

Estimating time and space in the evolution of the Lepidoptera

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Several aspects of estimating what happened when and where in the evolution of the Lepidoptera are discussed. Because of their scarcity and often poor preservation, fossils are not very helpful, but at least they demonstrate that, in the Oligocene some taxa of butterflies, perhaps at tribal level or higher, did occur in the Northern as well as in the Southern Hemisphere. The concept of a molecular clock is seen as a most needed test for vicariance explanations of disjunct distributions. Special emphasis is laid on the importance of calibration of the clock. The use of geological vicariance events as calibration points is rejected, because of circularity when vicariance explanations are to be tested. Fossils as calibration points should ideally be replaced by the minimum age of an apomorphous character state demonstrated by the fossil rather than a supposed identity on the basis of overall similarity. Some conditions that directed the evolution of Lepidoptera (called constraints here) are discussed for their possible use as calibration points. Estimation of the evolution in space through time (palaeobiogeography) as found in recent literature is discussed, the often supposed role (of the break-up) of Gondwana in the evolution of the butterflies is challenged, and an alternative hypothesis is given.

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Introduction

Estimating time and space of events in the evolution of life has been an important issue ever since the acceptance of the concept of evolution. A fair idea of these events is crucial in understanding how the evolution of a group of organisms has been shaped not only by intrinsic factors (mutation, population growth, food preference, etc.), but by extrinsic, environmental factors as well. Initially, and for a very long time, fossils formed the only clue to what had happened in deep history. Although the first fossil lepidopteron was described well before the idea of evolution had clearly been formulated (Charpentier 1843; described as *Sphinx atava* [Sphingidae], moved to Nymphalidae by later authors), fossil Lepidoptera remained too rare to play an important role in elucidating the evolutionary history of the Lepidoptera, both in time and space. Every attempt to estimate the origin of the Lepidoptera from fossils had to

extrapolate the data to far back in history and to make use of (reputed) circumstantial evidence. Thus, Forbes (1932), starting from a well preserved butterfly fossil (*Prodryas persephone* Scudder, 1878, about 20 Ma old), concluded that “there is a slight weight of probability that the Lepidoptera arose in the late Carboniferous or early Permian period ...” (i.e. some 280–300 million years ago). Not only fossils, also the study of recent taxa led some authors to unwarranted extrapolations and speculations on the origin of higher taxa. In a study of American Copper butterflies (Lycaeninae) Miller & Brown (1979) speculated that the basal split in the Lycaeninae took place over 100 million years ago and, thus, the origin of the “Lycaenoid root” should be placed much further back into the Mesozoic. More generally, Brown (1987), while discussing the evolution of Neotropical butterflies, suggested that pantropical groups at the level of subfamily and

tribe originated in the Mesozoic and the early super-families of the Lepidoptera in the Palaeozoic. Several developments have demonstrated the untenability of such broad speculations. The rise of cladistics, fast computer programs and molecular techniques in the second half of the 20th century have largely taken over the role of fossils in evolutionary studies. The same developments, enhanced by an incomparably better fossil record than found for Lepidoptera, have also led to a much better understanding of the evolution of the angiosperms (Soltis et al. 2005, Wikström et al. 2004), the foodplants of all Lepidoptera except the basal-most lineages and some secondary changes to other food sources. The dependence on foodplants set constraints on the estimation of the age of the Lepidoptera. Also other environmental factors, leading to particular adaptations, may help to date evolutionary events in Lepidoptera, if we know the age of the environmental factor.

In the present contribution several aspects of estimating divergence times in Lepidoptera are discussed, aiming at a better understanding of the interplay of evolutionary and distributional changes. The survey is not exhaustive, and emphasis is laid on the evolution of skippers and butterflies.

Estimating time

Fossils

Traditionally fossils are considered the key to the past. Indeed, without fossils we would have no idea of the enormous diversity of dinosaurs or extinct mammals. It is difficult to assess, however, how far fossils have contributed to our understanding of the phylogeny of the groups concerned and have changed patterns of relationship that had been derived from analysis of extant organisms. The finding of a new fossil is not different from the finding of a new extant species when it comes to allocation in an existing system, but while, in an extant species, all characters used to build up the system can be studied and analysed in a cladistic way, fossils are usually very fragmentary. In most cases, their place in the system is more determined by overall similarity than by a critical evaluation of apomorphic and plesiomorphic character states, as correctly stated by Kristensen & Skalski (1998). If a fossil shares an apomorphic state of a character with a group of extant taxa, but has retained the plesiomorphic state of one or some characters that have a derived state in the extant group, the fossil is placed at the root of that group. An example is provided by the famous butterfly fossils *Praepapilio colorado* and *gracilis*,

both described by Durden & Rose (1978) from the (middle Eocene) Florissant fossil beds in Colorado. The fossils demonstrate two papilionid apomorphies in the venation of the forewing, viz. the presence of a "basal spur" (term by Miller 1987; a cross-vein between Cu and 1A), and vein 2A curves to the hind margin instead of to 1A. Two other prominent apomorphies of the papilionids, viz., in forewing cubitus and lower discocellular vein in line (i.e., cubitus seemingly quadrid), and in hindwing only a single anal vein (only in *Baronia* there are two anal veins), are not present in *Praepapilio*, i.e. these conditions are in a plesiomorphous state. As a consequence, *Praepapilio* does not fit in our system of Papilionidae and the only logical place is at the root of the Papilionidae.

Notwithstanding the limitations, a fossil fixes a point in the evolution of a taxon in time and space, the aspects we are interested in, in this contribution. Unfortunately, fossil Lepidoptera are extremely rare. Kristensen & Skalski (1998; see also many references therein) estimate the total number known at some 600–700 specimens, covering about 200 million years (the oldest known fossil is *Archaeolepis mane*, described by Whalley (1985), from the Lower Lias of Dorset, England, based on a wing fragment with scales which show a similarity to the scales of the most primitive extant Lepidoptera, Micropterigidae). From the whole of the Mesozoic era only 19 specimens are known that are considered lepidopterous (Whalley 1986), all other Lepidoptera fossils are from the Tertiary, and a few from the Pleistocene. Remarkably, the proportion of butterflies among the fossils in number of specimens (some 80 specimens known) is close to the proportions among extant Lepidoptera in species.

Because of their scarcity, and also their often fragmentary nature, fossil Lepidoptera are not very helpful in estimating time and space in the evolution of the Lepidoptera, and conclusions are surrounded by many "ifs". Recently, Hermsen & Hendricks (2007) described a method for constraining the age of origination of derived characters with the help of fossils. However, for that method fossil taxa must be incorporated in a phylogenetic analysis of extant taxa. The authors recognize and discuss the problems associated with fragmentary and missing characters. It would seem that the lepidopterous fossils simply are too badly preserved for that purpose. But surely, as far as apomorphic character states can be recognized in a fossil, the minimum age of that character state can be plotted on the tree of extant taxa. This is actually what is done (or should be done) when fossils are used to calibrate the molecular clock (see

below), divergence being nothing else but the origination of a derived character state in one of two sister species.

A critical review of all known butterfly fossils will be published separately. In the present study only those fossils that have been used in literature for calibration of the molecular clock are discussed. The list provided by Braby et al. (2005) is incomplete (also for the time frame chosen) and uncritical, and the names have not been given in the original combination. In view of the scarcity and often fragmentary condition of fossil Lepidoptera, their usefulness for calibrating the molecular clock is limited, but at least they testify of the occurrence of the taxon of which an apomorphic trait has been preserved in the fossil at a certain time and place in deep history.

Molecular clock

The publication by Zuckerkandl & Pauling (1965), in which the authors introduced the idea of a molecular clock, must be one of the most cited papers in molecular phylogenetics. The initial idea that there would be a constant rate in nucleotide substitution in DNA evolution (the molecular clock) over time and across lineages, so that counting the substituted nucleotides would be a measure of time elapsed, proved to be an oversimplification, or simply wrong. There is an almost unsurvivable stream of publications on the application of a molecular clock, pro as well as contra (Graur & Martin 2004, for instance, compared the use of a molecular clock with reading the entrails of chickens), but the most critical voices seem to have become silent and there appears to be a general opinion that the clock may be used if allowance is made for variation in substitution rate. A well written summary of aspects of estimating divergence times from molecular data can be found in Arbogast et al. (2002). Several computer programmes have been designed to calculate divergence times in the presence of rate variation. Welch & Bromham (2005) give an overview, with the addresses of the websites where they can be found.

Crucial in applying a molecular clock with differential rate among lineages and branches of the same tree is the fixation of so-called calibration points, speciation events for which we (think to) have a fair idea of absolute age. It can not be emphasized strongly enough how important good calibration points are. Divergence times with confidence intervals may look impressively accurate, but with doubtful calibration points they have little meaning. For a discussion of problems involved in estimating divergence times in biogeography, see Heads (2005).

Calibration by fossils

As stated above, butterfly fossils are rare and usually difficult to assign to a taxon rank below subfamily. Therefore, their application as calibration points (minimum age) must be done with great care, and fossils should not be identified on the basis of similarity only, but on apomorphic characters.

Braby et al. (2006) used four fossil pierids to calibrate the molecular clock for their tree of the Pieridae. As the authors put it: "Because the nearest relatives of these fossils have been determined with some degree of certainty, the fossils served as useful calibration points." (p. 250). All four fossils are discussed here.

***Stolopsyche libytheoides* Scudder, 1889.** Lower Oligocene, Florissant, Colorado. According to Braby et al. (2006) the closest relative is the extant genus *Pieris*. Probably they based their judgement on Emmel et al. (1992), who said the fossil was closer to *Pieris* than any other living genus. Actually the fossil is so badly preserved that Zeuner (1942) could not even determine the family. The antennae show a very gradually thickened club which takes about 1/3 of the whole antennal length. If not for this character, the fossil could as well represent a non-papilionoid lepidopteron. The forelegs are long, a primitive character found in Papilionidae, Pieridae, Lycaenidae females, *Libythea* female, and Hesperidae, and generally in non-papilionoid Lepidoptera. Since the head is small for Hesperidae and *Libythea*, the forewing is long for Lycaenidae (c. 25 mm), and the palps are long for the Papilionidae. Scudder thought the Pieridae the most likely family. Not very strong arguments to consider it to belong in the ancestry of, or being sister to, *Pieris*.

***Oligodonta florissantensis* Brown, 1976.** Lower Oligocene, Florissant, Colorado. Listed by Braby et al. (2006) as a close relative of the *Catasticta* group (possibly *Leodonta*). Seen from the left; wings folded; head and thorax squashed and useless for identification; abdomen enveloped in anal area of hindwing. Only the wing shape and venation can yield useful characters, although obscured by the four wings being superimposed. If correctly interpreted the radius of the forewing is branched as follows: R1 and R2 unbranched, R3 and R4 forked, with M1 stalked on R3+4 and mdc (Brown: udc, but udc does not exist if M1 is stalked on R) just after the origin of R2. The stalking of M1 on R is a pierid apomorphy, but not unique. There is, however, a drawback. According to Brown the apical part of the termen of the forewing is crenulate with a short tooth at the end of M2. If there is a tooth, in some Pieridae and a number of Nymphalidae, it is at the end of M1 (or close to it), also in *Leodonta* (Pieridae), the genus

mentioned by Brown for comparison (followed by Smith e.a. 1994: "very closely related to the present day Andean genus *Leodonta* Butler."). It thus seems that either Brown's M2 is actually M1 (in that case the branching of R needs revision, and the fossil is more likely to be a nymphalid than a pierid), or the tooth was not reconstructed correctly (in this connection it must be remarked that Brown's drawing of the forewing does not exactly match the photograph of the whole fossil, especially the apex being shaped slightly differently). As the distal half of the forewing is obscured by the overlapping hindwing, the rest of the forewing venation remains uncertain. In the hindwing the cell seems to be open (a character of the Nymphalinae), possibly because of the ldc being too weak to be visible in the superimposed wings. Sc is very long for a member of the Pieridae (where it is usually much shorter and terminates on the costa), and more like the long Sc found in the Nymphalidae. Diagnostic features are thus weak in the fossil, and a family assignment must remain uncertain. It was placed in the Pieridae by Brown (followed by Emmel et al. 1992), apparently for want of a better placement.

***Coliates proserpina* Scudder, 1875.** Lower Oligocene, Aix-en-Provence, France. Braby et al. (2006) give as closest relative: *Delias-Prioneris* group (possibly *Aporia*). Only forewings available. It seems that R2 is missing or fused with R1, while M1 is stalked on the common stem of R3, R4 and R5. The latter condition is a pierid apomorphy. Scudder compared the fossil to *Delias* (Pieridae, India to Australia), but in that genus there are only three radial branches left. In most pierid genera two radial branches (R1 and R2) arise free from the cell. The fossil does not show further characters that could be helpful phylogenetically.

***Miopieris talboti* Zeuner, 1942.** Upper Miocene, Randecker Maar, Schwaben, Southwest Germany. According to Braby et al. (2006) belonging to the *Pontia* group, possibly *Pontia*. Badly preserved. Of the radial branches of the forewing only basal parts of R1, R2 and the common stem of R3, R4 and R5 are visible; M2 originates from the upper angle of the cell, M1 is apparently stalked on the common stem of R3, R4 and R5; probably one R branch lost as commonly found when M1 is stalked on R, but relevant part of wing missing. The distad movement of M1 along R and the shift of R2 towards the costa are apomorphic characters of the Pierinae. The light colour and dark spots (at end of cell and between M3 and CuA1, and between CuA1 and CuA2) agree with this. The condition of the fossil is too bad to allow further statements. Zeuner (1942) himself saw a similarity with *Pontia callidice* Hübner, 1800, an

extant species, widely distributed in the Holarctic, and with *Tatochila macrodice* Staudinger, 1899, an extant South American pierid. Perhaps best placed in the subtribe Pierina as recognized by Braby et al. (2006), a more exact place within that tribe not warranted on the basis of the few characters visible in the fossil.

This review does not leave much room for use of the putative pierid fossils in fixing calibration points close to the origin of extant genera. By using them in the way they did, Braby et al. (2006) may have overestimated the age of the genera, and with that, the age of the Pieridae as a whole.

Since fossil Lepidoptera are so rare, and usually do not show the desired characters for a reliable allocation in the existing system, their use in calibrating molecular clocks has been limited. One more example is Nazari et al. (2007), who used papilionid fossils for calibrating the molecular clock for their tree. Above, in the chapters on Fossils, we already discussed the position of *Praepapilio*, which on morphological grounds can only be placed at the root of the Papilionidae. Yet, Nazari et al. (2007) place it near the first split in the *Papilio* lineage, thus running the risk that they strongly overestimated the age of the genus *Papilio*. See also the chapter on Estimating space. Obviously, *Praepapilio* can have originated tens of millions of years before the moment it became fossilized, and still have been in existence when *Papilio* was already flying around, but there is no evidence for that, and we must stick to what we have.

Calibration by vicariance events

The main reason for estimating divergence times is to test whether a speciation event coincides with a geological or climatological vicariance event, and, thus, can be ascribed to that event. If the speciation event is younger, then dispersal must have played a role in the distribution as it is today. Clearly, if one wants to test a vicariance explanation, one should not use the age of a vicariance event as calibration point, i.e. as the age of the speciation (divergence) event, because in that case vicariance has already been chosen as driving force. It is an example of circular reasoning. Yet, it is not difficult to find examples in the literature. An interesting case outside the Lepidoptera can be found among the icons of vicariance by the break-up of Gondwana, viz. the Ratites, the large flightless birds of the southern continents. Because of their flightlessness it is supposed that they could not disperse across the water to the Gondwana fragments, but were present before the fragmentation took place. However, the conclusion only

holds if they lost power of flight only once, in their ancestor, and that is just an assumption. In New Zealand, the extinct moa and the extant kiwi are the sole representatives of the Ratites. If a molecular clock is applied that has been calibrated on the assumption that moas were in New Zealand when it became isolated (giving a calibration point at 82 Ma), then the kiwi, which originated later (under this model 68 Ma), must have arrived by dispersal (Waters & Craw 2006). And, as stated by these authors (p. 353): "... this conclusion clearly begs the question: if dispersal was possible for the ancestors of the kiwi, why not for the moa?" Interestingly, also the vicariance origin of another icon of Gondwanan vicariance, *Nothofagus* (southern beech), supposed to be a bad disperser, in New Zealand, has been challenged recently (Knapp et al. 2005). The vicariant origin of the greater part of the New Zealand biota has further been challenged by Trewick et al. (2007). As described by these authors, New Zealand is lying on an enormous piece of continental crust, called Zealandia (on which also the present-day Chatham Islands and New Caledonia are situated). By far most of the continental crust has always been under water. Modern New Zealand originated from plate boundary collision. It started abruptly 26 Ma. Also New Caledonia is the product of plate boundary collision, starting 35 Ma. While Zealandia drifted northwards, it thinned and sank some 2000–3000 m. As far as there was emergent land on the continental crust, it was gradually inundated. Possibly all dry land was totally immersed, obliterating all traces of possible Gondwanan biota, but geological evidence is still insufficient to be sure about it. If there has been permanent land all the time, it must have been tiny pieces, and most of the Gondwanan biota must have disappeared. It implies that most or all land life on modern New Zealand arrived there by long distance dispersal. This conclusion is at variance with the ancientness of New Zealand's biota as stressed by the panbiogeographic school (e.g., Craw et al. 1999). At the same time, it demonstrates that a supposed vicariant origin is unfit for calibrating a molecular clock.

Pellmyr & Leebens-Mack (1999) examined the evolution of mutualism between yuccas and yucca moths (Incurvarioidea: Prodoxidae). Age estimation is based on the age of the sister family, Cecidosidae, which "... combine a classical Gondwanan distribution with very low dispersal ability...". This is reminiscent of the Ratites and *Nothofagus*. A monophyletic group of six genera which are gall-makers on Anacardiaceae is found in South America and Africa. To allow for their vicariant origin, they must have been isolated since the separation of the two

continents, at least 95 Ma. True enough, it is much older than the age of the Anacardiaceae as supposed at the time (70 Ma; Wikström et al. 2001, estimate the age of the Anacardiaceae even younger, mid-Palaeocene), but it "is consistent with other biogeographic evidence", whatever that may be. Moreover, a new genus of Cecidosidae had just been discovered from New Zealand, indicating that the age of the family was at least 82 Ma (the Ratites line of reasoning: it must have been there before the separation, so its minimum age is the age of the separation). Since the Prodoxidae, as sister group, are equally old, a "conservative age of > 95" million years for the prodoxid-cecidosid divergence is derived. The authors felt their age estimate supported by further, indirect evidence: in 97 million years old leaf fossils characteristic mines had been found of the more derived Ditrysia, and thus, the more primitive incurvarioid stemgroup was present at the time. They did not make clear what this has to do with a crown group in the Incurvarioidea. This example has been described in some detail to demonstrate how difficult it is to estimate divergence times, but particularly that such a complex of assumptions, each with its own limited reliability, can easily fall apart if one of the assumptions (e.g., that dispersal did not play a role) proves wrong. So, how much reliability do we attach to the product of the assumptions? It should be added that a bit earlier Grehan (1991) dealt with the Prodoxidae in a panbiogeographic way. Apart from the assertion that the family "... may be oriented to a Pacific baseline ...", no conclusion is drawn (or is a "Pacific baseline" a conclusion in itself?).

In their paper on the genus *Papilio*, Zakharov et al. (2004) based their estimates of divergence times on calibration points derived from "biogeographical time constraints". These constraints are vicariance events. They do see problems with that: "Calibration of a molecular clock based on vicariance events presents a major problem for absolute dating when the selected events separate previously contiguous areas under a variety of scenarios, e.g., gradual vicariances that occurred over extended periods of time or multiple sequential events in which the same areas were separated and reunited repeatedly over time." (p. 1). This is certainly true, but they did not indicate the main problem, viz., that the divergence may not have been the result of vicariance but of dispersal. Now they only "prove" that the divergences are the result of vicariance events which they pre-supposed as the driving diverging factor to start with.

Similarly, Braby et al. (2005) hypothesized a role of Gondwanan fragmentation in the distribution and radiation of the Troidini (Papilionidae), based on vicariance events as calibration points, instead of

asking themselves the question: how far can the present distribution of diversity be ascribed to, respectively, vicariance and dispersal, and trying to find evidence outside the realm of vicariance and dispersal.

Hall et al. (2004) described a fossil riodinid butterfly, *Voltinia dramba*, from Oligocene-Miocene Dominican amber (15–25 Ma). The explicitly hypothesized sister species is *Voltinia danforthi* (Warren & Opler, 1999), an extant species occurring in northwestern Mexico. Because of this relationship and distribution, they hypothesized that the divergence of the two species date back to the period when the proto-Greater Antillean arc made range extension to Hispaniola possible, i.e., 40–50 Ma. They opt for a vicariance explanation because of the comparatively sedentary behaviour of the riodinids. However, in a time span of 25 million years everything is possible (see, e.g., the faunal exchange between Asia and Australia; de Jong 2003), and the assumption of vicariance is a weak reason for supposing that “a more ancient date of origin for many of the higher-level butterfly taxa than is often conceded” follows from this fossil.

Calibration by constraints

Obviously, adaptation to an environmental factor cannot have originated before the factor existed. Thus, the age of that factor constrains the age estimate of the adaptation. It must be clear that the reliability of the estimation of the age of the Lepidoptera clades concerned is dependent on the reliability of the age of the constraints. Three such constraints are discussed here.

Hearing organs

Hearing organs are widespread and come in different shapes and on different body parts in the Lepidoptera, particularly in the Macrolepidoptera (Minet & Surlykke 2003). There is growing evidence of their functioning in communication (courtship) (Spangler 1988), but the hearing organs of night-active moths are supposed to have evolved in response to predation by bats (Spangler 1988, Scoble 1992, Grimaldi & Engel 2005). Possibly, the hearing organs had more simple precursors used for escaping other predators before the rise of the bats, but such precursors are not known. Without evidence to the contrary, it is better to stick to what is known. Evasive behaviour of moths in the presence of bats is a common observation, and so far there is no reason to suppose that the occurrence of organs that can detect the bat's echo-location is not an apomorphy at the level of the family or superfamily level where the hearing organs occur. Clearly, the conclusions below are dependent

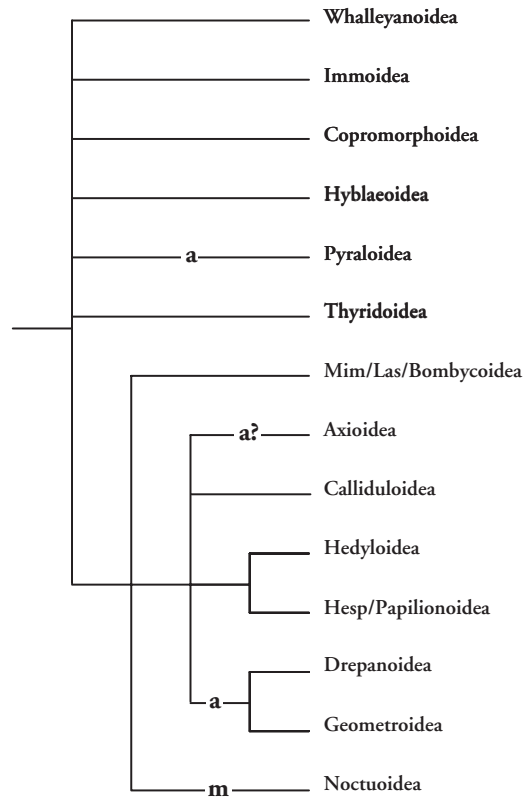


Fig. 1. Phylogeny of the superfamilies of Obtectomera, after Kristensen & Skalski (1998). a = abdominal hearing organ, m = metathoracic hearing organ.

on the correctness of the assumption that the hearing organs evolved in response to bat predation.

Most types are tympanal organs, consisting of a tympanum, a tracheal sac and a scoloparium. They fall into three categories according to their location: base of forewing, metathorax and antero-abdominal region. It is unlikely that the hearing organs in the forewing, found in Thyrididae, Hedyliidae and Nymphalidae, evolved in response to bat predation, since at least part of the species concerned are diurnal and do not come into contact with bats. The tympanal organs in metathorax and abdomen were considered homologous by Scott (1986a), but according to Minet & Surlykke (2003) this is highly unlikely, since the innervation is different. Abdominal tympanal organs are found in Dudgeonidae (provisionally placed in Cossioidea; Scoble 1992, Edwards et al. 1998), Pyraloidea, Geometroidea (including Uraniidae), and Drepanoidea (although in the latter there is no clear tympanum), while metathoracic tympanal

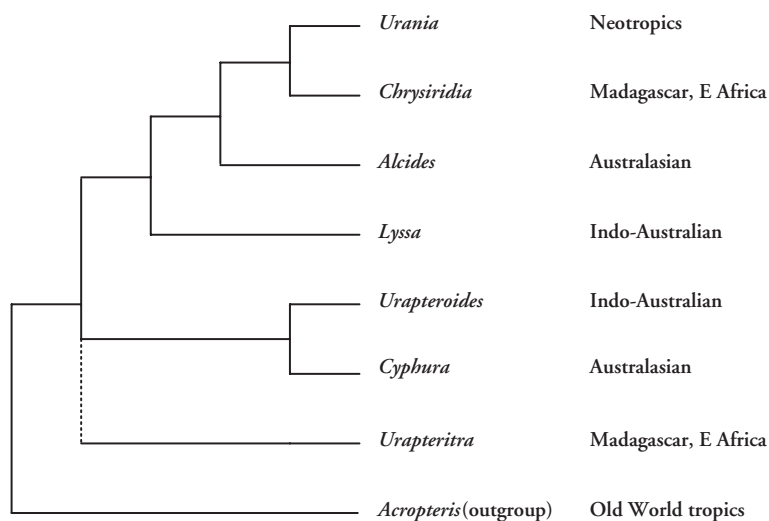


Fig. 2. Phylogeny of the Uraniinae, after Lees & Smith (1991) and Holloway (1998). The genus *Acropteris*, used as outgroup, is in the Microniinae. By adding genitalic characters, Lees found the same tree and an alternative tree with *Lyssa* and *Alcides* sister taxa (see Holloway 1998).

organs are confined to the Noctuoidea. Possible abdominal hearing organs are further found in Axioidea and in two genera of the Tineidae (*Harmaclona* and *Micrerethista*), but these need further study.

The “oldest definitive bat fossils are early to middle Eocene, distributed in North America (...), Europe (...), and Australia (...), and they were already specialized for flight and echolocation (...).” (Teeling et al. 2003: 582; see also references therein). These fossils do not belong to some intermediate form, but are fully-fledged Chiroptera. It is, therefore, not surprising that a molecular clock estimate gives a higher age for the origin of the bats, circa 64–71 Ma, i.e. around the K-T boundary (Springer 1997, Smith & Peterson 2002, Teeling et al. 2005). Consequently, echolocation in bats cannot be older than that age. Probably, it evolved more than once (Jones & Teeling 2006), but for our purpose, i.e. constraints on the estimation of time of divergence of higher Lepidoptera clades, only the first origin is of importance.

Unfortunately, the phylogeny of the superfamilies of the ditrysiid moths (making up about 95 % of all Lepidoptera) is still largely unresolved and little progress has been made over the last 15 years. The tree given by Kristensen & Skalski (1998, and repeated in Kristensen 2003) is essentially the same as the one presented by Minet (1991). Part of the tree is reproduced in Fig. 1. Yet, plotting the occurrence of hearing organs on the tree strongly suggests that not only the metathoracic and abdominal organs arose independently, but that, moreover, the abdominal organs arose more than once, viz. in Pyraloidea and Geometroidea/Drepanoidea. The relatively late origin of echolocation implies that also the

associated hearing organs arose relatively late, i.e. after the K-T boundary. In other words, the Pyraloidea, Geometroidea, Drepanoidea and Noctuoidea are not older than Tertiary.

The fossil history of the bats is too fragmentary and geographically biased (no fossils are known from tropical regions) to make them helpful in estimating where the bats originated. On the basis of the phylogenetic tree and present-day distribution, Teeling et al. (2005) concluded that the bats radiated in Laurasia before they colonized already separated Gondwana fragments and radiated and dispersed further from there. This agrees with the findings of Australian palaeontologists that bats entered Australia from south-eastern Asia as early as 30 Ma, i.e. well before Australia reached its present, more northern, position (Archer et al. 1996).

A northern origin for the bats cannot simply be translated into a northern origin for the moths with hearing organs, but, if these moths originated on Gondwana fragments, it must have been after the bats had spread to these fragments, implying a younger age for the moths. At the time of the origin of the bats (and thus, the maximum age for hearing organs), Africa, India, Madagascar and New Zealand had not been connected to other land masses for a long time, ranging from 15 to 75 million years (Smith et al. 1994, McLoughlin 2001). So, unless the superfamilies with hearing organs originated on one of these Gondwana fragments and later migrated from there to occupy the entire world, they arose elsewhere and later dispersed across the sea, in case of Madagascar and New Zealand, or possibly also over-land, in case of Africa and India, to these areas, where they

radiated to often very rich faunas. For Madagascar, for instance, 487 species of Pyraloidea, 711 species of Geometroidea, and 1815 species of Noctuoidea have been recorded (Lees & Minet 2003), while the moth fauna of southern Africa alone (south of Angola, Zimbabwe and Tanzania; there are no reliable figures for the rest of Africa) includes 1017 species of Pyraloidea, 1124 species of Geometroidea, and 2282 species of Noctuoidea (Vári et al. 2002). The fossil record of the moths is too scant to be helpful in deciding where these moths originated. The phylogeny of Pyraloidea, Geometroidea, Drepanoidea and Noctuoidea, as far as known, is not very helpful either, because of the very wide distributions of most of the higher taxa. In the first superfamily, for instance, the Pyralidae (as separate from the Crambidae) are divided into five subfamilies (Solis & Mitter 1992, Munroe & Solis 1998), four of which are cosmopolitan, while the fifth, Chrysauginae, with highest diversity in the Neotropics, is also found in North America and the tropics of Asia and Australia. To understand the constraint of the echolocation of the bats in the reconstruction of the palaeobiogeography of the moths with hearing organs, infra-subfamilial relationships may be more elucidating. As an example, we shall discuss the genera of the Uraniinae (Uraniidae, Geometroidea).

The Uraniinae form a small subfamily with circa 50 species in seven genera, including the brilliantly coloured, large, day-flying genera *Urania*, *Chrysidia* and *Alcides* (note that in day-flying moths tympanal organs have lost their function in bat evasion). Lees & Smith (1991) analysed the interrelationships of six of the seven genera (*Urapteritra* was excluded because of lack of data, but, at least externally, it looks like *Urapteroides* and *Cyphura*). Fig. 2 represents the interrelationships of the genera as well as their distribution. Discussing the evolutionary history of the subfamily in relation to its food preference (to be dealt with in the next section), Lees & Smith (1991) hypothesized an Australasian origin for the subfamily and a vicariance origin for the genera due to the break-up of Gondwana, even though in that case the origin of the subfamily must predate the separation of Africa from Australasia (> 100 Ma), and a number of additional assumptions are needed to explain the absence of the older taxa in the Neotropics. If tympanal organs arose in the ancestor of the Drepanoidea and Geometroidea not before the origin of the bats, c. 70 Ma, and thus all subfamilies within the superfamilies must be younger, a vicariance explanation is unlikely. Lees & Smith (1991: 332) stated that: "Vicariance acting on the original colonization of the foodplant genera by ancestral uraniines seems sufficient without the need to invoke long-distance

dispersal, including use of land bridges." However, long-distance dispersal must always have been involved, certainly for taxa with an Indo-Australasian distribution: either the genera originated by vicariance and later spread across land and sea to reach their present distribution limits, or their ancestor dispersed to other landmasses and diversified there in isolation. Moreover, at least the larger uraniines are strong flyers, and the genera *Alcides*, *Urania* and *Chrysidia* are famous for their migratory flights (Minet & Scoble 1998). An alternative hypothesis for the distribution of the genera will be discussed later.

Foodplants

The evolution of larval food preferences in Lepidoptera has been amply discussed by Powell et al. (1998), although not in the context of setting constraints to the estimation of divergence times. The fossil record for plants is incomparably better than for Lepidoptera. Moreover, molecular studies of plants have been numerous, leading to a strongly revised picture of the phylogeny of the plants, particularly the angiosperms, the food of 95% of the Lepidoptera. As a consequence, divergence times for the families of angiosperms are known with some reliability (Wikström et al. 2001, 2004). These times can be used as constraints in estimating the time of origin of those taxa that are dependent on the relevant plant family (or even genus), or in biogeographic considerations. Obviously, this works better, the more restrictive the foodplant choice of the Lepidoptera clade concerned is. In highly polyphagous taxa the spread in the age of the foodplants may be too large to be helpful as constraint. An assumption to be made a priori is that the preference for a single plant family has developed only once in the evolution of the lepidopterous clade under study. It is hard to see how, from an unknown ancestral food preference, taxa as far apart as, for example South Africa, New Guinea and New Zealand, all shifted to the same new plant family independently.

A few examples of the constraint by the age of the foodplant on the age estimation of a lepidopterous clade are given below.

Celaenorrhinus (Hesperiidae)

With c. 85 species one of the largest genera of the Hesperiidae, and the only pantropical genus, occurring in tropical and subtropical America, sub-Saharan Africa, Madagascar, and from India to the Philippines and the Moluccas. The monophyly of the genus is supported by a peculiar abdominal scent organ in the males (de Jong 1982). The phylogeny of the genus and the relationships between the species of the three large areas are unknown. The

disjunction is suggestive of a vicariance event following the separation of Africa and America. The separation of the two land masses was completed c. 84 Ma (Pitman et al. 1993). Possibly, Africa and South America remained close enough for an extended period to make occasional crossings of the widening sea way possible, but whatever the width of the stretch of sea, crossing means dispersal and not vicariance. Although in some cases additional foodplants are used, the predominant foodplant family in the Palaetropics as well as in the Neotropics is Acanthaceae. The age of this family is estimated at 40–45 Ma (Wikström et al. 2001), much too young for the vicariance event. Consequently, either a dispersal scenario including exchange between Africa and South America, or quite another hypothesis is needed to explain the present distribution, see the discussion below.

Libytheinae (Nymphalidae)

The modest size of this subfamily (two genera, *Libythea* in the Old World, *Libytheana* in the New World, with 7–9, and 1–4 species, respectively, depending on the treatment of island populations) is disproportional to its importance in phylogenetic analyses. The distribution is worldwide, but the subfamily is absent from the cooler and drier parts of the globe. In a morphological cladistic analysis of Papilionoidea and Hesperioidea with 19 nymphalid genera (de Jong et al. 1996), *Libythea*, as representative of the subfamily, ended up as sister to the rest of the Nymphalidae. In a much more extensive morphological study of the Nymphalidae only, including 95 genera, Freitas & Brown (2004) found the same position for the subfamily (represented by *Libytheana*). In a molecular analysis of the Nymphalidae (based on one mitochondrial and two nuclear genes; Wahlberg et al. 2003), *Libythea* was used as outgroup, since the inclusion of species from outside the Nymphalidae (Pieridae or Lycaenidae) led to spurious results, probably because of long branch attraction. However, it left the position of *Libythea* uncertain, unless it is, indeed, sister to the rest of the Nymphalidae. In a combined morphological and molecular study of the Papilionoidea and Hesperioidea (Wahlberg et al. 2005), the subfamily was sister to the Danainae in a maximum parsimony analysis, and sister to a group of five other subfamilies of the Nymphalidae in a Bayesian analysis. According to Wahlberg (pers. comm.), the non-basal position in the combined analysis probably is the result of poor taxon sampling.

A remarkable feature of the subfamily is the occurrence of an endemic species on the Marquesas (*Libythea collenettei* Poulton & Riley, 1928), in the middle of

the Pacific Ocean. Shields (1979) saw this as evidence for the now practically forgotten theory of an expanding Earth and considered *L. collenettei* as a relic of the initial opening of the Pacific in the Jurassic (146–208 Ma). All species of the subfamily live exclusively on the genus *Celtis* (Ulmaceae) (Ackery et al. 1995, Braby 2000, Igarashi & Fukuda 2000, Scott 1986b, and others). The age of this genus has been estimated at c. 25 Ma, much too young for whatever vicariance event. If Libytheinae is, indeed, sister to the rest of the Nymphalidae, this age is also much too young for the family, if only because older fossils are known (see above). The only possible hypothesis in this case is that, long after the split between Libytheinae and remainder of the Nymphalidae there occurred a shift in food preference, and only thereafter the subfamily reached its present wide distribution. Several species of Libytheinae are strong migrants, and this may have helped to attain a wide distribution.

Kawahara (2003) published a cladogram for the subfamily, confirming the sister group relationship between *Libythea* and *Libytheana*, and placing *L. collenettei*, the Marquesas endemic, as sister to the rest of *Libythea*. It makes one wonder, whether the ancestor of *Libythea* crossed the Pacific from America, leaving behind a population on the Marquesas to develop into *L. collenettei*.

Lycaeninae (Lycaenidae)

The Lycaeninae form a well-defined subfamily of the Lycaenidae, probably sister to the Polyommatae and Theclinae combined (Wahlberg et al. 2005). By far the most of the more than 100 species are found in the Holarctic region, but there are also species in East and South Africa, the Oriental region, New Guinea, New Zealand, and Guatemala. The subfamily has been divided into a number of genera which may or may not represent monophyletic groups. Most species are easily recognizable as belonging to the subfamily, but the mostly montane species of the Oriental genus *Heliophorus* look strongly different, and, together with the New Guinea *Melanolycaena* (two species) and the monotypic genus *Iophanus* in Guatemala, they have been placed in a separate tribe, the Heliophorini, leaving the remainder of the subfamily in the Lycaenini (Eliot 1973). A preliminary molecular analysis (de Jong & Van Dorp 2006) showed this division to be at variance with phylogenetic relationships. *Heliophorus*, *Melanolycaena* and the New Zealand coppers (divided by Zhdanko 1995, among *Lycaena* and the newly erected *Boldenaria*, a somewhat unhelpful action, not based on a phylogenetic analysis) appear to be more closely related to East Asian and North American taxa than to most of the West Palaearctic taxa, making the

isolation of the New Zealand coppers less severe. But still there is a large distributional gap between New Guinea and New Zealand. Miller & Brown (1979) considered the worldwide occurrence of Lycaeninae proof of their hypothesis that the coppers dated back to Pangaea. Apart from the fact that this would predate the radiation of the angiosperms and, thus, is unacceptable, the foodplant choice indicates that the distribution is not very old. All taxa, except some North American species that apparently switched to other hosts secondarily, live on Polygonaceae. This plant family is supposed to have originated c. 38 Ma (Wikström et al. 2001). As described by Trewick et al. (2007), modern New Zealand originated by plate boundary collision starting 26 Ma (see also section on Calibration by vicariance events). The arrival of the ancestor or ancestors (since only two of the four or five copper species of New Zealand were included in the molecular analysis, we cannot be sure that the New Zealand coppers together form a monophyletic group) may have been much younger. The nearest piece of dry land is the tiny Norfolk Island, about 750 km to the north, probably submerged for most or all of the Tertiary and only emergent in its current existence as land for 3 Ma. Buckley & Simon (2007) used the emergence of Norfolk Island to calibrate the molecular clock for the New Zealand cicada genus *Maoricicada* (through the genus *Kikihia*, of which one species, *K. convicta*, is restricted to Norfolk Island). Certainly, the emergence of Norfolk Island must have facilitated the spread of *Lycaena* to the south, but since the genus is absent from Norfolk Island, we cannot use the 3 Ma mark to calibrate the *Lycaena* tree, and we must leave the question of the age of the arrival of *Lycaena* in New Zealand unanswered for the time being.

Acraea (Nymphalidae)

The genus *Acraea* is, with about 250 species, among the largest genera of butterflies in the world. Since the morphological cladistic revision by Pierre (1987), the genera *Actinote* (up to that time considered a Neotropical genus) and *Bematistes* (up to that time considered an Afrotropical genus) are included in *Acraea*. Pierre (1987) distinguished two subgenera, *Acraea* in the Old World (Afrotropics, and from India to Australia, New Caledonia and the Solomon Islands), and *Actinote* in the Neotropics, and in the Afrotropics and Oriental region largely sympatric with *Acraea*, and occurring as far east as Java. The two subgenera are polyphagous. For Africa alone 12 families of hostplants have been recorded for *Acraea* and 19 for *Actinote* (Ackery et al. 1995). Although there is a slight overlap, the subgenera centre around different foodplants. *Acraea* has the most restricted

range of foodplants, with records from 12 families, but seven of these are single records of *Acraea* species using also other foodplant families. By far most foodplant records (80%) for *Acraea* relate to Passifloraceae, and the related families Flacourtiaceae, Violaceae and Turneraceae. With a few other families, these foodplant genera form a monophyletic group that is estimated to have originated around the K/T boundary (c. 65 Ma) (Wikström et al. 2001). In accordance with its larger distribution area, *Actinote* has a wider foodplant choice, with some 20 families recorded, but also here many family records relate to single *Actinote* species which make use of other plants as well. In Africa there are foodplant records for 42 species of *Actinote*, half of which use Urticaceae (not used by *Acraea*). In the Neotropics, *Actinote* seems to make use mainly of Urticaceae and Asteraceae, with an important role for the genus *Mikania* (Asteraceae) (Ackery 1988, DeVries 1987).

Two questions arise: 1, how did the disjunction in subgenus *Actinote* originate, and 2, why is subgenus *Acraea* restricted to the Palaeotropics? Since the age of the main foodplant families of *Actinote*, Urticaceae and Asteraceae, has been estimated at 45 Ma and 50 Ma, respectively (Wikström et al. 2001), a vicariance explanation is not likely. As to question no. 1, a possible solution, apart from long distance dispersal, will be discussed below in the section Estimating space. An answer to question no. 2 could possibly be found in two directions: a, subgenus *Acraea* possibly originated in the Old World too late to make a chance to reach the Neotropics, and/or b, in the Neotropics the related and speciose genus *Heliconius* (43 species; see <http://www.tolweb.org/tree?group=Heliconius&contgroup=Heliconiini>), of which the larvae exclusively live on Passifloraceae, has effectively blocked subgenus *Acraea* from entering the Neotropics. A relatively recent origin for speciose genera has, for instance, also been postulated for *Arhopala* (Lycaenidae, c. 200 species; Evans 1957) and *Agrodiaetus* (Lycaenidae, 57 species; Häuser & Eckweiler 1997), respectively 7–11 Ma (Megens et al. 2004) and 2.5–3.8 Ma (Kandul et al. 2004).

Uraniinae (Uraniidae)

Above, we discussed the origin of the Uraniinae in relation to the evolution of tympanal organs as devices for bat evasion, and we concluded that the subfamily is too young to explain the distribution of the genera as the result of the break-up of Gondwana. The same story is told by the foodplants. The subfamily exclusively lives on Euphorbiaceae, the age of which has been estimated at c. 70 Ma (Wikström et al. 2001), the same age as for the bats. Moreover, the genera of the Uraniinae live on few genera of

Euphorbiaceae only. Lees & Smith (1991) concluded that *Endospermum* was the ancestral foodplant genus of the Uraniinae, while there was a later shift to *Suregada* in *Urapteroides*, *Cyphura* and *Urapteritra*, and to *Omphalea* in *Urania*, *Chrysidia* and *Alcides*. The most advanced uraniine genera, the sister taxa *Urania* and *Chrysidia*, “feed on a monophyletic group of relatively advanced Neotropical and Afrotropical species of *Omphalea*.” Lees & Smith 1991: 331). The vicariant distribution of the two uraniine genera as well as of their foodplants (Neotropics and Afrotropics, respectively) is suggestive of being the result of a vicariance event, viz. the opening of the Atlantic between Africa and America. However, with an age of 70 Ma for the Euphorbiaceae as a whole, the age of an advanced monophyletic group of species of a particular genus must be considerably younger, much too young for this vicariance event.

According to Holloway et al. (2001), Uraniinae are sister to the Microniinae. The latter subfamily is restricted to the Old World tropics. The only genus for which foodplants are known is *Acropterus*. They are all in the Asclepiadaceae (now in Apocynaceae). According to Wikström et al. (2001), the Apocynaceae arose circa 50 Ma. This relatively young age does not challenge the supposed age of the Uraniinae, but as said, foodplants are not known for the other genera of the Microniinae.

Dry land

Being terrestrial animals, Lepidoptera are dependent on the occurrence of dry land. In cases where one or more of the taxa of the group under study are restricted to islands the subaerial age of which is known, this age can be used as maximum age for the taxon. It cannot be used for islands that became separated from the mainland, as in that case we would use a vicariance calibration point, while we cannot be sure how the taxon arrived there, by vicariance or dispersal, and thus, we could overestimate its age. Also, with islands that never had contact with other pieces of dry land, some care is needed. The island could be one in a series that appeared and disappeared one after the other, like the Hawaii Islands (Wagner & Funk 1995). In that case, the taxon could well be older than the dry land on which it occurs. See also the case of Norfolk Island as described under the section on Lycaeninae above.

This constraint was used by de Jong (2003) for setting a maximum age on the presence of *Ornithoptera goliath* Oberthür, 1888 (Papilionidae) on the Moluccan island of Seram, where it has a well differentiated subspecies compared with the forms flying in New Guinea. Since Seram emerged only 5–6 Ma (Audley-Charles 1986, 1993, Fortuin

& de Smet 1991), the differentiation cannot be older. Similarly, Nazari et al. (2007) used the age of the Greek island of Crete (3–11 Ma) as maximum age for the endemic *Zerynthia (Allancastria) cretica* Rebel, 1904 (Papilionidae). Such cases may be common, but difficult to find when one needs them. In the case of relatively young islands, like Seram and Crete, the use is limited, since the reliability of the estimate of substitution rate based on it will decrease with age, and older calibration points are needed to compensate for that.

Estimating space

It is unlikely that we, on the basis of extant taxa only, would ever have dreamed of a North American origin of the genus *Equus* (Mammalia). Yet, the rich fossil history dictates so (Simpson 1951). Similarly, how could we have deduced from the extant species only that the Proboscidea (elephants and relatives) originated in Africa, and once were distributed in a number of species and genera across North and South America as well (Soshani & Tassi 1996)?

Fossils

In most animal groups the fossil record is much poorer and, as discussed above, it is particularly poor for the Lepidoptera. Moreover, apart from being rare in time, and often very fragmentary, lepidopterous fossils are geographically biased, almost all fossils having been found in the Northern Hemisphere. Realizing their rarity, and considering that fossils assignable to a particular taxon generally are found in the present-day distribution area of that taxon, it is obvious that fossil Lepidoptera can add little to biogeographic considerations. Most interesting (from a biogeographic point of view) are those fossils that extend the distribution area of the taxon concerned considerably (as in the elephants), but such instances are rare and not always correctly interpreted. But surely, positive proof that a distribution area has not changed may be equally important in a biogeographic discussion. Three examples of a supposed extinction in a particular area are given.

Tindale (1985) described a fossil from the famous Oligocene deposits at Florissant, Colorado, consisting of two superimposed forewings, as *Dominickus castnioides*, a member of the Castniidae. According to the original description, the assignment to this family is based on similarity in wing venation with a member of the Australian extant genus *Synemon* as well as with a species of *Castnia* from Chile. Undoubtedly the venation is not butterfly-like or skipper-like, if only because of the presence of a well-marked median vein in the cell. How far there

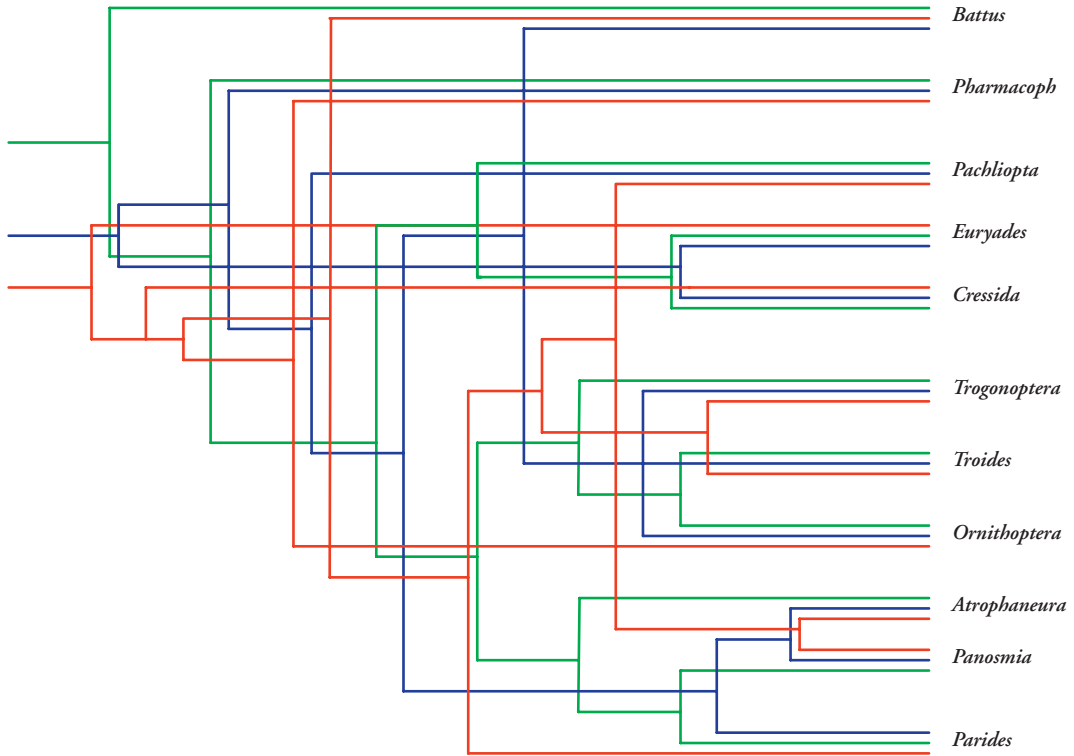


Fig. 3. Phylogeny of Troidini (Papilionidae), based on partly different sets of morphological characters. Green, after Miller (1987); blue, after Tyler et al. (1994); red, after Parsons (1996).

are apomorphic characters involved is not clear. Unfortunately the body is missing, the antennae (clubbed in the Castniidae) would have been decisive to assign the fossil to the correct taxon. If correctly identified as a castniid, the fossil has been found in a region where no castniids occur at present, the nearest extant species being found in Mexico, almost 2000 km to the south.

A forewing from the lower Oligocene from Aix-en-Provence (France) was described as *Pamphilites abdita* by Scudder (1875). Since there were no branched veins (an apomorphy of the Hesperidae, also found scattered among some moth groups), the wing shape was skipper-like, and the origin of M2 was closer to M3 than to M1, an apomorphy of the Hesperinae, Scudder identified the fossil as such. In many hesperiine species the male has a prominent stigma (patch of androconial scales), and since the fossil lacked any trace of it, Scudder thought it could be a female. However, there are also many hesperiine species in which a stigma is lacking in the male. Being an American, Scudder compared the fossil with

American skippers and found a resemblance in venation and markings with "*Pansydia mesogramma*" (now *Atalopedes mesogramma* (Latreille, 1824)), a species of the Greater Antilles, as well as with "*Carystus lucasi*" (now *Turesis lucas* (Fabricius, 1793)), a South American species. Therefore he decided on a South American relationship of this European fossil. The type specimen seems to be lost, and Nel & Nel (1986) designated a neotype that seems to be conspecific with it. They correctly remarked that the venation and markings agree with numerous extant hesperiine species in the Old World and New World, so that a South American affinity of the fossil is not obvious.

Another fossil from the rich fossil beds of Florissant, Colorado, was described as *Vanessa amerindica* by Miller & Brown (1989). Of the two specimens, one is fairly complete, with abdomen (squashed) and four wings, but without antennae or proboscis. In the forewing, radial veins 4 and 5 are stalked on each other, and together on R3 (a condition found in many Nymphalidae), and the cell is open

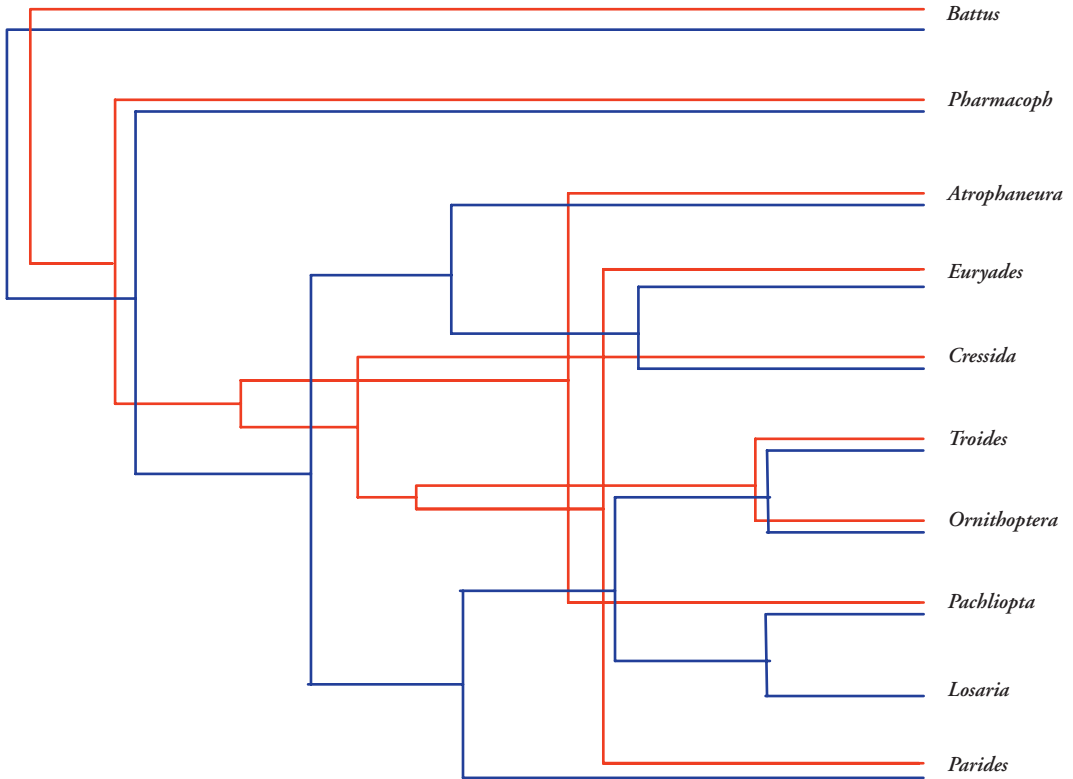


Fig. 4. Phylogeny of Troidini (Papilionidae), based on different genetic markers. Blue, after Morinaka et al. (1999); red, after Braby et al. (2005) (Bayesian Inference).

(internal apomorphy of Nymphalidae); the apex of the forewing is produced, with a lobe at M1-M2. In the hindwing the cell is open (apomorphy of several nymphalid groups). The forelegs are reduced (apomorphy of Nymphalidae). According to the authors the produced apex of the forewing with characteristic lobe at M1-M2 is indicative of the genus *Vanessa*. A similar lobe can, however, be found in several other nymphaline genera. The authors suggest that what is left of the pattern is reminiscent of the pattern of the extant Old World species *Vanessa indica* (Herbst, 1794). This may be so, but the pattern remnants a poor, and even if they would fully agree with those of *V. indica*, without indication of the apomorphies of the genus *Vanessa*, the similarity remains superficial (see also the interesting paper by Otaki et al. 2006, on the evolution of the color pattern in *Vanessa*). Moreover, in *Vanessa* the cell in the hindwing is generally closed, though the cross vein may be too weak to show up clearly in a fossil. Further, Sc in the hindwing is remarkably straight in the drawings of the fossil, different from the nicely curved

vein in *Vanessa*. The suggestion by the authors that the presence of a fossil butterfly of Old World affinities in North America may have something to do with migratory behaviour, is certainly premature and highly speculative. There are several extant *Vanessa* species in North America.

Although fossils of Lepidoptera do not have much impact on biogeographic studies, it is advisable, when dealing with the biogeography of a group of Lepidoptera, to have a fair knowledge of faunal development in general in the geographic area of their interest, since the Lepidoptera made part of that fauna and underwent its developments. The knowledge of movements in space through time gained from fossils of other animals may help to prevent too speculative statements or may give hints for solutions which may otherwise be overlooked.

Analytical approaches

Early interest in the distribution of Lepidoptera was mainly descriptive (e.g., Pagenstecher 1909, whole world; but also much later, e.g., Kostrowicki 1969,

Palaeartic), and aimed at subdividing the world in faunal regions or provinces, or the animal species in faunal elements belonging to a typical type of fauna. It described the distribution of Lepidoptera, often in relation to vegetation or other environmental factors, usually without trying to explain history. A rare exception was Toxopeus (1930), who saw species as a function of time and place, and tested his ideas with the Lycaenidae of Australasia. But he published his book (actually his thesis) in Dutch, and it did not receive the attention it deserved. Zeuner (1943) published a remarkable study on the genus *Troides* and its allies (Papilionidae), in which he presented the first phylogeny of the relevant genera on the basis of morphology (be it not in a cladistic way), and tried to understand the evolution of the taxa in relation to the geological history of the Australasian archipelago in a clear and well-reasoned way (see also below).

Analytical programs to examine distributions with the aim of giving a historical explanation started to appear in the 1970's. They were partly statistical (in particular Holloway, who directed his attention mainly to the Lepidoptera of the Oriental and Australian regions, e.g., Holloway 1973, 1974, 1991, 1997, 2003; Holloway & Jardine 1968), partly a logical extension of cladistics that, after the publication of Hennig (1966, an English translation and revision of his work of 1950 in German) rapidly developed into the dominating method for phylogenetic research. See Holloway & Nielsen (1998) for a review of various aspects of the biogeography of the Lepidoptera in the second half of the 20th century.

The biogeographical debate has long been dominated by the vicariance paradigm. Vicariance biogeography had its roots in Croizat's (1958) panbiogeography, but only got momentum when Croizat's ideas were combined with the rapidly developing ideas about cladistics after the publication of Hennig's (1966) book. It led to heated debates (see, e.g., Nelson & Rosen 1981), in which reasoned arguments sometimes got the worst of it, and the basal question: is a disjunction due to vicariance or dispersal, was no longer posed, but a priori answered (namely, by vicariance). It was pushed so far that similar vicariant distributions in widely divergent organisms, be it species, genera or higher taxa, were ascribed to a single vicariance event (particularly the break-up of Gondwana, but also on local scale), without even asking the question of whether the vicariant distributions were all of the same age. Instead, long debates were held on the meaning of "assumptions 0, 1 and 2", assumptions used to render incompletely congruent distribution patterns more comparable. People with a more differentiated point of view were (and sometimes still are; see frequent discussions on

the Taxacom list server, taxacom@mailman.nhm.ku.edu) easily branded "dispersalist". One reason for the emphasis laid on vicariance is that dispersal is not a generally directive process, it is different for different organisms and, for that reason, is supposed to be unable to lead to the kind of patterns found if only vicariance is involved. It is an unproven presupposition, and actually should be subject of study, but a point in favour of the explanatory power of vicariance is that, in a narrative way, with dispersal and selective extinction any distribution can be explained, and thus, nothing is explained of the interplay of geological and biological powers. On one hand, vicariance as an explanation has the beauty of simplicity, on the other, explaining every disjunction as the result of vicariance certainly underestimates the role of dispersal, just as in morphology explaining every similarity as a derived character state underestimates plesiomorphy and convergence. Sole interest in "proving" vicariance can easily induce circular logic. Waters & Craw (2006) describe how such an attitude can lead to incorrect conclusions in the case of New Zealand biogeography, if a vicariance provenance of the biota is taken for granted instead of being the subject of research.

With the conviction, or at least the hope, that a molecular clock makes it possible to estimate divergence times, a tool for testing vicariance explanations came within reach. The main reason for estimating divergence times by applying a molecular clock may be just that: testing the events (dispersal across existing barriers versus fragmentation of distribution) that may have led to the divergence. The results can be very much at variance with previous explanations. Trewick (2000), for instance, analysing mitochondrial DNA (COI) of flightless insects in four genera (two Coleoptera, one Orthoptera, and one Blattodea) occurring in New Zealand and the Chatham Islands to the east of New Zealand (shortest distance c. 600 km), concluded that the separation of the taxa on both island groups was of Pliocene age (2–6 Ma). Even allowing for much variation in substitution rate, it is much too young for a vicariance explanation (plausible for flightless insects), which would need a separation since at least 70 Ma. In Lepidoptera such dramatic differences are not known, although they can be expected, when the panbiogeographic principle is applied that determines that all speciation events are "an underlying pattern of geographical vicariance (...) upon which is superimposed "noise" caused by secondary, across-barrier, dispersal events" (Craw et al. 1999: 18), instead of considering the event that led to the speciation a subject for study.

The geographic origin of the butterflies

In a study on the tineid genera of Australia, Robinson & Nielsen (1993) wrote: "Few examples of 'Gondwanan' distribution have yet been demonstrated in the ditrysian Lepidoptera, suggesting that the radiation of the group postdates the Gondwanan fragmentation events. The Tineidae [because of their systematic position at the base of the Ditrysia] would be an appropriate group with which to test that hypothesis." However, it remains to be seen whether age is the decisive factor here. One of the crown groups, the butterflies, appeared in the fossil record in the Upper Palaeocene (about 54 Ma) (Kristensen & Skalski 1998), indicating that the group came into being before that time. Recent estimates (although based on disputable calibration of the molecular clock) suggest an age of about 115 million years. Braby et al. (2006), for instance, estimated the age of the Pieridae (a family that takes a middle position in the evolution of the butterflies, i.e. it originated after Hesperiiidae and Papilionidae, but before Lycaenidae, Riodinidae and Nymphalidae) at 112–82 Ma (with a mean of 95 Ma), but, as discussed above, the identity of the fossils used for the calibration of the molecular clock is problematic (at least, it is not based on apomorphy), and, as a consequence, the age of the supposedly associated genera could well be younger, and thus the Pieridae as a whole could be younger. Nevertheless, there is no reason to doubt that the butterflies are old enough to have undergone the fragmentation of the last part of Gondwana, the final separation of Australia, Antarctica and South America. By 35 Ma Antarctica was completely isolated and developed an ice cover. The separation of South America and Africa was completed by 84 Ma (Pitman et al. 1993) or earlier by other estimates: Smith et al. (1949), for example, estimated that the two continents were completely separated around 100 Ma. According to Braby et al. (2006), this vicariance event led to the split of the monotypic Pseudopontiinae (Africa) and Dismorphiinae (South America, Holarctic). If their age estimation is correct (but see above), then this would hardly be a possible scenario, and certainly not the only one (see below). The sister group of Pseudopontiinae+Dismorphiinae is the sister group Coliadinae+Pierinae. If the ancestor of the first two subfamilies had a Gondwanan distribution, then the ancestor of the next two subfamilies, which by definition had the same age, undoubtedly also was Gondwanan. Why then did not the break-up of Africa and South America leave traces in the other Pieridae? Or in the even older families Papilionidae and Hesperiiidae? Have they not been recognized so far, or are they simply absent?

Up to 2005, there was only a single case of sister group relationship between genera of butterflies known that was usually interpreted as the result of the separation of Australia from South America (through Antarctica), viz. the monotypic genus *Cressida* in the Australian region and *Euryades* (two species) in South America. The genera belong to the Troidini (Papilionidae, Papilioninae), one of the most intensively studied groups of butterflies. The intensity of the studies did not lead to much agreement (Figs 3 and 4). The sister group relationship of *Cressida* and *Euryades* was recovered in morphological studies by Miller (1987) and Tyler et al. (1994), and in a molecular study by Morinaka et al. (1999). De Jong (2003) estimated that the divergence time between the two genera was, at 31 Ma, too young to be the result of the fragmentation of the southern continents. Braby et al. (2005) challenged not only the age of divergence between *Cressida* and *Euryades*, which they estimated at 48–37 Ma, but also their sister group relationship. In their maximum likelihood tree the position of *Cressida* is unresolved and *Euryades* is sister to the South American genus *Parides*, in their Bayesian inference tree *Cressida* is sister to a group of four genera, *Euryades*+*Parides* (South American) and *Ornithoptera*+*Troides* (Indo-Australian). Above, we already discussed that the calibration points Braby et al. (2005) used, viz. events in the fragmentation of Gondwana, effectively prevented the use of the derived ages as proof of the effect of the fragmentation on the divergence of the genera. First vicariance events in the fragmentation of Gondwana were taken to derive divergence times, and then the divergence times were taken as "proof" of the effect of the vicariance events. It is not to say that their conclusions are wrong, but if correct (which still has to be proven), it is for the wrong reason.

Another point in the paper by Braby et al. (2005) that deserves some attention is the biogeography of the monophyletic group of three troidine genera *Trogonoptera*, *Ornithoptera* and *Troides*, which are related as follows: (*Trogonoptera* (*Ornithoptera*, *Troides*)). According to the authors, *Trogonoptera* is Oriental, *Ornithoptera* is Australian, and *Troides* is Oriental and Australian. They concluded that an Australian or an Oriental origin for the group are equally parsimonious, both involving two dispersal events and one extinction. This would be so, if their starting point was correct. Actually, *Troides* is not "Oriental and Australian", at least when it comes to origin. Of the 20 species, only one species, *T. oblongomaculatus* (Goeze, 1779), occurs east of Wallace's Line, in New Guinea, Central Moluccas, Sula Archipelago (east of Sulawesi) and the islands Salayar and Tanajampea

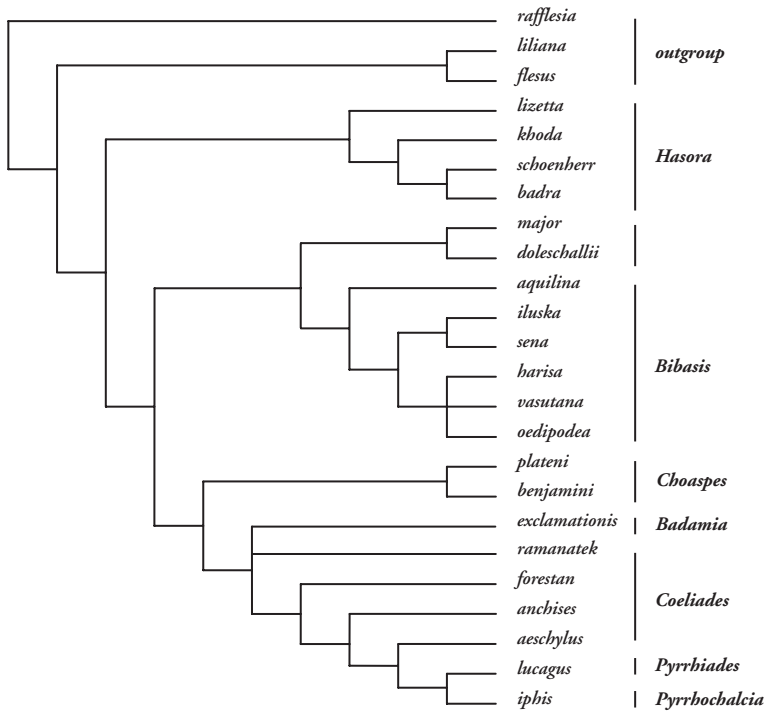


Fig. 5. Phylogeny of Coeliadinae (Hesperiidae). Strict consensus tree of six equally parsimonious trees, based on differentially weighed morphological characters; TL=195, CI=0.523, RI 0.789, RC 0.413; see text for further explanation.

south of Sulawesi (Tsukada & Nishiyama 1982). It is not a basal species but a crown species in the genus. There is no published cladistic analysis of the phylogeny of *Troides*, but the phylogenetic trees published by Zeuner (1943) and Tsukada & Nishiyama (1980) agree in considering *T. oblongomaculatus* and the Oriental species *T. helena* (Linnaeus, 1758) (India to Sulawesi and Sumbawa) sister species. Since they are both crown species, and the former species is the only *Troides* species in the Papuan region, we can only conclude that *T. oblongomaculatus* is an Oriental species by origin. In case of an Australian origin for *Trogonoptera*+*Ornithoptera*+*Troides*, we would need numerous dispersal events for *Troides* from Australia to the Oriental region to explain the present distribution, and not just one as in Braby's et al. (2005) study. There is growing evidence of repeated faunal exchange between Asia and Australia over millions of years (de Jong 2001, 2004, Braby & Pierce 2006), but the unidirectional exchange from the Australian region (not Australia itself) needed to explain the present-day distribution of *Troides* if the genus had Australian roots, is overstressing the probabilities. More than 60 years ago, Zeuner (1943) had already come to the conclusion that the group is of Oriental origin and later dispersed to the Papuan/Australian region.

With an Oriental origin of *Trogonoptera*+*Ornithoptera*+*Troides*, *Ornithoptera* originated from a dispersal event from the Oriental region to the Papuan/Australian region. Braby et al. (2005) estimated the origin of the divergence between *Ornithoptera* and *Troides* at 40 Ma. As stated above this estimate is based on an unjustified calibration of the molecular clock, but, for that reason, not per se wrong. However, with *Ornithoptera* an Oriental intruder in the Papuan/Australian region, it is highly unlikely that the divergence between *Ornithoptera* and *Troides* is that old, since at the time the position of the Australian plate was still far to the south and the probability of a successful long distance dispersal was very much lower than, say, 25–35 million years later, after Australia had drifted far to the north. Zeuner (1943) estimated that the evolution of the *Troides*-group (i.e., *Trogonoptera*+*Ornithoptera*+*Troides*) had required between three and twelve million years. Although it appears to be a more realistic figure in view of the geographic evolution of the area, Zeuner's estimate is based on the unproven assumption that the formation of a new species lasts half to one million years. So, for the time being the age of the divergence between *Ornithoptera* and *Troides* remains uncertain, but an Oriental origin for *Ornithoptera* appears to be inevitable.

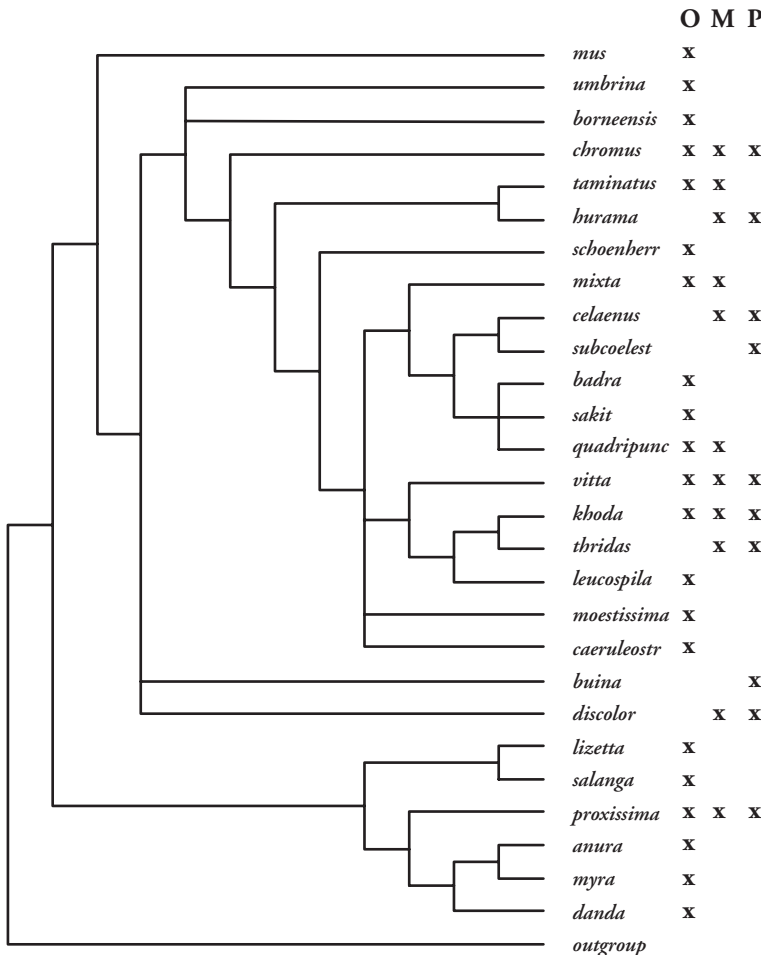


Fig. 6. Phylogeny of *Hasora* (Hesperiidae: Coeliadinae). Strict consensus tree of 20 equally parsimonious trees; TL=216, CI=0.431, RI 0.705, RC 0.304; see text for further explanation. O=Oriental, M=Moluccan, P=Papuan.

To be as close to the root of the butterflies and skippers as possible, the present author executed a morphological study of the subfamily Coeliadinae of the Hesperiiidae. On morphological (de Jong et al. 1996, Ackery et al. 1998) and molecular (Warren 2006) grounds, this subfamily is supposed to be sister to the remaining Hesperiiidae and thus, is the first offshoot of the Hesperiiidae, which in turn are the first offshoot of the skipper+butterfly lineage. It is a small group (c. 80 species, divided among 7–8 genera) of robust skippers, restricted to the Palaeotropics with slight extension into the East Palaearctic. A total of 55 characters and a selection of the species, covering all genera, were used in a Maximum Parsimony analysis (PAUP*, Swofford 2002). Not surprisingly, the (preliminary) results are dependent on the weighting of characters, either equally or differentially. In all cases, however, the three African genera form a

monophyletic crown group that is sister to an Indo-Australian genus, which in turn is three speciation events removed from the ancestor of the subfamily. Apparently, Africa was reached after a radiation of the group in the Indo-Australian area. Fig. 5 shows the strict consensus of six equally parsimonious trees, with structural characters (wing venation, genitalia, etc.) given a double weight compared to superficial characters (colour, wing design, development of spots) which apparently are subject to much selective pressure. The main difference with the strict consensus tree (of three equally parsimonious trees) when all characters have equal weight, is the position of *Badamia* which in the latter case is basal to the other Coeliadinae (a bootstrap analysis gives the position of *Badamia* as unresolved). *Badamia exclamationis* (Faricius, 1775) is a very widespread species, from Pakistan to Southeast Australia and into the Pacific

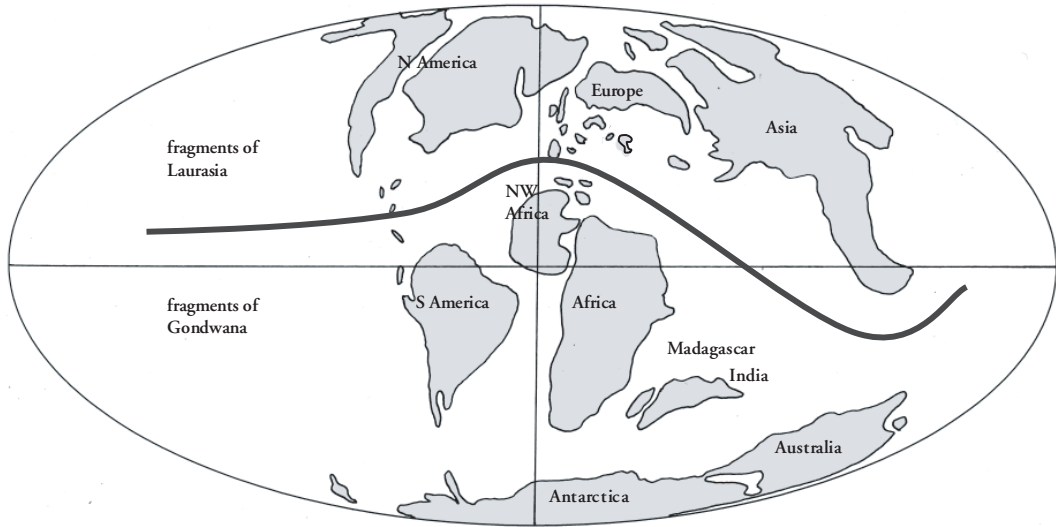


Fig. 7. Distribution of land and sea, 90 Ma. Mainly after Smith et al. (1994). NB - Much of East and Southeast Asia consists of terranes that had their origin on the Indian-Australian margin of Gondwana (at the time still connected to Laurasia in the supercontinent Pangaea); they drifted northwards in the Palaeozoic, and progressively accreted to the amalgated Siberia and Kazakhstan blocks (Metcalf 1999); c. 200 Ma, long before the supposed origin of the butterflies, these originally Gondwana terranes were already an integral part of the Northern Hemisphere.

as far as Samoa; it is a well-known and strong migrant (the only other species of the genus, *Badamia atrox* (Butler, 1877) is restricted to a few Pacific islands). The genera *Choaspes* and *Hasora* both have an Indo-Australian distribution, with a preponderance of Oriental species, but also with endemics east of Wallace's Line and species occurring east as well as west of Wallace's Line. *Bibasis* (including *Burara*) is Oriental, *Allora* is Papuan (New Guinea and surrounding islands, also reaching North Queensland, Australia). Thus, the Coeliadinae are, again, a group of butterflies for which Wallace's Line is a boundary that can easily be crossed.

Further, a preliminary Maximum Parsimony analysis was executed for 27 species of *Hasora* (four species of which only one sex was known, were omitted), based on 35 morphological characters (Appendices 3 and 4). Although the resulting tree (Fig. 6), with differential weighting as for the genus tree, must be treated with care, since for a number of taxa the characters of the female genitalia could not yet be filled in, and four taxa for which only one sex was known were deleted, it appears that there has been an initial radiation in the Oriental region (O) before parts of the Papuan region (M, P) were reached. Part of the eastward move may have been of relatively recent

age. Some species (*Hasora mixta* (Mabille, 1876), *Hasora quadripunctata* (Mabille, 1876), *Hasora taminanus* (Hübner, 1818)) did not make it beyond the Moluccas (M). According to Audley-Charles (1986, 1993) there was no dry land between the coast of Australia-New Guinea and Sulawesi until the Miocene emergence, and according to this author, Seram only emerged 6 Ma. Later authors (Fortuin & de Smet 1991), even estimated the time of emergence at 5 Ma. Consequently, occurrence on the Moluccas is of relatively recent age. It does not exclude the possibility that other species reached (proto-)New Guinea (P) by long distance dispersal, but the fact that there is little endemism east of Wallace's Line suggests that species have not been isolated there for more than a short time. Four species finally reached Australia, but did not even develop subspecies there, except for *Hasora khoda* (Mabille, 1876), which apparently develops local forms quite easily, as over its range from Assam to New Caledonia nine subspecies are recognized.

It is planned also to do a molecular analysis of the subfamily (with Andrew Warren and David Lees), to find support for (or rejection of) the morphological results, and to make an attempt to estimate divergence times. However, in view of the distribution of

land and sea around 80–100 Ma, there is no reason to suppose that the Coeliadinae arose in another area than where they occur today (or at least in the Northern Hemisphere), with the note that Africa was not part of the ancestral area.

So there is growing evidence of an “Oriental” origin of the Coeliadinae. We do not know their age, but being so close to the root of the butterfly/skipper lineage, it could be anything between, say, 80 and 100 Ma. Fig. 7 shows roughly what the world looked like 80 Ma. The Oriental region (as we know it today) has never been part of Gondwana (with the exception of India, see below), but at the time of the emergence of the butterflies, was part of the northern supercontinent Laurasia (including Eurasia and North America). Gondwana was far away and, although stray contacts may have been possible (Archer et al. 1996, for instance, thought it possible that Australia received rare northern elements while it was still connected to Antarctica), it seems highly unlikely that the Coeliadinae originated from an ancestor that strayed from Australia to the north. The climate was warmer and more equable, and the ancestor of the Coeliadinae may have occurred further north and further west than today (remember that even nowadays the subfamily reaches as far north as the Ussuri region in the extreme east of Russia).

Following Morley’s (1998) palynological arguments for a Gondwana contribution to the early flora of Tertiary Southeast Asia, we should also consider the possibility that the Coeliadinae originated in India, dispersed to Southeast Asia, differentiated there, and subsequently migrated westward to finally reach Africa and Madagascar. However, if the phylogeny of the Coeliadinae as represented in Fig. 5 is correct, the first split in the lineage is between *Hasora* and the rest of the Coeliadinae. In *Hasora*, the first species in the tree (Fig. 7) occurring in India is the very widespread *Hasora chromus* (Cramer, 1782) (Sri Lanka and South India to Australia, Fiji and Vanuatu [New Hebrides]; Evans 1949), a species well away from the base of the genus. In the remainder of the Coeliadinae species occurring in Sri Lanka and/or peninsular India are found scattered among the genera *Bibasis* (five of the 17 species), *Choaspes* (one of the eight or more species), and *Badamia* (one of the two species) (see Fig. 6). None of the species of Coeliadinae occurring in Sri Lanka and/or peninsular India is endemic to these areas. Since Sri Lanka/peninsular India apparently did not play a role in the basal differentiation of the Coeliadinae, there is no evidence of an origin of the subfamily in the Indian continent while drifting northward. It is in accordance with Holloway’s (1974: 479) conclusion for butterflies in general, based on a faunal centre survey, that

“a picture [is presented] of relatively recent invasion of South India from several centres in mainland Asia and from one in Africa.”

With Coeliadinae a Laurasian element, there are no vicariance events known that could explain the divergence of Coeliadinae and their sister group, the remaining Hesperidae. In other words, the divergence took place in this huge supercontinent. To be sure, Laurasia became fragmented (see Fig. 7), and these events may have been responsible for the early splits of the hesperiid lineage, but so far there is no evidence. If the root of the Hesperidae is in Laurasia, where then diverged the proto-Hesperidae from the proto-Papilionoidea? Could the whole butterfly/skipper lineage have started in Laurasia, contrary to the common belief that the break-up of Gondwana played an important role?

After the Hesperidae, the next group to branch off the butterfly lineage are the Papilionidae, perhaps the best studied Lepidoptera of all. As in the case of the Troidini (Papilioninae) discussed above, ‘much studied’ does not necessarily mean that there is agreement, even at the level of subfamilial relationships. Up to very recently there was general agreement that Baroniinae (with the single species *Baronia brevicornis* Salvin, 1893 from Mexico) was sister to the rest of the Papilionidae (e.g., Hancock 1983, Miller 1987, de Jong et al. 1996, Ackery et al. 1998, Caterino et al. 2001, Zakharov et al. 2004, Wahlberg et al. 2005), with the Parnassiinae either sister to Baroniinae or to the remaining Papilioninae. However, Nazari et al. (2007) came to a very different conclusion, with a basal split between “Graphiinae” (not named as such) and the remaining Papilionidae, and next a split between Papilioninae and *Baronia*+Parnassiinae, with *Baronia* sister to the Parnassiinae. This is the more remarkable, since the other two authors of the paper were also co-authors of Zakharov et al. (2004). No explanation has been given. Actually, they found different trees, depending on the analytical method, but they based their conclusions on the tree with “Graphiini” sister to the rest of the family, and Papilioninae sister to *Baronia*+Parnassiinae. It cannot all be true. Either *Baronia* is the oldest offshoot of the papilionid lineage, or it originated after Graphiinae and Papilioninae had split off. For the age of the Troidini (tribe of the Papilioninae) the authors referred to Braby et al. (2005), discussed above. There we casted doubt on the validity of the calibration of the clock. Further, they used the fossil *Praepapilio* as one of the calibration points, but they put it (with a question mark) in a remarkable place, viz. at the root of the genus *Papilio*. As discussed above, this is most unlikely, as in that case either two apomorphous characters

of Papilionidae returned to their plesiomorphous state well after the initial radiation of the family, or these apomorphous states arose several times independently. A similar situation occurs with respect to the position of *Baronia*. It is the only extant genus where two anal veins in the hindwing are present (as in all other butterflies). Did the character reverse to its plesiomorphous state, or does *Baronia* actually belong near the root of the Papilionidae? Has morphology here been drowned in a tsunami of molecular characters? With so much unexplained divergence of opinion, one fears that a fragile framework of interdependent parts has been built up for the phylogeny of the butterflies that can easily fall apart when one of the constituent parts proves false. Could the topology of the tree by Nazari et al. (2007) be so different because all taxa of Parnassiinae and *Baronia* were involved, and only a few other papilionids? The subject of the paper was the Parnassiinae, but still, the other taxa also played a role in the discussion. For the present discussion we shall follow the previous, well documented topologies with *Baronia* and Parnassiinae at the root of the Papilionidae.

Since all Parnassiinae are restricted to the Holarctic, and *Baronia* is restricted to a very small area in Mexico that historically also is part of the Northern Hemisphere, it is not surprising that several authors (e.g., Hancock 1983, Nazari et al. 2007) have concluded that the roots of these taxa are in the Northern Hemisphere. It also agrees with the provenance of the fossil taxa *Thaites ruminiana* Scudder, 1875 (Aix-en-Provence, France; lower Oligocene) and *Doritites bosniaski* Rebel, 1898 (Gabbro, Italy; upper Miocene), which both fit well in the Parnassiinae, but since there are hardly any fossil butterflies known from the Southern Hemisphere, the fact that these two fossils are from the Northern Hemisphere, although supporting a northern origin for the group, is not decisive.

Thus, at the base of the skipper/butterfly lineage first we have the initial radiation of the Hesperiiidae that took place in Laurasia, followed by the initial radiation of the Papilionidae that also took place in Laurasia. The sister group of the Papilionidae, the combined families Pieridae, Riodinidae, Lycaenidae and Nymphalidae is, by definition, as old as the Papilionidae. Its cosmopolitan occurrence at present does not give a clue as to where it originated, but it could have originated in Laurasia as well. There are further arguments in favour of the idea that Laurasia played a prominent role in the diversification of the butterflies. In the Pieridae, the Pseudopontiinae and Dismorphiinae (discussed above) are basal. Braby et al. (2006) hypothesized an origin in West Gondwana with a scenario of dispersals and extinctions to

explain the present-day distribution in the Palaearctic, the African rain forest and the Neotropics. It seems more likely that the monophyletic group consisting of Pseudopontiinae and Dismorphiinae originated in Laurasia and dispersed to Africa at a very early stage, and later to South America, after which they became extinct in North America.

Also the distribution of diversity in the Lycaenidae is illustrative. Since there is no published cladistic higher level (down to tribes) analysis of the Lycaenidae, the landmark work by Eliot (1973) is taken as starting point. All 33 tribes recognized occur in the Old World, where 28 are endemic. Only five tribes extend to America, and of these only two reach the Neotropics (three if we include Central America). Eliot's (1973) phylogeny of the family, although based on many morphological characters, is intuitive and not well resolved at the higher levels, but it does not contradict the findings of Wahlberg et al. (2005) for a very restricted set of taxa in the sense that the strong radiation in the Neotropics has occurred in two crown groups only, Polyommataini and Eumaeini (Polyommatainae), while all more basal groups occur in the Old World, except the small tribe Spalgini (Miletinae), with one genus (*Spalgis*) in the Afrotropical and Oriental regions, and one monotypic genus (*Feniseca*) in North America, apparently a relic distribution that can only be understood by assuming a former Laurasian distribution. There are no traces of a Gondwanan relationship in the Lycaenidae.

Basing his conclusions on a wealth of data on fossil insects, Eskov (2002) convincingly argued that there is an increasing number of "Gondwanan" insect taxa that have been found as fossils in Eurasia and North America, indicating that extant "Gondwanan" elements could well be relics of a former, broader distribution. Relationships between taxa on Gondwana fragments do not need to be direct (i.e., a result of the break-up of Gondwana), but the ancestor can have had a wider distribution and simply became extinct in the north. Consequently, Eskov concluded that "the value of the modern range appears to be of very limited significance" in drawing conclusions about a geographic origin of a taxon. Alternatively, the present occurrence in Gondwana fragments need not be as old as Gondwana itself, but could be a secondary phenomenon.

Conclusion

The broader picture that emerges is that the skippers and butterflies originated and radiated in the vast continent Laurasia, possibly mainly in the Asiatic part, under warmer and more humid conditions than there are nowadays in most of the area. As

opportunities arose they dispersed southward, to Africa in the first place, as that continent has always been closer than the other parts of Gondwana, climate being a greater barrier than distance. As shown by the frequent faunal exchange between Asia and Australia (see above), continents that were never connected since the Lepidoptera appeared on the scene, water may be a barrier, but not insurmountable, and exchange may have existed over a very extended period of time between the Northern Hemisphere and other Gondwana fragments. The presence of a putative satyrine nymphalid in an Oligocene deposit in Brasil, *Neorinella garciae* (Martins-Neto et al. 1993) is illustrative. It is reminiscent of the satyrine extinct genera *Neorinopsis* and *Pseudoneorina*, both from Oligocene deposits in France. All three genera bear a resemblance to the extant genus *Neorina*, which occurs in the Oriental region, and particularly *Neorinopsis sepulta* (Boisduval, 1841) closely resembles the extant species *Neorina lowii* Doubleday, 1849 from the Malay Peninsula, Sumatra, Borneo and Palawan (Eliot 1992). As early as the Oligocene, or even before, many butterflies may already have attained a semi-worldwide distribution. Butterflies do not rove freely across the globe, but they prove to be better wanderers than often thought. Apart from logical problems (explained above), it makes the use of vicariance events to calibrate the molecular clock very tricky.

Cooling and desiccation of large parts of the Northern Hemisphere finally wiped out the earlier traces. During the Palaeocene-Eocene thermal maximum, about 55 Ma, when the globe experienced a greenhouse condition, sea surface temperatures at the North Pole reached values of 23° C (Sluijs et al. 2006; see also Moran et al. 2006). After this maximum the Northern Hemisphere slowly cooled down. According to Larsson (1978: 185) the Eocene-Oligocene "Baltic amber fauna contains a large subtropical element. To a pronounced degree, these animals have their closest recent relatives in equatorial forests in South America, Africa and quite particularly frequently in East Asia. They are often found only in one of these regions of the world, often in several, but no matter the extent of their distribution, they must be regarded as the remains of groups which in the Eocene have had a much greater, often circumpolar distribution." Some tropical elements may have been very resistant against the cooling, or they returned later during a climatic optimum. An illustrative example from the Mammalia is the presence of fossil tapirs in deposits of upper Pliocene and lower Pleistocene age in Europe as far north as the Netherlands (Sluijs 1960), while nowadays tapirs are restricted to Sundaland and the Neotropics.

Finally, to complete the picture, the supposed sister group of the butterflies and skippers, the Hedyliidae (Wahlberg et al. 2005), are restricted to Central and South America. Would it be possible that the split between Hedyliidae and butterflies+skippers occurred by vicariance (fragmentation of Laurasia) or simply by differential evolution of populations at the geographically opposite ends of a pan-Laurasian distribution area?

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Appendix 1

List of characters used for the analysis of genera of Coeliadinae (Hesperiidae)

- 1 antennae, 0=less than twice width of scape apart, 1=more than twice width of scape apart
- 2 eyes, 0=without complete ring of reduced ommatidial facets, 1=with
- 3 forewing, 0=some radial veins branched, 1=all radial veins from cell
- 4 chaetosemata, 0=one pair, 1= two pairs
- 5 palpi third segment, 0=different from 1, 1=long, slender and perpendicular to second segment
- 6 nudum segments, 0=25–36, 1=<25, 2=>38
- 7 eyes, 0=bare, 1=hairy
- 8 mid tibiaE, 0=smooth, 1=spined
- 9 forewing male androconial patch, 0=absent, 1=along veins, 2=transverse
- 10 hind tibiae male, 0=no recumbent tuft, 1=with recumbent tuft
- 11 hind tibiae male, 0=no erectile tuft, 1=with erectile tuft
- 12 male abdominal sternal flap, 0=absent, 1=present
- 13 male coremata, 0=absent, 1=present
- 14 male hind tibiae, 0=without special scales, 1= white shining scales covering tuft, 2=comb of dark hairs enclosing tuft
- 15 uncus, 0=entire, may be indented at tip, 1=deeply indented, 2=complete divided
- 16 uncus tip, 0=narrowing to a more or less rounded point, 1=broad, more or less indented
- 17 uncus, 0=without horns, 1=with dorsal horns
- 18 uncus dorsal horns, 0=gently curving proximad, 1=gently curving distad, 2=abruptly curving distad and continued as bundle of fused hairs
- 19 male costa of valva, 0=simple, 1=extended
- 20 male costa of valva extension, 0=dorsal, 1=ventral or distal
- 21 forewing length of cell, 0=<dorsum, 1=dorsum, 2=>dorsum
- 22 forewing length of cell, 0=0.5–0.59 costa, 1=0.6–0.69 costa, 2=>0.69 costa
- 23 forewing vein 1, 0=smoothly curved, 1=acutely bisinuate near base
- 24 forewing base to origin vein 2/base to origin vein 4, 0=>0.30, 1=0.21–0.28, 2=0.16–0.2
- 25 forewing female base to origin vein 4/base to end vein 4, 0=0.54–0.6, 1=0.6–0.67, 2=0.67–0.72
- 26 forewing vein 5, 0=equidistant to vein 4 and vein 6, 1=nearer vein 6
- 27 forewing veins 6 to 8, 0=equidistant, 1=veins 7 and 8 approximate
- 28 forewing vein 12, 0=reaching costa far beyond end of cell, 1=almost to just beyond end of cell, 2=before
- 29 forewing male origin vein 3, 0=as in female, 1=displaced towards wing base
- 30 hindwing base of cell to origin of vein 2/base of cell to origin of vein 4, 0=>59%, 1=<56%
- 31 hindwing vein 3, 0=immediately before end of cell, 1=well before
- 32 hindwing skewness of cell, origin vein 4/origin vein 6, 0=0.77, 1=0.77–0.8, 2=>0.8
- 33 hindwing vein 5, 0=well marked, 1=obsolete to wanting
- 34 hindwing origin vein 7, 0=between veins 2 and 3, 1=before or opposite vein 2, 2=opposite vein 3, 3=beyond vein 3
- 35 hindwing length of cell, 0=<½ length of hindwing measured along vein 5, 1=>½ length of hindwing
- 36 colour upperside, 0=not sexually dimorphic, 1=male brownish, female bluish
- 37 forewing male hyaline spot in cell, 0=absent, 1=present
- 38 forewing male hyaline spot in space 2, 0=absent, 1=present
- 39 forewing male hyaline spot in space 3, 0=absent, 1=present
- 40 forewing male hyaline spot in space 6, 0=absent, 1=present
- 41 forewing male hyaline spot in space 7, 0=absent, 1=present
- 42 forewing female hyaline spot in cell, 0=absent, 1=present
- 43 forewing female hyaline spot in space 2, 0=absent, 1=present
- 44 forewing female hyaline spot in space 3, 0=absent, 1=present
- 45 forewing female hyaline spot in space 6, 0=absent, 1=present
- 46 forewing female hyaline spot in space 7, 0=absent, 1=present
- 47 forewing female hyaline spot in space 8, 0=absent, 1=present
- 48 underside hindwing black spot at wing base, 0=absent, 1=present
- 49 underside hindwing white cell spot, 0=absent, 1=present
- 50 underside hindwing pale band, 0=absent, 1=from costa/vein 8 to vein 1b or dorsum, 2=only ternal pale spot in space 1c(-2)
- 51 underside hindwing dark ternal lobe, 0=absent, 1=present
- 52 underside hindwing veins, 0=not outlined in black, 1=outlined in black
- 53 head, 0=concolourous with thorax, 1=red
- 54 underside abdomen, 0=not red-tipped, 1=red-tipped, rest dark
- 55 abdomen, 0=more or less banded (may be very reduced) at least on underside, 1=no traces of banding

Appendix 2

iphis	1110120000	0100000N11	2202201201	0211100000	0000000000	01111
lucagus	1110100000	01101N0N11	2202211201	0210100000	0000000000	00111
forestan	1110100000	1110000N11	2202211201	0210000000	0000000001	00000
aeschylus	1110100000	11101N0N11	2202211201	0210000000	0000000000	00111
anchises	1110100000	11101N0N11	2202211201	0210000000	0000000001	00000
ramanatek	1110100000	1100000N0N	2202201201	0210000000	0000000001	00000
oedipodea	1110100021	0001010N0N	0001000110	0001010000	0000000100	00000
vasutana	1110100001	0001010N0N	0001000100	0001010000	0000000100	00000
harisa	1110100001	000101110N	0001000100	0001010000	0000000100	00000
sena	1110100001	0001010N0N	0001000100	0001000000	0000000001	00000
iluska	1110100021	0001010N0N	0001000100	0001000000	0000000001	00000
aquilina	1110100001	0001010N0N	0001000110	0100000000	0000000000	00000
doleschallii	1110100100	000001100N	0101010101	0200000000	0000000012	00000
major	1110100100	000001100N	0101010101	0200000000	0000000012	00000
badra	1110100000	00002N1210	0111111111	0000000000	0111111012	10000
lizetta	1110100000	00002N0N10	0111111111	0000000000	0111110000	10000
khoda	1110100010	00002N1210	0111111111	0000000000	0011100001	10000
schoenherr	1110100020	00002N1211	0111111111	0000011111	1111111001	10000
exclamationis	1110100000	1100000N11	2201200201	1200001110	0111100002	00000
benjaminii	1110101001	1102000N11	1101111101	0210000000	0000000002	01000
plateni	1110101011	1102000N11	1101111101	0210000000	0000000000	01000
rafflesia	1111020100	0000000N11	1100100100	0200101110	0111000000	00010
flesus	1111010000	0000000N0N	0100210200	1201101111	1111111000	00000
liliana	1111010000	0000000N0N	1100111100	0210101111	1111111000	00000
machaon	00000N0100	0000N0N0N0N	000020N000	1201100000	0000000000	01000
Macrosoma	00000N0000	0000000N0N	010011N001	1203100000	0000000000	00000

Data matrix for the analysis of relationships between genera of Coeliadinae Hesperidae). N=not applicable. In the analysis resulting in the tree of Fig. 5, the non-hesperide taxa, *Papilio machaon* Linnaeus, 1758, and *Macrosoma*, have been omitted. For author and year of the other taxa, see Evans (1937, 1949).

Appendix 3

List of characters used for the analysis of species of *Hasora* (Hesperidae: Coeliadinae)

- | | | | |
|----|---|----|--|
| 1 | forewing vein 1, 0=gently curved, 1=acutely bisinuate near base | 13 | forewing female hyaline spot in space 8, 0=absent, 1=present |
| 2 | antennae nudum segments, 0=>30, 1=<30 | 14 | underside hindwing white cell spot, 0=absent, 1=present |
| 3 | forewing male hyaline spot in cell, 0=absent, 1=present | 15 | underside hindwing pale band, 0=absent, 1=from costa/vein8 to vein 1b or dorsum, 2=only ternal pale spot in space 1c(-2) |
| 4 | forewing male hyaline spot in space 2, 0=absent, 1=present | 16 | underside hindwing dark ternal lobe, 0=absent, 1=present |
| 5 | forewing male hyaline spot in space 3, 0=absent, 1=present | 17 | forewing male stigmata, 0=absent, 1=along veins, 2=transverse |
| 6 | forewing male hyaline spot in space 6, 0=absent, 1=present | 18 | distal edge genital plate, 0=regular, 1=irregular |
| 7 | forewing male hyaline spot in space 7, 0=absent, 1=present | 19 | dorsal sclerotization transition ductus/bursa, 0=absent, 1=present |
| 8 | forewing female hyaline spot in cell, 0=absent, 1=present | 20 | papillae anales, 0=broadly rectangular, 1=narrow and pointed |
| 9 | forewing female hyaline spot in space 2, 0=absent, 1=present | 21 | genital plate, 0=normal, 1=high |
| 10 | forewing female hyaline spot in space 3, 0=absent, 1=present | 22 | lateral sclerites 8th abdominal segment female, 0=widely separate, 1=close midventrally |
| 11 | forewing female hyaline spot in space 6, 0=absent, 1=present | 23 | hairs papillae anales, 0=normal, 1=few and mainly large |
| 12 | forewing female hyaline spot in space 7, 0=absent, 1=present | 24 | bursa, 0=ovate-elongate, 1=curving almost 90° |

vervolg Appendix 3

- 25 genital plate, 0=with narrow central indentation, deeper than wide, 1=shallow central indentation
 26 uncus arms in dorsal view, 0=more or less straight, 1=strongly curved
 27 uncus arms in lateral view, 0=more or less straight, 1=curved upwards
 28 cucullus, 0=distally more or less truncate and serrate, 1=distally narrowly rounded, may be serrate
 29 gnathos, 0=not or only slightly extending beyond uncus, 1=extending well beyond uncus
 30 uncus, 0=without horns ("bifid"), 1=2ith horns ("quadrifid")
 31 dorsal extension sacculus, 0=absent, 1=present
 32 costal process, 0=simple, 1=bifid, 2=trifid
 33 proximal edge tegumen, 0=evenly rounded, 1=more or less notched
 34 bases uncus horns, 0=wide apart, 1=approximate
 35 eyes, 0=bare, 1=hairy

Appendix 4

mus	1100000000	0000210???	??????0?0	?0?01
alta	1?00000???	??0010???	????00000	00001
lizetta	1100000111	1100010000	0100000000	00100
salanga	1?00000111	0000210???	??????0?0	?0?0?
proxissima	1100000011	00001100?0	0?0?1??0?0	?0?00
anura	1100011111	1111200???	??????0?0	?1?01
myra	1100000111	1100000000	0100000000	01000
danda	1?00000111	1110010???	??????0?0	?1?0?
zoma	1?00000000	0000010???	??????0?0	?1?0?
umbrina	1?00000011	0000210???	??????0?1	?0???
buina	1?00000000	0001200???	??????0?1	?0???
discolor	1100000000	0000100010	0000000001	00100
borneensis	1000000011	1100110???	??????0?1	?0???
chromus	1100000011	0000112000	0000000001	00000
taminatus	1100000011	0000112000	0110101001	10100
hurama	1100000000	0000112000	0110111011	10000
schoenherr	1111111111	1110112000	0100110111	00010
mixta	1100000111	1100212001	1110100111	11110
celaeus	1100000000	0000002001	1110100101	01100
badra	1100000111	1111210001	1110100101	11100
sakit	1?00000111	1101210???	??????1?1	?????
quadripunctata	1100000111	1101210???	??????1?1	?1???
wilcocks	1?????111	11100?0???	??????1?1	?????
subcoelestis	1100000000	000000???	??????1?1	?1???
vitta	1100110011	1000110110	0101011121	11010
moestissima	1100000011	1000110110	01010??1?1	?1???
caeruleostriata	1100000???	??0110???	?????001?1	11?10
perplexa	1?00000???	??01?0???	??????1?1	?1???
khoda	1000000011	1000111???	?????11121	12010
leucospila	1100000011	1000211???	??????1?1	?2???
thridas	1000000000	0000101???	?????11121	12010
outgroup	0000000000	0000000000	0000000000	00000

Data matrix for the analysis of relationships between species of *Hasora* (Hesperiidae: Coeliadinae). NB - the state of a number of characters in various species is still unknown (indicated by ?). For author and year of the other taxa, see Evans (1937, 1949).