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ABSTRACT

A new rhynchonellide brachiopod genus and species, *Skadarirhynchia semicostata* gen. et sp. nov., is described from the late Pliensbachian of Livari, Rumija Mountain, southeastern Montenegro. It occurs in shallow-water brachiopod-crinoid packstone beds (bioclastic limestones) of the periplatform facies of the Dinaric Carbonate Platform. Stratigraphy is constrained by means of $^{87}Sr/^{86}Sr$ dating indicating a late Pliensbachian age, and by the fact that the brachiopod beds lie immediately below the Toarcian marly limestones, which is consistent with the regional stratigraphical position. The new species has a circular to roundly pentagonal outline and semicostate shells with 10–12 strong angular ribs. Internally, it shows reduced dental plates, narrow and thin hinge plates inclined dorsally with small crural bases, crescent-like and laterally convex, and hamiform crura. The shell microstructure of the new taxon is characterised by a homogeneous secondary layer (a single layer with no sublayers) built of rhombic fibres that are typically of coarse-fibrous type (eurinoid pattern) 35–50 μm wide and 20–30 μm thick. Other co-occurring rhynchonellide species such as *Prionorhynchia fraasi* and *Cuneirhynchia dalmasi* are also described. Shell microstructures for the genus *Cuneirhynchia* are presented.

Introduction

Some of the first studies that focused on the Lower Jurassic brachiopods of the Montenegrin Dinaric Carbonate Platform were published in the second half of the nineteenth century. Eichenbaum (1883), Bittner (1895), and Mihajlović (1955) described the Sinemurian rhynchonellines from the white recrystallised limestones (rudstones) of Smokovac (near Risan, on the Gulf of Boka Kotorska). From the same locality, terebratulides were discussed and then described by Sandy et al. (2018, 2021, 2022). Pliensbachian brachiopod species from the marly limestones of Lovćen Mountain were described by Ćirić (1949). Bešić (1959) and Vörös (1980, 1984) considered this association to be Pliensbachian in age. Radulović (2008) described a new rhynchonellide genus and species *Livarirhynchia rajkae* and recorded the rhynchonellids *Prionorhynchia fraasi* and *Cuneirhynchia dalmasi* from the Pliensbachian of Livari (Rumija Mountain). Recently, Radulović (2022) erected the new rhynchonellide genus and species *Sepkoskirhynchia sphaerica* from the upper Pliensbachian brachiopod-crinoidal wackestone/packstone deposits. Toarcian brachiopods from the Rumija–Lovćen region are unknown.

At the beginning of the last century, Martelli (1906) described brachiopods from dark-grey oolitic limestones at Tijani and Livari, on the north-eastern slopes of Rumija Mountain and Čekanje (Lovćen Mountain). From these localities, he described 13 rhynchonellide taxa (including two new species and one subspecies) and four terebratulide taxa (one new species). By comparing brachiopod faunas from different localities in the Apennines and Alps, Martelli (1906) concluded that the brachiopods of Tejani, Livari and Čekanje were early Middle Jurassic (Aalenian).

The purposes of the present study are as follows: (i) to erect the new rhynchonellide genus and species *Skadarirhynchia semicostata* based on external, internal, and microstructural characters; (ii) to compare it with morphologically similar Lower Jurassic species of the genus *Sepkoskirhynchia* and *Soaresirhynchia* (family Basiliolidae); (iii) to describe the co-occurring rhynchonellide species from this area; (iv) to provide new results on the litho- and biostratigraphy of the study area; (v) to determine the relative age of the rhynchonellide assemblage based on $^{87}Sr/^{86}Sr$ dating; (vi) to reconstruct the palaeoenvironmental setting of the described rhynchonellide assemblage based on other associated brachiopod elements and facies relationships.

Geological setting

Rumija Mountain is located in the south-eastern margin of the Dinaric Carbonate Platform (Figure 1A; Radoičić 1966, 1982, 1987; Radoičić and D'Argenio 1999; Črne and Goričan 2008; Radulović 2008, 2022). The collapse of the internal shallow-water platform system, well established in the Dinaric area, by rifting and subsequent drowning triggered a high diversity of ecological niches and biotas. These events created a new palaeogeographic feature during the Lower Jurassic with a narrower platform space, as well as extensive and very long angular slopes. In some segments of the platform, slopes (differentially subsiding blocks), depressions and adjacent-open, semi-open and/or euxinic basins were formed.

Deposition of the Lower Jurassic micritic limestone above the Upper Triassic Dachstein Formation at Livari and Tejani was caused by drowning of the marginal areas of the Dinaric

Carbonate Platform around the Triassic–Jurassic boundary that primarily occurred due to tectonic subsidence (Radoičić 1987).

During the Early Jurassic and the Early Middle Jurassic, internal platform facies were deposited in the western part of the Rumija Mountain, whereas marginal platform belt facies, including also the Lovćen-Rumija depression facies, are characteristic of the successions from the central and eastern Rumija Mountain. The Lower Jurassic successions of these and other adjacent depressions of the Dinaric Carbonate Platform consist of thin- to medium-bedded, variably marly, nodular limestone containing brachiopods, crinoids and their fine detritus, and lagenid foraminifers among others (Radoičić 1987).

A transition from lithiotid limestone to wackestone and packstone with intraclasts is followed by peloidal grainstone, interpreted as a transition from shallow-water environments of the inner platform to a higher-energy environment of an open platform.

Along the Rumija Mountain, the Lower Jurassic–Lower Middle Jurassic succession laterally changes from carbonate facies (lower part with lithiotid limestone to the wackestones/packstones with intraclasts, succeeded by peloidal grainstones) in the shallow water environment of the inner part of the internal platform in the north-western part to those of the platform margin. This succession is characterised by dispersed coral-spongiomorph-sphinctozoan patches (in which lithiotids are sometimes observed) or knoll reefs, which gradually pass into deeper facies of the periplatform area in the central part, i.e. micritic limestones, fine-grained calcareous turbidites with chert, oolitic limestones, and brachiopod and crinoidal limestone beds, locally with chert, whereas farther eastwards the limestones are completely silicified (Miladinović 1964).

The rhynchonellide specimens currently under investigation were collected from the dark-grey Lower Jurassic bioclastic limestones (layers 10–40 cm thick) from the village of Livari exposed on the northeastern slope of Rumija Mountain, southern Montenegro (Figure 1B; geographical coordinates: 42° 07' 32"N; 19° 12' 37"E).

The Lower Jurassic rocks of the Livari succession have a total thickness of about 280 m (Figure 2) and were described by Čađenović et al. (2005, 2008) and Radulović (2022). At Livari, the Upper Triassic Dachstein limestones (Norian–Rhaetian) are directly overlain by 40 m of mudstones and wackestones with peloids, echinoderm fragments, ooids, and rare foraminifers (Lenticulina sp., Frondicularia sp., Ophthalmium sp., textularids).

The next unit, 60 m thick, is represented by resedimented limestones (packstones to wackestones) and mostly contains peloids and echinoderm fragments, foraminifers (Lenticulina sp., Frondicularia sp., Ophthalmium sp.), ooids and sponge spicules. The limestones are overlain by chert-free oolitic packstones, 45 m thick, with ooids, echinoderm fragments, and peloids.

Above these, 75 m of oolitic packstone levels were deposited, with cherts and peloids as well as echinoderm fragments, with intercalations of marly limestones. The uppermost 20 m of the Pliensbachian succession consists of bioclastic limestones with abundant brachiopods and crinoids. This succession consists of micritic limestone beds (wackestones/packstones) with crinoid ossicles and fine crinoidal detritus, very small echinoid spines, some bryozoans and rare foraminifers (Agerella martana, Spirillina sp., Lenticulina sp., Frondicularia sp., Trocholina sp.), rare ooids and mud-supported crinoidal packstones predominantly with crinoid fragments, sponge spicules, bryozoans, and a few lagenid foraminifers (Figure 3).

In thin-section, micrite matrix predominates, and the abundance of crinoids, brachiopod fragments and so on (Figure 3) indicates the occasional effect of higher energy currents, waves and tides. Observed black concentrations are most probably dispersed ferruginous matter whose presence indicates oxidation conditions. The bioclasts were not sorted; and judging by their shapes, they were not transported far. Their accumulation took place in a protected low-energy part of an inner shelf with a gentle slope.

In these layers, rhynchonellide brachiopods were observed, represented by Prionorhynchia fraasi (Oppel 1861), Cuneirhynchia dalmasi (Dumortier 1869), Livarirhynchia rajkae Radulović 2008, Sepkoskirhynchia sphaerica Radulović 2022 and the terebratulide genus Rhapidothyris. Ammonites and planktonic foraminifers are absent.

This part of the succession of brachiopods and crinoids is overlain by 10 m of Toarcian marly limestones alternating with marlstone with rare radiolarians, foraminifers and sponge spicules, indicating the deepest water depositional environment of the section (Črne and Goričan 2008; Čađenović et al. 2008). The observed succession ends with 30 m of early Middle Jurassic oolitic limestones, from which Martelli (1906) collected brachiopods. According to Alméras (1964), all the species figured and described by Martelli are Aalenian in age.
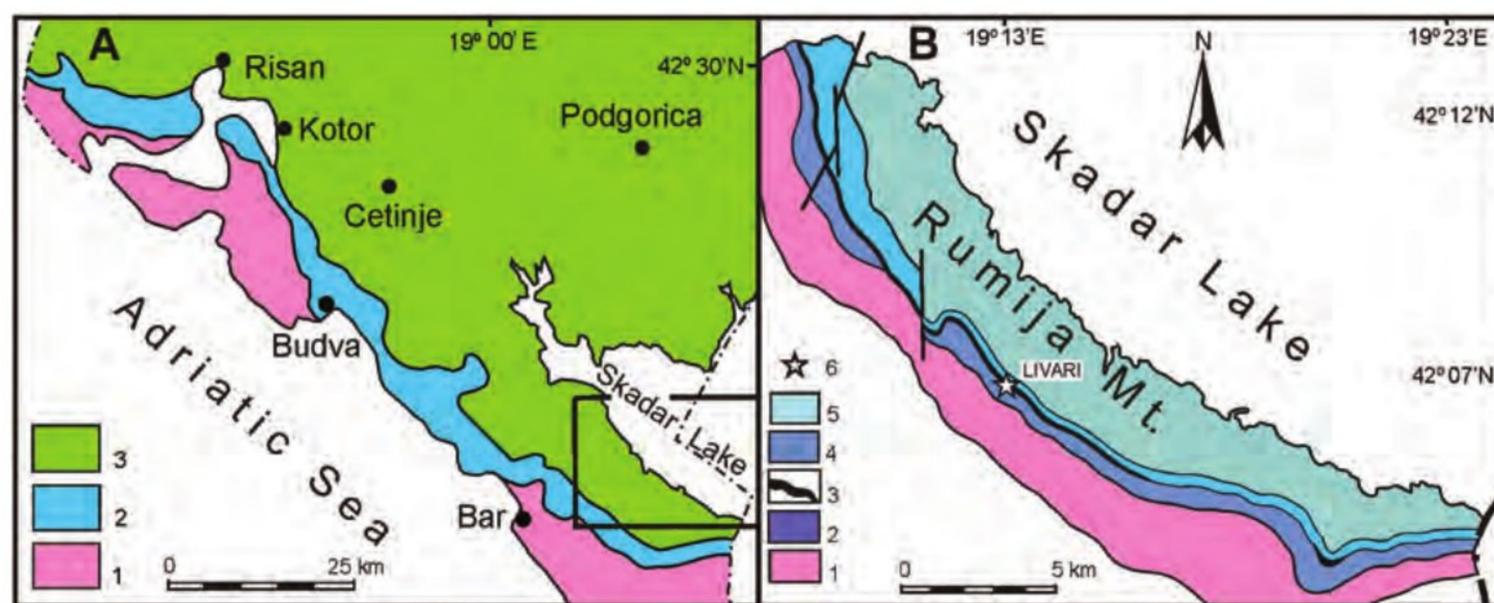
Figure 1. (A) Geological map of southern Montenegro; 1, Adriatic Carbonate Platform; 2, Budva Basin; 3, Dinaric Carbonate Platform; the study area is indicated by the rectangle. (B) Geological map of the northern Rumija Mountain area, modified after Miladinović (1964) ; 1, Upper Triassic (Norian–Rhaetian) limestones and dolomites; 2, Hettangian – lower Pliensbachian micritic limestones with cherts and ooidal limestones; 3, upper Pliensbachian peloidal limestones with brachiopods (2 and 3 periplatform facies); 4,Toarcian marly limestones and marlstones; 5, Middle Jurassic (Aalenian bioclastic limestones with brachiopods and crinoids and predominantly Bajocian–Bathonian ooidal limestones) and Upper Jurassic reefal limestones (marginal platform area facies); 6, Fossiliferous locality.

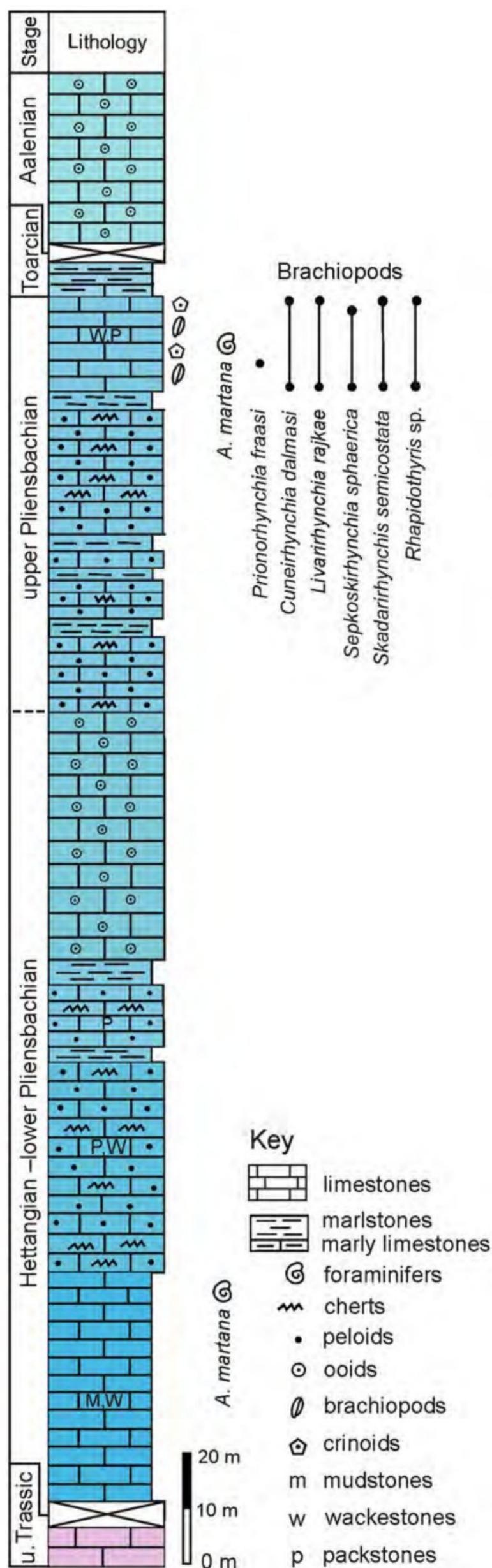**Figure 2.** Lower Jurassic lithostratigraphic section from Livari, modified after Črne and Goričan (2008), showing the distribution of brachiopod taxa. In the section, only the first and last occurrence of Agerella martana is indicated (Črne and Goričan 2008; present study). The RGB Color Codes are according to the Commission for the Geological Map of the World (CGMW), Paris, France.
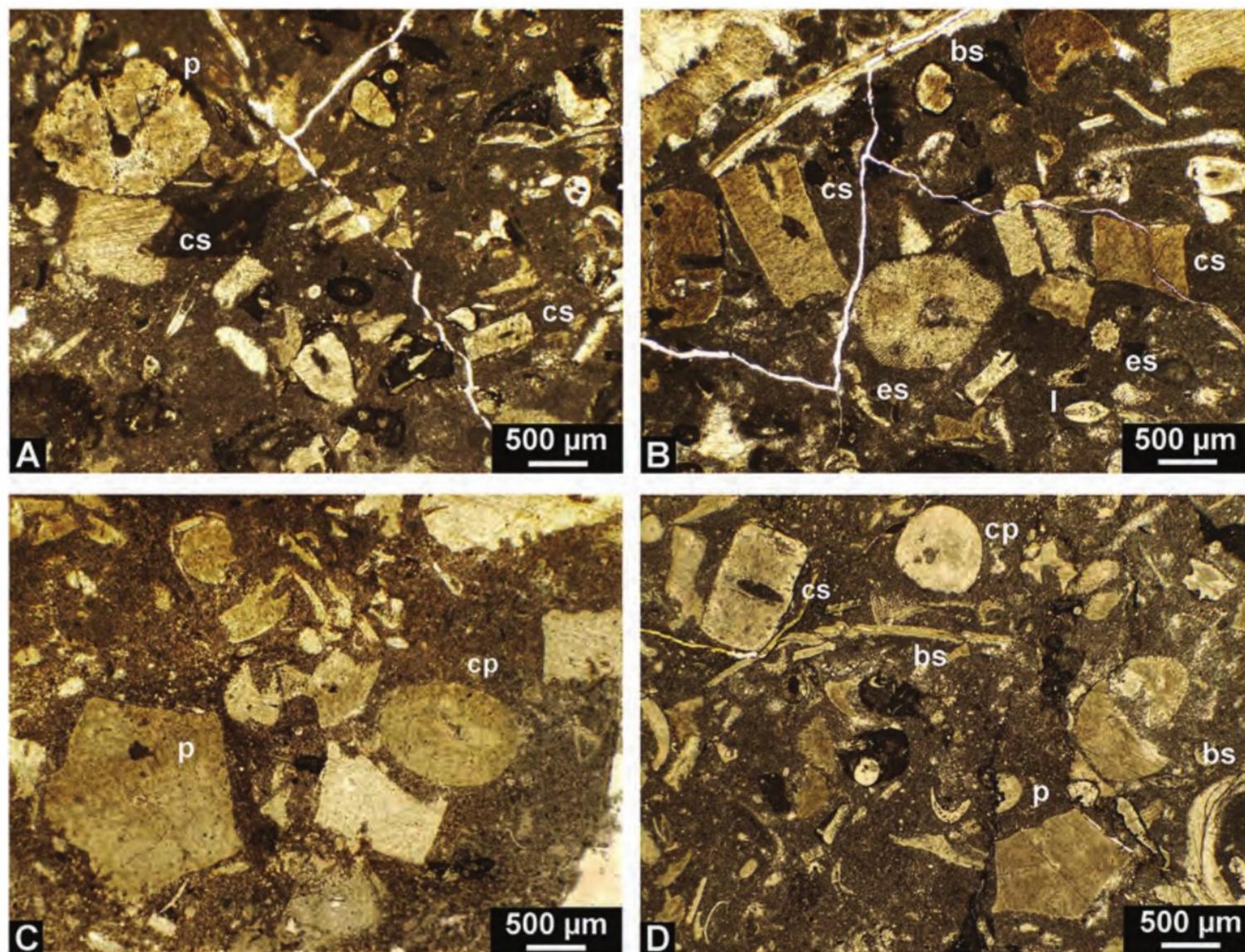
Figure 3. Thin-section photomicrographs of the upper Pliensbachian deposits of the Livari outcrop, Rumija Mountain, southern Montenegro. (A)–(D), Brachiopod-crinoid packstone levels (bioclastic limestones) with abundant crinoids, echinoids, brachiopod shells and rare benthic foraminifers. Abbreviations used: crinoid plate (cp), crinoid stem (CS), Pentacrinus sp. (p), echinoid spine (es), brachiopod shell (bs), *Lenticulina* sp. (l). A, RGF BR 91/A thin section; B, RGF BR 91/B thin section; (C) RGF BR 91/D thin section; (D) RGF BR 91/F thin section.

Based on the presence of the foraminifer *Agerella martana*, the 240 m thick succession between the Dachstein Limestone and the Toarcian marly limestone at Livari ranges from the Hettangian to the Pliensbachian, but a more precise age assignment of the individual units is currently not possible (Črne and Goričan 2008). Only the age of the last 20 m of this part of the succession, represented by bioclastic limestones (packstones/wackestones) with brachiopods and crinoids, is proven that these deposits lie immediately below the Toarcian marly limestones. The rhynchonellide brachiopods *Prionorhynchia fraasi* and *Cuneirhynchia dalmasi* are recorded from the Sinemurian to the upper Pliensbachian (Domerian). The greatest number of representatives of the terebratulide genus *Rhapidothyris* is recorded from the Pliensbachian (Tuluweit 1965; Tchorszevski 1985; Ager 1990; Lee et al. 2006; Vörös 2009), while a smaller number of species is known from the Sinemurian (Böse and Schlosser 1900; Vörös 2009). In the Montenegro section, the genus *Rhapidothyris* is represented by *R. cernagorensis* (Martelli 1906) and most probably by two new species. The fossil assemblages of brachiopod-crinoidal limestones (packstones/wackestones) of this part of the succession include, in addition to brachiopods (rhynchonellides, terebratulides), a wide variety of epifauna, i.e. crinoids, echinoids, microgastropods, and benthic foraminifers, inhabitants of a shallow marine inner platform.

Taphonomic features, such as brachiopod specimens with articulated shells and filled with the surrounding sediment suggest their autochthonous to parautochthonous fossilisation. There was no sorting of the specimens by size, and both adult and juvenile forms were found together. Specimens are variously orientated,

with no dominant direction noted. Thus, it is suggested that the shells suffered little to no post-mortem transport and were buried rapidly by sediment.

Material and methods

The rhynchonellide collection from Livari, southern Montenegro, consists of 34 well preserved articulated shells. *Prionorhynchia fraasi* includes a single specimen, *Cuneirhynchia dalmasi* is represented by 11 internal moulds with shell remains, 10 of which were measured (Table 1), while *Skadarirhynchia semicostata* sp. nov. is represented by 22 articulated shells, 19 of which were measured (Table 2).

The specimens chosen for transverse serial sectioning were calcined and then embedded in plaster. As a result of burning, the internal elements become white and distinct from the sediment and secondary mineralisation. Specimens were serially sectioned at a spacing of 0.1 or 0.2 mm between sections using a grinding apparatus (Cutrock of London; Cutrock manufactured a version of the 'Croft-Grinder', see Croft 1959). The sections were drawn using a binocular microscope (Carl Zeiss, Jena) on which was mounted a camera lucida. For each rhynchonellide specimen sectioned, we drew approximately 30 sections from which the most important are presented. Serial sections are drawn with the ventral valve oriented uppermost (see Motchurova-Dekova et al. 2008).

The shell microstructures of the specimens of *Cuneirhynchia dalmasi* and *Skadarirhynchia semicostata* were examined using a JEOL JSM–6460LV scanning electron microscope (SEM) at the

Table 1. Measurements (in mm) and ratios of *Cuneirhynchia dalmasi* (Dumortier 1869).

Specimen	L	W	T	W/L	T/L	T/W	Remarks
RGF BR 91/2	14.3	15.1	8.8	1.06	0.62	0.58	
RGF BR 91/3	15.8	15.4	10.9	0.97	0.69	0.71	
RGF BR 91/4	16.0	15.7	9.2	0.98	0.58	0.59	
RGF BR 91/5	17.0	18.7	11.6	1.10	0.68	0.62	Sectioned, Figure 6
RGF BR 91/6	17.0	15.9	11.8	0.93	0.69	0.74	Figure 5E–H
RGF BR 91/7	17.1	17.5	12.7	1.02	0.74	0.73	Figure 5I–L
RGF BR 91/8	17.2	17.3	11.8	1.01	0.69	0.68	
RGF BR 91/9	18.1	20.0	13.2	1.10	0.73	0.66	Figure 5 M–P
RGF BR 91/10	18.9	18.5	12.9	0.98	0.73	0.70	
RGF BR 91/11	18.1	20.0	13.2	1.10	0.73	0.66	Microstructure, Figure 7
Range	**14.3–18.9**	**15.1–20.0**	**8.8–13.2**	**0.93–1.10**	**0.58–0.74**	**0.58–0.74**	
Mean	**16.95**	**17.41**	**11.61**	**1.02**	**0.67**	**0.67**	

Table 2. Measurements (in mm) and ratios of *Skadarirhynchia semicostata* sp. nov.

Specimen	L	W	T	W/L	T/L	T/W	Remarks
RGF VR 91/43	15.8	16.0	10.6	1.02	0.68	0.66	
RGF VR 91/44	15.7	17.2	11.8	1.10	0.75	0.69	
RGF VR 91/45	14.2	15.2	10.7	1.07	0.75	0.70	
RGF VR 91/46	13.5	13.8	9.5	1.02	0.70	0.69	Figure 8A–D
RGF VR 91/47	13.4	15.6	9.0	1.16	0.67	0.58	
RGF VR 91/48	12.6	14.2	8.3	1.13	0.66	0.58	Figure 8E–H
RGF VR 91/49	12.5	13.2	7.8	1.06	0.62	0.59	
RGF VR 91/50	12.8	12.8	7.9	1.00	0.62	0.62	Figure 8I–L
RGF VR 91/51	12.9	14.0	8.3	1.09	0.64	0.59	Figure 8 M–P
RGF VR 91/52	14.7	14.5	9.5	0.99	0.65	0.66	
RGF VR 91/53	14.5	15.3	10.4	1.06	0.72	0.68	
RGF VR 91/54	14.7	15.3	11.2	1.04	0.76	0.73	Sectioned, Figure 9
RGF VR 91/55	14.8	15.1	9.2	1.02	0.62	0.61	
RGF VR 91/56	13.5	16.1	9.7	1.19	0.72	0.60	
RGF VR 91/57	10.4	11.4	5.4	1.10	0.52	0.47	
RGF VR 91/58	15.7	15.8	10.5	1.00	0.67	0.66	Figure 8Q–T
RGF VR 91/59	17.0	18.8	10.8	1.10	0.63	0.57	Holotype, Figure 9 U–X
RGF VR 91/60	14.0	14.1	9.3	1.00	0.66	0.65	Microstructure, Figure 10
RGF VR 91/61	12.7	14.4	9.7	1.13	0.76	0.67	
Range	**10.4–17.0**	**11.4–18.8**	**5.4–11.8**	**0.99–1.19**	**0.52–0.76**	**0.47–0.73**	
Mean	**13.97**	**14.04**	**9.45**	**1.01**	**0.67**	**0.63**	

Department of Biology and Ecology, Faculty of Science, University of Novi Sad (Serbia). The specimens were first embedded in 'Araldite' (a brand name of a two-part epoxy adhesive; resin and hardener) and then cut from the anterior and posterior ends perpendicular to the plane of symmetry, polished, etched with 5% HCl for 6 s, dried and finally coated with gold and photographed.

Additionally, the shell microstructures were examined using acetate peels of uncalcined specimens. They were properly oriented, embedded in araldite and then serially ground perpendicular to the plane of symmetry. For each specimen, up to 20 sections were made from the tip of the ventral valve to the maximum shell thickness, coinciding with the mid-shell length. After grinding, selected surfaces were properly polished and etched with a dilute solution of (5%) HCl for about 10 s, and finally acetate peels were prepared. The acetate peels were examined using an Olympus BH-2 light microscope and photographed using an Olympus E-410 digital camera.

The shell microstructure terminology of Kamyshan (1977, 1986) and Manceñido and Motchurova-Dekova (2010) is used. These authors distinguished two types of fibrous microstructures of the secondary layer in rhynchonellides: fine fibrous rhynchonellidine type (leptinoid) and coarse fibrous basiliolidine type (eurinoid).

The shell thickness and fibres of the secondary layer were measured at the maximum shell width, as recommended by Sass and Monroe (1967).

For photography of the brachiopods, they were coated with ammonium chloride sublimate, which accentuates the finer details of shell ornaments, and then photographed with a Nikon D7200 camera. All linear measurements (taken with a Vernier Calliper and rounded to 0.1 mm) are given in millimetres, and their ratios are also given. The brachiopod abbreviations of the measured parameters are L = length, W = width, T = thickness.

The classification of the brachiopods is based on Williams et al. (1996) presented in the revised edition of the Treatise on Invertebrate Palaeontology concerning rhynchonellide brachiopods (Savage et al. 2002).

The brachiopod specimens investigated in this contribution, were collected by Vladan Radulović and Barbara Radulović in the summer of 1989 and are stored in the authors' collection at the Department of Palaeontology, Faculty of Mining and Geology, University of Belgrade (RGF BR).

For Sr isotopic analyses, approximately 36 mg of sample material was dissolved in 1 N HCl, centrifuged for 30 min and evaporated to dry in PTFE beakers. The residue was re-dissolved in 8 N HNO_3. Samples were eluted on SrSpec® (EICHROM Company) ionic interchange PFA columns to extract and purify strontium. Sr isotopic ratios were determined with a TRITON PLUS thermal ionisation mass spectrometer equipped with 9 Faraday collectors at the Laboratorio Universitario de Geoquímica Isotópica (LUGIS), Instituto de Geofísica, Universidad Nacional Autónoma de México

(UNAM) in Mexico City. Isotopic measurements were made in static collection mode. Sr was loaded as chloride onto rhenium filaments and measured as metallic ions. The obtained $^{87}Sr/^{86}Sr$ ratio was normalised to a $^{86}Sr/^{88}Sr$ value of 0.1194. The $^{87}Sr/^{86}Sr$ value of the NBS 987 standard throughout this study was 0.712239 ± 12 (1SD, $n = 18$). The total procedural blank was 0.4 ng of Sr. Analytical errors are given as standard deviation (1SD) and referred to as the last two digits. The standard error of the mean (2SE) was calculated from 57 individual isotopic ratios of the sample and is given with the last digit.

Sr isotopic results

The age of the brachiopod horizon was calculated from $^{87}Sr/^{86}Sr$ measurements of a well preserved and microscopically controlled calcitic shell from a specimen of *Livarirhynchia rajkae* Radulovic, 2008, which co-occur with *Skadarirhynchia semicostata* sp. nov. The obtained $^{87}Sr/^{86}Sr$ value was 0.717177 ± 38 (1SD) ± 5 (2SE) from a total of 57 measurements. This $^{87}Sr/^{86}Sr$ ratio was compared directly to the $^{87}Sr/^{86}Sr$ seawater curve to determine a relative age using the LOWESS software from McArthur et al. (2001). Several interceptions between 144.6 and 191.0 Ma were observed. However, the younger ages between 144.6, 173.3 and 184.6 Ma are not consistent with the local stratigraphy, whereas the late Pliensbachian age (191.0 Ma) coincides well with the suggested age derived from present biostratigraphic studies (Figure 4).

Systematic palaeontology

Phylum Brachiopoda Duméril 1806
Subphylum Rhynchonelliformea Williams et al. 1996
Class Rhynchonellata Williams et al. 1996
Order Rhynchonellida Kuhn 1949
Superfamily Rhynchotretadoidea Licharev 1956
Family Prionorhynchiidae Manceñido and Owen in Savage et al. 2002
Genus *Prionorhynchia* Buckman 1918

Type species
Terebratula serrata J. de C. Sowerby 1825 in 1823–1825.

Prionorhynchia fraasi Oppel 1861
(Figure 5A–D)

1861 *Rhynchonella Fraasi* Oppel: 543, pl. 12, fig. 3.
1869 *Rhynchonella* cfr. *Fraasi* Opp.; Zittel: 130, pl. 14, fig. 18.
1868-1871 *Rhynchonella Fraasi* Opp.; Quenstedt: 147, pl. 40, fig. 82.
1883 *Rhynchonella* sp. ind. cfr. *Rh. Fraasi* Opp.; Canavari: 100, pl. 9, fig. 4.
1889 *Rhynchonella Fraasi* Opp.; Geyer: 52, pl. 6, figs. 18–24.
1893 *Rhynchonella Fraasi* Oppel; Böse: 643.
1907 *Rhynchonella Fraasi* Opp.; Dal Piaz: 31, pl. 2, fig. 7.
1907 *Rhynchonella Fraasi* Opp. var *paucicostata* n. v.; Dal Piaz: 32, pl. 2, fig. 8.
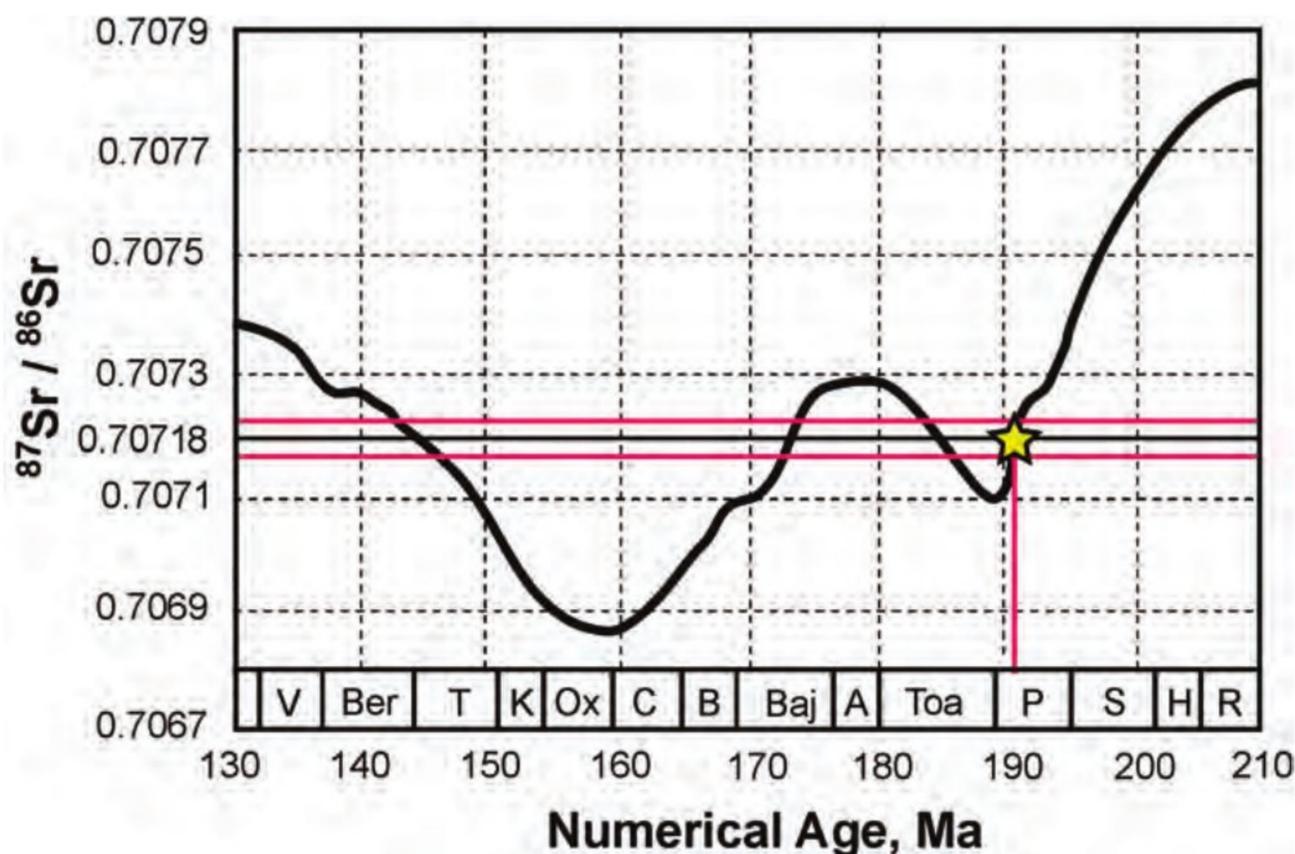
Figure 4. Diagram with the $^{87}Sr/^{86}Sr$ seawater evolution curve for the 130-210 Ma period adapted from McArthur et al. (2001). The obtained $^{87}Sr/^{86}Sr$ value for the Livari brachiopod sample investigated in this paper is 0.717177 and marked with the black horizontal line. Red horizontal lines refer to the $\pm$ 0.000038 (1SD) error. Four intersections with the seawater curve were obtained, but only the 191 Ma intersection (yellow star) is interpreted as the correct relative age of the brachiopod sample, which is consistent with the local stratigraphy.

Figure 5. (A)–(D), *Prionorhynchia fraasi* (Oppel 1861), RGF BR 91/1 specimen. E–P, *Cuneirhynchia dalmasi* (Dumortier 1869). (E)–(H), RGF BR 91/6 specimen; I–L, RGF BR 91/7 specimen; M–P, RGF BR 91/9 specimen. All from the upper Pliensbachian, Livari, Rumija Mountain. Images are arranged in dorsal, ventral, lateral, and anterior views respectively. Scale bar = 10 mm.
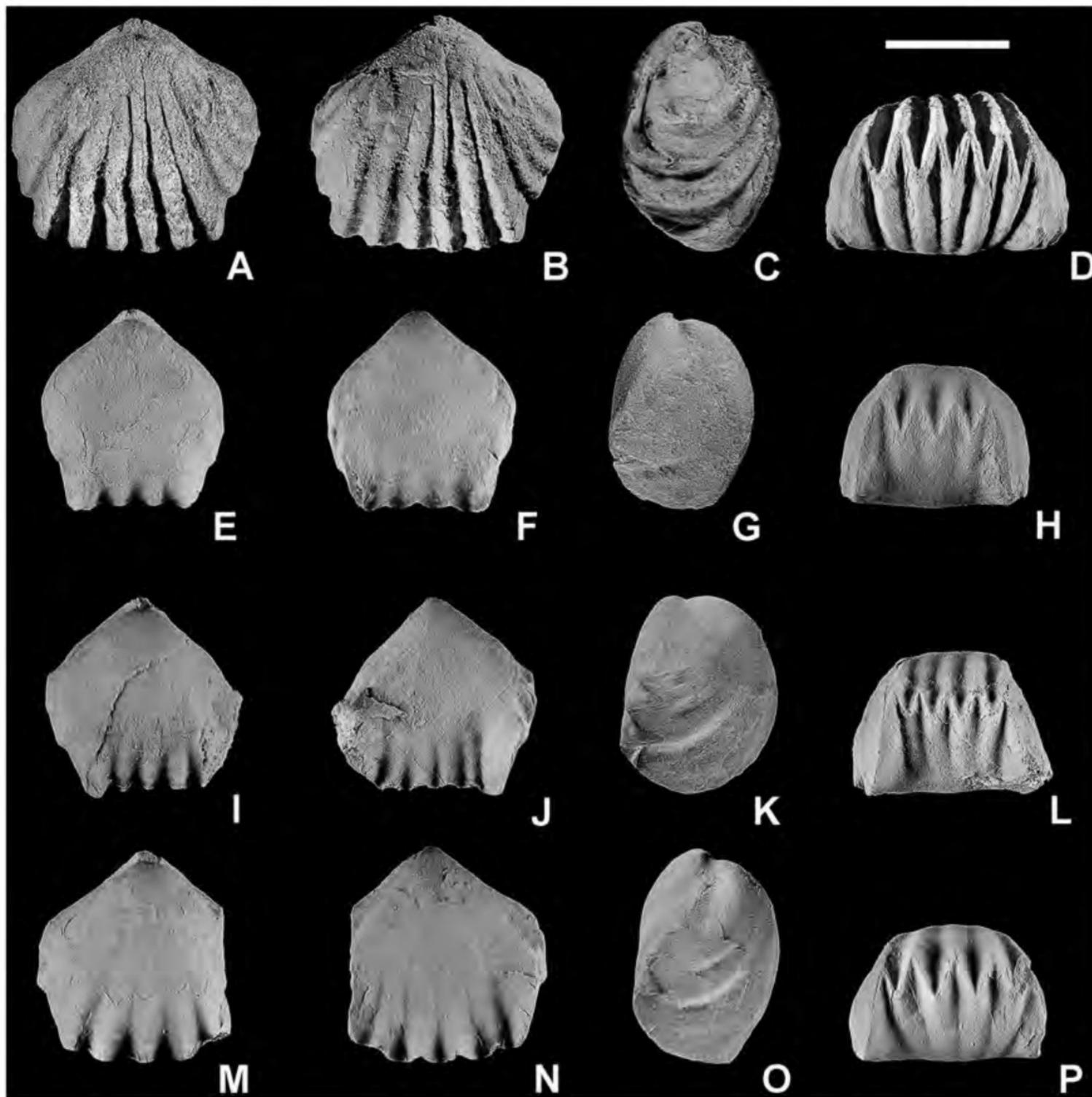
1937 *Rhynchonella fraasi* Oppel; Ormós: 30.
1964 '*Rhynchonella*' *fraasi* Oppel; Pevny: 164.
1993a '*Rhynchonella*' *fraasi* Oppel; Siblík: 969, pl. 1, figs. 7, ?8.
1993b '*Rhynchonella*' *fraasi* Oppel; Siblík: 128, pl. 2, figs. 7, 8.
1993 *Cuneirhynchia*? *fraasi* (Oppel); Vörös: 180.
1999 *Prionorhynchia fraasi* (Oppel); Siblík in Böhm et al.: 186, text-fig. 49, pl. 30, figs. 1–5,
2003 *Prionorhynchia fraasi* (Oppel); Vörös et al.: 65, 67, 72.
2003 *Cuneirhynchia fraasi* (Oppel); Dulai: 35, pl. 6, figs. 4–6.
2007 *Cuneirhynchia fraasi* (Oppel); Vörös and Dulai: 52, 54.
2008 *Prionorhynchia fraasi* (Oppel); Siblík in Siblík and Lobitzer: 64, pl. 1, fig. 6; pl. 3, fig. 1.
2013 *Prionorhynchia fraasi* (Oppel); Alméras and Cougnon: 47.

Material

An internal mould with shell remains of an adult individual (RGF BR 91/1).

Description

External characters. The shell medium in size (L = 19.8, W = 21.4, $T = 14.0$, W/L = 1.08, T/L = 0.71, T/W = 0.65), roundly pentagonal in outline, wider than long, with the maximum width and thickness at the midvalve. Characteristically flattened in anterior view. The ventral valve is moderately convex, and the dorsal valve is considerably more convex than the ventral one. The anterior commissure having trapezoidal uniplication. Each valve is ornamented with about 14 strong and angular costae. The dorsal fold with six costae, flat, low, prominent but not strongly elevated above the flanks; the ventral sulcus is broad, shallow, and occupied by five costae, both starting prior to the midvalve. Flanks with 4 weak costae. The beak is low, wide, and erect, with subangular beak ridges bounding a large concave interarea. The planarea is deep, but not sharply limited. The apical angle is around 112°.

Internal characters. Due to the paucity of material (one specimen found), no serial sections were performed, and the internal

morphology was not studied. Slightly ventrally convergent dental plates and a high and long dorsal median septum can be seen through the shell wall and in the broken side of the dorsal umbo.

Remarks

This species is very variable in the outline and convexity of the valves, but the trapezoidal anterior commissure and flattened shell are the essential external features for recognising the species. The specimen corresponds well to the description and figure given by Oppel (1861), but differs slightly in having fewer costae on the dorsal fold (6 compared to 10 in Oppel's original, pl. 12, fig. 3).

Geyer (1889), pl. 6, figs. 22–24) was the first who figured 3 transverse serial sections through the shell of this species. These sections show very slightly ventrally convergent dental plates, faintly ventrally inclined wide and slender hinge plates, small and crescent-like crural bases, vestigial dorsal median septum, and poorly crenulated globular teeth inserted nearly vertically in the large sockets agreeing well with the internal morphological characters of *P. fraasi* given by Siblík (in Böhm et al. 1999, text-fig. 49), as well as those of *Prionorhynchia serrata* (J. de C. Sowerby; Ager, 1956–1967, text-fig. 26), and *Prionorhynchia polyptycha* (Oppel 1861; Dulai 1992, text-fig. 8).

Geyer (1889) mentioned transitional forms from *Rhynchonella fraasi* to *Rhynchonella polyptycha*, the latter distinguished above all on the grounds of its more numerous ribs. Several attributions to the *Rhynchonella polyptycha* Oppel are considered synonymous with '*fraasi*' (see also Siblík in Böhm et al. 1999). Alméras and Cougnon (2013, p. 47) also stated that *Rhynchonella polyptycha* Oppel is synonymous with *Prionorhynchia fraasi* (Oppel).

Baeza-Carratalá (personal communication, 2024) had previously checked the material of both mentioned species housed in the Hungarian Natural History Museum in the Dulai and Vörös collections. The wider and elliptical outline, the convexity of both valves and the presence of bifurcate ribs suggest considering the Hungarian material as *P. polyptycha* instead of *P. fraasi* as [the] authors [herein] affirm.

The generic attribution of the species *fraasi* to *Prionorhynchia* or to *Cuneirhynchia*, is well demonstrated in the synonymic list included in this taxon, since both genera are internally very similar (see transverse serial sections of both genera in Siblík 1964, Siblík in; Böhm et al. 1999; Dulai 2003; only differences is in the orientation of dental plates and the height of the dorsal septum), and the external features here take on great relevance. Externally, *P. polyptycha* differs from *P. fraasi* in having width which exceeds length, elliptical outline (the *fraasi* outline is subpentagonal with straight anterior margin) and the ventral valve which is moderately convex (the *fraasi* ventral valve is flattened).

Occurrence

According to Alméras (1964), a Sinemurian–upper Pliensbachian (Domerian) age is reported for *Prionorhynchia fraasi*. It is recorded from Austria (Hierlatz, Adnet, Steinplatte, Schafberg), Italy (Sospirolo), Hungary (Bakony Mountains), and Montenegro (this study).

Superfamily Rhynchonelloidea d'Orbigny 1847
Family Rhynchonellidae d'Orbigny 1847
Subfamily Piarorhynchiinae Shi and Grant 1993
Genus **Cuneirhynchia** Buckman 1918

Type species
Rhynchonella dalmasi Dumortier 1869.

Cuneirhynchia dalmasi (Dumortier 1869)
(Figures 5E–P, 6, 7)

1869 *Rhynchonella dalmasi* Dumortier: 331, pl. 42, figs. 3–5 (= holotype).
1891 *Rhynchonella dalmasi* Dumortier; Di Stefano: 198, pl. 2, figs. 8–12.
1892 *Rhynchonella dalmasi* Dumortier; Parona: 32, pl. 1, fig. 22.
1900 *Rhynchonella dalmasi* Dumortier; Böse and Schlosser: 195, pl. 18, figs. 16, 17.
1907 *Rhynchonella dalmasi* Dumortier; Dal Piaz: 28, fig. 2.
1957–1967 *Cuneirhynchia dalmasi* (Dumortier); Ager: 125 (*non*), pl. 11, figs. 4, 5, text-fig. 78–80 [= *Cuneirhynchia raui* (Rollier 1917)].
1964 *Cuneirhynchia dalmasi* (Dumortier); Siblík: 172 (*non*), pl. 8, fig. 3 [= *Cuneirhynchia raui* (Rollier 1917)].
1967 *Cuneirhynchia dalmasi* (Dumortier); Sacchi Vialli and Cantaluppi: 83, pl. 12, figs. 12, 13.
1987 *Cuneirhynchia dalmasi* (Dumortier); Alméras and Elmi: 36, pl. 3, figs. 7, 8 (fig. 8 = refigured holotype).
2003 *Cuneirhynchia* aff. *dalmasi* (Dumortier); Vörös et al.: 78, pl. 8, figs. 20–22.
2007 *Cuneirhynchia dalmasi* (Dumortier); Alméras et al.: 72 (with extended synonymy).
2013 *Cuneirhynchia dalmasi* (Dumortier); Alméras and Cougnon: 71.
2013 *Cuneirhynchia dalmasi* (Dumortier); Baeza-Carratalá: fig. 5.5.
2020 *Cuneirhynchia dalmasi* (Dumortier); Baeza-Carratalá and García Joral: figs. 4.C1, C2.

Material
11 internal moulds with shell fragments, 10 of which were measured (Table 1).

Description
External characters. Medium-sized shells, up to 19 mm in length (Table 1), subtriangular rarely subpentagonal in outline, anterior margin straight and width exceeding length in most of the specimens. We determine the maximum width and convexity at/or slightly posterior to the mid-valve. The ventral valve is flattened in the lateral profile; the dorsal valve is nearly twice as convex as the ventral one. Trapezoidal and flattened outline in anterior view. Anterior commissure is highly uniplicated. The uniplication is trapezium-like and rather wide. Each valve is ornamented by 6–8 sharp costae developed only on the anterior half. Wide and very shallow ventral sulcus starts at about mid length, occupied by 3–4 strong sharp costae. The dorsal fold is flat, beginning at one-third the length, and broadens anteriorly, with 4–5 costae (in some shells two of the lateral costae are stronger and longer). The lateral flanks with 2–3 less pronounced ribs. Small, sub-erect, acute beaks with poorly defined lateral beak ridges. The foramen is small, circular and submesothyrid. The apical angle varies from 92° to 105°.

Internal characters (Figure 6). A pedicle collar is present. The delthyrial cavity is rectangular, bounded by relatively long and thin slightly convergent dental plates. The lateral umbonal cavities are large and semicircular in cross-section. The septalial plates are subparallel and suspended. Hinge teeth are very short, dorsally expanded and inserted into large sockets. Crenulation is poorly developed. Stout denticula are exposed laterally. The outer hinge plates are broad, thin, horizontal and clearly demarcated from broad inner socket ridges. The dorsal septum is long, extending as a low ridge beyond the ends of the crura.

Crura are thin, triangular in cross-section, expanded distally, ventrally divergent, and slightly curving ventrally. Crura are of the
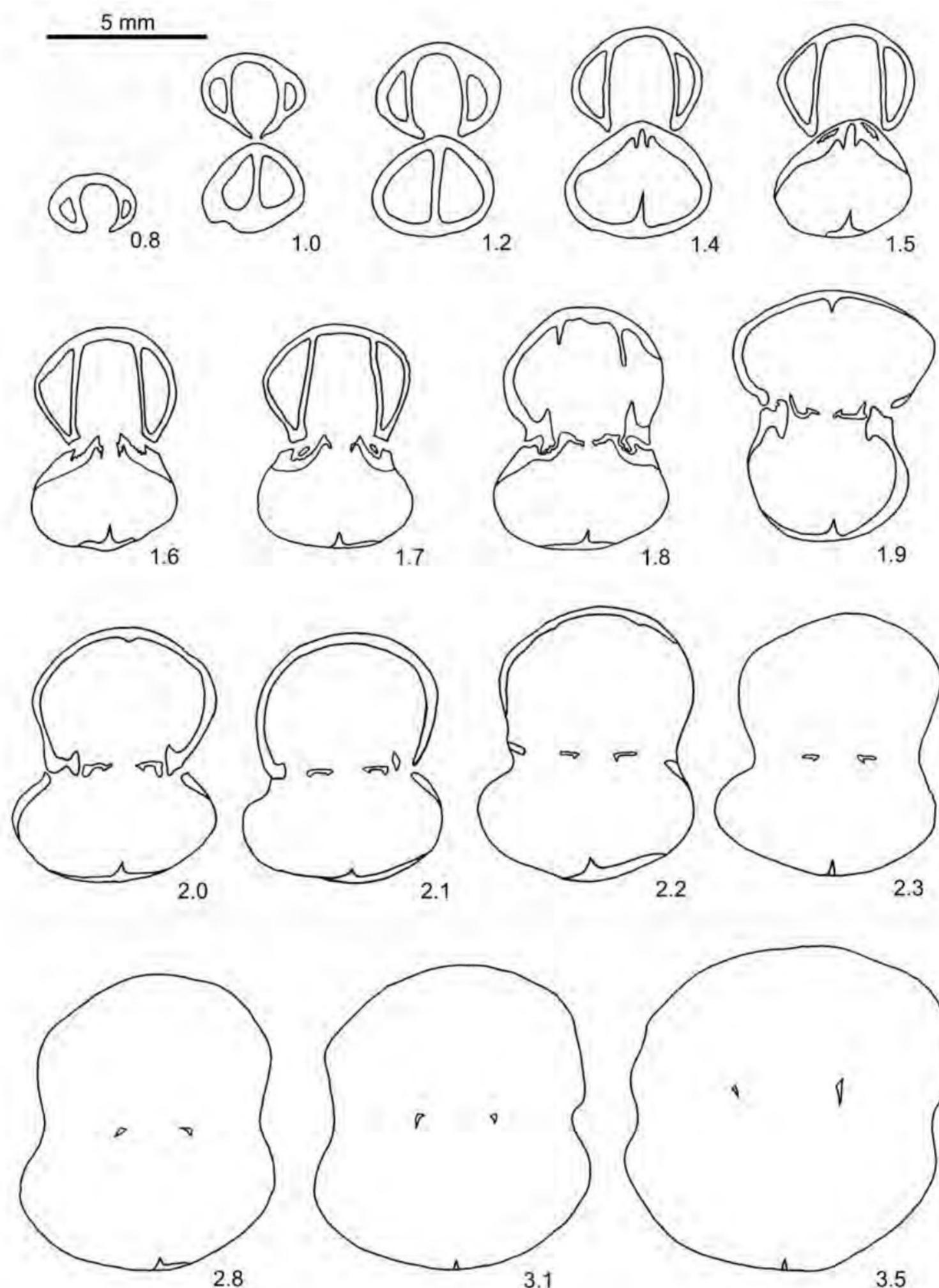
Figure 6. Transverse serial sections performed on the *Cuneirhynchia dalmasi* (Dumortier 1869), specimen RGF BR 91/5, upper Pliensbachian, Livari, Rumija Mountain, southern Montenegro. Original dimensions of the specimen (in mm): L = 17.0, W = 18.7, T = 11.6. Numbers indicate the distance in mm from the apex.

raduliform type, ending at a distance of 0.17 of the dorsal valve length from the dorsal umbo.

Shell microstructure (Figure 7A–F)

Shell microstructure was studied using one specimen; 12 SEM micrographs and 20 acetate peels were taken. The dorsal valve interior is with uncorrugated dental sockets bounded by well-developed socket ridges; hinge plates are anteriorly slightly ventrally inclined with small crural bases (Figure 7A, C, D); the dorsal median septum is high (Figure 7B). The primary layer was not preserved. The secondary layer is homogeneous (not differentiated in several packages) built of a single relatively thin layer, that is variable in thickness. In the dorsal valve, it is 350–450 μm thick in the tip of the costae and 150–200 μm thick in the corresponding sulci; it is somewhat thinner in the ventral
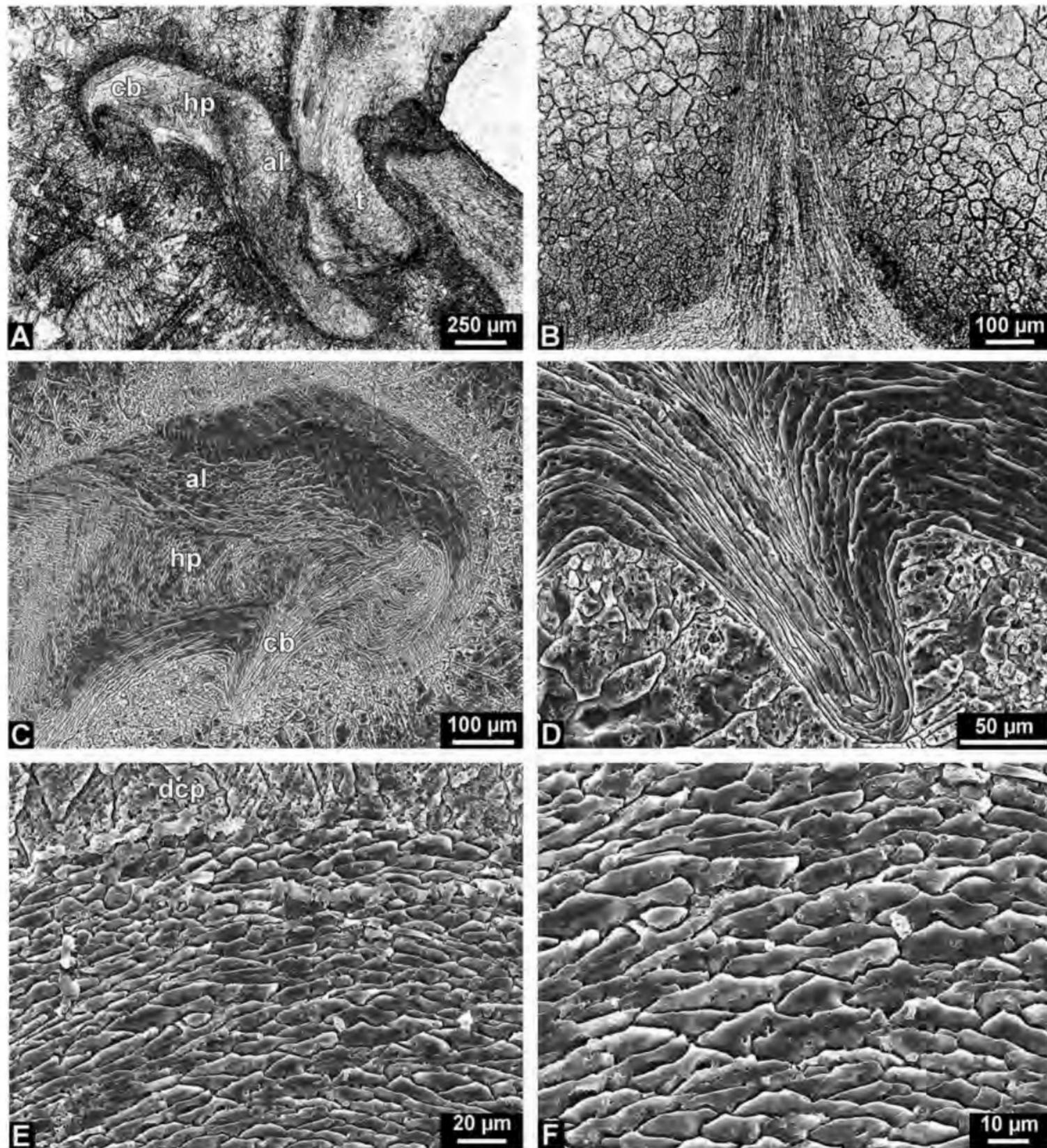
Figure 7. *Cuneirhynchia dalmasi* (Dumortier 1869), upper Pliensbachian, Livari, Rumija Mountain, southern Montenegro. Photomicrographs of the shell microstructure from acetate peels of successive transverse serial sections. Original dimensions of the specimen RGF BR 91/11 (in mm): L = 18.1, W = 20.0, T = 13.2. A, crural base (cb), hinge plate (hp), appositional layer (al),and tooth (t) are shown; B, section showing modified fibre of the dorsal median septum. (c)–(f), SEM micrographs of transverse sections of the shell RGF BR 91/11. C, note the hinge plate (hp), crural base (cb), and appositional layer (al); D, crural base. A–D serial sections taken at 1.90 mm from the ventral umbo. E, finer anisometric fibres of secondary layer overgrown by diagenetic calcite prisms (dcp) above, in the lower part, more rhomboidal fibres are shown.; F, detail of D showing the fine anisometric fibres of the secondary layer. E–F serial sections taken at 11.80 mm from the ventral umbo.

valve, 180–200 μm thick in the costae and 120–150 μm thick in the sulci. It is built up of fine anisometric fibres (i.e. leptinoids), finer close to the exterior shell surface that tend to have elongated rhombic sections (Figure 7E, F) 12–15 μm wide and 3–5 μm thick. The fibres gradually become larger, more elongated and irregular (polygonal) in the cross-section in the central and inner parts of the shell, averaging 20–30 μm wide and 5–10 μm thick. The secondary layer is overgrown by diagenetic calcite crystals perpendicular to the shell surface (Figure 7E).

The shell microstructure of a specimen of *Cuneirhynchia dalmasi* from the Pliensbachian of the westernmost Subbetic area has also recently been shown in Baeza-Carratalá and García Joral (2020), fig. 4.C1). The secondary layer of this specimen also consists of one layer of mainly anisometric and rarely rhombic fibres 30–45 μm wide and

10–15 μm thick, showing fibres with rhomboidal-shaped cross sections (fine fibrous pattern, i.e. leptinoids) and similar fibre dimensions as in the Montenegrin specimen (Figure 6E, F herein).

Remarks
Buckman (1918) erected the genus *Cuneirhynchia* with the type species *Rhynchonella dalmasi* Dumortier 1869 from the upper Pliensbachian (Domerian) of Privas (Ardèche, France). The holotype (Dumortier 1869, pl. 42, figs. 3–5) is a small specimen 10 mm in length, most likely a juvenile form, with a characteristic triangular (cuneiform) outline, straight anterior margin, and dorsal fold barely perceptible with 6 strong and angular costae. The specimens described in this work differ from the holotype in having significantly larger dimensions (maximum length of 19 mm instead of

10.5 mm for the holotype), a much more convex dorsal valve, and rarely a somewhat more subpentagonal outline. Four specimens of *Cuneirhynchia dalmasi* figured and described by Sacchi Vialli and Cantaluppi (1967) from the upper Pliensbachian (Domerian) of Prealpi Pienmontesi, Italy (maximum length is 19.2 mm), have similar dimensions to the specimens from Livari, Montenegro, and their external morphology matches well with the Montenegrin specimens.

Ager (1956–1967, p. 126, pl. 11, figs. 4, 5) described nine specimens as 'Cuneirhynchia dalmasi' from the 'lower Lias' (Jamesoni Zone, lower Pliensbachian) of Radstock, Somerset, England which differs from the type specimen in having a higher frontal uniplication with 3–4 costae on the fold, with a correspondingly wide and deep ventral sulcus, and rectangular linguiform extension on the ventral valve. His description of the latter specimens takes into account the holotype from the upper Domerian of Ardèche. Alméras et al. (2007) considered that these morphological differences and the different ages justify the separation of Ager's forms from the true *Cuneirhynchia dalmasi*. They considered that the English forms belong to *Cuneirhynchia raui*.

Recently, Baeza-Carratalá and García Joral (2020) figured a small specimen of *Cuneirhynchia dalmasi* from the Pliensbachian of the westernmost Subbetic area, Spain, which differs from the Montenegrin specimens in having a smaller size and triangular shell. In the same paper, they show the microstructure of the secondary layer as a single layer with a fine fibrous pattern (i.e. leptinoid).

So far, the interior of the true *Cuneirhynchia dalmasi* has not been studied (i.e. topotype material from the type locality). The internal characters of the specimen presented in Figure 5 herein agree entirely with the shape of the dental plates, the dorsal median septum, horizontal to slightly inclined hinge plates, and the presence of raduliform crura with serial sections given by Siblík (1964), p. 172, pl. 8, fig. 3, text-fig. 4) for *C. raui* (formerly known as 'dalmasi') and Alméras et al. (2007), p. 73, figs h.t. 7, 8) for *C. cartieri* (Oppel 1861). Transverse serial sections of a specimen of *Cuneirhynchia raui* Ager (1957–1967) from the Lower Lias (Jamesoni Zone) of Somerset (earlier referred to by Ager as *C. dalmasi*) show strong secondary shell thickening which masks internal skeletal elements. Only ventrally convergent dental plates, a strong dorsal median septum and raduliform crura can be observed.

According to Alméras and Cougnon (2013), *Cuneirhynchia lubrica*, *C. rastuensis* and *C. raui* from the lower Pliensbachian (lbex and Davoei zones) represent transitional forms from the Sinemurian species to the upper Pliensbachian *C. dalmasi*. *Cuneirhynchia lubrica* from the southern Italian Alps (Uhlig 1879, pl. 5, figs. 5–7) and from Hungary shows a wedge-rounded contour, and the sinus appears on the posterior third of the concave ventral valve in the frontal view and a raised, rounded dorsal median fold ornamented with four to five strong and angular costae. *Cuneirhynchia rastuensis* Benigni 1978 from Belluno (Ra Stua) differs from *C. lubrica* by the triangular outline of its shell with slightly rounded anterior margin, strongly flattened shell and lesser convexity of the dorsal valve, by a ventral less pronounced median sulcus as well as by costation (costae blunt of grandis type) limited to the anterior fifth. *Cuneirhynchia raui* could be considered synonymous with *C. dalmasi*, but it has an older stratigraphic age (lower Pliensbachian). It is recorded from the lower Pliensbachian of southwestern Germany (Swabia), France, Slovakia (Veľká Fatra), Spain, and England (Somerset). *Cuneirhynchia cartieri* (Oppel 1861) from the Sinemurian of Austria (Hierlatz near Hallstatt), Italy (Southern Alps) and Hungary (Geresce and Bakony Mountains), Sinemurian–lower Pliensbachian of western Algeria, and lower

Pliensbachian of Switzerland, Sicily and Spain (westernmost Subbetic area) are characterised by subcircular and globose shell, rectangular linguiform extension on the ventral valve, ventral sulcus wide and very shallow. 12 – 17 thin, acute, tetrahedra-like costae are arranged over the entire surface of the valves. *Cuneirhynchia retusifrons* (Oppel 1861, pl. 12, fig. 5) from the upper Hettangian to upper Pliensbachian of Austria (Hierlatz near Hallstatt), Italy (Southern Alps), Sicily and Hungary (Geresce and Bakony Mountains) differs in having a widened subpentagonal outline of its shell, more strongly and more regularly convex valves, a densely costate dorsal median flat fold (with six costae of which two lateral costae are stronger), straight anterior margin and a smooth stage present on the posterior half of the valves.

Occurrence

Vörös and Dulai (2007) recorded this taxon from the Sinemurian of Hungary (Bakony Mountains); Georgescu (1990) from the Late Sinemurian to the Early Domerian of Romania (Apuseni Mountains); Vörös et al. (2003) from the Sinemurian to the Pliensbachian of Austria (Alps, Salzkammergut). According to Alméras and Cougnon (2013), *Cuneirhynchia dalmasi* is reported from the late Pliensbachian (Domerian) of France (Ardèche and Vinezac), Algeria, and possibly Anatolia and Slovakia; Pliensbachian of Italy (Prealpi Piemontesi, Tyrol, Venice and Sicily), Spain (Andalusia, Alicante and Eastern Subbetic) and England (Somerset).

Superfamily Pugnacoidea Rzhonsnitskaia 1956
Family Basiliolidae Cooper 1959
Subfamily Basiliolinae Cooper 1959
Genus **Skadarirhynchia** gen. nov.

Type species

Skadarirhynchia semicostata sp. nov. by monotypy.

Diagnosis

Medium-sized, circular to rounded pentagonal dorsal outline, strongly dorsibiconvex, flattened; costae developed only anteriorly, with a long smooth posterior stage; anterior commissure uniplicate with tendency to asymmetry; dorsal fold poorly developed, ventral sulcus wide and shallow; beak small and erect, mesothyrid foramen small and circular; dental plates poorly developed, ventrally divergent, fused to shell wall, hinge plates broad and slender, dorsally inclined; low dorsal median septum, reduced; crura hamiform; secondary layer homogenous, composed of a single layer with coarse rhombic fibres.

Included species

Only the type species.

Derivation of name

After Skadar Lake, southern Montenegro.

Remarks

Based on the general shape and semicostate shell, internal characters (reduced dental plates and median dorsal septum, slender, dorsally inclined hinge plates, hamiform crura) and microstructure (coarse fibrous pattern). *Skadarirhynchia* is established as a distinct new genus within the semicostate stock of the family Basiliolidae.

Recently, Radulović (2022) introduced a new genus *Sepkoskirhynchia* with *S. sphaerica* as type species from the upper Pliensbachian brachiopod and crinoidal limestones from the same levels and locality. Its internal characters are almost identical to *Skadarirhynchia semicostata* sp. nov. Both species are characterised by short, poorly developed dental plates merged with the shell wall

by wide, slender and dorsally inclined hinge plates, reduced dorsal median septum and hamiform crura.

Microstructurally, the new genus has a homogenous secondary layer and consists of a single layer built of coarse fibres (i.e. eurinoid; sensu Manceñido and Motchurova-Dekova 2010) with the rhombic or rarely subquadrate outline in the cross-section. *Sepkoskirhynchia* differs in having a non-homogenous secondary layer differentiated into several sublayers, which was the most important characteristic for distinguishing this genus (Radulović 2022).

Based on the external morphology, and particularly the semicostate ornamentation of the valves and the outline, the new genus can be compared to stratigraphically younger *Almorhynchia* Ovcharenko 1983, with the type species *A. urtabusensis* (Moiseev 1935) from the Toarcian – lower Aalenian of southeastern Pamir. Externally, *Almorhynchia*, differs from *Skadarirhynchia* in having a smaller shell, circular outline and much less developed folding, a larger number of weaker and rounded costae (11–21) developed on the anterior half and a feebly defined fold. Internally, it differs in having long and ventrally convergent dental plates, wide, slender and dorsally inclined hinge plates, reduced dorsal median septum and hamiform crura. External and internal characters are very close to those in *Soaresirhynchia*. Manceñido and Owen (in Savage et al. 2002) considered that *Almorhynchia* may be a subjective synonym of *Soaresirhynchia*.

The new genus shows some external similarities, such as outline, convexity of the valves, beaks, and strong and deeply serrated costae developed anteriorly, with the Pliensbachian genus *Serratapringia* Vörös 2009 of the Northern Calcareous Alps (Austria), Bakony (Hungary) and probably Sicily, central Apennines and Southern Alps (Italy). This genus, attributed to the Basiliolinae, differs in having more convex valves, well developed ventrally convergent dental plates, and well developed delthyrial and lateral cavities (in *Skadarirhynchia*, dental plates are poorly developed and ventrally divergent, fused to the shell wall, and delthyrial and lateral cavities are not present). Both genera have hamiform crura.

It is interesting to note that Radulović et al. (2007), Manceñido and Motchurova-Dekova (2010), and Baeza-Carratalá and García Joral (2020) gave lists of post-Palaeozoic rhynchonellide taxa with coarse fibrous (i.e. eurinoid) microstructure, and all of them have a homogenous secondary layer with a single layer built of coarse fibres of rhomboidal to subquadrate sections.

Livarirhynchia rajkae Radulović 2008, *Sepkoskirhynchia sphaerica* Radulović 2022, and *Skadarirhynchia semicostata* sp. nov. from the upper Pliensbachian of Livari have isometric coarse (i.e. eurinoid microstructure) fibres, respectively. *Cuneirhynchia dalmasi* has more anisometric, partly fine isometric fibres (i.e. a leptinoid pattern). This clearly indicates that genetic control undoubtedly plays the most decisive role in the development of the shape and dimensions of fibres of the secondary layer of the shell. The same conclusion, but in relation to the presence of a single layer with several sublayers of the secondary layer in *Sepkoskirhynchia*, was given by Radulović (2022).

Occurrence
Upper Pliensbachian of southern Montenegro, Dinaric Carbonate Platform, Mediterranean Province.

Skadarirhynchia semicostata sp. nov.
(Figures 8A–X, 9, 10)

Derivation of name
Latin semicostata = costae developed on the anterior half of the shell.

Diagnosis
As for the genus.

Holotype
Articulated specimen RGF BR 91/59, illustrated in Figure 8U–X.

Type locality
Livari village, Rumija Mountain, Montenegro.

Type horizon
Bioclastic limestones (wackestones/packstones) of the upper Pliensbachian (Domerian).

Material
Twenty-two well-preserved articulated shells, 19 of which were measured (Table 2).

Description
External characters. The shell is medium-sized, up to 17.0 mm in length (Table 2), rounded pentagonal to rarely subcircular in dorsal outline, flattened in anterior view, strongly dorsibiconvex, with a long smooth stage posteriorly, always wider than long and anterior margin slightly rounded. The maximum width and thickness are at or slightly posterior of the midlength. The dorsal valve is about two times more convex than the ventral valve. Beaks are small, wide and erect, bounded with short subangular barely defined beak ridges. The foramen is small, circular and submesothyrid. The apical angle varies between 93° and 115°. Anterior commissure is widely plano-uniplicate and rarely slightly asymmetric. Dorsal folds are commonly noticeable, with ventral sulcus wide and shallow. Each valve is ornamented by about 10–12 strong and angular costae, developed only on the anterior third of the dorsal valve and the anterior half of the ventral valve, of which usually 4–6 costae are located on the dorsal fold with 3–5 in the ventral sulcus and with 2–3 weak costae on the lateral flanks of both valves.

Internal characters (Figure 9). The pedicle collar is thick and low. Dental lamellae are poorly developed, short, very slender and ventrally divergent, and fused to the shell wall. The hinge teeth are massive, linguiform and laterally inserted into small sockets with blunt denticula laterally. The inner socket ridges are very reduced. The dorsal median septum is low, reduced to a very low ridge, as long as the crura. The hinge plates are broad and slender and initially slightly inclined dorsally, anteriorly becoming much more inclined dorsally and attached to the ventral ends of the crural bases. The crural bases are crescent-shaped and slightly convex laterally. The crura of hamiform (= prefalciform) type, initially located in the commissural plane, anteriorly slightly diverge ventrally and very thin, terminating at a distance of 0.22 dorsal valve lengthfrom the dorsal umbo.
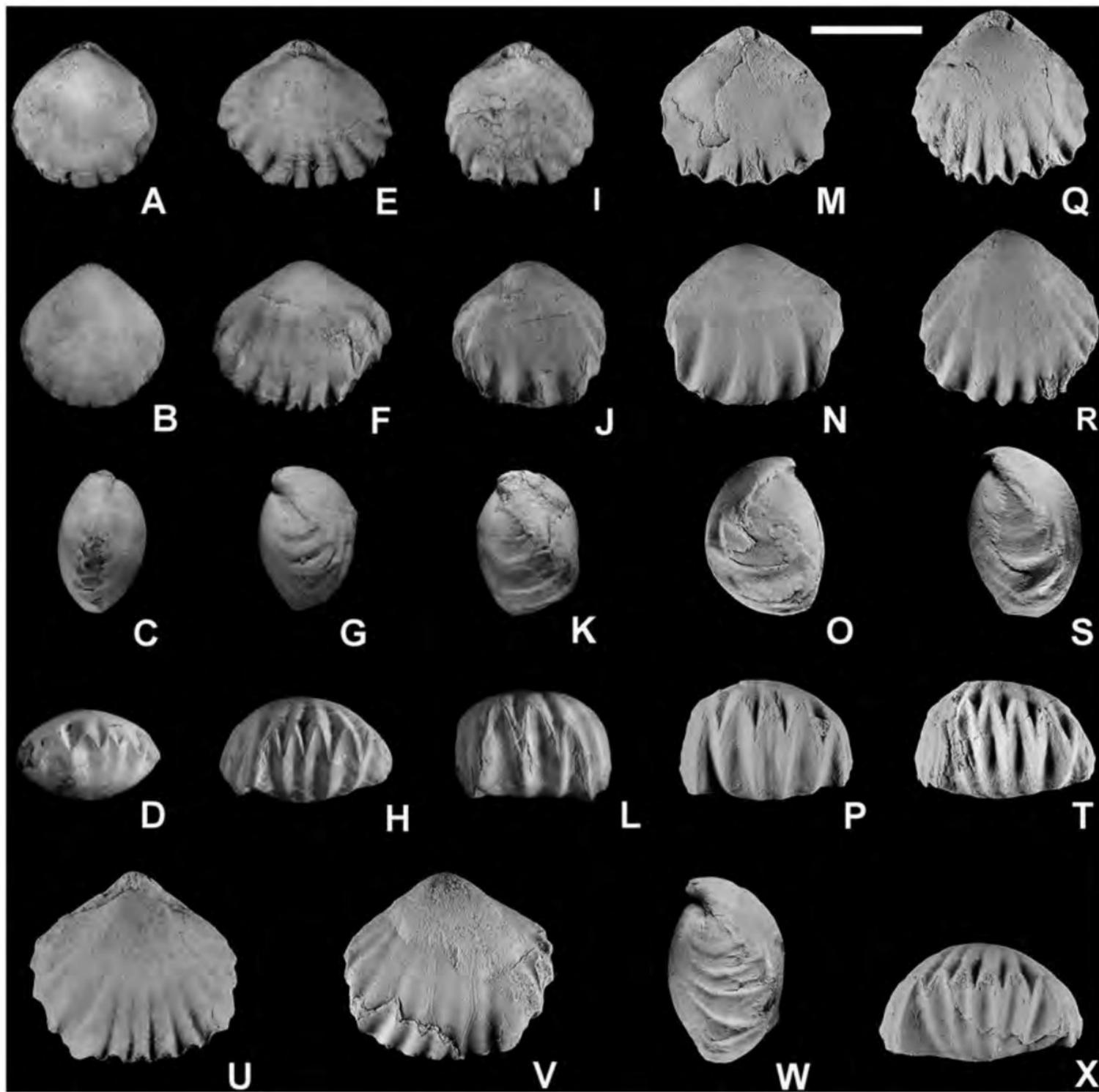
Figure 8. (A)–(X), *Skadarirhynchia semicostata* sp. nov., upper Pliensbachian, Livari, Rumija Mountain, southern Montenegro. Paratypes: (A)–(D), RGF BR 91/46 specimen; E–H, RGF BR 91/48 specimen; I–L, RGF BR 91/50 specimen; (M)–(P), RGF BR 91/51 specimen; (Q)–T, RGF BR 91/58 specimen; Holotype: (U)–(X), RGF BR 91/59 specimen. Images are arranged in dorsal, ventral, lateral, and anterior views respectively. Scale bar = 10 mm.

Shell microstructure (Figure 10A–F)

Shell microstructure was studied from one specimen using 8 SEM micrographs and 18 acetate peels. In a dorsal valve, hinge plates are dorsally inclined and the crural bases are convex laterally (Figure 10A, B). The shell is composed of two calcite layers, primary microgranular (not preserved) and secondary fibrous (Figure 10B–F). The primary layer is poorly observed and relatively thin (20 μm; Fig. 10E). The secondary fibrous layer is homogeneous, built of a single layer (no sublayers were observed). Total thickness of the secondary layer in the costae ornament is approximately uniform, in the costae, it is 350 μm thick (Figure 10C) and in the intercostal spaces (sulci), it is 300 μm thick (Figure 9D). It consists of isometric fibres that are of coarse fibrous type (eurinoid pattern) typically with a rhombic outline in cross-section, 50–60 μm wide and 25–35 μm thick (Figure 10C–F). Secondary diagenetic calcite prisms were also observed (Figure 10C, D, E). They are perpendicular to (or slightly inclined to) the internal shell surface and are considered to be the result of secondary diagenetic calcite precipitation without taxonomic significance.

These observations confirm the recent hypothesis of correlation between shell microstructure and crural type in post-Palaeozoic rhynchonellides (Radulović et al. 2007; Manceñido and Motchurova-Dekova 2010). The hamiform crura of the new species are associated with coarse fibrous (i.e. eurinoid) shell microstructure and confirm the attribution to the Pugnacoidea.

Remarks

Recently, Radulović (2022) erected the new genus and species *Sepkoskirhynchia* with the type species *S. sphaerica* from the upper Pliensbachian of the Livari outcrop, Rumija Mountain, (Montenegro, Dinaric Carbonate Platform). It differs externally from the new species, also found at the same locality and horizon, in having a much more circular outline, much more convex valves, in the anterior view the shell is spherical (in the new species herein the valves are flattened), less developed dorsal fold and no noticeable ventral sulcus. The internal structures of *Sepkoskirhynchia sphaerica* and *Skadarirhynchia semicostata* sp. nov. are very close, especially in having dental plates poorly developed, short, and fused to the shell wall (lateral cavities not developed), dorsally inclined
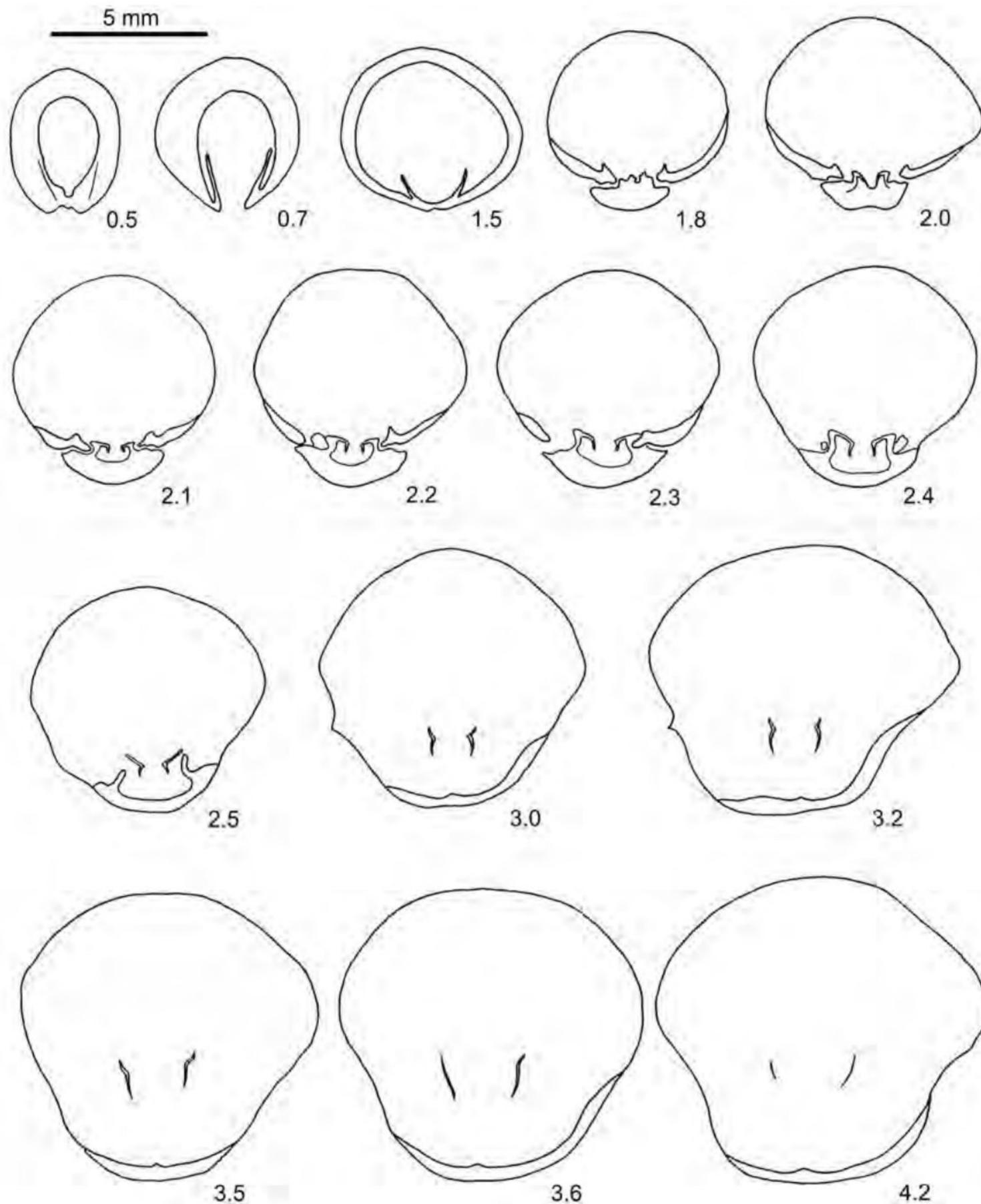
Figure 9. Transverse serial sections performed on *Skadarirhynchia semicostata* sp. nov., specimen RGF BR 91/54, upper Pliensbachian, Livari, Rumija Mountain, southern Montenegro. Original dimensions of the specimen (in mm): L = 14.7, W = 15.3, T = 11.2. Numbers indicate the distance in mm from the apex.

wide and slender hinge plates, teeth laterally inserted at the same angle into sockets, crescent-shaped crural bases and hamiform crura. Reduced dental plates merged into the shell wall are an important characteristic to distinguish between *Skadarirhynchia semicostata* and species of the genus *Soaresirhynchia*. Microstructurally, *Sepkoskirhynchia sphaerica* differs from *Skadarirhynchia semicostata* sp. nov. in having the non-homogenous secondary fibrous layer subdivided into six alternating sublayers with different sizes of coarse (i.e. eurinoid) rhombic fibres, which are considered quite different from *Soaresirhynchia bouchardi* (Davidson 1852), *Livarirhynchia rajkae* (Radulović 2008) and *Skadarirhynchia semicostata* sp. nov. All these latter species have a homogenous secondary layer consisting of a single layer built of coarse rhomboidal fibres.

One question about the brachiopod shell structure that arose during the current work was whether the six-layered secondary shell structure was consistent during growth in *Sepkoskirhynchia sphaerica* (Radulović 2022). The specimen in which the sublayers were originally observed (specimen number RGF BR 91/80, Radulović 2022, figure 5) was taken and additional serial sections were prepared from the maximum shell length to the anterior end of the specimen by BVR. Near the anterior end of the specimen, four sublayers were observed in the secondary shell. Another specimen revealed two sublayers (specimen RGF VR 91/72) and another 2–3 sublayers. The number of layers within the secondary shell layer of *Sepkoskirhynchia sphaerica* is therefore variable. Towards the posterior apical part of the shell two secondary sublayers have been observed, at the maximum width (approximating to
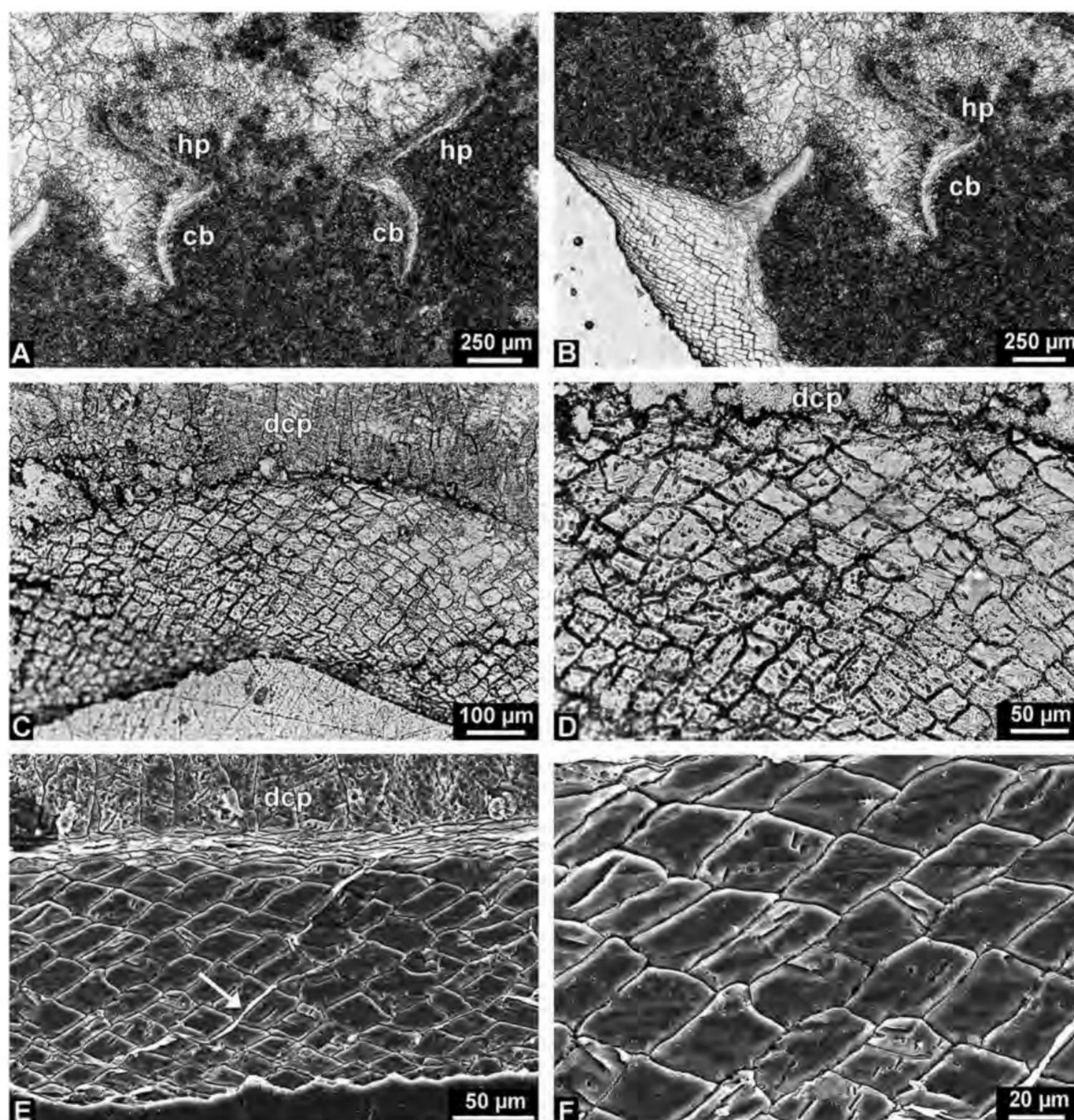
Figure 10. *Skadarirhynchia semicostata* sp. nov., upper Pliensbachian, Livari, Rumija Mountain, southern Montenegro. A–D, Photomicrographs of the shell microstructure from acetate peels of successive transverse serial sections. Original dimensions of the specimen RGF BR 91/60 (in mm): L = 14.0, W = 14.1, T = 9.3. A, crural base (cb) and hinge plate (hp) are shown; B, crural bases (cb), hinge plate (hp) and coarse rhombic fibres of the secondary layer observed in lower left corner. A and B serial sections taken at 2.30 mm from the ventral umbo. C, dorsal valve, sulcus near the plane of symmetry, boundary between whole shell thickness of the secondary layer composed of coarse isometric rhombic fibres and thick diagenetic calcite prisms (dcp) above. D, detail of C, dorsal valve sulcus coarse rhombic fibres of the secondary layer overgrown by diagenetic calcite prisms (dcp) above. E, F, SEM micrographs of transverse sections of the same specimen. E, dorsal valve, whole shell thickness of secondary layer, composed of isometric coarse rhombic fibres, silicified organic sheets developed (arrow) in the middle part, overgrown by diagenetic calcite prisms (dcp) above, the other part of the secondary layer is exhausted; F, detail of E showing the coarse rhombic fibres. C–F serial sections taken at 8.10 mm from the ventral umbo.

midlength) six, while the number of sublayers has been reduced to four near the anterior end.

Alméras and Cougnon (2013) listed 10 species belonging to the genus *Soaresirhynchia*. So far, *Soaresirhynchia bouchardi* is the only species of the genus for which shell microstructure has been investigated. Photomicrographs of the secondary layer of this species from the lower Toarcian (Serpentinus Zone) has been given by several authors: from the Gran Sasso Range (Central Apennines, Italy), from the Iberian Range, Spain by Graziano et al. (2006, fig. 11C); from the Iberian Range, Spain, by Baeza-Carratalá and García Joral (2020, fig. 1.B2, B3); from the Barranco de la Cañada, Iberian Range, Spain, Ullmann et al. (2020, fig. 3); and from Sierra Espuña, Murcia Province, Spain, by Radulović (2022). All of these microphotographs show a homogenous secondary layer, with neither sublayer/s nor different orientations of the fibres. The secondary layer consists of fibres that are of coarse fibrous type (eurinoid microstructure) typically with a rhombic outline in the cross-section. The dimensions of the fibres from the various localities vary from 50 to 90 μm in width and from 20 to 60 μm in thickness (for exact fibre dimensions see Radulović 2022). The dimensions of these fibres agree with those proposed by Manceñido and Motchurova-Dekova (2010) for the coarse (eurinoid) pattern.

Externally, *Livarirhynchia rajkae* Radulović 2008 from the same locality and horizon as *Skadarirhynchia* gen. nov. is quite different in having a fully costate shell (11–16 simple, strong and subangular costae) and a roundly subtriangular outline. Internally, it is very close to having very reduced and short dental plates and dorsally inclined, broad and slender hinge plates, but differs in possessing hamiform crura that are strongly ventrally curved.

Microstructurally, this species has a secondary layer with a single layer built of rhombic fibres of similar dimensions as in *Skadarirhynchia semicostata* (40–55 μm wide and 30–35 μm thick instead of 50–60 μm wide and 25–35 μm thick in *L. rajkae*).

Skadarirhynchia semicostata sp. nov. can be closely compared with some species of the genus *Soaresirhynchia*, namely, *S. bouchardi* (Davidson 1852), *S. renzi* (Choffat) Alméras 1994 and *S. rustica* (Dubar 1931). In contrast to the new species herein, the type species of the genus *Soaresirhynchia*, *S. bouchardi* from the lower Toarcian (Serpentinus Zone) of northwestern and southern Tethys, differs in having a somewhat smaller shell, generally more rounded outline, fewer and rounded costae (4–12 on each valve and 2–3 on the dorsal fold), that are coarser and much shorter. The closest species stratigraphically to *Skadarirhynchia semicostata* sp. nov. is *S. renzi* described by Alméras (1994) and Andrade (2006) from the upper Toarcian part of the north Lusitanian Basin (Portugal). The stratigraphically younger, *S. rentzi* differs externally from the new species in having smaller size (11–12 mm in the maximum length compared to up to 17 mm in the Montenegrin specimens), circular shell and less convex valves, 3–15 (usually 7–9) costae on the dorsal valve and 2–7 on the dorsal fold (usually 4). *Soaresirhynchia rustica* from the lower Toarcian of Portugal, Spain, Morocco, and Algeria differs from the Montenegrin *Skadarirhynchia semicostata* sp. nov. in having a generally more elongated shell and much longer and rounded costae.

From the upper Toarcian of the north Lusitanian Basin (Portugal), Alméras (1994) investigated the internal characters of 5 specimens of *Soaresirhynchia bouchardi*, 3 specimens of *S. renzi* and one specimen of both *S. rustica* and *S. flamandi*. From the Lusitanian Basin, Andrade (2006) figured serial sections of a single specimen of *S. renzi*. It is interesting to note that all sectioned specimens present the same internal characters including the characteristic shape of the dental plates with well-developed lateral cavities (not developed in our new species). According to Alméras (1994, pp. 73, 85) *Soaresirhynchia renzi* and *S. rustica* have the same internal characters as *S. bouchardi*.

Conclusions

A new rhynchonellide brachiopod genus and species, *Skadarirhynchia semicostata* gen. et sp. nov. from the upper Pliensbachian crinoidal-brachiopod bioclastic limestones (packstone/wackestone levels) at Livari, Rumija Mountain, Montenegro, is formally described based on examination of its external and internal morphology, as well as the shell microstructure. The locality is on the southeastern margin of the Dinaric Carbonate Platform.

The relative age of this assemblage as well as of the new species is determined as late Pliensbachian by means of ^{87}Sr/^{86}Sr dating, and the position of brachiopod beds lie immediately below the Toarcian marly limestones; both coincide well with the age derived from present biostratigraphic studies.

The main morphological features that distinguish the new species from close representatives of the basiliolid genus *Soaresirhynchia* are its subpentagonal and circular outline and semicostate shell (10–12 strong angular costae). Internally, it is characterised by having very reduced dental plates merged with the shell wall, narrow and thin-hinge plates, subhorizontal to slightly dorsally inclined with very small crural bases, crescent-like and laterally convex, and hamiform crura.

The shell microstructure of *Skadarirhynchia semicostata* sp. nov. reveals a secondary layer built of a single layer of coarse fibres (i.e.

eurinoid), rhomboidal in cross-section, isometric in shape, 35–50 μm wide and 20–30 μm thick, which is compatible with its placement in the Basiliolidae.

Other co-occurring rhynchonellides, such as *Prionorhynchia fraasi* and *Cuneirhynchia dalmasi* are also described. In addition to the external characters of these two species, the internal morphology and shell microstructures of *Cuneirhynchia dalmasi* are presented. The secondary layer of the shell wall is homogeneous and consists of a single layer built of anisometric and partly isometric fine fibres (i.e. leptinoid), with an average width of 20–30 μm and thickness of 5–10 μm.

Palaeoecological, taphonomic, and sedimentological data suggest that the rhynchonellide assemblage lived in a shallow-marine inner shelf environment, with a lime mud sea floor, in low energy conditions. The presence of articulated valves, both adult and juvenile forms were found together, with good preservation of the fauna and variously oriented specimens (no dominant direction was noted), indicating that transport and reworking of the rhynchonellide assemblage was insignificant (e.g. parautochthonous). The abundance of rhynchonellides in this assemblage at Livari is considered to be related to favourable environmental conditions.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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References

Ager DV. 1956–1967. A monograph of the British Liassic Rhynchonellidae. London: Paleontogr Soc.

Ager DV. 1990. British Liassic Terebratulida (Brachiopoda). Part. 1. London: Paleontogr Soc.

Alméras Y. 1964. Brachiopodes du Lias et du Dogger. Essai bibliographique et critique de Paléontologie stratigraphique. Doc Lab Géol Fac Lyon. 5:1–161.

Alméras Y. 1994. Le genre *Soaresirhynchia* (Brachiopoda, Rhynchonellacea, Wellerellidae) dans le Toarcien du Sous-bassin nord-lusitanien. Doc Lab Géol Lyon. 130:3–135.

Alméras Y, Cougnon M. 2013. Les Brachiopodes jurassiques (Spiriferida et Rhynchonellida). Principaux genres et leur évolution. Les espèces, extensions verticales et répartitions géographiques. Doc Lab Géol Lyon. 170:1–227.

Alméras Y, Elmi S. 1987. Évolution des peuplements de brachiopodes en fonction de l'environnement dans le Lias ardéchois. Cah Inst Catholique Lyon, sér Sci. 1:21–56.

Alméras Y, Elmi S, Fauré P. 2007. Les Brachiopodes liasiques d'Algérie occidentale. Doc Lab Géol Lyon. 163:1–241.

Andrade B. 2006. Los braquiópodos del tránsito Jurásico Inferior–Medio de la Cuenca Lusitánica (Portugal). Coloq Paleont. 56:5–194.

Baeza-Carratalá JF. 2013. Diversity patterns of Early Jurassic brachiopod assemblages from the westernmost Tethys (Eastern Subbetic). Palaeogeogr Palaeoclimat Palaeoecol. 381–382:76–91. doi: 10.1016/j.palaeo.2013.04.017.

Baeza-Carratalá JF, García Joral F. 2020. Linking Western Tethyan rhynchonellide morphogroups to the key post-Palaeozoic extinction and turnover events. Palaeogeogr Palaeoclimat Palaeoecol. 553:109791. doi: 10.1016/jpalaeo.2020.109791.

Benigni C. 1978. Revisione tassonomica dei Rhynchonellida liassici di ra stua (Belluno) e fanes (Bolzano). Riv Ital Paleont Stratigr. 84:121–168.

Bešić Z. 1959. Geologischer Führer durch die Volksrepublik Crna Gora. Société géologique du Monténégro 559. Titograd: Société géologique du Monténégro. [In Serbian with German summary].

Bittner A. 1895. Über die Gattung Rhynchonellina Gemm. Jb K-K Geol Reichsanstalt. 44(1894):547–572.

Böhm F, Ebli O, Krystyn L, Lobitzer H, Raküs M, Siblík M. 1999. Fauna, Stratigraphy and Depositional Environment of the Hettangian-Sinemurian (Early Jurassic) of Adnet (Salzburg, Austria). Abh Geol Bundesanst. 56 (2):143–271.

Böse E. 1893. Die Fauna der liasischen Brachiopodenschichten bei Hindelang (Algäu). Jb K-K Geol Reichsanstalt. 42(4):627–650.

Böse E, Schlosser M. 1900. Ueber die mittelliasischen Brachiopodenfauna von Südtyrol. Palaeontogr, Stuttgart. 46(5–6):175–212.

Buckman SS. 1918. The Brachiopoda of the Namyau Beds, Northern Shan States, Burma. Mem Geol Surv India, Palaeont Indica (New Ser). 3:1–299.

Čađenović D, Kilibarda Z, Radulović N. 2008. Late Triassic to Late Jurassic evolution of the Adriatic Carbonate Platform and Budva Basin, Southern Montenegro. Sed Geol. 204(1–2):1–17. doi: 10.1016/jsedgeo.2007.12.005.

Čađenović D, Radulović N, Milutin J, Ostojić Z. 2005. Jurassic formations of the Rumija Mt. plateau (Montenegro). Novi Sad: 14th Congress of Geologists of Serbia and Montenegro. 185–192.

Canavari M. 1883. Contribuzione III alla conoscenza dei Brachiopodi degli strati a Terebratula Aspasia MGH. nell'Appennino centrale. Ati Soc tosc Sci nat. 6 (1):70–110.

Ćirić B. 1949. Les brachiopodes du Lias de Lovćen. Glas Prirod muz Srpske zemlje, ser A. 2:159–172. [In Serbian with French summary].

Cooper GA. 1959. Genera of Tertiary and Recent rhynchonelloid brachiopods. Smithson Misc Collect. 139(5):1–90.

Črne AE, Goričan Š. 2008. The Dinaric Carbonate Platform margin in the Early Jurassic: a comparison between successions in Slovenia and Montenegro. Boll Soc Geol Ital. 127(2):389–405.

Croft WN. 1959. A parallel grinding instrument for the investigation of fossils by serial sections. J Paleont. 24:693–698.

Dal Piaz G. 1907. Sulla fauna liasica delle tranze di Sospirolo. Mem Soc Paleont Suisse. 33:1–64.

Davidson T. 1852. British fossil Brachiopoda, Oolitic and Liassic species 65–100. London: Palaeontogr Soc Monogr.

Di Stefano CD. 1891. Sul Lias inferiore di Taormina e de' suoi dintorni. G Sei Nat Econ Palermo. 3:121–270.

d'Orbigny A. 1847. Paléontologie Française. Description des Mollusques et Rayonnés fossiles. Terrains Crétacés. Brachiopodes. Paris: Victor Masson.

Dubar G. 1931. Brachiopodes liasiques de Catalogue et des régions voisines. Bull Inst catalana Hist nat, ser 2. 31(4):103–180.

Dulai A. 1992. The Early Sinemurian (Jurassic) brachiopod fauna of the Lókút Hill (Bakony Mts. Hungary). Fragm Mineral Paleont. 15:41–94.

Dulai A. 2003. A Dunántúli-középhegység hettangi és kora szinemuri (korajura) brachiopoda faunája II. Rendszertani leírások. [Hettangian and Early Sinemurian (Early Jurassic) brachiopods of the Tïansdanubian Central Range (Hungary) II]. Systematic Descr A Bakony természettudományi kutatásának eredményei. 27:1–144.

Duméril AMC. 1806. Zoologie analytique ou méthode naturelle de classification des animaux. Paris: Allais; xxiv.

Dumortier E. 1869. Études paléontologiques sur les dépôts jurassiques du Bassin du Rhône. 3ème partie: Lias moyen. Paris: F. Savy édit.

Eichenbaum J. 1883. Die brachiopoden von Smokovac bei Risano in Dalmatien. Jb K-K Geol Reichsanst. 33:713–720.

Georgescu DM. 1990. An attempt to the correlation of the brachiopod biozones in the Liassic deposits of the Northern Apuseni Mountains (Romania). Crisia. 20:517–541.

Geyer G. 1889. Uber die liassischen Brachiopoden des Hierlatz dei Hallstat. Abh K-K Geol Reichsanst. 15:1–88.

Graziano R, Buono G, Taddei Ruggiero E. 2006. Lower Toarcian (Jurassic) brachiopod-rich carbonate facies of the Gran Sasso range (central Apennines, Italy). Boll Soc Paleont It. 45(1):61–74.

Kamyshan VP. 1977. Organizational levels of the shell substance, structure and texture of the shell of Mesozoic and Cenozoic rhynchonellides. The Third All-Union Conference on Mesozoic and Cenozoic Brachiopods, Kharkov, Abstract p. 21–24. [In Russian].

Kamyshan VP. 1986. On the microstructure features of shell growth in the Jurassic rhynchonellides (Brachiopoda). Vesn Khar'kovskogo Univ, Seria Geol. 16:75–77. [In Russian].

Kuhn O. 1949. Lehrbuch der Paläozoologie 326 pp. Stuttgart: E. Schweizerbart.

Lee DE, Mackinnon DI, Smirnova TN, Baker PG, Yu-Gan J, Dong-Li S. 2006. Terebratulida. In: Kaesler R, editor. Treatise on Invertebrate Paleontology Vol. 5, Part H. Brachiopoda (revised). Boulder (CO): Geological Society of America and University of Kansas Press; p. 1965–2255.

Licharev BK. 1956. Super-family Rhynchotetradoidea. In: Rzhonsnitskaia M, Systematization of Rhynchonellida. Mexico: XX International Geological Congress; p. 125–126.

Manceñido MO, Motchurova-Dekova N. 2010. A review of crural types, their relationships to shell microstructure, and significance among post-Palaeozoic Rhynchonellida. Spec Pap Palaeont. 84:203–224. doi: 10.1111/j.1475-4983. 2010.00991.x.

Martelli A. 1906. Brachiopodi del Dogger montenegrino. Boll Soc Geol It. 25:281–320.

McArthur JM, Howarth RJ, Bailey TR. 2001. Strontium isotope stratigraphy: lowess version 3: best fit to the marine sr-isotope curve for 0–509 ma and accompanying look-up table for deriving numerical age. J Geol. 109 (2):155–170. doi: 10.1086/319243.

Mihajlović M. 1955. Quelques espèces Rhynchonellinae du calcaire jurassique à Smokovac près de Risan (Boka Kotorska). Geol An Balk Poluost. 23:67–73. [In Serbian with French summary.

Miladinović M. 1964. La géologie et la tectonique de la montagne Rumija et ses environs dans le littoral Montenegrin Vol. 96. Sarajevo: Institut géologique de Sarajevo. [In Serbian with French summary].

Moiseev AS. 1935. O Iurskikh brakhiopodakh, sobrannykh Tadzhiksko-Pamirskoi ekspeditsiei Moskva 1933 g. [On the Jurassic brachiopods collected by the 1933 Tajikistan-Pamirs expedition] Vol. 22, 128–130. Trudy Tadzhiksko-Pamirskaia Ekspeditsiia. [In Russian].

Motchurova-Dekova N, Radulović V, Bitner MA. 2008. Orientations of the valves when presenting serial sections of post-Palaeozoic brachiopods: tradition and utility versus the revised Treatise. Lethaia. 41(4):493–495. doi: 10. 1111/j.1502-3931.2008.00128.x.

Oppel A. 1861. Ueber di Brachiopoden des untern Lias. Zeitschr Deutsch geol Ges. 13(4):529–550.

Ormós E. 1937. Die Brachyopoden-Fauna der unteren Lias in Kékhegy (Bakonyerwald). Közl Debrec Egyet Ásv–Földt Int. 9:1–45.

Ovcharenko VN. 1983. Yurskie brakhiopody Pamira [Jurassic brachiopods of the Pamirs] 196. Dushanbe: Akad Nauk Tadzhikistana SSR, Inst geol. [In Russian].

Parona CF. 1892. Revisione della fauna liasica di Gozzano in Piemonte. Mem Reale Accad Sci Torino, sér. 2. 43:1–59.

Pevny J. 1964. On brachiopods from Northern Little Carpathians. Geol práce. 33:157–172.

Quenstedt FA. 1868–1871. Petrefactenkunde Deutschlands, vol. 2, Brachiopoden. Tübingen and Leipzig: Fuess ed.

Radoičić R. 1966. Microfacies du jurassique des Dinarides da la Yougoslavia. Geol Raspr Poroč. 9:5–375.

Radoičić R. 1982. Carbonate platforms of the Dinarides: the example of Montenegro-West Serbia sector. Bull Acad Serbe Sci Arts, Cl Sci Nat Math. 22:35–46.

Radoičić R. 1987. The Dinaric Carbonate Platform: adjacent basins and depressions. Mem Soc Geol It. 40:309–311.

Radoičić R, D'Argenio B. 1999. An outline of the geology of the External Dinarides and their Mesozoic. Early Tertiary facies. Rendicon Accad Sci Fis Mat. 61:181–243.

Radulović B. 2022. New Pliensbachian rhynchonellide (Brachiopoda) from Livari, (Rumija Mountain, Montenegro): the taxonomic implications of microstructure to disentangle cases of homeomorphism. Hist Biol. 34 (12):2304–2314. doi: https://doi.org/10.1080/08912963.2021.2014480.

Radulović B, Motchurova-Dekova N, Radulović V. 2007. New Barremian rhynchonellide brachiopod genus from Serbia and the shell microstructure of Tetrarhynchiidae. Acta Paleont Polonica. 52(4):761–782.

Radulović V. 2008. A new Pliensbachian rhynchonellide brachiopod from Livari (Rumija Mountain, Montenegro). In: Harper D, Long S, Nielsen C, editors. Brachiopods: fossil and recent Vol. 54, Fossils and strata; p. 183–192.

Rollier L. 1917. Synopsis des Spirobranches (Brachiopodes) jurassiques celto-souabes. Mém Soc Paléont Suisse. 42:71–184.

Rzhonsnitskaia MA. 1956. Systematization of Rhynchonellida. XX Congr Geol Int, Mexico, Resúmenes Trab Present. Report 20.

Sacchi Vialli G, Cantaluppi G. 1967. I nuovi fossili di Gozzano (Prealpi piemontesi). Mem Soc Ital Sci Nat Mus Civ Stor Nat Milano. 16(2):61–127.

Sandy MR, Radulović BV, Đaković M. 2021. Revisiting the Early Jurassic (Sinemurian) brachiopod fauna from Smokovac, Montenegro. The 13th Romanian Symposium of Palaeontology Iașa, September 16–17, 2021, Iași.

Sandy MR, Radulović BV, Peckmann J, Sulser H, Radulović VJ, Wu SY, Đaković M. 2018. Homeomorphy in an Early Jurassic rhynchonellide-dominated brachiopod coquina from Smokovac, Montenegro: an incertae sedis finds a home in the suborder Terebratellidina. Geological Soc Am, Abstr Program. 50(6). doi: 10.1130/abs/2018AM-323189.

Sandy MR, Radulović BV, Sulser H, Đaković M. 2022. New brachiopod family Arzonellinidae (Terebratulida) from the Early Jurassic (Sinemurian) of Montenegro, Southern Europe, Mediterranean Province. Hist Biol. 34 (5):917–929. published online 2021 Sep 25. 10.1080/08912963.2021.1952573;.

Sass DB, Monroe EA. 1967. Shell growth in recent Terebratuloid Brachiopoda. Palaeontology. 10:298–306.

Savage NM, Manceñido MO, Owen EF, Carlson SJ, Grant RE, Dagys AS, Dong-Li S. 2002. Rhynchonellida. In: Kaesler R, editor. Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised). Volume 4, Rhynchonelliformea. Boulder (CO): Geological Society of America and University of Kansas Press; p. 1027–1376.

Shi X, Grant RE. 1993. Jurassic Rhynchonellids: internal structures and taxonomic revisions. Smithson Smithson Contr Paleobiol. 73:iv + 190.

Siblík M. 1964. Brachiopodi severnej casti Malych Karpat. Geol pràce, Zpravy. 33:157–172.

Siblík M. 1993a. Lower Liassic Brachiopods from the Steinplatte–Kammerköhralm area near Waidring (Northern Calcareous Alps, Salzburg). Jb Geol B-A. 136:965–982.

Siblík M. 1993b. Review of the Early Liassic brachiopods of the Northern Calcareous Alps. In: Pálfy J, Vörös A, editors. Mesozoic Brachiopods of Alpine Europe. Budapest: Hungarian Geol Soc; p. 127–132.

Siblík M, Lobitzer H. 2008. A Jurassic Brachiopod Fauna from the Mitterwand Area near Hallstatt (Upper Austria). Jb Geol B-A. 148(1):59–87.

Sowerby J de C. 1823–1825. The Mineral Conchology of Great Britain Vol. 5, 168 pp. London: W. Ardling.

Tchorszevski E. 1985. New data of the lower Jurassic genus Rhapidothyris (Brachiopoda), its composition, structure of shell and spread. Paleont Sb. 22:34–40 [In Russian with English summary].

Tuluweit K. 1965. Die Terebratulidae und Zeilleriidae (Brachiopoda) des mittleren Lias Nordwestdeutschlands. N Jb Geol Palaont Abh. 122:50–126.

Uhlig V. 1879. Über die liasischen Brachiopodenfauna von Sospirolo bei Belluno. Sitzber Math-NATW Cl Kais Akad Wiss. 80:259–310.

Ullmann CV, Boyles R, Duarte LV, Hesselbo SP, Kasemanns SA, Kleins T, Lenton T, Piazza V, Aberhan M. 2020. Warm afterglow from the Toarcian Oceanic Anoxic Event drives the success of deep-adapted brachiopods. Sci Rep. 10:6549. doi: 10.1038/s41598-020-63487-6.

Vörös A. 1980. Lower and Middle Jurassic brachiopod provinces in the Western Tethys. Föl Közl. 110:395–416. [In Hungarian with English summary].

Vörös A. 1984. Lower and Middle Jurassic brachiopod provinces in the western Tethys. Ann Univ Sci Budapest, Sec Geol. 24:207–233.

Vörös A. 1993. Jurassic brachiopods of the Bakony Mts. (Hungary): global and local effects on changing diversity. In: Pálfy J, Vörös A, editors. Mesozoic Brachiopods of Alpine Europe. Budapest: Hungarian Geol Soc; p. 179–187.

Vörös A. 2009. The Pliensbachian brachiopods of the Bakony Mountains (Hungary). Geol Hung, Ser Palaeont. 58:3–300.

Vörös A, Dulai A. 2007. Jurassic brachiopods of the Transdanubian Range (Hungary: stratigraphical distribution and diversity changes). Fragmenta Palaeont Hung. 24–25:51–68.

Vörös A, Szabó J, Dulai A, Szente I, Ebli O, Lobitzer H. 2003. Early Jurassic fauna and facies of the Schafberg area (Salzkammergut, Austria). Fragm Palaeont Hung. 21:51–82.

Williams A, Carlson SJ, Brunton CHC, Holmer LE, Popov L. 1996. A supra-ordinal classification of the Brachiopoda. Phil Trans R Soc B. 351 (4):1171–1193. doi: 10.1098/rstb.1996.0101.

Zittel KA. 1869. Geologische Beobachtungen aus den Central Apenninen. Benecke's Geognost Pal Beitr. 2(2):91–177.