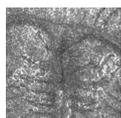


The morphology and affinities of *Skania fragilis* (Arthropoda) from the middle Cambrian Burgess Shale

DAVID A. LEGG



The enigmatic arthropod *Skania fragilis*, from the middle Cambrian (Series 3, Stage 5) Burgess Shale Formation (Yoho National Park, British Columbia, Canada), is redescribed based on 14 new specimens repositated at the Royal Ontario Museum. These specimens provide a clearer picture of the morphology of this taxon and help to resolve conflicting opinions regarding potential homology of particular features. Specifically, the anchor-shaped anterior, which has been compared to a similar structure in the putative Precambrian arthropod *Parvancorina*, is shown to represent an anterior cephalic doublure with features comparable to the mediolateral spines of marrellids, such as *Marrella*. Beyond a vaguely cordiform outline, no other features are shown to be shared between *Skania* and *Parvancorina*, weakening claims that crown-group arthropods were present in the Neoproterozoic. The removal of these taxa from Arthropoda is in keeping with recent molecular clock analyses, which demonstrate a Cambrian diversification of Euarthropoda. A phylogenetic analysis resolved *Skania* as the most basal member of Acerostraca, a clade of marrellomorphs including *Vachonisia* and *Xylokorys*, united by the presence of a cordiform dorsal shield. Similarities between these taxa and marrellids may indicate that the elongate posterior spines of *Marrella* and related taxa, and the dorsal shield of acerostracans have a common origin akin to the carapace anlagen of extant crustaceans. • Key words: marrellomorph, carapace formation, Burgess Shale.

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Since its original description in the posthumous manuscript of Walcott (1931), discussion regarding the affinities of the enigmatic arthropod *Skania fragilis*, from the middle Cambrian (Series 3, Stage 5) Burgess Shale Formation of British Columbia, has been equivocal. Although originally comparisons were made to *Marrella*, *Burgessia*, and *Naraoia*, notes associated with the original publication indicate that Walcott considered *Skania* to be a trilobite (Resser in Walcott 1931). This interpretation was followed by Størmer (1944) amongst others (e.g. Hupé 1953), who, based on the pliable nature of its exoskeleton, suggested it might represent a larval stage presumably of another Burgess Shale trilobite. Harrington (1968, p. O99), however, dismissed trilobite affinities for *Skania*, noting “[it] does not resemble any known trilobite meraspis”, although an alternative affinity was not proffered. A similar conclusion was also reached by Delle Cave & Simonetta (1975). They undertook a restudy of the 29 specimens assigned to *S. fragilis* by Walcott (1931) and concluded that only eight specimens were valid, none of which showed unequivocal arthropod features such as arthropodized appendages and

segmentation. Instead, Delle Cave & Simonetta (1975) emphasised similarities between *Skania* and the Precambrian *Parvancorina*, particularly pertaining to the putative guts of these taxa which were both considered to be anchor-shaped. Glaessner (1980) reaffirmed arthropod affinities for *Parvancorina* based in part on similarities to marrellomorphs, such as the shield-like carapace of *Vachonisia*. He was, however, sceptical of a close relationship between *Parvancorina* and *Skania*, a view not shared by many later workers (e.g. Gehling 1991, Conway Morris 1993, Simonetta & Insom 1993). In a subsequent phylogenetic analysis, Waggoner (1996) resolved *Parvancorina* as a stem-group arthropod, but considered *Skania* to represent a “true” arthropod due to its resemblance to purported protaspids of *Naraoia* from the Lower Cambrian Chengjiang biota (Hou *et al.* 1991). These supposed naraoiid larva where later assigned to their own genus and species, *Primitarica larvaformis* (Zhang *et al.* 2003), which, along with *Parvancorina* and *Skania*, were placed in the Parvancorinomorpha, as were other potential Precambrian arthropods and tentatively the Devonian *Vachonisia* (Lin *et al.* 2006).

This clade was thought to represent an incipient stage in the development of arachnomorph tagmosis. Similar topologies have not been recovered in recent phylogenetic analyses (Legg *et al.* 2012, 2013), which have instead resolved marrellomorphs, including *Skania* and *Vachonisia*, as stem-lineage mandibulates, although admittedly *Parvancorina* and other putative Precambrian arthropods were not included in these analyses. To resolve this phylogenetic confusion new specimens of *Skania fragilis* are described herein. These specimens are used to build a more complete picture of its morphology, which will aid in determining its phylogenetic affinities.

Materials and methods

The specimens deposited at the ROM were examined using a Nikon SMZ1500 binocular microscope with a drawing tube attached. All specimens, including the holotype, were photographed using a Canon EOS 5D Mark II digital SLR camera equipped with Canon macro lenses (EF 100 mm f/2.8 Macro and MP-E 65 mm f/2.8 1-5x Macro Photo) with a polarizing filter. A variety of lighting conditions were used, however the best results were obtained when using low-angle cross polarized light with specimens immersed in water (Schaarschmidt 1973, Bengtson 2000, Crabb 2001).

Phylogenetic analysis

Although *Skania fragilis* has been included in prior phylogenetic analyses of arthropods (*e.g.* Legg *et al.* 2012, 2013), character coding was based solely on previous descriptions and interpretations of this taxon, particularly those of Delle Cave & Simonetta (1975), and Lin *et al.* (2006). This taxon was thus recoded into an updated version of the Legg *et al.* (2013) data set (with subsequent modifications from Siveter *et al.* 2014), based on the examination and interpretation of new material presented herein, as were other non-marrellid marrellomorphs, namely *S. sundbergi* Lin *et al.* 2006, *Primicaris* Zhang *et al.* 2003, an undescribed acercostracan from Morocco (Van Roy *et al.* 2010), and the acercostracans *Xylokorys* Siveter *et al.* 2007, and *Vachonisia* (Kühl *et al.* 2008). A single character, “fusion of paratergal fold into a dorsal shield” (formerly character 69 of Legg *et al.* 2013), was removed from the original data set to account for observations made herein resulting in a total data set of 315 taxa and 752 characters (see online supplementary material).

The data set was converted into NEXUS file format (available as online supplementary material) and analysed using TNT v. 1.1. (Goloboff *et al.* 2008). All characters

were treated as non-additive and weighted using both equal character weighting and implied weighting with a variety of concavity constants ($k = 2, 3, 10$). Most Parsimonious trees (MPTs) were found using New Technology search options with 100 Random Addition Sequences using Parsimony Ratchet (Nixon 1999), Sectorial Searches, Tree Drifting and Tree Fusing (Goloboff 1999).

Systematic palaeontology

Unnamed rank Marrellomorpha Beurlen, 1930

Order Acercostraca Lehmann, 1955

Emended diagnosis. – Arthropod possessing an extensive cordiform carapace covering all appendages (emended from Tasch 1969).

Included taxa. – *Skania* Walcott, 1931, *Primicaris* Zhang *et al.*, 2003, “*Skania*” *sundbergi* Lin in Lin *et al.*, 2006, and *Vachonisiidae* Tasch, 1969.

Plesion (genus) *Skania* Walcott, 1931

Type species. – *Skania fragilis* Walcott, 1931 (by monotypy).

Emended diagnosis. – Arthropod with a cordiform carapace with an anterior doublure bearing lateral spines, and possessing elongate spines and slight serration on its postero-lateral edge, plus crescent-shaped anterior diverticulae extending into elongate lateral diverticulae with medially projecting secondary rami (emended from Lin *et al.* 2006).

General dimensions. – Specimens range in size from 7.5 mm (ROM 63029) to 13.5 mm (ROM 63027, 63032, 63034, and 63035), measured sagittally, and between 9 mm (USNM 83950) and 11.5 mm (ROM 63027 and 63032), measured transversely. Despite this variation in size, all specimens retain a width to length ratio of 1:1.2. The posterior spines measure between 10 and 15 percent of the total body length, except in the smallest individual, ROM 63029, in which they account for 20 percent of the total body length.

Remarks. – The diagnosis of Lin *et al.* (2006) was based, in part, on the assignment of “*Skania*” *sundbergi* to this genus, however, this taxon differs significantly from *S. fragilis*, perhaps indicating they should be placed in separate genera. For this reason the diagnosis of *Skania* is restricted to *S. fragilis*, pending further study of “*S.*” *sundbergi*.

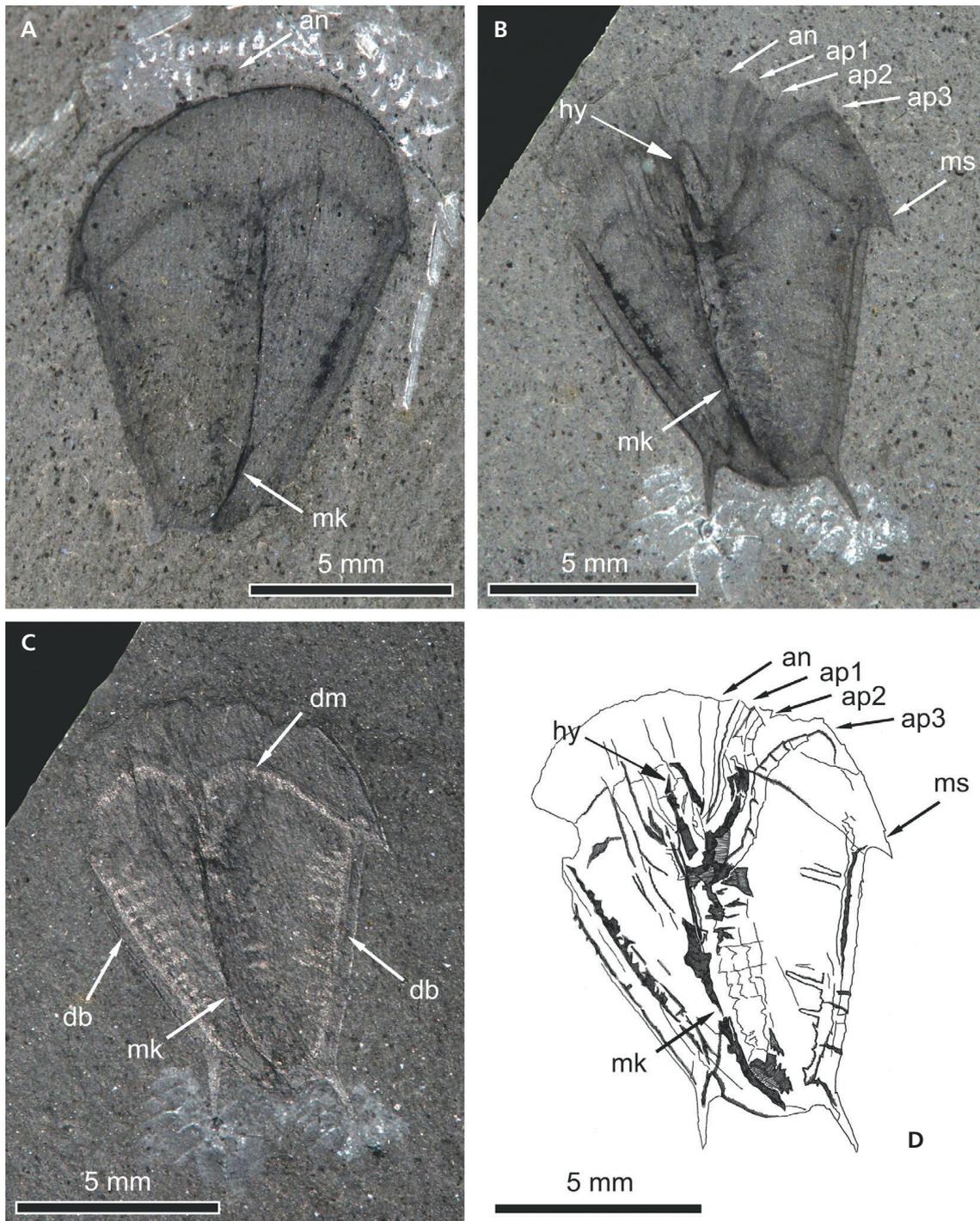


Figure 1. Holotype of *Skania fragilis* Walcott, 1931 (USNM 83950). • A, B – part and counterpart photographed using cross polarised light. • C – counterpart photographed using plain polarised light. • D – camera lucida drawing of the counterpart. Abbreviations: an – antenna, ap1-3 – appendages 1–3, db – doublure-like structure, dm – posterior margin of the doublure, hy – hypostome, mk – medial keel, ms – mediolateral spine.

Specimens

Fifteen specimens of *Skania fragilis* were examined: 14 undescribed specimens reposit at the Royal Ontario Museum (ROM), Toronto, Canada, and the holotype reposit

at the Smithsonian National Museum of Natural History, Washington DC, USA. All material was excavated from exposures of the middle Cambrian (Series 3, Stage 5, *Bathyriscus-Elrathina* Zone) Burgess Shale Formation situated along Fossil Ridge in Yoho National Park (British

Columbia, Canada). The holotype, USNM 83950 (Fig. 1), was recovered from the Walcott Quarry exposure (formerly USNM locality 35k) of the Walcott Quarry Shale Member (*Pagetia bootes* Subzone). Of the remaining specimens, 11 (ROM 60752, 63022, 63026, and 63028–63035; Figs 2C, E–H, 3) originated from the Raymond Quarry exposure of the Raymond Quarry Shale Member (*Pagetia walcotti* Subzone), and three (ROM 63023, 63025, and 63027; Fig. 2A, B, D) from the associated talus. Other specimens assigned to *S. fragilis*, reposit at the USNM and ROM, were also examined but no diagnostic characteristics were observed which might justify assignment to this taxon.

Morphological interpretation of *Skania fragilis*

Perhaps the most conspicuous feature of *Skania fragilis* is the cordiform dorsal shield (Figs 1–4). The exact composition of the dorsal shield has been unclear, specifically whether it is formed by the fusion of trunk tergopleurae, or represents a posterior outgrowth of the cephalic shield, *i.e.* a carapace (*sensu* Olesen 2013). Most previous works (*e.g.* Walcott 1931, Glaessner 1980, Lin *et al.* 2006, Rak *et al.* 2013) have favoured a trunk tergite derivation for the dorsal shield. Walcott (1931) thought the posterior dorsal shield was formed via the fusion of 14 or 15 segments whose borders were still evident. However, it was a lack of clear segmentation, which led Delle Cave & Simonetta (1975) to conclude *Skania* was not an arthropod. Nearly all specimens (Figs 2B–E, G, H, 3), including the holotype (Fig. 1), show delineations near the edge of the dorsal shield, which Walcott (1931) may have mistaken for segmental boundaries. However, these delineations are not part of the tergal exoskeleton and instead form part of a diverticulate network (Figs 3, 4). Lin *et al.* (2006) also suggested that the dorsal shield was formed of a single element and not composed of fused segments expressed as dorsal tergites, however, they did consider it essentially bipartite with an anterior “cephalic area” bearing genal spines and covering the antennae, and a fused posterior “trunk region” covering all other appendages. In their cladogram (Lin *et al.* 2006, fig. 9) the parvancorinomorphs, including *Skania*, were placed as sister-taxon to arachnomorphs based on the shared presence of a “pleural field”, the implication being that the dorsal shield was homologous to arachnomorph tergites, although articulation was a later acquisition in the latter group. The so-called “cephalic area” of Lin *et al.* (2006), is herein interpreted as an anterior cephalic doublure, akin to that of artiopodans. USNM 83950 (Fig. 1C), ROM 63026 (Fig. 2C), and ROM 60752 (Fig. 3A) demonstrate that a delineation (or the posterior margin of the doublure, labelled “dm”), is present anterior

of the diverticulae and first appendage pair (*contra* Lin *et al.* 2006). The association of the lateral spines with the anterior cephalic doublure (Figs 1, 2B, E, 3A, C–E) makes them unlike genal spines, as they have previously been identified (*e.g.* Walcott 1931, Lin *et al.* 2006), which are usually post-appendicular and associated with the posterolateral margins of the cephalon (Harrington 1968). Instead, they are more comparable to the mediolateral spines of marrellid marrellomorphs (Rak *et al.* 2013), which are pre-appendicular (García-Bellido & Collins 2006), and form part of a crescent-shaped anterior cephalon.

The extensive diverticulae of *Skania* have received considerable attention (*e.g.* Walcott 1931, Størmer 1944, Hupé 1953). In the majority of specimens the anterior diverticulae arch laterally in a contiguous line with the posterior boundary of the doublure (*e.g.* Fig. 3C). These lateral diverticulae originate from a medial triangular node (Fig. 3F), and continue posteriorly with the outer margin running parallel to the lateral margins of the dorsal shield (Fig. 3). The outer margins of these diverticulae give the impression of a marginal rim bordering the dorsal shield, however, a distinctive rim is lacking as evidenced by specimens lacking distinctive diverticulae, in particular ROM 63023 (Fig. 2A), however, a doublure-like structure can be observed in some specimens, *e.g.* USNM 83950 (Fig. 1) and ROM 63029 (Fig. 3C). Each lateral diverticula possesses a series of secondary channels which project perpendicular to the main diverticular axis towards the medial axis of the specimen (Fig. 3). The most anterior secondary diverticulae show noticeable curvature towards the anterior of the specimen (*e.g.* Fig. 3A, C) and may show additional branching (Fig. 3D). A putative gut runs from the triangular node to the posterior margin of the dorsal shield (Fig. 3F). The position of the mouth is uncertain but was presumably located at the posterior end of the hypostome (Fig. 1B).

The nature of the lateral diverticulae is unclear. Although they seem to connect to a putative gut structure it is possible they are associated through superposition rather than genuinely connected. ROM 63022 (Fig. 3B) shows differential preservation of the diverticulae and the putative gut, the latter is preserved in noticeable relief whereas the diverticulae are not. Furthermore, when some specimens were photographed using polarised light the lateral diverticulae and appendages became reflective, whereas the putative gut remained dull (Figs 1A, 3F). A reflective film is also preserved around the main body axis (Figs 2C, 3F). This area, and associated material in the appendages may indicate a cardiovascular nature, however, it resembles no other arthropod circulatory system. The diverticular network shows similarities to the ramified gut diverticulae of *Burgessia* (Hughes 1975) and *Naraoia* (Vannier & Chen 2002). Such diverticulae are restricted to the cephalic regions of these taxa, which in *Burgessia* shows considerable overlap of the trunk somites (Hughes

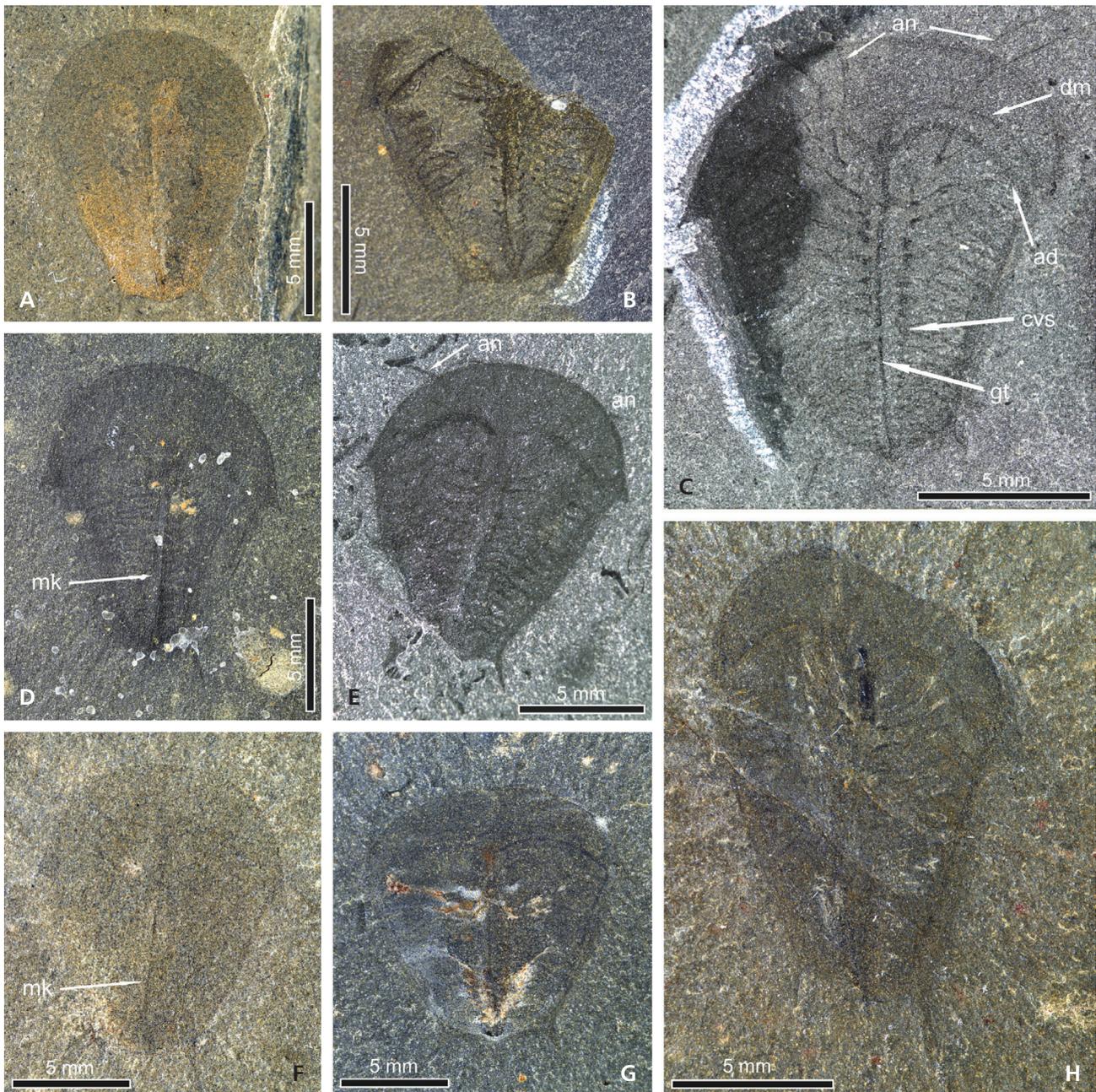


Figure 2. New specimens of *Skania fragilis* Walcott, 1931, from Raymond Quarry. All photographed using cross-polarised light. • A – ROM 63023. • B – ROM 63025. • C – ROM 63026. • D – ROM 63027. • E – ROM 63028. • F – ROM 63032. • G – ROM 63033. • H – ROM 63035. Abbreviations: ad – anterolateral diverticula, an – antenna, cvs – cardiovascular system, dm – posterior margin of the doublure, gt – gut, mk – medial keel-like structure.

1975), akin to a crustacean carapace (Olesen 2013). The similar arrangement in *Skania* may indicate that the dorsal shield represents a carapace that has become fused to the trunk, much as it is in extant malacostracans (Olesen 2013), rather than the fused pleurotergites of the trunk. Further support for this hypothesis comes from comparisons with other taxa bearing a dorsal shield, particularly *Vachonisia*, which early in ontogeny possesses a rounded dorsal shield, which becomes more cordiform and develops considerable

posterior expansions later in development (Kühl *et al.* 2008). A similar mode of development is shown by the carapace of the notostracan *Triops cancriformis*, which also develops considerable posterior expansions during later growth stages (Olesen & Møller 2014).

The morphology of the appendages of *Skania* has had only vague mention in previous works (*e.g.* Walcott 1931, Lin *et al.* 2006). These studies recognised putative antennae in the holotype and poorly preserved thoracic

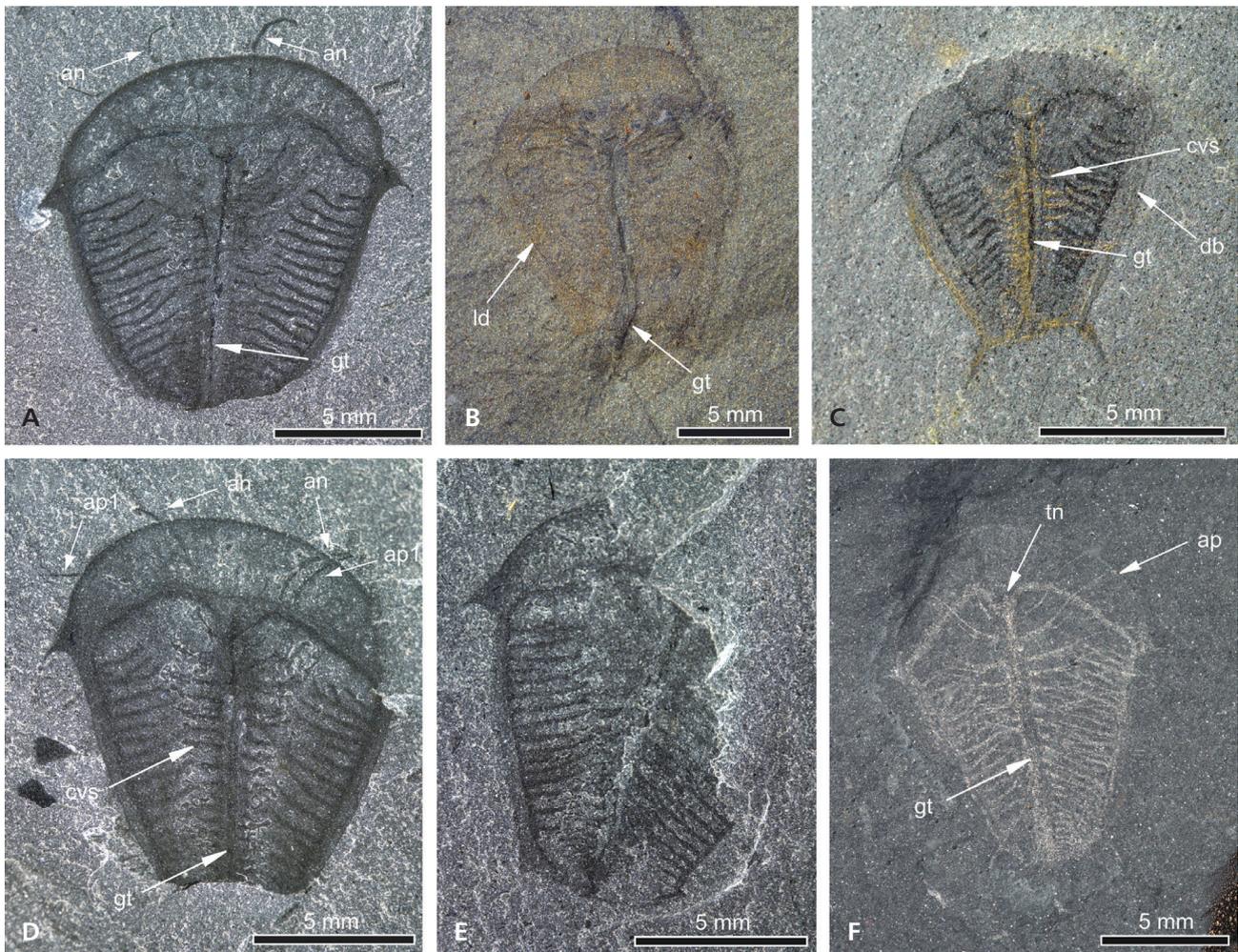


Figure 3. Digestive structures in new specimens of *Skania fragilis* Walcott, 1931. • A – ROM 60752. • B – ROM 63022. • C – ROM 63029. • D – ROM 63030. • E – ROM 63031. • F – ROM 63034. Abbreviations: ap – appendage, cvs – cardiovascular system, db – doublure-like structure, gt – gut, ld – lateral diverticula, tn – triangular node.

endopods. In fact, *Skania* appears to possess two sets of differentiated appendages. The anterior appendages are elongate and sigmoidal, extending beyond the anterior boundary of the cephalon (Figs 1B, 2C, 3A, D, F). At least five pairs are present, the anterior four of which abut an elongate labrum-like structure (Fig. 1B). Podomere boundaries are best observed in the holotype, in which the anterior-most appendage pairs possess small, sub-quadrate podomeres (Fig. 1A), and the more posterior sigmoidal appendages possess elongate, subrectangular podomeres (Fig. 1B). The arrangement of the anterior appendages, particularly their sigmoidal nature resembles the cephalic exopods of other acercostracans, particularly *Vachonisia* and *Xylokorys*. The posterior trunk appendages are differentiated from the cephalic appendages in being shorter, *i.e.* not extending beyond the carapace margins, and they show a lesser degree of curvature (Fig. 3A, D). Individual podomeres could not be observed.

Discussion

The status of Precambrian “arthropods”

Skania has frequently been linked to so-called Precambrian “arthropods”, particularly *Parvancorina* (Gehling 1991, Simonetta & Insom 1993, Lin *et al.* 2006), and thus potentially represents a late surviving member of a Precambrian body plan (Conway Morris 1993). Few phylogenetic analyses have possessed the taxon coverage to explore possible relationships of these taxa, as those including a variety of putative Precambrian arthropods have excluded *Skania* (*e.g.* Waggoner 1996), or vice versa (*e.g.* Legg *et al.* 2012, 2013). A notable exception is the phylogenetic analysis of Lin *et al.* (2006), which included both *Skania*, and a handful of Precambrian “arthropods”, namely *Mialsemia* (= *Bomakellia sensu* Dzik 2002), *Vendia*, *Praecambrium*, and *Parvancorina*. Such limited taxon sampling was

guaranteed to resolve *Skania* as an ingroup parvancorinomorphic and therefore does not represent a reliable test of affinities. The singular ingroup taxon, Parvancorinomorpha encompasses *Skania*, *Vendia*, *Praecambridium*, and *Parvancorina*, and was erected based on the shared presence of an anchor-shaped anteromedial ridge (Lin *et al.* 2006). The validity of this group therefore relies on reliable homology of these anchor-like structures. In *Skania* this anchor is composed of the anterior doublure and the medial keel on the carapace. This keel is weakly developed in *S. fragilis* (Figs 1, 2D) but more prominent in “*S.*” *sundbergi*, however it is not attached to the anterior doublure (Lin *et al.* 2006, fig. 2e–h). By contrast the anchor of *Parvancorina* is set back from the “anterior” margin and is therefore unlikely to be homologous to the doublure-like structure in *Skania*. Once we remove this character the only other character linking *Skania* and *Parvancorina* is a cordiform outline, however, this feature in *Parvancorina* shows considerable ontogenetic and interspecific variation (Naimark & Ivantsov 2009), and despite previous claims (Lin *et al.* 2006), does not show a similar growth trajectory to *Skania* (Naimark & Ivantsov 2009).

Analyses linking these taxa also relied heavily on the identification of appendages in *Parvancorina* (Glaessner 1980). These appendages were reported as attaching to the anterior anchor-shaped ridge (Glaessner 1980), unlike any known arthropod, which instead typically show considerable antero-posterior alignment of appendages and segments (Ortega-Hernández & Brena 2012), as seen in *Skania* and non-Precambrian “parvancorinomorphs”. Such patterning is caused by antero-posterior gene expression domains that show little or no relative lateral displacement (Ortega-Hernández & Brena 2012). This also weakened likely relationships between arthropods and taxa possessing glide reflection symmetry such as *Vendia*, and *Praecambridium* (Ivantsov 2001).

The removal of Precambrian “arthropods” from Arthropoda is in keeping with recent molecular clock estimates that indicate a Cambrian, rather than Precambrian, diversification of crown-group arthropods (Lee *et al.* 2013, Rota-Stabelli *et al.* 2013).

The affinities of *Skania* and relationships within Marrellomorpha

Phylogenetic analysis with equal character weighting resulted in 14 Most Parsimonious Trees (MPTs) of 1839 steps (CI = 0.518; RI = 0.873), and implied weighted analyses with a concavity constant of two, three, and 10 produced 12 MPTs of 173.95755 steps (CI = 0.515; RI = 0.871), 25 MPTs of 140.71591 steps (CI = 0.515; RI = 0.871), and 19 MPTs of 63.35458 steps (CI = 0.517; RI = 0.872), respectively.

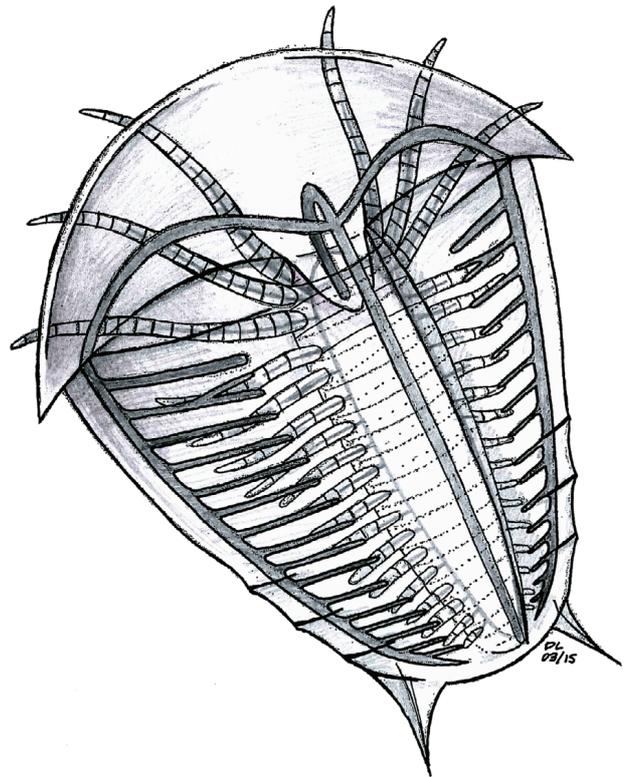


Figure 4. A reconstruction of *Skania fragilis* showing internal diverticular network.

Both inter- and intrarelations of *Skania* and the marrellomorphs were consistent over all iterations of the data set (Fig. 5). *Skania fragilis* resolved as the basal most member of a clade composed of *Primicaris*, “*S.*” *sundbergi*, and a polytomy including *Vachonisia*, *Xylokorys*, and an undescribed taxon from the Ordovician of Morocco (Van Roy *et al.* 2010). These taxa were all assigned to Parvancorinomorpha by Lin *et al.* (2006), however, the exclusion of vendiomorphs, particularly *Parvancorina*, from this clade renders this clade, as originally intended, polyphyletic. It also seems appropriate to reserve this clade name for a group including its namesake. The name Acercostraca was originally proposed for *Vachonisia* alone (Lehmann 1955) and was subsequently expanded to include *Xylokorys* (Rak *et al.* 2013), based on the shared presence of a cordiform dorsal shield (Siveter *et al.* 2007, Köhl *et al.* 2008). Both genera were also included in the family Vachonisiidae (Rak *et al.* 2013). Herein I propose retaining *Vachonisia*, *Xylokorys* and potentially the undescribed Moroccan acercostracan in Vachonisiidae and expanding Acercostraca to include those marrellomorphs which resolved closer to *Vachonisia* and *Xylokorys*, than to *Marrella*, *Furca* and *Mimetaster* (collectively = Marrellida), and possess a cordiform dorsal shield. Although the shape of the dorsal shield was not included as a character in the current analysis, this clade was supported by two

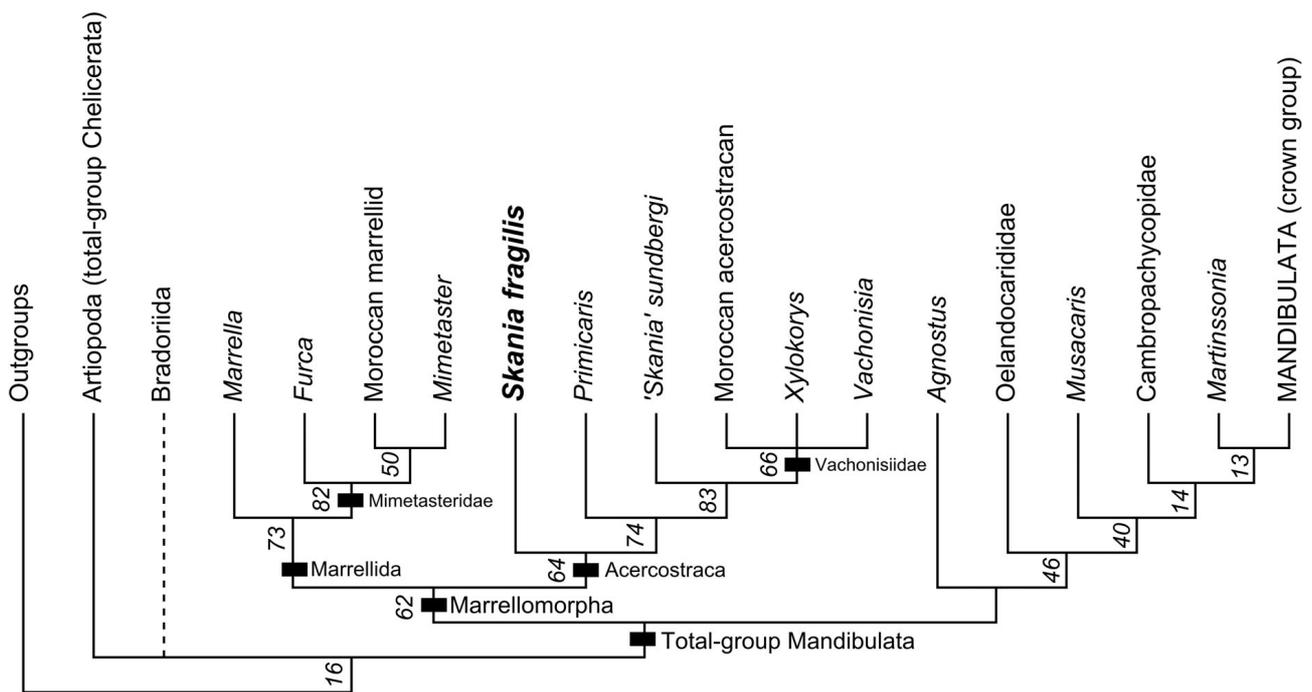


Figure 5. The phylogeny of marrellomorph arthropods as resolved in this study. The position of Bradoriida was unstable under different character weighting schemes, either resolving as sister-taxon to Artiopoda or total-group Mandibulata. Numbers associated with nodes are selected G/C frequency values produced under implied weighted searches with a concavity constant of three.

synapomorphies, the first of which was the presence of an expansive posterior carapace, and the second was the presence of an anterior cephalic doublure. Later taxa, namely *Vachonisia* and *Xylokorys* appear to have lost this doublure (Siveter *et al.* 2007, Köhl *et al.* 2008); this character resolved as a synapomorphy of Vachonisiidae, as did the presence of an anterior cephalic notch.

Skania fragilis, *Primicaris* and “*S.*” *sundbergi* resolved as successive plesions of Vachonisiidae, indicating “*S.*” *sundbergi* might not represent a species of *Skania*. Unlike *S. fragilis* and *Primicaris*, “*S.*” *sundbergi* lacks spines on the posterior margins of its dorsal shield, a feature it shares with vachonisiids and which resolved as a synapomorphy of a “*S.*” *sundbergi* + Vachonisiidae clade. “*S.*” *sundbergi* also differs from *S. fragilis* in possessing an expansive marginal rim on the dorsal shield and a significantly raised axial region. A lack of these features may be autapomorphies of *Skania fragilis*, although in the current analysis their presence resolved as synapomorphies of a clade including all acerrostracans to the exclusion of *S. fragilis*. Given the numerous differences between *S. fragilis* and “*S.*” *sundbergi* it seems appropriate to refer the latter to a new genus, however, I refrain from doing so at this time, pending a formal re-study of “*S.*” *sundbergi*.

A close relationship between the acerrostrans and marrellids has been recognised for a long time (Stürmer & Bergström 1976). In particular, workers have drawn atten-

tion to similarities in abdominal and cephalic appendage morphology (Lehmann 1955, Stürmer & Bergström 1976, Wills *et al.* 1998, Köhl *et al.* 2008). The monophyly of Marrellomorpha was supported in the current analysis by four synapomorphies: 1) a lack of paratergal pleurae, 2) an elongate trunk composed of more than 25 segments, 3) elongation of the cephalic exopods, and 4) the possession of rounded trunk endopod endites. The latter three characters were also used to support the monophyly of Marrellomorpha by Rak *et al.* (2013), and they also included two additional characters: 1) the presence of multisegmented trunk exopods with 2) medially directed filamentous setae. These characters are also present in many stem-mandibulates and in the current analysis resolved as a synapomorphy of total-group Mandibulata (all euarthropods closer to Mandibulata than Chelicerata). A similar relationship has been advocated by others (Waggoner 1996; Schram & Koenemann 2004; Siveter *et al.* 2007; Legg *et al.* 2012, 2013).

Although a sister-taxon relationship between marrellids and acerrostracans is little disputed (although see Hou & Bergström 1997), they do show a number of features which are hard to homologise between these clades, particularly the nature of the dorsal cephalic shield which in marrellids possesses extensive mediolateral and posterolateral extensions, and in the acerrostracans is expanded into a cordiform dorsal shield. The presence of lateral spines associated with a doublure in *Skania* increases

similarities between acercostracans and marrellids, however, it does little to inform on the ancestral morphology of Marrellomorpha, specifically whether the plesiomorphic condition of the clade is the possession of elongate cephalic spines or an expansive dorsal shield. Simonetta & Delle Cave (1981) hypothesised that the cephalon of marrellids evolved via the “erosion” of a *Vachonisia*-like carapace (although see Van Roy 2006 for a different hypothesis). A similar hypothesis is proposed herein. The presence of a posteriorly expansive carapace in other members of the mandibulate stem-lineage, such as *Henningsmoenicaris* (Haug *et al.* 2010) may indicate this represents the primitive condition of Marrellomorpha. If this is the case then the marrellids have secondarily lost their carapace. In extant crustaceans the carapace is formed from two posterior cephalic anlagen which fuse to form a shield like structure (Olesen 2013). The posteriolateral spines of marrellids may have formed from similar anlagen, in which case the serrated postero-lateral spines of *Marrella* and the serrated carapace margin of *Skania* may serve as another character linking these taxa.

Supplementary data

Appendix A – character list (www.geology.cz/bulletin/supplement/1532_Legg%20_APP_A.pdf).

Appendix B – supporting information for the phylogenetic analysis (www.geology.cz/bulletin/supplement/1532_Legg_APP_B.txt).

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