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

ŠTĚPÁN RAK, JAVIER ORTEGA-HERNÁNDEZ, and DAVID A. LEGG


The enigmatic marrellomorph arthropod Furca bohemica from the Upper Ordovician Letné 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 Letné 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, Letné Formation, Barrandian, Ordovician, Ostrý Hill, Czech Republic.

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Introduction

The Upper Ordovician (Sandbian) Letné 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 Letné 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 cheloniiellids, bivalved ?phylocarids 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 Hünsrück 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-
interpreted *Furca 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 *Furca bohemica* as the head shield of an unusual arthropod, having previously compared it to a trilobite pygidium (Perner 1918). *Furca 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
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
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 exter-

<table>
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**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 Barriél 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 2. Character matrix used for cladistic analysis. Question mark denotes uncertainty.

<table>
<thead>
<tr>
<th>Character</th>
<th>Marrella splendens</th>
<th>Naraoia compacta</th>
<th>Olenoides serratus</th>
<th>Vachonista rogeri</th>
<th>Furca bohemica</th>
<th>Minetaster hexagonalis</th>
<th>Xylokorys chledophilia</th>
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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 (A₁) and detailed view (A₂). 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.
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* 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). 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 that it is an exopod; although this appendage is uniramous, making it unclear whether it is an endopod or an exopod.

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).


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 crustaceomorphs. 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 crustaceomorphs (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.

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**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.


*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.

1908 *Furca bohemica* Barrande, 1946; Fritsch 1908a: 8–9, pl. 11: 1–3.

1999 *Furca pilosa* sp.; Rak, 2009: 16, fig. 1A.


1999 *Furca bohemica* Fritsch, 1908; Chlupáč 1999a: 79, 81–82, pl. 3: 1–4, text-fig. 2a.


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. *Furca bohemica* Fritsch, 1908; Van Roy 2006: 68, fig. 4.1b. *Furca pilosa* Chlupáč, 1999; Van Roy 2006: 68, fig. 4.1c.


2009 *Furca bohemica* Fritsch, 1908; Rak 2009: 15–16, fig. 1B–E, G, H. *Furca pilosa* Chlupáč, 1999; Rak 2009: 15–16, fig. 1F. *Furca* sp.; Rak, 2009: 16, fig. 1A.


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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 orientation and length (Fig. 7). The central portion of the cephalic shield is characterized by a pair of almost parallel, short anterolateral spines and delicate secondary spines of variable length. Longitudinal sulcus-like depression in the posterior half of the cephalic shield.

*Furca* 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 orientation and length (Fig. 7). The central portion of the cephalic shield is characterized by a pair of almost parallel, short anterolateral spines and delicate secondary spines of the cephalic shield. The front end 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 orientation and length (Fig. 7). The central portion of the cephalic shield is characterized by a pair of almost parallel, short anterolateral spines and delicate secondary spines of variable length. Longitudinal sulcus-like depression in the posterior half of the cephalic shield.

**Remarks.**—From the studied material, a single specimen (NML 40860a, 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.

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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 (E1) and detailed view of the posterolateral (E2), mediolateral (E3), and anterolateral (E4) 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.
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. 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.
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 (character 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 unambiguous 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...
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; Stürmer 1944; Simonetta 1962; Rolfe 1969). Later studies have favoured a benthic (Whittington 1971) 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 through 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 been 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 *Austromarrella 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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