

RELATIONSHIPS OF THE SWALLOWTAIL 'GENERA' *AGEHANA* MATSUMURA, *CHILASA* MOORE AND *ELEPPONE* HANCOCK (LEPIDOPTERA: PAPILIONIDAE)

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Abstract

Three Old World groups of Papilionini with apparent New World ancestors are reviewed. The Chinese *Agehana* Matsumura is transferred from a subgenus of *Chilasa* Moore to a subgenus of *Pterourus* Scopoli. The Indo-Papuan *Chilasa* and Australian *Eleppone* Hancock are treated as sister-genera derived from ancestral *Heraclides* Hübner. Dispersal is suggested to be Beringian in *Pterourus* (*Agehana*) and Gondwanan in *Chilasa* and *Eleppone*.

Introduction

Papilio Linnaeus *sens. lat.* is a worldwide genus of some 200+ species of swallowtail butterflies. Hancock (1983) divided it into six genera (*Pterourus* Scopoli, *Heraclides* Hübner, *Eleppone* Hancock, *Chilasa* Moore, *Priniceps* Hübner and *Papilio*) that are now [with the exception of *Chilasa*] generally regarded as subgenera (e.g. Häuser *et al.* 2005). Smith and Vane-Wright (2008) noted that a more detailed examination of individual species-groups might provide data enabling their monophyly to be tested and a more robust phylogenetic hypothesis to be produced.

Chilasa, *Eleppone* and *Agehana* Matsumura [placed by Hancock (1983) as a subgenus of *Chilasa*], include 14 species of Old World swallowtails that are apparently derived from New World ancestors (Hancock 1983). As such, they represent a small terminal group or groups that might help determine the status of their ancestral groups. Their relationships are reassessed below.

Wing shapes and patterns throughout these three groups have been so greatly modified by mimicry that they are completely unreliable as indicators of relationships. Hence, greater reliance must be placed on characters of the early stages and male genitalia. For the purposes of this study, the generic names recognised by Hancock (1983) are used below.

Agehana Matsumura

Agehana is an Oriental taxon of two closely related species: *A. elwesi* (Leech) from China and *A. maraho* (Shiraki & Sonan) from Taiwan. It was included within *Chilasa* by Igarashi (1976), placed as a subgenus of it by Hancock (1983) and regarded as a separate but closely related genus by Igarashi (1984). He *et al.* (1992) also treated it as a full genus. Miller (1987) did not include it in his study and it does not appear to have been a part of any molecular investigation.

Adults have exceptionally broad tails (uniquely enclosing two veins) and appear to be Batesian mimics of the distasteful troidine genus *Atrophaneura* Reakirt (Papilionidae) and/or the day-flying moth genus *Epicopeia* Westwood (Epicopeiidae) (Hancock 1983). Igarashi (1976) illustrated the

male genitalia. The valva has a broad clasper [= harpe] with a serrate apical lobe and a distinct apicoventral spine. Early stages were discussed and/or illustrated by Igarashi (1984: *maraho*) and He *et al.* (1992: both species).

Mature larvae are smooth, largely green above and blackish-brown below, with similarly dark markings on the prothorax, as a pair of metathoracic 'double eye-spots', as a narrow band along the posterior margin of the first abdominal segment, as a pair of subdorsal anterior spots or patches on the second abdominal segment and as a)(shaped pair of dark abdominal markings (viewed from above) which are separated dorsally but connect laterally with the dark lateroventral band; the 'eye-spots' are not connected by a dark band, there is a distinct series of blue abdominal spots below the spiracles and the osmeterium is white. Pupae are brown and relatively narrow but not stick-like; the head is truncate and the thoracic 'horn' is short and oblique. Larval food plants are *Liriodendron* (Magnoliaceae) for *A. elwesi* and *Sassafras* (Lauraceae) for *A. maraho* (Igarashi 1984).

The mature larvae of both species (He *et al.* 1992) are remarkably similar to those of *Pterourus* Scopoli (Tyler *et al.* 1994), retaining the)(shaped abdominal markings seen in subgenus *Pyrrhosticta* Butler (which often, but not always, connect dorsally in the latter taxon) and having the isolated metathoracic 'eye-spots' seen in subgenus *Pterourus* (which lacks the)(shaped abdominal markings). The shape of the abdominal markings, the dark lateroventral band and (especially) the series of blue subspiracular abdominal spots set the *Agehana* species apart from superficially similar larvae in the large, Old World genus *Princeps* [including the primitive *Pr. xuthus* (Linnaeus)] and are especially indicative of a close relationship with *Pterourus*. In *Princeps*, the lateroventral band is largely white and blue spots are absent. The eggs, pupae and larval food plants of *Agehana* are also similar to those of *Pterourus*. The male genitalia, especially the valva and clasper (Igarashi 1976), are very similar to those of subgenus *Pterourus* (Miller 1987, Tyler *et al.* 1994), particularly *Pt. esperanza* (Beutelspacher) (Beutelspacher 1975) from Mexico, which has *Pterourus*-like larvae (Tyler *et al.* 1994) and appears to be the most primitive species in that subgenus.

Chilasa Moore

Chilasa is a largely SE Asian taxon extending as far eastwards as New Guinea and the Solomon Islands. Eleven species are recognised: *C. clytia* (Linnaeus), *C. paradoxa* (Zinken-Sommer), *C. veiovis* (Hewitson), *C. osmana* (Jumalon), *C. carolinensis* (Jumalon), *C. agestor* (Gray), *C. epycides* (Hewitson), *C. slateri* (Gray), *C. laglaizei* (Depuiset), *C. toboroi* (Ribbe) and *C. moeneri* (Aurivillius). It was treated as a distinct genus by Igarashi (1976, 1984) and by Hancock (1983). The former also included the South American *Heraclides anchisiades* (Esper) and its allies within *Chilasa*, while the latter arrangement (*i.e.* excluding *Heraclides*) has been widely (but not universally) adopted in recent years (*e.g.* by Häuser *et al.* 2005).

Adults often have a pale-spotted frons, thorax and abdomen and appear to be Batesian mimics of various danaines (Nymphalidae) or (in the Papuan *laglaizei* group) the day-flying moth genus *Alcides* Hübner (Uraniidae). The male genitalia are not uniform in shape. The clasper is either broad (e.g. *clytia*, *paradoxa*, *veiovis*, *agestor*, *epycides*) or narrow (*slateri*, *laglaizei* group); there is no apicoventral spine but a posteroventral spine is present in *C. paradoxa*. The aedeagus is strongly curved. Early stages were discussed and illustrated by Straatman (1975), Igarashi (1984) and Müller (2001) and have been illustrated in various faunal works.

Eggs are laid singly or in batches and larvae are accordingly either solitary (*clytia*, *agestor*) or gregarious (*epycides*, *slateri*, *laglaizei*, *toboroi*). Mature larvae are variable in appearance but are generally dark with pale spots or patches; the prothorax, mesothorax, metathorax and abdominal segments 1-9 are distinctly tuberculate (except in *C. epycides*). In the *laglaizei* group, mature larvae are banded with large, white lateral spots and the tubercles are reduced (absent on prothorax). Pupae are generally brown and stick-like, resembling a broken twig; the thoracic 'horn' is rudimentary and parallel with the body axis. In the *laglaizei* group the pupa is yellow and robust with the thoracic 'horn' vestigial. Known larval food plants are species of *Litsea*, *Cinnamomum* and *Persea* (Lauraceae).

The dark, tuberculate mature larva and shape of the pupal thoracic 'horn' are likely to be homologous with those seen in several *Heraclides* species, although the pale larval markings are possibly independently derived. Solitary and gregarious larvae occur in both *Chilasa* and *Heraclides*. Igarashi (1976, 1984) also noted a close relationship between *Chilasa* and *Heraclides* based on their early stages and male genitalia, specifically the broad clasper although the similarities appear largely superficial and there are no apical or medioventral spines present in *Chilasa*.

***Eleppone* Hancock**

Eleppone was proposed for the sole Australian species *Papilio anactus* W.S. Macleay (Hancock 1979, 1983). It is currently regarded as a subgenus of *Papilio* (e.g. by Häuser *et al.* 2005), although Igarashi (1976, 1984) and Hancock (1983) had regarded it as either a part of or the sister-genus of *Chilasa*.

Adults have a pale-spotted frons, thorax and abdomen and, in both appearance and behaviour (A.G. Orr, pers. comm.), appear to be effective Batesian mimics of the distasteful troidine *Cressida cressida* (Fabricius). The male genitalia were illustrated by Miller (1987); the clasper is broad with a posteroventral spine and the aedeagus is strongly curved. Early stages were illustrated by Fisher (1978).

Eggs are laid singly and are unusually small (A.G. Orr, pers. comm.). Mature larvae are dark with pale spots and patches; the prothorax, mesothorax,

metathorax and abdominal segments 1-9 are distinctly tuberculate. Pupae are generally a variegated grey, brown and green, relatively straight and stick-like in shape but with the head not truncate; the thoracic 'horn' is rudimentary and parallel with the body axis. Larval food plants are various species of Rutaceae, including cultivated *Citrus*.

The early stages and male genitalia indicate a close relationship between *Eleppone* and *Chilasa* (Igarashi 1976, Hancock 1983), particularly the mature larval morphology, the shape of the pupal thoracic 'horn', the posteroventral spine on the male clasper and the curved aedeagus. However, the slightly curved pupa with a non-truncate head and the rutaceous larval food plants also indicate a close relationship with *Heraclides*, these characters being modified in *Chilasa*.

Discussion

The species currently included in *Agehana* do not appear to be as closely allied to those placed in *Chilasa* as previously believed; the early stages in particular are very different. The true relationships of the *Agehana* species appear to be with the American genus *Pterourus* and, wing shape and pattern aside, there do not appear to be any differences significant enough to recognise it as a separate genus. This, together with the apparent intermediate nature of the mature larva, between subgenera *Pterourus* and *Pyrrhosticta*, suggest that a subgeneric placement of *Pterourus* (*Agehana*) is the most appropriate, with subgenus *Pterourus* as its most likely sister-group.

The present distribution of the *Agehana* species in China and Taiwan appears to be a result of Beringian dispersal from a North American *Pterourus* (*Pterourus*) ancestor, possibly now represented by *Pt. esperanza*, which subsequently radiated throughout Central and North America as the *glaucus* and *troilus* groups of Hancock (1983). This dispersal appears to have occurred after the *Pterourus*-*Pyrrhosticta* split, which saw the latter subgenus radiate widely throughout South and Central America. Beringian dispersal from the Palaearctic to North America has evidently occurred in other papilionids, such as *Parnassius* Latreille and the *Papilio machaon* group, so movement in the other direction is not especially surprising.

Removal of the *Agehana* species from *Chilasa* enables the latter genus to be more rigidly defined and larval and genitalic similarities within both it and *Heraclides* (see Tyler *et al.* 1994) suggest that each genus is monophyletic. The relationship is thus one of common ancestry rather than a derivation of *Chilasa* from within *Heraclides*. Its present distribution in the Indo-Australian region is undoubtedly a result of Gondwanan dispersal from South America and this appears to have been accompanied by a switch in larval food plants from Rutaceae to Lauraceae.

Current distribution of the various *Chilasa* species closely mirrors that of the *Trogonoptera-Troides-Ornithoptera* lineage in tribe Troidini (see Hancock

2007), suggesting a possible centre of origin in the SE Asian (Sundaland) block rather than the Greater Indian block. The fact that SE Asian *Chilasa* species mimic danaines rather than troidines in the *Atrophaneura* group of genera [which appear to be primitively associated with the Greater Indian block: Hancock 2007] also suggests that they evolved apart. Dispersal eastwards to New Guinea and the Solomon Islands (as in the case of *Ornithoptera* Boisduval) is supported by the apparently derived nature of the *laglaizei* group, in which the larvae and pupae are highly modified.

Specific relationships within *Chilasa* are difficult to determine. Apart from the distinctive *laglaizei* group (*C. laglaizei*, *C. moeneri*, *C. toboroi*), the male genitalia (where known) do not show distinct patterns of similarity and life history details are unknown for several species. In the polymorphic *C. paradoxa* and *C. clytia* the hindwing vein Rs arises near the base of the discal cell, in *C. veiovis*, *C. osmana* and *C. carolinensis* it arises centrally and in the other species it arises closer to the apex of the cell. *C. veiovis* shows the large size and apically produced forewings typical of many Sulawesi swallowtails and has an uncertain mimetic association. Its hind wing retains the tooth to vein M₃ and position of vein Rs seen in *Eleppone anactus* and it is possibly a relict representative of the ancestral species.

Given its apparently intermediate position between *Heraclides* and *Chilasa*, the Australian *Eleppone* is best retained as a separate genus, sister to (but more primitive than) the Indo-Papuan genus *Chilasa*. Like the latter genus, it also appears to be a result of Gondwanan dispersal from a South American ancestor and its more primitive position suggests that *Chilasa* reached the Sundaland block via Australia. At some time in the past, *E. anactus* was presumably restricted to eastern Australia, developing its mimetic pattern following an overlap with *Cressida cressida*. Its present distribution beyond the range of the latter is presumably a result of *Citrus* cultivation in modern times. Its absence from most of northern Australia suggests that (unlike *C. cressida*: Hancock 2007) it is not an invader from the north. Unfortunately, this taxon was not considered by de Jong (2003) in his study of potential Gondwanan relicts but its apparent relationship with *Chilasa* and *Heraclides* suggests that a Gondwanan ancestry is likely.

Eleppone is also likely to be contemporaneous with the endemic Australian genus *Protographium* Munroe [tribe Leptocircini]. Male genitalic characters (particularly the shape of the clasper) show that American species included in the latter genus by Tyler *et al.* (1994) are better placed in *Protesilaus* Swainson [= *Mimoides* Brown, which grades into it via *P. asiis* (Fabricius) and *P. agesilaus* (Guérin-Méneville)] or *Eurytides* Hübner (see Hancock 1983). *Eurytides bellerophon* (Dalman) was transferred from *Protesilaus* by Tyler *et al.* (1994), while *Iphiclides* Hübner, *Graphium* Scopoli and *Lamproptera* Gray (see Miller 1987) appear to belong to a separate, Laurasian radiation (*c.f.* *Papilio* + *Princeps*).

The above discussion suggests that the current arrangement of recognising *Chilasa* as a separate genus and including *Pterourus*, *Heraclides* and *Eleppone* as subgenera of *Papilio* (e.g. Häuser *et al.* 2005) is untenable, since it results in a paraphyletic classification. Either all must be treated as subgenera of the 'supergen' *Papilio sens. lat.* (essentially following Miller 1987), or *Pterourus*, *Heraclides* and *Eleppone* must also be treated as distinct genera, as suggested by Hancock (1983). The latter arrangement enables a clearer expression of the diversity and relationships of the 200+ species of 'fluted' swallowtails by way of further subgeneric divisions.

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