Entomologie heute 22 (2010): 85-97

Overview and Descriptions of Fossil Stoneflies (Plecoptera) in Baltic Amber

Übersicht und Beschreibungen von fossilen Steinfliegen (Plecoptera) im Baltischen Bernstein

CELESTINE CARUSO & WILFRIED WICHARD

Summary: Three new fossil species of stoneflies (Plecoptera: Nemouridae and Leuctridae) from Eocene Baltic amber are being described: *Zealeuctra cornuta* n. sp., *Lednia zilli* n. sp., and *Podmosta attenuata* n. sp.. Extant species of these three genera are found in Eastern Asia and in the Nearctic region. It is very probably that the genera must have been widely spread across the northern hemisphere in the Cretaceous period, before Europe was an archipelago in Eocene. The current state of knowledge about the seventeen Plecoptera species of Baltic amber is shortly presented. Due to discovered homonymies, the following nomenclatural corrections are proposed: *Leuctra fusca* Pictet, 1856 in *Leuctra electrofusca* Caruso & Wichard, 2010 and *Nemoura affinis* Berendt, 1856 in *Nemoura electroaffinis* Caruso & Wichard, 2010.

Keywords: Fossil insects, fossil Plecoptera, Eocene, paleobiogeography

Zusammenfassung: In dieser Arbeit werden drei neue fossile Steinfliegen-Arten (Plecoptera: Nemouridae und Leuctridae) des Baltischen Bernsteins beschrieben: *Zealeuctra cornuta* n. sp., *Lednia zilli* n. sp., *Podmosta attenuata* n. sp.. Rezente Arten der drei Gattungen sind in Ostasien und in der nearktischen Region nachgewiesen. Sehr wahrscheinlich breiteten sich die Gattungen in der Kreidezeit über die nördliche Hemisphäre aus, noch bevor Europa im Eozän ein Archipel war. Der gegenwärtige Kenntnisstand über die siebzehn Plecoptera Arten des Baltischen Bernsteins wird kurz dargelegt. Wegen bestehender Homonymien werden folgende nomenklatorische Korrekturen vorgenommen: *Leuctra fusca* Pictet, 1856 in *Leuctra electrofusca* Caruso & Wichard, 2010 und *Nemoura affinis* Berendt, 1856 in *Nemoura electroaffinis* Caruso & Wichard, 2010.

Schlüsselwörter: Fossile Insekten, fossile Plecoptera, Eozän, Paläobiogeographie

1. Introduction

Systematic and taxonomic studies of stoneflies (Plecoptera) in Eocene Baltic amber started in the middle of the 19th century. PICTET (1856) and HAGEN (1856) described thirteen species, which are assigned to six genera whose extant species are mainly distributed in the Palaearctic. In the following hundred years only one new fossil species from Baltic amber, *Megaleuctra neavei* Ricker, 1936, was added. Today, this genus is represented in the Nearctic of North America by six species (BAUMANN 1973) and one species in Korea (HAM & BAE 2002; ZWICK 2010). With overall 14 described species only a few fossil taxa are known, which could be explained by the fact that Plecoptera are generally very rarely found in Baltic amber. In an amber collection exclusively of aquatic insects Plecoptera normally make up 4% at most. As aquatic insects make up almost 25% of all animal inclusions in Baltic amber (WICHARD et al. 2009), Plecoptera therefore represent only about 1% of all animal inclusions. They are even rarer in "unselected",

random collections of amber inclusions, where they represent only about 0,5% of encased animals (SONTAG 2003; HOFFEINS & HOFFEINS 2003; WICHARD & WEITSCHAT 2004). The fact that amber Plecoptera were seldom subject of study could be connected with the poor state of preservation of many amber inclusions, which are often not suitable for a determination based on criteria of modern taxonomy. The fine structure of the taxonomically important epiproct of the male abdominal end is frequently covered by the wings or by other embedded objects or are "verlumt" and therefore not sufficiently visible from different angles.

Nevertheless, this paper endeavours to examine and identify Plecoptera of Baltic amber in order to achieve an overview of the different fossil families, genera and species found in amber. Apart from the known species discovered by PICTET (1856), HAGEN (1856), and RICKER (1936) three further genera have been identified, whose extant species are surprisingly found in the Nearctic region. For this paper, over 200 fossil plecopteran inclusions of different collections were examined and assigned to four families. However, only six specimens were suitable for a taxonomic analysis.

2. Systematics

Family: Nemouridae

Genus: *Lednia* Ricker, 1952

Type species: *Lednia tumana* Ricker, 1952

Diagnosis (RICKER 1952; BAUMANN 1975): Head with large, bulging eyes, 3 ocelli present; mandibles fully developed, sclerotized, with distinct mola; maxilla with 5-segmented and labium with 3-segmented palps; terminal segment of the labial palps broadly rounded and flat (discoid); labium with 4 approximately equally long lobes of glossa and paraglossa; no gills at submentum or cervix, instead small round rudimental nubs present. Legs are with 3 tarsal joints, which is characteristic of this order; 2. segment is much shorter than 1. and 3.; wings are typical of this family, long and flat, covering the abdomen; wing venation with terminal costal crossvein, which connects costa C and radius R1. Vesicle (ventral lobe) of the ninth sternum absent, hypoproct (subgenital plate) broadened at base and towards the middle and narrows apically; the bent epiproct is basally broadened and almost wholly sclerotized, bilaterally symmetrical and distally narrowing into a slender tip; under the epiproct the 10th tergum forms a sclerotized and concave area, posterolaterally elongated into long, club-shaped prongs; cerci are one-segmented, relatively short and neither sclerotized nor modified.

Among the Nemouridae, the vesicle of the 9th sternite is only absent in the genera *Lednia* and *Paranemoura*. However, *Paranemoura* differs from *Lednia* in two conspicuous characters: In the wing venation of *Paranemoura* the terminal costal crossvein (Sc2) is connected to Sc1 instead of R. The 10th tergite of *Paranemoura* differs in structure as it is for example lacking the two lateral prongs.

The genus *Lednia* contains only one extant species, *Lednia tumana* Ricker, 1952, and is distributed in Nearctic region, i.e. in Montana and Washington (USA). Here nymphs are found in mountain meltwater-springs. *Lednia tumana* is therefore known under the common name "Meltwater Lednia Stonefly".

Lednia zilli n. sp.

(Figs. 1, 4)

Holotype: Male, embedded in Baltic amber, kept in the Geol.-Palaeontol. Institute and Museum of the University Hamburg, GPIMH (ex coll. GRÖHN 6945); almost completely preserved specimen, which enables the inspection of the abdominal end from different perspectives. For a better preservation the specimen was embedded into synthetic resin.

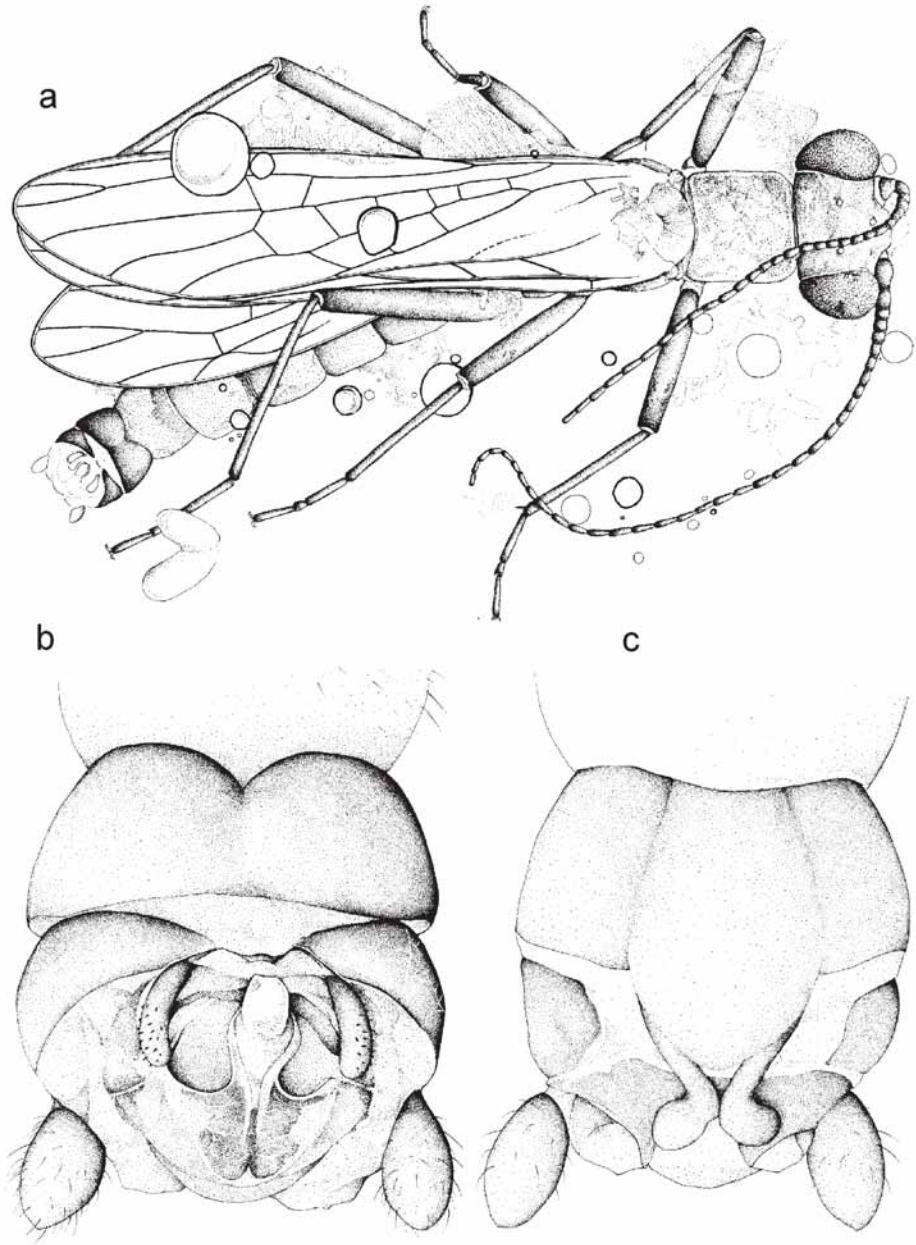

Fig. 1: Fossil stonefly *Lednia zilli* n. sp. (Plecoptera: Nemouridae); **a** male habit in dorsal view, **b** male genitalia in dorsal and **c** ventral view.
Abb. 1: Fossile Steinfliege *Lednia zilli* n. sp. (Plecoptera: Nemouridae); **a** Habitus des Männchens von dorsal; **b** männliches Genitale von dorsal und **c** von ventral.

Material: The fossil is well preserved in a clear amber; all taxonomic traits are visible.
Derivatio nominis: The species bears the name Zilli, an old family established in Sicily.
Description: Head: large, bulging eyes and three ocelli; no gills at submentum or cervix, instead, small, rudimental nubs; the filiform antennae consist of 35 segments, scapus and pedipalpus; glossa and paraglossa of the labium are equally long; terminal segment of 3-segmented labial palps broadened and flattened (discoid); maxillary palps 5-segmented, segments are long and oval, the last 3 segments are equally long, the first two are shorter; head with mouthparts are "verlumt", which makes a close observation difficult.
Thorax: Legs with 3 tarsal joints; 2. segment much shorter than 1. and 3.; in the first pair of forelegs 1. and 3. segment are approximately equally long; in the 2. and 3. pair of legs 1. tarsal segment much longer than 3. segment. Forewing length 3.5mm and do not exceed the abdomen lengthwise. The terminal costal crossveins of the wings connect costa C with radius R1.
Male genitalia: Cerci are one-segmented and relatively short, approximately twice as long as broad. Hypoproct (subgenital plate) is broad at the basis and forms apically a short lancet; the lanceolate apex is laterally flanked by two, rounded, slightly outcurved bulges. The dorsal epiproct is broad and flat, almost entirely sclerotized and terminates into a narrow, membranous tip. As the epiproct is dorsally covered by small, light-coloured objects and also the lateral view of the epiproct is not possible in this piece of amber, the exact structure and form of its tip can not be further described. Underneath the epiproct there is a sclerotized, concave area; the lateral areas are elongated into sclerotized prongs, which seem to be broad and oval from lateral view and slightly outcurved from dorsal view. The prongs bear short hair and their concave inner sides flank the median epiproct. The vesicle (ventral lobe) on the basis of the 9th sternite is absent.
Diagnosis: The new species is placed into the genus *Lednia* as the vesicle of the 9th abdominal sternite is lacking; the species does not belong to the genus *Paranemoura*, which is the only other nemourid genus with a lacking vesicle, as in the wing venation the terminal costal crossvein Sc2 joins radius R1 and not Sc1 as it is the case in *Paranemoura*. The fossil *Lednia zilli* n. sp. differs from the only extant species among this genus, *Lednia tumana*, in the form of the hypoproct, which has one, pointed apex in *L. tumana* and two, rounded apices in *L. zilli*. Moreover, the two prongs of the 10th tergite of *L. zilli* are not clubshaped but are broad and oval (auriculate) and flank the epiproct with their concave inner side.

Gattung: *Podmosta* Ricker, 1952

Type species: *Nemoura decepta* Frison, 1942

Diagnosis (RICKER 1952; BAUMANN 1975): Head with three ocelli and large, bulging eyes; no gills at submentum or cervix but instead small, rudimental nubs; labium with paired glossa and paraglossa, which are approximately equally long; terminal segment of the 3-segmented labial palps is large, flat and rounded (discoid); maxillary palps are 5-segmented; mandibles are fully developed and sclerotized, with distinct mola. Tarsi of legs are 3-segmented; 2. tarsal segment is much shorter than 1. and 3. segments; wings are long and flat and cover the body; wing venation shows the conspicuous family-typical X-structure formed by subcosta and the terminal costal crossvein that joins the radius R1; in the anal field A1 and A2 are not fused towards the wing margin. In the male genitalia the hypoproct is broad at its base and terminates into a long, narrow tip; median stripe, margins and apex are strongly sclerotized. Cerci are short and approximately 3 times as long as wide, not sclerotized and unmodified. The sclerotized epiproct is not completely recurved onto the dorsal side of

the body, but is directed upwards, forming an angle to the body axis. Vesicle (ventral lobe) is present on the 9th sternite.
Remark: The genus *Podmosta* currently contains 5 extant species that can be found in North America, Canada and Eastern Asia. Larvae prefer cold, oxygenated mountain springs and rivers.

***Podmosta attenuata* n. sp.**
(Figs. 2, 5)

Holotype: Male encased in a clear, well preserved piece of amber, embedded in synthetic resin, kept in Senckenberg Deutsches Entomologisches Institut, SDEI (ex coll. HOFFEINS 479-1)
Material: The fossil is embedded in a lateral position and the wings with the family-typical X-structure are clearly visible. The left side of head, antennae and mouthparts are visible. Thorax and abdomen has a ventrallateral turbidity ("Verlumung"); however, a lateral and ventral view of the abdominal end with its epiproct is possible, which enables the description of this specimen.
Derivatio nominis: The name attenuata (attenuatus = inconspicuous, inornate) refers the relatively inconspicuous and inornate stonefly.
Description: Head: bulging eyes with three ocelli; filiform right antenna with a length of 4 mm, consists of 35 segments, scapus, pedicellus and a longer 3rd segment (left antenna is probably incomplete and consists of 26 segments). The 3-segmented labial palp has a flat and cochleariform terminal segment (discoid); in the fossil male specimen not clearly visible (however, well visible in the female *Podmosta*, ex. coll. WITSCH); the 5-segmented maxillary palps are clearly visible, the last 3 segments are equally long, the first 2 segments much shorter; the mandibles are not visible from lateral view in this fossil.
Thorax: Legs with 3-segmented tarsi, 2. segment much shorter than 1. and 3. segment, which are equally long in the forelegs; mid and hindlegs of the male fossil specimen are lacking (they are, however, present in the female ex coll. Witsch, where 1. and 3. tarsal segments of the midlegs are also equally long; the 1. segment of the hindlegs is much longer than the 3. segment). Length of forewings 4.2 mm. Wings with the X-structure that is typical of this family; the terminal costal crossvein Sc2 joins the radius R1. In the anal field the veins A1 and A2 are not fused towards the wing margin.
Male genitalia: Hypoproct broad at base, elongate tip that reaches the base of the epiproct; apically (apparently) longitudinally divided and strongly sclerotized; Cerci short, approximately twice as long as wide, they seem unsclerotized and unmodified. Epiproct is complex in structure, bent upwards and inwards and is not completely recurved onto the dorsal side of the body but forms an approximately 45° angle to the body axis; epiproct broad at base and distally partly sclerotized, terminating in a cuspidate tip; 10. tergit inconspicuous, with a few, stout and short hair. Vesicle (ventral lobe) is present at the base of the 9th sternite; approximately 3 times as long as wide.
Diagnosis: The described fossil species is included into the genus *Podmosta* due to the following characters: No gills at submentum or cervix; instead small, rudimental nubs present. The veins A1 and A2 of the anal field of the forewings are not fused towards the wing margin (in *Soyedina* they are fused); the terminal costal crossvein (Sc2) joins R1 (in *Paranemoura* it joins Sc1); Cerci are unmodified, unsclerotized and approximately twice as long as wide (*Nemoura, Nemurella* and *Osctrocerca* have modified, long cerci). Vesicle is present.
Podmosta is similar to the genus *Prostoia* but differs from the latter in 2 clear characters:

1. in the length of the cerci, which are longer in *Prostoia* and approximately 3 times as long as wide (in *Podmosta* twice as long as wide)

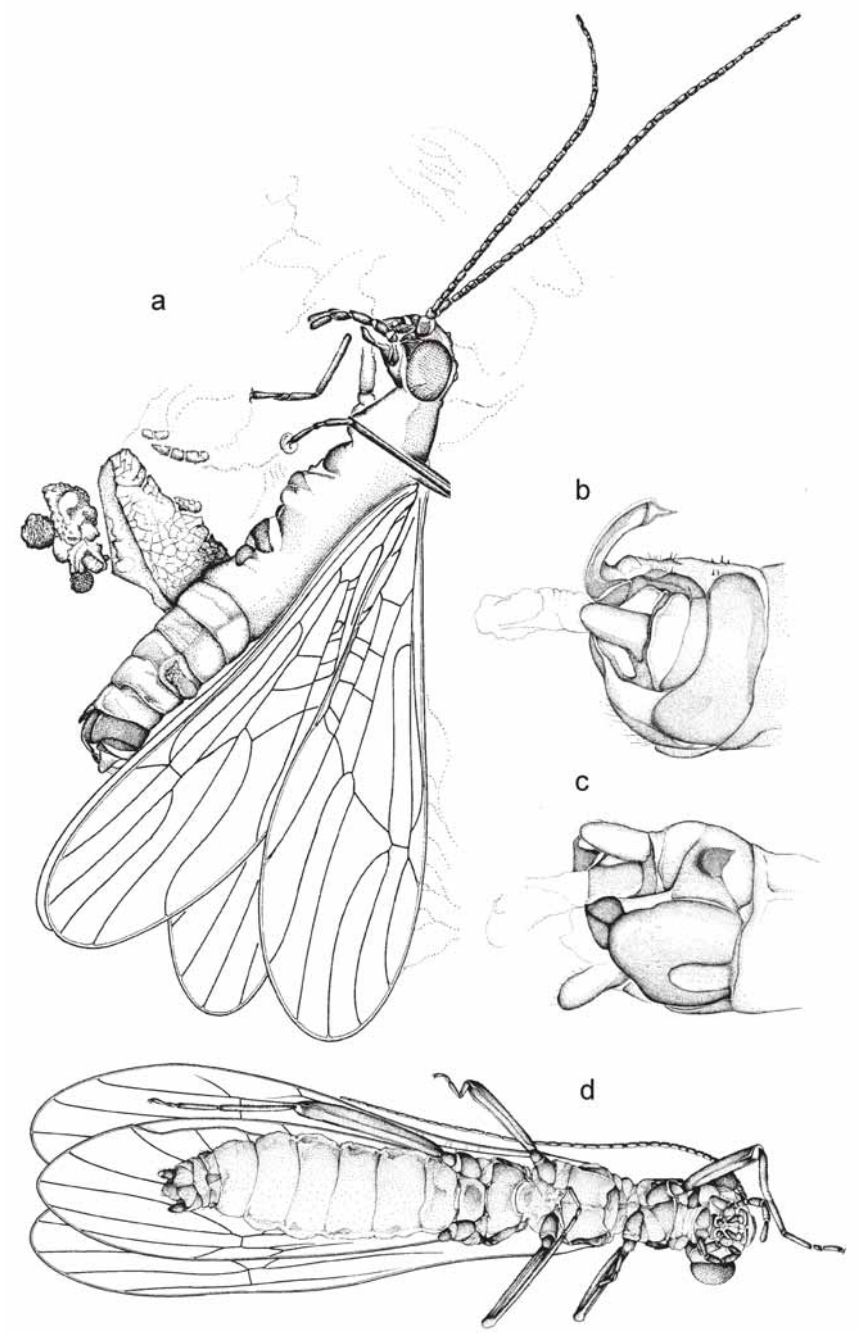

Fig. 2: Fossil stonefly *Podmosta attenuata* n. sp. (Plecoptera: Nemouridae); **a** male habit in dorsal view, **b** male genitalia in lateral and **c** in ventral view, **d** female habit in ventral view.
Abb. 2: Fossile Steinfliege *Podmosta attenuata* n. sp. (Plecoptera: Nemouridae); **a** Habitus des Männchens von dorsal, **b** männliches Genitale von lateral und **c** von ventral; **d** Habitus des Weibchens von ventral.

2. in the structure of the epiproct: In *Prostoia* the structure of the epiproct is simple and completely recurved onto the dorsal part of the body (parallel to the body axis) whereas in *Podmosta* it is more complex and not completely recurved (forms an angle to the body axis).

Podmosta attenuata n. sp. differs from all other extant *Podmosta* species in the structure of the epiproct, which bears for example sidewards directed, curved horns near the tip or deeply folded along the median line as in *P. macdunnoughi*. Furthermore, the epiproct of *P. attenuata* n. sp. seems to have only one tip (at least from lateral view), which is different in all other extant *Podmosta* species.

The females of *Podmosta* are characterized by a short, darkly sclerotized stripe on the median line of the 8th sternum. The shape of this stripe is species specific as it can for example be triangular-shaped. So far, two female specimens have been found in Baltic amber (coll. WICHARD and coll WITSCH, Fig. 2 d). They were identified as belonging to the genus *Podmosta* due to the following characters: Gills absent at submentum and cervix, instead small, oval, rudimental nubs present; 8th abdominal sternite narrow, much smaller than 7th sternite, overlapping onto the 9th sternite; median stripe present. Paraprocts triangular; Furthermore, the 8th sternite of both fossil female specimens bear lateral sclerotizations, the vaginal lobes, which are so distinctly visible only in *P. weberi* among extant *Podmosta* species. However, both fossil females differ from *P. weberi* in the shape of the median sclerotization, which is 3-4 times as long as wide in *P. weberi* and V-shaped and twice as long as wide in the fossil specimens. The female *Podmosta* specimens of Baltic amber provide further evidence about the presence of the genus *Podmosta* in Baltic amber. However, it is not possible to classify them as members of the species *Podmosta attenuata* n. sp.; they therefore remain unnamed.

Familie: Leuctridae

Gattung: *Zealeuctra* Ricker, 1969

Type species: *Leuctra claasseni* Frison, 1929

Diagnosis (RICKER & ROSS 1969; STARK & STEWART 1973; KONDRATIEFF & ZUELLIG 2004; GRUBBS 2005): Elongate, slender habitus; head with small, hemiglobose compound eyes; three ocelli present; labium with approximately equally long glossa and paraglossa; terminal segment of the 3-segmented labial palps are slender and longer than segments 1 and 2; the first two segments of the 5-segmented maxillary palps are short and the last 3 segment almost equally long; sclerotized mandibles are fully developed. No gills at submentum or cervix. Wings are long and rolled lengthwise around the body. In the forewings media M and Rs arise from separate points on R; in hindwings the crossvein m-cu joins cubitus CuA1 on the fork of CuA into CuA1 and CuA2. The subanal apparatus of the abdomen is not conspicuously long and divided into specilla and styli (titillator) as it is the case in most of leuctrid species, but it is fused into short, broad components. Cerci are one-segmented, long and terminate into a sometimes sclerotized tip, which can bear a cusp, or are fully sclerotized. The cerci bear a basal or subterminal hump or lobe. The hypoproct (subgenital plate) of males is never conspicuously long; 9th tergum is deeply cleft and the cleft can be V- or U-shaped; the corners of the cleft can be elongated into more or less long projections which can be curved in- or upwards. By the shape of the cerci, the subanal apparatus and above all the structure of the 9th tergite with its deep cleft and the elongate projections, *Zealeuctra* differs from all other Leuctrid genera.

***Zealeuctra cornuta* n. sp.**
(Figs. 3, 6)

Holotype: Male embedded in a well preserved piece of amber, which has been cut, grinded and polished for a better inspection from all

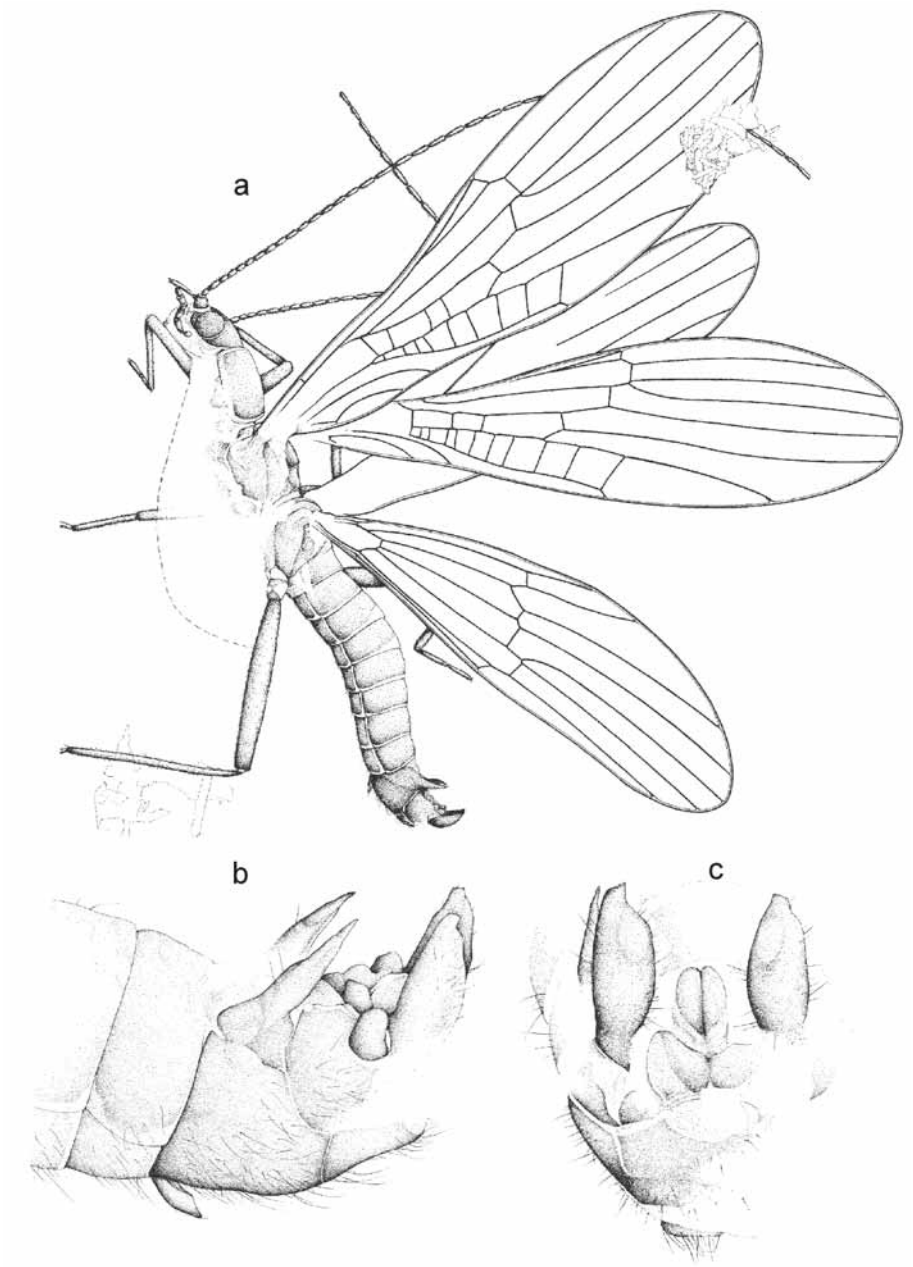

Fig. 3: Fossil stonefly *Zealeuctra cornuta* n. sp. (Plecoptera: Leuctridae); **a** male habit in lateral view, **b** male genitalia in lateral view and **c** in ventral view.
Abb. 3: Fossile Steinfliege *Zealeuctra cornuta* n. sp. (Plecoptera: Leuctridae); **a** Habitus des Männchens von lateral, **b** männliches Genitale von lateral und **c** von ventral.

sides and was embedded in synthetic resin for better preservation and conservation; the amber sample is kept in the Staatliches Museum für Naturkunde, Stuttgart, SMNS, ex. coll. WICHARD.

Material: All four wings of this adult specimen are spread and do not overlap much so that the wing venation is clearly visible. The body has ventrall turbidity („Verlumung") and covered by air bubbles from the head until the abdominal end; head and mouthparts are therefore barely visible. The male genitalia are visible from almost all sides.

Derivatio nominis: cornutus = horned. The two conspicuously long projections of the 9th tergite distinguish this species from all other species of *Zealeuctra*.

Description: Head: small, hemiglobose compound eyes; three ocelli present; filiform antennae (longer than the forewings), that consist of 41 segments, plus scapus and pedicellus (right antenna is shortened). The specimen has a family-typical slender habitus, which is slightly compressed in amber, and no gills; the body length from head until the end of the abdomen would comprise 4.5 mm, the forewings with 4.5 mm length would be equally long. The wings spread in amber would be overlapping the abdomen.

Thorax: The forewings have three veins in the anal field, the media M arises proximally, before R1 arises from the sector radii Rs; however, there is a slight asymmetry in this specimen, as M and Rs touch in the left forewing after the fork of the longitudinal veins and seem to cross each other whereas in the right forewing the two longitudinal veins do not touch each other and seem to be structured normally, as described above. In the hindwings the crossvein m-cu joins CuA1 shortly after CuA divides into CuA1 and CuA2. The tarsi of the legs are 3-segmented and the 1. and 3. segment are almost equally long whereas the 2. segment is shorter.

Male genitalia: The 9th abdominal tergite is medially depressed in a U-shape and sclerotized at the margins of the depression. Along this margin, two long, lateral projections arise which are directed backwards; the projections are conspicuously long and pointed, almost as long as the cerci. The cerci are one-segmented, broad and bear a terminal cusp; they bear a large basal hump. The epiproct is small, broad at its base – as far as recognisable – and distally terminating to a hooked tip. The subanal apparatus consists of two broad, round components, that are separated by a median line but seem to be partly fused.

Diagnosis: The new, described leuctrid specimen was identified as belonging to the genus *Zealeuctra* due to the wing venation and the structure of the male genitalia. In the forewing of *Zealeuctra cornuta* n. sp. sector radii Rs and media M arise from separate points on radius R1 as it is the case in most Leuctrid species (apart from *Perlomyia*, where M and Rs arise from the same point on R1). In the hindwings of *Z. cornuta* n. sp. the crossvein m-cu joins CuA1 after CuA divides into CuA1 and CuA2, whereas in *Leuctra, Moselia, Despaxia, Tyrrhenoleuctra* and *Pachyleuctra* the crossvein joins CuA before the fork of CuA into CuA1 and CuA2. *Zealeuctra* differs from *Rhopalopsole* and *Paraleuctra* in the structure of the 9th tergite which has a V- or U-shaped median cleft. In *Zealeuctra cornuta* n. sp. the margins of the cleft are elongated into one long projection on each side; the projection is broad at its base and thorn-shaped with a pointed tip. With these conspicuous projections of the 9th tergite *Z. cornuta* differs from all other extant species of the genus *Zealeuctra*.

3. Overview of the fossil Plecoptera in Baltic amber

The catalogue of known Plecoptera from Baltic amber currently includes seventeen species. Most of the specimens (holotypes) described by Hagen (1856) and Pictet (1856) are lost. These old descriptions, using the common wing venations instead of the male

genitalia, do not allow a significant reconstruction of the species. However, they provide an overview on the presence of the families and genera in Baltic amber.

Because of occurring homonymies, the following nomenclatural corrections have to be made.

1. *Leuctra electrofusca*, instead of *Leuctra fusca* Pictet, 1856, fossil (not: *Leuctra fusca* (Linné, 1758), extant)
2. *Nemoura electroaffinis*, instead of *Nemoura affinis* Berendt, 1856, fossil (not: *Nemoura affinis* Stephens, 1835, extant)

Order Plecoptera, Suborder Arctoperlaria

Familie Taeniopterygidae	
Taeniopteryx elongata Hagen, 1856	Holotype lost
Taeniopteryx ciliata Pictet, 1856	Holotype lost
Familie Leuctridae	
Leuctra gracilis Pictet, 1856	Holotype in MNHU
Leuctra linearis Hagen, 1856	Holotype lost
Leuctra electrofusca Caruso & Wichard, 2010	Holotype in MNHU
Leuctra minuscula Hagen, 1856	Holotype lost
Megaleuctra neavei Ricker, 1936	Holotype lost
Zealeuctra cornuta n.sp.	Holotype in MNHU
Familie Nemouridae	
Lednia zilli n.sp	Holotype in GPIMH
Nemoura ocularis Pictet, 1856	Holotype in MNHU
Nemoura electroaffinis Caruso & Wichard, 2010	Holotype in MNHU
Nemoura lata Hagen, 1856	Holotype lost
Nemoura puncticollis Hagen, 1856	Holotype lost
Podmosta attenuata n.sp	Holotype in SDEI
Familie Perlidae	
Perla prisca Pictet, 1856	Holotype in MNHU, currently lost
Familie Perlodidae	
Isoperla succinica (Hagen, 1856)	Holotype lost
Perlodes resinata (Hagen, 1856)	Holotype lost

Acronyms of depositories:

GPIMH - Geologisch-Paläontologisches Institut und Museum der Universität Hamburg
MNHU - Museum für Naturkunde der Humboldt Universität Berlin
SDEI - Senckenberg Deutsches Entomologisches Institut
SMNS - Staatliches Museum für Naturkunde Stuttgart

Fig. 4: Fossil stonefly *Lednia zilli* n. sp. (Plecoptera, Nemouridae) in Baltic amber.
Abb. 4: Fossile Steinfliege *Lednia zilli* n. sp. (Plecoptera, Nemouridae) in Baltischem Bernstein.
Fig. 5: Fossil stonefly *Podmosta attenuata* n. sp. (Plecoptera, Nemouridae) in Baltic amber.
Abb. 5: Fossile Steinfliege *Podmosta attenuata* n. sp. (Plecoptera, Nemouridae) in Baltischem Bernstein.
Fig. 6: Fossil stonefly *Zealeuctra cornuta* n. sp. (Plecoptera, Leuctridae) in Baltic amber.
Abb. 6: Fossile Steinfliege *Zealeuctra cornuta* n. sp. (Plecoptera, Leuctridae) in Baltischem Bernstein.

4. History of distribution

The list of the various Plecoptera found in Baltic amber represents almost the whole spectrum of Palaearctic and European families that are still living today. This gives the impression that the habitat conditions of the Eocene stoneflies were comparable to the present-day Holocene conditions in Europe. With exception of the Capniidae and Chloroperlidae, which are so far lacking in amber, the families Taeniopterygidae, Nemouridae, Leuctridae, Perlodidae and Perlidae gives a familiar picture that seems to correspond to extant European stonefly fauna (ILLIES 1965).

If, however, the genera are inspected, the similarity between the faunas of extant and Baltic amber stoneflies has to be questioned. Among the family Nemouridae, Baltic amber provides evidence for the genus *Nemoura*, which has a holarctic spread and the two genera *Podmosta* and *Lednia*, which are presently nearctic. Also among the family Leuctridae the holarctic genus *Leuctra* is found in Baltic amber, as well as the genera *Megaleuctra* and *Zealeuctra*, which are currently lacking in Europe and in the Palaearctic and have been exclusively found in the Nearctic. Two holarctic genera and four genera from nearctic regions are both co-occurring in Eocene Baltic amber and initiate a new discussion about the historical spread and distribution of Arctoperlaria and specifically of the Nemouridae and Leuctridae.

Continental drift and climate change are factors that have a great and continuous influence on the historical spread and the phylogenesis of terrestrial and freshwater organisms. In times of the Eocene amber forest, the origin of encased plants and animals in amber, the climate was subtropical and paratropical. Europe was an archipelago with large and smaller subcontinental islands that sometimes connected and broke apart again and were surrounded by the sea. The Archipelago was separated from Asia by the Turgai strait, in its south it was surrounded by the Thethys ocean, in its Northwest by the Atlantic, the Northern Sea and the Boreal sea (WICHARD et al. 2009).

A spread of species across Europe 55 - 34 million years ago had been impossible for a long time. It was not until the end of the Eocene that the climate changed (ZACHOS et al. 2001) which not only lead to the extinction of the amber forest but also of the subtropical plants and animals. Asia and Europe have since been connected, the temperature decrease lead to the icing of the Polar caps, the sea-level sank and the Turgai strate dried out. Nevertheless, there is no evidence for a European origin of the genera *Podmosta, Lednia, Megaleuctra* and *Zealeuctra* or for a Eurasian spread that reached North America whereas European species were dying out. Even if there are no older known fossil specimens of the four genera than the fossils of Eocene Baltic amber, it is probable that these genera must have been widely spread across the subtropical northern hemisphere already in the Cretaceous Period. The Nearctic species were apparently adapted to their habitats until today whereas the Eurasian species died out towards the end of the Eocene.

Acknowledgements

The described fossil stoneflies were provided by the private amber collection of CARSTEN GRÖHN (Glinde), CHRISTEL and HANS WERNER HOFFEINS (Hamburg) and FRANZISKA and GÜNTER WITSCH (Köln), to whom we would like to express our gratitute. We would like to thank AGNES GRAS for preparing and preserving the specimens which enabled the identification of the species, TIMO BUDER and CLAUS LÜER for the accurate and detailed drawings. We kindly thank Dr. WOLFGANG WEITSCHAT (Hamburg) for proofreading the manuscript. We exceptionally thank Prof. Dr. PETER ZWICK (Schlitz) for insightful comments and suggesting the necessary

change of names because of the existing homonymies. Last but not least we thank JOE MANGER, Leicester, for proofreading the English text.

References

BAUMANN, R.W. (1973): New *Megaleuctra* from the Eastern United States (Plecoptera: Leuctridae). Entomological News 84: 247-250.

BAUMANN, R.W. (1975): Revision of the stonefly family Nemouridae (Plecoptera): a study of the world fauna at the generic level. Smithsonian Contribution of Zoology 211: 3-74.

BERENDT, G.C. (ed. 1856): Die im Bernstein befindlichen organischen Reste der Vorwelt Band II. Nicolai; Berlin.

FRISON, T.H. (1929): Fall and Winter Stoneflies or Plecoptera of Illinois. Bulletin of Illinois Natural History Survey 18: 345-409.

FRISON, T.H. (1942): Studies of North American Plecoptera with special reference of the fauna of Illinois. Bulletin of Illinois Natural History Survey 22: 281-471.

GRUBBS, A.S. (2005): *Zealeuctra talladega***,** a new species of Leuctridae (Plecoptera) from Alabama, U.S.A. Illiesia, 1: 40-42.

HAM, S.A., & BAE, Y.J. (2002): The stonefly genus *Megaleuctra* (Plecoptera: Leuctridae) new to east Palaearctic region, with description of *Megaleuctra saebat* new species. Entomological News 113: 336-341.

HOFFEINS, C., & HOFFEINS, H.W. (2003): Untersuchungen über die Häufigkeit von Inklusen in Baltischem und Bitterfelder Bernstein (Tertiär, Eozän) aus unselektierten Aufsammlungen unter besonderer Berücksichtigung der Ordnung Diptera. Studia dipterologica 10: 381-392.

ILLIES, J. (1965): Phylogeny and zoogeography of the Plecoptera. Annual Review of Entomology 10: 117–140.

KONDRATIEFF, B.C., & ZUELLIG, R.E. (2004): A new species of *Zealeuctra* Ricker (Plecoptera: Leuctridae) and confirmation of *Hydroperla fugitans* (Needham and Claassen) (Plecoptera: Perlodidae) from Texas. Proceedings of the Entomological Society of Washington 106: 840-843.

PICTET, F.J., & HAGEN, H. (1856): Die im Bernstein befindlichen Neuropteren der Vorwelt Band 2: 40-122. In: BERENDT, G.C. (ed.): Die im Bernstein befindlichen organischen Reste der Vorwelt. Nicolai; Berlin.

RICKER, W.E. (1936): New Canadian Perlids (Part II). Canadian Entomologist 67: 256-264.

RICKER, W.E. (1952): Systematic studies in Plecoptera. Indiana University Publications, Science Series 18: 1-200.

RICKER, W.E., & ROSS, H.H. (1969): The genus *Zealeuctra* and its position in the family Leuctridae (Plecoptera, Insecta). Canadian Journal of Zoology 47: 1113-1127.

SONTAG, E. (2003): Animal inclusions in a sample of unselected Baltic amber. Acta zoologica cracoviensia 46 (Suppl. Fossil Insects): 431-440.

STARK, B.P., & STEWART, K.W. (1973): New species and descriptions of stoneflies (Plecoptera) from Oklahoma. Entomological News 84: 192-197.

WICHARD, W., & WEITSCHAT, W. (2004): Im Bernsteinwald. Gerstenberg; Hildesheim.

WICHARD, W., GRÖHN, C., & SEREDSZUS, F. (2009): Aquatic Insects in Baltic Amber – Wasserinsekten im Baltischen Bernstein. Verlag Kessel; Remagen.

ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E., & BILLUPS, K. (2001): Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686-693.

ZWICK, P. (2010): New species and new records of Plecoptera from Korea and the Russian Far East. Illiesa 6: 75-97.

cand. rer. nat. Celestine Caruso
Prof. Dr. Wilfried Wichard
Institut für Biologie
Universität zu Köln
Gronewaldstr. 2
D-50931 Koeln
E-Mail: ccaruso@uni-koeln.de
E-Mail: Wichard@uni-koeln.de