Rapid communication

A morphological and taxonomic appraisal of the oldest anomalocaridid from the Lower Cambrian of Poland

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Abstract

Material previously referred to as *Cassubia infercambriensis* was re-examined and found to represent a composite fossil of a *Peytoia*-like anomalocaridid frontal appendage and an arthropod of uncertain affinities comparable to some bivalved arthropod taxa. The frontal appendage is referred to the genus *Peytoia* based on the presence of elongated ventral spines bearing a single row of auxiliary spines. As well as representing the oldest example of an anomalocaridid in the fossil record (Series 2, Stage 3), *Peytoia infercambriensis* is also the only record of this group from the East European Craton, therefore extending both the temporal and geographic range of the anomalocaridid family Hurdiidae.

Keywords: *Peytoia nathorsti*, *Cassubia*, Zawiszyn Formation, Hurdiidae, Cambrian Explosion, Arthropoda.

1. Introduction

The soft-bodied arthropods of the Lower Cambrian Zawiszyn Formation of Poland represent the oldest record of Burgess Shale-type metazoans in the fossil record (Conway Morris 1989, Moczydłowska 2002; Gaines 2014). Lendzion (1975) described three soft-bodied arthropods from this fauna, namely ‘*Pomerania*’ *infercambriensis*, ‘*Livia*’ *convexa*, and ‘*L.*’ *plana*. Both generic names were preoccupied however, and replaced with *Cassubia* Lendzion, 1977 and *Liwia* Dzik & Lendzion, 1988, respectively. Although the morphology and affinities of *Liwia* are fairly well understood (Dzik & Lendzion 1988, Paterson *et al.* 2010), opinion regarding *Cassubia* has been more equivocal.

In its original description, *Cassubia*’was considered an aquatic chelicerate comparable to the Burgess Shale arthropod *Leanchoilia* (Lendzion 1975). The holotype was thought to consist of an 11 segmented thorax and an enlarged chelicera. The supposed thorax was subsequently reinterpreted as the proximal end of an anomalocaridid-type great-appendage and the chela as the distal region of the same appendage, showing ventral spines (Dzik & Lendzion 1988). The appendage was compared to *Anomalocaris nathorsti* (= *Peytoia nathorsti sensu* Daley & Bergström 2012) (Dzik & Lendzion 1988, Hou *et al*. 1995, Delle Cave *et al.*1998), with some workers suggesting *Cassubia* should be a junior synonym of *Anomalocaris* (e.g. Conway Morris & Robison 1988, Conway Morris 1989, Delle Cave & Simonetta 1991). At the time, *Peytoia* was considered a junior synonym of *Anomalocaris* (see Whittington & Briggs 1985, Collins 1996). Although anomalocaridid affinities for *Cassubia* were almost universally accepted, not everyone has accepted the morphological interpretation of Dzik & Lendzion (1988), with some favouring Lendzion's (1975) original interpretation (e.g. Bousfield 1995, Delle Cave *et al.* 1998). Most recently, the frontal appendages of *Cassubia* have been interpreted as an incipient condition between the elongate frontal appendages of anomalocaridids and the 'short-great-appendages' of megacheirans and chelicerae (Bousfield 1995, Haug *et al*. 2012), although given recent neurological data this hypothesis seems unlikely (Tanaka *et al*. 2013, Cong *et al.* 2014). To resolve this morphological and taxonomical confusion, a restudy *Cassubia infercambriensis* was undertaken.

2. Material and methods

The only known specimen of *Cassubia infercambriensis* (PIG 1432 II 22) was originally collected from a borehole drilled near Kościerzyna in northern Poland, approximately 60km southwest of Gdansk (Lendzion 1975). The specimen was found in Kościerzyna IG1 borehole, at a depth of 4920.8m. The matrix consists of medium grey, fine-grained mudstone, with the specimen preserved as a black, reflective carbon film. The specimen is deposited in the collections at the Geological Museum of the Geological Institute, Warsaw, Poland (PIG).

The age of the sediments containing the specimen was estimated as belonging to the *Fallotaspis* Zone of the Atdabanian, correlating to Cambrian Series 2, Stage 3. This age determination was based on the presence of *Mobergella* and acritarchs in the same interval and the presence of trilobites of the *Schmidtiellus mickwitzi* Zone found higher up in the core (Dzik & Lendzion 1988). This is older than other early Cambrian fossil Lagerstätten, namely the Chengjiang and Sirius Passet biotas (Dzik & Ledzion 1988, Zhang *et al.* 2001).

The specimen was examined and photographed both dry and immersed in water, using incident and cross-polarised lighting to increase contrast. A polariser was fitted to the camera lens in crossed orientation with a second polarised film at the light source. A Canon EOS 500D digital SLR Camera with Canon EF-S 60 mm Macro Lens was used for photography, and was controlled using the EOS Utility 2.8.1.0 program for remote shooting. Images were processed in Adobe Photoshop CS6, to make minor adjustments to contrast, exposure, colour balance and sharpness. Background was removed where necessary. Figures were made using Adobe Illustrator CS6.

3. Systematic palaeontology

‘*Cassubia*’ *infercambriensis* (Fig. 1a, b) is a composite fossil consisting of a *Peytoia*-like anomalocaridid appendage (Fig. 1c-e) in close association with an unidentifiable arthropod body of non-anomalocaridid origin (Fig. 2). The anomalocaridid appendage is located on a different level of rock from the arthropod body, with separation of 1-2mm, as indicated by the preparation marks delineating the anomalocaridid appendage from the arthropod body in the counterpart (arrow in Fig. 1b). Preservation of the appendage is darker, more complete and more highly reflective, as compared to the arthropod body. There are two elongated structures (app? in Fig. 2b) positioned next to the arthropod body on the same sediment level and with a similar style of preservation. They may be limbs associated with the arthropod body. Their elongated nature could be suggestive of anomalocaridid appendage ventral spines, however the width is not comparable to that of the ventral spines of the anomalocaridid appendage on this slab.

Genus *Peytoia* Walcott, 1911

Type species. Peytoia nathorsti Walcott, 1911 (by original designation).

Emended diagnosis. Anomalocaridid with body subdivided into two distinct tagmata. The non-segmented front part bears large dorsolateral eyes on stalks set well back on the head; a dorsolateral carapace; frontal appendages consisting of 11 subrectangular podomeres with dorsal spines on most podomeres, and 5 to 7 elongated, straight ventral spines with short auxiliary spines along length and straight distal tips; and anteroventral mouthparts consisting of a circlet of 32 radially arranged plates bearing short triangular spines, and with a square to rectangular central opening that lacks inner rows of teeth. The metameric trunk consists of a central body region bearing rows of setal blades, and 14 pairs of triangular body flaps with transverse lines that extend outward laterally and are broadest at segment 7 then tapering in size forward and back to a blunt body posterior. Tailfan lacking (*emended from* Collins 1996).

Remarks. Pending a complete redescription of *Peytoia*, this diagnosis has been substantially emended from Collins (1996) based on detailed descriptions of the frontal appendages (Daley & Budd 2010; Daley *et al.* 2013) and recent comparisons of *Peytoia* body structures such as the cephalic carapace (Daley *et al*. 2009), setal blades (Daley *et al.* 2009; Daley & Edgecombe 2014), and oral cone (Daley & Bergström 2012) with other anomalocaridid taxa.

Discussion. The anomalocaridid appendage described herein is similar to the appendages of taxa such as *Peytoia* and *Hurdia* (Daley *et al*. 2009, 2013), which have long, wide ventral spines and a relatively low number of podomeres (11 or fewer, as compared to 13 or more in taxa with short ventral spines, such as *Anomalocaris*) (Daley & Edgecombe 2014). In overall aspect this taxon is most similar to *Peytoia nathorsti* from the Burgess Shale, and is therefore referred to the same genus. Both appendages have straight ventral spines that do not curve at their distal tips, and which are angled forward distally (in contrast with *Hurdia*). *Peytoia* appendages often do not preserve dorsal spines (Fig. 13A-D in Daley *et al.* 2013) although rare specimens show they were present on all podomeres (Fig. 13E, F in Daley *et al.* 2013). A single specimen of *Peytoia* cf. *P. nathorsti* from the Balang Formation of China preserves only one dorsal spine on a middle podomere (Fig. 3 in Liu 2013). The lack of dorsal spines in *P. infercambriensis* could also be taphonomic. Only four ventral spines are preserved in *P. infercambriensis*, as compared to five in other species of *Peytoia*, however the two more proximal podomeres in *P. infercambriensis* are highly incomplete, and it is possible that one or both may have had ventral spines that have not been preserved.

Peytoia infercambriensis comb. nov.

Figs 1, 2.

Holotype and only known specimen. PIG 1432 II 22.

Justification of type designation: The original description of the Holotype specimen included both the anomalocaridid appendage and the arthropod body shown here to be non-anomalocaridid in origin. We designate the appendage specimen alone as the

Holotype, to the exclusion of the arthropod body found in close proximity. This is in agreement with Article 73.1.5 of The International Code of Zoological Nomenclature (ICZN). Our restriction of the holotype to the appendage stabilises the species name and associates it with an identified group (Radiodonta: Hurdiidae: *Peytoia*), rather than having it attached to a taxonomically unidentified arthropod body.

Diagnosis. Appendage with ventral spines that are half as wide as the ventral margin of the podomere to which they are attached. Pronounced distalward decrease in ventral spine length, with most proximal ventral spine at least four times longer than most distal ventral spine. Auxiliary spines of ventral spines tiny and closely spaced, with as many as 24 per ventral spine.

Description. The anomalocaridid appendage has a mostly complete distal region, and a partial proximal region. The attachment region is completely unknown. Nine podomeres are visible, but the first two most proximal podomeres are highly incomplete and preserve only the dorsal margin, which bear 1 mm long oval ridges arranged perpendicular to the margin (r in Fig. 1d). One oval ridge is present on the first podomere, and five on the second. Podomeres 3 to 8 are roughly rectangular, with wider dorsal margins as compared to the ventral margins. Boundaries between podomeres consist of simple lines with no visible arthrodial membranes, and are delineated along the dorsal margin by indentations at the boundary. Podomeres decrease in both height and length towards the distal end of the appendage, imparting a curved, tapering appearance to the appendage. The boundaries of podomere 8 are difficult to see, owing to old preparation marks (p8 in Fig. 1d). Podomere 9 is elongated and pointed, with a small triangular projection that may represent a dorsal spine (ds? in Fig. 1d). A small triangular projection is also seen on the most distal corner of the dorsal margin of podomere 5, which may be another dorsal spine (ds? in Fig. 1d).

Ventral spines project from the distal region of the ventral margins of podomeres 3 to 6 (vs1-vs4 in Fig. 1d). These are straight and angled forward distally, forming a diminishing angle with the podomere ventral boundary from 60° for ventral spine 3 to 45° for ventral spine 6. Podomeres 7, 8 and 9 do not have visible ventral spines, although this region has undergone extensive preparation that may have obscured some features. The ventral spines are about half as wide at their base as the total width of the ventral margin of the podomere to which they are attached. They taper gradually to a point. The length of the ventral spines decreases towards the distal end, with ventral spine 3 being nearly three times as long as the height of the podomere to which it is attached, while ventral spine 6 is only as long as its podomere is high. The bases of auxiliary spines are visible along most of the distal margin of ventral spine 3 (as in Fig. 1d). These are closely spaced, with less than 1 mm of space between spine bases that are only about 1 mm in width. The tips of the auxiliary spines were not preserved, given them a truncated appearance.

Remarks. *P. infercambriensis* differs from other species of *Peytoia* in the size and number of ventral spines, and the arrangement of auxiliary spines. In *P. nathorsti*, the ventral spine base is as wide as the ventral margin of the podomere to which it is attached (Fig. 13A-E in Daley *et al.* 2013), whereas the ventral spines in *P. infercambriensis* are only half as wide as their podomere (Fig. 1c-e). The distalward decrease in the length of the ventral spines is more pronounced in *P. infercambriensis*, with the most proximal ventral spine being at least four times longer than the most distal ventral spine. In *P. nathorsti*, the longest ventral spine is actually the second or third most proximal, which is still at most only twice as long as the shortest, most distal ventral spine (Daley *et al.* 2013). The arrangement of auxiliary spines in *P. infercambriensis* also differs from that of *P. nathorsti*, which is known to have up to eight widely-space auxiliary spines that are 1-3 mm in length, slender, and projecting at an angle to the ventral spine margin. The length of the auxiliary spines in *P. infercambriensis* is unknown, but the spacing is tight. At least 8 auxiliary spines (as in Fig. 1d) are visible on a well-preserved region of the most proximal ventral spine (vs1 in Fig. 1d), which accounts for only one third of the total length of the ventral spine, suggesting that as many as 24 auxiliary spines were present on that ventral spine. This high number of auxiliary spines is more similar to that seen in the ?*Peytoia* appendage (Daley & Budd, 2010) from the Tulip Beds locality (Fletcher & Collins 1998; Fletcher & Collins 2003, O'Brien & Caron 2012) of the Burgess Shale Formation. This appendage has upwards of 17 auxiliary spines along the distal margin of its ventral spines, and these are also closely spaced (Text-Fig. 8A in Daley & Budd, 2010) as is seen in *P. infercambriensis*. The *?Peytoia* appendage differs from *P. infercambriensis* in relative size and arrangement of ventral spines (similar to that described for *P. nathorsti* above) and also in the details of the terminal end of the appendage, which bears three large, curved dorsal spines not present in *P. infercambriensis*.

P. infercambriensis could also be compared to the frontal appendages found in the Ordovician Fezouata Biota of Morocco (Figs. 1l, S3c-d, and S4f in Van Roy & Briggs 2011). The two published specimens from this site were originally compared to the frontal appendages of *Peytoia* (Van Roy & Briggs 2011), sharing with this taxon and *P. infercambriensis* the presence of straight ventral spines angled towards the distal end, simple podomere boundary lines, and similar shape and size of podomeres. One of the appendages has prominent dorsal spines that arch over the distal end of the appendage and closely-spaced auxiliary spines on the ventral spines (fig.1l, S4f in Van Roy & Briggs 2011), similar to those in *?Peytoia* (Daley & Budd 2010). The second appendage differs from *P. infercambriensis* in having a protracted distal end with numerous terminal spines and widely spaced auxiliary spines on the ventral spines.

Arthropoda gen. et sp. indet.

Figs. 1a, b; 2

Description. The remaining material originally referred to *'Cassubia*' is here putatively identified as the abdomen of an indeterminate arthropod. A total of 13 segments are preserved, each with a slight convexity. Segments appear to transversely widen towards the posterior of the abdomen, reaching their widest at the sixth segment, although the more posterior segments are incompletely preserved in this aspect. The more anterior segments, one to seven, have a straight posterior margin, which becomes more convex due to the bending of the abdomen. This is most pronounced in segments eight and nine. In at least seven segments a medial keel-like structure can be observed. These keel-like structures extend between a third- and half-way into their associated tergites and taper to a point.

Anterior to the abdominal segments are several fragments of organic material (org in Fig. 2b) of unknown origin. The outermost of these fragments on both the left and right side are roughly oval or round in outline, though highly incomplete. They contain no distinct features, and are difficult to interpret owing to the extensive preparation marks in this region of the fossil. It is unknown if these organic fragments are associated with the arthropod abdomen described here.

A limb-like elongated structure is also associated with this material (app? in Fig. 2b), although its exact affinities are uncertain (see above). If this does indeed represent a limb then it possesses roughly 13 podomeres which taper towards the posterior of the specimen.

Remarks. The morphology of this putative arthropod abdomen is somewhat indistinct but shows some similarities to that of Cambrian bivalved arthropods, particularly *Nereocaris* (Legg *et al*. 2012; Legg & Caron 2014). *Nereocaris* also possesses wide abdominal somites with straight posterior edges, and in some specimens possess spines on their posterior somites (Legg & Caron 2014), which may be compressed to resemble the keel-like structure in the material described herein.

The keel-like structure is also reminiscent of the sagittal ridge of mollisoniids. While *Mollisonia* only possesses only 7 thoracic tergites (Briggs et al. 2008; Zhang et al. 2002b), the mollisoniid *Urokodia* is characterised by 14 or 15 thoracic tergites (Zhang et al. 2002a), in line with the 13 abdominal segments of the incomplete arthropod described here. Mollisoniid thoracic segments typically resemble each other in sagittal length and transverse width (Briggs et al. 2008; Zhang et al. 2002a, b; Caron et al. 2014) and may have elongated lateral spines along their margin (Zhang et al. 2002a; Caron et al. 2014), but neither of these characteristics is present in the arthropod described here. The two roughly oval fragments of organic material located anterior of the abdomen are similar in relative size and location to the eyes of *Mollisonia* from the Marble Canyon locality in the Burgess Shale (Caron et al. 2014), but the fragmentary nature of the material prevents a more conclusive identification of the anatomy of the anterior region.

Given the non-diagnostic nature of this material it is retained here in open nomenclature.

4. Discussion

Anomalocaridids with appendages bearing long ventral spines have been found in recent phylogenetic analyses (e.g. Vinther *et al.* 2014; Cong *et al.* 2014, Van Roy *et al.* 2015) to be a monophyletic group including the taxa *Peytoia* (Whittington & Briggs 1985; Daley *et al.* 2013), *Hurdia* (Daley *et al.* 2009; 2013), *Stanleycaris* (Caron *et al.* 2010) and

Schinderhannes (Kühl *et al*. 2009; Legg *et al*. 2013). *P. infercambriensis* has also been placed in this group (Daley & Edgecombe, in prep), which has been referred to as the family Hurdiidae (Vinther *et al.* 2014). Previously, the geologically oldest member of the group was *Peytoia* cf. *P. nathorsti* from the Balang Formation of China, with an age of Cambrian Series 2 Stage 4 (Liu 2013). The presence of *P. infercambriensis* in the Cambrian (Series 2, Stage 3) of Poland extends the range of the Hurdiidae family back in time, making these the oldest anomalocaridids in the fossil record. Indeed, *P. infercambriensis* and the associated arthropod body represent the oldest known examples of Burgess Shale-type preservation (Gaines 2014). By Series 3, Stage 5 of the Cambrian, members of the family Hurdiidae are relatively abundant and diverse, including: *Peytoia nathorsti, ?Peytoia, Hurdia* and *Stanleycaris* from the Burgess Shale (Daley *et al*. 2009, 2013; Daley & Budd 2010); *Hurdia* from the Spence Shale (Daley et al. 2013); and *Peytoia nathorsti* from the Marjum Formation (Briggs & Robison 1984). *Aegriocassis benmoulae* and other isolated anomalocaridid frontal appendages from the Fezouata Biota of Morocco show similarities to *Peytoia* and *Hurdia* appendages, and extend the range of the family Hurdiidae up into the upper Tremadocian and Lower Floian of the Ordovician (Van Roy & Briggs 2011; Van Roy *et al.* 2015). The possible anomalocaridid *Schinderhannes* with its *Hurdia*-like frontal appendages extends the range even further into the Early Emsian of the Devonian (Kühl *et al.* 2009). The morphology of anomalocaridid appendages with long ventral spines, as exemplified by *P. infercambriensis*, was therefore incredibly long-lived, existing for nearly 110 million years.

P. infercambriensis represents the only known example of an anomalocaridid from the East European Craton, the core of the Baltica continent. Throughout the early and middle Cambrian, Baltica is thought to have been a distinct continent located south of Laurentia, South China, and Siberia (Landing *et al.* 2013). *Peytoia* appendages are found later in the Cambrian on both South China and Laurentia. The presence of *P.*

infercambriensis on Baltica fills in a gap in the geographic range of the family Hurdiidae. *Peytoia* represents the second most geographically widespread morphology of anomalocaridid appendages, with only *Anomalocaris* being found on more continents in the Cambrian (Daley & Edgecombe, 2014).

5. Conclusions

The anomalocaridids have undergone numerous reinvestigations and interpretations of their anatomy, however, thanks to extensive restudy of pre-existing material and information from new specimens, a more complete and accurate understanding of their morphology and evolutionary history is starting to emerge. Our restudy of *Peytoia infracambriensis* demonstrates the longevity, both temporally and geographically, and conservative morphology of hurdiid anomalocaridids.

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References

BOUSFIELD, E. L. 1995. A contribution to the natural classification of lower and middle Cambrian arthropods: food-gathering and feeding mechanisms. *Amphipacifica* **2**, 3-34.

BRIGGS, D. E. G. & ROBISON, R. A. 1984. Exceptionally preserved nontrilobite arthropods and *Anomalocaris* from the Middle Cambrian of Utah. *The University of Kansas Paleontological Contributions* **111**, 1-23.

BRIGGS, D. E. G. , LIEBERMAN, B. S., HENDRICKS, J. R., HALGEDAHL, S. L., & JARRARD, R. D. 2008. Middle Cambrian arthropods from Utah. *Journal of Paleontology* **82**, 238-254.

CARON, J.-B., GAINES, R. R., MÁNGANO, M. G., STRENG, M. & DALEY, A. C. 2010. A new Burgess Shale-type assemblage from the “thin” Stephen Formation of the southern Canadian Rockies. *Geology* **38**, 811-14.

CARON, J.-B., GAINES, R. R., ARIA, C., MÁNGANO, M. G. & STRENG, M. 2014. A new phyllopod bed-like assemblage from the Burgess Shale of the Canadian Rockies. *Nature Communications* **5**, 3210.

COLLINS, D. 1996. The “evolution” of *Anomalocaris* and its classification in the arthropod Class Dinocarida (nov.) and Order Radiodonta (nov.). *Journal of Paleontology* **70**, 280-93.

CONG, P., MA, X., HOU, X., EDGECOMBE, G. D. & STRAUSFELD, N. J. 2014. Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* **513**, 553-42.

CONWAY MORRIS, S. 1989. The persistence of Burgess Shale-type faunas: implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **80**, 271-83.

CONWAY MORRIS, S. & ROBISON, R. A. 1988. More soft-bodied animals and algae from the middle Cambrian of Utah and British Columbia. *The University of Kansas Paleontological Contributions* **122**, 1-48.

DALEY, A. C. & BERGSTRÖM, J. 2012. The oral cone of *Anomalocaris* is not a classic "peytoia". *Naturwissenschaften* **99**, 501-4.

DALEY, A. C. & BUDD, G. E. 2010. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* **53**, 721-38.

DALEY, A. C. & EDGECOMBE, G. D. 2014. Morphology of *Anomalocaris canadensis* from the Burgess Shale. *Journal of Paleontology* **88**, 68-91.

DALEY, A. C., BUDD, G. E., CARON, J.-B., EDGECOMBE, G. D. & COLLINS, D. 2009. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. *Science* **323**, 1597-600.

DALEY, A. C., BUDD, G. E. & CARON, J.-B. 2013. Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *Journal of Systematic Palaeontology* **11**, 743-87.

DELLE CAVE, L. & SIMONETTA, A. M. 1991. Early Palaeozoic arthropods and problems of arthropod phylogeny; with some notes on taxa of doubtful affinities. In *the Early Evolution of Metazoa and the Significance of Problematic Taxa* (eds. Simonetta, A. M. & Conway Morris, S.), pp. 189-244. Cambridge University Press, Cambridge.

DELLE CAVE, L., INSOM, E. & SIMONETTA, A. M. 1998. Advances, diversions, possible relapses and additional problems in understanding the early evolution of the Articulata. *Italian Journal of Zoology* **65**, 19-38.

DZIK, J. & LENDZION, K. 1988. The oldest arthropods of the East European Platform. *Lethaia* **21**, 29-38.

FLETCHER, T. P. & COLLINS, D. H. 1998. The Middle Cambrian Burgess Shale and its relationship to the Stephen Formation in the southern Canadian Rocky Mountains. *Canadian Journal of Earth Sciences* **35**, 413-36.

FLETCHER, T. P. & COLLINS, D. H. 2003. The Burgess Shale and associated Cambrian formations west of the Fossil Gully Fault Zone on Mount Stephen, British Columbia. *Canadian Journal of Earth Sciences* **40**, 1823-38.

GAINES, R. R. 2014. Burgess Shale-type preservation and its distribution in space and time. In *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization. The Paleontological Society Papers, Volume 20* (eds. M. Laflamme, J. D. Schiffbauer & S. A. F. Darroch), pp. 123-46. The Paleontological Society.

HAUG, J. T., WALOSZEK, D., MAAS, A., LIU, Y. & HAUG, C. 2012. Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology* **55**, 369-99.

HOU, X.-G., BERGSTRÖM, J. & AHLBERG, P. 1995. *Anomalocaris* and other large animals in the lower Cambrian Chengjiang fauna of southwest China. *GFF* **117**, 163-83.

KÜHL, G., BRIGGS, D. E. G. & RUST, J. 2009. A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany. *Science* **323**, 771-3.

LANDING, E., GEYER, G., BRASIER, M. D. & BOWRING, S. 2013. Cambrian evolutionary radiation: Context, correlation, and chronostratigraphy – overcoming deficiencies of the first appearance datum (FAD) concept. *Earth-Science Reviews* **123**, 133-172.

LEGG, D. A. & CARON, J.-B. 2014. New middle Cambrian bivalved arthropods from the Burgess Shale (British Columbia, Canada). *Palaeontology* **57**, 691-711.

LEGG, D. A., SUTTON, M. D., EDGECOMBE, G. D. & CARON, J.-B. 2012. Cambrian bivalved arthropod reveals origin of arthrodization. *Proceedings of the Royal Society B* **279**, 4699-704.

LEGG, D. A., SUTTON, M. D. & EDGECOMBE, G. D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications* **4**:2485.

LENDZION, K. 1975. Fauna of the *Morgella* Zone in the Polish Lower Cambrian. *Kwartalnik geologiczny* **19**, 237-42.

LENDZION, K. 1977. *Cassubia* – a new generic name for *Pomerania* Lendzion 1975. *Kwartalnik geologiczny* **21**, 211.

LIU, Q. 2013. The first discovery of anomalocaridid appendages from the Balang Formtaion (Cambrian Series 2) in Hunan, China. *Alcheringa* **37**, 338-43.

MOCZYDŁOWSKA, M. 2002. Early Cambrian phytoplankton diversification and appearance of trilobites in the Swedish Caledonides with implications for coupled evolutionary events between primary producers and consumers. *Lethaia* **35**, 191-214.

O'BRIEN, L. J. & CARON, J.-B. 2012. A new stalked filter-feeder from the Middle Cambrian Burgess Shale, British Columbia, Canada. *PLoS One* **7**:29233.

PATERSON, J. R., EDGECOMBE, G. D., GARCÍA-BELLIDO, D. C., JAGO, J. B. AND GEHLING, J. G. 2010. Nektaspid arthropods from the Lower Cambrian Emu Bay Shale Lagerstätte, South Australia, with a reassessment of lamellipedian relationships. *Palaeontology* **53**, 377-402.

TANAKA, G., HOU, X., MA, X., EDGECOMBE, G. D. & STRAUSFELD, N. J. 2013. Chelicerate neural ground pattern in a Cambrian great appendage arthropod. *Nature* **502**, 364-7.

VAN ROY, P. & BRIGGS, D. E. G. 2011. A giant Ordovician anomalocaridid. *Nature* **473**, 510-3.

VAN ROY, P., DALEY, A. C. & BRIGGS, D. E. G. 2015. Anomalocaridid trunk limb homology revealed by a gient filter-feeder with paired flaps. *Nature* (advance online publication).

VINTHER, J., STEIN, M., LONGRICH, N. R. & HARPER, D. A. T. 2014. A suspension-feeding anomalocarid from the Early Cambrian. *Nature* **507**, 496-9.

WALCOTT, C. D. 1911. Cambrian geology and paleontology. II. Middle Cambrian holothurians and medusa. *Smithsonian Miscellaneous Collections* **57**, 41-68.

WHITTINGTON, H. B. & BRIGGS, D. E. G. 1985. The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London B* **309**, 569-609.

ZHANG, X., SHU, D. LI, Y. & HAN, J.2001. New sites of Chengjiang fossils: crucial windows on the Cambrian explosion. *Journal of the Geological Society* **158**, 211-8.

ZHANG, Z., HAN, J., & DEGAN, S. 2002a. New occurrence of the Burgess Shale arthropod *Sidneyia* in the Early Cambrian Chengjiang Lagerstätte (South China), and revision of the arthropod *Urokodia*, *Alcheringa* **26**, 1-8.

ZHANG, X., ZHAO, Y., YANG, R. & DEGAN, S. 2002b. The Burgess Shale arthropod *Mollisonia* (*M. sinica* New Species): New occurrence from the Middle Cambrian Kaili Fauna of Southwest China. *Journal of Paleontology* **76**, 1106-1108.

Figure 1. Composite fossil from the Lower Cambrian Zawiszyn Formation of Poland, showing *Peytoia infercambriensis* comb. nov. with an arthropod of uncertain affinity. Photographs of entire specimen (a) part and (b) counterpart. Arrow in (b) indicates preparation marks delineating the anomalocaridid appendage from the arthropod body, which are found on slightly different levels in the rock. (c–e) Closeup of *Peytoia infercambriensis* comb. nov. Holotype specimen PIG 1432 II 22. (c) Photograph of part. (d) Composite drawing from both part and counterpart. (e) Photograph of counterpart mirrored for consistent orientation. All photographs taken under cross polarised overhead lighting with specimen submerged in water. Abbreviations: ds – dorsal spines; org – unidentified organic material; p1-p9 – podomeres 1 to 9; r – raised oval ridges; vs1-4 – ventral spines 1 to 4. Scale bars represent 10 mm for (a–b) and 5 mm for (c–e).

Figure 2. Arthropoda gen. et. sp. indet. from the Lower Cambrian Zawiszyn Formation of Poland. Photographs of (a) part and (c) counterpart mirrored for consistent orientation, and (b) composite drawing from both part and counterpart. All photographs taken under cross polarised overhead lighting with specimen submerged in water. Numbers refer to body segments. Abbreviations: app? – possible appendage; k – medial keel-like ridges; org – unidentified organic material. Scale bars represent 10 mm.

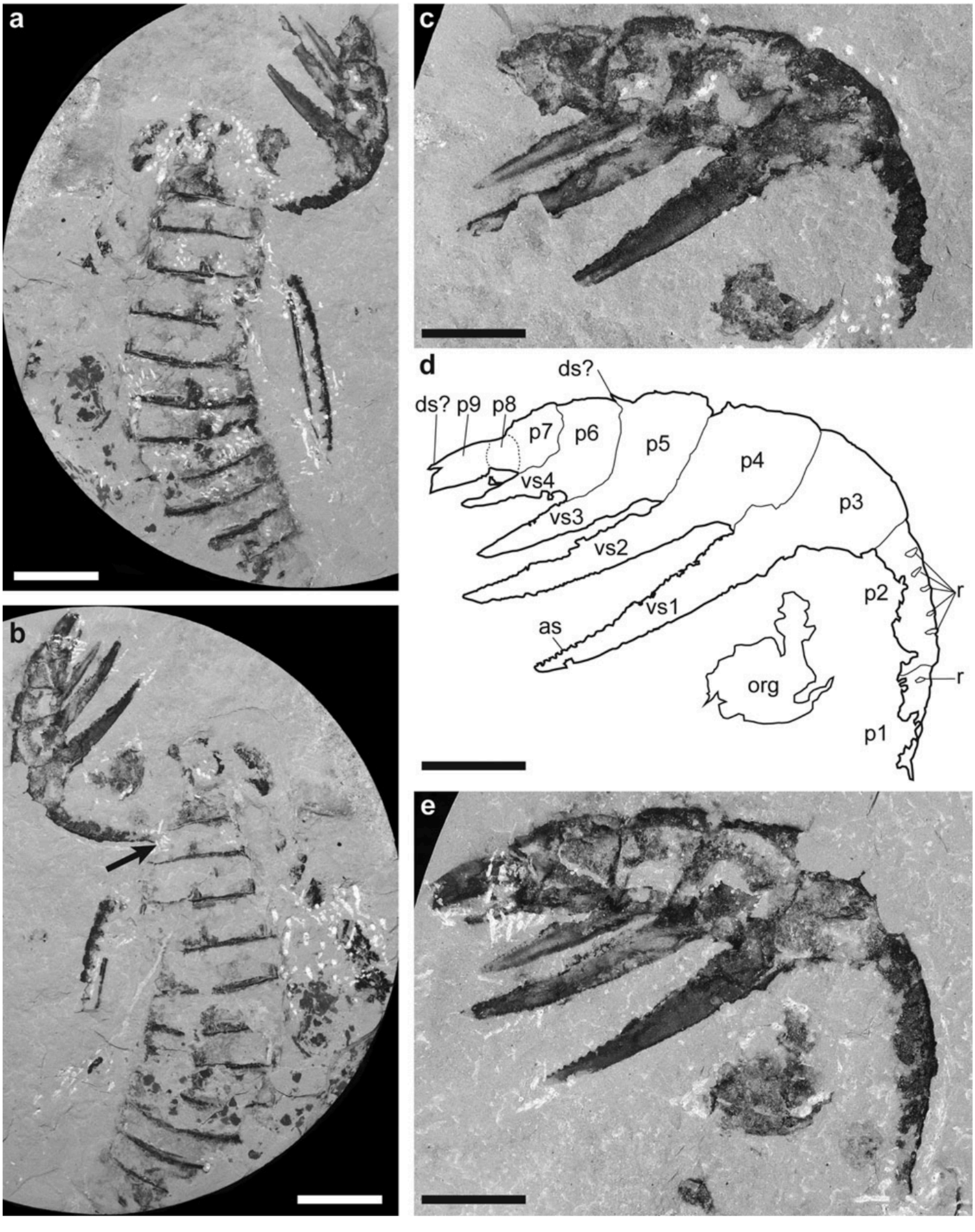

Figure 1

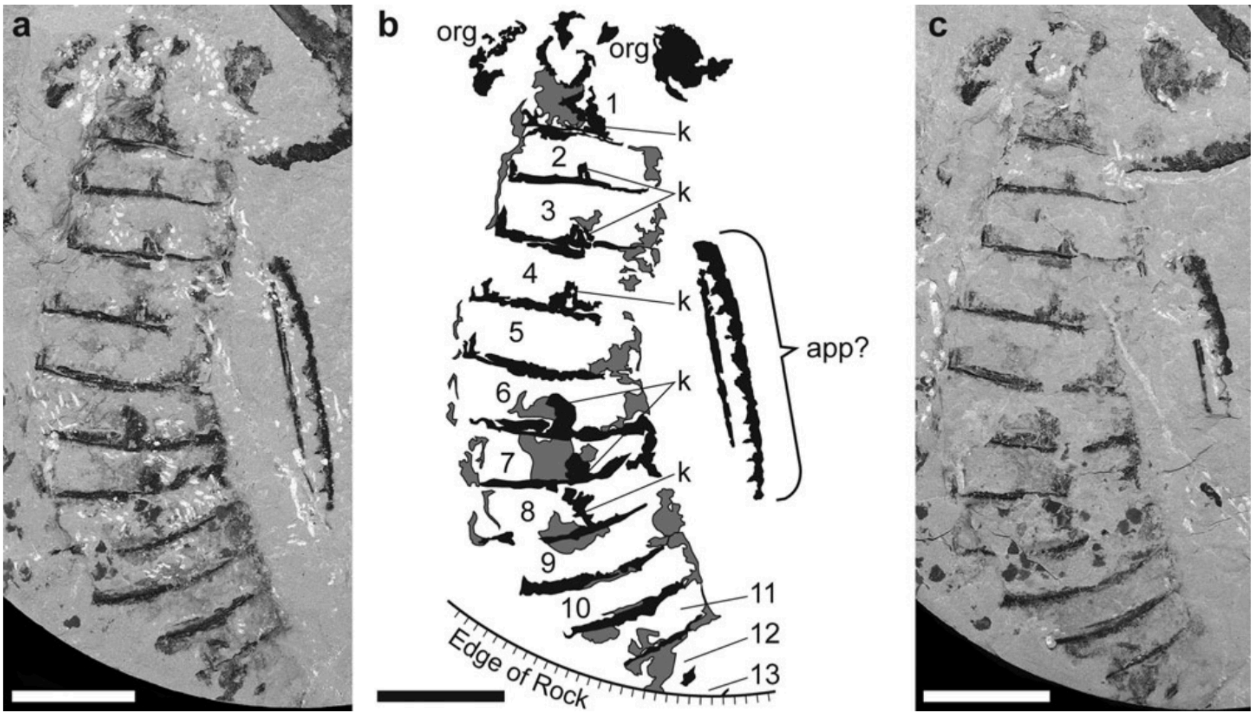

Figure 2