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New insights into dictyopteran early development: smallest Palaeozoic roachoid nymph found so far

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Abstract

Palaeozoic dictyopteran nymphs are quite rarely reported in the fossil record and, therefore, the early ontogeny of these Palaeozoic insects is largely unknown. The smallest Carboniferous dictyopteran nymphs known so far were found at the Piesberg quarry, northwestern Germany, and are about 8 to 9 mm in entire estimated body length. We present here two new findings of fossil roachoid nymphs, also from the Piesberg quarry, which are distinctly smaller than the ones previously discovered. For the documentation of these specimens, we compare and discuss different illumination settings. In these new fossils, anlagen of wings are prominent, but in comparison with the known specimens the wing pads seem to be less developed. Indicated by the body size and the developmental state of the wing pads, it seems likely that these nymphs represent younger stages of the earlier described nymphs. The smaller specimen represents a very early stage, possibly even a hatchling. In concordance with earlier findings, we can add further support to the hypothesis of an extremely gradual wing development in early insects.

Keywords: Dictyoptera, Carboniferous, development, fossil nymph, cross-polarized lighting.

1. Introduction

Insects are generally considered to be the most successful group of organisms in the modern fauna. Hence it is not surprising that also fossil remains of insects are commonly found from the late Palaeozoic onwards. The majority of these comparably numerous fossils found in the Palaeozoic are adult insects. Fossils of nymphs of this time are still rather rare. An exemption represents the fossil findings of Montceau-les-Mines, France, where a majority of fossil insect is assigned to juvenile representatives (POPLIN & HEYLER 1994; GARWOOD et al. 2012). Up to now, the most ancient undoubted known remains of pterygote nymphs are of Marsdenian (Namurian B, Bashkirian) age and were documented from Hagen-Vorhalle (BRAUCKMANN et al. 2003). The true identity of a supposed Devonian dicondylian nymph has been heavily debated (GARROUSTE et al. 2012, 2013; HÖRNSCHEMEYER et al. 2013). Among the relatively small number of fossil nymphs, representatives of Dictyoptera s.l., i.e., roach-like insects are dominating; the group with the second-most representatives is Palaeodictyoptera (e.g., WOOTTON 1972; KUKALOVÁ-PECK 1974; ROSS 2010).

The known Carboniferous nymphal specimens of dictyopteran insects were mainly described by SELLARDS (1903, 1904), ROLFE (1967), JARZEMBOWSKI (1987), KUKALOVÁ-PECK (1997), SCHNEIDER (1984), GARWOOD et al. (2012), HAUG JT & HAUG C (2013), HAUG JT et al. (2013a). The nymphs described therein appear to be mostly rather large and far developed. It therefore seems likely that these represent comparably late nymphal stages.

HAUG JT el al. (2013a) estimated body lengths of small roachoid nymphs based on fragments from the Piesberg quarry near Osnabrück, northwestern Germany, with the resulting entire body length of about 8-9 mm. This specimen currently represents the smallest Palaeozoic fossil roachoid nymph known so far; the smallest specimens described by SELLARDS (1903, 1904) and JARZEMBOWSKI (1987) are about 10 mm long.

Extant blattodean nymphs have significantly smaller hatchlings; as an example, hatchlings of *Periplaneta americana* have an entire body length of about 4 mm. This can also be shown for younger fossil deposits, in fact small specimens seem to be widespread in museum collections (Fig. 1), but were rarely mentioned in the literature.

Therefore, it seems that we have so far no specimens representing very early developmental stages in Palaeozoic insects; hence the early ontogeny of Palaeozoic insects remains unknown. This even applies to the probably best represented lineage Dictyoptera.

We report here new findings of dictyopteran (s.l.) nymphs from the Carboniferous Piesberg quarry. One of these specimens is significantly smaller than any other specimen known before and hence partly closes the gap of knowledge of early post-embryonic insect development in the late Palaeozoic.

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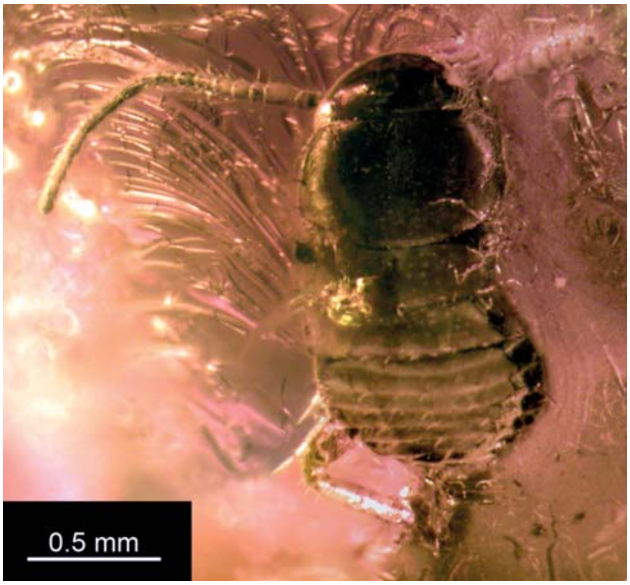

Fig. 1. Small blattoid nymph, ZMUC 901808, preserved in Baltic amber (40 – 50 mya). Entire body length (without appendages) is about 1.6 mm.

both Natural History Museum of Denmark, Copenhagen, provided access to the amber collection of the museum and to technical equipment and helped with work in the collection. MKH was kindly supported by the SYNTHESYS Project (FP 7) and supported by Steffen Harzsch, Greifswald. JTH is currently funded by the German Research Foundation (DFG HA 6300/3-1). Matthias J. Starck, Planegg-Martinsried, is thanked for his support. Russell Garwood, Manchester, and Carsten Brauckmann, Clausthal-Zellerfeld, provided very helpful comments to an earlier version of this manuscript.

2. Material and methods

2.1. Material

The here described specimens with the collection numbers PBH 500 and PBH 501 were part of the private collection of Helga Bech, Fröndenberg (Westphalia), but will be deposited in the collection of the Museum am Schölerberg (MAS Pal), Osnabrück. The specimens came from the Piesberg quarry, which is assigned to the Late Carboniferous (Pennsylvanian; about 308 mya, Leipner, pers. com.) and were found by Helga Bech, in the layers above the coal seam Flöz Zweibänke. For further information about the geological details, see e.g., Dunlop et al. (2008) and Haug JT et al. (2013a). Both specimens appear to be preserved in a kind of shale-type preservation (see Haug JT et al. 2013a).

A single comparative specimen of a nymphal dictyopteran preserved in amber comes from the collection of the Zoological Museum in Copenhagen with the collection number ZMUC 901808. The amber is of Baltic origin and therefore likely of Eocene age (40–50 mya).

2.2. Methods

Specimens PBH 500 and PBH 501 were photographed with a Canon Eos Rebel T3i, equipped with a MP-E 65 mm objective and a Canon MT 24 Macro Twin Flash. In order to reduce reflections and enhance the contrast between fossil and matrix, all specimens were photographed under cross-polarised light (Figs. 1, 2A, 3A, C; Haug C et al. 2011, 2012; Haug JT et al. 2012, 2013a, b). For comparison also pictures without polarization filters were taken (Figs. 2B, C, 3B), either with undirected light or with low-angle side light.

Specimen ZMUC 901808 was photographed with a Nikon Mikrophot-FX compound microscope equipped with a ToupTek DCM 510 ocular camera. Illumination was provided by two external cold light sources equipped with polarization filters. The image is a composite image recorded as stacks. Stacks were fused with Image Analyzer, CombineZM, or Combine ZP. Resulting sharp images were stitched either with Adobe Photoshop CS4 or Microsoft Image Composite Editor (e.g., Haug JT et al. 2008; Haug C et al. 2009).

All images were optimized for colour balance, saturation and sharpness in Adobe Photoshop CS4.

3. Results

3.1. Specimen PBH 500

Description: The specimen represents the remains, probably an exuvia (indicated by median gap of the thoracic tergites) of a roachoid insect nymph, preserved in dorsal aspect (Fig. 2). The entire body length is about 7.5 mm and maximum width about 5 mm. The head (ocular segment and post-ocular segments 1-5) is not visible (not preserved or covered by pronotum). Post-ocular segments 6-8 (thoracic segments: pro-, meso- and metathorax) each dorsally with a well sclerotised tergite (pro-, meso- and metanotum). Most anterior structure is the right half of the pronotum, which usually covers the head, with a length of about 2 mm. Left part of pronotum is missing. The pronotum is followed by the mesonotum, which is also is clearly made up of a right and a left half. Both are subsquare-shaped, slightly extending posteriorly towards the lateral edge and are medially about 1 mm, laterally about 2 mm long. The next structure is the metanotum. It roughly resembles the mesonotum, but is shorter in anterior-posterior axis medially (0.75 mm, laterally about 1.5 mm). Appendages of post-ocular segments

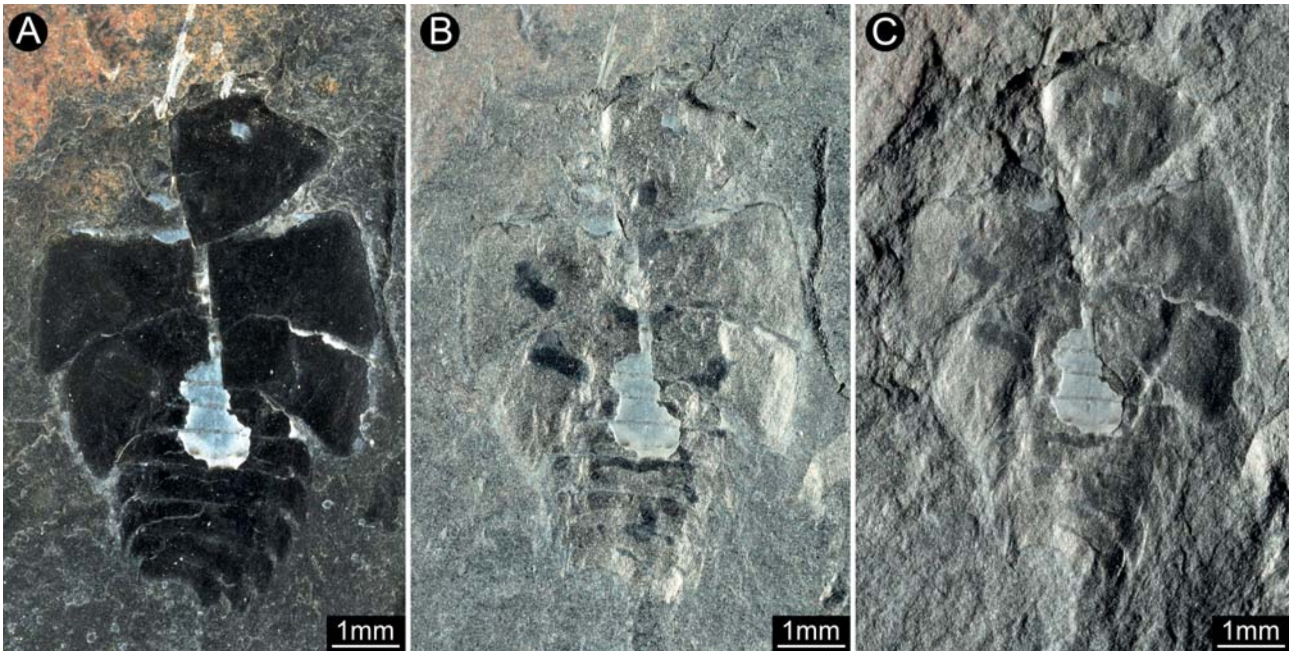

Fig. 2. Small dictyopteran nymph from the Piesberg quarry, PHB 500. A. Under cross-polarised light. B. Under undirected white light. C. Under low-angle side light. Note the good contrast under cross polarised light.

7 and 8 (legs) could be partly indicated by darker areas (Fig. 2B, C). Post-ocular segments 7 and 8 bear anlagen of wings (wing pads). The metanotum is followed by a series of abdominal tergites; nine abdominal segments are visible, each between 0.3 and 0.5 mm long. Entire length of the visible part of the abdomen is about 3.5 mm. Cerci are not preserved.

Remarks: The specimen represents a more complete nymphal exuvia than those reported before from the Piesberg quarry (Haug JT et al. 2013a). The specimen is also slightly smaller than the reconstructed smaller instar of Haug JT et al. (2013a). Based on the fact that the wing pads extending from the metanotum appear additionally slightly shorter than in the smallest specimen described in Haug JT et al. (2013a), it most likely represents the nymphal stage right before the latter. The alternative of representing another, smaller species is less likely due to the continuity of the length increase of the wing pad. In other words, not only the body length, but also the length of the wing pads in relation to the body length increase, as in an ontogenetic sequence can be expected.

3.2. Specimen PBH 501

Description: The specimen also represents a roachoid nymphal insect, preserved in dorso-lateral aspect (Fig. 3). The specimen appears partly incomplete; probably some pieces remained in the counterpart, which is not available. The entire body length is about 3.3 mm and the maximum width is about 1.8 mm. The head (ocular segment and post-ocular segments 1-5) is not visible (not preserved or covered by pronotum). Post-ocular segments 6-8 (thoracic segments: pro-, meso- and metathorax) each dorsally with a well sclerotised tergite (pro-, meso- and metanotum). Entire length of thorax is about 2 mm (median). Prothorax is incomplete preserved and about 1 mm long. The preserved part is about 1.3 mm wide, presumably about 1.6 mm in original condition. The mesonotum is medially about 0.75 mm long, laterally about 1 mm long and 1.8 mm wide. Metanotum is strongly curved, medially about 0.4 mm long and laterally about 0.7 mm long. Width is presumably about 1.9 mm.

Appendages of post-ocular segments 7 and 8 (legs) are not preserved. Post-ocular segments 7 and 8 bear anlagen of wings (wing pads). Abdomen presumably contains post-ocular segments 9-19 (as it is an insect), but not all segments are preserved. Five segments are clearly recognisable, but they cannot be clearly identified as specific segments. Visible segments are about 0.15 and 0.3 mm long. Preserved parts of the abdomen are slightly less than 1 mm wide, but presumably they were wider in original condition. Entire length of the visible parts of the abdomen is about 1.2 mm. Cerci are not preserved.

Remarks: Although the specimen is partly incomplete, it can be clearly identified as a "typical" dictyopteran nymph (based on large and wide thoracic tergites, especially the head covering pronotum; more slender abdominal tergites in relation to thoracic tergites). We can estimate

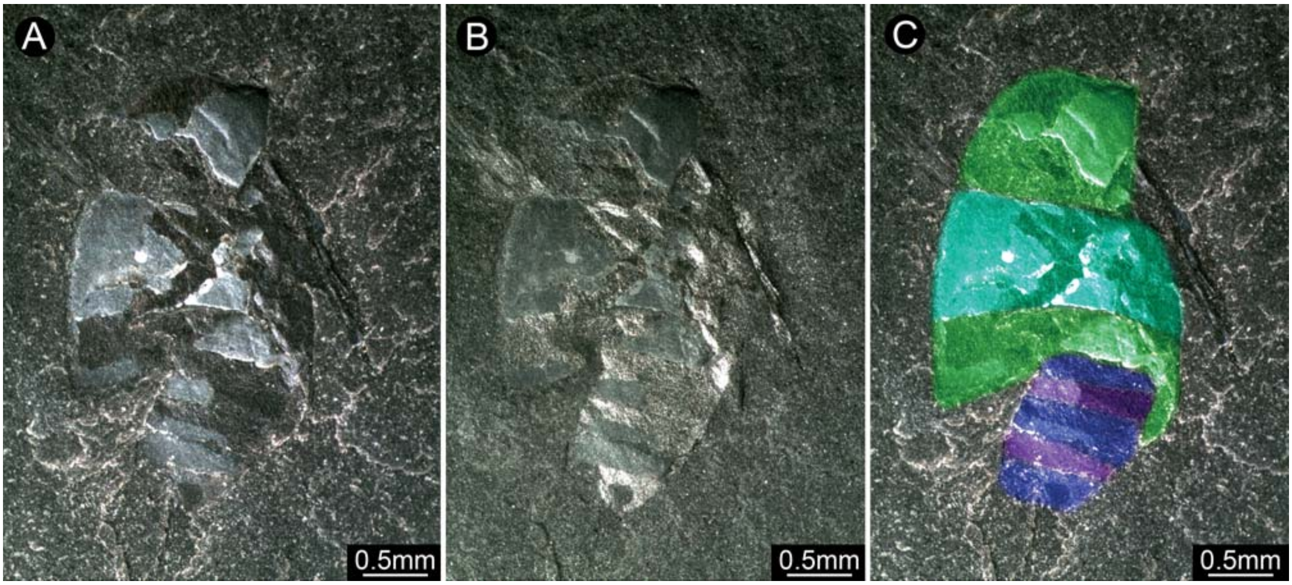

Fig. 3. Small dictyopteran nymph from the Piesberg quarry, PHB 501. A. Under cross-polarised light. B. Under undirected white light. C. Colour-marked version of A.

that the specimen would have measured slightly less than 4 mm in length originally.

3.3. Documentation evaluation

As put forward by Haug C et al. (2012) and Haug JT et al. (2012, 2013a), cross-polarised light provided the best contrast between fossil and matrix. Also fully reflected light, evenly distributed, provided some additional information, i.e., darker areas, which could indicate remains of thoracic appendages. Most problematic appears to be low-angle side light as it mixes surface colour information and relief information, without providing a good contrast.

4. Discussion

4.1. Nymphal nature of the specimens

A standard question when dealing with fossil specimens with immature characteristics is whether we can be sure that they indeed represent immatures. The clear answer is: no. We could also speculate that these specimens represent tiny, paedomorphic adults of a separate species. While this cannot be completely excluded, it seems more parsimonious that they indeed represent earlier stages of the same ontogenetic series indicated by the four fragmentary specimens depicted in Haug JT et al. (2013a). The correlation of overall size and the slight increase of wing pad length appear to be most compatible with this interpretation. Numerous wing remains and other parts of the body of adult insects from the Piesberg quarry still await description (Haug JT et al. 2013a), while already a comparably rich fauna of adult insects has been recognised (Brauckmann 1983, 1991, 1995; Brauckmann & Herd 2000, 2002, 2005, 2007; Zessin 2008; Béthoux & Herd 2009; Brauckmann et al. 2009); up to three species of dictyopterans may be among the still to be described material (Herd pers. obs.). A clear designation of nymphs and adults will demand for a more complete sequence and more ventral details.

The Piesberg quarry has already provided the smallest known specimen of the xiphosuran *Euproops* found so far (Schultka 2000; Haug C et al. 2012), and appears to continue to provide small Palaeozoic arthropod specimens.

4.2. Size and developmental state of the specimens

The two specimens represent the two smallest Palaeozoic insect nymphs known so far. The larger one most likely represents a nymphal stage right before the next larger specimen described by Haug JT et al. (2013a). The smaller one might well be three stages before the next one (Fig. 4; see Kutschera et al. 2012 for a discussion of the size increase per moult). Hence we appear to currently miss specimens representing two size classes, but a larger sample size will be necessary before clarifying this issue.

Even though the small specimen is very tiny, it already possesses quite apparent wing pads. This is fully compatible with a very gradual development of wing anlagen in Palaeozoic insects, leading to large nymphs with very long wing pads, unparalleled among their modern relatives

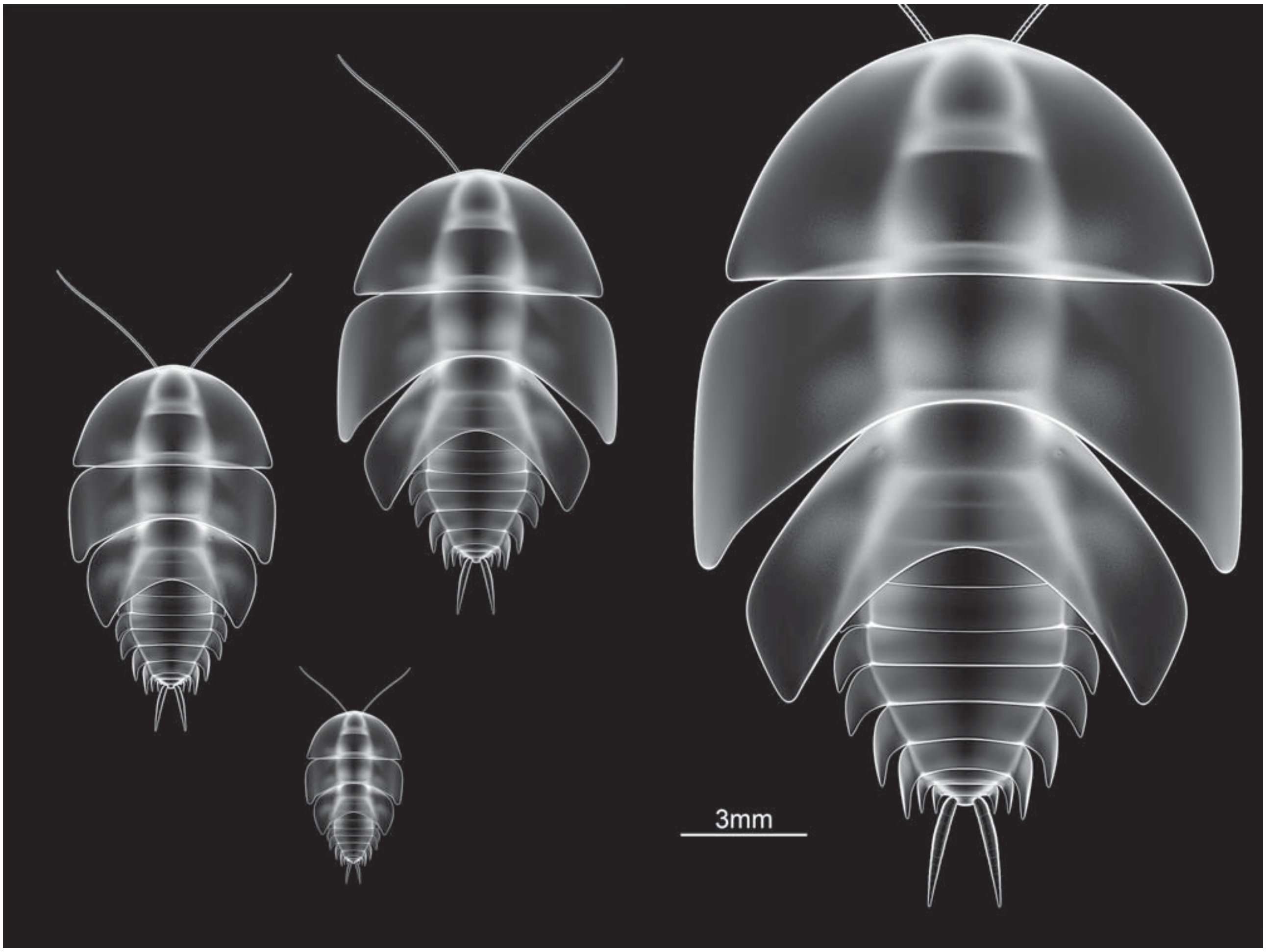

Fig. 4. Computer models of the four nymphal stages known from the Piesberg quarry. Some general features amended from other fossils (e.g., HAUG JT et al. early view). Note the size difference.

(HAUG JT et al. early view). Unlike larger dictyopteran and also palaeodictyopteran nymphs (e.g., KUKALOVÁ-PECK 1974, 1978, 1991; SHEAR & KUKALOVÁ-PECK 1990), there is no indication for an articulation of the wing pads; they seem to be continues with the tergum.

The specimen is quite incomplete and only very small aspects of the ontogeny are known, yet we can already see some differences to other Palaeozoic developmental sequences. KUKALOVÁ-PECK (1997) described that wing pads curve back in early nymphs of Palaeodictyoptera, but straighten more and more during ontogeny in palaeodictyopteran nymphal development. In the case of dictyopterans this does not seem to be the case. In the earlier stages described here, the wing pads appear to be straighter than in later stages from the same locality or very mature stages from other localities (HAUG JT et al. early view). Still, also this observation remains preliminary.

In modern forms the development of wing pads is clearly postponed into later stages, leading to a more metamorphic development in the modern representatives (see MIALL & DENNY 1886; BELL et al. 2007; HAUG JT & HAUG C 2013; HAUG JT et al. early view for a longer discussion).

4.3. A possible hatchling?

The very tiny size of the smaller specimen raises the question whether it could represent a hatchling. Hatching sizes of modern species are well in this range (e.g., ROTH & HAHN 1964; BELL et al. 2007). We do not know about the egg size in early dictyopterans. Their long and thin ovipositor indicate comparably small eggs. Yet, also in modern blattoids hatchlings with few millimetres hatch from astonishingly small eggs (ROTH & WILLIS 1955; ROTH & STAY 1962). Hence, the specimen could well represent a hatching stage, but we can currently not further support this interpretation. If not representing a hatchling, at least it must represent a very early nymph.

5. Conclusions

The specimens described herein

- represent the smallest Palaeozoic insect nymphs and earliest post-embryonic stages known so far,
- support the interpretation that wing development in early insects was extremely gradual (due to the already prominent developed wind pad in early nymphal stages in contrast to the more condensed ontogeny of early nymphs of modern species), and
- demonstrates that straightening of the wing pads during nymphal development is not always present in Palaeozoic nymphs.

6. References

Bell, W. J., Roth, L. M. & Nalepa, C. A. (2007): Cockroaches – Ecology, Behavior, and Natural History. 230 pp.; Baltimore (Johns Hopkins University Press).

Béthoux, O. & Herd, K. J. (2009): Discovery of an enigmatic and gigantic Pennsylvanian Archaeorthoptera. – Journal of Orthoptera Research, **18**: 23–28. DOI 10.1665/034.018.0112

Brauckmann, C. (1983): Ein Insektenrest (Odonata, Meganisoptera) aus dem Ober-Karbon des Piesberges bei Osnabrück. – Osnabrücker naturwissenschaftliche Mitteilungen, **10**: 7–14.

Brauckmann, C. (1991): Ein neuer Insekten-Rest (Megasecoptera) aus dem Ober-Karbon von Osnabrück. – Osnabrücker naturwissenschaftliche Mitteilungen, **17**: 25–32.

Brauckmann, C. (1995): Neue Insekten-Funde (Palaeodictyoptera: Breyeriida) aus dem Ober-Karbon von Osnabrück (Deutschland). – Osnabrücker naturwissenschaftliche Mitteilungen, **20/21**: 157–165.

Brauckmann, C. & Herd, K. J. (2000): Eine weitere neue Breyeriiden-Art (Insecta, Palaeodictyoptera) aus dem Ober-Karbon von Osnabrück (Deutschland). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2000** (6): 333–344.

Brauckmann, C. & Herd, K. J. (2002): Insektenfunde aus dem Westfalium D (Ober-Karbon) des Piesberges bei Osnabrück (Deutschland), Teil 1 Palaeoptera. – Osnabrücker naturwissenschaftliche Mitteilungen **28**: 27–69.

Brauckmann, C. & Herd, K. J. (2005): Insekten-Funde aus dem Westfalium D (Ober-Karbon) des Piesberges bei Osnabrück (Deutschland), Teil 2 Neoptera. – Osnabrücker naturwissenschaftliche Mitteilungen, **30/31**: 19–65.

Brauckmann, C. & Herd, K. J. (2007): A subcircular insect wing from the Late Carboniferous of Osnabrück, Germany. – Clausthaler Geowissenschaften, **6**: 79–85.

Brauckmann, C., Herd, K. J. & Leipner, A. (2009): Insekten-Funde aus dem Westfalium D (Ober-Karbon) des Piesberges bei Osnabrück. – Osnabrücker naturwissenschaftliche Mitteilungen, **35**: 5–30.

Brauckmann, C., Schöllmann, L. & Sippel, W. (2003): Die fossilen Insekten, Spinnentiere und Eurypteriden von Hagen-Vorhalle. – Geologie und Paläontologie in Westfalen, **59**: 1–89.

Dunlop, J.A., Brauckmann, C. & Steur, H. (2008): A Late Carboniferous fossil scorpion from the Piesberg, near Osnabrück, Germany. – Fossil Record, **11**: 25–32.

Garrouste, R., Clément, G., Nel, P., Engel, M. S., Grandcolas, P., D'Haese, C., Lagebro, L., Denayer, J., Gueriau, P., Lafaite, P., Olive, S., Prestianni, C. & Nel, A. (2012): A complete insect from the Late Devonian period. – Nature, **488**: 82–85.

Garrouste, R., Clément, G., Nel, P., Engel, M. S., Grandcolas, P., D'Haese, C., Lagebro, L., Denayer, J., Gueriau, P., Lafaite, P., Olive, S., Prestianni, C. & Nel, A. (2013): Garrouste et al. reply. – Nature, **494**: E4–E5.

Garwood, R., Ross, A., Sotty, D., Chabard, D., Charbonnier, S., Sutton, M., & Withers, P. J. (2012): Tomographic reconstruction of neopterous Carboniferous insect nymphs. – PloS one, **7(9)**: e45779.

Haug, C., Haug, J. T., Waloszek, D., Maas, A., Frattigiani, R. & Liebau, S. (2009): New methods to document fossils from lithographic limestones of southern Germany and Lebanon. – Palaeontologia Electronica, **12** (3); 6T; 12p; http://palaeo-electronica.org/2009_3/193/index.html

Haug, C., Mayer, G., Kutschera, V., Waloszek, D., Maas, A. & Haug, J. T. (2011): Imaging and documenting gammarideans. – International Journal of Zoology, art. 380829, DOI 10.1155/2011/380829

Haug, C., Van Roy, P., Leipner, A., Funch, P., Rudkin, D. M., Schöllmann, L. & Haug, J. T. (2012): A holomorph approach to xiphosuran evolution—a case study on the ontogeny of *Euproops*. – Development, Genes and Evolution, **222**: 253–268.

Haug, J. T., Haug, C. & Ehrlich, M. (2008): First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany). – Palaeodiversity, **1**: 103–109.

Haug, J. T. & Haug, C. (2013): An unusual fossil larva, the ontogeny of achelatan lobsters, and the evolution of metamorphosis. – Bulletin of Geosciences, **88**: 195–206.

Haug, J. T., Mayer, G., Haug, C. & Briggs, D. E. G. (2012): A Carboniferous non-onychophoran lobopodian reveals long-term survival of a Cambrian morphotype. – Current Biology, **22**: 1673–1675.

Haug, J. T., Leipner, A., Wappler, T. & Haug, C. (2013a): Palaeozoic insect nymphs: new finds from the Piesberg quarry (Upper Carboniferous, Germany). – Bulletin of Geosciences, **88**: 779–791.

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., Haug, C. & Garwood, R. (early view): Evolution of insect wings and development – new details from Palaeozoic nymphs. – Biological Reviews.

Hörnschemeyer, T., Haug, J. T., Béthoux, O., Beutel, R. G., Charbonnier, S., Hegna, T. A., Koch, M., Rust, J., Wedmann, S., Bradler, S. & Willmann, R. (2013): Is *Strudiella* a Devonian insect? – Nature, **494**: E3–E4.

Jarzembowski, E. A. (1987): The occurrence and diversity of Coal Measures insects – Journal of the Geological Society London, **144**: 507–511.

Kukalová-Peck, J. (1974): Pteralia of the Paleozoic insect orders Palaeodictyoptera, Megasecoptera, and Diaphanopterodea (Paleoptera). – Psyche, **81** (3–4): 416–430.

Kukalová-Peck, J. (1978): Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. – Journal of Morphology, **156**: 53–126.

Kukalová-Peck, J. (1991): Fossil history and the evolution of hexapod structures. – In: The Insects of Australia, pp. 141–179; Carlton (Melbourne University Press).

Kukalová-Peck, J. (1997): Mazon Creek insect fossils: the origin of insect wings and clues about the origin of insect metamorphosis. – Richardson's guide to the fossil fauna of Mazon Creek: 194–207.

KUTSCHERA, V., MAAS, A., WALOSZEK, D., HAUG, C. & HAUG, J. T. (2012): Re-study of larval stages of *Amphionides reynaudii* (Eucarida, Malacostraca) with modern imaging techniques. – Journal of Crustacean Biology, **36** (6): 916–930.

MIALL, L.C. & DENNY, A. (1886): The structure and life-history of the cockroach (*Periplaneta orientalis*). 224 pp. ; London (Lovelle Reeve & Co.). DOI 10.5962/bhl.title.48436

POPLIN, C. & HEYLER, D. (1994): Quand le Massif Central était sous l'Équateur: un écosysteme carbonifere a Montceau-les-Mines. – Mémoires de la Section des Sciences, **12**: 300 pp.; Paris (Comité des Travaux Historiques et Scientifiques).

ROLFE, W. D. I. (1967): *Rochdalia*, a Carboniferous insect nymph. – Palaeontology, **10** (2): 307–313.

ROSS, A. J. (2010): A review of the Carboniferous fossil insects from Scotland. – Scottish Journal of Geology, **46**: 157–168.

ROTH, L. M., & HAHN, W. (1964): Size of new-born larvae of cockroaches incubating eggs internally. – Journal of Insect Physiology, **10** (1): 65–72.

ROTH, L. M., & STAY, B. (1962): A comparative study of oocyte (?) development in false ovoviviparous cockroaches. – Psyche, **69** (4): 165–208.

ROTH, L. M., & WILLIS, E. R. (1955): Water content of cockroach eggs during embryogenesis in relation to oviposition behavior. – Journal of Experimental Zoology, **128** (3): 489–509.

SCHNEIDER, J. (1984): Die Blattodea (Insecta) des Paläozoikums. Teil II: Morphogenese der Flügelstrukturen und Phylogenie. – Freiberger Forschungshefte, (C), **391**: 5–34.

SCHULTKA, S. (2000): Zur Palökologie der Euproopiden im nordwestdeutschen Oberkarbon. – Fossil Record, **3** (1): 87–98.

SELLARDS, E. H. (1903): Some new structural characters of Paleozoic cockroaches. – American Journal of Science, Series 4, **15**: 307–315.

SELLARDS, E. H. (1904): A study of the structure of Paleozoic cockroaches, with descriptions of new forms from the Coal Measures. – American Journal of Science, Series 4, **18**: 113–134.

SHEAR, W. A. & KUKALOVÁ-PECK, J. (1990). The ecology of Paleozoic terrestrial arthropods: the fossil evidence. – Canadian Journal of Zoology, **68** (9): 1807–1834.

WOOTTON, R. J. (1972): Nymphs of Palaeodictyoptera (Insecta) from the Westphalian of England. – Palaeontology, **15**: 662–675.

ZESSIN, W. (2008): Überblick über die paläozoischen Libellen (Insecta, Odonatoptera). – Virgo, Mitteilungsblatt des Entomologischen Vereins Mecklenburg, **11** (1): 5–32.

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