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.
Ghavide-Syooki (2003) and Hairapetian et al. (2012). The best exposures are situated on the southern flank of the Bogenous Mountains (Fig. 1A). There the Silurian Niur Formation rests unconformably on siliciclastic sediments (green shale member) of the Ordovician Kaktuyeh 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 comprises intercalating beds of argillite, sandstone, siltstone, and bioclastic limestone. The Aeronian part of the section is characterized by a conodont assemblage including Distomodus staurognathoides (Walliser, 1964), Wurmiella ex. gr. excavata (Branson and Mehl, 1933), Ozarkodina spp. and Ootodus? spp., and a low diversity brachiopod fauna dominated by the rhynchonellides Stegocornu procerum Dürkoop, 1970 and Stegocornu densisae Popov, Modzalevskaya, and Ghabadi Pour in Hairapetian et al., 2012 (Fig. 1B). The brachiopods Jafarirhynchus alatus gen. et sp. nov., and Strisspirifer? ocellinus Popov, Modzalevskaya, and Ghabadi 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 Arianaagnathus jafariani Männik et al. (2015). The latter was known from the Derenjal Mountains, east-central Iran associated with several taxa including Pterospaathodus amorphognathoides lennarti Männik, 1999, 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 Kockeella ranuliformis (Walliser, 1964), suggesting an early Sheinwoodian (early Wenlock) age (Hairapetian et al. 2012).

Systematic palaeontology

Phyllocum Brachiopoda Dumeril, 1806
Subphylum Rhynchozheniformia Williams, Carlson, Brunton, Holmer, and Popov, 1996
Class Rhynchozhenella Williams, Carlson, Brunton, Holmer, and Popov, 1996
Order Rhynchozhenella Kuhn, 1949
Superfamily Rhynchozhenematoidea Schuchert, 1913
Family Jafarirhynchidae nov.

Diagnosis.—Aberrant Rhynchozhenematoidea 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 septalum supported by a dorsal medium septum; cardinal process septiform.

Remarks.—The family Jafarirhynchidae is unique within the order Rhynchozhenella 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 septalum supported by the median septum, a septiform cardinal process and long, raduliform crura, typical for the rhynchozhenella superfamiliy Rhynchozhenematoidea. 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, dorsi-ribiconvex, 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: L, 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 | Lw/ 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%  |
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. Medianfold 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, Llandovery, 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? oceissimus* Popov, Modzalevskaya, and Ghabadi 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 (A₁), ventral (A₂), lateral (A₃), and anterior (A₄) views, enlarged ventral interarea (A₅). B. AEU1501, a pair of conjoined valves, in anterior (B₁), ventral (B₂), dorsal (B₃), and lateral (B₄) views of a strongly asymmetrical specimen. C. AEU1502, dorsal view of a pair of conjoined valves (C₁), enlarged surface ornament (C₂). D. AEU1511, a pair of conjoined valves, in ventral (D₁), lateral (D₂), and dorsal (D₃) 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? octissimus Popov, Modzalevskaya, and Ghabadi Pour in Hairapetian et al., 2012

Figs. 3D, E, 4.
2012 Striispirifer? octissimus Popov, Modzalevskaya, and Ghabadi 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? octissimus from the underlying Aeronian deposits (Hairapetian et al. 2012) and are considered here as conspecific.

Stratigraphic and geographic range.—Niur Formation, Aeronian, Llandovery, 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 Gourvenec 1996; Alvarez et al. 1998; Popov et al. 1999), while the astrophic shell can be considered as plaeosimorphic 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-bearer brachiopods from Kazakhstan (Popov et al. 1999) that spiriferides evolved from an atyride (probably lissatrypoid) ancestor with a simple, centrally directed or planospiral spirallum. Therefore the strophic shell in spiriferides is an apomorphic character. Remarkably, the strophic shell evolved repeatedly several times in “astrophic spire-bearers”, including the atyride superfamily Davidsonioidea, the Devonian athyridide genera Anathyrella Khalfin in Gratsianova et al., 1961, and Anathyris Peetz, 1901, the Permian subfamily Comeli-caniinae 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 spire-bearer appearance of some genera of the family Platystrophidae; 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 Rynchonellidae 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 superfamly Rhychotrematoidea. From other side, shells of Striispirifer? octissimus, which occur at the same locality, have well preserved calcified spiralia (Fig. 4).

Fig. 4. Transverse serial sections of a cyrtioid spiriferid brachiopod Striispirifer? octissimus Popov, Modzalevskaya, and Ghabadi 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.
Striispirifer nant species in the oligotaxic rhynchonellid association with suggests a liberosessile mode of life for this species, which is no functional pedicle foramen in mature individuals. This sealed by the medially merged deltidial plates and there is lineae.

allatus

Jafarirhynchus shows a remarkable similarity to atrypid- es of the superfamily Davidsionioidea 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 Mehl, M.G. 1993, Conodonts from the Bainbridge Formation (Silurian) of Missouri. University of Missouri Studies 8: 39–52. Brice, D. 1999. Middle(?). Silurian rhynchonellid and spiriferid brachiopod faunas from eastern central Iran. *Annales de la Société géologique du Nord* 7: 5–12. Cocks, L.R.M. 1979. A silicified brachiopod fauna from the Silurian of Iran. *Bulletin of the British Museum (Natural History), Geology* 32: 25–42. Conrad, T.A. 1842. Observations on the Silurian and Devonian Systems of the United States, with descriptions of new organic remains. *Journal of the Academy of Natural Sciences of Philadelphia* 8: 228–280. Cooper, G.A. and Muir-Wood, H.M. 1951. Brachiopod homonyms. *Journal of Washington Academy of Sciences* 41: 195–196. Cooper, C. 2002. *Atyrida.* In: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised)*, 1475–1614. Geological Society of America and the University of Kansas Press, Boulder. Boucot, A.J. 1975. *Evolution and Extinction Rate Controls.* 426 pp. Elsevier Scientific Publishing Company, New York. Brandson, E.B. and Melh, M.G. 1993. Conodonts from the Bainbridge Formation (Silurian) of Missouri. *University of Missouri Studies* 8: 39–52. obese. It is suggested that this mode of life is similar to that of *Jafarirhynchus* and the family Ja- farirhynchidae 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 rhyncho- trematoid 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).

**Conclusions**

A strophic shell with well-developed ventral interarea convergently similar to those of spiriferides, and a libreros- sile mode of life make *Jafarirhynchus* and the family Ja- farirhynchidae 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 rhyncho- trematoid 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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