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THE RUDISTS OF SOUTHERN ISTRIA - AN EXAMPLE OF ENVIRONMENTALLY INDUCED SUCCESSION WITHIN SANTONIAN LIMESTONES

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Riassunto. Le rudiste sono bivalvi comuni alla piattaforme carbonatiche nel Cretaceo del Dominio tetideo. Il succedersi di due associazioni a rudiste lungo due sezioni stratigrafiche misurate nel Cretaceo Superiore di Capo Merlera (porzione meridionale della penisola Istriana) viene interpretato come controllato da fattori ambientali.

La prima successione inizia con calcari pelagici, si sviluppa con una associazione mista a radiolitidi e hippuritidi, per concludersi con biostrome a floatstone monogenerici a radiolitidi. I calcari pelagici della parte inferiore rappresentano condizioni marine relativamente aperte, mentre l'unità a radiolitidi sommitale viene interpretata come originata in condizioni marine più confinate.

La seconda successione inizia invece con floatstone a radiolitidi contenenti rari bouquets di *Gorjanovicia*. Verso l'alto, l'associazione a radiolitidi viene sostituita da una associazione mista a radiolitidi e hippuritidi in cui sono caratteristici floatstone a radiolitidi, ma con grandi esemplari di *Vaccinites*.

Per entrambe le sezioni, si ritiene che la causa più importante nella sostituzione delle associazioni sia la variazione eustatica. Le minori differenze che si osservano tra le due successioni possono venir attribuite ad un rilievo sottomarino più accentuato. Radiolitidi ed hippurutidi avrebbero occupato biotopi diversi nell'ambito degli ambienti subtidali della piattaforma carbonatica Adriatica. Gli hippuritidi avrebbero preferito ambienti subtidali più stabili e più profondi. Per contro, i radiolitidi avrebbero preferito le parti meno profonde dell'ambiente subtidale.

In conclusione, questi due maggiori gruppi di rudiste possono venir usati per identificare diverse condizioni paleoecologiche.

Abstract. Rudist bivalves thrived commonly in the shallow carbonate platforms of the Cretaceous Tethyan realm. The presence of two vertically separated Rudist assemblages along two well-preserved Upper Cretaceous sections of cape Mrlera (southern part of the Istrian peninsula) is interpreted as environmentally induced faunal replacement.

The first succession begins with pelagic limestones, followed by a mixed radiolitid-hippuritid assemblage, and by monogeneric floatstones-biostromes of radiolitids. The lower pelagic unit represents relatively open marine conditions while the uppermost radiolitid unit originated under more restricted marine conditions.

Radiolitid floatstones with rare *Gorjanovicia* bouquets represent the beginning of the second succession. A mixed radiolitid-hippuritid assemblage, characterised by radiolitid floatstones where rare large *Vaccinites* individuals occur, replaces the Radiolitid assemblages in vertical succession.

In both sections, sea level changes were the most important factor causing the replacement of rudist assemblages. Slight differences between the two successions could be attributed to differences in submarine topography. Radiolitids and hippuritids might have occupied different biotopes within subtidal environments of the Adriatic carbonate platform. Hippuritids preferred more stable and deeper subtidal environments. By contrast, radiolitids preferred the shallowest parts of subtidal areas.

Therefore, these two major rudist groups may be used for determination of different paleoecological conditions.

Introduction.

During the Upper Cretaceous rudist bivalves thrived in shallow carbonate platforms of the Tethyan realm (Polšak, 1965, 1967a; Philip, 1980, 1985; Masse & Philip, 1981; Ross & Skelton, 1993; Gili et al., 1995a). Rudist assemblages became established in environments ranging from carbonate complexes of the open sea margin, to isolated build-ups, open to inner shelf, and platform biostromes (Philip, 1972; Philip et al., 1978; Masse & Philip, 1981; Ross & Skelton, 1993; Simo et al., 1993). The successive vertical replacement of different rudist morphotypes in the development of rudist-bearing formations has been attributed to ecological succession (Kaufman & Sohl, 1974; Camoin et al., 1988). However, documentation alone of a predictable succession of different faunal assemblages is not sufficient evidence for ecological succession (Gili et al., 1995b). A helpful tool to more precisely determine the change in rudist succession is to analyze the intrinsic factors of depositional environments in which rudist communities thrived (Collins, 1988; Ross & Skelton, 1993). According to Gili et al. (1995b) it is possible to presume that two determining factors can cause vertical faunal change: (1) change in local environment caused largely by internal biotic factors (yielding ecologic succession) and (2) change in the environment caused by external physical

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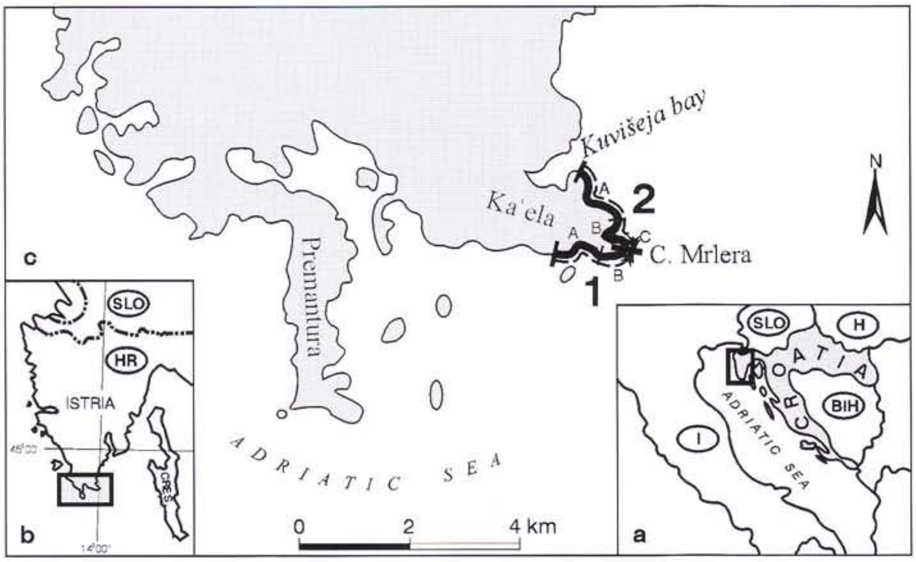


Fig. 1 - (a) Location of the study area. (b) Map of Istria with location of study area. (c) Geographic map of the study area with location of logged sections. 1 - The Kazela section (Units A and B). 2 - The Kuvišeja section (Units A, B and C). Arrows indicate direction of successions studied.

factors (yielding sedimentary succession). Classic ecologic succession requires that each community, or serial stage, has modified the local physical environment in such a way as to allow the establishment and/or maturation of several succeeding stages (Gili et al., 1995b). An example of that kind of succession is given by Kauffman & Sohl (1974) for the development of rudist reefs. A sedimentary succession, by contrast, is induced essentially by a change in physical environmental factors with no necessary biotic influence, as Gili et al. (1995b) showed for coral to rudist succession. In both cases there is an environmental change, although ecologic and sedimentary succession are still connected with different causative factors (Gili et al., 1995b). By recognizing this distinction it is possible to understand the evolution of the northern part (Fig. 1) of the Upper Cretaceous Adriatic carbonate platform and the nature of the environmental changes in this part of the Late Cretaceous Tethyan Ocean.

It is possible to presume that rudist assemblage successions were often controlled only by changes in environmental conditions forced by external factors. The description of sedimentary successions with rudists as exclusive representatives of the macrofauna, within pure carbonate sedimentation, is the main objective of this paper. Our examples are drawn from Santonian rudist formations of cape Mrlera in the southern part of the Istrian peninsula (Fig. 1). This locality offers an excellent opportunity to recognize possible environmental controls on the vertical and lateral distribution of rudists.

Geologic setting of sections.

The succession of the Kazela and Kuvišeja sections (Fig. 1) has been described by Polšak (1965, 1967a, b, 1970), Tišljar (1976) and Moro (1997a, b). The southern part of the Istrian peninsula exposes autochthonous Upper Cretaceous rocks (Maticec et al., 1996), comprising pure carbonate platform sediments without terrigenous influence. Continuous sedimentation characterized the southern Istria from the Albian to the Upper Santonian (Polšak, 1965; Velic et al., 1995; Moro, 1997a). Beds are generally oriented NE-NNE (the Kazela section) and SW-SSW (the Kuvišeja section) with dipping approximately 10-20° (Polšak, 1967b, 1970). No major tectonic influence was recorded (Polšak 1967b, 1970), which is supported by the normal succession of the fossil assemblage for both sections (Polšak, 1965, 1967a). Biostratigraphically, the most important forms among benthic foraminifers are *Pseudocyclammina sphaeroidea* Gendrot, *Moncharmontia apenninica* (De Castro), *Scandonea samnitica* De Castro and *Cuneolina* sp. In addition, sediments contain the algae *Aeolisaccus kotori* Radoicic and *Thaumatoporella parvovesiculifera* (Raineri). The listed microfossil assemblage correlates well with Fleury's CsB3 zone with *P. sphaeroidea* (Fleury, 1980) and corresponds chronostratigraphically to the Middle Turonian-Early Santonian time span. While benthic foraminifers suggest Fleury's (1980) zone CsB3 and the Middle Turonian-Early Santonian time interval, sequence stratigraphy data, together with numerous *Vaccinites* individuals, indicate that the sections investigated are probably Santonian in age (Moro, 1997a).

The depositional environment is described as shelf (Moro, 1997a, b), according to sedimentologic characteristics (Tucker & Wright, 1990), physiography of rudist formations (Ross & Skelton, 1993) and nearness to an emerged part of the platform (Island of Cres) where interruption in sedimentation occurred in the late Cenomanian-early Turonian (Mamuzic et al., 1982; Cosovic et al., 1994).

The coeval Upper Cretaceous limestones of both sections (Polšak, 1965, 1967a, b, 1970; Maticec et al., 1996; Moro, 1997a, b) are transgressively and discon-

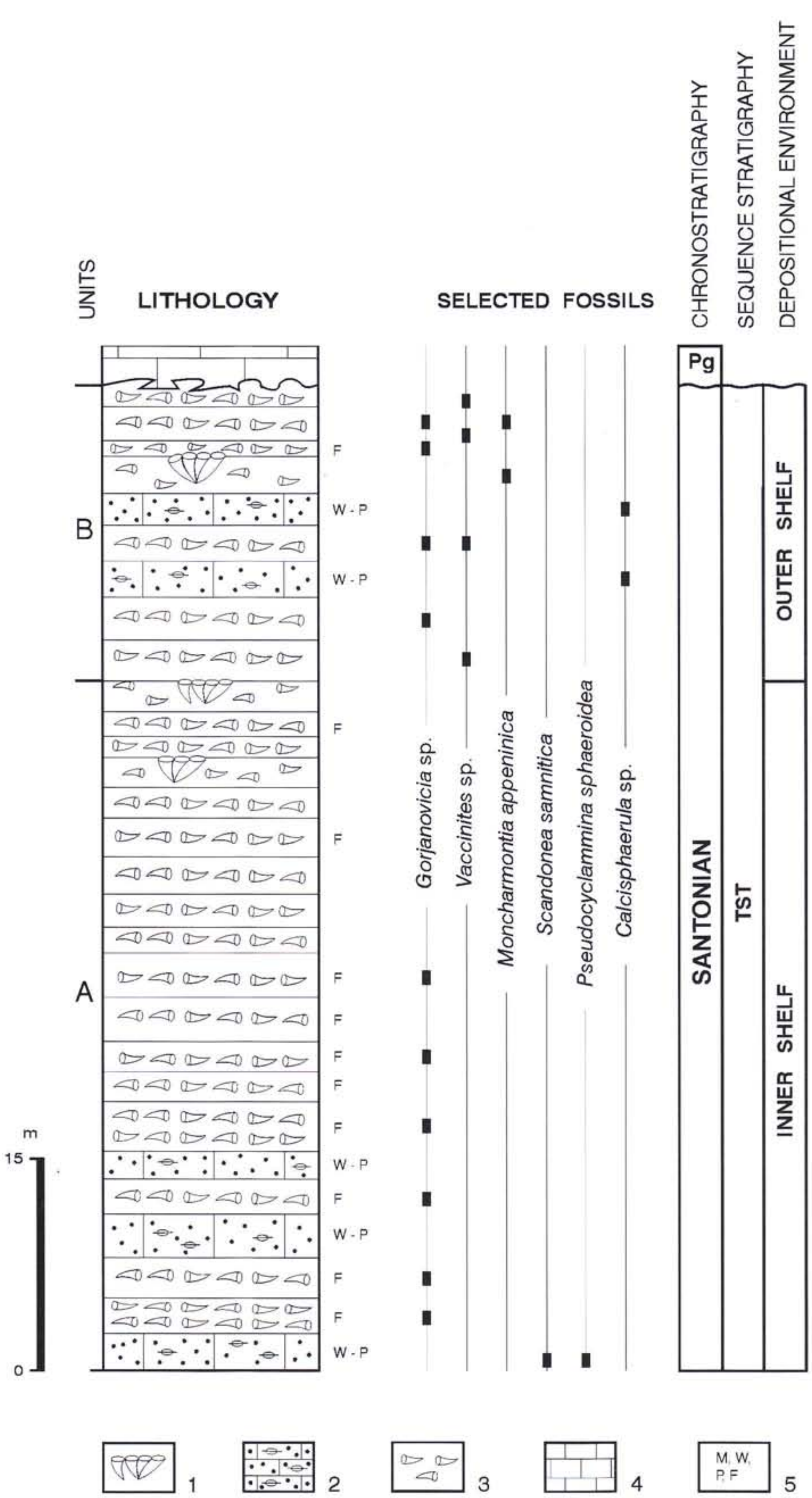


Fig. 2 - Simplified stratigraphic log of the Santonian limestones in the Kazela section. Thicknesses of the beds are shown schematically (not to scale). 1 - rudist bouquets, 2 - foraminiferal-peloidal wackestone-packstones, 3 - rudist floatstones, 4 - Paleogene limestones, 5 - M - mudstone, W - wackestone, P - packstone, F- floatstone.

formably overlain by the same Palaeogene layer (D'Ambrosi, 1940; Cosovic et al., 1994).

Semi-quantitative method estimating the proportion (Flügel, 1982) of selected fossils (Thaumatoporeliids, Bacinellas) was performed on a randomly selected area of 1 cm^2 for each thin-section. The frequency distribution of selected fossil groups was obtained throughout the sections studied.

Radiolitid-dominated to radiolitid-*Vaccinites*-dominated assemblage succession.

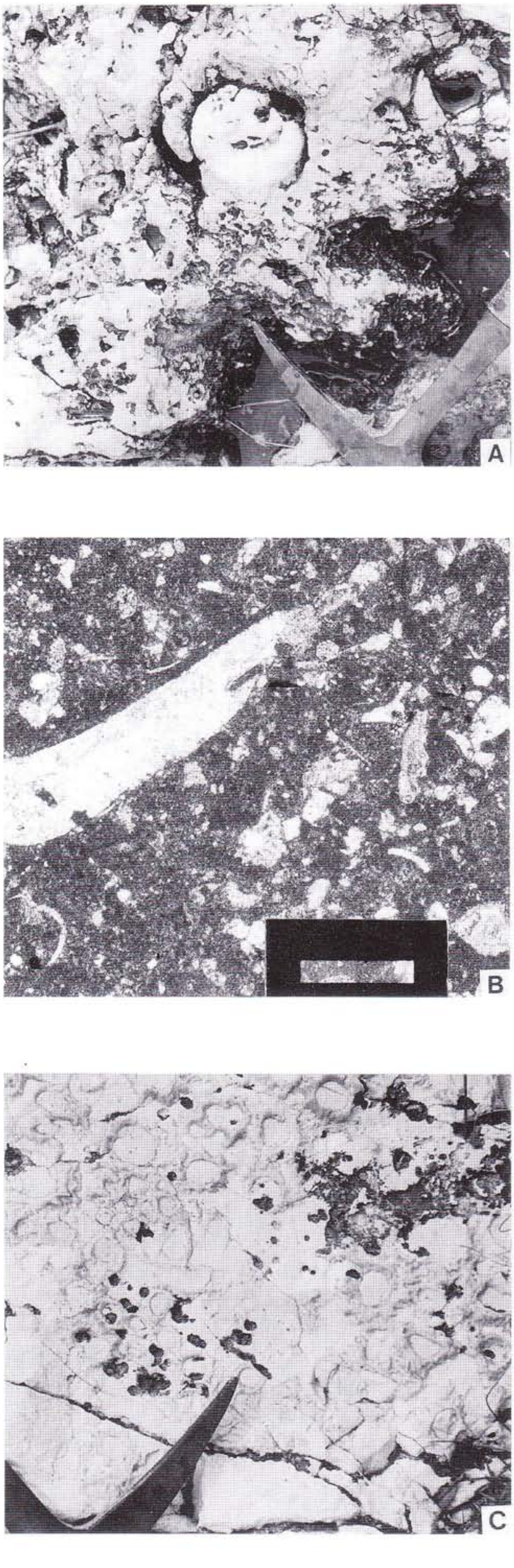
The first example of what we interpret as an environmentally induced succession is the Kazela section (Fig. 2), which comprises two units (from bottom to top): (Unit A) radiolitid floatstones and rare bouquets, and (Unit B) radiolitid floatstones with rare *Vaccinites*.

The succession begins with an exclusively radiolitid-dominated assemblage, followed by an association where radiolitids are abundant while rare *Vaccinites* occur too.

Description.

The total thickness of the Kazela section is 71 m. Beds are 30-70 cm thick, and are characterized by abundant radiolitids. Pelagic wackestones and rare hippuritids occur towards the top of the section (Fig. 2).

The 49 m thick vertical succession of Unit A shows peloidal wackestone-packstones with porcelaneous foraminifers in alternation with several rudist floatstones and few bouquets. As morphotypes, rudists are elevators (Skelton & Gili, 1991) and gregarious sediment-dwellers (Gili et al., 1995a), which achieved stabilization by implantation in



the sediment. The most common (or abundant) specimens belong to the genus *Gorjanovicia* whose height and outer commissural diameter range between 4 and 10 cm and 1 and 2.2 cm, respectively. The cylindrical *Gorjanovicia* specimens form "bouquets" locally (Philip, 1972; Moro, 1997a) (Fig. 3C). The peloidal wackestones-packstones contain a micrite matrix (often recrystallized into microsparite) with fine skeletal debris. The bioclastic wackestone-packstone is characterized by the presence of *Thaumatoporella parvovesiculifera* (Raineri) (up to 20% of the total biotic components). *Bacinellas* are less common (up to 2.5% of the total biota). Rare benthic foraminifers, *Scandonea samnitica* De Castro (Fig. 4A), *Pseudocyclammina sphaeroidea* Gendrot (Fig. 4C) and miliolids are scattered throughout the matrix. The peloidal nature of the sediments, the sparse foraminifers, the lack of abrasion of the bioclasts, the lime mud matrix and no orientation of the rudists indicate that Unit A was deposited under no water current energy conditions. Transition into Unit B is marked by the first appearance of hippuritids (*Vaccinites*).

Unit B is up to 21 m thick. It is composed of 30-70 cm thick-bedded peloidal-foraminiferal wackestone-packstones in alternation with floatstones (Fig. 3B). The most common rudists belong to the genus *Gorjanovicia*. Wackestones with *Calcisphaerulidae* (100-125 µm diameter, Fig. 4B) and pithonellas represent elements of an open marine influence. They occur in alternation with floatstones and wackestone-packstones towards the top of the unit. In the uppermost part of the section, in radiolitids floatstones, large solitary *Vaccinites* (Fig. 3A) are the most common macrofossils. The right valves of the rudists show no preferred orientation, suggesting the absence of any water current energy trend. Biotic components in the recrystallized microsparite matrix of the peloidal-foraminiferal wackestone-packstone are benthic foraminifers *Moncharmontia apenninica* (De Castro) and miliolids. Individuals of *Thaumatoporella parvovesiculifera* (Raineri) are less common than in sediments attributed to Unit A (always less than 5% of the total biota compared to 20% in Unit A).

Interpretation.

We interpret the transition from radiolitid-dominated to radiolitid-*Vaccinites* dominated assemblage succession to have developed as a consequence of the car-

Fig. 3 - The Kazela section. A - Limestone bed, in the upper part of the section (Unit B), with rare Vaccinites (*V. inaequicostatus* (Münster, 1840)). B - Rudist floatstones in the upper part of the section (Unit B). Scale bar 0.8 mm. C - Upper surface of the layer showing *Gorjanovicia* bouquet (Unit B).

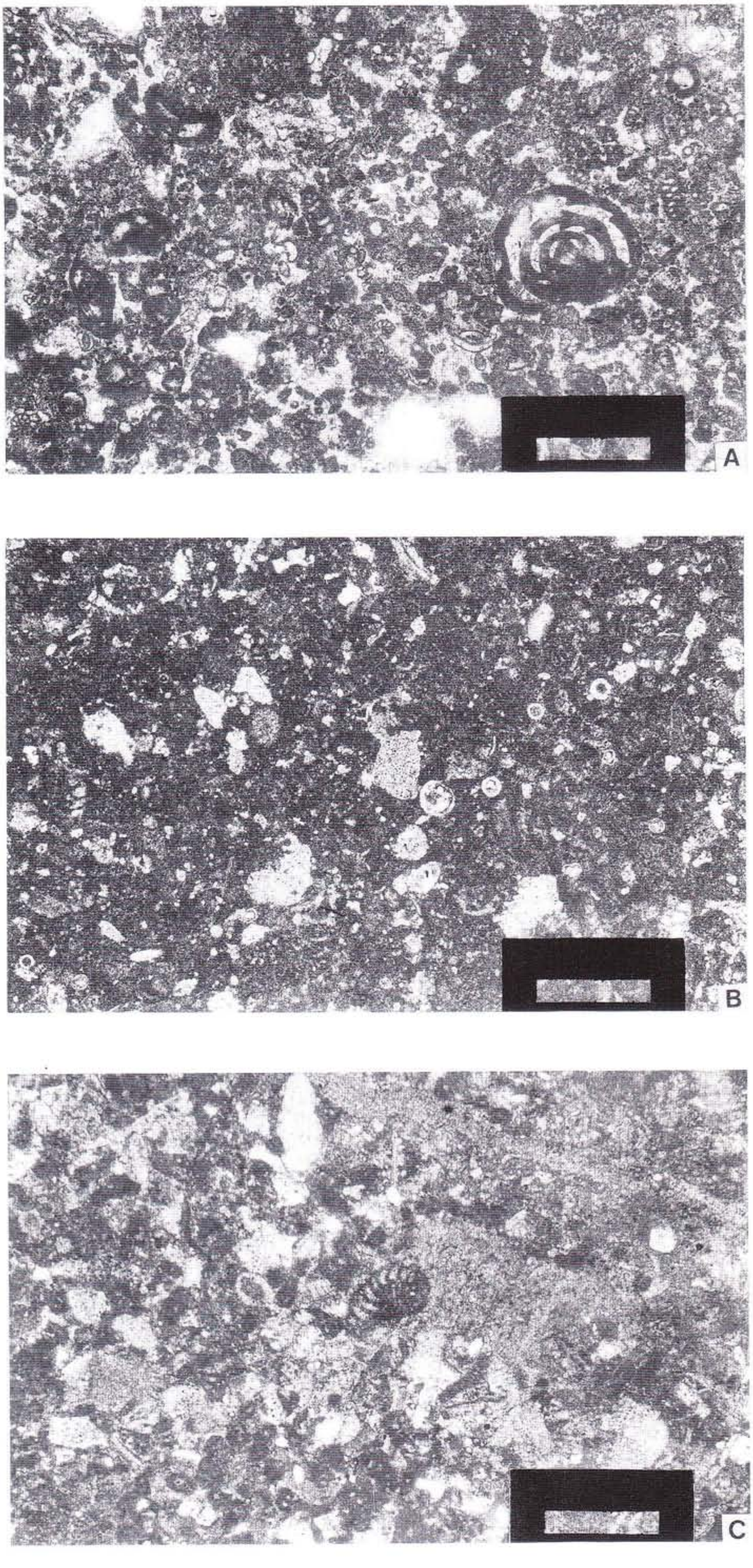


Fig. 4 - The Kazela section. A - *Scandonea samnitica* (De Castro). Unit A. Scale bar 0.8 mm. B - Pelagic wackestone with *Calcisphaerulidae*. Unit B. Scale bar 0.8 mm. C - *Pseudocyclammina sphaeroidea* Gendrot. Unit A. Scale bar 0.8 mm.

bonate platform drowning or opening. The drowning was caused by a relative sea level rise (Moro, 1997a). Paleontological evidence (i.e. composition and characteristics of rudists and benthic foraminifers associations) indicates that the lower part of the section was deposited under conditions appropriate for monogeneric radiolitid growth. The common development of radiolitid-dominated congregations in shallow, quiet water conditions of the carbonate shelves was emphasized recently by Ross & Skelton (1993).

The change from radiolitid dominated to radiolitid-*Vaccinites* dominated assemblage represents a change from a relatively shallow environment where such monogeneric elevator congregations survived, to a relatively deep and more open environment with pelagic influences, which allowed the appearance of large solitary elevators, i.e. *Vaccinites*, within radiolitid floatstones.

The paleoenvironmental interpretation of this vertical faunal change suggests that it resulted from a deepening of the depositional setting, caused primarily by a relative sea level change. Further evidence indicating that the change of rudist assemblages was triggered by variations in the sedimentary biotopes is provided by the presence of *Calcisphaerulidae* in the mixed radiolitid-*Vaccinites* floatstones.

Pelagic to radiolitid-*Vaccinites*-dominated, and radiolitid-dominated assemblage succession

The Kuvišeja section (Fig. 5) contains a rich rudist community, which consists of three distinct units (from bottom to top): (Unit A) pelagic limestones, (Unit B) radiolitid-*Vaccinites* floatstones and (Unit C) radiolitid thickets and floatstones.

Description.

The lowest unit (Unit A) of the succession is 58.4 m thick. It is made of well-bedded pelagic limestones (Fig. 6C; generally 10-20 cm thick), rich in *Calcisphaerulidae* (largest diameter of 110 (μm) and pithonellas (Fig. 7B). Among others, the planktonic foraminifers *Heterohelix* sp., *Hedbergella* sp. and *Marginotruncana* cf. *marginata* (Reuss) (Sliter, 1989) (Figs. 7B, 7C) are found along with fragments of pelagic crinoids, undetermined hyaline foraminifers and textulariids. The dominance of fine-grained sediments and planktonic foraminifers, and the lack of abraded detritus indicate a very low-energy depositional environment (Fig. 6C). These limestones occur in alternation (every 4-6 m) with wackestone-packstones where shallow marine biota, i.e. miliolids and rare *Cuneolina* sp., are found. The transition from Unit A to Unit B is sharp, marked by the appearance of rudists and the disappearance of predominantly pelagic biota.

Unit B is 25.6 m thick. It is composed of 40-60 cm thick-bedded wackestone-packstones, in alternation with floatstones rich in radiolitid-*Vaccinites* biota. As morphotypes, the rudists observed are elevators (upward growth of the entire commissure, stabilization achieved by passive implantation of the attached valve in the sediment). Among paucispecific rudist congregations the most common are *Gorjanovicia costata* Polšak, *G. acuticostata* Polšak, *G. lipparinii* Polšak, *G. paronai* (Wiontzek), *Medella zignana* (Pirona), *Sauvagesia raricostata* Polšak, *S. tenuicostata* Polšak, *S. kueni* Polšak, *S. meneghiniana* (Pirona), *Radiolites* sp., *hippuritids* (the species listed above are after Polšak (1965, 1967a) who determined 11 species of *Vaccinites*), *Praeradiolites* sp., and *Plagioptychus* sp. (P.W. Skelton, pers. obser.). The fauna preserved is rarely in life position, mostly overturned within floatstones. The right valves of the rudists show no preferred orientation, suggesting the absence of any water current energy trend. Locally, Radiolitids form bouquets or are congregated in sparse clusters. Besides microbored, micritic-coated rudist fragments (Fig. 7D) and echinoid fragments, the bioclastic wackestone-packstone matrix contain rare benthic foraminifers (*Moncharmontia apenninica* (De Castro) and miliolids), rare *Calcisphaerulidae* (25-40 μm diameter, Fig. 7D) and pithonellas. The transition to Unit C is marked by the presence of dense monogeneric radiolitid congregations and the absence of *Vaccinites*.

The overlying Unit C, composed of radiolitid thickets and floatstones (Fig. 6B), has a total thickness of 17 m. Well-bedded (40-60 cm thick) sediments are characterized by an abundant radiolitid fauna (Fig. 6A). As morphotypes, all observed rudists are elevators, exhibiting upward growth of the entire commissure (Fig. 6A). Among these the most common are specimens of the genus *Gorjanovicia* with typical cylindrical shells and pronounced ribs. The outer commissural diameter of *Gorjanovicia* specimens is up to 1 cm and its height ranges from 10 to 15 cm. The fauna is mostly preserved in growth position and forms dense monogeneric congregations (i.e. thickets) (Fig. 6A), except in floatstones where individuals had fallen in horizontal position. Most of the thickets consist of upright cylindrical *Gorjanovicia* individuals in wackestone matrix, while other macrofauna is missing. Bioclastic wackestone-packstones with sparse radiolitid shells are rare. Microscopic components within recrystallized lime mud are benthic foraminifers, including *Scandonea samnitica* De Castro, *Moncharmontia apenninica* (De Castro) (Fig. 7A), *Pseudocyclammina sphaeroidea* Gendrot, *Cuneolina* sp. and miliolids, as well as fragments of rudists.

Interpretation.

The first unit (Unit A) of this section represents pelagic limestones with rare alternations of shallow water deposits. These alternations imply probably an outer shelf "echo" of shallowing-upward cycles.

The transition from pelagic limestones to limestones with radiolitid-*Vaccinites* biota, i. e. from relatively distal to the relatively proximal part of the shelf, is indicated by the presence or absence of rudists. The change from a radiolitid-*Vaccinites* assemblage to a radiolitid dominated assemblage represents a change from relatively deep and open subtidal environment, where different rudist genera lived and thrived together, to a more shallow and proximal subtidal environment, where monogeneric radiolitid lithosomes occurred. This change from a mixed radiolitid-*Vaccinites* assemblage to a radiolitid dominated assemblage probably occurred when the habitat became even more shallow, and environmentally confined for monogeneric thickets. Although in the radiolitid dominated succession, Unit C of the shallowing-upward cycles (James, 1984) is absent, and neither the microbiota nor the structure and texture of the sediment record a shallowing of the environment, the monogeneric nature of the rudist thickets suggests the shallowest part of the subtidal zone, as in other parts of the Adriatic carbonate platform (Gušic & Jelaska,

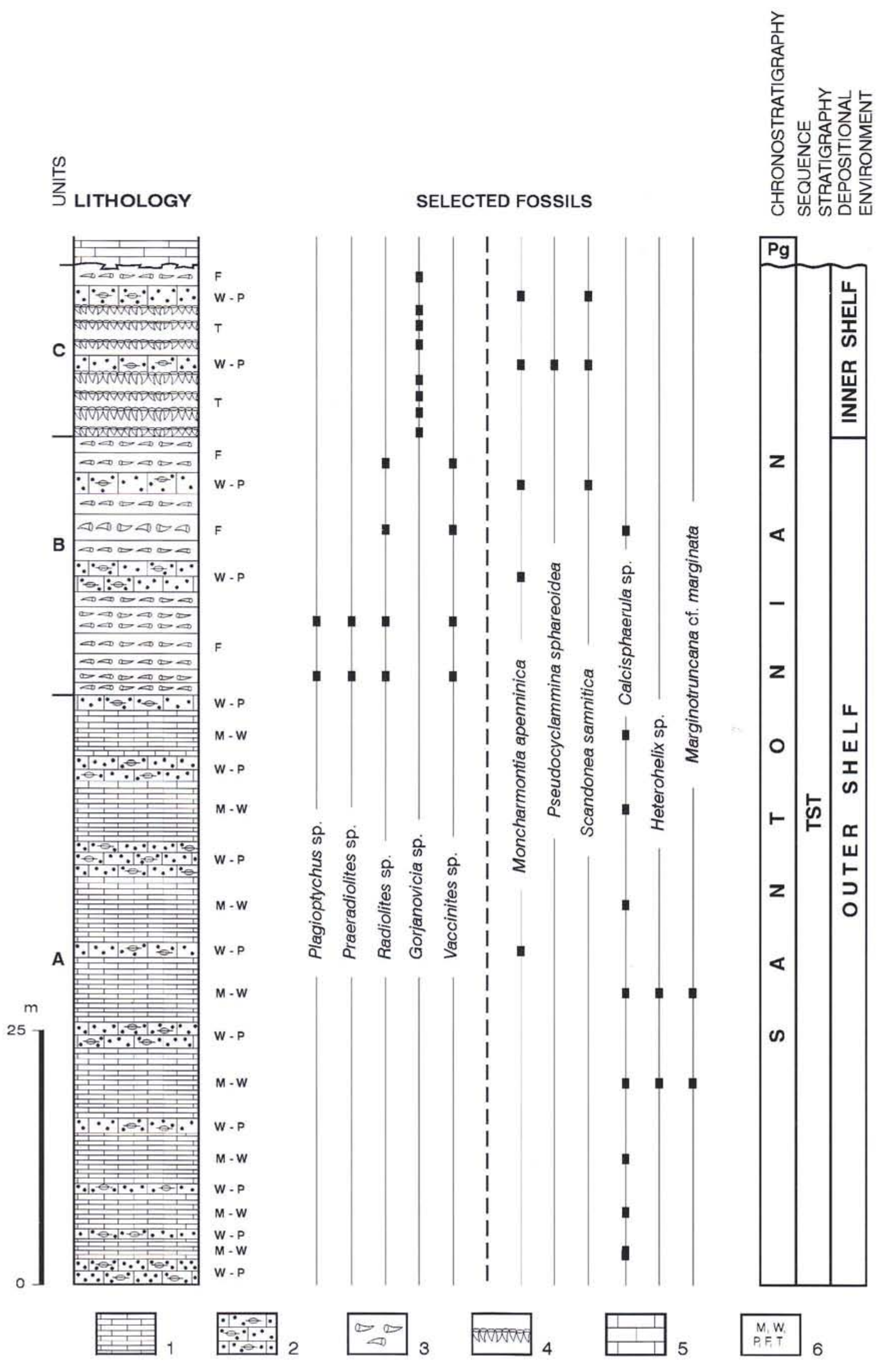


Fig. 5 - Simplified stratigraphic log of the Santonian limestones in the Kuvišeja section. Thicknesses of the beds are shown schematically (not to scale). 1 - pelagic mudstone-wackestones, 2 - foraminiferal-peloidal wackestone-packstones, 3 - rudist floatstones, 4 - rudist congregations, 5 - Paleogene limestones, 6 - M-mudstone, W- wackestone, P- packstone, F- floatstone, T- thicket.

Fig. 6 - The Kuvišeja section. A - Limestone bed showing dense biostrome (Unit C) composed of radiolitids. B - Radiolitid biostromes (Unit C). C - Thin-bedded limestones (Unit A) with pelagic particles.

1990; Fucek et al., 1990; Moro & Jelaska, 1994; Moro 1997a).

The dominance of pelagic sedimentation in the lowest unit (Unit A) of the succession indicates that initially conditions were not favourable for rudist growth. A significant shallowing, suggested by sporadic pelagic influence in the second unit (Unit B), records the end of unfavourable conditions for rudist growth, and the beginning of much more favourable environments where mixed radiolitid-hippuritid association developed. At the end of the succession, i.e. in Unit C, a further shallowing depositional trend result in settings suitable for colonization by the radiolitid elevators. This interpretation is reinforced by the vertical biotic zonation recorded for the Turonian of the cape Premantura (Moro, 1997a), which corresponds generally with the vertical zonation present in the sedimentary succession described here.

Discussion.

Both sections have similar facies (mixed radiolites-*Vaccinites*, and pure radiolites) characteristics (Figs. 2, 5).

According to the influence of pelagic sedimentation and the absence of the shallowing upward cycles, shelf deposits of the cape Mrlera sections may be considered as the beginning (i.e. TST, Tucker, 1993) of the third order sequence (Moro, 1997a). Simi-

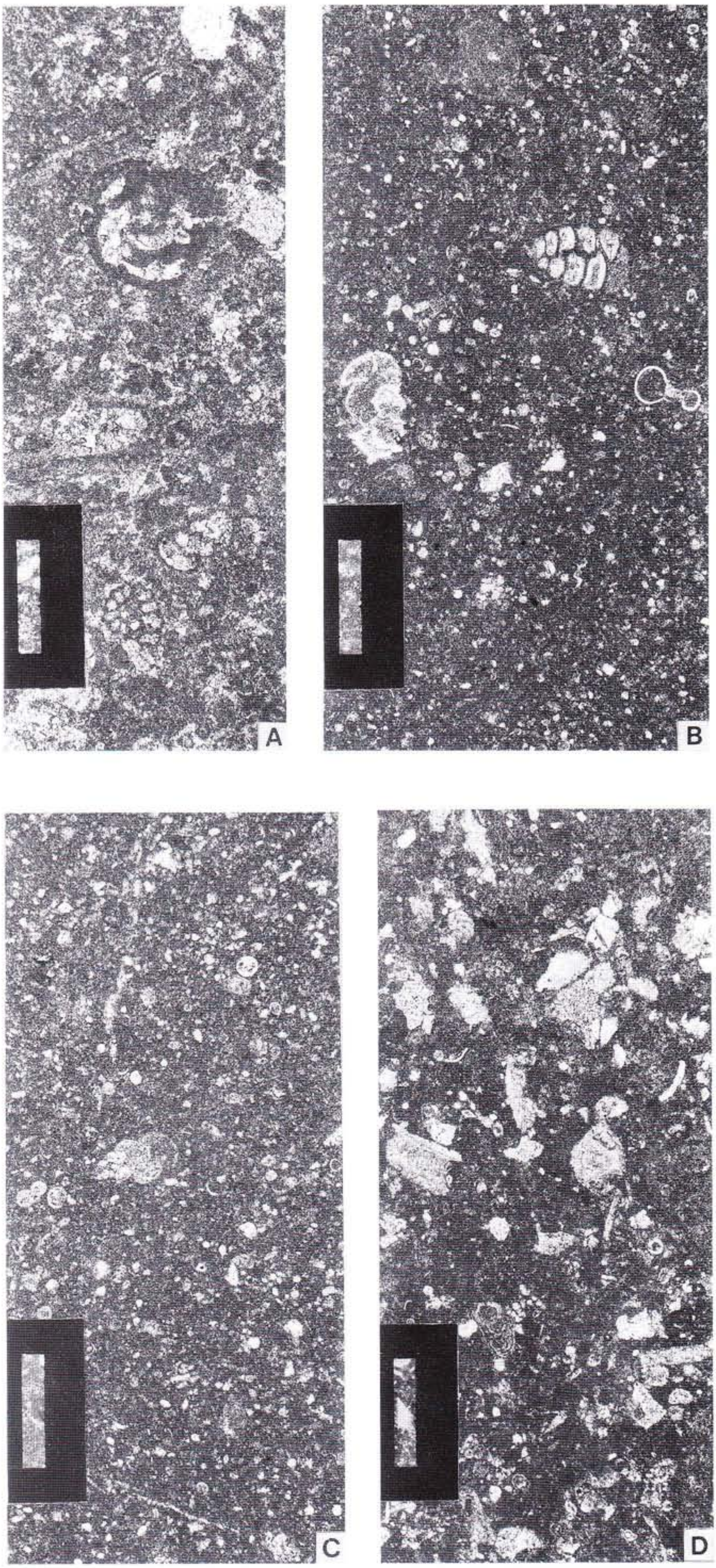


Fig. 7 - The Kuvišeja section. A - *Scandonea samnitica* (De Castro), *Moncharmontia apenninica* (De Castro) and *Thaumatoporella parvovesiculifera* (Raineri). Unit C. Scale bar 0.8 mm. B - Wackestone with *Calcisphaerulidae*, *Marginotruncana* cf. *marginata* (Reuss) and *Hedbergella* sp. Unit A. Scale bar 0.8 mm. C - Wackestone with *Calcisphaerulidae* and *Heterohelix* sp. Unit A. Scale bar 0.8 mm. D - Rudist floatstones with rare *Calcisphaerulidae*. Unit B. Scale bar 0.8 mm.

lar outer shelf facies with intercalations of pelagic sedimentation are observable in the Sezana formation of the southern part of the Trieste-Komen plateau (Jurkovšek et al., 1996), which corresponds to the Gornji Humac Formation of Brac Island (Gušic & Jelaska, 1990). In the Mediterranean region, outer shelf facies are observable in the Matese mountains (Ruberti, 1993, 1997), while outer shelf facies with intercalations of pelagic sedimentation are present in the Ostuni area in Apulia (Laviano, 1984; Laviano & Guarnieri, 1991). This renewed deepening is recorded by hemipelagic Santonian deposits at the Olmedo and Punta Negra localities of northwestern Sardinia (Carannante et al., 1995), by late Santonian pelagic levels in the Monte S. Angelo section of the Gargano promontory (Laviano & Marino, 1996), by pelagic sediments overlying evaporites in north Africa (Camoin, 1995), and by a deepening of the narrow shelf in Tyrol (Sanders, 1998).

Although both sections share this characteristic, the Kuvišeja section differs in its upper shallowing trend (Fig. 8). Since elevator rudists had little or no positive topographic expression (Philip, 1972), the

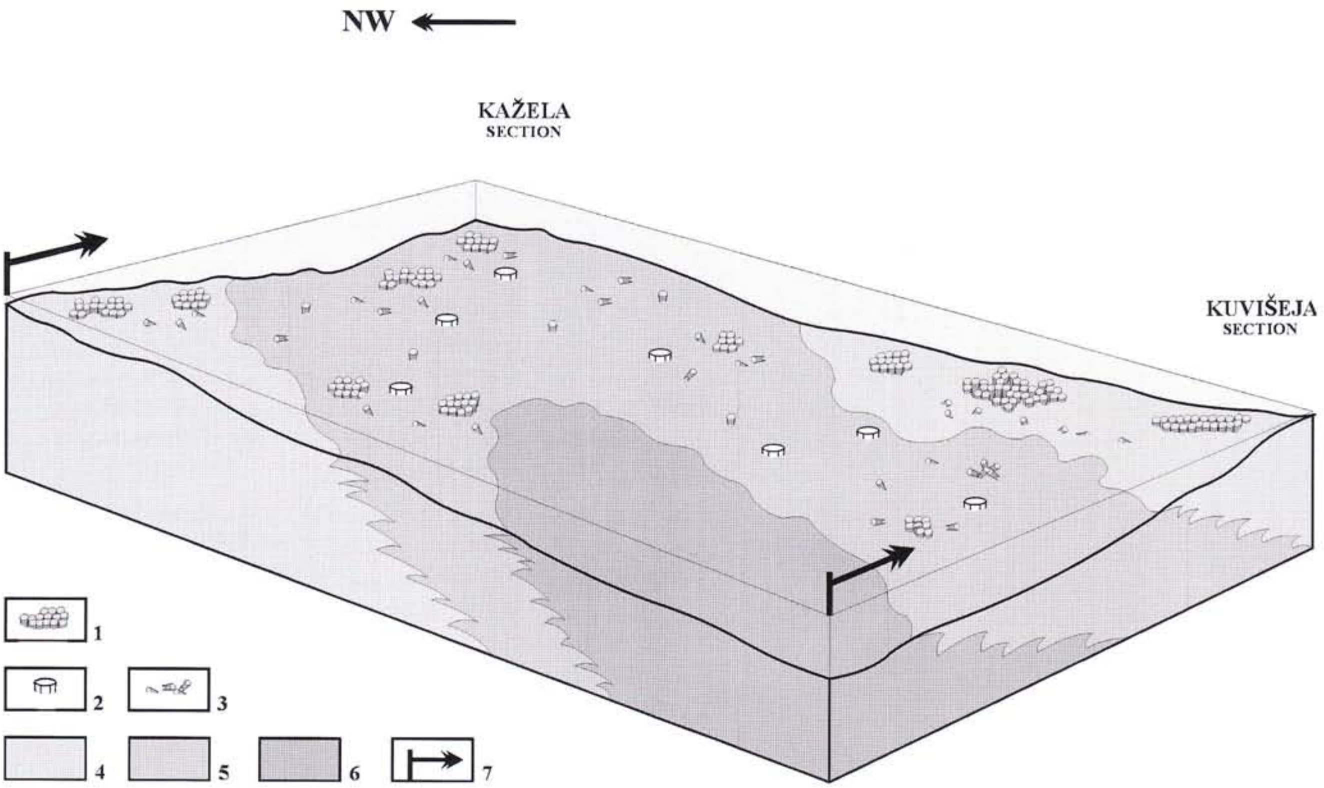


Fig. 8 - Reconstructed block-diagram of depositional environments of the cape Mrlera during the Santonian. Not to scale. 1 - radiolitid congregations, 2- solitary *Vaccinites*, 3- radiolitid floatstones, 4- radiolitid-dominated assemblage, 5- radiolitid-*Vaccinites*-dominated assemblage, 6 - pelagic (open sea) sedimentation, 7 - direction of the vertical development of the sections.

shallowing trend could be attributed to the more pronounced submarine relief. Actually, the absence of intertidal Unit C within the shallowing-upward cycles (James, 1984), typical of the shallowing-upward cycles on the Adriatic carbonate platform (Gušic & Jelaska, 1990; Fucek et al., 1990; Moro & Jelaska, 1994; Moro, 1997a), and the constant repeating of subtidal Unit B, reinforce this interpretation. Moreover, in the sections investigated the contact between pelagic and radiolitid-*Vaccinites* successions, as well as the radiolitid-*Vaccinites* and radiolitid successions, were always observed, (Figs. 2, 5, 8).

Elevator (Skelton & Gili, 1991) rudists inhabited shallow warm seas within the photic zone and commonly occurred in sediments deposited in quiet water (Freytet, 1973; Scott, 1981; Sartorio, 1986; Camoin et al., 1988; Collins, 1988). This is a general characteristic for elevators on the Adriatic carbonate platform (Gušic & Jelaska, 1990; Fucek et al., 1990; Moro & Jelaska, 1994).

Although much work remains to be done on the autecological characteristics of rudists (Gili et al., 1995a), there is some evidence that various genera had different degrees of tolerance towards fluctuations in environmental variables. The appearance of *Vaccinites* within deeper and more open subtidal environments (Fig. 8) is probably connected with biochemical attraction of conspecific recruits for hippuritids (Skelton et al., 1995). Moreover, their life strategies suggest that large-bodied *Vaccinites* were probably more K-strategists (Gili et al., 1995a) than radiolitids. The slightly deeper and probably more stable subtidal environment, compared to the peritidal, presumably was less prone to salinity fluctuations (Ross & Skelton, 1993). Hippuritids with their open system of pores and canals (Skelton, 1976) were hindered from sealing themselves off entirely from the water (Ross & Skelton, 1993). Similarly, the appearance of *Vaccinites* within a deeper and more open subtidal environment was observed in Brac Marbles of the Brac Island (Gušic & Jelaska, 1990) and in the Lipica formation of the Trieste-Komen plateau (Jurkovšek et al., 1996; Plenicar & Jurkovšek, 1996).

Monogeneric radiolitids thickets (Figs. 2, 5, 8), which preferred the shallowest parts of the subtidal zone (Moro, 1997a; Ross & Skelton, 1993), could also reflect rapid settlement of larvae on a biochemically attracted and temporarily available substratum (Skelton et al., 1995). In contrast to the hippuritids, some radiolitids (here *Gorjanovicia*, *Sauvagesia*, *Plagyopticus*, *Radiolites* and *Praeradiolites*) were probably more r-strategists with a short life span and few reproductions with large spawns (Gili et al., 1995a). Therefore, they preferred the shallowest parts of the subtidal environment where, through competitive interference with other taxa and probably higher adaptability to the temporary fluctuations in water chemistry (e.g. hypersalinity, Ross &

Skelton, 1993), they excluded other taxa. Radiolitids within the shallowest parts of the subtidal environment were observed on Brac Island (Gušic & Jelaska, 1990), and in peritidal deposits of Olib Island (Moro & Jelaska, 1994).

Conclusions.

We interpret the vertical succession of rudists assemblages in the rudist-dominated sections Kazela and Kuviševa of the cape Mrlera in the southern part of the Istrian peninsula as environmentally induced succession. This interpretation is supported by the relative sea-level change.

The appearance of *Vaccinites* at the top of the Kazela section is attributed to a its different tolerance of environmental factors such as deepening and opening of the environment in response to relative sea level changes. Slight differences between the two sections (shallowing in the upper part of the Kuviševa section) could be attributed to the influence of more pronounced submarine relief. Once the environment became relatively shallower or deeper, due to relative sea level changes, specific rudist communities appeared, as shown by typical congregations: a radiolitid-dominated assemblage succession evolving to monogeneric dense thickets or dense floatstones, and a radiolitid-*Vaccinites*-dominated assemblage evolving to radiolitid bouquets with solitary hippuritids or less dense floatstones.

It may be concluded that radiolitids and *Vaccinites* occupied different biotopes within subtidal environments of the Adriatic carbonate platform. *Vaccinites* preferred more stable, deeper subtidal environments. Although radiolitids appear also in deeper subtidal areas, according to the monogeneric nature of radiolitid thickets from the shallowest parts of the subtidal zone, it is possible to presume that they were more adaptable to extreme peritidal environments.

Therefore, these two rudist groups may be used for paleoenvironmental interpretations.

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REFERENCES

Camoin G. (1995) - Nature and origin of Late Cretaceous mud-mounds, north Africa. *Spec. Publ. Int. Assoc. Sedimentol.*, v. 23, pp. 385-400, Oxford.

Camoin G., Bernet-Rollande M.C. & Philip J. (1988) - Rudist-coral frameworks associated with submarine volcanism in the Maastrichtian of the Pacino area (Sicily). *Sedimentology*, v. 35, pp. 123-138, Oxford.

Carannante G., Cherchi A. & Simone L. (1995) - Chlorozoan versus foramol lithofacies in Upper Cretaceous rudist limestones. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, v. 119, pp. 137-154, Amsterdam.

Collins L.S. (1988) - The faunal structure of mid-Cretaceous rudist reef core. *Lethaia*, v. 21, pp. 271-280, Oslo.

Cosovic V., Baloncic D., Koic M., Marjanac T., Moro A., Gušic I. & Jelaska V. (1994) - Paleontological evidence of Paleogene transgression on Adriatic carbonate platform, *Géologie Mediterranee*, v. 21, pp. 49-53, Marseille.

D'Ambrosi C. (1940) - Scoperta di un lembo di calcare Eocenico presso punta Merlera a SE di Pola. *Boll. Soc. Adriatica Sci. Naturali Trieste*, v. 38, pp. 53-57, Udine.

Fleury J.J. (1980) - Les zones de Gavrovo-Tripolitza et du Pinde-Olonos (Gréce continentale et Péloponnése du Nord). Evolution d'une plate-forme et d'un bassin dans leur cadre alpin. *Publ. Soc. Géol. Nord*, v. 4, 651 pp., Villeneuve d'Ascq.

Flügel E. (1982) - Microfacies Analysis of Limestones. V of 633 pp., Springer-Verlag, Berlin.

Fucek L., Gušic I., Jelaska V., Korolija B. & Oštric N. (1990) - Stratigrafija gornjokrednih naslaga jugoistocnog dijela Dugog otoka i njihova korelacija s istovremenim naslagama otoka Braca (Upper Cretaceous stratigraphy of the SE part of the Dugi otok Island and its correlation with the corresponding deposits of the Brac Island (Adriatic carbonate platform)). *Geološki Vjesnik*, v. 43, pp. 23-33, Zagreb.

Freytet P. (1973) - Edifices recifaux developpés dans un environment detritique, example des biostromes a Hippurites (Rudistes) du Senonien Inférieur du sillon languedocien (region du Narbone, sud de la France). *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, v. 13, pp. 65-76, Amsterdam.

Gili E., Skelton W.P., Vinces E. & Obrador A. (1995a) - Corals to rudists-an environmentally induced assemblage succession. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, v. 119, pp. 127-136, Amsterdam.

Gili E., Masse J-P. & Skelton P.W. (1995b) - Rudists as gregarious sediment-dwellers, not reef-builders, on Cretaceous carbonate platforms. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, v. 118, pp. 245-267, Amsterdam.

Gušic I. & Jelaska V. (1990) - Stratigrafija gornjokrednih naslaga otoka Braèa (Upper Cretaceous stratigraphy of the Island of Braè within the geodynamic evolution of the Adriatic carbonate platform). *Opera Academiae Scient. Art. Slav. Meridional.*, v. 69, 160 pp, Zagreb.

James N.P. (1984) - Shallowing upward sequences in carbonates. In: Walker, R.G. (ed.) Facies models, pp. 213-228, *Geological Association Canada*, Toronto.

Jurkovšek B., Toman M., Ogorelec B., Šribar L., Drobne K., Poljak M. & Šribar Lj. (1996) - Formacijska geološka karta juznega dela Trzaško-Komenske planote 1:50000 (Geological map of the southern part of the Trieste-Komen plateau). *Inštitut za geologijo, geotehniko in geofiziko*, pp.1-143, Ljubljana.

Kauffman E.G. & Sohl N.F. (1974) - Structure and evolution of Antillean Cretaceous rudist frameworks. *Verh. naturf. Ges. Basel*, v. 84, pp. 399-467, Basel.

Laviano A. (1984) - Preliminary observations on the upper cretaceous coral-rudist facies of Ostuni (south-eastern Murge, Apulia). *Riv. Ital. Pal. Strat.*, v. 90, pp.177-196, Milano.

Laviano A. & Guarnieri G. (1991) - Rudists as a tool for paleoenvironmental reconstruction in Apulia (Italy). *Atti Accad. Pelor. Pericol.*, v. 67, Suppl. 1, pp. 45-75, Messina.

Laviano A. & Marino M. (1996) - Biostratigraphy and paleoecology of Upper Cretaceous carbonate successions in the Gargano promontory. *Mem. Soc. Geol. It.*, v. 51, pp. 685-701, Roma.

Mamuzic P., Polšak A., Grimani M. & Korolija B. (1982) - Geološki stup kroz naslage cenomana i donjeg turona u središnjem dijelu otoka Cresa (Une colonne stratigraphique á travers les couches du Cénomanien et du Turonien inférieur dans la partie centrale de l'île de Cres). *Geološki Vjesnik*, v. 35, pp. 65-70, Zagreb.

Masse J.P. & Philip J. (1981) - L'évolution des Rudistes au regard des principaux événement géologiques du Crétacé. *Bull. Centres Rech. Explor.* - Prod. Elf-Aquitaine, v. 10, n. 2, pp. 437-456, Pau.

Maticec D., Vlahovic I., Velic I. & Tišljar J. (1996) - Eocene Limestones Overlying Lower Cretaceous Deposits of Western Istria (Croatia): Did Some Parts of Present Istria Form Land During the Cretaceous?. *Geolog. Croat.*, v. 49/1, pp. 117-127, Zagreb.

Moro A. (1997a) - Stratigraphy, paleoecology and vertical succession of rudist biostromes in the Upper Cretaceous (Turonian-Santonian) limestones of southern Istria, Croatia. *Palaeogeog., Palaeoclimat., Palaeoecol.*, v.131, pp. 113-131, Amsterdam.

Moro A. (1997b) - Paleoekologija i evolucija sjevernog dijela Jadranske karbonatne pletforme u gornjoj kredi (Paleoecology and evolution of the northern part of the Adriatic carbonate platform during Upper Cretaceous). *Ph. D. thesis (unpublished)*, pp. 129, *University of Zagreb*, Zagreb.

Moro A. & Jelaska V. (1994) - Upper Cretaceous peritidal deposits of Olib and Ist islands (Adriatic Sea, Croatia). *Geol. Croat.*, v. 47/1, pp. 53-65, Zagreb.

Philip J. (1972) - Paléoécologie des formations á rudistes du Crétacé superieur-l'exemple du sud-est de la France. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, v. 12, pp. 205-222, Amsterdam.

Philip J. (1980) - Crétacé superiéur de Provence. *Geobios, Mém. spécial*, v. 4, pp. 99-109, Lyon.

Philip J. (1985) - Sur les relations des marges téthysiennes au Campanien et au Maastrichtien déduites de la distribution des Rudistes. *Bull Soc. géol. France*, v. 8, I, n. 5, pp. 723-731, Paris.

Philip J., Amico S. & Allemann J. (1978) - Role des Rudistes dans la sédimentation calcaire au Crétacé supérieur. *"Livre jubilaire Jacques Flandrin" - Docum. Lab. Géol. Fac. Sci. Lyon*, 4, pp. 343-359, Lyon.

Plenicar M. & Jurkovšek B. (1996) - Patch reef near Senozece (Grebenska zaplata pri Senozecah) Rasprave IV. razreda SAZU, XXXVII, v. 3, pp. 37-83, Ljubljana.

Polšak A. (1965) - Geologija juzne Istre s osobitim obzirom na biostratigrafiju krednih naslaga (Géologie de l'Istrie méridionale spécialement par rapport a la biostratigraphie des couches crétacées). *Geološki Vjesnik*, v. 18, pp. 415-509, Zagreb.

Polšak A. (1967a) - Kredna makrofauna juzne Istre (Macrofaune crétacée de l'Istrie méridionale, Yugoslavie). *Palaeontologia jugoslavica*, v. 8, pp. 1-219, Zagreb.

Polšak A. (1967b) - Osnovna geološka karta SFRJ, list Pula, 1:100000, L33-112 (Basic geological map of SFRY: Sheet Pula L33-112). *Instit. za geol. istraz.*, Zagreb, Savezni geološki zavod, Beograd.

Polšak A. (1970) - Osnovna geološka karta SFRJ1:100 000. Tumac za list Pula L33-112 (Explanatory notes for sheet Pula). - *Inst. za geološka istraz. Zagreb*, pp. 1-44, Savezni geološki zavod, Beograd.

Ross D.J. & Skelton P.W. (1993) - Rudist formations of the Cretaceous: a palaeoecological, sedimentological and stratigraphical review. *Sedimentology Review*, v. 1, pp. 73-91, Oxford.

Ruberti D. (1993) - Late Cretaceous carbonate shelf-to-slope facies in the central-western Matese (central Apennines, Italy). *Giornale di Geol.*, v. 55, pp. 21-36, Bologna.

Ruberti D. (1997) - Facies analysis of an Upper Cretaceous high-energy rudist -dominated carbonate ramp (Matese Mountains, central-southern Italy): subtidal and peritidal cycles. *Sedimentary Geology*, v. 113, pp. 81-110, Amsterdam.

Sanders D. (1998) - Tectonically Controlled Late Cretaceous Terrestrial to Neritic Deposition (Northern Calcareous Alps, Tyrol, Austria). *Facies*, v. 39, pp. 139-178, Erlangen.

Sartorio D. (1986) - Caprinid patch reef in the Cansiglio inner platform carbonate sequence (Southern Alps): a record of the earliest Aptian marine transgression. *Riv. Ital. Pal. Strat.*, v. 92, pp. 383-400, Milano.

Scott R.W. (1981) - Biotic relations in Early Cretaceous coral-algal-rudist reefs, Arizona. *Jour. of Paleont.*, v. 55, pp. 463-478, Menasha.

Simo J.A., Scott R.W. & Masse J-P. (1993) - Cretaceous Carbonate Platforms: an overview. In: Simo J.A., Scott R.W. & Masse J-P. (Eds.) Cretaceous Carbonate Platforms, *Amer. Assoc. Petrol. Geol. Memoir*, v. 56, pp. 1-13, Tulsa.

Skelton W.P. (1976) - Functional morphology of the Hippuritidae, *Lethaia*, v. 9, pp. 83-100, Oslo.

Skelton W.P. & Gili E. (1991) - Paleoecological classification of rudist morphotypes. In: *First International Conference* *on Rudists, October 1988, Proceedings (Ed. by M. Sladic-Trifunovic). Serbian Geological Society*, 71-86, Belgrade (Issued only as reprint from unpublished volume; paper resubmitted elsewhere).

Skelton W.P., Gili E., Vinces E. & Obrador A. (1995) - The growth fabric of gregarious rudist elevators (hippuritids) in a Santonian carbonate platform in the southern Central Pyrenees. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, v. 119, pp. 107-126, Amsterdam.

Sliter W. V. (1989) - Biostratigraphic zonation for Cretaceous planctonic foraminifers examined in thin section. *Journ. Foram. Res.*, v. 19, pp. 1-19, Lawrence.

Tišljar J. (1976) - Petrološka studija krednih sedimenata zapadne i juzne Istre (Sedimentologic study of the Cretaceous sediments in the western and southern Istria). *Ph. D. thesis (unpublished)*, 188 pp, *University of Zagreb*, Zagreb.

Tucker M. E. (1993) - Carbonate diagenesis and sequence stratigraphy. in Wright, V.P. (Ed.) *Sedimentology review*, v. 1, pp. 51-72, Oxford.

Tucker M. E. & Wright V.P. (1990) - Carbonate sedimentology. 482 pp., Blackwell Scientific publications, Oxford.

Velic I., Tišljar J., Maticec D. & Vlahovic I. (1995) - A Review of the Geology of Istria. In: Vlahovic I. & Velic I. (Eds.) - *1. hrvatski geološki kongres (First croatian geological congress) Vodiè ekskurzija (Excursion guide-book)*, pp. 21-30, Zagreb.