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A *Marrella*-like arthropod from the Cambrian of Australia: A new link between "Orsten"-type and Burgess Shale assemblages

JOACHIM T. HAUG, CHRISTOPHER CASTELLANI, CAROLIN HAUG, DIETER WALOSZEK, and ANDREAS MAAS



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An isolated exopod in uncompressed three-dimensional "Orsten"-type preservation from the Cambrian of Australia represents a new species of Marrellomorpha, *Austromarrella klausmuelleri* gen. et sp. nov. The exopod is composed of at least 17 annuli. Each of the proximal annuli carries a pair of lamellae: one lamella on the lateral side and one on the median side. The distal annuli bear stout spines in the corresponding position instead of lamellae, most likely representing early ontogenetic equivalents of the lamellae. The new find extends the geographical range of the taxon Marrellomorpha. Additionally, it offers a partial view into marrellomorph ontogeny. The occurrence of a marrellomorph fragment in "Orsten"-type preservation provides new palaeo-ecological insights into the possible connections between the "Orsten" biotas and other fossil Lagerstätten. Finding such connections is necessary for understanding the complex ecosystems of early Palaeozoic times.

Key words: Arthropoda, Marrellomorpha, *Austromarrella*, palaeoecology, Lagerstätte, phosphatization, Cambrian, Australia.

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Introduction

Marrellomorpha is a group of arthropods from the early to middle Palaeozoic that has gained quite a lot of attention in recent years. This attention was received due to three major causes: (i) re-investigations of long-known representatives of the group: *Marrella splendens* Walcott, 1912 (García-Bellido and Collins 2004, 2006), *Vachonisia rogeri* (Lehmann, 1955) (Kühl et al. 2008) and *Mimetaster hexagonalis* Gürich, 1931 (Kühl and Rust 2010); (ii) re-investigations of the seemingly forgotten species *Furca bohemica* Fritsch, 1908 (Chlupáč 1999; Van Roy 2006a, b; Rak 2009; Rak et al. 2013); and (iii) the discovery of new marrellomorphs: *Marrella* sp. from the Cambrian Chinese Kaili Konservat-Lagerstätte (Zhao et al. 2003), *Xylokoris chledophilia* Siveter, Fortey, Sutton, Briggs, and Siveter, 2007 preserved in three dimensions from the Silurian of the English Herefordshire Konservat-Lagerstätte (Siveter et al. 2007) and the beautifully-coloured specimens of *Furca* sp. from the Fezouata Konservat-Lagerstätte from the Ordovician of Morocco (Van Roy 2006a, b; Van Roy et al. 2010) which most likely represent two different species (Van Roy, personal communication 2011).

The low number of species of Marrellomorpha is not a reflection of abundance. Probably eight species have been determined in total. *Marrella splendens*, especially, is represented by thousands of individuals (e.g., García-Bellido and Collins 2006). Yet, the known occurrences ranging from Series 2 of the Cambrian up to the Lower Devonian suggest a much higher Palaeozoic diversity than that discovered thus far (Kühl et al. 2008; Kühl and Rust 2010). One can assume that Marrellomorpha played an important role in Palaeozoic ecosystems.

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A single, fragmentary specimen in "Orsten"-type preservation from the middle Cambrian of Australia is herein interpreted as representing a fragment of a marrellomorph arthropod (sensu Kühl et al. 2008; excluding obvious non-arthropods like *Marria walcotti* Ruedemann, 1931, cf. Simonetta 1961). Implications for the evolution of Marrellomorpha and also consequences for the biodiversity of the group and the understanding of early Palaeozoic ecosystems are briefly discussed.

Todays' ecosystems are characterized by a large set of interacting parameters including biotic and abiotic factors. Biotic factors include ontogenetic and species diversity, feeding strategy, and interactions of the trophic web. Abiotic factors include substrate consistency, temperature, oxygen availability, light intensity, water or substrate chemistry, environmental structure. Both biotic and abiotic factors influence the evolution of an ecosystem. These parameters can be investigated to describe and interpret a modern ecosystem. Ancient ecosystems are characterized by the same parameters, but in many cases, more difficult to describe or reconstruct. While often generally attributed to incomplete preservation, the causes are more complex:

- There is a bias toward the preservation of mineralized organisms (or parts thereof). Hard parts, become more easily fossilized, while non-biomineralized tissues have almost no chance of fossilization. Consequently, we have almost no fossil record of organisms that never develop any hard parts, such as flat worms, ribbon worms or gastrotrichs. Therefore, there is no complete access to the original taxonomic composition of a fossil biota.
- The structure/type of the sediment, the environment, and the diagenetic processes have a significant effect on the quality of preservation. Fine preservation not only preserves minute details but also minute organisms (including early ontogenetic stages). Coarse preservation leads to the lack of information on smaller organisms, while larger organisms or large fragments are well documented. The quality of preservation may be spatially variable as well. Consequently, Lagerstätten with coarse and fine preservation may display almost no significant taxonomic overlap.
- There is a bias in the ecological composition of fossil Lagerstätten. Organisms living in or on the substrate (benthos) have, in general, a much greater fossilization potential than those living in the water column above the substrate (pelagic and nektic).
- Many other biotic and abiotic parameters of ancient ecosystems may have affected the selectivity of preservation, but they are difficult to constrain in deep time.

Consequently, our knowledge of ancient ecosystems is, and will stay, much less complete than that of modern ecosystems. However, a few sedimentary deposits with exceptional fossil preservation can offer deep insights into the organization of these ancient ecosystems. The famous Cambrian "Burgess Shale-type" preservation (e.g., Burgess Shale of British Columbia, Canada; Chengjiang fossil lagerstätten, southern China) has often been used as a basis for reconstructing early Palaeozoic ecosystems (e.g., Conway Morris 1986; Vannier and Chen 2005; Vannier et al. 2007; Dunne et al. 2008). Yet, since the type of preservation in these Konservat-Lagerstätten tends to favour larger animals (some millimetres to several centimetres), they depict a view of only the macrobenthic community. As a consequence, our understanding of the ecosystems represented in these Konservat-Lagerstätten remains incomplete.

Marine biotic communities are often classified according to size, e.g., macro-, meio-, and microbenthos. The last two categories of organisms, likely due to their small size and seemingly low potential of preservation, are often neglected in palaeo-ecological reconstructions. Yet, modern aquatic ecosystems, as well as terrestrial ones, heavily depend on these tiny faunal organisms, such as nematodes, platyhelminths, crustaceans, mites, springtails, at least to name some major groups (Gerlach 1978; Warwick 1989; Coull 1990, 1999).

A window into such ecological niches of early Palaeozoic ecosystems is offered by the "Orsten"-type preservation, representing fossils of organisms equivalent to inhabitants of modern flocculent layer biotas, yielding mainly organisms of the meiobenthos. Known now from all over the world, this exceptional type of preservation—uncompressed, three dimensional, with soft parts such as membranous areas, eyes, setae and setules down to 0.2 μm—provides access to a meio-ecosystem (Maas et al. 2006). This includes various ecological niches, such as true filter feeders (a term often misused, but here represented in its strict sense by the branchiopod *Rehbachiella kinnekullensis* Müller, 1983; Walossek 1993), micro-predators (Haug et al. 2009a), possible benthic primary producers such as the cyanobacteria *Girvanella* sp. (currently under study) and parasites (Walossek and Müller 1994; Walossek et al. 1994; Waloszek et al. 2006; Castellani et al. 2011).

Thus, both the Burgess Shale-type and the "Orsten"-type fossil assemblages offer views on specific parts of Palaeozoic ecosystems. However, reconstructing the ecological system of that time in a wider framework demands an understanding of trophic interactions between both macro- and micro-fauna. Therefore, the rare cases of taxonomic overlap between the types of Lagerstätten are of special interest. One such example is that of agnostine euarthropods (see below; Müller and Walossek 1987; Haug et al. 2012). The marrellomorph exhibiting "Orsten"-type preservation from the middle Cambrian of Australia discussed here represents another such overlap among the arthropods.

Institutional abbreviations.—CPC, Commonwealth Palaeontological Collection of Geoscience Australia, Canberra, Australia; E_G, National Museums of Scotland, Edinburgh, United Kingdom; ROM, Royal Ontario Museum, Toronto, Canada; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UB, Steinmann Institute, University of Bonn, Germany; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA.

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Material and methods

The single investigated specimen, CPC 30719, was recovered from an "Orsten"-type nodule found at Mount Murray, Western Queensland, Australia (sample 7324). Details of the locality and the processing of the nodules to yield the fossil specimens are given by Walossek et al. (1993; see also Maas et al. 2007a, 2009; Haug et al. 2009b for material from this and adjacent localities). The specimen was studied under a Zeiss DSM 962 Scanning Electron Microscope at the Central Unit for Electron Microscopy, University of Ulm. Some images were recorded as composite images (Haug et al. 2008) using CombineZM, CombineZP, Microsoft Image Composite Editor and Adobe Photoshop CS3 and 4.

Systematic palaeontology

Arthropoda sensu stricto (sensu Maas, Waloszek, Chen, Braun, Wang, and Huang, 2004)

Marrellomorpha Beurlen, 1934 (sensu Kühl, Bergström, and Rust, 2008)

Genus *Austromarrella* nov.

Etymology: *Austro*, referring to its occurrence on the southern hemisphere; *marrella*, referring to the similarities to the eponymous taxon.

Type species: *Austromarrella klausmuelleri* sp. nov.; see below.

Diagnosis.—As for the monotypic species.

Austromarrella klausmuelleri sp. nov.

1993 "Multi-annulated limb fragment, possibly representing an exopod of a 'trilobitomorph' arthropod"; Walossek et al.1993: fig. 5A, B.

1993 "remarkable multi-annulated exopod with lamellate outgrowths on opposing sides"; Walossek et al. 1993: 13.

2009 "Multi-annulated limb fragment, possibly representing an exopod of a non-crustacean"; Maas et al. 2009: fig. 2F.

Etymology: In honour of the late Klaus J. Müller (1923–2010), Bonn, the discoverer of the "Orsten" assemblage in Sweden.

Holotype: CPC 30719, exopod fragment; sample 7324.

Type locality: Mount Murray, Western Queensland, Australia.

Type horizon: Excavation in top of Monastery Creek Phosphorite Formation, bedded phosphorite of Series 3 of the Cambrian (Late Templetonian to Early Floran age in the Australian system).

Material.—Holotype only.

Diagnosis.—Arthropod with multi-annulated exopod on post-antennular limbs. Exopod with at least 17 annuli, each of the proximal 14 annuli equipped with a pair of lamellae, one on the lateral, one on the median side. In a most likely immature ontogenetic stage, the most distal two annuli are equipped with a pair of bluntly rounded stout spines.

Description.—The description refers to the specific developmental stage represented by the only known specimen, which is most likely immature). Only known from a fragment of a post-antennular appendage, namely the exopod of about 970 μm in total length (Fig. 1A). The exopod is composed of at least 17 annuli, 16 of which are preserved; as the most distal preserved annulus is still a normal ring, the presence of at least one further distal, terminal element is assumed (Fig. 1B). The annuli are more or less circular to slightly compressed in anterior-posterior axis (Fig. 1A, B). The proximal annuli measure about 150 μm in diameter and about 60–70 μm in proximo-distal axis. Size decreases progressively distally, penultimate preserved annulus measures about 80 μm in diameter and 45 μm in proximo-distal axis (Fig. 1B).

Each of the proximal fourteen annuli is equipped with a pair of lamellae, one inserting medio-distally and one latero-distally. The lamellae are at least 560 μm long (Fig. 1B) and approximately lanceolate in shape (Fig. 1C) in lateral or median profile, i.e., having the largest width in anterior-posterior axis somewhere in the middle. At the base, a lamella measures 45 μm in width (Fig. 1C) and widens up to 100 μm, after two-fifth of the preserved length, becoming less wide toward the distal end again. The distal tip is not preserved. The thickness in medio-lateral axis of a lamella is about 18 μm throughout its length (Fig. 1B).

The distal two annuli do not bear lamellae but stout, chubby spines (Fig. 1B, D–F) in the corresponding positions (medio-distally and latero-distally). The base of such a spine measures 25 μm (anterior-posterior axis; Fig. 1D, E), its thickness (medio-lateral axis) is about 14 μm. In proximo-distal axis the spine measures about 32 μm (Fig. 1D). The tip is bluntly rounded (Fig. 1E, F).

Discussion

Affinities.—The single specimen of *Austromarrella klausmuelleri* clearly represents a fragment of an arthropod. Multi-annulated appendages are found in various groups of arthropods. Yet, the armature of certain structures reduces the number of possible interpretations on the systematic affinities of the specimen described herein. For example, the limb rod of fuxianhuiid arthropods may also be described as multi-annulated. However, it lacks any kind of armature, i.e., setae or spines. Also many antennae, in most cases antennulae (i.e., the deuterocerebral appendage; cf. Waloszek et al. 2005), of arthropods can be described as being multi-annulated, yet usually lack well-developed armature, i.e., setation on the median side of the articles. Exceptions are the great-appendage arthropods, in which the antennulae are developed as raptorial limbs with a strong median setation, but these differ from the specimen described here in being non-lamellate. Among modern arthropods post-antennular feeler structures and tarsi can be described as multi-annulated. Yet, these also lack well-developed armature.

Strong armature is developed on exopods of various euarthropods. Yet, exopods in the ground pattern of Arthropoda sensu stricto (sensu Maas et al. 2004) and also in the ground pattern of Euarthropoda (sensu Walossek 1999) are paddle-shaped and non-annulated. In the ground pattern of Arthropoda sensu stricto, Euarthropoda, Chelicerata, and even Eucheliceratа the post-antennular limbs are all similar, hence

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Fig. 1. SEM images of the holotype and single specimen CPC 30719 of marrellomorph *Austromarrella klausmuelleri* gen. et sp. nov., Mount Murray, Western Queensland, Australia; Series 3 of the Cambrian. **A**. Median or lateral view, exposing the more or less lanceolate lamellae. **B**. Anterior or posterior view. The 16 ringlets are well separated from each other. Letters indicate the direction of view in images D–F. **C**. Median or lateral view, opposing to side displayed in A. Here the insertion of the most proximal preserved ringlet is well apparent. **D**–**F**. Details of the stout spines on the most distal preserved annuli viewed as indicated in image B. **D**. View from latero/medio-proximal on the distal tip. **E**. View from lateral/median, same spine as in D. **F**. View from medio/latero-proximal. Spine on the other side of the same ringlet as in D and E.

the exopods of the various limbs also are not distinguishable. Crustacea sensu lato (sensu Stein et al. 2008), however, is characterized by two specialized head appendages, i.e., the first and second post-antennular appendages are quite different from the succeeding appendages (see below).

The exact condition of the exopods in the ground pattern of Euarthropoda may have been bipartite. This is exemplified by all post-antennular appendages of the chelicerate *Leanchoilia illecebrosa* (Hou, 1987) (cf. Liu et al. 2007), and also by the third and fourth post-antennular appendages, belonging to the head, and all trunk appendages of the crustaceans *Oelandocaris oelandica* Müller, 1983 (Stein et al. 2008) and *Henningsmoenicaris scutula* (Walossek and Müller, 1990) (Haug et al. 2010a). A tripartite exopod is developed on the last head appendage (= third post-antennular appendage) of *Agnostus pisiformis* (Wahlenberg, 1818) (Müller and Walossek 1987). Exopods with five elements, the distal one developed as a paddle, are known from the second head appendage of *Ercaia minuscula* Chen, Vannier, and Huang, 2001 (Chen et al. 2001), as well as from the post-antennular limbs of the trilobite *Ceraurus pleurexanthemus* Green, 1832 (cf. Størmer 1938). Multi-annulated exopods, in the strict sense of the word, are developed in three groups of Arthropoda sensu stricto: Marrellomorpha, Agnostina, and Crustacea sensu lato.

In Marrellomorpha all trunk limbs have, as far as known, multi-annulated exopods with up to 50 annuli. Like in the

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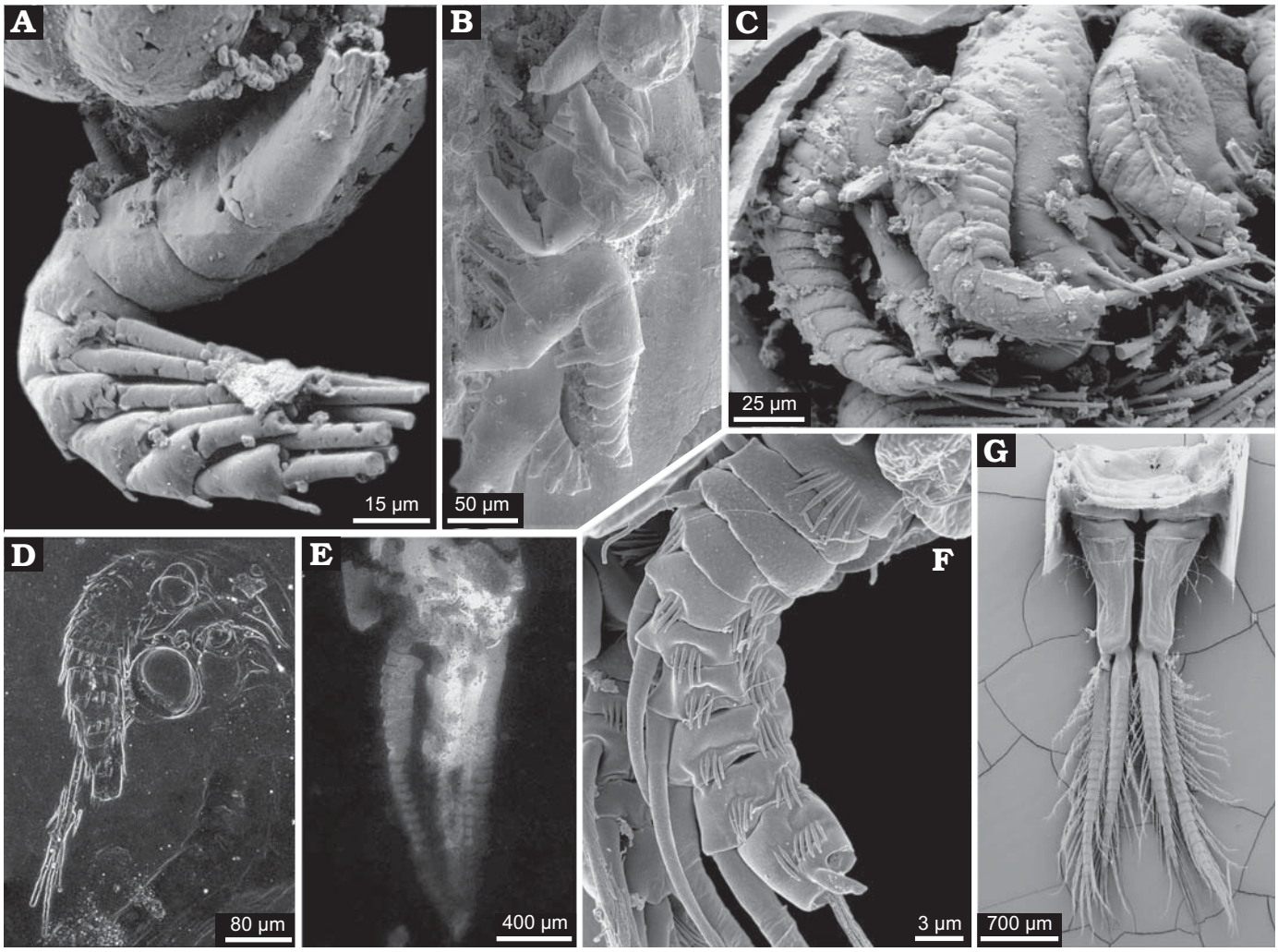


Fig. 2. Examples of multi-annulated exopods of fossil and extant representatives of the taxa Agnostina and Crustacea sensu lato. **A**. SEM image of the exopod of the second head appendage of *Agnostus pisiformis* (Wahlenberg, 1818) composed of nine articles. Each of the six distal articles bears a pair of long, outwardly directed setae, a short spinule close to the base of the setae and a short seta opposite of the long setae (cf. Müller and Walossek 1987: pl. 18.1). Series 3 of the Cambrian (*Agnostus pisiformis* Zone), UB 832. **B**. SEM image of appendages two and three of a stage two larva of the fossil micro-predator *Goticaris longispinosa* Walossek and Müller, 1990. Series 3 of the Cambrian (*Agnostus pisiformis* Zone), UB 98. Detail of pl. 2.5 of Haug et al. (2009b). **C**. SEM image of the appendages two to four of the phosphatocopine *Vestrogothia spinata* Müller, 1964, Furongian, Cambrian, UB 622. **D**. Light microscopic image (processed according to Haug et al. 2009a) of a putative thecostracan larva (E_G2010_16_2_1), from the Devonian Windyfield Chert (cf. Fayers and Trewin 2004). **E**. Composite fluorescence image (cf. Haug et al. 2008) of an undetermined natant decapod from the Solnhofen Lithographic Limestones, Upper Jurassic, Southern Germany (SMNS 70149, ex coll. Gebert, Iphofen). **F**. SEM image of the second antenna of the Recent mystacocarid *Derocheilocaris remanei* Delamare-Debouteville and Chappuis, 1951 (cf. Olesen 2001; Haug et al. 2011). Specimen from the collection of the Zoological Museum, Copenhagen. **G**. SEM image of a pleomeric segment with a pair of pleopods of the Recent amphipod *Gammarus roeselii* Gervais, 1835. Image courtesy Gerd Mayer, Ulm.

ground patterns of Arthropoda sensu stricto and Euarthropoda, the trunk appendages are serially similar in Marrellomorpha, but the two post-antennular head appendages are specialized (Kühl et al. 2008). In the ground patterns of both Agnostina and Crustacea sensu lato, head appendages two and three possess multi-annulated exopods (Haug et al. 2010a, 2013). The specific morphology of head appendages two and three in Agnostina and Crustacea sensu lato is interpreted as an autapomorphic character of a taxon Agnostina + Crustacea sensu lato (Stein et al. 2008; Haug et al. 2010a, b).

The fact that Marrellomorpha and the taxon (Agnostina + Crustacea sensu lato) possess multi-annulated exopods was one of the arguments for placing Marrellomorpha closer to the crustaceans (e.g., Wills et al. 1998; Siveter et al. 2007). Yet, the taxon (Agnostina + Crustacea sensu lato) is deeply nested within Euarthropoda (cf. Haug et al. 2010a, b). The stem species of Marrellomorpha (based on the proposed phylogeny of Kühl and Rust 2010) lacks crucial characters of Euarthropoda, such as a head comprising four appendage-bearing segments and a strong, rigid basipod on the post-antennular limbs. Instead, the head of the Marrellomorpha appears to comprise three segments in the ground pattern, an ocular segment plus two appendage-bearing segments; the postantennular limbs lack a rigid basipod as it is known

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from Euarthropoda. Marrellomorpha are, therefore, interpreted as representatives of Arthropoda sensu stricto, which had branched off before the evolutionary level of Euarthropoda. In consequence, the multi-annulated exopods of Marrellomorpha and (Agnostina + Crustacea sensu lato) are, most parsimoniously, interpreted as having evolved independently, as the ground pattern of Euarthropoda is characterized by paddle-shaped exopods (see above).

The multi-annulated exopods of the second and third appendages of *Agnostus pisiformis* (the only representative of Agnostina of which this detail is known) bear setation on their lateral side (Fig. 2A), while in the ground pattern of Crustacea sensu lato the median side of the multi-annulated exopods is setose (Fig. 2B–D, F). In certain crustacean ingroups multi-annulated exopods may also occur on more posterior limbs, e.g., in several derivatives of the evolutionary lineage towards Eucrustacea, such as Cambropachycopidae (Haug et al. 2009b), *Martinssonia elongata* Müller and Walossek, 1986 and *Musacaris gerdgeyeri* Haug, Waloszek, Haug, and Maas, 2010b (Haug et al. 2010b) or also in certain representatives of Phosphatocopina, such as *Vestrogothia spinata* Müller, 1964 (Maas et al. 2003) and even within Eumalacostraca (Fig. 2E). Representatives of the latter taxon bear lateral and median setation on the exopods of their trunk limbs (Fig. 2G), but this can be interpreted as autapomorphically evolved.

In Marrellomorpha, however, the exopods of the postantennular limbs do not bear setae in the strict sense, but the setae are modified into lamellae (Fig. 3A, B), a morphology also present in the new species *Austromarrella klausmuelleri* (Fig. 1C). No other arthropod taxon is known to possess this combination of characters, i.e., multi-annulated exopods with lamellae. While multi-annulated exopods are known from other groups than Marrellomorpha (see above) and the possession of lamellae on the exopods is also known from other groups of arthropods (e.g., *Naraoia longicaudata* Zhang and Hou, 1985, cf. Hou and Bergström 1997), the combination of multi-annulated exopods with lamellae is restricted to Marrellomorpha. In consequence, the specimen from the "Orsten" type of preservation described herein is most likely an exopod fragment of marrellomorph affiliation.

Austromarrella klausmuelleri differs in one significant aspect from the other representatives of Marrellomorpha: in marrellomorphs, for which the exopod morphology is known, lamellae are present only on the median side of the exopods (Fig. 3C). On the lateral side of the exopod *Marrella splendens* bears small spines (Fig. 3D). Additionally, for *Xylokoris chledophilia* also structures on the lateral side of the exopods can be recognized (Siveter et al. 2007: fig. 2I), yet these being significantly shorter than the lamellae on the median side. The exact nature and organization of these structures cannot be judged as the diameter of these structures is close to the resolution limit of the Herefordshire material and the method of extracting the information. In the new species, lamellae are located on both lateral and median side, no differentiation between the two sides is recognisable. Due to this unique morphology and since it is the first representative of a marrellomorph in Australia, we propose the fragment to represent a new species of Marrellomorpha.

The distal annuli of *Austromarrella klausmuelleri* hint to morphogenetic changes of the lamellae throughout ontogeny. The distal annuli do not possess lamellae. Instead they bear thick spine-like structures that appear to be not yet fully developed. This intepretation is based on their chubby shape. Similar shapes can, for example, be found in not yet fully developed spines in larval stages of extant crustaceans (e.g., Haug et al. 2011: figs. 7A, 8B, E). Furthermore, in such larval stages further distal structures are usually less developed compared to more proximal structures (cf. Haug et al. 2011: fig. 7A). This is seen as an indication that the lamellae developed from such spine-like structures and hints to the supposed immature status of the single specimen of *A. klausmuelleri*.

The exopod of *Austromarrella klausmuelleri* with its 16 preserved annuli is almost one millimetre long. If we assume that the exopod originally consisted of the same number of annuli as those of other marrellomorphs, between more than 25 and about 50, the entire exopod might have measured slightly less than three millimetres. Estimated from specimens of *Marrella splendens* this would indicate a body size of the entire animal of between four to nine millimetres.

Austromarrella klausmuelleri contributes to the knowledge about Marrellomorpha in expanding its geographical range (Fig. 4). Furthermore, the specimen was found in an "Orsten"-type of preservation. Therefore, it was originally part of a fauna, from which we know almost exclusively meiofaunal species or meiofaunal ontogenetic stages, but *A. klausmuelleri* was presumably too large to have been part of the meiofauna.

Overlap of Burgess Shale-type and "Orsten"-type lagerstätten.—*Austromarrella klausmuelleri* represents a new faunal overlap between the early Palaeozoic Burgess Shale and "Orsten" types of preservation. Other faunal overlaps are extremely rare. The "Orsten" assemblages are dominated by various crustaceans, mainly Phosphatocopina (Maas et al. 2003). In the Burgess Shale-like fossil assemblages no true crustaceans could be found until today (e.g., Dahl 1984 and references therein). It could be possible that phosphatocopines are also present in the Burgess Shale-type faunas. Many tiny bivalved specimens usually assigned to Bradoriida that make up the major part of the finds in the Burgess Shale (García-Bellido and Collins 2006) could indeed represent such examples, but this assumption still needs to be verified.

Chelicerata (sensu lato, sensu Chen et al. 2004) are represented in the Burgess Shale by predatory derivatives of the evolutionary lineage towards Chelicerata sensu stricto, the great-appendage arthropods (recent discussion in Haug et al. 2012). In the "Orsten" only a single representative of Chelicerata sensu stricto is known, *Cambropycnogon klausmuelleri* Waloszek and Dunlop, 2002. It also occupies a significantly different ecological niche than the chelicerates from the Bur-

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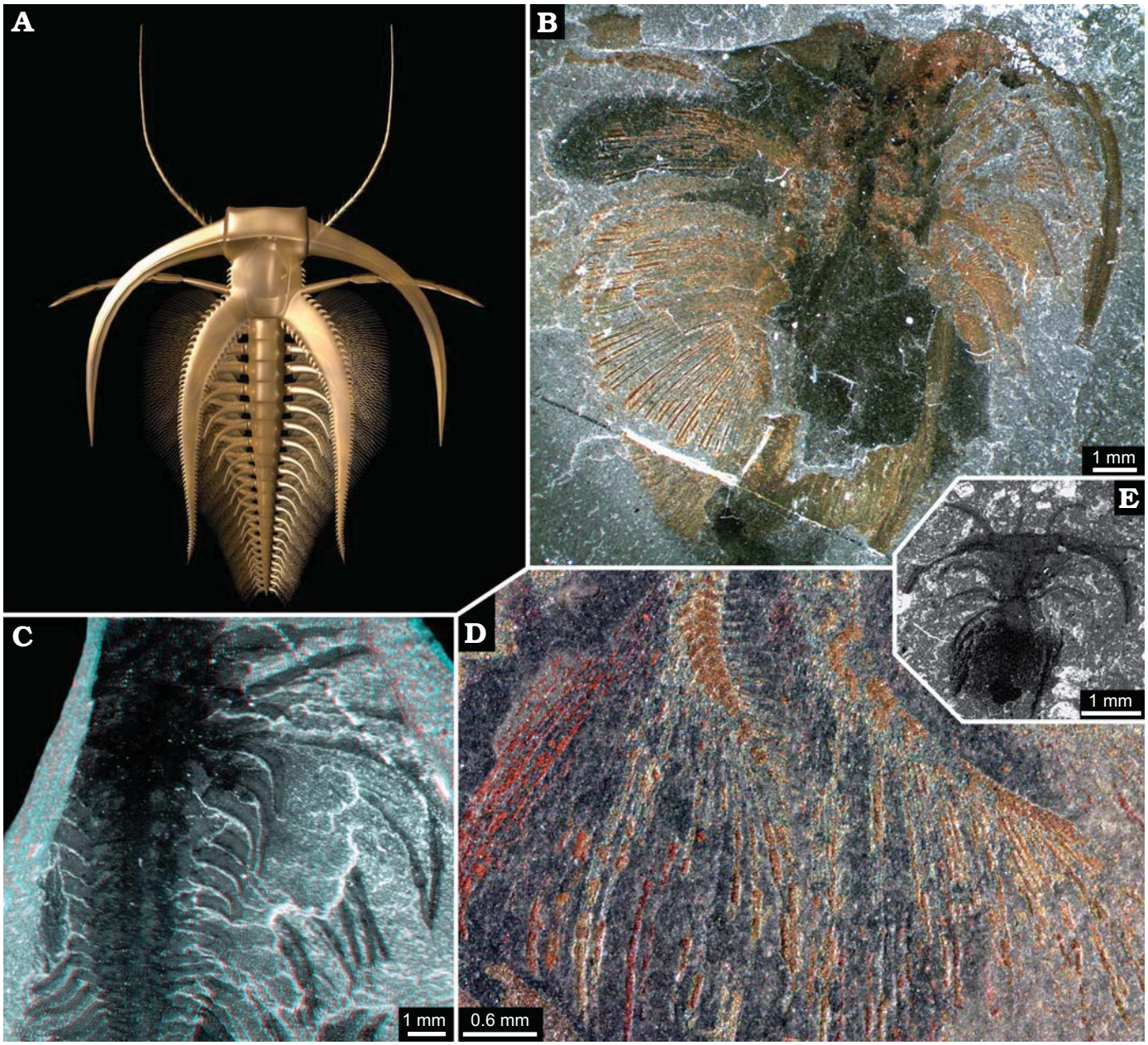


Fig. 3. Marrellomorph *Marrella splendens* Walcott, 1912, for comparison with *Austromarrella klausmuelleri* gen. et sp. nov., Mount Murray, Western Queensland, Australia; Series 3 of the Cambrian. **A**. Dorsal view on a rendered 3D model, based on own observations. **B**–**E**. Micrographs under polarized light. **B**. Beautifully preserved specimen USNM 83486f with the exopods in a "rusty" preservation (cf. García-Bellido and Collins 2006). **C**. Stereo image of specimen USNM 139665. Exopods of preceding limbs are super-imposing each other, separated by a thin layer of sediment. **D**. Detail of specimen ROM 56766A in "rusty" preservation. Here the spines on the lateral side of the exopod ringlets are well preserved. **E**. One of the smallest specimens of *M. splendens* USNM 219817e that possesses preserved appendage remains. The single fragmentary specimen of *A. klausmuelleri* could, based on its size, belong to an entire specimen of a comparable size.

gess Shale, as the only known (larval) semaphoront was presumably parasitic (Waloszek and Dunlop 2002).

Other parasites from the "Orsten" are species of Pentastomida (Castellani et al. 2011 and references therein). This taxon is well represented by ten described species, and possibly significantly more undescribed species in the "Orsten"-type faunas (Andres 1989; Castellani et al. 2011). Pentastomids are unknown from Burgess Shale-like fossil assemblages.

Derivatives of the evolutionary lineage towards Arthropoda sensu stricto are the tardigrades, which are not known from Burgess Shale-like, but only from "Orsten"-type deposits (Müller et al. 1995), and the lobopodians. The latter ones are well known from both Burgess Shale-like (Briggs et al. 1994; Liu et al. 2008) and "Orsten"-type fossil assemblages (Maas et al. 2007b), representing an important faunal overlap. However, only one single species, *Orstenotubulus evamuellerae* Maas, Mayer, Waloszek, and Kristensen, 2007b,

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Fig. 4. Localities, in which Marrellomorpha (sensu Kühl et al. 2008) have been found. 1, Monastery Creek Phosphorite Formation, Late Templetonian–Early Floran, Australia: *Austromarrella klausmuelleri* gen. et sp. nov. 2, Kaili, early middle Cambrian, China: *Marrella* sp. (Zhao et al. 2003). 3, Burgess Shale, middle Cambrian, British Columbia, Canada: *Marrella splendens* Walcott, 1912 (Whittington 1971; García-Bellido and Collins 2006). 4, Fezouata biota, Ordovician, Morocco: *Furca* spp. (Van Roy 2006a, b; Van Roy et al. 2010). 5, Letná Formation, Ordovican, Czech Republic: *Furca bohemica* Fritsch, 1908 (Chlupáč 1999; Van Roy 2006a, b; Rak 2009; Rak et al. 2013). 6, Herefordshire, Silurian, England: *Xylokoris chledophilia* Siveter, Fortey, Sutton, Briggs and Siveter, 2007 (Siveter et al. 2007). 7, Hunsrück slate, Lower Devonian, Germany: *Vachonisia rogeri* Lehmann, 1955 (Kühl et al. 2008); *Mimetaster hexagonalis* Gürich, 1931 (Kühl and Rust 2010). Table indicates occurrences.

is known from the "Orsten", and this is significantly smaller than the many species described from Burgess Shale-type lagerstätten.

The major faunal overlap between the Burgess Shale-like and the "Orsten"-type fossil assemblages are species of Agnostina. Yet, understanding and comparison of species of this taxon between the two types of fossil deposits is partly hindered as only the details of *Agnostus pisiformis* from the Swedish "Orsten" faunal assemblage are well known (Müller and Walossek 1987). Comparative studies of the hard parts of other agnostines indicated that not only *A. pisiformis*, but also other agnostines were living in a "box" formed by their head shield and pygidial shield, and were swimming and sweeping-in food particles with their large antennulae (Müller and Walossek 1987; Bruton and Nakrem 2005). Agnostine specimens from the Burgess Shale apparently also have the potential to preserve soft part details (Haug et al. 2012) and could, thus, be used for a more detailed comparison in the future.

The discovery of the exopod fragment of *Austromarrella klausmuelleri* marks an important faunal overlap between the Burgess Shale-like and the "Orsten"-type lagerstätten. Based on its size, the fragment of *A. klausmuelleri* should stem from an entire animal of a size comparable to middle-sized specimens of *Marrella splendens* (Fig. 3E). This is quite remarkable when considering the argumentation outlined in the following.

One could expect that Burgess Shale-like Konservat-Lagerstätten with their concentration of older developmental stages and adults would provide some individuals being the adults of larval forms known from the "Orsten". In other words, we could expect an ontogenetically triggered effect, i.e., a species can be a component of the "Orsten" fossil assemblage during its earlier developmental stages, while it becomes a component of the Burgess-Shale type lagerstätten after reaching a certain threshold size. However, this is exactly what we do not observe. Such an ontogenetically triggered overlap does not exist, neither in the lobopodians, nor in the agnostines. The new "Orsten" marrellomorph in fact demonstrates an overlap, but stems from an individual of more or less the size we already know from the Burgess Shale in numerous specimens. The presence of only a single specimen of the new marrellomorph species among hundreds of specimens from other taxa from the "Orsten" of Australia rather indicates that *Austromarrella klausmuelleri* was a component of the original "Orsten" biota in this area and at that time, but its ecological significance was much less than that of marrellomorphs in the original Burgess Shale biota. The same sample (7324), which yielded the here described exopod fragment, contained another fragmentary exopod (of a crustacean Walossek et al. 1993: fig. 5D), 11 specimens of the nemathelminth *Orstenoloricus shergoldii* Maas, Waloszek, Haug, and Müller, 2009a and fragments of nemathelminth palaeoscolecids. Sample 7323 (same locality) yielded eucrustacean type-A larva (Walossek et al. 1993: fig. 1A).

An important aspect in this respect is that the "Orsten" of Australia and the "Orsten" of Sweden differ in their taxonomic composition. Many crustacean species from the "Orsten" are

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mainly from the Swedish Lagerstätten, while the entire nemathelminths are from Australia (Maas et al. 2006, 2007a). A taxonomic overlap is restricted to a few specimens of Phosphatocopina from Australia vs. thousands of specimens from Sweden (Maas et al. 2006). The "Orsten" of China seems to link the two Lagerstätten, since it comprises both nemathelminths and crustaceans (Dong et al. 2004, 2005; Maas et al. 2006; Zhang, X. et al. 2007, 2010; Zhang, H. et al. 2011).

The new find underlines that even for understanding the autecology of a single species it is necessary to develop a more integrated view that is not limited to a certain fossil preservation type. That holds even more for a dem- or synecological approach. Macrofaunas of the early Palaeozoic of Australia are represented for example by fossils from the Emu Bay Shale (Jago et al. 2002) from the Botomian of Series 2 of the Cambrian. This Lagerstätte has not yet yielded a species of Marrellomorpha, but since investigation has just started it might do so in the future.

The new species also enhances the biodiversity of Marrellomorpha and, with this, supports the assumption that the fossil record of Marrellomorpha does not represent their original diversity (Kühl et al. 2008; Kühl and Rust 2010). Additionally, the biogeographical range is extended to include now also Australia (Fig. 4). Future comparative studies will provide a more integrated view on Marrellomorpha, since even more yet undescribed material is available (Van Roy et al. 2010).

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