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First butterfly (Papilionoidea) from Baltic amber by a characteristic egg pinpoints an Eocene minimal age of admirals (Nymphalidae: Limenitidinae) — a distinct step in the rise of the Papilionoidea

Thilo C. Fischer and Axel Hausmann

ABSTRACT

Inclusions in Eocene Baltic amber have been studied for a long time and manifold taxa, predominantly Arthropoda, have been scientifically described from it, also new orders. With respect to the insect order Lepidoptera (moths and butterflies) there have not yet been indisputable finds of butterflies. However, phylogenetic studies and direct fossil evidence from older sediments indicate that butterflies in a broad sense (Rhopalocera, comprising the Papilionoidea) have older origin as evidenced by a Hesperiidae from the Paleocene of Fur, Denmark (Kristensen and Skalski in Kristensen, 1999; de Jong, 2017). Earliest known Papilionoidea (butterflies in a strict sense) are from the Eocene Green River Shale of Colorado (Durden and Rose, 1978). Chazot et al. (2019) calculated the origin of butterflies (Papilionoidea) by divergence analyses with molecular data at between 89.5 and 129.5 mya with a median at 107.6 mya, corresponding to latest Early Cretaceous. This strongly supposes that butterflies also have been present in the Eocene Baltic amber forest ecosystem. Here, we report on first reliable fossil record of butterflies in Baltic amber. The find of an egg inclusion with a characteristic hexagonal sculpture can be identified as a Papilionoidea egg. Among these it can be affiliated to the subfamily Limenitidinae of Nymphalidae. Best known extant relatives of the find are butterflies of the genus *Limenitis,* admirals. The Eocene minimal age for Limenitidinae provides one of the few known calibration points by direct evidence at 33.9--37.8 mya for Baltic amber. The delicate eggshell structures have developed surprisingly early but then turned out to be quite conservative.

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INTRODUCTION

The fossil record of Lepidoptera is sparse, most likely for their most delicate structures and unfavorable taphonomy. But some time ago, the fossil record of Lepidoptera was reviewed thoroughly (Sohn et al., 2012; Sohn and Lamas, 2013; de Jong, 2017). Structures allowing for systematic affiliation are most likely to be preserved in ambers. However, there is strong bias against the preservation of larger adults, such as Papilionoidea (butterflies) and Macroheterocera. Macroheterocera records from ambers are from the family Geometridae, caterpillars (Grimaldi and Engel, 2005; Fischer et al., 2019) and a moth from Dominican amber (Sarto i Monteys et al., 2022). To date, butterflies in amber are known from Dominican amber, but not at all from Baltic amber (Grimaldi and Engel, 2005; Sohn et al., 2012; Sohn and Lamas, 2013). Here, we provide by a characteristic fossil egg a first record and a description of a member of the subfamily Limenitidinae (Nymphalidae, Papilionoidea). Fossil evidence for the genus *Limenitis* up to now is only from the Pliocene of Willershausen (Germany) by a forewing and partial thorax preserved in lacustrine sediments (Branscheid, 1977; Brauckmann et al., 2001; Sohn et al., 2012). Furthermore, resemblance to *Limenitis* was discussed by Comstock (1961) for *Apanthesis leuce* described from the Late Eocene Florissant Beds (Scudder, 1889). For the genus *Neptis* there seems to be no fossil evidence at all. The butterfly egg described here is an isolated finding, without association to other Lepidopteran remains or other syninclusions in this piece of Baltic amber, except stellate trichome hairs from leaves typical for this amber. Nevertheless, it may serve as another piece of information in the scarce fossil record of butterflies.

GEOLOGICAL SETTINGS / STUDY AREA

Baltic amber comes from Upper Eocene deposits (Prussian Formation, "Blue Ground"); the facies is that of lagoonal deltas, which embedded resin from forests over large areas of the Scandinavian and Baltic regions (Kharin and Eroshenko, 2017). Economically, the largest mine is that of Kaliningrad, where also most amber inclusions and the one described here originate.

MATERIAL AND METHODS

Authentication of the amber inclusion is ensured by purchase from a trusted salesperson known by long-term relations. The amber also contains a stellate trichome as a syninclusion with a typical form for Baltic amber. The amber shows the characteristic blue fluorescence with UV light. The pictures of the egg were produced by a stacked imaging approach. The specimen is kept at constant temperature in a plastic clip bag within a metal box, excluding excess oxygen and light, in the author's TCF collection under # 8660. It will be transferred as a holotype kept at the Bavarian State Collection of Zoology (# SNSB-ZSM-LEP amb012).

RESULTS

Systematic Palaeontology

Family NYMPHALIDAE Rafinesque, 1815

Taxon. Genus *EOLIMENITIS* gen. nov.

zoobank.org/6927C70F-A381-4EC4-99D5-1AFF0F566A6E

Species. *Eolimenitis baltica* nov. spec.

zoobank.org/EFB714D1-BD24-47BB-BCCE-BD2370C8499C

Name. Etymology: "limenitis" refers to the subfamily Limenitidinae. The prefix "Eo" in the genus name refers to the Greek word for (the godhead of) dawn "Eos". The genus *Eolimenitis* might also been used for future finds fossil eggs of Limenitidinae of other ages than Eocene. The species name *'baltica'* refers to the occurrence in Baltic amber and to the locus typicus.

Typus. Holotypus: Specimen SNSB-ZSM-LEP amb012.
Locus typicus: Amber mine of Yantarni, RU.
Stratum typicum: "Blaue Erde" (Upper Eocene to Lower Oligocene).
Repository: Bavarian State Collection of Zoology SNSB-ZSM-LEP amb012.

Diagnosis of genus. The genus *Eolimenitis* is established for fossil forms of the subfamily Limenitidinae and is currently only based on the egg phenotype. The fossil *Eolimenitis* egg - as described below - closely resembles eggs of the genera *Limenitis, Neptis, Parthenos,* and *Adelpha* (all Limenitidinae). The high number of 400 - 500 hexagonal fields seems characteristic in comparison to

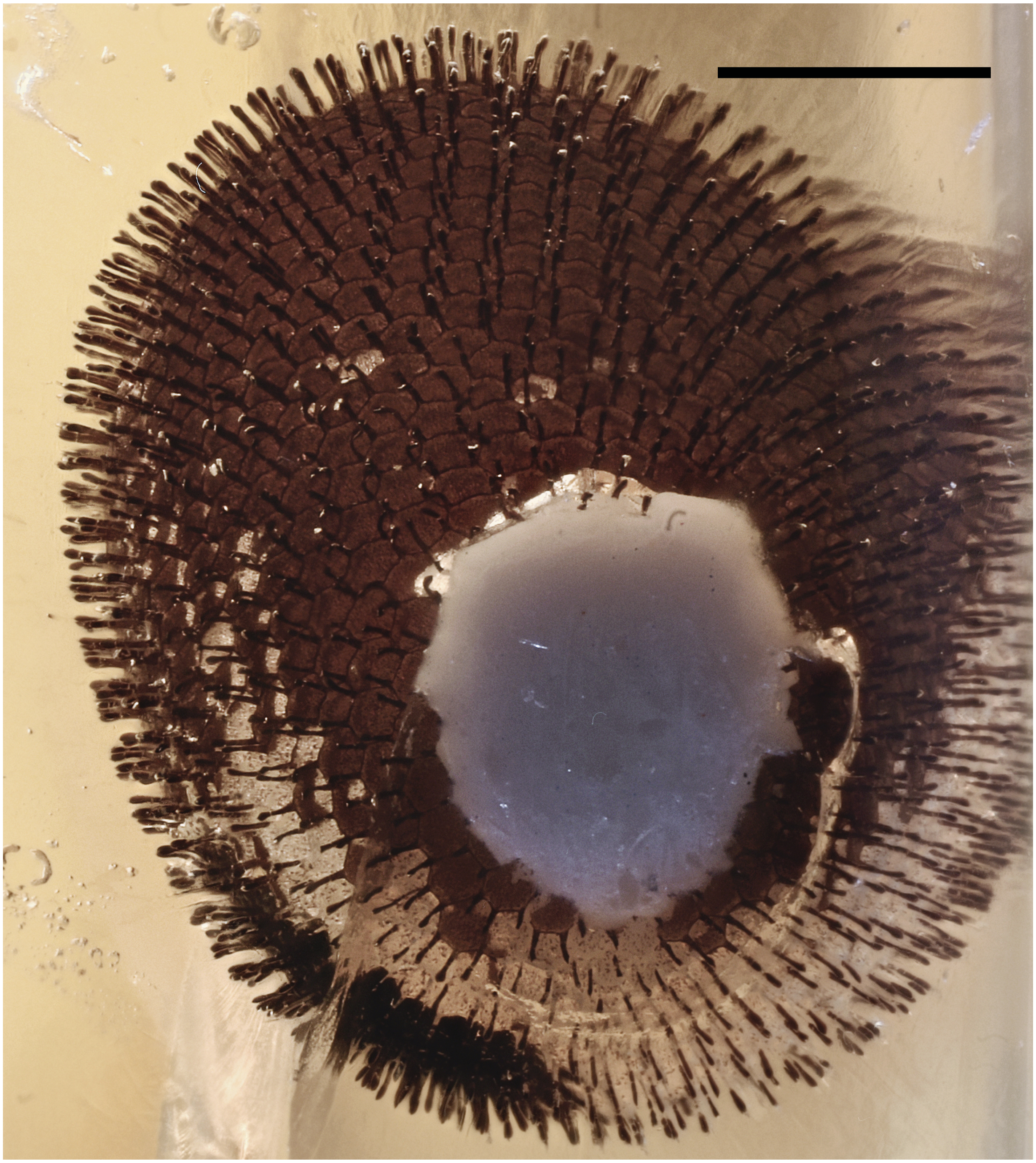

FIGURE 1. Inclusion of the Lepidoptera – Papilionoidea – Nymphalidae egg in Baltic amber (2 mm largest diameter), identified here as an egg of a member of Limenitidinae, *Eolimenitis baltica* nov. spec. Scale bar equals 0.5 mm.

extant Limenitidinae. In genus *Adelpha*, the number of hexagonal fields can reach 100 - 200 (Cossey, online resource), in *Limenitis* this is much lower (Döring, 1955).

Description of species. The general shape of the egg is a slightly elongated spheroid (Figure 1).

An irregular structure which, due to its position in amber is hardly visible, may represent the micropyle. Polishing of the batch of amber with this piece had touched the inclusion's surface, leading to partial filling of its cavity with white polishing powder. The surface of the egg is characteristically structured by a hexagonal pattern with fields of approx.

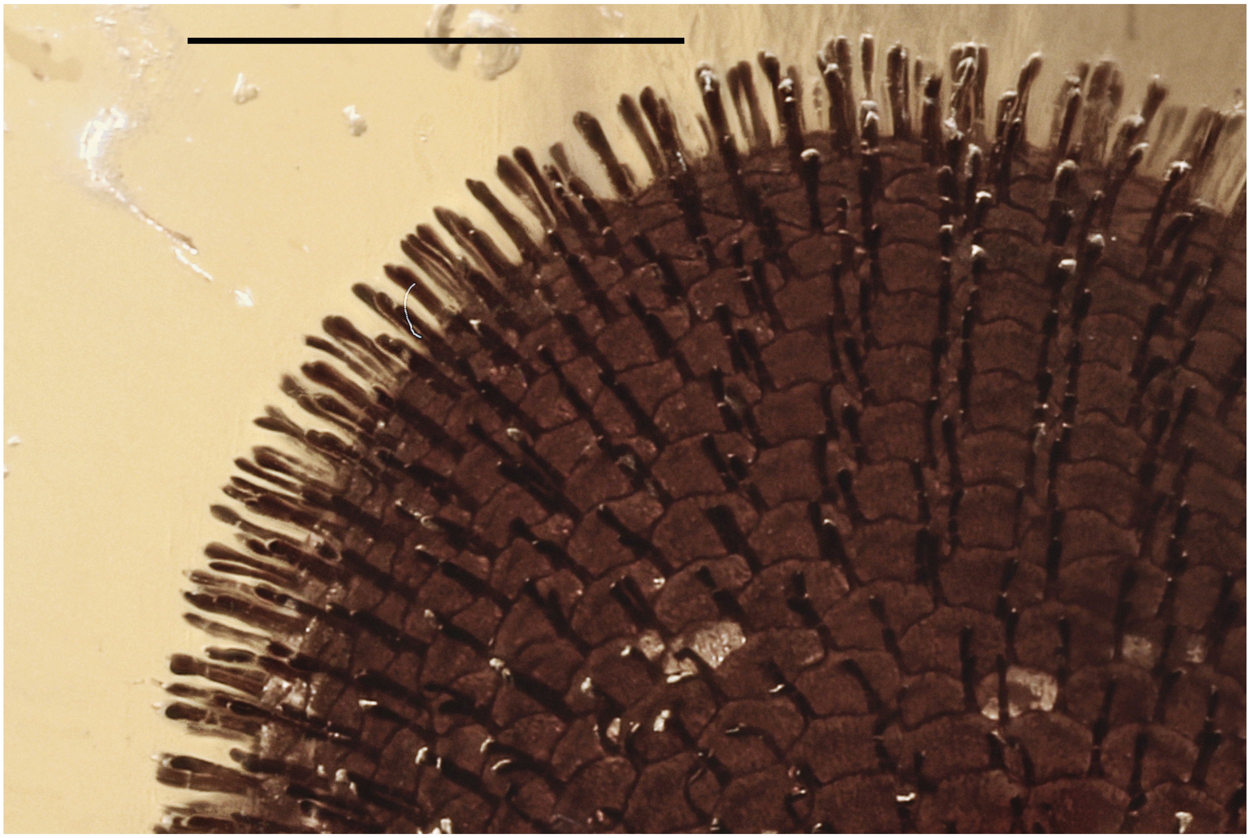

FIGURE 2. Detail of egg inclusion showing the surface sculpturing with hexagonal fields 100 µm in diameter and the club-ended spikes at the corners 130 µm in length. Scale bar equals 0.5 mm.

100 µm in diameter. Every corner of three-fields-joining carries a 130 µm spike, which is 10 µm thick and has a clubbed end of 15 µm in diameter (Figure 2). The total of hexagonal fields can be estimated to 400-500.

Orientation of the egg's micropylar axis to the substrate, whether upright (perpendicular to substrate) or flat (parallel) (for definition of types see Chapman, 1896), could not be determined, as the egg is an isolated find without substrate at all.

Taphonomy. The inclusion is preserved in a piece of clear Baltic amber 12 mm x 9 mm x 7 mm in size. It is 2 mm long with its large diameter. The only syninclusion is a stellate trichome, as often observed from Baltic amber.

Systematic Identification

The inclusion was first supposed to be a Lepidoptera egg and, subsequently, as an egg of the genus Limenitis or closely related taxa. In parallel, also a wider systematic approach for confirming its identification was taken. Eggs of all lepidopteran families and genera for which pictures of eggs are available at Lepiforum and those reported by Döring (1955) were checked. After an initial screening hit with *Limenitis* eggs (Limenitidinae) further focus was set on the other subfamilies of Nymphalidae, namely Heliconiinae, Apaturinae, Nymphalinae, Charaxinae, Satyrinae, Danainae, and Libytheinae (Dhungel and Wahlberg, 2018). Only among Nymphalidae – Subfamily Limenitidinae Behr, 1864 - tribes Limenitidini Behr, 1864 (admirals, german "Eisvögel"), Neptini Newman, 1870 ("Trauerfalter"), and Parthenini Reuter, 1896 ("Blaue / Braune Segelfalter") eggs comparable to the fossil find could be found. Eggs of the genera *Limenitis* Fabricius, 1807, *Adelpha* Hübner 1819 (Limentitidini), *Neptis* Fabricius, 1807, and *Parthenos* Hübner, 1819 were found to show a highly similar sculpture of hexagonal plates with spikes with clubbed ends at every corner of the hexagons (for *Adelpha* and *Partenos*, pers. comm. A.V.L. Freitas, 2024; Willmott, 2003). Similar egg figures were examined from *Limenitis populi, L. camilla, L. reducta, Neptis sappho,* and *N. rivularis* (Lepiforum, 2022). The same results from the study of Döring (1955) who presented accurate and detailed figures for the eggs of 618 European Lepidoptera species. The character "hexagonal egg pattern with clubbed spikes" was only found within

Limenitidinae in this study and has been described as a synapomorphy for the subfamily Limenitidinae (Freitas et al., 2004).

Ackery et al. in Kristensen (1999) reported on the specific structure of eggs of genera related to *Limenitis*: “While eggs of many Limenitini [sic!] are characteristically spined, appearing like ‘minute sea urchins’ (Corbet and Pendlebury, 1992), those of other subgroups….... are variable in form, without spines.”

Eggs of *Limenitis* and *Neptis* are about 0.9 mm in diameter (Natur-in-NRW online resource). The fields of the hexagonal pattern, however, have about the same size of 100 µm in diameter. The fossil egg has about a 2.2-fold diameter as in extant species, and, hence, correspondingly larger number of fields and spikes. There are some 400-500 fields, which is higher than in extant Limenitidinae. Closest is *Adelpha*, the number of hexagonal fields some 100-200 (Cossey, online resource).

DISCUSSION

With respect to careful examination, it must be considered if the inclusions could represent some other structure rather than an egg, like a compound eye of an insect. Also compound eyes are known to show hexagonal surface structure and compound eyes can bear setae between the ommatidia (e.g., honeybee, *Drosophila*, Noctuidae/Hadeninae). However, the number of hexagonal fields in compound eyes is much larger and the setae – if present – are much finer and longer and not clubbed. Most importantly, the whole inclusion is an almost complete globular structure, showing no attachment zone at all. Moreover, the borders of the hexagonal fields are notched rather than bulged over the surface. Consequently, the interpretation as a compound eye can be excluded.

Accepting the inclusion as an insect egg, it must be considered that this might belong to another order than Lepidoptera. However, screening through the internet, study of literature and asking advice from expert entomologists did not result in finding any alternative explanation for our inclusion. Therefore, we conclude here the egg belonging to Limenitidinae.

The egg is a single specimen from a collection with some 1400 Lepidopteran inclusions from Baltic amber. Eggs of moths (so called “Microlepidoptera”), in contrast, do occur in Baltic amber rarely. They are often associated with females of all abundant Baltic amber Lepidoptera families and genera. Findings of female adults with eggs are from cf. Gracillariidae (*Gracillariites* sp.) (2 specimens), Elachistidae (1), Oecophoridae (6), Depressariidae (1), Tineidae (7), and Gelechiidae (1, Bitterfeld amber) in the considered collection. Furthermore, there are two isolated finds of moth eggs, one of these caught in a spider web in the collection examined. It is unclear if the eggs, which are found in close relation to those female moths, are examples of egg laying caught in the act by the flowing resin (“frozen behaviour”) or, instead, being induced by the resin itself as a reaction and an attempt to save the eggs, or are due to a post-mortem process. Extant Limenitidinae are not known to feed on resin-producing plants. The presented butterfly egg is a single find, without even associated Lepidopteran scales or remains of leaves or other substrate from egg deposition. The egg could also have been transported onto the resin via air or water.

For the genera *Limenitis* and *Neptis*, egg deposition on the respective narrow range of feed plant taxa is described and fossil association with such leaves might have been expected. However, like with adults of butterflies there is a strong bias against preservation of larger leaves within resin and amber, respectively. There is fast erosion from any open side of an inclusion as regularly observed with larger inclusions. If egg deposition was on food plant leaves, rare separation of such eggs from leaves feed may have been a prerequisite favoring complete embedding in resin and subsequent preservation as an amber inclusion.

Extant European species of *Limenitis* are associated with a narrow spectrum of plants on which the caterpillars feed and on which eggs are deposited. These are trees of the genus *Populus (P. tremula, P. nigra)* for *Limenitis populi* (Düring, 2020) and species of the Caprifoliaceae genus *Lonicera (L. xylosteum, L. caprifolium, L. periclymenum, L. etrusca, L. implexa, L. alpigena, L. nummulariifolia)* for *Limenitis reducta* and *Limenitis camilla*, the latter also being found at non-endemic *Symphoricarpos albus* which originates in North America (Eber, 1993; Tolman and Lewington, 1998).

Caterpillars of *Neptis sappho* (syn. *Neptis aceris*) live on leaves of Fabaceae *(Lathyrus vernus, L. niger, Robinia pseudoacacia,* and on other Fabaceae in Asia) (Lepidorum). In contrast, *Neptis rivularis* places its eggs at leaves of Rosaceae and caterpillars feed on such *(Filipendula ulmaria* [Rosoideae], *Aruncus dioicus, Spiraea* spp. [both Spiraeoideae]) (Lepiforum, 2022).

Adelpha species (“sisters”) live in southern Northern America and South America (Neotropics)

(Lepiforum, 2024; Willmott, 2003). The genus has “certainly one of the widest host breadths of any nymphalid genus” (Willmott, 2003). The prominent North American *Adelpha bredowii* (California sister butterfly) feeds on oak *(Quercus* sp.) trees (Prudic et al., 2002).

Butterflies of extant genus *Parthenos* (Southeast Asia, India, Sri Lanka, Philippines, New Guinea) feed on tropical vines of *Adenia* (Passifloraceae) (pers. comm. A.V.L. Freitas, 2024). However, this plant genus has not been found in Baltic amber up to now. Caterpillars of the species *Parthenos sylvia* feed on a wide variety of plants, mainly *Adena* (Passifloraceae), but also Menispermaceae, and Cucurbitaceae (Nylin et al., 2013, Das-Tier-Lexikon).

There is only some direct evidence for the presence of the extant food-plant families of European *Limenitis* and *Neptis* in the Baltic amber forest (Spahr, 1993). A report on *Populus (“Populites”)* had been rejected, there is only evidence for the related genus *Salix. Lonicera* and *Symphoricarpus* (both Caprifoliaceae) are not known from Baltic amber, only *Viburnum* by pollen. Among Fabaceae (syn. Leguminosae) *Acacia succini* has been described. Some remains of Rosaceae are known from Baltic amber *(Pteropetalum palaeogonum,* and unspecified remains). The typical host plant families of *Parthenos* (Passifloraceae, Menispermaceae, Cucurbitaceae) seemingly are not known from Baltic amber (Spahr, 1993).

The habitat of extant European *Limenitis* and *Neptis* species are deciduous forests with *Populus* and *Lonicera*, but also dry, open, or mountainous forests *(L. reducta),* moist forests with *Quercus, Carpinus,* and often with *Robinia pseudoacacia (Neptis sappho),* moist or dry forests with *Aruncus* or *Filipendula*, or urban areas where *Spiraea* is cultivated there *(Neptis rivularis)* (Lepiforum, 2022).

Most interestingly, oak trees are hosts of the North American *Adelpha bredowii*. There is manifold evidence for several *Quercus* species and other Fagaceae in Baltic amber, most typical are their male inflorescences (Spahr, 1993; Sadowski, 2020). Also isolated trichomes might stem from these.

Today’s climate of the European / North African areal of the European genera *Limenitis* and *Neptis* is warm temperate (Köppen-Geiger, accessed 2020) (compare e.g., for *Limenitis populi* [Global Biodiversity Information Facility, accessed 2023]).

The climate of the Baltic amber forest (Sadowski, 2017) and the forest itself are reconstructed as “a thermophilic, humid-mixed forest similar to modern subtropical forests of Eastern and Southeastern Asia” (Alekseev, 2016). A later comprehensive study on Fagaceae hints to a warm temperate climate (Sadowski, 2020). Hence, today’s climate of the European genera of Limenitidinae to which the egg inclusion is related agrees with the climate reconstructed for the Baltic amber forest habitat.

The finding of the Limenitidinae egg from Eocene Baltic amber allows some conclusions on geological age of taxa: Wahlberg et al. (2013) date the origin of the family Nymphalidae to 90 mya and Chazotet al. (2019) the age of the superfamily Papilionoidea to 106,7 mya (lower to middle Cretaceous). There is fossil evidence of Nymphalinae already from the Late Eocene (Late Priabonian) of the Florissant Formation (US) (Scudder, 1889). Now, the finding of another subfamily (Limenitidinae) gives a minimum geological age and a calibration point, as well as direct fossil evidence for paleobiogeographical analyses (Chazot et al., 2021). The supposed age of Baltic amber was Mid Eocene (Lutetium) (44 mya by radiometric age dating of glauconite from Blue Earth) (Ritzkowski, 1997), revised to Upper Eocene (Priabonian, 33.9-37.8 mya) by paleontological evidence from Blue Earth (Kosmowska-Ceranowicz et al., 1997, Sadowski et al., 2020).

CONCLUSIONS

The find of a butterfly egg and its affiliation to the group of admirals (Limenitidinae) gives a minimum age for this subfamily of higher Lepidoptera by direct evidence, demonstrating also conservatism for the highly specialized egg sculpture. For taphonomy of amber inclusions, it shows that taxa not yet found and not to be expected to be preserved as adults can again be identified by their juvenile stages. Eggs or larvae are much smaller, often they have a different habitat. Consequently, embedding chances in amber-forming resins differ from that of adults.

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