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Article

Early Dalejan (Emsian) brachiopods from Hamar Laghdad (eastern Anti-Atlas, Morocco)

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With 16 figures and 1 table

Abstract: Late Emsian (early Dalejan, *Polygnathus inversus* Zone) brachiopods from Hamar Laghdad (eastern Anti-Atlas, Morocco) are examined on the basis of a collection of over 540 specimens coming from the Kess-Kess Formation. Two entirely different assemblages (no shared species) corresponding to mud mound and inter-mound carbonates are recorded. The assemblage A (inter-mound carbonates) includes 15 species and is dominated by *Kyrtatrypa* cf. *balda*, *Brachyspirifer*? sp., and *Sieberella*? sp. Other brachiopods include *Stenorhynchia ulrici* Halamski & Baliński n. sp., *Eoglossinotoechia marocanensis* and *Reticulariopsis*? sp. The assemblage A is a mixture of quieter water species and of brachiopods adapted to high energy environments. The assemblage D from cavities and small caves occurring within the Kess-Kess mud mounds is nearly monospecific, dominated (98%) by *Septatrypa tumulorum* Baliński & Halamski n. sp. This species was probably adapted to live around the outlets of active or inactive venting chimneys. Precise biogeographic analysis of the fauna is hampered by inadequate preservation and the necessity of using the open nomenclature resulting therefrom, but Bohemian affinities of the described brachiopods are clear.

Key words: Brachiopoda, Early Devonian, Morocco, mud mounds, palaeobiogeography.

1. Introduction

Brachiopods were a major element of the Devonian benthos and Morocco is arguably one of the best places of the world to study them thanks to richness, diversity and good state of preservation of fossils on the one hand and to the quality of outcrops on the other hand. Devonian brachiopods from the Anti-Atlas were first studied by Le Maître (1939, 1944; for a more detailed history of research, see Halamski & Baliński 2013, pp. 243-244) and then by Drot (1964), mainly on the basis of collections made by the geologist Henri Hollard during geological surveying work (e.g. Hollard 1974). Detailed studies of the brachiopod faunas based on systematic collecting by palaeontologists (Jansen 2001; Halamski & Baliński 2013) revealed that richness and diversity were even greater than expected.

In the following, we describe the brachiopod inventory of two of the assemblages collected from Hamar Laghdad (Tafilalt Platform, Eastern Anti-Atlas) for the first time. The structures of these two assemblages are discussed in the light of their ecological conditions.

2. Material and methods

Emsian and earliest Eifelian (late Early to earliest Middle Devonian) brachiopods from Hamar Laghdad in the eastern Anti-Atlas come from four locality groups with uniform brachiopod assemblages (Fig. 1).

Assemblage A has been collected from limestones of the intermound facies belonging to the Kess-Kess Formation (Saheb el Rhassel Group) cropping out in a small wadi (= oued, dry valley) dissecting the plateau of Hamar Lagh-

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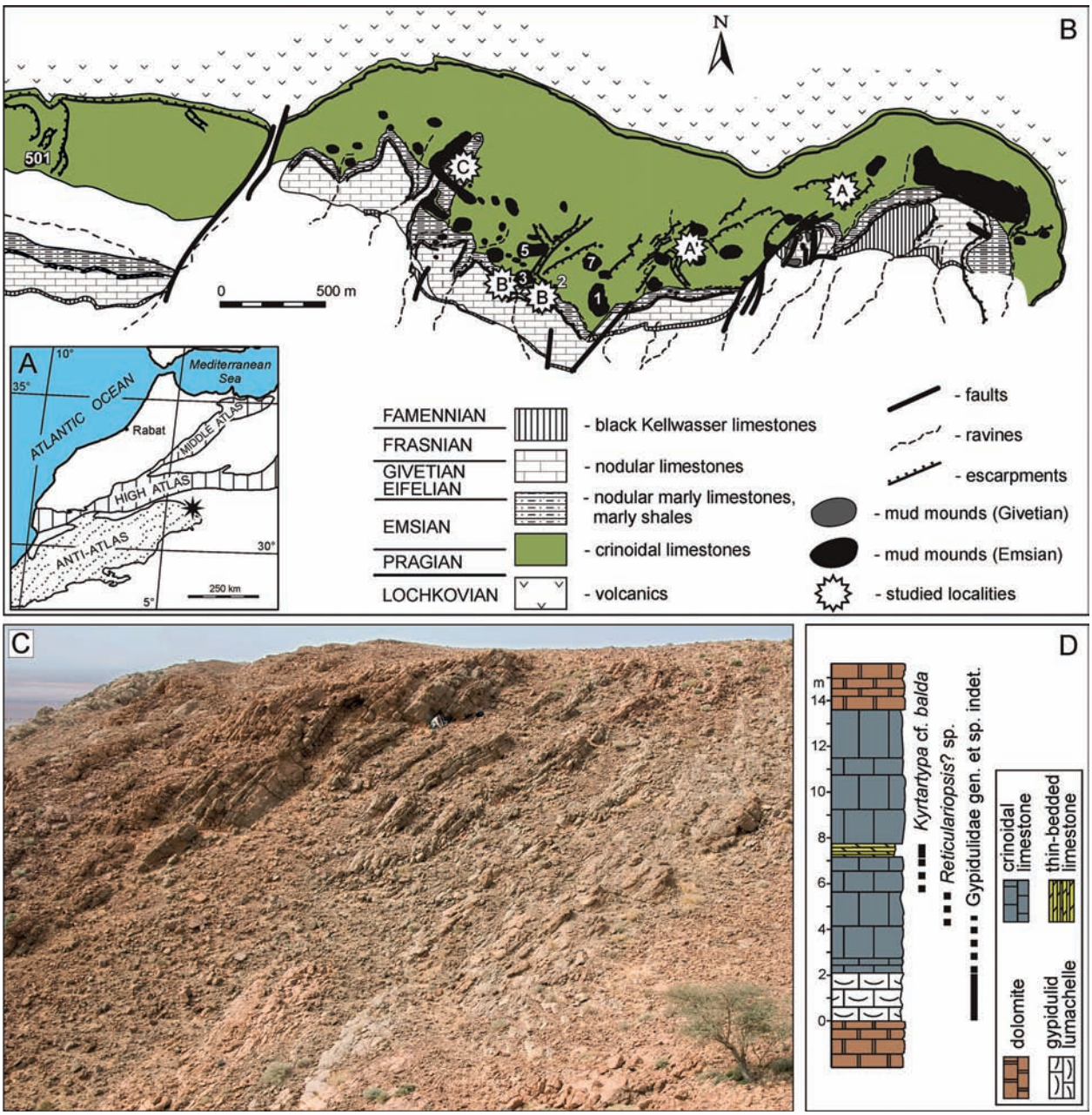

Fig. 1. Geographic and geological setting of the studied brachiopods. **A** – Tectonic framework of northwestern Africa showing the position of Hamar Laghdad hills. **B** – Geological map of Hamar Laghdad (after Berkowski & Zapalski 2014) showing the studied localities. The localities corresponding to assemblages A, B, and C are noted by asterisks. The mounds from which brachiopods have been collected (assemblage D) are denoted by numbers (according to the system by Brachert et al. 1992, supplemented by unpublished data of B. Berkowski & Z. Belka), the other mounds are left unnumbered. **C** – General view (from the east) of the locality A: the studied section begins with the gypidulide lumachelle about the solitary acacia in the bottom right corner of the image; ATH is just below the thin-bedded limestones with *Kyrtatrypa* cf. *balda* (top centre of the image). **D** – Lithological section of the locality A showing the distribution of those brachiopods from the assemblage A for which the data are available. See text for further explanation.

dad NW of the peculiar Givetian Mound 50 described by Berkowski (2006) (Fig. 1B, C; geographic coordinates of the locality 31.3824° N, 4.0374° W). About 12 m of limestone were recorded, whereas both underlying and overlying strata are dolomitised. The limestones yielding this assemblage are often rich in crinoids (see Fig. 1D for a detailed section). In the lower part, there is a single lumachelle bed of 2.10 m thickness with *Sieberella*? sp. and several beds in which the same brachiopods occur abundantly. In the upper part there are several thin beds (totally 0.60 m thick) of lumachelle containing predominant *Kyrtatrypa* cf. *balda*. According to unpublished conodont data (B. Berkowski, personal communication, 13.07.2016), these rocks might belong to the *Polygnathus inversus* Zone. The only articulated shell of *Brachyspirifer*? sp. was surface-collected in the same wadi further southwest (locality A'; approximate coordinates 31.3772° N, 4.0450° W ± 3") and may tentatively be considered as approximately coeval to the rest of assemblage A.

Assemblage B has been collected from marly shales belonging to the upper part of the Amerboh Group immediately south-eastward of Mound 3 at the southern edge of Hamar Laghdad; the photograph and lithological section of this locality was given by Berkowski (2008, 2012) and Berkowski & Klug (2012), approximate coordinates are 31.3744° N, 4.0525° W. Subordinately, material from the lower part of the Amerboh Group (nodular marly limestones) was also included. Additional material has been collected slightly further west, on the other (south-western) slope of a small pass immediately south of Mound 3 (locality B'; approximate coordinates 31.3747° N, 4.0536° W). The age of the assemblage B is thus mainly from the *Polygnathus serotinus* Zone to the *Polygnathus patulus* Zone, perhaps including portions of the latest *Polygnathus inversus* Zone (Aitken et al. 2002; Berkowski 2008; Z. Belka, unpublished data).

Assemblage C has been collected from early to earliest Middle Devonian strata cropping out around a small solitary hill of Middle Devonian limestone at 31.3789° N, 4.0569° W (our locality C). A very similar fauna was collected by C. Klug and M. Mergl from coeval strata at the famous "Red Cliff". According to us, the Red Cliff is situated ca. 100 m northeast of our locality C [thus about 31.3803° N, 4.0567° W; the geographic coordinates of the Red Cliff are 31.37694° N, 4.05778° W according to Klug et al. 2009 and 30.82453° N, 4.90210° W according to Klug et al. 2014, but in our opinion both seem erroneous].

Assemblage D has been collected from the cavities and small caves occurring within the Kess-Kess mud mounds number 1, 2, 3, 5, 7 (numbering after Brachert et al. 1992) and 501 (unpublished numbering of Z. Belka and B. Berkowski). The age of the Kess-Kess mud mounds corresponds to the *Polygnathus inversus* conodont zone (Aitken et al. 2002; Berkowski 2008 and references therein).

The description of the late Emsian to earliest Eifelian brachiopods from Hamar Laghdad is subdivided as follows:
a. our paper is devoted to the two older (early Dalejan) assemblages, called herein assemblages A and D;
b. the younger (middle to late Dalejan) brachiopods from the assemblage C are described by Michal Mergl (2018, this volume) on the basis of collections from the Red Cliff.

The collections corresponding to the assemblages A and D were made by Andrzej Baliński, Zdzisław Belka, Błażej Berkowski and Adam T. Halamski in February and March 2010. They are kept in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw and registered under the inventory number ZPAL Bp 80. The collection numbers of individual specimens incorporate field numbers of samples (M1, M2, ..., ATH-a, b, AB-a, b, ...) and the ordinary number of species in the entire collection, so a number like ZPAL Bp 80/AB-e-24/1 is to be read "Moroccan collection (Bp 80), sample AB-e, 24th species, first specimen". The number of a particular specimen within a sample is omitted if the entire sample is meant or if there is only a single specimen within the sample. Measurements are usually given as follows: (*a*-)*b*-*c*(-*d*), *e*, *N*, where *a* is the smallest measured value, *b* the first quartile, *c* the third quartile, *d* the highest measured value, *e* the arithmetic mean, and *N* the number of measured values.

3. Systematic descriptions

Phylum Brachiopoda Duméril, 1805
Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer & Popov, 1996
Class Strophomenata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order Strophomenida Öpik, 1934
Superfamily Strophomenoidea King, 1846
Family Rafinesquinidae Schuchert, 1893
Subfamily Leptaeninae Hall & Clarke, 1894
Leptaeninae gen. et sp. indet.
Fig. 2C, D

Material: One incomplete ventral valve (ZPAL Bp 80/ATH-f-35), two fragmentary dorsal valves and one fragment of an unidentified valve (ZPAL Bp 80/AB-e-35); all from Hamar Laghdad, assemblage A.

Description: The best preserved specimen is an incomplete ventral valve, subrectangular in outline, the preserved part being ca. 21 mm wide and ca. 16 mm long, showing fine concentric rugae (ca. 6 per 5 mm) and geniculation covered with striae. The other fragments show coarser rugae, ca. 3-4 per 5 mm and radial striae, ca. 2 per mm; the geniculation is always without rugae.

Remarks: These generically unidentifiable fragments (possibly representing more than one species) are reported to document the presence of strophomenides in assemblage A.

Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order Pentamerida Schuchert & Cooper, 1931
Suborder Pentameridina Schuchert & Cooper, 1931
Superfamily Gypiduloidea Schuchert *in* Schuchert & LeVene, 1929
Family Gypidulidae Schuchert *in* Schuchert & LeVene, 1929
Subfamily Gypidulinae Schuchert *in* Schuchert & LeVene, 1929

Remarks: The authorship of the subfamily Gypidulinae and of the coordinated name of the family is usually (e.g., Blodgett et al. 2002) credited to Schuchert & LeVene (1929). Following Bassett (1976), it is attributed to Schuchert alone.

Genus *Sieberella* Œhlert, 1887

Type species: *Pentamerus sieberi* von Buch in Barrande, 1847; Barrandian, Bohemia; Early Devonian.

Sieberella? sp.
Fig. 2J-L

Material: 64 specimens in total, mostly incomplete or fragmentary ventral valves (ZPAL Bp 80/ATH-f-36, AB-h-36) and single fragmentary dorsal valve (ZPAL Bp 80/AB-g-36); all from Hamar Laghdad, assemblage A.

Description: Ventral valves thick, probably about as long as wide, usually 25-30 mm wide, with a massive umbo and a strongly incurved beak. A flattened fold bordered by subvertical flanks begins at about 2/5 of the valve length. Dorsal valve moderately convex, subtriangular in anterior profile, with a shallow flat-bottomed sulcus beginning at mid-length. Costae acute, separated by V-shaped furrows, 3-5 on the fold, at least 3 per flank, visible on the entire fold and sulcus, and on the anterior third to two thirds of lateral flanks. Ventral interior: spondylium present; dorsal interior unknown.

Remarks: The distinction between *Gypidula* and *Sieberella* is based on the inner hinge plates being discrete or united, respectively (Blodgett et al. 2002). However, strong costation is characteristic for *Sieberella*, so this genus name has been used tentatively. Markedly and weakly costate individuals are considered as belonging to a single species; a similar variation was described in the Devonian pentameride *Gypidulina optata* (Barrande, 1847) by Havlíček (1985, p. 299).

Gypidulidae gen. et sp. indet.
Fig. 2A-B

Material: A single incomplete articulated shell (ventral beak lacking; ZPAL Bp 80/AB-e-18) from Hamar Laghdad, assemblage A.

Description: Shell pentagonal in outline, 15.3 mm wide, ca. 14 mm long, and 9.8 mm thick, weakly ventribiconvex, maximum width slightly anteriorly to mid-length. Dorsal valve subtriangular, ventral valve parabolic in anterior profile. Ventral umbo long, beak not preserved. No fold; a flat-bottomed sulcus developed only in the proximity of the anterior commissure. Anterior commissure unisulcate, tongue subtrapezoidal, 7.5 mm wide and 3.4 mm high. Shell smooth. Interior unknown.

Remarks: This brachiopod is included into the order Pentamerida on account of the inverse sulcation. In external form, it is quite similar to the Silurian *Ascanigypa ascania* Barrande, 1879 or the Devonian (?) *Wyella uralica* (Tschernyschew, 1893) (see Blodgett et al. 2002, text-figs. 681.3, 689.2). It differs from *Sieberella*? sp. in the absence of a fold and costation and from Pentamerida? fam., gen. et sp. indet. described below in the sulcation of the commissure.

Family unknown
Pentamerida? fam., gen. et sp. indet.
Fig. 2E-I

Material: Two articulated shells, one complete (ZPAL Bp 80/AB-h-23), one incomplete ZPAL Bp 80/ATH-f-23) and one ventral valve (ZPAL Bp 80/ATH-w-23); all from Hamar Laghdad, assemblage A.

Description: Shell elliptic in outline, wider than long (width-to-length ratio ca. 1.2), weakly to markedly ventribiconvex, maximum width at about mid-length. Dimensions of the two specimens in mm: width 22.2 and 28.2, length 18.7 and ca. 23, thickness 13.5 and ca. 17. Umbones thick, beaks strongly incurved. Anterior commissure straight, with a few low and rounded zigzags. Growth lines, where preserved, relatively strong, sometimes having appearances of rugae. Shells otherwise smooth, except for about six low undulations visible in the median part of the immediate proximity of the anterior commissure on the smaller shell (anterior region crushed in the larger shell).

The exfoliated smaller shell shows the presence of both a dorsal and a ventral median septum; otherwise interior unknown.

Remarks: The available material is insufficient for serial sectioning. The studied brachiopods are tentatively assigned to the pentamerides on the basis of external characters (very thick umbones covering the palintrope).

Order Rhynchonellida Kuhn, 1949
Superfamily Rhynchotrematoidea Schuchert, 1913
Family Trigonirhynchiidae Schmidt, 1965

Remarks: The authorship of this family was discussed by Brice et al. (2011, p. 77).

Genus *Stenorhynchia* Brice, 1981

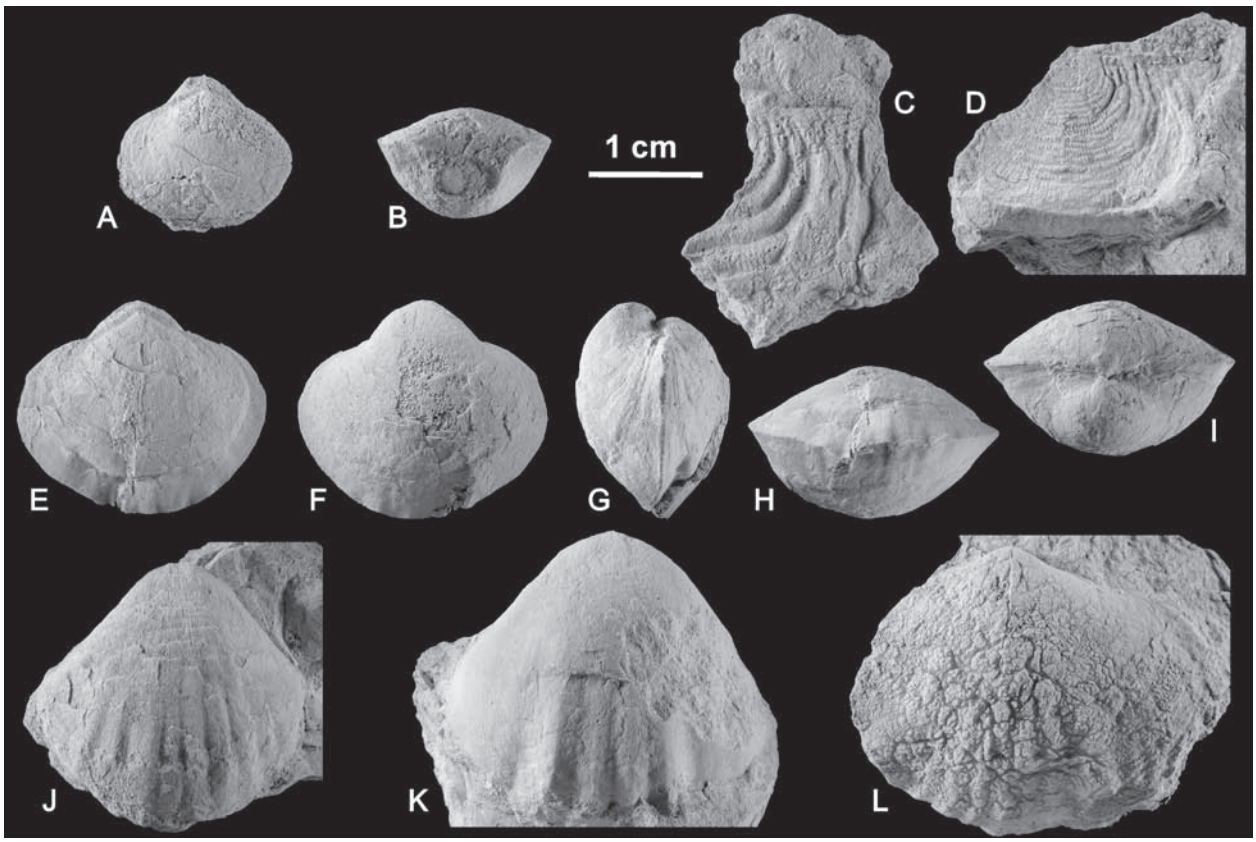

Fig. 2. Strophomenida and Pentamerida from the assemblage A. **A-B** – Gypidulidae gen. et sp. indet., incomplete articulated shell in dorsal, ventral and anterior views. **C-D** – Leptaeninae gen. et sp. indet. (assemblage A), incomplete ventral valve ZPAL Bp 80/ATH-f-35 and fragmentary dorsal valve ZPAL Bp 80/AB-e-35/1. **E-I** – Pentamerida? fam., gen. et sp. indet. articulated shell ZPAL Bp 80/AB-h-23/1 in dorsal, ventral, lateral, anterior and posterior views. **J-L** – *Sieberella*? sp., two ventral valves and one dorsal valve.

Type species: *Terebratula nympha* Barrande, 1847; Koněprusy, Barrandian, Bohemia; Koněprusy Limestone, Pragian.

Remarks: The genus *Stenorhynchia* is understood here broadly, following Brice (1981), Havlíček (1992) and Brice et al. (2011) but contrary to Sartenaer (2009, 2010; splitting of *Stenorhynchia* is rejected for reasons analogous to those given by Talent & Gratsianova 1991 in their discussion of Sartenaer's taxonomy).

Stenorhynchia ulrici Halamski & Baliński, n. sp.
Fig. 3K-DD, Fig. 4

1944 *Camarotoechia nympha*. – Le Maître, p. 47-48, pl. 6, figs. 25, 26.
1950 *Camarotoechia nympha*. – Termier & Termier, pl. 98, figs. 4-11.
1952 *Camarotoechia nympha*. – Le Maître, p. 112, pl. 21, figs. 40, 41.
2011 *Stenorhynchia briceae*. – Brice et al., p. 77-79; figs. 2-5.

Etymology: In honour of Dr. Ulrich Jansen (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany), in recognition of his contribution to the knowledge of Early Devonian brachiopods (Christian name latinised as *Ulricus*, genitive *Ulrici*, apposition).

Type locality: Small wadi dissecting the plateau of Hamar Laghdad hills NW from the Mound 50 *sensu* Berkowski (2006), 31. 3824° N, 4.0374° W; eastern-Anti-Atlas, Morocco.

Type horizon: Limestones (intermound facies) of the Kess-Kess Formation; probably *Polygnathus inversus* Zone, early Dalejan (late Emsian, Early Devonian).

Type material: Holotype (subcomplete articulated shell; ZPAL Bp 80/AB-e-24/4, figured in Fig. 3Z-AA); paratypes: nine articulated shells (four adult subcomplete, one juvenile,

Table 1. Comparison of biometric characters useful for distinguishing the species of *Stenorhynchia*.

Taxon	Stratigraphy	Adult shell width	Width index	Sulcus index	Source
S. nympha	Pragian, Koněprusy Limestone, Prague Basin (Bohemia)	10.6-17.2	1.02-1.25	0.70-0.81	Havlíček (1992)
S. ida	Pragian, Vinařice Limestone, Prague Basin (Bohemia)	9.8-18.3	1.07-1.40	0.63-0.71	
S. hetaera	Pragian, Koněprusy Limestone, Prague Basin (Bohemia)	6.4-11.0	1.04-1.18	0.76-0.81	
S. fryne		16.0-22.5	1.08-1.34	0.72-0.87	
S. pseudolivonica		16.0-22.5	1.15-1.36	?	
S. briceae (type sample)	early-late Emsian boundary, Asturias (Spain)	12.0-17.8	1.00-1.33	0.60-0.65	Truyols-Massoni & García-Alcalde (1994)
S. briceae (*S. nympha* sensu Brice 1981)	Emsian, Lézais, Brittany (France)	13.3	1.06	?	Brice (1981)
S. ulrici (*S. briceae* sensu Brice et al. 2011)	Emsian, Ougarta (Algeria) and Haci Remlia (Morocco)	14.8-18.3	1.20-1.41	0.65-0.71	Brice et al. (2001)
S. ulrici	early late Emsian, Hamar Laghdad (Morocco)	16.3-19.3	1.13-1.41	0.53-0.69	this work

two serially sectioned) and eight fragmentary ones (ZPAL Bp 80/AB-e-24); all from Hamar Laghdad, assemblage A.

Diagnosis: *Stenorhynchia* with large and transverse shell, flat-bottomed and relatively narrow sulcus, and rather low and weakly zigzagging tongue.

Description: Shell rounded pentagonal in outline, wider than long (width-to-length ratio 1.13-1.41, usually about 1.3), maximum width about mid-length, markedly dorsibiconvex. Usually 15-18 mm wide, maximum recorded width 19.3 mm, but an incomplete specimen has a reconstructed width of ca. 24 mm. Shoulder angle ca. 120°. Ventral umbo relatively fine, beak incurved. Fold and sulcus visible from the posterior third of the length; fold distinct, flatly rounded; sulcus flat-bottomed. Anterior commissure plicate, tongue subrectangular, occupying 0.53-0.69 of the shell width, high. Ornamentation of rounded (yet relatively high) costae separated by furrows of approximately the same width as the costae; costae arising from the umbonal region, 6-7 on the fold, 5-6 in the sulcus, sometimes 1 on the fold flank (parietal costa); costae on the lateral flanks similar in strength to those on the fold, becoming very thin near cardinal extremities, the latter seldom preserved, so the total number of lateral costae difficult to estimate, but 11 per flank in a single well-preserved specimen.

Dorsal interior: crural plates forming a deep, Y-shaped septalium; outer hinge plates horizontal, extending anteriorly beyond the septalium; crural bases with distinct ridges extending ventro-medially and hanging above septalium; crura rather short, slightly divergent and sharply bent ventrally, in cross-section proximally subtriangular and distally concave towards the front of the shell; sockets rather small, bordered by well marked socket ridges; median septum slender, thinning considerably anteriorly, high, reaching about 0.32-0.37 of the valve length. Ventral interior: dental plates rather slender, distinct, sub-parallel to slightly divergent ventrally; umbonal chambers distinct.

Remarks: This rhynchonellide is included in the family Trigonirhynchiidae on account of the shell outline, presence of a septalium, and absence of a cardinal process. The apparently uncovered septalium seems to point towards the subfamily Hemitoechiinae Savage, 1996 with the Ludlowian to Lochkovian genus *Hemitoechia* Nikiforova, 1970 possessing a long dorsal septum, a long septalium, and strong dental plates (Savage 1996) like in the described material. It is probable, however, that the uncovered septalium in two of our sectioned specimens may represent a preservational artefact. Similar coeval and slightly older representatives of the same subfamily include *Browneella*, *Losvia*, *Luterella*, *Nymphorhynchia*, and *Yanetoechia*. In *Browneella* Chatterton, 1973 (type species *B. browneae* from late Emsian or early Eifelian strata of New South Wales), the dorsal median septum is weak and the septalium short (Chatterton 1973; Savage 1996). In the Emsian *Losvia* Breivel & Breivel, 1976, the tongue is low to absent, the dental plates are thin and situated closely to the valve wall (Savage 1996); the latter is true for *Nymphorhynchia* Rzhonsnitskaia, 1956 (Savage 1996). In the late Silurian *Luterella*, the dorsal median septum is short (type species *L. altisulcata* Amsden, 1951 from the Ludlow–Pridoli Henryhouse Fm. of the Arbuckle Mts.; Amsden 1951, p. 86; Amsden & Barrick 1988, p. 20; Savage 1996, p. 1070). In the Emsian *Yanetoechia* Baranov, 1980, the dental plates

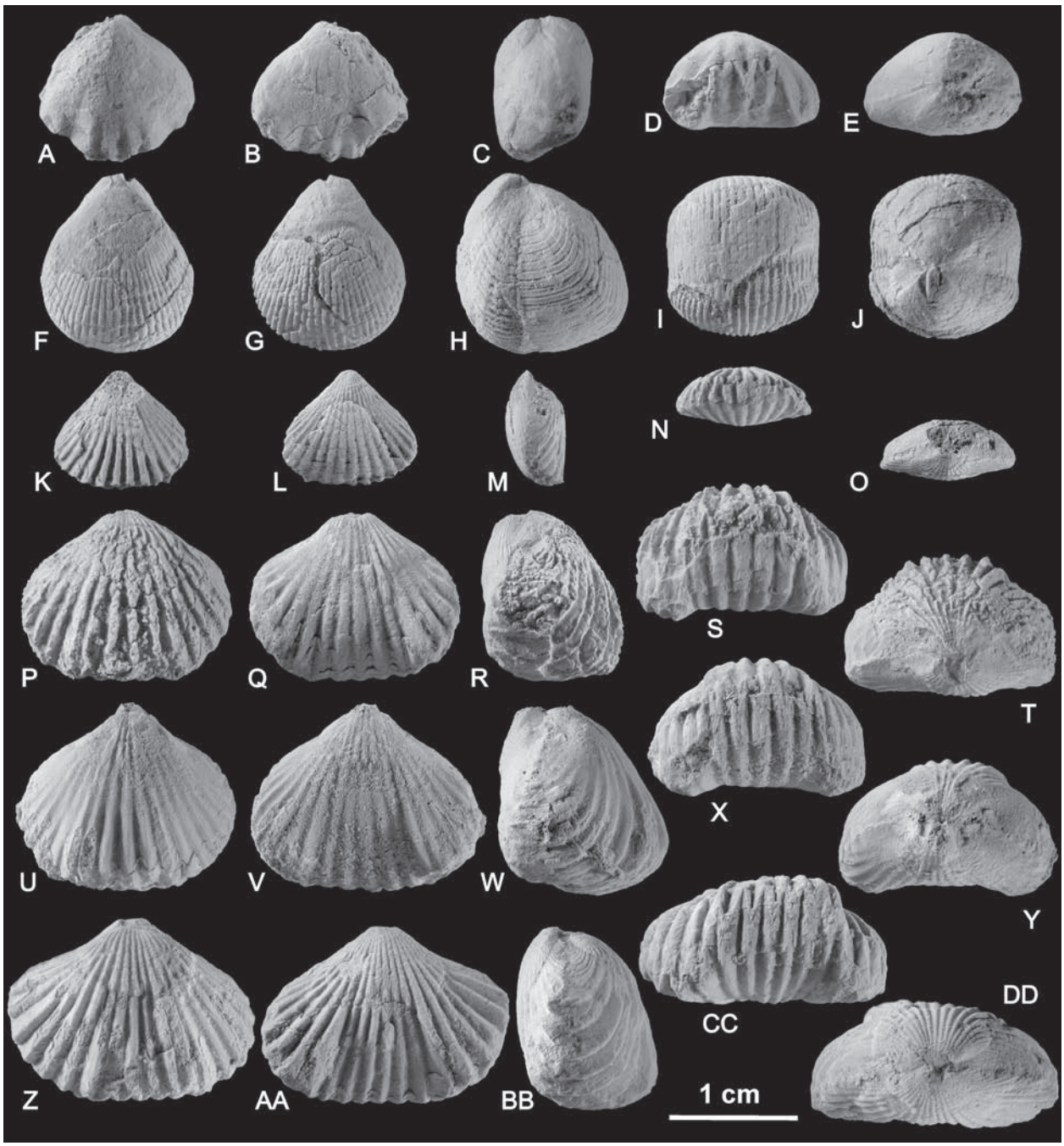

Fig. 3. Rhynchonellida from the assemblage A. Articulated shells in dorsal, ventral, lateral, anterior and posterior views. **A-E** – Rhynchonellida fam., gen. et sp. indet., ZPAL Bp 80/AB-h-37. **F-J** – *Eoglossinotoechia marocanensis* Drot, 1964, ZPAL Bp 80/ATH-v-16. **K-DD** – *Stenorhynchia ulrici* n. sp. K-O. ZPAL Bp 80/AB-e-24/5 (juvenile shell, paratype). P-T. ZPAL Bp 80/AB-e-24/6 (adult shell, paratype). U-Y. ZPAL Bp 80/AB-e-24/3 (adult shell, paratype). Z-DD. ZPAL Bp 80/AB-e-24/4 (adult shell, holotype).

are mostly fused to the valve wall and the dorsal median septum is absent. The placement of the described material within any of the above-mentioned genera does not appear satisfactory, wherefore the present authors consider that the lack of a septalium cover is a preservation artefact (distinct ridges above crural bases and hanging above the septalium might suggest a broken connectivum), all the more that the agreement of external and internal characters (except that

one) with Ludlowian to Emsian *Stenorhynchia* Brice, 1981 is nearly perfect (stratigraphic range after Savage 1996). A similar situation is apparently described by Latz (1992, p. 162) when describing the serial sections of her material of *S. nympha* from the Carnic Alps: "the opening of the septalium is somewhat covered by short processes from anterior ends of the cardinal plates". Unfortunately, drawings of the corresponding sections were not provided by Latz (1992).

The comparison of *Stenorhynchia* species from the Pragian and Emsian of Bohemia, Brittany, Asturias, and northern Africa is based largely on a few biometrical characters (Table 1). The presence or absence of septalium cover (connectivum) judged diagnostic by Truyols-Massoni & García-Alcalde (1994) cannot in fact be reliably estimated given the preservation (see above).

Specimens of *Stenorhynchia* from Hamar Laghdad are characterised by a relatively large size (shell width up to 19.3 mm in a small collection, when compared to maximum shell width of *S. nympha*, 17.2 mm, observed in a sample of about 300 specimens; Havlíček 1992), transverse shape (width index up to 1.41), and a relatively narrow sulcus (sulcus index up to 0.69, always over 0.7 in *S. nympha*, *S. hetaera*, and *S. fryne*). *Stenorhynchia ida* described by Havlíček (1992) from the Pragian Vinařice Limestone is quite similar in biometric characters, but possesses a longer ventral umbo with concave postero-lateral margins. *Stenorhynchia fryne* from the Pragian Koněprusy Limestone is similar in general shape, but has a higher tongue with sharper and strongly zigzagging margin. As a consequence, the material of *Stenorhynchia* from Hamar Laghdad is described herein as a new species. One may note, however, that this conclusion is based on the taxonomic treatment of Pragian species of *Stenorhynchia* by Havlíček (1992) who distinguished four species within a single lithological unit, the Koněprusy Limestone. It is not excluded that a critical reassessment of the Pragian representatives of the discussed genus may lead to a lumping of the possibly over-split genus and, in turn, to modifications in the systematics of Emsian species. Nonetheless, in the present state of knowledge, *Stenorhynchia ulrici* cannot be included in any species described heretofore.

Stenorhynchia from Ougarta and Hassi Remlia was identified by Brice et al. (2011) as *S. briceae*, but the reasons for that are unclear, especially given the marked shape difference between North African and Spanish samples (see Table 1 herein and comparison of width indices given by Brice et al. 2004, p. 79) summarised in the following comment "In spite of several differences, the specimens from Ougarta are assigned to *S. briceae*." One might suppose that the stratigraphic position of the described material (Emsian) was the reason why the name of an Emsian species was preferred over all the Pragian ones. In the view of the present authors, *Stenorhynchia briceae* (Asturias and Brittany) is very different from all the representatives of this genus from northern Africa: the former are weakly transverse (width index usually about 1.1) and with maximum width located anteriorly, whereas the latter are more transverse (width index usually about 1.3) and with maximum width located in the median third of the length.

Occurrence: Emsian, northern Africa.

Superfamily Uncinuloidea Rzhonsnitskaia, 1956
Family Glossinotoechiidae Havlíček, 1992
Genus *Eoglossinotoechia* Havlíček, 1959

Type species: *Eoglossinotoechia cacuminata* Havlíček, 1959; Dvorce, Bohemia; Pridoli.

Eoglossinotoechia marocanensis Drot, 1964
Fig. 3F-J

*1964 *Eoglossinotoechia sylphidea marocanensis* Drot, p. 135-138, pl. 16, figs. 8-10, text-figs. 58-60 [*ubi syn.*].
1992 *Eoglossinotoechia marocanensis.* – Havlíček, p. 98, pl. 6, fig. 9.

Material: Four articulated shells, one subcomplete (posterior part exfoliated), three other incomplete (ZPAL Bp 80/AB-e-16, ATH-s.n.-16) and one juvenile shell identified tentatively (ZPAL Bp 80/AB-g-19); all from Hamar Laghdad, assemblage A.

Description: Shell drop-shaped in outline, maximal width at anterior third of the length (dimensions of the complete shell: length 13.8 mm, width 11.9 mm, thickness 13.0 mm), markedly dorsibiconvex. Ventral valve moderately convex, umbo rather long, beak strongly incurved. Dorsal valve high, with vertical lateral flanks and moderately convex median region. Fold and sulcus absent. Anterior commissure uniplicate; tongue ca. 4 mm wide and ca. 2 mm high, irregular in shape and asymmetric. Ornamentation of ca. 40 flattened costae visible on the entire not exfoliated anterior half of the shell; costae separated by sublinear furrows and medially grooved on the paries geniculatus. Internal features revealed on exfoliated posterior part of the shell: dorsal median septum; dental plates.

Remarks: Despite internal characters being only partially known, the studied brachiopods may be identified at species level thanks to the very characteristic external form and ornamentation.

Occurrence: The type material of *Eoglossinotoechia marocanensis* is from outcrop i 867 sensu Drot (1964) [=AT 78 sensu Hollard unpubl.] situated in the western part of the Dra Plains (sheet Agadir-Tissint, SE from Jbel Hamsaïlikh; Drot 1964, p. 227). Two other specimens figured in the original publication come from localities AT 81 (very close to AT 78) and AT 91 (S from Iriqui). The specimen from AT 91 is identified with a quotation mark in the legend of the plate, but in the main text all the material from AT 91 is assigned to the discussed subspecies without further distinctions. The stratigraphic assignment of the type stratum according to Drot (1964) is "Tindouf Basin, upper Emsian with *Acrospirifer arduennensis*" [= Mdâour-el-Kbîr Formation]. It may be mentioned that Jansen (2001, pp. 224, 248) rejected Drot's identification of *Arduspirifer arduennensis arduennensis* and assigned her material to *Arduspirifer* cf. *mosellanus steiningeri* (Solle, 1953).

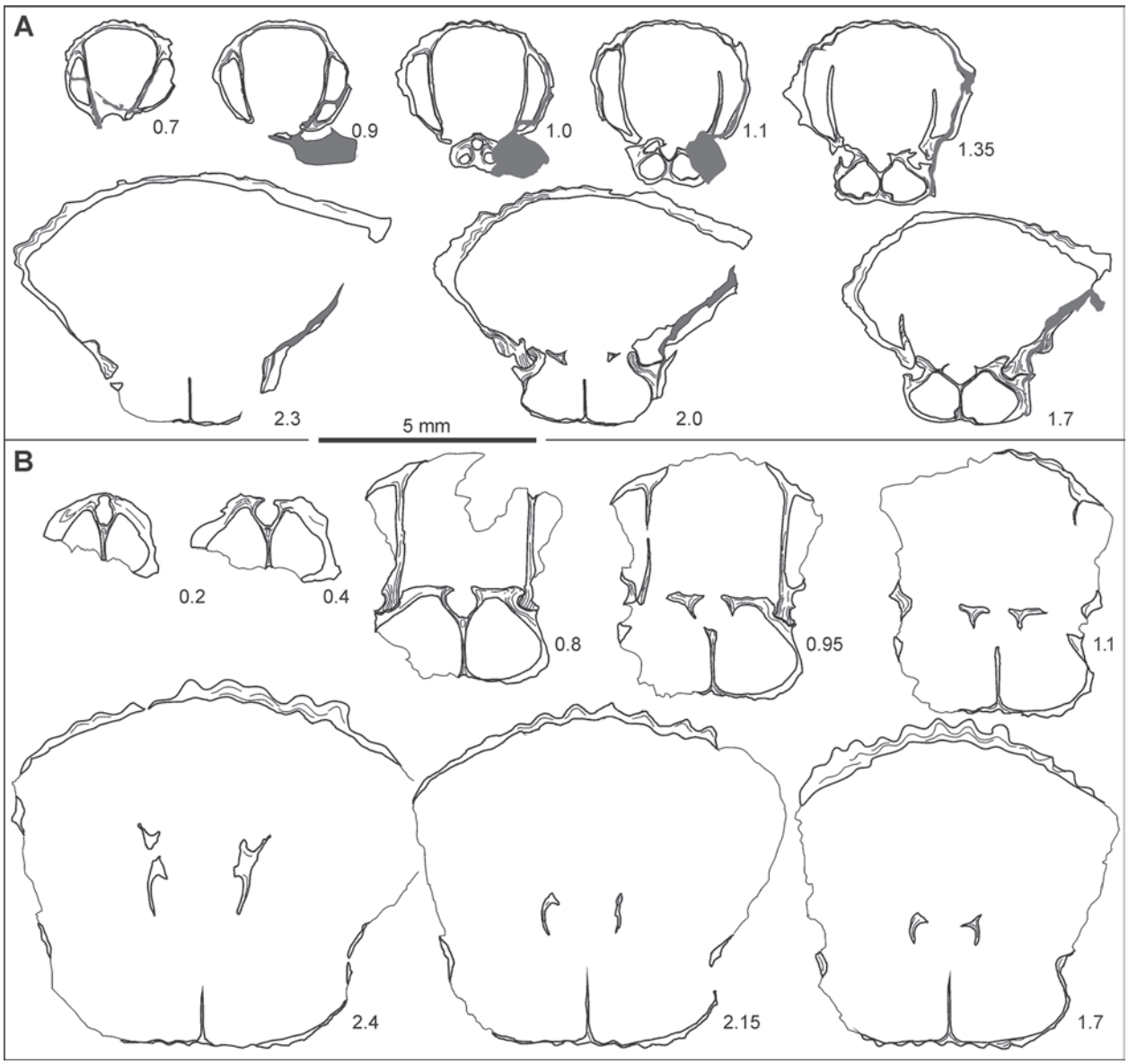

Fig. 4. Transverse serial sections of *Stenorhynchia ulrici* n. sp. (Barrande, 1847) through the shells ZPAL Bp 80/AB-e-24/1,2 (assemblage A). Greyed areas denote recrystallisation. Distances measured in millimetres from the tip of the ventral umbo.

Besides from the type locality, *Eoglossinotoechia marocanensis* was reported from several other Moroccan localities (Tarfaya province; Coude du Dra sheet; and Maïder, locality TM22 located north of Oufatène Srhir; Drot 1964); Hamar Laghdad, assemblage A; Prague Basin, Chýnice Limestone (late Zlichovian; Havlíček 1992).

Family and genus unknown
Rhynchonellida fam., gen. et sp. indet.
Fig. 3A-E

Material: Two articulated shells, one incomplete adult (ZPAL Bp 80/AB-h-37) and one juvenile shell (ZPAL Bp 80/AB-e-37); all from Hamar Laghdad, assemblage A.

Description: Shell pentagonal in outline, the adult one 12.3 mm wide, ca. 11 mm long, and 8.1 mm thick, maximum width near the anterior fourth of the length, markedly dorsibiconvex, shoulder angle ca. 100°. Umbones incompletely preserved. Fold flat, sulcus flat-bottomed, both visible only in the anterior half. Anterior commissure trapezoidal, sulcus ca. 9 mm wide, and ca. 6 mm high. Ornamentation of acute

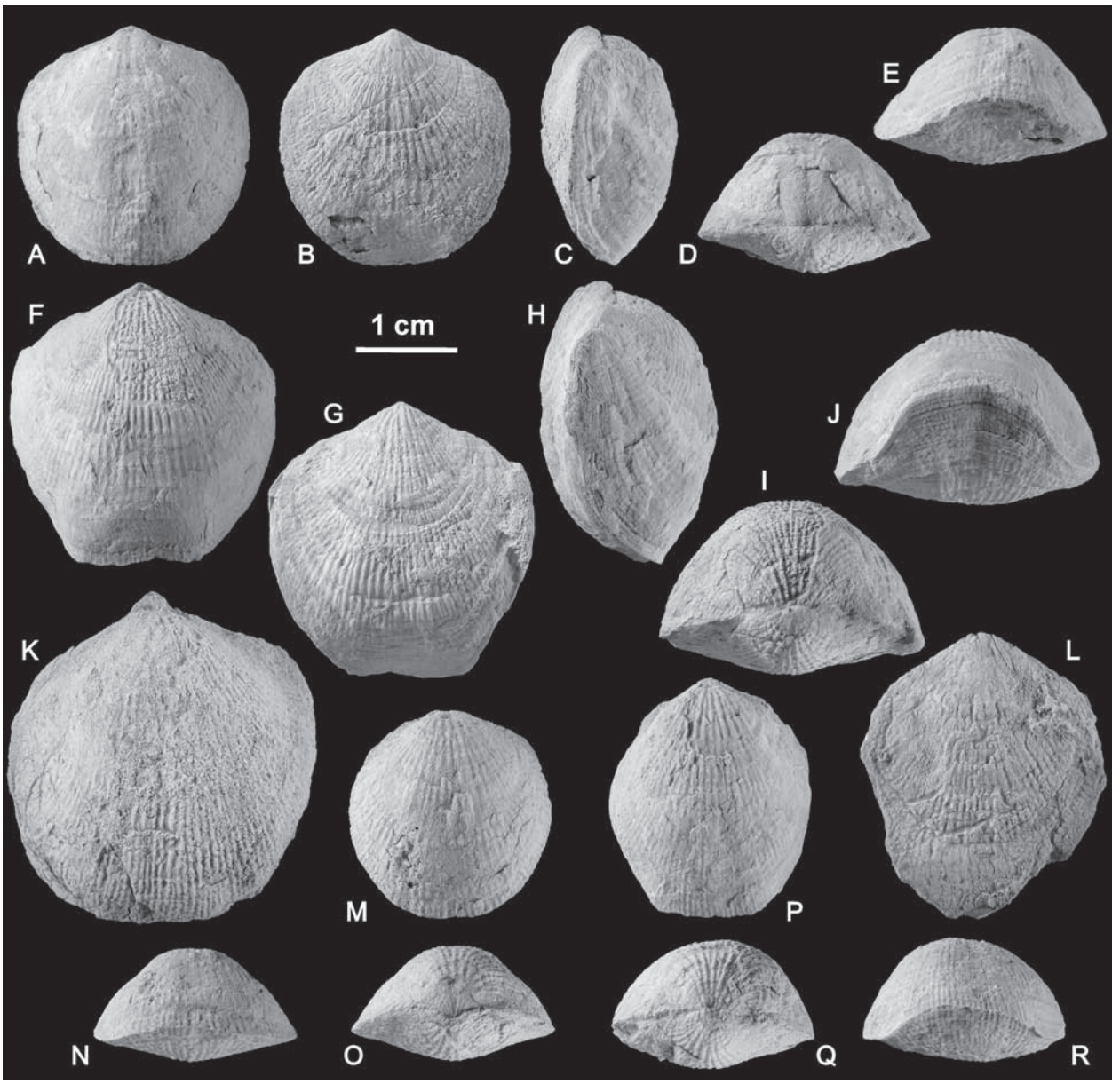

Fig. 5. *Kyrtatrypa* cf. *balda* Havlíček, 1987, the dominant species in the assemblage A. **A-E, F-J** – Articulated shells ZPAL Bp 80/AB-e-15/3, 4 in dorsal, ventral, lateral, posterior and anterior views. **K** – The largest articulated shell found ZPAL Bp 80/AB-e-15/6 in dorsal view. **L** – Subcomplete articulated shell ZPAL Bp 80/AB-e-15/5 with preserved frills (ventral view). **M-O, P-R** – Two articulated shells ZPAL Bp 80/AB-e-15/6, 7 in dorsal, posterior and anterior views.

costae separated by V-shaped furrows, 4 on the fold, 3 in the sulcus, 2 on a lateral flank (the other not preserved); costae visible in the anterior half of the valves, but well developed only in the anterior fourth.

Remarks: This rhynchonellide is clearly distinct from representatives of *Hemitoechia* and *Glossinotoechia* described above mainly because of the ornamentation. The material is too scanty for serial sectioning, which precludes any identification. *Septalaria subtetragona tarfayensis* Drot, 1964 from the early Eifelian of Jeraïfa in the Tarfaya Province (Morocco) is somewhat similar in size, shape and ornamentation, but the costae are rounded and the dorsal valve is flat (Drot 1964, pl. 20, figs. 1, 4).

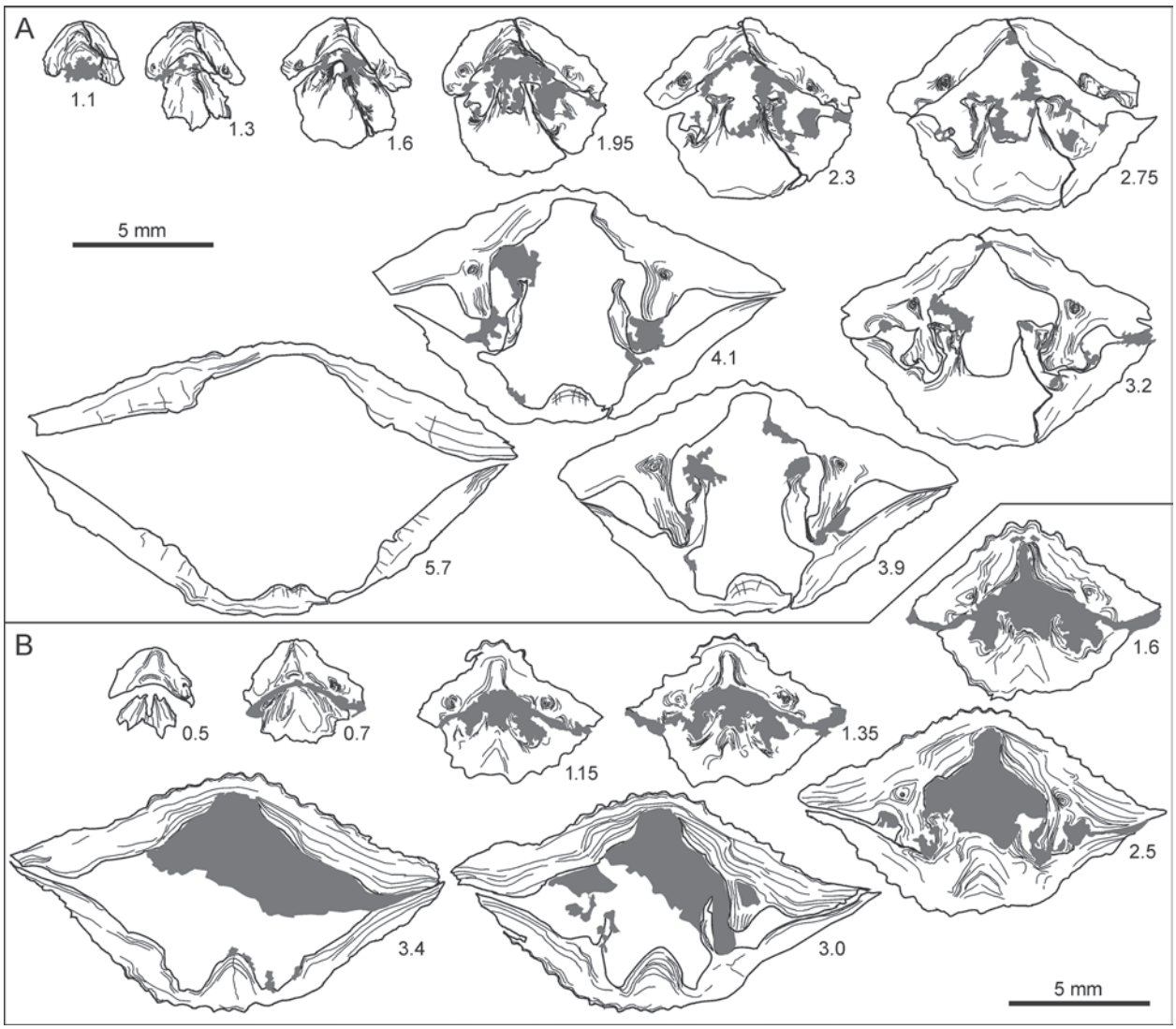

Fig. 6. Transverse serial sections of *Kyrtatrypa* cf. *balda* Havlíček, 1987 through the shells ZPAL Bp 80/AB-e-15/1,2 (assemblage A). Shaded areas denote recrystallisation. Distances measured in millimetres from the tip of the ventral umbo.

Order Atrypida Rzhonsnitskaia, 1952
Suborder Atrypidina Moore, 1952
Superfamily Atrypoidea Gill, 1871
Family Atrypidae Gill, 1871
Family Atrypinae Gill, 1871
Genus *Kyrtatrypa* Struve, 1966

Type species: *Atrypa* (*Kyrtatrypa*) *culminigera* Struve, 1966; southern Eifel; Eifelian.

Kyrtartypa cf. *balda* Havlíček, 1987
Fig. 5, Fig. 6

cf.*1987 *Kyrtatrypa balda* Havlíček, p. 67-69, pl. 3, figs. 1-5, pl. 4, figs. 2-5, pl. 5, figs. 3, 4, 7, text-fig. 2.

Material: 199 shells in total, largely complete articulated shells (two serially sectioned); inventory numbers ZPAL Bp 80/AB-e-15, AB-f-15, AB-h-15, ATH-e-15, ATH-f-15; all from Hamar Laghdad, assemblage A.

Description: Shell most often 23 to 28 mm wide (maximal recorded width 29.9 mm), about as long as wide, but in a few cases markedly longer than wide [length-to-width ratio (0.83-)0.96-1.05(-1.09), mean 0.99; *N*=30], dorsibiconvex. Ventral valve shield-shaped to rounded, weakly to moderately convex; dorsal valve most often strongly convex, parabolic in anterior view [thickness-to-width ratio (0.43-) 0.53-0.61

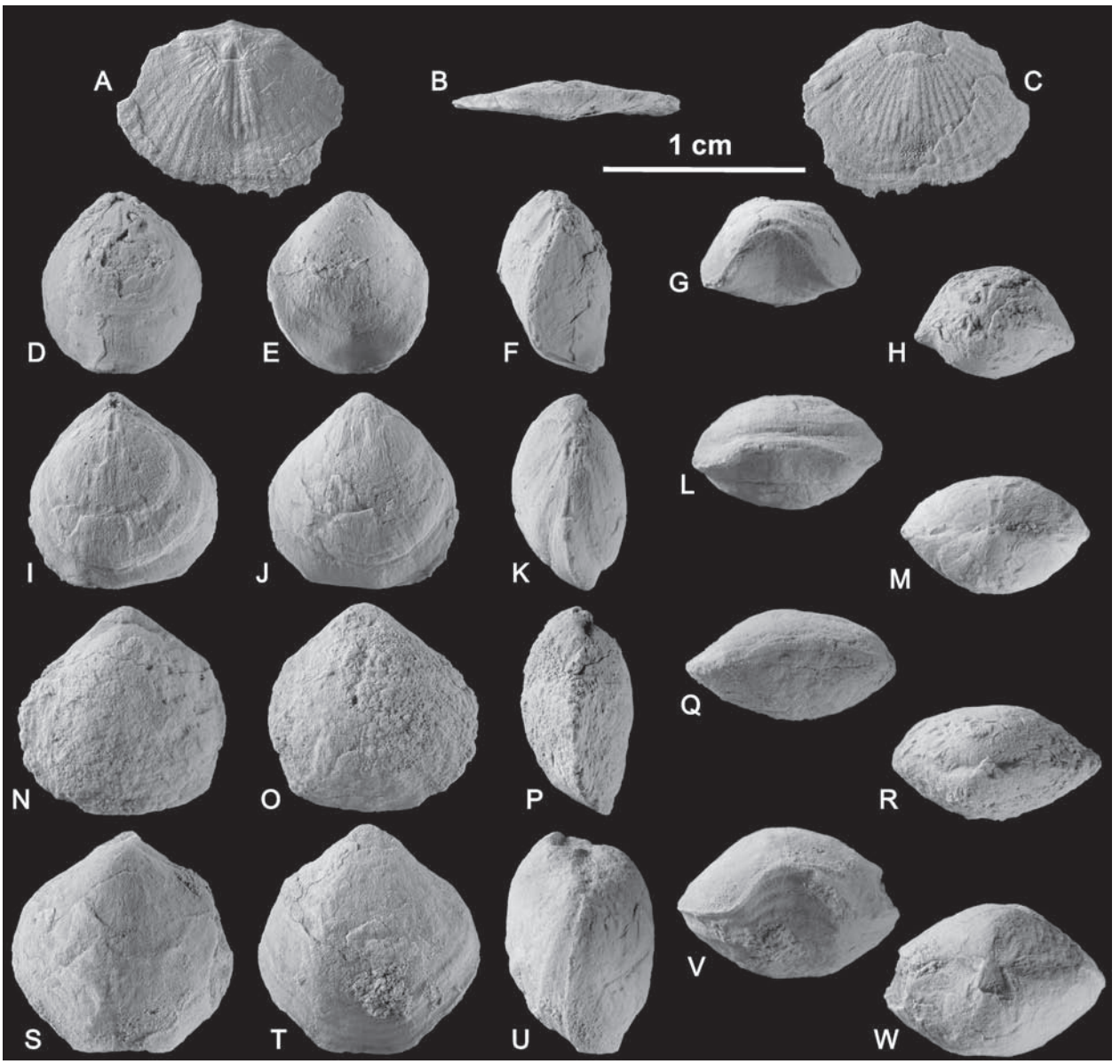

Fig. 7. Davidsoniidine and lissatrypidine atrypides from assemblage D and smooth atrypides, athyridides, and unidentified brachiopods from assemblage A. **A-C** – *Carinatina*? sp. (assemblage D), subcomplete articulated shell ZPAL Bp 80/42/M1/1 in dorsal, posterior and ventral views. **D-H** – Athyridida fam., gen. et sp. indet. (assemblage A), articulated shell ZPAL Bp 80/AB-e-19 in dorsal, ventral, lateral, anterior and posterior views. **I-M, N-R** – *Lissatrypa* sp. (assemblage A), articulated shells ZPAL Bp 80/AB-e-20/1, 2 in dorsal, ventral, lateral, anterior, and posterior views. **S-W** – Athyrididae? gen. et sp. indet. (assemblage A), articulated shell ZPAL Bp 80/AB-e-38/1 in dorsal, ventral, lateral, anterior and posterior views.

(-0.72)]. In adult shells, the ventral beak is overlapping the posterior part of the dorsal valve, the ventral interarea is not visible. Anterior commissure weakly to markedly, exceptionally strongly uniplicate. Ribs 5-7 per 5 mm both at 10 mm from umbo and at anterior commissure. Frills seldom preserved, observed length up to 6.5 mm (Fig. 5L).

Interior of ventral valve with thick pedicle layer well developed, but without pedicle collar; dental nuclei small, well-marked, without dental cavities; teeth thick, solid with lateral lobes; median groove deep, posteriorly filled up with shell material. Dorsal interior with deep sockets and distinct median socket ridges; cardinal process presumably present in cardinal pit, but poorly discernible due to the recrystallization of the interior; median septum broad and fairly long (Fig. 6A, sections at 3.9-5.7 mm; Fig. 6B, sections at 3.0-3.4 mm); spiralia and jugal processes not preserved.

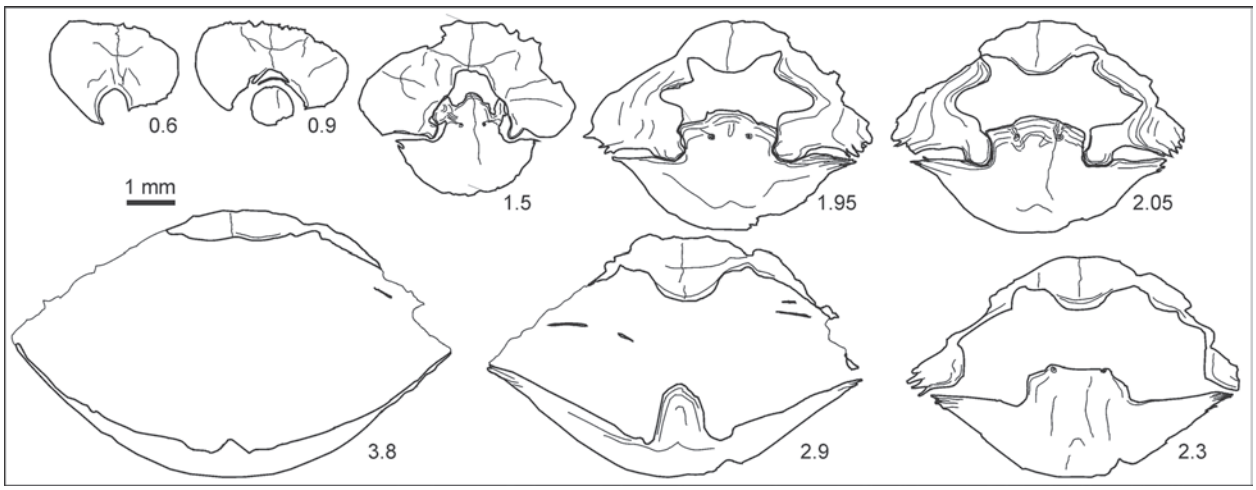

Fig. 8. Transverse serial sections of *Lissatrypa* sp. through the shell ZPAL Bp 80/AB-e-20/3 (assemblage A). Distances measured in millimetres from the tip of the ventral umbo.

Remarks: The described brachiopods are included in *Kyrtatrypa* Struve, 1966 on account of dorsibiconvex frilled shells with a uniplicate commissure, solid teeth, and presence of a thick pedicle callist (Copper 2002). The internal structures are much alike those of the Frasnian *K. teicherti* (Coleman, 1951) from Australia as illustrated by Grey (1978, text-fig. 6), especially in the form of the dorsal septum. They are similar to *K. balda* Havlíček, 1987 from the Pragian to Zlichovian (Emsian) of the Barrandian (Havlíček, 1987) in the form of the shell (width-to-length and thickness-to-width ratios) and of the beak as well as in the density of ornamentation. The only major difference is the lack of a dorsal septum in the Czech material (Havlíček 1987, text-fig. 2).
The Pragian *Kyrtatrypa canalibalda* Havlíček, 1987 from the Barrandian (reported also from the Southern Alps; Latz 1992) differs in having a dorsal groove. The late Lochkovian *K. exquisita* (Johnson, 1975) (generic attribution after Copper 1978) from Bathurst Island (arctic Canada) is more aequibiconvex and its commissure is nearly straight (Johnson 1975, p. 27; pl. 8, figs. 19-23). *K. globosa* (Barrois, 1889) from the upper 'Siegenian' to lower Emsian of Brittany (see discussion in Copper & Racheboeuf 1985, p. 78) is larger and aequibiconvex. *Kyrtatrypa* sp. from the Emsian of Queensland (Australia) has more inflated shell and possibly coarser ornamentation (Brock & Talent 1993), but scanty material and short description precludes any detailed comparison. *Atrypa nevadana* Merriam, 1940 from the Emsian *Eurekaspirifer pinyonensis* Zone of Nevada (Johnson 1970, pl. 41, figs. 5-17) is quite similar in form and ornamentation, but its interior is described in insufficient detail.

The Eifelian *Kyrtatrypa culminigera* (Struve, 1966) from the Eifel, the Givetian *Kyrtatrypa* sp. n. 2 from the Holy Cross Mts. (= *Kyrtatrypa pauli* nomen nudum sensu Halamski 2004 = *Kyrtatrypa* sp. sensu Zapalski 2005) and the Frasnian *K. barnimi* Halamski, 2013 from the Sudetes are all more aequibiconvex. The Eifelian *Kyrtatrypa* sp. n. 1 from the Holy Cross Mts. (= *Kyrtatrypa gertrudis* nomen nudum sensu Halamski 2004) is more transverse. The Frasnian *Kyrtatrypa*? *brandonensis* (Stainbrook, 1938) from Iowa has a coarser ornamentation (Stainbrook 1938, pl. 31, figs. 1, 2).

Occurrence: Hamar Laghdad, outcrop A (Emsian, possibly *inversus* Zone); *Kyrtatrypa balda* is known from the Pragian to early Emsian strata of the Barrandian.

Suborder Davidsoniidina Copper, 1996
Superfamily Davidsonioidea King, 1850
Family Carinatinidae Rzhonsnitskaia, 1960
Genus *Carinatina* Nalivkin, 1930

Type species: *Orthis arimaspus* Eichwald in von Buch, 1840; Eifelian, Urals.

Remarks: Following Cooper (2002), *Kaplicona* Havlíček, 1987 is considered a junior subjective synonym of *Carinatina*.

Carinatina? sp.
Fig. 7A-C

Material: A single incomplete articulated shell from Mound 1 (ZPAL Bp 80/42/M1/1) from Hamar Laghdad, assemblage D.

Description: The single available shell is incomplete and flattened (preserved width 11.2, preserved length 8.7 mm), presumably semi-elliptic in shape, with straight cardinal margin and lateral and anterior commissures forming a

continuous half of an ellipse. Dorsal valve with a narrow sulcus, ventral valve with a narrow fold. Ventral area ca 1.5 mm high, apsacline. Ornamentation of ca. 25 weak costae and costellae uniformly covering the entire shell surface.

Remarks: The single poorly preserved shell described herein belongs probably to the same species as a davidsoniidine, which is relatively common in the assemblages B and C. In the material representing the assemblage B and collected by the present authors, costate (= *Kaplicona* sp. sensu Mergl 2018, pl. 2, figs. 9-12; assemblage C) and smooth (= *Quasidavidsonia tenuissima* sensu Mergl 2018, pl. 2, figs. 13-14; assemblage C) shells co-occur and are otherwise undistinguishable. They might be considered as belonging to a single biological species (own, unpublished data).

Suborder Lissatrypidina Copper in Copper & Gourvennec, 1996
Superfamily Lissatrypoidea Twenhofel, 1914
Family Lissatrypidae Twenhofel, 1914
Genus *Lissatrypa* Twenhofel, 1914

Type species: *Lissatrypa atheroidea* Twenhofel, 1914; Anticosti, Canada; Llandovery.

Lissatrypa sp.
Figs. 7I-R, 8

Material: Three articulated shells (one serially sectioned) (ZPAL Bp 80/AB-e-20); all from Hamar Laghdad, assemblage A.

Description: Shell drop-shaped in outline, as wide as long, approximately aequibiconvex, rather thin (dimensions of two specimens in mm: width 10.4, 8.8; length 10.4, 8.8; thickness 5.6, 4.7). Ventral umbo relatively fine, beak suberect. Anterior commissure broadly and lowly plicate. Shell smooth with traces of growth lines in anterior region.

Internally, thick-shelled, especially posteriorly. Ventral valve with umbonal cavity infilled with thick pedicle callist; muscle scars deeply incised, divided by a thick and wide median ridge; teeth short, robust and blunt; dental cavities not developed. Dorsal interior with rather shallow sockets; posteriorly, cardinalia consist of strong socket plates and a lobate median bulge (Fig. 8, distance 1.5); anteriorly, cardinalia continue as massive, elevated hinge plate reinforced by secondary shell deposits and without a cardinal pit; the hinge plate extends anteriorly as a thick myophragm dividing paired adductor scars (Fig. 8).

Remarks: Another representative of the same genus is present in the assemblages B and C (= *Holynatrypa* sp. sensu Mergl 2018, pl. 4, figs. 1-4; assemblage C). It differs from *Lissatrypa* sp., described herein, in showing a median indentation of the anterior commissure. It does not possess a raised median septum, which is present in *Holynatrypa crucifera* Havlíček, 1973 (Havlíček 1998, Copper 2002), so in the opinion of the present authors it would be better classified as *Lissatrypa* (Halamski & Baliński, unpublished data).

Family Septatrypidae Kozłowski, 1929
Subfamily Septatrypinae Kozłowski, 1929
Genus *Septatrypa* Kozłowski, 1929

Type species: *Septatrypa secreta* Kozłowski, 1929; Podolia; Tajna beds, Lochkovian.

Septatrypa tumulorum Baliński & Halamski, n. sp.
Figs. 9-11

Etymology: Latin *tumulus* – mound, hillock; because of the occurrence in association with the mud mounds of Hamar Laghdad (*tumulorum*, genitive plural, apposition).

Type locality: Mud mound 1, Hamar Laghdad, eastern Anti-Atlas, Morocco.

Type horizon: Kess-Kess Formation, *Polygnathus inversus* Zone, early Dalejan (late Emsian, Early Devonian).

Type material: Holotype (complete articulated shell) ZPAL Bp 80/41/M1/1 from mud mound 1 (Fig. 9EE-II) and 123 mostly subcomplete articulated shells (paratypes: Mound 1 – 83 specimens, Mound 2 – 28 specimens, Mound 3 – 11 specimens, Mound 5 – 1 specimen, Mound 7 – 1 specimen, Mound 501 – 19 specimens), collection number ZPAL Bp 80/41; all from Hamar Laghdad, assemblage D.

Diagnosis: Shell medium-sized for the genus, usually 10-14 mm and up to 17.6 mm in width, dorsibiconvex; adults usually transverse in outline, rarely about as long as wide (width to length ratio 0.95 to 1.27, usually 1.1-1.2); anterior commissure uniplicate, with wide, usually rounded to sporadically trapezoidal tongue attaining up to 0.88 of the shell width.

Fig. 9. *Septatrypa tumulorum* n. sp., the monodominant species in the assemblage D; articulated shells in dorsal, ventral, lateral, anterior and posterior views. **A-E** – ZPAL Bp 80/41/M58/3 (paratype; Mound 58). **F-J** – ZPAL Bp 80/41/M58/2 (paratype; Mound 58). **K-O** – ZPAL Bp 80/41/M1/4 (paratype; Mound 1). P-T. ZPAL Bp 80/41/M1/3 (paratype; Mound 1). **U-Y** – ZPAL Bp 80/41/M58/1 (paratype; Mound 58). **Z-DD** – ZPAL Bp 80/41/M1/2 (paratype; Mound 1). **EE-II** – ZPAL Bp 80/41/M1/1 (holotype; Mound 1).

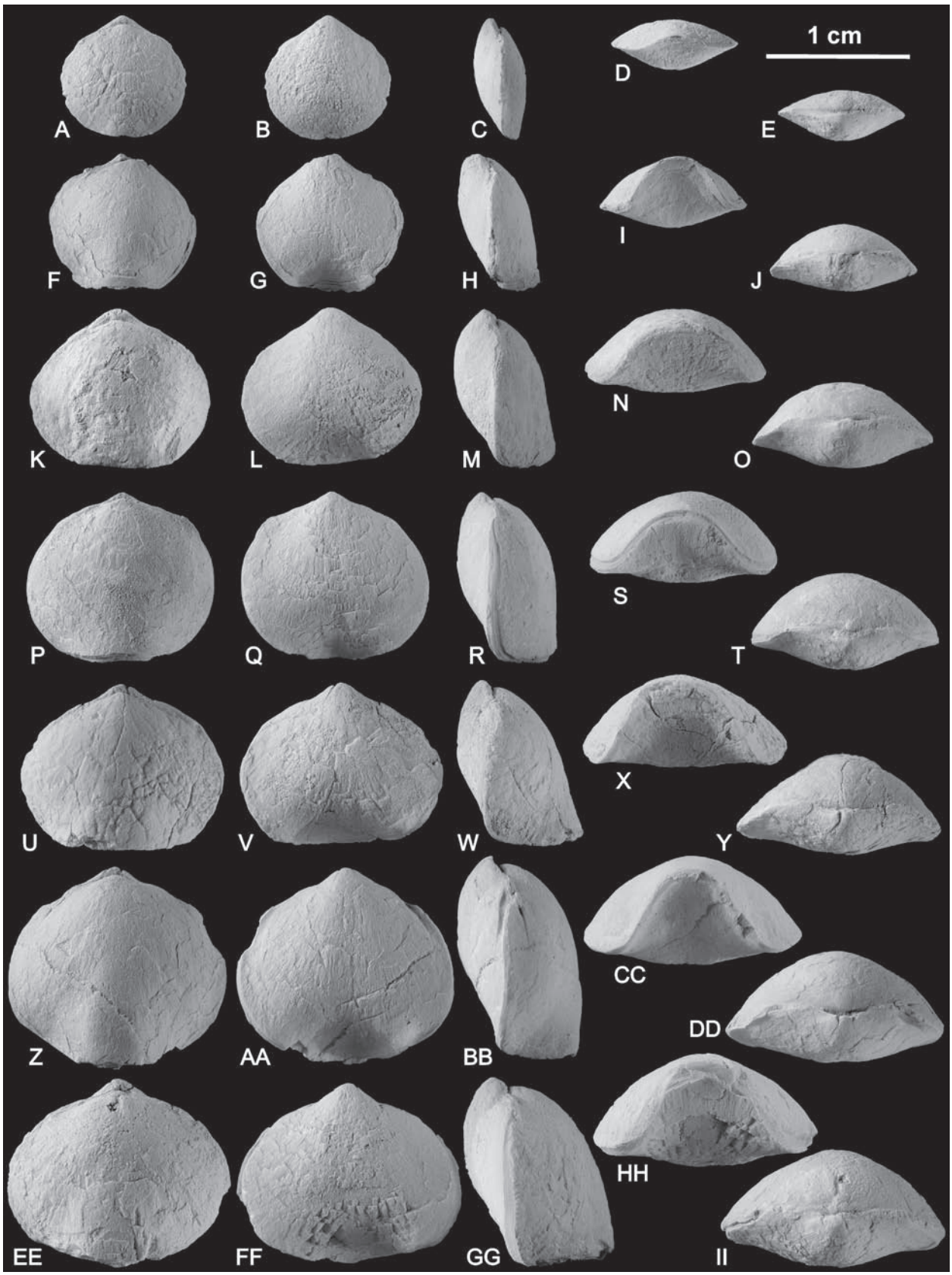

Fig. 9.

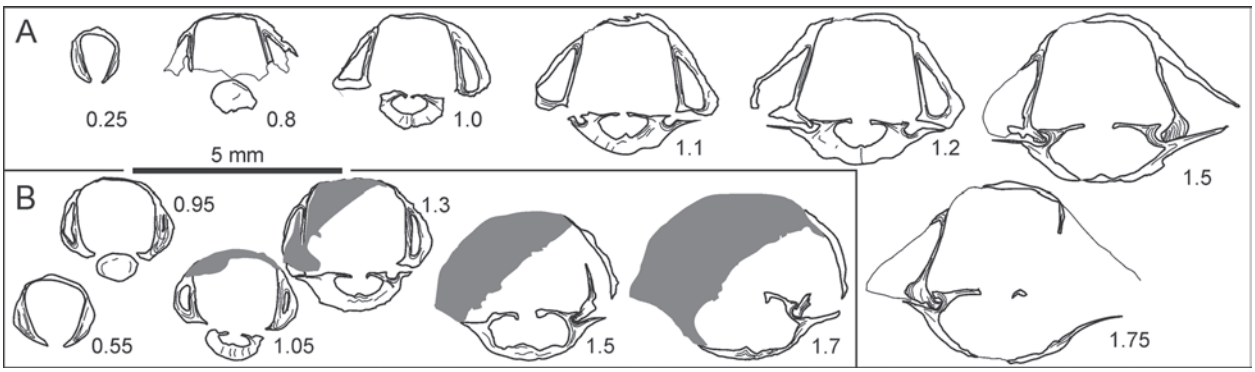

Fig. 10. Transverse serial sections of *Septatrypa tumulorum* n. sp. through the shells ZPAL Bp 80/41/M1/5, 6 (paratypes; assemblage D). Shaded areas denote recrystallisation. Distances measured in millimetres from the tip of the ventral umbo.

Description: Shell smooth, transverse, subelliptical to subpentagonal in outline, dorsibiconvex, (5.5-) 10.2-13.7 (-17.6) mm wide [mean 11.9, *N* = 54]; in adult shells (above 9 mm in length) the width-to-length ratio is (0.94-) 1.07-1.18 (-1.27) [mean 1.11, *N* = 43]. Maximal width at 3/5 to 4/5 of the length. Anterior commissure with a wide tongue occupying 0.53 to 0.88 of the shell width in adults (Figs. 9K-II, 11B). Ventral valve with a low anacline interarea and a wide, laterally rather poorly delineated sulcus that begins at about one-fourth of the valve length; flanks flattened to slightly concave; tongue rounded, more seldom trapezoidal. Dorsal valve with a poorly defined wide fold discernible anteriorly from about valve mid-length.

Interior of ventral valve with well developed, slightly ventrally convergent dental plates and wide dental cavities. Dorsal valve interior with very poorly developed median septum and thin, subhorizontal socket plates; valve thickened posteriorly (Fig. 9); other internal features not preserved, but in a few specimens plausible fragments of crushed and displaced spiral lamellae are recovered.

Growth changes. Measurements of 55 shells ranging from 6.9 to 17.6 mm in length show that younger individuals are more elongated than adults (Fig. 11A). The former generally are as wide as long until about 9 mm in shell length, whereas larger individuals become gradually more expanded transversally. The ventral sulcus appears in specimens reaching more than about 6 mm in length and with age its width gradually occupies a greater part of the shell anterior (Figs. 9, 11B).

Remarks: The degree of recrystallisation of interiors of this species was especially strong and initially, it could not be decided whether this brachiopod belongs to the rhynchonellides or to the atrypides. Confusions between *Septatrypa* and similar-looking rhynchonellides have occurred several times (see discussion by Copper 2004, p. 124) and are unavoidable without serial sectioning.

Septatrypa tumulorum appears to be most closely related with *Rhynchatrypa jesenia* Havlíček & Pek, 1986 described from the Eifelian of the Nizký Jeseník Mountains in Moravia (Havlíček & Pek 1986). According to the serial sections (Havlíček & Pek 1986, text-fig. 3) on the one hand and, on the other hand, congenerity of *Rhynchatrypa* and *Septatrypa* postulated by Copper (2002, 2004), the Moravian species is here regarded as a member of *Septatrypa*. The new species from Hamar Laghdad and *Septatrypa jesenia* share very similar general characters of shell exterior and interior. The former, however, is distinguished from the latter by generally

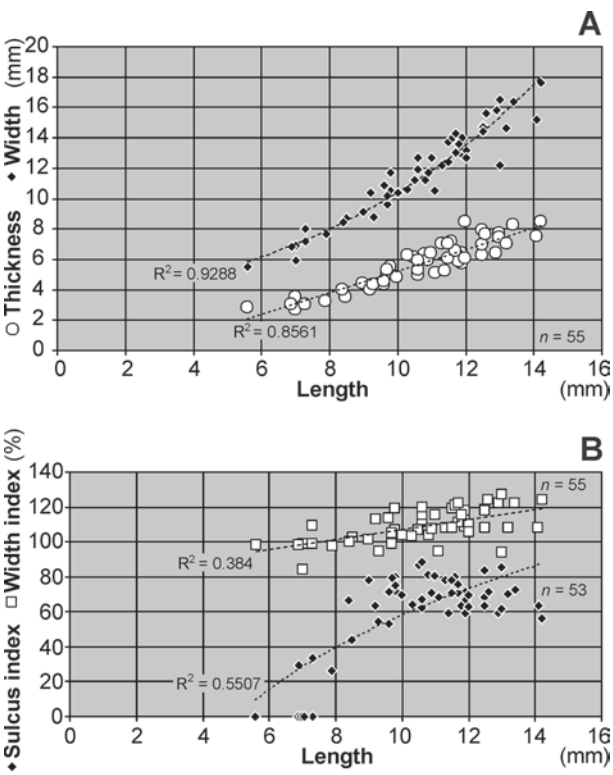

Fig. 11. *Septatrypa tumulorum* n. sp.; diagrams showing biometric characteristics of the sample. Width index = shell width/shell length; sulcus index = sulcus width/shell width.

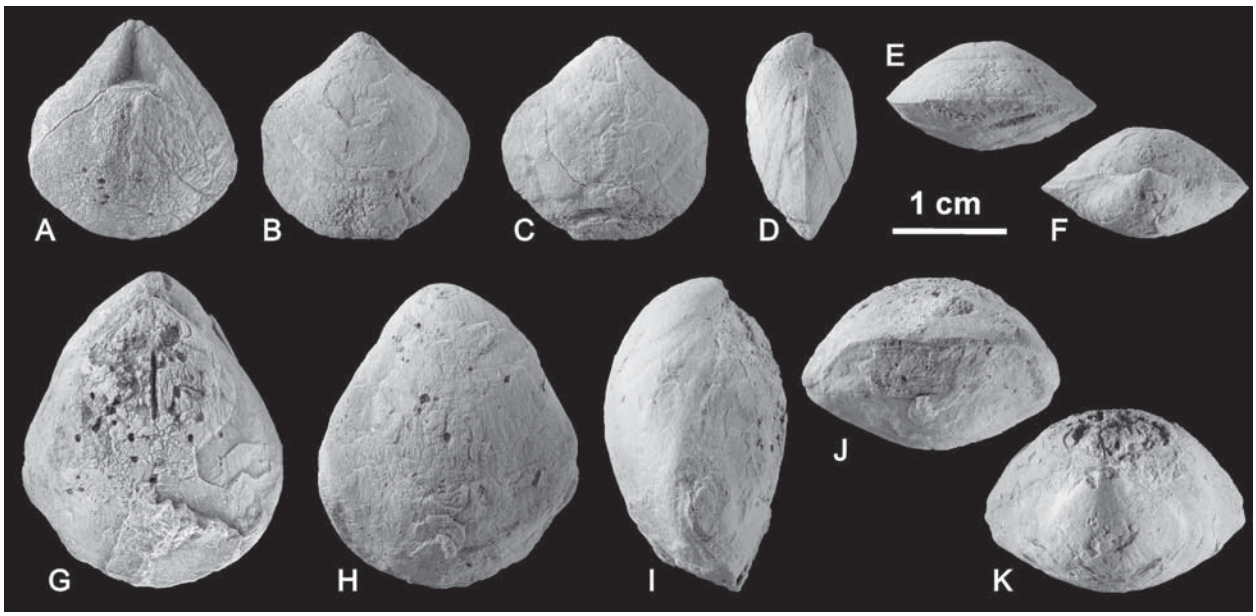

Fig. 12. Large athyridides from the assemblage A. **A-F** – *Camarium*? sp., corroded shell ZPAL Bp 80/ATH-f-14/3 showing the shoe-lifter process in dorsal view and articulated shell ZPAL Bp 80/AB-f-14/2 in dorsal, ventral, lateral, anterior, and posterior views. **G-K** – Meristellidae gen. et sp. indet., articulated shell ZPAL Bp 80/AB-e-19 in dorsal, ventral, lateral, anterior and posterior views.

slightly greater shell dimensions (*S. tumulorum* up to 17.6 mm in width; *S. jesenia* up to 13.8 mm), a more dorsibiconvex and proportionally wider shell aspect and a wider, more arched, and less angular ventral tongue.

Radimatrypa zelaria Havlíček in Havlíček & Kukal, 1990 from the Suchomasty and Acanthopyge limestones (Emsian–Eifelian) of the Barrandian area (Havlíček & Kukal 1990) is similar externally to *S. tumulorum*, but differs from the new species in having a frequently flat-bottomed, not gently concave sulcus, trapezoidal, not rounded tongue and internally in absence of dental plates. According to Copper (2002, p. 1463) the problematic genus *Radimatrypa* Havlíček in Havlíček & Kukal, 1990 is externally homoeomorphic with *Septatrypa* or *Cerasina* and absence of dental plates in the former genus should be verified.

Occurrence: Hamar Laghdad, assemblage D. This is nearly the only brachiopod species occurring in low-diversity assemblages associated with mud mounds.

Order Athyridida Boucot, Johnson & Staton, 1964
Order Athyrididina Boucot, Johnson & Staton, 1964
Superfamily Athyridoidea Davidson, 1881
Family Athyrididae Davidson, 1881
Athyrididae? gen. et sp. indet.
Fig. 7S-W

Material: Three articulated shells, two complete (ZPAL Bp 80/AB-e-38), one incomplete (ZPAL Bp 80/AB-h-38); all from Hamar Laghdad, assemblage A.

Description: Shell pentagonal in outline (the dimensions of a complete specimen in mm: length 11.0, width 10.0, thickness 8.2), weakly ventribiconvex. Both valves subtrapezoidal in anterior profile (i.e., with median regions somewhat flattened); dorsal fold and ventral sulcus nearly imperceptible; ventral umbo elongate. Anterior commissure uniplicate; tongue parabolic, occupying about half of the shell width. Shell smooth. Interior unknown.

Remarks: The tentative identification is based on external similarity with genera like *Athyris* McCoy 1844, *Bruntonites* Struve, 1992 or *Gonathyris* Baranov, 1994 (see Alvarez & Rong 2002). Late Emsian brachiopods comparable in external form to those described herein were reported under "*Athyris*" cf. *concentrica* (von Buch, 1834) from the upper part of the Moniello Formation in the Asturias, Spain (Alvarez 1990, p. 51). The late Emsian (Suchomasty Limestone) *Athyris odolens* Havlíček in Havlíček & Kukal, 1990 is larger, flatter, and has stronger growth lines.

Superfamily Meristelloidea Waagen, 1883
Family Meristidae Hall & Clarke, 1895
Genus *Camarium* Hall, 1859

Type species: *Camarium typum* Hall, 1859; Cumberland, Maryland, USA; Lower Helderberg Group, Lochkovian.

Camarium? sp.
Fig. 12A-F, Fig. 13

Material: 17 specimens, three complete, one subcomplete, the other incomplete or fragmentary (ZPAL Bp 80/AB-f-14, ATH-f-14); all from Hamar Laghdad, assemblage A.

Description: Shell subpentagonal to pentagonal in outline, about as long as wide (maximum recorded width 25.5 mm; incomplete shells suggesting width up to 30 mm), approximately aequibiconvex; maximum width situated about mid-length or more anteriorly. Beak weakly to strongly incurved; palintrope not visible. Anterior commissure rectimarginate in smaller shells, uniplicate in larger ones; tongue subtrapezoidal, occupying slightly more than half the shell width, low. Shell smooth.

Interior revealed through corroded shells and serial sections (Fig. 13); dorsal valve: septalium small, supported by thin and high median septum that extends to about mid-length of the valve; ventral valve: shoe-lifter process present; dental plates thin, subparallel posteriorly and slightly converging ventrally more anteriorly.

Remarks: The presence of a shoe-lifter process revealed both through serial sections (Fig. 13, section at 0.9-3.2 mm) and on corroded shells (Fig. 12A) allows the confident placing of the discussed brachiopods within the family Meristidae Hall & Clarke, 1895 (Alvarez & Rong 2002, p. 1570). The mystrochial plates being apparently absent, the brachiopods are included in *Camarium* Hall, 1859 (see Amsden 1968, Alvarez & Brime 2000); it cannot, however, be entirely excluded that such absence is a preservation artefact due to recrystallisation, in which case the brachiopods should be assigned to *Merista* Suess, 1851. The external form can be identical in both genera, as evidenced by *Merista herculea* (Barrande, 1847) (Alvarez & Rong 2002, fig. 1068.1) and *Camarium turgens* (Siehl, 1962) (Siehl 1962, pl. 39, fig. 9; generic attribution after Amsden, 1968, p. 89). Recently, Halamski & Baliński (2013, p. 285) pointed also to the uncertainty about internal structures of the type species of *Dicamara* Hall & Clarke, 1893 (the material hitherto sectioned is only presumably conspecific with the type species). The open nomenclature is used as a precaution.

Family Meristellidae Waagen, 1883
Meristellidae gen. et sp. indet.
Fig. 12G-K

Material: A single articulated shell (ZPAL Bp 80/AB-e-19) from Hamar Laghdad, assemblage A.

Description: Shell elongate, pentagonal, maximum width about the anterior fourth, 27.0 mm long, 22.7 mm wide, and 15.9 mm thick, weakly ventribiconvex. Anterior commissure plicate, tongue trapezoidal, ca. 20 mm wide and ca. 4 mm high. Interior: traces of a dorsal septum observed on the corroded valve; otherwise unknown.

Remarks: The family Meristellidae is composed largely of externally homoeomorphic species. This is why any identification at genus level is not attempted.

Family unknown
Athyridida fam., gen. et sp. indet.
Fig. 7D-H

Material: A single incomplete articulated shell (ventral umbo lacking) (ZPAL Bp 80/AB-e-19) from Hamar Laghdad, assemblage A.

Description: The only available shell is rounded subpentagonal in outline, 8.5 mm long, 8.0 mm wide with maximum thickness about mid-length, and 6.1 mm thick, moderately dorsibiconvex. Shell structure impunctate. Dorsal valve subtrapezoidal in anterior profile with an incipient fold in the anterior fifth. Ventral valve subtriangular in anterior profile, with a very shallow sulcus in the anterior fifth. Anterior commissure uniplicate; tongue subtrapezoidal, ca. 6 mm wide and ca. 3 mm high. Shell smooth. Interior unknown.

Remarks: The scarcity of available material precludes serial sectioning. The described brachiopod is interpreted as an athyridid on account of external form and lack of shell punctation. It differs from Athyrididae? indet. in having a much stronger tongue despite smaller dimensions.

Order Spiriferida Waagen, 1883
Suborder Delthyridina Ivanova, 1972
Superfamily Delthyridoidea Phillips, 1841
Family Hysterolitidae Termier & Termier, 1949
Genus *Brachyspirifer* Wedekind, 1926

Type species: *Brachyspirifer carinatus* Schnur, 1853 in 1853-54; Daleiden, Eifel; Wiltz Beds, early to middle part of the late Emsian.

Brachyspirifer? sp.
Fig. 14L-R

Material: 70 specimens from the assemblage A, but invariably incomplete or fragmentary; only three subcomplete valves (two ventral, one dorsal) and two incomplete juvenile articulated shells (ZPAL Bp 80/ATH-f-22). A single subcomplete adult articulated shell from outcrop A'; all from Hamar Laghdad, assemblage A.

Description: Shell up to about 50 mm in width (estimations based on the largest subcomplete specimen), transverse (width-to-length ratio ca. 1.7), biconvex; hinge line straight.

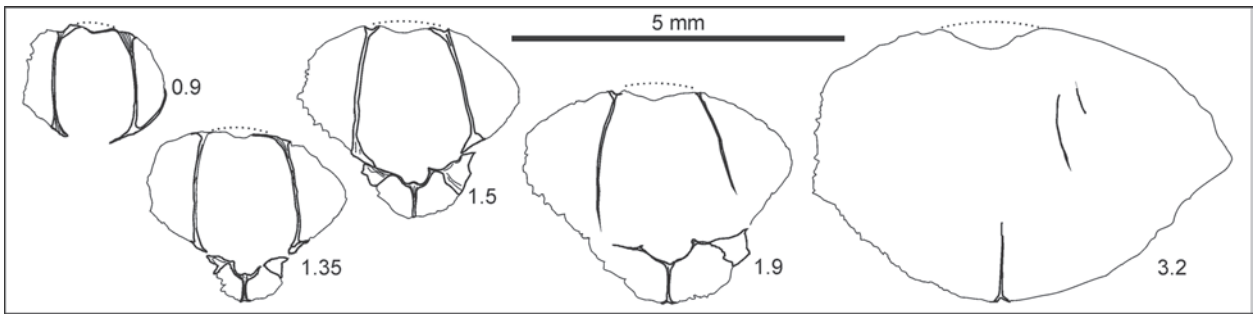

Fig. 13. Transverse serial sections of *Camarium*? sp. through the shell ZPAL Bp 80/AB-g-14/1 (assemblage A). Distances measured in millimetres from the tip of the ventral umbo.

Ventral valve with a deep, V-shaped and smooth sulcus originating at the beak, tongue low; interarea weakly apsacline (nearly catacline). Dorsal valve with an acute fold beginning at the beak and triangular in cross-section, flanks of the fold smooth. Lateral flanks with 10-12 rounded costae beginning at the beak or in immediate proximity, separated by furrows of about the same width as the costae. In a few places, dense growth lines are preserved on lateral costae.

Remarks: The identification without micro-ornamentation and interiors can be only tentative. However, the agreement of external characters (transverse, plicate shells with well-marked smooth sulcus and fold) with representatives of *Brachyspirifer* and particularly with *B. carinatus* is quite good (U. Jansen, pers. comm. 1st Feb. 2017), in spite of a slightly lower number of costae. In the type area (Rhenish Slate Mountains), *B. carinatus* is known from the middle part of the early Emsian to the middle part of the late Emsian (Solle 1971).

Superfamily Reticularioidea Waagen, 1883
Family Reticulariidae Waagen, 1883
Subfamily Reticulariopsinae Gourvennec, 1994
Genus *Reticulariopsis* Fredericks, 1916

Type species: *Spirifer* (*Reticularia*) *dereimsi* Œhlert, 1901; Santa Lucia, Spain; Emsian.

Reticulariopsis? sp.
Fig. 14A-K, Fig. 15

Material: Four complete to subcomplete articulated shells and 16 fragmentary specimens (ZPAL Bp 80/AB-e-39, AB-f-39); all from Hamar Laghdad, assemblage A.

Description: Shell medium-sized for the genus, up to 28.2 mm in width, transversely elliptical in outline with maximum width at shell mid-length or slightly posteriorly, subequally biconvex; cardinal margin attains 0.60-0.76 of the shell width, cardinal extremities rounded, anterior margin truncate to slightly emarginate, anterior commissure uniplicate. Ventral valve with suberect beak; interarea apsacline, gently concave, attaining 2.5 to 4.2 mm in height; delthyrium with an apical angle of 47-50°, occluded by a convex deltidium; lateral slopes gently convex; sulcus shallow to almost not defined, but with median longitudinal furrow starting at the umbo; tongue 2.7-5.2 mm high in the largest shells, trapezoidal, developed even in shells without a well-defined sulcus. Dorsal valve evenly convex in lateral profile; dorsal interarea poorly preserved, most probably apsacline, low; fold well defined, beginning in umbonal region, low and flat, sometimes with a weak longitudinal furrow, which is less developed than that on the ventral valve.

Shell macroscopically smooth, micro-ornamentation, if any, not preserved.

Interior of ventral valve with thick extrasinal dental plates partly buried posteriorly in thickened shell material (Fig. 15A, sections at 0.9-3.0 mm). Dorsal interior with short and low crural plates and a short, crenulated cardinal process.

Remarks: The tentative identification is based on external similarity with some reticularioid genera like *Reticulariopsis* Gourvennec, 1994, *Kymatothyris* Struve, 1970 or *Rhenothyris* Struve, 1970 (Struve 1970; Gourvennec 1994; Carter & Gourvennec 2006). The internal shell structure (dental plates, cardinal process, crural plates) is generally in agreement with the interior of *Reticulariopsis*. Unfortunately, poor preservation of the external shell surface does not allow assessing shell micro-ornamentation.

4. Palaeoecology

Assemblage A (N = 421) has been collected from limestones with numerous red and orange traces of weathering ferruginous substances. Most of the collected brachiopods come from the scree (this is why the assemblage is not subdivided further), but in the field, the authors noted the presence of

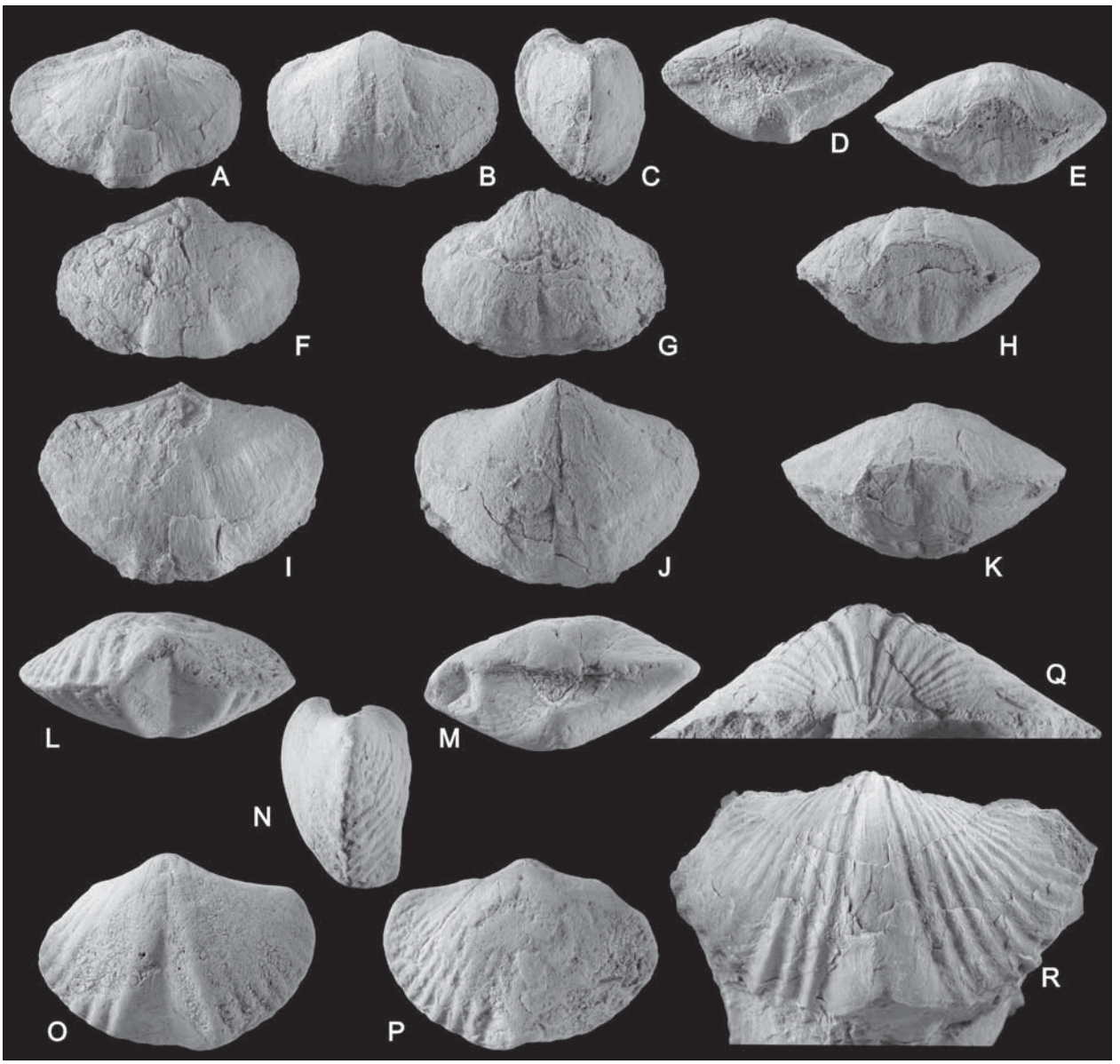

Fig. 14. Spiriferides from the assemblage A. **A-K** – *Reticulariopsis*? sp. A-E. Articulated shell ZPAL Bp 80/AB-e-39/2 in dorsal, ventral, lateral, posterior, and anterior views. F-H, I-K. Articulated shells ZPAL Bp 80/AB-e-39/3, 4 in dorsal, ventral, and anterior views. **L-R** – *Brachyspirifer*? sp. L-P. Articulated shell ZPAL Bp 80/ATH-y-22/1 from outcrop 1 bis in anterior, posterior, lateral, ventral, and dorsal views. Q-R. Isolated dorsal valve ZPAL Bp 80/ATH-f-22/1 from outcrop A' in posterior and dorsal views.

two lumachelle layers (Fig. 1D), one (lower) with *Sieberella*? sp., the other (upper) with *Kyrtatrypa* cf. *balda*. Brachiopods were also seen in beds between the two lumachelles. The shells of the dominant species *Kyrtatrypa* cf. *balda* are mostly relatively entire (articulated, not broken, so presumably having not undergone long transport) and the same may be said about *Meristella* sp. (largely), Athyrididae indet., and *Lissatrypa* sp. In contrast to this, *Brachyspirifer*? sp. and *Sieberella*? sp. are preserved solely as fragmented valves. The assemblage A as a whole is oligodominant (Fig. 16A), *Kyrtatrypa* cf. *balda* accounting for slightly less than half of the brachiopods, *Brachyspirifer*? sp. for 17%, *Sieberella*? sp. for 15%, and the remaining 12 species together for 20% (*Reticulariopsis*? sp. 5%, *Stenorhynchia ulrici* 4%, *Camarium*? sp. 4%, other <2% each). Besides numerous crinoid columnals, the remaining fauna is scarce: corals, rare pygidia of *Scutellum* s.l., a single *Platyceras* s.l., and a single acanthodian spine. The assemblage A should therefore be

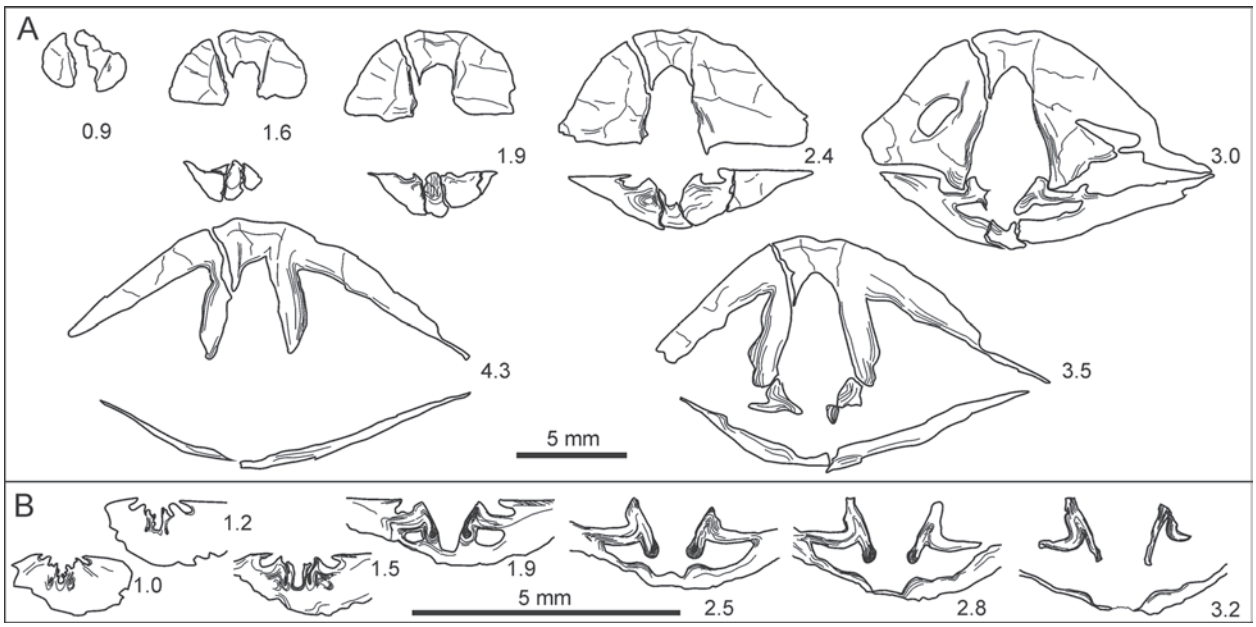

Fig. 15. Transverse serial sections of *Reticulariopsis*? sp. through the shell ZPAL Bp 80/AB-e-39/1 (assemblage A). Distances measured in millimetres from the tip of the ventral umbo.

interpreted as a mixture of quieter water species (the frills of *Kyrtatrypa* are an adaptation to soft bottom; same for the small smooth shells of Athyrididae indet. and *Lissatrypa* sp.; upper lumachelle) and of brachiopods adapted to high energy environments (thick-shelled gypidulids, costate spiriferides; lower lumachelle).

Assemblage D (*N* = 124), discovered in the cavities and small caves occurring within the Emsian Kess-Kess mud mounds may represent cryptic and/or vent biota. The assemblage is nearly monospecific (Fig. 16B), being composed of >120 *Septatrypa tumulorum* and only two other brachiopods (one probable spiriferide, one davidsoniidine atrypide). Such a low diversity was also found in the other groups inhabiting the cryptic environments within the Kess-Kess mud mouds. Apart from brachiopods, the cavities harboured single species of small solitary undissepimented rugose corals regarded as thermophilic (Berkowski 2004; Belka & Berkowski 2005), growing together with the tabulates and sponges around the outlets of active or inactive venting chimeys. The cavities are filled by younger grey laminated carbonate sediment with numerous *Scutellum* exuviae and orthoceratids.

5. Palaeobiogeography

The assessment of palaeobiogeographic affinities of the assemblage A is hampered by taxonomic problems, mostly due to poor preservation of the described fauna, more seldom to inadequate knowledge of other faunas. Despite that, a general statement about the similarity of the described fauna with that of the Prague Basin can be made. *Kyrtatrypa* cf. *balda* is much alike (possibly identical with) a Bohemian species and *Stenorhynchia fryne*, the species closest to *Stenorhynchia ulrici*, occurs in the Prague Basin as well.

As far as the assemblage D is concerned, the monodominant *Septatrypa tumulorum* is unknown outside the type locality, so any precise palaeofaunistic links cannot be ascertained; however, the two closest species (see remarks in the systematic part), *Rhynchatrypa jesenia* and *Radimatrypa zelaria*, are both from Bohemia. The single specimen described here as *Carinatina*? sp. is also strongly suggestive of a Bohemian species ("*Kaplicona*"; A.T. Halamski, A. Baliński & M. Mergl, unpublished data).

To sum up, despite the lack of precise data and impossibility of presenting a quantitative analysis, the Bohemian affinities of the described early Dalejan brachiopods are clear. Similar conclusions were obtained for the middle to late Dalejan brachiopods (Mergl 2018) and the rugosans (B. Berkowski, personal communication, March 2017) from Hamar Laghdad.

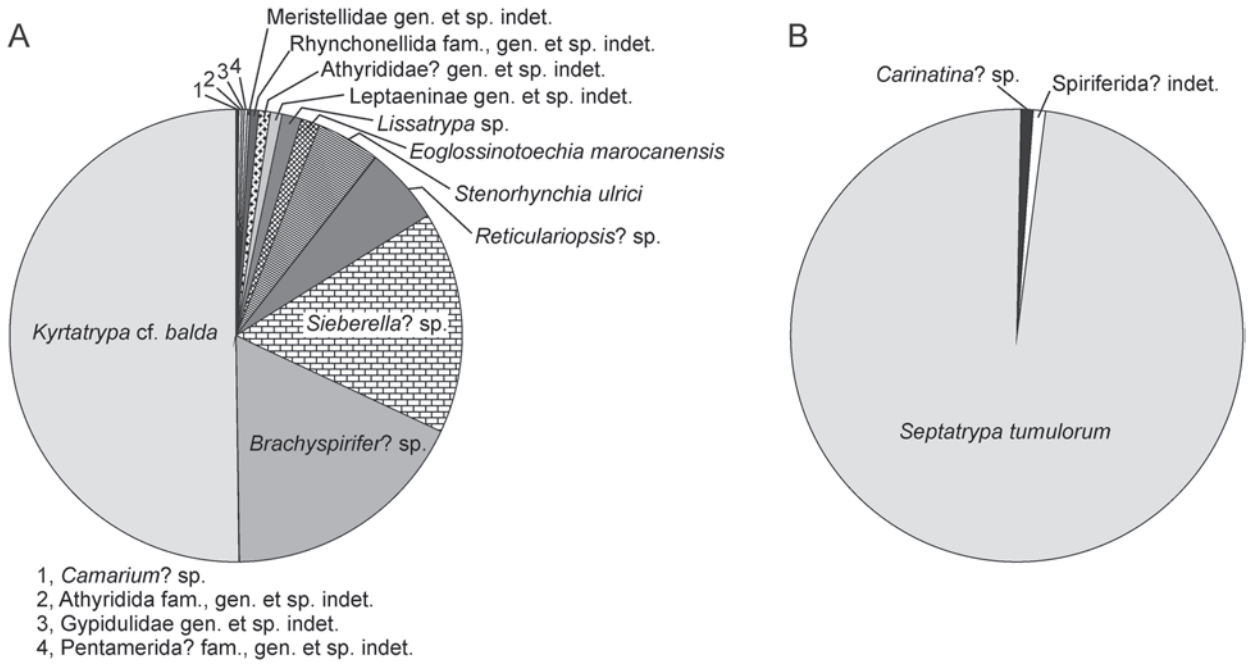

Fig. 16. Pie diagrams showing the percentages of taxa within the described assemblages A and D.

6. Conclusions

1. Early Dalejan (early late Emsian) brachiopods from Hamar Laghdad are represented by two very different assemblages (no species in common) corresponding to mud mound and inter-mound carbonates (assemblages A and D herein, respectively). Assemblage A is oligodominant, the most frequent taxa being *Kyrtatrypa* cf. *balda*, *Brachyspirifer*? sp. and *Sieberella*? sp. Assemblage D is nearly monospecific with *Septatrypa tumulorum* n. sp., accounting for over 98% of the brachiopods.

2. *Stenorhynchia ulrici* Halamski & Baliński n. sp. is characterised by a large and transverse shell, a flat-bottomed and relatively narrow sulcus, and a rather low and weakly zigzagging tongue. It is quite unlike the only other Emsian representative of the genus described up to now, *S. briceae*, which is subtriangular in shape. *Stenorhynchia fryne* from the Pragian of the Prague Basin is similar in shape but possesses a higher tongue, whereas *S. ida* (same area and stage) has similar biometric characteristics, but its ventral umbo is longer and with concave postero-lateral margins.

3. *Septatrypa tumulorum* Baliński & Halamski n. sp. is characterised by a smooth, transverse, dorsibiconvex shell of medium size and a usually rounded tongue. It is noteworthy that the occurrence of *S. tumulorum* in the Hamar Laghdad area is strictly confined to mud mounds suggesting that this brachiopod was probably adapted to live around the outlets of the active or inactive venting chimneys. The closest species are *Rhynchatrypa jesenia* Havlíček & Pek, 1986 from the Eifelian of the Nízký Jeseník Mountains in Moravia and *Radimatrypa zelaria* Havlíček in Havlíček & Kukal, 1990 from the Suchomasty and Acanthopyge limestones (Emsian–Eifelian) of the Barrandian.

4. The inadequate preservation and taxonomic problems do not allow to present a quantitative palaeobiogeographic analysis, but the Bohemian affinities of the described brachiopods are clear.

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