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Early Jurassic (latest Toarcian) brachiopods from the northeastern margin of the Western Tethys (Central Iran) and their paleobiogeographical significance*

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Abstract

Brachiopod fauna from central Iran, recorded in the upper part of the Shemshak Group and attributed to the upper Toarcian (Pseudoradosa-Aalensis zones), are reported for the first time in Iran. The assemblage recognized includes six different taxa: *Homoeorhynchia sepahanensis* nov. sp., formally described in this paper, *Globirhynchia subobsoleta*, *Pseudogibbirhynchia* sp., Tetrarhynchiidae sp. indet., *Monsardithyris?* aff. *haresfieldensis*, and *Zeilleria* cf. *leckenbyi*. Analysis of faunal affinities with other paleobiogeographical regions shows a free connection the central Iranian brachiopod fauna with wide areas of the northern shelf margin of the Tethys Ocean. This is due to an apparent disruption of bioprovinciality inferred for the late Toarcian-earliest Aalenian, congruent with a connection through the northern seaway across the peri-Laurasian epicontinental platforms.

Keywords:

Brachiopods

Systematic

Paleobiogeography

Central Iran

Early-Middle Jurassic transition

1. Introduction

Brachiopod communities flourished in the marine Paleozoic environments in north and central Iran (Popov et al., 2008, 2009a, 2009b, 2012; Gaetani et al., 2009 and references therein; Pour et al., 2011, 2012; Taghvaie et al., 2011; Bahrammanesh et al., 2011; Hairapetian et al., 2012; Angiolini et al., 2013; Basset et al., 2013), as they did elsewhere, even reaching the Permian-Triassic transition (Gaetani et al., 2009; Angiolini et al., 2010; Leda et al., in press, among others). After the significant end-Triassic event that brought substantial changes in these benthic filter-feeding communities (Dulai, 2001; Tomašových and Siblík, 2007), brachiopods were recorded again, although rarely, in the earliest Jurassic times in a few localities from the westernmost Tethys and northwest European platforms in the Hettangian and early Sinemurian (Rossi-Ronchetti and Brena, 1953; Dulai, 1993, 2001, 2003; Siblík, 1999; Böhm et al., 1999; Tomašových, 2006). After these earliest Jurassic records, a new episode of prosperity has been documented widely in the western Tethyan basins from the late Sinemurian to the early Toarcian (e.g., Oppel, 1861; Gemmellaro, 1874-1881; Canavari, 1880; Geyer, 1889; Böse and Schlosser, 1900; Manceñido, 1993; Ager, 1994; Alméras and Fauré, 2000; Siblík, 2002; Vörös and Dulai, 2007, Alméras et al., 2007a; Vörös, 2009; García Joral et al., 2011; Baeza-Carratalá, 2013).

Meanwhile, during this timespan, the Iran Plate and its surrounding basins, located in the most north-eastern Tethyan margin (Dercourt et al., 1993; Seyed-Emami et al., 2006, 2008; Fürsich et al., 2009; Wilmsem et al., 2009, among others), were characterized by the sedimentation of the Shemshak Formation (Assereto, 1966). This is a thick succession made up by a facies mosaic with a siliciclastic predominance that includes from marine platform carbonates to deltaic sediments, and from fluvial deposits to swamp and lake environments (Fürsich et al., 2005, 2009; Seyed-Emami et al., 2006, 2008). Most of these habitats offer unfavorable depositional conditions for brachiopod settlement.

In the late Early Jurassic, the non-marine facies in central Iran gave way to marine deposits, forming the uppermost part of the Shemshak Formation, due to the noteworthy transgression event that took place in the late Toarcian-early Aalenian (Seyed-Emami, 1988; Fürsich et al., 2005; Seyed-Emami et al., 2008). Consequently, in central-northern Iran the earliest brachiopods after the end-Triassic extinction occur during the Toarcian.

Previous authors have generically indicated brachiopod occurrences in some middle Toarcian-early Aalenian beds of the uppermost part of the Shemshak Formation. Thus, biplicate terebratulids were reported in storm-dominated shelf environments of Tazareh (Fürsich et al., 2005; Seyed-Emami

et al., 2006), and undetermined records were also documented in Level E of Sharif-Abad (Seyed-Emami et al., 2008) and in the Tabas Block (Wilmsen et al., 2009).

In this study, the find of a scarce but peculiar brachiopod fauna in the Laluk Mountain succession has enabled both taxonomical analysis and biostratigraphical calibration based on recent advances in the ammonoid biochronostratigraphy (Seyed-Emami et al., 2006, 2008). Hence, the Laluk record is remarkable because it provides new data among the very scarce brachiopod records of the Early-Middle Jurassic transition in the northeastern Tethys margin. Furthermore, this study enables the establishment of the paleobiogeographical affinities of this fauna within a peri-marginal Tethyan context. These were previously unknown for this time interval, as the Jurassic brachiopods already reported from regions currently close to Iran were in significantly different paleogeographical situations at that time (e.g., Cooper, 1989; Feldman et al., 1991, 2012) or are younger than in central Iran. Actually, all these records are from the Middle Jurassic, when the Boreal and Tethyan realms, as well as diversification in several Tethyan paleobioprovinces (Ethiopian, Caucasian, Himalayan and East Asian) were entirely effective, after the maximum provinciality detected from the Aalenian onwards (Vörös, 1984; Manceñido, 2002).

Additionally, this study enhances the late Toarcian brachiopod record, which is relatively scant when compared with the Early Jurassic record as a whole, even in the well-documented localities of the westernmost Tethys, despite some noticeable exceptions (García Joral and Goy 1984; García Joral et al., 1990; Ager, 1990; Alméras and Fauré, 2000; Andrade, 2006; Fauré and Alméras, 2006).

2. Geographical and geological setting

The brachiopod assemblage studied comes from the Laluk Mountain (N 33°12'14", E 51°49'46"). This fossil locality is approximately 80 km northeast of Isfahan and 45 km southwest of the city of Natanz; it is accessible from the Isfahan-Kashan highway (Fig. 1).

Jurassic sediments in the province are attributed to the Shemshak Group (Late Triassic-Middle Jurassic; Assereto, 1966), which is distributed widely from north to central and southeast Iran. It is almost exclusively made up by fine- to coarse-grained siliciclastic sediments that are associated with coal beds and carbonaceous shales at different stratigraphic levels (Shekarifard et al., 2012, among others). Their depositional conditions include marine to deltaic and fluvial to swamp and lake environments (Stampfli, 1978; Rad, 1982, 1986; Baudin and Tehrani, 1991; Fürsich et al., 2005, 2009; Seyed-Emami et al., 2006, 2008).

Early Jurassic deposits in the Isfahan province are different from place to place (Zahedi, 1976). In the northeast of Isfahan, the upper Triassic Nayband Formation is overlain conformably by a shale/sandstone sequence containing two thick limestone beds in its middle part, attributed to the

Toarcian (Zahedi, 1976). These facies are likely to be contemporaneous with one of the most conspicuous transgressive phases within the upper part of the Shemshak Group that occurred during the Toarcian-Aalenian (Fürsich et al., 2005; Seyed-Emami et al., 2008, among others).

In the Laluk region, the Early Jurassic beds are about 300 m-thick. They are therefore distinctly thinner than in north Iran, where a maximum thickness of 1027 m is reached (Asseretto, 1966). At the fossil locality, an approximately 150 m-thick succession is discernible. The basal layers of the stratigraphical section in Laluk Mountain are faulted. The section is mainly made up of fine-grained sandstones inter-bedded with yellowish sandy oolitic limestones (Fig. 1). These sandy limestone beds show a relatively abundant fossil fauna made of brachiopods, belemnites, and, to a lesser extent, some solitary corals and fragmentary bivalves (Fig. 2).

3. Material and methods

Before the prospection of several stratigraphical sections in the central Iran region (Fig. 1), where the Shemshak Formation outcrops with a wide distribution and great thickness, brachiopods have only been recorded in the Laluk Mountain section (Fig. 1).

All analyses were performed at a generic and specific level. Generic assignments follow the published systematics (mainly in *Treatise*: Kaesler and Selden, 1997-2007). For the taxonomical analysis, the main biometric parameters and indices were measured whenever possible. The internal structure was studied using the conventional method of taking acetate peels after making transverse serial sections; the distance between sections was 0.1 mm. All figured specimens are deposited at the Departamento de Ciencias de la Tierra y del Medio Ambiente (Universidad de Alicante, Spain).

The ammonite zonal scheme referred to follows the standard proposed by Cariou and Hantzpergue (1997) for the northwest European domain. Recent biochronostratigraphic data of Seyed-Emami et al. (2008) in the Shemshak group from northern Iran are also used.

The occurrence of common and very closely related species and genera was taken into account in the paleobiogeographical analysis, comparing the studied assemblage with other representative areas of the Western Tethys during the Early-Middle Jurassic transition. They were then summarized and plotted in a paleomap slightly modified from Bassoullet et al. (1993). It is worth noting that the paleobiogeographic relationships have been inferred on the basis of a single fauna, which is the unique record until now in central Iran, and consequently the accuracy of the analysis would be improved if further brachiopod faunas were to be found in the future.

4. Brachiopod fauna: Compositional analysis and biostratigraphical record

The brachiopod fauna from central Iran can be arranged in a single assemblage consisting of *Homoeorhynchia sepahanensis* nov. sp., *Globirhynchia subobsoleta* (Davidson), *Pseudogibbirhynchia* sp., Tetrarhynchiidae sp. indet., *Monsardithyris?* aff. *haresfieldensis* (Davidson), and *Zeilleria* cf. *leckenbyi* (Walker in Davidson). In this assemblage, taxonomic diversity is rather low. It is dominated by numerous polymorph specimens of *H. sepahanensis* nov. sp. (81%), whereas two species (*Globirhynchia subobsoleta* and *Monsardithyris?* aff. *haresfieldensis*) reach nearly 12% and the remaining taxa are very scarce. This paucispecific faunal diversity is not restricted to the central Iranian basin, as this is generally well known in the brachiopod records from this timespan (e.g., Alméras, 1964; Comas-Rengifo and Goy, 1978; Vörös, 1980, 1993, 1995; García Joral and Goy, 1984; García Joral et al., 1990; Sulser, 1999).

At supraspecific level, all the taxa show an ordinary-looking morphological appearance just as is usually recorded in several Tethyan basins during the Early-Middle Jurassic transition. In addition, their geographical distribution is global, and some of them are ubiquitous (e.g., *G. subobsoleta*). At species level, *H. sepahanensis* nov. sp. can be considered as a new specific component of the well-known “*cynocephala*-type” group (*sensu* Buckman, 1895) developed in this peri-marginal Tethyan area. The remaining taxa are widespread, chiefly in the central and westernmost Tethyan platforms. In this assemblage the presence of species with a pronounced polymorphism is also remarkable, as noted in those taxa with enough individuals to analyze their morphological pattern, such as *H. sepahanensis* nov. sp., but also in the less abundant *Globirhynchia subobsoleta* and in the smooth terebratulids group.

The presence of all of these faunal attributes in comparable records from the Early-Middle Jurassic transition in some other basins, such as the Iberian Range, were linked to habitats with environmental instability due to tectono-sedimentary changes (García Joral and Goy, 1984). This situation is in agreement with central Iran, where the brachiopod-bearing levels appear in transgressive phases greatly influenced by synsedimentary tectonic activity (Fürsich et al., 2005; Seyed-Emamy et al., 2008). It is also globally consistent with the progressive rifting stage noticed in other Tethyan paleomargins during the latest Toarcian-Middle Jurassic.

From a biostratigraphical point of view, the Iranian brachiopod fauna includes a variety of taxa whose distribution ranges from the late Toarcian to early Aalenian in several Tethyan basins. Thus, *G. subobsoleta* seems to be a cosmopolitan species in the Aalenian European records, ranging from the Opalinum to the Bradfordiense zones (Alméras and Elmi, 1987; García Joral et al., 1990; Shi and Grant, 1993; Ager, 1994; Goy et al., 1994; Fauré and Alméras, 2006; Alméras et al., 2007b), but it has also been recorded in the late Toarcian-early Aalenian (Aalensis-Opalinum zones) from the Western Balkans (Motchurova-Dekova et al., 2009).

The species *M.?* *haresfieldensis* was recorded in the uppermost Toarcian (Ager, 1990; Alméras and Fauré, 2000; Ruban, 2004, 2009) and from the late Toarcian-early Aalenian (Aalensis-Opalinum zones) by Fauré and Alméras (2006). Finally, *Zeilleria leckenbyi* was reported by Baker (1972) in the Aalenian (Murchisonae Zone), together with *G. subobsoleta*. The *G. subobsoleta*-*M.?* *haresfieldensis* assemblage, together with specimens belonging to the *Homoeorhynchia* genus, were also recorded in the Aalensis-Bradfordensis zones from the eastern Pyrenees (Fauré and Alméras, 2006). In England, Davidson (1852-1878) also reported *G. subobsoleta*, *M.?* *haresfieldensis* and *Z. leckenbyi* jointly in the Early-Middle Jurassic transition. Occasionally, some of the aforementioned taxa are also associated with *Pseudogibbirhynchia* spp. and/or some representatives of the *H. cynocephala* group (García Joral et al., 1990; Ruban, 2004, 2009) in the late Toarcian-early Aalenian interval, just as in central Iran.

Except for the British records (Davidson, 1852-1878; Baker, 1972), the most comparable assemblage in terms of faunal constituent affinities may be the F1 assemblage defined by Fauré and Alméras (2006) in the Pyrenees. These authors established the *Stroudithyris infraoolithica*-*S. stephanoides* Zone ranging from the upper Toarcian-lowermost Aalenian (Aalensis-Opalinum zones). In addition to the index species, this assemblage includes *Lobothyris haresfieldensis*, *Monsardithyris catzigrasae*, *Homoeorhynchia cynocephala*, and *Zeilleria* cf. *lycetti*, among others.

This first dating approach based on brachiopod taxa (late Toarcian-early Aalenian) can be calibrated by more accurate biostratigraphical markers. Actually, although ammonoids are practically inexistent in the prospected sections of the Laluk area, an isolated and moderately preserved ammonoid has been found in the brachiopod-bearing levels, in which diagnostic criteria attributable to *Paradumortieria elmii* Seyed-Emami et al., 2008 are recognized, such as its ribbing pattern and the distinctive ventral keel. According to the recent biochronostratigraphic data of Seyed-Emami et al. (2008), this species is a good marker of the upper Toarcian (Pseudoradosa-Aalensis zones) in central and northern Iran. Finally, it is worth noting that this brachiopod assemblage from the late Toarcian in central Iran reveals close affinities to the earliest Aalenian faunas recorded in some western Tethyan basins.

5. Systematic Paleontology

Order RHYNCHONELLIDA Khun, 1949

Superfamily RHYNCHONELLOIDEA d'Orbigny, 1847

Family RHYNCHONELLIDAE d'Orbigny, 1847

Subfamily RHYNCHONELLINAE d'Orbigny, 1847

Genus *Homoeorhynchia* Buckman, 1918

Homoeorhynchia sepahanensis nov. sp.

Figs. 3, 4

?2000. *Rhynchonelloidea ruthenensis* (Reynés, 1968) - Kebriaizadeh et al., pl. 2, fig. 9-12

Derivation of the name: From Sepahan, ancient name of the Isfahan Province, where this species has been recorded for the first time.

Types and material: 47 specimens (I.H.2 to I.H.48) with diverse state of preservation. Internal recrystallization of the specimens is dominant and they frequently show deformations as a consequence of diagenetic processes (compressed lateral profiles as well as specimens with the dorsal valve flattened are common). The specimen I.H.21 (Fig. 3(6); Table 1) is designated as the holotype. Three paratypes (I.H.2, I.H.5, and I.H.16) have been sectioned and are also represented (Fig. 4). Both the holotype and acetate peels are deposited at the Departamento de Ciencias de la Tierra y del Medio Ambiente collections (University of Alicante, Spain). Intraspecific variability is shown through the paratypes (Fig. 3) and measured in Table 1.

Distribution: In central Iran this species has been recorded together with *Paradumortieria elmii*, which is a biostratigraphical marker of the Pseudoradosa-Aalensis zones of the upper Toarcian (Seyed-Emami et al., 2008).

Diagnosis: *Homoeorhynchia* of medium size and planoconvex shell, with a trigonal outline and subcynocephalous profile. The beak is pointed and suberect to nearly straight. The lateral commissure is straight and the anterior one is strongly uniplicate. Sharp ribs (8-13) appearing only near the anterior margin (3-5 in the median fold). Septalium is V-shaped and deep. Dorsal septum very long, exceeding the length of the crura. Long raduliform crura, distally with a noticeable ventral progression.

Description:

External features (Fig. 3). Medium-sized planoconvex shells (Table 1), with the ventral valve very flat, a distinctive subcynocephalous-cynocephalous profile, and trigonal to slightly subpentagonal outline. L/W ratio is rather variable, but most of the specimens are close to being equidimensional. Thickness is about 3/4-3/5 of the length. Maximum width and thickness lie in the anterior third of the shell. The beak is pointed, suberect to nearly straight, with a small foramen; the beak ridges are long and sharp, developing narrow interareas.

The lateral commissure is straight in the entire shell except for the proximity of the beak where it is slightly arched with dorsal convexity. The anterior commissure is strongly uniplicate, with a rather narrow and highly pronounced median fold (sharper in the biggest specimens), trapezoidal in outline, giving the shell a distinctive trilobate aspect. Ribs only appear near the anterior margin; they are strong and sharp. Consequently there is a wide smooth stage in the posterior area of the shell (nearly

occupying from 2/3 to 1/2 of the entire surface) where some fine, spaced and concentric growth lines are the only ornamentation noted. Costation consisting of 8 to 13 ribs on each valve (10 in most individuals), 3-5 of which can be present in the median fold (4 is the most frequent) (Fig. 3).

Internal structure (Fig. 4). This species shows a short pedicle collar and disjunct deltidial plates. The delthyrial cavity is rectangular to subtrapezoidal. Dental plates are subparallel to slightly convergent ventrally. Hinge teeth and sockets are crenulated; weak denticula and accessory sockets are present. The septalium is deep and well-developed, showing a V-shaped (rarely W-shaped) cross section. The dorsal median septum is very large, even exceeding the length of the crura. Hinge plates are subhorizontal. Crural bases are triangular in cross section, giving rise to long crura of raduliform type that evolve distally to bracket-shaped laminae with a noticeably ventral development, resembling canaliform variants of raduliform developments.

Remarks: In addition to the main biometric ratios (Table 1), intraspecific variability mainly lies in the height of the dorsal median fold, thus conditioning the cynocephalous appearance of the shell. Referring to the biometric measurements, the general pattern tends towards equidimensionality, but some shells are longer than wide and *vice versa* (Table 1). Maximum width can be shifted towards the mid-length in some specimens. Those specimens with more cynocephalous outlines have a greater thickness coinciding with the presence of a sharper and more triangular median fold. The ribbing pattern is essentially conservative, except for a very few specimens. Usually the presence of additional ribs in the median fold depends on whether the specimen has a greater number of ribs on both flanks. There is no relationship between ribbing progression and ontogenetic development, as 3-4 ribs are present in the median fold of the juvenile as well as in adult individuals. Usually there are additional ribs in the widening expanded specimens.

Homoeorhynchia sepahanensis nov. sp. is very close to the distinctive group of *H. cynocephala* and related forms (*H. cynica*, *H. meridionalis*, and *H. capitulata*) and can be incorporated in those morphologies that Buckman (1895) identified as the “*cynocephala*-type” group. *Homoeorhynchia cynocephala* s.s. (also recorded in the late Toarcian-early Aalenian) is consistently small-sized, with very few ribs and only two of these in the dorsal median fold (García Joral and Goy, 1984; García Joral et al., 1990; Goy et al., 1994, 3:5; Alméras and Fauré, 2000; Alméras and Beaud, 2002; Alméras et al., 2010a, 2010b), or occasionally up to three (Davidson, 1852; Ager, 1956; Goy et al., 1994; Alméras et al., 2010a).

Referring to the outline, *H. cynocephala* has a much higher dorsal median fold conferring a noticeable cynocephalous profile to the shell. This conspicuous cynocephalous shape is only reached in the extreme forms of *Homoeorhynchia sepahanensis* nov. sp. and only in a very few specimens (Fig. 3(15, 16)). *H. sepahanensis* nov. sp. can also be distinguished because it is more widely

expanded and always has more ribs on the shell. Moreover, it shows a more pointed beak and triangular shape on the edges of the posterior third of the shell; additionally, crural tips are rather longer in *H. sepahanensis* nov. sp.

The most evident external similarity of *H. sepahanensis* nov. sp. is found in the Pliensbachian species (Spinatum Zone) *H. capitulata* (Tate, 1876), whose lectotype was figured by Ager (1956). *H. capitulata* presents a similar ribbing pattern and comparable size, but has the maximum width shifted towards the mid-length, thus showing a more expanded pentagonal outline with blunter and rounded edges. In this sense, in neighbouring paleogeographic basins like the Caucasus, the species *capitulata* (Tate, 1876) was proposed by Ruban (2004, 2009) to designate taxa from the late Toarcian belonging to the genus *Grandirhynchia*. This supraspecific designation cannot be assigned to the Iranian specimens because, although some particular features such as a large dorsal median septum are more usual in this genus, most of the diagnostic criteria of *Grandirhynchia* are imperceptible in the material studied here (very large size, greater beak, convexity of the shell, ribbing pattern). In addition, the biostratigraphical ranges are disconnected since *Grandirhynchia* is regarded hitherto as a representative genus from the Pliensbachian (Manceñido, 2000; Manceñido et al., 2002). Easternmost records of the *cynocephala*-type group were recorded in the Aalenian from Tibet through *H. bolinensis* (Sun, 1981), but they are rather different to the Iranian material. Last, *H. sepahanensis* nov. sp. also has a dorsal outline rather similar to *H. cynica* (Buckman, 1895) as described by this author and shown by Ager (1956), but the ribbing pattern is rather different, *H. cynica* showing stronger and larger ribs.

Thus, all the external and internal gathering features such as ribbing pattern, cynocephalous profile, smooth posterior stage, deep septalium, and raduliform crura point to the *Homoeorhynchia* genus. The very long dorsal septum and long crural developments also appear in the species formerly called *Rhynchonelloidella marini* Rousselle, 1975. This generic assignment has been questioned and updated as a possible relative of the *Homoeorhynchia* group (*Homoeorhynchia?* *marini* in Fernandez-Lopez et al., 1998; *Rhynchonelloidella?* *marini* in García Joral and Goy, 2010). Finally, it is worth noting that in southeastern Iran, Kebriaiizadeh et al. (2000) figured specimens with similar external features to *H. sepahanensis* nov. sp. as *Rhynchonelloidea ruthenensis* (Reynés, 1968). These specimens were recorded in a stratigraphical range (Opalinum-Murchisonae zones, Aalenian) relatively close to the central Iran material studied here. It seems that the southeastern Iran specimens have a noticeable posterior smooth stage, different from those specimens belonging to *Rhynchonelloidea* genus and also from *Rhynchonelloidea ruthenensis*, mainly represented in the Pyrenees from the Aalensis-Opalinum zones (Alméras, 1979; Alméras and Peybernès, 1979; Alméras and Fauré, 2000), where the smooth stage is absent.

Superfamily HEMITHIRIDOIDEA Rzhonsnitskaia, 1956

Family CYCLOTHYRIDIDAE Makridin, 1955

Subfamily CYCLOTHYRIDINAE Makridin, 1955

Genus *Globirhynchia* Buckman, 1918

Globirhynchia subobsoleta (Davidson, 1852)

Fig. 5(1)

1852. *Rhynchonella subobsoleta* n.sp. - Davidson, pl. 17, fig. 14.

1878. *Rhynchonella subobsoleta* - Davidson, pl. 28, fig. 42-44.

1918. *Globirhynchia subobsoleta* (Davidson) - Buckman, pl. 18, fig. 12.

?1979. *Globirhynchia subobsoleta* (Davidson) - Alméras and Peybernés, pl. 2, fig. 1-6.

1987. *Globirhynchia prava* (Rothpletz, 1886) aff. *G. subobsoleta* (Davidson) - Alméras and Elmi, pl. 4, fig. 19-20.

1990. *Globirhynchia subobsoleta* (Davidson) - García Joral et al., pl. 1, fig. 4.

1993. *Globirhynchia subobsoleta* (Davidson) - Shi and Grant, pl. 14, fig. 1-6; pl. 18, fig. 5-6.

1994. *Globirhynchia subobsoleta* (Davidson) - Goy et al., pl. 3, fig. 6.

2002. *Globirhynchia subobsoleta* (Davidson) - Manceñido et al. (*in Treatise*), fig. 901, 3.

2006. *Globirhynchia subobsoleta* (Davidson) - Fauré and Alméras, pl. 1, fig. 4.

Material: Three poorly preserved specimens (I.H.50 to I.H.52), two of them only showing partly incomplete double valves.

Distribution: Among the profuse Aalenian records of this widespread species that can be emphasized here are those from the Opalinum Zone of the southeastern margin of the French Massif Central (Alméras and Elmi, 1987); from the Opalinum-Murchisonae zones of the Iberian Range (García Joral et al., 1990); from England (Shi and Grant, 1993; Ager, 1994); from Russian platforms (Kamyshan and Migacheva, 1963); from Southern Alps (Benetti and Pezzoni, 1993); from the Murchisonae-Bradfordiense zones of the Eastern Pyrenees (Fauré and Alméras, 2006); from the Murchisonae-Bradfordiense zones of the High Atlas (Alméras et al., 2007b). The report from the Western Balkans (Motchurova-Dekova et al., 2009) was dated in the late Toarcian-early Aalenian (Aalensis-Opalinum zones). The Iranian specimens have been recorded together with *Paradumortieria elmii*, which is a biostratigraphical marker of the Pseudoradiosa-Aalensis zones of the upper Toarcian (Seyed-Emami et al., 2008).

Description: Medium-sized equibiconvex shells, with both ventral and dorsal valves globose and ovoid dorsal outline. Maximum width and thickness occur in the mid-length of the shell. The beak is moderate and suberect; beak ridges are sharp, developing significant interareas. The lateral

commissure is straight, except for the development of a poorly defined squama-glotta in the slightly depressed interareas. The anterior commissure is uniplicate with a fairly narrow and low dorsal fold, nearly arcuate in outline. The shells are fully costae, with 25-27 sharp and closely packed ribs on each valve (7-8 of which located in the median fold), without bifurcation. The internal features have not been studied because of the scarcity of specimens and their inadequate preservation.

Remarks: The poor preservation and paucity of specimens did not permit analysis of intraspecific variability in the Iranian material. Only some variations about the fold can be observed, ranging from arcuate to narrower and nearly square-shaped.

The specimens have been assigned to *Globirhynchia subobsoleta* (Davidson, 1852) on the basis of the recognition of most of the diagnostic criteria of this species, such as equibiconvex shells, massive beak, or sharp and triangular ribbing pattern. The collected specimens are in close accordance with the figures of García Joral et al. (1990), showing a clearer anterior uniplication and the dorsal outline less widely expanded than the Iberian ones. The Iranian specimens are also close to *G. prava* aff. *G. subobsoleta* (Almérás and Elmi, 1987), *G. prava* (Rothpletz, 1886) *sensu stricto* showing more rounded outlines.

Almérás and Peybernès (1979) depicted the specific variability of *G. subobsoleta*, essentially concerning the biconvexity of the shells, although Shi and Grant (1993) questioned that the sectioned specimen by Almérás and Peybernès (1979) belonged to *Globirhynchia*. On the other hand, the ribbing pattern of *G. subobsoleta* is also reminiscent of *G. cf. buckmani*, figured by Almérás and Peybernès (1979), which shows a more rectangular outline in lateral view.

Kamyshan and Babanova (1973) established the new species *G. davidsoni* from the Aalenian of the Caucasus, based on specimens considered by Davidson (1876-1878: 41-43) as synonymous of *G. subobsoleta*. Actually, the external morphology of *G. davidsoni* is closely related to *G. subobsoleta* except for a narrower and higher dorsal fold; however, when Shi and Grant (1993) compared the internal structure, they again suggested that its generic assignment within *Globirhynchia* was inappropriate.

Finally, Cooper (1989) established several new species of *Globirhynchia* in the Bajocian-Bathonian of Arabia, all similar to *G. subobsoleta* but with a stronger ribbing pattern. Among these, *G.? dubia* and *G. triangulata* have external features that are more comparable with *G. subobsoleta*, differing mainly in their size and stronger features of the beak. Further on, *G. subtriangulata* has a box-like appearance and *G. concinna* and *G.? crassa* show flatter valves and broader anterior uniplication, just as occurs with *G. tatei* figured by Davidson (1878), Shi and Grant (1993) and Almérás and Fauré (2008), or *G. grayi* reported by Almérás and Fauré (2008) from the early Bajocian of the Atlas.

Family TETRARHYNCHIIDAE Ager, 1965

Tetrarhynchiidae sp. indet.

Fig. 5(3)

Material: A single poorly preserved specimen (I.H.49), with its ventral valve flattened and deformed. The mean biometric parameters are L: 18.97 mm, W: 17.79 mm, T: 12.39 mm.

Distribution: This single specimen has been recorded in central Iran together with *Paradumortieria elmii*, which is a biostratigraphical marker of the Pseudoradosa-Aalensis zones of the upper Toarcian (Seyed-Emami et al., 2008).

Description: The inadequate preservation of this specimen does not allow an accurate determination. Even so, there are some diagnostic features that point to its assignation within the Family Tetrarhynchiidae, such as a prominent beak, its markedly dorsibiconvex shape, subtriangular (with the anterior edges rounded) dorsal outline, presence of a well-defined squama-glotta, and a clear dorsal arcuate uniplication. Moreover, the specimen shows a typical ribbing pattern consisting of a multicostate shell, with 22 dense, fine and sharp ribs in the entire shell surface (9 placed in the median fold). Except for the squama-glotta area, the lateral commissure is straight. Maximum width is placed in the mid-length of the shell. The study of its internal features was not possible.

Remarks: As discussed above, the external features of the recorded specimen point toward the Tetrarhynchiidae. In several currently neighbouring regions, different taxa referred to Tetrarhynchiidae have been recorded in a similar biostratigraphic range. Thus, the central Iranian specimen differs from those belonging to *Conarosia* Cooper, 1989, recorded from the Toarcian-Bathonian in Saudi Arabia, because this genus shows greater equibiconvexity of both valves, a spherical outline, a strongly incurved beak, and a large size. It can be also separated from *Baeorhynchia* Cooper, 1989, recorded in Saudi Arabia and in southeastern Iran (Kebriaiizadeh et al., 2000), because this genus has a dispersed and coarse ribbing pattern.

Among the most similar taxa are the widespread *Tetrarhynchia* Buckman, 1918. It also resembles the younger *Cymatorhynchia* Buckman, 1917, which was recorded in SE Iran (Kebriaiizadeh et al., 2000), Saudi Arabia (Cooper, 1989), Jordan (Feldman et al., 2012), and in the Aalenian of the eastern Pyrenees (Fauré and Alméras, 2006), in the latter case also coexisting with *G. subobsoleta*. It is also externally comparable to the usually younger *Rhactorhynchia* Buckman, 1918, recorded from Europe to China and from South America to Canada.

Superfamily PUGNACOIDEA Rzhonsnitskaia, 1956

Family BASILIOLIDAE Cooper, 1959

Subfamily PAMIRORHYNCHIINAE Ovcharenko, 1983

Genus *Pseudogibbirhynchia* Ager, 1962

Pseudogibbirhynchia sp.

Fig. 5(2)

Material: A single poorly preserved specimen (I.R.1), with the dorsal valve eroded and fragmented. The mean biometric parameters are: L: 11.62 mm, W: 11.20 mm, T: 6.35 mm.

Distribution: This single specimen has been recorded in central Iran together with *Paradumortieria elmii*, which is a biostratigraphical marker of the Pseudoradosa-Aalensis zones of the upper Toarcian (Seyed-Emami et al., 2008).

Description: Medium-sized equibiconvex shell, with both ventral and dorsal valves very flat, triangular dorsal outline, and rounded anterior edges. Maximum width is slightly shifted towards the anterior third of the shell. The beak is slightly sharp and suberect. It shows well-defined beak ridges and rather wide interareas. The lateral commissure is inclined towards the ventral valve. The anterior commissure is rectimarginate to gently uniplicate. The shell is fully costate, with 21 rounded but penetrating ribs on each valve, sometimes bifurcating. Bifurcation is always visible in the posterior half of the shell. The internal structure was not studied because of the inadequate preservation of the only specimen recorded.

Remarks: As a precise determination of its internal structure is lacking and taking into account its inadequate preservation, the specimen recorded has been ascribed to *Pseudogibbirhynchia* Ager, 1962. This was based on several recognizable external diagnostic features usually identified in diverse species frequently attributed to this genus by most of the previous authors, such as the small to medium size, flattened valves, straight to roughly uniplicate anterior commissure, and ribbing pattern with numerous and occasional bifurcating ribs.

Some external features of the recorded specimen, such as the shallow uniplication, the markedly trigonal dorsal outline, the ribbing pattern, and the developed interareas are also shared with representatives of the younger genus *Lacunaerhynchia* Alméras, 1966, widely found during the Bajocian-Bathonian in several places (France, Poland, Romania, Argentina, but also in paleogeographically neighbouring basins like Tibet; Manceñido et al., 2002). On the contrary, *Lacunaerhynchia* has never been recorded in Toarcian-Aalenian times, and together with their rather different internal structure, both genera can be externally distinguished by their greater size and the more widening-expanded outline of *Lacunaerhynchia*, among other features. Fully costate rhynchonellids with a triangular shape and comparable in age have also been documented, belonging to *Pamirorhynchia* Ovcharenko, 1983. According to Andrade (2006), the scarce species of this genus were recorded in the late Toarcian from the Lusitanian Basin and the Iberian Range and in the late

Aalenian-Bajocian from areas near Iran, like the Pamir basin; nevertheless *Pamirorhynchia* species show biconvex profiles, more noticeable uniplication, and fewer and stronger ribs than the specimen attributed to *Pseudogibbirhynchia* in Iran.

At a specific level, *Pseudogibbirhynchia* sp. shows both valves flatter than the congeneric taxa recorded in a comparable timespan (late Toarcian-Aalenian), such as *P. mutans* (Rothpletz, 1886), *P. bothenhamptonensis* (Walker, 1892), *P. heiningensis* (Rollier, 1917) or the numerous species of *Pseudogibbirhynchia* described by Kamyschan and Babanova (1973).

Some other attributes can help to differentiate these taxa with respect to the Iranian material. More biconvex profiles can be seen in *P. bothenhamptonensis* from the late Toarcian of the Armorican Massif (Alm eras et al., 2010a, 2010b) and from the Lusitanian Basin (Andrade, 2006). In addition, the Iberian peri-marginal records of *Pseudogibbirhynchia* were ascribed to *P. mutans* by Andrade (2006) in the Aalenian of the Lusitanian Basin, and to *P. bothenhamptonensis* in the upper Toarcian of Asturias (Garc a Joral and Goy, 2009), both with fewer and stronger ribs as well as a pentagonal outline. Besides these records, Alm eras and Faur e (2008) referred to *P. petitclerci* (Haas, 1890) in the Aalenian-Bajocian from the Middle Atlas in Morocco, and Alm eras and Beaud (2002) reported *P. heiningensis* (Rollier, 1917) in the late Toarcian from the southern border of the Armorican Massif, which have fewer and stronger ribs and show more globose profiles. In this sense, it must be taken into account that *P. heiningensis* was also reported in the late Toarcian from neighbouring basins like the Caucasus (Ruban, 2004, 2009), but assigned to the *Gibbirhynchia* genus.

In some Western Tethyan areas, specimens with approximately similar ages were formerly assigned to *Pseudogibbirhynchia*, although they are morphologically unrelated to the sample studied here. This applies to *Pseudogibbirhynchia?* n. sp. (Garc a Joral and Goy, 1984). This stock of multicostate rhynchonellids shows a more cynocephalous lateral view and a more widening expanded dorsal outline, and has recently been established as a new species of *Choffatirhynchia* (*C. turolensis*) by Garc a Joral and Goy (2004).

Order TEREBRATULIDA Waagen, 1893

Suborder TEREBRATULIDINA Waagen, 1893

Superfamily LOBOIDOTHYRIDOIDEA Makridin, 1964

Family LISSAJOUSITHYRIDIDAE Cooper, 1983

Subfamily LISSAJOUSITHYRIDINAE Cooper, 1983

Genus *Monsardithyris* Alm eras, 1971

Monsardithyris? aff. *haresfieldensis* (Davidson, 1876)

Fig. 5(5-7)

aff. 1876. *Terebratula punctata* var. *havesfieldensis* (sic) - Davidson, pl. 16, fig. 3-5.

aff. 1982. *Lobothyris subpunctata* (Davidson) transient *havesfieldensis* (Davidson) - Alméras and Moulán, pl. 8, fig. 6-7.

aff. 1990. *Lobothyris havesfieldensis* (Davidson) - Ager, pl. 2, fig. 5, 6.

aff. 2000. *Lobothyris havesfieldensis* (Davidson) - Alméras and Fauré, pl. 8, fig. 3-6.

Material: Four specimens (I.T.55 to I.T.58) with varying states of preservation.

Distribution: Comparable morphologies to the Iranian specimens were recorded in the upper Toarcian from England as *Lobothyris havesfieldensis* (Ager, 1990); in the Aalensis Zone of the upper Toarcian (Alméras and Fauré, 2000), and then in the Aalensis-Opalinum zones (Fauré and Alméras, 2006) from the Pyrenees. Finally, Ruban (2004, 2009) cited *Lobothyris havesfieldensis* (sic) in the upper Toarcian from the Caucasus. In Iran these specimens have been recorded together with *Paradumortieria elmii*, which is a biostratigraphical marker of the Pseudoradosa-Aalensis zones of the upper Toarcian (Seyed-Emami et al., 2008).

Description: Medium to large-sized terebratulids (Table 2) with biconvex to fairly ventribiconvex shells. The dorsal outline is pyriform to subcircular with the maximum width and thickness lying near the mid-length. The beak is strong and slightly incurved and the beak ridges are long, developing narrow interareas that are deeper near the beak. Medium-sized and permesothyrid pedicle foramen. The lateral commissure is straight to gently arcuate and the anterior one is rectimarginate, with some individuals showing a barely discernible uniplication. Smooth shells except for the numerous dense growth lines. The internal structure was not studied due to inadequate preservation of the material.

Remarks: The specimens collected show the usual morphological intraspecific plasticity of a large amount of smooth Toarcian-Aalenian terebratulids, such as *Monsardithyris*, *Loboidothyris*, or *Lobothyris*. These genera include species with a clear external intraspecific variability specially referring to individuals ranging from a wide and subcircular outline to a narrower anterior margin, and from slightly ventribiconvex to nearly biconvex shells. In the same way, they are usually medium-sized but there are exceptionally very large specimens as shown in Fig. 5.

The smooth terebratulids found in central Iran have been assigned to the *Monsardithyris*? aff. *havesfieldensis* group because the individuals with a pyriform dorsal outline show a great similarity with the original types of Davidson (1876) and Ager (1990). The specimens with more subcircular outlines are comparable to those depicted by Alméras and Fauré (2000).

Among similar taxa is the contemporaneous *Monsardithyris catzigrasae* (Alméras and Moulán, 1982), regarded as the origin of the genus *Monsardithyris* by Alméras and Fauré (2007) in the lowermost upper Toarcian (Thouarsense Zone). However, *M. catzigrasae* can be differentiated by its

wider and more massive beak and usually shows the anterior commissure clearly uniplicate (Alm eras and Faur e, 2000; Alm eras et al., 2010a, 2010b). Therefore, a tentative identification has been adopted here, as the scarce available specimens do not allow recognition of the folding pattern throughout its ontogeny. Taking this question into account, some other taxa are clearly distinguishable from these Iranian terebratulids because of their clear uniplicate anterior margin, such as the several species of *Monsardithyris* described in the Bajocian of Normandy (Alm eras and Gu egan, 2009), *Monsardithyris ventricosa* from the Bajocian of Arabia (Alm eras, 1987), and the diverse uniplicate species of *Monsardithyris* from the Aalenian-Bajocian of Algeria and Morocco (Alm eras and Faur e, 2008). Thus, the Iranian material is more comparable to the Aalenian (Murchisonae-Bradfordensis zones) taxon *M. trilineata*, whose morphologic variability has been well documented by Alm eras and Peybern es (1979) and Faur e and Alm eras (2006). Finally, similar but more biconvex shapes were reported as *Loboidothyris clemishawi* by Alm eras and Peybern es (1979) in the Murchisonae Zone from the Pyrenees.

Suborder TEREBRATELLIDINA Muir-Wood, 1955

Superfamily ZEILLERIOIDEA Allan, 1940

Family ZEILLERIIDAE Schuchert, 1929 (*nom. transl.* Allan, 1940)

Subfamily ZEILLERIINAE Allan, 1940

Genus *Zeilleria* Bayle, 1878

Zeilleria cf. *leckenbyi* (Walker in Davidson, 1878)

Fig. 5(4)

cf. 1878. *Waldheimia leckenbyi* n. sp., Walker in Davidson, pl. 23, fig. 1-4.

cf. 1972. *Zeilleria leckenbyi* (Walker in Davidson) - Baker, pl. 82, fig. 1-12.

cf. 1974. *Zeilleria leckenbyi* (Walker in Davidson) - Delance, pl. 7, fig. 8.

Material: Two moderately preserved articulated specimens labelled as I.Z.53 (L: 19.74 mm, W: 17.30 mm, T: 10.62 mm) and I.Z.54 (L: 22.45 mm, W: 17.30 mm, T: 10.86 mm).

Distribution: This species was reported together with *Globirhynchia subobsoleta*, among others, from England in the Aalenian (Murchisonae Zone) (Baker, 1972). In central Iran, it is recorded together with *Paradumortieria elmii*, which is a biostratigraphical marker of the Pseudoradiosa-Aalensis zones of the upper Toarcian (Seyed-Emami et al., 2008).

Description: Medium-sized and slightly ventribiconvex zeillerid, with the dorsal valve somewhat flattened in the anterior third of the shell. The dorsal outline is distinctly pentagonal with the anterior margin rather narrow. Maximum width lies in the mid-length and maximum thickness is slightly shifted towards the posterior third of the shell. The beak is strong, subcrotaliform and suberect; the

beak ridges are robust but slightly blunt. Interareas are well defined and deep. The foramen is medium-sized and permesothyrid. The lateral and anterior commissures are straight. The entire surface of the shell is smooth, except for some growth lines. The internal structure was not studied because of the paucity of the material, but traces of dorsal median septum and dental plates were ascertainable.

Remarks: The presence of a dorsal median septum, dental plates and the typical beak features described justify the assignment of these terebratulids to *Zeillerioidea* Allan, 1940. Moreover, the similarities with *Zeilleria leckenbyi* depicted by Baker (1972) are evident, mainly those figured in Baker (1972: pl. 82: 10-12), especially regarding the subpentagonal dorsal outline, flatter dorsal valve, maximum thickness lying in the posterior third of the shell and the strong beak and well-developed beak ridges. However, in the specimens recorded here, a smaller foramen than in those figured by Baker (1972) is noted. In addition, some specimens depicted by Baker (1972: pl. 82:1-9) have a more rounded dorsal outline, just as occurs with the specimen figured by Delance (1974). On the other hand, the original material illustrated by Davidson (1878) shows a slightly wider dorsal outline than the Iranian one.

On the other hand, *Zeilleria cf. leckenbyi* is completely different from the stock of zeillerids appearing in several basins from the Western Tethys after the Early Toarcian Anoxic Event (ETOAE), which meant a severe brachiopod crisis in terms of diversity and abundance (García Joral and Goy, 2000; Vörös, 2002; Gahr, 2005; Comas-Rengifo et al., 2006; García Joral et al., 2011; Baeza-Carratalá, 2013, among others). This post-ETOAE stock of zeillerids has some distinguishable external features in common like small global size, minute beak, or wider anterior margin (Andrade, 2006), and these were gathered within the genus *Neozeilleria* Andrade, 2006.

6. Contributions of Iranian brachiopod fauna to paleobiogeography

Until the Late Triassic, the Iran Plate and the surrounding basins were part of the northern margin of Gondwana. From this time onward, they moved northward and finally collided with the southern margin of Laurasia. Thus, the Iran Plate and the surrounding basins were located in the most northeastern Tethyan margin during the Early-Middle Jurassic transition (Dercourt et al., 1993; Seyed-Emami et al., 2006, 2008; Fürsich et al., 2009; Wilmsen et al., 2009, among others).

Early Jurassic brachiopod faunas from the Tethys Ocean have conventionally been settled within the classical Mediterranean and NW-European paleobioprovinces (Ager, 1967, 1971, 1973; Vörös, 1977, 1980, 1984, 2005; Manceñido, 2002, among others). In this framework, paleobiogeographical affinities of brachiopod faunas from the central and northeastern margins of the Western Tethys are far from being accurately settled because of the paucity of the record in the Early-Middle Jurassic

transition, except for some noticeable data (Kamyshan and Babanova, 1973; Ruban, 2004, 2009). In central Iran and its adjacent basins, this scarcity of brachiopod data is due to the fact that they are restricted to transgressive episodes that gave rise to marine calcareous bed intercalations within the Shemshak Group (Seyed-Emami et al., 2008).

For the establishment of the paleobiogeographical affinities of the Iranian brachiopods studied here, a correlation with other representative Tethyan basins was performed through a paleomap slightly modified from Bassoulet et al. (1993) (Fig. 6). The Iranian taxa show a clear NW-European or subboreal distribution, since they have chiefly been recorded in the western and northern Tethyan platforms from England (Davidson, 1852, 1876, 1878; Baker, 1972; Ager 1990), the Pyrenees (Alm eras and Peybern es, 1979; Alm eras and Faur e, 2000; Faur e and Alm eras, 2006), and the Great Caucasus and the Crimea (Kamyshan and Babanova, 1973; Ruban, 2004, 2009); to a lesser extent, they are also related to the records of the Iberian Range (Garc a Joral and Goy, 1984; Garc a Joral et al., 1990; Goy et al., 1994) and the margins of the Armorican French Massif (Alm eras et al., 2010a, 2010b). On the contrary, they seem to be very different from the early Aalenian brachiopods described in typical Mediterranean areas, such as the Northern Calcareous Alps (Rothpletz, 1886) and north Italy (Ferrari and Manara, 1972). Therefore, the Iranian brachiopod occurrences during the Early-Middle Jurassic transition apparently show influences of the NW-European paleobioprovince.

Only the ubiquitous *G. subobsoleta* is indistinctly distributed, showing records not only in the northwestern areas but also in the Trento Platform (Benetti and Pezzoni, 1993), or even in the southwestern marginal Tethyan areas of High Atlas (Alm eras et al., 2007b). However these cosmopolitan records, even including some *Pseudogibbirhynchia* spp. and *Monsardithyris* spp. occurrences, are paleogeographically significant, as probably the Early-Middle Jurassic transition was a timespan when the Boreal and Tethyan realms, as well as the subsequent splitting into several Tethyan paleobioprovinces (Ethiopian, Caucasian, Himalayan and East Asian), were not entirely effective, just before reaching the maximum of provinciality revealed from the Aalenian onward (e.g., V or s, 1986; Mance nido, 2002; Garc a Joral, 2005). Thus, these occurrences reveal a certain homogenization of biochoremas and consequently the provinciality in the brachiopod faunas was less clear in the late Toarcian-earliest Aalenian times than in other previous or subsequent intervals, probably as a consequence of the extinction related to the Early Toarcian Oceanic Anoxic Event (ETOAE).

This probable post-ETOAE disruption of the regional provinciality for the brachiopod faunas was previously presumed in several western Tethyan basins (Garc a Joral, 2005; Garc a Joral et al., 2011; Baeza-Carratal a et al., 2011; Baeza-Carratal a, 2013) and probably lasted in some basins until the Aalenian. Previous authors reported faunal elements from NW-European and Mediterranean

bioprovinces recorded together, as in the Northern Calcareous Alps (García Joral, 1993), the Iberian Range (García Joral, 2005) and the Lusitanian Basin (Andrade, 2006). Additionally, it should be remembered that the gradual opening of the Central Atlantic produced significant paleogeographic changes in the Toarcian. These changes may have boosted a free connection in wide areas of the Tethys Ocean, therefore supporting the aforementioned homogenization.

These free connections can be also inferred from several other fossil groups. Indeed, Seyed-Emami et al. (2008) recorded ammonite fauna with common elements from NW-European and Mediterranean provinces in the Shemshak deposits equivalent in age to the brachiopod-bearing sediments studied here (Pseudoradosa-Aalensis zones). This disruption of ammonoid provinciality was suggested by Macchioni and Cecca (2002) in the Western Tethys from the late Pliensbachian onwards. A similar condition is noted in the calcareous nannoplankton, as Sandoval et al. (2012) reported a marked Mediterranean character until the early Toarcian, and then cosmopolitan assemblages in the middle-late Toarcian in southern Spain.

The transitory unification of bioprovinces inferred above can be coeval with the distinctly northern Tethyan dispersion of common taxa or ones that are highly related to Iranian fauna. Actually, a clear southern peri-Eurasian distribution can be detected (Fig. 6). García Joral and Goy (1984) put forward that several taxa of the Middle Jurassic from Western Europe originated in the peri-marginal areas of the Iberian Massif, where the oldest records of their phyletic lineages have been found. Probably, these taxa subsequently connected with the French assemblages, due to possible faunal linkages to their adjacent basins, with communication branches to the Trento Platform also being achievable, and perhaps even to the High Atlas, via the Lusitanian Basin (Fig. 6). These taxa immediately became widespread, as highly-related faunal constituents are recorded in the central and northern Tethyan areas (e.g., Western Balkans, Caucasus and Iran), spreading through a peri-Eurasian seaway where they found a feasible route through wide and continuous platforms and epicontinental habitats (Fig. 6). This northern seaway for the brachiopod fauna in the Early-Middle Jurassic transition was already inferred by Andrade (2006). This author established evolutionary relationships between faunal constituents of the Lusitanian Basin such as *Pamirorhynchia*, *Soaresirhynchia* and *Pseudogibbirhynchia*, with highly related or even synonymous taxa from Pamir, via the southern French basins (Almérás and Elmi, 1998), the northern Calcareous Alps (Rothpletz, 1886), and the northwestern Caucasus (Kamyshan and Babanova, 1973) among other areas, supporting the connection by means of a free marginal northern Tethyan corridor.

Considering all the data, it can be postulated that both the disruption of Mediterranean/NW-European provinciality and good communication through the northern seaway across the peri-Laurasian epicontinental platforms, allowed an episodically free faunal connection between the

western and northeastern parts of the Tethys Ocean, this last region including central Iranian brachiopod fauna.

7. Conclusions

To date, the Laluk Mountain area has yielded the only Jurassic brachiopod record systematically recognized from the central Iran region. These brachiopods have been assigned to six different taxa, which have been identified for the first time in Iran. The recognized assemblage is dominated by the new species *Homoeorhynchia sepahanensis* nov. sp., which is formally described in this paper. Within the sediments of the Shemshak Group, this assemblage can be assigned to the upper Toarcian (Pseudoradosa-Aalensis zones) based on the brachiopod specimens collected, together with an ammonite biostratigraphical marker. However, this range could be extended from Pseudoradosa to Bradfordiense Zones (upper Toarcian-Aalenian) based on comparable brachiopod assemblages recorded in the westernmost Tethys areas.

An apparent homogenization of biochoremas and, consequently, a less clear provinciality of the brachiopod faunas in the late Toarcian-earliest Aalenian, is inferred, taking into account the distribution of taxa highly related to the Iranian fauna in the Tethys Ocean, explaining a free connection in wide areas of the Tethys. On the other hand, this can be congruent with the southern peri-Eurasian distribution detected. Thus, it can be postulated from brachiopod faunas that both the disruption of bioprovinciality and the free communication through the northern seaway across the peri-Laurasian epicontinental platforms allowed an episodically open faunal connection between the Western and northeastern parts of the Tethys Ocean, including central Iran.

Finally, the study of the Jurassic brachiopods from central Iran enhances the knowledge of this group in the northeastern Tethyan margins during the late Toarcian, a timespan when the entire brachiopod record is relatively scarce over the Tethys Ocean.

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Table and Figure captions

Table 1. Biometric measurements of the studied specimens of *Homoeorhynchia sepahanensis* nov. sp. L: total length; W: total width; T: total thickness (in mm); R: Ribs on each valve; Rb: Ribs on the dorsal median fold.

Table 2. Biometric measurements of the studied specimens of *Monsardithyris?* aff. *haresfieldensis* (Davidson, 1876). L: total length; W: total width; T: total thickness (in mm).

Figure 1. **A.** Geographical location of the study area. **B.** Lithostratigraphical sketch of the Early Jurassic deposits in the Laluk Mountain showing the occurrence of collected brachiopods (black arrow). **C.** Location of the Laluk Mountain in the Jurassic outcrops from the Esfahan area.

Figure 2. **A.** Brachiopod-bearing levels in the Laluk Mountains. **B.** Field-aspect of the sandy limestone levels with brachiopod accumulations. **C.** Outcrop detail of the brachiopod assemblage in the yellowish sandy limestone beds. **D.** Facies detail, showing belemnites recorded together with the brachiopod assemblage.

Figure 3. 1-16. *Homoeorhynchia sepahanensis* nov. sp. from the upper Toarcian (Pseudoradiosa-Aalensis zones) of the Laluk Mountain (central Iran). 1, I.H.7; 2, I.H.17; 3, I.H.27; 4, I.H.10; 5, I.H.15; 6, I.H.21, holotype; 7, I.H.33; 8, I.H.35; 9, I.H.48; 10, I.H.28; 11, I.H.34; 12, I.H.29; 13, I.H.47; 14, I.H.44; 15, I.H.39; 16, I.H.38. a: dorsal view; b: lateral view; c: anterior view. Scale bar: 1 cm.

Figure 4. Internal structure of *Homoeorhynchia sepahanensis* nov. sp. **A1.** Transverse serial sections through the I.H.2 specimen (distance from the apex in mm). **A2-4.** Microphotographs of acetate peels from the I.H.2 specimen. A2, section at 1.20 mm from the apex showing the main features of the cardinal area, dorsal median septum and septalium; A3, section at 1.50 mm from the apex showing hinge teeth and sockets and representative dorsal median septum and septalium; A4, section at 2.90 mm from the apex showing individualized crura. **B1.** Transverse serial sections through the I.H.5 specimen (distance from the apex in mm). **B2-4.** Microphotographs of acetate peels from the I.H.5 specimen: B2, section at 1.20 mm from the apex showing the main features of both ventral and dorsal valves; B3, detailed view of the slightly “W”-shaped septalium (section at 1.70 mm from the

apex); B4, section at 4.20 mm from the apex showing raduliform and bracket-shaped crura development. **C1**. Transverse serial sections through the I.H.16 specimen (distance from the apex in mm). **C2**. Microphotograph of acetate peels from the I.H.16 specimen showing the main internal features at 0.50 mm from the apex.

Figure 5. Some representative species of the brachiopod assemblage collected in the Laluk Mountain, Central Iran (upper Toarcian; Pseudoradosa-Aalensis zones). **1.** *Globirhynchia subobsoleta* (Davidson), specimen I.H.51. **2.** *Pseudogibbirhynchia* sp., specimen I.R.1. **3.** Tetrarhynchiidae sp. indet., specimen I.H.49. **4.** *Zeilleria* cf. *leckenbyi* (Walker in Davidson), specimen I.Z.54. **5-7.** *Monsardithyris?* aff. *haresfieldensis*. (Davidson); 5, specimen I.T.57; 6, specimen I.T.56; 7, specimen I.T.58. a: dorsal view; b: lateral view; c: anterior view; d: ventral view. Scale bar: 1 cm.

Figure 6. Paleogeographical map of the Early-Middle Jurassic transition (slightly modified from Bassoullet et al., 1993), showing the position of representative localities in the western Tethys with taxa highly related to, or common with the Iranian fauna. Black arrows show the spreading inferred by the preferentially southern peri-Eurasian distribution pattern. Sources cited in the text; (?) marks taxa not figured or possibly inconsistent taxonomical attributions as well as tentative connections.

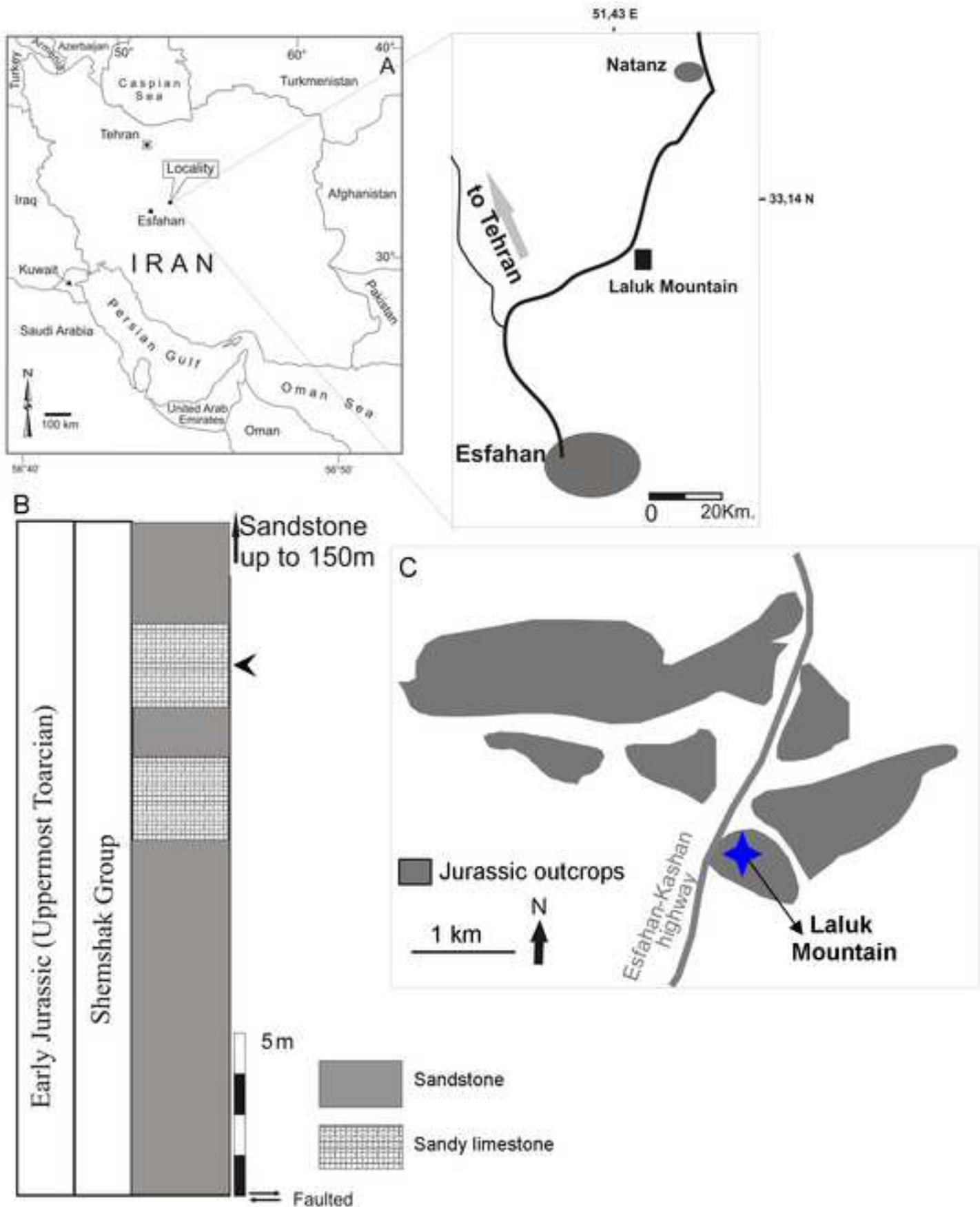
Table 1.

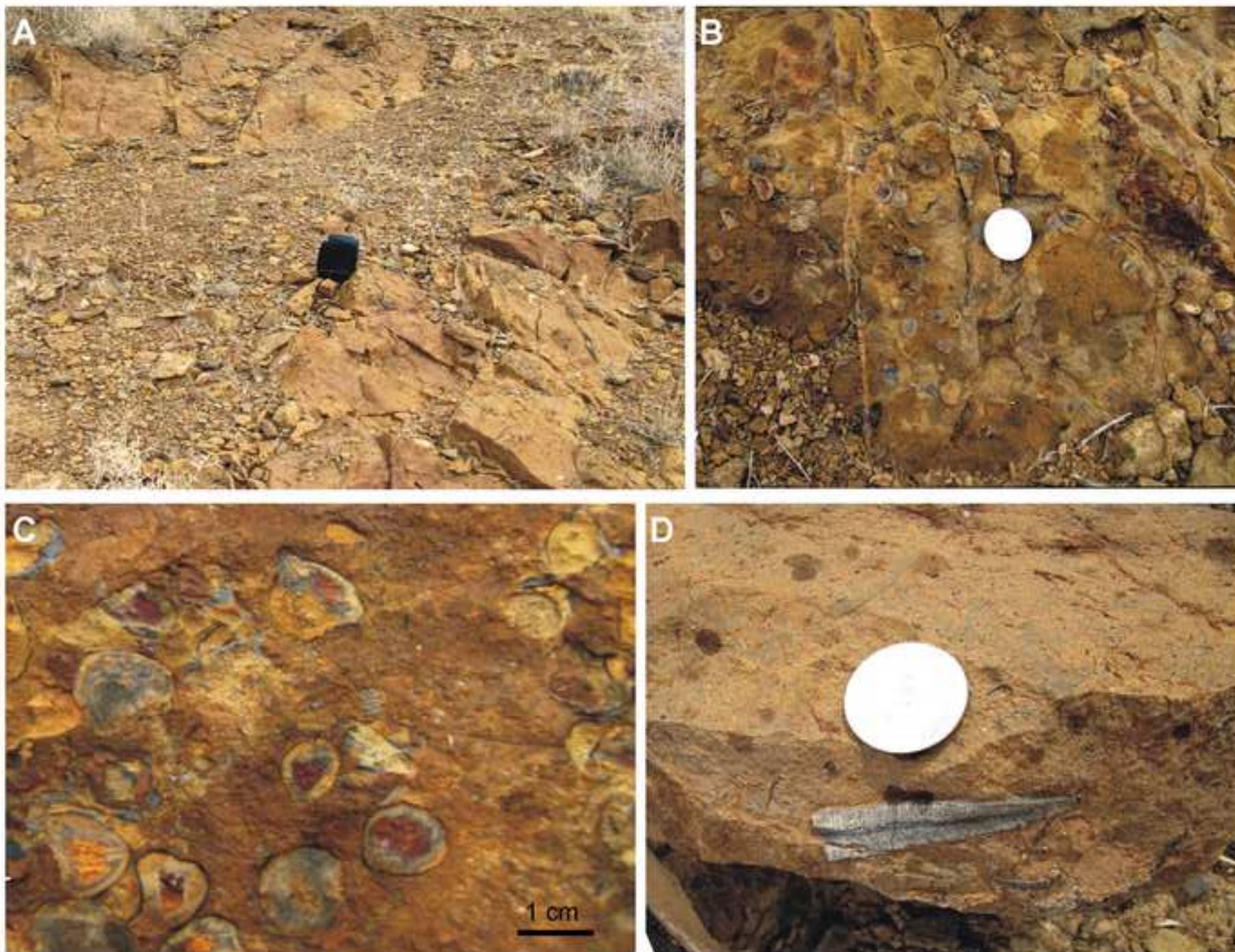
| Specimen | L | W | T | W/L | T/L | T/W | R | Rb |
|----------|-------|-------|-------|------|------|------|----|----|
| I.H.2 | 12.81 | 13.98 | 9.90 | 1.09 | 0.77 | 0.71 | 10 | 4 |
| I.H.3 | 15.69 | 17.81 | - | 1.13 | - | - | 13 | 5 |
| I.H.4 | 17.30 | 15.87 | 12.70 | 0.92 | 0.73 | 0.80 | 13 | 5 |
| I.H.5 | 15.64 | 15.81 | 10.36 | 1.01 | 0.66 | 0.65 | 10 | 4 |
| I.H.6 | - | 18.66 | 12.10 | - | - | 0.65 | 10 | 4 |
| I.H.7 | 9.17 | 9.17 | 5.53 | 1 | 0.60 | 0.60 | 9 | 3 |
| I.H.8 | 11.11 | - | - | - | - | - | 8 | 4 |
| I.H.9 | 10.39 | 11.44 | 8.52 | 1.10 | 0.82 | 0.74 | 10 | 4 |
| I.H.10 | 10.68 | 11.09 | 8.03 | 1.04 | 0.75 | 0.72 | 8 | 4 |
| I.H.11 | 13.39 | 14.13 | - | 1.05 | - | - | 10 | 4 |
| I.H.12 | 14.35 | 12.54 | 10.15 | 0.87 | 0.71 | 0.81 | 10 | 4 |
| I.H.13 | 12.00 | 11.91 | 9.76 | 0.99 | 0.81 | 0.82 | 10 | 4 |
| I.H.14 | 14.20 | 15.35 | 10.31 | 1.10 | 0.72 | 0.67 | 10 | 4 |
| I.H.15 | 13.37 | 13.35 | 9.95 | 1.00 | 0.74 | 0.74 | 8 | 4 |
| I.H.16 | 12.78 | 11.75 | 7.22 | 0.92 | 0.56 | 0.61 | 10 | 4 |
| I.H.17 | 12.80 | 11.84 | 7.85 | 0.92 | 0.61 | 0.66 | 9 | 3 |
| I.H.18 | 16.31 | - | 11.12 | - | 0.68 | - | 10 | 4 |
| I.H.19 | 14.49 | 12.61 | 8.00 | 0.87 | 0.55 | 0.63 | 8 | 4 |
| I.H.20 | 11.74 | 11.80 | 9.35 | 1.00 | 0.79 | 0.79 | 10 | 4 |
| I.H.21 | 13.26 | 11.85 | 9.15 | 0.89 | 0.69 | 0.77 | 10 | 4 |
| I.H.22 | 14.32 | 12.94 | 8.53 | 0.90 | 0.60 | 0.66 | 11 | 5 |
| I.H.23 | 13.80 | 13.07 | 9.90 | 0.95 | 0.72 | 0.76 | 8 | 4 |
| I.H.24 | 13.25 | 12.32 | 9.97 | 0.93 | 0.75 | 0.81 | 9 | 5 |
| I.H.25 | 14.59 | 15.60 | 10.47 | 1.07 | 0.72 | 0.67 | 10 | 4 |
| I.H.26 | 12.79 | 13.85 | 9.45 | 1.08 | 0.74 | 0.68 | 8 | 4 |
| I.H.27 | 11.26 | 11.82 | 6.98 | 1.05 | 0.62 | 0.59 | 9 | 3 |
| I.H.28 | 13.58 | 13.15 | 9.17 | 0.97 | 0.67 | 0.70 | 11 | 5 |
| I.H.29 | 15.13 | 14.73 | 9.90 | 0.97 | 0.65 | 0.67 | 11 | 5 |
| I.H.30 | 14.33 | 13.17 | 9.56 | 0.92 | 0.67 | 0.72 | 10 | 4 |
| I.H.31 | 13.22 | 12.83 | 8.49 | 0.97 | 0.64 | 0.66 | 10 | 4 |
| I.H.32 | 11.90 | 14.91 | 9.03 | 1.25 | 0.76 | 0.60 | 10 | 4 |
| I.H.33 | 13.64 | 13.25 | 8.61 | 0.97 | 0.63 | 0.65 | 8 | 4 |
| I.H.34 | 15.28 | 14.82 | 10.58 | 0.97 | 0.69 | 0.71 | 11 | 5 |
| I.H.35 | 13.16 | 11.93 | 9.06 | 0.91 | 0.69 | 0.76 | 10 | 4 |
| I.H.36 | 16.45 | 16.29 | 12.8 | 0.99 | 0.78 | 0.78 | 10 | 4 |
| I.H.37 | 11.70 | 12.70 | 9.00 | 1.08 | 0.77 | 0.71 | 8 | 4 |
| I.H.38 | 19.99 | 18.90 | 17.64 | 0.94 | 0.88 | 0.93 | 12 | 4 |
| I.H.39 | 17.40 | 16.67 | 15.46 | 0.96 | 0.89 | 0.93 | 12 | 4 |
| I.H.40 | 15.74 | 15.75 | 10.04 | 1.00 | 0.64 | 0.64 | 10 | 4 |
| I.H.41 | 17.03 | 16.58 | 11.05 | 0.97 | 0.65 | 0.66 | 10 | 4 |
| I.H.42 | 14.32 | 14.46 | - | 1.01 | - | - | 10 | 4 |
| I.H.43 | 15.87 | 15.65 | 8.53 | 0.99 | 0.54 | 0.54 | 11 | 5 |
| I.H.44 | 17.72 | 17.65 | 10.89 | 0.99 | 0.61 | 0.62 | 13 | 5 |
| I.H.45 | 19.22 | 16.96 | 10.73 | 0.88 | 0.56 | 0.63 | 11 | 5 |
| I.H.46 | 13.38 | 12.78 | 8.93 | 0.95 | 0.67 | 0.70 | 11 | 5 |
| I.H.47 | 14.65 | 15.20 | 10.31 | 1.04 | 0.70 | 0.68 | 10 | 6 |
| I.H.48 | 13.75 | 13.28 | 8.90 | 0.97 | 0.65 | 0.67 | 9 | 5 |

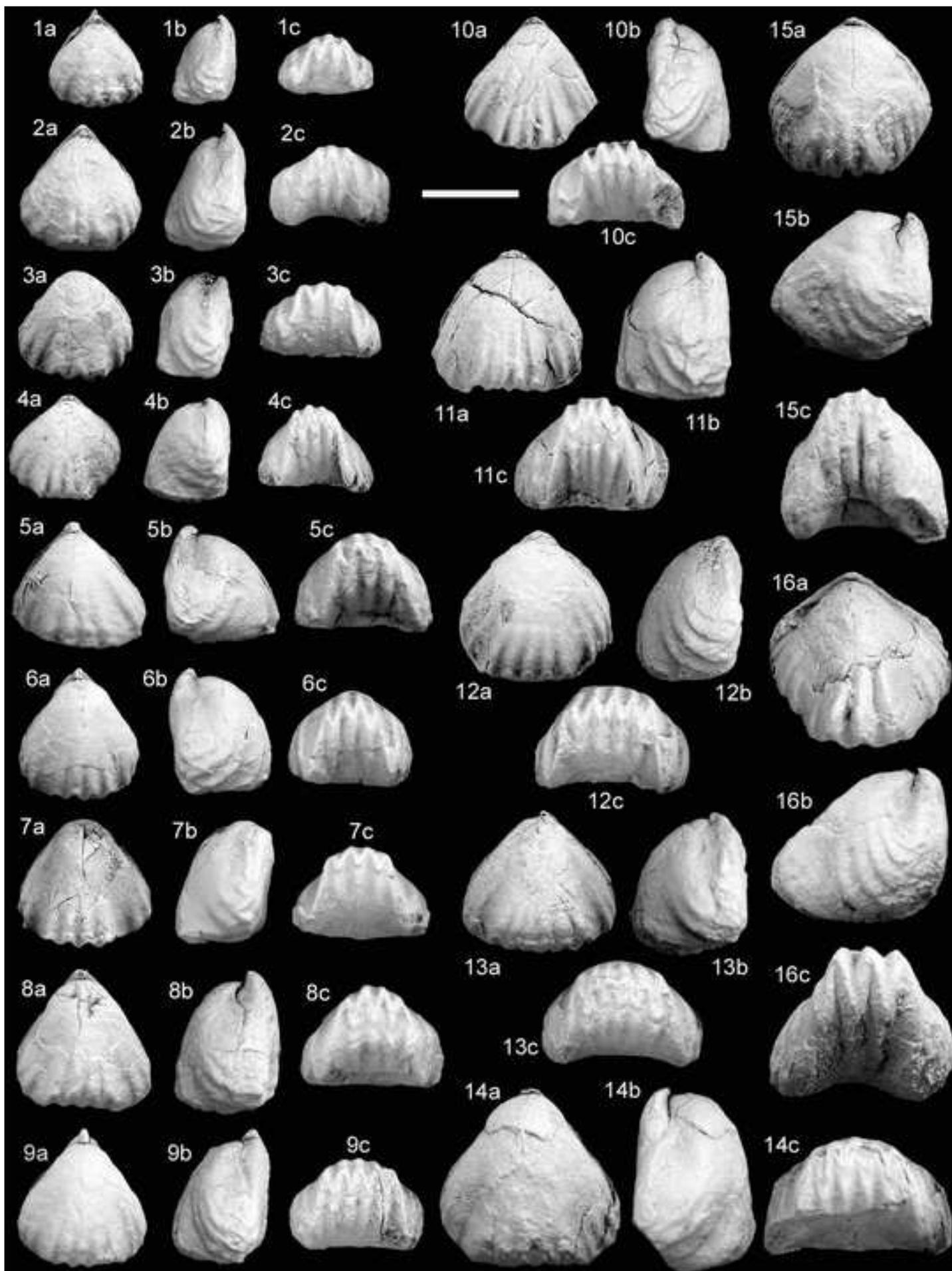
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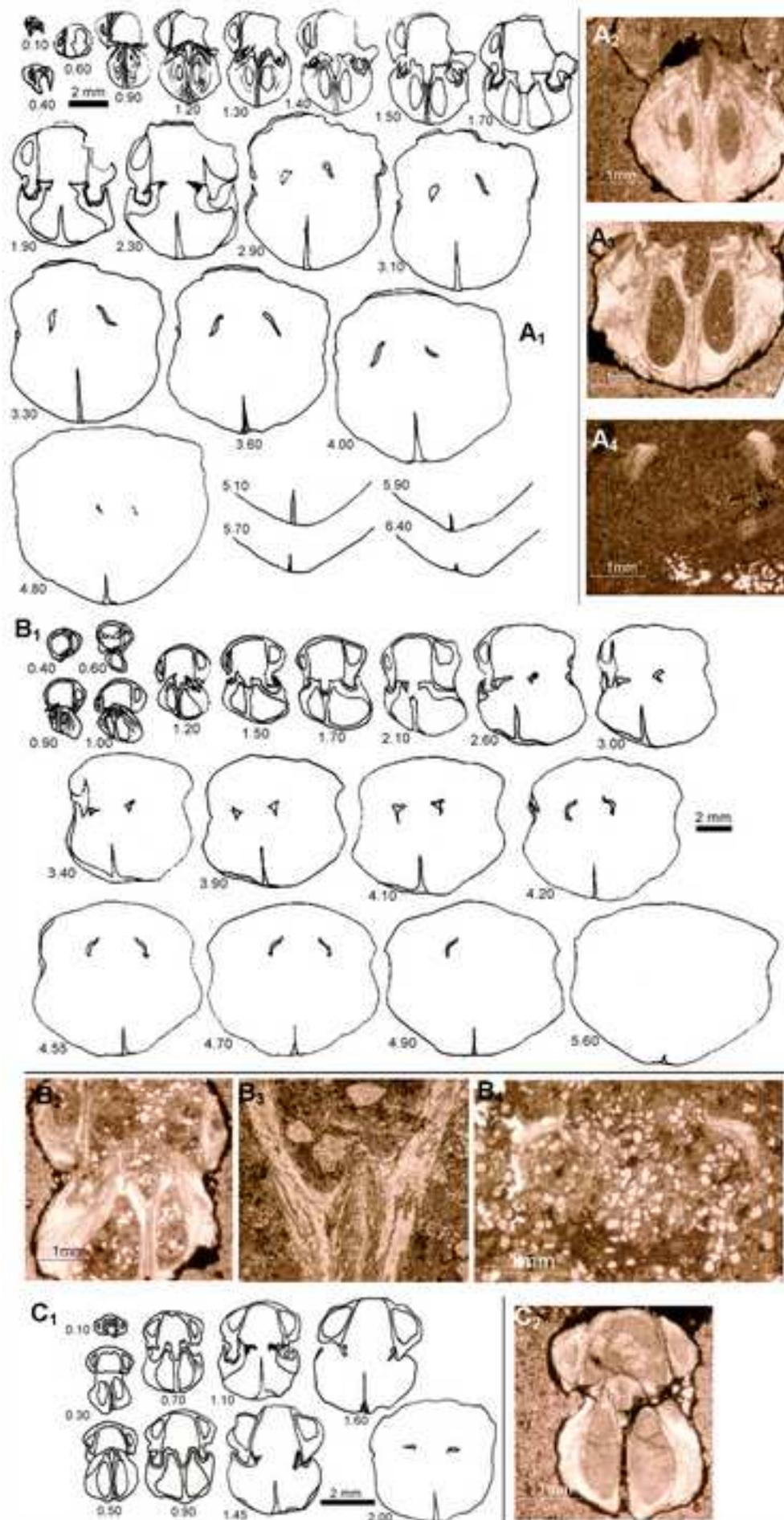
| Specimen | L | W | T | W/L | T/L | T/W |
|-----------------|----------|----------|----------|------------|------------|------------|
| I.T.55 | 40.28 | 31.38 | 21.50 | 0.78 | 0.53 | 0.68 |
| I.T.56 | 26.83 | 21.05 | 13.36 | 0.78 | 0.50 | 0.63 |
| I.T.57 | 28.48 | 23.96 | 18.25 | 0.84 | 0.64 | 0.76 |
| I.T.58 | 24.26 | - | 10.56 | - | 0.43 | - |

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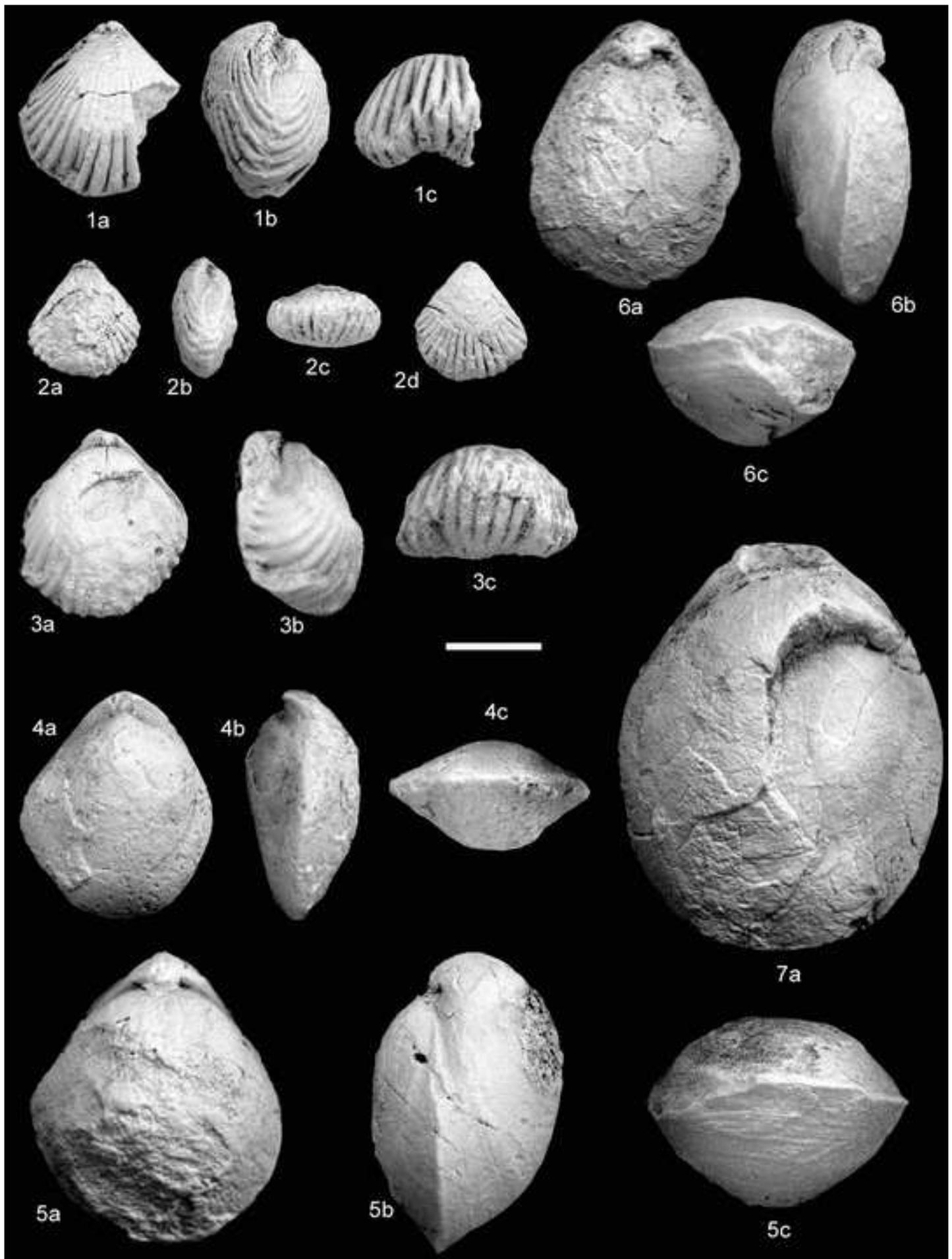


Figure 6

