Damselfly and dragonfly nymphs in Eocene Baltic amber (Insecta: Odonata), with aspects of their palaeobiology

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Abstract

All seven previously known damselfly larvae in Baltic amber are revised and eight new specimens are described. Some of these can be attributed to the Recent family group taxa Calopterygidae: Calopteryginae, Hypolestidae: Hypolestini, Megapodagrionidae: Argiolestinae, Synlestidae, and Lestida (= Lestinoidea sensu Fraser 1957), while others can only be attributed to different unidentified species of the paraphyletic "megapodagrionid" grade of damselflies. A further new specimen is a rather strange odonate larva, which seems to represent the first genuine Anisoptera larva in amber (probably Aeshnidae). Various taphonomic, palaeoecological and palaeobiological aspects of these amber inclusions are discussed. The relative abundance of damselfly larvae with saccoid caudal gills suggests the presence of well-oxygenated and fast flowing habitats.

Keywords: Baltic amber, Tertiary, Eocene, Odonata, Zygoptera, Calopterygidae, Hypolestidae, Megapodagrionidae, Synlestidae, Anisoptera, Aeshnidae, larva, exuvia, fossil, palaeoecology, palaeobiology.

Zusammenfassung

Alle sieben bisher bekannten Einschlüsse von Kleinlibellenlarven im Baltischen Bernstein werden revidiert und acht neue Exemplare beschrieben. Einige davon können den rezenten Familiengruppentaxa Calopterygidae: Calopteryginae, Hypolestidae: Hypolestini, Megapodagrionidae: Argiolestinae, Synlestidae und Lestida (= Lestinoidea sensu Fraser 1957) zugeordnet werden, während andere nur verschiedenen unbestimmten Arten aus dem paraphyletischen „Megapodagrioniden-Übergangsfeld" zugeordnet werden können. Ein weiteres neues Exemplar ist eine recht merkwürdige Libellenlarve, die wohl die erste echte Großlibellenlarve (vermutlich Aeshnidae) im Bernstein darstellt. Verschiedene Gesichtspunkte der Taphonomie, Palökologie und Paläobiologie dieser Bernsteineinschlüsse werden diskutiert. Die verhältnismäßige Häufigkeit von Kleinlibellenlarven mit sackförmigen Kaudalkiemen spricht für sauerstoffreiche und schnell fließende Habitate.

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1. Introduction

Even though fossil odonates are quite rare as inclusions in amber, adult specimens of Zygoptera or at last fragments of them are not as rare as often supposed.

Hagen (1854) mentioned five odonates and Handlirsch (1908) mentioned six odonates from Baltic amber. Handlirsch's list was incomplete and contained several errors, which unfortunately have been frequently perpetuated, although they had already been corrected by Ander (1942). The Odonata chapter in the well-known catalogue of amber fossils by Keilbach (1982: 208–209) was likewise incomplete and introduced additional errors.

Spahr (1992) and Bechly (1993, 1996b) provided the

first comprehensive lists of fossil odonates in amber. Bechly (1998) provided an updated list of 46 specimens. Meanwhile, there are numerous further specimens known (about 75; Bechly, unpublished data), even though most of them are not yet scientifically described.

However, being fully aquatic organisms, larval specimens of the order Odonata are of course extremely rare finds in amber. Previously, there were only seven specimens described or mentioned in the literature (Bechly 1998). All of these are damselfly larvae, because the larva considered by Pictet in Pictet-Baraban & Hagen (1856: 78) as a „*Gomphus* Larve", was shown to be a damselfly larva by Hagen (p. 80 in the very same publication), which was later confirmed by Bechly (1998: 54–56) as well as the present publication. This damselfly exuvia only lacks the apex of the abdomen with the caudal gills and therefore superficially resembles an anisopterid larva.

We here revise all seven previously known specimens of damselfly larvae in Baltic amber and describe nine new odonate larvae of different taxonomic affinities, including a first genuine Anisoptera larva.

Currently there are no known specimens of fossil odonate larvae in other kinds of amber, like Dominican amber, Mexican amber, Burmese amber, or Lebanon amber.

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For loan of material and/or hospitality during our visits we are most grateful to Mr. Carsten Gröhn (Glinde, Germany), Mr. Walter Ludwig (Berlin, Germany), Mr. Jörg Wunderlich (Straubenhardt, Germany), Mr. Alexander von dem Busche (Hamburg, Germany), Prof. Dr. Wieslaw Krzeminski (Polish Academy of Sciences, Cracow, Poland), Dr. Wolfgang Weitschat (GPIM, Hamburg, Germany), Dr. Mike Reich and Dr. Hans Jahnke (GZG, Göttingen, Germany), Dr. Christian Neumann (MNB, Berlin, Germany), and Dr. Philip D. Perkins (Museum of Comparative Zoology, Cambridge, USA).

We are indebted to Mr. Jerzy Stasiulewicz (San Diego, USA) for providing photos of the adult synlestid specimen from Baltic amber in his collection.

Finally, we thank Dr. André Nel (Muséum national d'Histoire naturelle, Paris), Dr. Jörg Ansorge (Ernst-Moritz-Arndt-Universität, Greifswald), and Dr. Ronald Böttcher (SMNS, Stuttgart) for numerous helpful comments on the manuscript.

Mr. C. Gröhn agreed to depose all types and voucher specimens from his amber collection by will to the Geological-Palaeontological Institute and Museum (GPIM) of the University Hamburg (Germany) (Dr. W. Weitschat).

2. Material and Methods

The drawings have been made with a camera lucida. A few older photos (Pl. 3, Figs. 2a–c; Pl. 5, Fig. 1d; and Pl. 8, Figs. 1a–b) have still been made with an analog SLR camera attached with an adapter to a stereomicroscope. All other photos have been made with the 8-megapixel digital camera Leica DFC490 on a Leica Z 16 Apo macroscope from z-image-stacks using Synchroscopy AutoMontage within the Leica LAS software to digitally increase the depth-of-field. All measurements have been made with the Leica LAS software. The photos and plates have been subsequently edited and polished with the Adobe Photoshop CS3 imaging software.

The used classification of the order Odonata is mainly based on Bechly (1996a, 2007).

Acronyms of depositories

GPIM	Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Germany
GZG	Geowissenschaftliches Zentrum der Universität Göttingen, Germany
MB	Museum für Naturkunde, Berlin, Germany
SMF	Naturmuseum Senckenberg, Frankfurt a. M., Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany

3. Taxonomy

Ordo Odonata Fabricius, 1793
Subordo Anisoptera Selys, 1854
Superfamilia Aeshnoidea Leach, 1815
Familia Aeshnidae Leach, 1815

Specimen 1
Pl. 1, Figs. 1a–c

Specimen without number from coll. Wieslaw Krzeminski at the Museum of Natural History in Cracow (Poland).

Description. – A very large and robust fossil odonate larva in a rather dirty piece of amber (Pl. 1, Fig. 1a), in which the inclusion is only poorly visible. The apex of the abdomen is missing and the abdomen is partly visible from inside, because the inclusion posteriorly opens to the outside of the piece of amber. Apparently, a faint imprint of an anisopterid anal pyramid is still visible in the ventral part of the end of the opened abdomen. Otherwise, the larva is completely preserved. The preserved part of the body is 26 mm long, the thorax is 4.9 mm wide, and the wing pads are 6.7–7.5 mm long (together spanning 8.2 mm in length). There are definitely no ecdysial sutures, thus it is a larva, not an exuvia. The legs are strong and relatively short (profemur 3.79 mm, protibia 4.04 mm, protarsus 2.07 mm; mesofemur 4.56 mm, mesotibia 3.41 mm, mesotarsus 2.26 mm; metafemur 5.26 mm).

The head is 5.6 mm wide. The compound eyes are rather small (Pl. 1, Fig. 1b), separated from each other by a distance of four times their width. The mask (Pl. 1, Fig. 1c) is of the aeshnid type, flat and without setae. It is 6.05 mm long, max. 3.63 mm wide, and min. 1.69 mm wide. The

prementum is basally narrowed and has a relatively straight anterior margin with a short apical cleft. The labial palps are very broad and flat (Pl. 1, Fig. 1c), with a straight apical margin without teeth, but with a strong movable hook. The antennae (Pl. 1, Fig. 1b) are 7-segmented (1st segment 0.35 mm, 2nd segment 1.07 mm, 3rd segment 0.94 mm, 4th segment 0.43 mm, 5th segment 0.73 mm, 6th segment 0.72 mm, and 7th segment 0.44 mm). The antenna is distinctly longer than the length of the head, about the length of the width of the head.

Discussion. – This very long antenna is very unlike most Recent Anisoptera, but is present in the anisopteroid *Nothomacromia* larvae from the Lower Cretaceous Crato Formation of Brazil, and in a few Recent species such as the aeshnid *Tetracanthagyna degorsi* (Lieftinck in Corbet 1999, fig. 5.11).

Otherwise, the body proportions, the relative proportion of the antennomeres, and especially the morphology of the mask and labial palps strongly suggest that this specimen represents an Anisoptera larva. Among Recent Anisoptera families, the group of libelluloid dragonflies called Cavilabiata (including Cordulegastridae, Neopetaliidae, Chlorogomphidae, Macromiidae, Corduliidae, Libellulidae) can be excluded because of their spoon-shaped type of mask without median cleft and with strongly serrated palps. Gomphidae can be excluded because they possess only 4 antennal segments and have no median cleft in their mask either. This leaves Petaluridae, Austropetaliidae and Aeshnidae as putative "candidates". They all have a flat mask without setae, entire broad palps and a median cleft. Austropetaliidae can be excluded because they have only 4- or 5-segmented antennae. Petaluridae can be excluded because they possess very different antennae with shorter antennomeres, and a different morphology of the mask (e. g. labial palps somewhat concave and with a strong spine overlapping the base of the movable hook). Similar relative proportions of the antennal segments are often found in Recent Aeshnidae. Also the shape of the head and of the abdomen is very aeshnid-like. Consequently, this fossil larva is here tentatively attributed to the family Aeshnidae s. l. (= Neoaeshnida sensu Bechly 1996a). Even though many aeshnid larvae do posses distinctly larger eyes, there are some species with comparably small eyes (e. g. *Nasiaeschna pentacantha* (Rambur), *Dendroaeschna conspersa* (Tillyard), *Boyeria vinosa* (Say), *Coryphaeschna ingens* (Rambur), and *Aeshna eremita* Scudder). Since it is a larva and not an exuvia in amber, and since the very long antennae suggest an unusual way of life for an Anisoptera, we believe that it is well possible that this animal was semiterrestrial or terrestrial, like the larva of the Australian aeshnoid species *Antipodophlebia asthenes* (Telephlebiidae) (Corbert 1999: 144). The long antennae might well be an autapomorphic adaptation to locate prey more easily on land.

Remarks. – A wing fragment of an adult Gomphaeschnidae in Baltic amber is present in the amber collection in Stuttgart with no. SMNS BB-2390 and could represent a potential imaginal stage of this larva (Bechly, in prep.).

Subordo Zygoptera Selys, 1854
Familia incertae sedis ("megapodagrionid" grade)

Specimen 2
Fig. 1; Pl. 2, Figs. 1a–d

Specimen no. MB.I.2225 in the amber collection Berendt in Berlin. It is labelled as "*Gomphus* sp.-Larve, Orig. zu Pictet & Hagen (1856), S. 78, 80, T.6, F.6, Baltischer Bernstein, coll. Berendt".

1848 *Gomphus resinatus*. – Hagen, p. 8 (nomen nudum, because without description).
1850 *Gomphus resinatus* Hagen, Nymphe. – Hagen in Selys-Longchamps, p. 358.
1852 *Gomphus resinatus* Hagen. – Giebel, p. 639.
1854 *Calopteryx* ?, Nymphenhaut. – Hagen, p. 227.
1856 *Libellula resinata*. – Giebel, p. 284.
1856 *Gomphus* (Larva). – Pictet in Pictet-Baraban & Hagen, p. 78, pl. 6, fig. 6 (first description).
1856 Agrionide. – Hagen in Pictet-Baraban & Hagen, p. 80, pl. 8, fig. 12 (supplementary description and detailed figure of the mask; the term „Larva" in the explanation of fig. 12 refers to *Agrion antiquum*).
1890 *Aeschna resinata* Hag. – Kirby, p. 168.
1908 *Calopteryx* ? (larva) Hagen. – Handlirsch, p. 896.
1908 *Gomphus resinatus* Hagen. – Handlirsch, p. 900.
1908 *Gomphus*-(larva) Hagen. – Handlirsch, p. 900.
1921 Calopterygidae, zweifelhafte Larve. – Handlirsch, p. 217.
1921 2 als *Gomphus* bezeichnete Formen. – Handlirsch, p. 217.
1942 Agrioniden-Larve 1. – Ander, p. 76. (considered *Gomphus resinatus* as a nomen nudum)
1957 *Gomphus* … have also been reported from Bavarian amber. – Fraser, p. 94.
1982 *Agrion spec.* Hagen in Berendt 1856, p. 80. – Keilbach, p. 209.
1982 *Gomphus* Larva Hagen in Berendt 1856, p. 80. – Keilbach, p. 209.
1982 *Gomphus resinatus* Pictet, 1856 in Berendt, p. 81. – Keilbach, p. 209.
1992 *Gomphus* Leach, 1815, p. 37. [Generic assignment of fossil (nymph) doubtful.] Hagen, 1848. – Carpenter, p. 81.
1992 *Calopteryx* Leach, 1815, p. 137. … Hagen, 1848, … . Oligo., Europe (Baltic), … – Carpenter, p. 87.
1992 Agrioniden-Larve 1. – Spahr, pp. 12–13.
1993 *Gomphus resinatus* Hagen, 1848. – Bridges, p. VII.196 (not treated as nomen nudum).
1993 A damselfly-larva (!) described by Hagen (1854) as *Calopteryx*. – Bechly, p. 14.
1993 A dragonfly larva (!), described by Hagen (1856) as *Gomphus*. – Bechly, p. 14.
1994 *Gomphus resinatus* Pictet, 1856 (in Berendt, 1856: 81) (d'après Keilbach, 1982) … Elle doit être considérée comme un Odonata Gomphidae (?) de position incertaine. – Nel & Paicheler, p. 57.
1994 *Gomphus* „larva" Hagen, 1856 (in Berendt) … Son attribution est très douteuse. – Nel & Paicheler, p. 57.

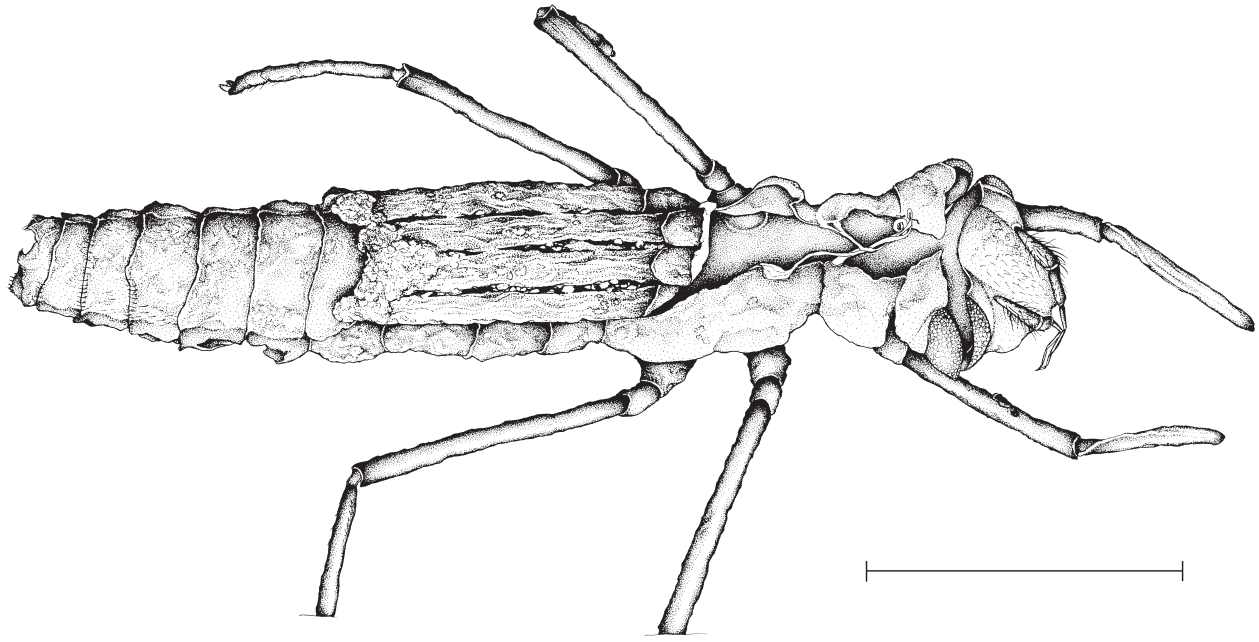

Fig. 1. Specimen 2 (Zygoptera: "megapodagrionid"); no. MB.I.2225, coll. BERENDT; male damselfly exuvia. – Scale: 5 mm.

1994 *Gomphus resinatus* HAGEN, 1848. – BRIDGES, p. VII.200 (not treated as nomen nudum).
1998 most probably an exuvia of a Coenagrionidea incertae sedis. – BECHLY, pp. 34–35.

Redescription. – This fossil damselfly nymph has widely split ecdysial sutures (Pl. 2, Fig. 1a) and thus represents an exuvia. The preserved part of the body is 16 mm long (head, thorax and abdomen, except the missing apex of the abdomen with the caudal gills). The antennae (Pl. 2, Fig. 1c) are 7-segmented with segments 1–4 being very elongate and about equally long, while segments 5–7 are very short. Segment 1 (scapus) and 2 (pedicellus) are much thicker than the remaining segments and furnished with numerous long hairs. The mask (Pl. 2, Fig. 1d) is flat and lacks setae. The apex of the prementum is bilobate (not just semicircular protruding as in many of the other amber larvae) and has a short median cleft. The legs are rather short (profemora 3.5 mm long, mesofemora 4.5 mm long, metafemora about 4.5–5 mm long), but the distal parts of the tibiae and all tarsi are missing (Pl. 2, Fig. 1b). All femora are laterally flattened.

Discussion. – The presence of a median swelling on the sternite of the 2nd abdominal segment, and of two swellings on the sternite of the 9th abdominal segment, clearly shows that this is a male specimen, as was already mentioned in the description of HAGEN in PICTET-BARABAN & HAGEN (1856: 80).

The figure of PICTET in PICTET-BARABAN & HAGEN (1856, pl. 6, fig. 6) is very imprecise, e. g. showing the tarsi although they are not preserved, and not showing the ecdysial sutures although they are clearly preserved in the fossil. According to BECHLY (1998) it seems rather unlikely that this exuvia was embedded at the original site of emergence, because the exuvia lacks all tarsi as well as the end of the abdomen with the caudal gills, so that this specimen is most likely an old exuvia that was blown (e. g. during a storm) into a blotch of resin and became embedded.

Based on a very brief study in 1996, BECHLY (1998) concluded in agreement with HAGEN in PICTET-BARABAN & HAGEN (1856: 80) that this inclusion most probably represents an exuvia of a Coenagrionoidea incertae sedis, but could neither confirm nor refute a conspecificity with *Platycnemis ? antiqua* (PICTET & HAGEN, 1856). Here we can clearly refute both attributions, because the type of mask with a distinct apical median cleft of the prementum shows that this exuvia cannot belong to the Coenagrionida (Pseudostigmatidae, Protoneuridae, Isostictidae, Platycnemididae, and Coenagrionidae). It rather represents a further taxon from the "megapodagrionid" grade basal of the coenagrionoid clade. Certainly it is not a Hypolestidae or Synlestidae, contrary to some other specimens described below.

Remarks. – Because this historic specimen showed significant signs of aging (cracks and reddish oxidation), which also hampered the visibility of the inclusion, we repolished this piece of amber and embedded it in a block of artificial resin for better protection, with friendly permission by the responsible curator Dr. C. NEUMANN from the Museum für Naturkunde in Berlin.

Specimen 3

Missing Zygoptera-larva in collection HAGEN.

1850 Agrion … Une petite nymphe, ou plutôt l'étui vide. – HAGEN in SELYS-LONGCHAMPS, p. 357.
1856 Eine unvollständige kleine Larve. – GIEBEL, p. 273.
1942 Agrioniden-Larve 2. – ANDER, p. 76.
1992 Agrioniden-Larve 2. – SPAHR, p. 13.
1998 Another Zygoptera-larva in collection HAGEN. – BECHLY, p. 56.

Remarks. – BECHLY (1998) reported that he could not find this specimen in the amber collections of the Museum of Comparative Zoology in Cambridge (laboratory of late F. M. CARPENTER), although most of the collection HAGEN is presently located in this institution. However, because GIEBEL (1856) described this specimen as an incomplete small larva, it cannot be totally excluded that this larva is identical with an incomplete specimen from the Königsberg amber collection described below (specimen 12), that is now deposited in Göttingen with the collection number GZG.BST.05504 (old no. III B 167).

Specimen 4

Missing odonata larva from the amber collection of the "physic.-oekonom. Gesellschaft zu Königsberg".

1830 *Libellula*. – BERENDT, p. 38. (the very first mention of fossil odonates in amber at all!)
1856 Libellen-Larve. – HAGEN in PICTET-BARABAN & HAGEN, p. 78.
1908 Odonata incertae sedis (Libellula) – BERENDT. – HANDLIRSCH, p. 904.
1942 Odonaten-Larve incert. sedis. – ANDER, p. 77 (this specimen might be identical with the specimen cited by HANDLIRSCH (1906–1908) as Odonata incertae sedis).
1992 Odonaten-Larve incert. sedis. – SPAHR, p. 12.
1993 A specimen classified by HANDLIRSCH as Odonata incertae sedis, was described by BERENDT (1830) as *Libellula* spec. – BECHLY, p. 14.
1998 an odonate 'larva' (certainly an exuvia) of uncertain affinities. – BECHLY, p. 56.

Remarks. – This specimen was indicated as missing by HAGEN in PICTET-BARABAN & HAGEN (1856: 78) with the comment "Auch eine Libellen-Larve im Bernstein, welche ich im älteren Inventar des Kabinets der physic.-oekonom. Gesellschaft zu Königsberg verzeichnet finde, fehlt gegenwärtig." ANDER (1942) considered it as probably lost. However, two damselfly larvae which are labelled as Libellulidae are present in the remains of the Königsberg amber collection in Göttingen (GZG, see specimens 12 and 15 described below). While one of these specimens is labelled as „*Gomphus* Larve", the other (GZG.BST.05504, old no. III B 167) is labelled as „Libelluliden-Larve" and therefore might represent this "missing larva". Consequently this larva could also be identical with specimen 3 described above.

Specimen 5
Pl. 2, Figs. 2a–b

Specimen no. Typ. Kat. Nr. 645 (SCHEELE nr. 1082) from the amber collection SCHEELE in Hamburg (GPIM). It is labelled as "Zygopteren-Larve, Zygoptera, gen. *Agrion* spec., *Platycnemis*?".

1958 *Platycnemis* ? *antiqua* ? – WEIDNER, p. 58, fig. 1
1996 Exuvie … Platycnemididae. – WICHARD & WEITSCHAT, p. 26.
1998 Zygoptera'larva'. – BECHLY, p. 57.

Redescription. – The length of the preserved part of the body is 13.0 mm, the wing pads are 4.1 mm long, and the head has a max. width of 4.16 mm. The elongate and basally narrowed mask (Pl. 2, Fig. 2b) is not very well visible (length 3.51 mm, max. width 2.43 mm, min. width 1.42 mm), but seems to have a semicircular projecting prementum that possibly lacks a median cleft. The antennae are not very well visible either (apparently only 5-segmented), but segments 2 and 3 are clearly the longest (segment 2 slightly longer than segment 3). The legs are relatively short (profemur 2.41 mm, protibia 3.27 mm, protarsus 1.37 mm, mesofemur 3.41 mm, metafemur 3.41 mm), but only the forelegs are completely preserved. The femora are laterally flattened. The apex of the abdomen with the caudal gills is not preserved.

Discussion. – This specimen was first mentioned and figured by WEIDNER (1958) who tentatively considered this Zygoptera "larva" as possibly belonging to Platycnemididae. According to WICHARD & WEITSCHAT (1996) it is not a true larva but represents an exuvia. This is clearly confirmed by the presence of widely split ecdysial sutures (Pl. 2, Fig. 2a).

However, since the larvae of all Coenagrionida (incl. Platycnemididae) have a prementum that is projecting as large triangle, an attribution of this specimen to Platycnemididae can be excluded with certainty. On the basis of the visible characters a safe attribution of this exuvia to any existing family is not possible, but most probably it belongs to the "megapodagrionid" grade.

Specimen 6
Figs. 2a–b; Pl. 3, Figs. 1a–c

Specimen no. 7513 in coll. CARSTEN GRÖHN in Glinde (Germany), donated by will to GPIM.

Description. – The fact that the ecdysial sutures on head and thorax are split and a part of the abdomen is detached (Pl. 3, Fig. 1a) shows that it is an exuvia (reconstructed length of preserved part, 10.8 mm). The apex of the abdomen and the caudal gills are missing. The legs are relatively short (metatibia 3.4 mm, metatarsus 1.36 mm). The head is 2.96 mm wide. The antennae are apparently

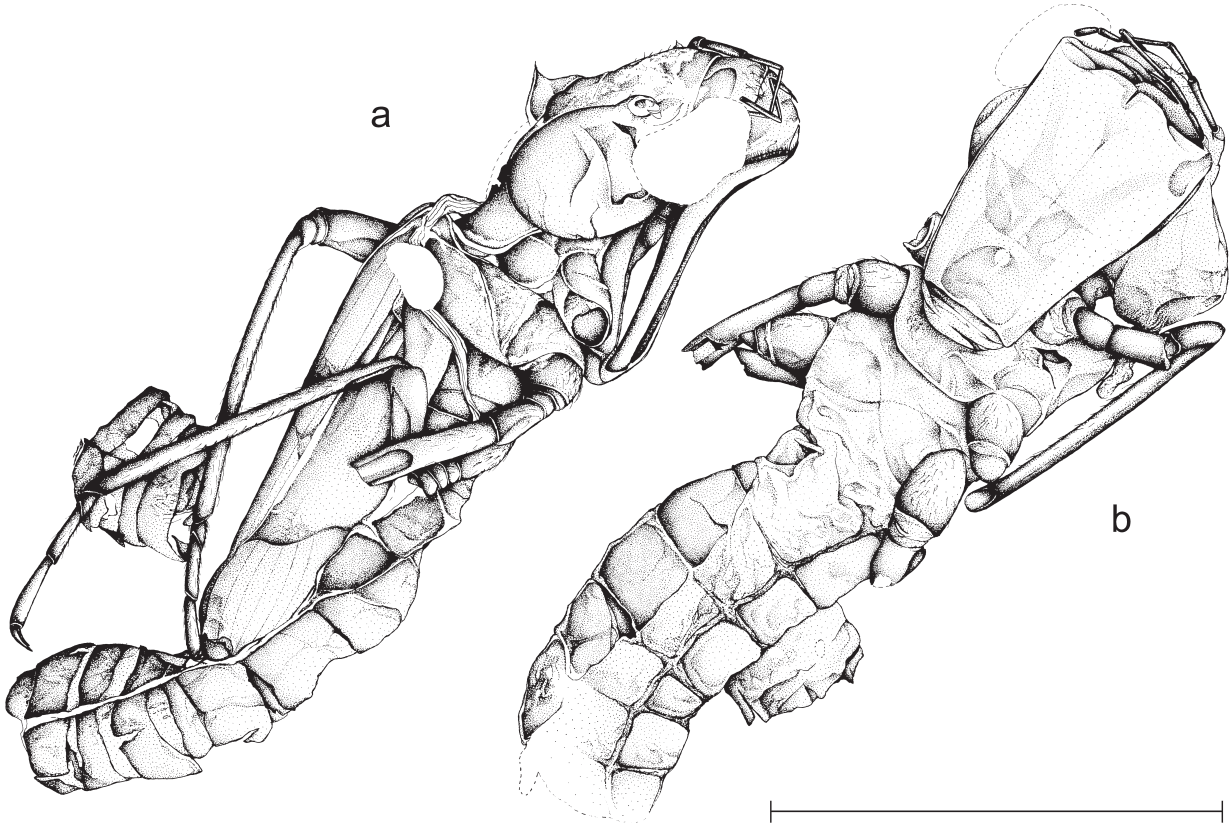

Fig. 2. Specimen 6 (Zygoptera: "megapodagrionid"); no. 7513 coll. GRÖHN; damselfly exuvia. – **a**. Lateral aspect; **b**. Ventral aspect. – Scale: 5 mm.

6 segmented (maybe 7-segmented), with segments 2, 3, and 4 being the longest. The mask (Pl. 3, Fig. 1c) is of the megapodagrionid type (length 3.19 mm, max. width 2.05 mm, min. width 1.15 mm), flat, without setae, and the elongate prementum is semicircular protruding, as well as slightly bilobate, with a very distinct apical cleft. The anterior margin of the prementum is furnished with a row of distinct denticles.

Discussion. – The row of premental denticles, the shape of the anterior margin of the prementum, and the elongate shape of the mask are differences to the other damselfly larvae described in this work and suggest the presence of a further undescribed species of the "megapodagrionid" grade.

Specimen 7
Pl. 4, Figs. 1a–b

Specimen without number in coll. CARSTEN GRÖHN in Glinde (Germany), donated by will to GPIM.

Description. – This damselfly larva has a very strange preservation (Pl. 4, Fig. 1a): There are no ecdysial sutures visible on head and thorax, thus it seems to be a larva rather than an exuvia at first sight. However, the abdomen is completely flattened and destroyed, and its apex with the caudal gills is missing. Probably this specimen represents the food remains from a predator or from ants. The head is 2.5 mm wide. Unfortunately, the mask is not well visible from below, but it might possess a median cleft. The antennae are not very well visible either (Pl. 4, Fig. 1b), but are 6-segmented with a short segment 1 (scapus), a very long segment 2 (pedicellus) which is as long as segments 3 and 4 together, followed by three equally long segments 3–5, and a very short ultimate segment 6. The legs are incompletely preserved, except for the right foreleg (profemur 2.9 mm, protibia 3.3 mm, protarsus 1.3 mm).

Discussion. – A determination of this specimen is not possible with the available characters.

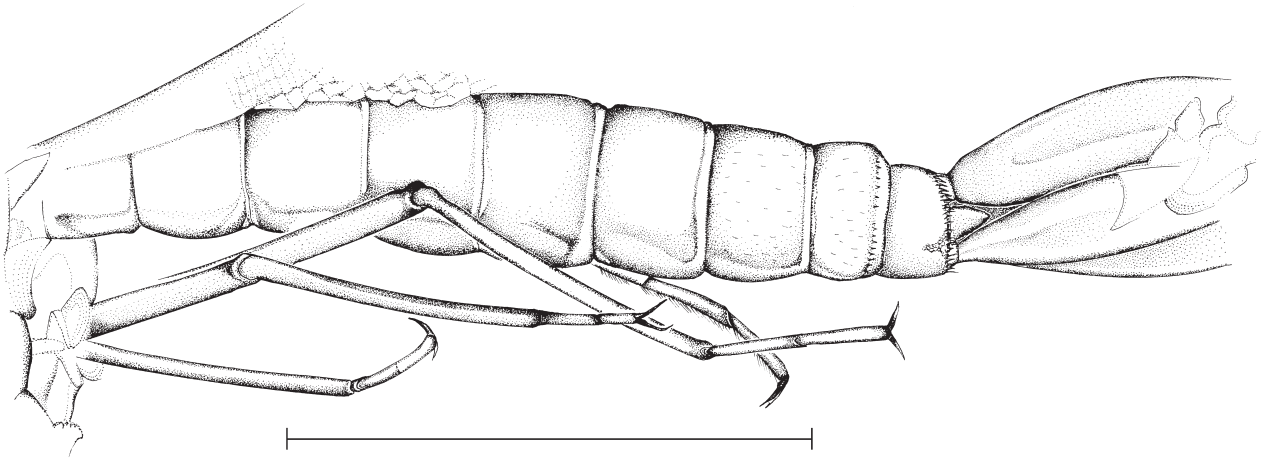

Fig. 3. Specimen 8 (Zygoptera: Lestinoidea incertae sedis); no. Bi 3801, coll. LUDWIG; damselfly exuvia (Lestida?). – Scale: 5 mm.

Superfamilia Lestinoidea CALVERT, 1901
(sensu FRASER 1957)
Familia incertae sedis

Specimen 8
Fig. 3; Pl. 4, Figs. 2a–b

Specimen no. Bi 3801 in coll. WALTER LUDWIG in Berlin (Germany).

Description. – This inclusion (total length 13.2 mm) obviously represents an exuvia of a damselfly larva. The abdomen is completely preserved (length 8.9 mm + 2.9 mm gills), but head and thorax are missing. Of the thorax only a part of the wing pads and four legs are preserved (Pl. 4, Fig. 2a). One hind leg is completely preserved (metafemur 3.24 mm, metatibia 3.53 mm, metatarsus 1.55 mm). The lack of an ovipositor shows that this is a male specimen. The caudal gills are foliate with a lateral midrib (Pl. 4, Fig. 2b), but the most distal part of the gill plates is broken off. However, the posterior curvature of the gill plate margins shows that not much of the gills can be missing.

Discussion. – There are no details preserved that would allow a save attribution on the family level, but the relatively long abdomen and the apparently short and foliate caudal gills that are held in vertical position resemble the larvae of Lestida or lestinoid damselflies (Perilestidae, Synlestidae, Megalestidae, and Lestidae), even though a coenagrionoid relationship cannot be excluded either. The relatively short legs and the much smaller dimensions exclude a specific identity with the synlestid specimen 9 described above.

Remarks. – Besides the two adult synlestid specimens mentioned in this publication, there also is a still undescribed adult Lestidae from Baltic amber in the private collection BUSCHE (Hamburg, Germany) with no. 109, and it is even more plesiomorphic in one character (area between IR2 and RP3/4 not widened) than all Recent Lestidae (BECHLY, in prep.).

The here described exuvia represents the only known odonate larva from the Bitterfeld amber outcrops in Saxonia, Germany! However, most specialists meanwhile agree that the Bitterfeld amber most probably is no autochthonous amber of Miocene origin, as was earlier believed, but only represents redeposited Baltic amber (WEITSCHAT 1997).

Familia Synlestidae TILLYARD, 1917

Specimen 9
Fig. 4; Pl. 5, Figs. 1a–d

Specimen no. SMF VI 1332 in Frankfurt a. M., labelled "Larve von 324, Libelle (Odonata), Slg. SAULIUS".

2002 Dicteriadidae (= Heliocharitidae) larva. – WEITSCHAT & WICHARD, p. 94, fig. 45.

Description. – Even though the dorsal side of this damselfly larva is concealed with white clouded substance (Pl. 5, Fig. 1a), it is well visible that the larva is still closed and thus does not represent an exuvia. The end of the abdomen with the caudal gills is missing (length of preserved part of larva, 16.5 mm). The very long and slender legs (Pl. 5, Fig. 1b) are similar to the Recent families Dicteriadidae and Synlestidae. The lengths of the leg segments are: profemur 4.15 mm, protibia 5.21 mm, protarsus 1.70 mm; mesofemur 5.0 mm, mesotibia 5.45 mm, mesotarsus not preserved; metafemur 6.22 mm, metatibia 7.06 mm, metatarsus 1.41 mm. There are no strong spines on the apex of the femora. The head is 3.86 mm wide. The lengths of the antennal segments are: 1st (scapus) 2.0 mm, 2nd (pedicellus) 0.87 mm, 3rd 0.53 mm, 4th 0.37 mm, 5th 0.21 mm, 6th 0.17 mm, and 7th (ultimate) 0.12 mm. The

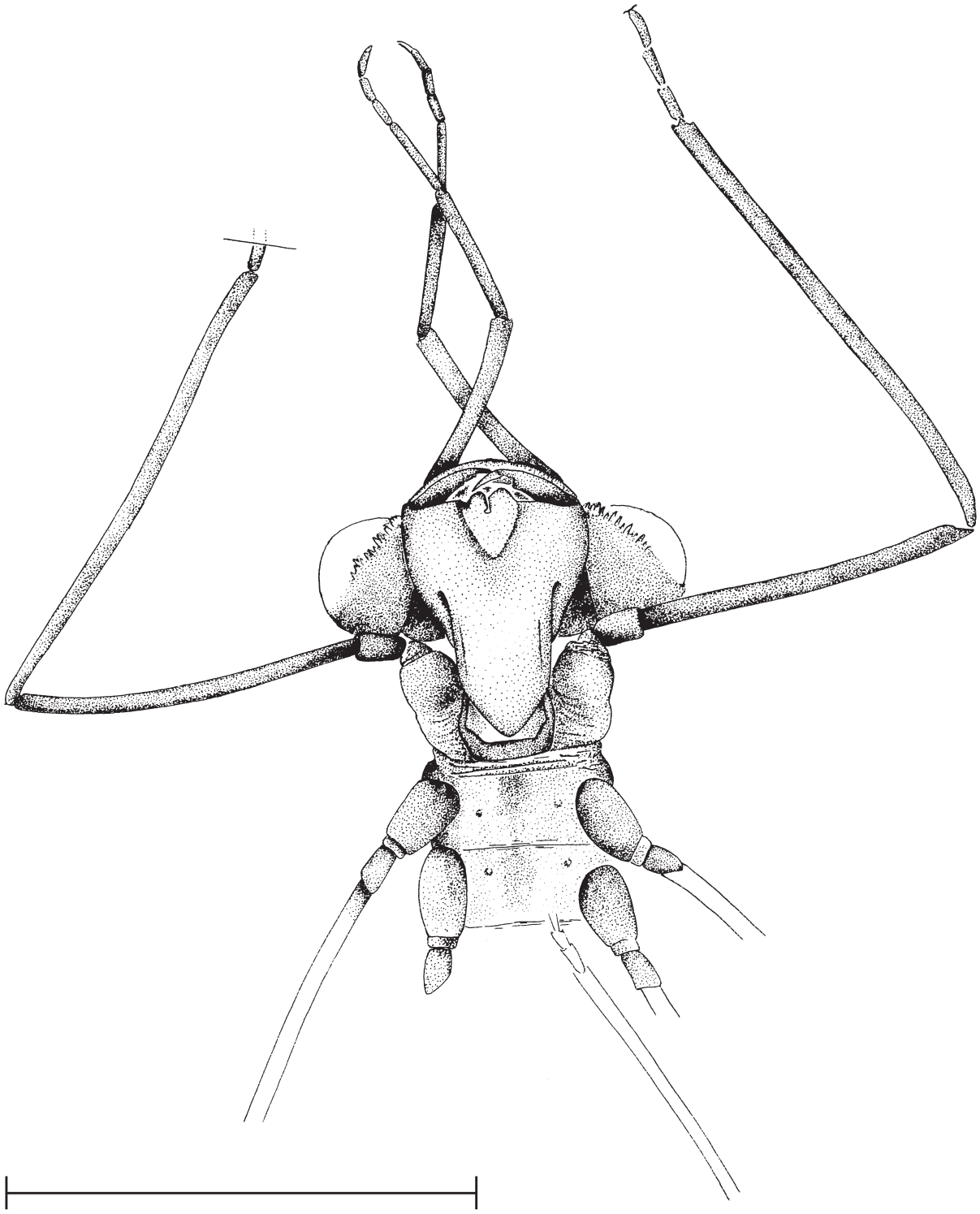

Fig. 4. Specimen 9 (Zygoptera: Synlestidae); no. SMF VI 1332 (coll. SAULIUS, no. 324); damselfly larva; ventral aspect. – Scale: 5 mm.

mask is of the megapodagrionid type (length 3.8 mm, max. width 2.83 mm, min. width 1.41 mm), flat, without setae, and with a strongly bilobate apex (length of protruding lobes 0.2 mm) of the prementum with a distinct median cleft that is 0.3 mm long (Pl. 5, Fig. 1c).

Discussion. – The very much elongated 1st segment

(scapus) of the antennae (Fig. 4; Pl. 5, Fig. 1b) is similar to the families Dicteriadidae and Synlestidae (and Calopterygidae) as well, and does not occur in any other families (in Synlestidae it is characteristic for the genus *Synlestes* only). The bilobate mask is very different from Dicteriadidae and Calopterygidae, but is typical for Synlestidae. Consequently, this larva most probably represents a Synlestidae close to the Recent relict genus *Synlestes* from Australia.

There is only one potentially conflicting character: beneath the antero-ventral margin of the left compound eye there is a row of spines visible (Pl. 5, Fig. 1d), of which the longest spines reach a length 0.125 mm. Such a row of strong spines shall represent a putative synapomorphy of the Recent genera *Diphlebia* SELYS and *Philoganga* KIRBY that have been included in a common family Diphlebiidae by BECHLY (1996a). The large size of the larva would also agree with the very large size of the Recent diphlebiids *Diphlebia* and *Philoganga*. Furthermore, an isolated pair of wings (length of preserved part of wing 28.5 mm) of a possible adult Diphlebiidae from Baltic amber (Pl. 7, Fig. 1) was acquired from coll. W. LUDWIG and is deposited at the SMNS (collection number SMNS BB-2389). It is still undescribed and is definitely different in venation from the amber amphipterygoid *Pamita hannahdaltonae* described by MAY & CARLE (2005), which probably is not an Amphipterygidae s. str. either, as is suggested by its rectangular discoidal cell. However, the undescribed specimen from coll. LUDWIG might also belong to another taxon of the "amphiterygoid complex" of damselflies like Thaumatoneuridae (incl. Dysagrioninae). It could even be conspecific with *Electrophenacolestes serafini* recently described by NEL & ARILLO (2006), which has a very similar dimension and wing venation, except for the origin of IR2 that is basal of the subnode, while it is distal of it in the SMNS specimen.

Remarks. – The detached foliate structure near the posterior abdomen of this specimen (Pl. 5, Fig. 1a) does not seem to be a caudal gill plate but rather a leaf of a plant, because it is too large, the "root" is distinctly bent, and the ventral surface structure is more plant-like (the dorsal surface is concealed by white clouded substance). If this structure should nevertheless be a detached gill plate, it would confirm the attribution to Synlestidae rather than the other options (Diphlebiidae or Dicteriadidae).

Two adult specimens of a still undescribed synlestid species (one wing fragment in private collection STASIULEWICZ (Pl. 5, Fig. 2), and a piece with a complete pair of wings in coll. SMNS with no. BB-2391) have also been found in Baltic amber (BECHLY, in prep.) and corroborate the presence of this taxon.

Superfamilia Calopterygoidea SELYS, 1850
Familia Calopterygidae SELYS, 1850

Specimen 10
Figs. 5a–b; Pl. 6, Figs. 1a–d

Specimen no. SMNS BB-2387 (ex coll. WUNDERLICH) in Stuttgart.

Description. – The ecdysial sutures in the dorsal thorax are widely split (Pl. 6, Fig. 1a), thus it is an exuvia. Head and body of this fossil damselfly exuvia have a total length of 13.8 mm. The wing pads are 4.7 mm long. Only the right fore- and midleg as well as the caudal gills are missing (Pl. 6, Fig. 1a). The head is 3.48 mm wide. One antenna is well visible (Pl. 6, Fig. 1b) and has three distinct segments (but the apex seems to be subdivided in further segments), of which the first is very strong and longer than all the other segments together (1st segment 1.87 mm, 2nd segment 0.78 mm, remaining segments 0.82 mm). The mask of this larva is 3.69 mm long and has a very deep and very wide (max. width 0.5 mm) rhomboid median cleft (Pl. 6, Fig. 1c), and is of the typical, unique and apomorphic shape of the calopterygid larval labium.

Discussion. – The shape of the median cleft resembles the derived structure in Calopteryginae much more than in the Neotropical subfamily Hetaerininae. The larva of Dicteriadidae, the putative sistergroup of Calopterygidae, still has a much smaller median cleft, and the larva of the most basal calopterygid subfamily Caliphaeinae seems to be still unknown, but most probably has a less developed median cleft as well. Therefore, this amber larva can be safely attributed to the jewelwing family Calopterygidae and even to the Recent subfamily Calopteryginae.

This larva has some further remarkable features: the posterior margin of the head has an unusual and distinct shape (Pl. 6, Fig. 1b); the abdominal segments 7–9 are armoured with distinct strong spines, and on the ventro-lateral side of segment 9 there are 2 strong triangular, spine-like projections (Pl. 6, Fig. 1d); the legs are very long and slender (right hind leg: trochanter and femur 6.5 mm, only femur 5.4 mm, tibia 6.57 mm, tarsus 1.49 mm). These features are also found in the larvae of many species of Recent Calopterygidae.

Remarks. – An undescribed isolated pair of wings (Pl. 6, Fig. 2) of an adult Calopterygidae in Baltic amber, that confirms the presence of this family in Baltic amber forest, was acquired from coll. DAMZEN and is deposited at the SMNS (collection number SMNS BB-2388).

A quite similar calopterygid exuvia from Baltic amber in coll. SERAFIN (Poland) will be described by FLECK et al. (submitted).

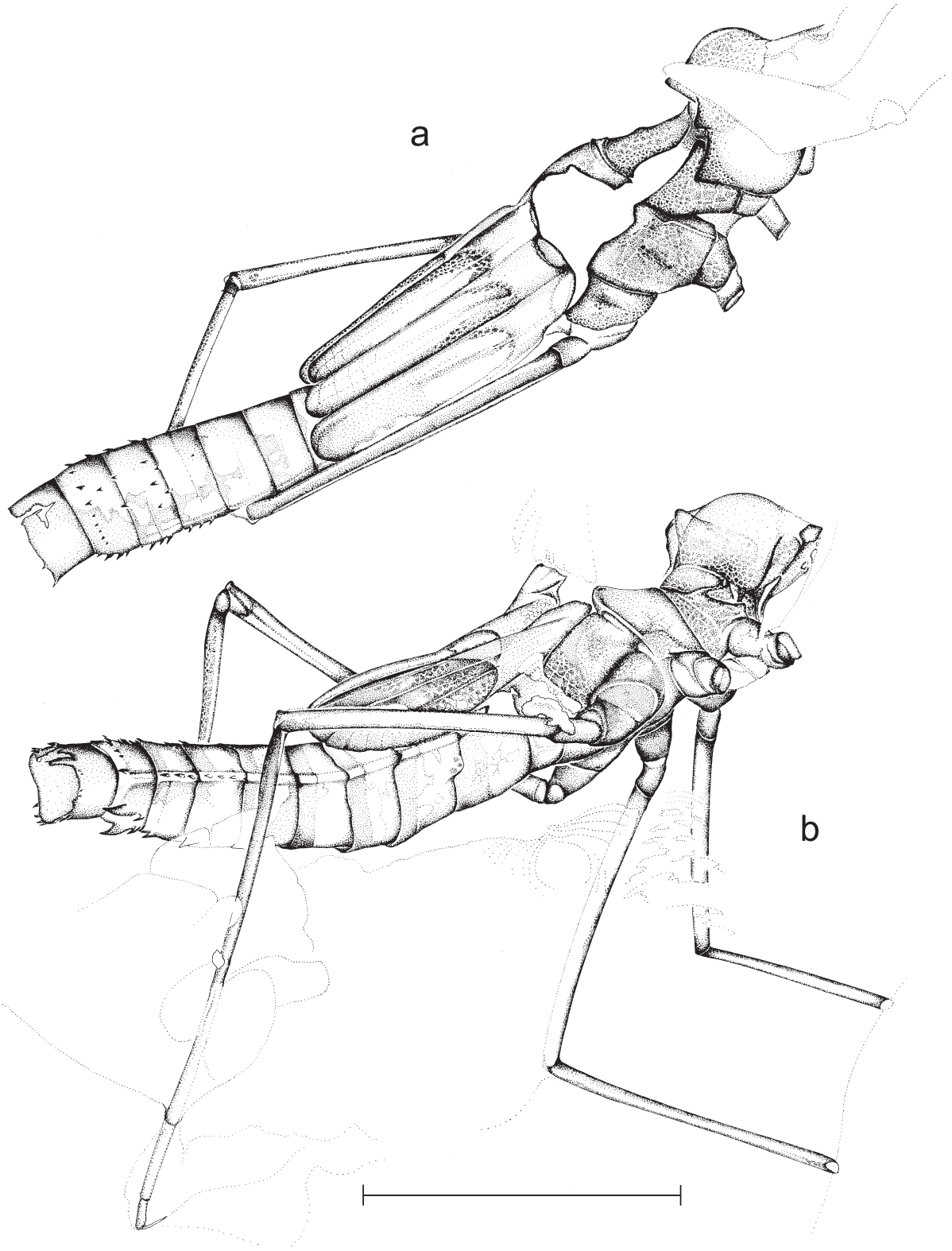

Fig. 5. Specimen 10 (Zygoptera: Calopterygidae); no. SMNS BB-2387 (ex coll. WUNDERLICH); calopterygid exuvia. – **a**. Dorsal aspect. **b**. Lateral aspect. – Scale: 5 mm.

Familia Megapodagrionidae CALVERT, 1913
Subfamilia Argiolestinae FRASER, 1957

Specimen 11
Pl. 3, Figs. 2a–c

Specimen no. 1639 in coll. ACHIM HERRLING in Bramsche (Germany) (ex coll. JONAS DAMZEN in Vilnius (Lithuana)).

Description. – This piece of amber shows a damselfly larva (total length 19.3 mm) in ventral aspect, which is more or less covered with white clouded substance (in German: "Verlumung" or "Verflohmung") (Pl. 3, Fig. 2a), so that no details of the mask are visible. The later effect is characteristic for Baltic amber inclusions and suggests that the larva was still wet, when it was embedded in the blotch of resin. The apical parts of the caudal gills (length about 5 mm) of the larva are broken off. The larva was a female specimen, because an ovipositor anlage is clearly visible (Pl. 3, Fig. 2c). The legs are relatively short, compared to the body length.

The same piece of amber also includes the distal halves of a right pair of wings and leg fragments of an adult damselfly (Pl. 3, Fig. 2b). Therefore, the larva might represent an exuvia, even though the dorsal side is invisible, thus it cannot be seen if the ecdysial sutures are split. Even if the larva would still be "filled", as is suggested by its shape and the "Verlumung", it would be rather likely that the adult specimen belongs to the same taxon, and the common embedding resulted from a common emergence of several conspecific specimens.

Discussion. – The larva has the typical morphology of a megapodagrionid argiolestine larva, with a rather stout body and all three gills held in horizontal plane (Pl. 3, Fig. 2c). The latter character is a unique autapomorphy of Megapodagrionidae. The slightly inflated caudal gill plates with distinct carinae are known from several Recent Argiolestinae (see LIEFTINCK 1976), e. g. *Caledargiolestes uniseries* (RIS, 1915). Also the general habitus of the larva is very much like Argiolestinae. Quite similar triquetral gills are known from some species of the Recent American coenagrionid genus *Argia*, but this genus has a very different wing venation than the wings preserved in the same piece of amber. These distal wing fragments (Pl. 3, Fig. 2b) clearly belong to a megapodagrionid damselfly, and the widened area between the veins RP1 and RP2 and the shape of IR1 agree with an attribution to Argiolestinae.

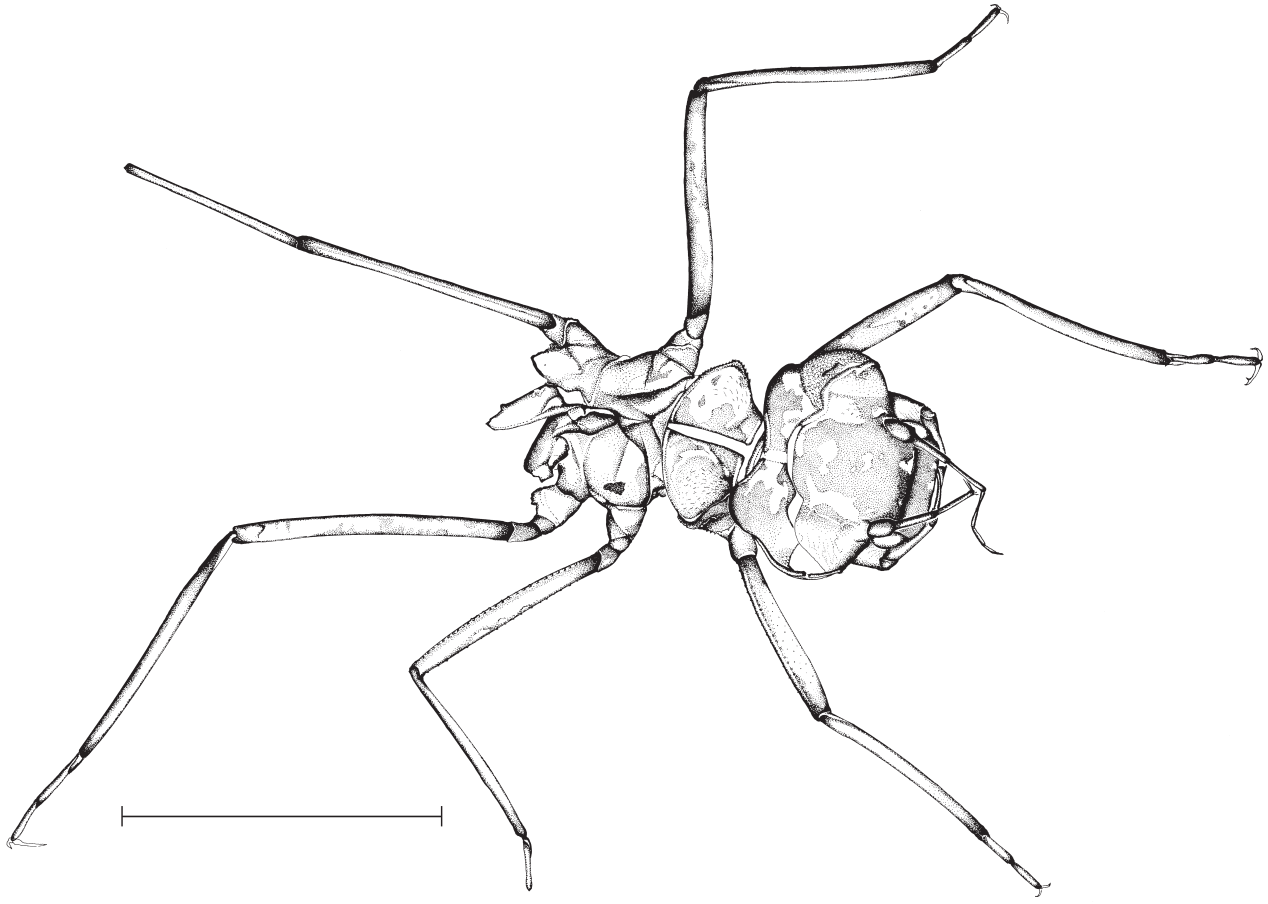

Fig. 6. Specimen 12 (Zygoptera: Hypolestidae); no. GZG.BST.05504; damselfly exuvia fragment. – Scale: 5 mm.

Familia Hypolestidae Tillyard & Fraser, 1938
Subfamilia Hypolestinae Tillyard & Fraser, 1938
Tribus Hypolestini Tillyard & Fraser, 1938

Specimen 12
Fig. 6; Pl. 7, Figs. 2a–c

Specimen no. GZG.BST.05504 (old no. III B 167) in Göttingen, labelled "B. S. d. Univers., Fam. Libellulidae, Gen. Libelluliden-larve, Koenigsberg i/Pr, V. 7". This specimen might be identical with either specimen 3 or specimen 4 mentioned above, or even with both.

Description. – This piece of amber is mounted in Canada balm on a microscope slide (Pl. 7, Fig. 2a). The inclusion shows only head, thorax, and legs of a damselfly larva; the abdomen is completely missing. Both sides of the inclusion are well preserved and perfectly visible in very clear amber. The ecdysial sutures are split (Pl. 7, Fig. 2b), thus it is an exuvia. Head and thorax are 6 mm long. The mask (Pl. 7, Fig. 2c) is of the megapodagrionid type, flat, without setae, the prementum semicircular protruding with an apical cleft. Beneath the ventral margin of the compound eyes there is a serration that is developed as small row of spines in the anterior portion. The 7-segmented antennae are relatively short (much shorter than in specimen 9), with segments 2, 3 and 4 being the longest (Pl. 7, Fig. 2b). The legs are distinctly shorter than in specimen 9 as well (profemur 3 mm long, mesofemur 4 mm long, metafemur 4.3 mm long; protibia 3.2 mm long, mesotibia 3.5 mm long, metatibia 4.5 mm long).

Discussion. – According to the preserved characters of antennae and mask, this animal might belong to the Recent family Hypolestidae (see chapter 3.1).

Specimen 13
Figs. 7a–b; Pl. 8, Figs. 1a–b

Specimen no. 490 in coll. Achim Herrling in Bramsche (Germany).

2004 Fangmaske einer Libellenlarve. – Wichard & Weitschat, p. 128, fig. without no.

Description. – An isolated mask of a damselfly (max. width 2.47 mm), which is very well visible from the dorsal (Pl. 8, Fig. 1a) and ventral (Pl. 8, Fig. 1b) side in a clear piece of amber. This mask is of typical megapodagrionid type, flat, and without any setae. The prementum is anteriorly semicircularly protruding with a distinct apical median cleft. The labial palps have three teeth, of which the median one is the longest, and a very long movable hook.

Discussion. – Even though such a type of mask is known from various taxa of the "megapodagrionid" grade, it perfectly agrees with the mask of the Recent genus *Hypolestes* of the family Hypolestidae.

Specimen 14
Figs. 8a–b; Pl. 9, Figs. 1a–e

Specimen no. SMNS BB-2386 (ex coll. W. Ludwig) in Stuttgart.

1998 probably Platystictidae or Megapodagrionidae. – Bechly, pp. 34–35, 57, figs. 1–4.

Redescription. – This unique inclusion shows a damselfly embedded during the process of emergence (Pl. 9, Fig. 1a), with the apex of the abdomen still concealed in the exuvia (Pl. 9, Fig. 1b), which is also completely preserved (Pl. 9, Fig. 1c). Unfortunately, the wings of the specimen were not yet unfolded (Pl. 9, Fig. 1b), so that the wing venation is completely invisible. The exuvia has a body length of 11.4 mm plus 5.7 mm length of the caudal gills. The head of the exuvia is only 2.8 mm wide, even though the head of the imago is 4.53 mm wide. The larval mask (Pl. 9, Fig. 1d) is of typical megapodagrionid type (length 2.68 mm, max. width 1.94 mm, min. width 0.99 mm), flat, without setae, the prementum is semicircularly protruding with a median cleft, and the labial palps possess three teeth of which the median one is the longest. The antennae are 7-segmented, with segments 2 and 3 being the longest. The larva has a well-developed ovipositor, thus it is a female specimen. The caudal gills are detached from the body and have a saccoid shape (3.3 mm long) with 2.4 mm long apical filaments (Pl. 9, Fig. 1e). The legs are completely preserved and folded under the body of the exuvia (profemur 1.78 mm, protibia 2.38 mm, protarsus 0.99 mm; mesofemur 2.47 mm, mesotibia 2.6 mm, mesotarsus 1.0 mm; metafemur 3.06 mm, metatibia 3.15 mm, metatarus 1.16 mm).

Discussion. – The presence of so-called "clouded white substance" around parts of the damselfly (Pl. 9, Fig. 1a) and the presence of stellate hairs is typical for genuine Baltic amber and clearly excludes a forgery of this remarkable fossil. The combination of characters suggests that this animal belongs to the family Hypolestidae (see chapter 3.1).

Specimen 15
Fig. 9; Pl. 7, Fig. 3

Specimen no. GZG.BST.05505 (old no. G 4.562) in Göttingen, labelled "B. S. d. Univers., Fam. Libellulidae, Gen. *Gomphus* Larve, Koenigsberg i/Pr".

Description. – This piece of amber is also mounted in Canada balm on a microscope slide (Pl. 7, Fig. 3). It shows a completely preserved damselfly larva in lateral aspect. Obviously the imago was just emerging, because the thorax is already very much swollen and on the verge of rupturing the larval skin. The body is 16.5 mm long, plus 6.5 mm of the caudal gills, which are saccoid with an

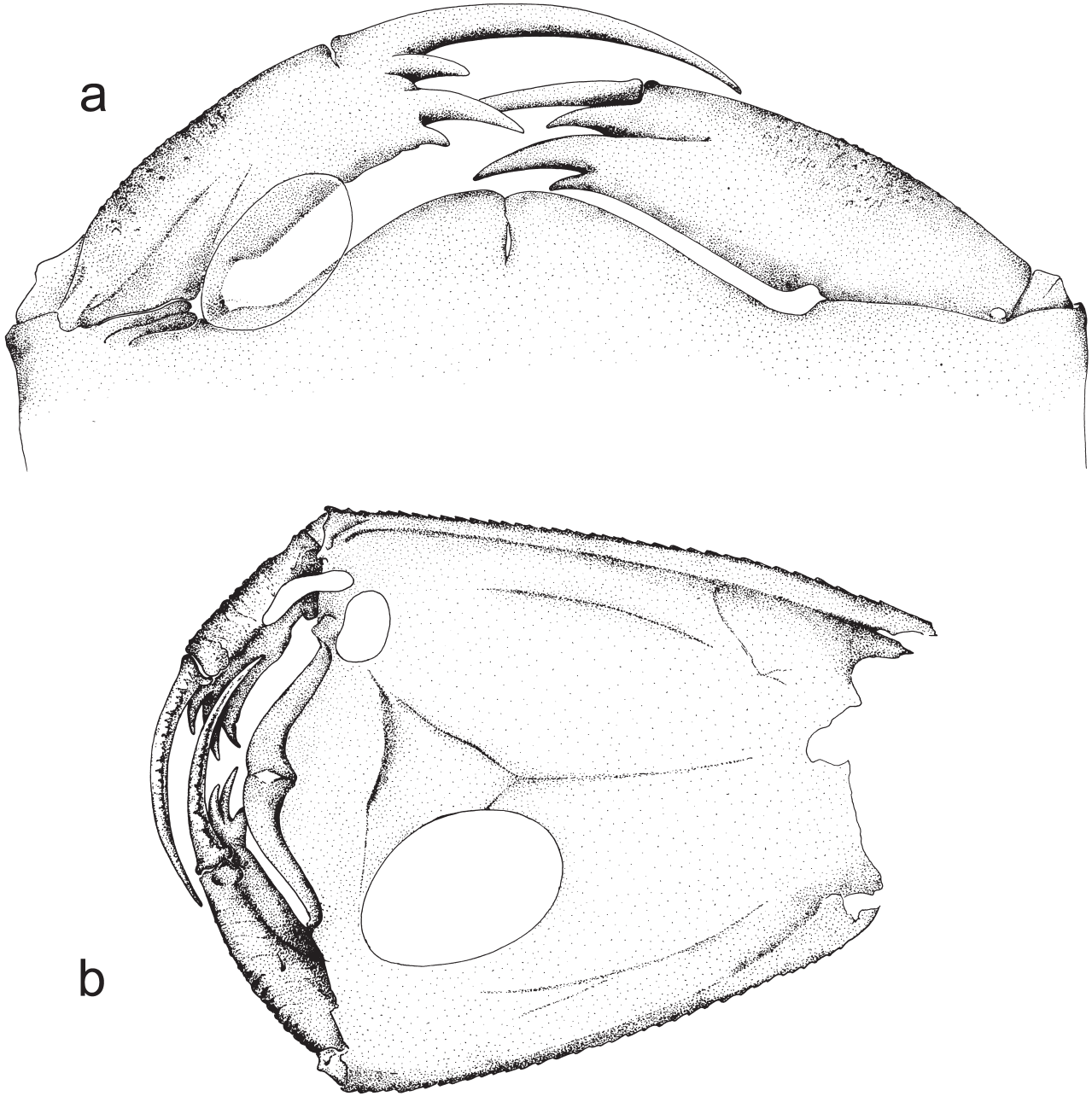

Fig. 7. Specimen 13 (Zygoptera: Hypolestidae); no. 490, coll. HERRLING; isolated mask of damselfly exuvia (max. width 2.47 mm). – **a**. Prementum and palps in ventral aspect. **b**. Complete mask in dorsal aspect. – Without scale.

apical filament. A distinct ovipositor shows that it is a female specimen. The antennae are not very well visible, but have 7 segments, of which segments 2 (pedicellus), 3, and 4 are the longest, while segments 1, 5 and 6 are distinctly shorter, and segment 7 is tiny. Unfortunately, due to the preparation as microscope slide, the prehensile mask is not visible from below, but it is clearly flat and of megapodagrionid shape. Beneath the anterior part of the ventral margin of the compound eyes there is a serration or small row of spines. The legs are not very long and slender (length of metafemur 6.0 mm), and the tarsi have well-developed „cleaning brushes".

Discussion. – This specimen is a further putative Hypolestidae (see chapter 3.1).

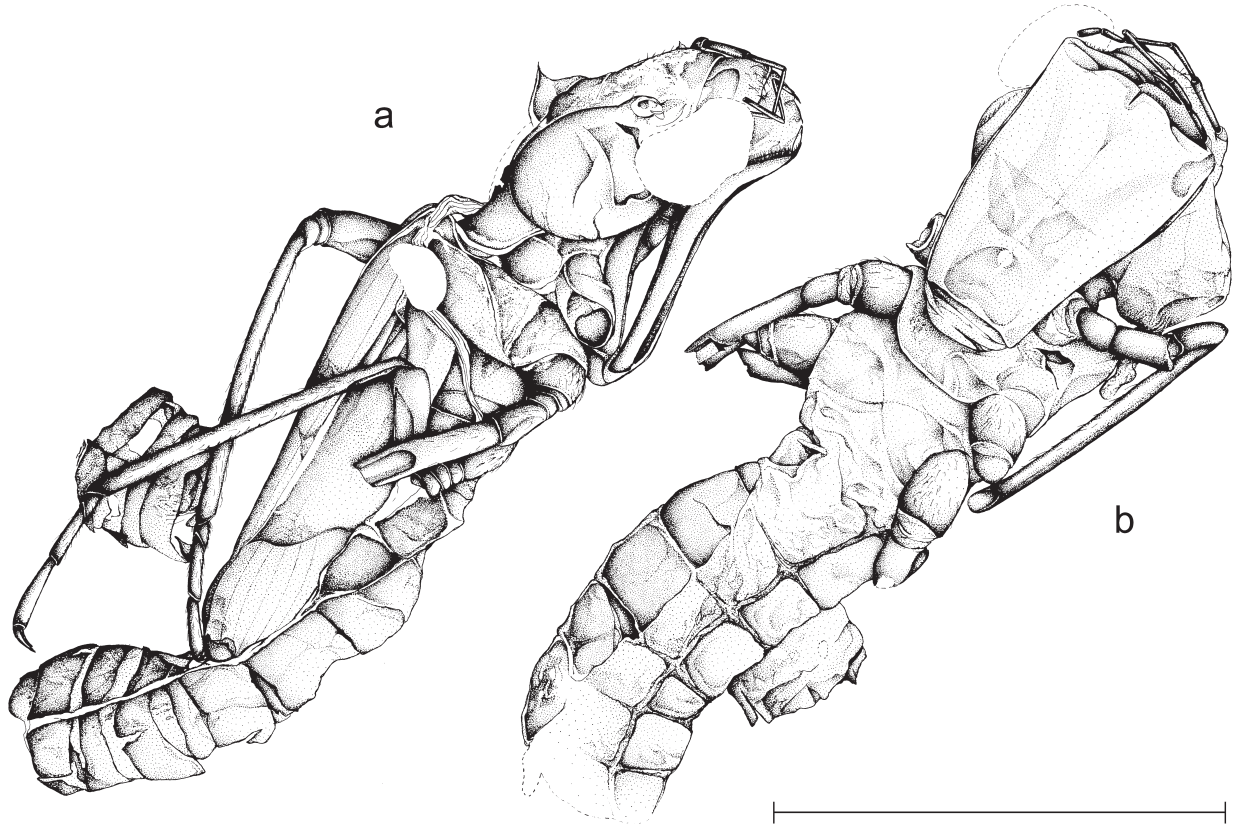

Fig. 8. Specimen 14 (Zygoptera: Hypolestidae); no. SMNS BB-2386 (ex coll. Ludwig); emerging imago and exuvia. – **a**. Lateral aspect. **b**. Ventral aspect. – Scale: 5 mm.

Specimen 16
Fig. 10; Pl. 8, Figs. 2a–b

Specimen no. 6902 in coll. Carsten Gröhn in Glinde (Germany), donated by will to GPIM.

Description. – This piece of amber includes a complete exuvia (body length 14.9 mm without gills) of a damselfly, as well as fragments (wing base, distal part of abdomen, and two tarsi of which the paired claws possess an apical tooth) of an adult male damselfly (Pl. 8, Fig. 2a). The wing fragment is still partly crumpled (the apparently acute cell is not the discoidal cell, but only an artefact!) (Fig. 10), indicating that it resulted from an incomplete emergence. Consequently, the exuvia and imago most probably belong to the same animal. Unfortunately, the imaginal remains do not show any important characters except on the abdomen, with two pairs of long claspers (the lower claspers are slender and the upper claspers are partly flattened), the primary male genital flaps, and the ligula of the secondary genital apparatus (Fig. 10).

The larva has saccoid caudal gills (length 3.6 mm) with a very long terminal filament (length 2.7 mm) that is gradually originating from the gill corpus (Pl. 8, Fig. 2b). The gills have been partly deflated during emergence. The wing pads are 5.7 mm long. Only the femora of the legs are well visible (profemur 2.29 mm, mesofemur 3.11 mm, metafemur 4.0 mm). The antennae are not visible, and the mask is not well visible either.

Discussion. – A save determination of the family is not possible with the few available characters. Nevertheless, it is quite possible that this animal represents a Hypolestidae as well (see chapter 3.1), just like specimen 14 described above.

3.1 Taxonomic significance of saccoid caudal gills

In three of the here described damselfly larvae from Baltic amber (specimens 14, 15, and 16) there are saccoid caudal gills preserved (Pl. 7, Fig. 3; Pl. 8, Fig. 2b; and Pl. 9, Fig. 1e), that are not known from the modern damselfly fauna of Middle and Northeastern Europe.

Recent damselfly larvae with saccoid caudal gills are known from the families Amphipterygidae, Diphlebiidae, Euphaeidae, Polythoridae, some Megapodagrionidae s. str., Platystictidae: Palaemnematinae, and a few Coen-

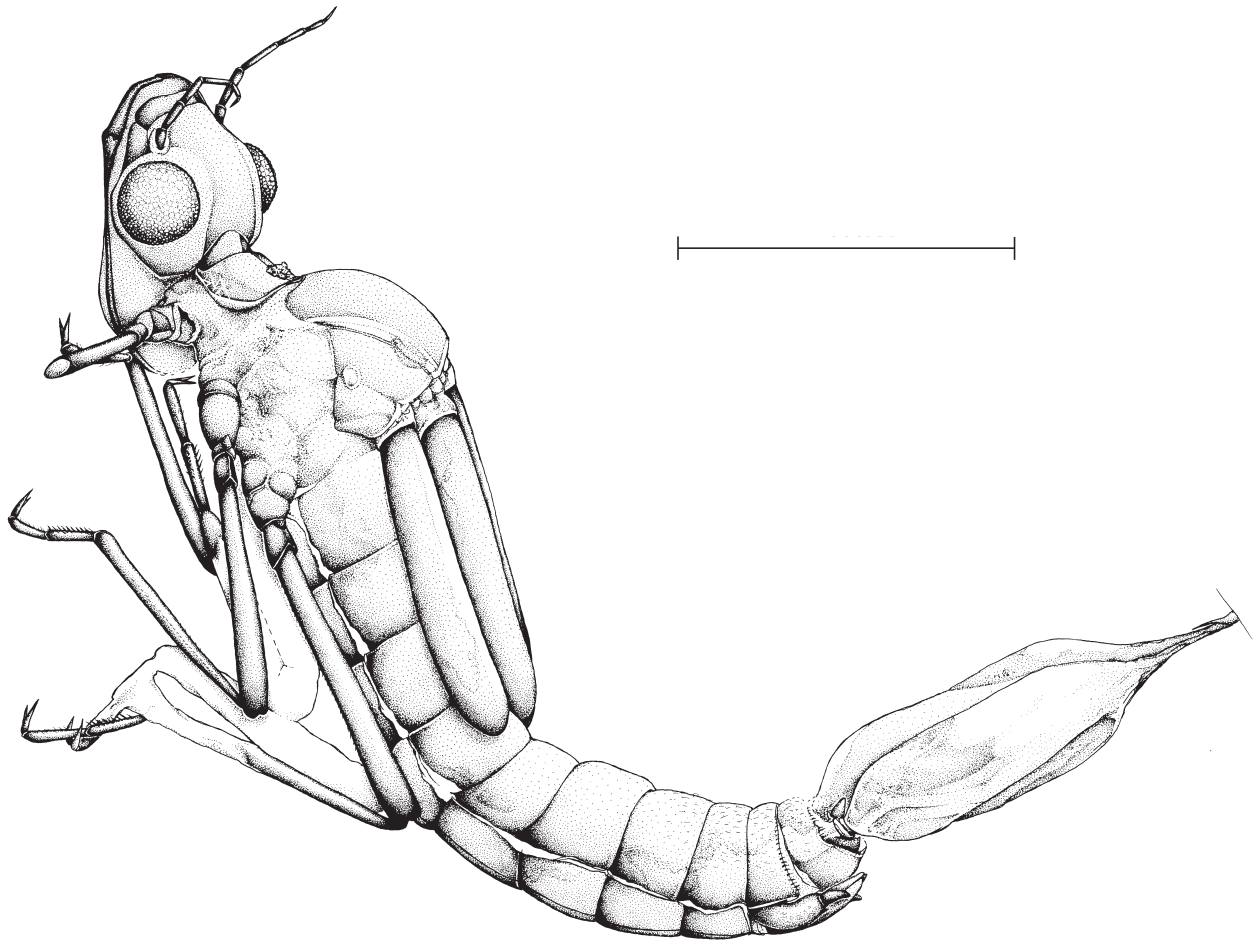

Fig. 9. Specimen 15 (Zygoptera: Hypolestidae); no. GZG.BST.05505; damselfly larva. – Scale: 5 mm.

agarionoidea s. str. (e. g. some Protoneuridae: Isostictinae, and some species of the Hawaiian endemic coenagrionid genus *Megalagrion*). Amphipterygidae can be excluded because of a totally different shape of their spine-like gills combined with the presence of unique gill tufts. Diphlebiidae can be excluded because they possess a very distinct row of strong spines beneath the ventral margin of the compound eyes (probably a synapomorphy of *Diphlebia* and *Philoganga*) that are absent in the fossil larvae (with possible exception of the specimen 9). Euphaeidae and Polythoridae can be excluded because they both posses lateral abdominal gills that are absent in all of the here described amber fossils. Furthermore, Polythoridae can be excluded because of a very different and unique shape of the swollen caudal gills with 3–6 finger-like projections. All lestinoids (incl. the basal groups Hemiphlebiidae, Chorismagrionidae, and Synlestidae) still have an apical median cleft retained in the prementum of the larval mask, but they can be excluded because they always posses flat and foliate caudal gills (synlestids also have a much deeper apical cleft). Those few coenagrionoids that do possess saccoid caudal gills can all be excluded, because they possess a very different and more derived type of mask with an triangular protruding prementum that has neither a bilobed apex nor an apical median cleft retained. Isostictinae can also be excluded because they possess a unique type of bipartite caudal gills that are divided into two parts by a constriction. Coenagrionida and Lestidae can be excluded because they all have prominent and large setae on the larval mask (even on the movable hook in Lestidae), that are absent in the concerning fossils. Platystictidae (Palaemnematinae) do not possess such setae and still have a median cleft retained, but have an autapomorphic very different shape of the prementum, which has its maximum width basal of the labial palps. This leaves the pantropical family Megapodagrionidae and the family Hypolestidae. Within Megapodagrionidae the subfamily Argiolestinae can be excluded, because they possess a distinct

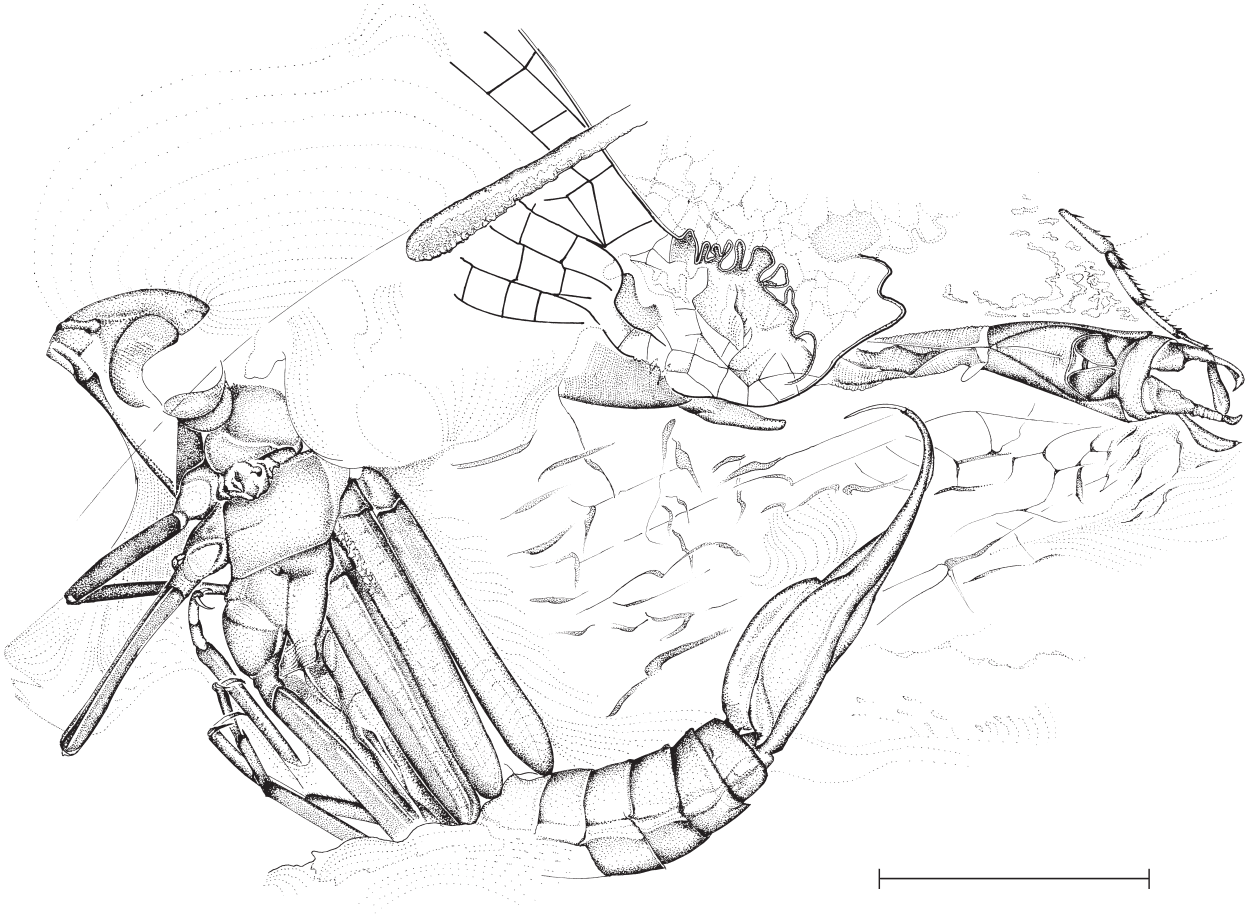

Fig. 10. Specimen 16 (Zygoptera: Hypolestidae); no. 6902, coll. Gröhn; damselfly exuvia and fragments of imago. – Scale: 5 mm.

type of caudal appendages, in which only the median appendage is more or less swollen, while the lateral appendages are flat and broad and held horizontally. In Megapodagrioninae the caudal gills are all foliate and held horizontally. Consequently, the respective fossil larvae from Baltic amber are here tentatively attributed to the family Hypolestidae (sensu Bechly 1996a), which includes the tree subfamilies Heteragrioninae (*Heteragrion* Selys and maybe other genera like *Oxystigma* Selys), Philogeniinae (*Philogenia* Selys and maybe *Paraphlebia* Hagen), and Hypolestinae with the three tribes Philosiniini (*Philosina* Ris, *Lestomima* May, and *Rhipidolestes* Ris), Hypolestini (*Hypolestes* Gundlach), and Lestoideini (*Lestoidea* Tillyard). Of these taxa the genus *Hypolestes* shows most similarities with these fossil larvae (proportion of antennal segments, length of legs, saccoid caudal gills with terminal filament, larval mask without setae and with an apical median cleft in the semicircular projecting prementum) (compare Westfall & May 1996, fig. 45). Furthermore, there is at least one undescribed adult fossil damselfly from Baltic amber in coll. Jürgen Velten (Bechly, in prep.), which agrees in wing venation very well with Hypolestinae. However, the mode of emergence of the fossil species was probably quite different from Recent *Hypolestes*, which emerges from large boulders just a few inches above the water (Westfall & May 1996: 158), because otherwise it wouldn't have been trapped that often in amber.

4. Taphonomy

The Baltic amber of Eastern Europe originated in the Upper Eocene (ca. 40–50 Mio. years b. p.) of Scandinavia, but is found in secondary deposits of glauconitic sands (Blue Earth) of the Upper Eocene to Lower Oligocene (ca. 30–40 Mio. year b. p.) mainly along the coast of the Baltic Sea. Based on the monograph of Conwentz (1890) and on the detailed studies of Schubert (1961) the Baltic amber-tree has long been assumed to be an extinct conifer that has been named *Pinus succinifera* (originally described as *Pinites succinifer* by Göppert 1836), although this taxon is

still undefined and could include five different species (SCHLEE 1986). However, KATINAS (1971) proposed that the Baltic amber was most likely produced by a cedar, close to the extant species *Cedrus atlanticus*, while LANGENHEIM (1995) favoured the kauri-pine genus *Agathis*. LARSSON (1978) and BECK (1999) also saw a closer chemical match of "*Pinus succinifera*" to Araucariaceae than to Pinaceae. However, ANDERSON & LEPAGE (1995) demonstrated that it is most likely that the amber producing tree has been a relative of the gold larch *Pseudolarix*. The Recent representatives of the latter tree genus also produce resin which contains succinic acid that is unique and typical for Baltic amber.

Even though most inclusions in Baltic amber represent terrestrial or aerial arthropods, there is a surprising diversity of aquatic organisms known from this type of amber (WICHARD & WEITSCHAT 1996, WICHARD 2005), including fully aquatic organisms like larvae of Ephemeroptera, Odonata, Nevrorthidae (Neuroptera / Planipennia), Gyrinidae and Dytiscidae (aquatic Coleoptera) and even Gammaridae (aquatic Crustacea – Amphipoda), of which at least some have not been embedded as exuviae but as still living animals. Thus, at least some aquatic habitats must have been close enough to the amber trees, so that such purely aquatic animals could become embedded, when they temporarily have been exposed outside the water because they left their habitat for emergence, or to escape from desiccation. A few specimens might also have been dropped by predators like birds.

The presence of exuviae of aquatic insect larvae as inclusions in amber is most easily explained by the fact the most aquatic insect larvae (including all odonates!) leave the water for the final emergence of the imago and climb stones or plants for this purpose, were they can get into contact with resin. Furthermore, dried exuviae are quite robust and enduring objects and could be transported by strong winds and then trapped by resin flows.

Of the 16 remains of odonate larvae mentioned in this work only 14 could be located and studied. In one specimen it was not visible if it represents an exuvia or a larva. Of the remaining 13 specimens, 7 clearly represent exuviae, 4 represent incomplete emergences or exuviae preserved with remains of the emerged adult, and only 2 represent complete larvae (Pl. 1, Fig. 1a and Pl. 5, Fig. 1a) that probably were embedded alive. According to the relative length of the nymphal wing pads all of the specimens seem to be ultimate larval stages, at least none can plausibly be attributed to earlier larval instars.

5. Palaeoecology and Palaeobiology

That odonate inclusions in amber can be of high palaeobiological interest was shown by POINAR (1996) with the description of an adult damselfly of the New World damselfly genus *Diceratobasis*, of which the Recent relatives are all known to oviposit in phytotelmata within bromeliads. Likewise, the damselfly larvae from Baltic amber provide some clues to the reconstruction of their palaeohabitat:

Of the 14 studied odonate larvae in Baltic amber, 11 can be attributed to the "megapodagrionid" and "amphipterygid" grade of damselflies that today have an exclusively pantropical distribution. Consequently, the damselfly larvae provide a further piece of evidence for a subtropical or even intertropical climate in the Baltic amber forest of the Late Eocene.

Only five of the 13 fossil Zygoptera larvae from Baltic amber studied by the authors of the present publication have the caudal gill appendages preserved, while in the other eight specimens the corresponding part of the abdomen is missing. Of these five larvae three have a saccoid type of gills (Pl. 7, Fig. 3; Pl. 8, Fig. 2b; and Pl. 9, Fig. 1e), while one specimen (Pl. 4, Fig. 2b) has foliate gills (probably Lestida) and one (Pl. 3, Fig. 2c) has foliate-triquetral gills (Megapodagrionidae: Argiolestinae). The single calopterygine larva (Pl. 6, Fig. 1a) does not have the caudal gills preserved, but it can be regarded as quite certain that they have been non-saccoid just as in Recent Calopterygidae, because the typical calopterygid type of gills is also present in the sistergroup Dicteriadidae. The only putative Anisoptera larva (Pl. 1, Fig. 1a) of course must have had an anal pyramid instead of caudal gills. Consequently, 50% of the damselfly larvae with preserved caudal gills have the saccoid type, which is surprising, even though the sample size is too small for a statistically significant result.

According to CORBET (1999: 82) a saccoid type of caudal gill appendages is found "predominantly among larvae that live in well-oxygenated habitats such as trickles, rapid streams, and situations out of water". Consequently, the large frequency of larvae with this type of gills suggests that the mentioned type of habitats must have been relatively abundant in the Baltic amber forest. This is also confirmed by the record of the rheophilic damselfly family Calopterygidae, as well as the fact that all mayfly larvae known from Baltic amber (*Succinogenia larssoni*) belong to the family Heptageniidae (= Ecdyonuridae), which has a similar preference for fast-flowing streams (LARSSON 1978, WICHARD 2005).

In Recent damselfly larvae with saccoid caudal appendages, these appendages usually are only poorly tracheated and with a thick cuticle and a lower surface area-to-volume ratio (CORBET 1999: 82), which demonstrates that they are less important as respiratorial devices. Consequently, these damselfly larvae may also more easily leave their aquatic habitat or climb higher plants for emergence, and thus are more likely to become trapped by resin flows.

Some might even had a semiterrestrial or terrestrial mode of life, similar to some species of the Recent coenagrionid genus *Megalagrion* from the Hawaii archipelago.

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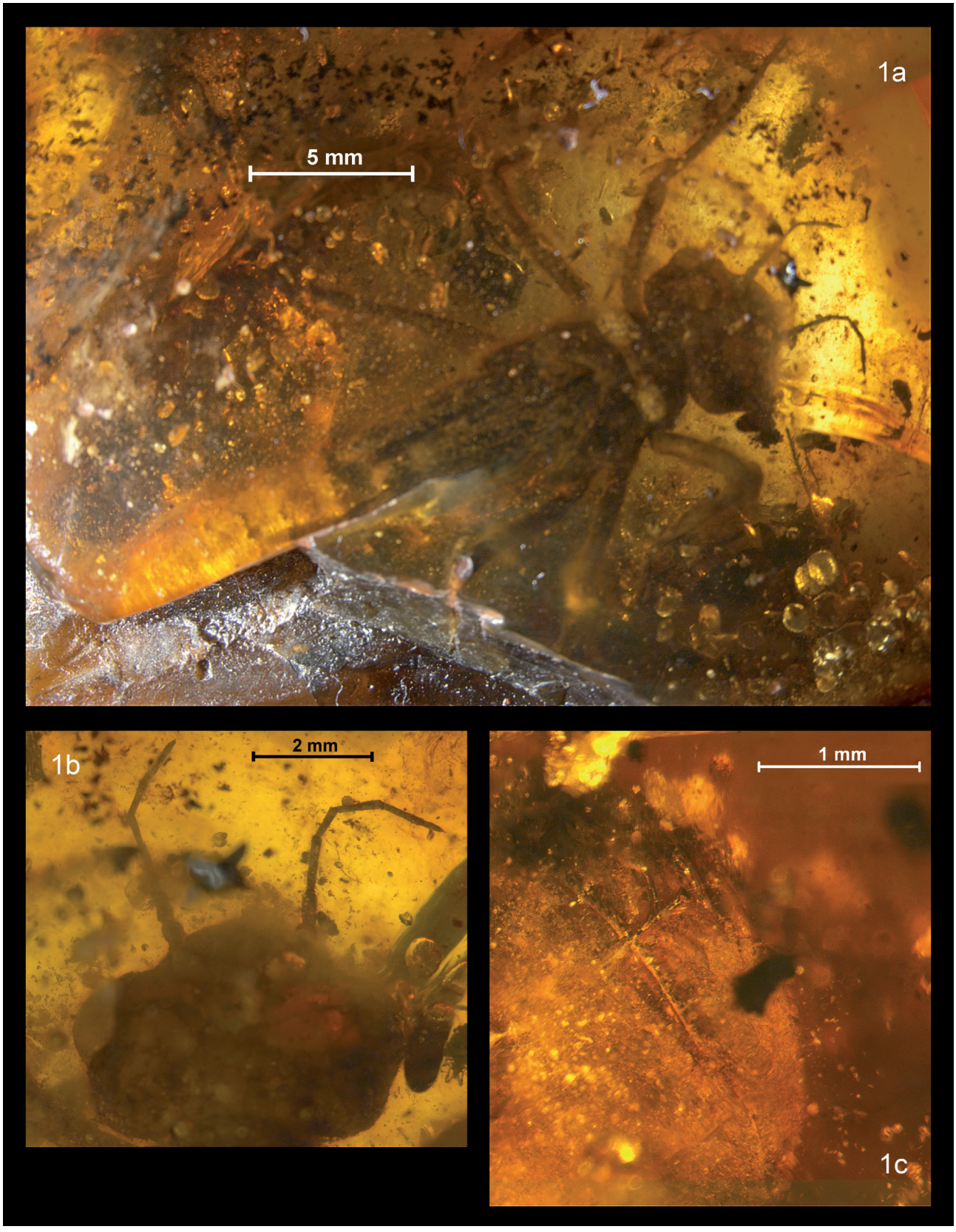
Plate 1

Fig. 1. Specimen 1 (Anisoptera: Aeshnidae); without no. in coll. KRZEMINSKI; dragonfly larva.
Fig. 1a. Dorsal aspect. – Scale: 5.0 mm.
Fig. 1b. Head and antennae; dorsal aspect. – Scale: 2.0 mm.
Fig. 1c. Mask (prementum and labial palps). – Scale: 1.0 mm.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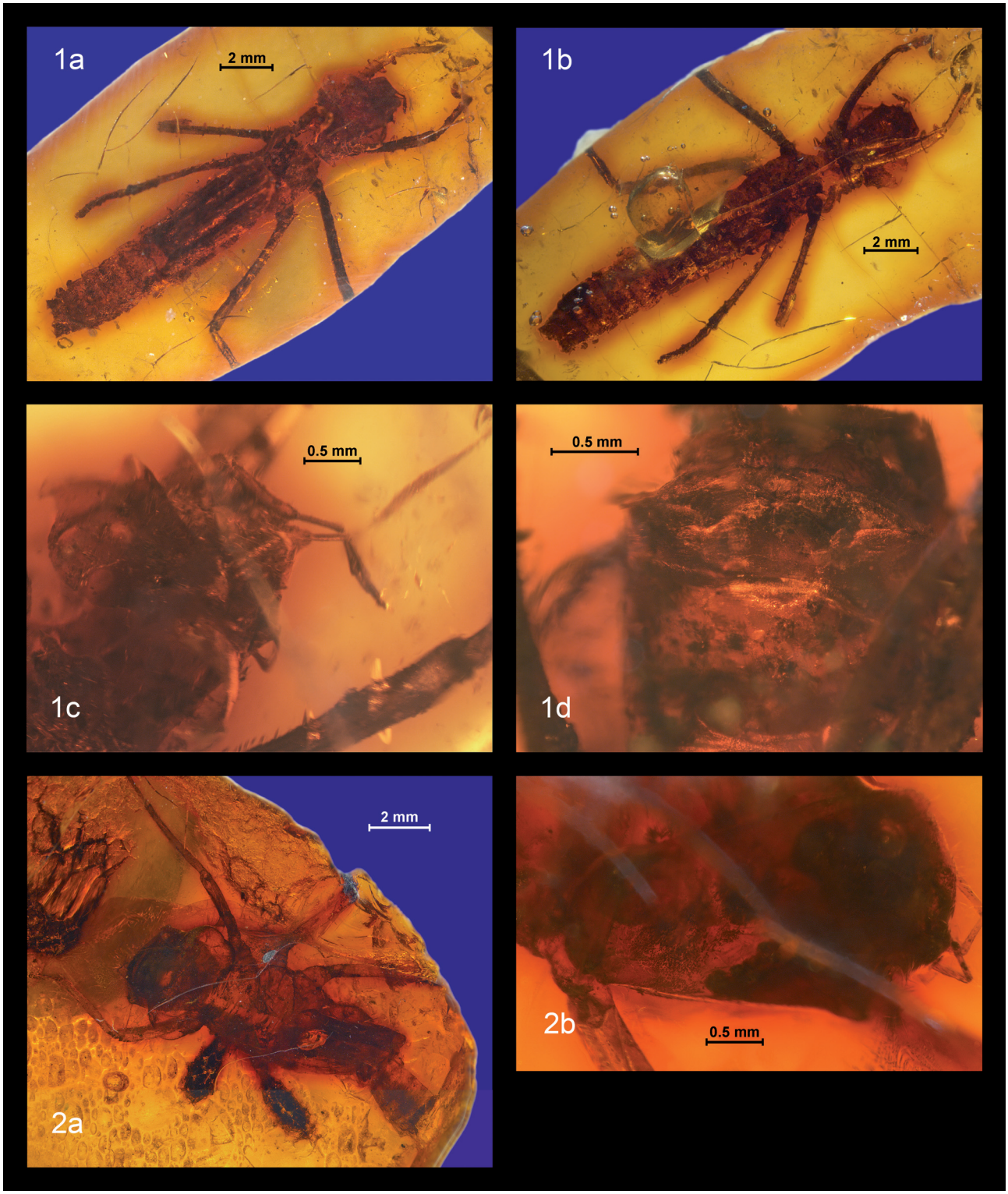
1c

Plate 2

Fig. 1. Specimen 2 (Zygoptera: "megapodagrionid"); no. MB.I.2225, coll. BERENDT; male damselfly exuvia.
Fig. 1a. Dorsal aspect. – Scale: 2.0 mm.
Fig. 1b. Ventral aspect. – Scale: 2.0 mm.
Fig. 1c. Head with antennae. – Scale: 0.5 mm.
Fig. 1d. Mask. – Scale: 0.5 mm.

Fig. 2. Specimen 5 (Zygoptera: "megapodagrionid"); no. GPIM no. 645, SCHEELE no. 1082; damselfly exuvia.
Fig. 2a. Dorsal aspect. – Scale: 2.0 mm.
Fig. 2b. Mask. – Scale: 0.5 mm.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2b
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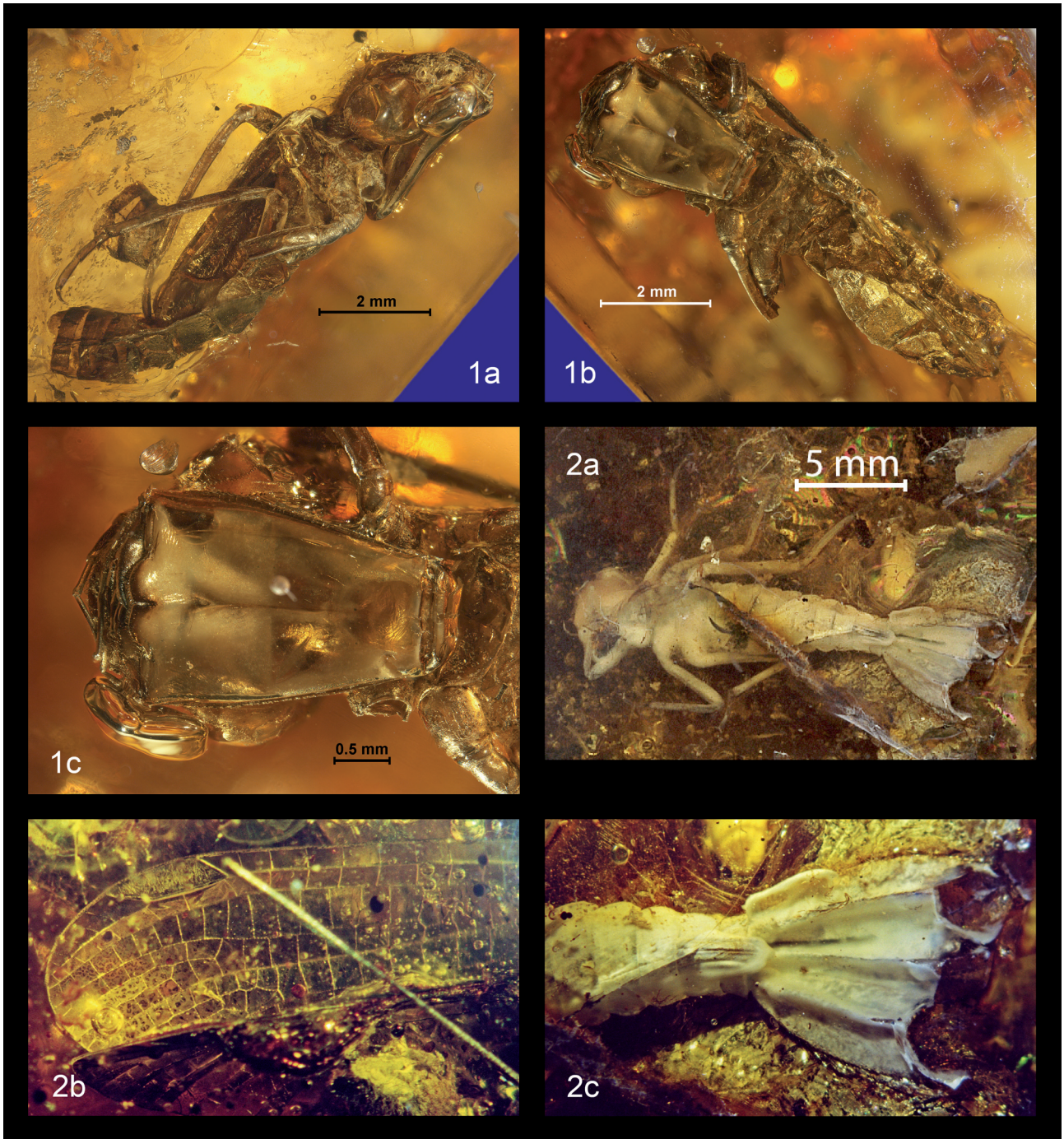
Plate 3

Fig. 1. Specimen 6 (Zygoptera: "megapodagrionid"); no. 7513, coll. GRÖHN; damselfly exuvia.
Fig. 1a. Lateral aspect. – Scale: 2.0 mm.
Fig. 1b. Ventral aspect. – Scale: 2.0 mm.
Fig. 1c. Mask. – Scale: 0.5 mm.

Fig. 2. Specimen 11 (Zygoptera: Megapodagrionidae: Argiolestinae); no. 1639, coll. HERRLING; damselfly larva and wings.
Fig. 2a. Larva; ventral aspect. – Scale: 5.0 mm.
Fig. 2b. Wing fragments of megapodagrionid damselfly. – Without scale.
Fig. 2c. Larval abdomen with ovipositor and caudal gills; ventral aspect. – Without scale.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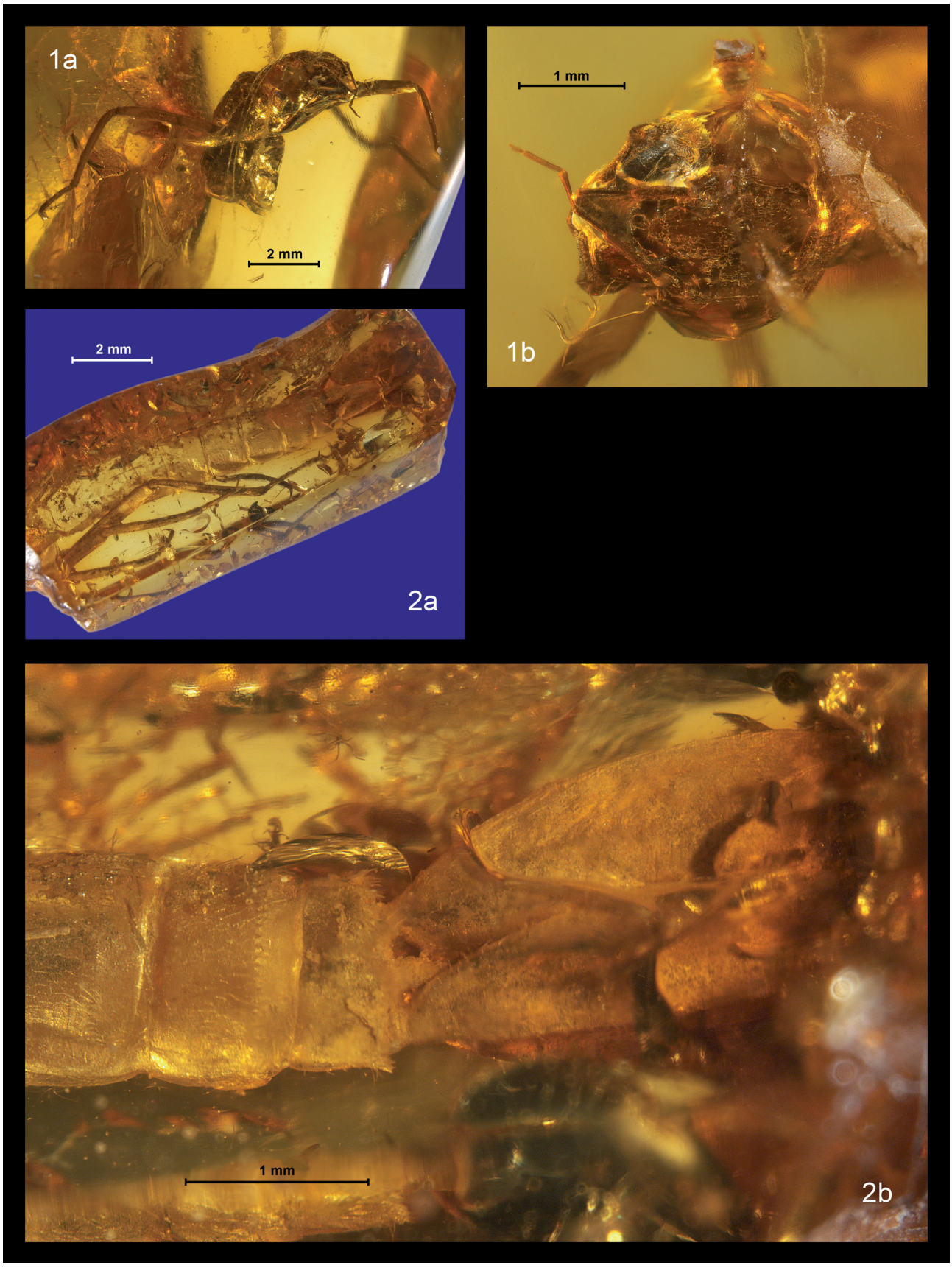
1c
0.5 mm
2a
5 mm
2b
2c

Plate 4

Fig. 1. Specimen 7 (Zygoptera incertae sedis); without no., coll. GRÖHN; damselfly exuvia.
Fig. 1a. Complete animal. – Scale: 2.0 mm.
Fig. 1b. Head with antennae. – Scale: 1.0 mm.

Fig. 2. Specimen 8 (Zygoptera: Lestinoidea incertae sedis); no. Bi 3801, coll. LUDWIG; damselfly exuvia (Lestida?).
Fig. 2a. Total inclusion in lateral aspect. – Scale: 2.0 mm.
Fig. 2b. Caudal gills in lateral aspect. – Scale: 1.0 mm.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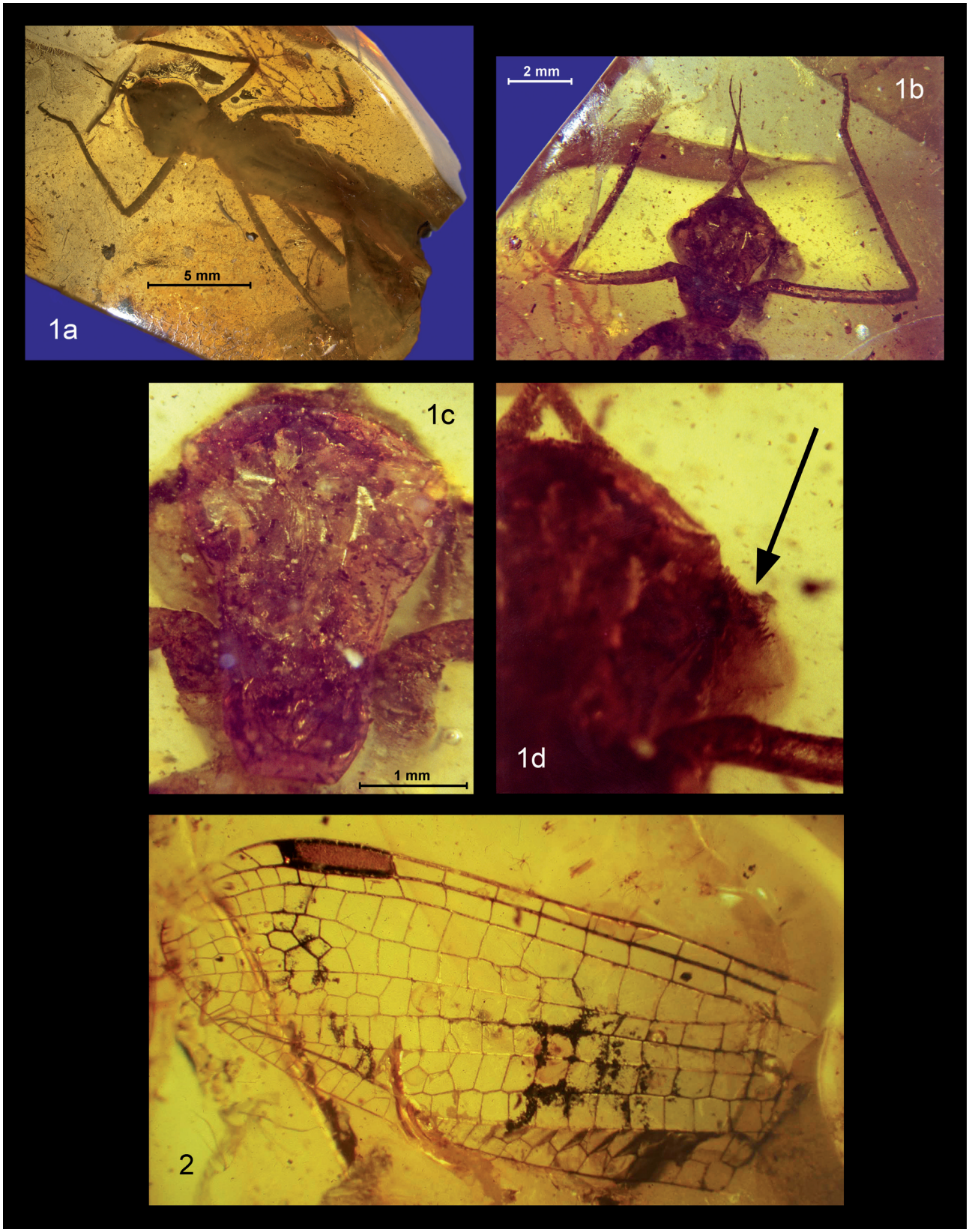
2b

Plate 5

Fig. 1. Specimen 9 (Zygoptera: Synlestidae); no. SMF VI 1332 (coll. SAULIUS, no. 324); damselfly larva.
Fig. 1a. Dorsal aspect. – Scale: 5.0 mm.
Fig. 1b. Ventral aspect. – Scale: 2.0 mm.
Fig. 1c. Mask. – Scale: 1.0 mm.
Fig. 1d. Compound eye with antero-ventral row of spines (arrow); without scale (longest spine 0.125 mm).

Fig. 2. Wing fragment of an adult Synlestidae in Baltic amber (coll. JERZY STASIULEWICZ, Baltic Amber Co., San Diego, CA, USA). – Without scale (photo: PAT CRAIG).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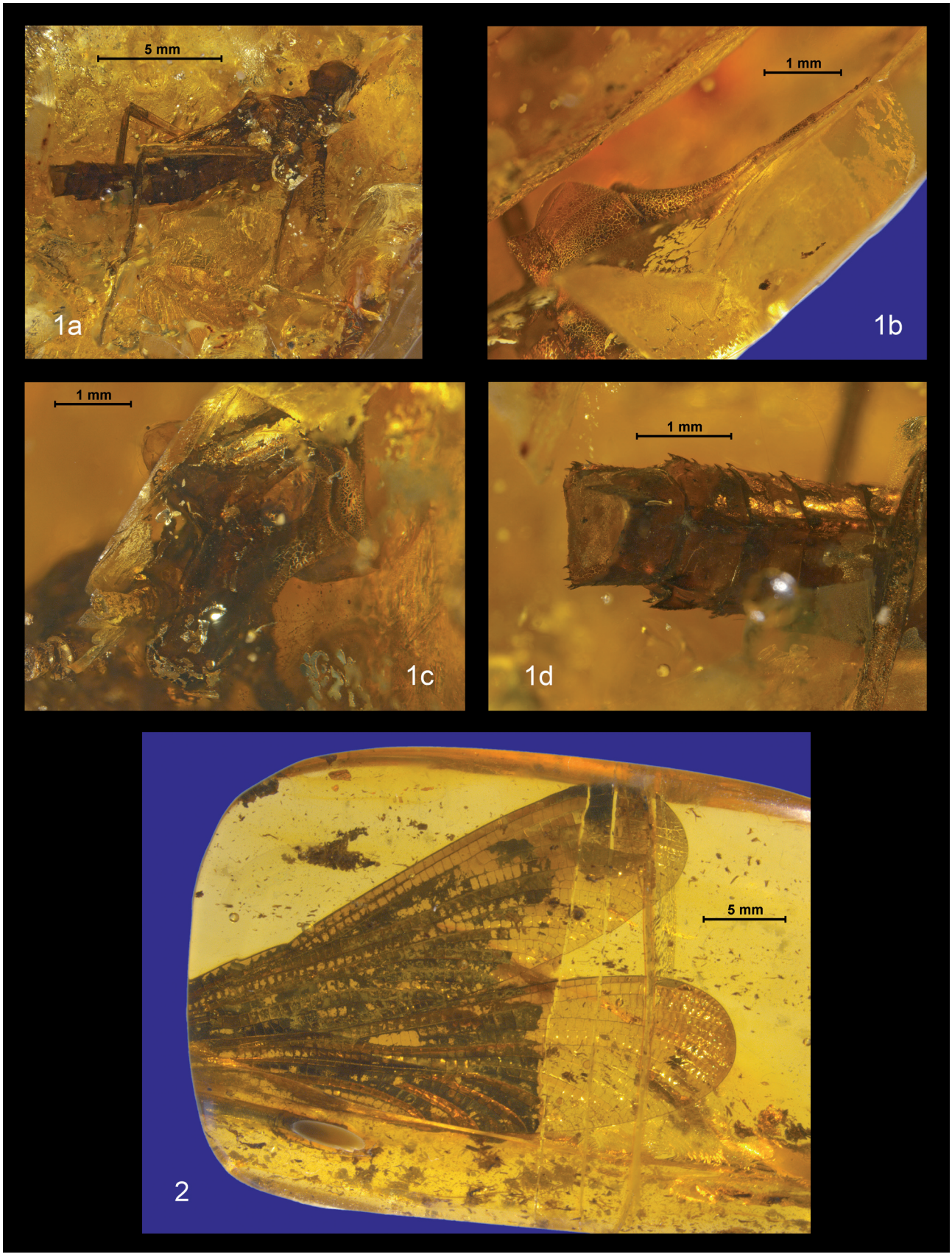
1 mm
1d
2

Plate 6

Fig. 1. Specimen 10 (Zygoptera: Calopterygidae); no. SMNS BB-2387 (ex coll. WUNDERLICH); exuvia.
Fig. 1a. Lateral aspect. – Scale: 5.0 mm.
Fig. 1b. Head and antenna. – Scale: 1.0 mm.
Fig. 1c. Mask. – Scale: 1.0 mm.
Fig. 1d. Abdominal spines. – Scale: 1.0 mm.

Fig. 2. Specimen SMNS BB-2388 (ex coll. DAMZEN); right pair of wings of an adult Calopterygidae; dorsal aspect. – Scale: 5.0 mm.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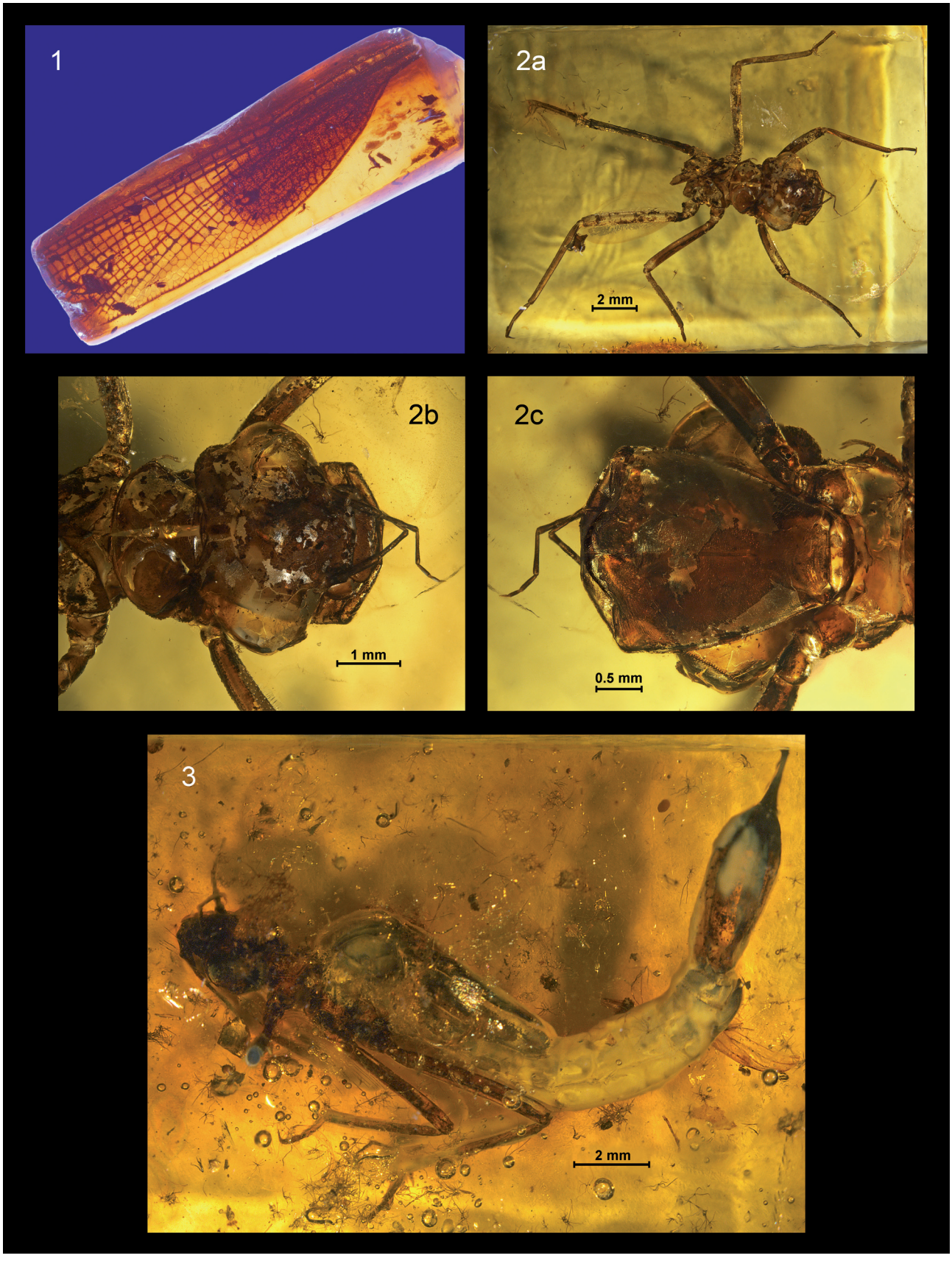
5 mm
2

Plate 7

Fig. 1. Specimen no. SMNS BB-2389 (ex coll. LUDWIG); isolated wing of a possible adult Diphlebiidae (maybe *Electrophenacolestes serafini*).

Fig. 2. Specimen 12 (Zygoptera: Hypolestidae); no. GZG.BST.05504; damselfly exuvia fragment.
Fig. 2a. Dorsal aspect. – Scale: 2.0 mm.
Fig. 2b. Head in dorsal aspect. – Scale: 1.0 mm.
Fig. 2c. Mask. – Scale: 0.5 mm.

Fig. 3. Specimen 15 (Zygoptera: Hypolestidae); no. GZG.BST.05505; damselfly larva; lateral aspect. – Scale: 2.0 mm.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3
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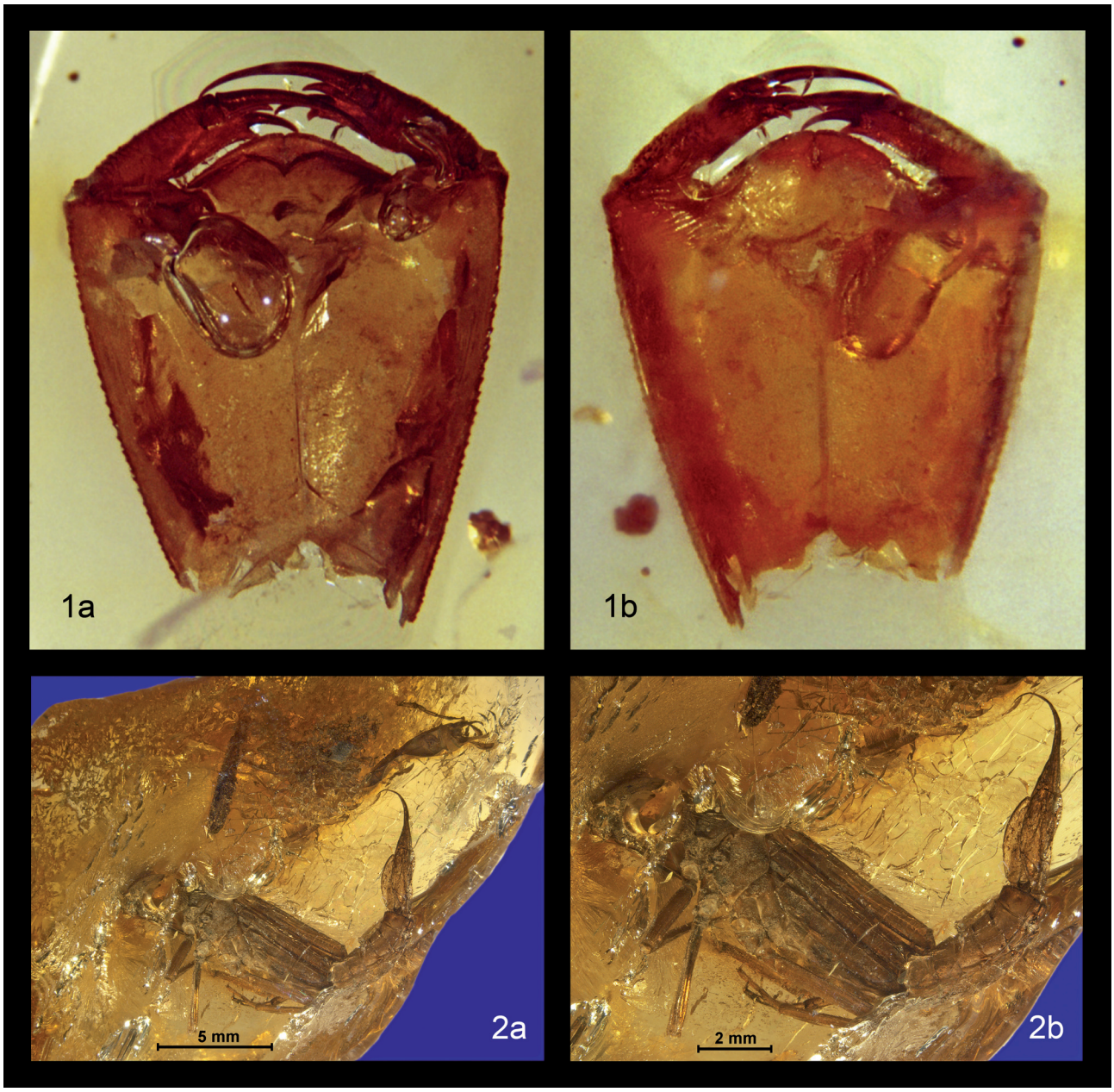
Plate 8

Fig. 1. Specimen 13 (Zygoptera: Hypolestidae); no. 490, coll. HERRLING; isolated mask of damselfly exuvia (max. width 2.47 mm).
Fig. 1a. Mask in dorsal aspect; without scale.
Fig. 1b. Mask in ventral aspect; without scale.

Fig. 2. Specimen 16 (Zygoptera: Hypolestidae); no. 6902, coll. GRÖHN; damselfly exuvia and fragments of imago.
Fig. 2a. Total view. – Scale: 5.0 mm.
Fig. 2b. Exuvia. – Scale: 2.0 mm.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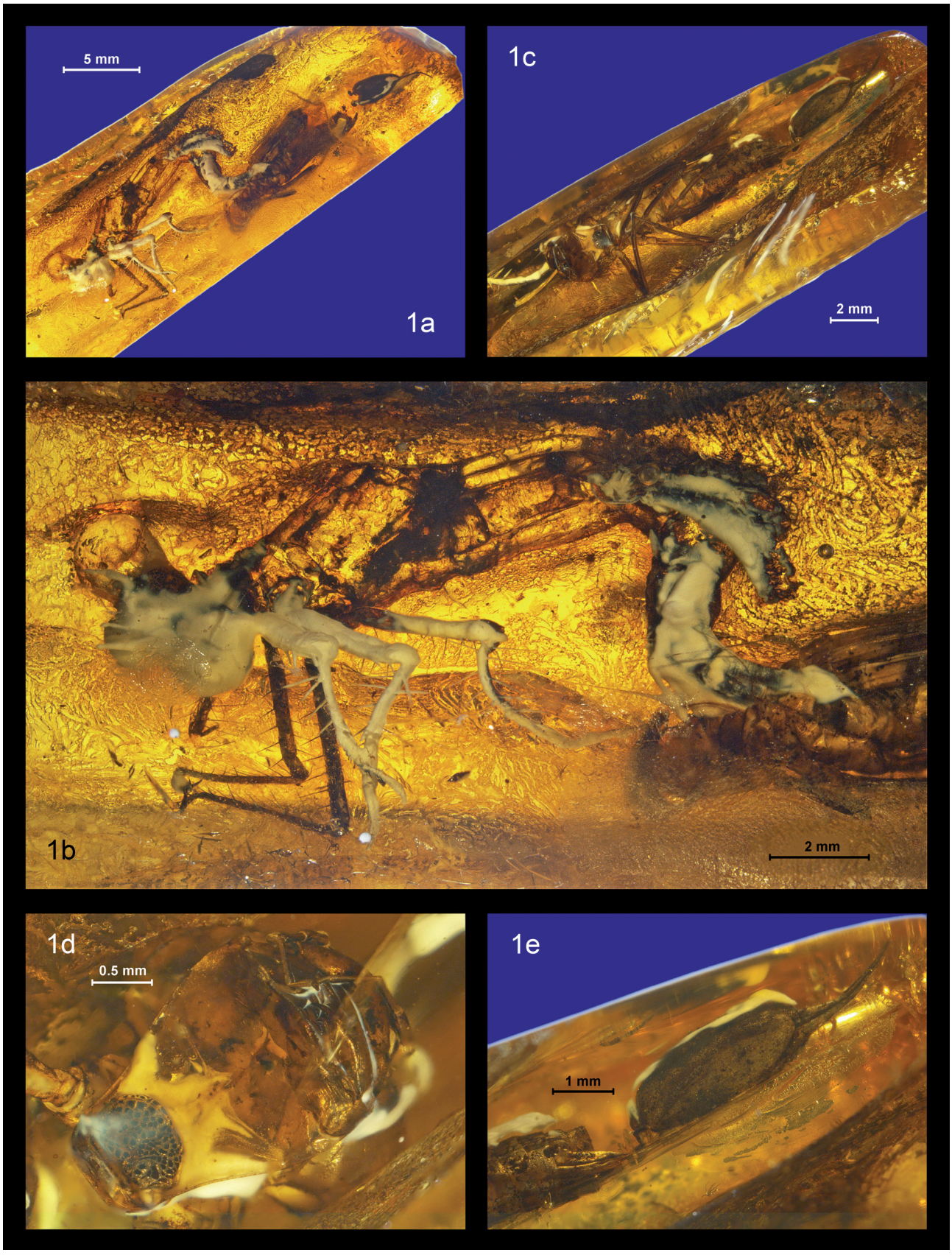
2b

Plate 9

Fig. 1. Specimen 14 (Zygoptera: Hypolestidae); no. SMNS BB-2386 (ex coll. LUDWIG); emerging imago and exuvia.
Fig. 1a. Lateral aspect. – Scale: 5.0 mm.
Fig. 1b. Imago in lateral aspect. – Scale: 2.0 mm.
Fig. 1c. Exuvia in ventral aspect. – Scale: 2.0 mm.
Fig. 1d. Larval mask. – Scale: 0.5 mm. Fig. 1e. larval ovipositor and caudal gills. – Scale: 1.0 mm.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