

# A new aglaspidid-like euarthropod from the lower Cambrian Emu Bay Shale of South Australia

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**Abstract** – A new euarthropod from the Emu Bay Shale (Cambrian Series 2, Stage 4) on Kangaroo Island, South Australia, is a rare component of this Konservat-Lagerstätte. The two known specimens of *Eozetetes gemmelli* gen. et sp. nov., in combination, depict a non-biomineralized euarthropod with a relatively short cephalic shield lacking dorsal eyes and bearing a flagelliform antenna, 18 trunk segments with broad tergopleurae and paired axial nodes/carinae, and an elongate, styliform tailspine. The new species compares most closely with taxa in the putative clade Vicissicaudata, which groups Aglaspidida, Cheloniellida and Xenopoda. A ring-like terminal tergite in *E. gemmelli* corresponds to the caudal tergite in cheloniellids and xenopodans. Incorporating *Eozetetes* into recent character sets for Cambrian euarthropods supports close affinities to either *Emeraldella* or to aglaspidids, but several plesiomorphic character states are inconsistent with membership in Aglaspidida *sensu stricto*. *Eozetetes* is among the earliest of various Cambrian taxa informally referred to as ‘aglaspidid-like euarthropods’.

Keywords: Euarthropoda, *Eozetetes gemmelli*, *Emeraldella*, Aglaspidida, Vicissicaudata.

## 1. Introduction

Among more than 50 species currently known from the Emu Bay Shale Konservat-Lagerstätte on Kangaroo Island, South Australia, euarthropods represent more than half that diversity and are numerically dominant at the level of individuals (Paterson *et al.* 2015), a pattern shared with other Cambrian Konservat-Lagerstätten (Caron *et al.* 2014). Fifteen field seasons at Buck Quarry since 2007 (Gehling *et al.* 2011) have yielded more than 5000 registered specimens in the South Australian Museum. A new non-biomineralized euarthropod described herein is known from two specimens that provide a fairly complete picture of the dorsal exoskeletal morphology, as well as information on the antenna, hypostome and doublure. This rare taxon constitutes the oldest record of aglaspidid-like euarthropods in Australia, with Aglaspidida Walcott, 1912 (*sensu stricto*) known from just one occurrence, in the upper Cambrian of Tasmania (Ortega-Hernández *et al.* 2010).

## 2. Material and methods

Two specimens (SAM P48369 and P46332) form the basis for the description of a new Emu Bay Shale euarthropod, and are housed in the palaeontological

collections at the South Australian Museum, Adelaide (prefix SAM P). Photography used a Canon EOS 5D digital SLR camera with a Canon MP-E 65 mm 1–5× macro lens and low-angle NW light to enhance relief. Camera lucida drawings were made under a Leica MZ6 stereomicroscope. Images were edited and plates assembled with Adobe Photoshop Version C5.

*Eozetetes gemmelli* gen. et sp. nov. was coded using the character matrices of Ortega-Hernández, Legg & Braddy (2013) and Stein *et al.* (2013), both of which scored a broad range of early euarthropods for 82 and 74 characters, respectively, the former employing a denser taxonomic sampling for Aglaspidida and aglaspidid-like euarthropods in particular. Parsimony analysis with TNT (Goloboff, Farris & Nixon, 2008) used equal character weights as well as implied weights with varied concavity constants. Heuristic searches used 10 000 random stepwise addition sequences saving 50 trees per replicate with TBR branch swapping. Node support was quantified using parsimony jackknifing for equal weights and symmetric resampling for implied weights. Jackknife frequencies and GC values, respectively, above 50 % are reported based on 1000 replicates of jackknife resampling with 36 % removal probability or 1000 replicates of symmetric resampling with 33 % change probability.

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### 3. Systematic palaeontology

EUARTHROPODA Lankester, 1904

VICISSICAUDATA Ortega-Hernández, Legg & Braddy, 2013

*Discussion.* Vicissicaudata was named (Ortega-Hernández, Legg & Braddy, 2013) for a putative clade composed of Aglaspida, Cheloniellida Broili, 1932 and a group referred to as Xenopoda Raymond, 1935. The last group conventionally includes *Sidneyia* Walcott, 1911 and *Emeraldella* Walcott, 1912, and has sometimes been expanded in scope to also include Cheloniellida (e.g. Hou & Bergström, 1997). Vicissicaudata was diagnosed by a postabdomen that lacks walking legs. Monophyly of Vicissicaudata has been defended in cladistic analyses using implied character weights for a broad range of artiopodan euarthropods by Ortega-Hernández, Legg & Braddy (2013), Legg, Sutton & Edgecombe (2013) and Legg (2014). A nearly identical clade had been recognized as ‘Clade 5’ of Cotton & Braddy (2004, fig. 8), united by a postabdomen lacking appendages, strongly curved posterior tergites compared to anterior ones and a pre-telson segment with paired, unsegmented appendicular derivatives, in the form of caudal flaps (Xenopoda), furci (Cheloniellida) or postventral plates (Aglaspida). Members of Vicissicaudata (*sensu* Ortega-Hernández, Legg & Braddy, 2013) were, however, resolved as non-monophyletic in a phylogenetic analysis by Stein *et al.* (2013), uniting with some additional, mostly Cambrian taxa (*Squamacula* Hou & Bergström, 1997; *Retifacies* Hou, Chen & Lu, 1989; *Molaria* Walcott, 1912; *Burgessia* Walcott, 1912; and *Marrellomorpha* Beurlen, 1934).

Genus *Eozetetes* gen. nov.

*Type species.* *Eozetetes gemmelli* sp. nov., by monotypy.

*Etymology.* Gr. *Eo-*, early; *zetetes*, searcher; for the fossil hunter after whom the type species is named.

*Diagnosis.* Euarthropod with relatively short (sag.), wide (tr.) cephalic shield; genal angles acute, lacking spines; dorsal eyes absent; moderately wide cephalic doublure; paradoublural line curving posteriorly adjacent to attachment of hypostome; 18 trunk tergites with tergopleurae and broad overlap of adjacent tergites; axial part of trunk tergites 1–18 arched anteriorly, bearing paired longitudinally ovate nodes that grade into carinae on posterior segments; caudal tergite (tergite 19) short, ring-like; styliiform tailspine longer than remaining part of trunk.

*Eozetetes gemmelli* sp. nov.

Figures 1–4

*Material.* Holotype, SAM P48369a, b (Figs 1, 2); 10.9 m above the base of the Emu Bay Shale; paratype SAM P46332a, b (Fig. 3), 10.8 m above the base of the Emu Bay Shale. Both from Buck Quarry (35° 34' 25" S 137° 34' 36" E), Big Gully, north coast of Kangaroo

Island, South Australia; Cambrian Series 2, Stage 4, *Pararaia janeae* Zone.

*Etymology.* After Mike Gemmell, a regular member of our field team, for moving a vast amount of Emu Bay Shale and finding many superb specimens, including the type specimens of this taxon.

*Diagnosis.* As for the genus.

*Description.* Holotype 29.5 mm in length, from anterior margin of cephalic shield to preserved (incomplete) posterior tip of tailspine; cephalon 4.9 mm (sag.), 13.5 mm wide across genal angles; trunk 11.7 mm long excluding tailspine; preserved extent of tailspine 13.0 mm long.

Anterior and lateral margins of cephalic shield evenly curved; posterior margin weakly arched anteriorly. Genal angle acute, blunt, lacking spine. Narrow marginal rim present along at least anterior and anterolateral margins of cephalic shield (Fig. 2a). Doublure moderately wide, its position indicated by strong paradoublural line in both specimens (Figs 2a, 3a, b); doublure gently narrowing posteriorly. Hypostomal suture indistinct; hypostome directly attached to doublure based on paradoublural line sharply flexed posteriorly, confluent with anterolateral margin of hypostome. Hypostome widening posteriorly; posterolateral angle rounded; posterior margin transverse; maximum width (tr.) of hypostome *c.* 25% width of posterior margin of cephalic shield; doublure and hypostome extending 90% length (sag.) of cephalic shield.

Antenna known only from one side in holotype (Figs 1, 2a); elongate flagelliform, with only slight tapering along preserved extent from its insertion at side of hypostome to where it curves inwards and is concealed by cephalic shield; articulations between a few articles preserved in a section a short distance from where antenna is exposed outside the cephalic shield, these articles all being of about equal length and width.

Trunk consists of 18 tergites with tergopleurae, tergite 2 being the broadest; trilobation distinct, axis set off from tergopleurae by break in slope, more pronounced in posterior part of trunk (Fig. 2c); tergopleurae broad along most of trunk, with straight posterior margins, curved anterolateral margins, and acute tips, markedly narrowing (tr.) from *c.* tergite 10 and becoming more strongly curved and pointed; broad overlap between adjacent tergites abaxially (Fig. 2b); pair of longitudinally ovate nodes on tergites 1–13 grading into more elongate carina-like ridges on tergites 14–18 (Figs 1, 2c). Tergite 19 (= caudal tergite) a short (sag.) ring lacking nodes, tergopleurae apparently lacking (Fig. 2c).

Tailspine as wide as caudal tergite at its base, rapidly tapering in its proximal *c.* 3 mm and then maintaining an even, narrow width; wider proximal part bearing a median carina (Figs 1b, 2c).

*Discussion.* The shape of the cephalic shield (especially the nearly transverse/weakly arched posterior margin), lack of dorsal eyes, proportions of the antenna, size of the hypostome, distinct trilobation, and shape and

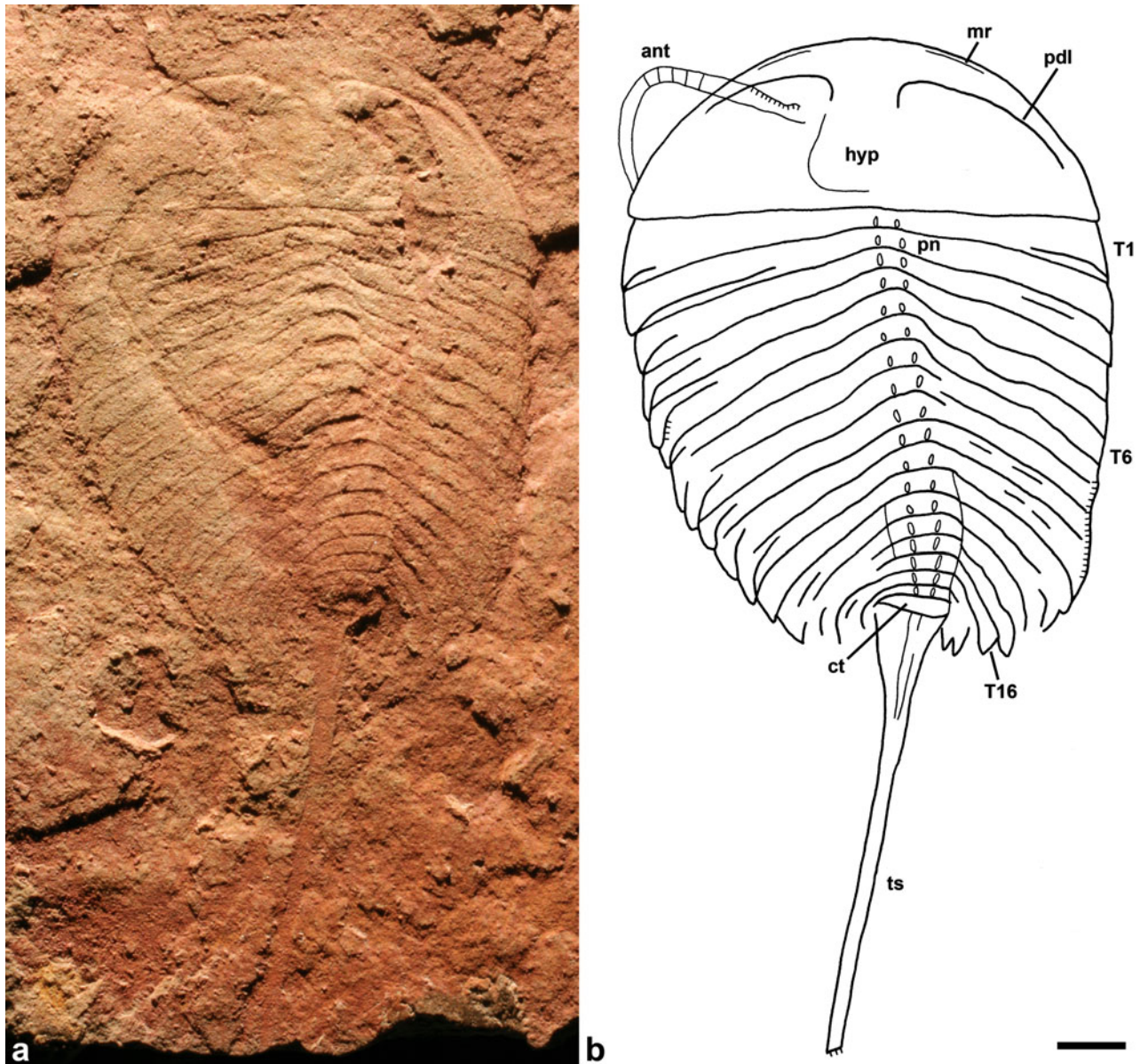


Figure 1. (Colour online) *Eozetetes gemmelli* gen. et sp. nov., from the Emu Bay Shale, Kangaroo Island, South Australia. Holotype SAM P48369a. (a) Dorsal view of articulated specimen. (b) Interpretive drawing. Abbreviations: ant – antenna; ct – caudal tergite; hyp – hypostome; mr – marginal rim on cephalic shield; pdl – paradoublural line; pn – paired longitudinally ovate nodes on axis; T – tergite; Tp – tergopleura; ts – tailspine. Scale bar 2 mm (same scale for both images).

length of the tailspine relative to the rest of the trunk (Fig. 4) are reminiscent of *Emeraldella* (Walcott, 1912; Bruton & Whittington, 1983; Stein, Church & Robison, 2011; Stein & Selden, 2012). Distinction of *Eozetetes* is justified based on its greater number of trunk tergites (18 with tergopleurae versus 10 or 11 in *Emeraldella*), greater relative width of the tergopleurae compared to the axis, absence of articulating ridges in the trunk, shorter caudal tergite and apparent absence of articulations in the tailspine. The caudal tergite of *Emeraldella* bears a prominent pair of caudal flaps, which are not known in *Eozetetes*. However, it is possible that the absence of these structures in the available material of *Eozetetes* is taphonomic, with the holotype being preserved in dorsal rather than ventral view. Given the diminutive size of the caudal tergite in *Eozetetes*

compared to that of *Emeraldella*, it might be expected that associated flaps, if present, would be smaller than those of *Emeraldella*. Transverse articulations on the tailspine have been observed in *Emeraldella brutoni* and *E. brocki* (Stein, Church & Robison, 2011). No articulations can be discerned in the tailspine of *Eozetetes gemmelli*, and given the quality of preservation in the holotype, we consider this to be a real absence.

*Eozetetes* displays a general similarity to Aglaspidida as well, and some results of phylogenetic analyses (discussed in Section 4 below) are consistent with a close relationship between these taxa. Membership in Aglaspidida *s.s.* (Van Roy, 2006; Ortega-Hernández, Legg & Braddy, 2013; Ortega-Hernández, Van Roy & Lerosey-Aubril, 2015) is opposed by *Eozetetes* having a non-biomineralized

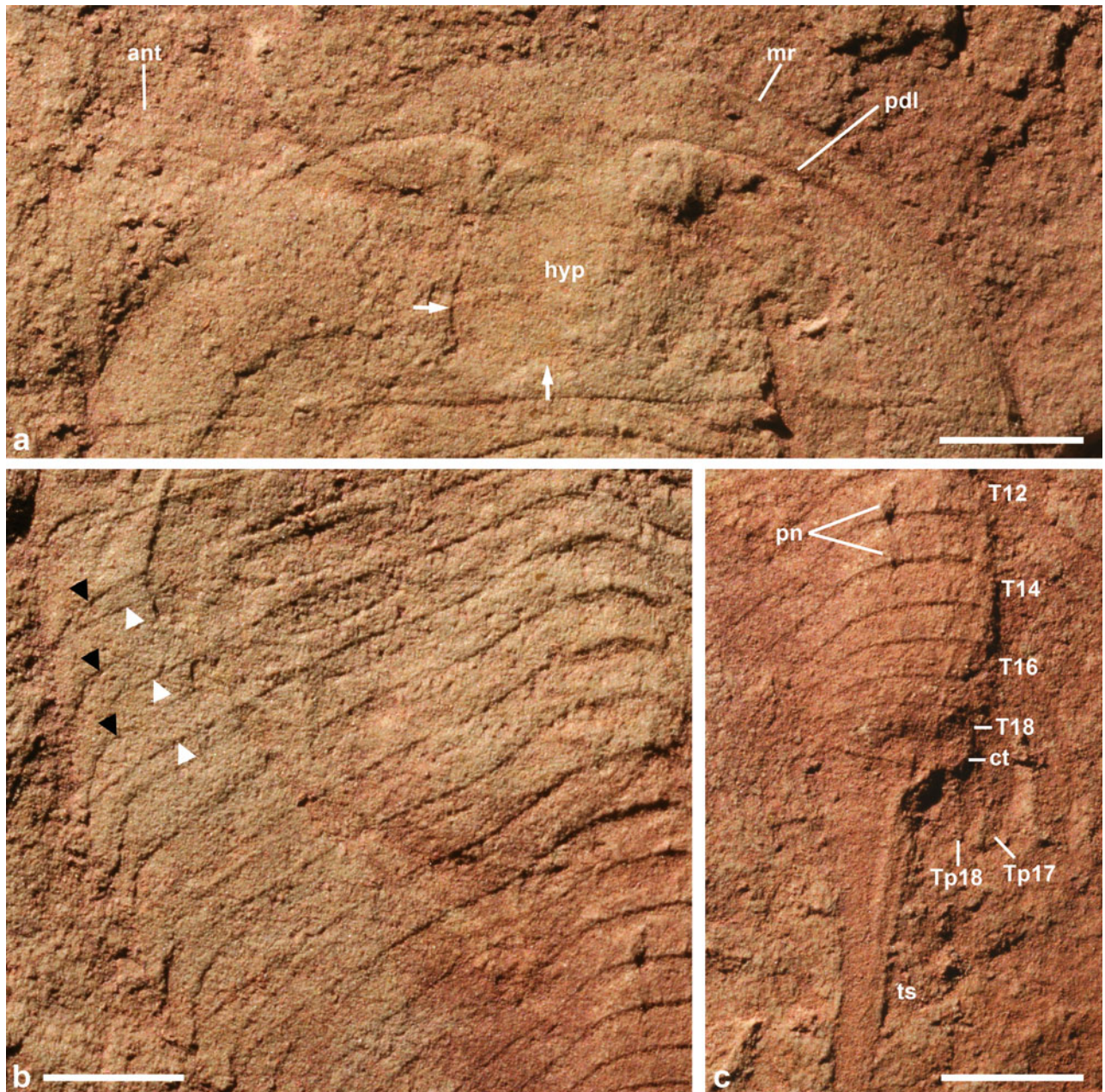


Figure 2. (Colour online) *Eozetetes gemmelli* gen. et sp. nov., from the Emu Bay Shale, Kangaroo Island, South Australia. Holotype SAM P48369a, all dorsal views (see Fig. 1 for overview). (a) Cephalic shield and left antenna; arrowheads indicate margins of hypostome. (b) Anterior part of trunk (left side) showing overlapping of tergopleurae; black arrowheads indicate anterior margins of tergopleurae; white arrowheads, posterior margins. (c) Posterior part of trunk, showing proximal part of tailspine. Abbreviations as in Figure 1. Scale bars 2 mm.

exoskeleton (versus phosphatic in Aglaspida), broadly overlapping rather than edge-to-edge tergite articulations, a markedly greater number of trunk segments compared to Cambrian aglaspids, and lacking dorsal eyes; however, it should be noted that aglaspid morphology varies within this clade with respect to the last three characters (Ortega-Hernández, Legg & Braddy, 2013; Ortega-Hernández, Van Roy & Lerosey-Aubril, 2015). A roughly ovate bulge at the right edge of the hypostome in SAM P48369 (Fig. 2a) could be compared in its position to the eyes of various aglaspids, but we regard it more likely to be sediment injected into the cephalic cavity limited by the doublure; the lack of a similar feature

on the other side of this specimen and in SAM P46332 (Fig. 3) supports this interpretation. One of the key autapomorphies of Aglaspida *s.s.*, postventral plates (Ortega-Hernández, Legg & Braddy, 2013; Ortega-Hernández, Van Roy & Lerosey-Aubril, 2015), is not observed in *Eozetetes*, and the preservation of the holotype compared to similarly preserved articulated aglaspids suggests they may be truly absent.

#### 4. Phylogenetic affinity

Comparison with *Emeraldella* and Aglaspida above signals membership in Vicissicaudata, a putative clade that includes *Emeraldella* and other artiopodans with

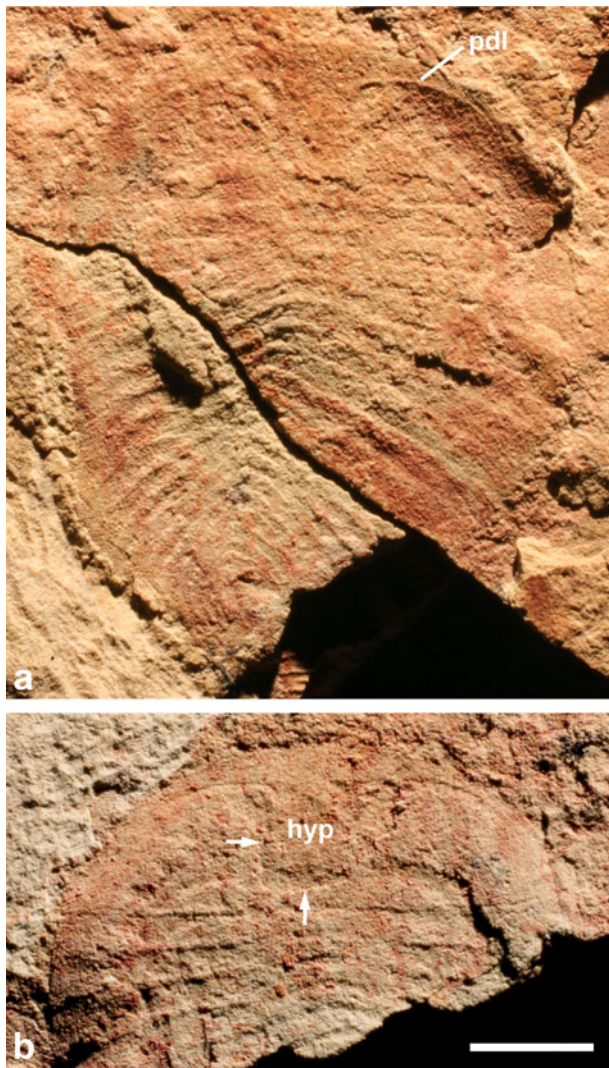


Figure 3. (Colour online) *Eozetetes gemmelli* gen. et sp. nov., from the Emu Bay Shale, Kangaroo Island, South Australia. Paratype SAM P46332. (a) Counterpart, SAM P46332a. (b) Part, SAM P46332b. Arrowheads indicate margins of hypostome. Abbreviations as in Figure 1. Scale bar 3 mm (same scale for both images).

a postabdomen that lacks walking legs but bears other paired ventral structures, at least some of which are convincingly regarded as appendicular (Ortega-Hernández, Legg & Braddy, 2013). The case for a caudal tergite in *Eozetetes* is inconclusive owing to the absence of associated appendicular derivatives, but evidence at hand is indicative of such a structure. The holotype allows for tergopleurae to be associated with the axial rings of the first 18 trunk segments, all of which bear paired axial nodes (Figs 1, 2c); the curved tergopleurae of tergite 18 run almost immediately against the base of the tailspine (Fig. 2c). The tergite immediately anterior to the tailspine (tergite 19) lacks the paired nodes that are present on all other tergites and has no associated tergopleurae. As such, we consider it most probable that the short, ring-like structure identified as tergite 19 corresponds to a caudal tergite, resembling that of Xenopoda in having reduced (apparently absent) tergopleurae. As discussed above in

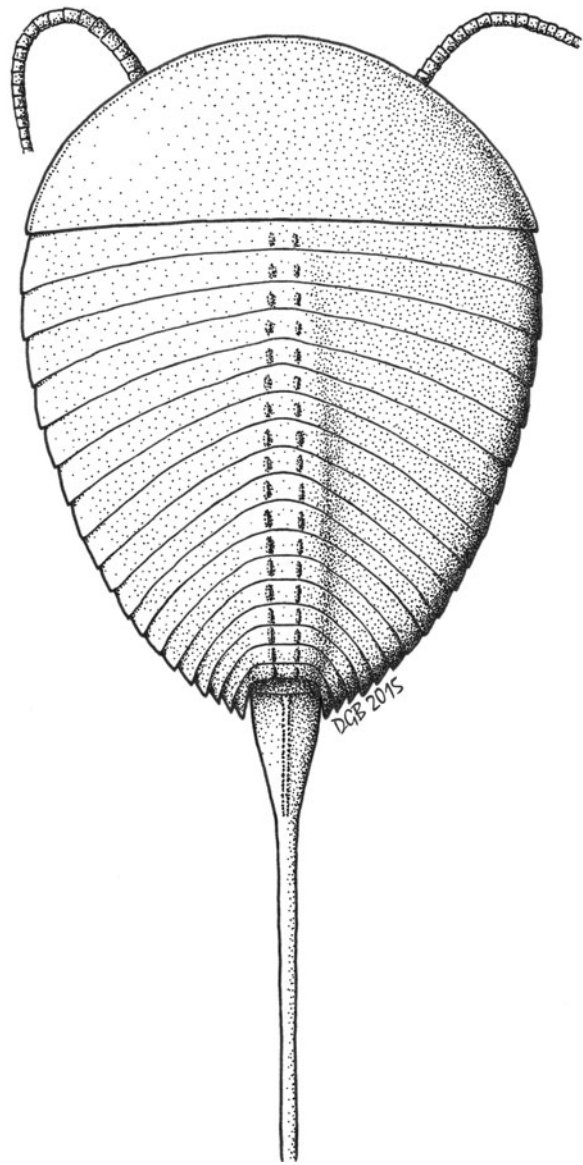


Figure 4. Reconstruction of *Eozetetes gemmelli* gen. et sp. nov.

comparison with *Emeraldella*, no caudal flaps or other ventral structures are associated with tergite 19 in *Eozetetes*, though the limited amount of available material provides a weak case for this apparent absence being real. An alternative interpretation of what we identify as tergite 19 would be that it represents an articulating structure at the anterior margin of the tailspine, but this is inconsistent with its distinct elevation relative to the tailspine.

Recent cladistic analyses of relevant taxa provide a more explicit basis for inferring the systematic position of *Eozetetes*. The character matrices of Ortega-Hernández, Legg & Braddy (2013) and Stein *et al.* (2013) were used unmodified (see online Supplementary Material available at <http://journals.cambridge.org/geo>). In both matrices, many characters are scored as missing (all appendage characters apart from a few antennal characters) or inapplicable for *Eozetetes*.

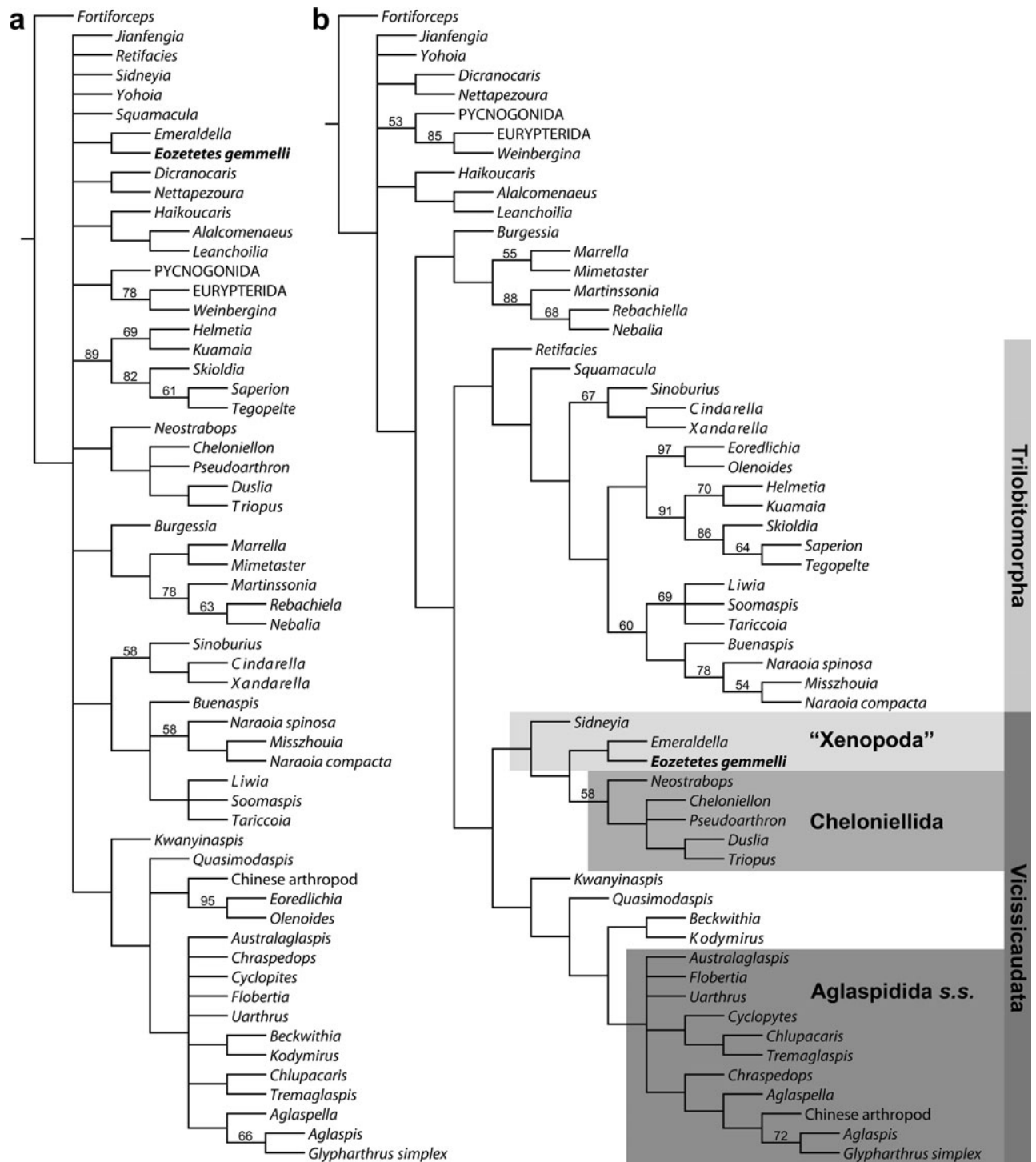


Figure 5. Cladograms with *Eozetetes gemmelli* coded in the 82-character matrix of Ortega-Hernández, Legg & Braddy (2013). (a) Strict consensus of 532 shortest cladograms (237 steps, Consistency Index 0.45, Retention Index 0.75) under equal character weights. Numbers at nodes are jackknife frequencies >50%. (b) Strict consensus of 90 shortest cladograms under implied character weights ( $k = 3$ ). Numbers at nodes are GC values >50%.

The Ortega-Hernández, Legg & Braddy (2013) matrix resolves *Eozetetes* as most closely related to *Emeraldella* under either equal or implied character weights (Fig. 5a, b). In the context of implied weights (Fig. 5b), *Eozetetes* and *Emeraldella* are members of a ‘xenopodan’ grade allied to Cheloniellida within a monophyletic Vicissicaudata. However, as in the original analyses of Ortega-Hernández, Legg & Braddy (2013, their

fig. 6), Vicissicaudata is sensitive to character weighting, not being retrieved under equal weights or more extreme concavity constants. In the implied weighted tree, *Eozetetes* and *Emeraldella* are united by their lack of lateral eyes and long tailspine (characters 18 and 70, respectively, of Ortega-Hernández, Legg & Braddy, 2013). They are more broadly united with Cheloniellida based on a single segment in the preabdomen. Although

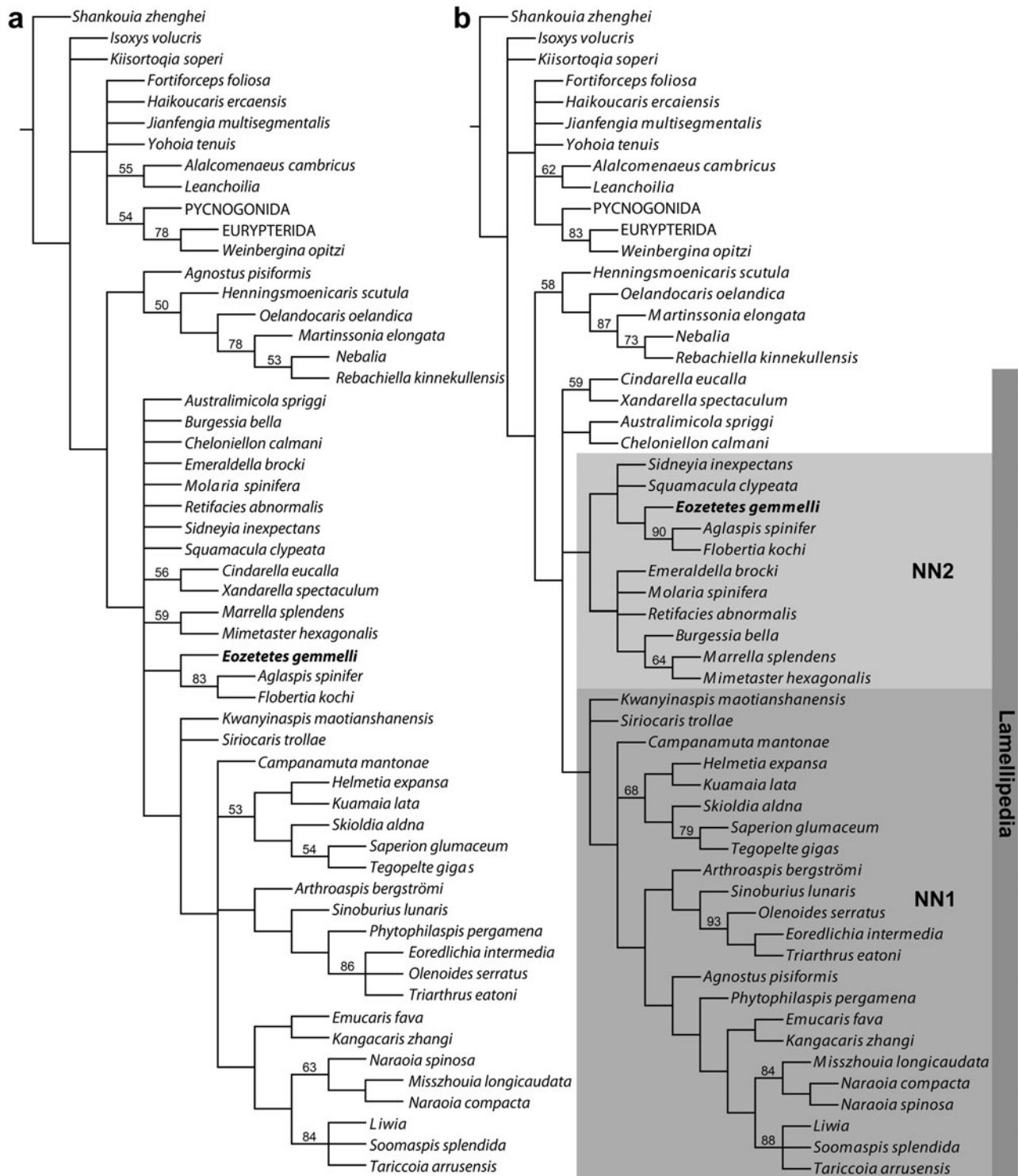


Figure 6. Cladograms with *Eozetetes gemmelli* coded in the 74-character matrix of Stein *et al.* (2013). (a) Strict consensus of 2820 shortest cladograms (180 steps) under equal character weights. Numbers at nodes are jackknife frequencies > 50 %. (b) Strict consensus of 63 shortest cladograms under implied character weights ( $k = 2-20$ ). Numbers at nodes are GC values > 50 % calculated for  $k = 3$ . NN1 and NN2 refer to two unnamed clades in the analysis of Stein *et al.* (2013).

this latter state was not coded for *Eozetetes*, discussion of tergite 19 above is consistent with the same coding as for *Emeraldella*. Membership of *Eozetetes* + *Emeraldella* within a ‘xenopodan’-cheloniellid clade resolved precisely as in Figure 5b is stable across a range of concavity constants ( $k = 2, 3, 4, 5$  and 6).

Including *Eozetetes* in the Stein *et al.* (2013) matrix, parsimony analysis with implied weights across concavity constants  $k = 2-20$  in TNT (see Section 2 above) finds 63 cladograms that invariably place *Eozetetes* within unnamed clade NN2 of Stein *et al.* (2013, fig. 16) as sister taxon to Aglaspida (Fig. 6b). All relationships depicted in the strict consensus for all analyses

are identical to those presented by Stein *et al.* (2013, fig. 16A) in their sets of 63 cladograms apart from two different resolutions of *Agnostus* and *Phytophilaspis* relative to Trilobita. In all shortest cladograms, including those retrieved under equal character weights (Fig. 6a), *Eozetetes* and Aglaspida are united by the shared presence of a cephalic marginal rim (character 42 of Stein *et al.* 2013).

Hence, determining the closest relative of *Eozetetes* – whether a ‘xenopodan’ or aglaspids – is sensitive to differences in taxonomic and character sampling in available data matrices. In either case, however, *Eozetetes* is apparently allied to taxa that have been informally grouped as ‘aglaspid-like (eu)arthropods’ (table 1 of Van Roy, 2006; table 2 of Ortega-Hernández, Legg & Braddy, 2013). Some of these taxa have subsequently been corroborated as close relatives of Aglaspida (e.g. *Kodymirus* Chlupáč & Havlicek, 1965; Lamsdell, Stein & Selden, 2013), although excluded from Aglaspida *sensu stricto*.

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### Supplementary material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0016756815001053>.

### References

- BEURLIN, K. 1934. Die Pygaspiden, eine neue Crustaceen–(Entomostracen–) Gruppe aus den Mesosaurier führenden Iraty–Schichten Brasiliens. *Paläontologische Zeitschrift* **16**, 122–34.
- BROILI, F. 1932. Ein neuer Crustacee aus dem rheinischen Unterdevon. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung* **1932**, 27–38.
- BRUTON, D. L. & WHITTINGTON, H. B. 1983. *Emeraldella* and *Leancoilia*, two arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* **300**, 553–85.
- CARON, J.-B., GAINES, R. R., ARIA, C., MANGANO, M. G. & STRENG, M. 2014. A new phyllopod bed-like assemblage from the Burgess Shale of the Canadian Rockies. *Nature Communications* **5**, 3210.
- CHLUPÁČ, I. & HAVLÍČEK, I. 1965. *Kodymirus* n. g., a new aglaspid merostome of the Cambrian of Bohemia. *Sborník Geologických Věd, Paleontologie* **6**, 7–20.
- COTTON, T. J. & BRADDY, S. 2004. The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**, 169–93.
- GEHLING, J. G., JAGO, J. B., PATERSON, J. R., GARCÍA-BELLIDO, D. C. & EDGEcombe, G. D. 2011. The geological context of the lower Cambrian (Series 2) Emu Bay Shale Lagerstätte and adjacent stratigraphic units, Kangaroo Island, South Australia. *Australian Journal of Earth Sciences* **58**, 243–57.
- GOLOBOFF, P. A., FARRIS, J. S. & NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–86.
- HOU, X. & BERGSTRÖM, J. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils & Strata* **45**, 1–116.
- HOU, X., CHEN, J. & LU, H. 1989. Early Cambrian new arthropods from Chengjiang, Yunnan. *Acta Palaeontologica Sinica* **28**, 42–52.
- LAMSDELL, J. C., STEIN, M. & SELDEN, P. A. 2013. *Kodymirus* and the case for convergence of raptorial appendages in Cambrian arthropods. *Naturwissenschaften* **100**, 811–25.
- LANKESTER, E. R. 1904. The structure and classification of Arthropoda. *Quarterly Journal of Microscopical Science* **47**, 523–82.
- LEGG, D. A. 2014. *Sanctacaris uncata*: the oldest chelicerate (Arthropoda). *Naturwissenschaften* **101**, 1065–73.
- LEGG, D. A., SUTTON, M. D. & EDGEcombe, G. D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications* **4**, 2485.
- ORTEGA-HERNÁNDEZ, J., BRADDY, S. J., JAGO, J. B. & BAILLIE, P. W. 2010. A new aglaspidid arthropod from the Upper Cambrian of Tasmania. *Palaeontology* **53**, 1065–76.
- ORTEGA-HERNÁNDEZ, J., LEGG, D. A. & BRADDY, S. J. 2013. The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics* **29**, 15–45.
- ORTEGA-HERNÁNDEZ, J., VAN ROY, P. & LEROSEY-AUBRIL, R. 2015. A new aglaspidid euarthropod with a six-segmented trunk from the Lower Ordovician Fezouata Konservat-Lagerstätte, Morocco. *Geological Magazine*, published online 30 October 2015. doi: [10.1017/S0016756815000710](https://doi.org/10.1017/S0016756815000710).
- PATERSON, J. R., GARCÍA-BELLIDO, D. C., JAGO, J. B., GEHLING, J. G., LEE, M. S. Y. & EDGEcombe, G. D. 2015. The Emu Bay Shale Konservat-Lagerstätte: a view of Cambrian life from East Gondwana. *Journal of the Geological Society*, published online 10 November 2015. doi: [10.1144/jgs2015-083](https://doi.org/10.1144/jgs2015-083).
- RAYMOND, P. E. 1935. *Leancoilia* and other Mid-Cambrian Arthropoda. *Bulletin of the Museum of Comparative Zoology at Harvard College* **76**, 205–30.
- STEIN, M., BUDD, G. E., PEEL, J. S. & HARPER, D. A. T. 2013. *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry. *BMC Evolutionary Biology* **13**, 99.
- STEIN, M., CHURCH, S. B. & ROBISON, R. A. 2011. A new Cambrian arthropod, *Emeraldella brutoni*, from Utah. *Paleontological Contributions* **3**, 1–9.
- STEIN, M. & SELDEN, P. A. 2012. A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and



- reassessment of its affinities. *Journal of Systematic Palaeontology* **10**, 361–83.
- VAN ROY, P. 2006. An aglaspigid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **96**, 327–50.
- WALCOTT, C. D. 1911. Cambrian geology and paleontology II. Middle Cambrian Merostomata. *Smithsonian Miscellaneous Collections* **57**, 17–40.
- WALCOTT, C. D. 1912. Cambrian geology and paleontology II. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. *Smithsonian Miscellaneous Collections* **57**, 145–229.