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Paleogeographic Distribution of Leuctridae and Nemouridae Genera Preserved in Baltic Amber, with the Description of *Palaeopsole weiterschani* n. gen., n. sp. (Plecoptera)

Die paläogeographische Verbreitung der Leuctridae- und Nemouridae-Gattungen des Baltischen Bernsteins, mit der Beschreibung von *Palaeopsole weiterschani* n. gen., n. sp. (Plecoptera)

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Summary: The description of the new fossil species *Palaeopsole weiterschani* n. gen., n. sp. adds the genus *Palaeopsole* to the extant six genera of the families Leuctridae and Nemouridae, which have been found in Eocene Baltic amber. These Eocene fossils are the oldest representatives of their extant genera, so far. But the Eocene European archipelago is neither place nor time in which these genera originated. The origin of these seven genera is unknown, but took very probably place in the northern hemisphere before the Eocene. After Laurasia had finally broken apart at early Jurassic, probably not till then the genera developed and spread out across the warm-temperate and subtropical northern hemisphere. The extant Nearctic genera – *Lednia*, *Megaleuctra*, and *Zealeuctra*, including the transberingian *Podmosta*, and including *Leuctra* and *Nemoura* which are nearly distributed all over the Holarctic region – spread probably across the northern hemisphere via the temporary Beringian and Turgai Strait land bridges at Cretaceous. Towards the end of Eocene the temperature decreased worldwide and forced the Nearctic and Holarctic genera to adapt to temperate and boreal climates, whereas the recent relatives of genus *Palaeopsole*, probably genus *Rhopalopsole*, continued and live in the subtropical area of the Oriental region and Southeast Asia.

Keywords: *Rhopalopsole*, fossil Plecoptera, Eocene, paleobiogeography

Zusammenfassung: Die Beschreibung der neuen, fossilen Art *Palaeopsole weiterschani* n. gen., n. sp. fügt die Gattung *Palaeopsole* den sechs Gattungen der Leuctridae und Nemouridae hinzu, die im eozänen Baltischen Bernstein nachgewiesen sind. Diese eozänen Fossilien sind die ältesten Vertreter der rezenten Gattungen. Dennoch ist der Europäische Archipel im Eozän weder Ort noch Zeitpunkt des Ursprungs dieser Gattungen. Der Ursprung der sieben Gattungen ist unbekannt, aber lag sicher in der nördlichen Hemisphäre und zeitlich vor dem Eozän. Nachdem Laurasia im unteren Jura endgültig auseinander fiel, erst danach entwickelten sich die Gattungen und breiteten sich über die subtropische nördliche Hemisphäre aus. Die rezenten, nearktischen Gattungen, *Lednia*, *Megaleuctra* und *Zealeuctra*, sowie die transberingische Gattung *Podmosta* und die Gattungen *Leuctra* und *Nemoura*, die nahezu überall in der Holarktis vorkommen, expandierten während der Kreidezeit über die zeitweiligen Landbrücken der Turgai- und Bering-Strasse. Gegen Ende des Eozäns sanken die Temperaturen; das geänderte Klima zwang die holarktischen Gattungen, sich dem gemäßigten und borealen Klima anzupassen, während die heutigen nächsten Verwandten von *Palaeopsole* (vermutlich *Rhopalopsole*) in der Subtropis der Orientalischen Region und in Südostasien fortleben.

Schlüsselwörter: *Rhopalopsole*, fossile Plecoptera, Eozän, Paläobiogeographie

1. Introduction

So far, all Plecoptera that have been found in Baltic amber belong to genera that still exist today (CARUSO & WICHARD 2010). This arouses questions about the degree of relationship to extant species and their paleobiogeographic distribution. Apart from *Taeniopteryx* (Taeniopterygidae), *Perla* (Perlidae), *Isoperla* and *Perlodes* (Perlodidae) seven further genera of Nemouridae and Leuctridae were found, which will be discussed in this paper: *Leuctra*, *Megaleuctra*, *Palaeopsole*, *Zealeuctra* (Leuctridae) and *Lednia*, *Nemoura*, and *Podmosta* (Nemouridae). The genus *Palaeopsole* is a new discovery in Baltic amber and is represented by the fossil species *Palaeopsole weiterschani* n. gen., n. sp.

Baltic amber has its origin in the Eocene, approximately 40-50 million years ago and its genesis is very probably connected to the tree resin of the amber-pine tree *Pinus succinifera*, which was a characteristic species of the Eocene amber forest (SCHUBERT 1961; WEITSCHAT & WICHARD 2002). From the Mid Jurassic to the Late Eocene, Europe was an archipelago and it was composed of several small islands in its south and one big, northern island, which was probably the location of the amber forest (SCOTESE 2002; WICHARD et al. 2009). In the Cretaceous period the islands were sometimes connected with Asia and formed temporary land bridges that enabled a continental spread of plants and animals between Europe and Asia (SCOTESE 2002; BARABOSHKIN et al. 2003). During the Eocene the European archipelago was not connected with any other neighbouring continent (SCOTESE 2002). It was not before the end of the Eocene, approximately 34 million years ago, that the Turgai Strait ran dry, which resulted in a permanent connection of Europe and Asia and created Eurasia.

The oldest fossils of the families Leuctridae and Nemouridae come from the Lower Cretaceous (SINITSHENKOVA 1997, 2003). The first fossil species of the family Nemouridae is *Dimoula dimi* from the Glushkovo formation (Lower Cretaceous) (SINITSHENKOVA 2005). Another extinct species (*Palaeoleuctra acuta*) of the family Leuctridae was described from Eocene Rovno amber (SINITSHENKOVA 2009). The Eocene species of the Leuctridae and Nemouridae that have been found in Baltic amber are the oldest fossil representatives of their extant genera (CARUSO & WICHARD 2010).

2. Systematics

Family: Leuctridae

Palaeopsole n. gen.

Type species: *Palaeopsole weiterschani* n. sp.

Derivatio nominis: The new extinct genus is named in combination after the related genus *Rhopalopsole* and after the fossil inclusion in Baltic amber.

Diagnosis: The male is characterized by following genital structures: Tergum 9 bears mid-posterior spine on the posterior margin, sternum 9 has basally an drumming appendage (ventral lamella), and furthermore sternum 9 is extended caudally forming a rounded subgenital plate which undergirds sternum 10. Lateral projections of tergum 10 are formed by broad, rounded, and sclerotised plates ending caudad in a concave margin with two sharp points. Subanal lobes are short, flat and plate-like, semicircular, with central furrow. The cerci are short and upturned, mesad extended to a small, dark hump and terminally bearing a small, light-coloured hump. In lateral view, the elongate, hyaline epiproct forms a hook-like projection, upturned, arising from a broad, membranous cushion.

Palaeopsole is very closely related to genus *Rhopalopsole* by the presence of a ventral lamella basally on sternum 9 and further by sternum 9 forming an extended subgenital plate that undergrids sternum 10, furthermore by the lateral projections of tergum

10 forming broad, rounded and sclerotised plates. Nevertheless the trait combinations of the male genitalia do not allow us to confidently assign the fossil form to one of the taxonomical groups of the recent *Rhopalopsole* suggested by Sivec et al. (2008). Moreover, *Palaeopsole* differs from genus *Rhopalopsole* by the small and upturned cerci, mesad a with dark hump and terminally with a light-coloured hump, which seems to be more typical for *Perlomyia*; otherwise in *Perlomyia* forewings Rs and M arise from the same point on R (Nelson & Hanson 1973). But *Palaeopsole* n. gen. has a typical leuctrid forewing venation and sector radii Rs and media M arise from separate points of radius R.

Fossil genus *Palaeopsole* n. gen. male is characterized by tergum 9 bearing a mid-posterior spine on the posterior margin and by sternum 9 bearing basally a ventral lamella and furthermore forming caudally a subgenital plate that undergirds sternum 10. Lateral projections of tergum 10 are formed by broad, rounded and sclerotised plates ending caudad with two sharp points. The cerci are short and upturned, mesad extended to a dark hump and terminally bearing a light-coloured hump.

Palaeopsole weiterschani n.sp.

(Figs. 1, 2)

Holotype: Male adult is well preserved in Baltic amber. The amber sample is kept in the Staatliches Museum für Naturkunde, Stuttgart, SMNS, ex coll. Thomas Weiterschan.

Material: The amber stone has been cut, grinded, polished, and in the end embedded in synthetic resin for a better inspection from all sides of the inclusion and for better preservation and conservation. The fossil is embedded in a good position: head, mouthparts, eyes, antennae, abdomen, and legs; the forewings are widely spread, but the hind wings are rolled and damaged. The male genitalia is visible in right lateral view and from ventral side. The dorsal sides of the abdomen and male genitalia are covered by the right forewing.

Derivatio nominis: The species is named after the amber collector Thomas Weiterschan, Höchst im Odenwald, who kindly made the fossil available for this study.

Description: Head wide with small, hemiglobose compound eyes; with 3 distinct ocelli; the filiform antennae are asymmetrical; the left antenna is almost as long as the forewings and consists of 34 small segments, plus scapus and pedicellus. The right antenna is shortened, half as long as the left antenna (if they are not cut), and consists of 11 longer segments, plus scapus and pedicellus, both antennae start with a small scapus, a smaller pedicellus, and an elongate 1st segment which is at least twice as long as the following segments of the filiform antennae. The specimen has a family-typical slender habitus, which is slightly compressed in amber; the body length from head until the end of the abdomen comprises ca. 4 mm, the forewings with ca. 4 mm length are equally long.

Thorax: The forewings are widely spread and the incomplete hind wings are rolled; forewings with typical leuctrid venations: three veins in the anal field, cubitus forked in Cu1 and Cu2, with 9 crossveins between; in the right forewing 5 crossveins connect cubitus Cu1 and media M, in the left forewing there are 6 crossveins; the media M arises proximally, before sector radius Rs arises from the radius R1; Rs forked in R_{2+3} and R_{4+5} at crossvein r; subcosta Sc2 is absent. Typical legs are with 3-segmented tarsi; segments 1 and 3 are almost equally long whereas segment 2 is shorter.

Male genitalia: Tergum 9 is sclerotized, distinctly wider than long, its posterior margin with a long, light-coloured, mid-posterior spine. Sternum 9 is basally with a tongue-like appendage (ventral lamella)

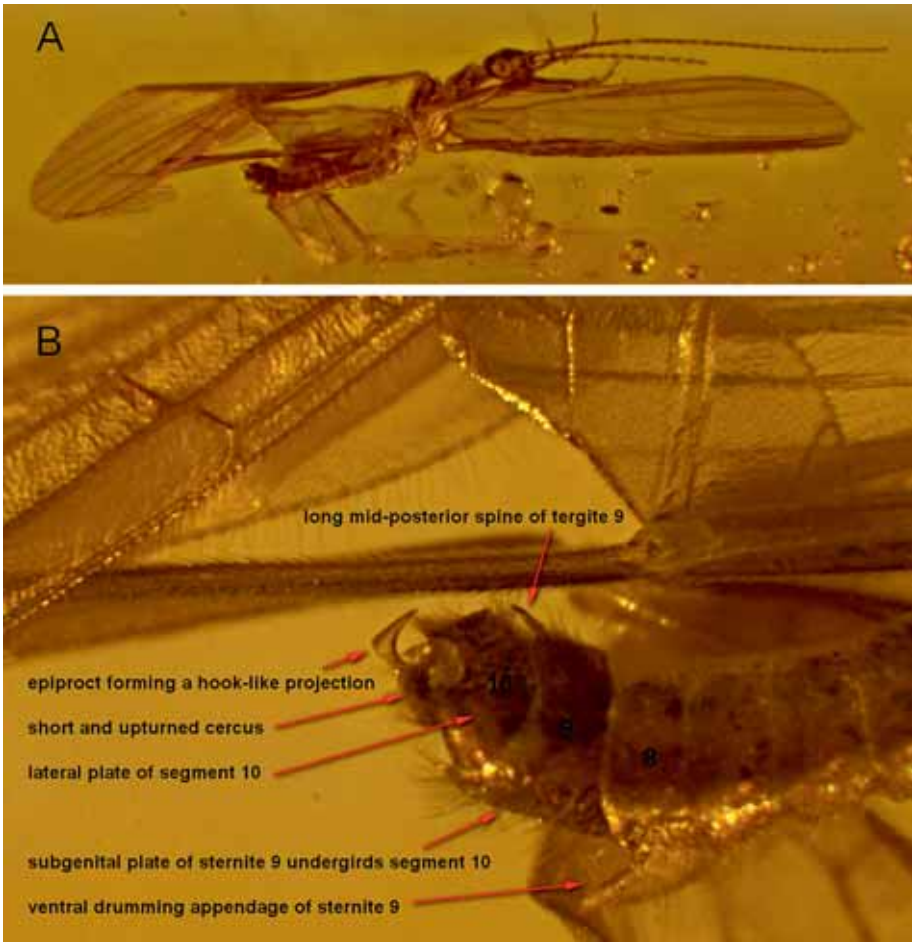


Fig. 1: *Palaeopsole weiterschani* n. gen, n. sp. embedded in Baltic amber. **A** Holotype in lateral view. **B** Male genitalia in lateral view.
Abb. 1: *Palaeopsole weiterschani* n. gen, n. sp. eingebettet im Baltischen Bernstein. **A** Holotyp in lateraler Ansicht. **B** Männliches Genitale, lateral.

and apically with a distinct subgenital plate as wide as long and rounded apically, which undergirds segment 10. The central plate of tergum 10 is covered by the right forewing and not visible from dorsal view. The lateral projections of tergum10 are developed into broad, rounded, and sclerotised plates ending caudad in two sharp peaks. Dorsal and ventral peaks are connected in a bow. In lateral view, the elongate and hyaline epiproct forms a hook-like projection arising from a broad and membranous cushion; its tip is rounded and turned forward. Subanal lobes are short, flat and plate-like, semicircular, with central furrow. The cerci are relatively short and upturned, mesad each with a small, dark hump and terminally each with a small, light-coloured hump.

Diagnosis: *Palaeopsole weiterschani* n. sp. is the type species of the extinct genus *Palaeopsole* n. gen. demonstrating a narrow relationship to the extant genera *Rhopalopsole*. Furthermore, *Palaeopsole weiterschani* n. sp. is charcterised by a long, light-coloured, mid-posterior spine on the posterior margin of

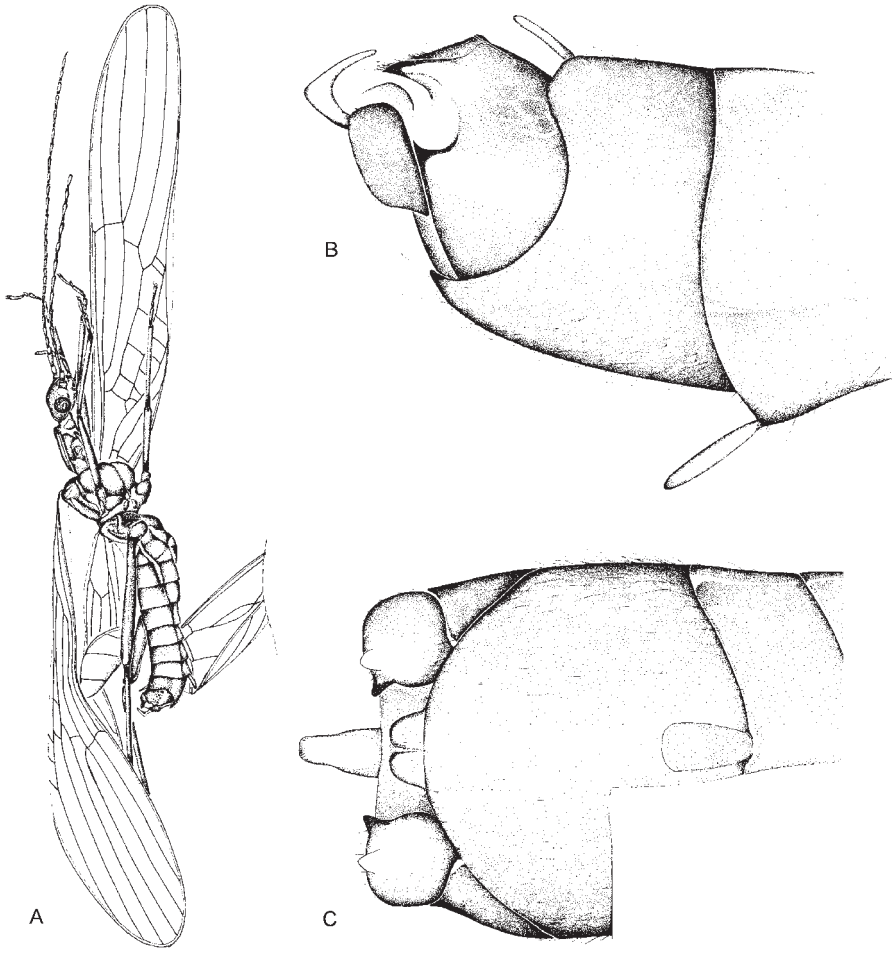
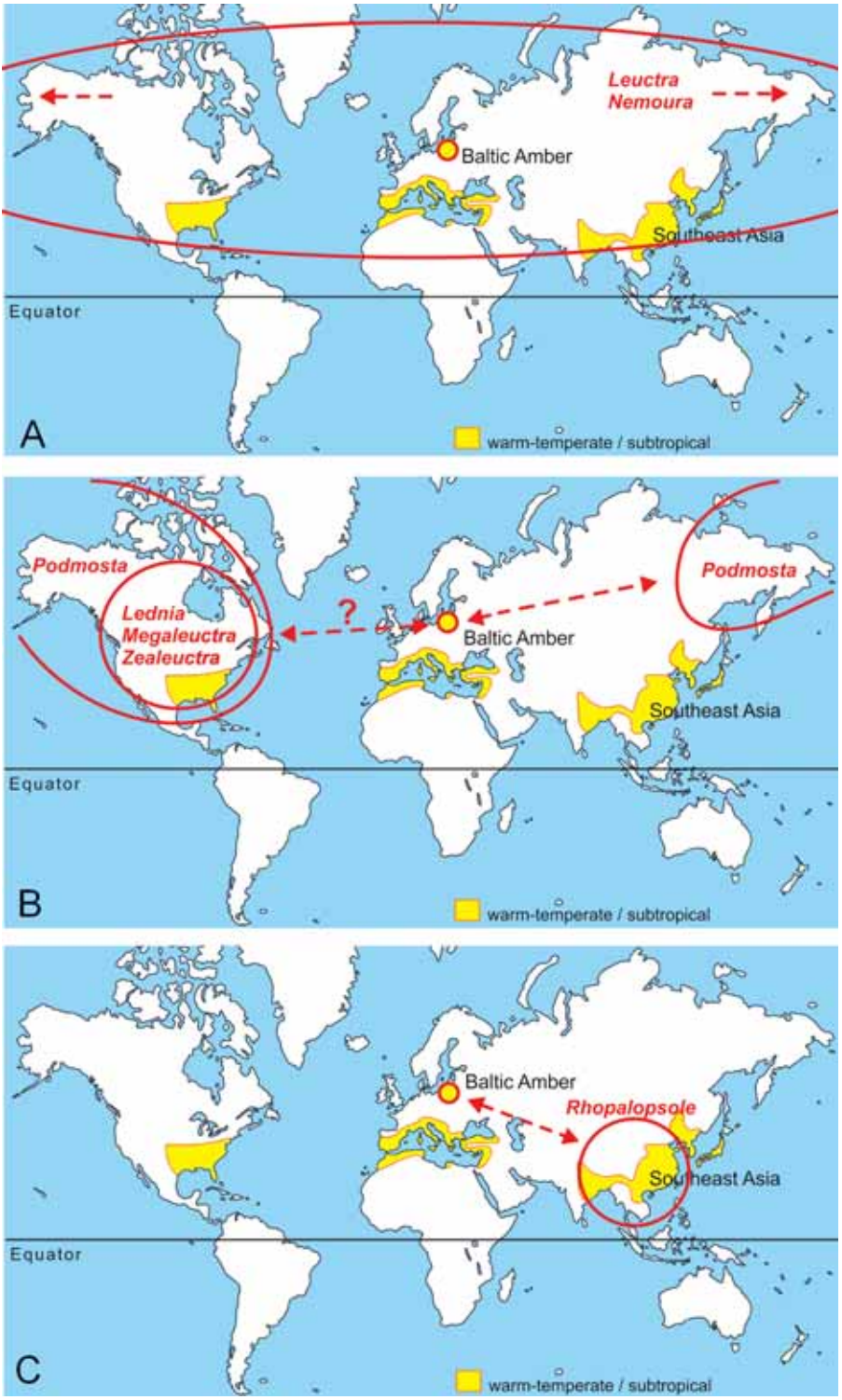


Fig. 2: *Palaeopsole weiterschani* n.sp., drawings. **A** Holotype in lateral view. **B** Male genitalia in lateral view. **C** Male genitalia in ventral view.
Abb. 2: *Palaeopsole weiterschani* n. gen, n. sp., Zeichnungen. **A** Holotyp in lateraler Ansicht. **B** Männliches Genitale, lateral.**C** Männliches Genitale, ventral.

tergum 9. Length of male 4 mm (tip of head to tip of abdomen, intraspecific variation not known).

3. Paleobiogeographic in discussion

The presently described fossil species *Palaeopsole weiterschani* n. gen., n. sp. contributes to the number of the plecopteran genera in the Eocene Baltic amber; among the Leuctridae the genera *Leuctra*, *Megaleuctra*, *Zealeuctra*, and *Palaeopsole* and among the Nemouridae the genera *Lednia*, *Nemoura*, and *Podmosta* have been discovered (Fig. 3). The Eocene fossils are the eldest representatives of their extant genera so far. Nevertheless, the points of origins of these genera are not the "amber forest" of the Eocene European archipelago. This implausible hypothesis would mean that the Eocene seven genera were only able to distribute and migrate across the Eurasian continent after the end of the


Leuctra
Nemoura
Baltic Amber
Southeast Asia
Equator
A
warm-temperate / subtropical
Podmosta
Lednia
Megaleuctra
Zealeuctra
?
Baltic Amber
Podmosta
Southeast Asia
Equator
B
warm-temperate / subtropical
Baltic Amber
Rhopalopsole
Southeast Asia
Equator
C
warm-temperate / subtropical

Eocene, when Europe and Asia were linked. If the Eocene European archipelago is neither place nor time of the origin of the genera, then the genera are distributed all over the northern hemisphere long before the Eocene.

Genus *Palaeopsole* n. gen. provides good clues about the possibility that the Baltic amber genera of Leuctridae and Nemouridae were existed already in the cretaceous, even if fossils are lacking so far. The species were adapted to a warm-temperate and subtropical climate, which occurred from the mid Jurassic to the mid Eocene, nearly in the whole northern hemisphere. Many plants and animals in Baltic amber – probably such as *Palaeopsole weiterschani* n. gen., n. sp. – have their next recent relatives in Southeast Asia and the Oriental region, as after the global climate changed and temperature decreased towards the end of the Eocene, whereas Southeast Asia and the Oriental region largely preserved its warm temperate climate up to today and the relatives of early *Palaeopsole* survived in the subtropical area of the Oriental region and Southeast Asia. The descendents are probably *Rhopalopsole*.

Area and age of origins of the Leuctridae and Nemouridae genera found in Baltic amber are unknown. Both families are cited to have existed in the early Cretaceous (Sinitshenkova 1997, 2003) and their family stem groups probably have their origins in the Jurassic Laurasia. Their extant genera are more recent and surely developed after Laurasia broke apart. Approximately 160 million years ago, the early Mesozoic continent, Laurasia, separated into Laurentia (North America) and Eurasia, and Europe formed an archipelago. Afterwards the genera in question had their origin somewhere in the northern hemisphere.

During the Cretaceous several land bridges were very probably formed at irregular intervals, in-between the continents of the northern hemisphere, the bridging of the Turgai Strait between the European archipelago and Asian continent (Scotese 2002; Baraboshkin et al. 2003) and of the Bering Strait between Northeast Asia and Alaska (Scotese 2002). Cretaceous Atlantic land bridges between Europe and North America are not recorded in paleogeographic studies. Vertebrate paleontologists studying the Cretaceous distribution of the dinosaur fauna and bird tracks in the northern hemispheric have hypothesised land bridges between Northeast Asia und North America (e.g. Russell 1993; Cifelli et al. 1997; Sereno 2000; Fiorillo 2008; Fiorillo et al 2010, 2011). However, studies about a comparable Cretaceous distribution of arthropods are lacking so far. Therefore it is remarkable that the species of the Plecopterean genera *Megaleuctra*, *Zealeuctra* and *Lednia* are today exclusively found in distinct Nearctic regions and as fossils in Eocene Baltic amber (Fig. 3B). It is quite possible that the north hemispherean dispersal of these stonefly genera occurred over the period of Cretaceous using the land bridges between the northern continents, before Europe was once again separated during the long period of Eocene. Afterwards cool-adapted species survived only in North America and Northeast Asia.

Fig. 3: North hemispherical distribution of extant Leuctridae and Nemouridae genera of which fossil species found in Baltic amber. **A** Holarctic distribution of *Leuctra* and *Nemoura*. **B** Transberingian distribution of *Podmosta* and nearctic distribution of *Lednia*, *Megaleuctra*, and *Zealeuctra*. **C** *Rhopalopsole* (recent narrow relative of *Palaeopsole*) in the Oriental region and Southeast Asia.

Abb. 3: Nordhemisphärische Verbreitung der rezenten Leuctridae- und Nemouridae-Gattungen, von denen fossile Arten im Baltischen Bernstein nachgewiesen sind. **A** Holarktische Verbreitung von *Leuctra* und *Nemoura*. **B** Transberingische Verbreitung von *Podmosta* und nearktische Verbreitung von *Lednia*, *Megaleuctra* und *Zealeuctra*. **C** *Rhopalopsole* (rezente Verwandte von *Palaeopsole*) in der orientalischen Region und in Südostasien.

Species of genus *Podmosta* occur on both sides of the Bering Strait (Fig. 3 B), extending westward into Asia and eastward into North America (BAUMANN 1975; LEVANIDOVA & ZHILTZOVA 1979; STEWART & RICKER 1997; ZASYPKINA & RYABUKHIN 2001; TESLENKO 2009). *Podmosta* is distributed in Northeast Asia with at least one species, *Podmosta weberi*, and in Alaska and Yukon with further species which are spread towards the south and southeast in the Nearctic. Species of *Podmosta* are nowadays cool-adapted, nevertheless the transberingian genus lived originally, at Creataceous, in warm-temperate climate and represents an interesting mode of distribution, which helps to explain the gap between the spread of cool-adapted Nearctic genera and their early existence in subtropical Cretaceous; fossils of Eocene Baltic amber indicate this. Genus *Megaleuctra* is adapted likewise. So far, one North Korean species (HAM & BAE 2002; ZWICK 2010) is eventually a relict of Cretaceous period surviving in the subtropical climate of Southeast Asia, and presently six species of North America are adapted at temperate climate. The fossil record of genus *Megaleuctra* in the North America (LEWIS 1969) indicates their early presence in Miocene; therefore we are confident in looking forward to Cretaceous fossils of North American *Megaleuctra*.

The extant Nearctic genera, *Lednia*, *Megaleuctra*, and *Zealeuctra*, including the transberingian *Podmosta* (Fig. 3 B) and including *Leuctra* and *Nemoura* which are distributed across the whole Holarctic region (Fig. 3 A), all known from Eocene Baltic amber spread probably across the northern hemisphere during subtropical Cretaceous and adapted probably to cool-temperate climate not till then the end of Eocene, whereas the warm-adapted relatives of *Palaeopsole* - probably the closely related *Rhopalopsyche* - survived in the subtropical Oriental region and in Southeast Asia (Fig. 3 C).

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