DIVERSITY PATTERNS IN MID-CRETACEOUS BENTHIC FORAMINIFERS AND DASYCLADALEAN ALGAE OF THE SOUTHERN PART OF THE MESOZOIC ADRIATIC PLATFORM, CROATIA

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ABSTRACT: The Mesozoic, mid-Cretaceous (Barremian to Cenomanian) deposits of southern Croatia comprise a succession of shallow tropical-water, inner-platform deposits that formed on a Bahama-type isolated Adriatic carbonate platform in the Dinarides. This succession is dominated by benthic foraminifers and dasycladalean algae, and is exposed in a nearly continuous outcrop section on the islands and along the coast of southern Croatia. It has been studied in terms of sedimentary facies, paleoecology, and biostratigraphy. The present study documents that several species of benthic foraminifers (cuneolinids, orbitolinids, alveolinids) and dasycladalean algae (*Salpingoporella*) have exceptional age-diagnostic value for mid-Cretaceous biostratigraphy. These are abundant, and they have a widespread distribution and a restricted stratigraphic range. They evolved rapidly and became extinct suddenly. The mid-Cretaceous benthic associations, including a total of 106 species and 57 genera of benthic foraminifers and 48 species and 20 genera of dasycladalean algae, were analyzed to establish the principal diversity patterns at (sub)stage level of resolution. The Early Aptian marked the foraminiferal diversity maximum, whereas significant diversity drops are recorded in the Late Aptian and Early Cenomanian. The foraminiferal distribution within the oligotrophic habitats of the platform interior was controlled primarily by relative sea-level oscillations, variations in oceanic circulation rate, and nutrient availability in surface waters. There is a positive correlation between episodes of increased diversification and the regional relative sea-level rises, whereas regressive episodes resulted in reduction of oligotrophic habitats and decreased species richness. The dasycladaleans were the most diversified during the tidal-flat-dominated Barremian, and from that peak diversity decreased through the Early Aptian. A significant diversity drop occurred in the Late Aptian, and it was contemporaneous with the maximum abundance of *Salpingoporella dinarica*. The mid-Cretaceous dasycladaleans never fully recovered from the Early Aptian platform deepening event, and their post-Aptian diversity pattern implies dependence on factors other than relative sea level and associated changes in habitats.

KEY WORDS: Cretaceous, Adriatic platform, foraminifera, algae, diversity

INTRODUCTION

The objective of this paper is to describe the characteristic mid-Cretaceous associations of the benthic foraminifers and dasycladalean algae of the southern part of the Adriatic platform, and to describe and interpret the possible driving forces behind their diversity patterns as a contribution towards a better understanding of the global distribution of these microorganisms during the mid-Cretaceous.

The Lower Cretaceous platform-interior deposits of the study area are characterized by generally scarce findings of macrofossils. Only locally, rudists occur in significant numbers in Late Barremian–Early Aptian perireefal environments. Subsequently, the rudists became important sediment producers in the Late Cretaceous, which coincided with the dasycladalean diversity low. Therefore, in the absence of macrofossils and due to lack of any index open-marine organisms (e.g., ammonites, planktonic foraminifers, etc.), which are commonly used in high-resolution biostratigraphy, paleontological investigations are focused on two groups of benthic microfossils: calcareous, predominantly dasycladalean algae, and foraminifers. The diversity of these two groups of organisms appears to be "cyclic" during the evolution of the Mesozoic Adriatic platform, characterized by an alternation of diversity lows, diversity highs, and intervals distinguished by abundance of a particular taxon.

Foraminiferal and algal communities have been used extensively for Mesozoic biostratigraphy of the Adriatic platform. There has been particular emphasis on the mid-Cretaceous period, with studies presenting local and regional schemes of stratigraphic distributions of benthic assemblages (e.g., Velić, 1977, 1988; Velić and Sokač, 1978, 1980, 1983; Sokač, 1987, 1996, 2004; Gušić, 1981; Velić and Vlahović, 1994; Velić et al., 1995; Husinec et al., 2000; Cvetko Tešović, 2000; Husinec, 2001, 2002; Husinec and Sokač, 2006). However, the major effort of micropaleontologists has been directed toward a description of the pattern of distribution of foraminifers and algae, not toward an understanding of where and how these organisms lived. Consequently, present paleoecological studies are usually restricted to occurrence patterns of individual taxa and/or typical associations. Rare attempts have been made to discuss the diversity patterns of these organisms and the complex background behind the diversity changes.

MATERIALS AND METHODS

The studied southern part of the Adriatic platform is characterized by nicely exposed and easily accessible outcrops of

Mesozoic platform-interior succession: limestones, dolomites, and paleosols represented by emersion breccias and residual clays. The outcrops occupy islands and coastal mountains of southern Croatia, and superb sections, spanning hundreds of meters and tens of millions of years, are available for detailed investigations. We selected the five probably most complete sections for an extensive biostratigraphic and sedimentary facies analysis (Fig. 1). These sections include two islands (Korčula and Mljet) and three coastal mountain localities (Dinara, Biokovo, and Hum near Dubrovnik), and were chosen because of their highest abundance of biostratigraphically important microfossils. The sections are generally continuous, with a considerable hiatus in the Late Aptian; locally shorter breaks in sedimentation occurred in the Barremian and Late Albian, less commonly in the Early Albian. The sections, representing the inner-platform deposits, are composed of shallow-water carbonates, and consequently yield shallow-water biota exclusively; the exception is an incidental occurrence of pelagic taxa in the Early Aptian. In order to get biostratigraphic control as precise as possible, the bed-by-bed logged sections were sampled more densely where microfossils were more abundant. Micropaleontological analysis is based on roughly 1,300 thin sections bearing benthic foraminifers and dasycladalean algae. The coeval relationships between the studied sections were determined by comparing the ranges of taxa and unconformity surfaces in all sections (Fig. 2).

LITHOFACIES AND DEPOSITIONAL ENVIRONMENTS

The regional distribution and depositional environments for many of the facies of the southern part of the Adriatic platform have been studied extensively (e.g., Velić et al., 1979; Tišljar and Velić, 1991; Tišljar et al., 2002; Husinec, 2002; Vlahović et al., 2005; Husinec and Jelaska, 2006). The mid-Cretaceous platform-interior facies of the study area include emersion breccia or residual clay (subaerial exposure), fenestral carbonates and microbial laminites (tidal flat), intraclast–bioclast–peloid packstone and grainstone (shoal water), skeletal–peloid mudstone, wackestone, and packstone (lagoon–subtidal), and dolomite.
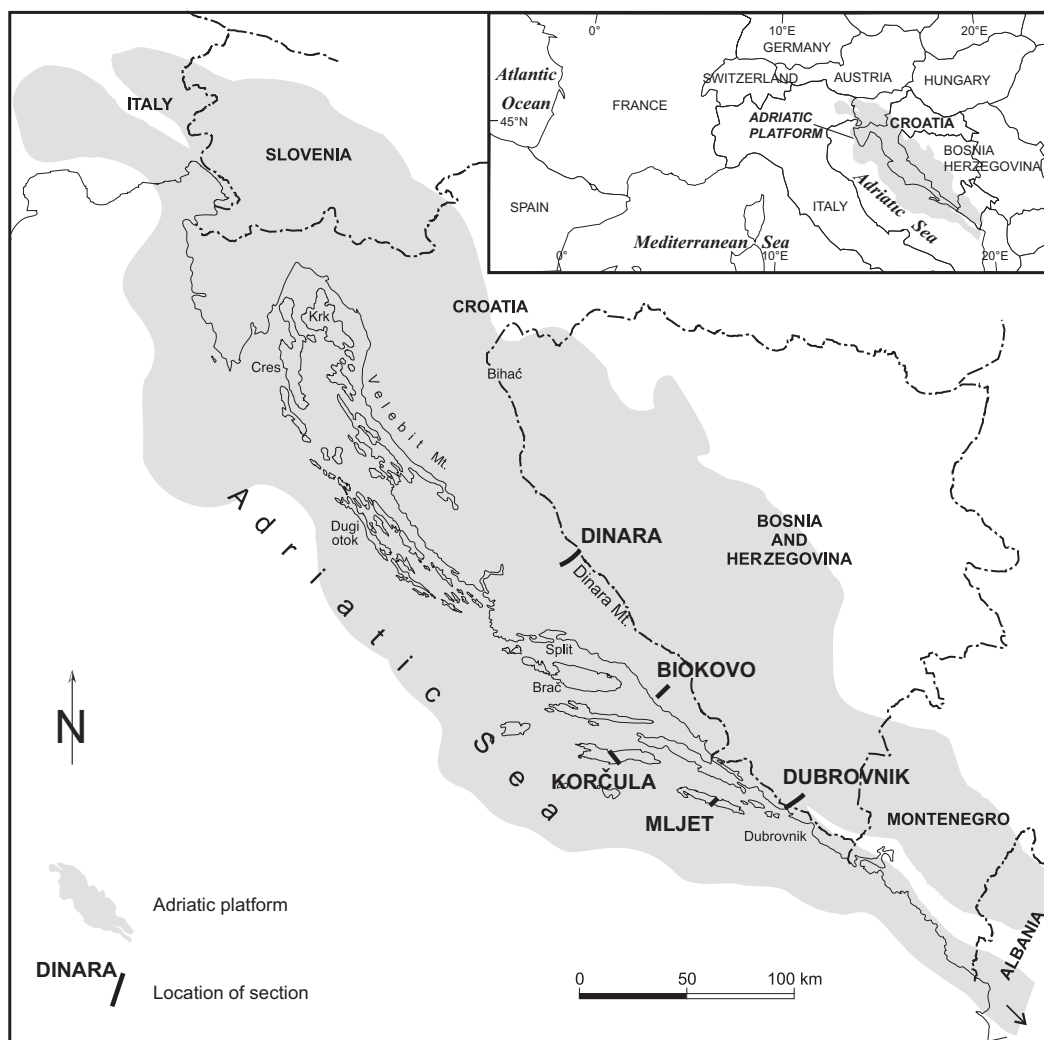

FIG. 1.—Location map showing outline of the Mesozoic Adriatic carbonate platform (after Grandić et al., 1999; Dragičević and Velić, 2002) with position of sections analyzed in this study. Inset map showing general location of Adriatic platform within Croatia and environs.
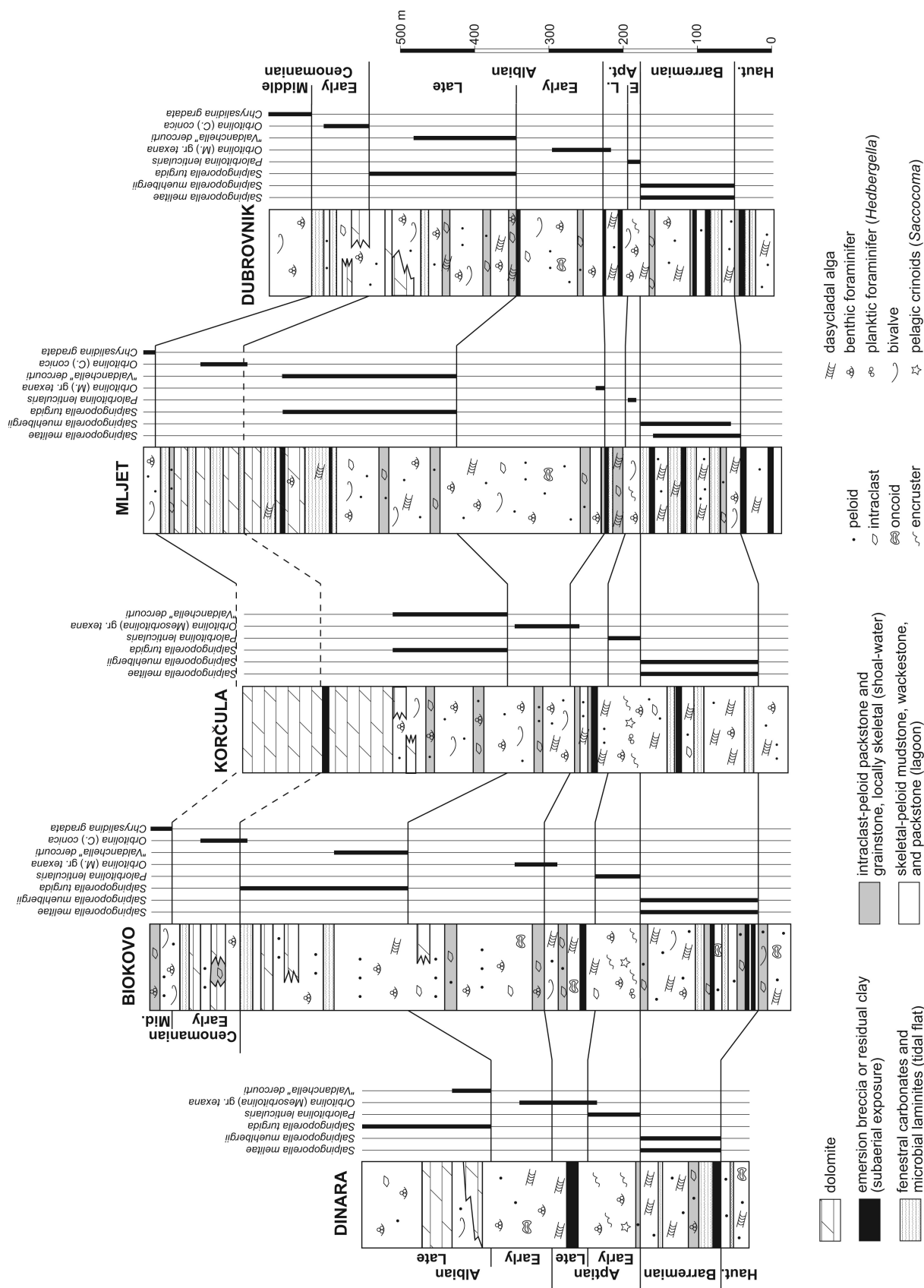
Fig. 2.—Stratigraphic subdivision and relationships of platform-interior sections of southern Croatia (for locations of composite sections see Figure 1; modified from Velić et al., 1979; Sokač and Tišljar, 1986; Husinec, 2002) with ranges of the most important dasycladalean algae and benthic foraminifers. The chronostratigraphic correlations are based on shallow-water benthic data (foraminifers and dasycladalean algae); chronostratigraphic boundaries are indicated by solid lines where biostratigraphic control is good, and dashed lines where concealed or inferred. The thickness of subaerial exposure intervals (in black) is exaggerated.

Emersion Breccia and Residual Clay (Subaerial Exposure)

The major subaerial exposure of the platform took place in the Late Aptian, as evidenced by decimeter-thick emersion breccia or residual clay sheets found throughout the study area. They are also common in the Barremian deposits, locally Upper Hauterivian, as well as in the Lower–Upper Cretaceous boundary strata. These intervals are thin, greenish, clay sheets or intraclastic limestone with a greenish clay or micrite matrix. The clasts, including black pebbles, were eroded from the underlying shallow-subtidal and intertidal–supratidal limestones. The angular shape of clasts and the absence of bauxites suggest that stratigraphic gaps were of limited duration. Breccia veneers and residual clay sheets resulted from prolonged subaerial exposure of the intertidal–supratidal facies due to relative sea-level fall. During subsequent transgression, some veneers were reworked into transgressive lags.

Fenestral Carbonates and Microbial Laminites (Tidal Flat)

Fenestral carbonates and microbial laminites are major Barremian facies, and are common in the Upper Albian and Lower Cenomanian succession. They also occur in less abundance in other parts of the succession but are generally absent in the Lower Aptian strata.

Fine, laminoid fenestral fabric consists of subparallel, closely-spaced, flattened, spar-filled voids. Sediments are generally flat-laminated lime mudstones and wackestones (less frequently packstones) with micritized foraminifers, dasycladalean algae, peloids, various bioclasts including rare ostracodes, and less frequently oncoids. Fine, tubular fenestral fabric is also common in these sediments. It consists of randomly oriented to subvertical tubular fenestrae which may bifurcate.

Microbial laminites are characterized by wavy or crinkly lamination and contain peloids, smaller intraclasts, benthic foraminifers, dasycladalean algae, and less commonly ostracodes. Polygonal desiccation cracks are common in microbial laminites of Cenomanian age only. Planar and micro-scalloped surfaces, with relief up to a few centimeters, developed locally on laminites, most commonly in the Barremian part of the succession.

Laminites formed in intertidal–supratidal settings with well developed microbial mat covers and low to moderate sediment influx (cf. Logan et al., 1974). The tidal storm-deposited sand–mud couplets were bound together by smooth algal mats (Kendall and Skipwith, 1968).

Intraclast–Bioclast–Peloid Packstone and Grainstone (Shoal Water)

This facies is the least common in the studied succession, being frequent only in the Barremian and periodically through the Albian. It is characterized by generally thin- to medium-bedded skeletal packstone and grainstone, less frequently rudstone, composed mainly of intraclasts, subangular to rounded skeletal grains, and peloids. Skeletal grains are mainly bivalve and gastropod fragments, whole and fragmented dasycladalean algae, and foraminifers.

Packstone and grainstone formed in shallow wave- and current-agitated subtidal settings by accumulation of resident dasycladaleans and foraminifers along with peloids and intraclasts derived from reworked muds or micritization of grains.

Skeletal–Peloid Mudstone, Wackestone, and Packstone (Lagoon–Subtidal)

Thick- to very thick-bedded lime mudstone and wackestone, less frequently packstone, contain variable amounts of lime mud, pellets, peloids, oncoids, intraclasts, and skeletal grains (dasycladalean algae, benthic foraminifers, encrusters, ostracodes, and gastropods). These limestones predominate in the Lower Aptian succession, where they are encrusted by *Bacinella irregularis*, one of the most common microfossils of the substage. Also this facies forms a major part of the Albian (excluding its topmost part), where it irregularly alternates with intraclast–bioclast packstone and grainstone.

The "deeper" subtidal environments are represented by skeletal–peloid mudstone and wackestone. Open-marine influence is evidenced only in the Lower Aptian deposits by local findings of planktonic foraminifers (*Hedbergella*) and fragments of pelagic crinoids (*Saccocoma*). Barren lime mudstone is found in the near-shore very shallow, low-energy restricted settings seaward of tidal flats, in the area where tidal currents and waves were extremely weak. Laterally, these shallow subtidal environments might have been associated with lacustrine environments, as suggested by the presence of charophytes.

Dolomite

The Upper Albian to Lower Cenomanian fenestral carbonates and microbial laminites are commonly dolomitized. They occur in an irregular, both vertical and lateral, alternation with limestone. The dolomite is commonly thick-bedded to massive with all the textures and fossil remains destroyed, but locally it contains well-preserved structures and textures suggesting shallowing to supratidal conditions, including fenestral fabric, desiccation cracks, microbial lamination, and dolomitized emersion breccia. Exceptionally, the Upper Albian deposits may locally contain kerogen-rich, dark, decimeter-thick dolomitized beds alternating with light-gray lime mudstone containing rare ostracodes and charophytes.

BIOSTRATIGRAPHY

Regional biostratigraphy was developed based on the studies of foraminiferal and dasycladalean assemblages from the mid-Cretaceous of the Adriatic platform. Numerous references with detailed taxon-range charts (see Introduction) show that there is a reasonable correlation with other Mediterranean localities where benthic biozones are calibrated with the established ammonite and planktonic foraminifera schemes (Hardenbol et al., 1998, and references therein).

One hundred and six species from 57 genera of benthic foraminifers and 48 species of dasycladalean algae from 20 genera were recovered from the studied sections. Since the morphological characteristics of these species are already well known, we restrict the brief remarks to clarifying the stratigraphical position and abundance and/or scarcity of the biostratigraphically most important species. Our selection of illustrated material (Figs. 3–6) is based primarily on the stratigraphic importance of a particular taxon, and its occurrence in the wider peri-Mediterranean region. Some of the dasycladaleans illustrated are less known from the literature, but they are regionally important and their type localities are within the study area.

The stratigraphic distribution of dasycladalean algae and benthic foraminifers for the study area is presented in Figures 7 and 8.

Barremian

Benthic Foraminifers.—

Despite being relatively rich, the benthic foraminiferal association lacks index taxa, with only one species—*Campanellula*
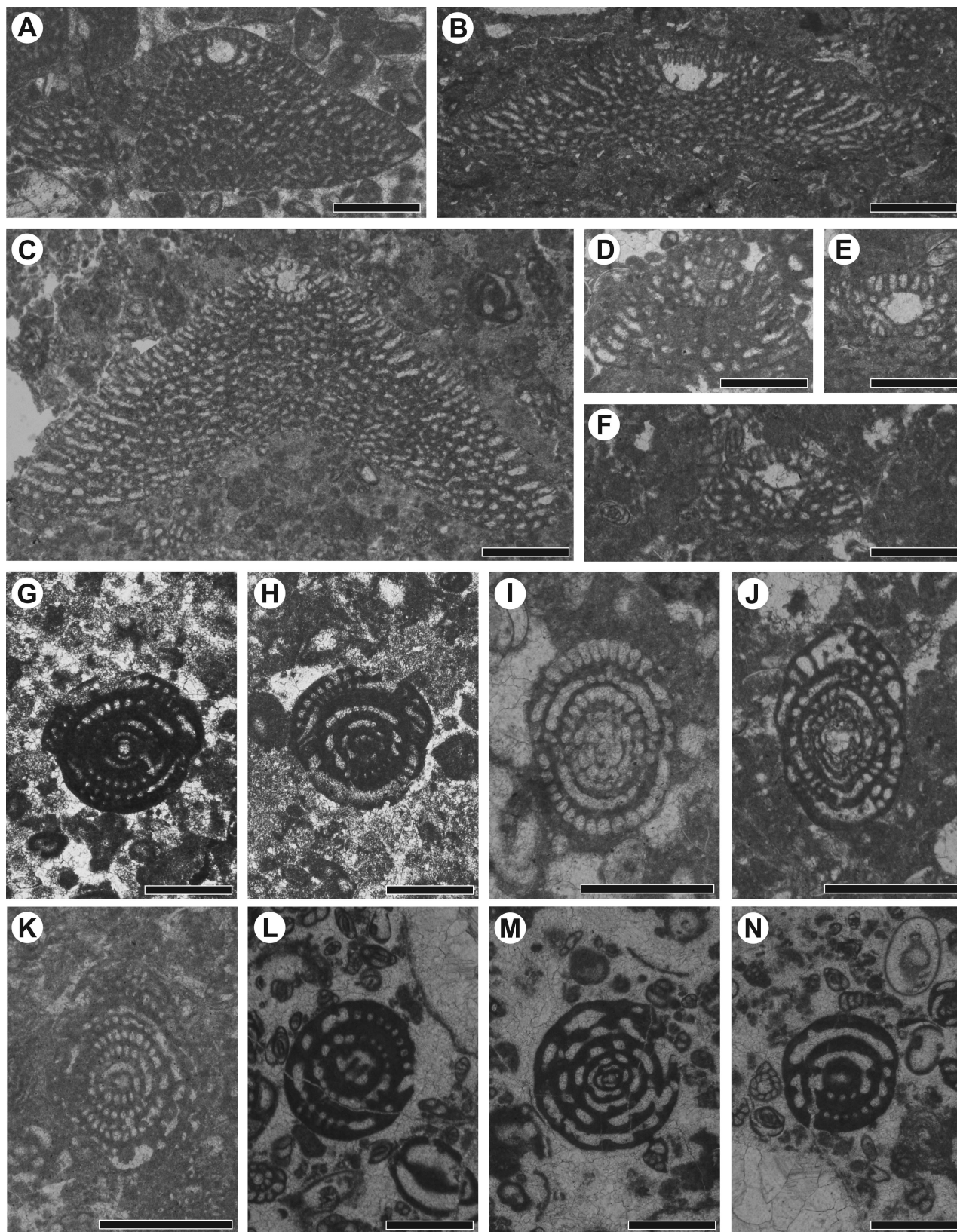
FIG. 3.—**A, B)** *Palorbitolina lenticularis*, Early Aptian, Biokovo (A) and Dinara (B) sections. **C–F)** *Orbitolina* (*Mesorbitolina*) *texana*, Late Aptian–Early Albian, Dinara; **G, H)** *Archaealveolina reicheli*, earliest Albian, Mljet. **I)** *Ovalveolina maccagnoae*, earliest Cenomanian, Biokovo. **J, K)** *Sellialveolina viallii*, earliest Cenomanian; Biokovo. **L–N)** *Ovalveolina crassa*, Biokovo. Scale bars represent 0.5 mm.

capuensis—with a rather narrow stratigraphic range. Its first occurrence (FO) is recorded in the Late Hauterivian, and the last occurrence (LO), in the Early Barremian.

Dasycladalean Algae.—

The beginning of the Barremian coincides with the middle part of the range of foraminifer *Campanellula capuensis*, and is characterized by the disappearance of some taxa characteristic of the Dinaric Neocomian (Berriasian to Hauterivian) and the FOs of several new species of the genus *Salpingoporella.* Besides FOs of *Salpingoporella melitae* (Figs. 5A, B), *S. muehlbergii* (Figs. 5C, D), and *S. genevensis*, the Early Barremian is characterized by LOs of *Actinoporella podolica* (Fig. 5F), *Clypeina*? s*olkani*, and *Falsolikanella danilovae.* The Late Barremian is characterized by FOs of genera *Triploporella*, *Korkyrella*, and *Biokoviella*, as well as by more frequent occurrences of *Salpingoporella dinarica* (Fig. 5E).

Early Aptian

Benthic Foraminifers.—

Palorbitolina lenticularis (Figs. 3A, B) is well known from numerous localities in the Karst Dinarides, where its stratigraphic range is generally defined as Early Aptian only. Other stratigraphically important taxa are *Voloshinoides murgensis* and *Praeorbitolina cormyi.*

Dasycladalean Algae.—

Following the disappearance of Barremian index taxa, the algal association reduces to generally scarce findings of several species of predominantly *Triploporella* and *Korkyrella*.

Other.—

Planktonic foraminifers (*Hedbergella* sp.), crinoids (*Saccocoma* sp.), encrusters (*Bacinella irregularis*, *Lithocodium aggregatum*), cyanobacteria (*Aeolisaccus* sp.), and microproblematica (*Coptocampylodon fontis*).

Late Aptian

Benthic Foraminifers.—

There are no taxa with a Late Aptian stratigraphic range exclusively. *Orbitolina* (*Mesorbitolina*) *parva* and *O*. (*M.*) *texana* (Figs. 3C–F) exhibit the narrowest range, i.e., Late Aptian–Early Albian.

Dasycladalean Algae.—

The exceptional abundance of *S. dinarica* (Fig. 5E) is what makes the Late Aptian succession of the Adriatic platform regionally recognizable.

Other.—

Microproblematica (*Coptocampylodon fontis*).

Early Albian

Benthic Foraminifers.—

The beginning of the Early Albian is characterized by the FOs of *Pseudonummoloculina heimi*, *Cuneolina pavonia*, and *C.*

parva. Archaealveolina reicheli (Figs. 3G, H) is known from both Aptian and lowermost Albian deposits of the Adriatic platform.

Dasycladalean Algae.—

Following the disappearance of *S. dinarica* (Fig. 5E), the dasycladalean association is extremely scarce and lacks index taxa.

Other.—

Microproblematica (*Coptocampylodon elliotti*).

Late Albian

Benthic Foraminifers.—

The association of orbitolinid species "*Valdanchella*" *dercourti* (Fig. 4C), *Neoiraqia insolita* (Figs. 4A, B), *N. convexa* (Fig. 4F), and less frequently *Paracoskinolina fleuryi* and *Simplorbitolina broennimanni* (Figs. 4D–E), is typical of the Upper Albian limestones of the Adriatic platform.

Dasycladalean Algae.—

The beginning of the Late Albian is regionally marked by the FO of *Salpingoporella turgida*. In the later levels of the Late Albian, *S. turgida* is accompanied by *Heteroporella lepina*, another index alga of the (sub)stage.

Other.—

Crinoids (*Saccocoma* sp.), algae (*Thaumatoporella parvovesiculifera*), microproblematica (*Coptocampylodon* sp.), charophytes, and ostracodes.

Early Cenomanian

Benthic Foraminifers.—

There are several species whose LOs and / or FOs occur during this (sub)stage. These include *Ovalveolina crassa* (Figs. 3L–N) and *O. maccagnoae* (Fig. 3I) with stratigraphic range Late Albian–Early Cenomanian, and *Orbitolina* (*Conicorbitolina*) *conica* (Figs. 4G, H) and *Sellialveolina viallii* (Figs. 3J, K) with Early to Middle Cenomanian range.

Dasycladalean Algae.—

Salpingoporella? sp.

Other.—

Red(?) alga *Marinella lugeoni*.

Middle Cenomanian

Benthic Foraminifers.—

The Middle Cenomanian is characterized by FOs of several stratigraphically important species, including *Biconcava bentori*, *Biplanata peneropliformis*, *Broeckina* (*Pastrikella*) *balcanica* (Figs. 4J, K), *Chrysalidina gradata* (Fig. 4I), *Pseudolituonella reicheli*, and *Pseudorhapydionina dubia.*
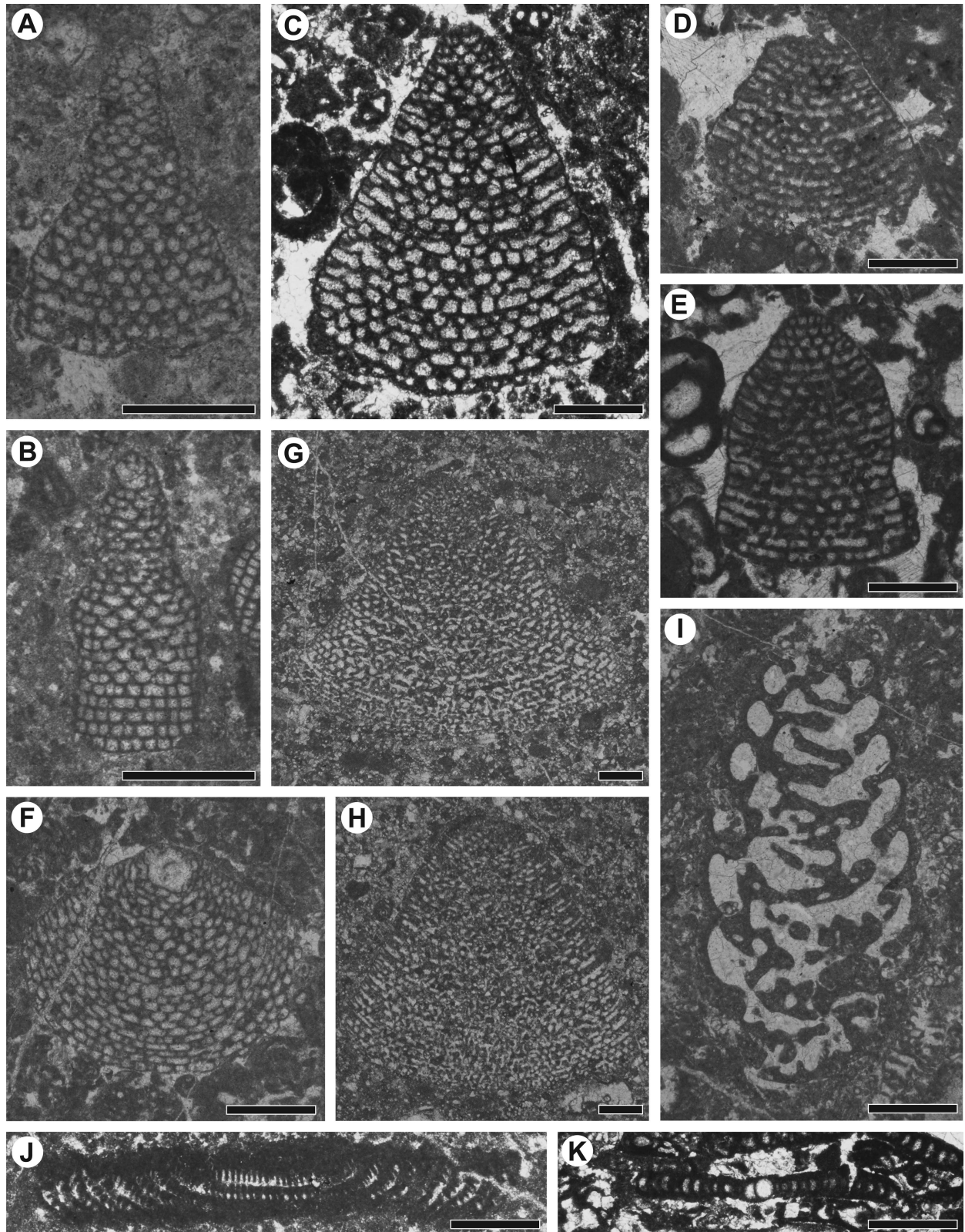
Fɪɢ. 4.—**A, B)** *Neoiraqia insolita*, Late Albian, Korčula section. **C)** "*Valdanchella*" *dercourti*, Late Albian, Mljet. **D, E)** *Simplorbitolina broennimanni*, Late Albian, Dubrovnik. **F)** *Neoiraqia convexa*, Early Cenomanian, Dubrovnik. **G, H)** *Orbitolina* (*Conicorbitolina*) *conica*, Early Cenomanian, Dubrovnik. **I)** *Chrysalidina gradata*, Middle Cenomanian, Biokovo. **J, K)** *Broeckina* (*Pastrikella*) *balcanica*, Middle Cenomanian, Mljet. Scale bars represent 0.5 mm.
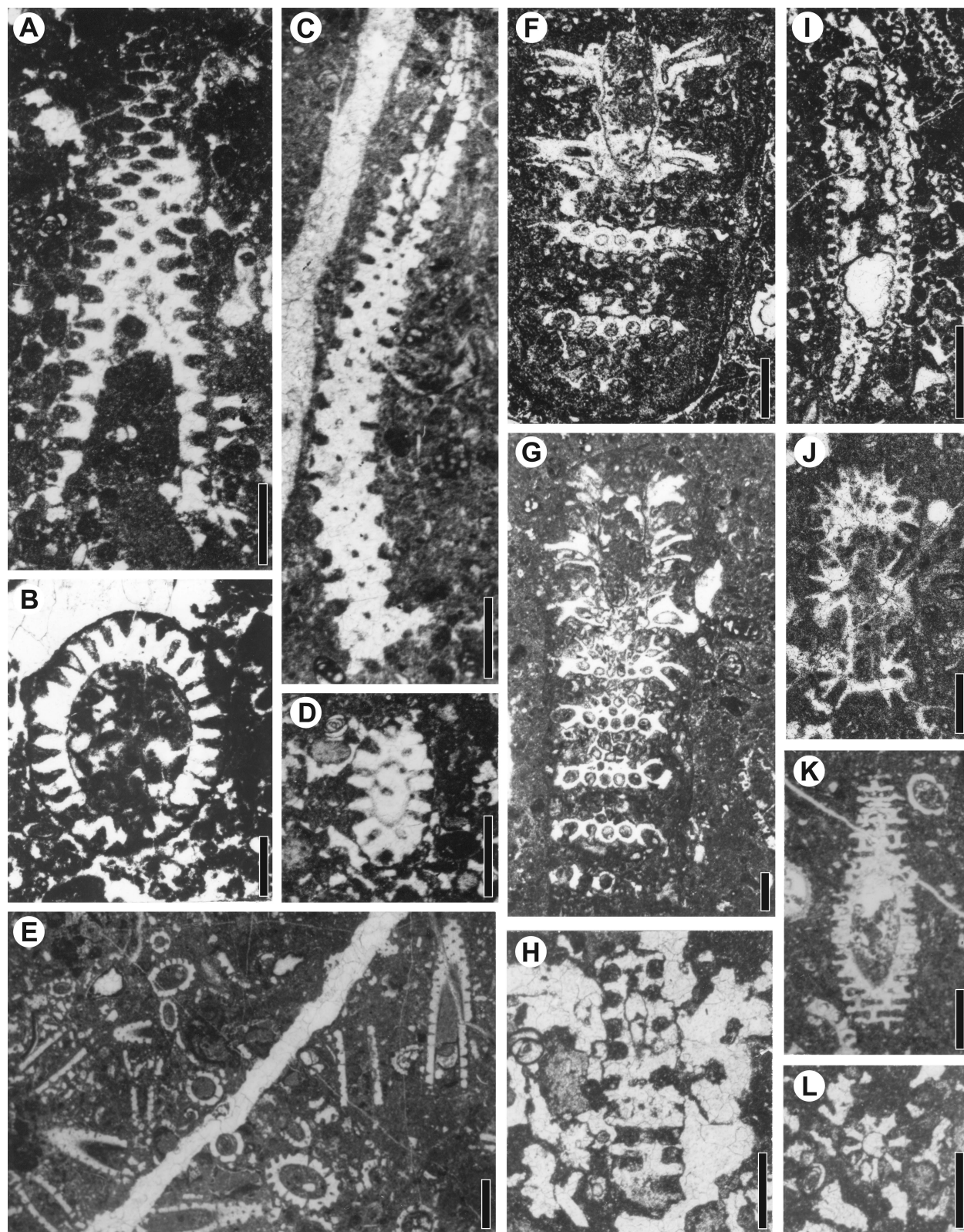
Fɪɢ. 5.—**A, B)** *Salpingoporella melitae*, Barremian, Mljet section. **C, D)** *Salpingoporella muehlbergii*, Barremian, Mljet. **E)** *Salpingoporella dinarica*, Late Aptian, Biokovo. **F)** *Actinoporella podolica*, Barremian, Mljet. **G)** "*Praturlonella*" *dalmatica*, Barremian, Korčula. **H, L)** *Salpingoporella biokoviensis*, Early Aptian, Biokovo. **I)** *Korkyrella texana*, Barremian, Mljet. **J)** *Falsolikanella nerae*, Barremian, Mljet. **K)** *Salpingoporella urladanasi*, Barremian, Dinara. Scale bars represent 0.5 mm.
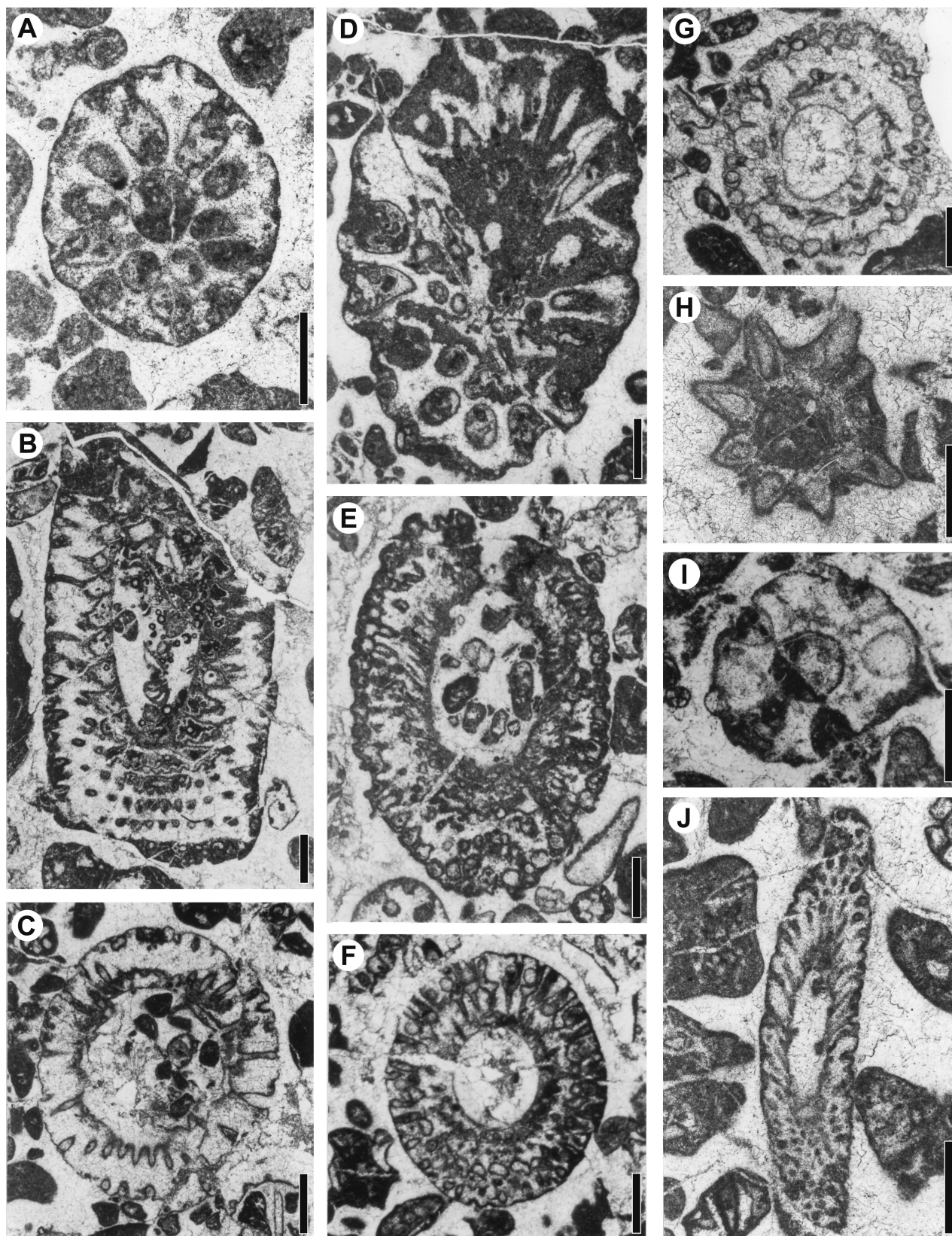
FIG. 6.—**A)** *Biokoviella robusta*, Barremian, Biokovo section. **B, C)** *Triploporella*? *sarda*, Barremian, Biokovo. **D)** *Salpingoporella patruliusi*, Barremian, Biokovo. **E, G)** *Linoporella vesiculifera*, Barremian, Biokovo. **F)** *Cymopolia velici*, Barremian, Biokovo. **H)** *Piriferella* sp., Barremian, Biokovo. **I)** *Megaporella nikleri*, Barremian, Biokovo. **J)** *Salpingoporela verticiliata*, Barremian, Biokovo.

Other.—

Alga *Thaumatoporella parvovesiculifera.*

SPECIES AND GENERA DIVERSITY (RICHNESS)

Taxon richness is by far the most commonly used measure of diversity, and is just one of many diversity facets (Purvis and Hector, 2000). Due to the patchy nature of the known fossil record, such a diversity measurement is affected by a number of assumptions regarding the data to be analyzed, including arbitrary choice of sample size and location, and potential error due to presumed clear and unambiguous classification of the subject matter. Despite its lack of theoretical elegance and the above-mentioned assumptions, Peet (1974) considered this taxon-counting approach to provide one of the simplest, most practical, and most objective measures of species richness. Accordingly, the diversity in this study is used in its simplest form, i.e., as a measure of the number of species and genera in a sample. Numerous microorganisms could not have been determined at either the species or the genus level, and were not included in diversity measurements. Due to the nature of collected bulk limestone samples, the diversity could have been studied only in thin sections. Because it was impossible to yield even a close-to-real number of individuals of each species from such material, neither heterogeneity nor equitability indices were used. We used therefore direct species and genera counts only.

In order to overcome sampling problems, in our study we took a regional approach, and tested whether the same pattern exists across a wider southern Adriatic area. Foraminiferal and dasycladalean data for Dinara, Biokovo, Korčula, and Dubrovnik were taken from Sokač et al. (1977, 1978), Sokač et al. (1979), Sokač and Tišljar (1986), and Husinec and Sokač (2006). However, in order to dismiss taxonomic artifacts, the foraminiferal data were revised and updated with regard to the taxonomic scheme of Loeblich and Tappan (1988).

Species Richness

Species richness of benthic foraminifers and dasycladalean algae for the Barremian to Middle Cenomanian of the southern part of the Adriatic platform is shown in Figure 9.

Benthic foraminifera species with author attributions and dates	BARREM.	APTIAN		ALBIAN		CENOMANIAN	
		EARLY	LATE	EARLY	LATE	EARLY	MIDDLE
Andersenolina molesta (Gorbatchik, 1959)	▬▬	▬▬					
Andersenolina sagittaria (Arnaud-Vanneau et al., 1988)	✳						
Archaealveolina reicheli (De Castro, 1966)					▬		
Archaeosepta coratina Luperto-Sinni and Masse, 1993		▬▬▬					
Belorussiella textilaroides (Reuss, 1863)	▬▬▬						
Biconcava bentori Hamaoui and Saint-Marc, 1965						▬▬	▬▬
Biplanata peneropliformis Hamaoui and Saint-Marc, 1970						▬▬	▬▬
Broeckina (Pastrikella) balcanica Cherchi et al., 1976						▬▬	▬▬
Campanellula capuensis De Castro, 1964	▪						
Charentia cuvillieri Neumann, 1965		▪					
Choffatella decipiens Schlumberger, 1903		▪					
Chrysalidina gradata diOrbigny, 1839						▬▬	▬▬
Cuneolina parva Henson, 1948				▬▬	▬	▬	▬
Cuneolina pavonia DiOrbigny, 1846			▬	▬	▬	▬	▬
Cuneolina sliteri Arnaud-Vanneau and Premoli Silva, 1995					▬▬		
Debarina hahounerensis Fourcade, Raoult and Vila, 1972		▬▬	▬	▬			
Glomospira urgoniana Arnaud-Vanneau, 1980				▬			
Haplophragmoides globosus Lozo, 1944		✳	▬				
Istriloculina granumtrici (Iovcheva, 1962)		▬▬					
Istriloculina elliptica (Iovcheva, 1962)	▬▬						
Mayncina bulgarica Laug, Peybernes and Rey, 1980	▬▬	▬					
Merlingina cretacea Hamaoui and Saint-Marc, 1970							▬▬
Nautiloculina cf. bronnimanni Arnaud-Vanneau and Peybernes, 1978	✳						
Neoiraqia convexa Danilova 1963					▬		
Neoiraqia insolita (Decrouez and Moullade, 1974)					▬	▬	
Neotrocholina aptiensis (Iovcheva, 1962)		▪					
Nezzazata conica (Smout, 1956)						▬	▬
Nezzazata gyra (Smout, 1956)						▬	▬
Nezzazata isabellae Arnaud-Vanneau and Sliter, 1995			▪				
Nezzazata simplex Omara, 1956					▬	▬	▬
Nezzazatinella cf. macoveii Neagu, 1979	▪						
Nezzazatinella picardi (Henson, 1948)				▬	▬	▬	▬
Novalesia cornucopia Arnaud-Vanneau, 1980	▬▬	▬					
Novalesia distorta Arnaud-Vanneau, 1980			✳				
Novalesia producta (Magniez, 1972)		▬	▬		▬		
Nummoloculina regularis Philippson, 1887							▬▬
Orbitolina (Conicorbitolina) conica (D'Archiac, 1837)						▬	
Orbitolina (Mesorbitolina) lotzei Schroeder, 1964		▪					
Orbitolina (Mesorbitolina) parva Douglass, 1960			▬				
Orbitolina (Mesorbitolina) subconcava Leymerie, 1878			▬				

Fɪɢ. 7.—Stratigraphic distribution of important mid-Cretaceous benthic foraminifers of southern Croatia.

Benthic Foraminifers.—

The species-richness dynamics of mid-Cretaceous benthic foraminifers is not characterized by any kind of stability (Fig. 9). Also, because various random factors make it highly unlikely that any two correlative intervals at different localities will contain exactly the same roster of taxa (Foote and Miller, 2007), there are local discrepancies. The general pattern of total species richness for the southern part of the Adriatic platform is described below.

Early Aptian Peak.—After a high diversification in the Barremian (33 species), the Early Aptian marked the benthic foraminiferal richness maximum (42 species) for the mid-Cretaceous as a whole.

Late Aptian Reduction.—A sharp decrease in the total species number occurred in the Late Aptian. However, the number of species present (29) was higher than during the Middle Cenomanian rise.

Albian Rise.—A gradual recovery that began in the Early Albian peaked in the Late Albian (37 species), marking the second-highest level of mid-Cretaceous benthic foraminiferal richness.

Early Cenomanian Reduction.—A high-diversity, shallow-water Late Albian foraminiferal association was replaced by a long interval of restricted taxonomic diversity. The Early Cenomanian marked the benthic foraminiferal low (18 species).

Middle Cenomanian Rise.—A recovery that began in the Middle Cenomanian did not compensate for the previous decrease. Consequently, the total species richness (25 species) was lower than during the Late Aptian reduction (29 species)

Dasycladalean Algae.—

Barremian Peak.—The Barremian marked the dasycladalean richness maximum (38 species) for the mid-Cretaceous as a whole (Fig. 9). In particular, this applies to the genus *Salpingoporella*, whose 13 species have been determined with *S. muehlbergii* (Figs. 5C, D) and *S. melitae* (Figs. 5A, B) being very abundant.

Early Aptian Decline.—Following the Barremian peak, the dasycladalean species richness decreased gradually in the Early Aptian. Still, the number of species (13) was high, and was not even closely reached in the remaining part of the mid-Cretaceous.

Late Aptian to Early Albian Low.—The Late Aptian and Early Albian marked the dasycladalean species-richness low. However, the Late Aptian shows an intriguing record of major algal anomaly, notably an enormous excess of *Salpingoporella dinarica* (Fig. 5E), whose individuals dramatically outnumbered all of the other organisms and became major rock-forming microfossils.

Benthic foraminifera species with author attributions and dates	BARREM.	APTIAN		ALBIAN		CENOMANIAN	
		EARLY	LATE	EARLY	LATE	EARLY	MIDDLE
Orbitolina (*Mesorbitolina*) *texana* (Roemer, 1849)				▬			
Orbitolinopsis aquitanica Schroeder and Poignant, 1964				▬			
Ovalveolina crassa De Castro, 1966						▬	
Ovalveolina maccagnoae De Castro, 1966					▬	▬	
Palorbitolina lenticularis (Blumenbach, 1805)		▬					
Paracoskinolina fleuryi Decrouez and Moullade, 1974					▬		
Peneroplis parvus De Castro, 1965							✳
Peneroplis turonicus Said and Kenawy, 1957							▬
Praechrysalidina infracretacea Luperto-Sinni, 1979	▬	▬	▬	▬	▬		
Praeorbitolina cormyi Schroeder, 1964		▬					
Protochrysalidina elongata Luperto Sinni, 1999					▬		
Pseudolituonella conica Luperto Sinni and Masse, 1993		▬					
Pseudolituonella reicheli Marie, 1952							▬
Pseudonummoloculina aurigerica Calvez, 1988			▬	▬			
Pseudonummoloculina heimi (Bonet, 1956)				▬	▬		
Pseudorhapydionina dubia (De Castro, 1965)							▬
Rumanoloculina minima (Tappan, 1943)					▬		
Rumanoloculina robusta (Neagu, 1968)	▬	▬	▬	▬			
Sabaudia auruncensis (Chiocchini and Di Napoli Alliata, 1966)			▬	▬			
Sabaudia briacensis Arnaud-Vanneau, 1980		▬					
Sabaudia capitata Arnaud-Vanneau, 1980				✳			
Sabaudia minuta (Hofker, 1965)	▬	▬	▬	▬			
Scandonea phoenissa Saint-Marc, 1974						▬	
Scandonea pumila Saint-Marc, 1974						▬	▬
Sellialveolina viallii Colalongo, 1963						▬	
Simplorbitolina broennimanni (Decrouez and Moullade, 1974)					▬		
Spiroloculina cretacea Reuss, 1854	▬						
Spiroloculina robusta Brady, 1884						▬	▬
Trochospira avnimelechi Hamaoui and Saint-Marc, 1970						▬	▬
"Valdanchella" dercourti Decrouez and Moullade, 1974					▬		
Vercorsella immaturata He, 1982			▬	▬	▬		
Vercorsella laurentii (Sartoni and Crescenti, 1962)	▬	▬	▬	▬			
Vercorsella scarsellai (De Castro, 1963)	▬	▬	▬				
Voloshinoides murgensis Luperto-Sinni and Masse, 1993		▬					

Fɪɢ. 7 (continued).—

Dasycladalean algae species with author attributions and dates	BARREM.	APTIAN		ALBIAN		CENOMANIAN	
		EARLY	LATE	EARLY	LATE	EARLY	MIDDLE
Acroporella radoicicae Praturlon, 1964	▪▪▪	▪▪▪					
Actinoporella podolica (Alth, 1878)	▬						
Biokoviella gusici Sokac, 2004	▬						
Biokoviella robusta (Sokac, 1993)	▬						
Clypeina? solkani Conrad and Radoicic, 1972	▬						
Cylindroporella lyrata Masse and Luperto Sinni, 1989	✳						
Cylindroporella sugdeni Elliott, 1957	▬						
Cylindroporella taurica Conrad and Varol, 1990					✳		
Cymopolia velici Sokac and Nikler, 1973	✳						
Falsolikanella danilovae (Radoicic, 1968)	▬						
Falsolikanella nerae (Dragastan, Bucur and Demeter, 1978)	▬	▬					
Heteroporella lepina Praturlon, 1966					✳		
Korkyrella texana (Johnson, 1965)	▬	▬					
Linoporella vesiculifera Sokac, 2005	✳						
Megaporella nikleri Sokac and Grgasovic, 2004	✳						
Neomeris cretacea Steinmann, 1899	▬						
Piriferella somalica (Conrad, Peybernes and Masse, 1983)	▬						
"Praturlonella" dalmatica (Sokac and Velic, 1978)	▬						
Salpingoporella biokoviensis Sokac and Velic, 1979	▬	▬					
Salpingoporella cemi (Radoicic, 1968)	✳						
Salpingoporella dinarica Radoicic, 1959	▪▪	▬	▬	▬	▬		
Salpingoporella genevensis (Conrad, 1969)	▪▪▪						
Salpingoporella hasi Conrad, Radoicic and Rey, 1976					✳		
Salpingoporella heraldica Sokac, 1996		▬					
Salpingoporella hispanica Conrad and Grabner, 1975	✳						
Salpingoporella melitae Radoicic, 1967	▬						
Salpingoporella muehlbergii (Lorenz, 1902)	▬						
Salpingoporella patruliusi Bucur, 1985	✳						
Salpingoporella polygonalis Sokac, 1996	✳						
Salpingoporella turgida (Radoicic, 1964)					▬		
Salpingoporella urladanasi Conrad, Peybernes and Radoicic, 1977	▬						
Salpingoporella verrucosa Sokac, 1996	✳						
*Salpingoporella verticiliata (*Sokac and Nikler, 1973)	✳						
Suppiluliumaella polyreme Elliott, 1968	▬						
Triploporella bacilliformis Sokac, 1985	▬	▬					
Triploporella imeccikae Jaffrezo, Piosson and Akbulut, 1978	✳						
Triploporella marsicana Praturlon, 1964	▬						
Triploporella sarda Jaffrezo, Bassoullet, Chabrier and Fourcade, 1978	✳						
Triploporella uragielliformis Conrad and Peybernes, 1976	▬						
Vermiporella tenuipora Conrad, 1970	✳						

FIG. 8.—Stratigraphic distribution of important mid-Cretaceous dasycladalean algae of southern Croatia.

Although the number of species was slightly higher in the subsequent Early Albian, none of them was even close in abundance to *S. dinarica* during the Late Aptian.

Late Albian Mini High.—This "mini" high turns out to be the swan song of mid-Cretaceous algae, with a doubling of recorded species (7) from the Late Aptian (3) to the Early Albian (4). However, the total number of species was lower than during the Early Aptian decline (13).

From this "peak", species richness declined dramatically during the Cenomanian.

Cenomanian Reduction.— The Late Albian association was decimated, with only one species being recorded in the Early Cenomanian, and none in the Middle Cenomanian.

Genus Richness

Benthic Foraminifers.—

Genus richness shows a pattern similar to that of species richness (Fig. 9). A minor difference in pattern is observed for the Late Aptian–Early Albian with a slight drop in genus richness, whereas species richness rises. Following the Barremian high genus richness (23 genera), the diversity maximum was reached in the Early Aptian (31 genera). Subsequent drop led to a Late Aptian–Early Albian plateau of low genus richness (19 and 18 genera, respectively). The Late Albian high (23 genera) was followed by a sudden drop in the Early Cenomanian, with the lowest richness for the mid-Cretaceous as a whole (12 genera). Subsequent recovery began in the Middle Cenomanian (20 genera). Except for the Early Aptian high and the Early Cenomanian low, it is evident that the overall diversity changes in benthic foraminifers resulted mostly in species (much less genus) turnovers.

Dasycladalean Algae.—

Genus richness shows a pattern similar to that of species richness, with even fluctuations being similarly pronounced (Fig. 9). The maximum in genus richness was reached in the Barremian (18 genera), and from this peak it declined through the Early Aptian (8 genera). This decline led to a plateau, with only 2 genera in the Late Aptian and Early Albian. Diversification increased in the Late Albian (4 genera), but then irretrievably declined to only
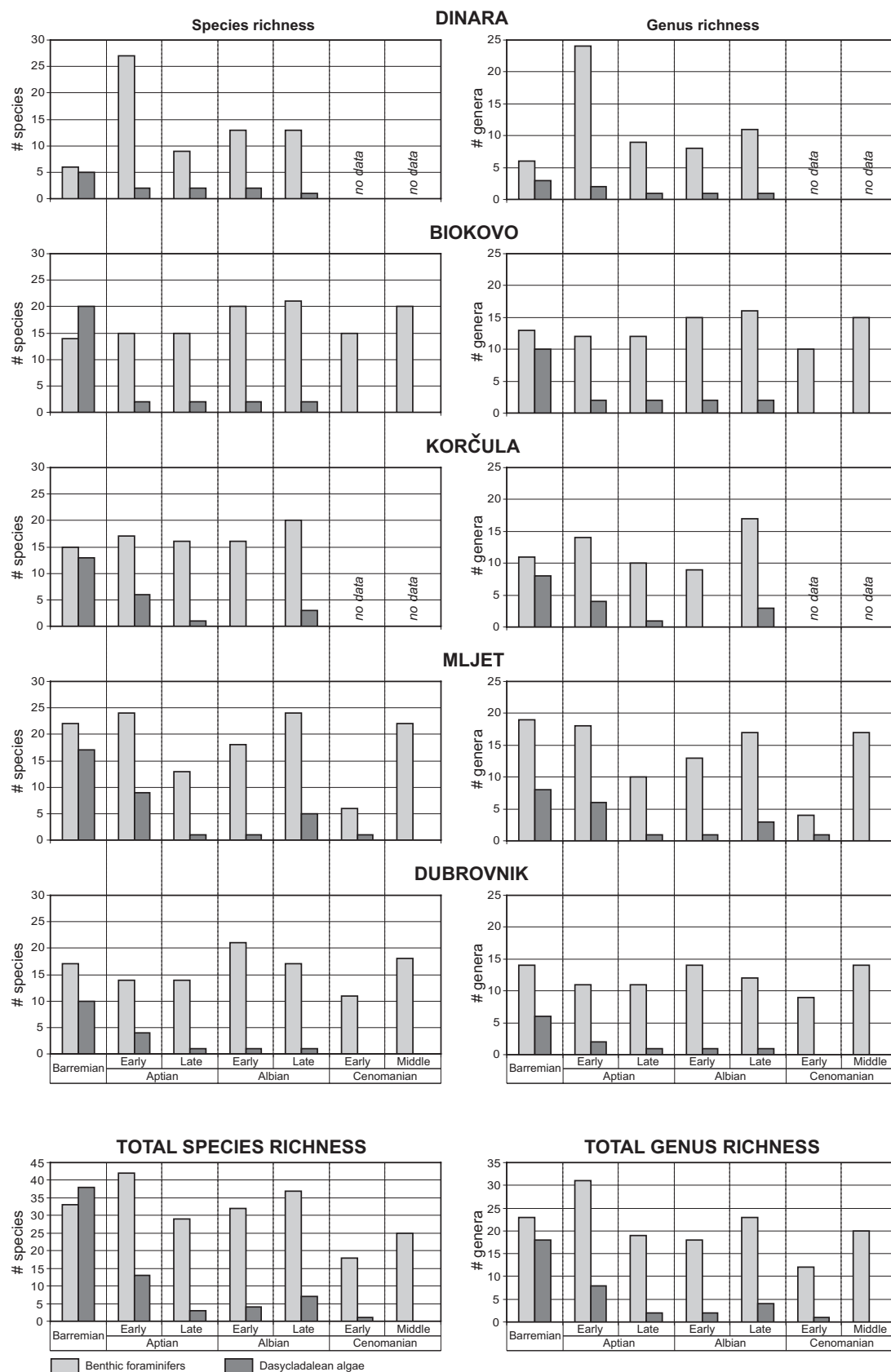
Fig. 9.—Histograms showing species and genus richness of the southern part of the Adriatic platform (for localities see Figure 1). Early to Middle Cenomanian thick-bedded to massive dolomites of Dinara and Korčula are devoid of fossils.

one genus in the Early Cenomanian. A minor difference in pattern is observed for Late Aptian–Early Albian with unchanged genus richness, whereas species richness increased in the Early Albian.

DISCUSSION

Sea-Level History

Because benthic foraminifers and dasycladalean algae of shallow tropical seas are sensitive to changes in sea level, we might expect their diversity to have been strongly affected by changes in relative water depths. Ever since the work of Newell (1967), the association between diversity pattern in the marine realm and eustatic sea-level change in the Mesozoic has been extensively elucidated. Recently, Smith et al. (2001) summarized that there are three plausible oceanographic events triggered by sea-level change that might drive biological extinction: (1) increased competition for space and resources among shallow benthic biota during lowstand, (2) enhanced surface-water productivity during transgression may trigger expansion of dysoxic or anoxic conditions and, (3) spread of oligotrophic oceanic waters associated with lower surface-water productivity during highstand.

The studied inner part of the platform, with its species' ecological tolerance and biota being restricted to intertidal or shallow subtidal zones, bears hardly any direct paleobiological evidence of sea-level history. Paleobiological evidence for sea-level change is very scarce and geographically restricted, with planktonic foraminifers and fragments of pelagic crinoids indicating deepening in the Early Aptian, and charophytes being indicators of local lacustrine environments in the Late Albian. The abundance or scarcity / absence of a group of organisms is also an unequivocal indicator of paleoenvironmental conditions, as is their diversity as well. Therefore, our knowledge of sea-level history rests predominantly on vertical facies distribution. This indicates repeated oscillations from subtidal to intertidal–supratidal settings with periodic subaerial exposure. According to Husinec (2002), transgressive periods favored intensified carbonate production, resulting in generally thicker beds deposited in subtidal environments of protected shoals and / or lagoons. In the study area, regressive periods are characterized by tidal-flat progradation and subsequent peritidal upward-shallowing cycles, commonly ending with emersion-breccia horizons at their tops. Husinec (2002) used reconstruction of vertical facies distribution and variability to construct a relative sea-level curve for the Mljet Island succession, which is also part of our study area (Fig. 1). Most of the facies changes were interpreted as changes in relative water depth, and consequently accommodation space across the area. For the mid-Cretaceous interval this curve shows relative sea-level rise in the Early Aptian followed by Late Aptian sea-level fall. Subsequent transgression in the Early Albian was followed by a relative sea-level fall during the Late Albian–Early Cenomanian. The ultimate transgression occurred in the Middle Cenomanian. Since the similar vertical facies distribution is present in all of our five sections in the study area (Fig. 2), we presume that Husinec's (2002) pattern of relative sea-level signature constructed for Mljet section is to some extent applicable for the entire studied area.

Barremian.—

The Barremian stage was characterized by upward-shallowing cycles of shallow subtidal to intertidal and supratidal facies with frequent short-lived exposures. This regional sea-level fall (Husinec and Jelaska, 2006) coincided with species-rich foramin-

iferal assemblage. This suggests that benthic foraminifers could simply have migrated as sea levels changed. During intervals when relative sea level was exceptionally low and the foraminifera-hostile intertidal–supratidal environments predominated in the interior of the platform, many taxa could have migrated into more hospitable low-energy shallow subtidal environments seaward of tidal flats. Mid-Cretaceous dasycladalean taxon diversity peaked in the Barremian (Fig. 9). Based on compilations by Deloffre and Granier (1992), Granier and Deloffre (1993, 1994), and Bucur (1999), Aguirre and Riding (2005) inferred a positive correlation between dasycladalean taxonomic diversity and periods of intermediate sea level, reflecting maximum extent of shallow tropical seas.

Early Aptian.—

Early Aptian diversification, during which benthic foraminifers reached their mid-Cretaceous all-time peak, coincided with a local sea-level high. Paleobiological evidence for deepening includes rare occurrences of planktonic foraminifers (*Hedbergella* sp.) and fragments of pelagic crinoids (*Saccocoma* sp.). During that transgression phase, foraminifers were able to diversify into various euphotic habitats, particularly in subtidal environments of the platform interior. On the contrary, dasycladalean diversity declined, which does not seem to match well with the coeval trends elsewhere in Tethys where this event occurred somewhat later, i.e., at the Early–Late Aptian transition (Masse, 1993; Bucur, 1999). This regional Early Aptian decline in dasycladalean taxon richness may have been triggered by reduction of niches preferentially occupied by dasycladaleans due to sea-level high.

Late Aptian.—

An apparent regional regression (see Vlahović et al., 2005; Husinec and Jelaska, 2006; and references therein) during the Late Aptian is evidenced by several clayey and / or emersion-breccia intervals. This subaerial exposure was a major factor in eliminating and changing diversity of subtidal biota. It broadly coincided with a sharp decrease in the number of total species and genera for both foraminifers and algae.

Albian.—

Benthic foraminifers show a gradual increase in taxon richness throughout the Albian. This improvement in living conditions in a shallow epicontinental sea indicates a gradual recolonization of the formerly subaerially exposed platform interior. It seems that a rising sea level improved connections with adjacent Umbria–Marche and Adriatic–Ionian basins, and enabled migration of new taxa and repopulation of the "Lazarus" taxa onto the platform. Unlike foraminifers, dasycladalean algae never recovered from this episode, and their richness in post-Aptian deposits of the Adriatic platform never got even close to that of the Early Cretaceous levels.

Early Cenomanian.—

Early Cenomanian foraminiferal assemblages became impoverished due to a regional regression episode that began already in the latest Albian. This regression at the Albian–Cenomanian transition is indicated throughout the region, either by emersion-breccia intervals or by dolomite with well-preserved structures and textures indicating shallowing to supratidal conditions. Thus this diversity low may reflect the poor quality of the fossil record due to intense dolomitization, but it may also be real,

and a useful indicator of genuinely low-abundance fauna in the aftermath of extinction (cf. Wignall and Benton, 1999).

Middle Cenomanian.—

Overall deepening and a shift towards intertidal (episodically supratidal) and shallow subtidal facies during the Middle Cenomanian facilitated recolonization of the platform interior. This renewal of benthic foraminiferal (not algal!) assemblages probably was a herald of the subsequent end-Cenomanian–Early Turonian relative sea-level rise and associated oceanic anoxic event (OAE 2: Schlanger and Jenkyns 1976; Jenkyns 1980; Arthur et al. 1990; Gušić and Jelaska, 1993).

Habitats

Hallock (1987) developed the argument that nutrient availability is a major factor influencing diversity of euphotic habitats, and nutrient supply controls depth of light penetration. The Cretaceous seas were extremely oligotrophic (Bralower and Thierstein, 1984), and in shallow euphotic waters light was not a limiting factor, in that algal-symbiont-bearing foraminifers could function as plants, i.e., deriving most of their energy by photosynthesis (Hallock, 1981). The Adriatic platform, occupying low latitudes and being isolated from sources of runoff and upwelling during its mid-Cretaceous evolution, seems to be one of the fine examples of such oligotrophic environments.

During the major mid-Cretaceous transgressive episode in the Early Aptian, organisms could have diversified into a cohort of euphotic habitats. At the close of that episode, when circulation of shallow platform waters increased, nutrient availability in surface waters increased, and the deepest, highly oligotrophic habitats were eliminated. Consequently, the apparent regional Late Aptian regression resulted in loss of "deeper" subtidal habitats, and the extinctions of organisms specialized to those habitats. This relationship between nutrients and euphotic habitats is stressed by Hallock (1988), who argued that an increase in deep ocean circulation that raised oceanic fertility worldwide to levels seen in the Atlantic today would probably eliminate level 4 (oligotrophic) and level 5 (highly oligotrophic) habitats, resulting in extinctions of up to 60% of the species living in euphotic environments. The Aptian episode of high (Early Aptian) and low (Late Aptian) diversity is much easier to understand in the context of this relationship. The Late Aptian regression resulted in abundant accumulation of nutrients that supported a dense growth of the alga *Salpingoporella dinarica* (Fig. 5E), the decay of which could have gradually depleted the shallow waters of oxygen. In addition, this event, which eliminated oligotrophic habitats, also could have reduced the preservation potential of the remaining taxa (Hallock, 1988). The benthic community (not algae!) gradually recovered in the Albian, aided by a transgression and associated decrease in fertility of platform waters. Regional onset of regression in the latest Albian again could have increased nutrient supplies to surface waters, reducing euphotic habitats. Subsequently, the Early Cenomanian was marked by numerous extinctions of shallow-water biota. An increased oligotrophy in the Middle Cenomanian could have provided a suite of euphotic habitats. These in turn provided niches for various agglutinated and porcelaneous forms of benthic foraminifers.

Temperature

In the Cretaceous, there were some warm peaks apparently associated with oceanic anoxic events (Jones and Jenkyns 2001;

Jenkyns 2003; Erba et al. 2004). In the study area, the foraminiferal diversity reached its maximum value in the Early Aptian (Fig. 9), presumably influenced by a regional transgression coeval to the Oceanic Anoxic Event 1A ("Livello Selli": Menegatti et al., 1998). This event is one of the best-documented oceanic anoxic events in the mid-Cretaceous, and it involved mass extinctions among the benthic platform biota on numerous Tethyan localities (e.g., Masse, 1989; Erba, 1994; Luperto Sinni and Masse, 1993; Skelton, 2003). However, in the study area there is neither sedimentological nor faunal evidence that anoxia spread into platform-interior settings where foraminiferal biodiversity was highest. Following the Late Aptian diversity minimum, the foraminiferal association gradually recovered through the Albian, reaching a peak in the Late Albian. This Albian increase in diversity again may have been initiated by the regional sea-level rise.

The diversity of unsophisticated carbonate secretors, such as dasycladalean algae, presumably was much more influenced by changes in seawater temperature. Aguirre and Riding (2005) compared the Veizer et al. (2000) temperature plots with dasycladalean algal biodiversity and argued for a strong link between long-term pattern of diversity and global fluctuations in temperature and sea level. Besides a broad positive correspondence between dasycladalean diversity and paleotemperatures for the Carboniferous–Pliocene, the authors acknowledged an anomaly for the Albian–Turonian, when despite high temperatures dasycladalean diversity declined. Such a discrepancy is also observed in the Albian succession of the studied area, which appears not to support a straightforward relationship between dasycladalean diversity and paleotemperature values.

Further stable-isotope studies are necessary to compare the dasycladalean diversity pattern and paleotemperature changes.

Calcite vs. Aragonite Seas

Oscillations in the carbonate mineralogy of dominant reef-building and sediment-producing organisms are in harmony with the oscillations in seawater chemistry controlled by changes in global spreading rates along mid-ocean ridges (Stanley and Hardie, 1998). Because dasycladalean algae control their mineralization only weakly, or simply induce it by modifying the chemistry of neighboring seawater (Lowenstam and Weiner, 1989), Stanley and Hardie (1998) argued that their productivity has been strongly affected by secular changes in seawater chemistry. With their thalli that can be heavily calcified, dasycladalean algae act as one of the major sediment producer on a shallow carbonate platform. Extant dasycladaleans are aragonitic, with rare possible exceptions (e.g., Simmons et al., 1991); this appears to have been the principal mineralogy of the group throughout its history (Berger and Kaever, 1992). Stanley and Hardie (1998) suggested that dasycladalean abundance matches with aragonite-sea episodes, with the only discrepancy for Late Jurassic and Early Cretaceous time. Recently, however, Aguirre and Riding (2005) have shown that both calcite and aragonite episodes include periods of high and low dasycladalean diversity. Our study shows a negative correspondence between the pattern of mid-Cretaceous dasycladalean taxon richness and Mg/Ca mole ratio model of Hardie (1996). It exhibits a peak of dasycladalean diversity in the Barremian (Fig. 9), i.e., when the Mg/Ca ratio plunged to a very low level (episode calcite II; Stanley and Hardie, 1998). It implies that aragonitic dasycladaleans were important sediment producers on tropical carbonate platforms even at times of calcite-sea highs. During a post-Barremian drop in taxon richness, we record an extreme abundance of *Salpingoporella dinarica* (Fig. 5E) in the Late Ap-

tian. Such a hypercalcification by this alga could be compared to a production of vast quantities of carbonate sediment by *Halimeda* in Neogene reefal lagoons (Hillis-Colinvaux, 1980). A "boom" of *Salpingoporella dinarica* occurred around the Mesozoic peak of calcite seas, which may have promoted probably calcitic (Simmons et al., 1991) *S. dinarica* to become a major carbonate producer within shallow platform interiors during the Late Aptian. Post-Aptian aragonitic dasycladaleans of the Adriatic platform are very scarce, which is in close agreement with the low Mg/Ca ratio of Stanley and Hardie (1998).

CONCLUSIONS

The mid-Cretaceous southern interior part of the Adriatic platform is characterized by exclusively shallow-water carbonate facies that were deposited in shallow-water, peritidal environments. The succession is characterized by a relatively rich association of shallow marine benthic organisms, primarily foraminifers and dasycladalean algae. Both the fossil record and the sedimentary record point to several episodes of change in relative sea level, paleoenvironments, and distribution of paleocommunities dominated by benthic foraminifers and dasycladalean algae. The taxon richness patterns of these benthic organisms in the study area appear related to regional changes in relative sea level, coupled with related changes in habitats, temperature, and possibly oscillations in carbonate mineralogy.

The observed taxon richness pattern of benthic foraminifers shows that after a relatively high diversification in the Barremian, the Early Aptian marked the foraminiferal taxon richness maximum. Foraminifers diversified into a suite of euphotic habitats backed by a relative sea-level rise that coincided with Oceanic Anoxic Event 1A. The regional regression in the Late Aptian resulted in loss of "deeper" subtidal habitats and, consequently, a drop in foraminiferal taxon richness. Transgression in the Early Albian and probable associated decrease in fertility of platform waters resulted in the gradual increase of taxon richness throughout the Albian. Regional onset of regression in the latest Albian again could have increased nutrient supplies to surface waters, and consequently, the subsequent Early Cenomanian foraminiferal association reached its mid-Cretaceous taxon richness minimum. The Middle Cenomanian relative sea-level rise led to a gradual recolonization of the platform interior and renewal of the benthic foraminiferal association.

The dependence on factors other than relative sea level and associated changes in habitats is much more pronounced in diversity patterns of aragonitic dasycladalean algae. The dasycladalean algae reached their taxon richness maximum in the Barremian, during maximum extension of tidal-flat environments. From this peak the diversity declined during the Early Aptian sea-level rise, reaching a plateau in the Late Aptian–Early Albian. The Late Aptian extreme abundance of the reputed calcitic alga *Salpingoporella dinarica* may have been triggered by the peak of the Mesozoic calcite II sea episode of Stanley and Hardie (1998). Subsequently, it seems that despite high temperatures and the renewal of vast tidal-flat environments during the Late Albian–Early Cenomanian, the mid-Cretaceous dasycladaleans never fully recovered from the Early Aptian platform deepening event.

ACKNOWLEDGMENTS

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