

The occurrence of giant bivalve Alatoconchidae from the *Yabeina* zone (Upper Guadalupian, Permian) in European Tethys

D. Aljinović^{a,*}, Y. Isozaki^b, J. Sremac^c

^a Faculty of Mining, Geology, and Petroleum Engineering, University of Zagreb, Pierottijeva 6, Zagreb 10000, Croatia

^b Department of Earth Science and Astronomy, University of Tokyo, Meguro, Tokyo 153-8902, Japan

^c Faculty of Science, Department of Geology, University of Zagreb, Horvatovac 102a, Zagreb 10000, Croatia

Received 5 June 2007; received in revised form 7 September 2007; accepted 19 September 2007

Available online 12 October 2007

Abstract

The Permian gigantic bivalve family Alatoconchidae forms a member of the tropical shallow marine fauna intimately associated with the Tethyan warm-water-adapted Verbeekiniidae fusulines, such as *Neoschwagerina* and *Yabeina*. The Velebit Mountains in central Croatia is one of the nine areas in the world that yielded Alatoconchidae, as first reported early in the 1970 s. In addition to the *Neoschwagerina* Zone (Wordian, Middle Guadalupian) originally described, we newly found Alatoconchidae from the *Yabeina* Zone (Capitanian, Upper Guadalupian) from the Brušane area in the central Velebit Mountains. Alatoconchidae occur in three stratigraphic levels of the Velebit Formation composed of black fusuline/algal wackestone/packstone with *Yabeina*. Although fragmented, the Alatoconchidae shell reach sizes over 40 cm long, and possess unique morphology with a lateral flange plus a prominent prismatic external layer in the double-layered shell structure. Our results confirm, for the first time in Europe and thus in the western Tethyan domain, that the stratigraphic range of the gigantic bivalve family extends up to the Capitanian as well as in the superocean Panthalassa. As no occurrence has been reported from the overlying Lopingian (Upper Permian), Alatoconchidae likely became extinct globally at the end of the Guadalupian, i.e., through the Guadalupian–Lopingian boundary mass extinction.

© 2007 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.

Keywords: Alatoconchidae; *Yabeina*; Capitanian; Tethys; Velebit; External Dinarides

1. Introduction

Alatoconchidae is a Permian aberrant bivalve family that has an extraordinary shell size (up to 1 m in length) and unique morphology with a wing-like flange on each valve. This family is so different from other ordinary bivalves that it was regarded as a paleontological problematica when first described from Japan in the late 1960s (Ozaki, 1968). Although the taxonomy of Alatoconchidae started with considerable confusion, Yancey and Boyd (1983) and Yancey and Ozaki (1986) finalized the controversial issue by proposing an overall model morphology and unique ligament structure as clear criteria for identification.

The occurrence of Alatoconchidae was reported from seven Tethyan areas, Tunisia, Croatia, Oman, Iran, Afghanistan,

Malaysia, and Thailand, and from two mid-Panthalassan domains currently in the Philippines and Japan, as summarized by Isozaki (2006) and Isozaki and Aljinović (in press). It is noteworthy that alatoconchids occur in close association with Early–Middle Permian Tethyan fusulines (Verbeekiniidae, Schwageriniidae), rugose corals (Waagenophyllidae), and abundant calcareous algae, a fact that suggests that the Alatoconchidae flourished in warm, shallow (photic) marine environments in low-latitude areas in Tethys (Yancey and Boyd, 1983). The occurrences of Alatoconchidae were reported from the Cisuralian–Guadalupian but its stratigraphic range has not yet been fully constrained. Isozaki (2006) recently emphasized that Alatoconchidae ranged up to the Capitanian (Upper Guadalupian) in Japan and became extinct at the end of the Guadalupian together with Verbeekiniidae and Waagenophyllidae.

The Velebit Mountains in central Croatia is one of the nine areas in the world that is located at the western end of the occurrences, i.e., in the *Cul-de-Sac* of Tethys, as well as Djebel

* Corresponding author. Tel.: +385 1 5535 790; fax: +385 1 48 36 057.

E-mail addresses: dunja.aljinovic@rgn.hr (D. Aljinović), isozaki@ea.c.u-tokyo.ac.jp (Y. Isozaki), jsremac@inet.hr (J. Sremac).

Tebaga in Tunisia (Fig. 1c). Kochansky-Devidé (1978) and Kochansky-Devidé and Ramovš (1987) reported an occurrence of Alatoconchidae from the Wordian (middle Guadalupian) limestone of the Permian Velebit Formation near Baške Oštarije,

ca. 10 km west of Gospić (Fig. 1a). Our recent fieldwork in the neighboring Brušane area in central Velebit Mountains, between Baške Oštarije and Gospić, documented a new locality of the Alatoconchidae. This article reports the occurrence of the strange

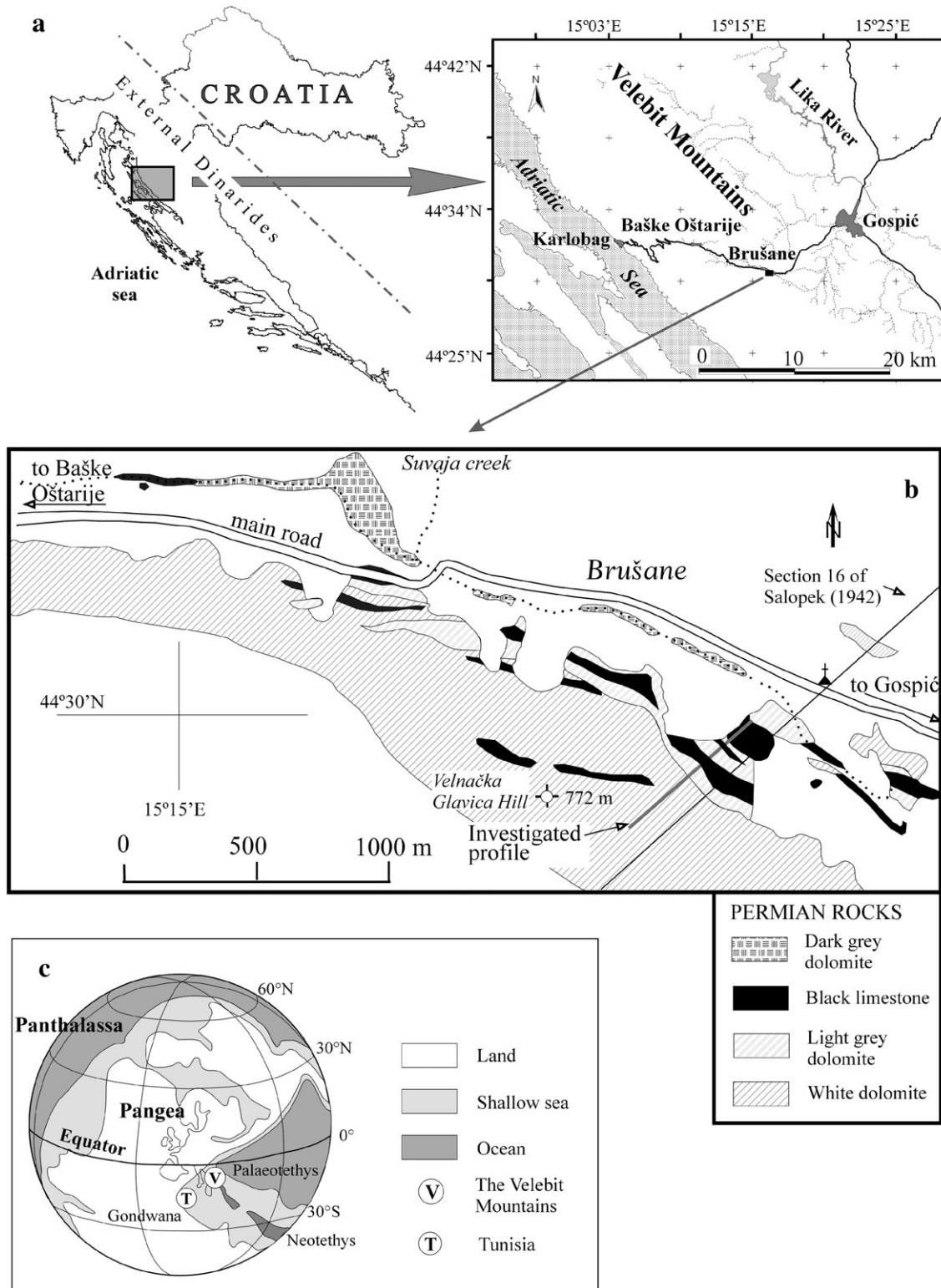


Fig. 1. Index map (a) and geologic map of the Brušane area (b) (modified after Salopek, 1942) in the central Velebit Mountains, central Croatia, and also paleogeographic map of Pangea in the Middle Permian (modified from Scotese and Lanford, 1995; Vai et al., 2000) (c). Note the Velebit Mountains in Croatia, together with Tunisia, formed a part of peri-Gondwana carbonate platform located in the western end of Tethys around the equator.

bivalve family Alatoconchidae from the Capitanian part of the Velebit Formation and discusses the geological implications particularly about the upper range limit of the Alatoconchidae in western Tethys.

2. Geologic setting

The External Dinarides along the northern margin of the Adriatic Sea form a geotectonic belt that continues for ca. 1000 km all the way from the Southern Alps in Austria/Italy to the Hellenides in Greece. This belt was derived primarily from Late Paleozoic–Triassic rifting of the Gondwana margin (Vlahović et al., 2005; Balini et al., 2006) and was later overprinted by Mesozoic–Cenozoic convergent tectonics, i.e., the

closure of Paleo-Tethys and new subduction along the northern margin of Neo-Tethys. As the entire External Dinarides is mostly composed of Mesozoic and Paleogene platform carbonates, often called the Adriatic Carbonate Platform (e.g., Vlahović et al., 2005), Paleozoic rocks in the External Dinarides are limited in distribution. The Permian rocks in Croatia are two-fold; a shallow marine carbonate-dominated facies in the Velebit Mountains in central Croatia (Fig. 1) and a terrigenous clastic-dominated facies in Gorski Kotar in western Croatia (e.g., Aljinović et al., 2003).

The Velebit Mountains located in the middle of the External Dinarides (Fig. 1a) is exceptional in containing extensive occurrences of Upper Paleozoic sedimentary rocks, in particular Middle–Upper Permian carbonate rocks (e.g., Salopek, 1942; Kochansky-Devidé, 1965; Sokač et al., 1976, Sremac, 2005).

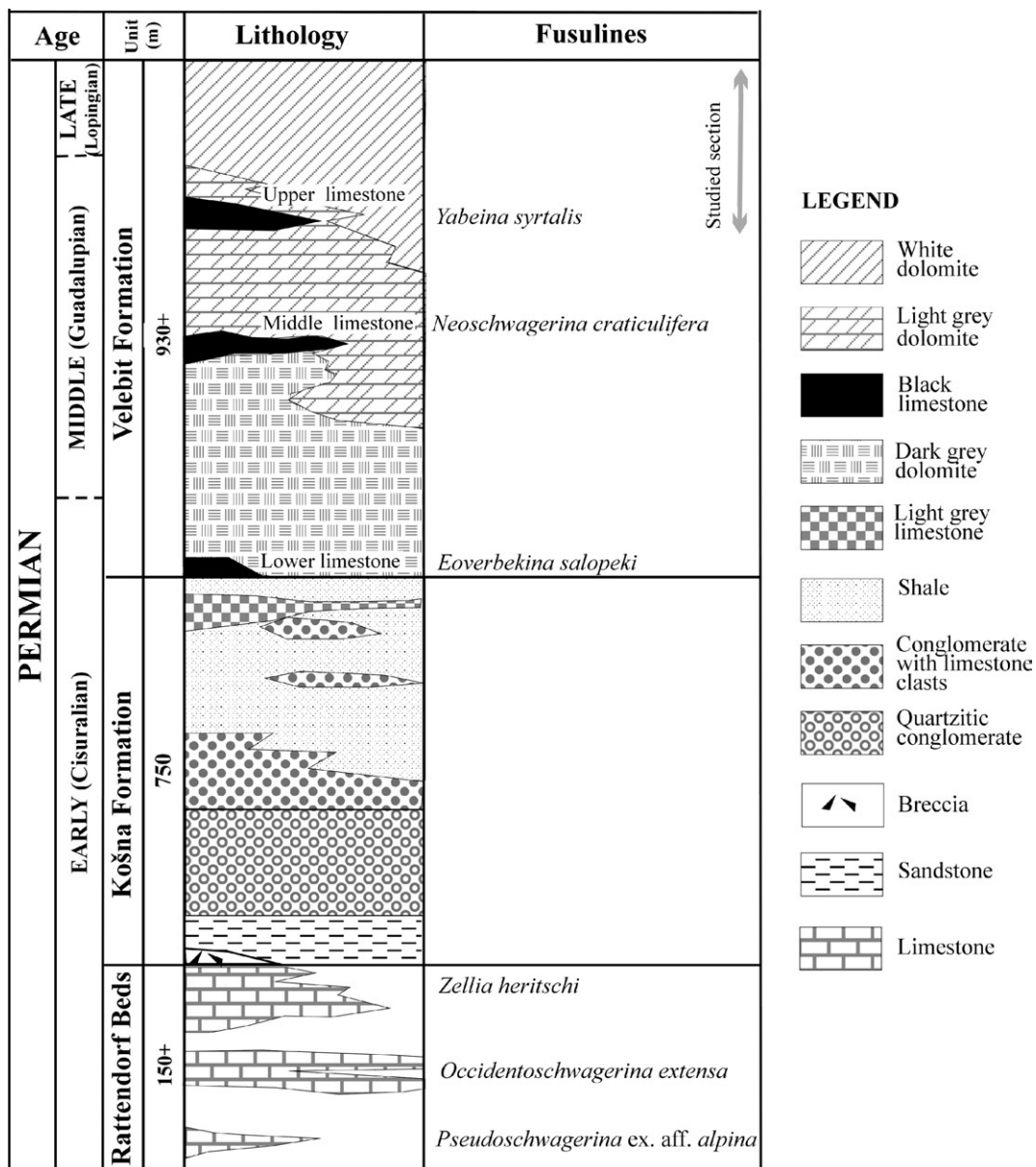


Fig. 2. Stratigraphic summary of the Permian System in the central Velebit Mountains, Croatia (modified after Kochansky-Devidé, 1982). The Permian in the Velebit Mountains is composed of Lower Permian and upper Middle–Upper Permian shallow marine carbonates with the upper Lower Permian terrigenous clastic wedge in between. This study focused on the upper limestone unit of the Velebit Formation that belongs to the Upper Guadalupian.

Salopek (1942) published a detailed geologic map of the Brušane area in the central Velebit Mountains, ca. 10 km to the west-southwest of Gospić (Fig. 1a, b). His contribution built a foundation for subsequent geological researches in the area in several aspects, in particular paleontological and sedimentological studies (e.g., Kochansky-Devidé, 1965; Flügel, 1977; Kochansky-Devidé, 1978; Kochansky-Devidé and Ramovš, 1987; Sremac, 1991, 2005).

According to Flügel (1977) and Kochansky-Devidé (1982), the Permian rocks in the Velebit Mountains comprise three distinct stratigraphic units: the Sakmarian (Cisuralian) Rattendorf Beds (carbonate), probably early Guadalupian clastic Košna Formation, and the Guadalupian–Lopingian Velebit Formation (carbonates) in ascending order (Fig. 2). In other words, the Permian platform carbonate sequence in the Velebit Mountains is intercalated in its centre with a terrigenous clastic wedge.

On the basis of previous analyses of sedimentary facies and environments and on geologic structures (Kiessling et al., 2003; Sremac, 2005; Vlahović et al., 2005), we briefly summarize the tectonic evolution of the Velebit Mountains as follows. This part of Croatia started to develop as a part of the Carboniferous to Early Permian epeiric platform along northern Gondwana (Fig. 1c), accumulating shallow marine carbonates and terrigenous clastics. In the late Early Permian this primary setting was punctuated by intermittent rift-related extensional tectonism that broke the platform into several horsts and grabens. The Velebit Mountains probably represents one of these Permian topographic-highs (horsts) isolated from the main carbonate platforms in the Southern Alps, whereas the clastic rocks in the Gorski Kotar in western Croatia filled the Permian inter-platform basins (grabens) prior to the Early Triassic carbonate deposition (Aljinović, 1997; Aljinović et al., 2006). The Permian clastic wedge (Košna Formation) intercalated between carbonates (the Rattendorf Beds and Velebit Formation; Fig. 2) probably represents a temporary terrigenous cover over the platforms.

The Velebit Formation *sensu* Flügel (1977), ca. 930 m thick, is mainly composed of dolomite with three lenticular bodies of limestone: lower, middle, and upper limestone (Salopek, 1942; Kochansky-Devidé 1965, 1982, Fig. 2). These three limestone lenses are the main source of fossils from the Velebit Formation, such as gastropods, bivalves, brachiopods, cephalopods, rugose coral, sponges, bryozoans, fusulines, smaller foraminifers, and calcareous algae, all forming typical Tethyan elements (Kochansky-Devidé, 1965, 1979; Kochansky-Devidé, 1982; Sremac, 1991). The rock types and fossil content clearly indicate that the Velebit Formation formed in a shallow marine, warm-water environment. By analyzing the middle limestone (middle Guadalupian) in particular, Sremac (1991) emphasized the key role of sponges and algae in the development of patch reefs and carbonate mud mounds on a carbonate platform.

The lower limestone yielded fusuline (*Eoverbeekina salopeki*) of Artinskian (Late Cisuralian) age (Kochansky-Devidé, 1965; Fig. 2). The middle limestone is replete with various macro- and micro-fossils including the above-mentioned reef-builders; e.g. gastropods (*Bellerophon*, *Pleurotomaria*, *Murchisonia*), bivalves (*Shikamaia*, *Edmondia*), brachiopods (spiriferids, enteletids, productoids, oldhaminoids), cephalopods (*Orthoceras?*), rugose

coral (*Waagenophyllum*), calcisponges, bryozoans, fusulines (*Eoverbekina*, *Neoschwagerina*, *Chusenella*), smaller foraminifers (*Paraglobivalvulina*, *Agathammina*, *Hemigordius*), and calcareous algae (*Mizzia*, *Vermiporella*, *Gymnocodium*, *Permo-calculus*) (Kochansky-Devidé, 1965, 1979; Sremac, 1991). On the basis of the occurrence of *Neoschwagerina craticulifera* (Schwager), Kochansky-Devidé (1965, 1979) and Sremac (1991) concluded a Wordian (or Murgabian; Middle Guadalupian) age for the middle limestone (Fig. 2).

The upper limestone yields abundant fusulines with minor amounts of rugose corals (*Waagenophyllum*), brachiopods, gastropods, and calcareous algae (Kochansky-Devidé, 1965). The occurrence of the index fusuline *Yabeina syrtalis* (Douville) indicates a Capitanian (or Midian; Late Guadalupian) age for the upper limestone (Fig. 2). The megafossil assemblage of the upper limestone is similar to that of the middle limestone, but differs in recording the first occurrence of some brachiopods (*Derbya*, *Streptorhynchus*, *Orthotetes*) and a gastropod (*Temnochelius*) (Salopek, 1942; Kochansky-Devidé, 1982). The upper limestone is conformably overlain by a thick (>200 m) less-fossiliferous dolomite that merely yields gymnocodiacean algae in the lower part, and small foraminifers (mostly Earlandiacea) in the uppermost part (Fig. 2) but they are not diagnostic for dating.

We investigated the stratigraphy and fossil contents, in particular the mode of occurrence of the large-shelled bivalve, in the upper part of the Velebit Formation in the Brušane area (Figs. 1b and 2). We measured a section in detail near Velnačka glavica in Brušane (44° 29' 41" N, 15° 16' 04" W; Fig. 1a, b) on the south of a small stream (Suvaja creek), collected more than 100 rock samples for indoor analyses, and made 60 thin sections of carbonate samples for observing sedimentary textures. The studied section, named here the Brušane section (Figs. 1b and 3), partly corresponds to Profile no. 16 illustrated by Salopek (1942). Paleontological data of the section were later added by Kochansky-Devidé (1979) and Sremac (1991).

3. The Brušane section

3.1. Lithostratigraphy

The Brušane section exposes the upper part of the Velebit Formation, i.e., a ca. 250 m-thick interval from the upper limestone to the topmost dolomite (Figs. 2 and 3). The section is composed of 2 distinct rock types: a predominant light gray dolomite and a minor black limestone intercalated in the former as thin lenses. As shown in Fig. 3, the latter occurs in 3 horizons, and here we name them as L-1, L-2, and L-3 in ascending order (Fig. 3). Kochansky-Devidé (1979) and Sremac (1991) previously correlated L-1 to the middle limestone of Kochansky-Devidé (1965), and both L-2 and L-3 to their upper limestone, respectively (Fig. 2). Photographs of the outcrop at Brušane and thin section views of samples are illustrated in Figs. 4 and 5.

L-1 is 45 m thick and consists of dark gray, well-bedded, bioclastic wackestone or packstone and lime mudstone (Fig. 4a) with various bioclasts. The wackestone/packstone (biomicrite) mainly consists of fine-to coarse-grained peloids and bioclasts of foraminifera, algae, bryozoans, echinoderms, corals, bivalves,

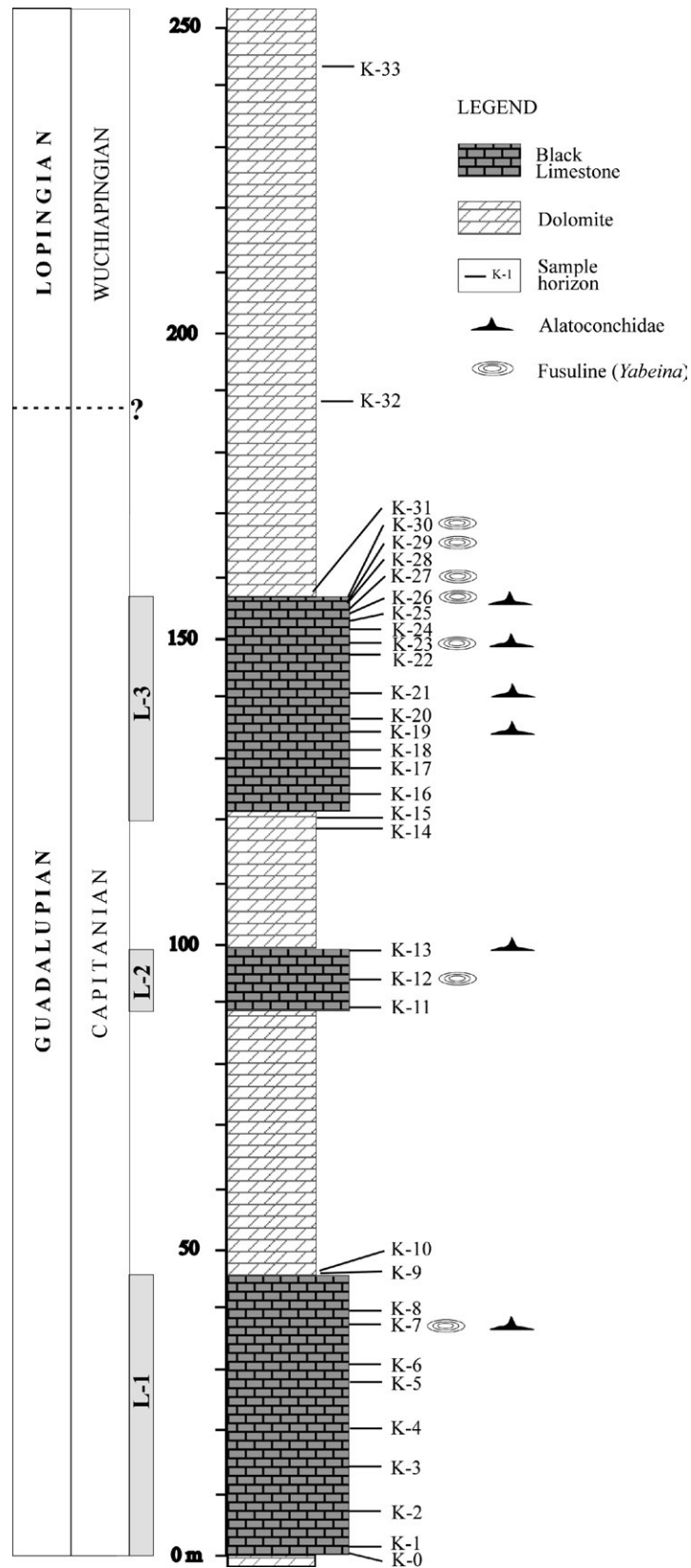


Fig. 3. Stratigraphic column of the Guadalupian Velebit Formation at the Brušane section near Velnačka glavica. See Fig. 1a, b for the location. This section exposes the upper part of the Velebit Formation from the upper limestone to the topmost dolomite (see Fig. 2).



Fig. 4. Photographs of the Guadalupian Velebit Formation at Brušane, central Velebit Mountains. a) bedded packstone–wackestone and lime-mudstone intercalating in L-1, a hammer for scale in circle; b) *Alatoconchidae* gen et sp. indet. (>25 cm-long large bivalve) in black lime mudstone (Sample K-13, L-2), the shell has a U-turn fold on the right-hand side end; c) *Alatoconchidae* gen et sp. indet. (>30 cm long) in black lime mudstone (Sample K-12, L-2); d) a juvenile form of *Alatoconchidae* in lime mudstone (Sample K-26, L-3), e) thickly-bedded wackestone with large bioclasts in the basal part (Sample K-21, L3) with a white arrow pointing a fragment of large bivalves; f) basal part of fusuline (mostly *Yabeina*) packstone (middle-upper) and lime mudstone of the underlying bed (lower) (Sample K-27, L-3).

gastropods, and microbial problematica, in a micritic matrix. See Sremac (1991) for thin section views of L-1 limestone. Small fragmented bivalve shells (*Alatoconchidae*) occur in the basal parts of some thick packstone/wackestone beds. Trace fossils (*Zoophycos*-type) occur in the muddy wackestone and lime-mudstone beds (Sremac, 1991).

L-1 is conformably overlain by a ca. 50 m-thick, light gray dolomite exhibiting microcrystalline texture, in which dasycladacean algae are still discernable in the field and in thin sections (Fig. 5a). The common occurrence of dasycladacean algae suggests that the dolomite was originally deposited as algal limestone. Fairly preserved primary bioclastic detritus and

microcrystalline texture suggests possibly early diagenetic dolomitization in supratidal conditions.

L-2 forms an 11 m-thick lens of thick-bedded, black wackestone/packstone containing abundant large-size fusulines (*Verbeekinae*) and a minor amounts of rugose coral (*Waagenophyllidae*), bryozoans, and large bivalves (*Alatoconchidae*) (Figs. 4b,c and 5b). In addition to fusulines, bioclasts also include less abundant brachiopods, gastropods and fragments of echinoderms, algae, bryozoans, and microbial problematica (right half of Fig. 5b).

Another dolomite, ca. 20 m thick, occurs between L-2 and L-3. The dolomite is polymodal, anhedral to subhedral, micro- to

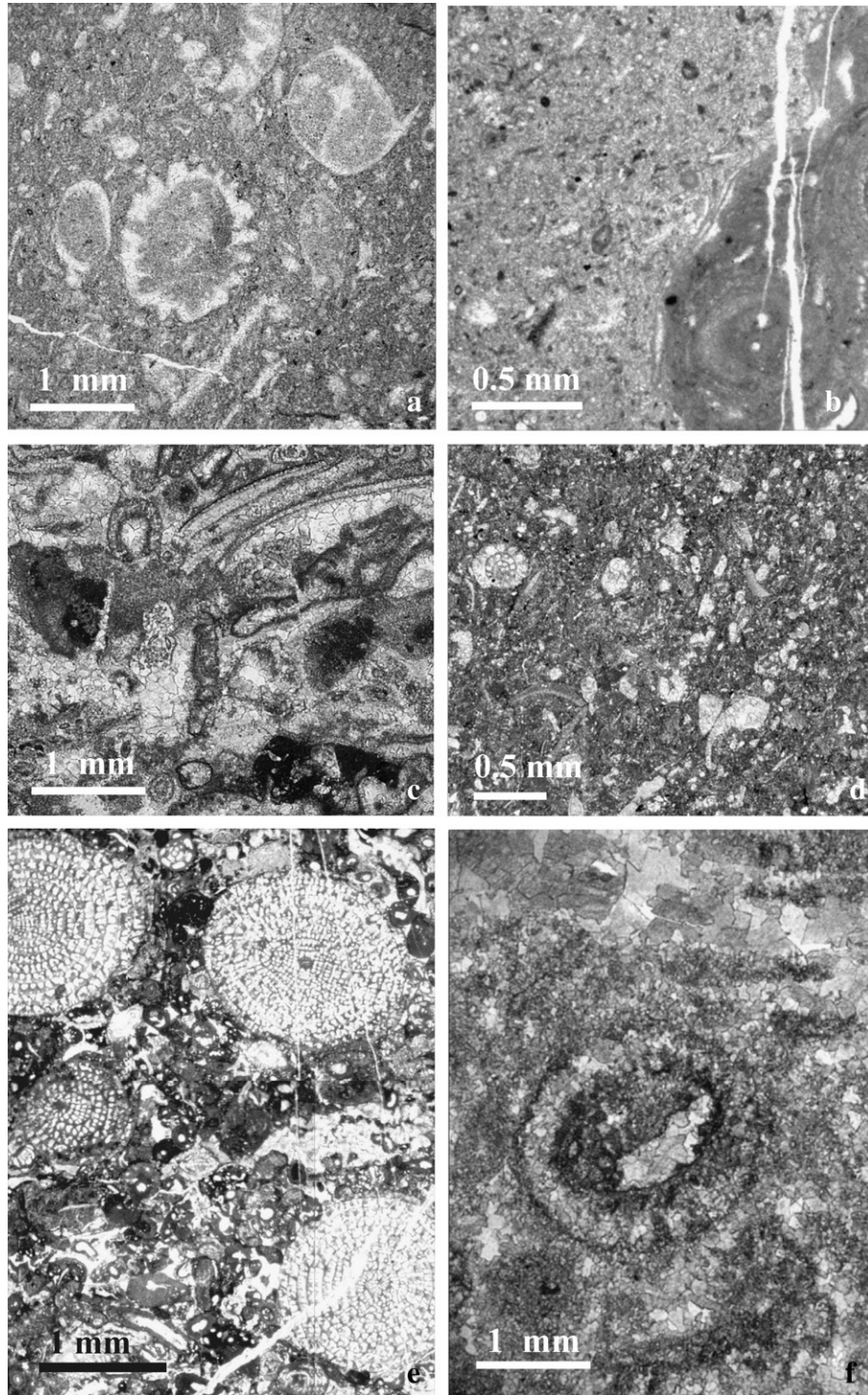


Fig. 5. Photomicrographs of the Guadalupian limestones at Brušane. a) bioclasts of algae and gastropod in a light grey dolomite overlying L-1 limestone. Well preserved primary bioclastic components and microcrystalline texture suggest possibly early diagenetic dolomitization, K-10; b) wackestone with various sand sized bioclasts (left side) and a large fragment of *Shamovella* (= *Tubiphytes*) microbial problematica (right side of a photo) illustrate the dominant rock type of L-2 limestone, K-16; c) Polymodal anhedra to subhedra micro to coarse-crystalline dolomite overlying L-2 limestone. Note that some of primary bioclastic components are mimically replaced by dolomite crystals, K-14; d) fusuline packstone (mostly *Yabeina*), K-29, L-3; f) macrocrystalline polymodal anhedra to subhedra dolomite with faintly preserved algal fragments overlies the L-3 limestone. Its fabric suggests dolomitization in a burial stage, K-33.

macro-crystalline. Primary components (mostly bioclasts) are mimically replaced whereas the matrix-replacing dolomite consists of homogenous anhedra to subhedra coarse crystals (Fig. 5c). This dolomite unit has likely suffered shallow burial dolomitization.

L-3 is approximately 37 m thick, and is composed of thick-bedded bioclastic wackestone/packstone and lime mudstone. The basal part of each bed is composed of coarser-grained wackestone/packstone (Fig. 5d) that grades upward into lime

Table 1

List of fossils from the Brušane section reported in previous studies (fossils with asterisk were reported by Kochansky-Devidé, 1979, and the rest by Sremac, 1991)

L-1
Fusuline
<i>Dunbarula nana</i> *
<i>Ozawainella</i> sp.
<i>Reichelina</i> sp.
<i>Staffella</i> cf. <i>elegantula</i>
<i>Nankinella waageni</i>
<i>Sphaerulina croatica</i>
<i>Schubertella</i> sp.
<i>Kahlerina pachytheca</i> *
<i>Chusenella velebitica</i>
<i>Dunbarinella velebitica</i>
<i>Eoverbeekina</i> cf. <i>paklenicensis</i>
<i>E.</i> cf. <i>salopeki</i>
<i>Neoschwagerina craticulifera</i> *
<i>N. occidentalis</i> *
<i>N. rotunda</i>
<i>Yabeina syrtalis</i> *
Smaller foraminifera
<i>Agathammina pusilla</i>
<i>Baisalina pulchra</i>
<i>Climacammina</i> sp.
<i>Glomospira</i> sp.
<i>Glovivalvulina</i> sp.
<i>Hemigordius renzi</i>
<i>H. irregulariformis</i>
<i>H.</i> cf. <i>ovatus</i>
<i>Palaeonubecularis</i> sp.
Algae
<i>Vermiporella nipponica longipora</i> *
<i>V. longipora</i>
<i>V. serbica</i>
<i>Velebitella triplicata</i>
<i>Mizzia velebitana</i>
<i>M. yabei</i>
<i>M. cornuta</i>
<i>Gymnocodium bellerophontis</i> *
<i>Permalculus tenellus</i> *
<i>P. plumosus</i> *
Rugose coral
<i>Waagenophyllum</i> sp.
Bivalve
<i>Tanchintongia</i> (= <i>Shikamaia</i>) <i>ogulinea</i>
<i>Edmondia permiana</i>
Gastropod
<i>Bucania kattaensis</i>
<i>Pleurotomaria</i> sp.
<i>Murchisonia</i> sp.
Brachiopod
<i>Martinia velebitica</i>
Sponge
<i>Guadalupia cyllindrica</i>
Microbial
<i>Shamovella</i> (= <i>Tubiphytes</i>) <i>obscura</i>
<i>S.(T.) carinthiaca</i>
Dolomite between L-1 and L-2
Algae
<i>Gymnocodium</i> sp.*
L-2: same as L-1
Dolomite between L-2 and L-3: barren

Table 1 (continued)

L-3: same as L-1 plus below*
Fusuline
<i>Verbeekina</i> sp.*
<i>Reichelina cribroseptata</i> *
Algae
<i>Permalculus fragilis</i> *
Dolomite above L-3
Fusuline
<i>Staffella</i> sp.*
Smaller foraminifera
<i>Glomospira</i> sp.*
<i>Hemigordius</i> sp.*
<i>Glovivalvulina</i> sp.*
Algae
<i>Mizzia</i> sp.*
<i>Gymnocodium bellerophontis</i> *
<i>Permalculus</i> cf. <i>fragilis</i> *

Fossils with asterisk were reported by Kochansky-Devide, 1979 and the rest by Sremac, 1991.

mudstone of the upper part. Sand-sized bioclasts form occasionally faint parallel to ripple cross lamination. Large bioclasts (e.g., brachiopod, gastropod fragment), as well as fragmented shells of large bivalves (Alatoconchidae), occur occasionally in the basal part (Fig. 4e). The black lime mudstone of the top part of each bed contains small amount (less than 10%) of fine-grained siliciclastics. In the upper part of the L-3, some packstone beds are composed almost entirely of large fusulines (*Yabeina*) (Figs. 4f and 5e).

Above the L-3, a ca. 100 m-thick massive, less-fossiliferous, white dolomite occur that has a macrocrystalline polymodal, anhedral to subhedral fabric with faintly preserved algal fragments (Fig. 5f). The dolomite possibly suffered several stages of dolomitization but in the present stage its structure indicates recrystallization of burial dolomites. This dolomite corresponds to the “transitional dolomite” *sensu* Salopek (1942) and Kochansky-Devidé (1982). The top of this dolomite is not exposed but apparently it is overlain by undivided, Triassic-aged, reddish conglomerate and bedded limestone.

3.2. Fusuline biostratigraphy

Fossil distribution in the Brušane section is shown in Tables 1, 2 and Fig. 3. Table 1 lists all fossils reported in previous studies, whereas Table 2 shows those found in the present study. Among the three limestone units in the studied sections, L-1 is outstanding in having a great variety of fossils. Despite the apparent richness in faunal composition, the sole fossil group useful for dating is fusuline, in particular Verbeekiniidae that includes the index genus *Yabeina*.

The fossil content of L-1 was fully analyzed by Kochansky-Devidé (1979) and Sremac (1991). As L-1 yields *N. craticulifera* (Schwager), Kochansky-Devidé (1979) and Sremac (1991) once assigned a Wordian (Middle Guadalupian) age for L-1; however, the co-occurrence of *Y. syrtalis* (Sremac, 1991; Table 1) presents a difficulty in this age assignment. *Y. syrtalis* is one of the advanced forms of *Yabeina* that characterizes the Capitanian

Table 2
List of fossils from the Brušane section found in the present study

L-1	K-7: Alatoconchidae gen. et sp. indet. <i>Neoschwagerina craticulifera</i> (Schwager)*
L-2	K-12: <i>Yabeina syrtalis</i> (Douville) <i>Neoschwagerina</i> sp., <i>Chusenella velebitica</i> Kochansky-Devidé <i>Eoverbeekina salopeki</i> Kochansky-Devidé <i>Sphaerulina croatica</i> Kochansky-Devidé <i>Dunbarinella nana</i> (Kochansky-Devidé) <i>Kahlerina pachythea</i> Kochansky-Devidé <i>Nankinella</i> sp.
	K-13: Alatoconchidae gen. et sp. indet.
L-3	K-19: Alatoconchidae gen. et sp. indet. K-21: Alatoconchidae gen. et sp. indet. K-23: Alatoconchidae gen. et sp. indet. <i>Yabeina</i> sp. K-26: Alatoconchidae gen. et sp. indet. <i>Yabeina</i> sp. K-27: <i>Yabeina syrtalis</i> (Douville) <i>Neoschwagerina</i> sp. <i>Chusenella velebitica</i> Kochansky-Devidé <i>Eoverbeekina salopeki</i> Kochansky-Devidé <i>Sphaerulina croatica</i> Kochansky-Devidé <i>Dunbarinella nana</i> (Kochansky-Devidé) <i>Kahlerina pachythea</i> Kochansky-Devidé <i>Nankinella</i> sp.
	K-29: <i>Yabeina</i> sp. K-30: <i>Yabeina</i> sp.

Refer to main text for details about *Neoschwagerina craticulifera** from K-7. Fossils with asterisk were reported by Kochansky-Devidé, 1979 and the rest by Sremac, 1991.

(Late Guadalupian) interval, as well as *Y. globosa* that represents the nominal species of the *Y. globosa* Zone in Japan (e.g. Toriyama, 1967; Ozawa and Nishiwaki, 1992; Zaw Win, 1999; Ota and Isozaki, 2006). Such advanced forms of *Yabeina* generally co-occur solely with advanced *Neoschwagerina*, such as *N. margaritae*, but never accompany primitive forms like *N. craticulifera* (H. Igo, personal communication). Sremac (2005) recently reported the abraded shape of *N. craticulifera* from the same horizon (from K-7 as illustrated in plate 4, fig. 1 of Sremac, 2005), and this suggests a possible reworked origin of *Neoschwagerina*; thus requires caution in age assignment. On the basis of these relations, L-1 is likely correlated with the Capitanian in West Texas (rather than the Wordian), with the Midian in Transcaucasia, and with the upper Maokouan in South China.

L-2 and L-3 are both dominated by large-tested fusulines, such as *Y. syrtalis*, *Chusenella velebitica*, *E. salopeki*, and *Neoschwagerina* sp., as shown in Table 2 and Figs. 4f and 5e, in accordance with the preliminary report by Kochansky-Devidé (1979). We could not confirm that *N. craticulifera* occurs both in L-2 and L-3. The dominance of well-evolved *Yabeina* suggests that both L-2 and L-3 are also correlated with the Capitanian. After all, it seems likely that the three limestone lenses are all correlated with the Capitanian; therefore, the *Neoschwagerina/Yabeina*

Zone boundary (= Wordian/Capitanian boundary) probably lies in a much lower horizon below L-1. The dolomite between L-1 and L-2, and the one between L-2 and L-3 lack good age indicators.

On the other hand, the top of the Capitanian (or Guadalupian) has not been constrained (Fig. 3), although the overlying Lopingian interval is inferred in the >100 m-thick dolomite above L-3 and below the Triassic rocks. The sole occurrence of *Staffella* sp. from the top dolomite (Table 1) may support this assumption.

It is noteworthy that all the large bivalves (Alatoconchidae) occur in L-1, L-2 and L-3. Sremac (1991) first reported the occurrence of *Tanchintongia* (= *Shikamaia*) *ogulineci* (Kochansky–Devidé), one of the species of Alatoconchidae, from L-1 in this section (Table 1). The present study also confirms the occurrence of juvenile forms of Alatoconchidae gen. et sp. indet. from the upper part of L-1 (Sample K-7). The largest specimen of Alatoconchidae from the Brušane section, ca. 40 cm long, was found in L-2 (K-13; Figs. 4b, c and 6a, c). L-3 only yielded smaller shell fragments (K-21; Fig. 4e) and juvenile forms (K-28; Fig. 4d). Thus in the Brušane section, the stratigraphic range of Alatoconchidae overlaps entirely with that of *Yabeina*.

3.3. Sedimentary facies

We studied 60 thin sections under the microscope to check the sedimentary facies of the Brušane section. Among the various bioclasts, calcareous algae are the most abundant, not only in the three black limestone lenses but also in the less-fossiliferous dolomites in-between. Particularly in the black limestone of L-1, a rich flora composed of 5 genera and 10 species was reported by Kochansky-Devidé (1979) and Sremac (1991). Although we need further detailed analyses of the floral composition of the algae, their ubiquitous occurrence throughout the section clearly indicates that the Velebit Formation as a whole was deposited mostly in a very shallow marine environment of the photic zone on a carbonate platform, as primarily suggested by Kochansky-Devidé (1965) and Flügel (1977). As for the black wackestone/packstone of L-1, L-2 and L-3 (Figs. 4b,c,e,f, 5b,d,e and 6c), abundant reworked bioclasts of various shallow marine biota, including microproblematica *Shamovella* (= *Tubiphytes*) (Sremac, 1991) of probable microbial origin, indicate a subtidal to possibly intertidal regime.

Likewise, the lime mudstone was probably deposited in a lagoonal environment with a very limited influx of fine-grained terrigenous clastics. The good preservation of fossils and trace fossils of mud-feeding organisms supports the predominance of a low-energy environment; however, the occasional development of current ripple cross lamination implies the occasional influx of fine-to coarse-grained bioclastic material by currents into a quiet lime mud lagoon. Wave megaripples and wave ripple cross lamination also suggest reworking of clasts by oscillatory wave action.

The remainder of the Velebit Formation, more than 90%, is composed of apparently massive dolomite. Judging from the remnant algal textures, in particular those of dasycladacean algae like *Mizzia* (Fig. 5a, Table 1), these dolomites were likely derived

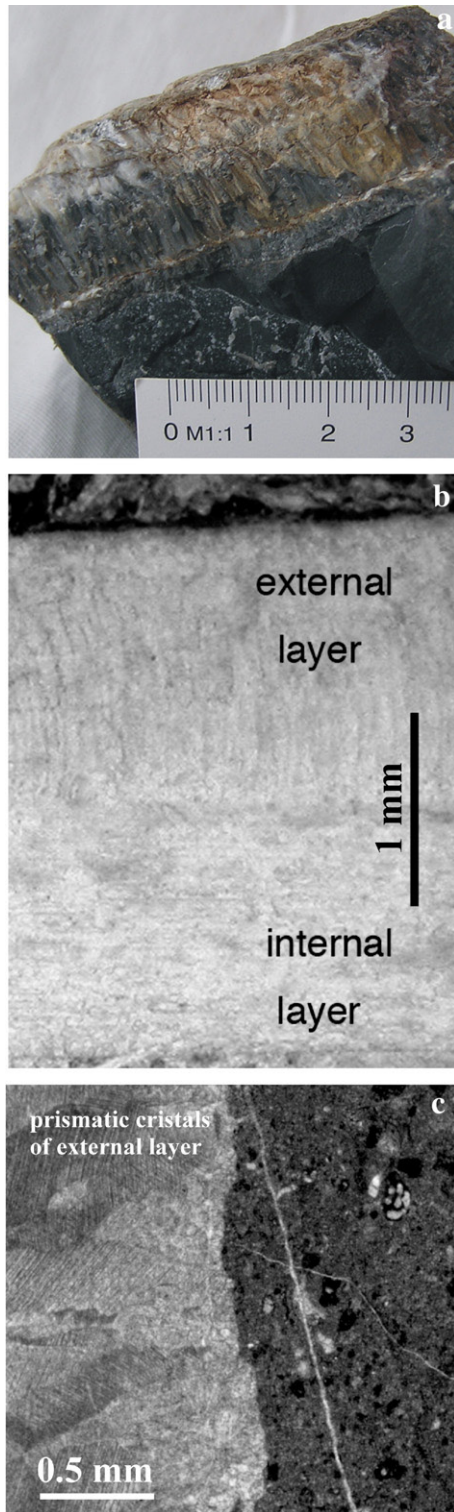


Fig. 6. Photographs of the shell structure in Alatoconchidae from the Brušane section a) the external layer of Alatoconchidae shell characterized by prismatic calcite (enlarged part of the specimen in Fig. 4b; Sample K-13, L-2; b) photomicrograph of a double-layered shell of Alatoconchidae, Sample K-21, L-3; c) photomicrograph of the external layer of the shell in a wackestone under polarized light, Sample K-13, L-2. Note the double-layered shell structure, particularly with a unique external layer composed of prismatic calcite crystals aligned perpendicularly to the shell surface.

primarily from a shallow marine limestone that underwent early diagenesis under possible supratidal conditions, although early diagenetic fabrics may have been overprinted by later diagenesis.

4. Large bivalves

We found Alatoconchidae from L-1, L-2, and L-3 in the Brušane section. In L-1 and L-3, shell fragments of large individuals rarely occur in packstone/wackestone, (Fig. 4e), whereas juvenile forms less than 5 cm long are in lime mudstone (Fig. 4d). L-2 yields many large specimens of Alatoconchidae including the biggest specimen in the studied section, the shell of which is about 40 cm long and 2 cm thick (Fig. 4b,c).

Most of the bivalve shells were broken into smaller fragments and densely lithified together with the matrix, thus free individual specimens are rare. The size of the broken bivalve shells is mostly 5–30 cm long and 0.5–2 cm thick, suggesting an abundance of extraordinarily large individuals. As our observation is limited to sections of shells on surface exposures and those on randomly sliced rock slabs, three-dimensional morphology of the whole bivalve shell is not well documented. No well-preserved hinge/ligament parts of valves or inner shell ornamentation has been recognized. Nonetheless, we can identify these shells as Alatoconchidae, because of their unusually large and thick shells (Fig. 4b) and the prominent U-shaped folds of shells in sections are unique to Alatoconchidae, but quite distinct from other Permian bivalves.

In addition, macroscopic and microscopic observations confirmed that the shells have a unique double-layered structure as illustrated in Fig. 6; the external layer is composed of long, prismatic calcite crystals aligned perpendicular to the shell surface, whereas the internal layer consists of a microgranular mosaic calcite (Fig. 6b). Each prismatic calcite crystal in the external layer generally ranges from 1 to 5 mm in length and 100 to 500 μm in diameter with the longest reaching nearly 10 mm (Fig. 6a). This is another significant feature that supports the identification as Alatoconchidae. In this article, we tentatively describe these bivalves from the Brušane section as Alatoconchidae gen. et sp. indet. More detailed paleontological study is obviously needed, and the results will be reported elsewhere.

Kochansky-Devidé (1978) reported the occurrence of large isolated specimens within the same family with the name of *Tanchintongia ogulineci* Kochansky-Devidé from the *Neoschwagerina* Zone of the Velebit Formation in the neighboring Baške Oštarije area.

The originally-described *Tanchintongia ogulineci* Kochansky-Devidé was later renamed as *Shikamaia ogulineci* (Kochansky-Devidé) according to the taxonomic synonymy pointed out by Boyd and Newell (1979). Accordingly, the specimen of *T. ogulineci*, described from L-1 from the studied section (Sremac, 1991), is here re-assigned in the genus *Shikamaia* (Table 1). It is noteworthy that alatoconchids from the *Neoschwagerina* Zone (Kochansky-Devidé, 1978) are much larger (over 40 cm in length) than those from the *Yabeina* Zone, as this tendency in size change may represent a general polarity in the unique bivalve evolution (Isozaki and Aljinović, in press).

5. Discussion

5.1. Range of Alatoconchidae

The present results prove for the first time that the stratigraphic range of the family Alatoconchidae extends up to the Capitanian, Late Guadalupian, and not only in the Velebit Mountains in Croatia but also in southeastern Europe representing the western Tethyan domain (Fig. 1c). Previous studies in the Velebit Mountains (Kochansky-Devidé, 1978; Kochansky-Devidé and Ramovš, 1987) recognized the occurrence of *S. ogulineci* (Kochansky-Devidé) from the middle limestone of the Wordian *N. craticulifera* Zone.

An occurrence of *S. ogulineci* (Kochansky-Devidé) was also reported from a Saikra bioherm complex at Djebel Tebaga in Tunisia that also belongs to the *Neoschwagerina* Zone. This marks the highest horizon ever reported from western Tethys including both Croatia and Tunisia, as there has been no report from the well-defined Capitanian *Yabeina* Zone.

According to paleogeographic reconstructions (Scotese and Lanford, 1995; Vai et al., 2000; Kiessling et al., 2003; Gaetani et al., 2003), the Permian carbonates in the Velebit Mountains and Djebel Tebaga in Tunisia belong to the same carbonate platform

in a broad sense at the western end of equatorial Tethyan realm (Fig. 1c). Thus in the *Cul-de-Sac* of the western Tethys, the large aberrant bivalve family likely thrived in shallow carbonate platforms throughout the Middle Permian, i.e., commonly in the Wordian, and up to Capitanian (Fig. 7). The same range for Alatoconchidae up to the *Lepidolina* Zone of Capitanian was recently confirmed in Japan (Isozaki, 2006). As the Japanese sections originated primarily from the mid-Panthalassan domain, their occurrence in both Croatia and Japan indicates that the Alatoconchidae survived up to the Capitanian in both Tethys and Panthalassa.

In contrast, no Alatoconchidae have been reported to date from the Lopingian. On the basis of all the previous and current data, the aberrant bivalve family Alatoconchidae likely became extinct at the end of the Guadalupian, in other words at the Guadalupian–Lopingian boundary extinction event (Jin et al., 1994; Stanley and Yang, 1994; Isozaki, 2007), simultaneously in Tethys and Panthalassa almost on the opposite sides of the globe.

5.2. Paleogeographic distribution of Alatoconchidae

The ecology and taxonomy of bivalves have been investigated in several studies (e.g., Kondo et al., 2006). The occurrence of Alatoconchidae is highly limited to low-latitude areas. As summarized by Isozaki (2006) and Isozaki and Aljinović (in press), the occurrence of Alatoconchidae has been hitherto reported from 9 areas in the world, i.e., Tunisia (Boyd and Newell, 1979), Croatia (Kochansky-Devidé, 1978; Kochansky-Devidé and Ramovš, 1987; and this report), Oman (Pillecut, 1993), Iran (Thiele and Ticky, 1980), Afghanistan (Termier et al., 1973), Malaysia (Runnegar and Gobbett, 1975), Thailand (Udchachon et al., 2006), the Philippines (Kiessling and Flügel, 2000), and Japan (Ozaki, 1968; Yancey and Ozaki, 1986; Isozaki, 2006). The first three areas belong to the peri-Gondwanan carbonate platform, whereas the 4 examples from the Middle East and South Asia are from the Cimmerian landmasses, which rifted from the northern margin of Gondwana and migrated northward to the equatorial zone (Fig. 1c). On the other hand, the last two examples were from accreted paleo-atoll complexes that primarily originated in the middle of Panthalassa (Isozaki et al., 1987; Isozaki, 2006; Isozaki and Aljinović, in press). Therefore, regardless of their tectonic setting and/or facing oceans, all the Alatoconchidae-bearing rocks were deposited in low-latitude, tropical to subtropical domains of Tethys and Panthalassa.

The concentrated occurrence of Alatoconchidae in low-latitude areas appears concordant with their closely associated fossil assemblage composed of abundant large-tested fusulines (Verbeekiniidae, Schwageriniidae) and rugose corals (*Waagenophyllum*) that represent the typical Tethyan fauna well adapted to warm-water environments (Yancey and Boyd, 1983; Isozaki, 2006). The reason why Alatoconchidae is absent in the western Pangean margin (e.g., West Texas) remains enigmatic; however, this may have resulted from sampling bias or from local environmental factors.

Nonetheless it is noteworthy that the aberrant bivalve family Alatoconchidae became extinct at the end of the Guadalupian almost simultaneously in both western Tethys and Panthalassa

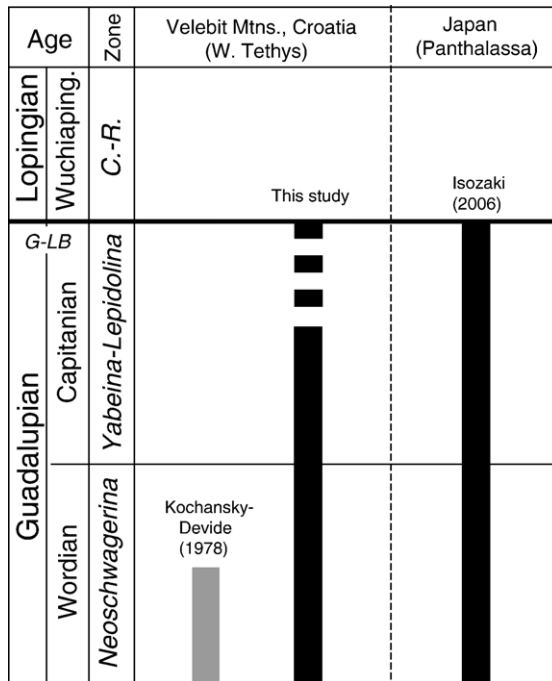


Fig. 7. Schematic range chart showing the upper limit of Alatoconchidae in the Velebit Formation in Croatia and in the mid-Panthalassan limestone in Japan. Not to scale. Keys: G–LB: Guadalupian–Lopingian boundary, C–R: *Codonofusiella–Reichelina*. The topmost horizon of the occurrence of Alatoconchidae was confirmed in the Capitanian (Upper Guadalupian) in this study. Despite the geographical separation between Croatian (western Tethys) and Japanese (mid-Panthalassa) sections, this aberrant bivalve group became extinct almost at the same time at the end of Capitanian, together with large-tested Verbeekiniidae (fusuline) and Waagenophyllidae (rugose coral). The extinction of “the tropical trio” may have been driven by the Kamura cooling event (Isozaki et al., 2007a,b) immediately before the Guadalupian–Lopingian boundary.

(Fig. 7). Their probable extinction at the end of the Guadalupian, together with the extinction of large-tested fusulines and most rugose corals, suggests that unfavorable environmental conditions may have appeared in the Late Guadalupian on a global scale and terminated long-lasting, warm-water-adapted fauna in low-latitude areas that Isozaki (2006) called the “tropical trio”.

The appearance of a cool interval in the Capitanian (Kamura event) in the tropical zone was recently proposed by Isozaki et al. (2007a,b) on the basis of stable carbon isotope chemostratigraphy. Similarly, cooling in the Middle–Late Permian was also suggested in concurrent high latitude domains (Beauchamp and Baud, 2002). In general, cooling is critical to the survival of most tropical biota that are too well adapted to a warm climate. With respect to the extinction pattern of Alatoconchidae, a possible kill mechanism and relevant environmental change is discussed elsewhere (Isozaki and Aljinović, in press).

6. Conclusions

The occurrence of the Permian large bivalve family Alatoconchidae from the Capitanian (Upper Guadalupian) *Ya-beina* Zone is confirmed for the first time in Europe, (i.e., at the western end of Paleo-Tethys). This aberrant bivalve family became dominant and attained an extraordinarily large size during the Middle Guadalupian in low-latitude areas in both Tethys and Panthalassa. In turn, they became extinct at the end of the Guadalupian together with large-tested fusulines (Verbeekiniidae and Schwageriniidae) and a large variety of rugose corals (Waagenophyllidae). A possible kill mechanism for “the tropical trio” may have been the Capitanian cooling (Kamura event) in the tropics; however, further study is needed, particularly from the viewpoint of physiology of the tropical trio in an oligotrophic condition in low-latitude carbonate platforms.

Acknowledgments

Adam Woods, Hiroyoshi Sano, an anonymous reviewer, and M. Santosh provided valuable comments on the manuscript. Hisayoshi Igo identified fusulines from the studied area and gave instructive suggestions. Corrado Venturini introduced us to the latest information on paleogeography of western Tethys. Brian Windley corrected the English. This research was supported by the Croatian Ministry of Science, Education and Sport (no. 195-1953068-2704 and 119-1951293-1162) and a Grant-in-Aid of the Japan Society of Promoting Science (no. 16204040).

References

- Aljinović, D., 1997. The Upper Palaeozoic (Permian) and Lower Triassic Sedimentary Facies in Gorski Kotar Region. PhD Thesis. University of Zagreb, Faculty of Mining, Geology and Petroleum Engineering, Zagreb, 146 pp. (in Croatian with English summary).
- Aljinović, D., Sremac, J., Ibrahimpašić, H., 2003. Permian and Lower Triassic facies of Velebit Mt. and the Gorski Kotar region (NW part of External Dinarides). In: Vlahović, I., Tišljarić, J. (Eds.), Evolution of Depositional Environments from the Palaeozoic to the Quaternary in the Karst Dinarides and the Pannonian Basin. Field Trip Guidebook of the 22nd Int. Assoc. Sedimentology Meeting (Opatija), pp. 183–206.
- Aljinović, D., Kolar-Jurkovšek, T., Jurkovšek, B., 2006. The Lower Triassic Shallow Marine Succession in Gorski Kotar Region (External Dinarides, Croatia): lithofacies and conodont dating. Riv. Ital. Paleontol. Stratigr. 112, 35–53.
- Balini, M., Jurkovšek, B., Kolar-Jurkovšek, T., 2006. New Ladinian ammonoids from Mt. Svilaja (External Dinarides, Croatia). Riv. Ital. Paleontol. Stratigr. 112, 383–395.
- Beauchamp, B., Baud, A., 2002. Growth and demise of Permian biogenic chert along northwest Pangea: evidence for end-Permian collapse of thermohaline circulation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 187, 37–63.
- Boyd, D.W., Newell, N.D., 1979. Permian pelecypods from Tunisia. Am. Mus. Novit. 2686, 22 pp.
- Flügel, E., 1977. Environmental models for Upper Paleozoic benthic calcareous algal communities. In: Flügel, E. (Ed.), Fossil Algae. Springer, Berlin, pp. 314–343.
- Gaetani, M., Dercourt, J., Vrielynck, B., 2003. The Peri-Tethys programme: achievements and results. Episodes 26, 79–93.
- Isozaki, Y., 2006. Guadalupian (Middle Permian) giant bivalve Alatoconchidae from a mid-Panthalassa paleo-atoll complex in Kyushu, Japan: a unique community associated with Tethyan fusulines and corals. Proc. Jpn. Acad. 82B, 25–32.
- Isozaki, Y., 2007. Guadalupian–Lopingian boundary event in mid-Panthalassa: Correlation of accreted deep-sea chert and mid-oceanic atoll carbonate. In: Wong, T.E. (Ed.), Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy 2003, Royal Dutch Acad. Art. Sci., Amsterdam, pp. 111–124.
- Isozaki, Y., Aljinović, D., in press. End-Guadalupian extinction of the Permian gigantic bivalve Alatoconchidae: End of gigantism in tropical seas by cooling. Palaeogeogr. Palaeoclimatol. Palaeoecol.
- Isozaki, Y., Amischaray, E.A., Rillon, A., 1987. Permian, Triassic and Jurassic bedded radiolarian cherts in North Palawan Block, Philippines: Evidence of Late Mesozoic subduction–accretion. J. Geol. Soc. Philipp. 41, 79–93.
- Isozaki, Y., Kawahata, H., Ota, A., 2007a. A unique carbon isotope record across the Guadalupian–Lopingian (Middle–Upper Permian) boundary in mid-oceanic paleoatoll carbonates: the high-productivity “Kamura event” and its collapse in Panthalassa. Glob. Planet. Change 55, 21–38.
- Isozaki, Y., Kawahata, H., Minoshima, K., 2007b. The Capitanian (Permian) Kamura Cooling Event: the beginning of the Paleozoic–Mesozoic transition. Palaeoworld 16, 16–30.
- Jin, Y.G., Zhang, J., Shang, Q.H., 1994. Two phases of the end-Permian mass extinction. In: Embry, A.F., Beauchamp, B., Glass, D.J. (Eds.), Pangea: Global Environments and Resources. Mem. Canad. Soc. Petrol. Geol., vol. 17, pp. 813–822.
- Kiessling, W., Flügel, E., 2000. Late Paleozoic and Late Triassic limestones from North Palawan block (Philippines): microfacies and paleogeographical implications. Facies 43, 6–16.
- Kiessling, W., Flügel, E., Golonka, J., 2003. Patterns of Phanerozoic carbonate platform sedimentation. Lethaia 36, 195–226.
- Kochansky-Devidé, V., 1965. Die fusuliniden Foraminiferen aus dem Karbon und Perm in Velebit und in der Lika (Kroatien) Mittleres und Oberes Perm. Acta Geol. 5 (Bull. Sci. Yugosl., 35), 101–148, (in Croatian with German abstract).
- Kochansky-Devidé, V., 1978. *Tanchintongia* — eine aberrante permische Bivalve in Europa. Paleontol. Z. 52, 213–218.
- Kochansky-Devidé, V., 1979. Excursion D, Brušane, Velebit Mt. — Permian. 16th European Micropaleontological Colloquium (Ljubljana), pp. 163–170.
- Kochansky-Devidé, V., 1982. Gornji paleozoik Velebita. In: Sremac, J. (Ed.), IGCP Project No. 5, Yugoslav working group field meeting, Field guide to Velebit Mt., pp. 8–16 (in Croatian with English summary).
- Kochansky-Devidé, V., Ramovš, A., 1987. Distribution of the Bivalve *Tanchintongia ogulincei* in Velebit. Geologija 28/29, 151–155 (in Slovenian with English summary).
- Kondo, Y., Kozai, T., Kikuchi, N., Sugawara, K., 2006. Ecologic and taxonomic diversification in the Mesozoic brackish-water bivalve faunas in Japan, with emphasis on infaunalization of heterodonts. Gondwana Res. 10, 316–327.
- Ota, A., Isozaki, Y., 2006. Fusuline biotic turnover across the Guadalupian–Lopingian (Middle–Upper Permian) boundary in mid-oceanic carbonate buildups: Biostratigraphy of accreted limestone in Japan. J. Asian Earth Sci. 26, 353–368.

- Ozaki, K., 1968. Problematical fossils from the Permian limestone of Akasaka, Gifu prefecture. Yokohama National Univ. Sci. Rep. (sect. 2) Biol. Geol. Sci. vol. 14, 27–33.
- Ozawa, T., Nishiwaki, N., 1992. Permian Tethyan biota and sedimentary facies of the Akasaka Limestone Group. Field Trip Guidebook B13 of International Geological Congress (Kyoto), pp. 189–195.
- Pillevert, A., 1993. Les bloc exotiques du Sultanat d'Oman. Evolution paleogeographique d'une marge massive flexurale. Mem. Geol. Lausanne 17, 249 pp.
- Runnegar, B., Gobbett, D., 1975. *Tanchintongia* gen. nov., a bizarre Permian myalinid bivalve from West Malaysia and Japan. Palaeontology 18, 315–322.
- Salopek, 1942. Upper Palaeozoic of Velebit near Brušane and Baške Oštarija (O gornjem paleozoiku Velebita u okolini Brušana i Baških Oštarija). Hrvat. Akad. Znan. Umjet. 274, 218–282 (in Croatian).
- Scotese, Lanford, 1995. Pangea and the paleogeography of the Permian. In: Scholle, P.A., Peryt, T.M., Ulmer-Scholle, D.S. (Eds.), The Permian of Northern Pangea. Paleogeography, Paleoclimates, Stratigraphy, vol. 1. Springer-Verlag, Berlin-Heidelberg, pp. 3–19.
- Sremac, J., 1991. Zone *Neoschwagerina craticulifera* in the Middle Velebit Mt. (Croatia, Yugoslavia). Geologija 34, 7–55.
- Sremac, J., 2005. Equatorial shelf of the Paleozoic Supercontinent — Cradle of the Adriatic Carbonate Platform. Geol. Croat. 58, 1–20.
- Sokač, B., Ščavničar, B., Velić, I., 1976. Explanation of sheet Gospić. Basic Geological Map of SFR Yugoslavia 1: 100 000, Savezni geološki zavod, Beograd, (in Croatian with English abstract).
- Stanley, S., Yang, 1994. A double mass extinction at the end of the Paleozoic era. Science 266, 1340–1344.
- Termier, H., Termier, G., De Lapparent, A.F., 1973. Grands bivalves recifaux du Permien superieur de l'Afghanistan central. Ann. Soc. Geol. Nord 93, 75–80.
- Thiele, O., Ticky, G., 1980. Über das Auftreten von *Tanchintongia* (Bivalvia) im Perm des Iran. Karinthin 82, 166–173.
- Toriyama, R., 1967. Fusulinacean zones of Japan. Mem. Fac. Sci., Kyushu Univ., Ser. D Biol. 18, 35–260.
- Udchachon, M., Chonglakmani, C., Campbell, H., 2006. Paleocology of the Permian Alatoconchidae bivalves from north-central Thailand. Abst. 2nd International Palaeontological Congress (Beijing), p. 215.
- Vai, G.B., Izart, A., Broutin, J., Chuvashov, B.I., Vaslet, D., 2000. Artinskian palaeogeographical map (scale 1:10.000.000). In: J. Dercourt, M. Gaetani et al. (Eds). Peri-Tethys Atlas and explanatory notes, map 2, 11–18, CCGM/CGMW, Paris.
- Vlahović, I., Tišljarić, J., Velić, I., Matičec, D., 2005. Evolution of the Adriatic Carbonate Platform: Palaeogeography, main events and depositional dynamics. Palaeogeogr. Palaeoclim. Palaeoecol. 220, 333–360.
- Yancey, T.E., Boyd, D.W., 1983. Revision of the Alatoconchidae: a remarkable family of Permian bivalve. Palaeontology 26, 497–520.
- Yancey, T.E., Ozaki, K., 1986. Redescription of the genus *Shikamaia* and clarification of the hinge characters of the family Alatoconchidae (bivalvia). J. Paleontol. 60, 116–125.
- Zaw Win, C., 1999. Fusuline biostratigraphy and palaeontology of the Akasaka Limestone, Gifu Prefecture, Japan. Bull. Kitakyushu Mus. Nat. Hist. 18, 1–76.