New Barremian rhynchonellide brachiopod genus from Serbia and the shell microstructure of Tetrarhynchiidae

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A new rhynchonellide brachiopod genus *Antulanella* is erected based on the examination of the external and internal morphologies and shell microstructure of "*Rhynchonella pancici*", a common species in the Barremian shallow-water limestones of the Carpatho-Balkanides of eastern Serbia. The new genus is assigned to the subfamily Viarhynchiinae, family Tetrarhynchiidae. The shell of *Antulanella* is small to rarely medium-sized, subglobose, subcircular, fully costate, with hypothyrid rimmed foramen. The dorsal euseptoidum is much reduced. The dental plates are thin, ventrally divergent. The hinge plates are straight to ventrally convex. The crura possess widened distal ends, rarely raduliform or canaliform. The shell is composed of two calcitic layers. The secondary layer is fine fibrous, homogeneous built up of predominantly anisometric anvil-like fibres. Although data on the shell microstructure of post-Palaeozoic rhynchonellides are still incomplete, it is possible to distinguish two types of secondary layer: (i) fine fibrous typical of the superfamilies Rhynchonelloidea and Hemithiridoidea and (ii) coarse fibrous typical of the superfamilies Pugnacoidea, Wellerelloidea, and Norelloidea. The new genus *Antulanella* has a fine fibrous microstructure of the secondary layer, which is consistent with its allocation in the Hemithiridoidea. *Antulanella pancici* occurs in association with other brachiopods showing strong Peritethyan affinity and close resemblance to the Jura fauna (= Subtethyan fauna).

Key words: Brachiopoda, Rhynchonellida, Tetrarhynchiidae, taxonomy, shell microstructure, Cretaceous, Barremian, Serbia.

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Introduction

The Barremian shallow-water carbonate limestones, abounding with brachiopods, bivalves and echinoids, are widespread at many localities of the Carpatho-Balkanides of eastern Serbia (Antula 1903; Petković 1911, 1930; Sučić 1953, 1961; Jankičević 1978; Radulović 2000; Polavder and Radulović 2005). The brachiopods constitute the best represented group of fossils found in these strata. However, their descriptions are incomplete, being based solely on external shell characters (Antula 1903; Petković 1930; Sučić 1953; Polavder and Radulović 2005). From such strata at Crnoljevica (Svrljiške Planine Mountains) Antula (1903) described three new species and one new subspecies of brachiopods, including a new rhynchonellide "*Rhynchonella pancici*". About a century later, Radulović (2000) and Polavder and Radulović (2005) tentatively assigned this species to the genus *Cyclothyris*. This study provides new data on external and internal features of the shell and shell microstructure, which suggest classification of "*R. pancici*" Antula, 1903 in a new monotypic genus. The shell microstructure of related brachiopods is summarized and future research directions are suggested.

Geological setting

"*Rhynchonella pancici*" Antula, 1903 occurs widely in the Barremian shallow-water limestones of the eastern Serbian Carpatho-Balkanides. The material studied herein was collected near the village of Crnoljevica, Svrljiške Planine Mountains, which is the type locality of "*R. pancici*" (Fig. 1). The locality belongs to the Kučaj-Svrljig Zone, which is a part of the Geticum Unit (Murgoci 1912).

The layers bearing "*Rhynchonella pancici*" are composed of bioclastics, marly and argillaceous limestones with a very rich fossil association of other brachiopods (listed below), bivalves (*Rostellum rectangulare*, *Aetostreon latissimum*, *A. crassinodus*, *Mimachlamys robinaldina*, *Neithea atava*, *N. neocomiensis*, *Plicatula placunaea*), echinoids (*Holaster cordatus*, *H. intermedius*, *Pseudodiadema grasi*, *Psamechinus hiselyi*), cephalopod (*Eucymatoceras* aff. *plicatum*), benthic foraminifera (*Neotrocholina* cf. *aptiensis*, *Nezzazata* sp., *Haplophragmoides* sp., *Trocholina* sp.), and algae (*Actinoporella podolica*, *Pseudoactinoporella fragilis*, *Pseudoactinoporella*? *silvaeregis*, *Suppiluliumella praebalcanica*) listed by Antula (1903) and Radulović (2000). This macrofossil assemblage has a wide stratigraphical distribution. The

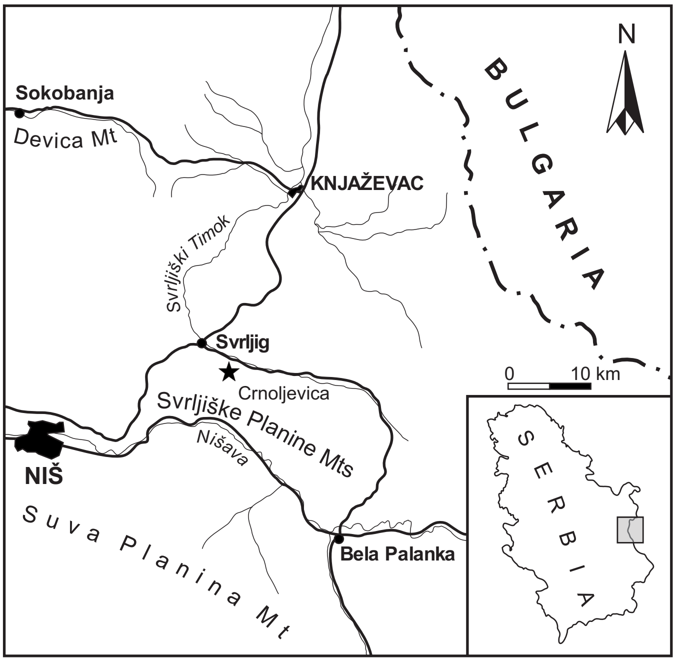


Fig. 1. Location map of the brachiopod locality (black star) in eastern Serbia, Carpatho-Balkanides.

occurrence of the above-mentioned green algae species in the brachiopod-bearing strata allows the age of the brachiopod fauna to be defined as Barremian (Radulović 2000).

At the locality of Crnoljevica, "*Rhynchonella pancici*" occurs in association with other Barremian brachiopods showing a strong Peritethyan affinity and bearing close similarity to the Jura fauna: *Cyclothyris desori* (Loriol in Pictet, 1872), *C. gillieroni* (Pictet, 1872), *C. renauxiana* (d'Orbigny, 1847), *C. rostriformis* (Roemer, 1836), *Loriolithyris russillensis* (Loriol, 1866), *L. valdensis* (Loriol, 1868), *Musculina sanctaecrucis* (Catzigras, 1948), *Sellithyris carteroniana* (d'Orbigny, 1847), *S. essertensis* (Pictet, 1872), *Timacella timacensis* (Antula, 1903), *Dzirulina pseudojurensis* (Leymerie, 1842), and *Oblongarcula*? *exquisita* (Loriol in Pictet, 1872). Only a few brachiopods from this assemblage, such as *C. rostriformis* (Roemer, 1836), *Musculina sanctaecrucis* (Catzigras, 1948), and *Sellithyris carteroniana* (d'Orbigny, 1847), are typical Boreal forms (Radulović 2000).

Material and methods

The described collection consists of 59 articulated shells, 28 of which were measured and statistically processed. Seven specimens were serially sectioned to study their internal morphology. Additionally, the shell microstructure of four other adult specimens was examined using a JEOL JSM-6460LV scanning electron microscope (SEM) at the Department of Biology and Ecology, Faculty of Science, University of Novi Sad (Serbia). The specimens were first embedded in araldite, and then cut from the anterior and posterior ends perpendicular to the plane of symmetry, polished, etched with 5% HCl for 6 seconds, dried, and finally coated with gold and photographed. Simultaneously, acetate peels were prepared. The shell thickness and fibres of the secondary layer were measured at the maximum shell width, and close to the plane of symmetry, as recommended by Sass and Monroe (1967).

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; IRScNB, Royal Institute of Natural Sciences of Belgium, Brussels; NHM, Natural History Museum, Belgrade, Serbia; NMNHS, National Museum of Natural History, Sofia, Bulgaria; RGF VR, Faculty of Mining and Geology, University of Belgrade, Serbia.

Other abbreviations.—L, length; W, width and T, thickness of the specimen; w, width and t, thickness of the fibres of the secondary layer in cross section.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

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

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

Order Rhynchonellida Kuhn, 1949

Superfamily Hemithiridoidea Rzhonsnitskaia, 1956

Family Tetrarhynchiidae Ager, 1965

Subfamily Viarhynchiinae Manceñido and Owen, 2002

Genus *Antulanella* nov.

Type species: *Rhynchonella pancici* Antula, 1903, monotypic; Barremian (Early Cretaceous) of Crnoljevica, Svrljiške Planine Mountains, eastern Serbia.

Derivation of the name: In honour to the Serbian geologist and palaeontologist Dimitrije Antula (1870–1924), who first described the species *R. pancici* and other fauna from Crnoljevica. His Ph.D. thesis was published in Austria-Hungary under the name Anthula (Anthula 1899) and some later authors followed this spelling. In Serbian, the spelling of his surname is Antula, therefore we recommend using this spelling.

Diagnosis.—Small to very rarely medium-sized, costate, subglobose, variable in outline, symmetrical, acutely biconvex rhynchonellides. Beak suberect, hypothyrid auriculate foramen, beak ridges well developed. Squama and glotta present, but not well developed. Anterior commissure uniplicate. Fold and sulcus poorly developed. Ornamented by 32–36 simple costae. Deltidial plates disjunct. Dental plates short, ventrally divergent. Hinge plates slightly ventrally deflected in the juvenile stage, becoming subhorizontal to horizontal, slender and wide, straight to rarely ventrally convex. Dorsal euseptoidum low. Crural bases crescent-shaped. Crura with widened distal ends, rarely typically raduliform or canaliform. Shell composed of two calcitic layers. Secondary layer built up of

Table 1. Summary of the external, internal and shell microstructure characters of *Antulanella* gen. nov. and all other genera included in the subfamily Viarhynchiinae Manceñido and Owen, 2002. Data for *Septatoechia* are taken only from its type species. * characters in *Septatoechia,* which seem to deviate from the norm in the subfamily Viarhynchiinae are shown in italics.

Genera		*Antulanella* gen. nov.	*Viarhynchia* Calzada Badia, 1974b	*Hemithyropsis* Kats, 1974	*Septatoechia* Lobacheva and Titova, 1977 (based on *S. inflata* from the type locality)
External morphology	Size	small, rarely medium	large	small to medium	medium to large
	Outline and shape	subcircular, roundly pentagonal or slightly transversely elliptical; subglobular	elongate oval; subglobular	roundly pentagonal, elongate oval, roundly triangular; subglobular	subtriangular, subpentagonal or oval; subglobular to globular
	Convexity	acutely and subequally biconvex, subglobose	acutely and equibiconvex, subglobose	acutely and equibiconvex, subglobose	acutely and dorsibiconvex, globulose
	Beak	suberect	slightly incurved	suberect	slightly incurved * *to erect*
	Foramen	hypothyrid	hypothyrid	hypothyrid	hypothyrid
	Deltidial plates	disjunct	disjunct		disjunct
	Ribs	subangular (26–32)	rounded (26–36)	subangular, bifurcating (28–40)	rounded or subangular (25–40)
	Fold and sulcus	poorly developed	poorly developed	poorly developed	* *well developed*
Internal morphology	Dental plates	ventrally divergent	ventrally divergent		* *parallel to ventrally convergent*
	Hinge plates	subhorizontal to horizontal, rarely ventrally convex	dorsally directed	hinge plates and socket ridges fused	ventrally divergent
	Euseptoidum or dorsal median septum	euseptoidum	euseptoidum	absent	* *very high dorsal median septum, slender, short, possible septalium*
	Crura	widened distal ends, rarely raduliform or canaliform	raduliform, concave distal ends	raduliform?	raduliform
Shell microstructure and texture	Shell thickness (in μm)	150–480			* *1000–2000*
	Primary layer thickness (in μm)	20–30			>30
	Fibre shape	predominantly anvil-like to elongate rhombic			rhombic, rarely anvil like or subhexagonal
	Fibre size (in μm)	w = 15–30; t = 5–10			w = 15–32; t = 8–12
	Microtexture	homogeneous, thin myotest			* *not homogeneous, built of several sublayers, very thick myotest*
Age		Barremian	Upper Campanian–Maastrichtian	Campanian–Maastrichtian	Maastrichtian

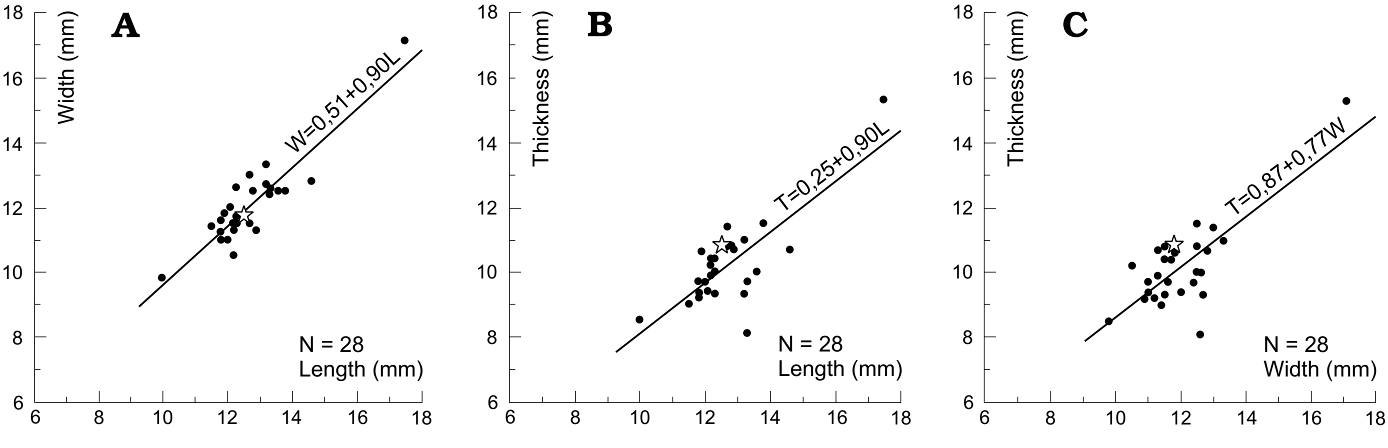


Fig. 2. Intraspecific variability of *Antulanella pancici* (Antula, 1903) from Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. Scatter diagrams plotting length/width (**A**), length/thickness (**B**), width/thickness (**C**): linear correlation. Open star indicates lectotype; N, number of specimens.

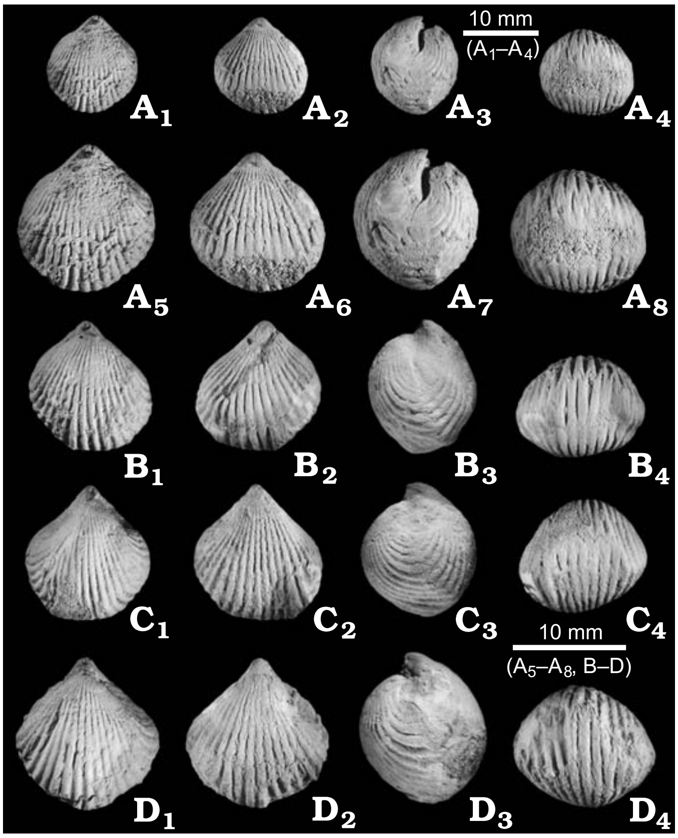


Fig. 3. Rhynchonellide brachiopod *Antulanella pancici* (Antula, 1903), Barremian (Early Cretaceous), Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. **A**. NHM 484/3, lectotype, dorsal (A_1, A_5), ventral (A_2, A_6), lateral (A_3, A_7), and anterior (A_4, A_8) views. **B**. NHM 484/8, paralectotype, dorsal (B_1), ventral (B_2), lateral (B_3), and anterior (B_4) views. **C**. NHM 484/9, paralectotype, dorsal (C_1), ventral (C_2), lateral (C_3), and anterior (C_4) views. **D**. NHM 484/6, paralectotype, dorsal (D_1), ventral (D_2), lateral (D_3), and anterior (D_4) views.

predominantly anisometric anvil-like fibres. Secondary layer microstructure fine fibrous, homogeneous.

Antulanella gen. nov. differs from *Viarhynchia* Calzada Badía, 1974b in its smaller size and variable outline (see also Table 1). Internally both genera share widened distal ends of the crura (with diabolo-like sections). Data about *Hemithyropsis* Kats, 1974 are incomplete, no serial sections being available for comparison. However, the new genus differs externally from *Hemithyropsis* in having a more circular outline and internally in having subhorizontal to horizontal, rarely ventrally convex hinge plates. *Antulanella* differs from *Septatoechia* Lobacheva and Titova, 1977 in its smaller size, more poorly developed fold and sulcus, and much thinner shell wall. Internally *Antulanella* is characterized by ventrally divergent dental plates, reduced dorsal euseptoidum and crura with generally widened distal ends (see later discussion suggesting revising the taxonomical position of *Septatoechia*). In addition to the above-mentioned differences, the three genera presently assigned to the Viarhynchiinae are stratigraphicaly younger than the new genus.

Discussion.—Some external and internal shell features, such as a nearly equibiconvex and subspherical shell with ill developed dorsal fold, and incurved beak, lack of a septalium and type of crura, suggest placement of the new genus in the subfamily Viarhynchiinae, family Tetrarhynchiidae within the Hemithiridoidea.

Dorso-ventrally widened distal ends of crura (giving rise to diabolo-like sections) among the Mesozoic rhynchonellides are reported only in members of the superfamily Hemithiridoidea. This term was introduced by Ager (1967: 143) who stated that the diabolo-like sections, however, do not correspond to the “various processes that are sometimes found at the distal ends of crura in the rhynchonellids”. Among Cyclothyridinae, these types of crural sections are known in the Early Jurassic *Squamirhynchia* Buckman, 1918, the Middle Jurassic *Globirhynchia* Buckman, 1918, the Late Jurassic *Bicepsirhynchia* Shi, 1990, the Middle Jurassic to Early Cretaceous *Septaliphoria* Leidhold, 1921, the Early Cretaceous *Lamellaerhynchia* Burri, 1953, the Early to Late Cretaceous *Cyclothyris* McCoy, 1844, the Late Cretaceous *Almerarhynchia* Calzada Badía, 1974a and in *Owenirhynchia* Calzada in Calzada and Pocovi, 1980. Within Viarhynchiinae, they are present in the Late Cretaceous *Viarhynchia* Calzada Badía, 1974b and in the Barremian *Antulanella*.

The diabolo appearance of the crura is sometimes accompanied by distal splitting of the crura into two, approximately parallel, plates. This feature has been noted so far in a few species of the above-mentioned genera: the Sinemurian–Pliensbachian *Squamirhynchia squamiplex* (Quenstedt, 1871), the Aalenian *Globirhynchia subobsoleta* (Davidson, 1852), the Oxfordian *Septaliphoria paucicosta* Childs, 1969, *S. arduennensis* (Oppel, 1858), *S. sobolevi* Makridin, 1964, *S. pectunculoides* (Etallon, 1860), *S. moeschi donetziana* (Makridin, 1952), and *Bicepsirhynchia asperata* Shi, 1990, the Cenomanian *Cyclothyris* sp. of Nekvasilova (1973), the Turonian *Cyclothyris zahalkai* Nekvasilova, 1973, and the Campanian–Santonian *Almerarhynchia reigi* Calzada, 1989.

Smirnova (1972) also reported crura with widened distal ends in three Early Cretaceous (Valanginian–Late Barremian) species of *Belbekella* (= *Cyclothyris*) from the Crimea and Caucasus: *B. rectimarginata* Smirnova, 1972, *B. irregularis* (Pictet, 1872), and *B. adducta* Smirnova, 1972. Other species of *Belbekella* have simple raduliform crura. No parallel plates are observed.

It is worth noting that in *Cyclothyris irregularis* (Pictet, 1872), the crura may be raduliform (Lobacheva in Bogdanova and Lobacheva 1966: 40, fig. 11) or distally widened (i.e., diabolo-type) (Smirnova 1972: 39, fig. 12).

In *Cyclothyris*? *globata* (Arnaud, 1877) from the Campanian of Guča, western Serbia and from the Early Campanian of Nanos, Slovenia, the crura have widened distal ends (Radulović and Motchurova-Dekova 2002) but those from other localities in north-eastern Bulgaria (Motchurova-Dekova 1995), and Croatia (Radulović and Motchurova-Dekova 2002), have narrow distal ends (i.e., typical raduliform crura).

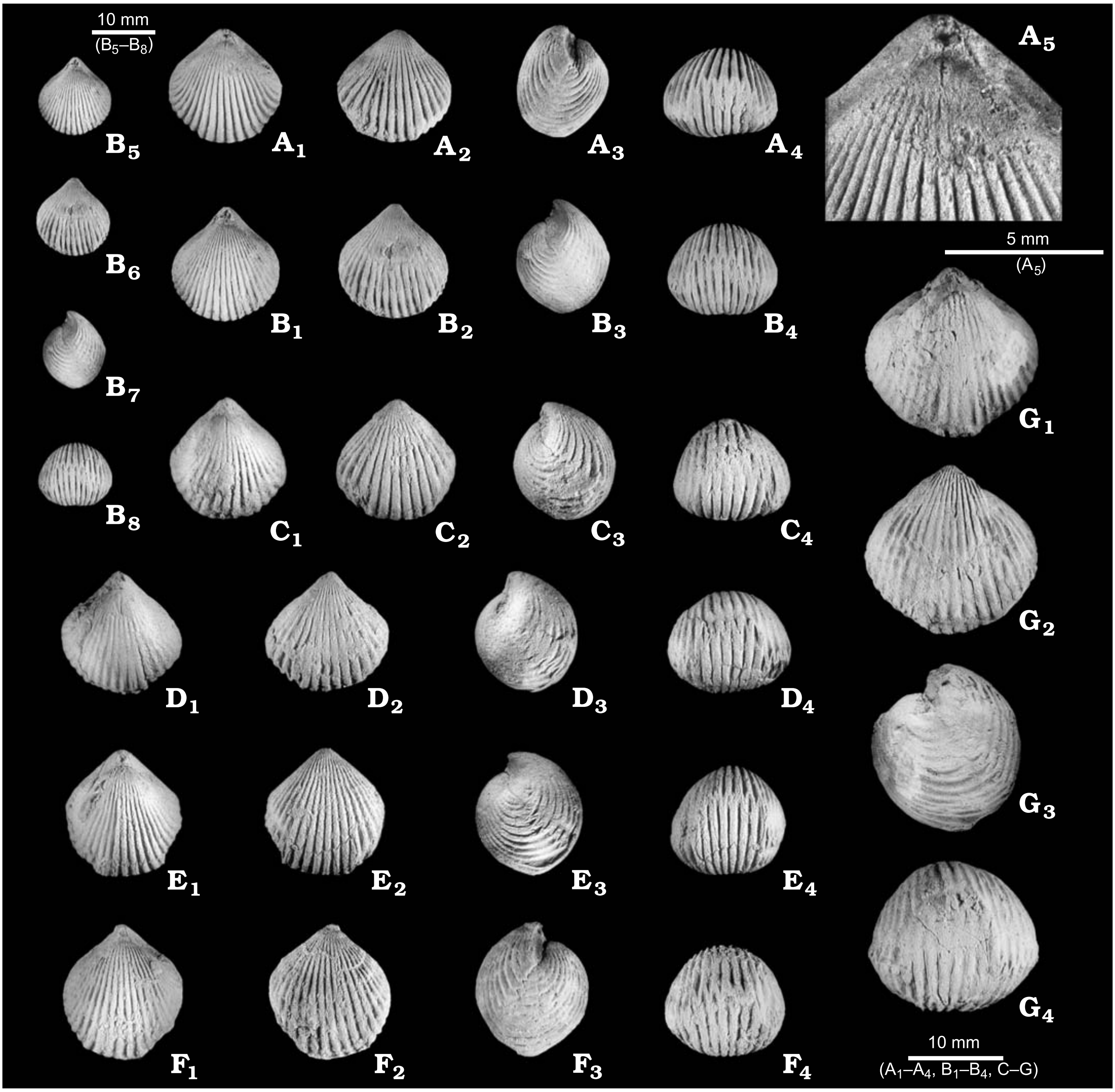


Fig. 4. Rhynchonellide brachiopod *Antulanella pancici* (Antula, 1903), Barremian (Early Cretaceous), Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. **A**. RGF VR 25/288, topotype, dorsal (A_1), ventral (A_2), lateral (A_3), and anterior (A_4) views; A_5, dorsal view shows interarea, deltidial plates and rimmed foramen. **B**. RGF VR 25/290, topotype, dorsal (B_1, B_5), ventral (B_2, B_6), lateral (B_3, B_7), and anterior (B_4, B_8) views. **C**. RGF VR 25/314, topotype, used for transverse serial sections, dorsal (C_1), ventral (C_2), lateral (C_3), and anterior (C_4) views. **D**. RGF VR 25/313, topotype, juvenile form, used for transverse serial sections, dorsal (D_1), ventral (D_2), lateral (D_3), and anterior (D_4) views. **E**. RGF VR 25/316, topotype, used for transverse serial sections, dorsal (E_1), ventral (E_2), lateral (E_3), and anterior (E_4) views. **F**. RGF VR 25/289, topotype, dorsal (F_1), ventral (F_2), lateral (F_3), and anterior (F_4) views. **G**. RGF VR 23/81, topotype, largest specimen, dorsal (G_1), ventral (G_2), lateral (G_3), and anterior (G_4) views.

Recently, Simon (2003) described a new species *Almerarhynchia kunradensis* from the Upper Maastrichtian of Limburg, the Netherlands. He figured serial sections of two specimens. In one specimen the crura are clearly canaliform but in the other specimen, the crura display very close to diabolo-like sections; moreover they terminate with two approximately parallel plates. These plates are also known in *Almerarhynchia reigi* Calzada, 1989.

The above examples suggest that crura in different specimens of one species may be narrow (typically raduliform) or widened and incurved at the distal ends (diabolo shape). Thus, this may be considered as an intraspecific variation and should not be given taxonomical weight.

The distal splitting of the crura into two plates does not always occur in the forms with diabolo crura. The non-occurrence of these plates is most likely a morphogenetic feature. It should also be noted that the plates are very short and that they might be overlooked when sectioned.

Stratigraphic and geographic range.—The Barremian of eastern Serbian Carpatho-Balkanides (Crnoljevica, Prekonozi, Novo Selo, Skrobnica, Bežište).

Antulanella pancici (Antula, 1903)

Figs. 2–12.

1903 *Rhynchonella Pančići* sp. nov.; Antula 1903: 34, pl. 1: 1–4.
1911 *Rhynchonella Pančići* Antula; Petković 1911: 7.
1930 *Rhynchonella Pančići* Antula; Petković 1930: 103, pl. 2: 7D (only).
1953 *Rhynchonella pančići* Antula; Sučić 1953: 86, 87, 108, pl. 2: 5–7.
1961 *Rhynchonella pančići* Ant.; Sučić 1961: 51, 82.
1978 *Rhynchonella pančići* Antula; Jankičević 1978: 126, 129, 149, 154.
2000 *Cyclothyris pancici* (Antula): Radulović 2000: 122, 124, pl. 1: 4, 5.
2005 *Cyclothyris*? *pancici* (Antula); Polavder and Radulović 2005: 57, figs. 2A–D, 3A, B.

Lectotype (designated herein).—Specimen NHM 484/3, illustrated in Fig. 3A. In Antula's collection housed in NHM under the No. M 484, there were 19 syntype specimens, not singly numbered. In the inventory book it is stated that there should be 27 specimens, collected by Antula in 1893 and 1894. Four specimens figured by Antula (1903: pl. 1: 1–4) are drawings, possibly partly modifying the outline of the originals (see Fig. 12). Unfortunately, we can not recognize any of Antula's figured specimens among the present 19 specimens. We propose herein the best preserved specimen as a lectotype, the remaining 18 specimens now becoming paralectotypes. Recently, we collected also additional topotype material from Crnoljevica.

Diagnosis.—Same for the genus.

Material.—The lectotype, 18 paralectotypes and 40 topotype specimens from Crnoljevica.

Measurements (in mm; see also Fig. 2):

Registration number of specimen	L	W	T	W/L	T/L	T/W
NHM 484/3, lectotype (Fig. 3A)	12.5	11.8	10.9	0.94	0.87	0.92
NHM 484/8, paralectotype (Fig. 3B)	11.8	11.2	9.2	0.95	0.78	0.82
NHM 484/9, paralectotype (Fig. 3C)	12.2	11.3	9.9	0.93	0.81	0.88
NHM 484/6, paralectotype (Fig 3D)	13.6	12.6	10.0	0.92	0.74	0.79
RGF VR 25/288, topotype (Fig. 4A)	11.5	11.4	9.0	0.99	0.78	0.79
RGF VR 25/290, topotype (Fig. 4B)	11.8	11.0	9.4	0.93	0.80	0.85
RGF VR 25/314, topotype (Fig. 4C)	12.3	11.7	10.4	0.95	0.85	0.89
RGF VR 25/313, topotype (Fig. 4D)	12.3	12.6	10.1	1.02	0.82	0.80
RGF VR 25/316, topotype (Fig. 4E)	12.7	11.5	10.8	0.91	0.85	0.94
RGF VR 25/289, topotype (Fig. 4F)	13.8	12.5	11.5	0.91	0.83	0.92
RGF VR 23/81, topotype (Fig. 4G)	17.5	17.1	15.3	0.98	0.87	0.89

Description.—*External morphology*: Shell small to very rarely medium-sized, subglobose, outline variable, from subcircular to roundly pentagonal, or slightly transversely elliptical. In juvenile specimens, valves equally biconvex, in adults strongly biconvex with dorsal valve somewhat more convex. Length slightly surpassing width in most specimens, very rarely as long as wide, or wider than long. Maximum width and thickness situated at about mid-length. Beak strong, pointed and suberect. Beak ridges very distinct, delimiting a moderately wide concave interarea. Hypothyrid foramen slightly auriculate, minute, circular, rarely oval. Deltidial plates disjunct. Squama and glotta present, but not well expressed. Anterior commissure highly and roundly uniplicate. Each valve ornamented with 26–32 simple subtriangular costae, 6–8 on fold, 5–7 in sulcus. Fold and sulcus poorly developed anteriorly, not sharply separated from lateral flanks. Apical angle ranges from 90 to 95 degrees.

Internal morphology: Seven specimens were sectioned of which four are figured (Figs. 5–8). Deltidial plates disjunct but very close together, relatively thick, inwardly curved. Dental plates ventrally divergent to subparallel, slender, largely confined to ventral umbo. Hinge-teeth subquadrate, or spherical, crenulated, with distinct denticulae, nearly vertically inserted in large well-developed sockets. Pedicle collar absent. Well defined inner and outer socket-ridges. Hinge plates slightly ventrally deflected in early stages, becoming anteriorly subhorizontal to horizontal, slender and wide, straight or gently arched ventrally. Septalium not present. Euseptoidum reduced to a short and low ridge (Fig. $11A_1$, A_2). Crural bases crescentic, not clearly separated from hinge plates (Fig. $11A_3$, B_1). Crura with dorso-ventrally widened distal ends (giving rise to a diabolo appearance) (Figs. 9A–C, $10A_5$, B), rarely raduliform, or canaliform (Fig. 9D), all these types belonging to the radulcal group *sensu* Manceñido (2000).

Shell microstructure: Four specimens were studied (Figs. 10, 11). The impunctate shell of *Antulanella pancici* is composed of two calcitic layers, primary microgranular and secondary fibrous. Calcite prisms perpendicular or slightly inclined to the internal shell surface were also observed (Figs. $10A_2$, $11A_1$). They are similar to those described by Motchurova-Dekova (2001) and are considered to be the result of

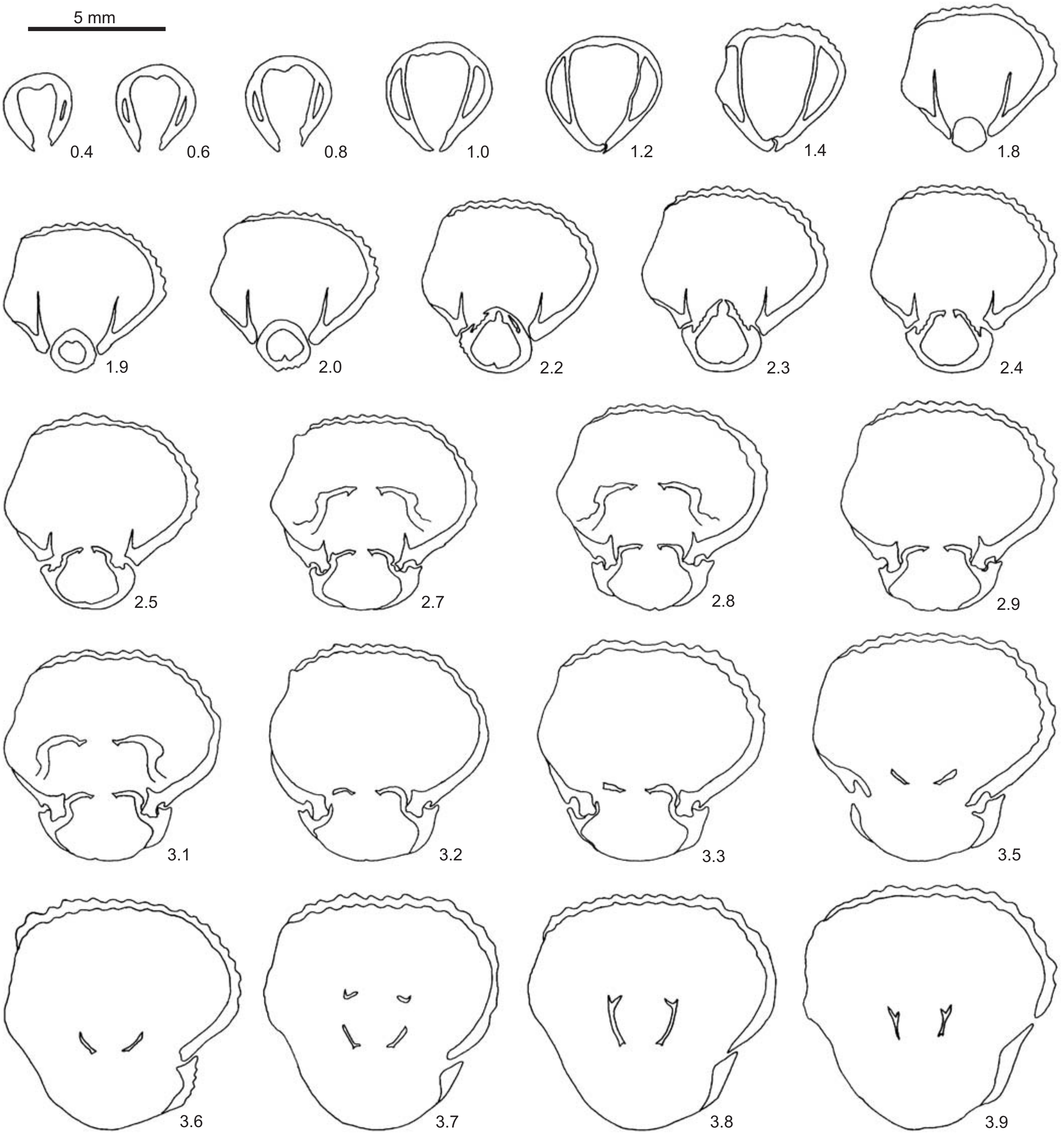


Fig. 5. Transverse serial sections of *Antulanella pancici* (Antula, 1903) through specimen RGF VR 25/314, illustrated in Fig. 4C. Barremian, Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. Original dimensions of the specimen (in mm): L = 12.3, W = 11.7, T = 10.4. Numbers indicate distance in mm from the tip of the ventral umbo.

secondary diagenetic calcite formation and should not be confused with tertiary prismatic layer.

The primary layer is 20 μm thick in the sulci and 30 μm in the ribs and preserved only in the shell parts covered with sediment. It is composed of elongate microgranular calcite crystals, perpendicular to the secondary layer (Figs. $10A_1$–A_3, $11A_1$).

The secondary layer is homogeneous (not differentiated in several packages), variable in thickness, 210–450 μm in costae and 130–250 μm in sulci. It is built up of anisometric fibres, finer close to the exterior shell surface, 12–15 μm wide and 3–5 μm thick, which gradually become larger in the central and inner part of the shell, 15–30 μm wide and 5–10 μm thick. The majority of the fibres have anvil-like cross-

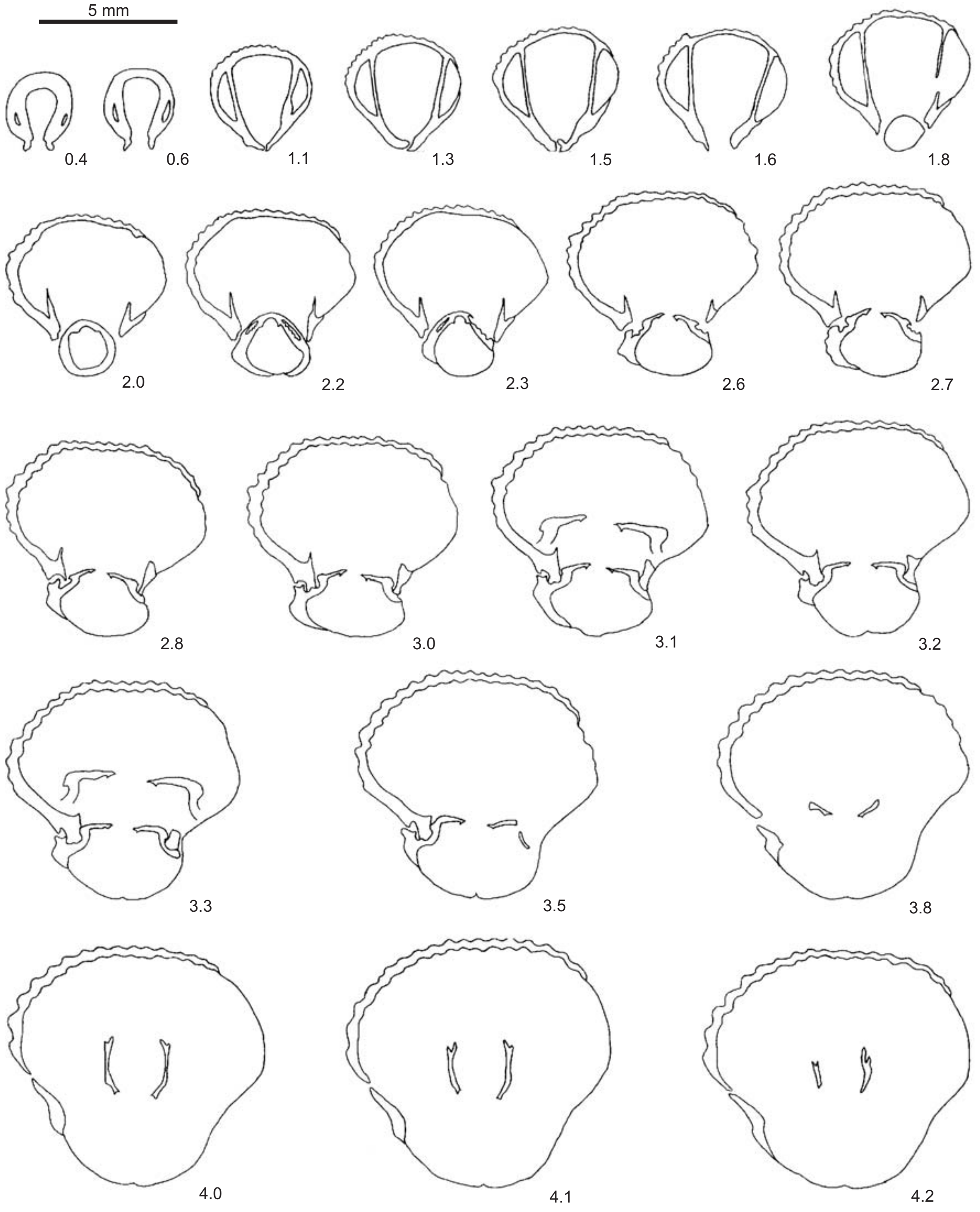


Fig. 6. Transverse serial sections of *Antulanella pancici* (Antula, 1903) through specimen RGF VR 25/313, illustrated in Fig. 4D. Barremian, Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. Original dimensions of the specimen (in mm): L = 12.3, W = 12.6, T = 10.1. Numbers indicate distance in mm from the tip of the ventral umbo.

sections, but some of them tend to have elongate rhombic sections (Figs. $10A_1$–A_4, $11A_1$). Diagenetic modifications of the fibres including fused fibrous elements were also observed (Fig. $10A_3$). Relatively thin myotest (not illustrated herein) is developed in the muscle fields.

The internal skeletal structures consist of modified fibres smaller than those building the secondary layer. The fibres forming the inner hinge plates are the largest, 12–15 µm wide and 5–8 µm thick. Fibres bounding the inner socket ridges are 8–12 µm wide and 4–6 µm thick, while fibres in the hinge teeth (Fig. $11B_2$, B_3) are smaller, 6–8 µm wide and 4–6 µm thick.

Remarks.—Antula (1903) appropriately described the variability of the external morphology of this species (Fig. 12). He classified specimens from the type locality into three morphological groups: (i) equally long and wide, strongly convex, almost globose with no sulcus in the anterior;

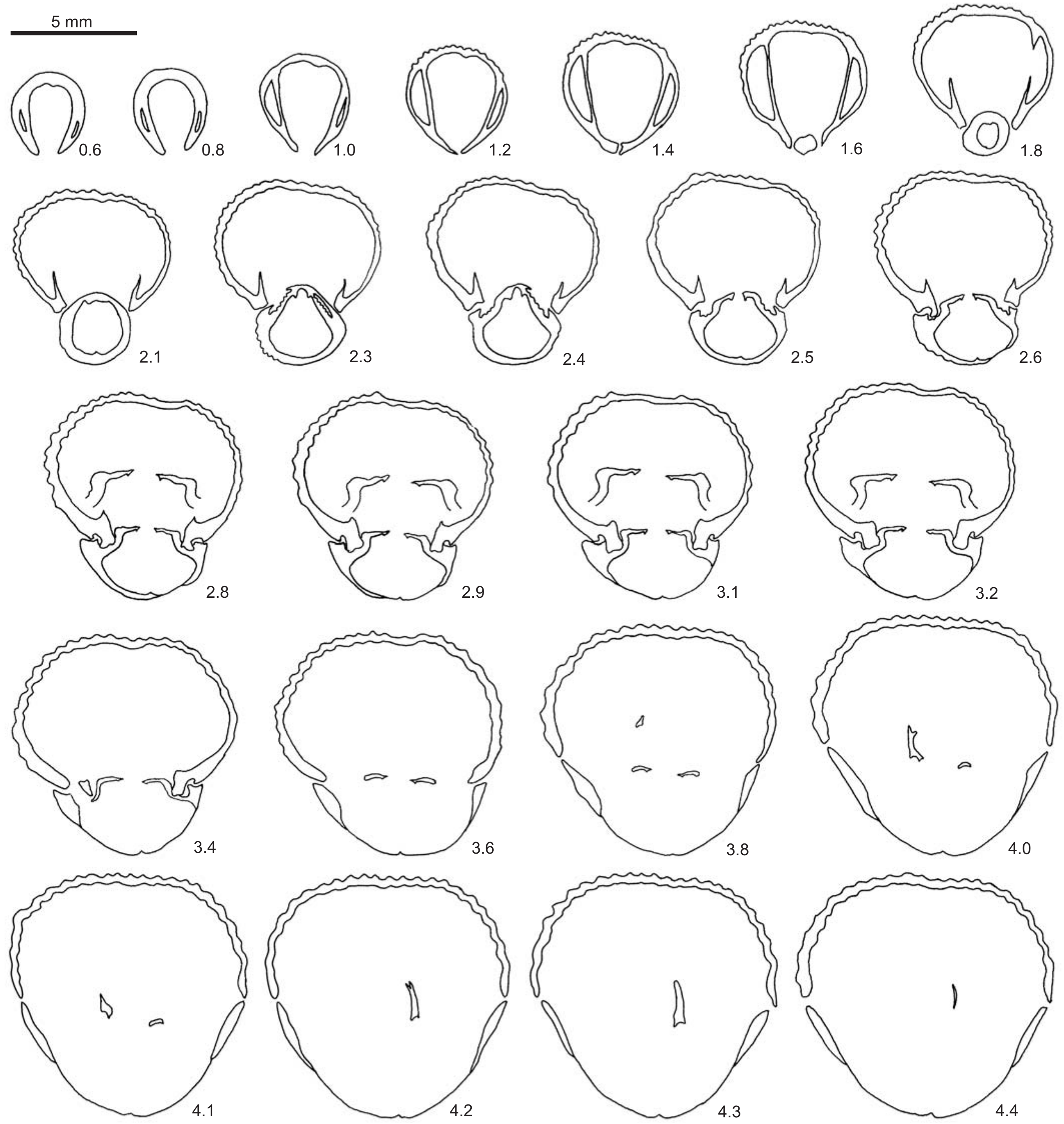


Fig. 7. Transverse serial sections of *Antulanella pancici* (Antula, 1903) through specimen RGF VR 25/316, illustrated in Fig. 4E. Barremian, Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. Original dimensions of the specimen (in mm): L = 12.7, W = 11.5, T = 10.8. Numbers indicate distance in mm from the tip of the ventral umbo.

(ii) width somewhat greater than length, moderately convex; ventral valve with sulcus in the anterior part; (iii) length almost equal to the width, convexity smaller than in others; sulcus slightly pronounced.

The average length of the specimens from Crnoljevica is 12.0 mm and only one relatively large specimen (17.5 mm in length) was found (Fig. 4G).

On the basis of external characters, such as transversely elliptical outline and the type of ribs, the described species resembles Valanginian–Hauterivian *Lamellaerhynchia picteti* Burri, 1953 (ex. *Rhynchonella lata* d'Orbigny, 1847; partim. Pictet, 1872) known from the Jura region. For this reason, Petković (1930) and Sučić (1953) assigned the transversely elliptical forms of this species to *Rhynchonella lata* d'Orbigny,

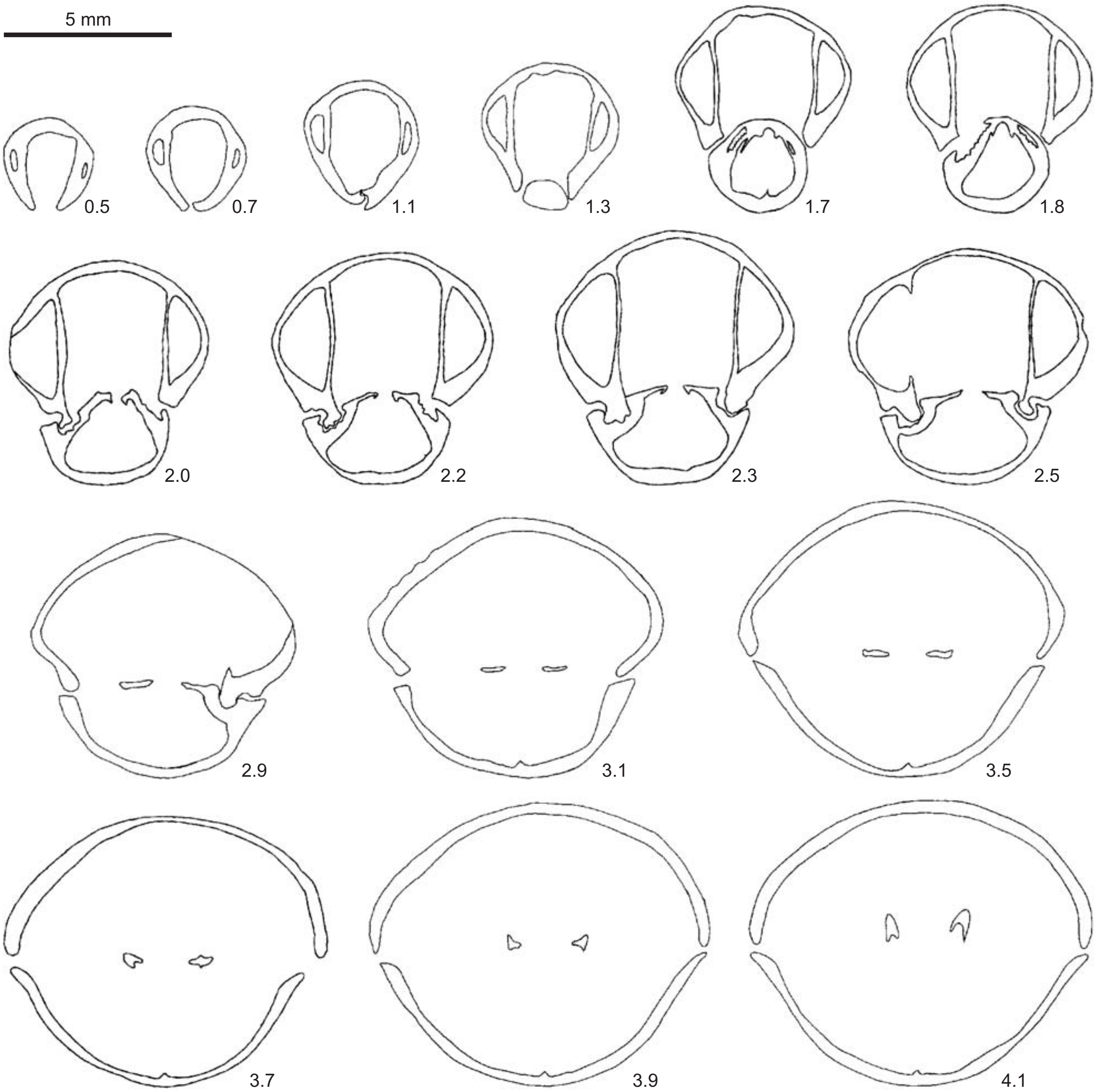


Fig. 8. Transverse serial sections of *Antulanella pancici* (Antula, 1903) through specimen RGF VR 23/83, Barremian, Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. Original dimensions of the specimen (in mm): L = 13.2, W = 12.7, T = 9.3. Numbers indicate distance in mm from the tip of the ventral umbo.

1847. Apart from being stratigraphically younger, *Antulanella pancici* differs from *L. picteti* in having much smaller dimensions and generally less numerous ribs.

Orbirhynchia asymmetrica Smirnova 1972 (32–33, pl. 1: 10; the same specimen was later refigured by the same author in 1990: 8, pl. 1: 8) from the Late Barremian of North Caucasus is a rhynchonellide brachiopod which externally has a subglobose shell and outline very similar to *Antulanella pancici*, judging from the published illustrations. However, *O. asymmetrica* has a somewhat larger size, greater number of ribs (34–36) and "asymmetric anterior end", as stated in the description of this species. It is curious that Smirnova (1972, 1990) wrote that the anterior commissure of her species is asymmetrical yet each of her figured specimens displays a symmetrical anterior commissure. *A. pancici* and *O. asymmetrica* are clearly distinguished by their internal morphology, especially by the development of two different types of crura: with widened distal ends, rarely raduliform or canaliform in *Antulanella* and falciform in *Orbirhynchia*, which places them in two different superfamilies.

Stratigraphic and geographic range.—*A. pancici* is known only from a few Barremian localities of the east Serbian Carpatho-Balkanides. The specimens from the type locality

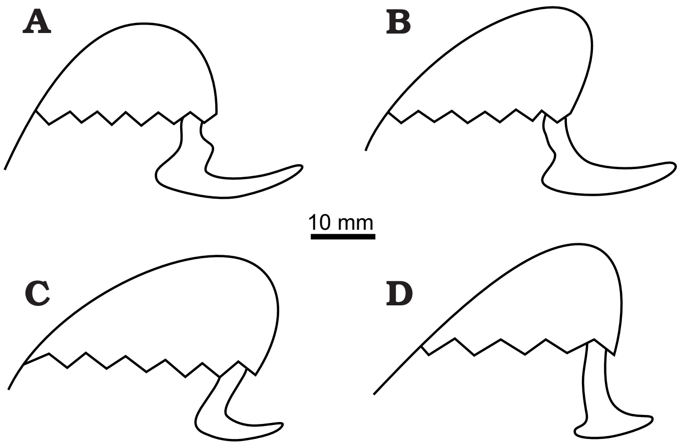


Fig. 9. Sketch reconstructions of the crura of *Antulanella pancici* (Antula, 1903), lateral views. **A**. RGF VR 25/314, from serial sections shown in Fig. 5. **B**. RGF VR 25/313, from serial sections shown in Fig. 6. **C**. RGF VR 25/316, from serial sections shown in Fig. 7. **D**. RGF VR 23/83, from serial sections shown in Fig. 8.

could not be precisely dated using the associated macrofossils and microfossils. Based on the associated orbitolinid species *Paracoskinolina*? *jourdanensis*, the specimens of *A. pancici* from the Prekonozi locality are dated as Early Barremian (Polavder and Radulović 2005).

Discussion

Taxonomic and phylogenetic implications of the shell microstructure in post-Palaeozoic rhynchonellides

The impunctate rhynchonellide shell is composed of three layers: organic periostracum, primary microcrystalline calcite layer and secondary organo-calcite layer (Williams 1997). In the past, using mostly observations on imprints of the shell on acetate peels, some authors (Dagys 1974; Smirnova 1984; Radulović 1991; Motchurova-Dekova 1992, 1994) misidentified secondary diagenetic calcite prisms in some rhynchonellide genera as a tertiary prismatic layer. Later extensive observations under SEM have shown that such prisms are diagenetic (Motchurova-Dekova 2001). Here we consider that there is no unambiguous evidence for the presence of a tertiary prismatic layer in post-Palaeozoic rhynchonellides. The periostracum is usually not preserved in the fossil state. The primary layer plays an important role in the formation of some microsculptural elements of the shell (the fine ornamentation, spines, radial fine striation, etc.), thus having importance in generic diagnoses. However, there are no specific studies discussing the taxonomic importance of the primary layer, since in the fossil state it is most commonly re-crystallised, or not preserved.

Thus, the only possible shell layer having potential for use in taxonomy is the secondary fibrous layer. The first attempt to distinguish different types of secondary layer microstructures was made by Kamyshan (1977) who, using mainly Jurassic rhynchonellides, distinguished two major types of shell microstructures in Mesozoic and Cenozoic rhynchonellides: (i) fine fibrous rhynchonellidine type and (ii) coarse fibrous basiliolidine type. According to him, the fine fibrous rhynchonellidine type is characterized by small fibres, usually less than 30–35 μm in cross section, while the coarse fibrous basiliolidine type has larger fibres, usually more than 50 μm wide in cross section. Later Kamyshan (1986) subdivided the rhynchonellides into two suborders, Rhynchonellidina and Basiliolidina, based essentially on the two different types of secondary layer microstructure. He suggested that the different size and morphology of the fibres were conditioned by two different secretory regimes in the respective suborders. According to him, in Basiliolidina, the growth of fibres tends to be more or less regular in width and thickness, producing more isometric fibres in cross sections, whereas in Rhynchonellidina, the growth is faster in width and slower in thickness, thus resulting in more anisometric fibres in cross sections. Thus, the ratio width/thickness (w/t) in the coarse fibrous type is lower than in the fine fibrous type.

Kamyshan's papers (1977, 1986) were published in Russian and regrettably he did not illustrate either of his secondary layer fabrics. This could be the reason why only a few subsequent authors, mainly Slavonic speaking (Smirnova 1984; and papers published after 2000; see Table 2), followed this classification. Kamyshan's classification was not adopted in the revised Treatise (Williams 1997; Savage et al. 2002) and his proposed suborders are still not widely accepted.

Recently Lee and Motchurova-Dekova (in press) suggested that the terms "basiliolidine" and "rhynchonellidine" type microstructure have a broader relevance, as the available sparse data show "rhynchonellidine" type microstructure in Hemithiridoidea and Rhynchonelloidea, and "basiliolidine" type in Pugnacoidea, Norelloidea, and Wellerelloidea. Lee and Motchurova-Dekova (in press) also suggested that the terminology proposed by Kamyshan (1977) needed amendment in order to avoid confusion with the nominative rhynchonellide families. Presently collected data generally confirm the validity of the classification proposed by Kamyshan (1977). Here we propose using only the descriptive terms (i) fine fibrous type and (ii) coarse fibrous type (Table 2, Fig. 13).

Our SEM observations on several rhynchonellide genera reveal that the outline of the cross section of fibres in the central part of both valves is often anvil-like (or halberd-like) and not strictly rhombic as postulated by Kamyshan (1977) for the fine fibrous type (Fig. 13). The anvil-type of section was first illustrated and described by Williams (1966) as a typical fibre cross section for Recent rhynchonellides (*Notosaria* and *Hemithyris*) and terebratulides without proposing any descriptive terms for the outline of such sections (see Williams 1966: 1148, figs. 5, 6). Laterally, from the mid line, the fibre cross-sections may change to rhombic or modified rhomb-like. Rhynchonellides with a coarse fibrous type

Table 2. Compilation of the shell microstructure and texture data for the secondary layer in post-Palaeozoic rhynchonellides. Numbers given after the superfamily name in the first column, as for instance 6 (39) for Pugnacoidea, indicating the number of genera for which there are published microstructure data: 6 *versus* the total number of genera in parentheses: (39); *Measurements and descriptive terms in italics* are not originally given in the respective references. Such measurements are taken by us using the published illustrations, and the descriptive terms are deduced from the text and the illustrations. We suspect that most of such measurements are not standard (i.e., taken at the central part of the shell at the maximum shell thickness); * genera for which we suspect some discrepancy (mistake in the papers) of the fibre size or the type of the crura determination are marked with an asterisk. Such data do not fit the hypothesis summarized in Fig. 13.

Superfamily	Family/subfamily	Genus/range	Type microstructure	Fiber size in mm	Homogeneity of the secondary layer	Type of the crura	Reference
Pugnacoidea 6 (39)	Basiliolidae	*Orbirhynchia* Cretaceous	coarse fibrous	w = 35–120; t = 10–50	homogeneous	falciform	Nekvasilova 1974; Smirnova 1984; Motchurova-Dekova 2001
		Lacunosella Middle Jurassic–Early Cretaceous	coarse fibrous	w = 125–130		falciform	Smirnova 1984
		B. (new genus in Dulai et al. in press) Paleocene	coarse fibrous	w = 40–56; t = 19–24	homogeneous	subfalciform	Dulai et al. in press
		Homaletarhynchia (= ex *Cretirhynchia* (*Homaletarhynchia*)) Late Cretaceous	coarse fibrous prevail; sublayers with fine fibrous type	w_1 = 30–45; t_1 = 10–23 w_2 = 30–40; t_2 = 5–12	non-homogeneous	subfalciform	Motchurova-Dekova and Simon 2007
	Erymnariidae	*Erymnaria* Late Cretaceous	coarse fibrous	w = 22–45	homogeneous	septiform	Ali-zade et al. 1981; Motchurova-Dekova and Taddei Ruggiero 2000
		Costerymnaria Late Cretaceous	coarse fibrous	w = 30–55; t = 14–40	homogeneous	septiform	Motchurova-Dekova and Taddei Ruggiero 2000
Rhynchotetradoidea 1 (8)	?Austrirhynchiidae	*Austrirhynchia** Late Triassic		*w = 60; t = 20*		raduliform	Michalík 1993
Wellerelloidea 3 (18)	Wellerellidae	*Euxinella* Late Triassic	*coarse fibrous*	*w = 50-60; t = 25–30*	*homogeneous*	hamiform	Dagys 1974
		? *Robinsonella* Late Triassic	*coarse fibrous?*	*w = 45–55; t = 10–15*	*homogeneous*		Dagys 1974
	?Allorhynchidae	*L.* (new genus in Radulović in press) Early Jurassic	coarse fibrous	w = 40–50; t = 30–35	homogeneous	hamiform	Radulović in press
Rhynchonelloidea 2 (64)	Rhynchonellidae	*Ivanoviella* Middle–Late Jurassic	fine fibrous	w = 15–20		calcariform	Kamyshan and Abdalla 1979
		Grasirhynchia Cretaceous	fine fibrous	w = 15–25; t = 2–5	homogeneous	calcariform	Motchurova-Dekova 2001
Norelloidea 5 (40)	Norellidae	*Monticlarella* Middle Jurassic–Late Cretaceous	coarse fibrous	w = 40–150	*homogeneous*	arcuiform	Nekvasilova 1977; Smirnova 1984
	Frieleiidae	*Frieleia* Paleogene–Recent	coarse fibrous	w = 40–50	*homogeneous*	spinuliform	Motchurova-Dekova et al. 2002
		Parasphenarina Recent	coarse fibrous	w = 50–100; t = 20–40	homogeneous	spinuliform	Motchurova-Dekova et al. 2002
		Manithyris Recent	*coarse fibrous*	*w = 50*		spinuliform	Foster 1974
		Compsothyris Recent	*coarse fibrous*	*w = 40*		spinuliform	Foster 1974

Hemithiridoidea 20 (88)	Cyclothyrididae		*Cyclothyris* Cretaceous	fine fibrous	w = 15–30; t = 2–10	non-homogeneous	raduliform to canaliform	Motchurova-Dekova 2001
			Almerarhynchia Late Cretaceous	fine fibrous	w = 25–35; t = 4–10	homogeneous	canaliform	Motchurova-Dekova 2001
			Fissirhynchia (= *Costirhynchopsis*) Middle–Late Triassic	fine fibrous	w = 38–45	*homogeneous*	raduliform	Radulović 1992
			Fissirhynchia Late Triassic–Early Jurassic	fine fibrous	*w = 25; t = 10*		canaliform	Michalík 1993
			Globirhynchia Middle Jurassic	fine fibrous	w = 30–42		canaliform	Kamyshan and Abdalla 1979
			Lamellaerhynchia Early Cretaceous	fine fibrous	w = 10–30; t = 3–15	non-homogeneous	canaliform	Motchurova-Dekova 2001
			Praecyclothyris (= *Septaliphoria*) Middle Jurassic–Early Cretaceous	fine fibrous	w = 30–42		canaliform	Kamyshan and Abdalla 1979
			Septaliphoria Middle Jurassic–Early Cretaceous	fine fibrous	w = 30–42		canaliform	Kamyshan and Abdalla 1979
			Serbiorhynchia (= *Torquirhynchia*) Middle–Late Jurassic	fine fibrous	w = 23–26	*homogeneous*	raduliform to canaliform	Radulović 1991
	Tetrarhychiidae	Tetrarhynchiinae	*?Belbekella* Lower Cretaceous	fine fibrous	w = 15–40; t = 2–6		raduliform	Motchurova-Dekova 2001
		Gibbirhynchiinae	*Burmirhynchia* Middle Jurassic	fine fibrous	w = 26–29	*homogeneous*	raduliform	Radulović 1991
		Kallirhynchiinae	*Rhactorhynchia* Middle Jurassic–Late Jurassic	fine fibrous	w = 30–42		raduliform to canaliform	Kamyshan and Abdalla 1979
		Isjuminellinae	*Sardorhynchia* (= *Isjuminella*) Middle Jurassic	fine fibrous	*w = 35–45; t = 10–12*	*homogeneous*	raduliform	Taddei Rugiero and Ungaro 1983
			Mosquella Late Jurassic	fine fibrous	w = 5–7		raduliform	Kamyshan and Abdalla 1979
			Russirhynchia Late Jurassic	fine fibrous	w = 10–15		raduliform	Kamyshan and Abdalla 1979
		Viarhynchiinae	*Septatoechia* Cretaceous	fine fibrous	w = 15–40; t = 8–30	non-homogeneous	raduliform	Motchurova-Dekova 2001
			Antulanella Barremian	fine fibrous	w = 15–30; t = 5–10	homogeneous	widened distal ends; raduliform or canaliform	this paper
		Cretirhynchiinae	*Cretirhynchia* sensu lato Late Cretaceous	fine fibrous	w = 20–40; t = 10–25	homogeneous	raduliform	Motchurova-Dekova 2001
			Cretirhynchia plicatilis Late Cretaceous	fine fibrous	w = 15–30; t = 8–10	homogeneous	raduliform	Motchurova-Dekova et al. in press
			Burrirhynchia Cretaceous	fine fibrous	w = 20–50; t = 5–10	homogeneous	raduliform	Motchurova-Dekova 2001
	Notosariidae		*Notosaria* Miocene–Recent	fine fibrous	*w = 7–15; t = 4*		raduliform	Williams 1968
	Uncertain		*C.* (new genus in Lee and Motchurova-Dekova in press) Late Cretaceous	fine fibrous	w = 8–30; t = 0.5–7	non-homogeneous; two sublayers	raduliform	Lee and Motchurova-Dekova in press

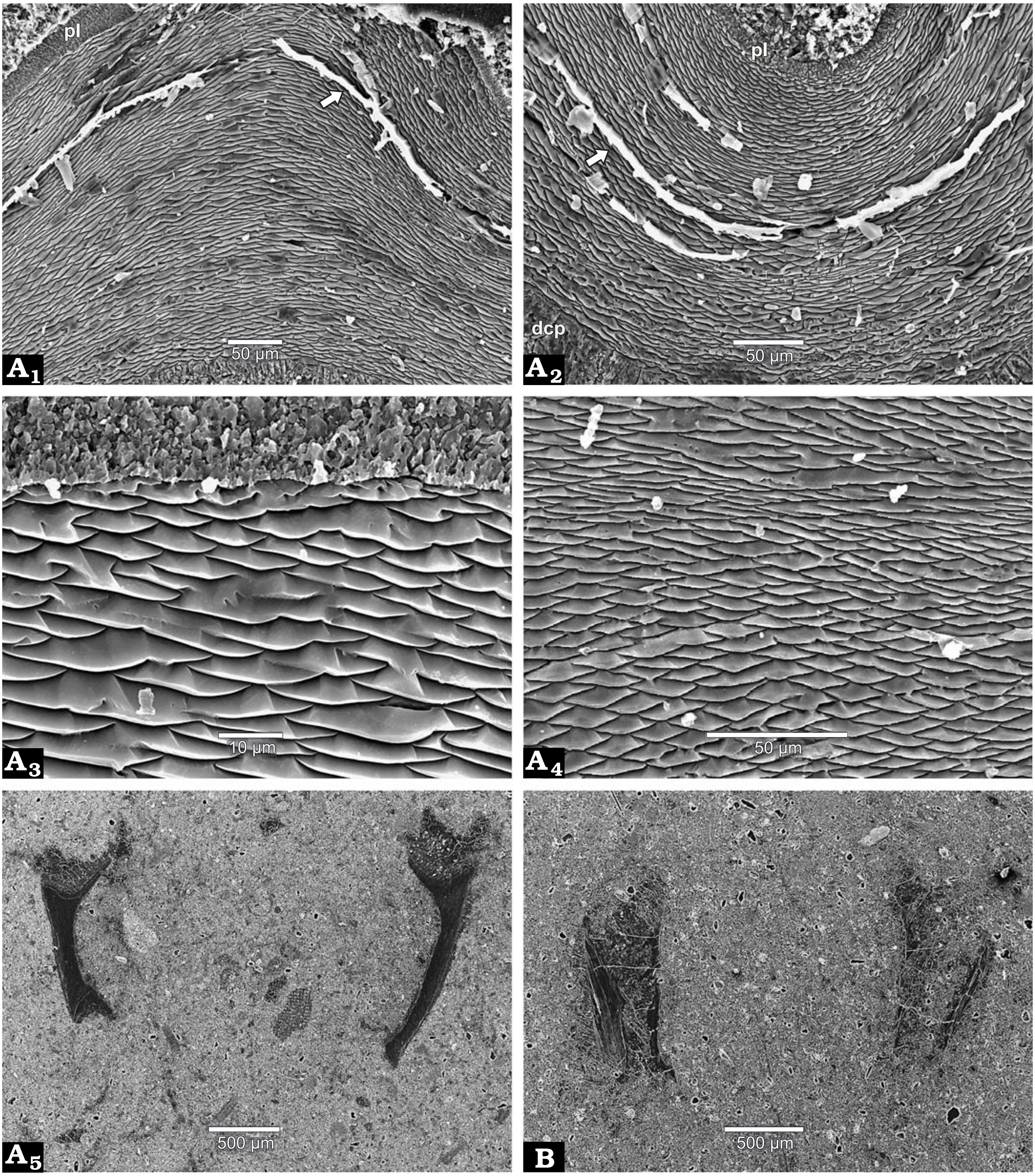


Fig. 10. Rhynchonellide brachiopod *Antulanella pancici* (Antula, 1903), Barremian, Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. **A**. SEM micrographs of transverse sections of the shell RGF VR 24/61. A_1. Rib of ventral valve, primary microgranular layer (pl), secondary layer. Silicified organic sheets crossing the section (arrow). A_2. Sulcus of ventral valve, primary microgranular layer (pl) above, secondary layer with finer fibrous sublayer, overgrown by diagenetic calcite prisms (dcp). Subparallel silicified organic sheets crossing the shell (arrow). A_3. Boundary between the primary microgranular layer and secondary fibrous layer, finer anisometric fibres in the outermost part of the shell, close to boundary; rib of a ventral valve. A_4. Anisometric anvil-like fibres of the secondary layer in a sulcus. A_5. "Diabolo" type sections of the crura. **B**. Distal splitting of the crura into parallel plates; better seen on the right crus, specimen RGF VR 25/484 (SEM micrograph taken from an acetate peel).

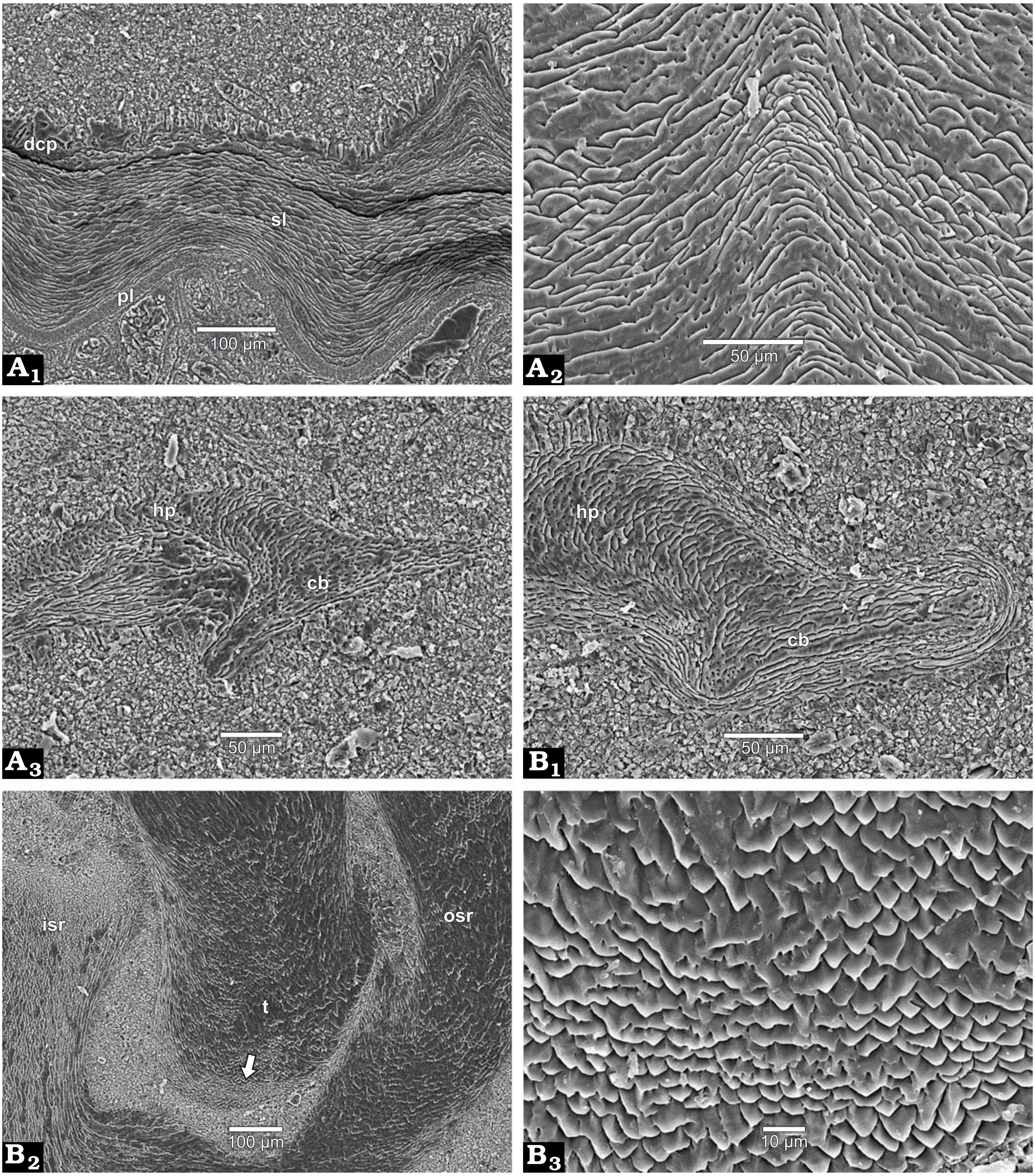


Fig. 11. Rhynchonellide brachiopod *Antulanella pancici* (Antula, 1903), Barremian, Crnoljevica, Svrljiške Planine Mountains, eastern Serbia. **A**. SEM micrographs of transverse sections of the shell RGF VR 25/310. A_1. Section through two ribs, sulci and euseptoidum; preserved primary layer (pl) and secondary layer (sl) overgrown with diagenetic calcite prisms (dcp). A_2. Section showing modified fibres of the euseptoidum. A_3. Hinge plate (hp) and crural base (cb). **B**. SEM micrographs of transverse sections of the shell RGF VR 24/61. B_1. Hinge plate (hp) and crural base (cb). B_2. Right tooth (t), inner socket ridge (isr) and outer socket ridge (osr). B_3. Close-up of fibres of hinge tooth from the area arrowed in B_2 showing also slight diagenetic fusion of the fibrous elements.

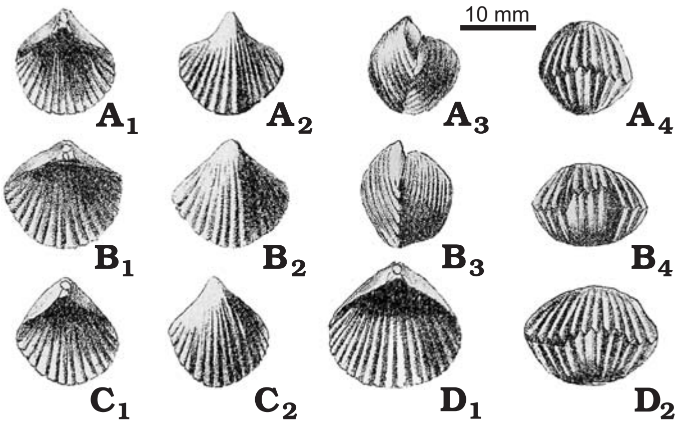


Fig. 12. Antula's (1903: pl. 2: 1–4) original drawings of four specimens of *Antulanella pancici* (Antula, 1903), from the Barremian, Crnoljevica, Svrljške Planine Mountains, eastern Serbia. **A**. Adult specimens, dorsal (A_1), ventral (A_2), lateral (A_3), and anterior (A_4) views. **B**. Fully adult specimen, dorsal (B_1), ventral (B_2), lateral (B_3), and anterior (B_4) views. **C**. Dorsal (C_1) and ventral (C_2) views. **D**. Dorsal (D_1) and anterior (D_2) views.

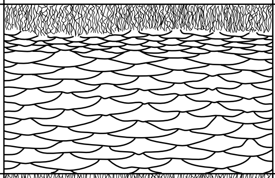
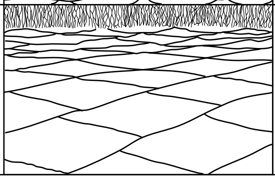
Type of secondary layer microstructure	Stylized section of the shell	Associated type of crura	Superfamilies
Fine fibrous		raduliform and variations canaliform calcariform	Rhynchonelloidea Hemithiridoidea
Coarse fibrous		falciform subfalciform septiform hamiform arcuiform spinuliform	Pugnacoidea Wellerelloidea Norelloidea

Fig. 13. Correlation of shell microstructure and type of crura in the various superfamilies of post-Paleozoic Rhynchonellida (unpublished data of NM-D and Miguel Manceñido; published with permission).

microstructure of the secondary layer (Table 2, Fig. 13) have larger, most commonly rhombic (Fig. 14B), but also rectangular or subquadrate sections of fibres.

Published data concerning the shell microstructure of rhynchonellides are still scarce. To the best of our knowledge, of all 257 post-Palaeozoic rhynchonellide genera included in the revised Treatise (Savage et al. 2002) and published after 2002, data (sometimes very fragmentary) are known only for 37 genera, that is some 14.4% of all Mesozoic and Cenozoic genera. The available shell microstucture data about the secondary layer in post-Palaeozoic rhynchonellides are summarized in Table 2. Most of the papers provide brief mention of, or just illustrate, a single fragment of a cross section. There is no evidence that such sections have been cut in any consistent standardized fashion (Sass and Monroe 1967). In the majority of the papers, there are only short descriptions of the shell microstructure based on a small number of individuals from one species only of a given genus.

The data compiled in Table 2 represent a very preliminary attempt to summarize the current state of knowledge on rhynchonellide microstructure and texture but not necessarily providing microstructural diagnoses of respective genera. In papers published after 2000 there has been a tendency to standardize the measurements and describe morphologically and measure the cross sections of the fibres in the mid shell length or at the maximum shell thickness. A future goal should be that such standard measurements are collected from a set of species for all genera. Additionally, more characters may be included, e.g., peculiarities of the longitudinal sections, which are still practically unknown.

Lee and Motchurova-Dekova (in press) suggested that the crura of the raducal group (*sensu* Manceñido 2000) are associated with *fine fibrous rhynchonellidine type*, as has been noted here for *Antulanella*, while the crura of the septifal group (*sensu* Manceñido 2000) are characterized as coarse fibrous basiliolidine type. We will add here that coarse fibrous type might also be typical of genera having crura from the arcual group (*sensu* Manceñido 2000). The correlation of crural types with the two types of secondary layer microstructure is illustrated in Fig. 13. This idea will be fully discussed elsewhere (paper in preparation by NM-D and Miguel Manceñido).

A character which is still poorly investigated and could possibly have potential use in taxonomy of rhynchonellides is the microtexture of the shell. Texture is here used in its petrological meaning in order to describe the geometric aspect of, and the mutual relations among, its component particles. It should include size, shape and arrangement of the constituent elements. Thus the description of the two types of shell microstructure could be regarded as one of the elements of the microtexture describing the size and the shape of the cross sections of the fibres. Regarding the constituent elements of the shell at the microstructural level, it was noted that some of the investigated genera have a monotonous and homogeneous arrangement of the fibres in the secondary layer (Fig. 14B, D), while in others, the secondary layer is built of several bundles (sheaves) of differently oriented

Fig. 14. SEM micrographs of transverse sections of the shells. **A**. "*Cretirhynchia*" (*Harmignirhynchia*) *obourgensis* Simon and Owen, 2001, IRScNB: IST 10847, holotype, Late Campanian, *Belemnitella woodi* Zone, Harmignies, Belgium. Non-homogeneous secondary layer in ventral valve. Note the primary microcrystalline layer (top) and sublayers of rhombic and anvil-like fibres. Specimen sectioned and figured by Simon and Owen (2001: 89, fig.17). **B**. *Orbirhynchia mantelliana* (J. de C. Sowerby, 1826), specimen NMNHS 31365, Middle Cenomanian, Cran d'Escalles, Cap Blanc-Nez, Pas-de-Calais,

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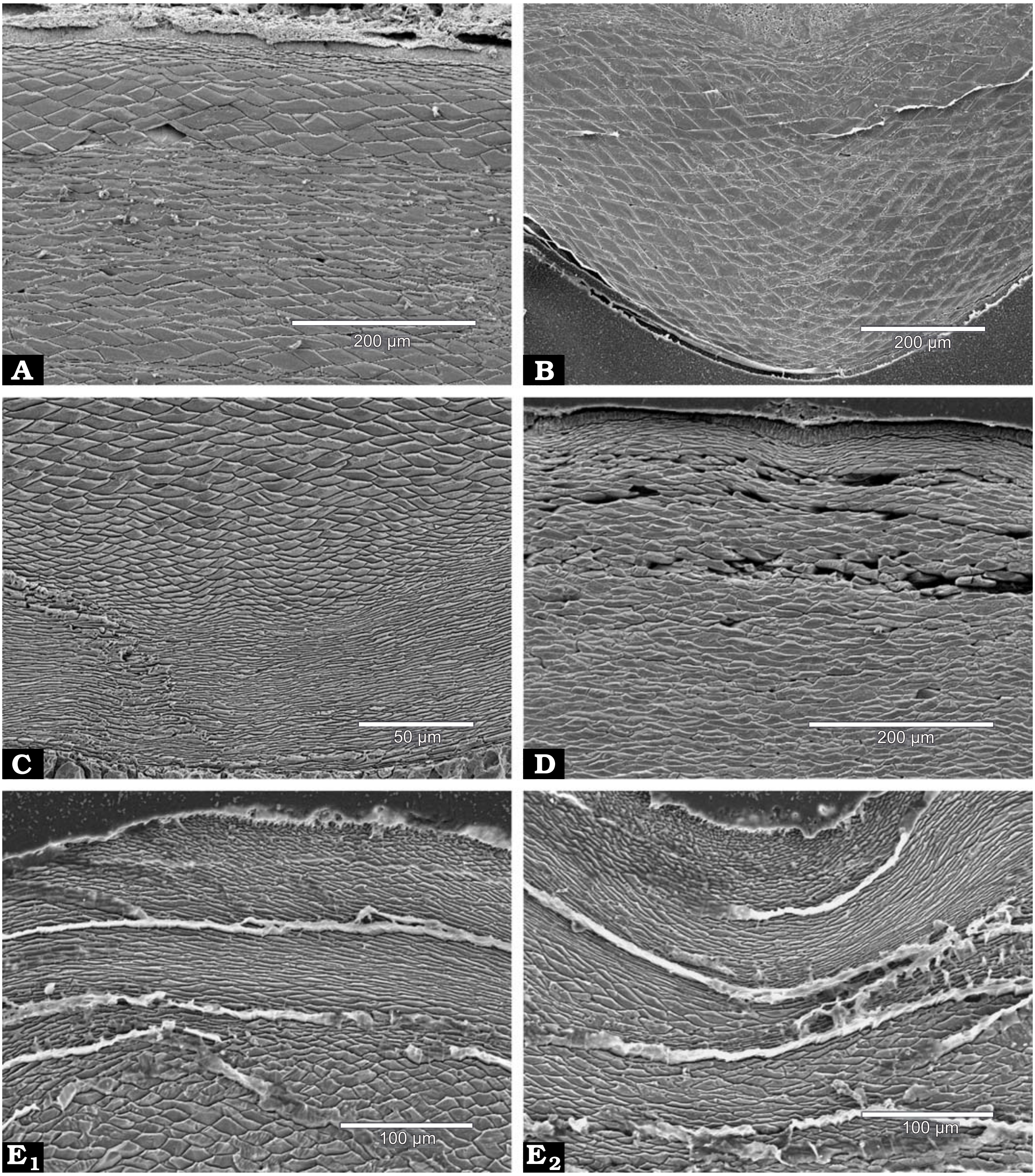

France. Section through a rib in the dorsal valve showing the homogeneous arrangement of rhombic fibres, coarse fibrous type microstructure, thin portion of the primary layer preserved. **C**. Gen. et sp. nov. to be described in Lee and Motchurova-Dekova (in press), specimen NMNHS F-31311, Campanian–Maastrichtian, Kahuitara Tuff, Tupuangi Point, Pitt Island, New Zealand. Non-homogeneous secondary fibrous layer, fine fibrous type, internal surface of the shell below, external surface not seen, note the inner sublayer of finer fibres and the outer sublayer of larger fibers. **D**. *Burrirhynchia leightonensis* (Walker in Lamplugh and Walker, 1903), specimen BMNH BF 62, Early Albian, Leighton Buzzard, Bedfordshire, England. Homogeneous arrangement of the fibres in the secondary layer, fine fibrous type. **E**. *Septatoechia inflata* Titova in Lobacheva and Titova, 1977, specimen NMNHS 31364, Late Maastrichtian, Tuarkir, Turkmenistan. Complete sections of the ventral valve in a rib (E_1) and sulcus (E_2), respectively. Internal surface of the shell below. Sections showing non-homogeneous arrangement of different sublayers of fine fibrous type. Boundaries between the sublayers marked by high relief silicified organic sheets.

fibres, each differing in the shape and size of their cross sections. Such texture is here described as non-homogeneous (Fig. 14A, C, E_1, E_2; see also Table 2). It is possible that the homogeneity of the arrangement of the fibres in the secondary layer could have taxonomic importance at the subfamily, genus, or species level. However, its potential at family and subfamily levels is still unclear, since in most cases there are data only about a single representative of the families.

The shell microstructure and microtexture of Tetrarhynchiidae

The following is a review including some new data about the shell microstructure and microtexture of some representative genera of the family Tetrarhynchiidae. Our aim is to establish whether shell microstructural and microtextural characters can potentially be used to discriminate new genera and assist placement of taxa in specific families and/or subfamilies.

The new genus *Antulanella* displays a typical fine fibrous microstructure, which is consistent with its placement within the Hemithiridoidea. Furthermore, *Antulanella* is classified in the Tetrarhynchiidae because of external and internal similarities with genera allocated to this family and, more specifically, the subfamily Viarhynchiinae mainly because of its closest similarity to the type genus *Viarhynchia* (Table 1).

Among genera belonging to Viarhynchiinae, the microstructural characters have been investigated only in *Septatoechia* (Motchurova-Dekova 2001). To avoid confusion, in Table 1 we provide data only on its type species (*S. inflata*), as we consider some of the species presently attributed to *Septatoechia* may belong to another genus. *Septatoechia* differs from *Antulanella* in having a very thick shell, reaching 1–2 mm, composed of many packages of differently oriented rhombic or anvil-like fibres (Fig. 14E_1, E_2). The primary layer is also thicker—30–50 µm. The cross sections of the fibres in *Septatoechia* are somewhat larger and thicker than in *Antulanella* (15–40 µm wide and 8–30 µm thick). *Septatoechia* displays a microstructure of the fine-fibrous type, however, it should be noted that the cross sections of the fibres are somewhat larger than those typical for the fine fibrous type microstructure. The most important differences between the two genera are (i) the much thickened shell and consequently much thicker myotest, and (ii) the clearly non-homogeneous microtexture of *Septatoechia*. All these microstructural differences between *Antulanella* and *Septatoechia* may suggest revising the detailed taxonomic position of the latter. These microstructural differences prompted us to review more critically the external and internal characters of the shell morphology in viarhynchiines (see Table 1). Comparing the diagnostic characters for *Viarhynchia, Hemithyropsis*, *Septatoechia*, and *Antulanella*, it can be noted that *Septatoechia* differs macroscopically in some important characters from the other three genera of the same subfamily, viz. by having: (i) a much more incurved beak, (ii) a well developed fold and sulcus, (iii) parallel to ventrally convergent dental plates and (iv) a very high slender dorsal septum and a possible septalium (Table 1). These discrepancies could perhaps lead to considering the removal of *Septatoechia* from the Viarhynchiinae. However, the microstructure of *Viarhynchia* requires to be checked in order to test whether or not *Antulanella* and the type genus of the Viarhynchiinae have similar microstructures.

For the subfamily Cretirhynchiinae, scarce data are known for *Cretirhynchia* and *Burrirhynchia* only, both genera having fine fibrous secondary layer (Motchurova-Dekova 2001; Motchurova-Dekova et al. in press). *Burrirhynchia* has a secondary layer microtexture similar to that of *Cretirhynchia* sensu stricto (Fig. 14D; Motchurova-Dekova 2001), homogeneous, which supports the allocation of the two genera together in one subfamily. However, the fibre size in *Burrirhynchia* is somewhat larger (Table 2). The data published in Motchurova-Dekova (2001) on the genus *Cretirhynchia* were not based on the type species. Only recently Motchurova-Dekova et al. (in press) established that the type species *C. plicatilis* possesses a typical homogeneous fine fibrous microstructure and texture. A subsequent investigation of some other species originally referred to *Cretirhynchia* revealed a coarse fibrous microstructure, which served as the basis for a thorough taxonomic revision which resulted in their removal to a separate new genus within the Pugnacoidea (Motchurova-Dekova and Simon 2007, see also Table 2 for *Homaletarhynchia*). Details about the microstructure of *Cretirhynchia* will be discussed in a separate paper. It should be noted that the shell microstructure study of *Cretirhynchia* is the first instance where certain species attributed to one genus (*Cretirhynchia*), in one superfamily (Hemithiridoidea), have been transferred to a new genus (*Homaletarhynchia*) within another superfamily (Pugnacoidea) based primarily on the shell microstructure differences (Motchurova-Dekova and Simon 2007). Data on other representatives of Tetrarhynchiidae are summarized in Table 2.

Comparing *Antulanella* with genera from different families, the following conclusions can be reached. *Antulanella* has several external and internal features in common with the genus *Cyclothyris* M’Coy, 1844 (subfamily Cyclothyridinae Makridin, 1955, family Cyclothyrididae Makridin, 1955), including the rimmed hypothyrid foramen, ventrally divergent dental plates, crescentic crural bases (i.e., “forked” hinge plates *sensu* Owen 1962), and a reduced dorsal median septum. The new genus is distinguished from *Cyclothyris* externally by its smaller size, subspherical shell and constant lack of asymmetry (this latter feature allocating the two genera to two different families). Although they both display similarities in fine fibrous structure and in the size and shape of fibres, the shell microstructure of the two genera also differs. Motchurova-Dekova (2001) studied the shell microstructure of five species of *Cyclothyris* and emphasized that all species are characterized by the predominance of anisometric anvil-shaped (to rarely rhomboidal) fibres in the secondary layer, 15–30 µm wide and 2–10 µm thick, shell thickness 0.3–1 mm, and thickness of the primary layer 50–80 µm. In contrast, the shell thickness in *Antulanella* is significantly less, 130–450 µm, and the primary layer is thinner, 20–30 µm. In *Cyclothyris*, the secondary layer is usually composed of several packages of fibres with different orientations, while in *Antulanella* this layer is homogeneous. It is maintained that all these microstructural differences are important enough for the two genera to be placed in different families or subfamilies.

Palaeoecologic, taphonomic and palaeobiogeographic implications

Antulanella pancici was collected in association with autochthonous elements including other brachiopods (rhynchonellides, terebratulidines, and terebratellidines), bivalves, echinoids, benthic foraminifera, and green algae, as well as allochthonous nautiloid cephalopods. The characters of the sedimentary rocks (bioclastic limestone, marly limestone, and clayey limestone) in which the brachiopods occur suggest a depositional environment covered with fine mud. Fine-grained clastic material was also noted as a sediment component, which is a likely indication of coastal proximity. The bioclastic limestone contains fossils belonging to a diverse population inhabiting a shallow-water environment of a partly protected carbonate platform. The fossil content of the upper beds in the section include sponge spicules and Lenticulinae, which indicate a deepening and less energetic environment below wave base.

Specimens of *Antulanella pancici* and other brachiopods were infilled with the same sediment that encloses them, which suggests their fossilisation in the environment of their existence. There are both adult and juvenile forms. All the specimens have both valves preserved, and are very rarely mechanically damaged. Specimens are variously oriented (no dominant direction was noted) and sorted. Thus, it is suggested that the shells were post-mortally transported only a very short distance away from their life position, or were even buried *in situ*.

Representatives of *Antulanella pancici* and other rhynchonellides populated a muddy sea bottom of the inner sublittoral. They probably lived on sediments with their beaks directed into the sea bed, semi-buried in the sediments. The very small foramen suggests the presence of a thin rooted pedicle, which probably fixed or served to anchor the brachiopod in place during periods of stronger bottom currents. On the contrary, the presence of a relatively large foramen and pedicle collar in various associated terebratulides and terebratellides suggests that each lived attached by its pedicle to solid biogenic remains or pebbles.

The Barremian brachiopod fauna from Crnoljevica adds to our understanding of the palaeobiogeography of the Early Cretaceous in Europe. Most brachiopod species found at Crnoljevica, except the two new Antula (1903) species (*Antulanella pancici* and *Timacella timacensis*), are widely distributed along the northern margin of Tethys and closely resemble the Early Cretaceous fauna of the French and Swiss Jura (Jura fauna *sensu* Middlemiss 1984; Subtethyan fauna *sensu* Michalik 1992; Gaspard 1999). Numerous Early Cretaceous Jura-type brachiopod taxa, even those previously considered to be strictly confined to the Jura province, are now reported from southeastern Romania (Georgescu 1996) and eastern Serbia (Radulović 2000). Thus it seems that the faunal boundary between Peritethyan and Jura provinces is rather indistinct.

Concluding remarks

A new rhynchonellide brachiopod genus *Antulanella* is proposed based on examination of the external and internal morphologies and shell microstructure of "*Rhynchonella pancici*", a common species in the Barremian shallow-water limestones of the Carpatho-Balkanides of eastern Serbia. Based on similarities with the closest genus *Viarhynchia*, *Antulanella* is assigned to the subfamily Viarhynchiinae, family Tetrarhynchiidae, thus further extending backwards in time the range of the Viarhynchiinae from Barremian to Maastrichtian. A time gap still remains between *Antulanella* and the Campanian forms, thus future representatives may be expected to occur between Barremian and Campanian.

Data on shell microstructure of post-Palaeozoic rhynchonellides are still scarce. However, it is possible to distinguish two types of secondary layer microstructure (i) fine fibrous, typical of the superfamilies Rhynchonelloidea and Hemithiridoidea and (ii) coarse fibrous, typical of the superfamilies Pugnacoidea, Wellerelloidea, and Norelloidea. The new genus *Antulanella* is characterized by a fine fibrous microstructure of the secondary layer, which is compatible with its allocation in the Hemithiridoidea.

As only scarce data are accessible it is still too early to appropriately evaluate the taxonomic importance of the shell microstructure for low level taxonomy. However, the case of *Antulanella* and *Septatoechia* described above suggests that such potential exists. Also in the case of *Cretirhynchia*, it has been possible to use the type of the secondary layer microstructure and texture to remove some species wrongly classified in that genus based on poorly investigated material (Motchurova-Dekova and Simon 2007). Thus, we suggest that shell microstructure has a good and not yet fully exploited potential for taxonomic purposes. This, however, requires extensive investigations on larger numbers of adult specimens of a given species and on representative numbers of species of each genus.

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