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Fossil butterflies, calibration points and the molecular clock (Lepidoptera: Papilionoidea)

Rienk de Jong

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Fossil butterflies, calibration points and the molecular clock (Lepidoptera: Papilionoidea)

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Abstract

Fossil butterflies are extremely rare. Yet, they are the only direct evidence of the first appearance of particular characters and as such, they are crucial for calibrating a molecular clock, from which divergence ages are estimated. In turn, these estimates, in combination with paleogeographic information, are most important in paleobiogeographic considerations. The key issue here is the correct allocation of fossils on the phylogenetic tree from which the molecular clock is calibrated. The allocation of a fossil on a tree should be based on an apomorphic character found in a tree based on extant species, similar to the allocation of a new extant species. In practice, the latter is not done, at least not explicitly, on the basis of apomorphy, but rather on overall similarity or on a phylogenetic analysis, which is not possible for most butterfly fossils since they usually are very fragmentary. Characters most often preserved are in the venation of the wings. Therefore, special attention is given to possible apomorphies in venational characters in extant butterflies. For estimation of divergence times, not only the correct allocation of the fossil on the tree is important, but also the tree itself influences the outcome as well as the correct determination of the age of the fossil. These three aspects are discussed.

All known butterfly fossils, consisting of 49 taxa, are critically reviewed and their relationship to extant taxa is discussed as an aid for correctly calibrating a molecular clock for papilionoid Lepidoptera. In this context some aspects of age estimation and biogeographic conclusions are briefly mentioned in review. Specific information has been summarized in four appendices.

Key words: biogeography, calibration points, evolutionary history, morphology, molecular clock phylogeny

Introduction

The rarity of fossilized butterfly remains cannot simply be attributed to the frailness of the butterflies or their powers of flight (Fox 1948; Shields 1976). Most butterflies are not frail in the first place, certainly not if compared with many other insects, such as Diptera, of which many more fossils are known. The powers of flight exhibited by many butterflies cannot explain the scarcity of butterfly fossils as well, since they do not prevent fossilization. Instead, the, or at least one, reason for such scarcity must rather be sought in life habits of butterflies that rarely brings them into favorable circumstances for fossilization, such as burial in shallow water sediment or entombment in dripping resin[1]). As remarked by Martínez-Declòs *et al.* (2004) and Peñalver & Grimaldi (2006), the wing surface of a butterfly easily repels fluids and is resistant to wetting. This repellent effect could be a reason why butterfly fossils are rare in Paleogene and Neogene ambers and lacustrine deposits. However, it would appear that the wing vestiture of non-papilionoid Lepidoptera has the same effect, yet they more frequently occur in amber. Remarkably, an obvious possibility has apparently been overlooked: fossil butterflies intrinsically may be rare because the butterflies were rare in the environment or perhaps because they are relatively large insects, and the conditions for preserving a large fossil are more stringent. These two aspects of butterfly occurrence could be linked, in that larger insects also tend to be rarer.

Apart from the butterfly fossils being rare, the localities where they have been found are very unevenly distributed across the globe (Fig. 1, Appendix 4). From the Southern Hemisphere only a few fossils are known from the Oligocene in Brazil, from the Holocene or Pleistocene in Colombia and a Pleistocene fossil has been

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1. The author once did some experiments with freshly caught butterflies, which were pressed into fresh resin of *Agathis* dripping from trees in the forests of Northern Sulawesi. After a year the resin had completely dried out and had become brittle, practically destroying the butterflies. It is not that easy for a butterfly to become an amber insect.

found in Tanzania. Consequently, there is no material evidence of the occurrence of butterflies on remnants of Gondwana prior to the Oligocene, and any suggestion that they did is at best dependent on the interpretation on circumstantial evidence. In the Northern Hemisphere the distribution of fossil localities also is very uneven. Apart from an allegedly Pleistocene fossil from Japan and equisitely preserved fossils in Dominican amber, all Northern Hemisphere fossils are from Western Europe and the USA, with more than 25 % originating solely from two localities only, Florissant in Colorado and Aix-en-Provence in Southern France.

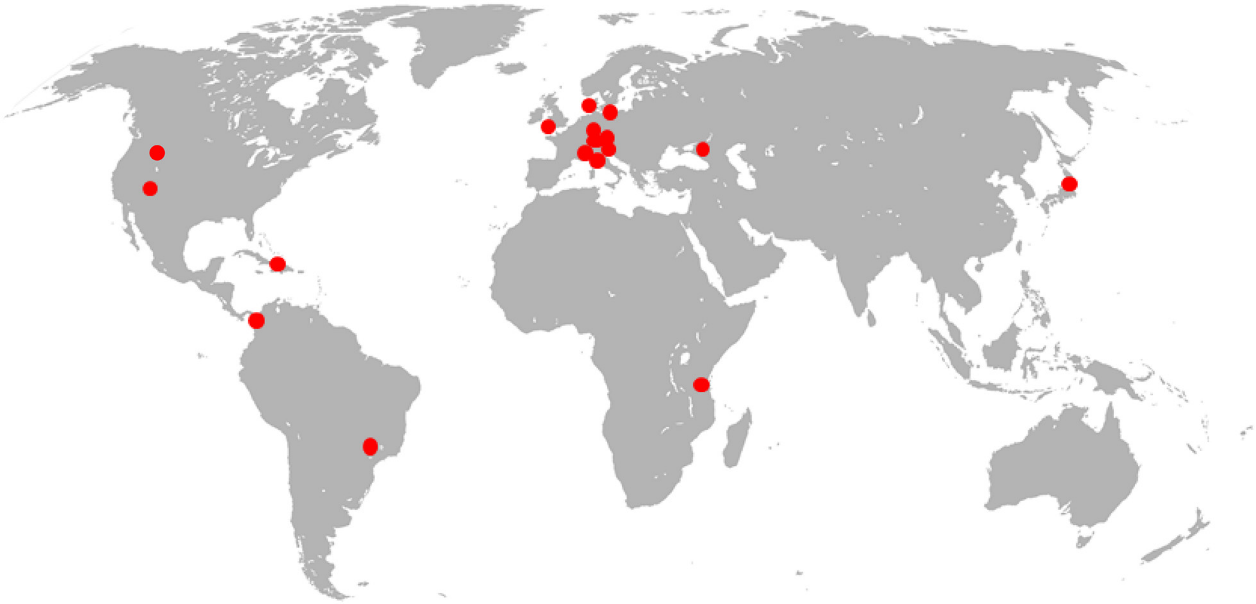


FIGURE 1. Localities of fossil butterflies plotted ion a modern map. See Table 1 for further, complementary information.

In addition to their paucity and sporadic global distribution (first quantitatively demonstrated by Labandeira & Sepkoski 1993) there is an uneven distribution of fossil butterflies in time. The oldest fossil is about 55 million years old (de Jong 2016). About 37 % of all species have been found in a ten-million-year-long interval largely coinciding with the Oligocene Epoch. With such a poor representation in time and space one may wonder how far the fossil record can contribute to an understanding of butterfly evolution. For a long time the contribution of the fossil record was meagre indeed, in spite of the conviction of some authors that fossils are crucial for understanding the phylogeny of organisms (see next paragraph). However, with the expansive rise of DNA analysis and the use of a "molecular clock" (see, e.g., Hillis *et al*. 1996; Page & Holmes 1998; Salemi & Vandamme 2003) fossils now play a crucial part in estimating divergence times, since they provide necessary calibration points for the clock. The position of the fossil on the phylogenetic tree determines the speed of the clock and since all estimates of divergence time (and with it, biogeographic considerations) are extrapolations from this point, the position of the fossil can hardly be accurate enough. Obviously, fossils provide other types of data that are unavailable in modern organisms. Fossils offer combinations of characters and the documentation of extinct lineages that are not available by just examining recent organisms, thus helping to understand evolution. However, the evolution of the butterflies is beyond the scope of the present study, which focuses on the allocation of butterfly fossils in phylogenetic trees based on extant species. In addition, poor as the butterfly fossil record may be, the fossils are the only material testimony of former distributions. The paleobiogeography of the butterflies will briefly be discussed at the end of the paper.

Throughout the text Ma stand for "million years ago" or "million years old". Thus, a fossil of 50 Ma means that it is 50 million years old, an event of 50 Ma means that it occurred 50 million years ago.

Fossils, evolution and phylogeny

Fossils are proof that in the deep past organisms existed that are different from what we find today. Evolution is the link between extinct and extant organisms. Without fossils, an evolution theory would not be needed as explanation for the extant diversity of life, a unique creation event would be enough. Evolution theory teaches us that all extant organisms are interrelated. The relationships are the subject of a phylogenetic study. Therefore, indirectly fossils are indispensable for phylogenetic research. Opinions differ widely with regard to a more direct value of fossils for phylogenetic research. Some authors consider them indispensable for phylogenetic reconstruction (e.g., Gingerich 1979: 74, "The fossil record is of fundamental importance for understanding phylogeny"; Nekrutenko 1965: 149, "[...] the genuine test of validity for any phylogenetic construction must be based on evolutionary data from different time periods"). Others (e.g., Hennig 1966a, 1969; de Jong 1980; Patterson 1981; Sober 1988; Wiley 1981) do not set special value on fossils for phylogenetic reconstruction, since the interpretation of character states in fossils is, generally spoken, subject to the same restrictions as in extant species, and the discovery of a new extant taxon could have the same impact as a fossil on a phylogenetic analysis by adding characters. These opposing views should not be taken too strictly. There are three possible situations: (a), all characters visible in the fossil are found in extant taxa as well; (b), the fossil shows a character not found in extant taxa; and (c), the fossil shows a combination of characters found in extant taxa, but not in this particular combination. In situation (a), the fossil does not influence the phylogeny deduced from extant taxa. Based on its characters it is placed on a still extant lineage, and it does not influence the relationship of this lineage to other lineages. In situation (b), it is concluded that the fossil represents an extinct lineage. On the basis of its further characters, the fossil is linked to a still extant lineage. Obviously, it complements the known phylogeny—as expressed in a tree—by adding a dead-end lineage, and it deepens our insight in the evolution of the higher taxon the fossil belongs to, but it does not influence the relationship of the extant lineage to other lineages. In situation (c), the autapomorphic characters still exist, but not in the combination as found in the fossil. This situation would seriously challenge the relationship of the taxa, of which the autapomorphic traits are combined in the fossil. Taking the relationship between Papilionidae and Pieridae as an example, in none of the phylogenetic analyses of the butterflies since Kristensen (1976), the two families have been considered monophyletic. However, discovery of a fossil displaying an autapomorphic trait of the Papilionidae as well as an autapomorphic trait of the Pieridae, would seriously challenge this concept. Disregarding possible convergent evolution, the most obvious conclusion would be that the combination of these traits is an apomorphy itself, and that the lineage split into two (now still existing) lineages, both of which lost one of the apomorphies.

In conclusion, by exhibiting combinations of characters fossils can prompt us to reconsider our views of character evolution (and thus of phylogeny) based on the study of extant taxa only. As will be shown below, such examples are not known among Papilionoidea. For a well-balanced evaluation of the use of fossils, see also Novacek (1992).

While fossils have an impact on phylogenetic relationships as concluded from extant taxa in special cases only, they exhibit an essential aspect of the evolution of the group under study: a time dimension (see also Forey 1992). Fossils, and not extant organisms, provide a minimum age for the characters visible in the fossil. If the character is apomorphic, the fossil provides a minimum age not only for the character, but also for the taxon that has been recognized on the basis of the apomorphy. Obviously, the correct identification of the fossil and its characters is essential. This is the main objective of the present paper.

Since the 1980's, butterfly phylogeny has been analyzed by applying computer programs capable of processing an increasing amount of data. The Hennigian method (Hennig 1966a) of building a tree based on an *priori* assessment of apomorphic character states was replaced by computer programs that resulted in trees, from which apomorphic characters states are deduced *a posteriori*. Because of the usually fragmented nature of fossils, with only few characters available, it is, in most cases, practically useless to include the fossil in a cladistics analysis to find its place in the phylogeny. Instead, we use the trees based on extant taxa as a coat rack, and try to allocate the fossil taxon on it using an apomorphic character as coat hanger.

Age determination of fossils

As a taxonomist, the lepidopterist does not determine the age of a fossil, but he/she is dependent on the information received from geologists. Obviously the age can rarely be determined very exactly, usually a range is given. This is the more so in cases where the insect may not have been fossilized on the spot, but for instance has been accumulated with debris in a depression, or has been washed ashore as with Baltic amber.

If an age range is given, the question arises: do we take the minimum age, the maximum age, or the average? Obviously, the choice has an impact on the estimates of divergence times. For example, a source of exceedingly well-preserved fossil butterflies is Dominican amber. According to Iturralde-Vinent & MacPhee (1996) (geologists), the age of Dominican amber is 15–20 Ma. Suppose we have a fossil that reliably can be identified as "very close" to an extant genus and we place it near the origin of the genus, then we have an indication of the rate of the molecular clock, if we know the number of substitutions between the extant genus and its sister group. Choosing the older age for calibration, the molecular clock ticks 33 % more slowly (same number of substitutions over a longer period) than choosing the youner age. In other words, the choice of the fossil's age has an influence on the divergence estimates (higher in case of a slower clock), and therefore also on possible correlations with geological or other changes in the past.

The main search is for divergence times of older nodes, not younger nodes. We might be more interested in the origin of Pieridae than in the origin of *Pieris brassicae* (Linnaeus). This means that often the divergence time estimates are extrapolations from the age of the fossil, not intrapolations. Here is a simplified example of what this could mean. If the fossil has a supposed age of 15–20 Ma, a fivefold extrapolation (roughly five times as many substitutions) results in an estimated age range of 75–100 Ma. One may wonder if a range of this magnitude, equivalent to the time elapsed since about the middle of the Oligocene to the present, is still meaningful for biogeographical considerations.

If we don't want to use the entire range for calibration, but the younger, middle or older value, I recommend taking the most recent age of the range given by geologists. Obviously, a fossil gives a minimum age for the origin of a particular character: it may have originated a little, much, or even very much earlier, but not later. By choosing the older age from a range, the fossil no longer provides a minimum age, but a more ambiguous age: the character may have originated earlier, but also later; we simply don't know.

Characters, taxa and calibration points

This study intends to offer reliable calibration points for molecular clock analyses in butterflies and it refers to calibration points used for such analyses in literature. It is not intended to execute such analyses, which will be done by a team led by Maria Heikkilä (USNM, Washington DC) for all Lepidoptera. People interested in the practice of fossil calibrations are advised to study the paper by Parham *et al*. (2012).

The strong focus on the recognition of taxa and relationships among taxa, as exemplified by the development of DNA-barcoding, is important in its own right. However, this focus has obscured the concept that taxa are just a cross-section of a lineage, the parts of which—be it specimens, species or higher categories—are held together by common descent. We may specify a cross-section of the same lineage at another time the same taxon, but such specification depends on how we define the taxon. Without the definition we would not be able to study, for example, the transformation of a species: we consider *Pieris brassicae* of the year 1800 as the same morphologically as *Pieris brassicae* of the year 2000. An analogy may be similr to that of a river: the course of the river may not change, but the water is constantly changing. One may not see the difference, but after 200 years *Pieris brassicae* has undoubtedly changed genetically.

By characterizing the entirety of the lineage, the delimitation of taxa becomes blurred. In an evolutionary context, this is what one would expect. The delimitation of a particular taxon, based on our own definition, does not change, it just fades away and becomes irrelevant. What is more evolutionarily interesting is the internal gene-based changes of characters that are reflected externally by the phenotype. This is what is documented in the fossil record, not changing taxa, but changing characters.

Recognition and identification of recent species is generally based on similarity with named specimens in a collection or reference to illustrations of known species. Apomorphy or plesiomorphy do not play a part here. Placement of a species in a genus and recognition of genera is accomplished in a similar way, notwithstanding that a genus, certainly since the time of Hennig, is considered a monophyletic group of species. With the rise of computer programs for phylogenetic analysis, and especially with the fast development of DNA-based research, the recognition of apomorphies and plesiomorphies, became very important prior to the development of large analytical programs (see, e.g., de Jong 1980). Character polarity became a conclusion based on an analysis in which there was no *a priori* recognition of apomorphy and plesiomorphy. The growing number of phylogenies based on molecular characters has not always been implemented seamlessly with the *a posteriori* recognition of apomorphies and plesiomorphies in morphological characters. A good example of a study where morphological characters are described and discussed in the context of a phylogeny, based on an analysis of molecular and morphological characters, is Warren *et al.* (2008, 2009). Such an analysis does not automatically lead to the recognition of apomorphic characters for higher-level taxa, as is clear from the detailed discussions of subfamilies and tribes in Warren *et al.* (2009), but at least it is discussed.

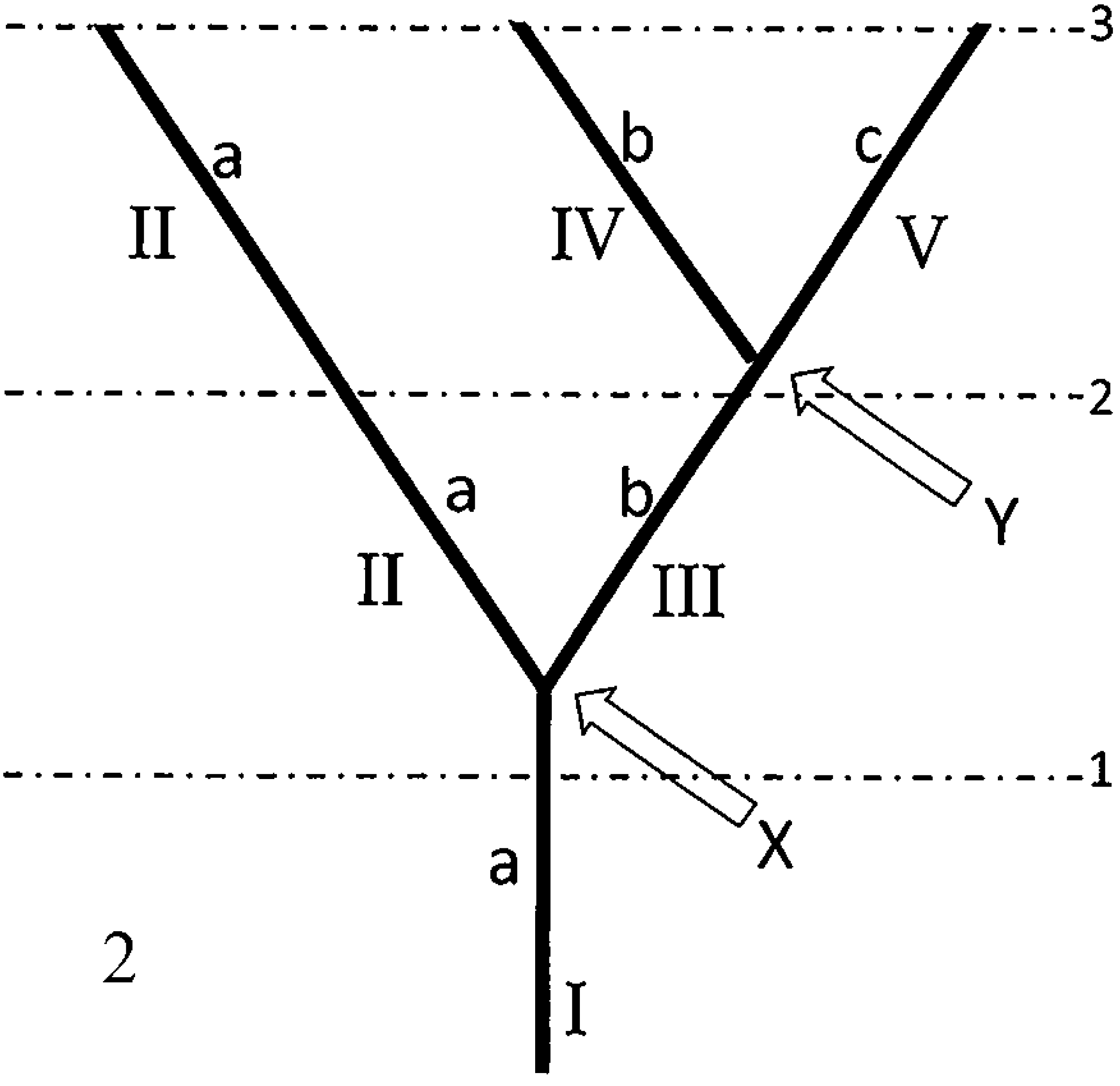


FIGURE 2. Apomorphies, their placement on a tree, and the assignment of calibration points. See text for explanation.

The taxonomic position of a fossil has been and generally is approached in the same way as extant taxa, specifically by similarity to extant taxa. However, from the discussion above, it may be clear that in evolutionary terms we are not seeking similarity between a fossil taxon and an extant taxon, but the evolution of characters that, again in an evolutionary context, can be divided into plesiomorphic and apomorphic characters. The Hennigian concept, that plesiomorphy is no measure of relationship, is widely practised but regularly not followed in the study of fossils, although in fossils Hennig's concept can be pursued just as it is in recent organism. Instead of searching for "related" extant taxa on the basis of similarity, which at best is a mix of plesiomorphies and apomorphies, the student of fossils should look for apomorphic characters of extant taxa in fossil taxa (see also the explicit account by Hennig 1966b). If found we have a minimum age for the character, and if we have defined the extant taxon on the basis of that particular character, we also have a minimum age for the taxon. If the "relationship" of a fossil to an extant taxon is based on plesiomorphy, even though it gives a minimum age for the character, it does not do so for the extant taxon, as the apomorphy-based relationship of the fossil to the extant taxon remains uncertain. In addition to apomorphic characters of extant taxa, which we hope to find in fossils, fossils may have apomorphic characters of their own that have gone lost in extant organisms. Such characters may be helpful in finding relationships between fossil taxa, but obviously, they do not indicate relationships with extant taxa.

Thus, apomorphy of characters and not overall similarity should determine the position of a fossil on the phylogenetic tree and with that its use as calibration point (see also de Jong 2007). Suppose we have a taxon I with character state "a" at level 1 (Fig. 2). It splits into taxa II and III with, respectively, character state "a" and "b" of character a at level 2. Taxon II may evolve further, but at level 3 remains inseparable taxonomically from II between levels 1 and 2. Taxon III splits into taxon IV, with character state "b", and taxon V with character state "c" of the same character. Thus at level 3 (present day) we have three taxa, II, IV and V, with character states "a", "b", and "c", respectively. Now we find a fossil with character state "b". We do not know the phylogenetic background; we only know that there are three extant species, II, IV and V, with character states "a", "b" and "c", respectively. Not knowing the phylogeny, we would tend to relate the fossil to IV and to place the fossil (and with that, the calibration point) at "Y", the origin of species IV, but if "b" is plesiomorphous at "Y", the correct allocation would be at "X", where the character state originated. In case of species the difference could possibly be around 5 million years, but in case of higher taxa the difference could be 10 or 20 million years, giving an enormous bias in estimates of divergence times.

In view of the often very fragmented nature of butterfly fossils, the search for characters in fossils that are apomorphic within the extant butterflies may be in vain, but it should at least be attempted and discussed before a fossil is assigned a taxonomic position. Placing a fossil as calibration point near an extant genus A because author X, without evidence, is of the opinion that it "is closest to that genus", is in validated by scientific reasoning.

How to recognize a fossil as a butterfly

The theoretical considerations in the foregoing chapter do not automatically lead to the identification of a fossil as a butterfly. Ideally, we should find an autapomorphy of the Papilionoidea in the fossil. Here we meet two kinds of problems. First, the character composition of the Papilionoidea. De Jong *et al*. (1996) listed six characters that could support the monophyly of what at the time was known as Papilionoidea + Hesperioidea. Further, they discussed ten characters that could possibly throw light on their relationship with Hedyloidea, at the time considered the sister clade to the Papilioidea+Hesperioidea, and came to the conclusion that none of these characters were universal and unique collectively to the three superfamilies. Recent analyses (Regier *et al*. 2009; Heikkilä *et al*. 2011; Kawahara & Breinholt 2014; Timmermans *et al*. 2014), using an increasing number of taxa and genes, have provided evidence that the traditional concept of butterfly phylogeny, as expressed in Wahlberg *et al*. 2005a, is in need of revision. Through the use of different gene sets, they came to similar conclusions about the relationships of the traditional butterfly families. All four studies agree in an interchangable position of Papilionidae and Hesperiidae compared to earlier schemes, and where Hedylidae have been included in the analysis, the latter turned up as sister group of Hesperiidae. Whatever their exact interrelationships, for the assembled grouping, which could still be termed Papilionoidea although with a different meaning, there are no universal and unique morphological characters known. Thus, although we can rather easily identify a lepidopteran as belonging to one of the constituent families based on an apomorphy, we can only identify it as a butterfly on the basis of a phylogenetic analysis, and not on the basis of an apomorphic character. In other words, if we do not find an apomorphic character of an extant butterfly family in a fossil, we cannot be certain the fossil belongs to a butterfly.

The second kind of problem we encounter is the fragmented nature of the fossil. Structures of head and thorax are usually poorly preserved or otherwise absent, and often only wings are available, and in many cases fragmented or superimposed upon each other. If the wing is fairly complete, the generally broad shape of a butterfly wing can help exclude other families of Lepidoptera to be considered. The same is true for size. There is an enormous overlap in size between various lepidopteran superfamilies and in none of them can a particular size range be considered a unique apomorphy within the Lepidoptera. For example, there is no butterfly as small as a micropterigid and vice versa. Occasionally, part of the wing pattern is visible by discoloration of the sedimentary or amber matrix, but there is no summary study detailing apomorphies and plesiomorphies in wing pattern of butterflies. Thus for the identification of a fossil as a butterfly, various characters must be considered simultaneously, while no character in particular is an apomorphy of the butterflies.

In addition to the problem of finding unique and universal butterfly apomorphies in extant as well as in fossil taxa, it is as yet uncertain which taxon is the sister group of the butterflies. In Kristensen *et al.* (2007) and in the Tree of Life Project (2010), the Macrolepidoptera clade to which the butterflies belong is largely unresolved. In a study on the reconstruction of the evolution of the ditrysian clade of the Lepidoptera by Regier *et al.* (2009), the butterflies as currently conceived (the traditional families with Hedylidae added) do not even constitute a monophyletic group, but are dispersed in a clade with four other superfamilies. In analyses of the phylogeny of the butterflies outgroups are chosen for rooting the tree. Generally, outgroups are chosen that are thought to be not too distantly related to the butterflies, but obviously such rather arbitrarily chosen outgroups cannot be used for sister group determination.

Identification of a fossil is a preliminary task and a subsequent task is understanding its relationships with other clades. For this we need apomorphies. Since wing venation provides the most important available clue, explanation is given here to avoid repeating descriptions and discussions.

Wing venation

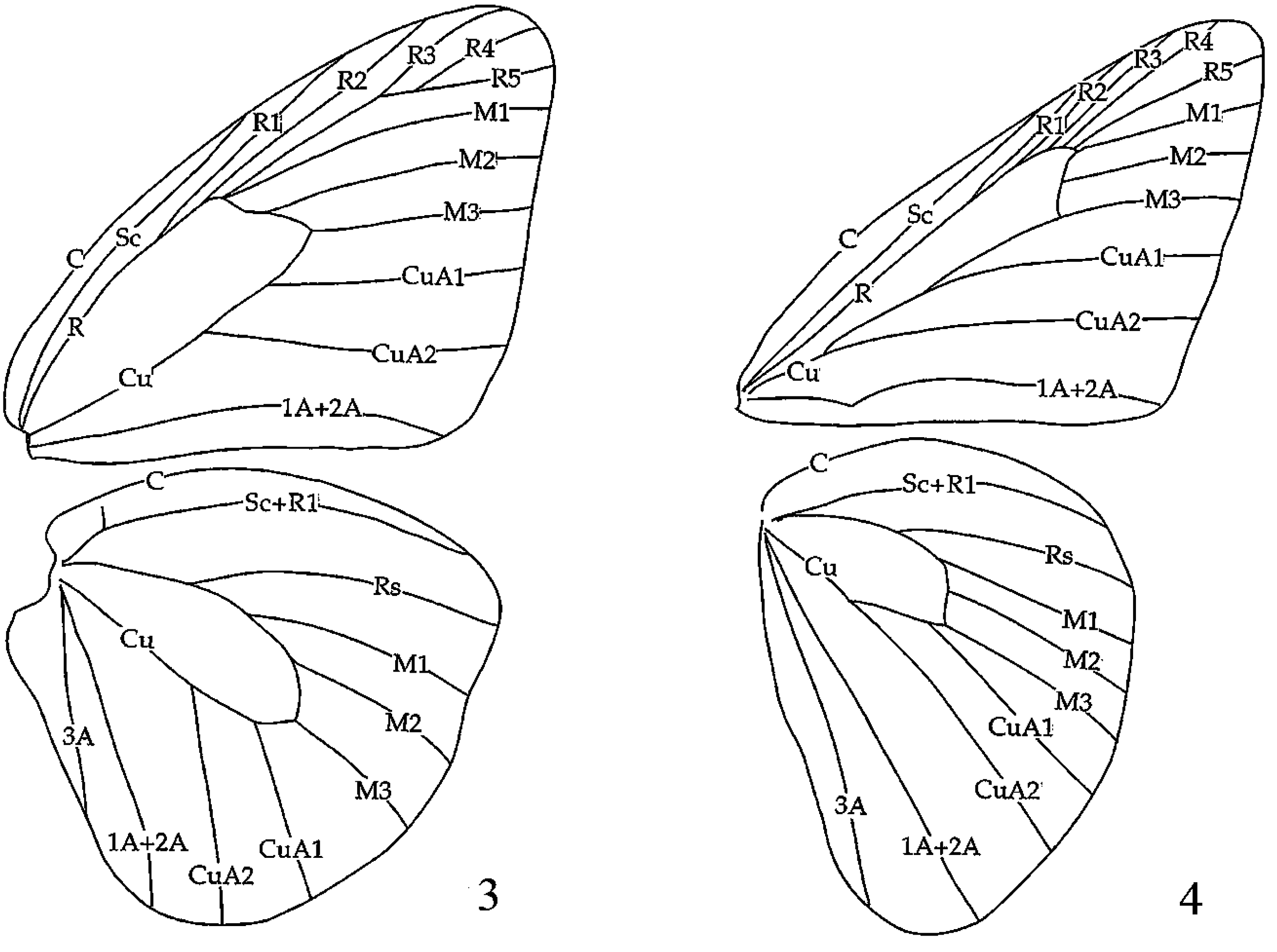
Nomenclature. The names of veins has changed considerably since the first fossil butterflies were formally described. Consequently, it is important to state explicitly the nomenclature followed in this paper.

Currently two systems are in use among lepidopterists: (a) a simple numbering system, dating back to Herrich-Schäffer whose works (1843–1856) involved the numbering of veins from 1 to 12 from starting at the rear of the wing; and (b) the more widely used system devised by Comstock and Needham and usually simply called the Comstock system (Comstock 1918). The Comstock system is based on the pupal wing tracheae, around which the veins are formed, allowing comparison between various insect orders. This comparability is because veins with the same name are hypothesized to be homologous in all insect orders. However, tracheation has been shown to be a fallacious guide to vein identification in various instances. For this reason Wootton (1979) used fold lines and flexion lines as a guide to vein homology. Nevertheless, the system recommended by Wooton is hardly different from Comstock's, other than the naming of branches of the radial sector (see below). The most elaborate and consistent system so far is the one described by Kukalová-Peck (1991), based on an extensive study of fossil insects. Her presentation, reflecting the evolutionary history of the structures in their names, is quite convincing. For comparisons among orders this may be essential, but for a study at a lower taxonomic level it may be overly circumscribed and can be confusing. With respect to Kukalová-Peck's analogy of embryonic wing-bud tracheae to adult wings, although the flippers of a dolphin are homologous with the forelegs of other mammals, we still call them flippers. Therefore, we follow the convention of Nielsen & Common (1991) who, although aware of Kukalová-Peck's conclusions and largely following Comstock's system, preferred to use a nomenclature that allows for comparison with other literature on Lepidoptera. See also Miller (1970) for a review of different systems for naming veins.

In the butterflies the veins of the forewing are as follows (Figs. 3–4):

- *costal vein* (C), runs along the front wing margin;
- *subcostal vein* (Sc), from the wing base to the costal vein, undivided;
- *radius* (R), from the wing base, forming the anterior margin of the discal cell (see below). R branches into R1 (Kukalová-Peck: RA, radius anterior) and the so-called radial sector (Rs; Kukalová-Peck: RP, radius posterior); the latter branches into four branches (some of which may be lost); the branches of Rs are usually named R2, R3, R4 and R5, respectively, in Lepidoptera and we shall follow that system here, in agreement with Nielsen & Common (1991) and Scoble (1992), but contrary to Wootton (1979) who strongly recommended to name the branches of the radial sector Rs1 to Rs4 and to Kukalová-Peck (1991), who called the same branches RP1 to RP4;

- *media* (M), from the basal part of the discal cell, but usually completely lost, sometimes with remnants present at the distal end of the discal cell and traces of the course may be visible by dark pigmentation. The media consists of three branches: M1, M2, M3, running from distal end of the discal cell to the outer wing margin (but M1 may branch off from Rs). In Kukalová-Peck's notation M1 and M2 belong to MA, media anterior, and M3 belongs to MP, media posterior. An autapomorphy of the Lepidoptera is the fusion of M4 with CuA1 (Kukalová-Peck: MP4 and CuA1+2), except in the primitive moth *Agathiphaga* (Common 1973; Hennig 1981);
- *cubitus* (Cu), forming posterior margin of the discal cell; there are two main branches, an anterior CuA (again branching into CuA1 and CuA2) and a posterior CuP; the latter is largely or entirely lost in butterflies, but traces of its course are sometimes visible by darker pigmentation and/or by the distribution of spots in the area between CuA2 and 1A; CuP was called the first anal vein by Comstock;
- *anal veins* (A); in butterflies there is one long anal vein and a short one (which may be partly or entirely missing) at the base running into the long vein (thus forming a loop) or to the hind margin; the small vein is generally considered the second anal vein, and the long vein is often called 1A+2A from the point of fusion (or over its whole length if the small vein is lost); however, if the small vein running to 1A is homologous with the small vein running to the hind margin, it is less confusing to call the long vein 1A and the small vein 2A, and thus consider the small vein to end on 1A and not to run as a vein fused with 1A to the outer margin; sometimes the small vein is called 3A, possibly a remnant of the Comstock notation, where CuP was called 1A.



FIGURES 3–4. Wing venation of (A) *Pareronia* Bingham, 1907 (Pieridae), and (B) *Hasora* Moore, 1881 (Hesperiidae). See text for explanation.

The area between radius and cubitus is called the *discal cell*, or simply 'cell' in butterflies; the cell is usually closed by cross veins, but may be open by loss of the cross vein between M2 and M3. The cross veins are often called udc (upper discocellular cross vein, between R and M1; absent if M1 branches off R), mdc (middle discocellular cross vein, between M1 and M2) and ldc (lower discocellular cross vein, between M2 and M3).

The front margin of the cell is not a separate vein. In the Hesperiidae it actually consists of, successively, R, Rs, R2+(R3+(R4+R5)), R3+(R4+R5), and R4+R5 (the "+" sign denotes a common stem). In other butterflies it is formed by, at most, R, Rs, R2+(R3+(R4+R5)) and, in rare cases, a short part of R3+(R4+R5). Thus, in Hesperiidae there are five radial veins seemingly originating from the cell, whereas in the other butterflies there are generally only three radial veins originating from the cell.

The space between two veins is termed a cell, or better space, so as to avoid confusion with the discal cell. For the sake of simplicity they are named after the vein above it and denoted with a lower case letter. Thus space m3 is the space between M3 and CuA1.

In the hindwing the venation is as in the forewing, but more simplified (Figs. 3–4). The subcosta and R1 are largely or totally fused (Sc+R1); often there is a short, straight or curved vein in the basal part between costa and subcostal (humeral area), known as the precostal or humeral vein; the radial sector is not branched (Rs); there are again three branches of the media (M1, M2, M3) and two of the anterior cubitus (CuA1, CuA2); CuP is lost and there are two anal veins (in Papilionidae, one), 1A+2A and 3A; also in the hindwing the cell may be open by loss of the crossvein between M2 and M3.

Plesiomorphy and apomorphy

For the discussion below I refer to the phylogenetic tree as given in Fig. 22.

Although the studies agree regarding the interrelationships of butterfly families, they strongly differ in the position of the butterflies within the Order Lepidoptera. These differences are not surprising since they employ very different sets of non-butterfly taxa. Consequently, pointing to a family or group of families as sister clade of the butterflies is not a productive statement at the moment. This indecisiveness implies that a discussion of possible apomorphies and plesiomorphies in the wing venation of the butterflies can be little more than a description of various patterns of venation and their occurrence across the families. If a pattern is present in one family only that is not at the root of the tree, this pattern considered autapomorphic for that family. A pattern occurring in all or almost all families, including the basal most one, is considered plesiomorphous within the butterflies. However, it could turn out to be autapomorphic for the butterflies as a group, once we know the sistergroup of the butterflies. The following discussion is meant to support the identifications of the fossils.

For the sake of simplicity we shall use a formula expressing the branching of the radial veins. The front margin of the cell is taken as if it represents a vein of its own from which the radial veins originate. In the formula used herein the radial branches are numbered 1–5. If a comma separates them, it means that they originate from the cell directly. If they are connected by a "+" sign, it means that their common stem originates from the cell. Three veins connected by a "+" sign and with two veins enclosed in brackets indicate a pectinate branching pattern.

Venational patterns of the forewing

- All radial branches originating from cell. This is considered an autapomorphy of the Hesperiidae, recurring in some subordinate taxa of a few other superfamilies (e.g. Adelidae, Incurvariidae, Psychidae, Hyblaeidae), where invariably the wing shape is very different, being much more elongate. There are other characters, such as the wide head of the Hesperiidae, that separate the Hesperiidae from other Lepidoptera, but it such characters are not preserved in any known fossil. According to Comstock (1918) and Kukalová-Peck (1991) the branching of the radius was originally dichotomous. Remnants of this dichotomy, particularly the fork formed by R4 and R5, are visible in the cell of many non-hesperiid butterflies.
- Radial formula 1, 2, 3, 4+5. Found in Hedylidae and some Papilionidae, such as the spectacular Birdwing butterflies (*Ornithoptera*).
- Radial formula 1, 2+3, 4+5 (R2 and R3 separate close to apex). Found in Papilionidae: Parnassiinae: Parnassini only.
- Radial formula 1, 2, 3+(4+5). Widely found in Papilionidae, Pieridae, Lycaenidae, Riodinidae and Nymphalidae. In view of the wide distribution of this pattern it could well be part of the groundplan of the butterflies or, in other words, a plesiomorphy within the butterflies. Alternatively (but much less parsimonious) the formula 1, 2, 3, 4+5 could be part of the groundplan, and the branching of 4+5 from 3 could be a homoplasious development in the five families. Whatever the case, discovery of this pattern in a fossil would be minimally helpful in identification of a potential specimen to family.

- Reduction of number of radial branches. A five-branched radius occurs in all butterfly families, but reduction of the number of branches is found in all families except Hesperiidae and apparently is a homoplasious development. Reduction is, thus, no clue to family membership. Usually only one of the branches, taken to be the fifth, is lost, but sometimes only three branches are present. This condition occurs in a number of Lycaenidae and in some Pieridae (Pseudopontiinae, some Pierinae and Coliadinae), but in the latter case only in combination with a shift of the origin of M1 (see below).
- R2 usually originates from the distal part of the upper border of the cell. In some Pieridae, Lycaenidae, Riodinidae and Nymphalidae the R2 has moved outwards, branching off from the common stem of R3–R5. This apparently is a homoplasious development in the four families and is of little help for identification, but the observation of this character in a fossil makes it highly unlikely that the fossil belongs to Papilionidae, Hedylidae or Hesperiidae.
- M1 usually originates from the distal end of the cell. In many Pieridae, a number of Lycaenidae and in the nymphalid genus *Microtia* (Nymphalinae) the M1 has moved to the common stem of R3–R5, to Rs, or even to R (Pieridae-Dismorphiinae only). Again, the observation of this character in a fossil is not decisive in assigning the fossil to a family, but at least it excludes an affiliation to Papilionidae, Hedylidae and Hesperiidae.
- The crossvein between M2 and M3 (ldc) makes an almost sharp angle with the vein that connects the origins of M3 and CuA1. The latter is in continuation of CuA, and thus the cubitus looks trifid. In all Papilionidae the crossvein between M2 and M3 is in continuation of CuA, making the cubitus appearing quadrifid. Outside the Papilionidae, this condition is only found in Pieridae-Dismorphiinae, apparently a homoplasious development.
- In all butterflies except Papilionidae, if well developed, 2A coalesces with 1A; in all Papilionidae, and only in this family, it runs to the hind margin of the wing.
- The crossvein between M2 and M3 (ldc) usually is well developed, but it is weak or has disappeared altogether in many Nymphalidae taxa. It is not a universal apomorphy of the Nymphalidae, as it evolved has independently in various genera.
- One or more basally swollen veins occur in most, but not all, Nymphalidae-Satyrinae. Two of the genera in which the veins are not swollen are *Melanitis* and *Lethe*. The character is usually taken as one of the characters defining Satyrinae, but it recurs in some other Nymphalidae, like *Mestra* and *Ariadne* (Biblidinae) (Ackery *et al.* 1999). Currently, no unique and universal apomorphies are known for the Satyrinae.
- In all Papilioninae, and nowhere else, there is a short vein in the basal area between Cu and 1A, also known as basal spur (Miller 1987) and Cu-V (Durden & Rose 1978). This vein is a useful diagnostic character, but it is uncertain whether it is an autapomorphy of the Papilioninae (a *de novo* development), or alternatively a remnant of the lost CuP. See further notes regarding *Praepapilio colorado*.

Venational patterns of the hindwing

The hindwing venation offers few characters useful at higher taxonomic levels in the butterflies:

- Generally all veins are unstalked and originate either from the wing base or from the cell. Rs and M1 are stalked in a few Pieridae-Dismorphiinae, Nymphalidae-Satyrinae, Nymphalidae-Danainae-Ithomiini, and Riodinidae.
- M2 is virtually absent in many Hesperiidae-Hesperiinae.
- In almost all butterflies (as well as in other Lepidoptera) there are two anal veins. The Papilionidae is an exception by having only one, a condition that is considered autapomorphic for the family, the genus *Baronia* being an exception.
- The cell is generally closed, but it is open (by failure of the crossvein between M2 and M3 to develop) in many Nymphalidae, and not only in species in which the cell of the forewing is open.

Consequently, the groundplan of the hindwing venation can be described as follows: all veins unstalked; Sc and R1 completely fused or almost so; Rs, M1, M2, M3, CuA1 and CuA2 originating from cell; CuP absent; two anal veins; cell closed.

Annotated list of fossil butterflies

A catalogue of all known fossil and subfossil Lepidoptera of the world was published by Sohn *et al.* (2012), including information on nomenclature, depository and age, but without discussion of the fossils and their identification. The present chapter focusses on the identification of the butterfly fossils.

Abbreviations for depositories

AIOSU	Amber Institute, Oregon State University, Corvallis, Oregon, U.S.A.
AMNH	American Museum of Natural History, New York, New York, U.S.A.
BHM	Black Hills Institute of Geological Research, Hill City, South Dakota, U.S.A.
BMNH	Department of Paleontology, Natural History Museum, Londen, United Kingdom;
DGUG	Departamento de Geociêncis, Universidade de Guarulhos, São Paulo, Brazil;
FFNM	Florissant Fossil Beds National Monument, Teller Co., Colorado, U.S.A.
FMNH	Field Museum of Natural Hiastory, Chicago, Illinois, U.S.A.
FMUF	Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.
GPUG	Geologisch-Paläontologisches Institut, Universität Göttingen, Göttingen, Germany;
IGEO	Museu Nacional et Instotuto de Geociências da Universidade Federal, Rio de Janeiro, Brazil;
IGMF	Centre Géologique et Géophisique de Montpellier, Montpellier, France;
MCZH	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MNHN	Institut de Paléontologie, Muséum National d'Histoire Naturelle de Paris, Paris, France;
MVMF	Muséum d'Histoire Naturelle de Marseille, Marseille, France;
NHMW	Naturhistorisches Museum Wien, Vienna, Austria;
NSMT	Department of Paleontology, National Science Museum, Tokyo, Japan;
PIRAS	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia;
PMUZ	Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland;
PLME	Prehistoric Life Museum, Evanston, Illionois, U.S.A.
USNM	United States National Museum of Natural History, Washington, DC, U.S.A.
ZMUC	Zoologisk Museum, Statens Naturhistoriske Museum, Copenhagen, Denmark.

Nomenclature. The butterfly fossils are listed alphabetically by their species name to facilitate referencing. In cases when a fossil could not be assigned to an extant genus by its student, a "fossil" genus was created, which signifies that the genus is no longer in existence. In many cases, later authors moved a fossil species to another genus, either to an extant genus or to another extinct genus. Such an action is a nomenclatural nuisance for extant species, but generally although not always justified by changing insights in relationships. It is generally assumed that extant genera are defined explicitly by autapomorphies and consequently they are different from other extant genera. In fossils, however, the situation is different. At least in groups with a sparse fossil record like butterflies, there are no groups (“genera”) of fossils with autapomorphic characters that differ from contemporaneous such groups. They may have existed and become extinct, but have not yet been found. A "fossil" genus must be seen as a category for convenience. Moving an extinct, fossil species from one "fossil" genus to another is only justified, if such fossil species shows an apomorphy of the other "fossil" genus. In the absence of autapomorphic characters for the genus, placing different fossil species in the same fossil genus does not imply closer relationship, contrary to extant taxa. Moving a fossil species from one undefined genus to another is, thus, not very meaningful.

In Appendix 2, all genera to which fossil butterflies originally have been assigned are listed, with their type species.

Fossils described or identified to species level

Since all relevant literature prior to 1875 has been dealt with extensively by Scudder (1875), reference to older literature has only been made, if necessary for improvements in understanding.

It is assumed that a character state assigning a fossil to a particular taxon at the same time assigns the fossil to all more inclusive taxa even though the autapomorphies of the higher taxa may not be apparent in the fossil.

References are given to published figures. A nice, but incomplete collection of copies of published figures is given by Murata (1998).

abdita. Pamphilites abdita **Scudder, 1875**

Hesperiidae: Hesperiinae.

France, Bouches-du-Rhône, Aix-en-Provence; Chattian–Aquitanian, Late Oligocene–early Miocene.

Depositories: MVMF (holotype lost); MNHN (neotype: IPM B-24308).

Published figures: Scudder (1875: Pl. III, Figs. 14, 17, 18); Leestmans (1983: Figs 11, 12); Nel & Nel (1986: Fig. 1a-b, Pl. I Fig. 1).

One forewing only. All veins originate from the cell, showing attribution of the fossil to the Hesperiidae; the character recurs in a few subordinate taxa in other superfamilies, but associated with different wing shape. Origin of M2 closer to M3 than to M1, within the Hesperiidae a unique but non-universal character of the Hesperiinae (Ackery *et al*. 1999). Wing shape and spotting agree with this subfamily.

Scudder thought it probable that the fossil wing belonged to a female, apparently only because he found a resemblance with *Pansydia mesogramma* Latreille (now in *Atalopedes*), a species of the Greater Antilles in which the male has a stigma. The fossil wing lacks any trace of a stigma, but so do the males of many Hesperiinae. Scudder also found a resemblance with *Carystus lucasii* (Fabricius), now *Turesis lucas* (Fabricius), a South American species. Therefore, he decided a South American relationship for this European fossil. Scudder remarked that R4 terminated on the termen close to the apex. I have not seen this condition in any Hesperiidae, R4 always terminating on the costa just or well before the apex.

The type of the fossil species 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 Hesperiinae species in the Old World and New World, so that a South American affinity of the fossil species is not obvious. If used for calibration, the fossil should be used as an estimated minimum age for the root of Hesperiinae.

alexae. Dynamine alexae **Peñalver & Grimaldi, 2006**

Nymphalidae: Biblidinae.

Dominican Republic, Cordillera Septentrional between Santago and Puerto Plata, Dominican Amber; Aquitanian, early Miocene.

Depository: AMNH (holotype, DR-18-2).

Published figures: Peñalver & Grimaldi (2006: Figs 3–5).

Most of the left wings with the color pattern still partly preserved, abdomen with male genitalia and distal part of mid- and hind legs. The allocation of the fossil to the extant genus *Dynamine* (Nymphalidae, Biblidinae) is based on the striking wing pattern, the dark brown abdomen with a white underside, and the rounded outer margin of the hindwing without expansions or tails. It is similar to the extant genus *Lucinia*, that however has larger wing ocelli and the margin of the hindwing is not rounded. No further structural reasons for the allocation of the fossil are given. Unfortunately, the apomorphy of Biblidinae (the hypandrium) is not mentioned or discussed in Peñalver & Grimaldi (2006), although they extensively discuss the genitalia that are adjacent to the hypandrium (cf. Freitas & Brown 2004). This is regrettable since wing pattern is more likely attributable to convergence and mimicry than to structural characters. This issue is exemplified by the remark by Peñalver & Grimaldi (2006) that a similar pattern is found in *Lucinia*. In the expansive analysis of Nymphalidae by Wahlberg *et al*. (2009), the subfamily is split into two monophyletic groups. In Wahlberg *et al*. (2009) *Dynamine* and *Lucinia* are in the same group, but distant from each other, with *Dynamine* being the first offshoot of the group (of which 18 genera have been included), while *Lucinia* is five divergence events later nearer to the crown. These relationships suggest that their similarity is either due to convergence, or alternatively to a symplesiomorphy. In the absence of structural arguments, and if the fossil is used for calibration, then it should be placed near the root of the Biblidinae. This is precisely where Wahlberg *et* *al*. (2009) put the calibration point. However, they put a minimum date on this point of 20 Ma. According to Iturralde-Vinent & MacPhee (1996), the age of Dominican amber is 15–20 Ma. By choosing the higher age, the derived divergence estimate may be 33 % too high, if 15 Ma would be the correct age for the amber.

amerindica. Vanessa amerindica **Miller & Brown, 1989**

Fig. 5

Nymphalidae: Nymphalinae; Nymphalini.

USA, Colorado, Florissant; late Priabonian, late Eocene.

Depository: FFNM (holotype: FLFO-108), FMUF (CHT: UF21999; PT UF22000).

Published figures: Emmel *et al*. (1992: Figs 1/12 and opp. title page); Miller & Brown (1989: Figs. 1–5); Murata (1998: Figs 53–55).

Two specimens, both ventral view; one specimen fairly complete with abdomen (squashed) and four wings, having the hindwings superimposed on forewings, the other specimen consisting of the distal three-fourths of the two left wings. No antennae or proboscis present. Palp visible, third segment one-third length of second segment. Veins in forewing not basally swollen, radial formula 1, 2, 3+(4+5) (a plesiomorphous condition), cell open (internal apomorphy of Nymphalidae); hindwing with faint indication of humeral vein (but not indicated in Fig. 3 of the original description), two anal veins, cell open, an apomorphy of several nymphalid groups. Apex of forewing produced, with lobe at M1-M2. Forelegs reduced.

According to the authors the produced apex of the forewing with the characteristic lobe at M1–M2 is indicative of the genus *Vanessa* (Nymphalidea, Nymphalinae). A similar lobe can be found in several other genera of the Nymphalinae, particularly Nymphalini sensu Wahlberg *et al*. (2005b), to which *Vanessa* and genera like *Aglais*, *Nymphalis* and *Precis* belong (Wahlberg *et al*. 2009), and can be considered an autapomorphy. Miller & Brown (1989) suggest that what is left of the pattern is reminiscent of the pattern of the extant Old World species *Vanessa indica* (Herbst), but they remark that the pattern remnants are very poor and not easy to interpret since the forewings and hindwings are superimposed. Moreover, in the figures accompanying the description of the fossil, the holotype and the paratype, the spots in the apical area do not seem to be exactly alike. Even if the pattern would fully agrees with those of *V. indica*, without indication of the apomorphies in wing pattern of the genus *Vanessa*, the similarity remains superficial and does not indicate a close relationship. Moreover, in *Vanessa* the cell in the hindwing is generally closed, though the crossvein 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, and is obviously straight in the photo of the paratype, 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 behavior, is premature and highly speculative.

Vane-Wright & Hughes (2007) mentioned *Vanessa amerindica* in their extensive description and discussion of the extant *Vanessa* species, but took the opinion of Miller and Brown that the fossil is most like *Vanessa indica* at face value. In the analysis of extant species of the genus *Vanessa* by Otaki *et al*. (2006) there is no evidence that the wing design in *Vanessa indica* (or the *Vanessa indica* group sensu Otaki *et al*.) is apomorphic. Consequently, I do not see convincing evidence for placing this fossil otherwise than as a member of the Nymphalini sensu Wahlberg *et al*. (2005b). On the basis of the suggestion in the original description that the fossil belongs to the genus *Vanessa*, Wahlberg (2006), Wahlberg *et al*. (2009) and Heikkilä *et al*. (2011) have used the fossil as calibration point for the split between *Vanessa* and its sister group, while in my opinion it would have been correct on the basis of available evidence to place the fossil lower down in the tree, at the base of the Nymphalini, making the molecular clock faster, consisting of more substitutions in the same time period yielding younger divergence times. See also comments by Brower & Vane-Wright 2011.

antiqua. Lithopsyche antiqua **Butler, 1889**

Incertae sedis.

United Kingdom, England, Isle of Wight, Gurnet Bay, Bembridge Marls; late Priabonian, late Eocene.

Depository: BMNH (holotype, I.19984).

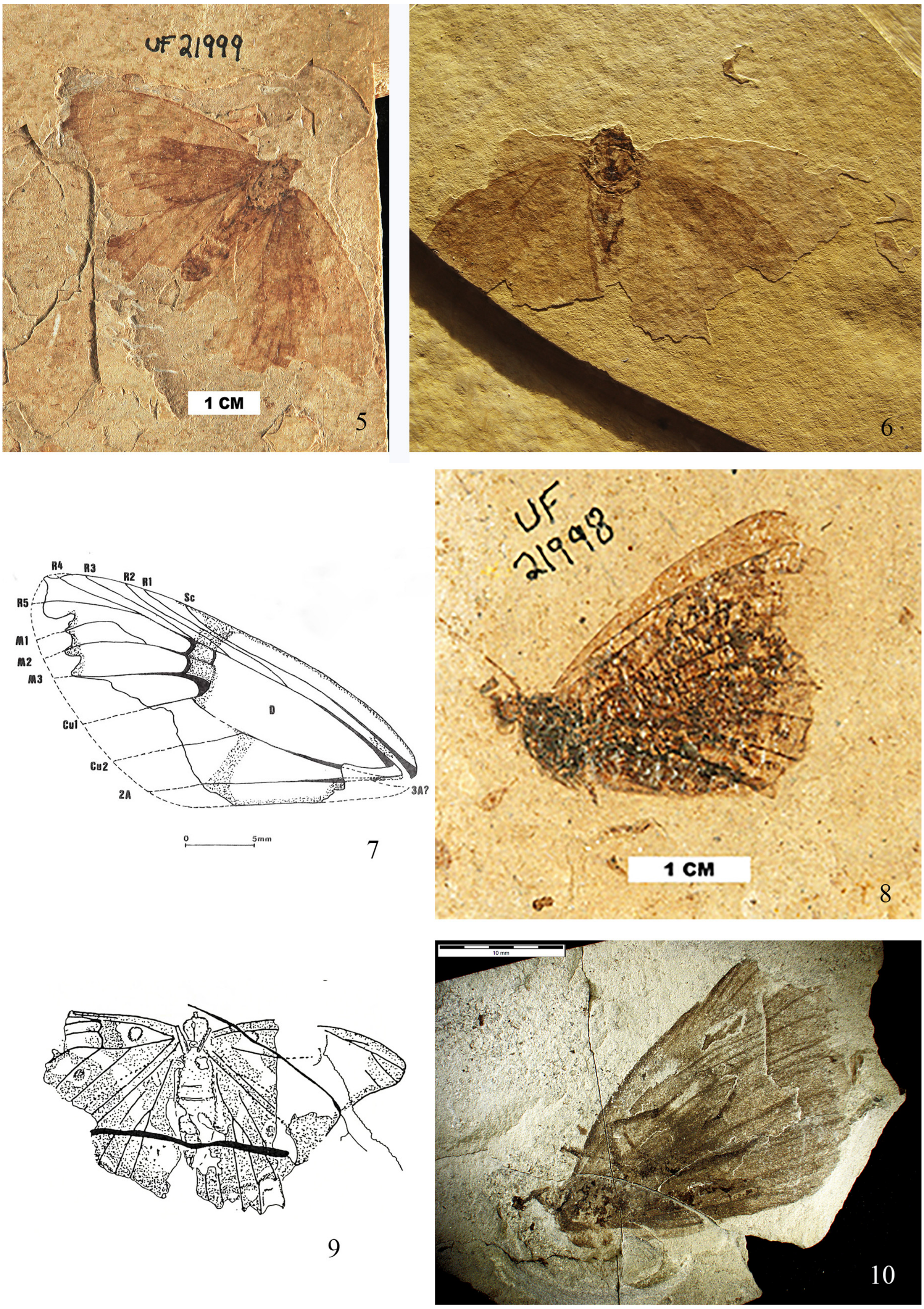


FIGURE 5. *Vanessa amerindica* Miller & Brown, 1989, holotype, collections of Invertebrate Paleontology, University of Florida. Photo by Roger Portell. Fig. 6. *Pseudoneorina coulleti* Nel & Descimon, 1984. France, Dép. Alpes-de-Haute-Provence, Dauphin, specimen in coll. M. Henrotay; photo by courtesy of M. Henrotay. Fig. 7. *Archaeolycorea ferreirai* Martins-Neto, 1989. Fig. 4A of original description. Fig. 8. *Oligodonta florissantensis* Brown, 1976, holotype, collections of Invertebrate Paleontology, University of Florida. Photo by courtesy of Akito Kawahara. Fig. 9. *Neorinella garciae* Martins-Neto, Kucera-Santos, de Moraes Vieira & de Campos Fragoso, 1993. Fig. 3A of original description. Fig. 10. *Protocoeliades kristenseni* de Jong, 2016, holotype, Zoologisk Museum, Copenhagen, Denmark. Photo by Department of Paleobiology, National Museum of Natural History, Washington DC, USA.

Published figures: Butler (1889: Pl. XXXI Figs 3, 6); Jarzembowski (1980: Figs. 44, 77).

Butler identified the fossil on the basis of traces of spots, which he considered similar to those in members of the "Euschemidae" (Geometridae). Jarzembowski (1980) redescribed the specimen (part and counterpart) and gave a more detailed description, including the venation, based on the left pair, since the right pair are superimposed and their anterior parts are missing. Body and wings preserved. Body without much detail; long palps visible; head and thorax relatively slender. Two cubital and three median veins visible, M2 slightly closer to M1 than to M3; parts of three radial veins can be seen, but apical part and much of the front margin of the forewing is missing, Cu2 branching off cell at about one-third from base. In both wings, cell probably closed. In forewing udc in missing anterior part, mdc not visible, ldc weak; 2A weakly indicated, terminating on 1A. Hindwing with long curving humeral vein, making a sharp angle with Sc+R1; humeral angle rounded with margin thickened on inner side.

According to Jarzembowski (1980) wing shape and venation are close to those of a number of extant Neotropical Riodinidae species, such as *Metacharis ptolomaeus* (Fabricius), *Mesene phareus* (Cramer) and *Anteros formosus* (Cramer). However, either M1 originates from the upper end of the cell next to R3+(4+5) or it branches off R3 before R4+5 branches off. In Riodinidae R5 tends to move distally, branching off R4 increasingly closer to the apex, disappearing altogether in a number of genera. Since much of the apex is missing, it cannot be decided which radial veins are visible, but they do not appear to branch off each other. Extrapolating the vein trajectories representing the radial veins in Jarzembowski's figure towards the cell, an arrangement could be established typical for Hesperiidae, with all veins originating from the cell separately. In extant Riodinidae the palps are not long. Moreover, in Riodinidae as well as in other butterflies Cu2 generally originates at or (well) beyond the middle of the cell. There appears to be a general evolutionary trend of the origin of Cu2 moving distally. This is apparent in Hesperiidae, where in the Coeliadinae, the first subfamily branching off, Cu2 generally originates well before the middle of the cell, while in the crown group, the Hesperiinae, it may originate well beyond the middle of the cell. Thus, the venation of the forewing is reminiscent of Hesperiidae, in particular Coeliadinae, but the long curving humeral vein in the hindwing is unknown among Hesperiidae, and what is left of the head seems too narrow for Hesperiidae. In addition, extant Hesperiidae do not have long palps.

The hindwing venation is indeterminate for an identification. The origin of Cu1 and M3 from the same spot at the lower outer corner of the cell can be found in a number of Hesperiidae, many Nymphalidae (if the cell is closed), Riodinidae and Lycaenidae. Considering all these observations, the identification of the fossil cannot be more precise than a butterfly of unknown affinities, thus of no utility for calibrating a molecular clock.

Butler (1889) thought to see so much of the spots on the wings that he reconstructed the insect (Pl. XXXI Fig. 6) as a dark brown, white-spotted geometrid-like moth with filiform antennae (no antennae visible in the fossil), but according to Jarzembowski (1980), what is left of wing design is difficult to see and indeterminate. It does not imply that Butler's (1889) observations were incorrect. Particularly in older compression fossils—especially those collected during the 1800's or before—some of the fine details, such as wing eye spots and bars or even delicate veins may have preservationally deteriorated or even lost, rendering modern observations less accurate than the old descriptions taken over 100 years ago.

***atava. Sphinx atava* Charpentier, 1843**

Nymphalidae: Nymphalinae (?).

Croatia, Radoboj; Burdigalian, early Miocene.

Depository: specimen probably lost.

Published figures: Scudder (1875: Pl. I Figs 1, 3, 7).

Only part of forewing. Judging from the detailed description by Heer (see Scudder 1875: 42) the radial formula is 1, 2, 3+(4+5) (R2 not clearly seen), with M1 originating from the cell. The cell is open (as far as can be judged). What is left of the apical part of the outer margin seems to be dentate, but the fossil is too much damaged to be certain.

Described by Charpentier (1843) as belonging to Sphingidae (Sphingoidea), but Heer (see Scudder 1875) stated that the costa was too strongly curved for a hawkmoth, and he placed it, under the name "*attavina*", in the nymphalid genus *Vanessa*. He was followed by Kirby (1871) who misspelled the name "*atovina*", but later (1877: 733) he listed it under the correct name in *Nymphalis*. Kozlov (1988) listed the fossil as belonging to the fossil genus *Nymphalites*. Scudder (1875) assigned the fossil to the genus *Eugonia*, which is closely related to *Vanessa* and *Nymphalis* (the present use of these genus names is slightly different, but not important here). The radial arrangement is a plesiomorphic condition. The open cell is an apomorphy of the Nymphalinae, but recurs in some other nymphalids. The dentate apex is suggestive of the apex in the Nymphalini (probably an apomorphy of the tribe), but the fossil is not very clear in this character. What is left of the markings (darker and lighter patches) is very similar to what is found in many Nymphalini, such as *Aglais urticae* (Linnaeus), *Nymphalis vau-album* (Schiffermüller), *Polygonia c-album* (Linnaeus), etc. This design is possibly apomorphic for the Nymphalini, as is the dentate apex. The fossil does not appear to show any apomorphic character of an extant genus. It could be used as calibration point at the root of Nymphalini, but since its age is relatively young, a calibration age will not be helpful.

bosniaskii. Doritites bosniaskii **Rebel, 1898**

Papilionidae: Parnassiinae: Luehdorfiini.

Italy, Gabbro (near Pisa), Italy; Messinian, late Miocene.

Depository: NHMW (holotype, 1898/0013/0001; counterpart holotype, 1898/0013/0002).

Published figures: Demoulin (1975: Fig 1); Murata (1998: Figs. 35, 36); Ponomarenko & Schultz (1988: Pl. 7 Fig. 1); Rebel (1898: Pl. I Figs 1–3).

Reasonably well preserved butterfly: head, thorax, abdomen, right forewing partly overlapped by right hindwing, basal parts of left wings, all seen from the underside. Forewing radial formula: 1, 2, 3+(4+5). The posterior margin of the cell is reconstructed as quadrifid, a papilionid autapomorphy. A cubital spur (also a papilionid autapomorphy) is not apparent. Further apomorphies of the Papilionidae, such as the second anal vein on the forewing running to the dorsum, and the single anal vein on the hindwing, are not apparent in the fossil. Rebel (1898: 736) remarked: "Die länglichen Hinterflügel zeigen, wie in der Gattung *Parnassius* Latr., einen stark ausgeschnittenen Innenrandtheil [...]" ("As in the genus *Parnassius* Latr., the oblong hindwings have a dorsum that strongly curves inwards […]"), but the fossil is not decisive here (see also Zeuner 1961). At the tip of the abdomen a sphragis is visible, indicating that the fossil is a fertilized female (or at least that it has mated). A sphragis is found in members of the Parnassiinae and some Papilioninae. It could, at most, be an apomorphy at the family level and is plesiomorphic within the subfamilies. Probably as a convergent development, a sphragis also can be found in some Nymphalidae, such as the genus *Actinote* (see Paluch *et al*. 2003). With its rounded and untailed wings the fossil is similar to species of the genera *Parnassius* and *Archon* of the subfamily Parnassiinae. Monophyly of the Parnassinae is only weakly based on characters that are not visible in the fossil (Ackery *et al*. 1999). Yet, the similarity with species in this subfamily is so striking, that it most probably belongs here. On the basis of recent analyses based on mitochondrial DNA (Omoto *et al*. 2004) and mitochondrial and nuclear DNA as well as morphology (Nazari *et al*. 2007), three monophyletic groups can be recognized in the subfamily, that were given tribal rank by Nazari *et al*. (2007) as follows: Parnassiini+(Luehdorfiini+Zerynthiini). In the fossil the precostal (=humeral) vein on the hindwing is simple. This is found in Luehdorfiini and Zerynthiini, while in Parnassiini this vein is forked. The unforked condition is supposed to be apomorphic with respect to the forked condition by Hancock (1983), who based his conclusions on morphological characters only. According to modern analyses based on DNA (Zakharov *et al*. 2004) or on DNA and morphological characters (Simonsen *et al*. 2011) the relationship of the subfamilies of the Papilionidae is Baroniinae+(Parnassiinae+Papilioninae), although Nazari *et al*. (2007), who also used molecular as well as morphological data found a sister group relationship between Baroniinae and Parnassiinae. A forked precostal vein is found in Baroniinae, part of the Parnassiinae (Parnassiini) and in most of the Papilioninae. In Pieridae the condition is unforked, if present; in Nymphalidae both conditions occur, in Riodinidae the precostal vein is unforked, in Lycaenidae generally absent. Such a distribution makes it difficult to attach much value to this character. If the unforked condition is apomorphic within the Papilionidae, it evolved in Parnassiini and Papilioninae, and it evolved several times in distantly related groups of Nymphalidae. If so, the simple condition of the precostal vein in *Doritites bosniaskii* is a plesiomorphy and need not point to a close relationship with Zerynthiini and Luehdorfiini, but does not contradict it either.

The forewing has a dark outer border, which according to Rebel (1898: 737) was probably hyaline, but this idea was apparently prompted by the assumption that the fossil was in the direct ancestry of *Parnassius*. Further, there are four bands, one subapical between cell and apex and extending from costa to halfway between M1 and M2, one at the end of the cell, one across the central part of the cell, and one more basally in the cell. Elements of these markings can be found throughout the Parnassiinae and in some Papilioninae as well (for instance, *Iphiclides*, some *Papilio* species), though the exact place may differ a little. It is considered to be part of the original papilionid design (Schwanwitsch 1943), and the fact that it resembles for instance the markings of *Parnassius delphius* Eversmann (cf. Rebel 1898) cannot be considered evidence of close relationship with the latter. The hindwing shows a dark outer border of which the proximal edge is less well defined than in the forewing, and a dark oblique band over the discocellular veins continuing to the costa. In Parnassiinae a similar oblique band is only found in *Luehdorfia* though elements of such a band can be found in *Sericinus* (female) and *Hypermnestra* (underside), and less clearly, in *Allancastria* and *Zerynthia*. Some elements of the band, namely a bar or irregular spot over the discocellular veins and a spot on the costa, are probably plesiomorphic within the Parnassiinae. In that case, the well-defined band of *Doritites* and *Luehdorfia* could well be synapomorphic.

Rebel (1898) thought the fossil to be closely related to the genus *Dorites* (now *Archon*), hence the name *Doritites*. Munroe (1961) assigned the fossil to *Luehdorfia*, as did Bryk (1913) half a century earlier. In view of the discussion above, a relationship of the fossil with the tribe Luehdorfiini (consisting of the genera *Archon* and *Luehdorfia*) seems supported by the evidence. Hancock (1983) considered *Doritites* an offshoot of the *Allancastria*/*Zerynthia* ancestral line (i.e. Zerynthiini), but did not give supporting characters. Nazari *et al*. (2007) included *Doritites* in their analysis, where it ended as sister taxon of *Archon*. At this position they used it as calibration point. As discussed under *Praepapilio colorado*, such an inclusion in the analysis must be rejected. If used for calibration purposes, the fossil should be placed at the ancestral line of the Luehdorfiini, a closer relationship with *Archon* not being supported by evidence.

The colours and hindwing tail of *Doritites* depicted by Bryk (1914: Pl. 6 Fig. 46) were invented by him to make the relationship to *Luehdorfia* seems more plausible. Later (Bryk 1934: 112) he wrote: “[...] ob der abweichende Praecostalsporn des Hinterflügels, der einfach distal gekrümmt und nicht 2ästig ist, tatsächlich so gebaut war oder unrichtig rekonstruiert wurde, sei dahingestellt.” ("[…] whether the deviating precostal thorn of the hindwing really was simply curved and not branched, or was reconstructed incorrectly, remains undecided.").

References with regard to this fossil up to 1934 can be found in Bryk (1934). A single paper may be mentioned here, that of Turati (1918). This author considered *Doritites bosnaskii* the ancestor of two subspecies of different *Parnassius* species: *apollo pumilus* Stichel and *mnemosyne calabricus* Turati. More recent opinions can be found in Verity (1947) who, without much comment, assigns the fossil to “Zerynthiinae-Lühdorfiidi”, and in Demoulin (1975) who followed Bryk's (1914) suggestion. With or without valid arguments, recent authors are thus unanimous in assigning the fossil to the Palaearctic tribes Zerynthiini+Luehdorfiini.

Larsen’s (1974: 34) remark that “*Parnassius*-like butterflies, close to *Archon apollinus*, have been found in Baltic Amber” and uncritically quoted by Shields (1976) must be based on a misunderstanding. Larsson (1978), while dealing with all insects in Baltic Amber, does not mention any butterfly. Larsen’s remark must refer to *D. bosniaskii* or to *Thaites ruminiana*, the only *Parnassius*-like fossil butterflies known, but not from amber.

With two other papilionid fossils, this fossil was used for calibration by Condamine *et al.* (2012), see discussion under *Praepapilio colorado*.

candiope. Charaxes candiope **(Godart, 1824)**

Nymphalidae: Charaxinae.

Pleistocene copal from East Africa (Zanzibar), but see the comments below.

Copal is half-fossilized resin, an intermediate stage of polymerization and hardening.

Depository: unknown.

Published figures: A picture of the fossil has not been published. Good pictures of the extant species can be found in many books on African butterflies.

This specimen was listed by Skalski (1976) without further information. It is a widespread extant species, occurring over most of sub-Saharan Africa. It is highly remarkable that dripping resin could trap a member of this genus of strong and fast-flying species, unless it was already dead or crippled.

The fossil is listed by Sohn *et al*. (2012) as originating from "Tanzania: Zanzibar Island". However, as explained by Evers (1907), the so-called Zanzibar-Copal does not originate from the island, but from the costal area of Tanzania between Bagamoyo to Lindi. The name "Zanzibar-Copal" may refer to the time when there was a sultanate of Zanzibar that covered the island as well as a large part of present Tanzania.

According to Evers (1907), the Zanzibar-Copal is only two- to three thousand years old. It is too young to be of interest for calibration purposes, and since there is no way to check Skalski's record, it seems better to dismiss its relevance.

***charon. Jupiteria charon* Scudder, 1889.**

Nymphalidae: Nymphalinae.

USA, Colorado, Florissant; late Priabonian, late Eocene.

Depository: USNM; originally it was in the private collection R.D. Lacoe, Pittston, Pennsylvania, USA (holotype, 2100), but the owner died soon after the American Civil War.

Published figures: Scudder (1889: Pl. LII, Figs 14, 15); Scudder's Fig. 15 was copied by Emmel *et al.* (1992: Fig. 1/7).

Wings reasonably well preserved, seen from above, forewings largely overlapping hindwings, apical parts of forewing missing; head, thorax and abdomen present; markings hardly present at all, a few light spots along costa on forewing and hindwing. Cells of forewing and hindwing open (or at least, discocellular veins too weak to have left traces in the fossil). This places the fossil in Nymphalidae. Open cells are found in many Nymphalinae (in which subfamily Emmel *et al.* 1992, placed the fossil), as well as in some members of other subfamilies (Ackery *et al.* 1999). Radial formula 1, 2+(3+(4+5)), with M1 originating halfway between R1 and R2. Usually R1 and R2 are free in Nymphalinae. A stalked R2, however, (by basad movement of M1) occurs in several groups, and an arrangement as in the fossil is common in what was called the “Melitaeen-Gruppe” by Schatz & Röber (1892). There is a remarkable similarity between the venation of *Jupiteria charon*, the Palaearctic genus *Melitaea* and the Mexican species *Chlosyne ehrenbergii* (Hübner), which by the way is unspotted. How far, however, the similarity is due to synapomorphy cannot be decided at the moment, but for the time being it appears safe to assign the fossil to the Nymphalinae. Scudder (1889) could not find much similarity with any extant species and he supposed the fossil to be most closely related to the fossil species *Lithopsyche styx* Scudder and *Prodryas persephone* Scudder. I see, however, no phylogenetic evidence for this opinion. If used as a calibration point it should be at the root of the Nymphalinae.

***colorado. Praepapilio colorado* Durden & Rose, 1978**

Papilionidae.

USA, Colorado, Ray Dome, Rio Blanco Co.; early Lutetian, middle Eocene.

Depository: private collection Hugh Rose, New Hampshire, USA (holotype, 1).

Published figures: Durden & Rose (1978: Figs 1, 6A–B); Murata (1998: Figs 1, 2, 5).

Rather well preserved, seen from above, with wings spread. Length of forewing 37 mm. Two papilionid autapomorphies are present, both in the forewing: crossvein Cu-1A (Durden & Rose: Cu-V; Miller 1987: basal spur) present, and 2A (Durden & Rose: V3) terminates on dorsum. In the hindwing there are two anal veins, a primitive condition, which in the Papilionidae is found in *Baronia* (Baroniinae) only. The posterior margin of the forewing cell is strongly trifid, a plesiomorphic condition not found in extant Papilionidae. In the forewing CuP seems to be present (interpreted by Durden & Rose as a sclerotized crease), a primitive character not found in other Papilionoidea, although the course of the lost vein can be visible in extant Hesperiidae by separate spots in the upper and lower part of the area between CuA2 and 1A+2A. Durden & Rose also interpreted a possible crease in the hindwing as CuP, but this seems unlikely, since it seems to originate from the base of 1A+2A, and it may be an artefact. Contrary to what is found in Papilioninae, there are only four radial branches in the forewing (formula: 1, 2, 3+5 (according to Miller 1987, R4 is missing); R2 originates at upper corner of cell. *Baronia* also has a 4-branched radius in the forewing, but so do *Parnassius* and *Hypermnestra*, as well as species of Pieridae (where even more radial veins may be lost), Lycaenidae, Riodinidae and Nymphalidae, suggesting that the loss of a radial branch occurred more than once in the evolution of the butterflies. Therefore, this character state in *Praepapilio* cannot be seen as a measure of close affinity with *Baronia*. According to Miller (1987) the crossvein Cu-1A is an apomorphy of the subfamily Papilioninae. Durden & Rose (1978) state that the patagia have a narrow elongate sclerotization. This is an apomorphy of Baroniinae (Ackery *et al*. 1999), but these authors indicate that the sclerotization is variable in butterflies, although generally not so much reduced as in *Baronia*. It is unlikely that this character is well visible in the fossil. It is even more unlikely that Durden & Rose have actually seen a narrow sclerotic band uniting the cervical sclerites beneath the neck, as they state in the list of characters agreeing with the Papilionidae, in a fossil that is seen from above.

The remark by Durden & Rose (1978: 6) that "Based on wing shape, abdominal dimensions preserved as deformation of matrix, and position of abdominal margin of hindwing, this specimens is a female", must be considered speculative, and their remark (Durden & Rose 1978: 8), based on a single specimen, that "Range of individual variation within sex, between sexes, and within species may be comparable to that found in the modern *Baronia brevicornis* …" lacks evidence.

Miller's (1987) remark that "the discovery of *Praepapilio* confirms that genera within the Papilionidae are at least 48 million years old", is not particularly meaningful, since the recognition of a supraspecific taxon is subjective and all extant genera could well be younger. Apart from *Praepapilio* many other genera may have existed that presently no longer occur, so why would extant genera be of such antiquity? The discovery of the fossil does confirm that some of the apomorphies of the Papilionidae, Baroniinae and Papilioninae are at least the age of the fossil.

The genus *Praepapilio* and the subfamily Praepapilioninae, erected by Durden & Rose (1978) for this species and its supposed fossil congener *P. gracilis* (see below), are not based on autapomorphic character states, but on the absence of apomorphies of other Papilionidae. In recent analyses (e.g. Zakharov *et al*. 2004; Simonsen *et al*. 2011) the extant Papilionidae are subdivided in Baroniinae, Parnassiinae and Papilioninae, which are interrelated as follows: Baroniinae+(Parnassiinae+Papilioninae). (The Baroniinae is monotypic, consisting solely of *Baronia brevicornis* Salvin, 1893.) An attempt to find the taxonomic position of *Praepapilio* in the phylogeny of the Papilionidae is hampered by the fact that only venational characters of the fossil are helpful. On the basis of the trifid condition of the posterior margin of the forewing cell *Praepapilio* is more primitive than the extant Papilionidae. The primitive condition agrees with the apparent presence of (a remnant of) CuP in the forewing. Moreover, it shares with *Baronia* another plesiomorphic trait, the presence of two anal veins in the hindwing. The the basal spur in the forewing is a character only found in Papilionidae, but it is absent in Baroniinae and many Parnassiinae as well as in the genus *Teniopalpus* of the Papilioninae (Ackery et al. 1999), indicating that it was probably lost several times. Alternatively, it could quite well be a remnant of the otherwise lost CuP, and without further evidence its presence is no criterion for close relationship within Papilionidae. Summing up this evidence, if we want to use *Praepapilio* as a calibration point, it is best placed at the root of the Papilionidae and not higher up.

Placing *Praepapilio* at the stem node of Parnassiinae+Papilioninae, Simonsen *et al.* (2011) found an estimated time of origin of the Papilionidae at 68 (53–87) Ma. Nazari *et al*. (2007) included the fossil as well as two other fossil Papilionidae, in their analysis of extant Papilionidae, making use of morphological and molecular characters, even though the fossils obviously lacked most characters. In this analysis *Praepapilio* turned up as sister to the genus *Papilio*. Using the fossils as well as some other information for calibration, Nazari *et al*. (2007) found an estimated age for the Papilionidae of c. 100 million years, strongly contrasting with the age as found by Simonsen *et al*. (2011) on the basis of a more realistic position of *Praepapilio*. The reason for this large difference is aptly discussed by Simonsen *et al.* (2011). Using *Praepapilio* as well as *Thaites ruminiana* and *Doritites bosnaskii* for calibration, Condamine *et al*. (2012) estimated the earliest split in the papilionid lineage at about 52 Ma, agreeing with an age for the family not very different from Simonsen's *et al*. (2011) conclusion.

corbieri. Lethe (?) corbieri **Nel, Nel & Balme, 1993.**

Nymphalidae: Satyrinae (subdivisions not yet generally agreed upon).

France, Dép. de Vaucluse, Céreste; Rupelian, early Oligocene.

Depository: holotype, Musée du Parc Naturel Régional du Lubéron, Apt, Vaucluse, France.

Published figures: Nel, Nel & Balme (1993: Figs. 1–3); ? Pfretzschner (1998: Figs. 1–3).

A nicely preserved specimen, probably female. Antennae tricarinate (autapomorphy of Nymphalidae, cf. Ackery et al. 1999), club weakly developed. Eyes hairy. Forelegs reduced (as in all Nymphalidae and males of most Lycaenidae). Forewing with vein 2A missing; radial formula 1, 2, 3+(4+5); R-branches and M1 originating very closely together from upper corner of cell; cell closed, about half as long as costa; Sc and 2A are weakly but distinctly swollen at their base; outer margin indented between M3 and Cu1 (or apically produced); prominent white-centred eye-spot between M1 and M2, and a small dark dot directly beneath it. Hindwing venation without special characters; cell closed; veins M3 and Cu1 originating from the same point (as in many Nymphalidae); outer margin indented between M2 and M3; in the original description it is interpreted as a slight extension at the end of vein M3 reminiscent of a rudimentary tail. Rather well preserved pattern of eye-spots and a submarginal line on forewing and hindwing.

A swollen base of Sc and 2A in the forewing is an apomorphy of Satyrinae. It is, however, not universal, and absent in genera like *Melanitis* and *Lethe* (Ackery *et al*. 1999; see also below). Moreover, a swollen base of Sc is also found in various other nymphalid genera, as mentioned below, under *Satyrites reynesii*, but in that case the forewing cell is open, or practically so. The eyespot between M1 and M2 also is widespread but not universal in Satyrinae.

The authors discussed the fossil at length and compared it with the information in the monograph of Miller (1968). They arrived at the conclusion that it most probably belongs to the “groupe de *Lethe*”, at present in the tribe Satyrini. Since they could not identify the fossil more precisely, "nous nous contenterons de le placer dans le genre *Lethe sensu lato*" ("we must be satisfied with placing it in the genus …"), as an indication that the fossil belongs to the group of genera considered closely related to *Lethe* by Miller (1968). In their nomenclature they tried to express this by naming the fossil "*Lethe (?) corbieri n.sp*." However, the "groupe de *Lethe*", apparently the same as what was called "*Lethe*-series, *sensu stricto*" by Miller (1968), contains 26 nominal genera that nowadays are divided among at least two tribes (Satyrini and Elymniini) in the classification followed by the Natural History Museum, London, in their catalogue of butterflies and moths of the world (http://www.nhm.ac.uk/our-science/data/butmoth/), which is based on the spreadsheet of Lamas_Genera_041108.xls. Moreover, the use of the genus name, even with a question mark, suggests a closer relationship than may be real. In extant *Lethe* there are no basally swollen veins in the forewing (Ackery *et al*. 1999; Schatz & Röber 1892: Pl. 33); at most, Sc is thicker in its proximal part than the radius, or fused with the proximal part of the radius to a thicker vein (see, e.g., Bascombe *et al*. 1999, Fig. 9.10). It is uncertain if such a subtle difference is clearly visible in a fossil.

Peña & Wahlberg (2008) used the fossil for calibrating the molecular clock of their phylogenetic tree of Satyrinae, placing it at the point of divergence of *Lethe* and *Neope*, the only two genera of Miller's (1968) "*Lethe*-series, *sensu stricto*" included in their analysis. Wahlberg *et al.* (2009) included more genera of this group in their analysis of the Nymphalidae. *Lethe* ended up as sister to the genera *Satyrodes* and *Enodia* combined; together they were sister to the genus *Rhaphicera*, which in Miller's (1968) study was closer to the "*Pararge*-series", and the four genera together were sister to *Neope*. In this study the fossil was used to constrain the split between *Lethe* and its sister group (*Satyrodes*+*Enodia*) to the age of the fossil (supposed to be 25 Ma). This is not the same calibration point as in Peña & Wahlberg (2008). Supposing the relationship as found in Wahlberg *et al*. (2009) is correct, the calibration point in Peña & Wahlberg (2008) is too low down in the tree. Since the number of substitutions since the split between *Neope* and its sister group must have been greater than since the split of *Lethe* and its sister group, the substitution rate was higher, consisting of more substitutions over the same period), favoring the calibration point of Peña & Wahlberg (2008) rather than with the calibration point of Wahlberg *et al*. (2009). A higher substitution rate leads to lower divergence time estimates. If all 10 genera of the subtribe Lethina (Wahlberg & Peña 2015) had been included in the analysis, the outcome may have again been different. Whether in this case the difference would be significant, remains to be seen. I just draw attention to a) the importance of finding the correct position of the fossil on the tree, and b) the large impact of the tree itself, for making reliable estimates of divergence times. Since there is still so much uncertainty about the phylogeny of the subfamily and the exact position of the fossil on the tree is difficult to ascertain, this fossil can, for the time being, only be used as minimum age calibration point at the root of the Satyrinae, based on similarities rather apomorphies.

Pfretzschner (1998) recorded a partly damaged forewing from Céreste as belonging to the same taxon. He again described (and figured) the basally swollen Sc and 2A, and the eyespot between M1 and M2 in the forewing. Since the length of the cell (as far as can be deduced from what is visible of the veins, and extrapolating the front margin and termen to the probable position of the apex) is *ca.* 40 % of the length of the wing), whereas it is about half the length of the wing in *Lethe (?) corbieri*, it could well be the remnant of a different taxon. According to Pfretzschner (1998) the wing design and the uniform pigmentation of the wing surface are identical to *Lethe (?) corbieri*; but since the fossil is so fragmentary, and the external similarity of many extant satyrine taxa can be confusing, identification of this fossil with *Lethe (?) corbieri* seems premature. See also the discussion on the plasticity of wing pattern under *Neorinopsis sepulta* (Boisduval). Moreover, in the satyrine tribes Brassolini, Morphini and Amathusiini, the eyespot of the forewing may be present on the underside only, and since the thin chitinous wing surface may be completely lost in the fossil and only the melanin may be preserved (see Pfretzschner 1998 for chemical background; see also Labandeira *et al*. 2016 for detection of melanin-bearing eyespots in much older insects), it cannot be decided whether the eyespot in the living insect was on the upperside or underside of the wing.

***coulleti. Pseudoneorina coulleti* Nel & Descimon, 1984**

Fig. 6.

Nymphalidae: Satyrinae (subdivisions not yet generally agreed upon).

France, Dép. Alpes-de-Haute-Provence, Céreste and Dauphin; Rupelian (= "Stampien"), early Oligocene.

Depositories: holotype from Céreste in Collection Nel, La Ciotat, Bouches-du-Rhône, France (nr 2486); paratype from Céreste in Collection Coullet, Barrème, Alpes-de-Haute-Provence, France; additional specimen from Dauphin in Collection Michel Henrotay (Liège, Belgium).

Published figures: Henrotay (1986); Murata (1998: Figs 7, 8); Nel & Descimon (1984: Figs 1–5); Nel & Nel (1986: Fig. 2e).

Three specimens, in varying states of preservation. Eyes naked. Forewing without vein 2A; radial formula 1, 2, 3+(4+5); stalk of R3-R5 and M1 originating from same spot at upper corner of cell; M2 at its base much closer to M1 than to M3; cell closed; base of Cu lightly swollen; rounded spot between M1 and M2; darker area between base, cubitus, M3 and hind margin, extending from base to about two-thirds towards termen; outer margin probably straight. Hindwing with Sc+R1 arising far from base: distance from base to Sc 3.6 mm, from Sc to Rs 4.5 mm; cell closed; round dark spot between Cu1 and Cu2 (according to the original description and in their photograph Figure 2A and in the reconstruction in Figure 5; in the description, it is given as between Cu1 and M3); outer margin possibly extended tail-like at the end of M3 (as it is in extant *Neorina*; in fig. 5 at the end of Cu1), but since the relevant part of the wing is absent in the fossil, this is speculative.

In their well-documented discussion the authors conclude that the fossil is close to the recent genus *Neorina* (Nymphalidae, Satyrinae), but differs in the origin of Sc in the hindwing being further from base than in any recent satyrine butterfly: in *Pseudoneorina* Sc originates at 44.4% of distance from base to Rs, further than in any extant species, in *Neorina* it originates at almost 22% of this distance. Apparently this feature was an autapomorphic character that was lost with the extinction of the taxon.

The venational characters of the fossil as well as the position of the rounded spots (in extant satyrines eyespots), although agreeing with extant *Neorina*, can be found in other extant genera as well, e.g. *Zophoessa* (considered a subjective synonym of *Lethe* [subtribe Lethina of Satyrini] by Wahlberg & Peña 2015), but to belong to another tribe, Elymniini, in the classification accepted at the Natural History Museum, London, www.nhm.ac.uk/our-science/data/butmoth/, which follows the database Lamas_Genera_04ii08.xls. Wahlberg & Peña (2015) classify *Pseudoneorina* within the subtribe Lethina, and *Neorina* as belonging to another tribe, Zetherini. Earlier *Neorina* was also placed outside Satyrini, as sister taxon to *Penthema*, in a clade that is sister taxon to Amathusiini (Wahlberg *et al*. 2009). According to Miller (1968) *Neorina* belongs to the Lethini, in which it, with its closest relatives, is mainly diagnosed by possessing naked eyes, a character found frequently throughout the butterflies and not very indicative of relationship. As long as there are no apomorphies known that unambiguously support relationships, I would hesitate to classify the fossil either as belonging to Satyrini or to Zetherini (see also Figures 18–20 under *Neorinopsis sepulta*, for the still unsettled interrelationhips among the tribes of Satyrinae).

A fossil from another locality about 18 km to the east, Dauphin (Dép. Alpes-de-Haute-Provence), Lower Oligocene, Stampien (= Rupelian), ca. 30 Ma, was figured but not named by Henrotay (1986). It was recognized as belonging to the same taxon by André Nel, co-author of the name (pers. comm. Henrotay, 16 Dec. 2015).

crataegi. Aporia crataegi fossilis Kernbach, 1967

Pieridae.

Germany, Hesse, Brandenburg, Willershausen; Plazencian, late Pliocene.

Depository: GPUG (one specimen, 596-12[13589]).

Published figures: Branscheid (1968: Figs 1, 2); Branscheid (1969: Figs 2–5); Kernbach (1967: Fig. 12). Numerous figures of the extant species in identification guides for European butterflies.

Kernbach (1967) recorded one forewing and two hindwings from the clay of Willershausen as belonging to this extant Palaearctic species. The fossils are not described apart from the observation that the dark stripe between veins 1A+2A and CuA2 in the hindwing is visible, and that the specimens were apparently larger in the Pliocene. In the accompanying photo of the hindwing the venation is rather similar to that of *A. crataegi* (Linnaeus), except for Sc+R1 being much less strongly curved and the cell being distinctly shorter than in the recent species. Actually it is not clear what is typical about the *Aporia* hindwing venation, a similar venation also being found in the widespread recent genus *Pieris* and some other pierid genera. Also the stripe mentioned, which actually indicates the lost CuP, is not restricted to *Aporia*. Kernbach described the fossil as *Aporia crataegi fossilis*, rather prematurely since it is not even certain that the fossil is conspecific with the extant species.

Apparently, the forewing, mentioned but not described by Kernbach (1967) was reported by Branscheid (1968). It shows the pierid apomorphy of M1 branching off the common stem of R4 and R5 (R3 is considered being lost by various authors). Sc is reconstructed as ending on the costa just beyond the end of the cell, but this may be a misinterpretation, even in fresh *Aporia* specimens it may be difficult to see where exactly Sc ends on the costa, this vein at its distal end running close to R1. Since the wing is incomplete, the general shape cannot be made out and its identification as belonging to *Aporia* is not without doubt.

Further wings from the same locality were described by Branscheid (1969) as most probably belonging to *Aporia*, although he was not sure about the (number of) species, since he found marked differences in size. For calibration purposes these fossils are hardly of interest. Not only are they rather young, but since they cannot reliably be identified even to the subfamily level, we could only use them as calibration point at the root of the Pieridae. (For a recent study of the phylogeny, see Wahlberg *et al*. 2014, in which the late Pliocene appears far too recent for a divergence time.)

In view of the extreme scarcity of butterfly fossils it is remarkable that so many specimens of a single genus or maybe even species have been found in the same locality. A possible explanation could be gregarious behavior on wet spots involving so called mud puddling that can be observed in many butterflies, including *Aporia crataegi* and many other Pieridae.

crawshayi. Belenois crawshayi Butler, 1894

Pieridae: Pierinae.

Tanzania, opposite Zanzibar (African copal, see Zeuner, 1942); late Pleistocene or Holocene.

Depository: BMNH (one specimen, I.3004).

Published figures: Zeuner did not give an illustration of the (sub)fossil. Illustrations of the extant species can be found in many books on African butterflies.

Described by Butler (1894) as a recent species. A complete, well preserved male butterfly (only head missing) recorded by Zeuner (1942). It agrees entirely with the extant *Belenois crawshayi* (Pieridae, Pierinae) (distribution: Cameroon and Angola to East Africa) in size, venational pattern, coloration and shape of valva. It is not surprising to find that a recent species has been present in part of its distributional area for the last 10,000 or perhaps 100,000 years.

dramba. Voltinia dramba Hall, Robbins & Harvey, 2004

Riodinidae: Riodininae: Mesosemiini: *Voltinea*.

Dominican Republic, Cordillera Septentrional between Santiago and Puerto Plata, Dominican amber; Burdigalian, early Miocene.

Depositories: USNM (holotype); Murata coll., Kyota, Japan (paratype); Morrone coll., Torino, Italy (paratype); AMNH (one specimen, DR-18-1).

Published figures: Hall *et al*. (2004: Fig. 1); Peñalver & Grimaldi (2006: Figs 1, 2).

The fossil was described by Hall *et al*. (2004) as a member of the extant genus *Voltinia* (Riodinidae) after five female specimens "that collectively represent probably the best-preserved fossil record for any lepidopteran." An additional fossil specimen belonging to the same taxon was described by Peñalver & Grimaldi (2006). Because of the exceptionally good quality of the fossils, there is little reason to doubt its taxonomic position, the more so since Hall (2003) had published a phylogenetic reassessment based on morphology of the tribes of Riodininae, the genus *Voltinia* belongs to, and thus, characters of all related extant genera were well known and evaluated. Very recently an extensive molecular phylogenetic analysis of the family was published (Espeland *et al*. 2015) covering all subfamilies, tribes and subtribes, and 98 out of 145 described genera of the Riodinidae, including *Voltinia*. The taxonomic position of the fossil was used as one of the calibration points (placed at the common stem of *Voltinia* and *Napaea*), with an age of 15–25 Ma as given by Hall *et al*. (2004). Since the Burdigalian lasted from 20.43 Ma to 15.97 Ma, the latter (younger) age should be used for calibration. However, recent studies, soon to be published, suggest that the allocation of the fossil needs revision (Noemy Seraphim Pereira, pers. comm.), and it may be wise to postpone the use of the fossil for calibration until its position is better known.

ferreirai. Archaeolycorea ferreirai **Martins Neto, 1989**

Fig. 7.

Family incertae sedis.

Tremembé Formation, Taubaté Basin, State of São Paulo, Brasil; (Rupelian)—(Aquitanian); late Oligocene—early Miocene.

Depository: IGEO (holotype, no. 5618-I).

Published figure: Martins-Neto (1989: Fig. 4A).

Part of a forewing of which the distal area, about 1/4 of the wing surface, is missing. The reconstruction of the termen in Fig. 4A of the publication and with that, the shape of the wing, is, therefore, uncertain. The venation shows a most unusual arrangement: M1 branches off M2 shortly before the middle of the latter. In many butterfly genera (particularly in Pieridae) M1 branches off R5, but I have not yet found such an arrangement illustrated in any extant butterfly genus. It could be an incorrect interpretation of the fossil, but apart from being clear in the figure, it is also explicitly described so in the text. The remainder part of the venation is not helpful. Since it is not clear in the figure where exactly is the distal end of the discoidal cell, either R3 and R4+5 have a common stem (an arrangement commonly found in butterflies), or R3 is separate and R4 and R5 have a common stem, an unusual arrangement in butterflies, but at least found in *Papilio antimachus* Drury from the Afrotropics. In summary, the taxonomic position of this fossil is unclear and the suggestion implied by the name that it is in the ancestral line of the extant genus *Lycorea* (Nymphalidae, Danainae) is not supported by evidence.

florissantensis. Oligodonta florissantensis **Brown, 1976**

Fig. 8.

Nymphalidae: Libytheinae.

USA, Colorado, Florissant; late Priabonian, late Eocene.

Depository: FFNM (holotype).

Published figures: Brown (1976: Figs 1–3); Emmel *et al*. (1992: Fig. 1/2, and at back of color plate III); Kawahara (2013: Fig. 62).

For a good description and interpretation of the fossil, see Kawahara (2013).This author synonymized it with *Barbarothea florissanti* (see below) and placed it in the extant genus *Libytheana* (Nymphalidae), see description below. It was placed in the Pieridae by Brown (1976) (followed by Emmel *et al*. 1992), because of the unjustly supposed similarity with *Leodonta*. Subsequently, Braby *et al*. (2006) used the fossil as calibration point on the phylogenetic tree of the Pieridae as a close relative of the *Catasticta* group, if not the genus *Leodonta*.

florissanti. Barbarothea florissanti Scudder, 1892

Nymphalidae: Libytheinae.

USA, Colorado, Florissant; late Priabonian, late Eocene.

Depository: Scudders' specimen is presumed lost (Shields 1985).

Published figures: Emmel *et al*. (1992: Fig. 1/2).

Very similar to the fossil *Prolibythea vagabunda* and also placed in the subfamily Libytheinae (Nymphalidae) by Scudder (1892), followed by Emmel *et al*. (1992). Fairly well preserved. Antenna tricarinate (autapomorphy of Nymphalidae), club very gradual. Two legs visible, not reduced, possibly middle legs. Palpi, 2nd segment oblique; apical joint horizontal, only a little more than two-thirds the length of the 2nd (i.e., relatively longer than in most butterflies, but shorter than in any known member of the Libytheinae). Venation as in *Prolibythea vagabunda* Scudder that is plesiomorphic and not indicating relatedness. Hindwing relatively broad and rounded, costa concave, termen crenulate. Forewing slightly falcate. The long palpi agree with the Libytheinae, but apparently they had not yet reached the state found in extant members of the subfamily. Although the palpi of Libytheinae are relatively long, they are not unique, some other nymphalids having similarly long palpi and a similar venation as well (e.g. *Eunica*, a member of the Biblidinae). The apomorphic character states of the Libytheinae mentioned by Ackery *et al*. (1999) are not visible in the fossil, but the extension of the termen of the forewing at the end of M2 seems to occur in Libytheinae only as judged from the numerous venational diagrams in Schatz & Röber (1892). In other butterflies, if there is an extension (a tooth) it is at or just below M1. It is not clear why Scudder did not place it in *Prolibythea*, although he mentioned the similarity. See also the discussion by Kawahara (2013), who synonymized it with *Oligodonta florissantensis* and placed it in the extant genus *Libytheana* on the basis of an analysis of morphological characters. However, since apomorphies are not clear and the palpi are definitely shorter than in extant members of *Libythea* and *Libytheana*, I hesitate placing it in an extant genus and suggest that it should be placed at the stem node of the subfamily, if used for calibration purposes. See also under *Prolibythea vagabunda*.

fossilis. Pyrameis fossilis Nekrutenko, 1965

Nymphalidae: Nymphalinae.

Russia, Kraj Stavropol, Stavropol, N. Caucasus; late Miocene.

Depository: PIRAS (holotype, PIN 254/2753).

Published figures: Nekrutenko (1965: Fig. 4).

Fragment of hindwing only. Judging from Nekrutenko's figure (1965: Fig 4) the cell is open, an apomorphy found (but not exclusively) in many Nymphalinae. However, the author considered the fossil congeneric with *Vanessa atalanta* (Linnaeus), *Cynthia cardui* (Linnaeus) (considered to belong to the genus *Vanessa* now), etc. (Nymphalinae), where the cell is closed, though the cross vein may be weak. Because of some proportional similarities, he suggested a close relationship with *C. cardui*, although he admitted that the material is not complete enough for a reliable identification. He described the fossil under the "nomen conditionalis", *Pyrameis fossilis*, a term not recognized by the International Code of Zoological Nomenclature. I found different venational proportions in the species from those mentioned by Nekrutenko. The proportions may be variable and not a reliable guide for relationship. The venational arrangement as far as visible in the fossil is found in many extant nymphalines and it is of little help in establishing closer relationships. In view of the deficient useful characters in the fossil I wonder why Kozlov (1988) synonimized it with *Vanessa amerindica* Miller & Brown (see comments above).

freyeri. Pierites freyeri Heer, 1849

Papilionoidea (?).

Croatia, Radoboj; early Miocene.

Depository: material probably lost, see Sohn *et al*. (2012) under *Pontia freyeri*.

Published figures: Scudder (1875: pl II, Figs 16, 18).

Original description and figure copied by Scudder (1875). Only one forewing present. Venation, particularly in apical part, hardly visible at all. Scudder placed this fossil in the recent genus *Pontia* (Pieridae: Pierinae) on the basis of obscure markings. He was followed by Kozlov (1988). However, I agree with Zeuner (1942) in considering the condition of the fossil too poor to make any reliable observations about its relationship.

gabbroensis. Lycaenites gabbroensis Rebel, 1898

Lycaenidae.

Italy, Tuscany, Gabbro (near Pisa); late Miocene.

Depository: NHMW (holotype, 1898/0013/0005; counterpart holotype, 1898/0013/0006).

Published figures: Murata (1998: Fig. 37); Rebel (1898: Pl. I Figs 5, 7).

A very badly preserved small insect. As correctly stated by Rebel, the strongly bent subcosta (Rebel: costa) of the hindwing shows that it is a butterfly and not a broad-winged moth. For the rest of the hindwing venation is so faulty that I have little confidence in Rebel's reconstruction (Pl. I Fig. 7), which, moreover, does not agree with his habitus drawing (Pl. I Fig. 5). Because of its size (forewing length 11 mm) and absence of a precostal vein (=humeral vein) in the hindwing, Rebel assigned the fossil to the Lycaenidae. In the description it is stated that a radial fork distally of the cell is visible in the forewing and prominent in the reconstructed wing venation, although not in the drawing of the habitus of the fossil. Consequently, the fossil cannot belong to the Hesperiidae. Moreover, the head is smaller than the thorax, which in Hesperiidae is only known from the strictly American *Megathymus* group (Hesperiinae), of which the extant species are much bigger and built much more heavily. Among further extant butterflies only Pieridae, in particular *Eurema* species, can approach consideration for an assignment in view of its small size. However, in *Eurema* M1 branches off the common stem of R3+R4 (see, e.g., Jeratthitikul *et al.* 2009), while in the reconstruction of Rebel, the origin of M1 is far apart from the origin of this common stem. The conclusion that the fossil apparently belongs to the Lycaenidae, is not very helpful in terms of divergence time of the family, since older fossils of the sister group, Riodinidae, are known and even assignable to extant genera.

garciae. Neorinella garciae Martins-Neto, Kucera-Santos, de Moraes Vieira & de Campos Fragoso, 1993

Nymphalidae: Satyrinae, Elymniini.

Brazil, State of São Paulo, Taubaté Basin, Tremembé Formation; Chattian–Aquitanian, late Oligocene—early Miocene.

Depository: DGUG (holotype).

Published figures: Martins-Neto *et al.* (1993: Figs 2, 3, pls I, II); Murata (1998: Figs 9–11).

Partly visible forewings and hindwings and compressed body. In addition to wing shape and venation (partly visible) a paler colored band across forewings and hindwings is visible; there is an eyespot in the cell of the forewing, in R4-R5 (visible in the photo, not represented in the drawing), and in CuA1-CuA2 (?) of the forewing and, vaguely, in Cu1-Cu2 of the hindwing. The length of the forewing is 31.7 mm. No visible swollen bases of forewing veins. Most remarkable in the venation of the forewing is the common origin of M3 and Cu1 from the lower distal corner of the cell. Among extant Papilionoidea it is a unique autapomorphy of the satyrine genus *Elymnias* (Miller 1968). For the rest, the reconstruction of the wings (Fig. 2 in the original publication, reproduced here as Fig. 9) is hypothetical for those parts of the wings that are absent in the fossil. Moreover, in the forewing the radial branching cannot have been correctly reproduced: in Fig. 2 of the original description two radial veins branch off before the end of the cell, at which point R2 originates. One of these veins coalesces over some distance with R2 before ending on the front margin. This part of the wing is absent in the fossil.

The fossil, which has been placed in a genus of its own, is supposed (in the original publication) to be related to the extant genus *Neorina* (Nymphalidae, Satyrinae) as well as to the fossil genera *Neorinopis* (see under *sepulta*) and *Pseudoneorina* (see under *coulleti*). Apparently, this is based on similarity in wing shape and wing pattern. Realizing the variation in these characters for extant *Neorina* species as well as in related genera, these characters are unreliable indicators of relationship. A structural character like venation appears more reliable. In combination with *Neorinopsis* and *Pseudoneorina*, *Neorinella* has been classified, without comment, as belonging to the subtribe Lethina of the tribe Satyrini, while *Neorina* has been placed in the tribe Zetherini by Wahlberg & Peña (2015). This, again, must be based on wing shape and design. If we take venation as indicator of relationship, both *Neorinella* and *Neorinopsis* should be classified as Elymniini. See further the discussion under *Neorinopsis sepulta*.

gracilis. Praepapilio gracilis **Durden & Rose, 1978**

Papilionidae.

USA, Colorado, Ray Dome, Rio Blanco Co.; Lutetian, middle Eocene.

Depositories: private collection Hugh Rose, New Hampshire, USA (holotype, 2a); BHM (counterpart holotype, 2b).

Published figures: Durden & Rose (1978: Figs 2, 3 6C–D); Murata (1998: Fig. 3).

Similar to *Praepapilio colorado*, but less well preserved, large parts of the wings (e.g., the important apical part of the forewing) missing. The forewing length is smaller, estimated as 32.6 mm of which the supposed precision is noted, although the apical part of the wing is missing. Moreover, it is of more slender built than *P. colorado*. Possibly a female: the authors record a possible sphragis. Of the radial system of the forewing, only R1 and R2, and part of R3 visible. The area where R4 and possibly R5 should branch off, is missing. The terminal quarter or third of the hindwing is missing, such that the lobed shape depicted by Durden & Rose (1978) is speculative. For the rest of the wing, the venation is like *P. colorado*. Apart from size and shape, the present fossil differs from *P. colorado* in pattern, prompting Durden & Rose (1978) to describe it as a separate species.

Since the fossil is apparently closely related to *Praepapilio colorado*, and is of the same age but less well preserved, it is not important for calibration.

irenaei. Aquisextana irenaei **Théobald, 1937**

Lycaenidae (?).

France, Bouches-du-Rhône, Aix-en-Provence; Chattian–Aquitanian, late Oligocene–early Miocene.

Depository: IGMF (holotype, Ma 1).

Published figures: Théobald (1937: Figs 2, 3); Leestmans (1983: Fig. 19).

A fairly well preserved specimen, showing all wings (partly overlapping), head with appendices, thorax and abdomen. According to the original description, the fossil is seen from the underside. If correct, the legs are lost. The antennae thicken gradually towards the club. They are supposed to be inserted before the eyes. This is an impossible antennal inserting area and if the insect is really seen from the underside, the insertion of the antennae should not be seen at all. Eyes elongate-oval, hairy. No emargination at the base of the antennae (apomorphy of Lycaenidae) mentioned, but otherwise not visible in ventral view. Forewing, length 21 mm; radial formula 1, 2, 3+4, with R4 ending on the outer margin just below the apex. This radial formula is found in Pieridae (e.g. *Eurema* Hübner, [1819]) and many Lycaenidae. In most Lycaenidae R4 terminates at the apex or on the costa close to the apex, in the Pieridae and in a few Lycaenidae, such as *Curetis* Hübner, [1819], an Oriental genus. In the Liphyrinae, an Old-World subfamily [see Eliot 1973], mentioned by Théobald (1937), the arrangement is not comparable, there being five radial branches and R4 terminates on the outer margin. As remarked by Théobald (1937), *Curetis* has a heavier thorax. Moreover, *Curetis* has a very different wing shape, triangular, with a straight outer margin and rectangular tornus, contrasting with the more elongate wing of the fossil, possessing a convex outer margin and rounded tornus.

On the wings a number of small dark spots are visible. Because of these spots, the general appearance and the eyes, Théobald believes his fossil to be a lycaenid, which is not close enough to any recent genus for assignment. Therefore, he erected a new genus for the fossil. From the discussion above it may be clear that evidence for a lycaenid relationship is hardly more convincing than for a pierid relationship, except that the modest size and the small dark spots that point to Lycaenidae. For want of better evidence, we follow Théobald and list this fossil under the Lycaenidae.

***japonica*. *Hestina japonica* (C. et R. Felder, 1862)**

Nymphalidae: Apaturinae.

Japan, Tochigi Pref., Shiobara; late Pleistocene, 37,800 BP. Same locality as the fossil of *Papilio* (cf) *maacki* Ménétries, see below.

Depository: NSMT (one specimen, PA12228).

Published figures: Illustrations of the extant species can be found in many books on East Asian butterflies.

Fujiyama (1983) reported on finding of the proximal half of a left forewing of which the basal part was missing. The open forewing cell and the branching off of the median veins are quite visible, as well as white patches and streaks. Venation and wing design agree completely with those of *Hestina japonica*, an extant species widely distributed in Japan, Korea, China and Taiwan. If this wing fragment had been found in a spider web, nobody would have doubted its identity.

***karaganica*. *Vanessa karaganica* Nekrutenko, 1965**

Nymphalidae.

Russia, Kraj Stavropol, Stavropol, N. Caucasus; late Miocene.

Depository: PIRAS (holotype, PIN 254/2936a).

Published figures: Nekrutenko (1965: Figs. 2, 3).

Hindwing only, of which tornal quarter and dorsal border are missing. Cell open, a nymphaline apomorphy found, for instance, in the recent genera *Aglais*, *Inachis*, *Nymphalis*, but also in some members of other subfamilies, e.g. *Apatura* (Apaturinae), *Neptis* (Limenitidinae), etc. According to Nekrutenko, the venation is typical for *Vanessa*, and he compares the fossil with "*V. urticae* L." This species is now placed in *Aglais*; *Vanessa*, as currently understood (type species *Papilio atalanta* Linnaeus), has the hindwing cell closed. It is not clear what is typical (i.e. apomorphic) about the venation of *Vanessa* sensu Nekrutenko, and therefore I consider the assignment of the fossil to an extant genus unwarranted. Moreover, it lacks the apparently apomorphic character of a crenulate hindwing termen, commonly found in vanessoid genera.

The pattern of the wing (underside) is also visible in the fossil. It resembles that of *A. urticae*, and it is reminescent of forms of *A. urticae* bred at elevated temperatures. Nekrutenko (1965) concluded that this condition could be of paleogeographical importance. Similar patterns on the underside of the hindwing, however, are not only found in several nymphaline genera, but also in a number of satyrine genera. Since the pattern is clearly cryptic, parallel and convergent evolution may be expected. The little evidence taken together does not allow a further identification than Nymphalidae. The assignment of this fragmentary fossil to the extant genus *Aglais* by Kozlov (1988), already hinted at by Nekrutenko, lacks convincing evidence.

***kristenseni*. *Protocoeliades kristenseni* de Jong, 2016**

Fig. 10.

Hesperiidae: Coeliadinae.

Denmark, Jutland, Island of Fur; late Paleocene–early Eocene, 55 Ma.

Depository: ZMUC (holotype, part and counterpart, Danekræ DK 136).

Published figures: de Jong (2016: Figs 1–5).

For an extensive description and discussion, see the original publication.

Oldest butterfly fossil known. A rather badly preserved specimen of moderate size, total wing length estimated at 22–23 mm inclusive of the missing apex. Apparently, all radial veins in forewing unbranched, an autapomorphy of the Hesperiidae. Estimated length of the cell about 60 % of wing length. The relative cell length is variable within Hesperiidae and it does not place the fossil in a particular clade (Warren *et al.* 2009). The (reconstructed) origins of CuA1 and CuA2 indicate relationship with Coeliadinae. The origin of CuA2 at about 20 % of the cubitus from cell base to origin of M3 is universal in Coeliadinae, but also is found in Euschemoninae and several genera of Pyrginae and Eudaminae. The origin of CuA1 close to the middle of the cubitus is found in Coeliadinae only, and within this subfamily in all species of *Hasora* and some species of *Burara*. It could be a good character to use for calibration, but the phylogeny of Coeliadinae needs further attention. For the time being, if used for calibrating the molecular clock, it should be placed at the stem node of the Coeliadinae.

leuce. Apanthesis leuce Scudder, 1889

Incertae sedis.

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depository: MCZH (holotype, 16354).

Published figures: Emmel *et al*. (1992: Fig. 1/10); Scudder (1889: Pl. LII Figs. 12, 13).

One forewing only, with venation and design well preserved. Radial formula 1, 2, 3+(4+5), udc absent, M1, R3+(4+5) and mdc almost originating from the same point; ldc weak. According to Scudder, the radial branching is typical for the "tribe Vanessidi" (Nymphalidae), but I do not know what is so typical about it, except for the weak ldc. Comstock (1961: 181) observed a closer similarity to *Limenitis*, with which also the markings correspond with a uniformously brown hue with a submarginal band parallel to termen and consisting of light-coloured, slightly kidney-shaped spots, and vague spots between the band and termen in intervenal areas). Because *Limenitis* and *Anaea* share characters in the male genitalia, Comstock (1961) considered the discovery of *Apanthesis leuce* an indication of a northern origin of *Anaea*. This is, however, an unwarranted speculation. The venational arrangement could as well be plesiomorphic and is, for instance, also similar to the arrangement in the pierid genus *Eronia*. *Euronia* was considered a primitive member of the pierid tribe Pierini by Klots (1931) based on morphological grounds. Braby *et al*. (2006) concluded from a molecular analysis of the Pieridae, that *Euronia* was grouped in the *Colotis* group of genera, the first offshoot of the Pierinae. The weakness of ldc may be an argument in favor of Nymphalidae, but it remains to be seen whether in a fossil of some 35 Ma of age the weak ldc in, e.g., *Limenitis*, can be distinguished from the rather weak ldc in *Eronia*. The only reason for considering the fossil a member of the Nymphalidae is, therefore, the similarity in wing markings to some recent species, a rather weak argument. Emmel *et al*. (1992) followed Scudder's decision; they did not mention Comstock's remarks. I think it is wise to consider the fossil as without clear affinities, as long as elements of the wing design remain unstudied in a phylogenetic context.

libytheoides. Stolopsyche libytheoides Scudder, 1889

Family incertae sedis.

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depository: MCZH (holotype, no.11077).

Published figures: Scudder (1889: Pl. LIII Figs. 1–3); Emmel *et al*. (1992: Fig. 4/1); Murata (1998: Figs. 42, 43).

This specimen is poorly preserved; according to Zeuner (1961) this fossil is too poor for attempting an assignment to a particular family. Antennae with 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 lepidopteran. Forelegs long, only a little shorter than middle legs. This is a plesiomorphic character found in Papilionidae, Pieridae, Lycaenidae females, *Libythea* females, and Hesperiidae. It could place the fossil in the ancestry of any butterfly family. Since the head is small for Hesperiidae and *Libythea*, the forewing is long for Lycaenidae (ca. 25 mm), and the palps long for Papilionidae, Scudder thought the Pieridae the most likely family for the fossil. Apparently the fossil has too few characters preserved to be of any use for phylogenetic research. I cannot find any evidence supporting the claim by Emmel *et al*. (1992) that the fossil "was closer to *Pieris* than any other living genus."

Apparently, Braby *et al*. (2006) based their use of this fossil as calibration point in the phylogenetic tree of Pieridae close to the origin of *Pieris* on the unsupported assumption of Emmel *et al*. (1992) (l.c.)—an unwarranted and probably erroneous assumption.

maackii. Papilio cf. maackii Ménétries, 1859

Papilionidae: Papilioninae: Papilio (?).

Japan, Tochigi Pref., Shiobara; late Pleistocene, 37,000 BP (see Fujiyama 1983).

Depository: NSMT (one specimen, no. 7141).

Published figures: Fujiyama (1968: Fig. 1, Pl. 1 Fig. 1); illustrations of the extant species can be found in many books on East Asian butterflies.

Reported by Fujiyama (1968). A forewing only is present, of which almost half is missing. Two papilionid apomorphies present: crossvein Cu-A1 (but see above, *Venational patterns of the forewing*) and 2A terminating on dorsum. Radial formula 1, 2, 3, 4+5, R3 and the common stem of R4 and R5, both originating from the upper corner of the cell. After comparison with extant papilionine species in Japan and adjacent areas, Fujiyama concluded on the basis of overall similarity (as far as overall similarity is possible with only half a wing), but principally determined by the proportions of the cell, that the fossil falls within the variation of the extant species *Papilio maackii*. However, Fujiyama (1968) does not make clear that the fossil does not fall within the variation of other *Papilio* species as well. The identification by Fujiyama is based on comparison with the extant fauna of the region, not on apomorphies, and, thus, is questionable. In view of its relatively recent age, the fossil is not of interest for calibration purposes. *Papilio maacki* has a wide distribution in East Asia. The fossil was found in a lake deposit, which presumably formed when it was 5–5.5^{0}C colder than at present, corresponding with the last ice age.

montana. *Lethe montana* Miller, Miller & Ivie, 2012

Nymphalidae: Satyrinae.

USA, Montana, Canyon Ferry Reservoir; Rupelian, early Oligocene.

Depository: holotype, Museum of Rockies, Montana State University, Bozeman (part and counterpart, MOR No. MV-152).

Published figures: CoBabe *et al*. (2002, Fig. 4c), Miller *et al*. (2012: Figs 1–5.

The fossil consists of a well preserved part and counterpart of a forewing. In their diagnosis the authors state that "… the unbranched forewing radial veins … indicate thet this fossil is … not a member of the Hesperioidea." Rather, this should read "the branched forewing radial veins", but the conclusion is correct. Moreover, the absence from the cubital spur and vein 3A eliminates Papilionidae from consideration. The authors also eliminate Pieridae, since M1 branches off the cell, although branching of M1 off R3 is widespread in Pieridae but not universal. The remark that Riodinidae or Lycaenidae can be eliminated because the "… veins are not simple in that they do not arise from the base or from the radius or cubitus proper …", is not clear to me. The authors arrive at the conclusion that the fossil belongs to the Nymphalidae, and since the forewing cell is closed, the subcostal vein is thickened at its base and there is a prominent ocellus in M1-M2, assignment to the Satyrinae seems obvious. The only problem is, that the basal part of the wing with the swelling of the subcostal vein, as represented in their reconstruction in Fig. 5, is absent from the fossil (Fig. 1) and from the interpretation of the fossil in Fig. 2.

See also the discussion under *Lethe* (?) *corbieri* on the absence of a basal swelling in *Lethe*. There is no convincing evidence for treating *Lethe montana* differently than *Lethe* (?) *corbieri* as far as its use as calibration point concerns. They are approximately the same age.

See also under *Biogeographic considerations*.

neander. Andronymus neander Plötz, 1884

Hesperiidae: Hesperiinae: *Andronymus ? neander.*

Locality uncertain, copal; Pleistocene.

Depository: BMNH (one specimen, no. 58522).

Published figures: Illustrations of the extant species can be found in various books on African butterflies.

Andronymus is a hesperiid genus restricted to sub-Saharan Africa. Evans, who was not sure of the correct species name and put a question mark on the label, identified the fossil in the collection of The Natural History

Museum (London). Apparently, this species name was copied by Skalski (1976) under the genus name *Androgynus*), but without the question mark, and without any details or references. Claire Mellish of the Palaeontology Department of The Natural History Museum (London) kindly sent me images of the fossil, in which the unbranched radial veins in the forewing are clearly visible, identifying the fossil as belonging to the Hesperiidae. The stout antennal club with upturned apiculus and the wide head also point to this family. The wings are relatively narrow and have an estimated length of about 20 mm. The third palpal segment is long, thin, sharply pointed, and appears to curve a bit over the vertex, similar to what is found in the distantly related genera *Acleros* and *Teniorhinus*. In the forewing, three well-developed subapical spots are visible, with the one in space R5 relatively large and trapezoidal and placed further to the termen than the smaller, elliptical spots in R3 and R4, which are placed one above the other. There is a large elliptical spot in the upper, outer corner of the cell. Possible additional spots are not clearly visible in the fossil. Among extant genera this arrangement of characters is only found in *Andronymus*. Of the about ten extant species (Larsen 2005), *A. neander*, *A. gander* and *A. evander* share the same arrangement of spots visible in the fossil. At the same time, this arrangement is not found in *Acleros* and *Teniorhinus*, and for this reason the identification of the fossil as a member of *Andronymus* appears correct.

According to Skalski (1976) and Sohn *et al.* (2012) the fossil originated from Tanzania (Zanzibar), East Africa. Since *A. neander* is the only extant *Andronymus* species occurring in East Africa, the idea that the fossil may have been this species seems obvious. However, the fossil was purchased, together with other fossil material, from J.C. Rees in 1867, without indication of locality, but assumed to be Baltic amber by subsequent early authors (Claire Mellish, pers. comm.). However, all specimens were preserved in copal and possibly originated from East Africa, although there is no proof. It is not clear why subsequently it was assumed to have come from Zanzibar.

Like most skippers, the *Andronymus* species are fast flying. As in the case of *Charaxes candiope* (see above) that was found in East African copal, it is remarkable that this swift skipper was trapped in dripping resin.

***nympha. Riodinella nympha* Durden & Rose, 1978**

Incertae sedis.

USA, Colorado, Rio Blanco Co., Ray Dome; early Lutetian, middle Eocene.

Depositories: PLME (holotype, no. 3a), BHM (counterpart, no. 3b).

Published figures: Durden & Rose (1978: Figs 4, 5, 6E–F); Murata (1998: Figs 4, 5).

Described as belonging to Lycaenidae (at the time including Riodinidae) and compared, among others, to the extant genus *Riodina*. In addition to photos of the holotype, a reconstruction of the wing venation and an extensive description is given. In the reconstruction of the hindwing a long tail at the end of M3 and CuA1 has been reproduced, or rather produced, since it is not present in the fossil. Hall *et al.* (2004) extensively explain that in wing venation there is nothing to link the fossil exclusively to the Riodinidae; several of the venational characters also are found in Papilionidae, Pieridae and Nymphalidae. Hall *et al.* (2004) conclude that it should be treated as an unplaced butterfly, with which I can fully agree.

According to the original description “the male genitalia are definitely comparable to modern members of this subtribe”, but the genitalia are not described except for a structure "in the anterior third of the capsule". This structure is interpreted as representing a Y-shaped furca, an interpretation that is considered unreliable. Apparently the specimen is supposed to be a male, but under “Characters agreeing with the family” [Lycaenidae] is listed “Prothoracic femur 0.6 of mesothoracic femur in female” (Durden & Rose 1978)

***obscurum. Nymphalites obscurum* Scudder, 1889**

Nymphalidae.

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depository: MCZH (holotype, no. 7768).

Published figures: Emmel *et al.* (1992: Fig. 1/8); Scudder (1889: Pl. LIII Figs 10–13).

A badly preserved fossil with a stout body. Possibly a male, as parts of the uncus (“curving sides of the tapering hook of the upper organ”) seem to be present. According to the original description the “ordinary form of superior apical branching seen in the subcostal vein [now considered to be the radius] of the fore wings of Nymphalinae appears also here.” This is a rather cryptic description, and not supported by Scudder’s own figure, where few venational details are discernible. Moreover, the usual radial arrangement in Nymphalidae, the formula 1, 2, 3+(4+5), apparently is plesiomorphic. Forelegs reduced, terminal tarsal joint with short slender spines instead of the normal claw. This is an apomorphy of Nymphalidae and Lycaenidae (males only). Because of the size of the insect (wing span is estimated at 63 mm), it is unlikely that it belongs to the Lycaenidae, the Nymphalidae thus being the most likely family. Nothing more can be said about the systematic position of the fossil. It is not clear on which evidence Emmel *et al.*’s (1992) remark is based that “its closest affinities seem to be with *Marpesia* and *Anaea* from Mexico and Central America” which, according Freitas & Brown (2004), based on morphology, and Wahlberg *et al*. 2009, based on molecular analysis, are in separate subfamilies of Nymphalidae; *Marpesia* is in Cyrestinae, *Anaea* in Charaxinae).

persephone. Prodryas persephone **Scudder, 1878**

Nymphalidae.

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depository: MCZH (holotype, no. 394).

Published figure: Emmel *et al*. (1992: Fig. 1/5, and at back of color plate III); Murata (1998: Figs 46–49); Scudder (1889: Pl. LII Figs. 1–10).

After the original decription (Scudder 1878), the author described and figured this specimen extensively in 1889. A well preserved, medium-sized (length of forewing 24.5 mm) and strongly built insect. The forewing, radial formula is 1, 2+(3+(4+5)), udc originates between R1 and R2 (slightly closer to R1); M1 and M2 originate close together near upper cell corner; cell open. In the hindwing Rs originates far basad; cell open; tail at M3, from here to tornus termen crenulate. The open cell in forewing and hindwing is an apomorphy found in many Nymphalinae and separately derived in some members of other nymphalid subfamilies. Emmel *et al*. (1992) assigned the fossil to this subfamily, but in the absence of additional apomorphies, we cannot be sure about the subfamily.

On the basis of overall similarity with extant genera, earlier authors have discussed its identification. According to Forbes (1932) and Brown (1978) the fossil is very close to the modern genus *Hypanartia*. This genus occurs, with eight species, in Central and South America (DeVries 1987). This author thought this fossil was a close relative of the African genus *Antanartia* (see also Brown & Heineman 1972), but Wahlberg *et al*. (2009) place *Hypanartia* as sister to *Vanessa*, and *Antanartia* as sister to *Aglais*, *Polygonia*, *Nymphalis* and *Kaniska*. One species of *Hypanartia* may occasionally stray into the southern USA (Scott 1986). Wahlberg *et al*. (2005a, 2009) and Heikkilä *et al*. (2011) followed Forbes and Brown in additionn to personal information from Willmot that the fossil is very close to *Hypanartia* and used the fossil as calibration point for the split between *Vanessa* and *Hypanartia*. This is an undesirable situation, since any information on characters, let alone apomorphies, is missing. Brown's (1978: 8) remark: "Careful examination of Scudder's type has led to the realization that it is little different, if any, from the modern genus *Hypanartia*." sounds reassuring, but does not convey much information on the presence of apomorphic characters. It is reminiscent of the case of *Vanessa amerindica* (see above), which is considered a member of the genus *Vanessa* because of the presence of a produced forewing apex with a lobe at M1-M2, a character that does not seem to be restricted to this genus.

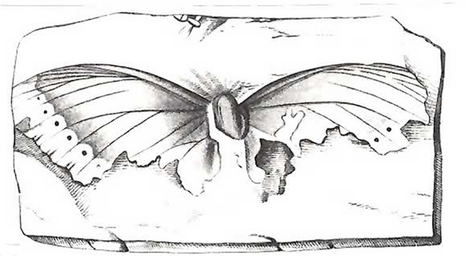
It must be remarked that the double spot between M2 and M3, clearly indicated in Scudder’s figures, is unlike any feature found in recent butterflies. If there is a spot in this space, it is always single, and if there is a spot between M1 and M2, it is close to the spot between M2 and M3 and not placed further basad. It seems possible that the division of the spot between M2 and M3 in the fossil is an artefact.

pluto. Vanessa pluto **Heer, 1849**

Figs 11–13.

Pieridae: Coliadinae+Pierinae.

Croatia, Radoboj, Croatia; Burdigalian, early Miocene.



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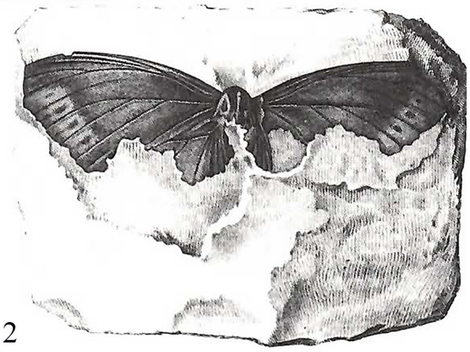

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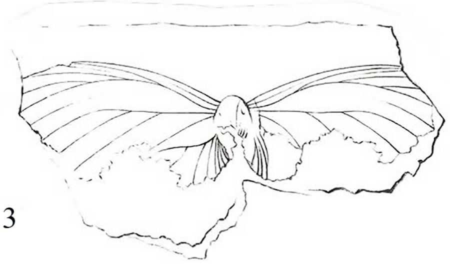

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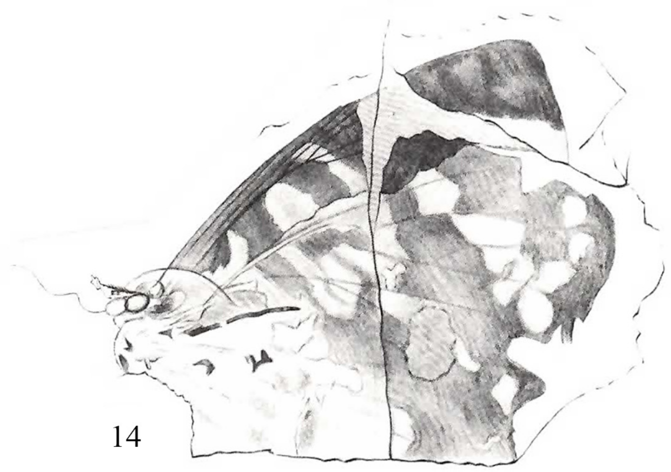

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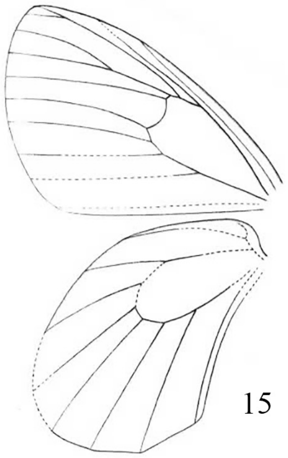

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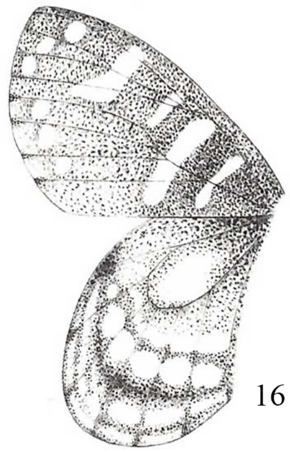

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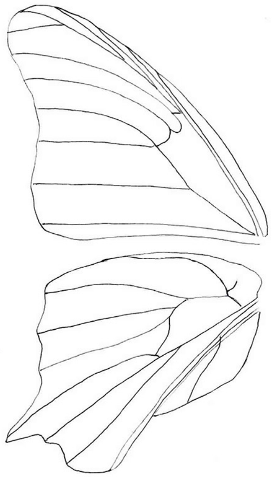


17

18

FIGURES 11–13. *Vanessa pluto* Heer, 1849. Figures copied from (1875), Plate II, figures 1, 17 and 7, respectively. (A), copied by Scudder from original description by Heer; (B) and (C), figures sent to Scudder by Mr. Brunner de Wattenwyl, made after the same object. Note differences in wing shape and other details. Figs 14–16. *Thaites ruminiana* Scudder, 1875. Figures copied from Scudder (1875), Plate III, figures 9, 1 and 3, respectively. (A), underside of fossil; (B), reconstruction of venation; (C), reconstruction of markings. In (A) two separate subcostal veins have been drawn in the forewing, an impossible configuration in Lepidoptera, and apparently a mistake, corrected in (B) and (C). Fig. 17. *Cyllo sepulta* Boisduval, 1841, wing venation after Scudder (1875). Fig. 18. Butterfly fossil recorded by Wangrin (1939), but shown to be a fraud by Ansorge (2015). Photo kindly provided by J. Ansorge, Horst, Germany (see text for explanation).

Depository: NHMW (holotype, no. 1940/0001/0011).

Published figure: Murata (1998: Figs 27, 28); Pongrácz (1928: Fig. 30); Scudder (1875: Pl. II Figs 2, 7, 17).

This specimen consists of the greater part of both forewings and basal fragments of hindwings. Original description and figure copied in Scudder (1875: 44–50). Considered to belong to Nymphalidae by Heer (and followed by some other authors, see discussion by Scudder) on the basis of a peculiar and highly unlikely venational arrangement: Sc arising from R halfway between base and apex, together with the common stalk of R1 and R2 (which forks shortly thereafter) and the common stalk of R3, R4 and R5, while M1 originates from the radial stem before this trichotomy; the cell is open. Such an arrangement is not found in any extant species.

Scudder's interpretation is very different, with Sc from base as usual; the radial branching is not clearly visible, partly because the apex is broken, but it seems that M1 branches off an R-branch (formula R1, R2, (R3+M1)). This arrangement, with M1 branching off an R-branch, is found in a number of genera belonging to Coliadinae and Pierinae (see phylogeny by Wahlberg *et al*. 2014), and Scudder apparently was correct in considering the fossil attributable to the Pieridae. He placed it in his genus *Mylothrites* (followed by Kozlov 1988) and compared it to the recent genera *Mylothris* (Africa) and *Hebomoia* (Southeastern Asia) (Pieridae: Pierinae), both which have only three radial veins. Three radial veins are also found in the American genus *Nathalis* (Pieridae: Coliadinae), so we cannot identify the fossil more precisely than belonging to Coliadinae+Pierinae. Pongrácz (1928) re-examined the type and concluded that it was close to the satyrine genus *Satyrus* (Nymphalidae). However, in view of the state of preservation of the fossil of which a photograph of the holotype has been published by Ponomarenko & Schultz 1988: Pl. 7 Fig. 2, Pongrácz's reconstruction (his Fig. 30) must have been erroneous. Without providing reasons, Handlirsch (1908) mentioned the fossil under “Papilionidae”, Handlirsch (1925) under “Papilioninae”, and Zeuner (1942) under "Nymphalinae".

proserpina. Coliates Scudder, 1875

Family incertae sedis.

France, Bouches-du-Rhône, Aix-en-Provence; late Oligocene–early Miocene.

Depository: MNHN (probably).

Published figures: Leestmans (1983: Fig. 5); Scudder (1875: Pl. II Fig. 5).

Only forewings are available in this specimen. 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 widespread in Pieridae, but recurs in some Lycaenidae and in one genus (*Microtia*) of Nymphalidae and, thus, is insufficient to identify the fossil as a pierid. Scudder compared the fossil to *Delias* (Pieridae, India to Australia), but in this genus there are only three radial branches present. In most pierid genera two radial branches (R1 and R2) arise free from the cell. The fossil does not exhibit additional further characters that could be helpful phylogenetically; we can only identify the fossil as belonging to the Pieridae. Apparently based on Scudder's comparison of the fossil with *Delias* and not on a personal inspection of the fossil or of the description, Braby *et al*. (2006) considered the closest relative the *Delias-Prioneris* group (possibly *Aporia*), and used it as calibration point for this node in the phylogeny of the Pieridae, thus taking the risk that it greatly overestimates the divergence ages in Pieridae.

reynesii. Satyrites reynesii Scudder, 1872

Nymphalidae: Satyrinae.

France, Bouches-du-Rhône, Aix-en-Provence; late Oligocene–early Miocene.

Depository: MVMF (holotype).

Published figures: Leestmans (1983: Figs 9–10); Scudder (1875: Pl. I Figs 2, 5).

The original description (Scudder 1872) is repeated by Scudder (1875), who erected a new genus for the fossil: *Lethites*. Kozlov (1988) accepted Scudder's genus switch. The poorly preserved specimen bears only the forewings, which yield some usable characters. Subcosta basally strongly swollen; radial formula 1, 2, 3+(4+5), cell closed. A swollen subcosta is typical, but not universal, for Satyrinae (Nymphalidae), but this character occurs in some genera of the Biblidinae as well (*Biblis*, *Ergolis*, *Eurytela*, *Hypanis*, *Vila*). In Nymphalinae with swollen

Sc, the cell is usually open or at least, the ldc is weak. In the fossil ldc seems to be fairly strong. Thus, it is plausible to consider the fossil a member of the Satyrinae. According to Scudder it is similar to the recent genera *Lethe* and *Cercyonis*, but it is not clear why it should be more similar to these genera than to any other satyrine genus. The similarity is not an indication of relationship, since *Lethe* and *Cercyonis* are only remotely related (Wahlberg *et al*. 2009). Moreover, in *Lethe* there are no basally swollen veins in the forewing (Ackery *et al*. 1999).

Neorinopsis, Pseudoneorina, *Neorinella* and *Satyrites* have been classified, without comment, as fossil genera belonging to the subtribe Lethina of the tribe Satyrini by Wahlberg & Peña (2015), but these choices are not supported by apomorphies. For further details, see the discussion under *Neorinella garciae* and *Neorinopsis sepulta*.

ruminiana. Thaites ruminiana **Scudder, 1875**

Figs. 14–16

Papilionidae: Parnassiinae: Parnassiini.

France, Bouches-du-Rhône, Aix-en-Provence; late Oligocene–early Miocene.

Depository: PMUZ (holotype).

Published figures: Demoulin (1975: Fig. 2); Leestmans (1983: Figs 1–4); Murata (1998: Figs 12–15); Scudder (1875: Pl. III Figs 1, 3, 6–10).

This specimen is only partly preserved; most of the venation and much of the pattern is discernible. Although Scudder usually is very accurate in his figures and descriptions, his figure of the left underside of the fossil (pl. III Fig. 9) must be incorrect in that it shows two subcostal veins in the forewing. In his reconstruction of the venation (Pl. III Fig. 1) the normal, single subcostal vein is depicted. The radial formula is: 1, 2+3, 4+5, with R2 and R3 separate close to the apex. Posterior margin of cell quadrifid, an apomorphy of Papilionidae. A cubital spur, another apomorphy of Papilioninae, is not apparent. Hindwing with single anal vein, an apomorphy of Papilionidae. Starting from the assumption that the radial formula 1, 2, 3+(4+5) belongs to the groundplan of the Papilionidae, the fossil cannot belong to the ancestry of any taxon in this family where the plesiomorphic condition has been retained. With slight variations, this is the case for all papilionid genera except for *Parnassius* and *Hypermnestra*. Therefore, only these genera can be considered as close relatives of *Thaites ruminiana*. *Parnassius* and *Hypermnestra* are thought to be sister groups by Hancock (1983), Omoto *et al*. (2004) and Nazari *et al*. (2007), the ancestor of which has lost R3 by fusion with R2; in some *Parnassius* species a further fusion seems to take place in a terminal anastomosis of R1 and R2. *Thaites* fits in quite well here, as sister group of both. According to Hancock (1983) *Thaites* is an offshoot of the ancestral line of Parnassiini, which is unlikely, as is his opinion that *Archon* belongs here, although it has retained the plesiomorphic radial vein arrangement. In the Parnassiini sensu Nazari *et al*. (2007) the tribe consists of *Parnassius* and *Hypermnestra* only, with which the fossil shares the apomorphic condition of the radial vein venation. Consequently, the fossil should be placed as sistergroup of Parnassiini sensu Nazari *et al*. (2007). However, Nazari *et al.* (2007) had included the fossil in their phylogenetic analysis of the morphology and molecular characters of extant species (see also under *Doritites bosniaskii* and *Praepapilio colorado*). In the analysis it appeared as an offshoot of the Parnassiini lineage, before it split into *Parnassius* and *Hypermnestra*. For the calibration of the clock such a switch of a taxonomic assignment may be of little consequence, since it concerns a sister group, but yet it is preferable to have relationships explicitly stated. New information, such as more or other molecular data or additional taxa, may prompt another rearrangement of genera and then the date of the calibration point should be clear.

For the sake of historical completeness but without impact on the discussion above, the following information is provided. Principally because of similarities in wing pattern apparently based on symplesiomorphies, Scudder (1875) considered the fossil a close relative of *Thais rumina* (Linnaeus), now allocated in the genus *Zerynthia*, hence the name. Stichel (1907) and Verity (1947) assigned the fossil to the tribe Zerynthiini, without much comment. Bricoux (1975) followed Verity (1952) in considering *Thaites ruminiana* as the ancestor of *Zerynthia rumina*, what is most unlikely because of the venation issues as explained above. Demoulin (1975) is of the opinion (based on venation) that the fossil is a precursor of *Parnassius*; he does not mention *Hypermnestra*.

With two other papilionid fossils, this fossil was used for calibration by Condamine *et al.* (2012), see discussion under *Praepapilio colorado*.

scudderi. Nymphalites scudderi Beutenmüller & Cockerell, 1908

Incertae sedis.

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depositories: AMNH (holotype), UCNH (counterpart?).

Published figures: Cockerell (1908: Pl. V Fig. 6); Emmel *et al*. (1992: Fig. 1/9).

The specimen is a large insect, with a forewing length of 39 mm. Venation not visible. According to the original description in Cockerell (1908), the pattern is uniformly dark with abroad, unsharp, pale, submarginal band and is reminiscent of *Basilarchia* (now *Limenitis*). Since this is the only reason for considering the specimen a member of the Nymphalidae, the position of the fossil is highly uncertain. The size of the forewing, if compared to modern taxa, suggests that the fossil either belonged to Nymphalidae or Papilionidae, but we do not know what these butterflies looked like, say, 30 million years ago. Emmel *et al*. (1992) placed the fossil in Nymphalinae, apparently only because of the superficial resemblance to *Limenitis weidemeyerii* Edwards in wing markings, although they remarked that the shape of the forewing is different.

sepulta. Cyllo sepulta Boisduval, 1841

Fig. 17.

Nymphalidae: Satyrinae.

France, Bouches-du-Rhône, Aix-en-Provence, France; Chattian–Aquitanian, late Oligocene–early Miocene.

Depository: MNHN (holotype, IPM B-24309).

Published figures: Leestmans (1983: Figs 6–8, 18); Murata (1998: Figs 17–23); Nel & Nel (1986: Fig. 2a, Pl. I Fig. 2); Scudder (1875: Pl. I Figs 8–17).

Original description (Boisduval 1841) cited by Scudder (1875) who dedicated a long discussion to the fossil. Further discussed by Nel & Nel (1986). The wing venation and pattern is rather well preserved. The thorax and legs (hindlegs only) lack diagnostic characters. The forewing radial formula is 1, 2+(3+(4+5)) according to Scudder, 1, 2, 3+(4+5) according to Nel & Nel (who studied the holotype), M3 and Cu1 originating from the same point at the lower distal end of the cell, meaning that ldc runs from the origin of Cu1 to M2, cell closed but crossvein weak, basally swollen veins absent. Hindwing with two anal veins, cell closed but crossvein weak. Forewing with falcate apex, hindwing forming a tail at M3. Scudder considered the visible wing pattern to be that of the upperside, but Nel & Nel (1986) convincingly showed it to be the pattern of the underside.

This specimen is generally placed in Satyrinae on basis of wing shape and pattern (submarginal ocelli). Boisduval (1841) assigned it to a recent genus, *Cyllo*, which is a junior synonym of *Melanitis*, see Hemming (1967). Butler (1873, cited by Scudder 1875) erected the genus *Neorinopsis*, although Scudder misspelled the fossil *Neorinopis*, repeated by later authors. In wingspan and pattern it is intermediate between recent satyrine genera *Neorina* (Southeast Asia), *Antirrhaea* (South America), and *Anchiphlebia*, a junior objective synonym of *Antirrhaea* (see Hemming 1967). Nel & Nel (1986) are clear in their opinion about this similarity: "… le rapprochement indiqué par Scudder (1875, tableau p. 28) avec des genres sud-américains (*Anthirrhaea*, *Anchiphlebia*), perd ainsi toute raison d'être." ("… therefore, the similarity to South American genera (*Anthirrhaea*, *Anchiphlebia*), indicated by Scudder (1875, table p. 28), lacks any credibility."). According to Scudder (1875), the venation is reminiscent of *Neorina*, *Lethe*, *Zophoessa* and *Debis*, of which the latter two are synonyms of *Lethe* (see Gaede 1931), but the radial vein arrangement is different, a remarkable observation by Scudder, since the common origin of M3 and Cu1 of the forewing in *Neorinopsis* does not agree at all with the situation in these genera, but is similar to what is found in the extant genus *Elymnias*.

The Satyrinae do not have a unique and universal morphological apomorphy (Ackery *et al.* 1999; but see Freitas & Brown 2004: 369), and the justification for its maintenance as a monophyletic group comes from a combined analysis of morphological end molecular data (Wahlberg *et al.* 2009). Similarly, even though the nine satyrine tribes recognized in a recent molecular analysis of the subfamily by Peña & Wahlberg (2008) largely agree with morphological studies, an analysis of the apomorphies of the tribes still is wanting. Thus, opinions of relationship to date have been based on similarity.

On the basis of the wing pattern Nel & Nel (1986) agree with Butler (1873) and Scudder (1875) about a close relationship with the recent satyrine genus *Neorina*. They indicate that *Neorinopsis*, *Neorina* and *Pseudoneorina coulleti* (also a fossil species, see under the species name) form a monophyletic group whose ancestor lived in the Eocene or earlier, maybe Upper Cretaceous, f Europe or Asia. As correctly remarked by Nel & Nel (1986), the common origin of veins M3 and Cu1 in the forewing is a character found in recent taxa only in the satyrine tribe Elymniini (Old World Tropics), which is not closely related to *Neorina* (tribe Zetherini, Peña & Wahlberg 2008). Since wing shape in Elymniini is generally crenulate and the pattern is very different, Nel & Nel (1986) conclude that the venational similarity is due to convergence. Alternatively, the similarity of *Neorina*, *Neorinopsis* and *Pseudoneorina* in wing design could well be based on symplesiomorphy or convergence, and probably the mimetic wing pattern of Elymniini, mimicking, among others, Danainae, may well have evolved after the common origin of M3 and Cu1 arose in an ancestor of *Neorinopsis* and Elymniini. In view of the variability and plasticity in the development of eyespots in Satyrinae, where even seasonal changes may lead to very different patterns (Brakefield *et al*. 1996), one should hesitate in providing more weight for similarity in wing design than for similarity in a unique structural character. In this context, the recent publication on Mesozoic kalligrammatid lacewings (Neuroptera) with a surprisingly butterfly-like appearance, including eyespots (Labandeira *et al*. 2016), which lived several tens of millions of years before the origin of butterflies must be mentioned. This study emphasizes that appearance alone is not a reliable guide to relationship. In an interesting examination, Martins-Neto *et al*. (1993) described a fossil butterfly from Brasil (*Neorinella garciae*) with the same remarkable connate origin of M3 and Cu1 from the forewing cell as found in *Neorinopsis* and *Elymnias* (see also *Neorinella garciae*).

Pseudoneorina, *Neorinella*, *Satyrites* and *Neorinopsis* have been classified by Wahlberg & Peña (2015), without comment, as fossil genera belonging to the subtribe Lethina of the tribe Satyrini, while *Neorina* has been placed in the tribe Zetherini. For *Neorinopsis* and *Neorinella* this placement appears incorrect in view of the venation, and for *Satyrites* it is not certain at all (see the discussion under *reynesii*). However, insights in the interrelationships among the tribes of Satyrinae are still in flux and would be altered with new analyses that apply other or new (molecular) characters and other sets of taxa. Consequently, Wahlberg & Brower (2006) presented the phylogeny of the tribes of Satyrinae quite differently from the scheme of Peña & Wahlberg (2008) for the same tribes, and one year later the situation has again changed drastically (Wahlberg *et al*. 2009) (Figs 19–21). Evidently, if *Neorinopsis sepulta* (about 28–34 Ma) or *Neorinella garciae* (about 20–30 Ma) are used to calibrate the molecular clock for Satyrinae, and the calibration point is placed at the base of Elymniini, it makes considerable difference whether it is done in the tree of Fig. 19 or in the tree of Fig. 20.

As to geographical relationship, if *Neorinopsis* and *Neorinella* are assigned to Elymniini on the basis of the connate origin of M3 and Cu1 from the forewing cell, *Neorinella* would be an example of a fossil found on another continent than the most closely related extant taxa, particularly as Elymniini currently are restricted to tropical Asia with a single species in Africa (see http://tolweb.org/Elymniini/70274). See the section on *Biogeographic considerations*.

spec. *Pierella* (teste Warren 2015)

Nymphalidae: Satyrinae: Haeterini: *Pierella*.

Colombia, Santander Department, copal; Holocene/Pleistocene

Depository: FMNH.

The specimen is a remarkably well-preserved fossil, so much that A.D. Warren (pers. comm.), who saw the specimen in July, 2015, thought it was a fake. According to Warren it exactly resembles the extant *Pierella helvina* Hewitson (Nymphalidae: Satyrinae), which is distributed from Nicaragua to Ecuador with Colombia being the type locality, except for the reddish color of the extant species. However, the fossil has not yet been studied in detail. In view of the young age of the fossil it is of little interest for calibration of the molecular clock, except for the evolution within the genus *Pierella*.

spec. *Theope*

Riodinidae: Riodininae: Nymphidiini.

Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata; Dominican amber, Burdigalian, early Miocene.

Depository: AIOSU (one specimen).

Published figure: DeVries & Poinar (1997: Fig. 1).

DeVries & Poinar (1997) described a fossil caterpillar that differs little from modern-day *Theope* (Riodinidae). They pointed out that the combined presence of tentacle nectary organs, vibratory papillae, and balloon setae which seem to be present, are found only on riodinid caterpillars in the tribe Nymphidiini, and nowhere else among the Lepidoptera (Cottrell 1984; Harvey 1987; DeVries 1997). In the extensive molecular phylogenetic analysis by Espeland *et al*. (2015), the genus was assigned to the tribe Nymphidiini, and they placed the calibration point of 15–20 Ma on the stem of *Theope virgilius* (Fabricius) and *T. philotes* (Westwood), apparently on the basis of overall similarity of the larva. There are, however, no synapomorphies known for the larvae of *Theope* and a more conservative calibration point would be at the base of Nymphidiini.

styx. Lithopsyche styx **Scudder, 1889**

Nymphalidae.

USA, Colorado, Teller County, Florissant; Late Priabonian, Late Eocene.

Depository: MCZH (holotype).

Published figures: Emmel *et al*. (1992: Fig. 1/2); Murata (1998: Figs 51, 52); Scudder (1889: Pl. LII Figs. 11, 16, 17).

This specimen presents only an overlapping forewing and hindwing, the former without an apex. The forewing has a radial formula of radial formula 1, 2+(3+(4+5)) (forking of R4-R5 reconstructed, missing in fossil), R2 originating very close to upper corner of cell, cell closed. The hindwing cell is open. The wing pattern is obscure and irregular.

According to Scudder (1889) this fossil is closer to *Jupiteria charon* from the same excavation site than it is to any living species (see entry under that species). The open hindwing cell is an apomorphic character state in (part of) the Nymphalidae. The assignment also agrees with the radial vein arrangement. Any further statement about the relationship is unwarranted. Because of Scudder's remark on its relationship to *Jupiteria*, Emmel *et al*. (1992) listed the fossil under Nymphalinae.

Lithopsyche Scudder, 1889, is a junior homonym of *Lithopsyche* Butler, 1889 (type-species *Lithopsyche antiqua* Butler, see above). Cockerell (1909) replaced it with *Lithodryas*.

talboti. Miopieris talboti **Zeuner, 1942**

Pieridae.

Germany, Baden-Würtemberg, Esslingen, Randecker Maar; Burdigalian, early Miocene.

Depository: BMNH (holotype).

Published figures: Murata (1998: Fig. 38); Zeuner (1942: Fig. 1).

This specimen is poorly preserved. Of the radial branches of the forewing only the basal parts of R1, R2 and the common stem of R3, R4 and R5, assuming the latter two are present, 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 the relevant part of the wing missing. The distad trajectory of M1 along the common stem of R3-5 is found throughout the Pieridae, but also occurs in a number of Lycaenidae and in the nymphalid genus *Microtia*. The light colour and dark spots at end of cell and between M3 and CuA1, and CuA1 and CuA2, agree with Pieridae, and not with other butterflies with a distally translocated M1. The condition of the fossil is too poor to allow further statements. However, Zeuner (1942) saw a similarity with *Pontia callidice* Hübner and *Tatochile macrodice* Staudinger. Perhaps on the basis of Zeuner's remark, Braby *et al*. (2006) considered the "*Pontia* group (possibly *Pontia*)" the closest relative of the fossil and used it accordingly as a calibration point.

vagabunda. Prolibythea vagabunda **Scudder, 1889**

Nymphalidae, Libytheinae (based on similarity rather than on apomorphy).

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depository: MCZH (holotype, no. 16353).

Published figures Scudder (1889: Pl. LIII Figs. 4–9); Emmel *et al*. (1992: Fig. 1/43); Murata (1998: Figs 44, 45); Kawahara (2013: Fig. 63).

The rather poorly preserved specimen shares at least one apomorphic character with Nymphalidae, tricarinate antennae. The very long palps are shared with the Libytheinae, but are also found in some other nymphalids (see above under *Barbarothea florissanti*). The relatively broad abdomen suggests a female, also indicated by the foreleg bearing complete tarsal claws. The latter is a plesiomorphic character, but in the Nymphalidae found only in Libytheinae, a feature in agreement with palpal characters. As far as visible the venation shows plesiomorphic characters, with a radial vein formula 1, 2, 3+(4+5), but large segments of the veins cannot be made out. Hindwing costa apically extended as in recent *Libythea celtis* (Fuessly). Apomorphic character states unique for the Libytheinae are not visible in the fossil, so its assignment to the Libytheinae, in agreement with Emmel *et al*. (1992), must be based on similarity only. Scudder emphasized that the fossil is more similar to Old World than to New World Libytheinae. Kawahara (2009, 2013) discussed the fossil at length. On the basis of a phylogenetic analysis of all taxa of Libytheinae, fossil and recent, he placed the fossil in the extant genus *Libytheana*, together with another fossil from the same fossil bed, *Barbarothea florissanti* (=*Oligodonta florissantensis*) (see comments under these names.). The difference between *Libytheana vagabunda* and *L. florissanti* is that in the latter the forewing apex is less strongly falcate. Indeed, the relatively strong falcation in *L. vagabunda* is not an observation, but Scudder's reconstruction, indicated by a dashed line. The insects were fossilized ca 34 Ma in a lake environment. The area has been suitable for fossilization of butterflies for a long period, a million to several million years (Smith *et al*. 2008). Consequently, *Libytheana vagabunda* and *L. florissanti* may have fossilized at times separated long enough for differences to evolve, possibly even at species level.

L. vagabunda as well *as L. florissanti* were used as calibration point for the molecular clock of the Nymphalidae by Wahlberg *et al*. (2009), the first also employed by Misof *et al*. (2014) in their paper on insect evolution for calibrating Macrolepidoptera. See also the section on *Fossils and calibrating the molecular clock*.

vetula. Vanessa vetula **von Heyden, 1859**

Incertae sedis.

Germany, Rheinland-Pfalz, Siebengebirge, Rott; Chattian, late Oligocene.

Depository: BMNH (holotype, but not found).

Published figures: von Heyden (1859: Pl. 1 Fig. 10); Scudder (1875: Pl. III Figs 12, 16, as *Thanatites juvenalis*).

The original description and figure of this specimen was reproduced by Scudder (1875), who corrected previous mistakes and compared the fossil to the hesperiid *Thanaos juvenalis* (Fabricius) (Pyrginae; now in *Erynnis*). Because of supposed similarities, Scudder (1875) erected the genus *Thanatites* for the fossil. There is, however, very little to support this opinion. As remarked by Scudder (1875: 65), the fossil "…is excessively obscure at the present time, and no fossil object I have ever studied has proved so difficult to decipher as this." The venation is too obscure to be helpful. The only character that could point to Hesperiidae is the presence of a costal fold, an apomorphy of part of the Hesperiidae. However, it is not mentioned in the original description, and only casually so by Scudder. Moreover, it is not shown in the figure. Scudder's assumption that the nearest living allies occur in tropical America is pure speculation, especially since it is not even certain that the fossil belongs to the Hesperiidae. There are no indications either, that the fossil belongs to the Nymphalidae, as supposed by von Heyden (1859). Kirby (1871) placed it in the recent genus *Araschnia*, apparently following von Heyden who compared it to *Vanessa levana* Linnaeus, now in *Araschnia*). Unless the specimen can be found and studied in greater detail, it is inconsequential for understanding either the timing or relationships of butterflies. Kozlov (1988) listed the fossil as "*Thanaites vetulinus* (Heyden)".

wilmattae. Chlorippe wilmattae Cockerell, 1907

Nymphalidae: "nymphalines" (Nymphalinae+Biblidinae+Cyrestinae+Apaturinae).

USA, Colorado, Teller County, Florissant; late Priabonian, late Eocene.

Depositories: MCZH (holotype, no. B602) and USNM (one specimen, no. 58682).

Published figures: Cockerell (1907: Pl. 10); Emmel *et al*. (1992: Fig. 1/11).

The original description does not provide structural details except for “The venation agrees with that of *Chlorippe*, with the same open cell.” The remainder of the almost three pages of description concerns wing pattern, which is compared to that of extant species of *Chlorippe*, now split into *Asterocampa* in North America and *Doxocopa* in Central and South America. It is unknown if there is a significant phylogenetic signal in the pattern, the pattern itself amenable to convergence and mimicry. An open forewing cell is found in several subfamilies, ostensibly in the Nymphalinae, Biblidinae, Cyrestinae and Apaturinae of the informal section “nymphalines” (Wahlberg *et al*. 2009) and, although not universal in these subfamilies, this feature can be considered an apomorphy of this grouping. For calibration purposes the taxonomic position of the fossil should be placed at the stem of this group.

Cockerell (1913) recorded a second specimen of which the preservation was poorer. The fossil was mentioned by Howe (1975) under Apaturinae and by Emmel *et al*. (1992) under Nymphalinae, in which they included Apaturinae, both without further comment.

zeuneri. Nymphalites zeuneri Jarzembowski, 1980

Nymphalidae.

England, Isle of Wight, Bembridge Marls; late Priabonian, late Eocene.

Depository: BMNH (holotype, no. I.10384; counterpart holotype).

Published figures: Jarzembowski (1980: Figs 72, 75, 76); Murata (1998: Fig. 6, as *Protoeuthalia brittanica*).

This specimen consists of remains of both pairs of wings. The forewing: cell closed; probable radial vein formula 1, 2, 3+(4+5), but of R3-R5 only the common stem and an indication of the first forking remains, since the rest of the apical region is lacking and it cannot be decided if all radial veins were present, or whether R4 or R5 had become obsolete. M1 from anterior apical corner of cell, M2 closer to M1 than to M3; udc absent, mdc concave to termen, ldc straight; Cu trifid (CuA2, CuA1, M3); 1A+2A faintly discernible, single, basal third invisible because of superimposed hindwing. Hindwing: margins missing except for basal part of anterior margin; cell open; humeral vein straight, unforked, from fork of Sc+R, directed toward humerus. Area between Sc and anterior margin apparently narrow; Sc straight except basally, but greater part missing. M2 closer to M1 than to M3. One anal vein visible, but anal area largely missing. Traces of crescent-shaped markings on the underside.

According to the original description the specimen is medium-sized; length of forewing cell 13.5 mm. This species of Nymphalidae is close to the extant species of *Neurosigma siva* (Westwood), *Abrota mirus* (Fabricius) of tropical Asia and *Cymothoe theobene* Doubleday & Hewitson, now placed in *Harma*, of Africa, in wing form and venation. However, since the wing margins are almost entirely missing, we can only speculate on the wing form and the short, broad wing tail between M2 and M3 of the hindwing in Fig. 75 of Jarzembowski (1980) is likely speculation of the artist who made the drawing, since the margin cannot be reconstructed from the fossil. The open hindwing cell is an apomorphy of part of the Nymphalidae. Notably, it is the only character on which the assignment of the fossil to the family Nymphalidae can be based. The radial branches in the forewing are incomplete, but what can be seen does not contradict an affinity to the Nymphalidae, at the same time this feature does not prove that it is a member of the Nymphalidae as the Nymphalidae generally have a plesiomorphic condition for the branching of the radial veins.

The fossil was mentioned by Zeuner (1961) without description, except that it was "so closely related to the recent genus *Euthalia* (Nymphalidae) that it could easily be placed there." He added that "The description will shortly be published elsewhere." This did not happen until 19 years later by Jarzembowski (1980). It is not clear where the names *Protoeuthalia brittanica*, used by Murata (1998) for this fossil, originates from. Possibly it is a manuscript name; apparently, the name is an objective junior synonym.

Additional records of butterfly fossils

The following records of butterfly fossils concern specimens that have not been identified to species or of which the identification is very doubtful, or otherwise do not fit well in the review above. The records below are listed alphabetically according to author.

Bachofen-Echt (1949) mentioned a species of *Papilio* and one *Lycaenites* found in amber without further information.

Brito & Ribeiro (1975: Pl. I Fig. 3, Pl. II) reported the finding of a butterfly fossil of the Tremembé Formation (Chattian–Aquitanian) in the Taubaté Basin of southern Brasil. The lacustrine shales are rich in fossils, but Lepidoptera are extremely rare. The fossil, consisting of a forewing and hindwing, has not been named, but is said to belong to the Danainae with greatest similarity to the extant genus *Lycorea*. The reconstruction of the forewing venation (their Fig. 2) has R2 branching off the frontal edge of the cell well before the end of the cell, while in *Lycorea* it originates very close to R3, and mdc has an unusable shape, strongly protruding into the cell and then sharply curving to the origin of M1 and R3. This configuration of R3 is unlike venational patterns known to me and possibly may not be entirely correct. It is different from the fossil of the same area that was described by Martins-Neto (1989) as *Archaeolycorea ferreirai*.

Evers (1907) recorded a butterfly inclusion in "Zanzibar copal" originating from the African mainland west of the island of Zanzibar. The fossil probably was only 2,000–3,000 years in age. According to Evers, the venation suggests the nymphaline genus *Precis*, though the forewing cell seems to be closed. The photograph accompanying Evers' paper is insufficiently clear to reveal relevant details. Of even more recent age is an inclusion in "Zanzibar copal" thought by Evers to represent a satyrine butterfly. The recency and the rather poor preservation relegates these fossils to insignificance.

Gravenhorst (1835) recorded a larva in Baltic amber that was supposed to belong to the Lycaenidae. The record was not included in Larsson (1978). At the time, Baltic amber was assumed to be of Oligocene age, but the actual date is more likely to be late Eocene (Labandeira 2014).

Hammond & Poinar (1998) described and figured (Figs 1–3) a well-preserved caterpillar from Dominican amber. According to the authors exact age unknown, estimates vary from 15–45 million years, but Iturralde-Vinent & MacPhee (1996) pointed out that the age is 15–20 Ma. On the basis of the structure of the sharp-branching spines, they place the fossil taxonomically in the *Nymphalis* group of genera of the Nymphalinae and consider it as a "prototypic ancestor of the *Pycina*-*Vanessa* lineage." They note that the fossil is very similar to the caterpillar of the genus *Smyrna*. It is unclear whether this type of spine is apomorphic for the lineage. Wahlberg *et al*. (2009) used the fossil as calibration point at the node of *Smyrna* and its sister group, but in view of the uncertainty about the apomorphies it may be wiser to place it four nodes lower down, at the base of the Nymphalinae (see the detailed phylogenetic tree in Wahlberg *et al*. 2009). Wahlberg *et al*. (2009) took as age 20 Ma, in accordance with the findings of Iturralde-Vinent & MacPhee (1996) (see also the chapter *Age determination of fossils* about the age of Dominican amber.)

Heer (1849) described a broken wing from Radoboj (Croatia) of lower Miocene age under the name *Phalaenites crenatus* as a *Phalaena*-like (Noctuidae) fossil. According to Pongrácz (1928) this specimen hardly is a recognizable member of the butterflies.

Henrotay (1986) reported on the discovery of an undescribed butterfly fossil from Dauphin, France, in Alpes-de-Haute-Provence (Fig. 6). Later, the fossil was recognized as *Pseudoneorina coulletti* Nel & Descimon, 1994, by Dr André Nel (Sohn *et al*. 2012) (see entry under *coulletti*.)

Jarzembowski (1980: 284) described a fossil from the Bembridge Marls, late Eocene (Priabonian)–early Oligocene (Rupelian) of the Isle of Wight, England, which "probably belongs to the Papilionoidea, though in the absence of further material the placing is uncertain".

Kernbach (1967) reported finding five unidentifiable butterfly wings in the Pliocene clay of Willershausen, in addition to what he identified as wings of *Aporia crataegi* (see entry under that species).

In addition to a survey of fossil Lepidoptera found in France, Leestmans (1983) published five photographs of lepidopterous fossils from Aix-en-Provence of early Oligocene age taken by Théobald around 1935. One of the photographs (Fig. 13) apparently represents a parnassiine butterfly, the wing pattern of which is reminiscent of *Thaites ruminiana* found in the same excavations. The fossils were sent to the Muséum National d'Histoire Naturelle in Paris in 1935. Until 1983 the fossils had not been recovered, but later A. Nel discovered them in the Department of Paleontology of the same Paris museum (R. Leestmans, pers. comm.).

Lutz (1984) reported the finding of a fossil from the lower Oligocene of Céreste, Southern France (pl. 5; Figs 19, 20). Right forewing and hindwing are largely present, whereas left wings are largely absent. On the basis of reduced forelegs, size (length of forewing appr. 43 mm) and presence of eyespots the specimen should be assigned to the Nymphalidae. Veins of the forewing are not swollen basally. A large eyespot on forewing between veins CuA1 and CuA2, and a smaller one between M1 and M2; also, a large eyespot is present on the hindwing. There is a pale band from middle of costa of forewing across the forewing and hindwing, and in direction of the hindwing tornus. The outer margin of the wings are largely broken.

Poinar (1992) published a colour photograph of a lycaenid (Pl. 7, "Lycaenidae or Riodinidae") in Dominican amber. This specimen is not included in the list of Lepidoptera found in Dominican amber (p. 287) and further details are wanting. The age of Dominican amber has been said to vary from 15 to 40 million years (see also Woodruff 1994). According to Iturralde-Vinent & MacPhee (1996) the amber is 15–20 million years old.

Van Schepdael (1974) listed a member of the Papilionidae and one of the Lycaenidae as amber fossils. He refers to Bachofen-Echt (1949) (see above) who in turn referred to Handlirsch (1908). Handlirsch (1908) listed the fossils known to him and among others was the alleged lycaenid larva recorded by Gravenhorst (1835) (see above), but there was no papilionid amber specimen.

Wangrin (1939) produced a photograph (but no description) of a fossil of middle Oligocene age found near Szczecin (Poland) in a so-called "Stettiner Kugel" consisting of a sandstone, an unlikely substrate for a butterfly fossil. The fossil presumably was a butterfly. The photograph (and apparently the condition of the fossil) was too poor to be of any assistance. The remark by Shields (1976) that's figure possibly represents a pierid, is not based on any definitive features. Urbahn & Urbahn (1939) had seen the specimen and remarked that it was very similar to the extant *Maniola jurtina* (Linnaeus) (Nymphalidae: Satyrinae). They suggested a more thorough examination by the noted lepidopterologist Hans Rebel in Vienna, but the owner did not want to part from his treasure. The fossil supposedly was lost during the Second World War. It was listed as a *genus incertae sedis* of the Satyrinae by Sohn *et al.* (2012), following Urbahn & Urbahn (1939). Recently, the matter received a hilarious denouement when the original "fossil" was offered for sale at the website eBay by one of the grandchildren of Wangrin, together with the original publication and an original photograph (Ansorge 2015). The item turned out to be a forgery, an impression made in plaster and stuck to the surface of a broken "Stettiner Kugel" (Fig. 18) (see Ansorge 2015 for the entire story).

Westwood (1854) depicted the remnants of what according to him could have been the hindwings of butterflies (Lower Purbecks, Durdlestone Bay). His Fig. 27 on plate XVIII shows a part of a wing, although the venation does not agree with any known butterfly. It appears to be a hindwing on which two anal veins and a cubital vein are visible. If this interpretation is correct, then there is a well-developed vein in the cell, a situation not found in the butterflies. Any other interpretation of the veins seems to be even more doubtfulWestwood's Fig. 30 is in poorer conditions. It shows six veins diverging from what seems to be a common point or area, unlike any arrangement found in recent butterflies, or other Lepidoptera, for that matter.

Zeuner (1930) recorded a fossil caterpillar from the upper Miocene of Böttingen, Southern Germany. Without giving a description, he noted that the specimen was similar to caterpillars of the recent genus *Apatura* (Nymphalidae). Apparently, Zeuner meant that the unspined, spindle-shaped body and the two long horns on the head are also found in *Apatura*. This is the general body shape and ornamentation in Apaturinae. Splendid images of caterpillars of other Apaturinae (*Chitoria, Helcyra, Sasakia, Hestinalis, Sephisa, Herona*) can be found in Igarashi & Harada (2015). Rather similar shapes also can be found in various Satyrinae, but in this subfamily the body is more slender and the tails usually prominently two-pronged. Presently, the fossil caterpillar may be classified as belonging to the Apaturinae. In view of the age of the fossil—between 11 and 5 Ma—it is not an exciting date for divergence time.

Fossils excluded from butterflies

incertus. Satyrites incertus Daudet, 1876

Daudet (1876) described and depicted a supposed fossil caterpillar (France, Bouches-du-Rhône, Aix-en-Provence; early Oligocene), with a bifid tail. For this reason, he described it as belonging to Nymphalidae: Satyrinae, although this character occurs in some other subfamilies of the Nymphalidae as well (Ackery *et al*. 1999), and even assigned it to a fossil genus described by Scudder (1872). Nel & Nel (1985) found many similar fossils at the same locality and concluded that they were not caterpillars, but conifer catkins, that with some fantasy are reminiscent of caterpillars.

Unidentified "butterfly"

In a book on an Eocene lake desposit in southwestern Wyoming (Green River Formation, c. 53–51 Ma,) Grande (2013) published two photos of an alleged fossil butterfly. The photos do not show details that can identify the fossil as a butterfly. Maria Heikkilä (pers. comm.) saw the actual fossil and confirmed that no such details can be seen.

On which tree should the fossil be allocated?

The start of the study on the phylogeny of the butterflies was rather slow. Kristensen (1976) published the first tree based on cladistic principles. The author discussed the interrelationships of the five butterfly families recognized at the time and they collectively were considered a monophyletic group: Hesperiidae, Papilionidae, Pieridae, Nymphalidae and Lycaenidae (including Riodinidae), on the basis of 42 characters. The next phylogenetic tree established for butterflies appeared twenty years after Kristensen's paper (de Jong *et al*. 1996), and was based on 74 taxa (59 butterflies and 15 outgroups) and 103 morphological characters. Consequently, the tree was considerably more detailed than Kristensen's (1976) tree, but still entirely based on morphology. Nine years later the morphological database of de Jong *et al.* (1996) was combined with molecular characters from three gene regions, resulting in the most detailed tree available at the time (Wahlberg *et al*. 2005a). More recent studies based on more genes and larger sets of taxa have changed our perception of butterfly phylogeny (Regier *et al*. 2009; Heikkilä *et al*. 2011; Kawahara & Breinholt 2014; Timmermans *et al*. 2014). Recently, more extensive datasets have been analysed for entire families, subfamilies or larger datasets of genera such as Papilionidae (Miller 1987; Simonsen *et al*. 2011), Papilionidae: Parnassiinae (Nazari *et al*. 2007), Papilionidae: Troidini (Braby *et al*. 2005; Silva-Brandão *et al*. 2005), Papilionidae: *Parnassius* (Omoto *et al*. 2004), Papilionidae: *Papilio* (Zakharov *et al.* 2004), Hesperiidae (Warren *et al*. 2008, 2009), Pieridae (Braby *et al*. 2006; Wahlberg *et al*. 2014), Nymphalidae (Freitas & Brown 2004; Wahlberg *et al*. 2009), Nymphalidae: Nymphalinae (Wahlberg *et al*. 2005b), Nymphalidae: Satyrinae (Peña & Wahlberg 2008), Nymphalidae: Danaini (Brower *et al*. 2010), Nymphalidae: Ithomiini (Willmott & Freitas 2006; Brower *et al*. 2006, Brower *et al*. 2014; Garzón-Otduña 2015), Nymphalidae: Acraeini (Silva- Brandão 2008), Nymphalidae: Libytheinae (Kawahara 2009, 2013), Nymphalidae: Brassolini (Penz *et al*. 2013), Nymphalidae Heliconiini (Brower & Egan 1997; Kozak *et al*. 2015), Nymphalidae: Phyciodina (Wahlberg & Freitas 2007), and Riodinidae (Espeland 2015). For the Lycaenidae a recent analysis for the entire family based on morphological and molecular data is still wanting, but for the time being the intuitive phylogenetic tree by Eliot (1973) can be used as a start, but without molecular data age estimation by way of a molecular clock is obviously currently impossible. There is a growing number of phylogenies encompassing larger datasets of genera of Lycaenidae based on molecular data such as Rand *et al*. (2000), *Chrysoritis*; Megens *et al*. (2004), *Arhopala*; Kandul *et al*. (2004), *Agrodiaetus*; Fric *et al*. (2007), *Phengaris-Maculinea*; Talavera *et al*. (2013), *Elcalyce* affinities; Ugelvig *et al.* (2011), *Glaucopsyche*; Wiemers *et al*. (2010), *Polyommatus* and *Plebicula*. However, there is no suitable fossil lycaenid for calibration purpose.

Currently, trees contain a large number of taxa, so in principle the placement of a fossil, given the right characters and the correct interpretation, can be relatively precise. It must be realized, however, that trees are liable to change when more and/or other taxa and more and/or other characters are included, possibly leading to alternative estimates of divergence times if the same fossil is used on different trees. An example is given and discussed under *Lethe* (?) *corbieri*, below.

In Fig. 22 butterfly fossils, as far as assignable to family or higher category and with the exception of fossils from Pleistocene or younger deposits (7 species) and those fossils not assignable to a particular family (8), have been indicated on the phylogenetic tree. This tree has been compiled from the published information for all families

(Heikkilä *et al*. 2011), Papilionidae (Simonsen *et al*. 2011), Hesperiidae (Warren *et al*. 2009), Pieridae (Wahlberg *et al.* 2014), Lycaenidae (Wahlberg *et al*. 2005a) and Riodinidae (Espeland *et al*. 2015). It emphasizes that the distribution of fossil butterflies is very uneven not only across the globe and over time, but on the phylogenetic tree as well. (In Appendices 1 and 2 a survey is given of all butterfly fossils arranged by family and their possible use as calibration points are indicated.)

Fossils and calibrating the molecular clock

A comprehensible introduction to calibrating molecular clocks was given by Benton *et al*. (2009). De Jong (2007) provided a review of various criteria for clock calibration in Lepidoptera, among which the age of fossils played a key role. As explicitly expressed by Brower and Vane-Wright (2011), in estimating divergence times "*The only direct link to an absolute time scale in molecular dating is the empirical ages of fossils (or other geological events) attached to particular nodes on the tree.*" All age estimates based on fossil butterflies are derivatives of these direct links, and interpolations and extrapolations frequently derived from the Bayesian statistical program BEAST (Drummond & Rambaut 2007). Brower and Vane-Wright (2011) emphasized the crucial role of the precision of taxonomic affinity of the fossils used as calibration points: "*When those anchors are tossed overboard to accommodate contradictory results from an algorithm that uses them as calibration points (we note that BEAST puts 95% confidence intervals even on its externally calibrated nodes), we see a problem - the model has become more "real" than the data, and in the process 'history' becomes fiction* …" In this connection I also approvingly quote from a recent message (September 2016) from Brower: "*For example, in BEAST, the most plausible model option for the age of a node calibrated by a fossil is a normal distribution with a truncated upper bound, but this makes most "likely" the upper bound age and deemphasizes the crucial caveat that a fossil represents a minimum age for the node to which it is assigned. This factor by itself tends to bias the clock towards faster rate*."

A recurrent theme is the discrepancy between ages estimated on the basis of a molecular clock and those of the oldest fossils of the group under study ("rock/clock discrepany"). A good reference to this problem can be found in O'Leary *et al*. (2013) in a discussion on placental mammals, and is dealt with in the superb paper by Wilf & Escapa (2014) using Gondwana plants, but it is apparent in butterflies as well, where the oldest known fossil is 55 Ma (*Protocoeliades kristenseni*), while recent estimates of the origin of the butterflies are about 100 Ma (Heikkila *et al*. 2012). The discrepancy could partly be due to a methodological bias (Rodriguez-Trelles *et al*. 2002), but in many cases, and certainly in the case of butterflies with their meagre fossil record, to the incompleteness of the fossil record. This problem was tackled for fossil in general by Marshall (1997) by establishing confidence intervals for the origin of a fossil lineage based on (1) the preservational potential of the lineage (e.g. lepidopteran are low compared to beetles); and (2), the density of the fossil record for that particular lineage (e.g. marsupial fossils are considerably more sparse than placentals. However, even for such an approach the density of butterfly fossils may be too low. Another factor may play a part. In angiosperms, where the fossil record is incomparably richer than in insects, and certainly than in butterflies, there is also a large discrepancy between the so-called rock and clock ages, which in view of the very rich fossil record can hardly be contributed to the fossils. Magallón (2014) published a most interesting review of the effect of several factors in the estimation of angiosperm age. She concluded that model misspecification (see also the remark by Brower & Vane-Wright 2011 above) might play a role in the observed molecular clock/fossil discrepancy. At the same time she remarked that (p. 18): "… all studies have recognized the crucial impact of calibrations on age estimation."

A factor possibly influencing the clock rate for butterflies not examined (or at least not mentioned) to date is the cooling of the climate worldwide around the Eocene–Oligocene transition. After the long-standing equal warm temperate to subtropical conditions of the Eocene, the annual mean temperature dropped sharply within a few million years (Crowley & North 1991; Behrensmeyer *et al*. 1992; Prothero & Berggren 1992; Berggren & Prothero 1993; Prothero 1994). In North America, for instance, the temperature dropped by 10–15°C. It undoubtedly had an impact on generation time and number of generations per year for butterflies, although there might have been large local or regional differences. It has been postulated (Page & Holmes 1998) that substitution rate should be counted as generations rather than years. There are good reasons for this to be the case in mammals as well as in plants, where plant age at first flowering rather than generation time could be a relevant measure. I am not aware of analogous tests with butterflies. Under equal tropical conditions butterflies tend to have a maximum of, perhaps, 12 generations per year, indicative of year-roundproduction, while in temperate zones the speed of reproduction may slow down dramatically to one generation per year. Could it be that the substitution rate and thus the clock has slowed down since, say, the Oligocene? Suppose we have an Oligocene fossil reliably placed at the node of two sister genera. The clock rate is the number of substitutions between the two genera divided by the number of (million) years of the fossil. On the basis of this clock rate we want to estimate the age of one node down, specifically the origin of the ancestor of the two sister genera combined and their sister group. If the clock ticked at the same pace before the Oligocene, there would be a linear relation between number of substitutions and time elapsed, but if the clock ticked faster for the substitutions before the Oligocene, the age of the last node would be overestimated. If and how far this phenomenon may have influenced recent estimations is unknown.

Obviously, the less detailed a tree is, the less precise the position of the calibration point can be. In this context, the expansive tree published by Misof *et al*. (2014), covering all insect orders and many subordinate taxa, is illustrative. Although detailed at the level of orders, there is very little detail at lower levels. Only ten Lepidoptera genera have been included, among which are two butterflies, *Parides* of the Papilionidae and *Polyommatus* of the Lycaenidae. The divergence between Trichoptera and Lepidoptera is dated at about 210 Ma and the first split in the Lepidoptera lineage (*Micropteryx* versus the rest) at about 150 Ma. In their tree (their Fig. 1), the authors estimate the split between *Polyommatus* and *Parides* at about 40 Ma. This is younger than the age of the oldest known butterfly fossil, *Protocoeliades kristenseni*, which is 55 Ma old (see above). The latter fossil belongs to the Hesperiidae, which according to recent analyses (Regier *et al*. 2009; Heikkilä *et al*. 2011; Timmermans *et al*. 2014) (Fig. 22) arose after Papilionidae and thus, the Papilionidae must be older. The discrepancy with the Misof *et al*. (2014) estimate must (at least partly) be due to the use of a fossil butterfly, *Libytheana vagabunda* (by Misof *et al*. 2014 dated as 34,07 Ma exactly), for calibration. The problem with using this fossil in this particular tree is that it belongs to the Nymphalidae, a family that originated after Papilionidae (to which *Parides* belongs) and before Lycaenidae (to which *Polyommatus* belongs). So where exactly should one place the calibration point? Or, to say it more plainly, is this fossil acceptable for calibrating this particular tree?

Whatever considerations and models are used for divergence time estimations, it must be clear that there is no material evidence for a deeper age of the butterflies (employing either the old or newer concepts) than the oldest fossil recognizable as a butterfly. The oldest butterfly is *Protocoeliades kristenseni*. All age estimates of the origin of the butterfly families, plausible as they may be, are what they are—estimates—dependent (apart from the discussion above) on the correct allocation of fossils to the trees and on the trees themselves, and thus liable to change. Sweeping conclusions about paleobiogeography based on these estimates also must be considered with reservation.

Biogeographic considerations

In view of their rarity and uneven geographic distribution across the globe, the known butterfly fossils presently offer little direct information on the distributional history of higher butterfly taxa. This is in stark contrast to what has been found for other organisms, such as vertebrates with as striking example the horses (MacFadden 1992) as well as several groups of insects (Grimaldi & Engel 2005). Yet, there are two fossil butterfly taxa (*Protocoeliades*, *Neorinella)* that have been found on a continent where their supposed closest relatives currently do not live, suggesting large-scale extinction. Obviously, such observations are dependent on correct identification of the fossils. For instance, *Lethe montana*, a fossil from Montana in North America, is supposed to belong to the extant genus *Lethe* (Miller *et al*. 2012; see above). The extant species of the genus are confined to temperate and tropical East and Southeast Asia. If the assignment of the fossil to *Lethe* is correct – in other words, if the fossil shows an apomorphy of the extant genus—it may lead to considerations of the faunal origin, exchange and large-scale extinction of this taxon. However, since the fossil does not show an apomorphy that undoubtedly assigns its position on the phylogenetic tree, there is no evidence for such considerations. This deficit does not mean that the conclusion of a once widespread genus *Lethe* is wrong, but if correct, it is for the wrong reason. Without evidence, it is just speculation.

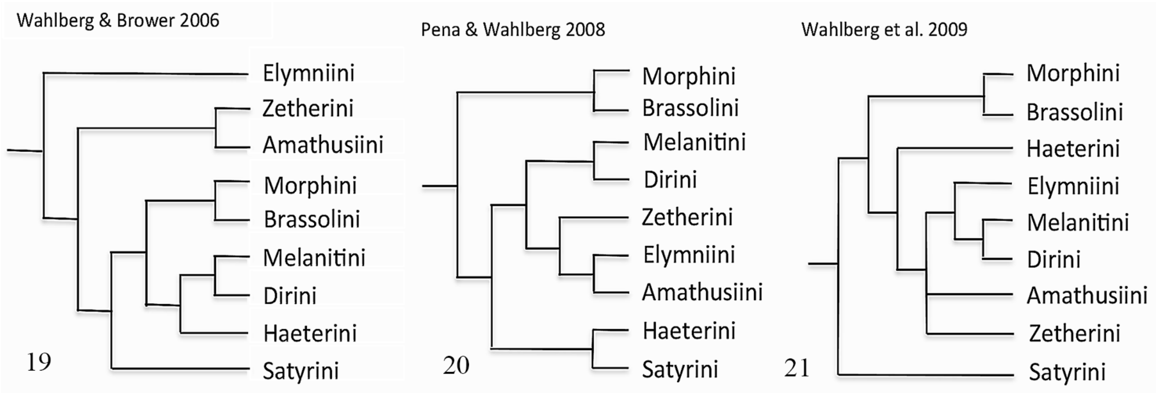
Generally, biogeographic considerations emerge from a phylogenetic analysis and an estimation of divergence times. Such biogeographic discussion can provide the geographic history of the group under study in isolation, but not as part of an evolving fauna. Although much information on faunal evolution can be found in literature, it is rarely considered in the taxonomic literature, probably because students are more interested in the group under study and have less concern for the general picture of insect or biotal evolution. I strongly advise students examining the history of their group to consider it as part of a fauna and not as an isolated tree in a forest of other isolated trees. As an example there is the tendency of some students to see an important role of the break-up of Gondwana in the diversification of the butterflies. This perspective is a widespread tendency (Vane-Wright 2004; Peñalver & Grimaldi 2006). A recent estimate for the earliest split in the Papilionidae lineage (Condamine *et al.* 2012), the first offshoot of the butterfly lineage (a.o., Heikkilä *et al.* 2011), demonstrate that the divergence of this family started much too late (52–53 Ma) to have been influenced by the breaking-up of Gondwana, contrary to the conclusion by Braby *et al.* (2005) for a subordinate taxon of this family.

In addition to critically evaluating their own considerations, students are advised to read, for example, Eskov (2002), regarding the numerous insect taxa that now are restricted to the Southern Hemisphere. These taxa have relatives that have been found in Cretaceous and Paleogene entomofaunas of Eurasia and/or North America. A striking example is the chironomid midge subfamily Aphroteniinae, now restricted to South Africa, Australia and South America, which comprise a typical Gondwanan distribution, but also are found in late-Cretaceous amber of Northern Siberia. Using similar reasoning, Larsson (1978), while discussing Baltic amber, concluded, "*The 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 present distribution, they must be regarded as the remains of groups which in the Eocene have had a much greater, often circumpolar distribution.*" There is no reason to suppose that this pattern is different with butterflies.

The oldest butterfly fossil known, *Protocoeliades kristenseni*, was found in Denmark, although probably most closely related extant genera, *Hasora* and *Burara*, together with additional genera, are confined to Southeastern Asia (some species of *Hasora* extend into the Pacific and into Australia). The relevant subfamily, Coeliadinae, occurs across Africa and Madagascar. Consequently, these taxa conform to the pattern just described and it indicates that the subfamily during the Paleogene had a wider or at least a different biogeographical distribution. At the time that *Protocoeliades* was an inhabitant of what now is Denmark, the Tethys Ocean still widely separated the northern continents from the southern Gondwanan continents, and India was distant and had not yet docked with Asia, but was transported northerly across Tethys and traversed the paleoeqator (Fig. 23). If *Protocoeliades* was distributed across Gondwana remnants, it could only have reached such a wide distribution by crossing very wide stretches of ocean. However, if it was confined to the northern hemisphere, a, periodically broken, wide land connection between Europe and Asia facilitated a wide distribution in proto-Eurasia (see relevant maps in Smith *et al.* 1994). The two available phylogenetic trees for Coeliadinae (de Jong 2016: Figs. 8, 9), although differing considerably, agree in placing the African members at a high position in the tree, suggesting that the subfamily diversified in Eurasia before Africa approached sufficiently close enough to be colonized. The latter pattern is intriguing, since the Coeliadinae is the first offshoot of the Hesperiidae lineage (Warren *et al.* 2008, 2009), and the Hesperiidae are rather basal (after Papilionidae) in the butterfly hierarchy (e.g. Heikkilä *et al.* 2011). As such, the early geographic history of the Coeliadinae may shed some light on the early geographic diversification of butterflies, as mentioned earlier by de Jong (2007).

A second fossil butterfly agreeing with the pattern of a northern continental occurrence during the Paleogene and the presence of its relatives in the modern tropics, is *Neorinopsis sepulta*, from the lower Oligocene in Southern France. On the basis of a venational character, it appears to belong to the Elymniini (Nymphalidae, Satyinae), a tribe that at present is found exclusively in tropical Asia, but with a single species in Africa. The pattern appears to be a repetition of the Coeliadinae case.

Surprisingly, a fossil with the venational apomorphy of Elymniini, *Neorinella garciae*, and of approximately the same estimated age as *Neorinopsis sepula*, was found in Southern Brazil. The occurrence of relatives in Africa and South America is suggestive of Gondwanan origin, but tropical Asia, where almost all species occur, has never been part of Gondwana. Moreover, Africa and South America became separated (Smith *et al.* 1994) around the time when the butterflies were supposed to have originated, although there are no reliable estimates beyond about 90 Ma (de Jong 2016). The major tectonic fragmentation of Gondwana occurred long before the Elymniini originated. Either the venational similarity among taxa of Elymniini is due to convergence or a different distributional history than that of a Gondwanan origin must be examined. In view of the finding of the same character during the same time interval in Southern France, the idea of a Gondwanan history is unlikely.



FIGURES 19–21. Three phylogenetic trees for Nymphalidae: Satyrinae. See text for explanation.

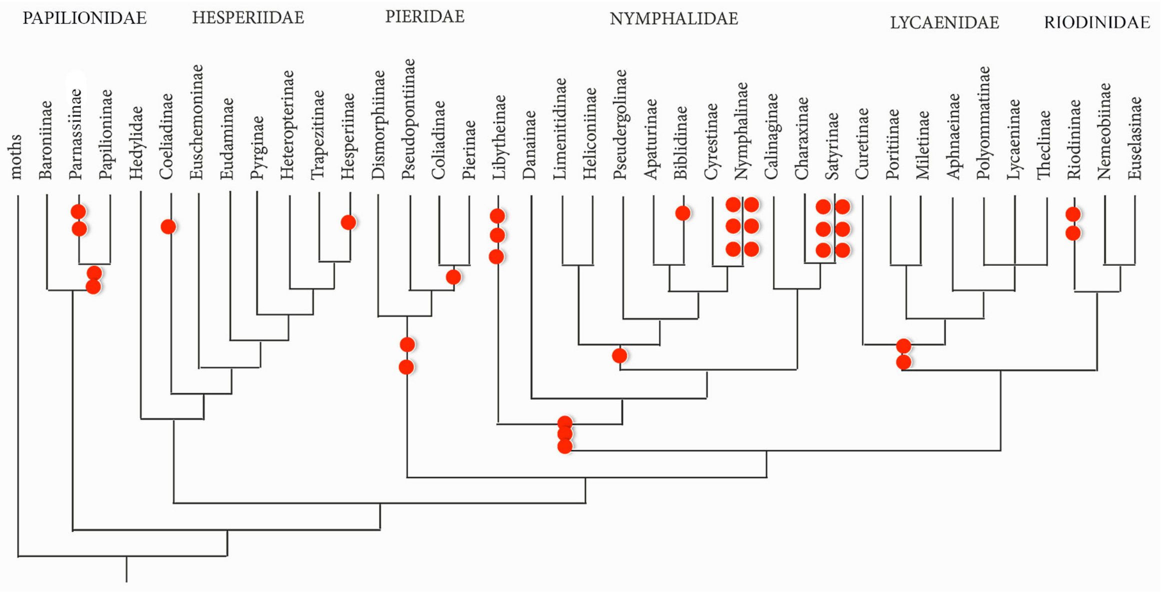


FIGURE 22. Fossils marked on phylogenetic tree of "redefined" butterflies (Heikkilä *et al*. 2011), with family trees according to Simonsen *et al*. (2011, Papilionidae), Warren *et al*. (2009, Hesperiidae), Wahlberg *et al*. (2014, Pieridae), Wahlberg *et al*. (2005, Lycaenidae), and Espeland *et al*. (2015, Riodinidae).

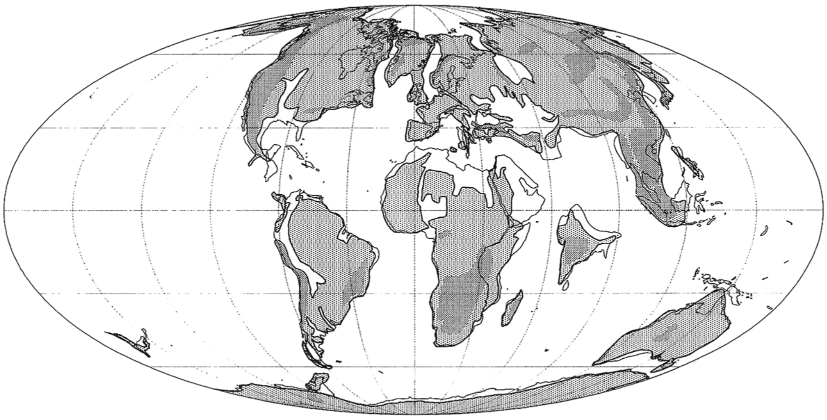


FIGURE 23. Distribution of land, epicontinental seas (flooded continental areas) and oceans during the middle Paleocene (Thanetian Stage) at 60 Mya. From Smith, A.G., Smith, D.G. & Funnell, B.M. (1994); with permission of Cambridge University Press and University of East Anglia.

The impact of the break-up of Gondwana has considerable currency, not only in butterflies but in plants as well. In a paper on Gondwanan origins of various plant lineages, Wilf & Escapa (2014: 283) uttered the plea "… we urge significantly greater caution when using molecular dating to interpret the biological impacts of geological events." Ironically, in this case molecular data gave younger ages than fossils. According to the authors this was due to a then very incomplete fossil record from South America, and the tendency to place calibration points at too low of a position on the tree, in a stem position instead of a crown position. Such a position makes crown lineages younger than when placed in a crown position. Since nothing is said on plesiomorphy or apomorphy (Wilf & Escapa 2014), it is difficult for an entomologist to judge, but it is certainly true that the discovery of a butterfly fossil, say, 70 or 80 million years of age in South America, or in any other continent for that matter, would open a fascinating perspective.

A Gondwanan distribution is a term for a vicariant distribution of sister taxa across remnants of Gondwana. This is a description, not an explanation, as long as there is no evidence of a vicariant geographic event having caused it. The idea that a vicariant distribution is evidence of a former continuous distribution has perennially dominated biogeographic thinking, even to the effect that geological events were postulated to accommodate distribution patterns, and people with a more balanced view of biogeography were easily assigned to the "dispersalist" camp. The rise of molecular clock methods has challenged this idea. Trewick (2000) provided a striking example. This author examined four genera of flightless insects from three insect orders with sister-group taxa in New Zealand and the Chatham Islands, 800 km apart in the Pacific Ocean. The biota of the isolated Chatham Islands was supposed to have survived the tectonic movements that separated the islands from the remainder of Gondwana, some 70 million years ago. However, using mitochondrial DNA, Trewick (2000) found that the flightless insects of the Chatham Islands had not been separated from their New Zealand sister-groups by more than 2–6 million years. The temporal data indicate that long distance dispersal was inevitable, even though the means of transport remains obscure.

A perversion of the concept that vicariant distributions are the result of vicariant events is the use of the vicariant events for calibration points of the molecular clock (e.g., Braby *et al.* 2005). This approach was rejected by Peñalver & Grimaldi (2006) and de Jong (2007) as circular reasoning.

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APPENDIX 1. Fossil butterflies arranged by family, with possible calibration points indicated

Within families butterfly fossils have been arranged alphabetically based on the genus in which they were originally placed (see main text for possible later combinations). Switching fossil species between fossil genera is problematic, since none of the fossil genera is defined by an autapomorphy.

If used as a calibration point, the fossil should be placed at the stem node of the taxon where it originated, split from its sister clade and it is given the designation "C -". Generally speaking, the older the fossil is, and the higher up it is positioned in the crown of the tree, the more relevant it will be for use as a calibration point. Evidently, those species listed as "incertae sedis" cannot be used for calibration, except at the level of the stem node of all butterfly lineages. As such, they are too young to be of any use.

The age ranges are according to Walker *et al*. (2013).

Papilionidae

Doritites bosniaskii Rebel, 1898
  Late Miocene: Messinian (7.2–5.3 Ma). Italy, Toscana, Gabbro.
  C – Papilionidae: Parnasiinae: Luehdorfiini.
Papilio cf. *maackii* Ménétries, 1859
  Late Pleistocene, 37.800 BP; Japan, Shiobara.
  C – Papilionidae: Papilioninae: Papilio; in view of young age not relevant.
Praepapilio colorado Durden & Rose, 1978
  Middle Eocene: Early Lutetian (47.8–41.2 Ma). USA Colorado, Ray Dome.
  C—Papilionidae.
Praepapilio gracilis Durden & Rose, 1978
  Middle Eocene: Early Lutetian (47.8–41.2 Ma). U.S.A., Colorado, Ray Dome.
  C—Papilionidae.
Thaites ruminiana Scudder, 1875
  Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (± 23 Ma). France, Dépt. Bouches-du-Rhône, Aix-en-Provence.
  C—Papilionidae: Parnassiinae: Parnassiini.

Hesperiidae

Andronymus neander Plötz, 1884
  Late Pleistocene (20 Ka?). Tanzania, Zanzibar.
  C—Hesperiidae: Hesperiinae: *Andronymus*; in view of young age, not relevant.
Pamphilites abdita Scudder, 1875
  Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). France, Dépt. Bouches-du-Rhône, Aix-en-Provence.
  C—Hesperiidae: Hesperiinae.

Protocoeliades kristenseni de Jong, 2016
  Late Paleocene–Early Eocene (Thanetian– Ypresian) (±55 Ma). Denmark, Jutland, Isle of Fur.
  C—Hesperiidae: Coeliadinae.

Pieridae

Aporia cf. *crataegi* (Linnaeus, 1758)
  Late Pliocene (3.6–2.6 Ma); Germany, Willershausen.
  C—Pieridae; in view of the young age not relevant.
Belenois crawshayi Butler, 1894
  Pleistocene or post-Pleistocene (± 20 Ka?). Tanzania, Zanzibar.
  C—Pieridae: Pierinae; in view of the young age not relevant.
Miopieris talboti Zeuner, 1942
  Early Miocene: Burdigalian (20.4–16 Ma). Germany, Baden-Würtemberg, Randecker Maar.
  C—Pieridae.
Vanessa pluto Heer, 1849
  Early Miocene: Burdigalian (20.4–16 Ma). Croatia, Radoboj.
  C—Pieridae: Coliadinae+Pierinae.

Lycaenidae

Aquisextana irenaei Théobald, 1937
  Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). France, Dépt. Bouches-du-Rhône, Aix-en-Provence.
  C—Lycaenidae(?).
Lycaenites gabbroensis Rebel, 1898
  Late Miocene (11.6–5.3 Ma). Italy, Toscana, Gabbro.
  C - Lycaenidae.

Riodinidae

Theope spec.
  Early Miocene: Burdigalian (20.4–16 Ma); Dominican Amber.
  C—Riodinidae: Riodininae: Nymphidiini.
Voltinia dramba Hall, Robinson & Harvey, 2004
  Early Miocene: Burdigalian (20.4–16 Ma); Dominican Amber.
  C—Riodinidae: Riodininae: Mesosemiini: *Voltinea*. However, allocation of the fossil uncertain (Noemy Seraphim Pereira, pers. comm.); a new study will be published soon.

Nymphalidae

Barbarothea florissanti Scudder, 1892
  Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
  C—Nymphalidae: Libytheinae.
Charaxes candiope Godart, 1824
  Late Pleistocene (± 20 Ka?). Tanzania, Zanzibar.
  C—in view of young age not relevant.
Chlorippe wilmattae Cockerell, 1907
  Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
  C—Nymphalidae: Nymphalinae+Biblidinae+Cyrestinae+Apaturinae.
Cyllo sepulta Boisduval, 1841
  Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). France, Dépt. Bouches-du-Rhône, Aix-en-Provence.
  C—Nymphalidae: Satyrinae.
Dynamine alexae Peñalver & Grimaldi, 2006
  Early Miocene: Burdigalian (20.4–16 Ma). Dominican amber.
  C—Nymphalidae: Biblidinae.
Hestina japonica (C. et R. Felder, 1862)
  Late Pleistocene, 37.800 BP; Japan, Shiobara.
  C—Nymphalidae: Apaturinae; in view of young age not relevant.
Jupiteria charon Scudder, 1889

Late Eocene: Late Priabonian (33.9–28.1 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae: Nymphalinae.

Lethe montana Miller, Miller & Ivie, 2012
Early Oligocene: Rupelian (33.9–28.1 Ma). USA, Montana, Canyon Ferry Reservoir.
C—Nymphalidae: Satyrinae (see also the discussion under this species).

Lethe (?) *corbieri* Nel, Nel & Balme, 1993
Early Oligocene: Rupelian (33.9–28.1 Ma). France, Dépt. Vaucluse, Céreste.
C—Nymphalidae: Satyrinae (see also the discussion under this species).

Lithopsyche styx Scudder, 1889
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae.

Neorinella garciae Martins Neto *et al*., 1993
Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). Brazil, State of São Paulo, Tremembé.
C—Nymphalidae: Satyrinae: Elymniini.

Nymphalites obscurum Scudder, 1889
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae.

Nymphalites zeuneri Jarembowski, 1980
Late Eocene: Late Priabonian (35–33.9 Ma). Great Britain, Isle of Wight, Bembridge.
C—Nymphalidae.

Oligodonta florissantensis Brown, 1976
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae: Libytheinae.

Pierella spec. (teste Warren)
Holocene/Pleistocene (±12 Ka?). Colombia, Santander Department. Copal.
C—too young to be relevant.

Prodryas persephone Scudder, 1878
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae.

Prolibythea vagabunda Scudder, 1889
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae: Libytheinae (based on overall similaity rather than apomorphy).

Pseudoneorina coulleti Nel & Descimon, 1984
Early Oligocene: Stampien (= Rupelian) (33.9–28.1 Ma). France, Dépt. Alpes-de-Haute-Provence, Céreste and Dauphin.
C—Nymphalidae: Satyrinae.

Pyrameis fossilis Nekrutenko, 1965
Middle Miocene: Langhian (16–13.8 Ma). Russia, Caucasus, Stavropol.
C—Nymphalidae: Nymphalinae.

Satyrites reynesii Scudder, 1872
Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). France, Dépt. Bouches-du-Rhône, Aix-en-Provence.
C—Nymphalidae: Satyrinae.

Sphinx atava Charpentier, 1843
Early Miocene: Burdigalian (20.4–16 Ma). Croatia, Radoboj.
C—Nymphalidae: Nymphalinae.

Vanessa amerindica Miller & Brown, 1989
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
C—Nymphalidae: Nymphalinae: Nymphalini.

Vanessa karaganica Nekrutenko, 1965
Middle Miocene: Langhian (16–13.8 Ma). Russia, Caucasus, Stavropol.
C—Nymphalidae.

Species incertae sedis

Apanthesis leuce Scudder, 1889
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.

Archaeolycorea ferreirai Martins-Neto, 1989
Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). Brazil, State of São Paulo, Tremembé.

Coliates proserpina Scudder, 1875
Late Oligocene–Early Miocene boundary: Chattian–Aquitanian (±23 Ma). France, Dép. Bouches-du-Rhône, Aix-en-Provence.

Stolopsyche libytheoides Scudder, 1889
Late Eocene: Late Priabonian (35–3.94 Ma). U.S.A., Colorado, Florissant.
Lithopsyche antiqua Butler, 1889
Late Eocene: Late Priabonian (35–33.9 Ma). Great Britain, Isle of Wight, Bembridge.
Nymphalites scudderi Beutenmüller & Cockerell, 1908
Late Eocene: Late Priabonian (35–33.9 Ma). U.S.A., Colorado, Florissant.
Pierites freyeri Heer, 1849
Early Miocene: Burdigalian (20.4–16 Ma). Croatia, Radoboj.
Riodinella nympha Durden & Rose, 1978
Middle Eocene: Early Lutetian (47.8–44 Ma). U.S.A., Colorado, Ray Dome.
Vanessa vetula Von Heyden, 1859
Late Oligocene: Chattian (28.1–23 Ma). Germany, Rheinland-Pfalz, Rott.

APPENDIX 2. Usable calibration points.

Redundant calibration points, such as younger ages of a more inclusive taxon than of one of its constituent taxa, or younger ages for the same taxon, could be problematical for divergence-time analysis. For instance, two fossils that are identifiable as Pieridae but not more precisely, are much younger than many fossils of the younger Nymphalidae, and their use as calibration points could easily yield incorrect results. Similarly, the oldest papilionid fossils are 48.6–44 Ma, consaiderably younger than the oldest hesperiid fossil, although the latter family is younger than the papilionids according to modern analyses. As a result, many fossils are insufficiently useful for calibration, as can be concluded from the following list (compare with Appendix 1 for details).

Papilionidae	Parnassiini	23 Ma	
	Luehdorfiini	7.2–5.3 Ma	
Hesperiidae	Coeliadinae	55 Ma	
	Hesperiinae	23 Ma	
Pieridae	Coliadinae+Pierinae	20.4–16 Ma	
Lycaenidae	23 Ma		
Riodinidae	Riodininae	Nymphidiini	20.4–16 Ma
	Riodininae	Mesosemiini	20.4–16 Ma
Nymphalidae	Libytheinae	35–34 Ma	
	Nymphalinae	Nymphalini	35-34 Ma
	Satyrinae	34–28.4 Ma	
	Satyrinae	Elymniini	23 Ma
	Biblidinae	20.4–16 Ma	

APPENDIX 3. Genera to which fossil butterflies have been assigned, and their type species

The names of genera of which the type species is a fossil, have been printed in bold.

Andronymus Holland, 1896	*Pamphila philander* Hopffer, 1855
Apanthesis Scudder, 1889	*Apanthesis leuce* Scudder, 1889
Aporia Hübner, [1819]	*Papilio crataegi* Linnaeus, 1758
Aquisextana Théobald, 1937	*Aquisextana irenaei* Théobald, 1937
Archaeolycorea Martins-Neto, 1989	*Archaeolycorea ferreirai* Martins- Neto, 1989
Barbarothea Scudder, 1892	*Barbarothea florissanti* Scudder, 1892
Belenois Hübner, [1819]	*Papilio calypso* Drury, [1773]
Chlorippe Doubleday, 1844	*Nymphalis laurentia* Godart, [1824]
Coliates Scudder, 1875	*Coliates proserpina* Scudder, 1875
Cyllo Boisduval, 1832 junior objective synonym of *Melanitis* Fabricius, 1807	*Papilio leda* Linnaeus, 1758
Dynamine Hübner, [1819]	*Papilio mylitta* Cramer, [1780]
Doritites Rebel, 1898	*Doritites bosniaskii* Rebel, 1898
Hestina Westwood, 1850	*Papilio assimilis* Linnaeus, 1758
Jupiteria Scudder, 1889	*Jupiteria charon* Scudder, 1889
Lethe Hübner, 1891	*Papilio europa* Fabricius, 1775
Lethites Scudder, 1875	*Satyrites reynesii* Scudder, 1872

junior objective synonym of *Satyrites* Scudder, 1872	
Lithodryas Cockerell, 1909	*Lithopsyche styx* Scudder, 1889
replacement name for *Lithopsyche* Scudder, 1889	
Lithopsyche Butler, 1889	*Lithopsyche antiqua* Butler, 1889
Lithopsyche Scudder, 1889	*Lithopsyche styx* Scudder, 1889
junior homonym of *Lithopsyche* Butler, 1889	
Lycaenites Rebel, 1898	*Lycaenites gabbroensis* Rebel, 1898
Miopieris Zeuner, 1942	*Miopieris talboti* Zeuner, 1942
Mylothrites Scudder, 1875	*Vanessa pluto* Heer, 1849
Neorinella Martins Neto *et al.*, 1993	*Neorinella garciae* Martins Neto *et al.*, 1993
Neorinopsis Butler, 1873	*Cyllo sepulta* Boisduval, 1841
Nymphalites Scudder, 1889	*Nymphalites obscurum* Scudder, 1889
Oligodonta Brown, 1976	*Oligodonta florissantensis* Brown, 1976
Pamphilites Scudder, 1875	*Pamphilites abdita* Scudder, 1875
Papilio Linnaeus, 1758	*Papilio machaon* Linnaeus, 1758
Pierella Westwood, 1851	*Papilio nereis* Dreury, 1782
Pierites Heer, 1849	*Pierites freyeri* Heer, 1849
Praepapilio Durden & Rose, 1978	*Praepalio colorado* Durden & Rose, 1978
Prodryas Scudder, 1878	*Prodryas persephone* Scudder, 1878
Prolibythea Scudder, 1889	*Prolibythea vagabunda* Scudder, 1889
Protocoeliades de Jong, 2016	*Protocoeliades kristenseni* de Jong, 2016
Pseudoneorina Nel & Descimon, 1986	*Pseudoneorina coulleti* Nel & Descimon, 1986
Pyrameis Hübner, [1819]	*Papilio atalanta* Linnaeus, 1758
junior objective synonym of *Vanessa* Fabricius, 1807	
Riodinella Durden & Rose, 1978	*Riodinella nympha* Durden & Rose, 1978
Satyrites Scudder, 1872	*Satyrites reynesii* Scudder, 1872
Sphinx Linnaeus 1758	*Sphinx ligustri* Linnaeus, 1758
Stolopsyche Scudder, 1889	*Stolopsyche libytheoides* Scudder, 1889
Thaites Scudder, 1875	*Thaites ruminiana* Scudder, 1875
Thanatites Scudder, 1875	*Vanessa vetula* Von Heyden, 1859
Vanessa Fabricius, 1807	*Papilio atalanta* Linnaeus, 1758
Voltinia Stichel, 1910	*Esthemopsis radiata* Godman & Salvin, [1886]

APPENDIX 4. Localities of fossil butterflies.

N America	Colorado, Ray Dome	Middle Eocene
	Colorado, Florissant	Late Eocene - Early Oligocene
	Montana, Canyon Ferry Reservoir	Early Oligocene
C America	Hispaniola, Dominican Republic	Early Miocene
S America	Colombia, Dep. Santander	Pleistocene/Holocene
	Brazil, State of São Paulo, Tremembé	Late Oligocene—Early Miocene
Europe	Denmark, Jylland, Fur	Late Paleocene
	Germany, Rheinland-Pfalz, Rott	Late Oligocene
	Germany, Bayern, Randecker Maar	Late Miocene
	Germany, Niedersachsen, Willershausen	Pliocene
	Poland, Szczecin	Middle Oligocene (forgery)
	Croatia, Krapina-Zagorje, Radoboj	Early Miocene
	Russia, Caucasus, Stavropol	Late Miocene
	Great Britain, Isle of Wight, Bembridge	Late Eocene—Early Oligocene
	France, Alpes-de-Haute-Provence, Céreste	Early Oligocene
	France, Alpes-de-Haute-Provence, Dauphin	Early Oligocene
	France, Bouches-du-Rhône, Aix-en-Provence	Late Oligocene—Early Miocene
	Italy, Toscana, Gabbro	Middle Miocene
Africa	Tanzania, Zanzibar	Pleistocene
Asia	Japan, Honshu, Shiobara	Pleistocene