

STABLE ISOTOPE SCLEROCHRONOLOGY OF *VACCINITES CORNUVACCINUM* (HIPURITIDAE) FROM BEOTIA (GREECE)

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ABSTRACT

The carbon and oxygen isotopic composition was analysed in several shells of *Vaccinites cornuvarcinum* (Bronn) from late Santonian-Campanian transgressive deposits of Beotia (central Greece). Elemental compositions and good preservation of the fibrous prismatic structure indicate only minor diagenetic alterations of the outer shell layers. Originally aragonitic inner shell layers have been altered by either dissolution and subsequent precipitation of clear calcite spar, or by calcitization in geochemically more closed systems, resulting in an irregular mosaic of dull-grey calcite. In the latter case, original isotopic compositions have been partially retained, as indicated by higher ^{13}C and ^{18}O contents when compared to the outer shell layers.

Two shells were analysed in sclerochronological profiles through the outer layer. Juvenile shells apparently recorded complete annual records of palaeotemperature variations while growth deceleration during summer occurred in the adult stage of a larger shell. Periods of reduced shell growth are marked by distinct growth lamellae, dark-coloured growth lines, and a change in shell structure; they probably correspond to reproductive cycles. Annual growth increments of the two studied shells amount to 40 mm in the juvenile phase and decrease to less than 10 mm in the adult shell.

Key words: Sclerochronology, oxygen stable isotope, carbon isotope, aragonite, calcite, palaeotemperature, annual growth.

RESUMEN

Fue analizada la composición isotópica del carbono y el oxígeno en varias conchas de *Vaccinites cornuvarcinum* (Bronn) provenientes de los depósitos transgresivos del Santoniano tardío-Campaniano de Beocia (Grecia central). La composición de los elementos y la buena conservación de la estructura fibroso-prismática indican alteraciones diagenéticas menores de las capas externas de la concha. Las capas internas de la concha, originalmente aragoníticas, han sido alteradas ya sea por disolución y subsecuente precipitación de espato de calcita clara, o bien por calcitización en sistemas geoquímicamente más cerrados, que da por resultado un mosaico irregular de calcita gris opaca. En el último caso, las composiciones isotópicas originales se conservaron parcialmente, como lo indica el contenido más alto de ^{13}C y ^{18}O en comparación con las capas externas de la concha.

Fueron analizados perfiles esclero cronológicos de la capa externa de dos conchas. En las conchas juveniles se encontró, aparentemente, registros anuales completos de variaciones de paleotemperatura, en tanto que en el estado adulto de una concha más grande se registró un retardo en el crecimiento durante el verano. Los períodos de crecimiento lento de la concha se marcan por láminas de crecimiento diferentes a las normales, por líneas de crecimiento de color oscuro y por un cambio en la estructura de la concha; estos períodos, probablemente, corresponden a ciclos reproductivos. El incremento de crecimiento anual en las dos conchas estudiadas alcanzó 40 mm en la fase juvenil y disminuyó a menos de 10 mm en la concha adulta.

Palabras clave: Esclero cronología, isótopos de oxígeno, isótopos de carbono, aragonita, calcita, paleotemperaturas, crecimiento anual.

INTRODUCTION

Sclerochronological analyses of recent bivalves have proven that environmental and physiological changes such as temperatures, tides and reproductive events affect shell growth patterns (e.g., Pannella and MacClintock, 1968; Rhoads and Pannella, 1970; Lutz and Rhoads, 1980). Therefore, invertebrates with continuously accreted skeletons store information about their life history in their hard parts. Additionally, the oxygen isotopic compositions of shell carbonate along profiles through recent bivalve shells were found to monitor precisely the seasonal variations in ambient water temperature (e.g., Killingley and Berger, 1979; Jones *et al.*, 1983; Jones *et al.*,

1984). In contrast to several other marine invertebrates, molluscs incorporate oxygen into their shells in—or near to—isotopic equilibrium with ambient water (Wefer and Berger, 1991). Variations in $\delta^{13}\text{C}$ have been traced back to periods of upwelling (Killingley and Berger, 1979), salinity events, and the effect of marine productivity on the composition of dissolved inorganic carbon (Arthur *et al.*, 1983), although vital effects usually cause disequilibrium fractionation between marine HCO_3^- and shell CaCO_3 (Wefer and Berger, 1991). Isotopic analyses of fossil molluscs were focused on diagenetic alterations of the calcitic and aragonitic skeletons (e.g., Buchardt and Weiner, 1981; Morrison and Brand, 1988). Their recognition is most important for well-founded palaeoclimatic and palaeoecologic interpretations (e.g., Tourtelot and Rye, 1969; Stevens and Vella, 1981; Saltzman and Barron, 1982) of the isotopic composition of fossil shells.

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First data on Cretaceous sea-water temperatures in connection with the palaeogeographic distribution of rudists were provided by Lowenstam and Epstein (1959). These implications were based on analyses of co-occurring belemnites and not of the rudist shells themselves. Polšak and Leskovsek-Sefman (1973) analysed several rudist shells, however, without paying attention to mineralogically and structurally different shell layers of hippuritids, radiolitids and caprinids. The diagenesis of rudist shells was investigated by a combination of textural, geochemical, and stable isotope analyses (Al-Aasm and Veizer, 1986a, 1986b; Woo *et al.*, 1993).

As their massive outer shell layer is composed of diagenetically stable low-Mg calcite (Skelton, 1976), hippuritid rudist bivalves can be expected to be particularly well suited for palaeoclimatic and palaeoecologic studies. Furthermore, their large size promises the resolution of annual growth increments by closely spaced sampling along the growth axis.

LATE SANTONIAN-CAMPANIAN RUDIST BIO-STROMES OF BEOTIA

Rudists are frequently observed in the basal levels of Cretaceous transgressive deposits in Beotia, central Greece (Figure 1). The folded Triassic-Jurassic basement of the region—Pelagonian continental fragment—(Mountrakis, 1986) was flooded by several transgressive pulses since the Aptian

(Steuber *et al.*, 1993). During the Cretaceous, the neritic depositional environments of the Pelagonian of Beotia were located marginally to the Pindos Ocean, which separated the Apulian and Pelagonian platforms during most of the Mesozoic.

One of the major transgressive intervals was dated to be of late Santonian-Campanian age by abundantly preserved rudists (Steuber *et al.*, 1993; Steuber, 1993, 1994). It postdates a regional period of emersion, when formerly marine realms of south Beotia and the bordering Parnassus platform were subjected to karstification (Caminiti, 1985; Konertz, 1987). Late Santonian-Campanian deposits, therefore, follow conformably over Coniacian karstified limestones in south Beotia and unconformably over folded pre-Aptian sediments or ophiolitic volcanics in North Beotia (Steuber *et al.*, 1993). Rudists can be studied in life position in several outcrops of these transgressive deposits. By far dominating among the hippuritids is *Vaccinites cornuvaccinum* (Bronn, 1831). It is associated with a diverse radiolitid and caprinid assemblage, comprising: *Bournonia africana* Douvillé, 1910; *Bournonia fourtaui* Douvillé, 1910; *Durania katzeri* (Sliskovic, 1984); *Durania martellii* Parona, 1911; *Fossulites dionysii* Steuber, 1994; *Fossulites aff. undaesaltus* (Astre, 1954); *Gorjanovic boeotica* Steuber, 1994; *G. costata* Polšak, 1967; *G. gracilis* (Wiontzek, 1934); *G. kayae* Özer, 1982; *G. lipparinii* Polšak, 1967; *Medeella cf. zignana* (Pirona, 1869); *Praeradiolites echennensis* Astre, 1954; *Radiolites subradius* Toucas, 1908; *Sauvagesia meneghiniana* (Pirona, 1869); *Sauvagesia tenuicostata* Polšak, 1967; and *Mitrocaprina beotica* (Munier-Chalmas, 1867).

Vaccinites cornuvaccinum (Bronn) was found to occur with several growth morphotypes. At Keratovouno hill (Figure 1), the type locality of "*Hippurites gaudryi* Munier-Chalmas 1867", shells are preserved in a reclined life position. At other localities, erect elevators dominate and sometimes formed clusters of 4–5 individuals. These various growth morphologies indicate adaption to different sedimentation rates and water agitations (Skelton and Gili, 1991). Various sedimentary environments are also indicated by changing radiolitid associations. *V. cornuvaccinum* with a reclined growth habit at Keratovouno hill occurs together with the recumbent *Mitrocaprina beotica* and the "clinger" *Praeradiolites echennensis*, both of which could not cope with high sedimentation rates.

CARBON AND OXYGEN ISOTOPIC COMPOSITION OF VACCINITES CORNUVACCINUM SHELLS

Only a small number of collected shells was sufficiently well preserved for isotopic analyses, because the outer shell layer was usually perforated by boring organisms. Preservation of unbored outer shell layers is generally good, revealing growthbanding in thin section (Plate 1, figure e) and a fibrous prismatic shell structure with divergent prisms on radially broken surfaces (Plate 1, figures a, b). Four elemental analyses (ICP-AES) of the outer shell layer of the specimen on Figure 5

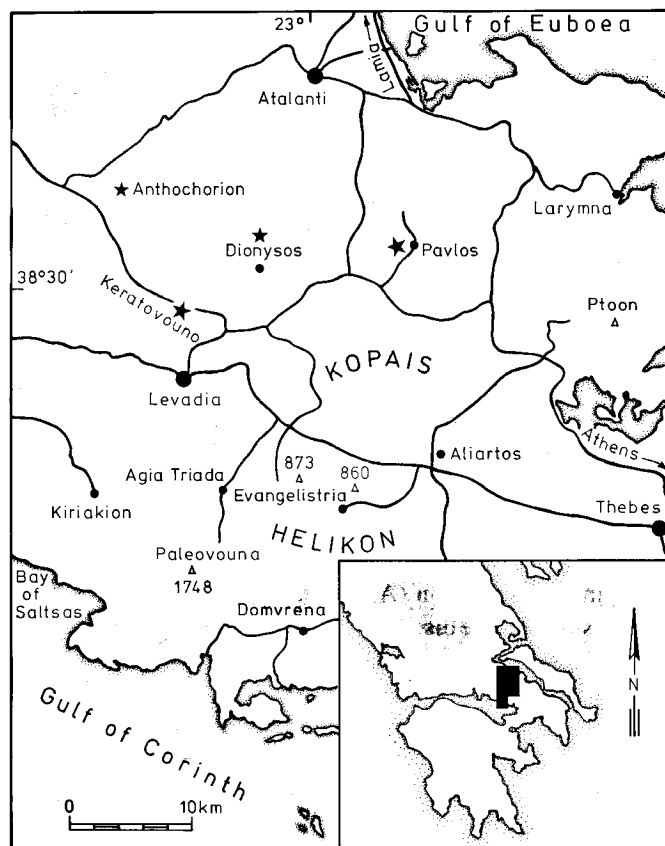


Figure 1. Location map. Asterisks indicate collection sites of *Vaccinites cornuvaccinum* (Bronn).

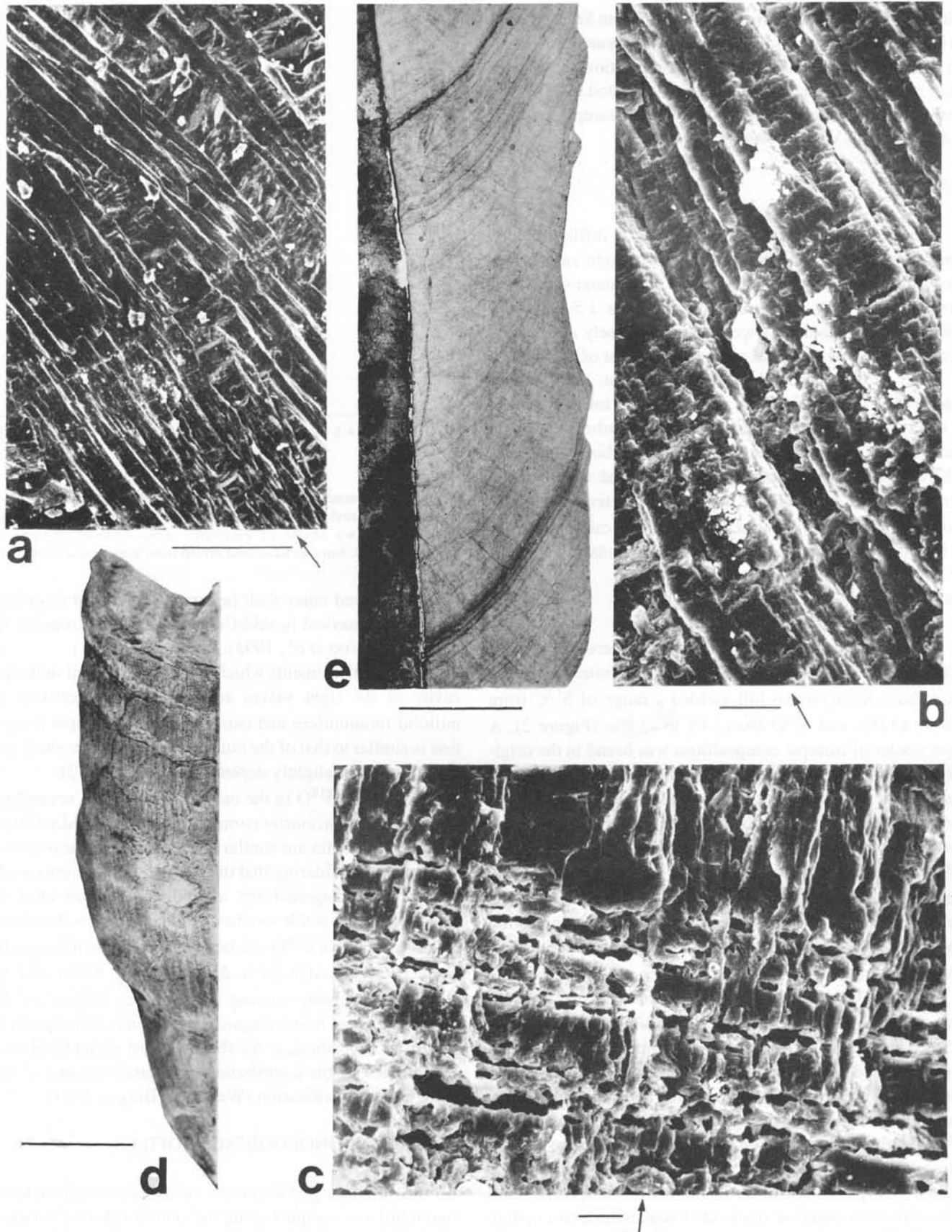


Plate 1. SEM micrographs of radial fractures of the outer shell layer (a-c) of the specimen on Figure 2 show prismatic structure (a) and closely spaced growth lines of prisms (b). Intercalated are thin layers (c) with small dissolution pits which correspond to growth lamellae of the sculpture (d) and major dark growth lines which are visible in thin section (e). Arrows indicate direction of growth. Scale bar: 100 mm in figure a, 10 mm in figures b and c, 20 mm in figure d, and 3 mm in figure e.

yielded 1,117–1,443 ppm Mg; 1,243–1,373 ppm Sr; 7–14 ppm Mn and Fe concentrations below 80 ppm—instrumental detection limit at the chosen dilution. This composition agrees with recent calcitic mollusc shells (Harriss, 1965; Dodd, 1967) and corresponds to the least diagenetically altered samples studied by Al-Aasm and Veizer (1986a).

METHODS

The shells were sampled with a dental drilling device from transverse and longitudinal sections of right valves. Isotope profiles from longitudinal sections of the outer shell layer were obtained with a 0.5-mm drill bit from 1.5-mm-thick polished sections. Samples were taken as closely as possible in consecutive rows and had an average weight of 0.5–1 mg.

The carbonate samples were roasted at 180°C under vacuum for 5–8 hours because organic matter incorporated in the outer shell layers was found to cause disturbance of mass spectrometric analyses. After digestion of carbonate samples with H₃PO₄, the CO₂ samples were measured with either a Finnigan Delta S or MAT 252 mass spectrometer. Repeatability of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was better than $\pm 0.1\text{‰}$ as calculated from the results of multiple analyses of NBS19 standard.

RESULTS

Samples which were drilled from transverse sections of the outer shell layer of two specimens of *Vaccinites cornuaccinum* from Keratovouno hill yielded a range of $\delta^{13}\text{C}$ from +1.9 to +3.0‰ and $\delta^{18}\text{O}$ from -4.5 to -2.8‰ (Figure 2). A larger scatter of isotopic compositions was found in the originally aragonitic inner layers. In the studied shells, they are preserved as diagenetic calcite, however, with a non-uniform fabric. Large parts, especially teeth and posterior myophores have been completely dissolved and voids were later filled with clear, equant calcite spar. These are the most ^{13}C and ^{18}O -depleted constituents of the shells with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ as low as -3.5‰ and -6.8‰, respectively (Figure 2), indicating precipitation from meteoric fluids or at elevated burial temperatures.

Most of the inner shell layer now consists of dull-grey, subhedral calcite with $\delta^{13}\text{C}$ of up to +4‰ and $\delta^{18}\text{O}$ of up to -1.5‰. The isotopic difference between this and the outer shell layer corresponds approximately to different equilibrium fractionations in the systems calcite-water and aragonite-water. Aragonite is found to be enriched by 0.7‰ in ^{18}O and by 1‰ in ^{13}C relatively to coexisting calcite at relevant temperatures (Grossman, 1984; Grossman and Ku, 1986). Therefore, the original isotopic composition in the former aragonitic shell layer of the two analysed shells has been retained to a certain extent. This implies the transformation from aragonite to calcite in a closed system, perhaps along intergranular alteration films (Pington, 1982). Comparable isotopic relationships be-

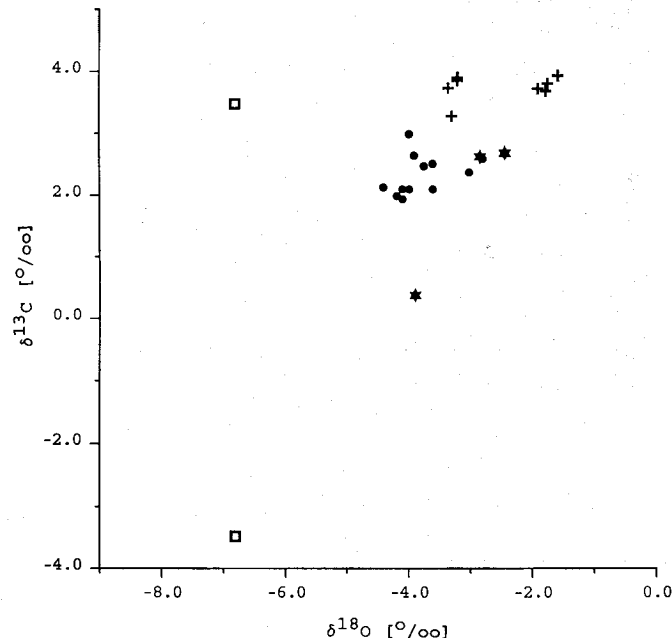


Figure 2. $\delta^{13}\text{C}$ versus $\delta^{18}\text{O}$ of outer shell layers (dots), calcitized inner shell layers (+), internal sediments (asterisks), and diagenetic sparry calcite (squares) of two shells of *Vaccinites cornuaccinum* (Bronn) from Keratovouno hill. Samples have been drilled from transverse sections.

tween unaltered outer shell layers and calcitized inner layers have been observed in mid-Cretaceous rudists from the Gulf of Mexico (Woo *et al.*, 1993).

Internal sediments which have been trapped in the body cavity of the right valves are clay-rich wackestones with miliolid foraminifera and ostracods. Their isotopic composition is similar to that of the outer shell layer in one shell, in the other, however, slightly depleted in ^{13}C (Figure 2).

$\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in the outer shell layers of several other right valves of *Vaccinites cornuaccinum* collected at different localities in Beotia are similar to those from Keratovouno hill (Figure 3). Considering that the original isotopic composition has not been diagenetically altered, this species must have thrived in rather stable environmental conditions, because the observed range in $\delta^{18}\text{O}$ can be ascribed to precipitation from Cretaceous seawater (-1‰ $\delta^{18}\text{O}$ SMOW; Savin and Yeh, 1981) at seasonally varying temperatures (Figure 3). $\delta^{13}\text{C}$ deviates slightly from inorganic equilibrium. This agrees with isotopic compositions of the shells of most extant bivalves and is explained by the contribution of a certain amount of metabolic CO₂ to calcification (Wefer and Berger, 1991).

SCLEROCHRONOLOGICAL PROFILES

A small shell of *Vaccinites cornuaccinum* from Keratovouno hill was sampled along the ventral side of a dorso-ventral longitudinal section (Figure 4). As the shell is curved around the dorsal side, larger growth increments along the ventral side allow the best resolution of isotopic variations.

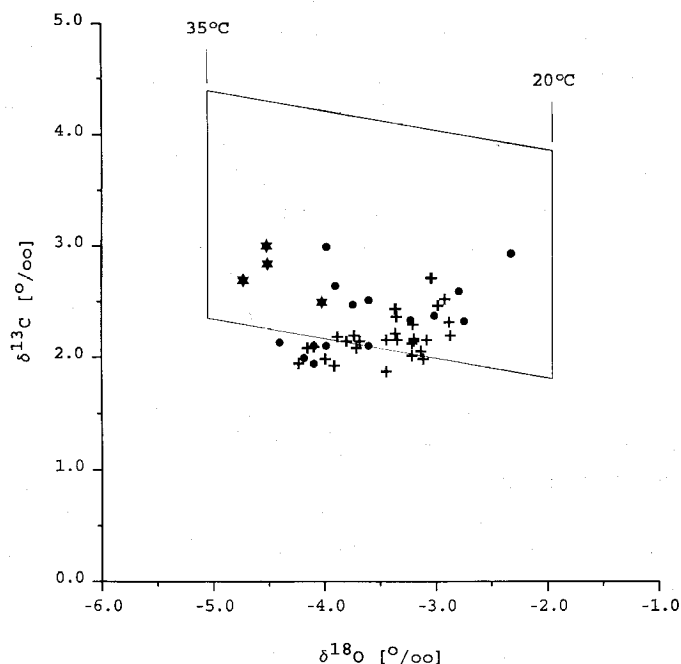


Figure 3. $\delta^{13}\text{C}$ versus $\delta^{18}\text{O}$ in outer shell layers of seven shells of *Vaccinites cornuvarcinum* (Bronn) from three Beotian localities: Anthochorion (asterisks), Dionysos (dots), and Keratovouno hill (+). Box delimits compositions of CaCO_3 in isotopic equilibrium with Cretaceous sea water (-1‰ $\delta^{18}\text{O}$ SMOW, 0 to $+2\text{‰}$ $\delta^{13}\text{C}$ HCO_3^-) in the temperature range of 20 to 35°C (fractionations from Anderson and Arthur [1983] and Emrich and coworkers [1970]).

The oxygen isotopic record starts with -4.8‰ in the ontogenetically youngest part of the shell and $\delta^{18}\text{O}$ then gradually increases to -3‰ . After a sharp drop below -5‰ , there is a return to -3‰ and a gradual decrease to -4.5‰ $\delta^{18}\text{O}$ in the upper part of the shell. $\delta^{13}\text{C}$ slightly increased from $+0.9$ to $+1.8\text{‰}$ during growth and shows a similar negative shift in the middle part of the sampled interval as observed in $\delta^{18}\text{O}$.

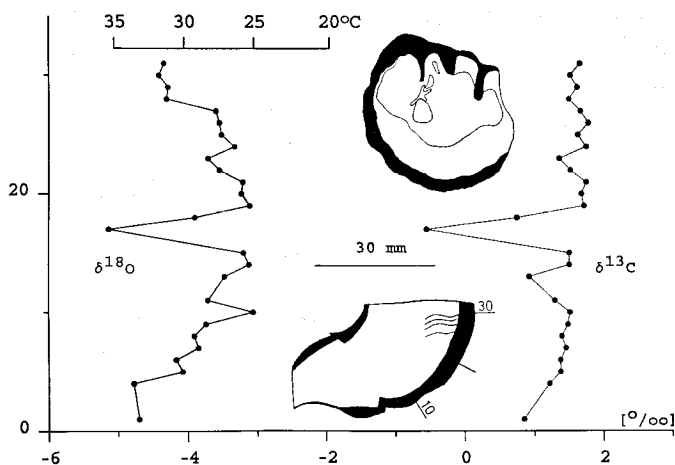


Figure 4. Sclerochronological $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variations within the outer shell layer of a *Vaccinites cornuvarcinum* from Keratovouno hill. Numbers on the y-axis correspond to successively taken samples indicated along the drawing of the longitudinal section of the right valve.

The overall trend in $\delta^{18}\text{O}$ can be readily ascribed to seasonal variations in temperature, which would amount to 8°C according to the palaeotemperature equation of Epstein and coworkers (1953). The negative shift in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ probably indicates a period of reduced salinity, when freshwater is mixed with marine waters. Meteoric waters are generally characterized by dissolved HCO_3^- which is depleted in ^{13}C when compared with marine HCO_3^- because their dissolved inorganic carbon is derived from phylogenetic CO_2 (Deines *et al.*, 1974; Steuber and Klinke, 1993). Therefore, the carbon isotopic composition of dissolved bicarbonates in estuarine environments was found to be well correlated with salinity (Mook, 1971). If -8‰ $\delta^{18}\text{O}$ (SMOW) and -15‰ $\delta^{13}\text{C}$ HCO_3^- are estimated for freshwater which discharged from the Pelagionian hinterland and mixed with Cretaceous sea water in littoral environments, a decrease in salinity from 35 to 28‰ would have produced the isotopic shift observed in the shell (Figure 5). There are no indications of contamination by diagenetic cements or changes in growth rate in this part of the shell, as inferred from the presence and spacing of growth bands.

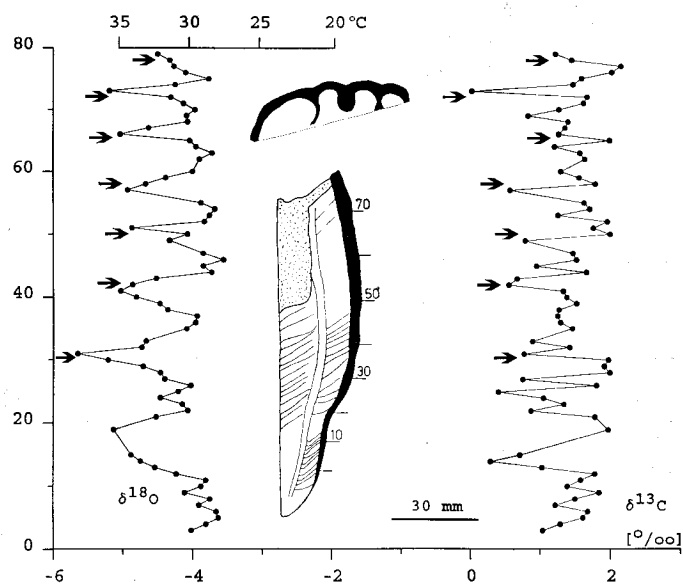


Figure 5. Sclerochronological $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variations within the outer shell layer of a *Vaccinites cornuvarcinum* from Pavlos. Numbers on the y-axis correspond to successively taken samples indicated along the drawing of the anterior longitudinal section of the right valve. Arrows indicate growth lamellae visible on a posterior view of the shell (Plate 1, figure d) which correspond to dark growth bands within the outer shell layer (Plate 1, figure e).

Although the ontogenetically youngest portion of the shell is not preserved, it can be concluded that the analysed *V. cornuvarcinum* began growing at the beginning of a warm season and grew more than 40 mm along its ventral side during the course of one year. An apparent influx of fresh water which occurred during the cold season did not leave any disturbance in the growth banding or shell structure as observed in this section.

Another shell of *Vaccinites cornuaccinum* from which a sclerochronological record was analysed (Figure 5) has been collected near Pavlos, to the north of the Kopais (Figure 1). There, hippuritids are not preserved in life position but were redeposited in marly coquinalimestones. However, reworking must have been moderate, as longitudinal costae and growth lamellae are well preserved (Plate 1, figure d). The straight right valve with tabulae perpendicular to the shell axis indicates an elevator mode of life. It was sampled along the anterior side of an anterior-posterior longitudinal section (Figure 5).

The $\delta^{18}\text{O}$ curve shows seven cycles ranging from -5.6 to -3.6‰ which most probably correspond to annual temperature variations during seven years of shell accretion (Figure 5). Although the average $\delta^{18}\text{O}$ composition is lower, the range of $\delta^{18}\text{O}$ is similar to that of the small *Vaccinites cornuaccinum* from Keratovouno hill and indicative of seasonal temperature fluctuations of 8°C. $\delta^{13}\text{C}$ varies between 0.0 and +2.2‰ and is not correlated with $\delta^{18}\text{O}$. Annual vertical growth increments amount to 23 mm in the first recorded year and decrease to less than 10 mm in the adult phase.

In order to substantiate these results, the ontogenetically oldest part of the shell was additionally sampled along a posterodorsal longitudinal section. The curve of oxygen isotopic compositions of these more closely spaced samples fits well with that of the anterior transect (Figure 6). Similarities in $\delta^{13}\text{C}$ are not evident which might be due to differing vital effects along the mantle margin of the rudist.

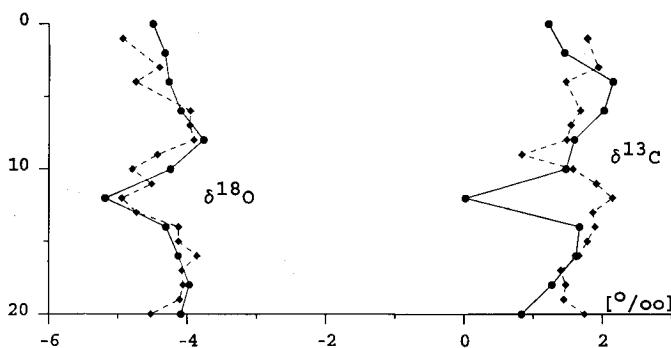


Figure 6. Comparison of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ variations in the last recorded year of growth in the anterior (—) and posterodorsal (---) shell shown in Figure 5.

The $\delta^{18}\text{O}$ curve is more or less sinusoidal in the first year of recorded growth but negative shifts are more abrupt in the following years, when the shell reached a certain diameter and the upwardly directed growth component predominated. Once this adult phase of shell growth was established, lamellae dominate the shell sculpture (Plate 1, figure d). They correspond to the negative peaks of the $\delta^{18}\text{O}$ curve. Obviously, shell growth rates were reduced during the warm season in this adult phase. Such a pattern of seasonal growth deceleration is probably related to periods of reproduction when physiological

energy was not available for shell growth. Similar growth patterns are known from recent molluscs (Pannella and MacClintock, 1968; Rye and Sommer, 1980). Other reasons for reduced shell growth could be too high ambient water temperatures or bad nutrition during summer. Both are considered to be unlikely because juvenile shells apparently recorded annual temperature changes more completely.

Decelerated growth during the warm season is further indicated by dark growth lines (Plate 1, figure e). They mark narrow zones with particularly short prisms and small dissolution pits along the former growth surfaces (Plate 1, figure c). Therefore, it cannot be ruled out that the isotopic composition of these 50–100 μm thick parts of the shells might be diagenetically altered. However, alteration was obviously restricted to partial dissolution and not to a considerable precipitation of diagenetic calcite. As only one sample within each annual cycle touched these zones, the overall trend in $\delta^{18}\text{O}$ distribution would not change significantly if the original isotopic composition was lost in these particular parts of the shell. On the other hand, $\delta^{18}\text{O}$ minima of each cycle do not always correspond exactly to these zones but were recorded in structurally unaltered parts above or below dark growth bands within most cycles (Figure 5).

DISCUSSION

Variations in the oxygen isotopic composition of the two analysed shells of *Vaccinites cornuaccinum* indicate that rudists stored valuable informations about their growth patterns, changes in ambient water temperatures, and perhaps tolerance against salinity fluctuations in their shells. Although annual temperature ranges of 7–8°C which are recorded within the shells appear to be reasonable, the calculation of absolute palaeotemperatures is problematic. The oxygen isotopic composition of Cretaceous seawater can only be estimated and was probably as variable as in today's oceans (Veizer, 1983). Another problem is posed by possible disequilibrium precipitation of low-Mg calcite by the rudist mantle. Although recent molluscs are among the most faithful recorders of ambient water temperatures when compared to other organisms with calcareous skeletons (Wefer and Berger, 1991), deviations from the inorganic isotope equilibrium cannot be ruled out. This problem was discussed by Woo and coworkers (1993). In their study, well preserved calcitic shell layers of other bivalves were found to contain more ^{18}O than those of several rudist families. The isotopic compositions of rudist shells presented in their study are similar to those of *Vaccinites cornuaccinum* from Beotia. They argued that lower ^{13}C and ^{18}O concentrations in the outer shell layer, when compared to the less well preserved inner layers, reflect disequilibrium precipitation of low-Mg calcite. They, however, did not consider different fractionations in the systems water-calcite and water-aragonite as discussed above.

If -1‰ $\delta^{18}\text{O}$ SMOW for Cretaceous seawater is assumed (Savin and Yeh, 1981), the calculated palaeotemperatures vary between extremes of 25 and 33.5°C for the small *Vaccinites cornuvaccinum* (Figure 4) and between 27.5 and 38°C for the large one (Figure 5). Both absolute temperatures and annual ranges are reasonable and similar to those in the recent Samoan habitat of *Tridacna maxima* where temperatures range from 28 to 34°C (Jones *et al.*, 1986).

Considering the above discussed uncertainties in the calculation of absolute palaeotemperatures, much more data have to be collected to detect possible vital effects on the isotopic compositions of rudist shells. Nevertheless, the determination of annual growth increments is an important tool for palaeoecological consideration of this peculiar group of Cretaceous molluscs. Flexible shell growth allowed them to occupy various habitats and to compete with corals in shallow water environments (Scott, 1979; Kauffman and Johnson, 1988; Ross and Skelton, 1993). In this connection, the delineation of annual growth rates and the evaluation of tolerance against environmental perturbations is most important for understanding their spectacular success and subsequent decline on the Cretaceous carbonate platforms.

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