A revision of the Late Ordovician marrellomorph arthropod *Furca bohemica* from Czech Republic

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The enigmatic marrellomorph arthropod *Furca bohemica* from the Upper Ordovician Letná Formation, is redescribed. Based on existing museum specimens and new material collected from the southern slope of Ostrý Hill (Beroun, Czech Republic), the morphology and taphonomy of *F. bohemica* is reappraised and expanded to produce a new anatomical interpretation. The previously distinct taxa *F. pilosa* and *Furca* sp., are synonymised with *F. bohemica*, the latter being represented by a tapho-series in which decay has obscured some of the diagnostic features. A cladistic analysis indicates close affinities between *F. bohemica* and the Hunsrück Slate marrellomorph *Mimetaster hexagonalis*, together forming the Family Mimetasteridae, contrary to previous models for marrellomorph internal relationships. As with other representatives of the group, the overall anatomy of *F. bohemica* is consistent with a benthic, or possibly nektobenthic, mode of life. The depositional setting of the Letná Formation indicates that *F. bohemica* inhabited a shallow marine environment, distinguishing it palaeoecologically from all other known marrellomorphs, which have been reported from the continental shelf.

Key words: Arthropoda, *Marrella*, *Mimetaster*, shallow marine, Letná Formation, Barrandian, Ordovician, Ostrý Hill, Czech Republic.

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Introduction

The Upper Ordovician (Sandbian) Letná Formation, located in the Prague Basin, contains one of the most fossiliferous and diverse assemblages of Early Palaeozoic invertebrates in the region. The quartzite beds of the Letná Formation have long been known to contain abundant fossil remains (Barrande 1846), most notably trilobites and brachiopods, but are also distinguished by the preservation of rare arthropods such as cheloniellids, bivalved ?phyllocarids and putative aglaspidids (Chlupáč 1965, 1999a, b; Rak et al. 2009; Ortega-Hernández et al. 2010). Arguably one of the most unusual arthropods from this formation is *Furca bohemica* Fritsch, 1908. Despite being known for over a century (e.g., Hawle and Corda 1847), this taxon has only recently (Van Roy 2006) been unequivocally recognized as a member of the Marrellomorpha, a group of arthropods which includes forms known only from sites with exceptional preservation such as *Marrella splendens* Walcott, 1912, from the middle Cambrian Burgess Shale (Whittington 1971; García-Bellido and Collins 2006) and also from the middle Cambrian Kaili Formation (Zhao et al. 2003), *Mimetaster hexagonalis* (Gürich, 1931) and *Vachonisia rogeri* (Lehmann, 1955) from the Lower Devonian Hünsruck Slate (Gürich 1932; Stürmer and Bergström 1976; Kühl et al. 2008; Kühl and Rust 2010), and *Xylokorys chledophilia* Siveter, Fortey, Sutton, Briggs, and Siveter, 2007 from the Silurian Herefordshire Lagerstätte (Siveter et al. 2007; Kühl et al. 2008).

Remains of *F. bohemica* were initially discovered by Joachim Barrande who, despite not formally publishing the find, labelled specimens in the National Museum of Prague as this taxon. These specimens were subsequently mentioned in the "*Thesaurus siluricus*" (Bigsby 1868), but no illustration was provided. Hawle and Corda (1847) were the first to illustrate *F. bohemica*, interpreting it as the hypostome of the trilobite *Prionocheilus pulchrum mendax* (Vaněk 1965) (previously *Pharastoma pulchrum* Barrande, 1852). Fritsch (1908a, b) formally described *F. bohemica* as a separate taxon. He re-

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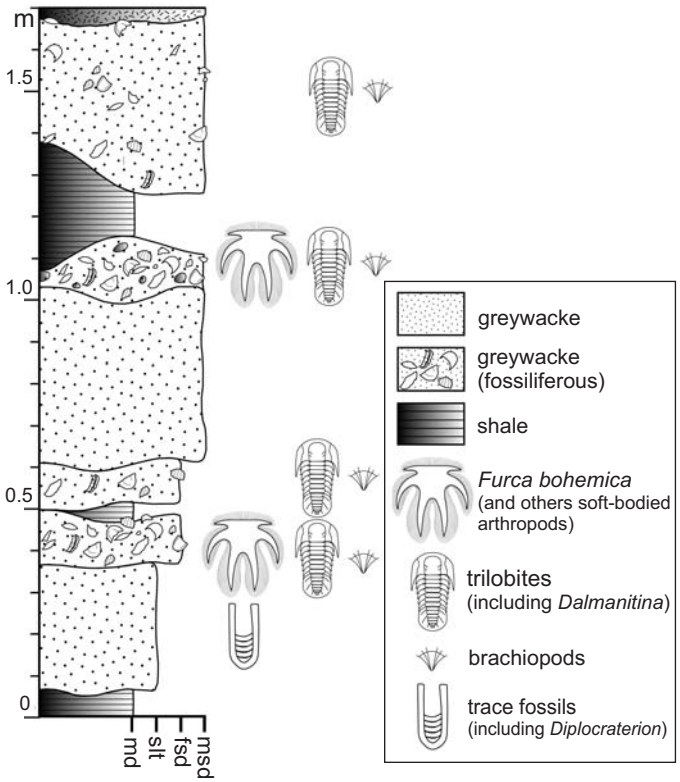

Fig. 1. Stratigraphic section of the Letná Formation at Ostrý Hill. Abbreviations: md, mudstone; slt, siltstone; fsd, fine sandstone; msd, medium sandstone.

interpreted *F. bohemica* as a juvenile echinoderm, and considered the raised area in the centre of specimens as an attachment site for a crinoid-like holdfast. It was not until the description of *Ma. splendens* that Perner (1919) recognised *F. bohemica* as the head shield of an unusual arthropod, having previously compared it to a trilobite pygidium (Perner 1918). *F. bohemica* was overlooked for almost 80 years, until Chlupáč (1999a, b) revised material from Ostrý Hill near Beroun, housed at the National Museum of Prague. From this collection, Chlupáč (1999a) defined a second species, *Furca pilosa*, which differs from the type species by the possession of a fringe of elongate secondary spines. Although Chlupáč (1999a) adopted Perner's (1919) interpretation of *Furca* as a marrellomorph arthropod, he did not rule out the possibility that it could represent the hypostome of the cheloniellid *Duslia insignis* Jahn, 1893, by virtue of the spinose outline characteristic of both taxa.

The discovery of a new fossiliferous locality by ŠR and Filip Novotný in the vicinity of Beroun (Barrandian area, Czech Republic) has resulted in additional collections of abundant new material, thus prompting a revision of the morphology and taphonomy of *F. bohemica*. The phylogeny and palaeoecology of *F. bohemica* are also reappraised in order to encompass recent advances in marrellomorph relationships and functional morphology.

Institutional abbreviations.—MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; NHMW, Natural History Museum in Vienna, Austria; NML, National Museum of Prague, Czech Republic; YPM, Yale Peabody Museum, New Haven, USA.

Geological setting

New specimens of *F. bohemica* (n = 31) were found by ŠR and other collectors in a recently discovered section of the Letná Formation (Havlíček 1998) on the southern slope Ostrý Hill in Beroun and in a debris of the classical site Veselá Gorge (Beroun District, Central Bohemian Region) (see Chlupáč 1965, 1999a for locality details). The Letná Formation consists of thick, complex layers of sandstone, greywacke, siltstone and pelitic shale deposited within a shallow, near-shore basin (Kukal 1958, 1963). The presence of dark shale and siltstone layers in the studied section (Fig. 1) indicates that it belongs to the upper part of the Letná Formation (Röhlich 1960), which is considered Sandbian (Late Ordovician) in age (Havlíček and Vaněk 1966).

Preservation and taphonomy

Fossil preservation in the Letná Formation commonly consists of internal and external moulds of generally disarticulated metazoans, including arthropods, brachiopods, molluscs, conulariids, and echinoderms, frequently associated with sandstone or quartzite layers (Chlupáč 1965, 1999a). Heavily biomineralized organisms, such as trilobites (mainly *Dalmanitina socialis* Barrande, 1846 and *Deanaspis goldfussi* Barrande, 1846), are covered by a substantial layer of limonite that replaces the calcium carbonate fraction of the exoskeleton, giving them a characteristic bright orange colouration and three-dimensional preservation. Non-biomineralized or thin-shelled animals (e.g., *Duslia* Jahn, 1893; *Drabovaspis* Barrande, 1872), on the other hand, display minute amounts of the aforementioned ore (Chlupáč 1988; Ortega-Hernández et al. 2010), have a less homogeneous colour and show little relief. The preservation of *F. bohemica* is more akin to that of non-biomineralizing organisms (Chlupáč 1999a) (Figs. 2–6).

With the exception of specimens NML 32998 (Fig. 3A, B) and NML 33001 (Fig. 3B, C), which are preserved in fine sandstone, most of the studied material is preserved in medium to coarse sandstone, predominantly in convex relief; the few concave specimens available (e.g., Figs. 3C, 5B, E, H, 6B) were collected in association with their counterparts. In most cases, the outline of the fossils is clearly defined by the contrast of its colour and relief with the surrounding matrix. Additional features of the cephalic shield, such as the axial sulcus and secondary spines, are preserved with varying degrees of slight three-dimensionality (Figs. 2B, C, 3A–C, 5C, E, F; 6B). In internal moulds, the central region of the cephalic shield is consistently the most convex and intact structure, while the

Fig. 2. The marrellomorph arthropod *Furca bohemica* Fritsch, 1908 from the Upper Ordovician (Sandbian) of Bohemia (Ostrý Hill and Veselá, Beroun District). **A**. NML 32991. **B**. NML 32992. **C**. NML 32993. **D**. NML 32994a. **E**. NML 32994b. **F**. NML 32995. **G**. NML 32996. **H.** NML 32997. **I**. NML 33000. Scale bars 10 mm.

primary spines are often broken and/or eroded to various degrees, giving them a much flatter appearance (e.g., Figs. 2A, B, F–H, 3B, 6C).

An interesting morphological and colouration bias can be observed in several weathered specimens. In these cases, the cephalic shields are mostly devoid of complete secondary spines, but instead possess a dark halo that shrouds the fossil's outline (Figs. 2A, D–F, H, 3D, E). A closer inspection of this region demonstrates the presence of numerous triangular stubs on the margins of the cephalic shield (Fig. 5E), which are identical to the bases of the well-preserved secondary spines in specimen NML 32998, the latter notable in not displaying the different colour patterning (Fig. 3A). Chlupáč (1999a) interpreted the different colouration as a result of Mn

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and/or C. Considering the mould preservation of the fossils in coarse sandstone, the presence of any carbonaceous remains seem highly unlikely, and thus cannot account for the dark shade distributed exclusively around the specimens. Allen (2002) has shown that, in low Fe environments, iron haloes form in the sediment around decaying carcasses. Taking into consideration the widespread occurrence of limonite on the fossils (Chlupáč 1988), these observations suggest that the dark halo may have a ferric composition, and have originated as a consequence of the initial stages of decay of the most distal and fragile regions of the body, the secondary spines. In the case of specimen NML 23998 (Fig. 3A), it appears that decay was minimum, as evidenced by the remarkably pristine morphology of the delicate secondary spines and the homogeneous colour of the cephalic shield with respect to the rock matrix. It is therefore proposed that the genus *Furca* in the Letná Formation consists of a single species that is represented by a tapho-series reflecting various stages of decay. As such, the distinction between *F. bohemica* and *F. pilosa* is an artefact of preservation, as the only character that differentiates these species is the length of the secondary spines. Chlupáč (1999a) also reported a specimen denominated *Furca* sp., described as lacking the anterolateral spines and the secondary spine fringe (Fig. 3C). This again consists of a typical *F. bohemica* specimen in which a more advanced degree of decay has stripped down the secondary spines from the margins, and the orientation of burial obscured the anterolateral spines.

Material and methods

A total of 49 specimens (including 12 counterparts) of *F. bohemica* were studied, including previously described material (Table 1). The fossils are preserved as low relief external moulds in coarse quartzites associated with a reddish-brown colouration due to weathering and the Fe content of the matrix (see Preservation); no curatorial preparation was performed. The specimens were photographed with a Nikon D80 digital camera fitted with a Sigma 50 mm Macro Lens; light source orientated from the NW with a 15°–45° inclination to enhance both colour and relief contrast.

Phylogenetic analysis.—A phylogenetic analysis of seven taxa and 16 characters (Table 2) was performed to test the monophyly of Marrellomorpha and to explore internal relationships amongst marrellomorph arthropods. Terminal taxa include all formally described species currently assigned to Marrellomorpha: *F. bohemica*, *Ma. splendens*, *Mi. hexagonalis*, *V. rogeri*, and *X. chledophilia*. Due to the uncertainties regarding marrellomorph affinities (Van Roy 2001, 2006; Kühl et al. 2008; Kühl and Rust 2010), two outgroup taxa were used, as per the recommendations of Barriel and Tassy (1998): the corynexochid trilobite *Olenoides serratus* (Rominger, 1887); and the nektaspid trilobitomorph *Naraoia compacta* Walcott, 1912. The data matrix was analysed us-

Table 1. Morphometric data of *Furca bohemica*. Asterisked are fragmentary structures. Abbreviations: 1, total length of head shield; 2, length of head shield minus primary spines; 3, width between tips of anterolateral primary spines; 4, maximum width of head shield; 5, minimum width of head shield between mediolateral and posterolateral primary spines; 6, width between tips of mediolateral primary spines; 7, width between tips of posteriolateral primary spines.

Specimen	Measurement type (mm)						
	1	2	3	4	5	6	7
NML 27715	31	15	19	29	11	31	9
NML CD 748–7845a, b	26	14	20	22	11	25	9*
NML CD 784–9413a, b	27	12	21*	26	11	25	9
NML 32990	21	9	18	21	9	23*	7
NML 32991	24	12	21	22	9	21	7
NML 32992	23	11	15	20	8	22	8
NML 32993	22	12	11	18	7	21*	8
NML 32994a, b	26	13	19	21	9	24	12
NML 32995	31	16	26	25	12	24	12
NML 32996	24	13	18	20	9	19	9
NML 32997	23	13	15	21	9	22	8
NML 32998	22	10	12	18	7	23	8
NML 32999	23	11	15	20	8	26	9
NML 33000	28	14	22	23	12	23	8
NML 33001a, b	26	14	11	21	12	22	9
NML 40860a, b	25	12	22	22	8	26	8
NML 40861	31	15	15*	–	11	–	10
NML 40862	26	13	16*	–	9	–	6*
NML 40863a, b	24	13	18	–	8	–	8
NML 40864a, b	26	13	19	22	9	23	9
NML 40865	27	13	–	24	10	23*	8
NML 40866	25*	12*	–	27	10	26	10
NML 40867	26	14	19	22	9	22	9
NML 40868	28	18	–	–	–	–	–
NML 40869	28	15	21*	–	10	–	7*
NML 40870	–	–	–	–	9	–	–
NML 40871	24	13	17*	20*	8	–	9
NML 40872a, b	27	13	19	22	10	25	8
NML 40873	28	14	–	–	10	–	8*
NML 40874	27	14	21	24	9	25	8
NML 40875	30	16	22*	23	10	23	9*
NML 40876a, b	–	–	–	–	8	23	9
NML 40877a, b	24	13	20	20	10	21	7
NML 40878a, b	–	–	–	–	10	–	9
NML 40879	26	14	19	22	9	22	9
NML 40881	23	11	19*	20	9	–	7
NML 40886	28	13	21	22	9	25	9

Table 2. Character matrix used for cladistic analysis. Question mark denotes uncertainty.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Olenoides serratus	0	?	?	?	–	0	1	1	0	0	0	0	0	0	0	0
Naraoia compacta	0	0	0	0	–	0	0	1	0	0	0	0	0	0	0	0
Marrella splendens	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1
Furca bohemica	**0**	**1**	**1**	**1**	**1**	**1**	**?**	**?**	**?**	**?**	**?**	**?**	**?**	**?**	**?**	**?**
Mimetaster hexagonalis	0	1	1	1	1	1	1	0	?	0	0	1	1	1	1	1
Vachonisia rogeri	1	0	0	0	–	0	0	1	1	1	1	1	1	1	1	1
Xylokorys chledophilia	1	0	0	0	–	0	0	1	1	1	1	1	1	1	1	1

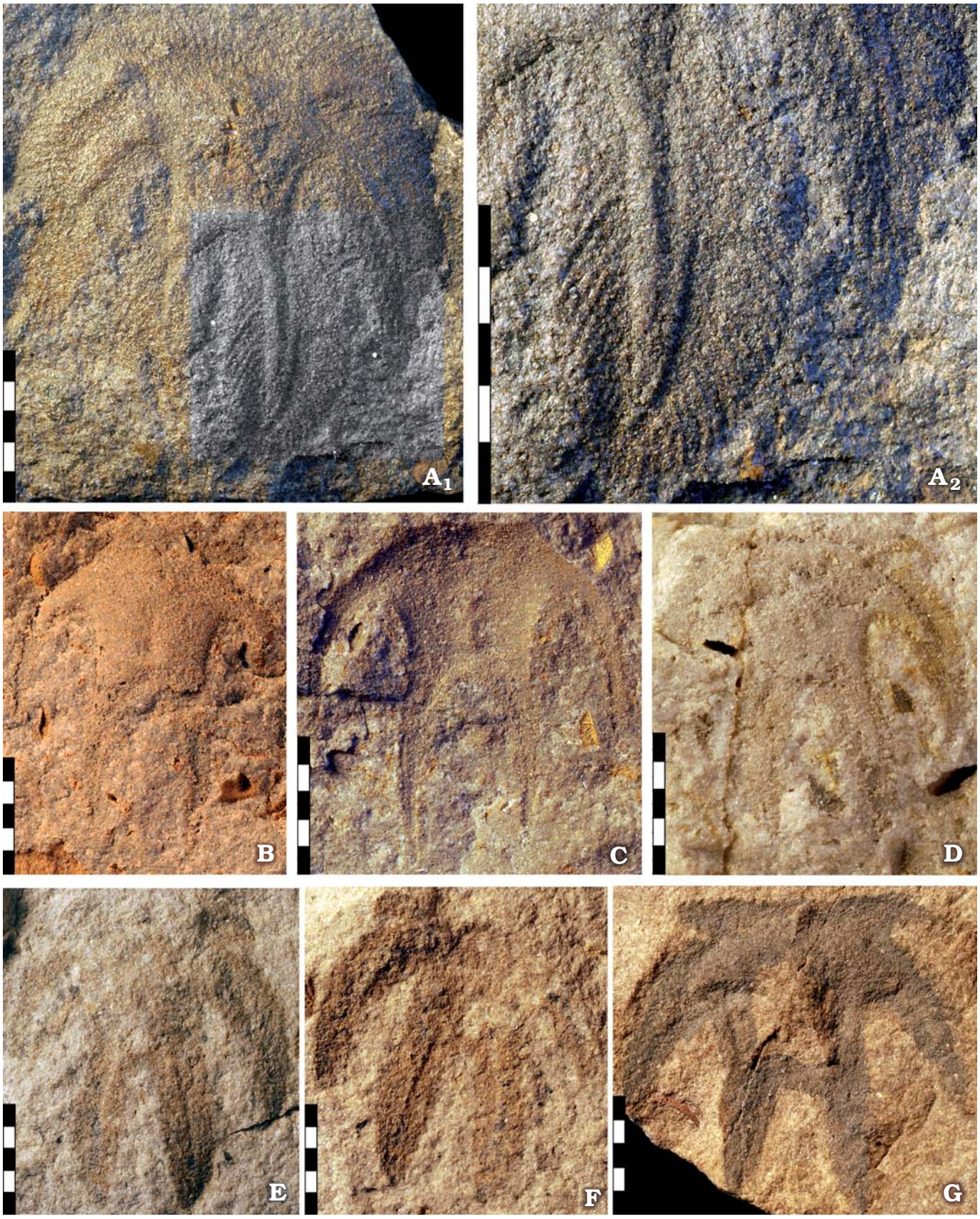

Fig. 3. The marrellomorph arthropod *Furca bohemica* Fritsch, 1908 from the Upper Ordovician (Sandbian) of Bohemia (Ostrý Hill and Veselá, Beroun District). **A**. NML 32998 (A_1) and detailed view (A_2). **B**. NML 33001a. **C**. NML 33001b. **D**. NML 40881. **E**. NML CD784-9143a. **F**. NML CD784-9143b. **G**. NML CD748-7845b. Scale bars 10 mm.

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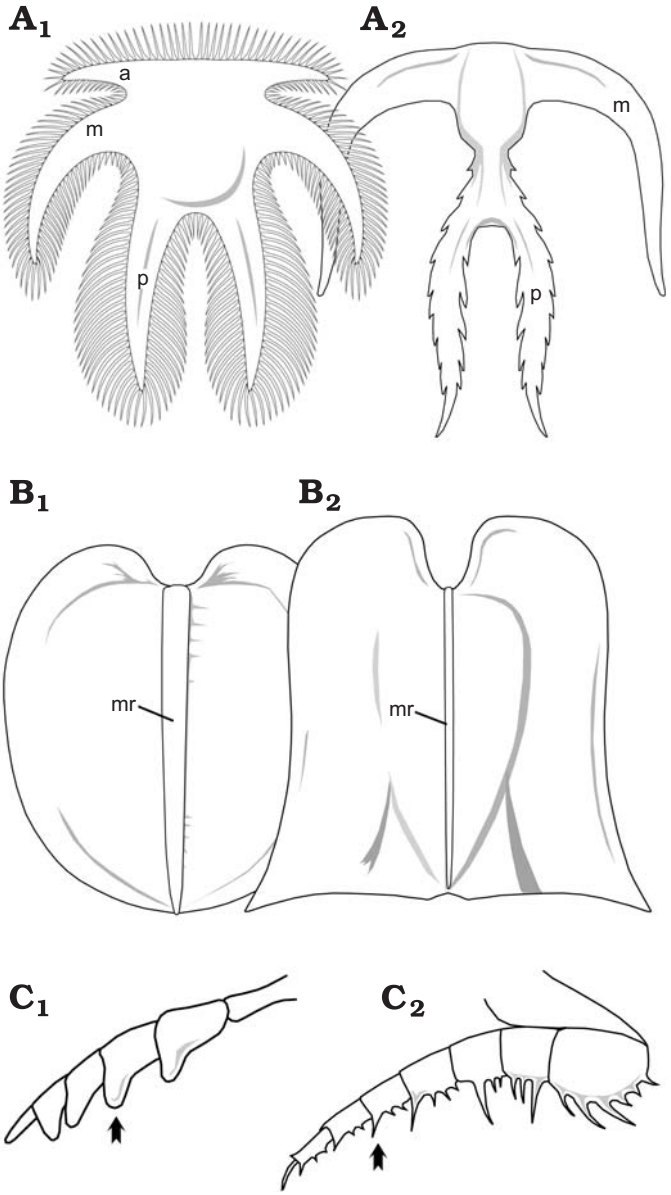

Fig. 4. Diagrammatic representations of character and character states. **A**. The cephalic morphology of the marrellids *Furca* (A_1) and *Marrella* (A_2). **B**. Morphological variation of the dorsal shield of the acercostracans *Xylokorys* (B_1) and *Vachonisia* (B_2). **C**. Comparison of the rounded endopod endites of *Marrella* (C_1: arrowed) and the spinose endites of *Olenoides* (C_2). Abbreviations: a, anterolateral spines; m, mediolateral spines; p, posterolateral spines; mr, median ridge.

ing TNT v. 1.1 (Goloboff et al. 2008) with an exact search (implicit enumeration), first with equal character weighting and subsequently with implied character weighting. During implied weighting the following convexity constants (k) were used: 1, 3, and 5. Nodal support was measured using Jackknife resampling (Farris et al. 1996) and Bremer support (Bremer 1994) for equally weighted trees, and Symmetric resampling (Goloboff et al. 2003) for implied weighted trees. Jackknifing used 1000 replicates, each a heuristic search with 100 random stepwise addition sequences and TBR branch swapping, with 36% deletion. Bremer support was calculated for suboptimal trees obtained during exact searches. Symmetric resampling used 1000 replicates each a heuristic search with a change probability of 33%.

Characters and coding.—Terminology for marrellomorph morphology follows Whittington (1971), and Stürmer and Bergström (1976), with the following exceptions: The anterior-most spines on the cephalic shields of *F. bohemica* and *Mi. hexagonalis* are herein referred to as anterolateral spines; the "lateral" spines of *Ma. splendens* (sensu Whittington 1971), are considered homologous to *F. bohemica*'s mediolateral spines and thus referred to as such (see character 3 for discussion); the posterior cephalic spines (including *Ma. splendens* "median" spines, sensu Whittington 1971) of all aforementioned taxa are referred to as posterolateral spines (Fig. 4A).

1. Single dorsal shield with ventral shelf and median ridge: (0) absent, (1) present. The head and trunk of *X. chledophilia* and *V. rogeri* are covered by a dorsal shield. Homology with other arthropod structures is unclear (Kühl et al. 2008), although Lin et al. (2006) considered the dorsal shield of parvancorinomorphs to be homologous. The dorsal shields of *X. chledophilia* and *V. rogeri* possesses a flat doublure on the edge outer margins of the dorsal shield (Fig. 4B), i.e., a ventral shelf (sensu Kühl et al. 2008), and a medial ridge-like structure. The latter is not to be mistaken with the "median keel" in the rostrum of *Mimetaster* (sensu Kühl and Rust 2010).

2. Anterolateral spines: (0) absent, (1) present. This and other characters that refer to the spines in the cephalic shield of marrellmorphs (characters 2–4) are coded as uncertain for *Olenoides*, as their relationship, if any, with the genal spines of trilobites cannot be reliably established.

3. Mediolateral spines: (0) absent, (1) present. The medial spines of *F. bohemica* are similar in morphology to the "lateral" spines of *Ma. splendens* (Fig. 4A) and are therefore considered homologous. Further evidence for the homology of the medial spines of *F. bohemica* and *Mi. hexagonalis* with the "lateral" spines of *Ma. splendens* comes from an aberrant specimen of the latter species that bears an additional pair of anterior spines (Whittington 1971: pl. 18: 3). This specimen has been interpreted by Van Roy (2006) as a possibly atavistic individual, thus suggesting that *F. bohemica* and *Mi. hexagonalis* display the plesiomorphic condition of this character. Under this scheme, the anterolateral spines (as defined herein) have been secondarily lost in *Ma. splendens*.

4. Posterolateral spines: (0) absent, (1) present.

5. Secondary spines: (0) absent, (1) present. The cephalic spines of *F. bohemica* and *Mi. hexagonalis* are fringed with delicate secondary spines. All specimens of *Ma. splendens* have serrated posterolateral spines (Whittington 1971; García-Bellido and Collins 2006), but no secondary spines are present (Fig. $4A_2$). The serration is not considered homologous to the secondary spines, as the latter appear to be separate from the cephalic shield and possibly detachable; a close relationship between the serrated edges of *Ma. splendens* and

the triangular bases of the secondary spines observed in *F. bohemica* remains a possibility.

6. Inflated cephalic shield: (0) absent, (1) present. The cephalic shields of *F. bohemica* and *Mi. hexagonalis* have a raised central area. In *Mi. hexagonalis* this area is associated with a pair of median eyes.

7. Compound eyes: (0) absent, (1) present.

8. Biramous cephalic appendages: (0) absent, (1) present.

9. Cephalic exopods much longer than the endopods: (0) absent, (1) present. The cephalic exopods of *V. rogeri* (Kühl et al. 2008), and *X. chledophilia* (Siveter et al. 2007) are considerably longer than their corresponding endopods. The second cephalic appendage of *Ma. splendens* is setiferous (see García-Bellido and Collins 2006: fig. 11B), thus suggesting that it is an exopod; although this appendage is uniramous, we interpret the secondary loss of the endopod and thus score this character as present in *Ma. splendens.* This character is coded as uncertain for *Mi. hexagonalis* as it is unclear is the uniramous cephalic appendages of this taxon are endopods or exopods due to the lack of setae.

10. Chelate cephalic endopods: (0) absent, (1) present.

11. Antenniform fifth appendage: (0) absent, (1) present. The fifth cephalic appendage of *V. rogeri* and *X. chledophilia* is antenniform. This appendage is uniramous and non-setiferous, making it unclear whether it is an endopod or an exopod.

12. High number of trunk somites in adults: (0) absent (< 25), (1) present (> 25).

13. Trunk endopod endites: (0) spiniferous, (1) rounded. Unlike many arthropods (e.g., trilobites, nektaspidids), which have spiniferous endites on their trunk endopods, marrellomorphs have rounded endites (Fig. 4C).

14. Trunk exopod setae: (0) lamellate, (1) filamentous. Marrellomorphs were previously placed in the Lamellipedia Hou and Bergström, 1997, based on the presence of lamellate respiratory organs on the trunk exopods. The exopod setae of *Ma. splendens*, however, are filamentous (García-Bellido and Collins 2006: fig. 13C), as are the setae of *Mi. hexagonalis* (Kühl and Rust 2010: fig. 3b). The setae of *X. chledophilia* are poorly preserved, as such this character is coded as uncertain. The lanceolate exopod setae of *V. rogeri* are coded as filamentous. Lamellate exopod setae are characteristic of trilobites (e.g., *Olenoides*) and trilobite-like arthropods (e.g., *Naraoia*) (see Ortega-Hernández et al. 2013: fig. 4).

15. Trunk exopod setae orientation: (0) laterally-directed, (1) medially-directed. This character is specific to the appendage's setae in the trunk region. Cotton and Braddy (2004) suggested that the presence of medially-directed exopod setae is synapomorphic for marrellomorphs and crustaceanomorphs. Although both taxa possess medially-directed setae, they are not considered homologous herein. The medially-directed exopod setae of marrellomorphs are restricted to the trunk appendages, whereas those of fossil crustaceanomorphs (e.g., *Martinssonia* Müller and Walossek 1986) are restricted to the cephalon, with the trunk exopods bearing laterally directed setae. This character can be hard to code from dorso-ventrally flattened specimens, but is clearer from isolated limbs. The exopod setae of *Olenoides* and *Naraoia* are laterally directed (see Hou and Bergström 1997: fig. 41; Ortega-Hernández et al. 2013: fig. 4).

16. Trunk exopod multisegmented with individual setae on each podomere: (0) absent, (1) present. As with character 15, this character refers exclusively to the exopod setae of the trunk appendages and not the cephalic appendages.

Systematic palaeontology

Phylum Arthropoda von Siebold 1848

Class Marrellomorpha Beurlen, 1930

Family Mimetasteridae Birenheide, 1971

Genus *Furca* Fritsch, 1908

Type species: *Furca bohemica* Fritsch, 1908, Sandbian, Late (previously interpreted as Middle) Ordovician, Bohemia, Czech Republic.

Emended diagnosis.—Small to medium sized arthropods characterized by a subtrapezoidal cephalic shield with three pairs of prominent primary spines: anterolateral, mediolateral, and posterolateral. Anterolateral spines of variable length and degree of curvature. Mediolateral spines long and strongly curved posteriorly. Posterolateral spines long and weakly curved. Outline of cephalic shield with fringe of secondary spines (modified from Chlupáč 1999a: 81).

Remarks.—The diagnosis of this genus has been emended to account for novel observations of *F. bohemica* made herein, and for observed features in, as yet, formally undescribed species from the Ordovician of Morocco that might be referable to this genus (Van Roy 2006; Van Roy et al. 2010).

Furca bohemica Fritsch, 1908

Figs. 2–7.

1847 *Pharastoma pulchrum* (Barrande, 1846); Hawle and Corda 1847: 88, pl. 5: 49a.
1868 *Furca bohemica* Barrande, 1946; Bigsby 1868: 192 (nomen nudum).
1908 *Furca bohemica* Barrande, 1946; Fritsch 1908a: 8–9, pl. 11: 1–3.
1908 *Furca bohemica* Barrande, 1946; Fritsch 1908b: 797–798.
1918 *Furca bohemica* Barrande, 1946; Perner 1918: 12.
1919 *Furca bohemica* Barrande, 1946; Perner 1919: 32–33.
1999 *Furca bohemica* Fritsch, 1908; Chlupáč 1999a; 79, 81–82, pl. 3: 1–4, text-fig. 2a.
1999 *Furca pilosa* sp. nov.; Chlupáč 1999a: 79, 81–82, pls. 2: 1, 3: 5.
1999 *Furca* sp.; Chlupáč, 1999a: 79, 82, pl. 3: 6.
1999 *Furca bohemica* Fritsch, 1908; Chlupáč 1999b: 395, fig. affiliation: 1.1.8.
1999 *Furca pilosa* Chlupáč, 1999; Chlupáč 1999b: 396, fig. 1.1.9.
2006 *Furca bohemica* Fritsch, 1908; Van Roy 2006: 68, fig. 4.1b.
2006 *Furca pilosa* Chlupáč, 1999; Van Roy 2006: 68, fig. 4.1c.
2006 *Furca* sp.; Van Roy 2006: 68.
2009 *Furca bohemica* Fritsch, 1908; Rak 2009: 15–16, fig. 1B–E, G, H.
2009 *Furca pilosa* Chlupáč, 1999; Rak 2009: 15–16, fig. 1F.
2009 *Furca* sp.; Rak, 2009: 16, fig. 1A.
2010 *Furca bohemica* Fritsch, 1908; Ortega-Hernández et al. 2010: 427.

Lectotype: NML 27715 from Děd Hill (formerly Drabow), near Beroun,

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Czech Republic, Late Ordovician. Figured by Fritsch (1908). Lectotype selected by Chlupáč (1999a) from two Fritsch's (1908) syntypes.

Emended diagnosis.—*Furca* with vaulted cephalic shield, short anterolateral spines and delicate secondary spines of variable length. Longitudinal sulcus-like depression in the posterior half of the cephalic shield.

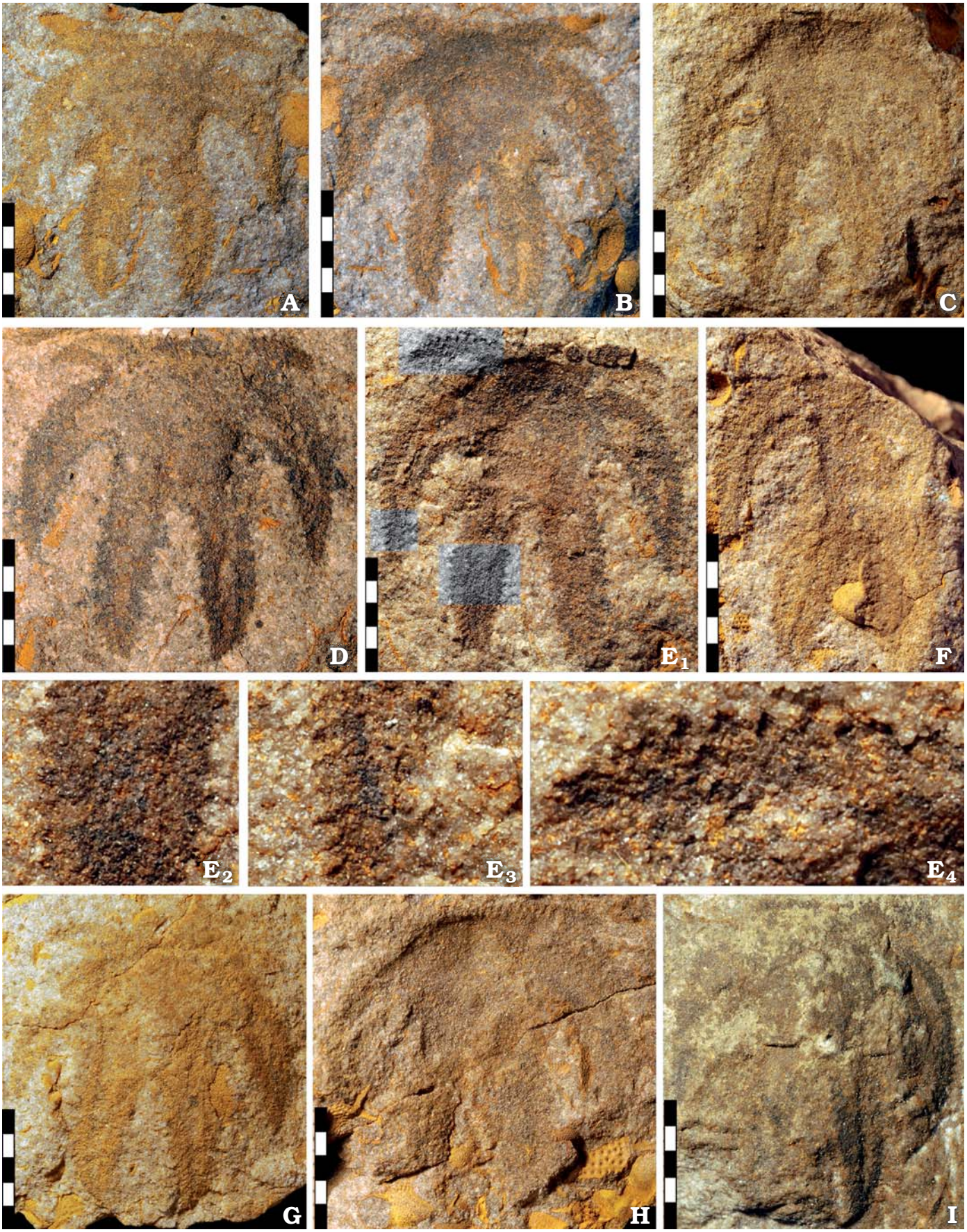
Referred material.—A number of collections outside the NML house a limited amount of *F. bohemica* material. These include the Yale Peabody Museum (YPM IP 014784), the Museum of Comparative Zoology, Harvard University (MCZ 6068a, b, MCZ 6069), and the Natural History Museum in Vienna (NHMW 1901/004/0011).

Description.—As reported by Chlupáč (1999a), the overall morphology of *F. bohemica* consists of a central body from which three pairs of large spines develop, each with a distinct orientation and length (Fig. 7). The central portion of the cephalic shield has a slightly elongated subtrapezoidal (wider anteriorly) shape, and is characterized by its conspicuous convexity, evident in both external and internal moulds (Figs. 2–6). The only prominent feature of the central body is a small fusiform depression, or sulcus, that occupies a posterior position in the axial plane of the cephalic shield (Figs. 2B, C, E, G, 3B, C, 5); the location of the median sulcus is suggestive of a role in cephalic muscle attachment, probably functioning as an apodeme, but the quality of preservation does not allow making further inferences about the significance of this structure. The front end of the cephalic shield has a straight margin that develops laterally into a pair of short anterolateral spines, which occasionally display a subtle degree of curvature on their inner facets, giving the impression of backward-facing horns (Figs. 2A, D–H, 3B, D, G, 5A–F, 6B, C). Immediately posterior to the aforementioned structures, the cephalic shield extends into a pair of large mediolateral spines. These are considerably arched and face backwards, with the tips reaching beyond the posterior margin of the central body; this represents the widest section of the cephalic shield in most specimens (Table 1). The bases of the mediolateral spines are widely attached to the main body of the cephalic shield, extending from the base of the anterior spines to the anterior-most tip of the axial sulcus. The posterior of the cephalic shield is characterised by a pair of almost straight spines that are directed backwards, and which are subequal in length to the mediolateral spines. The bases of the posterolateral spines are in mutual contact on their inner faces, and thus the posterior border of the cephalic shield has an inverted "U" shape (Figs. 3–6). As in *Ma. splendens* (Whittington 1971; García-Bellido and Collins 2006) and *Mi. hexagonalis* (Stürmer and Bergström 1976; Kühl and Rust 2010), the bases of the mediolateral and posterolateral spines are not in direct contact with each other, and thus define the slender posterior half of the cephalic shield (Table 1). The most striking feature of *F. bohemica* is the presence of a prominent fringe that consists of dozens of delicate secondary spines (Figs. 4A, 7). The secondary spines are gently curved backwards and vary in length from 1.5 to 7 mm, depending on their position, and are connected to the cephalic shield margins by distinctly triangular bases. The longest secondary spines are located on the most distal parts of the cephalic shield, such as 1/3 from the tips of the primary spines, giving the latter a rather leaf-like appearance (Figs. 4A, B, 7); this contrasts with Chlupáč's (1999a) interpretation, which portrayed the spines as having very little variation in length and perfectly straight outlines. In most specimens the secondary spines are lost or badly preserved, and the only traces left consist of the triangular stubs (Figs. 5E, 6A–C); however, the outline of the secondary spines can be clearly traced by the dark halo that surrounds the specimens (Figs. 3C–I, 4E, F, 5C–I, 6A). Secondary spines have been described in *Mi. hexagonalis* (Stürmer and Bergström 1976; Kühl and Rust 2010), although in this case the spines consist of less numerous, but longer, straight spines respectively. *Ma. splendens* shows the presence of small serrations restricted to the posterolateral primary spines (Whittington 1971; García-Bellido and Collins 2006); despite their resemblance to the triangular stubs observed in various specimens of *F. bohemica* in which the secondary spines have not become completely preserved, these structures are probably not homologous (see character 5).

Remarks.—From the studied material, a single specimen (NML40860a, b) displays a peculiar morphological abnormality (Fig. 5A, B); the left side (right in counterpart) of the posterolateral spine base bears a short but conspicuous structure whose shape closely resembles the tip of a backward facing supernumerary spine. This extra spine is preserved as a flat impression in both part and counterpart, which is consistent with the preservation of the other spines on the specimen, where most of the convexity has been lost. The homogeneous colouration between the supernumerary spine and the rest of the fossil adds support to its authenticity, as an alien superimposed fragment would be expected to have a different preservation, as is the case for a small piece of trilobite shell on the left anterior spine (Fig. 5A, B). The extra spine differs morphologically in the absence of any traces of the marginal fringe of secondary spines, or at least their triangular bases, which are clearly observable in the posterolateral spines. Apart from this asymmetrical structure, however, the rest of the fossil does not have any further malformations or traces of injury.

The occurrence of abnormalities in Palaeozoic arthropods is a relatively infrequent phenomenon that has been most extensively reported in trilobites (e.g., Owen 1985; Babcock 1993), although a single case is known in marrellomorph arthropods (Whittington 1971: pl. 18: 3). In most cases, however, it is difficult to assess the origin of the malformation.

Fig. 5. The marrellomorph arthropod *Furca bohemica* Fritsch, 1908 from the Upper Ordovician (Sandbian) of Bohemia (Ostrý Hill and Veselá, Beroun District). **A**. NML 40860a. **B**. NML 40860b. **C**. NML 40886. **D**. NML 40864a. **E**. NML 40864b (E_1) and detailed view of the posterolateral (E_2), mediolateral (E_3), and anterolateral (E_4) primary spines, showing triangular stubs corresponding to the secondary spines. **F**. NML 40878b. **G**. NML 40872b. **H**. NML 40877b. **I**. NML 40879. Scale bars 10 mm. →



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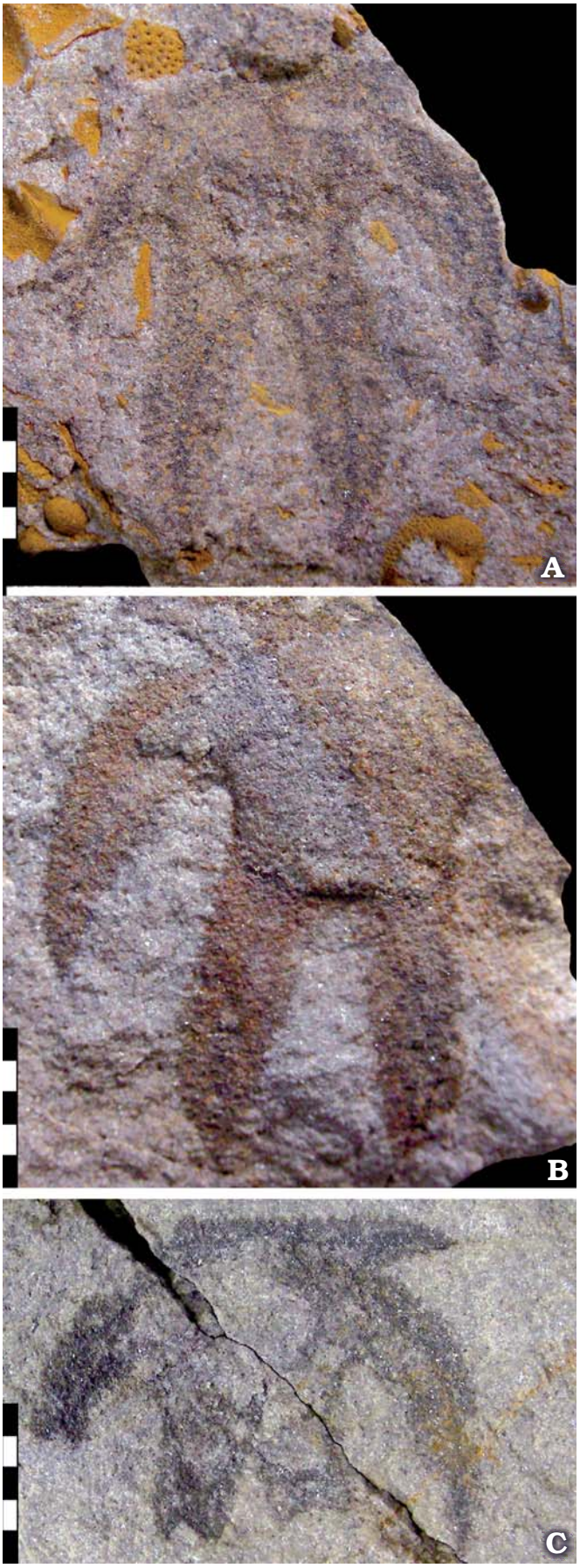

Fig. 6. The marrellomorph arthropod *Furca bohemica* Fritsch, 1908 from the Upper Ordovician (Sandbian) of Bohemia (Ostrý Hill and Veselá, Beroun District). **A**. NML 40865. **B**. NML 40861. **C**. NML 40875. Scale bars 10 mm.

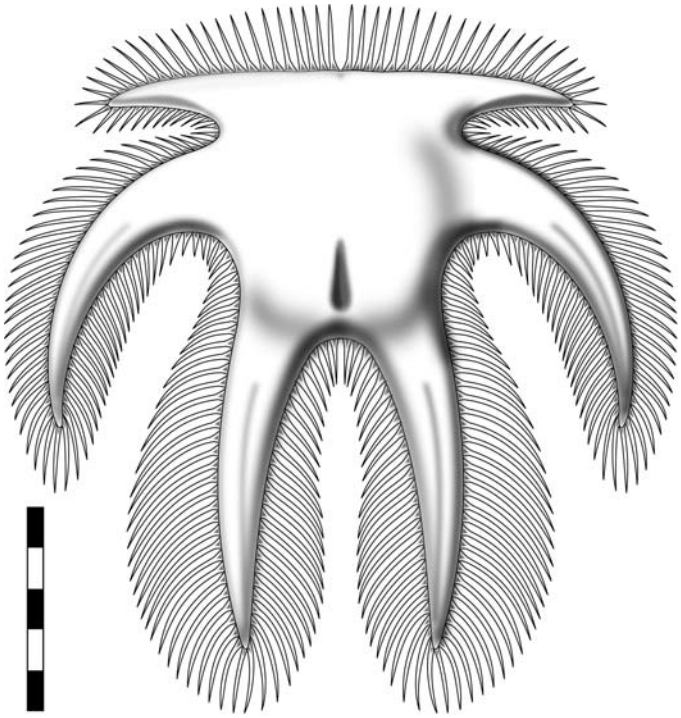

Fig. 7. A new morphological reconstruction of the marrellomorph arthropod *Furca bohemica* Fritsch, 1908 in dorsal view. Scale bar 10 mm.

Some asymmetrical abnormalities can be broadly explained through predation and injury healing (Babcock 1993), but many malformations have a developmental origin (i.e., teratologies) and do not necessarily follow this rule. The specimen of *Ma. splendens* illustrated by Whittington (1971) bears a pair of supernumerary processes attached to the anterior margin of the lateral spines; in this case, it seems plausible to argue that this is the result of a teratological condition as opposed to a healed injury. Van Roy (2006) discussed Whittington's (1971) specimen and reached the conclusion that it may represent an atavistic individual, in which a previously suppressed pair of spines associated with an inconspicuous head segment, as indicated by the number of primary spines, reappeared due to a developmental abnormality (see character 3). The model proposed by Van Roy (2006) is supported by the overall correlation between the number of head segments and primary spines in the cephalic shield of various marrellomorphs, as well as the highly symmetrical nature of the malformation in the aforementioned *Ma. splendes* specimen. In the case of the aberrant *F. bohemica*, however, the situation is not as straightforward, as the malformation is clearly confined to the left side of the cephalic shield and there are not any other abnormal features. It seems rather unreasonable to rely on the same argument as Van Roy (2006)

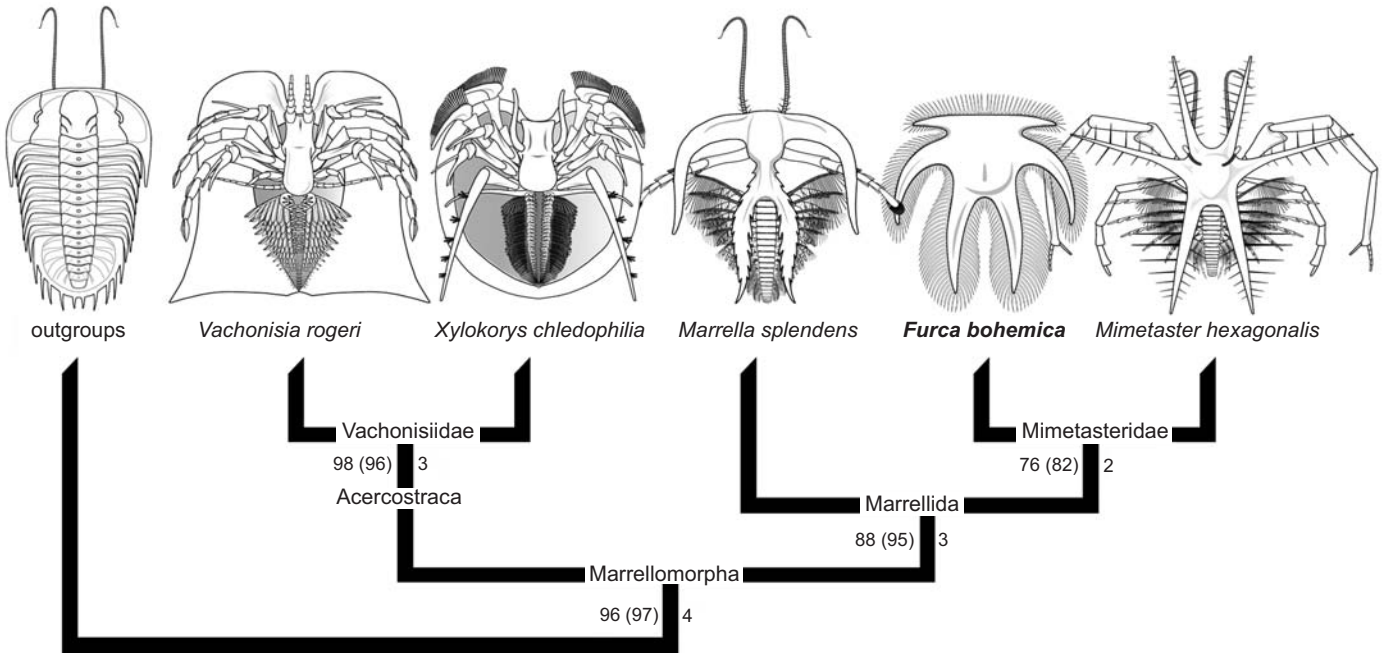

Fig. 8. Phylogeny of marrellomorph arthropods. Single MPT (most parsimonious tree) (CI = 0.941; RI = 0.941). Tree length is 17 steps with equally weighted characters. With implied weighting tree length equals 0.1667 (k = 5), 0.25 (k = 3) and 0.50 (k = 1). Numbers on the left of the branches indicate support values for jackknifing, and those in brackets are for symmetric resampling. Numbers on the right of branches indicate Bremer support values. Outgroup taxa are represented by trilobite *Olenoides serratus*.

to account for this additional structure, as that would imply a more primitive four-segmented condition for the marrellomorph head, which cannot be supported due to the absence of any appendage data for *Furca* or the recognition of other phylogenetically related organisms. As such, the simplest solution is to interpret this structure as a localized mutation, the result of an abnormal healing process due to injury or even a case of parasitism.

Results of phylogenetic analysis and the affinities of *Furca bohemica*

Kühl et al. (2008) and Kühl and Rust (2010) reviewed the systematics and relationships of marrellomorph arthropods, but did not support their phylogeny with a cladistic analysis. They recognised two clades of marrellomorphs: those with a dorsal cordate shield (i.e., *Xylokorys* and *Vachonisia*), and those with prominent cephalic spines (i.e., *Furca*, *Marrella*, and *Mimetaster*). The phylogenetic position of *Furca* with respect to other marrellomorphs was left unresolved mainly due to uncertainty on the character polarity.

All analyses with equal character weighting resulted in a single most parsimonious tree of 17 steps (Fig. 8). This topology was not affected by subsequent analyses with character weighting. The overall topology resembles that of Kühl et al. (2008) and Kühl and Rust (2010), the main difference being that *F. bohemica* was resolved as the sister-taxon to the *Mi. hexagonalis*. This relationship is supported by two unambiguous synapomorphies: the presence of anterolateral spines (character 2) and an inflated cephalic shield (chracter 6). These taxa also share the possession of a fringe of secondary spines (character 5), however, the current dataset has not allowed to determine the polarity of this character. The results indicate that *Furca* should be removed from Marrellidae (sensu Chlupáč 1999a) and instead placed in Mimetasteridae. Although the presence of anterolateral spines resolved as an unambiguous synapomorphy in the analysis, the presence of anterolateral spines in possibly atavistic specimens of *Ma. splendens* (see e.g., Van Roy 2006) may indicate that this feature is actually a synapomorphy of a more inclusive clade (*Marrella* + Mimetasteridae = Marrellida Raymond, 1920 sensu Chlupáč 1999a). The latter clade is also supported by three unambiquous synapomorphies: the presence of both mediolateral spines (character 3) and posterolateral spines (character 4), and the presence of uniramous cephalic appendages (character 8).

The interrelationships of the ingroup (Marrellomorpha) were unaffected by outgroup choice, indicating its monophyly (see Lin et al. 2006), the latter supported by six synapomorphies: the presence of multisegmented exopods (character 16) with filamentous (character 14) medially-directed setae (character 15), the presence of rounded endites on the trunk endopods (character 13), a high number of trunk segments (character 12) and the presence of long cephalic exopods (character 9). The current analysis provides a much clearer

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Table 3. Stratigraphic and palaeoecological comparison of marrellomorph arthropod species.

Taxon	Locality	Series	Environment	Mode of life	References
Marrella splendens	Burgess Shale Formation	Middle Cambrian	continental shelf	nektobenthic	Whittington 1971; García-Bellido and Collins 2006
Marrella sp.	Kaili Formation	Middle Cambrian	continental shelf	nektobenthic	Zhao et al. 2003; Lin 2009
Undescribed marrellomorph	Fezouata Formation	Lower Ordovician	continental shelf	benthic/ nektobenthic	Van Roy 2006; Van Roy et al. 2010
Furca bohemica	Letná Formation	Upper Ordovician	shallow marine	benthic/ ?nektobenthic	Chlupáč 1999a; this study
Xylokorys chledophilia	Herefordshire Lagerstätte	Silurian	continental shelf	benthic	Siveter et al. 2007
Mimetaster hexagonalis	Hünsruck Slate	Lower Devonian	continental shelf	benthic	Stürmer and Bergström 1976; Khül and Rust 2010
Vachonisia rogeri	Hünsruck Slate	Lower Devonian	continental shelf	benthic	Stürmer and Bergström 1976; Khül et al. 2008

resolution of the internal relationships within Marrellomorpha, but is clearly insufficient for determining the precise phylogenetic position of this clade with respect to other major Palaeozoic arthropod groups (e.g., Legg et al. 2012; Ortega-Hernández et al. 2013).

Mode of life

The absence of appendage information in *F. bohemica* hampers the interpretation of its palaeoecology, particularly those aspects related to its feeding strategies. However, it is possible to make general inferences about its mode of life based on comparison with other marrellomorphs and the depositional environment of the Letná Formation (Table 3). Early interpretations of marrellomorph palaeoecology depicted them as active swimmers that spent most of their time in the water column (e.g., Walcott 1912; Størmer 1944; Simonetta 1962; Rolfe 1969). Later studies have favoured a benthic (Whittington 1971; Stürmer and Bergström 1976; Kühl et al. 2008) or nektobenthic (Zhao et al. 2003; García-Bellido and Collins 2006) mode of life, arguing that the considerable bulk of the head shield would have only allowed these arthropods to hover near the substrate, with occasional resting episodes on the bottom. Stürmer and Bergström (1976) considered that *Vachonisia*'s prominent head shield would have hampered free swimming and this animal most likely dwelled in muddy bottoms, similarly to extant horseshoe crabs. Considering the morphological similarity of *Furca* with both *Marrella* and *Mimetaster*, it is not unreasonable to envisage a benthic lifestyle for the former. Although the possibility of a nektobenthic mode of life cannot be ruled out entirely, it is not possible to make further inferences until the appendage anatomy of *Furca* is discovered and described in detail. Of special palaeoecological interest is the shared presence of a fringe of secondary spines in *Furca* and *Mimetaster*. Rolfe (1969) considered the long secondary spines of *Mimetaster* as an adaptation for a pelagic lifestyle, an interpretation that has fallen out of favour in more recent studies. Bergström (1973) and Van Roy (2006) have regarded the presence of these structures among marrellomorphs as a defensive adaptation based on the wide coverage of the spines over the body. Kühl and Rust (2010) reported the association of tentaculitoids and sponges with *Mimetaster*, with most of the epibionts attached to the spines and dorsal margins of the cephalic shield. Although the biological significance of this association requires further investigation, it suggests that the secondary spines may have played an important ecological role by interacting with other marine organisms, possibly though commensalism. No unequivocal epibionts have yet been identified in *F. bohemica*. Chlupáč (1999a) considered that specimen NML 32998 (Fig. 3A) showed possible traces of organic activity, maybe ostracods, expressed as a pair of oval cavities on the centre of the head shield. Although the features highlighted by Chlupáč (1999a) cannot be verified as having being the result of epibiontic activity, this association was not observed in any other specimen, making it likely an artefact of preservation.

The depositional environment of the Letná Formation sets *F. bohemica* apart from other known marrellomorphs, as most representatives of this group have been described from open shelf settings (Table 3). The presence of *F. bohemica* in a shallow marine environment indicates that marrellomorph arthropods probably had a much wider distribution and ecological versatility than that suggested by most Palaeozoic sites of exceptional preservation.

Note added in proof

Since the acceptance of this manuscript, there have been new discoveries of marrellomorph arthropods, including *Australomarrella klausmuelleri* from the middle Cambrian of Australia (Haug et al. 2013 this paper), and a *Marrella*-like form from the early Cambrian of China (Liu 2013).

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References

Allen, R.E. 2002. Role of diffusion—precipitation reactions in authigenic pyritization. *Chemical Geology* 182: 461–472.

Babcock, L.E. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology* 67: 217–229.

Barrande, J. 1846. Noveaux Trilobites. *Supplément et la Notice préliminaire sur le Systême silurien et les Trilobites de la Bohême*. 40 pp. J.G. Calve, Prague.

Barrande, J. 1852. *Systême silurien du centre de la Bohême Vol. 1. Trilobites*. 70 pp. Published by the author, Prague.

Barrande, J. 1872. *Systême silurien du centre de la Bohême: I. Partie, Supplement au Vol. 1. Trilobites, Crustacés divers et Poissons*. 72 pp. Published by the author, Prague.

Barriel, V. and Tassy, P. 1998. Rooting with multiple outgroups: consensus versus parsimony. *Cladistics* 14: 193–200.

Bergström, J. 1973. Organization, life and systematics of trilobites. *Fossils and Strata* 2: 1–69.

Beurlen, K. 1930. Vergleichende Stammesgeschichte. Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschritte der Geologie und Palaeontologie* 8: 317–586.

Bigsby, J. 1868. Thesaurus siluricus. The flora and the fauna of the Silurian period. 214 pp. Taylor and Francis, London.

Birenheide, R. 1971. Beobachtung am "Scheinsten" *Mimetaster* aus dem Hünsruck-Schiefer. *Senckenbergiana lethae* 52: 77–91.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10: 295–304.

Chlupáč, I. 1965. Xiphosuran merostomes from the Bohemian Ordovician. *Sbornik Geologických Věd, Paleontologie* 5: 7–38.

Chlupáč, I. 1988. The enigmatic arthropod *Duslia* from the Ordovician of Czechoslovakia. *Palaeontology* 31: 611–620.

Chlupáč, I. 1999a. Some problematical arthropods from the Upper Ordovician Letná Formation of Bohemia. *Journal of the Czech Geological Survey* 44: 79–87.

Chlupáč, I. 1999b. Unusual arthropod from the Bohemian Ordovician. A review. *Acta Universitatis Carolinae, Geologica* 43: 393–396.

Cotton, T.J. and Braddy, S.J. 2004. The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Transactions of the Royal Society of Edinburgh* 94: 169–193.

Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D., and Kluge, A.G. 1996. Parsimony jackknifing outperforms neighbour-joining. *Cladistics* 12: 99–124.

Fritsch, A. 1908a. Problematica silurica. *In*: J. Barrande (ed.), *Systême silurien du centre de la Bohême*. 28 pp. Bellman, Prague.

Fritsch, A. 1908b. Über eine Echinodermenlarve aus dem Untersilur Böhmens. *Zoologische Anzeiger* 33: 797–798.

García-Bellido, D.C. and Collins, D.H. 2006. A new study of *Marrella splendens* (Arthropoda, Marrellomorpha) from the Middle Cambrian Burgess Shale, British Columbia, Canada. *Canadian Journal of Earth Sciences* 43: 721–742.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J., and Szumik, C.A. 2003. Improvements to resampling measures of group support. *Cladistics* 19: 324–332.

Goloboff, P.A., Farris, J.S. and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Gürich, G. 1931. *Mimaster hexagonalis*, ein neuer Kruster aus dem unterdevonischen Bundenbacher Dachschiefer. *Paläontologische Zeitschrift* 13: 204–238.

Gürich, G. 1932. *Mimetaster* n. gen. (Crust.) statt *Mimaster* Gürich, 1931. *Senckenbergiana* 14: 193.

Haug, J.T., Castellani, C., Haug, C., Waloszek, D., and Maas, A. 2013. A *Marrella*-like arthropod from the Cambrian of Australia: A new link between "Orsten"-type and Burgess Shale assemblages. *Acta Palaeontologica Polonica* 58: 629–639.

Havlíček, V. 1998. Paleozoic of the Barrandian (Cambrian to Devonian). *In*: I. Chlupáč, V. Havlíček, J. Kříž, Z. Kukal, and P. Štorch (eds.), *Paleozoic of the Barrandian (Cambrian to Devonian)*. 183 pp. Czech Geological Survey, Prague.

Havlíček, V. and Vaněk, J. 1966. The biostratigraphy of the Ordovician in Bohemia. *Sborník geologických věd, Paleontologie* 8: 7–69.

Hawle, I. and Corda, A.J.C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. *Abandlungen kaiser-böhmische Gessel-Wissenschaft* 5: 1–176.

Hou, X.-G. and Bergström, J. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils & Strata* 45: 1–116.

Jahn, J.J. 1893. *Duslia*, eine neue Chitonidengattung aus dem böhmischen Untersilur, nebst einigen Bemerkungen über die Gattung *Triopus* Barr. *Sitzungsberichte Jungen der koniglichen Akademia für Wissenschaften, Wien* 102: 591–603.

Kukal, Z. 1958. The petrographic research of the Letná Beds of the Barrandian Ordovician [in Czech, with English summary]. *Sborník Ústředního Ústavu Geologického, Oddělení geologie* 24 (1): 7–111.

Kukal, Z. 1963. Composition and origin of the Ordovician sediments of the Třenice and Mílina Beds [in Czech, with English summary]. *Sborník Ústředního Ústavu Geologického, Oddělení geologie* 28 (1): 265–307.

Kühl, G. and Rust, J. 2010. Re-investigation of *Mimetaster hexagonalis*: a marrellomorph arthropod from the Lower Devonian Hunsrück Slate (Germany). *Paläontologische Zeitschrift* 84: 397–411.

Kühl, G., Bergström, J., and Rust, J. 2008. Morphology, paleobiology and phylogenetic position of *Vachonisia rogeri* (Arthropoda) from the Lower Devonian Hunsrück Slate (Germany). *Palaeontographica Abteilung A* 286 (Lieferung 4–6): 123–157.

Legg, D.A., Sutton, M.D., Edgecombe, G.D., and Caron, J.-B. 2012. Cambrian bivalved arthropod reveals origin of arthrodization. *Proceedings of the Royal Society B* 279: 4699–4704.

Lehmann, W.M. 1955. *Vachonisia rogeri* n. g. n. sp., ein Branchiopod aus dem unterdevonischen Hunsrückschiefer. *Paläontologische Zeitschrift* 29: 126–130.

Lin, J.-P. 2009. Review of the depositional environment of the Kaili Formation (Cambrian Series 2–3, boundary interval: China). *Memoirs of the Association of Australasian Palaeontologists* 37: 131–149.

Lin, J.-P., Gon III, S.M., Gehling, J.G., Babcock, L.E., Zhao, Y.-L., Zhang, X.-L., Hu, S.-X., Yuan, J.-L., Yu, M.-Y., and Peng, J. 2006. A *Parvancorina*-like arthropod from the Cambrian of South China. *Historical Biology* 18: 33–45.

Liu, Q. 2013. The first discovery of *Marrella* (Arthropoda, Marrellomorpha) from the Balang Formation (Cambrian Series 2) in Hunan, China. *Journal of Paleontology* 87: 391–394.

http://dx.doi.org/10.4202/app.2011.0038

Müller, K.J. and Walossek, D. 1986. *Martinssonia elongata* gen. et sp. n., a crustacean-like euarthropod from the Upper Cambrian "Orsten" of Sweden. *Zoologica Scripta* 15: 73–92.

Perner, J. 1918. [no title]. *In*: O. Novák (ed.), Trilobiti pásma D-d1 gama z okolí pražského (Die Trilobiten der Zone D-d1 gama von Prag und Umgebung). *Palaeontolographica Bohemiae* 9: 1–51.

Perner, J. 1919. *Furca bohemica* – zástupce nové čeledi korýšů v českém siluru. *Časopis Musea Království Českého* 93: 32–33.

Ortega-Hernández, J., Braddy, S.J., and Rak, Š. 2010. Trilobite and xiphosuran affinities for the putative aglaspidid arthropods *Caryon* and *Drabovaspis*, Upper Ordovician, Czech Republic. *Lethaia* 43: 427–431.

Ortega-Hernández, J., Legg, D.A., and Braddy, S.J. 2013. The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics* 29: 15–45.

Owen, A.W. 1985. Trilobite abnormalities. *Transactions of the Royal Society of Edinburgh* 76: 255–272.

Rak, Š., Bergström, J., Fatka, O., and Budil, P. 2009. The Upper Ordovician arthropod *Zonozoe draboviensis* Barrande (Libeň and Letná formations, Sandbian, Barrandian area, Czech Republic). *Bulletin of Geosciences* 84: 185–187.

Röhlich, P. 1960. Ordovizium des nordöstlichen Teils von Prag. *Rozpravy České Akademie věd, Řada matematických a přírodních věd* 70: 1–64.

Rolfe, W.D. I. 1969. Arthropoda *incertae sedis*. *In*: R.C. Moore (ed), *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4*, R620–R625. Geological Society of America and University of Kansas Press, Lawrence.

Rominger, C. 1887. Description of primordial fossils from Mount Stephens, 348 N. W. Territory of Canada. *Proceedings Academy of National Science* 1: 12–19.

Siebold, C.T. von 1848. Lehrbuch der vergleichenden Anatomie der Wirbellosen Thiere. *In*: C.T. von Siebold and H. Stannius (eds.), *Lehrbuch der vergleichenden Anatomie*, 1–679. Verlag von Veit and Company, Berlin.

Simonetta, A.M. 1962. Note sugli artropodi non trilobiti della Burgess Shale, Cambriano Medio della Columbia Britannica (Canada). 1° contributo: II genere *Marrella* Walcott, 1912. *Monitore Zoologico Italiano* 69: 172–185.

Siveter, D.J., Fortey, R.A., Sutton, M.D., Briggs, D.E.G., and Siveter, D.J. 2007. A Silurian "marrellomorph" arthropod. *Proceeding of the Royal Society B* 274: 2223–2229.

Størmer, L. 1944. On the relationships and phylogeny of fossil and recent Arachnomorpha. *Skrifter Utgitt av det Norske Videnskaps-Akademi I Oslo, I: Matematisk-naturvidenskapelig Klasse* 5: 1–150.

Stürmer, W. and Bergström, J. 1976. The arthropods *Mimetaster* and *Vachonisia* from the Devonian Hunsrück Slate. *Paläontologische Zeitschrift* 50: 78–111.

Vaněk, J. 1965. New species of the suborder Calymenina Swinnerton, 1915 (Trilobita) from the Barrandian area. *Sborník geologických věd, Paleontologie* 6: 21–37.

Van Roy, P. 2001. Marrellomorpha. *Geologica Belgica* 2: 243–245.

Van Roy, P. 2006. *Non-trilobite Arthropods from the Ordovician of Morocco*. 230 pp. Unpublished Ph.D. thesis, Ghent University, Ghent.

Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., el Hariri, K., and Briggs, D.E.G. 2010. Ordovician faunas of Burgess Shale type. *Nature* 465: 215–218.

Walcott, C.D. 1912. Cambrian Geology and Paleontology 2. No. 6. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. *Smithsonian Misccellaneous Collection* 57: 145–229.

Whittington, H.B. 1971. Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia. *Bulletin of the Geological Survey of Canada* 209: 1–24.

Zhao, Y.-L., Yuan, J.-L., Zhu, M.-Y., Yang, X.-L., and Peng, J. 2003. The occurrence of the genus *Marrella* (Trilobitoidea) in Asia. *Progress in Natural Science* 13: 708–711.