Fragmenta entomologica, 52 (2): 137–167 (2020)

eISSN: 2284-4880 (online version)
pISSN: 0429-288X (print version)

Research article

Submitted: June 14th, 2020 - *Accepted*: September 18th, 2020 - *Published*: November 15th, 2020

Challenges for understanding lacewings: how to deal with the incomplete data from extant and fossil larvae of Nevrorthidae? (Neuroptera)

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Abstract

Within Neuroptera, the group of lacewings, the ingroup Nevrorthidae is special in several aspects: 1) the group may represent the sister group to all other neuropterans; 2) the group is quite species-poor with only 19 extant species known so far; 3) its representatives show a disjunct relict distribution; 4) it has very unusual appearing larvae. These larvae are very elongate, almost worm-shaped. Our overall knowledge of these larval forms is still very limited. We here review all known occurrences of extant larvae, amended by fossil larvae, all preserved in amber. So far there have been only 17 extant larval specimens of Nevrorthidae depicted in the literature. We also present new fossil larvae, with this reaching a total number of 16 known fossil larvae of Nevrorthidae. When plotting measured lengths, larvae cluster into more than three clusters. Also reconstructed size gains between these clusters indicate that Nevrorthidae might in fact develop through more than three larval stages, unlike other lacewings. A special subdivision of the trunk segments observed in many larvae indicates a specialisation for moving in confined spaces. Comparison of syn-inclusions and literature data make it likely that not all larvae lived in running waters, as previously assumed. Overall our knowledge remains rather limited, yet the data allow to draw some new conclusions about the life and evolution of these larval forms.

Key words: Neuroptera, diversity, larva, pupa, post-embryonic development.

Introduction

In terrestrial ecosystems the dominating group of metazoan animals is Insecta, but to be more precise, one of its ingroups, namely Holometabola. Holometabola comprises numerous ingroups, among them the "big four": Hymenoptera – bees, wasps, ants, etc.; Coleoptera – beetles; Lepidoptera – moths and other butterflies; Diptera – midges and flies. Yet, there are also some smaller ingroups of Holometabola. "Small" is a relative term in this respect, as some of these "smaller" groups also include several thousands of species. Among them is Neuropterida with three major ingroups, Raphidioptera and Megaloptera, with few hundred species each, and Neuroptera with about 6,000 formally described extant species (Tauber et al. 2003). This makes Neuroptera a comparably evolutionary successful group with an expected ecological importance as well.

Understanding ecological roles of neuropterans and knowing their evolutionary history including extinction and diversification events should thus be beneficial for understanding such processes in general. Thanks to the extensive work of Ulrike Aspöck and co-workers (e.g. Aspöck & Aspöck 2007, 2010; Aspöck et al. 2012, 2017) we have gained quite some insight into many ingroups of Neuroptera. Still, some neuropteran ingroups remain more difficult to understand.

Nevrorthidae is a small ingroup of Neuroptera, comprising only 19 formally described extant species (all recently reviewed in Aspöck et al. 2017) as well as 10 fossil species (Wichard 2016). The group has long been interpreted as the sister group to all other neuropterans (e.g. Aspöck et al. 2012; Verineuroptera of Haug et al. 2019), with this occupying a crucial position for reconstructing the evolutionary history for the entire group Neuroptera. Yet, this relationship has been recently challenged (Winterton et al. 2010, 2018; Engel et al. 2010). This dispute demonstrates our still limited knowledge on the early evolution of Neuroptera and that Nevrorthidae may play an important role in further resolving this issue. Furthermore, the representatives of Nevrorthidae show a distinct relict distribution easily prone to endangerment (already indicated for some species; Markovic et al. 2016). Additionally, larval forms of Nevrorthidae have a certain potential to be used as bio-indicators (Malicky 1984).

As for all holometabolans also representatives of Nevrorthidae spend a considerable time of their life as larvae (for challenges of this term see Haug 2020), hence this is a phase of ecological and evolutionary importance. The larvae of Nevrorthidae seem to be mostly rheophilic, living in fast running streams (Zwick 1967, Malicky 1984). As for (almost) all neuropteran larvae the mandibles are large and prominent, forming a pair of piercing-sucking stylets together with parts of the maxillae. In other neuropteran larvae these stylets inject venom into the prey and then its body fluids are sucked out; this can also be assumed for larval forms of Nevrorthidae. These larvae are easily distinguishable from those of other neuropterans due to the following combination of the characters:

1. Their mandibles are proximally straight but curved at the tip (e.g. Zwick 1967, Malicky 1984, Beutel et al. 2010); in this arrangement the stylets can move against each other for producing enough force to pierce the prey (also possible with curved mandibles), in other lineages stylets are either straight or curved entirely.
2. The head is connected to the next sclerite (cervix) by a distinct joint (originally termed 'Rollengelenk'; Zwick 1957; Beutel et al. 2010) absent in other larvae of Neuroptera.
3. The collar-like sclerite (cervix) following the head (possibly a sclerotisation between head and first true tergite, the pronotum) is very prominent and elongate.
4. The entire body is very elongate, elateriform, almost worm-shaped.

These specialised larvae were identified as representatives of Nevrorthidae by Zwick (1967), since then only few studies have explicitly dealt with these larvae in detail, Malicky (1984) and Beutel et al. (2010) being notable examples. Therefore, we have to state that our knowledge on the larval stages of Nevrorthidae is unfortunately still very limited (as for most groups of Neuroptera and Holometabola; see e.g. Gepp 1984). Among the fossil forms of Nevrorthidae numerous larval specimens are known. Yet, with our limited knowledge on modern forms it becomes even more difficult to incorporate fossil larvae into an evolutionary framework.

As a starting point for further research we here: 1) compile all available data on larval forms of Nevrorthidae, 2) present additional fossil larval specimens, and 3) explore how we can draw conclusions about ecology and evolutionary history based on such a comparably incomplete data set.

Material and methods

Basic approach

As pointed out in the introduction there are not many reports of extant larval forms of Nevrorthidae available in the literature. Many of the drawings available have been re-figured repetitively. Given the rather rare nature of these larval specimens we treat them differently from a common approach, more similar to the way fossils are usually treated, i.e. we list the first occurrence of a specimen and also where it has been re-figured. With this, we provide a solid database that can be further expanded with future records.

To make some literature reports that seem to have been regularly overlooked better available, we provide interpretive drawings for every specimen. This appeared necessary to us to perform measurements on each specimen. Only in depicting interpreted borders the reader can comprehend correctly which dimensions have been measured on each specimen. Additionally, some of the original depictions contain so far uninterpreted information, hence an interpretive drawing was used as a basis also for functional-morphological interpretations.

Fossil larval specimens from the literature were treated in the same manner. Alternatively, the fossil has been re-documented if available to the authors. Also new specimens are presented.

Material

In total, eight specimens of fossil larvae of the group Nevrorthidae preserved in amber were directly investigated and documented. Specimens came from collections of the Senckenberg Museum Frankfurt (SMF) and from the collections of two of the authors (Gröhn, Müller; summarised in Table 1).

Documentation methods

All available specimens were documented on a Keyence VHX-6000 digital microscope. Each specimen was documented with a stack of images of shifting focus and fused to a single sharp image. Larger specimens were documented with several stacks of adjacent image details, and stitched to panoramas (e.g. Haug et al. 2011a; especially beneficial for amber e.g. Haug et al. 2013a; Hörnig et al. 2016). In most cases each image was additionally recorded with several exposure times (HDR function; Haug et al. 2013b, 2018). Each specimen was recorded with unpolarised ring light illumination and cross-polarised co-axial illumination. The image providing the better contrast was used here. If both images show complementary details, both are shown. Images were processed with the software implemented in the microscope and further optimised in Adobe Photoshop CS2. Drawings were prepared in Adobe Illustrator CS2.

Measurements

For every specimen numerous morphological (= morphometric) distances were measured. To make the most out of the available specimens, distances were chosen after inspecting the specimens. Only lengths along the main body

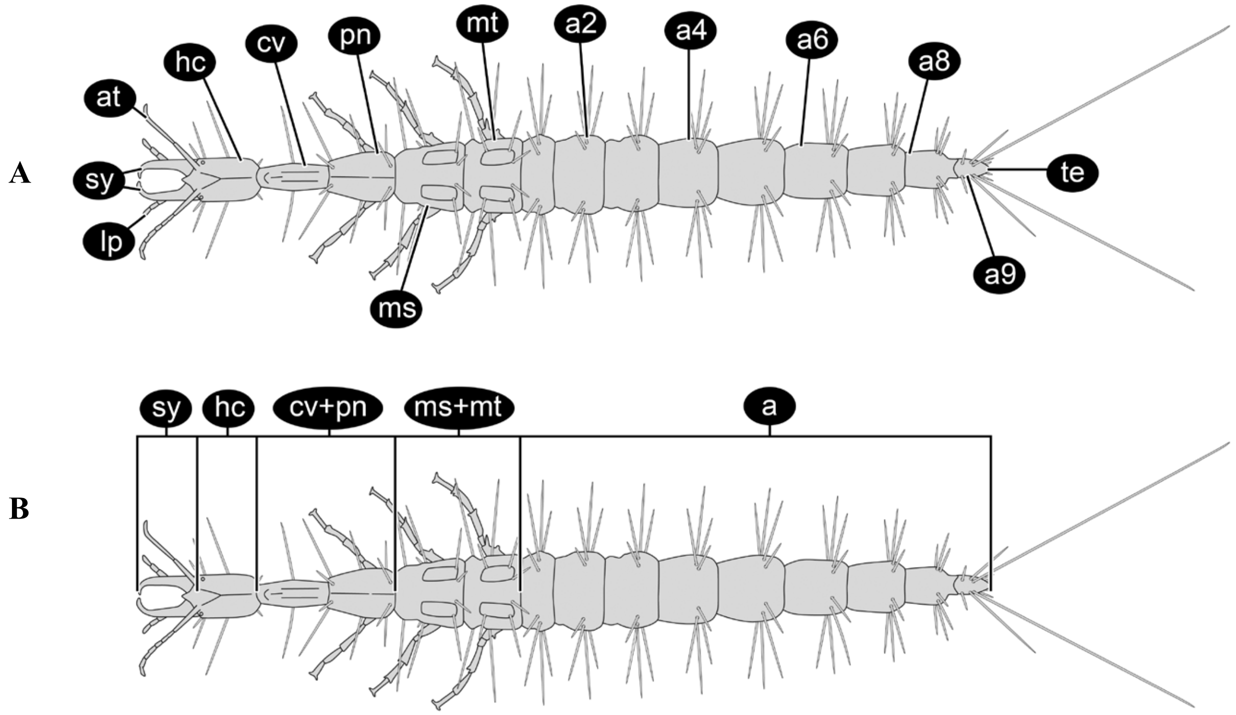

Fig. 1 – General morphology of larval forms of Nevrorthidae. **A,** Most prominent structures. **B,** Measured dimensions. Drawing simplified from Riek (1970: fig. 29–11F). Abbreviations: a = abdomen; a2–9 = abdominal segment 2–9; at = antenna; cv = cervix (neck); hc = head capsule; lp = labial palp; ms = mesonotum; mt = metanotum; pn = pronotum; sy = stylet; te = trunk end.

axis are used, this allows to include specimens that are only accessible in a limited amount of views (dorsal, ventral or lateral view). All major structures and measured distances are shown in Fig. 1.

In many cases a scale is missing from the published drawings of the larvae of Nevrorthidae. For quantitative aspects we are therefore limited to using ratios (Table 1). Although ratios are known to be inferior in removing size-related artefacts other standard methods cannot be used due to the lack of scale. As discussed in the following, also this "less sharp" approach can reveal some interesting aspects of this limited data set.

Results

Extant larval representatives of Nevrorthidae depicted in the literature

All occurrences are listed chronologically. Cases in which the same specimen has been re-figured are also included chronologically with reference to the original occurrence (see also Table 1). While this includes a certain redundancy, it should represent the most complete way of cross-referencing, avoiding interpreting the same specimen as two independent occurrences.

1) Takahashi (1942) was the first who figured a larval representative of Nevrorthidae (specimen 1). A single specimen was presented as a drawing in dorsal view (Takahashi 1942: fig 1; Fig. 2A). Also details of the head were figured (Takahashi 1942: fig. 2). The position of the specimen, as depicted, indicates that the drawing is based directly on a real specimen and not strongly stylised. The specimen was interpreted originally as a larval form of the neuropteran ingroup Dilaridae by Takahashi (1942), but recognised as representative of Nevrorthidae by Zwick (1967). Due to the disjunctive distribution of Nevrorthidae (e.g. Wichard et al. 2009) the specimen described by Takahashi (1942) is most likely a representative of *Nipponeurorthus* Nakahara, 1958. Since Zwick (1967), the specimen seems to have been largely ignored (examples for exceptions: Malicky 1984, Monserrat & Gavira 2014) leading to the impression that the larvae of *Nipponeurorthus* are unknown (e.g. Gepp 1984, Tauber et al. 2003). Based on comparison to other specimens (see below) the specimen is most likely a late larval stage. No scale is available to provide any hint for the overall size of the specimen.

2) Zwick (1967) first described and recognised the larval forms treated here as representatives of Nevrorthidae. Habitus of the single larval specimen of *Nevrorthus fallax* (Rambur, 1842) (specimen 2) was depicted as a stippled drawing in dorsal view (Zwick 1967: fig. 1; Fig. 2B). The position of the appendages indicates that this drawing is based on an actual specimen and not summarised from several specimens. The specimen most likely represents a

Table 1 – Summary of all specimens, including origin, interpretation in this contribution and measurements. Columns 10–15 (“head with stylet” to “abdomen total”) contain relative sizes, i.e., the measured body part divided by entire body length.

specimen	original source	species interpretation	sex	original fig,	Fig.	group	size group	absolute size in mm	head with stylet	head without stylet	prothorax (incl. neck)	meso+ metathorax	thorax total	abdomen total
1	Takahashi 1942	*?Nipponeurorthus* sp.	–	1	2A	extant	larva (?)	–	0,07	0,14	0,07	0,10	0,16	0,27
2	Zwick 1967	*Nevrorthus fallax*	–	1	2B	extant	larva (4)	13	0,09	0,16	0,08	0,14	0,20	0,34
3	Riek 1970	*Austroneurorthus* sp.	–	29-11G	3A	extant	larva (?)	–	0,07	0,15	0,08	0,17	0,15	0,33
4	Gepp 1984	*Nevrorthus* sp.	–	12a	2C	extant	larva (4)	12	0,08	0,16	0,08	0,13	0,20	0,33
5	Malicky 1984	*Nevrorthus fallax*	–	5aA	3B	extant	larva (2)	4,2	0,11	0,23	0,11	0,17	0,14	0,31
6	Malicky 1984	*Nevrorthus iridipennis*	–	5aB	2D	extant	larva (4)	11,2	0,08	0,16	0,08	0,16	0,23	0,39
7	Malicky 1984	*Nevrorthus iridipennis*	–	5aC	3C	extant	pre-pupa	–	–	0,09	0,16	0,16	0,32	0,59
8	Malicky 1984	*Nevrorthus iridipennis*	–	5aD	3D	extant	pre-pupa	–	–	0,11	0,34	0,20	0,54	0,35
9	Malicky 1984	*Nevrorthus iridipennis*	–	5bE-G	3E	extant	pupa	–	–	0,10	0,15	0,17	0,32	0,58
10	Wichard et al. 1995	*Nevrorthus* sp.	–	60a	3F	extant	pre-pupa	–	–	0,09	0,20	0,19	0,38	0,53
11	Wichard et al. 1995	*Nevrorthus iridipennis*	–	61b	3G	extant	pupa	–	–	0,12	0,12	0,18	0,30	0,58
12	Grimaldi & Engel 2005	*Nevrorthus fallax*	–	9.13	4A	extant	larva (4)	12	0,09	0,16	0,08	0,16	0,21	0,37
13	Aspöck & Aspöck 2010	*Nevrorthus apatelius*	–	5	3H	extant	larva (?)	–	0,08	0,15	0,07	0,14	0,24	0,38
14	Beutel et al. 2010	*Austroneurorthus* sp.	–	1	4B	extant	larva (3)	9,5	0,11	0,23	0,12	0,23	0,16	0,38
15	Gavira et al. 2012	*Nevrorthus reconditus*	–	1	4C	extant	larva (3)	9,6	0,10	0,19	0,09	0,17	0,16	0,33
16	Markovic et al. 2016	*Nevrorthus ?apatelios*	–	2	3I	extant	larva (3)	9	0,11	0,20	0,09	0,21	0,19	0,40
17	https://www.mdfrc.org.au/bugguide/	*Austroneurorthus* sp.	–	–	4D	extant	larva (4)	11	0,07	0,15	0,08	0,16	0,17	0,33
18	Wichard & Weitschat 1996	–	–	plate 10 lower	5A	fossil	larva (?)	–	0,08	0,13	0,06	0,12	0,20	0,32
19	Wichard et al. 2009	*?Rophalis ?relicta*	–	07.20a	5C	fossil	larva (1)	1,1	0,34	0,2	0,16	0,16	0,32	0.37
20	Wichard et al. 2009	*?Rophalis ?relicta*	–	07.21a, c	5D	fossil	larva (1)	0,9	0,31	0,49	0,18	0,20	0,23	0,43
21	Wichard 2017	–	–	2a	5E	fossil	larva (?)	–	–	–	–	–	–	–
22	Wichard 2017	–	–	2b	6	fossil	larva (2)	6,2	0,07	0,17	0,10	0,13	0,15	0,28
23	Lu et al. 2018	*?Cretarophalis ?patrickmuelleri*	–	10, 11	5B	fossil	larva (?)	–	–	–	–	–	–	–
24	this contribution (Gr 1341A)	–	–	–	7	fossil	larva (3)	8,1	0,09	0,18	0,09	0,15	0,19	0,34
25	this contribution (Gr 1341B)	–	–	–	8	fossil	larva (3)	8,2	0,09	0,17	0,08	0,19	0,18	0,37
26	this contribution (Gr 7668)	–	–	–	9	fossil	larva (3)	8	0,10	0,17	0,06	0,16	0,21	0,37
27	this contribution (Gr 2518)	–	–	–	10	fossil	larva (3)	7,8	0,09	0,18	0,09	0,16	0,18	0,33
28	this contribution (Gr 7095)	–	–	–	11	fossil	larva (3)	8,5	0,10	0,16	0,07	0,16	0,18	0,35
29	this contribution (Gr 2768)	–	–	–	12	fossil	larva (2)	5,6	0,11	0,20	0,09	0,17	0,19	0,36
30	this contribution (SMF 256)	–	–	–	13	fossil	larva (2)	5,6	0,10	0,10	0,14	0,22	0,35	0,49
31	this contribution (Gr 2769)	–	–	–	14	fossil	larva (2)	5,2	0,16	0,08	0,1	0,17	0,27	0,55
32	this contribution (Gr 1383A)	–	–	–	15	fossil	larva (1)	0,8	0,40	0,60	0,20	0,16	0,13	0,28
33	this contribution (Gr 1383B)	–	–	–	16	fossil	larva (1)	0,7	0,25	0,47	0,22	0,18	0,21	0,39
adult	Aspöck & Aspöck 2017	*Nipponeurorthus fuscinervis*	female	2c	–	extant	adult	–	–	0,10	0,12	0,21	0,33	0,57
adult	Aspöck & Aspöck 2017	*Nipponeurorthus flinti*	male	4e	–	extant	adult	–	–	0,09	0,10	0,21	0,31	0,59
adult	Aspöck & Aspöck 2017	*Nipponeurorthus qinicus*	male	12f	–	extant	adult	–	–	0,11	0,10	0,27	0,37	0,52
adult	Aspöck & Aspöck 2017	*Nevrorthus apatelios*	female	2a	–	extant	adult	–	–	0,09	0,10	0,24	0,34	0,57
adult	Aspöck & Aspöck 2017	*Sinoneurorthus yunnanicus*	female	2d	–	extant	adult	–	–	0,11	0,12	0,21	0,33	0,55
adult	Aspöck & Aspöck 2007	*Nevrorthus apatelios*	–	73	–	extant	adult	–	–	0,09	0,11	0,21	0,32	0,58
adult	Monserrat & Gavira 2014	*Nevrorthus fallax*	–	18	–	extant	adult	–	–	0,11	0,10	0,22	0,32	0,57
adult	Monserrat & Gavira 2014	*Nevrorthus apatelios*	–	19	–	extant	adult	–	–	0,11	0,11	0,19	0,30	0,59
adult	Monserrat & Gavira 2014	*Nevrorthus iridipennis*	–	20	–	extant	adult	–	–	0,12	0,11	0,19	0,30	0,58
adult	Monserrat & Gavira 2014	*Nevrorthus reconditus*	–	1	–	extant	adult	–	–	0,14	0,10	0,21	0,31	0,54

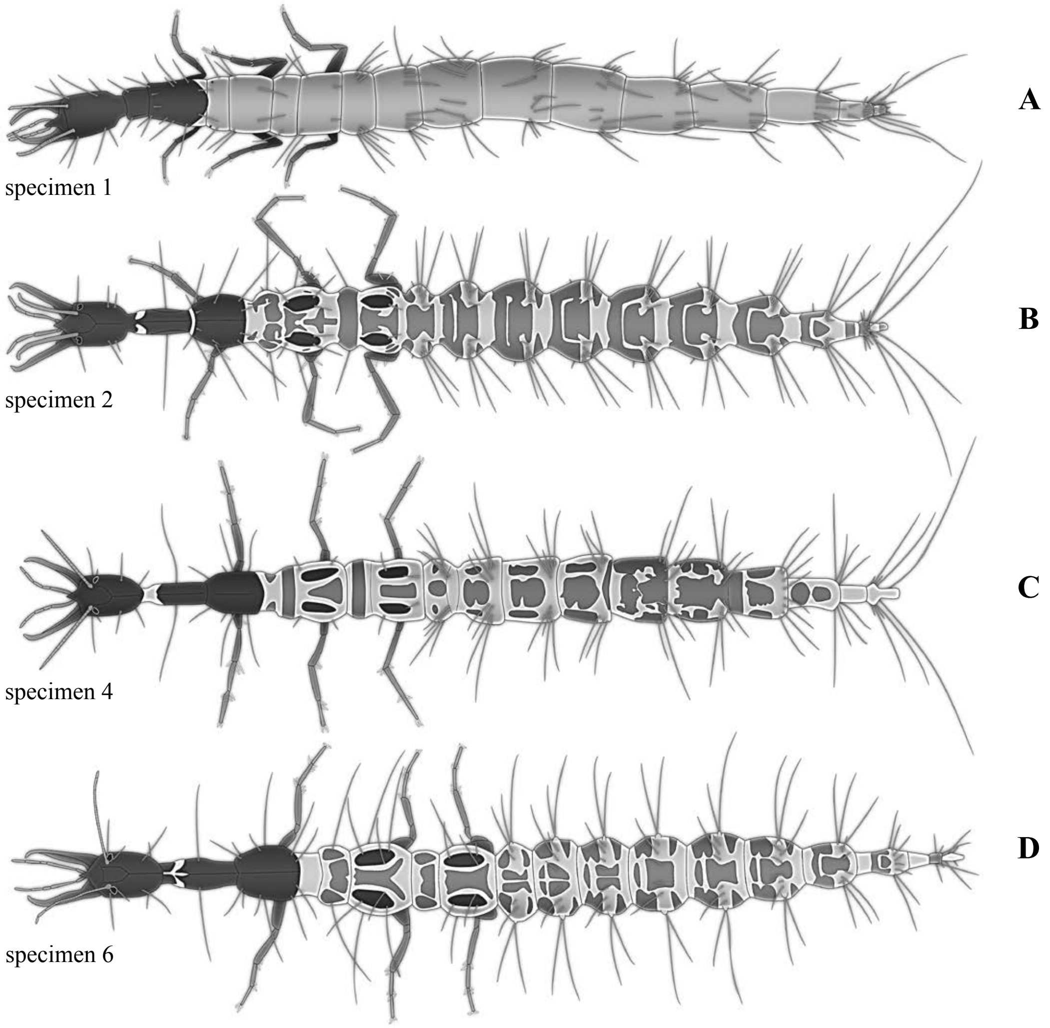

Fig. 2 – Nevrorthidae; extant immature specimens, interpretative drawings. All specimens seem to be ultimate larval stages. **A,** Specimen 1; ?*Nipponeurorthus* sp.; from Takahashi (1942: fig. 1). **B,** Specimen 2; *Nevrorthus fallax* (Rambur, 1842); from Zwick (1967: fig. 1). **C,** Specimen 4; *Nevrorthus* sp.; from Gepp (1984: fig. 12a). **D,** Specimen 6; *Nevrorthus iridipennis* Costa, 1863; from Malicky (1984: fig. 5aB).

late larval stage. Additional details were provided also as drawings in the following figures (Zwick 1967: figs 2–7). A simplified drawing of a ventral view of a larval specimen was depicted in a phylogram (Zwick 1967: fig. 8). It remains unclear whether this drawing was based on an actual additional specimen or whether it was the same specimen as in his figure 1; due to this uncertainty it is not considered further. Zwick (1967) mentions that while his paper was in press, other authors (MacLeod, Riek) would have recognised similar appearing larvae. Riek apparently published his specimen in 1970 (see under 3); we were not able to identify the supposed paper of MacLeod. In his important work on comparative head anatomy of neuropteran larvae (MacLeod 1964) no larval representative of Nevrorthidae is figured. The drawing of Zwick (1967) was re-figured by Wichard & Weitschat (1996) and Weitschat & Wichard (1998, 2002). Zwick reported that the figured larva is about 13 mm in length and that most of the specimens he had handled measure about 12–13 mm. He furthermore mentions that he had smaller specimens with about 10 mm that he interpreted as representatives of an earlier developmental stage, an interpretation further supported by a lower number of antenna elements.

3) Riek (1970) figured a larval representative of Nevrorthidae (specimen 3) in dorsal view (Riek 1970: fig. 29-11F; Fig. 3A). The drawing appears slightly simplified or generalised. Additionally, a close-up of the head is provided (Riek 1970: fig. 29–11G), indicating that despite simplification the drawings should have been based on an actually observed specimen. This interpretation is further supported by statements in the text, about observations on a specimen out in the field. As the overall publication deals with insects from Australia, it seems most likely that the specimen is a larval form of a species of *Austroneurorthus* Nakahara, 1958. The drawing has been re-figured in New

(1989, 1991, 1992, 2004) and Tauber et al. (2003). There is no indication of a scale or of the size of the larva.

4) Gepp (1984) summarised current knowledge on neuropteran larvae at the time; his paper is an important database-like work. He also depicted an original shaded drawing of the habitus of a larva (specimen 4) of *Nevrorthus* sp. ("*Neurorthus* spec.") in dorsal view (Gepp 1984: fig. 12a; Fig. 2C). The degree of detail indicates that an actual specimen was used as the basis for the drawing, yet it cannot be totally excluded that several specimens are sub-summarised here. Gepp (1984) states that the larva is 12 mm in length.

5) Malicky (1984) described the autecology of the larval stages of different species of *Nevrorthus* Costa, 1863. He also figured habitus drawings of several specimens in considerable details: a supposed penultimate larval stage of *N. fallax* (specimen 5) in dorsal view (without the legs; Malicky 1984: fig. 5aA; Fig. 3B), about 4.2 mm in overall length; a supposed ultimate larval stage of *N. iridipennis* Costa, 1863 (specimen 6) in dorsal view (Malicky 1984: Fig. 5aB; Fig. 2D), about 11.2 mm in length; an ultimate larval stage of *N. iridipennis* (specimen 7) close to moulting into the pupa ("Präpuppe", pre-pupa) in lateral view Malicky 1984: fig. 5aC; Fig. 3C), about 10.4 mm in length (measured along the curvature of the body); an ultimate

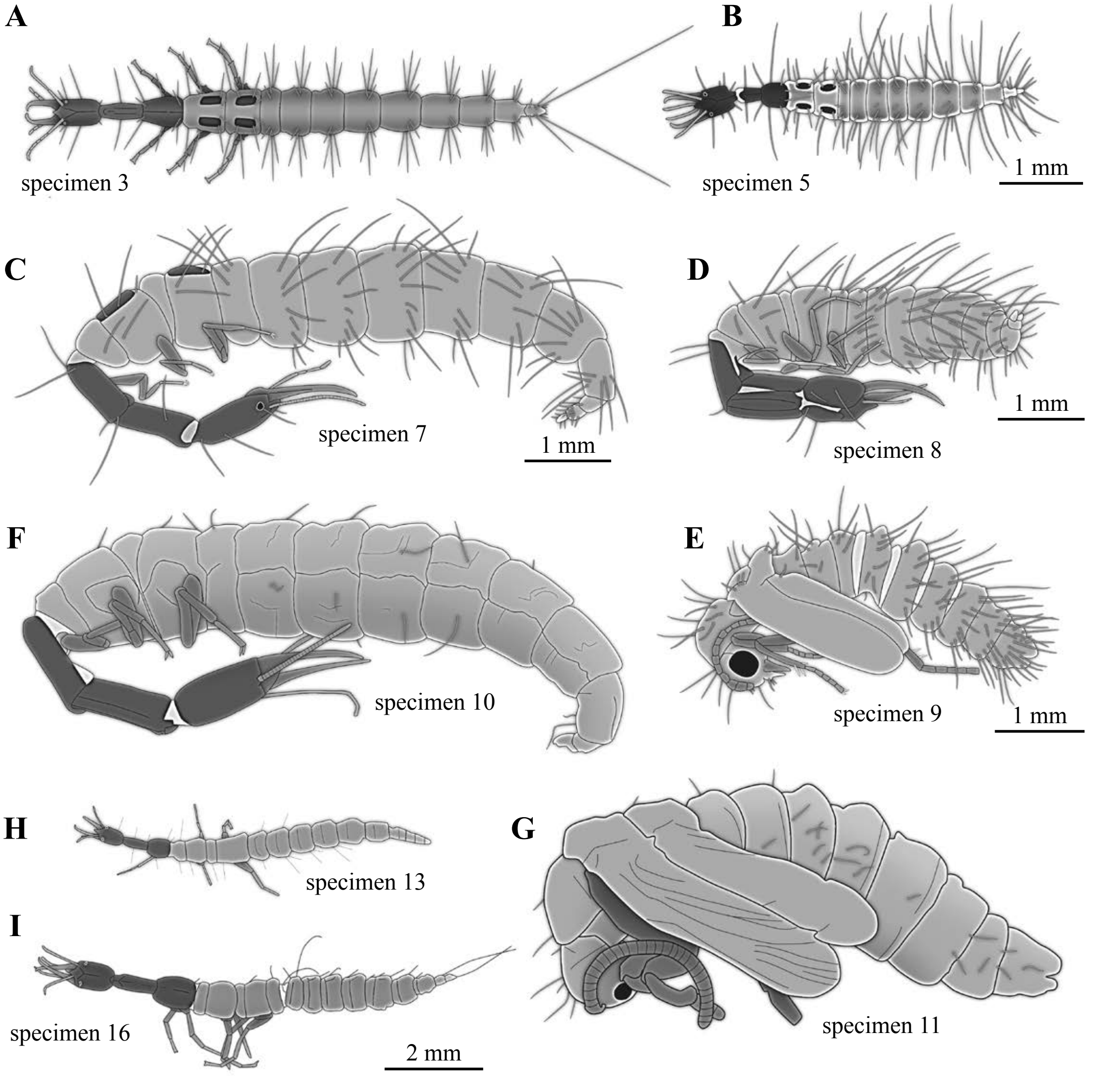

Fig. 3 – Nevrorthidae; extant immature specimens, interpretative drawings (continued). **A,** Specimen 3; *Austroneurorthus* sp.; from Riek (1970: fig. 29–11F); possibly ultimate larval stage. **B,** Specimen 5; *Nevrorthus fallax* (Rambur, 1842); from Malicky (1984: fig. 5aA); possibly penultimate larval stage. **C,** Specimen 7; *N. iridipennis* Costa, 1863; from Malicky (1984: fig. 5aC); later ultimate larval stage ("Präpuppe"). **D,** Specimen 8; *N. iridipennis*; from Malicky (1984: fig. 5aD); later ultimate larval stage ("Präpuppe"). **E,** Specimen 9; *N. iridipennis*; from Malicky (1984: fig. 5bE); pupa. **F,** Specimen 10; *Nevrorthus* sp.; from Wichard et al. (1995: fig. 60a); apparently later ultimate larval stage ("Präpuppe"). **G,** Specimen 11; *N. iridipennis*; from Wichard et al. (1995: fig. 61b); pupa. **H,** Specimen 13; *N. apatelius* Aspöck, Aspöck & Hölzel, 1977; from Aspöck & Aspöck (2010: fig. 5); possibly ultimate larval stage. **I,** Specimen 16; *N. ?apatelius*; from Markovič et al. (2016: fig. 2); possibly ultimate larval stage.

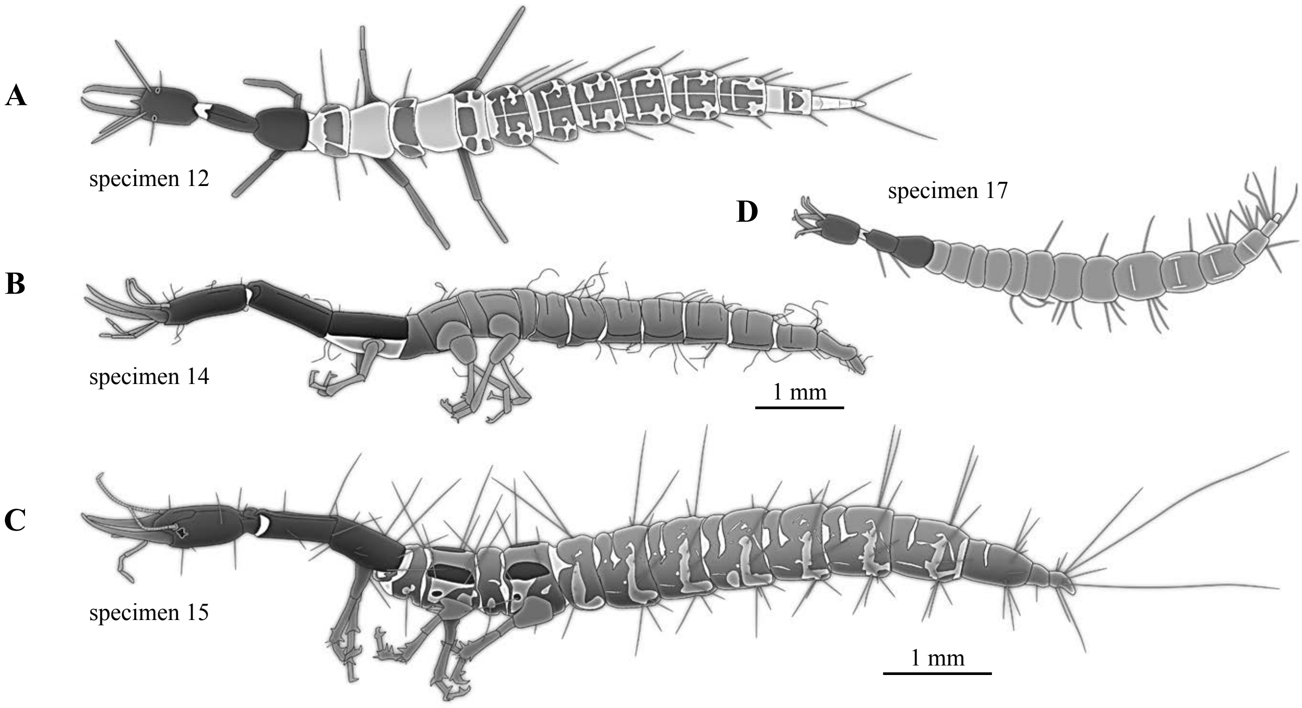

Fig. 4 – Nevrorthidae; extant immature specimens, interpretative drawings (continued). **A,** Specimen 12; *Nevrorthus fallax* (Rambur, 1842); from Grimaldi & Engel (2005: fig. 9.13); possibly ultimate larval stage. **B,** Specimen 14; *Austroneurorthus* sp.; from Beutel et al. (2010: fig. 1); unclear which larval stage. **C,** Specimen 15; *N. reconditus* Monserrat & Gavira, 2014; from Gavira et al. (2012: fig. 1); possibly ultimate larval stage. **D,** Specimen 17; *Austroneurorthus* sp.; from The Identification and Ecology of Australian Freshwater Invertebrates (https://www.mdfrc.org.au/bugguide/ retrieved June-8-2020); possibly ultimate larval stage.

larval stage of *N. iridipennis* (specimen 8) even closer to moulting into the pupa (advanced "Präpuppe", pre-pupa) in lateral view (Malicky 1984: fig. 5aD; Fig. 3D), about 7 mm in total length. Additionally, he also figured a pupa of *N. iridipennis* (specimen 9) in lateral (Fig. 3E), ventral and dorsal view (Malicky 1984: figs 5bE–G), about 6.2 mm in total length. All drawings appear to have been based on actual specimens. The drawings of the pupa have been re-figured in Wichard et al. (1995). All drawings have been re-figured in Aspöck & Aspöck (2010).

6) New (1989) re-figured specimen 3, i.e. the drawing by Riek (1970) and referenced the source. Also a detail from Zwick (1967: fig. 2) was re-figured (but incorrectly cited as Zwick 1977).

7) New (1991) re-figured specimen 3, i.e. the drawing by Riek (1970). This source was not directly seen by the current authors, the information is based on a reference in Tauber et al. (2003); therefore the figure number remains unknown.

8) New (1992: fig. 12) depicted a simplified version of specimen 3, i.e. the drawing in Riek (1970), without source reference.

9) Wichard et al. (1995) figured SEM images of an ultimate larval stage (specimen 10) of an undetermined species of *Nevrorthus* ("*Neurorthus* spec.") and a pupa (specimen 11) of *Nevrorthus iridipennis*. The larva was already far developed representing what Malicky (1984) termed "Präpuppe" (pre-pupa). It was depicted in lateral view (Wichard et al. 1995: fig. 60a; Fig. 3F). Additional details were highlighted with close-up SEM images (Wichard et al. 1995: figs 60b–f). The pupa was also shown in lateral view (Wichard et al. 1995: fig. 61b; Fig. 3G). Also here details were highlighted with close-up SEM images (Wichard et al. 1995: figs 61A, c–f). Additionally, the drawings of the pupa of Malicky (1984) were re-figured (Wichard et al. 1995: figs 7–3). There is no scale or absolute size provided, but a magnification factor. Based on this information, specimen 10 is about 8.5 mm (measured along the curvature of the back), and specimen 11 about 5.6 mm.

10) Wichard & Weitschat (1996) mostly figured amber specimens (see further below). Yet, they also re-figured specimen 2 (Wichard & Weitschat 1996: fig. 12), i.e. the drawing by Zwick (1967).

11) Weitschat & Wichard (1998) mostly figured amber specimens (see further below). Yet, they apparently also re-figured specimen 2, i.e. the drawing by Zwick (1967). Remark: this source was not seen by the current authors,

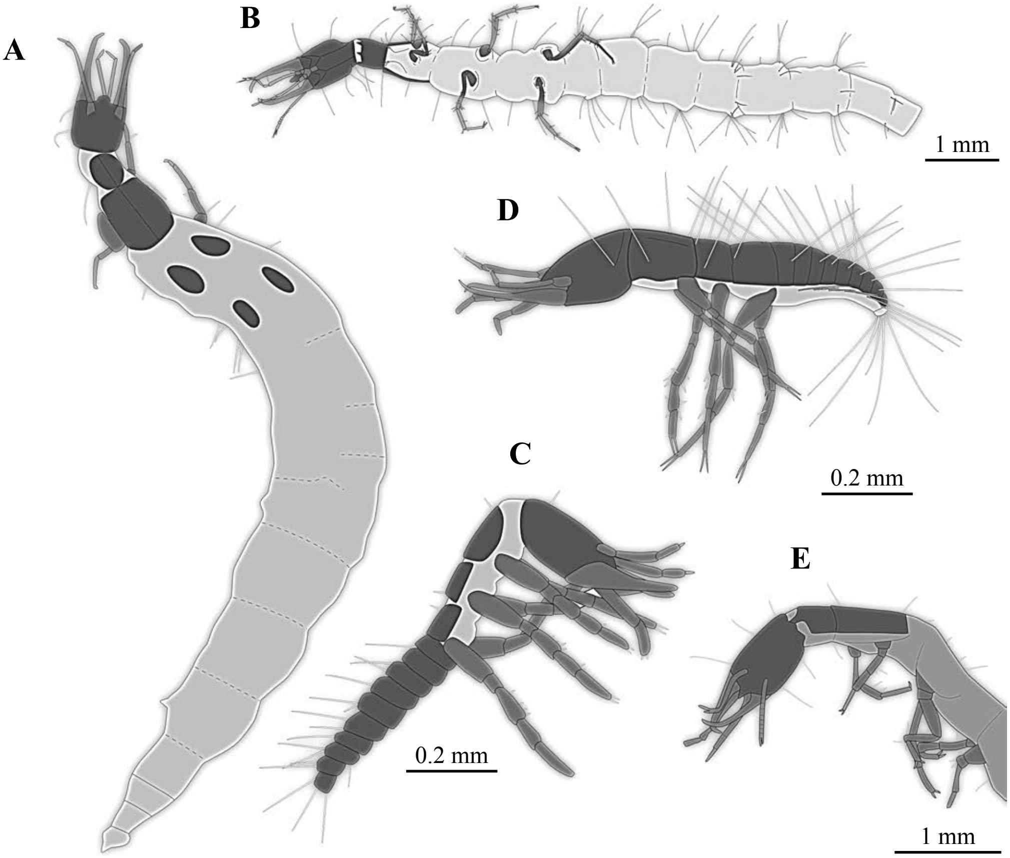

Fig. 5 – Nevrorthidae; fossil immature specimens, interpretative drawings. **A,** Specimen 18; from Wichard & Weitschat (1996: plate 10 bottom). **B,** Specimen 23; ?*Cretarophalis patrickmuelleri* Wichard, 2017; from Lu et al. (2018: figs. 10, 11). **C,** Specimen 19; ?*Rophalis relicta* (Hagen, 1856); from Wichard et al. (2009: fig. 07.20a). **D,** Specimen 20; ?*R. relicta*; from Wichard et al. (2009: fig. 07.21a, c). **E,** Specimen 21; from Wichard (2017: fig. 2a).

the information comes from one of the original authors (Wichard, pers. comm. 2019).

12) Weitschat & Wichard (2002) is a new edition of the book by Weitschat & Wichard (1998). Similar to the earlier edition mostly amber specimens are depicted, but also specimen 2, i.e. the drawing by Zwick (1967) (see Weitschat & Wichard 1998: fig. 68).

13) Tauber et al. (2003: fig. 4) re-figured specimen 3, i.e. the drawing of Riek (1970), but cited it as New (1991).

14) New (2004: fig. 3C) re-figured specimen 3, i.e. the drawing by Riek (1970), yet citing New (1991) as the source.

15) Grimaldi & Engel (2005) provided a photograph of a larva (specimen 12) of *Nevrorthus fallax* (Grimaldi & Engel 2005: fig. 9.13; from the courtesy of Aspöck & Aspöck; Fig. 4A). The image is not in a very high resolution, but allows the identification of at least some setation and details of the body surface, i.e. borders between segments and other structures necessary for measuring are clearly apparent. The specimen was re-figured in Aspöck & Aspöck (2007); there the length is stated with 12 mm.

16) Aspöck & Aspöck (2007: fig. 30) re-figured specimen 12, i.e. the photo from Grimaldi & Engel (2005).

17) Aspöck & Aspöck (2010: fig. 5; Fig. 3H) figured a larval specimen (specimen 13) of *Nevrorthus apatelius* Aspöck, Aspöck & Hölzel, 1977. The resolution of the photograph is not too good and was figured as a grey scale version. No scale or size has been provided. The image was re-figured in Aspöck et al. (2017) in a version with slightly higher resolution and in colour (used for interpretative drawing here). They also re-figured drawings from Malicky (1984): larvae and pre-pupae (Aspöck & Aspöck 2010: fig. 6) and the pupa (Aspöck & Aspöck 2010: fig. 8). Additionally, they re-figured details from Zwick (1967) (Aspöck & Aspöck 2010: fig. 7).

18) Beutel et al. (2010) provided a detailed discussion on the head anatomy of larvae of the group Nevrorthidae. They provided an SEM image of the habitus of a larval specimen (specimen 14) of *Austroneurorthus* sp. in lateral

view (Beutel et al. 2010: fig. 1; Fig. 4B), its size is about 9.5 mm. Additional details of this specimen were provided: i.e. drawings of the head (Beutel et al. 2010: fig. 2) and SEM close-ups of the head (Beutel et al. 2010: figs 3, 4). Furthermore, details of a head of a larval specimen of *Nevrorthus* sp. were depicted: volume render of synchrotron-μ-CT scan (Beutel et al. 2010: fig. 5), labelled 3D reconstructions (Beutel et al. 2010: figs 6, 7) and images of histological sections (Beutel et al. 2010: fig. 8).

19) Gavira et al. (2012) reported the first representatives of Nevrorthidae from the Iberian peninsula (Spain), based on four larval specimens. One of these specimens (specimen 15) was figured in lateral view (Gavira et al. 2012: fig. 1; Fig. 4C). Although the figure captions state 'reconstruction', the overall impression is that it is a photographic image (composite image?). The image provides many details and is probably the so far best published photograph of a larval representative of Nevrorthidae. Based on the provided scale, the specimen is about 9.6 mm in length. The image was reused in Monserrat & Gavira (2014).

20) Monserrat & Gavira (2014: fig. 9) re-figured the image from Gavira et al. (2012) and identified the larval specimen as a representative of the newly described species *Nevrorthus reconditus* Monserrat & Gavira, 2014.

21) Markovic et al. (2016) reported a first occurrence of a larval representative of Nevrorthidae from Serbia. They provided a single photograph (Markovic et al. 2016: fig. 2; specimen 16; Fig. 3I) in dorsal view: Most likely the specimen is a representative of *Nevrorthus*, possibly *N. apatelios* Aspöck, Aspöck & Hölzel, 1977. The resolution and contrast of the image are not optimal, for example setae are not visible due to overexposure in front of white background; only after optimising the images few setae become apparent. Still, boundaries between segments and structures such as sclerites or appendages are well apparent. Based on the provided scale, the specimen is 9 mm in length.

22) Aspöck et al. (2017) provided a taxonomical treatment of all formally described species of Nevrorthidae. They also re-figured (Aspöck et al. 2017: fig. 2b) the image of specimen 13, i.e. a larva of *Nevrorthus apatelius* from Aspöck & Aspöck (2010), this time in higher resolution and in colour.

23) Websites are usually not considered a "good" source for scientific research. Yet, given the scarceness of appearances of larval representatives of Nevrorthidae in the literature we decided to include also websites. Unfortunately, also in web repositories very few images were found figuring larval representatives of Nevrorthidae (while many other neuropteran larvae are available in vast numbers). Only a single occurrence was not identified as a re-figuring of one of the above mentioned cases. This website appears to additionally have an official character and is therefore included here: *The Identification and Ecology of Australian Freshwater Invertebrates* (https://www.mdfrc.org.au/bugguide/ retrieved June-8-2020) depicted a single larval representative of Nevrorthidae (specimen 17; Fig. 4D) identified as *Austroneurorthus bruneipennis* (Esben-Petersen, 1929). Yet, according to Aspöck et al. (2017) it is not possible to distinguish larval specimens of *Austroneurorthus* reliably to species level, hence the specimen should be better treated as *Austroneurorthus* sp. The image is not very detailed, yet allows the identification of segment borders and hence can be used for measurements. No scale or length was provided, only a size range of 10–12 mm.

Fossil larval representatives of Nevrorthidae depicted in the literature

Here also all occurrences are listed chronologically (see also Table 1). Also, re-figured cases are included chronologically despite the redundancy (see above).

24) Wichard & Weitschat (1996) figured a single larval representative of Nevrorthidae preserved in Baltic amber (specimen 18; Wichard & Weitschat 1996: plate 10 bottom; Fig. 5A). It is accessible in dorsal view. Also, a close-up of the anterior region is shown (Wichard & Weitschat 1996: plate 10 top). No scale or size was provided. The specimen was re-figured in Weitschat & Wichard (1998, 2002) and Wichard et al. (2009).

25) Weitschat & Wichard (1998) re-figured the specimen from Wichard & Weitschat (1996). Remark: this source was not seen by the current authors, the information comes from one of the original authors (Wichard, pers. comm. 2019).

26) Weitschat & Wichard (2002: figs 54d, e) re-figured the specimen from Wichard & Weitschat (1996).

27) Grimaldi et al. (2002: fig. 28e) figured a specimen preserved in Burmese Amber of about 2.5–3 mm in length, which they labelled "? Nevrorthidae (larva)". The image is difficult to evaluate, the preservation is at least challenging. We cannot exclude, yet also not support, the interpretation of Grimaldi et al. (2002) based on the available image. Due to this uncertainty, the specimen is not further considered here. If this specimen is indeed a larval individual of Nevrorthidae it would be very important, as with its specific size it would represent a growth stage so far not reported elsewhere. It should be investigated in more detail.

28) Wichard et al. (2009) re-figured the specimen from Wichard & Weitschat (1996) and also the close-up of the anterior region (Wichard et al. 2009: figs 07.18a, b). Additionally, they figure numerous very small specimens (about 0.9 mm overall length) all being very similar in appearance (Wichard et al. 2009: figs 07.19, 07.20b, c). They

have been interpreted as likely first instar larvae of *Rophalis relicta* (Hagen, 1856). Two specimens have been depicted in higher resolution, both in lateral view (specimen 19, Wichard et al. 2009: fig. 07.20a, Fig. 5C; specimen 20, Wichard et al. 2009: fig. 07.21a, c, Fig. 5D). Specimen 19 measures about 1.1 mm; specimen 20 measures 0.9 mm. Accompanying these images is another drawing of a specimen in dorsal view. It remains unclear whether this is specimen 20 seen from another direction. Due to this uncertainty this drawing is not further considered here. Specimen 20 has been re-figured in Gröhn (2015).

29) Gröhn (2015: fig. 7574 on page 253) re-figured one of the small-sized specimens (specimen 20) interpreted as larvae of *Rophalis relicta*.

30) Wichard (2017) figured two larval representatives of Nevrorthidae preserved in Burmese amber. Of the first specimen (specimen 21) only the anterior region is shown (Wichard 2017: fig. 2a; Fig. 5E), the first two abdominal segments are still partly in the image. The second specimen (specimen 22) is depicted as an overview (Wichard 2017: fig. 2b). Specimen 22 lies back to back to a cockroach. The specimen is re-figured in this contribution (Fig. 6). The preserved part of specimen 21 is about 3.5 mm in length. The entire length could have measured up to 10 mm. Specimen 22 measures about 6.2 mm.

31) Lu et al. (2018) figured a larval representative of Nevrorthidae (specimen 23) preserved in Burmese amber (Lu et al. 2018: figs 10–13; Fig. 5B), suggested to be a representative of *Cretarophalis patrickmuelleri* Wichard, 2017. The specimen is accessible from the ventral body side, the posterior end is apparently not accessible. The preserved part is 9.2 mm long, the entire specimen might have measured about 10 mm.

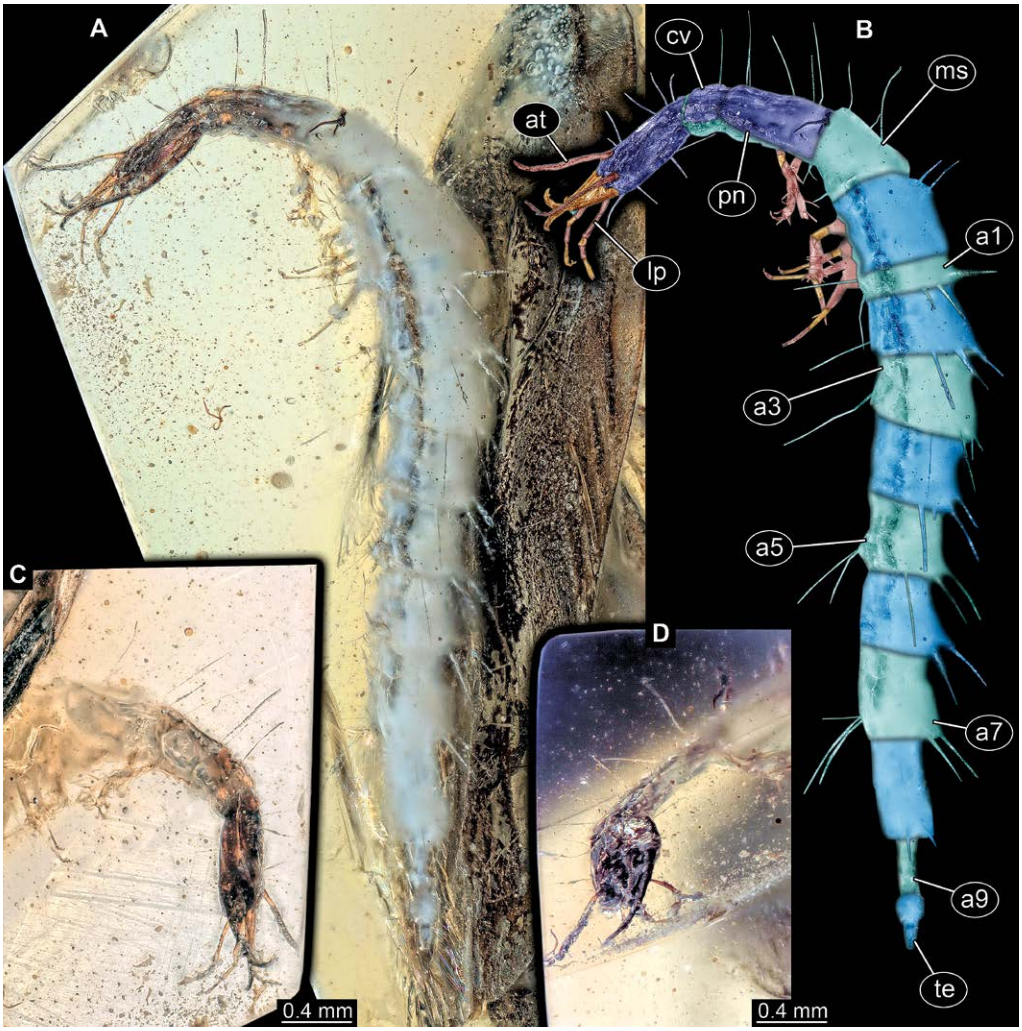

Fig. 6 – Nevrorthidae; fossil larva preserved in Burmese amber (BUB 0795); specimen 22. **A,** Composite image. **B,** Colour-marked version. **C,** Close-up of head from the other side. **D,** Close-up of head from anterior. Abbreviations: a1–9 = abdominal segments 1–9; at = antenna; cv = cervix (neck); lp = labial palp; ms = mesothorax; pn = pronotum; te = trunk end.

Additional fossil larval representatives of Nevrorthidae

To expand the data set, we figure here additional larval specimens of Nevrorthidae and present new photographs of one already published specimen; all specimens are preserved in amber.

32) Specimen 22 (BUB 0795), originally figured in Wichard (2017), is re-figured here (Figs 6A, B). Additionally, close-ups of the head are shown in different angles (Figs 6C, D). The specimen has a rather short cervix. It measures about 6.2 mm. A prominent syn-inclusion is an adult cockroach.

33) Specimen 24 (Gr 1341A) is accessible in dorsal view, other aspects are not accessible. Not only the overall body organisation (Figs 7A, B), but also some details of the head structures (Fig. 7C) and the thoracic appendages are accessible (Figs 7D, E). The specimen measures about 8.1 mm in total length. A second specimen is present in the same piece of amber (see next point). The specimen shows the overall slender morphology known for older larvae of Nevrorthidae. Anterior body well accessible, showing clear outlines of head capsule, cervix and prothorax. All further posterior segments visible in outline, but details largely obscured by Verlumung (Fig. 7A). Head capsule with prominent moulting suture (Fig. 7C). Head appendages include antenna, stylets and labial palps. Antenna is elongated and shows subdivision into numerous elements (about 17), Stylets taper distally; they are straight proximally, but sharply curved more distally. Labial palps shorter than antennae, about half the length. Subdivision into at least four elements well apparent distally, proximal region obscured. Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 7D).

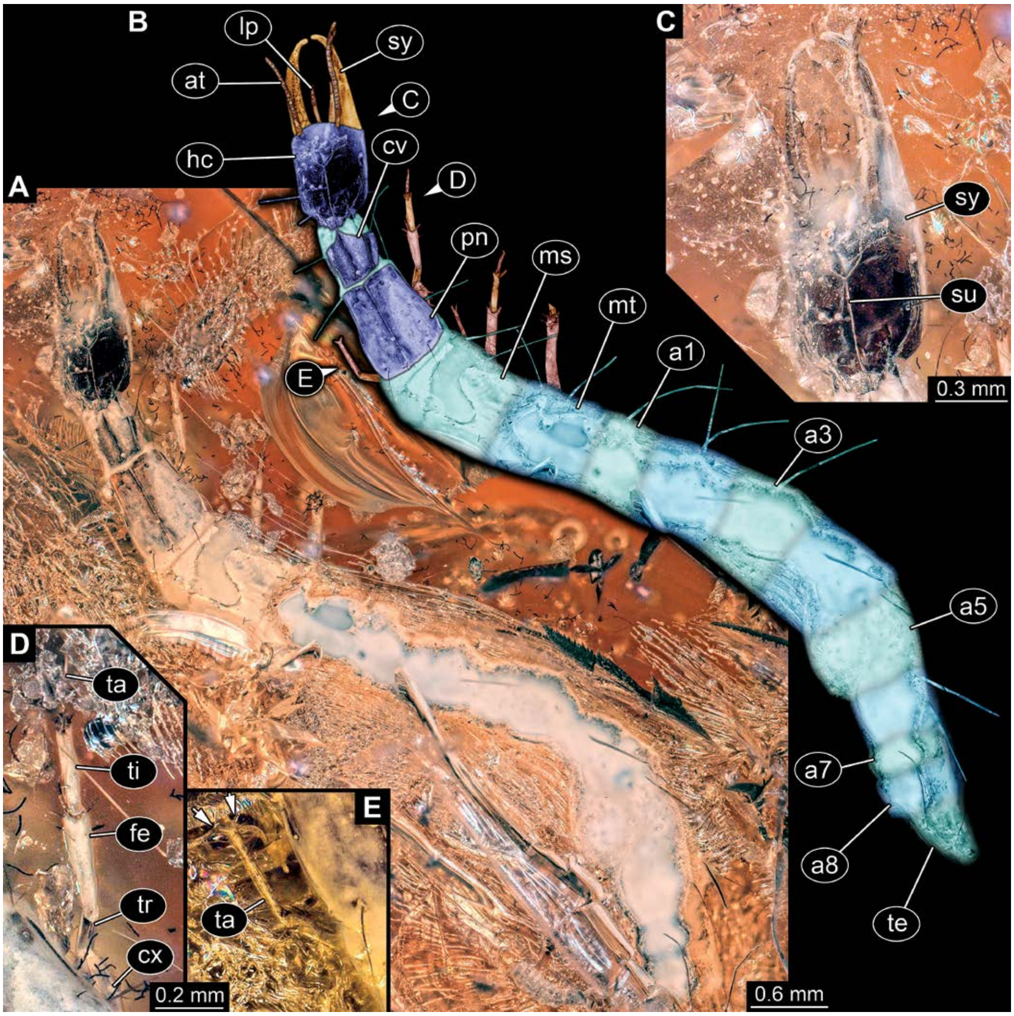

Fig. 7 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 1341A); specimen 24. **A,** Composite image, dorsal view. **B,** Colour-marked version of A. **C,** Close-up on head. **D,** Close-up on thoracic appendage. **E,** Close-up on tarsus of thoracic appendage; arrows indicate tarsal claws. Abbreviations: a1–9 = abdominal segments 1–9; at = antenna; cv = cervix (neck); cx = coxa; fe = femur; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pn = pronotum; su = suture; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

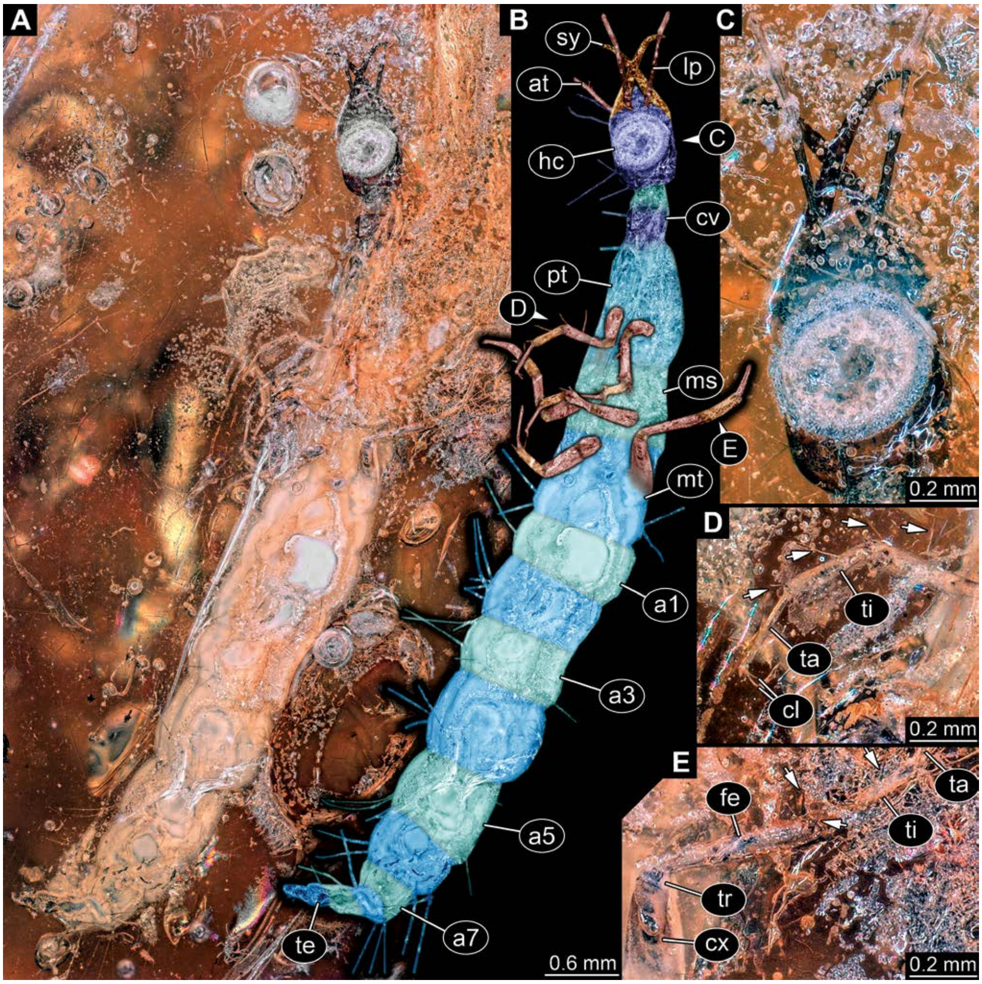

Fig. 8 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 1341B); specimen 25. **A,** Composite image, ventral view. **B,** Colour-marked version of A. **C,** Close-up on head. **D, E,** Close-ups on thoracic appendages. Abbreviations: a1–9 = abdominal segments 1–9; at = antenna; cl = tarsal claws; cv = cervix (neck); cx = coxa; fe = femur; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

Coxa appears tubular, elongate; trochanter similar, but shorter; femur significantly longer and thicker; tibia slightly shorter and thinner again; tarsus quite slender, elongate but shorter than tibia; distally with a pair of claws (Fig. 7E). Body carrying numerous elongate setae, yet their insertion areas are mostly obscured.

34) Specimen 25 (Gr 1341B) is accessible in ventral view, other aspects are not accessible; it is preserved in the same amber piece as specimen 24. The specimen measures about 8.2 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae (Figs 8A, B). Overall outline well accessible, yet most details, especially of the more posterior body obscured by Verlumung and numerous bubbles. Head with antennae, stylets and labial palps, but details, such as subdivision largely obscured (Fig. 8C). Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 8E). Coxa tubular, elongate; trochanter similar, but shorter; femur significantly longer and thicker; tibia slightly shorter and thinner again; tarsus quite slender, elongate but shorter than tibia; distally with a pair of claws (Fig. 8D). Body carrying numerous elongate setae, yet their insertion areas are mostly obscured.

35) Specimen 26 (Gr 7668) is accessible from both lateral sides of the body. The amber is very clear, hence the overall body is easily accessible (Figs 9A–C). The specimen measures 8 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae. The specimen is strongly curved dorsally, basically adopting a U-shaped posture (Fig. 9A–C). The head is seen in lateral view, hence dorsal and ventral details are not accessible. Head with antennae, stylets and labial palps. Antennae elongate slender, subdivision apparent in the distal region (Fig. 9D). Stylets curved, tapering distally. Labial palps prominent. Subdivided into five major elements. Element 1 rather short; 2 very long, mak-

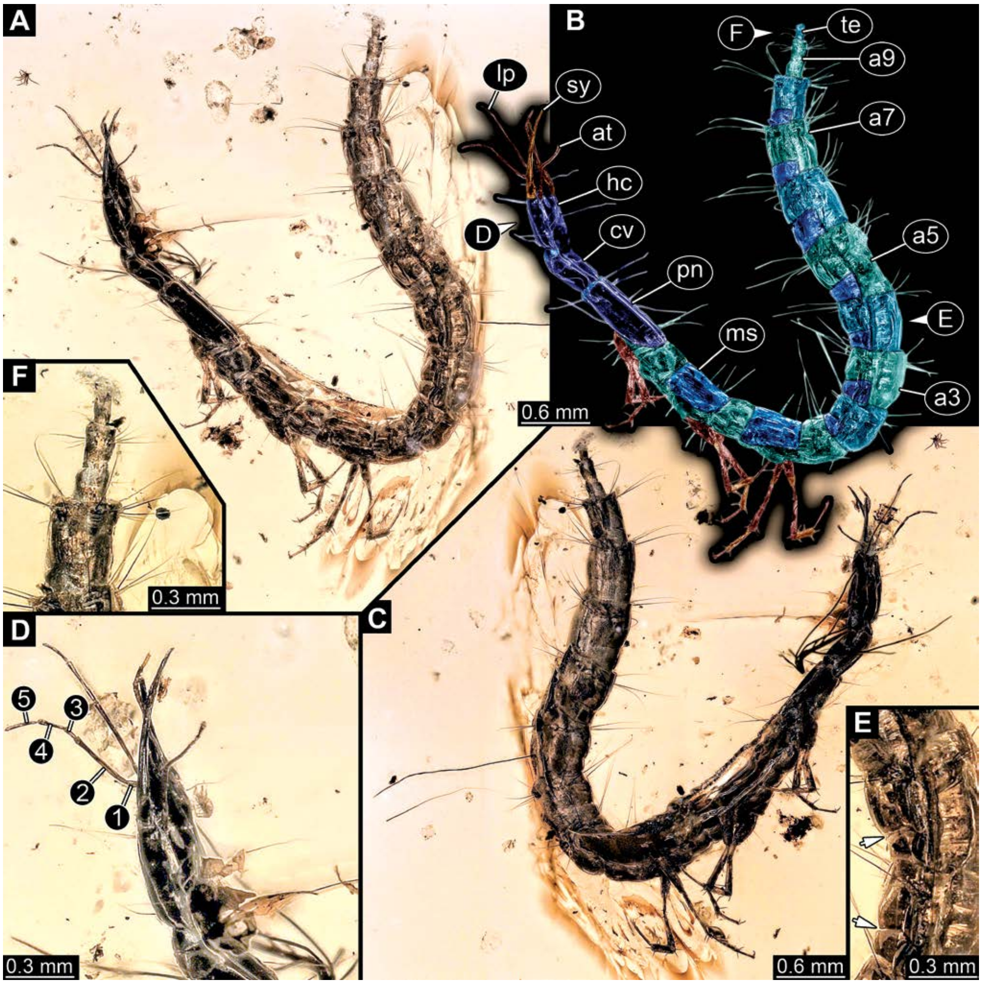

Fig. 9 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 7668); specimen 26. **A,** Composite image lateral view, left. **B,** Colour-marked version of A. **C,** Composite image lateral view, right. **D,** Close-up on head. **E,** Close-up on trunk segment subdivision; arrows mark inter-segmental folds. **F,** Close-up on trunk end. Abbreviations: 1–5 = antenna elements 1–5; a3–9 = abdominal segments 3–9; at = antenna; cv = cervix (neck); hc = head capsule; lp = labial palp; ms = mesothorax; pn = pronotum; sy = stylet; te = trunk end.

ing up half of the length of the palp; 3 quite short, similar to element 1; 4 a bit longer again; 5 about as long as 4, distally rounded. Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 9A–C). Coxa tubular, elongate; trochanter similar, but shorter; femur significantly longer and thicker; tibia slightly shorter and thinner again; tarsus quite slender, elongate but shorter than tibia; distally with a pair of claws (Fig. 9A–C). Prominent setae arise from the appendage elements. Femur and tibia distally with a set of three setae each. Few, less prominent setae also apparent further proximally, no clear pattern apparent. All trunk segments posterior to the prothorax with distinct pattern of dorsal specialisation. After anterior third of the segment a distinct fold is apparent, subdividing the dorsal region of each segment into two distinct subregions (Fig. 9E). Trunk segments with prominent long setae. These arise close to the posterior end of each segment and appear to form a kind of ring around the segment. This is especially apparent in the very posterior segments. In the last three segments there appear to be four setae dorsally and six ventrally (Fig. 9F).

36) Specimen 27 (Gr 2518) is accessible in dorsal and ventral view. The specimen measures 7.8 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae (Fig. 10A–C). Overall outline well accessible, yet most details, especially of the more posterior body obscured by Verlumung and numerous bubbles. Head with antennae, stylets and labial palps. Antenna is elongated and shows subdivision into numerous elements (about 16), Stylets taper distally; they are straight proximally, but sharply curved more distally. Labial palps slightly shorter than antennae, subdivided into five elements (Fig. 10D). Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 10C, E). Coxa conical, elongate; trochanter similar, but shorter; femur significantly longer and thicker; tibia slightly shorter and thinner again; tarsus quite slender, elongate

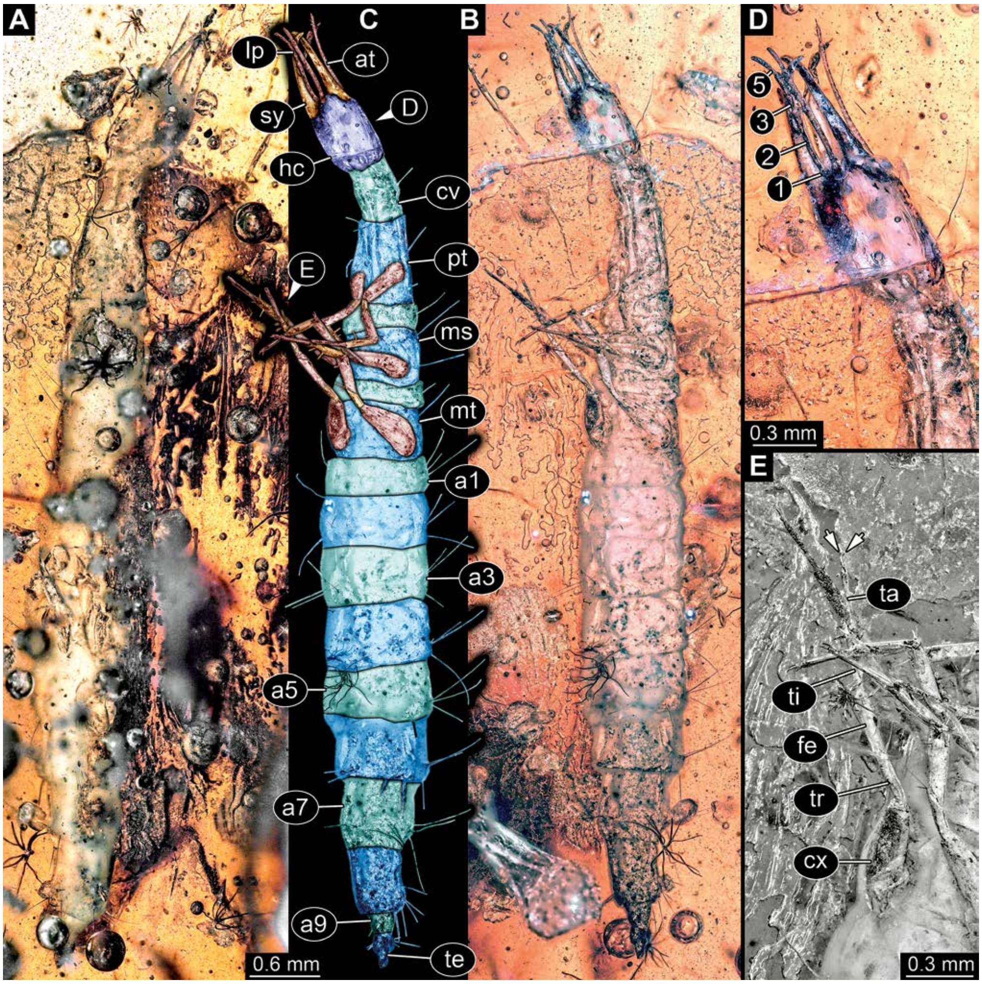

Fig. 10 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 2518); specimen 27. **A,** Composite image, dorsal view. **B,** Composite image, ventral view. **C,** Colour-marked version of B. **D,** Close-up on head. **E,** Close-up on thoracic appendage (desaturated to remove disturbing colour effects); arrows mark tarsal claws. Abbreviations: 1–5 = antenna elements 1–5; a1–9 = abdominal segments 1–9; at = antenna; cv = cervix (neck); cx = coxa; fe = femur; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

but shorter than tibia; distally with a pair of claws (Fig. 10E). Prominent setae arise from the appendage elements, exact arrangement difficult to assess. Trunk segments with prominent long setae; insertion areas obscured.

37) Specimen 28 (Gr 7095) is accessible in lateral view (Figs 11B, C). The specimen is largely surrounded by whitish opaque resin (“Verlumung”) and only few details are accessible (Fig. 11D). It measures about 8.5 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae (Fig. 11B, C), but appears a bit more “fat” than other specimens. Despite the Verlumung, head outline and appendages (antennae, stylets and labial palps) are apparent, yet details remain obscured (Fig. 11B, C). Trunk appendages are strongly verlumt, only vague outlines become apparent; one can guess the subdivisions (Fig. 11D). Numerous long setae arise from the trunk, yet due to the Verlumung their insertion areas are obscured. Interestingly, the specimen is preserved with several syn-inclusions. In addition to the larval representative of Nevrorthidae, this piece of amber contains a single specimen of a pupa of the genus *Mycetobia* Meigen, 1818 (Diptera: Anisopodidae; Fig. 11A), two adult long-legged flies (Diptera: Dolichopodidae), two worker-type ants of the species *Lasius schiefferdeckeri* Mayr, 1868, an adult caddisfly (Trichoptera) and two unidentifiable euarthropodan specimens (?Insecta) covered with thick, white film.

38) Specimen 29 (Gr 2768) is accessible from both lateral sides of the body. The amber is very clear, hence the overall body is easily accessible (Figs 12A–C). Also, smaller details of the head (Fig. 12D) and of the thoracic appendages (Fig. 12E) are well preserved. The specimen appears much more massive (“stocky”) than most of the other fossils. The specimen measures about 5.6 mm in total length.

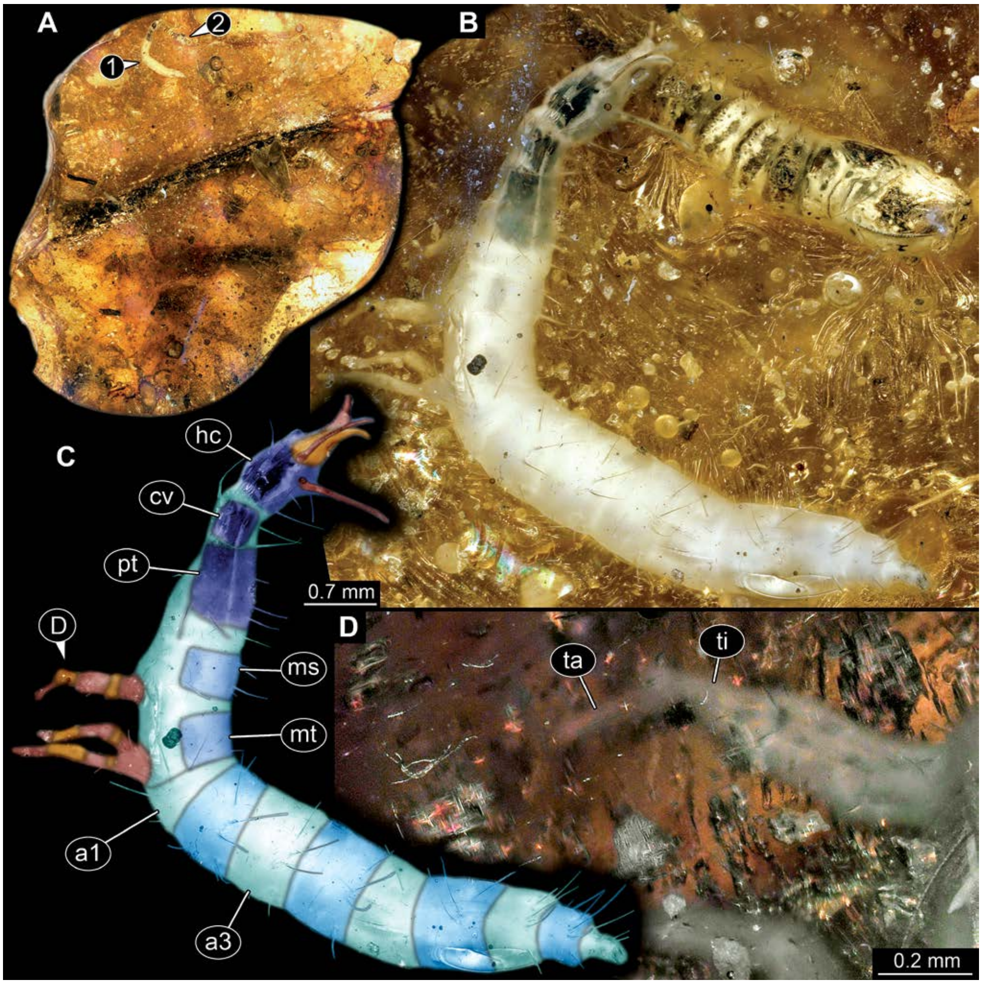

Fig. 11 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 7095); specimen 28. **A,** Overview of the amber piece; 1 marks the larva, 2 marks a pupa of the dipteran group *Mycetobia*. **B,** Composite image, lateral view. **C,** Colour-marked version of B. **D,** Close-up on thoracic appendage. Abbreviations: a1–3 = abdominal segments 1–3; cv = cervix (neck); hc = head capsule; ms = mesothorax; mt = metathorax; pt = prothorax; ta = tarsus; ti = tibia.

The specimen shows the overall slender morphology known for older larvae of Nevrorthidae (Fig. 12A, B, D), but appears less slender, more stout. The head is seen in lateral view, hence dorsal and ventral details are not accessible. Head with antennae, stylets and labial palps. Antennae elongate slender, subdivided into about 15 elements (Fig. 12C). Stylets curved, tapering distally. Labial palps slightly shorter than antennae, subdivision only apparent in the distal region. Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus), but proximal elements not well visible; distally with a pair of claws (Fig. 12E). Prominent setae arise from the appendage elements. Femur and tibia distally with a set of three setae each. Few less prominent setae also apparent further proximally, no clear pattern apparent. Mesothorax and metathorax with distinct pattern of dorsal specialisation. After anterior third of the segment a distinct fold is apparent, subdividing the dorsal region of each segment into two distinct subregions. Such a subdivision is not apparent in further posterior segments. Numerous elongate setae arising from the trunk segments. They seem to form rings around the posterior ends of the trunk segments, most apparent in the more posterior ones. At least ten insertions apparent on one body side on one segment, evenly distributed. Yet, the dorsal setae appear longer than the ventral ones; lateral setae appear even shorter.

39) Specimen 30 (SMF 256) is well accessible from the dorsal side (Figs 13A, B) and less well from the ventral side (Fig. 13C). Accessible details include aspects of the head appendages (Fig. 13D) and of the trunk subdivision (Fig. 13E). The specimen measures about 5.6 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae (Fig. 13A–C), but appears less slender, more stout. Head outline well apparent in dorsal view. Head with antennae, stylets and labial palps. Antennae elongate slender, subdivided into about 17 elements (Fig. 13D). Stylets curved, tapering dis-

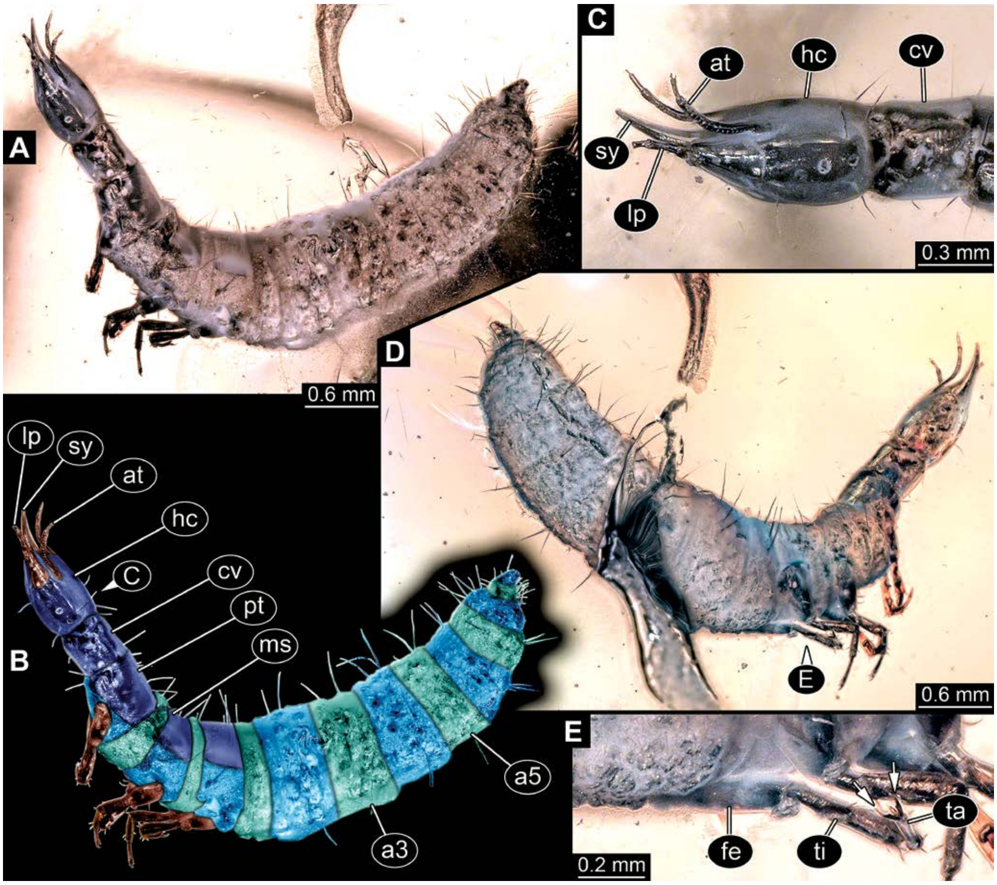

Fig. 12 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 2768); specimen 29. **A,** Composite image, lateral view, left. **B,** Colour-marked version of A. **C,** Close-up on head. **D,** Composite image, lateral view, right. **E,** Close-up on thoracic appendages; arrows mark tarsal claws. Abbreviations: a3–5 = abdominal segments 3–5; at = antenna; cv = cervix (neck); fe = femur; hc = head capsule; lp = labial palp; ms = mesothorax; pt = prothorax; sy = stylet; ta = tarsus; ti = tibia.

tally. Labial palps slightly shorter than antennae, subdivision into at least four elements apparent, proximal region not accessible. Trunk appendages most probably with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 13C); details largely obscured by Verlumung. Sclerotised neck (cervix) with pattern of numerous tightly arranged pits or dimples (Fig. 13A, B). All trunk segments posterior to the prothorax with distinct pattern of dorsal specialisation. After anterior third of the segment a distinct fold is apparent, subdividing the dorsal region of each segment into two distinct subregions. Stronger expressed in mesothorax and metathorax, but still apparent in anterior abdomen segments. Further posterior abdomen segments partly concealed by Verlumung. In the posterior region of both mesothorax and metathorax, a pair of sclerites is apparent. Almost as long as the posterior region, each with a width of about 20% of the trunk width, hence longer than broad, slightly more than 2x. Inner edge of sclerite stronger curved than outer edge, gibbous. Three setae arising from each sclerite, one anterior, one postero-median, one postero-lateral. Numerous elongate setae arising from the trunk segments. Insertion areas largely obscured by Verlumung.

40) Specimen 31 (Gr 2769) is accessible from both lateral sides of the body; it is well accessible from one direction (Figs 14A, B, D, E) and only partly from the other (Fig. 14C) where the specimen is largely obscured by a syninclusion, a late nymphal instar of a plecopteran with well preserved thoracic gills. The segments of the posterior abdomen are rather short and more massive than in most specimens, with the exception of specimen 29. The specimen measures 5.2 mm in total length. Yet, the abdomen is only incompletely known. Abdominal segments 2 and 3 appear faint and may have been distorted. The specimen might have been shorter in this region originally. The head is seen in lateral view, hence dorsal and ventral details are not accessible. Head with antennae, stylets and labial palps. Details obscured (Fig. 14D). Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 14E). Coxa tubular, elongate; trochanter similar, but shorter; femur significantly longer and thicker; tibia slightly shorter and thinner again; tarsus quite slender, elongate but shorter than tibia; distally with a pair of claws (Fig. 14E). Numerous elongate setae arising from the trunk segments. Insertion areas largely obscured by Verlumung.

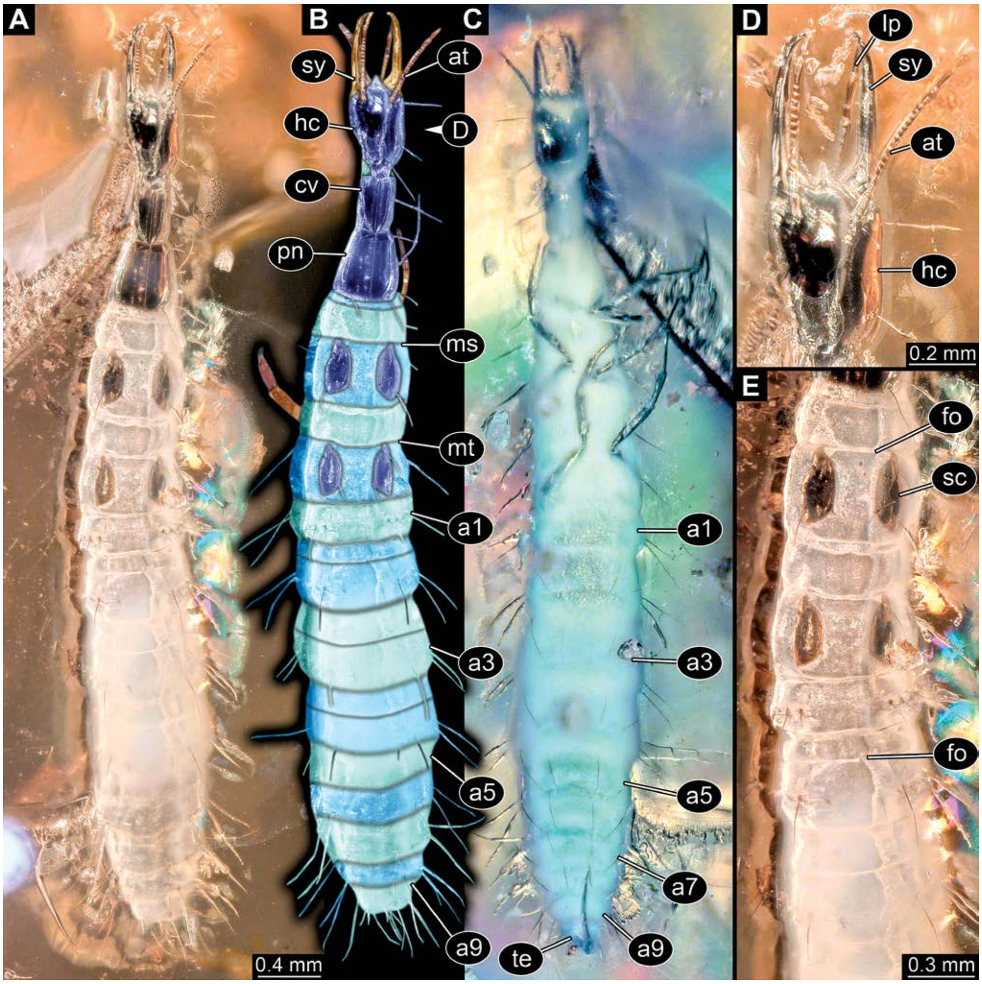

Fig. 13 – Nevrorthidae; fossil larva preserved in Baltic amber (SMF 256); specimen 30. **A,** Composite image, dorsal view. **B,** Colour-marked version of A. **C,** Composite image, ventral view. **D,** Close-up on head. **E,** Close-up on trunk segment subdivision. Abbreviations: a1–9 = abdominal segments 1–9; at = antenna; cv = cervix (neck); hc = head capsule; fo = fold; lp = labial palp; ms = mesothorax; mt = metathorax; pn = pronotum; sc = sclerite; sy = stylet; te = trunk end.

41) Specimen 32 (Gr 1383A) is accessible in ventral view (Figs 15A–C) and sits very deep within the amber piece. As the amber piece contains multiple inclusions it is not possible to further grind it down. The specimen measures 0.8 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae in the anterior region, especially the posterior trunk but appears much less slender, the segments of the abdomen are extremely short. Head outline well apparent in ventral view. Head with antennae, stylets and labial palps. Antennae elongate slender, but much stouter than in other specimens; subdivision into at least three elements (Fig. 15A–C). Stylets curved, tapering distally. Labial palps slightly shorter than antennae, subdivision into at least three elements apparent. Trunk appendages well preserved, but all six are entangled into each other, partly obscuring subdivision and details. Sclerotised neck region (cervix) behind head quite short, especially in comparison to pronotum. Mesothorax and metathorax with distinct pattern of dorsal specialisation. A distinct fold is apparent, subdividing the dorsal region of each segment into two distinct subregions, with the anterior one being very short. Abdomen segments very short, even shorter than the cervix, Numerous elongate setae arising from the trunk segments; exact arrangement not revolvable due to optical limitations of the amber. In the same amber piece a comparable specimen is preserved (see next point), as well as a larval specimen of Sisyridae (figured in Wichard et al. 2009: fig. 07.07c).

42) Specimen 33 (Gr 1383B) is preserved in lateral view (Fig. 16). The specimen measures 0.7 mm in total length. The specimen shows the overall slender morphology known for older larvae of Nevrorthidae in the anterior region (Fig. 16A–D), especially the posterior trunk but appears much less slender, the segments of the abdomen are extremely short. Head outline well apparent in lateral view. Head with antennae, stylets and labial palps. Anten-

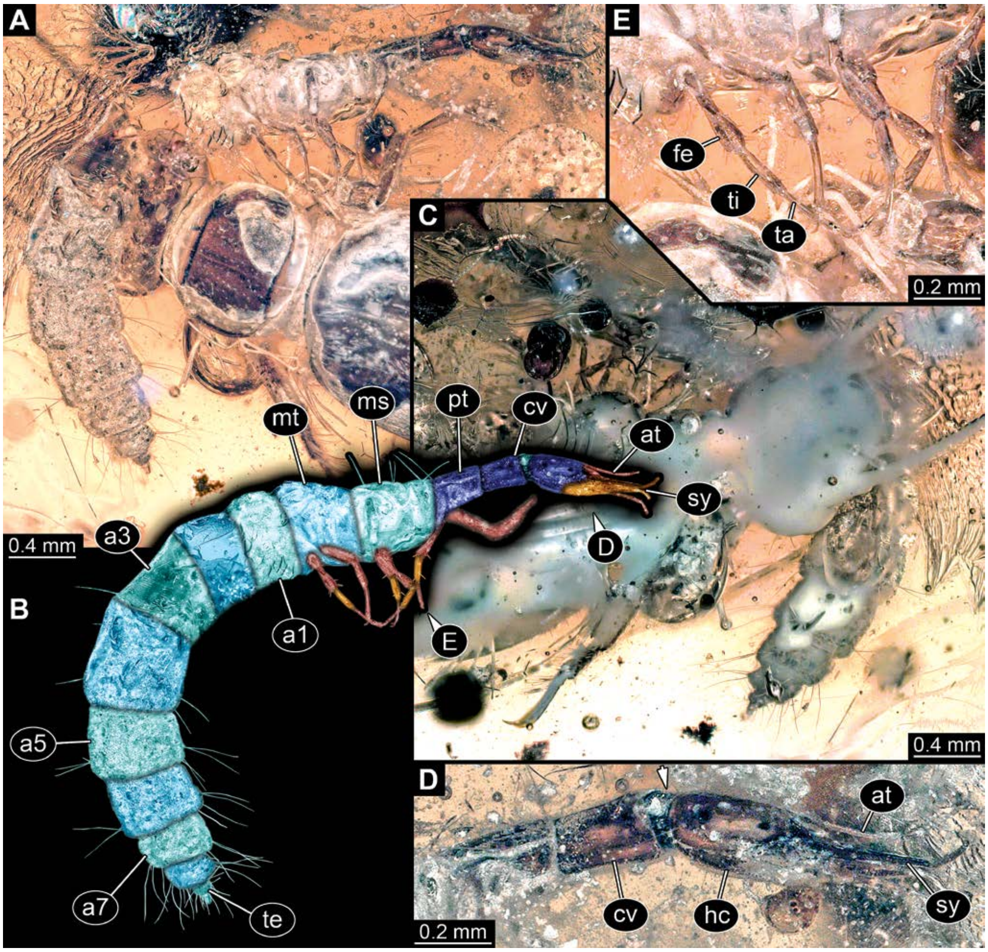

Fig. 14 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 2769); specimen 31. **A,** Composite image, lateral view, right. **B,** Colour-marked version of A. **C,** Composite image, lateral view, left. **D,** Close-up on head; arrow marks Rollengelenk. **E,** Close-up on thoracic appendages. Abbreviations: a1–7 = abdominal segments 1–7; at = antenna; cv = cervix (neck); fe = femur; hc = head capsule; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; te = trunk end; ti = tibia.

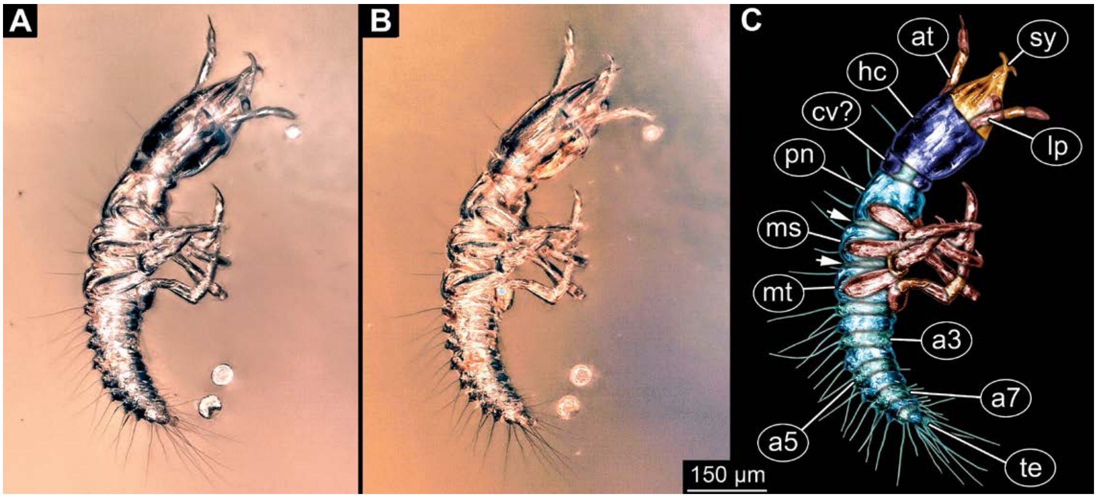

Fig. 15 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 1383A), specimen 32. **A–C,** Composite images, ventral view. **A,** Under cross-polarised light. **B,** Under ring light. **C,** Colour-marked version of A; arrows mark anterior set-off regions of mesothorax and metathorax. Abbreviations: a3–7 = abdominal segments 3–7; at = antenna; cv? = possible cervix (neck); hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pn = pronotum; sy = stylet; te = trunk end.

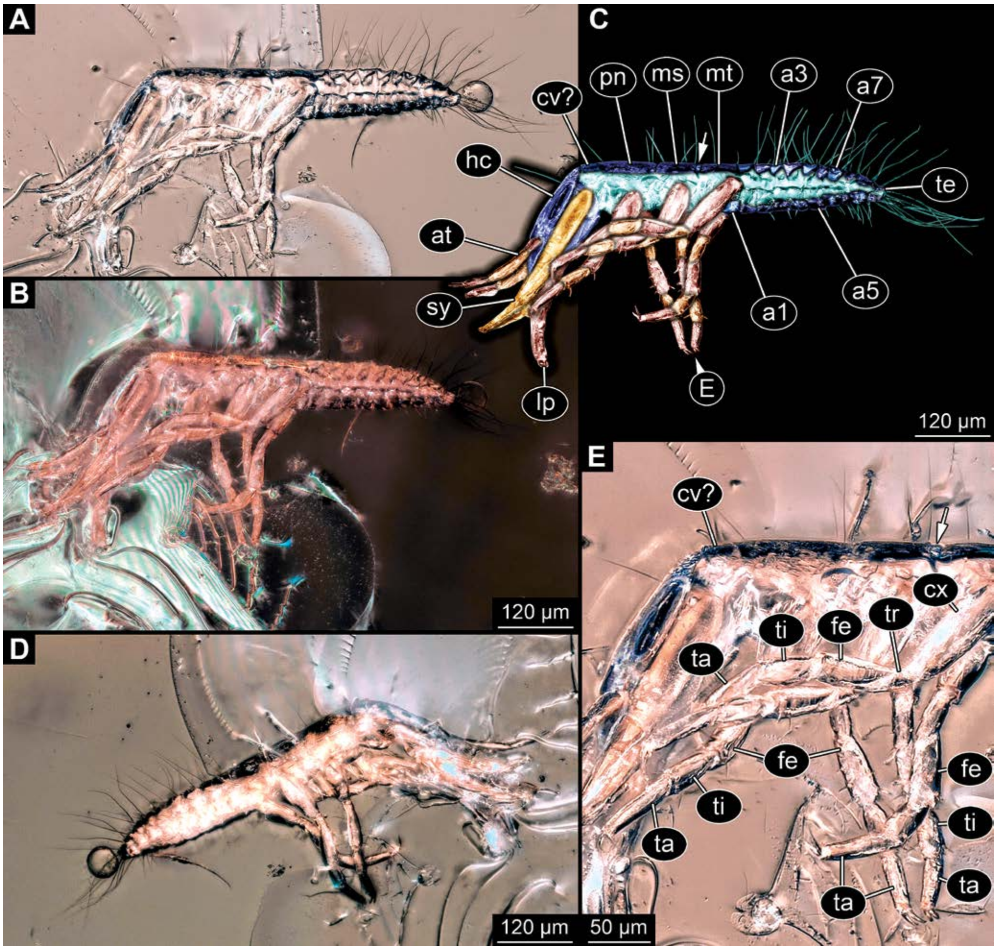

Fig. 16 – Nevrorthidae; fossil larva preserved in Baltic amber (Gr 1383B); specimen 33. All images flipped; composite images, lateral view. **A–C, E,** Right side. **D,** Left side. A, C–E under ring light, B under cross-polarised light. **C,** Colour-marked version of A; arrow marks anterior set-off regions of metathorax. **E,** Close-up on anterior trunk region; arrow marks anterior set-off region of metathorax. Abbreviations: a1–7 = abdominal segments 1–7; at = antenna; cv? = possible cervix (neck); cx = coxa; fe = femur; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pn = pronotum; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

nae elongate slender, but much stouter than in other specimens; subdivision into at least three elements (Fig. 16A–D). Stylets curved, tapering distally. Labial palps slightly shorter than antennae, no clear subdivision apparent. Trunk appendages with five major elements (coxa, trochanter, femur, tibia, tarsus; Fig. 16E). Coxa tubular, elongate; trochanter similar, but shorter; femur longer; tibia slightly shorter; tarsus quite slender, elongate but shorter than tibia; distally with a pair of claws (Fig. 16E). Short setae arise from the appendage elements. Femur and tibia distally with a set of at least two setae each. Few less prominent setae also apparent further proximally, no clear pattern apparent. Sclerotised neck region (cervix) behind head quite short, especially in comparison to pronotum. Metathorax with distinct pattern of dorsal specialisation. A distinct fold is apparent, subdividing the dorsal region of each segment into two distinct subregions, with the anterior one being very short; possibly also the case for the mesothorax, yet not well apparent. Abdomen segments very short, even shorter than the cervix. Numerous elongate setae arising from the trunk segments; exact arrangement not revolvable due to optical limitations of the amber. Dorsal setae appear longer than ventral ones. Specimens 32 and 33 are both tiny specimens similar to those depicted in Wichard et al. (2009). Although the amber piece is not as clear as in the specimens in Wichard et al. (2009), there are enough details accessible to identify them as similar. An important difference is that they appear to have a cervix, as well as a subdivision of mesothorax and metathorax.

Discussion

The data set

As outlined above, we have a data set of 33 specimens of immatures of Nevrorthidae. This includes various different stages and reports from extant and fossil fauna as well.

It is interesting that only 17 of these reports are extant and 16 are fossil. Also, it is interesting to note that especially small individuals are only known as fossils.

It is also unfortunate that quality of the input in the data set differs. Of some specimens we have considerable details available, of others we have only a vague overview. Often also no scales are available. It is important to note that extant specimens are not necessarily known in finer details than the fossils. Still, it is possible to measure certain aspects of the body of the immatures to at least gather some quantitative information, also regarding the specimens with only rather few accessible details.

Even with adult specimens, used here for some comparisons, there are some difficulties. Figures in the literature not always show the entire specimen, which makes them difficult to incorporate in a measuring approach. Also, in many needled specimens the abdomen has collapsed and can therefore not be used for measuring as well.

Post-embryonic development of representatives of Nevrorthidae

Number of instars. From the extant specimens we mainly know the later post-embryonic development. Most known specimens have been interpreted to be late larval stages (specimens 1–4, 6, 12–17), pre-pupae (specimens 7, 8, 10) or pupae (specimens 9, 11). Only a single specimen appears to represent an earlier, penultimate larval stage (specimen 5).

Last larval stages appear to reach sizes of about 10 mm or even slightly above; this is also true for some of the fossils. Zwick (1967) believed that the larger specimens of about 12–13 millimetres are ultimate stages, while specimens of about 10 mm would represent a smaller stage. This would require a size increase of about 30%, which is a realistic size gain for a single moult for many representatives of Euarthropoda (see discussion in Kutschera et al. 2012 and references therein).

Yet, this interpretation was not supported by the observations of Malicky (1984). He presented a penultimate larva (specimen 5) that seems to be slightly longer than 4 mm (excluding stylets). If Malicky (1984) was correct, this would consequently indicate two things:

1. The last larval stage of Nevrorthidae would show considerable variation concerning size, but also number of subdivisions of antenna elements as observed by Zwick (1967). Such a strong variation could also partly explain the specimen shown by Beutel et al. (2010; specimen 14), in which the abdomen appears rather short, possibly due to shrinking artefact during the drying process or showing a certain degree of flexibility of this region (also apparent in formation of the pre-pupa).
2. The body length has to increase by slightly more than 100%, roughly doubling its size in one moult. This is a remarkable increase compared to many representatives of Euarthropoda outside Insecta (cf. Kutschera et al. 2012), but for an insect species and also neuropteran species this is theoretically possible (e.g. Legaspi et al. 1994).

Even if we assume an increase of 100% for each moult, we run into an interesting observation: Late stage larvae of the group Nevrorthidae reach sizes of about 10 mm (excluding stylets). We furthermore know that the earliest stages, assumed to represent hatchlings, known from the fossil record, are about 0.6 mm (excluding stylets). If we assume increases of about 100% per moult we could expect a second stage of slightly more than 1.2 mm in size, a third stage of a bit more than 2.4 mm, a fourth stage with about 4.8 mm in size and an ultimate larval instar five with about 10 mm. However, if we simply plot the sizes of all measurable larvae provided with a scale (Fig. 17A) we see four more or less distinct "clusters" or "clouds". The data set is considerably too unbalanced and incomplete to apply any statistic test regarding this "clustering". Yet, it supports to a certain degree the observations by Zwick (1967) who indirectly assumed a moderate size gain of about factor 1.3. We have a more or less distinct "cluster" of four specimens representing possible first instar larvae. All specimens measure about 1 mm in total length (specimens 19, 20, 32, 33). Then there is a large gap further indicating that we lack stages in between (the specimen reported by Grimaldi et al. 2000 might partly fill this gap). The next "cluster" includes specimens that measure between 4 mm to slightly more than 6 mm. The "clustering" is not very tight here and the specimens may in fact represent different instars. In this loose "cluster" we find specimen 5, the one that Malicky (1984) interpreted as a penultimate instar. Also three of the fossil specimens plot here that appear less elongate than most of the larger specimens (specimens 29 to 31), a character shared with specimen 5. This could be a further argument that at least these three specimens indeed represent a single developmental stage. The largest specimen of this loose "cluster" measures more than 6 mm; it differs from the three other specimens as it resembles the larger larvae in overall sleekness. The remaining larvae form two "clusters", one with sizes ranges of about 8 mm to slightly less than 10 mm, and another one with specimens of 11 mm to 13 mm.

If we assume a first stage with 1 mm overall length, we could expect a second stage with about 1.3 mm in length if we assume a size increase of 130%. Such a stage is not represented by any specimen. A third hypothetical stage would be around 1.7 mm in length. A fourth stage with about 2.2 mm is also not represented. A fifth stage with 2.8 mm could be represented by the specimen of Grimaldi et al. (2002). A sixth stage would measure about 3.7 mm, but is also not represented by an actual specimen. A seventh stage with about 4.8 mm could be represented by at least four of the specimens of "cluster" 2. The largest specimens of this "cluster" could represent an eighth stage which should have about 6.3 mm. "Cluster" 3 could represent a

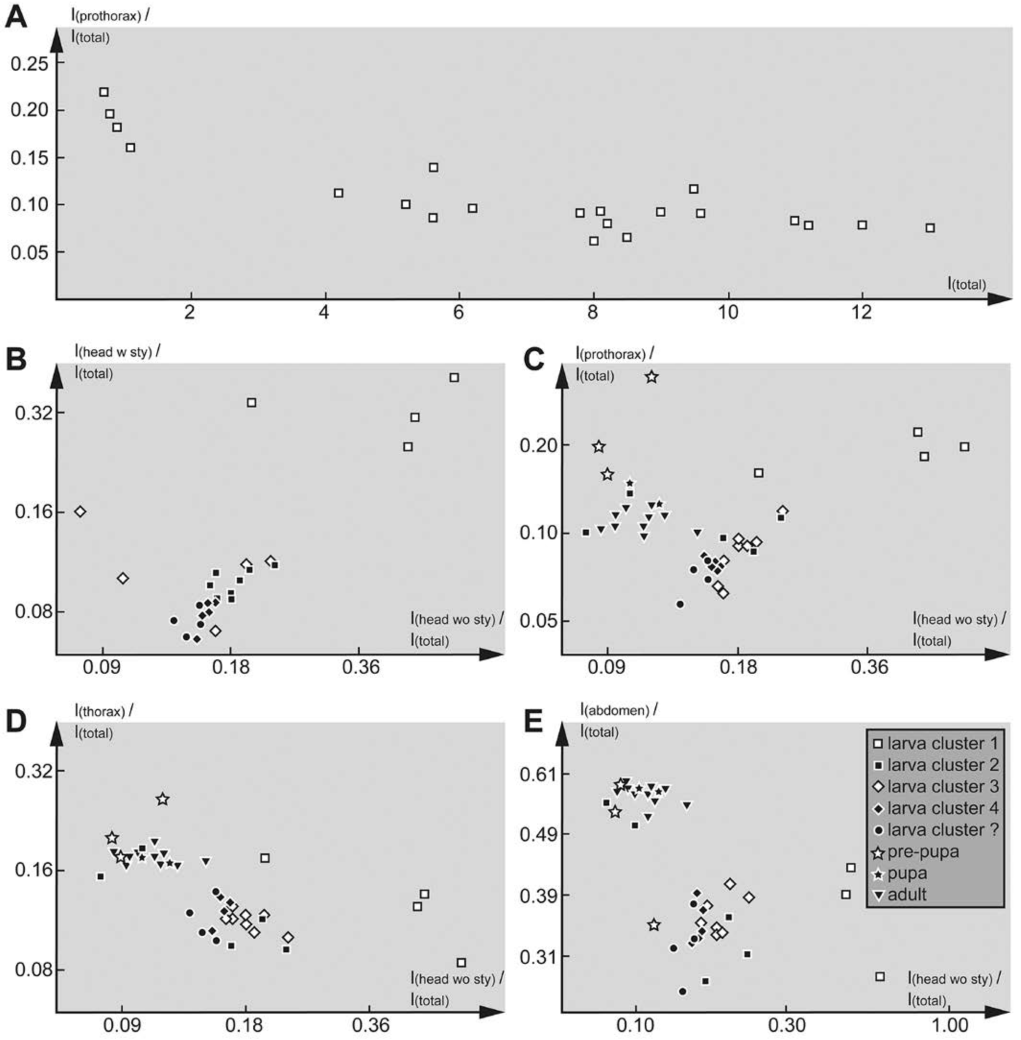

Fig. 17 – Scatterplots of measurements. **A,** Ratio (length of prothorax divided by total length) versus total length (in mm); note the four apparent groupings ("clusters"); the other plots refer to these four "clusters". **B,** Ratio (length of head including stylets divided by total length) versus ratio (length of head without stylets divided by total length). **C,** Ratio (length of prothorax divided by total length) versus ratio (length of head without stylets divided by total length). **D,** Ratio (length of entire thorax divided by total length) versus ratio (length of head without stylets divided by total length). **E,** Ratio (length of abdomen divided by total length) versus ratio (length of head without stylets divided by total length).

ninth stage which is expected to measure 8.2 mm. A last larval stage, expected to measure 10.6 mm would then be represented by "cluster" 4. Also plotting other aspect ratios separates the larger larval specimens not very sharply, further supporting the original assumption by Zwick (1967) that his specimens represent two separate stages. In any case it seems that the observed sizes of larvae of Nevrorthidae do not easily fit into the assumed 3-larval-stages type of development. Representatives of Nevrorthidae seem to have more, possibly five (or more) larval instars. Representatives of Raphidioptera and Megaloptera have a higher number of larval stages (up to 8?). The fixation to exclusively three larval stages (only further derived in very few ingroups) could hence represent an autapomorphy of Verineuroptera (monophyletic ingroup of Neuroptera excluding Nevrorthidae). While not all recent phylogenetic reconstructions favour such a sister group relationship of Nevrorthidae and Verineuroptera (e.g. Winterton et al. 2010, 2018; Engel et al. 2018) this estimation of number of larval stages could be seen as a support for such a relationship.

Formation of the pupa. Also the transition of the late larva to the pupa is worth noting upon. The known pre-pupa stages document a gradual transition from a very elongate larva to the much stouter pupa. While there is no moult to the pre-pupa, the morphology of the specimen indeed changes significantly. At first the ultimate larva seems to become only slightly thicker, as exemplified by a fossil larva (Fig. 11). In this stage the larva appears to be still mobile. In a later phase of the same instar (Figs 3C, F) the anterior body folds strongly ventrally. In this state the larva is most likely no longer mobile. In a much later pre-pupa (Fig. 3D) the body appears highly contracted, especially the abdomen. The neck seems to almost rip open. In comparison to the pupa we can guess that the head is so far retracted that it lies within the neck of the outer cuticle. In summary, we seem still to lack many aspects of post-embryonic development of representatives of Nevrorthidae. Yet, a general reconstruction of the development is already possible (Fig. 18).

Ontogenetic changes: antenna

Obvious changes during the larval phases include the elongation of the abdomen and the increase of the overall size. Additionally, a differentiation of the antenna is apparent (Fig. 19). It does not only show elongation, but also an increasing subdivision of the middle region. The degree of differentiation of the antenna may prove important to better understand the number of stages in Nevrorthidae. Unfortunately, this character is often not accessible and so far better documented for fossil specimens than for extant ones.

Quantitative morphological aspects: adult versus immatures

Plotting aspect ratios of body organisation reveals easily that adults are well separated from larvae, i.e. they are different in overall morphology (Figs 17C–E). Pupae are already organised similar to adults, later pre-pupae as well. Furthermore apparent is that adults cluster rather tightly together, i.e. there is not much variation between the different specimens and species in the adult phase (Figs 17C–E). Quite on the contrary, larvae seem to differ quite drastically in overall organisation in different larval stages. Already if only considering the later larval stages (“cluster” 2, 3 and 4), the larvae show more variation in the measured characters than the adults (Figs 17C–E). Even more so, in most aspects early larvae differ more from later larvae than these differ from adults (Fig. 17B). This means that diversity of morphology is not among the adults but in the larvae. Surely, the adults could show more differences when considering, for example, genitalia. Still, the gener-

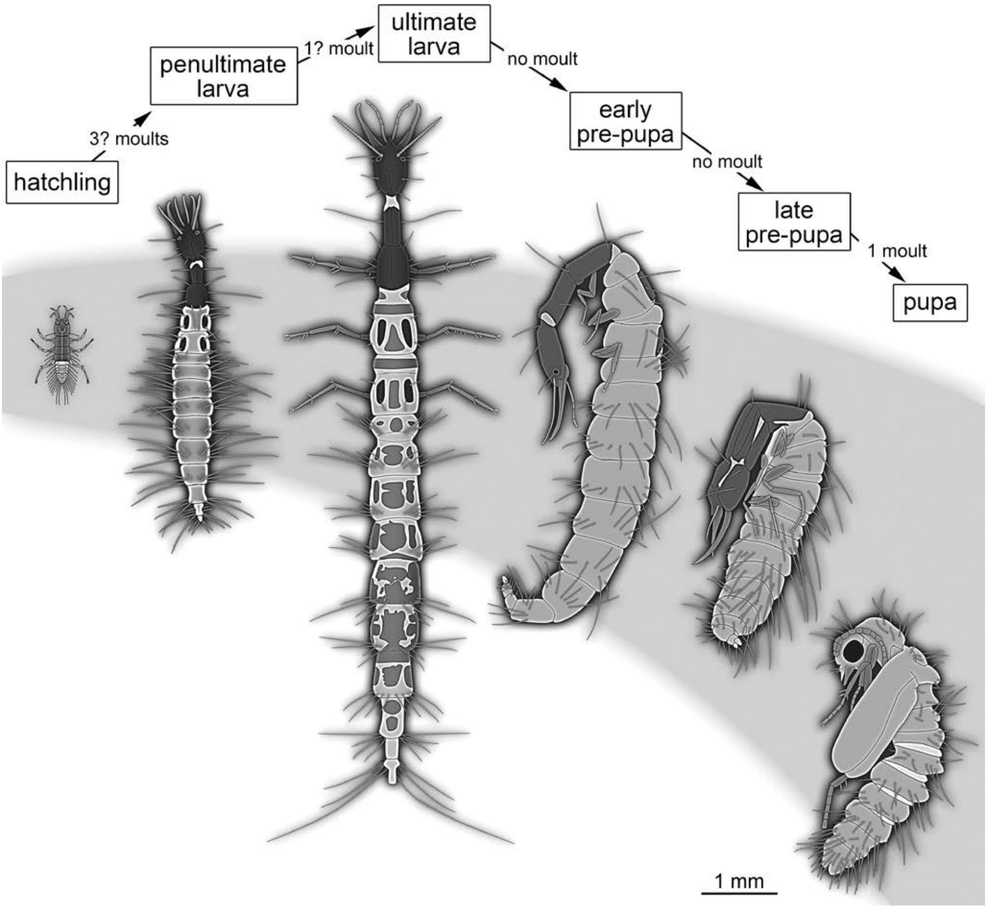

Fig. 18 – Generalised reconstruction of the post-embryonic development of representatives of Nevrorthidae. Based on actual specimens, besides the hatchling, this drawing combines the information of several specimens. Scale bar gives a general size impression.

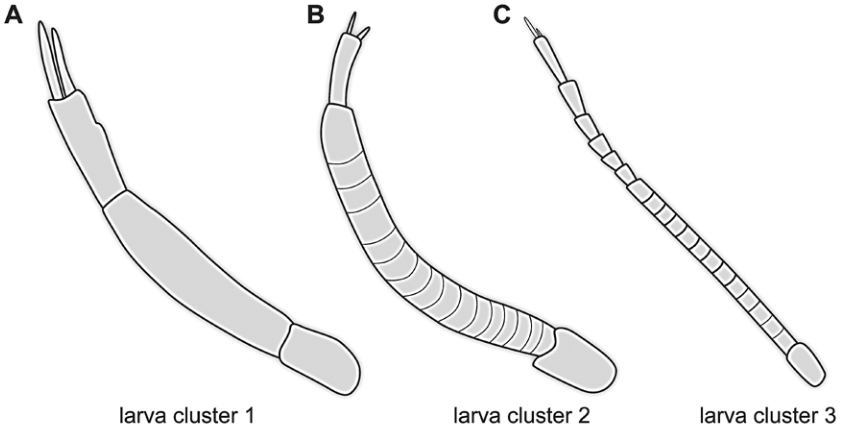

Fig. 19 – Generalised reconstruction of the post-embryonic development of representatives of Nevrorthidae, continued. Details of the morphological changes of the antenna. **A,** Antenna of "cluster" 1 larvae (based on Fig. 16). **B,** Antenna of "cluster" 2 larvae (based on Fig. 12). **C,** Antenna of "cluster" 3 larvae (combined, based on Figs. 7, 10). Antenna details of later stages (larva of "cluster" 4, prepupa, pupa) not accessible.

al body organisation at least provides some clues about the differences in life styles. The very strong similarities indicate that there is not very much differentiation between the different adult forms of Nevrorthidae. Among the larvae it seems that these fulfil quite different functions in different stages. This is already apparent by looking at the size: the 1 mm-sized specimens will hunt quite different prey than the more than 10 mm large specimens. For truly understanding the ecological impact of Nevrorthidae a much more detailed knowledge of the larval life will be necessary. It also emphasises that the common idea that the larval phase of species of Holometabola equals "one stage in life" is a mere oversimplification, as within the phase quite some morphological differences can be recognised.

Functional morphological interpretation

To repeat the obvious: our knowledge about the life habits of larvae of the group Nevrorthidae is still very limited. So far we know that larvae of some species occur in fast running waters and even pupate under water (Malicky 1984). At least one specimen has been observed in wet leaf litter, i.e. outside of the water (Riek 1970). As outlined above (and in Haug & Haug 2014), if the knowledge on extant forms is limited we should treat them more similar to fossils.

We therefore consider the functional aspects of the body organisation of larval representatives of Nevrorthidae. The mesothorax and the metathorax are usually depicted as each being subdivided into two regions by a distinct fold and a distinct constriction in dorsal view (Figs 2A–D, 3H, I, 4A, D) as well as in lateral view (Figs 4B, C). This is still apparent in the pre-pupa (Figs 3C, D, F). Only in specimen 3 (Fig. 3A) this is not really apparent, yet as pointed out the original drawing appears slightly simplified.

This subdivision is also not apparent in younger larval stages (e.g. specimen 5, Fig. 3B) and may hence be restricted to the presumed penultimate and ultimate larval stage (with about 8–9 mm and 11–13 mm). The subdivision of the segments separates an anterior part, about one third of the entire segment, from a more posterior region. The subdivision is also expressed by the sclerotisations of the cuticle. The more rigid sclerites are restricted to the posterior part, no sclerite crosses the division line.

Less apparent is a subdivision also of the further posterior segments, i.e. abdominal segment 1–8. Here, a subdivision is not expressed with a distinct constriction, also a fold is only rarely apparent. The division is mainly recognisable by the sclerotisations. A distinct line of weaker sclerotised cuticle is especially apparent in specimen 2 (Fig. 2B) and specimen 12 (Fig. 4A). A combination with a slight fold is furthermore apparent in lateral view on specimens 14 and 15 (Figs 4B, C). Specimen 14 (Fig. 4C) is especially interesting in this aspect as it is originally known from a SEM image. Less apparent, but at least recognisable is the subdivision in specimens 4 (Fig. 2C), 6 (Fig. 2D), 13 (Fig. 3H), 16 (Fig. 3I) and 17 (Fig. 4D).

In most of the fossils such a subdivision is not apparent. Yet, in specimen 26 the subdivisions of the abdominal segments are very distinct. In many of the fossils the abdominal segments appear to be partly covered, e.g. by opaque regions of the resin ("Verlumung"), hence such details may be obscured. Specimen 26 clearly shows not only distinct sclerites and a prominent fold, but also a slight constriction dividing the segments (Fig. 9E).

In specimen 30 (Fig. 13) we likewise see a strong subdivision of mesothorax and metathorax, but also of the anterior abdominal segments (Fig. 13E). Distinct folds clearly divide the anterior third of the segment from the posterior one.

After recognising this specialisation, a subdivision of all major trunk segments, we have to ask whether we know a comparable arrangement in other groups. Very notable examples are two ingroups of Myriapoda, namely Symphyla and *Craterostigmus* Pocock, 1902 . In both groups numerous trunk segments do not form a single sclerotisation dorsally, i.e. one tergite, but have two tergites per segment (Pocock 1902; Tiegs 1945; Edgecombe & Giribet 2008). Yet, this case differs from the condition of larval representatives of Nevrorthidae. In representatives of both myriapodan groups the "twin tergites" are very distinct plates, and both plates of a segment are extremely similar. In the larval forms of Nevrorthidae, the subdivision is not even. The dorsal side is divided into about one third anteriorly and two thirds posteriorly. Furthermore, the two entities are not clearly separated tergites.

More similar to the larval forms of Nevrorthidae appears the arrangement in representatives of Mystacocarida. Mystacocaridan crustaceans possess distinct folds in their trunk tergites (see Olesen 2000; Haug et al. 2011b; Olesen & Haug 2014 for details). This most likely provides them with additional flexibility. The same can be assumed for larval forms of Nevrorthidae. The subdivision transforms a usually inflexible segment into two subunits that can move against each other slightly, although most likely not as much as two segments can move against each other.

Mystacocaridan crustaceans live between sand grains and use their flexible, almost worm-shaped bodies to move in this rather restricted space. Mystacocaridan crustaceans are much smaller than larval forms of Nevrorthidae. Mystacocaridan adults reach only 500 µm in overall length, hence ultimate larval stages of Nevrorthidae are significantly larger. Yet, they do not live between sand grains, but apparently in fast running waters. In such streams the bottom is usually covered by smaller stones or pebbles. Larval forms of Nevrorthidae would therefore benefit from being very flexible to move in the confined spaces between these. Also if larvae of some species would move between leaf litter, high flexibility and movability would be of advantage. We therefore suggest that the subdivision of trunk segments in ultimate larvae of Nevrorthidae is best interpreted as a functional specialisation that allows them to move swiftly in confined spaces.

The habitat of larval forms of Nevrorthidae

The larvae of Nevrorthidae have been mostly reported to be rheophilic, living in fast running streams (Zwick 1967, Malicky 1984). However, Riek (1970) reported that extant larval specimens of Nevrorthidae also occur in moist, apparently terrestrial, leaf litter. This report is especially interesting in the light of some of the fossils reported here.

The habitat of larval forms of Nevrorthidae, especially that in the ground pattern of Nevrorthidae, has implications beyond the group itself and is of special importance for reconstructing the natural history of Neuroptera and closely related lineages. Nevrorthidae plays a key role in reconstructing the ground pattern of Neuroptera as it has been suggested to represent the sister group of all remaining ingroups of Neuroptera, Verineuroptera (e.g. Wichard et al. 2009). Within Verineuroptera, Sisyridae might represent the sister group to the remaining part of Verineuroptera. In such phylogenetic reconstructions, Osmylidae is usually interpreted as the sister group to the further remaining part of Verineuroptera (Verineuroptera without Sisyridae). With both Nevrorthidae and Sisyridae having aquatic larvae in at least the majority of species and aquatic larvae in some lineages of Osmylidae (Parfin & Gurney 1956, Gepp 1984, Weißmair 1999) aquatic larvae can be reconstructed for the ground pattern of Neuroptera. This would fit well with the aquatic larvae in Megaloptera, which is the supposed sister group of Neuroptera (e.g. Misof et al. 2014). Altogether, this would represent an ecologically very conclusive scenario: aquatic larvae in the ground pattern of the group that comprises Megaloptera and Neuroptera and terrestrial larvae having evolved in an ingroup of Neuroptera (Neuroptera without Nevrorthidae and Sisyridae) as well as in some lineages of Nevrorthidae.

Other, now less popular reconstructions have favoured Osmylidae and Sisyridae as ingroups of Hemerobiiformia, which is sister group to Myrmeleontiformia, both together (Verineuroptera) forming the sister group to Nevrorthidae (Aspöck et al. 2012). Even other reconstructions have favoured Coniopterygidae as sister group to all other neuropterans (Winterton et al. 2018). Still, even in the latter reconstruction aquatic larvae in the ground pattern of Neuroptera are possible (Winterton et al. 2018).

It seems therefore very important to explore which representatives of modern day Nevrorthidae possess truly aquatic larvae and which possess terrestrial larvae or whether there is an ontogenetic transition between the two ecological modes. Aside from urgently needed careful observations on the biology of extant species of Nevrorthidae, reconstructing conditions at the time of fossilisation can provide valuable insights into the ecology of the fossil forms and with this for the reconstruction of the ecological history of the neuropteran lineages as a whole.

Taphonomical aspects of syn-inclusions

Taphonomical assemblages, also called taphocoenoses, describe several fossils preserved together. Such taphocoenoses, ideally representing former living communities (biocoenoses), can give important insights about the palaeoecology of fossil organisms. Taphonomical assemblages in some cases can be formed over long periods of time and can inhabit enormous spatial dimensions (e.g. Konzentratlagerstätten, such as bonebeds). Amber pieces, on the other hand, along with other occasions, such as single layers of fine laminated sediment, represent remains of organisms that died during a short period of time, usually much less than a year. Additionally, these organisms died in a spatially very confined place. We can use the term 'micro-taphocoenosis' for such assemblages of organisms preserved in amber. There is of course the possibility that a drop of resin captures different habitats until the polymerisation has progressed enough to prevent animals from getting trapped, for example, by falling into leaf litter or into a pond. Still, syn-inclusions in amber pieces as micro-taphocoenoses can be considered to be much more informative than the overall taphocoenosis of the complete amber Lagerstätte. The syn-inclusions preserved together with larval forms of Nevrorthidae are therefore presented here in a database-like table (Table 2; Fig. 20) to avoid ambiguity as good as possible. Specimen 21 (Burmese amber) is preserved together with a typical terrestrial, non-aquatic organism, a cockroach. This indicates that this larval specimen of Nevrorthidae was not inside the water when being trapped in the amber. Yet, it could be argued that the cockroach fell into the water before being preserved together with the larva. The amber matrix is rich in small pieces of debris and some bubbles, which are typical for preserved aquatic or semi-aquatic environments (see e.g. de Lourdes Serrano Sánchez et al. 2015), but also for terrestrial leaf litter fauna (e.g. Sánchez García & Engel 2016).

Specimen 28 (Baltic amber) is preserved together with quite a number of different animals. Among these the two worker ants of *Lasius schiefferdeckeri* have limited value for reconstructing the palaeo-habitat, as representatives of *Lasius* have a quite large range in geography and habitats (Dlussky 2011). Larvae of wood gnats (Anisopodidae) are mostly saprophagous and occur in a variety of moist habitats with rotting plants or even animal remains and are often found in phytotelmata, small bodies of water provided by trees or other plants (Hancock 2017). Interestingly, larvae of the wood gnat group *Mycetobia* have also been found on trees at exudation points of tree saps (Hancock 2017), which would explain well their occurrence in amber. Adults of Dolichopodidae are predators who mostly feed on soft bodied organisms (e.g. annelids and larval forms of Holometabola) and often occur at or in proximity of water bodies (Grichanov & Brooks 2017). A likely interpretation for this micro-taphocoenosis could be that the larvae of Nevrorthidae lived in a small body of water (e.g. a tree hole) on or at the resin producing tree, where also the pupa of *Mycetobia* was. The adult ants could have been attracted by the water body.

Specimen 31 (Baltic amber) is preserved very close to a plecopteran nymph (Fig. 14A) strongly suggesting an aquatic habitat. Additionally, the morphology of the nymphs itself provides a good clue towards an aquatic lifestyle. The soft gill tubes on the thoracic body segments (Fig. 14E) are typical for plecopteran nymphs and can easily be interpreted as specialisations for respiration in water.

The presence of two larvae of Nevrorthidae (specimens 32 and 33; Figs 15, 16) and one larva of Sisyridae (not depicted in the figures) is quite remarkable, as the latter are exclusively aquatic, feeding on freshwater sponges and bryozoans (Parfin & Gurney 1956; Weißmair 1999). The preservation of the three specimens within the same amber piece seems to be a good indicator for an aquatic habitat.

Although data are limited, in the fossil record especially younger (and smaller) specimens seem to be preserved with typical faunal elements indicating an aquatic habitat, while especially later stages seem to be preserved with elements of the terrestrial fauna. In summary, it should not be assumed that all larval representatives of Nevrorthidae are aquatic. This also means that not every fossil larva of Nevrorthidae is a direct indicator of an aquatic habitat.

Based on these observations, it remains unclear how the ground pattern condition for Nevrorthidae looked like. This has so far been rarely taken into account, but has in fact severe consequences for our understanding of the evolutionary history of Nevrorthidae.

The origin of the larval neck in neuropteran insects

The subdivision of the trunk segments in late stage larvae of Nevrorthidae has further reaching implications concerning the evolutionary history of Nevrorthidae and also of Neuroptera as a whole. A prominent autapomorphy of Neuroptera is the presence of a sclerotised region between head and pronotum, the neck or cervix (e.g. Beutel et al. 2010). Generally, the origin of this sclerite has been considered a de novo sclerotisation of the membranous area between head and pronotum.

Within the group Euarthropoda, de novo sclerotisations of membranous areas seem to have occurred repeatedly in various lineages. The coxal element (most likely not equivalent to the coxa in representatives of Insecta; Bäcker et al. 2008, Haug in Hädicke et al. 2014) in the proximal appendage regions in crustaceans in the wide sense apparently evolved in this way (Walossek & Müller 1990; Waloszek 2003a,b; Waloszek et al. 2007; Haug et al. 2010a,b, 2013c). Among mantis shrimps a special joint allows them to erect their anterior body. The fold system enabling them to do so is stabilised by numerous additional de novo sclerotisations of the joint membrane (Haug et al. 2012). Even the soft-appearing larvae of dipterans demonstrate this phenomenon. Numerous larvae of culicomorphan and bibionomorphan dipterans, living in interstitial environments (upper soil, aquatic hyporheos) show a secondary pseudo-segmentation. Here the abdominal, and sometimes thoracic segments appear divided by “secondary annulations” into two or more parts. Most notable examples of such a “secondary segmentation” are larvae of the window gnats (Diptera: Anisopodidae). Here, the abdominal segments 1–7 appear divided into two unequal parts, and abdominal segment 8 appears divided into three unequal parts (Keilin & Tate 1940). Another group of flies in which the larvae exhibit pseudo-segmentation is Leptoconopinae, an ingroup of biting-midges (Diptera: Ceratopogonidae), where abdomen and thorax appear subdivided into 20 annular pseudo-segments (Borkent 2017). In most of these cases the membranous area between two segments appears enlarged and as hard (or soft) as the main segment, causing the impression of a subdivision. Hence, the principle idea that the cervix is a de novo sclerotisation in a membranous area is well founded as it assumes the

Table 2 – Systematic and ontogenetic information on each fossil larval specimen of Nevrorthidae and each animal inclusion associated with them. IDs are given for each individual inclusion (first column) as well as for each taphonomic community within a single piece of amber (micro-taphocoenosis, see discussion; second column).

ID (individuals)	ID (microtaphocoenosis)	narrowest systematic group	species if available	life stage	Institution	Collection #	Publication	figure in external publication	Specimen # (this publication)
1	1	Nevrorthidae		larva	Collection Patrick Müller	BUB 0795	this study		22
2	1	Blattodea		adult	Collection Patrick Müller	BUB 0795	this study		
3	2	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 1341A	this study		24
4	2	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 1341B	this study		25
5	3	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 7095	this study		28
6	3	Mycetobia		pupa	Collection Carsten Gröhn	Gr 7095	this study		
7	3	Dolichopodidae		adult	Collection Carsten Gröhn	Gr 7095	this study		
8	3	Dolichopodidae		adult	Collection Carsten Gröhn	Gr 7095	this study		
9	3	Lasius	*schiefferdeckeri* Mayr, 1868	adult	Collection Carsten Gröhn	Gr 7095	this study		
10	3	Lasius	*schiefferdeckeri* Mayr, 1868	adult	Collection Carsten Gröhn	Gr 7095	this study		
11	3	Trichoptera		adult	Collection Carsten Gröhn	Gr 7095	this study		
12	3	Euarthropoda			Collection Carsten Gröhn	Gr 7095	this study		
13	3	Euarthropoda			Collection Carsten Gröhn	Gr 7095	this study		
14	4	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 2769	this study		31
15	4	Plecoptera		larva	Collection Carsten Gröhn	Gr 2769	this study		
16	5	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 1383A	this study		32
17	5	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 1383B	this study		33
18	5	Sisyridae		larva	Collection Carsten Gröhn	Gr 1383	this study		
19	6	Nevrorthidae		larva			Wichard & Weitschat 1996	plate 10 lower	18
20	7	Nevrorthidae		larva			Wichard et al. 2009	07.20a	19
21	8	Nevrorthidae		larva			Wichard et al. 2009	07.21a, c	20
22	9	Nevrorthidae		larva	Collection Carsten Lammerskötter		Wichard 2017	2a	21
23	10	Nevrorthidae		larva	Collection Xiao Jia	PCXJ BA-0009	Lu et al. 2018	10, 11	23
24	11	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 7668	this study		26
25	12	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 2518	this study		27
26	13	Nevrorthidae		larva	Collection Carsten Gröhn	Gr 2768	this study		29
27	14	Nevrorthidae		larva	Senckenberg Museum Frankfurt	SMF 256	this study		30

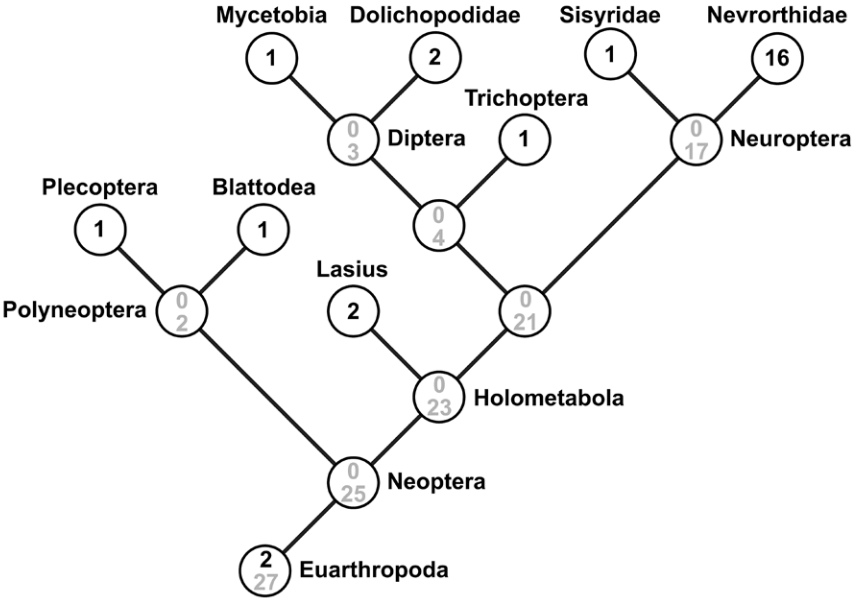

Fig. 20 – Graphical representation of the abundance of animal inclusions associated with fossil larval specimens of Nevrorthidae amended with information about the phylogenetic relationships between the preserved organisms. Single numbers as well as the upper numbers in the circles with two numbers show the abundance of fossils of a specific group represented by that tip or node of the tree; lower numbers in the circles represent the summed-up abundance of fossils of the specific group represented by that node in the tree. Summed-up numbers and zeros are shaded in grey for better comprehensibility.

evolution of a novel structure by a known and apparently common process.

Yet, the fact that the further posterior trunk segments are subdivided should be considered in this aspect. In other words: could the cervix and the presumed pronotum not simply represent two sclerotic regions of a former continuous pronotum? The advantage of this interpretation is simple. The subdivision of the posterior trunk segments in the ultimate larval stages of the group Nevrorthidae would be similar to that in the first thoracic segment. This should not indicate that the subdivision of the posterior trunk segments would be part of the ground pattern of Neuroptera; it is very likely a feature that evolved in the lineage of Nevrorthidae. Yet, it would not require an additional mechanism for the subdivisions of the further posterior segments in larval representatives of Nevrorthidae.

Deciding which of these two possibilities, de novo sclerotisation of a membranous area or a subdivision of the pronotum, has happened, would be easy if we would have more complete information about post-embryonic development of extant representatives of Nevrorthidae. Possible first stage larvae, apparently so far exclusively known from amber, seem to still lack an expressed cervix as they also lack subdivision of the further posterior trunk segments. Yet, two specimens reported here have tiny subdivisions of mesothorax and metathorax as well as an indication for a neck. It remains unclear whether these are differentiations of the outer cuticle or whether structures forming inside the outer cuticle (factually the pharate next instar) become apparent also on the outside. In extant forms, however, there should be a chance to observe the mechanism how the cervix is formed.

Why modern forms of Nevrorthidae are not "living fossils"

The term "living fossil" has been applied to modern representatives of Nevrorthidae. We doubt the value of the term "living fossil" in general. In most discussions it can easily be shown that it does not reflect the expectation behind it, largely due to a lack of concept. Hence, while often the expression "living fossil" is rather meaningless as it is not tied to any testable criterion, some authors use it more specifically. As a positive example, Aspöck & Aspöck (2007) provide clear criteria why they consider the modern representatives of Nevrorthidae as "living fossils". They cite Thenius (2000) for the following criteria:

1) isolated position in the (phylogenetic) system;
2) small number of extant species;
3) relic distribution;
4) slow speed of evolution in comparison to other lineages;
5) retention of old characters or character states.

Let us consider these criteria in general, i.e. in how far they indeed represent testable criteria, but also in how far they apply to the case of Nevrorthidae.

Concerning point 1): What does "isolated" mean in a phylogenetic context? Should it imply that a group is a sister group to another group? That would be the case for every thinkable lineage. We doubt that this criterion can be applied as it may look like one, but can in fact not be clearly delineated.

Concerning point 2): If a group comprises only a small number of extant species heavily depends on the point of comparison. Aspöck & Aspöck (2007) also apply the term "living fossils" to the group Raphidioptera, with more than 200 extant species. Does small number hence mean "any lineage with less than 200 species"? That would apply to numerous groups of Neuroptera besides Nevrorthidae, for example Ithonidae, Polystoechotidae, Berothidae, Dilaridae, Psychopsidae, Crocinae, Nymphidae, and in fact many more.

Concerning point 3): Relic distribution is indeed an interesting aspect. Especially fossils in amber have shown that many ingroups of Insecta have once had a much more global distribution and are now more disjunct and more restricted (e.g. Wedmann & Yeates 2008; Wedmann et al. 2010, 2011; Wappler et al. 2015). While the case of Nevrorthidae is an obvious one, this in fact applies to many more lineages (also within Neuroptera). Hence, while the criterion appears in principle applicable, it in fact attributes to many more cases than generally accepted (for example Ithonidae).

Concerning points 4 and 5): These two criteria are inter-connected. In principle, both can be boiled down to cases in which a modern form is said to strongly resemble a fossil one. This aspect is often only a matter of degree of detail. A detailed look will then easily show that apparently well-known cases only hold true if we remain on a very coarse level of comparison. Here are two such examples in which some of the authors were involved:

A) *Triops cancriformis* (Bosc, 1801), a tadpole shrimp (Notostraca Sars, 1867), was believed to have remained unchanged and to be still the same species since the Triassic, i.e., since roughly 200 million years. This was caused by the fact that the fossils provide little characters for finding differences (in fact they are similar to many modern species of Notostraca). Showing that these are in fact not the same species is philosophically challenging due to the fact that our concepts concerning species through time are still underdeveloped (Haug & Haug 2017). Yet, at least its ontogenetic sequence did not remain unchanged, but has undergone heterochronic shifts (Wagner et al. 2017).

B) Cockroaches are often assumed to have remained unchanged since the Carboniferous, hence since about 300 million years. Yet, their breeding biology has seen tremendous changes. Palaeozoic species appear to have laid single eggs into a substrate with the aid of a long, thin ovipositor. Modern day cockroaches produce complex egg packages in a special pouch that includes a tiny hidden ovipositor (Hörnig et al. 2018).

Yet, how about the case of Nevrorthidae? We indeed have fossils from the Cretaceous that strongly resemble their modern counterparts. However, this is also true for many other lineages of Neuroptera. Another weakness of this aspect is the age of the fossils. Many metazoans could be identified as living fossils if, for example, Pliocene fossils with their relatively young age are taken into account. In summary: Presumed criterion 1 is not a testable criterion; criteria 4 and 5 in fact relate to the same underlying characters. Hence three criteria remain: small number of species (about 200 or less), relic distribution, modern representatives resemble fossil forms in overall morphology. The group Nevrorthidae fulfils all these criteria, yet many others as well. Also the groups Ithonidae, Psychopsidae and Nymphidae fulfil all three criteria. If one insists on applying the term "living fossil" to Nevrorthidae, the same would also have to be applied to other groups of Neuroptera, at least to Ithonidae, Psychopsidae and Nymphidae, but possibly to many more. This would of course diminish the value of the term as pointing out a special condition for few groups.

In our view, some of the individual criteria, such as disjunct distribution of a group, are much more telling than the term "living fossil". As outlined also by others, the term "living fossil" should be abandoned.

Why the name Nevrorthiformia is an unnecessary term

Often Nevrorthidae is treated as a subordinate group of "Nevrorthiformia". This supposed group is content-wise identical to its single ingroup Nevrorthidae and can also not be differentiated from it by any means, besides taxonomic rank. "Nevrorthiformia" is thus a monotypic taxon (sensu Mayr 1969). Ranks are a questionable concept per se as there are no criteria that would allow to identify a rank of a specific monophyletic group (see e.g. Ereshefsky 2002; Laurin 2010; recent discussion by Satoh et al. 2014; Lambertz & Perry 2015, 2016; Giribet et al. 2016; Irie et al. 2018). The phenomenon of the "empty shell" such as "Nevrorthiformia" demonstrates one of the costs (hence downsides) of the concept of ranks. The same group carries two names, complicating general communication.

"Nevrorthiformia" has been introduced at the same taxonomic rank of Hemerobiiformia and Myrmeleontiformia. Yet, "Nevrorthiformia" would be sister group to Hemerobiiformia + Myrmeleontiformia, hence could also be interpreted to be one rank higher. Also, current phylogenetic hypotheses indicate that Myrmeleontiformia is in fact nested within Hemerobiiformia (e.g., Wichard et al. 2009; Winterton et al. 2018). This would in consequence mean that numerous lineages would need to be raised to the same rank as Myrmeleontiformia. This shows that trying to "balance" a tree for ranks is a hopeless enterprise and there is no gain in having several names for the same entity. "Balancing" the ranks based on new phylogenetic results always leads to many groups being renamed. The process of renaming groups can produce confusion as older literature still contains the old names that were valid at the time of publication (see discussion in Queiroz & Gauthier 1990). It seems therefore to be the most simple solution to abandon the term "Nevrorthiformia" and use Nevrorthidae as a general substitute.

Outlook and summary

Aspöck & Aspöck (2017) figured a map (their fig. 15) with numerous occurrences of larvae of *Austroneurorthus*. This means that larval specimens seem rather common in some areas of the world. We still have a limited knowledge on larvae of Nevrorthidae, despite the possibly crucial phylogenetic position of the group within Neuroptera. It is therefore urgent, but also well possible to study especially extant larvae for the aspects outlined and hypothesised here. Among these are:

- Larvae of Nevrorthidae appear to develop through more than three larval stages. This could be tested by breeding observations, or at least statistics on a large dataset from a single population.
- Larvae of Nevrorthidae appear to be specialised to move in confined spaces. This could be tested by field observations.
- Field observations and analysis of syn-inclusions make it possible that not all larvae of Nevrorthidae live or lived in running streams. This could also be tested by field observations.
- The ontogeny of Nevrorthidae might provide important clues for understanding the occurrence of the sclerotised neck in Neuroptera. Embryonic and early larva data would be necessary to further elaborate on this aspect.
- Finally, two more philosophical aspects are tied to Nevrorthidae: first, the grouping Nevrorthiformia is an unnecessary one; second, the modern forms of Nevrorthidae should not be considered to represent living fossils.

Acknowledgements – We thank Mónica Morayma Solórzano Kraemer, Frankfurt, for providing access to the collections. Wilfried Wichard and an anonymous reviewer are thanked for helpful comments on an earlier version of the manuscript. The Volkswagen Foundation kindly funds JTH with a Lichtenberg Professorship. JTH and CH thank J. Matthias Starck, Munich, for continuous support. We highly appreciate the effort of all people involved in providing open access, open source and low cost software. This is LEON publication #09.

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