Overview and descriptions of Nevrorthidae in Baltic amber (Insecta, Neuroptera)

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Overview and descriptions of Nevrorthidae in Baltic amber (Insecta, Neuroptera)

Wilfried Wichard

Abstract

This paper gives an overview of nine extinct species assigned to five genera of the neuropteran family Nevrorthidae found in Eocene Baltic amber. Three species are described new: *Balticoneurorthus elegans* n. gen., n. sp., *Palaeoneurorthus eocaenus* n. sp. and *Proberotha dichotoma* n. sp. Moreover, the genus *Proberotha* Krüger, 1923, originally assigned to the family Berothidae, is now transferred to the family Nevrorthidae. *Proberotha prisca* Krüger, 1923, exhibits significant traits of the Nevrorthidae Nakahara, 1958, a family which has not yet been established at that time.

Keywords: Taxonomy, Eocene, Baltic amber, Nevrorthidae, Neuroptera, *Proberotha*.

1. Introduction

The fossil record of Nevrorthidae in Baltic amber began with the description of "*Sisyra (Rophalis) relicta*" and "*Sisyra (Rophalis) amissa*" Hagen, 1856 (in Berendt 1845–1856). Handlirsch (1906–1908) placed the two species in the newly established family Sisyridae. Makarkin & Perkovsky (2009) studied *Rophalis relicta* found in Eocene Ukrainian amber and transferred this species to the family Nevrorthidae. *Rophalis amissa* is missed and was doubted (*nomen nudum*) by Krüger (1923) and by Makarkin & Perkovsky (2009).

Another Neuroptera species from Baltic amber, *Proberotha prisca*, was described by Krüger (1923) and originally recognized for the family Berothidae. Recently, Wedmann et al. (2013) and Wichard (2014) proposed to transfer *Proberotha* to the family Nevrorthidae.

Nakahara (1958) subordinated the lacewings of the former extant genera *Neurorthus*, *Nipponeurorthus* and *Austroneurorthus* into the subfamily Neurorthinae, however, within the family Sisyridae. The analysis of nevrorthid larvae (Zwick 1967) erected finally the subfamily into an own family Nevrorthidae Nakahara, 1958. Nine extinct species and five genera are known from Eocene Baltic amber so far; the extinct genera are *Balticoneurorthus* n. gen, *Electroneurorthus* and *Palaeoneurorthus* as well as *Proberotha* and *Rophalis.*

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2. Material and methods

All fossil nevrothids are from the Eocene Baltic amber. The specimens were examined under a Leica M5 or MZ12.5 dissecting microscope (Leica, Wetzlar, Germany). Pictures were taken using a Leica stereomicroscope M 420 Apozoom in combination with Canon EOS 600D, EOS utility software and the Zerene Stacker software or were taken by the digital microscope Keyence VHX-900F. All illustrations were edited with Adobe Photoshop CS4.

Acronyms of depositories: BMNH – British Natural History Museum, London, U.K.; GPIMH – Geologisch-Paläontologisches Institut und Museum, University of Hamburg, Germany; GZG – Geoscience Museum, University of Göttingen, Germany; SDEI – Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany.

Terminology: The terminology of the genitalia follows generally that of Aspöck & Aspöck (1980, 2008): e – ectoproct (10^{th} tergite), gx9 – gonocoxites of 9^{th} segment, gst9 – gonostyli of 9^{th} segment, gp9 – gonapophyses of 9th segment, psa – pseudoapex of sternite 9 (derivative of 10^{th} segment), S – Sternite, T – tergite.

The wing venation terminology (Fig. 1) follows Kukalova-Peck & Lawrence (2004) using the venation abbreviations in text and figures: A – Analis; CuA – Cubitus Anterior; CuP – Cubitus Posterior; MA – Media Anterior; MP – Media Posterior; R – Radius; RA – Radius Anterior; RP – Radius Posterior and RP1, RP2, RP3, RP 4 or RP3+4 – subordinate branches of

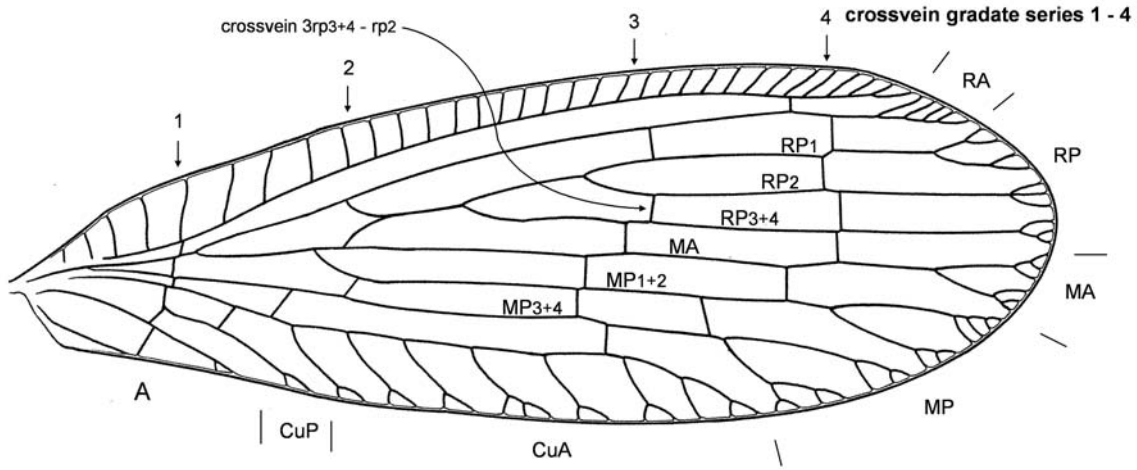

Fig. 1. Blueprint of the forewing of family Nevrorthidae with the longitudinal veins (RA, RP, MA, MP, CuA, CuP, A) and four crossvein gradate series (1 – basal, 2 – inner, 3 – middle and 4 – outer gradate series). In forewings crossvein "3rp3+4 – rp2" present in the extinct genera *Balticoneurorthus, Electroneurorthus, Palaeoneurorthus* and *Proberotha* but absent in extinct *Rophalis.*

Radius Posterior (sequence sensu KUKALOVA-PECK & LAWRENCE 2004); Sc – Subcosta.

Following OSWALD (1993) the forewing crossveins are arranged in more or less aligned gradate series. These series are numerically designated 1 to 4 starting at the base of the wing: 1 – basal, 2 – inner, 3 – middle, 4 – outer crossvein gradate series.

3. Systematic palaeontology

Order Neuroptera LINNAEUS, 1758

Family Nevrorthidae NAKAHARA, 1958

D i a g n o s i s of the extinct Nevrorthidae in Baltic amber:

H e a d: Ocelli absent; filiform antennae with slightly enlarged scapus, smaller pedicellus and uniform cylindrical flagellomeres, with about 25 (*Rophalis relicta*) or about 35 or more flagellomeres (all other extinct species). Maxillary palps 5-segmented, labial palps 3-segmented, their terminal segments pointed.

W i n g s: Forewing lengths 4.5–9.5 mm, about oval, apically rounded, translucent, small setae in rows along on veins. Costal cross-veins simple (*Rophalis, Electroneurothus, Palaeoneurothus*) or partly branched (*Proberotha, Balticoneurorthus*), in hindwings always all simple. In fore- and hindwings subcosta (Sc) and radius anterior (RA) running parallel each other distantly and connected distally by a short crossvein. The area between RA and RP interrupted by usually three crossveins: 2ra–rp, 3ra–rp and 4ra–rp, in *Balticoneurothus* some more crossveins present, similar to some extant nevrorthids: e.g. *Austroneurorthus.* Cross-vein 2ra-rp participates in the inner crossvein gradate series, crossvein 3ra-rp in the middle crossvein gradate series and crossvein 4ra-rp in the outer crossvein gradate series (Fig. 1). In forewings radius posterior pectinate, 3-branched in the subordinate branches RP1, RP2, RP3+4 (*Rophalis, Electroneurothus, Palaeoneurothus, Proberotha prisca*) or dichotomus, 4-branched in the subordinate branches RP1, RP2, RP3, RP4 (*Balticoneurorthus, Proberotha eocaenus*). In hindwings RP always 3-branched. In forewing crossvein 3rp3+4 – rp2 absent in *Rophalis* and present in all other genera. MA usually simple and MP with dichotomous branch in MP1+2 and MP3+4. The longitudinal veins in fore- and hindwings, e.g. R and M, always divided apically into small terminal branches at margin. CuA running parallel to margin with terminal branches; CuP simple. Anal veins simple, running separately to anal margin.

Male and female genitalia of extinct species often incompletely visible, but of extant nevrorthid species described and analysed by ASPÖCK & ASPÖCK (2008).

Genus *Rophalis* HAGEN, 1856

T y p e s p e c i e s: *Sisyra* (*Rophalis*) *relicta* HAGEN, 1856 in BERENDT 1856: 87, pl. 8, fig. 19.

N e o t y p e: *Rophalis relicta* HAGEN, 1856, designated in WICHARD et al. 2009: 96–100, figs. 7.10–7.12.

D i a g n o s i s: *Rophalis* differs definitely from all extant and extinct Nevrorthidae in Baltic amber by the low number of 25 flagellomeres and by the absence of crossvein "3rp3+4 – rp2" in forewings.

Rophalis relicta (HAGEN, 1856)
Figs. 2, 3

1856 *Sisyra* (*Rophalis*) *relicta* HAGEN, 1856. – BERENDT: 87, pl. 8, fig. 19.

2009 *Rophalis relicta* (HAGEN, 1856). – MAKARKIN & PERKOVSKY: 137–144.

2009 *Rophalis relicta* HAGEN, 1856. – WICHARD et al.: 96–100.

H o l o t y p e is lost, neotype illustrated in Fig. 2 (designated by WICHARD et al. 2009: 96–100, figs. 7.10–7.12.): Female

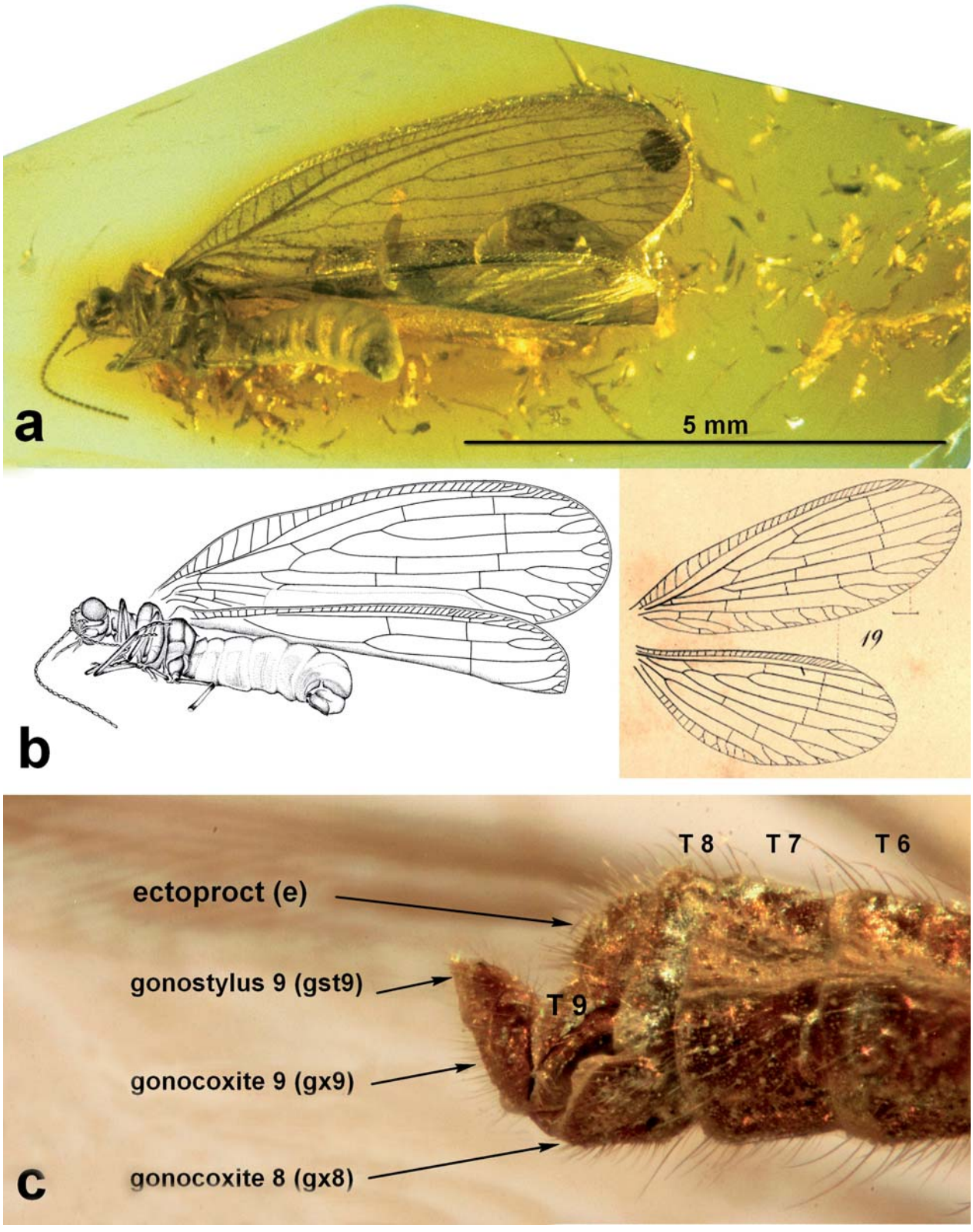

Fig. 2. *Rophalis relicta* (HAGEN, 1856), female; **a**: neotype, designated by WICHARD et al. (2009), "Westpreussisches Landesmuseum" in Münster-Wolbeck, Inv.-Nr. 467; **b**: Drawing of the neotype compared with the drawing by HAGEN in BERENDT 1856: 87, pl. 8, fig 19; **c:** female genitalia in lateral view.

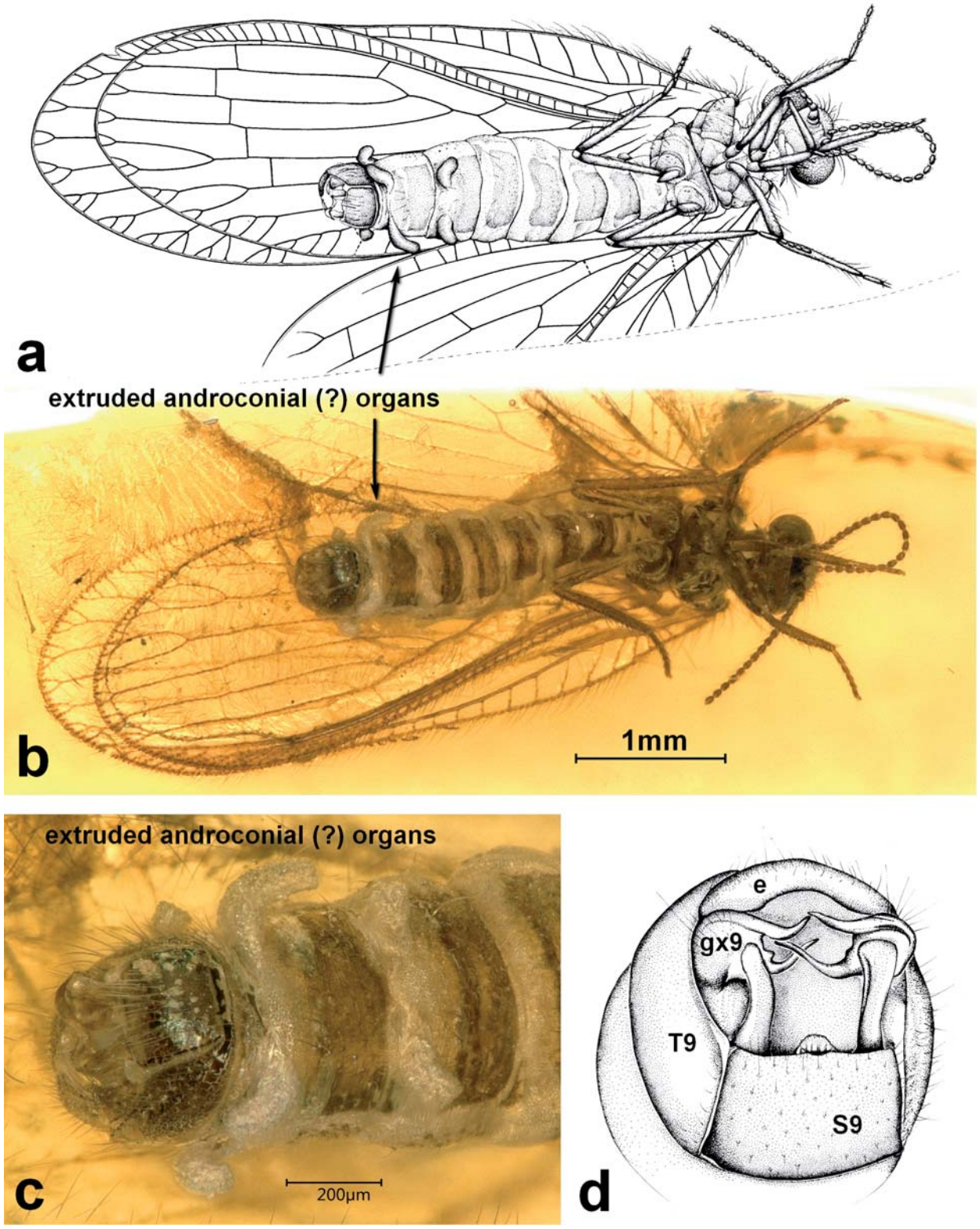

Fig. 3. *Rophalis relicta* (HAGEN, 1856), male with extruded androconial (?) organs; **a**: drawing in ventral view; **b**: photograph in ventral view; **c**: male genitalia and extruded androconial (?) organs, distal of 6th and of 7th segments in ventral view; **d**: drawing of male genitalia in ventral view.

from the amber collection of HELM (1826–1902) and MENGE (1808–1880) originally kept in the "Westpreussisches Provinzialmuseum" of Danzig, now partially kept in the "Westpreussisches Landesmuseum" in Münster-Wolbeck, Inv.-Nr. 467, formerly no. 398.

Diagnosis: In addition to family-traits of the Nevrorthidae *Rophalis relicta* is characterised by filiform antennae with about 25 flagellomeres including slightly enlarged scapus and pedicellus. In fore- and hindwings the crossvein "3rp3+4 – rp2" is absent. Furthermore the males bearing distally of the 6th and 7th abdominal segments at most 6 extruded and eversible tubes which can be probably interpreted as androconial glands. Extant males, e.g. *Nevrorthus*, possess also these eversible tubes (ASPÖCK & ASPÖCK 1983). Similar analogical organs are found in some amphiesmenopteran insects as well as in some males of fossil Trichoptera in Baltic amber (WICHARD 2013). In *Rophalis relicta* two tubes located lateroventral between 6th and 7th abdominal segments and respectively between 7th and 8th abdominal segments two tubes lateroventral and two tubes laterodorsal (Fig. 3). Forewing length 4.5–5.5 mm.

Male genitalia (Fig. 3c, d): The 9th sternite rectangular and almost square-cut; the four edges being nearly equally in lengths and slightly rounded at the corners; the lateral edges touching the 9th tergite, forming together the closed ring of the 9th segment. The distal margin of the quadrate sternite medially bears a small lobe, probably the pseudoapex derived from the 10th segment (sensu ASPÖCK & ASPÖCK 2008). Two strong and elongate appendages protrude at the laterodistal margin of 9th sternite; probably belonging to the 10th segment. They extended to the cavity of the gonocoxite, where the elongate appendage distally expanded into a tetrahedral, rounded structure. Each gonocoxite of the 9th segment, basally broad, curved, changing distally into curved, sinusoidal gonostyli running to the middle. At the base of each 9th gonocoxite a gonapophyses, sinusoidal and denticulate, running parallel to the gonostylus. Dorsally the genital is covered by a broad and pre-bulged ectoproct (compare WICHARD et al. 2009: 108, fig. 7.17 b).

Female genitalia: Most often "verlumt", therefore the outer genitalia often not visible; exceptionally the typical nevrorthid female genital structures are partly shown in lateral view in Fig. 2c.

Remarks: *Rophalis relicta* is the most common nevrorthid species in Baltic amber; single adults are also found in the Eocene Rovno amber (MAKARKIN & PERKOVSKY 2009) and in the Bitterfeld amber (WICHARD et al. 2009; RAPPSILBER 2016).

Genus *Electroneurorthus* WICHARD et al., 2010

Type species: *Electroneurorthus malickyi* WICHARD et al., 2010: 447–449, figs. 3–4.

Diagnosis: The extinct genus *Electroneurorthus* is closely related to the extinct genus *Palaeoneurorthus.* They coincide with the antennae consisting of about 34–36 segments including a larger scapus and a smaller pedicellus. In forewings crossveins 3rp3+4 – rp2 present, in hindwings absent. *Electroneurorthus* differs from *Palaeoneurorthus* in the male genitalia by the absence of needle-shaped gonapophyses of the 9th gonocoxites. Moreover 9th sternite is elongate, compactly stick-shaped and apically slightly forked, whereas 9th sternite in *Palaeoneurorthus* dorsoventrally flattened, apically with a small tongue. In forewings *Electroneurorthus* and *Palaeoneurorthus* differ from the genera *Balticoneurorthus* n. gen. and from *Proberotha* by the absence of some branched crossveins between costa and subcosta.

Electroneurorthus malickyi WICHARD et al. 2010
Fig. 4

Holotype: Male embedded in Baltic amber, GPIMH (ex coll. GRÖHN 7078).

Diagnosis: As for the genus. Adults of small body size; male forewing length 6–7 mm.

Male genitalia: The 9th abdominal ring segment is ventrally interrupted by the derived 9th sternite orientated mediad to the genital centre. The 9th sternite is much longer than wide, elongate and stick-shaped, apically slightly forked. The forked apex and/or the bulbous structures at both sides of the basal 9th sternite are probably elements of 10th segment. Basally broad gonocoxites of the 9th segment as a pair of robust claspers terminally with gonostyli bend mediad. The gonapophyses of the 9th gonocoxites not visible basoventrally.

Genus *Palaeoneurorthus* WICHARD, 2009

Type species: *Palaeoneurorthus hoffeinsorum* WICHARD, 2009 in WICHARD et al. 2009: 101–105, figs. 7.13–7.14.

Diagnosis: Adults of small body size; male forewing length 5.5–7 mm, body light brown, wings translucent.

Head: Ocelli absent. Filiform antennae with slightly enlarged scapus, smaller pedicellus and 34 – 36 following uniform flagellomeres. 5-segmented maxillary palps and the 3-segmented labial palps terminate in a pointed final segment.

Wings: Costal crossveins are simple in both wings. Sc and radius RA approximated each other distally, connected apically by a short crossvein. Fore- and hindwings characterized by 4 rows of crossveins (Fig. 1). In forewings the crossvein 3rp3+4 – rp2 present; in hindwings crossvein 3rp3+4 – rp2 absent.

Male genitalia: The 9th abdominal ring segment ventrally interrupted by the modified sternite. The 9th sternite much longer than wide, elongate, folded down and often dorsoventrally flattened; the tongue-shaped apex of the 9th sternite probably derived from the 10th segment (interpreted as pseudoapex of 9th sternite sensu ASPÖCK & ASPÖCK 2008). Gonocoxites of the 9th segment as a pair of basally broad claspers terminally with gonostyli bend mediad, claw-like in most *Palaeoneurorthus*. Basoventrally the gonocoxites bearing gonapophyses with a set of two or three pointed needles or two thorns. The ectoproct (10th tergite) distally modified to a broad, curved sclerite (compare WICHARD et al. 2013: 108, fig. 7.17c).

Comparisons: The genus *Palaeoneurorthus* differs from *Electroneurorthus* by the male genital, from *Balticoneurorthus* n. gen. and *Proberotha* by the simple, unbranched crossveins between costa and subcosta in the forewings. *Palaeoneurorthus* differs from genus *Rophalis* by the number of flagellomeres (*Rophalis*: 25, *Palaeoneurorthus*: ca. 35) and the crossveins between subordinate branches of radius posterior in forewings (in *Rophalis* crossvein 3rp3+4 – rp2 absent).

Palaeoneurorthus bifurcatus WICHARD, 2009
Fig. 6a, b

Holotype: Male embedded in Baltic amber, GPIMH 4523 (ex coll. GRÖHN 7076).

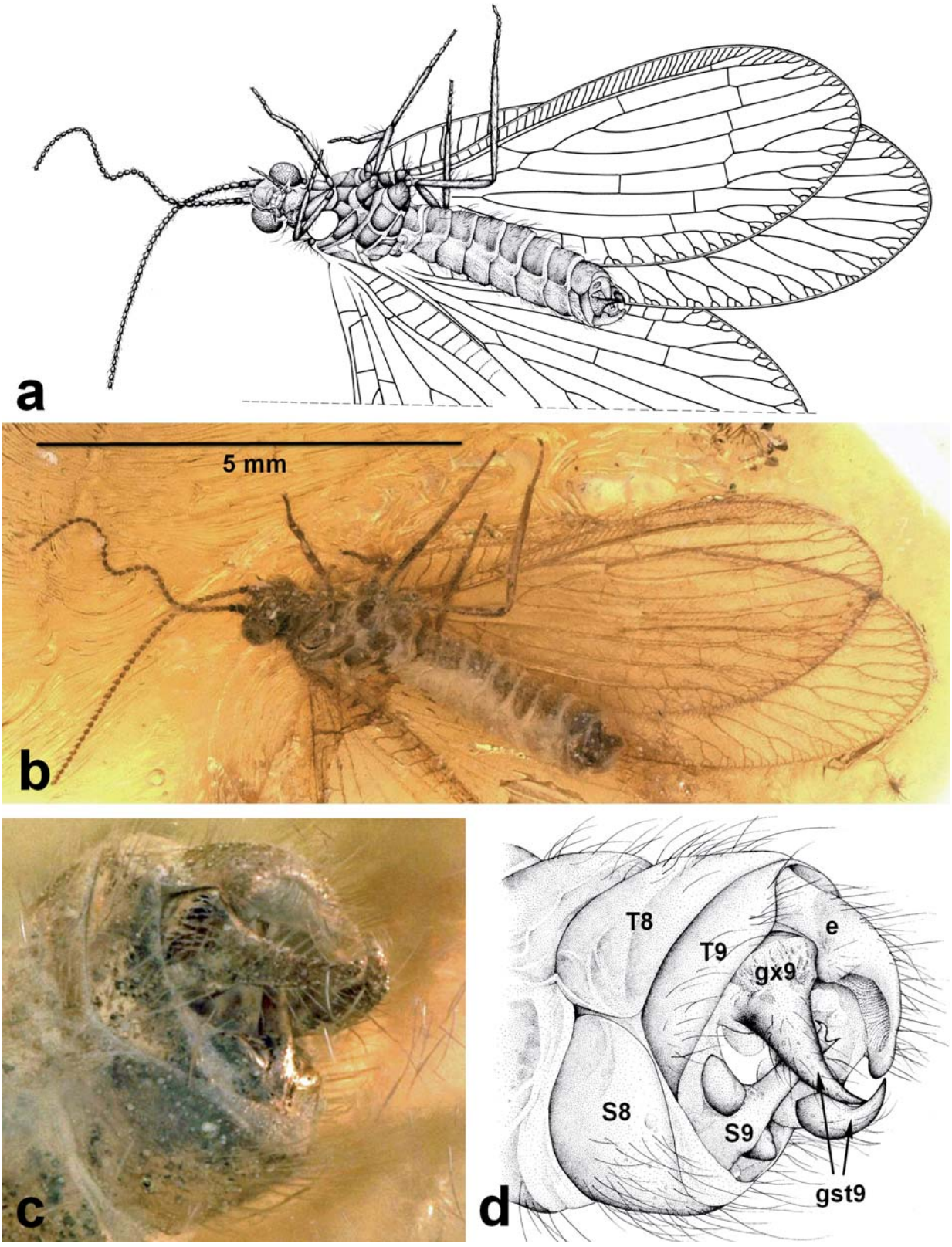

Fig. 4. *Electroneurorthus malickyi* WICHARD et al., 2010, male holotype, GPIMH (ex coll. GRÖHN 7078); **a**: drawing in ventral view; b: photograph in ventral view; **c**: male genitalia; d: drawing of male genitalia in lateroventral view.

Diagnosis: Male forewing length 5 mm. *Palaeoneurorthus bifurcatus* differs from all other *Palaeoneurorthus* species by the modified gonocoxites of 9th segment bearing basally gonapophyses consisting of a pair of distinct thorns instead of the set of two or three needles, present in other extinct *Palaeoneurorthus* species.

Male genitalia: The 9th sternite long, slender and bearing a terminal membranous tongue-shaped lobe, probably as pseudoapex derived from 10th segment. The gonocoxites of the 9th segment broad at their base bent distad into digitiform structures. At apex each gonocoxite bearing a gonostylus consisting of a short and pointed cone, beaked. A pair of thorns-shaped gonapophyses orginates at base of the gonocoxite, in lateral view subtriangular and apically bent dorsad and pointed. 10th tergite dorsally slightly bulging forming the curved ectoproct.

Palaeoneurorthus hoffeinsorum Wichard, 2009
Fig. 6c, d

Holotype: Male embedded in Baltic amber, SDEI (ex coll. Hoffeins 1124-3).

Diagnosis: Male forewing length 5.0–6.0 mm. *Palaeoneurorthus hoffeinsorum* differs from all other fossil species of genus *Palaeoneurorthus* in the set of three straight needles-shaped gonapophyses of 9th gonocoxites.

Male genitalia: The 9th abdominal segment separating the genitalia from the abdomen by a closed small ring consisting of a small border of the 9th tergite and a short basal part of the slender 9th sternite. The 9th sternite long, flattened, narrows dorsad and bearing a conical, membranous extension at its end, probably pseudapex, a derivate of 10th segment. The robust 9th gonocoxites with terminal gonostyli running mediad. Each 9th gonocoxite bearing basoventrally bizarre gonapophyses, consisting of a set of three dark and pointed needles arranged in a row of decreasing length, the ventral one longest. Ectoproct broad and bulging.

Palaeoneurorthus groehni Wichard et. al., 2010
Fig. 6e

Holotype: Male embedded in Baltic amber, GPIMH (ex coll. Gröhn 7081).

Diagnosis: Male forewing length 5.5–6.5 mm. *Palaeoneurorthus groehni* differs clearly from all other fossil species of *Palaeoneurorthus* by the modification of a baggy 9th gonapophyses bearing two needles.

Male genitalia: The abdominal 9th segment ring ventrally interrupted by the flattened 9th sternite, folded down to the genital center. Gonocoxites of 9th segment present as a pair of strong claspers, terminally with gonostyli, bent and running towards each other until touching medially. Baggy gonapophyses on each 9th gonocoxite bearing two needles; the ventral (outer) one a long needle, in distal part slightly ampullate, enlarged and pointed, the dorsal (inner) one a small needle with one third of the length of the dorsal needle. Ectoproct broad and bulging.

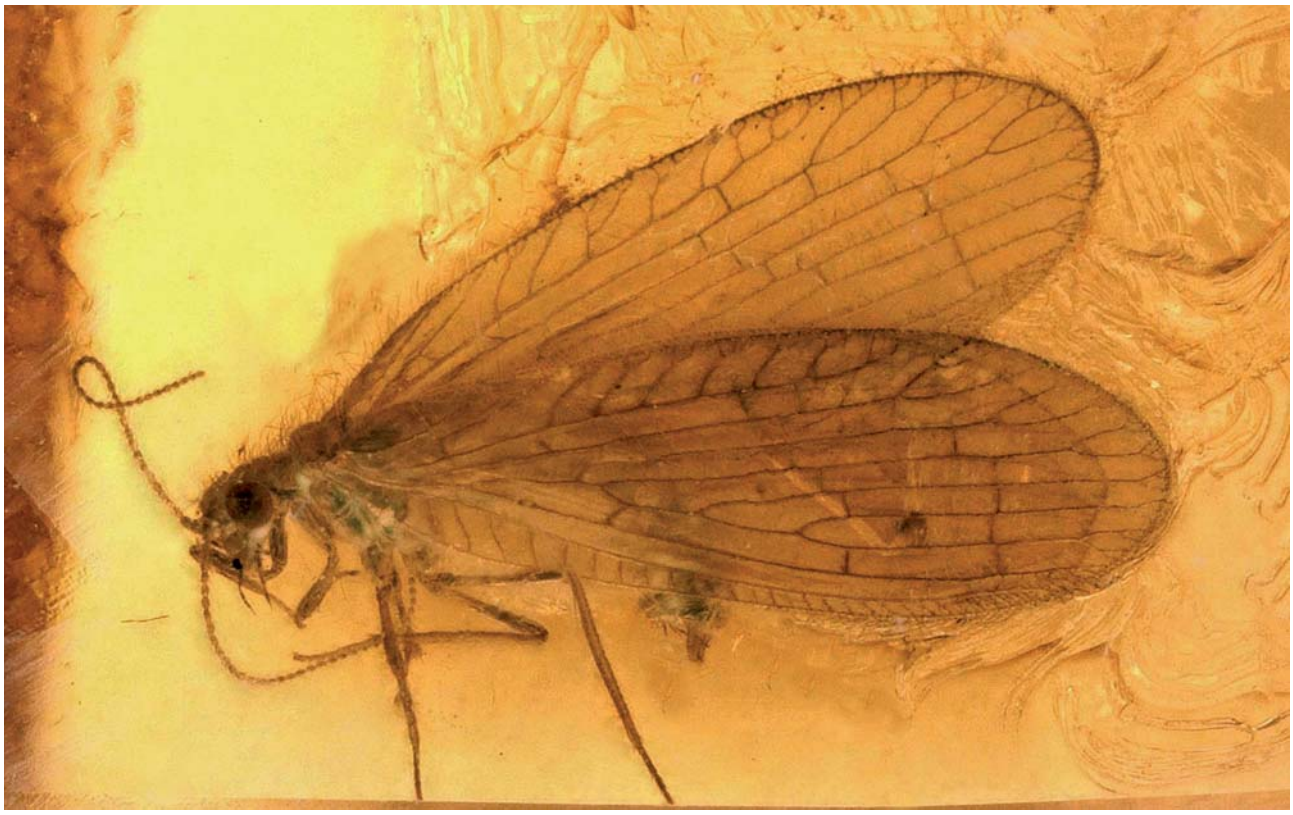

Fig. 5. *Palaeoneurorthus eocaenus* n. sp., male holotype, SMNS BB-2817 (ex coll. Wichard) embedded in Baltic amber.

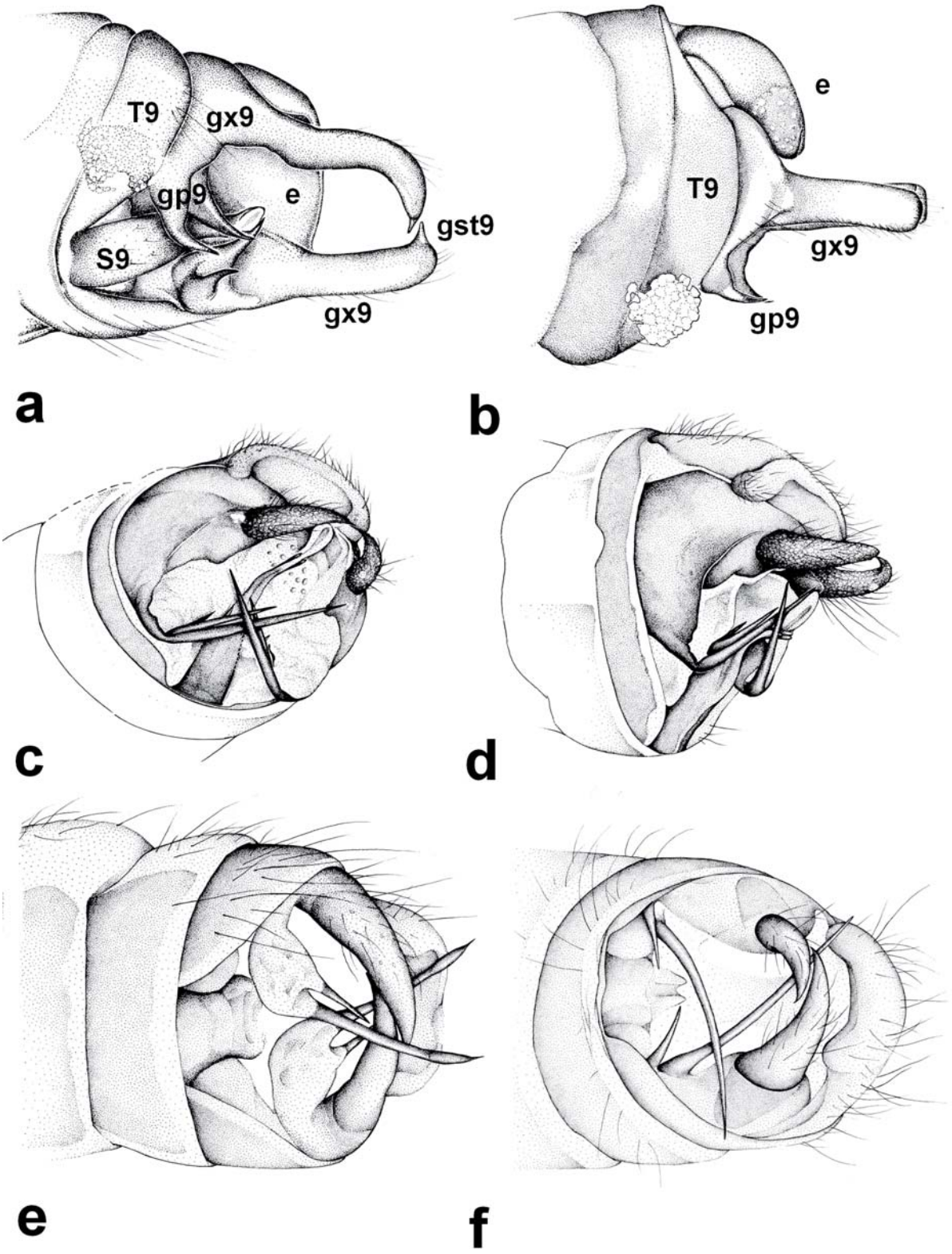

Fig. 6. *Palaeoneurorthus*, drawings of male genitalia; **a**: *Palaeoneurorthus bifurcatus* WICHARD, 2009 in lateroventral view; **b**: *Palaeoneurorthus bifurcatus* WICHARD, 2009 in lateral view; **c:** *Palaeoneurorthus hoffeinsorum* WICHARD, 2009 in lateroventral view; **d**: *Palaeoneurorthus hoffeinsorum* WICHARD, 2009 in lateral view; **e**: *Palaeoneurorthus groehni* WICHARD et al., 2010 in ventral view; **f**: *Palaeoneurorthus eocaenus* n. sp. in ventral view.

Palaeoneurorthus eocaenus n. sp.
Figs. 5, 6f

Holotype: Male embedded in Baltic amber, kept in the Staatliches Museum für Naturkunde Stuttgart, SMNS no. BB-2817 (ex coll. WICHARD). Forewings cover partly hindwings and abdomen; male genitalia visible in ventral and lateral view; head, antennae and the legs well preserved.

Etymology: The species *eocaenus* is named after the Eocene period of the Baltic amber.

Diagnosis: The male genitalia of *Palaeoneurorthus eocaenus* n. sp. is similar to the genital structure of *Palaeoneurorthus groehni*. They differ strongly in the gonapopyhses of the 9th gonocoxites. In the new species (*P. eocaenus* n. sp.) the basal baggy part of the gonapophyses is missing, but the apical two neddles are present in both species. However, in a further different way from *P. groehni*, the ventrally orientated (outer) needle is much smaller as in *P. groehni*, the dorsally orientated (inner) needle is longer than in *P. groehni* and about 5 x longer than the ventral one of *P. eocaenus* n. sp.. The needles are not ampullate enlarged as in *P. groehni*.

Description: Male forewing length 5.5 mm, wings and body light brown, wings ovoid, apically rounded, hindwing with 4.5 mm length smaller than forewing.

Head: Ocelli absent. Filiform antennae with enlarged scapus, smaller pedicellus and 34 uniform flagellomeres. The 5-segmented maxillary palps and the 3-segmented labial palps terminate in a pointed final segment.

Wings: Costal crossveins are simple in both wings. SC and RA running parallel to margin and connected apically by a short crossvein, RP 3-branched. In both wings crossvein gradate series present. In forewings the crossvein 3rp3+4 – rp2 present; in hindwings crossvein 3rp3+4 – rp2 absent.

Male genitalia: The modified 9th sternite is basally moderately broad, dorsoventrally flattened, folded down, mediad; the pseudoapex not visible. The gonocoxites of the 9th segment broad at their base, apically the gonostyli claw-like, pointed. Basoventrally the 9th gonocoxites bearing gonapophyses each with a set of two fine needles, a long one dorsally orientated and a smaller one ventrally orientated, about 1/5 in length of the inner dorsad needle. The broad, curved ectoproct distally modified of the 10th segment visible in ventral and lateral view.

Genus *Balticoneurorthus* nov.

Type species: *Balticoneurorthus elegans* n. sp., monotypic.

Diagnosis: *Balticoneurorthus* with its type species *Balticoneurorthus elegans* n. sp. differs from all extinct Baltic amber Nevrorthidae in the forewing length of 9.5 mm, in the forewing venation with partially forked subcostal crossveins and numerous irregular crossveins (Fig. 7c), and moreover in the male genitalia showing ventrally a pair of long sclerotized rods (Fig. 7b).

Balticoneurorthus elegans n. sp.
Fig. 7a–c

Holotype: Male embedded in Baltic amber, kept in Staatliches Museum für Naturkunde Stuttgart, SMNS no. BB-2818 (ex coll. WICHARD). Well preserved, forewings and hindwings visible. Male genitalia visible in posterior and partly lateral view. Head, antennae and legs are present.

Etymology: The new species bears the Latin name "elegans", a beautiful and exclusive species and the largest nevrorthid adult in Eocene Baltic amber.

Diagnosis: See diagnosis of genus *Balticoneurorthus.*

Description: Adults of relatively large body size; forewing length 9.5 mm and hindwing length 8mm. Wings light brown, translucent, apical margin rounded.

Head: Ocelli absent. Antennae filiform, half as long as forewings, consisting of a strong scapus, approximately twice the length of the short pedicellus, following 39 flagellomeres, each slightly ovoid, surrounded by fine setae. Maxillary palps 5-segmented, labial palps 3-segmented, their terminal segments pointed.

Forewings (Fig. 7c): Wing venation conspicuous by numerous crossveins, more common than usually in the crossvein gradate series 1–4 of other extinct Nevrorthidae. (Two extant nevrorthid species of genus *Austroneurorthus*: *A. horstaspoecki* and *A. brunneipennis* with similar numerous crossveins.) Costal crossveins at least partially forked, others simple and unbranched. (Branched crossveins between costa and subcosta present in the extinct genus *Proberotha* and the extant genera *Nipponeurothus* and *Austroneurorthus*.) Radius anterior running straight to the apical margin, parallel to Sc; RA and Sc bridged apically by a short crossvein. Radius posterior dichotomous 4-branched in subordinate branches RP1, RP2, RP3, RP4. MA simple, MP branched in MP1+2 and MP3+4. CuA running parallel to posterior wing margin with some terminal branches; CuP simple. Anal veins 1–3 running separate to anal margin.

Hindwings (Fig. 7c): All crossveins between costa and subcosta simple, unbranched; 9 crossveins between RA and RP1; 4 crossveins between MA and MP1+2. Outer gradate crossvein series present. RP pectinate, 3-branched in subordinate branches RP1, RP2, RP3+4. MA simple, MP branched in MP1+2 and MP3+4. CuA running parallel to posterior wing margin with some terminal branches; CuP simple. Anal veins 1–3 running separate to anal margin. In fore- and hindwings all longitudinal veins ramified apically in a last step into small terminal branching.

Male genitalia (Fig. 7a, b): Genital structure with dominant ectoproct and coxopodite of 9th segment. Ectoproct strong and broad, concaved medially on posterior margin, posterolateral corner little amplified and rounded. 9th coxopodite present as robust claw, in ventral view basally broad, convex, trapeziform, terminally with a thorn-shaped gonostylus curved mediad, in lateral view the distal end tapered, in posterior view the distal end forming a small edge. Ectoproct and gonostylus densely covered with fine setae. Ventrally a pair of long sclerotised rods drawing a bow, running parallel about 1 mm in length, mediad and spread afterwards apart. The two ventral rods originate a deep furcation, probably distal of the 9th sternite or of a modification of 10th segment present as a pair of widely protruding rods.

Remarks: The pair of the long sclerotized rods in the male genitalia of *Balticoneurorthus elegans* n. sp. is extremely distinct and unknown in all other extinct nevrorthids in Baltic amber. Clarifying details about the origin of the furcated rods are not visible in the embedded fossil.

ASPÖCK et al. (1980), MONSERRAT & GAVIRA (2014) illustrated the variable 9th sternites of the five species of the genus *Nevrorthus*; *N. apatelios* possesses terminally a rounded lobe whereas the

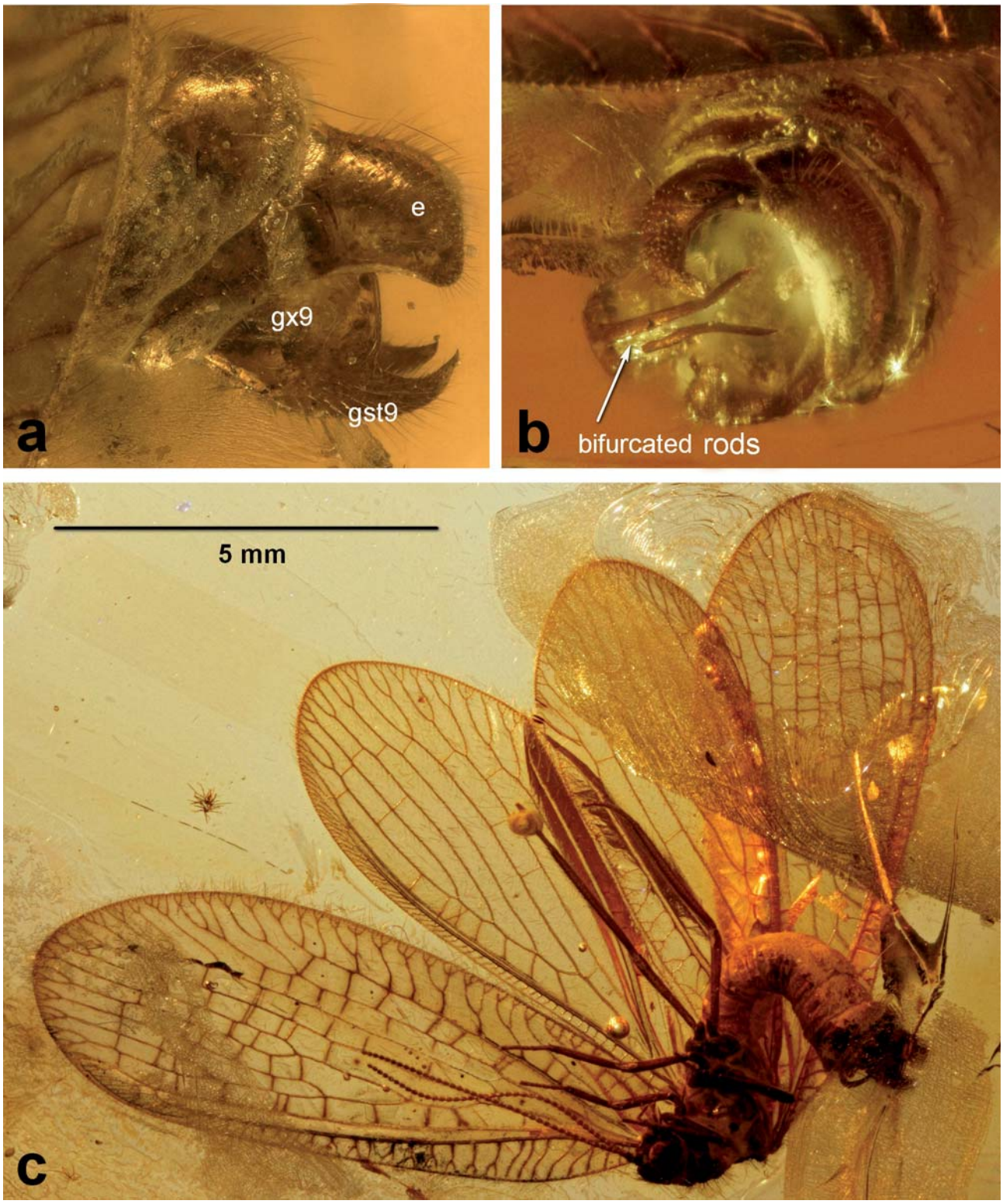

Fig. 7. *Balticoneurorthus elegans* n. gen. n. sp. male holotype, SMNS BB-2818 (ex coll. WICHARD); **a:** male genitalia in lateral view; **b**: male genitalia in posterior view; **c**: male in overall view.

other species show a tendency to furcation and *N. iridipennis* bears a branched apex, but in *Balticoneurorthus elegans* n. sp. the furcation is much longer and its genesis unknown.

Genus *Proberotha* KRÜGER, 1923

Type species: *Proberotha prisca* KRÜGER, 1923: 81–83.

Neotype: *Proberotha prisca* KRÜGER, 1923, designated M. S. ENGEL, NHM I.15997 BMNH, Natural History Museum, London.

Diagnosis: The genus *Proberotha* was established by KRÜGER (1923) on the base of wing venations in fore- and hindwings (however, not illustrated), originally placed in the family Berothidae. In *Proberotha* the fore- and hindwing venations concur with the wing venations of the known extinct nevrorthid species in Baltic amber. In forewings Sc and RA running parallel to apical wing margin and connected apically by a crossvein as in all other nevrothids. Radius posterior 3-branched in subordinate branches RP1, RP2, RP3+4 (*Proberotha prisca*) or dichotomus, 4-branched in subordinate branches RP1, RP2, RP3, RP4 (*Proberotha dichotoma*). Media M 3-branched, MA simple, unbranched, MP branched in the subordinate branches MP1+2 and MP3+4. CuA running to margin with 9 terminal branches; CuP simple. Furthermore the middle and outer crossvein gradate series are present in *Proberotha* and in all extinct Nevrorthidae.

Remarks: The genus *Proberotha* belongs to the family Nevrorthidae NAKAHARA, 1958. In forewings the costal crossveins partially forked as in the extinct *Balticoneurorthus* gen. nov. *Proberotha* differs from the extinct genera *Rophalis*, *Electroneurothus* and *Palaeoneurorthus* by the partially branched costal crossvein.

Proberotha prisca KRÜGER, 1923
Figs. 8–10

Holotype is lost, neotype designated by M. S. ENGEL, unpublished, NHM I.15997, BMNH, Natural History Museum, London.

Material:

1. NHM I.15997 Natural History Museum, London, male (ROSS 1998: fig. 133); Figs. 8a, 9a, b.
2. GZG.BST.05230 Geoscience Centre, University of Göttingen, Museum; Fig. 8b.
3. female adult in coll. WICHARD, Bonn, probably belonging to *Proberotha prisca*; Fig. 10.
4. no. 7074 in coll. GRÖHN, Hamburg (see SCHEVEN 2004: fig. on p. 74, left); Fig. 9c, d.

Four adults in clear Baltic amber. Fore- and hindwing, antennae, maxillary palps, labial palps, legs as well as male and female genitalia visible, however, partially "verlumt".

The old amber inclusions of Natural History Museum, London, NHM I.15997, originally from "Museum STANTIN & BECKER", and of Geoscience Centre, University of Göttingen, GZG.BST.05230, originally from "B.S. d. Univers Königsberg i.Ps." are mounted on standard microscope slides, embedded probably in Damar resin (TORNQUIST 1911; NEUMANN 2010) and covered by a thin cover slip (Fig. 8).

Re-description: Small adult male and female, forewing length 7 mm. Wings ovalness, apical rounded, hindwings smaller than forewings.

Fig. 8. *Proberotha prisca* KRÜGER, 1923, historical amber inclusens mounted on standard microscope slides; **a** (top): neotype, designated by M. S. ENGEL, NHM I.15997 Natural History Museum, London; **b** (bottom): GZG.BST.05230 Geoscience Museum, University of Göttingen.

Head: Ocelli absent; filiform antennae with slightly enlarged scapus, smaller pedicellus and about 35 flagellomeres in male neotype and apparently 33 in female. Maxillary palps 5-segmented, labial palps 3-segmented, their terminal segments pointed.

Forewing (Fig. 9c, d): Costal cross-veins partially branched. Subcosta (Sc) and radius anterior (RA) running parallel to wing margin, apically connected by a short crossveins. The area between RA and RP interrupted by usually three crossveins: 2ra-rp, 3ra-rp and 4ra-rp. The gradate series of crossveins present. Radius posterior (RP) pectinate, 3-branched in subordinate branches RP1, RP2, RP3+4. Crossvein 3rp3+4 – rp2 present. Media MA simple and MP with dichotomous branch in MP1+2 and MP3+4. CuA running parallel to margin with terminal branches; CuP simple. Anal veins (1A, 2A, 3A) simple, running separately to anal margin.

Hindwing: Costal cross veins all simple; in subcostal area Sc and RA running separately and parallel to margin, connected only by a basal and a distal cross vein. Between RA and RP three crossveins: 2ra-rp, 3ra-rp and 4ra-rp. RP pectinate, usually 3-branched; crossvein 3rp3+4 – rp2 absent. MA unusually simple, MP with dichotomous branch in MP1+2 and MP3+4, apically divided into small terminal branches at margin. CuA running parallel to margin with terminal branches; CuP simple.

Genitalia: Male genitalia of the neotype (Fig. 9b) in part "verlumt", in ventral view the ectoproct (e) broad, curved, concaved medially; the gonocoxites (gx9) basally abundant, bulged, inside concave, the apical part (gonostylus gst9) small, distad tapered and pointed. Female genitalia in part strong shrunken (together with the abdomen) and verlumt, compare Fig. 10.

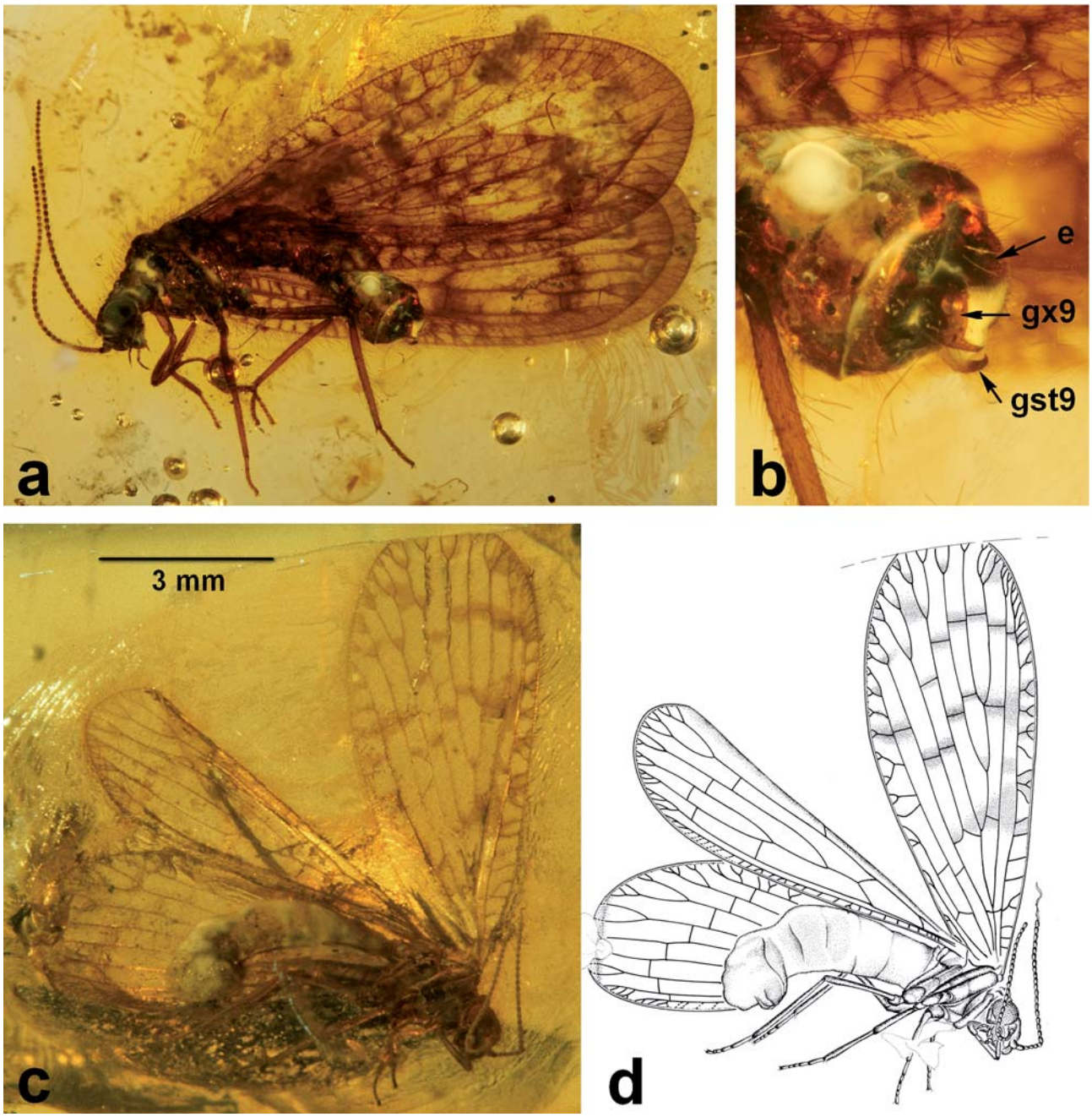

Fig. 9. *Proberotha prisca* KRÜGER, 1923; **a**: male neotype in lateral view, NHM I.15997 Natural History Museum, London; **b**: male genitalia of the neotype, partially "verlumt", ectoproct and gonocoxite with gonostylus visible; **c**: adult in coll. GRÖHN, Glinde, in ventral view; **d**: drawing of the adult.

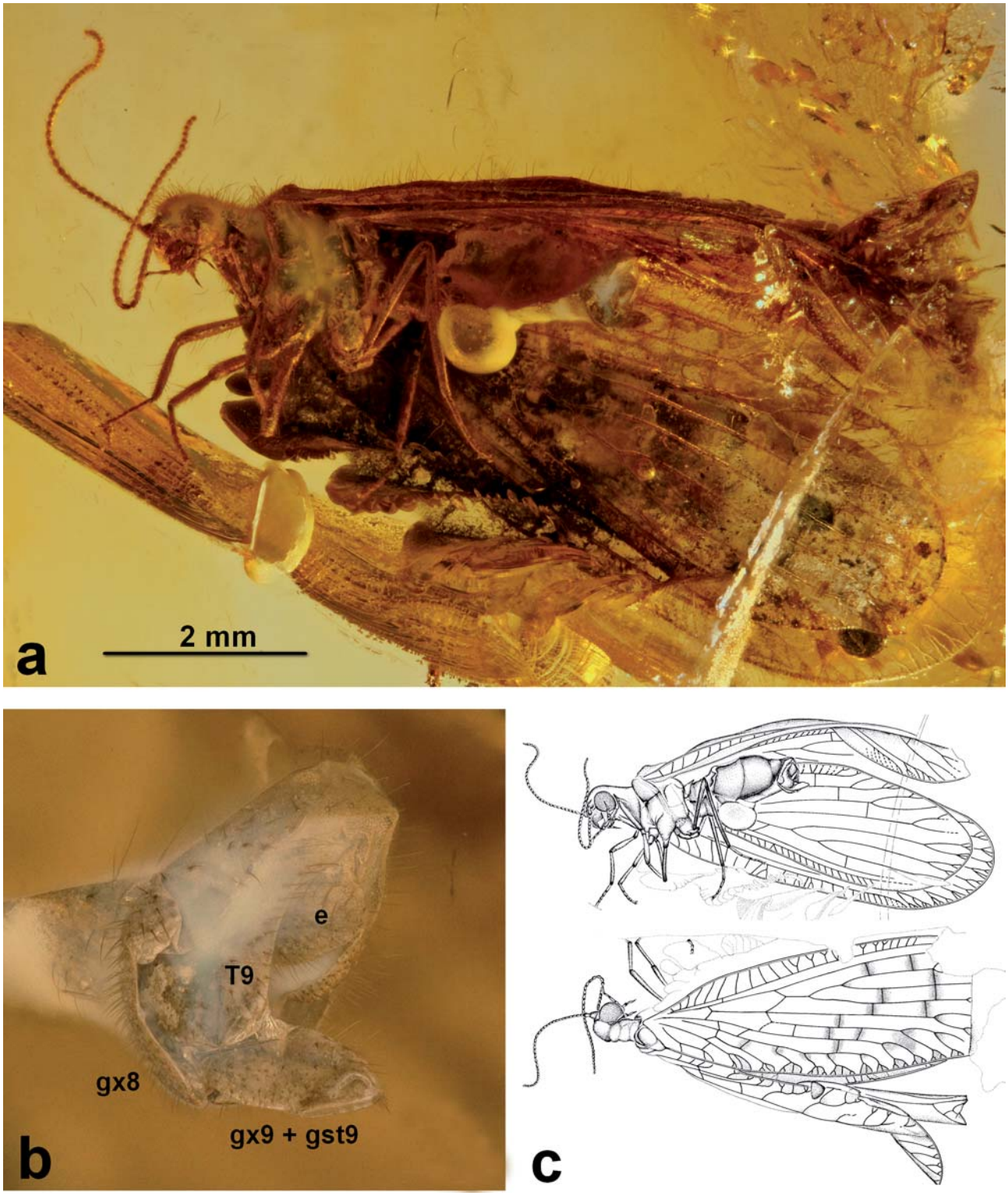

Fig. 10. *Proberotha* cf. *prisca* KRÜGER, 1923, female in coll. WICHARD, Bonn; a: female adult in lateral view; **b**: female genitalia and last abdominal segments strongly shrunken; **c**: drawings in ventral and dorsal view.

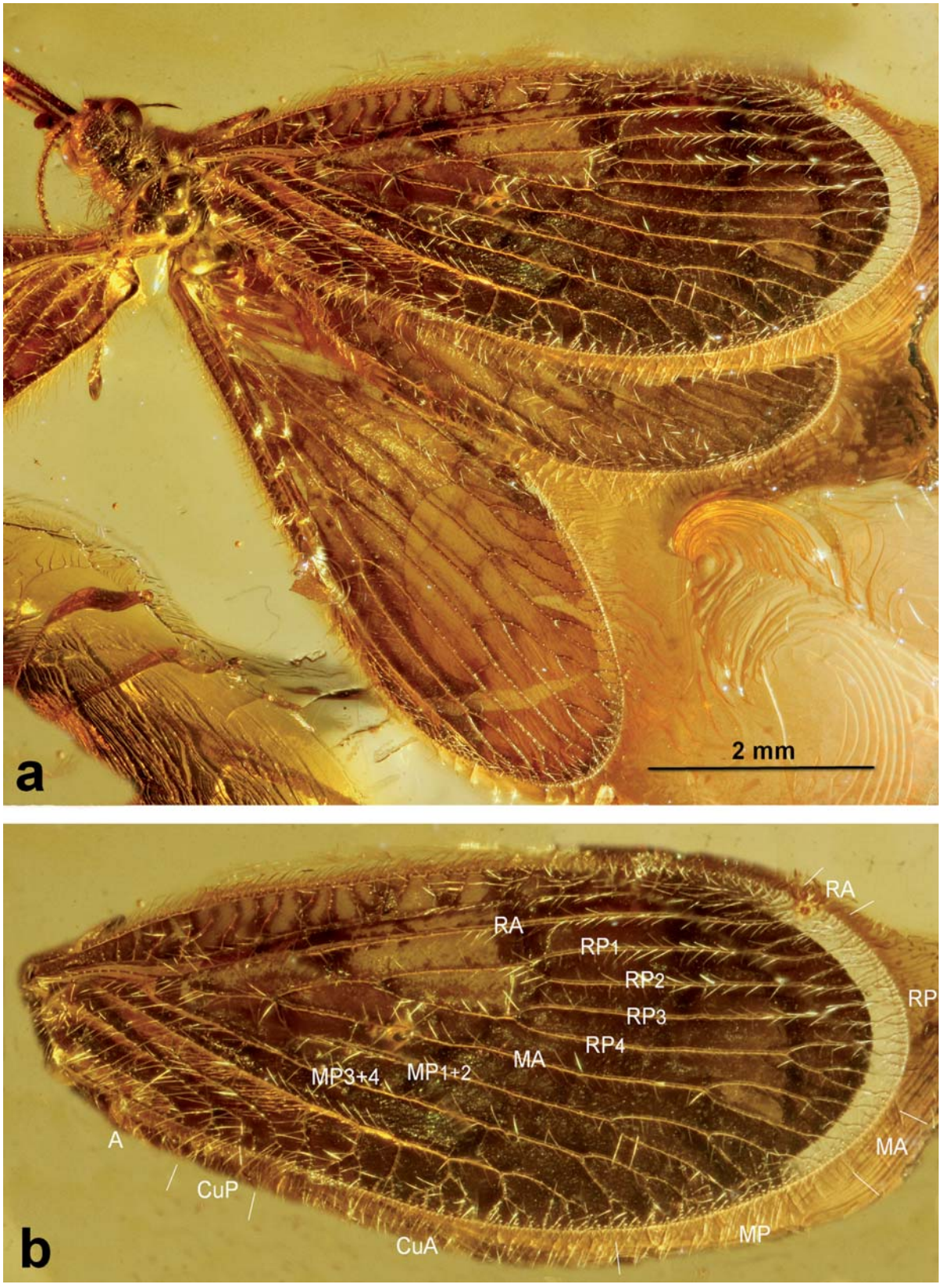

Fig. 11. *Proberotha dichotoma* n. sp. holotype, GPIMH (ex coll. GRÖHN 7156); **a**. adult in dorsal view; **b**: forewing with characteristic vein venation (dichotomy of 4 subordinate branches of RP).

Proberotha dichotoma n. sp.
Fig. 11

H o l o t y p e : Female embedded in Baltic amber, deposited in the Geologisch-Paläontologisches Institut und Museum, University of Hamburg, GPIMH (ex coll. GRÖHN 7156). Well preserved in Baltic amber but body partially "verlumt", left forewing absent.

E t y m o l o g y : The name is derived from the Latin and pointed to the dichotomous venation of the subordinate branches of radius posterior in forewings.

D i a g n o s i s : The new species differs from *Proberotha prisca* by the forewing venation. Radius posterior branched dichotomous and forming four subordinate branches of equal lengths RP1, RP2, RP3, and RP4, instead of the pectinate 3-branched RP in *Proberotha prisca*. The dichotomous branching is also known from the extinct *Balticoneurorthus elegans* n. gen. n. sp. and from the extant nevrorthid *Sinoneurorthus yunnanicus* LIU, H. ASPÖCK & U. ASPÖCK, 2012.

D e s c r i p t i o n : Small adult female, forewing length 7 mm. In fore- and hindwings rows of setae along the wing veins; crossveins often indistinct, but the crossvein gradate series present.

H e a d : Ocelli absent; filiform antennae with slightly enlarged scapus, smaller pedicellus about 35 segments. Maxillary palps 5-segmented, labial palps 3-segmented, their terminal segments pointed.

F o r e w i n g : Costal cross veins partially branched. Sc and RA running parallel and connected distally by a short crossvein. The area between RA and RP interrupted by usually three crossveins: 2ra-rp, 3ra-rp and 4ra-rp. The gradate series of cross-veins can be discerned. Radius posterior dichotomous, 4-branched in subordinate branches RP1, RP2, RP3, RP4. Crossvein between 3rp3 and 3rp2 present (3rp3-rp2). MA simple and MP with dichotomous branch in MP1+2 and MP3+4. Longitudinal veins apically divided into small terminal branches at margin. CuA running parallel to margin with terminal branches; CuP simple. Anal veins simple, running separately to anal margin.

H i n d w i n g : Costal cross veins all simple; so far visible, in subcostal area Sc and RA running separately and parallel to margin, connected by a basal crossvein, digital part not visible. RP pectinate, usually 3-branched; crossvein 3rp3+4 - rp2 absent. MA simple, MP with dichotomous branch in MP1+2 and MP3+4. CuA running parallel to margin with terminal branches; CuP simple. Anal veins (1A, 2A, 3A) simple, running separately to anal margin.

3. Key of adults of Nevrorthidae in Baltic amber

1	number of flagellomeres about 25, forewing crossvein (3rp3+4 – rp2) absent	*Rophalis relicta*
-	number of flagellomeres more than 30, forewing crossvein (3rp3+4 – rp2) present	2
2	forewing subcostal crossveins simple	3
-	forewing subcostal crossveins partially branched	7
3	9th sternite elongate, stick-shaped	*Electroneurothus malickyi*
-	9th sternite elongate, dorsoventrally flattened	4 (*Palaeoneurorthus*)
4	9th gonapophyses thorn-shaped	*P. bifurcatus*
-	9th gonapophyses needle-shaped	5
5	set of three needle-shaped 9th gonapophyses	*P. hoffeinsorum*
-	set of two needle-shaped 9th gonapophyses	6
6	long ventral and short dorsal 9th gonapophyses	*P. groehni*
-	short ventral and long dorsal 9th gonapophyses	*P. eocaenus*
7	forewings with numerous irregular crossveins	*Balticoneurorthus elegans*
-	forewings with crossveins in gradate series	8 (*Proberotha*)
8	forewings RP 3-branched	*Proberotha prisca*
-	forewings RP 4-branched	*Proberotha dichotoma*

4. Discussion

At present, 19 extant species of four genera belong to the small family Nevrorthidae. The distribution of the Nevrorthidae is limited to three disjunct geographical regions: the Mediterranean region with five species of the genus *Nevrorthus (*MONSERRAT & GAVIRA 2014), Southeast Asia with eleven species of the genus *Nipponeurorthus* (LIU et al. 2014) and one species of the genus *Sinoneurorthus* (LIU et al. 2012). The genus *Austroneurorthus* is distributed with two species in southeast Australia (ASPÖCK 2004). Nevrorthidae are adapted to a warm-temperate climate, which predominate in all geographical regions in which the family appears (Fig. 12).

In contrast, nine extinct species belonging to five extinct genera of the Nevrorthidae, all are found in the Eocene Baltic amber. At that time the fossil nevrorthid species lived probably under warm-temperate conditions (SCOTESE 2001; HEROLD et al. 2014). A warm-humid climate of the Eocene promoted probably the so-called amber-forests in northern Europe. In the Eocene period Europe was an archipelago, consisted of several southern islands and a large northern island separated from Asia by the epicontinental Turgai Strait, which connected the Arctic Sea and the Tethys Ocean for a long time. The separation ended step-by-step with the beginning of the Oligocene, when a decrease of temperature froze at least the North Pole (SCOTESE 2001). The sea level fall and caused the drying-up of the Turgai Strait and caused finally – in combination with further geological events – the conjunction of Europe and Asia to Eurasia (SANMARTIN et al. 2001). The change of climate and the decrease of temperature induced gradually the end of the typical Baltic amber forest and provoked to a great extent the extinction of the

Fig. 12. Worldwide distribution of extant and extinct genera of the family Nevrorthidae.

subtropical fauna and flora (Akhmetiev & Beniamovski 2009; Weitschat & Wichard 2010; Wegierek & Zyla 2011). Of course, the extant Nevrorthidae did not derive from the extinct species of the Eocene Baltic region. The extant species living predominantly in warm temperate refuges and the extinct species of the Eocene amber forest have, however, common ancestors, back to Pangea.

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