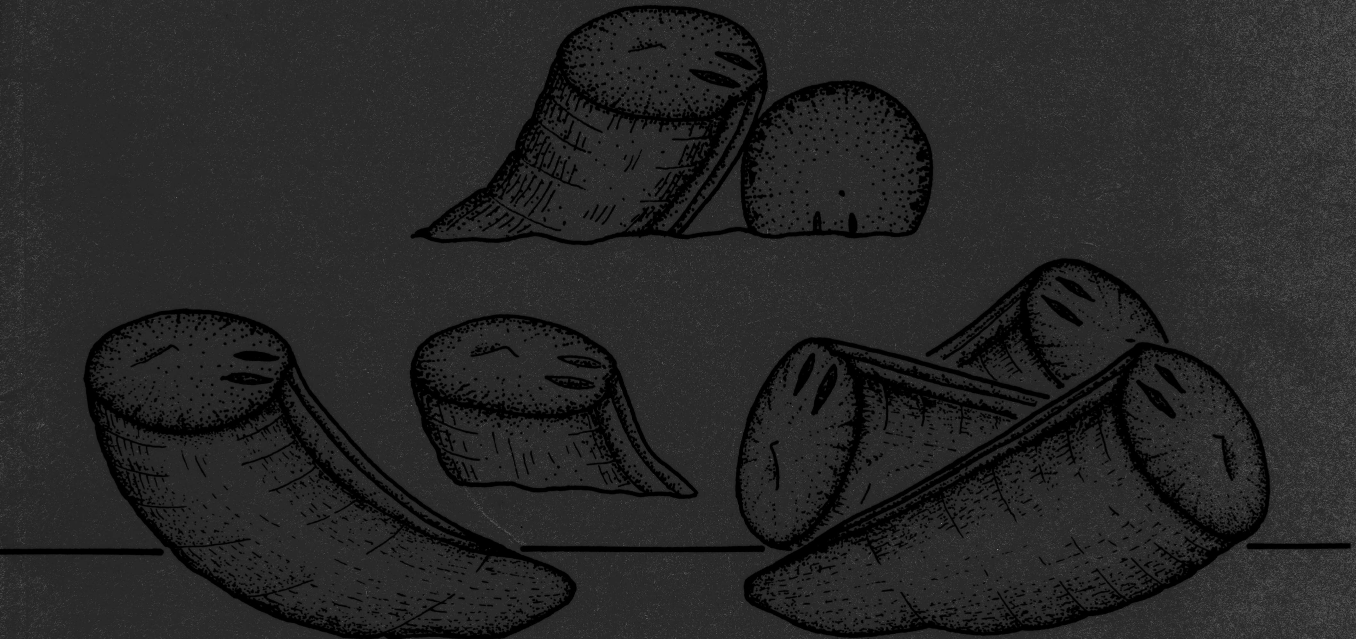
SPECIAL PAPERS IN PALAEONTOLOGY · 61

Cretaceous rudists of Boeotia, central Greece



THE PALAEONTOLOGICAL ASSOCIATION

PRICE £60

SPECIAL PAPERS IN PALAEONTOLOGY NO. 61

CRETACEOUS RUDISTS OF BOEOTIA, CENTRAL GREECE

BY

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with 26 plates, 21 tables and 90 text-figures

THE PALAEONTOLOGICAL ASSOCIATION
LONDON

Printed in Great Britain

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ABSTRACT. Diverse rudist associations were widely distributed on the western margin of the Pelagonian micro-continent, now exposed in Boeotia, during the late Cretaceous, while only few caprotinid rudists and Radiolitidae have been found in marginal-marine and predominantly siliciclastic deposits of early Aptian to Cenomanian age.

Sixty-one rudist species of Aptian to Maastrichtian age are described, with emphasis on the delineation of intraspecific variability. *Horiopleura*? *juxi* sp. nov. is described from Aptian conglomerates near Levadia. *Praelapeirousia*? sp. nov. from Upper Turonian–?Coniacian limestones of the Ptoon Mountains is provisionally left in open nomenclature. A revision of *Vaccinites cornuvaccinum* (Bronn) is based on abundant material from Boeotia and several palaeontological collections, and includes the installation of a neotype.

Rudists are particularly abundant in Santonian–Campanian limestones that were deposited on top of karst-bauxites in southern Boeotia, and which overlie disconformably Triassic–Lower Cretaceous rocks in northern Boeotia. *Vaccinites cornuvaccinum* (Bronn) dominated among the Hippuritidae and thrived in protected subtidal lagoons as well as on landward slopes and probably on the crests of current-swept shoals. Different growth-strategies existed in environments with various rates of water agitation and sediment accumulation. Less adaptable Plagioptychidae and Radiolitidae were associated with *V. cornuvaccinum* in changing faunal compositions.

Diversity patterns of Greek rudists are similar to those of other Mediterranean regions and close affinities with faunas from Italy and the Dinarids are evident. The Greek associations can be attributed to either African or central Mediterranean faunal provinces, but provincial separation faded during periods of high sea-level.

COMPARED with other Mediterranean regions, knowledge about the occurrence of rudists from Greece remained rather fragmentary until the last decade, although the presence of rudist limestones in Boeotia (central Greece) was known since the pioneering studies of Boblaye and Virlet (1833), Gaudry (1862–67) and Bittner (1880). In his landmark monograph on the Hippuritidae, Douvillé (1892*a*, 1895, 1897*a*) described several specimens from various Boeotian and other Greek localities. The current state of knowledge is founded mainly on the monographic descriptions of rudist occurrences in the Parnassus Mountains (Caminiti 1985), Vermion Mountains (Kollmann *et al.* 1985) and Argolis (Mermighis 1989; Philip *et al.* 1989*b*; Mermighis *et al.* 1991). Additional associations were reported from the Ionian Islands (Accordi *et al.* 1989).

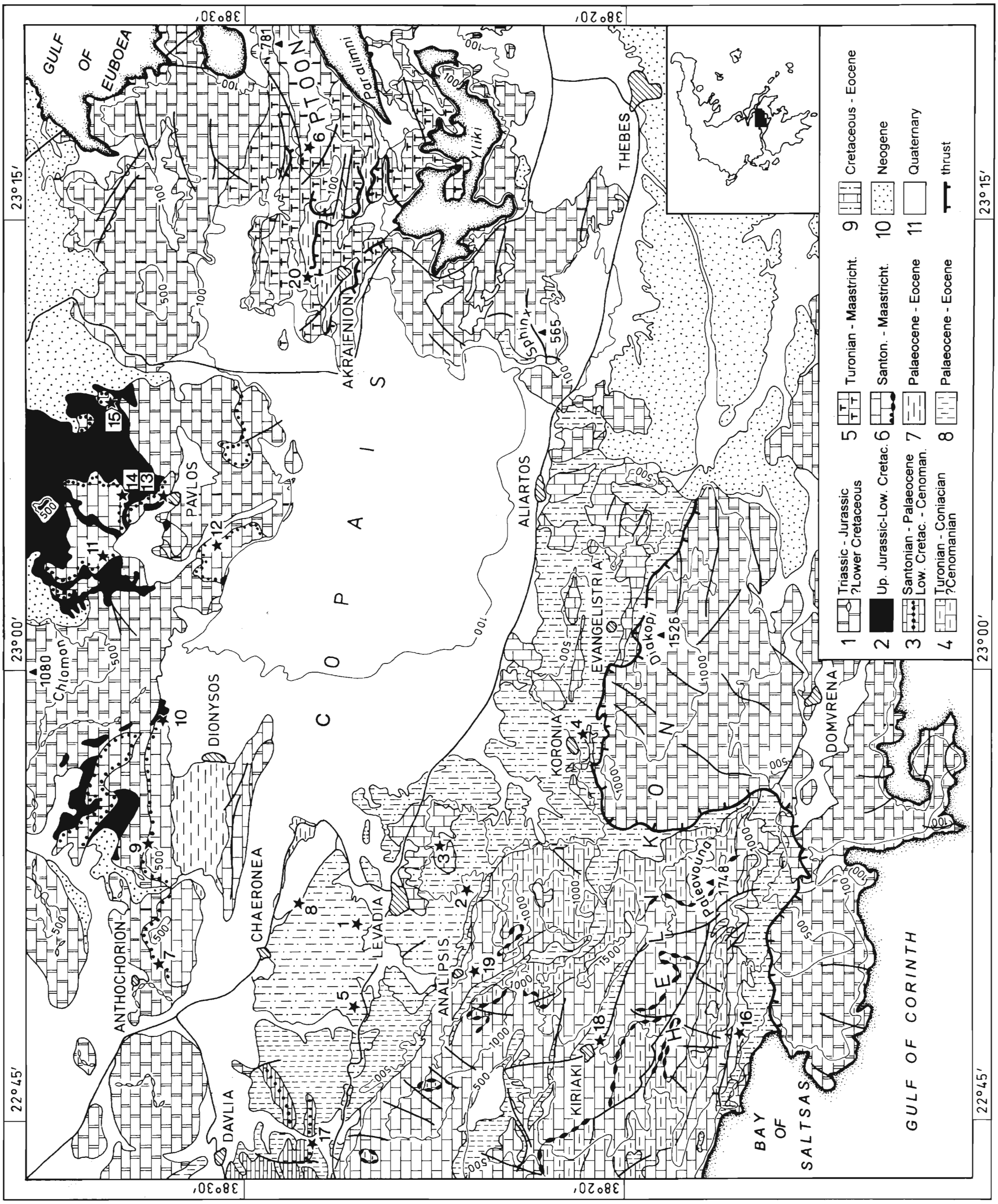
Until the 1970s biostratigraphical investigations of the widely exposed Cretaceous deposits of Boeotia (Text-fig. 1) had been limited to various sections or restricted areas (e.g. Nöth 1931*b*; Renz and Reichel 1948; Clément 1970; Clément and Ferrière 1973). The existence of differing coeval facies in closely adjacent areas was previously related to the emplacement of tectonic nappes from contiguous isopic zones. In contrast to this tectonostratigraphical interpretation of varying sedimentary facies, a rather autochthonous position of facies belts has been revealed by detailed biostratigraphical and microfacies analyses (Jux *et al.* 1987; Konertz 1987; Steuber *et al.* 1993, 1997; Raeder 1994; Walter 1996). A palaeogeographical reconstruction of the Cretaceous in Boeotia has been published elsewhere (Steuber *et al.* 1993) and is briefly summarized below.

CRETACEOUS STRATIGRAPHY AND PALAEOGEOGRAPHY OF BOEOTIA

The Boeotian rudist deposits described here formed on a continental fragment, called the Pelagonian platform, situated between the Cretaceous Pindos Ocean to the west and the Axios Ocean to the east (Text-fig. 2A). Transgressions from the Pindos Ocean controlled the evolution of the gradually subsiding western margin of the Pelagonian continental fragment from the Barremian until the Campanian (Text-fig. 2B). Carbonate production by rudist bivalves became increasingly important during the late Cretaceous, as high sea-levels provided extended environments for the establishment of rudist populations. The abundance of rudists at the basal levels of transgressive sequences is an important key for chronostratigraphical correlations of these palaeogeographically important episodes.

The older Mesozoic basement of the Pelagonian micro-continent in Boeotia consists of Jurassic–Triassic platform carbonates (Simon and Steuber 1993) which were folded during the earliest Cretaceous (Eohellenian orogeny, Jacobshagen *et al.* 1976). The folding was pre-dated by a deepening of depositional environments during the late Jurassic. Ophiolitic volcanics, hyalo- and siliciclastics are intercalated in radiolarites and ammonitico-rosso limestones of Tithonian age (Simon 1987).

[Special Papers in Palaeontology No. 61, 1999, pp. 1–229, 26 pls]


GULF OF EUBOEA
PTOON
781
Paralimni
Yliki
THEBES
AKRAIFNION
C O P A I S
Sphinx
565
ALIARTOS
PAVLOS
EVANGELISTRIA
Diakopi
1526
KORONIA
H E L I C O N
DOMVRENA
Chlomon
1080
DIONYSOS
ANTHOCHORION
CHAERONEA
LEVADIA
ANALIPSIS
KIRIAKI
Paleovouna
1748
DAVLIA
BAY OF SALTSAS
GULF OF CORINTH
38°30′
38°20′
23°15′
23°00′
22°45′
1 Triassic - Jurassic ?Lower Cretaceous
2 Up. Jurassic-Low. Cretac.
3 Santonian - Palaeocene Low. Cretac. - Cenoman.
4 Turonian - Coniacian ?Cenomanian
5 Turonian - Maastricht.
6 Santon. - Maastricht.
7 Palaeocene - Eocene
8 Palaeocene - Eocene
9 Cretaceous - Eocene
10 Neogene
11 Quaternary
thrust

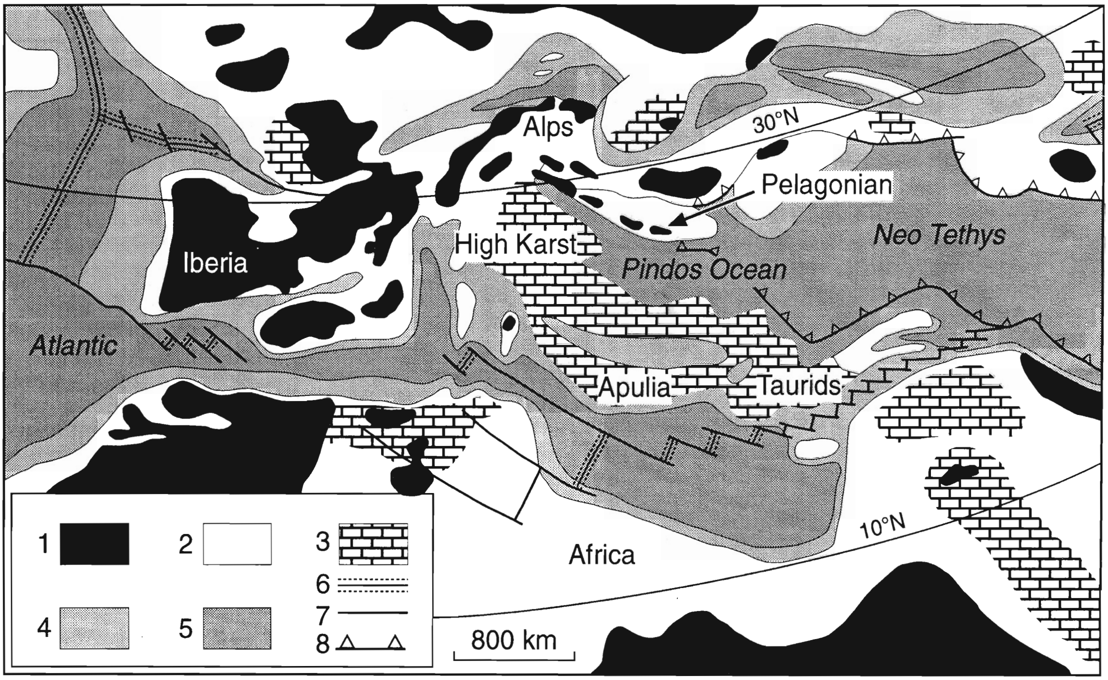
Clastic deposits to the north of the Copais plain range into the Lower Cretaceous (Schiefer-Hornstein-series; Renz 1913). Other Lower Cretaceous sedimentary rocks of Boeotia are variegated marls, shales and limestones with tintinnids of Berriasian age (Boeotian flysch; Celet and Clément 1971; Clément 1971). These flysch-type deposits resulted from the Eohellenian orogenic movements which were linked to the closure of the Axios Ocean in the east, and perhaps to the subduction of oceanic crust of the Pindos Ocean in the west (Jones and Robertson 1994). There is controversy as to whether the ophiolites that were obducted onto the Pelagonian platform during this episode were derived from Axios, or Pindos, oceanic crust (Robertson 1991). The folded Mesozoic basement of the Pelagonian platform was subsequently covered by polymict conglomerates with a high amount of serpentinized 'ophiolitic' components, derived from the erosion of previously obducted slabs of oceanic crust. The debris of reef- and platform carbonates was intercalated in these terrigenous deposits after the Hauterivian (Raeder 1994). Rudists, not older than Aptian, are known only from a few localities, but are mostly represented by fragments which are insufficiently preserved for further taxonomic classification. Above the Albian, rudists, with almost all families, are recognized as dominant constituents of such thin limestone intercalations.

Calcareous sedimentation dominated from the Turonian. Biomicrites with abundant planktic foraminifera indicate the deepening of previously marginal marine depositional environments in the Helicon range (Konertz 1987). Further to the north, in the Ptoon Mountains, Turonian rudist limestones unconformably overlie Triassic and Jurassic limestones (Nöth 1931*b*; Renz and Reichel 1948; Bignot and Guernet 1968; Steuber *et al.* 1993) and mark a global sea-level highstand.

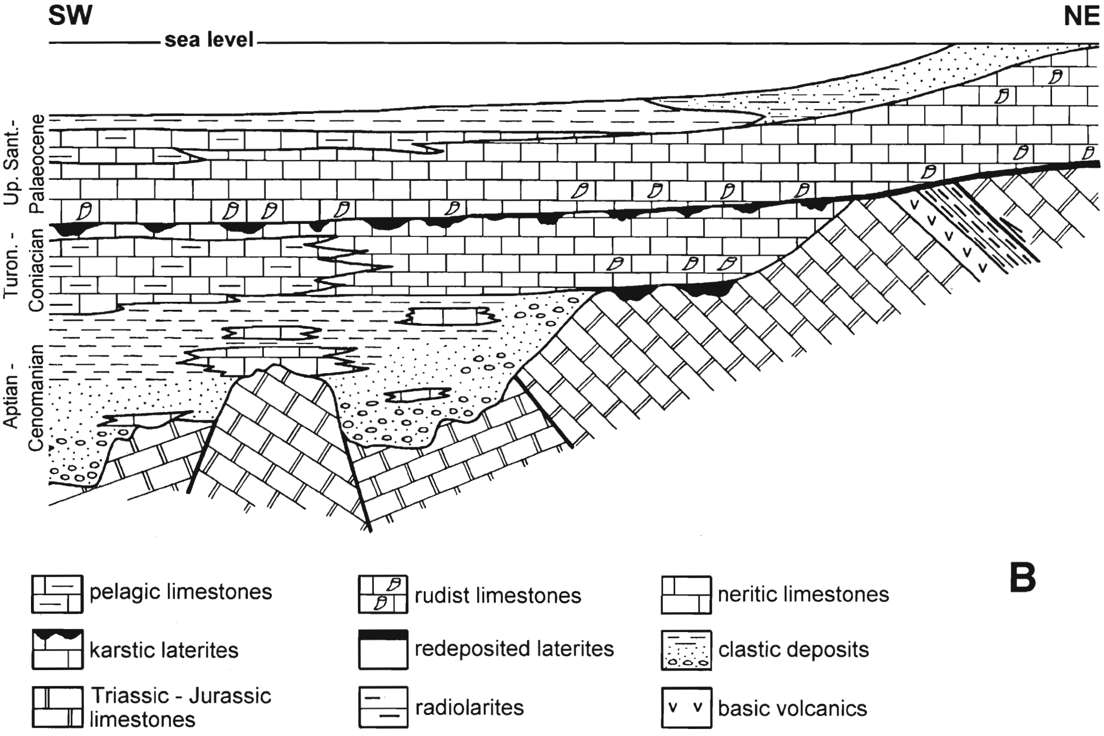
Marine sedimentation at the Pelagonian margin was interrupted during the Coniacian–early Santonian. Subaerial exposure is indicated by a palaeokarst that is sealed with pisolithic bauxites. The subsequent transgression, for the first time during the Cretaceous, encroached over internal areas of the Pelagonian continental fragment which are located now to the north of the Copais plain (Steuber *et al.* 1993). There, rudist limestones of Santonian–Campanian age unconformably overlie the folded early Mesozoic basement. A coeval transgressive onlap is known from several other areas of the internal Hellenids and was accompanied by the widespread deposition of rudist limestones (Aubouin *et al.* 1960). These deposits are indicated as 'conglomerates with *Hippurites*' of the transgressive Cretaceous on the official geological maps of Boeotia (Maratos *et al.* 1965, 1967). Diverse rudist-associations are preserved in life position at several localities, allowing for the reconstruction of palaeoenvironments and growth fabrics.

The Santonian–Campanian transgression initiated the development of an extended carbonate platform, on which north–south facies successions became increasingly accentuated in the late Campanian–Maastrichtian. Hemipelagic wackestones with planktic foraminifera of early to mid Maastrichtian age in the south interfinger with neritic and littoral carbonates to the north (Walter 1996). The late Maastrichtian and early Paleocene are only incompletely recorded, as incipient crustal movements dissected the distal platform during this time. Ferrophosphatic stromatolitic crusts formed on tectonic highs during late Paleocene periods of non-deposition (Kalpakis 1979; Walter 1996). This tectonically produced relief was buried from the late Paleocene by red pelagic marls that grade into Eocene flysch-type

TEXT-FIG. 1. Geological map and rudist localities of the area studied (after Maratos *et al.* 1965, 1967; Tataris *et al.* 1970*a*, 1970*b*; Papastamatiou *et al.* 1971; Katsikatsos *et al.* 1978; Bornovas *et al.* 1984; Jux *et al.* 1987; Hess 1993; and own field observations). Asterisks mark numbered rudist localities referred to in the text. (1) lime- and dolostones with bauxitic horizon; hyaloclastic sediments, sandstones and mafic volcanics are regionally intercalated in the Upper Jurassic/Lower Cretaceous; (2) peridotites, mafic volcanics and hyaloclastic sediments; (3) limestones of the Parnassus-platform (to the south of Davlia); (4) limestones; (5) rudist limestones, at the base lateritic iron ores on karst surface; (6) rudist limestones, overlying bauxites on karst surface or impure lateritic clastics; (7) light brown sandstones and pelitic rocks (flysch-type deposits); (8) red pelitic marls passing into brownish-grey sandstones and pelitic rocks (flysch-type deposits); (9) tectonic melange of variegated marls and thin limestone intercalations (early Cretaceous 'Boeotian' Flysch), ophiolitic conglomerates, sandstones, pelitic rocks and thin limestone intercalations (transgressive Lower Cretaceous–Cenomanian), units 7 and 8 of this map, and undivided limestones of predominantly Cretaceous age; (10) fluviatile gravels and conglomerates, sands, limnic limestones (molasse); (11) lacustrine sediments in the Copais, otherwise alluvial deposits.


Alps
30°N
Pelagonian
High Karst
Iberia
Pindos Ocean
Neo Tethys
Atlantic
Apulia
Taurids
10°N
Africa
1
2
3
4
5
6
7
8
800 km

A


SW
NE
sea level
Up. Sant.- Palaeocene
Turon. - Coniacian
Aptian - Cenomanian
pelagic limestones
rudist limestones
neritic limestones
karstic laterites
redeposited laterites
clastic deposits
Triassic - Jurassic limestones
radiolarites
basic volcanics

B

deposits. In northern Boeotia, Maastrichtian platform limestones with sparsely distributed rudists are followed by flysch-type arenaceous deposits with late Paleocene foraminifera and phytoplankton (Gotzes 1993). Both facies interfinger across the Cretaceous/Tertiary boundary in the north-eastern Helicon Mountains, where allodapic limestones are intercalated in red pelagic marls (Walter 1996).

From the Aptian until the Campanian, facies patterns along the western Pelagonian margin were controlled predominantly by global sea-level changes (Steuber *et al.* 1993). This was not the case on the Parnassus carbonate platform, located to the west of the considered region, nor was the Parnassus platform affected by the early Cretaceous Eohellenian orogenic movements which are evident on the Pelagonian micro-continent. On the Parnassus platform, thick limestone sequences had accumulated since the Triassic, although three major periods of emersion, during the mid–late Jurassic, Kimmeridgian–Tithonian, and Albian–Turonian, are indicated by intercalated bauxites. This intra-oceanic platform was left unaffected by clastic sedimentation which, as noted above, dominated at the Pelagonian margin during the early Cretaceous. The differing lithostratigraphical evolution of the Pelagonian and Parnassus platforms lasted until the Coniacian. The global Turonian sea-level highstand can be detected in the flooding of the previously continental Pelagonian basement of the Ptoon Mountains, and further to the south (Helicon Mountains), marine depositional environments deepened considerably. The Parnassus platform, in contrast, remained emerged from the Cenomanian until the Santonian–Campanian, and only marginal areas were flooded during the Turonian sea-level highstand (Celet 1962; Combes *et al.* 1981). Consequently, the late Cretaceous period of emersion lasted longer on the Parnassus platform than on the Pelagonian margin. As facies evolution at the Pelagonian margin accords well with global sea-level changes (Haq *et al.* 1988), the differing evolution of the Parnassus platform must be related to tectonic movements. It most probably collided with the Pelagonian continental fragment during the late Cenomanian–Turonian. Evidence for a connection between the Parnassus platform and the Pelagonian micro-continent during the Santonian–Campanian includes economically important bauxites which accumulated on the Parnassus platform during this time, and which must have been derived from the weathering of the Pelagonian ophiolites (Combes 1977). As a result of the considerably longer-lasting emersion, karstification on the Parnassus platform penetrated more deeply than on the Pelagonian margin. The depth of dolines and the abundance and thickness of bauxites decreases to the north-east (Valeton 1991), and indications of a coeval long-lasting emersion are absent in the Ptoon Mountains.

No differences in sedimentary facies between Pelagonian and Parnassus are evident after the Santonian–Campanian transgression. Rudists dominate the biofacies of these littoral and neritic limestones. The biostratigraphy and microfacies of these deposits have been studied in both the Parnassus and Helicon Mountains (Caminiti 1985; Konertz 1987).

It is generally accepted that the closure of the Pindos Ocean was linked to subduction under the continental crust of the Pelagonian micro-continent (Dercourt *et al.* 1986; Mountrakis 1986; Clift 1992). This was supported by the recognition of oceanic basalts of Cretaceous age in Argolis (Clift and Robertson 1989) and agrees with the outlined convergent evolution of sedimentary facies during the late Cretaceous (Steuber *et al.* 1993).

The structural architecture of Boeotia resulted both from early Cretaceous and Tertiary orogenies. Tertiary compressional tectonics induced the detachment of the rigid blocks of Late Cretaceous and Triassic–Jurassic platform limestones and thrusting of them over Early Cretaceous and Tertiary siliciclastic sediments of the external Pelagonian margin. However, remote nappe transport is not evident, and the former facies belts remained in a parautochthonous position (Steuber *et al.* 1993). The siliciclastic sequences now form a mosaic of thrusted sheets to the south and south-west of the Copais; their complicated tectonic structures cannot be indicated on the scale of Text-figure 1. Neither a widespread

TEXT-FIG. 2. A, palaeogeography of the Mediterranean during the Santonian–Campanian (after Dercourt *et al.* 1986). (1) land, (2) thick continental crust, (3) platform-carbonates, (4) thin continental crust, (5) oceanic crust, (6) active spreading ridge, (7) fault, (8) subduction zone. B, schematic cross section of the Pelagonian continental margin in Boeotia before Tertiary deformation, showing gradual onlap of Cretaceous deposits. Thickness of Cretaceous sediments amounts to more than 1500 m in the south-west; horizontal distance exceeds 50 km (after Steuber *et al.* 1993).

occurrence of Tertiary rocks (Clément 1970; Tataris *et al.* 1970*a*) nor of early Cretaceous 'Eohellenian' flysch-type deposits (Papastamatiou *et al.* 1971) was recognized to the south and south-west of the Copais. Instead, marginal marine deposits of Aptian to Cenomanian age are widely distributed (Jux *et al.* 1987), allowing for the reconstruction of Barremian–Cenomanian facies of the Pelagonian margin (Raeder 1994).

Tectonic structures are more simple to the north of the Copais, where incompetent Early Cretaceous siliciclastics are absent. However, minor thrusting of Late Cretaceous limestone blocks over Tertiary flysch-type deposits did occur in the Ptoon Mountains (Renz and Reichel 1948).

Younger extensional tectonics formed the gulfs of Corinth and Euboea, and exposed older Mesozoic deposits along the margins of these grabens (Text-fig. 1). The Copais depression, which is filled with limnic sediments and was drained by karstic sinkholes into the Gulf of Euboea, as well as the depression of Thebes, extend parallel to these major neotectonic lineaments.

RUDIST LOCALITIES AND BIOSTRATIGRAPHY

Several studies have focused on various stratigraphical and palaeontological aspects of the Boeotian Cretaceous: Konertz 1987 (Helicon Mountains), Steuber 1993*a* (Turonian hippuritids), Raeder 1994 (Lower Cretaceous–Cenomanian), Steuber 1994 (Santonian–Campanian radiolitids), Walter 1996 (Cretaceous/Tertiary transition), Abdel-Gawad and Gameil 1995 (corals), Löser and Raeder 1995 (corals), Steuber *et al.* 1997 (Pelagonian-Parnassus transitional facies). In order to present a complete account of the fossil associations known from individual localities, and to constrain the age of rudist occurrences by independent biostratigraphical evidence obtained from over- or underlying beds, the taxa listed or described in the above-mentioned publications are listed below together with the recognized rudist species.

Preservation of rudists in life-position was noted at only nine of the 23 studied localities. Such assemblages are commonly characterized by descriptive terms coined from the studies of coral-algal-hydrozoan frameworks. Transferring this nomenclature to patterns of colonization and construction observed in various rudist associations proved to be difficult. In addition to purely morphological aspects of the rudists themselves (Philip 1972), the distribution of other organisms is important for the comparison of such reefoid communities (Kauffman and Sohl 1973; Höfling 1997). The occurrence of certain rudist morphotypes with environmental factors, such as type of substratum, turbulence, as well as type and rate of background sedimentation (Skelton and Gili 1991), affected the growth and dimensions of these lithosomes as much as the distribution of, and interrelations with, framework-builders and -binders. The following terms are used.

Groups of few individuals grew without contact of their shells in limited areas. Various morphotypes are observed in relation to substratum and water-agitation. More complexly structured communities that are listed below frequently evolved from pioneering *groups* of rudists.

Bouquets were formed by several conjoined individuals which projected more or less (Gili *et al.* 1995) above the sediment surface. These mono- or oligospecific pseudocolonies thrived only for the lifespan of one or a few generations.

Biostromes formed by lateral merging of *bouquets*; other calcifying organisms (corals, algae, hydrozoans) may be common, rare or absent.

Banks developed when rudist biostromes persisted for numerous generations and topographic elevations were formed by the accumulation of shell debris on which later generations settled. These associations are commonly mono- or oligospecific; other organisms are sparsely distributed.

Reefs. Dissent has been expressed from the view of rudists as reef builders, i.e. as constructors of self-supporting, superstratal fabrics (e.g. Ross and Skelton 1993; Gili *et al.* 1995), as most growth fabrics of elevator rudists were essentially sediment supported (Gili *et al.* 1995; Skelton *et al.* 1995; Steuber *et al.* 1998). Bound frameworks of corals and rudist have been reported from only a few localities (e.g. Polšak 1981; Camoin *et al.* 1988; Höfling *et al.* 1996) and are generally of limited size. Their existence raises several questions concerning the synecology of rudists and other reef-building organisms (Scott *et al.* 1990; Scott 1995).

Aptian

Perachorion (1). Ophiolitic conglomerates with intercalated limestone blocks are exposed near the village of Perachorion, along the dirt-road linking the towns of Levadia and Chaeronea (Text-fig. 1). Diverse associations of colonial corals, comprising more than 30 species, are found in the conglomerates (Abdel-Gawad and Gameil 1995; Löser and Raeder 1995), their good preservation indicating only moderate reworking.

Foraminifera and dasycladacean algae which are characteristic of the Lower–Upper Aptian transition have been found in the limestone blocks (Raeder 1994): *Palorbitolina lenticularis* (Blumenbach), *Orbitolina* (*Mesorbitolina*) sp., *Trocholina* cf. *aptiensis* Iovcheva, *Coscinophragma cribrosum* (Reuss), *Cylindroporella* cf. *elitzae* Bakalova, and *Triploporella marsicana* Praturlon.

The limestone blocks are considered as parautochthonous within the conglomeratic sequence, as algal-hydrozoan associations and microbial crusts dominate their biofacies, indicating low water agitation and cryptic environments (Raeder 1994). Several sections of caprotinid rudists, not well enough preserved for generic determination, and *Horiopleura*? *juxi* sp. nov. have been collected.

Albian

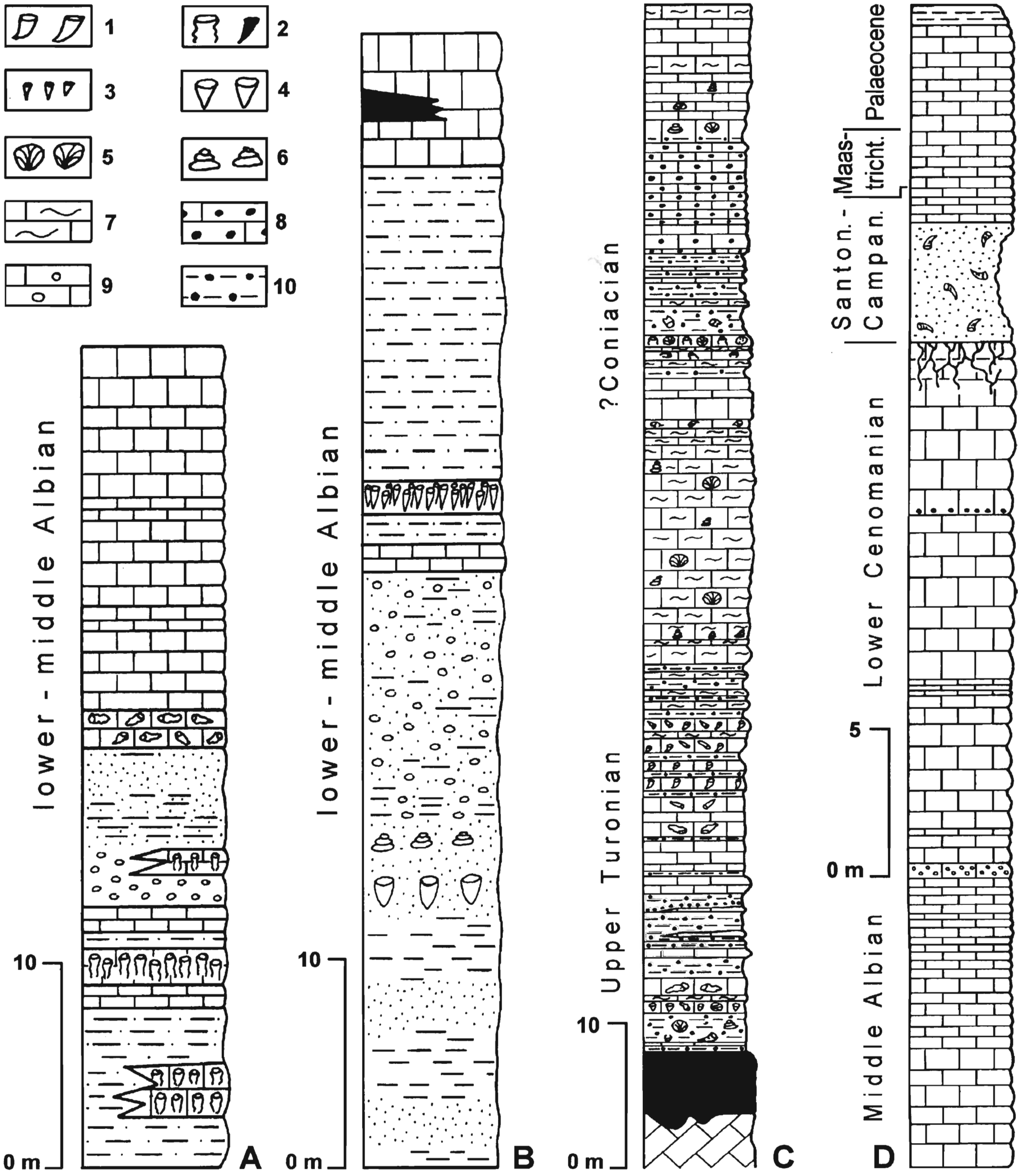
Analipsis (2). Marls with numerous bouquets of *Eoradiolites davidsoni* (Hill) overlie ophiolitic conglomerates and sandstones (Text-fig. 3A) 4 km east of the village of Analipsis (Sourpi). Each of these bouquets comprises ten to 20 conjoined shells. Their establishment in this marginal marine environment lasted not longer than for two or three generations, before the shells were buried by marls which contain abundant orbitolinid foraminifera. Macrospheric foraminifera dominate so that these deposits are considered as littoral taphocoenoses (Raeder and Steuber 1994). Solitary corals (*Ellipsosmilia* sp.) are sparsely distributed in the lower part of the section. A subsequent decrease in terrigenous sedimentation provided more favourable conditions for *Eoradiolites davidsoni* which formed biostromes up to 2 m thick, exposed 10 m above the base of the section. As with the isolated bouquets below, they were blanketed by marls with abundant orbitolinid foraminifera. The following massive limestones predominantly consist of diagenetically altered and partly dolomitized fragment of *Eoradiolites*.

An early to middle Albian age of this section (Raeder 1994) is indicated by benthic foraminifera (Schroeder and Neumann 1985), such as *Orbitolina* (*Mesorbitolina*) *subconcava* Leymerie, *Simplorbitolina conulus* Schroeder and *Pseudocyclammina hedbergi* Maync, and agrees with the stratigraphical range of *Eoradiolites davidsoni* (Hill) which is common in the Middle and Upper Albian (Coogan 1977).

Agia Barbara (3). The predominantly siliciclastic Early Cretaceous deposits of Boeotia are particularly fossiliferous in an outcrop 200 m to the east of the chapel of Agia Barbara near Levadia (Text-fig. 3B). *Horiopleura lamberti* Douvillé was found in life position between cerioid colonies of *Actinastrea dodecaphylla* (Trautschold) in polymict sand-siltstones which overlie ophiolitic conglomerates.

This level is followed by argillaceous deposits with abundant gastropods (Brunner and Kollmann 1983): *Echinobathra tricorollata* Kollmann, *Megalonoda* sp., *Neoptyxis incavata* (Bronn), *Neoptyxis symeonidisi* Kollmann and *Paraglauconia lujani* (Verneuil).

The latter horizon is overlain by ophiolitic conglomerates and marls with orbitolinid foraminifera. The same species as at Analipsis indicate an early to mid Albian age (Raeder 1994). Above these orbitolinid-bearing marls, an up to 0·5 m high biostrome of *Monopleura marcida* White is exposed. Its thickness is almost constant laterally for 40 m of exposure. Upwardly directed growth of younger shells along or on top of older conspecifics resulted in a dense growth fabric. Considering the average height of the shells (40 mm), a suitable environment was provided for approximately 20 successive generations of this species. In contrast to monopleurid associations described from Texas (Perkins 1974), at Agia Barbara small bouquets at the basal level merged quickly to form a laterally extending biostrome. As with the conditions observed at Analipsis, marls with orbitolinid foraminifera buried the biostrome at Agia Barbara and mark the transition to terrigenous sedimentation of marls and sandstones.



TEXT-FIG. 3. Measured sections: A, Analipsis; B, Agia Barbara (after Raeder 1994); C, Marmeko quarry (Ptoon Mountains) and, D, Paleokastron Hill. Symbols are used on Text-figures 4, 86–88: (1) hippuritids; (2) radiolitids, elongated compact-shelled morphotypes shown in black; (3) *Monopleura*; (4) *Horiopleura*; (5) chaetetids; (6) gastropods; (7) flaser-bedded limestones; (8) limestones with chert nodules; (9) conglomeratic limestones; (10) marls with limestone-nodules; other symbols as on Text-figure 2B.

Koronia (4). Along the dirt-road from Koronia to Evangelistria, 500 m east of Koronia, biohermal limestones are intercalated in ophiolitic conglomerates, sandstones and argillaceous deposits. Encrusting algae and sponges have been identified as the major framebuilders. *Coscinophragma cribosum* (Reuss) and *Orbitolina* (*Mesorbitolina*) *subconcava* Leymerie indicate an Albian age (Raeder 1994). Reworked rudist remains (*Horiopleura* sp., *Eoradiolites* sp.) are restricted to bioclastic limestones of the backreef.

Cenomanian

Tsoukalades (5). To the east of the village of Tsoukalades, an allochthonous block of massive lithobioclastic limestones is exposed in Tertiary flysch-type deposits. The limestones contain numerous pebbles of radiolarite reworked from the Eohellenian basement. Large bioclasts are almost exclusively remnants of caprinid shells. Among them are a few complete left valves of *Caprina baylei* (Gemmellaro) and *Sphaerucaprina woodwardi* Gemmellaro which are known from the Cenomanian of the eastern Mediterranean. *Orbitolina* (*O.*) *concava* (Lamarck), *O.* (*Conicorbitolina*) *conica* (d'Archiac) and *O.* (*Conicorbitolina*) *corbarica* Schroeder constrain an early Cenomanian age (Schroeder and Neumann 1985; Raeder 1994).

Middle Turonian–?Coniacian

Marmeko (6). Mining activities in the Ptoon Mountains which have taken place for more than a century, stimulated early scientific interest in the Cretaceous limestones overlying the lateritic iron ores of the region (von Zsigmondy 1914; Renz and Reichel 1948): *Radiolites sauvagesi* (d'Hombres-Firmas), *R. lusitanicus* (Bayle) and *Vaccinites grossouvrei* (Douvillé) have been described from there (Nöth 1931*b*).

A 70 m thick sequence has been studied in the Marmeko quarry on the slope of Tsekoureli Mountain, where Late Cretaceous transgressive deposits are particularly well exposed (Text-fig. 3C). The following rudist species have been recognized: *Biradiolites angulosus* d'Orbigny, *Durania* cf. *montisferrati* Astre, *Lapeirousella aumalensis* (Douvillé), *Praelapeirousia*? sp. nov., *Praeradiolites ponsianus* (d'Archiac), *Praeradiolites* cf. *urnalis* Astre, *Radiolites lusitanicus* (Bayle), *Radiolites praegalloprovincialis* Toucas, *Radiolites sauvagesi* (d'Hombres-Firmas), *Hippuritella resecta* (Defrance), *Vaccinites inferus* (Douvillé), *V. ljalintzenis* Pamouktchiev, *V. praegiganteus* (Toucas), *V. praepetrocoriensis* (Toucas), *V. ptoonensis* Steuber and *V.* cf. *grossouvrei* (Douvillé).

Redeposited shells of *Vaccinites* cf. *grossouvrei*, *V. inferus*, *Radiolites lusitanicus* and *R. sauvagesi* together with nerineids and chaetetids ('*Diplochaetetes hellenicus* Nöth') accumulated in coquinas that overlie basal pisolithic iron ores. *Biradiolites angulosus* encrusted on shells of *R. sauvagesi* prior to redeposition. These coquinas contain abundant pisoliths of haematite in an argillaceous-marly matrix. *Lapeirousella aumalensis* and *Praelapeirousia*? sp. nov. are sparsely distributed. The excellent preservation of sculpture of the radiolitids indicates a single event of redeposition, probably during a storm. Most species of the basal coquinas are found in life position in the following horizon. Monospecific or mixed bouquets of *R. sauvagesi* and *V. inferus* formed in sandy marls. In such pseudocolonies, single right valves of *V. inferus* with a diameter of 45 mm reached up to 230 mm long. *R. lusitanicus* and *V.* cf. *grossouvrei* lived in groups of slender elevator morphotypes. Nerineids and chaetetids dominated in areas that were less densely occupied by rudists. Chaetetids are frequently found in rudist associations, but encrustation of rudist shells was not observed.

Rudist remains are sparsely distributed in the following 14 m of impure nodular limestones. Groups of *V. praegiganteus* in geniculate life position and broad-conical morphotypes of vertically grown radiolitids are preserved in several banks of micritic limestones above. Only a few specimens of radiolitids (*Praeradiolites ponsianus*, *P.* cf. *urnalis*) were obtained from these compact limestones. Weathered sections of other large radiolitids with large prisms are most probably from *Sauvagesia* or *Durania*. In contrast with the basal rudist-beds, broad-conical morphotypes as well as the geniculate life-habit of *Vaccinites* indicate lower sedimentation rates.

Few rudist shells have been observed in the middle part of the section. They are redeposited and occur together with remnants of nerineids and chaetetids. Rudists are completely absent in levels with

Actaeonella. They reappear 49 m above the base of the section in several horizons that contain *Durania* cf. *montisferrati* and large chaetetids which are up to 250 mm high. The skeletons of both are commonly silicified. They formed groups of widely spaced individuals sticking in fine-grained, pure lime mud. Elongate or broad-conical morphotypes developed in response to varying rates of sedimentation. Within each horizon a remarkable similarity in shape of rudist and chaetetid morphotypes is noted, so that distinguishing between them on weathered surfaces is only possible after inspection of the structures of shells or coenostea, respectively. The section continues with thin-bedded and platy limestones with nodular chert.

The stratigraphical range of most of the Hippuritidae from the Marmeko quarry is Middle to Upper Turonian. Only *V. praegiganteus* is known from deposits as high as Lower Coniacian (Bilotte 1982*b*; Philip 1982*b*). Radiolitids from Marmeko have been reported from the Turonian–Coniacian of the Mediterranean.

As species of *Vaccinites* which are indicative of the Middle–Upper Turonian are restricted to the basal parts of the section, the overlying deposits could be of Coniacian age. Alternatively, depositional facies could be the major controlling factor for the vertical distribution of these associations, because not only have typical Turonian species disappeared in the upper parts of the sequence but also those radiolitids (*R. sauvagesi*) which are frequently found in Coniacian deposits of the western Mediterranean.

Benthic foraminifera give no additional information concerning a more precisely constrained age of the deposits at Marmeko (Upper Cenomanian to Lower Turonian, Renz and Reichel 1948; Lower Senonian, Bignot and Guernet 1968): *Aeoliosaccus kotori* Radoičić, *Neoendothyra apenninica* De Castro, *Barkerina* spp., *Minouxia* spp., *Cuneolina* ex gr. *pavonia* d'Orbigny, *Dicyclina* ex gr. *schlumbergeri* Munier-Chalmas, *Tetraminouxia* spp., *Nummoloculina robusta* Torre, *Keramosphaerina tergestina* (Stache) and '*Rotalina*' *cayeuxi* De Lapparent are present.

Santonian–Campanian

Santonian–Campanian transgressive deposits of northern Boeotia are described in detail in a later section (p. 190), with particular emphasis on the sedimentary facies, growth fabrics and patterns of establishment of rudist communities. Therefore, only the fossil taxa found at numerous localities are listed here (Table 1).

The Santonian–Maastrichtian comprises 20·8 My which is almost two-thirds of the duration of the entire Late Cretaceous (Gradstein *et al.* 1995). Eastern and central Mediterranean rudist associations from this long interval have been subdivided into only two coenozones (Santonian–early Campanian and late Campanian–Maastrichtian; Polšak *et al.* 1982). Even this rough subdivision is disputed (Gušić and Jelaska 1990) and is obviously incorrectly correlated to chronostratigraphy (Swinburne *et al.* 1992). As in other Mediterranean regions, a subdivision of the Santonian–Campanian proved to be difficult in Boeotia because age indicative fossils other than rudists are rare. Only at the Bay of Saltsas (16) and at Paleokastron Hill (17) do planktic foraminifera in pelagic limestones that overlie rudist beds provide independent and more precise biostratigraphical datums.

To the north of the Copais, rudist associations of the basal levels of the Late Cretaceous transgressive deposits are remarkably similar at several localities: *Vaccinites cornuvaccinum* (Bronn) is accompanied by changing radiolitid communities. Only to the east, at Tsouka Hill, is *V. cornuvaccinum* replaced by *V. chaperi* (Douvillé). It is shown in the taxonomic part of this monograph that *V. chaperi* was anagenetically derived from *V. cornuvaccinum.* This implies a decrease in age from west to east of the north Boeotian rudist beds in the Santonian–Campanian. Additional evidence is provided by changes in the associations of radiolitids: *Petkovicia*? *verajana* Slišković was found with *V. chaperi* at Tsouka Hill and with *Sauvagesia meneghiniana* (Pirona) at Loutsion whilst other radiolitids which are abundant further to the west are missing. *S. meneghiniana* is the only species which occurs with either *V. cornuvaccinum* (Dionysos, Megali Lakka) or *V. chaperi* (Tsouka). These changes in radiolitid associations support the assumption of decreasing age of the northern Boeotian rudist beds from west to east, but no independent evidence was obtained from the distribution of other fossils.

TABLE 1. Rudist species found at localities (7) Anthochorion, (8) Keratovouno Hill, (9) Makrokastron, (10) Dionysos, (11) Megali Lakka, (12) Kalamos Hill, (13) Pavlos, (14) Loutsion and (15) Tsouka Hill.

	7	8	9	10	11	12	13	14	15
Mitrocaprina boeotica (Munier-Chalmas)	–	X	–	–	–	X	–	–	–
Bournonia africana Douvillé	–	–	–	X	–	–	–	–	–
Durania katzeri (Slišković)	–	–	–	–	X	X	X	–	–
D. martellii Parona	–	–	–	–	X	–	X	–	–
Fossulites dionysii Steuber	–	–	–	X	–	–	–	–	–
F. aff. *undaesaltus* (Astre)	–	–	–	X	–	–	–	–	–
Gorjanovicia boeotica Steuber	–	X	–	X	X	–	–	–	–
G. costata Polšak	–	X	–	X	X	–	–	–	–
G. gracilis (Wiontzek)	–	–	–	X	X	–	–	–	–
G. kayae Özer	–	–	–	X	–	–	–	–	–
G. lipparinii Polšak	–	–	–	X	–	–	–	–	–
Gorjanovicia sp.	X	–	–	–	–	X	X	–	–
Hippuritella variabilis (Mun.–Chal.)	–	–	–	–	–	–	–	–	X
Medeella cf. *zignana* (Pirona)	–	X	–	X	–	–	–	–	–
Petkovicia? verajana Slišković	–	–	–	–	–	–	–	X	X
Praeradiolites echennensis Astre	–	X	–	–	–	X	–	–	–
Radiolites subradiosus Toucas	X	–	X	–	–	X	–	–	–
Sauvagesia meneghiniana (Pirona)	–	–	–	X	X	–	–	X	X
S. tenuicostata Polšak	X	–	–	X	–	–	–	–	–
Vaccinites cornuvaccinum (Bronn)	X	X	X	X	X	X	X	–	–
V. chaperi (Douvillé)	–	–	–	–	–	–	–	–	X

Bay of Saltsas (16). A 1400 m thick section of Coniacian to Paleocene deposits is exposed along the southern slope of Kakotopia Mountain at the Gulf of Corinth. This region of the Helicon Mountains is attributed to the Parnassus isopic zone on the official geological map (Papastamatiou *et al.* 1971). However, thick Early Cretaceous limestone sequences which would be indicative for the Parnassus platform have not been recognized in the Helicon Mountains during several field seasons. In contrast with the Parnassus platform, the limestones below the bauxite deposits in the Helicon Mountains range into the Coniacian (Konertz 1987).

At the Bay of Saltsas, a 900 m thick pile of Coniacian–Santonian limestones was thrust over rudist limestones of Campanian age. Shearing occurred along argillaceous marls of Paleocene age (Walter 1992). The Campanian limestones contain *Hippuritella variabilis* (Munier-Chalmas), *Vaccinites boehmi* (Douvillé) and *V. cornuvaccinum* (Bronn). Most shells are more or less strongly bioeroded and encrusted, and complete valves are rare. Insignificant banking, bad sorting of allochems and bioclasts as well as the sporadic presence of planktic foraminifera characterize these slope deposits of the Pelagonian platform margin. Biomicrites with planktic foraminifera of late Campanian or early Maastrichtian age dominate in higher parts of the section (Steuber *et al.* 1993): *Globotruncana linneiana* (d'Orbigny), *G. ventricosa* White, *Globotruncanita stuartiformis* (Dalbiez) and *Rosita fornicata* (Plummer) all occur.

Paleokastron Hill (17). A 200 m thick section of overturned Cretaceous deposits is exposed at Paleokastron Hill, 17 km west of Levadia and to the north of the road Levadia–Arachova (Text-fig. 3D). The top of Paleokastron Hill is formed by massive and in some horizons impure limestones that contain foraminifera of late Albian age (Raeder 1994): *Orbitolina* (*Mesorbitolina*) *aperta* (Erman) and *O.* (*Mesorbitolina*) *subconcava* Leymerie. Large bioclasts of colonial corals, encrusted by numerous calcareous algae, fragments of sponges (*Acantochaetetes* sp.) and radiolitid shells are indicative of talus deposits of a carbonate platform. In younger parts of the section (below the previously described unit, as the section is overturned), beds of coarse-grained platform debris alternate with biomicrites that contain

Middle Albian to Lower Cenomanian planktic foraminifera (Raeder 1994): *Praeglobotruncana* sp., *Rotalipora ticinensis* (Gandolfi) and *Ticinella roberti* (Gandolfi).

The succeeding well-sorted grain- and rudstones with bio-, intra- and ruditic lithoclasts of volcanic and lateritic rocks were deposited in more shallow environments. The youngest, 15 m thick deposits of the Albian–Cenomanian sequence are cut by neptunian dykes which clearly demonstrate the tectonic overturning of the sequence, and indicate a prolonged period of emersion after the early Cenomanian. The neptunian dykes are filled by wacke- and packstones with bioclasts and lithoclasts of volcanic and lateritic origin in a red-coloured micritic matrix.

The surface of non-deposition is covered by lithoclastic calcareous arenites that are followed by olistostromes with blocks and pebbles of serpentinized basic volcanics, radiolarites and pisolithic laterites. Rudist shells are abundantly dispersed in these deposits, without preferential orientation or horizontal accumulation: *Mitrocaprina bayani* (Douvillé), *Radiolites angeiodes* (Lapeirouse), *Hippurites* cf. *canaliculatus* Rolland du Roquan, *Hippurites colliciatus* Woodward, *Vaccinites boehmi* (Douvillé), *V. inaequicostatus* (Münster, *in* Goldfuß), *V. praesulcatus* (Douvillé), *V. sulcatus* (Defrance) and *V. vredenburgi* (Kühn).

Corals are also abundant: *Adelocoenia*? sp., *Agathelia* cf. *asperella* (Reuss), *Dimorphocoenia* sp., *Ellipsocoenia* sp., *Fungiastrea* cf. *conferta* (Milne-Edwards and Haime), *Heliastrea* sp., *Mycetophyllopsis antiqua* (Reuss), *Pachygyra bellula* Hackemesser, *Phyllocoenia toucasi* (Fromentel) and *Phyllocoenia* sp. (Abdel-Gawad and Gameil 1995; and determinations by H. Löser, Dresden).

Only *R. angeiodes* was found in life position in lithoclastic calcareous arenites of the youngest horizon of this unit. After a sharp unconformity, thick-bedded bioclastic limestones follow from which the Upper Campanian *Lepidorbitoides* sp. and *Pseudosiderolites* sp. have been identified (Steuber *et al.* 1997). Lateritic lithoclasts are still common in older horizons of these limestones. Subsequent deepening of depositional environments is recorded in thin-bedded, biomicritic limestones with Lower and 'middle' Maastrichtian planktic foraminifera (Robaszynski *et al.* 1984; Steuber *et al.* 1997): *Gansserina* cf. *gansseri* (Bolli), *Globotruncana arca* (Cushman), *Globotruncana linneiana* (d'Orbigny), *Globotruncana* cf. *ventricosa* White, *Globotruncanita* cf. *stuartiformis* (Dalbiez) and *Rosita fornicata* (Plummer).

Pelagic sedimentation was sporadically interrupted by the input of coarse debris from shallow marine environments. Micritic limestones with the Upper Paleocene foraminifera *Morozovella aequa* (Cushman and Renz), *M.* cf. *angulata* (White), *M.* cf. *velascoensis* (Cushman), *Planorotalites chapmani* (Parr) and *Pl.* cf. *pseudomenardii* (Bolli) follow without notable change in facies. Late Maastrichtian and early Paleocene deposits have not been recognized, but Late Cretaceous extraclasts are common in older horizons of the Tertiary limestones of Paleokastron Hill (Steuber *et al.* 1997). The contact to flysch-type argillaceous marls and sandstones at the base of the section is tectonically disturbed.

The facies development of the Paleokastron section differs significantly from that of the Pelagonian margin in Boeotia (Steuber *et al.* 1997). Thick limestones of early Cretaceous age and an Early Cenomanian to Campanian hiatus are characteristics of the sedimentary successions of the Parnassus platform. At Paleokastron, the emerged and karstified mid Cretaceous limestones are not sealed with bauxites as on the Parnassus platform, but are covered by terrigenous siliciclastics. This implies a palaeogeographical position marginal to the Parnassus platform and close to the emerged Pelagonian hinterland. This setting also explains the overturning of the sequence which is rather extraordinary compared with the regional style of tectonic deformation. During the early Tertiary the deposits became wedged in and tilted over between the rigid blocks of the Pelagonian and Parnassus platforms (Steuber *et al.* 1997).

Rudists from Paleokastron Hill can be assigned to the Santonian–early Campanian coenozone (sensu Polšak *et al.* 1982) which is in accordance with the late Campanian age of the overlying limestones. Therefore, the rudist beds of Paleokastron Hill must be contemporaneous with the transgressive rudist beds of northern Boeotia, although the associations are significantly different. In fact, not a single species occurs in both palaeogeographical settings.

Kiriaki (18). To the east of Kiriaki village (Helicon Mountains) rudist limestones are exposed which were covered by late Paleocene red argillaceous marls after a period of subaerial exposure (Walter 1996). Cross sections of conjoined rudist shells in life position are exposed on a north-east dipping bedding plane. *Vaccinites chaperi* (Douvillé) and thick-shelled radiolitids which could not be isolated from the compact, pure limestones formed a dense biostrome.

Road from Analipsis to Elikonas (19). Massive and thick-bedded limestones with abundant rudist remains are exposed along the road from Analipsis to Elikonas villages which ascends the northern slope of the Helicon Mountains. They contain *Vaccinites chaperi* (Douvillé) and *V. vesiculosus* (Woodward).

Maastrichtian

Akraifnion (20). North of the Copais, flysch-type sediments overlie thick-bedded Maastrichtian limestones (Christodoulou and Tsaila-Monopolis 1975; Konertz 1987); early Paleocene deposits are absent (Gotzes 1993). In contrast with the deepening of depositional environments on the distal Pelagonian platform, conglomeratic limestones with echinoderms and orbitoid foraminifera indicate periods of littoral redeposition on the proximal Pelagonian platform in northern Boeotia. A palaeokarst surface which developed locally during the Cretaceous/Tertiary transition in the Helicon, Parnassus and Othrys Mountains (Richter 1976; Richter and Mariolakos 1977; Walter 1996) has not been observed in northern Boeotia (Steuber *et al.* 1993).

Although rudist remains are commonly present in limestones below Paleocene flysch-type deposits, determinable shells have only been found at Akraifnion village, 30 m below the Cretaceous-Tertiary boundary. *Hippuritella lapeirousei* (Goldfuß) and *Hippurites cornucopiae* Defrance are abundant. *Orbitoides media* (d'Archiac) and *O. apiculata* Schlumberger have been mentioned from these limestones (Christodoulou and Tsaila-Monopolis 1975).

(21) Antikyra. The age of the youngest rudist beds of the region is well constrained at a locality on the isthmus of Kefallinia Peninsula in the Gulf of Antikyra (38° 21′ 34″ north, 22° 37′ 44″ east, out of the region shown on Text-fig. 1). There, a horizon with groups of *Hippuritella lapeirousei* (Goldfuß) is conformably overlain by micritic limestones with planktic foraminifera of the 'middle' Maastrichtian *Gansserina gansseri*-zone (Robaszynski *et al.* 1984): *Gansserina gansseri* (Bolli), *Globotruncana arca* (Cushman), *Globotruncana falsostuarti* Sigal, *Globotruncanella pschadae* (Keller), *Globotruncanita stuartiformis* (Dalbiez), *Rosita fornicata* (Plummer).

Rudist coenozones in Boeotia

According to the biostratigraphical data, the Boeotian rudist associations can be grouped into six coenozones (Table 2). The co-occurrence of rudists and benthic foraminifera provides a chronostratigraphical correlation of the Aptian to Cenomanian deposits. The Maastrichtian is indicated by planktic and orbitoid foraminifera. Stratigraphical correlations of Mid Turonian–Campanian deposits are based on comparisons of the Boeotian rudist associations with those of other Mediterranean regions, and especially with those from the external Dinarids (Polšak *et al.* 1982), the chronostratigraphy of which is, as noted above, not generally accepted. Within the Santonian–Campanian interval, further biostratigraphical evidence is provided for the rudist taphocoenosis from Paleokastron Hill (εb) which cannot be younger than late Campanian in age because of planktic and orbitoid foraminifera found in the overlying limestones. A diachronous deposition of the northern Boeotian rudist limestones (εa, εc) is indicated by the anagenetic lineage *Vaccinites cornuvaccinum* (Bronn)–*V. chaperi* (Douvillé) and by different radiolitid associations.

Although not a single species is shared by the associations εa and εb, both belong to the Santonian–Lower Campanian coenozone of Polšak *et al.* (1982). Additionally, the palaeogeographical reconstruction of depositional environments indicates that they must be contemporaneous.

Rudist localities in the Vermion Mountains (Macedonia)

Several rudist species have been reported from the Upper Cretaceous of the Vermion Mountains

TABLE 2. Cretaceous rudist coenozones in Boeotia.

(α) Aptian

Horiopleura? *juxi* sp. nov.

(β) Albian

Horiopleura lamberti Douvillé
Monopleura marcida White
Eoradiolites davidsoni (Hill)
Eoradiolites sp.

(γ) Cenomanian

Caprina baylei (Gemmellaro)
Sphaerucaprina woodwardi Gemmellaro

(δ) Middle Turonian - ?Coniacian
Biradiolites angulosus d'Orbigny
Durania cf. *montisferrati* Astre
Lapeirousella aumalensis (Douvillé)
Praelapeirousia? sp. nov.
Praeradiolites ponsianus (d'Archiac)
Praeradiolites cf. *urnalis* Astre
Radiolites lusitanicus (Bayle)
Radiolites praegalloprovincialis Toucas
Radiolites sauvagesi (d'Hombres-Firmas)
Hippuritella resecta (Defrance)
Vaccinites cf. *grossouvrei* (Douvillé)
Vaccinites inferus (Douvillé)
Vaccinites ljalintzensis Pamouktchiev
Vaccinites praegiganteus (Toucas)
Vaccinites praepetrocoriensis (Toucas)
Vaccinites ptoonensis Steuber

(ε) Santonian-Campanian

a)
Mitrocaprina boeotica (Munier-Chalmas)
Bournonia africana Douville
Bournonia fourtaui Douvillé
Durania martellii Parona
Durania katzeri (Slišković)
Fossulites dionysii Steuber
Fossulites aff. *undaesaltus* (Astre)
Gorjanovicia boeotica Steuber
Gorjanovicia costata Polšak
Gorjanovicia gracilis (Wiontzek)
Gorjanovicia kayae Özer
Gorjanovicia lipparinii Polšak
Medeella cf. *zignana* (Pirona)
Praeradiolites echennensis Astre
Radiolites subradiosus Toucas
Sauvagesia meneghiniana (Pirona)
Sauvagesia tenuicostata Polšak
Vaccinites cornuvaccinum (Bronn)

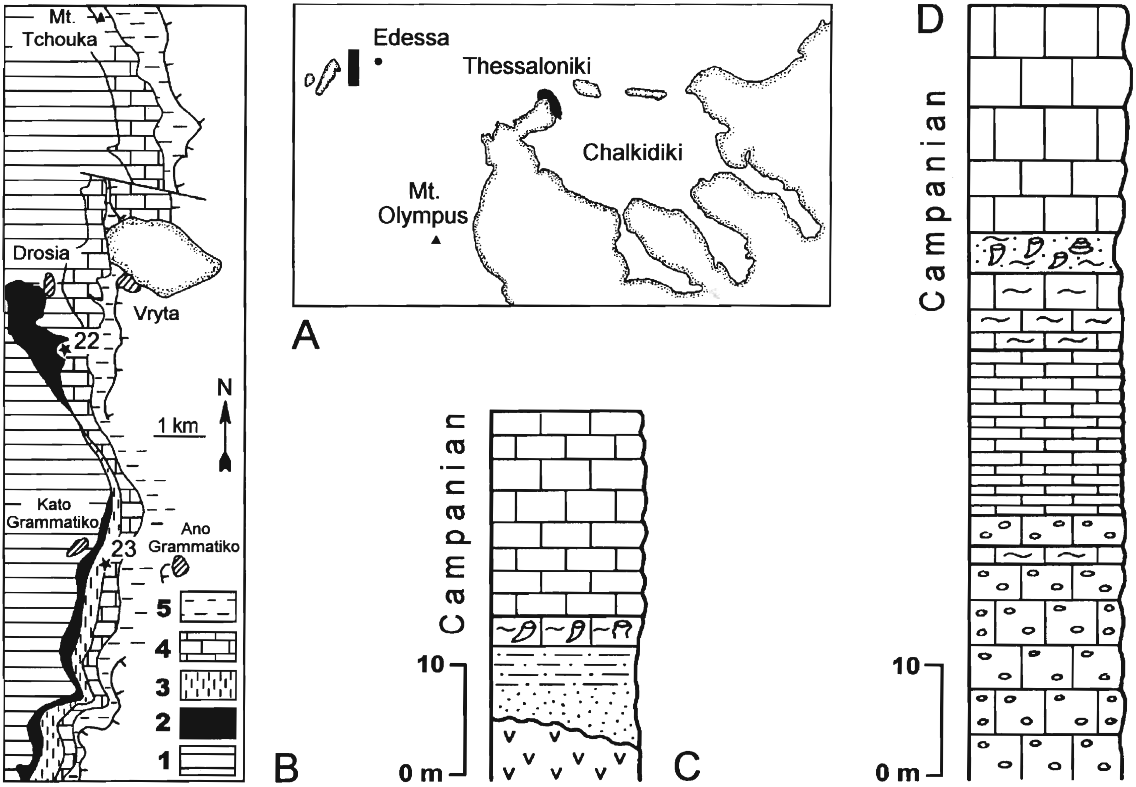
b)
Mitrocaprina bayani (Douvillé)
Radiolites angeiodes (Lapeirouse)
Hippurites cf. *canaliculatus* Rolland du Roquan
Hippurites colliciatus Woodward
Vaccinites boehmi (Douvillé)
Vaccinites aff. *cornuvaccinum* (Bronn)
Vaccinites giganteus (d'Hombres-Firmas)
Vaccinites inaequicostatus (Münster)
Vaccinites kuehni (Pejović)
Vaccinites praesulcatus (Douvillé)
Vaccinites salopeki (Polšak)
Vaccinites sulcatus (Defrance)
Vaccinites vredenburgi (Kühn)
Vaccinites sp.

c)
Petkovicia? *verajana* Slišković
Sauvagesia meneghiniana (Pirona)
Hippuritella variabilis (Munier-Chalmas)
Vaccinites chaperi (Douvillé)
Vaccinites vesiculosus (Woodward)

(μ) Maastrichtian

Hippurites cornucopiae Defrance
Hippuritella lapeirousei (Goldfuß)

(Mitzopoulos 1959; Mercier 1973; Kollmann *et al.* 1985). Rudist limestones that unconformably overlie the Pelagonian basement are well exposed between the towns of Edessa and Florina (Text-fig. 4). They were deposited on the eastern margin of the Pelagonian micro-continent, bordering the Cretaceous Axios Ocean (Mercier 1973), in contrast with the Boeotian sequences that formed on the western Pelagonian margin that bordered the Cretaceous Pindos Ocean. In the northern Vermion Mountains, the late Cretaceous transgressive onlap diachronously proceeded from the south to the north: the deposits are of Campanian age at Grammatiko village and at Moukharemi Hill, and of Maastrichtian age at Tsouka



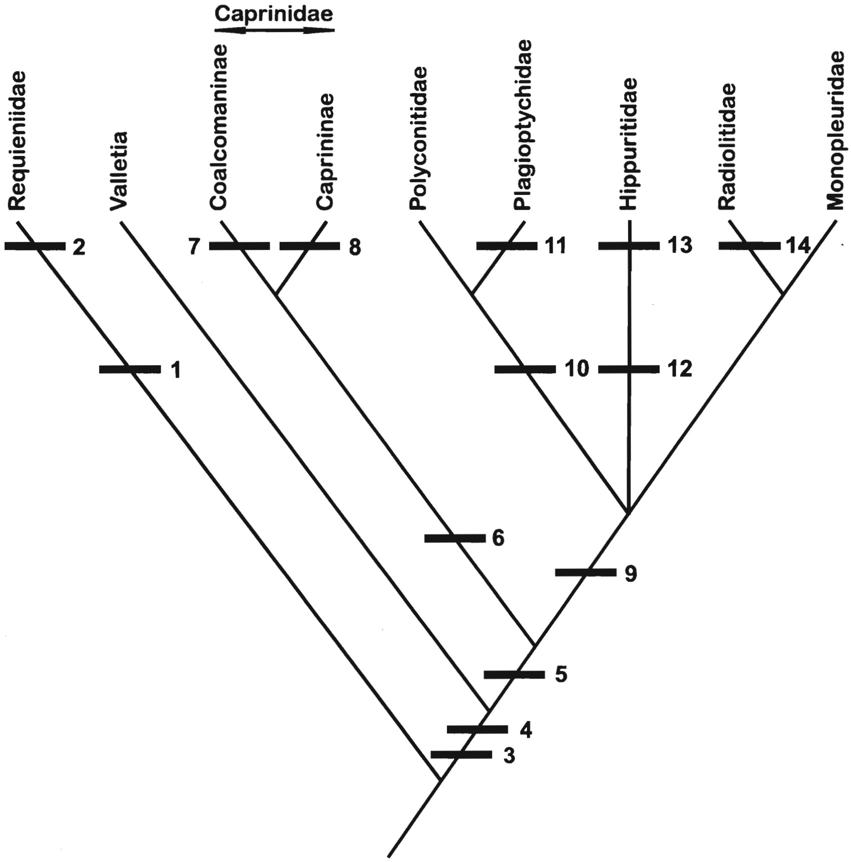
TEXT-FIG. 4. Rudist localities and measured sections in the Vermion Mountains. A, map; B, detail of black rectangle; (1) Triassic–Jurassic limestones; (2) basic volcanics; (3) conglomeratic limestones, ?Cenomanian–?Turonian; (4) rudist-limestones, Campanian–Maastrichtian; (5) flysch-type deposits, Maastrichtian–Tertiary. Geological map after Mercier (1973). C, section at Moukharemi Hill (22); D, section along dirt-road between the villages of Ano- and Kato-Grammatiko (23).

Mountain (Mercier 1973). Two localities are described here, from both of which rudists have hitherto not been reported.

Northern slope of Moukharemi Hill (22). To the south of the road linking Edessa and Florina, sandstones and argillaceous marls that overlie serpentinized basic volcanics (Text-fig. 4C) contain abundant corals (Abdel-Gawad and Gameil 1995): *Columnocoenia* sp., *Cunnolites* (*Paracunnolites*) *scutellum* (Reuss), *Fungiastraea* cf. *conferta* (Milne-Edwards and Haime), *Glyphephyllia crassisepta* Hackemesser, *Nefophyllia* sp., *Phyllocoenia corollaris* (Reuss), *Phyllosmilia aegiale* Felix, *Placosmiliopsis* sp. and *Pseudocoeniopsis* sp.

Impure limestones above contain *Cunnolites*, abundant debris of radiolitid shells and numerous bivalved specimens of *Vaccinites chaperi* (Douvillé) in a reclining life position. The shells are rarely in contact, predominantly curved around the dorsal side and the left valves are facing upwards. The overlying limestones are unsorted float- and rudstones with rudist and coral bioclasts that are heavily bored and partly encrusted by corallinacean algae. *Lapeirousia* sp. has been recognized in thin section among abundant rudist debris.

Grammatiko (23). A thick sequence of Cretaceous limestones is exposed along the dirt-road leading from Kato Grammatiko to Ano Grammatiko (Text-fig. 4D). Conglomeratic limestones with pebbles of the



TEXT-FIG. 5. Tentative reconstruction of the phylogeny of the Hippuritoidea. Derived characters: (1) LV = attached valve; (2) thickened outer shell layer; (3) RV = attached valve; (4) two cardinal teeth in LV, and one tooth, which is reduced in some taxa, in RV; (5) ligament invaginated; (6) inclined to erect lamina in RV, running from central tooth to posteroventral shell wall to demarcate omp′; (7) LV mp insertion surface facing outwards onto mp′ of RV, the latter on posterior shell wall; (8) LV mp insertion surface facing inwards onto outward facing mp′ of RV, the latter on erect myocardinal lamina; (9) thick outer shell layer in RV; (10) mp′ of RV on thickening of posterior shell (*Polyconites*), that may be raised to extend parallel to the commissure or is even slightly tilted backwards (*Horiopleura*); (11) canals in inner shell layer; (12) mp′ of RV tilted backwards, in tapering socket that receives elongated mp of LV; (13) pores and canals in LV outer shell layer; (14) cellular structure of outer shell layer in one or both valves. Phylogeny of Caprinidae d'Orbigny, after Skelton and Masse (1998); Coalcomaninae Coogan includes *Retha* Cox, and Caprininae d'Orbigny includes *Pachytraga* Paquier.

reworked Eohellenian basement unconformably overlie Triassic–Jurassic marbles. The thickness of these conglomerates increases from 100 m at Grammatiko to more than 800 m further to the south. Their precise age is unknown (Mercier 1973), but similar deposits contain gastropods and corals of presumed Cenomanian age (Brunn 1956) at other localities. At Grammatiko, thin bedded limestones overlie this sequence (Text-fig. 4D). These bioturbated biomicrites contain no age indicative fossils other than calcispheres and pithonellids and could have been deposited during the Turonian sea-level highstand. Overlying an erosional unconformity are red-brown flaser-bedded limestones and red, impure limestones (wacke-packstones). They contain groups of *Vaccinites chaperi* (Douvillé) and *V. archiaci* (Douvillé). Pseudocolonies of conjoined, finger-thick and up to 200 mm long valves of *Lapeirousia* sp. in a vertical life position follow. The overlying massive limestones contain a few valves of *V. chaperi* at the base, but

TABLE 3. Abbreviations. For additional explanations refer to Text-figures 6–9.

RV	right valve
LV	left valve
(1)	anterior tooth
(1′)	socket of anterior tooth
(2)	central tooth
(2′)	socket of central tooth
(3)	posterior tooth
(3′)	socket of posterior tooth
L	ligament
ma	anterior myophore of LV
ma′	anterior myophore or muscle scar of RV
mp	posterior myophore of LV
mp′	posterior myophore or muscle scar of RV
o	main body cavity
oma	accessory cavity anteriorly of ma of LV (Caprotinidae)
omp	accessory cavity posteriorly of mp of LV (Caprotinidae)
omp′	accessory cavity between more or less erect posterior lamina and shell wall of RV
o2′	accessory cavity extending ventrally from 2’ (Caprinidae)
Vb	ventral radial band along the external surface of the ventral shell (Radiolitidae)
Pb	posterior radial band along the outer surface of the posteroventral shell (Radiolitidae)
Ib	interband, on the outer surface between Vb and Pb (Radiolitidae)
Vs	ventral pseudopillar, modification of shell structure of Vb (Radiolitidae)
Ps	posterior pseudopillar, modification of shell structure of Pb (Radiolitidae)
P0	anterior pillar, ‘ligamental ridge’, ‘arête cardinale’ (Hippuritidae)
P1	central pillar (Hippuritidae)
P2	posterior pillar (Hippuritidae)

the amount of radiolitid shell debris decreases to the top. Rudist bioclasts of these rud-, pack-, and floatstones are commonly encrusted by *Pseudolithothamnium album* Pfender.

The presence of *Vaccinites chaperi* (Douvillé) is restricted to the coenozone εc in Boeotia. The association with *V. archiaci* (Douvillé) which was identified in Mid Campanian deposits of the Pyrenees (Vicens 1992), is indicative of a stratigraphically elevated level of the rudist beds at Grammatiko within the Santonian–Campanian coenozone.

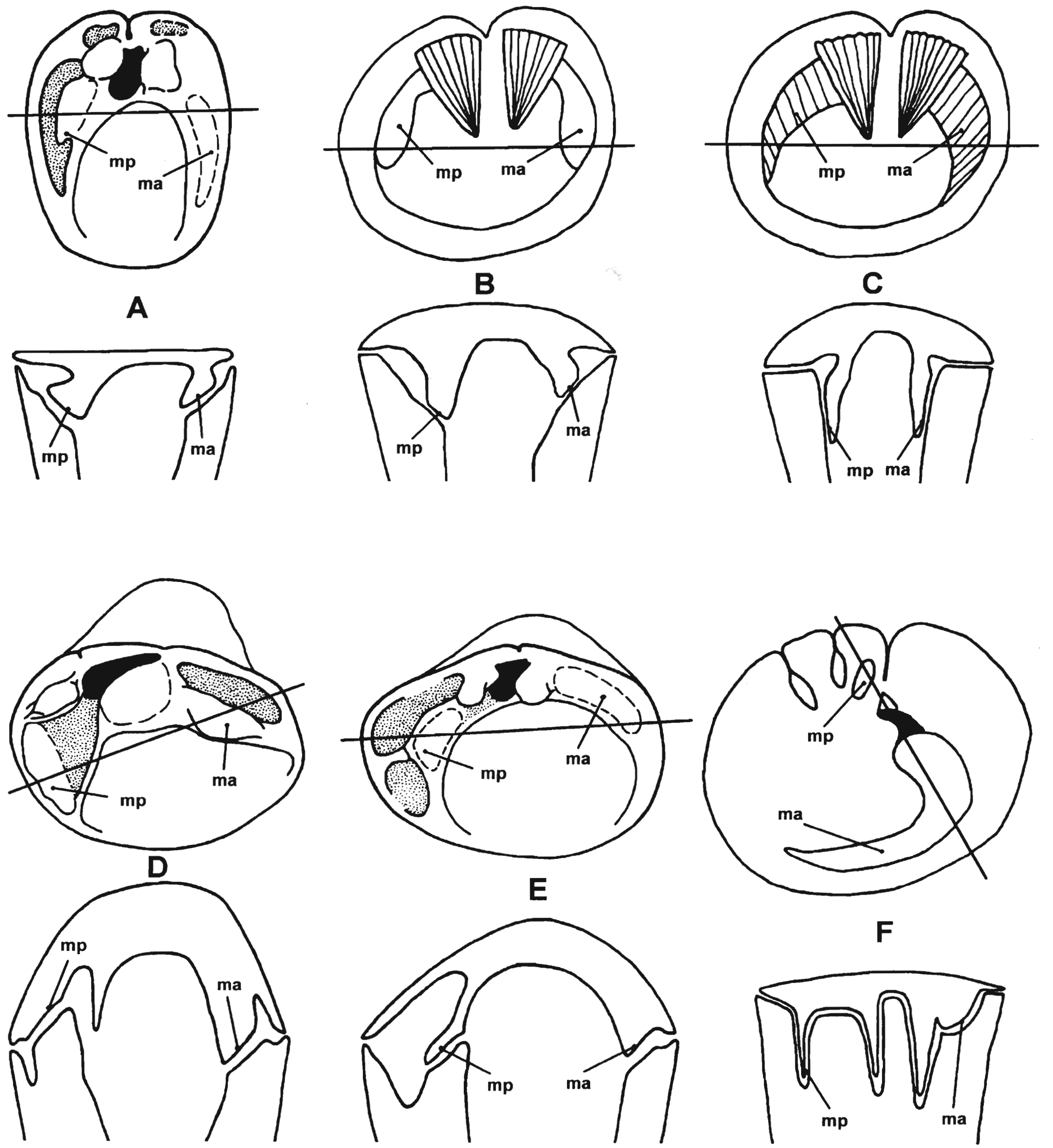
TAXONOMY

Phylogeny and terminology

Hippuritoidea Gray, 1848 comprises inequivalve, predominantly attached bivalves, the major clade of which shows a phylogenetic trend of shell uncoiling (Skelton 1978). Highly specialized forms evolved during the Cretaceous (Text-fig. 5) which were variously well-adapted to an epifaunal life habit (Masse and Philip 1986; Ross and Skelton 1993). A pronounced plasticity of growth allowed successful radiation in various shelf environments, some of which were at other times dominated by coral-algal-hydrozoan communities for most of the Phanerozoic.

The heterodont hinge of the Hippuritoidea has two prominent teeth (1, 3) in one valve and a single tooth (2) that is atrophied in some taxa, in the other. Two adductor muscles are inserted either directly on the shell wall, on a cardinal platform, or on more or less prominent myophores.

Myocardinal elements. The following explanations (Table 3; Text-figs 5–9) refer only to those taxa that were attached by the right valve (RV) and which have an anterior (1) and posterior (3) tooth in the free left



TEXT-FIG. 6. Arrangement of adductor attachment in some groups of the Hippuritoidea. A, *Polyconites*; B, *Agriopleura*; C, *Radiolites*; D, *Pachytraga*; E, *Caprotina*; F, *Vaccinites* (extended after Skelton 1978).

valve (LV) and a single tooth (2), which was atrophied in some genera, in the RV. Taxa with this type of hinge were much more successful in the colonization of shallow marine environments when compared with the Diceratidae Dall, 1895 and Requieniidae Douvillé, 1915*c*. Only a few taxonomists (e.g. Masse and Philip 1986; Mainelli 1992*b*) have followed the proposition to discriminate two suborders, Sinistrodonta Pcelintcev, 1959 and Dextrodonta Pcelintcev, 1959, on the basis of these differences in dentition.

Spirogyrate growth, only, was accomplished in the Diceratidae and Requieniidae by a continuous posterior dislocation of the active ligament during ontogeny (Skelton 1978). The invagination of the ligament occurred first in the paraphyletic Caprotinidae Gray, 1848, and was an important cornerstone of rudist phylogeny as it resulted in complete uncoiling and an efficient, almost complete translation of shell accretion to vertical (or horizontal) tubular growth. These major morphogenetic innovations induced several modifications in the design of the myocardinal elements. The cardinal teeth became aligned parallel to the growth axis, lengthened considerably and projected into deep sockets (1′, 3′) of the RV.

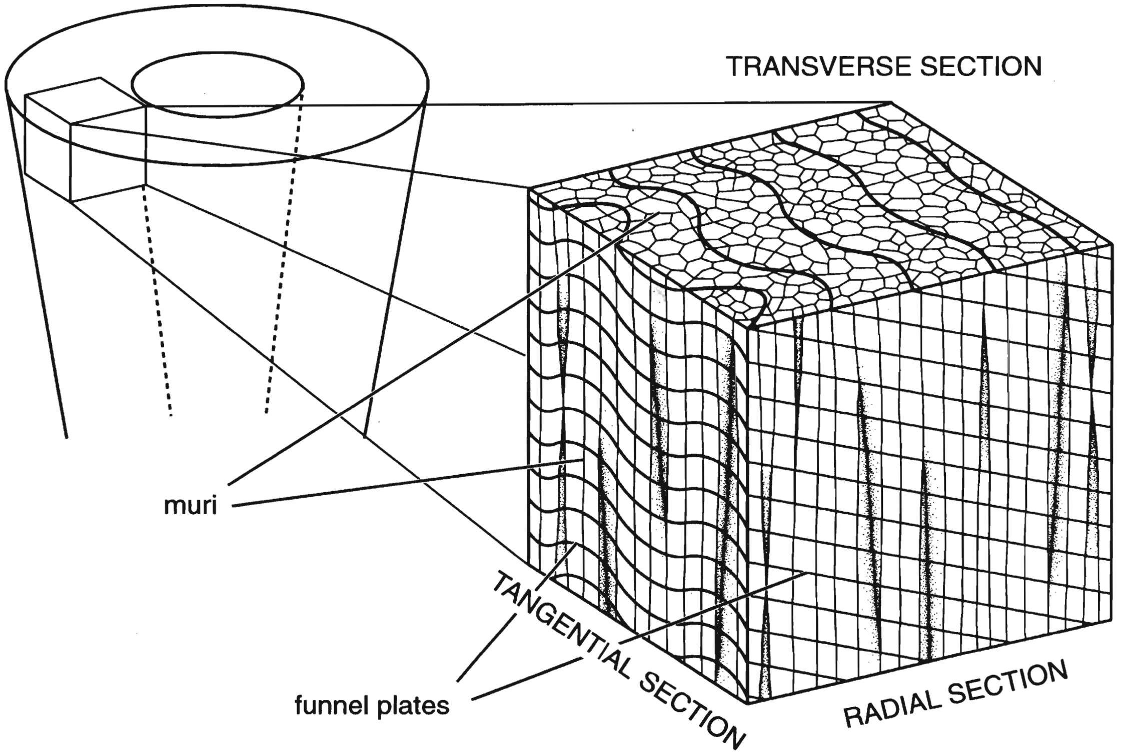
Two major lineages emerged in the caprotinid rudists and are delineated by different rotations of the posterior adductor (Skelton 1991; Skelton and Masse 1998). In the LV of *Monopleura*, and becoming more pronounced in *Agriopleura*, two thickenings of the inner shell layer project slightly over the commissural plane into the RV and form the anterior and posterior myophores (ma, mp; Text-fig. 6A–B). The anterior and posterior attachment sites of the adductors in the RV (ma′, mp′) are thickenings of the inner shell layer. This arrangement was only slightly modified in the Radiolitidae d'Orbigny, 1847 which were widely distributed until the end of the Cretaceous. Arrangement of the LV myophores was similar in the latter but they projected more deeply into the RV (Text-fig. 6C). The adductor muscles, now acting parallel to the commissural plane, attached on the outer surfaces of ma and mp so that uneconomical thickening of the RV inner shell to support the muscle scars was reduced.

In certain clades of caprotinid rudists, mp rotated out of the LV into the RV so that the adductor scar is situated on the interior surface of mp (Text-fig. 6D–F); mp′ forms a ridge or septum of the cardinal platform and demarcates a posterior accessory cavity (omp′). The RV posterior adductor scar is located on the exterior side of this septum. This reorganization of posterior muscle attachment during the Hauterivian (*Pachytraga* Paquier, 1900) was coeval with the start of a marked increase in diversity of the group (Smith 1994). The rotation of the myophores into the RV induced the formation of accessory cavities (oma, omp) that are diagnostic for most genera of caprotinid rudists. A *Pachytraga*-type of mp was refined in more evolved forms of the Caprininae d'Orbigny, 1847. In *Retha* Cox, 1965 which is considered to be ancestral within the Coalcomaninae Coogan 1973, mp′ retained its position close to the posterior shell wall (Skelton and Masse 1998). Similar to the conditions in the Caprininae, in more evolved forms of the Coalcomaninae which are restricted to the New World, an erect myocardinal lamina separates omp′ from the main body cavity, but the muscle insertion of mp faces outwards, and mp′ is located on the posterior shell wall (Chartrousse 1998). A relocation of the sites of myophoral attachment is noted also in other groups of the Hippuritoidea (Text-fig. 5). Among taxa with thick calcitic outer shell layers that could be related to *Monopleura*, an elevation of mp′ from the posterior shell wall into a position parallel to the commissure or even slightly tilted backwards occurred in the Polyconitidae Mac Gillavry, 1937 (Skelton and Masse 1998) and, more pronounced, in the Hippuritidae Gray, 1848, in which mp as well as (1) and (3) are considerably prolonged and project deeply into sockets of the RV.

The ligament lost its original function during the course of this myocardinal re-arrangement and was atrophied in several Radiolitidae, Hippuritidae and Plagioptychidae.

Shell sculptures and structures. Further evolution of the accessory cavities within the inner, aragonitic shell that are diagnostic of the caprotinid rudists occurred in the Caprinidae. A phylogenetic trend towards complex patterns of so-called pallial canals that finally invaded the entire LV, and the RV of some groups, has been noted (Mac Gillavry 1937). In transverse sections, these canals are either irregularly outlined, pyriform, polygonal or cylindrical and can be arranged in several successive rows along the posteroventral shell (Text-fig. 23). This hollow structure was probably formed by papillae of the mantle margin and, in addition to the economic use of $CaCO_3$, was certainly a pitfall for boring organisms (Vogel 1979). In contrast to the Hippuritidae and Radiolitidae, the outer calcitic shell layer is thin in the Caprinidae and in some caprotinid rudists.

Radiolitidae: The outer shell layer of the Radiolitidae is commonly formed by lamellae that are arranged in a tiled pattern of stacked, overlapping funnels. Various styles of folding and sculptures of the lamellae are diagnostic at the generic and species level. The outer shell consists of small, originally hollow cells that are formed by two major constructional elements (Text-fig. 7): Sub-horizontal plates delineate the former position of the outer mantle lobe during successive stages of shell formation and probably formed in



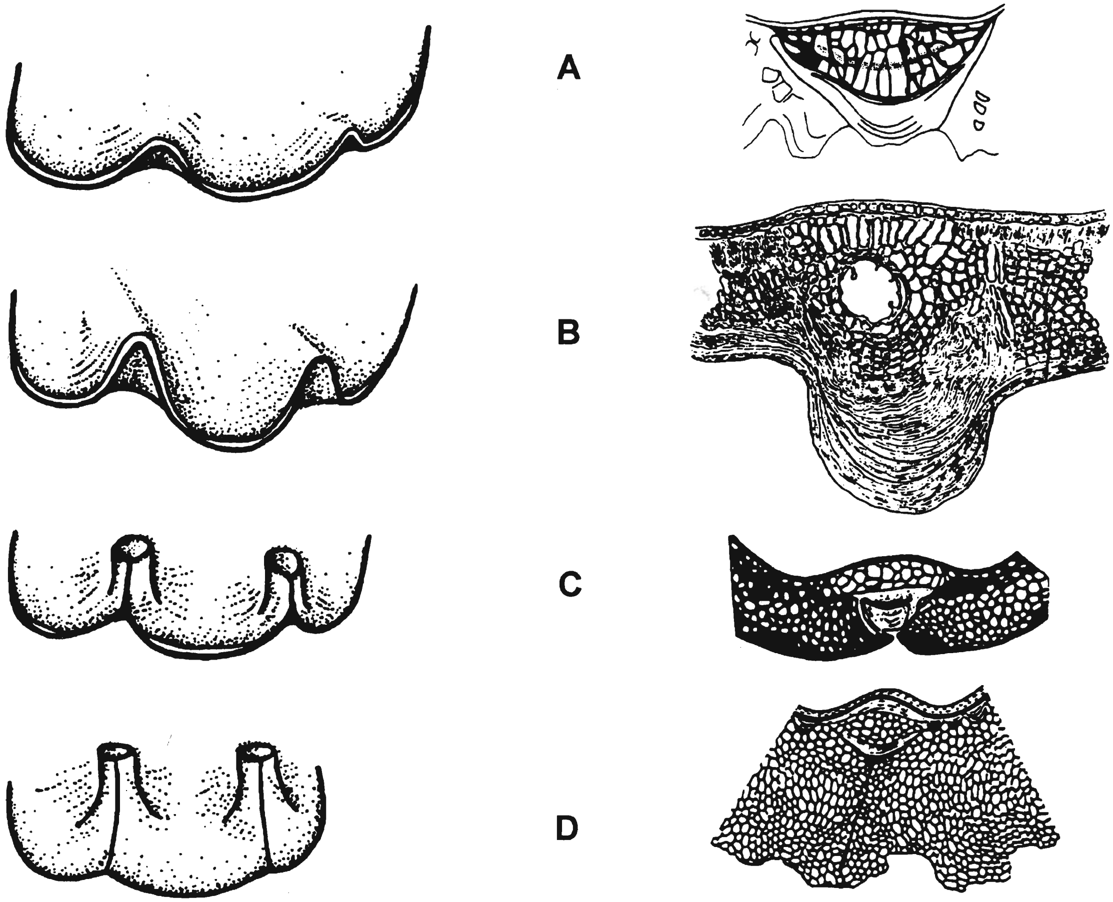
TEXT-FIG. 7. Shell structure of the Radiolitidae in various sections.

regular intervals (Amico 1978). The outer parts of these funnel plates are more or less distinctively folded, and they are commonly inclined towards the growth axis of the shell. In simple structures (*Eoradiolites* Douvillé, 1909), the funnel plates are crossed by thin radial blades that form the vertical structural elements. In transverse section, the intersections of these radial muri with the inclined funnel plates form rectangular hollow prisms. In more complicated structures, the muri branch distally or are complemented by tangential muri to form a pattern of hollow cells that appear irregular or sub-polygonal in transverse section. In most regular structures, the muri enclose angles of 120° and form similarly sized, even hexagons.

The importance of the cellular structure of the outer shell layer for the taxonomy and phylogeny of Radiolitidae was noted early by Douvillé (1910). Nevertheless, shell structures have been documented in only a few species and are frequently neglected, even in modern descriptions. A comparison of structural patterns and dimensions observed in Boeotian Radiolitidae with the few published data (e.g. Amico 1978) revealed remarkable similarities, confirming the high diagnostic value of this character.

Both cellular and compact, fibrous prismatic structures are known to occur in the outer shell layer of several genera of the Radiolitidae; compact and cellular structures can alternate in a single shell (Masse and Philip 1972). In several taxa, the cellular structure can be traced in compact layers (Pl. 11), whilst the compact layers of others have simple fibrous prismatic ultrastuctures as in the Hippuritidae. Compact structures commonly occur in thin-shelled, elongate morphotypes and reflect rapid vertical shell accretion (Cestari 1992*a*; Steuber 1996*a*).

Particular attention is generally given to structural modifications along the posteroventral shell where two radial bands can be discerned. A ventral (Vb) and a posterior (Pb) radial band are marked either by pronounced plications of the shell lamellae or by externally smooth or delicately ribbed sectors that differ from the sculpture



TEXT-FIG. 8. Pseudopillars of Radiolitidae. Left, infoldings of the posteroventral mantle margin of LVs. Right, corresponding shell structures of RVs in transverse sections. A, *Lapeirousella*; B, *Pseudopolyconites*, transverse section after Milovanović 1938*a*; C, *Lapeirousella*; D, *Lapeirousia*, transverse section after Milovanović 1938*a*.

of the rest of the shell. Radial bands in several caprotinid rudists and Caprinidae are developed as shallow, inconspicuous depressions that can be traced from the apex to the commissure. In the Radiolitidae, the sculpture of the radial bands and of the interband (Ib) are considered diagnostic at the genus and species level.

The functional implications of the radial bands are still discussed. It has been suggested that they mark the outlet of siphons or the sites of inhalant and exhalant currents (e.g. Yonge 1967; Kauffman 1969; Philip 1972); the most recent functional interpretation considers them as ejection sites of faeces and pseudofaeces (Skelton 1979*a*).

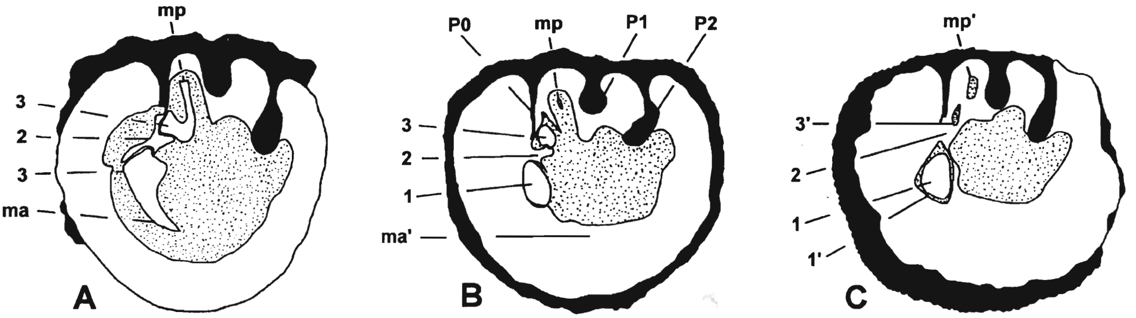
In transverse section through the radial bands, the exterior shell margin of most Radiolitidae is either incised or slightly bulging. The inner shell margin of the radial bands forms a straight sector or bulges towards the interior of the shell. The traces of the funnel plates observed in transverse section delineate the folding of the shell lamellae and, thus, the internal structure of the radial bands which formed by folding of the mantle margin. Although the radial bands are distinctively sculptured in many Radiolitidae, their internal structure is commonly similar to that of the rest of the shell. In other taxa, pseudopillars (Vs, Ps) are developed (Text-fig. 8) which had been previously misinterpreted as siphonal tubes (Klinghardt 1931) or siphonal cylinders (Wiontzek 1934). These peculiar structures are formed by oval or round, bowl-shaped depressions of the funnel plates (Milovanović 1938*a*; Astre 1957*b*). To the exterior, they are demarcated by steeply erected funnel plates that are embraced around the outside by the outer shell in advanced groups (Text-fig. 8B). The infoldings of the mantle margin that gave rise to these structures correspond to those of the LV, which, however, is rarely well preserved (Text-fig. 8). In primitive forms shallow arches formed at the commissural margin, which roofed small commarginal openings (Pl. 12, fig. 1) that remained open when the valves were tightly closed. The ontogenetic development of these arches can be traced from the apex to the commissure as a radial bulge that broadens commissurally. In other Radiolitidae, two inflections of the posteroventral shell margin of the LV are more steeply raised apically and were periodically reconstructed during ontogeny. Consequently, two galleries of imbricated arches developed over circular or oval depressions on the RV margin that formed the pseudopillars (e.g. *Petkovicia*? *verajana* Slišković, 1968*b*; Text-fig. 36C). In more advanced forms, the infoldings became continuously more erect (*Thyrastylon* Chubb, 1956), moved apically, and were finally embraced exteriorly by mantle lobes (*Lapeirousia* Bayle, 1878). This resulted in a continuous shift of the two posteroventral openings from a commarginal position to a chimney-like position on top of the LV. Adopting the functional interpretation of the radial bands as ejection sites of faeces and pseudofaeces (Skelton 1979*a*), an adaptive effect of this phylogenetic development would be that unwanted material was ejected above the commissure and was more efficiently removed by currents. The return of previously rejected material by currents could occur when waste was ejected through commarginal openings, as it was the case in more primitive radiolitids.

Similar folds of the RV mantle margin – almost a mirror image of those of the LV – resulted in the formation of pseudopillars (Text-fig. 8). With increasing apical dislocation of the LV openings (Text-fig. 8C–D), the pseudopillars of the RV bulge inwards. The bowl-shaped depressions in the outer shell are bordered on their outer sides by steeply erected lamellae (Pl. 10, fig. 3) which extended beyond the commissure, and occluded the hollow spaces between the closed valves towards the exterior so that gaping of the valves in Vb and Pb was only minor.

The two hollow spaces that resulted from the described modification of the posteroventral outer shell probably functioned as collecting sinks for faeces and pseudofaeces that were occasionally ejected through the openings formed by the LV. Alternatively, ejection of unwanted material could have been restricted to the posterior radial band. Food particles that were entrapped by the mantle margin could have been transported by ciliary action along the mantle margin to the ventral radial band, from where they might have passed towards the interior of the shell. The latter explanation agrees with the conventional denomination of the ventral radial band as the inhalant, and the posterior band as the exhalant site of the shell. It seems unlikely, however, that the observed structures simply functioned in channelling water currents, but it is premature to exclude the possibility that siphons were retracted into the described hollow spaces. There is still the need for detailed analysis of sufficiently well preserved specimens to constrain possible functional properties of the radial bands and concurrent structural modifications.

Inconspicuous arches at the posteroventral LV margin and corresponding depressions on the RV growth surface are known from Cenomanian and Turonian Radiolitidae such as *Neoradiolites* (Mermighis 1993), *Lapeirousella aumalensis* (Douvillé, 1915*b*) and *Praelapeirousia*? sp. nov. Faint pseudopillars have been reported even from late Aptian eoradiolitids (Masse and Gallo Maresca 1997), but prominent, inwardly bulging pseudopillars that are related to the formation of openings perpendicular to the commissure apparently did not develop before the Santonian–Campanian. It is tempting to unite radiolitids with pseudopillars in a single higher taxon. Unfortunately, the internal structures of radial bands have been examined only in a few species, and in many genera only the RVs are known. The taxonomy of the group is rather confusing, as some genera have been founded on characters of the LV whilst pseudopillars are considered diagnostic in others. The close relation between internal structures of radial bands and associated characters of the LV have generally been ignored. Pseudopillars are known in the RV of several genera, some of them with pronounced differences in the overall structure of the cellular outer shell. This indicates that pseudopillars developed convergently in several phylogenetic lineages of the Radiolitidae, which certainly do not belong to a monophyletic taxon.

Inner and/or outer shell layers of the LV of several genera are perforated by canals. Such canaliculate structures are apparently restricted to latest Cretaceous Radiolitidae and are commonly associated with the presence of pseudopillars. The cardinal teeth and myophores of most Radiolitidae are not constructed of



TEXT-FIG. 9. Transverse sections of three RVs of *Vaccinites cornuvaccinum* (Bronn). Distance from commissure increases from A to C. Black, outer shell layer; white, inner shell layers; dotted, body cavity, filled with internal sediments.

compact aragonite but are stiffened by ledges that enclose hollow spaces (Klinghardt 1931). Canaliculate structures that have been observed in the LV inner shell of Radiolitidae can thus be interpreted as a lightweight construction of the basal teeth and myophores and probably did not function as canals. The existence of true canals in the outer shell of the LV of certain Radiolitidae is not generally accepted (Pejović 1984; Alencáster and Pons 1992). Additionally, LV and RV have been confused in the description of several genera so that the systematics of this group is currently rather unstable. Neither pseudocanals of the inner shell nor canals of the outer shell have been noted in the LVs of Boeotian radiolitids.

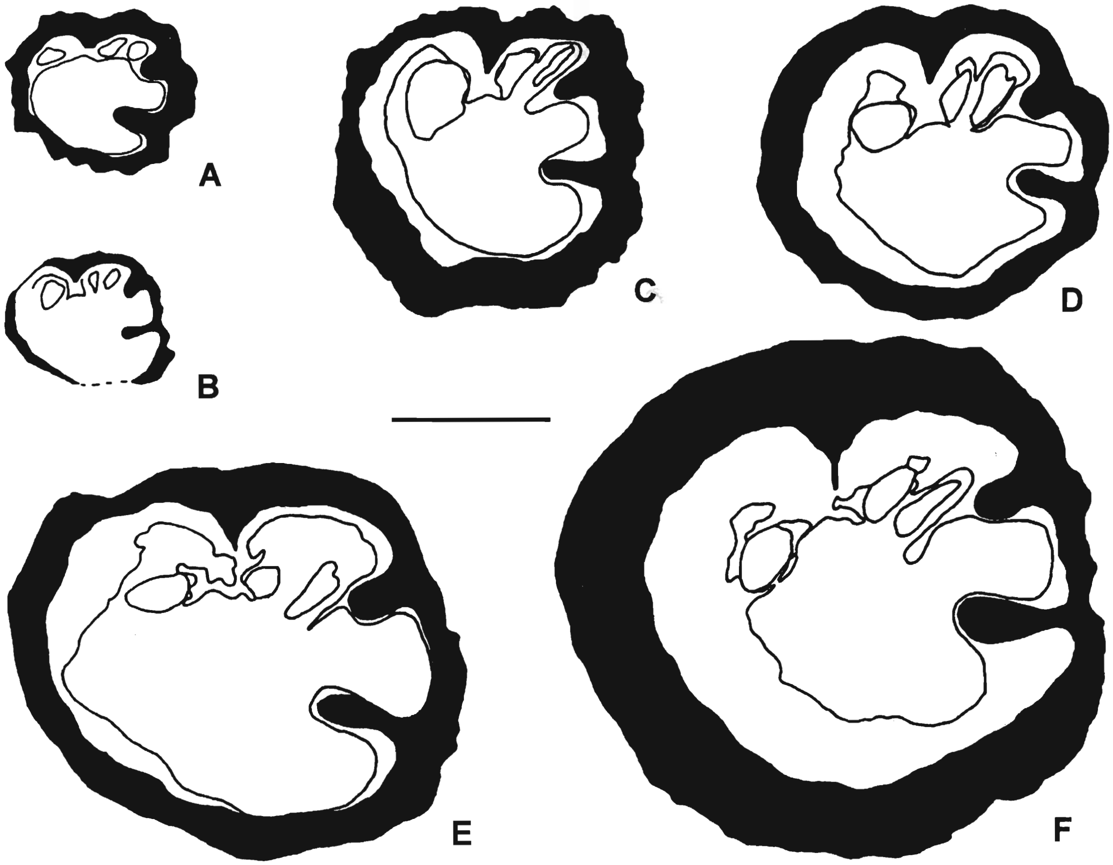
The most recent comprehensive diagnoses of radiolitid genera (Dechaseaux and Coogan 1969*b*) are misleading, particularly concerning the structures of the outer shell layer. Subfamilies were defined on the basis of the presence or absence of pseudopillars and ligamental ridge, but both characters developed convergently in different lineages. Additionally, the complete character suite of both valves of many genera is still unknown so that a division of Radiolitidae into subfamilies has been renounced in the taxonomic part of this monograph.

Hippuritidae: A thick, compact outer shell layer of fibrous prismatic calcite is found in Hippuritidae. Their sculpture of more or less pronounced and regularly spaced longitudinal ribs is mainly controlled by environmental factors and has only minor taxonomic implications (Vicens 1992). Two or more pillars which were formed by deep infoldings of the mantle margin are diagnostic features of the family (Text-fig. 9). Remnants of a ligament (Pl. 23, figs 1, 4) may be found at the tip of the anteriormost, dorsal pillar (P0). The ligament is reduced (Pl. 23, figs 2, 6) or completely absent in more evolved species, and the tip of P0 is rounded (Pl. 23, figs 3, 5). The loss of the ligament was also reported to occur during ontogeny (Douvillé 1910) but has never been unambiguously documented, and was not noted in the studied Boeotian Hippuritidae. The taxonomy of species with an atrophied ligament is difficult (Kühn 1933*a*; Mac Gillavry 1937; Vicens 1992), as the tapering tips of rounded P0 can be broken or diagenetically altered and thus mimic the existence of a ligament.

Two other prominent infoldings (P1, P2) posterior to P0 have been traditionally interpreted as marking the siphonal region of the shell. In certain late Cretaceous Hippuritidae, additional infoldings of the outer shell layer can protrude deeply and in regular patterns similar to scleractinian septa into the shell (e.g. *Pironaea* Meneghini).

The operculate LV of the Hippuritidae is covered by a network of small pores that cover radial canals which empty on the more or less steeply raised margin of the RV (Pl. 22). Pores and canals are formed by the outer shell layer. This construction has been convincingly interpreted to have channelled water currents. Accordingly, food particles were not trapped by ctenidia but by the mantle margin and passed over to the mouth by ciliary action (Skelton 1976). Another interpretation assumes an adaptation to photosymbiosis, suggesting that the porous surface of the LV allowed for the exposure of extended areas of the mantle to sunlight (Philip 1972; Cowen 1983).

Pores of the LV surface can be reticulate, polygonal, round, linear or vermiform and empty as simple funnels or complex sub-reticulate pores into the radial canals below (Douvillé 1891). The pores and radial

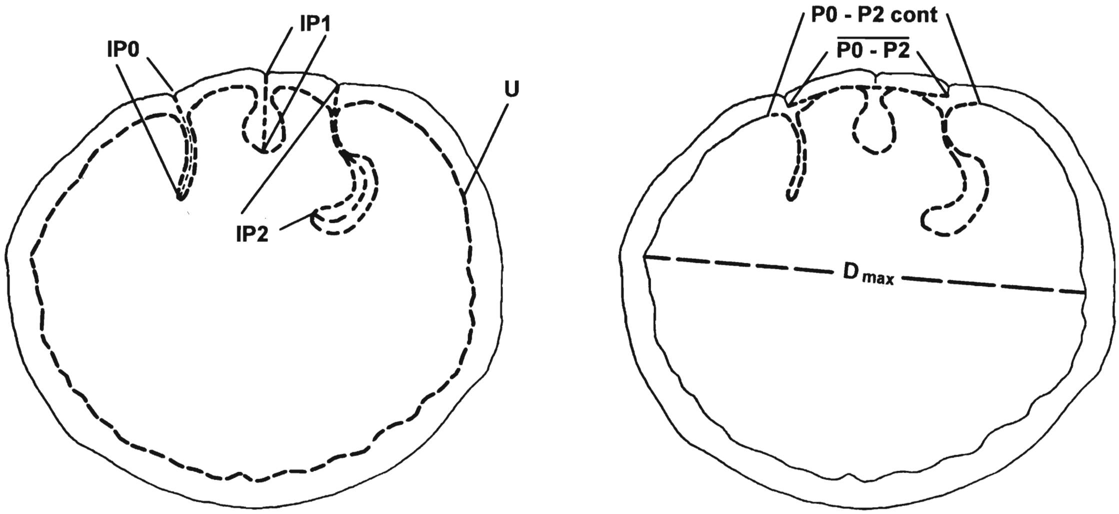


TEXT-FIG. 10. Example of a phylogenetic lineage of the Hippuritidae. A, *Hippurites incisus* (Coniacian); B, *H. matheroni* (Lower Santonian); C, *H. canaliculatus* (Upper Santonian–Lower Campanian); D, *H. vidali* (Middle Campanian); E, *H. lamarcki* (Upper Campanian–Lower Maastrichtian); F, *H. radiosus* (Lower Maastrichtian); after Douvillé (1893, 1895) and Vicens (1992). Scale bar represents 30 mm.

canals are diagnostic on the genus- and species-level but, unfortunately, not often preserved. The outline and arrangement of the pillars has developed similarly in several lineages and exhibits a pronounced intraspecific variation so that a safe determination based only on pillar morphology can be difficult.

Infoldings of the RV mantle that produced the characteristic pillars corresponded to two oscula of the LV pore system above the heads of P1 and P2. The oscula have been traditionally explained as inhalant and exhalant siphonal openings. According to a modern functional analysis they were ejection sites of faeces and pseudofaeces (Skelton 1976). Siphons would have been superfluous in hippuritids (Milovanović 1958), if trapping of food was not accomplished by ctenidia but by the mantle margin (Skelton 1976, 1979*b*), especially as the oscula were blocked by the pillar heads below, when the valves were closed. As outlined above for the Radiolitidae, the ventral osculum can alternatively be explained as an inhalant site for water which swept inside food particles that were collected by the mantle margin and transported around the margin by ciliary action. Ejection of faeces and pseudofaeces was probably restricted to the dorsal osculum.

The morphology of pillars and their distribution along the posterior shell are traditionally regarded as the most important species-diagnostic characters of the Hippuritidae. Phylogenetic evolution comprises the pinching of the stems of P1 and P2, an elongation of P0 and the reduction of the ligament, as reflected by the reduction of the surface of ligament insertion. Another trend was noted in lineages in which the



TEXT-FIG. 11. Explanation of measured distances and contours (broken lines) on transverse sections of RV of *Vaccinites chaperi* (Douvillé, 1897*a*).

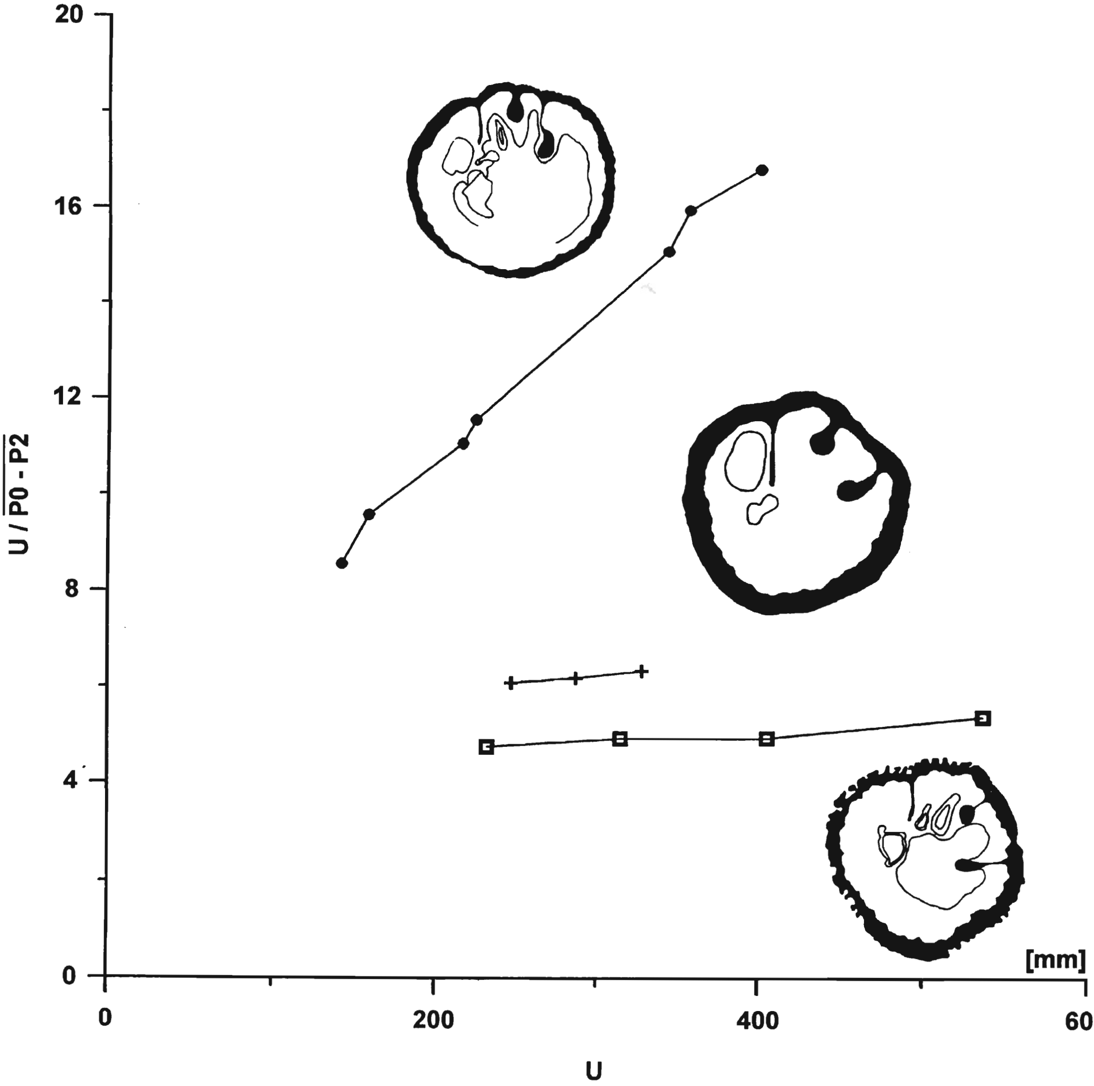
ligament was lost during early phylogeny: P0 is reduced and the corresponding infolding can disappear completely. In this case, the anterior tooth and myophore approach the dorsal shell (*Hippurites* Lamarck, 1801; *Hippuritella* Douvillé, 1908*a*).

The phylogenetic lineage *Hippurites incisus* Douvillé, 1895 – *H. matheroni* Douvillé, 1893 – *H. canaliculatus* Rolland du Roquan, 1841 – *H. vidali* Matheron, 1880 – *H. lamarcki* Douvillé, 1893 – *H. radiosus* des Moulins 1826 (Coniacian–Maastrichtian; Bilotte 1985; Vicens 1992) is characterized by the first morphological and functional evolution of P0 described above (Text-fig. 10), and by an overall increase in size which is frequently noted in evolutionary lineages of the Hippuritoidea. The broad surface of ligamental insertion of *H. incisus* is reduced, then rounded at its termination (loss of ligament) in *H. vidali* and elongated in *H. radiosus*. This example illustrates the relatively minor morphological changes that occurred during the long time span of the Coniacian–Maastrichtian and, consequently, the problems of taxonomic and biostratigraphical assignments if only a small number of specimens or single shells are considered. A pronounced ontogenetic and intraspecific variability complicates the taxonomy of the group. Therefore, morphometric analyses are an important tool to delineate the variation of morphospecies and to objectively compare specimens from various localities.

Morphometric analysis of Hippuritidae

Various approaches to morphometric analyses have been applied to the Hippuritidae (van Dommelen 1971; Laviano and Guarnieri 1989; Cestari 1992*a*). Much less attention has been paid to the qualitative and quantitative delineation of ontogenetic changes of diagnostic characters such as arrangement of pillars and myocardinal elements (Skelton and Wright 1987; Steuber 1993*a*), which are particularly important in phylogenetic considerations of the group.

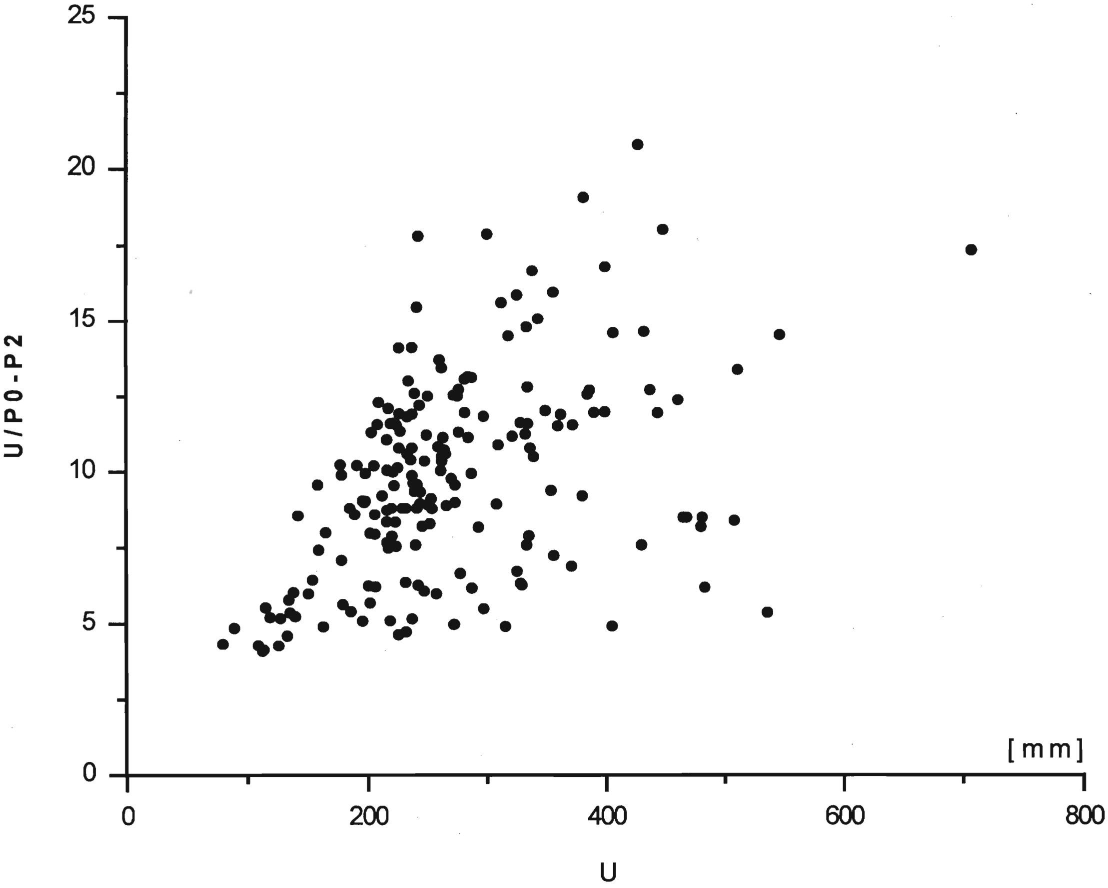
The arrangement of pillars is conventionally measured as angles between lines drawn from the centre of the RV through various characteristic reference points of the pillars (e.g. Laviano and Guarnieri 1989). As these angles vary in relation to the departure of the RV transverse section from circularity, which in turn depends on the available space during growth, such measurements are not always reliable. Environmentally driven morphological variations can be excluded, when the distance between the sutures of P0 and P2 ($\overline{\mathrm{P0-P2}}$) is compared with the length of the contour (U) of the inner margin of the outer shell layer (Text-fig. 11). By this approach, the distance of the sutures of the pillars is



TEXT-FIG. 12. Explanation of U/$\overline{P0-P2}$-diagrams with examples of the ontogeny of one RV, respectively, of (dots) *Vaccinites chaperi* (Douvillé, 1897*a*), (crosses) *V. inaequicostatus* (Münster, *in* Goldfuß, 1840) and (boxes) *V. vesiculosus* (Woodward, 1855).

related to the original length of the mantle margin. Measurements can only be taken from original material, as the scaling is imprecise or incorrect in many publications. Another premise is that transverse sections are cut exactly perpendicular to the growth axis, as oblique sections would bias the measurements.

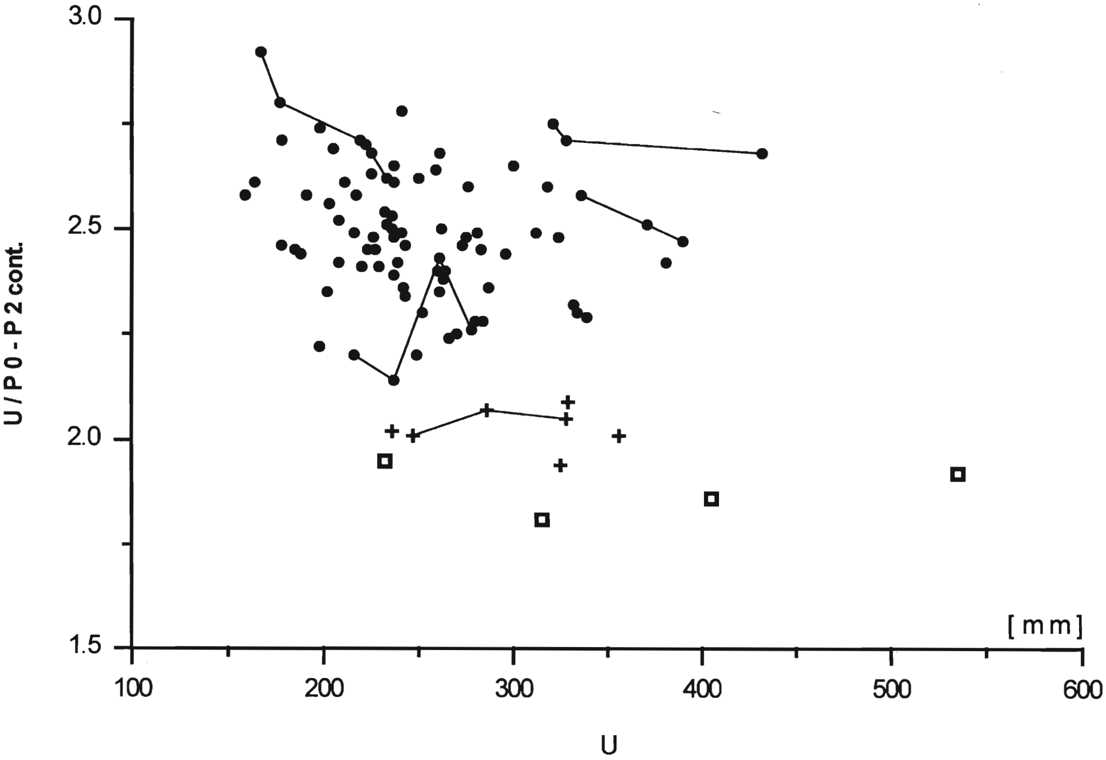
To evaluate intra- and interspecific variations of pillar arrangement, it is necessary to determine its ontogenetic evolution. It has been previously reported that the bases of the pillars move closer together with increasing individual age and diameter of RV (Douvillé 1910; Philip 1981), but this morphogenetic evolution has been quantified only in a few cases (Steuber 1993*a*). Although rarely evident by visual inspection (e.g. Pl. 24, fig. 5), it can be shown that the ratio U/$\overline{P0-P2}$ increases in all analysed species with the length of the contour U (Text-fig. 12). Consequently, the three pillars move proportionately



TEXT-FIG. 13. Plot of all measurements of pillar arrangement taken from numerous species of *Vaccinites* Fischer, 1887; see Text-figure 11 for measurements.

closer together with increasing length of the mantle margin. This trend is more pronounced in species with primarily closely distanced pillars such as *Vaccinites cornuvaccinum* (Bronn, 1831) or *V. chaperi* (Douvillé, 1897*a*), and less distinct in species in which the pillars are distributed around the posterodorsal quarter of the shell such as *V. vesiculosus* (Woodward, 1855) or *V. inaequicostatus* (Münster, *in* Goldfuß 1840). All measurements converge with decreasing length of the contour (U) to a ratio of $U/\overline{P0-P2} \cong 4$ (Text-fig. 13); this corresponds to the pillar arrangement of the oldest known species of *Vaccinites* Fischer, and is apparently retained in early ontogenetic stages of all analysed species.

The curvature of the stem of P2 that is commonly seen in transverse section of late growth stages traces the anterior relocation of this pillar during ontogeny (e.g. Text-fig. 11). This morphogenetic evolution could be related to an enlargements of the gills, as the expansion of the soft body was limited during the growth of cylindrical morphotypes. Only minor changes in pillar arrangement are noted in species with widely spaced pillars, and P2 frequently remains straight in adult shells (Text-fig. 85). This group comprises many species with broad-conical shells, but also others which commonly developed cylindrical morphotypes so that functional implications of these differences in ontogenetic development are difficult to constrain. An additional, adaptive aspect of this allometric shell growth that involves a disproportional expansion of the ventral shell is discussed below (see p. 197).

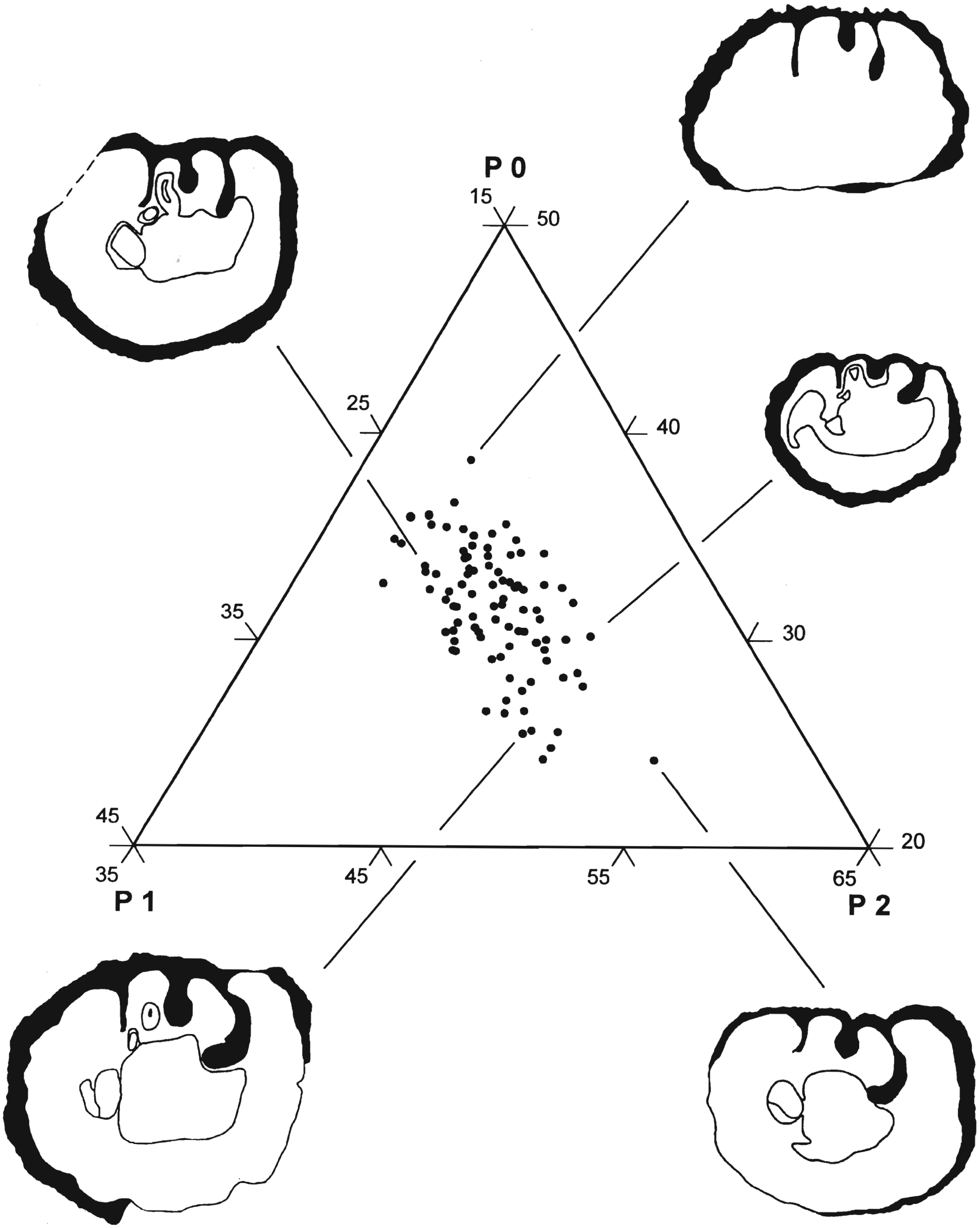


TEXT-FIG. 14. Fraction of infolded outer shell layer, plotted against the contour length (U) of the inner margin of outer shell layer (see Text-fig. 11). Dots, *Vaccinites cornuvaccinum* (Bronn, 1831); crosses, *V. inaequicostatus* (Münster, *in* Goldfuß, 1840); boxes, *V. vesiculosus* (Woodward, 1855). Ontogenetic stages of individual valves are connected by lines, respectively.

To assess if the tangential growth component was similar along the mantle margin, the length of the contour of the inner margin of the outer shell layer (U) has been compared in several ontogenetic stages to the fraction of this contour as measured between the anterior insertion of P0 and the posterior insertion of P2 ($\overline{\text{P0–P2}}$cont). The results show no distinct patterns (Text-fig. 14): one-third to more than half of the mantle was infolded to form the pillars. Successively extended parts of the mantle contributed to pillar formation during ontogeny of three RVs of *Vaccinites cornuvaccinum*, but this trend is not evident in another shell of the same species as well as in RVs of *V. inaequicostatus* and *V. vesiculosus*.

The relative length of P0, P1 and P2 (Text-fig. 11) are expressed in ternary diagrams (Text-fig. 15). This presentation involves the calculation of ratios so that unknown or imprecise scalings can be neglected and measurements taken from published figures can be used. The relative length of the three pillars have hitherto found little attention in taxonomic studies, but this method allows for a clear expression of intraspecific variations and provided interesting results in the comparison of closely related species.

The inclination of the hinge with respect to the radial axis of P0 is a diagnostic character of hippuritid genera (Toucas 1903, 1904; Bilotte 1982*c*). It can only be reliably determined on RVs with a straight P0 (Skelton and Wright 1987; Steuber 1993*a*), whereas such measurements are rather arbitrary in cases when P0 is curved (Kühn 1948). Therefore, this parameter has not been included in the morphometric analyses of the Hippuritidae.



TEXT-FIG. 15. Example of a P0-P1-P2 ternary diagram showing the intraspecific variation in relative length of pillars of *Vaccinites cornuvaccinum* (Bronn, 1831) from Boeotia.

SYSTEMATIC PALAEONTOLOGY

The taxonomic part of this monograph focuses on the description of variations that occur in the recognized morphospecies. Existing taxonomic inconsistencies are discussed or, when possible, solved. Specimens of unclear systematic position are described in open nomenclature.

In the synonymy lists, reference is given to the catalogues of Kühn (1932) and Sánchez (1981), but some differing opinions are expressed here and missing accounts are complemented. References that are listed in these catalogues are only included when the original material was examined. Complete lists are given with revised species. Synonymies are annotated with the symbols listed in Matthews (1973).

The separation of families of the Hippuritoidea follows the diagnoses given in Skelton (1978), those of genera refer to Dechaseaux and Perkins (1969*a*, 1969*b*, 1969*c*), and Dechaseaux and Coogan (1969*a*, 1969*b*).

Repository. The studied material is kept in the palaeontological collection of the Geological Institute of the University of Cologne, Germany. The numbers given in the descriptions and figure captions (e.g. C103) are added to one of three inventory numbers: (1) GIK 1491 (Caprinidae, Monopleuridae, Polyconitidae, Plagioptychidae), (2) GIK 1492 (Radiolitidae) and (3) GIK 1493 (Hippuritidae). The fossils are archived by a combination of these numbers (e.g. GIK 1491-C103).

Numbers of studied and figured specimens from other collections are given with the following abbreviations: BSM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; EM, Ecole des Mines de Paris, now at Lyon, Université Claude Bernard; MNHB-KC, Museum für Naturkunde der Humboldt-Universität zu Berlin, Klinghardt collection; PIB-GC, Palaeontological Institute, University of Bonn, Goldfuß collection.

Family POLYCONITIDAE Mac Gillavry, 1937

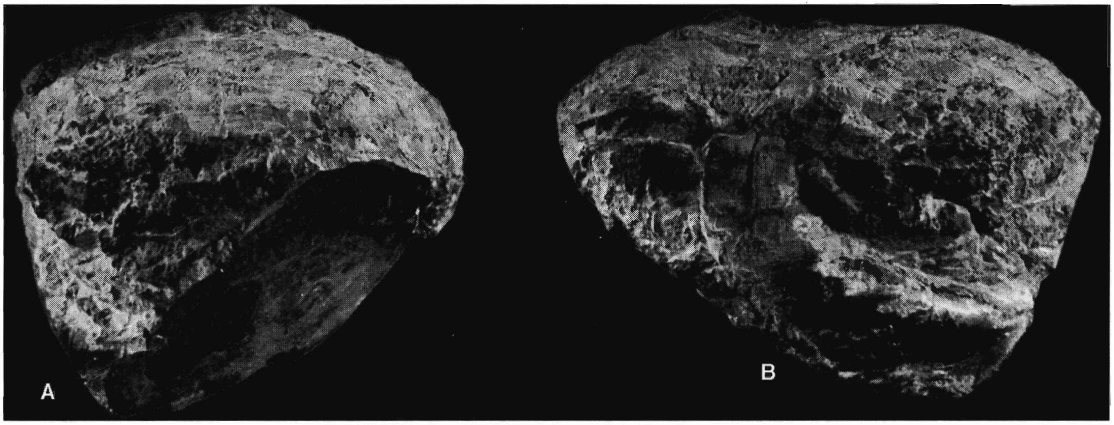
Genus HORIOPLEURA Douvillé, 1889

Type species. *Horiopleura Lamberti* Douvillé, 1889.

Horiopleura lamberti Douvillé, 1889

Text-figures 16–17

1867 *Monopleura Lamberti* Mun. Ch. *in litt.*; Hébert, p. 330 [*nomen nudum*].
1888a *Horiopleura Lamberti*; Douvillé, p. 233 [*nomen nudum*].
1882 *Oriopleura Lamberti* M.-Ch.; Lacvivier, p. 539 [*nomen nudum*].
1888 *H. Lamberti* M.-Ch.; Munier-Chalmas, p. 819 [*nomen nudum*].
*1889 *Horiopleura Lamberti* Mun-Ch.; Douvillé, p. 639, pl. 16, figs 1–4.
1890 *Horiopleura Lamberti* Munier-Chalmas; Seunes, p. 269.
1892b *Hor. Lamberti*; Douvillé, p. 80.
1898a *Horiopleura Lamberti*? M.-Ch.; Douvillé, p. 147.
1905 *H. Lamberti* Mun.-Chalm. *in* Douvillé; Paquier, p. 56, pl. 13, fig. 4.
1912 *Horiopleura Lamberti* Munier-Chalmas; Pervinquière, p. 297, pl. 21, figs 11a–b, 12; text-figs 5–6.
?1932 *Horiopleura* cf. *lamberti* Munier-Chalmas *in* Douvillé; Astre, p. 53.
1934 *Horiopleura lamberti* Mun.-Chalm. *in litt.*; Kutassy, p. 145 [with synonymy].
1935 *Horiopleura* cf. *lamberti* Munier-Chalmas; Astre, p. 91.
1937 *Horiopleura lamberti* (Mun.-Chalm.); Mac Gillavry, text-fig. 4 [p. 96].
1959 *Horiopleura lamberti* Mun. Chal.; Dubertret, *in* Arambourg *et al.*, p. 203.
1966 *Horiopleura lamberti* Mun.-Chal.; Dubertret, p. 304.
1969b *Horiopleura lamberti* (Munier-Chalmas); Dechaseaux and Perkins, p. N785, text-fig. E254,2a–b [cop. Douvillé 1889], 2c [cop. Mac Gillavry 1937].
1979 *H. lamberti*; Masse, p. 280.
1979 *Horiopleura lamberti*; Peybernès, text-fig. 1.
1986 *H. lamberti*; Skelton, *in* Pudsey *et al.*, p. 160.
1992 *Horiopleura lamberti* Bayle and Coquand; Masse *et al.*, p. 206, text-fig. 2.
1996 *Horiopleura lamberti* (Munier-Chalmas); Masse, p. 249, pl. 6, fig. 1.



TEXT-FIG. 16. *Horiopleura lamberti* Douvillé, 1889; C103, Agia Barbara; × 1. A, posterior aspect, overhanging beak of LV is seen to the right; B, ventral aspect.

Syntypes. Douvillé (1889), plate 16, figures 1–4. Douvillé (1889, pp. 639–640) noted that both genus and species were first described and figured by himself. The nomination of *H. Lamberti* M.-Ch. (Munier-Chalmas 1888) was not accompanied by any indication so that the authorship of both names has to be attributed to Douvillé (1889).

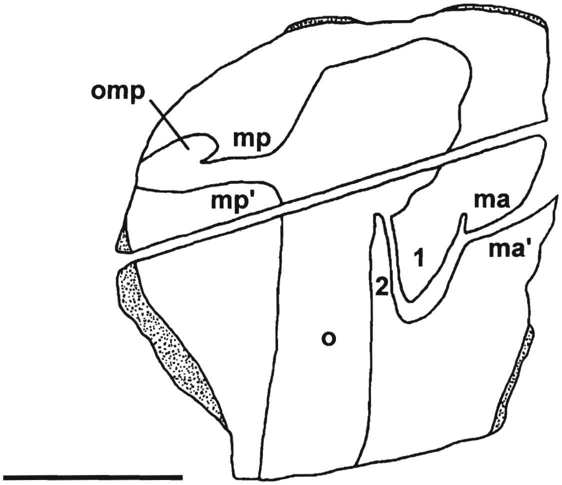
Material. Two specimens with both valves conjoined from Agia Barbara (C102, C103).

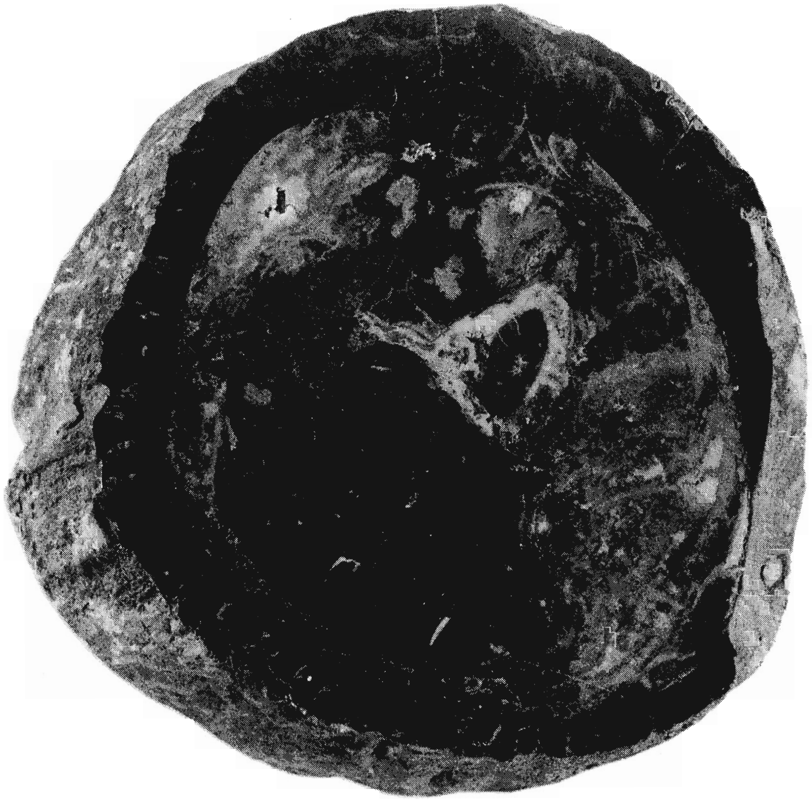
Description. LV gently convex, with flat median bulge that is flanked by shallow depressions. Exterior surface almost smooth, except for inconspicuous growth bands; beak slightly overhanging and inflected over the dorsal RV margin. Commissural diameter of RV is 90 mm. The commissure is oblique with respect to the longitudinal axis of RV. A 90 mm high fragment of the RV is preserved of which only the ventral segment is free from enclosing sediment. There, it has an ornament of inconspicuous growth lines. Vb is indicated by a shallow, rounded longitudinal furrow which is bordered posteriorly by a wide longitudinal bulge that corresponds to the median bulge of the LV. Pb was observed in transverse section only and is formed by a shallow depression of the outer shell margin.

The outer shell layer of the smaller, second specimen is only preserved fragmentarily. A longitudinal section shows the characteristic arrangement of hinge and posterior myophore (Text-fig. 17): (1) has a broad base and tapers distally, (2) is seen in a ventral, tangential section; it has a sub-quadrangular shape and a diameter of 9 mm in a commissural transverse section. Ma is slightly inclined towards the body-cavity and separated by a narrow furrow from (1). Mp forms a broad plate with a lower surface that parallels the commissural plane. It is pinched at its base, leaving space for omp that anteriorly extends further apically and towards the shell's interior. Mp′ is a broad platform that projects towards the body-cavity and ends interiorly at a rounded edge, which forms an angle of 100° with the posterior margin of the body-cavity.

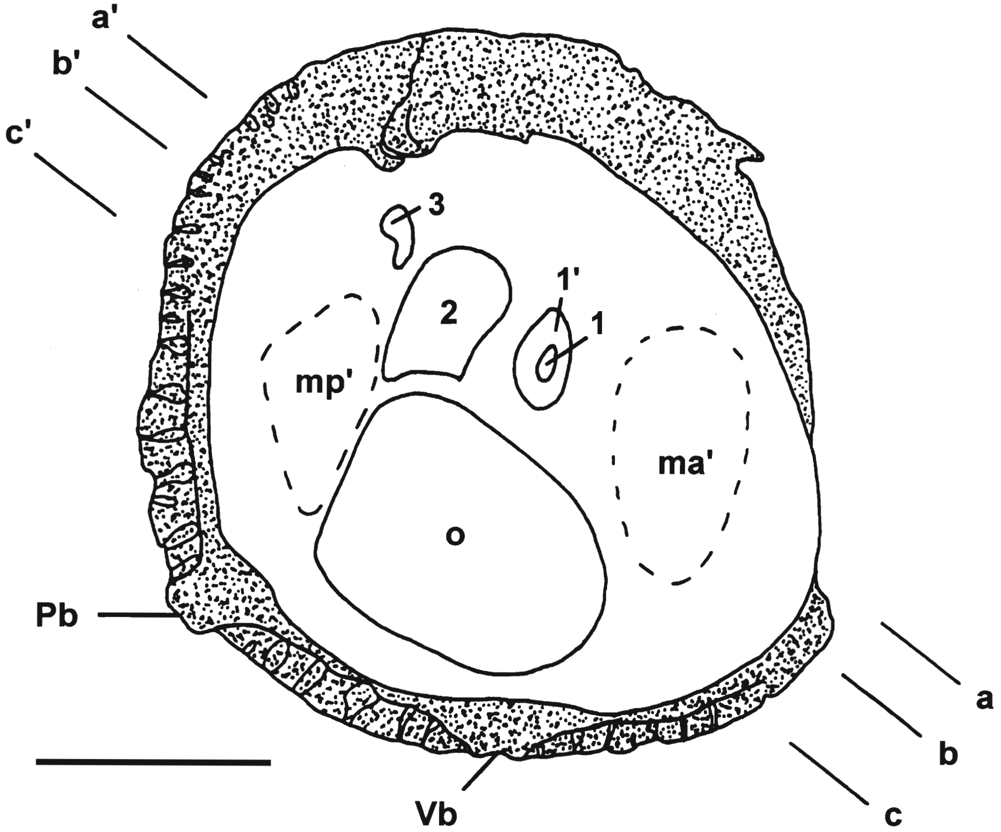
Remarks. Only a few specimens of *Horiopleura* have been described in detail so that a safe distinction of species is still problematical. In addition to a phyletic size increase, there seems to be a successive backward tilting of mp′ in the lineage *H. baylei* Coquand, 1865 – *H. almerae* Paquier, 1905 – *H. lamberti* through the Upper Aptian–Middle Albian. In *H. lamberti*, a prominent crest of mp′ demarcates the body cavity from a shallow omp′, whilst mp′ is tilted inwards in *H. baylei*, and is subhorizontal or slightly tilted backwards in *H. almerae*. Tangential or longitudinal sections through mp′ can be misleading, when their position is not precisely known. The section of the Boeotian specimen (Text-fig. 17) appears to resemble *H. almerae*, but it cuts mp′ obliquely, and its inner crest and inclination would thus appear more prominent in a section that cuts mp′ at a larger angle. This argues for *H. lamberti* and against *H. almerae*, although a safe distinction of these chronospecies affords a better knowledge of variation and microevolution within this lineage.

TEXT-FIG. 17. Anteroventral–posterodorsal longitudinal section of *Horiopleura lamberti* Douvillé, 1889; C102, Agia Barbara. Scale bar represents 30 mm.





TEXT-FIG. 18. *Horiopleura*? *juxi* sp. nov.; C150, Perachorion; × 1. Slightly oblique transverse section of RV, abapical view. Section runs 35 mm below the commissure ventrally and almost touches the commissure dorsally. For location of myocardinal elements see Text-figure 19.



TEXT-FIG. 19. Drawing of slightly oblique transverse section of RV of *Horiopleura*? *juxi* sp. nov. (see Text-fig. 18) showing location of myocardinal elements; abapical view; C150, Perachorion. Scale bar represents 30 mm.

Distribution. Upper Aptian–Albian of Portugal, Spain, the Pyrenees and southern France, Ibiza, Tunisia and Lebanon. *Horiopleura lamberti* Douvillé, 1889 is probably a senior synonym of *H. haydeni* Douvillé, 1926 and *H. desioi* Rossi Ronchetti, 1965 from northern Pakistan (Pudsey *et al.* 1986).

Horiopleura? *juxi* sp. nov.

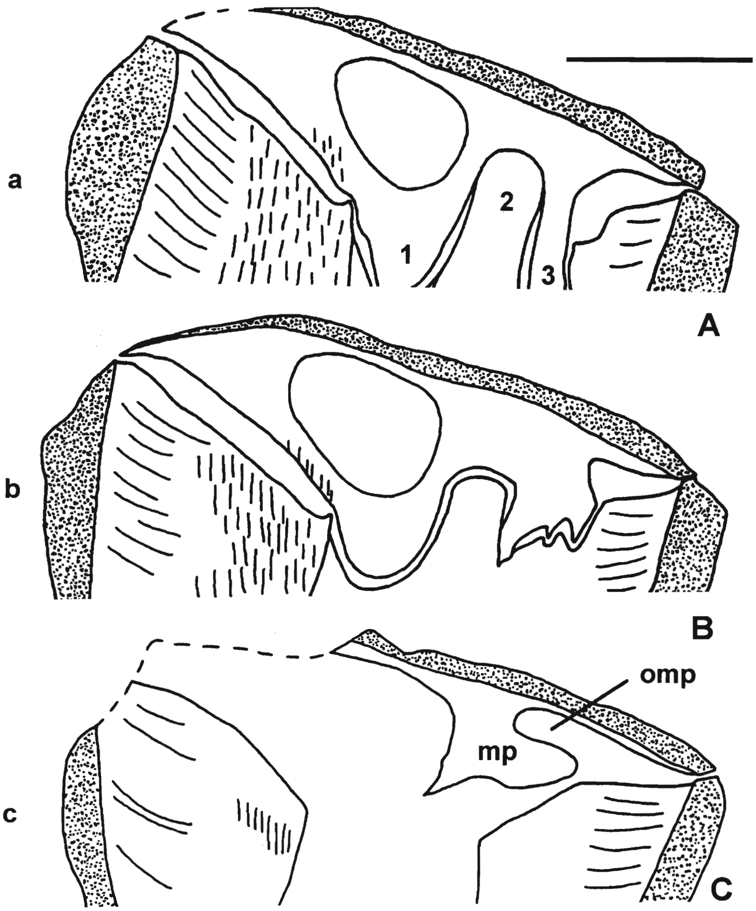
Text-figures 18–21

Derivation of name. After Ulrich Jux, who inspired this study of Boeotian rudists.

Type locality. Aptian conglomerates near Perachorion, Boeotia (lat. 38°27′03″, long. 22°51′31″).

Holotype. LV, conjoined with a commissural fragment of the RV, from Perachorion, C150.

Description. LV operculate, slightly convex and dorsally bent towards the commissure but not overhanging. External surface smooth except for inconspicuous growth lines. RV is preserved as a 50 mm long fragment with a commissural diameter of 115 mm. Posteriorly, it has narrow longitudinal furrows with a spacing of 3–5 mm. Vb and Pb are formed by 5 mm wide, rounded and gently protruding longitudinal ribs. The outer shell layer is 15 mm thick dorsally and has a fibrous-prismatic structure. Longitudinal furrows are formed by pyriform infoldings within the outer shell layer. These



TEXT-FIG. 20. Longitudinal sections of *Horiopleura*? *juxi* sp. nov.; C150, Perachorion. For orientation of sections refer to Text-figure 19. Vertical broken lines indicate remnants of myostracal structures. Scale bar represents 30 mm.

infoldings protrude deeply into the outer shell posteriorly and decrease in depth dorsally and ventrally. Growth lines are inflected commissurally in these infoldings (Text-fig. 21). The inner margin of the exterior portion of the outer shell layer that is involved in these infoldings is marked by a vague dark line posteriorly which fades dorsally. It leads towards the exterior margin of the shell in Vb and Pb so that it is interrupted in both radial bands. Ventrally it can be traced beyond the infolded segment of the shell. The invaginated ligament is found at the tip of a spout-shaped interior projection of the outer shell layer. Its suture runs obliquely to the anterior shell and opens in the region of the bent-down beak of the LV. A ligamental cavity is not discernible.

The axis through (1) and (3) is inclined towards the anterior shell. (1) is narrow and oval in transverse section; (3) has a sickle-shaped outline in transverse section. A large umbonal cavity in the LV is seen in longitudinal section over the base of (1); (1) and (3) are of equal length. (2) is strongly developed, has a broadly rounded top, and is subrectangular in transverse section. Ma is not thickened – at least not in its ventral portion – and is only recognized by remnants of the myostracum. Immediately ventral of (3) the lower surface of mp bears grooves and ridges that fit into the corresponding upper surface of mp′. A small cavity (omp) is seen above mp in longitudinal section. Farther ventrally, the lower surface of mp is undulating, the base of mp is thinned so that omp extends far towards the shell's interior. It is uncertain if the grooved dorsal part of mp that is seen in section B–B′ (Text-fig. 20B) functioned as a myostracum, as no structural remnants are preserved in the diagenetically altered inner shell of both valves. Ma′ is set off from the anterior shell, it has an oval outline and extends far ventrally; remnants of the myostracum are seen in longitudinal section. The inner shell exterior of ma′ is tabulate. The surface of ma′ slopes gently towards the body

TEXT-FIG. 21. *Horiopleura*? *juxi* sp. nov.; C150, Perachorion; × 7·5. A, tangential section of infoldings of outer shell layer at the posterior side; B, transverse section of posterior band (bottom) and posterior part of the shell with infoldings of the outer layer; C, transverse section of posterior shell with infoldings of outer layer.

cavity but is bordered interiorly by a prominent ridge. Mp′ is narrower than ma′, located between (3) and Pb and set off from the outer shell as is ma′. Mp′ slopes gently towards the body cavity and forms an acute edge with the posterior wall of the body cavity. The inner shell between mp′ and the outer shell layer is tabulate.

Systematic position. The arrangement of the myocardinal elements and especially that of mp, and the omp

TEXT-FIG. 22. *Monopleura marcida* White, 1884, Agia Barbara. A–B, C151; × 2; C–D, C152. A, twisted RV; furrow which indicates the invaginated ligament is seen apically to the left, to the right, a faint sculpture of longitudinal costae and growth rugae is visible; B, anterodorsal aspect of the commissural part; C, adapical view of RV, sockets of cardinal teeth are visible at the dorsal (upper) margin; × 4; D, adapical view of a RV with preserved cardinal platform; × 4·2.

as well as the broad platform of mp′, are diagnostic characters of *Horiopleura*. However, the sloping of mp′ towards the body cavity also resembles that in *Polyconites* Roulland, 1830, and the denticulate surface of mp in the ventral prolongation of (3) is also seen in the type specimen of *Polyconites operculatus* Roulland, 1830 (d'Orbigny 1850, pl. 547). On the other hand, deep infoldings of the outer shell layer and structurally differentiated radial bands have been reported previously from neither *Horiopleura* nor from *Polyconites*. These characters are commonly found in Radiolitidae and are rather complicated when compared with other caprotinid rudists. The pyriform infoldings of the outer shell layer are considered to have developed from the typical longitudinal ribbing of *Horiopleura* which is generally most pronounced along the posterior shell, i.e. where the infoldings of *Horiopleura*? *juxi* sp. nov. are most pronounced.

Pyriform infoldings of the outer shell layer are also a diagnostic feature of the problematical, monotypic genus *Palus* Palmer, 1928 from the Cenomanian of Mexico. An investigation of the syntypes of *Palus corrugatus* Palmer, 1928 (2 RVs) showed that the infoldings penetrate more deeply into the outer shell and are regularly distributed around the entire RV. The syntypes are rather badly preserved in the region of the radial bands, but it is discernible that Vb and Pb are formed either by a simple, broad furrow or a rounded rib. Not much is preserved from the hinge, but the cardinal platform is much thinner than in *Horiopleura* and indicates an arrangement of the myocardinal elements parallel to the dorsal margin. Consequently, *Palus* is more closely related to the Radiolitidae and *Monopleura* Matheron, 1842 than to Polyconitidae, and has no other characters in common with *Horiopleura*? *juxi* sp. nov.

Horiopleura obviously had a wide palaeogeographical distribution in the Tethyan realm during the Aptian–Albian (Pudsey *et al.* 1986), although records and descriptions have not been frequent. Therefore, it seems premature to decide whether the structural characters observed in the Boeotian specimen fall into the range of variability of the genus.

The phylogenetic evolution of *Horiopleura* during the Aptian–Albian was linked to an increase in size (P. Skelton, pers. comm. 1994). *Horiopleura*? *juxi* sp. nov. was found in deposits that formed during the early/late Aptian transition (Raeder 1994) and is remarkably large when compared with other species of *Horiopleura* of equivalent age.

Family MONOPLEURIDAE Munier-Chalmas, 1873

Genus MONOPLEURA Matheron, 1842

Type species. *Monopleura varians* Matheron, 1842.

Monopleura marcida White, 1884

Text-figure 22A–D

*1884 *Monopleura marcida* sp. nov. White, p. 96, pl. 3, figs 1–10; pl. 4, figs 1–9.
1889 *Monopleura marcida* White; Roemer, p. 288, pl. 33, fig. 1a–d.
1901 *Monopleura marcida*; Hill, p. 240, pl. 33, fig. 2.
?1901 *Monopleura marcida* White; Schnarrenberger, p. 200, pl. 3, fig. 2a–c [?=*Monopleura Schnarrenbergeri* Parona, 1909, p. 36].
1909 *Monopleura marcida*; Grabau and Shimer, p. 548, text-fig. 751c–d.
?1918 *Monopleura marcida* White; Douvillé, p. 12, text-figs 3–5.
1927 *Monopleura marcida* White; Scott, p. 252.
1928 *Monopleura marcida* White; Adkins, p. 144, pl. 2, fig. 4.
1928a *Monopleura marcida*; Klinghardt, pl. 24, fig. 7 [cop. Roemer 1889].
?1928*b* *Monopleura marcida* White; Klinghardt, p. 178, pl. 16, fig. 9.
1929 *Monopleura marcida* White; Klinghardt, p. 512, pl. 33, fig. 2.
1934 *Monopleura marcida* White; Kutassy, p. 117 [with synonymy].
1969a *M. marcida* White; Dechaseaux and Perkins, p. N783, text-fig. E250,3b [cop. White 1884].
1977 *Monopleura marcida* White; Coogan, p. 39, pl. 2, figs 1–2 [cop. White 1884], figs 3–4, 6.
*non*1979*b* *Monopleura marcida* White; Skelton, pl. 2, figs 2–3, 5 [=*Monopleura pinguiscula* White; P. Skelton, pers. comm. 1997].
1981 *Monopleura* cf. *M. marcida* White; Scott, p. 471, text-fig. 4a–c.
1983 *Monopleura marcida* White; Mainelli, p. 193.
1990 *Monopleura marcida* White; Yanin, tab. 1.

Syntypes. White (1884) plate 3, figures 1–10, plate 4, figures 1–9.

Material. More than 100 specimens from Agia Barbara, predominantly RVs (C126, C151, C152, C153).

Description. RVs sub-cylindrical-elongate, up to 45 mm long and with a commissural diameter of up to 16 mm, rarely straight, but more or less curved and twisted. Transverse sections are oval or anteriorly truncated. Outer shell layer 0·5–0·7 mm thick and exteriorly almost smooth, except for delicate growth rugae. Several shells are ornamented with inconspicuous longitudinal riblets that are spaced by 2–3 mm and together with the growth lines produce an even, rectangular ornament. The ligamental invagination is marked exteriorly by a narrow groove that is bordered anteriorly by a shallow longitudinal bulge. The commissure is oblique with respect to the longitudinal axis of the RV.

LV is flatly operculate and ornamented with concentric growth lines. (1) is of equal size or slightly larger than (3), while ma′ is considerably stronger than mp′. Ma and mp do not project deeply into the RV.

Remarks. Distinguishing small-shelled species of *Monopleura* and *Petalodontia* Počta, 1889 can be difficult. The described specimens are considered to belong to *Monopleura* because of the lack of salient myophores and sub-equal anterior and posterior teeth of the LV.

Distribution. The species is known from the Albian of Texas. There are no safe records from the Old World. The occurrence in the Abruzzi Mountains is doubtful (Parona 1909). Douvillé (1918) described a LV from the Barremian of France. Mainelli (1983) mentioned the species to occur together with *Eoradiolites rousseli* (Toucas, 1907) in the Albian of the Apennines.

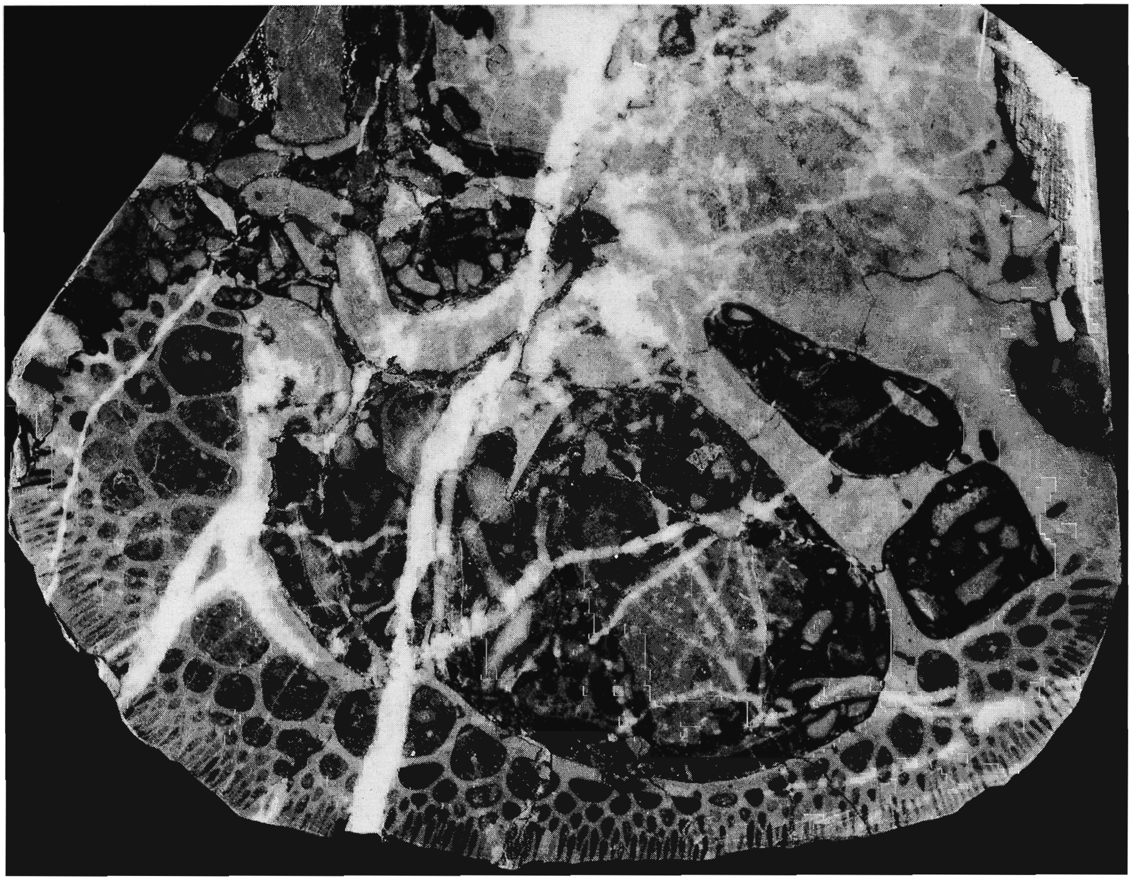
Family CAPRINIDAE d'Orbigny, 1847

Genus CAPRINA d'Orbigny, 1822

Type species. *Caprina adversa* d'Orbigny, 1822.

Caprina baylei (Gemmellaro, 1865)

*1865 *Caprinella baylei* Gemmellaro, p. 232, pl. 3, figs 1–4.
1865 *Caprinella caput-equi* Gemmellaro, p. 230, pl. 2, figs 5–9; pl. 4, fig. 1.
p1865 *Caprinella sharpei* Gemmellaro, p. 235, pl. 4, figs 2, 4.
1892*a* *Schiosia carinata*, n. sp? Boehm, p. 146, pl. 9, figs 1–2.
p1892 *Cornucaprina carinata* Böhm; Futterer, p. 87.
p1895 *Caprina schiosensis* Boehm; Boehm, p. 122.
1897b *Caprina schiosensis* var. *carinata*; Douvillé, p. 161.
1908*a* *Caprina carinata* (Boehm); Parona, p. 332, text-figs 13–19.
1926 *Caprina carinata* (Boehm); Parona, p. 41.
1934 *Caprinella baylei* Gemm.; Kutassy, p. 177.
1934 *Caprinella caput-equi* Gemm.; Kutassy, p. 178.
1934 *Caprina carinata* Boehm; Kutassy, p. 151.
1961 *Caprina carinata* Boehm; Pleničar, p. 40, pl. 6, fig. a; text-fig. 1.
1963 *Caprina carinata* Boehm; Pleničar, p. 573, pl. 1, fig. 1.
1965b *Caprina carinata* Boehm; Polšak, p. 431.
1967 *Caprina carinata* Boehm; Pleničar and Buser, p. 152.
1967*b* *Caprina carinata* (Boehm); Polšak, pp. 39, 162, pl. 12, figs 1–2.
1968a *Caprina carinata* (Boehm); Slišković, p. 13.
1969 *Caprina carinata* (Boehm); Polšak and Mamužić, p. 237.
1971 *Caprina carinata* (Boehm); Carbone *et al.*, p. 140, text-fig. 5.
1971a *Caprina carinata* (Boehm); Slišković, p. 22.
1975d *Caprina carinata*; Slišković, p. 139.
1976 *Caprina carinata* (Boehm); Praturlon and Sirna, p. 86.
1980 *Caprina carinata* (Boehm); Carbone *et al.*, p. 202.
1980 *Caprina carinata*; Laviano and Sirna, p. 69.
1981 *Caprina carinata* (Boehm); Carbone and Sirna, p. 435, text-fig. 6.
1981 *Ichthyosarcolites baylei* (Gemmellaro); Sánchez, p. 122.
1981 *Ichthyosarcolites caputequi* (Gemmellaro); Sánchez, p. 122.
1982 *Caprina carinata*; Accordi *et al.*, p. 762.
1982 *Caprina carinata* Boehm; Pleničar, p. 7.
1982 *Caprina carinata* (Boehm); Polšak *et al.*, text-fig. 3.
1982 *Caprina carinata* (Boehm); Sirna, p. 80.
1983 *Caprina carinata* Boehm; Pleničar and Premru, p. 191.
1984b *Caprina carinata* Boehm; Slišković; p. 214.
1987 *Caprina carinata*; Accordi *et al.*, p. 138.
1988*a* *Caprina* cf. *carinata* (Boehm); Özer, p. 162, pl. 1, fig. 7; text-fig. 4.
1989b *Caprina carinata*; Cestari and Sirna, tab. 1.
1991 *C. carinata* Boehm; Šribar and Pleničar, p. 175.
1992a *Caprina carinata* Boehm; Mainelli, p. 79.
1993 *Caprina carinata* Böhem [*sic*]; Cherchi *et al.*, text-fig. 2.
1993 *Caprina carinata* Böhem [*sic*]; Ruberti, p. 959.
1996 *Caprina baylei* (Gemmellaro); Bonanno and Sirna, p. 144, pl. 1, figs 1, 3–6; pl. 2, fig. 3; text-fig. 1a, c.
1996 *Caprina carinata*; Sanders, p. 851.



TEXT-FIG. 23. *Sphaerucaprina woodwardi* Gemmellaro, 1865; C49, Tsoukalades; × 1. Transverse section of LV, adapical view.

Syntypes. Gemmellaro (1865) plate 3, figures 1–4.

Material. A single LV from Tsoukalades, section in compact limestones (C46).

Description. Fragment of LV is 65 mm high, uncoiled but curved. Even, radially elongated and not tabulated canals are present along the ventral shell margin. Several larger canals are seen anterior of ma; large cavity ventrally of the ligament. A broad septum runs from the anteroventral edge of (1) to the ventral shell and separates a wide o2′ from the main body-cavity. (1) and (3) project into this accessory cavity and thus demarcate (2′) from o2′. The diagnostic ventral carina is prominent in the young growth stage but fades with ontogenetic age and is hardly discernible in the adult shell.

Remarks. The single character that separates *C. baylei* from *C. schiosensis* Boehm, 1892*a* is the ventral carina. Boehm (1892*a*) noted the ontogenetic reduction of this carina and doubted its taxonomic significance. It should be investigated on better preserved material whether the additional, internal characters mentioned by Parona (1908*a*) are sufficient to separate different species.

Distribution. Cenomanian of the southern Alps, the Apennines, Sicily, Slovenia, Croatia and the western Taurids.

Genus SPHAERUCAPRINA Gemmellaro, 1865

Type species. *Sphaerucaprina Woodward* Gemmellaro, 1865.

Sphaerucaprina woodwardi Gemmellaro, 1865

Text-figure 23

*1865 *Sphaerucaprina Woodward* Gemmellaro, p. 222, pl. 1, figs 1–5.
1892*a* *Sphaerucaprina forojuliensis* n. sp. Boehm, p. 142, pl. 6, fig. 1; text-fig. 2.
1892*a* *Sphaerucaprina*?; Boehm, p. 143, text-fig. 3.
1895 *Sphaerucaprina forojuliensis*; Boehm, p. 127, text-fig. 5 [cop. Boehm 1892*a*].
1895 *Sphaerucaprina* sp.; Boehm, p. 128, text-fig. 21 [cop. Boehm 1892*a*].
1897b *Sphaerucaprina forojuliensis*; Douvillé, p. 162.
1908*a* *Sphaerucaprina forojuliensis* Boehm; Parona, p. 344, text-fig. 30a–b.
1910 *Sphaerocaprina* [*sic*] *Woodwardi*; Douvillé, p. 30, text-figs 31–35.
1916 *Sphaerucaprina Woodwardi* Gemm.; Parona, p. 272.
1922 *Sphaerucaprina woodwardi* Gemm.; Harris and Hodson, pl. 5, figs 10–11 [cop. Douvillé 1910].
1934 *Sphaerucaprina forojuliensis* Boehm; Kutassy, p. 156 [with synonymy].
1934 *Sphaerucaprina woodwardi* Gemm.; Kutassy, p. 157 [with synonymy].
1937 *Sphaerucaprina woodwardi* Gemm.; Mac Gillavry, pl. 6, fig. 2IIe [cop. Douvillé 1910].
1963 *Sphaerucaprina forojuliensis* Boehm; Pleničar, p. 574, pl. 1, fig. 2.
1965b *Sphaerucaprina forojuliensis* Boehm; Polšak, p. 434.
1967 *Sphaerucaprina* cf. *forojuliensis* Boehm; Pleničar and Buser, p. 153.
1969c *Sphaerucaprina woodwardi*; Dechaseaux and Perkins, p. N797, text-fig. E262, 1a, 1b [cop. Douvillé 1910].
1969 *Sphaerucaprina forojuliensis* Boehm; Polšak and Mamužić, p. 237.
1971 *Sphaerucaprina forojuliensis* Boehm; Carbone *et al*., p. 143, text-fig. 9.
1976 *Sphaerucaprina forojuliensis* Boehm; Praturlon and Sirna, p. 99, text-fig. 17a–b.
1980 *Sphaerucaprina forojuliensis* Boehm; Carbone *et al*., p. 204.
1980 *Sphaerucaprina forojuliensis* Boehm; Iannone and Laviano, p. 223, text-fig. 28.
1980 *Sphaerucaprina forojuliensis*; Laviano and Sirna, p. 69.
1981 *Sphaerucaprina forojuliensis* Boehm; Carbone and Sirna, p. 435, text-fig. 6.
1982 *Sphaerucaprina forojuliensis*; Accordi *et al*., p. 762.
1983 *Sphaerucaprina forojuliensis* Boehm; Camoin, p. 219, pl. 5, fig. 9.
1983 *Sphaerucaprina forojuliensis* Böhm; Mainelli, p. 193.
1983 *Sphaerucaprina forojuliensis* Boehm; Pleničar and Premru, p. 191.
1985 *Sphaerucaprina forojuliensis* Boehm; Caminiti, p. 130, pl. 29, fig. 2.
1987 *Sphaerucaprina forojuliensis*; Accordi *et al*., p. 139.
1989 *Sphaerucaprina woodwardi* (Gemmellaro); Accordi *et al*., p. 167, pl. 4, fig. 2.
1989 *Sphaerucaprina forojuliensis*; Luperto Sinni and Borgomano, p. 101.
1989b *Sphaerucaprina forojuliensis* Boehm; Philip *et al*., p. 1381.
1989 *Sphaerucaprina forojuliensis* Boehm; Sartorio, p. 94, pl. 1 [cop. Parona 1908*a*].
1990 *Sphaerucaprina forojuliensis* (Boehm); Cestari and Pantosti, p. 45.
1991 *Sphaerucaprina forojuliensis* Boehm; Mermighis *et al*., p. 550.
1991 *Sphaerucaprina forojuliensis* Boehm; Šribar and Pleničar, p. 175.
1992a *Sphaerucaprina forojuliensis* Boehm; Mainelli, p. 79.
1993 *Sphaerucaprina forojuliensis* Bohem [*sic*]; Cherchi *et al*., p. 93, pl. 4, fig. 3.
1993 *Sphaerucaprina forojuliensis* Böhem [*sic*]; Ruberti, p. 959.
1996*b* *Sphaerucaprina forojuliensis* Böhm; Laviano, text-fig. 4.

Syntypes. Gemmellaro (1865), plate 1, figures 1–5; Douvillé (1910), text-figures 31–35.

Material. Two LVs from Tsoukalades (C49, C48).

Description. Dmax 152 and 119 mm, respectively. The larger LV has an interior row of sub-polygonal canals which are largest posteriorly, diminish in size ventrally and become larger again anteriorly, but without reaching the dimensions of the posterior canals. Exterior to these, a continuous row of smaller sub-cylindrical canals follows. A third row of sub-cylindrical canals fades ventrally, and a fourth, irregular row is only developed posteriorly. Radially elongated canals with occasionally bifurcating septa form an exterior row. LV bulges anterodorsally and has three large oma; it is crushed beyond the anteriormost oma. In adapical sections of the LV, the number of oma is constant but the canals within the inner shell are recrystallized and indiscernible. The LV is dorsally crushed but the invaginated ligament is preserved. A septum that separates o from (2′) and o2′ is only preserved dorsally and ventrally where it emerges from (1) and the ventral inner shell.

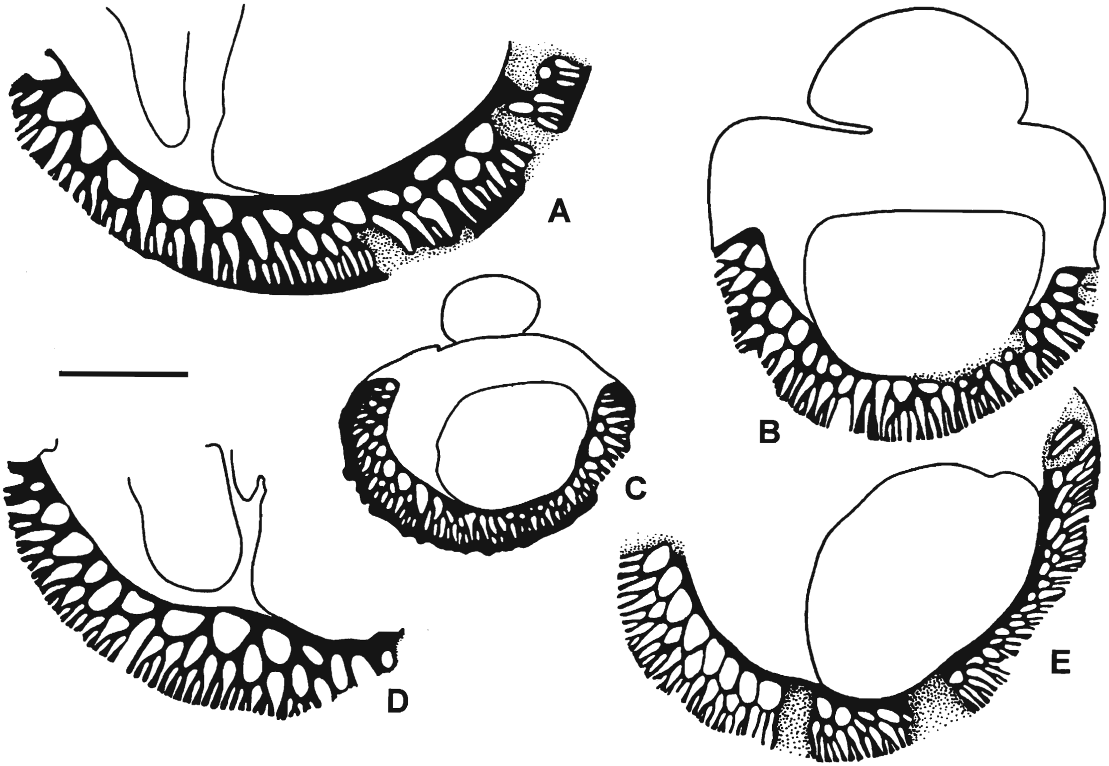
System of pallial canals of the second, smaller LV is more simple. An inner row of sub-cylindrical canals is accompanied only near to the dorsoventral septum by additional, small and oval canals. The inner shell is badly recrystallized along the outer margin so that bifurcations of the partitions of the outer, radially elongated canals are not discernible. Three large oma are seen anterodorsally, of which the two anteriormost are separated by a 0·5 mm thin, partly crushed partition. (1) strongly developed, sub-rectangular with concave sides in transverse section; a septum emerges from its anteroventral edge and runs towards the ventral shell. The posteroventral edge of (1) separates (2′) from o2′. (2′) and o2′ are constricted by a prominent (3) that projects considerably deeper into the body-cavity than the ventrally conjoined mp. Ma forms a prominent ledge along the interior shell adjacent to the two anteriormost oma. Invagination of ligament is much narrower and more inconspicuous when compared to the larger LV described previously.

Remarks. The holotype of *Sphaerucaprina forojuliensis* is a rather poorly preserved LV which Boehm (1892*a*, p. 143) assigned to the genus because 'die in Textfigur 2 dargestellten Kanäle einigermaßen an *Sphaerucaprina Woodwardi*, Gemmellaro erinnern' (the canals shown in text-fig. 2 to some extent resemble those of *Sphaerucaprina woodwardi* Gemmellaro); he did not give a differential diagnosis with respect to the type species. Parona (1908*a*) determined a LV from northern Italy as *S. forojuliensis*, but mentioned the minor differences in shape, number and size of the pallial canals when compared with those of *S. woodwardi*. Gemmellaro's original material of *S. woodwardi* was described for the first time in detail by Douvillé (1910); the pattern of pallial canals and the number of oma are identical with the LV assigned to *S. forojuliensis* by Parona (1908*a*). Douvillé (1910), however, did not mention these similarities and gave no reference to Parona's (1908*a*) study. Later, the designation *S. forojuliensis* became popular and relied predominantly on the disposition of the ventral pallial canals, with one exception of a LV from the Abruzzi Mountains (Praturlon and Sirna 1976).

The type specimen of *S. forojuliensis* differs from the syntypes of *S. woodwardi* only by the fading of sub-polygonal canals along the interior margin of the ventral LV. The description of *Mitrocaprina boeotica* (see below) suggests by analogy that such differences in the disposition of pallial canals of the Caprinidae are well within the range of intraspecific variability. A comparison of specimen figured as *S. forojuliensis* or *S. woodwardi* supports the opinion of considering *S. woodwardi* as a senior synonym of *S. forojuliensis*.

The shape and number of oma also varies to a certain extent. Three oma are seen in the Boeotian LVs as well as in the syntypes of *S. woodwardi* and Parona's specimen (1908*a*) from northern Italy, whilst as many as nine oma are present in a LV from the Cenomanian of the Abruzzi Mountains (Praturlon and Sirna 1976). The partition between the oma disappears close to the commissure so that a large, single oma is connected with (2′) in commissural sections. It also seems possible that *Schiosia forojuliensis* Boehm, 1895 and *Sphaerucaprina*? *carezi* Douvillé, 1910, both of which differ from *Sphaerucaprina woodwardi* by the number of oma, could fall within the still insufficiently known range of variability of *S. woodwardi*. American specimens that were originally assigned to *Sphaerucaprina* were later included in other genera (Palmer 1928; Mac Gillavry 1937), or are of doubtful systematic position (e.g. *Sphaerucaprina seafieldensis* Chubb, 1967) so that the occurrence of the genus in the New World is uncertain (Mac Gillavry 1937). Should this be substantiated, the number of species that belong to *Sphaerucaprina* is reduced from six (Kutassy 1934) to a single one, the type species.

Distribution. Cenomanian of the circum-Adriatic region, of Parnassus Mountains and Argolis.



TEXT-FIG. 24. Transverse sections of pallial canals of *Mitrocaprina bayani* (Douvillé, 1888*b*), LVs, adapical view, Paleokastron Hill; A, C55; B, C114; C, C111; D, C51; E, C113. Scale bar represents 10 mm.

Family PLAGIOPTYCHIDAE Douvillé, 1888*b*

Genus MITROCAPRINA Boehm, 1895

Type species. Coralliochama Bayani Douvillé, 1888*b*.

Mitrocaprina bayani (Douvillé, 1888*b*)

Text-figure 24

*1888*b* *Coralliochama Bayani* Douvillé, p. 725, pl. 25, fig. 7, text-fig. 9.
1892b *Sphaerucaprina Bayani* (Douvillé); Boehm, p. 561.
1895 *Mitrocaprina Bayani* (Douvillé); Boehm, p. 103.
1897b *Mitrocaprina Bayani*; Douvillé, p. 162.
1932 *Mitrocaprina bayani* (Douvillé); Muellerried, p. 177.
1934 *Mitrocaprina bayani* Douvillé; Kutassy, p. 158 [with synonymy].
1937 *Mitrocaprina bayani* (Douvillé); Mac Gillavry, p. 164, pl. 7, figs 3, 9.
p1937 *Sphaerucaprina* sp.; Vermunt, p. 275.
1950 *Mitrocaprina bayani* Douvillé; Rengarten, p. 43, pl. 9, fig. 2; text-fig. 18.
1959 *Mitrocaprina bayani* Douv.; Rengarten, p. 257.
1965b *Mitrocaprina bayani* (Douvillé); Polšak, pl. 6.
1966 *Mitrocaprina bayani*; Astre, text-figs 1–10.
1967*b* *Mitrocaprina bayani* (Douvillé); Polšak, pp. 50, 168, pl. 17, fig. 2–2b.
1969 *Mitrocaprina polšaki* nov. sp. Astre, p. 11.

1969c *Mitrocaprina bayani* (Douvillé); Dechaseaux and Perkins, p. N795, text-fig. E259,2a [cop. Douvillé 1888*b*].
1982 *Mitrocaprina bayani* (Douvillé); Polšak *et al.*, text-fig. 3.
1985 *Mitrocaprina polsaki* Astre; Tomić, p. 85.
1996 *Mitrocaprina bayani* (Douvillé); Rojas and Iturralde-Vinent, p. 293.
1997 *Mitrocaprina bayani* (Douvillé); Steuber *et al.*, p. 179.

Syntypes. Douvillé (1888*b*), plate 25, figure 7, text-figure 9.

Material. Eight LVs from Paleokastron Hill (C51, C55, C110, C111, C113, C114, C117, C125).

Description. LVs globose, narrow and symmetrically coiled; Dmax 56 mm, one large fragment suggests a commissural diameter of up to 80 mm. Inner shell layer including myocardinal elements badly recrystallized, but (2′), o2′ and mp that bulges slightly into o2′ are recognizable.

Thin outer, calcitic shell layer, 0·1–0·2 mm thick. Pallial canals within the inner, originally aragonitic shell are present in a zone that runs from (3) along the ventral shell to the region of ma; no oma. Arrangement of pallial canals more complex anteriorly and posteriorly than ventrally. An inner row of sub-polygonal or sub-cylindrical canals is followed exteriorly by a row of pyriform or radially elongated canals with dichotomizing partitions. The inner row of canals is not continuous in all LVs, but is frequently interrupted ventrally by pyriform canals. Sub-cylindrical canals are also frequent in the external spandrels of the inner canals, but do not form a continuous second row. The apical parts of the shells are badly recrystallized so that observations on the ontogeny of the canal patterns are impossible. However, no relation exists between the overall dimensions and the complexity of arrangement of pallial canals.

Remarks. The Boeotian LVs, together with those described from Istria (Polšak 1967*b*), are among the largest known of the species.

Mitrocaprina polsaki Astre, 1969 was separated from *M. bayani* because of a discontinuous second row of large sub-cylindrical canals. Such variations occur in the syntypes as well as in the Boeotian specimens.

Distribution. Upper Santonian–Campanian of southern France, Istria, Caucasus and Cuba.

Mitrocaprina boeotica (Munier-Chalmas, *in* Gaudry 1867)

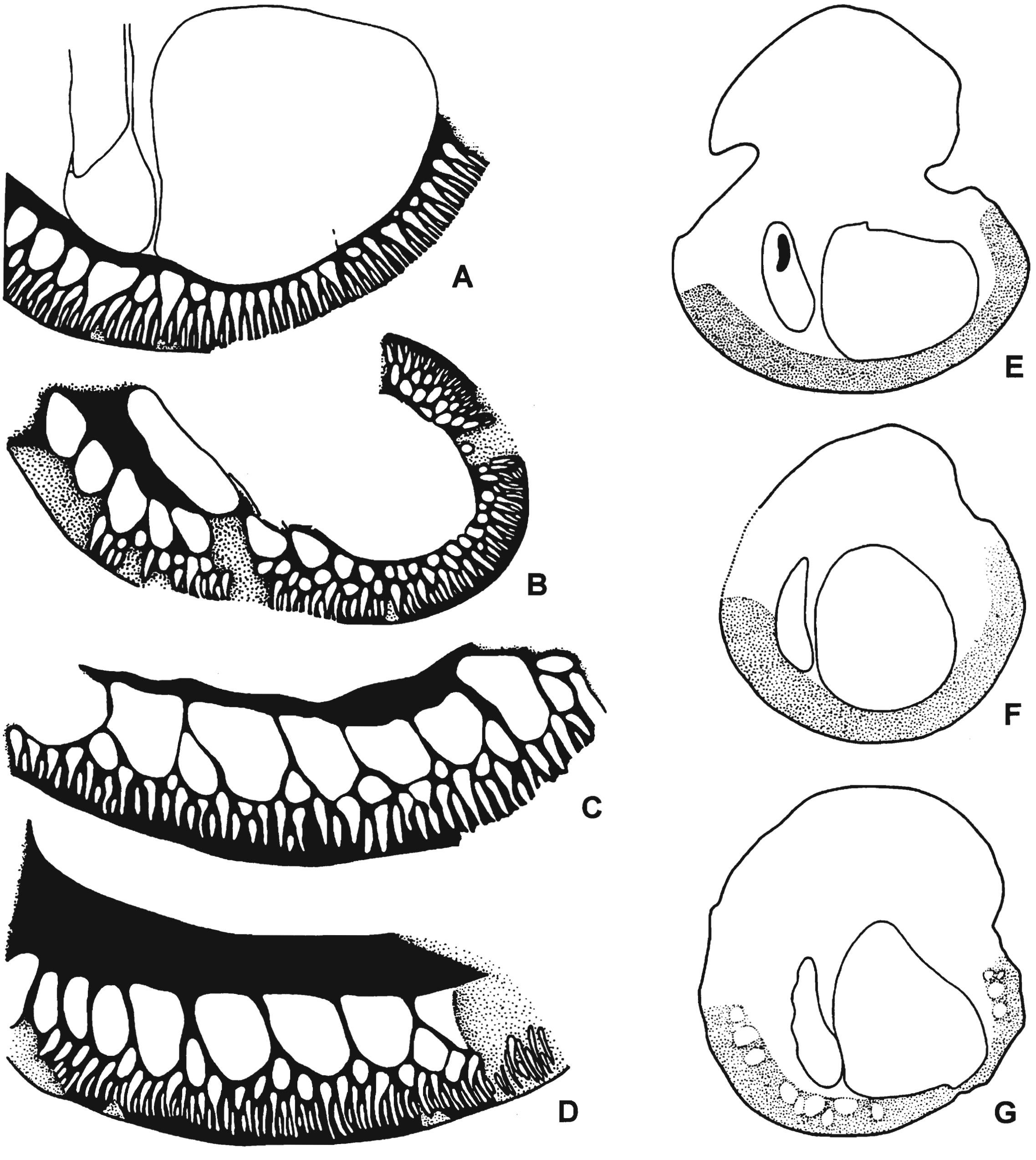
Text-figures 25–28

*1867 *Plagioptychus boeoticus* Munier-Chalmas *in* Gaudry, p. 391 [*nomen dubium*].
1888 *Plagioptychus beoticus*; Munier-Chalmas, p. 819 [*nomen dubium*].
1934 ?*Plagioptychus beoticus* Mun.-Chalm.; Kutassy, p. 173 [*nomen dubium*, with synonymy].
v.1943 *Plagioptychus toucasi* Matheron; Klinghardt, p. 129; text-fig. 6.
1949*b* *Mitrocaprina beotica* Munier-Chalmas; Mennessier, p. 395, text-figs 1–3.
v.1950 *Mitrocaprina* sp.; Mennessier, p. 529, text-figs 1–2.
?1950 *Mitrocaprina corbarica* n. sp. Mennessier, p. 532, text-figs 3–8.
1965 *Mitrocaprina beotica* (Munier-Chalmas); Tzankov, p. 14.
1993b *Plagioptychus toucasi* Matheron; Steuber, p. 44.
1993 *Mitrocaprina beotica* (Munier-Chalmas); Steuber *et al.*, text-fig. 10.

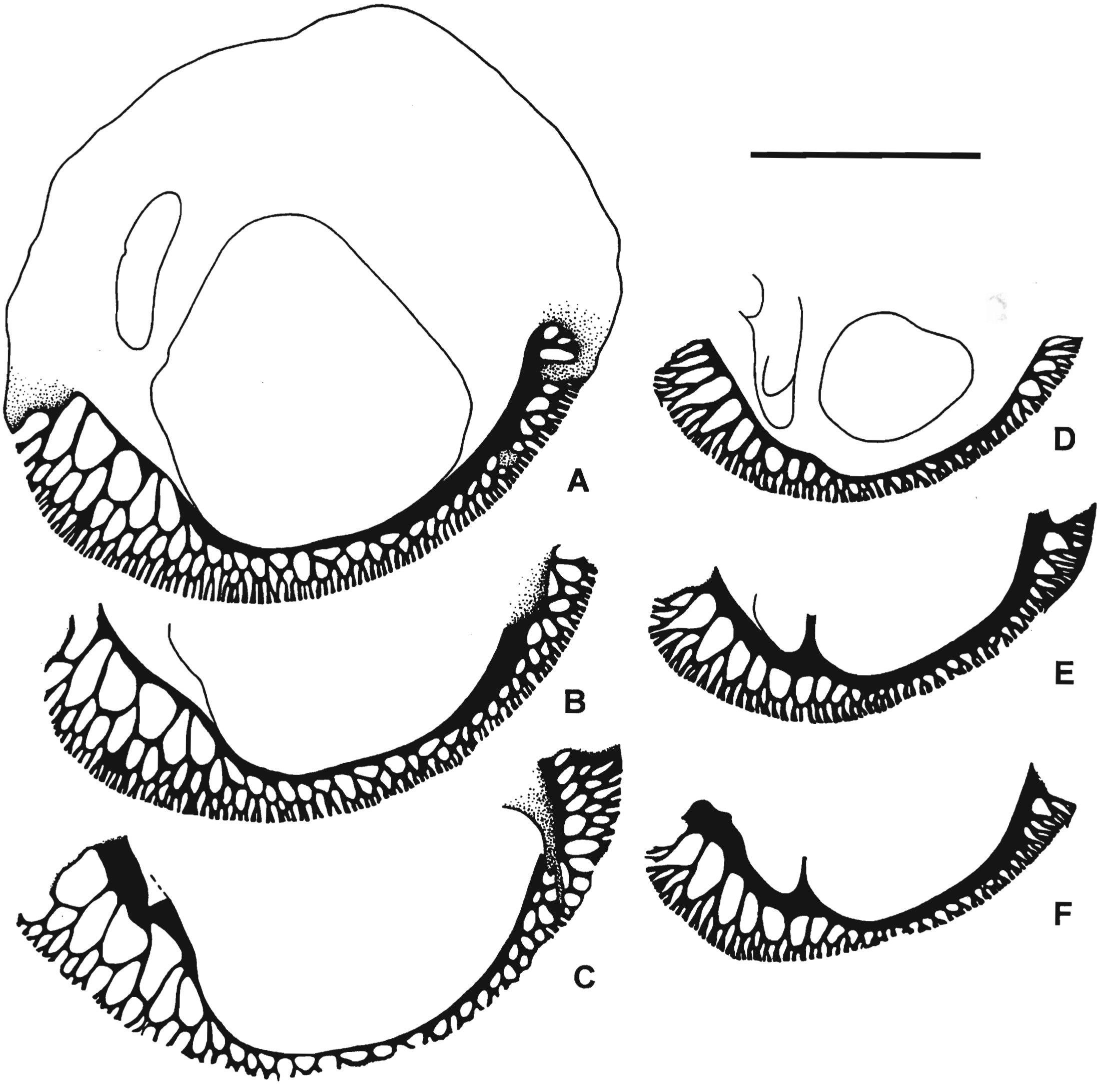
Syntypes. Mennessier (1949*b*), text-figures 1–3; Mennessier (1950), text-figures 1–2.

Material. More than 40 specimens, most of them LVs from Keratovouno Hill (C2, C3, C4, C9, C10, C34, C52, C53, C58, C59, C74, C75, C77, C78, C81, C84, C85, C86, C88, C90, C91, C92, C93, C94, C95, C127) and from Kalamos Hill (C119, C121, C122).

Description. Highly domed, globose LVs of which a few are symmetrically, but most asymmetrically coiled (Text-fig. 25E–G). Dmax up to 90 mm. Exterior surface smooth except for fine commarginal growth lines. RV is a wide cone or is conical-elongated and has hardly visible growth lines. Thickness of outer shell layers is 0·2 mm in LV and up to 2 mm in RV.



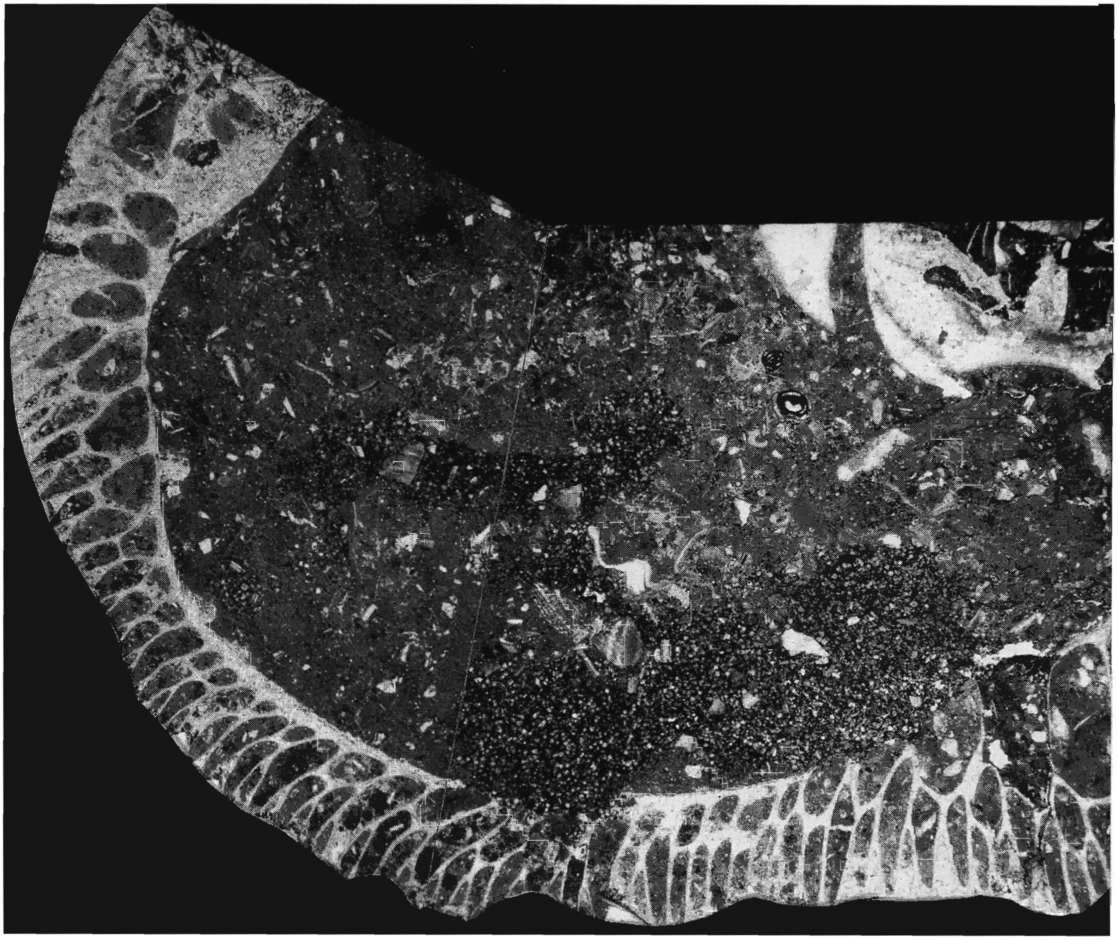
TEXT-FIG. 25. Transverse sections of LVs and pallial canals of *Mitrocaprina boeotica* (Munier-Chalmas, *in* Gaudry, 1867); A–E, G, Keratovouno Hill; F, Kalamos Hill. Zone of pallial canals dotted in E–G. A, C3; B, C94; × 1·2. C, C93; D, C127; × 2. E, C95; F, C119; G, C86; × 0·8.



TEXT-FIG. 26. A–F, *Mitrocaprina boeotica* (Munier-Chalmas, *in* Gaudry, 1867), Keratovouno Hill; A–C, C58; D–F, C9; transverse sections of LVs. Ontogenetic age increases from A to C and D to F, respectively. Distances between sections along the ventral margin are 5 mm (A–B), 20 mm (B–C), 12 mm (D–E) and 5 mm (E–F). Scale bar represents 30 mm.

Pallial canals along the interior margin of LV inner shell are sub-cylindrical to sub-polygonal, exterior canals are pyriform or radially elongated (Text-fig. 25A–D). The interior canals are particularly large in the posterior shell and small, irregular sub-polygonal canals can be intercalated in their distal spandrels. The interior canals are notably smaller anterior to the dorso-ventral septum that separates o2′ from the main body cavity, and they are absent in the ventral shell of some LVs in which only pyriform or radially elongated canals are developed (compare *Mitrocaprina palmeri* Mac Gillavry, 1937). Sub-polygonal canals are present anteriorly in all shells and may form up to three rows, but do not reach the size of the posterior canals; their radial partitions often dichotomize twice, or three times in large LVs. No tabulae have been noted in sub-cylindrical, sub-polygonal or radially elongated canals.

The external trace of the ligamentary infolding is seen in a furrow in both the LV and RV. A dorso-ventral septum separates the main body-cavity from a narrow (2′) which only in a few shells is subdivided from o2′ by a shallow



TEXT-FIG. 27. *Mitrocaprina boeotica* (Munier-Chalmas, *in* Gaudry, 1867); C84, Keratovouno Hill; × 4·8. Thin section of a juvenile LV, abapical view.

projection of the inner shell between (3) and mp (Text-figs 26, 28). In most shells, the inner surface of conjoined (3) and mp is smooth. (2) is broad and massive, with a beak-shaped termination, flanked anteriorly by (1′) and posteriorly by (3′); (3) shorter than (1). A shallow cavity between the anterodorsal margin and ma as well as ma′ resembles the larger and deeper oma of the Caprinidae. In adapical transverse sections of RV, ma′ and mp′ are discernible as swellings (Text-fig. 28A), but in commissural sections a shallow omp′ is present outside of mp′ that is joined with 3′ (Text-fig. 28B).

Ontogeny and *variability of arrangement of pallial canals*. Not much has been reported about the variability and ontogeny of the pattern of pallial canals in *Mitrocaprina*. The large quantity of well preserved LVs from Keratovouno Hill offers the opportunity to study such variations among a few successive populations.

Pallial canals are well preserved only in the commissural part of most shells. Juvenile growth stages are commonly recrystallized and the arrangement of the canals is not clearly discernible. Constant patterns have been noted in serial sections of up to 25 mm thick segments of LVs. An ontogenetic development of sub-polygonal canals by constriction of the internal bulges of pyriform canals has been observed in neither an adult nor in a small-sized shell (Text-fig. 26). No relation was noted between the size of LV and the complexity of arrangement of pallial canals. A rather small LV (Text-fig. 27) has an almost continuous interior row of sub-polygonal canals and a generally more complicated pattern than a considerably larger LV (Text-fig. 25A). This is similar to the variation observed in *Mitrocaprina tschoppi* (Palmer, 1933) by Mac Gillavry (1937). Thus, despite its conservative ontogeny (Douvillé 1888*b*), the intraspecific variation of the pattern of pallial canals is pronounced. In several LVs the inner ventral shell has a continuous row of sub-cylindrical canals but in others, these canals pass into radially elongated canals more or less anterior to the dorso-ventral septum. The large posterior canals vary in shape: They are sub-polygonal when their partitions are thin (Text-fig. 25C) and become sub-cylindrical and oval with increasing thickness of the partitions (Text-figs 25A, 26). One of the syntypes and several other LVs have regularly arranged, small sub-cylindrical canals in the spandrels of the large internal posterior canals (Text-fig. 25C–D) that form a continuous second row. In other LVs this second row of sub-cylindrical canals is completely absent or the canals are much more irregularly developed.

Remarks

The diagnosis of Munier-Chalmas (1867) is insufficient for a safe recognition of the species. The first detailed description of the type material from Keratovouno Hill was provided by Mennessier (1949*b*, 1950). Previously, Klinghardt (1943) had figured a specimen from the type locality and despite the clearly visible sub-polygonal pallial canals misidentified it as *Plagioptychus toucasi* Matheron, 1842. Only three specimens of this species, documented exclusively from the type locality, have been figured hitherto.

Systematic position. Diagnostic characters of the LV of *M. boeotica* are large sub-cylindrical or sub-polygonal canals within the posteroventral inner shell layer and a narrow o2′. They separate *M. boeotica* from *M. bayani* (Douvillé, 1888*b*) and *M. palmeri* Mac Gillavry, 1937 which have similar patterns of pallial canals.

In *M. tschoppi* (Palmer, 1933), two rows of evenly sized sub-polygonal canals are found along the ventral shell and o2′ is much wider than in *M. boeotica*.

The pallial canals of *M. corbarica* Mennessier, 1950 are known only from the posteroventral part of a single specimen and fall into the range of variation observed in *M. boeotica*. A description of better preserved shells from the type locality in southern France is necessary for a conclusive decision on its taxonomic position.

M. bulgarica Tzankov, 1965 from the Campanian (Swinburne *et al.* 1992) of Bulgaria is very similar to *M. boeotica*. It can be distinguished by three rows of sub-polygonal canals and a less highly domed LV. Its larger size and the more complicated pattern of pallial canals strongly suggest derived characters of a closely related species.

Distribution. Upper Santonian–Campanian; known only from Boeotia; perhaps also from southern France (*M. corbarica* Mennessier, 1950).

Family RADIOLITIDAE d'Orbigny, 1847

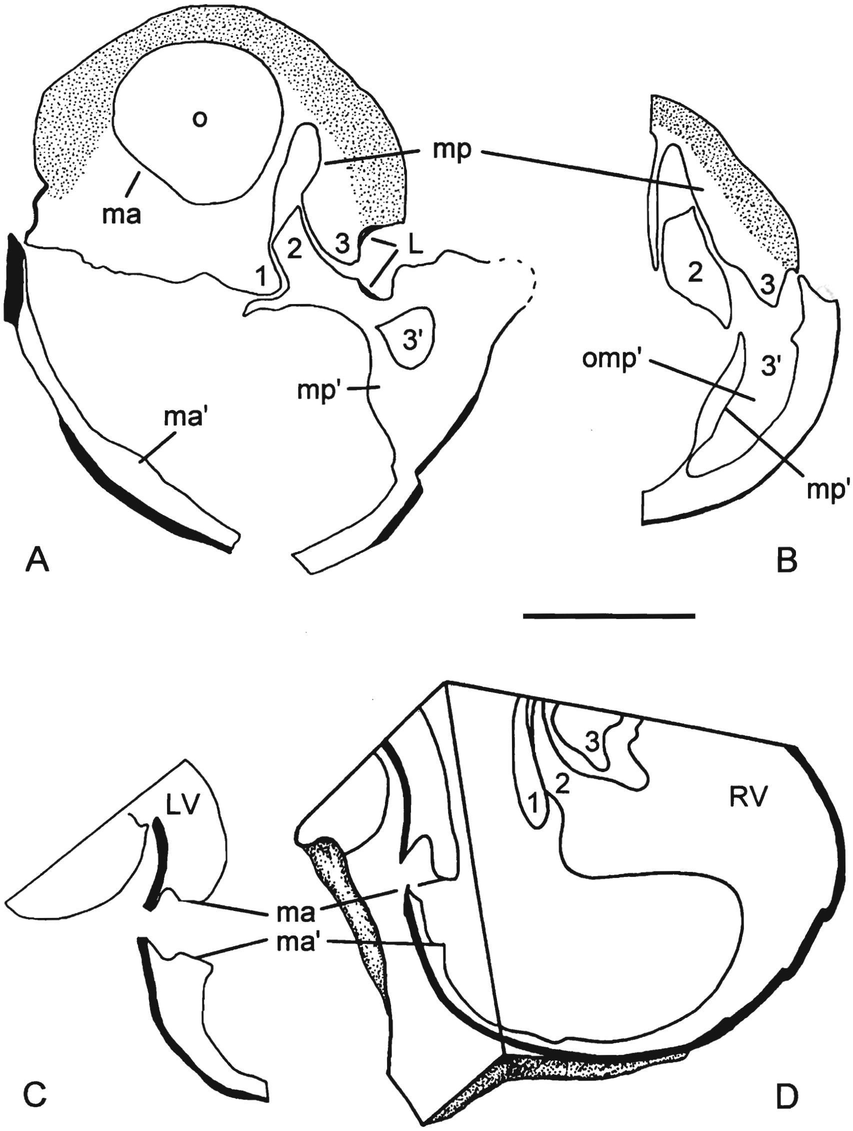
Genus BIRADIOLITES d'Orbigny, 1850

Type species. Biradiolites canaliculatus d'Orbigny, 1850.

Biradiolites angulosus d'Orbigny, 1850

Plate 3, figures 4–5

*non*1842*a* *Radiolites angulosa* d'Orbigny, p. 183.
*non*1850 *Radiolites angulosa* d'Orb.; d'Orbigny, p. 220, pl. 562, figs 1–4.
*1850 *Biradiolites angulosa* d'Orb.; d'Orbigny, p. 233, pl. 574, figs 7–11.
1850 *Biradiolites quadrata* d'Orb.; d'Orbigny, p. 232, pl. 574, figs 1–6.



TEXT-FIG. 28. Myocardinal arrangement of *Mitrocaprina boeotica* (Munier-Chalmas, *in* Gaudry, 1867). A, transverse section of both valves, adapical view, slightly inclined ventrally in both valves; B, transverse section through RV, 9 mm above section shown in A and close to commissure; C, anterodorsal–posteroventral section of LV and commissural part of RV showing ma and ma′; D, anterodorsal–posteroventral section 8 mm farther ventrally than in C. The section to the right (posterodorsal–anteroventral) was cut at almost right angles to that on the left and shows the cardinal teeth. RV is sectioned tangentially. A–B, C122; C–D, C95. Scale bar represents 30 mm.

p1856 *Radiolites angulosus* d'Orb.; Bayle, p. 379, pl. 15, figs 1, 3–5.
v1856 *Radiolites angulosus* d'Orb.; Bayle, p. 379, pl. 15, fig. 2.
1901 *Radiolites quadrata* d'Orb.; Söhle, p. 39.
1902 *Bir. angulosus*; Douvillé, p. 473.
1904a *Bir. angulosus*; Douvillé, p. 175.
1908b *B. angulosus*; Douvillé, p. 309.

1910 *Biradiolites angulosus* d'Orbigny; Toucas, p. 251.
1913*b* *Birad. angulosus*; Douvillé, p. 416.
p*1932* *Biradiolites angulosus* d'Orbigny; Kühn, p. 83 [with synonymy].
1932 *Biradiolites quadratus* d'Orbigny; Kühn, p. 83 [with synonymy].
1937 *Biradiolites ? angulosus* d'Orbigny; Oosterbaan, p. 111, text-fig. 26.
*non*1941 *Biradiolites ?angulosus* d'Orbigny; Montagne, p. 63, pl. 4, figs 9–10.
1966 *Biradiolites angulosus* d'Orbigny; Torre, p. 7, pl. 1, figs 2–3.
1969 *Biradiolites angulosus* d'Orbigny; Polšak and Mamužić, p. 238.
p1972*b* *Biradiolites angulosus* d'Orbigny; Campobasso, p. 441, pl. 3, fig. 2.
1974 *B. angulosus* (d'Orb.); Lapparent *et al.*, p. 313.
1974 *Biradiolites angulosus* (d'Orb.); Philip, p. 112.
1978 *Biradiolites angulosus* d'Orb.; Amico, p. 68, pl. 16, figs 3–5.
1978 *Biradiolites quadratus* d'Orb.; Amico, p. 67.
1978a *Biradiolites angulosus*; Philip *et al.*, p. 84.
1980 *Biradiolites angulosus*; Laviano and Sirna, p. 69.
p*1981* *Biradiolites angulosus* d'Orbigny; Sánchez, p. 69 [with synonymy].
1981 *Biradiolites quadratus* d'Orbigny; Sánchez, p. 81 [with synonymy].
1982 *Biradiolites angulosus* d'Orb.; Philip, *in* Platel, p. 93.
1982 *B. quadratus* (d'Orb.); Philip, *in* Platel, p. 93.
1984 *Biradiolites angulosus* d'Orbigny; Laviano, p. 185.
1985 *Biradiolites angulosus* d'Orbigny; Laviano, p. 327, pl. 12, figs 2–3; pl. 14, fig. 2.
1987 *Biradiolites angulosus* d'Orbigny; Pejović and Radoičić, p. 123, fig. 3.
1987 *Biradiolites quadratus* d'Orbigny; Pejović and Radoičić, p. 126, fig. 3.
1989 *Biradiolites angulosus* d'Orbigny; Accordi *et al.*, p. 168, tab. 1.
1989 *Biradiolites angulosus*; Luperto Sinni and Borgomano, p. 105.
1989 *Biradiolites angulosus*; Pieri and Laviano, p. 352.
1991 *Biradiolites angulosus*; Floquet, text-fig. 285.
1992 *Biradiolites angulosus* d'Orbigny; Cestari *et al.*, p. 360.
1994 *Biradiolites angulosus* d'Orbigny; Pleničar and Dozet, p. 189.
1996 *Biradiolites angulosus* d'Orbigny; Paris and Sirna, p. 192, pl. 2, figs 3–4.
1996 *Biradiolites quadratus* (d'Orbigny); Paris and Sirna, p. 192, pl. 2, fig. 6.

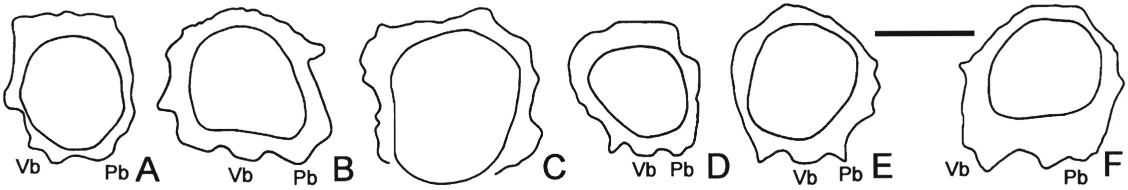
Syntypes. D'Orbigny (1850), plate 574, figures 7–11. The designation *Radiolites angulosus* d'Orbigny, 1842*a* was obviously not a mistake, as assumed by Bayle (1856), because the syntypes of this species (d'Orbigny, 1850, pl. 562, figs 1–4) have a ligamental ridge. The name is, therefore, excluded from the synonymy of *Biradiolites angulosus* d'Orbigny, 1850.

Material. Five specimens from Marmeko quarry, encrusting on *Radiolites sauvagesi* (d'Hombres Firmas, 1838); R531, R535, R540.

Description. Up to 45 mm long, 25 mm wide; attached with the anterior shell on RVs of *Radiolites sauvagesi* (d'Hombres Firmas, 1838). Steeply erected shell lamellae of RV surmount the commissure anteriorly and dorsally by up to 7 mm. LV thin, its centre deeply depressed. RV anterodorsally ornamented with three to five longitudinal ribs that appear rather faint due to the encrusting life habit, whereas the ribs that border Vb and Pb are prominent. Posteroventral bands are more or less elevated from the bases of wide furrows, and their surfaces are smooth or longitudinally depressed. Vb is wider than Pb. Bands either occupy the total area between the bordering ribs from which they are then separated by narrow furrows, or they occupy less than half of this area and the bordering furrows are almost as wide as the bands. In the range of this variability, Vb and Pb are commonly dissimilarly developed in the same specimen.

Radial muri of the outer shell layer are rarely branched distally so that rectangular cells dominate in transverse sections. Funnel plates are downfolded in the longitudinal ribs as well as in Vb and Pb while they are upfolded in the furrows.

Remarks. Bayle (1856) considered *Biradiolites angulosus* d'Orbigny, 1850 and *Biradiolites quadratus* d'Orbigny, 1850 together with *Biradiolites irregularis* d'Orbigny, 1850 as synonyms of *Radiolites angulosus* d'Orbigny, 1842*a*. However, *R. angulosus* bears a ligamental ridge (see above) and *Birad.*



TEXT-FIG. 29. Transverse sections of *Bournonia africana* Douvillé, 1910 from Dionysos; A, R285; B, R353; C, R359; D, R368; E, R376; F, R369. Scale bar represents 10 mm.

irregularis belongs to *Bournonia* (Toucas 1909; Kühn 1932). Later, *Birad. angulosus* and *Birad. quadratus* were considered as distinct species by Toucas (1909). This view was generally adopted in subsequent works.

According to the differential diagnosis, *Biradiolites quadratus* d'Orbigny, 1850 has wider posteroventral bands than *B. angulosus*. They should occupy almost the complete area between the bordering ribs in *B. quadratus*, but should be separated from these ribs by wide furrows in *B. angulosus*. These characters are combined in several RVs from Marmeko quarry, in which one band is developed as in *B. angulosus*, the other as in *B. quadratus*. Accordingly, distinguishing the two species is impossible.

Distribution. Upper Turonian of the Pyrenees, of France, Italy, Istria, Dalmatia (Sánchez 1981), Sardinia, the Ionian Islands and of Afghanistan. Middle Turonian–Lower Coniacian of northern Castile (Floquet 1991).

Genus BOURNONIA Fischer, 1887

Type species. *Sphaerulites bournoni* des Moulins, 1826.

Bournonia africana Douvillé, 1910

Text-figure 29A–F

*v1910 *Bournonia africana* n. sp. Douvillé, p. 45, pl. 2, fig. 11, text-figs 23, 53.
1932 *Bournonia africana* Douvillé; Kühn, p. 94.
1966 *Bournonia africana* Douvillé; Pamouktchiev, p. 31, pl. 3, fig. 3.
1969 *Bournonia* cf. *africana*; Polšak and Mamužić, p. 238.
1972a *B. africana* Douv.; Campobasso, text-fig. 1/1 [cop. Douvillé 1910].
1972*a* *Bournonia putignanensis* n. sp. Campobasso, p. 364, pl. 1, fig. 1a–b; pl. 2, figs 1–2; text-fig. 1/7.
1981*b* *Bournonia africana* Douvillé; Pamouktchiev, p. 196, pl. 92, fig. 5 [cop. Pamouktchiev 1966].
1981 *Bournonia africana* Douvillé; Sánchez, p. 86 [with synonymy].
1982 *Bournonia putignanensa* Campobasso; Pamouktchiev, p. 232, pl. 4, fig. 5.
1986*a* *Bournonia africana* Douvillé; Pamouktchiev, p. 92, pl. 1, fig. 8.
1987 *Bournonia africana* Douvillé; Pejović and Radoičić, p. 128.
1991 *Bournonia africana*; Caffau and Pleničar, p. 209.
1992 *Bournonia putignanensa* Campobasso; Swinburne *et al.*, text-fig. 2.

Holotype. Douvillé (1910), plate 2, figure 11, text-figures 23, 53.

Material. Six RVs from Dionysos (R285, R353, R359, R368, R369, R376).

Description. RVs more than 50 mm high, maximum width 22 mm, ornamented ventrally with prominent longitudinal ribs of varying width. Among these, Vb is formed by an anterior or central rib which is broadly truncated or has a longitudinal central depression. One or two prominent ribs are found anteriorly of Vb. Pb is narrower or of equal width as Vb, distally tapering, broadly truncated or centrally depressed, but not as salient as in *Bournonia gardonica* (Toucas, 1907). The remaining sculpture is formed by inconspicuous longitudinal ribs that are unevenly spaced: a single rib on the posterior shell can be more prominent. Shape of inner shell margin irregularly round or oval. Fine growth bands are visible on the smooth outer surface of the shells that lack protruding lamellae. Structure of outer shell layer compact, growth lines are upfolded in Vb and Pb.

Remarks. The described specimens lived in clusters of a few conjoined shells. The development of longitudinal ribs and posteroventral bands was thus dependent on available space. The characteristic ventral rib is more prominent in the Boeotian shells than in the type specimen, and can be displaced anterodorsally. The ribbing pattern of such shells is identical with *B. putignanensis* Campobasso, 1972*a* (Text-fig. 29F).

Distribution. Santonian–Campanian of Algeria (Douvillé 1910); Upper Senonian of northern Italy (Caffau and Pleničar 1991); Turonian of Bulgaria and the external Dinarids (Polšak and Mamužić 1969; Pamouktchiev 1986*a*).

Bournonia fourtaui Douvillé, 1910

v*1910 *Bournonia Fourtaui* n. sp. Douvillé, p. 49, pl. 3, fig. 8; text-figs 22, 54.
v.1913*a* *Bournonia Fourtaui* Douvillé; Douvillé, p. 249, pl. 17, fig. 6 [cop. Douvillé 1910]; text-fig. 8.
1915*a* *Bournonia Fourtaui* Douvillé; Douvillé, p. 166, pl. 8, fig. 5; text-fig. 1.
1932 *Bournonia fourtaui* Douvillé; Kühn, p. 96 [with synonymy].
1934 *Bournonia fourtaui* Douvillé; Wiontzek, p. 13, text-fig. 5.
1949 *Bournonia fourtaui* Douvillé; Dechaseaux, pl. 4, fig. 3; text-fig. 3.
1954 *Bournonia fourtaui* Douv.; Jux, p. 176.
1968a *Bournonia fourtaui* Douvillé; Slišković, p. 43.
1972a *B. fourtaui* Douv.; Campobasso, text-fig. 1/5 [cop. Douvillé 1910].
1982 *Bournonia fourtaui* Douvillé; Pamouktchiev, p. 237, pl. 4, fig. 3.
1981 *Bournonia fourtaui* Douvillé; Sánchez, p. 88 [with synonymy].
1982 *Bournonia* cf. *fourtaui* Douvillé; Pleničar, p. 21, pl. 8, fig. 1.
1982 *Bournonia fourtaui* Douvillé; Polšak *et al.*, text-fig. 3.
1987 *Bournonia fourtaui* Douvillé; Pejović and Radoičić, p. 136.
1992 *Bournonia fourtaui* Douvillé; Swinburne *et al.*, text-fig. 2.

Syntypes. Douvillé (1910), plate 3, figure 8, text-figures 22, 54.

Material. Fragment of a single RV in compact limestones at Agia Pelagia monastery, Ptoon Mountains; Senonian (R577).

Description. Three prominent, rounded longitudinal ribs ventrally, the two anteriormost border Vb. Pb is developed as a broad, rounded rib. Preserved portion of the shell (dorsal shell is missing) smooth, with the exception of a single, posterodorsal rib. Structure of outer shell layer compact, except for a single row of rectangular cells that disappear anterodorsally and in Pb.

Remarks. Age assignments for *B. fourtaui* are controversial. According to Douvillé (1910, 1913*a*, 1915*a*) the syntypes were collected from Turonian deposits ('couche *e* d'Abou Roach' after Fourtau 1900, cited in Douvillé 1913*a*). Kühn (1932) indicated a Campanian age in the *Fossilium Catalogus* although the species was then known only from the locus typicus. This erroneous stratigraphical age was adopted by Sánchez (1981). Jux (1954) mentioned the species together with *Eoradiolites liratus* (Conrad) and *Durania gaensis* (Dacqué) from the Cenomanian of Abu Roash. It was found by Pamouktchiev (1979) in the Maastrichtian of Bulgaria and reported by Slišković (1968*a*) from the Campanian–Maastrichtian of Herzegovina.

Numerous small-shelled species of *Bournonia* differ only in details of the posteroventral bands and the distribution on longitudinal ribs. However, these characters are rather variable even in the few specimens of *B. africana* Douvillé, 1910 from Dionysos (Text-fig. 29). A study of richer associations would certainly result in a better-founded taxonomy of the group, which is probably formed by a single, conservative species. This is supported by the fact that all frequently identified, morphologically similar taxa have remarkably extended stratigraphical ranges (*B. fourtaui*, *B. africana*, *B. excavata* d'Orbigny, 1850).

Genus DURANIA Douvillé, 1908*b*

Type species. *Hippurites cornupastoris* des Moulins, 1826.

Durania martellii Parona, 1911*a*

Plate 1, figures 1–2 (cf.), 4, 7; Plate 2, figures 1–3

*1911*a* *Durania Martellii* n. f. Parona, p. 386, text-figs 1–2.
1911c *Durania Martellii* Par.; Parona, p. 292.
1922 *Durania Martellii* Parona; Klinghardt, pp. 9, 35.
1928a *Durania Martellii* Parona; Klinghardt, pl. 13, fig. 15 [cop. Parona 1911*a*]; pl. 14, fig. 8 [cop. Parona 1911*a*].
1930 *Durania Martellii* Par.; Zuffardi-Comerci, p. 14.
1931 *Durania Martellii* Par.; Desio, p. 423.
1932 *Durania martellii* Parona; Kühn, p. 107 [with synonymy].
1958 *Durania martellii* Parona; Tavani, p. 174.
1963 *Durania martellii* Par.; Ambrosetti, p. 213.
1966 *Durania martellii* Parona; Torre, p. 15, pl. 5.
1972 *Biradiolites martellii* (Parona); Pejović, p. 119, text-fig. 1 [cop. Parona 1911*a*].
1975*c* *Milovanovicia dobrunensis* n. sp. Slišković, p. 65, pl. 2, figs 1–4; pl. 3, figs 1–2; pl. 4, figs 1-6; pl. 5, figs 3–5; pl. 6, figs 1–6; pl. 7, figs 1–4; pl. 8, figs 1–2.
1978a *Biradiolites martellii* (Parona); Philip *et al.*, p. 84.
1979 *Biradiolites martellii* (Parona); Polšak, pp. 206, 224.
1981 *Biradiolites martellii* (Parona); Polšak, p. 454.
1984 *B. martellii* (Parona); Laviano, p. 185.
1985 *Milovanovicia dobrunensis* Slišković; Caminiti, p. 140, pl. 31, fig. 4.
1987 *Milovanovicia dobrunensis* Slišković; Accordi *et al.*, p. 139, pl. 1, fig. 4.
1987 *Biradiolites martellii* (Parona); Pejović and Radoičić, p. 127.
1987 *Milovanovicia dobrunensis* Slišković; Pejović and Radoičić, p. 128.
1989 *Biradiolites martellii* (Parona); Accordi *et al.*, p. 168, tab. 1.
1989 *Milovanovicia martellii*; Pieri and Laviano, p. 352.
1990 *Biradiolites* cf. *martellii* (Parona); Cestari and Pantosti, p. 47, text-fig. 4.
1990 *Milovanovicia dobrunensis*; Gušić and Jelaska, text-fig. 7.
1992*b* *Durania martellii* Parona; Peza, p. 297, pl. 2, fig. 3.
1992 *Durania martellii* Parona; Pleničar *et al.*, p. 233.
1993 *Milovanovicia dobrunensis* Slišković; Carannante *et al.*, p. 25.
1993 *Milovanovicia dobrunensis* Slišković; Cherchi *et al.*, p. 95, text-fig. 2.

EXPLANATION OF PLATE 1

Figs 1–2. *Durania*. cf. *martelli* Parona, 1911*a*; R548, Pavlos. 1, posterior aspect; 2, transverse section, adapical view. Both × 0·7.

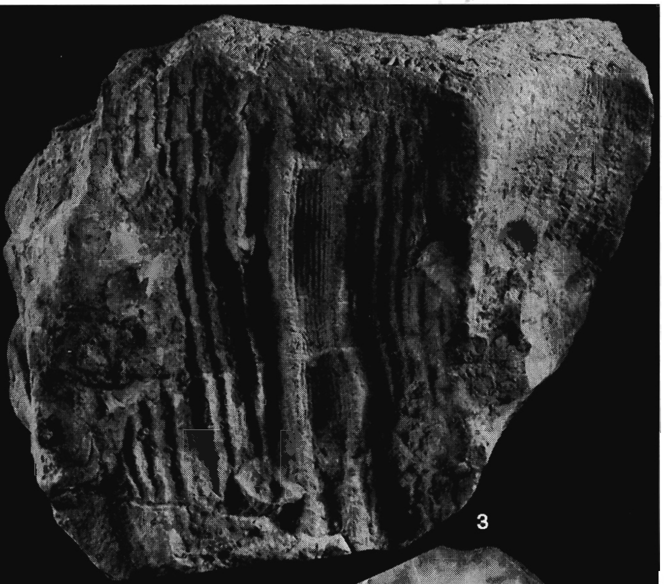
Figs 3, 5–6. *Durania katzeri* (Slišković, 1984*a*). 3, posterior aspect; R631, Pavlos. 5, anterodorsal aspect; R554, Megali Lakka. 6, the same valve as on fig. 5, posteroventral aspect. All × 0·7.

Figs 4, 7. *Durania martellii* Parona, 1911*a*. 4, transverse section, adapical view; R550, Pavlos. 7, transverse section, adapical view; R566, Megali Lakka. Both × 0·7.

Upper side is dorsal in all transverse sections.

PLATE 1


1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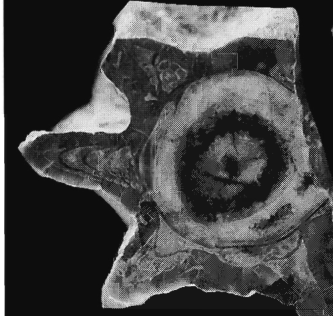
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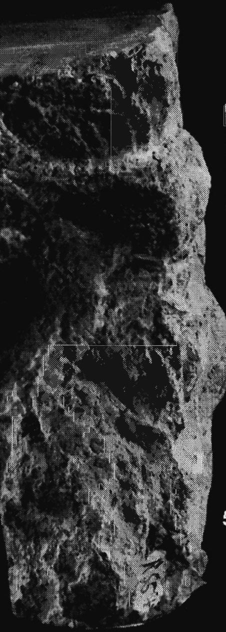
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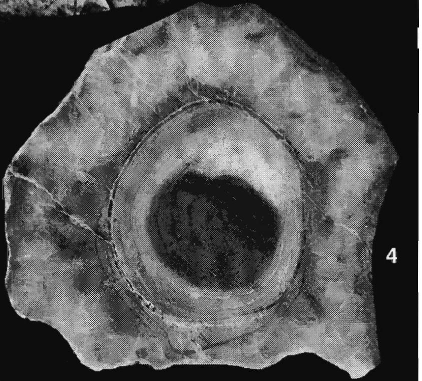
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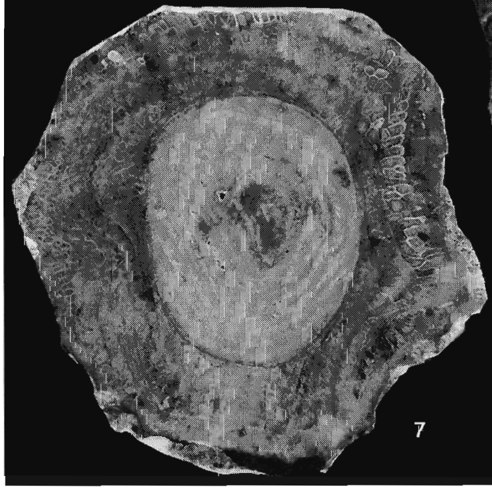
7

STEUBER, *Durania*

1993 *Milovanovicia dobrunensis* Slišković; Ruberti, p. 965, pl. 7, fig. 3.
p1996 *Milovanovicia martellii* (Parona); Laviano and Pejović, p. 93, text-figs 1, ?4–5.
1996 *Milovanovicia dobrunensis* Slišković; Paris and Sirna, p. 187.
1996 *Milovanovicia dobrunensis*; Sanders, p. 852.
1997 *Milovanovicia dobrunensis* Slišković; Ruberti, tab. 1.

Syntypes. Parona (1911*a*), text-figures 1–2.

Material. Five RVs from Pavlos (R548 [cf.], R550, R622, R630, R632, R633) and one from Megali Lakka gorge (R566).

Description. RVs more than 180 mm long, reaching 100 mm in diameter; they are ornamented with six to eight protruding ribs that bear 1–2 mm wide costellae. Spacing of costellae is commonly wide and irregular, and in one specimen only, costellae and furrows of equal width alternate evenly. The outer shell layer is commonly thin between the protruding ribs, but attains almost the same thickness as the ribs in shells with almost circular outline. The distance between Vb and Pb amounts to more than one-quarter of the shell's total circumference; they are separated by two prominent ribs. The bands are either deeply depressed as wide furrows or protrude between the bordering ribs. They are ornamented with up to 12 costellae. In one RV, the bands are raised to the same level as the outer shell margin and are only discernible by the delicate ribbing. Outline of inner shell margin oval, dorso-ventrally elongated. Hinge and LV are not preserved.

Structure of outer shell layer varies from compact to cellular; both types occur in thin-shelled as well as in thick-shelled morphotypes, but all shells have a thick cortical layer. Funnel plates are more or less steeply inclined and are downfolded in the protruding ribs. The more pronounced these ribs, the higher the amplitudes of plication. Funnel plates are widely spaced, so that the height of cells (3–6 mm) occasionally exceeds the vertical spacing of tabulae within the body chamber which is less than 6 mm. Radial and tangential muri are delicate in comparison with the thick (0·05–1 mm) funnel plates. Muri rarely run parallel in radial and tangential section but converge and diverge irregularly. Cellular structure of thin-shelled morphotypes is commonly restricted to the ribs and radial bands, whereas the rest of the shell has a compact structure. No peculiar structures have been noted in the radial bands. Cells are commonly rectangular in transverse section in thin-shelled morphotypes, but muri are inflected in the ribs. The characteristic *Durania*-type pattern of large (3·5 mm mean diameter) penta-, hexa- or heptagonal cells is noted in thick-shelled morphotypes, but irregularly rounded cells may be found in the crest of the major ribs.

Remarks. *Milovanovicia* Polšak, 1967*a* was originally separated from *Durania* Douvillé, 1908*b* because of a compact structure of the outer shell layer. This structural character has been dismissed as a diagnostic feature at the genus level (Cestari 1992*a*), as it occurs more or less commonly in several genera of Radiolitidae (Masse and Philip 1972; Amico 1978). Slišković (1975*c*, 1984*a*) included four additional new species with irregular, large cells of the outer shell layer in *Milovanovicia*. Consequently, the diagnosis of the genus had to be changed and *Milovanovicia* was separated from *Durania* because of its steeply inclined funnel plates and primitive structure of the outer shell layer with inflected muri (Slišković 1975*c*). The Bosnian specimens of this group are particularly thin-shelled, and the large, irregular cells may be considered primitive. However, the shell structure of thick shelled RVs among the Boeotian specimens is indistinguishable from that of *Durania* (Pl. 1, fig. 7). Inflected muri cannot be considered to be a diagnostic character, as they also occur in *Durania* and *Sauvagesia* (cf. Pl. 5, fig. 4). Thus, the only remaining character for separation would be the steep inclination of the funnel plates. As the funnel plates delineate former surfaces of shell accretion, their inclination reflects environmentally controlled changes in growth rate and, thus, this is a ecophenotypic character. Even in the holotype of '*Milovanovicia dobrunensis*' (Slišković 1975*c*, pl. 2, figs 2–3) the inclination of the funnel plates varies, and they are oriented perpendicular to the growth axis of the RV in some parts of the shell. Additionally, there are neither

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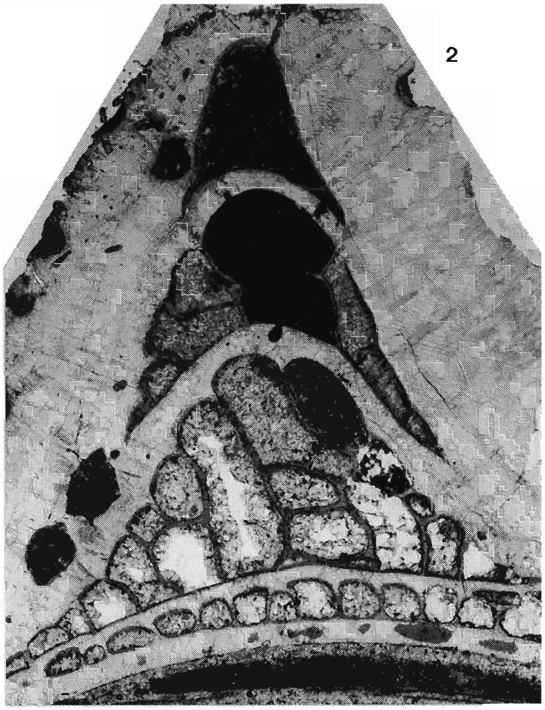
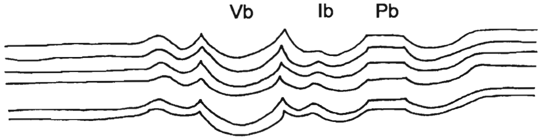
EXPLANATION OF PLATE 2

Figs 1–3. Shell structures of *Durania martelli* Parona, 1911a; R622, Pavlos. 1, radial section of ventral band. 2, transverse section of longitudinal rib. 3, tangential section of longitudinal rib. All × 7·5.



STEUBER, *Durania*



TEXT-FIG. 30. Folds of funnel plates in the posteroventral shell of *Durania* cf. *montisferrati* Astre, 1954.

distinct internal structures in the radial bands of '*Milovanovicia*' (Pl. 2, fig. 1) nor any conspicuous characters of the LV (Slišković 1984*a*) so that a separation from *Durania* appears to be unjustified. Finally, the delicately ribbed radial bands are a diagnostic character of *Durania*.

The only remarkable character is the large size and especially the height of the cells of the outer shell layer. However, although only a few species of *Durania* have been investigated for their shell structure so that a well-founded comparison is still difficult, the dimensions found in '*Milovanovicia*' are probably within the range that can be expected to occur in *Durania*.

Distribution. Lower Senonian of Sardinia, the Apennines, Parnassus and from Kefallinia (Ionian Islands); Turonian–Senonian of Sofrana (Aegean, Desio 1931), Albania (Peza 1992*b*); Santonian–Lower Campanian of Herzegovina (Slišković 1968*a*); Coniacian of the Apennines and the Adriatic island Brač (Accordi *et al*. 1987; Gušić and Jelaska 1990).

Durania katzeri (Slišković, 1984*a*)

Plate 1, figures 3, 5–6

*1984*a*	*Milovanovicia katzeri* n. sp. Slišković, p. 201, pl. 4, figs 1–6; pl. 5, fig. 5; text-fig. 3.
1985	*Biradiolites* cf. *martellii* (Parona); Laviano, p. 327, pl. 13, fig. 1a.
p1996	*Milovanovicia martellii* (Parona); Laviano and Pejović, p. 93, text-figs 2–3.
?1996	*Milovanovicia* cf. *martellii* (Parona); Paris and Sirna, p. 192, pl. 2, fig. 5.

Material. Five RVs from Pavlos (R618, R621, R625, R631), two from Megali Lakka gorge (R552, R554) and one from Kalamos Hill (R281).

Remarks. *D. katzeri* is here only provisionally separated from *D. martelli*. The 'species' differs by the number of longitudinal ribs on the interband: one in *D. katzeri* and two in *D. martelli*. As Ib occupies less than one-quarter of the total circumference of the RV, Vb and Pb are more closely spaced in *D. katzeri*. One RV differs slightly by a regular pattern of ribbing and protruding shell lamellae (Pl. 1, figs 5–6).

Considering the observed variation of *D. martellii*, it seems probable that the four species from the Lower Senonian of Bosnia and Herzegovina which were previously included in '*Milovanovicia*' (Slišković 1975*c*, 1984*a*) belong to a single species. Slight differences occur in the morphology of the radial bands and in the ribbing pattern of Ib. Not much is known about the range of morphological variations, as the description of the four installed species were based on 14 specimens, and there is a similarly small amount of Boeotian material.

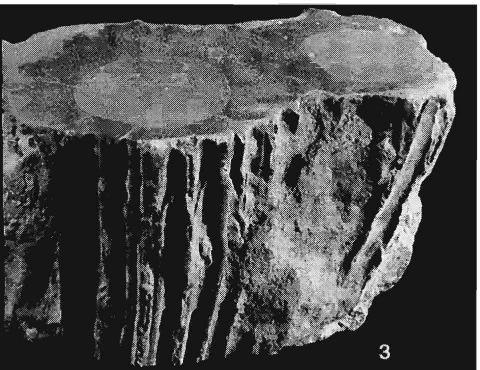
EXPLANATION OF PLATE 3

Figs 1–2. *Durania* cf. *montisferrati* Astre, 1954; R749, Marmeko. 1, posterior side; 2, ventral aspect. Both × 1.

Fig. 3. *Lapeirousella aumalensis* (Douvillé, 1915*b*); R753, Marmeko; posteroventral aspect; × 1.

Figs 4–5. *Biradiolites angulosus* d'Orbigny, 1850; Marmeko. 4, posteroventral aspect, specimen attached to *Radiolites sauvagesi* (d'Hombres-Firmas, 1838); R531. 5, three specimens in posteroventral aspect, attached to *Radiolites sauvagesi* (d'Hombres-Firmas, 1838); R535. Both × 1·4.

1



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Durania cf. *montisferrati* Astre, 1954

Plate 3, figures 1–2; Plate 4, figures 1–5; Plate 5, figures 4–5; Plate 14, figure 1; Text-figure 30

*1954	*Durania montisferrati* nov. sp. Astre, p. 59, pl. 5, figs 2–6; text-fig. 20.
1955a	*Durania montisferrati* Ast.; Astre, p. 11.
1957*b*	*Durania montisferrati* Ast.; Astre, p. 63, text-fig. 17.
1981	*Durania montisferrati* Astre; Sánchez, p. 108.

Syntypes. Astre (1954), plate 5, figures 2–6, text-figure 20.

Material. Twenty-three specimens from Marmeko quarry (R2, R141, R146, R157, R167, R245, R248, R251, R258, R587, R588, R589, R590, R734, R742, R743, R744, R745, R746, R747, R748, R749, R750.)

Description. Most RVs are broadly conical, a few are elongated sub-cylindrical. One particularly depressed RV has a commissural diameter of 160 mm and a length of 85 mm, while elongated specimens reach 125 mm in commissural diameter and exceed 270 mm long. Low-amplitude folding of shell lamellae occurs only in the posteroventral shell, including the radial bands and small segments that border them. Shell lamellae protrude in irregular intervals and are ornamented with rounded, evenly spaced longitudinal ribs that are regularly wrinkled. Furrows and ribs are of equal width, four to six ribs are found on segments 10 mm wide. LV preserved in fragments only, its outer margin is smooth and particularly thin.

The external ornamentation of both radial bands is preserved in one RV, another specimen shows only that of Vb; both RVs have a commissural diameter of 110 mm. Vb of the first, more completely preserved RV is shallowly indented so that the transverse section is V-shaped; its commissural width is 26 mm and it bears 28 delicate costellae. Vb is formed by a downfold of shell lamellae; it is bordered by the anterior and posterior, angular and slightly salient culminations of this fold. Width of Ib is 30 mm, lamellae are downfolded and form two unequal longitudinal ribs which are covered by costellae similar to those around the rest of the valve. Pb is 15 mm wide and bears 14 costellae. Shell lamellae run parallel to the commissure in Pb and are downfolded in a single fold dorsally of Pb. Vb of the second RV is 23 mm wide, with a shallow, V-shaped indentation as in the other specimen, and ornamented with 25 costellae.

Sculptures are only partly preserved in the other RV, but Vb and Pb can be recognized by characteristic plications of the funnel plates. The relative widths of Vb, Ib and Pb, as well as the general style of folding of the funnel plates varies only insignificantly (Text-fig. 30): In all specimens, Vb is wider than Pb, Ib is of equal width or wider than Vb; funnel plates are downfolded in Vb, they are downfolded and undulating in Ib and run parallel to the commissure in Pb. The outer shell layer is thickest anterodorsally and much thinner in the opposite, posteroventral segment. Anterodorsally, its thickness may exceed the diameter of the inner shell as measured between the inner margins of the outer shell layer. Outline of inner shell oval, slightly bulging at the sites of radial bands in some shells.

(1) is more prominent than (3), (1) and (3) are dorsally furrowed; furrows interlock with longitudinal ridges of (1′) and (3′). Ma is located far distally, at the margin of the general cavity; mp is rooted more centrally than ma and, consequently, projects obliquely from the LV to the inner margin of the RV.

The cellular shell structure has been analysed in two specimens. Maximum height of cells is 0·85 mm, spacing of funnel plates becomes successively closer when approaching the upper and lower border of a lamella. In transverse section, the cells are predominantly angular and tangentially elongated, often hexagonal, less commonly penta- or heptagonal, mean length is 0·75–1·25 mm; anterodorsally and near to the outer shell wall, cells are often irregularly rounded or tangentially elongated up to 2·75 mm; undulating muri are common. Cellular pattern of the other RVs is more irregular, as angular hexagonal cells are rarely developed. Instead, tangentially elongated or vermiform cells dominate and are up to 10 mm long. The muri undulate and are frequently interrupted so that cells are not always

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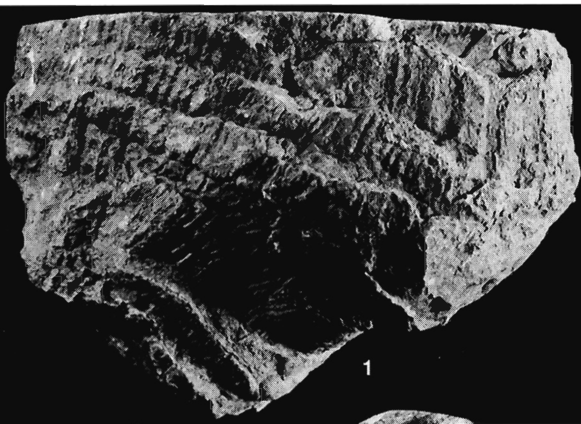
EXPLANATION OF PLATE 4

Figs 1–5. *Durania* cf. *montisferrati* Astre, 1954; Marmeko. 1, RV with well-preserved sculpture, posterodorsal aspect; R258. 2, flat-conical, bivalve specimen, dorsal aspect; R245. 3, large elongated RV with partially protruding shell lamellae, anteroventral aspect; R742. 4, same valve as on fig. 3, dorsal aspect; fine longitudinal ribs are preserved in the commissural part. 5, RV with well-preserved sculpture, dorsal aspect; R750. All × 0·7.



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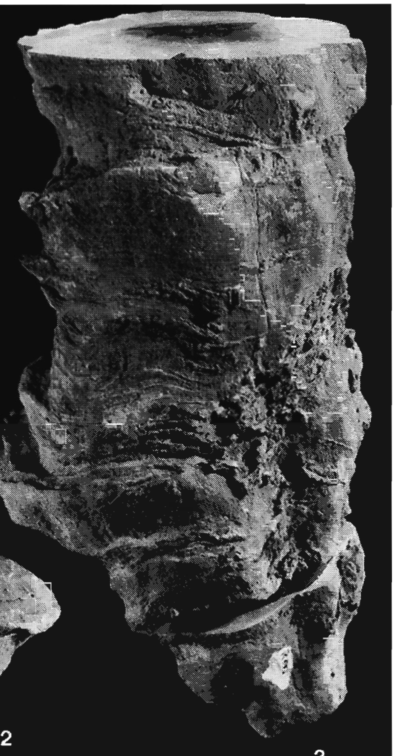

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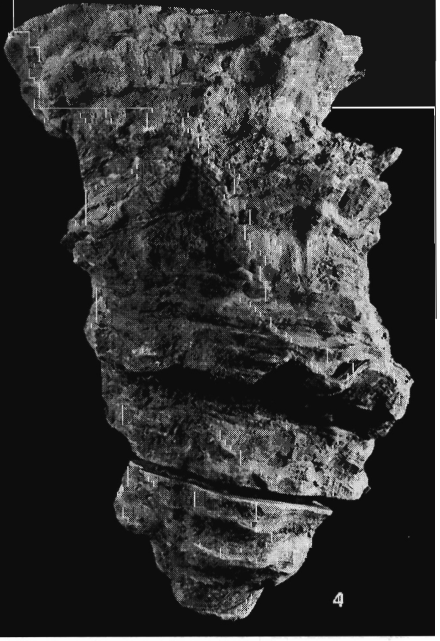

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STEUBER, *Durania*

enclosed and form a labyrinthic pattern. In both shells, the arrangement and outline of cells becomes increasingly irregular when approaching the outer shell wall.

Remarks. Only a few, rather incompletely preserved specimens of *D. montisferrati* have been described from the Upper Turonian of the Pyrenees. Their radial bands have fewer costellae than the Boeotian shells. According to the diagnosis, Pb is ornamented with only five or six costellae, and Vb of a subsequently described specimen (Astre 1957*b*) has nine delicate ribs. In contrast, more than twice as many costellae are found on the radial bands of the Boeotian shells. The overall shape of the valves, the flaky appearance of the shell lamellae and their regular ribbing is very similar to the syntypes.

Flat-conical morphotypes and protruding, flaky shell lamellae are rarely developed in other species of *Durania*. Similar morphotypes of *D. cornupastoris* (des Moulins, 1826) and *D. arnaudi* (Choffat, 1891) have been described from Portugal (Choffat 1902, pl. 7, figs 15, 18; pl. 8, fig. 13a–b; Berthou 1973, pl. 53, fig. 1); both 'species' are rather arbitrarily separated because of differing width of Ib (Cobban *et al.* 1991). The Boeotian specimens resemble *D. cornupastoris* by their broad Ib. However, protruding, flaky shell lamellae occur both in depressed-conical and sub-cylindrical-elongated RVs from Marmeko quarry and appear to be a diagnostic character of the shells. Additionally, the relative widths of the radial bands show only insignificant variations, and the exceptionally large number of costellae is considered to exclude an attribution to *D. cornupastoris*. However, knowledge of morphological variability in this taxon and other species of *Durania* is still very insufficient.

Genus EORADIOLITES Douvillé, 1909

Type species. *Radiolites davidsoni* Hill, 1893.

Remarks. Although several Aptian–Albian species of *Eoradiolites* have been revised recently (Gallo Maresca 1994; Masse and Gallo Maresca 1997), the taxonomy of the group is still confusing. The genus comprises more than 40 species, and little is known about ecophenotypic variations. Type specimens of several species are transverse sections of RVs embedded in compact limestones, and differential diagnoses are predominantly concerned with minor differences in outlines of radial bands. Compared with other European representatives, the Boeotian specimens are among the best preserved, and show remarkable variations in characters that are conventionally considered diagnostic at the species level.

Eoradiolites davidsoni (Hill, 1893)

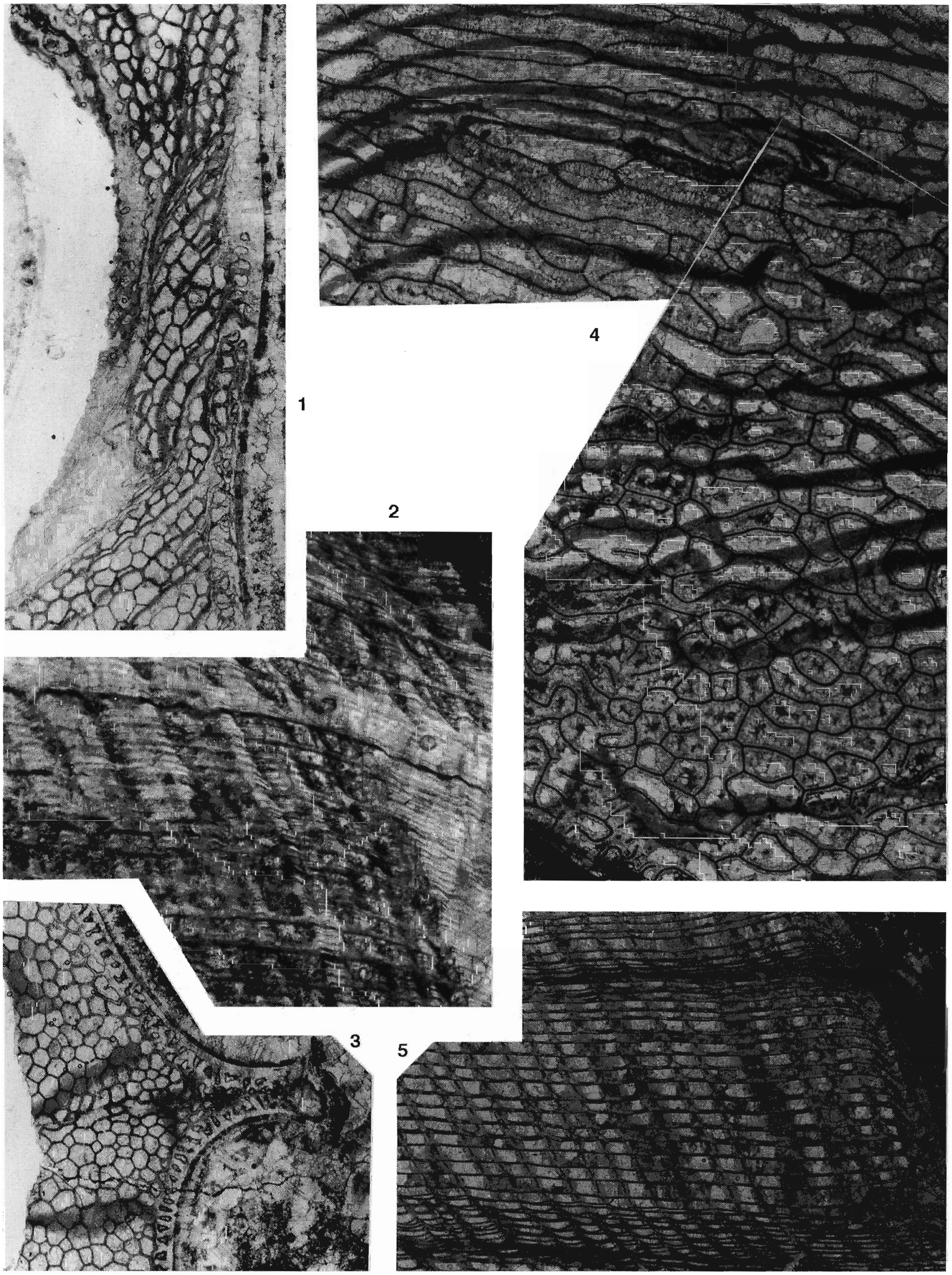
Plate 6, figures 1–12; Plate 7, figures 1–5; Text-figures 31–32

*1893 *Radiolites davidsoni* sp. nov. Hill, p. 106, pl. 13.
1898b *Rad. Davidsoni*; Douvillé, p. 388.
v.1900*a* *Radiolites Davidsoni* Hill; Douvillé, p. 218, text-fig. 15.
v.1902 *Praeradiolites davidsoni* Hill; Douvillé, p. 468, pl. 15, fig. 7.
v.1907 *Agria Davidsoni* Hill; Toucas, p. 24, pl. 2, fig. 1, 1a.
p1930 *Eoradiolites quadratus* n. sp. Adkins, p. 80 [*teste* Coogan 1977].

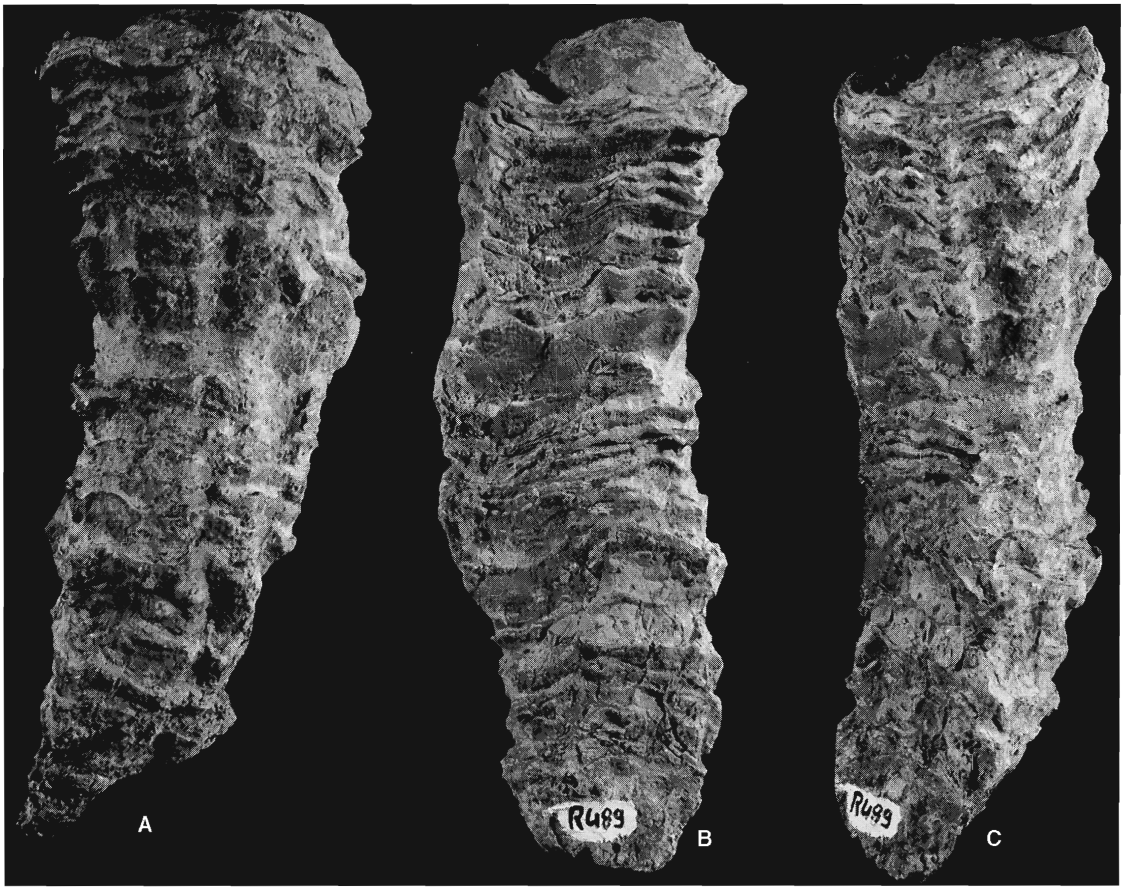
EXPLANATION OF PLATE 5

Figs 1–3. *Sauvagesia meneghiniana* (Pirona, 1869). 1, transverse section of posterior band; R361, Dionysos. 2, radial section of posterior band; R573, Tsouka Hill. 3, transverse section of dorsal part of outer shell layer with ligamental ridge; R361, Dionysos. 1, 3, × 11·5; 2, × 23·1.

Figs 4–5. *Durania* cf. *montisferrati* Astre, 1954; R589, Marmeko. 4, transverse section, anterodorsal; 5, radial section; both × 8·3.



STEUBER, *Sauvagesia, Durania*



TEXT-FIG. 31. *Eoradiolites davidsoni* (Hill, 1893); R489, Analipsis; × 1. A, bivalve specimen with steeply inclined, closely imbricated and smooth shell-lamellae; posteroventral aspect; B, ventral aspect, profile of posterior band is seen to the right; C, anterior side.

1932 *Eoradiolites davidsoni* (Hill) Douvillé; Kühn, p. 111 [with synonymy].
?1934 *Eoradiolites davidsoni* Hill; Wiontzek, p. 12, text-figs 2–4.
?*1935* *Eoradiolites rousseli*; Douvillé, pl. 23a [cop. Douvillé 1900*a*].
?1948 *Eoradiolites durdurensis* nov. sp. Tavani, p. 151, pl. 11, fig. 4a–b.
1965 *Eoradiolites davidsoni* (Hill) Douvillé; Torre, p. 74, pl. 2, fig. 3a–d.
1973 *Eoradiolites davidsoni* (Hill); Coogan, p. 63, text-fig. 7.
1974 *Eoradiolites davidsoni*; Pejović, p. 130.
?1974 *Eoradiolites metohiensis* n. sp. Pejović, p. 130.
.1977 *Eoradiolites davidsoni* (Hill); Coogan, p. 44, pl. 5, figs 1, 3–6, 8.
p1977 *Eoradiolites quadratus* (Adkins); Coogan, p. 46.
1980 *Eoradiolites davidsoni*; Laviano and Sirna, p. 69.
1981 *Eoradiolites davidsoni* (Hill) Douvillé; Czabalay, tab. 1.
1981 *Eoradiolites davidsoni* (Hill); Sánchez, p. 113 [with synonymy].
1985 *Eoradiolites davidsoni* (Hill); Czabalay, p. 124, text-figs 2, 4, 5b.
1987 *Eoradiolites davidsoni* (Hill); Alencáster, p. 117.
1988 *Eoradiolites davidsoni*; Collins, p. 278.
1988 *Eoradiolites davidsoni* (Hill); Pamouktchiev, p. 256, pl. 1, fig. 3.

*non*1992*b* *Eoradiolites* cf. *davidsoni* (Hill); Özer, pl. 1, fig. 11.
1994 *Eoradiolites davidsoni* (Hill); Gallo Maresca, p. 24, pl. 1, figs 1–5; text-fig. 8 [cop. Douvillé 1910].
1996 *Eoradiolites davidsoni* (Hill); Alencáster and Aguilar-Pérez, p. 118.
1996 *Eoradiolites davidsoni* Hill; Corona-Esquivel and Alencáster, p. 188.

Syntype. Hill (1893), plate 13, text-figure 1.

Material. Ninety specimens from Analipsis, many of them with conjoined valves (R398, R401, R403, R406, R407, R408, R412, R414, R417, R418, R421, R423, R424, R427, R428, R430, R431, R437, R441, R449, R450, R455, R457, R458, R460, R464, R477, R478, R481, R482, R483, R485, R486, R488, R489, R494, R496, R501, R505, R506, R507, R508, R509, R511, R602, R603, R638, R641, R735).

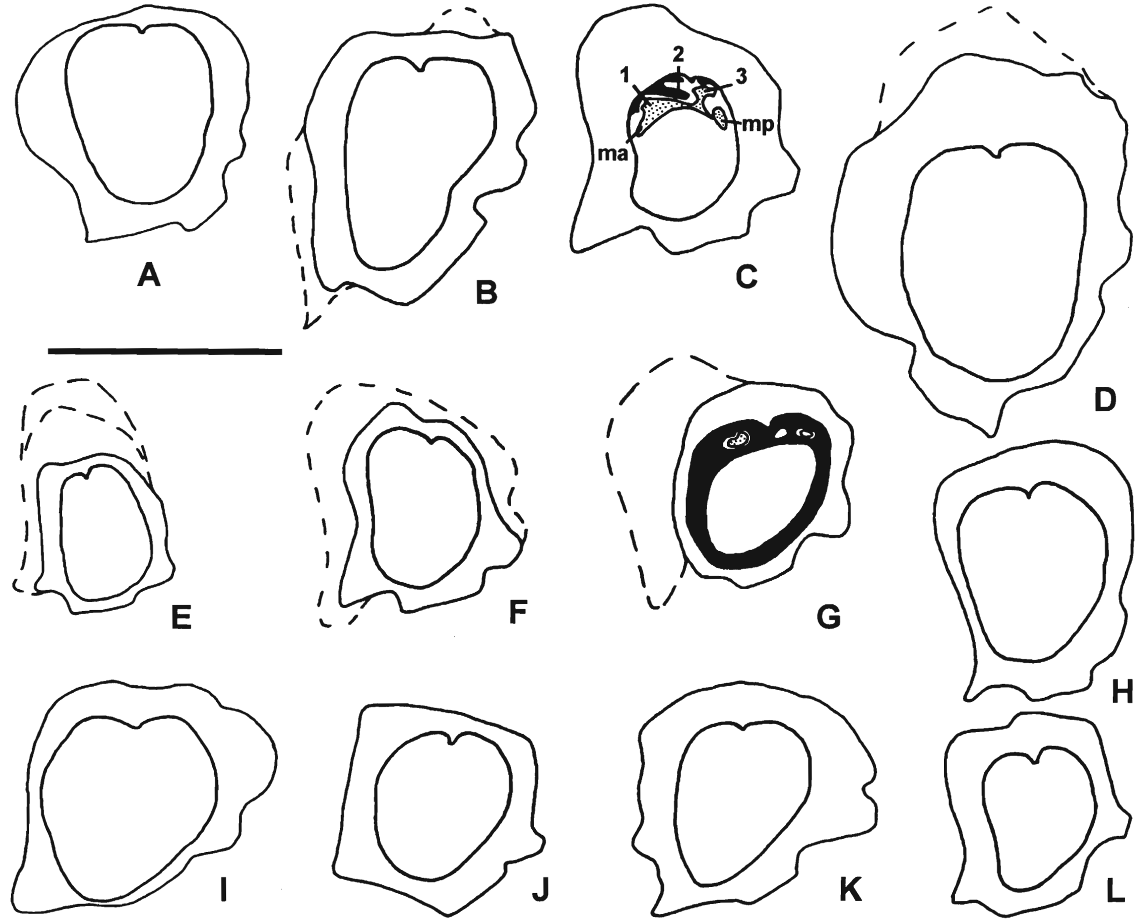
Description. RVs elongated-conical or sub-cylindrical, exceeding 120 mm long, commissural diameter up to 59 mm. Shell lamellae more or less steeply inclined, but externally protruding or even adapically inflected in some specimens; commonly ornamented with faint longitudinal ribs in the dorsal half of the shell. The ribbing pattern of many RVs cannot be recognized, as the delicate ribs are corroded. Shell lamellae form an acute or rounded, salient plication at the ventral shell; a rounded furrow of variable width and depth is located posterior to this ventral fold that is bordered posteriorly by Vb. Lamellae project in Vb to form a wide, exteriorly truncated bulge. Pb is similarly developed, but considerably narrower and has a less pronounced exterior truncation. Ib is formed by a rounded, narrow furrow. Neither Ib nor the furrow between the ventral fold and Vb is ribbed.

The LV is flatly convex and deeply depressed between inclined lamellae of the RV. (1) and (3) are externally fluted with one or two furrows that fit into ridges of (1′) and (3′). (1) is considerably stronger and longer than (3). (2) projects obliquely from the anterodorsal inner shell margin to the shell's interior. In adapical transverse sections it is joined to a septum that runs dorsally from the anterior to the posterior inner shell and demarcates (1′) and (3′) ventrally. Ligamental ridge wide and truncated or internally tapering, commonly posteriorly inflected; close to the commissure it is surrounded by a cavity that can be traced down toward the apex but becomes smaller adapically; it is located anteriorly of (3) and at the ventral tip of the ligamental ridge. Ma is more robust than mp, both project only shallowly into the RV.

Structure of outer shell layer is compact in thin-shelled specimens with tightly inclined lamellae. Cellular structure is commonly restricted to thick, externally projecting lamellae. Steeply inclined funnel plates are stacked in regular intervals of 0·5–0·75 mm and are crossed regularly by simple, radial muri. Tangential muri are not developed. This pattern results in rectangular cells when viewed in transverse section. Rectangles are more or less radially elongated, depending on the inclination of the funnel plates. Branching of the 0·08–0·1 mm thick muri occurs rarely and has only been noted in externally expanding lamellae. Generally, additional radial muri are intercalated distally when the cells exceed 0·3 mm in tangential width.

Variability and *systematic position*. Elongated-conical specimens dominate at Analipsis. Sub-cylindrical shells are less abundant and may reach overall dimension of 120 × 25 mm. Lamellae of most shells are steeply inclined but may be projecting horizontally near the commissure. Projection occurs preferentially around the dorsal shell but downturning of lamellae is exceptional. Lamellae are always inclined and fit tightly in the radial bands. RVs with considerably projecting lamella resemble a specimen described as *E.* cf. *perforata* (Palmer, 1928) from the Albian of Texas (Coogan 1977, pl. 4, fig. 5a–b), although ribbing is coarser in this shell when compared with the Boeotian specimens. The position of the ligamental invagination is indicated in several shells by a prominent longitudinal furrow in which the lamellae converge towards the apex (Pl. 6, fig. 10). Such specimens resemble *Praeradiolites*? *hedini* Douvillé, 1916 which, however, differs in having rounded radial bands and in the lack of a conspicuous ventral plication. In most RVs, the position of the ligamental ridge is not discernible from the external ornamentation.

The Boeotian shells differ from the Texan specimens of *E. davidsoni* by the large number of stacked lamellae. The vertical spacing amounts to 25 mm in some shells, while several lamellae only 2 mm thick may be stacked in other shells that, consequently, have a flaky appearance and lack longitudinal ribs. The latter morphotype departs considerably from the usual appearance of the species. The ventral fold, Vb and Pb are clearly accentuated in transverse sections (Text-fig. 32), and vary only by the degree of projection. The dorsal shell margin is either straight, as in *E. plicatus*, or rounded.



TEXT-FIG. 32. Transverse sections of RVs of *Eoradiolites davidsoni* (Hill, 1893) from Analipsis. Black, inner shell layers of RV; dotted, myocardinal elements of LV; outline of shell lamellae below the figured plane is marked by broken lines. A, R505; B, R641; C, R427; D, R638; E, R477; F, R427; G, R464; H, R602; I, R406; J, R403; K, R482; L, R417. Scale bar represents 30 mm.

EXPLANATION OF PLATE 6

Figs 1–12. *Eoradiolites davidsoni* (Hill, 1893); Analipsis. 1, posterior aspect of a slender RV; profile of ventral band is seen to the left; R477. 2, anteroventral view of the ventral folds and ventral band of same valve as on fig. 1; profile of posterior band is seen to the right. 3, ventral aspect of same valve as on figs 1–2; profile of Pb is seen to the right. 4, anterodorsal aspect of RV with prominent longitudinal ribs; ventral fold to the right; R507. 5, same valve as on fig. 4, posterodorsal aspect. 6, posterior side of a RV with protruding shell-lamellae, ventral and posterior bands badly preserved; R505. 7, same valve as on fig. 6, dorsal aspect. 8, anterior aspect of RV with steeply inclined, longitudinally ribbed shell-lamellae; R482. 9, ventral aspect of a ventrally compressed RV; R602. 10, same valve as on fig. 9, dorsal aspect; position of ligament is indicated by adapically convergent shell-lamellae. 11, anterodorsal aspect of a RV with distinct longitudinal ribs; R478. 12, shape of RV with (from top to bottom) angular posterior and ventral bands, and ventral fold, adapical view; R494. 1–5, 8–10, 12, × 1; 6–7, 11, × 0·8.

PLATE 6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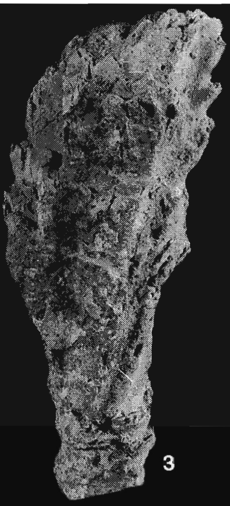
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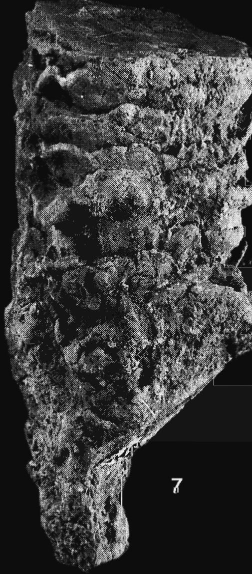
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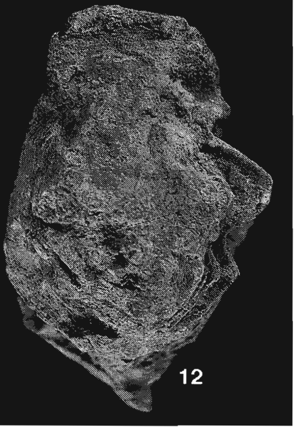
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STEUBER, *Eoradiolites*

The ribbing of RVs is rather variable: In several RVs lamellae are longitudinally ribbed around the complete shell, except for the posteroventral segment. Ribs are lacking on the anterior flank of the ventral plication of many RVs, and in some shells only a thin antero- or posterodorsal segment is ribbed. Specimens with completely smooth lamellae are rare. The ribbing is thus much less pronounced as in *E. franchii* Parona, 1921. *E. durdurensis* Tavani, 1948 can probably be included in the variability of *E. davidsoni*, even though the ribbing is slightly coarser when compared with the Boeotian and Texan specimens. *E. plicatus* Conrad, 1852 is insufficiently known, but apparently has smooth lamellae, a sub-quadrangular outline and inconspicuous radial bands. Gallo Maresca (1994) described several specimens from Upper Aptian–Lower Albian circum-Mediterranean localities as *E. plicatus*, and concluded that they differ from *E. davidsoni* only by the ventral position of Vb and Pb, less salient longitudinal ribs, and by a relatively thin outer shell layer. These characters are highly variable in the Boeotian specimens (Text-fig. 32). However, the available descriptions of type specimens of *E. plicatus* are too imprecise for a concluding decision about the justification of separating *E. plicatus* and *E. davidsoni*. These taxa, including *E. liratus* (Conrad, 1852), probably belong to an anagenetic lineage, characterized by increasing size, relative thickness of outer shell layer and prominence of longitudinal ribbing during the Late Aptian–Albian.

Distribution. Albian of Texas, Mexico, Egypt, Iran (Sánchez 1981), Hungary, Apulia, Somalia; Cenomanian of Serbia (Pejović 1974); Lower Cenomanian of Bulgaria (Pamouktchiev 1988); Cenomanian–Lower Turonian of Apulia (Laviano and Sirna 1980).

Eoradiolites sp.

Material. Two RVs from Koronia (R738, R704); Albian.

Description. The larger of the two RVs exceeds 100 mm long and has a commissural diameter of 75 mm; the outer shell layer is only 4–7 mm thick. Shell lamellae are steeply inclined and have inconspicuous, blunt ribs of irregular width that become slightly more salient ventrally, in the vicinity of Pb. The posteroventral shell is corroded, but a wide, externally truncated bulge of Vb is discernible close to the commissure. It is anteriorly bordered by a salient ventral fold of the lamellae. The anterior shell was conjoined with two other radiolitids, presumably of the same species, so that their attached fragments preclude the description of the anterior sculpture.

The second specimen is preserved as a corroded fragment with a commissural diameter of 55 mm. The ornamentation is preserved only on the posterior shell. There, lamellae are unevenly ribbed and folded dorsally to Pb. The amplitudes of plications decrease dorsally. Pb is formed by a 4 mm wide, externally truncated bulge. The anterior shell is crushed.

Compact and cellular structures alternate in the outer shell layer. Funnel plates and radial muri form cells that appear rectangular in transverse section. Spacing of funnel plates is close but irregular and rarely exceeds 0·3 mm. The transition between compact and cellular structures occurs by thickening of the radial muri.

Remarks. A safe determination of the two specimens from Koronia is precluded by the bad preservation of the posteroventral shells. The sculpture resembles those of *E. costicillatus* Torre, 1948, *E. hungaricus* Czabalay, 1981, *E. franchii* Parona, 1921 and *E. robustus* (Palmer, 1928 *sensu* Coogan 1977), but longitudinal ribs are less salient and less regularly distributed. The ribbing pattern of *E. murgensis* Torre, 1965 is most similar.

EXPLANATION OF PLATE 7

Figs 1–5. *Eoradiolites davidsoni* (Hill, 1893); Analipsis, shell structures. 1, transverse section, anterior part; R488; × 12. 2, detail of fig. 1; × 33·3. 3, transverse section of dorsal part of shell with myocardinal elements, abapical view; R735; × 3·9. 4, radial section of posterior band; R455; × 7·1. 5, transverse section of dorsal part of shell with myocardinal elements, abapical view; R488; × 4·4.

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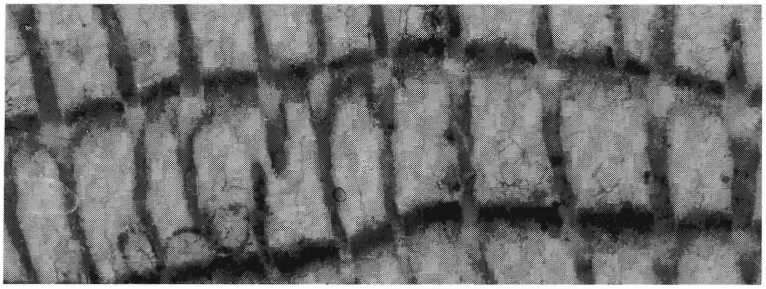

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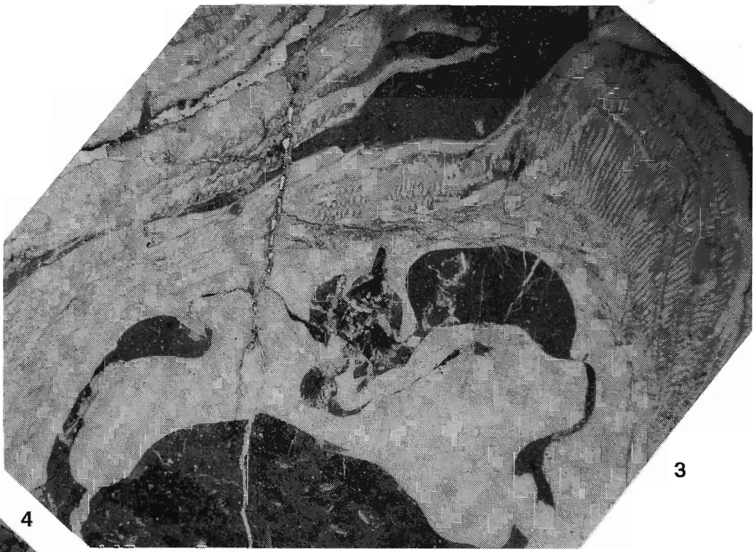

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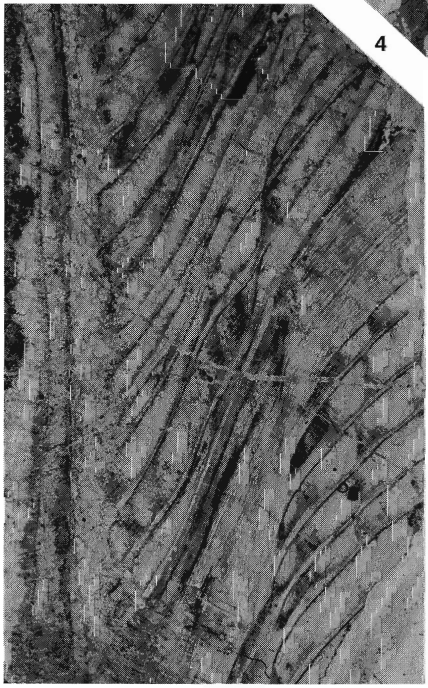

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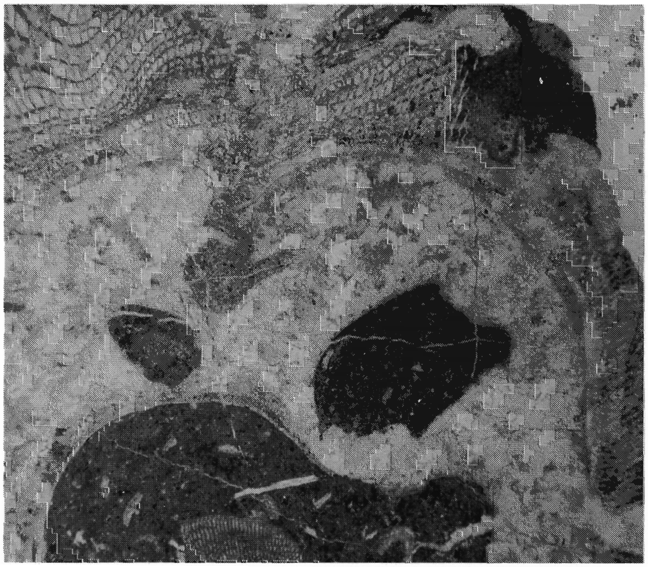

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STEUBER, *Eoradiolites*

Genus FOSSULITES Astre, 1957*b*

Type species. *Medeella undaesaltus* Astre, 1954.

Fossulites dionysii Steuber, 1994

1993 *Fossulites dionysii* Steuber; Steuber *et al*., text-fig. 10 [*nomen nudum*].
*1994 *Fossulites dionysii* n. sp. Steuber, p. 48, text-figs 4–9, 29, 31.

Holotype. Steuber (1994), text-figures 4, 7–9, 31 (GIK 1055).

Material. Holotype and 11 paratypes (GIK 1056–1066) from Dionysos.

Description. See Steuber (1994).

Fossulites aff. *undaesaltus* (Astre, 1954)

*1954 *Medeella undaesaltus* nov. sp. Astre, p. 41, text-fig. 14a–d.
1994 *Fossulites* aff. *undaesaltus* (Astre); Steuber, p. 51, text-fig. 12 [with synonymy and description].

Syntypes. Astre (1954), text-figure 14a–d.

Material. One fragmentary RV from Dionysos (GIK 1067).

Description. See Steuber (1994).

Distribution. Coniacian–Lower Santonian of the western Mediterranean region; Santonian–Lower Campanian of Bosnia (Slišković 1985); Upper Senonian (?Maastrichtian) of Slovenia (Drobne *et al*. 1988; Šribar and Pleničar 1991).

Genus GORJANOVICIA Polšak, 1967*b*

Type species. *Gorjanovicia costata* Polšak, 1967*b*.

Gorjanovicia boeotica Steuber, 1994

1993 *Gorjanovicia boeotica* Steuber; Steuber *et al*., text-fig. 10 [*nomen nudum*].
*1994 *Gorjanovicia boeotica* n. sp. Steuber, p. 54, text-figs 14, 19–22, 24–26, 28, 30.

Holotype. Steuber (1994), text-figures 14a, 19–20 (GIK 1068).

Material. Holotype, six paratypes (GIK 1069–1074) from Dionysos, three specimens (GIK 1075–1077) from Megali Lakka (locality called 'Loutsion' in Steuber 1994) and one RV from Keratovouno Hill (GIK 1078).

Description. See Steuber (1994).

Gorjanovicia costata Polšak, 1967*b*

1964 *Gorjanovicia costata* n. sp. Polšak, p. 67 [*nomen nudum*].
1965b *Gorjanovicia costata* n. sp. Polšak, p. 451 [*nomen nudum*].
1965 *Gorjanovicia costata* Polšak; Slišković, p. 373 [*nomen nudum*].
*1967*b* *Gorjanovicia costata* n. sp. Polšak, pp. 103, 202, pls 61–66, 69; pl. 70, figs 1–2; text-fig. 28.
1994 *Gorjanovicia costata* Polšak; Steuber, p. 55 [with synonymy and description].
1995*b* *Gorjanovicia costata* Polšak; Caffau and Pleničar, p. 232, pl. 4, figs 1, 1a, 2, 2a.

?1995*b* *Radiolites dario* (Catullo); Caffau and Pleničar, p. 235, pl. 1, fig. 2, 2a; pl. 9, figs 1–2.
?1996*a* *Gorjanovicia* cf. *costata* Polšak; Steuber, p. 315, text-fig. 1.

Holotype. Polšak (1967*b*), plate 61, figure 1, 1a; plate 62, figure 1.

Material. One RV from the southern Parnassus Mountains near Arachowa (GIK 1080) and one from Keratovouno Hill (GIK 1081), respectively, 11 RVs from Dionysos (GIK 1082–1092) and four RVs from Megali Lakka (GIK 1079 [*G*. cf. *costata*], GIK 1093–1095, locality called 'Loutsion' in Steuber 1994).

Description. See Steuber (1994).

Remarks. The systematic position of *Gorjanovicia costata* Polšak, 1967*b* and related species is confusing as there are several potential senior synonyms (Steuber 1994). Numerous species of this group have been incorporated into *Radiolites dario* (Catullo, 1834) on the basis of morphometric analyses (Cestari 1992*b*), but without considering the diagnostic character of the posteroventral pseudopillars.

Distribution. Santonian–Campanian of the external Dinarids, of Italy and Greece (Parnassus Mountains).

Gorjanovicia gracilis (Wiontzek, 1934)

*1934 *Medeella gracilis* nov. sp. Wiontzek, p. 24, pl. 1, figs 6–8; text-fig. 17.
1994 *Gorjanovicia gracilis* (Wiontzek); Steuber, p. 56, text-figs 15–18, 27 [with synonymy and description].

Holotype. Wiontzek (1934), plate 1, figures 6–8, text-figure 17.

Material. Five RVs from Dionysos (GIK 1096–1100), four RVs from Megali Lakka (GIK 1101–1104, locality called 'Loutsion' in Steuber 1994).

Description. See Steuber (1994).

Distribution. Santonian–Campanian of Istria and Greece.

Gorjanovicia kayae Özer, 1982

*1982 *Gorjanovicia kayae* n. sp. Özer, p. 231, pl. 1, fig. 3.
1994 *Gorjanovicia kayae* Özer; Steuber, p. 56, text-figs 10–11 [with synonymy and description].

Holotype. Özer (1982), plate 1, figure 3.

Material. One RV from Dionysos (GIK 1105).

Description. See Steuber (1994).

Distribution. Campanian of north-western Anatolia.

Gorjanovicia lipparinii Polšak, 1967*b*

1964 *Gorjanovicia lipparinii* n. sp. Polšak, p. 67 [*nomen nudum*].
1965b *Gorjanovicia lipparinii* n. sp. Polšak, p. 451 [*nomen nudum*].
*1967*b* *Gorjanovicia lipparinii* n. sp. Polšak, pp. 107, 205, pl. 67, fig. 1; text-fig. 31.
1994 *Gorjanovicia lipparinii* Polšak; Steuber, p. 58, text-fig. 13 [with synonymy and description].
1995*b* *Gorjanovicia lipparinii* Polšak; Caffau and Pleničar, p. 233, pl. 5, figs 1–3; text-fig. 4.

Holotype. Polšak (1967*b*), plate 67, figure 1.

Material. One fragmentary RV from Dionysos (GIK 1106).

Description. See Steuber (1994).

Distribution. Santonian–Campanian of Istria, ?Apulia.

Genus LAPEIROUSELLA Milovanović, 1938*a*

Type species. Lapeirousia (*Lapeirousella*) *orientalis* Milovanović, 1938*a*.

Lapeirousella aumalensis (Douvillé, 1915*b*)

Plate 3, figure 3; Plate 8, figures 1–4; Plate 9, figures 1–4, Plate 12, figure 1; Text-figures 33–35, 38B

Systematic position. '*Lapeirousia*' *aumalensis* from the Turonian of Aumale was previously considered as the stratigraphically oldest species of *Lapeirousia* Bayle, 1878. Phylogenetic analyses of the genus were repeatedly based on this taxon (Kühn 1934; Milovanović 1938*a*, 1951*b*), although its shell structure was insufficiently known. *Lapeirousella* Milovanović, 1938*a* was separated from *Lapeirousia* because of the rudimentary development of the pseudopillars that hardly project into the shell interior. *Lapeirousella* was, however, not considered as the ancestor of *Lapeirousia*, being known only from deposits which are younger than those in which the oldest representatives of *Lapeirousia* had been found. Consequently, the comparatively simple structure of the pseudopillars was considered as a phylogenetic reduction of the more complicated structures in *Lapeirousia* (Milovanović 1938*a*, 1951*b*). Obviously, the shell structure of '*Lapeirousia*' *aumalensis* Douvillé, 1915*b* is of considerable importance for the evolution of radiolitid pseudopillars so that the type specimens have been reinvestigated, and their first detailed description and figures are given here.

*v1915*b*	*Lapeirousia aumalensis* n. sp. Douvillé, p. 26, text-fig. 1.
1932	*Lapeirouseia* [*sic*] *aumalensis* Douvillé; Kühn, p. 118.
1934	*Lapeirouseia* [*sic*] *aumalensis* Douv.; Kühn, p. 373.
1938a	*L. aumalensis* Douvillé; Milovanović, p. 87.
1951b	*Lapeirouseia* [*sic*] *aumalensis* Douvillé; Milovanović, pp. 158, 210.
1981	*Lapeirouseia* [*sic*] *aumalensis* Douvillé; Sánchez, p. 132.
1992b	*Lapeirousia aumalensis* Douvillé; Özer, p. 138.

Syntype. Douvillé (1915*b*), text-figure 1; hereby designated as lectotype.

Material. One specimen with conjoined valves as well as five fragmentary RVs from Marmeko quarry (R178, R752–753), and the type specimens (EM 15634–15635).

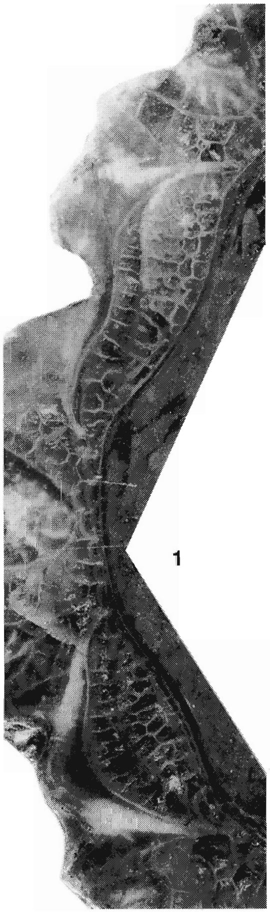
Redescription of lecto- and paratype. The lectotype (EM 15634; Pl. 8; Text-figs 33, 38B) figured by Douvillé (1915*b*, text-fig. 1) is mounted on a cardboard with the following label:

'*Aumale*
Radiolites Nicaisei
Coquand
étage Rhotomagien'.
An additional row is not legible.

EXPLANATION OF PLATE 8

Figs 1–4. *Lapeirousella aumalensis* (Douvillé, 1915*b*); lectotype, EM 15634. 1, transverse section of posteroventral shell; × 7·5. 2, transverse section of ventral pseudopillar; × 17·6. 3, transverse section of posterior pseudopillar; × 17·6. 4, transverse section of dorsal shell; × 15.

PLATE 8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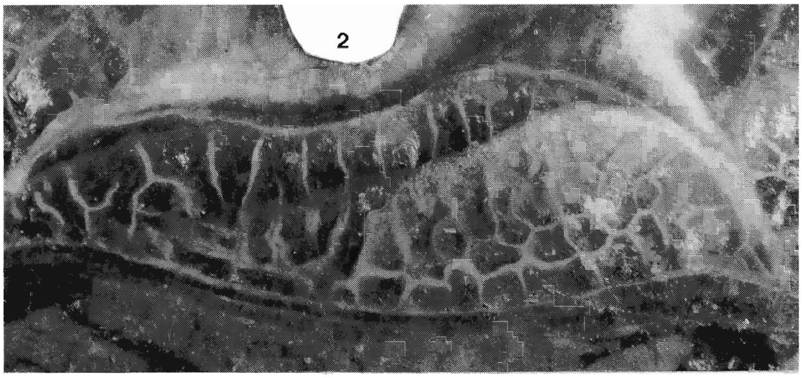
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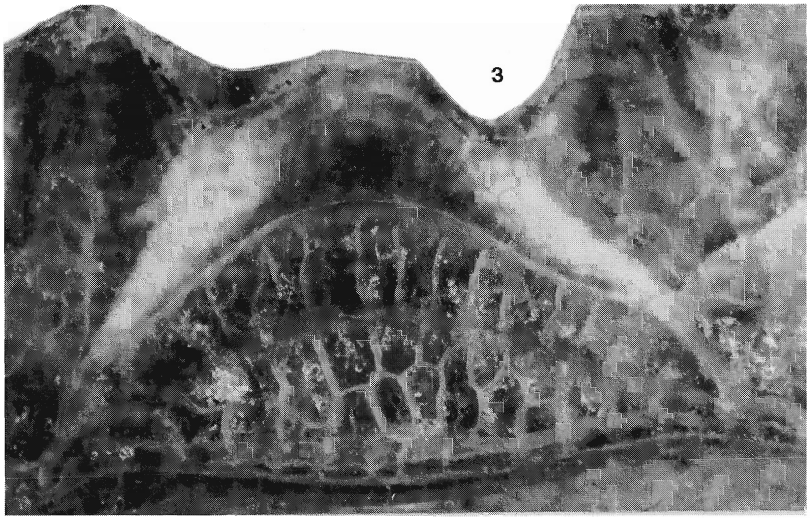
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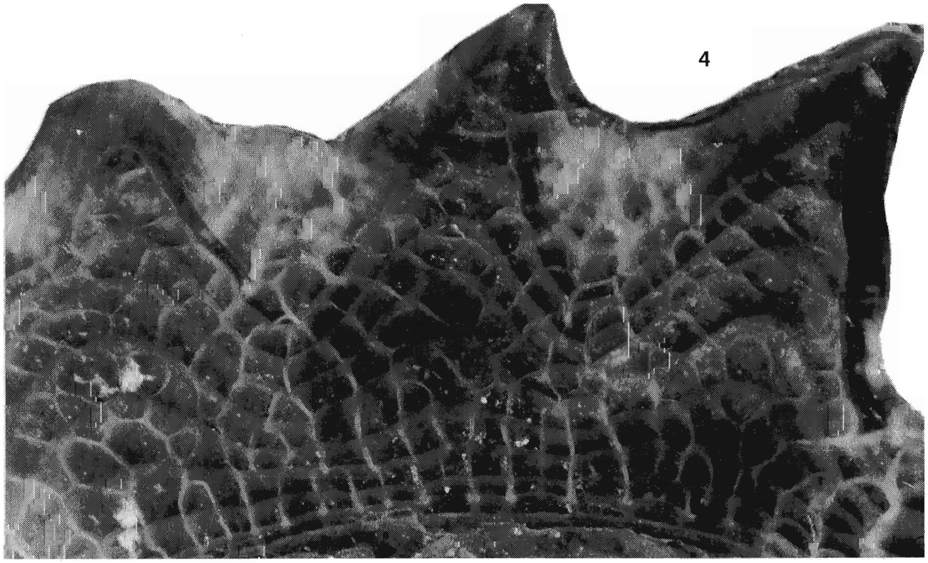
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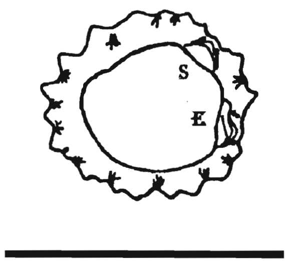
STEUBER, *Lapeirousella*



TEXT-FIG. 33. Reproduction of the single previously published figure of *Lapeirousella aumalensis* (Douvillé, 1915*b*), lectotype; EM 15634. Scale bar represents 30 mm.

It is a 33 mm high fragment of a RV with a commissural diameter of 22 mm that has been transversally sectioned and polished on the commissural and apical surfaces. The commissural section is the original of the single previously published figure of the species. This drawing was published with a reduction of 10 per cent. and is reproduced in Text-figure 33. The outer shell layer consists of rectangular cells along the inner margin and irregular polygonal cells further distally; its outer margin is formed by a compact cortex 0·5 to 0·8 mm thick. Inclination of funnel plates towards the shell's interior is steep in the furrows, and more shallow in the ribs that produce the ornament of the shell. Cells of Vs and Ps are sub-polygonal, and the pseudopillars are bordered by a compact layer that extends towards the exterior and produces a rounded rib that projects more or less distinctively from the base of a wide furrow. Ib has two ribs. The funnel plates are steeply inclined towards the interior of the shell in Vs and Ps. The inner margin of the outer shell layer slightly bulges into the interior of the shell in Vs and Ps. It is crushed dorsally so that no safe indications can be given about the presence of a ligamental ridge. The apical transverse section has a diameter of 14 mm and clearly shows the absence of a ligamental ridge. In this section, the outer shell layer is compact and the pseudopillars are marked by sickle-shaped, externally convex bands. As in the commissural section, the inner margin of the outer shell is slightly inflected towards the centre of the shell.

The paratype (EM 15635) is labelled as:

'Loc.Aumale
Etage. Cénomanien
D.p.M. Peron
L'échantillon de droite montre le début des Lapeirousia H. D.
Lap. Aumalensis 9.19.14'

The fragment is 11 mm long and 25 mm wide and conjoined to a slightly larger fragment of *Durania cornupastoris* (des Moulins, 1826). The shell is crushed but well preserved posteroventrally; ribbing and shell structure correspond to those of the lectotype, with the exception of more regular, hexa- and pentagonal cells of the outer shell layer.

The type locality of *Lapeirousella aumalensis* is only indicated as 'Aumale' on both labels. As the specimens were collected by A. Peron, a pioneer of North African Cretaceous stratigraphy, this denotes most probably Aumale (Hodna Mountains) in Algeria.

Description of Boeotian specimens. RV elongated-conical, commissural diameter up to 59 mm, with acute, irregularly salient and unevenly spaced longitudinal ribs that are up to 12 mm wide, and are rarely interrupted by inconspicuous terraces that form widely spaced lamellae. Vb and Pb are formed by rounded, more or less protruding ribs; Ib has three acute ribs that are less salient than those of the remaining shell, or two ribs that are indistinguishable from other ribs. Vs and Ps bulge slightly into the body-cavity or simply form two straight segments along the inner margin of the shell.

Funnel plates are shallowly inclined towards the interior of the shell and are downfolded in the longitudinal ribs. The outer shell layer is predominantly cellular, but commonly compact in Vs and Ps. Cells along the inner margin are rectangular or sub-polygonal, but farther distally they are predominantly hexagonal, while others are penta- to heptagonal; average width of cells is 15 mm and they do not exceed 0·9 mm high. The transition to a compact structure occurs by widening of the bases of the muri. Vs and Ps are round or oval depressions of the funnel plates, that are

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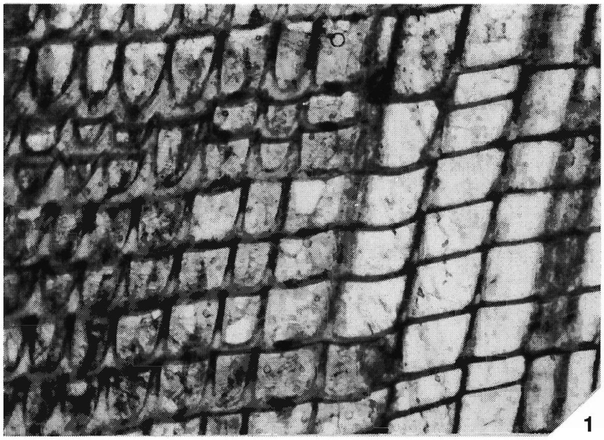
EXPLANATION OF PLATE 9

Figs 1–4. *Lapeirousella aumalensis* (Douvillé, 1915*b*); shell structures; R178, Marmeko. 1, dorsal tangential section; × 12. 2, transverse section, anterodorsal; × 8·3. 3, dorsal radial section; × 12. 4, detail of fig. 3; × 37·5.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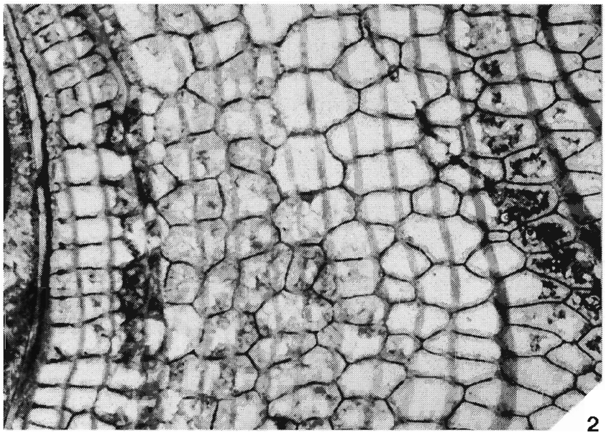
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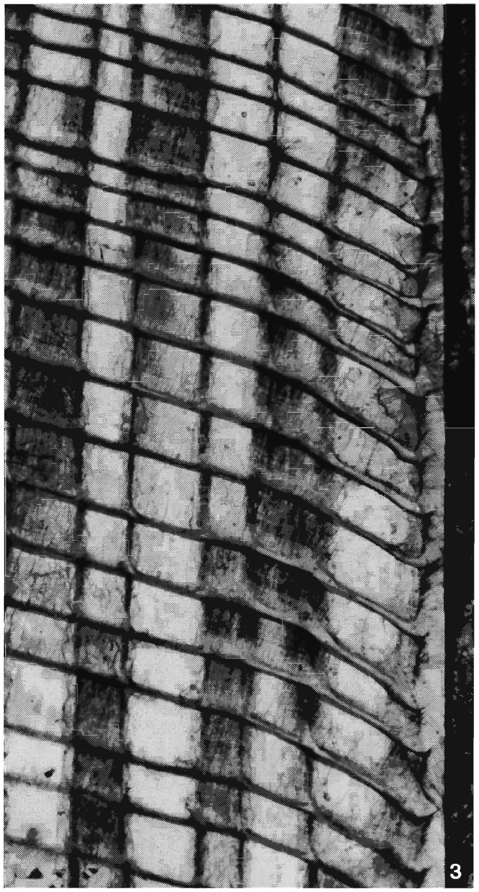
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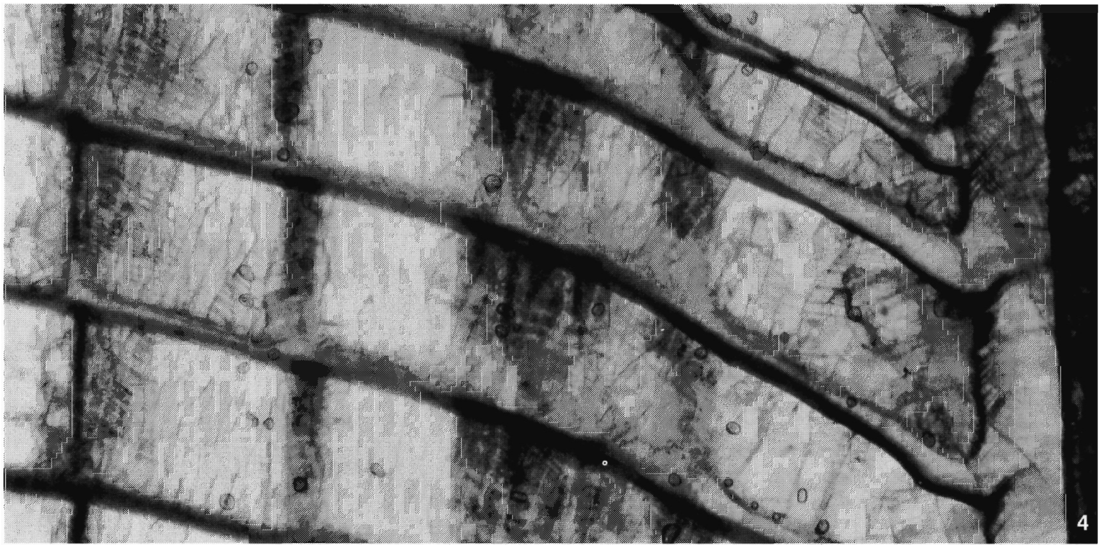
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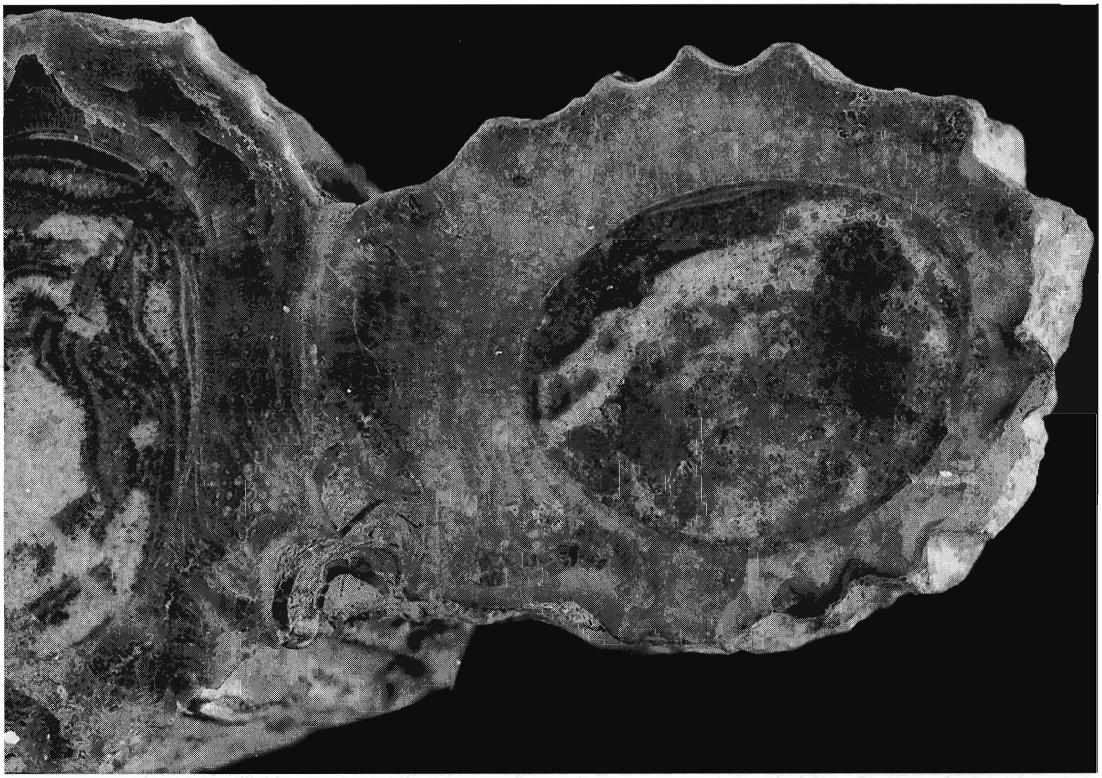
STEUBER, *Lapeirousella*



TEXT-FIG. 34. *Lapeirousella aumalensis* (Douvillé, 1915*b*); R178; Marmeko; × 2. Transverse section of two RVs, adapical view.

bordered distally and laterally by steeply inclined, crowded funnel plates that appear as compact, dark layers in transverse section. Externally, these layers form the rounded longitudinal ribs of Vb and Pb.

The LV is flatly convex, radially ribbed so that ribs of the LV pass at the commissure into furrows of the conjoined RV. The RV furrows in which Vb and Pb form elevated, rounded ribs correspond to suspiciously broad ribs of the LV which lack depressions that would correspond to the radial bands of the RV. Consequently, round openings with a diameter of 2 mm are formed at the commissure above Vb and Pb.

Myocardinal elements obviously short, as only mp and (3′) are visible in a transverse section that was cut 13 mm below the commissure of the bivalve specimen which has a commissural diameter of 59 mm. In this section, mp extends ventrally as far as Ps.

Remarks. The two type specimens are considerably smaller than the Boeotian specimens, but are very similar even in details of the ribbing pattern and shell structure. The stunted growth of the type specimens

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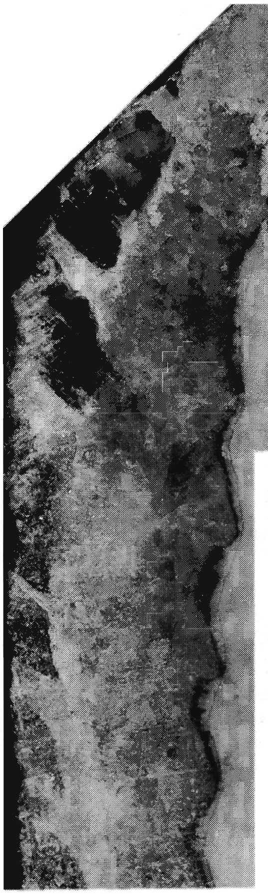
EXPLANATION OF PLATE 10

Figs 1–2, 4–5. *Petkovicia*? *verajana* Slišković, 1968*b*; shell structures; R570, Tsouka. 1, radial section of posterior pseudopillar of LV; × 7·5. 2, tangential section of ventral pseudopillar of RV; × 7·5. 4, slightly oblique transverse section of RV, crossing the commissure ventrally, adapical view of RV; × 1·25. 5, apical transverse section of same RV as on fig. 4, adapical view; × 1·25.

Fig. 3. *Praelapeirousia*? sp. nov.; R580, Marmeko; radial section of ventral pseudopillar, external side is to the right; × 8·3.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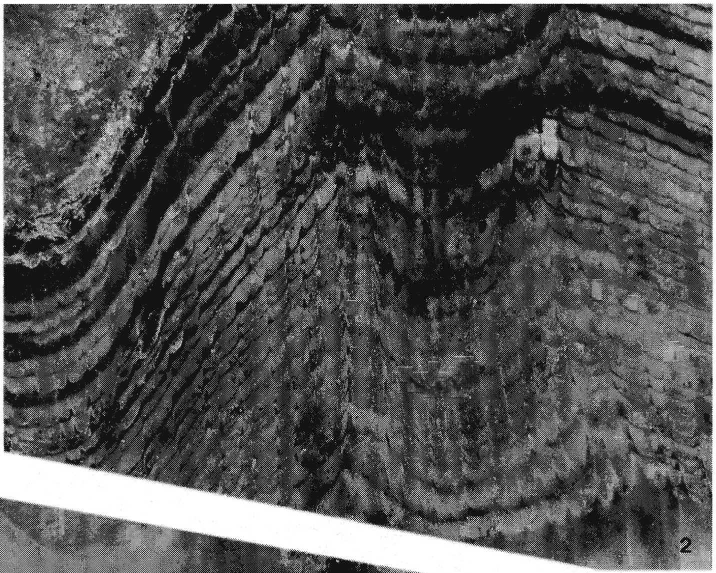
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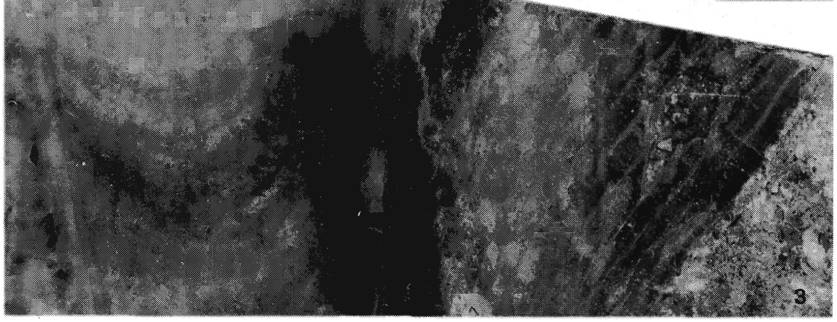
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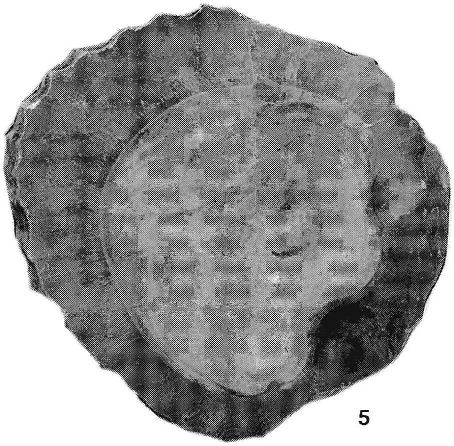
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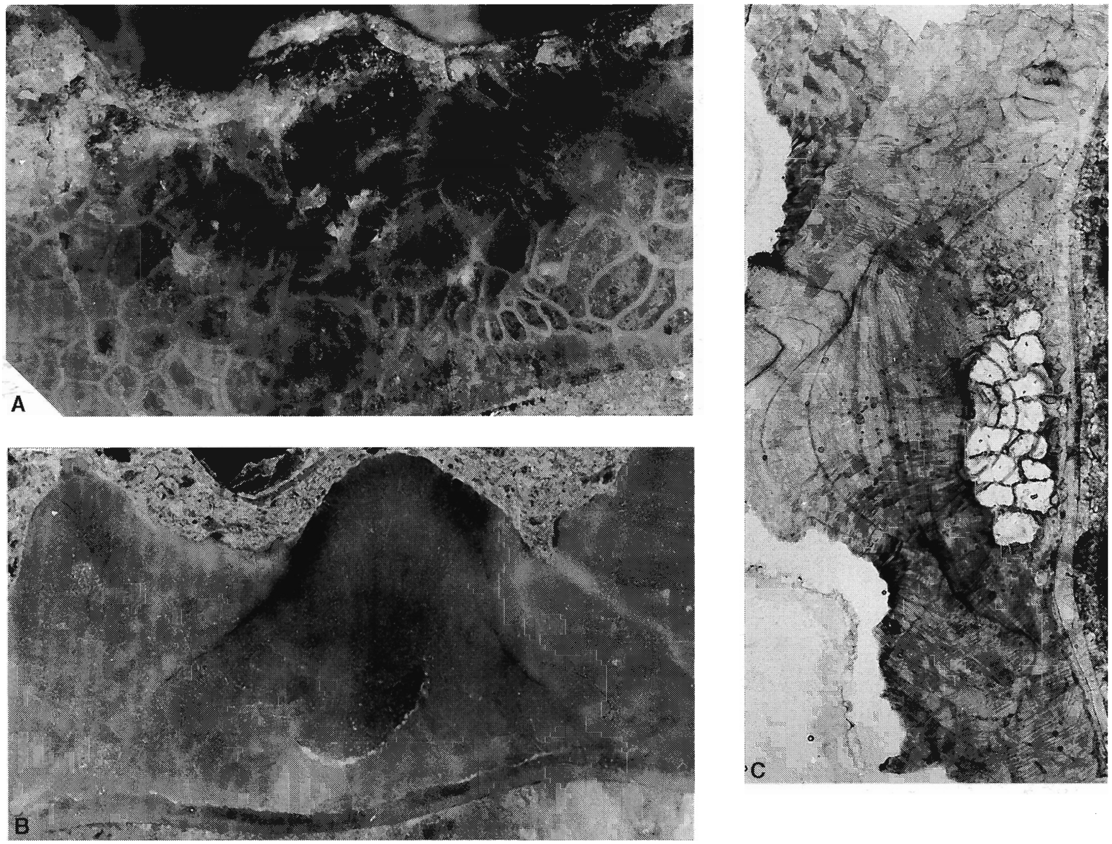
STEUBER, *Petkovicia*?, *Praelapeirousia*?



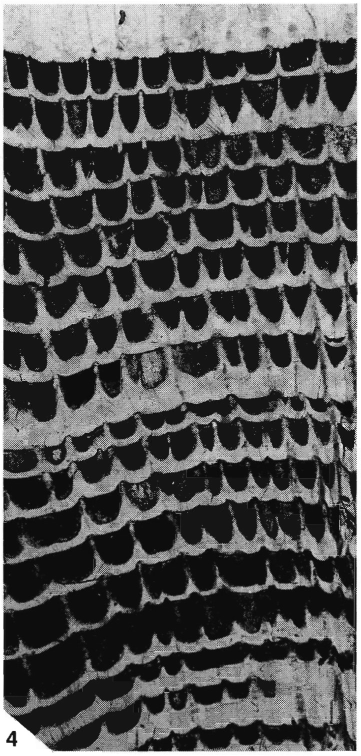
TEXT-FIG. 35. *Lapeirousella aumalensis* (Douvillé, 1915*b*); Marmeko. A, transverse section of posterior band; R753; × 12·5; B, transverse section of posterior band; R752; × 9·7; C, transverse section of ventral band, thin section micrograph; R178; × 7.5.

could be related to environmental factors, as the conjoined shell of *Durania cornupastoris* (des Moulins, 1826) are remarkably small as well. Much larger shells of the latter species are known from Portugal, France and Egypt.

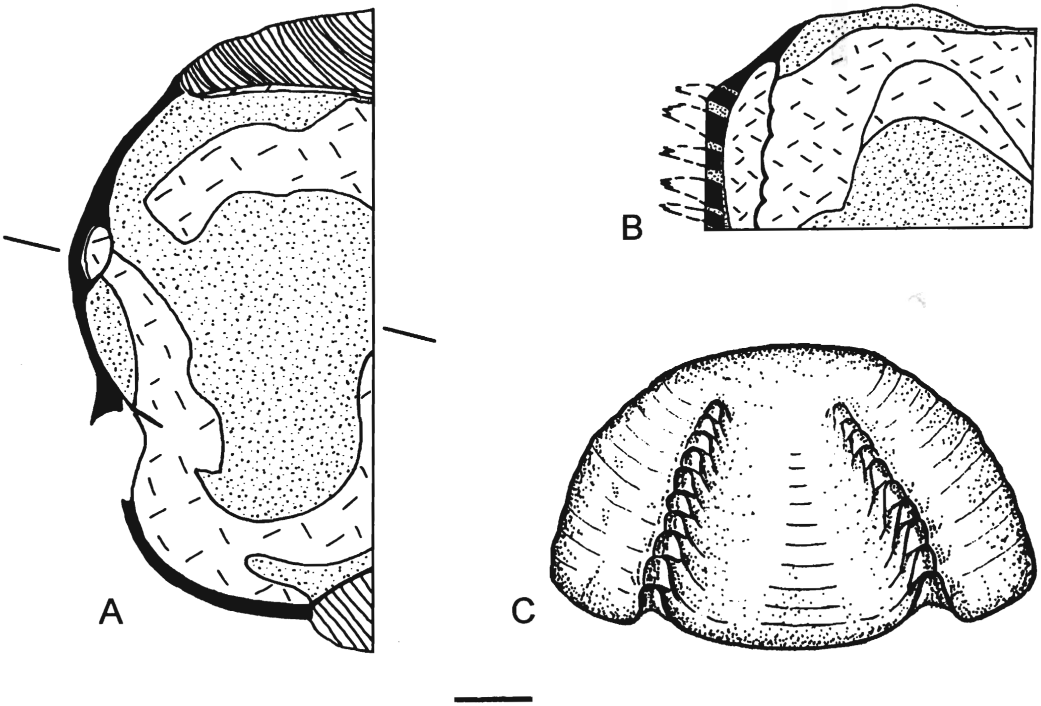
The structure of Vs and Ps corresponds to the definition of *Lapeirousella* Milovanović, 1938*b*. Consequently, there remain no arguments to consider the simple structure of the pseudopillars in *Lapeirousella* as a secondary reduction of the more complicated structures in *Lapeirousia*. They are better explained as primitive characters and it appears likely that *Lapeirousia* became separated as a sister group of *Lapeirousella*. During the course of the Late Cretaceous, the infoldings of the posteroventral mantle margin were accentuated; they finally bulged deeply towards the centre of the shell and became embraced by mantle flanges that converged exteriorly (see Text-fig. 8). The oscula in the LV of *Lapeirousia*, therefore, are dislocated apically while they form small commarginal openings in *Lapeirousella aumalensis*.

EXPLANATION OF PLATE 11

Figs 1–5. *Petkovicia*? *verajana* Slišković, 1968*b*; shell structures; R518a, Loutsion. 1, transverse section of anterodorsal shell. 2, transverse section of posteroventral shell. 3, transverse section of posterior pseudopillar. 4, tangential section. 5, transverse section of ventral pseudopillar. All × 7·3.



STEUBER, *Petkovicia*?



TEXT-FIG. 36. *Petkovicia*? *verajana* Slišković, 1968*b*; R570. A, oblique transverse section across commissure. Black, outer shell layer of LV; hatched, inner shell layers; dotted, internal sediments; lines in the outer shell layer of RV are obliquely cut funnel plates; × 1·5. B, radial section of posterior pseudopillar of LV; external parts of outer shell layer are not preserved. Ornament as in A; × 1·5. C, reconstruction of posteroventral flank of LV of *Petkovicia*? *verajana* Slišković, 1968*b* showing Vb (left) and Pb (right). Scale bar represents 10 mm.

Distribution. Middle to Upper Turonian (because of the association with *Durania cornupastoris*) of Aumale (?Algeria).

Genus MEDEELLA Parona, 1924

Type species. *Radiolites zignana* Pirona, 1869.

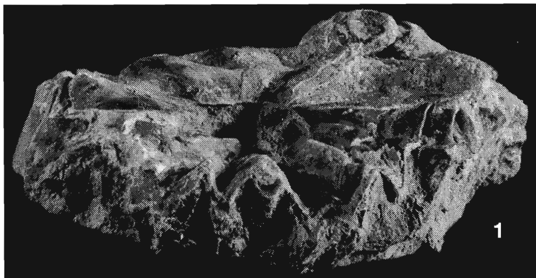
Medeella cf. *zignana* (Pirona, 1869)

cf.1869 *Radiolites Zignana* n. sp. Pirona, p. 419, pl. 22, figs 1–11.
1994 *Medeella* cf. *zignana* (Pirona); Steuber, p. 59 [with synonymy and description].
1995*b* *Medeella zignana* (Pirona); Caffau and Pleničar, p. 234, pl. 8, fig. 2.
1996a *Medeella zignana*; Laviano, p. 5.

Description. See Steuber (1994).

EXPLANATION OF PLATE 12

Fig. 1. *Lapeirousella aumalensis* (Douvillé, 1915*b*); R752, Marmeko; posteroventral aspect of bivalve specimen, small circular opening is seen between valves at ventral band in the centre of the figure; × 1.
Fig. 2. *Praeradiolites ponsianus* (d'Archiac, 1835); R137, Marmeko; posteroventral aspect; × 1.
Fig. 3. *Praelapeirousia*? sp. nov.; R579, Marmeko; posteroventral aspect; × 0·9.
Figs 4–5. *Praeradiolites* cf. *urnalis* Astre, 1954; R177, Marmeko. 4, posteroventral aspect; 7, anterodorsal aspect; × 1.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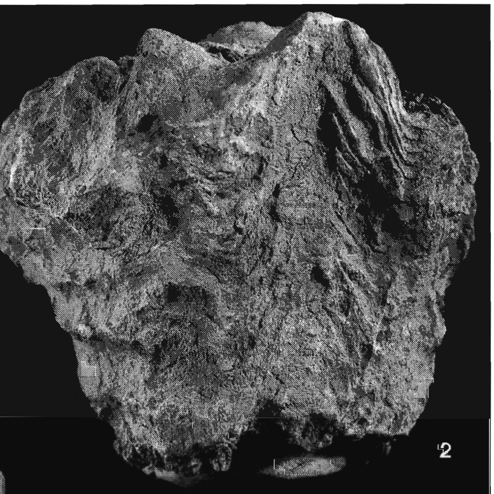
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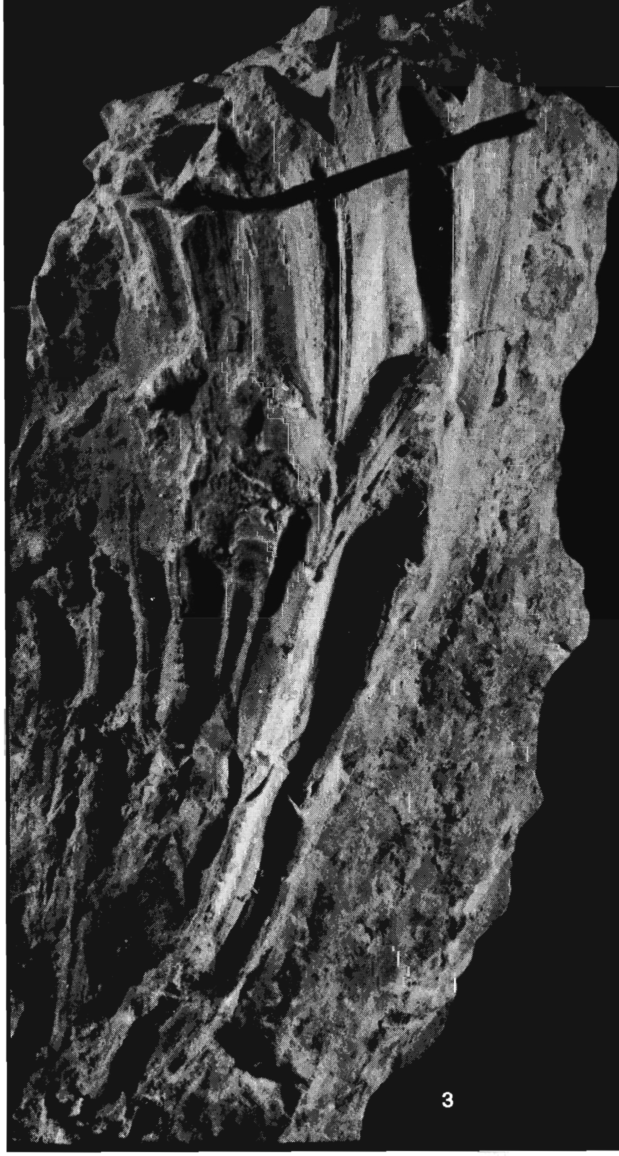
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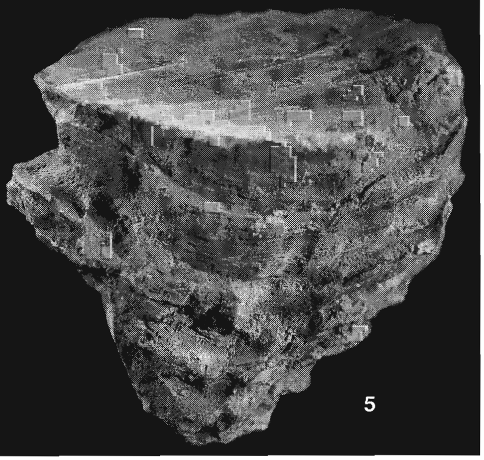
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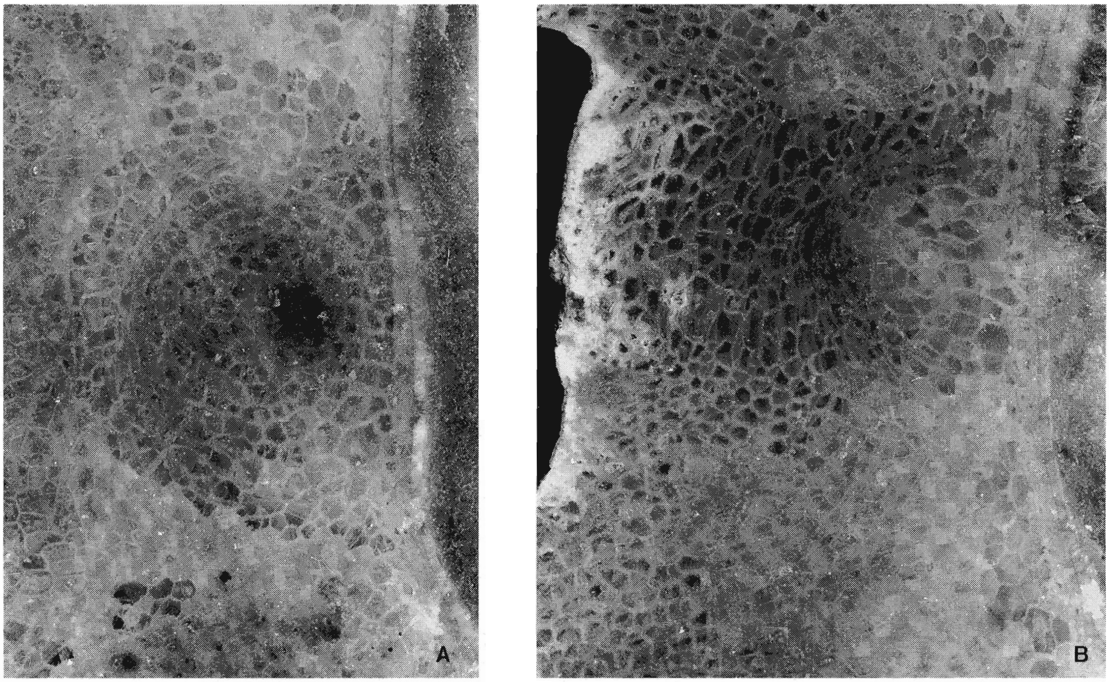
STEUBER, rudists



TEXT-FIG. 37. *Praelapeirousia*? sp. nov.; R579, Marmeko; × 7·5. Transverse sections of, A, ventral and, B, posterior pseudopillars.

Distribution. Santonian–Campanian of Italy and the Dinarids, Maastrichtian of Brač, Adriatic Sea (Gušić and Jelaska 1990). Klinghardt (1943) described *Medeella zignana* from Keratovouno Hill.

Genus PETKOVICIA Kühn and Pejović, 1959

Type species. *Petkovicia prima* Kühn and Pejović, 1959.

Petkovicia? *verajana* Slišković, 1968*b*

Plate 10, figures 1–2, 4–5; Plate 11, figures 1–5; Text-figure 36A–C

1968a *Petkovicia verajana* n. sp. Slišković, p. 44 [*nomen nudum*].
*1968*b* *Petkovicia verajana* n. sp. Slišković, p. 87, pl. 8, figs 1–3.
1969 *Petkovicia verajana* Slišković; Polšak and Mamužić, p. 240.

EXPLANATION OF PLATE 13

Figs 1–10. *Praeradiolites echennensis* Astre, 1954. 1–3, bivalve specimen in, 1, dorsal, 2, posteroventral and, 3, anteroventral aspect; R206, Kalamos. 4–10, specimens from Keratovouno Hill. 4, RV with almost rectangular bands; R101. 5, posteroventral aspect of RV with anteriorly projecting ventral and posterior bands and wide interband; R106. 6–8, bivalve specimen in, 6, ventral, 7, dorsal and, 8, anterior aspect; R257. 9, posterior band projecting posteriorly; R114. 10, RV with narrow, projecting bands; R33. All × 0·7.

PLATE 13

STEUBER, *Praeradiolites*

1971a *Petkovicia verajana* n. sp. Slišković, p. 45.
1971b *Petkovicia verajana* n. sp. Slišković, p. 93, pl. 8, figs 1–3 [cop. Slišković 1968*b*].
1973 *Petkovicia verajana* Slišković; Slišković, p. 18.
1975a *Petkovicia verajana* Slišković; Slišković, p. 45.
1981 *Petkovicia verajana* Slišković; Sánchez, p. 146.
1982 *Petkovicia verajana* Slišković; Polšak *et al.*, text-fig. 3.
1988 *Petkovicia verajana*; Pejović, p. 148.
1989 *Petkovicia verajana* Slišković; Accordi *et al.*, p. 167, tab. 1.
?1989*a* *Petkovicia verajana* Slišković; Cestari and Sirna, p. 135, tab. 1; pl. 4, figs 2–3.

Holotype. Slišković (1968*b*), plate 8, figure 1, 1a.

Material. Sixteen RVs from Loutsion (R516a, R518, R718–19, R723–724, R726, R728–729) and three specimens from the quarry at Tsouka Hill (R570, R634–635), one of them with both valves conjoined.

Description. RV elongated-conical, commissural diameter up to 47 mm, exceeding 140 mm long, with an ornament of evenly spaced, slightly salient, acute longitudinal ribs that are 3–4 mm broad. Vb and Pb rise more or less distinctively as rounded ribs from the bases of wide furrows; Ib has two ribs that are similar to those of the rest of the shell. Vs and Ps bulge considerably towards the shell's interior.

Structure of outer shell layer predominantly compact. A simple cellular structure is formed by thick, slightly inclined funnel plates that are crossed by radial muri which rarely branch distally. More intense branching of radial muri and the development of an irregular, *Durania*-type cellular pattern was noted only near the exterior margin of a thick-shelled specimen. Funnel plates are downfolded in the ribs. Radial muri are broad at their bases and taper towards the funnel plate above; they fit into radial grooves on the lower, apical surfaces of the funnel plates (Pl. 11, fig. 4). The transition from compact to cellular structure occurs by thickening of the basal parts of the radial muri which can be traced even in completely compact shells as dark-coloured structural elements, crossed by distinct growth bands. As in the holotype, the thickened radial muri are visible as vague radial striations in transverse section of compact-shelled morphotypes. (Pl. 11, figs 1–3, 5). Vs and Ps are round or oval, deep depressions of the funnel plates. In transverse sections, the depressed funnel plates of shell layers above are seen as circular or oval traces, and the radial muri appear as denticles (Pl. 11, figs 2–3, 5).

LV almost hemispherical, reaching 13 mm high in a specimen with a commissural diameter of 35 mm; its outer, compact shell layer is 1 mm thick. Above Vs and Ps of the RV, the outer shell layer of the LV is thickened and forms two cupolas that open at the commissure. Consequently, in transverse section close to the commissure, the outer shell layer branches to enclose an almond-shaped, 2 mm wide and 5·5 mm long cavity above Ps; it thins to 0·15 mm in the interior and to 0·75 mm in the exterior branch (Text-fig. 36A). Vs of LV crushed but apparently similar to Ps. Further apically, the outer shell layer of the LV is partly eroded, but tangential polishing of the posteroventral shell revealed narrow, apically convex embayments of growth lines above Ps and Vs of the RV. These embayments form stacked arches with openings between their culminations that are now filled with internal sediment. In radial section of Ps, the inner branch of the outer shell layer is corrugated; the stacked arches that are visible in tangential section are cut in a plane which runs through their culminations and shows the openings in-between (Pl. 10, fig. 1; Text-fig. 36B). The area between the branched outer shell layer is filled with dark-coloured calcite which is assumed to have formed by diagenetic alteration of an originally aragonitic, inner shell layer. A cavity would have been in contact with the openings between the stacked arches of the outer shell layer and would have been filled, like the openings themselves, with internal sediment. This structural modifications of the radial band in the LV indicate the existence of depressions on the mantle margins that mirror the bowl-shaped depressions on the growth surface, and thus the mantle margin of the RV. The remnants of formerly aragonitic inner shell layer which are found in the LV pseudopillars suggest that aragonite-precipitating portions of the mantle margin were involved in their formation. The pits in the LV opened to the outside and were protected by arches formed by the outer shell layer. These arches were reconstructed successively during growth, while the ontogenetically older openings were abandoned (Text-fig. 36C). Diagenetically altered shell layers within the depressions of the LV are perhaps remnants of a pallial myostracum.

(1) much stronger than (3), both are joined in a transverse section 8 mm below the commissure by a broad septum (Pl. 10, fig. 4). Rounded ridges on the external surfaces of (1) and (3) interlock with longitudinal furrows of (1′) and (3′). A prominent projection of the inner shell borders both (1′) and (3′) ventrally. Ma is irregularly thickened, it terminates far ventrally; mp extends ventrally as far as the site of Ps.

Systematic position. Description of species that have been included in *Petkovicia* Kühn and Pejović, 1959 are so insufficient concerning the structural composition of the outer shell and the pseudopillars that well-founded comparisons are difficult. The LV of the genus was unknown, except for the myocardinal elements of the type species. The genus comprises shells without ligamental ridge, compact shells and pseudopillars that bulge towards the shell's interior. The structure of the outer shell layer of the type species is probably of *Vaccinites*-type and lacks the radial muri that are typical of the Boeotian specimens. Such radial elements are apparently present in the holotype of *Petkovicia verajana*, but are also in that of *Katzeria hercegovinaensis* Slišković, 1966, although the shell structure of the latter has never been described in detail. The doubtful generic classification of *Petkovicia verajana* was also mentioned by Pejović (1988). Apparently, the structures of the pseudopillars within the discussed group is similar and related to bowl-shaped depressions of the funnel plates. This character developed convergently in different lineages of Radiolitidae so that detailed investigations of the shell structures and LVs are necessary to clarify their systematic positions and phylogenetic relations.

The explanation to the figure of *P. verajana* in Cestari and Sirna (1989*a*, pl. 4, fig. 2) is misleading, as it indicates a ligamental ridge that is not visible on the plate (field photograph).

Distribution. Maastrichtian of the external Dinarids (Herzegovina), ?Apennines.

Genus PRAELAPEIROUSIA Wiontzek, 1934

Type species. Praelapeirouseia kossmati Wiontzek, 1934.

Praelapeirousia? sp. nov.

Plate 10, figure 3; Plate 12, figure 3; Text-figure 37A–B

Material. Four specimens from Marmeko quarry, two of them with both valves conjoined (R579, R580).

Description. RV of the largest specimen is 185 mm long and has a dorso-ventral commissural diameter of 65 mm; the body chamber is 30 mm wide. It is sculptured with 16 acute or rounded, broad and irregularly spaced longitudinal ribs. The largest rib is 20 mm, the widest furrow 23 mm wide. Two projecting terraces interrupt the smooth ribs and furrows. Vb is formed by a salient rib that is externally truncated, Pb forms a shallow band at the base of a wide furrow, and Ib has one acute rib. The inner margin of the shell bulges slightly in Vs and forms a straight segment in Ps.

LV is radially ribbed, ribs of the LV interfinger with furrows of the RV at the commissure. Two prominent elevations are located above the RV pseudopillars. The margin of the LV is deeply inflected adapically above Vs so that it forms a 15 mm high and 9 mm wide commissural opening. Pb, which is located at the base of a furrow, projects over the commissure and fits into the LV without gaping.

The myocardinal elements are asymmetrically developed; ma reaches further ventrally than mp which terminates dorsally of Ps and projects obliquely from the LV to the inner margin of the RV. (1) and (3) probably had cavities that are now filled by diagenetic calcite which form contrasting, dark-coloured ledges that point obliquely towards the centre of the shell. A dorsal ridge bears remnants of a ligament; (2) was not recognized.

Funnel plates are downfolded in the longitudinal ribs and are more ore less steeply inclined; bowl-shaped depressions form Vs and Ps which are externally bordered by steeply raised funnel plates (Pl. 10, fig. 3). Mean diameter of irregular sub-polygonal, penta- or hexagonal cells is 0·55 mm; vertical spacing of funnel plates is less than 0·5 mm.

Systematic position. The systematic position of comparable taxa is confusing. The ornamentation and shell structure of the RV have been considered diagnostic (Polšak 1967*b*) whereas, in other cases, modifications of the radial bands of the LV were used to define new genera (Astre 1957*b*). It remained unconsidered that infoldings or other modifications of the posteroventral mantle margin must have had effects on the shell structures of both valves. Other genera were separated because of canals or pseudocanals in the LV. Among the valid genera with ligamental ridge and similar pseudopillars, the following taxa can be considered: *Praelapeirousia* Wiontzek, 1934, *Fossulites* Astre, 1954, *Medeella* Parona, 1924 and *Gorjanovicia* Polšak, 1967*b*.

The LV of *Praelapeirousia kossmati* Wiontzek, 1934 probably bears *Lapeirousia*-type oscula, whereas the LV of *Praelapeirousia macutensis* Slišković, 1984*a* resembles that of *Fossulites*. Nothing is known about the LV of *Medeella*; that of *Gorjanovicia* most probably has no distinct modifications (Polšak 1967*b*). It is obvious that the discussed genera are insufficiently distinguished (Steuber 1994). The Boeotian specimens are tentatively included in *Praelapeirousia* because of their prominent longitudinal ribs. Pejović (1984) discovered pseudocanals within the inner shell layer of the LV of *Praelapeirousia*, but gave no indications about Vs and Ps, so that the systematic position of the studied specimens remains obscure.

Genus PRAERADIOLITES Douvillé, 1902

Type species. *Radiolites fleuriausa* d'Orbigny, 1842*a*.

Praeradiolites echennensis Astre, 1954

Plate 13, figures 1–10; Plate 14, figures 3–5

v.1943 *Radiolites lusitanicus* (Bayle) Parona, var. *rigida* Choffat; Klinghardt, p. 122, pl. 7, figs 1–2.
*1954 *Praeradiolites echennensis* nov. sp. Astre, p. 63, pl. 6, figs 5–8; text-fig. 21a.
1954 *Praeradiolites echennensis* [nov.] var. *batidopsis* nov. var. Astre, p. 64, pl. 6, figs 9–10; text-fig. 21b.
1955a *Praeradiolites echennensis* Ast., et var. *batidopsis* Ast.; Astre, p. 11.
1957*b* *Praeradiolites echennensis*; Astre, text-fig. 4.
1962 *Praeradiolites echennensis* Astre var. *montsecanus* nov. Baudelot and Souquet, p. 501, pl. 1, figs 1–2; text-figs 1–3.
1968 *Pr. echennensis*; Astre, p. 213.
1977 *Praeradiolites echennensis* Astre; Pons, p. 67, pl. 44, figs 1–3; pl. 45, figs 1–3.
1980 *P. echennensis*; Bilotte, p. 57.
1981 *Praeradiolites echennensis* Astre; Sánchez, p. 149 [with synonymy].
1982 *Praeradiolites echennensis* Astre; Pons, tab. 3.
1983 *Praeradiolites echennensis*; Babinot *et al.*, tab. 4.
1983 *P. echennensis*; Philip and Bilotte, tab. 1.
1985 *Pr. echennensis*; Bilotte, tab. 42.
1993 *P. echennensis*; Vicens, p. 65.

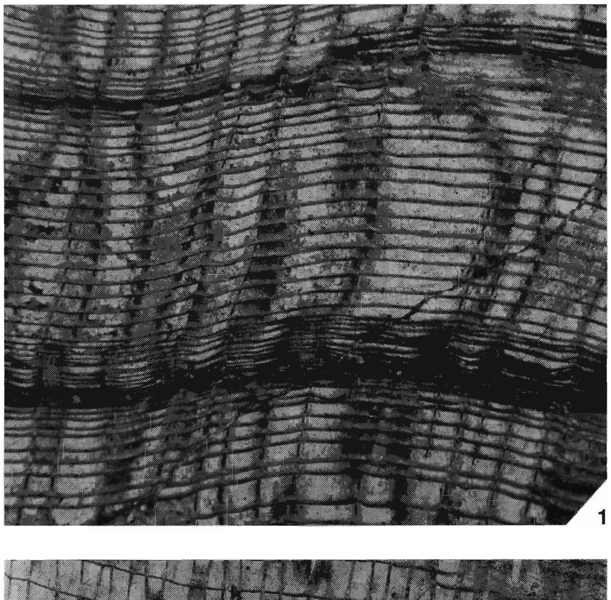
Holotype. Astre (1954), plate 6, figures 5–8.

Material. Twenty-two specimens from Keratovouno Hill (R28–R29, R33, R101–R116, R257, R545, R607), nine of them with both valves conjoined, and one bivalve specimen from Kalamos Hill (R206).

Description. RVs broadly conical, almost of equal width and height, commonly dorso-ventrally compressed (Table 4). Shell lamellae are saliently protruding and have a flaky appearance; dorsally they protrude horizontally, i.e. perpendicular to the growth axis. At the anterior and posterior shell, the lamellae are sharply inflected towards either the apex or commissure, or they protrude horizontally. Vb and Pb are formed by sub-rectangular upfoldings, each of them being bordered by a single downfold in which the lamellae are turned down. Downfoldings are almost generally wider than Vb and Pb.

EXPLANATION OF PLATE 14

Fig. 1. *Durania* cf. *montisferrati* Astre, 1954; R589, Marmeko; anterodorsal tangential section; × 6·1.
Fig. 2. *Sauvagesia meneghiniana* (Pirona, 1869); R361, Dionysos; anterodorsal tangential section; × 12.
Figs 3–5. *Praeradiolites echennensis* Astre, 1954; R607, Keratovouno Hill. 3, anterodorsal radial section; × 5·3. 4, transverse section, dorsal; × 12. 5, transverse section, dorsal; × 7·5.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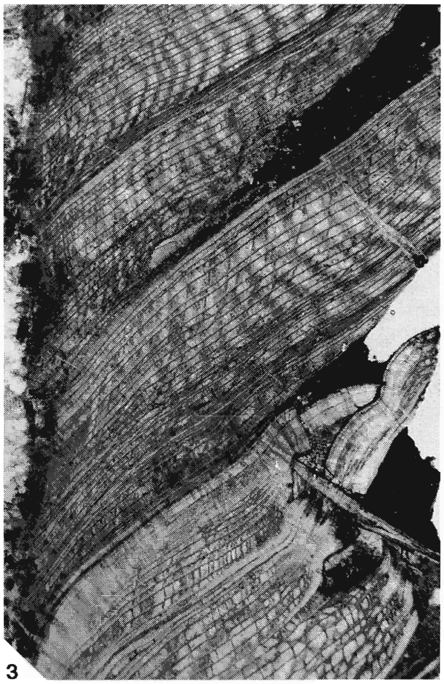
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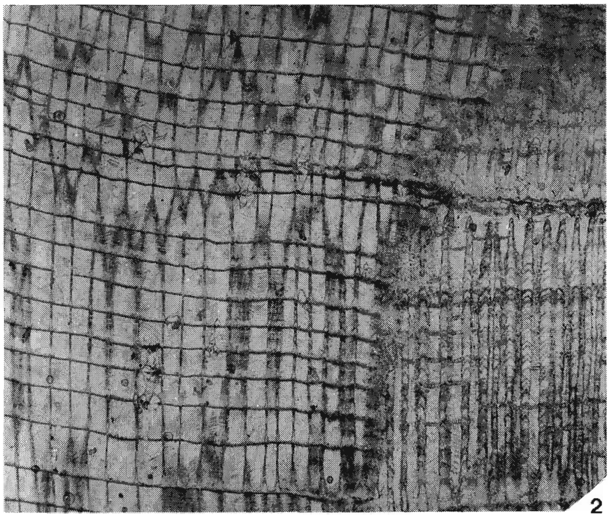
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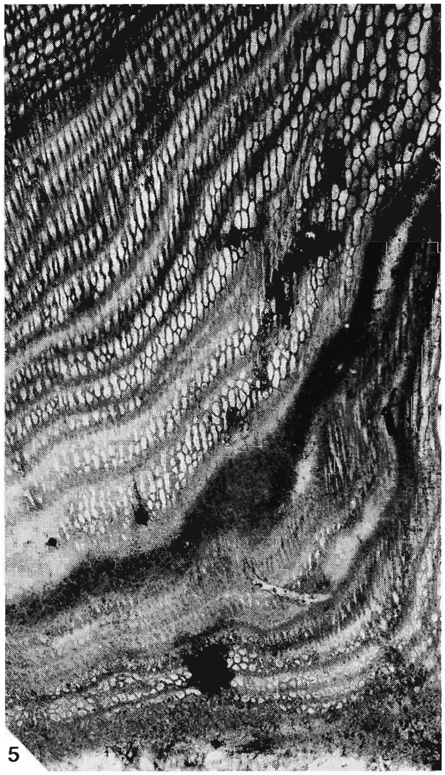
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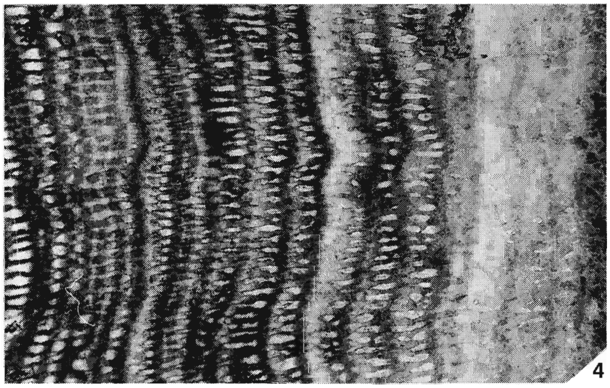
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TABLE 4. Heights and commissural diameters of RVs, and distances between ventral and posterior band (measured between culminations of shell-lamellae) of *Praeradiolites echennensis* Astre, 1954. Maximal widths are marked with an asterisk when measured dorso-ventrally; all others occur between the anterior and posterior shell margin. The distance between ventral and posterior bands was measured at the commissure. All measurements are in mm.

No.	Height	Width min.	Width max.	Distance Vb-Pb
R33	71	51	59	18
R33a	>53	60	60	20
R101	>39	48	56	27
R104	>87	60	88	23
R105	>47	58	59	23
R106	61	61	75	30
R107	>56	54	87	19
R108	48	47	*60	27
R109	67	52	78	31
R111	>74	68	82	28
R112	74	55	*79	–
R113	70	–	–	30
R114	58	48	*60	31
R206	101	58	79	38
R545	>81	65	69	21
R607	97	67	88	24

LV flatly conical, without canals or pseudocanals. The dorsal surfaces of (1) and (3) are grooved. Ma and mp are thickened, ma′ is bordered ventrally by a projection of the inner shell. The ventral tip of mp reaches as far as to the centre of Pb. Projections of the inner shell border (1′) and (3′) ventrally.

Funnel plates are inflected in correspondence with undulations of the shell lamellae. Their vertical spacing is rather variable but does not exceed 0·45 mm. Muri are irregularly thickened, so that cells are narrower than muri in certain areas. Radial muri dominate in transverse sections so that the cellular pattern resembles that of *Eoradiolites*. Tangential muri are rare and irregularly distributed, they diverge towards the exterior and delineate the tangential extension of the lamellae. Sub-polygonal cells are developed irregularly and only in small areas of the shell.

Variability and *systematic position*. The morphology and width of the posteroventral bands are to a certain extent variable: In laterally compressed RVs, Vb and Pb can be closely spaced and their radial axes parallel each other (Pl. 13, fig. 10). In other RVs, the radial axes of Vb and Pb diverge and may include angles of up to 50°; Ib is much wider than Vb or Pb in such shells (Pl. 13, figs 5, 9) which resemble *P. caderensis* Toucas, 1907 but differ in having a less depressed overall appearance. The shell lamellae of several RVs are only slightly turned down in Ib and posterior to Pb (Pl. 13, fig. 4), whilst the posterior fold is considerably accentuated in a specimen from Kalamos Hill so that Pb is partially concealed (Pl. 13, fig. 2). Within this variability, there are several specimens that are almost identical to the holotype (Pl. 13, figs 6–8); other RVs with inclined lamellae at the posterior and anterior shell correspond to the variety *montsecanus* (Baudelot and Souquet 1962).

Vicens (1993) discussed the probable synonymy of *Praeradiolites echennensis*, *P. aristidis* Toucas, 1907 and *P. subtoucasi* Toucas, 1907. The Boeotian specimens, despite their described morphological variation, can be distinguished from the other two species by the following characters: lamellae of the dorsal shell protrude widely and almost horizontally; sub-rectangular, externally protruding Vb and Pb that are raised as high as the apex of the LV; wide folds of the shell lamellae anterior and posterior of the radial bands.

Remarks. P. echennensis is abundant at Keratovouno Hill. It has been listed frequently under other names from this locality but was never described in detail. Munier-Chalmas (*in* Gaudry 1867) mentioned a variety of '*Sphaerulites Desmoulinsi*, Bayle', and Bittner (1880) gave a short description of a '*Sphaerulites Desmoulinsi* Bayl.' This species is identical with *Praeradiolites plicatus* (Lajard, Negrel and Toulouzan) [Toucas 1907] and differs from *P. echennensis* by the less prominent, rounded plications of the radial bands, narrower folds and slightly protruding shell lamellae. Klinghardt (1943) described the shells from Keratovouno Hill erroneously as *R. lusitanicus* var. *rigida* Choffat.

Radiolites hellenicus Munier-Chalmas, 1867 [*nomen dubium*] from Keratovouno Hill is most probably identical with *Biradiolites hellenicus* Munier-Chalmas, 1888 [*nomen nudum*]. According to Toucas (1909, p. 126) the latter is an indeterminable fragment. The fragments of *Radiolites hellenicus* Munier-Chalmas, 1867 and *Biradiolites hellenicus* Munier-Chalmas, 1888 (Toucas 1909), each described with a single sentence, probably belong to *Gorjanovicia* Polšak, 1967*b*, which is abundant at the locality. The original material could not be traced in the collection of the Ecole des Mines, but there exists an undetermined specimen, labelled 'Grèce, probablement de Caprena' that corresponds to *Praeradiolites echennensis*, Astre 1954.

Distribution. Upper Santonian–Maastrichtian of the Pyrenees (Pons 1977; Philip and Bilotte 1983; Bilotte 1985).

Praeradiolites ponsianus (d'Archiac, 1835)

Plate 12, figure 2

*1835 *Sphaerulites Ponsiana* d'Archiac, p. 182, pl. 11, fig. 6a–g.
*1842*b *Radiolites ponsiana* (*Sphaerulites ponsiana* d'Archiac); d'Orbigny, p. 155.
1857 *Sphaerulites ponsianus* d'Archiac; Bayle, p. 693.
1904b *Praeradiolites ponsianus*; Douvillé, p. 542.
v.1904*c* *Praeradiolites ponsianus*, d'Archiac; Douvillé, p. 244, pl. 33, figs 1–2, 4.
v1907 *Praeradiolites* cf. *ponsi*; Toucas, p. 31, pl. 3, fig. 5.
1908b *Pr. ponsianus*; Douvillé, p. 309.
v1910 *Praeradiolites ponsianus* d'Archiac, var. *egyptiaca*; Douvillé, p. 48, pl. 3, figs 6a–b, 7.
v1913*a* *Praeradiolites ponsianus* d'Archiac, race *aegyptiaca*; Douvillé, p. 248, pl. 15, figs 1a–b, 2 [cop. Douvillé 1910].
?1928*a* *Praeradiolites Ponsi* d'Archiac; Klinghardt, pl. 21, fig. 16.
1932 *Praeradiolites ponsianus* (d'Archiac) Douvillé; Kühn, p. 130 [with synonymy].
1932 *Praeradiolites ponsianus* var. *aegyptiaca* Douvillé; Kühn, p. 130 [with synonymy].
1954 *Praeradiolites ponsianus* d'Archiac var. *bouiretensis* nov. var. Astre, p. 25, pl. 2, figs 4–5; text-fig. 6a–c.
1955a *Praeradiolites ponsianus* d'Arch. et var. *bouiretensis* Astre; Astre, p. 10.
1957a *Praeradiolites ponsianus* d'Arch.; Astre, p. 191.
1957a *Praeradiolites ponsianus* d'Arch. var. *bouiretensis* Ast.; Astre, p. 191.
1964 *Praeradiolites ponsianus* (d'Archiac); Polšak, p. 67.
1965b *Praeradiolites ponsianus* (d'Archiac); Polšak, p. 444.
1969 *Praeradiolites ponsianus* (d'Archiac); Polšak and Mamužić, p. 238.
1978 *Praeradiolites ponsi* d'Archiac; Amico, p. 28, pl. 2, figs 1–4.
1981 *Praeradiolites ponsianus* (d'Archiac); Sánchez, p. 154 [with synonymy].
1981 *Praeradiolites ponsianus egyptiaca* Douv.; Sánchez, p. 155 [with synonymy].
1982b *Praeradiolites ponsianus*; Bilotte, tab. 2.
1982 *Praeradiolites ponsi* (D'Arch.); Philip, *in* Platel, p. 93.
1982 *Praeradiolites ponsianus* (d'Archiac); Polšak *et al.*, text-fig. 3.
1985 *Praeradiolites ponsianus*; Bilotte, tab. 17.
1987 *Praeradiolites ponsianus aegyptiacus* Douvillé; Kora and Hamama, p. 296.
1995 *Praeradiolites ponsianus aegyptiacus* Douvillé; Kora and Genedi, p. 226.

Syntypes. d'Archiac (1835), plate 11, figure 6a–g.

Material. RV with apex missing, from Marmeko quarry (R137).

Description. The fragmentary RV is sub-cylindrical-conical, 56 mm high; its apical diameter is 44 mm, the commissural diameter is 65 mm. Shell lamellae are steeply inclined towards the shell's interior but turned down in the downfolds that border Vb and Pb. Pb is slightly wider and is formed by a higher fold than Vb; Ib is a wide downplication. Anterior and posterior of the radial bands the shell lamellae are folded with five wide plications, respectively, with successively decreasing amplitudes. These folds are stronger along the posterior shell when compared with those of the anteroventral shell. Lamellae of the anterodorsal quarter of the shells remained unfolded.

Remarks. Specimens in which the shell lamellae are folded posterior to the Pb – as noted in the Boeotian RV – have been defined as *Praeradiolites ponsianus* var. *egyptiaca* by Douvillé (1910).

Distribution. Turonian of the Pyrenees, of southern France, Italy, Hungary, Algeria, Tunisia, Egypt, Iran (Sánchez 1981) and probably of Turkey (Nöth 1931*a*); Upper Turonian of the external Dinarids (Polšak *et al.* 1982); Middle to Upper Turonian of the Pyrenees (Bilotte 1985).

Praeradiolites cf. *urnalis* Astre, 1954

Plate 12, figures 4–5

*1954	*Praeradiolites urnalis* nov. sp. Astre, p. 29, pl. 4, fig. 1; text-fig. 8a–b.
1955a	*P. urnalis* Ast.; Astre, p. 11.
1957a	*Pr. urnalis* Ast.; Astre, p. 191.
1981	*Praeradiolites urnalis* Astre; Sánchez, p. 158.
1982b	*P. urnalis*; Bilotte, tab. 2.

?Syntypes. Astre (1954), plate 4, figure 1; text-figure 8a–b. Astre (1954) gave no indication about the number of specimens examined. The drawings and photographs probably show the same, single shell.

Material. One RV from Marmeko quarry (R177).

Description. The conical RV is more than 55 mm long, its dorso-ventral commissural diameter is 60 mm. Shell lamellae smooth, dorsally turned down in the lower part of the shell, protruding horizontally or steeply inclined near the commissure. Vb wider than Pb, with weakly folded lamellae that are slightly depressed in the centre. Pb is a high, wide upfold of lamellae that ascends towards the commissure posterior to Vb so that Ib is located on the ventral flank of Pb. Lamellae are slightly undulating anterior to Vb and posterior to Pb, and are smooth along the anterodorsal half of the RV.

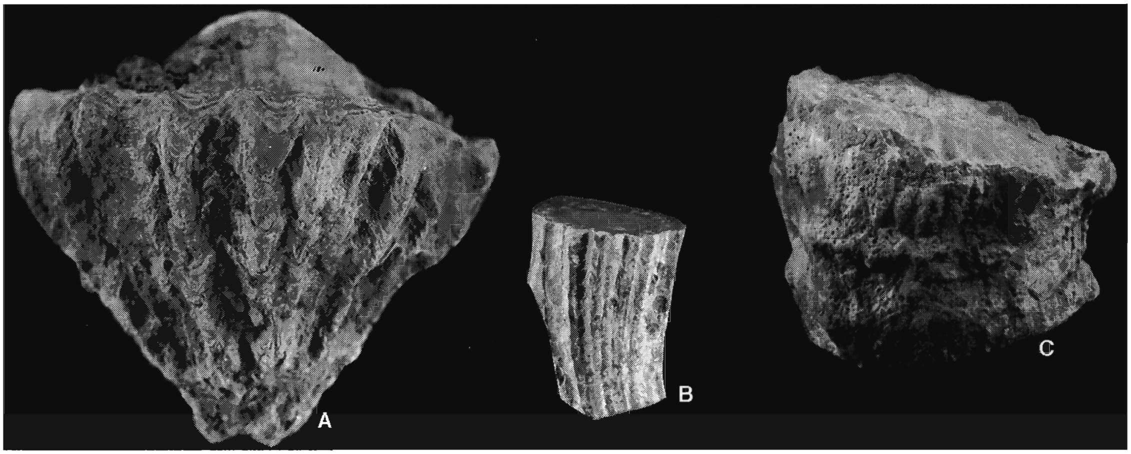
Ligamental ridge is strongly developed, extends 5 mm from the inner margin into the shell, thins to 0·6 mm and then again widens to 3 mm at the inner termination. (1) and (3) are coarsely grooved dorsally, the other myocardinal elements are not preserved.

Remarks. In contrast with *P. ponsianus* (d'Archiac, 1835), the shell lamellae of *P. urnalis* are not turned down in the downfolds. The Boeotian specimen slightly differs from the Pyrenean *P. urnalis* by a less pronounced plication of Ib and, therefore, resembles *P. ponsianus* var. *bouiretensis* Astre, 1954.

Distribution. Upper Turonian of the Pyrenees.

Genus RADIOLITES Lamarck, 1801

Type species. Ostracites angeiodes Lapeirouse, 1781.



TEXT-FIG. 38. A, *Radiolites angeiodes* (Lapeirouse, 1781); R707, Paleokastron; × 1; posteroventral aspect. B, *Lapeirousella aumalensis* (Douvillé, 1915*b*); lectotype, EM 15634; × 1; posteroventral aspect. C, *Sauvagesia tenuicostata* Polšak, 1967*b*; R241, Dionysos; × 0·8; dorsal aspect.

Radiolites angeiodes (Lapeirouse, 1781)

Plate 19, figures 1–2; Text-figure 38A

*1781 *Ostracites angeiodes* Lapeirouse, p. 40, pls 12–13.
v.1908 *Radiolites angeiodes* Picot de Lapeirouse; Toucas, p. 77, pl. 15, figs 11, 13.
1932 *Radiolites angeiodes* (Lapeirouse) Lamarck; Kühn, p. 135 [with synonymy].
1932 *Radiolites angeiodes* Picot de Lapeirouse; Milovanović, p. 43, pl. 1, figs 1–3.
1933 *Radiolites angeiodes* (Lapeirouse) Lamarck; Milovanović, pp. 83, 154, text-figs 15, 19–23.
1935 *Radiolites angeiodes* Picot de Lapeirouse; Klinghardt, p. 25, pl. 2, fig. 1.
1935 *Radiolites angeiodes* (Pic. de Lap.); Parona, p. 131.
1937 *Radiolites angeiodes* (Lapeirouse); Milovanović, p. 128.
1937 *Radiolites angeiodes* Lam.; Zapfe, p. 76.
1939 *Radiolites angeiodes* (Lapeirouse) Lamarck; Klinghardt, p. 133, pl. 2, fig. 12.
?1944 *Radiolites angeiodes* (Lapeirouse) Lamarck; Klinghardt, p. 202, pl. 5, figs 1–4.
1947 *Radiolites angeiodes*; Kühn, p. 187.
1950 *Radiolites angeiodes* Picot de Lapeirouse; Rengarten, p. 64, pl. 11, fig. 4.
1951a *Radiolites angeiodes* (Lapeirouse) Lamarck; Milovanović, p. 18.
1955a *R. angeiodes* Lap.; Astre, p. 11.
1956 *Radiolites angeiodes* Matheron; Brunn, p. 136
1957a *Radiolites angeiodes* Lap.; Astre, p. 193.
1959 *Radiolites angeiodes* Lap.; Kühn and Pejović, p. 981.
1959 *Radiolites angeiodes* (Lapeirouse); Petković *et al.*, p. 286.
1959 *Radiolites angeiodes* Pic. de Lap.; Rengarten, p. 257.
1961 *Radiolites angeiodes* Picot de Lapeirouse; Bobkova, text-fig. 6.
1962 *Radiolites* cf. *angeiodes* Lapeirouse; Kaumanns, p. 310.
1963 *Radiolites angeiodes* Pic de Lap.; Ambrosetti, p. 213.
1965 *Radiolites angeiodes* Picot de Lapeirouse; Benkö-Czabalay, p. 402.
1965 *Radiolites angeiodes* (Lapeirouse); Pamouktchiev, p. 31, pl. 3, fig. 2.
1966 *Radiolites angeiodes* (Lapeirouse); Pamouktchiev, p. 28, pl. 2, fig. 2; pl. 4, fig. 1.
1967 *Radiolites angeiodes* Lapeirouse; Lupu and Lupu, p. 308.
1968 *Radiolites angeiodes* Lapp.-Lam.; Bogdanović, p. 76.
1969 *Radiolites angeiodes* (Lapeirouse); Polšak and Mamužić, p. 239.
1970 *Radiolites angeiodes* Picot de Lapeirouse; Benkö-Czabalay, p. 283.
1972*b* *Radiolites angeiodes* (Lapeirouse); Campobasso, p. 447, pl. 8, fig. 2.

v?1973 *Radiolites angeiodes* (Lapeirouse); Sakellariou-Mané, p. 397, pls 1–2.
1974 *Radiolites angeiodes* (Lapeirouse); Lupu, p. 53, pl. 2, fig. 7.
1974 *Radiolites angeiodes* (Lapeirouse); Slišković, p. 133.
1976 *Radiolites angeiodes* (Picot de Lapeyrouse); Andrusov, p. 15.
1978 *Radiolites angeiodes* Picot de Lapeirouse; Amico, p. 58, pl. 14, figs 4–6.
1978 *Radiolites angeiodes* (Lapeirouse); Pamouktchiev, tab. 1.
?1979*a* cf. *Radiolites angeoides* [*sic*] (De Lapeirouse); Skelton, p. 91, text-figs 2–4.
1980 *Radiolites angeoides*; Bilotte, p. 57.
1981 *Radiolites angeiodes* P. de Lap.; Bilotte, text-fig. 2.
1981*b* *Radiolites angeiodes* (Lapeirouse); Pamouktchiev, p. 185, pl. 92, fig. 3.
1981 *Radiolites angeiodes* (Lapeirouse); Sánchez, p. 168 [with synonymy].
1982 *Radiolites angeiodes* (Lapeirouse); Pons, tab. 2.
1983 *Radiolites angeiodes* P. de Lap.; Czabalay, p. 187.
1983 *R. angeiodes*; Philip and Bilotte, tab. 2.
non 1984 *Radiolites angeiodes* (Lapeirouse); Pejović, p. 95, pl. 1, figs 1–2; pl. 2, figs 1–5; pl. 3, figs 1, 4; pl. 4, fig. 1; pl. 5, figs 1–3.
1985 *R. angeiodes*; Bilotte, tab. 31, 42.
1985 *Radiolites angeiodes* (Lapeirouse); Höfling, p. 31, pl. 6, fig. 6.
1985 *R. angeiodes* Lap.; Lupu, p. 21.
1987 *Radiolites angeiodes* (Lapeirouse); Pejović and Radoičić, p. 130, tab. 1.
?1989 *Radiolites angeiodes* (Lapeirouse); Accordi *et al.*, p. 167, tab. 1., pl. 4, fig. 3.
?1989*a* *Radiolites angeiodes* (de Lapeirouse); Cestari and Sirna, p. 135, tab. 1, pl. 7, fig. 4.
1989*b* *Radiolites angeiodes* (De Lapeirouse); Cestari and Sirna, p. 20, tab. 1, pl. 7, fig. 1.
1989 *Radiolites angeoides* [*sic*] (P. de Lap.); Pascual *et al.*, p. 224, text-fig. 3.
1990 *Radiolites angeiodes*; Gušić and Jelaska, text-fig. 15.
1990 *Radiolites angeiodes*; Leiss, p. 61.
1991 *Radiolites angeoides* [*sic*]; Caffau and Pleničar, p. 209.
1992 *Radiolites angeiodes*; Caffau *et al.*, p. 164, pl. 1, fig. 8.
1992 *Radiolites angeiodes* (Lapeirouse); Swinburne *et al.*, text-fig. 2.
1993 *Radiolites angeiodes* (Lapeirouse) Lamarck; Pleničar, p. 50, pl. 1, figs 1–5; pl. 2, figs 1–3.
1996a *Radiolites angeioides* [*sic*]; Laviano, p. 7.
1997 *Radiolites angeiodes* (Lapeirouse); Steuber *et al.*, p. 179, pl. 1, fig. 15.

Material. Eight specimens from Paleokastron Hill (R650, R653, R707, R709).

Description. RV conical, more than 60 mm long, commissural diameter up to 70 mm. Shell lamellae are regularly and acutely plicated. Lamellae hardly protrude so that the regular plications form almost uninterrupted, salient longitudinal ribs which reach a width of 5–7 mm at the commissure of a large RV. Vb is depressed between two ribs and is 10 mm wide in a shell which is 40 mm long and 64 mm in diameter. Ib is twice as wide as Vb and ornamented with three longitudinal ribs. Pb rises as a rib, which is slightly less salient than others, from a 10 mm wide furrow between two pronounced, acute ribs. Margin of LV flat and with plications that correspond to those of the RV, forming a prominent cone above the RV interior. No commissural openings have been detected at Vb and Pb, but above Pb the LV margin is straight, and not downfolded as it is above other ribs.

Cells of the outer shell layer are regularly penta- or octagonal, predominantly hexagonal, not exceeding 0·5 mm in diameter. Rudimentary radial or tangential muri project into larger cells (*appendices cloisonnaux*, Amico 1978). Funnel plates are intensely folded, even close to the inner margin of outer shell layer. No structural modifications in Vb, but funnel plates have a oval or round depression in Pb (Pl. 19, fig. 2). This character is found in all specimens from Paleokastron, and has also been noted by Klinghardt (1935, pl. 2, fig. 1, bands are wrongly labelled) in *R. angeiodes* of unknown provenance, as well as by Pleničar (1993, pl. 1, figs 4–5; pl. 3, fig. 3) in a specimen from Slovenia. Comparable dissimilar structures of the two radial bands have been described from *Sauvagesia aliciae* Pons, 1977.

Remarks. In the LVs of some specimens that have been determined as *R. angeiodes*, canals have been noted in the inner or outer shell layer (Klinghardt 1944; Pejović 1984). The systematic position of these specimens has been questioned, as no canals were recognized in the LVs of syn- and topotypes (Alencáster and Pons 1992). No canals were found in the LVs of the Boeotian specimens.

Distribution. Campanian–Maastrichtian of France, the Gosau, southern Alps, of Algeria, Tunisia, the external Dinarids, Serbia, north-western Anatolia, Iran (Kühn 1932), the Pyrenees, Romania (Sánchez 1981), Apulia, Greece (?Kefallinia Island, Pindos Mountains) and of Caucasus. Upper Santonian of France (Bilotte 1981); Upper Santonian–Lower Campanian of the Pyrenees (Bilotte 1985); Maastrichtian of Brač, Adriatic Sea (Gušić and Jelaska 1990).

Radiolites lusitanicus (Bayle, 1857)

Plate 15, figures 1–6; Plate 16, figures 1–5'

*1857 *Sphaerulites lusitanicus* Bayle, pp. 683, 692 [*nomen dubium*].
1886 *Sphaerulites lusitanicus* Bayle; Choffat, p. 32, pl. 4, figs 2–8 [with synonymy].
1886 *Sphaerulites Peroni* Choffat, p. 33, pl. 5.
v.1901 *Sphaerulites lusitanicus* Bayle; Choffat, p. 144, pl. 11, fig. 1.
1901 *Sphaerulites lusitanicus* Bayle; Choffat, p. 144, pl. 10, figs 3–6; pl. 11, figs 2–5.
non 1903 *Sphaerulites Peroni* Choffat; Dacqué, p. 375, pl. 36, figs 1–2.
v.1908 *Radiolites lusitanicus* Bayle; Toucas, p. 62, pl. 11, fig. 10.
v.1908 *Radiolites Peroni* Choffat; Toucas, p. 61, pl. 11, figs 3–4, 6–9.
v1913*a* *Radiolites Peroni* Choffat, race *sinaitica*; Douvillé, p. 249, pl. 15, fig. 3.
1930 *Radiolites lusitanicus* Bayle; Nöth, p. 367.
1931*b* *Radiolites lusitanicus* Bayle; Nöth, p. 158.
1931*b* *Radiolites lusitanicus* Bayle var.; Nöth, p. 159, pl. 16, fig. 2.
1932 *Radiolites lusitanicus* (Bayle) Parona; Kühn, p. 145 [with synonymy].
1932 *Radiolites peroni* (Choffat) Douvillé; Kühn, p. 150 [with synonymy].
1932 *Radiolites lusitanicus* (Bayle); Parona, p. 101.
1932 *Radiolites Peroni* (Choff.); Parona, p. 101.
?*1933* *Radiolites lusitanicus* Bayle; Müllerried, p. 270.
1942 *Radiolites lusitanicus* (Bayle); Parona, p. 87.
1942 *Radiolites Peroni*; Parona, p. 90.
v *non* 1943 *Radiolites lusitanicus* (Bayle) Parona, var. *rigida* Choffat; Klinghardt, p. 122, pl. 7, figs 1–2.
1954 *Radiolites lusitanicus* Bayle var. *fortovanus* nov. var. Astre, p. 23, pl. 2, fig. 3; text-fig. 5a–b.
1955a *Radiolites lusitanicus* Bayl. et var. *fortovanus* Astre; Astre, p. 10.
1955a *Radiolites peroni* Choff.; Astre, p. 10.
1957a *Radiolites lusitanicus* Bayl. var. *fortovanus* Ast.; Astre, p. 190.
1957a *Radiolites peroni* Choff.; Astre, p. 191.
1964 *R. lusitanicus* (Bayle); Polšak, p. 67.
1964 *R. lusitanicus porericus* n. subsp. Polšak, p. 67 [*nomen nudum*].
1964 *Radiolites peroni* (Choffat); Polšak, pp. 66–67.
1965b *Radiolites lusitanicus* (Bayle); Polšak, p. 444.
1965b *Radiolites lusitanicus porericus* n. subsp. Polšak, p. 444 [*nomen nudum*].
1965b *Radiolites peroni* (Choffat); Polšak, p. 444.
1967*b* *Radiolites lusitanicus porericus* n. subsp. Polšak, pp. 60, 174, pl. 29, figs 8–9; pl. 30, figs 1–4.
1968a *Radiolites peroni* (Choffat); Slišković, p. 31.
1969 *Radiolites lusitanicus* (Bayle); Polšak and Mamužić, p. 238.
1969 *Radiolites peroni* (Choffat); Polšak and Mamužić, p. 233.
1971 *Radiolites peroni* (Choffat); Berizzi Quarto di Palo and Busson, p. 526, pl. 39, fig. 12.
1971a *Radiolites peroni* (Choffat); Sliskovic, p. 34.
1972 *Radiolites lusitanicus* Bayle; Babinot *et al*., text-fig. 2.
1972 *Radiolites peroni* (Choffat); Babinot *et al*., text-fig. 2.
1972*c* *Radiolites peroni* (Choffat); Campobasso, p. 528, pl. 2, figs 1–3.
1973 *Radiolites lusitanicus* (Bayle); Berthou, pl. 55, figs 1–2.
1973 *Radiolites peroni* (Choffat); Berthou, pl. 56, fig. 3.
1973 *Radiolites lusitanicus* (Bayle); Berthou and Philip, p. 238.
1973 *R. peroni* (Choffat); Berthou and Philip, p. 238.
1974 *Radiolites lusitanicus* (Bayle); Pleničar, pp. 140, 175, text-figs 12–13.
1974 *Radiolites lusitanicus* (Bayle); Slišković, p. 133.
1975b *R. lusitanicus* (Bayle); Slišković, p. 57.

1978 *Radiolites lusitanicus* Bayle; Amico, p. 45, pl. 6, figs 1–6; pl. 7, figs 1–3.
1978 *Radiolites peroni* Choffat; Amico, p. 45.
1978 *Radiolites peroni* (Choffat); Pamouktchiev, tab. 1.
1978b *Radiolites lusitanicus* & *peroni* Chof.; Philip *et al.*, tab. 5.
1979 *Radiolites lusitanicus* (Bayle); Mamužić *et al.*, p. 103, tab. 1.
1979 *Radiolites peroni* (Choffat); Mamužić *et al.*, p. 102, tab. 1.
1980 *R. lusitanicus*; Laviano and Sirna, p. 69.
1981 *Radiolites lusitanicus* (Bayle); Carbone and Sirna, p. 435, text-fig. 6.
1981*b* *Radiolites peroni* (Choffat); Pamouktchiev, p. 185, pl. 87, fig. 2, fig. 2a [cop. Pamouktchiev 1969].
1981 *Radiolites lusitanicus* (Bayle); Sánchez, p. 176 [with synonymy].
1981 *Radiolites lusitanicus porericus* Polšak; Sánchez, p. 176 [with synonymy].
1981 *Radiolites peroni* (Choffat); Sánchez, p. 182 [with synonymy].
1982 *Radiolites lusitanicus* (Bayle); Polšak *et al.*, text-fig. 3.
1982 *Radiolites lusitanicus porericus* Polšak; Polšak *et al.*, text-fig. 3.
1982 *Radiolites peroni* (Choffat); Polšak *et al.*, text-fig. 3.
1982 *Radiolites lusitanicus* (Bayle); Pons, tab. 1.
non 1983 *Sphaerulites lusitanicus* Bayle; El-Asa'Ad, p. 94 [*teste* El-Asa'Ad 1987].
non 1983 *S. Peroni* Choffat; El-Asa'ad, p. 94 [*teste* El-Asa'Ad 1987].
1983 *Radiolites peroni* (Choffat) Douvillé; Mainelli, p. 193.
1987 *Radiolites peroni sinaiticus* Douvillé; Parnes, p. 146, pl. 1, fig. 6; pl. 5, fig. 11.
1988 *Radiolites peroni* (Choffat); Yanin, p. 286, pl. 14, figs 1–4.
1989b *Radiolites lusitanicus*; Cestari and Sirna, tab. 1.
1989*b* *Radiolites peroni*; Cestari and Sirna, tab. 1, pl. 7, fig. 2.
1989a *Radiolites lusitanicus*; Philip *et al.*, p. 110.
1989a *Radiolites peroni*; Philip *et al.*, p. 110.
1991 *Radiolites lusitanicus*; Floquet, text-fig. 285.
1991 *Radiolites lusitanicus* (Bayle); Šribar and Pleničar, p. 177.
non 1994 *Sphaerulites lusitanicus*; El-Nakhal and El-Naggar, p. 406.
non 1994 *Sphaerulites peroni*; El-Nakhal and El-Naggar, p. 406.
1994 *Radiolites lusitanicus* (Bayle); Peza and Pirdeni, p. 224.
1994 *R. peroni* (Choffat); Peza and Pirdeni, p. 224.
1995 *Radiolites peroni* (Choffat); Kora and Genedi, p. 226.
1996 *Radiolites peroni* (Choffat); Caffau *et al.* p. 96, pl. 4, fig. 3.
1996 *Radiolites peroni* Douvillé; Paris and Sirna, p. 191, pl. 1, fig. 7.
1997 *S. lusitanicus* Bayle subsp. *rigida* Choffat; Metwally and Abd El Azeam, p. 276.
1997 *Sphaerulites peroni* (Choffat); Metwally and Abd El Azeam, p. 276.

Syntype. Choffat (1901), plate 11, figure 1; Toucas (1908), plate 11, figure 10.

Material. Thirty-one specimens from Marmeko quarry (R131, R142–R143, R150, R159, R164, R166, R168, R175, R246, R250, R254, R267, R269–R272, R520–R526, R528–R529, R536).

Description. RVs more than 180 mm long, commissural diameter up to 102 mm. Shell lamellae are irregularly, more or less tightly plicated, steeply inclined in most shells, rarely horizontally protruding or slightly turned down. Culminations of folds are wide and asymmetrical, whereas the downfolds are narrower and more pronounced so

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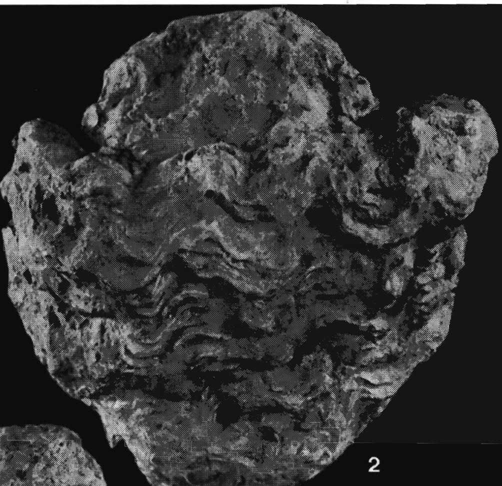
EXPLANATION OF PLATE 15

Figs 1–6. *Radiolites lusitanicus* (Bayle, 1857), Marmeko. 1, posteroventral aspect of large RV with irregularly folded lamellae which are turned down in the single interband fold near the commissure; R526. 2, posteroventral aspect of bivalve specimen with dome-shaped LV, lamellae of RV interband projecting horizontally and turned down in the adjacent folds; R246. 3, RV with weakly folded shell lamellae, dorsal aspect; R520. 4, RV with closely spaced, intensively folded shell lamellae; R269. 5, posteroventral aspect of RV with steeply inclined lamellae and two ribs (folds) in the interband; R164. 6, posteroventral aspect of RV with steeply inclined lamellae and two longitudinal ribs (folds) in the interband; R267. All × 0·7.

PLATE 15


1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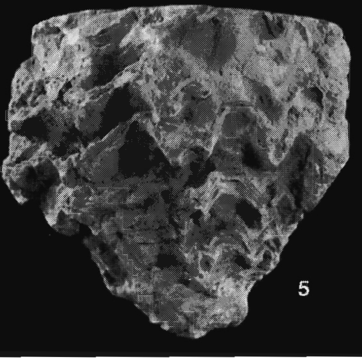
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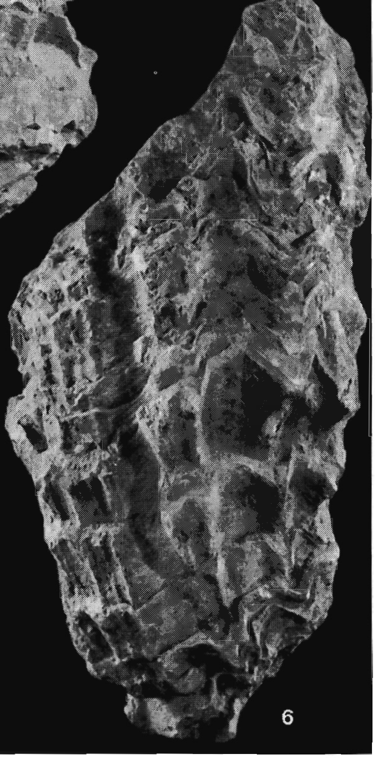

6

STEUBER, *Radiolites*

that unevenly spaced longitudinal ribs contribute to the ornamentation of shells with steeply inclined lamellae (Pl. 15, fig. 6). Vb and Pb are formed by broadly culminating upfolds which are commonly somewhat depressed or more inclined towards the interior than other plications; only rarely do they protrude exteriorly. Vb of similar width as Pb or twice as wide; Ib has one to three plications. The ornamentation of Ib is preserved in 16 RVs: 12 of them have two plications on Ib, and two have one or three plications, respectively. In several RVs the lamellae ascend dorsally in Ib and the posterior fold of Ib is less prominent. The lamellae of the dorsal and posteroventral shell are slightly turned down in some RVs. Downturned lamellae are also present in the radial bands of some shells.

LVs are more or less convex, hemispherical in some specimens; apex sub-central, shifted dorsally. No canals or pseudocanals have been recognized. The ligamental ridge is narrow and short. (1) slightly stronger than (3), the dorsal surface of both is delicately grooved. (1′) and (3′) are bordered ventrally by a projection of the inner shell. Ma is narrow and projects far ventrally, mp is thicker and terminates dorsally of Pb.

Cells of the outer shell layer are irregularly polygonal, radially elongated or sub-rectangular. Sub-polygonal cells are commonly restricted to the inner margin of the outer shell layer, and elongated sub-rectangular or vermiform cells that reach 3·5 mm long dominate distally. Radial muri are irregularly curved. In radial sections, tangential muri are abundant only near the inner margin of the outer shell. They are irregularly distributed and diverge towards the exterior (Pl. 16, fig. 4). In tangential section, cells are separated by funnel plates and radial muri, and appear predominantly rectangular, while the broad, oblique sections of tangential muri are rarely noted (Pl. 16, fig. 5). Maximum vertical spacing of funnel plates is 0·45 mm, but on average is much smaller. Cortical layer is 0·25 mm thick.

Remarks. According to the differential diagnosis, *Radiolites lusitanicus* is separated from *Radiolites peroni* (Choffat, 1886) by the number of plications on Ib: three to four in the former, only one or two in the latter (Choffat 1886, 1901). Additionally, the folding of the shell layer is more pronounced around the whole shell in *R. lusitanicus*. However, Toucas (1908) included RVs with only two plications on Ib in *R. lusitanicus*, and one of the syntypes of *R. lusitanicus* (Choffat 1901, pl. 11, fig. 1) has only two folds on Ib, one of them even developed only during late ontogeny.

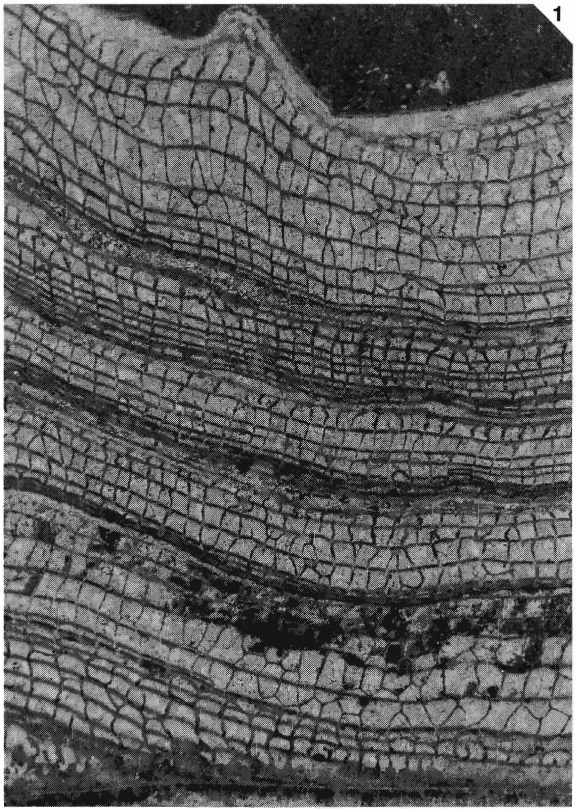
The intense plication of the shell lamellae of the Boeotian specimens argues for *R. lusitanicus*, although the number of plications of Ib is indicative of *R. peroni* (*sensu* Choffat 1886). The same applies to *R. lusitanicus* from the Upper Turonian–Coniacian of Istria (Polšak 1967*b*). The ornamentation of the interband is obviously variable and does not provide a safe distinction. On the other hand, the intensity of plication is difficult to assess in the absence of type material for comparison, and the RVs of Marmeko quarry, although collected from a single horizon, show a considerable variation in this character (Pl. 15, figs 2, 4). The structural composition of the outer shell layers also does not provide any differing characters (Amico 1978). As both taxa have been frequently reported to co-occur at several localities and have the same stratigraphical range (e.g. Polšak 1967*b*; Berthou 1973; Philip *et al.* 1978*b*, 1989*a*), *Radiolites peroni* (Choffat, 1886) is considered to be a junior synonym of *R. lusitanicus*.

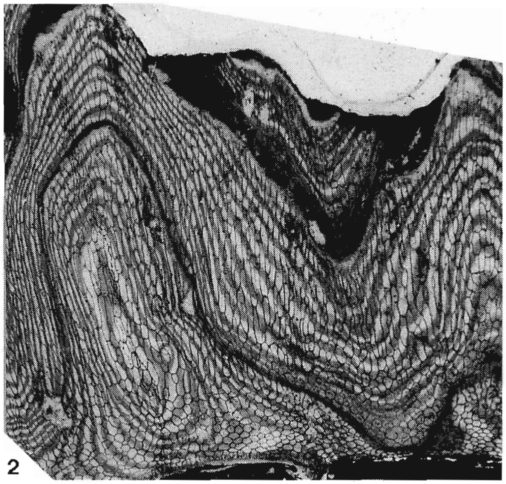
RVs with lamellae that are turned down in the radial bands and the bordering plications have been reported from several localities (Choffat 1901; Astre 1954; Pašić 1957; Polšak 1967*b*) and also occur at Marmeko quarry. They have been defined as *R. lusitanicus* var. *fortovanus* Astre, 1954 or *R. lusitanicus porericus* Polšak, 1967*b*. As they co-occur with the typical *R. lusitanicus* and the inclination of shell lamellae obviously varies during ontogeny, the separation of a subspecies is inappropriate.

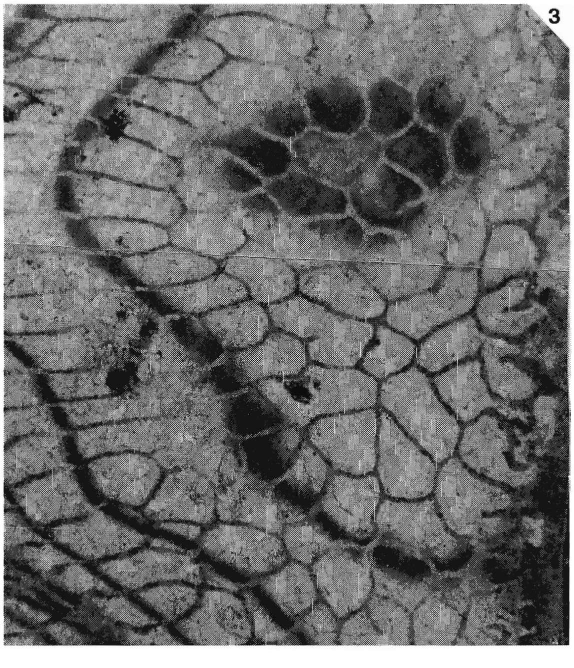
Distribution. Cenomanian–Coniacian of the external Dinarids (Polšak and Mamužić 1969; Polšak *et al.* 1982), the Apennines, of Serbia (Pašić 1957; Pejović 1957), Greece (Ptoon Mountains, Attica [Mitzopoulos and Kühn 1963]), Somalia, Caucasus, ?Mexico; Upper Cenomanian of south-western Europe (Berthou and Philip 1973; Philip 1978; Philip *et al.* 1978*b*), Albania (Peza and Pirdeni 1994), Egypt (Metwally and Abd El Azeam 1997), Afghanistan and Tunisia (Berizzi Quarto di Palo and Busson 1971); Middle Turonian–Lower Coniacian of northern Castile (Floquet 1991).

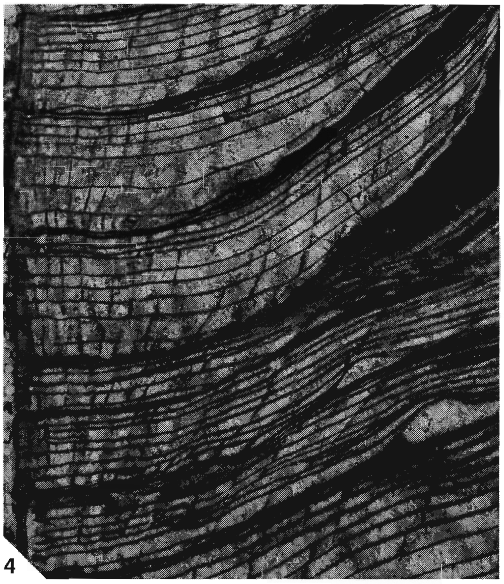
EXPLANATION OF PLATE 16

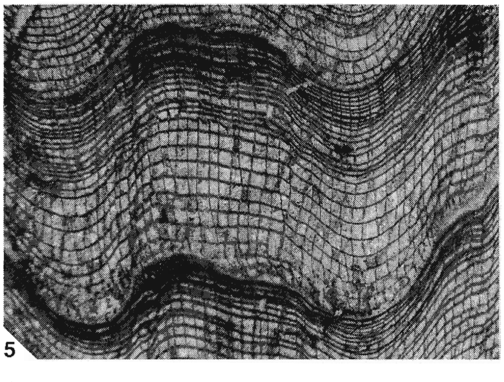
Figs 1–5. *Radiolites lusitanicus* (Bayle, 1857); shell structures; 1, 3–4, R175; 2, 5, R522; all from Marmeko. 1, transverse section, anteroventral; × 12·5. 2, transverse section, dorsal; × 3·4. 3, transverse section, anterodorsal; × 25. 4, anterodorsal radial section; × 9·1. 5, dorsal tangential section; × 5·5.



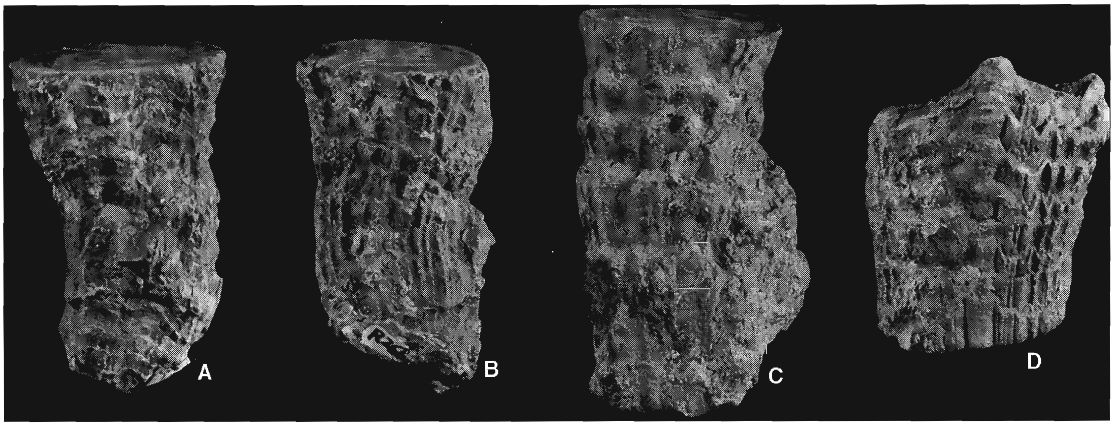








STEUBER, *Radiolites*



TEXT-FIG. 39. *Radiolites praegalloprovincialis* Toucas, 1908; Marmeko; × 0·77. A–B, R266; A, posteroventral, B, anterior aspect. C, posteroventral aspect; R140. D, posteroventral aspect; R264.

Radiolites praegalloprovincialis Toucas, 1908

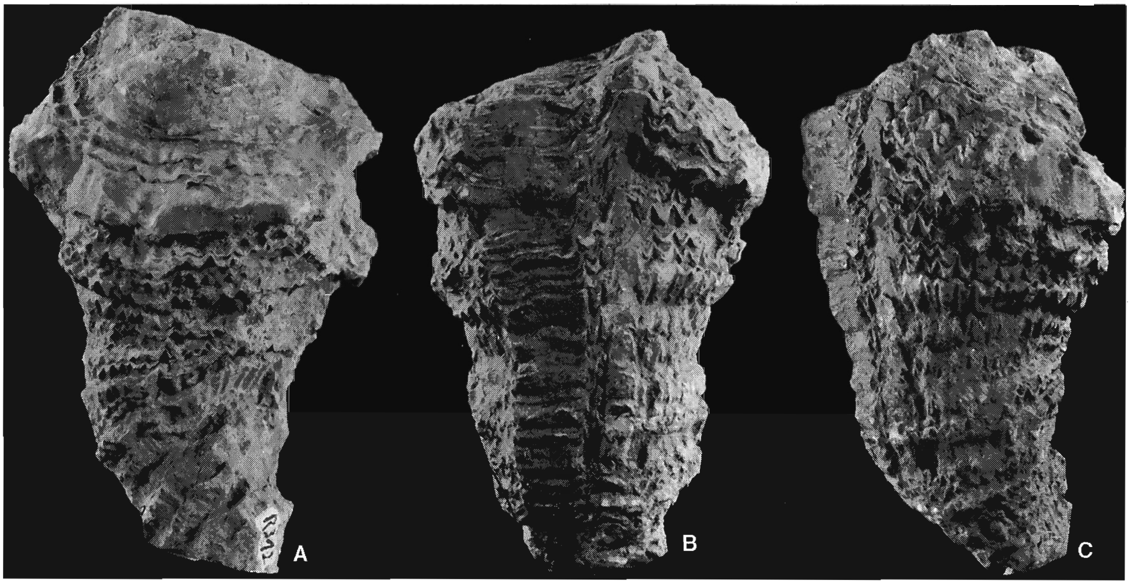
Text-figure 39A–D

v*1908 *Radiolites praegalloprovincialis* nov. sp. Toucas, p. 75, pl. 14, figs 8, 11, ?12.
*1908 *Radiolites praegalloprovincialis* nov. sp. Toucas, p. 75, pl. 14, figs 9, 9a, 10.
1932 *Radiolites praegalloprovincialis* Toucas; Kühn, p. 151.
?*1932* *Radiolites praegalloprovincialis* var. *crassa* Toucas; Kühn, p. 151.
1954 *Radiolites praegalloprovincialis* Toucas var. *campsinus* nov. var. Astre, p. 40, pl. 4, figs 4–5.
1955a *R. praegalloprovincialis* Touc. var. *campsinus* Ast.; Astre, p. 11.
1957a *Radiolites praegalloprovincialis* Toucas var. *campsinus* Ast.; Astre, p. 191.
1959 *Radiolites praegalloprovincialis* Toucas; Petković *et al.*, p. 282.
1964 *R. praegalloprovincialis* Toucas; Polšak, p. 67.
1965b *Radiolites praegalloprovincialis* Toucas; Polšak, p. 447.
1969 *Radiolites praegalloprovincialis* Toucas; Polšak and Mamužić, p. 238.
1973 *Radiolites praegalloprovincialis* Toucas; Pleničar, pp. 188, 219, pl. 1, fig. 1.
1974 *Radiolites praegalloprovincialis* Toucas; Slišković, p. 133.
1980 *R. praegalloprovincialis*; Laviano and Sirna, p. 69.
1981 *Radiolites praegalloprovincialis* Toucas; Sánchez, p. 183 [with synonymy].
1982b *R. praegalloprovincialis*; Bilotte, tab. 2.
1982 *Radiolites praegalloprovincialis* Toucas; Polšak *et al.*, text-fig. 3.
1985 *R. praegalloprovincialis*; Bilotte, tab. 17.
1989 *R. praegalloprovincialis* Toucas; Pascual *et al.*, p. 218, text-fig. 3.
1991 *Radiolites praegalloprovincialis* Toucas; Šribar and Pleničar, p. 178.

Holotype. Toucas (1908), plate 14, figure 8.

Material. Three specimens from Marmeko quarry, one with fragments of the LV (R140, R264, R266).

Description. RVs elongated-conical, more than 75 mm high, commissural diameter not exceeding 44 mm. Shell lamellae are steeply inclined and regularly folded; narrow folds form ribs that can be traced on the vertically stacked and widely spaced (up to 14 mm) lamellae. Vb wider or of the same width as Pb, slightly projecting or centrally depressed; Pb is always depressed. Lamellae reach the same height in Vb and Pb. Pb of the bivalve specimen projects over the commissure, Vb is crushed. Ib is narrower than Pb and has either two similar or a single, salient rib with undulating posterior margin. The preserved margin of the LV is smooth (see var. *campsinus* [Astre, 1954]). (1) and (3) are dorsally grooved, ma is narrow, mp broader. Both myophores project not far ventrally, mp terminates well dorsally of Pb.



TEXT-FIG. 40. *Radiolites sauvagesi* (d'Hombres-Firmas, 1838); R312; Marmeko; bivalve specimen with asymmetrically domed LV; × 0·8. A, anterodorsal aspect; B, ventral aspect, Ib with two folds; C, posterior aspect.

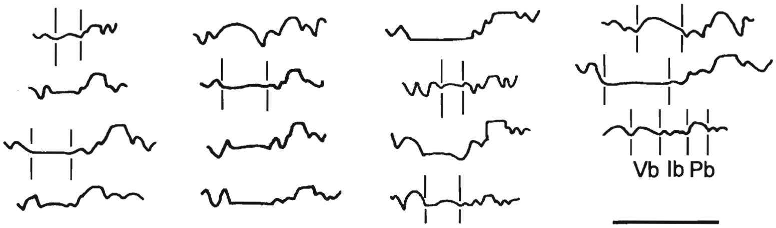
Cells are irregularly polygonal, predominantly penta- and hexagonal. Their diameter does not exceed 0·85 mm, and they are much smaller at the inner and outer margin of the outer shell layer.

Distribution. 'Zone de passage Turonien-Coniacien' of the Pyrenees (Bilotte 1982*b*); Coniacian–Lower Santonian of the external Dinarids (Polšak *et al.* 1982; Šribar and Pleničar 1991); Lower Senonian of Serbia (Pašić 1957); Upper Turonian–Senonian of Apulia (Laviano and Sirna 1980); Campanian of Slovenia (Pleničar 1961).

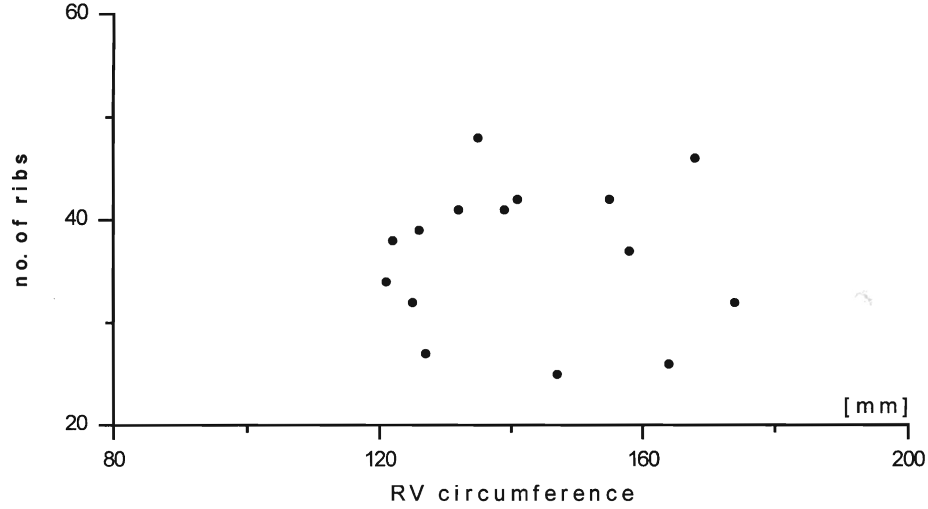
Radiolites sauvagesi (d'Hombres-Firmas, 1838)

Plate 17, figures 1–14; Plate 18, figures 1–5; Text-figures 40–41

*1838	*Hipp. Sauvagesii* d'Hombres Firmas, p. 193, pl. 2, figs 1–8.
1839	*Hippurites Sauvagesi*; d'Hombres Firmas, p. 15.
v.1881	*Sphaerulites Lefebvrei* Bayle; Bayle, *in* Rolland, p. 526, pl. 15, figs 5–6.



TEXT-FIG. 41. Folds of shell lamellae along posteroventral shell of RVs of *Radiolites sauvagesi* (d'Hombres-Firmas, 1838) from Marmeko quarry. Figured sections are transverse to the steeply inclined shell lamellae. Vertical lines indicate limits of ventral (Vb), inter- (Ib), and posterior bands (Pb) in one example (cf. Table 5). Ventral bands are indicated on several other examples to show delimitation to Ib. Scale bar represents 30 mm.



TEXT-FIG. 42. Number of folds of shell lamellae ('ribs') in relation to the circumference of RVs of *Radiolites sauvagesi* (d'Hombres-Firmas, 1838) from Marmeko quarry.

?1889–93	*Radiolites lefebvrei* Bayle; Peron, p. 287, pl. 28, figs 20–23.
1890	*Sphaerulites sauvagesi* d'Hombr. F. sp., d'Orb. (*pars*), emend. Bayle; Blanckenhorn, p. 86.
v.1908	*Radiolites sauvagesi* d'Hombres-Firmas; Toucas, p. 65, pl. 12, fig. 10; text-figs 34–36.
v.1910	*Rad. sauvagesi*; Douvillé, text-fig. 13.
1930	*Radiolites Sauvagesi* d'Hombre Firmas; Nöth, p. 367.
1931*b*	*Radiolites sauvagesi* d'Hombre-Firmas; Nöth, p. 158, pl. 16, fig. 1.
1932	*Radiolites sauvagesi* (d'Hombre Firmas) d'Orbigny; Kühn, p. 154 [with synonymy].
1937	*Radiolites sauvagesi* (d'Hombre Firmas) d'Orbigny; Oosterbaan, p. 109, pl. 2, figs 17–18.
1954	*Radiolites sauvagesi* d'Hombres-Firmas var. *aqualninus* nov. var. Astre, p. 38, text-fig. 13.
1955a	*Radiolites sauvagesi* d'Homb. Firm.; Astre, p. 10.
1955a	*Radiolites sauvagesi* d'Homb. Firm. var. *aqualninus* Ast.; Astre, p. 11.
1957a	*Radiolites sauvagesi* d'Hombr. Firm. var. *aqualninus* Ast.; Astre, p. 192.
1959	*Radiolites sauvagesi* (d'Hombre Firmas); Petković *et al.*, p. 282.
1961	*Radiolites lefebvrei* Bayle; Rossi Ronchetti and Albanesi, p. 267.
1964	*R. sauvagesi* (d'Hombres-Firmas); Polšak, p. 67.
1965b	*Radiolites sauvagesi* (d'Hombres-Firmas); Polšak, p. 444.
1968a	*Radiolites sauvagesi* (d'Hombres-Firmas); Slišković, p. 35.
1969	*Radiolites sauvagesi* (d'Hombres-Firmas); Polšak and Mamužić, p. 238.
p*1972*	*Radiolites praesauvagesi* Toucas; Bartov *et al.*, p. 80.
1973	*R. sauvagesi* d'H.-F.; Freytet, p. 68.
1974	*Radiolites sauvagesi* d'H. Firmas; Philip, p. 112.
1974	*Radiolites sauvagesi* (d'Hombres-Firmas); Slišković, p. 133.
1978	*Radiolites sauvagesi* d'Hombres Firmas; Amico, p. 50, pl. 9, figs 3–4.
1978	*Radiolites sauvagesi* var. *aqualninus* Astre; Amico, p. 50, pl. 9, figs 5–6.
1981	*Radiolites sauvagesi* (d'Hombres Firmas); Sánchez, p. 185 [with synonymy].
1982b	*Radiolites sauvagesi*; Bilotte, tab. 2.
1982	*Radiolites sauvagesi* (d'Hombres-Firmas); Polšak *et al.*, text-fig. 3.
1982	*Radiolites sauvagesi* (d'Hom.-Firm.); Pons, tab. 1.
1983	*Radiolites sauvagesi*; Philip and Bilotte, tab. 1.
1985	*Radiolites sauvagesi*; Bilotte, tab. 17.
1987	*Radiolites lefebvrei lefebvrei* (Bayle); Parnes, p. 139, pl. 2, figs 4–15.
1987	*Radiolites lefebvrei senescens* n. ssp. Parnes, p. 140, pl. 3, figs 1–8.
1989	*Radiolites sauvagesi* (d'Hom.-Firm.); Pascual *et al.*, p. 224, text-fig. 3.

TABLE 5. Measurements (in mm) and number of ribs of RVs of *Radiolites sauvagesi* (d'Hombres-Firmas, 1838), taken close to the commissure. Delimitation of ventral- (Vb), inter- (Ib), and posterior bands (Pb) is indicated on Text-figure 41.

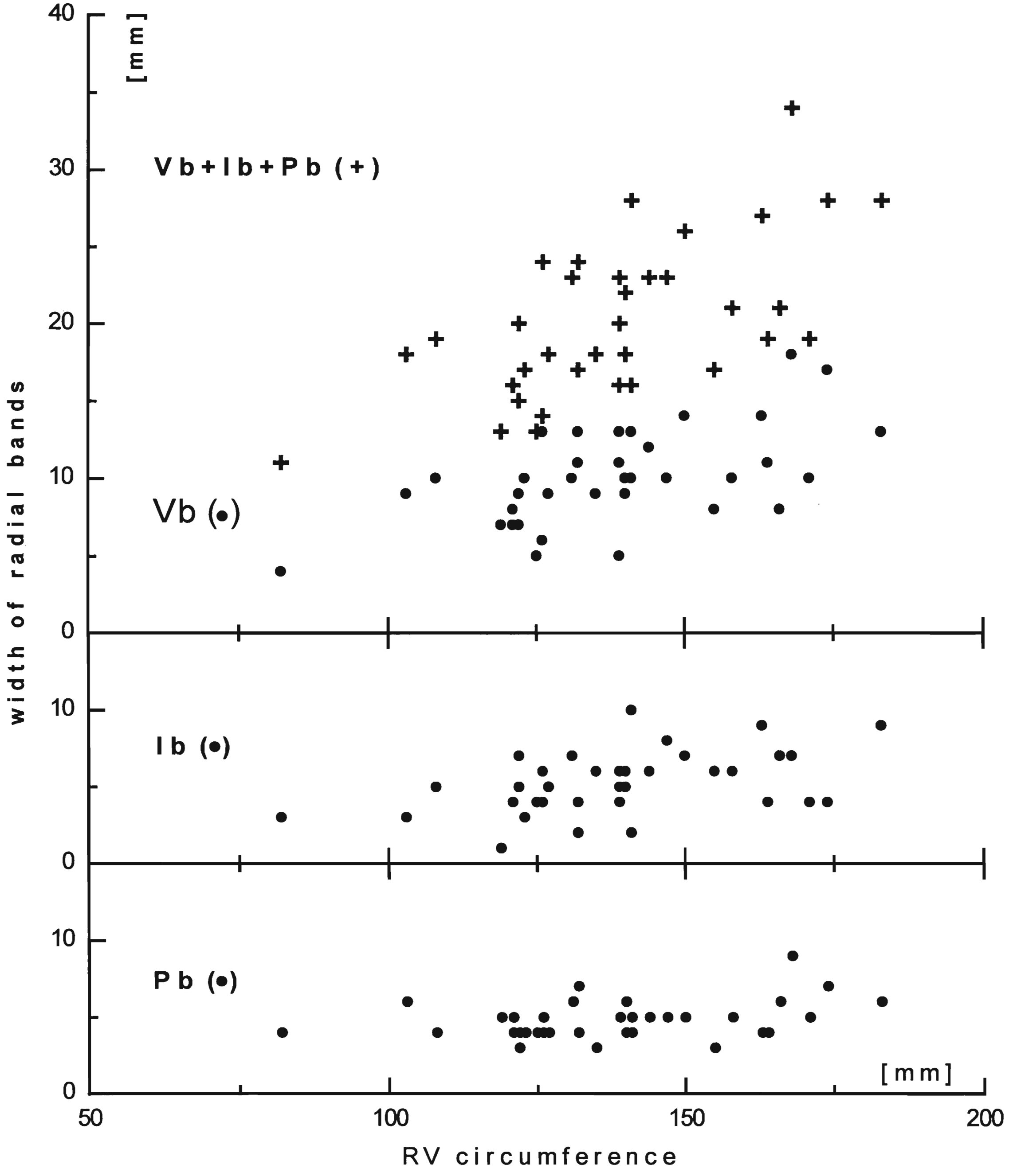
No.	RV length	Circumference	Σ Ribs	Vb	Ib	Pb	Ribs on Ib
R124	>72	119	–	7	1	5	1
R127	67	135	48	9	6	3	2
R128	>71	155	42	8	6	3	2
R135	>69	183	–	13	9	6	2
R144	>96	168	46	18	7	9	2
R152	>52	174	32	17	4	7	1
R158	>58	131	–	10	7	6	2
R160	>69	141	–	13	10	5	2
R165	>45	132	41	13	4	7	2
R174	>47	163	–	14	9	4	2
R247	>59	127	27	9	5	4	2
R249	63	121	–	7	4	5	1
R265	>73	126	–	13	6	5	2
R313	>64	123	–	10	3	4	1
R314	67	140	–	10	6	6	2
R315	74	140	–	9	5	4	2
R316	>74	166	–	8	7	6	3
R318	>29	103	–	9	3	6	1
R319	>37	122	38	7	5	3	2
R321	>93	122	–	9	7	4	2
R323	>55	108	–	10	5	4	1
R324	>45	121	34	8	4	4	2
R527	>59	139	–	11	4	5	2
R529	>56	139	–	13	5	5	1
R530	>79	139	41	5	6	5	2
R533	>80	150	–	14	7	5	3
R537	>85	164	26	11	4	4	1
R540	120	126	39	6	4	4	3
R661	>97	171	–	10	4	5	2
R663	>83	144	–	12	6	5	2
R757	>82	132	–	11	2	4	1
R766	>88	141	42	10	2	4	1
R767	>73	158	37	10	6	5	2
R769	>102	147	25	10	8	5	2
R770	>64	125	32	5	4	4	3

1991 *Radiolites sauvagesi*; Breyer, p. 32, pl. 15, text-fig. 4.
1991 *Praeradiolites sauvagesi*; Floquet, text-fig. 286.

Syntypes. d'Hombres Firmas (1838), plate 2, figures 1–8.

Material. Ninety-five specimens from Marmeko quarry, many of them with both valves conjoined (R3, R4, R7, R12–R13, R122–R128, R130, R133, R135, R138–R139, R144–R145, R151–R152, R154–R155, R158, R160–R163, R165, R169–R171, R174, R243, R247, R249, R251, R265, R309, R312–R324, R527, R529–R530, R533–R534, R535, R537–R538, R540, R661–R663, R683, R692, R756–R776).

Description. RVs elongated-conical, up to 120 mm high. Shell lamellae are regularly plicated and steeply inclined, which results in an ornamentation of almost continuous, slightly rounded or acute longitudinal ribs. Vb and Pb are



TEXT-FIG. 43. Width of ventral (Vb), inter- (Ib), and posterior bands (Pb) in relation to the circumference of RVs of *Radiolites sauvagesi* (d'Hombres-Firmas, 1838) from Marmeko quarry. Measurements taken as closely as possible to the commissure.

clearly accentuated; Vb is more or less deeply depressed between two bordering ribs, or protrudes externally and is then bordered by acute furrows. Width of Vb ranges from being similar to that of Pb to three times the width of Pb. Ib has at least a single, inconspicuous undulation of shell lamellae, commonly two and rarely three salient ribs. In most RVs, the lamellae ascend in Ib towards the posterior shell and have a more commissural position in Pb. Pb is a more or less deep, trench-like depression; it is never protruding. Lamellae are steeply inclined in Pb and stacked almost seamlessly so that the exterior surface of Pb is rather smooth.

LV flat to strongly convex, apex in a sub-central, dorsal position. Vb and Pb of strongly convex LVs formed by radial bulges. (1) and (3) are dorsally grooved, as are (1′) and (3′). Sockets of RV ventrally bordered by projections of inner shell. Ma and mp developed symmetrically, inner shell layer thickened in ma′ and mp′, mp′ is bordered ventrally, and dorsally of Pb, by a projection of the inner shell.

Cells of outer shell layer of variable size (mean diameter 0·35 mm, not larger than 0·75 mm), penta- hexa- or heptagonal muri are rarely curved. Funnel plates are slightly inclined towards the shell's interior, often incompletely developed or discontinuous and continue exteriorly in a higher or lower position; vertical spacing less than 0·65 mm.

Variability and *systematic position*. The number of radial plications varies considerably among specimens of similar size (Table 5; Text-fig. 42). These folds form slightly salient undulations of lamellae in some RVs (Pl. 17, fig. 8), but pronounced longitudinal ribs in others (Pl. 17, figs 1, 11–12). Morphotypes with irregularly and weakly folded lamellae from the Upper Turonian of Istria have been defined as *R. praesauvagesi communis* Polšak, 1967*b*; they differ from similar Boeotian RVs by a less complicated Ib.

Symmetrical ribs and furrows are distributed regularly around the shell of many specimens, but the plications are asymmetrical and the furrows wider than the ribs in other RVs. Such sculptural variations can alternate in a single RV.

Even though the RV apex is not preserved in any of the Boeotian specimens, the ontogenetic development can be traced in approximately four-fifths of the total length in numerous shells. Only in a few cases it has been noted that hardly visible undulations of apical lamellae gave rise to salient longitudinal ribs during shell growth; the ribbing pattern thus remained rather constant during ontogeny. This is also the case in the ornamentation of Ib.

The widths of Vb, Ib and Pb in RVs of similar size vary considerably: the most evident relation exists between the length of commissural circumference of RVs and the width of the complete posteroventral region of radial bands, whilst there is hardly any correlation between the length of circumference and the width of Ib (Text-fig. 43).

The plication of Ib shows considerable variation in the RVs from Marmeko quarry (Text-fig. 41). Ib can have a simple undulation in some shells (Pl. 17, fig. 10) but has three salient ribs in others (Pl. 17, fig. 13); the ornament consists of two plications in most RVs (Table 5). Therefore, the Boeotian specimens correspond to the diagnosis of *R. sauvagesi*.

Similar shells have been described by Parnes (1987) from the basal Upper Turonian of Sinai Peninsula as *R. lefebvrei* (Bayle, *in* Rolland, 1881). This taxon was included in the synonymy of *R. sauvagesi* as early as by Toucas (1908), because it only differs in having ascending lamellae in Ib, which consequently have a more commissural position in Pb. This is also a common character of the RVs from Marmeko quarry, but shells in which lamellae are commarginally parallel in Vb and Pb are equally abundant so that the opinion of Toucas (1908) is adopted. *R. lefebvrei senescens* Parnes, 1987 was installed for morphotypes in which shell lamellae are less steeply inclined in adult growth stages when compared to the juvenile shell. This morphological variation certainly corresponds to environmental factors rather than genetic differences. *R. lefebvrei* from the Sinai Peninsula (Parnes 1987) is therefore indistinguishable from *R. sauvagesi*. Ib of these valves are slightly narrower when compared with the Boeotian specimens, but still structured by undulating lamellae ('subplicated', Parnes 1987, p. 140).

R. praesauvagesi Toucas, 1908 was separated from *R. sauvagesi* because of an unfolded Ib. *R. praesauvagesi* was reported to co-occur with *Vaccinites praegiganteus* (Toucas, 1904) in the Turonian of Gatigues (southern France), whilst *R. sauvagesi* occurs together with *Vaccinites moulinsi* (d'Hombres-Firmas, 1838) in the Coniacian of the same region (Toucas 1908). In the Sinai Peninsula, morphotypes with plicated Ib obviously occur as low as at the base of the Upper Turonian. This raises the question of the systematic and stratigraphical position of *R. praesauvagesi*. The following observations were made during the analysis of the abundant material of *R. sauvagesi* and *R. praesauvagesi* from southern France kept in the Toucas collection and the collection of the Ecole des Mines: (1) The relative height of individual lamellae in Vb and Pb is variable in specimens from several localities; (2) RVs with unstructured Ib (*praesauvagesi*) co-occur at several localities with specimens in which Ib has one or more plications. Consequently, *R. praesauvagesi* and *R. sauvagesi* should not be separated as biospecies, if the generally accepted diagnoses are considered.

Compared with *R. sauvagesi* from Boeotia, '*Radiolites lefebvrei*' from the basal Upper Turonian of the Sinai Peninsula is slightly smaller (up to 90 mm long), and Ib is, on average, slightly narrower and less plicated. This could indicate a younger stratigraphical age of the specimens from Marmeko quarry, which is supported by other biostratigraphical evidence. Ib of *R. sauvagesi* from the Coniacian of Gatigues (Toucas 1908, pl. 12, fig. 10) is considerably wider than in the discussed Turonian specimens. However, the width and plication of Ib obviously vary considerably even in a few almost contemporaneous populations (Text-fig. 41; Table 5), so that the microevolution of the group can only be clarified by morphometric analyses of numerous specimens of precisely known stratigraphical age.

Distribution. Coniacian of southern France, Istria, Bosnia, Serbia, Greece (Ptoon Mountains), of the Sinai Peninsula (Sánchez 1981) and of Sardinia (Oosterbaan 1937); Upper Turonian–Coniacian of the external Dinarids (Polšak *et al.* 1982); 'zone de passage Turonien-Coniacien'–Santonian of the Pyrenees (Bilotte 1982*b*; Pascual *et al.* 1989); basal Upper Turonian of the Sinai Peninsula (Parnes 1987); ?Campanian of northern Castile (Floquet 1991).

Radiolites subradiosus Toucas, 1908

Plate 19, figures 3–5; Text-figure 44A–B

*1908	*Radiolites subradiosus* nov. sp. Toucas, p. 71, pl. 13, fig. 8.
v1931	*Radiolites subradiosus* Toucas; Klinghardt, p. 39, pl. 3, fig. 12; text-fig. 11.
1932	*Radiolites subradiosus* Toucas; Kühn, p. 158 [with synonymy].
1933*b*	*Radiolites subradiosus* Toucas; Kühn, p. 242.
1944	*Radiolites subradiosus* Toucas; Klinghardt, p. 204.
1955a	*Radiolites subradiosus* Touc.; Astre, p. 11.
1957a	*Radiolites subradiosus* Touc.; Astre, p. 191.
1964	*R. subradiosus* Toucas; Polšak, p. 67.
1964	*R. subradiosus angeiodiformis* n. subsp. Polšak, p. 67 [*nomen nudum*].
1965b	*Radiolites subradiosus* Toucas; Polšak, p. 450.
1965b	*Radiolites subradiosus angeiodiformis* n. subsp. Polšak, p. 450 [*nomen nudum*].
1967*b*	*Radiolites subradiosus angeiodiformis* n. subsp. Polšak, pp. 68, 179, pl. 39, fig. 1; pl. 40, fig. 4.
1969	*Radiolites subradiosus* Toucas; Polšak and Mamužić, p. 239.
1974	*Radiolites subradiosus* Toucas; Lupu, p. 54, pl. 1, fig. 1.
1981	*Radiolites subradiosus* Toucas; Sánchez, p. 190 [with synonymy].
1981	*Radiolites subradiosus angeiodiformis* Polšak; Sánchez, p. 190.
1982	*Radiolites subradiosus* Toucas; Polšak *et al.*, text-fig. 3.

EXPLANATION OF PLATE 17

Figs 1–14. *Radiolites sauvagesi* (d'Hombres-Firmas, 1838); Marmeko. 1, posteroventral aspect of RV with uniformly folded lamellae; R530. 2, same valve as on fig. 1, anterodorsal aspect. 3, posteroventral aspect of bivalve specimen with deeply sunken Pb and dome-shaped LV; R661. 4, dorsal aspect of bivalve specimen with slightly domed LV; R318. 5, posteroventral aspect of bivalve specimen with slightly domed LV; R316. 6, posteroventral aspect of RV with broad ventral band; R314. 7, posterior aspect of RV with projecting lamellae in ventral band; R165. 8, posteroventral aspect of RV attached with anterior side to *Vaccinites inferus* (Douvillé, 1891); R313. 9, posteroventral aspect of RV with projecting Vb; Ib has three ribs in commissural part; R762. 10, posteroventral aspect of RV with simple interband; R124. 11, dorsal aspect of strongly ribbed RV; R265. 12, same valve as on fig. 11, posteroventral aspect. 13, posteroventral aspect of RV with broad Vb and three folds in Ib; R135. 14, posterior aspect of bivalve specimen with asymmetrically domed LV; R758. All × 0·8.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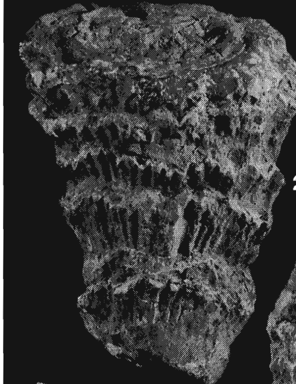
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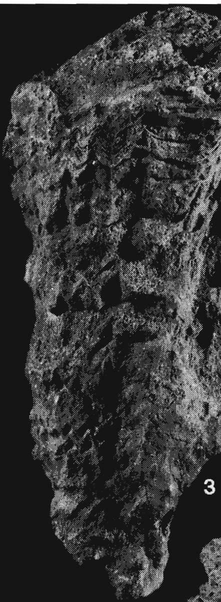
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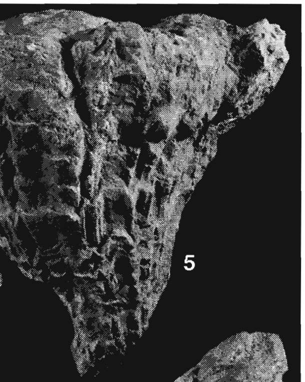
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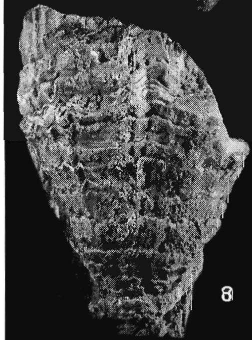
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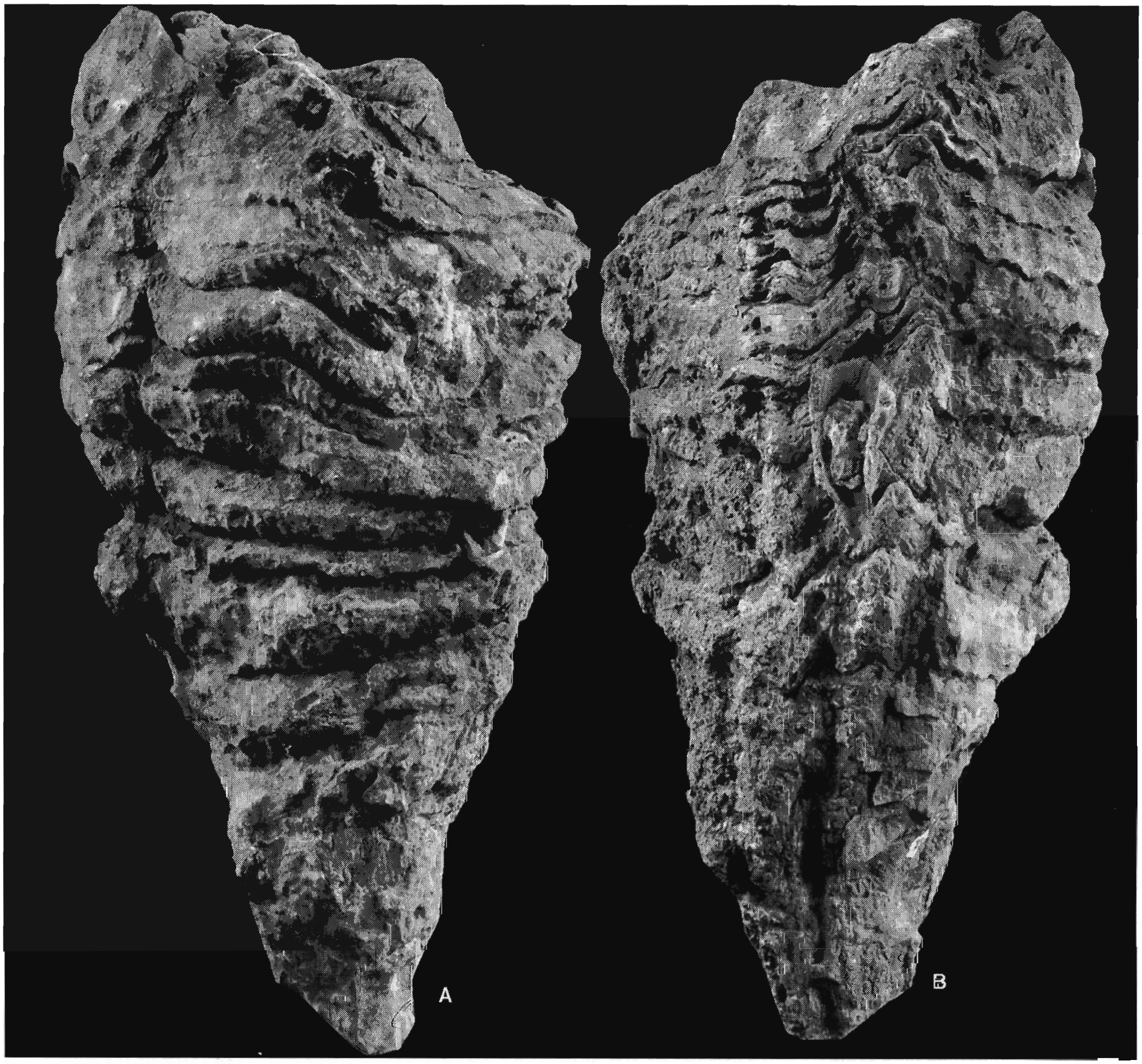
STEUBER, *Radiolites*



TEXT-FIG. 44. *Radiolites subradiosus* Toucas, 1908; R644, Anthochorion; × 0·8. A, dorsal aspect; B, posteroventral aspect.

EXPLANATION OF PLATE 18

Figs 1–5. *Radiolites sauvagesi* (d'Hombres-Firmas, 1838); shell structures. 1–2, R622; 3–5, R692; all from Marmeko. 1, transverse section of Vb (top) and Pb (bottom); × 7·9. 2, transverse section, anterodorsal; × 7·9. 3, transverse section with ligamental ridge; × 7·5. 4, dorsal radial section; × 12. 5, dorsal tangential section; × 12.

PLATE 18

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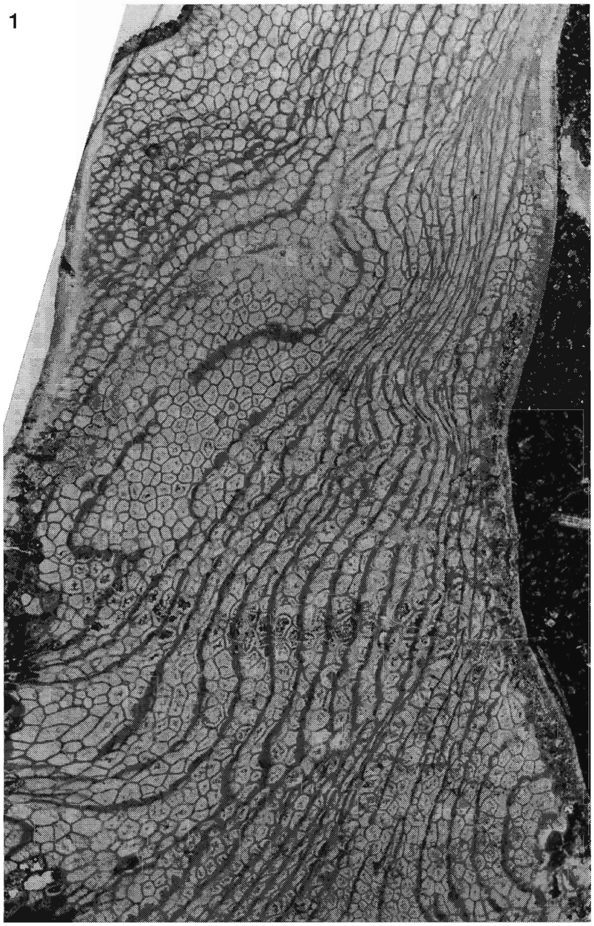

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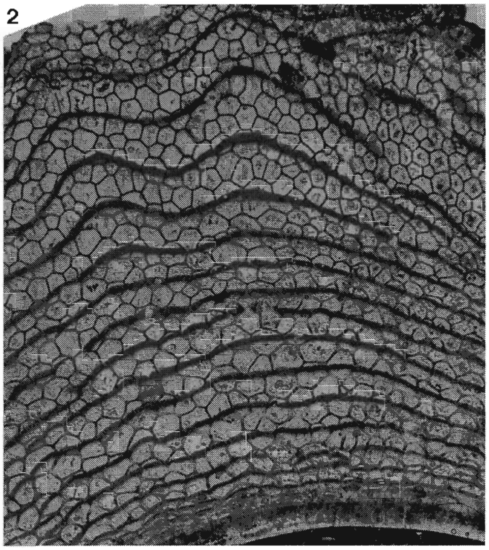

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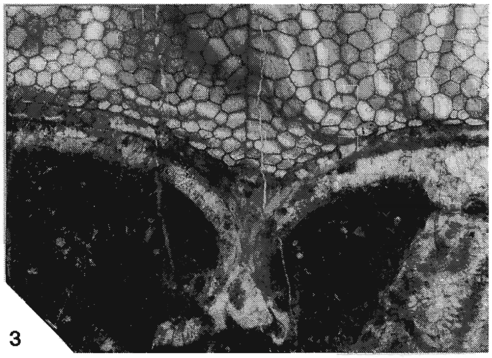

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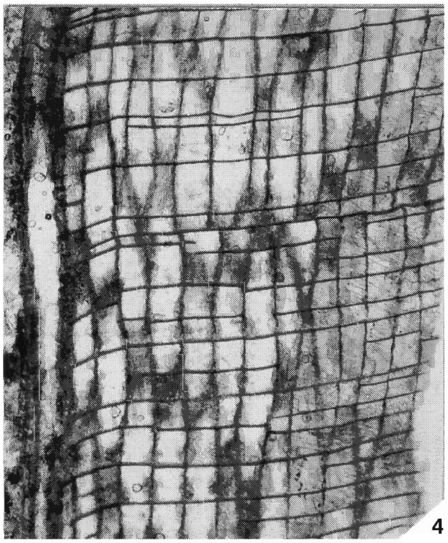

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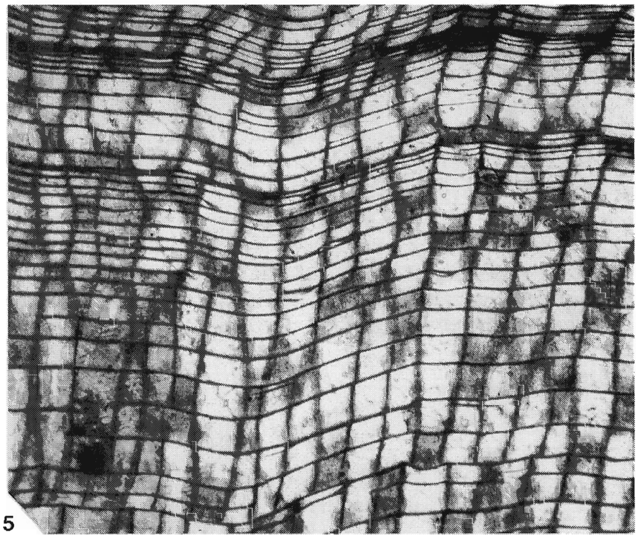

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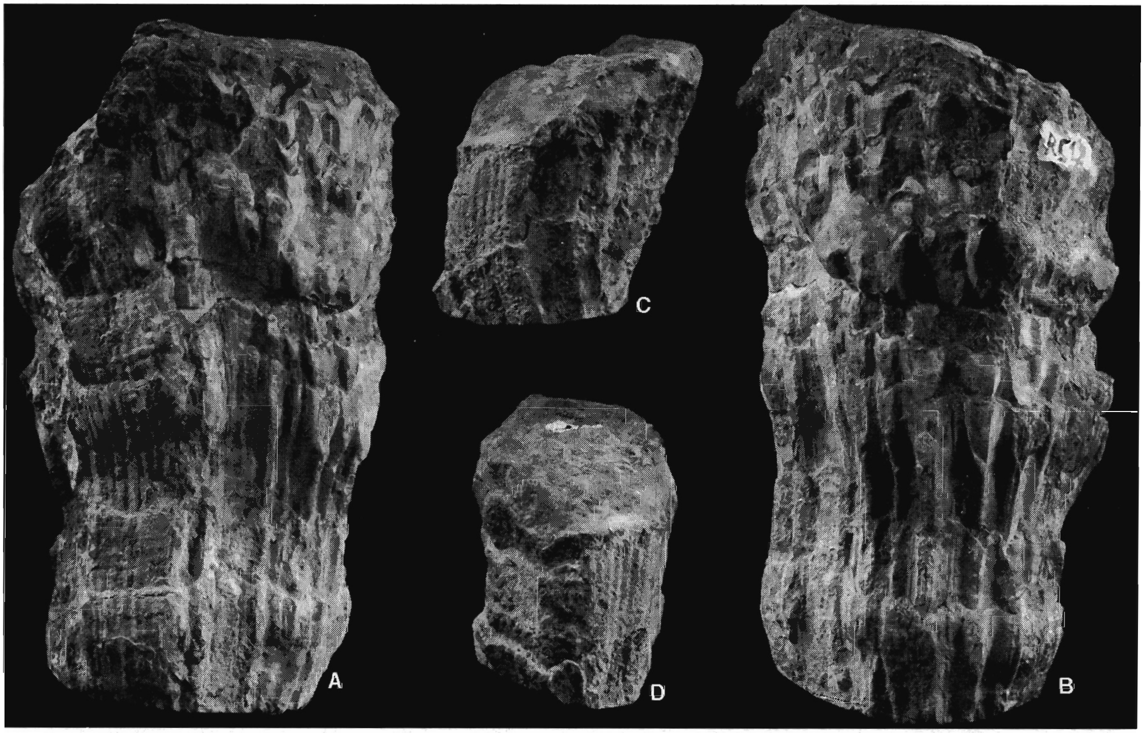

TEXT-FIG. 45. *Sauvagesia meneghiniana* (Pirona, 1869). A–B, R519; Tsouka Hill; C–D, R362; Dionysos; all × 0·8. A, posteroventral aspect; B, posterodorsal aspect; posterior band is seen to the left; C, posteroventral aspect, costellated ventral band to the left; D, ventral aspect.

1982 *Radiolites subradiosus angeiodiformis* Polšak; Polšak *et al.*, text-fig. 3.
1982 *Radiolites subradiosus* Toucas; Pons, tab. 2.
1984 *Radiolites subradiosus* Toucas; Höfling, pl., fig. 3.
1985 *Radiolites subradiosus* Toucas; Höfling, p. 32, pl. 6, fig. 7 [cop. Höfling 1984].
1989 *R. subradiosus* Toucas; Pascual *et al.*, p. 224, text-fig. 3.

Holotype. Toucas (1908), plate 13, figure 8.

Material. Four RVs from Makrokastron Hill (R180, R182, R184, R189), one RV from Anthochorion (R644) and one specimen with both valves conjoined from Kalamos Hill (R207).

Description. RVs conical or elongated-conical, exceeding 195 mm long, commissural diameter up to 109 mm. Shell lamellae have a more or less horizontal orientation with respect to the growth axis, but in small segments can be turned down or erected; they are less regularly folded posteroventrally when compared with the rest of the shell. Lamellae are folded with low amplitudes; slightly salient, acute and evenly spaced riblets are visible on the lower surface of inclined

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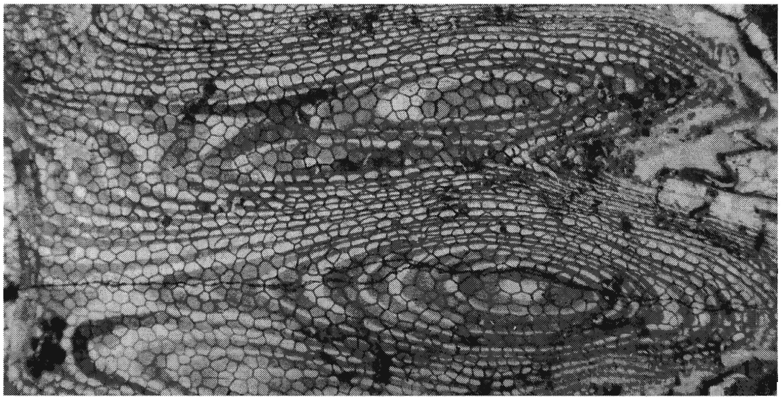
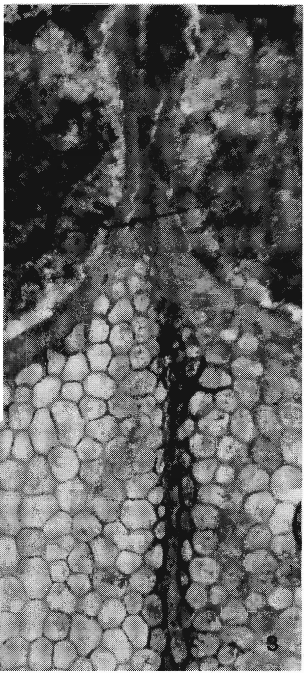
EXPLANATION OF PLATE 19

Figs 1–2. *Radiolites angeiodes* (Lapeirouse, 1781); R709, Paleokastron Hill; shell structures. 1, transverse section, dorsal; × 5·1. 2, transverse section of posterior pseudopillar; × 7·5.
Figs 3–5. *Radiolites subradiosus* Toucas, 1908; R180, Makrokastron; shell structures. 3, transverse section with ligamental ridge; × 10·7. 4, dorsal tangential section; × 7·5. 5, transverse section of anterior shell; × 3·4.





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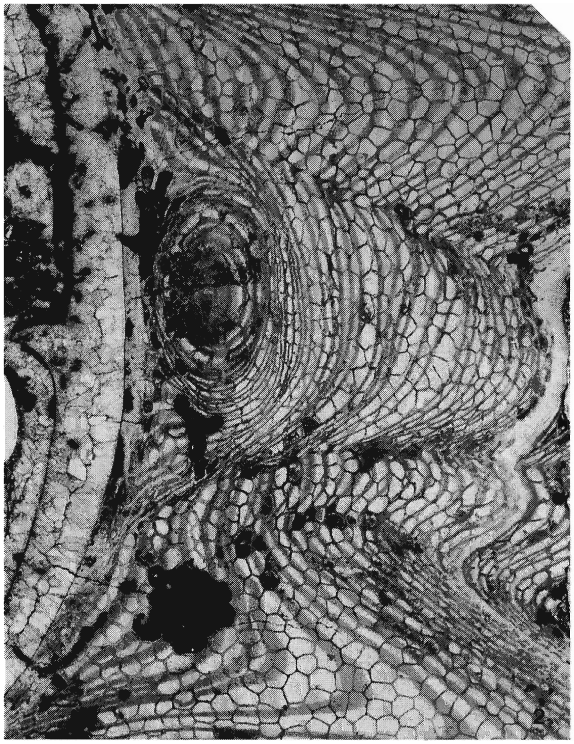

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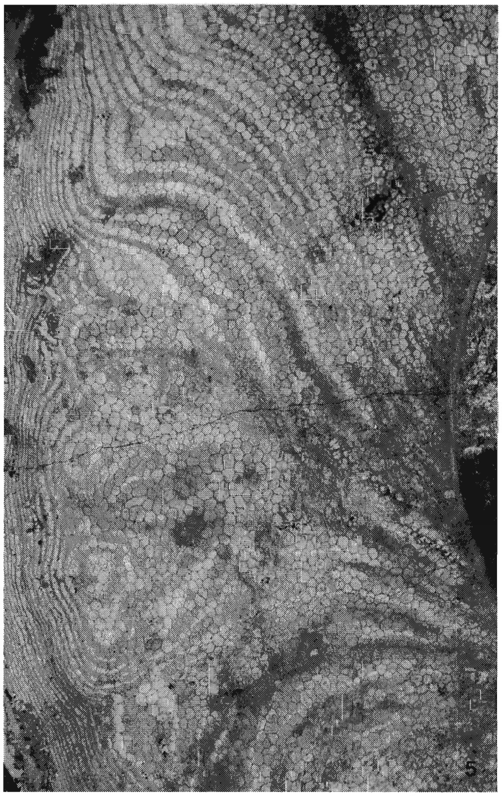
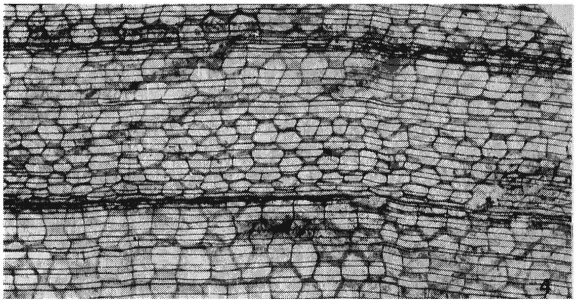


5



4

STEUBER, *Radiolites*

lamellae. As the inclination of lamellae varies, undulating lamellae and riblets of their lower surfaces alternate on the exterior surface. Vb and Pb hardly differ in amplitude from other irregular posteroventral plications. Lamellae are horizontal in Vb; Ib is wider than Vb and has two or three plications that ascend posteriorly; Pb is a simple fold with a slightly larger amplitude and is narrower than Vb.

LV convex, not sufficiently well preserved to discern its sculpture. (1) and (3) are dorsally grooved, their sockets are bordered ventrally by prominent projections of the inner shell. Mp short, rather thin distally and projecting ventrally beyond Pb; ma severely bioeroded.

Cells of the outer shell layer are regularly polygonal, predominantly hexagonal, their mean diameter is 0·5 mm; vertical spacing of funnel plates rarely up to 0·5 mm, on average less than 0·25 mm.

Remarks. The diagnostic feature of *R. subradiosus angeiodiformis* Polšak, 1967*b* is a regular longitudinal ribbing of shell lamellae. This ornament is seen in Boeotian specimens on the lower surface of steeply inclined shell lamellae. The RV figured on Text-figure 44 shows the variation in external ornament as a result of varying inclination of shell lamellae. At the type locality, *R. subradiosus angeiodiformis* occurs together with the nominal type species, and the differences in ornamentation are considered to be related to ecological factors.

R. subradiosus is known from the Coniacian–Lower Santonian of southern France and the Pyrenees (Toucas 1908; Pons 1977); the specimens from Istria (Polšak 1967*b*) and Boeotia are slightly younger and differ by more densely plicated lamellae.

Distribution. Coniacian–Lower Campanian of France, the Pyrenees, Gosau, of Istria, Serbia, northern Anatolia (Pons 1977; Sánchez 1981; Polšak *et al*. 1982).

Genus SAUVAGESIA Choffat, 1886

Type species. *Sphaerulites Sharpei* Bayle, 1857.

Sauvagesia meneghiniana (Pirona, 1869)

Plate 5, figures 1–3; Plate 14, figure 2; Text-figure 45A–D

*1869 *Sphaerulites Meneghiniana* Pirona, p. 408, pl. 16, figs 1–12.
v.1909 *Sauvagesia meneghini* Pirona; Toucas, p. 90, pl. 17, figs 11–12.
1932 *Sauvagesia meneghiniana* (Pirona) Toucas; Kühn, p. 164 [with synonymy].
?1941 *Sauvagesia meneghiniana* (Pirona); Montagne, p. 63, pl. 4, fig. 11.
1950 *Sauvagesia meneghini* Pirona; Rengarten, p. 70, pl. 16, fig. 5; text-fig. 34.
1959 *Sauvagesia meneghiniana* (Pirona); Petković *et al*., p. 282.
1959 *Sauvagesia meneghiniana dalmatica* n. subsp. Polšak, pp. 68, 74, pl. 2, figs 3–4; text-fig. 3.
1964 *Sauvagesia meneghiniana* (Pirona); Polšak, p. 67.
1965b *Sauvagesia meneghiniana* (Pirona); Polšak, p. 450.
1965b *Sauvagesia meneghiniana dalmatica* Polšak; Polšak, p. 450.
1969 *Sauvagesia meneghiniana* (Pirona); Polšak and Mamužić, p. 240.
1969 *Sauvagesia meneghiniana dalmatica* Polšak; Polšak and Mamužić, p. 240.
1972*b* *Sauvagesia meneghiniana* (Pirona); Campobasso, p. 452, pl. 4, fig. 2.
1975 *Sauvagesia meneghiniana* (Pirona); Civitelli and Mariotti, p. 95, text-fig. 7.
1978 *Sauvagesia meneghiniana* (Pirona); Polšak *et al*., p. 190.
1979 *Sauvagesia meneghiniana* (Pirona); Polšak, pp. 206, 224.
1980 *Sauvagesia meneghiniana*; Laviano and Sirna, p. 69.
1981 *Sauvagesia meneghiniana* (Pirona); Polšak, p. 454.
1981 *Sauvagesia meneghiniana* (Pirona); Sánchez, p. 199 [with synonymy].
1981 *Sauvagesia meneghiniana dalmatica* Polšak; Sánchez, p. 199 [with synonymy].
1982 *Sauvagesia meneghiniana* (Pirona); Polšak *et al*., text-fig. 3.
1982 *Sauvagesia meneghiniana dalmatica* Polšak; Polšak *et al*., text-fig. 3.
1990 *Sauvagesia* cf. *meneghiniana*; Cestari and Pantosti, text-fig. 4.
1990 *Sauvagesia meneghiniana*; Gušić and Jelaska, text-fig. 15.

1993 *Sauvagesia meneghiniana* (Pirona) Toucas; Pleničar, p. 53, pl. 4, figs 2–4.
1995*b* *Sauvagesia meneghiniana* (Pirona); Caffau and Pleničar, p. 237, pl. 8, fig. 3.

Syntypes. Pirona (1869), plate 16, figures 1–12.

Material. Five RVs from Loutsion (R515, R516b, R716–R717, R720), three from Tsouka Hill (R519, R573, R576), three from Dionysos (R361–R362, R388) and one from Megali Lakka gorge (R555).

Description. Dimensions of RVs and characters of the radial bands are listed in Table 6. RVs conical or elongated-conical, ornamented with prominent longitudinal ribs that are interrupted at varying distances by terraces formed by steeply inclined shell lamellae. Furrows appear V-, U- or box-shaped, depending on the spacing of the bordering ribs; furrows and ribs have one to two costellae. Vb is depressed between two ribs or protrudes externally as far as the tips of the bordering ribs, it is ornamented with seven or eight delicate costellae. Ib is narrow and has one, rarely two longitudinal ribs. Pb is more or less deeply depressed, wider than Ib and about half as wide as Vb; costellae are only preserved on Pb of one RV.

LV not preserved, but one RV reveals dorsally grooved sockets of (1) and (3), and a large transverse section of (1) that almost completely occupies (1′), and a much smaller (3) that was sectioned near its tip. (1′) and (3′) are bordered ventrally by pronounced projections of the inner shell. The posterior projection, ventrally of (3′), is extended towards the shell's anterior to form a thin septum that separates (3′) from the main body-cavity. It thickens anteriorly and forms (2). Anterior and posterior of the ligamental ridge are two sub-cylindrical cavities.

Cellular structure of outer shell layer is regularly hexagonal and has only a few sub-polygonal, rectangular or pentagonal cells; mean diameter of cells is 0·3 mm. Maximum vertical spacing of funnel plates is 0·7 mm; they are shallowly inclined, undulate exteriorly and are downfolded in the longitudinal ribs. Vb and Pb have a thick cortex of compact structure. In conical, thick-shelled specimens, the outer shell is spotted with compact areas; the cells are slightly smaller and funnel plates are more closely spaced when compared with slender, thin-shelled RVs.

TABLE 6. *Sauvagesia meneghiniana* (Pirona, 1869); Σ= number of longitudinal ribs except those on the ventral–, inter–, and posterior bands. Minimum and maximum widths of the interior shell (body cavity) have been measured in commissural transverse sections only. All measurements in mm.

		width commiss.		apical		interior		width Vb		Ib		Pb		ribs			
No.	length	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.	Σ	Vb	Ib	Pb
R519	>127	68	70	41	49	38	41	14	15	6	10	9	9	21	7	1	6
R576	>108	55	65	26	29	39	45	14	25	3	7	6	9	24	7	1	–
R515	>84	67	75	13	15	42	48	9	22	2	10	–	7	23	7	2	–
R516	>73	–	–	25	27	14	18	3	10	–	–	–	–	–	–	–	–
R361	>67	36	45	22	29	–	–	10	11	2	–	5	5	>9	–	1	–
R362	>48	37	47	25	34	–	–	12	13	2	–	5	6	20	7	1	–
R573	>116	–	69	21	27		46	5	18	3	–	3		–	8	2	–
R717	>105	49	59	–	–	38	42	–	13	–	6	–	8	–	9	–	–

Remarks. Shell structures and diameters of cells of other species of *Sauvagesia* from the Santonian–Lower Campanian of Istria (Polšak 1967*b*) are very similar. In contrast, the stratigraphically older *S. nicaisei* (Coquand, 1862) has much larger cells of more irregular outline (Amico 1978).

Distribution. Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982), southern Alps, Apennines, Caucasus; Maastrichtian of the Adriatic island Brač (Gušić and Jelaska 1990).

Sauvagesia tenuicostata Polšak, 1967*b*

Plate 20, figures 1–5; Text-figure 38C

1964 *S. tenuicostata* n. sp. Polšak, p. 67 [*nomen nudum*].
1965b *Sauvagesia tenuicostata* n. sp. Polšak, p. 451 [*nomen nudum*].
*1967*b* *Sauvagesia tenuicostata* n. sp. Polšak, pp. 86, 189, pl. 50, figs 1–5; pl. 51, figs 1–4; pl. 52, figs 1–7; pl. 53, figs 1–11.
1969 *Sauvagesia tenuicostata* Polšak; Polšak and Mamužić, p. 240.
1973 *Sauvagesia tenuicostata* Polšak; Pleničar, p. 192, pl. 3, fig. 1.
1975 *Sauvagesia tenuicostata* Polšak; Civitelli and Mariotti, p. 97, text-fig. 9.
1976 *Sauvagesia tenuicostata* Polšak; Lupu, p. 133, pl. 21, figs 3a–b, 4.
1977 *Sauvagesia tenuicostata* Polšak; Pons, p. 75, pl. 73, figs 1–4.
1980 *S. tenuicostata*; Laviano and Sirna, p. 69.
1981 *Sauvagesia tenuicostata* Polšak; Sánchez, p. 203.
1982 *Sauvagesia tenuicostata* Polšak; Accordi *et al.*, p. 772, pl. 4, figs 1, 5.
1982 *Sauvagesia tenuicostata* Polšak; Polšak *et al.*, text-fig. 3.
1982 *Sauvagesia tenuicostata* Polšak; Pons, tab. 2.
1983 *Sauvagesia tenuicostata*; Gallemi *et al.*, tab. 3.
1985 *Sauvagesia tenuicostata* Polšak; Laviano, p. 332, pl. 8, fig. 2; pl. 10, figs 1, 3; pl. 11, fig. 3; pl. 16, figs 3–4.
1987 *Sauvagesia tenuicostata*; Accordi *et al.*, p. 139.
1989 *Sauvagesia tenuicostata*; Pieri and Laviano, p. 352.
1989 *Sauvagesia tenuicostata*; Sirna and Cestari, p. 712.
1990 *Sauvagesia tenuicostata* (Polšak); Cestari and Pantosti, p. 45, text-fig. 4.
1990 *Sauvagesia tenuicostata*; Gušić and Jelaska, text-fig. 15.
1990 *Sauvagesia tenuicostata* (Polšak); Sirna, p. 25.
1991 *S. tenuicostata* Polšak; Šribar and Pleničar, p. 179.
1992 *Sauvagesia tenuicostata* Polšak; Cestari *et al.*, p. 360.
1993 *Sauvagesia tenuicostata* Polšak; Carannante *et al.*, p. 28.
?1993 *Sauvagesia tenuicostata* Polšak; Cherchi *et al.*, p. 95, pl. 5, fig. 2 [cf.].
1993 *Sauvagesia tenuicostata* Polšak; Gili, tab. 1.
1993 *Sauvagesia tenuicostata* Polšak; Ruberti, p. 965.
1995*b* *Sauvagesia tenuicostata* Polšak; Caffau and Pleničar, p. 238, pl. 11, figs 1–3.
1996 *Sauvagesia tenuicostata* Polšak; Paris and Sirna, p. 193, pl. 2, fig. 10.
1996 *Sauvagesia tenuicostata*; Sanders, p. 852.
1997 *Sauvagesia tenuicostata*; Höfling, pl. 20, fig. 2.
1997 *Sauvagesia tenuicostata* Polšak; Ruberti, tab. 1.

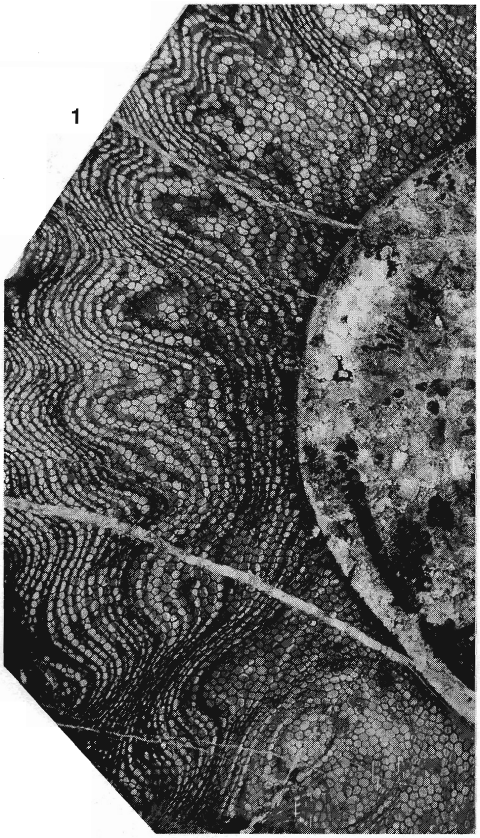
Holotype. Polšak (1967*b*), plate 50, figure 1, 1a, 1b.

Material. Eight specimens from Dionysos (R229, R240–R241, R286, R338, R346), one of them with both valves conjoined (R237), and one RV from Anthochorion (R192).

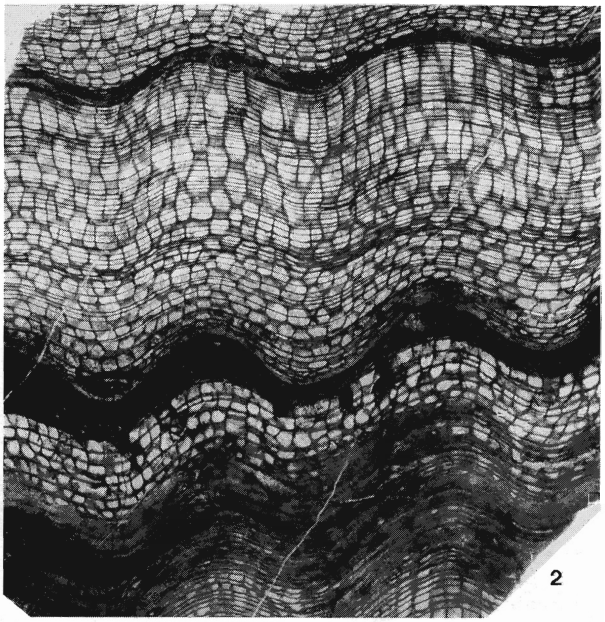
Description. Conical or elongated-conical RVs have a commissural diameter of up to 60 mm and exceed 90 mm long. Sculpture is formed by evenly spaced, delicate longitudinal ribs and hardly protruding shell lamellae that produce a zigzag pattern on the exterior surface. Broad Vb, narrow Ib and Pb are discernible in transverse sections of some specimens but their delicate costellae are not preserved. The ligamental ridges of some RVs are short, triangular and have an undulating inner surface and, thus, resemble that of the holotype. In other specimens the ligamental ridge is narrow and has a straight truncation at its inner termination. The LV is almost hemispherically convex, without canals or pseudocanals. (1) and (3) are dorsally grooved and are structured by oblique ledges that point towards the centre of the shell. Prominent projections of the

EXPLANATION OF PLATE 20

Figs 1–5. *Sauvagesia tenuicostata* Polšak, 1967*b*; R229, Dionysos; shell structures. 1, transverse section, anterodorsal; × 3·4. 2, anterodorsal tangential section; × 7·5. 3, radial section of Vb; × 7·5. 4, transverse section, anterodorsal; × 7·1. 5, transverse section of ventral and posterior band; × 3·3.



1



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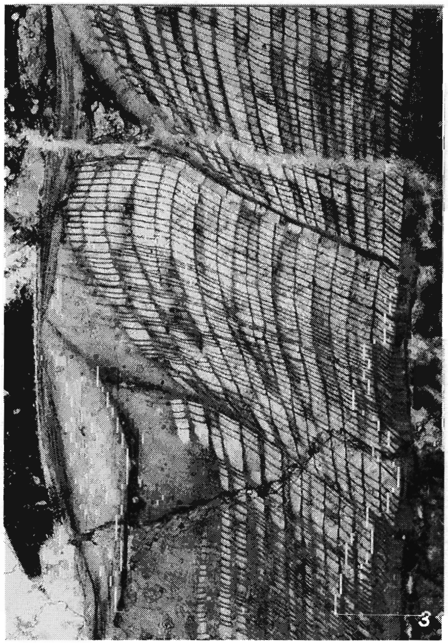

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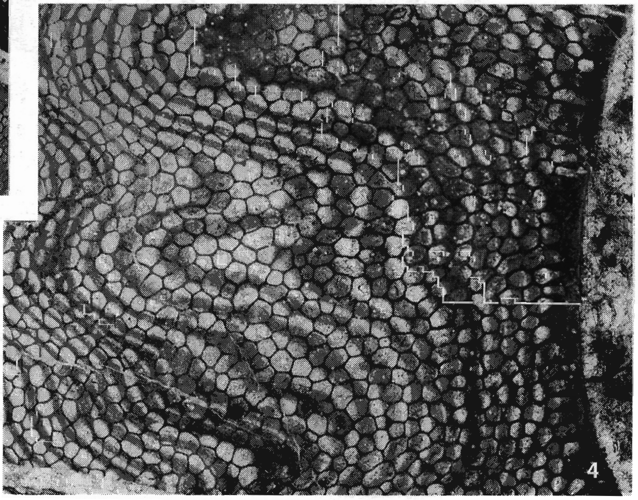

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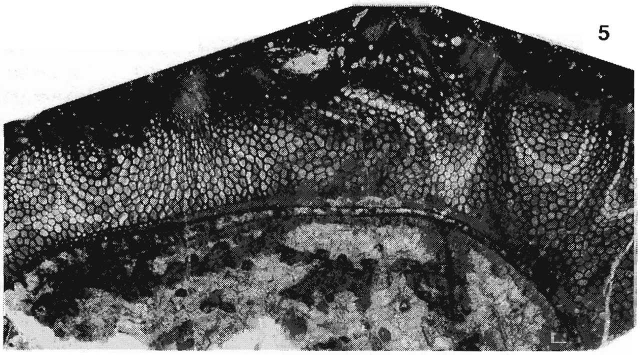
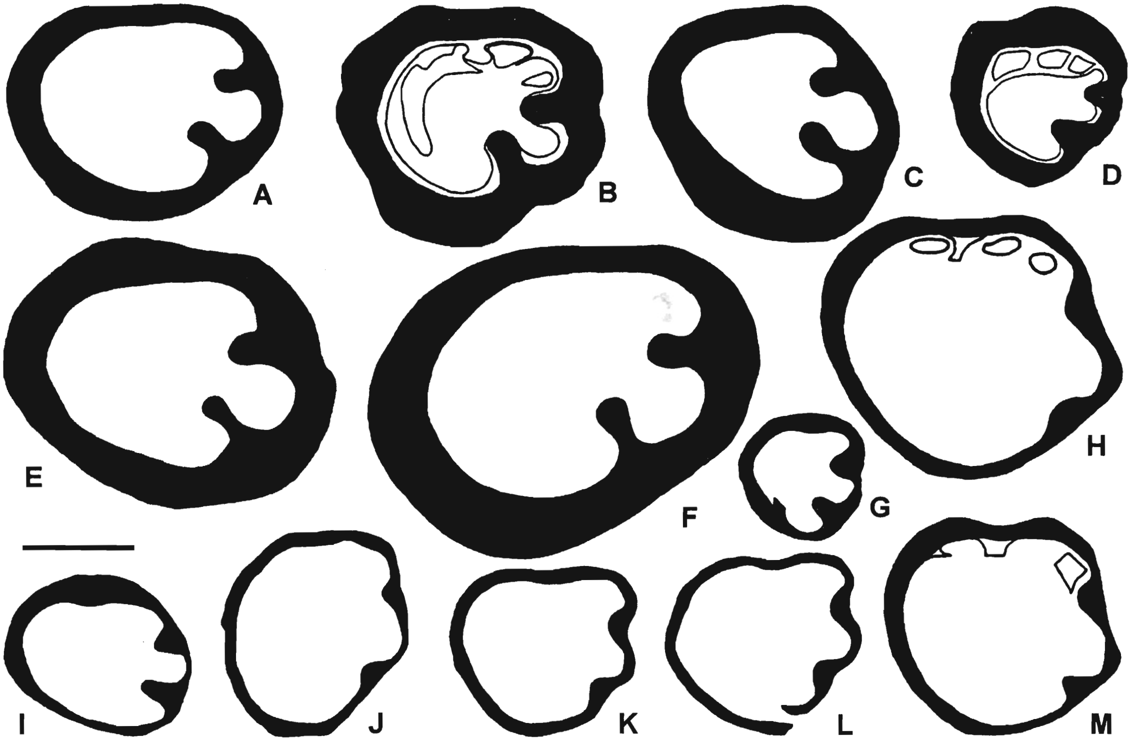


5

STEUBER, *Sauvagesia*



TEXT-FIG. 46. A–C, E–F, *Hippurites cornucopiae* Defrance, 1821; A, C, E–F, Akraifnion; B, Tuz Gölü, Turkey. D, G, I, *Hippuritella variabilis* (Munier-Chalmas, *in* Gaudry, 1867); G, I, Kakotopia Mountain; D, Tsouka Hill. H, J–M, *Hippuritella lapeirousei* (Goldfuß, 1840), Akraifnion. RV sections; A, H573; B, H325; C, H265; D, H533; E, H574; F, H337; G, H567; H, H255; I, H568; J, H569; K, H570; L, H260; M, H571. Scale bar represents 10 mm.

inner shell border (1′) and (3′) ventrally. Ma extends further ventrally than mp, both are rather narrow. Anterior and posterior of the ligamental ridge, respectively, is a small cavity triangular or round in outline.

Cells of the outer shell layer are remarkably regular, hexagonal, less commonly penta- or heptagonal, and very rarely sub-polygonal. Mean diameter of cells is 0·4 mm. Vertical spacing of funnel plates amounts to 0·4 mm, but is commonly much lower. Funnel plates are intensely plicated without any structural modification of the radial bands. The outer shell layer tends to disintegrate along the funnel plates so that their plications can be perfectly studied on such fragments.

Distribution. Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982), Pyrenees, Apennines, of Istria and Romania; Maastrichtian of the Adriatic Island Brač (Gušić and Jelaska 1990).

Family HIPPURITIDAE Gray, 1848

Genus HIPPURITELLA Douvillé, 1908*a*

Type species. *Hippurites maestrei* Vidal, 1878.

Hippuritella lapeirousei (Goldfuß, 1840)

Text-figure 46H, J–M

*v1840	*Hippurites Lapeirouseii* Goldfuß, p. 303, pl. 165, fig. 5a–c, e–f.
v1895	*Hippurites Lapeirousei* Goldfuss; Douvillé, p. 164, pl. 24, figs 7–8.
non 1900	*Hippurites Lapeirousei* Goldfuss; Parona, p. 11, pl. 1, figs 2–3.
non 1900	*Hippurites Lapeirousei* Goldf.; Redlich, p. 26, pl. 2, fig. 2a–d.

?1926 *Hippurites* (*Orbignya*) *Lapeirousei* Goldf.; Parona, p. 15.
1928*a* *Hippurites* (*Orbignya*) *Lapeirousei* Goldfuß; Klinghardt, pl. 23, fig. 10; pl. 24, fig. 13.
1932 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuß; Kühn, p. 54 [with synonymy].
?*1932* *Hippurites* (*Orbignya*) *Lapeirousei* Goldf.; Parona, p. 99.
1933 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Milovanović, p. 137, text-figs 64–67.
1934 *Orbignya Lapeirousei* Goldf.; Boissevain, p. 164, text-fig. 27.
?1934 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Milovanović, p. 223, text-fig. 18.
1935 *Hipp.* (*Orbignya*) *lapeirousei* Goldfuß; Klinghardt, p. 23.
1935 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Milovanović, p. 50.
1936 *Hippurites* (*Orb.*) *lapeirousei* Goldfuss; Milovanović, p. 41.
1937 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Milovanović, p. 128.
1938*b* *H.* (*Orbignya*) *lapeirousei* Goldfuss; Milovanović, p. 245.
1940 *Orbignya Lapeirousii* (Goldfuss); van de Geijn, p. 52, text-figs 1–4.
1946*a* *Hippurites* (*Orbignya*) *Lapeirousei* Goldfuss; Stchépinsky, p. 129, pl. 21, fig. 1,1a.
1946b *Hipp.* (*Orbignya*) *lapeirousei* Goldfuss; Stchépinsky, p. 354.
1956 *Hippurites Lapeirousei* Goldf.; Brunn, p. 128.
1958 *Hippurites* (*Orbignya*) *lapeirousei* Goldf.; Tavani, p. 171.
1959 *Hippurites* (*Orb.*) *lapeirousei* Goldf.; Petković *et al.*, p. 287.
1963 *Hippurites* (*Orbignya*) *lapeirousei*; Ambrosetti, p. 213.
1964 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Slišković and Luburić, p. 7.
1965 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Mamužić, p. 344.
1965 *Orbignya lapeirousei* (Goldfuss); Pamouktchiev, p. 26, text-fig. 1.
1965a *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Polšak, p. 337.
1968 *Hippurites lapeirousei* Goldf.; Bogdanović, p. 76.
1968a *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Slišković, p. 44.
1969 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Polšak and Mamužić, p. 240.
1969 *Hippurites* (*Orbignya*) *lapeirousei* n. subsp.; Polšak and Mamužić, p. 239.
1972 *Hippurites* (*O.*) *lapeirousei* Goldfuss; Sladić-Trifunović, text-fig. 13b [cop. Goldfuß 1840].
1972 *Hippurites* (*Orbignya*) cf. *lapeirousei* Goldfuss; Sladić-Trifunović, pp. 131, 147, pl. 11, fig. 1; pl. 12, fig. 1; text-fig. 14a.
1973 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Slišković, pp. 15, 18.
1975 *Hippurites lapeirousei* Goldfuss; Lupu, p. 222, pl. 4, fig. 10.
1975 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Pleničar, pp. 87, 107, pl; 1, fig. 1; text-fig. 2.
1975d *Hippurites* (*O.*) *lapeirousei*; Slišković, p. 139.
1977 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Sladić-Trifunović, p. 258.
1978 *Hippurites lapeirousei*; Sladić-Trifunović, pp. 428, 440.
1980 *H. lapeirousei*; Laviano and Sirna, p. 69.
1980 *Hippurites* (*O.*) *lapeirousei* Goldfuss; Sladić-Trifunović, p. 293.
1981 *Hippuritella lapeirousei* (Goldfuss); Sánchez, p. 10 [with synonymy].
1982a *Hippuritella lapeirousei* Gold.; Bilotte, p. 1020.
1982c *Hippuritella lapeirousei* Gold.; Bilotte, p. 111.
non 1982 *Hippurites lapeirousei* Goldfuss; Czabalay, pp. 44, 81, pl. 24, fig. 1.
1982 *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Polšak *et al.*, text-fig. 3.
1982 *Hippuritella lapeirousei* (Goldfuss); Pons, tab. 3.
?*1983* *H. lapeirousei*; Czabalay, text-fig. 3.
1983 *Hippuritella lapeirousei*; Gallemi *et al.*, tab. 3.
?1983 *Hippurites* (*Orbignya*) cf. *lapeirousei* Goldfuss; Özer, p. 18, pl. 3, fig. 3.
1983 *Hippuritella* cf. *lapeirousei* Goldf.; Philip, p. 90, fig. 4.
1983 *Ha. lapeirousei*; Philip and Bilotte, tab. 2.
1983 *Hippurites lapeirousei*; Sladić-Trifunović, tab. 1.
1983 *Hippurites* (*O.*) *lapeirousei*; Slišković, p. 12.
1984 *Hippuritella lapeirousei* (Goldf.); Bilotte, pl. 39, fig. 9.
1984b *Hippurites* (*Orbignya*) *lapeirousei* Goldfuss; Slišković, p. 215.
1985 *Hippuritella lapeirousei* Gold.; Bilotte, p. 340, tab. 42.
1985 *Hippurites* (*Orbignya*) *lapeirousei* (Goldfuss); Polšak, pp. 4, 17.
1986*b* *Hippuritella espaillaciana espaillaciana* (d'Orbigny); Pamouktchiev, p. 100, pl. 2, figs 1–3 [cop. d'Orbigny 1847], figs 4–5 [cop. Toucas 1903], fig. 6 [cop. Douvillé 1895].

1986*b* *Hippuritella espaillaciana toucasi* subsp. n. Pamouktchiev, p. 101, pl. 1, figs 4–5 [cop. Toucas 1903].
1986*b* *Hippurites lapeirousei* Goldfuss; Pamouktchiev, p. 98, pl. 1, fig. 1 [cop. Goldfuß 1840], figs 2–3 [cop. Douvillé 1895].
1988b *H. lapeirousei*; Özer, p. 49.
1989 *Hippurites lapeirousei*; Accordi *et al.*, p. 165.
1989 *Hippuritella lapeirousei* (Goldf.); Pascual *et al.*, p. 225, text-fig. 3.
1989 *H. lapeirousei* Goldfuss; Sladić-Trifunović, p. 149.
1990 *Hippurites lapeirousei*; Gušić and Jelaska, text-fig. 11.
1991 *Hippurites (Ha.) lapeirousei*; Floquet, text-fig. 286.
1992b *Hippurites lapeirousei* Goldfuss; Özer, p. 133.
1992 *Hippuritella lapeirousei* (Goldfuss); Swinburne *et al.*, text-fig. 2.
1992 *Hippuritella lapeirousei* (Goldfuss); Vicens, p. 125, pl. 1, figs 16–20; text-figs 4f, 8a–c.
1993b *Hippurites lapeirousei* Goldfuss; Steuber, p. 47.
1993 *Hippurites lapeirousei* Goldfuss; Steuber *et al.*, text-fig. 11.
1993 *Hippurites lapeirousei* Goldfuss; Swinburne and Noacco, p. 33.
1995*a* *Hippuritella lapeirousei* (Goldfuss); Caffau and Pleničar, p. 124, pl. 1.
1995*b* *Hippuritella lapeirousei* (Goldfuss); Caffau and Pleničar, text-fig. 2b [cop. Vicens 1992], 2d [cop. Douvillé 1895].
?1995 *Hippurites* aff. *lapeirousei* Goldfuss; Morris and Skelton, p. 292, pl. 5, figs 1–2.
1997 *Hippuritella lapeirousei* (Goldfuss); Höfling, pl. 17, figs 5–6.

Syntypes. Goldfuß (1840), plate 165, figure 5a–c, e–f.

Material. Fifteen transverse sections in compact limestones from Akraifnion, together with *Hippurites cornucopiae* Defrance, 1821; H255, H260, H262–H263, H268, H546, H569–H571. Three RVs (transverse sections in limestones) from Kefallinia Peninsula near Antikyra (H401).

Description. RV elongated-conical, outer shell layer thin, without prominent longitudinal ribs; Dmax 23 mm. Inner margin of outer shell layer slightly inflected dorsally. P1 and P2 formed by projecting thickenings of the outer shell layer, the position of each is indicated externally by a wide, shallow longitudinal furrow. $(1')$, (2) and $(3')$ located close to the dorsal shell margin, mp$'$ between $(3')$ and P1.

Remarks. The thin outer shell layers and the faintly projecting pillars allow a safe recognition of the Boeotian specimens, which are almost identical to the syntypes of *Hl. lapeirousei*. Thick-shelled valves with similar hinge and pillars that have been reported from equivalent stratigraphical horizons of other eastern Mediterranean localities (Sladić-Trifunović 1972; Laviano 1985) are difficult to separate from *Hl. lapeirousei*.

Distribution. Maastrichtian of the Mediterranean region, Iran, Afghanistan, probably in the Arabian Peninsula, and in the Boreal Realm (type locality near Maastricht); Upper Campanian of northern Castile (Floquet 1991).

Hippuritella resecta (Defrance, 1821)

*1821 *Hippurites resecta* Defrance, p. 196.
1993*a* *Hippuritella resecta* (Defrance); Steuber, p. 39, text-fig. 3c–3d [with synonymy and description].
1993 *Hippuritella resecta* (Defrance); Steuber *et al.*, p. 258.

Syntype. Douvillé (1892*a*), plate 5, figure 9, 9a.

Material. Three RVs, in pseudocolony with *Vaccinites inferus* (Douvillé, 1891), from Marmeko quarry (H251).

Description. See Steuber (1993*a*).

Distribution. Middle to Upper Turonian of the Mediterranean region.

Hippuritella variabilis (Munier-Chalmas, *in* Gaudry, 1867)

Text-figure 46D, G, I

*1867 *Hippurites variabilis* Munier-Chalmas; Munier-Chalmas, *in* Gaudry, p. 390 [*nomen dubium*].
v1892*a* *Hippurites variabilis* Munier-Chalmas; Douvillé, p. 50, pl. 7, fig. 17.
v.1910 *Hippurites* (*Hippuritella*) *variabilis* Mun.-Chalm.; Douvillé, p. 40, pl. 2, fig. 8.
1932 *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Kühn, p. 72 [with synonymy].
1933 *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Milovanović, p. 174.
1934 *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Milovanović, pp. 187, 253.
1937 *H.* (*Hippuritella*) *variabilis* Munier-Chalmas; Milovanović, p. 128.
1946*a* *Hippurites* (*Orbignya*) *variabilis* Munier-Chalmas; Stchépinsky, p. 126, pl. 17, figs 6–9.
1946b *Hipp.* (*Orbignya*) *variabilis* Munier-Chalmas; Stchépinsky, p. 353.
1951a *H.* (*Hippuritella*) *variabilis* Munier-Chalmas; Milovanović, p. 18.
1963 *H. variabilis* Mun. Chal.; Ambrosetti, p. 213.
1965a *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Polšak, p. 337.
1965 *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Slišković, p. 373.
1966 *Hippurites variabilis* Munier-Chalmas; Todiriţă-Mihăilescu, p. 72, pl. 48, fig. 6.
1968 *Hippurites variabilis* Mun.-Chalm.; Bogdanović, p. 76.
1968a *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Slišković, p. 43.
1969 *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Polšak and Mamužić, p. 240.
1978 *H.* (*Hippuritella*) *variabilis* Munier-Chalmas; Caus *et al.*, p. 457.
1978 *Hippuritella variabilis* (Munier-Chalmas); Pamouktchiev, p. 238, tab. 1.
1978 *H.* (*O.*) *variabilis* Munier-Chalmas; Polšak *et al.*, p. 190.
1979 *Hippurites* (*Orbignya*) *variabilis* Munier-Chalmas; Polšak, pp. 205, 224, pl. 10, fig. 3.
1981 *H. variabilis* Mun.-Chalm.; Bilotte, text-fig. 2.
1981*b* *Hippuritella variabilis variabilis* (Munier-Chalmas); Pamouktchiev, p. 161, pl. 78, fig. 1, 1a.
1981 *Hippurites* (*Orbignya*) *variabilis* Munier-Chalmas; Polšak, p. 454, text-fig. 7c [cop. Polšak 1979].
1981 *Hippuritella variabilis* (Munier-Chalmas); Sánchez, p. 14 [with synonymy).
1982c *Hippuritella variabilis* Mun.-Ch.; Bilotte, p. 111.
?1982 *Hippurites variabilis* Munier-Chalmas; Czabalay, pp. 44, 80, pl. 25, figs 3–5; text-fig. 23.
1982 *Hippurites* (*Hippuritella*) *variabilis* Mun.-Chalm.; Polšak *et al.*, text-fig. 3.
1982 *Hippuritella variabilis* (Mun.-Chalm.); Pons, tab. 2.
1983 *Ha. variabilis*; Philip and Bilotte, tab. 1.
1983 *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Slišković, pp. 3, 12.
1984 *Hippuritella variabilis* (Munier-Chalmas); Busulini *et al.*, p. 251, text-fig. 1.
1984b *Hippurites* (*Hippuritella*) *variabilis* Munier-Chalmas; Slišković, p. 214.
1985 *Hippuritella variabilis* Mun.-Ch.; Bilotte, p. 340, tab. 31.
1987 *Hippuritella variabilis*; Accordi *et al.*, p. 140.
1989 *Hippurites nabresinensis* Futterer; Özer, p. 339, pl. 1, fig. 10.
1989 *Hippuritella variabilis* (Mun.-Chal.); Pascual *et al.*, p. 224, text-fig. 3.
1990 *Hippuritella variabilis*; Gušić and Jelaska, text-fig. 11.
1991 *Hippurites* (*Ha.*) *variabilis*; Floquet, text-fig. 286.
1992a *Hippuritella variabilis* Munier-Chalmas; Peza, p. 88.
1992 *Hippuritella variabilis* Munier-Chalmas; Swinburne *et al.*, text-fig. 2.
.1992 *Hippuritella variabilis* (Douvillé); Vicens, p. 123, pl. 1, figs 9–10 [cop. Douvillé 1892*a*], figs 11–15; text-fig. 7.
1993 *Hippurites* (*Hippuritella*) *variabilis*; Camoin, p. 157.
1993*b* *Hippuritella variabilis* (Munier-Chalmas); Steuber, p. 46, pl. 1, fig. 3.
1993b *Hippurites* cf. *socialis* Douvillé; Steuber, p. 46.
1993 *Hippuritella variabilis* (Munier-Chalmas); Steuber *et al.*, text-fig. 8.

Syntypes. Douvillé (1892*a*), plate 7, figures 4–7, 9–12, 14–15, 18. The first diagnosis of the species (Munier-Chalmas, *in* Gaudry, 1867) is insufficient ('Petite espèce très variable extérieurement, qui abonde à l'Eschert'), and is part of a list-type description of the rudists of Keratovouno Hill. Munier-Chalmas gave the original material of *Hl. variabilis* from Leychert to Douvillé, who provided a detailed description in 1892. Later, a badly preserved, squashed RV from the Munier-Chalmas collection from Keratovouno Hill was figured as *Hippurites maestrei* Vidal, 1878 (Douvillé 1897*a*, pl. 32, fig. 7). I did not find *H. maestrei*, *Hl. variabilis*, or morphologically similar shells at this locality.

Material. Ten RVs in compact limestones from the southern slope of Kakotopia Mountain at the Bay of Saltsas (H83, H284/2, H286–H288, H567–H568), and one RV from the quarry at Tsouka Hill (H533).

Description. RV elongated-conical, without distinct longitudinal ribs. Dmax 15 mm, more than 50 mm long. P0 formed by inconspicuous inflection and swelling of outer shell layer. P1 located posterodorsally, P2 posteroventrally, both with broad bases, and flanks that converge towards the interior of the shell. The hinge is preserved in the specimen from Tsouka Hill (Text-fig. 46D): (1′), (2) and (3′) located immediately adjacent to the dorsal outer shell, as is mp′ which is found between (3′) and P1.

Distribution. Campanian of the Pyrenees, Dinarids, and Romania (Sánchez 1981). Campanian of Sardinia, the Apennines and Turkey. Middle Campanian of the southern Pyrenees (Vicens 1992); Coniacian ('primitive forms') of Algeria (Camoin 1993); Upper Santonian-Campanian of northern Castile (Floquet 1991).

Genus HIPPURITES Lamarck, 1801

Type species. Hippurites bioculata Lamarck, 1801.

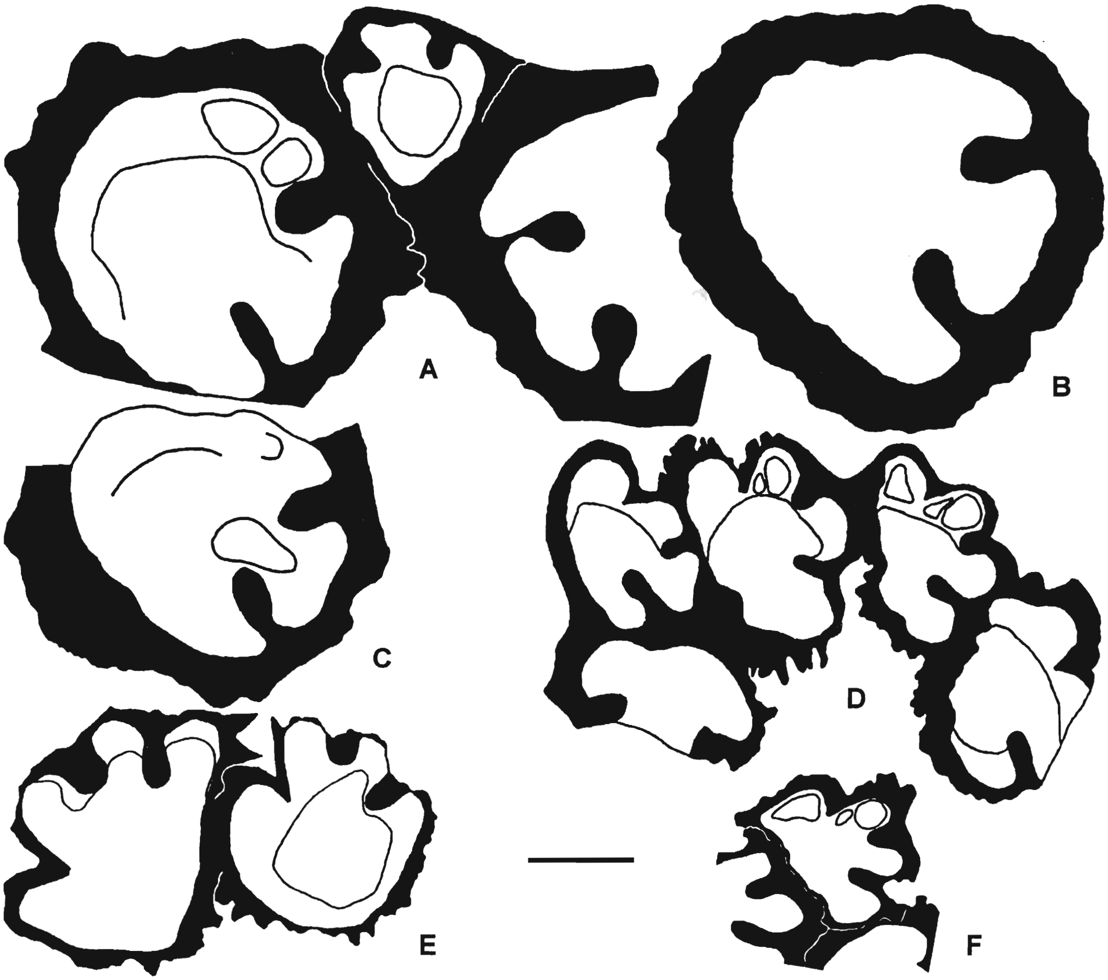
Hippurites cf. *canaliculatus* Rolland du Roquan, 1841

Text-figure 47D–F

*1841	*Hippurites canaliculata* Rolland du Roquan, p. 50, pl. 3, figs 2–4; pl. 7, fig. 2.
v1893	*Hippurites canaliculatus* Rolland du Roquan; Douvillé, p. 61, pl. 8, figs 6–10.
v1893	*Hippurites crassicostatus* n. sp. Douvillé, p. 63, pl. 8, figs 11–13; pl. 9, fig. 1; text-fig. 45.
v1895	*Hippurites canaliculatus* Rolland du Roquan; Douvillé, p. 173, pl. 26, figs 8a, 9, 9a.
1932	*Hippurites* (*Orbignya*) *canaliculatus* Rolland du Roquan; Kühn, p. 40 [with synonymy].
1932	*Hippurites* (*Orbignya*) *crassicostatus* Douvillé; Kühn, p. 45 [with synonymy].
1932	*Hippurites* (*Orbignya*) *canaliculatus* Roll. du Roq.; Parona, p. 99.
1936	*O. canaliculata* Roll. du Roq.; Antonini, p. 120.
1937	*Hippurites* (*Orbignya*) *canaliculatus* Rolland du Roquan; Oosterbaan, p. 103, pl. 2, figs 19–21.
1938	*O. canaliculata* Rolland du Roquan; Antonini, p. 172.
1950	*Orbignya canaliculata* Rolland du Roquan; Rengarten, p. 47, pl. 8, fig. 2a–b; text-fig. 20.
1957a	*O. canaliculata* Roll. du Roq.; Astre, p. 193.
1959	*Orbignya canaliculata* Roll. du Roq.; Rengarten, p. 257.
1965	*H.* (*O.*) *canaliculata* Rolland du Roquan; Mamužić, p. 344.
1969	*Hippurites* (*Orbignya*) *canaliculatus* Rolland du Roquan; Polšak and Mamužić, p. 239.
1981	*H.* (*H.*) *canaliculatus* R. du R.; Bilotte, text-fig. 2.
1981	*H.* (*H.*) *crassicostatus* Douv.; Bilotte, text-fig. 2.
1981	*Hippurites canaliculatus* Rolland du Roquan; Sánchez, p. 16 [with synonymy].
1981	*Hippurites crassicostatus* Douvillé; Sánchez, p. 17 [with synonymy].
1982c	*Hippurites* (*H.*) *canaliculatus* R. du R.; Bilotte, p. 109.
1982	*Hippurites canaliculatus* Roll. du Roq.; Pons, tab. 1.
1983	*H. canaliculatus*; Philip and Bilotte, tab. 1.
1984	*Hippurites* (*Hippurites*) *canaliculatus* Rolland du Roquan; Bilotte, pl. 38, fig. 5.
1985	*Hippurites* (*H.*) *crassicostatus* Douv.; Bilotte, p. 342, tab. 31.
1985	*Hippurites* (*H.*) *canaliculatus* R. du R.; Bilotte, p. 342, tab. 31.
1989	*H. canaliculatus* Roll. du Roq.; Pascual *et al.*, p. 224, text-fig. 3.
p1992	*Hippurites canaliculatus* Rolland du Roquan; Vicens, p. 131, pl. 4, figs 1–3 [cop. Douvillé 1893], figs 5–11; text-figs 4c, 10a–d.
1997	*Hippurites* cf. *canaliculatus* Rolland du Roquan; Steuber *et al.*, p. 178, text-fig. 3j.

Syntypes. Rolland du Roquan (1841), plate 3, figures 2–4; plate 7, figure 2.

Material. Three pseudocolonies with nine, 11, and two RVs, respectively, from Paleokastron Hill (H523, H543, R652).



TEXT-FIG. 47. A–C, *Hippurites colliciatus* Woodward, 1855; D–F, *Hippurites* cf. *canaliculatus* Rolland du Roquan, 1841; all from Paleokastron Hill. RV sections; A, H381; B, H416; C H380; D, F, H523; E, R652. Scale bar represents 10 mm.

Description. All shells are grown in contact with conspecifics. Outer shell layers of juveniles less than 0·5 mm thick when in contact with other shells, but reaching 3 mm thick when free; ornamented irregularly with salient longitudinal ribs up to 3 mm wide. Position of pillars indicated on the exterior shell by deep longitudinal furrows, that of P0 being particularly prominent. Transverse section of P0 short and triangular, somewhat prolonged in several RVs, with blunt inner termination. Flanks of P1 predominantly parallel or sub-parallel, slightly pinched in a few RVs. P2 reaches almost double the length of P1, its flanks are parallel or slightly pinched. (1′) large, located close to the dorsal shell margin. Shape of (1′) is variable depending on the shape of the RV. (3′) much smaller than (1′), located posterior to P0. Mp′ between (3) and P1, immediately adjacent to the dorsal margin of the outer shell.

Remarks. According to the diagnosis given by Douvillé (1893), *Hippurites crassicostatus* Douvillé, 1893 differs from *H. canaliculatus* only in size and longitudinal ribbing. Other characters fail to separate both species clearly (Vicens 1992, p. 134). *Hippurites striatus* Defrance, 1821 differs in a strongly convex LV and details of its pore system (Toucas 1903), whereas the RV is rather similar to that of *H. canaliculatus*. Both morphospecies occur in the same stratigraphical horizon so that the variability of their LVs has to be assessed to decide whether *H. striatus* is an older synonym of *H. canaliculatus* (Vicens 1992).

Morphometric analyses have indicated an increase in diameter of RVs of *H. canaliculatus* from three successive horizons across the Santonian-Campanian boundary of the Sierra de Montsec (Vicens 1992). Dmax of the RVs from Paleokastron Hill ranges from 15 mm to 26 mm which corresponds to the size of shells from the lowermost horizon of the southern Pyrenees.

Distribution. Santonian–Lower Campanian of the southern Pyrenees (Pascual *et al*. 1989; Vicens 1992), Sardinia, Croatia and the Caucasus.

Hippurites colliciatus Woodward, 1855

Plate 25, figure 2; Text-figure 47A–C

*1855 *Hippurites colliciatus*, n. sp. Woodward, p. 58, pl. 4, fig. 5.
1897*a* *Hippurites colliciatus* Woodward; Douvillé, p. 221, pl. 32, fig. 8 [cop. Woodward 1855].
v.1897*a* *Hippurites colliciatus* Woodward; Douvillé, p. 221, pl. 32, fig. 9.
non 1900 *Hippurites colliciatus* Woodward var. *romanica* n. v. Redlich, p. 25, pl. 2, fig. 1a, 1b.
1932 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Kühn, p. 42 [with synonymy].
1933 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Milovanović, p. 172.
1934 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Milovanović, p. 187.
1934 *Orbignya colliciata* Woodward; Wiontzek, p. 9.
1935 *Hippurit*. (*Orbig*.) *colliciatus* Woodward; Klinghardt, p. 26.
1937 *H*. (*Orbignya*) *colliciatus* Woodward; Milovanović, p. 128.
1937 *Hippurites* (*Orb*.) *colliciatus* Woodw.; Zapfe, p. 76, text-fig. 3.
1944*b* *Hippurites* (*Orbignya*) *colliciatus* Woodward; Stchépinsky, p. 238, pl. 7, figs 1–2.
1946a *Hippurites* (*Orbignya*) *colliciatus* Woodward; Stchépinsky, p. 129, pl. 21, figs 2–3 [cop. Stchépinsky 1944*b*].
1946b *Hipp*. (*Orb*.) *colliciatus* Woodward; Stchépinsky, p. 354.
1959 *Hippurites colliciatus* Woodward; Aubouin, p. 152, pl. 16, fig. 2a.
1959 *Hippurites colliciatus* Woodward; Petković *et al*., p. 284.
1960 *Hippurites colliciatus* Woodward; Aubouin *et al*., p. 465.
1960 *Hippurites* (*Orbignya*) *exaratus* Zittel; Lupu and Lupu, p. 251, pl. 4, fig. 49; text-fig. 19.
1961 *H. colliciatus*; Lupu and Lupu, p. 275.
1962 *Hippurites* cf. *colliciatus* Woodw.; Celet, pl. 6, fig. 2a–b.
1962 *Hippurites exaratus* Zittel; Kaumanns, p. 303, text-fig. 5.
1963 *Hippurites colliciatus* Wood.; Ambrosetti, p. 213.
1965 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Benkö-Czabalay, p. 402.
1969 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Polšak and Mamužić, p. 240.
1970 *Hippurites* (*Orbignya*) *colliciatus* Wood.; Benkö-Czabalay, p. 277.
1974 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Slišković, p. 133.
1975d *H*. (*O*.) *colliciatus*; Slišković, p. 139.
1976 *Hippurites colliciatus* (Woodward); Kühn, *in* Andrusov, p. 14.
1978 *Hippurites colliciatus* Woodward; Pamouktchiev, p. 235, tab. 1.
1978 *Hippurites colliciatus* Woodward; Sladić-Trifunović, pp. 435, 443, fig. 8/1 [cop. Woodward 1855], fig. 8/2 [cop. Douvillé 1897*a*]. fig. 8/3 [cop. Kaumanns 1962]
1980 *Hippurites colliciatus* Woodward; Carbone *et al*., p. 206, pl. 5, fig. a.
1980 *H. colliciatus*; Laviano and Sirna, p. 69.
?1980 *Hippurites colliciatus* Woodward; Sladić-Trifunović, pp. 294, 299, pl. 5, fig. 1.
1981 *Hippurites colliciatus* Woodward; Carbone and Sirna, p. 437, text-fig. 6.
1981*b* *Hippurites colliciatus* Woodward; Pamouktchiev, p. 157, pl. 77, fig. 1, 1a.
1981 *Hippuritella colliciatus* Woodward; Sánchez, p. 10 [with synonymy].
1982 *Hippurites colliciatus* Woodward; Accordi *et al*., p. 770, pl. 4, figs 4, 7.
1982 *Hippurites colliciatus* Woodward; Czabalay, pp. 43, 80, pl. 10, figs 6–7; text-fig. 22.
1983 *H. colliciatus*; Czabalay, text-fig. 3.
1982 *Hippurites* (*O*.) *colliciatus* Woodward; Polšak *et al*., text-fig. 3.
1983 *Hippurites* (*Orb*.) *colliciatus* (Woodward); Pleničar and Premru, p. 194.
1983 *Hippurites colliciatus*; Sladić-Trifunović, tab. 1.

1984 *H. colliciatus* Woodward; Laviano, p. 187.
1984b *Hippurites* (*Orbignya*) *colliciatus* Woodward; Slišković, p. 216.
1985 *Hippurites colliciatus* Woodward; Laviano, p. 323, pl. 12, fig. 4.
1985 *Hippurites colliciatus* Woodw.; Lupu, p. 21.
1986 *H. colliciatus* Woodward; Kaya *et al.*, p. 14.
1986 *Hippurites colliciatus* Woodward; Negra and Philip, p. 51, pl. 1, fig. 2; pl. 2, fig. 2.
1987 *Hippurites colliciatus* Woodward; Accordi *et al.*, p. 140, pl. 1, fig. 10.
1987 *Hippurites colliciatus* (Woodward); Pejović and Radoičić, p. 132, tab. 2.
1989 *Hippurites colliciatus* Woodward; Accordi *et al.*, p. 165, tab. 1, pl. 2, fig. 4.
1989 *Hippurites colliciatus*; Borgomano and Philip, text-fig. 4.
1989*a* *Hippurites colliciatus* Woodward; Cestari and Sirna, p. 135, tab. 1, pl. 3, fig. 3.
1989*b* *Hippurites colliciatus* (Woodward); Cestari and Sirna, p. 19, pl. 1, fig. 1, tab. 1.
1989 *Hippurites colliciatus*; Luperto Sinni and Borgomano, p. 111.
1989 *Hippurites colliciatus*; Pieri and Laviano, p. 352.
?1989 *Hippurites colliciatus* Woodward; Sirna and Cestari, p. 712, text-fig. 3.
1989 *Hippurites colliciatus* Woodward; Sladić-Trifunović, p. 149.
1990 *Hippurites colliciatus* Woodward; Sirna, p. 25.
1992a *H. colliciatus* Woodward; Peza, p. 87.
1992*b* *Hippurites colliciatus* Woodward; Peza, p. 293, pl. 1, fig. 2; text-fig. 5.
.1992 *Hippurites colliciatus* (Woodward); Reali, p. 94, text-figs 3–4, tabs 2–3, pl. 1.
1992 *Hippurites colliciatus* Woodward; Swinburne *et al.*, text-fig. 2.
1993 *Hippurites colliciatus* Woodward; Carannante *et al.*, p. 25.
1993 *Hippurites colliciatus* Woodward; Cherchi *et al.*, p. 95, pl. 5, fig. 3.
1993 *Hippurites colliciatus* Woodward; Ruberti, p. 965, text-fig. 4b.
1993b *Hippurites colliciatus* Woodward; Steuber, p. 46.
1994 *Hippurites* (*Orbignya*) *colliciatus* Woodward; Fenerci, p. 1.
1996a *Hippurites colliciatus*; Laviano, p. 7.
1996b *Hippurites colliciatus*; Laviano, p. 145.
1996 *H. colliciatus*; Sanders, p. 852.
1997 *Hippurites colliciatus* Woodward; Ruberti, tab. 1, text-fig. 11c
1997 *Hippurites colliciatus* Woodward; Steuber *et al.*, p. 179, text-fig. 3i.
1998 *Hippurites colliciatus* Woodward; Steuber *et al.*, p. 389, text-fig. 3f.

Holotype. Woodward (1855), plate 4, figure 5 (drawing); Douvillé (1897*a*), plate 32, figure 8 (photograph).

Material. Four RVs from Paleokastron Hill (H380, H381, H416) and one RV found in limestone block at Agia Barbara (H269).

Description. RVs elongated-conical, grown solitary or in pseudocolonial contact with conspecifics; ornamented with irregularly spaced, low and rounded longitudinal ribs. Dmax 31 mm, length exceeding 110 mm. Inner margin of outer shell layer undulating, slightly bulging at the dorsal shell to form P0. P1 in juvenile specimens with sub-parallel flanks that become parallel or slightly pinched in adult shells. P2 quadrangular to oval, straight or curved posteriorly, slightly pinched. (1′) and (3′) near to the dorsal shell margin, as is mp′, which is located between (3′) and P1.

Remarks. The holotype is characterized by sub-parallel flanks of P1 and P2, whereas the pillars of almost all RVs that were subsequently attributed to this species are slightly pinched (for differences from *Hippurites cornucopiae* Defrance, 1821, see below). The variability of pillar morphology of this species was demonstrated with pseudocolonies from the Apennines (Reali 1992). P1 and P2 of most of these shells are pinched, more often and more intensely in P2 when compared with P1; pedunculate pillars were not found. Considering these characters and the general dimensions, the Boeotian shells are particularly similar to those that have been reported from Italy (Carbone *et al.* 1980; Cestari and Sirna 1989*b*; Reali 1992).

Distribution. Santonian of the Gosau, Apennines, Dinarids, Romania, Greece, Turkey and Iran (Sánchez 1981). Campanian–Maastrichtian of the Apennines (Cestari and Sirna 1989*b*), Carpathians (Andrusov 1976) and Tunisia

(Negra and Philip 1986). Middle Campanian of Bulgaria (Swinburne *et al.* 1992), Maastrichtian of southern Italy (Borgomano and Philip 1989). Lower Campanian of Turkey (Steuber *et al.* 1998).

Hippurites cornucopiae Defrance, 1821

Text-figure 46A–C, E–F

*1821 *Hippurites cornucopia* Defrance, p. 196.
1824 Hippurite, corne d'abondance; Defrance, Cahier 31, pl. 20, fig. 1, 1a–c [?*non* fig. 1, *teste* Douvillé 1897*a*].
v1897*a* *Hippurites cornucopiae* Defrance; Douvillé, p. 223, pl. 32, fig. 12.
v.1910 *Hippurites* (*Hippuritella*) *cornucopiae* Defrance; Douvillé, p. 79, pl. 7, figs 3–4.
1932 *Hippurites* (*Hippuritella*) *cornucopiae* Defrance; Kühn, p. 43 [with synonymy].
?1934 *Orbignya cornucopiae* Defrance sp., ex. aff. Rasse *rennensis* Douvillé; Wiontzek, p. 8.
1936 *Hippurites* (*Orb.*) *cornucopiae* Defrance; Milovanović, p. 41.
1944 *Hippurites cornucopiae* Defr.; Kühn, p. 23, figs 1–2.
1949 *Hippurites* (*Hippuritella*) *cornucopiae* Defr.; Tavani, p. 13, pl. 4, figs 7, 9.
1949 *Hippurites* (*Hippuritella*) *somalicus* n. sp. Tavani, p. 14, pl. 4, fig. 6 [*teste* Pons *et al.* 1992].
1952 *Hippurites cornucopiae*; Milovanović, p. 28.
1963 *Hippurites* (*Orbignya*) *cornucopiae*; Ambrosetti, p. 213.
1965a *Hippurites* (*Hippuritella*) *cornucopiae* Defrance; Polšak, p. 337.
1968 *Hippurites cornucopiae* Defr.; Bogdanović, p. 76.
1969 *Hippurites* (*Hippuritella*) *cornucopiae* Defrance; Polšak and Mamužić, p. 240.
1972 *Hippurites* (*Hippuritella*) *cornucopiae* Defrance; Sladić-Trifunović, pp. 131, 147, pl. 11, figs 2–3; pl. 13, figs 2–3.
1975d *H.* (*O.*) *cornucopiae*; Slišković, p. 139.
1981 *Hippuritella cornucopiae* (Defrance); Sánchez, p. 10 [with synonymy].
1982 *Hippurites cornucopiae* Defrance; Matteucci *et al.*, p. 81, text-fig. 4.
1983 *Hippurites cornucopiae* Defrance; Camoin, p. 223, pl. 7, fig. 1.
1983 *Hippurites cornucopiae* Defrance; Camoin *et al.*, p. 1093.
1983 *Hippurites cornucopiae* Defrance; Özer, p. 17, pl. 3, figs 6–7.
1983 *Hippuritella cornucopiae*; Sladić-Trifunović, tab. 1.
1984 *Hippuritella cornucopiae* (Defrance); Busulini *et al.*, p. 251, figs 1, 8.
1984b *Hippurites* (*Orbignya*) *cornucopiae* Defrance; Slišković, p. 216.
1985 *Hippurites* (*Hippuritella*) *cornucopiae* Defrance; Polšak, pp. 4, 17.
1987 *Hippurites cornucopiae* Defrance; Accordi *et al.*, p. 140, pl. 1, fig. 12.
1988 *Hippurites cornucopiae* Defrance; Camoin *et al.*, p. 130, text-fig. 4d.
1988b *H. cornucopiae*; Özer, p. 49.
1989 *Hippuritella cornucopiae* Defrance; Sladić-Trifunović, p. 149.
1990 *Hippurites cornucopiae* Defrance; Skelton *et al.*, p. 528, tab. 1.
1992*a* *Hippurites cornucopiae* Defrance; Özer, p. 77, pl. 1, figs 1–2.
1992b *Hippurites cornucopiae* Defrance; Özer, p. 133.
1992a *H. cornucopiae* Defrance; Peza, p. 87.
1992 *Hippurites cornucopiae* Defrance; Pons *et al.*, p. 224, text-fig. 8a–e.
1993 *Hippurites cornucopiae* Defrance; Özer, p. 169, fig. 2.
1993b *Hippuritella cornucopiae* (Defrance); Steuber, p. 47.
1993 *Hippuritella cornucopiae* (Defrance); Steuber *et al.*, text-fig. 11.
1994 *Hippurites cornucopiae*; Parente, p. 160.
1994 *Hippurites cornucopiae* Defrance; Pons *et al.*, p. 284, pl. 3, figs 1–3; text-fig. 3.
1995 *Hippurites cornucopiae* Defrance; Morris and Skelton, p. 292, pl. 5, figs 4–7.
1996a *Hippurites cornucopiae*; Laviano, pp. 3, 9.
1996b *Hippurites cornucopiae*; Laviano, p. 147.

Syntypes. Defrance (1824), Cahier 31, plate 20, figure ?1, 1a–c.

Material. More than 20 sections of RVs in compact limestones from Akraifnion (H259, H261, H264–H267, H337, H573–H574), together with *Hippuritella lapeirousei* (Goldfuß, 1840); other material from Gökdag, east of Tuz Gölü, Turkey (compare Özer 1983); H325–H333.

Description. RVs elongated-conical, Dmax 35 mm, more than 110 mm long; no distinct longitudinal ribbing. Outer shell layer thick when compared with diameter of RV; 0·1–0·3 mm wide, light- and dark-coloured segments alternate radially. Position of P0 indicated in a few RVs by a slight inflection of the dorsal shell, but this inflection is absent in most shells. P1 with parallel or slightly pinched bases. P2 slightly pinched, straight or slightly curved either posteriorly or anteriorly. No shells with preserved hinge have been found in Boeotia. A RV from Tuz Gölü is more complete and shows the arrangement of the myocardinal elements (Text-fig. 46B): as the transverse section was cut close to the commissure, (1) and ma are joined. Ma projects ventrally beyond the dorsal half of the shell. (1) embraces (2) ventrally with a tapering projection; (3) triangular and located close to the dorsal shell margin. Posterior flank of mp rounded, tapering anteriorly.

Systematic position. Since the detailed description by Douvillé (1897*a*), the pinched base of P2 is considered diagnostic of the species, although some of the subsequently figured RVs have parallel sides of P2. Similar specimens have been reported from Somalia (Pons *et al.* 1992) and are difficult to distinguish from *Hippurites colliciatus* Woodward, 1855. The problem of separating RVs of *H. cornucopiae* and *H. colliciatus* was also discussed by Parona (1900). The following characters are considered to separate the Boeotian specimens from *H. colliciatus*: (1) outer shell layer thick with respect to the diameter of RV; light-dark-coloured alternating radial stripes are seen in transverse section of the outer shell layer; (2) inner margin of outer shell layer dorsally smooth or inconspicuously inflected; and (3) smaller distance between P1 and P2.

RVs without preserved hinge are almost identical to those of *Hippurites bioculatus* Lamarck, 1801. Slightly smaller pillars and a strongly pinched P2 are barely sufficient to distinguish RVs of *H. bioculatus* and *H. cornucopiae* considering the intraspecific variability of both species. The determination of the Boeotian specimens is supported by their association with the late Campanian–Maastrichtian *Hippuritella lapeirousei* (Goldfuß, 1840), whereas the stratigraphical range of *H. bioculatus* is restricted to the Santonian.

Remarks. In the eastern Mediterranean, *H. cornucopiae* is found predominantly in compact, pure limestones. Therefore, it has frequently been described from transverse sections, but hinge and LV are known only from a few specimens (e.g. Özer 1983; Morris and Skelton 1995).

Distribution. Maastrichtian of the Apennines, Sicily, the Dinarids, Iran (Sánchez 1981), Sardinia, Albania, Turkey, Oman, United Arab Emirates and Somalia.

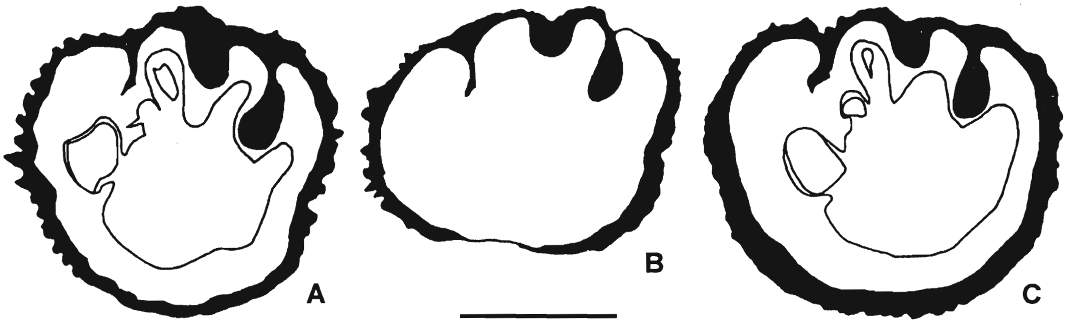
Genus VACCINITES Fischer, 1887

Type species. Hippurites cornuvaccinum Bronn, 1831.

Vaccinites archiaci (Douvillé, 1892*a*)

Plate 23, figure 1; Text-figure 48A–C

*1892*a* *Hippurites archiaci* Munier Chalmas; Douvillé, p. 45, pl. 5, figs 1–2, text-figs 30–33.
v*1892*a* *Hippurites archiaci* Munier Chalmas; Douvillé, p. 45, pl. 5, fig. 3.
v.1895 *Hippurites archiaci* Munier-Chalmas; Douvillé, p. 160, pl. 23, figs 5–6.
1932 *Hippurites* (*Vaccinites*) *archiaci* Munier-Chalmas; Kühn, p. 37 [with synonymy].
1959 *Vaccinites archiaci* Mun. Chal.; Aubouin, p. 63, pl. 1, fig. 1b.
1960 *Vaccinites archiaci* Mun.-Chal.; Aubouin *et al.*, p. 459.
1965 *Hippurites* (*Vaccinites*) *archiaci* Munier-Chalmas; Benkö-Czabalay, p. 402.
1966 *Hippurites* (*Vaccinites*) *archiaci* Munier-Chalmas; Todiriţă-Mihăilescu, p. 72, pls 21–22.
1967 *Hippurites* (*Vaccinites*) *archiaci* Douv.; Lupu and Lupu, p. 308.
1969 *Hippurites* (*Vaccinites*) *archiaci* Munier-Chalmas; Polšak and Mamužić, p. 239.



TEXT-FIG. 48. *Vaccinites archiaci* (Douvillé, 1892*a*) from Grammatiko, Vermion Mountains. RV sections; A, H465; B, H532; C, H466. Scale bar represents 30 mm.

1970 *H.* (*V.*) *archiaci* Munier-Chalmas; Benkö-Czabalay, p. 283.
1971 *Vacc. archiaci* (Douv.); Vogel, p. 65.
1974 *Hippurites archiaci* Mun.-Chal.; Patrulius, p. 173.
1975 *Hippurites* (*Vaccinites*) *archiaci* Munier-Chalmas, *manuscr.*; Pleničar, pp. 95, 110, pl. 8, figs 1–2; pl. 9, fig. 1.
1976 *Hippurites archiaci* (Munier-Chalmas); Kühn, *in* Andrusov, 14.
1978 *H.* (*V.*) *archiaci* Munier-Chalmas; Polšak *et al.*, *190.*
1979 *H.* (*V.*) *archiaci* Munier-Chalmas; Polšak, pp. 205, 224.
1980 *V. archiaci*; Bilotte, p. 57.
1980 *Vaccinites archiaci* (Munier Chalmas); Czabalay, p. 284, pls 1–2.
1981 *H.* (*V.*) *archiaci* Munier-Chalmas; Polšak, p. 454.
1981 *Vaccinites archiaci* Munier-Chalmas; Sánchez, p. 37 [with synonymy].
1982a *Vaccinites archiaci* Mun.-Ch.; Bilotte, p. 1021.
1982c *Vaccinites archiaci* Mun.-Ch.; Bilotte, p. 111.
1982 *Vaccinites archiaci* (Munier-Chalmas),[?]; Czabalay, pp. 37, 75, pl. 10, fig. 2; pl. 23, figs 4–5, text-fig. 14.
p1982 *Vaccinites chalmasi* (Douvillé); Czabalay, pp. 36, 75, pl. 13; pl. 15, figs 4, 7.
1982 *Vaccinites archiaci* (Mun.-Chalm.); Pons, tab. 2.
1983 *Vaccinites archiaci*; Babinot *et al.*, tab. 3.
1983 *V. archiaci*; Philip and Bilotte, tab. 2.
1983 *H.* (*Vacc.*) *archiaci* Munier-Chalmas; Pleničar and Premru, p. 194.
1984 *Vaccinites archiaci* Munier-Chalmas; Bilotte, pl. 41, fig. 7.
1985 *Vaccinites archiaci* Mun.-Ch.; Bilotte, p. 340, tab. 42.
1985 *V. archiaci*; Lupu, text-fig. 6.
1989 *Vaccinites archiaci* (Mun.-Chal.); Pascual *et al.*, p. 225, text-fig. 3.
1991 *Vaccinites archiaci*; Floquet, text-fig. 286.
1991 *H.* (*Vaccinites*) *archiaci* Munier-Chalmas; Šribar and Pleničar, p. 178.
1992 *V. archiaci* Munier-Chalmas; Pleničar and Šribar, p. 305.
1992 *Vaccinites archiaci* Munier-Chalmas; Swinburne *et al.*, text-fig. 2.
1992 *Vaccinites archiaci* (Douvillé); Vicens, p. 139, pl. 6, fig. 7 [cop. Douvillé 1892*a*], 8–13, text-fig. 4a., tabs 9–10.

Syntypes. Douvillé (1892*a*) plate 5, figures 1–3. Munier-Chalmas was generally indicated as the author of this species but he only labelled specimens from Benaix and Leychert (Ariège) with '*Hippurites archiaci*' (Douvillé 1892*a*, p. 45). Vicens (1992) corrected this long-purported mistake.

Material. Four specimens from Grammatiko (Vermion Mountains), one of them bivalve (H465–H467, H532).

Description. LV convex, pores denticulate, diameter 0·5-0·7 mm. Radial canals reach a maximum diameter of 2·5 mm.

TABLE 7. Measurements (mm) of RVs of *Vaccinites archiaci* (Douvillé, 1892*a*).

	Dmax	U	$\overline{P0-P2}$	$\overline{P0-P2}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H532	60	224	30	98	1·6	0·8	0·5
H466	62	245	30	104	1·4	0·7	0·5
H465	59	250	28	107	1·0	0·5	0·5

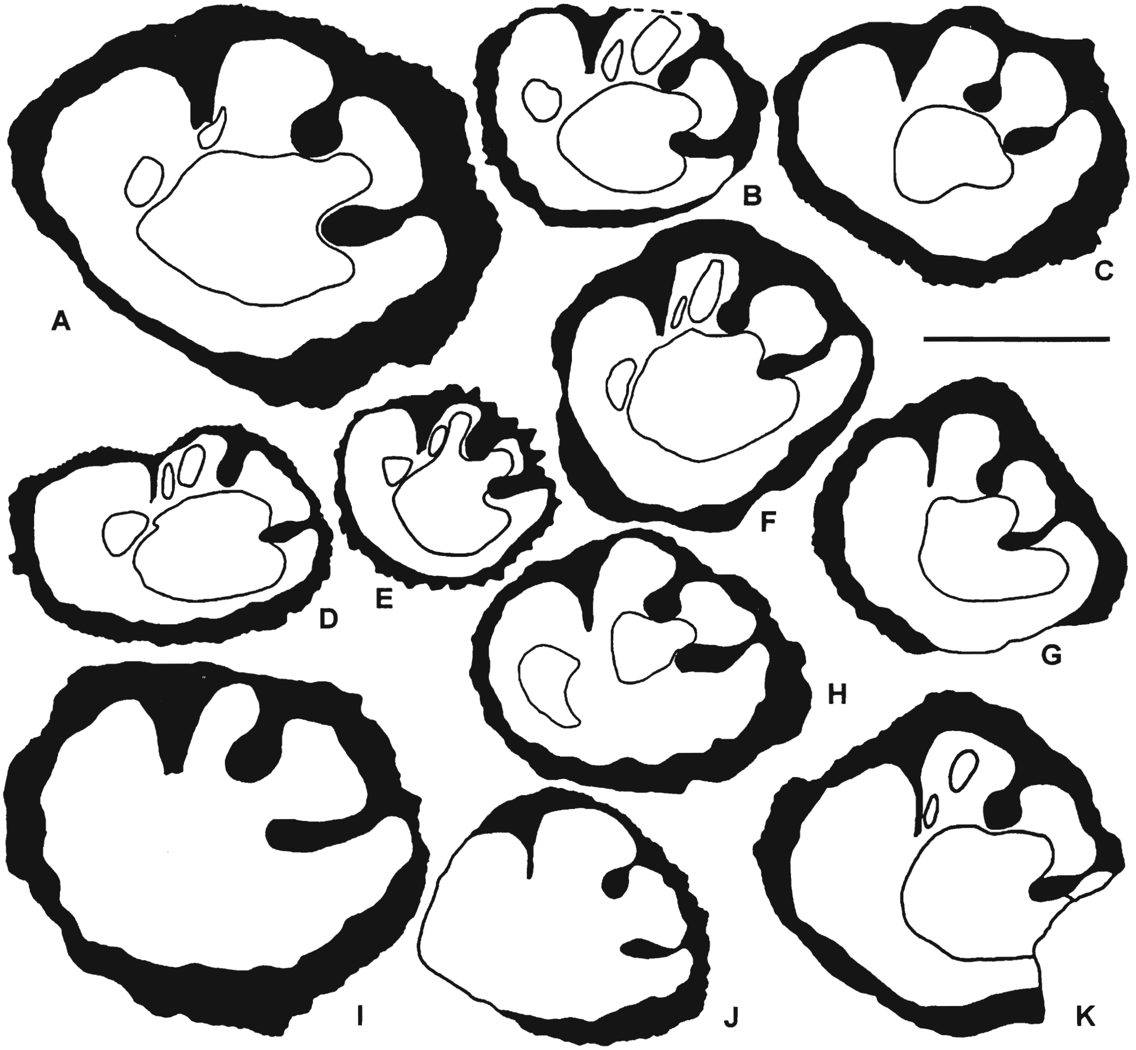
Pustules mark the insertion points of distal radial canals. RVs geniculate, more than 160 mm long, with up to 5 mm wide, prominent longitudinal ribs. P0 strongly developed, curved towards the shell's anterior, inner termination obliquely truncated with broad insertion of ligament, the remains of which are clearly visible. P1 thick, with sub-parallel flanks. P2 broad and massive, base slightly pinched. $U/\overline{P0-P2}$ varies in the range of 7·6 to 8·9 (Text-fig. 73). Dimensions of pillars agree perfectly with those of one of the syntypes (Text-fig. 74). (1) in prolongation of P0, (2) bears rounded but not considerably prolonged excrescences towards the shell's interior, and (3) is located towards the shell's interior and far posteriorly. Ventral tip of mp points to the centre of RV and projects further inward than the tip of P1.

Distribution. Campanian of France, the Pyrenees, Dinarids, of Hungary, Romania, Bulgaria, (Sánchez 1981), Afghanistan (Vogel 1971) and Greece (Aubouin 1959, Othrys Mountains); Middle Campanian of the southern Pyrenees (Vicens 1992); Santonian-Campanian boundary of northern Castile (Floquet 1991).

Vaccinites boehmi (Douvillé, 1897*a*)

Text-figures 49d, g–h (cf.), j (cf.), k, 82a–b (cf.)

*1897*a* *Hippurites Boehmi* Douvillé, p. 197, pl. 30, figs 1–2; pl. 34, fig. 7.
v1897*a* *Hippurites Chalmasi* nov. sp. Douvillé, p. 210, pl. 34, figs 3–4.
1932 *Hippurites* (*Vaccinites*) *boehmi* Douvillé; Kühn, p. 39 [with synonymy].
1932 *Hippurites* (*Vaccinites*) *chalmasi* Douvillé; Kühn, p. 41 [with synonymy].
1933*a* *Hippurites* (*Vaccinites*) *chalmasi* Douvillé; Kühn, p. 153.
1937 *H. böhmi* Douv.; Zapfe, p. 75.
1939 *Hippurites* (*Vaccinites*) *boehmi* Douvillé; Klinghardt, p. 137, pl. 3, fig. 4, 4a.
1942 *Hippurites boehmi* Douvillé; Kühn and Andrusov, p. 458.
1947 *H. boehmi* Douv.; Kühn, p. 185.
?1947 *Hippurites* (*Vaccinites*) *boehmi* Douvillé *pars*; Müllerried, p. 390, text-figs 20–25.
1954 *H.* (*V.*) *boehmi* Douvillé; Milovanović, p. 164.
1959 *Hippurites boehmi* Douv.; Andrusov, p. 208.
1959 *Hipp.* (*Vacc.*) *boehmi* Douvillé; Petković *et al.*, p. 287.
1960 *V. chalmasi* Douv.; Aubouin *et al.*, p. 462.
1960 *H. boehmi* Douv.; Milovanović, p. 367.
1961a *Hippurites* (*V.*) *boehmi* Douvillé; Polšak, p. 422.
1961*b* *Hippurites* (*Vaccinites*) *boehmi* Douvillé- Polšak, p. 442, pl. 2, fig. 2.
1964 *H.*(*V.*) *boehmi* Douvillé; Polšak, p. 67.
1965b *Hippurites* (*V.*) *boehmi* Douvillé; Polšak, p. 451.
1968 *Hippurites boehmi* Douvillé; Kennedy and Taylor, p. 326, text-fig. 1.
1968a *Hippurites* (*Vaccinites*) *boehmi* Douvillé; Slišković, p. 39.
1969 *Hippurites* (*Vaccinites*) *boehmi* Douvillé; Polšak and Mamužić, p. 239.
1974 *Hippurites* (*Vaccinites*) *boehmi* Douvillé; Lupu, p. 63, pl. 5, fig. 20, 20a–b.
1974 *Vaccinites boehmi* Douv.; Patrulius, p. 173.
1974 *Hippurites* (*Vaccinites*) *boehmi* Douvillé; Slišković, p. 133.
1974 *Hippurites* (*Vaccinites*) *boehmi* n. subsp.; Slišković, p. 133.
1975a *H.* (*V.*) *boehmi* Douvillé; Slišković, p. 43.
1978 *Vaccinites chalmasi* (Douvillé); Pamouktchiev, p. 235, tab. 1.
1980 *Vaccinites boehmi* (Douvillé); Carbone *et al.*, p. 206, pl. 4, figs a, c–d.
1980 *Vaccinites boehmi*; Laviano and Sirna, p. 69.
1981 *Vaccinites boehmi* Douvillé; Carbone and Sirna, p. 436, text-figs 4b, 6.



TEXT-FIG. 49. A–B, F, I, *Vaccinites praesulcatus* (Douvillé, 1897*a*); C, *Vaccinites* sp.; E, *V. sulcatus* (Defrance, 1821); D, K, *V. boehmi* (Douvillé, 1897*a*); G–H, J, *V.* cf. *boehmi* (Douvillé, 1897*a*); all from Paleokastron Hill. RV sections; A, H412; B, H396; C, H428; D, H392; E, H436; F, H520; G, H419; H, H426; I, H414; J, H524; K, H423. Scale bar represents 30 mm.

1981*b*	*Vaccinites chalmasi* (Douvillé); Pamouktchiev, p. 171, pl. 85, figs 1–2.
1981	*Vaccinites boehmi* (Douvillé); Sánchez, p. 39 [with synonymy].
1981	*Vaccinites chalmasi* (Douvillé); Sánchez, p. 40 [with synonymy].
non 1982	*Vaccinites chalmasi* (Douvillé); Czabalay, pp. 36, 75, pl. 13, fig. 9; pl. 15, figs 4, 7.
1982	*Hippurites* (*Vaccinites*) *boehmi* Douvillé; Polšak *et al.*, text-fig. 3.
1985	*Vaccinites boehmi* Douvillé; Lupu, *in* Kollmann *et al.*, p. 129, pl. 4, figs 15–20.
1985	*H.* (*V.*) *boehmi* Douvillé; Slišković, p. 17.
?1989*b*	*Vaccinites boehmi* (Douvillé); Cestari and Sirna, p. 19, tab. 1, pl. 1, fig. 2.
1989	*Vaccinites boehmi* Douvillé; Mermighis, p. 79, pl. 22, fig. 5; text-fig. 22.
1989b	*V. boehmi* Douv.; Philip *et al.*, p. 1382.
1990	*Hippurites* (*V.*) *boehmi* Douv.; Cestari and Pantosti, p. 45, text-figs 4, 5b.

1990 *Hippurites* (*Vaccinites*) *boehmi*; Leiss, p. 63.
1992a *V. boehmi* Douvillé; Peza, p. 87.
1993b *Vaccinites chalmasi* (Douvillé); Steuber, p. 46.
1993 *Vaccinites chalmasi* (Douvillé); Steuber *et al.*, text-fig. 8.
1997 *Vaccinites boehmi* (Douvillé); Steuber *et al.*, p. 179, text-fig. 3h.

Holotype. Douvillé (1897*a*), plate 30, figure 1; plate 34, figure 7.

Material. Eighteen RVs from Paleokastron Hill with preserved myocardinal elements (H342, H383–H384, H392, H397, H412, H423, H429, H549), ten with mp not preserved (*V.* cf. *boehmi*, H390, H419, H426, H521, H524, H535–H536, H539, H548, H563), some of them in clusters with *Vaccinites praesulcatus* (Douvillé, 1897*a*); two RVs from the southern slope of Kakotopia Mountain at the Bay of Saltsas (H82, H284/1).

Description. RVs elongated-conical, exceeding 180 mm long, ornamented with acute, 2·5–3·5 mm wide longitudinal ribs that are separated by narrow furrows. P0 slightly longer than P1, relatively shorter in relation to P1 and P2 when compared with the holotype (Text-fig. 83). Inner termination of P0 bluntly truncated, with V-shaped incision, or rounded and with reduced area of ligamental insertion. P1 more or less strongly pinched, but not pedunculate. P2 pinched, straight or curved towards P0. U/$\overline{\text{P0}-\text{P2}}$ is in the range of 4·5 to 5·6 (Text-fig. 76). (3) located posterior to P0, not surpassing the tip of P0; mp far dorsally.

TABLE 8. Measurements (mm) of RVs of *Vaccinites boehmi* (Douvillé, 1897*a*).

	Dmax	U	$\overline{\text{P0}-\text{P2}}$2	$\overline{\text{P0}-\text{P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H392	46	163	33	78	0·9	0·7	0·8
H419	43	179	32	96	1·1	0·9	0·8
H426	46	195	38	114	1·1	0·7	0·7

Remarks. The species differs from *V. gosaviensis* (Douvillé, 1890) by a more dorsally located mp. Unfortunately, mp is not preserved in several of the Boeotian RVs (*V.* cf. *boehmi*). *Vaccinites chalmasi* (Douvillé, 1897*a*) has been considered to be a synonym of *V. boehmi* by Toucas (1904) and Parona (1926). Kühn (1932, 1933*a*) separated *V. chalmasi* again, regarding a triangular P0 as a diagnostic character of the species. The opinion of Toucas (1904) and Parona (1926) is followed here because of the considerable variability in the shape of P0 among the RVs from Paleokastron Hill. Some of the specimens figured as *V. chalmasi* by Czabalay (1982) belong to *Vaccinites archiaci* (Douvillé, 1892*a*).

Life habit. At Paleokastron Hill *Vaccinites boehmi* occurs in pseudocolonies together with *V. praesulcatus* (Douvillé, 1897*a*). Monospecific pseudocolonies of *V. boehmi* have been reported from the Carpathians (Kühn and Andrusov 1942) and the Apennines (Carbone *et al.* 1980).

Distribution. Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982). Santonian–Campanian of the Gosau, the Dinarids and Carpathians (Sánchez 1981), of Albania and Greece (Macedonia, Trapezona, Argolis). Probably also in the Senonian of Mexico (Müllerried 1947).

Vaccinites chaperi (Douvillé, 1897*a*)

Plate 21, figure 1; Plate 22, figures 2, 4; Plate 23, figures 3, 5; Text-figures 51–53, 72E–F

?1865 *Hippurites Taburnii* n. sp. Guiscardi, p. 2, pl. 1, fig. 1.
v*1897*a* *Hippurites Chaperi* nov. sp. Douvillé, p. 214, pl. 30, fig. 7.
v*non* 1897*a* *Hippurites Chaperi* nov. sp. Douvillé, p. 214, pl. 30, fig. 6.
v.1897*a* *Hippurites Taburnii*? Guiscardi; Douvillé, p. 216, pl. 30, fig. 8.
1899 *Hippurites Taburnii* Guisc.; de Alessandri, p. 183, pl. 14, figs 1, 4.

non 1904 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Toucas, p. 107, text-figs 170–171; pl. 16, fig. 2.
1907 *Hippurites atheniensis* Ktenas, p. 698, 1 text-fig.
non 1911*b* *H. Chaperi* Douv.; Parona, p. 888, text-fig. 1.
1916 *Hippurites Chaperi*; Frech, p. 296.
?1926 *Hippurites* (*Vaccinites*) *Chaperi* Douv.; Parona, p. 20, pl. 1, fig. 3; pl. 2, fig. 6.
1927 *Hippurites Chaperi*; Douvillé, *in* Renz, p. 502.
1932 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Kühn, p. 38.
p*1932* *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Kühn, p. 41.
p*1932* *Hippurites* (*Vaccinites*) *taburni* Guiscardi; Kühn, p. 70
1932 *Vaccinites Taburnii* Guiscardi; Milovanović, p. 51, pl. 2, fig. 2.
1934 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Milovanović, p. 199, text-figs 4–5.
1934 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Milovanović, p. 202, text-fig. 6 [cop. Ktenas 1907], 7–13.
1947 *H. atheniensis* Ktenas; Kühn, p. 187.
1948 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Kühn, p. 174, text-figs 2–3.
1948 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Kühn, p. 179, text-fig. 6.
?1951 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Pejović, p. 92, pl. 1, fig. 1.
1954 *H.* (*V.*) *atheniensis* Ktenas; Milovanović, p. 164.
1954 *H.* (*V.*) *atheniensis* Ktenas var. *serbicus* nov.var. Milovanović, p. 165, text-figs 1–2.
1954 *H.* (*V.*) *chaperi* Douvillé; Milovanović, p. 164.
1957 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Pašić, p. 119, pl. 35, fig. 1; pl. 37, fig. 1; text-fig. 60.
1957 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Pejović, p. 95, pl. 24, fig. 1; pl. 25, fig. 1; pl. 26, fig. 1; pl. 27, fig. 1.
1959 *Hippurites chaperi* Mun. Chal.; Aubouin, p. 61.
1959 *Hippurites atheniensis* Ktenas; Kühn and Pejović, p. 981.
1959 *Hipp.* (*Vacc.*) *atheniensis* Ktenas; Petković *et al.*, p. 282.
1959 *Hipp.* (*Vacc.*) *chaperi* Douvillé; Petković *et al.*, p. 287.
p1959 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Polšak, pp. 58, 73, pl. 1, figs 1–3; pl. 2, fig. 2; pl. 3, fig. 1; text-fig. 1.
1960 *Vaccinites atheniensis* Ktenas; Aubouin *et al.*, p. 458.
1960 *Hippurites chaperi* Mun.-Chal.; Aubouin *et al.*, p. 459.
1960 *Hippurites atheniensis* Ktenas; Kühn, p. 48.
1960 *Hippurites atheniensis* Ktenas; Milovanović, p. 367.
1960 *H. chaperi* Douv.; Milovanović, p. 367.
?1960 *Hippurites chaperi* Douv.; Pejović and Kühn, p. 137.
1961 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Sakellariou, p. 160, pls 1–3.
1962 *Hippurites atheniensis* Ktenas; Kaumanns, p. 296.
1962 *Hippurites* (*Vacc.*) *atheniensis* Ktenas; Slišković *et al.*, p. 130.
?1963*b* *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Slišković, p. 8, pl. 1, fig. 1.
1964 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Polšak, p. 67.
1965 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Benkö-Czabalay, p. 402.
1965 *H.* (*V.*) *atheniensis* Ktenas; Mamužić, p. 344.
1965b *Hippurites* (*V.*) *atheniensis* Ktenas; Polšak, p. 451.
1967 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Pleničar and Buser, p. 156, pl. 7, fig. 1.
1967*b* *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Polšak, pp. 118, 210, pl. 73, figs 1–2; text-fig. 39.
1967*b* *Hippurites atheniensis* Ktenas; Sladić-Trifunović, pp. 267, 281, text-figs 1 [cop. Ktenas 1907], 2 [cop. Milovanović 1932], 3–15, 16 [cop. Polšak 1959], 17, 18 [cop. Milovanović 1934], 19 [cop. Polšak 1959], 20–21.

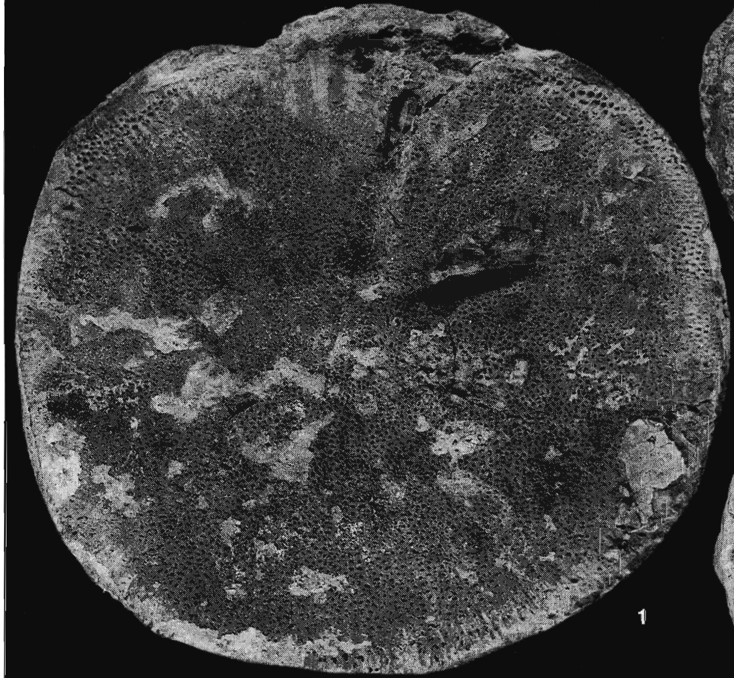
EXPLANATION OF PLATE 21

Fig. 1. *Vaccinites chaperi* (Douvillé, 1897*a*); H531, Moukharemi Hill (Vermion Mountains); × 1.

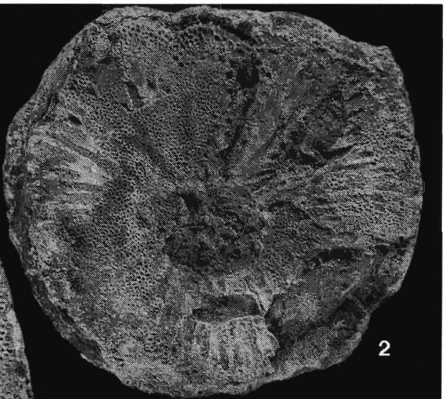
Figs 2, 4–5. *Vaccinites cornuvaccinum* (Bronn, 1831). 2, H75; Keratovouno Hill; 4, H476; Keratovouno Hill; 5, H183, Anthochorion. All × 1.

Fig. 3. *Vaccinites praegiganteus* (Toucas, 1904); H249, Marmeko; × 1.

Fig. 6. *Vaccinites inaequicostatus* (Münster, *in* Goldfuß 1840); holotype, BSM AS VII 135; × 2.



1



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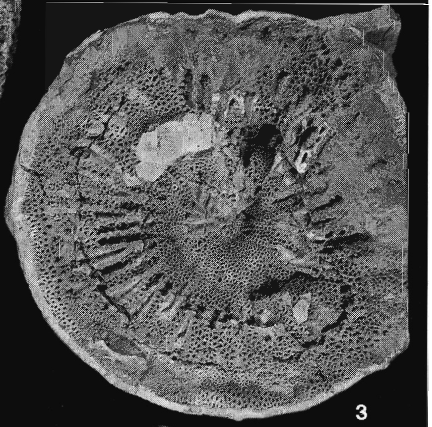

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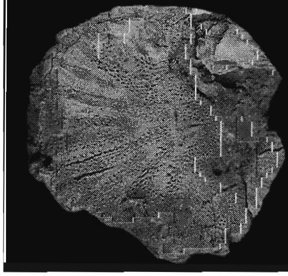
4



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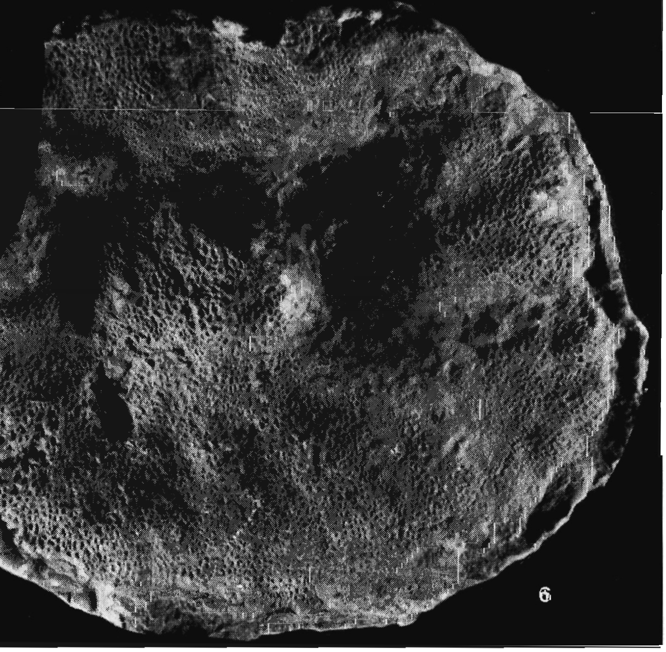
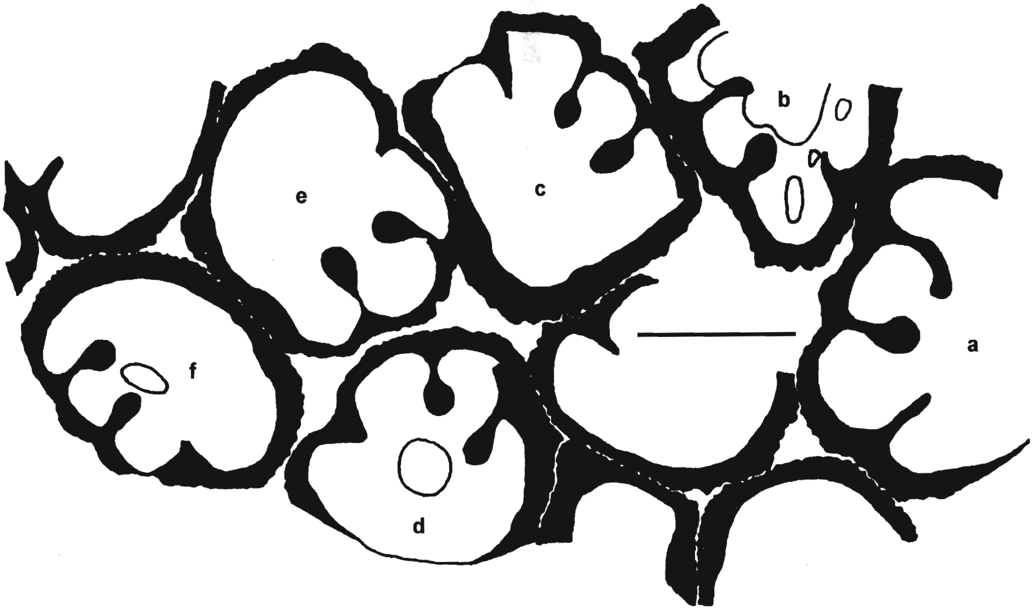


6

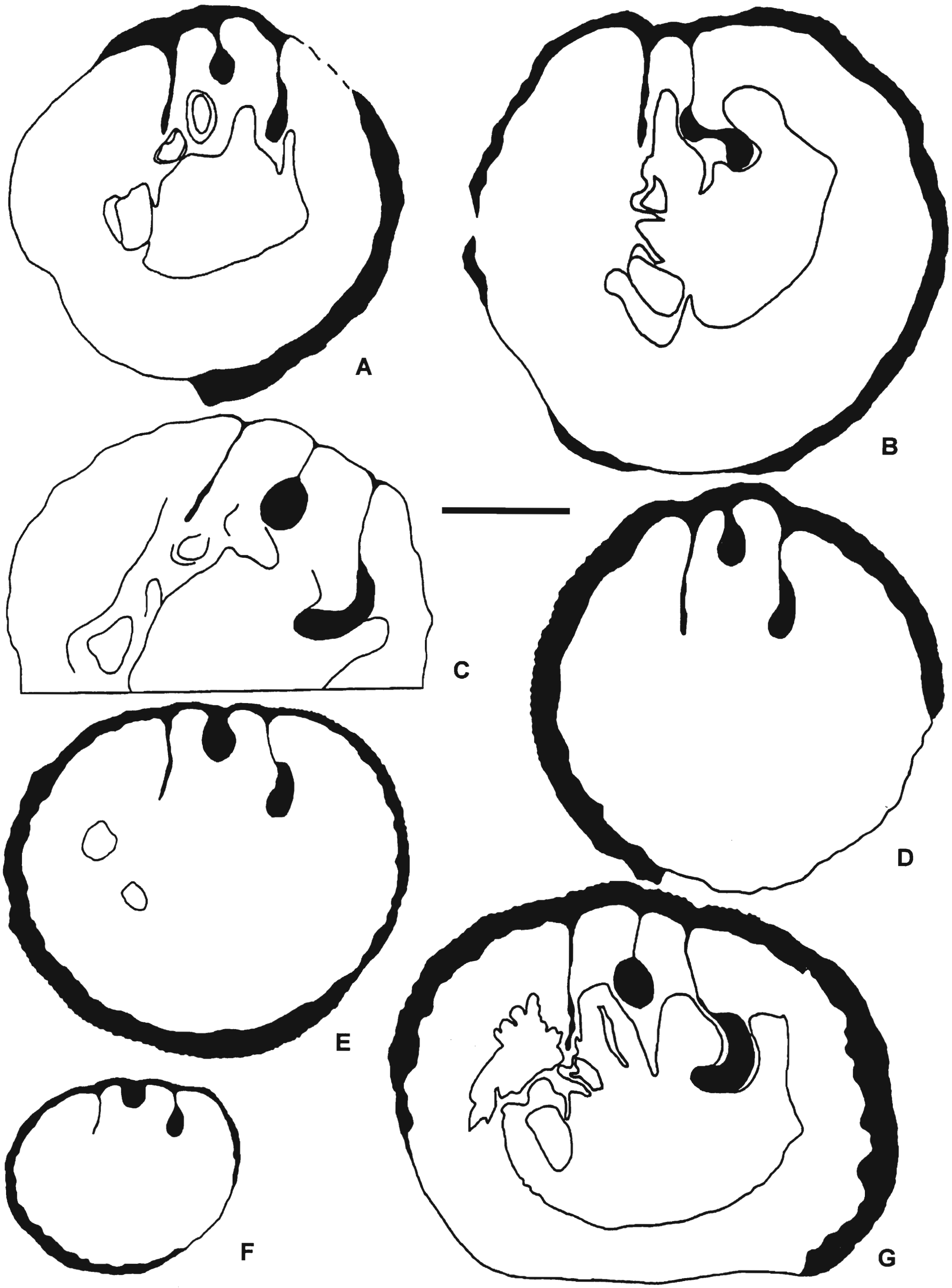
STEUBER, *Vaccinites*



TEXT-FIG. 50. Pseudocolony with (a) *Vaccinites* cf. *boehmi* (Douvillé, 1897*a*) and (b–f) *V. praesulcatus* (Douvillé, 1897*a*) from Paleokastron Hill. RV sections; H563. Scale bar represents 30 mm.

1967*b* *Hippurites atheniensis grubici* n. subsp. Sladić-Trifunović, pp. 278, 282, text-figs 23 [cop. Polšak 1959], 24 [cop. de Alessandri 1899], 25–26 [cop. Pašić 1957].
1967*b* *Hippurites atheniensis serbicus* Milovanović; Sladić-Trifunović, pp. 277, 282, text-fig. 22 [cop. Milovanović 1954].
1967 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Slišković, p. 23, pls 1–3; text-figs 1–5.
1967 *V. atheniensis* Ktenas; Sornay, *in* Freneix and Lefèvre, p. 762.
1968a *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Slišković, p. 38.
1968a *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Slišković, p. 38.
1969 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Polšak and Mamužić, p. 239.
1969 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Polšak and Mamužić, p. 239.
1970 *Hippurites atheniensis* (Ktenas); Benkö-Czabalay, p. 277.
1971a *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Slišković, p. 40.
1971a *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Slišković, p. 40.
1973 *Vaccinites atheniensis* Ktenas; Mercier, p. 311, pl. 1, fig. 1.
1973 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Sakellariou-Mané, p. 399, pl. 4, figs 1–2.
1974 *Vac. chaperi* (Douv.); Philip, p. 112.
1975 *Hippurites* (*Vaccinites*) *chaperi* Douvillé; Pleničar, pp. 98, 111, pl. 13, fig. 1; pl. 14, figs 1–2.
1976 *Vaccinites chaperi* Douvillé; Lupu, p. 116, pl. 5, fig. 3; pl. 37, fig. 4.
1978 *Vaccinites atheniensis* Ktenas; Pamouktchiev, p. 238, tab. 1.
1978a *Vaccinites chaperi* (Douvillé); Philip *et al.*, p. 84.
1978 *H.* (*V.*) *atheniensis* Ktenas; Polšak *et al.*, p. *190.*
1979 *H.* (*V.*) *atheniensis* Ktenas; Polšak, pp. 205, 224.
1980 *V. chaperi*; Laviano and Sirna, p. 69.
?*1981* *Ps. chaperi* Douv.; Bilotte, p. 124.
1981 *Vaccinites atheniensis* (Ktenas); Combes *et al.*, p. 353.

TEXT-FIG. 51. *Vaccinites chaperi* (Douvillé, 1897*a*). RV sections; A, holotype; B, D–G, RVs from Moukharemi; E–F, H559, different growth stages of one valve; C, holotype of '*Hippurites atheniensis* Ktenas, 1907'; B, H561; D, H558; G, H562. Scale bar represents 30 mm.


A
B
C
D
E
F
G

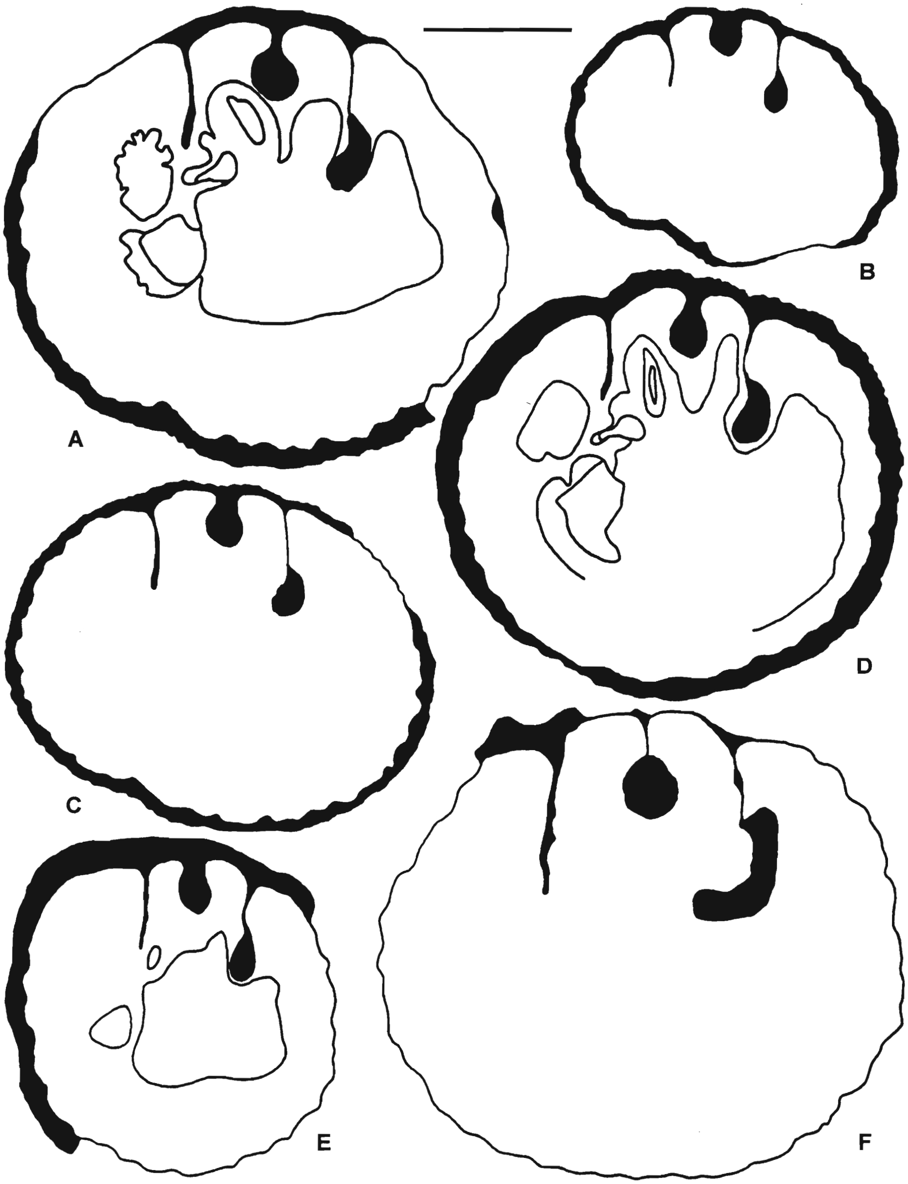
non 1981*b* *Vaccinites atheniensis* (Ktenas); Pamouktchiev, p. 177, pl. 86, fig. 3.
1981 *H.* (*V.*) *atheniensis* Ktenas; Polšak, p. 454.
1981 *Vaccinites atheniensis* (Ktenas); Sánchez, p. 38 [with synonymy].
1981 *Vaccinites atheniensis grubici* (Sladić-Trifunović); Sánchez, p. 38 [with synonymy].
1981 *Vaccinites chaperi* (Douvillé); Sánchez, p. 41 [with synonymy].
1982 *Vaccinites atheniensis* (Ktenas); Accordi *et al.*, p. 770, pl. 4, figs 2, 6.
1982c *Pseudovaccinites chaperi* Douv.; Bilotte, p. 112.
1982 *Vaccinites atheniensis* Ktenas; Czabalay, pp. 34, 74, pl. 11, fig. 3; pl. 12, fig. 1; text-fig. 13.
1982 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Polšak *et al.*, text-fig. 3.
1982 *Vaccinites chaperi* (Douvillé); Pons, tab. 1.
1983 *Vaccinites atheniensis* (Ktenas); Czabalay, p. 187.
1983 *Vaccinites chaperi*; Gallemi *et al.*, tab. 3.
1983 *H.* (*Vacc.*) *atheniensis* Ktenas; Pleničar and Premru, p. 192.
1983 *Vaccinites atheniensis*; Sladić-Trifunović, tab. 1.
1985 *Pseudovaccinites chaperi* Douv.; Bilotte, p. 345.
?1985 *Vaccinites atheniensis* (Ktenas); Caminiti, p. 133, pl. 30, fig. 1.
1987 *Vaccinites atheniensis*; Accordi *et al.*, p. 139.
1987 *Vaccinites gaudryi* (Munier-Chalmas); Konertz, pl. 1, fig. 4.
1987 *Vaccinites atheniensis* (Ktenas); Pejović and Radoičić, p. 126, tab. 2.
1989b *Vaccinites atheniensis* Ktenas; Philip *et al.*, p. 1382.
1990 *Vaccinites atheniensis*; Gušić and Jelaska, text-figs 8, 11.
1991 *Hippurites* (*Vaccinites*) *atheniensis* Ktenas; Šribar and Pleničar, p. 179.
1991 *H.* (*Vacc.*) *chaperi* Douvillé; Šribar and Pleničar, p. 179.
1992a *V. atheniensis* (Ktenas); Peza, p. 87.
1992a *V. chaperi* Douvillé; Peza, p. 87.
1992 *Vaccinites atheniensis* Ktenas; Swinburne *et al.*, text-fig. 2.
1993 *Vaccinites atheniensis* (Ktenas); Cherchi *et al.*, p. 95, pl. 5, fig. 1.
?1993 *Vaccinites taburni* (Guiscardi); Cherchi *et al.*, p. 95, pl. 5, fig. 4.
1993 *Vaccinites chaperi* (Douvillé); Gili, tab. 1.
1993b *Vaccinites* cf. *chaperi* (Douvillé); Steuber, p. 44.
1993b *Vaccinites atheniensis* (Ktenas); Steuber, p. 46.
1993 *Vaccinites atheniensis* (Ktenas); Steuber *et al.*, p. 260, text-fig. 9.
1994 *Vaccinites atheniensis*; Jerinić *et al.*, text-fig. 2.
p1996 *Vaccinites fortisi* (Catullo); Cestari *et al.*, p. 171, text-figs 1, 2a–n, 3o–z.
1996 *Vaccinites atheniensis*; Sanders, p. 852.

Holotype. Douvillé (1897*a*), plate 30, figure 7.

Material. Six RVs from the top of Paleovouna Mountain, Helicon range, (H257–H258, H289), one from Kiriaki village (H528), two from the quarry at Tsouka Hill (H497, H556) and 21 from the Vermion Mountains (Moukharemi, Grammatiko, Drosia; H3–H10, H531, H557–H562, H565, H581).

Description. LVs slightly convex; polygonal pores with an average diameter of 0·6–0·8 mm, elongated pores up to 1 mm in diameter; commonly denticulate with two, rarely three teeth which are only exceptionally fused (Pl. 22, figs 2, 4). Radial canals distally 2–2·5 mm wide, ridges between canals 1 mm wide. Osculum above P1 28 mm long and 4 mm wide, above P2 15 mm long and 5 mm wide.

RV is a wide cone or is elongated-conical, more than 500 mm high, Dmax up to 114 mm; ornamented with inconspicuous, 1–3 mm wide longitudinal ribs and narrow furrows. P0 rather long, commonly with undulating sides, and rounded inner termination without ligamental remains. P1 with parallel sides, in juvenile growth stages, that become pinched and finally pedunculate with increasing diameter of RV (Text-fig. 65B); P2 is pedunculate even in early ontogenetic growth stages, its shape changes from oval to crescentic during growth and it becomes more and more curved anteriorly. P0 on average one-and-a-half times longer than P1, in some valves more than twice as long (Text-fig. 71). The variability of ratios of length of P0 and P2 are even more pronounced (Text-fig. 54). On average, P1 is shorter in RV from the Vermion Mountains when compared with other specimens from the eastern Mediterranean (Text-fig. 54). $U/\overline{P0-P2}$ increases from 8·3 in juveniles to 18·0 in adult shells (Text-fig. 55). P1 and P2 can be fused (Text-figs 51B, 72F), as in '*Vaccinites atheniensis grubici* (Sladić-Trifunović, 1967*b*)'. Accessory cavity shallow and



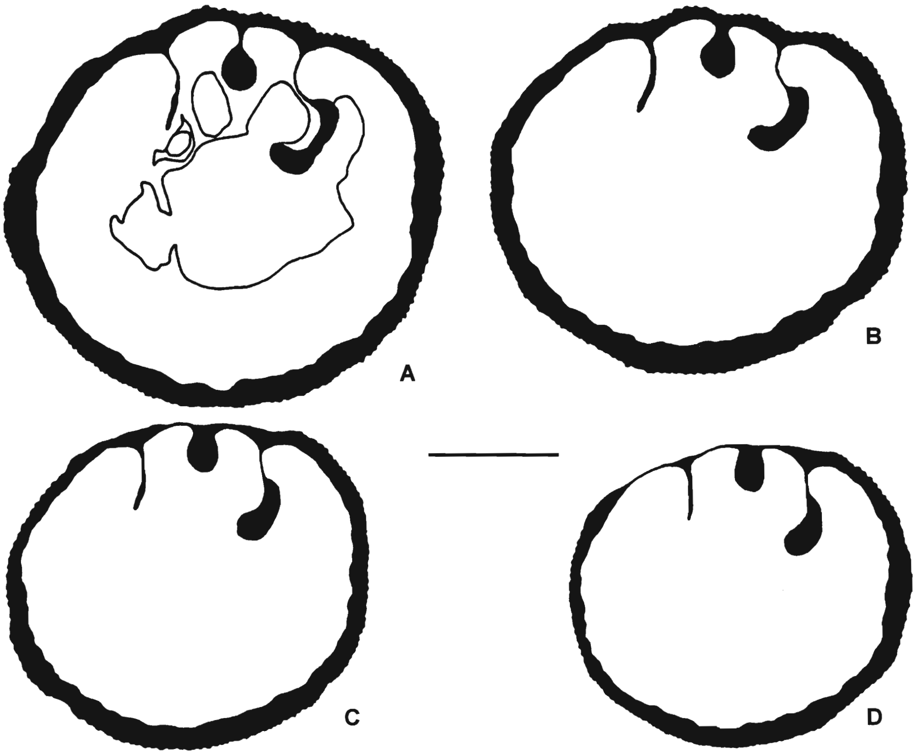
TEXT-FIG. 52. *Vaccinites chaperi* (Douvillé, 1897*a*) from Vermion Mountains. RV sections; A–C, H560; Moukharemi; different growth stages of one valve; D, H531; E, H557; F, H3; Moukharemi. Scale bar represents 30 mm.

compartmentalized by protruding excrescences of inner shell. (1) in prolongation of P0, (3) at various places in front of or posterior to P0; mp between P0 and P1, at some distance from the dorsal shell.

Remarks. When comparing the type specimens (Text-fig. 51A, C), it is obvious that *V. atheniensis* (Ktenas, 1907) was installed for an adult growth stage of *Vaccinites chaperi* (Douvillé, 1897*a*). The intraspecific variability within a few generations of the species is demonstrated by numerous specimens that have been collected from a single horizon at Moukharemi Hill (Vermion Mountains) where the shells are preserved

TABLE 9. Measurements (mm) of RVs of *Vaccinites chaperi* (Douvillé, 1897*a*).

	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
holotype	92	406	28	160	1·6	0·9	0·6
Douv. 1897*a*, pl. 30, fig. 8	114	556	42	269	1·1	0·6	0·5
Vermion (n = 7)							
min.	70	314	24	130	1·3	0·5	0·4
max.	106	546	38	270	1·9	1·0	0·6
mean	92	430	31	190	1·5	0·7	0·5



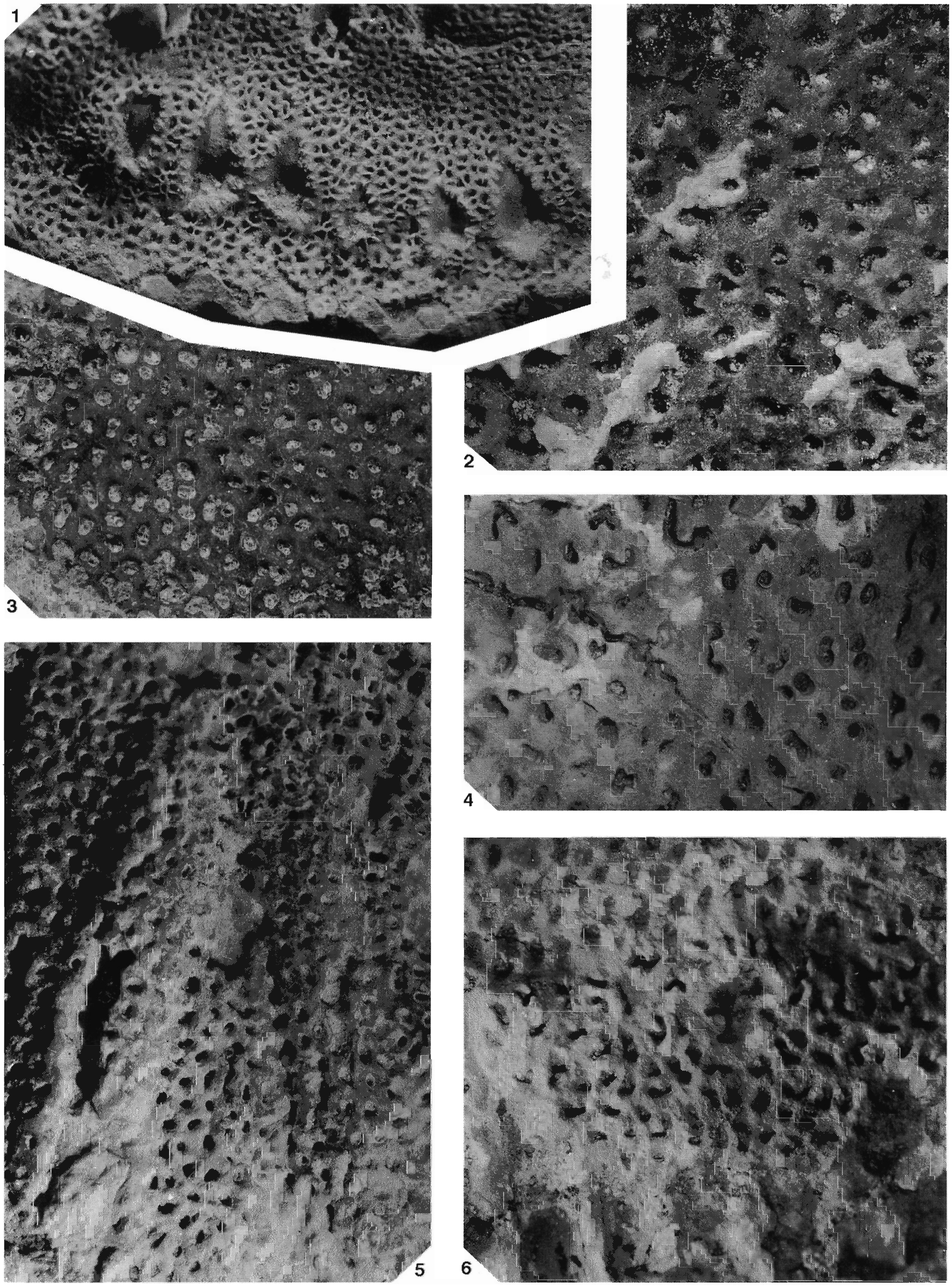
TEXT-FIG. 53. A–D, Consecutive transverse sections through RV of *Vaccinites chaperi* (Douvillé, 1897*a*) from Moukharemi; H565. Scale bar represents 30 mm.

EXPLANATION OF PLATE 22

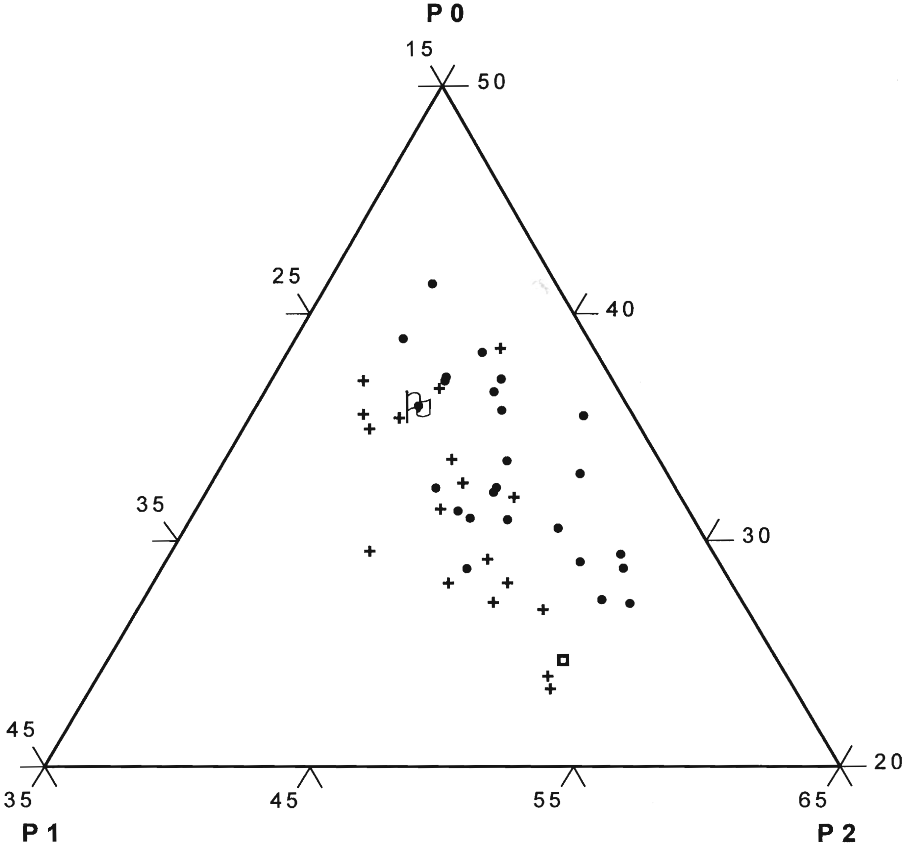
Fig. 1. *Vaccinites inferus* (Douvillé, 1891); H253, Marmeko; margin of LV with reticulate pores; × 7.

Figs 2, 4. *Vaccinites chaperi* (Douvillé, 1897*a*); Moukharemi Hill (Vermion Mountains); sub-polygonal pores of LV. 2, H581; × 7·7. 4, H558; × 7·1.

Figs 3, 5–6. *Vaccinites cornuvaccinum* (Bronn, 1831); Keratovouno Hill; sub-polygonal, partly denticulate pores of LVs. 3, H69; 5, H580; 6, H476. All × 7·3.



STEUBER, *Vaccinites*



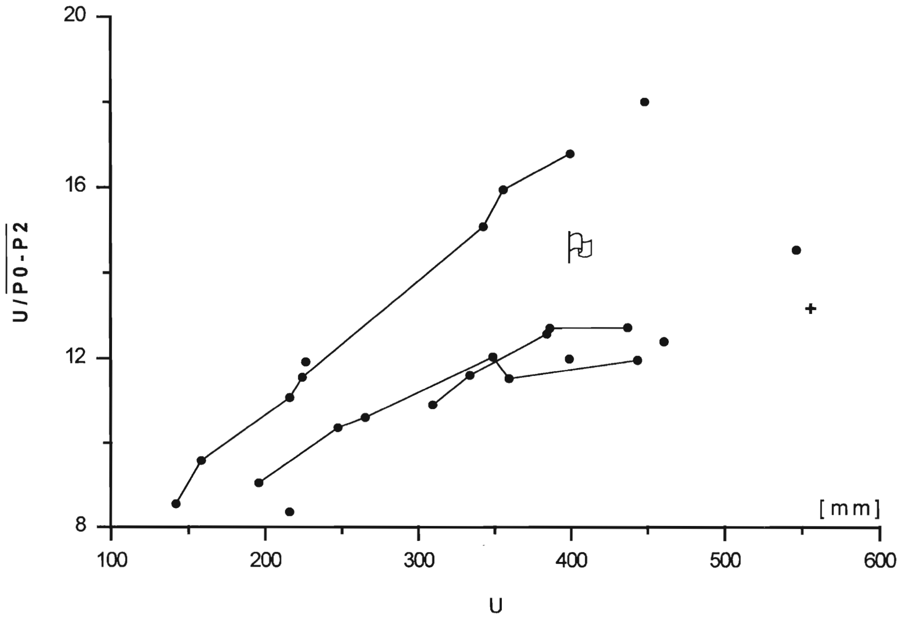
TEXT-FIG. 54. Relative length of P0, P1 and P2 in *Vaccinites chaperi* (Douvillé, 1897*a*) from Vermion Mountains (dots) and other eastern Mediterranean localities (+) after Ktenas (1907); Milovanović (1934); Kühn (1948); Milovanović (1954); Polšak (1967*b*); Sladić-Trifunović (1967*b*;) Slišković (1967); holotype (flag), and (box) holotype of *Vaccinites taburnii* (Guiscardi, 1865). See Text-figure 11 for measurements.

in life position (Text-figs 51–53); the type specimens of *V. chaperi* and *V. atheniensis* fit well into the series of observed morphotypes. Douvillé (1897*a*, pl. 30, fig. 6) figured, together with the holotype and under the same name, a RV of *Vaccinites cornuvaccinum* (Bronn, 1831) from Antinitza (Othrys Mountains). This certainly has induced some confusion concerning the taxonomy of *V. chaperi*.

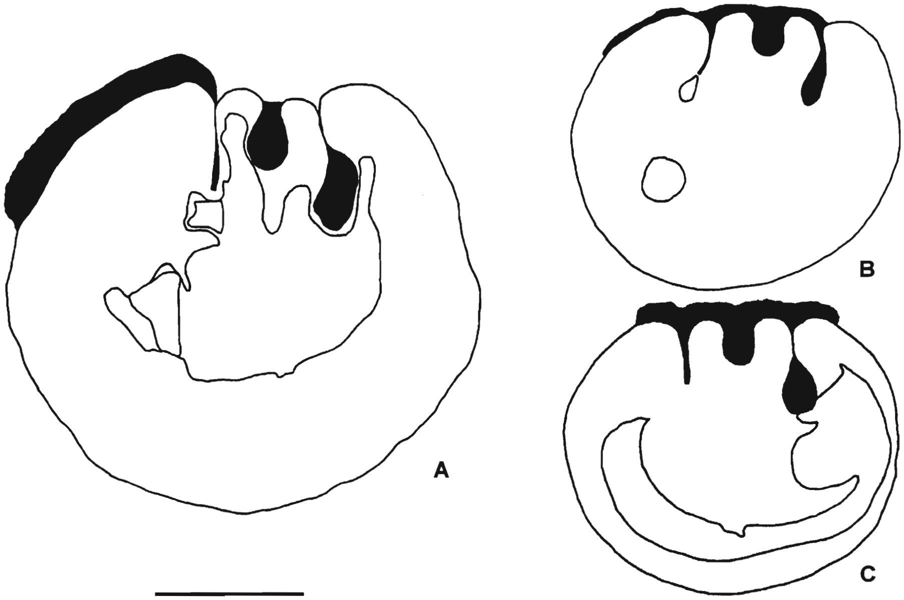
V. chaperi has probably been described earlier as *Vaccinites taburnii* (Guiscardi, 1865), the type specimen of which was insufficiently described for a safe recognition. A short P0 that has frequently been considered characteristic of *V. taburnii*, is certainly not useful for a separation, taking into account the variability of that character (Text-fig. 54).

Life habit. At Moukharemi Hill (Vermion Mountains) ventrally convex, reclined and geniculate shells are found in life position in marly siltstones and impure limestones. This life habit is similar to that of *Vaccinites cornuvaccinum* (Bronn, 1831) from Keratovouno Hill (Boeotia) which is described in detail below. In Boeotia, no shells of *V. chaperi* have been found in life position.

Distribution. Santonian–Campanian of the ?Pyrenees, of Sardinia, the southern Alps, Gosau, the Apennines, of Hungary, the Carpathians, Dinarids, Hellenids and Taurids, ?Bulgaria and Albania. *V. chaperi* is associated



TEXT-FIG. 55. Arrangement of pillars plotted against the length of contour of inner margin of outer shell layer (U) in *Vaccinites chaperi* (Douvillé, 1897*a*) from Vermion Mountains (dots), the holotype (flag) and in '*Hippurites Taburnii*?' (+, after Douvillé 1897*a*, pl. 30, fig. 8). Ontogenetic stages of individual valves are connected by lines, respectively. See Text-figure 11 for measurements.



TEXT-FIG. 56. *Vaccinites cornuvaccinum* (Bronn, 1831). RV sections; A–B, neotype, PIB-GC 1062, transverse sections 23 mm below commissure in A and 73 mm above apex of RV in B; C, topotype, MNHB-KC 80 I 5. Scale bar represents 30 mm.

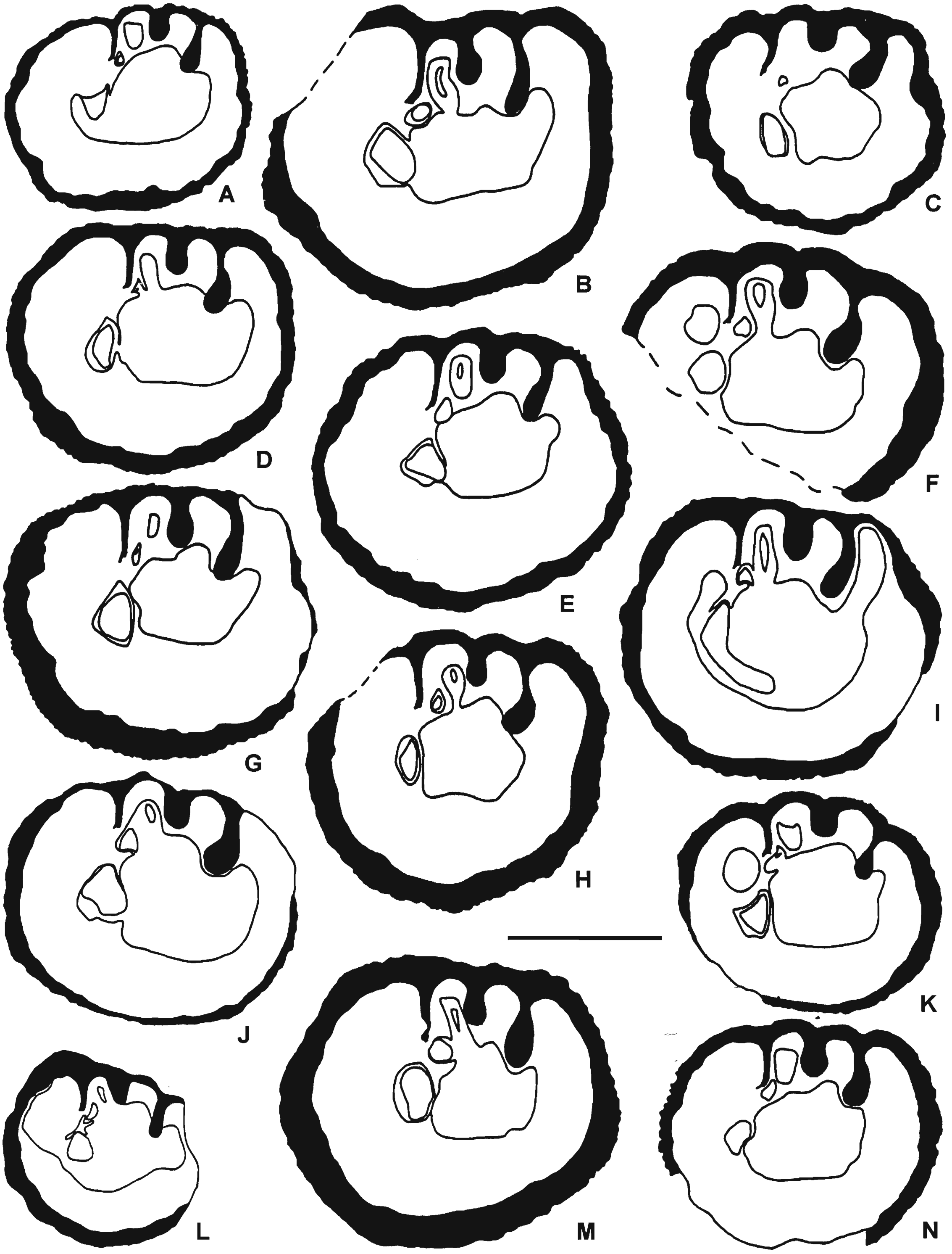
with *V. archiaci* (Douvillé, 1892*a*) in the Vermion Mountains and with *V. vesiculosus* (Woodward, 1855) in the Helicon Mountains. This faunal association indicates a Campanian age. Neither in northern Greece nor in Boeotia, has *V. chaperi* been found with *V. cornuvaccinum* (Bronn, 1831).

Vaccinites cornuvaccinum (Bronn, 1831)

Plate 21, figures 2, 4–5; Plate 22, figures 3, 5–6; Plate 23, figures 2, 6; Plate 24, figures 1–6; Plate 25, figures 4–5; Text-figures 56–63

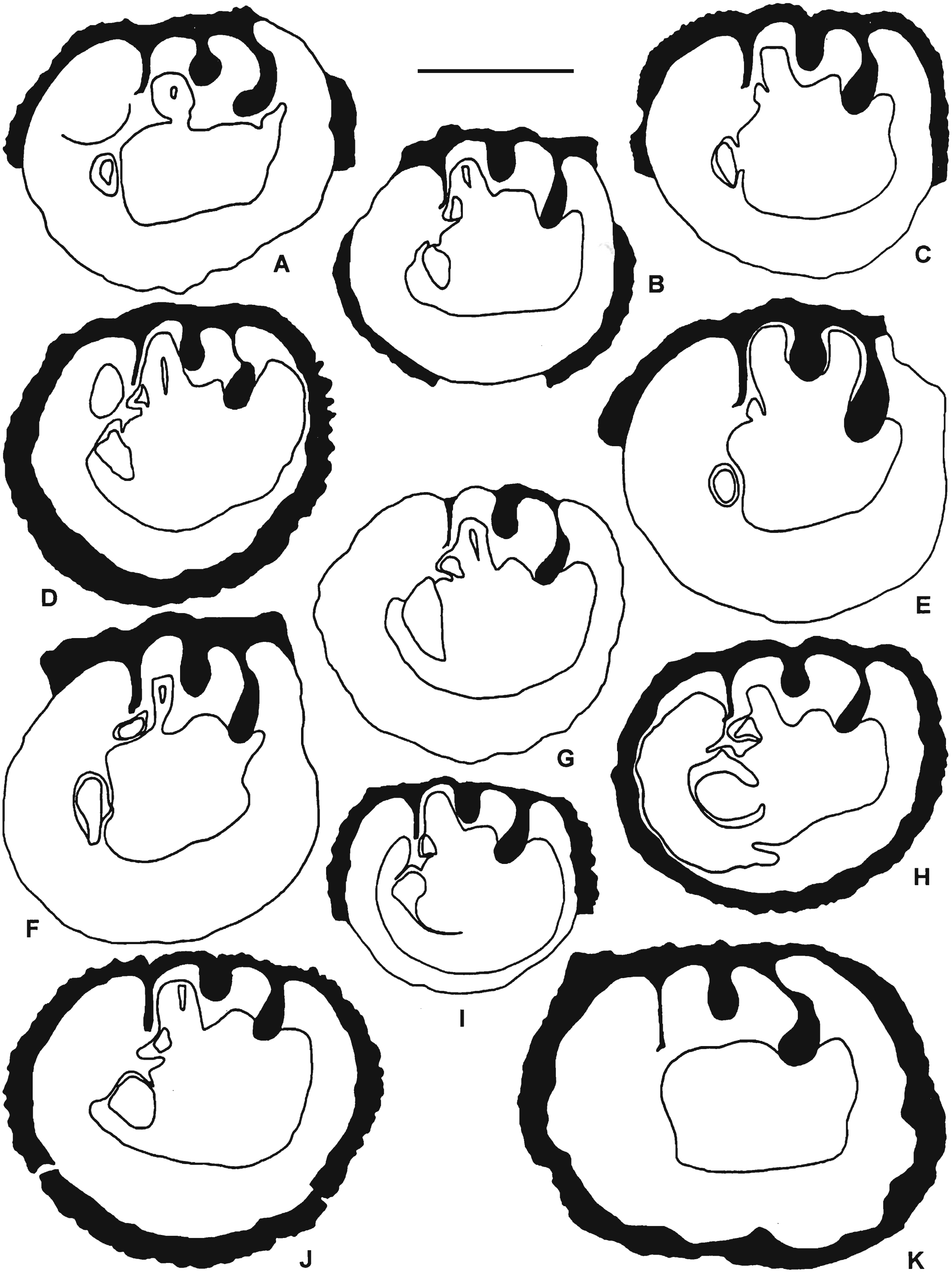
1827 *Hippurites Fortisii* Catullo, p. 171, pl. 6, figs B, b.
*1831 *H. cornu-vaccinum* n. s. Bronn, p. 374.
1832 *Hippurites cornu vaccinum* n. sp. Bronn, p. 172.
1838 *Hippurites cornuvaccinum*; Bronn, p. 634, pl. 31, fig. 2a–b.
v.1840 *Hippurites Cornu vaccinum* Bronn; Goldfuß, p. 302, pl. 165, fig. 1.
non 1850 *Hippurites cornu-vaccinum* Bronn; d'Orbigny, p. 162, pl. 526, fig. 4; pl. 527, fig. 2.
?1850 *Hippurites cornu-vaccinum* Bronn; d'Orbigny, p. 162, pl. 526, figs 1–3; pl. 527, fig. 1.
?1852 *Hippurites cornuvaccinum*; Quenstedt, p. 536, pl. 45, figs 3–4.
p1855 *Hippurites cornu-vaccinum*; Woodward, p. 43, pl. 4, figs 2–3, text-fig. 8.
v *non* 1857 *Hippurites cornu-vaccinum* Bronn; Bayle, p. 665, pl. 15, figs 1–3.
1857 *Hippurites cornu-vaccinum*; Bayle, p. 673.
1863 *Hippurites Cornu vaccinum* Bronn; Goldfuß, p. 287, pl. 165, fig. 1 [cop. Goldfuß 1840].
p*1863* *Hippurites costulatus*; Goldfuß, p. 288, pl. 165, fig. 2a.
1865 *H. cornu-vaccinum* Bronn; Guiscardi, p. 2.
non 1865 *Hippurites cornu-vaccinum* Bronn; Vaillant, p. 280 [*teste* Kühn 1932].
1866 *Hippurites cornuvaccinum*; Coquand, p. 501.
*non*1866 *Hippurites cornu-vaccinum* Bronn; Zittel, p. 135, pl. 21, figs 1–7 [*teste* Douvillé 1891, Kühn 1932].
p1866 *Hippurites Toucasianus* d'Orb.; Zittel, p. 140, pl. 23, fig. 3 [= *Hippurites alpinus teste* Douvillé 1897*a*].
1866 *Hippurites Toucasianus* d'Orb. var. *turbinata*; Zittel, p. 141, pl. 23, fig. 6 [= *Hippurites alpinus teste* Douvillé 1897*a*].
?*1867* *Hippurites cornu-vaccinum*; Hébert, p. 364.
1867 *Hippurites Gaudryi* Munier Chalmas; Munier-Chalmas, *in* Gaudry, p. 390.
1867 *Hippurites cornuvaccinum*; Quenstedt, p. 818, pl. 64, figs 22–23; text-fig. 305.
1880 *Hippurites cornu vaccinum* Bronn cf.; Bittner, p. 40.
1885 *Hippurites cornu-vaccinum* Bronn; Boehm, p. 548.
1885 *Hippurites cornuvaccinum* Bronn; Peron, p. 263.
1888 *Hippurites Gaudryi* M.-Ch.; Munier-Chalmas, p. 819.
1891 *Hippurites cornuvaccinum* Bronn; Douvillé, p. 6, pl. 1, figs 1 [cop. Bronn 1838], 2 [cop. Goldfuß 1840], 3 [cop. Woodward 1855].
v.1891 *Hippurites cornuvaccinum* Bronn; Douvillé, p. 6, pl. 1, fig. 4.
.1892*a* *Hippurites gaudryi* Munier Chalmas; Douvillé, p. 48, pl. 7, fig. 2; text-fig. 34.
v.1892*a* *Hippurites gaudryi* Munier Chalmas; Douvillé, p. 48, pl. 7, figs 1, 3.
1897*a* *Hippurites alpinus* nov. sp. Douvillé, p. 217, pl. 34, fig. 5.
v *non*1897*a* *Hippurites alpinus*?; Douvillé, p. 217, pl. 32, figs 1–2.
v. p1897*a* *Hippurites Chaperi* nov. sp. Douvillé, p. 214, pl. 30, fig. 6.
1897*a* *Hippurites cornuvaccinum* Bronn; Douvillé, p. 212, pl. 31, fig. 2.
v.1897*a* *Hippurites cornuvaccinum* Bronn; Douvillé, p. 212, pl. 31, figs 3–4.
v.1897*a* *Hippurites Gaudryi* Munier-Chalmas; Douvillé, p. 213, pl. 31, figs 5–6; pl. 34, figs 1–2.
p1901 *Hippurites Taburni* Guisc.; Parona, p. 212, pl. 1, fig. 14.
1903 *Hippurites cornuvaccinum*; Deprat, p. 238.
1903 *Hippurites Gaudryi*; Deprat, p. 238.
1904 *Hippurites* (*Vaccinites*) *alpinus* Douvillé; Toucas, p. 99, text-fig. 156 [cop. Douvillé 1897*a*].
1904 *Hippurites* (*Vaccinites*) *gaudryi* Munier-Chalmas; Toucas, p. 100, text-fig. 157.

TEXT-FIG. 57. *Vaccinites cornuvaccinum* (Bronn, 1831) from Keratovouno Hill. RV sections; A, H102; B, H63; C, H56; D, H28; E, H78; F, H79; G, H77; H, H70; I, H37; J, H74; K, H36; L, H479; M, H69; N, H68. Scale bar represents 30 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M
N

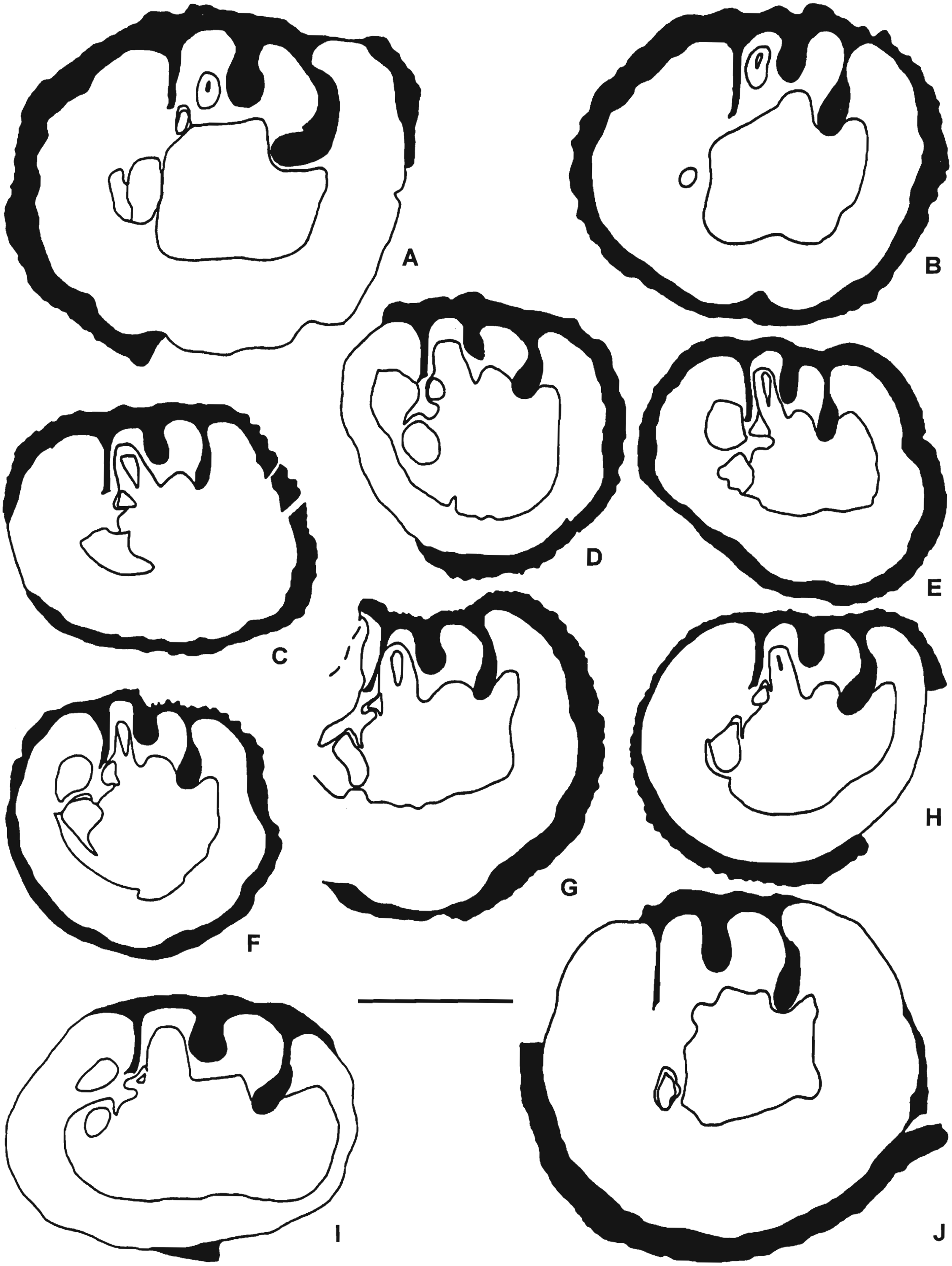
1904 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Toucas, p. 100, text-fig. 158.
1908*b* *Hippurites* (*Vaccinites*) *Chaperi* Douv.; Parona, p. 147, text-fig. 6.
1908*b* *Hippurites* (*Vaccinites*) *Gaudryi* Mun.-Chalm.; Parona, p. 148, text-fig. 8.
non 1910 *Hippurites cornu-vaccinum* (Goldf.); Fraas, p. 158, text-fig. 99a–b [=*Hippurites* (*Vaccinites*) *gosaviensis* (Douvillé, 1890) *teste* Kühn 1932].
v. p1910 *Hippurites* (*Vaccinites*) *Taburni* Guiscardi; Douvillé, p. 41, pl. 2, figs 1, 2, 2a.
1912 *Hippurites cornuvaccinum* Br.; Schubert, p. 62.
?1912 *Hippurites Gaudryi* M. Ch.; Schubert, p. 62, text-fig. 21.
1914 *H. cornu vaccinum*; von Zsigmondy, p. 388.
1916 *Hippurites Gaudryi*; Frech, p. 296.
1917 *Hippurites* (*Vaccinites*) *Gaudryi* Mun. Chalm.; Parona, p. 588, pl. 1, fig. 1, 1a; text-fig. 1a–b.
1922 *Hippurites cornuvaccinum* Matheron; Klinghardt, p. 63
1922 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Klinghardt, pl. 4, fig. 3.
p1926 *Hippurites* (*Vaccinites*) *Gaudryi* Mun. Chalm.; Parona, p. 21, pl. 1, fig. 4a–b; pl. 2, fig. 5a–b.
1927 *Hippurites Gaudryi*; Douvillé, *in* Renz, p. 502.
1931 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Klinghardt, p. 35, pl. 3, figs 10–11; text-fig. 9.
1931*b* *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Nöth, p. 161.
1931*b* *Hippurites* (*Vaccinites*) *gaudryi* Mun. Chalm.- Nöth, p. 161.
1932 *Hippurites* (*Vaccinites*) *alpinus* Douvillé; Kühn, p. 37.
1932 *Hippurites* (*Vaccinites*) *cornu-vaccinum* Bronn; Kühn, p. 44.
1932 *Hippurites* (*Vaccinites*) *gaudryi* Munier-Chalmas; Kühn, p. 48.
1932 *Hippurites* (*Vaccinites*) *Gaudryi* Mun. Chalm.; Parona, p. 100.
1934 *Hippurites Gaudryi* Munier-Chalmas; de Lapparent, p. 1163.
1934 *Hippurites* (*Vaccinites*) *cornu-vaccinum* Bronn; Milovanović, p. 215, text-fig. 16.
1935 *Hipp. cornuvaccinum*; Klinghardt, p. 30.
1937 *Hippurites* (*Vacc.*) *cornu-vaccinum* Bronn; Zapfe, p. 74.
1939 *Hippurites* (*Vaccinit.*) *alpinus* Douvillé; Klinghardt, p. 135.
?*1939* *Hippurites* (*Vaccinites*) *cornu-vaccinum* Bronn; Klinghardt, p. 137.
1939 *Hippurites* (*Vaccinit.*) *cornuvaccinum* Bronn, var. *crassa* Klinghardt; Klinghardt, p. 135.
1939 *Hippurites* (*Vaccinit.*) *gaudryi* Munier-Chalmas; Klinghardt, pp. 133, 135.
1941 *Hippurites* (*Vacc.*) *gaudryi* Munier-Chalmas; Montagne, p. 61, pl. 4, fig. 4.
?1941 *Hippurites cornuvaccinum* Bronn; Stchépinsky, p. 17.
?*1941* *Hippurites cornuvaccinum* Bronn; Tromp, p. 608.
non 1942 *Hippurites cornuvaccinum* Bronn; Stchépinsky, p. 53, pl. 7, fig. 14.
.1943 *Hippurites* (*Vaccinites*) *gaudryi* Munier-Chalmas; Klinghardt, p. 128, pl. 8, fig. 9.
v.1943 *Hippurites* (*Vaccinites*) *gaudryi* Munier-Chalmas; Klinghardt, p. 128, text-fig. 5.
1944 *Hippurites* (*Vaccinites*) *alpinus* Douv.; Klinghardt, p. 201, pl. 4, fig. 4.
1944 *Hippurites* (*Vaccinites*) *gaudryi* Munier-Chalmas; Klinghardt, p. 201, pl. 4, figs 6–7.
non 1946*a* *Hippurites cornuvaccinum* Bronn; Stchépinsky, p. 125, pl. 16, fig. 7 [cop. Stchépinsky 1942].
?*1946b* *Hippurites cornuvaccinum* Bronn; Stchépinsky, p. 353.
1947 *H. cornu-vaccinum* Bronn; Kühn, p. 187.
1947 *H. gaudryi* Douv.; Kühn, p. 187.
1948 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn var. *gaudryi* (Mun.-Ch.) Kühn; Kühn, p. 180, pl. 27, fig. 1; text-figs 8–11.
p1948 *Hippurites* (*Vaccinites*)*fortisi* Catullo; Kühn, p. 177, text-fig. 5 [cop. Parona 1908*b*].
?1951 *Hippurites* (*Vaccinites*) *cornu-vaccinum* Bronn; Pejović, p. 93, pl. 3, fig. 1.
1954 *H.* (*V.*) *cornuvaccinum* Bronn var. *gaudryi* (Mun.-Ch.); Milovanović, p. 166, text-figs 3 [cop. Toucas 1904], 5 [cop. Kühn 1948].
v.1954 *Hippurites* (*Vaccinites*) *klinghardti* nov. spec. Milovanović, p. 167, text-fig. 4 [cop. Klinghardt 1943].
?1957 *Hippurites* (*Vaccinites*) *alpinus* Douvillé; Pašić, p. 119, pl. 34, fig. 5.
1957 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn var. *gaudryi* (Mun.-Chal.) Kühn; Pašić, p. 123, text-fig. 62.
1957 *Hippurites* (*Vaccinites*) *taburni* Guiscardi; Pašić, p. 130, pl. 37, fig. 2.

TEXT-FIG. 58. *Vaccinites cornuvaccinum* (Bronn, 1831) from Dionysos. RV sections; A, H207; B, H349; C, H196; D, H272; E, H197; F, H195; G, H246; H, H212; I, H200; J, H201; K, H203. Scale bar represents 30 mm.

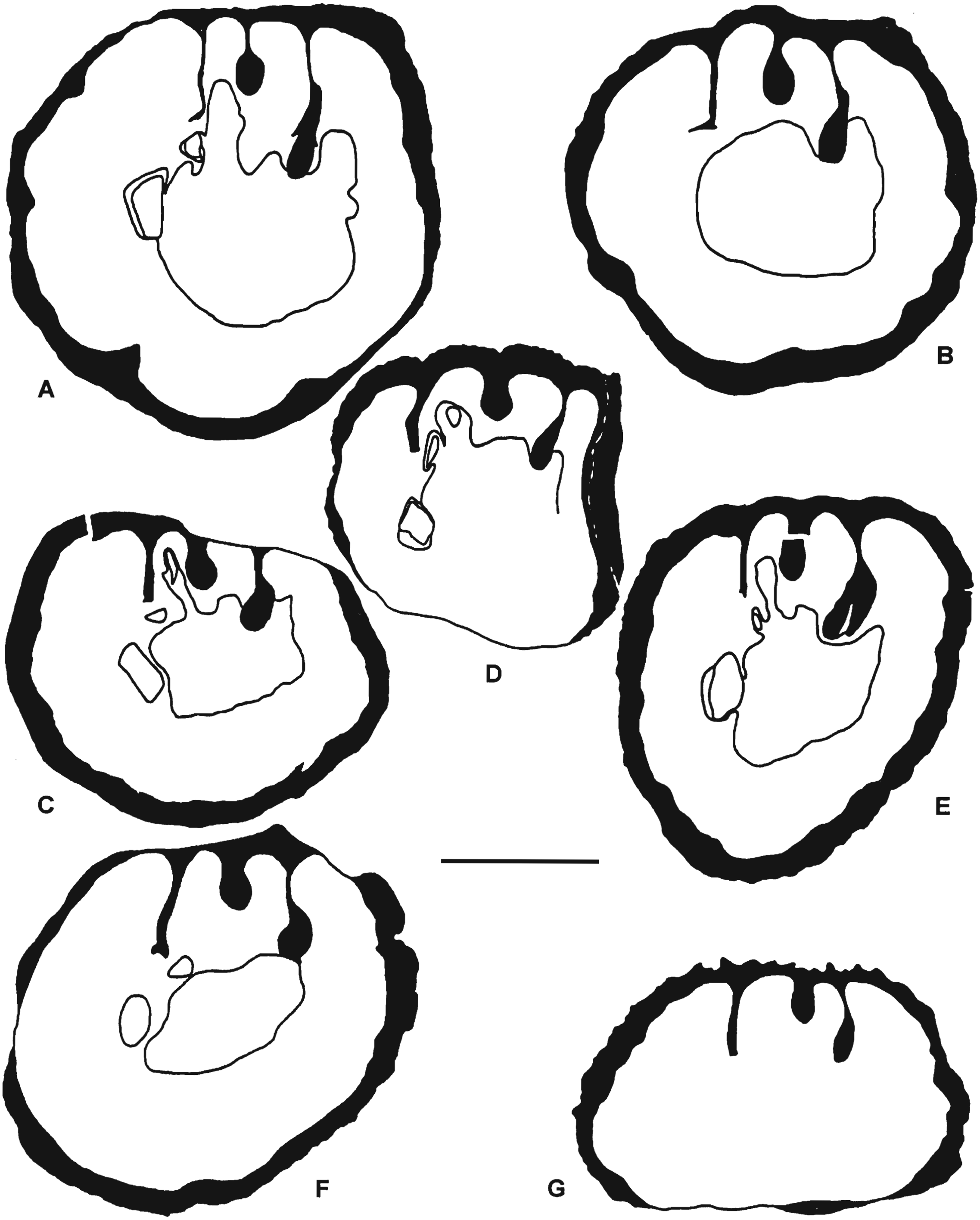

A
B
C
D
E
G
F
H
I
J
K

non 1959 *Vaccinites gaudryi* Mun. Chal.; Aubouin, p. 62, pl. 1, fig. 1a.
?1959 *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* (Mun.-Chalm.) Kühn; Polšak, pp. 64, 74, pl. 5, figs 1–3; pl. 6, figs 1–2; text-fig. 2.
1960 *Vaccinites gaudryi* Mun.-Chal.; Aubouin *et al.*, p. 458.
1960 *Hippurites cornuvaccinum* Bronn; Kühn, p. 48.
1960 *Hippurites gaudryi* Munier-Ch.; Kühn, p. 48.
1960 *Hippurites* (*Vaccinites*) *archiaci* Mun. Chalmas Form B; Lupu and Lupu, p. 246, pl. 2, fig. 39; text-fig. 11.
1960 *H. cornuvaccinum* Bronn; Milovanović, p. 367.
1960 *H. gaudryi*; Milovanović, p. 367.
1960 *H. cornuvaccinum* Bronn var. *gaudryi* (Mun.-Ch.); Milovanović, p. 367.
1960 *Hippurites cornuvaccinum* Bronn; Pejović and Kühn, p. 137.
1961 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn var. *gaudryi* (Mun.-Ch.) Kühn; Pleničar, p. 54, text-figs 11–12.
?1961 *Hippurites gaudryi* Munier-Chalmas?; Pleničar, p. 56, pls 10–11, 14.
1961a *Hippurites* (*V.*) *cornuvaccinum* Bronn; Polšak, pp. 422, 432.
1961a *Hippurites* (*V.*) *cornuvaccinum gaudryi* (Mun.-Chalm.) Kühn; Polšak, pp. 422, 432.
1961*b* *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Polšak, pp. 436, 451, pl. 1, figs 1–2.
1961*b* *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* (Mun.-Chalm) Kühn; Polšak, pp. 438, 451, pl. 2, fig. 1.
non 1962 *Vaccinites* cf. *gaudryi* M. Ch.; Celet, pl. 13, fig. 1.
non 1962 *Hippurites cornuvaccinum* Bronn; Kaumanns, p. 300, text-fig. 3.
?1962 *Hippurites cornuvaccinum gaudryi* (Mun.-Ch.) Kühn; Kaumanns, p. 302, text-fig. 4.
1962 *H. cornuvaccinum* Bronn; Pleničar, p. 42.
1962 *Hippurites* (*Vacc.*) *cornuvaccinum* Bronn; Slišković *et al.*, p. 131.
1962 *Hippurites* (*Vacc.*) *cornuvaccinum Gaudryi* (Mun. Chalm.) Kühn; Slišković *et al.*, p. 131.
1962 *Vaccinites gaudryi* M. Ch.; Sornay, *in* Celet, p. 187, pl. 6, fig. 3a–b; pl. 7, fig. 4a–b.
1963*b* *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Slišković, p. 9, pl. 2, fig. 1.
1963*b* *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* (Mun.-Chalmas) Kühn; Slišković, p. 10, pl. 2, fig. 2; pl. 3, fig. 1.
1964 *Vaccinites gaudryi* Mun.-Chal.; Dercourt, p. 197.
1964 *H.* (*V.*) *cornuvaccinum* Bronn; Polšak, p. 67.
1965 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Benkö-Czabalay, p. 402.
1965 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Mamužić, p. 344.
1965 *H.* (*V.*) *cornuvaccinum gaudryi* (Mun.-Chalm.); Mamužić, p. 344.
1965b *Hippurites* (*V.*) *cornuvaccinum* Bronn; Polšak, p. 451.
?1966 *Vaccinites cornuvaccinum gaudryi* (Munier-Chalmas); Pamouktchiev, p. 26, pl. 3, fig. 1.
?1966 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn var. *gaudryi* (Munier-Chalmas) Kühn; Todiriţă-Mihăilescu, p. 73, pls 23–24.
1967*b* *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Polšak, pp. 120, 211, text-fig. 41.
1967 *H.* (*V.*) *cornuvaccinum*; Slišković, p. 30.
1968a *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Slišković, p. 38.
1968a *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* Kühn; Slišković, p. 38.
1969 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Polšak and Mamužić, p. 239.
1969 *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* (Munier-Chalmas); Polšak and Mamužić, p. 239.
1969 *H. cornuvaccinum* Bronn; Sladić-Trifunović, text-figs 23 [cop. Bronn 1838], 24 [cop. Milovanović 1934].
1970 *H. gaudryi* Munier-Chalmas; Benkö-Czabalay, p. 283.
1971a *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Slišković, p. 40.
1971a *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* Kühn; Slišković, p. 40.
1971 *Vacc. cornuvaccinum* (Bronn); Vogel, p. 65.
1973 *Vaccinites gaudryi* Mun. Chal.; Mercier, p. 314.
1974 *Hippurites* (*Vaccinites*) *cornuvaccinum cornuvaccinum* Bronn; Lupu, p. 59, pl. 4, fig. 15, text-fig. 7.
1974 *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* Munier-Chalmas; Lupu, p. 60, pl. 4, fig. 16, text-fig. 8.
1974 *Vaccinites gaudryi* (Mun.-Chalm.); Patrulius, p. 170.

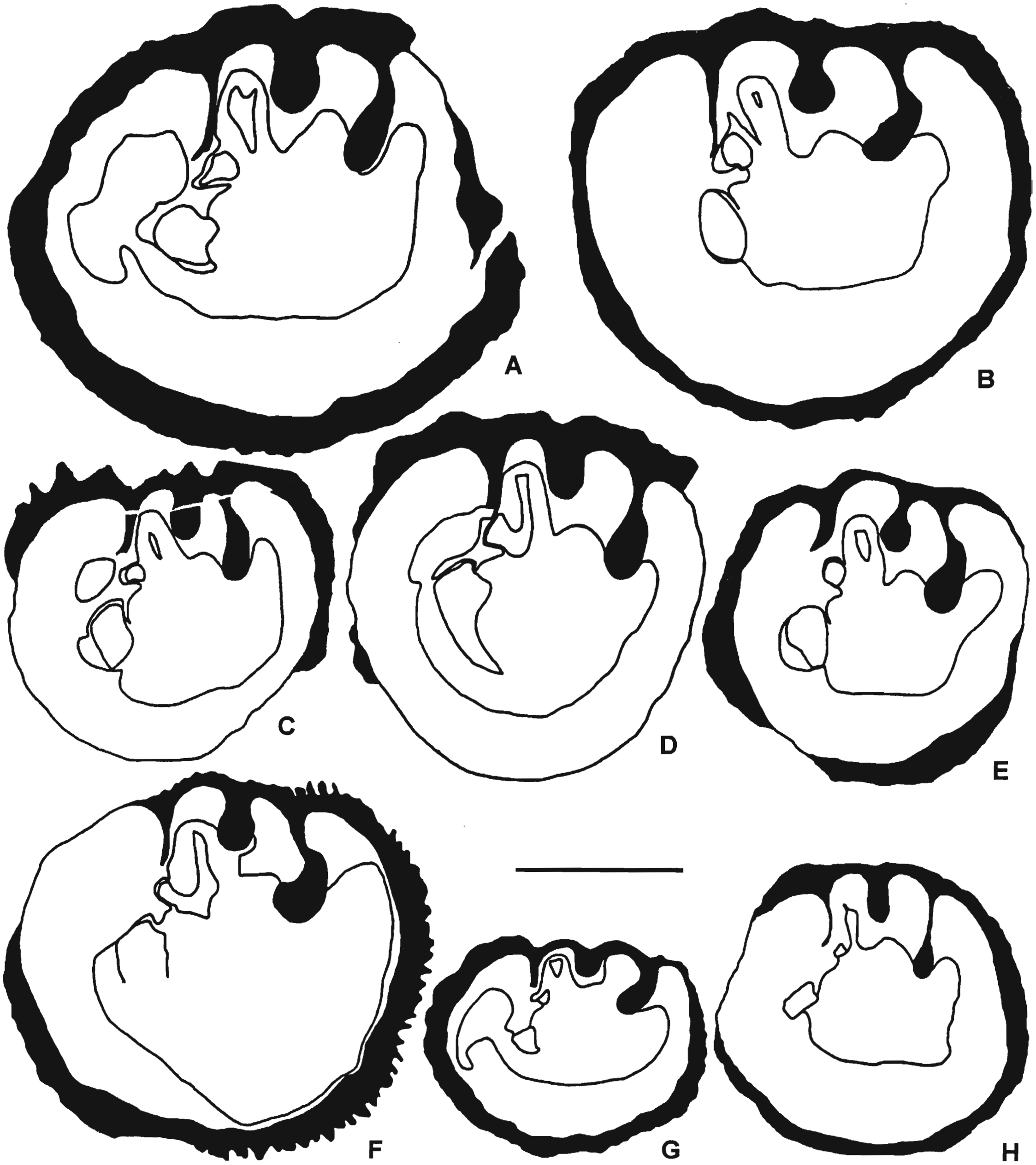
TEXT-FIG. 59. *Vaccinites cornuvaccinum* (Bronn, 1831) from Anthochorion. RV sections; A, H508; B, H507; C, H511; D, H515; E, H26; F, H72; G, H71; H, H180; I, H77a; J, H34. Scale bar represents 30 mm.


A
B
C
D
E
F
G
H
I
J

1974 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Slišković, p. 133.
1974 *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* Kühn; Slišković, p. 133.
1975 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Pleničar, pp. 100, 111, pl. 15, figs 2–3.
1975 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn var. *gaudryi* (Munier-Chalmas) Kühn; Pleničar, pp. 101, 112, pl. 16, figs 1–3; pl. 17, figs 1–3.
1975a *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Slišković, p. 43.
1975a *H.* (*V.*) *cornuvaccinum gaudryi* Kühn; Slišković, p. 43.
1976 *Vaccinites cornuvaccinum* (Bronn); Andrusov, p. 19, text-figs 6–8.
1976 *Vaccinites gaudryi* (Munier-Chalmas); Andrusov, p. 20, text-figs 9–10.
1976 *Vaccinites cornuvaccinum* Bronn; Lupu, p. 112, pl. 7, fig. 3, pl. 35, figs 7–8.
1976 *Vaccinites cornuvaccinum gaudryi* Munier-Chalmas; Lupu, p. 112, pl. 9, fig. 5; pl. 36, fig. 8.
1978 *V. cornuvaccinum gaudryi* (Munier-Chalmas); Pamouktchiev, p. 235, tab. 1.
1978 *H.* (*V.*) *cornuvaccinum cornuvaccinum* Bronn; Polšak *et al.*, p. 190.
1978 *H.* (*V.*) *cornuvaccinum gaudryi* Munier-Chalmas; Polšak *et al.*, p. 190.
1978 *Hippurites cornuvaccinum* Bronn; Sladić-Trifunović, text-figs 6/1 [cop. Bronn 1838], 6/3 [cop. Toucas 1904].
1978 *H. cornuvaccinum gaudryi* (Mun. Chalm.); Sladić-Trifunović, text-fig. 5/2 [cop. Kühn 1948].
?1979 *Hippurites* (*Vaccinites*) *cornuvaccinum cornuvaccinum* Bronn; Polšak, pp. 205, 224, pl. 10, fig. 1.
1979 *H.* (*V.*) *cornuvaccinum gaudryi* Munier-Chalmas; Polšak, p. 205.
1980 *V. cornuvaccinum*; Laviano and Sirna, p. 69.
?1981*b* *Vaccinites cornuvaccinum gaudryi* (Munier-Chalmas); Pamouktchiev, p. 170, pl. 84, fig. 1 [cop. Pamouktchiev 1966], fig. 1a.
?*1981* *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Polšak, p. 454, text-fig. 7a [cop. Polšak 1979].
1981 *Vaccinites alpinus* (Douvillé); Sánchez, p. 37 [with synonymy].
1981 *Vaccinites cornuvaccinum* Bronn; Sánchez, p. 41 [with synonymy].
1981 *Vaccinites cornuvaccinum gaudryi* Munier-Chalmas; Sánchez, p. 42 [with synonymy].
1982 *Vaccinites taburni* (Guiscardi); Accordi *et al.*, p. 771, pl. 5, fig. 3.
1982c *Vaccinites cornuvaccinum* Bronn; Bilotte, p. 111.
non 1982 *Vaccinites cornuvaccinum gaudryi* (Munier-Chalmas); Czabalay, pp. 35, 74, pl. 10, fig. 1.
non 1982 *Vaccinites cornuvaccinum* Bronn; Matteucci *et al.*, p. 81, pl. 1, fig. 5.
1982 *Hippurites* (*V.*) *cornuvaccinum* Bronn; Polšak *et al.*, text-fig. 3.
1982 *Vaccinites alpinus* (Douvillé); Pons, tab. 1.
1983 *Vaccinites alpinus*; Gallemi *et al.*, tab. 3.
1983 *H.* (*Vacc.*) *cornuvaccinum* Bronn var. *gaudryi* (Munier-Chalmas) Kühn; Pleničar and Premru, p. 192.
?1984 *Vaccinites cornuvaccinum* Bronn; Bilotte, pl. 41, fig. 8.
?1984 *Hippurites* (*Vaccinites*) *cornuvaccinum cornuvaccinum* Bronn; Höfling, pl., figs 4–5.
1985 *Vaccinites cornuvaccinum* Bronn; Bilotte, p. 340.
?1985 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn; Höfling, pp. 35, 65, pl. 7, figs 4, 6 [cop. Höfling 1984]; pl. 7, fig. 5.
1985 *V. cornuvaccinum* Bronn; Lupu, p. 21.
1985 *V. gaudryi* Mun.-Chalm.; Lupu, p. 21.
1985 *V. cornuvaccinum gaudryi* Mun.-Chalm.; Lupu, p. 22.
?1985 *Vaccinites cornuvaccinum gaudryi* Munier-Chalmas; Lupu, *in* Kollmann *et al.*, p. 129, pl. 1, fig. 1.
non 1987 *Vaccinites gaudryi* (Munier-Chalmas); Konertz, pl. 1, fig. 4.
1989*b* *Vaccinites taburni* (Guiscardi); Cestari and Sirna, p. 20, tab. 1, pls 4–6.
?1989 *Vaccinites sulcatus* Defrance; Özer, p. 337, pl. 1, figs 7–9.
1989 *Vaccinites cornuvaccinum*; Pieri and Laviano, p. 352.
1990 *Vaccinites cornuvaccinum gaudryi*; Gušić and Jelaska, text-figs 7–8, 11.
1991 *Vaccinites cornuvaccinum*; Caffau and Pleničar, p. 209.
1991 *H.* (*Vacc.*) *cornuvaccinum* Bronn; Šribar and Pleničar, p. 179.
1991 *Hippurites* (*Vaccinites*) *cornuvaccinum* Bronn var. *gaudryi* (Munier-Chalmas) Kühn; Šribar and Pleničar, p. 178.
?1992*a* *Vaccinites cornuvaccinum* Bronn; Chikhi-Aouimeur, p. 173, pls 1–3.
1992*a* *Vaccinites cornuvaccinum gaudryi* (Mun.-Chalmas) Kühn; Chikhi-Aouimeur, p. 174, pl. 4.
p1992*b* *Vaccinites taburnii* Guisc.; Chikhi-Aouimeur, pl. 3, figs 6–7 [cop. Douvillé 1910], pl. 4 [without label: cop. Pašić 1957], pl. 5 [without label: cop. Parona 1901, cop. 'Sirna 1982' = Accordi *et al.* 1982, cop. 'Sirna 1988' = Cestari and Sirna 1989*b*].

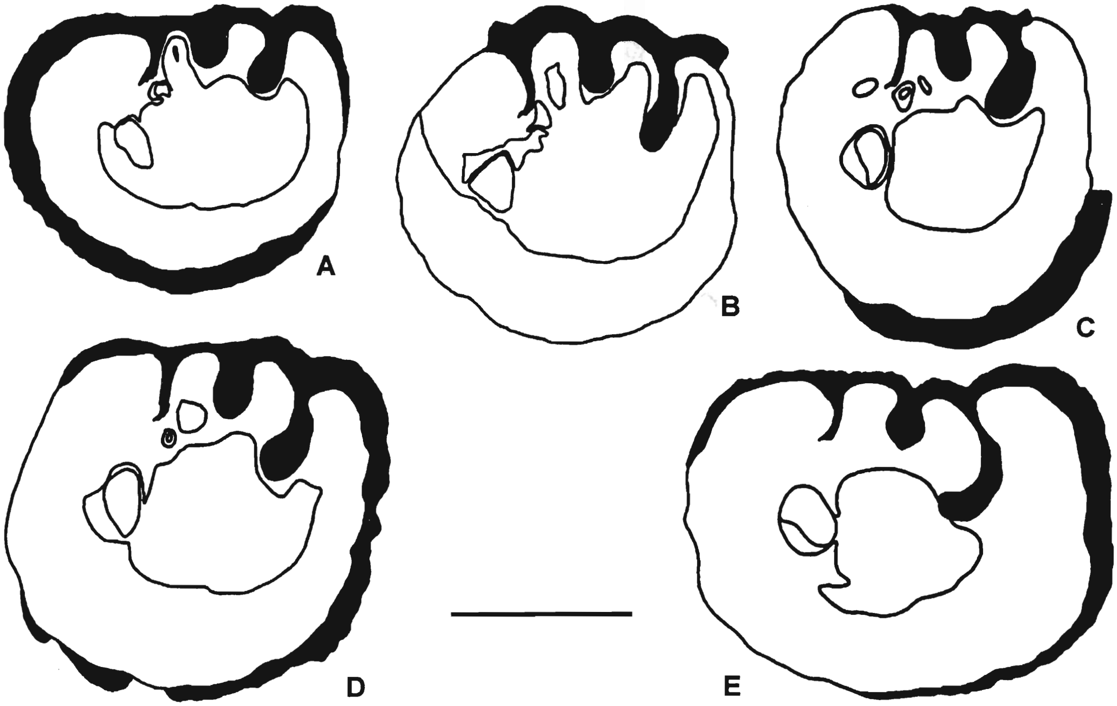


TEXT-FIG. 60. *Vaccinites cornuvaccinum* (Bronn, 1831) from Anthochorion. RV sections; A, H33; B, H31; C, H178; D, H517; E, H518; F, H503; G, H516. Scale bar represents 30 mm.



TEXT-FIG. 61. *Vaccinites cornuvaccinum* (Bronn, 1831). RV sections; A–G, from Pavlos; H, from Makrokastron; A, H495; B, H480; C, H494; D, H481; E, H489; F, H490; G, H585; H, H166. Scale bar represents 30 mm.

1992a	*V. cornuvaccinum* Bronn; Peza, p. 87.
1993	*Vaccinites taburni* Guiscardi; Carannante *et al.*, p. 28, text-fig. 2a.
1993	*Vaccinites gaudryi* Munier-Chalmas; Cherchi *et al.*, p. 95, text-fig. 2.
1993	*Vaccinites taburni* (Guiscardi); Ruberti, p. 970, pl. 9, figs 4–5; pl. 10, fig. 2 [cop. Carannante *et al.* 1993].

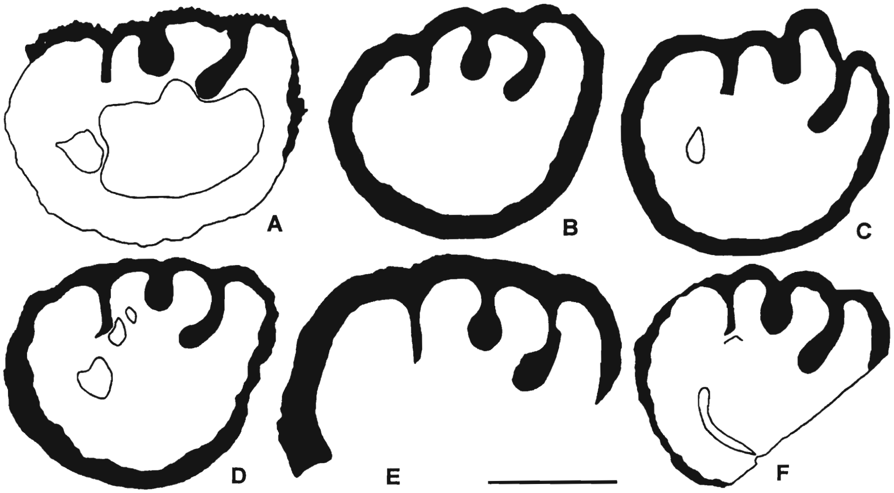


TEXT-FIG. 62. *Vaccinites cornuvaccinum* (Bronn, 1831) from Kalamos Hill. RV sections; A, H241; B, H234; C, H232; D, H230; E, H236. Scale bar represents 30 mm.

1993*b* *Vaccinites alpinus* (Douvillé); Steuber, p. 44, pl. 1, fig. 7.
1993*b* *Vaccinites cornuvaccinum* (Munier-Chalmas); Steuber, p. 44, pl. 1, fig. 5.
1993*b* *Vaccinites gaudryi* (Munier-Chalmas); Steuber, p. 44, pl. 1, fig. 6.
1993*b* *Vaccinites* cf. *boehmi* (Douvillé); Steuber, p. 46, pl. 1, fig. 4.
1993 *V.* aff. *boehmi* (Douvillé); Steuber *et al.*, text-fig. 8.
1993 *Vaccinites alpinus* (Douvillé); Steuber *et al.*, text-fig. 10.
1993 *V. cornuvaccinum* (Bronn); Steuber *et al.*, text-fig. 10.
1993 *Vaccinites gaudryi* (Munier-Chalmas); Steuber *et al.*, text-fig. 10.
1996*b* *Vaccinites cornuvaccinum* (Bronn); Steuber, p. 308, pl. 1.
p1996 *Vaccinites fortisi* (Catullo); Cestari *et al.*, p. 171, text-figs 1, 2a–n, 3o–z.
1997 *Vaccinites taburni* Guiscardi; Ruberti, tab. 1.

Neotype. Designated herein: Goldfuß (1840, pl. 165, fig. 1.); Plate 24, figures 1–6, Text-figure 56A–B; PIB-GC 1062.

Greek material. More than 200 specimens, numerous of them with both valves preserved, from Keratovouno Hill (H28, H36–H37, H56, H63, H68–H70, H74–H75, H77–H79, H102, H476, H479), Anthochorion (H26, H31, H33–H34, H71–H72, H77a, H178, H180, H183, H503, H507–H509, H511–H512, H515–H518), Makrokastron (H155, H158–H160, H164, H166, H170, H173), Dionysos (H193, H195–H197, H200–H201, H203, H207, H212, H245–H246, H272, H349–H350), Pavlos (H441, H443–H445, H480–H482, H489–H490, H493–H495, H585), from Kalamos Hill (H217, H227, H229–H234, H236, H241, H525), from the southern slope of Kakotopia Mountain at the Bay of Saltsas (H81, H275, H279, H285, H409), and one RV from Panourgias, Othrys Mountains (H409).



TEXT-FIG. 63. *Vaccinites cornuvaccinum* (Bronn, 1831). RV sections; A–D, F, from Kakotopia Mountain; E, from Panourgias; A, H278; B, H279; C, H275; D, H285; E, H409; F, H81. Scale bar represents 30 mm.

Additional material. The specimen figured by Goldfuß (1840, pl. 165, fig. 1); the holotype of *Vaccinites alpinus* (Douvillé, 1897*a*), several figured originals and topotypes from the collection of the Ecole des Mines (Lyon), and another topotype (MNHB-KC 80 I 5).

Remarks. Douvillé (1891, p. 7) succeeded neither in finding the syntypes described by Bronn nor in tracing a relatively well preserved shell figured by Goldfuß (1940) and, without being able to study these specimens, considered the inner termination of P0 to be rounded (Douvillé 1892*a*, p. 49). Previously, Woodward (1855) had presented a first description of the hinge and the morphology of the pillars. Subsequently, several specimens from the type locality (Untersberg) and other Gosau localities were described in detail (Douvillé 1897*a*); since then, the termination of P0 is known to be truncated and the pores of the LV to be polygonal. The synonymy list shows that the lack of a type specimen still has negative effects on a stable systematic position of the species.

The problems of separating *V. cornuvaccinum* and *Vaccinites taburnii* (Guiscardi, 1865) have been addressed frequently (e.g. Chikhi-Aouimeur 1992*a*, 1992*b*). RVs with short, truncated P0 have been attributed to *V. taburnii*, although the drawing of the holotype clearly shows a short P0 with a rounded inner termination. Therefore, a short, truncated P0 has been regarded diagnostic of *V. taburnii* by several taxonomists (Accordi *et al.* 1982; Cestari and Sirna 1989*b*), while others consider its rounded termination as a characteristic feature (Chikhi-Aouimeur 1992*a*). *V. gaudryi* has been considered a variety (Kühn 1948), subsequently a subspecies (Polšak 1959) of *V. cornuvaccinum*, and was finally regarded to be

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EXPLANATION OF PLATE 23

Fig. 1. *Vaccinites archiaci* (Douvillé, 1892a); H465, Grammatiko (Vermion Mountains); ligamental ridge with remnants of strong ligament; × 17·6.

Figs 2, 6. *Vaccinites cornuvaccinum* (Bronn, 1831); ligamental ridge with reduced ligament. 2, H512, Anthochorion. 6, H493, Pavlos. Both × 43.

Figs 3, 5. *Vaccinites chaperi* (Douvillé, 1897*a*); Vermion Mountains; 'ligamental ridge' without ligament insertion. 3, H560, Moukharemi Hill; 5, H6, Drosia. Both × 50.

Fig. 4. *Vaccinites* aff. *cornuvaccinum* (Bronn, 1831); H413, Paleokastron Hill; ligamental ridge with remnants of ligament; × 27·3.


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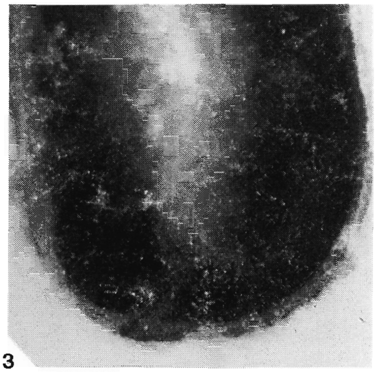
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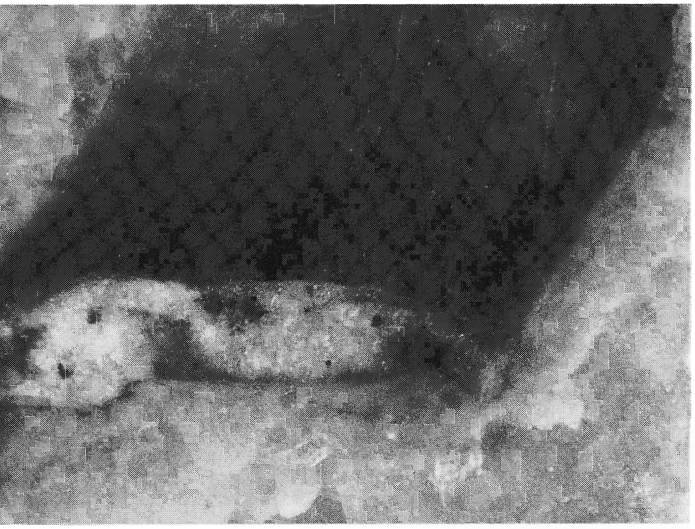
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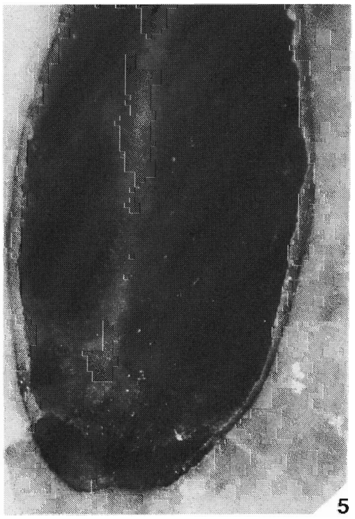
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6

STEUBER, *Vaccinites*

indistinguishable from *V. cornuvaccinum* (Höfling 1985). In respect of this taxonomic confusion it seems useful to define *Vaccinites cornuvaccinum* clearly by the installation of a neotype. This taxon is not only one of the longest known hippuritids but also the type species of *Vaccinites* Fischer, 1887.

As the syntypes are untraceable, the selection of a lectotype is not possible. The University of Heidelberg refused to receive Bronn's rudist collection, which was subsequently sold by Bronn to North America. The purchasing institution or individual was not named to the University (H. Bahlburg, pers. comm. 1994). A topotypic, bivalve shell was figured by Goldfuß (1840) and is remarkably well preserved in comparison with other specimens from the Untersberg locality, as the hinge and remnants of the LV pore system are visible. This specimen was thought to be lost after the inquiries of Douvillé (1891, p. 7) but is still part of the Goldfuß collection of the Palaeontology Institute of the University of Bonn. Most likely, Goldfuß received the specimen from his contemporary Bronn, so that the selected shell could be a lectotype. However, manuscripts of Goldfuß do not exist any more at the Palaeontology Institute in Bonn (M. Sander, pers. comm. 1994).

Descriptions

Neotype. Pores of LV preserved in a few small areas only and strongly worn. Their shape is polygonal, diameter 0·5 mm. Radial canals preserved only near the centre of LV, not exceeding 1 mm wide ridges between canals are up to 1·2 mm wide. RV elongated-conical, curved around the dorsal shell, length ventrally 277 mm, dorsally 219 mm; Dmax is 95 mm. Outer shell layer preserved anterodorsally in a 100 mm long fragment; other remnants apically, but badly worn. Longitudinal furrows 0·5–0·7 mm wide, separating thin, acute ribs.

Transverse section 20 mm below commissure: inner margin of outer shell layer somewhat undulating, P0 slightly curved anteriorly, its dorsal part diagenetically thinned by pressure dissolution, inner termination truncated. P1 with considerably pinched base and oval head. P2 has a long peduncle and an oval head which is curved anteriorly. (1) anterior to P0, triangular; (2) bears a posterodorsally tapering ridge that projects into the body-cavity; (3) in the prolongation of P0, with sub-rectangular outline and concave anterior, dorsal and ventral sides; ($3'$) anterodorsally excavated. Mp 20 mm long, max. 3 mm wide, dorsally and ventrally rounded, aligned sub-parallel to P0 and pointing to the centre of the valve, projecting interiorly 6·5 mm over the tip of P0.

Transverse section 23 mm below the commissure: General morphology of pillars unchanged, but diagenetic thinning of P0 is more pronounced. (1) separates anteroventral cavity; (2) projects with a ventral ridge that borders $1'$ into the body-cavity; (3) with sub-rectangular outline but less concave sides when compared with the higher section, dorsal excavation of ($3'$) less distinct. Mp 11 mm long, ventrally tapering and not projecting ventrally past the tip of P0.

Transverse section 75 mm above apex of RV: P0 curved anteriorly, increasing in thickness towards its inner termination which is truncated and bears remnants of the ligament. Sides of P1 sub-parallel, only the posterior side is slightly pinched. Base of P2 pinched, head oval-elongated and curved anteriorly. Shape of ($1'$) not clearly outlined, located posterior to the prolongation of P0; (3) immediately ventral of the tip of P0. $U/\overline{P0-P2}$ increases from 12·5 in this juvenile stage to 20·8 in the adult shell (Text-fig. 64).

The neotype differs from *V. chaperi* (Douvillé, 1897*a*) in the truncated P0 that bears remnants of a ligament (cf. Pl. 23, figs 3, 5; Pl. 24, figs 1–3).

Boeotian specimens. LV pores polygonal, diameter 0·6 to 0·8 mm, up to 1 mm in elongated pores; commonly denticulate with two, rarely three teeth that are only exceptionally fused. In some LVs simple polygonal pores dominate, in others more than two-thirds of all pores are denticulate. No relationship between these variations in pore

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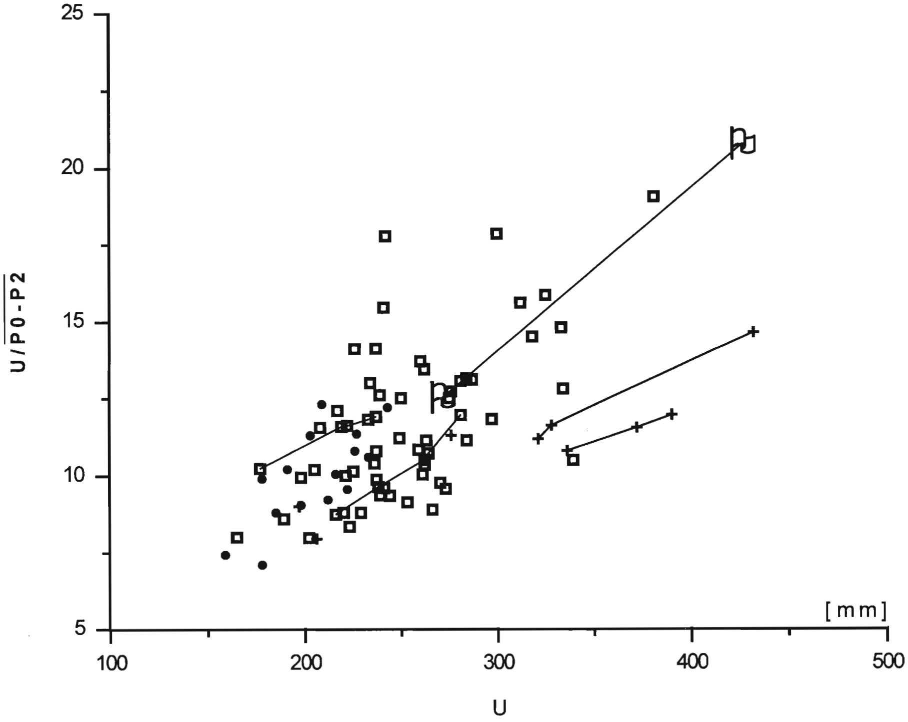
EXPLANATION OF PLATE 24

Figs 1–6. *Vaccinites cornuvaccinum* (Bronn, 1831); neotype; PIB-GC 1062. 1, transverse section of RV, 23 mm below commissure, adapical view. 2, transverse section of RV, 20 mm below commissure, abapical view. 3, transverse section of RV, 75 mm above apex, adapical view. 4–5, anterodorsal and dorsal aspects of both valves. 6, detail of LV with remnants of pores. 1–3, × 1; 4–5, × 0·3; 6, × 12.

PLATE 24

STEUBER, *Vaccinites*



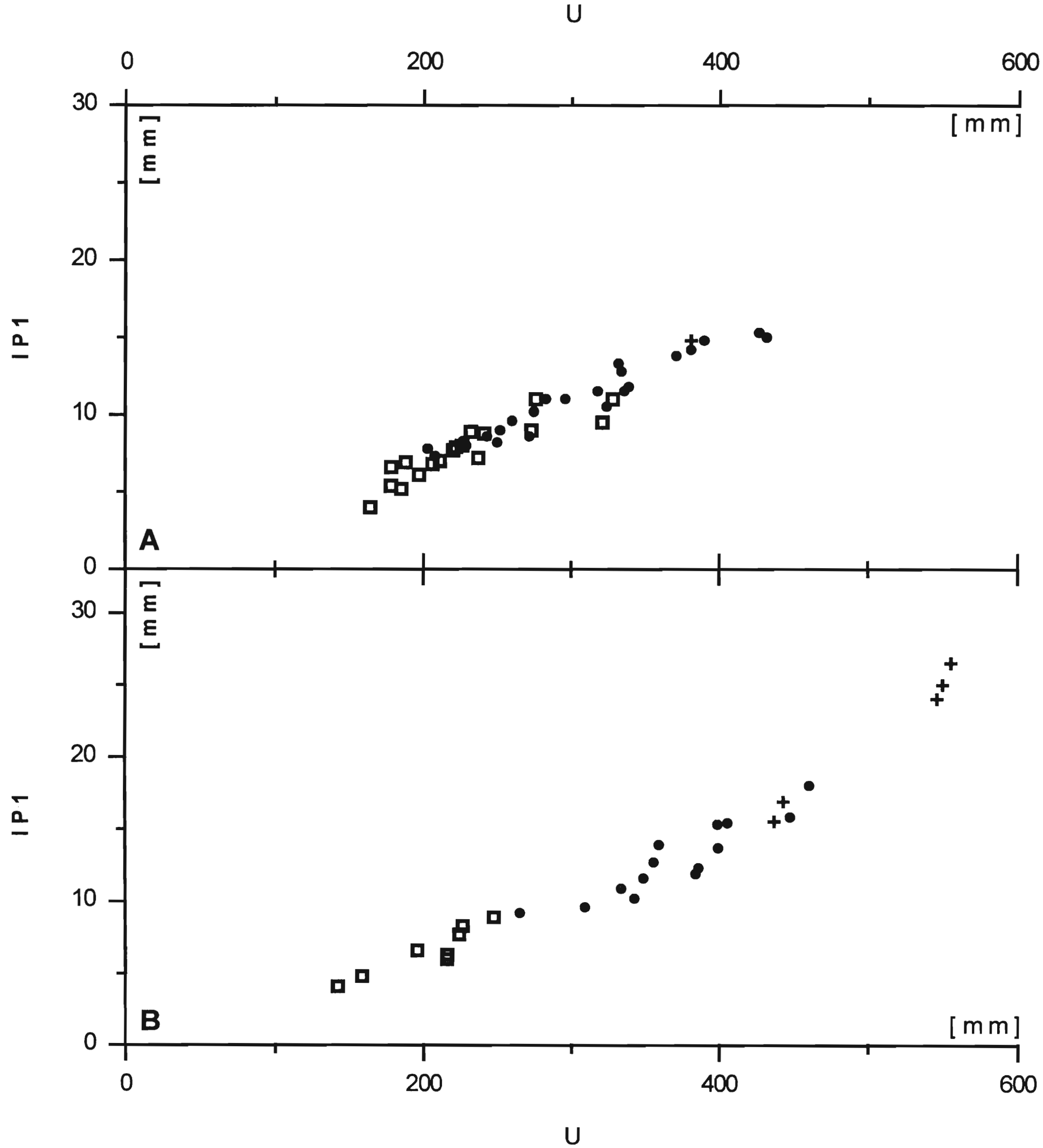
TEXT-FIG. 64. Arrangement of pillars plotted against the length of contour of inner margin of outer shell layer (U) in *Vaccinites cornuvaccinum* (Bronn, 1831). Neotype (flag), topotypes (+), topotypes of '*Hippurites gaudryi* Munier-Chalmas, *in* Gaudry 1867' (dots), *V. cornuvaccinum* from Boeotia (boxes). Ontogenetic stages of individual valves are connected by lines, respectively. See Text-figure 11 for measurements.

shape and ontogenetic age or other morphological characters of both valves was found. LV surface of weakly ribbed RVs smooth, but radially undulating; spotted with pustules in specimens with coarsely ribbed RVs; pustules mark the insertion sites of new radial canals that intercalate distally between older canals; mean width of radial canals is 1·5–1·7 mm, in a few specimens up to 2 mm; ridges between canals are 0·5–0·7 mm wide.

RVs elongated-conical, very rarely depressed-conical, up to 435 mm long. Dmax commonly between 55 mm and 60 mm, up to 75 mm. Thickness of outer shell layer varies in shells of approximately the same size (Text-fig. 57E, H, M), and amounts to 8 mm in a shell with Dmax of 77 mm. Longitudinal ribs in some RVs coarse and angular, sometimes thickened to form a beaded pattern; in other shells, longitudinal ribs are absent and the sculpture is dominated by transverse growth bands.

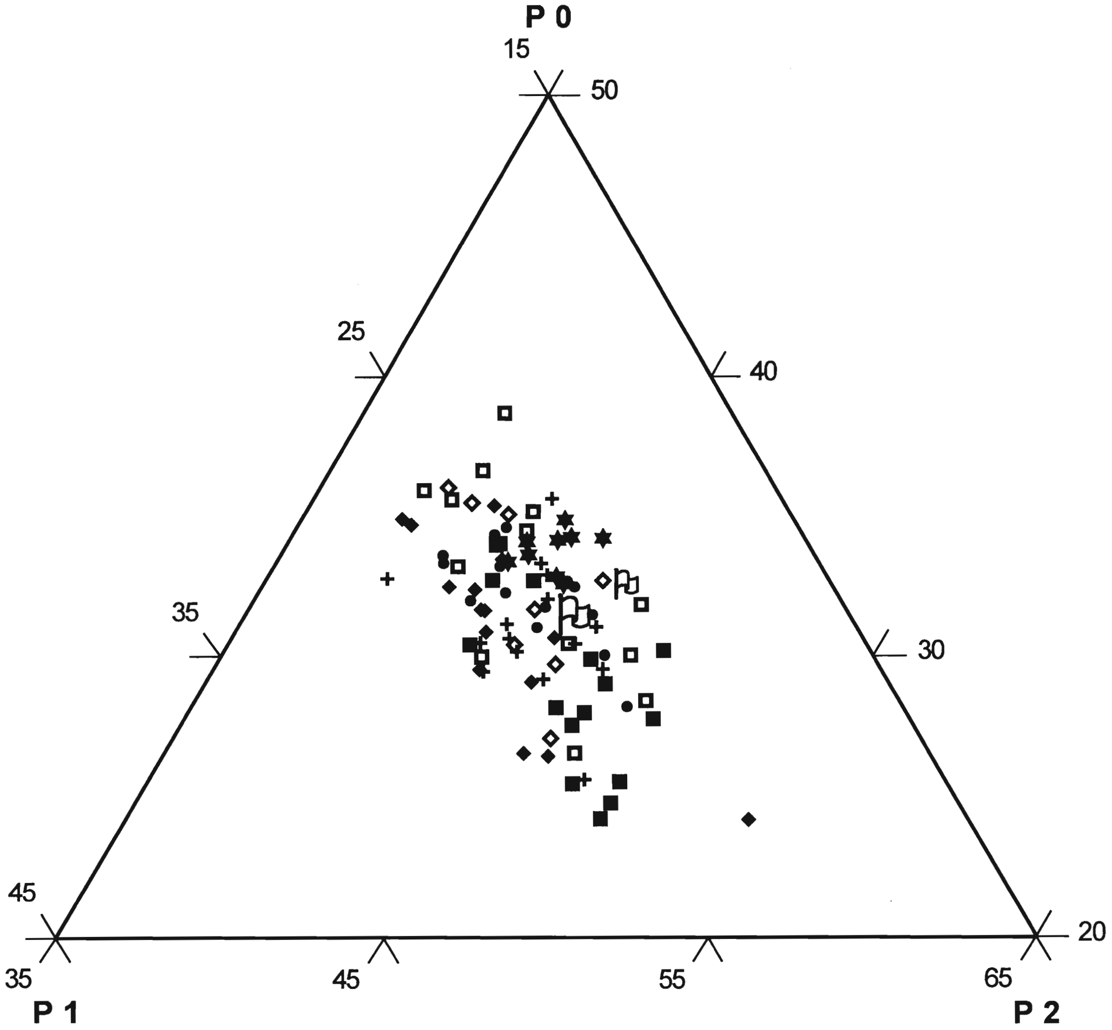
Pillars located close together at the dorsal shell, their bases move closer together during ontogeny (Text-fig. 64). Inner margin of outer shell layer smooth or undulating, one or two ventral undulations are more or less pronounced in some shells ('secondary pillars', Text-fig. 60A). P0 straight or curved anteriorly, its inner termination rectangularly or obliquely truncated, boot-shaped in some specimens, in others tapering and with reduced area of ligamental insertion (Pl. 23, fig. 2). P1 either with sub-parallel, parallel or pinched sides, only exceptionally with pedunculate base (Text-fig. 60A). P2 spatula- or kidney-shaped, with pinched or, less commonly, pedunculate base. The degree of pinching of P1 increases with U; P1 with parallel sides occur up to U = 340 mm, pinched bases are developed when U exceeds 200 mm (Text-fig. 65A). Length of P1 relatively invariable when compared with strongly varying ratios between lP0 and lP2 (Text-fig. 66). P2 almost generally longer than P0 or P1. LP0/lP1 ranges from 0·9–1·8, a ratio of 1·2 occurs most commonly (Text-fig. 67).

(1) and (2) in prolongation of P0. Location of (3) variable: in front of P0, posteroventrally or posteriorly of P0. Mp is frequently incised dorsally, shorter than (1) and (3); its insertion between P0 and P1 varies from positions deeply engulfed at the dorsal margin of the inner shell, to positions in front of the inner termination of P1. Positions of (3) and mp vary independently of each other. RVs with a long P0 are generally characterized by a narrow ligamental insertion (Pl. 23, figs 2, 6).



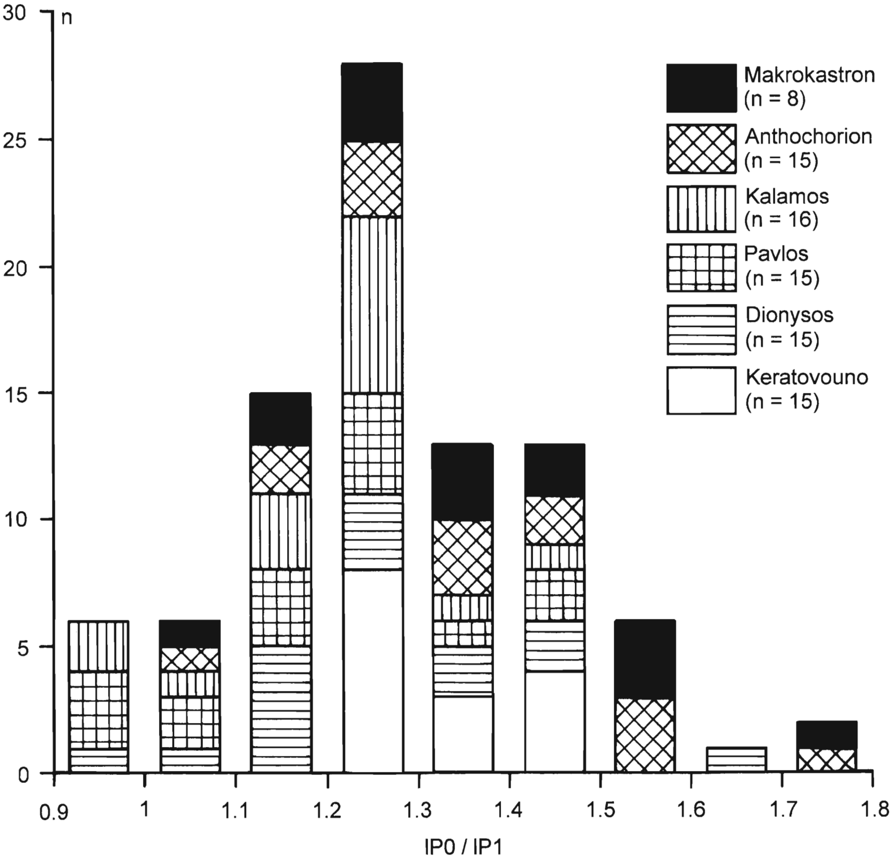
TEXT-FIG. 65. Length and shape of P1 plotted against U; A, *Vaccinites cornuvaccinum* (Bronn, 1831); B, *V. chaperi* (Douvillé, 1897*a*). Boxes, P1 with parallel sides; dots, P1 with pinched base; +, P1 with peduncled base.

Systematic position. Douvillé (1892*a*) was the first to figure and describe *Vaccinites gaudryi* (Munier-Chalmas, *in* Gaudry, 1867); he originally separated the species from *V. cornuvaccinum* because of its truncated P0, but emphasized their close relationship. At this time *V. cornuvaccinum* was only very insufficiently described, its P0 was considered to be rounded and, thus, not bearing a ligament. After the



TEXT-FIG. 66. Relative length of P0, P1 and P2 in *Vaccinites cornuvaccinum* (Bronn, 1831). Neotype (big flag = adult stage, small flag = juvenile stage); topotypes (asterisks); from Keratovouno Hill (dots, topotypes of '*Hippurites gaudryi* Munier-Chalmas, *in* Gaudry 1867'); Dionysos (+); Makrokastron (white diamonds); Kalamos Hill, (black diamonds); Anthochorion (white boxes); Pavlos (black boxes). See Text-figure 11 for measurements.

recognition of a truncated P0 in *V. cornuvaccinum* (Douvillé 1897*a*), it was stressed that P0 was short and curved anteriorly in *V. gaudryi*, and longer and straight in *V. cornuvaccinum*. This was linked to minor differences of hinge and mp. The line connecting (1) and (3) is more inclined with respect to the radial axis of P0 in *V. gaudryi* when compared with *V. cornuvaccinum* (Douvillé, 1897*a*). Despite their similarity, both species were maintained, even though Douvillé (1897*a*, p. 213) proposed that they could be races of the same species. Kühn (1948) considered *V. gaudryi* to be a variety of *V. cornuvaccinum*, and Polšak (1959), consequently, regarded *V. gaudryi* as a subspecies of *V. cornuvaccinum*. Because of their sympatric distribution, Höfling (1985) suggested abandoning these subspecies and included *V. cornuvaccinum gaudryi* in the synonymy of *V. cornuvaccinum*. These taxonomic changes have been rather intuitive, as the morphological variation of the species was never documented by morphometric analyses.

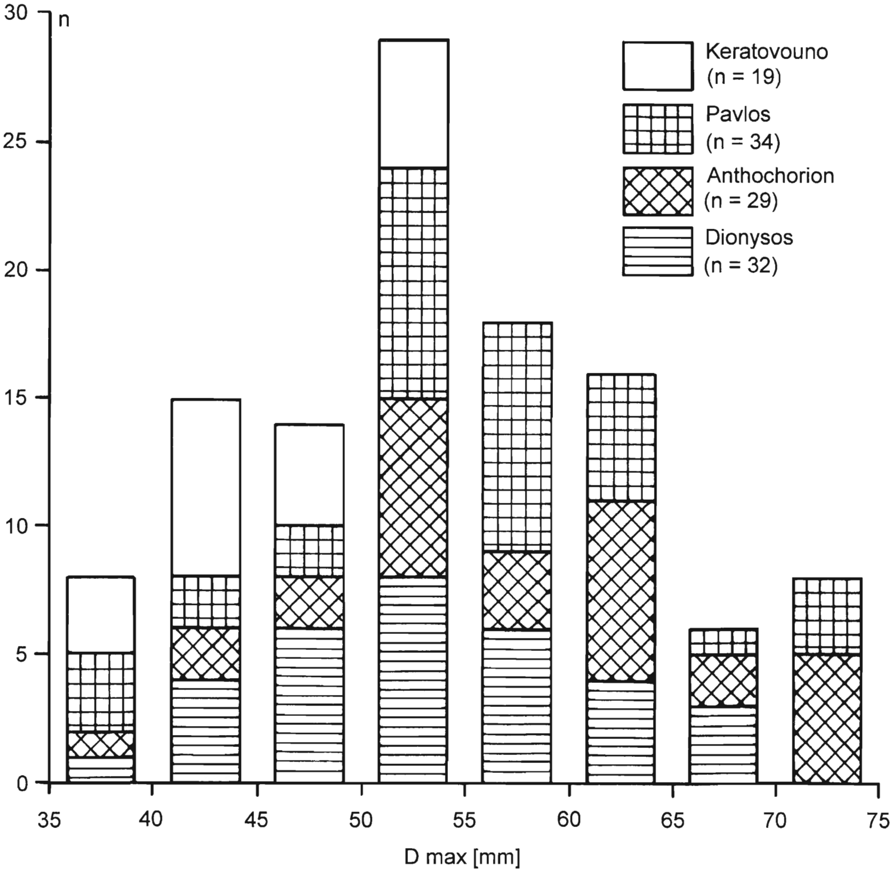


TEXT-FIG. 67. Histogram of ratios of length of P0 and P1 in *Vaccinites cornuvaccinum* (Bronn, 1831) from Boeotian localities.

RVs with anteriorly curved P0 and (3) posterior of P0 (Text-fig. 57) which agree well with the diagnosis of *V. gaudryi* given by Douvillé (1892*a*) are very abundant at Keratovouno Hill, the type locality of *Vaccinites gaudryi* (Munier-Chalmas, 1867). However, even among these shells, the morphology of P0 and especially the position of (3) is variable. Among the Boeotian specimens from several localities, about half correspond to the diagnosis of *V. cornuvaccinum*, and the other half to that given for *V. gaudryi* by Douvillé (1892*a*, p. 48; 1897*a*, p. 212). The specimens from Keratovouno Hill do not differ in the measurements taken (Text-figs 64, 66–68), except that they are smaller (Text-fig. 68). This could be related to trophic conditions or the life habit at this locality. A curvature of the RV around the dorsal shell which is frequently observed in *V. cornuvaccinum* from Keratovouno Hill, could have induced an escape of P0 to the anterior, and of (3) and mp to the posterior shell during growth, but this relationship between life habit, resulting morphotypes and arrangement of the myocardinal elements is not evident in the extensive material studied.

Vaccinites alpinus was separated from *V. cornuvaccinum* because of its pustulose pore system of the LV (Douvillé 1897*a*). Its RV is ornamented with coarse longitudinal ribs and P1 is considered to be not pinched, even in adult shells. It has been shown that these characters are rather variable within one species, and that coarsely ribbed morphotypes are often characterized by a pustulose LV (Douvillé 1894; Vicens 1992).

The taxonomic problems concerning *V. taburnii* (Guiscardi, 1865) have been discussed recently by Chikhi-Aouimeur (1992*b*) and are caused by an insufficient knowledge of the holotype. The drawing

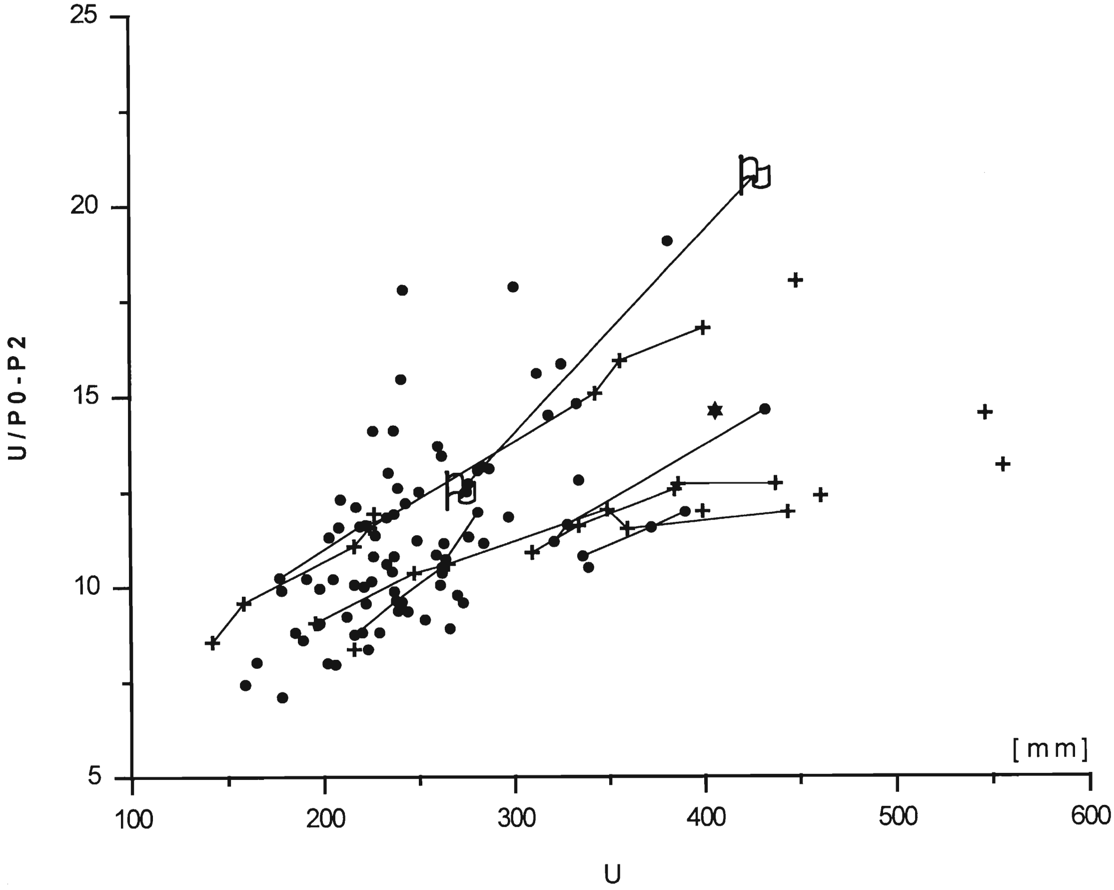


TEXT-FIG. 68. Histogram of Dmax of *Vaccinites cornuvaccinum* (Bronn, 1831) from Boeotian localities.

(Guiscardi 1865) of the type specimen shows a transverse section with a short P0 that is distinctly rounded at its tip. However, several taxonomists followed Parona (1901) who also used the name for RVs with truncated P0. Morphometric studies show that the relation of lP0 to the length of the other pillars is extremely variable in *Vaccinites cornuvaccinum*, and that RVs with P0 shorter or of equal length to P0 are common (Text-figs 66–67, Table 10). Shells that have been determined as *V. taburnii* which have a truncated P0 have, therefore, been included in the synonymy of *V. cornuvaccinum*. A redescription of the type specimen of *V. taburnii* is necessary to clear up its taxonomic status. If P0 actually does not have remnants of a ligament, the holotype would fall into the variability of *V. chaperi* (Text-fig. 54).

Vaccinites ultimus (Milovanović, 1935) has similar pillar morphology but belongs to a different phylogenetic lineage because of reticulate pores of the LV.

Vaccinites chaperi (Douvillé, 1897*a*) differs from *V. cornuvaccinum* by a completely atrophied ligament, as indicated by the rounded tip of P0. The pedunculate base of P2 which formed during early ontogeny is a less reliable character, because it has been noted exceptionally also in *V. cornuvaccinum*. On average, $U/\overline{P0{-}P2}$ is smaller in *V. chaperi* (Text-fig. 69), and P1 is shorter in relation to P0 and P2 when compared with *V. cornuvaccinum* (Text-figs 70–71), but the ranges observed in both species overlap. The relative increase in length of P0 in *V. chaperi* does not reflect shape change along a single allometric curve in specimens of *V. cornuvaccinum* and *V. chaperi* from Greece (Text-fig. 71A). Instead, an ontogenetic trend of decreasing lP0/lP1 in most shells of *V. chaperi* results from the pinching and, thus, elongation of



TEXT-FIG. 69. Arrangement of pillars plotted against U in (dots; flag = neotype) *Vaccinites cornuvaccinum* (Bronn, 1831) and (+, asterisk = holotype) *V. chaperi* (Douvillé, 1897*a*). Ontogenetic stages of individual valves are connected by lines, respectively. See Text-figure 11 for measurements.

P1. Therefore, low lP0/lP1 ratios are common in large specimens of *V. chaperi* (Text-fig. 71A), which may conceal to some extent the distinction of both species in a histogram of ratio values (Text-fig. 71B).

The pinching of P1 occurs at similar sizes (U) in both species (Text-fig. 65), and the pores of the LV show no diagnostic differences. (3) and mp insert in more ventral positions in *V. chaperi*, but this is also noted in RVs of *V. cornuvaccinum* with long P0 and reduced ligamental insertion area. The characters of such specimens correspond to the phenon '*cornuvaccinum*', as it was separated by Douvillé (1897*a*) from the phenon '*gaudryi*'; they represent, within the intraspecific variability of *V. cornuvaccinum*, the transition to *V. chaperi*. A clear distinction is only provided by the loss of the ligament in *V. chaperi*.

In addition to the overlapping variations that are evident in several characters, the similarity of the LV pore system argues for a close relation and a monophyletic heritage of both species. The loss of the ligament, the increase in length of P0 (Text-fig. 71), the increasing pinching of the pillar bases, and the general increase in length and diameter of the shells are considered as typical features of phylogenetic lineages in *Vaccinites* (Toucas 1904; Philip 1981; cf. Text-fig. 10). In *V. chaperi*, these characters are either apomorphic (loss of ligament) or trend towards a more evolved development (increase in length of P0, formation of peduncle in P2, increase in overall size). In this context, the descriptions given by Polšak (1959) of *Hippurites* (*Vaccinites*) *cornuvaccinum gaudryi* from a Dalmatian locality are remarkable. The

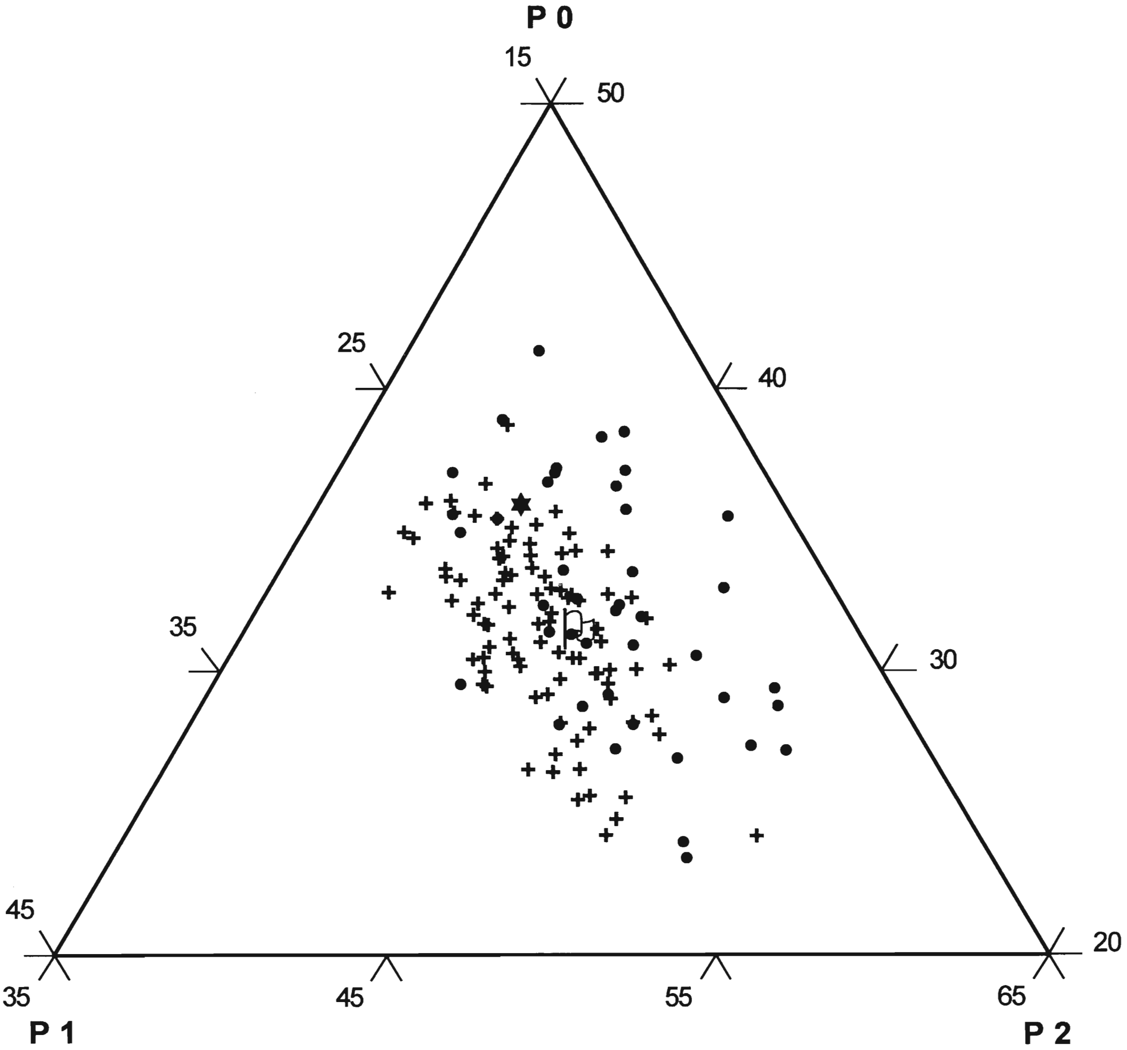
TABLE 10. Measurements (mm) of RVs of *Vaccinites cornuvaccinum* (Bronn, 1831).

	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
neotype:							
adult	98	427	21	158	1·4	0·7	0·5
juvenile	69	272	22	100	1·5	0·7	0·5
topotypes:							
Douv. 1891, pl. 1, fig. 4							
adult	105	432	30	161	1·4	0·7	0·5
juvenile	81	321	29	117	1·5	0·8	0·5
Douv. 1897*a*, pl. 31, fig. 3							
adult	92	390	33	158	1·4	0·8	0·6
juvenile	81	336	31	130	1·6	0·8	0·5
Douv. 1897*a*, pl. 31, fig. 4	52	197	22	76	1·6	0·8	0·5
Keratovouno (n = 14)							
min.	44	159	17	62	1·2	0·6	05
max.	57	232	25	99	1·5	0·8	0·7
mean	50	204	21	81	1·3	0·7	0·6
Anthochorion (n = 14)							
min.	50	217	16	84	1·0	0·6	0·5
max.	75	381	30	157	1·8	1·0	0·7
mean	66	280	22	107	1·4	0·8	0·6
Dionysos (n = 17)							
min.	46	188	14	76	1·0	0·5	0·5
max.	69	312	26	125	1·6	0·9	0·7
mean	59	248	21	99	1·3	0·7	0·6
Kalamos (n= 4)							
min.	52	198	16	72	1·0	0·5	0·4
max.	69	283	26	116	1·4	0·8	0·8
mean	59	241	21	97	1·2	0·7	0·6
Pavlos (n = 16)							
min.	45	164	17	63	0·9	0·5	0·4
max.	75	339	32	148	1·4	0·8	0·6
mean	60	239	25	106	1·2	0·6	0·5

inner termination of P0 of the juvenile shell in one specimen is truncated, in adult specimens it is rounded or tapering. Unfortunately, the figures (Polšak 1959, pl. 5, figs 1–3) do not reveal whether the ligament was actually ontogenetically atrophied, but the pedunculate P2 of this RV from Rakićev Umac indicates a high evolutionary level. A pronounced reduction of the area of ligamental insertion during ontogeny was noted in several Boeotian specimens, but the ligament was in no case completely lost. On the other hand, no indication of a ligament was found in juvenile growth stages of the RVs of *V. chaperi* that have been studied.

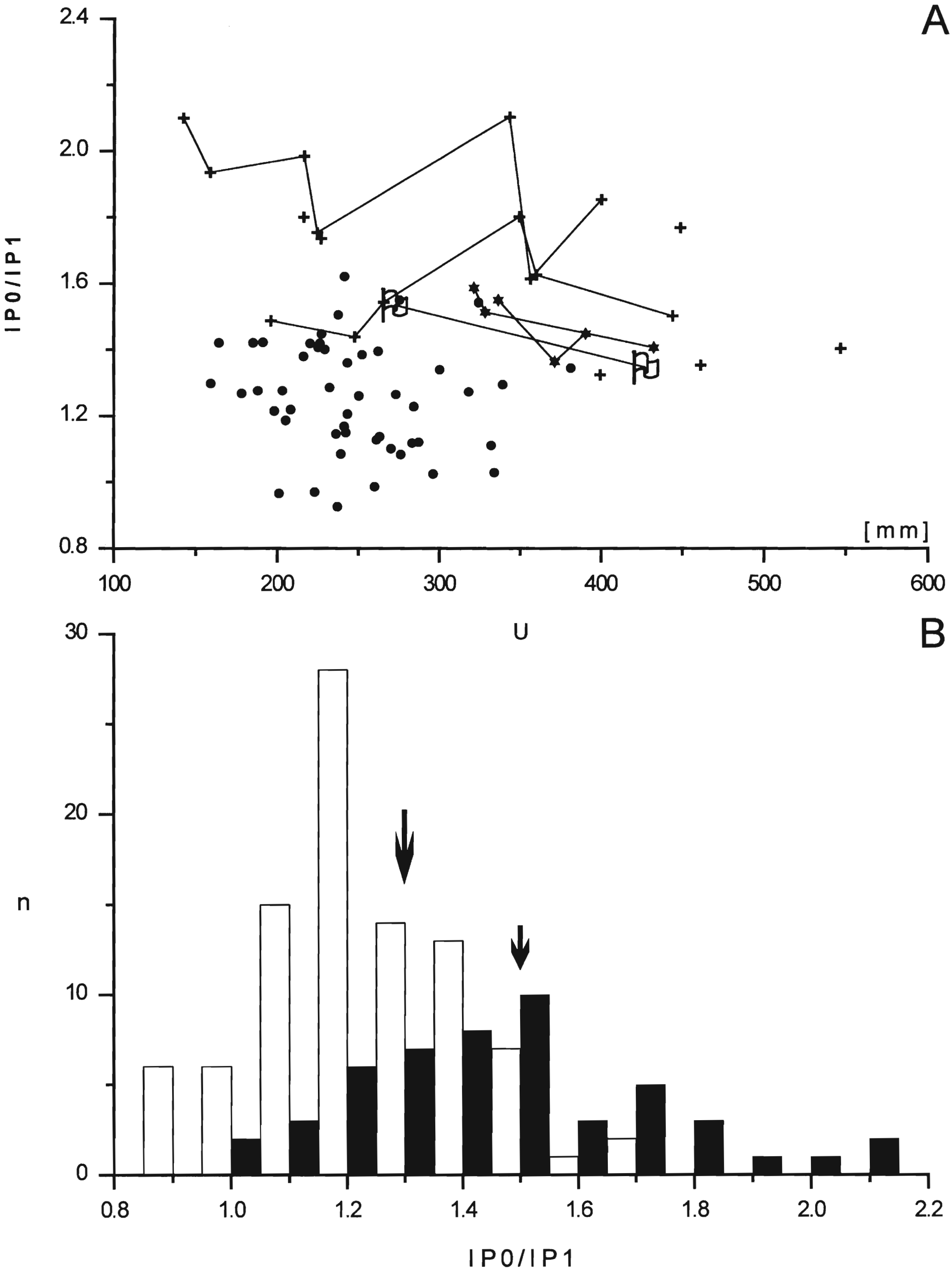
V. cornuvaccinum and *V. chaperi* do not co-occur at any of the studied Greek localities, although they are generally considered to be of the same stratigraphical age (Santonian–Campanian) and have been listed as members of a single coenozone (Slišković 1968*a*; Polšak *et al.* 1982). An important exception is the type locality of *V. chaperi*, Antinitza, from where a specimen and *V. cornuvaccinum* and *V. gaudryi*, respectively, have been figured (Douvillé 1897*a*, pl. 30, fig. 6; pl. 31, fig. 6). However, Douvillé (1897a, pl. 31, captions of figs 5–6) expressed doubts about the Greek localities indicated by Chaper, the collector of the specimens. The Antinitza locality was not rediscovered during my own field studies.

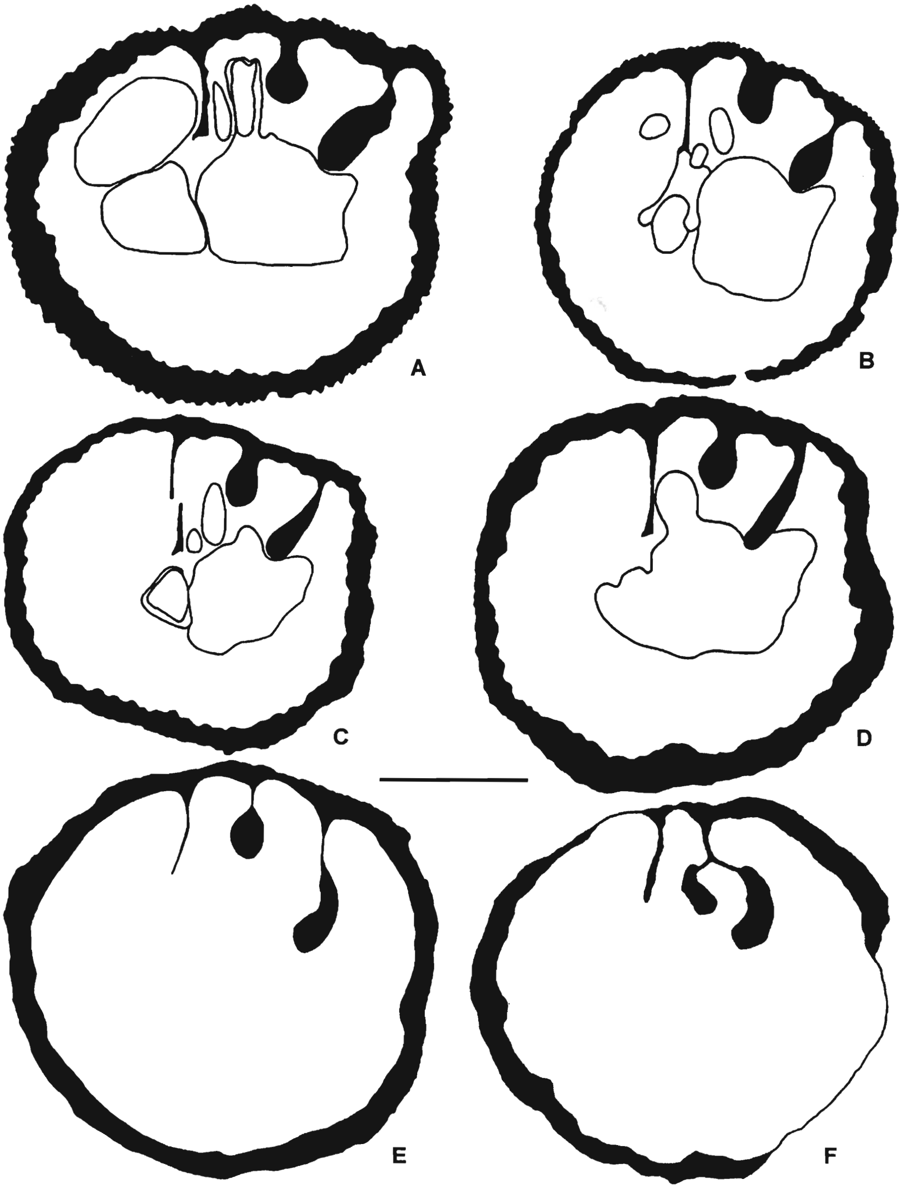
A review of other available descriptions and indications of localities revealed that the co-occurrence of *Vaccinites cornuvaccinum* and *V. chaperi* has never been clearly demonstrated. Kühn (1947, p. 187; 1965,



TEXT-FIG. 70. Relative length of P0, P1 and P2 in (+, flag = neotype) *Vaccinites cornuvaccinum* (Bronn, 1831) and (dots, asterisk = holotype) *V. chaperi* (Douvillé, 1897*a*). See Text-figure 11 for measurements.

p. 254) repeatedly mentioned the occurrence of both species from the Gosau and the Bakony Mountains ('*atheniensis-gaudryi-*' or '*atheniensis-cornuvaccinum*-reef') as well as from Carinthia (Kühn 1965). As descriptions or figures were not given, these indications could not be assessed. A study of the rudist association of the Bakony Mountains (Czabalay 1982) substantiated only the occurrence of *V. chaperi* (= *V. atheniensis*). However, the arguments for a stratigraphical succession of both species are also poorly constrained and lack confirmation of independent biostratigraphical evidence. The association of *V. chaperi* with hippuritids that are known from the Campanian only, such as *V. archiaci* (Douvillé, 1892*a*) in the Vermion Mountains and *V. vesiculosus* (Woodward, 1855) in Boeotia, is not sufficient for a clear stratigraphical distinction from the rudist beds with *V. cornuvaccinum* in Boeotia. Nevertheless, the phylogenetic development of *V. chaperi* from *V. cornuvaccinum* is considered to be well constrained on the basis of morphometric data.


A
IP0/IP1
2.4
2.0
1.6
1.2
0.8
[mm]
100
200
300
400
500
600
U
B
n
30
20
10
0
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
IP0/IP1



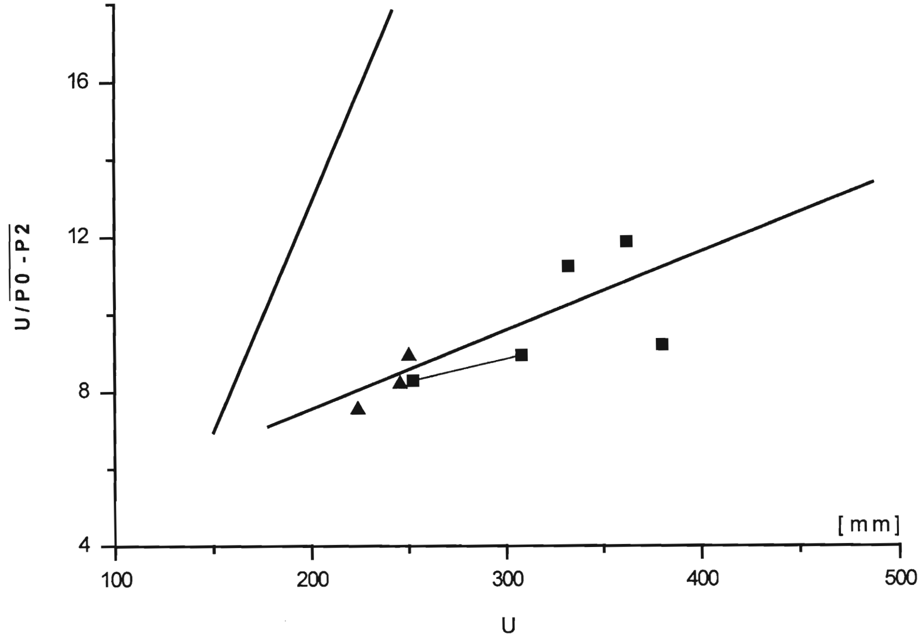
TEXT-FIG. 72. A–D, *Vaccinites* aff. *cornuvaccinum* (Bronn, 1831) from Paleokastron Hill; E–F, *V. chaperi* (Douvillé, 1897*a*) from Tsouka Hill. RV sections; A, H413; B, H551; C, H537; D, H550; E, H497; F, H556. Scale bar represents 30 mm.

TEXT-FIG. 71. A, lP0/lP1 plotted against U in (dots; flag = neotype; asterisks = topotypes) *Vaccinites cornuvaccinum* (Bronn, 1831) and (+) *V. chaperi* (Douvillé, 1897*a*) from Greece. Ontogenetic stages of individual valves are connected by lines, respectively. See Text-figure 11 for measurements. B, histogram of ratios of length of P0 and P1 in (white bars) *V. cornuvaccinum* (Bronn, 1831), material from Boeotia, other Greek localities, as well as specimens and topotypes from the Ecole des Mines collection; arrow to the left indicates value of neotype. Black bars, *V. chaperi* (Douvillé, 1897*a*), material from Boeotia, Vermion Mountains, collection Ecole des Mines, and after Ktenas (1907); Milovanović (1934); Kühn (1948); Milovanović (1954); Polšak (1967*b*); Sladić-Trifunović (1967*b*); Slišković (1967); Lupu (1976); arrow to the right indicates value of holotype.

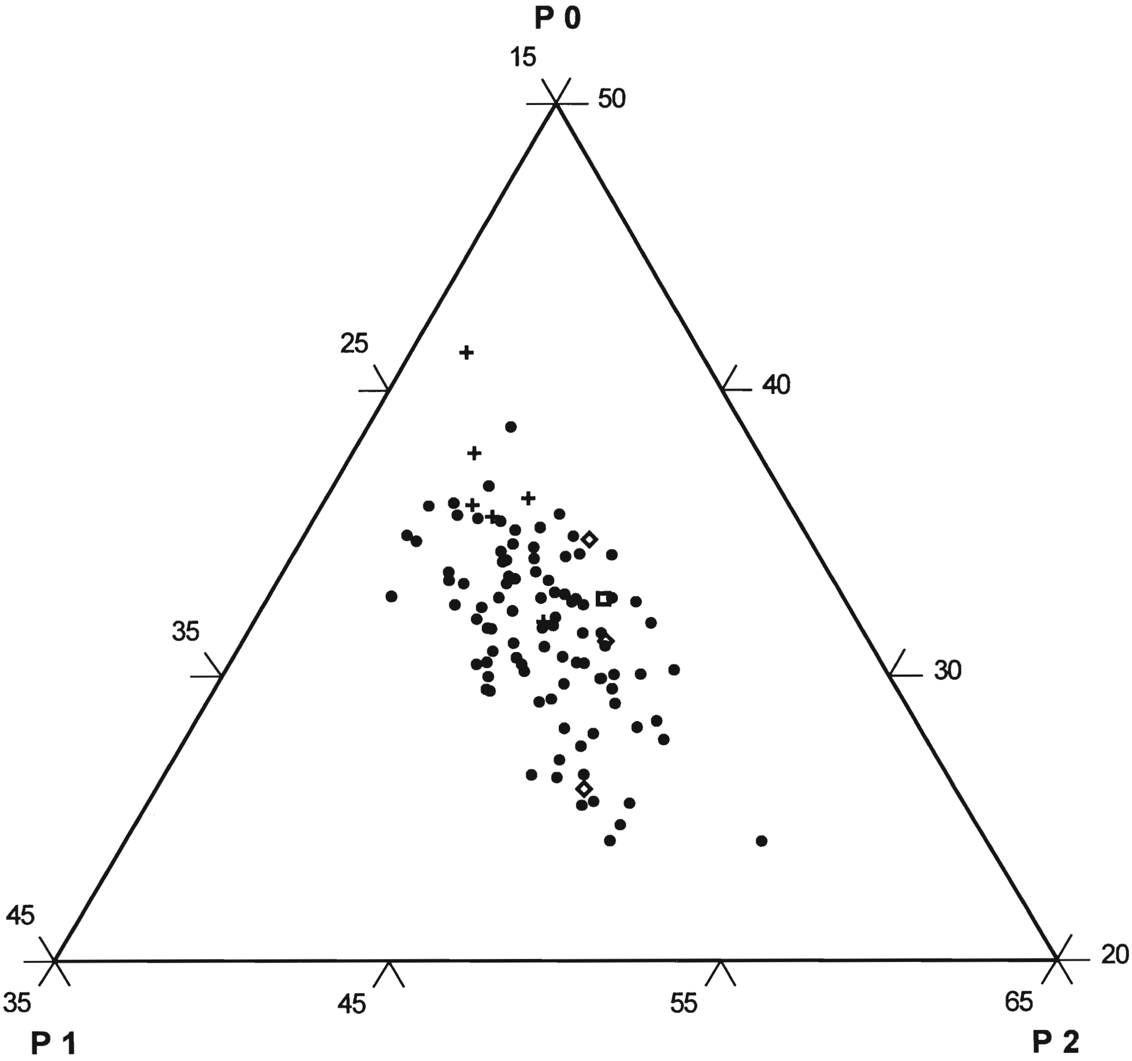
TABLE 11. Measurements (mm) of RVs of *Vaccinites* aff. *cornuvaccinum* (Bronn, 1831).

	Dmax	U	$\overline{P0 - P2}$	$\overline{P0 - P2}$cont	lP0/lP1	lP0/lP2	lP1/lP2
H413	84	380	41	171	1·3	0·7	0·6
H537	70	331	30	142	1·9	1·1	0·6
H550	80	361	30	153	1·5	0·9	0·6
H551	68	308	34	134	1·6	1·0	0·6

The name *Vaccinites fortisi* (Catullo, 1827) was rarely used, presumably because of a rather insufficient original description, although a drawing of a transverse section of the type specimen was later figured by Parona (1908*b*) and assigned to *V. chaperi* (Douvillé, 1897*a*). Both the superficial original description and Parona's arbitrary taxonomic treatment were certainly responsible for the name, subsequent to Gemmellaro (1848), being considered valid only by Kühn (1948), Polšak (1961*b*) and Czabalay (1982). In a recent revision of *V. fortisi* (Cestari *et al.* 1996), the inner termination of P0 was mentioned to be truncated but this statement was not supplemented by a redescription or new figures of the type specimen. Cestari *et al.* (1996) listed 15 species as junior synonyms of *V. fortisi*, including *Vaccinites chaperi* (Douvillé, 1897*a*), *V. gaudryi* (Munier-Chalmas, 1867) and *V. taburnii* (Guiscardi, 1865). The taxonomic position of *V. cornuvaccinum* remained unconsidered in this revision although this species certainly belongs to the group in question and, consequently, should be included in the synonymy of *V. fortisi*. Such a taxonomic procedure, however, would introduce further instability to the nomenclature of the group as it affects the validity of the type species of *Vaccinites* Fischer, 1887. The present confusion resulted from the imperfect



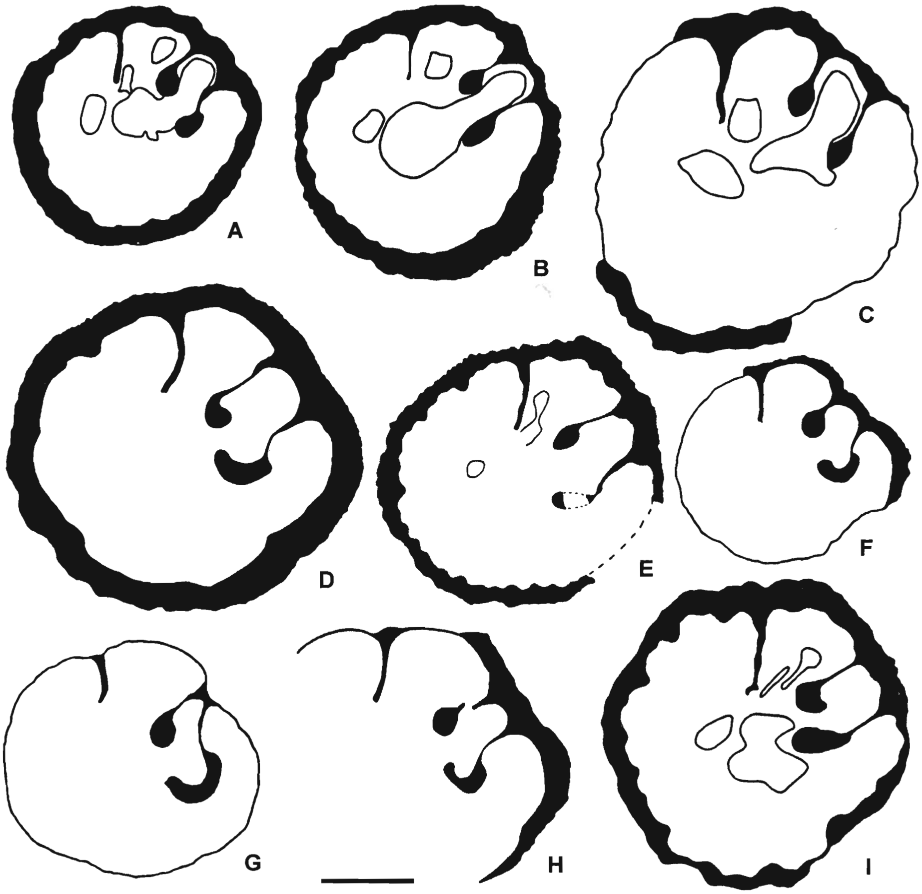
TEXT-FIG. 73. Arrangement of pillars plotted against U in (triangles) *Vaccinites archiaci* (Douvillé, 1892*a*) and (boxes) *V.* aff. *cornuvaccinum* (Bronn, 1831). Bold lines delimit the intraspecific variation of *V. cornuvaccinum* (cf. Text-fig. 64). See Text-figure 11 for measurements.



TEXT-FIG. 74. Relative length of P0, P1 and P2 in (diamonds, box = syntype) *V. archiaci* (Douvillé, 1892*a*), after Douvillé 1892*a*, pl. 5, fig. 3, and (+) *V.* aff. *cornuvaccinum* (Bronn, 1831) compared with measurements taken on *V. cornuvaccinum* (dots) from various localities (further explained on Text-fig. 66). See Text-figure 11 for measurements.

knowledge of the type specimen of *V. fortisi*. The important diagnostic character of ligamental insertion was only cleared up recently (Cestari *et al.* 1996), and the LV of the type specimen is not preserved. Therefore, it is proposed to suppress the rarely used name *Vaccinites fortisi* (Catullo, 1827) and conserve the name *Vaccinites cornuvaccinum* (Bronn, 1831).

Distribution. *V. cornuvaccinum* is known from Coniacian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982; Šribar and Pleničar 1991) and the Alps, Carpathians, Balkans, Italy, northern Africa and the eastern Mediterranean to Afghanistan. This regional distribution includes specimens that have been attributed to *V. gaudryi* and *V. alpinus*. A late Coniacian–early Campanian age was indicated for *V. taburnii* (Guiscardi, 1865) by Cestari and Sirna (1989*b*). The occurrence of *V. cornuvaccinum* (or *V. alpinus*) in the Pyrenees (Klinghardt 1931; Gallemi *et al.* 1983; Bilotte 1984) is controversial (Vicens 1992, p. 140).



TEXT-FIG. 75. A–B, *Vaccinites giganteus* (d'Hombres-Firmas, 1838) from Paleokastron Hill; C–G, I, *V. vredenburgi* (Kühn, 1933*a*) from Paleokastron Hill and, H, from Kefallinia. RV sections; A, H415; B, H420; C, H538; D, H544; E, H542; F, H430; G, H389; H, H405; I, H545. Scale bar represents 30 mm.

Vaccinites aff. *cornuvaccinum* (Bronn, 1831)

Plate 23, figure 4; Text-figure 72A–D

Material. Seven RVs from Paleokastron Hill (H413, H537, H550–H551).

Description. RVs wide-conical, up to 158 mm long, ornamented with evenly spaced, 2 mm (dorsally 3 mm) wide, rounded longitudinal ribs and furrows. Dmax up to 82 mm. Inner margin of outer shell layer with pronounced undulations. Posterior side of P0 straight or undulating, P0 thins at its centre and then widens towards the inner, truncated termination. P1 is pinched to a varying extent, P2 is strongly pinched, straight or curved anteriorly and oval to sickle-shaped. $U/\overline{P0-P2}$ ranges from 8·3 to 11·9 (Text-fig. 73). (1′) located in prolongation of P0, (2) is strongly developed and X-shaped, (3′) oval, located posterior of P0 and slightly projecting over the inner termination of P0. Mp inserts posterior to P0 and (3′), is sub-parallel to P0 and points with its tip towards the centre of the shell.

Systematic position. The shape and alignment of the pillars closely resemble *V. cornuvaccinum*, even though $U/\overline{P0-P2}$ is on average smaller when compared to similar-sized RVs of *V. cornuvaccinum*

TABLE 12. Measurements (mm) of RVs of *Vaccinites giganteus* (d'Hombres-Firmas, 1838).

	Dmax	U	$\overline{P0-P2}$	$\overline{P0-P2}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H415	68	334	42	180	0·9	0·8	0·9
H420	80	370	53	184	0·9	0·7	0·8

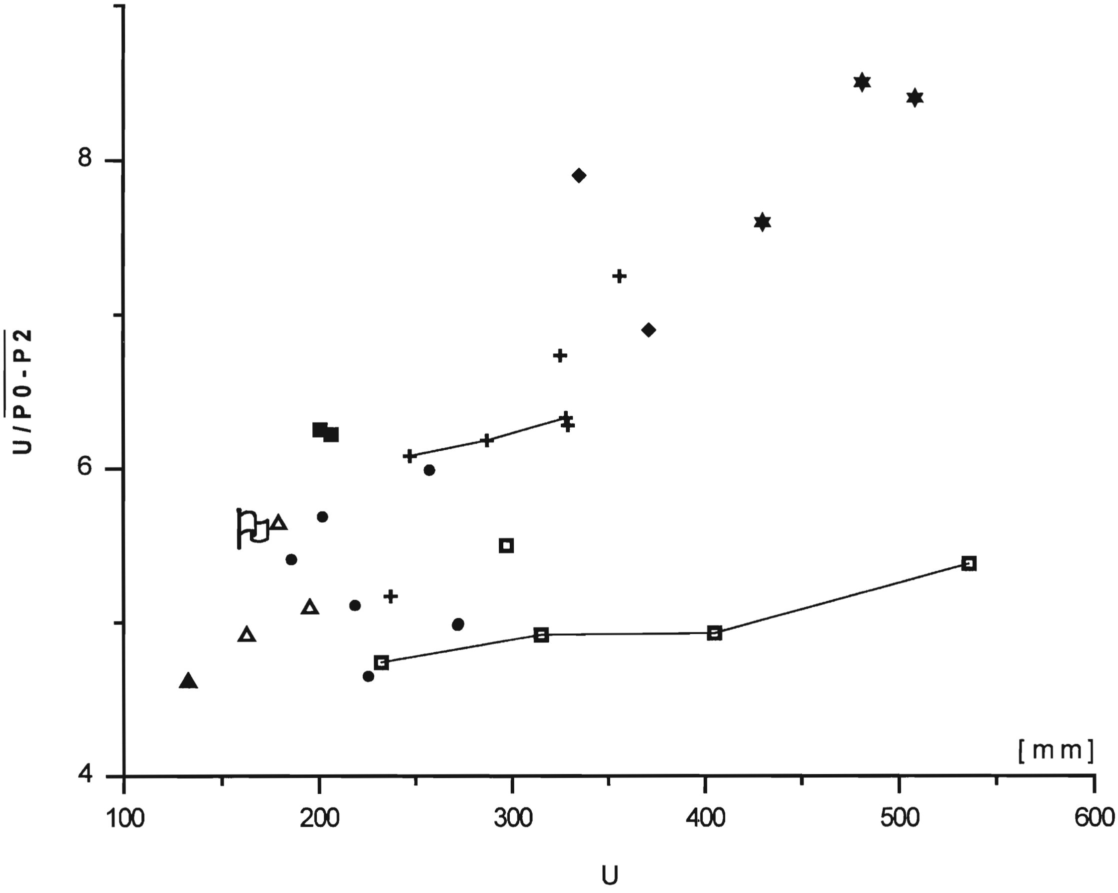
(Text-fig. 73), and P0 is longer in relation to lP1 and lP2 (Text-fig. 74). Doubts about the taxonomic position are raised because of the position of $(3')$ posterior to P0, as, in similar morphotypes of *V. cornuvaccinum* with long P0, $(3')$ is generally located ventrally or posteroventrally of the tip of P0.

The broad and anteriorly projecting surface of ligamental insertion resembles *V. ultimus* (Milovanović, 1935), which differs in having more closely spaced bases of the pillars that diverge towards the shell's interior. A further discussion of the systematic position is difficult, as the LVs are not preserved.

Vaccinites giganteus (d'Hombres-Firmas, 1838)

Text-figure 75A–B

*1838 *Hippurites gigantea* d'Hombres-Firmas, p. 198, pl. 4, fig. 1.
v.1891 *Hippurites giganteus* d'Hombres-Firmas; Douvillé, p. 19, pl. 3, fig. 5; text-fig. 7.
v1895 *Hippurites giganteus* d'Hombres Firmas; Douvillé, p. 152, pl. 22, fig. 1.
v1904 *Hippurites* (*Vaccinites*) *giganteus* var. *major* Toucas, p. 95, text-fig. 150.
1914 *H. giganteus*; von Zsigmondy, p. 388.
1932 *Hippurites* (*Vaccinites*) *giganteus* d'Hombre-Firmas; Kühn, p. 49 [with synonymy].
1932 *Hippurites* (*Vaccinites*) *giganteus* var. *major* Toucas; Kühn, p. 49 [with synonymy].
?*1933* *Hippurites* (*Vaccinites* Fischer) *giganteus* d'Hombres-Firmas var. *major* Toucas; Müllerried, p. 270.
1935 *Hipp. giganteus* var. *major*; Klinghardt, p. 30.
?*1936* *Vaccinites giganteus* d'Hombres-Firmas var. *major* Toucas; Müllerried, p. 39.
1938 *Hippurites* (*Vaccinites*) *giganteus* d'Hombre-Firmas; Voorwijk, p. 57, pl. 2, fig. 2.
1949a *Vaccinites giganteus* d'Hombres-Firmas; Mennessier, p. 315.
1955b *Hippurites* (*Vaccinites*) *giganteus* d'Homb.-Firm.; Astre, p. 109.
1957a *Vaccinites giganteus* d'Hombr.-Firm.; Astre, p. 193.
1959 *Hipp.* (*Vacc.*) *giganteus* d'Hombre-Firmas; Petković *et al.*, p. 282.
1964 *H.* (*V.*) *giganteus* d'Hombres-Firmas; Polšak, p. 67.
1964 *H.* (*V.*) *giganteus medulinus* n. subsp. Polšak, p. 67 [*nomen nudum*].
1965b *Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Polšak, p. 451.
1965b *Hippurites* (*V.*) *giganteus medulinus* n. subsp. Polšak, p. 451 [*nomen nudum*].
1965 *H.* (*V.*) *giganteus medulinus* Polšak; Slišković, p. 373 [*nomen nudum*].
1967*b* *Hippurites* (*Vaccinites*) *giganteus medulinus* n. subsp. Polšak, pp. 110, 207, pl. 72, figs 2, 4.
1968a *Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Slišković, p. 38.
1968a *Hippurites* (*Vaccinites*) *giganteus major* Toucas; Slišković, p. 39.
1968a *Hippurites* (*Vaccinites*) *giganteus medulinus* Polšak; Slišković, p. 39.
1971 *Vaccinites giganteus* (d'Hombre Firmas); Vogel, p. 57.
1971 *Vacc. giganteus major* Toucas; Vogel, p. 57.
1973 *Vaccinites giganteus* Touc.; Freytet, p. 68.
1974 *V. giganteus* (d'H. Firmas); Philip, p. 112.
1974 *V. giganteus* var. *major* Touc.; Philip, p. 112.
1974 *Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Slišković, p. 133.
1974 *Hippurites* (*Vaccinites*) *giganteus medulinus* Polšak; Slišković, p. 133.
?1975 *Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Pleničar, pp. 94, 110, pl. 6, fig. 1; pl. 7, figs 1–2.
1978a *Vaccinites giganteus* (d'H. Firmas); Philip *et al.*, p. 83.
1978a *Vaccinites giganteus* var. *major* Toucas; Philip *et al.*, p. 84.

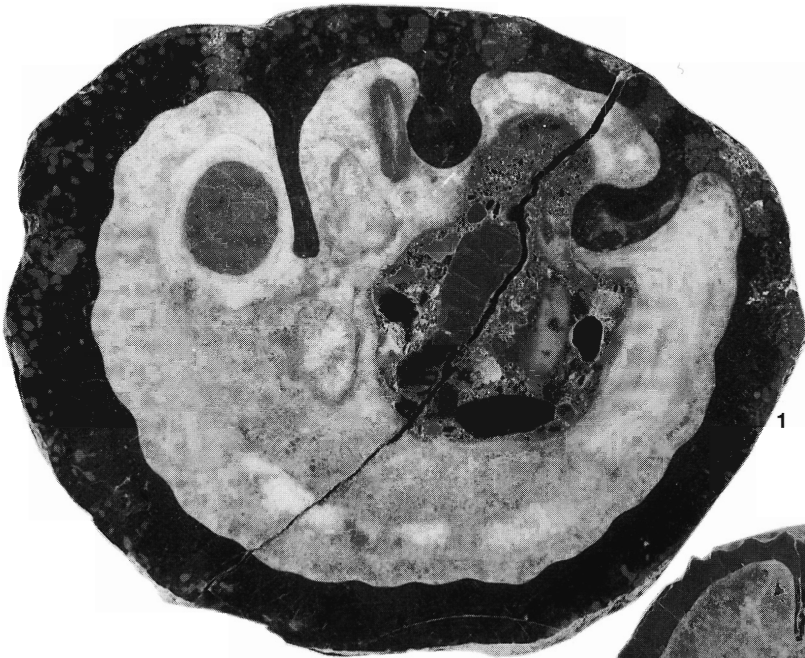


TEXT-FIG. 76. Arrangement of pillars plotted against U in (+, flag = holotype) *Vaccinites inaequicostatus* (Münster, *in* Goldfuß, 1840); white boxes, *V. vesiculosus* (Woodward, 1855); diamonds, *V. giganteus* (d'Hombres-Firmas, 1838); asterisks, *V. vredenburgi* (Kühn, 1933*a*); dots, *V. praesulcatus* (Douvillé, 1897*a*); black boxes, *Vaccinites* sp.; white triangles, *V. boehmi* (Douvillé, 1897*a*); black triangle, *V. sulcatus* (Defrance, 1821). Ontogenetic stages of individual valves are connected by lines, respectively. See Text-figure 11 for measurements.

1978	*H.* (*V.*) *giganteus* d'Hombres-Firmas; Polšak *et al.*, p. 190.
non 1979	*Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Polšak, pp. 205, 224, pl. 9, fig. 7.
1979*b*	*Vaccinites giganteus* (d'Hombres-Firmas); Skelton, pl. 3, fig. 1.
1980	*Vaccinites giganteus*; Laviano and Sirna, p. 69.
non 1981	*Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Polšak, p. 454, text-fig. 8d [cop. Polšak 1979].
1981	*Vaccinites giganteus* (d'Hombres Firmas); Sánchez, p. 45 [with synonymy].

EXPLANATION OF PLATE 25

Fig. 1. *Vaccinites inaequicostatus* (Münster, *in* Goldfuß, 1840); H424, Paleokastron Hill.
Fig. 2. *Hippurites colliciatus* Woodward, 1855; H416, Paleokastron Hill.
Fig. 3. *Vaccinites vredenburgi* (Kühn, 1933*a*); H545, Paleokastron Hill.
Figs 4–5. *Vaccinites cornuvaccinum* (Bronn, 1831). 4, H201, Dionysos; 5, H68, Keratovouno Hill.
All transverse sections of RVs; × 1.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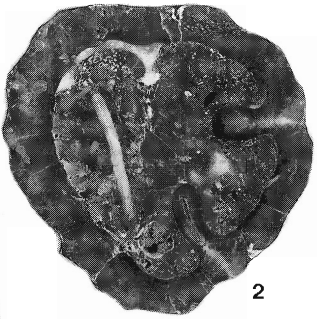
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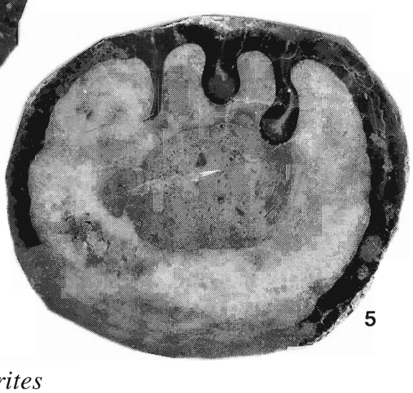
3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STEUBER, *Vaccinites, Hippurites*

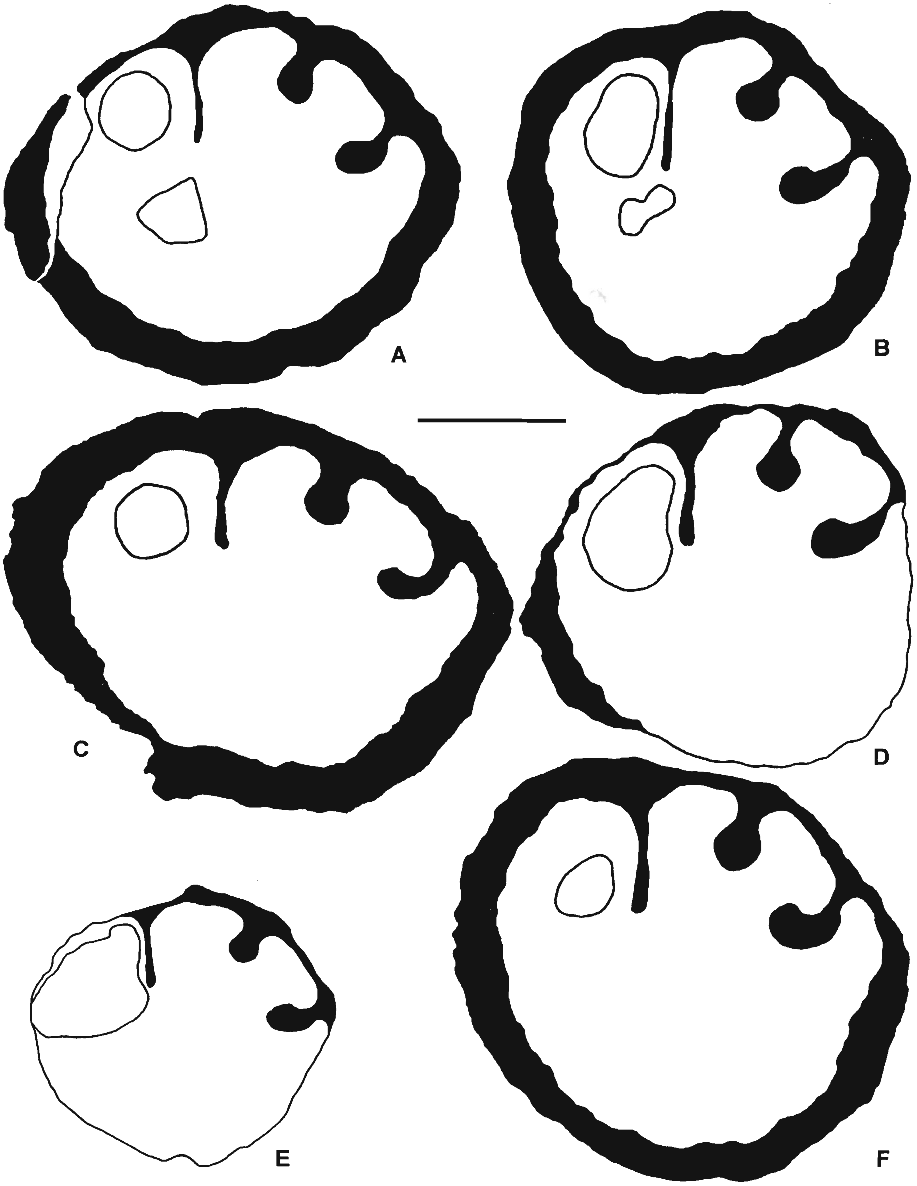
1981 *Vaccinites giganteus medulinus* (Polšak); Sánchez, p. 45 [with synonymy].
1981 *Vaccinites giganteus major* Toucas; Sánchez, p. 46 [with synonymy].
1982 *Vaccinites giganteus* (d'Hombres-Firmas); Accordi *et al.*, p. 771, pl. 5, figs 6–7.
1982b *Pseudovaccinites giganteus* (H.F.); Bilotte, p. 98, tab. 2.
1982c *Pseudovaccinites giganteus* H.F.; Bilotte, p. 112.
1982 *V. giganteus*; Devalque *et al.*, p. 67, tab. 2.
1982 *Vaccinites giganteus major*; Gili, p. 982.
1982a *Vaccinites giganteus* (d'H. Firmas); Philip, p. 997.
1982b *V. giganteus*; Philip, text-fig. 2b.
1982 *Vaccinites giganteus* (d'H. Firmas); Philip *in* Floquet *et al.*, text-fig. 2; pl. 1, fig. b.
1982 *Hippurites* (*Vaccinites*) *giganteus medulinus* Polšak; Mariotti, p. 888.
1982 *Hippurites* (*V.*) *giganteus* d'Hombres-Firmas; Polšak *et al.*, text-fig. 3.
1982 *Vaccinites giganteus* (d'Hom.-Firm.); Pons, tab. 1.
1982 *Vaccinites giganteus major* Toucas; Pons, tab. 1.
1983 *Vaccinites giganteus*; Gallemi *et al.*, tab. 3.
1983 *Vaccinites giganteus major*; Gallemi *et al.*, tab. 3.
1983 *V. giganteus*; Philip and Bilotte, tab. 1.
1983 *V. giganteus-major*; Philip and Bilotte, tab. 1.
1984 *Pseudovaccinites giganteus* (d'Hombres-Firmas); Bilotte, pl. 41, fig. 2.
1984 *Pseudovaccinites giganteus* var. *major* Toucas; Bilotte, pl. 41, fig. 3.
1985 *Pseudovaccinites giganteus* H.F.; Bilotte, p. 345, tab. 17.
1985 *Pseudovaccinites giganteus* var. *major* Toucas; Bilotte, p. 345, tab. 31.
1985 *Vaccinites giganteus* d'Hombre-Firmas; Lupu, p. 22.
1986 *Vaccinites giganteus* d'Hombres-Firmas; Mercadier, p. 73.
1986 *Vaccinites giganteus* (d'H.-Firmas) var. *major* Toucas; Philip, *in* Mercadier, p. 73, pl. 13, figs a–b.
?1989*b* *Vaccinites giganteus* (d'Hombres-Firmas); Cestari and Sirna, p. 19, tab. 1, pl. 2, fig. 1.
p1989 *Vaccinites vredenburgi* Kühn; Laviano and Guarnieri, p. 80, pl. 1, figs 1–4, 6.
1989 *Vaccinites giganteus*; Sirna and Cestari, p. 715.
1989 *Vaccinites giganteus* Hombres-Firmas; Yanin, p. 179, pl. 16, fig. 1.
1990 *Hippurites* (*V.*) *giganteus* (d'Homb.-Firm.); Cestari and Pantosti, p. 45, text-figs 4, 5a.
1991 *Vaccinites giganteus* d'Hombres-Firmas; Breyer, p. 28, pl. 11, figs 5, 7–8.
1991 *Vaccinites giganteus*; Floquet, text-fig. 286.
1991 *H.* (*Vacc.*) *giganteus* d'Hombres-Firmas; Šribar and Pleničar, p. 178.
1992 *Vaccinites giganteus major* Toucas; Gili, p. 321.
1992a *V. giganteus* d'Hombre-Firmas; Peza, p. 87.
1993 *Vaccinites giganteus*; Alonso *et al.*, text-fig. 6.
1993 *Pv. giganteus*; Bilotte, text-fig. 4.
1993 *Vaccinites giganteus major* Toucas; Gili, tab. 1.
1993 *Vaccinites giganteus*; Philip, tab. 1.
1995 *Vaccinites giganteus major* Toucas; Skelton *et al.*, p. 115.
1997 *Vaccinites giganteus* (d'Hombre-Firmas); Steuber *et al.*, p. 179, text-fig. 3a.

Holotype. D'Hombres-Firmas (1838), plate 4, figure 1. The holotype has been considered lost since the last century, so the first detailed description (Douvillé 1891) was based on para- and topotypes.

Material. Two RVs from Paleokastron Hill (H415, H420).

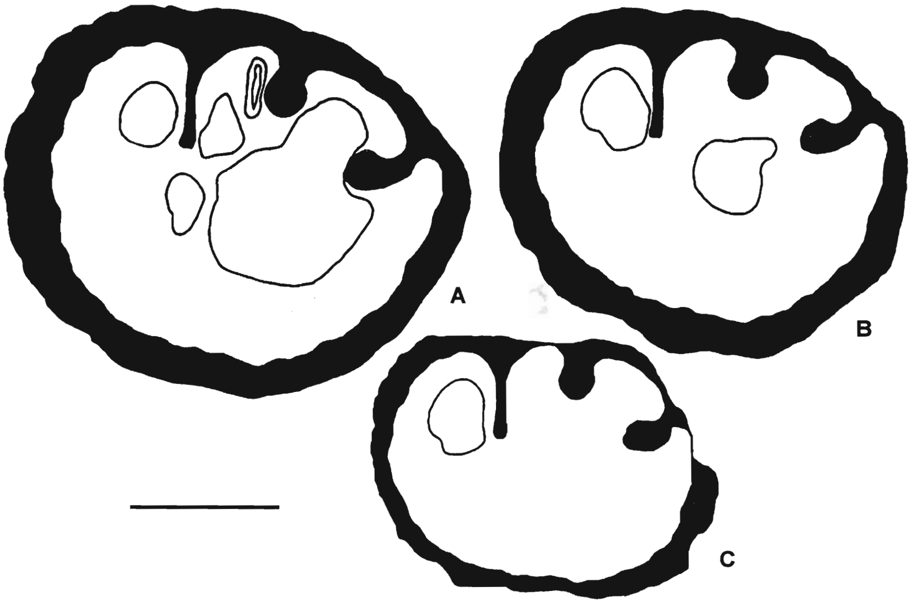
Description. RVs elongated-conical, up to 225 mm long, ornamented with both acute and centrally depressed longitudinal ribs that are 2–3 mm wide and separated by deep, rounded furrows. P1 and P2 pedunculate, the stalks are sub-parallel, closely spaced and inclined by 40–50° against P0. $U/\overline{P0-P2}$ is 6·9 and 7·9 (Text-fig. 76). Inner termination of P0 rounded, head of P1 slightly inflected posteriorly. $(1')$ anterior to P0, (3) runs parallel to P0 and surpasses its tip ventrally. Mp' located close to the dorsal shell, near the base of P1.

Remarks. The two RVs differ only by smaller Dmax and the rounded tip of P0 from several other RVs (Text-figs 76, 79) of the same locality that are attributed to *V. vredenburgi* (Kühn, 1933*a*).



TEXT-FIG. 77. *Vaccinites inaequicostatus* (Münster, *in* Goldfuß, 1840) from Paleokastron Hill. RV sections; A, H427; B, H398; C, H391; D, H425; E, H385; F, H399. Scale bar represents 30 mm.

Distribution. Coniacian–Campanian of Spain, southern France, Sardinia, Apulia, Romania, the Dinarids, (Sánchez 1981), Albania and the Caucasus; Upper Turonian of the north-eastern Pyrenees (Bilotte 1993). The species was originally described from the Coniacian of southern France, later from the Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982). Specimens from the Campanian of Apulia (Laviano and Guarnieri 1989) that have been determined as *V. vredenburgi* (Kühn, 1933*a*) do not differ substantially from *V. giganteus*.



TEXT-FIG. 78. A–C, ontogeny of a RV of *Vaccinites inaequicostatus* (Münster, *in* Goldfuß, 1840) from Paleokastron Hill; H424. Scale bar represents 30 mm.

Vaccinites cf. *grossouvrei* (Douvillé, 1894)

*v1894 *Hippurites Grossouvrei* n. sp. Douvillé, p. 118, pl. 18, figs 1–4.
1993*a* *Vaccinites* cf. *grossouvrei* (Douvillé); Steuber, p. 40 [with synonymy and description].
1993 *Vaccinites* cf. *grossouvrei* (Douvillé); Steuber *et al.*, p. 259.

Holotype. Douvillé (1894), plate 18, figure 1.

Material. Eight RVs from Marmeko quarry (H113, H119, H131, H133, H144, H339–H341).

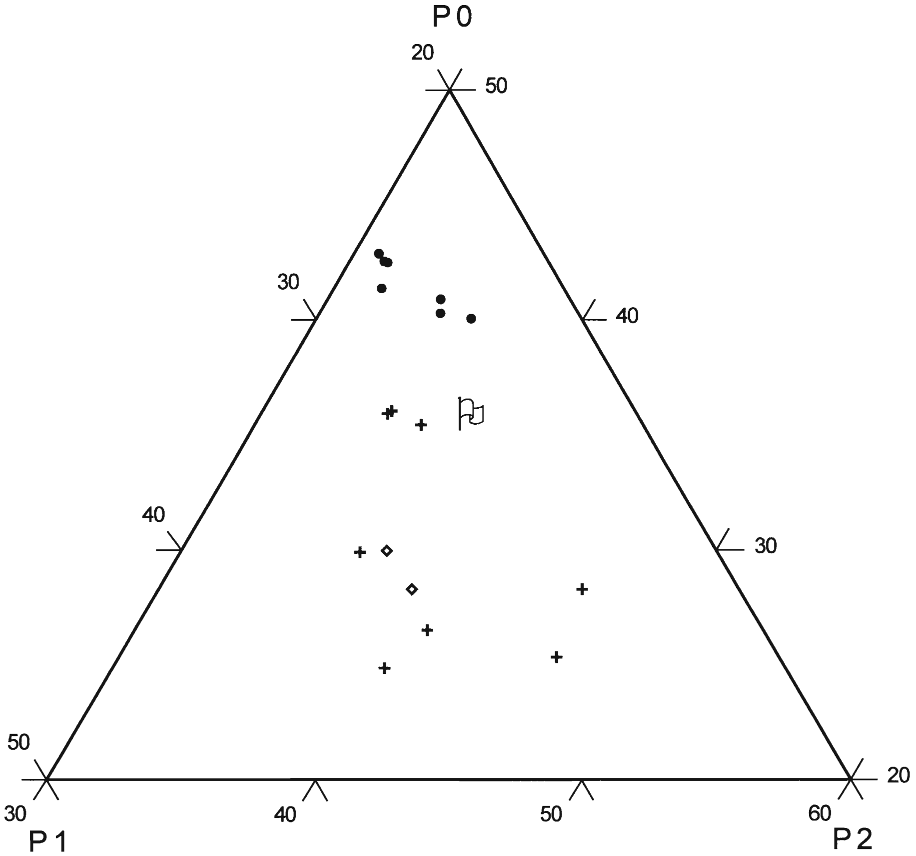
Description. See Steuber (1993*a*).

Distribution. Middle to Upper Turonian of the Mediterranean region, Turonian–Coniacian of Caucasus.

Vaccinites inaequicostatus (Münster, *in* Goldfuß 1840)

Plate 21, figure 6; Plate 25, figure 1; Text-figures 77–78

*v1840 *Hippurites inaequicostatus* Münster, *in* Goldfuß, p. 303, pl. 165, fig. 4.
v.1897*a* *Hippurites inaequicostatus* Munster; Douvillé, p. 199, pl. 30, fig. 3.
1897*a* *Hippurites inaequicostatus* Munster; Douvillé, p. 199, pl. 30, fig. 5; pl. 33, figs 2–3.
v?1897*a* *Hippurites inaequicostatus* Munster; Douvillé, p. 199, pl. 30, fig. 4.
1899 *Hippurites inaequicostatus* Münst.; de Alessandri, p. 181, pl. 14, fig. 5; pl. 16, figs 2, 4–6.
1932 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Kühn, p. 52 [with synonymy].
?1937 *Vaccinites inaequicostatus macgillavryi* (Palmer); Mac Gillavry, p. 111, pl. 4, figs 1–8; pl. 10, fig. 2.
?1937 *Vaccinites inaequicostatus vermunti* n. sbsp. Mac Gillavry, p. 118, pl. 5, fig. 2.
1937 *H. inaequicostatus* Münst.; Zapfe, p. 88.
1939 *Hippurites* (*Vaccinites*) *inaequicostatus* Douvillé; Klinghardt, p. 137.
1941 *Hippurites inaequicostatus* Münster; Tromp, p. 609.



TEXT-FIG. 79. Relative length of P0, P1, and P2 in (dots) *Vaccinites inaequicostatus* (Münster, *in* Goldfuß, 1840), (+, flag = holotype) *V. vredenburgi* (Kühn, 1933*a*) and (diamonds) *V. giganteus* (d'Hombres-Firmas, 1838). See Text-figure 11 for measurements.

?1942 *Hippurites inaequicostatus* Münster; Kühn and Andrusov, p. 459, pl. 28, fig. 2; pl. 29.
?1942 *Hippurites inaequicostatus* Münster var. *carpathica* n. var. Kühn and Andrusov, p. 459, text-fig. 1.
?1946*a* *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Stchépinsky, p. 126, pl. 17, fig. 5.
1946b *Hipp.* (*Vacc.*) *inaequicostatus* Münster; Stchépinsky, p. 353.
?1949 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster var. *MacGillavryi* (Palmer); Tavani, p. 12, pl. 4, figs 1–2, 10.
non 1951 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Pejović, p. 95, pl. 2, fig. 1.
1954 *H.* (*V.*) *inaequicostatus* Münster; Milovanović, p. 164.
1957a *Vacc.* cf. *inaequicostatus* Munst.; Astre, p. 194.
1959 *H. inaequicostatus* Münst.; Andrusov, p. 208.
non 1959 *Hippurites inaequicostatus* Münster; Mitzopoulos, p. 83, text-fig. 1.
1960 *H. inaequicostatus* Münster; Milovanović, p. 367.
1960 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Moisescu, p. 111, pl. 3, figs 12–13; pl. 4, figs 16–17.
1961a *Hippurites* (*V.*) *inaequicostatus* Münster; Polšak, pp. 422, 432.
1962 *Hippurites* (*Vacc.*) *inaequicostatus* Münster; Slišković *et al.*, p. 130.
1963a *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Slišković, p. 66.
1964 *H.* (*V.*) *inaequicostatus* Münster; Polšak, p. 67.
1965b *Hippurites* (*V.*) *inaequicostatus* Münster; Polšak, p. 451.
1965 *H.* (*V.*) *inaequicostatus* Münster; Slišković, p. 373.

TABLE 13. Measurements (mm) of five RVs from Boeotia and the holotype of *Vaccinites inaequicostatus* (Münster, *in* Goldfuß, 1840).

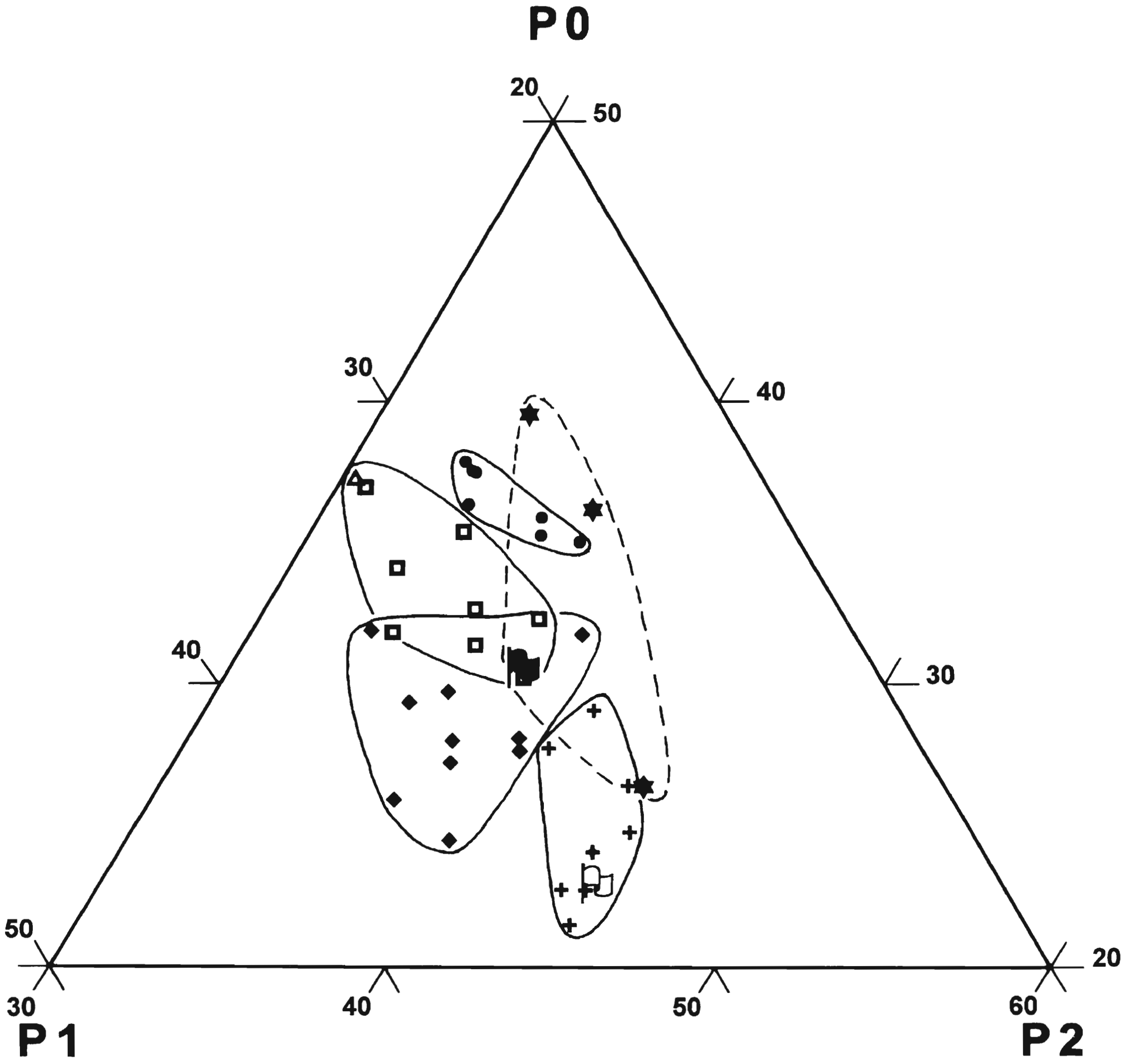
	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
min.	58	236	46	118	1·5	1·1	0·7
max.	83	356	52	177	1·7	1·4	0·9
mean	74	315	50	156	1·6	1·3	0·8
holotype	41	166	30	87	1·3	1·0	0·8

p1966 *Vaccinites inaequicostatus* (Münster); Pamouktchiev, p. 24, pl. 1, fig. 2.
1967 *Hippurites* (*Vaccinites*) *inaequicostatus* Münst.; Lupu and Lupu, p. 309.
1968a *Hippurites* (*Vaccinites*) *inaequicostatus* Munier-Chalmas; Slišković, p. 39.
1969 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Polšak and Mamužić, p. 239.
?1971 *Pseudovaccinites inaequicostatus macgillavryi* (Palmer); van Dommelen, p. 24, text-fig. 4B–D, G [cop. Mac Gillavry 1937].
?1971 *Pseudovaccinites inaequicostatus vermunti* (Mac Gillavry); van Dommelen, p. 25, text-fig. 4E–F [4F = cop. Mac Gillavry 1937].
1978 *Vaccinites inaequicostatus* (Münster); Pamouktchiev, p. 235, tab. 1.
non 1979 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Polšak, pp. 205, 223, pl. 9, figs 5–6.
?1981*b* *Vaccinites inaequicostatus* (Münster); Pamouktchiev, p. 168, pl. 82, fig. 2, fig. 2a [cop. Pamouktchiev 1966].
non 1981 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Polšak, p. 454, text-fig. 8b–c [cop. Polšak 1979].
1981 *Vaccinites inaequicostatus* (Munster); Sánchez, p. 48 [with synonymy].
1982 *H.* (*Vaccinites*) *inaequicostatus* Münster; Mariotti, p. 888.
1982 *Vaccinites inaequicostatus* Münster; Özer, p. 229.
1982 *Hippurites* (*V.*) *inaequicostatus* Münster; Polšak *et al.*, text-fig. 3.
1983 *H.* (*Vacc.*) *inaequicostatus* Münster; Pleničar and Premru, p. 194.
1985 *Vaccinites inaequicostatus* Münster; Lupu *in* Kollmann *et al.*, p. 128, pl. 1, figs 5–6; pl. 3.
1985 *V. inaequicostatus* Münst.; Lupu, p. 21.
1989 *V. inaequicostatus*; Pieri and Laviano, p. 352.
1992a *V. inaequicostatus* (Münster); Peza, p. 87.
1996 *Vaccinites inaequicostatus* Munster; Philip and Platel, p. 262, pl. 1, fig. 4.
?*1996* *Vaccinites inaequicostatus macgillavryi* (Palmer); Rojas *et al.*, p. 279.
1996 *Vaccinites inaequicostatus macgillavryi* (Palmer); Rojas and Iturralde-Vinent, p. 293.
1996 *Vaccinites inaequicostatus vermunti* Mac Gillavry; Rojas and Iturralde-Vinent, p. 293.
1997 *Vaccinites inaequicostatus*; Sanders *et al.*, p. 363.
1997 *Vaccinites inaequicostatus* (Münster); Steuber *et al.*, p. 179, pl. 1, fig. 14, text-fig. 3d–e.

Holotype. Münster, *in* Goldfuß (1840), plate 165, figure 4; Douvillé 1897*a*, plate 30, figure 3. The description of Münster is insufficient for a safe recognition, and the indication of the type locality is rather vague ('Findet sich bei Salzburg'). Douvillé's (1897*a*) definition has been generally adopted. He figured a transverse section of a broken RV (pl. 30, fig. 3), that was sent to him by Zittel, and noticed such a resemblance with the holotype 'que l'on peut se demander si ce n'est pas l'échantillon figuré lui-même' (Douvillé 1897*a*, p. 200). A comparison of the specimen in question and the figure of the holotype shows, that they are in fact identical. The LV of the holotype is figured here for the first time (Pl. 21, fig. 6).

Material. Ten RVs from Paleokastron Hill (H385, H391, H398–H399, H417, H424, H425, H427, H431).

Description. RVs elongated-conical, more than 160 mm high, outer shell layer thick but worn or bioeroded. P0 straight, thinning after one-third of its length and widened at the top which is rounded. Pinching is slight in P1 but more strongly developed in P2, the head of which is inflected anteriorly. Pinching of P1 and P2 only slightly increased during ontogeny (Text-fig. 78). LP0 large in relation to lP1 and lP2, variation in relative length of pillars is small (Text-fig. 79). Accessory cavity anterior of P0 reaches deeply into RV and can be recognized in almost all transverse



TEXT-FIG. 80. Relative length of P0, P1, and P2 in (+, white flag = holotype) *Vaccinites vesiculosus* (Woodward, 1855), after Woodward (1855); Sladić-Trifunović (1967*a*); Slišković (1968*c*); Laviano and Gallo Maresca (1992), and Text-figure 85A, F of this study; (black flag = holotype) *V. inaequicostatus* (Münster, *in* Goldfuß, 1840), specimens from Paleokastron Hill (dots) and the southern Alps (asterisks, after Douvillé 1897*a*); *V. macgillavryi* Palmer, 1933 from Somalia (diamonds, after Pons *et al.* 1992); *V. inaequicostatus macgillavryi* Palmer, 1933 from Cuba (boxes, after Mac Gillavry 1937); *V. inaequicostatus vermunti* Mac Gillavry, 1937 from Cuba (triangle, after Mac Gillavry 1937). See Text-figure 11 for measurements.

sections. U/$\overline{\text{P0}-\text{P2}}$ increases from 5 to 7·5 with increasing Dmax of RV (Text-fig. 76). (1′) in prolongation of P0, (3′) large and triangular, posterior to P0 and projecting ventrally over the tip of P0. Mp long, slender, located ventrally of P1. The RVs from Paleokastron Hill are remarkably large when compared with previously described specimens.

Remarks. The systematic relations between *Vaccinites inaequicostatus* from the Mediterranean region and similar forms of the group around *V. inaequicostatus macgillavryi* (Palmer, 1933) that have been reported from Cuba and Somalia are still unresolved (Mac Gillavry 1937; van Dommelen 1971; Pons *et al.* 1992).

V. inaequicostatus from localities of the Old World differs in having a more complex, sub-reticulate pore system, the axis (1)-(3) being less inclined against P0, and by a mp that inserts further dorsally. The characters of the pore system strongly argue against a close relation between *V. inaequicostatus* and similar Somalian and Cuban taxa. *V. vesiculosus* (Woodward, 1855) is also very similar and shares the character of reticulate pores with the specimens of *V. macgillavryi* that have been described from Somalia (Pons *et al.* 1992). A comparison of the relative lengths of the pillars shows clearly separated clusters of values measured on the Cuban specimens and *V. vesiculosus* from the Mediterranean region; the Somalian shells occupy an intermediate position (Text-fig. 80). A high variability of lP0/lP2-ratios is evident, when these three groups of specimens that lived in disjunct regions are considered together. The range of variation in this character is remarkably similar (see Text-figs 54, 66) to that of *V. chaperi* (Douvillé, 1897*a*) and *V. cornuvaccinum* (Bronn, 1831). Therefore, the discussed taxa could be allopatric subspecies. For further clarification, studies of the LV pore system of the Cuban specimens are required, as these have so far only been investigated in longitudinal sections (Mac Gillavry 1937).

Without referring to other characters, the morphometric analysis of pillar length alone does not give conclusive evidence of the relations between the taxa in question. It is, however, remarkable that the range of variation differs in the considered groups. A high variability noticed in *V. inaequicostatus* from several localities of the Alps (Text-fig. 80) is comparable to that of *V. cornuvaccinum* or *V. chaperi*. The ratios of pillar length are much more constant in other groups, even if the measured RVs come from far distant regions, as in the case of *V. vesiculosus*.

Distribution. Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982). Campanian of the Gosau, the southern Alps, Dinarids and Romania (Sánchez 1981); Lower Campanian of Oman (Philip and Platel 1996). Santonian–Campanian of the Apennines, Slovac Republic, Turkey, Albania and northern Greece (Vermion Mountains); perhaps also in the Santonian–Campanian of Cuba (Mac Gillavry 1937; Rojas and Iturralde-Vinent 1996).

TABLE 14. Measurements (mm) of 15 RVs of *Vaccinites inferus* (Douvillé, 1891) from Marmeko quarry.

	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
min.	23	79	18	39	0·6	0·4	0·5
max.	40	154	29	72	1·5	1·1	0·9
mean	32	123	24	60	1·1	0·8	0·7

Vaccinites inferus (Douvillé, 1891)

Plate 22, figure 1

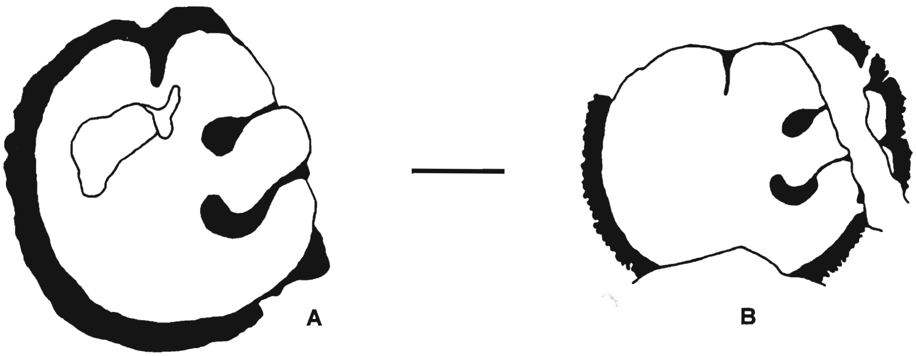
*1891 *Hippurites inferus* n. sp. Douvillé, p. 23, pl. 2, fig. 6.
1993*a* *Vaccinites inferus* (Douvillé); Steuber, p. 41, text-figs 2a–i, 3a–f, 8/1–8/3 [with synonymy and description].
1993*b* *Vaccinites inferus* (Douvillé); Steuber, p. 42, pl. 1, fig. 1.
1993 *V. inferus* (Douvillé); Steuber *et al.*, p. 259.

Holotype. Douvillé (1891), plate 2, figure 6.

Material. More than 30 specimens from Marmeko quarry, several of them with both valves conjoined (H105–H106, H117, H121, H251–H252, H254).

Description. See Steuber (1993*a*).

Distribution. Middle–Upper Turonian of the Mediterranean region, Turonian–Coniacian of Caucasus.



TEXT-FIG. 81. *Vaccinites kuehni* (Pejović, 1957) from Kefallinia. RV sections; A, H402; B, H403. Scale bar represents 30 mm.

Vaccinites kuehni (Pejović, 1957)

Text-figure 81

*1957 *Hippurites kühni* n. sp. Pejović, pp. 99, 139, pl. 41, fig. 1; text-fig. 44.
1964 *H.* (*V.*) *kühni* Pejović; Polšak, p. 67.
1967*b* *Hippurites* (*Vaccinites*) *kuehni* Pejović; Polšak, pp. 124, 212, pl. 79, fig. 3.
1967*b* *Hippurites* (*Vaccinites*) cf. *kuehni* Pejović; Polšak, p. 125, pl. 79, fig. 1.
1968a *Hippurites* (*Vaccinites*) *kuehni* Pejović; Slišković, p. 39.
1981 *Vaccinites kuehni* (Pejović); Sánchez, p. 49.
1982 *Hippurites* (*Vaccinites*) *kühni* Pejović; Polšak *et al.*, text-fig. 3.

Holotype. Pejović (1957), plate 41, figure 1; text-figure 44.

Material. Two RVs collected loose from Kefallinia peninsula near Antikyra, stratigraphical horizon not known (H402–H403).

Description. RVs elongated-conical, ornamented with 2–4 mm broad, rounded longitudinal ribs, some of them with a shallow central furrow; rounded furrows between ribs 1 mm wide. P0 short but thick, rounded at its inner termination. P1 pedunculate, head oval; P2 pedunculate or strongly pinched, head sickle-shaped and inflected dorsally. Peduncles of P1 and P2 run parallel and are inclined by 70° with respect to P0. (1′) anterior to P0, (2) ventral to P0 and dorsally excavated.

Remarks. *V. kuehni* differs from *V. vredenburgi* (Kühn 1933*a*) by the lost ligament. *V. giganteus* (d'Hombres-Firmas, 1838) has a longer P0, and P1 and P2 insert farther dorsally. A safe distinction from *V. vredenburgi*, however, is difficult, as only a few RVs of *V. kuehni* from Istria and Serbia have been described and figured, and the LV is unknown.

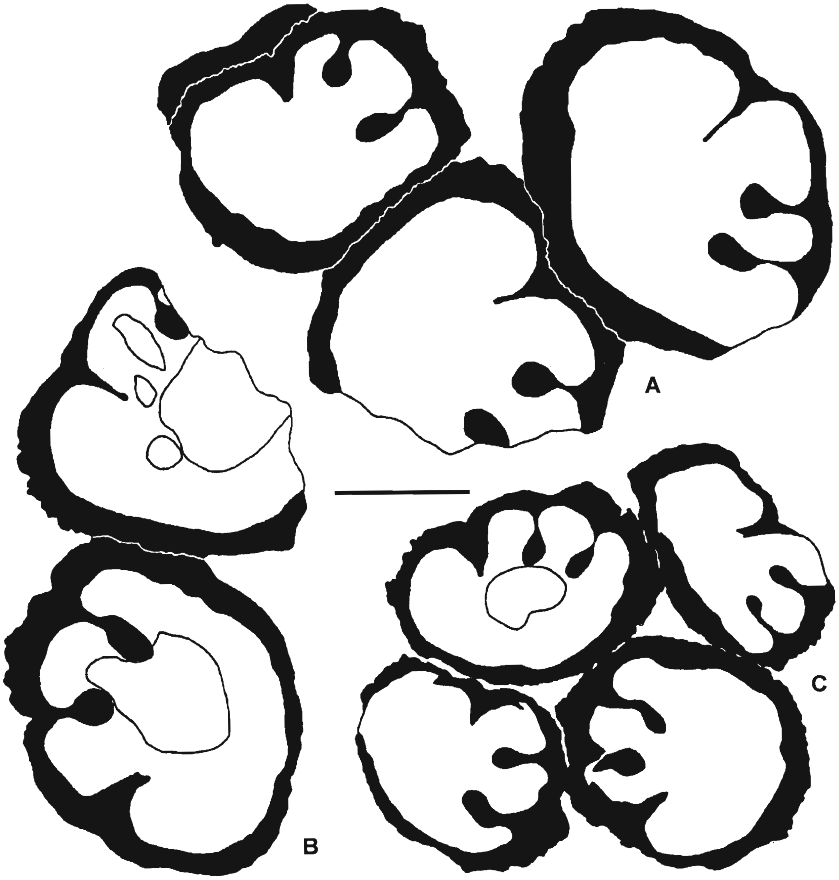
Distribution. Santonian–Campanian of Serbia and Istria.

Vaccinites ljalintzensis Pamouktchiev, 1975

*1975 *Vaccinites ljalintzensis* sp. n. Pamouktchiev, p. 37, pl. 1, fig. 1a–c.
1993*a* *Vaccinites ljalintzensis* Pamouktchiev; Steuber, p. 44, text-fig. 8/7 [with synonymy and description].
1993 *V. ljalintzensis* Pamouktchiev; Steuber *et al.*, p. 259.

Holotype. Pamouktchiev (1975), plate 1, figure 1a–c.

Material. Two fragments of RVs from Marmeko quarry (H251a, H310).



TEXT-FIG. 82. Pseudocolonies with, A–B, *Vaccinites* cf. *boehmi* (Douvillé, 1897*a*), *V. praesulcatus* (Douvillé, 1897*a*) and, C, *Vaccinites* sp. and *V. praesulcatus* (Douvillé, 1897*a*) from Paleokastron Hill. RV sections; A–B, H412; C, H428. Scale bar represents 30 mm.

Description. See Steuber (1993*a*).

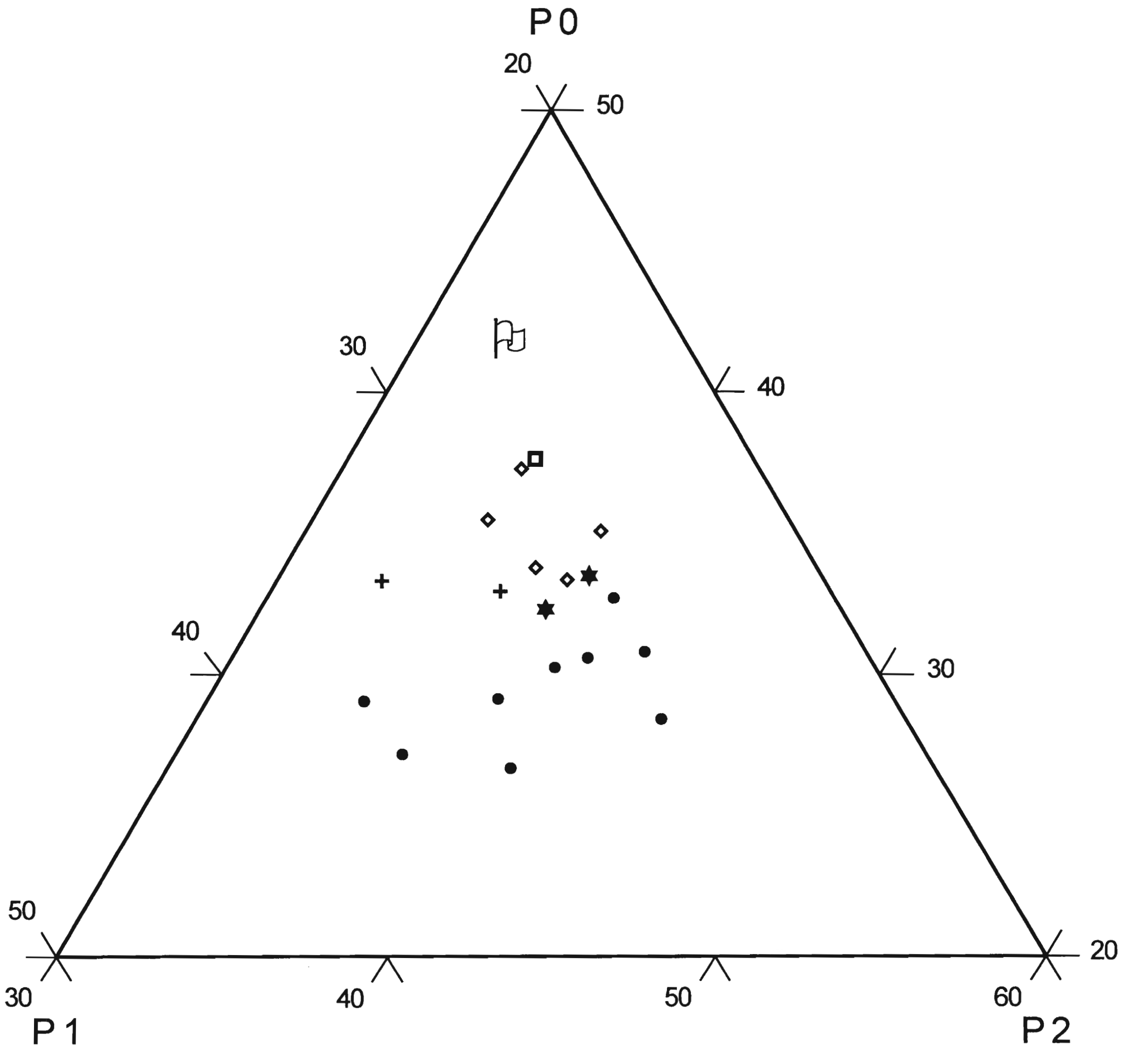
Distribution. Turonian of southern Bulgaria.

Vaccinites praegiganteus (Toucas, 1904)

Plate 21, figure 3

*1904 *Hippurites* (*Vaccinites*) *praegiganteus* nov. sp. Toucas, p. 91, pl. 13, fig. 2, 2a; text-figs 142–145.
1993 *Vaccinites praegiganteus*; Philip, tab. 1.
1993*a* *Vaccinites praegiganteus* (Toucas); Steuber, p. 46, text-figs 6a–h, 8/6, 8/8 [with synonymy and description].
1993*a* *Vaccinites praegiganteus* (Toucas) var. *glaensis*; Steuber, p. 46, text-figs 6g–h, 8.
1993*b* *Vaccinites praegiganteus* (Toucas); Steuber, p. 42, pl. 1, fig. 2.
1993 *V. praegiganteus* (Toucas); Steuber *et al.*, p. 259.
1993 *V. praegiganteus* (Toucas) var. *glaensis* Steuber; Steuber *et al.*, p. 259.

Holotype. Toucas (1904), plate 13, figure 2, 2a, text-figure 142.



TEXT-FIG. 83. Relative length of P0, P1, and P2 in (+) *Vaccinites* sp.; (dots, asterisks = syntypes, after Douvillé 1897*a*, pl. 32, fig. 7) *V. praesulcatus* (Douvillé, 1897*a*); (diamonds, flag = holotype) *V. boehmi* (Douvillé, 1897*a*), and (box) the holotype of '*V. chalmasi* (Douvillé, 1897*a*)'. See Text-figure 11 for measurements.

Material. Fourteen specimens from Marmeko quarry, several of them with both valves conjoined (H1, H16, H18, H80, H249, H307, H311).

Description. See Steuber (1993*a*).

Distribution. Middle Turonian–Lower Coniacian of the Mediterranean region; according to my observations, also in the Turonian of Abu Roash (Egypt).

Vaccinites praepetrocoriensis (Toucas, 1904)

*1904 *Hippurites* (*Vaccinites*) *praepetrocoriensis* nov. sp. Toucas, p. 70, pl. 8, fig. 1, 1a; text-figs 104–108.

1993*a* *Vaccinites praepetrocoriensis* (Toucas); Steuber, p. 48, text-fig. 8/4 [with synonymy and description].
1993 *V. praepetrocoriensis* (Toucas); Steuber *et al.*, p. 259.

Holotype. Toucas (1904), plate 8, figure 1, 1a, text-figure 104.

Material. One RV from Marmeko quarry (H2).

Description. See Steuber (1993*a*).

TABLE 15. Measurements (mm) of seven RVs of *Vaccinites praegiganteus* (Toucas, 1904) from Marmeko quarry.

	Dmax	U	$\overline{P0-P2}$	$\overline{P0-P2}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
min.	52	216	27	94	0·8	0·7	0·6
max.	73	293	42	137	1·4	0·9	0·9
mean	61	254	33	112	1·1	0·8	0·7

Distribution. Middle–Upper Turonian of the northern Mediterranean region, Bulgaria.

Vaccinites praesulcatus (Douvillé, 1897*a*)

Text-figures 49A–B, F, I, 50, 82A–C

*1897*a* *Hippurites praesulcatus* nov. sp. Douvillé, p. 209, pl. 32, fig. 7, 7a.
1932 *Hippurites* (*Vaccinites*) *praesulcatus* Douvillé; Kühn, p. 62 [with synonymy].
1937 *H. praesulcatus* Douv.; Zapfe, p. 75.
1939 *Hippurites* (*Vaccinites*) *praesulcatus* Douvillé; Klinghardt, p. 133.
1941 *Hippurites* (*Vacc.*) *sulcatus* Defrance; Montagne, p. 62, pl. 4, fig. 5.
non 1941 *Hippurites* (*Vacc.*) *praesulcatus* Douvillé; Montagne, p. 62, pl. 4, fig. 6.
?1944 *Hippurites* (*Vaccinites*) *praesulcatus* Douv.; Klinghardt, p. 198, pl. 4, fig. 5.
1959 *Hipp.* (*Vacc.*) *praesulcatus* Douvillé; Petković *et al.*, p. 282.
1959 *Vaccinites praesulcatus* Douv.; Rengarten, p. 256.
1961a *Hippurites* (*V.*) *praesulcatus* Douvillé; Polšak, pp. 422, 432.
1968a *Hippurites* (*Vaccinites*) *praesulcatus* Douvillé; Slišković, p. 36.
1969 *Hippurites* (*Vaccinites*) *praesulcatus* Douvillé; Polšak and Mamužić, p. 239.
1974 *V. praesulcatus* Douv.; Patrulius, p. 172.
1975 *Hippurites* (*Vaccinites*) *praesulcatus* Douvillé; Pleničar, pp. 91, 109, pl. 2, figs 5–6; pl. 3, figs 1–2.
1981 *Vaccinites praesulcatus* (Douvillé); Sánchez, p. 54 [with synonymy].
non 1982 *Vaccinites praesulcatus* (Douvillé); Czabalay, pp. 31, 71, pl. 15, fig. 3.
1983 *Vaccinites praesulcatus*; Sladić-Trifunović, tab. 1.
1985 *Vaccinites praesulcatus* Douvillé; Lupu *in* Kollmann *et al.*, p. 126, pl. 1, fig. 2.
?1989 *Vaccinites praesulcatus* Douvillé; Mermighis, p. 76, pl. 22, figs 1–2, text-fig. 19.
non 1989 *Vaccinites praesulcatus pelagoniensis* nov. subsp. Mermighis, p. 81, pl. 21, figs 3–5, 7–9, text-figs 25–26.

TABLE 16. Measurements (mm) of seven RVs of *Vaccinites praesulcatus* (Douvillé, 1897*a*).

	Dmax	U	$\overline{P0-P2}$	$\overline{P0-P2}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
min.	49	186	34	94	0·5	0·4	0·7
max.	69	272	55	152	0·9	0·6	1·0
mean	58	233	45	127	0·7	0·5	0·8

TEXT-FIG. 84. *Vaccinites salopeki* (Polšak, 1967*b*), Paleokastron Hill. RV section; H434. Scale bar represents 30 mm.

1989b *Vaccinites praesulcatus* Douvillé; Philip *et al*., p. 1381.
1991 *H*. (*Vacc*.) *praesulcatus* Douvillé; Šribar and Pleničar, pp. 178–179.
1997 *Vaccinites praesulcatus* (Douvillé); Steuber *et al*., p. 179, text-fig. 3f–g.

Holotype. Douvillé (1897*a*), plate 32, figure 7.

Material. Eighteen RVs from Paleokastron Hill, most of them in pseudocolonies with *Vaccinites boehmi* (Douvillé, 1897*a*) and *Vaccinites* sp. (H396, H412, H414, H419, H422, H428, H432, H435, H438, H520, H522, H535, H541, H563).

Description. RVs elongated-conical, more than 160 mm long, remarkably thick-shelled and large-sized. Longitudinal ribbing delicate on contact surfaces of conjoined pseudocolonial shells, otherwise particularly coarse with up to 6 mm wide, triangular ribs which are commonly structured by furrows of varying width. P0 short, triangular, with a broad terminal truncation; relative length of P0 variable (Text-fig. 83). P1 and P2 are strongly pinched. Pillars are almost evenly spaced, but P1 approaches P0 in a few RVs (Text-figs 49I, 82A). U/$\overline{\mathrm{P0}-\mathrm{P2}}$ ranges from 4·7 to 6·0 (Text-fig. 76). (1) lies far anterior to P0, axis (1)-(3) consequently strongly inclined with respect to P0. Location of (3) variable: in front of or posterior to P0, in the latter case aligned parallel to P0. Mp runs parallel to the (1)-(3) axis but lies posterior to the prolongation of this axis.

Remarks. *V. praesulcatus pelagoniensis* Mermighis, 1989 from the Turonian of Argolis is a juvenile shell of either *V. inferus* (Douvillé, 1891) or *V. grossouvrei* (Douvillé, 1894).

Distribution. Santonian–Campanian of the Gosau, Dinarids, Romania (Sánchez 1981), Greece (Vermion Mountains) and Caucasus. Turonian–Coniacian of Argolis (Philip *et al*. 1989*b*).

Vaccinites ptoonensis Steuber, 1993*a*

*1993*a* *Vaccinites ptoonensis* n. sp. Steuber, p. 49, text-figs 7a–b, 8/5.
1993 *V. ptoonensis* Steuber; Steuber *et al*., p. 259.

Holotype. Steuber (1993*a*), text-figures 7a, 8/5 (GIK 1031).

Material. Two RVs from Marmeko quarry (GIK 1031, GIK 1032).

Description. See Steuber (1993*a*).

Distribution. Middle Turonian–?Coniacian of Marmeko quarry (Boeotia).

Vaccinites salopeki (Polšak, 1967*b*)

Text-figure 84

1964 *H.* (*V.*) *salopeki* n. sp. Polšak, p. 67 [*nomen nudum*].
1965b *Hippurites* (*V.*) *salopeki* n. sp. Polšak, p. 451 [*nomen nudum*].
*1967*b* *Hippurites* (*Vaccinites*) *salopeki* n. sp. Polšak, pp. 112, 208, pl. 80, figs 1–3, 5; text-figs 34–35.
1968a *Hippurites* (*Vaccinites*) *salopeki* Polšak; Slišković, p. 39.
1969 *Hippurites* (*Vaccinites*) *salopeki* Polšak; Polšak and Mamužić, p. 239.
1974 *Hippurites* (*Vaccinites*) *salopeki* Polšak; Lupu, p. 66, pl. 3, fig. 14; text-fig. 15.
1974 *Hippurites* (*Vaccinites*) *salopeki* Polšak; Slišković, p. 133.
1975 *Hippurites* (*Vaccinites*) *salopeki* Polšak; Pleničar, pp. 96, 110, pl. 9, figs 2–3.
1981 *Vaccinites salopeki* (Polšak); Sánchez, p. 55.
1982 *Hippurites* (*Vaccinites*) *salopeki* Polšak; Polšak *et al.*, text-fig. 3.
1985 *H.* (*V.*) *salopeki* Polšak; Slišković, p. 17.
1991 *H.* (*Vacc.*) *salopeki* Polšak; Šribar and Pleničar, p. 179.

Holotype. Polšak (1967*b*), plate 80, figure 2.

Material. One bivalve specimen and one RV from Paleokastron Hill (H434).

Description. Pores of LV not preserved, radial canals widen towards the shell margin to 2–2·5 mm, canals separated by up to 3 mm wide ridges. RVs elongated-conical, worn and severely bioeroded. P0 short, triangular and rounded at its inner termination; P1 pinched, head circular; P2 strongly pinched, head oval and slightly inflected anteriorly. P1 and P2 are remarkably large and shorter than P0. Cardinal teeth strongly developed, Axis (1)-(3) is considerably inclined against P0. Mp is not clearly recognized in transverse section 4 mm below the commissure, its posterior relocation probably induced a pathological modification of the shell between P0 and P1.

Remarks. The systematic position of *V. salopeki* remains speculative. The LV was unknown and its pore system is not preserved in the Boeotian specimen.

Distribution. Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982) and Gosau (Lupu 1974).

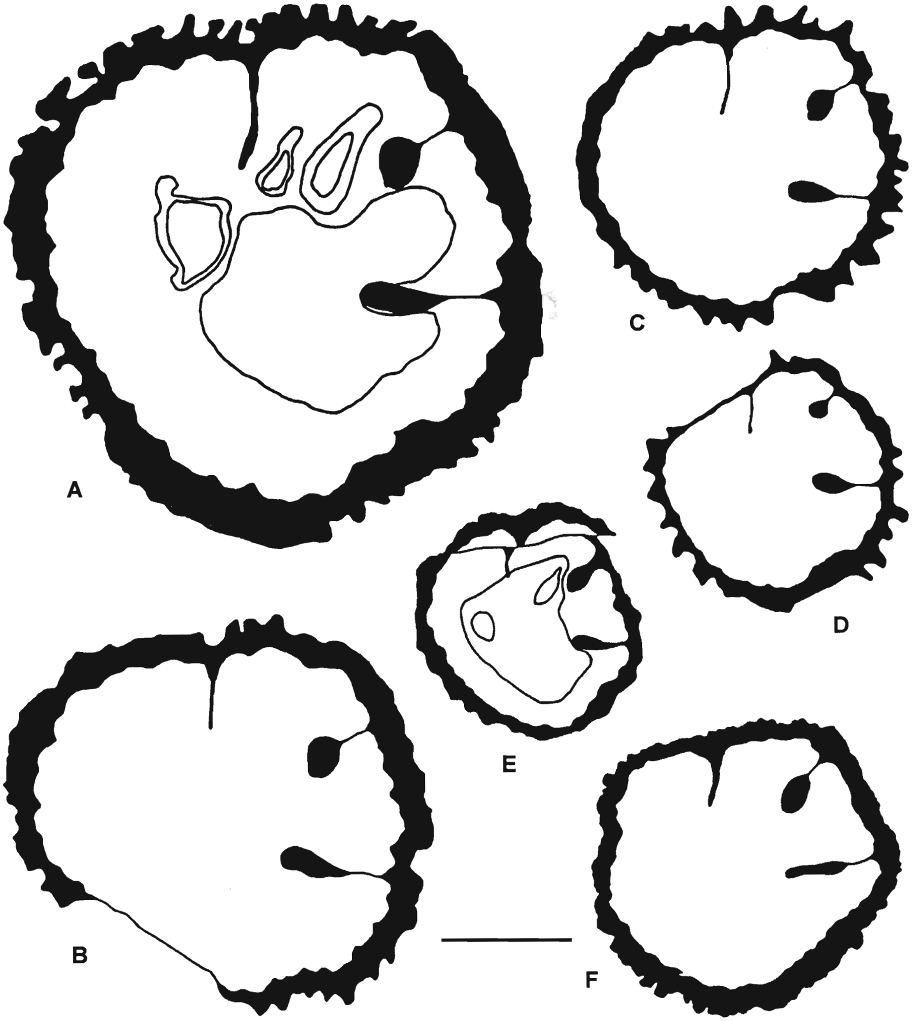
Vaccinites sulcatus (Defrance, 1821)

Text-figure 49E

*1821 *Hippurites sulcata* Defrance, p. 196.
1824 Hippurite sillonnée; Defrance, Cahier 31, pl. 20, fig. 3.
1892*a* *Hippurites sulcatus* Defrance; Douvillé, p. 43, pl. 5, figs 4–5 [cop. Defrance 1821].
v.1892*a* *Hippurites sulcatus* Defrance; Douvillé, p. 43, pl. 5, figs 6–8.
v.1895 *Hippurites sulcatus* Defrance; Douvillé, p. 159, pl. 23, fig. 2.
v.1897*a* *Hippurites sulcatus* Defrance; Douvillé, p. 207, pl. 32, figs 4-6.
1932 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Kühn, p. 68 [with synonymy].
1935 *Hippurit.* (*Vaccinit.*) *sulcatus* Defrance; Klinghardt, p. 26.
1935 *Hipp.* (*Vaccinites*) *sulcatus* var. *maastrichtiensis* Kühn; Klinghardt, p. 23.
1937 *Hippurites sulcatus* Defr.; Zapfe, p. 74, text-figs 2, 7, 10/4.
1941 *Hippurites* (*Vacc.*) *praesulcatus* Douvillé; Montagne, p. 62, pl. 4, fig. 6.
non 1941 *Hippurites* (*Vacc.*) *sulcatus* Defrance; Montagne, p. 62, pl. 4, fig. 5.
1947 *H. sulcatus* Defr.; Kühn, p. 186.
1954 *H.* (*V.*) *sulcatus* Defrance; Milovanović, p. 164.
1957a *Vaccinites sulcatus* Defr.; Astre, p. 194.
1959 *Hippurites sulcatus* Dfr.; Andrusov, p. 215.
1959 *Hipp.* (*Vacc.*) *sulcatus* Defrance; Petković *et al.*, p. 282.
1960 *H. sulcatus* Defr.; Milovanović, p. 367.
1960 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Moisescu, p. 109, pl. 1, figs 5–9; pl. 3, fig. 14.
1961a *Hippurites* (*V.*) *sulcatus* Defrance; Polšak, pp. 422, 432.

1964 *H.* (*V.*) *sulcatus* Defrance; Polšak, p. 67.
1965 *Hippurites* (*Vaccinites*) *sulcatus* Defr.; Benkö-Czabalay, p. 402.
1965b *Hippurites* (*V.*) *sulcatus* (Defrance); Polšak, p. 452.
1966 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Todiriţă-Mihăilescu, p. 73, pl. 26, figs 1–2.
1967 *Hippurites* (*Vaccinites*) *sulcatus* Defr.; Lupu and Lupu, p. 308.
1969 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Polšak and Mamužić, p. 239.
1970 *H.* (*V.*) *sulcatus* Defrance; Benkö-Czabalay, p. 283.
1972*b* *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Campobasso, p. 454, pl. 10, fig. 2.
1974 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Lupu, p. 63, pl. 5, figs 18–19; text-figs 11–12.
1974 *Vaccinites sulcatus* Defr.; Patrulius, p. 172.
1975 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Pleničar, pp. 92, 109, pl. 3, figs 3–5.
1978 *Vaccinites sulcatus* (Defrance); Pamouktchiev, p. 235, tab. 1.
1978 *H.* (*V.*) *sulcatus* Defrance; Polšak *et al.*, p. 190.
1979 *H.* (*V.*) *sulcatus* Defrance; Polšak, p. 205.
1981 *Ps. sulcatus* Def.; Bilotte, text-fig. 2.
1981 *Vaccinites sulcatus* Defrance; Carbone and Sirna, p. 437, text-fig. 6.
1981a *Vaccinites sulcatus* Defrance; Pamouktchiev, p. 405, text-fig. 1.
1981*b* *Vaccinites sulcatus* (Defrance); Pamouktchiev, p. 173, pl. 85, figs 6–7.
1981 *H.* (*V.*) *sulcatus* Defrance; Polšak, p. 454.
1981 *Vaccinites sulcatus* (Defrance); Sánchez, p. 55 [with synonymy].
1982c *Vaccinites sulcatus* Defrance; Bilotte, p. 111.
p1982 *Vaccinites sulcatus* (Defrance); Czabalay, pp. 30, 71, pl. 13, figs 1–8; pl. 15, figs 5–6, 8–12; text-fig. 10.
1982 *Hippurites* (*V.*) *sulcatus* Defrance; Polšak *et al.*, text-fig. 3.
1982 *Vaccinites sulcatus* (Defrance); Pons, tab. 2.
1983 *Vaccinites sulcatus*; Babinot *et al.*, tab. 3.
1983 *V. sulcatus* (Defr.); Czabalay, p. 187.
1983 *V. sulcatus*; Philip and Bilotte, tab. 1.
1983 *H.* (*Vacc.*) *sulcatus* Defrance; Pleničar and Premru, p. 192.
1983 *Vaccinites sulcatus*; Sladić-Trifunović, tab. 1.
1984 *Vaccinites sulcatus* Defrance; Bilotte, pl. 41, fig. 6.
1984 *Hippurites* (*V.*) *sulcatus* Defrance; Laviano, p. 187.
1985 *Vaccinites sulcatus* Defrance; Bilotte, p. 340, tab. 31.
1985 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Höfling, pp. 108, 145.
1985 *V. sulcatus* Defr.; Lupu, p. 21.
1985 *Vaccinites sulcatus* Defrance; Lupu, *in* Kollmann *et al.*, p. 126, pl. 1, fig. 7.
1987 *Vaccinites sulcatus* (Defrance); Accordi *et al.*, p. 139, pl. 1, figs 1, 8.
1988 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Höfling, p. 134.
non 1989 *Vaccinites sulcatus* Defrance; Özer, p. 337, pl. 1, figs 7–9.
1989 *V. sulcatus*; Pieri and Laviano, p. 352.
1990 *Hippurites* (*V.*) *sulcatus* Defrance; Cestari and Pantosti, p. 45, text-fig. 4.
1990 *V. sulcatus* (Defrance); Sirna, p. 25.
1991 *H.* (*Vacc.*) *sulcatus* Defrance; Šribar and Pleničar, p. 178.
1992 *V. sulcatus* (Defrance); Cestari *et al.*, p. 366.
1992a *V. sulcatus* Defrance; Peza, p. 87.
1992*b* *Vaccinites sulcatus* (Defrance); Peza, p. 295, pl. 2, fig. 2, text-fig. 7.
1992 *Vaccinites sulcatus* (Defrance); Vicens, p. 139, pl. 6, fig. 1 [cop. Douvillé 1892*a*], figs 2–6.
1993 *Hippurites sulcatus*; Moussavian *et al.*, p. A3/15.
1996 *Vaccinites sulcatus*; Sanders, p. 852.
p1997 *Hippurites* (*Vaccinites*) *sulcatus* Defrance; Höfling, pp. 50, 81, pl. 18, figs 1, 3, 5–6, [*non* fig. 8]; pl. 19, fig. 4.
?1997 *Vaccinites* ‘*sulcatus*’; Sanders and Baron-Szabo, p. 71, pl. 23, fig. 2.
1997 *Vaccinites sulcatus* (Defrance); Steuber *et al.*, p. 179, text-fig. 3k.
1998 *Vaccinites sulcatus* (Defrance); Steuber *et al.*, in press.

Syntype. Defrance (1824), Cahier 31, figure 3. The generally accepted definition of the internal characters are based on the description of topotypes (Douvillé 1892*a*). The syntype was obviously not available to Douvillé.



TEXT-FIG. 85. *Vaccinites vesiculosus* (Woodward, 1855). RV sections; A–D, ontogeny of RV from Bayburt, Turkey; H44. E, H534; F, H500; RVs from Analipsis, Boeotia. Scale bar represents 30 mm.

Material. One RV from Paleokastron Hill (H436).

Description. RV ornamented with regularly spaced, acute longitudinal ribs that are up to 3 mm wide. P0 triangular with broad area of ligamental insertion. Anterior and posterior sides of P1 and P2 parallel, not pinched. (1′) in front of and ventral to P0, (3′) posterior to P0, aligned parallel to the posterior margin of P0 and not surpassing its tip. U/$\overline{\text{P0–P2}}$ is 4·6 (Text-fig. 76).

TABLE 17. Measurements (mm) of RV of *Vaccinites sulcatus* (Defrance, 1821).

	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H436	34	133	29	66	1·1	0·8	0·8

Remarks. Vaccinites praesulcatus (Douvillé, 1897*a*) and *V. sulcatus* differ only in the pinching of P1. This character is generally variable in *Vaccinites* and the degree of pinching increased during ontogeny. Therefore, it can be assumed, that *V. sulcatus* is a juvenile growth stage of *V. praesulcatus*. This is supported by the fact that both species commonly occur together (e.g. at Paleokastron Hill). The name '*praesulcatus*' is misleading because it implies an allochrony with *V. sulcatus* which does not exist; it resulted from the erroneous assumption of a Turonian age of the type stratum. However, the number of specimens from Paleokastron is insufficient for a further evaluation of the ontogeny of P1.

Distribution. Santonian–Lower Campanian of the external Dinarids (Polšak *et al.* 1982), Upper Santonian–Lower Campanian of the Pyrenees, of southern France, the Gosau, Apennines, Hungary, Romania (Sánchez 1981), the Slovac Republic, Bulgaria, Albania and Greece (Vermion Mountains).

Vaccinites vesiculosus (Woodward, 1855)

Text-figure 85A–F

*1855 *Hippurites vesiculosus* n. sp. Woodward, p. 59, pl. 4, fig. 6.
1897*a* *Hippurites vesiculosus* Woodward; Douvillé, p. 201, pl. 29, fig. 7.
v1897*a* *Hippurites vesiculosus* Woodward; Douvillé, p. 201, pl. 29, fig. 8a–b; text-fig. 71.
1927 *Hippurites vesiculosus* Woodward; Böhm, p. 208, pl. 17, fig. 5.
1932 *Hippurites* (*Vaccinites*) *vesiculosus* Woodward; Kühn, p. 73 [with synonymy].
1933a *Hippurites bithynicus* nov. spec.; Kühn, p. 169.
1941 *Hippurites vesiculosus* Woodward; Tromp, p. 609.
1944*a* *H. vesiculosus* Woodw. Stchépinsky, p. 97.
1944*b* *Hippurites* (*Vaccinites*) *vesiculosus* Woodward; Stchépinsky, p. 237, pl. 3, fig. 1; pl. 4, figs 1, 5; pl. 5, figs 1, 3; pl. 7, fig. 3.
1946a *Hippurites* (*Vaccinites*) *vesiculosus* Woodward; Stchépinsky, p. 129, pl. 20, fig. 1a–b [cop. Stchépinsky 1944*b*].
1946b *Hipp.* (*Vacc.*) *vesiculosus* Woodward; Stchépinsky, p. 354.
1949 *Vaccinites vesiculosus* Woodward; Erentöz, p. 22, pl. 1, figs 3–4.
1951 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Pejović, p. 95, pl. 2, fig. 1.
1967*a* *Hippurites braciensis* n. sp. Sladić-Trifunović, pp. 141, 152, pls 1–4; text-figs 1–3, 9 [cop. Pejović 1951], 10 [cop. Kaumanns 1962], 11–12, 13 [cop. Woodward 1855].
1968a *Hippurites* (*Vaccinites*) *braciensis* Sladić-Trifunović; Slišković, p. 43.
1969 *Hippurites* (*Vaccinites*) *braciensis* Sladić-Trifunović; Polšak and Mamužić, p. 240.
1975 *Hippurites* (*Vaccinites*) *braciensis* Sladić-Trifunović; Pleničar, pp. 103, 112, pl. 22, fig. 2; pl. 23, fig. 1.
1975d *H.* (*V.*) *braciensis*; Slišković, p. 139.
1976 *Vaccinites braciensis* Sladić-Trifunović; Karacabey-Öztemür, p. 75, pl. 4, fig. 2; pl. 5, figs 1, 3–4.
1978 *Hippurites* (*Vaccinites*) *braciensis* Sladić-Trifunović; Polšak *et al.*, p. 190.
1978 *Hippurites braciensis* Sladić-Trifunović; Sladić-Trifunović, p. 432, text-figs 7/1 [cop. Sladić-Trifunović 1967*a*] 7/2–7/3, 7/4 [cop. Kaumanns 1962].
1979 *Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Polšak, pp. 205, 224, pl. 9, fig. 7.
1979 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Polšak, pp. 205, 224, pl. 9, figs 5–6.
1981 *Hippurites* (*Vaccinites*) *giganteus* d'Hombres-Firmas; Polšak, p. 454, text-fig. 8d [cop. Polšak 1979].
1981 *Hippurites* (*Vaccinites*) *inaequicostatus* Münster; Polšak, p. 454, text-fig. 8b–c [cop. Polšak 1979].
1981 *Vaccinites bracensis* [*sic*] (Sladić); Sánchez, p. 40 [with synonymy].
1981 *Vaccinites vesiculosus* (Woodward); Sánchez, p. 57 [with synonymy].
1982 *Hippurites* (*Vaccinites*) *braciensis* Sladić-Trifunović; Polšak *et al.*, text-fig. 3.
1983 *V. braciensis* (Sladić-Trifunović); Czabalay, p. 187.
1983 *H.* (*Vacc.*) *braciensis* Sladić-Trifunović; Pleničar and Premru, pp. 192, 194.
1983 *Vaccinites braciensis*; Sladić-Trifunović, tab. 1.
1984b *Hippurites* (*Vaccinites*) *braciensis* Sladić-Trifunović; Slišković, p. 214.
1985 *Vaccinites braciensis* Sladić-Trifunović; Caminiti, p. 135, pl. 30, fig. 4.
1986 *Vaccinites braciensis* Sladić-Trifunović; Negra and Philip, p. 51, pl. 1, fig. 1.
1986 *Vaccinites braciensis* Sladić-Trifunović; Özer, p. 101, pl. 1, figs 3–4; text-fig. 2.
1987 *Vaccinites vesiculosus*; Pejović and Radoičić, tab. 2.

TABLE 18. Measurements (mm) of RVs of *Vaccinites vesiculosus* (Woodward, 1855) from Bayburt, Anatolia (H44) and Analipsis, Boeotia (H500).

	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H44 adult	114	535	100	279	1·3	0·9	0·7
H44 juvenile	52	232	49	119	1·3	0·6	0·5
H500	64	297	54	161	0·9	0·7	0·7

1987 *Vaccinites braciensis* (Sladić-Trifunović); Pejović and Radoičić, p. 132, tab. 2.
1988b *V. braciensis*; Özer, p. 49.
1989 *Vaccinites bracensis* [*sic*]; Pieri and Laviano, p. 352.
1989 *Vaccinites braciensis* Sladić-Trifunović; Sladić-Trifunović, p. 151, pl. 5, fig. 7.
1990 *Vaccinites braciensis*; Gušić and Jelaska, text-fig. 11.
1990 *Vaccinites braciensis* Sladić-Trifunović; Skelton *et al.*, p. 537, tab. 1.
1990 *Vaccinites vesiculosus* (Woodward); Skelton *et al.*, tab. 2, fig. 9h.
1991 *Vaccinites vesiculosus* (Woodward); Skelton and Gili, pl. 1, fig. 3.
1991 *H.* (*Vacc.*) *braciensis*; Šribar and Pleničar, p. 182.
1992 *Vaccinites vesiculosus* (Woodward); Laviano and Gallo Maresca, p. 49, text-figs 2–9 [with synonymy].
1992b *Vaccinites braciensis* Sladić-Trifunović; Özer, p. 134.
1992 *V. braciensis* Sladić-Trifunović; Pleničar and Šribar, p. 307.
1993 *Vaccinites braciensis* Sladić-Trifunović; Özer, p. 167, fig. 2.
1993 *V. braciensis* Sladić-Trifunović; Plenicar, p. 49.
1994 *Vaccinites vesiculosus* (Woodward); Platel *et al.*, p. 151, pl. 2, figs 5–6.
1995 *Vaccinites vesiculosus* (Woodward); Morris and Skelton, p. 290, pl. 4, fig. 3; pl. 5, fig. 3.
1995 *Vaccinites vesiculosus*; Schumann, p. 191, pl. 38, figs 3, 5; pl. 39, fig. 4; pl. 40, fig. 1, text-fig. 4.
1996a *Vaccinites vesiculosus*; Laviano, p. 7.
1996 *Vaccinites vesiculosus* Woodward; Philip and Platel, p. 262, pl. 1, fig. 5.

Holotype. Woodward (1855), plate 4, figure 6; Douvillé (1897*a*), plate 29, figure 7.

Material. Four RVs from Analipsis (H500–H502, H534); three RVs from Bayburt (eastern Turkey) for comparison (H42–H44).

Description. Boeotian RVs more than 185 mm long, those from Bayburt more than 250 mm long; elongated-conical. Longitudinal ribs rounded, commonly broadening distally, then club-shaped in transverse section. Inner margin of outer shell layer with pronounced irregular undulations. No remnants of ligamental insertion are visible at the tip of P0 which is straight or slightly inflected either anteriorly or posteriorly. Head of P1 round or oval, base strongly pinched or pedunculate. P2 straight or slightly inflected dorsally, pedunculate, head elliptical. Ratios of lP0 and lP2 variable (Text-fig. 80). U/$\overline{\text{P0–P2}}$ ranges from 4·7 to 5·4. (Text-fig. 76). (1) anterior to P0, (3) posterior to P0 and projecting ventrally over the tip of P0. Axis (1)-(3) strongly inclined against P0. Mp located between (3) and P1. Axis (1)-mp aligned parallel to P1.

Remarks. The Boeotian RVs are small when compared with those from eastern Turkey and, thus, resemble the holotype and specimens described from Apulia (Laviano and Gallo Maresca 1992). RVs from Serbia that have been described as *Hippurites braciensis* (Sladić-Trifunović, 1967*a*) are considerably larger. In these shells, the formation of peduncles is more pronounced even in juvenile growth stages (Text-fig. 85D). It would be interesting to evaluate if these morphological patterns have a stratigraphical implication. However, pillar morphology does not allow for a differentiation of the Serbian, Boeotian and Turkish specimens. Therefore, *V. braciensis* and *V. vesiculosus* are considered synonymous, following the suggestion of Laviano and Gallo Maresca (1992).

TABLE 19. Measurements (mm) of RVs of *Vaccinites vredenburgi* (Kühn, 1933*a*).

	Dmax	U	$\overline{\mathrm{P0-P2}}$	$\overline{\mathrm{P0-P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H538	108	481	57	224	1·2	1·0	0·8
H542	85	430	56	230	0·8	0·7	0·7
H544	98	508	61	281	0·7	0·6	0·9

Distribution. Campanian–Maastrichtian (Polšak *et al.* 1982; Platel *et al.* 1994; Philip and Platel 1996) of the Alps, Apennines, Dinarids, of Greece (Parnassus Mountains), Turkey, Tunisia, Egypt, Iran and Oman. This stratigraphical age is supported by associated rudists at Bayburt (Fenerci 1994): *Hippuritella sulcatoides* (Douvillé, 1892*a*), *Vaccinites ultimus* (Milovanović, 1935).

Vaccinites vredenburgi (Kühn, 1933*a*)

Plate 25, figure 3; Text-figure 75C–I

1932	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn, p. 73 [with synonymy, *nomen nudum*].
**1933a*	*Hippurites* (*Vaccinites*) *vredenburgi* sp. nov. Kühn, p. 156, text-figs 1–2.
1938*b*	*H.* (*Vaccinites*) *vredenburgi* Kühn; Milovanović, p. 249, pl. 1, fig. 2.
1957	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Pejović, p. 105, pl. 39, fig. 2; text-figs 47–48.
1959	*Hippurites vredenburgi* Kühn; Nazemi and Grubić, p. 950, text-fig. 4.
1959	*Hipp.* (*Vacc.*) *vredenburgi* Kühn; Petković *et al.*, p. 287.
1960	*H. vredenburgi*; Milovanović, p. 367.
1960	*Vaccinites vredenburgi* Kühn; Vogel, p. 280.
1961a	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Polšak, pp. 422, 432.
1962	*Hippurites vredenburgi* Kühn; Grubić, p. 108, text-figs 1–12.
1962	*Hippurites vredenburgi* v. *persicus* n. var. Grubić, p. 115, text-figs 14–15.
1962	*Hippurites vredenburgi* v. *nazemi* n. var. Grubić, p. 116, text-fig. 13.
1962	*Hippurites vredenburgi* v. *occidentalis* n. var. Grubić, p. 117, text-figs 16–19.
1962	*Hippurites* (*Vacc.*) *vredenburgi* Kühn; Slišković *et al.*, p. 130.
1964	*H.* (*V.*) *vredenburgi* Kühn; Polšak, p. 67.
1965b	*Hippurites* (*V.*) *vredenburgi* Kühn; Polšak, p. 451.
1965	*H.* (*V.*) *vredenburgi* Kühn; Slišković, p. 373.
1967*b*	*Hippurites* (*Vaccinites*) *taburni* Guiscardi; Polšak, pp. 119, 211, pl. 74, figs 1–3; text-fig. 40.
1968a	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Slišković, p. 38.
1969	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Polšak and Mamužić, p. 239.
1974	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Slišković, p. 133.
1975	*Hippurites vredenburgi occidentalis* n. subsp. Grubić, p. 145, pl. 1.
1975	*Hippurites nazemi* n. sp. Grubić, p. 146, pl. 2.
1975	*Hippurites Polšaki* n. sp. Grubić, p. 146, pl. 3.
1975	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Pleničar, pp. 97, 111, pl. 10, figs 1–2; pl. 11, figs 1–2; pl. 12, figs 1–2.
1975a	*H.* (*V.*) *vredenburgi* Kühn; Slišković, p. 43.
1977	*Hippurites* (*Vaccinites*) *bacevicensis* n. sp. Sladić-Trifunović, pp. 258, 266, pl. 1, figs 1–2; text-fig. 1.
1978	*Vaccinites vredenburgi* Kühn; Pamouktchiev, p. 238, tab. 1.
1978	*H.* (*V.*) *vredenburgi* Kühn; Polšak *et al.*, p. 190.
1979	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Polšak, pp. 205, 224, pl. 9, fig. 4.
1981*b*	*Vaccinites vredenburgi* Kühn; Pamouktchiev, p. 176, pl. 86, fig. 2.
1981	*Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Polšak, p. 454, text-fig. 8a [cop. Polšak 1979].
1981	*Vaccinites vredenburgi* (Kühn); Sánchez, p. 57 [with synonymy].
1981	*Vaccinites vredenburgi nazemi* (Grubić); Sánchez, p. 57 [with synonymy].
1981	*Vaccinites vredenburgi occidentalis* (Grubić); Sánchez, p. 58 [with synonymy].
1981	*Vaccinites vredenburgi persicus* (Grubić); Sánchez, p. 58 [with synonymy].
?1982	*Vaccinites vredenburgi* (Kühn); Czabalay, pp. 31, 72, pl. 10, fig. 4; pl. 25, fig. 2.

p1982 *Vaccinites gosaviensis* (Douvillé); Czabalay, pp. 33, 72, pl. 17, figs 2–3.
1982 *Vaccinites vredenburgi* Kühn; Pamouktchiev, p. 223, pl. 9, fig. 3.
1982 *Hippurites* (*Vaccinites*) *vredenburgi* Kühn; Polšak *et al.*, text-fig. 3.
1983 *H.* (*Vacc.*) *vredenburgi* Kühn; Pleničar and Premru, p. 192.
1983 *Vaccinites bacevicensis*; Sladić-Trifunović, tab. 1.
non 1989 *Vaccinites vredenburgi* Kühn; Laviano and Guarnieri, p. 80, pl. 1, figs 1–3, 6; text-figs 2–3.
1989 *Vaccinites vredenburgi* Kühn; Mermighis, p. 80, pl. 22, fig. 8; text-fig. 24.
1989 *Vaccinites vredenburgi hellenica* nov. subsp. Mermighis, p. 83, pl. 22, fig. 6; text-fig. 28.
1989b *V. vredenburgi* Kühn; Philip *et al.*, p. 1382.
1989 *V. vredenburgi*; Pieri and Laviano, p. 352.
1990 *Vaccinites vredenburgi*; Gušić and Jelaska, text-figs 8, 11.
1991 *Hippurites vredenburgi*; Caffau and Pleničar, p. 209.
1991 *H.* (*Vacc.*) *vredenburgi* Kühn; Šribar and Pleničar, p. 178.
1992 *Vaccinites vredenburgi* Kühn; Swinburne *et al.*, text-fig. 2.
1993 *Vaccinites vredenburgi* Kühn; Cherchi *et al.*, p. 95, pl. 6, fig. 4.
1994 *Vaccinites vredenburgi* (Kühn); Platel *et al.*, p. 156.
1996 *Vaccinites vredenburgi* Kühn; Philip and Platel, p. 262, pl. 1, fig. 6.
1997 *Vaccinites vredenburgi* (Kühn); Steuber *et al.*, p. 179, text-fig. 3b–c.

Holotype. Kühn (1933*a*), text-figure 1.

Material. Eight specimens, one of them with both valves conjoined, from Paleokastron Hill (H386, H389, H395 [cf.], H430, H538, H542, H544–H545) and one RV, collected loose from Kefallinia peninsula near Antikyra (H405).

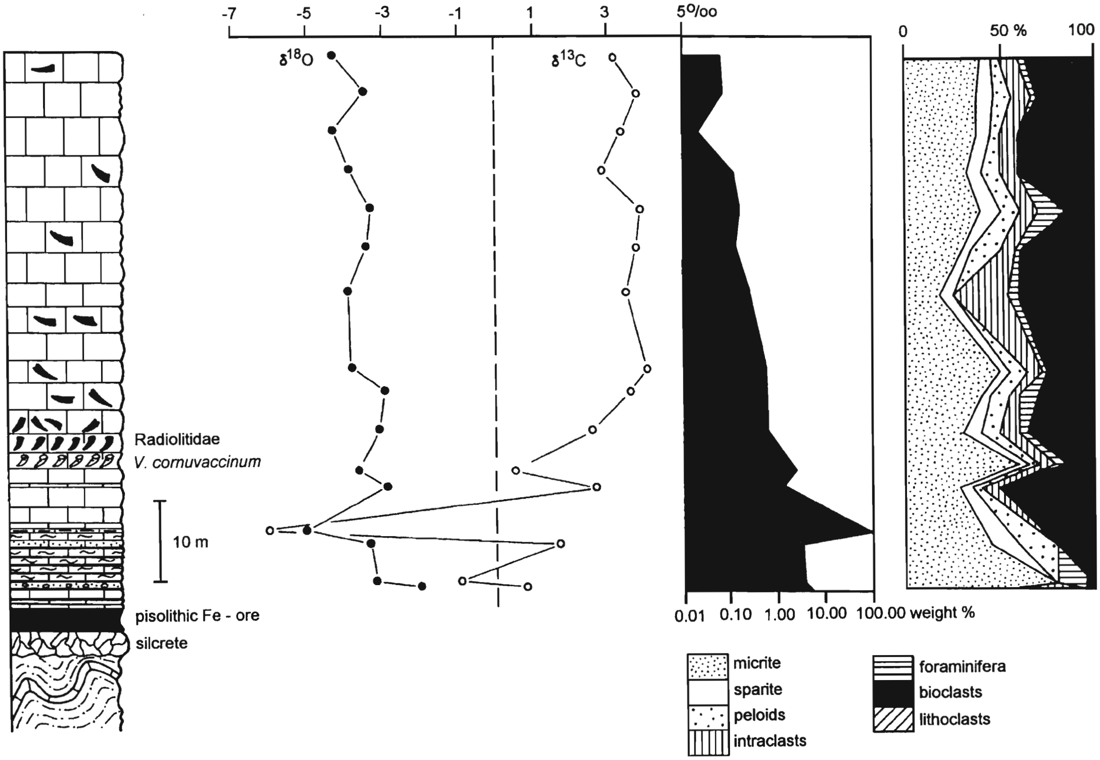
Description. LV 25 mm high, apex in a sub-central, anterodorsal position; radial canals distally 1·2–1·5 mm wide, as are the separating ridges. Reticulate pores only preserved in small areas of the surface, at other places worn to reveal denticulate pores with an average diameter of 0·8 mm. Small osculum above P1 (2·5 mm wide, 15 mm long), osculum above P2 is 6 mm wide and 18 mm long.

RVs elongated-conical, exceeding 220 mm long, ornamented with 2–4 mm wide, rounded longitudinal ribs and furrows. Inner margin of outer shell layer more or less undulating. Outer shell layer shows alternating light-dark coloured, 12–18 mm thick growth banding in one shell. P0 long and strongly developed, its tip is inflected anteriorly. Inner termination truncated and in some shells widened, with distinct remnants of ligament. P1 pedunculate in most RVs, strongly pinched in others, head oval or sickle-shaped and inflected towards P2. Base of P2 pedunculate and thin, head oval or sickle-shaped and inflected anteriorly. P1 and P2 are located close to each other, their peduncles are parallel and offset from P0. Relative length of the three pillars is rather variable (Text-fig. 79). $U/\overline{P0-P2}$ ranges from 7·6 to 8·5 (Text-fig. 76). The myocardinal elements are preserved in one shell only (Text-fig. 75I): (1′) anterior to P0; (3′) posterior to P0, outline long-elliptically and radially aligned. Axis (1′)-(3′) inclined at 40° with respect to P0. Mp′ aligned parallel to (3′), shifted posterodorsally and distally extended.

Remarks. The problematical definitions of *V. vredenburgi*, *V. giganteus* (d'Hombres-Firmas, 1838) and *V. gosaviensis* (Douvillé, 1890) have been discussed by Laviano and Guarnieri (1989). In their study, morphometric analyses failed in providing a distinction between *V. giganteus* and *V. vredenburgi*. However, only RVs with rounded P0 had been considered. Certainly, these Apulian specimens are indistinguishable from *V. giganteus* or *V. giganteus major*. Although mp is located far dorsally between P0 and P1 in *V. giganteus*, and more centrally, often ventrally of P1 in *V. vredenburgi*, some RVs have been defined as *V. vredenburgi* var. *occidentalis* (Grubić, 1962) that are similar to *V. giganteus* in this character, but in which P0 is not rounded.

The described taxonomic problems result from the definition of *V. vredenburgi* in which shells with both rounded and truncated P0 have been incorporated (Kühn 1933*a*). Most probably, the varying shape of P0 is of diagenetic origin, as noted earlier in other *Vaccinites* with long and slender P0 (Milovanović 1934; Grubić 1962). Nevertheless, the drawing of the holotype clearly shows a truncation of P0, which provides a safe distinction from *V. giganteus*. An additional character for differentiation probably is the presence of particularly narrow radial canals in the LV of *V. vredenburgi*, but this needs further substantiation as the LV of this species is still insufficiently known.

V. bacevicensis (Sladić-Trifunović, 1977) was based on the description of a single RV from eastern



TEXT-FIG. 86. Litho- and microfacies (principal components), whole-rock isotopic compositions (versus PDB), and HCl-insoluble residues in measured section at Keratovouno Hill. Samples for analysis of whole-rock isotopic compositions have been drilled from counterparts of thin sections free of sparry calcite cements.

Serbia. The hinge is unknown and no differential diagnosis was given concerning the separation from the very similar *V. vredenburgi* (Kühn, 1933*a*). The type specimen of *V. bacevicensis* differs only by a thicker P0 and the pinching of P1 from the typical *V. vredenburgi*. These characters are generally rather variable so that a separation of two species is considered inappropriate.

The RVs from Paleokastron Hill resemble those described from Istria and Slovenia (Polšak 1967*b*; Pleničar 1975) because of the sickle-shaped and anteriorly inflected P2. RVs that were figured by Polšak (1967*b*) as *V. taburni* (Guiscardi, 1865) and *V. vredenburgi* co-occur at several localities, and are considered to delineate the intraspecific variety of the species.

A thick P0 and the stout peduncles of P1 and P2 indicate an early phylogenetic level of the specimens from Paleokastron Hill in contrast with those that have been figured from other localities, including those from Iran (Grubić 1962). This is supported by the stratigraphical position of the rudist beds at Paleokastron which are not younger than early Campanian.

Distribution. Santonian–Campanian (Grubić 1962; Polšak *et al.* 1982; Philip and Platel 1996) of Hungary, southern Italy, Croatia, Serbia, the Peloponnese and Turkey, Iran, Pakistan, Afghanistan (Sánchez 1981), Bulgaria and Oman.

Vaccinites sp.

Text-figures 49C, 82C

Material. Three RVs, two of them in pseudocolonial congregation with *V. praesulcatus* (Douvillé, 1897*a*); H410, H428.

TABLE 20. Measurements (mm) of RVs of *Vaccinites* sp.

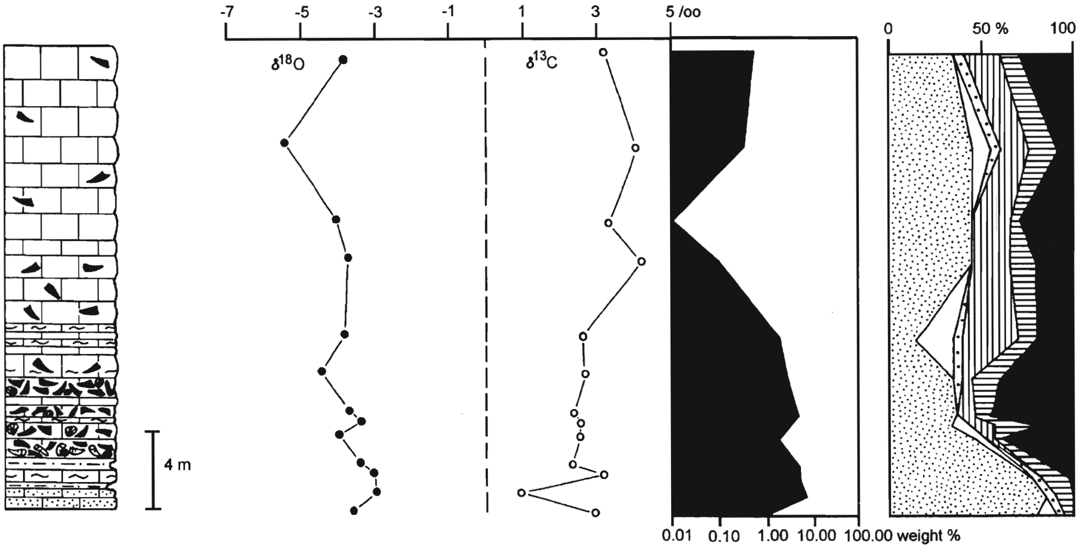
	Dmax	U	$\overline{\text{P0–P2}}$	$\overline{\text{P0–P2}}$ cont	lP0/lP1	lP0/lP2	lP1/lP2
H428/1	49	207	33	110	0·8	0·7	0·8
H428/2	51	201	32	110	0·8	0·8	1·0

Description. RVs elongated-conical with unevenly spaced, 1–2 mm wide longitudinal ribs. Base of P0 broad, tapering and with remnants of a ligament at its inner termination. P1 strongly pinched or pedunculate, commonly inflected towards P0; P2 pedunculate, head inflected towards P0.

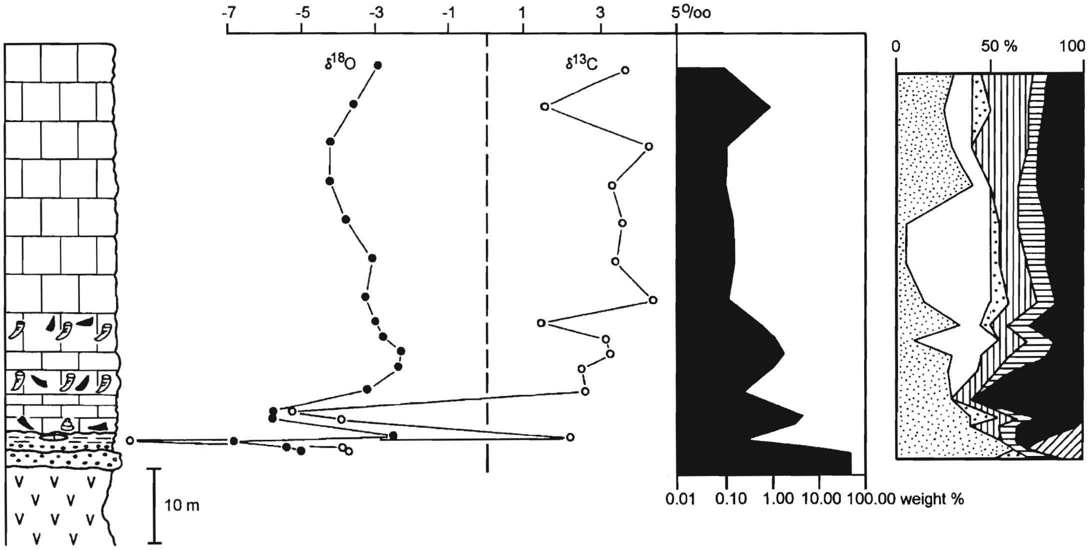
Systematic position. The RVs that are preserved in dense congregations differ from *V. praesulcatus* (Douvillé 1897*a*) in having more strongly pinched or even pedunculate P1 and P2 that insert more closely to P0 (Text-fig. 76); the relative length of pillars are very similar in both species (Text-fig. 83). The RVs resemble *Vaccinites loftusi* (Woodward, 1855) because of the broad, triangular P0. In *V. loftusi*, however, P1 and P2 are not pedunculate.

SANTONIAN–CAMPANIAN RUDIST FORMATIONS OF NORTHERN BOEOTIA

In Boeotia the global Santonian–Campanian sea-level highstand (Haq *et al.* 1988) is recorded in a regionally extensive transgressive marker horizon (Steuber *et al.* 1993; Text-figs 1–2). Preceding the marine transgression, the palaeokarst of the external Pelagonian was sealed with laterites in the Helicon and Parnassus Mountains that are now mined as high-quality karstic bauxites. The overlying limestone facies is rather uniform in the Parnassus and Helicon Mountains; its biostratigraphy and carbonate microfacies was studied in detail (Caminiti 1985; Konertz 1987; Walter 1992). In north-eastern Boeotia, Late Santonian–Campanian rudist limestones follow disconformably over the folded Eohellenian basement. Reworked laterites cover the transgressive surface but are less pure and of minor economic



TEXT-FIG. 87. Litho- and microfacies, whole-rock isotopic compositions, and HCl-insoluble residues in a measured section at Dionysos. Symbols of principal component composition as in Text-figure 86.



TEXT-FIG. 88. Litho- and microfacies, whole-rock isotopic compositions, and HCl-insoluble residues in a measured section at Kalamos Hill. Symbols of principal component composition as in Text-figure 86.

importance due to the vicinity to the ophiolitic nappes of the hinterland. Rudists dominate the biofacies of the overlying limestones and are preserved in life position at several localities. One of them is Keratovouno Hill near Chaeronea, known since the pioneering studies of Gaudry (1862–67) and Bittner (1880). It is the type locality of *Hippurites gaudryi* Munier-Chalmas and *Plagioptychus boeoticus* Munier-Chalmas, and Douvillé (1892*a*, 1895, 1897*a*) figured several specimens from there in his monograph of the Hippuritidae. A subsequent study by Klinghardt (1943) focused on the description of fossils and their biostratigraphical implications, but it remained unmentioned that rudists are preserved in life position at Keratovouno Hill.

Sections

Keratovouno Hill. The limestones that form Keratovouno Hill are exposed along the south-eastern flank of a narrow valley to the South-West of Chaeronea (Text-fig. 1, locality 8). Variegated marls with intercalations of graded-bedded, up to 0·4 m thick limestone banks are exposed at the opposite slope of the valley. They are considered as Tertiary flysch-type deposits on the regional geological map, Levadia Sheet, 1:50·000 (Papastamatiou *et al.* 1971), and limestones of the Keratovouno are interpreted to have been thrusted upon these clastics. A Lower Cretaceous microflora (Steuber 1993*b*) and calpionellids that have been found in the intercalated limestones (Raeder 1994), however, indicate that this sequence belongs to the tectonostratigraphical unit of the Boeotian Flysch (Celet and Clément 1971). This sequence is disconformably followed by a 2–3 m thick silcrete and 3 m of pisolithic iron ores (Text-fig. 86) which have been studied by Rosenberg (1984).

The iron ore is followed conformably by a polymictic conglomerate that contains numerous lateritic components. It grades into an alternation of marls and thin limestone banks with several 20–30 mm thin beds of pisolithic limonite. Micritic limestones nodules are common in the basal marly horizons. Gastropod shells are the only macrofossils found in these marl-limestone alternations. The first rudist remains, fragments of small-shelled radiolitids, occur 10 m above the ore horizon. The following 8 m thick succession of thick-bedded limestones contains only a few redeposited radiolitid shells. It is followed by the main rudist lithosome of Keratovouno Hill. *Vaccinites cornuvaccinum* (Bronn) dominates by far in the 2 m thick impure, marly-sandy limestones. Well preserved shells of *Praeradiolites echennensis* have been found abundantly whereas the valves of *Mitrocaprina boeotica* (Munier-Chalmas) are commonly crushed and preserved in fragments only. Klinghardt (1943) mentioned *Radiolites lusitanicus* (Bayle) var. *rigida* Choffat from this locality, but his figures (Klinghardt 1943, pl. 7, figs 1–2) show *Praeradiolites echennensis* Astre.

Some confusion about the origin of specimens which have been reported from the region resulted from imprecise indications in older monographs. Douvillé (1897*a*, p. 216, pl. 30, fig. 8) described a specimen of *Hippurites taburnii*? Guiscardi [=*Vaccinites chaperi* (Douvillé)] from 'Caprena'. This denomination, the old name of Chaeronea, was frequently used to indicate the locality at Keratovouno Hill. There are no subsequent records of *V. chaperi* (Douvillé) from Keratovouno Hill, and the species was not found there during my own field studies.

On top of the lithosome with *V. cornuvaccinum*, a 50 m thick succession of thick bedded and massive limestones is exposed. At the base they contain abundant *Gorjanovicia* Polšak and *Medeella* Parona in dense associations and in vertical life position. Their abundance decreases quickly upsection and only a few redeposited shells have been found in the topmost 40 m of limestones. Other radiolitids are preserved only in indeterminable fragments and hippuritids are absent.

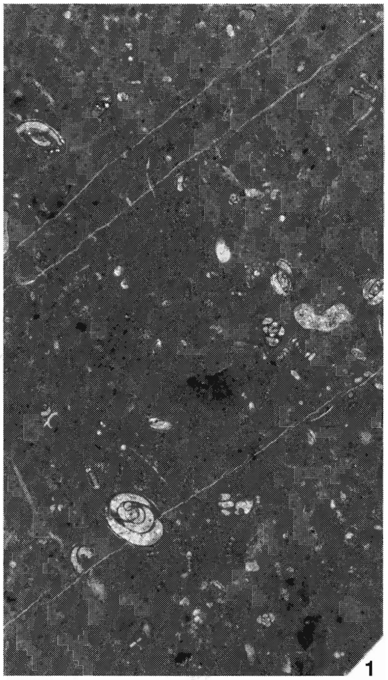
Dionysos. Late Cretaceous limestones (Text-fig. 87) follow unconformably over hyaloclastics and serpentinites to the north-north-east of Dionysos (Text-fig. 1, locality 10). The base of the section consists of a thin alternation of impure, marly-arenaceous limestones and marls. It is followed by several rudist coquinas exposed along an 8 m high escarpment. More or less complete but often disarticulated shells of *Vaccinites cornuvaccinum*, *Gorjanovicia* spp. and *Sauvagesia* spp. accumulated in up to 0·5 m thick beds without any preferred orientation. Few shells of *Gorjanovicia* and vast numbers of *Blastochaetetes flabellum* (Michelin) settled on this substratum. Each of the coquinas is blanketed by thin, fining upward sequences of arenaceous limestone. The top of the section is formed by thick-bedded limestones with a few redeposited rudist remains.

Kalamos Hill. South of Pavlos, the late Cretaceous transgressive surface is formed by serpentinized basic volcanics (Text-fig. 88). The basal levels of the section at Kalamos Hill (Text-fig. 1, locality 12) are several, 150–250 mm thick layers of redeposited pisolithic bauxites, alternating with beige-coloured marls. They are followed by siliciclastic arenites and thin conglomerates with variegated chert, volcanics and redeposited laterites. Grain size decreases continuously upsection. Thin layers of marl are followed by impure, flaser-bedded limestones that grade into more pure, banked limestones. The first rudist remains have been recorded 5 m above the base of the section and are associated with gastropod shells. A hippuritid horizon follows after 3 m, but its unfavourable exposure precludes further observations about growth fabrics and the orientation of the valves within the sediment. The same applies to another horizon, overlying 7 m of flaser-bedded limestones. Hippuritids were collected loose and are represented exclusively by *Vaccinites cornuvaccinum* (Bronn). *Radiolites subradiosus* Toucas and *Mitrocaprina boeotica* (Munier-Chalmas) are less common.

EXPLANATION OF PLATE 26

Figs 1–5. Microfacies of Santonian–Campanian transgressive limestones of northern Boeotia. 1, wackestone with miliolids and ostracods, restricted lagoonal environment below horizon with *Vaccinites cornuvaccinum* (Bronn) at Keratovouno Hill. 2, grainstone with miliolids and diverse bioclasts but rare rudist remains; fine-grained material underneath bivalve-shell was sheltered from winnowing in this turbulent environment (Kalamos) which was not occupied by rudists. 3, rudist bioclast infested by clionid sponges; matrix consists largely of chips that resulted from sponge boring (Pavlos). 4, radiolitid bioclast encrusted by *Pseudolithothamnium album* Pfender and *Thaumatoporella* sp.; seaward slope of *Gorjanovicia*-bank at Keratovouno Hill. 5, detail of fig. 4. 1, 4, × 12·5; 2–3, × 7·7; 5, × 33·3.

PLATE 26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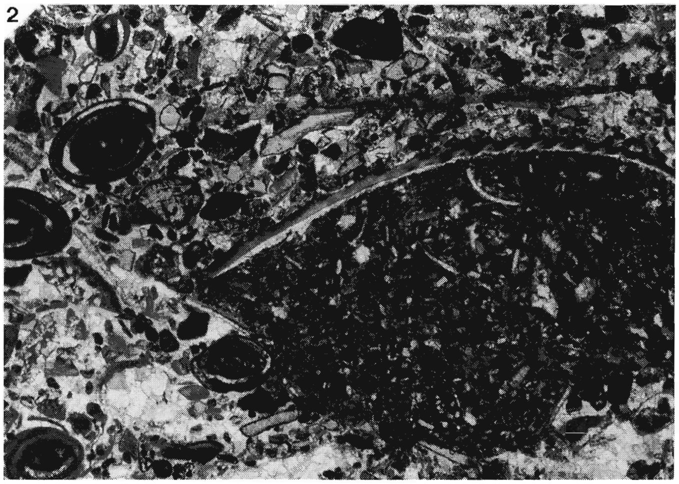
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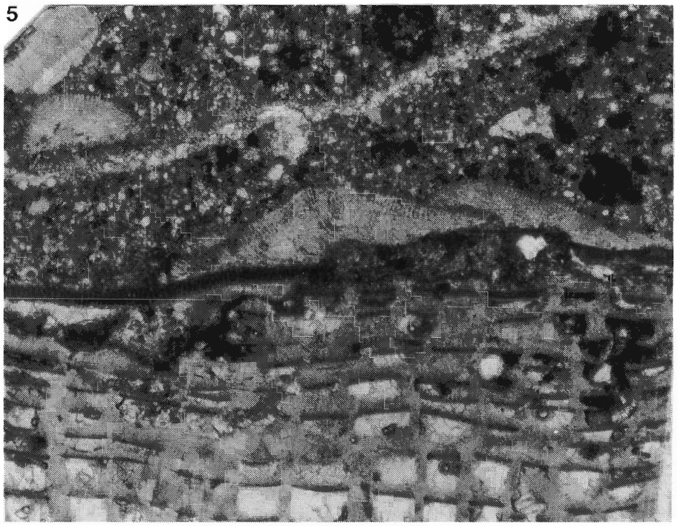
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STEUBER, limestone microfacies

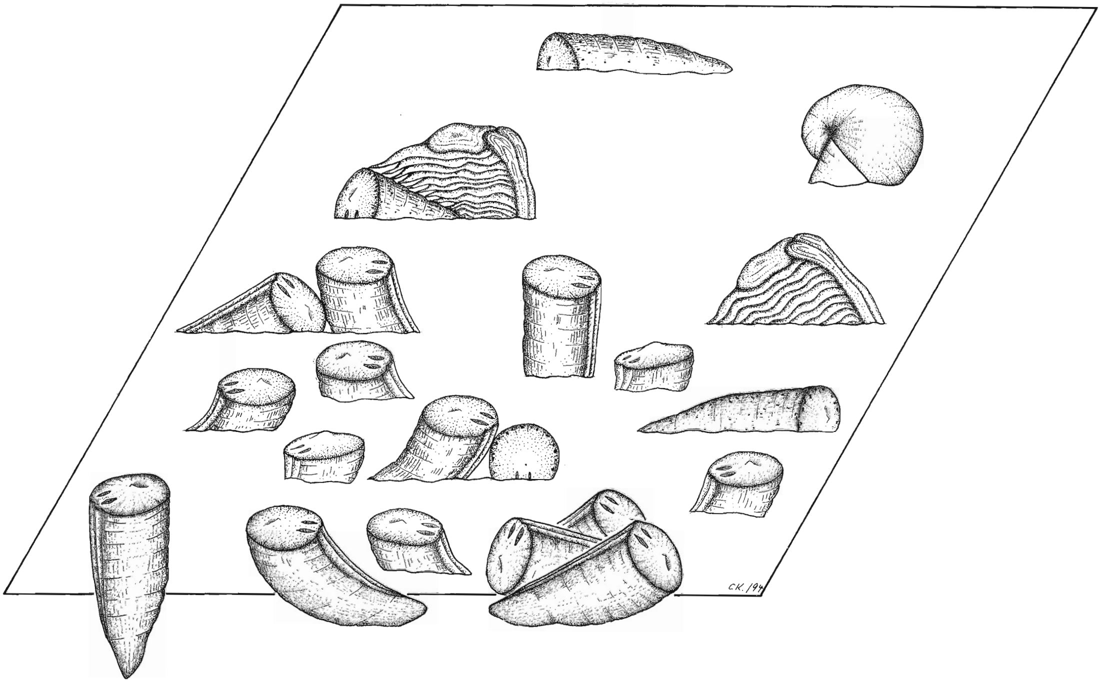
TEXT-FIG. 89. Rudist habitats during the Santonian–Campanian on the Pelagonian platform (not to scale).

Facies successions

The variegated lithofacies of the transgressive siliciclastics and impure limestones that follow over the pisolithic iron-ores at Keratovouno Hill, and over serpentinites near Dionysos and at Kalamos Hill indicate marginal marine depositional environments in the basal levels of the Santonian–Campanian transgressive sequence. Conglomerates and redeposited laterites are repeatedly intercalated. Impure, nodular or flaser-bedded limestones of the basal levels are intramicrites with muddy intraclasts, small thin-shelled ostracods and small gastropods (Pl. 26, fig. 1). The matrix of the overlying micritic limestones is partially winnowed, indicating deposition above wave base or in areas of occasionally increased current velocities; bioturbation was common. Several beds with abundant faecal pellets, porostromate cyanophyceans, *Bacinella irregularis* Radoičić and various benthic foraminifera (*Moncharmontia apenninica* (De Castro) and ataxophragmiids) mark the transition to normal marine environmental conditions. Redeposited fragments of radiolitids (*Gorjanovicia* sp.) occur in these biomicritic pack- and wackestones for the first time in the sedimentary successions.

The matrix of the lithosome with *Vaccinites cornuvaccinum* at Keratovouno Hill is micritic to arenitic without indication of winnowing, and contains abundant muddy intraclasts. Fragments of hippuritid shells and scarce radiolitid bioclasts are found in these wacke- and packstones; some fragments are encrusted by serpulids. Benthic foraminifera are common but are represented exclusively by miliolids. With the exception of more abundant rudist bioclasts, this microfacies closely resembles that of horizons below. This includes the amount of siliciclastics, which again is elevated (Text-fig. 86). The same type of sediments is found internally within the shells. The hippuritid horizons at Kalamos Hill are characterized by a similarly monotonous facies and restricted microfaunas and -floras.

High rates of water turbulence are indicated by the sedimentary fabrics of the *Gorjanovicia* bank that follows over the lithosome with *Vaccinites cornuvaccinum* at Keratovouno Hill. The interstitial sediments between the vertically grown shells that form dense, more or less mutually supporting fabrics, are bioclastic packstones with unsorted, mechanically reworked rudist debris. Indications of bioerosion are restricted to fine borings of cyanophyceans that penetrated rarely deeper than 0·5 mm into the shells. Foraminifera are exclusively represented by thick-shelled miliolids. A corresponding shift to turbulent depositional environments is evident in thick rudist-coquinas at Dionysos. There, most rudist remains have been infested by clionid sponges, and large numbers of chaetetid sponges encrusted the coarse rudist shell rubble. Elongate morphotypes of *Gorjanovicia* only occasionally managed to become established in this



TEXT-FIG. 90. Life position of *Vaccinites cornuvaccinum* (Bronn, 1831), *Mitrocaprina boeotica* (Munier-Chalmas, *in* Gaudry, 1867) and *Praeradiolites echennensis* Astre, 1954 at Keratovouno Hill.

environment. The associated calcareous microfaunas of this unit are exceptionally poor both near Dionysos and at Keratovouno Hill.

The corresponding high energy deposits at Kalamos Hill (Pl. 26, fig. 2) are well-sorted foraminiferal grainstones with *Moncharmontia apenninica* (De Castro), *Pseudocyclammina* cf. *massiliensis* Maync, Verneuilinidae, Ataxophragmiidae and thick-shelled Miliolidae. Rudist remains are common among other bioclasts (*Pseudolithothamnium album* Pfender, echinoids), but are not dominant components.

The microfacies of the overlying limestones is rather monotonous in all three sections. This is also expressed in rather constant compositions of principal components (Text-figs 86–88). Biointramicrites with occasionally packed, unsorted skeletal grains dominate. Among the bioclasts, rudist remains of various sizes dominate by far. Larger fragments are angular, others are rounded and almost completely disintegrated by clionid sponges and microborers (Pl. 26, fig. 3), or infested by various encrusters such as *Pseudolithothamnium album* Pfender, *Thaumatoporella* sp. (Pl. 26, figs 4–5) and *Bacinella irregularis* Radoičić. Foraminifera are more diverse in this unit: *Cuneolina* sp. *Dicyclina schlumbergeri* Munier-Chalmas, *Dicyclina* sp. *Pseudocyclammina* sp., Miliolidae, Ataxophragmiidae and Rotaliidae. Only a few bioclasts of porostromate algae, dasycladaceans and solitary corals have been noted.

The succession of depositional environments as recorded in the three sections is rather uniform: terrigenous and partly siliciclastic sediments are overlain by limestones that were deposited in calm lagoonal environments. Both biofacies and low $\delta^{18}O$ as well as $\delta^{13}C$ of whole rock samples of these mud- and wackestones indicate sporadic hyposaline conditions (Text-figs 86–88). Thin-shelled miliolids, ostracods and microgastropods probably thrived as epiphytes on sea grasses that were apparently widely distributed during the late Cretaceous (Den Hartog 1970; Brasier 1975; Höfling 1985). The coeval influx of freshwater and terrigenous debris to near-shore environments is indicated by co-varying $\delta^{13}C$ and amounts of HCl-insoluble residues (Text-figs 86–88). Extended rudist communities became established as soon as normal marine conditions prevailed (Steuber *et al.* 1993): within the measured sections both the isotopic composition of the matrix sediments and of the rudist shells mark the transition to stable, normal marine salinity.

The biofacies of the rudist habitats is remarkably monotonous. Encrusting organisms are sparsely distributed and species-rich associations of benthic foraminifera are restricted to the debris of the rudist communities. Only the eroding activity of clionid sponges and cyanophyceans is frequently recognized by their characteristic boring patterns (Pl. 26, fig. 3). Even borings of clionid sponges that are among the most common bioeroders to attack rudist shells are rare in the densely packed *Gorjanovicia* banks at Keratovouno Hill which were destroyed predominantly by wave action. In one specimen of *V. cornuvaccinum* both valves were infested by oysters, but the commissure was not blocked so that it cannot be excluded that these epibionts settled on the shell while the rudist was still alive.

A sparse distribution of encrusters has been frequently reported from various rudist associations (Kauffman and Sohl 1973; Höfling 1985; Schumann 1995), and was explained by biochemical halos that prevented the settling of other organisms (Kauffman and Sohl 1973; Kauffman and Johnson 1988). Toxins are physiologically expensive to produce and were probably not simply sprayed into the surrounding water, but mucus from the mantle lobes may have inhibited many settlers. On the other hand, coral-rudist associations are known in which both groups of organisms coexisted (Schumann 1995), encrusted each other and are interpreted to have formed rigid frameworks (Höfling *et al.* 1996).

Sediments that overlie the *Vaccinites* horizons at Keratovouno and Kalamos Hill were deposited in more agitated waters, and correspond to the coquina limestones of the section near Dionysos. Consequently, the Pelagonian platform was sheltered by offshore shoals from the surf of the Pindos Ocean (Text-fig. 89). The establishment of larger rudist communities was obviously restricted in such turbulent environments, as they are absent from the grainstones with foraminifera at Kalamos Hill. The fast-growing *Gorjanovicia* (Steuber 1996*a*) was apparently best-adapted to elevated turbulence and rapidly accumulating or unstable sediments. Dense associations and the concurrent high $CaCO_3$ production (Steuber 1996*c*) characterize the *Gorjanovicia* banks at Keratovouno Hill as reefoid elevations above the original topography.

Limestones of the upper part of all three sections were deposited below storm wave base. Sedimentation was dominated by the debris of the rudist banks, and low amounts of terrigenous components indicate that depositional environments were remote from the continental hinterland (Text-figs 86–88). This is also evident in the rather constant carbon and oxygen isotopic compositions of the limestones (Text-figs 86–88). Other calcareous organisms, with the exception of calcareous algae and foraminifera in the debris of the rudist banks, did not contribute significantly as primary sediment producers.

Patterns of establishment and growth fabrics

Vaccinites cornuvaccinum (*Bronn*). Keratovouno Hill provides an excellent exposure to study the life position of *V. cornuvaccinum.* On several square metres of the lower surface of the lithosome, the embedding sediment has been removed by erosion so that numerous horn-shaped specimens with both valves conjoined are visible. The inspection of a weathered section of the same bed shows that several generations were buried in place, and no indications of redeposition are obvious. Density of association is largest at the base and decreases towards the top of this 2 m thick bed. Both field observations and more than 70 collected specimens show that almost all valves are ventrally convex, curved around the dorsal shell. Their life position on the arenaceous-muddy sediment was reclined, with the ventral shell at the bottom and the dorsal shell facing upwards. Such a reclined growth position has been frequently reported from hippuritids (Zapfe 1937; Skelton and Gili 1991). Multigeniculate, almost semicircularly curved shells seem to have grown into the sediment first and then curved to grow out of the substratum again, but this orientation of the apex is entirely secondary and resulted from multiple toppling and geniculate recovery growth.

No juvenile shells that are attached to older shells have been found at Keratovouno Hill, although rudist larvae required a firm substratum for initial attachment (Skelton 1979*b*), and dense associations in the basal lithosome left almost no choice for larval attachment except for the shells of older individuals. It is assumed that larvae initially settled on the shells of adult conspecifics, but came loose relatively early during ontogeny and fell on the soft sediment between the older shells. The commissure with the mantle tissue that was important for respiration and feeding was subsequently elevated above the sediment surface by allometric growth. Where vertical growth exceeded the rate of ambient sedimentation, such shells escaped the danger of burial. However, rapid vertical shell accretion was disadvantageous in environments with low sediment supply or even sporadic erosion. Vertically projecting shells became unstable so that minor water agitation induced toppling of individuals that were not sufficiently embedded. Sclerochronological stable isotope analyses of a curved shell of *Vaccinites cornuvaccinum* from Keratovouno Hill have shown that toppling resulted in increased allometric growth which lifted the commissure back in a position parallel to the sediment surface. Once this was achieved, growth increments were significantly reduced to less than 10 mm/year (Steuber 1997).

The distribution of clionid borings provides additional indications of the postmortal position of the shell within the sediment (Text-fig. 90). Borings are most common in the commissural part of the shells that was not covered by sediment after death, and are commonly restricted to the upper part of the dorsal shell that comprises the infoldings of the pillars. Such individuals apparently did not succeed in raising the commissure in a position parallel to the sediment surface after dislocation and died, most probably as a result of toppling. This interpretation of the distribution of sponge borings assumes that *Vaccinites cornuvaccinum* managed to prevent infestation of the shell by bioeroders during life.

The orientation of the valves at Keratovouno Hill is not random. Among 60 shells that have been analysed from the basal layers of the *Vaccinites* horizon, the LVs of 27 face to the south, 15 others face to the north and 18 have other orientations. The preferred north-south orientation probably resulted from weak currents. It must have occurred early during ontogeny as torsion of RV axes was not observed, although this was obviously possible in *Vaccinites*, but has been very rarely reported (e.g. Schumann 1995). Irrespective of their orientation, 80 per cent. of the RVs have a ventrally convex curvature. Toppling of vertically growing shells due to sporadically increased, directed water turbulence would have resulted in a random distribution of curvature of the valves. The permanent turbulence in the habitat must have been low, as the sediment is predominantly fine grained and the fabric mud-supported. Consequently, toppling of the shells as a result of occasional turbulence is assumed to have occurred only rarely. Instead, vertical growth was responsible for a continuous, destabilizing elevation of the centre of gravity. Vertically grown shells of *Vaccinites* are not a simple, elongated, well-balanced cone (Text-fig. 90), but the ventral shell margin expanded disproportionally during growth (cf. Text-fig. 64). This asymmetry predetermined a ventral direction of toppling where the shells were not sufficiently stabilized by sedimentation during growth. Once the curvature was established by reorientation of the growth axis and the commissure was lifted back in a position more or less perpendicular to the sediment surface, further growth again induced instability on soft bottoms in areas with low sedimentation rates. Repeated sinking of the curved, heavy commissural part of such shells eventually produced the semicircularly curved morphotypes which have been found at Keratovouno Hill.

The allometric expansion of the ventral shell has been noted in all of the various analysed species of *Vaccinites* (Text-figs 12–13; Steuber 1993*a*), and can also be traced in the phylogeny of the genus (Kühn 1948; Philip 1981). The morphologically predetermined direction of toppling on the ventral shell had the consequence that the oscula of the LVs were not blocked by sediment. The blocking of a ventral portion of the pore and canal system was certainly not fatal for the organism, but the oscula most probably had a vital, although still disputed, function (e.g. Vogel 1960; Skelton 1976). Dislocation by storms would have resulted in a random orientation of toppled shells, and individuals that fell on the dorsal shell and the oscula of which were blocked by sediment could perhaps not have maintained their life functions. The disproportional expansion of the ventral shell of elongated-conical valves of *Vaccinites* can thus be explained as an adaptation to the epifaunal life habit, as it predetermined the direction of toppling in case that sedimentation rates were too low to stabilize the vertically projecting shells within the sediment. This interpretation is supported by the observation that RVs of *Vaccinites* that are curved around the ventral shell, i.e. which are dorsally convex, are generally much less common when compared with RVs that are ventrally convex. This is not only observed at Keratovouno Hill, but is a general feature of the genus.

Broad-conical morphotypes which are commonly developed in other Hippuritidae, have not been observed in *V. cornuvaccinum*, although they would have been perfectly adapted to the environment reconstructed at Keratovouno Hill. In contrast, the adult growth rates of a geniculate shell from Keratovouno Hill (Steuber 1997) and a straight, elongated morphotype from Kalamos Hill (Steuber 1996*b*) are very similar (8–10 mm/year) so that sedimentation rate probably did not control the rate of vertical shell accretion. However, the biogeochemical data (Steuber 1996*a*, 1996*b*, 1996*c*, 1997) are still insufficient for a well-founded interpretation of factors controlling growth rates in various environments.

A low ambient sedimentation during the formation of the *Vaccinites* lithosome at Keratovouno Hill is also indicated by morphotypes of other less abundant rudists that shared the same habitat. The large, globose and spirogyrate LV of *Mitrocaprina boeotica* (Munier-Chalmas) prevented rapid elevation of the commissure above the sediment surface. Such morphotypes lived reclining on soft bottoms in areas with low sedimentation rates (Skelton and Gili 1991; Ross and Skelton 1993). The broad, conical RVs of *Praeradiolites echennensis* Astre with laterally projecting shell lamellae indicate slow vertical growth and the attempt of stabilization by lateral support. Several shells were found at Keratovouno Hill that clutched with their extended lamellae on to toppled shells of *V. cornuvaccinum* or conspecifics to obtain a stable position (Text-fig. 90).

The field studies on orientation of the shells within the sediment, microfacies, and growth rates as determined by stable isotope sclerochronology (Steuber 1996*b*, 1997), delineate a lagoonal environment with low mean annual sedimentation (<5 mm/year) during the formation of the *V. cornuvaccinum* lithosome at Keratovouno Hill. It was subjected to weak but probably directed (?tidal) currents in the shallow to middle subtidal, and protected from the surf of the open ocean by offshore shoals.

V. cornuvaccinum was, however, not restricted to such environments along the Pelagonian margin of Boeotia. Sclerochronological stable isotope analyses of an elongate specimen from Kalamos indicate regular vertical annual growth increments of *c.* 10 mm in the adult shell (Steuber 1996*b*). In contrast with the conditions at Keratovouno Hill, the shell was stabilized by continuously accumulating sediment so that rates of sediment supply must have been in the range of adult vertical growth. Such morphotypes probably lived together with elongated-conical morphotypes of *Radiolites subradiosus* Toucas with hardly any lateral projection of shell lamellae (Text-fig. 44) on the landward flanks of shoals with elevated sedimentation rates (Text-fig. 89).

Particularly large specimens of *V. cornuvaccinum* that formed monospecific pseudocolonies of conjoined elongated shells are abundant near Anthochorion. Mutual interaction during growth resulted in a pronounced variation of pillar morphology in these shells (Text-figs 59–60). Most RVs are coarsely ribbed, enhancing the frictional surface of the conjoined shells (Philip 1972).

The exposures near Anthochorion do not allow for a more detailed analyses of the life position of these morphotypes. The gregarious life habit could be the result of absent firm surfaces so that only adult shells were available for initial larval attachment. Competition could be expected to have resulted either in removal of the juvenile shells as at Keratovouno Hill, or in bouquets of laterally diverging shells (Gili *et al.* 1995; Skelton *et al.* 1995). Vertical growth in mutual contact could indicate dense associations with no space for lateral divergence. This implies favourable trophic conditions in well aerated water which agrees with the large size of the specimens. In such dense and to some extent self-stabilizing communities, rapid vertical growth was essential in competition with other individuals. Such communities probably thrived on turbulent areas of shoals (Philip 1972) and formed dense associations similar to the *Gorjanovicia* banks at Keratovouno Hill (Text-fig. 89).

The morphotypes of *V. cornuvaccinum* observed in different sedimentary environments document a remarkable adaptation to various rates of sedimentation and water agitation. Protected lagoonal soft bottoms, the landward flanks of shoals and probably their crests that were subjected to the surf of the open ocean were suitable for the establishment of dense associations (Text-fig. 89). A comparison of the diameters that were reached by shells from these different environment reveals interesting patterns (Text-fig. 68). Small diameters of RVs that were collected at Keratovouno Hill could be due to unfavourable trophic conditions. However, it seems more probable that imperfect conditions are related to the reclined life habit that was forced upon this typical elevator due to low ambient rates of sedimentation. This environment was tolerated, but the adaptation to a pseudocolonial life habit and rapid vertical growth was more efficiently expressed on shoals

(Anthochorion) and their landward flanks (Kalamos Hill), where higher rates of sedimentation stabilized the vertically growing shells.

Radiolitidae. Compact-shelled Radiolitidae (*Gorjanovicia*, *Fossulites*, *Medeella*; Steuber 1994) dominate on top of the lithosome with *Vaccinites cornuvaccinum* at Keratovouno Hill and produced reefoid mounds. Dense associations of vertically grown shells are embedded in coarse-grained, mechanically reworked, arenitic-ruditic rudist debris, indicating a turbulent environment exposed to the surf of the open ocean. These bouquets did not merge to stable barriers because binding and encrusting calcareous organisms were absent. Consequently, the radiolitid banks were formed by intermittent colonization and destruction, each colonization and establishment phase probably having lasted only a few years.

At other localities, various species of *Gorjanovicia* occur in similar environments. Slender morphotypes of *Gorjanovicia boeotica* Steuber, up to 200 mm long, which show several reorientations of the growth axis, grew on the thick coquinas near Dionysos. A specimen of *Gorjanovicia* cf. *costata* Polšak that was collected from a similar facies at Megali Lakka has been analysed by stable isotope sclerochronology (Steuber 1996*a*). It belonged to a group of slender morphotypes that grew on top of and between large, redeposited fragments of *Vaccinites*. Several adjacent individuals of approximately the same ontogenetic age reacted synchronously to perturbations that afforded a shift in direction of growth. Remarkably high annual growth increments of up to 54 mm indicate the effort to elevate the commissure rapidly from the bottom of this turbulent milieu, endangered by the sporadic input of coarse grained rudist debris. Relatively thick, compact outer shell layers and rapid vertical growth are necessary adaptations in such environments.

Other radiolitids are much less common in the Upper Santonian–Campanian of northern Boeotia and, therefore, do not allow for a well-founded reconstruction of their life habits and environmental preferences. The list of species of the Boeotian localities (Table 1) shows that *Vaccinites cornuvaccinum* occurs together with changing associations of radiolitids and plagioptychids that were more strictly bound to the prevailing environmental conditions. The landward slopes of shoals were inhabited with groups of *Radiolites subradiosus* Toucas and *Durania martellii* Parona. Both species reacted to changing sedimentation rates by the formation of either elongated or conical morphotypes, but formed only loose associations and did not merge to form pseudocolonies of conjoined shells.

Compact-shelled radiolitids of the genera *Gorjanovicia*, *Fossulites* and *Medeella* were particularly abundant in turbulent outer shelf environments exposed to the open ocean. This group has also been reported from oligotrophic and hypersaline intraplatform settings (Caminiti 1985; Cestari 1992*b*), but only redeposited shells have been found in near-shore, mixohaline environments of northern Boeotia.

PALAEOBIOGEOGRAPHY OF BOEOTIAN RUDISTS

Rudist occurrences in Greece

Rudist taxa that have hitherto been reported from Greece are listed in Table 21. In a previous review, Kühn (1948) was able to list only 12 species; even experienced authorities of the regional geology such as Renz and Philippson were apparently not aware of additional localities with determinable fossils (Kühn 1948, p. 169). Detailed studies of the regional geology by French geologists (Brunn 1956, northern Pindos Range, Macedonia; Aubouin 1959, northern Greece; Celet 1962, Parnassus Mountains; Mercier 1973, central Macedonia) confirmed the known localities and emphasized the widespread occurrence of rudist limestones, but only in a few cases described previously unknown material. Therefore, until 1985, only 37 per cent. of the species listed in Table 21 were known. Subsequently, descriptions of rudist occurrences of the Parnassus Mountains (Caminiti 1985), Vermion Mountains (Kollmann *et al.* 1985), Ionian Islands (Accordi *et al.* 1989) and Argolis (Mermighis 1989; Philip *et al.* 1989*b*; Mermighis *et al.* 1991) significantly improved the knowledge of Greek rudists. The present description of Boeotian rudists supplements these investigations so that the faunal inventory is now comparable to that of other Mediterranean regions.

Nevertheless, the Greek rudist associations are still imperfectly known for well-founded palaeobiogeographical analyses. Additional occurrences have been reported from several other regions (e.g. Vermion Mountains, Othrys Mountains, Klokova-Varassova Mountains), but their detailed investigations are still missing. The eastern margin of the Pelagonian micro-continent that faced the Cretaceous Axios Ocean is of special biogeographical importance, as it allows comparisons with the eastern European localities of Bulgaria and Romania. It is well exposed in the Vermion Mountains, but only a few localities have been studied (e.g. Kollmann *et al.* 1985).

For well-founded chorological studies, the present knowledge about stratigraphical and regional distributions of rudists is still imperfect in many other circum-Mediterranean areas (Gili *et al.* 1987). Major obstacles are the lack of a consistent taxonomy and imperfect chronostratigraphic correlations (Philip 1985). Therefore, a quantitative comparison of diversity patterns of the Greek rudist associations with those of other regions is considered to be premature.

Rudist occurrences in Argolis and Boeotia thrived on the western margin of the Pelagonian micro-continent, which bordered the Cretaceous Pindos Ocean in the east (Text-fig. 2A). The same palaeogeographical position is assumed for the Parnassus Platform during the late Cretaceous, while the rudist formations of the Ionian Island belong to the Apulian Plate and thus to the western coast of the Pindos Ocean (Praeapulian Zone). Therefore, it is not surprising that rudist associations of the external Hellenids have a strong affinity to those of southern Italy (Accordi *et al.* 1989), and biogeographical differences between the external Hellenids and the western Pelagonian margin were minor during the late Cretaceous: during the Cenomanian–early Turonian, 15 per cent. of all species known from Greece (Table 21) were restricted to the external Hellenids (Apulia); during the Santonian–Campanian this fraction amounts to 10 per cent., and only during the Maastrichtian, a larger fraction (38 per cent.) is known only from the external Hellenids. The higher diversity along the western Pindos coast of Apulia during the Maastrichtian was probably caused by environmental

TABLE 21. Compilation of rudist species known from Greece.

Aptian

Eoradiolites plicatus (Conrad)
Horiopleura cf. *baylei* (Coquand)
Horiopleura? *juxi* sp. nov.
Offneria italica Masse
O. nicolinae (Mainelli)
Pachytraga paradoxa (Pictet and Campiche)
Polyconites distefanoi Parona
Requienia ammonia (Goldfuß)
Toucasia carinata (Matheron)

Albian

Horiopleura lamberti Douvillé
Monopleura marcida White
Eoradiolites davidsoni (Hill)

Cenomanian–lower Turonian

Caprina adversa d'Orbigny
C. baylei (Gemmellaro)
C. schiosensis Boehm
Sphaerulites foliaceus Lamarck

middle Turonian–?Coniacian

Biradiolites angulosus d'Orbigny
Distefanella montagnei Slišković
D. raricostata Slišković
D. cf. *lombricalis* (d'Orbigny)
Durania martellii Parona
D. cf. *montisferrati* Astre
Lapeirousella aumalensis (Douvillé)
Praelapeirousia? sp. nov.
Praeradiolites ponsianus (d'Archiac)
P. cf. *urnalis* Astre
Radiolites lusitanicus (Bayle)
Radiolites peroni (Choffat)
Radiolites praegalloprovincialis Toucas
Radiolites sauvagesi (d'Hombres-Firmas)
Hippuritella resecta (Defrance)
Vaccinites grossouvrei (Douvillé)
V. inferus (Douvillé)
V. ljalintzensis Pamouktchiev
V. narentanus (Slišković)
V. praegiganteus (Toucas)

TABLE 21. Compilation of rudist species known from Greece (continued).

Neocaprina gigantea Pleničar
Neocaprina nanosi Pleničar
Orthoptychus striatus Futterer
Schiosia carinatoformis Polšak
Sphaerucaprina woodwardi Gemmellaro
Ichtyhosarcolites bicarinatus (Gemmellaro)
I. triangularis (Desmarest)
Distefanella douvillei Parona
Neoradiolites epidavricus Mermighis
N. helladensis Mermighis
N. kosjerici Pašić
N. majdanensis Pašić
N. pelagoniensis Mermighis
N. peloponnesiacus Mermighis
N. piadensis Mermighis
N. scrapensis Pašić
N. turonensis Pašić
Radiolites cremai Parona
R. radiosus d'Orbigny
Sauvagesia nicaisi (Coquand)
S. praesharpei Toucas
S. sharpei (Bayle)
S. villei (Toucas)
G. lipparinii Polšak
Lapeirousia zitteli Douville
Medeella zignana (Pirona)
Petkovicia? *verajana* Slišković
Praeradiolites echennensis Astre
Pseudopolyconites laskarevi Milovanović and Sladić

Ps. ovalis apuliensis Sladić-Trifunović and Campobasso
Radiolites angeiodes (Lapeirouse)
Radiolites galloprovincialis Matheron
Radiolites styriacus (Zittel)
Radiolites subradiosus Toucas
Rajka spinosa Milovanović
Sauvagesia meneghiniana (Pirona)
Sauvagesia tenuicostata Polšak
Hippuritella variabilis (Munier-Chalmas)
Hippurites cf. *canaliculatus* Rolland du Roquan
H. colliciatus Woodward
H. heritschi Kühn
H. socialis Douvillé
Pseudopironaea hellenica Lupu
Tetravaccinites macedoniensis Lupu
Vaccinites archiaci (Douvillé)
V. boehmi (Douvillé)
V. chaperi (Douvillé)
V. cornuvaccinum (Bronn)
V. douvillei (de Alessandri)
V. giganteus (d'Hombres-Firmas)
V. gosaviensis (Douvillé)
V. praepetrocoriensis (Toucas)
V. praesulcatus (Douvillé)
V. ptoonensis Steuber

Santonian–Campanian

Mitrocaprina bayani (Douvillé)
M. boeotica (Munier-Chalmas)
Plagioptychus aguilloni (d'Orbigny)
Sabinia aniensis Parona
Biradiolites angulosissimus Toucas
Bournonia africana Douvillé
B. fourtaui Douvillé
B. wiontzeki Pejović
Durania katzeri (Slišković)
Durania martellii Parona
Fossulites dionysii Steuber
Gorjanovicia boeotica Steuber
G. costata Polšak
G. gracilis (Wiontzek)
G. kayae Özer

V. inaequicostatus (Münster)
V. kuehni (Pejović)
V. oppeli (Douvillé)
V. praesulcatus (Douvillé)
V. salopeki (Polšak)
V. sulcatus (Defrance)
V. vesiculosus (Woodward)
V. vredenburgi (Kühn)

Maastrichtian

Mitrocaprina bulgarica Tzankov
Sabinia aniensis Parona
Bournonia dinarica Slišković
B. wiontzeki Pejović
Durania apula (Parona)
Joufia reticulata Boehm
Pseudopolyconites laskarevi Milovanović and Sladić
Ps. ovalis apuliensis Sladić-Trifunović and Milovanović

Radiolitella maestrichtiana Pejović
Radiolites angeiodes (Lapeirouse)
Rajka spinosa Milovanović
Hippuritella lapeirousei (Goldfuß)
Hippurites cornucopiae Defrance
H. colliciatus Woodward
H. heritschi Kühn
H. socialis Douvillé

differences. The carbonate platform at the western Pelagonian margin subsided rapidly and was dissected into horsts and grabens, reducing the environments suitable for the establishment of rudist communities, while the shelf of the Praeapulian Zone remained largely unaffected from such tectonic perturbations (Accordi *et al.* 1989).

The Pindos Ocean, consequently, did not act as a barrier for the dispersal of rudist taxa between the Apulian and Pelagonian platforms (Text-fig. 2A). The width and tectonic significance of the Pindos Ocean in the puzzle of eastern Mediterranean micro-continents is still debated (e.g. Robertson *et al.* 1991; Surmont *et al.* 1991; Thiébault *et al.* 1994), but it is well constrained that its northern termination was located near the palaeolatitude of the High Karst (Dercourt *et al.* 1986). In addition to transoceanic dispersal by planktic larvae, faunal migrations could, therefore, certainly have occurred along its northern coast.

Palaeobiogeographical relations

Until the Aptian, rudist associations were very similar on a global scale (Skelton 1982). A previously suggested southern Caribbean endemism of *Amphitriscoelus* Harris and Hodson during the Aptian (Masse 1987; Masse and Rossi 1987) appears to be more broadly Caribbean after discoveries of the genus in Mexico and Cuba (Pantoja-Alor *et al.* 1994; Rojas *et al.* 1996). Migrations into the Caribbean presumably occurred from the Mediterranean (Douvillé 1900*b*; Masse and Philip 1986) and were supported by westward surface currents in the central Tethys (Masse 1987; Barron and Peterson 1989).

The opening of the central Atlantic was linked to the shaping of an American (Caribbean) rudist province, and during the Albian a sharp increase in the number of endemic genera in the New World is noted (Coates 1973; Skelton 1982). Subsequently, the Caribbean province became more or less isolated, although sporadic migrations from the Mediterranean Tethys occurred (e.g. Hippuritidae, Skelton 1982). Only a few Caribbean genera (*Torreites* Palmer, *Thyrastylon* Chubb) succeeded in crossing the late Cretaceous Pacific. They reached Oman and Iran (Skelton 1988), but did not invade the Mediterranean Tethys.

Early Cretaceous. Not much is known about the oldest rudists from Greece (Baron-Szabo and Steuber 1996). However, they were presumably rather diverse, as *Glossomyophorus* sp., *Sellaea* sp., *Praecaprina* sp. (Masse 1985), *Retha* sp. (Combes *et al.* 1981), *Monopleura* sp. and *Himeraelites* spp. (Baron-Szabo and Steuber 1996) from the Aptian of the Parnassus Mountains have to be added to the species listed in Table 21. *Valletia* sp. and *Monopleura* sp. (Combes *et al.* 1981) from the Parnassus are probably of Valanginian age.

During the Aptian, a European and an African rudist province evolved in the Mediterranean Tethys (Masse 1985). However, radiolitid provincialism in the Mediterranean seems to be low or absent (Masse and Gallo Maresca 1997). Both the Parnassus platform and Apulia belong to the African province. Early Aptian caprotinids and Caprinidae found in xenoliths within Tertiary flysch-type deposits of the Parnassus platform have been attributed to the western Pelagonian margin, and show pronounced affinities with Apulian association (Baron-Szabo and Steuber 1996). Consequently, the provincialism was related to the barrier of the Pelagonian micro-continent, preventing dispersal to the north and north-east, and not to the deep basin of the Pindos Ocean. Provincialism faded during the Albian (Masse and Philip 1986), probably as a result of globally rising sea level. Among the Boeotian rudists, *Eoradiolites davidsoni* (Hill) is known from Texas, Somalia and Iran. The occurrence of *Monopleura marcida* White in the Mediterranean Tethys is not well documented.

Cenomanian–Early Turonian. While peri-Mediterranean regions are characterized by similar rudist associations, a central Mediterranean province with pronounced endemism began to take shape during the Cenomanian (Philip 1982*a*).

In contrast with Boeotia (Table 2), the associations of the external Hellenids, Parnassus platform and of Argolis are remarkably diverse (Table 21), and can be divided into three groups: *Caprina adversa* d'Orbigny, *Ichthyosarcolites* Desmarest, *Radiolites radiosus* Lamarck, *Sauvagesia* Choffat and *Sphaerulites* Lamarck were widely distributed in the Mediterranean Tethys. *Orthoptychus striatus* Futterer and *Sphaerucaprina* Gemmellaro are known only from the circum-Adriatic regions while *Caprina baylei* (Gemmellaro) and *Neocaprina* Pleničar occur also in the Taurid Mountains (Özer 1988*a*): *Neoradiolites* Milovanović was restricted to the Cenomanian of Greece and the Dinarids. The central Mediterranean province, consequently, comprised not only the Adriatic platforms, but extended across the Pindos Ocean to the western Pelagonian margin. Dispersal further to the north-east was apparently again inhibited by the emerged Pelagonian micro-continent because typical central Mediterranean taxa are missing in Bulgaria. It remains to be proven if this province extended into the still insufficiently studied Taurid Mountains.

The early Turonian was a crucial period for the development of carbonate platforms globally. An important sea level rise, linked to tectonic movements and increased terrigenous influx (Philip 1981), as well as perturbations in oceanic circulation (anoxic events) have been stressed as possible causes for the extinction of numerous rudist genera, among them all Caprinidae (Philip and Airaud-Crumiere 1991).

Cenomanian-Turonian boundary sections are not well exposed in Boeotia. At the Bay of Saltsas, a late Cenomanian–early Turonian succession of shallow marine limestones that pass into calcareous turbidites and finally pelagic biomicrites is exposed (Raeder 1994). In the Helicon Mountains, pelagic sedimentation lasted from the Turonian until the Coniacian (Konertz 1987). A pelagic episode and the interruption of rudist occurrences at the Cenomanian–Turonian transition was also reported from Argolis (Philip *et al.* 1989*b*). The coeval emersion of the Parnassus platform sharply contrasts with these regional facies patterns.

Late Turonian–Coniacian. During the mid Turonian, a re-establishment of rudist communities and the rapid dispersal of Hippuritidae was initiated. Hippuritidae subsequently dominated many rudist associations until the Maastrichtian. Their sudden appearance in the Lower Turonian (Philip 1978), connected to fundamental morphofunctional innovations, is one of the most fascinating events in the phylogeny of rudists.

Almost all Turonian species that are known from Greece have been found at Marmeko quarry. This is a good example of how insecure the quantification of diversity of Greek rudist associations still is, as the faunal composition of a single locality can considerably change the known distribution patterns. The highly diverse association of Marmeko comprises species which are widely distributed in the circum-Mediterranean region and extend as far as Caucasus; this applies also to much less diverse associations of Megara (Mitzopoulos and Kühn 1963) and Argolis (Philip *et al.* 1989*b*). In contrast, *Distefanella montagnei* Slišković and *D. raricostata* Slišković that have been reported from the Parnassus platform (Combes *et al.* 1981) are restricted to the central Mediterranean.

The diversity of the Turonian rudists from Greece is similar to that of the external Dinarids (Polšak *et al.* 1982), but higher when compared with the Adriatic platforms of the Apennines (Pons and Sirna 1992). Greek associations are similar to those of the western Mediterranean, whilst various species of *Distefanella* Parona dominate in the Apennines and external Dinarids.

The most diverse Coniacian and Lower Santonian rudist associations are known from the classical areas of rudist research in southern France and the Pyrenees. Both on the Ebro High and in Provence, they formed in a transitional belt of siliciclastic and calcareous sedimentary environments (Philip 1974; Pons and Sirna 1992). On the intra-oceanic platforms of the Apennines (Pons and Sirna 1992), in the external Dinarids, and on the Pelagonian margin, regressions and emersions restricted the rudist habitats during this time. There are no safe records of Coniacian–Lower Santonian rudists in Greece.

Santonian–early Campanian. During the late Santonian–early Campanian, the diversity of rudist associations reached its maximum in Spain and Italy (Pons and Sirna 1992). This correlates with a global rise of sea level and a relative highstand during the Campanian. The western Mediterranean faunas differ significantly from those of the central Mediterranean so that provincialism, which was almost absent during the Turonian, is again accentuated during the Santonian–Campanian. The previously diminished diversity in central Mediterranean regions must have increased due to migrations from eastern regions, as the western Mediterranean associations appear to have developed rather independently (Pons and Sirna 1992).

The Greek associations show strong affinities to those of the external Dinarids and of the Alpine Gosau. Slightly lower similarity exists to the platforms of the Apennines. The presence of *Mitrocaprina bayani* (Douvillé), *Vaccinites giganteus* (d'Hombres-Firmas), *Hippuritella variabilis* (Munier-Chalmas), *Hippurites* cf. *canaliculatus* Rolland du Roquan in Boeotia, and *V. archiaci* (Douvillé) in the Vermion Mountains indicates a faunal exchange with the western Mediterranean.

It has been previously mentioned that coeval rudist associations of northern Boeotia and Paleokastron Hill differ significantly. Both have central Mediterranean affinities but share not a single species. An association similar to that found at Paleokastron has been reported from the Vermion Mountains (Mitzopoulos 1959; Kollmann *et al.* 1985) and from Argolis (Philip *et al.* 1989*b*). It is also widely distributed in the Alps as well as in the external and internal Dinarids (Milovanović 1934, 1960; Pašić 1957; Polšak 1967*b*) and is generally referred to as a Gosau-type association. It commonly co-occurs with corals and gastropods in marginal marine environments with a prominent influx of siliciclastics (Zapfe 1937). The northern Boeotian associations, dominated by *Vaccinites cornuvaccinum* (Bronn), in contrast, established only when salinity remained stable and the input of terrigenous clastics had ceased (see above). The absence or restricted distribution of typical species of the Gosau-type association on the platforms of the Apennines and Apulia, therefore, is presumably related rather to environmental conditions and not to biogeographical isolation, as the preferred environments in the transitional belt of siliciclastic and calcareous sedimentation was not available on the central and southern Italian intra-oceanic platforms.

Upper Campanian–Maastrichtian. Incipient crustal movements that were related to the final closure of Tethys induced significant changes in the peri-Mediterranean depositional environments. Regressions and the concurrent loss of suitable habitats impoverished the endemic associations of the Pyrenees (Philip 1985), and emersions terminated the development of rudist formations on the platforms of the Apennines (Pons and Sirna 1992). On the other hand, typical central Mediterranean species occurred in southern Spain (*Pironaea* Meneghini, *Vaccinites ultimus* (Milovanović)), and species-rich associations of apparently highly specialized rudists developed in Arabia, the internal Dinarids, Anatolia, as well as on the Apulian and northern Adriatic platforms ('*Pironaea-Pseudopolyconites*-Senonian', Sladić-Trifunović 1989). The origin of these genera and their migration paths are problematical, because most of them cannot be attributed to phylogenetic lineages of the central Mediterranean. Apparently, they invaded the region from the east and spread as far as southern Spain (Philip 1985).

For several of the latest Cretaceous species listed in Table 21, it is questionable if their stratigraphical range actually extended into the Maastrichtian. Independent biostratigraphical evidence exists in the cases of *Hippurites cornucopiae* Defrance and *Hippuritella lapeirousei* (Goldfuß) from Boeotia. Both were widely distributed in the entire Mediterranean region, and *H. lapeirousei* extended even into the endemic province of the Pyrenees and the Boreal Realm. A Maastrichtian age is also well-founded for *Sabinia* sp., *Hippurites heritschi* Kühn, *Pseudopolyconites laskarevi* Milovanović and *Bournonia dinarica* Sliskovic from the Parnassus Mountains (Caminiti 1985). In summary, rudists are sparsely distributed in the uppermost Cretaceous of Greece. In Boeotia, the Pelagonian platform was tectonically dissected, and pelagic limestones were deposited. Similar conditions have been reported from Argolis (Philip *et al.* 1989*b*) Depositional environments in the Vermion Mountains varied considerably over short distances (Mercier 1973): Near Grammatiko, Maastrichtian flysch-type deposits follow over pelagic limestones, whereas a few kilometres to the north, at Tsouka Mountain (Text-fig. 4B), Maastrichtian limestones follow transgressively over the metamorphic basement. My own field studies proved the presence of *Hippuritella lapeirousei*, *Hippurites cornucopiae* and *Bournonia* sp. in these Maastrichtian limestones. The record of *Pironaea* sp. (Mercier 1973) in Macedonia is particularly noteworthy. This genus is widely distributed in the uppermost Cretaceous of almost the complete Mediterranean region, but seems to be absent from Greece. The specimen mentioned by Mercier (1973) and indicated as an index fossil on the official geological maps of the region is a single fragment found in conglomeratic limestones, and is now lost (Mercier, pers. comm. 1994). According to current knowledge, the distribution of highly specialized rudists of the uppermost Cretaceous of the Pelagonian is thus restricted to the Parnassus platform. The sparse distribution of the '*Pironaea-Pseudopolyconites*-Senonian' is attributed to the prevailing pelagic environments that dominated on the

Pelagonian during its acme in the late Campanian (Swinburne *et al.* 1992), as the association was apparently not restricted to a certain shallow-marine environment (Sladić-Trifunović 1989).

During the late Maastrichtian, the disappearance of the rudists from the platforms of the Mediterranean region occurred gradually (Philip 1985), and was almost everywhere related to a drastic deepening of depositional environments or the onset of terrigenous or flysch-type sedimentation. These tectonic movements that culminated in pronounced palaeogeographical changes during the Cretaceous–Tertiary transition, successively restricted the rudist habitats and were certainly a major reason for the extinction of the group that was already considerably reduced in diversity in the mid Maastrichtian.

Acknowledgements. This monograph is part of a habilitation thesis which was prepared during an assistant professorship at the Chair of Palaeontology at the University of Cologne. I am indebted to Prof. U. Jux for his guidance, encouragement and many helpful suggestions. I thank the following persons who helped with advice on locating material and rudist occurrences, or with fruitful discussions: Prof. G. Eleftheriadis (Thessaloniki), Prof. I. Gedik (Trabzon), Prof. E. K. Kempf (Cologne), Dr D. Lupu (Bukarest), Prof. J. Mercier (Paris), Prof. J. M. Pons (Barcelona), Prof. D. Schumann (Darmstadt), Dr I. Sharp (Edinburgh), Dr P. W. Skelton (Milton Keynes), Dr V. Tselepidis (Athens) and Prof. H. Wopfner (Cologne). Field work in Greece was only possible with the kind support of the Directors Dr B. Andronopoulos, Dr C. Katagas, Prof. I. Mariolakos and G. Traganos of the Institute of Geology and Mineral Exploration (I.G.M.E), Athens, which is gratefully acknowledged. Several field seasons were shared with Dr P. Aslanidis, Dr M. Raeder and Dr J. Walter, whose help and lively discussions were greatly appreciated. I am most grateful to Dr Helms (Berlin), Prof. R. Höfling (Munich, now Erlangen), Dr D. Pajaud (Paris), Dr A. Prieur (Lyon) and Dr M. Sander (Bonn) for providing access to and information about the collections in their care. I further thank Mrs C. Krings for her careful work on many figures and Mrs K. Nengelken for her help with the photography. Dr P. W. Skelton and Dr J.-P. Masse provided valuable comments on the manuscript.

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Typescript received 10 April 1997
Revised typescript received 7 September 1998