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ORIGINAL ARTICLE

Reconstructing a 55-million-year-old butterfly (Lepidoptera: Hesperiidae)

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Abstract. The oldest butterfly fossil known, which was formed about 55 Ma in what is now Denmark, is described. The fragments of its forewing venation indicates it belongs to the Hesperiidae. Further reconstruction indicates that it fits in the Coeliadinae and is close to the extant genera *Hasora* and *Burara*. It is here described as *Protocoeliades kristenseni* gen. et sp. n. It is the first butterfly fossil found on a continent (Europe) where its closest relatives do not currently occur. Its position on the phylogenetic tree of the Coeliadinae and its importance in understanding the time dimension in the evolution of butterflies, and their ecological and biogeographic implications are discussed.

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INTRODUCTION

Butterfly fossils are very rare. To date 48 fossil butterfly species are named (de Jong, in prep.). In addition, a number of purported butterfly fossils are mentioned in the literature. Sohn et al. (2015, Table 2) cites 142 fossil butterflies. This number, however, relates to specimens, not taxa (Sohn, pers. comm.), and does not include identified taxa other than the 48 recorded so far (see also their additional file with literature sources). While modern estimates place the origin of the butterflies before the Cretaceous-Paleogene boundary (see chapter Importance of this fossil for determining the time dimension in the evolution of the butterflies), the oldest recorded fossils of butterflies date from the Early Lutetian, Middle Eocene, 48 Ma (*Praepapilio*; Durden & Rose, 1978). The present paper describes (and names) an older fossil, from near the Paleocene/Eocene boundary, initially dated at 57 Ma (Rust, 1998), but more recent estimates give a date of about 55 Ma (Pedersen et al., 2004), i.e. very early Eocene. This fossil was shown to me in 1996 by the late Niels Peder Kristensen, lepidopterist at the Zoologisk Museum, Copenhagen, with the request that I identify and describe it. Although I identified it as a member of the Hesperiidae I did not describe it. A photograph of the fossil was published by Kristensen & Skalski (1999: 29), with the caption "An apparent hesperioid butterfly…". The fossil was listed in Sohn et al. (2012: 62) under Hesperiidae, but with "genus incertae sedis". At long last I fulfil my commitment to Niels with this paper, but regret that it appears after his untimely death on December 6th, 2014. I feel it is appropriate to name the fossil after him.

MATERIAL AND METHODS

The fossil (Fig. 1) was found in the Fur formation on the island of Fur in the Limfjord in N Denmark. It is a 60 m thick marine deposit of diatoms and clay minerals with many layers of volcanic ash. It was formed shortly after the Paleocene to Eocene transition, about 55 Ma (Pedersen et al., 2004) and previously estimated at 57 Ma (Rust, 1998). The deposit is famous for its many fossils, not only marine animals but also terrestrial animals, which apparently were blown into the sea or actively flew over the water. Among the numerous insect fossils only the present fossil can be identified as a butterfly.

The fossil is of a relatively broad-winged insect with wings folded down enclosing the legs. Outline of hindwings difficult to make out and most of the head is missing, but the dark lines in front of it may be remnants of palpi. Apex and greater part of termen of forewings are absent. Because of its fine detail the specimen in Fig. 1a is thought to be the compressed insect (although little is left except coloration of the substrate), of which the imprint is preserved in the counterpart illustrated in Fig. 1b. Therefore, the uppermost forewing is supposed to be the right wing. In the rest of the fossil the veins of four wings are lying on top of each other, making it difficult to decide which vein belongs to which wing. Part of the underlying (left) forewing is free and, although in this wing the apex is missing, several veins are clearly visible and there are no structures lying under it and blurring the picture. The venation of the "free" part of the (supposed) left forewing (right part of the fossil in Fig. 1a) was drawn on a transparent sheet and slid over the other forewing. By moving the

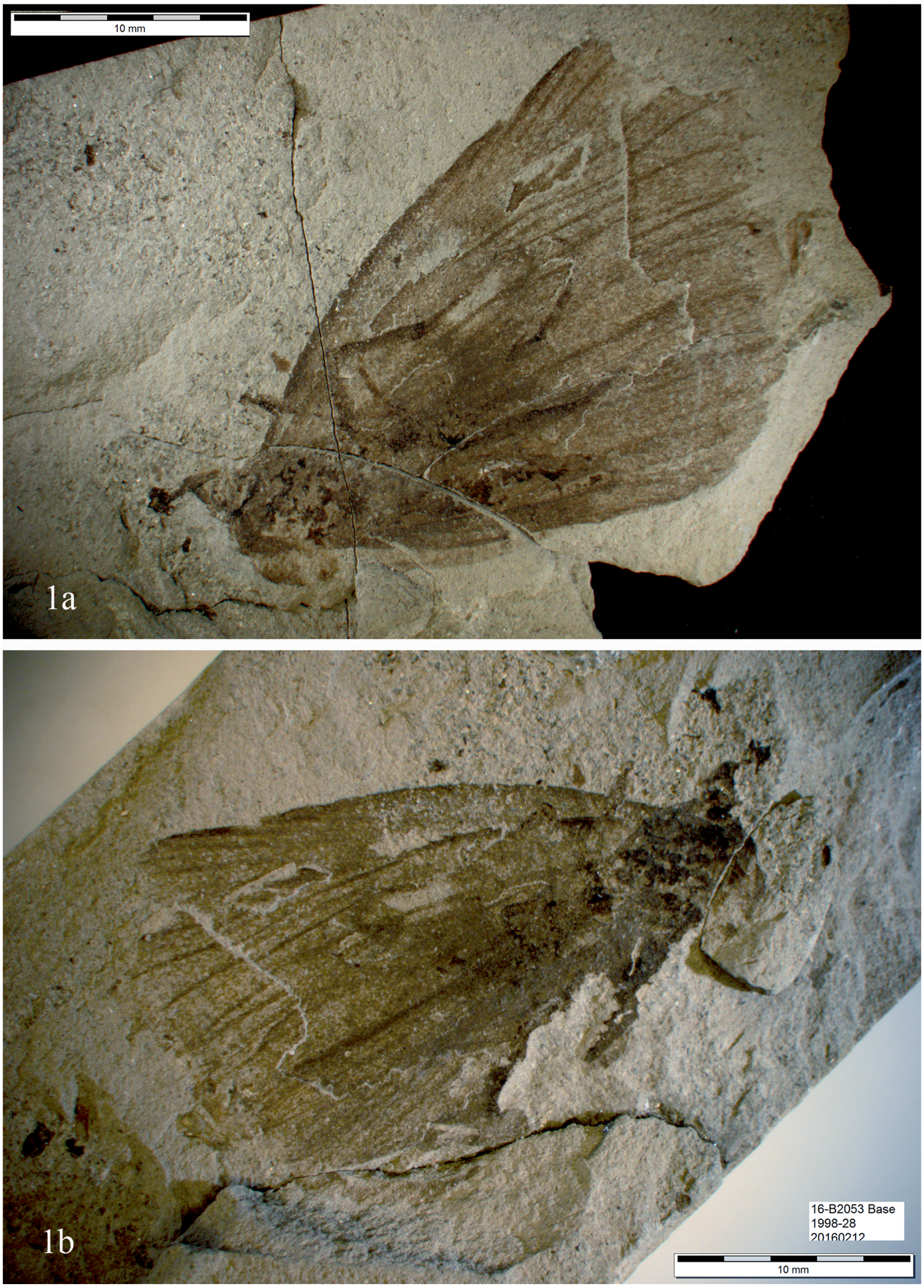


Fig. 1. *Protocoeliades kristenseni*, holotype, Zoological Museum, Copenhagen, registered as “Danekrae DK 136”. 1a and 1b – imprints, see text. Photographs provided by USNM, Smithsonian Institution, Washington.

sheet to give the best fit, several dark lines in the apical part of the right forewing and other structures were identified.

The dark stripe approximately following the course of vein CuA_2 is much too broad to be this vein and is interpreted as a wing fold, which includes CuA_2. Another dark stripe, still broader and further to the hind margin of the wing, is apparently overlying and obscuring vein 1A+2A and is possibly part of a leg.

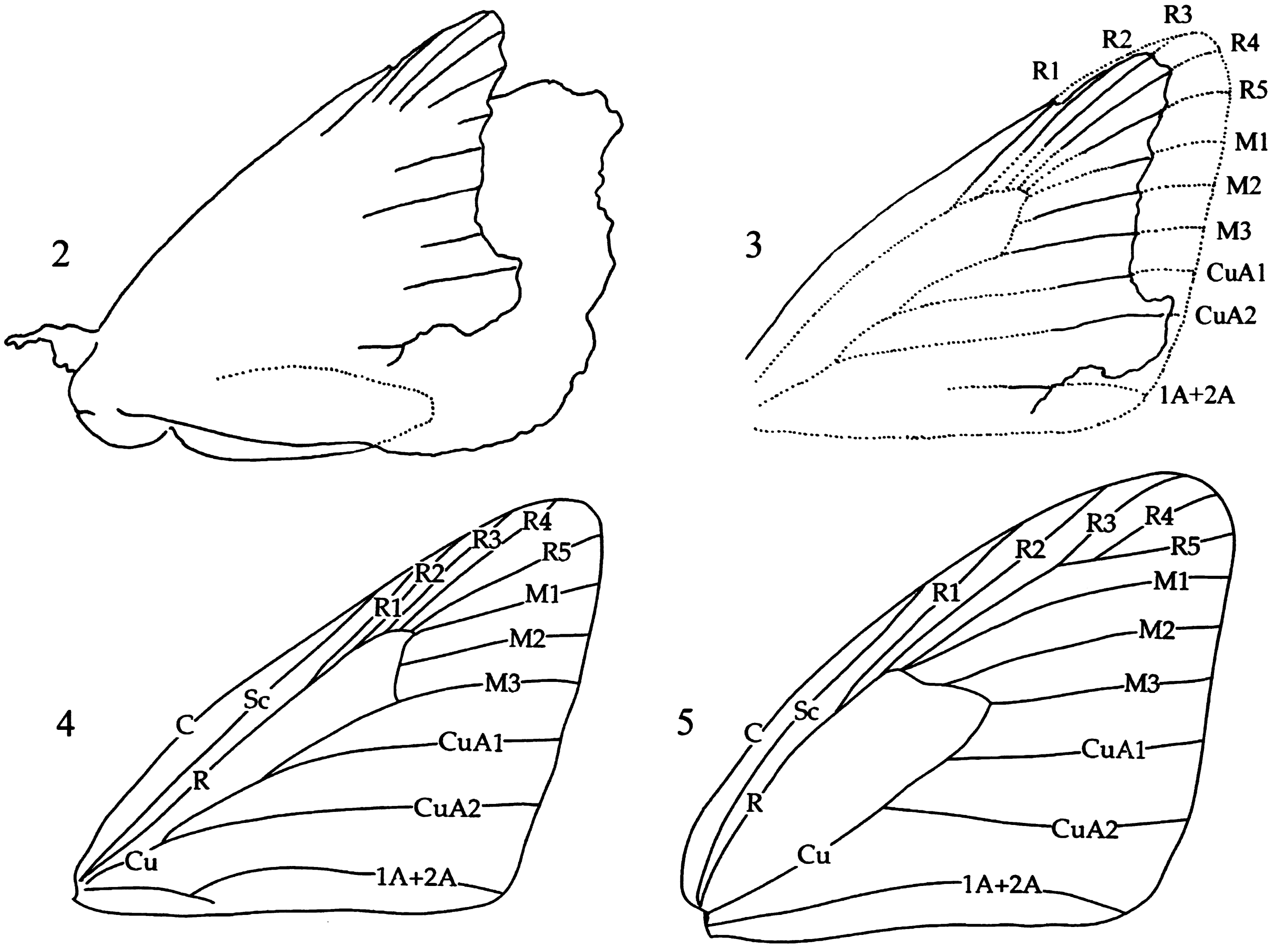
The nomenclature of the veins follows the convention of Nielsen & Common (1991), who broadly adopted the old Comstock system (Figs 4 and 5).

Genus *Protocoeliades* gen. n.

ZooBank taxon LSID:
E771863A-8D48-4480-8D1A-72B216B9F31D

Type species: *Protocoeliades kristenseni* sp. n.

Length of preserved part of forewing 23 mm, actual wing length estimated at about 25.6 mm. In the right forewing, five radial veins (R_1–R_5) are clearly visible. Although it is difficult to make out exactly what part of the cell they



Figs 2–5. Forewing venation. 2 – *Protocoeliades kristenseni*, outline of fossil, with the veins in right forewing that can be identified. 3 – same, but only right forewing and venation reconstructed based on the pieces of veins in Fig. 2, Sc omitted since there is no trace of it in the fossil. 4 – *Hasora vitta* (Butler, 1870) (Hesperiidae), with vein nomenclature following Nielsen & Common (1991). 5 – *Pareronia valeria* (Cramer, 1776) (Pieridae).

originate from, their course clearly shows that they are unbranched (Figs 2 and 3; compare with Fig. 5) and do not branch off each other. Reconstruction of the possible complete forewing venation (Fig. 3; subcosta omitted, since no trace of it can be found in the fossil; it is not diagnostic) leads to the following observations. Cell length about 60% of wing length. The origins of CuA$_1$ and CuA$_2$ are not visible on the fossil, but if extrapolated (by following their course) towards their apparent (but approximate) origin from the cubitus, CuA$_1$ originates about halfway between wing base and origin of M$_3$, while CuA$_2$ originates about halfway between wing base and origin of CuA$_1$.

Etymology. The name *Protocoeliades* indicates that the fossil is an early member of the Coeliadinae (see discussion on taxonomic position), of which *Coeliades* is the type genus. Its gender is feminine.

Protocoeliades kristenseni sp. n.

ZooBank taxon LSID:
F03B6458-8A67-4822-8B64-D032E7631962

Type material. Holotype in Zoologisk Museum, Copenhagen, registered as “Danekræ DK 136”. Imprint of fossil in part and counterpart, both of which were conserved.

Type locality. Island of Fur, Limfjord, Denmark.

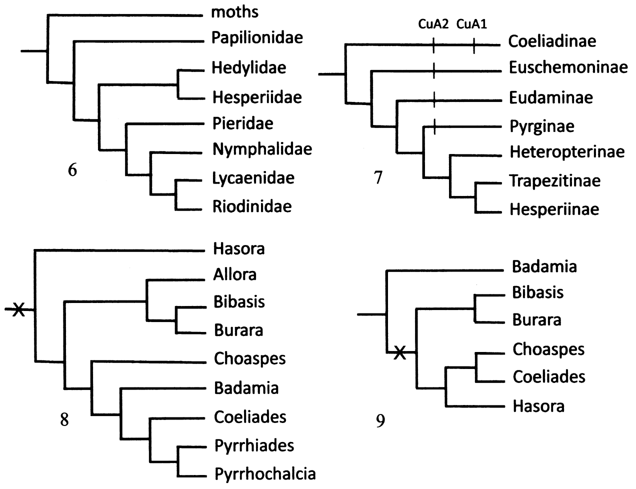
Characters as for the genus, of which it is the sole representative.

Etymology. The new species is named after the late Niels Peder Kristensen (Zoologisk Museum, Copenhagen), who was the first to recognize the fossil as something special and trusted the author with its description.

Taxonomic position

Within the butterflies (as defined by Heikkilä et al., 2011) the five unbranched radial veins in the forewing are a universal autapomorphy of the Hesperiidae (Ackery et al., 1999), in all other butterflies branching of some of the radial veins (sometimes including one median vein as well) occurs and often the radial veins are also reduced. Unbranched radial veins are very rarely found also in other Lepidoptera, but always combined with a very different, much narrower wing shape (see, e.g., Kristensen & Skalski, 1999). Thus, this character identifies the fossil as a member of the Hesperiidae.

Cell length relative to wing length is variable throughout the Hesperiidae and a relative length of 60% does not place this fossil in any particular extant subfamily as recognized by Warren et al. (2009). It cannot be decided whether M$_2$ approaches M$_3$ at their origins (indicating relationship with



Figs 6–9. Phylogenetic trees. 6 – redefined butterflies (Heikkilä et al., 2012). 7 – Hesperiidae (Warren et al., 2008, 2009). 8 – Coeliadinae (de Jong, 2007). 9 – Coeliadinae (Warren et al., 2008, 2009). X = allocation of *Protocoeliades* as possible calibration point, see text for further explanation.

Hesperiinae), since the relevant part of the wing is too blurred, but it is unlikely that it approaches M$_3$ suddenly in the blurred basal part of the veins, since in the extant species where M$_2$ approaches M$_3$, it does so very gradually.

The origin of CuA$_2$ at 15% to about 25% of the cubitus from the base of the cell is universal in the Coeliadinae (Fig. 4), and found in some other Hesperiidae, viz. in the single species of Euschemoninae, and in various genera of Pyrginae (e.g., *Oxynetra* Felder & Felder, 1862, *Gerosis* Mabille, 1903, and *Tagiades* Hübner, 1819) and Eudaminae (e.g., *Phocides* Hübner, 1819, *Epargyreus* Hübner, 1819). In the extensive phylogenetic analysis of the Hesperiidae by Warren et al. (2008, 2009) these subfamilies are successively basal in the phylogenetic tree (Fig. 7). Since the Hesperiidae are not basal in recent trees for the butterflies (e.g., Fig. 6, based on Heikkilä et al., 2011), and this character does not occur in other butterflies (Ackery et al., 1999), it appears to be a non-universal apomorphy of the Hesperiidae. It either originated once at the root of the Hesperiidae, was lost in many taxa in the evolution of Eudaminae and Pyrginae and the common ancestor of Heteropterinae, Trapezitinae and Hesperiinae, or it originated separately in Coeliadinae, Euschemonidae, Eudaminae and Pyrginae (Fig. 7).

The origin of CuA$_1$ about halfway along the cubitus is found only in Coeliadinae (although it is approached in *Oxynetra*, a genus of Pyrginae restricted to the Neotropics), and within this subfamily it is found in all species of *Hasora* Moore, 1881 (Fig. 4) (but sex-linked in some species) and some species of *Burara* Swinhoe, 1893. The phylogenetic tree of the Coeliadinae is still uncertain. The phylogenetic tree in Fig. 8 was obtained by analyzing 55 morphological characters and 26 species (representing all nine genera of Coeliadinae and five outgroups) (de Jong, 2007). The only other tree available is a part of the large tree which includes 210 hesperiid taxa (Warren et al., 2009), of which only six are Coeliadinae (representing six of the nine genera currently recognized; Fig. 9). Not surprisingly these trees differ considerably, but agree in not placing *Hasora* and *Burara* as sister groups. A partial molecular tree for Coeliadinae (viz. for the species occurring in Japan) is provided by Dodo et al. (2008), which only includes the genera *Burara*, *Choaspes*, *Badamia* and *Hasora*. Also in this partial tree *Burara* and *Hasora* are not sister groups, the first being a sister group to the other three combined.

If that position of the origin of CuA$_1$ originated only once and was lost several times, this fossil could be placed either at the root of the Coeliadinae (Fig. 8), or one node up (Fig. 9) (indicated by an X in both figures). If the character originated several times independently, the fossil could be placed at two independent places in any of the two trees, making it useless for calibration purposes (see below). A double origin (in *Hasora* and *Burara*) may be the most parsimonious solution for this character, but without a simultaneous analysis of other characters of this fossil, it is not wise to speculate. There is an easy character for separating *Hasora* and *Burara*: in the former there is a sharp bend in the basal part of vein 1A+2A (Fig. 4), while in *Burara* 1A+2A is more or less straight or gently curved as is usual in butterflies. Unfortunately the basal part of this vein is not visible in this fossil. Since the fossil cannot be assigned to either *Hasora* or *Burara*, the genus *Protocoeliades* was erected to accommodate this fossil. For further discussion on the phylogeny of the Coeliadinae see the next chapter.

Importance of this fossil for determining the time dimension in the evolution of the butterflies

Exciting as it may be to have the oldest known butterfly in hand, its importance for estimating divergence times in butterfly or hesperiid phylogeny is moderate. Recent analyses indicate that several butterfly families younger than the Hesperiidae (based on phylogenies reported in several recent studies, such as Heikkilä et al., 2011; see Fig. 6) originated before the Cretaceous-Paleogene (K-Pg) boundary. For the four younger families the estimates are as follows: Pieridae 81–112 Ma (Braby et al., 2006), Nymphalidae 90 Ma (Wahlberg et al., 2009), Riodinidae 81–96 Ma (Espeland et al., 2015), Lycaenidae, as sister to the Riodinidae, should be similar in age. In addition, the age of the older family Papilionidae was recently estimated at 68 (53–87) Ma (Simonsen et al., 2011). Clearly, this cannot be true at the same time, with the youngest family at the root. Differences and uncertainties are due to difficulties with calibration (and possibly the trees can still be improved). For instance, for the calibration of the Pieridae tree four fossils were used, the identification of which is doubtful if not incorrect (de Jong, 2007). But we are not concerned with the butterflies as a whole in this paper. Whatever the correct ages of the "younger" families, the Hesperiidae must be older and finding the universal hesperiid apomorphy of unbranched radial veins in a fossil of 55 million years old does not alter this fact.

Similarly the basal move in the origin of vein CuA$_2$ is of limited value for calibration. It occurred once and was lost many times, or many times independently. In both cases we need to determine the minimum age for its occurrence at the root of the Hesperiidae.

Only the basal move in the origin of vein CuA$_1$ has some potential for calibration. It is found in only two genera. Depending on the phylogenetic tree, it first arose at the root of the Coeliadinae (Fig. 8), or one node up (Fig. 9). Evidently, a new analysis of Coeliadinae, based on morphology and molecular markers, and including all genera, is needed for a fruitful further discussion.

Such a new analysis is not only crucial for estimating divergence times in Coeliadinae, but also for butterflies in general. In Fig. 8, *Hasora* is at the root of the Coeliadinae. It only feeds on Fabaceae, the age of which varies from 56 to 82 Ma depending on the authors (see next chapter), and thus, the first split in the hesperiid lineage in Fig. 8 cannot be older than that. Since the Hesperiidae are rather low in the butterfly tree (see Fig. 6), this could considerably constrain the estimates for the entire tree. If, on the other hand, *Hasora* is in the position in Fig. 9, or another non-basal position, the constraint would be less.

Apart from a Pleistocene copal hesperiid fossil assigned to an extant species, *Andronymus neander* (Plötz, 1884) (Skalski, 1976), there is just one other fossil hesperiid, *Pamphilites abdita* Scudder, 1875. It is assignable to the subfamily Hesperiinae (de Jong, in prep.) and of Oligocene/Miocene age (around 25 Ma). The Hesperiinae are predominantly grass feeders. Their expansion and radiation undoubtedly coincided with the evolution of the other large group of grass feeding butterflies, the Satyrinae (Nymphalidae) in the Oligocene (Peña & Wahlberg, 2008), long after the origin of the present fossil. Being less than half the age of the present fossil, it would be of interest to compare *P. abdita* with *P. kristenseni* as a calibration point (the first at the root of the Hesperiinae) using a molecular clock analysis. *Vanessa vetula* von Heyden, thought to be a hesperiid by Scudder (1875) who erected the genus *Thanatites* for it, cannot be assigned to any particular butterfly family (de Jong, in prep.).

Ecological and biogeographic considerations

The extant species of the Coeliadinae feed on a wide range of food plants, belonging to some 30 families (Vane-Wright & de Jong, 2003; Larsen, 2005; Cock, 2010), the estimated age of which collectively range from 30 to 110 million years (Hedges & Kumar, 2009; estimates differ considerably between authors; here a recent publication was used). Almost all genera of Coeliadinae are polyphagous, and consequently their food plants are not the maximum constraint on their age (except the 110 million year boundary for the subfamily, just mentioned). Two genera are an exception. The West African endemic and monotypic genus *Pyrrhiades* Lindsey & Miller, 1965, is only known from Malpighiaceae (Larsen, 2005), a plant family (estimated age 65–71 Ma; Hedges & Kumar, 2009) also widely used by other Coeliadinae. Moreover, Chiba (2009) concludes that *Pyrrhiades* is not monotypic, but also contains a number of species previously included in *Coeliades*. This taxonomy needs additional supporting evidence, which does not concern us here. *Pyrrhiades* sensu Chiba lives on Malpighiaceae and Asclepiadaceae (also widely used by *Coeliades*). The relatively large Oriental genus *Hasora* (extending to Australia and into the Pacific as far as the Sandwich Islands) is confined to Fabaceae. The age of this family is given as 56–68 Ma by Wikström et al. (2001), 59.9 Ma for the entire order Fabales by Magallon & Sanderson (2001), and 76–82 Ma by Forest & Chase (2009). This gives a maximum constraint for the age of *Hasora*, although the wide range is not very helpful. *Protocoeliades* is younger than the oldest food plants for *Hasora* and *Burara* (the food plants of which belong to Malpighiaceae, Combretaceae, Araliaceae, Myristicaceae and Myrsinaceae, according to Vane-Wright & de Jong, 2003), or in other words it falls within the maximum constraint for both genera.

The extant subfamily Coeliadinae occurs throughout the tropics from Africa to Australia and far into the Pacific, with a very slight extension in East Asia to Japan and the Amur region (Southeast Siberia) (Evans, 1937, 1949). It can be divided into eight or nine genera, three of which are confined to Africa, and five or six to Asia and Australia. *Hasora* and *Burara* belong to the latter group. The first genus covers almost the entire area of the subfamily in Asia/Australia.

The fossil described was formed at a time when tropical and subtropical conditions were prevalent in large parts of Europe. Worldwide the Early Eocene was the warmest period in the Cenozoic; with some fluctuations it was a continuation of the warm climate in the Cretaceous (Crowley & North, 1991). Relationships of fossil taxa from the Cretaceous and Paleogene in the Northern Hemisphere with extant taxa nowadays restricted to tropical areas, are well known (Eskov, 2000; Larsson, 1978). *P. kristenseni* is the first record of a butterfly fossil found on a continent (i.e., Europe), where at present its closest relatives do not live, and it fits in the pattern of a once, in the early Paleogene, widespread tropical fauna that largely or totally became restricted to tropical areas around the equator by cooler and drier climates from the Eocene onwards.

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REFERENCES

Ackery P.R., de Jong R. & Vane-Wright R.I. 1999: The butterflies: Hedyloidea, Hesperioidea and Papilionoidea. In Kristensen N.P. (ed.): *Handbook of Zoology IV (35), Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin, New York, pp. 263–300.

Braby M.F., Vila R. & Pierce N.E. 2006: Molecular phylogeny and systematics of the Pieridae (Lepidoptera: Papilionoidea):

higher classification and biogeography. — *Zool. J. Linn. Soc.* **147**: 239–275.

Chiba H. 2009: A revision of the subfamily Coeliadinae (Lepidoptera: Hesperiidae). — *Bull. Kitakyushu Mus. Nat. Hist. Hum. Hist. (A, Nat. Hist.)* **7**: 1–51.

Cock M.J.W. 2010: Observations on the biology of Afro-tropical Hesperiidae (Lepidoptera) principally from Kenya. Part 1. Introduction and Coeliadinae. — *Zootaxa* **2547**: 1–63.

Crowley T.J. & North G.R. 1991: *Paleoclimatology*. Oxford University Press, New York, 339 pp.

Dodo Y.T., Saigusa T., Chiba H., Nishiyama T., Hirowatari T., Ishii M., Yagi T., Hasebe M. & Mohri H. 2008: Molecular phylogeny of Japanese skippers (Lepidoptera, Hesperiidae) based on mitochondrial *ND5* and *COI* gene sequences. — *Trans. Lepidopt. Soc. Jap.* **59**: 29–41.

Durden C.J. & Rose H. 1978: Butterflies from the Middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). — *Pearce-Sellards Ser.* **29**: 1–25.

Eskov K.Yu. 2002: Geographical history of insects. In Rasnitsyn A.P. & Quicke D.L.J. (eds): *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston, London, pp. 427–435.

Espeland M., Hall J.P.W., DeVries P.J., Lees D.C., Cornwall M., Hsu Y.-F., Wu L.-W., Campbell D.L., Talavera G., Vila R., Salzman S., Ruehr S., Lohman D.J. & Pierce N. 2015: Ancient Neotropical origin and recent recolonization: Phylogeny, biogeography and diversification of the Riodinidae (Lepidoptera: Papilionoidea). — *Mol. Phylogenet. Evol.* **93**: 296–306.

Evans W.H. 1937: *A Catalogue of the African Hesperiidae in the British Museum*. British Museum (Natural History), London, 212 pp., 30 pls.

Evans W.H. 1949: *A Catalogue of the Hesperiidae from Europe, Asia and Australia in the British Museum (Natural History)*. British Museum (Natural History), London, 502 pp., 53 pls.

Forest F. & Chase M.W. 2009: Eurosids I. In Hedges S.B. & Kumar S. (eds): *The Time-Tree of Life*. Oxford University Press, Oxford, pp. 188–196.

Hedges S.B. & Kumar S. (eds) 2009: *The Time-Tree of Life*. Oxford University Press, Oxford, 551 pp.

Heikkilä M., Kaila L., Mutanen M., Peña C. & Wahlberg. N. 2011: Cretaceous origin and repeated tertiary diversification of the redefined butterflies. — *Proc. R. Soc. Lond. (B)* **279**: 1093–1099.

de Jong R. 2007: Estimating time and space in the evolution of the Lepidoptera. — *Tijdschr. Entomol.* **150**: 319–346.

Kristensen N.P. & Skalski A.W. 1999: Phylogeny and palaeontology. In Kristensen N.P. (ed.): *Handbook of Zoology IV (35), Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin, New York, pp. 7–25.

Larsen T.B. 2005: *Butterflies of West Africa.* Apollo Books, Stenstrup, Text Volume, 595 pp., Plate Volume 125 pls.

Larsson S.G. 1978: *Baltic Amber – A Palaeobiological Study.* Scandinavian Science Press, Klampenborg, 192 pp.

Magallon S. & Sanderson M.J. 2001: Absolute diversification rates in angiosperm clades. — *Evolution* **55**: 1762–1780.

Nielsen E.S. & Common I.F.B. 1991: Lepidoptera. In CSIRO, Division of Entomology: *The Insects of Australia. 2nd ed.* Melbourne University Press, Melbourne, pp. 817–915.

Pedersen S.A.S., Steffensen J. & Pedersen C.P. 2004: Clay content of a clayey diatomite, the Early Eocene Fur Formation, Denmark. — *Bull. Geol. Soc. Denmark* **51**: 159–177.

Peña C. & Wahlberg N. 2008: Prehistorical climate change increased diversification of a group of butterflies. — *Biol. Lett.* **4**: 274–278.

Rust J. 1998: Biostratinomie von Insekten aus der Fur-Formation von Dänemark (Moler, oberes Paleozän/unteres Eozän). — *Paläontol. Z.* **72**: 41–58.

Scudder S.H. 1875: Fossil butterflies. — *Mem. Am. Assoc. Adv. Sci.* **1**: 1–99.

Simonsen T.J., Zakharov E.V., Djernaes M., Cotton A.M., Vane-Wright R.I. & Sperling F.A.H. 2011: Phylogenetics and divergence times of Papilioninae (Lepidoptera) with special reference to the enigmatic genera *Teinopalpus* and *Meandrusa*. — *Cladistics* **27**: 113–137.

Skalski A.W. 1976: Les lépidoptères fossiles de l'ambre. Etat actuel de nos connaissances (2e partie). — *Linneana Belg.* **6**: 195–208.

Sohn J.-C., Labandeira C., Davis D. & Mitter C. 2012: An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. — *Zootaxa* **3286**: 3–132.

Sohn J.-C., Labandeira C.C. & Davis D.R. 2015: The fossil record and taphonomy of butterflies and moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time estimates. — *BMC Evol. Biol.* **15**: 12.

Vane-Wright R.I. & de Jong R. 2003: The butterflies of Sulawesi; annotated checklist for a critical island fauna. — *Zool. Verh.* **343**: 1–267.

Wahlberg N., Leneveu J., Kodandaramaiah U., Peña C., Nylin S., Freitas A.V.L. & Brower A.V.Z. 2009: Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. — *Proc. R. Soc. Lond. (B)* **276**: 4295–4302.

Warren A.D., Ogawa J.R. & Brower A.V.Z. 2008: Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperiidae (Lepidoptera: Hesperioidea). — *Cladistics* **24**: 642–676.

Warren A.D., Ogawa J.R. & Brower A.V.Z. 2009: Revised classification of the family Hesperiidae (Lepidoptera: Hesperioidea) based on combined molecular and morphological data. — *Syst. Entomol.* **34**: 467–523.

Wikström N., Savolainen V. & Chase M.W. 2001: Evolution of the angiosperms: calibrating the family tree. — *Proc. R. Soc. Lond. (B)* **268**: 2211–2220.

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