NEW AND REVISED SMALL SHELLY FOSSIL RECORD FROM THE LOWER CAMBRIAN OF NORTHERN IRAN

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Abstract: Small shelly fossils (SSFs) are highly informative of the 'Cambrian explosion'. Their palaeobiodiversity has been documented from lower Cambrian deposits worldwide but it remains elusive in areas such as Iran, despite this region occupying a critical position on the north-western Gondwana margin during the early Cambrian. This new study of the SSFs of the lower Cambrian of northern Iran provides a large dataset from this understudied area. We revise the micropalaeontological signal of the Soltanieh Formation of the Alborz Mountains and introduce novel data from the Soltanieh and overlying Barut Formations of the Soltanieh Mountains. The new, solid taxonomic and stratigraphic SSF data enable us to distinguish two successive microfaunal assemblages. The first occurs in the Soltanieh Formation of the Soltanieh and Alborz Mountains and is dominated by anabari-tids (Anabarites trisulcatus, A. ex gr. trisulcatus, A. tristichus, A. dalirense sp. nov., Cambrotubulus decurvatus) along with protoconodonts (Protohertzina anabarica and P. unguliformis), maikhanellids (Maikhanella multa, Purella squamulosa and Purella sp.), Aethelicopalla adnata, indeterminate cones and irregular tubes. The second assemblage, from the Barut Formation, is dominated by a diverse assemblage of molluscs (Oelandiella korokkovi and cap-shaped morphotypes). Siphogonuchitid sclerites also occur in both assemblages. The two SSF assemblages are characteristic of the Terreneuvian. Our dataset enables us to assess the sequence of faunal change of the Ediacaran–Cambrian transition; in contrast to the tube–sclerite–brachiopod succession presented in the literature, the Iranian fauna changes from one dominated by tubes and sclerites, to one dominated by molluscs and sclerites.

Key words: small shelly fossils, Cambrian, Iran, Terreneuvian, Alborz Mountains, micropalaeontology.

In recent decades, our knowledge of the ‘Cambrian explosion’ has benefited from studies of a large amount of fossil data, especially from the famous, exceptionally preserved biotas such as those of the Maotianshan Shale (South China; e.g. Hou et al. 2017) and of the Burgess Shale (Canada; e.g. Briggs et al. 1994), among others. The small shelly fossils (SSFs), a polyphyletic group of microfossils generally preserved in phosphate that thrived at the beginning of the Cambrian (during the so-called ‘pre-trilobitic’ Cambrian), can also largely contribute to our understanding of the explosion of biomineralizing animal life in the Cambrian, especially of its initial phase. Their palaeobiodiversity has been documented in early Cambrian deposits from all of the palaeocontinents and has proven to be of significant use for biostratigraphy (e.g. Devaere et al. 2019), palaeobiogeography (e.g. Yang et al. 2015), and phylogenetic (e.g. Shu et al. 2014) and palaeoecologic reconstructions (e.g. Budd & Jackson 2016).

In some critical areas, however, information on SSFs has remained elusive, although it is of major importance for the validation of their different uses. This is the case for Iran: early Cambrian SSFs were reported for the first time from the Soltanieh Formation of the Alborz Mountains by Hamdi (1989) and Hamdi et al. (1989), without any taxonomic descriptions. In Hamdi (1989), the palaeobiodiversity of SSFs is presented as a list of occurrences. Part of the listed taxa are illustrated and a composite stratigraphical column showing the stratigraphic range of some of the listed taxa is provided for the Soltanieh Formation at two localities of the Alborz Mountains. The two localities are called Dalir and Valiabad, from the name of the villages located close to the north–south road crossing the Alborz Mountains between Chalus and Tehran (the village of Dalir is located 40 km to the south-west of the town of Marzan-Abad, and Valiabad is located 30 km to the south of Marzan-Abad). The authors failed...
to find SSFs at other localities (two sections in the Soltanieh Mountains and one at Hasanakdar, also along the Chalus road in the Alborz Mountains). Hamdi et al. (1989) presented the palaeobiodiversity of the SSFs of the Soltanieh Formation as a list of faunal and floral sequences with few illustrations, and part of their distribution is reported in a composite stratigraphical column for the Soltanieh Formation of the same two localities, although the column shows the first appearance datum points of the main early skeletal fossil taxa. Later, Hamdi (1995) published a report on the Precambrian–Cambrian deposits in Iran (in Persian), in which a biostratigraphic framework with five assemblage zones and a chronostratigraphic interpretation is proposed for the Soltanieh Formation based on the data from the previous publications. That work is accompanied by expanded illustrations of the small shelly fauna from Dalir and Valiabad. In addition to the SSFs of the two aforementioned sections, rare SSFs from the lower Cambrian of Yazd are also illustrated: molluscs and hyoliths from the Bonloukhi section, Bafq area and chancelloriids from the Chah-Shour section, Saghand area (Hamdi, 1995). A field meeting was then organized in 1996 by Hamdi for the International Geological Coordination Program (IGCP) 366, at which Neoproterozoic to Ordovician successions of the Alborz Mountains were visited, including the previously studied, SSF-yielding localities (Zhuravlev et al. 1996). After these studies in the 1990s, very few studies on SSFs were conducted in Iran. CiaBeGhodsi et al. (2006) focused on the trace fossil Trichophycus pedum at the Soltanieh type section. They mention the presence of Anabarites sp. and Protohertzina sp. in the Soltanieh Formation at the type section but no specimen is illustrated. Tashayoee et al. (2012) listed and illustrated SSFs from the Soltanieh Formation at the Garmab section (village of Hasanakdar) of the Alborz Mountains and proposed two SSF assemblage zones. Both studies failed to provide a description and stratigraphic range for the identified taxa, which are essential information for any further biostratigraphic and palaeobiogeographic interpretations. Finally, Shahkarami et al. (2017a, b) focused on the ichnofossils of the Soltanieh Formation but synthesized the results on the SSFs from the previous studies for discussion. Despite the deficiencies of the previous studies, the figured material attests to the relative abundance, diversity and preservation of the SSFs from the critical Ediacaran–Cambrian transition.

This new study on the SSFs of northern Iran was therefore conducted to improve and enlarge on the promising data from this key area. The Soltanieh Formation of the Alborz Mountains is revised for its micropalaeontological content at the sections of Dalir and Valiabad. In addition, novel micropalaeontological studies are presented from the Soltanieh Mountains for the Soltanieh Formation, but also for the fossiliferous overlying Barut Formation. The aim of this new work is to provide solid SSF data (with taxonomy and stratigraphic extension) for further biostratigraphic and palaeobiogeographic interpretations. This substantial dataset enables us to: (1) identify distinct microfaunal assemblages; (2) provide a revised biochronostatigraphic interpretation of the succession; and (3) offer new considerations for the interpretation of the evolution of biodiversity in the framework of the Cambrian explosion.

GEOLOGICAL SETTING

This work focuses on the SSFs of the lower Cambrian of Iran, which outcrops best in the Soltanieh and Alborz Mountains in the northern part of the country (Fig. 1A). The Soltanieh Mountains, located to the south of the cities of Zanjan and Soltanieh, are a narrow mountain range located close to and south of the central Alborz Mountains and run in a north-west–south-east direction (Fig. 1B). The width of the Soltanieh Mountains ranges between 10 and 12 km and the length extends to more than 150 km. The range corresponds to an uplift of Mesozoic, Palaeozoic and Precambrian rocks produced by a fault zone aligned to the north-east border of the range (Fig. 1B, D, E; Stöcklin, 1968; Hassanzadeh et al. 2008; Ghadimi et al. 2012). This longitudinal fault zone is accompanied by cross-faults of various directions, producing a complicated mosaic pattern (Fig. 1B, D, E; Stöcklin et al. 1964, 1965; Hassanzadeh et al. 2008; Ghadimi et al. 2012). The Alborz Mountains are a sinuous, narrow (c. 120 km wide), east–west-trending mountain range that extends for 2000 km from eastern Turkey to Afghanistan along the southern margin of the Caspian Sea (Fig. 1B; Zanchi et al. 2006; Zandkarimi et al. 2016). It is a double-verging transpressional fold-and-thrust belt complex (Guest et al. 2006, and references therein; Etemad-Saeed et al. 2016; Etemad-Saeed & Najafi 2019). Oblique convergence is accommodated through a combination of left-lateral strike-slip and thrust faulting (Fig. 1C; Ballato et al. 2011). The Alborz, and most probably the Soltanieh Mountains, resulted from the Alpine orogeny, from the Late Triassic Cimmerian phase (resulting from the collision of the Central Iranian Block with Eurasia) to the post-Oligocene stage of intracontinental deformation (related to the collision between the Arabian and Eurasian plates) (Stöcklin et al. 1964, 1965; Stöcklin, 1968; Zanchi et al. 2009; Ballato et al. 2011; Zandkarimi et al. 2016; Etemad-Saeed et al. 2016, Madanipour et al. 2017; Etemad-Saeed & Najafi 2019).

During the Ediacaran–Cambrian transition, the Iranian blocks were originally part of a series of peri-Gondwana terranes that bordered the north-western margin of
Gondwana (the so-called Proto-Palaeotethyan margin sensu Lasemi 2001 and Proto-Tethyan margin sensu Stampfli & Borel 2002). This part of the peri-Gondwanan margin is interpreted either as a thermally subsiding passive margin of the Afro-Arabian platform that was formed after the late Proterozoic rifting of the north-western Gondwana supercontinent (Stöcklin, 1968; Berberian & King 1981; Husseini 1989; Talbot & Alavi 1996; Lasemi 2001, 2007, 2017) or alternatively as an active continental margin with Cadomian arc plutonism and volcanism resulting from the southwards subduction of the Proto-Tethys ocean along the northern margin of Gondwana (Ramezani & Tucker 2003; Hassanzadeh et al. 2008; Horton et al. 2008; Moghadam et al. 2015, 2016, 2017; Malek-Mahmoudi et al. 2017; Etemad-Saeed & Najafi 2019).

The lower Cambrian of the Soltanieh and Alborz Mountains, on which this study focuses, is recorded in the mixed carbonate–siliciclastic successions of the Soltanieh and Barut Formations. The Soltanieh Formation was defined by Stöcklin et al. (1964) from ridges east of the village of Chopoghlu (or Chopoqlu) in the Soltanieh Mountains, to the south of the town of Soltanieh (Fig. 1B). The Soltanieh Formation is 1160 m thick and is composed of three...
members at the type locality, described by Stöcklin et al. (1964) from bottom to top as follows.

1. The lowest member is the Lower Dolomite Member, which is 123 m thick and consists of yellow, recrystallized, well-bedded dolostone with many black and white chert bands up to 50 cm thick.

2. The Chopoghlu Shale Member is 247 m thick and consists of dark green–grey argillaceous, siliceous and silty-micaceous slaty shales. In the uppermost part, blue–black, thin-platy, nodular, partly siliceous limestones and calcareous shales are interbedded within the shales.

3. The Upper Dolomite Member is very thick (790 m) and is composed of white to yellow, massive, recrystallized dolostone. Within the dolostone, two levels (5 m and 73 m) of green, micaceous, slaty shales are intercalated. In the uppermost part, dark grey, well-bedded dolostones and limestones with nodules of black chert are present.

The overlying Barut Formation was defined by Stöcklin et al. (1964) in hills north-west of the village of Barut-Aghaji in the Soltanieh Mountains. It corresponds to a 714-m-thick succession of alternating purple to green shales and sandstones and dark, laminated dolostones and limestones with chert nodules. The Soltanieh Formation was later recognized in the Alborz Mountains by Hamdi and Golshani in 1983 in Hamdi 1989. In the Alborz Mountains, Hamdi (1989) identified five members in the Soltanieh Formation at Dalir and Valiabad due to the presence of a thicker shale intercalation in the Upper Dolomite Member as defined by Stöcklin et al. (1964). Therefore, Hamdi (1989) described from bottom to top: (1) the Lower Dolomite Member (165 m thick); (2) the Lower Shale Member (120 m thick); (3) the Middle Dolomite Member (180 m thick); (4) the Upper Shale Member (90 m thick); and (5) the Upper Dolomite Member (580 m thick). The stratigraphic subdivisions of Stöcklin et al. (1964) and Hamdi (1989) have not been formally defined according to the International Stratigraphic Guide and such a procedure is beyond the scope of this paper. However, for practical purposes, this terminology is used in the rest of the paper, with the subdivisions of Stöcklin et al. (1964) and Hamdi (1989) used for the successions of the Soltanieh and Alborz Mountains, respectively.

In this study, the Soltanieh and Barut Formations were also investigated in the Soltanieh Mountains, around the type locality of the Soltanieh Formation (Fig. 1D) and of the Barut Formation (Fig. 1E). The type section of the Soltanieh Formation was visited and limestone levels sampled for SSFs but they did not yield any fossils. A second section was studied and sampled for SSFs (sample numbers starting with CH reported in Fig. 2) to the south-east of the type section, in a valley midway between the villages of Chopoghlu and Qafas Abad (coordinates of the start of the section N36.17998°; E48.92794°; Fig. 1D). Above the recognizable Bayandor Formation, we identified the Lower Dolomite Member, which is c. 100 m thick and consists of yellow, recrystallized, massive dolostone with numerous black and white chert bands (only the upper part is represented in Fig. 2). The Chopoghlu Shale Member is 108 m thick and dominated by shales (Fig. 2). In the lower part, limestone nodules and irregular beds are observed (Fig. 2). Massive, yellow, recrystallized dolostone constitutes most of the Upper Dolomite Member, which is 617 m thick (Fig. 2). Blue and finely laminated limestones are intercalated in the Upper Dolomite Member: a 22 m interval is present in the lowermost part and a 50 m interval at 136 m above the base of the member (Fig. 2). The Barut Formation overlies the Soltanieh Formation and its base corresponds to 24 m of blue, finely bedded limestones alternating with thin shale beds in the section south-east of the village of Chopoghlu (Fig. 1B, C). The base of the Barut Formation was also studied and sampled for SSFs at the type locality, where it consists of finely bedded blue limestones interbedded with rare shales (Fig. 2; sample numbers starting with D). The Lower Dolomite Member contains thick, massive, yellow dolostone and black cherts. The Chopoghlu Shale Member (delimited by the first and last occurrence of shale beds) is dominated by crumbly, grey, slaty shales in the lower part and centimetre-sized beds of cherty dolostone in the upper part. A 5-m-thick, dark limestone and 5-m-thick, yellow dolostone are intercalated in the upper part of the Chopoghlu Shale Member (Fig. 3). The Middle Dolomite Member consists of 67 m of massive, yellowish dolostone (Fig. 3). The Upper Shale Member is delimited by the first and last occurrence of shale beds. In its lower 35 m, alternations of thin beds of shales with dolostone and then phosphatic limestones are present (Fig. 3). The upper 68 m of the Upper Shale Member is dominated by dark shales (Fig. 3). The lowermost 8 m of the Upper Dolomite Member corresponds to thinly bedded, grey limestone (Fig. 3). The rest of the Upper Dolomite Member consists of massive, yellowish dolostone. At Valiabad (N36.27268°; E51.27462°), the succession is more difficult to study due to intense
vegetation cover and the presence of a large fault along the trail where the best outcrops are present, therefore only part of it has been sampled and is represented in Fig. 4. We could observe the Lower Dolomite Member, which was largely dominated by cherts. The Chopoghlu Shale Member is dominated by shales in the lower part, while the upper part is more cherty. The Middle Dolomite Member consists of massive, yellow dolostone except for a few metres of cherts in the lowermost part (sample numbers starting with V reported in Fig. 4). The lower
22 m of the Upper Shale Member contains thinly bedded, blue, phosphatic limestone beds alternating with dark shales (Fig. 4), and the upper part contains only dark shales. The contact between the Upper Shale Member and the Upper Dolomite Member was not observed due to intense vegetation cover. The Upper Dolomite Member produces abrupt cliffs, which makes access to the overlying Barut Formation too difficult in the two localities of the Alborz Mountains.

MATERIAL AND METHOD

In the Soltanieh Mountains 86 carbonate samples were collected from the SE Chopoghlu section and 8 at the Barut section exclusively for micropalaeontological studies (Fig. 2). Samples from the Alborz localities were also collected for micropalaeontological studies: 22 at the Dalir section (Fig. 3) and 17 at the Valiabad section (Fig. 4).

For micropalaeontological analyses, a minimum of 1 kg of each carbonate sample was processed in acid. For samples productive of SSFs, more material was processed (up to 2.5 kg). All the acid processing was performed at the Museum für Naturkunde Berlin (MfN). Samples were first broken into fragments and dissolved, either with c. 10% acetic acid when dealing with limestone or with c. 8% formic acid for the slightly dolomitic limestone. The acid-resistant residues were washed in water, wet-sifted (>50 μm), dried, and the microfossils manually picked from the dried residues under a stereomicroscope. The SSFs were stuck on stubs with carbon tape, coated with carbon and observed and imaged with a scanning electron microscope (JEOL-6610 LV) at the MfN. The described and figured material is housed in the collections of University Lille (USTL; Université des Sciences et Technologie de Lille) following the recommendation of the International Commission on Zoological Nomenclature.

RESULTS

This new study of the SSFs of the Soltanieh and Barut Formations of the Soltanieh and Alborz Mountains provides detailed, new and revised occurrences of SSFs in northern Iran. In this paper we excluded the siphogonuchitids and maikhanellids from the systematic section, although they are present in the successions along with the described taxa. Only their range is reported in the figures and is discussed (Figs 2–4). Another paper will focus on the systematic and detailed description of recovered siphogonuchitids and their phylogenetic implications.

In the Soltanieh Mountains, SSFs are relatively rare, and this is the first report of SSFs from this area. At the locality we studied, south-east of the village of Chopoghlu, SSFs first occur in the finely bedded, blue limestones of the lower middle part of the Upper Dolomite Member (sensu Stöcklin et al. 1964; Fig. 2). The SSFs of the Upper Dolomite Member in the Soltanieh Mountains are restricted to protoconodonts (Protohertizia anabarica Missarzhevsky, 1973 and P. unguliformis Missarzhevsky, 1973; Fig. 2). SSFs were then recovered in the Barut Formation at the SE Chopoghlu section and at the Barut type section (Fig. 2). They correspond to Oelandiella korobkovi Vostokova, 1962 and various other molluscs and siphogonuchitids (Lomasulcachites macrus Qian & Jiang in Jiang, 1980, Lopochites latazonalis Qian, 1977 and Siphogonuchites triangularis Qian, 1977).

In the Alborz Mountains, SSFs are well preserved, abundant and diversified. The lowest recoveries of SSFs are in the upper part of the Chopoghlu Shale Member at Dalir and in the lower part of the Upper Shale Member at Valiabad. At Dalir, 18 species are identified from the upper part of the Chopoghlu Shale Member to the lower part of the Upper Dolomite Member (sensu Hamdi 1989), and include (Fig. 3) protoconodonts (Protohertizia anabarica and P. unguliformis), anarbitids (Anarbites trisulcatus Missarzhevsky in Voronova & Missarzhevsky, 1969, A. ex gr. trisulcatus Missarzhevsky in Voronova & Missarzhevsky, 1969, A. tristichus Missarzhevsky in Rozanov et al., 1969, A. dalirense sp. nov., Cambrotubulus decoratus Missarzhevsky in Rozanov et al., 1969), Aetholicopalla adnata Conway Morris in Bengtson et al., 1990, and indeterminate cones and irregular tubes, all of which are described in this paper. Siphogonuchitids (Lomasulcachites macrus Qian & Jiang in Jiang, 1980, Lopochites latazonalis Qian, 1977, Siphogonuchites triangularis Qian, 1977 and siphogonuchitid sp. A and B) and maikhanellids (Maikhanella multa Zhegallo in Voronin et al., 1982, Purella squamulosa Qian & Bengtson, 1989 and Purella sp.) are also present and their stratigraphic ranges reported (Fig. 3), but they will be thoroughly described in another paper. At Valiabad, the same species are present but are
found only in the Upper Shale Member, except for *Anabarites dalirense*, *Purella* sp. and siphogonuchitid sp. A, which are absent (Fig. 4). No macrofossils were detected in the field or in the samples at any of the studied localities, except for *Chuaria* Walcott, 1899 in the Chopoghlu Shale Member.

**DISCUSSION**

This work constitutes a comprehensive study of the SSFs from the lower Cambrian of northern Iran. It includes a revision of the taxonomy and stratigraphic extension of the SSFs of the Soltanieh Formation of the Alborz Mountains at Dalir and Valiabad (Figs 3, 4), which were first described by Hamdi (1989, 1995) and Hamdi et al. (1989). It is extended by novel data on the SSFs of the Soltanieh and Barut Formations of the Soltanieh Mountains (Fig. 2). This substantial dataset enables us to discuss the following points.

**SSF assemblages of the lower Cambrian of northern Iran**

In order to take previous data into account for the identification of SSF assemblages from the Soltanieh and Barut Formations of the Soltanieh and Alborz Mountains, the taxonomic data from this study and from Hamdi (1989, 1995) and Hamdi et al. (1989) are compared, to enable the identification of a number of synonyms (Table 1). Some of the species (*Alborzinites iranensis*, *Cambroclavus fangxianensis*, *Dabashanites mirus*, *Hyolithellus vladimirovae*, *Lopothyrella isp.*, *Aethioclypea adha*), and *VasTorbiella spinulosa* from the lower Cambrian of northern Iran
Hyolithellus sp., Igorella? cyrtiformis, Igorella cf. hamata, Obtusoconus longicornic, Obtusoconus rostripteta, Palaeophirrhabda complexa, Pelagiella lorenzi, Psammathopalas amphidos, Pseudovalithecra crassa, P. glabella, Purella tainzhushanensis, Rugatotheca typica and Thambetolepis dalensis) listed (but not figured) by Hamdi (1989, 1995) and Hamdi et al. (1989) have not been recovered in the present study despite detailed observations in the field, thorough sampling and careful processing. The figured specimens assigned by Hamdi (1995) to Bemella simplex, Ginella savitzkii, Ginella orectes, Igorella vali-abadensis, Igorella mioribis and Yunnanopleura biformis show few diagnostic characters and fall in the range of morphological variations of the specimens referred to as cap-shaped molluscs in the present study. Hamdi (1995) assigned broken specimens to the species Coleolella reeta and Heraulitpegmina sp. but his material is too fragmentary to permit identification. In addition to the figured specimens, Hamdi (1989) listed many other species of SSFs in the description of the stratigraphy and fauna of the Soltanieh Formation at Dalir and Valiabad. However, without illustration, assessment of their taxonomic validity is impossible.

With regard to the taxonomic assessment of Hamdi (1989, 1995) and Hamdi et al. (1989), discrepancies were noted between the stratigraphic extension in those studies and that of the species identified in our study. According to our data, the stratigraphic extension of the SSFs is restricted to the interval from the upper part of the Upper Shale Member to the lower part of the Upper Barat Formation, whereas Hamdi (1989) and Hamdi et al. (1989) reported (without illustration) Hyolithellus sp., Igorella sp., monoplacophora?, Olivooides multisulcatus, Protohertzina sp., Sibellitides, Rugatotheca sp., phosphatic tubes and figured Archaeooides granulatus, Hyolithellus cf. filiformis, Rugatotheca typica, and biglobular fossils (Hamdi, 1995) from the Lower Dolomite Member at Valiabad. Despite careful observation and sampling of the Lower Dolomite Member at Dalir and Valiabad and in the valley south-east of Chopoghlu, no microfossils were recovered from this member. Moreover, according to Hamdi (1989, 1995), molluscs (species of Bemella, Igorella, Oelandiella, Obtusoconus, Protoconus, Purella, Scenella, Sinocomus, Xiangongconus etc. are listed but not figured) first occur in the upper part of the Upper Shale Member exclusively at Valiabad. Tashayee et al. (2012) also figure a possible specimen of Obtusoconus rostriptetae from the Upper Dolomite Member at Garmab (Alborz Mountains). In our study, no molluscs were recovered from the upper Shale Member, or from the lower part of the Upper Dolomite Members, the limestones of which were thoroughly investigated at Dalir. The upper part of the Upper Shale Member and the lower part of the Upper Dolomite Member were not accessible at Valiabad due to thick vegetation cover. We recovered molluscs only from the Barut Formation in the Soltanieh Mountains. It is possible, according to Hamdi (1989, 1995) and Hamdi et al. (1989), that molluscs occur below the level suggested by our new data, the upper part of the Upper Shale Member, and that they were recorded only in limited areas (Valiabad and Garmab). However, at Valiabad, the section is located close to a fault (Fig. 1C). In this context, it is also possible that the samples of the mollusc assemblages in Hamdi (1989, 1995) and Hamdi et al. (1989) may actually come from the Barut Formation (or even from an overlying formation such as the Zaigun, Lalun or Mila Formations; Fig. 1C) and not from the Upper Shale Member.

Based on the stratigraphic range of all the SSFs identified in each section derived from this study (Figs 2–4), we suggest the identification of two microfaunal assemblages. The first assemblage corresponds to SSFs occurring in the entire Soltanieh Formation in the Soltanieh and Alborz Mountains. It is composed of protoconodonts (Protohertzina anabaria and P. unguliformis), anabaritids (Anabarites trisulcatus, A. ex gr. trisulcatus, A. tristichus, A. dalirensis, Cambrotubulus decorvatus), maikhanellids (Maikhanella milta, Purella squamulosa and Purella sp.) and of Aetholicopalla adnata, indeterminate cones and irregular tubes. The biodiversity and abundance of this assemblage are dominated by tubes of anabaritids. The second assemblage is dominated, in diversity and abundance, by molluscs of the Barut Formation, which include Oelandiella korobkovi and various cap-shaped morphotypes. Along with the taxa of both assemblages there also occur siphogonuchitid sclerites of Lomasulcachites macrus, Lopochites latazonalis, Siphogonuchites triangularis and two morphotypes of unidentified siphogonuchitid species.

Interpretations of SSF assemblages and of the resulting chronostratigraphy should be considered with caution, considering recent advances in the identification of various factors affecting the SSF record. Indeed, SSF data are the result of acid extraction of microfossils from carbonate rocks. Therefore, the record of SSFs is strongly affected by the sampling procedure, given that only carbonate levels are targeted, leaving gaps in fossil data from the siliciclastic and dolomitic intervals. The extraction technique also introduces biases into the fossil record, given that originally calcareous shells are dissolved in the process (Jacquet et al. 2019). Phosphatization (replacement of the calcareous shell) and phosphogenesis (phosphatic coating or mould) are necessary for the recovery of the originally calcareous shells from acid-resistant residues, whereas originally siliceous and phosphatic shells are not affected (Jacquet et al. 2019). Phosphatization and phosphogenesis are the result of particular depositional and taphonomic processes outlined in Pruss et al. (2018).
| Species | Occurrence | Species | Figure | Occurrence |
|---------|------------|---------|--------|------------|
| Anabarites trisulcatus | CSM + MDM + USM + UDM | Anabarites trisulcatus | Hamdi et al. (1989): fig. 3h | MDM + USM |
| Anabarites tristichus | USM | Anabarites trisulcatus | Hamdi (1989): pl. 4, figs 4–5, 7 | MDM + USM |
| Protohertzina anabarica | CSM + MDM + USM | Protohertzina anabarica | Hamdi (1989): pl. 1, figs 3, 6–7 | MDM + USM |
| | | Protohertzina cf. anabarica | Hamdi (1995): pl. 5, figs 17, 18 | USM |
| | | Protohertzina robusta | Hamdi (1989): pl. 2, figs 4–8 | MDM |
| | | Protohertzina unguliformis | Hamdi (1989): pl. 1, fig. 1 | MDM |
| | | Protohertzina anabarica | Hamdi et al. (1989): fig. 3g | USM |
| | | Protohertzina cf. unguliformis | Hamdi (1989): pl. 1, fig. 10; pl. 3, fig. 1 | MDM |
| | | Protohertzina cf. siciformis | Hamdi (1995): pl. 5, figs 11–13 | USM |
| | | Hastina sp. | Hamdi (1989): pl. 1, figs 4, 5 | MDM |
| | | Cambrotubulus decurvatus | Hamdi et al. (1989): fig. 3e | USM |
| Siphogonuchites triangularis | CSM + MDM + USM + UDM + BF | Siphogonuchites triangularis | Hamdi (1995): pl. 6, figs 5–9, 13; pl. 10, fig. 1 | USM |
| | | Palaeosulcachites cf. biformis | Hamdi (1989): pl. 3, fig. 7 | USM |
| Lopochites latazonalis | CSM + MDM + USM + UDM + BF | Lopochites latazonalis | Hamdi (1995): pl. 6, figs 14, 15 | MDM |
| | | Drepanochites dilatatus | Hamdi (1995): pl. 6, figs 10–12 | MDM |
| | | Quadrochites disjunctus | Hamdi (1995): pl. 8, figs 4, 5 | MDM |
| | | Lopochites cf. latazonalis | Hamdi (1995): pl. 10, fig. 2 | MDM + USM |
| | | Lomasulcachites macrus | Hamdi (1995): pl. 14, figs 2, 3 | USM |
| Aetholicopalla adnata | CSM + MDM + USM | Archaeospira granulata | Hamdi (1995): pl. 7, fig. 5 | MDM + USM |
| Maikhanella multa | USM | Lapidites emeiensis | Hamdi (1995): pl. 7, figs 1–3, 6–8 | MDM |
| | | Maikhanella cf. multa | Hamdi (1995): pl. 9, figs 2, 4 | MDM |
| | | Maikhanella multa | Hamdi et al. (1989): fig. 3d | USM + UDM |
| Oelandiella korobkovi | BF | Latouchella cf. korobkovi | Hamdi (1995): pl. 11, figs 1, 2, 8, 9, 12; pl. 16, figs 11, 12 | USM + UDM |
| Irregular tube | USM | Hubeispira nitida | Hamdi (1995): pl. 11, figs 3, 11 | USM |
| Indeterminate cones | USM | Latouchella maidipingensis | Hamdi (1995): pl. 11, figs 4–6, 7, 10; pl. 16, figs 7–10 | USM + UDM |
| | | Latouchella korobkovi | Hamdi (1989): pl. 6, figs 1, 2 | USM |
| | | Latouchella sp. | Hamdi (1995): pl. 12, figs 3, 7, 9, 11, 12 | USM |
| | | Latouchella ex gr. korobkovi | Hamdi (1989): pl. 6, figs 3, 4 | USM |
| | | Archaeospira ornata | Hamdi (1995): pl. 12, figs 6, 8, 10 | USM |
| | | Archaeospira regularis | Hamdi (1995): pl. 14, figs 1, 2 | USM |
| | | ?Aldanella sp. | Hamdi et al. (1989): fig. 3b | n.a. |

BF, Barut Formation; CSM, Chopoghlu Shale Member; MDM, Middle Dolomite Member; n.a., not applicable; UDM, Upper Dolomite Member of the Soltanieh Formation; USM, Upper Shale Member.
and references therein) and Freeman et al. (2019 and references therein), which therefore introduce a bias into the distribution of SSFs in sections. SSF distribution thus appears to be influenced by facies (e.g. Jacquet et al. 2019) and additionally by palaeoenvironmental conditions (e.g. bathymetry; Jacquet et al. 2019). The impact on regional biostratigraphy and the global correlation of shell mineralogy, extraction technique, palaeoenvironmental, depositional and taphonomic conditions associated with SSF data should thus be considered.

The SSF data from northern Iran presented in this paper, as are any traditional SSF data, are subject to the biases described above. Indeed, the SSFs were mostly extracted by acetic acid digestion from limestone levels. Limestone intervals were preferentially sampled from the mixed carbonate–siliciclastic succession of the Soltanieh and Barut Formations. However, it was possible to reduce the gaps in the SSF distribution in the siliciclastic intervals of the sections thanks to the presence of limestone intercalations within the shales, which were sampled, dissolved and picked for SSFs (Figs 2–4). Dolostones, which represent a considerable thickness of the Soltanieh Formation, are also unfavourable to the extraction of SSFs but efforts were made to sample the less dolomitic beds, which were dissolved with formic acid for SSF extraction (Figs 2–4). Acid extraction of SSFs also introduced a bias in the SSF distribution due to the mineralogy of their shells. The shells of the recovered anabaritids, maikhanellids, siphonogonuchitids and Aetholicopalla adnata are interpreted as calcareous. These taxa are preserved as phosphatic replacement of the shells/tests (Anabarites trisulcatus, Aetholicopalla adnata), phosphatic internal coatings (Anabarites tristichus, A. trisulcatus, A. dalirense, Cambrotubulus decurvatus) and/or external coatings (Aetholicopalla adnata), and/or internal moulds (Anabarites tristichus, A. trisulcatus, A. ex gr. trisulcatus, A. dalirense, Cambrotubulus decurvatus, Oelandiella korobkovi, Aetholicopalla adnata). The original mineralogy of the shells of the indeterminate cones and irregular tubes also described in this study is not known, therefore the taphonomic impact on their record cannot be assessed with certainty, but they are preserved as internal moulds, which suggests a calcareous mineralogy. As stated by Jacquet et al. (2019), the occurrences of these calcareous taxa are strongly related to facies (i.e. depositional environment and preservation potential) and therefore to palaeoenvironmental conditions. In order to evaluate how lithological and taphonomic constraints influence the stratigraphic distribution of the SSFs in northern Iran, detailed microfacies and multivariate analyses associated with the micropalaeontological data presented in this paper will be integrated in a future study (following Jacquet et al. 2019). The only originally phosphatic elements from the described Iranian assemblages are the protoconodonts Protohertzina anabarica and P. unguliformis. According to Jacquet et al. (2019), given that the distribution of phosphatic taxa is more reliable than that of calcareous taxa, the range of Protohertzina anabarica and P. unguliformis in the Iranian sections should therefore be prioritized in biostratigraphic and correlation discussions.

Revision of biochronostratigraphic interpretations of the lower Cambrian of northern Iran

Most of the taxa identified in the Soltanieh and Barut Formations of northern Iran have a wide palaeogeographic distribution and a relatively well-described stratigraphic range that enable their use for biostratigraphic studies and chronostratigraphic interpretations of the sections. It appears that, from the composite stratigraphic range of globally distributed taxa (Fig. 5), the sampled and fossiliferous studied intervals of the Soltanieh and Barut Formations correspond to the Terreneuvian

FIG. 5. Range of globally distributed taxa recorded in the Soltanieh and Barut Formations (see Table S1 for detailed references). Occurrence data in black refer to species described in this work and occurrence data in grey refer to those that are currently unpublished.
(Figs 2–4). Only one species (*Aethelicopterrella adnata*) of the 12 biostatigraphically significant species has a stratigraphic range extending up to the Cambrian Stage 3 (Fig. 5). Only two formally identified species are restricted to the Fortunian: *Maikhanella multa* and *Purella squamulosa* (Fig. 5). Therefore, the upper limit of the Fortunian can be interpreted at or above the highest occurrence of those taxa. Hence, the transition from the Fortunian to the Cambrian Stage 2 is most probably located in the lower part of the Upper Shale Member, where the highest occurrences of *Maikhanella multa* and *Purella squamulosa* are reported at Dalir and Valiabad (Figs 3, 4). *Maikhanella multa* and *Purella squamulosa* were not recovered in the Soltanieh Mountains, therefore the position of the transition from the Fortunian to the Cambrian Stage 2 cannot be identified based on biostatigraphic data (Fig. 2), but can be inferred from lithological correlations with the record from the Alborz Mountains. No SSF restricted to the Cambrian Stage 3 has been recovered from the Soltanieh and Barut Formations of the Alborz and Soltanieh Mountains.

Our chronostratigraphic interpretation of the Soltanieh Formation of the Alborz Mountains differs from that of Hamdi (1989, 1995) and Hamdi *et al.* (1989), which was further promoted by Shahkarami *et al.* (2017a, b). They considered the upper part of the Soltanieh Formation to be Cambrian Stage 3. Such an interpretation is questionable due to several lines of evidence. A Cambrian Stage 3 age is deduced from the ichnostratigraphy by Shahkarami *et al.* (2017a, b), who identified four ichnozones. Ichnozone 1 spans the middle interval of the Chopoghlu Shale and is similar to the ichnofauna of the Ediacaran (Shahkarami *et al.* 2017a). However, due to the interpretations of Hamdi (1989, 1995) and Hamdi *et al.* (1989), which suggest that Fortunian SSFs occurred in the Lower Dolomite Member, and due to environmental settings associated with this ichnofauna in Iran, Shahkarami *et al.* (2017a) concluded that Ichnozone 1 is a distal expression of the Fortunian *Treptichnus pedum* Zone. Ichnozone 2 corresponds to the upper part of the Chopoghlu Shale Member; it the Middle Dolomite Member, and the lower part of the Upper Shale Member; it is defined by the first occurrence of *Treptichnus pedum*, and is regarded as Fortunian in age (Shahkarami *et al.* 2017a). Such an interpretation is congruent with the first occurrence of SSFs in the upper part of the Chopoghlu Shale at Dalir and in the lower part of the upper Dolomite (*sensu* Stöcklin *et al.* 1964; equivalent to the Middle Dolomite of Hamdi 1989) south-east of Chopoghlu, as shown in the present study. Ichnozone 3 represents the middle part of the Upper Shale Member and is interpreted as Fortunian to Cambrian Stage 2 (Shahkarami *et al.* 2017a), as suggested by the SSF distribution in the present study. Ichnozone 4, defined by the first occurrence of *Psammichnites gigas*, corresponds to the uppermost part of the Upper Shale Member and is regarded as Cambrian Stage 2–3 (Shahkarami *et al.* 2017a).

**Contribution of the SSFs from northern Iran to our knowledge of the evolution of palaeobiodiversity during the Cambrian explosion**

The identification of two distinct, successive microfaunal assemblages in the Terreneuvian successions of northern Iran can be compared with the few global and regional patterns of faunal changes during the pre-trilobitic Cambrian advanced in the literature. Maloof *et al.* (2010), Porter (2010) and Kouchinsky *et al.* (2012) presented sequences of first appearance of various clades of metazoans at the global scale, by considering biomineralization events; whereas Li *et al.* (2007) and Zhu *et al.* (2017) reconstructed early Cambrian metazoan fossil
sequential occurrences for south China from a biodiversity perspective, and Budd & Jackson (2016) presented global faunal sequences from an evolutionary perspective. The raw data on which these faunal sequences have been interpreted are, however, not detailed and it would be necessary to have access to the raw data to evaluate the interpretations. In each sequence, anabaritids and protoconodonts are part of the first faunal assemblage (protoconodonts are slightly delayed compared with anabaritids for Li et al. 2007, Maloof et al. 2010, Kouchinsky et al. 2012 and Zhu et al. 2017). They are accompanied by sclerites (grouped as the debated ‘coeloscleritophorans’) in Maloof et al. (2010) and Porter (2010), whereas sclerites appear later in south China according to Li et al. (2007). Other tubular organisms (hyolithelminths and the rather conical hyoliths) are directly associated with the assemblage of anabaritids, protoconodonts and sclerites according to Maloof et al. (2010) and Porter (2010), whereas they are slightly delayed according to Li et al. (2007), Kouchinsky et al. (2012) and Zhu et al. (2017). In the Maloof et al. (2010) study, molluscs appear later than anabaritids, protoconodonts, and sclerites. However, the first appearance of ‘cap-shaped fossils’ is reported simultaneously as protoconodonts and sclerites by Maloof et al. (2010), who include under this term possible univalved molluscs, but also sclerites of halkieriids or other ‘coeloscleritophorans’ and isolated valves of possible brachiopods. For Li et al. (2007), Porter (2010) and Kouchinsky et al. (2012), molluscs first occur simultaneously in the assemblage with anabaritids, protoconodonts and coeloscleritophorans, whereas they are reported as occurring later by Zhang et al. (2017). Budd & Jackson (2016) proposed a sequence of faunal change for the Ediacaran–Cambrian transition by grouping taxa under the informal term ‘X world’ according to the type of assemblage (Fig. 6). According to the authors, the terminal Ediacaran is characterized by problematic tubes best represented by Cloudina. Similarly, the basalmost part of the Cambrian is also dominated by an assemblage of tubes of uncertain affinities, notably of anabaritids and by protoconodonts of the genus Protohertzina and sponge spicules and ctenophores, which has been named ‘tube world’ (Budd & Jackson 2016). Then, various cap-shaped fossils including the ‘scaly’ shells Purella and Maikhanella, halkieriids and many other taxa dominate the upper half of the Fortunian in the ‘sclerite world’. In Cambrian Stage 2, the assemblages are dominated by brachiopods (‘brachiopod world’) and hyolithids, and by archaeocyaths with associated fauna in reef settings (Budd & Jackson 2016). The Cambrian Stage 3 is marked by the appearance and rapid diversification of trilobites (‘trilobite world’; Budd & Jackson 2016). This pattern is deduced from global data on the early Cambrian at the time of writing and is expected to change with additional information. Our work on the SSFs of northern Iran provides new data to review these faunal sequences. No terminal Ediacaran tubes were recovered in this study. From this work, it appears that most of the Fortunian of northern Iran records what we have described as the first microfaunal assemblage, which is dominated by tubes of anabaritids (Anabarites and Cambrotubulus) and the protoconodont Protohertzina (Fig. 6), along with a minority of maikhanelids (Maikhanella and Purella). This is relatively congruent with the interpretations of Li et al. (2007), Maloof et al. (2010), Porter (2010), Kouchinsky et al. (2012) and Zhang et al. (2017), although hyoliths and

**FIG. 6.** Sequence of faunal change in the Cambrian based on Budd & Jackson (2016) (above) and this study of small shelly fossils (SSFs) from northern Iran (below).
hyolithelminths are missing from northern Iran. It corresponds to the tube world and part of the sclerite world of Budd & Jackson (2016). Our second assemblage, interpreted as Cambrian Stage 2, is dominated by molluscs in diversity and abundance, and is called the ‘mollusc world’ (Fig. 6). This sequence, with a delayed appearance of molluscs compared with the assemblage of anabaritids, protoconodonts and sclerites, is similar to the sequence described by Zhang et al. (2017) but differs from the interpretations of Li et al. (2007), Maloof et al. (2010) and Porter (2010), although data on the actual species that these authors consider as molluscs would be necessary for appraisal of the interpretation. The mollusc assemblage was not recognized by Budd & Jackson (2016). In Iran the siphogonuchitid sclerites also occur in both assemblages, therefore part of the sclerite world of Budd & Jackson (2016) occurs as a background signal during the entire Terreneuvian in northern Iran (Fig. 6). The discrepancies in the sequence of faunal changes for the pre-trilobitic Cambrian demonstrate the necessity to precisely identify the sequence of faunal changes by constructing taxonomically solid databases, first at the regional scale, so that datasets can then be compared between regions to identify a possible global signal, but such a work is beyond the scope of this study.

CONCLUSION

This work on the Soltanieh and Barut Formations of the Soltanieh and Alborz Mountains provides new and revised data on occurrences of SSFs from the lower Cambrian of northern Iran. One part of the study focuses on the novel report of SSFs from the Soltanieh and Barut Formations of the Soltanieh Mountains, and the other part consist of new data used for a revision of work previously conducted in the Soltanieh Formation of the Alborz Mountains for the taxonomy and stratigraphic range of the SSFs (Hamdi 1989, 1995; Hamdi et al. 1989). Regarding the results from the SSFs, two distinct microfaunal assemblages are identified in the successions. The first assemblage of SSFs occurs from the upper part of the Chopoghlu Shale Member to the lower part of the Chopoghlu Shale Member and the lower part of the Barut Formation, therefore this result differs completely from the interpretation of Hamdi (1989, 1995) and Hamdi et al. (1989), who classified most of the Upper Dolomite Member as corresponding to the Cambrian Stage 3 based solely on the occurrence of one species, the assignment of which is doubtful. Our dataset on the Terreneuvian faunal evolution of northern Iran enables us to discuss the sequence of faunal change for the Ediacaran–Cambrian transition proposed by Li et al. (2007), Maloof et al. (2010), Porter (2010), Kouchinsky et al. (2012), Budd & Jackson (2016) and Zhang et al. (2017). The successive Terreneuvian tube, sclerite, and brachiopod worlds of Budd & Jackson (2016) are better represented in northern Iran by successive tube and mollusc worlds, both with a sclerite background.

Institutional abbreviation. USTL, Université de Sciences et Technologie de Lille, France.

SYSTEMATIC PALAEONTOLOGY

by Léa Devaere, Dieter Korn and Abbas Ghaderi
Phylum ?CHAETOGNATHA Leuckart, 1854
Class, Order & Family UNCERTAIN
Genus PROTOHERTZINA Missarzhevsky, 1973

Type species. Protohertzina anabatica Missarzhevsky, 1973; Fortunian, mouth of the Kotujkan River, Siberia, Russia.

Diagnosis. See Qian & Bengtson (1989).

Remarks. Part-based taxonomy is applied here for the identification of the spine-shaped phosphatic elements from the Soltanieh Formation. They are assigned to the genus Protohertzina because of the laterally slightly compressed spine-shape of the simple elements, which are characteristic for this genus.
Kouchinsky et al. (2017) restudied the topotype material of *P. anabarica*, in which the morphological variation led those authors to unify *P. anabarica*-type elements or *P. unguliformis*-type elements under the species *P. anabarica*. However, in the Iranian material, specimens assigned to *P. anabarica* and *P. unguliformis* described below are clearly different and are characterized by very distinct morphologies without any continuous morphological transition; this does not support an amalgamation of *P. anabarica*-type and *P. unguliformis*-type elements under the species *P. anabarica* in a context of part-based taxonomy. They might represent different elements from the same apparatus but it is not possible to confirm this in the absence of articulated apparatus and/or statistical analysis of the distribution of both morphological groups. Also, *P. anabarica* and *P. unguliformis* do not necessarily co-occur in all of the samples: they co-occur only in six samples, whereas *P. unguliformis* occurs alone in eight samples and *P. anabarica* in one sample. The two distinct morphological groups from the Alborz Mountains are therefore assigned to two different species.

**Protohertzina anabarica** Missarzhevsky, 1973

*Figure 7A–J*

1973 Protohertzina anabarica Missarzhevsky; pp 54–55, figs 1–3, pl. 9 figs 1, 2, 4, 6.
1977 Protohertzina robusta Qian; p. 268, pl. 2 figs 13–14.
1977 Protohertzina anabarica Missarzhevsky; Qian, p. 267–
268, pl. 2 figs 7, 8, 11, 12.
1979 Protohertzina anabarica Missarzhevsky; Qian et al., pl. 4 figs 3–4.
1980 Protohertzina cf. anabarica; Conway Morris & Fritz, fig. 3a–c.
1981 Protohertzina anabarica Missarzhevsky; Missarzhevsky & Mambetov, fig. 16.9.
1983 Protohertzina anabarica Missarzhevsky; Azmi, pl. 5 figs 1–2, 14. pl. 6 figs 1, 6. 8.
1983 Protohertzina unguliformis Missarzhevsky; Azmi, p. 384, pl. 5 figs 3, 4, 11–13.
1984 Hastina quadrigoniata Yang & He; p. 38–39, pl. 2 figs 4–5.
1984 Protohertzina robusta Qian; Chen, pl. 1 fig. 13.
1984 Protohertzina anabarica Missarzhevsky; Xing et al., pl. 3
figs 24–25.
1984 Protohertzina anabarica Missarzhevsky; Xing et al.,
pl. 14 figs 12–13.
1984 Protohertzina anabarica Missarzhevsky; Luo et al., pl 7
figs 6, 6a.
1984 Protohertzina dabashanensis Yang & He; p. 41, pl. 2
figs 1–3.
1985 Protohertzina anabarica Missarzhevsky; Nowlan et al.,
p. 245, fig. 8A–F.
1985 Protohertzina sp. B; Nowlan et al., p. 246, pl. 9.
1987 Protohertzina anabarica Missarzhevsky; Brasier & Singh,
p. 333–334, figs 5.1–8, 14–16, 21–22, 24–25.
1988 Protohertzina unguliformis Missarzhevsky; Mambetov,
p. 152, fig. a.

1989 Protohertzina anabarica Missarzhevsky; Hamdi, pl. 1
figs 3, 6–7.
1989 Protohertzina robusta Qian; Hamdi, pl. 2 figs 4–8.
1989 Protohertzina anabarica Missarzhevsky; Qian, pp 212–
213, pl. 47 figs 1–2, pl. 53 figs 1–5, pl. 86 figs 5, 6.
1989 Protohertzina anabarica Missarzhevsky; Qian &
Bengtson, pp 68–69, fig. 40.
1989 Protohertzina anabarica Missarzhevsky; Landing et al.,
p. 765, fig. 7.2.
1991 Protohertzina anabarica Missarzhevsky; Bhatt, fig. 4A.
1995 Protohertzina cf. anabarica Missarzhevsky; Hamdi, pl. 5
figs 17–18.
1996 Protohertzina anabarica Missarzhevsky; Esakova &
Zhegallo, p. 99, pl. 4, fig. 1.
2004 Protohertzina anabarica Missarzhevsky; Azmi & Paul,
fig. 3f.
2004 Protohertzina anabarica Missarzhevsky; Steiner et al.,
fig. 3.8.
2006 Protohertzina anabarica Missarzhevsky; Pyle et al., p.
316 figs 6.5–6.8.
2007 Protohertzina anabarica Missarzhevsky; Steiner et al.,
fig. 4A.
2014 Protohertzina anabarica Missarzhevsky; Guo et al., figs
2g–h, 5n1–n2.
2014r Protohertzina anabarica Missarzhevsky; Yang et al.,
fig. 12A–B.
2016 Protohertzina anabarica Missarzhevsky; Yang et al.,
fig. 7K.
2017 Protohertzina unguliformis Missarzhevsky; Kouchinsky
et al., p. 396–400, fig. 57H–J.

**Diagnosis.** See Qian & Bengtson (1989).

**Material.** 30 complete or broken elements including the figured specimens USTL3198-6, USTL3200-1 and USTL3223-7.

**Preservation.** Almost complete elements preserved as phosphatic walls with internal cavity partially filled with phosphatized material (Fig. 7A–F) or as phosphatized internal moulds broken at the base (Fig. 7G–J).

**Description.** The generally complete elements are robust, spine-shaped, bilaterally symmetrical (Fig. 7A, G, J) with a height between 1.465 and 2.635 mm. A moderate lateral compression and gentle (Fig. 7I) to strong (up to 56°) curvature occurs in the median plane (plane of bilateral symmetry); the apical part has a slight curvature, while the maximum curvature can be seen at the base (Fig. 7B–E). The apex has a sharp angle of divergence of c. 9° (between 7° and 11°; Fig. 7A, G, J) and a circular cross-section. The base is flared with a semi-circular cross-section elongated in the plane perpendicular to the median plane (Fig. 7D). Aperture width (W, distance between the opposite lateral ridges at the aperture): c. 0.640 µm; aperture length (L, distance between the convex and planar sides at the aperture): c. 0.410 µm; W/L, c. 1.55. The cross-section of the elements is semi-circular due to the presence of two sides differentiated at one-third of the height below the apex: one rounded,
smooth, convex side is opposite one relatively planar side with a weakly defined median ridge. The two sides are separated by well-defined, prominent lateral ridges arranged at a right angle (Fig. 7B, D, E, I). Lateral ridges appear at the apex and are first marked by a triangular area (arrow in Fig. 7A). When the shell is preserved, its thickness is c. 35 µm (Fig. 7D).
Remarks. The Iranian specimens described here are assigned to *P. anabarica* because of the absence of a median keel and the absence of a lateral depression, both of which are typical of *P. yudomica* Demidenko, 2006. They differ from *P. biformis* Qian, 1989 and *P. dabashanensis* Yang & He, 1984 by the stronger lateral compression, and from *P. siciformis* Missarzhevsky, 1973 by the weaker lateral compression. The present specimens share most morphological characters with *P. unguliformis* Missarzhevsky, 1973. However, they can be separated from *P. unguliformis* by the weaker lateral compression, the well-defined, non-merging, prominent lateral ridges that separate the broader convex side from the planar sides, and by the more continuous transition between the adapical part and the base.

Distribution. Terreneuvian, Soltanieh Formation, Iran: samples CH109, CH68, CH69 and CH70 of the SE Chopoghlu section, and V20 of the Valiabad section, Alborz Mountains; samples D2, D4, D6, D7 and D10 of the Dalir section and samples V13 and V20 of the Valiabad section, Alborz Mountains; samples USTL3199-1, USTL3205-1, 3211-4 and USTL3222-2, 3224-1, 3224-3, 3224-5.

**Protohertzina unguliformis** Missarzhevsky, 1973

*Figure 7K–AE*

1973 *Protohertzina unguliformis* Missarzhevsky; p. 55, text-figs 4, 5, pl. 9 fig. 3.

1975 *Protohertzina unguliformis* Missarzhevsky; Matthews & Missarzhevsky, pl. 3, figs 5, 6.

1977 *Protohertzina unguliformis* Missarzhevsky; Bengtson, fig. 9.

1977 *Protohertzina anabarica* Missarzhevsky; Qian, p. 267–268, pl. 2 figs 9–10.

1979 *Protohertzina anabarica* Missarzhevsky; Qian *et al*., pl. 4 figs 2, 5–6.

1982 *Emeida primitiva* Chen; p. 258, pl. 1, fig. 35.

1983 *Protohertzina unguliformis* Missarzhevsky; Azmi, p. 384, pl. 5 figs 3, 4, 11–13.

1983 *Protohertzina unguliformis* Missarzhevsky; Azmi & Pancholi, p. 367, pl. 1 figs 9, 10, 13.

1983 *Protohertzina unguliformis* Missarzhevsky; Bengtson, p. 8, figs 1a–1e.

1984 *Hastina bialata* Yang *et al*.; pl. 2, figs 7–9.

1984 *Protohertzina unguliformis* Missarzhevsky; Qian & Yin, p. 112, pl. 5 figs 6, 7.

1984 *Protohertzina unguliformis* Missarzhevsky; Wang *et al*., pl. 5 figs 4a, 4b.

1984 *Protohertzina anabarica* Missarzhevsky; Xing *et al*., pl. 21 fig. 2, pl. 28 fig. 16.

1984 *Hastina bialata* Yang & He; p. 39, pl. 2 figs 14–21.

1985 *Protohertzina unguliformis* Missarzhevsky; Nowlan *et al*., p. 245, fig. 8g–k.

1987 *Protohertzina anabarica* Missarzhevsky; Brasier & Singh, figs 5, 9, 10–13, 19–20, 23, 26–28.

1989 *Protohertzina unguliformis* Missarzhevsky; Hamdi, pl. 1 figs 1–2.

1989 *Protohertzina cf. unguliformis*; Hamdi, pl. 1 fig. 10, pl. 3 fig. 1.

1989 *Protohertzina cf. siciformis*; Hamdi, pl. 5 figs 11–13.

1989 *Hastina sp.*; Hamdi, pl. 1 figs 4–5.

1989 *Protohertzina anabarica* Missarzhevsky; Hamdi *et al*., fig. 3g.

1989 *Protohertzina unguliformis* Missarzhevsky; Missarzhevsky, pl. 25 fig. 1.

1989 *Protohertzina unguliformis* Missarzhevsky; Qian, p. 213, pl. 53 figs 6–13, pl. 58 figs 8, 9.

1989 *Protohertzina unguliformis* Missarzhevsky; Qian & Bengtson, p. 69, text-figs 41, 42.

1995 *Protohertzina unguliformis* Missarzhevsky; Hamdi, pl. 5 figs 7–10.

1996 *Protohertzina unguliformis* Missarzhevsky; Esakova & Zhegallo, p. 100, pl. 4 figs 2, 3.

2004 *Protohertzina anabarica* Missarzhevsky; Azmi & Paul, fig. 3d, e.

2004 *Protohertzina unguliformis* Missarzhevsky; Qian *et al*., fig. 1 F, K.

2004 *Protohertzina anabarica* Missarzhevsky; Steiner *et al*., figs 3.11–12, 6.11, 8.11.

2007 *Protohertzina unguliformis* Missarzhevsky; Steiner *et al*., fig. 4B.

2010 *Protohertzina unguliformis* Missarzhevsky; Parkhaev & Demidenko, p. 927, pl. 29 figs 2, 3.

2012 *Protohertzina unguliformis* Missarzhevsky; Tashyoeae *et al*., pl. 1, fig. 7.

2012 *Protohertzina siciformis* Missarzhevsky; Tashyoeae *et al*., pl. 2, fig. 4.

2014 *Protohertzina anabarica* Missarzhevsky; Guo *et al*., figs 2d–f, 5p.

2014 *Protohertzina anabarica* Missarzhevsky; Yang *et al*., fig. 12C.

2014 *Protohertzina anabarica* Missarzhevsky; Yang *et al*., fig. 2O–P.

2016 *Protohertzina unguliformis* Missarzhevsky; Budd & Jackson, fig. 6a.

2016 *Protohertzina anabarica* Missarzhevsky; Yang *et al*., fig. 7L–J.

2017 *Protohertzina unguliformis* Missarzhevsky; Kouchinsky *et al*., pp 396–400, fig. 57A–G, K.

Diagnosis. See Qian & Bengtson (1989).

Material. 215 complete or fragmentary elements including the figured specimens USTL3199-2 and USTL3201–2, 3201-10, 3202–4, 3201-1, 3211–4 and USTL3222–2, 3224–1, 3224–3, 3224–5.

Preservation. The elements are almost complete and preserved as phosphatic walls with an internal cavity that is partially filled with phosphatized material (Fig. 7K, M, U–AE) or as phosphatized internal moulds (Fig. 7L, N–T).

Description. The spine-shaped, bilaterally symmetrical elements (Fig. 7L, P, AC) range in height from 1.565 to 3.645 mm. They are slender with strong lateral compression and strongly curved in the median plane (up to 90°; Fig. 7N, R, T, V, X–AB). Apical part with moderate curvature, maximum curvature at the base. Sharp apex with angle of divergence of c. 3° with a range from 1.6° to 6° (Fig. 7L, P, AC) and a circular cross-section. Flared base with nearly heart-shaped cross-section elongated in the plane perpendicular to the median plane (Fig. 7L, P, Z, AA). Apertural width, c. 485 µm; apertural length, c. 410 µm; W/L, c. 1.18. The shape of the cross-section of the adapical part of the element is due to presence of two sides differentiated very shortly after the apex.
(Fig. 7O, Q, AC, AD); one rounded, convex side with a faint median ridge (Fig. 7T, AB) opposite one subdivided by a prominent median ridge into two planar to concave surfaces (Fig. 7L, M, O, P, AC). The two sides are separated by well-defined lateral ridges (Fig. 7N, R, U, V, X–AC) that appear around the apex and are first marked by a triangular area (arrow in Fig. 7K, Z). The wall of thickness c. 30 \( \mu \)m is, when preserved, composed of multiple layers of 2–11 \( \mu \)m in thickness (Fig. 7AC–AE). The external surface of the wall layers is composed of longitudinally oriented fibres (Fig. 7V–W).

**Remarks.** The Iranian specimens are assigned to *Protohertzina ungaformis* because of the absence of a median keel and a lateral depression, which are characteristic of *P. yadomica* Demidenko, 2006. They differ in the degree of lateral compression from *P. biformis* Qian, 1989 and *P. dabashanensis* Yang & He, 1984 (stronger compression) as well as from *P. sicformis* Misarzhevsky, 1973 (weaker compression). The specimens from Iran are morphologically most similar to *P. anabarica* (for separating characters, see discussion for this species above).

**Distribution.** Terreneuvian, Soltanieh Formation, Iran: samples D2, D4, D6, D7, D9a, D10, D13, D16 and D17 of the Dalir section and samples V9, V12, V13, V14 and V17 of the Valiabad section, Alborz Mountains; samples CH109, CH111, CH114, CH68 and CH69 of the SE Chopoghlu section, Soltanieh Mountains.

**Phylum ?Cnidaria Hatschek, 1888**

**Class & order UNCERTAIN**

**Family ANABARITIDAE Misarzhevsky, 1974**

**Genus ANABARITES Misarzhevsky in Voronova & Misarzhevsky, 1969**

**Type species.** *Anabarites trisulcatus* Misarzhevsky in Voronova & Misarzhevsky, 1969; Fortunian, mouth of the Kotujkan River, Anabar Uplift, Siberia, Russia.

**Diagnosis.** See Kouchinsky et al. (2009).

**Anabarites tristichus** Misarzhevsky in Rozanov et al., 1969

**Figure 8**

1965 *Hyolithellus* sp. Sysoev, p. 13, fig. 2.
1967 *Anabarites tristichus* Misarzhevsky; p. 20 [nomen nudum].
1969 *Anabarites tristichus* Misarzhevsky; Rozanov et al., pp 156–157, pl. 8 figs 1, 14, 19.
1975 *Jakutiochrea tristicha* (Misarzhevsky); Val’kov, pl. 13 fig. 9.
1975 *Anabarites tristichus* Misarzhevsky; Matthews & Misarzhevsky, pl. 2 fig. 8.
1982 *Jakutiochrea* sp.; Val’kov, p. 78–79, pl. 13 fig. 20.
1982 *Jakutiochrea tristicha* (Misarzhevsky); Val’kov, pl. 13 figs 17–19.
1983 *Anabarites tristichus* Misarzhevsky; Sokolov & Zhuravleva, p. 160, pl. 51 fig. 2.
1984 *Anabarites gracilis* Chen; p. 62, pl. 1 fig. 9.
1987 *Jakutiochrea solita* Val’kov; pp 111–112, pl. 14 figs 1–5.
1987 *Jakutiochrea lenta* Val’kov; p. 114, pl. 14 figs 7–8.
1987 *Jakutiochrea portentosa* Val’kov; p. 113, pl. 14 fig. 6.
1989 *Anabarites trisulcatus* Misarzhevsky; Brasier, pl. 7A fig. 9.
1989 *Anabarites trisulcatus* Misarzhevsky; Hamdi, pl. 4, figs 4–5, 7.
1989 *Anabarites tristichus* Misarzhevsky; Khomentovsky & Karlova, p. 56, pl. 6 fig. 4.
1989 *Jakutiochrea tristicha* (Misarzhevsky); Misarzhevsky, pl. 13 figs 3, 16–17.
2002 *Jakutiochrea tristicha* (Misarzhevsky); Kouchinsky & Bengtson, figs 2–5.
2009 *Anabarites tristichus* Misarzhevsky; Kouchinsky et al., pp 273–274, figs 26–28.
2012 *Jakutiochrea lenta* Mokova & Valko; Tashayoei et al., pl. 1 fig. 6.
2017 *Anabarites tristichus* Misarzhevsky; Kouchinsky et al., pp 420, fig. 76A–C, F.

**Diagnosis.** See Kouchinsky et al. (2009).

**Material.** 39 specimens including the figured material USTL3206–6, 3207–2, 3211–5, 3216–5 and USTL3220–7, 3220–8, 3224–2, 3225–10.

**Preservation.** The tubes are preserved as a thin phosphatic internal coating (c. 22 \( \mu \)m in thickness) partially or completely filled with phosphatic material (Fig. 8L–N, T, AC, AF) or as multiple-layered, thick phosphatic internal coating with individual layers from 3 to 46 \( \mu \)m in thickness for a total thickness of up to c. 58 \( \mu \)m, but without internal filling (Fig. 8G, D, H, I, L, Q, Z, AA). Internal surface of internal coating made of contiguous spherical phosphatic structures (Fig. 8O, AA). Simple, coarse internal phosphatic mould may also be present (Fig. 8A, E, K, Y, AG, AH). Different preservations may possibly be combined in the same specimen (Fig. 8A–E, H, I).

**Description.** The fragmentary tubes are open at both ends and have a length of between 0.995 and 4.360 mm, and are slightly (Fig. 8W, X, AC–AE) to relatively strongly (Fig. 8F, J–L, U, Y, AG, AH) irregularly helically curved. The cross-section is distinctly trilobate along the entire length and gives the specimens a triradial symmetry (Fig. 8A, D, E, H, L–N, Q, Y–AA, AC, AF). The diameter of the cross-section increases slowly and gradually towards the aperture (angle of divergence c. 2.50°). The apertural diameter varies between c. 190 and c. 470 \( \mu \)m. The trilobate cross-section is caused by equidistant longitudinal depressions (Fig. 8A–G, J–M, Q–T, V–Z, AC–AH) that vary from circular (diameter c. 20 \( \mu \)m; Fig. 8G, P, U) to elongated notches (length up to c. 60 \( \mu \)m; Fig. 8AB, AH, AI) that run along the length of the tube in a groove. The distance between notches ranges from 115 to 215 \( \mu \)m. Transverse striations on the external surface of
internal coatings and moulds are smooth, irregular, fine and packed (Fig. 8AB), or thick and distant (Fig. 8A–E), or absent (Fig. 8G, J–L, V–Z, AC–AG).

Remarks. The Iranian specimens have the typical triradial symmetry of Anabarites and are assigned to A. tristichus because of the presence of three chains of notches. These are situated in the grooves that separate the lobes and are only found in this species. Notches are also diagnostic of Anabarites valkovi (Bokova in Bokova & Vasil’eva, 1990), but in that species they are aligned longitudinally in the middle part of the three lobes, rather than in the grooves separating the lobes as in A. tristichus.

Distribution. Terreneuvian, Soltanieh Formation, Iran: samples D9a, D10, D13, D14 and D16 of the Dalir section and samples V9, V11, V12, V13 and V14 of the Valiabad section, Alborz Mountains.

Anabarites trisulcatus Missarzhevsky in Voronova & Missarzhevsky, 1969

Figure 9

1967 Anabarites trisulcatus Missarzhevsky; 20 [nomen nudum].
1969 Anabarites trisulcatus Missarzhevsky; Voronova & Missarzhevsky, p. 209, pl. 1 figs 8–9.
1969 Anabarites trisulcatus Missarzhevsky; Rozanov et al., p. 156, pl. 8 fig. 10.
?1970 Anabarites trisulcatus Missarzhevsky; Val’kov & Sysoev, p. 97, pl. 1 figs 3–5.
1975 Anabarites trisulcatus Missarzhevsky; Matthews & Missarzhevsky, pl. 2 figs 4, 16.
?1975 Anabarites trisulcatus Missarzhevsky; Val’kov, pl. 13 figs 3–5.
?1977 Anabarites rotundus Qian; p. 260, pl. 1 figs 11–12.
1977 Anabarites trisulcatus Qian; p. 259, pl. 1 figs 9–10, 18–19.
1978 Anabarites trisulcatus Missarzhevsky; Qian, p.15, pl. 3 figs 2–3, 12–13, pl. 4 figs 1–2.
1978 Anabarites obliquasulcatus Qian; p. 16, 3 figs 6–8.
1978 Anabarites sulcoconvex Qian; p. 16, 3 figs 9–10.
?1978 Anabarites undulatus Qian; pp 16–17, pl. 3 fig. 11.
1979 Anabarites trisulcatus Missarzhevsky; Qian et al., pl. 2 figs 6–7.
?1981 Anabarites signatus Missarzhevsky & Mambetov; p. 73, pl. 3 figs 11, 17, 18.
1982 Anabarites trisulcatus Missarzhevsky; Val’kov, p. 74, pl. 11 figs 15–17.
1982 Anabarites trisulcatus Missarzhevsky; Luo et al., p. 171, pl. 14 figs 7,9.
1982 Anabarites primitivus Qian & Jiang; Luo et al., p. 172, pl. 14 fig. 10.
?1982 Anabarites grandis Val’kov; pp 74–75, pl. 11 fig. 18.
?1984 Anabarites trisulcatus Missarzhevsky; Chen, p. 54, pl. 1 fig. 1.
?1984 Anabarites cf. trisulcatus; Chen, pp 54–55, pl. 1 figs 19–20.
1985 Anabarites trisulcatus Missarzhevsky; Nowlan et al., p. 242, fig. 6.

?1989 Anabarites rotundus Qian; Conway Morris & Chen, pp 620–628, figs 6–9, 12a, b.
?1989 Anabarites sulcatus (Bokova); Qian, p. 146, pl. 23, figs 10–15.
1989 Anabarites sulcoconvex Qian; p. 147, pl. 23 figs 3–9.
1989 Anabarites tenuisulcatus Qian; p. 145, pl. 23 figs 1–2.
?1989 Anabarites trisulcatus Missarzhevsky; Qian, p. 147, pl. 23, figs 16–19, pl. 24 figs 1–4.
1989 Anabarites trisulcatus Missarzhevsky; Qian & Bengtson, pp 125–127, fig. 84.
1989 Anabarites trisulcatus Missarzhevsky; Conway Morris & Chen, pp 628–629, fig. 12c–k.
1989 Anabarites trisulcatus Missarzhevsky; Missarzhevsky, pl. 13 fig. 19, pl. 14 figs 1, 3–4.
1989 Anabarites trisulcatus Missarzhevsky; Hamdi et al., fig. 3h.
1991 Anabarites trisulcatus Missarzhevsky; Khomentovsky & Karlova, pl. 1 fig. 2.
1991 Anabarites trisulcatus Missarzhevsky; Hamdi et al., pp 1–6, pl. 10 figs 5–7.
2002 Anabarites trisulcatus Missarzhevsky; Qian et al., text-fig. 4.15–16.
2004 Anabarites trisulcatus Missarzhevsky; Steiner et al., fig. 3.14.
2004 Anabarites trisulcatus form sulcoconvex; Steiner et al., fig. 3.15.
2004 Anabarites trisulcatus form oblquasulcatus; Steiner et al., fig. 3.16.
2005 Anabarites Missarzhevsky; Chen & Peng, figs 3, 4.
2005 Anabarites rotundus Qian; Peng, fig. 2A, B.
2005 Anabarites trisulcatus Missarzhevsky; Feng, fig. 2C, D.
?2005 Anabarites sp.; Feng, fig. 2E–H.
2006 Anabarites trisulcatus Missarzhevsky; Pyle et al., p. 815 fig. 6.1–4.
2007 Anabarites trisulcatus Missarzhevsky; Steiner et al., fig. 2D, E, F, I.
2009 Anabarites trisulcatus Missarzhevsky; Kouchinsky et al., pp 255–258, figs 6, 7A–E, 11A–V, 12D.
2010 Anabarites trisulcatus Missarzhevsky; Rozanov et al., p. 85, pl. 53 figs 6, 7.
2012 Anabarites lutus Val’kov & Sysoev; Tashayoe et al., pl. 1 fig. 5.
2012 Anabarites tripartitus Missarzhevsky in Rozanov et al.; Tashayoe et al., pl. 2 fig. 3.
2014 Anabarites trisulcatus Missarzhevsky; Guo et al., figs 2i–j, 4o–p.
2015 Anabarites trisulcatus Missarzhevsky; Kouchinsky et al., p. 499, fig. 69A, E.
2017 Anabarites trisulcatus Missarzhevsky; Kouchinsky et al., pp 417–419, fig. 74A–F, H, I, K.

Diagnosis. See Kouchinsky et al. (2009).

Material. Several thousands of complete and fragmentary specimens including the figured material USTL3203–1, 3204–4,
Preservation. The tubes are preserved as coarse phosphatic internal moulds with a fine outer surface reproducing the internal surface of the tube in detail (Fig. 9A–H, I–K, O–S) or with thin phosphatic internal coating of a thickness between 4 and 44 μm (Fig. 9X–AI). Rare specimens are preserved with thin internal coating and coarse phosphatic material made of botryoidal amalgamation of coccoidal pseudomorphs within the internal cavity (Fig. 9T, X–AB, AF–AH). One specimen possesses a coarse phosphatic replacement of the wall (Fig. 9L, M).

Description. Complete and fragmented tubes are open at both ends (originally or by fragmentation) with a length of between 0.765 and 5.325 mm. The tubes are relatively straight (Fig. 9B, C, E, F), undulating (Fig. 9A, D, I, L, M, R, S), curved (Fig. 9J, K, O–Q) or strongly helically curved (Fig. 9AC–AE, AJ). When the apex is preserved, it is always open, with a circular cross-section (Fig. 9G, V, W); longitudinal furrows, grooves or depressions are absent at the apical part (Fig. 9A, B, G, H, Q, R, V, W). In one specimen, the apical part is angled from the abapical part of the tube (Fig. 9H, J, K), otherwise progressive transition occurs from the apical to the abapical part of the tube with a rapid increase in diameter (Fig. 9G, V, W). The cross-section of the abapical part of the tube is slightly trilobate along the entire length, giving the diameter (Fig. 9G, V, W). The cross-section is slightly trilobate caused by equidistant shallow, wide and not well-delimited longitudinal depressions (Fig. 9A–E, I–P, R–T, X, Z, AC–AI). Transverse striations may occur on the external surface of internal coatings and moulds; they are irregular, indistinct, coarse and distant (Fig. 9I, N, S, AC, AI), and often absent (Fig. 9A–E, J, K, O–R, T, AC–AE, AJ).

Remarks. The specimens from the Alborz Mountains have the typical triradial symmetry of Anabarites and are assigned to A. trisulcatus because they possess the slowly expanding general shape of the tubes, showing three rounded lobes separated by shallow grooves or depressions. The few and barely visible imprints of transverse striations on the internal moulds/coatings do not show a clear curvature towards the aperture in the grooves. However, this character is highly variable in specimens of A. trisulcatus (e.g. Kouchinsky et al. 2009, figs 6, 7) and is not diagnostic of the species. The coarse phosphatic material in the internal cavity, which consists of a botryoidal amalgamation of coccoidal pseudomorphs, is similar to the preserved digestive tracts of hyoliths (e.g. Devaere et al. 2014). However, the preservation in the Iranian anabaritid specimens is too coarse to enable any conclusions to be reached regarding the nature of the structure.

Distribution. Terreneuvian, Soltanieh Formation, Iran: samples D2, D7, D8, D9, D9a, D10, D11, D13, D14, D15, D16, D18, D20, D21 and D22 of the Dalir section and samples V6, V8, V9, V11, V12, V13, V14, V16, V17, V18, V19 and V20 of the Valiabad section, both Alborz Mountains.

Anabarites ex gr. trisulcatus Missarzhevsky in Voronova & Missarzhevsky, 1969

Figure 10

Material. Complete and fragmented specimens including the figured material USTL3203-2, 3209-2, 3216-8 and USTL3217-3, 3219-1.

Preservation. The tubes are preserved as a phosphatic internal mould with a delicate outer surface reproducing the internal surface of the tube in detail (Fig. 10C, M–N).

Description. Fragmented tubes open at both ends with a length of between 1.315 and 5.335 mm. The tubes are relatively straight (Fig. 10A, I), or slightly curved (Fig. 10H–L) to strongly helically curved (Fig. 10B, D–F). The cross-section is slightly trilobate along the entire length, giving the specimens a triradial symmetry (Fig. 10C, E, H–J, L). Diameter of cross-section slightly and gradually increases towards the aperture (angle of divergence, c. 5.5°). Apertural diameter varies between c. 287 and c. 820 μm. Trilobate cross-section caused by equidistant, shallow, sharp and narrow longitudinal furrows (Fig. 10). Transverse striations on the external surface of internal moulds fine, regular and close (Fig. 10C, M, N) but absent on most specimens (Fig. 10A, B, D–L, O).
**Anabarites dalirense** sp. nov.

*Figure 11*

**Remarks.** The Iranian specimens show the typical triradial symmetry of *Anabarites*, and are assigned to *Anabarites* ex gr. *trisulcatus* following Kouchinsky et al. (2009). They possess the slowly expanding general shape of *A. trisulcatus*, with the three rounded lobes separated by longitudinal structures. The specimens described above have only some affinities with *A. trisulcatus* given that the structures separating the lobes are very distinct shallow, sharp and narrow furrows and clearly differ from the shallow but wide and not well-delimited depressions typical of *A. trisulcatus*. However, this variation may fall within the limits of the species; the notation ‘ex gr.’ is used to indicate that the specimens described here might belong to an unresolved species complex as suggested by Kouchinsky et al. (2009). The Iranian specimens are similar to *Anabarites* ex gr. *trisulcatus* form 1 of Kouchinsky et al. (2009).

**Distribution.** Terreneuvian, Soltanieh Formation, Iran: samples D2, D7, D9a, D10, D11, D13, D14, D16 and D18 of the Dalir section and samples V8, V9, V13, V14, V16 and V19 of the Vali-abad section, Alborz Mountains.

**Anabarites dalirense** sp. nov.

*Figure 11*

**LSID.** urn:lsid:zoobank.org:act:17D9727B-0781-40FA-902A-64EC6EE5A901

**Derivation of name.** Named after the village of Dalir, which is on the access road to the section.

**Holotype.** Specimen USTL3213-1, Fig. 11A–E; phosphatic internal coating; Soltanieh Formation, Dalir Section located along the trail to the phosphate mine above the village of Dalir, Alborz Mountains, Iran.

**Material.** 9 specimens including the figured material USTL3211-7, 3213-1, 3214-8 and 3215-3.

**Diagnosis.** Species of *Anabarites* with a strongly curved tube forming a ring with a wide central gap. Internal moulds and coatings expressing three slightly rounded lobes separated by shallow, sharp and narrow longitudinal furrows. Low, irregular transverse plications on the external surface of internal coatings and moulds.

**Preservation.** The tubes are preserved as a thick internal coating that consists of an assemblage of phosphatic spheres (Fig. 11A, E, I) and/or as a coarse phosphatic internal mould with a fine outer surface (Fig. 11F–H, J–P); both preservation modes reproduce the internal surface of the tube in detail.

**Description.** Fragmentary tubes are open at both ends; they are strongly curved to form a half to a complete ring. Complete rings correspond to a curvature at 360° of the tube in one plan (Fig. 11A–K), with two overlapping extremities (Fig. 11A, E, F–H, I, J, K). Coiling of the tube is loose and forms a wide central gap with a diameter of between 530 and 665 µm (Fig. 11A, F). Incomplete rings correspond to the breakage of a tube (Fig. 11D) or to a strongly helically curved tube (Fig. 11L–O). The length of tube ranges from 1.870 to 2.345 mm. Apical and apertural extremities are never preserved but the cross-section at one extremity has a smaller diameter than at the other (Fig. 11J, L). The cross-section is oval (Fig. 11J) to slightly trilobate along the entire length and gives the specimens a triradial symmetry (Fig. 11D, L). Three equidistant shallow, sharp and narrow longitudinal furrows are present along the entire length of the tube (Fig. 11A–D, F–H, J–P). Low, irregular transverse plications are visible on the external surface of internal coatings and moulds (Fig. 11C, F–H, P).

**Remarks.** The triradial symmetry is produced by three furrows that separate the three lobes of the tube; this assigns the specimens to the genus *Anabarites* with certainty. The strong curvature of the tube, forming a loose ring, has never been reported for another species in the genus, and hence a new species is introduced here. Except for the ring shape, other...
important characters of the specimens and especially the shallow, sharp and narrow longitudinal furrows are similar to that of *Anabarites* ex gr. *trisulcatus*. Some specimens from Iran assigned to *A.* ex gr. *trisulcatus* have a strong helical curvature (Fig. 10D–F) that tends towards the configuration of *A. dalirense*. This could correspond to variations in the same species. In the absence of the complete sequence of gradual morphological variations, they are considered separate herein. Some other taxa organized as tubes that are curved to form a ring that can be compared to *A. dalirense* are *Spirellus groenlandicus* Peel, 1988, which differs by the presence of multiple superimposed whorls; and *Obruchevella* Reitlinger, 1948, which differs in the helical twisting of whorls of an organic-walled microfossil.

**Distribution.** Terreneuvian, Soltanieh Formation, Iran: samples D10, D13 and D14 of the Dalir section, Alborz Mountains.

Genus CAMBROTUBULUS Missarzhevsky in Rozanov et al., 1969

**Type species.** *Cambrotubulus decurvatus* Missarzhevsky in Rozanov et al., 1969, Terreneuvian, mouth of the Ary-Mas-Yuryakh Creek, Kotuj River, Siberia, Russia.

**Diagnosis.** See Kouchinsky et al. (2009).

*Cambrotubulus decurvatus* Missarzhevsky in Rozanov et al., 1969

Figure 12

1967 *Cambrotubulus decurvatus* Missarzhevsky; p. 20 [nomen nudum].
1968  
*Platysolenites sibirica* Val’kov; pp 116–117, figs 2–5.

1969  
*Cambrotubulus decurvatus* Missarzhevsky; Rozanov et al., p. 160, pl. 7 figs 5–7, 10.

1975  
*Cambrotubulus decurvatus* Missarzhevsky; Matthews & Missarzhevsky, pl. 2 fig. 6.

?1975  
*Cambrotubulus sibiricus* (Val’kov); Val’kov, pl. 14 figs 2–5.

1979  
*Cambrotubulus decurvatus* Missarzhevsky; Qian et al., p. 217, pl. 2 figs 13–16.

1982  
*Cambrotubulus decurvatus* Missarzhevsky; Val’kov, p. 72, pl. 11 figs 1–12.

?1982  
*Cambrotubulus sibiricus* (Val’kov); Val’kov, pp 72–73.

1983  
*Cambrotubulus decurvatus* Missarzhevsky; Sokolov & Zhuravleva, p. 160, pl. 51 figs 3–4.

1984  
*Cambrotubulus decurvatus* Missarzhevsky; Chen, p. 56, pl. 1 fig. 2.

?1987  
*Cambrotubulus plicativus* Val’kov; pp 110–111, pl. 13 figs 19–21.

1989  
*Cambrotubulus decurvatus* Missarzhevsky; pl. 13 figs 9–10.

1989  
*Cambrotubulus conicus* Missarzhevsky; pl. 12 fig. 7.

**FIG. 11.** *Anabarites dalirense* sp. nov. from the Soltanieh Formation at Dalir, Alborz Mountains, Iran. A–E, I, USTL3213-1: A, lateral view, outlined area magnified in E to show detail of internal coating and gap; B–C, lateral views; D, view of the openings, outlined area magnified in I to show detail of internal coating. F–H, J–K, P, USTL3214-8: F, lateral view, outlined area magnified in K to show overlap; G, oblique lateral view, outlined area magnified in P to show transverse folds; H, oblique lateral view; J, view of openings. L, USTL3211-7 in aperture view. M–O, USTL3215-3: M, lateral; N–O, oblique lateral views. Scale bars represent: 200 μm (A–D, F–H, L–O); 50 μm (E, P); 20 μm (I); 100 μm (J, K).
1989 *Cambrotubulus decurvatus* Missarzhevsky; Hamdi, pl. 4, figs 1–3, 6.
1989 *Cambrotubulus decurvatus* Missarzhevsky; Hamdi et al., fig. 3e.
1990 *Cambrotubulus crassus* Fedorov; Pel’man et al., p. 25, pl. 2 fig. 1.
1995 *Rugathecata* cf. typica; Hamdi, pl. 5 fig. 14.
1996 *Conotheca subcurvata* Yu; Hamdi, pl. 5 figs 15–16.
1996 *Cambrotubulus decurvatus* Missarzhevsky; Esakova & Zhegallo, p. 95, pl. 3 figs 12–16.
2002 *Cambrotubulus conicus* Missarzhevsky; Kouchinsky & Bengtson, fig. 8A–D.
2009 *Cambrotubulus ex gr. decurvatus*; Kouchinsky et al., p. 286, figs 12B, 14M, 42–44.
2012 *Conotheca subcurvata* Yu; Tashayoee et al., pl. 1 fig. 4.
2012 *Cambrotubulus*; Tashayoee et al., pl. 2 fig. 5.
2017 *Cambrotubulus decurvatus* Missarzhevsky; Kouchinsky et al., p. 425, fig. 79D–J, P.

**Diagnosis.** See Kouchinsky et al. (2009).

**Material.** Several thousand complete and fragmentary specimens including the figured material USTL3204–2, 3206–1, 3207–5, 3207–11, 3208–2, 3209–3, 3209–9, 3211–3, 3212–9, 3212–10, 3214–3, 3214–9, 3215–3, 3216–6, 3217–1, 3220–5, 3221–4, 3225–5, 3224–9, 3224–9 and 3227–8.

**Preservation.** The complete or fragmentary tubes are preserved in two modes: (1) as coarse phosphatic internal molds with outer surface reproducing the internal surface of the tube in detail (Fig. 12A–S, U, AA–AK); or (2) as an internal coating consisting of an assemblage of phosphatic spheres (thickness of coating between 4.7 and 43.46 µm; Fig. 12A, T, V–X). Rare specimens are preserved with coarse phosphatic material made of a botryoidal amalgamation of coccoidal pseudomorphs within the internal cavity (Fig. 12W–Y); others are preserved with phosphatic filamentous structures on the surface of the internal mould (Fig. 12J–K).

**Description.** The tubes are open at both ends (originally or by fragmentation) with highly variable length, between 0.868 and 6.408 mm (see variation of size in the top right frame; Fig. 12A, T, V–X). Rare specimens of *Cambrotubulus decurvatus* are preserved with coarse phosphatic material made of a botryoidal amalgamation of coccoidal pseudomorphs within the internal cavity (Fig. 12W–Y); others are preserved with phosphatic filamentous structures on the surface of the internal mould (Fig. 12J–K).

**Remarks.** In the absence of the apical part and operculum, it is sometimes difficult to differentiate *Cambrotubulus* from *Conotheca* (Kouchinsky et al., 2009). However, many specimens recovered from Iran are preserved with the apical part, which is strongly tapered and always open, and no operculum has been recovered despite the recovery of several thousands of tubes. These characters are typical of *Cambrotubulus* and the specimens are therefore assigned to this genus. The specimens are assigned to the species *C. decurvatus*, which is interpreted to be the only valid species in the genus. *Conotheca conicus* Missarzhevsky, 1989, *C. crassus* Fedorov in Pel’man et al., 1990, *C. plicatus* Val’kov, 1987 and *C. sibiricus* (Val’kov, 1968) are regarded as synonyms of *C. decurvatus*. *Conotheca corniformis* Elicki, 1994 cannot be assigned with certainty to the genus *Cambrotubulus* because the apical end is not known. As for some of the Iranian specimens of *Anabarites trisulcatus*, some specimens of *Cambrotubulus decurvatus* exhibit an unidentified phosphatic structure in the internal cavity. The phosphatic filaments present on the surface of internal molds are interpreted as internal molds of traces of the activity of endolithic microborers within the now-gone tube walls.

**Distribution.** Terreneuvian, Soltanieh Formation, Iran: samples D6, D7, D8, D9, D9a, D10, D11, D13, D14, D15, D16, D18, D19, D20, D21 and D22 of the Dalir section, and samples V6, V7, V8, V9, V11, V12, V13, V14, V16, V17, V18, V19 and V20 of the Valiabed section, both Alborz Mountains.

**FIG. 12.** *Cambrotubulus decurvatus* Missarzhevsky in Rozanov et al., 1969, from the Soltanieh Formation at Dalir and Valiabad, Alborz Mountains, Iran. A, USTL3206–1. B, USTL3207–5. C, USTL3208–2. D, USTL3224–9. E, R–S, U, USTL3227–8. F, O–Q, AI, USTL3221–9: G, lateral view; R, apertural view; U, lateral view, outlined area magnified in S to show the apical end. F, USTL3204–2. G, AI–AK, USTL3212–10: G, lateral view; AI, apical view, outlined area magnified in AK to show transverse striations. H, O–Q, AI, USTL3212–9: H, lateral view; O, apical view, outlined area magnified in AI to show the circular cross-section of open end; P, lateral view, outlined area magnified in Q to show the apical part separated from the abapical area by a furrow. I, USTL3209–9, J–K, USTL3207–11: J, lateral view, outlined area magnified in K to show phosphatic filaments. L–N, USTL3221–4: L, lateral view, outlined area magnified in M to show the distant and fine transverse striations; N, apertural view. T, V, USTL3209–3: T, apertural view, outlined area magnified in V to show detail of the thick internal coating. W–X, USTL3220–5: W, lateral view, outlined area magnified in X to show the unidentified phosphatic internal structure. Y, USTL3214–3. Z–AA, AG, USTL3214–9: AA lateral view, outlined area magnified in Z to show apical part; AG, oblique apertural view. AB, USTL3217–1. AC, USTL3215–5. AD, AH, USTL3216–6: AD, lateral view, outlined area magnified in AH to show apical part. AE, USTL3211–3. AF, USTL3225–5. Scale bars represent: 500 µm (A–I, W, Y, AE); 200 µm (J, L, N, R, T, U, AC, AD, AF); 50 µm (K, M, Q, Z, AH); 20 µm (S, V, AI, AK); 100 µm (O, P, AA, AG, AI); 10 µm (X); 1 mm (AB).
Type species. Oelandiella korobkovi Vostokova, 1962, Cambrian
Stage 2, Kotuj River, East Krasnoyarsk Region, Siberia, Russia.

Diagnosis. See Gubanov & Peel (1999).

Oelandiella korobkovi Vostokova, 1962

Figure 13

1962 Oelandiella korobkovi Vostokova; p. 52, pl. 1 figs 1–4.
1962 Oelandiella sibirica Vostokova; p. 52, pl. 1 figs 5–7.
1969 Latouchella korobkovi (Vostokova); Rozanov et al., p. 142, pl. 3 figs 4a, 7, 11, 12, 19, 20, pl. 4 fig. 17.
1979 Anabarella emeiensis Yu in Lu, pl. 3, fig. 15 [nomen nudem].
1979 Latouchella raricostata Yu in Lu, pl. 3 figs 4–9.
1979 Archaeospira imbricata Yu, p. 255, pl. 3 figs 24–27.
1980 Archaeospira ornata Yu, p. 255, pl. 4 figs 14–17.
1980 Latouchella cf. membrabilis; Yu, p. 252, pl. 3 fig. 20.
1980 Yangtzespira exima Yu, p. 255, pl. 4 figs 18–21.
1980 Archaeospira ornata Yu; Zhao et al., p. 51.
1980 Archaeospira ornata Yu; Yin et al., p. 156, pl. 13 figs 9, 10.
1980 Archaeospira sp.; Yin et al., p. 156, pl. 13 figs 17, 18.
1980 Remella jacutica (Missarzhevsky in Rozanov & Missarzhevsky); Yin et al., p. 156, pl. 13 figs 4, 5.
1980 Igorella cf. ungulata; Jiang, pl. 3 fig. 8.
1980 Latouchella korobkovi (Vostokova); Jiang, p. 122, pl. 3 fig. 1a–c.
1980 Latouchella korobkovi (Vostokova); Missarzhevsky, pl. 6 figs 2, 3, 5a.
1980 Latouchella korobkovi (Vostokova); Yin et al., p. 156, pl. 13 fig. 8 (cf. korobkova [sic]).
1980 Latouchella songlengpoensis Chen & Zhang, p. 195, pl. 1 figs 39, 46.
1980 Maidipingoconus maidipingensis (Yu); Yin et al., p. 155, pl. 14 figs 1–3, 10, 11.
1980 Yangtzespira regularis Jiang; p. 120, pl. 3 fig. 2.
1980 Yangtzespira regularis Jiang; Luo et al., p. 99, pl. 1 fig. 24.
1980 Yunmanospira multiribis Jiang; p. 120, pl. 3 fig. 23.
1980 Yunmanospira multiribis Jiang; Luo et al., pl. 1 fig. 27.
1981 Huanglingella polycostata Chen et al., p. 37, pl. 1 fig. 19.
1981 Hubeispira nitida Yu; p. 534, pl. 14 figs 14–19.
1981 Yangtzespira xindianensis Yu; p. 553, pl. 1 figs 11–13.
1982 Igorella ungulata Missarzhevsky in Rozanov et al.; Luo et al., p. 191, pl. 20 fig. 4.
1982 Latouchella korobkovi (Vostokova); Luo et al., p. 190, pl. 19 figs 8, 9.
1982 Latouchella korobkovi (Vostokova); Voronin et al., p. 43, pl. 1 fig. 1.
1982 Latouchella minuta Zhegallo in Voronin et al.; p. 44, pl. 1 fig. 4.
1982 Latouchella sibirica (Vostokova); Voronin et al., p. 44, pl. 1 fig. 2.
1982 Yangtzespira exima Yu; Luo et al., p. 189, pl. 19 fig. 14.
1982 Yangtzespira regularis Jiang; He & Yang, pl. 3 figs 10–12.
1982 Yangtzespira regularis Jiang; Luo et al., p. 189, pl. 19 fig. 10.
1982 Yunmanospira multiribis Jiang; Luo et al., p. 189, pl. 19 fig. 13.
1983 Latouchella korobkovi (Vostokova); Zhegallo in Sokolov & Zhuravleva, p. 99, pl. 33 fig. 9.
1984 Archaeospira ornata Yu; Xing et al., pl. 5 fig. 13.
1984 Archaeospira ornata Yu; Yu, p. 30, pl. 2 fig. 12.
1984 Archaeospira sp.; Chen, p. 58, pl. 1 fig. 14.
1984 Maidipingoconus maidipingensis (Yu); Chen, p. 58, pl. 1 fig. 14.
1984 Gibbaspira acutumonalis He; p. 27, pl. 2 figs 1–4.
1984 Uncinaspira pristina He; p. 25, pl. 2 figs 16, 17.
1984 Uncinaspira ruidocostata He; p. 25, pl. 2 figs 10–13.
1984 Yangtzespira exima Yu; Luo et al., pl. 10 fig. 1.
1984 Yangtzespira exima Yu; Yu, p. 28, pl. 2 figs 10, 11.
1984 Yangtzespira multicoostata He in Xing et al.; pl. 13 figs 8, 9.
1984 Yangtzespira regularis Jiang; Xing et al., pl. 10 fig. 13.
1984 Yunmanospira multiribis Jiang; Luo et al., pl. 10 fig. 2.
1984 Yunmanospira multiribis Jiang; Xing et al., pl. 10 fig. 20.
1984 Archaeospira sp.; Yu, pl. 44 figs 1–2, pl. 45 figs 1–6.
1984 Yangtzespira exima Yu; Yu, pl. 5 figs 11–13, pl. 4 figs 6–8.
1984 Archaeospira imbricata Yu; Yu, p. 196, pl. 43 figs 7–10, pl. 46 figs 4–6, pl. 48 figs 2, 3, 5–8, pl. 49 figs 6–9, pl. 54 figs 4–6.
1984 Archaeospira ornata Yu; Yu, p. 194, text-figs 29a–29c, 57, pl. 43 figs 4–6, pl. 48 figs 1, 4, 9, pl. 49 figs 1–5, 10–12, pl. 50 figs 1–9, pl. 51 figs 1–7, pl. 53 figs 5–7, pl. 54 figs 1–3, pl. 58 fig. 9.
1984 Archaeospira sp.; Yu, p. 198, pl. 40 figs 1, 2, 5, 6, 10, 11, pl. 46 figs 9–11, pl. 47 figs 8, 9, pl. 53 figs 8, 9, pl. 54 figs 7–12.
1984 Hubeispira nitida Yu; Yu, p. 206, pl. 55 figs 1–7, pl. 56 figs 5–8.
1984 Latouchella cf. korobkovi; Yu, p. 185, pl. 39 figs 1–6, pl. 43 figs 1–3, pl. 46 figs 1–3, 7, 8, pl. 47 figs 3–7.
1984 Yangtzespira exima Yu; Yu, p. 211, text-figs 22, 29d, 29e, 64, pl. 47 figs 1, 2, pl. 53 figs 1–4, pl. 57 figs 1–8, pl. 58 figs 1–8, pl. 59 figs 1–7.
1984 Latouchella vetula Val’kov, pl. 1 fig. 1.
1984 Latouchella angusta (Cobbold); Kerber, p. 171, pl. 7 figs 7–10, 14–15, 17.
1984 Yangtzespira exima Yu; Yu, figs 8–10.
1984 Archaeospira cf. ornata; Qian & Bengtson, p. 116, fig. 74.
1984 Archaeospira cf. songlengpoensis; Qian & Bengtson, p. 116, text-fig. 75.
1984 Archaeospira ornata Yu; Qian & Bengtson, p. 112, text-figs 72, 73.
FIG. 13. *Oelandiella korobkovi* Vostokova, 1962, from the Barut Formation at Barut Aghaji and Chopoghlu, Soltanieh Mountains, Iran. A–E, USTL3230-6: A, lateral; B, posterior; C, anterior; D, upper; E, oblique lateral view. F–I, USTL3228-3: F, oblique lateral view, outlined area magnified in I to show polygonal imprints at the umbilicum; G, oblique anterior view; H, lower view. J, USTL3229-3 in oblique posterior view. K–L, USTL3229-9: K, oblique anterior; L, oblique posterior view. M–Q, USTL3230-9: M, upper; N, lateral; O, oblique lateral; P, anterior; Q, posterior view. R–U, USTL3230-3: R, posterior; S, anterior; T, oblique lateral; U, upper view. Scale bars represent: 500 µm (A–H, J–U); 100 µm (I).
Description. The univalve conchs are laterally compressed and coiled into half a whorl (Fig. 13N, O, T) to almost a complete whorl (Fig. 13A, F, L). The conch length ranges from 1.511 to 2.776 mm, the width from 0.413 to 1.128 mm and the height 2.776 mm, the width from 0.413 to 1.128 mm and the height 0.607 to 1.398 mm. The coiling is mainly planispiral with a slight asymmetric component (Fig. 13A, F, L). Expansion of conchs rapid with a large aperture in some specimens (Fig. 13A, E, F, H, N, O, T). Maximum distance between ribs (from 0.739 to 1.869 mm), elongated along the anteroposterior axis (Fig. 13H). Lateral fields straight (Fig. 13P, Q) to slightly concave (Fig. 13B, C, G, L), affected by deformation in some specimens (Fig. 13, O–T). External surface of internal moulds with commarginal ribs that always cross the dorsum in the best-preserved specimens (Fig. 13A–E, G, M–U) but slightly faded in the dorsal area in the worn specimens (Fig. 13K). Ribs fading toward the umbilicum (Fig. 13A, E, F, H, N, O, T). Maximum distance between ribs is 157–422 µm. High variability in number and distance between ribs (compare Fig. 13A and Fig. 13F). Specimens densely ribbed due to presence of intermediate ribs rapidly disappearing toward the umbilicum and flanked by two primary ribs (Fig. 13F, G, J). Ribs roughly triangular in transverse section, rounded (Fig. 13F–I) to sharp (Fig. 13A–E, M–U) depending on the preservation. Polygonal imprints present on the surface of internal moulds near the umbilicum (Fig. 13I).

Remarks. The specimens from Iran are assigned to the genus Oelandiella due to their typical coiling and the presence of ribs crossing the dorsum. Oelandiella selindeica (Val’kov, 1987) and O. vetula (Val’kov, 1987) are probably junior synonyms of O. korobkovi; they differ only in the expression and number of ribs, which is interpreted as intraspecific by Devaere et al. (2013). Oelandiella selindeica (Bokova, 1990) is tightly coiled exclusively and clearly dextrally, whereas the present specimens are subsymmetrical. Oelandiella memorabilis (Missarzhevsky in Rozanov et al., 1969) clearly differs from the Iranian specimens in the presence of an antispinal sinus on the ribs.

Material. A few hundred broken to complete internal moulds including the figured specimens USTL3228–3, 3229–3, 3229–9, 3230–3, 3230–6 and 3230–9.

Preservation. Specimens are preserved as internal moulds.
Distribution. Terreneuvian, Barut Formation, Iran: samples B5 and B8 of the Barut Aghaji section and samples CH7 and CH12 of the SE Chopoghlu section, Soltanieh Mountains.

CAP-SHAPED MOLLUSCS

Various internal moulds of univalved, cap-shaped molluscs were recovered from the limestone beds at the base of the Barut Formation in the sections of Barut Aghaji (samples B5 and B8) and of the valley south-east of Chopoghlu (sample CH10, CH12). All of them possess an apex overhanging the apertural margin (Fig. 14A, B, E, G, J, M, N). The first morphotype (Fig. 14A–D) is higher than wide and as long as high, laterally compressed and coiled for less than half a whorl (Fig. 14C, D). It has irregular folds that extend from one lateral field to the other, crossing the dorsum (Fig. 14C, D). The specimens are superficially similar to Oelandiella korobkovi but clearly differ in the coiling and ornaments: Oelandiella korobkovi is more tightly coiled than this first morphotype and has strong co-marginal ribs always crossing the dorsum, whereas in the first morphotype of cap-shaped molluscs, the co-marginal folds are faint and irregular. The second and third morphotypes are low (height smaller than width and length; Fig. 14E–J, M, N). The second morphotype is wide (Fig. 14E, H) whereas the third morphotype is similar to some specimens of Bemella Missarzhevsky in Rozanov et al., 1969: it is slightly compressed laterally (Fig. 14J, K, M) and possesses polygonal imprints at the apertural margin and on the dorsum (Fig. 14L, O).

FIG. 14. Various cap-shaped molluscs from the Barut Formation at Barut Aghaji and Chopoghlu, Soltanieh Mountains, Iran. A–D, USTL3230-5: A, lateral; B, oblique posterior; C, oblique anterior; D, oblique upper view. E–H, USTL3230-7: E, upper; F, anterior; G, lateral; H, posterior view. I–O, USTL3197-7: I, lateral view; J, posterior view, outlined area magnified in L to show polygonal imprints under the apex; K, anterior view; M, upper view, outlined area magnified in O to show polygonal imprints on the surface of the internal mould; N, lateral view. Scale bars represent: 500 µm (A–D); 200 µm (E–K, M, N); 20 µm (L); 50 µm (O).
Phylum, Class, Order & Family UNCERTAIN
Genus AETHOLICOPALLA Conway Morris in Bengtson et al., 1990

Type species. Aetholicopalla adnata Conway Morris in Bengtson et al., 1990, Cambrian Stage 3, Curramulka, Yorke Peninsula, Stansbury Basin, Australia.

Diagnosis. See Bengtson et al. (1990).

Aetholicopalla adnata Conway Morris in Bengtson et al., 1990

1988 Archaeooides granulatus Qian; Kerber, p. 189, pl. 11 figs 13–20.
1990 Aetholicopalla adnata Conway Morris in Bengtson et al., p. 338, figs 213–216.
1992 Archaeooides granulatus Qian; Elicki & Schneider, pl. 16 figs 8, 9.
1998 Aetholicopalla adnata Conway Morris; Elicki, p. 58, pl. 1 figs 6–9, pl. 2.
2001 Aetholicopalla adnata Conway Morris; Demidenko in Gravestock et al., pl. 12 figs 7–8.
2004 Aetholicopalla adnata Conway Morris; Wrona, p. 51, fig. 26D, E.
2009 Aetholicopalla adnata Conway Morris; Topper et al., p. 219, figs 6S–U.
2010 Archaeooides granulatus Qian; Rozanov et al., p. 87, pl. 54 fig. 6.
2013 Aetholicopalla adnata Conway Morris; Devaere et al., p. 66, figs 25.1–23.
2014a Aetholicopalla adnata Conway Morris; Yang et al., fig. 13P.
2015 Aetholicopalla adnata Conway Morris; Kouchinsky et al., fig. 73A.
2015 Aetholicopalla adnata Conway Morris; Yang et al., fig. 7U.
2017 Archaeooides granulatus Qian; Kouchinsky et al., fig. 82G.

Diagnosis. See Bengtson et al. (1990).

Material. 46 complete to broken phosphatic specimens including the figured material USTL3209-1, 3212-1 and 3226-5.

Preservation. The specimens are preserved as phosphate replacement of the test with pyrite overgrowth (Fig. 15A–F) or as internal mould (Fig. 15J) with partial external coating (Fig. 15G–I).

Description. The test is spherical (Fig. 15G–J) to ellipsoidal in shape (Fig. 15A–F; average flattening of 0.85) and 0.596–1.489 mm

FIG. 15. Aetholicopalla adnata Conway Morris in Bengtson et al., 1990 from the Soltanieh Formation at Dalir and Valiabad, Alborz Mountains, Iran. A–F, USTL3209-1: A, upper view; B, view of cross-section, outlined area magnified in F to show microstructure; D, lateral view, left outlined area magnified in C to show the external surface with pyrite crystals, and right outlined area magnified in E to show the contact between the microfossil and substrate. G–I, USTL3212-1: G, lateral view, lower outlined area magnified in H and upper outlined area magnified in I. J, USTL3226-5. Scale bars represent: 500 μm (A, B, D); 50 μm (C, H, I); 100 μm (E, F); 200 μm (G, J).
in diameter. Most specimens show a differentiated attachment area, which is either isolated (Fig. 15I) or still attached to the encrusted substrate (Fig. 15A, B, D, E, G, H). The attachment surface can be completely flat, but also convex or concave. The surface of the internal moulds is covered with slightly projecting tubes or pillars when filled with phosphatic material (Fig. 15G–I) up to 25 µm in height. The pillars are connected to a continuous external coating (Fig. 15G, H), whereas the tubes are connected to the external coating and appear as holes on the external surface (Fig. 15J). In one specimen, the test is completely replaced by a thick, recrystallized layer of phosphate (Fig. 15B, F) and pyrite crystals that are present on the outer surface of this thick layer (Fig. 15C–E). The internal surface of the thick layer is irregular and constituted of joined phosphatic rounded structures (Fig. 15B, F). The internal cavity is hollow (Fig. 15B, F).

Remarks. The specimens from Iran are assigned to the genus Aetholicopalla and particularly to the single species Aetholicopalla adnata, because of tubes or pillars and attachment surfaces that differentiate it from the comparable genus Archaeoides Qian, 1977.

Distribution. Terreneuvian, Soltanieh Formation, Iran: samples D4, D7, D8, D10 and D13 of the Dalir section and samples V9 and V19 of the Valiabad section, Alborz Mountains.

Indeterminate conical microfossils (32 specimens) are present in the interval of the Soltanieh Formation corresponding to the Fortunian (samples D9a, D10, D13 and D14 of the Dalir section and sample V9 of the Valiabad section). They are robust, conical, phosphatized internal moulds (Fig. 16) with a height range from 1.694 to 2.940 mm. They exhibit a moderate lateral compression and gentle curvature in the plane of bilateral symmetry (Fig. 16G, H, I–N). The apex is sharp (Fig. 16J) with an oval to circular cross-section (Fig. 16E, H). A ridge, located under the apex, connects it to the aperture and sharply separates the two lateral sides of the cone (Fig. 16C, H, I). The angle of divergence is wide at the base and ranges between 51° and 84° (Fig. 16C, D, I, O). The basal part has an irregular margin caused by a breakage (Fig. 16A–D, F–I, K–O). The cross-section of the aperture is teardrop-shaped, with a length between 0.890 and 1.448 mm and a width between 0.396 and 0.930 mm (Fig. 16F, G, M). The surface of the internal mould is smooth (Fig. 16).

Many Early Cambrian conical objects with indeterminate affinities were described and can be compared with the Iranian indeterminate cones. Some are ornamented cones, such as Zhijinites Qian, 1978 and Stoibostrombus Conway Morris & Bengtson in Bengtson et al., 1990, and some are problematic cones as described by Kouchinsky et al. (2015, fig. 45). Their preservation with phosphatic walls is different from the preservation of...

**FIG. 16.** Indeterminate cones from the Soltanieh Formation at Dalir and Valiabad, Alborz Mountains, Iran. A–F, USTL3214-6. G–I, USTL3220-3. J–O, USTL3212-7. Scale bars represent: 500 µm (A–D, F–I, K–O); 50 µm (E); 100 µm (J).
Iranian specimens as internal moulds, making direct comparison difficult. *Archaeopetasus* Conway Morris & Bengtson in Bengtson et al., 1990 and *Fontitchella* Missarzhevsky in Rozanov et al., 1969 are more flared at the base, less laterally compressed and lack the subapical ridge visible in the Iranian specimens. The problematic cones from Iran can also be compared to protoconodont elements, especially of *Mongolodus* Missarzhevsky, 1977, although the latter are much more compressed laterally.

**INDET. IRREGULAR TUBES**

Figure 17

Indeterminate irregular tubes (37 specimens) come from samples D10, D13, D14 and D16 of the Dalir section and samples V8, V9 and V12 of the Valiabad section. They correspond to phosphatic internal moulds of tubes open at both ends; their length ranges from 2.020 to 6.822 mm (Fig. 17). The tubes are helically curved and twisted (Fig. 17B–D, F–K). The cross-section is rounded triangular along the length in the shortest specimens (Fig. 17A, C, G, J) and subcircular in the longest specimens (Fig. 17E). The diameter of the cross-section increases towards the aperture, where the angle of divergence reaches c. 18°. The apertural diameter ranges between 0.580 and 1.352 mm. The tubes are organized into three low convex to flat surfaces separated by rounded ridges (Fig. 17B, G–I). This causes the rounded triangular shape of the cross-section, which is reminiscent of that of *Anabarites*. However, in the irregular tubes, the circular cross-section occurs in the largest specimens and is thus opposite in *Anabarites*.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article (https://doi.org/10.1002/spp2.1391):

Table S1. Global stratigraphic and geographic range of species identified in ‘New and revised small shelly fossil record from the lower Cambrian of northern Iran’.

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