Caught in the act of hatching – a group of heteropteran nymphs escaping from their eggs preserved in Dominican amber

Authors: Hörnig, Marie K., Fischer, Thilo C., and Haug, Joachim T.

Caught in the act of hatching – a group of heteropteran nymphs escaping from their eggs preserved in Dominican amber

Marie K. Hörnig, Thilo C. Fischer & Joachim T. Haug

Abstract

Insects enclosed in amber can provide unique insights into the morphology, but also behavioural aspects of extinct species, due to their often exceptional preservation. This is especially true in the cases of so-called 'frozen behaviour', were animals were caught in the fresh and viscid resin while e.g. mating, egg laying, capturing prey or in rare cases, hatching. Here, we report a group of heteropteran insect nymphs preserved together with their eggs in 15–20 million-year-old Dominican amber. Two of the nymphs were caught in the act of hatching. The eggs form a cluster of 47 individuals and possess a morphology, as occurs in the eggs of some extant Reduviidae, especially Hapactorinae. Most notable are the operculum surrounding elongated extensions of the chorion at the apical part of the elongated eggs. The cluster strongly resembles the appearance of a composite flower. Details of the egg morphology of extinct insects are very scarce, and even if fossil remains can be identified as insect eggs, the corresponding insect group can rarely be determined. Rare cases of 'frozen behaviour', such the herein described, allow to observe aspects of the hatching process, but can also help to shed light on the morphology of the eggs from different extinct insect groups.

K e y w o r d s : Heteroptera, Hemiptera, 'frozen behaviour', fossil hatching.

1. Introduction

Fossils provide us with a view into the history of life. Fossil remains of animals enclosed in amber have a peculiarly high potential for the investigation of many different aspects of such organisms, including the morphology, development and distribution of today extinct organisms. In contrast to many other types of fossil preservation, inclusions in amber are often exceptionally detailed and preserved in nearly life-like conditions (ARILLO 2007) and with no compressions of the body. A similar detailed preservation, but compressed, can be found in many famous Lagerstätten such as the Burgess Shale (e.g., GAINES et al. 2008; GOULD 1990; HAUG et al. 2012a).

Especially for the reconstruction of behavioural aspects, amber fossils can provide important insights. Cases of the so-called 'frozen behaviour' have been described for fossils of several ingroups of Insecta, such as representatives of e.g. Diptera, Hymenoptera, Coleoptera, Dictyoptera, and Lepidoptera (e.g., WEITSCHAT & WICHARD 2002; WEITSCHAT 2009; BOUCOT & POINAR JR. 2010; POINAR JR. 2010; GRÖHN 2015; FISCHER & HÖRNIG 2019). These animals were enclosed in the still viscid resin during various actions, such as feeding, mating, egg laying (but note, that most of these cases could reflect false oviposition due to death stress) or capturing prey (ARILLO 2007; BOUCOT & POINAR JR. 2010; POINAR JR. 2010; GRÖHN 2015). The resulting fossils represent a kind of snapshots of a specific moment of the life of the animal. Yet, the interpretations of these fossils are not straightforward in every case and so conclusions about behaviour and lifestyle should always be careful discussed (e.g., GRIMALDI 1996; BOUCOT & POINAR JR. 2010).

Cases of fossils showing euarthropodan species (the larger arthropodan group including insects and their more distant relatives such as other crustaceans and representatives of Euchelicerata) captured during the hatching process are exceptional rare. In BOUCOT & POINAR JR. (2010), a piece of Mexican amber with hatching uropodid mites was reported. GRÖHN (2015) depicted a group of cockroaches hatching from an ootheca in Baltic amber. PÉREZ-DE LA FUENTE et al. (2019) described pieces of Lebanese amber containing groups of hatchlings of neuropteran insects (Chrysopoidea) and corresponding remains of eggs. A further example, remarkably not preserved in amber, has been described by ROY & FÅHRAEUS (1989) from the Early Ordovician Orsten conservation type, corresponding to a nauplius larva, which was fossilised during hatching.

Strikingly, fossil eggs of Insecta have rarely been reported in the literature. Some known examples of such eggs are oothecae, or egg packages of dictyopterans, especially roaches and mantodeans (BOUCOT & POINAR 2010; GRÖHN 2015). One reason for the little knowledge about eggs of extinct euarthropodan species could be that isolated eggs can be difficult to identify in the fossil record. In most cases, clearly identifiable eggs of representatives of Insecta are preserved together with the adult. Examples are fossils of numerous groups such as Diptera, but also Collembola, Lepidoptera and Dictyoptera (e.g., GRIMALDI & ENGEL 2005; BOUCOT & POINAR 2010; HÖRNIG et al. 2018; GAO et al. 2019).

Yet, some ingroups of Insecta have a conspicuously characteristic egg morphology. Among these are many ingroups of Lepidoptera or Phasmatodea (e.g., Arbogast et al. 1980; Forister et al. 2006; García-Barros & Martín 1995; Sellick 1997). Another group of extant insects with a remarkable characteristic egg morphology is Reduviidae, the group of assassin bugs, which is an ingroup of Heteroptera, true bugs (Barber 1923; Coscaron et al. 2002; Gil-Santana & Forero 2010; Pikart et al. 2012; Schaefer & Wolf 2003; Shurtz & McPherson 2005; Vennison & Ambrose 1990; Voss & McPherson 2003). Eggs of Reduviidae are elongated in general shape, often with extensions of the chorion surrounding the prominent operculum forming a collar, are never embedded in plant tissues and frequently arranged in compact cluster in vertical or horizontal position (Southwood 1956).

The group Reduviidae contains about 7,000 formally described species; its representatives occur worldwide, with a major distribution in the tropics (Weirauch et al. 2014). The representatives of this insect group are raptorial and feature a wide range of morphological adaptations to various strategies for capturing prey, such as subchelate and chelate raptorial appendages ("legs") or glands for producing sticking secretions on the legs, as for example in the group Harpactorinae (Weirauch et al. 2014).

Here we report a single piece of Dominican amber containing a group of eggs and nymphs. The latter most likely represent assassin bugs captured in the moment of hatching.

2. Material and methods

2.1. Material

The single piece of Dominican amber studied herein was kindly provided by Jens Urban and it is housed at the collection of Naturkunde Museum Mauritianum Altenburg with the collection number GP 10958.

The age of Dominican amber is much debated in the literature. The youngest and most currently accepted proposed age for Dominican amber is 15–20 Million years (Iturralde-Vinent & MacPhee 1996, 2019), but the assumptions reach up to an age of 30–45 Million years (see conclusions in Poinar & Poinar 1999; Vitali 2009; Penney 2010).

2.2. Documentation methods

Macro-Photography: The specimen was photographed with a Canon EOS 70D, equipped with a Canon MP-E 65 mm objective and a Canon Twin Flash MT-24. For close-up images with high magnification, additional extension tubes were used. To avoid reflexions, polarisation filters were fixed in front of flashes and objective, resulting in cross-polarised light. To reduce distortions based on irregularities, convexities, concavities or scratches of the amber surface, a drop of glycerine was applied and covered by a cover slip (e.g., Haug et al. 2013b; Hörnig et al. 2016).

Z-stacks, images composed of multiple photographs (10–15) taken at successive focal depths, were obtained from every part of the specimen in overlapping areas. Subsequently, the Z-stacks were fused to consistently sharp images with CombineZM (Alan Hadley) and stitched together with Adobe Photoshop CS4 to generate high-resolution composite images. Further adjustments (colour, contrast, etc.) were done with Adobe Photoshop CS4.

X-ray Micro-computed tomography: Micro-computed tomography (µCT) was performed with using an XRadia XCT-200 (Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with switchable scintillator-objective lens units. The tomography was recorded using magnification of 0.39x objective and X-ray source setting at 30 kV and 6 W for 18 s acquisition time. Image stack properties are 6.36 µm system based calculated pixel size, 2048 x 2048 px. Tomography projections were reconstructed using the XMReconstructor software (Carl Zeiss Microscopy GmbH, Jena, Germany), resulting in image stacks (TIFF format). Scan and reconstruction were performed using Binning 1 (full resolution) to avoid information loss. Volume renderings were generated using Amira 6 (FEI, Hillsboro, OR, USA).

3. Results

Eggs: The amber specimen GP 10958 contains 47 eggs, mostly arranged in the same orientation (Fig. 1), as well as five nymphs (Figs. 1–3). Eggs and nymphs form a cluster, which is arranged, approximately, in a hexagonal pattern, i.e., in apical view each egg not situated in the periphery is surrounded by six other eggs. Each egg is about 2 mm long, with a diameter of about 0.75 mm. The shape of all eggs is elongated and rounded at the base. The apical side (operculum) is flattened, round and composed by a central area surrounded by circularly arranged structures forming a collar, which gives the eggs a flower-like appearance (Fig. 4C). The surface of the central area has a porous appearance (possibly a micropilar area). The surrounding collar is formed by an outer and an inner ring of structures. The outer ring has about ten (varies between the eggs slightly) petal-like fibrous structures (extensions of the chorion) forming a collar which are tapering towards the apex. The inner ring is formed by a row of about 18–20 fine stick-like opercular extensions, which are distinctly shorter than those on the outer ring.

Nymphs: The specimen GP 10958 contains five nymphs (Figs. 1–3), two of them preserved while hatching from their eggs. All nymphs are equal in size, with a body length of about 1.7 mm (without appendages). Body is distinctly organised into head and trunk.

The rather flat head is about as long as wide (Fig. 4). Head segments form a capsule. The head capsule is rounded in shape. Ocular segment and post-ocular segments 1–5 (insect terminology [IT]: antennal, intercalary,

Fig. 1. Overviews of specimen GP 10958; **A** – Overview of the piece of amber; **B** – overview of enclosed eggs and heteropteran nymphs.

mandibular, maxillary and labial segment) are dorsally contributing to the head capsule. The head capsule is freely articulated against the next posterior segment.

Recognisable features of the head are prominent compound eyes (ocular segment) which are about 0.2 x 0.3 mm in size, antennae with an entire length of about 2 mm (appendages of post-ocular segment 1) and massively developed mouthparts (appendages of post ocular segment 3–5) (Fig. 4A, B, D). The antennae, with an entire length of about 2 mm, contain a more massive proximal part (scapus) and a distal part with three elements each bearing numerous setae. The recognisable parts of the mouthparts form a beak (for piercing and sucking) and are about 0.9 mm long, with the labium forming the outer visible part, most likely subdivided in several elements (exact number not clearly visible).

The thorax (pro-, meso- and metathorax, which resembles post-ocular segment 6–8) is about 0.4 mm long and equipped with three pairs of appendages (pro-, meso- and

metathoracic legs), composed of (from proximal to distal) coxa, trochanter, femur, tibia and tarsus, further subdivided into two tarsal elements. All pairs of legs are similar in size. The coxae and trochanters of all legs are about as long as wide; femora are about 4 times longer than wide. The tibiae are longer than femora and about 10 times longer than wide. Femora and especially tibiae are equipped with fine and long setae (more than twice as long as tibia width). Tarsi are about 4 times as long as wide and distally equipped with a paired claw (Fig. 4E).

The posterior trunk, the abdomen, has 10 visible segments (post-ocular segments 9–18), the last one possibly representing undivided abdomen segments 10 and 11 (post-ocular segments 18–19). The entire abdomen is about 0.75 mm long, with a maximum width of 0.5 mm.

"B y c a t c h": The CT data reveal another animal between the eggs (Fig. 5). The animal has an overall worm-shaped appearance, yet the body is clearly organised into discrete segments (Fig. 5B, F). More than a dozen units are

apparent, yet the borders between the posterior more ones are less clear, hindering a reliable recount. The first two units appear to be more strongly sclerotised. The first one appears to be the head. Ventral indications of mouthparts (the most prominent a possible labium; Fig 5A) are apparent. The second more strongly sclerotised unit is most likely the prothorax. No indications of true legs are apparent. The specimen is most likely a larva of a representative of Holometabola. As most details are not accessible, a reliable identification remain impossible; the specimen could in principle be a representative of Diptera (flies, mosquitoes) but also a specialised larva of Coleoptera (beetles).
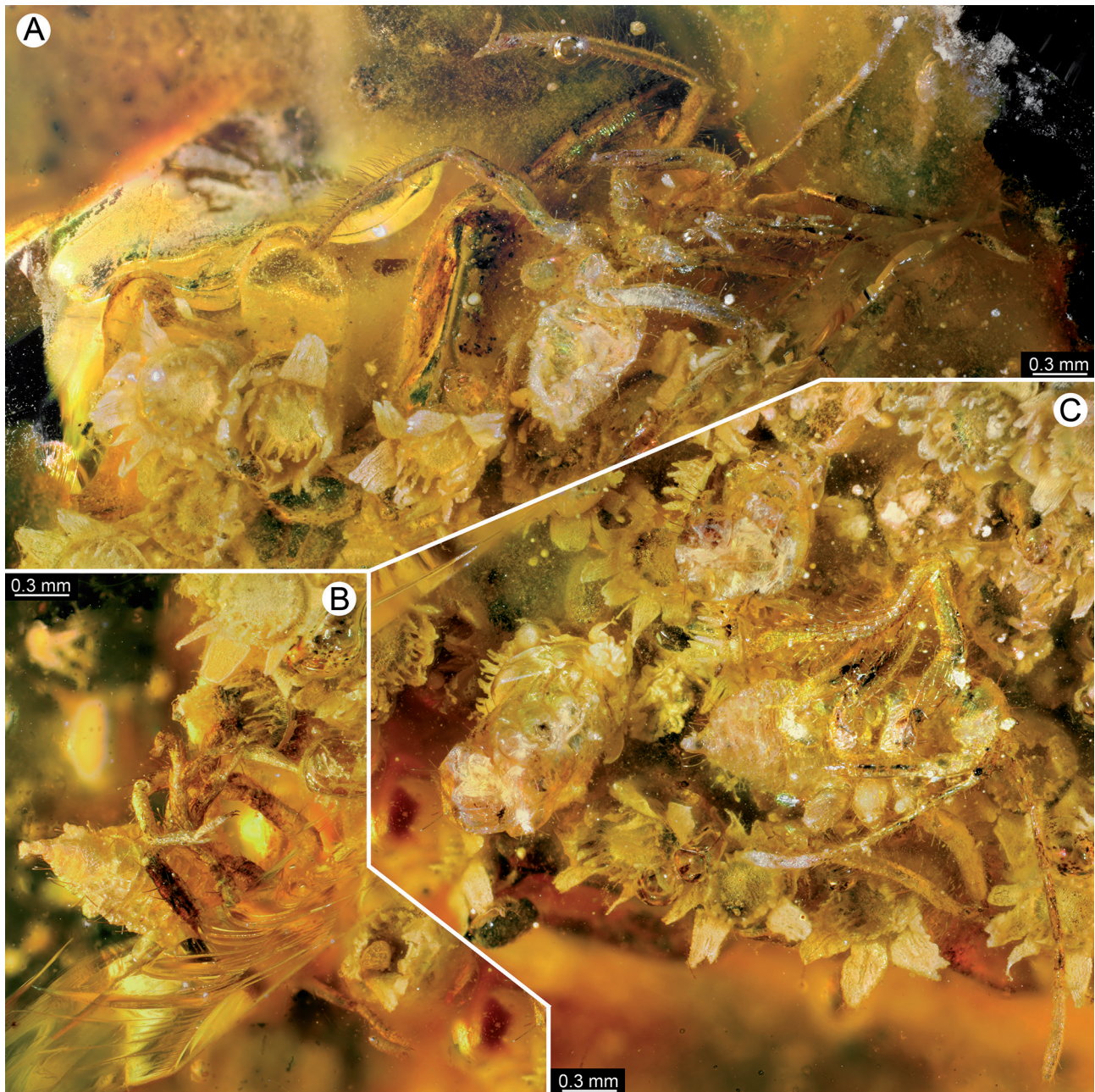
Fig. 2. Close-up images of the five heteropteran nymphs; **A** – heteropteran hatchling (marked in yellow in Fig. 5); **B** – Posterior part (abdomen) and legs of heteropteran hatchling (marked in dark blue in Fig. 5); **C** – Completely hatched heteropteran nymph (marked in red in Fig. 5) and two nymphs captured during hatching (marked in green and light blue in Fig. 5).
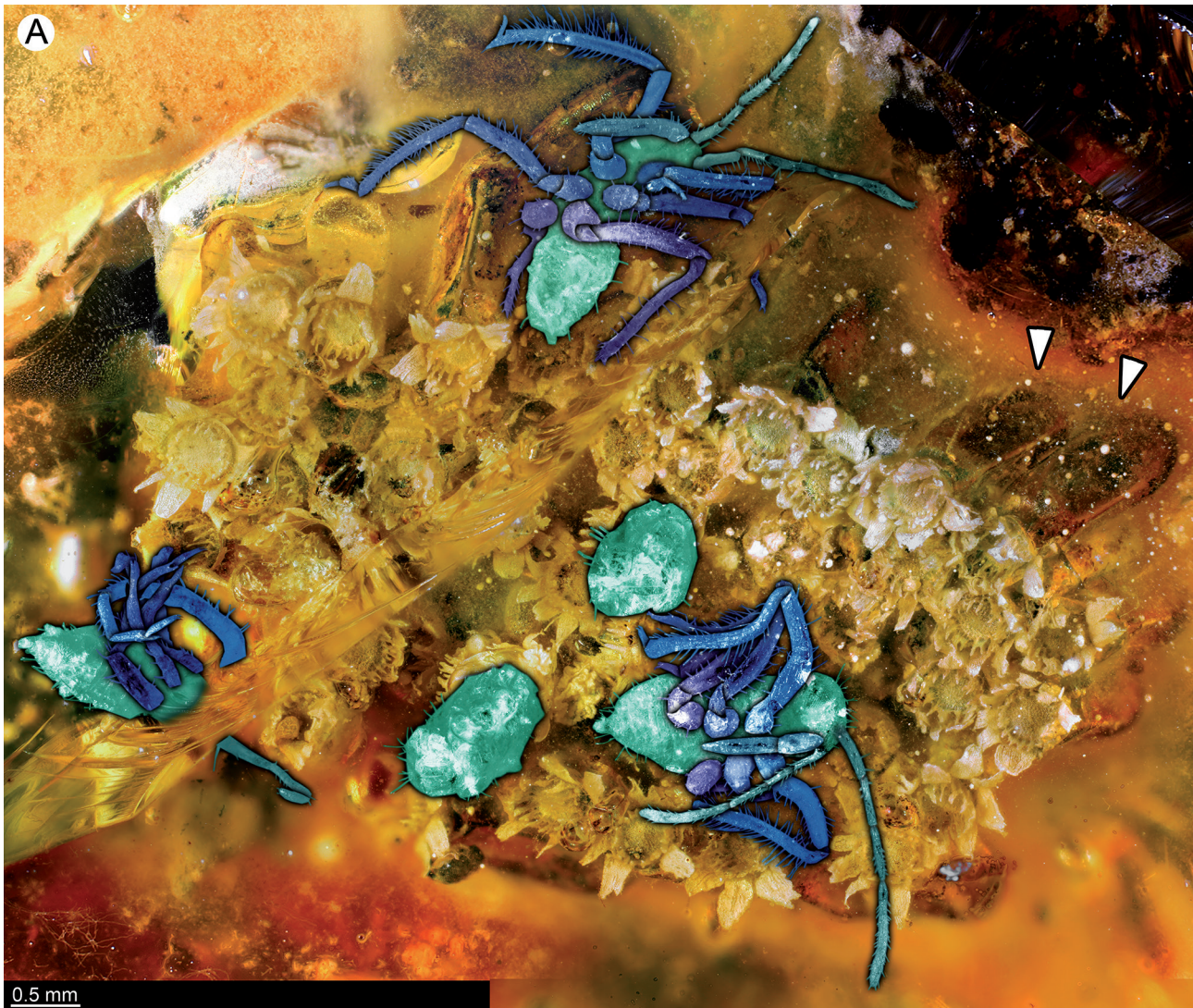
Fig. 3. Colour-marked overview of enclosed eggs and heteropteran nymphs (colour-marked version of Fig. 1B). Arrows point eggs in anterior-lateral view (close-up in Fig. 4C).

4. Discussion

The piece of amber described herein contains a cluster of 47 eggs with characteristic shape and five nymphs, two of them captured right in the moment of hatching. The identification of fossil nymphs of Insecta, especially hatchlings, to a specific narrow group is often challenging, because descriptions of morphological characters for identifying phylogenetic groups are mainly based on adults. Moreover, even if the specimens are well preserved, not every character is accessible. In this case, we have the possibility to obtain further information from the very characteristic eggs in order to narrow down to a specific systematic group.

4.1. Identification: Morphology of the enclosed eggs and nymphs

The enclosed nymphs possess mouthparts forming a distinct beak for piercing and sucking. This identifies the specimens as representatives of Hemiptera. The position of this beak is rather anterior on the head, clearly identifying the specimens as representatives of Heteroptera, true bugs (SCHUH & SLATER 1995). The most proximal part of the antennae appears more massive and articulated to the next distal antennal element. It seems plausible that the antennae were functionally geniculate in original condition. This would indicate that the nymphs are representatives of Reduviidae (BÄHRMANN 2011).

Further characters are provided by the morphology of the eggs. The eggs are elongated in shape, not inserted to plant tissue, arranged in a cluster (not singly), with no recognisable structures of the chorion (beside the apical part) and a symmetrical operculum. Most notable are the operculum surrounding elongated extensions of the chorion, which forming a collar. It can be recognised as a true operculum as the two of the nymphs are preserved in the moment of hatching right at this side of the egg, with the operculum removed. Altogether, this character clearly contradicts an interpretation as eggs of Anthocoridae, Cimicidae, Aradidae, Miridae, Nabidae, Tingidae (the latter three possess a collar, but the eggs are always inserted into plant tissue), and Polyctenidae (vivipar) (SOUTHWOOD 1956; COBBEN 1968). Also, an interpretation as eggs of Microphysidae seems unlikely based on the size of the eggs (2 mm length of the herein described specimen, 0.5 mm length e.g. in *Loricula elegantula*, COBBEN 1968). All characters stated above, especially the length and shape of the elongated extensions of the chorion, is present in eggs of Reduviidae, more precisely in eggs of Hapactorinae (BARBER 1923; COSCARON et al. 2002; GIL-SANTANA & FORERO 2010; HARIDASS 1986; PIKART et al. 2012; SCHAEFER & WOLF 2003; SHURTZ & MCPHERSON 2005; VENNISON & AMBROSE 1990; VOSS & MCPHERSON 2003). A quite similar type of collar can be found in eggs of Priatinae, but these are always lain into the soil and are characterised by specific structures of the surface of the eggs which are not recognisable in the herein reported fossil eggs (HARIDASS 1985). Moreover, eggs of Apiomerinae resemble in principle those of some species of Hapactorinae; yet, the operculum seems to be rather low and sunken in the middle (SOUTHWOOD 1956).

Within Harpactorinae, the specific flower-like appearance of the collar could resemble eggs of e.g. for *Rhinocoris* (HARIDASS et al. 1987, fig. 2E), but especially those of *Sinea* (e.g., MYLES & SMITH 1986; SCHAEFER & WOLF 2003; SHURTZ & MCPHERSON 2005; VOSS & MCPHERSON 2003). Furthermore, the porous central area with an inner ring of stick-like structures (opercular extensions) also reminds of those of *Sinea,* but cannot clearly be determined, as the amber specimen does not allow to investigate this area in more detail. Yet, there are at least two types of egg arrangement within *Sinea*. It has been reported that *Sinea spinipes* and *S. diadema* lay eggs in double rows, but at least *S. rileyi* (MYLES & SMITH 1986) and *S. confusa* (SCHAEFER & WOLF 2003) in rather circular arranged groups, which would be more similar to the here reported fossil eggs.

In extant forms of Reduviidae and within Hapactorinae, size and arrangement of egg clusters differs significantly in different groups (if the eggs are laid in clusters). The eggs within a cluster are in several ingroups of Reduviidae glued with cementing materials on the substrate and/or to each other (VENNISON & AMBROSE 1990), also the usage of resin is possible (Apiomerinae; CHOE &

RUST 2007). Smaller clusters include between 2 to 15 eggs (VENNISON & AMBROSE 1990). Larger clusters are known in several species such as e.g. *Sycanus galbanum* (Hapactorinae; NITIN et al. 2017), or *Sycanus recliizatus* (VENNISON & AMBROSE 1990), with up to 90 eggs per cluster. Yet, the pattern of exact arrangement and number of eggs per cluster, even the orientation of the cluster itself seems to be very variable also within groups between species. For example, the group *Endochus* (Hapactorinae) contains at least three species with strong differences of the egg laying arrangement (SRIKUMAR et al. 2014). The orientation of the cluster is not necessarily parallel to the substrate (so that every base of every egg is in contact with the substrate), it can also be arranged as rows were the eggs of the first row are attached lying on the side. All further rows are stacked over one another, resulting in further rows that are not in contact to the substrate. Such a type of vertical arrangement could be also be the case for the here described enclosed cluster, as there seems no remain of a substrate preserved; yet this cannot be further supported. The number of eggs seems to be also highly variable within a species, for example in *Rhynocoris albopilosus* (Hapactorinae) the number of eggs per cluster can vary at least between 23 and 134 (KWADJO et al. 2017).

In consequence for the here described specimens, the number of eggs and the way of arrangement in the cluster cannot used for identifying a specific position within Hapactorinae, yet it seems highly likely that they are representatives of this group.

S y n c h r o n i s e d h a t c h i n g : Five nymphs are visible in the fossil specimen. Three of them apparently just have hatched, still sitting on the eggs. Two more are in the process of hatching. It therefore should be considered whether these nymphs could have synchronised their moment of hatching, at least to a certain degree. In groups of predatory organisms, it seems widespread that times of vulnerability are synchronised to avoid cannibalism and use the positive effects of the law of the large number. There are for example indications of synchronised moulting in the fossil record coupled to these effects (see discussion in HAUG et al. 2013a). It remains unclear how the synchronisation of hatching could be communicated among the individuals. Possible mechanisms include pheromones, but also vibrations (e.g., ENDO et al. 2019).

4.2. Interpretation of the egg morphology

The morphology of the eggs is remarkable due to their strong resemblance to a composite flower, i.e., an inflorescence, most similarly found in the group Asteraceae (syn. Compositae) (e.g., ZOMLEFER 1994). For the identification of these structures as eggs, μCT proved to be a helpful
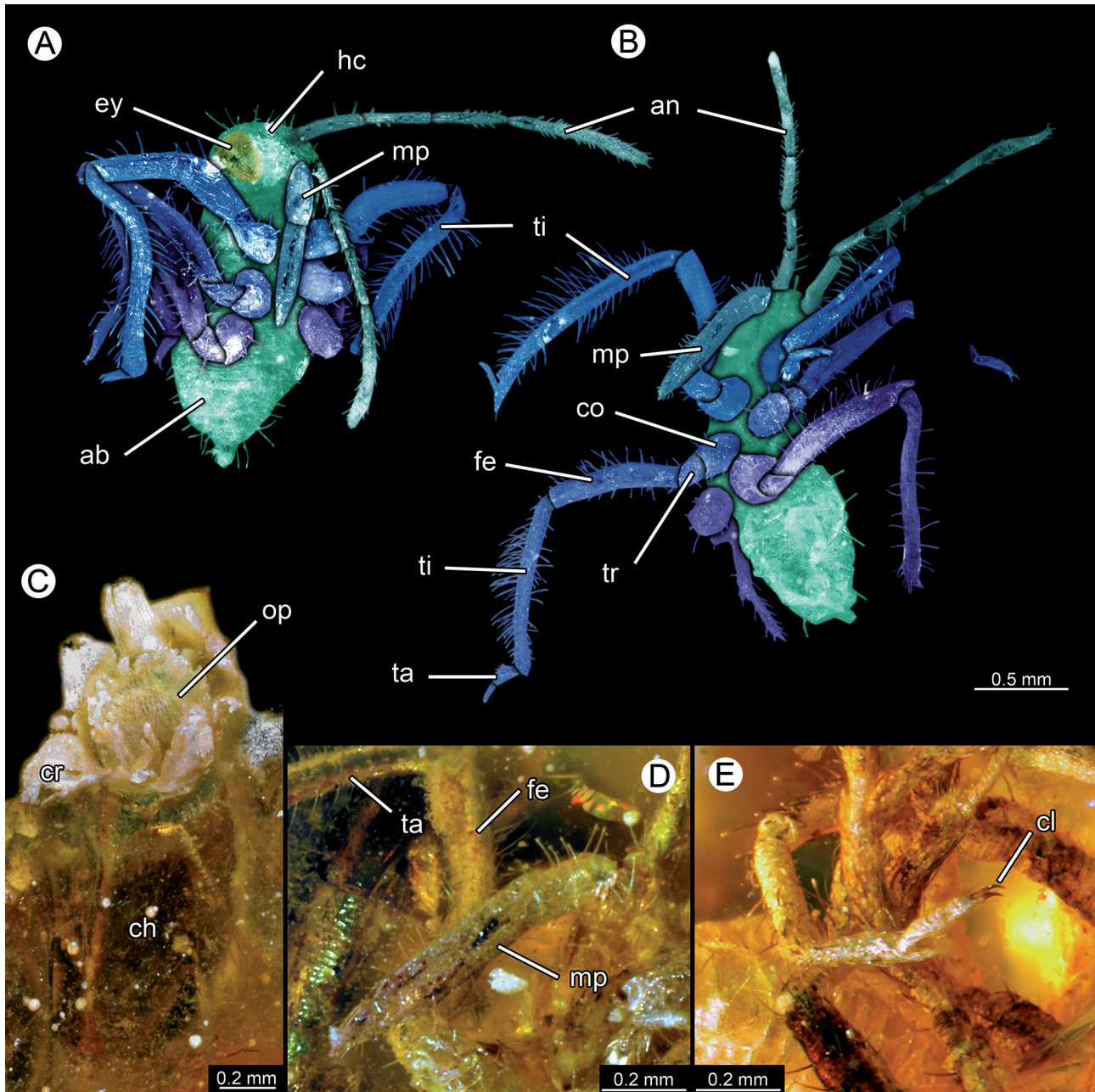
Fig. 4. Close-up images of heteropteran nymphs and one egg; **A** – colour-marked version of nymph (marked in red in Fig. 5); **B** – colour-marked version of nymph (marked in yellow in Fig. 5); **C** – close-up image of egg in antero-lateral view; **D** – close-up image of mouthparts of nymph shown in Fig. 4B; **E** – close-up image of mesothoracic leg (hindleg) of nymph (marked in dark blue in Fig. 5). Abbreviations: ab = abdomen; an = antenna; ch = chorion; cl = tarsal claw; co = coxa; cr = collar; ey = compound eye; fe = femur; hc = head capsule; mp = maxillary palp; op = operculum with lateral extensions; ta = tarsus; ti = tibia; tr = trochanter.

tool, as the inclusion can only be viewed from one side of the amber piece (all other sides are covered by strong irregularities). The µCT data allowed investigating the base of the structures (Fig. 5). These are rounded at the base, egg-like, with no indications of any further plant-related attachment area.

Hence, the question of whether the morphology and arrangement of the eggs could represent a case of flower mimicry arises. Each egg with its ring of protuberances resembles a single flower of a composite inflorescence; also, the entire egg arrangement resembles a complete inflorescence. Within the group Asteraceae, species of the

group *Xenophyllum* (FUNK 1997) seems most similar to the morphology of the here described eggs. Extant representatives of the group *Xenophyllum* live in Central America, however, and has its habitats in mountainous regions. This is a quite different habitat to the tropical forests with the resin producing forms of the group *Hymenaea,* which have been compared to the reconstructed Miocene amber forest of the Dominican Republic (POINAR & POINAR 1999).

A possible Asteraceae form from modern day Central American tropical forest whose inflorescences could have been mimicked by the egg arrangements has not yet been identified, but possibly could be found studying such floras much more closely. If the here described specimen indeed represents a case of mimicry, the flower-like appearance could be a strategy preventing the eggs to be identified as such by predators.
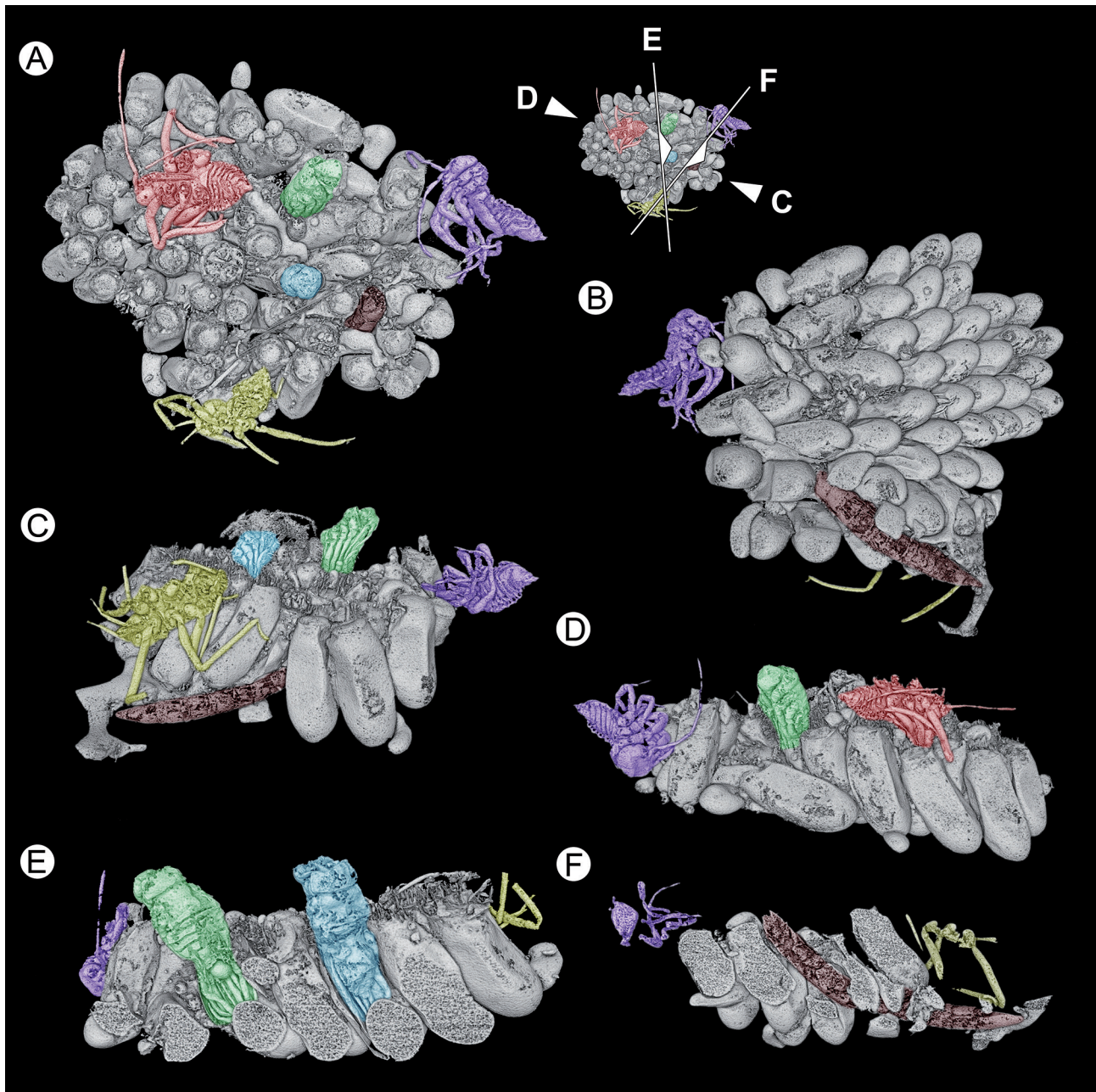
Fig. 5. Colour-marked Volume renderings based on μCT (Amira 6, Adobe Photoshop CS4); **A** – overview topside; **B** – Overview underside; **C, D** – lateral view; **E** – sliced projection showing two nymphs with the anterior part already outside and the posterior part inside the egg case; **F** – sliced projection showing holometabolan larva in the egg cluster.

Several types of mimicry are frequently occurring within Heteroptera. This is also true for nymphal stages, e.g. in some groups which feed on flowers or seed. These nymphs posses the same colourations (and also shape in some cases) as the seeds or flowers on which they developed (summarised e.g. in Schuh & Slater 1995). Also, in forms of Reduviidae such mimicry can be seen, e.g. elongate and slender body, which resembles the grass and sedge stems or leaves of the habitat. Some tropical representatives of Reduviidae show colour patterns and structural modifications, which resemble flowers on which they sit and wait for prey (e.g. summarised in Schuh & Slater 1995). Thus, to our knowledge, no reports of mimicry of eggs are known so far in Heteroptera, and the interpretation remains plausible, but speculative.

Another interesting point regarding the function of the long extensions of the collar was raised by Myles & Smith (1986). They reported that the corollar of *Sinea rileyi* (Harpactorinae) can contract if the eggs were submerged under water and open again when drying. The corolla of *Sinea rileyi* is composed of long aeropilar outgrowths, which indeed, look quite similar to the chorion extensions at the apical part of the herein described eggs of specimen GP 10958 (Myles & Smith 1986: figs. 1–4). The authors interpreted the function of the structure as plastron, whereby air bubbles persists between the eggs to preserve respiration processes. A similar observation was also reported for *Loricula elegantula* (Microphysidae) by Cobben (1968).

4.3. General background: the fossil record of hatchlings and early immature stages

Euarthropoda is a mega-diverse group of animals including four major recognised groups: insects (also called hexapods in Anglo-American literature), chelicerates (spiders, mites, scorpions and all their lesser known relatives), myriapods (centipedes, millipedes and some smaller relatives of these) and the various forms of eucrustaceans (prawns, shrimps, lobsters, crabs, woodlice and many more). The various forms of Euarthropoda are not only everywhere in the modern-day fauna, but have already dominated many ecosystems of the past as shown by an incredible fossil record.

While we easily recognise adult forms of Euarthropoda and accept their ecological impact, we tend to partly forget that these organisms have to develop from an egg to become the forms we know so well. Thus, it may not be astonishing that for most groups of Euarthropoda we know most aspects about the adult, but less so for the many immature stages such as zoeae (decapod crustaceans), nymphs (many insects some chelicerates), pupoids (hatching stages of at least some millipedes), or naiads (aquatic immatures of some groups of flying insect).

Naturally, we face a similar problem concerning the work on fossil material. Many studies focus on adult specimens. Yet the fossil record is in fact full of immatures euarthropods and there is in fact also a still growing faction of studies dealing with them, yet, still the number of studies does not reflect the amount of available material. In other words, studies on fossil immature euarthropods are still underrepresented.

Even more so, we can identify a differentiation among the different immatures. Put simply larger immatures, mostly also meaning later developmental stages seem to be favoured, either to be preserved or to be recognised. This means that if we know aspects of the immatures' development of fossil euarthropods we tend to know more about the late phase and less so about the earlier and earliest phase. Very special seems to be the preservation of first stage immatures or hatchlings. Still there are quite some impressive examples available.

One of the oldest examples is an about 480-million-year-old nauplius larva in Orsten-type preservation that is hatching from its egg (Roy & Fåhraeus 1989). More generally, Orsten-type preservation has provided numerous examples of first stage individuals of various crustaceans (modern eucrustacean-type larvae; Waloszek & Müller 1998; Maas et al. 2006; Haug et al. 2014), but also those of early representatives of the crustacean lineage prior to the split of myriapods, insects and eucrustaceans (Maas & Waloszek 2001; Waloszek 2003; Haug et al. 2012b) as well as early chelicerates (Waloszek & Dunlop 2003).

Comparable to the Orsten-type fossils in their three-dimensionality are fossils from the Herefordshire Lagerstätte. Some of these fossils have been reported to co-occur with their offspring (Siveter et al. 2007; Briggs et al. 2016a). Yet, here the smaller individuals are so small that resolution prohibits the access of details. The smaller specimens may represent embryos (so not yet hatched forms) or even parasites (Piper 2016; but see Briggs et al. 2016b). Similarly, other very old fossils that have been interpreted to show cases of brood care (Siveter et al. 2014; Caron & Vannier 2016) largely represent cases in which the degree of detail of the supposed early stage specimens is clearly not comparable to Orsten-type fossils and hence they are challenging to interpret in a biological context.

Younger occurrences include the cuticular remains of the hatching stage of a scorpion (so-called "embryo II") and a very tiny dictyopteran insect nymph (Dictyoptera is the group including cockroaches, mantodeans and termites), both from the Carboniferous of north-western Germany (Braun 1997; Hörnig et al. 2014).

An especially interesting type of preservation for hatchlings is fossilised resin, or amber. Here numerous examples have been recognised as hatching stages for example of myriapods (Haug et al. 2018) but especially various insect groups including jumping bristletails (Haug et al. 2015) and cockroaches (Gröhn 2015; Hörnig et al. 2016).

The fossil record of arthropod hatchlings is still very fragmentary, also in relation to descriptions of adult representatives. To understand more about the evolution of arthropod groups and their phylogeny it is necessary to consider immature stages. Especially due to their ecological impact, research on fossil immatures is important for the reconstruction of living environments of different geological periods.

The specimen presented herein represents an extremely rare case of 'frozen behaviour' of a hatching process of heteropteran nymphs from about 15–20 million years ago. If the hatchlings are indeed representatives of Reduviidae, the morphology of the eggs and type of egg cluster resembles strongly these, which can be found today in this group. This indicates that this type of egg laying strategy evolved more than 15–20 million years ago.

5. References

Arbogast, R. T., Lecato, G. L. & Van Byrd, R. (1980): External morphology of some eggs of stored-product moths (Lepidoptera Pyralidae, Gelechiidae, Tineidae). – International Journal of Insect Morphology and Embryology, **9** (3): 165–177.

Arillo, A. (2007): Paleoethology: fossilized behaviours in amber. – Geologica Acta, **5** (2): 159.

Bährmann, R. (2011): Bestimmung wirbelloser Tiere. Heidelberg (Spektrum).

Barber, G. (1923): Notes on *Sinea diadema* (Fabr.); Hemiptera. – Psyche, **30** (2): 74–76.

Boucot, A. J. & Poinar Jr, G. O. (2010): Fossil Behavior Compendium. Boca Raton (CRC Press).

Braun, A. (1997): Vorkommen, Untersuchungsmethoden und Bedeutung tierischer Cuticulae in kohligen Sedimentgesteinen des Devons und Karbons. – Palaeontographica, (A), **245**: 83–156.

Briggs, D. E. G., Siveter, D. J., Siveter, D. J., Sutton, M. D. & Legg, D. (2016a): Tiny individuals attached to a new Silurian arthropod suggest a unique mode of brood care. – Proceedings of the National Academy of Sciences, **113** (16): 4410–4415.

Briggs, D. E. G., Siveter, D. J., Siveter, D. J., Sutton, M. D. & Legg, D. (2016b): Reply to Piper: Aquilonifer's kites are not mites. – Proceedings of the National Academy of Sciences, **113** (24): E3320–E3321.

Caron, J. B. & Vannier, J. (2016): *Waptia* and the diversification of brood care in early arthropods. – Current Biology, **26** (1): 69–74.

Choe, D. H. & Rust, M. K. (2007): Use of plant resin by a bee assassin bug, *Apiomerus flaviventris* (Hemiptera: Reduviidae). – Annals of the Entomological Society of America, **100** (2): 320–326.

Cobben, R. H. (1968): Evolutionary trends in Heteroptera, Part I, Eggs, architecture of the shell, gross embryology and eclosion. – Laboratorium voor Entomologie, Wageningen, Mededeling, **151**: 1–475.

Coscaron, M. E., Melo, M. E. & Oi-Iashi, D. V. (2002): Description of the egg and fourth instar of *Cosmoclopius curacavencis* (Heropterea: Reduviidae: Harpactorinae). – Faceiya, **18**: 59–61.

Endo, J., Takanashi, T., Mukai, H. & Numata, H. (2019): Egg-cracking vibration as a cue for stink bug siblings to synchronize hatching. – Current Biology, **29** (1): 143–148.

Fischer, T. C. & Hörnig, M. K. (2019): Mating moths (Tineidae, Ditrysia, Lepidoptera) preserved as frozen behavior inclusion in Baltic Amber (Eocene). – Palaeontologia Electronica, **22** (1): 1–11.

Forister, M. L., Fordyce, J. A., Nice, C. C., Gompert, Z. & Shapiro, A. M. (2006): Egg morphology varies among populations and habitats along a suture zone in the *Lycaeides idas-melissa* species complex (Lepidoptera: Lycaenidae). – Annals of the Entomological Society of America, **99** (5): 933–937.

Funk, V. A. (1997): *Xenophyllum*, a new Andean genus extracted from *Werneria* s.l. (Compositae: Senecioneae). – Novon, **7**: 235–241.

Gaines, R. R., Briggs, D. E. G. & Yuanlong, Z. (2008): Cambrian Burgess Shale-type deposits share a common mode of fossilization. – Geology, **36** (10): 755–758.

Gao, T., Shih, C., Labandeira, C. C., Liu, X., Wang, Z., Che, Y., Yin, X. & Ren, D. (2019): Maternal care by Early Cretaceous cockroaches. – Journal of Systematic Palaeontology, **17** (5): 379–391.

García-Barros, E. & Martín, J. (1995): The eggs of European satyrine butterflies (Nymphalidae): external morphology and its use in systematics. – Zoological Journal of the Linnean Society, **115** (1): 73–115.

Gil-Santana, H. R. & Forero, D. (2010): Taxonomical and biological notes on Neotropical Apiomerini (Hemiptera: Heteroptera: Reduviidae: Harpactorinae). – Zootaxa, **2331** (1): 57–68.

Gould, S. J. (1990): Wonderful life: the Burgess Shale and the nature of history. New York (Norton & Co.).

Grimaldi, D. A. (1996): Captured in amber. – Scientific American, **274** (4): 84–91.

Grimaldi, D. A. & Engel, M. S. (2005): Evolution of the Insects. Cambridge (Cambridge University Press).

Gröhn, C. (2015): Einschlüsse im Baltischen Bernstein. Kiel & Hamburg (Wachholtz Verlag & Murmann Publishers).

Haug, C., Haug, J. T., Maas, A. & Waloszek, D. (2014): Fossil larvae (head larvae, nauplii, and others) from the Cambrian in Orsten preservation. In: Martin, J. W., Olesen, J. & Høeg, J. T. (eds.): Atlas of Crustacean Larvae: 17–26; Baltimore (Johns Hopkins University Press).

Haug, J. T., Briggs, D. E. G. & Haug, C. (2012a): Morphology and function in the Cambrian Burgess Shale megacheiran arthropod *Leanchoilia superlata* and the application of a descriptive matrix. – BMC Evolutionary Biology, **12** (1): 162.

Haug, J. T., Castellani, C., Haug, C., Waloszek, D. & Maas, A. (2012b): A *Marrella*-like arthropod from the Cambrian of Australia: A new link between "Orsten"-type and Burgess Shale assemblages. – Acta Palaeontologica Polonica, **58** (3): 629–640.

HAUG, J. T., CARON, J.-B. & HAUG, C. (2013a): Demecology in the Cambrian: synchronized molting in arthropods from the Burgess Shale. – BMC Biology, 11: art. 64.

HAUG, J. T., MÜLLER, C. H. G. & SOMBKE, A. (2013b): A centipede nymph in Baltic amber and a new approach to document amber fossils. – Organisms Diversity & Evolution, 13: 425–432.

HAUG, J. T., HÄDICKE, C. W., HAUG, C. & HÖRNIG, M. K. (2015): A possible hatchling of a jumping bristletail in 50 million years old amber. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 278 (2): 191–199.

HAUG, J. T., HAUG, C., NEUMANN, C., SOMBKE, A. & HÖRNIG, M. K. (2018): Early post-embryonic bristly millipedes (Myriapoda, Polyxenida) from Saxonian amber (Eocene). – Bulletin of Geosciences, 93 (1): 1–11.

HARIDASS, E. T. (1985): Ultrastructure of the eggs of Reduviidae: I. Eggs of Piratinae (Insecta – Heteroptera). – Proceedings of the Indian Academy of Sciences, Animal Sciences, 94 (5): 533–545.

HARIDASS, E. T. (1986): Ultrastructure of the eggs of Reduviidae: II eggs of Harpactorinae (Insecta: Heteroptera). – Proceedings of the Indian Academy of Sciences, Animal Sciences, 95 (2): 237–246.

HARIDASS, E. T., BALU, A., & MORRISON, M. N. (1987): Feeding and behavioural parameters and egg ultrastructure in the biosystematics of Reduviidae (Insecta – Heteroptera). – Proceedings of the Indian Academy of Sciences, Animal Sciences, 96 (5): 485–497.

HÖRNIG, M. K., HAUG, C., HERD, K. J. & HAUG, J. T. (2014): New insights into dictyopteran early development: smallest Palaeozoic roachoid nymph found so far. – Palaeodiversity, 7: 159–165.

HÖRNIG, M. K., HAUG, C., SCHNEIDER, J. W. & HAUG, J. T. (2018): Evolution of reproductive strategies in dictyopteran insects – clues from ovipositor morphology of extinct roachoids. – Acta Palaeontologica Polonica, 63 (1): 1–24.

HÖRNIG, M. K., SOMBKE, A., HAUG, C., HARZSCH, S. & HAUG, J. T. (2016): What nymphal morphology can tell us about parental investment – a group of cockroach hatchlings in Baltic Amber documented by a multi-method approach. – Palaeontologia Electronica, 19 (1): 1–20.

ITURRALDE-VINENT, M. A. & MACPHEE, R. D. E. (1996): Age and paleogeographical origin of Dominican amber. – Science, 273 (5283): 1850–1852.

ITURRALDE-VINENT, M. A. & MACPHEE, R. D. E. (2019): Remarks on the age of Dominican amber. – Palaeoentomology, 2 (3): 236–240.

KWADJO, K. E., KRA, K. D., DOUAN, B. G. & DOUMBIA, M. (2017): Natural enemies and prey of Rhynocoris albopilosus (Heteroptera, Reduviidae) in Grand-lahou, Southern Côte d'Ivoire". – International Journal of Current Research, 9 (6): 52414–52417.

MAAS, A. & WALOSZEK, D. (2001): Cambrian derivatives of the early arthropod stem lineage, pentastomids, tardigrades and lobopodians an 'Orsten'Perspective. – Zoologischer Anzeiger, 240 (3–4): 451–459.

MAAS, A., BRAUN, A., DONG, X. P., DONOGHUE, P. C., MÜLLER, K. J., OLEMPSKA, E., REPETSKI, J. E., SIVETER, D. J., STEIN, M. & WALOSZEK, D. (2006): The 'Orsten' – more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. – Palaeoworld, 15 (3–4): 266–282.

MYLES T. G. & SMITH R. L. (1986): Contractability of a chorionic opercular corolla on eggs of the assassin bug Sinea rileyi Montandon (Heteroptera: Reduviidae). – International Journal of Invertebrate Reproduction and Development, 11: 317–322.

NITIN, K. S., SHIVARAMA BHAT, P., RAVIPRASAD, T. N. & VANITHA, K. (2017): Biology, behaviour and predatory efficiency of Sycanus galbanus Distant (Hemiptera: Reduviidae: Harpactorinae) recorded in Cashew plantation. – Journal of Entomology and Zoology Studies, 5: 524–530.

PENNEY, D. (2010): Dominican amber. In: PENNEY, D. (ed.): Biodiversity of fossils in amber from the major world deposits: 22–41; Castleton (Siri Scientific Press).

PÉREZ-DE LA FUENTE, R., ENGEL, M. S., AZAR, D. & PEÑALVER, E. (2019): The hatching mechanism of 130-million-year-old insects: an association of neonates, egg shells and egg bursters in Lebanese amber. – Palaeontology, 62 (4): 547–559.

PIKART, T. G., SOUZA, G. K., ZANUNCIO, T. V., ZANUNCIO, J. C. & SERRÃO, J. E. (2012): Eggshell structure of the predator Harpactor angulosus (Hemiptera: Reduviidae). – Annals of the Entomological Society of America, 105 (6): 896–901.

PIPER, R. (2016): Offspring or phoronts? An alternative interpretation of the "kite-runner" fossil. – Proceedings of the National Academy of Sciences, 113 (24): E3319–E3319.

POINAR JR, G. (2010): Palaeoecological perspectives in Dominican amber. – Annales de la Société entomologique de France, 46 (1–2): 23–52.

POINAR, G. O. & POINAR, R. (1999): The amber forest: a reconstruction of a vanished world. Princeton (Princeton University Press).

ROY, K. & FÅHRAEUS, L. E. (1989): Tremadocian (Early Ordovician) nauplius-like larvae from the Middle Arm Point Formation, Bay of Islands, western Newfoundland. – Canadian Journal of Earth Sciences, 26 (9): 1802–1806.

SCHAEFER, C. W. & WOLF, K. W. (2003): Notes on the harpactocorine genus Sinea (Hemiptera: Heteroptera: Reduviidae). – Entomologica Americana, 111 (4): 227–235.

SCHUH, R. T. & SLATER, J. A. (1995): True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Ithaka (Cornell University Press).

SELLICK, J. (1997): The range of egg capsule morphology within the Phasmatodea and its relevance to the taxonomy of the order. – Italian Journal of Zoology, 64 (1): 97–104.

SHURTZ, R. A. & MCPHERSON, J. E. (2005): Life history and laboratory rearing of Sinea spinipes (Heteroptera: Reduviidae) with descriptions of immature stages. – Annals of the Entomological Society of America, 98 (1): 18–36.

SIVETER, DA. J., SIVETER, DE. J., SUTTON, M. D. & BRIGGS, D. E. G. (2007): Brood care in a Silurian ostracod. – Proceedings of the Royal Society, (B), 274 (1609): 465–469.

SIVETER, DA. J., TANAKA, G., FARRELL, Ú. C., MARTIN, M. J., SIVETER, DE. J. & BRIGGS, D. E.G. (2014): Exceptionally preserved 450-million-year-old Ordovician ostracods with brood care. – Current Biology, 24 (7): 801–806.

SOUTHWOOD, T. R. E. (1956): The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. – Transactions of the Royal Entomological Society of London, 108 (6): 163–221.

SRIKUMAR, K. K., BHAT, P. S., RAVIPRASAD, T. N., VANITHA, K., SAROJ, P. L. & AMBROSE, D. P. (2014): Biology and behavior of six species of reduviids (Hemiptera: Reduviidae: Harpactorinae) in a cashew ecosystem. – Journal of Agricultural and Urban Entomology, 30 (1): 65–82.

VENNISON, S. J. & AMBROSE, D. P. (1990): Diversity of eggs and ovipositional behaviour in Reduviids (Insecta, Heteroptera, Reduviidae) of South India. – Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologisches Museum und Institut für Spezielle Zoologie, 66 (2): 319–331.

Vitali, F. (2009): Two new longhorned beetles from Dominican amber (Coleoptera, Cerambycidae). In: Berning, B. & Podenas, S. (eds.): Amber – Archive of deep time: 223–230; Linz (Biologiezentrum der Oberösterreichischen Landesmuseen).

Voss, S. C. & McPherson, J. E. (2003): Life history and laboratory rearing of *Sinea diadema* (Heteroptera: Reduviidae) with descriptions of immature stages. – Annals of the Entomological Society of America, **96** (6): 776–792.

Waloszek, D. (2003): The 'Orsten' window – a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda. – Paleontological Research, **7** (1): 71–88.

Waloszek, D. & Dunlop, J. A. (2003): A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian 'Orsten' of Sweden, and the phylogenetic position of pycnogonids. – Palaeontology, **45** (3): 421–446.

Waloszek, D. & Müller, K. J. (1998): Cambrian 'Orsten'-type arthropods and the phylogeny of Crustacea. In: Fortey, R.

A. & Thomas, R. H. (eds.): Arthropod Relationships. – The Systematics Association, Special Volume Series, **55**: 139–153; Dordrecht (Springer).

Weirauch, C., Bérenger, J. M., Berniker, L., Forero, D., Forthman, M., Frankenberg, S., Freedman, A, Gordon, E., Hoey-Chamberlain, R., Hwang, W. S., Marshall, S. A., Michael, A., Paiero, S. M. Udah, O., Watson, M, Yeo, M., Zhang, G. & Zhang, J. (2014): An illustrated identification key to assassin bug subfamilies and tribes (Hemiptera: Reduviidae). – Canadian Journal of Arthropod Identification, **26** (2): 1–115.

Weitschat, W. (2009): Jäger, Gejagte, Parasiten und blinde Passagiere – Momentaufnahmen aus dem Bernsteinwald. – Denisia, **26** (86): 243–256.

Weitschat, W. & Wichard, W. (2002): Atlas of Plants and Animals in Baltic Amber. München (Pfeil).

Zomlefer, W. B. (1994): Guide to flowering plant families. Chapel Hill (University of North Carolina Press).

Addresses of the authors:

Marie K. Hörnig (corresponding author), Universität Greifswald, Zoologisches Institut und Museum, Cytologie und Evolutionsbiologie, Soldmannstraße 23, 17489 Greifswald, Germany; e-mail: marie.hoernig@palaeo-evo-devo.info

Thilo C. Fischer, Förderverein der Bayerischen Staatssammlung für Paläontologie und Geologie München, Richard-Wagner-Straße 10, 80333 München, Germany; e-mail: thilo.fischer@4gene.de

Joachim T. Haug, LMU Munich, Biocenter – Department of Biology II and GeoBio-Center, Großhaderner Str. 2; 82152 Planegg-Martinsried, Germany; e-mail: joachim.haug@palaeo-evo-devo.info