Tunis, G., Özer, S., Radoičić, R., Săsăran, L., Tarlao, A. and Tentor, M. 2013. The state of the knowledge of the genus *Pseudopolyconites*. *Caribbean Journal of Earth Science*, **45**, 107-118. © Geological Society of Jamaica. Available online 14th September 2013.

The state of the knowledge of the genus *Pseudopolyconites*

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ABSTRACT. The genus *Pseudopolyconites* is distributed in Upper Cretaceous successions of the Central Tethys. Specimens have been recovered from carbonate, siliciclastic, volcanoclastic or mixed carbonate/siliciclastic successions dated from the late Santonian or early Campanian to the latest Maastrichtian, but often only fragmented shells have been collected and described. Many species have been established but the constructional morphology of individuals and, in particular, the characters of the outer shell layer were seldom adequately examined by rudistologists. Currently two species can be recognized with certainty: *Pseudopolyconites hirsutus* (late Santonian-early Campanian) and *Pseudopolyconites serbicus* (late Campanian). Currently, the phylogenetic relationships within the genus during the Santonian to latest Maastrichtian remain obscure. It is speculated that the examples of *Pseudopolyconites* found at the type-locality of Bačevica developed particular shell growth strategies in response to a peculiar environment where they thrived.

Key words: *Pseudopolyconites*; morphology; palaeo-biogeographic distribution; Upper Cretaceous.

1. INTRODUCTION

The rudist bivalve genus *Pseudopolyconites* was established in 1934 by the Serbian palaeontologist Branislav Milovanović (1934a). The first specimens of this rudist were found close to the village of Bačevica (eastern Serbia) which is considered the type-locality of the genus. Due to the complete disappearance of all the holotypes and paratypes of the numerous species of *Pseudopolyconites* established by the Serbian rudistologists from Bačevica, we have surveyed and examined many times the lithological and faunal succession cropping out in the area in question. The scope of the latest investigation has been aimed at collecting examples of *Pseudopolyconites* and at examining the faunal assemblages close to the *Pseudopolyconites* bearing strata. Successively we have expanded the research upon the *Pseudopolyconites* specimens found in Rumania and Turkey and we have examined the literature concerning all known *Pseudopolyconites* bearing strata both within carbonate and clastic successions. In some cases we have surveyed carbonate successions cropping out in the Adriatic region.

The aim of this paper is to discuss different aspects concerning the genus *Pseudopolyconites*: that is, morphological characters, faunal assemblages, age, palaeobiogeographical distribution, phylogeny and possible developments of the research.

2. LITHOLOGICAL AND FAUNAL CHARACTERISTICS OF THE BAČEVICA SUCCESSION

Due to the shortage of outcrops in the environs of Bačevica (**Figure 1**) and the low quality of the exposures, it is only possible to make a brief assessment of the lithological succession and the field relationships. The lower part of the Bačevica succession is characterized by rhythms consisting of a lower unit of thick limestone breccias containing fragmented rudist shells and an upper thinner unit composed of silty limestones with abundant, often intact rudists. The rhythms record multiple events of transport and reworking of sediments and of recolonization by rudists (Tarlao et al., 2010). The upper part of the Bačevica succession is represented mainly by weathered sandstones and siltstones with subordinate conglomerates and silty limestones. Because of the rare and very limited outcrops and the shallow dip of the strata, the total thickness of the section is very difficult to estimate.

In the absence of strontium isotope analyses (SIS), the inferred age of the upper part of the Bačevica section is Campanian on the basis of close similarities with the Gavlo section (see below).

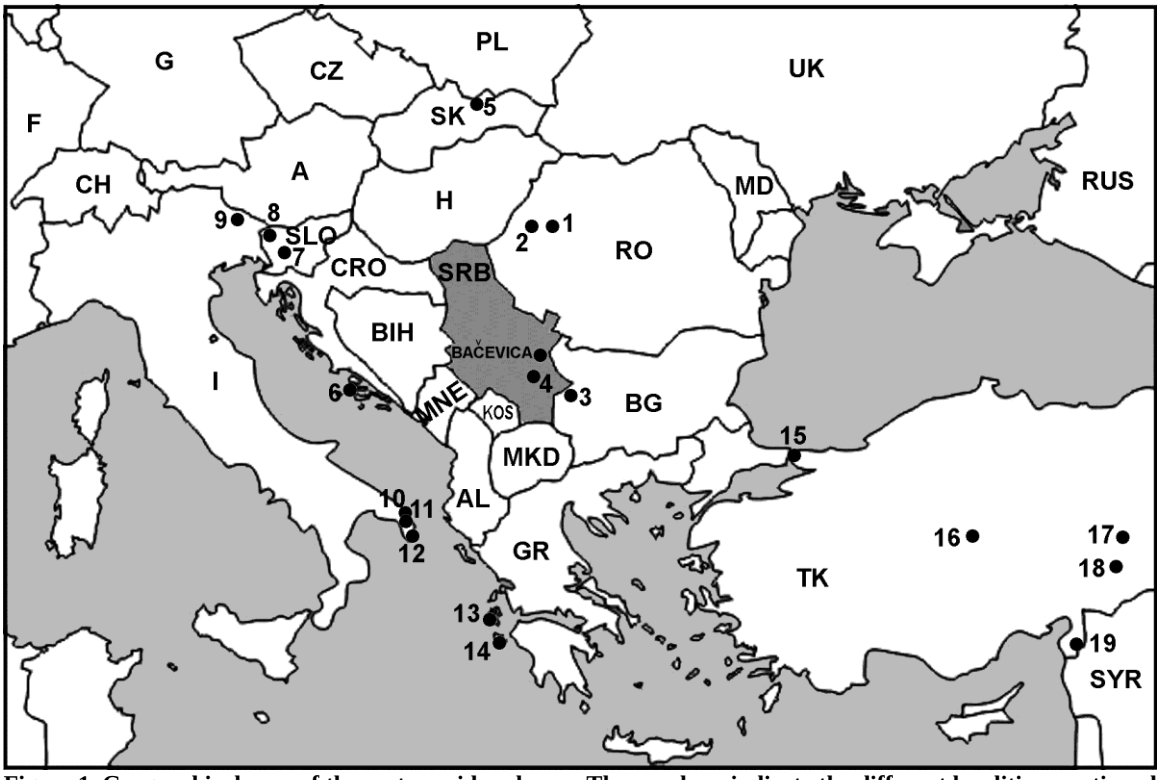

Figure 1. Geographical map of the vast considered area. The numbers indicate the different localities mentioned in the text: 1, Remeti valley; 2, Dealul Magura; 3, Garlo; 4, Vrla Strana, Vina; 5, Hron valley; 6, Hvar island; 7, Mt. Nanos; 8. Anhovo; 9, Maniago; 10, Cava Soframa; 11, Vitagliano; 12, Ciolo cove; 13, Zakynthos island; 14, Lefkas island; 15, Kocaeli peninsula; 16, Tuz Lake basin; 17, Malatya basin; 18, Kahta-Adiyaman; 19, Yayladağ-Antakya.

The faunal succession of the upper part of the section shows an alternation of low diversity and high diversity assemblages of rudists. Several dozen specimens of *Pseudopolyconites* have been found and more than 90% of them have been recovered in a small area (Liljekar) where a rich monospecific assemblage is present. The individuals are mainly large in size, always isolated, separated from one another, and mostly in grwoth position and often fully articulated. The finding of this rudist outside this area is remarkably rare.

It is not easy to explain the reason for the abundance of specimens of *Pseudopolyconites* in this small area. Due to the poor quality of the exposures, both lithology and sedimentology are not much help and the interpretation of the depositional setting is questionable. It is speculated that *Pseudopolyconites* individuals grew in unconsolidated sediments on silty substrates in a shallow shelf environment. The sediment included between the spines of *Pseudopolyconites* consists of ochreous clayey-silt suggesting that these rudists thrived in muddy, low energy settings. The rudists herein were presumably adapted to a life in turbid, depositional environments. The life of individual rudists was probably terminated suddenly by rapid burial by sediments during a single sedimentation episode (Tarlao et al., 2010).

3. RELEVANT CHARACTERISTICS OF *PSEUDOPOLYCONITES* AND THE QUESTION OF THE *PSEUDOPOLYCONITES* SPECIES INSTITUTED AT BAČEVICA

All the examples of *Pseudopolyconites* recovered at Bačevica show a dense coat of tubules or spines (**Figure 2a**) emerging from the shell wall and then curving downwards (**Figure 2b**) (Milovanović, 1937). This character is rarely found in other localities where *Pseudopolyconites* has been recovered. The tubules at the base are thin and short but they became progressively larger and longer during the growth of individuals. The thickness of the wall of the tubules is large in comparison with the diameter of the internal hole which is narrow.

The origin of the spines in *Pseudopolyconites* was explained by Pons and Vicens (2008) by examining the outer shell layer constructional pattern which is considered the main diagnostic character of the Radiolitidae since its pattern is used both in the phylogeny and taxonomy of the family.

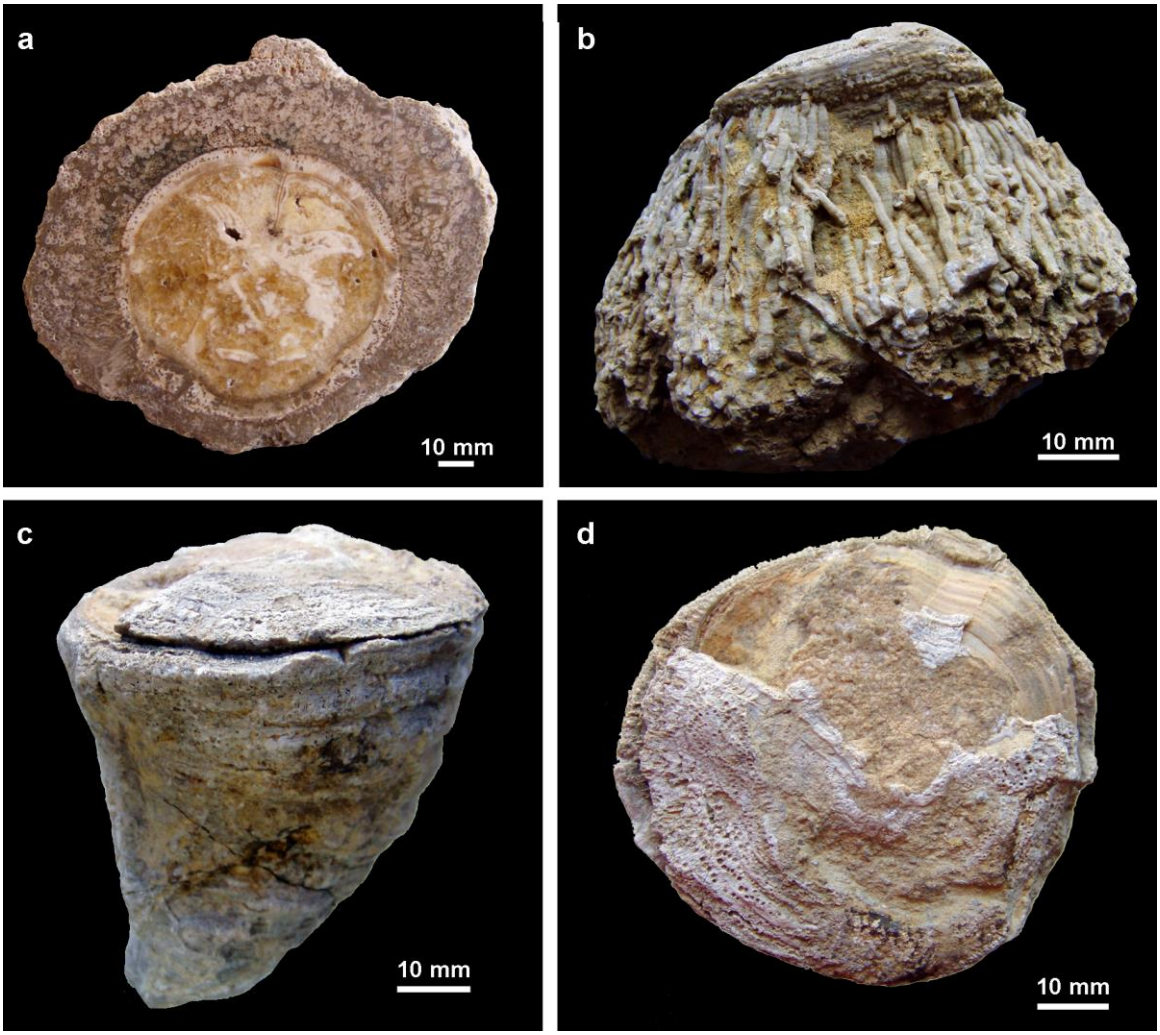

Figure 2. a) Transverse section of a right valve of a *Pseudopolyconites* serbicus specimen from Liljekar (Serbia); b) right valve of a *Pseudopolyconites serbicus* individual showing the dense coat of spines emerging from the shell wall; c) entire specimen of *Pseudopolyconites serbicus* from Liljekar; d) View from high of the left valve of the specimen shown in c).

A transverse section and a radial section of an example of *Pseudopolyconites* collected at Bačevica are shown respectively in **Figures 3**-**4**. The repetitive closed invaginations of the radial downfolds in the growth lamellae, projecting outwards as spines (**Figure 4**), is the main characteristic of the outer shell layer structure of *Pseudopolyconites* and this represents the extreme case of the radial folding of the growth lamellae in radiolitid rudists (Pons and Vicens, 2008).

However, one of us (Rajka Radoičić) hypothesizes that the tubules are not integral parts of the shell and may represent epizoa. Besides, *Pseudopolyconites* tubules were explained by Misik (1966, pl. LXXV, fig. 1) as serpulid worm tubules (*Filigrana* sp.) from the serpula-bioherm limestones of the Brezova Mountains (Western Carpathians, Slovakia).

The Serbian rudistologists erected numerous species of *Pseudopolyconites* in the environs of Bačevica. The Branislav Milovanović old collection of rudists included the five holotypes of the first *Pseudopolyconites* species erected by Milovanović (1934a, 1935a) and it was housed at the Institute of Paleontology (Faculty of Philosophy) of the the Belgrad University: it was lost during World War II when the building was set on fire. Unfortunately, the holotypes of the species established successively by Milovanović and Sladić (1957) and by Sladić-Trifunović (1986) have also vanished.

The most significant criterion selected by the Serbian workers for establishing different species of *Pseudopolyconites* was founded on the characteristics of the ligamental ridge in the transverse section (e.g., shape, length and thickness). Minor characteristics concerning the

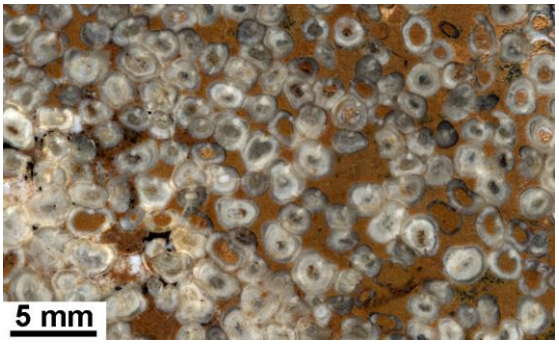

Figure 3. Spines seen in transverse section of the right valve of a *Pseudopolyconites serbicus* specimen (Liljekar).

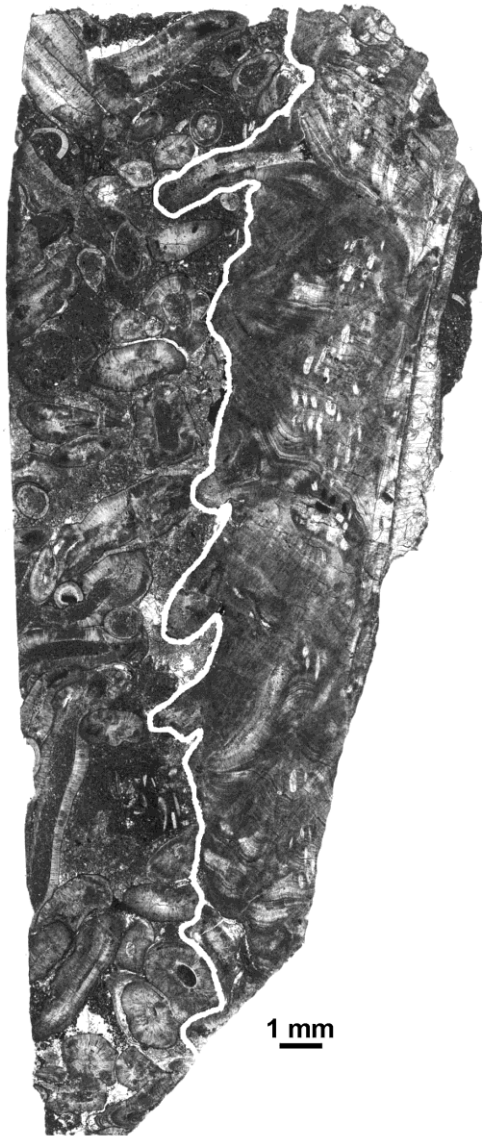

Figure 4. Vertical section of the right valve of a *Pseudopolyconites serbicus* specimen (Liljekar) showing the outwards expansion of the spines (white line). Shell wall on the right.

radial structures and the ornamentation have been observed and discussed mainly by Sladić-Trifunović (1983). Moreover, according to this author, the shape of the ligamental ridge of *Pseudopolyconites* individuals was remarkably transformed through ontogenetic development of the right valve, and this was the main criterion used for discrimining species.

Tarlao et al. (2010) have considered all species of *Pseudopolyconites* erected at Bačevica as simple eco-morphotypes which may be attributed to just one species, *Pseudopolyconites serbicus*, the earliest one established by Milovanović (1934a).

It is stressed here that the level rich in examples of *Pseudopolyconites* is included within a thin fossiliferous lithosome and occupies a precise stratigraphic position (i.e., Liljekar) along the Bačevica section. We hypothesize also that this situation was not different at the time the original research was carried out by Milovanović and Sladić-Trifunović as they often mention the place name of Liljekar where we have found the majority of the specimens of *Pseudopolyconites*.

4. *PSEUDOPOLYCONITES* BEARING STRATA WITHIN THE CARBONATE SUCCESSIONS OF THE CENTRAL TETHYS

Examples of *Pseudopolyconites* have been found within late Campanian carbonate successions cropping out in the northern Adriatic region (NE Italy, Slovenia, Croatia, Bosnia), in southwestern Italy and western Greece (**Figure 1**). Other species of *Pseudopolyconites* were erected on the basis of the usual criterion, that is, the change of the shape of the ligamental ridge. *Pseudopolyconites ovalis apuliensis* was described from Poggiardo (Apulia, southern Italy) by Sladić-Trifunović and Campobasso (1980) and *Pseudopolyconites campobassoi* was described from Pokonj Dol (Hvar, Croatia) by Sladić-Trifunović (1980).

The Upper Cretaceous limestones exposed on the islands of Hvar and Brač typify the Adriatic carbonate platform system. *Pseudopolyconites* individuals, together with other radiolitids, are embedded in massive bioclastic packstone to rudstone of the Brač Marbles Unit of Pučišća Formation. The foraminiferal association of *Orbitoides tissoti* and *Pseudosiderolites vidali* is referred to the middle or early late Campanian by Gušić and Jelaska (1990) and was recalibrated by strontium isotope stratigraphy to Middle Campanian by Steuber et al. (2005).

Large fragments of massive valves of *Pseudopolyconites* were collected within bioclastic deposits at Mt. Nanos, Western Slovenia (Pleničar,

2005), Mt. Jouf, NE Italy (Sladić-Trifunović and Nereo, 1990) and, more recently from an olistolith at Anhovo, northwestern Slovenia (Pleničar and Jurkovšek, 2009). *Pseudopolyconites manjae* Milovanovic & Sladic was erected on material from Mt. Jouf. Numerical ages derived from the strontium isotope stratigraphy indicated, in general, a late Campanian age for the *Pseudopolyconites* bearing strata at Mt. Jouf (Swimburne and Noacco, 1993). *Pseudopolyconites slovenicus* Pleničar & Jurkovšek recovered from Anhovo is the latest species added to the conspicuous catalog of the genus in question.

The rudist shell beds of all the previously mentioned localities from Croatia to Apulia can be considered hydraulic shell concentrations which were deposited under the influence of hydraulic processes with the input of surrounding bioclastic sediments. Thus, due to the hard lithology, it is difficult to collect good examples of *Pseudopolyconites*.

Recently, late Cretaceous platform carbonate successions containing specimens of *Pseudopolyconites* from the Salento peninsula (southern Italy) were studied by strontium isotope stratigraphy (Schlüter et al., 2008a). The rudist associations of the S. Cesarea Limestone exposed in the quarry near Vitagliano (late Campanian) and those of the overlying Ciolo Limestone exposed in the Cava Soframa and Ciolo cove (late Maastrichtian), from a time interval of more than 10 Ma years, are surprisingly similar. Successively (Steuber et al., 2007), numerical ages of well preserved rudist shells from breccias and megabreccias of the slope of the same Apulian Platform exposed on the Ionian islands (W. Greece) also indicate a late Maastrichtian age. Some characteristic genera, such as, *Joufia*, *Pseudosabinia* and other caniculate recumbents, are abundant throughout this time interval both in the Salento peninsula and in the Ionian islands. Many of these rudists (*Pseudopolyconites* sp., *Hippurites cornucopiae*, *Plagioptychus* sp., *Pironaea polystila*, *Joufia reticulata*, *Pseudosabinia* sp., *Mitrocaprina* sp., etc.) are also present in the clastic successions cropping out in the environs of Bačevica, Gavlo (Bulgaria) and in some localities of Turkey.

5. PRESENCE OF *PSEUDOPOLYCONITES*-BEARING STRATA WITHIN CLASTIC SUCCESSIONS OF SOUTHEASTERN EUROPE, TURKEY AND WITHIN CARBONATE SUCCESSIONS OF THE MIDDLE EAST

Rudist shells are abundant in the Campanian and Maastrichtian rudist-bearing deposits of the Peri-Adriatic intra-oceanic carbonate platforms, but they are usually reworked and broken and often beyond taxonomic recognition.

Examples of *Pseudopolyconites* have been found within mixed carbonate-siliciclastic or volcanoclastic Campanian successions (**Figure 1**) in Eastern Serbia (Rtanj and Vrla Strana, Vina), Bulgaria (Gavlo), Rumania (Magura Hill and Remeti valley) and Turkey (Kocaeli peninsula-Istanbul zone, Tuz Lake-Central Anatolia, Malatya-Eastern Anatolia, Adiyaman and Antakya-Southeastern Anatolia). Rudists here are often well preserved, isolated and in growth position.

The Bulgarian outcrops at Garlo (Breznik area) are about 120 km from those of Bačevica-Vrbovac and are closely related: both sequences are underlain by lavas and tuffs and consist mainly of sandstones and siltstones with subordinate conglomerates, marlstones and limestones. Excluding the plethora of rudist species, concerning in particular the genera *Pironaea* and *Biradiolites*, studied by Milovanović (1934b and 1935b) and Pamouktchiev (1964, 1975, 1979) respectively, both the Bačevica and Garlo successions have very similar rudist faunas. Given these strong similarities it is supposed that the age of the deposits in eastern Serbia and western Bulgaria is similar. The age of the *Pironaea-Joufia-Pseudopolyconites* assemblage at Garlo, as determined from strontium isotopes is late Campanian (Swinburne et al., 1992).

The finding of *Pseudopolyconites* specimens is rare at Garlo. A new species *Pseudopolyconites garlensis* was established by Pamouktchiev (1979). But the poor description and illustrations of this form mean that we cannot form an opinion on the validity of this species.

Late Santonian-early Maastrichtian(?) rudist-bearing strata widely crop out on the Apuseni Mountains (Rumania). The Apuseni Mountains comprise a sedimentary succession comparable to the well-studied Gosau Group in the Eastern Alps and in other regions of the Alpine-Carpathians chain (Western Carpathians and Transdanubian range). The estimates of the ages of these deposits rely on nannofossils, benthic foraminifers and rudist bivalve biostratigraphy but not on strontium isotope stratigraphy.

Pseudopolyconites is a rare rudist bivalve in Rumania. It was found only in two localities of Apuseni Mountains: Magura Hill (*Pseudopolyconites hirsutus*, Patrulius, 1974; *Pseudopolyconites parvus*, Săsăran et al., 2013) and Remeti Valley (*Pseudopolyconites milovanovici*, Lupu, 1969, 1974).

A good example of *Pseudopolyconites* was found in Hron Valley, Slovakia (Mišik, 1966; Lupu, 1976).

Specimens of *Pseudopolyconites* have been recovered in late Campanian-Maastrichtian transgressive mixed siliciclastic-carbonate successions of Turkey, from the Istanbul zone (Kocaeli peninsula, northwestern Turkey), Tuz Lake Basin (central Anatolia), Malatya Basin (eastern Anatolia) to Adıyaman and Antakya areas (southeastern Turkey) but they are not abundantly represented (Özer, 1982, 1983, 1992 a, b, 2002; Özer et al., 2008, 2009; Steuber et al., 2009). However, most examples of *Pseudopolyconites* are well preserved, isolated, generally large, in growth position and free of sediment matrix which makes it possible to observe all the internal and external characteristics of both valves.

The Hereke area (Kocaeli peninsula) is the type locality of *Pseudosabinia*, where some *Pseudopolyconites* specimens are also reported as occurring together with *Gorjanovicias* by Özer (1982, 1992a) and Fenerci (1999). The previous studies suggest a Campanian, Campanian-Maastrichtian or Maastrichtian age for the rudist fauna, however the Sr-isotope data of the rudist shells indicate a late Campanian age for the rudist-bearing limestones in the Hereke area (personal communication with T. Steuber).

The transgressive sequence of Tuz Lake basin contains well-preserved specimens of *Pseudopolyconites* (Özer, 1983) together with abundant hippuritids (Özer, 2002). The Sr-isotope analysis of the equivalent levels of the rudist-bearing limestones in the north of the basin, around Ankara, indicate a late Campanian age (personal communication with T. Steuber).

Rudists are widespread and very abundant in the Campanian-Maastrichtian transgressive-regressive systems tracts of the Malatya Basin (Özer et al., 2008). In the southern part of this basin, around Yeşilyurt village, Sr-isotope data obtained from rudists of the *Pseudopolyconites*-bearing limestones just below the *Orbitoides apiculatus* level indicate a late Campanian age (Özer et al., 2008; Schlüter et al., 2008a; Schlüter, 2008b).

The Kahta-Adıyaman and Yayladağı-Antakya areas are the type localities of the several rudist taxa that are endemic to the Arabian platform-plate (Özer, 1986, 1992b; Steuber et al., 2009). The rudist-bearing limestone lenses within the clastic sequence contain some specimens of *Pseudopolyconites* (Özer, 1986, 1991; Özer et al., 2008). Strontium isotope analysis of rudist shells indicates a late Campanian age for the *Pseudopolyconites*-bearing limestone lenses in the transgressive sequence in the Kahta and Yayladağı areas (Özer et al., 2008; Schülter et al., 2008b; Steuber et al., 2009).

As far as the Middle East is concerned, the best outcrops of late Campanian-Maastrichtian rudist bearing sequences are in Iran (Khazaei et al., 2010 with bibliography) but *Pseudopolyconites* specimens have not been found so far in Iran (Khazaei and Özer, 2011). Rudist collections from NW and NE Syria with similar rudist assemblages to those of southeastern Anatolia have been recently examined by one of us (S. Ö.) indicating a late Campanian-early Maastrichtian age. But, unfortunately, *Pseudopolyconites* has not been found. The rudists are very limited in the Upper Cretaceous sequences of Jordan and they are only observed in the Cenomanian and Turonian beds (Bandel and Mustafa, 1994; Özer and Ahmad, 2011) indicating that it seems impossible to find *Pseudopolyconites* specimens. The late Campanian-Maastrichtian rudist fauna of NE Iraq showing close resemblances with those of southeastern Anatolia and Iran have been recently presented by Özer et al. (2012), but *Pseudopolyconites* specimens have not been observed.

Our knowledge of the rudist fauna of the Middle East has been improved recently by Steuber and Schlűter (2012) who presented a strontium-isotope stratigraphy of Upper Cretaceous rudist bivalves of the Arabian Plate. Due to the presence of *Pseudopolyconites* in southeastern Anatolia (Özer, 1986, 1991, 1992b; Steuber et al., 2009) and in the United Arab Emirates (Morris and Skelton, 1995), the existence of this taxon in other localities of the Middle East is highly probable.

6. ANCESTORS OF THE CAMPANIAN-MAASTRICHTIAN *PSEUDOPOLYCONITES* SPECIES

The oldest representative of *Pseudopolyconites* is considered to be *Pseudopolyconites hirsutus* (=*Duranddelgaia hirsuta*) Patrulius, 1974, described from the Apuseni Mountains, Romania. Pejovic and Sladić-Trifunovic (1977) were the first authors who observed that the specimens described as *Duranddelgaia hirsuta* (Patrulius, 1974) have all the specific characters of the genus *Pseudopolyconites* and so there was no need to establish the new genus *Duranddelgaia*. Specimens of *P. hirsutus* (Patrulius) from Măgura Hill (Apuseni Mountains) are represented by the holotype, two paratypes and six specimens that are housed at the Geological Museum in Bucarest (**Figure 5**). Of these six specimens, four are poorly preserved right valves and the two others are large fragments of the right valve embedded in rock. Previously, *P. hirsutus* (Patrulius) was considered to be an Early Santonian representative of

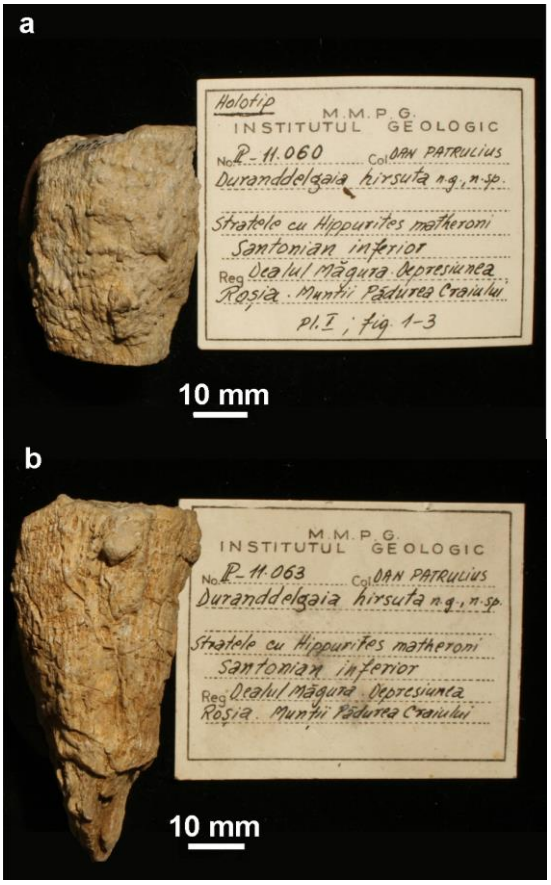

Figure 5. a) Holotype P11060 of *Pseudopolyconites hirsutus*: dorsal side of right valve with tubular excrescences; b) specimen 11063A of *Pseudopolyconites hirsutus*: right valve with ventral radial band. Original specimens collected by Patrulius (1974) are in the custody of the Geological Museum in Bucharest (Rumania).

Pseudopolyconites based on Patrulius (1974). Recently, new detailed investigations on the rudist fauna from Măgura Hill have been made and independent biostratigraphic data (e.g., nannoplankton) as well as the rudist assemblages suggest a Late Santonian-Early Campanian age (Săsăran et al., 2013). Additionally, new rudist taxa (*Pseudopolyconites parvus* and *Pseudosabinia klinghardti*) were described for the first time from these deposits (Săsăran et al., 2013).

The specimens of *P. hirsutus* and *P. parvus* described from Măgura Hill by Săsăran et al. (2013) have smaller dimensions as compared to specimens describes from Serbia (Bačevica, Lesak) (Pejovic and Sladić-Trifunovic, 1977; Sladić-Trifunovic, 1983) and have no long spines. Also, detailed taxonomical investigations revealed an intraspecific variability of external morphological features of both valves of *P. hirsutus* as follows: the shape of left valves varies from flat and very thin to slightly convex and thicker while the shape of right valves varies from conical to cylindrical-conical, slightly curved in some specimens. Also, in the right valve the ventral radial band is always flat, without tubular excrescences while the posterior radial band usually is not discernable on the surface of the, but may appear as a narrow furrow with one fine, longitudinal costa in some specimens (Săsăran et al., 2013). The same variability of external morphological features of both valves in small species of *Pseudopolyconites* has been also observed by Sladić-Trifunovic (2004) within the rudist fauna from Lesak (Serbia).

Pseudopolyconites hirsutus and *P. parvus* have been found in mixed siliciclastic-carbonate deposits at Măgura Hill that transgressively overlie Mesozoic tectonic units (Codru Nappe complex). The stratigraphic succession is 40 m-thick and starts with basal conglomerates which are succeeded by sandstone/marlstone intercalations with plant remains and mollusc fragments. These are followed by gastropod-rich limestones dominated by actaeonellids and nerineids, with rare rudists. These limestones are overlain by marls and marly limestones rich in solitary and meandroid colonial corals. The succession continues with interlayers of marls/sandstones/conglomerates containing three calcareous levels (Săsăran et al., 2013).

Specimens of *P. hirsutus* were also recognized by Pejović and Sladić-Trifunović (1977) in a large olistolith characterized by abundant rudist fauna at Svračija Stena, Lešak (southwestern Serbia). According to these authors, the forms of *P. hirsutus* recovered at Lešak are identical with the presumed coeval rudist bivalves from Măgura Hill. Based on species of *Sulcoperculina* aff. *cubensis* (Palmer) Radoičić ascribes the Lešak olistholit to Campanian or Upper Santonian-Campanian.

Successively, Sladić-Trifunović (1983) established the new species *P. leposavicensis* from Svračija Stena and in her last paper (2004) she instituted *Pseudopolyconites pantici* in place of *P. hirsutus* and *P. leposavicensis*. We find it impossible to understand the reason for the emendation by changing the name of *P. hirsutus* made by Sladić-Trifunović (1983; 2004) because we consider that the two mentioned species of *P. leposavicensis* and *P. pantici* are synonymous with *P. hirsutus* falling into intraspecific variability of this species. *P. parvus* was previously known only from Late Campanian sequences from Eastern Serbia (Bačevica).

7. DISCUSSION

Examples of *Pseudopolyconites* were found mostly

within the late Campanian successions. They have been found in many localities but they are almost never abundant except close to Bačevica. In particular, owing to reworking in high energy environments typical of the Central Tethys carbonate platforms during the Campanian, complete specimens of *Pseudopolyconites* are very rare and, often, only fragmented shells have been collected. Moreover, the outer shell layer characters of *Pseudopolyconites* established far from Bačevica are partly preserved or, in some cases, quite lacking because they were removed during the mechanical breakdown in the high-energy environments. Only photos of poorly preserved *Pseudopolyconites* and/or large fragments of the right valves of the same in addition to cross sections are available in most cases. We stress that, in spite of long and laborious research carried out in Belgrad, the original palaeontological material with all the holotypes and paratypes of the species of *Pseudopolyconites* established by the Serbian rudistologists both in Serbia and abroad has not been found, making comparative analysis between the holotypes and topotypes impossible. To sum up, it is difficult to hold for certain the validity of all the species of *Pseudopolyconites* established by the various authors (i.e., *P. campobassoi*, *P. ovalis apuliensis*, *P. manjae*, but also *P. garlensis*, *P. milovanovici* and *P. slovenicus*). Further, the numerous 'species' of *Pseudopolyconites* from Bačevica have been considered as simple eco-morphotypes (Tarlao et al., 2010). The proliferation of species made by rudistologists at Bačevica is not only peculiar to the genus *Pseudopolyconites*. For instance, three different 'species' of *Pironaea* established by Milovanović (1934b) have been recovered by us within the same fossiliferous level (see also Swimburne et al., 1992 and Munujos Vinyoles, 1989, for discussion about the determination of *Pironaea* species).

Pseudopolyconites was not present only during the late Campanian since specimens have been recovered in other Late Cretaceous successions of Central Tethys-Vardar zone. The earliest forms of *Pseudopolyconites* were recovered from Dealul Magura (Patrulius, 1974) and from the Lešak olistolith (Pejović and Sladić-Trifunović, 1977) and were considered to be the same species. In the absence of age diagnostic fossils and of strontium-isotope analysis, a precise chronological attribution of the deposits cropping out in these two localities is not yet established. However, the rudist taxa of Magura Hill and other biostratigraphic data (e.g., nanoplankton) suggest a late Santonian-early Campanian age (Săsăran et al., 2013). All the original examples from Lešak seem to have vanished and, moreover, the Serbian locality is at present unreachable. It is just on the boundary between Kosovo-Metohia region and Serbia. Only photos of selected transverse sections of *Pseudopolyconites* from Lešak but fine entire examples from Magura Hill are available. A few slight differences concerning mainly the different shape of the tip of the ligamental ridge were observed by Sladić-Trifunović (2004). Furthermore, the individuals from Rumania seem to be larger in size in comparison with the Serbian ones. To sum up the synonymy of these two old forms of *Pseudopolyconites* is probable. Transitional forms of *Pseudopolyconites* from Santonian to late Campanian are not known. An "evolutionary phylogenetic jump" (sensu Sladić-Trifunović, 2004) characterized mostly by size increase and by the development of a rich coat of tubules.

Pseudopolyconites individuals are relatively abundant in the late Campanian deposits: the so-called specific *Pironaea-Pseudopolyconites* association, widely distributed in the Central Tethys, represents an important palaeo-biogeographic and biostratigraphic event in the area in question (Milovanović and Grubić, 1971; Sladić-Trifunović, 1983). Following the datum that the sea-water Sr/Ca had reached a particularly high value in the Campanian (Stanley and Hardie, 1998; Steuber and Veizer, 2002) and coeval rudist shells were calcite-dominated (Steuber, 2002), it may be that *Pseudopolyconites* shells benefitted by the relative abundance of calcite by developing very much their growth lamellae structure. This may be one of the possible reasons for the extraordinary growth of tubules in late Campanian *Pseudopolyconites*. Another hypothesis is that *Pseudopolyconites* which lived in siliciclastic (or vulcanoclastic) settings developed peculiar functional adaptations of the shells different from the specimens which thrived in carbonate settings (see also Steuber, 1997).

Pseudopolyconites representatives undoubtedly attributed to the early Maastrichtian are not yet known. *Pseudopolyconites* examples have been recovered within rudist-bearing deposits dated back to the latest Maastrichtian of the Apulian carbonate platform (Steuber et al., 2007; Schlüter et al., 2008a). Unfortunately the *Pseudopolyconites* examples recognized within these deposits are poorly preserved and the collection of complete shells or larger fragments for detailed descriptions is almost impossible. It would be very important to take fine examples from the hard rock to evaluate possible differences between late Campanian and latest Maastrichtian *Pseudopolyconites*. The palaeontological data presented by Steuber et al. (2007) and Schlüter et al. (2008a) provide evidence

that the rudist associations existing in the latest Maastrichtian, close to the K-P boundary of the Apulian carbonate platform are remarkably similar to the rudist assemblages recognized within the late Campanian limestones of the same platform. The rudist associations of Bačevica and of the nearby locality of Vrbovac, characterized by a conspicuous group of caniculate rudists, are also surprisingly similar to those of the Apulian Plate exposed in Salento (S. Italy) and in the Ionian islands (Greece).

Because of the superb preservation of *Pseudopolyconites* our conjectures concerning the palaeoecology are entirely based on the Bačevica *Pseudopolyconites*-rich site (i.e., Liljekar). It is observed that both the short and long spines reach the base of the lower valve in *Pseudopolyconites*. It is speculated that the spines were useful for attaching the shells to the substrate. The spines emerging from the outer shells of *P. hirsutus* seem to curve upwards. In that case, they probably had a different function in comparison with those of *P. serbicus*, maybe acting as a defense against possible predators.

Pseudopolyconites from Bačevica thrived in moderate to low energy settings, maybe in, or close to, shallow channels and creeks of muddy tidal flats. It is hypothesized that the group of caniculate rudists found within the rudist-bearing lithosomes of Bačevica and Vrbovac colonized intertidal zones of protected marine environments (Özer and Ahmad, 2011). Shallow lagoons and/or tidal flats are sufficiently represented both in the carbonate and siliciclastic Central Tethys realm during the late Campanian. But, due to the general drowning and, sometimes, demise of the carbonate platform system in the Central Tethys during the Maastichtian, tidal flat environments are extremely rare in the early Maastrichtian seas of the Central Tethys and scarcely documented during the late Maastrichtian (Dercourt et al., 1993). This may explain the relative rarity of *Pseudopolyconites* during the Maastrichtian.

Lastly, as far as the taxonomy of *Pseudopolyconites* is concerned, Sladić-Trifunović (1983) proposed the segregation from radiolitids as a new family (i.e., *Pseudopolyconitidae*) for the genera *Pseudopolyconites*, *Fundinia* (Sladić-Trifunović and Pejovic, 1977) and *Kurtinia* (Karacabay-Öztemur, 1980) based on the outer shell layer structure are the growth lamellae, which project outwards as spines. Pons and Vicens (2008) showed that this character alone may not be used to define monophyletic groups. Moreover, *Kurtinia* cannot be ascribed to *Pseudopolyconites*. *Fundinia* also cannot be regarded as a member of the "pseudo-family". In fact *Fundinia* and *Kurtinia* have no spines emerging from the shell wall which are the most remarkable elements in the structure of *Pseudopolyconites*.

The new updated phylogenetic classification of rudist bivalves proposed by Skelton (2013) definitively obliterates the family of Pseudopolyconitidae.

8. CONCLUSIONS

Pseudopolyconites can be considered a rare component of Upper Cretaceous faunal assemblages. Many late Campanian species of *Pseudopolyconites* were instituted in the environs of Bačevica and elsewhere. Many species were based on poorly preserved specimens and, often using cross sections. This makes it difficult or even impossible to evaluate all the characters necessary for an unequivocal separation amidst the previously established species.

Thus, at the present state of knowledge, many specimens of *Pseudopolyconites* previously assigned to different species might fall within the biological variability of a single species. A few characters allow us to separate some late Santonian-early Campanian representatives of the genus from the late Campanian ones, but it is not possible to form an opinion concerning poorly preserved *Pseudopolyconites* from the latest Maastrichtian. It may be that *Pseudopolyconites* preserved unaltered the peculiar characters from the late Campanian up to the latest Maastrichtian, analogously to a conspicuous group of caniculate rudist which seem to have passed the fore-mentioned long lapse of time without significant changes of the skeletal characters. Thus, the topic of functional adaptations, growth rates and different shell growth strategies of *Pseudopolyconites* from the Santonian to the latest Maastrichtian should be adequately examined in the future, considering also the different environments where these radiolitids thrived, for instance, carbonate versus siliciclastic/volcanoclastic settings.

Specimens of *Pseudopolyconites* found at Bačevica are considered herein as rudist bivalves which developed particular shell growth strategies in response to the peculiar environments where they thrived, probably in muddy tidal flats.

This paper may underestimate the true richness of *Pseudopolyconites*, but without more well-preserved material this cannot be considered. Undoubtedly phylogenetic relationships within the genus in question are obscure and a future job concerning accurate descriptions and character analysis both of historical and new examples will be needed.

Acknowledgements. *This paper has benefited from the careful reviews by Simon Mitchell and one anonymous. We are most grateful to Josè Maria Pons who read our paper at the 9th International Congress on Rudist bivalves in Kingston, Jamaica in 2011.*

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Accepted 21st June 2013