# A New, Unusual Rhynchonellide Brachiopod with a Strophic Shell from the Silurian of Iran

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# A new, unusual rhynchonellide brachiopod with a strophic shell from the Silurian of Iran

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A new, unusual rhynchonellide brachiopod *Jafarirhynchus alatus* assigned to the newly established family Jafarirhynchidae is described from the Silurian (Telychian) of the Boghu Mountains in east-central Iran. It forms a low diversity association with the spiriferide *Striispirifer*? *ocissimus*, which exhibits well preserved calcified brachial supports. A strophic shell, well-developed ventral interarea and liberosessile mode of life make this taxon unique among Palaeozoic rhynchonellide brachiopods. In spite of a superficial similarity to spiriferides and the atrypide family Davidsonioidea, *Jafarirhynchus* retains the typical rhynchotrematoid cardinalia with a septalium supported by the median septum, a septiform cardinal process and long, raduliform crura. It is considered as an offshoot of the local lineage, which includes two successive species of *Stegocornu* (family Rhynchotrematidae) which proliferated in Central Iran and adjacent Afghanistan during Aeronian time.

Key words: Rhynchonellida, morphology, taxonomy, Silurian, Telychian, Iran.

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## Introduction

The existing record of Iranian Silurian brachiopods remains sparse and incomplete apart from the rich Aeronian brachiopod faunas of Central Iran and Kopet-Dagh, which are well documented in publications by Cocks (1979), Brice (1999), and Hairapetian et al. (2012). The major focus of this paper is to describe a small, oligotaxic brachiopod association from the Telychian deposits of the Boghu Mountains in the vicinity of the town of Kashmar, which are situated at the northern margin of the Tabas block in the north-eastern part of the Central Iran plate. The most distinctive component of this association is an unusual rhynchonellide with a strophic shell and a well-developed ventral interarea assigned to a new genus and species *Jafarirhynchus alatus*.

*Institutional abbreviations*.—AEU, Azad University, Esfahan, Iran; NMW, Department of Geology, National Museum of Wales, Cardiff, UK; CNIGR, F. N. Chernyshev Central Research and Geological Exploration Museum, St Petersburg, Russia.

*Other abbreviations*.—Lv, Ld, maximum length of ventral and dorsal valves; max, maximum observed size; min, minimum observed size; N, number of specimens; S, standard deviation from the mean; SLw, SLh, maximum width and height of the sulcus/median folds; W, T; maximum width, thickness of the shell; X, mean.

## Geological and geographical setting

The Boghu Mountains are situated about 25 km south-west of the town of Kashmar (Fig. 1). An outline of the Lower Palaeozoic geology of the area can be found in publications by

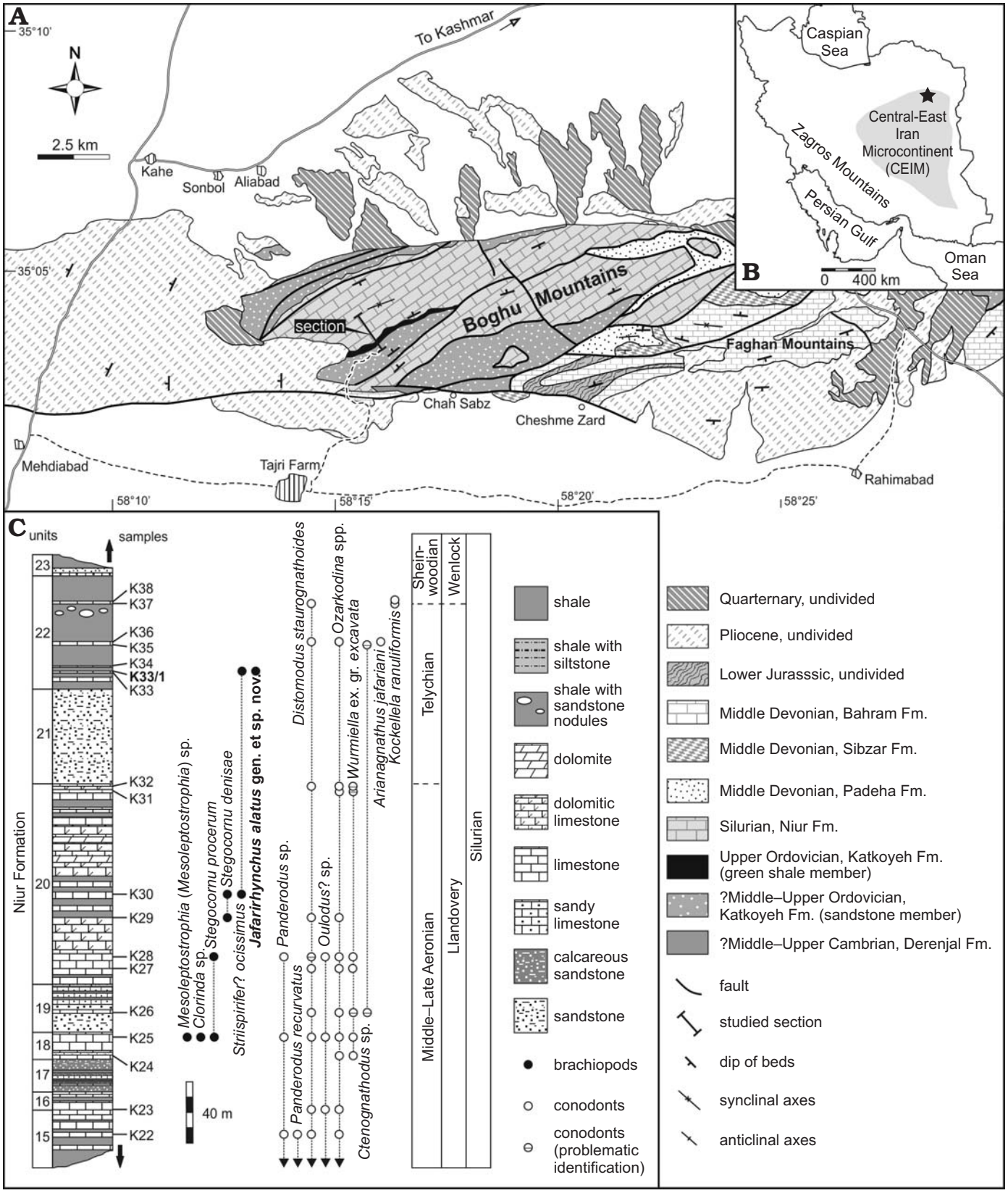


Fig. 1. **A**. Geographic and geologic setting of the studied material showing position of studied section (modified after Taheri 2001). **B**. Schematic map showing position of studied locality (asterisk). **C**. Stratigraphical column of the Boghu Section showing the informal lithostratigraphical subdivision of the Niur Formation, position of fossil samples, and stratigraphical distribution of brachiopods and conodonts. Arrows below and above the log indicate that the section continues in both directions (for a complete log see Hairapetian et al. 2012). Arrows at the lowermost of distribution line of some taxa indicates that these also occur in lower strata.

Ghavidel-Syooki (2003) and Hairapetian et al. (2012). The best exposures are situated on the southern flank of the Boghu Mountains (Fig. 1A). There the Silurian Niur Formation rests unconformably on siliciclastic sediments (green shale member) of the Ordovician Katkoyeh Formation (Fig. 1B). The base of the measured section is situated at 34°4′6.2″N, 58°15′48.8″E, altitude 1222 m. The Niur Formation comprises intercalating beds of argillite, sandstone, siltstone, and bioclastic limestone. The Aeronian part of the section is characterised by a conodont assemblage including *Distomodus staurognathoides* (Walliser, 1964), *Wurmiella* ex. gr. *excavata* (Branson and Mehl, 1933), *Ozarkodina* spp. and *Oulodus*? sp., and a low diversity brachiopod fauna dominated by the rhynchonellides *Stegocornu procerum* Dürkoop, 1970 and *Stegocornu denisae* Popov, Modzalevskaya, and Ghobadi Pour in Hairapetian et al., 2012 (Fig. 1B).

The brachiopods *Jafarirhynchus alatus* gen. et sp. nov. and *Striispirifer*? *ocissimus* Popov, Modzalevskaya, and Ghobadi Pour in Hairapetian et al., 2012 were sampled from the bed of grey bioclastic limestone at 12 m above the base of unit 22 (Fig. 1; sample K33/1). It is separated from the last occurrence of *Wurmiella* ex. gr. *excavata* (Fig. 1B; sample K32) by a barren sandstone unit about 61.8 m thick (Fig. 1B; Unit 21). A conodont assemblage collected from sample K36 at 23.3 m above sample K33/1 includes *Distomodus staurognathoides* and *Arianagnathus jafariani* Männik et al. (2015). The latter was known from the Derenjal Mountains, east-central Iran associated with several taxa including *Pterospathodus amorphognathoides lennarti* Männik, 1998, suggesting the *P. amorphognathoides lennarti* Conodont Zone of mid Telychian age (Männik et al. 2013, 2015).

The uppermost conodont occurrences in the studied succession are in samples K37 and K38 (43.4 m above sample K33/1; Fig. 1B). They contain *Kockelella ranuliformis* (Walliser, 1964), suggesting an early Sheinwoodian (early Wenlock) age (Hairapetian et al. 2012).

# Systematic palaeontology

## Phyllum Brachiopoda Dumeril, 1806

## Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996

## Class Rhynchonellata Williams, Carlson, Brunton, Holmer, and Popov, 1996

## Order Rhynchonellida Kuhn, 1949

## Superfamily Rhynchotrematoidea Schuchert, 1913

## Family Jafarirhynchidae nov.

*Diagnosis*.—Aberrant Rhynchotrematoidea with a coarsely costate, alate, strophic shell, a wide, straight hinge line, a well-developed ventral interarea, a strong ventral sulcus and a dorsal median fold extending from the beak. Anterior commissure strongly bisulcate. Dental plates and septalium supported by a dorsal medium septum; cardinal process septiform.

*Remarks*.—The family Jafarirhynchidae is unique within the order Rhynchonellida in having a strophic shell with a wide, straight hinge line and a well-developed ventral interarea. These features in combination with cyrtomatodont teeth are considered diagnostic for spiriferides (Jaanusson 1971); however, the family Jafarirhynchidae has dorsal cardinalia with a septalium supported by the median septum, a septiform cardinal process and long, raduliform crura, typical for the rhynchonellide superfamily Rhynchotrematoidea. The serial sections demonstrate the lack of calcified spiralia.

### Genus *Jafarirhynchus* nov.

*Type species*: *Jafarirhynchus alatus* sp. nov.; monotypic; see below.

*Etymology*: After Professor Mohammad-Ali Jafarian (1935–2013) in appreciation of his valuable contributions to the Palaeozoic palaeontology and stratigraphy of Iran.

*Diagnosis*.—As for the family.

*Stratigraphic and geographic range*.—Silurian, Llandovery, Telychian; Niur Formation of east-central Iran.

### *Jafarirhynchus alatus* sp. nov.

Figs. 2, 3A–C; Table 1.

*Etymology*: After the alate shape of the shell.

*Type material*: Holotype: AEU1500, a pair of conjoined valves. Paratypes*:* AEU1501, 1501–1510, NMW 2011.11G.400–456, CNIGR136/12600, total 62 articulated shells and four ventral valves from sample K-33/1.

*Type locality*: Boghu Mountains about 25 km south-west of the town of Kashmar, Iran.

*Type horizon*: Sample K-33/1, lower–middle Telychian, Llandovery, Silurian.

*Measurements* (in mm): Paratype AEU1501, Lv = 14.0, Ld = 12.3, W = 25.6, T = 10.0, SLw = 7.6, SLt = 8.3; AEU1503, Lv = 17.6, Ld = 15.6, W = 28.1, T = 13.6, SLw = 9.9, SLt = 9.4.

*Diagnosis*.—As for the genus.

*Description*.—Shell variably asymmetrical, strophic, dorsibiconvex, strongly alate, transverse, subtriangular in outline about three-fifths as long as wide, with maximum width at or slightly anterior to hinge line, and two-thirds as thick

Table 1. Basic measurements (in mm) of 13 shells of *Jafarirhynchus alatus* gen. et sp. nov.; Llandovery, Telychian, Niur Formation, sample K33/1, Boghu Mountains. Abbreviations: Lv, Ld, maximum length of ventral and dorsal valves; max, maximum observed size; min, minimum observed size; n, number of specimens; s, standard deviation from the mean; SLw, SLh, maximum width and height of the sulcus/median folds; W, T; maximum width, thickness of the shell; x, mean.

| | Lv | Ld | W | T | SLw | SLh | Lv/W | Ld/W | T/Lv | SLw/W |
|---|---|---|---|---|---|---|---|---|---|---|
| n | 13 | 13 | 13 | 13 | 13 | 13 | 13 | 13 | 13 | 13 |
| x | 15.7 | 14.1 | 26.8 | 10.2 | 8.7 | 9.8 | 58.5% | 52.6% | 65.3% | 32.5% |
| s | 1.20 | 1.21 | 1.35 | 1.17 | 1.15 | 1.67 | 4.4 | 4.5 | 6.2 | 4.9 |
| min | 14.2 | 12.25 | 24.7 | 8.7 | 6.8 | 7.4 | 48.5% | 43.4% | 55.8% | 23.2% |
| max | 17.8 | 15.8 | 29.25 | 13.5 | 10.3 | 14.2 | 63.6% | 58.9% | 75.8% | 41.7% |

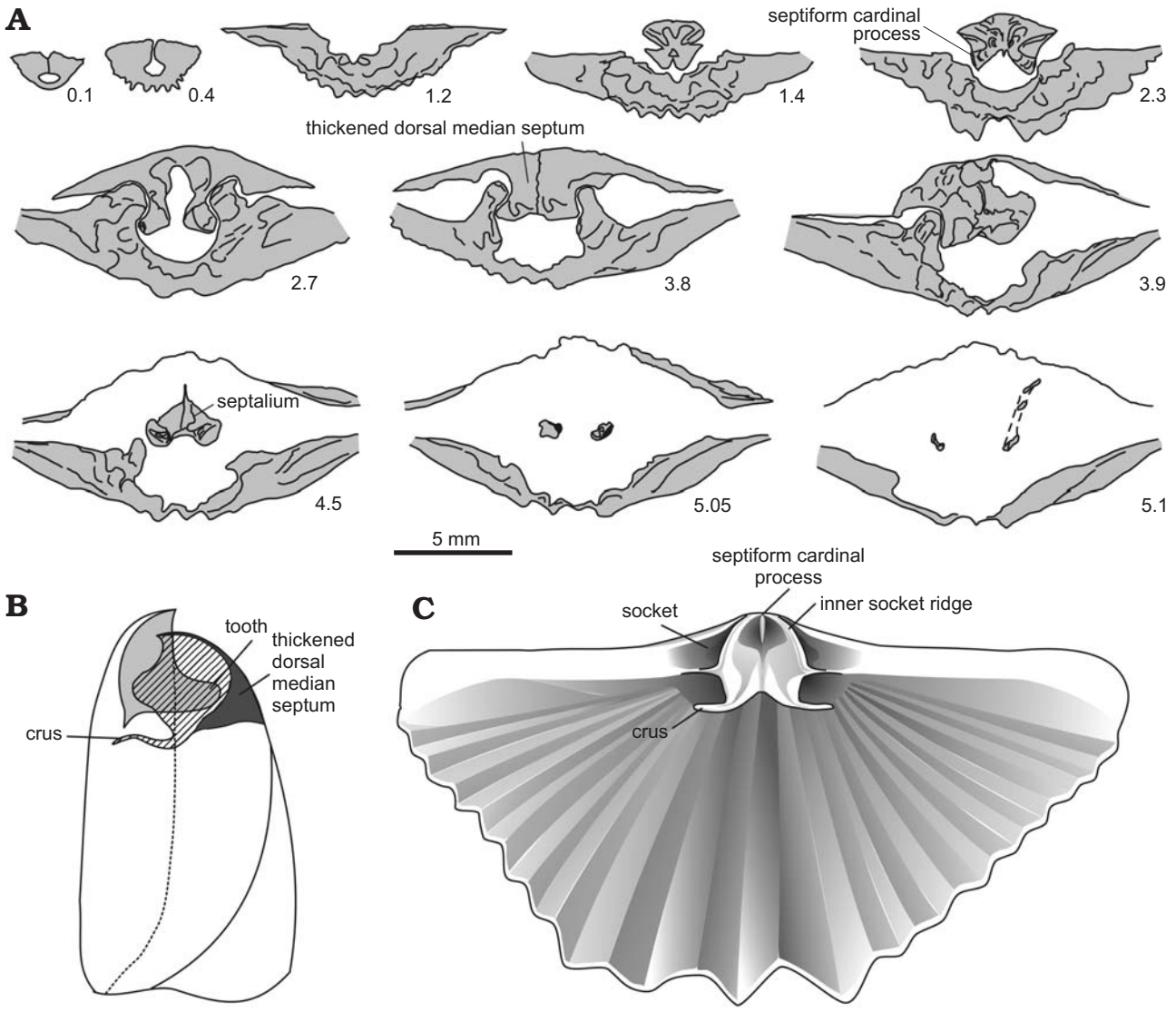


Fig. 2. Rhynchonellide brachiopod *Jafarirhynchus alatus* gen. et sp. nov. from Llandovery, Telychian, Niur Formation, sample K33/1, Boghu Mountains, CNIGR136/12600. **A**. Transverse serial sections (L = 18.4; W = 23.2; T = 10.5). **B**. Sagittal section of the shell. **C**. Dorsal valve interior. Numbers indicate distance in mm from the tip of the ventral umbo.

as long. Cardinal extremities slightly rounded. Lateral commissures almost straight, converging anteriorly. Anterior commissure strongly bisulcate. Ventral valve gently convex with a sulcus originating at the umbo and strongly deepening anterior to mid-length, bearing a single rib. Ventral interarea, planar, almost orthocline, with a broad, triangular delthyrium completely covered by the medially merged deltidial plates. Lateral profile of dorsal valve strongly convex with maximum height between mid-length and the anterior valve margin or at the anterior margin. Median fold with steep lateral slopes originating at the umbo, bearing two strong, high ribs, occupying about one-third maximum valve width at the anterior margin. Radial ornament of 17–22 strong, tubular ribs separated by interspaces of equal size. Two prominent subangular ribs on the dorsal median fold and a pair of subangular ribs on the flanks of ventral sulcus about twice as high and wide as other ribs. Concentric ornament of fine, regularly spaced concentric lamellae, becoming more prominent and densely crowded close the anterior margin of the mature individuals.

Ventral interior with strong, oblique teeth supported by the short, strongly thickened dental plates. Ventral muscle field strongly impressed with adductor scars completely enclosed by larger diductor scars. Strongly thickened pedicle callist mainly occupying the floor of the small delthyrial cavity. Dorsal interior with massive hinge plates and a small septalium supported by a strongly thickened, short median septum. Cardinal process septiform. Crura faint, radulifer, gently curved dorsolaterally. No calcified brachial supports.

*Stratigraphic and geographic range*.—Niur Formation, Aeronian, Llandowery, Silurian, Central Iran.

## Order Spiriferida Waagen, 1883

## Suborder Spiriferidina Waagen, 1883

## Superfamily Cyrtioidea Frederiks, 1924

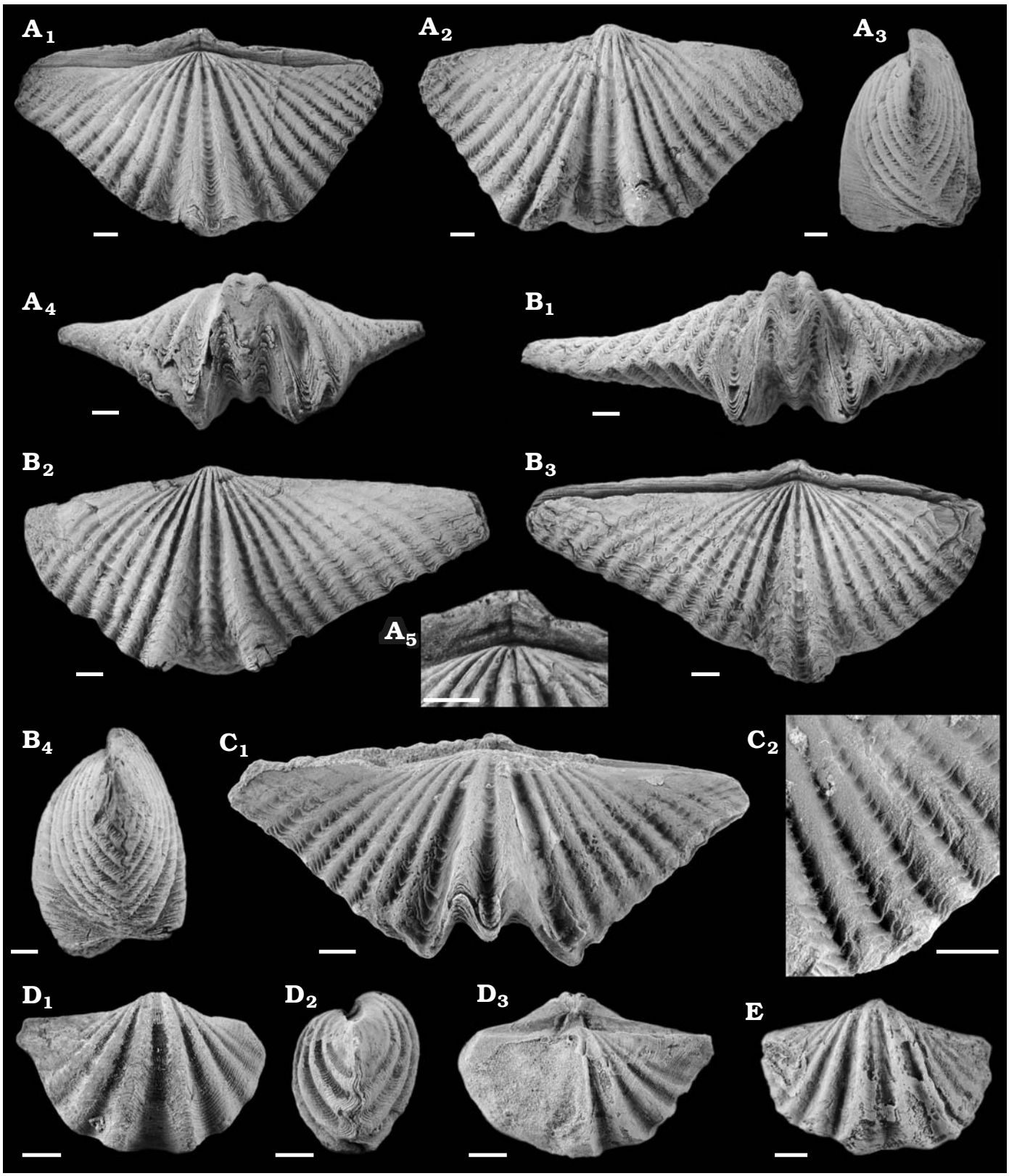


Fig. 3. Rhynchonellide brachiopod *Jafarirhynchus alatus* gen. et sp. nov. (**A–C**) and spiriferide *Striispirifer*? *ocissimus* Popov, Modzalevskaya, and Ghobadi Pour in Hairapetian et al., 2012 (**D**, **E**) from Niur Formation, Telychian, Llandovery, Silurian, sample K33/1, Boghu Mountains. **A**. AEU1500, holotype, a pair of conjoined valves, in dorsal ($A_1$), ventral ($A_2$), lateral ($A_3$), and anterior ($A_4$) views, enlarged ventral interarea ($A_5$). **B**. AEU1501, a pair of conjoined valves, in anterior ($B_1$), ventral ($B_2$), dorsal ($B_3$), and lateral ($B_4$) views of a strongly asymmetrical specimen. **C**. AEU1502, dorsal view of a pair of conjoined valves ($C_1$), enlarged surface ornament ($C_2$). **D**. AEU1511, a pair of conjoined valves, in ventral ($D_1$), lateral ($D_2$), and dorsal ($D_3$) views. **E**. AEU1512, ventral valve exterior. Scale bars 2 mm.

Family Cyrtioidae Frederiks, 1924

Subfamily Eospiriferinae Schuchert, 1929

Genus *Striispirifer* Cooper and Muir-Wood, 1951

*Type species*: *Delthyris niagarensis* Conrad, 1842; Niagara Group, Wenlock, Silurian, Lockport, New York, USA.

*Striispirifer*? *ocissimus* Popov, Modzalevskaya, and Ghobadi Pour in Hairapetian et al., 2012

Figs. 3D, E, 4.

2012 *Striispirifer*? *ocissimus* Popov, Modzalevskaya, and Ghobadi Pour 2012; Hairapetian et al. 2012: 101, figs. 6R-T, 11.

*Material*.—AEU1510–1512, NMW 2011.11G.457–469. Total six pairs of conjoined valves and nine ventral valves.

*Remarks*.—Specimens from the Telychian have spiralia with up to seven whorls. Except for their smaller size, these shells are morphologically identical to those of *Striispirifer*? *ocissimus* from the underlying Aeronian deposits (Hairapetian et al. 2012) and are considered here as conspecific.

*Stratigraphic and geographic range*.—Niur Formation, Aeronian, Llandowery, Silurian, Central Iran.

# Discussion

There is a general consensus that the earliest "astrophic spire-bearers" with calcified brachial supports evolved monophyletically from a rhynchonellide ancestor (Copper and Gourvennec 1996; Alvarez et al. 1998; Popov et al. 1999), while the astrophic shell can be considered as plaesiomorphic feature inherited by the early spire-bearers from rhynchonellides. Rong and Zhan (1996) also published convincing evidence, subsequently supported by a study of the early spire-bearing brachiopods from Kazakhstan (Popov et al. 1999) that spiriferides evolved from an atrypide (probably lissatrypoid) ancestor with a simple, centrally directed or planospiral spiralium. Therefore the strophic shell in spiriferides is an apomorphic character. Remarkably, the strophic shell evolved repeatedly several times in "astrophic spire-bearers", including the atrypide superfamily Davidsonioidea, the Devonian athyridide genera *Anathyrella* Khalfin in Gratsianova et al., 1961, and *Anathyris* Peetz, 1901, the Permian subfamily Comelicaniinae and the Mesozoic superfamily Koninckinoidea (for details see Alvarez and Rong 2002). Wright (1979) argued in favour of the origin of spiriferides from orthides, based on a superficial spiriferide appearance of some genera of the family Platystrophiidae; however, this view was not supported by subsequent studies by Rong and Zhan (1996).

There is no previous record of a similar strophic shell in rhynchonellides through their entire evolutionary history from the Ordovician to Recent. Hence the family Jafarirhynchidae is unique within the order Rhynchonellida in having a strophic shell with a wide, straight hinge line and a well-developed ventral interarea. These features, in combination with cyrtomatodont dentition, are considered diagnostic for the spiriferides (Jaanusson 1971); however, brachiopods assigned to the family Jafarirhynchidae lack calcified brachial supports and show the dorsal cardinalia with a septalium supported by the median septum, a septiform cardinal process and long, raduliform crura, typical for the rhynchonellide superfamily Rhynchotrematoidea. From other side, shells of *Striispirifer*? *ocissimus*, which occur at the same locality, have well preserved calcified spiralia (Fig. 4).

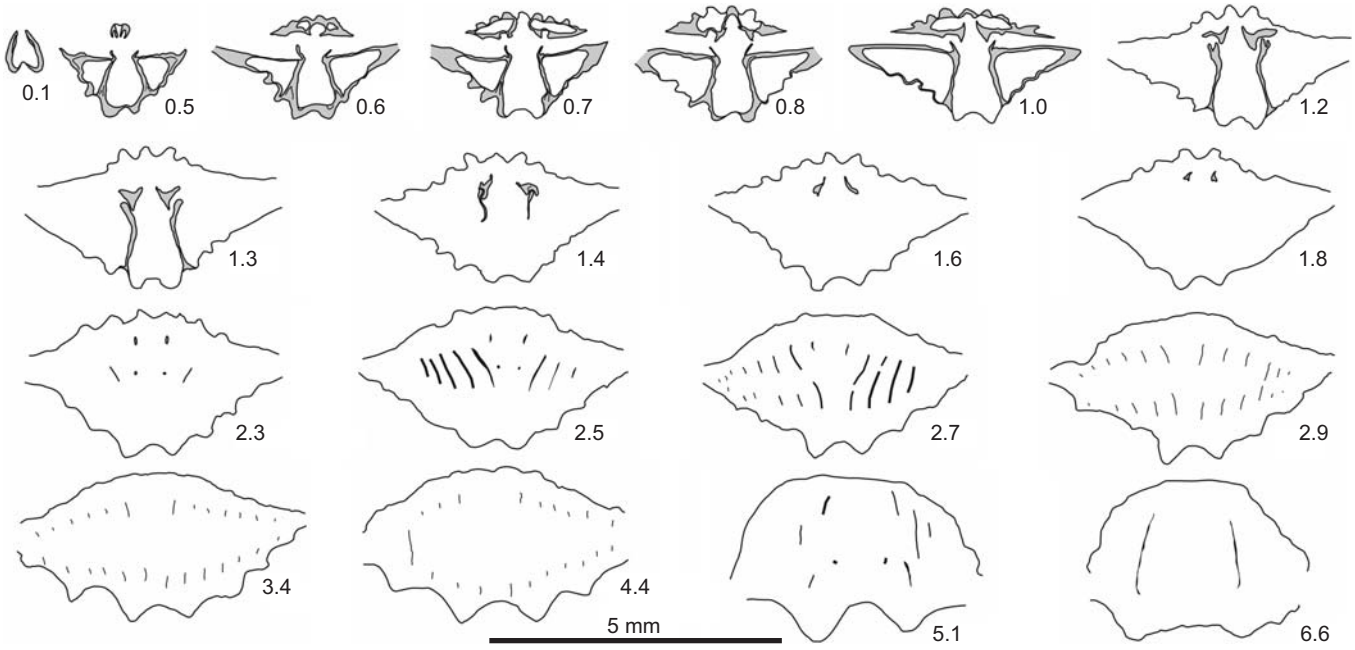


Fig. 4. Transverse serial sections of a cyrtioid spiriferid brachiopod *Striispirifer*? *ocissimus* Popov, Modzalevskaya, and Ghobadi Pour in Hairapetian et al., 2012; NMW 2011.11G.457 from Llandovery, Telychian, Niur Formation, sample K33/1, Boghu Mountains. Numbers indicate distance in mm from the tip of the ventral umbo.

*Jafarirhynchus* itself can be linked to the Aeronian lineage of rhynchotrematid *Stegocornu* represented by two succeeding species *S. procerum* Dürkoop, 1970 and *S. denisae* Popov, Modzalevskaya, and Ghobadi Pour in Hairapetian et al., 2012 in a number of localities across Central Iran (Hairapetian et al. 2012; Popov and Cocks 2013). Indeed, *S. denisae* shows an erect beak, an almost straight hinge line that is only slightly shorter than maximum shell width and a delthyrium mainly covered by converging deltidial plates (Hairapetian et al. 2012: fig. 6S, T). In comparison with the ancestral taxon *S. procerum*, *S. denisae* is also characterized by its wider, dorsoventrally compressed shell and narrower fold and sulcus in relation to the maximum shell width. All these tendencies are progressed further in *Jafarirhynchus alatus*, which possibly represents the last member of that lineage.

The delthyrium in *Jafarirhynchus alatus* is completely sealed by the medially merged deltidial plates and there is no functional pedicle foramen in mature individuals. This suggests a liberosessile mode of life for this species, which is unusual in rhynchonellides. *Jafarirhynchus alatus* is a dominant species in the oligotaxic rhynchonellid association with *Striispirifer*? *ocissimus* as a minor component. In the early Telychian of the Kashmar area this association replaced the *Stegocornu* association characteristic of the Aeronian (Hairapetian et al. 2012). Both associations inhabited the shallow shelf environments on a carbonate ramp and can be assigned to the Benthic Assemblage Zone 2 of Boucot (1975).

*Jafarirhynchus* shows a remarkable similarity to atrypides of the superfamily Davidsonioidea in the morphology of the ventral interarea and delthyrial covers (Copper 2002: fig. 937.2); however, that similarity is superficial and represents no more than homoplasy, since *Jafarirhynchus* retains typical rhynchonellide cardinalia with a septalium. Recent rhynchonellides have a spirolophe lophophore with dorsally directed apices of cones. They lack calcified supports, but it is likely that their basic morphology remained unchanged since the early Palaeozoic. The strongly transverse shell renders this type of lophophore dysfunctional in *Jafarirhynchus*, therefore the eversion model of lophophore cones developed from the laterally directed axis of spiralia, proposed by Rong and Zhan (1996) for spiriferides, was probably applicable also for *Jafarirhynchus*.

# Conclusions

A strophic shell with well-developed ventral interarea convergently similar to those of spiriferides, and a liberosessile mode of life make *Jafarirhynchus* and the family Jafarirhynchidae unique among the Palaeozoic rhynchonellide brachiopods. In spite of its unusual morphology and life style, previously unknown in the early Palaeozoic representatives of the order, *Jafarirhynchus* retains characteristic rhynchotrematoid cardinalia and can be considered as a terminal member of a local lineage, which evolved in Central Iran during the Aeronian, where it is represented by two succeeding species of *Stegocornu* (Hairapetian et al. 2012).

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