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Late Campanian Rudist Assemblages and Biometrical Analysis of *Pseudopolyconites* from Bačevica (Eastern Serbia)

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Abstract: The lithological and faunal succession cropping out close to the famous palaeontological locality of Bačevica (Eastern Serbia) is described along a very discontinuous and ill-exposed section. Since the section is dominated by clastic sediments, no-vestige of the so-called 'Vrbovac reef' has been observed. Rhythms consisting of a limestone breccia lower unit and a fossil-rich upper part characterize the base of the section while rare silt and sand-rich limestone breccias and prevailing silty/sandy soils are the lithologies observed in the upper part of the same. The faunal succession shows an alternation of monospecific-paucispecific assemblages and much more diverse assemblages of rudists. The stratigraphic distribution of the different examples of rudist bivalves recovered at Bačevica may represent a significant tool for biostratigraphic correlations as far as the late Campanian deposits in the Central Tethys area are concerned. In particular, the *Pseudopolyconites*-bearing strata seem to be included within a few fossiliferous lithosomes. Therein the Serbian rudistologists instituted twenty species of *Pseudopolyconites* on the base of the characteristics of their ligamental ridge. Biometrical analyses have been made on the transverse sections of the right valves of the *Pseudopolyconites* holotypes illustrated in the scientific literature. It is suggested that the wide variability of the ligamental ridge shape alone does not warrant the institution of so many species of the genus in question but the existing ones should probably be re-considered as simple eco-morphotypes.

Key Words: Bačevica, Serbia, Late Campanian, lithological and faunal succession, rudist bivalves, *Pseudopolyconites* species

Bačevica (Doğu Sırbistan)'da Bulunan *Pseudopolyconites*'in Biyometrik Analizi ve Geç Kampaniyen Rudist Topluluğu

Özet: İyi tanınan paleontoloji lokalitesi Bačevica (Doğu Sırbistan)'ya oldukça yakın bir alanda yüzeyleyen litolojik ve faunal istif süreksiz ve kötü korunmuş bir kesitte tanımlanmıştır. Kesitin klastik tortullarca baskın olduğu yerlerde 'Vrbovac reef' olarak tanımlanan fasiyes gözlenememiştir. Kesitin taban bölümü, kireçtaşı breşlerinden oluşan alt birim ve fosilce zengin üst kısımdan yapılıdır. Üst kısımda aynı zamanda, seyrek silt ve kumca baskın kireçtaşı breşleri ve siltli/kumlu topraklar gözlenir. Faunal istif, monospesifik-posispesifik topluluklarının ardalanmasını ve oldukça çeşitli rudist topluluklarını içerir. Bačevica'da tanımlanan farklı rudist örneklerinin stratigrafik dağılımı, Orta Tetis bölgesi'ndeki geç Kampaniyen tortullarının biyostratigrafik korelasyonu için önemli bir veri teşkil etmektedir. Özellikle *Pseudopolyconites* içeren düzeyler, birkaç fosilli lithosoma dahil edilebilir gibi görünmektedir. *Pseudopolyconites*'in yirmi türü ligament çıkıntısının özelliklerine dayanılarak Sırbistan rudist uzmanlarınca tanımlanmıştır. Literatürde örneklendirilmiş olan *Pseudopolyconites*'in sağ kavkısının enine kesitlerinde biyometrik analizler yapılmıştır. Ligament çıkıntısındaki genişlik değişiminin tek başına birçok türün tanımlanması için sağlıklı bir veri olmadığı ve olasılıkla basit bir eko-morfotip olabileceği anlaşılmıştır.

Anahtar Sözcükler: Bačevica, Sırbistan, Geç Kampaniyen, litolojik ve faunal istif, rudist bivalviaları, *Pseudopolyconites* türleri

Introduction

The rudist genus *Pseudopolyconites* was established in 1934 by the famous Serbian palaeontologist Branislav Milovanović. The first specimens of this rudist were found close to the village of Bačevica (Eastern Serbia) which is considered the type-locality of this genus. Tubular excrescences on the shell of *Pseudopolyconites* individuals and other minor characteristics made this genus different from the other genera of Radiolitiidae and, due to the tubules, probably one of the most bizarre and specialized rudists known up to that time (Milovanović 1934, 1935a, b, 1937a, b).

According to Milovanović (1932) and Milovanović & Grubić (1971), specimens of the new genus together with a large variety of rudists, including also new genera and species, created a well-developed bioherm, the so-called 'Vrbovac reef' characterized by a specific '*Pironaea-Pseudopolyconites*' association.

Very few geologists have had the opportunity to visit the Bačevica area (Figure 1). Four field investigations in this zone have been carried out by Alceo Tarlao who spent two weeks during the late spring and early autumn 2006 and two weeks, together with Maurizio Tentor, during the summers 2008 and 2009 in order to: (i) inspect the architecture of the expected rudist constructions and of their associated facies and (ii) examine the rudist assemblages of the area in question. A second aim of this research regards the question of the large number of *Pseudopolyconites* species instituted in the Bačevica locality (Milovanović 1934, 1935a; Milovanović & Sladić 1957; Sladić-Trifunović 1986) in order to verify the foundation of the criteria used by the Serbian rudistologists in establishing so many species of the fore-mentioned genus.

Geological Context and the Lithological/Faunal Succession of Bačevica

The upper Cretaceous deposits of Eastern Serbia were formed in the central area of Tethys, on the southern margin of the European Plate. The rudist-bearing deposits usually overlie andesite and andesitic pyroclastics of the Timok eruptive area (Djordjević & Benjesević 1996). The late Senonian palaeogeography of the Carpatho-Balkanides of Eastern Serbia illustrated by Sladić-Trifunović (1998) shows a group of islands (archipelago?), some of which were of volcanic origin, separated by deep sea basins. This picture is consistent with the palaeogeographic reconstruction proposed by other authors (e.g., Dercourt *et al.* 1993). The stratigraphy of the upper Cretaceous sediments in Eastern Serbia (Sladić-Trifunović 1998) shows the following succession from the base to the top: (i) limestone breccias; (ii) sandstone and marls with planktonic foraminifers, (iii) andesites and andesitic tuffs, (iv) deposits characterized by recurrent horizontal and vertical alternations of different facies. These different facies include biohermal and biostromal rudist reef deposits, limestone breccias, sandy limestones with orbitoids, sandstone with actaeonellids and *Cyclolites*, sandy marlstones with *Inoceramus* and others. The so-called '*Inoceramus* marlstones' containing *Inoceramus*, *Belemnitella* and planktonic foraminifers rest on the fore-mentioned facies (Figure 2).

As far as the age of the rudist-bearing strata is concerned, Sladić-Trifunović (1986, 1998, 2004) seems to be inclined to assign an early Maastrichtian age and, doubtfully, a late Campanian age. Rajka Radoičić considering the micropalaeontological content consisting of *Siderolites vidali* and *Orbitoides tissoti*, set the Vrbovac beds in the Campanian.

Swimburne *et al.* (1992) provided Sr-isotope data on similar palaeontological assemblages from Bulgaria and determined a late Campanian age. Steuber *et al.* (2005, 2007) and Schlüter *et al.* (2008) have also supplied numerical ages from Sr-isotope analysis made on unaltered calcite shells of radiolitids and hippuritids from a few localities of the island of Brac (Croatia) and Salento peninsula (southern Italy) where *Pseudopolyconites* individuals have also been found. The fore-mentioned authors established a middle Campanian age.

A.T. during the field investigations in the area between Bačevica, Vrbovac and Liljekar hill has observed only rare exposures. Due to the shortage of the cropping out strata and to the reduced thickness of the recovered successions, only a very discontinuous profile has been traced through the area, some 1050 m east of Bačevica small square and

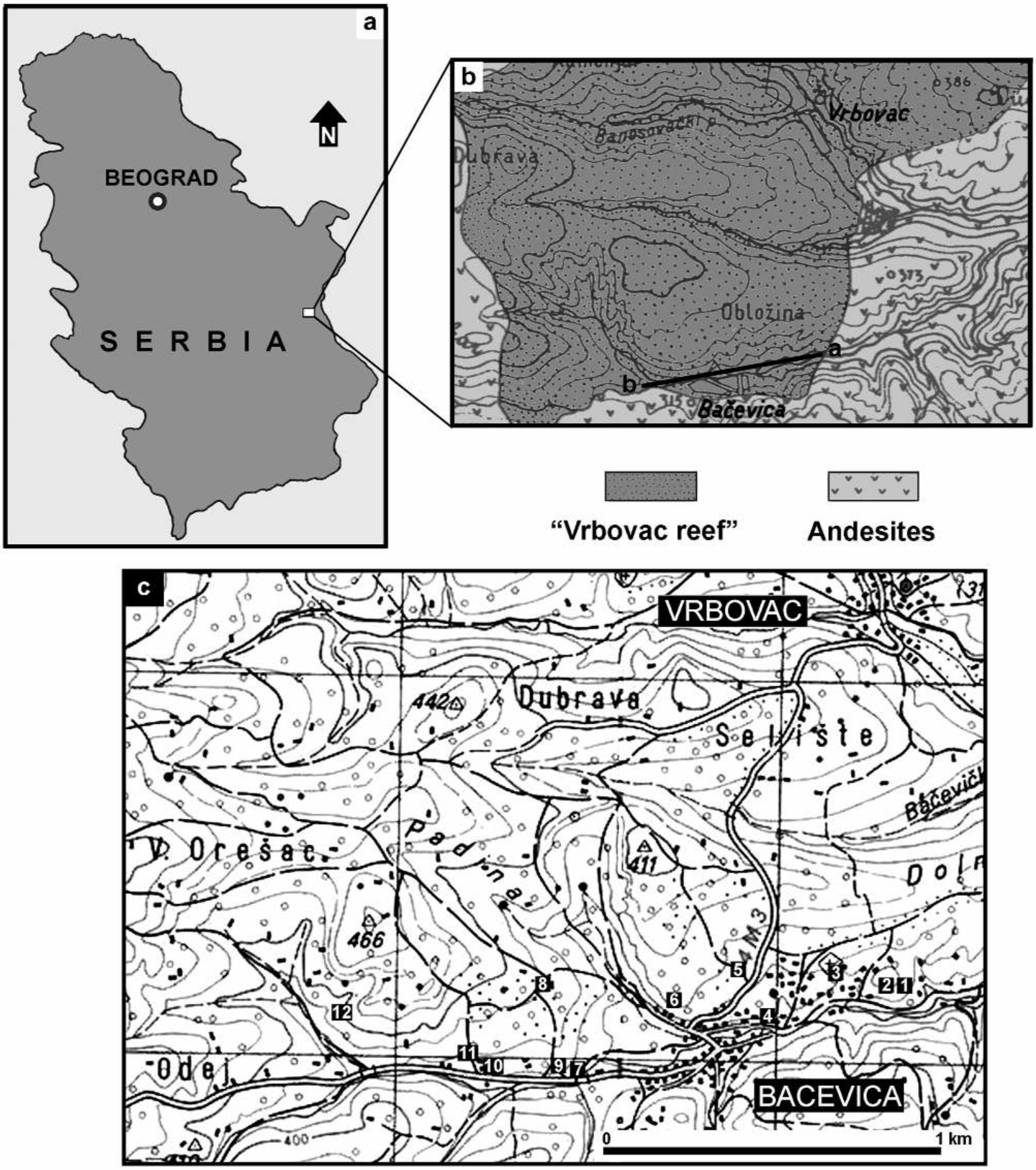

Figure 1. **(a)** Location map of the examined zone; **(b)** geological map of the area between Bačevica and Vrbovac after Milovanović (1935a) with the approximate track of the examined profile a–b; **(c)** map showing the observation points quoted in the text (a and b in the Figure 1b correspond to point 1 and to point 12, respectively).

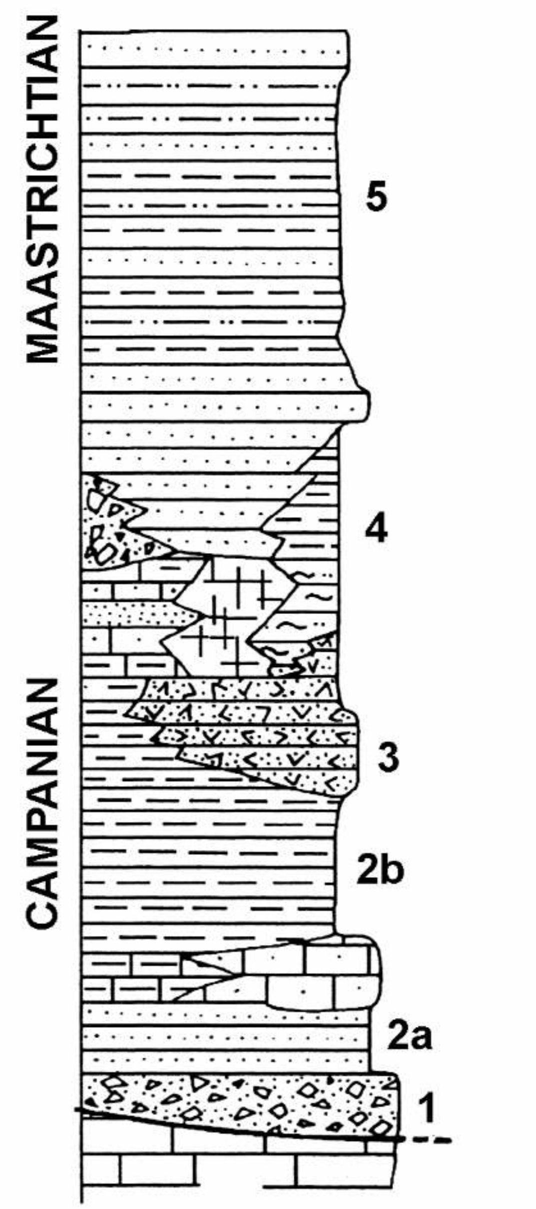

Figure 2. Schematic stratigraphical section (without scale) of the 'Senonian graben' in Eastern Serbia characterized by rudist-bearing strata (modified after Sladić-Trifunović 1998). 1– limestone breccias, 2a– sandstones and marly limestones, 2b– marlstone with planktonic foraminifers, 3– andesite pyroclastics, 4– 'different facies' (see the text), 5– '*Inoceramus*' marlstones.

1400 m W of the same. Twelve datum-points referring to the poor visible exposures are numbered from E to W (Figure 1c). Due to a fault, the beds are sub-vertical (75°W) at point 1. The beds dip to the west (30–35 degrees) at points 2 and 3, then they progressively dip more and more gently to the west so much that they are sub-horizontal between Bačevica and Liljekar (point 7 as far as point 12). Andesitic/dacitic tuffs and andesites crop out to the east, west and to the south of the profile. The maximum thickness of the exposed successions does not reach 8 metres (point 2). The first three short successions (point 1 to point 3) are characterized by rhythms up to about 70 cm in thickness, but they are usually 30–40 cm thick. Each rhythm consists of (i) a lower thicker clastic unit with random oriented specimens of diverse corals and rudists and (ii) an upper thinner part with more or less abundant, mostly intact rudists. A rather abrupt contact between the underlying and overlying rhythms is usually observed. The lower unit consists of a limestone breccia with a nodular or strongly nodular appearance due to a significant silty fraction. This unit is represented by a rather wide spectrum of bioclastic lithologies characterized by either angular or rounded coarse debris (i.e. coarse rudstone to grainstone/packstone). Large quantities of rudist and coral fragments compose the bioclasts; peloids are fairly common while benthic foraminifers, always beyond the taxonomic recognition, are uncommon. Sporadic, intact rudists and ahermatypic corals are locally present. Rare blocks of coral have been also observed within the clastic unit. The upper unit is characterized by weathered silty limestones, silt and sand and by rare, well rounded, multicoloured (white, red, grey and black) quartz pebbles, ranging in diameter from 0.5 to 8 cm. The rudists herein are not reworked; they are mostly in growth position (point 3), often fully articulated (approximately 50–60% of the examples) and without evidence of bioerosion. The specimens are mostly isolated from each other and no-type of congregation of individuals has been detected. Rare *Vaccinites* sp. and common *Radiolites* sp. have been found at point 1, while rare examples of *Plagyopticus toucasianus* together with abundant radiolitids are visible at point 2. Due to the hard rock, the rudists can be extracted only with difficulty. Point 3, in the vicinity of Bačevica cemetery, is marked by *Joufia reticulata*, common specimens of *Lapeirousia jouanneti* and rare *Lapeirousia crateriformis* (Plate 1). The *Lapeirousia* individuals are big and elongated in some places, while they are large and short in the neighbouring places. A monospecific assemblage represented by *Joufia reticulata* has been observed at point 4. Abundant examples of *Praeradiolites* cf. *orientalis* together with rare *Vaccinites* cf. *gaundry* occur at point 5. One clump made of small examples of *Hippuritella variabilis* (2 specimens), *Vaccinites loftusi* (1) and *Radiolites* sp.(1) has been recovered here (Figure 3). An oligo-specific assemblage of common *Joufia reticulata* and *Plagyopticus. toucasianus* (Plate 1) has been observed at point 6.

The rare visible beds from point 7 to point 12 are represented by silty limestones or silt and sand-rich limestone breccias containing rudists, solitary corals (*Cyclolites* sp.) and abundant quartz pebbles, but the prevailing sediments consist of silt and sand. The quartz grains are well rounded while the carbonate grains are angular to sub-angular. The rudists are mainly fully articulated and in growth position or slightly oblique with respect to the bedding. Rudists are nearly always isolated and they do not form any biogenic concentrations.

The first specimens of *Pseudopolyconites* sp. (Plate 1) associated with rare *Plagyoptycus* cf. *toucasianus* have been recovered at point 7 together with both small and large fragments of *Pseudopolyconites* tubules. An abundant ochrous silty matrix is commonly observed among the tubules of *Pseudopolyconites* individuals A rich association made of solely large specimens of actaeonellids (Figure 4) has been recovered at point 8 which is located 1 km north of point 7. A much more diverse assemblage of rudists with common specimens of *Vaccinites loftusi* (predominant specimens), *Lapeirousia jouanneti*, *Lapeirousia crateriformis*, *Hippuritella variabilis*, *Pironaea polystila* (small examples), rare *Branislavia bacevicensis* (Plate 1) together with very common *Cyclolites* occurs at point 9. Very rare and tiny clusters made of *Hippuritella cornucopiae* have also been observed. The breccia bed at point 10 (i.e. only the top of the clastic unit is visible) contains a lower diversity and abundance of rudists in comparison with point 9. Vertically growing individuals of *Pseudopolyconites* sp. dominate the low-diversity rudist assemblage. Only large specimens of *Pseudopolyconites* have been found in the vicinity (point 11). Point 12 is characterized by rare, large examples of *Pironaea polystila* var. *milovanovici* and *Vaccinites ultimus*. A more diverse assemblage has been observed at the western end of the out-crop 12 with abundant *Biradiolites acuticostatus*, *Biradiolites fissicostatus*, *Biradiolites stoppanianus*, *Praeradiolites subtoucasi* and rare, small specimens of *Pironaea polystila*. Small clusters of *Hippuritella cornucopiae* have been sporadically observed.

In addition to what is described above, rudists are common in the Bačevica area but are less abundant in the environs of Vrbovac (Figure 5). Rudists have been observed along creeks, on the bottom of the dirt roads crossing the area, inside the low party walls which separate the properties of the peasants. Rudists have been also recovered in fields, in soils presumably derived from the weathering of breccia beds and/or tuffaceous arenites.

In general, large, elongated, cylindro-conical, thick-shelled rudist bivalves dominate the faunal assemblages everywhere. The rudists are highly diversified in some places but they also form pauci-specific or monospecific assemblages (e.g., at points 4, 10 and 11). According to Milovanović & Grubić (1971), the *Pironaea-Pseudopolyconites* rudist association and corals characterize the 'Vrbovac reef'. It is pointed out that the the *Pironaea-Pseudopolyconites* association does not dominate the faunal assemblages observed at Bačevica since it is inferred that the relative abundance of the rudist species varies from one zone to another.

Barring the examples found within the clastic unit at points 1 and 2, the rudists are mainly well preserved and fully articulated. Usually, the external structures of the rudist shells preserve all their morphological features. For instance, the specimens of *Branislavia bacevicensis* show all the delicate details of the right valve (Plate 1). But, when the upper valves of the fore-mentioned examples are cut, the resulting transverse sections show only incomplete, faint traces of the canals. A large example of *Pironaea polystila* has been cut and serial sections have been made. The matrix at the 3-cm-thick basal part of the shell consists of silty limestone with rare unidentified microfossils while, above, the matrix is rich in silt and clayey minerals and, moreover, very little or nothing of the internal

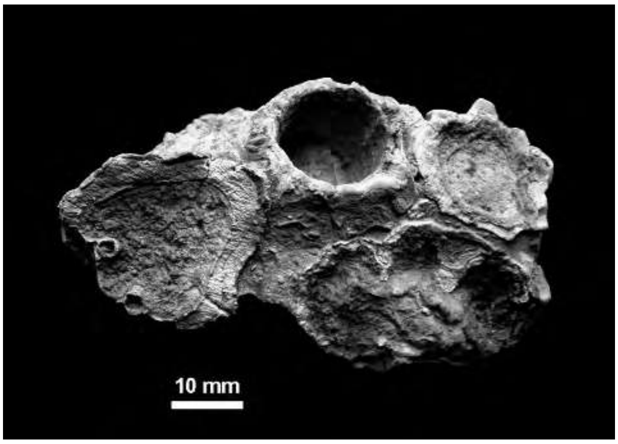

Figure 3. Small clump with *Hippuritella variabilis* (two examples), *Vaccinites loftusi* and *Radiolites* sp.

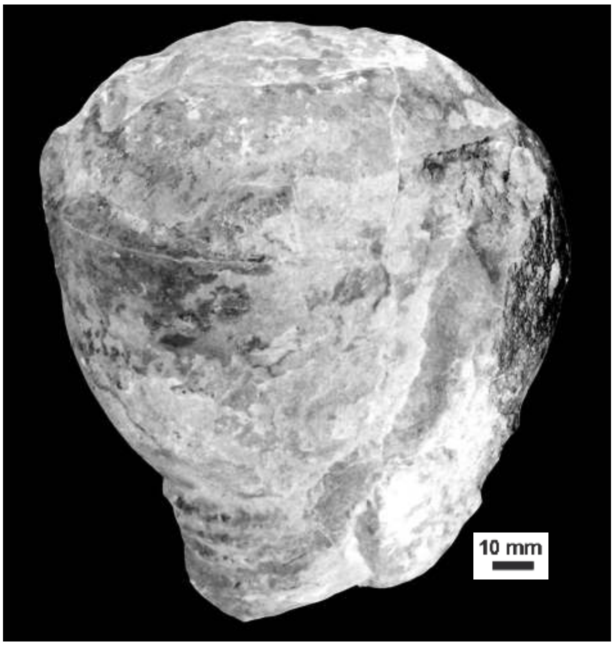

Figure 4. A large specimen of *Actaeonella* sp. (point 9).

structure of the specimen is visible. This occurrence is presumably due to circulation of silica-rich fluids during the diagenesis. By the way, the filling sediments of the rudist shells are often characterized by variable amounts of detrital quartz (mostly 10–15%), clayey minerals (illite, chaolinite and smectite), and very low amounts of feldspars, horneblende and biotite.

Figure 5. Large example of an unidentified rudist (new genus?) recovered in the vicinity of Vrbovac.

Palaeoenvironmental Interpretation

No vestige of the Vrbovac reef postulated by Milovanović & Grubić (1971) was found during the field investigations. Pauci-specific associations of rudists, which were able to co-exist with corals, yielding complex coral-rudist reefs are well known in the geological record (Masse & Philip 1981; Scott *et al.* 1990; Götz 2003a). Rudist-coral biostromes were found even associated with volcanic or volcaniclastic rocks (Camoin *et al.* 1988; Mitchell 2002; Schafhauser *et al.* 2003; Mitchell *et al.* 2004).

Many corals were observed in the explored area and they either belong to one genus of solitary coral (Figure 6a) or are represented by scattered, both small and large examples, diverse ahermatypic corals found within the clastic unit at points 1 and 2. Therefore, calcareous deposits created by sessile organisms do not seem to represent the case of Bačevica. Anyway, it is to be pointed out that Milovanović in his last paper on the Bačevica faunas

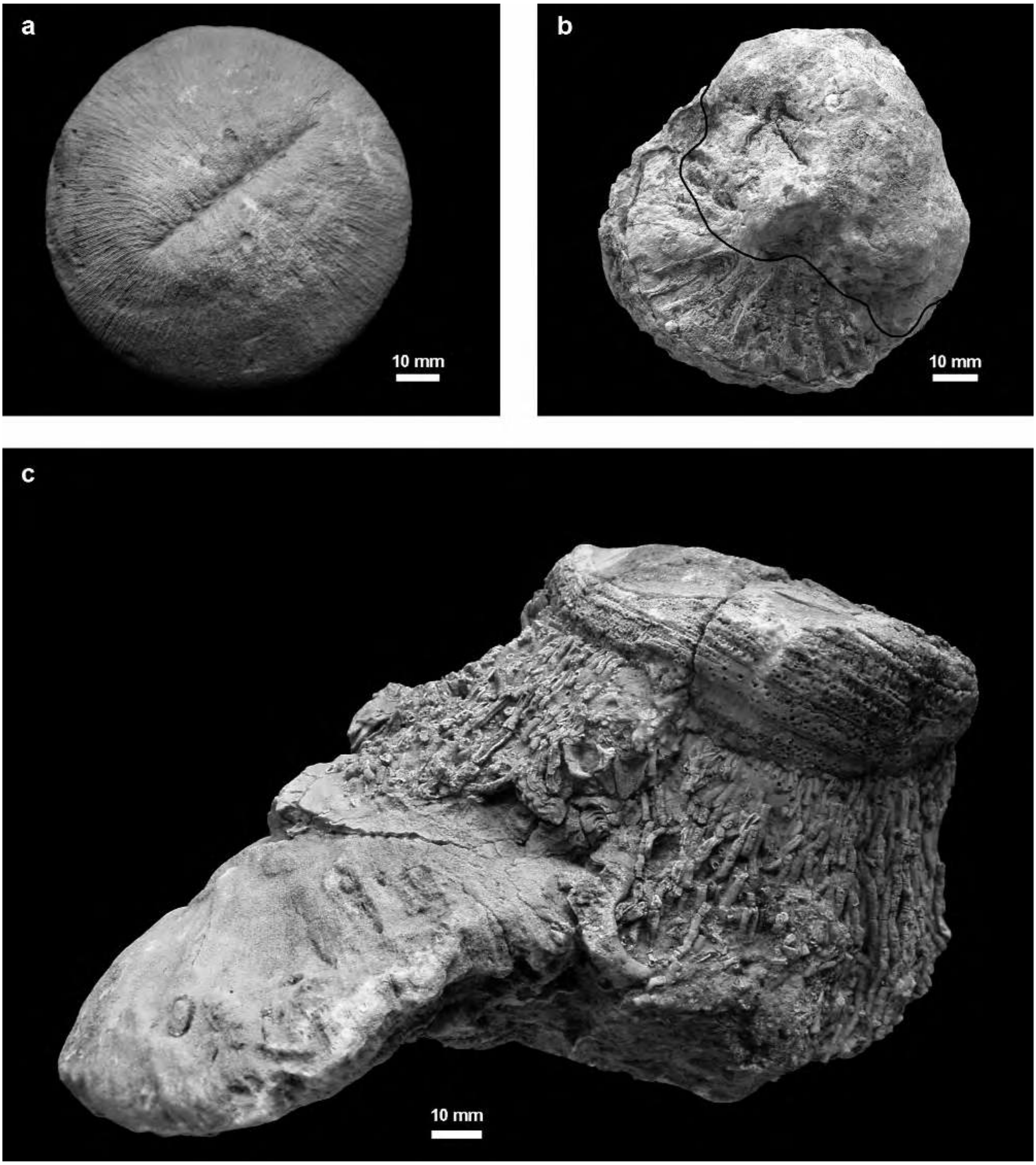

Figure 6. (a) *Cyclolites* sp. (on the left); **(b)** *Milleporidium* sp. settled on the upper valve of a rudist (on the right); **(c)** *Pseudopolyconites* specimen settled on a *Cyclolites* example.

(Milovanović & Grubić 1972) seems to contradict his model of the rudist-coral reef in Vrbovac.

In general, in agreement with Sladić-Trifunović (1998), it is probable that rudists lived in different, clastic, shallow sea habitats close to the active andesitic Timok volcanic complex. However, due to both the rarity of exposures of rudist-bearing strata and the scarce thickness of the same out-crops, the interpretation of the depositional setting is questionable.

The rhythms observed at points 1, 2 and 3 presumably record the interplay of multiple events of transport and reworking and of following colonizations by rudists. Since no hermatypic coral and no cluster or clump of rudists have been detected within the breccia beds it is hypothesized that rudists and corals thrived mainly isolated from each other in the same environment or, more likely, they lived in adjacent habitats (shoreface to inner shelf environment?). A few cases show a small coral (*Milleporidium* sp.) on the upper valve of a rudist (Figure 6b) and a *Pseudopolyconites* specimen settled on a solitary coral (Figure 6c). It is also supposed that the fossiliferous lithosomes were periodically dismantled and that the carbonate materials together with rare well-rounded quartz pebbles, sand and silt were transported far away from the primary places of deposition. The provenance of the quartz pebbles and quartz sand grains is problematic since both the parent rocks close to the Timok complex and the source areas are unknown to us. Quartz pebbles may be related to small coarse-grained fluvio-deltaic systems or to coarse clastic beaches (beach-face, shoreface) localized near eroding cliffs of an island. The ultimate cause of the rhythms and of the lower unit in particular is as difficult to postulate. The rhythms may have been originated by sea-level changes and/or by volcanic related events or, more likely, by storm surges that periodically afflicted the coastal zones of the island which was situated within the late Cretaceous monsoonal belt (Price *et al.* 1995).

The palaeoenvironmental interpretation of rudist-bearing strata rich in silt and sand (from point 7 to point 12) is also intriguing.

The rudists probably settled and thrived in low to moderate-energy regimes. For instance the material included among the tubules of *Pseudopolyconites* is made exclusively of ochraous silt and this led to postulate that these rudists thrived in muddy, low-energy settings. While the large and short-sized *Lapeirousia* examples recovered within sandy soils allow the hypothesis of a relatively high-energy regime. Thus, it is speculated that the rudist bivalves grew in loose sediments, occupying silty and subordinately sandy substrata on a shallow shelf environment. The rudists herein were presumably adapted to a life in turbid, depositional environments due to their potential for rapid upward-growth (Steuber 1997) and their filter-feeding mode of life. Under a high rate of sediment accumulation, under fast shifting of the clastic substrata or under volcanic episodes, the flourishing of rudist individuals in the depositional environment was suddenly stopped by burial with sediments (Sanders & Pons 1999). In fact, it is observed that the filling sediments of the rudist shells consist mainly of silt, in particular at points 9 and 12, while the sediments all around the rudist bivalves are made of a mixture of well-rounded sand grains and silt with abundant pebbles. It is previously outlined that the diagenesis of the rudist shells might represent another complex question.

In conclusion, it is suspected that local volcanic related forcing was a significant control factor of sedimentation during the periods of colonization by rudists. But the hypothesis of episodic hurricanes that punctuated the sedimentation cannot be ruled out.

The Species of *Pseudopolyconites* Instituted in Bačevica

Considering the sub-horizontalitry of the *Pseudopolyconites*-bearing strata cropping out between points 7 and 11, only a few fossiliferous lithosomes may be inferred. Thus, it is a little surprising that a plethora of species of *Pseudopolyconites* has been instituted by the Serbian palaeontologists in this zone (Plate 2). Milovanović (1934, 1935a) instituted the following species: *Pseudopolyconites serbicus*, *Pseudopolyconites parvus*, *Pseudopolyconites ovalis*, *Pseudopolyconites mirabilis* and *Pseudopolyconites serbicus* var. *triangularis*. Other eight species have been established by Milovanović & Sladić (1957): *Pseudopolyconites bacevicensis*, *Pseudopolyconites balkanicus*, *Pseudopolyconites dechaseauxi*, *Pseudopolyconites giganteus*, *Pseudopolyconites laskarevi*, *Pseudopolyconites manjae*, *Pseudopolyconites orientalis* and *Pseudopolyconites timacensis*. Lastly, Sladić-Trifunović (1986) added eight new species to those previously instituted: *Pseudopolyconites boljevacensis*, *Pseudopolyconites concavatus*, *Pseudopolyconites djuroi*, *Pseudopolyconites ljubicae*, *Pseudopolyconites minor*, *Pseudopolyconites pejovicae*, *Pseudopolyconites robustus* and *Pseudopolyconites triangularis* (ex *serbicus* var. *triangularis*).

After a careful reading of the relevant literature it appears that the most significant criterion selected by the Serbian rudistologists in the specific identification of *Pseudopolyconites* is founded on the characteristics of the ligamental ridge (e.g., shape, length and thickness). Other minor characteristics of the *Pseudopolyconites* species have been observed and discussed mainly by Sladić-Trifunović (1983). On the base of the fore-mentioned criterion, other *Pseudopolyconites* species have been instituted in Rumania (Lupu 1975), in Hvar Island, Croatia (Sladić-Trifunović 1980), in Apulia, Southern Italy (Sladić-Trifunović & Campobasso 1980), in Bulgaria (Pamouktchiev 1982), in Serbia (Sladić-Trifunović 1986) and in Friuli, NE Italy (Sladić-Trifunović & Nereo 1990).

Sladić-Trifunović (1980, 2004) distinguished three ontogenetic stages in the development of the lower valves of the *Pseudopolyconites* species marked by distinct changes of the ligamental system: i.e. the early (juvenile) stage, the middle stage and the late stage. Cross-cuts through the *Pseudopolyconites* species (Plate 2) show a similar gondola-like shape of the ligamental ridge during the early ontogenetic stage (Sladić-Trifunović 2004). The ligamental ridge-shape changes remarkably in the trasverse sections cut through the middle and upper parts of the lower valve. It is pointed out that research regarding the ontogenetic development of rudist bivalves is usually carried out on continuous serial sections of the shells by techniques of 3D reconstruction (Pons & Vicens 1988; Götz 2003b).

According to Sladić-Trifunović (1983, 1986), the shape of the ligamental ridge of near-commissure (1.5 cm below) sections examined in 'adult' individuals is the conclusive element for determining the species of *Pseudopolyconites*.

Material and Methods

A biometrical approach integrated with the classical palaeontological analysis has been applied in order to gain some more data regarding the *Pseudopolyconites* species. The biometrical approach is usually based on measurements of significant shell characteristics from the specimens illustrated in scientific literature and/or from fossils collected in the field. To check the morphological variability of the *Pseudopolyconites* species, some linear and angular measurements have been taken from the drawings and subordinately from the cross-cut photographs chosen from the published literature representing the holotypes of these species. It is pointed out that often the quality of the illustrated material is not good or homogeneous. Thus, only the material illustrated by Milovanović (1937a), Milovanović & Sladić (1957), Sladić-Trifunović (1983, 1986) has been chosen for this analysis.

Significant shell parameters suggested by Cestari (1992) have been detected. In particular, by drawing the 'LSE triangle', the following distances and angles among L (ligamental crest), S (posterior) and E (anterior) radial structures have been measured (Figure 7).

The drawings and photographs of the *Pseudopolyconites* holotypes have been sent to a computer and the relative images have been digitized by means of the Matrox-Meteor programme. This system allows numerous areal and linear measurements of fossil specimens.

Measurements Made on the Pseudopolyconites Holotypes

The distances on the LSE triangle between the ligament ridge L and the S and E structures fall in the intervals: $41<LS<97.3$ mm; $54<LE<98$ mm; $28<SE<67$ mm. The ratio LS/LE falls between 0.68 and 0.98, the ratio LS/SE falls between 0.97 and 1.58; the ratio LE/SE falls between 1.26 and 1.93 (Table 1). The measurements of the A1, A2 and A3 angles indicate that their values fall in the intervals: $32<A1<51$degrees; $74<A2<99$ degrees ; $43<A3<74$.

Some values have been plotted in histograms (e.g., distances and angles on the LSE triangle) and in

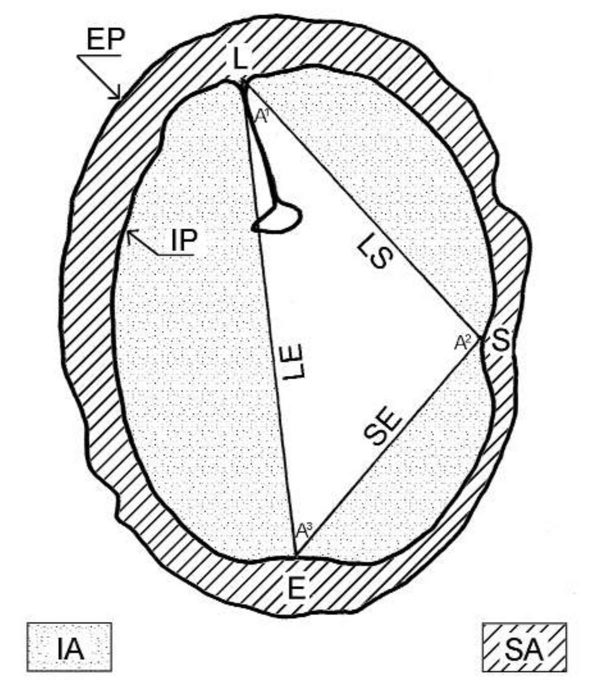

Figure 7. Drawing of the LSE triangle from the lower valve of a *Pseudopolyconites* with the measured shell parameters. L– ligamental crest, S– posterior radial structure, E– anterior radial structure, LS– distance between L and S, LE– distance between L and E, SE– distance between S and E, A1– angle between LS and LE, A2– angle between LE and SE, A3– angle between LS and SE, IP– inner perimeter, EP– external perimeter, IA– inner area, SA- shell area.

scatter diagrams (e.g., linear measurements versus the inner area of the shells) which are not figured here. A few groups of Pseudopolyconites species have been tentatively singled out but the boundaries between these 'kinds' of similar morphological types can be aleatory. Therefore, the long and unproductive discussion of the results obtained by the numerical approach is not dealt with here. Synthetically, the analysis and the comparison between the different parameters, which should represent the morphostructural characters of the shells of the 18 *Pseudopolyconites* species, show only ill-matched values. Anyway it is admitted that a great number of measurements on *Pseudopolyconites* specimens showing well-preserved ligamental crest should be made in order to define the inter-intraspecific variability of these rudists.

Discussion

The palaeontological analysis of the *Pseudopolyconites* examples recovered close to Bačevica does not find significant differences in the shells. Furthermore, some trasverse or slightly oblique sections of specimens recovered at Bačevica increased our doubts about the criterion of classification of the *Pseudopolyconites* species. In fact, by contouring the ligamental part on the cross-cuts of some examples, other shapes of the ligamental ridge have been detected not previously illustrated in literature. However, it is unlikely that the specimen in Figure 8 represents a further species. On the other hand, it is observed that other authors found classification difficulties of the *Pseudopolyconites*

Table 1. Measurements made on *Pseudopolyconites* holotypes illustrated in the literature (see Plate 2).

Species	Author	Year	Material	Type	LS mm^2	LE mm^2	SE mm^2	LS/SE mm^2	LE/SE mm^2	A_1 dg.	A_2 dg.
P. ovalis	Milovanović	1935a	Milovanović 1937a, p. 18	holotype	48	53	48	1	1.1	47	90
P. parvus	Milovanović	1935a	Milovanović 1937a, p. 12	holotype	41	61	42	0.97	1.45	45	91
P. serbicus	Milovanović	1935a	Milovanović 1937a, p. 25	holotype	56	65	40	1.4	1.62	41	84
P. serbicus var. *triangularis*	Milovanović	1935a	Milovanović 1937a, p. 31	holotype	40	48	37	1.08	1.3	49	77
P. bacevicensis	Milovanović & Sladić	1957	p. 218	holotype	62	72	54	1.15	1.33	47	77
P. balcanicus	Milovanović & Sladić	1957	p. 229	holotype	52	59	40	1.3	1.47	40	80
P. dechaseauxi	Milovanović & Sladić	1957	p. 211	holotype	51	73	45	1.18	1.62	39	97
P. giganteus	Milovanović & Sladić	1957	p. 226	holotype	70	75	48	1.46	1.56	40	74
P. laskarevi	Milovanović & Sladić	1957	Sladić-Trifunovic 1983 plate XXI	holotype	59	78	45	1.28	1.69	36	96
P. manjae	Milovanović & Sladić	1957	" " p. 214	holotype	62	72	40	1.55	1.8	34	88
P. orientalis	Milovanović & Sladić	1957	" " p. 223	holotype	45	54	38	1.18	1.42	45	80
P. timacensis	Milovanović & Sladić	1957	" " p. 221	holotype	56	67	39	1.43	1.72	37	90
P. djuroi	Sladić & Trifunović	1986	plate 3, figure 2	holotype	40	55	30	1.33	1.83	34	99
P. pejovicae	Sladić & Trifunović	1986	plate 4, figure 2	holotype	58	71	60	0.96	1.18	55	75
P. triangularis	Sladić & Trifunović	1986	plate 6, figure 2	? paratype	47	65	43	1.09	1.51	41	94

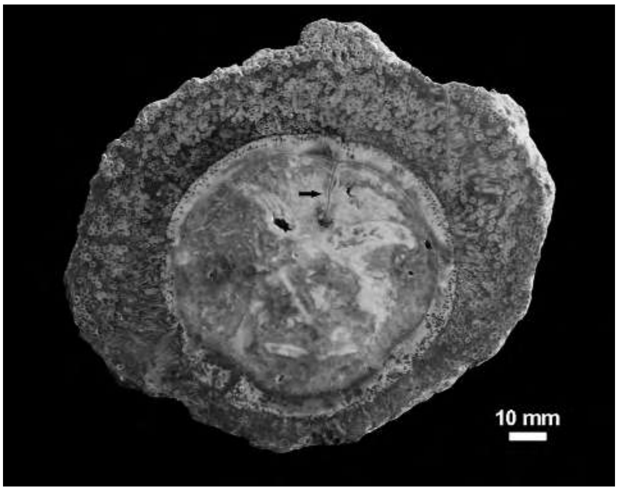

Figure 8. *Pseudopolyconites* specimen from the observation point no 11. The arrow points at a thread-like shape of the ligamental ridge. The cross section is cut close to the commissural plane.

species (Karacabey 1970; Karacabey-Öztemür 1980; Özer 1986, 1988; Cestari & Sartorio 1999; Cestari & Sirna 2002), with a few exceptions (Morris & Skelton 1995; Pleničar 2005).

To sum up, the wide variability of the ligamental ridge close to the commissure does not seem to support by itself the institution of so many species of *Pseudopolyconites*. In most radiolitids the mantle-secretive activity is considered dynamically adapted to their peculiar ecological needs. Thus, the various shapes of the ligamental ridge marking the different ontogenetic stages of *Pseudopolyconites* were presumably originated by particular shell-growth strategies developed in response to the interaction of the individual intrinsic palaeobiology with the palaeoenvironmental controls (Cestari 1992).

Summary and Conclusions

A very discontinuous section through the upper Campanian rudist-bearing strata cropping out in the vicinity of the famous fossiliferous locality of Bačevica (Eastern Serbia) has been delineated. The lithological succession together with the faunal succession characterized by rudists and other macrofossils has been described.

At its base the section examined is marked by rhythms consisting of a lower thicker limestone breccia unit and an upper part made of silty limestone, silt and sand with abundant, often intact rudists. The rhythms record multiple events of transport and reworking of sediments and of re-colonization by rudists. The rudist-bearing strata at the middle-upper part of the section are represented by weathered limestone-breccias, but the strata become richer and richer in sand towards the top of the succession. Thus the expected vestiges of the 'Vrbovac reef' have not been detected in the explored territory.

It is suggested that, due to the vicinity of the active andesitic Timok complex, episodic volcanic events may have influenced the sedimentation and perhaps the diagenetic processes.

Rudists are the most prominent faunal elements present on the Bačevica territory. The faunal succession shows an alternation of low diversity assemblages of rudists and of richer assemblages of the same. The rudists are found mainly in growth position, intact, fully articulated, without evidence of bio-erosion. The examples are isolated from each other and no type of congregations of individuals has been observed along the entire section.

It is suggested that the distribution of the different examples of rudist-bivalves recovered at Bačevica may represent a significant tool for bio-stratigraphic correlations of the upper Campanian rudist-bearing deposits in the Central Tethys.

The examples of *Pseudopolyconites*, which represent the most peculiar genus recovered at Bačevica, seem to be confined to a few fossiliferous lithosomes.

A large number of species of *Pseudopolyconites* collected in the environs of Bačevica has been established by Serbian rudistologists. According to the Serbian workers, the change of the shape of the ligamental ridge near to the commissure is the fundamental criterion for distinguishing the different species of *Pseudopolyconites*. A careful reading of the specific literature, minute inspections both of intact individuals and of some cross-cuts of different *Pseudopolyconites* specimens and, finally, an approach based on biometrical analysis of the various holotypes illustrated in the scientific literature led to the belief that the existing ones should be reconsidered within the concepts of the inherent variability of the biological species. The mantle secretive activity of the individuals could have formed slightly different shell-shapes and internal structures (e.g., the ligamental ridge) which have been taxonomically interpreted as different species of *Pseudopolyconites*. Thus, all these species may be regarded as simple ecomorphotypes.

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PLATE 1

Different views of common rudist examples at different observation points.

(a) *Lapeirousia crateriformis* (point 3);
(b) *Lapeirousia jouanneti* (point 3);
(c) *Plagyoptychus toucasianus* (point 6);
(d) *Pseudopolyconites* sp.;
(e) *Vaccinites loftusi* (point 9);
(f) *Branislavia bacevicensis* (point 9);
(g) *Pironaea polystila milovanovici* (point 12).

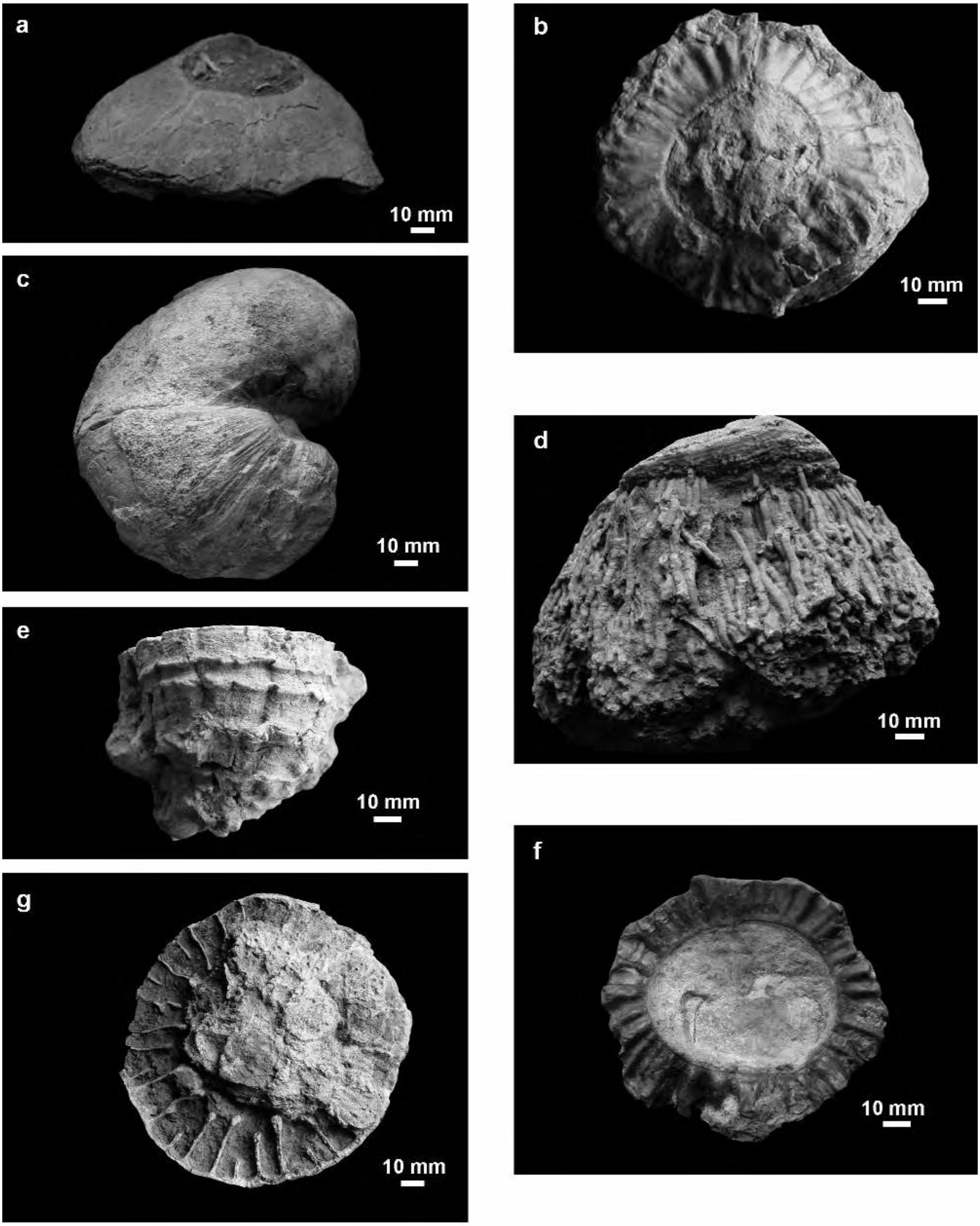
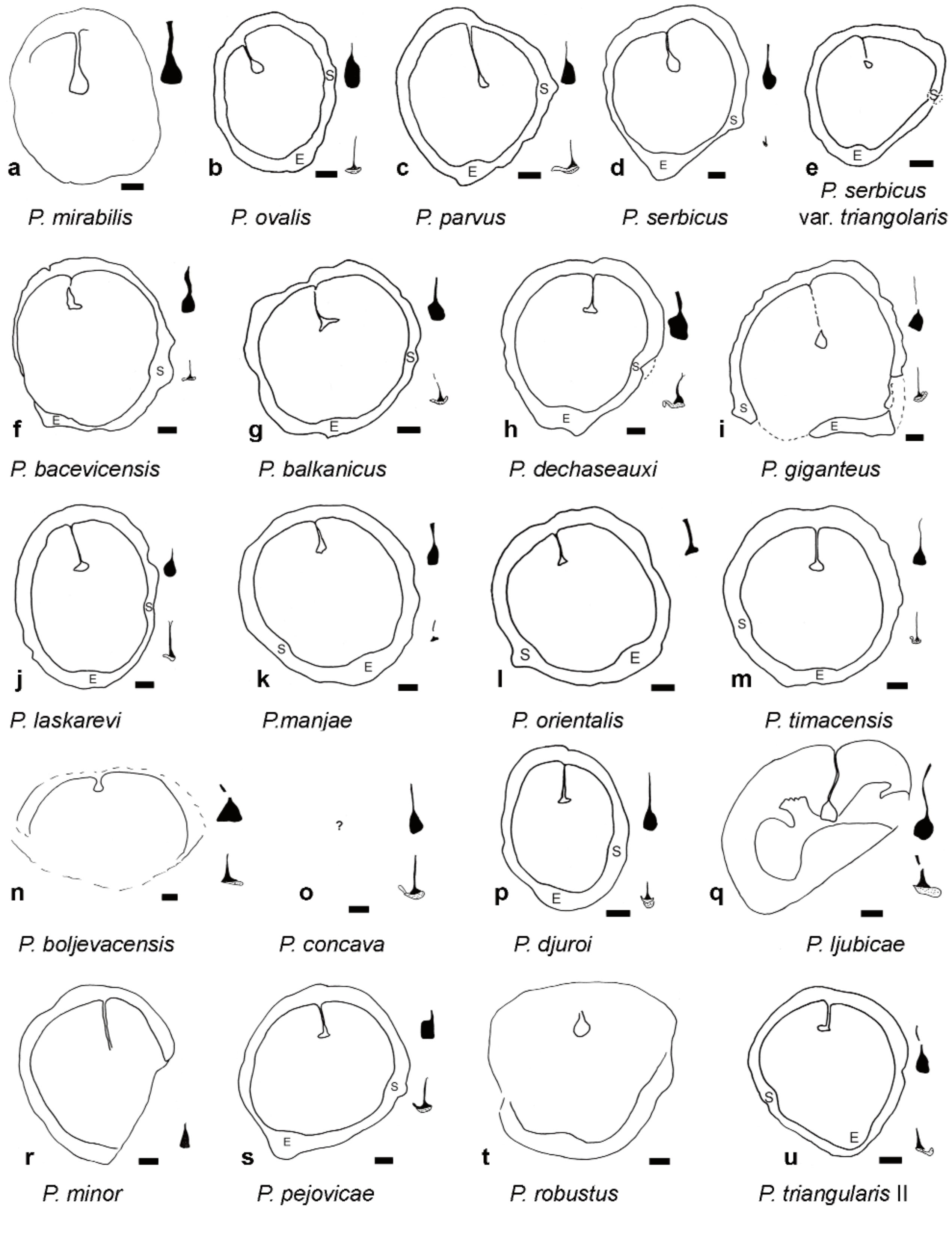

a
10 mm
b
10 mm
c
10 mm
d
10 mm
e
10 mm
f
10 mm
g
10 mm

PLATE 2

Selected transverse sections cut near to the commissural plane across the lower valves of the *Pseudopolyconites* species:

- **(a)** section after Sladić-Trifunovic (1983);
- **(b–e)** sections after Milovanović (1937a);
- **(f–m)** sections after Milovanović & Sladić (1957); J section after Sladić-Trifunović (1983);
- **(n–u)** sections after Sladić-Trifunović (1986). Ligamental crest shapes characteristic of the early ontogenetic stage (on the bottom, if figured) and of the late ontogenetic stage (above) (after Sladić-Trifunović 1983). Bar-scale for all the sections = 10 mm.


a P. mirabilis
b P. ovalis
c P. parvus
d P. serbicus
e P. serbicus var. triangolaris
f P. bacevicensis
g P. balkanicus
h P. dechaseauxi
i P. giganteus
j P. laskarevi
k P.manjae
l P. orientalis
m P. timacensis
n P. boljevacensis
o P. concava
p P. djuroi
q P. ljubicae
r P. minor
s P. pejovicae
t P. robustus
u P. triangularis II
S
E
?