

Stegocornu and associated brachiopods from the Silurian (Llandovery) of Central Iran

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Abstract. A Llandovery (mid-upper Aeronian) brachiopod fauna is described for the first time from the Niur Formation of Central Iran. It is dominated by two succeeding rhynchonellide species *Stegocornu procerum* Dürkoop, 1970 and *Stegocornu denisae* sp. nov. In addition, there are three common and four rarer brachiopod species, including *Dalejina? rashidii* sp. nov., *Isorthis (Ovalella) inflata* sp. nov. and *Striispirifer? ocissimus* sp. nov. The *Stegocornu* Association gives a distinct biogeographic signature to the mid to late Llandovery rhynchonellide-dominated shallow-water brachiopod faunas of Central Iran, Kope-Dagh and Afghanistan. Its proliferation in temperate latitude peri-Gondwana was one of the earliest signs of biogeographical differentiation of the brachiopod faunas in the early Silurian. The affinities of *Stegocornu* and *Xerxespirifer* are discussed.

Key words: Silurian, Aeronian, Brachiopoda, taxonomy, biogeography, Iran.

INTRODUCTION

The only published report on the occurrence of Silurian brachiopods in Central Iran is the paper by Brice (1999). Her study was based on a small collection sampled by the late A. F. de Lapparent in 1973, from a small outcrop of Silurian sediments, now assigned to the Shabdjereh Formation, in the vicinity of the Khanuk village. A more substantial record of the Silurian brachiopods from Kope-Dagh in northeastern Iran can be found in the paper by Cocks (1979) where he described 23 taxa. His study was based on a collection sampled at 2.5 km northeast of Robat-e-Qarabil, from a single bed about 33 m above the base of the Qarabil Limestone Formation designated in that publication. This is the type locality of *Xerxespirifer iranicus* Cocks, 1979, which for some time became a taxonomic puzzle. In particular, Carter et al. (1994) suggested that *Xerxespirifer* is not a spiriferidine, but more likely has rhynchonellide or leptocoellid affinity. Alvarez & Rong (2002) questionably assigned this genus to the athyridide family Retziellidae, whereas Brice (1999) and Savage et al. (2002) considered *Xerxespirifer* as possible junior objective synonym of *Stegocornu*, which has found support in the present study.

The rhynchonellide *Stegocornu* is a core taxon in the shallow-water fauna of the Benthic Assemblage Zone 2 (BA 2) in Central Iran, which can be termed as the *Stegocornu* Association. It occurs also in Robat-e-Qarabil and the Saluk Mountains, both located in the Kope-Dagh region of northeastern Iran (Fig. 1; Cocks 1979 and new unpublished observations by M. Ghobadi Pour), and in Afghanistan (Dürkoop 1970). The age of the *Stegocornu* fauna is defined as mid- to late Aeronian by co-occurrence with characteristic conodonts.

OUTLINE OF FOSSIL LOCALITIES

Kashmar region

The major source of the studied brachiopods in the area is Silurian deposits of the Niur Formation, exposed in the Boghu Mountains about 25 km southwest of the town of Kashmar (Fig. 1). The geographical coordinates of the base of the measured section are 34°04'6.2"N, 58°15'48.8"E, altitude 1222 m. The geographical coordinates for the top of the section are 35°04'43.3"N, 58°15'14.7"E, altitude 1266 m. Here a succession of the lower to middle Silurian sediments, assigned to the Niur Formation, is well exposed on the southern flank of the

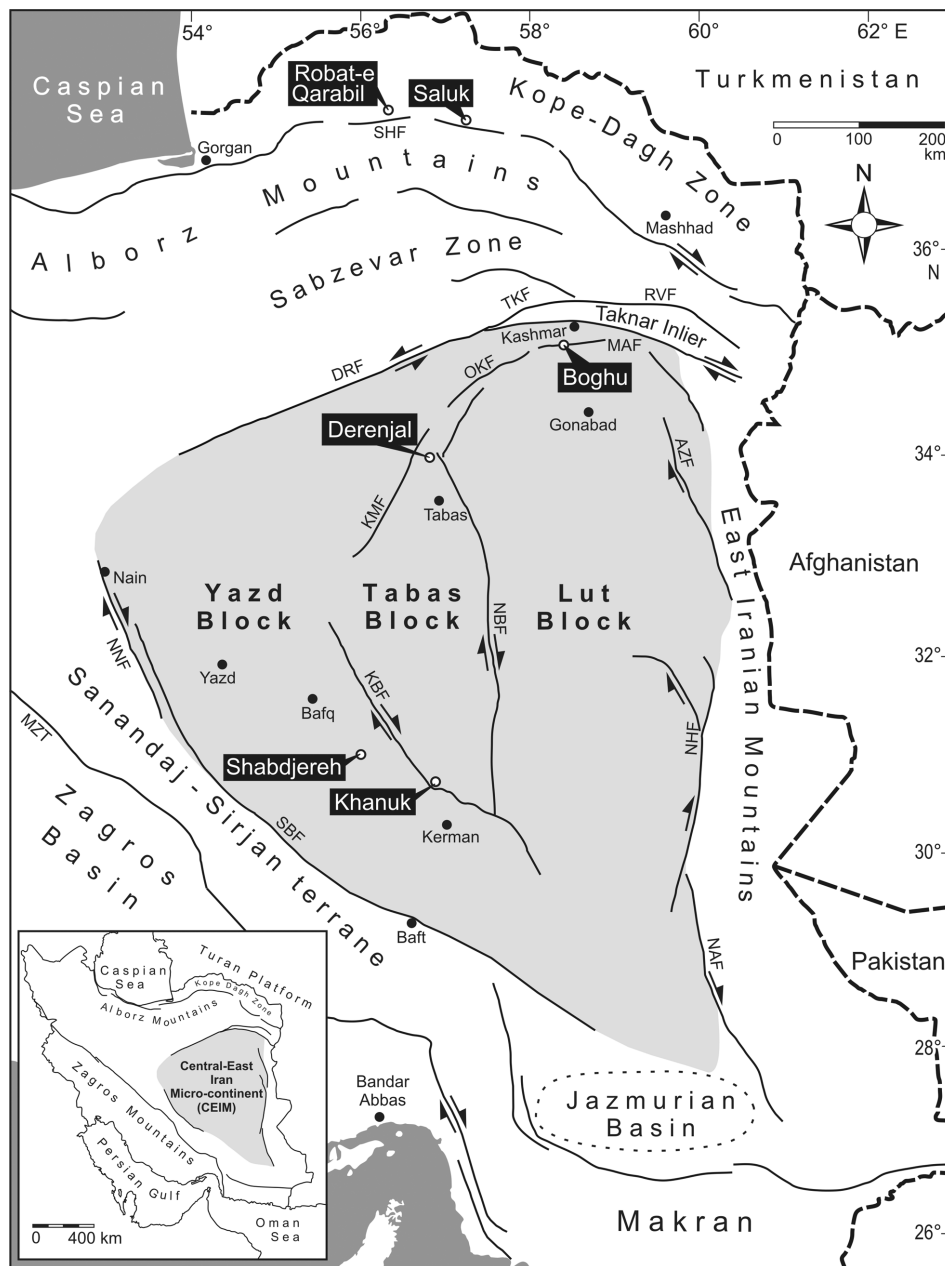


Fig. 1. Map of Iran showing Silurian brachiopod fossil localities discussed in the paper (mainly after Ramezani & Tucker 2003, with modifications; structural data compiled from various sources, e.g. Berberian & King 1981; Lindenberg et al. 1984; Alavi 1991; GSI 2001b; Ramezani & Tucker 2003). Abbreviations: AZF, Abiz fault; DRF, Doruneh fault; KBF, Kuhbanan fault; KMF, Kalmard fault; MAF, Mehdiabad fault; MZF, Main Zagros thrust; NAF, Nostratabad fault; NBF, Nayband fault; NNF, Nehbandan fault; NNF, Nain fault; OKF, Ozbak Kuh fault; RVF, Rivash fault; SBF, Shahre-Babak fault; SHF, Syahkuh fault; TKF, Taknar fault.

Boghu Mountains. It is underlain by an unnamed formation of Upper Ordovician siliciclastic rocks. The sampled section consists of highly fossiliferous limestones, shales and sandstone/siltstone units. The lowermost part of the measured section comprises green siltstone/shale beds intercalating with thin tentaculitid limestones and sandstones, which were assigned to the Niur Formation and dated by conodonts as lowermost

Llandovery on the geological map of Kashmar (GSI 2001a, sheet 1:100 000). However, the occurrence of *Icriodella* in association with *Amorphognathus* within this interval (Fig. 2, unit 1, samples K5–K10) clearly indicates an Upper Ordovician (Sandbian–Katian) age (P. Männik and C. G. Miller, pers. comm. 2011).

Conodonts from sample K25 (Fig. 2, unit 18) have been identified as *Distomodus staurogathoides* (Walliser, 1964),

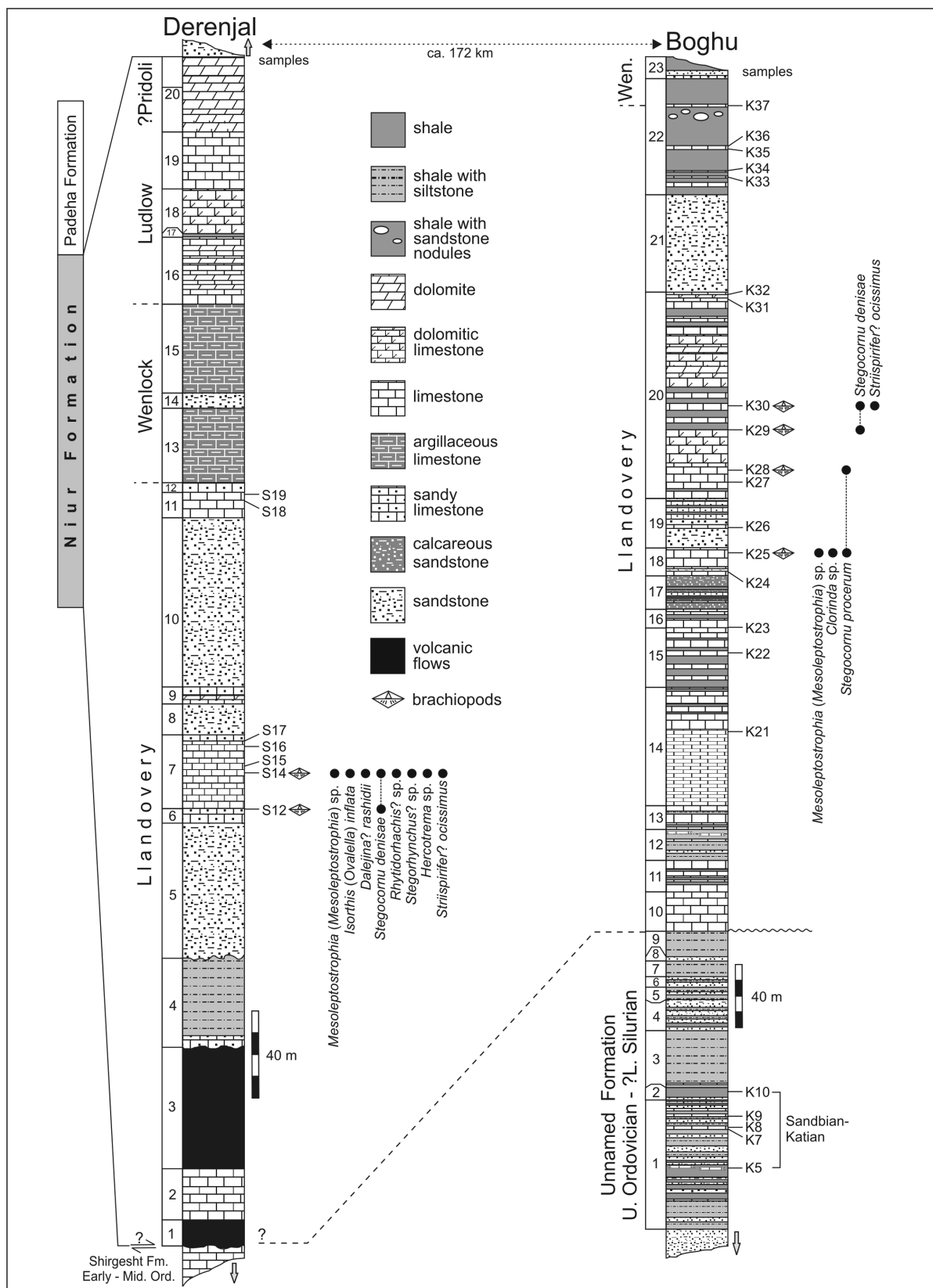


Fig. 2. Stratigraphical columns of the Derenjal and Boghu sections, showing informal lithostratigraphical subdivision of the Niur Formation, position of sampled horizons and stratigraphical distribution of brachiopods.

Wurmiella ex. gr. *excavata*, *Ozarkodina* spp. and *Oulodus?* sp., suggesting an age not older than the mid-Aeronian. Samples K28 and K29 (Fig. 2, unit 20) contain a similar conodont fauna, including *Distomodus staurogathoides*. The latter species is also documented from sample K37 (Fig. 2, unit 22), where it occurs together with *Kockelella ranuliformis* (Walliser, 1964), suggesting an early Sheinwoodian age.

In the Boghu section *Stegocornu procerum* Dürkoop, 1970 was sampled from two horizons (Fig. 2). In the lowermost sample K25 it occurs in association with a few specimens of *Clorinda* sp. and *Mesoleptostrophia* (*Mesoleptostrophia*) sp., whereas in sample K28 it forms a monotaxic association. The first occurrence of *Stegocornu denisae* sp. nov. is documented from sample K29, about 25 m above sample K28. The second horizon with *Stegocornu denisae* in association with a few *Striispirifer?* *ocissimus* sp. nov. is about 15 m higher (Fig. 2, sample K30).

Derenjal Mountains

The area is located about 65 km northwest of Tabas (Fig. 1; see also Ruttner et al. 1968; Hairapetian et al. 2008). Here Silurian sediments assigned to the Niur Formation are exposed on the eastern side of the Dahaneh-e-Kolut gorge and have a faulted contact against the lower Early–Middle Ordovician Shirgesht Formation (Bruton et al. 2004; Ghobadi Pour et al. 2006). The upper boundary of the Niur Formation represents a conformable contact with the presumably Lower Devonian Padeha Formation (Ruttner et al. 1968).

A measured section of the Niur Formation, in total 551 m thick, is exposed in three major hills named A, B and C (Hairapetian et al. 2008). The sedimentary succession through Hill A (units 1–4) consists of medium- to thin-bedded limestones, siltstones and argillites with abundant corals, brachiopods, ostracods, crinoids and trilobites (Fig. 2). Unit 2 is sandwiched between two horizons of volcanic rocks representing submarine basaltic lava flows (Fig. 2, units 1 and 3). The sedimentary unit was dated as mid-Aeronian, based on ostracods and brachiopods (Hairapetian et al. 2011).

Silurian deposits exposed on Hill B (base of the section at 34°5'2.9"N, 56°48'14"E; altitude 1040 m) comprise sandstone and bioclastic sandy limestone. The limestone beds yield an abundant fauna of brachiopods, corals, cephalopods, tentaculitids, conodonts, ostracods and trilobites. The *Stegocornu* Brachiopod Association was sampled from a single sample S14 in the middle part of Unit 7 (Fig. 2). It is dominated by two species, namely *Isorthis* (*Ovalella*) *inflata* sp. nov. (54%) and *Stegocornu denisae* sp. nov. (32%). Other associated brachiopod taxa include *Dalejina?* *rashidii* sp. nov.

(4%), *Hercotrema* sp. (<2%), *Mesoleptostrophia* (*Mesoleptostrophia*) sp. (1%), *Rhytidorhachis?* sp. (<1%) and *Striispirifer?* *ocissimus* sp. nov. (6%).

A conodont assemblage from the underlying Unit 6 (Fig. 2, sample S12) contains *Wurmiella excavata* cf. *puskuensis* (Männik, 1994), *Distomodus staurogathoides* (Walliser), *Ozarkodina* sp. and a few elements of *Panderodus* and *Oulodus?* suggesting a mid- to late Aeronian age (unpublished data by P. Männik, C. G. Miller and V. Hairapetian). Similar conodonts were recovered also from the overlying Unit 7 (Fig. 2; S15, S16 and S17). The occurrence of *Pterospirifer?* *amorphognathoides lennarti* Männik, the index species of the conodont biozone, in sample S19 in the uppermost part of Unit 11 (Fig. 2) indicates a mid-Telychian age (unpublished data by P. Männik, C. G. Miller and V. Hairapetian). Thus from the available conodont data the age of the brachiopod fauna from sample S14 is probably mid- to late Aeronian.

The part of the Niur Formation exposed on Hill C (Fig. 2, units 13–20) is dated from Wenlock to Pridoli (Flügel & Saleh 1970; Hairapetian et al. 2008). It comprises dark grey argillaceous limestones, dolomitic limestones and dolomites with abundant brachiopods, gastropods, ostracods, corals and fish microremains.

Kerman region

Geographical coordinates of the locality, in the vicinity of the Khanuk village published by Brice (1999) are undoubtedly erroneous and the precise location and sedimentary logs of the sampled section remain unknown. Probably it was located somewhere southeast of the village, where the Shabdjereh Formation is exposed (Fig. 1). The specimens of *Stegocornu* aff. *procerum* Dürkoop, 1970 (here re-assigned to *Stegocornu denisae* sp. nov.) have been identified from two individual samples. According to Brice (1999), they occur in association with *Hedeinopsis* spp. and *Nikiforovaena?* sp. The latter shells are probably assignable to *Striispirifer?* *ocissimus*.

The precise taxonomical affiliation of two other taxa referred to *Howellella* and *Rhynchotrema* is questionable.

Another small collection from the Kerman region was handed to T. L. Modzalevskaya by the late Prof. Stepanov (St Petersburg University) and has recently been donated to the Central Geological Research and Exploration Tschernyshev Museum (St Petersburg). These brachiopods were sampled by an anonymous Iranian geologist from an outcrop in the vicinity of the Shabdjereh village (Fig. 1). Geological and geographical information for the collection is not available. The specimens were most likely derived from a loose sample, as they include both *Stegocornu procerum* and *Stegocornu denisae*, which do not co-occur in the same horizon.

SIGNIFICANCE OF THE FAUNA

In Central Iran *Stegocornu* is represented by two species, namely *Stegocornu procerum* and *Stegocornu denisae*, which succeed each other in the sequence. Both species either dominated in low-diversity associations, usually including *Striispirifer?* (Kashmar and Kerman regions), or were an important part of more diverse associations together with various orthides, spiriferides and strophomenides (e.g. the Derenjal Mountains and Kope-Dagh).

In the Derenjal Mountains abundant *Stegocornu denisae*, and *Striispirifer? ocissimus* and rare *Hercotrema* sp. and *Rhytidorhachis?* sp. occur as conjoined valves, whereas *Isorthis (Ovalella) inflata* and *Dalejina? rashidii* are preserved as numerous disarticulated valves in shell accumulations with a few disarticulated valves of *Stegocornu*. It is probable that the brachiopod association from sample S14 represents a mixture of mainly autochthonous rhynchonellide and spiriferide shells, and allochthonous shells of *Isorthis (Ovalella)* and *Dalejina?*, which were transported into the area during seasonal storms.

In the type locality in Dascht-e-Nawar, eastern Afghanistan, *Stegocornu procerum* occurs together with conodonts identified as *Lonchodina* cf. *fluegeli* (Walliser, 1964) (Dürkoop 1970, p. 159), which may be an element of *Aspelundia? fluegeli* (Walliser, 1964) known from the late Aeronian–Telychian. In the Kashmar section, eastern Central Iran, *Stegocornu procerum* co-occurs with a conodont assemblage, suggesting an age not older than mid-Aeronian. The succeeding species *Stegocornu denisae* is found in the Shirgesht section well below the first documented appearance of the index species of the mid-Telychian *Pterospathodus amorphognathoides lennarti* Biozone and within the range of *Wurmiella excavata* cf. *puskuensis* (Männik), which is considered as the early member of the *W. excavata* lineage. These finds suggest that the proliferation of *Stegocornu* in Afghanistan and Central Iran took place within a narrow time span from the mid- to late Aeronian.

Dispersion of the *Stegocornu* Association in Central Iran, Kope-Dagh and Afghanistan in the late Aeronian represents a significant regional event. *Stegocornu* has a short stratigraphic range and its occurrence can be considered as a good indication of Aeronian age, in particular, for the faunas described earlier by Cocks (1979) from Kope-Dagh and by Brice (1999) from the Kerman Region.

Boucot & Blodgett (2001) consider the presence of *Xerxespirifer* (= *Stegocornu*) in Iran as indication of biogeographical differentiation within their North Silurian Realm in Wenlock time. New data suggest

that proliferation of the *Stegocornu* Association had occurred already in the mid- to late Llandovery. At that time peri-Gondwanan terranes of Central Iran, Kope-Dagh and Afghanistan supported shallow-water faunas bearing a common biogeographical signature, suggesting their position in relative proximity to each other, and probably in temperate southern palaeolatitudes.

SYSTEMATIC PALAEOLOGY

Abbreviations for parameters measured on specimens are: W, L, T = maximum width, length, thickness of the shell; Lv, Ld = maximum length of the ventral and the dorsal valve; Iw = maximum width of the interarea; Sw, St = width and depth of the sulcus at the anterior margin; Mw, Ml = width, length of the muscle field; SVl = length of the ventral median septum; BBw = distance between outer margins of brachiofores; BBl = brachiofores length; Sl = distance from the umbo to anterior termination of the median ridge; X = mean; S = standard deviation from the mean; N = number of specimens; max = maximum observed size; min = minimum observed size. All measurements are in millimetres.

The illustrated and described material is housed in the National Museum of Wales, Cardiff (NMW), in the Central Geological Research and Exploration Tschernyshev Museum (St Petersburg) and Azad University, Esfahan (AEU). The authorship of the new taxa is as follows: Popov, Modzalevskaya & Ghobadi Pour.

Order STROPHOMENIDA Öpik, 1934

Superfamily STROPHOMENOIDEA King, 1846

Family LEPTOSTROPHIIDAE Caster, 1939

Genus *Mesoleptostrophia* Harper & Boucot, 1978

Type species. *Mesoleptostrophia kartalensis* Harper & Boucot, 1978 (*nom. nov. pro Stropheodonta (Leptostrophia) explanata* Paeckelman & Sieverts, 1932, *non* Sowerby, 1842); Lower Devonian, Emsian, Kartal-Schichten, Turkey.

Mesoleptostrophia (Mesoleptostrophia) sp.

Figure 3A, B

Material. NMW 2011.11G.10, 11, ventral valves; NMW 2011.11G.8, 9, 12, dorsal valves; sample K25, Boghu Mountains. NMW 2011.11G.6, 7, ventral valves; sample S14, Derenjal Mountains. Total four ventral and three dorsal valves.

Description. Shell weakly concavoconvex to almost biplanate, transverse subrectangular with maximum width slightly anterior to the hinge line; anterior commissure rectimarginate.

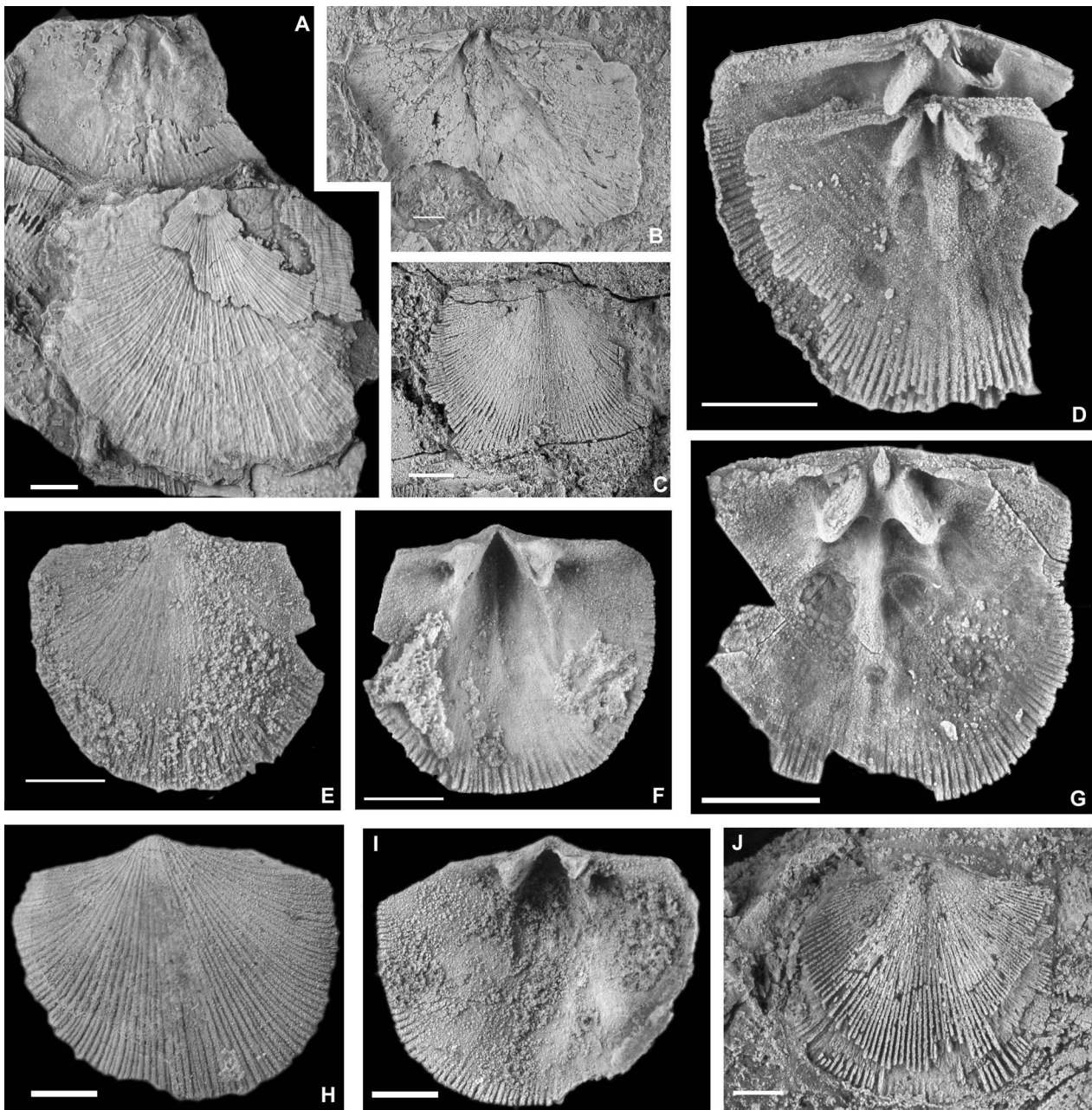


Fig. 3. A, B, *Mesoleptostrophia* (*Mesoleptostrophia*) sp.; Llandovery, mid-late Aeronian, Niur Formation; A, NMW 2011.11G.8, dorsal valve interior and NMW 2011.11G.8, 9, dorsal valve exterior, sample K25, Boghu Mountains; B, NMW 2011.11G.6, ventral valve interior, sample S14, Derenjal Mountains. C–J, *Isorthis* (*Ovalella*) *inflata* sp. nov. Llandovery, mid-late Aeronian, Niur Formation; sample S14, Derenjal Mountains; C, NMW 2011.11G.114.6, dorsal valve exterior; D, NMW 2011.11G.191, 192, dorsal valve interiors; E, F, NMW 2011.11G.15, ventral valve exterior, interior; G, NMW 2011.11G.190, dorsal valve interior; H, I, NMW 2011.11G.14, ventral valve exterior, interior; J, NMW 2011.11G.115, dorsal valve exterior. All scale bars 2 mm.

Ventral valve very weakly convex with a low, planar, apsacline interarea; delthyrium covered by a small pseudodeltidium. Dorsal valve planar anteriorly, weakly concave between the umbo and midlength. Dorsal interarea linear, anacline. Radial ornament subequally parvicostellate with one, rarely two parvicostellae between

accentuated ribs and with up to 9 ribs per 3 mm in mature specimens. Concentric ornament of regular, very fine, densely spaced fila.

Ventral interior with transverse denticulate plates on both sides of the delthyrium and a large, open anteriorly, subtriangular muscle field terminated almost

at midvalve and bisected medially by a faint median ridge. Posterolateral muscle bounding ridges prominent, straight, widely divergent.

Remarks. In shell outline and characters of ventral and dorsal interior Iranian specimens show close similarity to the shells from the Llandovery (Telychian) of Britain illustrated by Harper & Boucot (1978, pl. 1, figs 12–15, 18). They differ from two other British Llandovery (Telychian) species *Mesoleptostrophia* (*Mesoleptostrophia*) *tenuis* (Williams, 1951) and *Mesoleptostrophia* (*Mesoleptostrophia*) *ostrina* (Cocks, 1967) in having obtuse cardinal extremities, more prominent ventral muscle bounding ridges and subequally parvicostellate radial ornament with only one or two parvicostellae between accentuated ribs. The Iranian shells also lack distinct rugellae in the posterior part of the shell reported in the British species. They may represent a new, not yet recognized species of *Mesoleptostrophia* (*Mesoleptostrophia*), but inadequate preservation of the cardinalia makes its formal taxonomic designation impossible.

Order ORTHIDA Schuchert & Cooper, 1932
 Suborder DALMANELLIDINA Moore, 1952
 Superfamily DALMANELLOIDEA Schuchert, 1913
 Family ISORTHIDAE Schuchert & Cooper, 1931
 Genus *Isorthis* Kozłowski, 1929
Isorthis (*Ovalella*) Walmsley & Boucot, 1975

Type species. *Dalmanella* (*Isorthis*) *szajnochai* Kozłowski, 1929; Lower Devonian, Borshchov Formation, Podolia, Ukraine.

Isorthis (*Ovalella*) *inflata* sp. nov.
 Figures 3C–J, 4; Tables 1, 2

Derivation of name. Latin *inflatus* – swollen.

Holotype. NMW 2011.11G.91, holotype, dorsal valve, Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains, Iran.

Paratypes. NMW 2011.11G.373 (L = 11.8, W = 12.5, T = 6.2, Iw = 11.2); NMW 2011.11G.14–89, 114.3, 114.5, ventral valves; NMW 2011.11G.90, 91–112, 114.1, 114.2, 114.4, 114.6, 114.7, 115–192, dorsal valves; locality and stratum as for the holotype. Total one articulated shell, 78 ventral and 95 dorsal valves.

Diagnosis. Shell dorsibiconvex; transverse suboval to almost subrectangular outline, with maximum width between hinge line and midlength; radial ornament multicostellate, with 11–13 rounded ribs per 3 mm along the anterior margin; ventral muscle field large, bilobed,

elongate, extended anterior to midlength; cardinal process undivided.

Description. Shell dorsibiconvex, slightly transverse suboval to almost subrectangular in outline, about 95% as long as wide, with maximum width between hinge line and midlength. Hinge line about four fifths as wide as the shell; cardinal extremities rounded. Anterior commissure weakly sulcate. Lateral profile of the ventral valve moderately and evenly convex with maximum height slightly posterior to midlength; transverse profile subcarinate. Ventral interarea gently curved, apsacline, with an open delthyrium. Dorsal valve lateral profile gently convex with maximum height at about one third valve length from the umbo. Dorsal sulcus originating at the umbo, slightly deepening towards midvalve and fading towards anterior margin in mature specimens. Dorsal interarea low, planar, anacline. Radial ornament finely and equally multicostellate with 11–13 rounded ribs per 3 mm along the anterior margin of mature specimens.

Ventral interior with small subtriangular teeth supported by slightly divergent dental plates. Ventral muscle field bilobed, elongate, strongly impressed, extending beyond the midvalve length and surrounded by faint muscle bounding ridges. Ventral median ridge long and narrow, slightly widening anteriorly. Ventral *vascula media* short, divergent. Dorsal interior with a small, bulbous undivided cardinal process bearing posteriorly a crenulated myophore and supported anteriorly by faint, ridge-like shaft. Brachiophores blunt, subtriangular, slightly divergent anteriorly with almost subparallel bases. Dental sockets large, subtriangular, supported by thickened socket pads. Dorsal adductor muscle field narrow, elongate, surrounded by faint muscle bounding ridges, extending anteriorly beyond midlength and bisected by low and broad median ridge.

Remarks. Distinctive features of *Isorthis* (*Ovalella*) and its affinity to *Isorthis* (*Arcuella*) were discussed repeatedly in publications by Walmsley & Boucot (1975), Zhang (1989), Strusz (2002) and Li & Copper (2006). The Iranian shells are referred to *Isorthis* (*Ovalella*), because they have a narrow ventral median ridge, an undivided cardinal process, low and broad dorsal median ridge and indistinctly quadripartite, weakly defined dorsal adductor muscle field. *Isorthis* (*Ovalella*) *inflata* sp. nov. differs from other species of the genus in having a large ventral muscle field extending slightly anterior to midvalve and a long, very narrow ventral median ridge bisecting the muscle field. It differs also: (a) from *I. (Ovalella) beechhillensis* Walmsley & Boucot, 1975 (Llandovery, Rhuddanian, of Nova Scotia, Quebec) in having a wider delthyrium and maximum shell width only

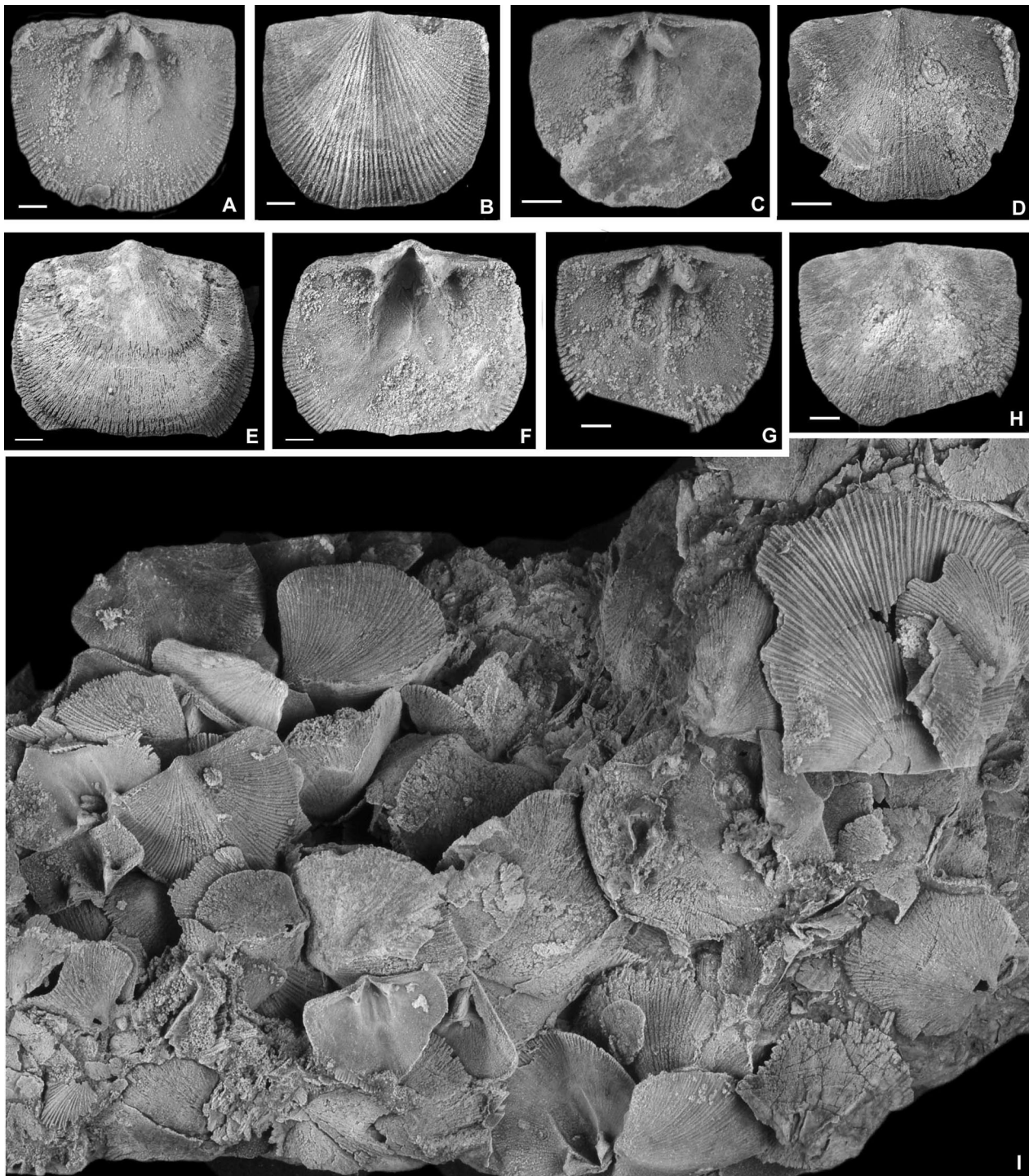


Fig. 4. *Isorthis (Ovalella) inflata* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains. **A, B**, NMW 2011.11G.91, holotype, dorsal valve interior, exterior; **C, D**, NMW 2011.11G.92, dorsal valve interior, exterior; **E, F**, NMW 2011.11G.28, ventral valve exterior, interior; **G, H**, NMW 2011.11G.90, dorsal valve interior, exterior; **I**, NMW 2011.11G.193, slightly dissolved surface of a shell bed showing accumulation of disarticulated valves of *Isorthis (Ovalella) inflata* sp. nov. All scale bars 2 mm.

Table 1. Basic statistics of 20 ventral valves of *Isorthis (Ovalella) inflata* sp. nov.; Llandoverly, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains

S14	Lv	W	Iw	T	MI	Mw	Lv/W	Iw/W	T/Lv	MI/Lv
N	20	19	17	19	15	15	19	17	19	15
X	8.4	10	8.2	3.18	4.8	3.1	85.3%	81.8%	37.2%	55.6%
S	1.61	1.84	1.73	0.8	0.91	0.79	3.8	6.1	2.5	4.5
Min	5.5	6.7	5.6	2.0	3.7	1.8	76.6%	71.4%	31.9%	48.8%
Max	11.9	14.8	12.2	5.0	7.2	5.2	91.7%	95.1%	42.0%	66.7%

Table 2. Basic statistics of 21 dorsal valves of *Isorthis (Ovalella) inflata* sp. nov.; Llandoverly, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains

S14	Ld	W	Iw	T	MI	Mw	Lv/W	Ld/W	T/Lv	MI/Lv
N	21	21	18	17	16	15	21	18	17	16
X	9.0	10.7	9.5	2.9	4.9	3.7	83.6%	87.0%	30.9%	56.0%
S	1.67	1.58	1.26	0.66	1.00	0.85	5.7	5.6	4.4	5.1
Min	6.0	7.6	7.4	1.9	3.4	2.4	73.9%	74.7%	21.8%	43.5%
Max	12.6	13.9	12.3	4.2	7.0	5.8	94.4%	93.7%	41.3%	64.1%

slightly anterior to the hinge line; (b) from *I. (Ovalella) mackenziei* Walmsley, 1966 (Llandoverly, Telychian to lower Wenlock of New Brunswick, Maine and Wales) in having a more transverse shell with maximum width posterior to midlength.

Isorthis (Ovalella) arndellensis Laurie, 1991, from the Llandoverly, Westfield Sandstone of Tasmania and *I. (Ovalella) naticoteca* Li & Copper, 2006, from the Llandoverly, Rhuddanian, of Anticosti Island, have a bilobed cardinal process unlike *I. (Ovalella) inflata*, which is undivided.

Family RHIPIDOMELLIDAE Schuchert, 1913
Subfamily RHIPIDOMELLINAE Schuchert, 1913
Genus *Dalejina* Havlíček, 1953

Type species. *Dalejina hanusi* Havlíček, 1953; Lower Devonian, Pragian, Zlichov Limestone, Bohemia.

Dalejina? rashidii sp. nov.
Figure 5A–P

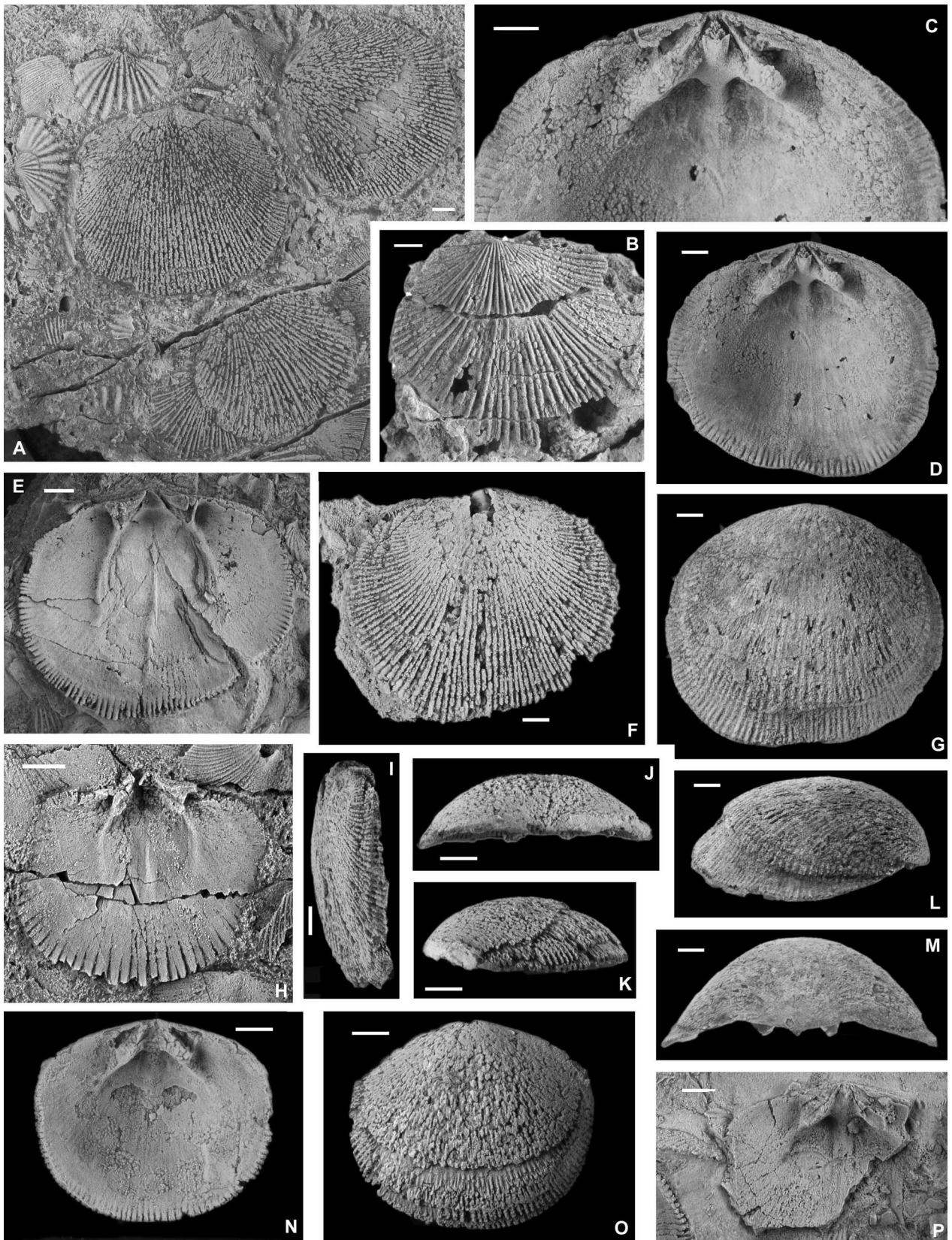
Derivation of name. After Dr Koorosh Rashidi (Payame Noor University of Ardakan) in recognition of his kind assistance during the fieldwork in the Tabas region.

Holotype. NMW 2011.11G.205 (Ld = 19.0, W = 19.0, T = 7.4, BBw = 6.2, BBl = 3.5, Sl = 4.6), Llandoverly, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains, Iran.

Paratypes. NMW 2011.11G.194, 197 (Lv = 13.6, W = 16.4), 198 (Lv = 10.2, W = 12.9, Iw = 9.7, MI = 5.8, Mw = 5.7, Sl = 6.6), 199, 200 (Lv = 15.2, W = 18.0, MI = 7.6, Mw = 5.8, SVI = 9.5), 201 (Lv = 16.2, W = 19.8, Iw = 11.3, MI = 9.8, Mw = 7.3, Sl = 11.9), 208, ventral valves; NMW 2011.11G.195 (Ld = 17.3, W = 20.1; T = 4.4), 202, 206 (Ld = 12.5, W = 14.7, T = 4.3, BBw = 4.7, BBl = 2.8, Sl = 4.1), 208–212, 370, dorsal valves; locality and stratum as holotype. Total seven ventral and nine dorsal valves.

Diagnosis. Shell strongly dorsibiconvex, about 80% as long as wide; anterior commissure weakly uniplicate; ventral muscle field large, subcordate, slightly elongated, extending anterior to the midvalve and bisected by long median ridge terminating at about one third valve length from the anterior margin; dorsal interior with undivided cardinal process with a broad shaft on a high notothyrial platform; brachiophores stout, divergent at about right angle; dorsal median ridge terminated at about middle of a weakly impressed dorsal adductor muscle field.

Fig. 5. *Dalejina? rashidii* sp. nov.; Llandoverly, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains. **A**, NMW 2011.11G.194–196, two dorsal valves and one ventral valve on the bedding surface; **B**, NMW 2011.11G.204, ventral valve exterior; **C, D, G, L, M**, NMW 2011.11G.205, holotype, dorsal valve, enlarged view of cardinalia, interior, exterior, side and posterior views; **E**, NMW 2011.11G.201, ventral valve interior; **F, I**, NMW 2011.11G.203, ventral valve exterior, side view; **H**, NMW 2011.11G.200, ventral valve interior; **J, K, N, O**, NMW 2011.11G.206, dorsal valve, posterior and lateral views, interior, exterior; **P**, NMW 2011.11G.202, incomplete dorsal valve interior. All scale bars 2 mm.



Description. Shell strongly dorsibiconvex, slightly transverse suboval, about four fifths as long as wide. Hinge line about two thirds of maximum shell width at midlength, cardinal extremities broadly rounded. Anterior commissure weakly uniplicate. Ventral valve sagittal profile gently convex with maximum height at about one third valve length from the umbo. Ventral interarea low, curved with an open, triangular delthyrium. Ventral sulcus very broad and shallow, almost indistinguishable, originating at 3–4 mm from the umbo. Dorsal valve strongly and evenly convex in sagittal and transverse profiles, with rudimentary, strongly apsacline interarea. Radial ornament equally multicostellate with up to 6 ribs per 3 mm along the anterior margin of mature specimens. Concentric ornament of fine, evenly spaced fila and growth lamellae, in the anterior half of the shell.

Ventral valve interior with strong teeth and short, widely divergent dental plates. Ventral muscle field strongly impressed, large, subcordate, about four fifths as long as wide, extending well beyond the midvalve, surrounded by strong muscle bounding ridges. Thickened pedicle callist present in the posterior part of the delthyrial cavity bottom. Ventral median ridge bisecting the entire muscle field, extending anteriorly and terminating at about one third valve length from the anterior margin. Ventral diductor muscle scars large, strongly impressed, enclosing completely weakly defined adductor muscle scars in the posterior half of the muscle field.

Dorsal interior with high, stout brachiophores divergent at about right angles and deep, subtriangular dental sockets supported by socket pads. Fulcral plates present. Cardinal process undivided, with a broad, thickened shaft and crenulated myophore facing posteriorly, situated on a high, subtriangular notothyrial platform. Dorsal adductor muscle field weakly impressed, with only smaller anterior pair of adductor scars clearly discernable. Dorsal median ridge very short, terminated at the midpart of the adductor muscle field.

Remarks. The generic assignment of *Dalejina? rashidii* sp. nov. is questionable, because, unlike almost all other known species of the genus (e.g. Boucot et al. 1965), it has a simple, undivided cardinal process. It probably represents the oldest documented species of *Dalejina*. Williams & Harper (2000) considered the stratigraphic range of *Dalejina* as Wenlock to Emsian, however, there is a species assignable to *Dalejina* from the Llandoverly of the East Baltic, described originally as *Rhipidomelloides phaseola* Rubel, 1963, from the Adavere Regional Stage (Telychian) of Estonia. Unlike Iranian shells it has a bilobed cardinal process, a strongly dorsibiconvex shell and a larger ventral muscle field extending anterior to midvalve.

Dalejina? rashidii sp. nov. differs from *Dalejina hybrida* (J. de Sowerby, 1839), which is widespread in the Wenlock to Ludlow of Britain and Baltoscandia, in having a simple, undivided cardinal process, a more strongly dorsibiconvex shell, a weakly defined anterior border of the ventral muscle field, a very short dorsal median ridge and coarser radial ornament. Iranian shells are also almost twice as large as the average size of *Dalejina hybrida* given by Bassett (1972).

Among the early species of the genus, *Dalejina phedodra* Bassett, 1972 from the Wollhope Limestone (base of the Wenlock Series) of the Welsh Borderland is probably the closest species to the newly described taxon. It also has a large, weakly defined anteriorly ventral muscle field, an undivided, inflated cardinal process, a short dorsal median ridge and a relatively large shell size. Iranian shells can be distinguished from the British species in complete absence of the dorsal sulcus and in having a ventral median ridge extending beyond the anterior border of the muscle field, a very short dorsal median ridge bisecting only the posterior half of the dorsal muscle field and less strongly transverse adult shells.

Order PENTAMERIDA Schuchert & Cooper, 1931

Suborder PENTAMERIDINA Schuchert & Cooper, 1931

Superfamily CLORINDOIDEA Rzhonsnitskaya, 1956

Family CLORINDIDAE Rzhonsnitskaya, 1956

Subfamily CLORINDIDINAE Rzhonsnitskaya, 1956

Genus *Clorinda* Barrande, 1879

Type species. *Clorinda armata* Barrande, 1879, Hlubočepy Limestone, Prague region, Czech Republic.

Clorinda sp.

Figure 6N–Q

1979 *Clorinda?* sp.; Cocks, p. 36, fig. 27.

Material. Conjoined valves: NMW 2011.11G.1 (Lv = 16.1, Ld = 13.5, T = 10.8, Sw = 8.6), sample K25, Boghu Mountains.

Remarks. A single specimen from the Niur Formation of the Boghu Mountains is characterized by a low, flattened ventral sulcus and dorsal median fold originating at the umbonal area and smooth flanks. It shows distinct similarity to the ventral valve of *Clorinda?* sp. illustrated by Cocks (1979, fig. 27). These shells may well be conspecific, but the limited material and absence of data on the interior of both valves makes their precise taxonomic discrimination impossible.

Order RHYNCHONELLIDA Kuhn, 1949
 Superfamily RHYNCHOTREMATOIDEA Schuchert,
 1913

Family RHYNCHOTREMATIDAE Schuchert, 1913
 Subfamily RHYNCHOTREMATINAE Schuchert, 1913
 Genus *Stegocornu* Dürkoop, 1970

Type species. *Stegocornu procerum* Dürkoop, 1970;
 Silurian, Aeronian, Dascht-e Nawar, eastern Afghanistan.

Remarks. *Stegocornu* was originally described by Dürkoop (1970) from eastern Afghanistan, but was subsequently also identified by Brice (1999) from a small collection of the Silurian brachiopods sampled by A. F. de Lapparent in 1973 northwest of Kerman. Brice also pointed out the close resemblance of these shells to *Xerxespirifer iranicus* Cocks, 1979 from the Silurian Qarabil Formation of Kope-Dagh. There was, however, an issue of taxonomic relationship of the illustrated specimens with the holotype of *Xerxespirifer iranicus*, which represents a small, strongly biconvex shell with a short hinge line, a single narrow rib in the sulcus and four ribs on flanks of the ventral valve. It looks rather atypical for *Stegocornu* according to Brice (1999). Subsequently Savage et al. (2002) also considered *Xerxespirifer* as junior objective synonym of *Stegocornu*.

From the studied collection it is likely that the holotype of *Xerxespirifer iranicus* is within the margins of significant morphological variability characteristic of *Stegocornu procerum*, but additional study based on the topotype material is still required to resolve the problem of taxonomic relationships between *Stegocornu* and *Xerxespirifer*.

Stegocornu procerum Dürkoop, 1970
 Figures 7A–H, 8; Table 3

1970 *Stegocornu procerum* Dürkoop; p. 186; Abb. 48,
 text-fig. 1; pl. 18, figs 1–6.

1979 *Xerxespirifer iranicus* Cocks; p. 40, figs 35–39
 (?non fig. 34).

2002 *Stegocornu procerum* Dürkoop; Savage et al.,
 fig. 708.3a–n.

Holotype. GPBIO 59, deposited in the Palaeontological Institute, Bonn, Germany, conjoined valves; Silurian, Llandovery, mid-late Aeronian, Shoroj-Sang, Dasht-e Nawar, eastern Afghanistan.

Material. NMW 2011.11G.213 (L_v = 12.7, L_d = 11.3, W = 15.0, T = 9.9, Sw = 7.3), 252–268, CNIGR 12600/128, 129, AEU 1267–1300, articulated shells; sample K25; NMW 2011.11G.214 (L_v = 12.7, L_d = 11.3, W = 15.0, T = 9.9, Sw = 7.3), 215–251 conjoined valves; sample K28; both samples from the Boghu Mountains. CNIGR

12600/130–133, articulated shells, loose sample, vicinity of Shabdjereh. Total 94 articulated shells.

Diagnosis. See Dürkoop (1970, p. 186).

Remarks. The specimens from samples K25 to K28 of the Boghu section are almost identical in morphological characters to the topotypes and considered here as conspecific. The only difference is in the presence of fine crowded concentric lamellae in the anterior half of the Iranian shells, which may be explained by partial exfoliation of the shells studied by Dürkoop (1970), as is evident from the provided illustrations. Earlier Brice (1999) suggested that the majority of the shells illustrated by Cocks (1979) under the name *Xerxespirifer iranicus* Cocks, with the exception of the holotype, are probably conspecific to *Stegocornu procerum*. This synonymy is also accepted here. Delthyrial plates in *S. procerum* are completely merged anterior to the pedicle foramen as shown in Fig. 8A.

Stegocornu denisae sp. nov.
 Figures 7I–Y, 9, 10; Tables 4, 5

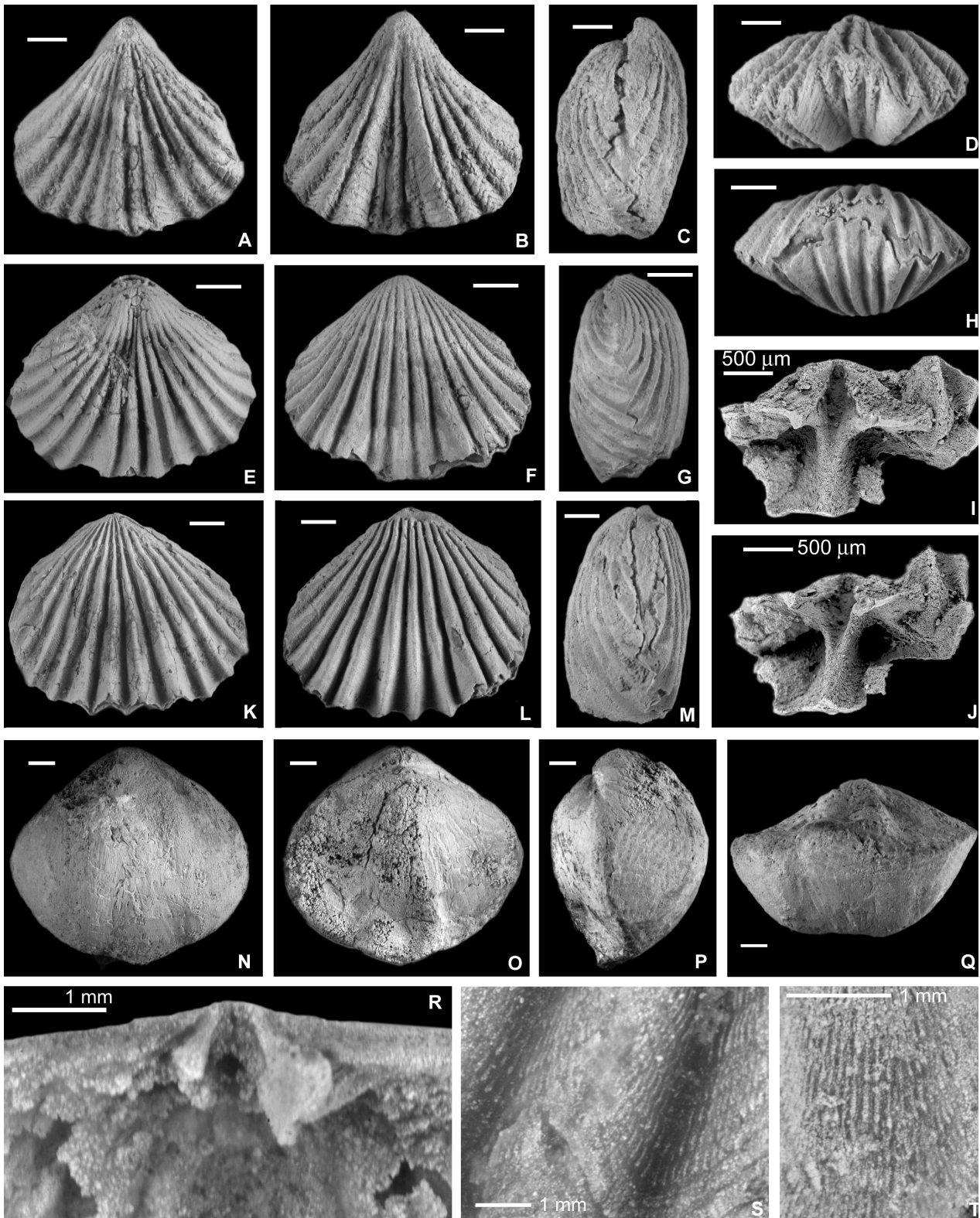
1999 *Stegocornu* aff. *procerum* Dürkoop; Brice, p. 7;
 pl. 1, figs 1–6.

Derivation of name. After Prof. Denise Brice (University of Lille) who reported for the first time on the occurrence of *Stegocornu* in Central Iran.

Holotype. NMW 2011.11G.269 (L_v = 13.8, L_d = 11.9, W = 18.8), conjoined valves; Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains, Iran.

Paratypes. NMW 2011.11G.271–326, conjoined valves; NMW 2011.11G.270, 327, 328, ventral valves; NMW 2011.11G.329, 330, dorsal valves; sample S14, Derenjal Mountains. NMW 2011.11G.336–354, AEU 1368–1475, articulated shells; NMW 2011.11G.355, ventral valve, NMW 2011.11G.357, 358, dorsal valves, sample K29; Boghu Mountains. NMW 2011.11G.331–333, conjoined valves; NMW 2011.11G.334, ventral valve; NMW 2011.11G.335, dorsal valve; sample K30, Boghu Mountains. CNIGR 12600/126, 127 conjoined valves; loose sample, vicinity of Shabdjereh. Total 184 articulated shells, five ventral and five dorsal valves.

Diagnosis. Subequally biconvex transverse shell with maximum width slightly anterior to the hinge line or at the hinge line, about 50–60% as thick as long; with a strong ventral sulcus and dorsal median fold originating at the umbonal area and occupying about 40% of maximum shell width; radial ornament with a single rib in a sulcus, two ribs on a dorsal fold and 4–7 on valve flanks; ventral median rib of equal size with ribs on



valve flanks; ventral beak erect; delthyrial plates merged anterior to the elongate, submesothyrid pedicle foramen.

Description. Shell subequally biconvex, transverse, semioval in outline, about 80% as long as wide with maximum width slightly anterior to the hinge line or at hinge line and 50–60% as thick as long. Hinge line relatively wide, almost straight; anterior commissure strongly sulcinate. Ventral valve sagittal profile moderately convex with maximum height at midlength. Beak erect to gently curved. Delthyrial plates thick, conjunct anterior to the elongate, submesothyrid pedicle foramen. Sulcus deep and narrow, with steep lateral slopes, originating at the umbonal area and terminating with a trapezoidal tongue occupying about 40% of maximum shell width. Dorsal valve moderately convex with maximum height at midlength. Dorsal median fold high, originating at the umbonal area. Radial ornament of coarse angular ribs with a single rib in the ventral sulcus, two ribs on the dorsal median fold and 4–7 ribs on flanks of the dorsal valve. Rib in the sulcus about the same size as ribs on the valve flanks. Concentric ornament of fine crowded growth lamellae covering anterior half of the shell surface and with fine, evenly spaced fila in the posterior half of the shell of the mature specimens.

Ventral interior with strong, oblique teeth supported by the rudimentary dental plates mainly fused to the valve walls. Ventral muscle field strongly impressed with adductor scars completely enclosed by larger diductor scars. Strongly thickened pedicle callist mainly occupying a bottom of the small delthyrial cavity. Dorsal interior with massive united hinge plates and a small septalium supported by a very short median septum. Cardinal process septiform. Crura faint, radulifer, gently curved dorsolaterally.

Remarks. *Stegocornu denisae* sp. nov. in the Boghu section succeeds the type species *Stegocornu procerum* Dürkoop in the stratigraphical sequence. It differs from the former in having a more dorso-laterally compressed shell (only 50–60% as thick as long against 75% in *S. procerum*), a narrow median fold and dorsal sulcus (on average 40% as wide as the shell against 50% in *S. procerum*) and an erect ventral beak. The median rib

in the ventral sulcus in *S. denisae* is of about equal size to the ribs on the valve flanks, whereas in *S. procerum* it is considerably smaller. The number of ribs on the flanks overlaps significantly in both species, however, in *S. procerum* specimens with four ribs on flanks of the dorsal valve are the most common and the number of ribs does not exceed six, whereas in *S. denisae* specimens with 5–6 ribs are the most characteristic and shells with seven ribs do occasionally occur. Unlike *S. procerum* shells of *S. denisae* are transverse suboval, with maximum width slightly anterior of the hinge line or at the hinge line, and may be slightly alate.

Subfamily LEPIDOCYCLINAE Cooper, 1956
Genus *Rhytidorhachis* Jin & Caldwell, 1990

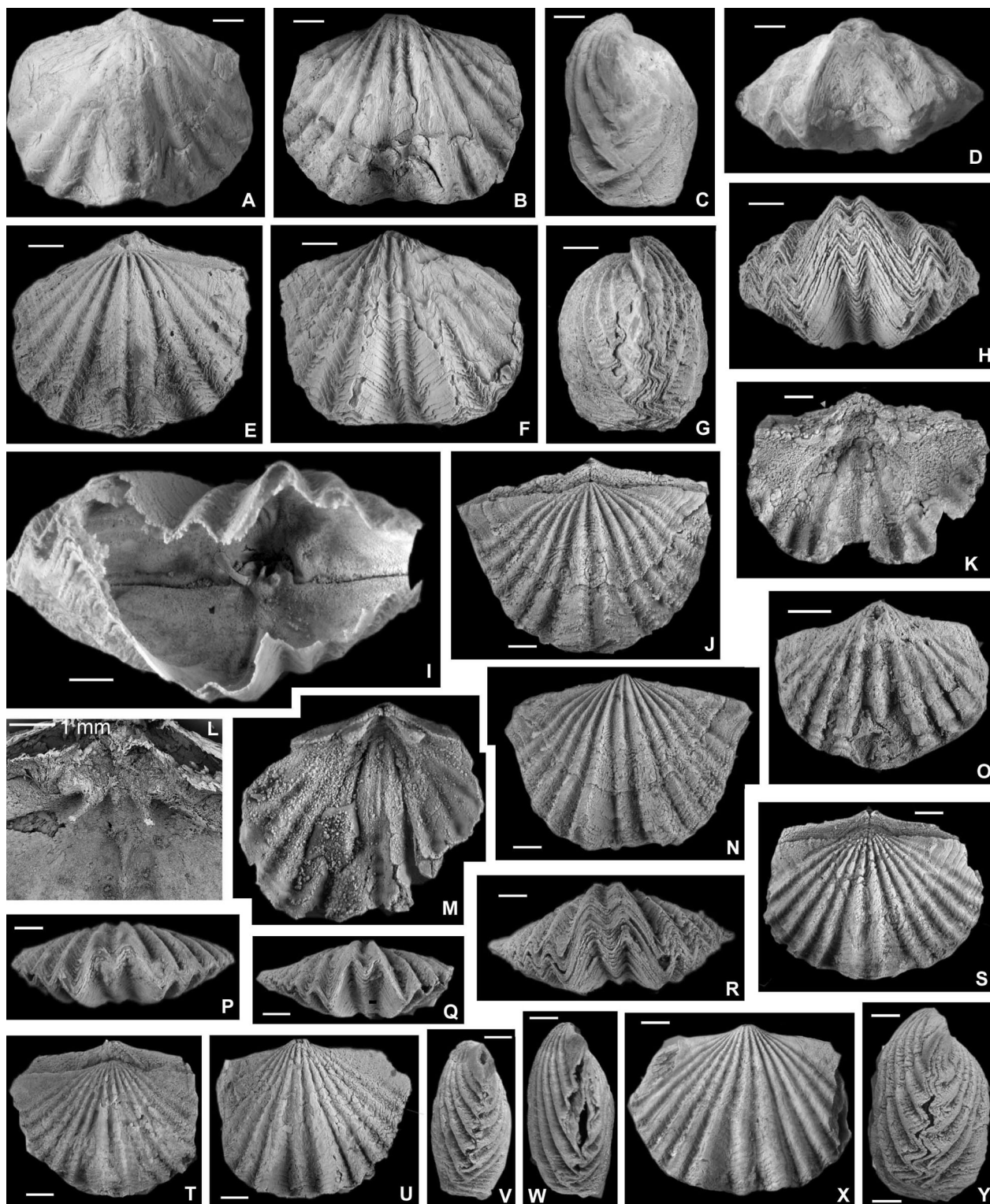
Type species. *Rhytidorhachis hudsonensis* Jin & Caldwell, 1990; Silurian, Llandovery, Ekwan River Formation, Hudson Bay Lowlands, Canada.

Rhytidorhachis? sp.
Figure 6A–D

Material. NMW 2011.11G.2 (Lv = 10.0, Ld = 8.0, W = 10.3, T = 5.7, Sw = 5.0), articulated shell, sample S14, Derenjal Mountains.

Description. Shell rostrate, subtriangular, subequally biconvex almost as long as wide; hinge line very narrow, curved. Anterior commissure uniplicate. Ventral valve with an erect, acuminate beak. Pedicle foramen large, submesothyridid. Delthyrium covered by thick deltidial plates merged distally. Ventral sulcus originating at the umbo, narrow and deep, with steep lateral slopes terminating in a semioval tongue. Dorsal valve evenly convex with a narrow fold originating at the umbo. Radial ornament with six subangular ribs on flanks. Ventral sulcus with a single costa in the umbonal area and a pair of smaller ribs intercalating at about mid-length. Dorsal median fold with two costae bifurcating anteriorly. Concentric ornament of prominent, regular growth lamellae about 3 per 1 mm forming a characteristic zig-zag pattern on the rib crests. Interior of both valves unknown.

Fig. 6. A–D, *Rhytidorhachis?* sp.; Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains; NMW 2011.11G.2, conjoined valves, dorsal, ventral, lateral and anterior views. E–J, *Hercotrema* sp.; Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains; E–H, NMW 2011.11G.3, conjoined valves, dorsal, ventral, lateral and anterior views; I, J, shell fragment showing cardinalia in ventral valve, tooth and vestigial dental plate in dorsal valve. K–M, *Stegerhynchus* sp.?; Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains; NMW 2011.11G.372, conjoined valves dorsal, ventral and lateral views. N–Q, *Clorinda* sp.; Llandovery, mid-late Aeronian, Niur Formation, sample K25, Boghu Mountains; NMW 2011.11G.1, conjoined valves, ventral, dorsal, lateral and anterior views. R–T, *Striispirifer?* *ocissimus* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation sample S14, Derenjal Mountains; R, NMW 2011.11G.362, enlarged dorsal valve interior showing cardinalia; S, T, NMW 2011.11G.366, enlarged ventral valve surface showing microornament. All scale bars except I, J and R–T are 2 mm.



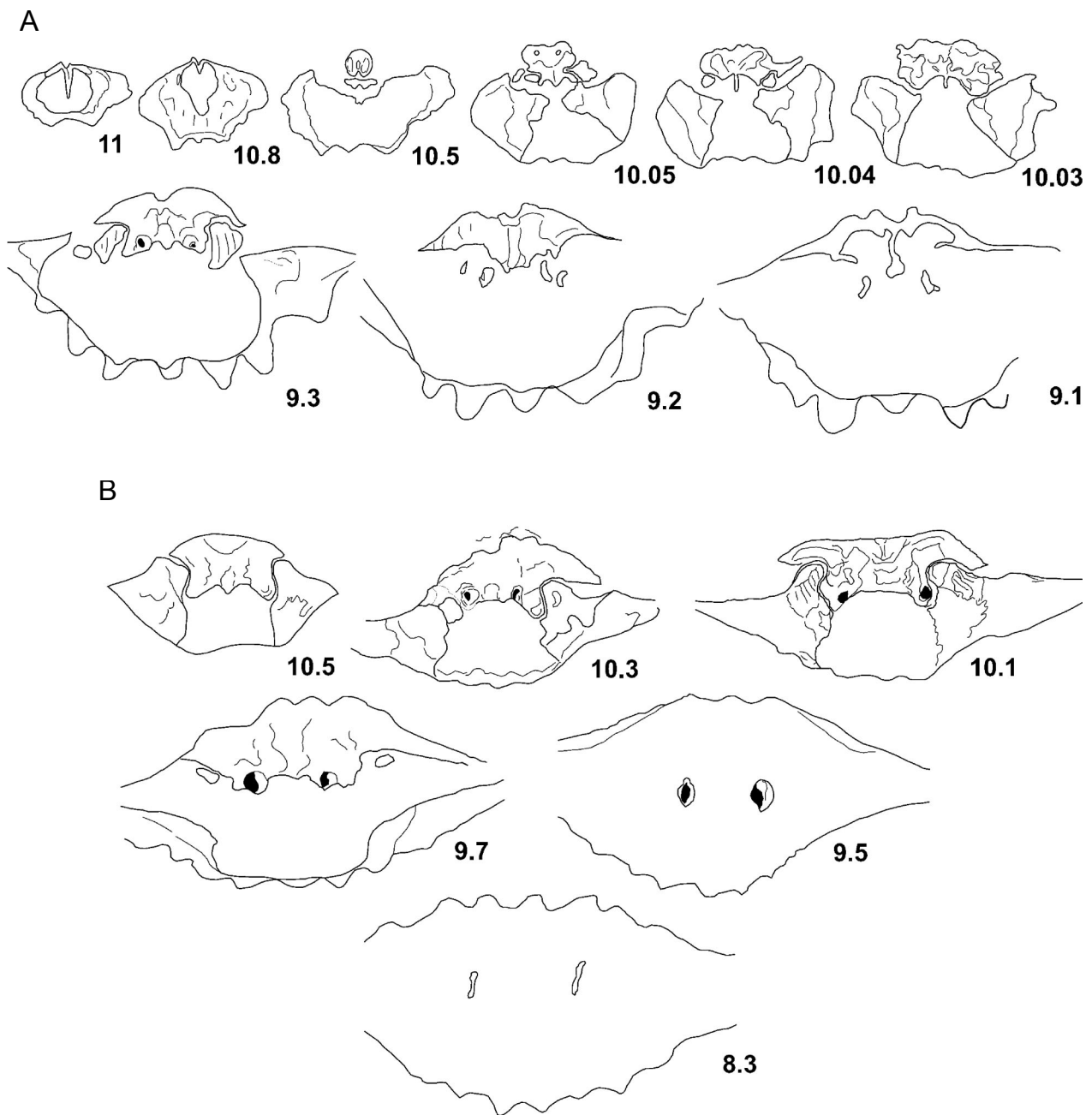


Fig. 8. Transverse serial sections of *Stegocornu procerum* Dürkoop, 1970; Llandovery, mid-late Aeronian, Niur Formation, sample K25, Boghu Mountains; **A**, CNIGR 12600/128 (L = 11.2, W = 13.6, T = 8.4); **B**, CNIGR 12600/129 (L = 10.7, W = 15.4, T = 10.5). Numbers indicate distances (mm) from the apex of the shell.

Fig. 7. A–H, *Stegocornu procerum* Dürkoop, 1970; Llandovery, mid-late Aeronian, Niur Formation, sample K28, Boghu Mountains; A–D, NMW 2011.11G.214, conjoined valves, dorsal, ventral, lateral and anterior views; E–H, NMW 2011.11G.213, conjoined valves, dorsal, ventral, lateral and anterior views, sample K25. **I–Y,** *Stegocornu denisae* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation; L, sample K29 and I, M, O, sample K30, both Boghu Mountains; I, NMW 2011.11G.331, oblique anterior view of broken conjoined valves showing cardinalia; J–K, N, P–Y, sample S14, Derenjaj Mountains; J, N, R, Y, NMW 2011.11G.269, holotype, dorsal, ventral, anterior and lateral views of conjoined valves; K, NMW 2011.11G.270, ventral valve interior; L, NMW 2011.11G.358, umbonal part of the dorsal valve; M, NMW 2011.11G.334, ventral valve interior; O, NMW 2011.11G.332, ventral view of conjoined valves; P, S, W, X, NMW 2011.11G.271, anterior, dorsal, lateral and ventral views of conjoined valves; Q, T–V, NMW 2011.11G.272, anterior, dorsal, ventral and lateral views of conjoined valves. All scale bars except L are 2 mm.

Table 3. Basic statistics of 24 shells of *Stegocornu procerum* Dürkoop, 1970; Llandovery, mid-late Aeronian, Niur Formation, sample K28, Boghu Mountains

K28	Lv	Ld	W	T	Sw	St	Lv/W	Ld/W	T/Lv	Sw/W
N	24	24	24	24	22	18	18	18	18	18
X	14.0	12.7	17.7	10.4	8.8	7.9	79.3%	71.9%	74.2%	50.0%
S	0.87	0.85	0.97	1.13	0.95	1.21	5.6	4.7	7.1	5.0%
Min	12.8	11	15.8	7.5	7.2	5.9	70.3%	64.8%	58.6%	41.0%
Max	16.5	14.1	19.2	12	10.5	9.9	89.0%	84.1%	85.8%	59.1%

Table 4. Basic statistics of 10 shells of *Stegocornu denisae* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation, sample K29, Boghu Mountains

K29	Lv	Ld	W	T	Sw	St	Lv/W	Ld/W	T/Lv	Sw/W
N	10	10	10	10	10	9	10	10	10	10
X	15.3	14.3	20.6	9.3	8.3	5.9	74.6%	69.9%	60.2%	40.3%
S	1.49	1.36	2.33	1.79	1.30	1.23	5.8	6.4	7.6	4.3
Min	12.7	11.8	17	6.3	6.4	4.5	67.4%	60.5%	49.6%	35.2%
Max	17.4	16.2	24.2	12.5	9.7	8.1	82.9%	81.8%	75.3%	49.2%



Fig. 9. Surface of a shell bed showing accumulation of *Stegocornu denisae* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation, sample S12, Derenjal Mountains; scale bar 10 mm.

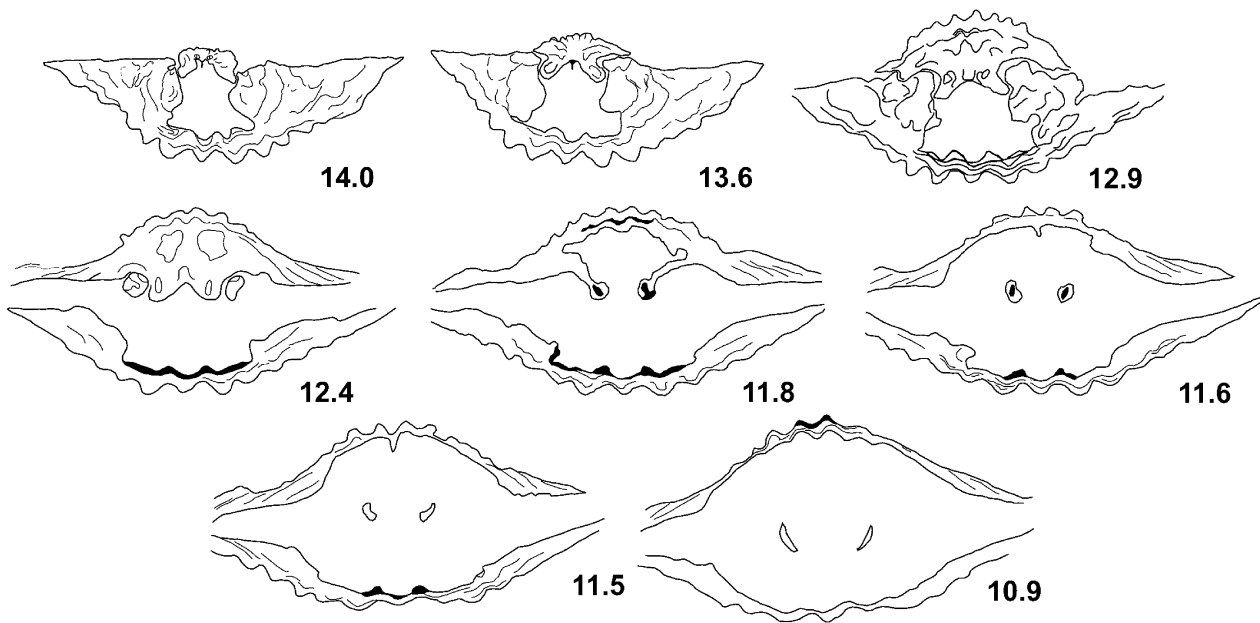


Fig. 10. Transverse serial sections of *Stegocornu denisae* sp. nov.; Llandovery, mid-late Aeronian, Shabdjereh Formation, loose sample, vicinity of Shabdjereh; CNIGR 12600/126 ($L > 14.0$, $W = 22.5$, $T = 10.5$). Due to damaged ventral beak, numbers indicate distances (mm) from the anterior margin of the shell.

Table 5. Basic statistics of 28 shells of *Stegocornu denisae* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains

S14	Lv	Ld	W	T	Sw	St	Lv/W	Ld/W	T/Lv	Sw/W
N	28	28	29	29	26	26	28	28	28	26
X	11.1	9.9	14.2	5.5	5.8	4.1	79.4%	69.8%	49.7%	41.3%
S	1.88	1.66	2.60	1.15	1.23	1.55	8.3	5.7	7.7	7.2
Min	7.7	7.0	9.7	3.2	3.8	2.2	67.8%	59.2%	39.8%	22.8%
Max	15.9	14.2	20.2	7.9	8.8	8.9	100.0%	77.9%	60.0%	53.1%

Remarks. Lack of data on the interior of both valves makes the generic affiliation of the specimen tentative. It is assigned provisionally to *Rhytidorhachis* because it has a rostrate shell with a delthyrium covered by thick medially conjunct deltidial plates and prominent concentric ornament. It differs from the type species *R. hudsonensis* Jin & Caldwell, 1990 from the Silurian, Llandovery, Ekwon River Formation of Hudson Bay Lowlands, Canada, in having a single rib in the ventral sulcus and two ribs on the dorsal fold posterior to midlength and coarse concentric growth lamellae. The Iranian shell differs from *Rhytidorhachis diodonta* (Dalman, 1828) from the Silurian Klintberg Beds (upper Wenlock–lower Ludlow) of Gotland in having finer radial ornament with up to six ribs on flanks and a pair of additional costellae originating in the ventral sulcus and a dorsal median fold anterior to midlength.

Genus *Stegerhynchus* Foerste, 1909

Type species. *Rhynchonella (Stegerhynchus) whittii-praecursor* (= *Stegerhynchus praecursor*) Foerste, 1909. Silurian, Llandovery, Aeronian. Clinton Beds, Clinton, Tennessee, USA.

Stegerhynchus? sp. Figure 6K–M

Material. NMW 2011.11G.372 ($Ld = 12.7$, $W = 13.7$, $T = 6.7$, $Sw = 7.6$), articulated shell; sample S14, Derenjal Mountains.

Remarks. A single specimen from the Niur Formation of the Derenjal Mountains occurs in association with the shell referred to *Hercotrema* sp. It also has three ribs in the ventral sulcus, four ribs in the dorsal fold,

but differs in having angular ribs, a subrectangular, not semioval tongue, a more strongly dorsibiconvex shell with a dorsal valve profile having maximum height close to the anterior margin. Without knowing the characters of the cardinalia the generic affiliation of this shell is uncertain, but it is more likely not congeneric with *Hercotrema* sp. from the same locality. In general shell shape and characters of radial ornament, the specimen resembles *Stegerhynchus penobrealis* (Twenhofel, 1928), as revised by Jin & Copper (2004), but differs in its slightly larger size and less transverse shell outline.

Family TRIGONIRCHYNCHIDAE Schmidt, 1965
 Subfamily ROSTRICELLULINAE Rozman, 1969
 Genus *Hercotrema* Jin, 1989

Type species. *Hercotrema bulbicostatum* Jin, 1989; Silurian, Llandovery, Jupiter Formation, Anticosti Island, Quebec, Canada.

Hercotrema sp.
 Figure 6E–J

Material. NMW 2011.11G.3 (Lv = 9.0, Ld = 8.6, W = 10.7, T = 5.0, Sw = 5.7), 4, 5 (Lv = 12.9, Ld = 12.2, W = 13.3, T = 7.5, Sw = 7.2), articulated shells, sample S14, Derenjal Mountains.

Description. Shell slightly dorsibiconvex, subpentagonal in outline, slightly wider than long and about three fifths as high as long. Anterior commissure uniplicate. Ventral valve lateral profile moderately convex with maximum height at about one third valve length from the umbo. Delthyrium open, narrow, triangular. Ventral median sulcus originating at about 3–4 mm from the umbo, gently deepening anteriorly and terminating in a low, semioval tongue slightly wider than half the maximum shell width. Dorsal valve lateral profile moderately and unevenly convex with maximum height at about one third valve length from the anterior margin. Dorsal median fold low, evenly convex in transverse profile, originating slightly posteriorly to the midvalve. Radial ornament with simple rounded costae, with three ribs in the ventral sulcus, four ribs in the dorsal median fold and 5–6 ribs on flanks. Concentric ornament of very fine, evenly spaced fila.

Ventral interior with delicate teeth and thin, short dental plates. Dorsal interior with a short, narrow septalium supported by a short median septum. Cardinal process absent (Fig. 6H, I).

Remarks. The shells from the Niur Formation show strong simple ribs, a ventral sulcus and dorsal median fold originating at some distance from the beak, rudimentary dental plates and a small cruralium lacking a cardinal

process, all suggesting affiliation to *Hercotrema* Jin, 1989. They differ from the type species *Hercotrema bulbicostatum* in having three ribs in the ventral sulcus and four ribs on the dorsal median fold.

Order SPIRIFERIDA Waagen, 1883
 Suborder SPIRIFERIDINA Waagen, 1883
 Superfamily CYRTIOIDEA Frederiks, 1924
 Family CYRTIOIDAE Frederiks, 1924
 Subfamily EOSPIRIFERINAE Schuchert, 1929
 Genus *Striispirifer* Cooper & Muir-Wood, 1951

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

Striispirifer? ocissimus sp. nov.
 Figures 6R–T, 11

Derivation of name. After Latin *ocissimus*, appearing, occurring earliest.

Holotype. NMW 2011.11G.365 (Lv = 11.0, Ld = 9.2, T = 7.9, W = 15.2, Sw = 3.9), conjoined valves, Llandovery, mid-late Aeronian, Niur Formation, sample S14, Derenjal Mountains, Iran.

Material. NMW 2011.11G.359 (L = 15.5, W = 23.2, T = 14.2), conjoined valves; NMW 2011.11G.360 (L = 10.2, W = 14.0, Sw = 4.9), ventral valve; sample K30. NMW 2011.11G.361.1, 2, disarticulated conjoined valves; NMW 2011.11G.364 (Lv = 9.1, Ld = 7.9, T = 6.9, W = 12.1, Sw = 3.2), 366 (Lv = 9.2, Ld = 7.0, W = 11.5, T = 6.7, Sw = 3.4), 367 (Lv = 7.8, Ld = 6.1, T = 6.6, W = 11.6, Sw = 3.1), 368 (Lv = 7.3, Ld = 6.8, W = 15.2, T = 5.6), conjoined valves; NMW 2011.11G.363, 369, ventral valves; NMW 2011.11G.362, dorsal valve; sample S14, Derenjal Mountains. Total eight articulated shells, three ventral valves and one dorsal valve.

Diagnosis. Shell strongly ventribiconvex, transverse, subtrapezoidal and about three quarters as long as wide, with maximum width slightly anterior to the hinge line; cardinal extremities obtuse; ventral sulcus and dorsal median fold narrow, flattened, slightly more than one quarter as wide as the shell; dorsal median fold bisected by a fine groove; radial ornament of 5–7 plications on flanks and superimposed very fine striae, about 9–11 per 1 mm; dental plates sulcus-bounding, cardinal process smooth.

Description. Shell ventribiconvex, strongly transverse, subtrapezoidal in outline, about three quarters as long as wide, with maximum width slightly anterior to the hinge line, and about three quarters as thick as long. Cardinal extremities obtuse; anterior commissure uniplicate. Ventral valve lateral profile strongly convex with maximum

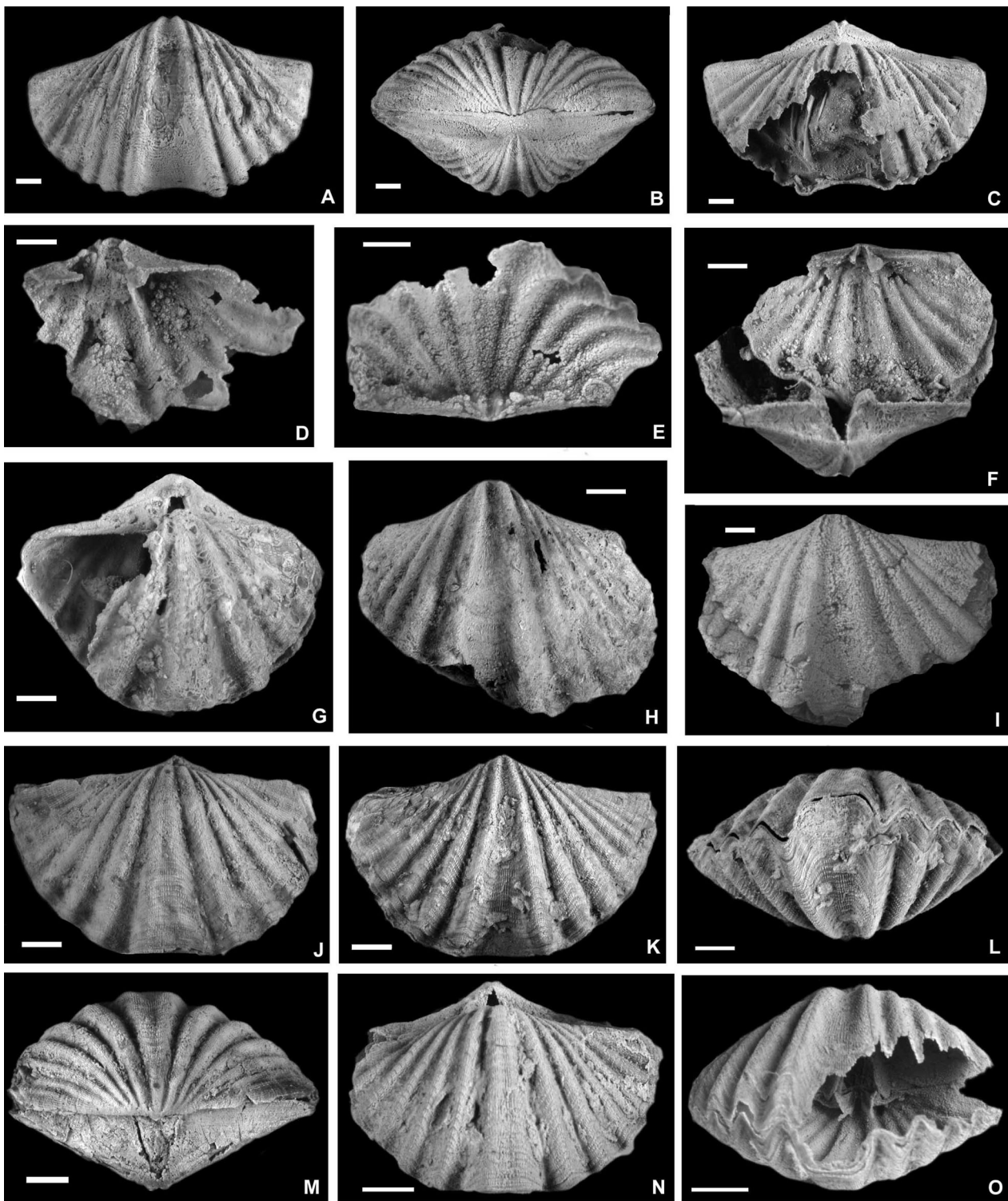


Fig. 11. *Striispirifer? ocissimus* sp. nov.; Llandovery, mid-late Aeronian, Niur Formation; A–C, I, sample K30, Boghu Mountains; D–H, J–O, sample S14, Derenjal Mountains; A–C, NMW 2011.11G.359, conjoined valves, ventral, anterior and dorsal views showing silicified spiralia; D, NMW 2011.11G.361.1, incomplete ventral valve interior; E, NMW 2011.11G.361.2, oblique posterior view of dorsal valve interior; F, NMW 2011.11G.362, dorsal valve interior and NMW 2011.11G.363, ventral valve interarea; G, NMW 2011.11G.364, broken conjoined valves, dorsal view; H, NMW 2011.11G.364, broken conjoined valves, ventral view; I, NMW 2011.11G.360, broken conjoined valves, ventral view; J–M, NMW 2011.11G.365, conjoined valves, dorsal, ventral and anterior views; N, O, NMW 2011.11G.366, conjoined valves, posterior and dorsal views.

height above the hinge line. Ventral interarea high, curved, apsacline with an open, narrow triangular delthyrium. Ventral sulcus narrow, strongly curved, originating at the umbo and terminating in a subtrapezoidal tongue about 25–30% valve width. Dorsal valve moderately and evenly convex with a low, anacline interarea and a narrow, flattened median fold originating at the umbo and often bisected by a fine groove. Radial ornament with 5–6 strong, rounded plications on the flanks of the dorsal valve and 6–7 plications on the flanks of the ventral valve, separated by broad, U-shaped interspaces. Microornament of very fine, striae about 10–12 per 1 mm. Concentric ornament of fine, evenly spaced fila.

Ventral interior with rounded, long, slightly divergent, sulcus-bounding dental plates. Dorsal interior with thin, short, slightly divergent crural plates, straight, short rod-like crura (Fig. 11O), and a smooth cardinal process.

Discussion. The Iranian shells are provisionally assigned to the genus, because they have broad, rounded in cross section interspaces between the ribs and a flattened dorsal median fold, unlike other species of *Striispirifer* (e.g. Boucot 1963; Rong et al. 1974; Rong & Yang 1978).

Rounded in cross section interspaces between the ribs are considered as diagnostic for *Macropoleura* (Boucot 1963). However, Iranian shells differ from other species assigned to this genus in having sulcus-bounding, not distinctly extrasinal, dental plates and a relatively narrow dorsal median fold bisected by a faint groove. In addition, they differ from the type species *Macropoleura macropoleura* (Conrad, 1840) in having more plications (up to 7) on the lateral sides of the valves and a high, apsacline, not strongly curved ventral interarea.

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***Stegocornu* ja kaasnevad brahhiopoodid Kesk-Iraani Silurist (Llandovery)**

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Esmakordselt on kirjeldatud Kesk-Iraani Niuri kihistu Llandovery (hilise Aeroni) vanusega brahhiopoodifaunat, milles kõige tähtsamad on kaks järjestikku levivat rhynchonelliidset liiki *Stegocornu procerum* Dürkoop, 1970 ja *Stegocornu denisae* sp. nov. Lisaks on seal levinud ka kolm tavalist ja neli harvem esinevat liiki, nende hulgas *Dalejina? rashidii* sp. nov., *Isorthis (Ovalella) inflata* sp. nov. ning *Striispirifer? ocissimus* sp. nov. *Stegocornu* koosluse levik annab sellele madalaveelisele faunale spetsiifilise biogeograafilise tunnuse, mis tõstab esile Kesk-Iraani, Kopetdagi ja Afganistani vastavate faunade ühtsust ning samal ajal on seal varasemaid märke Vara-Siluri brahhiopoodide biogeograafilise diferentseerumise algusest. Töös on arutatud perekondade *Stegocornu* ja *Xerxespirifer* sugulusuhteid.