

Vicariance and ecological dispersal in *Papilio* subgenus *Achillides* (Papilionidae) and some other butterflies of Asia and the Southwest Pacific

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ABSTRACT

Biogeographic patterns are reviewed for four widespread Southeast Asia butterfly groups in the superfamily Papilionoidea: *Papilio* subgenus *Achillides* Hübner, 1819 (Papilionidae), the birdwing butterflies (Papilionidae tribe Troidini), Genus *Polyura* Billberg, 1820 (Nymphalidae), and Genus *Vanessa* Fabricius, 1807 (Nymphalidae). The patterns of allopatry and sympatry are shown to be consistent with the vicariance of widespread ancestors with distributions including parts of Asia and Australasia, followed by secondary range expansion. Aspects of the distributions that are correlated with tectonic structures provide evidence of the age and origin of these butterflies in South-east Asia and Australasia. The transpacific affinities of the Troidini are consistent with a Pacific ancestry linked with former Cretaceous landscapes. The multi-island ranges of many of the butterfly species in Southeast Asia represent examples of metapopulation structure in which groups survive and persist in a region over long periods of time, even where individual islands are ephemeral.

INTRODUCTION

Butterflies are generally vagile organisms capable of flight over extended distances, sometimes even between continents. It is therefore not surprising that many species are widespread over continental regions and, often, multiple oceanic islands. In contrast, though, many butterfly species and some higher taxa

have geographically localized distributions, even when there are no obvious barriers to range expansion. Both widespread and localized butterfly taxa may show patterns of allopatry where sister taxa (species level or higher) occupy different geographic sectors, so they effectively ‘replace’ each other in geographic space. Allopatry is a recurrent

characteristic of many taxa spanning almost all taxonomic levels in both animals and plants. It is evolutionarily significant because isolation is required for differentiation to occur between different localities (Croizat 1958, Craw et al. 1999, Heads 2012, 2014, 2017).

Traditional attempts to provide a mechanism for allopatry have relied on an evolutionary model of chance dispersal. In this historical model, migrations from one set of localities (center of origin) manage to fortuitously cross a barrier one time (or just a few times) so that the colonists are isolated and can diverge. This is Darwin's (1859) model of evolution – organisms are constantly migrating away from centers of origin to colonize new regions (Croizat 1964). It is a model of evolution in which movement is used to explain divergence, and it has been widely applied to studies of butterfly allopatry (e.g. Aduse-Poku et al. 2009; Condamine et al. 2013a, b, Sahoo et al. 2018). The problem with this model is that it requires single or rare dispersal events that somehow land colonizers in different places so that all the descendants are neatly allopatric. Most allopatric distribution patterns are common to many taxa, but in the chance dispersal theory, every individual pattern requires a separate dispersal event (that happens only once in each taxon) – there is no common cause (Heads 2012).

The adoption of center of origin and dispersal explanations has been justified by widespread acceptance of two problematic principles. The first is the assumption that dispersal-vicariance programs provide empirical evidence of chance dispersal or vicariance. The second is that fossil-calibrated molecular divergence dates provide an accurate (even if sometimes imprecise) representation of the age of taxa.

Dispersal-vicariance analyses are widely used to support sequential chance dispersal (usually unidirectional) as the mechanism of for the evolution of butterfly allopatry (e.g. Aduse-Poku et al. 2009, Condamine et al. 2013a, b,

2015, Kodandaramaiah et al. 2018). But these programs assume that a paraphyletic basal grade in area A indicates a centre of origin in A. For example, if four taxa in two areas, A and B, have a phylogeny A (A (A+B)), a centre of origin in A is proposed, followed by dispersal to B. However, this common pattern can also be explained by differentiation of a widespread ancestor already present in A and B, followed by overlap in A (Heads 2014, 2017). The result of such programs is to show support for sequential chance dispersal when none actually exists.

The introduction of molecular dating at first sight seems to be an ideal method for assigning a definitive age to the origin of taxa. It also made biogeography easy for the specialist, as there was no further need to have a general knowledge of biogeographic patterns; each taxon could be assigned its own, unique history, rather than having a shared history with other taxa through tectonic processes (Croizat 1958). Every group could be studied in isolation with a simple demarcation between dispersal and vicariance depending on the group's age. If a taxon was only 10 million years old, for example, it could not have been influenced by tectonic events dating as much as 100 million years ago.

If fossil-calibrated divergence estimates represented actual or maximum clade ages, this approach would indeed provide a general method for evaluating the evolution of allopatry. But no matter how many studies have misrepresented fossil-calibrated estimates as actual or maximal ages, it does not change the fact that they cannot represent anything but minimum clade age and they cannot be turned into anything else (Heads 2005, 2014). Reliance on fossil-calibrated molecular clock ages for clades has resulted in decreased attention being given to the details of distribution and tectonics (Heads 2019). In reality, fossil-calibrated molecular estimates cannot falsify earlier origins of groups, and these may be predicted from other methods of dating, such as

correlation between clade distribution and tectonic events (Heads 2019).

An alternative biogeographic approach presented here examines the relationship between phylogenetic affinity and geographic distribution to identify the extent and nature of allopatry between sister clades in *Papilio* subgenus *Achillides* of Asia and the Southwest Pacific. This method is based on the general biogeographic principle that allopatry constitutes evidence of vicariance, while geographic overlap of taxa is evidence of subsequent range expansion by ecological dispersal (Craw et al. 1999, Heads 2012, 2014, 2017). In this vicariance model, ecological dispersal allows a group to survive and even expand its range, but does not itself lead to divergence; divergence requires isolation through geological or ecological disruption of the ancestral distribution range. Patterns of allopatry and distributional overlap in *Achillides* are documented here to assess the relative impact of vicariance and dispersal in a tectonically complex region. Comparisons are also made with other Asian and Southwest Pacific butterflies to characterize examples of butterfly allopatry in these regions and assess their historical significance with respect to geological evolution.

MATERIALS AND METHODS

Distributional and phylogenetic information on *Achillides* (from Condamine et al. 2013a) is mapped below in the following sequence:

1. The distribution ranges of the four principle *Achillides* clades (referred to as clades 1-4) are mapped to illustrate the extent of allopatry and sympatry.
2. Three of the *Achillides* clades that have multiple species are mapped to species level with respect to the phylogenetic structure of the subclades.
3. Distribution patterns are assessed for their consistency with the expectations of

allopatric differentiation (vicariance) or dispersal (as secondary range expansion).

4. Comparisons are made among the Papilionoidea butterfly groups *Polyura* (Nymphalidae), tribe Troidini (Papilionidae) and *Vanessa* (Nymphalidae).

5. Examples of distributional relationships or boundaries that coincide with tectonic features are discussed along with the historical implications of the correlations for dating evolution.

These steps in methodology reflect the assumption that the actual geographic patterns of distribution are historically informative about the biogeographic significance of phylogenetic divergence (Craw et al. 1999). The principal geographic distinction is between allopatry (which is consistent with a general biogeographic model of in situ allopatric divergence, i.e. vicariance), and geographic overlap of taxa (which is consistent with range expansion by subsequent ecological dispersal) (Croizat 1958, 1964, Craw et al. 1999, Heads 2012, 2014, 2017). Since the individual distributions of taxa are historically informative, this approach does not require the a priori subdivision of geography into predefined areas, such as ‘Wallacea’ (e.g. Lohman et al. 2011).

Most of the distributional ranges of *Achillides* species mapped by Condamine et al. (2013a) are at a very broad geographic scale and may be locally imprecise, particularly for distributional limits within mainland Asia. However, for the purposes of this article, the distributional boundaries provided by Condamine et al. (2013a) are sufficient to identify patterns of allopatry and range overlap. Future mapping of distribution for this group at a finer geographic level will also allow more precise biogeographic evaluation, although this will be unlikely to significantly alter the general patterns of overall allopatry outlined here. Some taxa treated as species by Condamine et al. (2013a) include more localized forms that have been treated as species in other works. The

location and names of these forms are included in the distribution maps by Condamine et al. (2013a).

RESULTS

Papilio subgenus *Achillides*

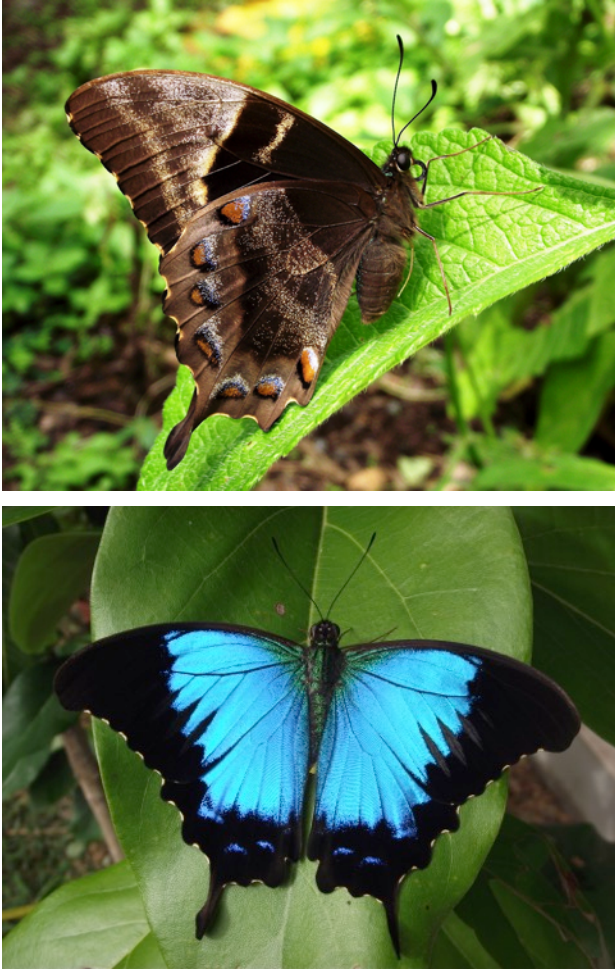


Fig. 1. Habitus of the New Caledonian *Papilio montrouzieri*, top: lateral view, bottom: dorsal view. Photos by Thierry Salesne.

This subgenus comprises about 25 species (an example in Fig. 1) and extends over much of eastern Asia (between India, the Russian Far East and Japan), and south east to northern Australia, New Caledonia and the Solomon Islands (Fig. 2). The genus has four major clades (Condamine et al. 2013a) that show some geographic overlap (Fig. 2).

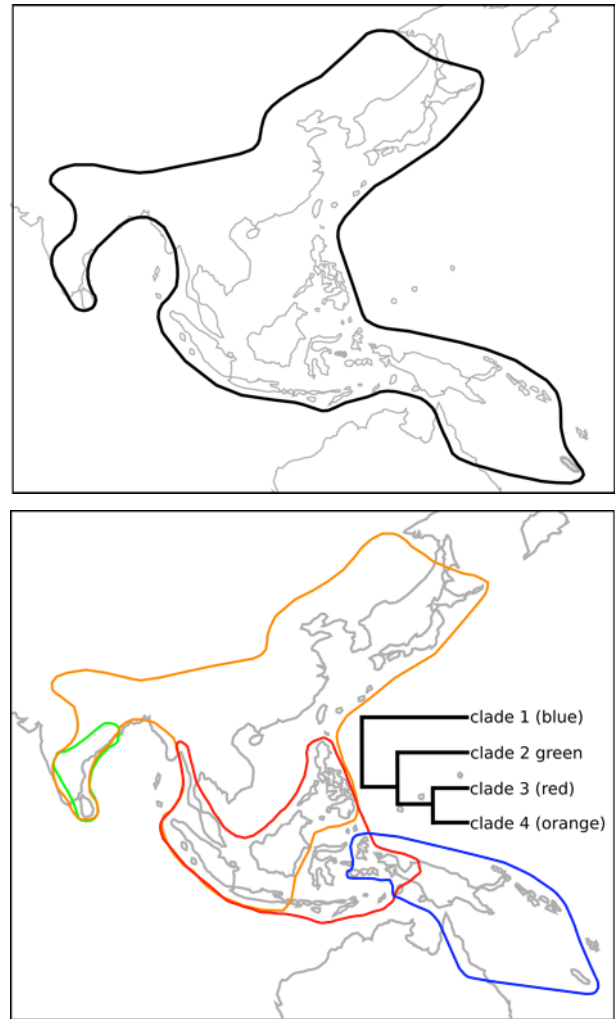


Fig. 2. Distribution of *Papilio* subg. *Achillides*. Top: overall distribution, bottom: distribution of its four main clades.

The distributions of clade 1 and clade 4 are reciprocally allopatric, while clade 3 fills in the geographic gap separating them from each other and also partially overlapping both. The distribution of Clade 2, comprising the single species *Papilio crino* Fabricius, 1792, is enclosed within the distribution of clade 4. The distribution pattern of the four clades together is consistent with vicariance of a widespread ancestor followed by range expansion of two or more descendants. The phylogenetic status of the single species in Clade 2 is not fully resolved. Condamine et al. (2013a) noted that “All species are clearly assigned to four well-resolved clades that exhibit distinctive

geographical distributions, with the exception of *P. crino*. The latter species is found in an enigmatic and moderately supported position as sister to the C3–C4 clade ... in contrast to its traditional placement within the *palinurus* group [clade 4]...We anticipate that the addition of *P. buddha*, also traditionally placed in the *palinurus* group and occurring in India as well, may bring more resolution on the issue of the phylogenetic position of *P. crino*.”

The initial phylogenetic break separating the basal clade 1 from the rest occurred in the vicinity of northwestern New Guinea and the Moluccas archipelago (Fig. 2). The next break occurs with the separation of clade 2 from 3 + 4, although clade 2 is currently of uncertain phylogenetic status. As the two most widespread clades, clade 3 and clade 4 also show extensive overlap, but clade 3 is mostly in southeastern Asia, while clade 4 extends over a greater area of mainland Asia. These differences can be explained as remnants of the original allopatry of the two clades.

Clade 1

Clade 1 comprises two allopatric species, with *Papilio ulysses* Linnaeus, 1758 widespread across New Guinea, the Moluccas, Bismarks, Solomon Islands, and northern Queensland, and *P. montrouzieri* Boisduval, 1859 endemic to New Caledonia, including both Grande Terre and the Loyalty Islands (Thierry Salasne pers. comm.). This pattern (Fig. 3) is consistent with vicariance of a widespread ancestor established prior to the tectonic separation of part of the New Caledonia region from eastern Gondwana. The partial overlap of clade 1 with clade 3 represents local range expansion by one or both clades.

Clade 3

Clade 3 comprises two subclades that are that are almost entirely allopatric, with the overlap restricted to Sulawesi (Fig. 4). This pattern is

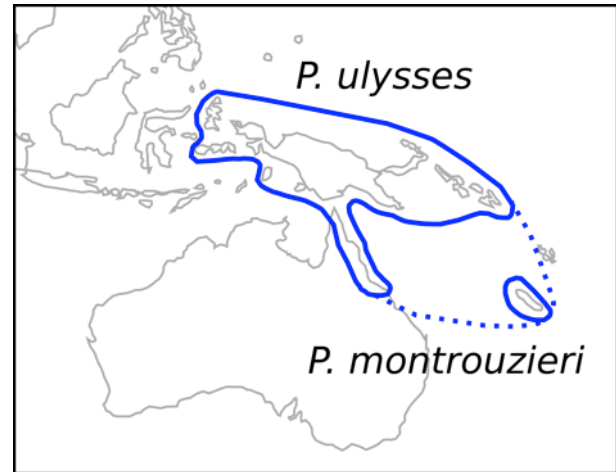


Fig. 3. Distribution of *Papilio* subg. *Achillides* Clade 1, with two allopatric sister species.

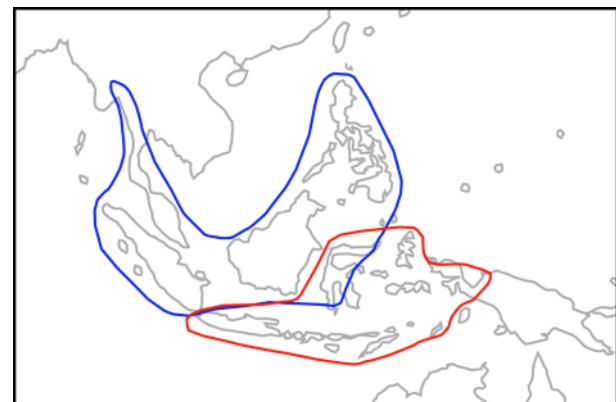


Fig. 4. Distribution of *Papilio* subg. *Achillides* Clade 3, with subclade 3a (blue) and subclade 3b (red).

consistent with vicariance followed by marginal range expansion by one or both taxa. The northern clade 3a comprises three allopatric species, with *Papilio blumei* Boisduval, 1836 (Sulawesi) sister to the other two (Fig. 5). This pattern is consistent with vicariance of the common ancestor, with *P. blumei* diverging first. The southeastern clade 3b comprises four allopatric species, again consistent with vicariance in the common ancestor (Fig. 6). The allopatry within clade 3b comprises two bands, one in the north with *P. peranthus* Fabricius, 1787 and *P. lorquinianus* C. & R. Felder, 1865, and one in the south with *P. pericles* Wallace,

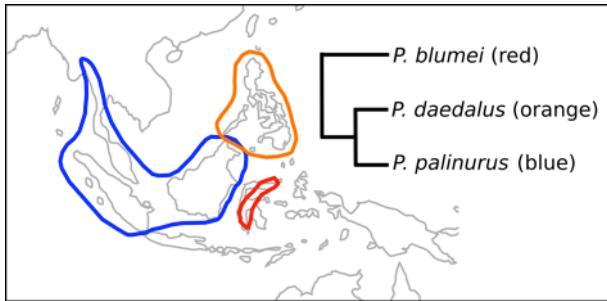


Fig. 5. Distribution of *Papilio* subg. *Achillides* Clade 3a, with three allopatric species.

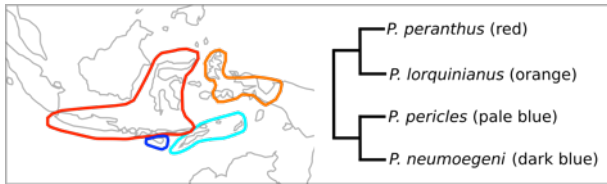


Fig. 6. Distribution of *Papilio* subg. *Achillides* Clade 3b, with four allopatric species.

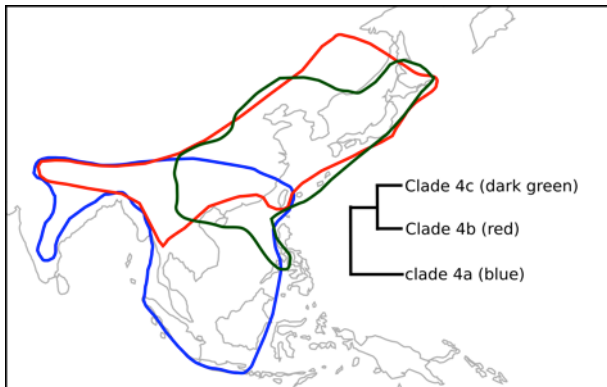


Fig. 7. Distribution of the three main subclades of *Papilio* subg. *Achillides* Clade 4.

1865 and *P. neumoegei* Honrath, 1890 on the eastern Lesser Sunda islands. The wide range of *P. peranthus* across Sulawesi, Java, and parts of the Lesser Sunda suggests that the geographic overlap of clades 3a and 3b is the result of range extension by *P. peranthus*.

Clade 4

There are three main subclades (here labeled a, b, and c), and these show considerable geographic overlap. This is interpreted here as

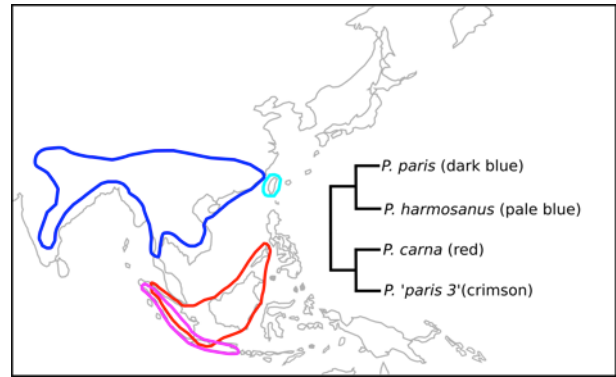


Fig. 8. Distribution of *Papilio* subg. *Achillides* subclade 4a.

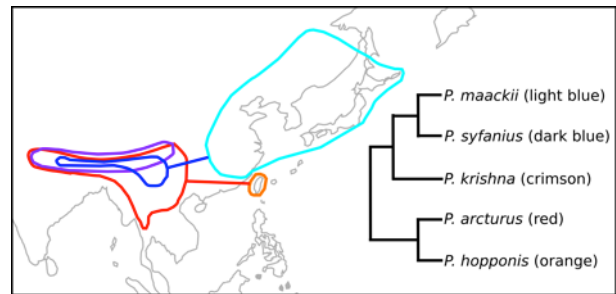


Fig. 9. Distribution of *Papilio* subg. *Achillides* subclade 4b.

evidence of extensive dispersal following initial vicariance (Fig. 7). Within clade 4a there are two allopatric and disjunct sister species groups – a northern pair: *P. paris* Linnaeus, 1758/*P. hermosanus* Rebel, 1906, and a southern pair: *P. karna* C. & R. Felder, 1864/*P. 'paris 3'* (Fig. 8). The species in the northern group are allopatric and adjacent to each other, while in the southern group there is marginal overlap. The pattern conforms to vicariance followed by range expansion between *P. karna* and *P. 'paris 3'*. The original differentiation between the mainland *P. paris* and *P. hermosanus* of Taiwan may have been influenced by seafloor extension in the Taiwan Strait, as has been suggested for ghost moths (Hepialidae) endemic in the region (Buchsbbaum et al. 2018).

In clade 4b there are two subclades that overlap in the Himalayan region (Fig. 9). The basal species *P. krishna* Moore, 1857 in the Himalayan region is the sister group of two

species, one also in the Himalayan region (*P. syfanius* Oberthür, 1886), and the other (*P. maackii* Ménétries, 1859) ranging widely over eastern Asia and Japan, but allopatric with all the other species of clade 4b. The second subclade comprises the disjunct sister species *P. arcturus* Westwood, 1842, widespread in central-southern Asia, and *P. hopponis* Matsumura, 1907 in Taiwan. Even though there is considerable overlap in central-southern Asia, two distinct ancestral ranges are still discernible – one in the northeast (*P. maackii*-*P. syfanius*) and the other in the southeast (*P. arcturus*-*P. hopponis*). The pattern is consistent with two widespread ancestral distributions followed by range expansion in central-southern Asia, perhaps as a consequence of the Himalayan and Tibetan Plateau uplift.

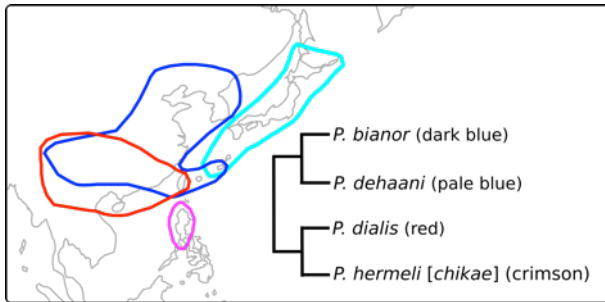


Fig. 10. Distribution of *Papilio* subg. *Achillides* subclade 4c.

The third group, clade 4c, is also widespread in eastern Asia, but does not extend so far west into the Himalayan region (Fig. 10). Clade 4c comprises two groups of sister species that partially overlap in China. In the northern group *P. bianor* Cramer, 1777 and *P. dehaani* C. & R. Felder, 1864 are allopatric, and vicariance may be the result of the back arc extension that formed the Sea of Japan. The second group of sister species is also allopatric, with *P. dialis* in mainland of China and northern Southeast Asia disjunct from *P. hermeli* Nuyda, 1992 on the island of Mindoro

in the Philippines. This vicariance could be explained by the tectonic extension that formed the South China Sea basin (cf. Grehan et al. 2019). [Note: *P. hermeli* has been designated a subspecies of *P. chikae* Igarashi, 1965 of Luzon Island, Philippines (CoP18Prop.47 2019) which was not included by Condamine et al. (2013)].

THREE COMPARATIVE EXAMPLES OF BUTTERFLY ALLOPATRY

(a) *Polyura* (Papilionoidea: Nymphalidae)

As with *Papilio* subg. *Achillides*, the distribution of *Polyura* spans Southeast Asia and adjacent regions (Toussaint & Balke 2016). The two subclades, '*Eudamippus*' and '*Pyrrhus*', are allopatric apart from local overlap in Sumatra (Fig. 11a). This pattern is consistent with vicariance in a widespread ancestor, followed by secondary range expansion in the descendants. The *Pyrrhus* group comprises five allopatric clades, with the basal clade disjunct between western Malesia and the Solomon Islands (Fig. 11b). All five clades are allopatric, except for the overlap of two in the Solomon Islands. This is consistent with a simple vicariance origin of the five clades, with secondary range expansion of either one or two clades within the Solomon Islands.

(b) Birdwing butterflies (Papilionoidea: Troidini)

The birdwing butterflies comprise 12 genera. Three genera form a monophyletic group that ranges from India to Australia (Fig. 12a). Of these three genera, *Trogonoptera* Rippon, 1890 and *Ornithoptera* Boisduval, 1832 are allopatric, while the widespread *Troides* Hübner, 1819 encloses the range of *Trogonoptera* and partly overlaps the range of *Ornithoptera*. This pattern can be explained by an original allopatric differentiation of the three genera, with subsequent range expansion of *Troides*.

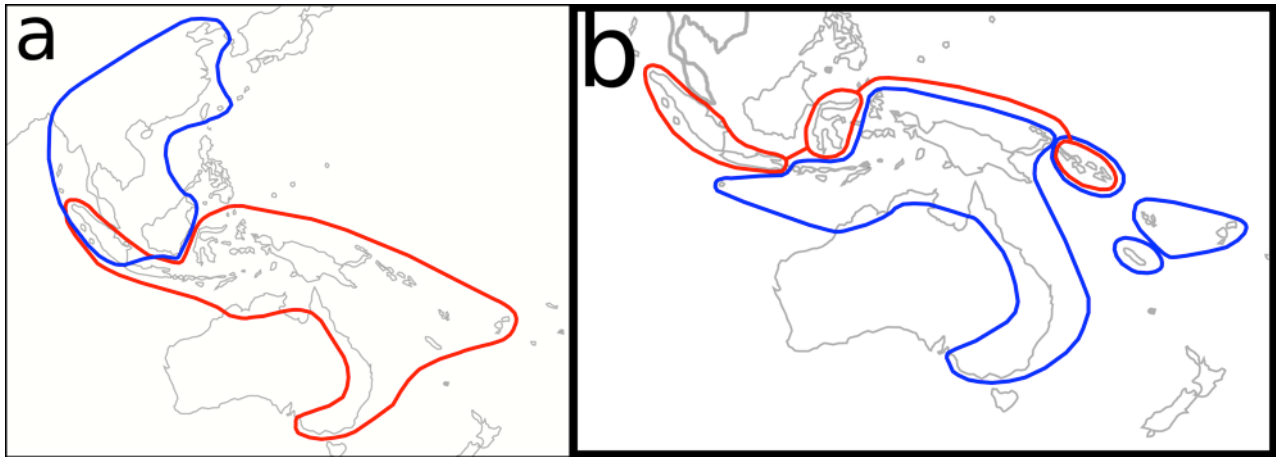


Fig. 11. Distribution of *Polyura*: (a) two mostly allopatric clades, with *Eudamippus* in Asia and northern South-east Asia (blue outline), and *Pyrrhus* in Australasia and Southeast Asia (red outline); (b) Distribution of *Polyura* subg. *Pyrrhus*, with five allopatric clades. The basal clade (red) is disjunct across New Guinea in a pattern that corresponds to terrane movement along a strike slip fault system (from Heads 2019, fig. 9).

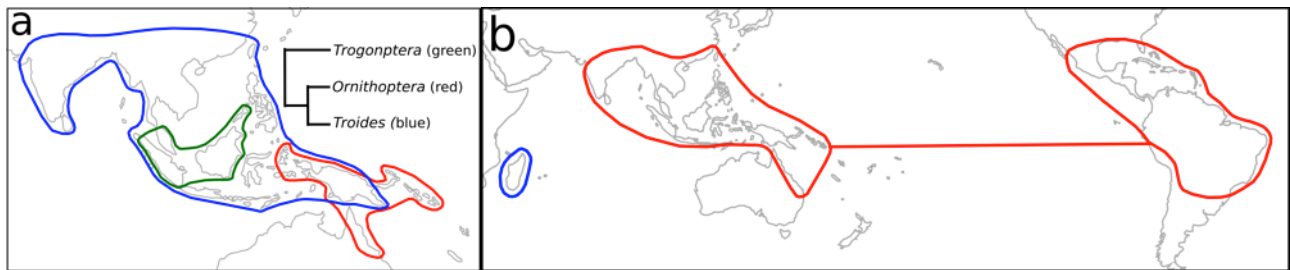


Fig. 12. Distribution of the tribe Troidini, the birdwing butterflies. (a) A clade of three genera ranging from India to Australia; (b) The East Asian clade of Troidini, shown in Fig. 12a, together with its American sister group (red outline) and the basal sister group *Pharmacophagus* (blue outline).

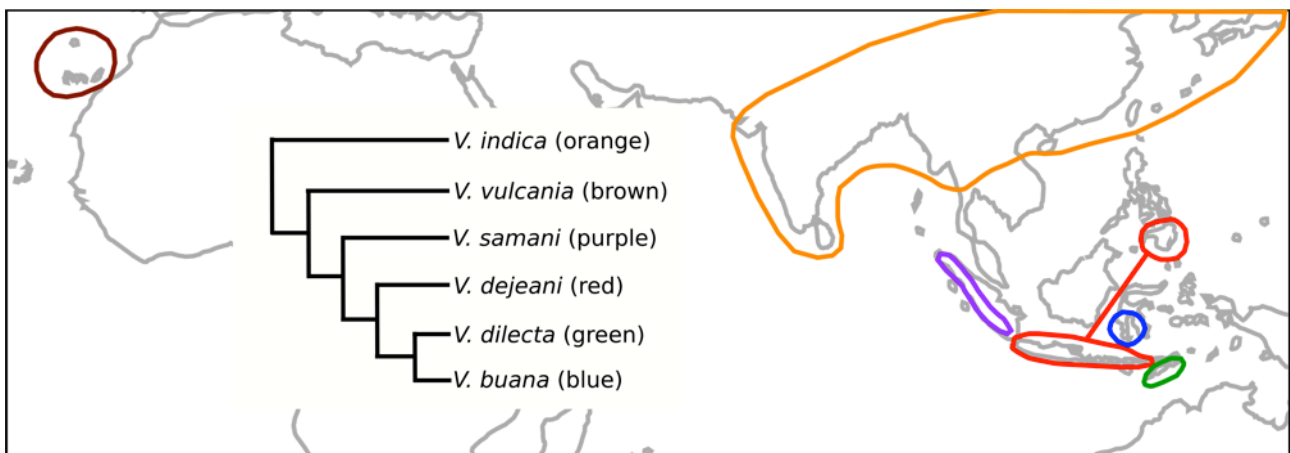


Fig. 13. Distribution of the south-east Asian *Vanessa* species and their sister group in Macaronesia. Map modified from Grehan (2017, fig. 21).

Of special biogeographic interest is the absence of *Troides* from the Bismarck Archipelago, even though it is only 70 km from mainland New Guinea, and the ocean gap includes small islands. In contrast to *Troides* is *Ornithoptera priamus* (Linnaeus, 1758) which is widespread on most islands of the Bismarks, with several subspecies (e.g. *O. priamus admiralitatus* (Rothschild, 1915) and *O. priamus bornemanni* (Pagenstecher, 1894)) endemic to that area. *Papilio ulysses* also has a number of subspecies endemic to the area (*P. ulysses gabrielis* [Rothschild, 1898] on Manus, *P. ulysses kallinikos* Fruhstorfer, 1903 on New Ireland and *P. ulysses ambiguus* Rothschild, 1895 on New Britain). The Bismarck Archipelago-New Guinea faunistic boundary is found in many other organisms, including birds, which suggests that there is a general explanation. The Bismarck Archipelago forms part of an island arc that has encroached from the Pacific, and the ancestors of the groups that are absent from it were probably never there.

The phylogenetic analysis of Condamine et al. (2013a) classifies the tropical American genera *Parides* Hübner, [1819] and *Euryades* C. Felder & R. Felder, 1864 (Fig. 12b) as the sister group of the three birdwing genera shown in Fig 12a. This trans-Pacific pattern indicates that the presence of the birdwing butterflies in South-east Asia is of Pacific origin and is consistent with an ancestral Pacific distribution that has been displaced east and west by the Pacific spreading ridges (Heads 2014). The distribution suggests that the ancestral range occupied the extensive island arcs and Cretaceous magmatic plateaus in the central Pacific, along with many other Pacific and trans-Pacific taxa (cf. Heads 2012). A combined molecular and morphological analysis by Simonsen et al. (2011) also supported the trans-Pacific pattern in Troidini, but proposed a larger Old World clade that also included *Cressida* Swainson, 1832 (Australasia) and *Losaria* Moore, [1902] (India-Australia) (Braby et al. 2005 gave a similar reconstruction). The sister group to these

butterflies is *Pharmacophagus* Haase, 1891 of Madagascar. The separation of this genus and its trans-Pacific sister represents the initial phylogenetic break, perhaps dating from formation of the Indian Ocean (cf. Heads 2012).

(c) Genus *Vanessa* - red admiral butterflies (Nymphalidae)

Four species of *Vanessa* Fabricius, 1807 in South East Asia form a clade and have allopatric distributions, although one species ranges across several islands (Fig. 13). This allopatry is consistent with vicariance of a widespread ancestor in the region. The sister group of these butterflies is *V. vulcania* (Godart, 1819) in Macaronesia, while *V. indica* (Herbst, 1794), distributed between India and Japan, is the next related species. The Asia – Macaronesia disjunction can be explained by extinction in intermediate localities, perhaps resulting from closure of the former Tethys Sea with the suturing of India and Africa with Eurasia (Grehan 2017).

DISCUSSION

Tectonics

The phylogeny and distribution of *Papilio* subg. *Achillides* provides biogeographic evidence for both vicariance and ecological dispersal (as range expansion). The higher proportion of allopatry at lower taxonomic levels (especially among species) is not surprising, as these represent more recent events with less time for subsequent range expansion to obscure the original allopatry. Many of the *Papilio* subg. *Achillides* species that span multiple islands in South East Asia have allopatric boundaries that are adjacent or in close proximity. This geographically precise and non-random pattern of spatial differentiation is inconsistent with their origin by unidirectional, chance dispersal events (as proposed by Condamine et al. 2013a).

The simplest explanation for the high levels of allopatry in *Papilio* subg. *Achillides* is *in situ* vicariance, and there is no need for any

allopatric lineage or species to be sequentially derived from any allopatric sister group, regardless of whether they are disjunct or adjacent. For example, the disjunct New Caledonian *Papilio montrouzeri* can be explained as the result of vicariance of a widespread ancestor (clade 1), either by tectonic extension along coastal Gondwana or by accretion of the Loyalty-Three Kings Ridge (cf. Heads 2019). It has been suggested by various biogeographers that New Caledonia was completely submerged until 34–37 Ma (review in Heads 2019), and so the entire biota must have been derived from long-distance trans-oceanic dispersal. This view was accepted by Condamine et al. (2013a) to justify the origin of *P. montrouzeri* by chance dispersal. However, the geological evidence they cited indicates submersion of different parts of New Caledonia at different times – there is no geological evidence for complete submersion at any one time (Heads 2014, 2019). In addition, chance dispersal does not account for the repetition of similar distributions in large numbers of groups with different ecology and means of dispersal. For example, the overall distribution range of *Papilio* clade 1 is similar to the eastern range of the plant *Deplanchea* Vieill. (Fig. 14).

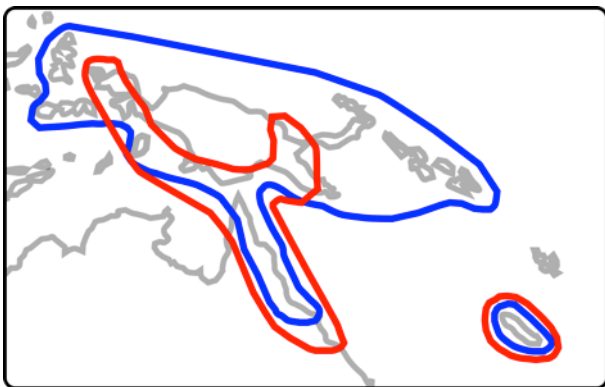


Fig. 14. Comparison of distribution range of eastern *Deplanchea* (Bignoniaceae) – red outline, and *Papilio* subg. *Achillides* clade 1 – blue outline. *Deplanchea* distribution from Heads (2003: fig. 112).

Evidence for the widespread presence of ancestral *Papilio* subg. *Achillides* in Southeast Asia is suggested by shared distributional boundaries and tectonic correlations. This is illustrated by the biogeographic boundary (or node) between Sulawesi and the Moluccas. The Moluccas archipelago marks the western boundary of *Achillides lorquinianus* (Fig. 6), *Papilio ulysses* (Fig. 3), *Ornithoptera* (Fig. 12a), and *Pyrrhus* clades 2-5 (Fig. 11b). Similar phylogenetic breaks between the Moluccas and Sulawesi occur in many plants and animal groups, including birds of paradise. A tectonic explanation for this break is available, as there has been ~2000 km westward movement of the Halmahera arc along the northwestern edge of New Guinea since early or mid Miocene time (Heads 2001). The *Pyrrhus* clade 1 disjunction between the Greater Sunda Islands and the Solomon Islands corresponds spatially with long-distance terrane translation on major, east–west strike-slip faults (Heads 2014, 2019).

Many butterfly distribution patterns in South East Asia include boundaries that prove to be of great biogeographic interest when examined in detail. For example, the two sister species groups in *Papilio* clade 3b (Fig. 6) display precise allopatry, even though individual species range over multiple islands. Bearing in mind that butterfly distributions in this region are not perfectly documented (although butterflies are the best collected invertebrates) the allopatry within clade 3b is striking. In Clade 3b, group 1, the distribution of *P. peranthus* extends along the Inner Banda Arc of the Lesser Sunda to Alor Island (Fig. 15). On the next island to the east is Wetar with *P. pericles* of group 2 with a range that extends further east to the island of Pulau, and southwest to the outer Banda Arc island of Timor while its sister species *P. neumogeni* is endemic to Sumba Island of the outer arc (Fig. 14). Although different in detail, the distribution of *Vanessa* along the Banda Arcs also shows a divergence between *V. dijeani* distributed along the inner arc from Java to Sumbawa (Field 1971), while its sister group is

made up of the species pair *V. dilecta* on west Timor (Hanafusa 1992) and *V. buana* in southern Sulawesi (Field 1971) (Fig. 13).

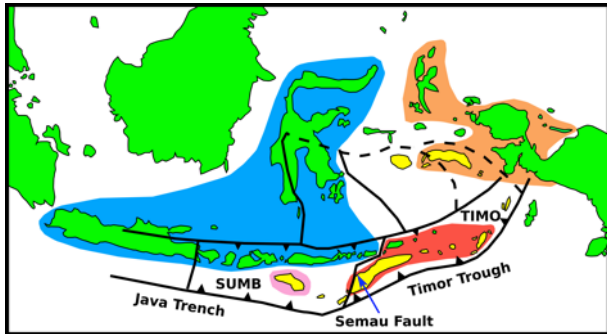


Fig. 15. Distribution of *Papilio* subg. *Achillides* Clade 3b (cf. Fig. 6) in the Lesser Sunda (Islands east of Java) and regional tectonic features. *P. peranthus* group 1 (blue), *P. lorquinianus* group 1 (orange), *P. neumogeni* group 2 (crimson) and *P. pericles* group 2 (red). Black lines – major faults, barbed lines – subduction zones (barbs on over-riding plate). SUMB – Sumba tectonic block, TIMO – Timor tectonic block. Islands of the Outer Banda Arc shaded in yellow.

The Inner Banda Arc is volcanic in origin and was initiated in Late Miocene time, while the Outer Banda Arc comprises allochthonous rocks from the Asian margin along with Neogene volcanism (Hall 2002). Timor is of Australian continental margin origin, while Sumba represents a micro-continental fragment thought to have originally been located near west Sulawesi (Satyana & Purwaningsih 2011, Hall 2012). The boundary between group 1 and group 2 along the inner Banda Arc coincides with a narrow strait between the islands of Alor and Wetar that is only 20 km across. Within this strait is the Semau Fault, which extends between the thrust fault to the north of Wetar and obliquely south west of Timor to connect with the main thrust fault south of the Lesser Sunda. The Semau Fault provides the structural link between the fore-arc (outer Banda islands) and the back-arc (inner Banda islands) (Koulali et al. 2016). Geological activity along this fault would

explain the divergence between the two groups in *Papilio* subg. *Achillides* clade 3b along the inner arc, as the ancestor became established across this region during collision between the Australian margin and the Banda volcanic arc.

Condamine et al. (2013a, p. 94) did acknowledge (in reference to the Papilionidae) that fossils provide information only on the minimum age of a taxon (“The age and divergence times of Papilionidae were inferred using fossils as minimum age constraints”). However, they also decided that a maximum age could be imposed on papilionid clades with reference to angiosperm divergence dates proposed by Bell et al. (2010). But the angiosperm divergence estimates were also fossil-calibrated, so they too provide only a minimal timescale that cannot logically be transmogrified into maximum ages. Consequently, the age estimate of ~ 21 Ma for *Papilio* subg. *Achillides* is only a minimum age of the subgenus. The use of spatially related geological events or structures to date clades was regarded by Condamine et al. (2013a) as “very dangerous”, because divergence may have occurred even earlier and because geological reconstructions are not immutable. They did not specify examples in which these possibilities were more problematic than the misrepresentation of minimum fossil calibrated ages as actual or maximum dates. Geological or tectonic correlations certainly cannot be taken for granted, and some are more problematic or uncertain as to timing than others. For example, some tectonic structures, such as faults, can be reactivated at different times, so these considerations have to be taken into account. As noted by Condamine et al. (2013a), a disjunction in a taxon across a particular ocean basin could have originated before the opening of the basin, and a full analysis of a group and its relatives is necessary. For example, some taxa disjunct across the Tasman Sea have been attributed to events occurring before the opening of the Tasman basin (Heads 2017). A divergence date based on geological/tectonic correlation is an approximation, whereas one

based on fossil calibration is always a minimum (Heads 2012).

Allopatry

The extent of allopatry in the butterfly groups analyzed here is explained more simply by vicariance than by chance dispersal from localized centers of origin. The patterns of phylogeny and distribution are consistent with divergence by vicariance of widespread ancestors followed by various degrees of range expansion. Apart from the monotypic clade in southern India (clade 2), each *Achillides* clade retains some portion of its original allopatry. Within clade 1 the two species are allopatric. In clade 3 all subclades are allopatric or nearly so. Only in clade 4 is there extensive overlap of the three subclades, and this occurs only within the Asian mainland. Further overlap occurs in two of the three subclades, again mostly on the Asian mainland. These characteristics indicate that despite many species having multi-island distributions in Southeast Asia, allopatry is much more prevalent in the island regions than in mainland Asia. In the genera of Troidini mapped in Fig. 12, the distribution of *Troides* almost encompasses that of the other two genera, but *Ornithoptera* and *Trogonoptera* remain reciprocally allopatric.

Allopatry in each group is consistent with the view that their ancestral ranges included Southeast Asia along with adjacent regions. In other words, the ancestor initially occupied the entire current range of each group prior to local differentiation. In this context none of the allopatric descendants are derived from any other. Indications of the age of particular clades may be inferred from spatially correlated tectonic features. For example, the disjunct distribution of *Pyrrhus* clade 1 between the Solomon Islands and Sulawesi (Fig. 11b) corresponds with the model of Hall (2002). In this model, Halmahera has moved west from a position in the vicinity of present day Solomon Islands from Oligocene time (Hall 2009, 2012). This correlation suggests a 30 Ma existence for

this disjunction and a minimal divergence age for clade 1 with respect to the rest of the *Pyrrhus* group. Subg. *Achillides* Clade 1 and *Ornithoptera* also have a western boundary at Halmahera and are present in the Solomon Islands, consistent with a similar age. The isolation of *Papilio montrouzeri* in what is now New Caledonia is explicable by the seafloor spreading that separated the region from Australia (at about 50 Ma). Another possibility is that the ancestor was amalgamated to New Caledonia at ~ 35 Ma along with the Loyalty – Three Kings Ridge (Heads 2017).

Metapopulation biogeography

Current ‘ancestral area’ algorithms generate results that often explain allopatry by a chance dispersal process. In this approach, dispersal – the mobility of organisms – is presented as a mechanism for the differentiation of allopatric taxa. In order to explain the members of a group that are all allopatric, this dispersal has to occur just once in the entire history of each allopatric member, which is often millions of years, and it is a theoretical notion with no empirical grounding. Widespread species of *Achillides* often show evidence of local differentiation as subspecies, especially in the Southeast Asian region (mapped in detail by Condamine et al. 2013a), and in the future some of these local entities may prove to be good species. Evidence for local differentiation suggests that these butterfly species are not dispersing in an open-ended, random way, but are more closely tied to local ecology and geography than might be assumed by their flight capability. For example, *Papilio ulysses* is a fragile species that is easily damaged – especially its wings. It is probably very short lived, and in captivity a 10 day old specimen is in a derelict condition. This species typically inhabits rainforest – especially along rivers – and does not venture far outside forests or over open habitat (John Nielsen pers. comm.).

Empirical observations of dispersal as an ecological process show that the movement

of organisms allows them to occupy and colonize new habitats as they become available, and to occupy multiple disjunct habitats ('habitat islands') over the range of a distribution (Fig. 16). By this multiple habitat occupancy species comprise metapopulations, or populations of populations. Because of this, species may continue to persist; some habitats

are obliterated through geological or climate upheaval, but other habitats come into existence through these geological and climatic events and are subsequently occupied. This concept of a metapopulation structure in species distribution is well accepted in the science of ecology, but it is far less acknowledged in evolutionary biogeography (Heads 2018).

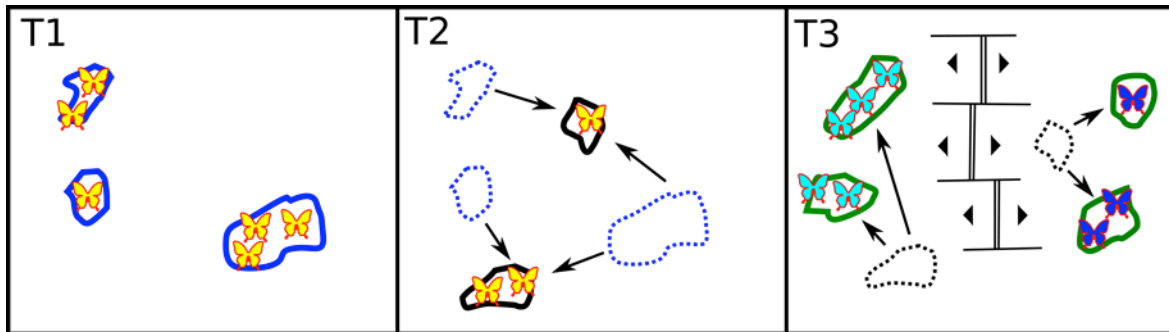


Fig. 16. Metapopulation persistence and vicariance. T1 – taxa inhabiting three islands, T2 – Islands eroded or subside, but taxa survive having dispersed onto new, nearby islands (arrows); T3 – Islands in T2 now submerged following dispersal onto newer islands (green outline) that are also being displaced by formation of a spreading ridge resulting in vicariance of the two island biotas. This same model is equally applicable if the islands were individual habitat islands on a continent (modified from Heads 2017: fig. 4).

The metapopulation concept provides a significant mechanism for the origin and evolution of butterfly allopatry. Ancestral distributions are established through normal ecological dispersal which may result in range expansion, but does not generate differentiation. In this context the movement of organisms is not the cause of allopatry. Allopatric differentiation requires isolation, and this may occur within an ancestral range as the result of geological or climatic disruption of the ancestral range. This is why distributions often show boundaries that are correlated with tectonic structures that caused geological disruption. If a butterfly distribution spans multiple, disjunct habitats, the species will be able to persist in its overall region for millions of years if new habitat areas are constantly being formed. This will be true even if each of the individual habitats are submerged at one time or another, or reduced to very small localities such as volcanic islands (which may

support very high levels of diversity – Heads 2012).

Metapopulation persistence by the colonization or re-colonization of habitats means that a species or higher taxon can be much older than the geological age of the islands (or habitat islands) that it occupies. The metapopulation concept also means that there does not need to be a direct 'landbridge' connection between areas to establish an ancestral range. Heads (2014) noted that biogeographers have often assumed that groups on continental crust have had a different history from those on oceanic island arcs. For example, Lohman et al. (2011) classified many Philippine and Wallacean islands as oceanic, because they had had no terrestrial connections to surrounding land since first emerging. The authors argued that this meant that the islands' biota arose 'predominantly' by dispersal rather than vicariance (Lohman et al. 2011 did not explain how vicariance could still sometimes be

applicable to that situation). But if terrestrial and reef clades on oceanic crust can persist as metapopulations in dynamic archipelagos, they can also undergo vicariance, whether or not all the land originally occupied was directly connected (Fig. 16, T3) (Heads 2014). Lohman et al. (2011) noted that terranes moving around what is now the South China Sea did not necessarily remain above sea level and that submergence would presumably have extinguished all terrestrial and freshwater life they may have hosted. But different parts of these terranes may well have remained subaerial at different times, and so some of their biota may have persisted with a metapopulation distribution structure.

Metapopulation biogeography represents a meeting point between ecological processes that maintain the distribution range of species (by normal means of dispersal among subpopulations) and evolutionary processes of isolation responsible for differentiation (Heads 2018). The concept provides a broad framework for the initial establishment of ancestral distributions in *Papilio* subg. *Achillides* and other butterflies. It also provides a mechanism for the persistence of allopatric distributions in the Malay Archipelago, in a changing landscape of continental areas and oceanic islands.

Ancestral origins

The Malesian region comprises both continental and accreted oceanic terranes (especially island arcs) of different ages and sources. The region is also biogeographically diverse with groups that encompass the entire region, while others have more restricted distributions (Heads 2014). Many taxa in this region have highly localized distributions along with broad disjunctions; both patterns have no obvious relationship to current geography but correlate spatially with various tectonic features (Heads 2003). A prevalent view of Malesian biogeography has treated the biota as derived by chance dispersal from nearby centers of origin, usually continental sources such as

Australia and Asia (e.g. Lohman et al. 2003). This view is inconsistent with the allopatry within *Papilio* subg. *Achillides* and *Vanessa*, as well as the disjunct allopatry of two Troidini clades. An alternative to the chance dispersal model proposes that each group has evolved by vicariance of a widespread ancestor whose distribution range also included other regions.

The sister group of *Papilio* subg. *Achillides* comprises two subgenera – 'Menelaides 2' which is also distributed over parts of South East Asia and Southwest Pacific, and 'Princeps 3' in Africa and India (Condamine et al. 2013a did not delineate their distributions in detail). This pattern, found in many animal and plant groups, can be explained by ancestors having had typical Gondwanan ranges connecting Africa and South East Asia across the Indian Ocean (Croizat 1958, Craw et al. 1995). The phylogenetic relationships of the Malesian *Vanessa* with Macaronesia, then India-Asia, and more distantly with a Laurasian clade could be the result of an ancestral distribution that extended along the Tethys shoreline (see Heads 2014 for other examples). In the Troidini the Malesian genera are allopatric to their sister group in America, and together they are allopatric to the basal sister group in Madagascar. The Pacific relationship is typical for many plant and animal groups (e.g. *Masteria* spiders, Fig. 17), although many biogeographers have assumed that the Pacific is nothing more than an originally empty region accidentally penetrated by waifs and strays.

The frequent assumption of the Pacific basin as a permanent scattering of small, oceanic islands is not consistent with a range of tectonic and geological studies that provide evidence for the formation of massive magmatic plateaus in the Cretaceous. These include the super plateau Ontong Java Nui that comprised the present day Ontong Java, Hikurangi, Manihiki plateaus in the west Pacific, and the Gorgona plateau in Colombia (Hochmuth et al. 2015). Geological evidence from sediments and even terrestrial plant fossils

indicate that that these plateaus were partially subaerial and were associated with large volcanic islands. These would have supported a Pacific biota that itself could have been inherited from island arcs formed along the subduction zones of earlier Pacific plates. The plateaus were eventually broken up and dispersed around the east and west Pacific by plate movement, and this would have also displaced their biota, including butterflies ancestral to those now in the Old and New Worlds (Heads 2012, 2014, 2017). With respect

to the broader affinities of *Papilio* subg. *Achillides*, *Vanessa*, and the Triodini, it is suggested that their shared presence in Malesia is the result of three polymorphic, ancestral butterfly species, each with a broad ancestral range (as found with some extant butterflies). The ancestral forms were centered on different regions (Gondwanic, Tethyan, Pacific) and were tectonically combined within the geologically composite region of the Malay Archipelago.

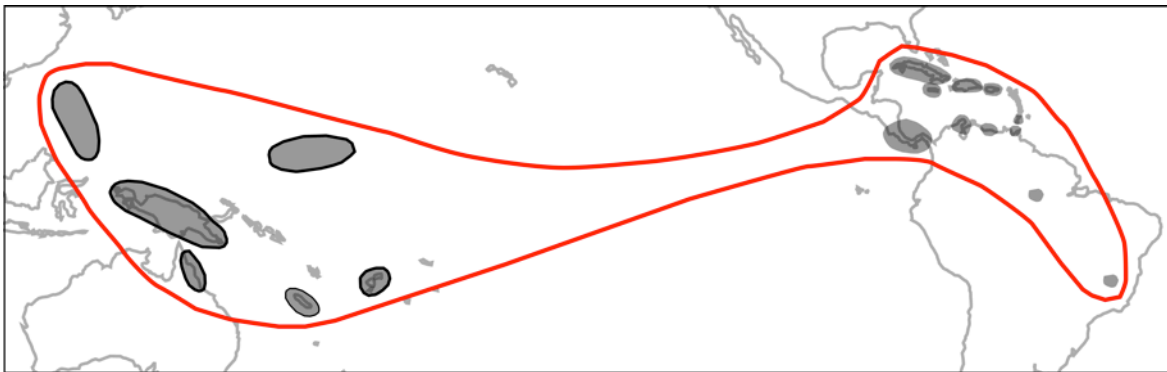


Fig. 17. Biogeography of *Masteria* spiders (Dipluridae). Note the group's presence in the Caribbean, consistent with a Pacific origin of the Caribbean plate. Modified from Heads (2014 fig.8.8) and with additional data from Pedroso et al. (2015).

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