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Aquatic lacewings of family Nevrothidae (Neuroptera) in Baltic amber¹

W. WICHARD, T. BUDER & C. CARUSO

Abstract: From Baltic amber there are currently five known fossil species in three fossil genera. *Electroneurothus malickyi* nov.gen., nov.sp. and *Palaeoneurothus groehni* nov.sp. are going to be described in this paper. On the basis of the fossil species, a preliminary phylogenetic tree of the family Nevrothidae is suggested. Extant Nevrothidae can be regarded as "living fossils", as their morphology and probably their biology match with the currently oldest known fossil Nevrothidae from Baltic amber. It is possible that the subtropical Nevrothidae expanded across Eurasia during the Cretaceous Period, when land bridges existed for a short amount of time between Asia und Europe, even before Europe was once again separated from Asia by the marine Turgai Strait during the whole Eocene.

Key words: Baltic amber, fossil Nevrothidae, Turgai Strait, Cretaceous, palaeobiogeography, phylogeny.

Introduction

It was a paper of Hans MALICKY (1984) that inspired the research of Nevrothidae in the past years. This small family within the order Neuroptera is represented in the Mediterranean (*Nevrothus*), in Southeast Asia (*Nipponeurothus*) and in Australia (*Austroneurothus*) by one genus each. ZWICK (1967) had previously described the larva of *Nevrothus fallax* (RAMBUR, 1842) and he not only analysed the particular structure of the prothoracal segment but also established the monophyletic group of the Nevrothidae as a new own family. In his paper, MALICKY (1984) dealt with the distribution, biology and ecology of the genus *Nevrothus* in the Mediterranean area and described the biology of larvae and pupae, which he observed in Greece, Sicily, Sardinia and Corsica. According to his observations the agile larvae live mostly in small, mountain springs that are characterized by a particular clearness of the water, a low saprobiological pollution and high oxygen content. The mature larvae construct a loosely spun outer cocoon and a tightly spun inner cocoon for their pupation, which takes place in the water on the bottom side of stones (MALICKY 1984). The fine structure of the two cocoons when observed with a scanning electron microscopic (SEM) show matted, unregularly spun areas (WICHARD et al. 2002), in which air can be stored, covering the whole pupal body, thereby enabling respiration and thus allowing the pupa to survive under the water surface. Dissolved oxygen diffuses from the water via the air store into the pupal body. As the pupa is isolated by the air store from the surrounding water no osmosis is taking place and the aquatic pupae do not require osmoregulation.

¹ This paper is dedicated to Prof. Dr. Hans Malicky on the occasion of his 75th birthday.

Based on first descriptions (*Nevrorthus* COSTA, 1863, *Nipponeurorthus* NAKAHARA, 1958 and *Austroneurorthus* NAKAHARA, 1958, summarized by MONSERRAT 1977), studies of the last years were made systematically and phylogenetically. Apart from the new descriptions of the currently fourteen discovered species (ASPÖCK U. 2004, ASPÖCK H. et al. 1977, 1980, ASPÖCK U. & H. ASPÖCK 1983, 2007, 2008) morphological and molecular biological analysis provide evidence about the suborder Nevorthiformia with its only family Nevorthidae being a sister group to all other Neuroptera (Myrmeleontiformia, Hemerobiiformia) (ASPÖCK U. et al. 2001, ASPÖCK U. 2002, HARING & U. ASPÖCK 2004). The so far oldest nevrorthid fossils come from Eocene Baltic amber (WEITSCHAT & WICHARD 2002, WICHARD et al. 2009) and from Eocene Ukrainian amber (MAKARKIN & PERKOVSKY 2009). *Rophalis relict*a (HAGEN, 1856 in BERENDT 1845-1856) is the first verified fossil species (Figs 1, 2a-c), followed by four further fossil species in Baltic amber: *Palaeoneurorthus hoffeinsorum* WICHARD, 2009, *Palaeoneurorthus bifurcatus* WICHARD, 2009 and now two new described species are added: *Palaeoneurorthus groehni* nov.sp. and *Electroneurorthus malickyi* nov.gen., nov.sp.

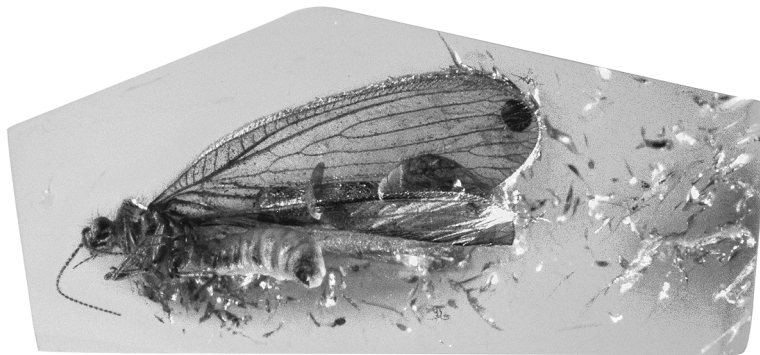


Fig. 1: *Rophalis relict*a (HAGEN, 1856), neotype, female (compare WICHARD et al. 2009).

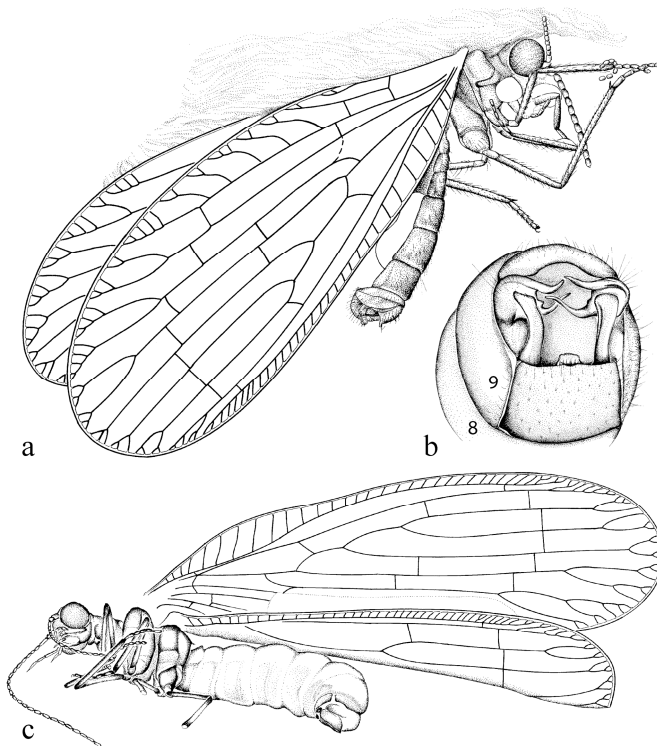


Fig. 2: *Rophalis relict*a (HAGEN, 1856), drawings (a) male in lateral view; (b) male genitalia; (c) female, the neotype, kept in "Westpreussisches Landesmuseum" in Münster-Wolbeck (ex Coll. Menge & Helm no. 398).

Systematik

***Electroneurorthus* nov.gen.**

Type species: *Electroneurorthus malickyi* nov.sp.

Derivatio nominis: The name *Electroneurorthus* refers to the word electron, the Greek term for amber.

Diagnosis:

Head: Ocelli are absent; filiform antennae with slightly enlarged scapus, smaller pedicellus and ca. 34 following uniform antennal segments. The five-segmented maxillary palps and the three-segmented labial palps terminate in a pointed final segment.

Wings: Fore- and hindwings are almost uniform. Subcostal crossveins are simple in both wings. Subcosta and radius R1 approximate each other distally and are connected distally by a short crossvein. Fore- and hindwings are characterized by the inner and outer crossvein gradate series 3 and 4 (Figs 3a-b, 4a, 8). In forewings the crossvein 3rs3-rs2 is present and in hindwings absent.

Male genitalia: The 9th abdominal ring segment is ventrally interrupted by the derived, elongate 9th sternite. The 9th sternite is much longer than wide, elongate and stick-shaped. At the base of the 9th sternite there are bulbous structures at both sides, probably interpretable as elements of 10th segment. The broad gonocoxites bear apically strong gonostyli that are bent and running medially towards each other. The gonocoxites do not bear visible parameres (gonapophyses). Likewise a median bridge of the gonostyli of the (11th) segment is missing. (Probably both the parameres of the gonocoxites and the gonostyli of the 11th segment are hidden within the genitalia and therefore not visible in the amber preservation.)

The fossil genus *Electroneurorthus* nov.gen. differs from fossil genus *Rophalis* and the extant genus *Nipponeurorthus* in the elongated 9th sternite and from the extant genera *Neurorthus* and *Austroneurorthus* in the missing of the dorsodistal, median bridge of the gonostyli of the (11th) segment. Moreover *Electroneurorthus* differs from the fossil genus *Palaeoneurorthus* 1. in the elongate and compactly stick-shaped 9th sternite, which is dorsoventrally flattened in *Palaeoneurorthus* and 2. in loss of the outdoor, needle-shaped parameres of the gonocoxites.

***Electroneurorthus malickyi* nov.sp. (Figs 3a-b, 4a-b)**

Holotype: Male arranged in Baltic amber, which is embedded in synthetic resin, prepared by Agnes Gras, Köln, deposited in Geol.-Paläontol. Institute and Museum, University of Hamburg, GPIMH (ex. Coll. Gröhn 7078). The male is well preserved with the head and antennae, with thorax and all legs and the left fore- and hindwings, and with the abdomen and the male genitalia, but the right fore- and hindwings are cut.

Paratype: Male embedded in clear Baltic amber, deposited in Coll. Wichard. The male is well preserved in amber, but the male genitalia is covered by an air bubble, which hinder the view and the interpretation.

Derivatio nominis: Dedicated to Univ.-Prof. Dr. Hans Malicky's 75th birthday. Hans Malicky greatly contributed to the present knowledge of aquatic entomology by his studies on the taxonomy, biology and biogeography of aquatic insects and especially of Trichoptera.

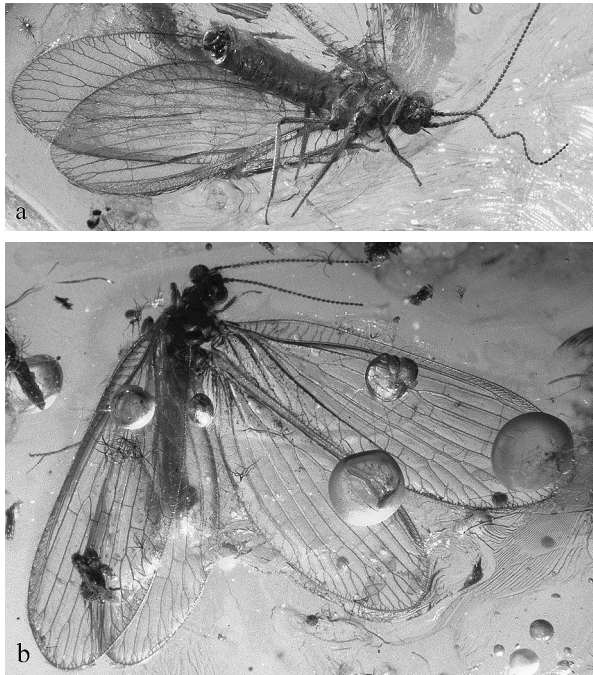


Fig. 3: *Electroneurorthus malickyi* nov.gen., nov.sp. (a) holotype; (b) paratype.

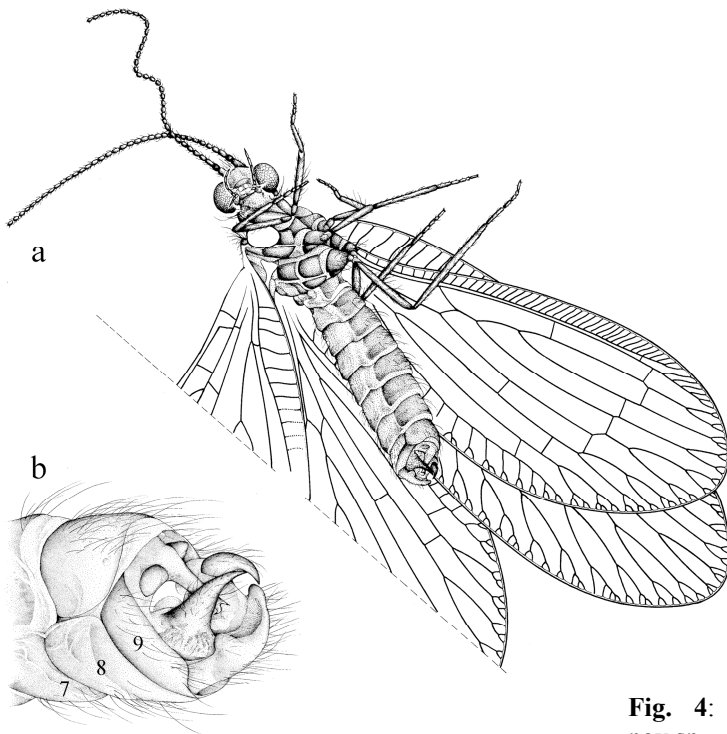


Fig. 4: *Electroneurorthus malickyi* nov.gen., nov.sp., drawings (a) holotype in ventral view; (b) male genitalia in lateral view.

Description:

Head: Large male, the distance between the bulging eyes is ca. 0.7 mm, without additional ocelli, with filiform antennae, consisting of ca. 36 segments, including a large scapus, a smaller pedicellus, and a third segment, which is twice as long as the following antennal segments; mouthparts with five-segmented maxillary palps with pointed final segment and with three-segmented labial palps, pointed the last segment.

Wings: Length of left forewing is ca. 6.5 mm (forewings of the paratype = ca. 7 mm). Wings are not spotted, hyaline; wing venation in fore- and hindwings with an inner and outer row of crossveins. In forewings crossvein 3rs3-rs2 is present, but absent in hindwings. Subcosta and radius 1 are close together at apex and connected by a short crossvein; crossveins between costa and subcosta are not forked but simple.

Male genitalia: The 9th abdominal ring segment is ventrally interrupted by the derived 9th sternite. The 9th tergite forms dorsobilaterally a cufflike structure. The 9th sternite is much longer than wide, elongate and covered basally by a membrane of the 8th segment. The long and cylindrically rounded, stick-shaped 9th sternite is distally narrowed and forked into two short and curved spines at the end. Laterally, at the base of the 9th sternite there are bulbous-formed structures at both sides, which are probably elements of 10th segment. The basally broad gonocoxites bear apically strong gonostyli that are bent and running towards each other medially. The gonocoxites do not possess needle-like parameres (gonapophyses) as in genus *Palaeoneurorthus*; the parameres are absent or, probably, engrained inside and basally of the gonocoxites and therefore not visible. The 10th tergite is dorsally broadly bulging and forms laterally convex epiprocts.

Diagnosis:

The fossil *Electroneurorthus malickyi* nov.gen., nov.sp. differs from the fossil *Rophalis relict*a:

1. in the number of the antennal segments (*Rophalis*: ca. 25, *Electroneurorthus*: ca. 36),
2. in the distribution of the crossveins (in forewings the crossvein 3rs3-rs2 are normally absent in *Rophalis*, but present in *Electroneurorthus*)
3. in the structure of the 9th sternite (quadrate in *Rophalis*, elongate in *Electroneurorthus*)

The fossil *Electroneurorthus malickyi* nov.sp. differs furthermore from the fossil *Palaeoneurorthus hoffeinsorum* and fossil *Palaeoneurorthus bifurcates*:

1. in the elongate stick-shaped 9th sternite, which is dorsoventrally flattened in *Palaeoneurorthus*
2. in absence of the needle- or thorn-shaped parameres of the gonocoxites.

***Palaeoneurorthus* WICHARD, 2009**

Type species: *Palaeoneurorthus hoffeinsorum* WICHARD, 2009.

Diagnosis:

Head: Ocelli are absent; filiform antennae with slightly enlarged scapus, smaller pedicellus and ca. 34 following uniform antennal segments. The five-segmented maxillary palps and the three-segmented labial palps terminate in a pointed final segment.

Wings: Fore- and hindwings are almost uniform. Subcostal crossveins are simple in both wings. Subcosta and radius R_1 approximate each other distally and are connected by a short crossvein. Fore- and hindwings are characterized by inner and outer rows of crossveins. In forewings the crossvein 3rs3-rs2 is present; in hindwings the crossvein 3rs3-rs2 and 3rs3-rs3 are absent.

Male genitalia: The 9th abdominal ring segment is ventrally interrupted by the derived 9th sternite. 9th sternite is much longer than wide, elongate and dorsoventrally flattened. The gonocoxites of the 9th segment are broad at their base and bear apically equally strong gonostyli that are bent and approximate each other until they almost touch medially. The gonostyli consist of pointed cones. Ventrally both gonocoxites bear bizarre parameres (gonapophyses) with a set of two or three pointed needles or thorns.



Fig. 5: *Palaeoneurorthus gröhni* nov.sp., male holotype, together with a female, probably *P. gröhni*.

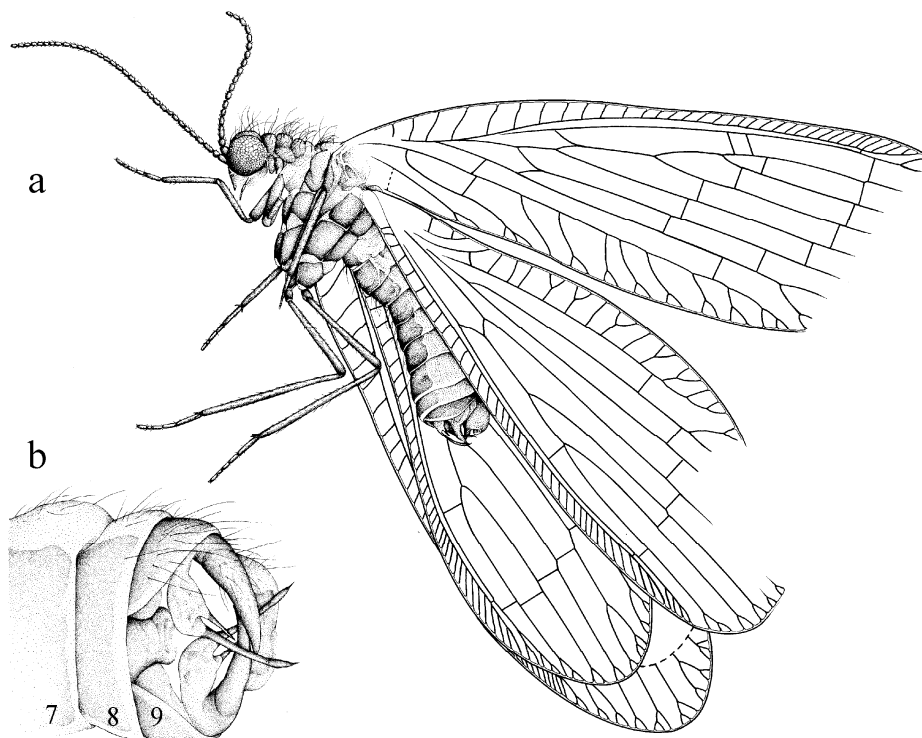


Fig. 6: *Palaeoneurorthus gröhni* nov.sp., drawings (a) holotype in lateral view, (b) male genitalia in ventral view.

***Palaeoneurorthus groehni* nov.sp. (Figs 5, 6a-b)**

H o l o t y p e : Male is in a piece of clear Baltic amber together with a female that possibly belongs to the described male and species, together embedded in synthetic resin, prepared by Agnes GRAS, Köln. The male genitalia can be seen in lateral and ventral view. The prepared amber piece is kept in the amber collection of the Geol.-Palaeontol. Institute and Museum of the University of Hamburg, ex. Coll. GRÖHN 7081.

D e r i v a t i o n o m i n i s : Dedicated to Carsten GRÖHN, Glinde. Carsten Gröhn made many nevrorthid specimens in Baltic amber available for scientific use.

D e s c r i p t i o n :

Head: Large, bulging eyes, without additional ocelli, with filiform antennae; both antennae are broken into two pieces in the amber sample, consist of all ca. 36 segments, including a large scapus and a small pedicellus; five-segmented maxillary palps and the three-segmented labial palps, both with pointed final segments.

Wings: Length of forewings ca. 6 mm, whereas the female has forewings with a length of ca. 7 mm, wings are not spotted, but hyaline. Wing venation in fore- and hindwings have inner and outer rows of crossveins. In forewing crossvein 3rs3-rs2 present, but lacking in hindwing. The holotype has asymmetrical wings; the left forewing has a crossvein 3rs3-rs which is absent in the right forewing. Between R1 and Rs the crossvein 3r1-rs is present twice in fore- and hindwing. Subcosta and radius are apically close together and connected by a short crossvein, the crossveins between costa and subcosta are not forked but simple.

Male genitalia: The 9th abdominal ring segment is ventrally interrupted by the derived 9th sternite. The 9th abdominal segment forms a slender cufflike structure with an almost annular tergite and is interrupted ventrally by the 9th sternite. The 9th sternite is long, slender and flattened; the distal part is probably hidden on the inside of the male genitalia and not visible. Amalgamated spicular sclerites laterally at the 9th sternite are not clearly visible. The gonocoxites of the 9th segment are broad at their base and end distad into a strong gonostyli that are bent and running towards each other until they almost touch medially. A ventral lobe of the gonocoxites bears two needle-shaped parameres (gonapophyses); the ventral one is short and pointed; the dorsal one is long, distally ampullae-shaped enlarged and pointed rearwards. The 10th tergite is dorsally slightly bulging and forms the lateral epiprocts.

D i a g n o s i s :

The new described species belongs to the genus *Palaeoneurothus* within the family Nevrothidae by the combination of following characteristic features.

1. the antennae with ca. 36 segments, 2. the wing venation with apical crossveins between Sc and R₁, 3. the crossveins 3rs3-rs2 in the forewing and 4. crossvein gradate series 3 and 4. Also the male genitalia characteristics 5. a slender and flattened 9th sternite and 6. the needle-shaped parameres of the gonocoxites. *Palaeoneurorthus groehni* nov.sp. differs clearly from the other two fossil species of *Palaeoneurorthus* by shape differentiations of the parameres.

Male genus key of Nevrorthisidae

- 1 Antennae ~25-segmented; in forewings crossvein 3rs3-rs2 absent †*Rophalis*
- Antennae ~36-segmented; in forewings crossvein 3rs3-rs2 present 2
- 2 9th sternite shorter than wide, or as long as wide, semicircular *Nipponeurorthis*
- 9th sternite much longer than wide, elongate 3
- 3 9th sternite elongate, dorsoventrally flattened 4
- 9th sternite elongate, stick-shaped †*Electroneurorthis* nov.gen.
- 4 Parameres needle-shaped, in forewings crossveins 3rs3-rs2 and without 3rs-rs3 5
- Parameres lobus-shaped; in forewings crossveins 3rs3-rs2 and 3rs-rs3 *Austroneurorthis*
- 5 Elements of 11th segment forming a median bridge, dorsodistal *Nevrorthis*
- Median bridge not dorsodistal ... (absent or positioned on the inside of the male genitalia, therefore not visible in amber preservation) †*Palaeoneurorthis*

Palaeobiogeography

Currently, fourteen extant and five fossil species belong to the family Nevrorthisidae, which is composed of overall six genera, three of which are fossil. All of the fossil species are found in Eocene Baltic amber. The distribution of the extant Nevrorthisidae is limited to three disjunct areas, the Mediterranean with four species of the genus *Nevrorthis*, Southeast Asia with eight species of the genus *Nipponeurorthis* and the Australian eastcoast with two species of the genus *Austroneurorthis*. In their biology, Nevrorthisidae are adapted to a subtropical climate, which can be found in all three geographical regions in which this family appears. Only the larvae with their aquatic way of life are accommodated to the moderate water temperature of streams (MALICKY 1984). Similarly, also fossil nevrorthid species of the Eocene lived under subtropical conditions (Fig. 7). From the Mid Jurassic period to the end of the Eocene, the global temperature was at its maximum, the polar caps of the North and South Pole were ice-free and Spitzbergen had subtropical vegetation. The climate conditions of the Eocene, which was characterized by a high amount of precipitations, were similar to the extreme conditions of the earlier Carboniferous. This warm-humid climate of the Eocene caused a development of tropical and subtropical rain forests, to which also the amber forest of northern Europe belonged.

Taking into account the background of fossil Nevrorthisidae of the subtropical Eocene of northern Europe, new questions about the biogeography of currently living, endemic genera are raised. In the Eocene period, Europe was an archipelago and consisted of several islands, which were drawn together or torn apart by continental drift and constantly changed their form and size as the sea level was fluctuating (SCOTese 2001, SANMARTIN et al. 2001, BARABOSHkin et al. 2003). Europe was separated from Asia by the epicontinental Turgai Strait, which connected the Arctic Sea and the Tethys Ocean for a long time. The separation started in the Mid Jurassic, approximately 160 million years ago, and ended with the beginning of the Oligocene, approximately 34 million years ago, when a decrease of temperature froze the North and South Pole and the sea level therefore sank, which caused the Turgai Strait to dry out. When Europe and Asia were finally connected, the climate changed and a decrease of temperature caused the end of the amber forest and prevented the fauna and flora to spread across Eurasia.



Fig. 7: Worldwide distribution of fossil and extant genera of family Nevrorthisidae in subtropical (grey) areas.

In the Oligocene and the following periods, the temperature decreased, which made a spread of the Eocene subtropical Nevrorthisidae in the continental triangle between northern Europe, Southeast Asia and the Mediterranean unlikely. It is, however, more likely that the expansion and distribution took place even before the global decrease of temperature and before the separation of Europe and Asia. Even if the Turgai Strait existed for approximately 125 million years (Middle Jurassic to Early Oligocene) it dried out from time to time when the sea level fell. In the Cretaceous period, continental drifts caused Europe and Asia to draw together and the Turgai Strait was interrupted from about the Aptian-Coniacian by a series of intermittent land bridges, which enabled a continental expansion of subtropical plants and animals, such as the nevrorthisids across Eurasia (SCOTSE 2001, BARABOSHKIN et al. 2003).

Even earlier in the geological past, between the Early Triassic and the Early Jurassic (approximately 245-195 million years ago) the supercontinent Pangea allowed land animals to spread across its surface and to migrate from the South Pole to the North Pole. The spread of Nevrorthisidae across Pangea was discussed to explain the presence of the genus *Austroneurorthus* in Southeast Australia (ASPÖCK U. & H. ASPÖCK 1994). However, the remarkably close relationship between fossil species of Eocene Skandinavia and extant Nevrorthisidae from Australia, Southeast Asia and the Mediterranean contradicts the hypothesis of an very early, pangean spread that took place more than 200 million years ago, even if the fossil specimens are frequently called "living fossils". If the nevrorthisid stem group had been distributed from the pangean North Pole (Skandinavia) to the pangean South Pole (Australia), an uncountable number of populations must have existed and spread across the continent and during a long geological time they would have probably brought out numerous new species with a high variety of characteristic features. However, neither fossil nor extant Nevrorthisidae provide evidence for such a variety.

In fact, extant Nevrorthisidae can be seen as "living fossils", as their morphology and probably their biology match with fossil Nevrorthisidae from the Eocene Baltic amber. The fourteen discovered extant and five fossil species hardly differ, e.g. in the venation of their fore- and hindwings (Fig. 8). The species of *Nipponneurorthus*, *Palaeoneurorthus*, *Electroneurorthus*, and *Nevrorthis* are almost identical in the organization of the longitudinal veins and of the crossveins. In the forewings of all species the characteristic crossvein 3rs3-rs2 is present

whereas the crossvein 3rs-rs2 is absent in the hindwings. Only *+Rophalis relict*a (Figs 1, 2a-c) differs by the lacking crossvein 3rs3-rs2 in the forewings. In contrast to all other genera, the genus *Austroneurorthus* has additional crossveins and is characterized by the crossvein 3rs3-rs in its forewings. Apart from this regularity of the wing venations, all nevrorthids tend to show a more or less developed intraspecific asymmetry in the crossveins, e.g. in some few specimens of *Rophalis relict*a the crossvein 3rs3-rs2 is also present in the right or left forewing and in genus *Palaeoneurorthus* the crossvein 3rs3-rs sometimes appears in one of the forewings, in addition to the characteristic crossvein 3rs3-rs2. Sometimes the crossveins occur also twice in the same wings, e.g. in the forewing of *Palaeoneurorthus groehni* nov.sp. with two crossveins 3rs-r1 on left wing only (Fig. 6). These intraspecific asymmetries hint at a tendency in the family Nevorthidae to complete the 3rd gradate series of the crossveins in the forewing and do not stand in contrast to the general high morphological similarity of fossil and extant Nevorthidae.

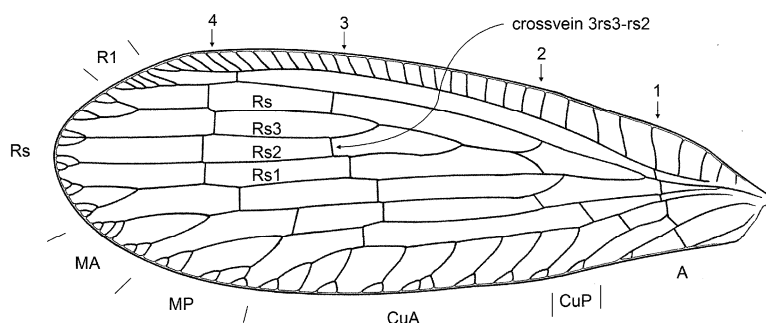


Fig. 8: Blueprint of the forewing of the family Nevorthidae with the longitudinal veins (R1, Rs, MA, MP, CuA, CuP, A) and with four crossvein gradate series (1-4). The terminology follows OSWALD (1993) in the interpretation of MAKARKIN & PERKOVSKY (2009). In forewing the crossvein 3rs3-rs2 is present in fossil *Palaeoneurorthus* and *Electroneurorthus* and in extant *Nipponeurorthus* and *Nevorthus*, but absent in fossil *Rophalis*.

On the basis of the fossil species and of the morphological characters of their male genitalia we suggest a preliminary phylogenetic tree of the family Nevorthidae (Fig. 9) and include the extant taxa as far as possible, e.g. the sistergroup of *Nevorthus* and *Austroneurorthus* proposed by ASPÖCK U. (2004).

The morphological traits are:

1. Apomorphy of the family Nevorthidae: The aquatic larvae are characterised by prothoracal differentiations (ZWICK 1967).
2. Sympleisiomorphy of the sistergroup of *Rophalis* and *Nipponeurothus*: The 9th abdominal segment forms a closed ring by the dorsobilateral, horseshoe-shaped 9th tergite and the ventral, quadrate 9th sternite (Fig. 2b).
3. Apomorphy of the group consists of fossil *Electroneurorthus*, *Palaeoneurorthus* and the extant *Nevorthus* and *Austroneurorthus*: The abdominal 9th segment ring is ventrally interrupted by the derived, elongate 9th sternite (Figs 4b, 6b).
4. Apomorphy of extant *Nipponeurorthus*: The 9th quadrate sternite is derived, much shorter than wide and semicircular (NAKAHARA 1958, ASPÖCK U. & H. ASPÖCK 2008).

5. Apomorphy of fossil *Electroneurorthus*: The 9th elongate sternite is cylindrically rounded and stick-shaped (Fig. 4b).
6. Apomorphy of fossil *Palaeoneurorthus*, including the extant *Nevrorthus* and *Austroneurorthus*: The 9th elongate sternite is dorsoventrally flattened (Fig. 6b).

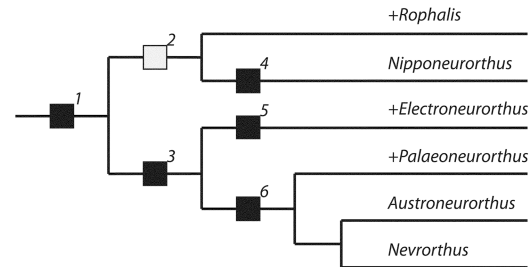


Fig. 9: Proposal of a preliminary phylogenetic tree of the family Nevorthidae on the basis of the fossil taxa, descriptions of the traits in the text.

We think, that the expansion of the nevorthid stem group is likely to go back to the Cretaceous period; their earliest evidence was found in Eocene Baltic amber. The prevailing tropical and subtropical climate in the Cretaceous period enabled the Eurasian spread of the warm-adapted nevorthids in times when Asia and Europe were connected. The idea of the Tethys-spread of nevorthids along the continental margins (ASPÖCK U. & H. ASPÖCK 1994) is acceptable but not verified and does not take into account the existence of nevorthids in Baltic amber. It is more likely that the stem group spread out from an unknown Cretaceous Eurasian location into different directions and populated distant areas, e.g. in the north, south and east of Eurasia, where the nevorthids survived and established new genera in disjunct areas (Fig. 7). Eocene Baltic amber provides evidence about plants and animals whose extant closest relatives are frequently found today in Southeast Asia - as it is the case with the family Nevorthidae - and seldom in the Mediterranean or in other subtropical regions. This leads to the conclusion that a stem group of both the relicts of disjunct areas and the inclusions of Eocene Baltic amber had a wide Eurasian-continental spread by the end of the Aptian-Coniacian, even before Europe was again separated from Asia and isolated as an archipelago.

Zusammenfassung

Aus dem Baltischen Bernstein sind derzeit fünf fossile Arten in drei fossilen Gattungen bekannt, von denen hier *Electroneurorthus malickyi* nov.gen., nov.sp. und *Palaeoneurorthus groehni* nov.sp. beschrieben werden. Auf der Grundlage der fossilen Arten schlagen wir einen vorläufigen Stammbaum der Familie Nevorthidae vor. Die heutigen Nevorthiden können als "lebende Fossilien" bezeichnet werden, weil sie morphologisch und wahrscheinlich auch biologisch mit den derzeit ältesten fossilen Nevorthiden aus dem Baltischen Bernstein nahezu übereinstimmen. Möglicherweise breiteten sich die wärmeliebenden Nevorthiden während der Kreidezeit im subtropischen Eurasien aus, als für kurze Zeiten Landbrücken zwischen Asien und Europa bestanden, noch bevor Europa durch die marine Turgai Senke wieder einmal und für die Dauer des Eozäns von Asien getrennt wurde.

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Authors' addresses:

Prof. Dr. Wilfried WICHARD
Timo BUDER, Celstine CARUSO
Institut für Biologie
Universität Köln
Gronewaldstr. 2
D-50931 Köln, Germany
E-mail: Wichard@uni-koeln.de

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