

SHORT NOTE

ADDITIONAL BRACHIOPOD FINDINGS FROM THE LOPINGIAN SUCCESSION OF THE ALI BASHI MOUNTAINS, NW IRAN

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Key words: New species, brachiopod miniaturization, nutrient-deficient settings, phylogenetic relationships.

Abstract. Aim of this note is to describe additional findings of Lopingian brachiopods along the Main Valley section and at Localities 1, 3, and 4 of the Ali Bashi Mountains, NW Iran. Here we provide:

1) taxonomic descriptions of two newly recorded taxa, one of which is a new species, *Meekella julfensis* n. sp.;

2) more information on the stratigraphic range of brachiopods from the Ali Bashi Mountains, which show a greater abundance and diversity in the upper part of the Julfa Formation, in the Ali Bashi Formation, and in the Boundary Clay. The newly collected faunas are characterized by miniaturization which is considered to be a response to deep water conditions in well oxygenated, but trophic resource-limited settings, and not a Lilliput-effect related to the end-Permian crisis;

3) a discussion on the phylogenetic relationships between *Ara-xathyris* and *Transcaucasathyris*, proposing that the former may have evolved from the latter by the convergence of the dental plates to form a spondylium, that was probably a structure that functioned to optimize the muscle length in response to greater shell volumes.

Introduction

At the end of September 2013, a Chinese-Iranian-Italian research group visited the sections of the Ali Bashi Mountains near Julfa, in NW Iran (Angiolini et al. 2013), described in Ghaderi et al. (this volume) to

which reference is made for the location map, the stratigraphic log and the geological setting.

The main aim of the fieldwork was to sample in detail for conodonts, brachiopods, and geochemistry, the upper part of the Julfa Formation, the Ali Bashi Formation, the Boundary Clay and the base of the Elikah Formation. The primary goals were 1) to establish a refined conodont biozonation for the Changhsingian of NW Iran, and 2) to study the evolution of biomineralization at the Permian-Triassic boundary based on the ultrastructure and geochemistry of brachiopod shells.

Notwithstanding the fact that these sections are well known and have been sampled since the sixties of last century up to very recently (see references in Ghaderi et al. this volume), we have still found new data.

In this short note, we describe the additional findings of brachiopods along the Main Valley section (Ghaderi et al. this volume) and at Localities 1, 3, and 4 of Teichert et al. (1973). We provide not only additional taxonomic descriptions of two newly recorded taxa, one of which a new species, but also more information on the stratigraphic range and evolution of the Lopingian brachiopods from the Ali Bashi Mountains.

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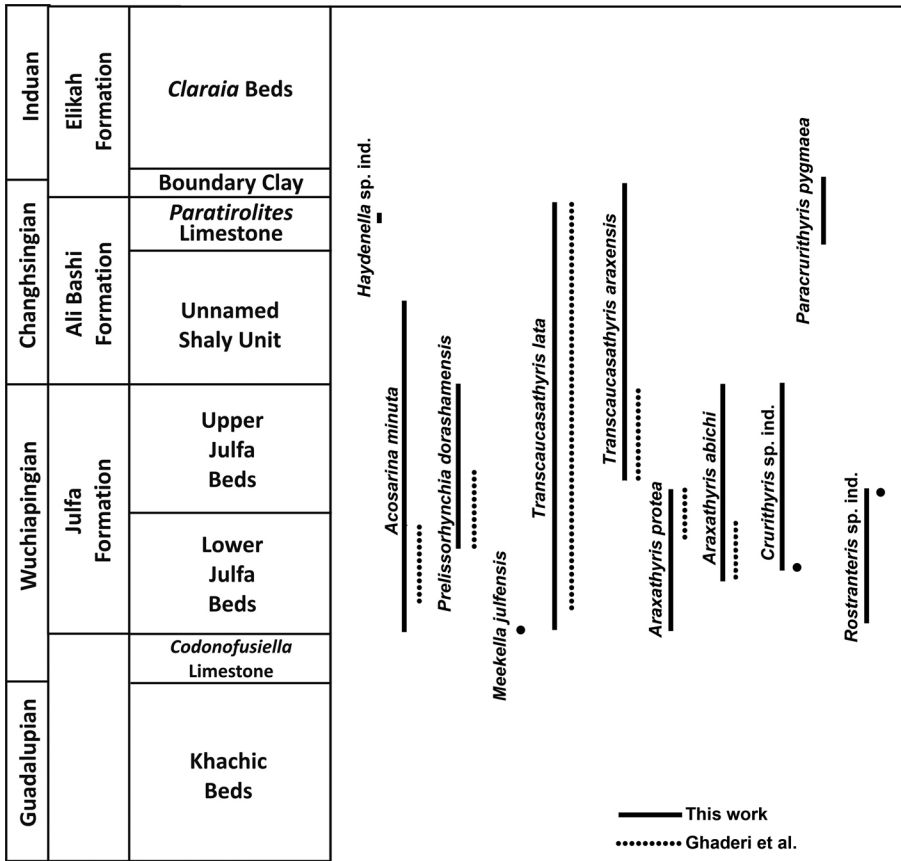
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Tab. 1 - Synthetic range chart showing the new record of the stratigraphic ranges of the brachiopod species described in this paper.

Brachiopod stratigraphic ranges

As shown by Ghaderi (this volume), the Julfa Formation is very rich in brachiopods, but these decline abruptly in both diversity and abundance in the overlying Ali Bashi Formation.

More specifically, Ghaderi et al. (this volume, fig. 4) recorded a rich fauna from the Julfa Formation, especially in its lower part, but only one specimen each of two species (*Transcaucasathyris lata* and *Dielasma* sp. ind.) at the top of the *Paratirolites* Limestone in the Ali Bashi Formation (samples G271 and G273).

As a result of this current study we were able to extend previous records of abundance and diversity for the upper part of the Julfa Formation, the unnamed shaly unit, and *Paratirolites* Limestone, which together form the Ali Bashi Formation, and very importantly, for the Boundary Clay.

We have extended the range of *Acosarina minuta* and *Rostranteris* sp. ind. down to the first metre and to the first three metres from the base of the Julfa Formation respectively. We have also found *Araxathyris protea* and *Transcaucasathyris lata* together in the same bed at 3.4 metres from the base of the Julfa Formation. We have extended upward to the top of the Julfa Formation the ranges of *Araxathyris abichi*, *Crurithyris* sp. ind. and *Prelissorhynchia dorashamensis*. We have found *Acosarina minuta* and several species of *Transcaucasathyris* in

the unnamed shaly unit and *Haydenella* sp. ind., *T. araxensis*, and *Paracrurithyris pygmaea* in the *Paratirolites* Limestone. Finally, we have recorded several specimens of *T. araxensis* and *Paracrurithyris pygmaea* from the Boundary Clay (Tab. 1).

Lopingian brachiopod miniaturization

The specimens recorded from the upper ten metres of the Julfa Formation, from the Ali Bashi Formation, and the Boundary Clay, are characterized by their small size, relatively high surface area to volume ratio and smooth shells. These features have been previously interpreted to indicate conditions of low oxygen and/or limited trophic resources (e.g., Alexander 1977; Thayer 1986; Oschmann 1994; Levin 2003; Payne et al. 2009, 2011), as they may facilitate respiration and nutrient intake in oxygen- and nutrient-deficient settings. Higher surface area to volume ratio may favor oxygen transport and thus respiration, which in brachiopods takes place through the epithelia of the mantle lobes and lophophore (Peck et al. 1997).

Smooth, small or thin shelled brachiopods have been considered characteristic of deep-water, resource-poor environments also in well oxygenated conditions (e.g. Fürsich & Hurst 1974; Mancenido 1993; Vörös 2005), such as those recorded in the Wuchiapingian-

Changhsingian succession of Julfa, as size and surface to volume ratio are also controlled by food availability (Payne et al. 2011 and reference therein).

Small sized faunas near the Permian-Triassic boundary have been interpreted to be a result of a protracted primary productivity collapse causing a mass extinction. Twitchett (2006) used the term Lilliput Effect to define this type of stunting of marine organisms.

In comparison, the miniaturization of the brachiopods recorded herein is considered to be a response to protracted deep water conditions in well oxygenated, but trophic resource-limited settings, and not a Lilliput-effect related to the end-Permian crisis, as recognized in other end-Permian to lowermost Triassic successions (e.g. Twitchett 2006, 2007; He et al. 2007). The small sized faunas already occur at the top of the Julfa Formation, well before the mass extinction interval. The success in smooth brachiopods colonizing deep-water settings in the Late Palaeozoic lends credit to the hypothesis of Vörös (2005) that brachiopods flourished in bathyal and abyssal zones well before the Mesozoic.

Phylogenetic relationships between *Araxathyris* and *Transcaucasathyris*

Collection of new material from the Ali Bashi Mountains sections has allowed the analysis of the internal characters of a larger number of specimens through serial sections (cf. Alvarez & Brunton 2008). This has proved to be very valuable in clarifying the phylogenetic relationships between *Araxathyris* Grunt in Ruzhentsev & Sarytcheva, 1965 and *Transcaucasathyris* Shen, Grunt & Jin, 2004, that was previously attempted by Angiolini & Carabelli (2010). The two genera are externally similar, but *Transcaucasathyris* has a less strongly biconvex profile and separate dental plates instead of a spondylium in the ventral valve.

According to Angiolini & Carabelli (2010), *Transcaucasathyris* could have evolved from *Araxathyris* by the lack of convergence of bowl-like dental plates on the floor of the valve to form a spondylium through pedomorphism, as also indicated by its weakly biconvex profile. More specifically, they suggested that *Transcaucasathyris kandevani* (Fantini Sestini & Glaus, 1966) might have been derived from *Araxathyris bruntoni* Angiolini & Carabelli, 2010, as supported by their stratigraphic range, with the latter ranging from the Wuchiapingian to the Changhsingian, whereas the former appeared later and occurred higher in the Lopingian succession of the Alborz Mountains, N Iran.

The analysis of the new material (Figs 1-2) confirms that the species of *Transcaucasathyris* are characterized by separate dental plates which are rather closely set in the early ontogenetic stages and become

wider apart anteriorly with age (see also Ghaderi et al. this volume, plate 5, figs 1-13). The two dental plates are also distinct from a low median septum set in between them. The configuration in *Araxathyris/Transcaucasathyris* is instead characterized by the development of a spondylium (Figs 1-2; see also Ghaderi et al. this volume, plate 5, figs 14-26).

However, the stratigraphic record of *Araxathyris* and *Transcaucasathyris* both in Transcaucasia (Ruzhentsev & Sarytcheva 1965) and in the Ali Bashi Mountains (Ghaderi et al. this issue), which better covers the lower Wuchiapingian interval, does not support this pattern of evolution, due to an earlier occurrence of *T. araxensis* and *T. lata* with respect to the first occurrences of all species of *Araxathyris*. In fact, our newly collected data record the simultaneous occurrence of both genera in the same bed at the base of the Julfa Formation making more difficult the interpretation of their relationships. It is clear though that species of *Transcaucasathyris* are abundant since their first occurrence, whereas species of *Araxathyris*, except for the new finding of one single specimen at 3.4 metres from the base of the formation, occur only above 8 metres from the base. In addition, species of *Araxathyris* are restricted to the Julfa Formation, whereas those of *Transcaucasathyris* range higher up to the Boundary Clay (Tab. 1).

Most Carboniferous-Permian genera of the Comelicianiidae Merla, 1930 *sensu* Shen et al. (2004) have separate dental plates, except for the Araxathyriinae Shen, Grunt & Jin, 2004, which are characterized by a spondylium, and for the Comelicianiinae Merla, 1930, which have no dental plates. These two subfamilies are also the youngest among the family, the former being Wuchiapingian-Changhsingian, and the latter being restricted to the Changhsingian. The acquisition of the spondylium or the loss of dental plates can thus be considered to be derived characters.

In the light of the new findings, it is thus proposed that *Araxathyris* may have evolved from *Transcaucasathyris* by the convergence of the dental plates, very closely set in the early growth stages, to form a spondylium. In addition, *Araxathyris* is more convex than *Transcaucasathyris* and its spondylium may represent a structure that functions to optimize the length of the diductor and adductor muscles in shells with greater volume. The evolution in *Araxathyris* of a shell with increased internal space, lead to a more spacious mantle cavity and thus to a larger volume of the lophophore, which, together with the increased volume to surface area ratio, is indicative of higher metabolic rate and energy requirement. As shown by McGhee (1999), biconvex brachiopods tend to maximize internal volumes to shell surface areas in order to favor their feeding system of water filtration via the lophophore and growth to large size. However, the palaeoenvironmental change

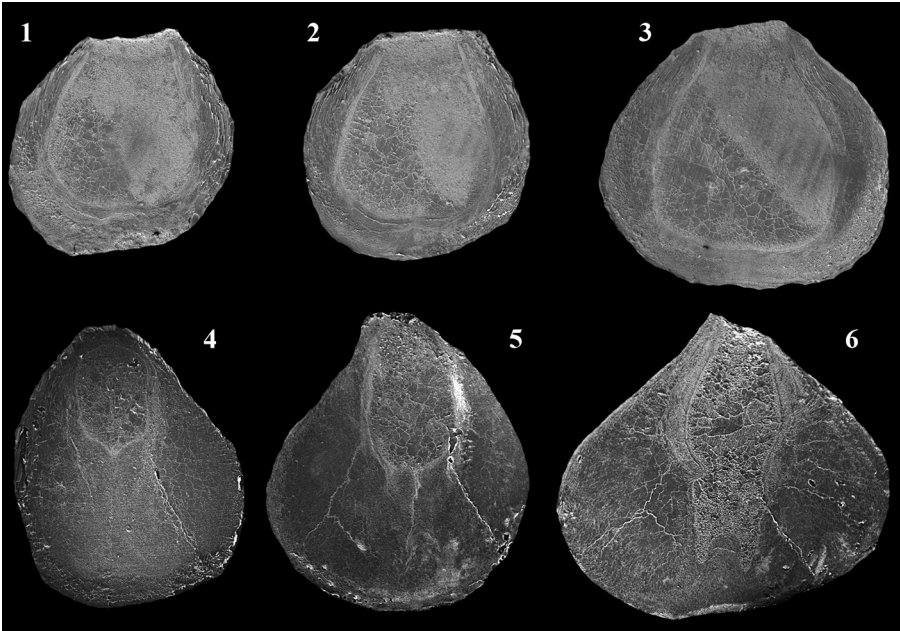


Fig. 1 - 1-3) Serial section of *Transcaucasathyris lata*, MPUM 11302 (JU111) at 0.2, 0.3 and 0.6 mm from the umbo respectively; 4-6) serial section of *Araxathyris protea*, MPUM11303 (JU111) at 0.3, 0.5 and 0.9 mm from the umbo respectively. All x 10.

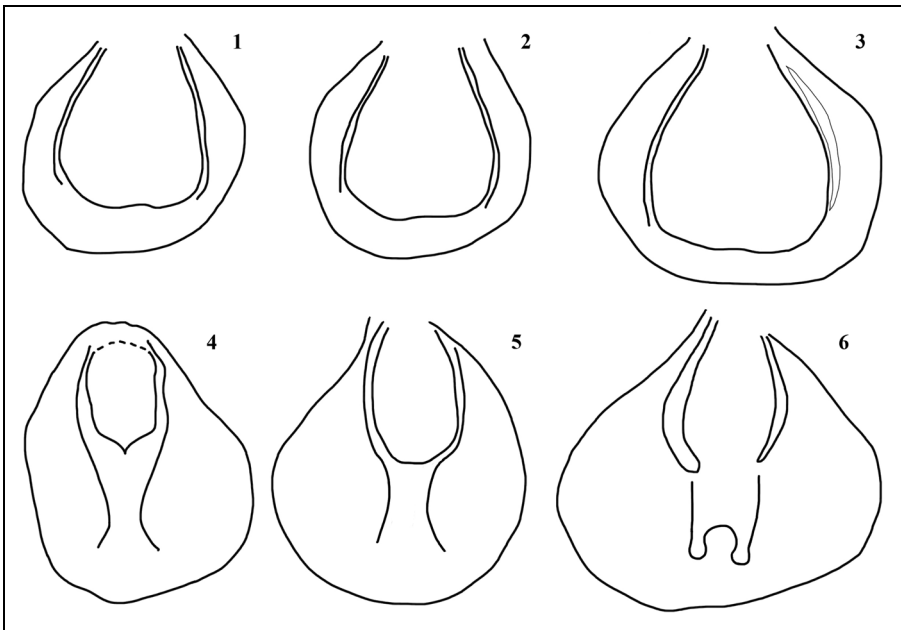


Fig. 2 - Line drawings of the serial sections of Fig. 1; 1-3) *Transcaucasathyris lata*, MPUM 11302 (JU111), drawings corresponding to photos 1-3 of Fig.1 respectively; 4-6) *Araxathyris protea*, MPUM 11303 (JU111), drawings corresponding to photos 4-6 of Fig. 1 respectively. All x 10.

recorded in the upper part of the Lopingian succession of NW Iran seems to have favored organisms with high surface area to volume ratio and lower metabolic rates, able to survive in areas where food supplies were low; hence the longer range of *Transcaucasathyris* versus the demise of *Araxathyris* at the top of the Julfa Formation.

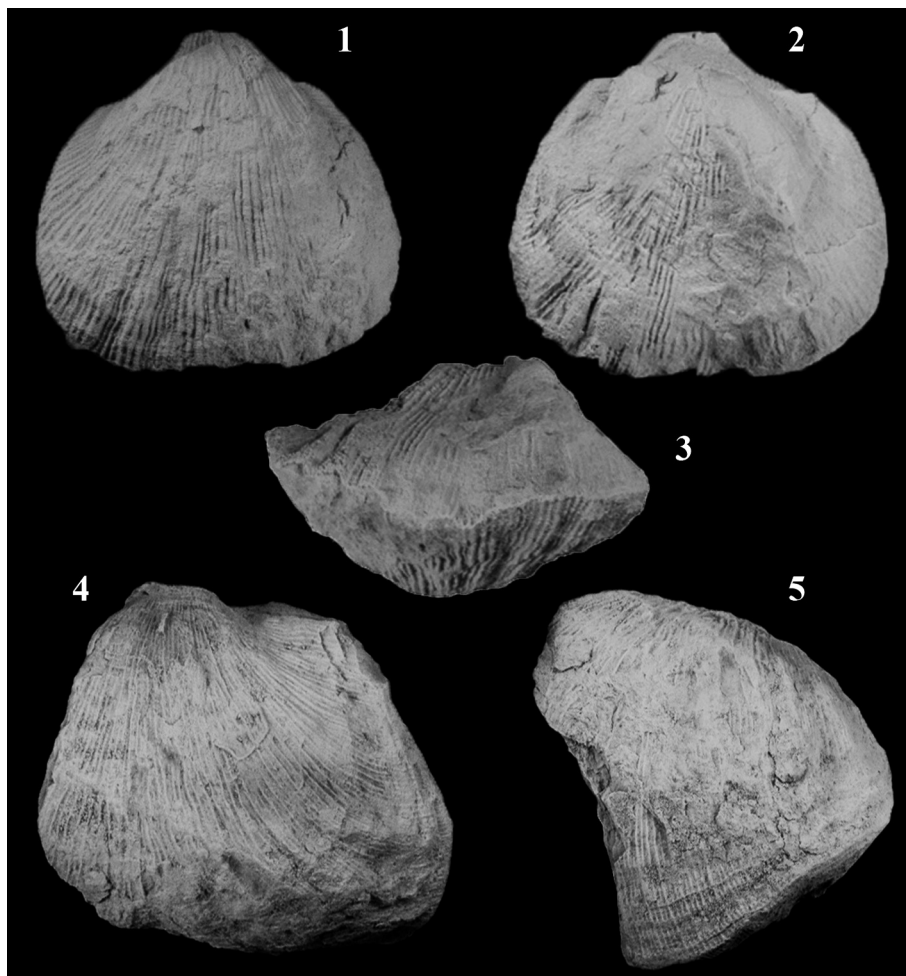
The acquisition, through evolution, of a spondylium is also known in other families of the Athyridida, for example some Devonian-Carboniferous subfamilies of the Ordovician-Carboniferous family Meristidae Hall & Clarke, 1895 (Grunt, pers. comm. 2013). The Athyridida are not the only taxa characterized by this type of evolution, it also occurs in the Clitambonitidina, where the spondylium is considered to be a derived

character that evolved in highly convex shells (Vinn & Rubel 2000)

Systematic descriptions

- Order **Orthotetida** Waagen, 1884
- Suborder **Orthotetidina** Waagen, 1884
- Superfamily Orthotetoida Waagen, 1884
- Family Meekellidae Stehli, 1954
- Subfamily Meekellinae Stehli, 1954
- Genus *Meekella* White & St. John, 1867
- Type species: *Plicatula striatocostata* Cox, 1857
from the Moscovian of Iowa.

Fig. 3 - 1-3) *Meekella julfensis*, MPUM11296 (JU1), holotype, ventral, dorsal and anterior views respectively, x2; 5-6) *Meekella julfensis*, MPUM11297 (JU120), ventral and dorsal views respectively, x 1.5.



***Meekella julfensis* n. sp.**

Fig. 3

1965 *Orthothenina peregrina* - Sokolskaja in Ruzhentsev & Sarytcheva, p. 206, pl. 30, figs 7a-c (non figs 6a-c).

2010 *Meekella* aff. *M. heterofolda* - Angiolini & Carabelli, p. 65, pl. 3, figs 2-5; pl. 4, figs 2-3.

Holotype: MPUM11296 (JU1), an articulate specimen from the base of the Julfa Formation, Ali Bashi Mountains (38°56'21,1"N, 45°30'43,8"E).

Derivation of name: From the town of Julfa in NW Iran near the border with Azerbaijan.

Material: One figured articulated shell: MPUM11297 (JU120).

Diagnosis: Medium to large sized *Meekella* with poorly and irregularly developed plicae, but with uniformly branching costellae numbering 10-11 per 5 mm both at mid-length and at the anterior margin.

Description. Medium to large sized, sub-equally biconvex shell with subovate outline; maximum width ranging from 25.1 to 49.0 mm at mid-length, and maximum length ranging from 23.2 to 41.8 mm; cardinal margin about half the width of the shell; broadly unisulcate anterior commissure.

Ventral valve convex, conical with pointed umbo, interarea relatively high, apsacline with pseudodelti-

dium. Dorsal valve slightly more convex with subovate outline, and a very shallow sulcus. Ornamentation of ventral valve with regularly branching costellae, somewhat sinuous or distorted, which number 10-12 per 5 mm both at mid-length and at the anterior margin; plication weak, irregular, slightly oblique, mostly developed anteriorly to mid-length; growth lamellae, more visible anteriorly.

Interior of ventral valve with dental plates converging apically to form a sessile pseudospondylium; anteriorly dental plates are separated and slightly divergent on the valve floor.

Remarks. The new species is the most similar to *Meekella heterofolda* Liang, 1990 as described by Shen & Shi (2007, p. 17, pl. 4, figs 1-4) based on its outline and irregularly developed, weak plicae. However, *Meekella julfensis* n. sp. differs from *M. heterofolda* by its weaker dorsal sulcus, by the number of costellae, which remains constant (10-12 per 5 mm) from mid-length to the anterior margin, and by its less divergent dental plates.

One of the specimens described by Sokolskaya in Ruzhentsev & Sarytcheva (1965) as *Orthothenina peregrina* is irregularly and weakly plicate and fits with the description of the new species.

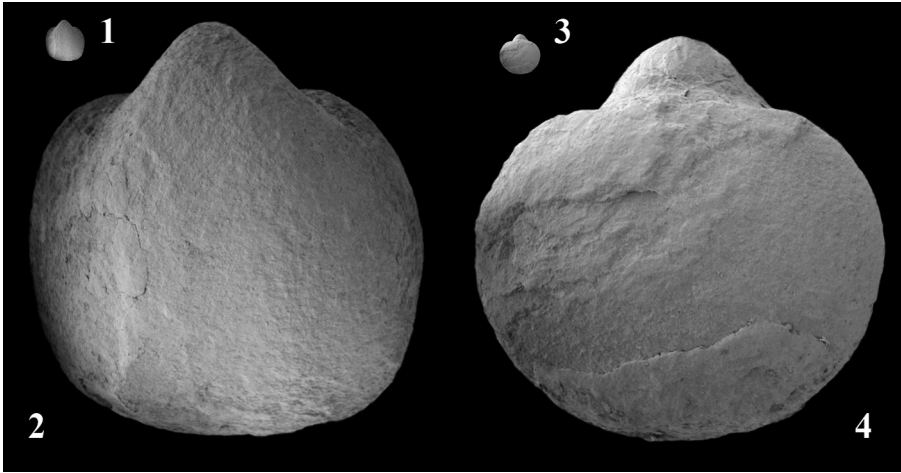


Fig. 4 - 1-2) *Paracrurithyris pygmaea*, MPUM 11299 (JU148-4), ventral view of an articulated specimen, x1 and x10 respectively; 3-4) *Paracrurithyris pygmaea*, MPUM11298 (JU148-1), dorsal view of an articulated specimen, x1 and x10 respectively.

Ruzhentsev & Sarytcheva (1965) reported another species, *Meekella arakeljani* (Sokolskaya in Ruzhentsev & Sarytcheva, 1965), from the Guadalupian-early Wuchiapingian Khachik Formation of Transcaucasia. However, this species is characterized by stronger plications, more numerous costellae and the absence of a dorsal sulcus and thus it is different from the new species.

Occurrence. JU1 float at the base of the Julfa Formation at 38°56'21,1"N, 45°30'43,8"E, NW of the Main Valley section; JU120 at 10.70 metres from the base of the Julfa Formation along the Main Valley section (Ghaderi et al., this volume); Wuchiapingian *Permophriconothyrus ovata* Biozone, Ali Bashi Mountains.

Distribution. Wuchiapingian part of the Nesen Formation of the Alborz Mountains, N Iran (Angiolini & Carabelli 2010); Wuchiapingian *Araxilevis* beds of Transcaucasia (Ruzhentsev & Sarytcheva 1965).

Order Spiriferida Waagen, 1883

Superfamily Ambocoelioidea George, 1931

Family Ambocoeliidae George, 1931

Subfamily Ambocoeliinae George, 1931

Genus *Paracrurithyris* Liao, 1981

Type species: *Crurithyris pygmaea* Liao, 1980 from the Lopingian of China.

***Paracrurithyris pygmaea* (Liao, 1980)**

Fig. 4

?1979 *Paracrurithyris pygmaea* Liao, p. 207, figs 4-7.

1980 *Crurithyris pygmaea* Liao, p. 264, pl. 8, figs 1-4.

1981 *Paracrurithyris pygmaea* - Liao in Zhao et al., p. 54, pl.1, figs 4-7.

1984 *Crurithyris pygmaea* - Liao, p. 285, pl. 2, figs 26, 27.

2012 *Paracrurithyris pygmaea* - He et al., p. 523, fig. 7.

Material: Two articulated figured shells: MPUM11298 (JU148-1), MPUM11299 (JU148-4); eight articulated shells: MPUM11300

(JU148,-2,-3,-5,-6,-7,-8,-9,-10, JU85); one dorsal valve: MPUM11301 (JU83).

Description. Small sized plano-convex shell, with subcircular to subelliptical outline; maximum width ranging from 3.3 mm to 6.7 mm, corresponding length from 2.9 mm to 6.8 mm; cardinal margin straight, line about 5/6 shorter than the maximum width that is at mid-length. Ventral valve strongly convex with hooked umbo; ventral interarea apsacline with an open delthyrium; ventral sulcus from subtle to weakly developed. Dorsal valve nearly flat with a relatively wide anacline interarea. Both valves with smooth surface.

Remarks. According to Xu & Grant (1994), Liao in 1979 illustrated the species as *Paracrurithyris pygmaea* without giving it a description. Liao then described *Crurithyris pygmaea* in 1980, but the genus *Paracrurithyris* was only erected in 1981. We did not have access to Liao (1979), so we consider the species as first established in 1980. The external features of the specimens under study are consistent with the illustration and description of *Paracrurithyris pygmaea* given by previous authors, in particular regarding the outline, plano-convex shape and the absence of any type of ornamentation on both valve surfaces.

Occurrence. JU85 *Paratirolites* Limestone, Locality 1 of Teichert et al. (1973) at 38°56'22.5"N, 45°31'13.0" E; JU83, JU148 Boundary Clay, Locality 1 of Teichert et al. (1973) at 38°56'22.5" N, 45°31'13.0" E.

Distribution. Changhsingian of South China (He et al. 2012).

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