Cretaceous rudists of Boeotia, central Greece
CRETAEOUS RUDISTS OF BOEOTIA, CENTRAL GREECE

BY

THOMAS STEUBER

with 26 plates, 21 tables and 90 text-figures
# CONTENTS

<table>
<thead>
<tr>
<th>ABSTRACT</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>5</td>
</tr>
<tr>
<td>CRETACEOUS STRATIGRAPHY AND PALAEOGEOGRAPHY OF BOEOTIA</td>
<td>5</td>
</tr>
<tr>
<td>RUDIST LOCALITIES AND BIOSTRATIGRAPHY</td>
<td>10</td>
</tr>
<tr>
<td>Aptian</td>
<td>11</td>
</tr>
<tr>
<td>Albian</td>
<td>11</td>
</tr>
<tr>
<td>Cenomanian</td>
<td>13</td>
</tr>
<tr>
<td>Middle Turonian—?Coniacian</td>
<td>13</td>
</tr>
<tr>
<td>Santonian—Campanian</td>
<td>14</td>
</tr>
<tr>
<td>Maastrichtian</td>
<td>17</td>
</tr>
<tr>
<td>Rudist coenozones in Boeotia</td>
<td>17</td>
</tr>
<tr>
<td>Rudist localities in the Vermion Mountains (Macedonia)</td>
<td>17</td>
</tr>
<tr>
<td>TAXONOMY</td>
<td>21</td>
</tr>
<tr>
<td>Phylogeny and terminology</td>
<td>21</td>
</tr>
<tr>
<td>Morphometric analysis of Hippuritidae</td>
<td>29</td>
</tr>
<tr>
<td>SYSTEMATIC PALAEONTOLOGY</td>
<td>34</td>
</tr>
<tr>
<td>Family Polyconitidae Mac Gillavry, 1937</td>
<td>34</td>
</tr>
<tr>
<td>Genus <em>Horiopleura</em> Douvillé, 1889</td>
<td>34</td>
</tr>
<tr>
<td>Family Monopleuridae Munier-Chalmas, 1873</td>
<td>41</td>
</tr>
<tr>
<td>Genus <em>Monopleura</em> Matheron, 1842</td>
<td>41</td>
</tr>
<tr>
<td>Family Caprinidae d’Orbigny, 1847</td>
<td>42</td>
</tr>
<tr>
<td>Genus <em>Caprina</em> d’Orbigny, 1822</td>
<td>42</td>
</tr>
<tr>
<td>Genus <em>Sphaerucaprina</em> Gemmellaro, 1865</td>
<td>44</td>
</tr>
<tr>
<td>Family Plagioptychidae Douvillé, 1888b</td>
<td>46</td>
</tr>
<tr>
<td>Genus <em>Mitrocaprina</em> Boehm, 1895</td>
<td>46</td>
</tr>
<tr>
<td>Family Radiolitidae d’Orbigny, 1847</td>
<td>51</td>
</tr>
<tr>
<td>Genus <em>Biradiolites</em> d’Orbigny, 1850</td>
<td>51</td>
</tr>
<tr>
<td>Genus <em>Bournonia</em> Fischer, 1887</td>
<td>54</td>
</tr>
<tr>
<td>Genus <em>Durania</em> Douvillé, 1908b</td>
<td>57</td>
</tr>
<tr>
<td>Genus <em>Eoradiolites</em> Douvillé, 1909</td>
<td>65</td>
</tr>
<tr>
<td>Genus <em>Fossulites</em> Astre, 1957b</td>
<td>72</td>
</tr>
<tr>
<td>Genus <em>Gorjanovicia</em> Polšak, 1967b</td>
<td>72</td>
</tr>
<tr>
<td>Genus <em>Lapeirrousella</em> Milovanović, 1938a</td>
<td>74</td>
</tr>
<tr>
<td>Genus <em>Medeella</em> Parona, 1924</td>
<td>81</td>
</tr>
<tr>
<td>Genus <em>Petkovicia</em> Kühn and Pejović, 1959</td>
<td>83</td>
</tr>
<tr>
<td>Genus <em>Praelapeirousia</em> Wiontzek, 1934</td>
<td>87</td>
</tr>
<tr>
<td>Genus <em>Praeradiolites</em> Douvillé, 1902</td>
<td>88</td>
</tr>
<tr>
<td>Genus <em>Radiolites</em> Lamarck, 1801</td>
<td>92</td>
</tr>
<tr>
<td>Genus <em>Sauvagesia</em> Choffat, 1886</td>
<td>112</td>
</tr>
<tr>
<td>Family Hippuritidae Gray, 1848</td>
<td>116</td>
</tr>
<tr>
<td>Genus <em>Hippuritella</em> Douvillé, 1908a</td>
<td>116</td>
</tr>
</tbody>
</table>
Genus Hippurites Lamarck, 1801
Genus Vaccinoides Fischer, 1887

Santonian–Campanian Rudist Formations of Northern Boeotia

Sections
Facies successions
Patterns of establishment and growth fabrics

Palaeobiogeography of Boeotian Rudists
Rudist occurrences in Greece
Palaeobiogeographical relations

Acknowledgements
References
ABSTRACT. Diverse rudist associations were widely distributed on the western margin of the Pelagonian microcontinent, now exposed in Boeotia, during the late Cretaceous, while only few caprotnid 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. *Praelepeirousia?* 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 Plagiopychidae 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 (1892a, 1895, 1897a) 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.* 1989b; 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 1931b; 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 teckonostratigraphical 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.

**CRETAEOUS STRATIGRAPHY AND PALEOGEOGRAPHY 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).
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 Eoothellenian 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 serpentinitized ‘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 Albion, rudists, with almost all families, are recognized as dominant constituents of such thin limestone intercalations.

Clastiferous 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 1931b; 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
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 Alban–Turonian, are indicated by intercalated bauxites. This intra-oceanic platform was left unaffected by elastic 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 thrust 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. 1970a) 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 1993a (Turonian hirudinids), Raeder 1994 (Lower Cretaceous–Cenomanian), Steuber 1994 (Santonian–Campanian radioïds), 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 syncology 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., *Troccholina* cf. *aptiensis* Iovcheva, *Coscinophragma cribrosum* (Reuss), *Cylindroporella* cf. *elizae* Bakalova, and *Triplopora 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 caprotimid 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 orbitolind 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 orbitolind 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*) *subconca* Leymerie, *Simplorbitolina conulus* Schroeder and *Pseudocyclammina hedbergi* Mayne, 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 pyritic 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., *Neoptyx incavata* (Bromm), *Neoptyx symeonidisi* Kollmann and *Paraglaucoria lujani* (Verneuil).

The latter horizon is overlain by ophiolitic conglomerates and marls with orbitolind foraminifera. The same species as at Analipsis indicate an early to mid Albian age (Raeder 1994). Above these orbitolind-bearing marls, an up to 0.5 m high biostrome of *Monopleura marcidia* 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 orbitolind 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, biothermal 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 (*Horiopeura* 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 Eoheleanian basement. Large bioclasts are almost exclusively remnants of caprinid shells. Among them are a few complete left valves of *Caprina baylei* (Gemellaro) and *Sphaerucaprina woodwardi* Gemellaro 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 laterite 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 1931b).

A 70 m thick sequence has been studied in the Marmeko quarry on the slope of Tsekiourei 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 aumaensis* (Douvillé), *Praelapeiroisia?* 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* Pamoukitchiev, *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 aumaensis* and *Praelapeiroisia?* 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 coenosteae, 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 1982b; Philip 1982b). 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. sauvegesi) 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 Guinet 1968): Aeoliosaccus kotori Radojičić, Neondotheia apenninica De Castro, Barkerina spp., Minouxia spp., Cuneolina ex gr. pavonia d’Orbigny, Discyclina ex gr. schlumbergeri Munier-Chalmas, Tetramouxiella 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 ecozones (Santonian–early Campanian and late Campanian–Maastrichtian; Polšák 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 cornu vaccinum (Bronn) is accompanied by changing radiolitid communities. Only to the east, at Tsouka Hill, is V. cornu vaccinum replaced by V. chaperi (Douvillé). It is shown in the taxonomic part of this monograph that V. chaperi was anagenetically derived from V. cornu vaccinum. 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 Loutson whilst other radiolitids which are abundant further to the west are missing. S. meneghiniana is the only species which occurs with either V. cornu vaccinum (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>
<thead>
<tr>
<th></th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mitrocaprina boeotica</em> (Munier-Chalmas)</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bourbonia africana</em> Douvillé</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Durania kateri</em> (Slišković)</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. martellii</em> Parona</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fossulites dionysii</em> Steuber</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>F. aff. undaealtus</em> (Astre)</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gorjanovicia boeotica</em> Steuber</td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. costata</em> Polšak</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. gracilis</em> (Wiontze)</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. kaya</em> Özer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. lipparini</em> Polšak</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gorjanovicia</em> sp.</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hippuritella variabilis</em> (Mun.-Chal.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Medellia</em> cf. <em>zignana</em> (Pirona)</td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Petkovicia</em> verrajana Slišković</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Praruadiolites echemensis</em> Astre</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Radiolites subradiolus</em> Toucas</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sauvagesia meneghiniana</em> (Pirona)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. tenuiocastata</em> Polšak</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Vacucites cornucucumin</em> (Iron)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>V. chaperi</em> (Douvillé)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

Bay of Salthas (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 isoclinic 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 Salthas, 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), *Vacucites boehmi* (Douvillé) and *V. cornucucumin* (Iron). Most shells are more or less strongly bioereoded and encrusted, and complete valves are rare. Ipprinent 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): *Globotruncanina linnetiana* (d’Orbigny), *G. ventricosa* White, *Globotruncanita stuartiformis* (Dalbiez) and *Rosita fornicate* (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. 3b). 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)* *subconcaua* Leymerie. Large bioclasts of colonial corals, immersed by numerous calcareous algae, fragments of sponges (*Acanthochaetes* 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 ricinensis (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 anegioides (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), Heliaestra sp., Mycetophyllopsis antiqua (Reuss), Pachygyra bellula Hackemesser, Phyllocoenia toucasi (Fromental) and Phyllocoenia sp. (Abdel-Gawad and Gameil 1995); and determinations by H. Löser, Dresden).

Only R. angeioides 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, biomigmatic limestones with Lower and ‘middle’ Maastrichtian planktic foraminifera (Robaszynski et al. 1984; Steuber et al. 1997): Gansserina cf. gansseri (Bolli), Globotruncanca arca (Cushman), Globotruncanca linneiana (d’Orbigny), Globotruncanca cf. ventricosa White, Globotruncanca cf. stuartiformis (Dalbiez) and Rostia 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 extracasts 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 coenozoic (sensu Pölšak 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* (Douville) 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* (Douville) and *V. vesiculosus* (Woodward).

*Maastrichtian*

*Aakraifion (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 i993). In contrast with the deepening of depositional environments on the distal Pelagonian platform, conglomeratic limestones with echinodermats and orbitoid foraminifera indicate periods of littoral redeposition on the proximal Pelagonian platform in northern Boeotia. A palæokarst 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 Aakraifion village, 30 m below the Cretaceous-Tertiary boundary. *Hippuritella lapeirootse* (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 lapeirootse* (Goldfuß) is conformably overlain by micritic limestones with planktic foraminifera of the ‘middle’ Maastrichtian *Gansserina gansseri*-zone (Robaszynski et al. 1984): *Gansserina gansseri* (Bolli), *Globotruncanca arca* (Cushman), *Globotruncanella falsostuartii* 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 (eb) 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 (ea, ec) is indicated by the anagenetic lineage *Vaccinites cornuvaccinum* (Bromn)—*V. chaperi* (Douville) and by different radiolitid associations.

Although not a single species is shared by the associations ea and eb, 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.**

<table>
<thead>
<tr>
<th>Stage</th>
<th>Coenozone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aptian</td>
<td>Horiopleura? juxi sp. nov.</td>
</tr>
<tr>
<td>Albian</td>
<td>Horiopleura lamberti Douvillé</td>
</tr>
<tr>
<td></td>
<td>Monopleura marcida White</td>
</tr>
<tr>
<td></td>
<td>Eoradiolites davidsoni (Hill)</td>
</tr>
<tr>
<td></td>
<td>Eoradiolites sp.</td>
</tr>
<tr>
<td>Cenomanian</td>
<td>Caprina baylei (Gemmellaro)</td>
</tr>
<tr>
<td></td>
<td>Sphaerocaprina woodwardi Gemmellaro</td>
</tr>
<tr>
<td>Middle Turonian - ?Coniacian</td>
<td>Durania cf. montisferrati Astre</td>
</tr>
<tr>
<td></td>
<td>Lapeirousella aqualensis (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Praealpeirousia? sp. nov.</td>
</tr>
<tr>
<td></td>
<td>Praealpeirousia? sp. nov.</td>
</tr>
<tr>
<td></td>
<td>Radiolites lusitanicus (Bayle)</td>
</tr>
<tr>
<td></td>
<td>Radiolites praegalloprovincialis Toucas</td>
</tr>
<tr>
<td></td>
<td>Radiolites sauvesi (d’Hombres-Firmas)</td>
</tr>
<tr>
<td></td>
<td>Hippuritella resecta (Defrance)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites cf. grossouvrei (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites inferus (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites ljalinzensis Pamouktsiev</td>
</tr>
<tr>
<td></td>
<td>Vaccinites praegiganteus (Toucas)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites praepetrocruensis (Toucas)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites ptoonensis Steuber</td>
</tr>
<tr>
<td>Santonian-Campanian</td>
<td>b) Mitrocaprina bayani (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Radiolites angeiodes (Lapeirouse)</td>
</tr>
<tr>
<td></td>
<td>Hippurites cf. canaliculatus Rolland du Roquan</td>
</tr>
<tr>
<td></td>
<td>Hippurites colliciatus Woodward</td>
</tr>
<tr>
<td></td>
<td>Vaccinites boehni (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites aff. corruvaccinum (Bromn)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites giganteus (d’Hombres-Firmas)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites inaequicostatus (Münster)</td>
</tr>
<tr>
<td></td>
<td>Vaccinite kuehni (Pejovic)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites praesulcatus (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites salopeki (Polšak)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites sulcatus (Defrance)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites vredenburgi (Kühn)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites sp.</td>
</tr>
<tr>
<td>a)</td>
<td>Petkovicia? varjana Slišković</td>
</tr>
<tr>
<td></td>
<td>Sauvagesia meneghiniana (Pirona)</td>
</tr>
<tr>
<td></td>
<td>Hippuritella variabilis (Munier-Chalmas)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites chaperi (Douvillé)</td>
</tr>
<tr>
<td></td>
<td>Vaccinites vesticulosus (Woodward)</td>
</tr>
<tr>
<td>(Mu) Maastrichtian</td>
<td>(μ) Maastrichtian</td>
</tr>
<tr>
<td></td>
<td>Hippurites cornucopiæ Defrance</td>
</tr>
<tr>
<td></td>
<td>Hippuritella laperousei (Goldfuß)</td>
</tr>
</tbody>
</table>

(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 Vernon 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 Mouskaremí 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 Mouskaremí 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): Columnocenia sp., Cunolites (Paracumnolites) scutellum (Reuss), Fungiastrea cf. conferta (Milne-Edwards and Haimé), Glyphophyllia crassisepta Hackemesser, Nefophyllia sp., Phyllocenia corollaris (Reuss), Phyllosmilia aegiale Felix, Placosmilopsis sp. and Pseudocumnolites sp.

Impure limestones above contain Cunolites, abundant debris of radiolitid shells and numerous bivalved specimens of Vaccinides chaperi (Douville) 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 corallineacean 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 omph'; (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 overlies 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. 4p). These bioturbated bimicrites 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 Vacciniites chaperi (Douville) and V. archiaci (Douville). 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.

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

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 (Douville) is restricted to the coenozoic sc in Boeotia. The association with V. archiaci (Douville) 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 coenozoic.

TAXONOMY

Phylogeny and terminology

Hippuritoida 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 Hippuritoida 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

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 Requieniaeae Douville, 1915c. Only a few taxonomists (e.g. Masse and Philip 1986; Mainelli 1992b) have followed the proposition to discriminate two suborders, Sinistrodonta P減intcev, 1959 and Dextrodon+ P減intcev, 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 paraplyetic 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 myocardinial 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 Caprinidae d’Orbigny, 1847. In Retha Cox, 1965 which is considered to be ancestral within the Coalcomaninidae Coogan 1973, mp’ retained its position close to the posterior shell wall (Skelton and Masse 1998). Similar to the conditions in the Caprinidae, in more evolved forms of the Coalcomanidae which are restricted to the New World, an erect myocardinial 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 Hippuritoidae (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 Polycomitidae 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 myocardinial 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 CaCO₃, 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
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 ultrastructures as in the Hippuritidae. Compact structures commonly occur in thin-shelled, elongate morphotypes and reflect rapid vertical shell accretion (Cestari 1992a; Steuber 1996a).

Particular attention is generally given to structural modifications along the posterovertral 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.
of the rest of the shell. Radial bands in several caprothin 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 1979a).

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 1938a; Astre 1957b). To the exterior, they are
demarcated by steeply erected funnel plates that are emplaced 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 rooted 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 commisurally. 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, 1968b; Text-fig. 36c). In more advanced forms, the infoldings became continuously more erect (Thyraysterion 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 1979a), 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 aualensis (Douville, 1915b) and Praepaelapousia? sp. nov. Faint pseudopillars have been reported even from late Apterian eoepilamellids (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
compact aragonite but are stiffened by ledges that enclose hollow spaces (Klinghardt 1931). Canalicate 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 1969b) 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 values 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 1933a; 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. Pironaeca 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
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, 1979b), 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
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, 1908a).

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 1992a). 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 (Skeiiton and Wright 1987; Steuber 1993a), 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 (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
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 (Douville 1910; Philip 1981), but this morphogenetic evolution has been quantified only in a few cases (Steuber 1993a). Although rarely evident by visual inspection (e.g. Pl. 24, fig. 5), it can be shown that the ratio U/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. 12. Explanation of U/P0—P2-diagrams with examples of the ontogeny of one RV, respectively, of (dots) Vaccinum chaperi (Douville, 1897a), (crosses) V. inaequicostatus (Münster, in Goldfuß, 1840) and (boxes) V. vesiculosus (Woodward, 1855).
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 (Brön, 1831) or V. chaperi (Douville, 1897a), and less distinct in species in which the pillars are distributed around the postero-dorsal quarter of the shell such as V. vesiculosus (Woodward, 1855) or V. inaequicostus (Münster, in Goldfuß 1840). All measurements converge with decreasing length of the contour (U) to a ratio of \( U/P_0-P_2 \approx 4 \) (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 cornuacuminum* (Bromm, 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 (P0–P2cont). 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 cornuacuminum*, 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 1982c). It can only be reliably determined on RVs with a straight P0 (Skelton and Wright 1987; Steuber 1993a), 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).


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 Douville, 1889

Type species. Horiopleura Lamberti Douville, 1889.

_Horiopleura lamberti_ Douville, 1889

Text-figures 16–17

1867 Monopleura Lamberti Mun. Ch. in litt.; Hébert, p. 330 [nomen nudum].
1888a Horiopleura Lamberti; Douville, p. 233 [nomen nudum].
1882 Oriopleura Lamberti M.-Ch.; Lacovier, p. 539 [nomen nudum].
1888 H. Lamberti M.-Ch.; Munier-Chalmas, p. 819 [nomen nudum].
*1889 Horiopleura Lamberti Mun.-Ch.; Douville, p. 639, pl. 16, figs 1–4.
1890 Horiopleura Lamberti Munier-Chalmas; Seunes, p. 269.
1892b Hor. Lamberti; Douville, p. 80.
1898a Horiopleura Lamberti? M.-Ch.; Douville, p. 147.
1905 H. Lamberti Mun.-Chalm. in Douville; Péquier, 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 Douville; 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.
1979 H. lamberti; Masse, p. 280.
1979 Horiopleura lamberti; Peybernès, text-fig. 1.
1986 H. lamberti; Skelton, in Pudey 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 lamberi* 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. M1a is slightly inclined towards the body-cavity and separated by a narrow furrow from (1). M1p 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. M1p 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 myocardial 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 Horiopterus? 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 sub-rectangular 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 diagnostically 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
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 caprotnid 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? juxii* 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? juxii* 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

<table>
<thead>
<tr>
<th>Year</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1884</td>
<td><em>Monopleura marcida</em> sp. nov. White, p. 96, pl. 3, figs 1–10; pl. 4, figs 1–9.</td>
</tr>
<tr>
<td>1889</td>
<td><em>Monopleura marcida</em> White; Roemer, p. 288, pl. 33, fig. 1a–d.</td>
</tr>
<tr>
<td>1901</td>
<td><em>Monopleura marcida</em>; Hill, p. 240, pl. 33, fig. 2.</td>
</tr>
<tr>
<td>1901</td>
<td><em>Monopleura marcida</em> White; Schnarrenberger, p. 200, pl. 3, fig. 2a–c [=?Monopleura Schnarrenbergeri Parona, 1909, p. 36].</td>
</tr>
<tr>
<td>1909</td>
<td><em>Monopleura marcida</em>; Grabau and Shimer, p. 548, text-fig. 751c–d.</td>
</tr>
<tr>
<td>1918</td>
<td><em>Monopleura marcida</em> White; Douvillé, p. 12, text-figs 3–5.</td>
</tr>
<tr>
<td>1927</td>
<td><em>Monopleura marcida</em> White; Scott, p. 252.</td>
</tr>
<tr>
<td>1928</td>
<td><em>Monopleura marcida</em> White; Adkins, p. 144, pl. 2, fig. 4.</td>
</tr>
<tr>
<td>1928a</td>
<td><em>Monopleura marcida</em> White; Klinghardt, pl. 24, fig. 7 [cop. Roemer 1889].</td>
</tr>
<tr>
<td>1929</td>
<td><em>Monopleura marcida</em> White; Klinghardt, p. 178, pl. 16, fig. 9.</td>
</tr>
<tr>
<td>1934</td>
<td><em>Monopleura marcida</em> White; Kutassy, p. 117 [with synonymy].</td>
</tr>
<tr>
<td>1977</td>
<td><em>Monopleura marcida</em> White; Coogan, p. 39, pl. 2, figs 1–2 [cop. White 1884], figs 3–4, 6.</td>
</tr>
<tr>
<td>1979b</td>
<td><em>Monopleura marcida</em> White; Skelton, pl. 2, figs 2–3, 5 [=Monopleura pinguiscula White; P. Skelton, pers. comm. 1997].</td>
</tr>
<tr>
<td>1981</td>
<td><em>Monopleura cf. M. marcida</em> White; Scott, p. 471, text-fig. 4a–c.</td>
</tr>
<tr>
<td>1990</td>
<td><em>Monopleura marcida</em> White; Yanin, tab. 1.</td>
</tr>
</tbody>
</table>

**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 ligamentary 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 Albion 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 rouselli* (Toucas, 1907) in the Albion of the Apennines.

Family **Caprinidae** d’Orbigny, 1847

Genus **Caprina** d’Orbigny, 1822

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

**Caprina baiyeli** (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.
1892a Schiosia carinata, n. sp? Boehm, p. 146, pl. 9, figs 1–2.
p1892 Cornucaprina carinata Böhm; Futterer, p. 87.
p1895 Caprina schiosensis Böhm; Boehm, p. 122.
1897b Caprina schiosensis var. carinata; Douvillé, p. 161.
1908a 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.
1965a Caprina carinata Boehm; Polšak, p. 431.
1967 Caprina carinata Boehm; Pleničar and Buser, p. 152.
1967b 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.
1988a Caprina cf. carinata (Boehm); Özer, p. 162, pl. 1, fig. 7; text-fig. 4.
1989b Caprina carinata; Čestari and Sirna, tab. 1.
1992a Caprina carinata Boehm; Mainelli, p. 79.
1993 Caprina carinata Böhm [sic]; Cherci et al., text-fig. 2.
1993 Caprina carinata Böhm [sic]; Ruberti, p. 959.
1996 Caprina baiyeli (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.
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 anterioventral 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, 1892a is the ventral carina. Boehm (1892a) 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 (1908a) 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 Woodwardi* Gemmellaro, 1865.

*Sphaerucaprina woodwardi* Gemmellaro, 1865

Text-figure 23

*1865 Sphaerucaprina Woodwardi* Gemmellaro, p. 222, pl. 1, figs 1–5.
*1892a Sphaerucaprina forojulienis* n. sp. Boehm, p. 142, pl. 6, fig. 1; text-fig. 2.
*1892a Sphaerucaprina?;* Boehm, p. 143, text-fig. 3.
*1895 Sphaerucaprina forojulienis*; Boehm, p. 127, text-fig. 5 [cop. Boehm 1892a].
*1895 Sphaerucaprina sp.;* Boehm, p. 128, text-fig. 21 [cop. Boehm 1892a].
*1897b Sphaerucaprina forojulienis*; Douvillé, p. 162.
*1908a Sphaerucaprina forojulienis* Boehm; Parona, p. 344, text-fig. 30a–b.
*1922 Sphaerucaprina woodwardi* Gemm.; Harris and Hodson, pl. 5, figs 10–11 [cop. Douvillé 1910].
*1934 Sphaerucaprina forojulienis* Boehm; Kutassy, p. 156 [with synonymy].
*1934 Sphaerucaprina woodwardi* Gemm.; Kutassy, p. 157 [with synonymy].
*1937 Sphaerucaprina woodwardi* Gemm.; Mac Gillavry, pl. 6, fig. 21le [cop. Douvillé 1910].
*1963 Sphaerucaprina forojulienis* Boehm; Pleničar, p. 574, pl. 1, fig. 2.
*1965b Sphaerucaprina forojulienis* Boehm; Polšak, p. 434.
*1967 Sphaerucaprina cf. forojulienis* Boehm; Pleničar and Buser, p. 153.
*1969 Sphaerucaprina forojulienis* Boehm; Polšak and Mamužič, p. 237.
*1971 Sphaerucaprina forojulienis* Boehm; Carbone *et al.*, p. 143, text-fig. 9.
*1976 Sphaerucaprina forojulienis* Boehm; Praturlon and Sirna, p. 99, text-fig. 17a–b.
*1980 Sphaerucaprina forojulienis* Boehm; Carbone *et al.*, p. 204.
*1980 Sphaerucaprina forojulienis* Boehm; Iannone and Laviano, p. 223, text-fig. 28.
*1980 Sphaerucaprina forojulienis*; Laviano and Sirna, p. 69.
*1981 Sphaerucaprina forojulienis* Boehm; Carbone and Sirna, p. 435, text-fig. 6.
*1983 Sphaerucaprina forojulienis* Boehm; Camoin, p. 219, pl. 5, fig. 9.
*1983 Sphaerucaprina forojulienis* Böh m; Mainelli, p. 193.
*1983 Sphaerucaprina forojulienis* Boehm; Pleničar and Premru, p. 191.
*1985 Sphaerucaprina forojulienis* Boehm; Caminiti, p. 130, pl. 29, fig. 2.
*1987 Sphaerucaprina forojulienis*; Accordi *et al.*, p. 139.
*1989 Sphaerucaprina woodwardi* (Gemmellaro); Accordi *et al.*, p. 167, pl. 4, fig. 2.
*1989b Sphaerucaprina forojulienis* Boehm; Philip *et al.*, p. 1381.
*1989 Sphaerucaprina forojulienis* Boehm; Sartorio, p. 94, pl. 1 [cop. Parona 1908a].
*1990 Sphaerucaprina forojulienis* (Boehm); Cestari and Pantosti, p. 45.
*1992a Sphaerucaprina forojulienis* Boehm; Mainelli, p. 79.
*1993 Sphaerucaprina forojulienis* Boehm [sic]; Cherchi *et al.*, p. 93, pl. 4, fig. 3.
*1993 Sphaerucaprina forojulienis* Böh m [sic]; Ruberti, p. 959.
*1996b Sphaerucaprina forojulienis* Böh m; 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 adanal 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 dorsovenal 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 anterovenal 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 (1892a, 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 (1908a) 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 (1908a). Douvillé (1910), however, did not mention these similarities and gave no reference to Parona’s (1908a) 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 (1908a) 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 Schistosia 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 seafiel densis 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, 1888b), LVs, adapical view, Paleokastron Hill; A, C55; B, C114; C, C111; D, C51; E, C113. Scale bar represents 10 mm.

Family **PLAGIOPTYCHIDAE** Douvillé, 1888b

Genus **MITROCAPRINA** Boehm, 1895

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

*Mitrocaprina bayani* (Douvillé, 1888b)

Text-figure 24

*1888b* 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.
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); Polšák, pl. 6.
1966 Mitrocaprina bayani; Astre, text-figs 1–10.
1967b Mitrocaprina bayani (Douvillé); Polšák, 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 18886].

1982 *Mitrocaprina bayani* (Douvillé); Polšak *et al.*, text-fig. 3.

1985 *Mitrocaprina polsaki* Astre; Tomič, p. 85.

1996 *Mitrocaprina bayani* (Douvillé); Rojas and Ituralde-Vinent, p. 293.

1997 *Mitrocaprina bayani* (Douvillé); Steuber *et al.*, p. 179.

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

**Material.** Eight LVs from Palekastron 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 spindles 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 1967b), 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 boeticus*; Munier-Chalmas, p. 819 [nomen dubium].

1934 *Plagioptychus boeoticus* Mun.-Chalm.; Kutassy, p. 173 [nomen dubium, with synonymy].

v.1943 *Plagioptychus touca* Matheron; Klinghardt, p. 129; text-fig. 6.


v.1950 *Mitrocaprina* sp.; Mennessier, p. 529, text-figs 1–2.


1993b *Plagioptychus touca* Matheron; Steuber, p. 44.

1993 *Mitrocaprina boeotica* (Munier-Chalmas); Steuber *et al.*, text-fig. 10.

**Syntypes.** Mennessier (1949b), 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 coiled (Text-fig. 25e–g). Dmax up to 90 mm. Exterior surface smooth except for fine comm marginal 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.
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...
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 (Douville 1888b), 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-fgs 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 Keratouvevou Hill was provided by Mennessier (1949b, 1950). Previously, Klinghardt (1943) had figured a specimen from the type locality and despite the clearly visible sub-polygonal pallial canals misidentified it as _Plagiotochus toucasii_ 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 α2'. They separate _M. boeotica_ from _M. bayani_ (Douville, 1888b) 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 α2' 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 1842a** | *Radiolites angulosus* d’Orbigny, p. 183. |
| **non 1850** | *Radiolites angulosus* d’Orbigny, p. 220, pl. 562, figs 1–4. |
| ***1850** | *Biradiolites angulosus* d’Orbigny, p. 233, pl. 574, figs 7–11. |
| **1850** | *Biradiolites quadrata* 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, adpalical 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.
1913b Birad. angulosus; Douvillé, p. 416.

p1932 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.

non1941 Biradiolites ? angulosus d’Orbigny; Montagne, p. 63, pl. 4, fgs 9–10.
1966 Biradiolites angulosus d’Orbigny; Torre, p. 7, pl. 1, fgs 2–3.
1969 Biradiolites angulosus d’Orbigny; Polšak and Manušić, p. 238.
p1972b 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.
1978a Biradiolites angulosus; Philip et al., p. 84.
1980 Biradiolites angulosus; Laviano and Sirma, p. 69.
p1981 Biradiolites angulosus d’Orbigny; Sánchez, p. 69 [with synonymy].
1987 Biradiolites quadratus d’Orbigny; Sánchez, p. 81 [with synonymy].
1982 Biradiolites angulosus d’Orb.; Philip, in Plate, p. 93.
1982 B. quadratus (d’Orb.); Philip, in Plate, p. 93.
1984 Biradiolites angulosus d’Orbigny; Laviano, p. 185.
1985 Biradiolites angulosus d’Orbigny; Laviano, p. 327, pl. 12, fgs 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 Sirma, p. 192, pl. 2, fgs 3–4.
1996 Biradiolites quadratus (d’Orbigny); Paris and Sirma, p. 192, pl. 2, fig. 6.

Syntypes. D’Orbigny (1850), plate 574, figures 7–11. The designation Radiolites angulosus d’Orbigny, 1842a was obviously not a mistake, as assumed by Bayle (1856), because the syntypes of this species (d’Orbigny, 1850, pl. 562, fgs 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). Steeplipped 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, 1842a. However, R. angulosus bears a ligamental ridge (see above) and Birad.
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 poster-oventral 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 Marmekö 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

*1910* *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*; Polšák and Mamužič, p. 238.

1972a *B. africana* Douvillé; Campobasso, text-fig. 1/1 [cop. Douvillé 1910].

1972a *Bournonia putignanensis* n. sp. Campobasso, p. 364, pl. 1, fig. 1a–b; pl. 2, figs 1–2; text-fig. 1/7.

1981b *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.

1986a *Bournonia africana* Douvillé; Pamouktchiev, p. 92, pl. 1, fig. 8.

1987 *Bournonia africana* Douvillé; Pejović and Radoičić, p. 128.

1991 *Bournonia africana*; Caffau and Plenčar, 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 unfolded in Vb and Pb.

**Remarks.** The described specimens lived in clusters of a few conjoined shells. The development of longitudinal ribs and posterodorsal 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, 1972a (Text-fig. 29F).

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

---

**Bournonia fourtau** Douvillé, 1910

*1910* *Bournonia Fourtau* n. sp. Douvillé, p. 49, pl. 3, fig. 8; text-figs 22, 54.
*1913a* *Bournonia Fourtau* Douvillé; Douvillé, p. 249, pl. 17, fig. 6 [cop. Douvillé 1910]; text-fig. 8.
*1915a* *Bournonia Fourtau* Douvillé; Douvillé, p. 166, pl. 8, fig. 5; text-fig. 1.
*1932* *Bournonia fourtau* Douvillé; Kühn, p. 96 [with synonymy].
*1934* *Bournonia fourtau* Douvillé; Wiontzek, p. 13, text-fig. 5.
*1949* *Bournonia fourtau* Douvillé; Dechaseaux, pl. 4, fig. 3; text-fig. 3.
*1954* *Bournonia fourtau* Touv.; Jux, p. 176.
*1968a* *Bournonia fourtau* Douvillé; Slišković, p. 43.
*1972a* *B. fourtau* Douv.; Campobasso, text-fig. 1/5 [cop. Douvillé 1910].
*1982* *Bournonia fourtau* Douvillé; Pamoukchiev, p. 237, pl. 4, fig. 3.
*1981* *Bournonia fourtau* Douvillé; Sánchez, p. 88 [with synonymy].
*1982* *Bournonia cf. fourtau* Douvillé; Plenčar, p. 21, pl. 8, fig. 1.
*1982* *Bournonia fourtau* Douvillé; Polšak et al., text-fig. 3.
*1987* *Bournonia fourtau* Douvillé; Pejović and Radoičić, p. 136.
*1992* *Bournonia fourtau* 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 monastary, Ptoon Mountains; Senonian (RS77).

**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. fourtau* are controversial. According to Douvillé (1910, 1913a, 1915a) the syntypes were collected from Turoanian deposits ("couche e d'Abou Roach" after Fourtau 1900, cited in Douvillé 1913a). 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 Pamoukchiev (1979) in the Maastrichtian of Bulgaria and reported by Slišković (1968a) from the Campanian–Maastrichtian of Herzegovina.

Numerous small-shelled species of *Bournonia* differ only in details of the posterodorsal 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. fourtau*, *B. africana*, *B. excavata* d’Orbigny, 1850).

**Genus Durania Douvillé, 1908b**

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

**Durania martelli** Parona, 1911a

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

*1911a Durania Martelli* n. f. Parona, p. 386, text-figs 1–2.
1911c *Durania Martelli* Par.; Parona, p. 292.
1922 *Durania Martelli* Parona; Klinghardt, pp. 9, 35.
1928a *Durania Martelli* Parona; Klinghardt, pl. 13, fig. 15 [cop. Parona 1911a]; pl. 14, fig. 8 [cop. Parona 1911a].
1931 *Durania Martelli* Par.; Desio, p. 423.
1932 *Durania martelli* Parona; Kühn, p. 107 [with synonymy].
1958 *Durania martelli* Parona; Tavani, p. 174.
1963 *Durania martelli* Par.; Ambrosetti, p. 213.
1966 *Durania martelli* Parona; Torre, p. 15, pl. 5.
1972 *Biradiolites martelli* (Parona); Pejović, p. 119, text-fig. 1 [cop. Parona 1911a].
1975c *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 martelli* (Parona); Philip et al., p. 84.
1979 *Biradiolites martelli* (Parona); Polšák, pp. 206, 224.
1981 *Biradiolites martelli* (Parona); Polšák, p. 454.
1984 *B. martelli* (Parona); Laviano, p. 185.
1985 *Milovanovicia dobrunensis* Slišković; Caminiti, p. 140, pl. 31, fig. 4.
1987 *Milovanovicia dobrunensis* Slišković; Accardi et al., p. 139, pl. 1, fig. 4.
1987 *Biradiolites martelli* (Parona); Pejović and Radočič, p. 127.
1987 *Milovanovicia dobrunensis* Slišković; Pejović and Radočič, p. 128.
1989 *Biradiolites martelli* (Parona); Accardi et al., p. 168, tab. 1.
1990 *Biradiolites* cf. *martelli* (Parona); Cestari and Pantosti, p. 47, text-fig. 4.
1990 *Milovanovicia dobrunensis*; Gušić and Jelaska, text-fig. 7.
1992b *Durania martelli* Parona; Peza, p. 297, pl. 2, fig. 3.
1992 *Durania martelli* Parona; Pleničar et al., p. 233.
1993 *Milovanovicia dobrunensis* Slišković; Caramante 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, 1911a; R548, Pavlos. 1, posterior aspect; 2, transverse section, adapical view. Both $\times 0.7$.

Figs 3, 5–6. *Durania katzeri* (Slišković, 1984a). 3, posterior aspect; R631, Pavlos. 5, anterodorsal aspect; R554, Megali Lakka. 6, the same valve as on fig. 5, posteroventral aspect. All $\times 0.7$.

Figs 4, 7. *Durania martelli* Parona, 1911a. 4, transverse section, adapical view; R550, Pavlos. 7, transverse section, adapical view; R566, Megali Lakka. Both $\times 0.7$.

Upper side is dorsal in all transverse sections.
1993  *Milovanovicia dobrunensis* Slišković; Ruberti, p. 965, pl. 7, fig. 3.

p1996  *Milovanovicia martelli* (Parona); Laviano and Pejović, p. 93, text-figs 1, ?4–5.


1996  *Milovanovicia dobrunensis*; Sanders, p. 852.

1997  *Milovanovicia dobrunensis* Slišković; Ruberti, tab. 1.

**Syntypes.** Parona (1911a), 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 *Dura*nia-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, 1967a was originally separated from *Durania* Douvillé, 1908b 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 1992a), as it occurs more or less commonly in several genera of Radiolitidae (Masse and Philip 1972; Amico 1978). Slišković (1975c, 1984a) included four additional new species with irregular, large cells of the outer shell layer in *Milovanoviciia*. Consequently, the diagnosis of the genus had to be changed and *Milovanovicia* was separated from *Dura*nia because of its steeply inclined funnel plates and primitive structure of the outer shell layer with inflected muri (Slišković 1975c). 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 *Dura*nia (Pl. 1, fig. 7). Inflected muri cannot be considered to be a diagnostic character, as they also occur in *Dura*nia 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 1975c, 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

---

**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
distinct internal structures in the radial bands of ‘Milovanovicia’ (Pl. 2, fig. 1) nor any conspicuous characters of the LV (Slišković 1984a) 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 1992b); Santonian–Lower Campanian of Herzegovina (Slišković 1968a); Coniacian of the Apennines and the Adriatic island Brač (Accordi et al. 1987; Gušić and Jelaska 1990).

Durania katzeri (Slišković, 1984a)

Plate 1, figures 3, 5–6

*1984a Milovanovicia katzeri n. sp. Slišković, p. 201, pl. 4, figs 1–6; pl. 5, fig. 5; text-fig. 3.

1985 Biradiolites cf. martelli (Parona); Laviček, p. 327, pl. 13, fig. 1a.

p1996 Milovanovicia martelli (Parona); Laviček and Pejović, p. 93, text-figs 2–3.

?1996 Milovanovicia cf. martelli (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. martelli, it seems probable that the four species from the Lower Senonian of Bosnia and Herzegovina which were previously included in ‘Milovanovicia’ (Slišković 1975c, 1984a) 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


Fig. 3. Lapeirousella australiensis (Douville, 1915b); 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); R533. Both × 1–4.
STEUBER, rudists
Durania cf. montisferrati Astre, 1954

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


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 Ibb 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, Ibb 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, Ibb is of equal width or wider than Vb; funnel plates are downfolded in Vb, they are downfolded and undulating in Ibb 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 veriform cells dominate and are up to 10 mm long. The muri undulate and are frequently interrupted so that cells are not always

---

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.
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 1957b) 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 eco-phenotypic 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.1900a *Radiolites Davidsonii* Hill; Douvillé, p. 218, text-fig. 15.

v.1902 *Praeradiolites davidsoni* Hill; Douvillé, p. 468, pl. 15, fig. 7.

v.1907 *Agric Davidsonii* 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; x 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 rousselii; Douville, pl. 23a [cop. Douville 1900a].
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.
1977 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.
STEUBER: CRETACEOUS RUDISTS OF BOEOTIA

non1992b  *Eoeradiolites* cf. *davidsoni* (Hill); Özer, pl. 1, fig. 11.
1994  *Eoeradiolites davidsoni* (Hill); Gallo Maresca, p. 24, pl. 1, figs 1–5; text-fig. 8 [cop. Douvillé 1910].
1996  *Eoeradiolites davidsoni* (Hill); Alencáster and Aguilar-Pérez, p. 118.
1996  *Eoeradiolites davidsoni* Hill; Corona-Esquivel and Alencáster, p. 188.

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


**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. 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, myocardial 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.
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. Albion 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 Czablay, 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.
STEUBER, Eoradiolites
Genus Fossulites Astre, 1957b

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).


Genus Gorjanovicia Polšak, 1967b

Type species. Gorjanovicia costata Polšak, 1967b.

Gorjanovicia boeotica Steuber, 1994

1993 Gorjanovicia boeotica Steuber; Steuber et al., text-fig. 10 [nomen nudum].


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, 1967b

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].
*1967b 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].
1995b Gorjanovicia costata Polšak; Caffau and Plenčičar, p. 232, pl. 4, figs 1, 1a, 2, 2a.
Holotype. Polšak (1967b), 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 ‘Loutson’ in Steuber 1994).

Description. See Steuber (1994).

Remarks. The systematic position of Gorjanovicia costata Polšak, 1967b 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 1992b), 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 ‘Loutson’ 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).


Gorjanovicia lipparinii Polšak, 1967b

1964 Gorjanovicia lipparinii n. sp. Polšak, p. 67 [nomen nudum].
1965b Gorjanovicia lipparinii n. sp. Polšak, p. 451 [nomen nudum].
*1967b 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].
1995b Gorjanovicia lipparinii Polšak; Caffau and Pleničar, p. 233, pl. 5, figs 1–3; text-fig. 4.

Holotype. Polšak (1967b), plate 67, figure 1.
Material. One fragmentary RV from Dionysos (GIK 1106).

Description. See Steuber (1994).


Genus LAPEIROUSELLA Milovanović, 1938a

Type species. Lapeirosia (Lapeirosella) orientalis Milovanović, 1938a.

Lapeirosella aimalensis (Douvillé, 1915b)

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. ‘Lapeirosia’ aimalensis from the Turonian of Aumale was previously considered as the stratigraphically oldest species of Lapeirosia Bayle, 1878. Phylogenetic analyses of the genus were repeatedly based on this taxon (Kühn 1934; Milovanović 1938a, 1951b), although its shell structure was insufficiently known. Lapeirosella Milovanović, 1938a was separated from Lapeirosia because of the rudimentary development of the pseudopillars that hardly project into the shell interior. Lapeirosella was, however, not considered as the ancestor of Lapeirosia, being known only from deposits which are younger than those in which the oldest representatives of Lapeirosia had been found. Consequently, the comparatively simple structure of the pseudopillars was considered as a phylogenetic reduction of the more complicated structures in Lapeirosia (Milovanović 1938a, 1951b). Obviously, the shell structure of ‘Lapeirosia’ aimalensis Douvillé, 1915b 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.

*a1915b Lapeirosia aimalensis n. sp. Douvillé, p. 26, text-fig. 1.
1932 Lapeiroseia [sic] aimalensis Douvillé; Kühn, p. 118.
1934 Lapeirososeia [sic] aimalensis Douvillé; Kühn, p. 373.
1938a L. aimalensis Douvillé; Milovanović, p. 87.
1981 Lapeiroseia [sic] aimalensis Douvillé; Sánchez, p. 132.

Syntype. Douvillé (1915b), 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 (1915b, 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. Lapeirosella aimalensis (Douvillé, 1915b); 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.
STEUBER, Lapeirousella
TEXT-FIG. 33. Reproduction of the single previously published figure of *Lapeirousella aumalensis* (Douville, 1915b), 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:

*Loci Aumalae*

*Etage. Cenomanien*

D.p.M. Peron

*L'échantillon de droite montre le début des Lapeiroisia H. D.*


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 *Lapeiroisella 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 pentato 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

---

**EXPLANATION OF PLATE 9**

Figs 1–4. *Lapeiroisella aumalensis* (Douville, 1915b); 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.
STEUBER, Lapeirousella
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

**Explanation of Plate 10**

Figs 1–2, 4–5. *Petkovicia? verajana* Slišković, 1968b; 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; × 1–2.5. 5, apical transverse section of same RV as on fig. 4, adapical view; × 1–2.5.

Fig. 3. *Praelapeirusia?* sp. nov.; R580, Marmeko; radial section of ventral pseudopillar, external side is to the right; × 8–3.
STEUBER, *Petkovicia*, *Praelapeirousia*?
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 *Lapeirosella* Milovanović, 1938b. Consequently, there remain no arguments to consider the simple structure of the pseudopillars in *Lapeirosella* as a secondary reduction of the more complicated structures in *Lapeirosia*. They are better explained as primitive characters and it appears likely that *Lapeirosia* became separated as a sister group of *Lapeirosella*. 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 *Lapeirosia*, therefore, are dislocated apically while they form small commarginal openings in *Lapeirosella aumalensis*.

---

**EXPLANATION OF PLATE 11**

Figs 1–5. *Petkovicia*? *verajana* Slišković, 1968b: 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, 1968b; 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, 1968b 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* Pironia, 1869.

*Medeella* cf. *zignana* (Pironia, 1869)

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

Description. See Steuber (1994).

**EXPLANATION OF PLATE 12**

Fig. 1. *Lapeirousella aumalensis* (Douville, 1915b); 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 ponsiantus* (d’Archiac, 1835); R137, Marmeko; posteroventral aspect; × 1.

Fig. 3. *Praealpeirousia*? sp. nov.; R579, Marmeko; posteroventral aspect; × 0:9.

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, 1968b

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*].
1968b *Petkovicia verajana* n. sp. Slišković, p. 87, pl. 8, figs 1–3.
1969 *Petkovicia verajana* Slišković; Polšak and Mamužič, p. 240.

Explanation of Plate 13

Figs 1–10. *Præradiolites 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.
STEUBER, Praeradiolites
Holotype. Slišković (1968b), plate 8, figure 1, 1a.

Material. Sixteen RVs from Loutision (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 marl 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 *Kateria hercegovinaensis* Slišković, 1966, although the shell structure of the latter has never been described in detail. The doubtfull 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 (1989a, 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 **Praelapoeirosia** Wiontzek, 1934

**Type species.** *Praelapoeirosia kossmati* Wiontzek, 1934.

*Praelapoeirosia* 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 intertongue with furrows of the RV at the commissure. Two prominent elevations are located above the LV 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 arc 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 (Polšák 1967b) whereas, in other cases, modifications of the radial bands of the LV were used to define new genera (Astre 1957b). 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: *Praelapoeirosia* Wiontzek, 1934, *Fossulites* Astre, 1954, *Medeella* Parona, 1924 and *Gorjanovicia* Polšák, 1967b.
The LV of *Praelapeirousia kossmati* Wiontecz, 1934 probably bears *Lapeirousia*-type oscula, whereas the LV of *Praelapeirousia macutensis* Sliškovič, 1984a resembles that of *Fossilites*. Nothing is known about the LV of *Medella*; that of *Gorjanovicia* most probably has no distinct modifications (Polšak 1967b). 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 pseudocamels 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, 1842a.

**Praeradiolites echennensis** Astre, 1954

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


*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.


1957b *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. *Sauvaginea 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.
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.

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

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 inlaid 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 Kalantos 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. aristedis Toucas, 1907 and P. subtoucasii 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 picatus* (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 indeterminate 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 *Gorjano victia* Polšak, 1967b, 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 Bilote 1983; Bilote 1985).

*Praeradiolites ponsianus* (d’Archiac, 1835)

Plate 12, figure 2

*1835*  
*Sphaerulites Ponsiana* d’Archiac, p. 182, pl. 11, fig. 6a–g.

*1842b*  
*Radiolites ponsiana* (Sphaerulites ponsiana d’Archiac); d’Orbigny, p. 155.

*1857*  
*Sphaerulites ponsianus* d’Archiac; Bayle, p. 693.

*1904b*  
*Praeradiolites ponsianus*; Douvillé, p. 542.

*1904c*  
*Praeradiolites ponsianus*, d’Archiac; Douvillé, p. 244, pl. 33, figs 1–2, 4.

*1907*  
*Praeradiolites cf. ponsi*; Toucas, p. 31, pl. 3, fig. 5.

*1908b*  
*P. ponsianus*; Douvillé, p. 309.

*1910*  
*Praeradiolites ponsianus* d’Archiac, var. *egyptiaca*; Douvillé, p. 48, pl. 3, figs 6a–b, 7.

*1913a*  
*Praeradiolites ponsianus* d’Archiac, race *egyptiaca*; Douvillé, p. 248, pl. 15, figs 1a–b, 2 [cop. Douvillé 1910].

*1928a*  
*Praeradiolites Ponsi* d’Archiac; Klinghardt, pl. 21, fig. 16.

*1932*  
*Praeradiolites ponsianus* (d’Archiac) Douvillé; Kühn, p. 130 [with synonymy].

*1932*  
*Praeradiolites ponsianus* var. *egyptiaca* Douvillé; Kühn, p. 130 [with synonymy].

*1954*  
*Praeradiolites ponsianus* d’Archiac var. *bouirensis* nov. var. Astre, p. 25, pl. 2, figs 4–5; text-fig. 6a–c.

*1955a*  
*Praeradiolites ponsianus* d’Arch. et var. *bouirensis* Astre; Astre, p. 10.

*1957a*  
*Praeradiolites ponsianus* d’Arch.; 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*; Bilote, 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*; Bilote, tab. 17.

*1987*  
*Praeradiolites ponsianus* *egyptiaca* Douvillé; Kora and Hamama, p. 296.

*1995*  
*Praeradiolites ponsianus* *egyptiaca* 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 downflection. 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 1931a); Upper Turonian of the external Dinarids (Polšák 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.
Radiolites angeioides (Lapeirous, 1781)

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


v.1908 Radiolites angoioides Picot de Lapeirous; Toucas, p. 77, pl. 15, figs 11, 13.

1932 Radiolites angoioides (Lapeirous) Lamarck; Kühn, p. 135 [with synonymy].

1932 Radiolites angoioides Picot de Lapeirous; Milovanović, p. 43, pl. 1, figs 1–3.

1933 Radiolites angoioides (Lapeirous) Lamarck; Milovanović, pp. 83, 154, text-figs 15, 19–23.

1935 Radiolites angoioides Picot de Lapeirous; Klinghardt, p. 25, pl. 2, fig. 1.

1935 Radiolites angoioides (Pic. de Lap.); Parona, p. 131.

1937 Radiolites angoioides (Lapeirous); Milovanović, p. 128.

1937 Radiolites angoioides Lam.; Zapfe, p. 76.

1939 Radiolites angoioides (Lapeirous) Lamarck; Klinghardt, p. 133, pl. 2, fig. 12.

1944 Radiolites angoioides (Lapeirous) Lamarck; Klinghardt, p. 202, pl. 5, figs 1–4.

1947 Radiolites angoioides; Kühn, p. 187.

1950 Radiolites angoioides Picot de Lapeirous; Rengarten, p. 64, pl. 11, fig. 4.

1951a Radiolites angoioides (Lapeirous) Lamarck; Milovanović, p. 18.

1955a R. angoioides Lap.; Astre, p. 11.

1956 Radiolites angoioides Matheron; Brunn, p. 136.

1957a Radiolites angoioides Lap.; Astre, p. 193.


1959 Radiolites angoioides (Lapeirous); Petković et al., p. 286.


1961 Radiolites angoioides Picot de Lapeirous; Bobkova, text-fig. 6.


1963 Radiolites angoioides Pic de Lap.; Ambrosetti, p. 213.

1965 Radiolites angoioides Picot de Lapeirous; Benkö-Czabalay, p. 402.

1965 Radiolites angoioides (Lapeirous); Pamoukchchiev, p. 31, pl. 3, fig. 2.

1966 Radiolites angoioides (Lapeirous); Pamoukchchiev, p. 28, pl. 2, fig. 2; pl. 4, fig. 1.

1967 Radiolites angoioides Lapeirous; Lupu and Lupu, p. 308.

1968 Radiolites angoioides Lapp.-Lam.; Bogdanović, p. 76.

1969 Radiolites angoioides (Lapeirous); Polšak and Mamužič, p. 239.

1970 Radiolites angoioides Picot de Lapeirous; Benkö-Czabalay, p. 283.

1972b Radiolites angoioides (Lapeirous); Campobasso, p. 447, pl. 8, fig. 2.
Radiolites angioides (Lapeirouse); Sakellariou-Mané, p. 397, pls 1–2.
1974 Radiolites angioides (Lapeirouse); Lupu, p. 53, pl. 2, fig. 7.
1974 Radiolites angioides (Lapeirouse); Slišković, p. 133.
1976 Radiolites angioides (Picot de Lapeyrouse); Andrusov, p. 15.
1978 Radiolites angioides Picot de Lapeirouse; Amico, p. 58, pl. 14, figs 4–6.
1978 Radiolites angioides (Lapeirouse); Pamouktchiev, tab. 1.
1980 Radiolites angioides; Bilotte, p. 57.
1981 Radiolites angioides P. de Lap.; Bilotte, text-fig. 2.
1981b Radiolites angioides (Lapeirouse); Pamouktchiev, p. 185, pl. 92, fig. 3.
1981 Radiolites angioides (Lapeirouse); Sánchez, p. 168 [with synonymy].
1982 Radiolites angioides (Lapeirouse); Pons, tab. 2.
1983 R. angioides; Philip and Bilotte, tab. 2.

non 1984 Radiolites angioides (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. angioides; Bilotte, tab. 31, 42.
1985 Radiolites angioides (Lapeirouse); Höfling, p. 31, pl. 6, fig. 6.
1985 R. angioides; Lupu, p. 21.
1987 Radiolites angioides (Lapeirouse); Pejović and Radičić, p. 130, tab. 1.
?1989 Radiolites angioides (Lapeirouse); Accordi et al., p. 167, tab. 1., pl. 4, fig. 3.
?1989a Radiolites angioides (de Lapeirouse); Cestari and Sirna, p. 135, tab. 1, pl. 7, fig. 4.
1989b Radiolites angioides (De Lapeirouse); Cestari and Sirna, p. 20, tab. 1, pl. 7, fig. 1.
1989 Radiolites angioides [sic] (P. de Lap.); Pascual et al., p. 224, text-fig. 3.
1990 Radiolites angioides; Gušić and Jelaska, text-fig. 15.
1990 Radiolites angioides; Leiss, p. 61.
1992 Radiolites angioides; Caffau et al., p. 164, pl. 1, fig. 8.
1992 Radiolites angioides (Lapeirouse); Swinburne et al., text-fig. 2.
1993 Radiolites angioides (Lapeirouse) Lamarck; Pleničar, p. 50, pl. 1, figs 1–5; pl. 2, figs 1–3.
1996a Radiolites angioides [sic]; Laviano, p. 7.
1997 Radiolites angioides (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. angioides 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. angioides, 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 (?Kéfallinia 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.
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.
1903 *Sphaerulites Peroni* Choffat; Dacqué, p. 375, pl. 36, figs 1–2.
1908 *Radiolites lusitanicus* Bayle; Toucas, p. 62, pl. 11, fig. 10.
1908 *Radiolites Peroni* Choffat; Toucas, p. 61, pl. 11, figs 3–4, 6–9.
1913a *Radiolites Peroni* Choffat; race sinaitica; Douvillé, p. 249, pl. 15, fig. 3.
1930 *Radiolites lusitanicus* Bayle; Nöth, p. 367.
1931b *Radiolites lusitanicus* Bayle; Nöth, p. 158.
1931b *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.
1933 *Radiolites lusitanicus* Bayle; Müllerried, p. 270.
1942 *Radiolites lusitanicus* (Bayle); Parona, p. 87.
1942 *Radiolites Peroni*; Parona, p. 90.
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.
1957a *Radiolites lusitanicus* Bayl. var. fortovanus Ast.; Astre, p. 190.
1957a *Radiolites peroni* Choff.; Astre, p. 191.
1964 *R. lusitanicus* (Bayle); Polšák, p. 67.
1964 *R. lusitanicus porericus* n. subsp. Polšák, p. 67 [nomen nudum].
1964 *Radiolites peroni* (Choffat); Polšák, pp. 66–67.
1965b *Radiolites lusitanicus* (Bayle); Polšák, p. 444.
1965b *Radiolites lusitanicus porericus* n. subsp. Polšák, p. 444 [nomen nudum].
1965b *Radiolites peroni* (Choffat); Polšák, p. 444.
1967b *Radiolites lusitanicus porericus* n. subsp. Polšák, pp. 60, 174, pl. 29, figs 8–9; pl. 30, figs 1–4.
1968a *Radiolites peroni* (Choffat); Slišković, p. 31.
1969 *Radiolites lusitanicus* (Bayle); Polšák and Mamuzić, p. 238.
1969 *Radiolites peroni* (Choffat); Polšák and Mamuzić, p. 233.
1971 *Radiolites peroni* (Choffat); Berizzi Quarto di Palo and Busson, p. 526, pl. 39, fig. 12.
1971a *Radiolites peroni* (Choffat); Slišković, p. 34.
1972 *Radiolites lusitanicus* Bayle; Babinot et al., text-fig. 2.
1972 *Radiolites peroni* (Choffat); Babinot et al., text-fig. 2.
1972c *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); Plenicač, 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.
1981b *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-As’a Ad, p. 94 [teste El-As’a Ad 1987].
nor 1983 *S. Peroni* Choffat; El-As’a ad, p. 94 [teste El-As’a Ad 1987].
1983 *Radiolites peroni* (Choffat) Douvillé; Mainelli, p. 193.
1987 *Radiolites peroni sinicus* 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.
1989b *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 Plenicač, p. 177.
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 Azeem, p. 276.
1997 *Sphaerulites peroni* (Choffat); Metwally and Abd El Azeem, p. 276.

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


*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

---

**Explanation of Plate 15**

Figs 1–6. *Radiolites lusitanicus* (Bayle, 1857), Marmeko. 1, posterovertral aspect of large RV with irregularly folded lamellae which are turned down in the single interband fold near the commissure; R526. 2, posterovertral 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, posterovertral aspect of RV with steeply inclined lamellae and two ribs (folds) in the interband; R164. 6, posterovertral aspect of RV with steeply inclined lamellae and two longitudinal ribs (folds) in the interband; R267. All × 0.7.
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 posterodorsal 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 veriform 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 the shell is indicative of R. peroni (sensu Choffat 1886). The same applies to R. lusitanicus from the Upper Turonian–Coniacian of Istria (Polšak 1967b). 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 1967b; Berhou 1973; Philip et al. 1978b, 1989a), 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 1967b) and also occur at Marmeko quarry. They have been defined as R. lusitanicus var. fortovanus Astre, 1954 or R. lusitanicus porericus Polšak, 1967b. 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 Mamužič 1969; Polšak et al. 1982), the Apennines, of Serbia (Pašić 1957; Pejović 1957), Greece (Poon Mountains, Attica [Mitzopoulos and Kühn 1963]), Somalia, Caucasus, Mexico; Upper Cenomanian of south-western Europe (Berhou and Philip 1973; Philip 1978; Philip et al. 1978b), Albania (Peza and Piridni 1994), Egypt (Mewally and Abd El Azeem 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, anteroventral; × 25. 4, anteroventral section; × 9.1. 5, dorsal tangential section; × 5.5.
Radiolites praegalloprovincialis Toucas, 1908

Text-figure 39A–D

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; Polšák, p. 67.
1965b Radiolites praegalloprovincialis Toucas; Polšák, p. 447.
1969 Radiolites praegalloprovincialis Toucas; Polšák 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; Blotte, tab. 2.
1982 Radiolites praegalloprovincialis Toucas; Polšák et al., text-fig. 3.
1985 R. praegalloprovincialis; Blotte, tab. 17.
1989 R. praegalloprovincialis Toucas; Pascual et al., p. 218, text-fig. 3.

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 īods 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; x 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 1982b); Coniacian–Lower Santonian of the external Dinarids (Polšak et al. 1982; Štrbar 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

*1839 Hippurites Sauvagesii*; d’Hombres Firmas, p. 15.
*v.1881 Sphaerulites Lefevrei* 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’Hembr. F. sp., d’Orb. (pars), emend. Bayle; Blanckenhorn, p. 86.
1908  *Radiolites sauvagesi* d’Hombres-Firmas; Toucas, p. 65, pl. 12, fig. 10; text-figs 34–36.
1910  *Rad. sauvagesi*; Douvillé, text-fig. 13.
1930  *Radiolites Sauvagesi* d’Hombre Firmas; Nöth, p. 367.
1931b  *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.
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); Polšák, p. 67.
1965b  *Radiolites sauvagesi* (d’Hombres-Firmas); Polšák, p. 444.
1968a  *Radiolites sauvagesi* (d’Hombres-Firmas); Slišković, p. 35.
1969  *Radiolites sauvagesi* (d’Hombres-Firmas); Polšák and Mamuzić, p. 238.
1972  *Radiolites praeauvagesi* 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. *aqualinus* 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); Polšák et al., text-fig. 3.
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.
1989  *Radiolites sauvagesi* (d’Hom.-Firm.); Pascual et al., p. 224, text-fig. 3.
<table>
<thead>
<tr>
<th>No.</th>
<th>RV length</th>
<th>Circumference</th>
<th>Σ Ribs</th>
<th>Vb</th>
<th>lb</th>
<th>Pb</th>
<th>Ribs on lb</th>
</tr>
</thead>
<tbody>
<tr>
<td>R124</td>
<td>&gt;72</td>
<td>119</td>
<td>–</td>
<td>7</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>R127</td>
<td>67</td>
<td>135</td>
<td>48</td>
<td>9</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>R128</td>
<td>&gt;71</td>
<td>155</td>
<td>42</td>
<td>8</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>R135</td>
<td>&gt;69</td>
<td>183</td>
<td>–</td>
<td>13</td>
<td>9</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>R144</td>
<td>&gt;96</td>
<td>168</td>
<td>46</td>
<td>18</td>
<td>7</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>R152</td>
<td>&gt;52</td>
<td>174</td>
<td>32</td>
<td>17</td>
<td>4</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>R158</td>
<td>&gt;58</td>
<td>131</td>
<td>–</td>
<td>10</td>
<td>7</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>R160</td>
<td>&gt;69</td>
<td>141</td>
<td>–</td>
<td>13</td>
<td>10</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R165</td>
<td>&gt;45</td>
<td>132</td>
<td>41</td>
<td>13</td>
<td>4</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>R174</td>
<td>&gt;47</td>
<td>163</td>
<td>–</td>
<td>14</td>
<td>9</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>R247</td>
<td>&gt;59</td>
<td>127</td>
<td>27</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>R249</td>
<td>63</td>
<td>121</td>
<td>–</td>
<td>7</td>
<td>4</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>R265</td>
<td>&gt;73</td>
<td>126</td>
<td>–</td>
<td>13</td>
<td>6</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R313</td>
<td>&gt;64</td>
<td>123</td>
<td>–</td>
<td>10</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>R314</td>
<td>67</td>
<td>140</td>
<td>–</td>
<td>10</td>
<td>6</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>R315</td>
<td>74</td>
<td>140</td>
<td>–</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>R316</td>
<td>&gt;74</td>
<td>166</td>
<td>–</td>
<td>8</td>
<td>7</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>R318</td>
<td>&gt;29</td>
<td>103</td>
<td>–</td>
<td>9</td>
<td>3</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>R319</td>
<td>&gt;37</td>
<td>122</td>
<td>38</td>
<td>7</td>
<td>5</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>R321</td>
<td>&gt;93</td>
<td>122</td>
<td>–</td>
<td>9</td>
<td>7</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>R323</td>
<td>&gt;55</td>
<td>108</td>
<td>–</td>
<td>10</td>
<td>5</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>R324</td>
<td>&gt;45</td>
<td>121</td>
<td>34</td>
<td>8</td>
<td>4</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>R527</td>
<td>&gt;59</td>
<td>139</td>
<td>–</td>
<td>11</td>
<td>4</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R529</td>
<td>&gt;56</td>
<td>139</td>
<td>–</td>
<td>13</td>
<td>5</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>R530</td>
<td>&gt;79</td>
<td>139</td>
<td>41</td>
<td>5</td>
<td>6</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R533</td>
<td>&gt;80</td>
<td>150</td>
<td>–</td>
<td>14</td>
<td>7</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>R537</td>
<td>&gt;85</td>
<td>164</td>
<td>26</td>
<td>11</td>
<td>4</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>R540</td>
<td>120</td>
<td>126</td>
<td>39</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>R661</td>
<td>&gt;97</td>
<td>171</td>
<td>–</td>
<td>10</td>
<td>4</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R663</td>
<td>&gt;83</td>
<td>144</td>
<td>–</td>
<td>12</td>
<td>6</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R757</td>
<td>&gt;82</td>
<td>132</td>
<td>–</td>
<td>11</td>
<td>2</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>R766</td>
<td>&gt;88</td>
<td>141</td>
<td>42</td>
<td>10</td>
<td>2</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>R767</td>
<td>&gt;73</td>
<td>158</td>
<td>37</td>
<td>10</td>
<td>6</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R769</td>
<td>&gt;102</td>
<td>147</td>
<td>25</td>
<td>10</td>
<td>8</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>R770</td>
<td>&gt;64</td>
<td>125</td>
<td>32</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
</tbody>
</table>

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.


**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. praesaungesis communis Poljak, 1967b; 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 Marmoko 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. sauagesis.

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. sauagesis 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 Marmoko 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. sauagesis. Ib of these valves are slightly narrower when compared with the Boeotian specimens, but still structured by undulating lamellae (‘subduplicated’, Parnes 1987, p. 140).

R. praesaungesis Toucas, 1908 was separated from R. sauagesis because of an unfolded Ib. R. praesaungesis was reported to co-occur with Vaccinites praegiganteus (Toucas, 1904) in the Turonian of Gâtiguès (southern France), whilst R. sauagesis occurs together with Vaccinites moulinisi (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. praesaungesis. The following observations were made during the analysis of the abundant material of R. sauagesis and R. praesaungesis 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 (praeasauvagesi) co-occur at several localities with specimens in which Ib has one or more plications. Consequently, *R. praeasauvagesi* 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 (Polšák et al. 1982); ‘zone de passage Turonien-Coniacien’—Santonian of the Pyrenees (Büttel 1982b; 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.

*1931* *Radiolites subradiosus* Toucas; Klinghardt, p. 39, pl. 3, fig. 12; text-fig. 11.

*1932* *Radiolites subradiosus* Toucas; Kühn, p. 158 [with synonymy].

*1933b* *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; Polšák, p. 67.

*1964* *R. subradiosus angeiodiformis* n. subsp. Polšák, p. 67 [nomen nudum].

*1965b* *Radiolites subradiosus* Toucas; Polšák, p. 450.

*1967b* *Radiolites subradiosus angeiodiformis* n. subsp. Polšák, p. 450 [nomen nudum].

*1969* *Radiolites subradiosus* Toucas; Polšák 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* Polšák; Sánchez, p. 190.

*1982* *Radiolites subradiosus* Toucas; Polšák 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.
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.
STEUBER, Radiolites
TEXT-FIG. 45. Sauvagesia meneghiniana (Pirona, 1869). A-B, R519; Tsouka Hill; C-D, R362; Dionysos; all × 0.8. A, posteroveentral aspect; B, posterodorsal aspect; posterior band is seen to the left; C, posteroveentral 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 posteroveventrally 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

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.
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 posterointernal 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, 1967b 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 1967b) 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 meneghiniana* 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 meneghiniana* (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.

1972b *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.
1995b  *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 ventradly by prominent projections of the inner shell. The posterior projection, ventradly 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.

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

**Remarks.** Shell structures and diameters of cells of other species of *Sauvagesia* from the Santonian–Lower Campanian of Istria (Polšak 1967b) 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, 1967b

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

1964 Sauvagesia tenuicostata n. sp. Polšak, p. 67 [nomen nudum].
1965b Sauvagesia tenuicostata n. sp. Polšak, p. 451 [nomen nudum].
*1967b 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 Sauvagesia 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; Galleffi 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.
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.
1995b 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 (1967b), 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 Lb 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, 1967b; 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.
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 (Gusić and Jelaska 1990).

**Family HIPPURITIDAE Gray, 1848**

**Genus HIPPURITELLA Douvillé, 1908**

*Type species.* *Hippurites maestrei* Vidal, 1878.

**Hippuritella lapeirousei** (Goldfuß, 1840)

Text-figure 46H, I–M

*vl840* *Hippurites Lapeirousei* Goldfuß, p. 303, pl. 165, fig. 5a–c, e–f.

*vl895* *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.
Hippurites (Orbignya) Lapeirousei Goldfuß; Parona, p. 15.

Hippurites (Orbignya) Lapeirousei Goldfuß; Klinghardt, pl. 23, fig. 10; pl. 24, fig. 13.

Hippurites (Orbignya) lapeirousei Goldfuß; Kühn, p. 54 [with synonymy].

Hippurites (Orbignya) Lapeirousei Goldfuß; Parona, p. 99.

Hippurites (Orbignya) lapeirousei Goldfuß; Milovanović, p. 137, text-figs 64–67.

Orbignya Lapeirousei Goldfuß; Boisseveain, p. 164, text-fig. 27.

Hippurites (Orbignya) Lapeirousei Goldfuß; Milovanović, p. 223, text-fig. 18.

Hippurites (Orbignya) lapeirousei Goldfuß; Milovanović, p. 50.

Hippurites (Orb.) lapeirousei Goldfuß; Milovanović, p. 41.

Hippurites (Orbignya) Lapeirousei Goldfuß; Milovanović, p. 128.

H. (Orbignya) lapeirousei Goldfuß; Milovanović, p. 245.

Orbignya Lapeirousei (Goldfuß); van de Geijn, p. 52, text-figs 1–4.

Hippurites (Orbignya) Lapeirousei Goldfuß; Stchépinsky, p. 129, pl. 21, fig. 1,1a.

Hipp. (Orbignya) lapeirousei Goldfuß; Stchépinsky, p. 354.

Hippurites Lapeirousei Goldfuß; Brunn, p. 128.

Hippurites (Orbignya) lapeirousei Goldfuß; Tavani, p. 171.

Hippurites (Orb.) lapeirousei Goldfuß; Petković et al., p. 287.

Hippurites (Orbignya) lapeirousei; Ambrosetti, p. 213.

Hippurites (Orbignya) lapeirousei; Slišković and Luburić, p. 7.

Hippurites (Orbignya) lapeirousei Goldfuß; Mamužić, p. 344.

Orbignya lapeirousei (Goldfuß); Pamouktchev, p. 26, text-fig. 1.

Hippurites (Orbignya) lapeirousei Goldfuß; Polšak, p. 337.

Hippurites lapeirousei Goldfuß; Bogdanović, p. 76.

Hippurites (Orbignya) lapeirousei Goldfuß; Slišković, p. 44.

Hippurites (Orbignya) lapeirousei Goldfuß; Polšak and Mamužić, p. 240.

Hippurites (Orbignya) lapeirousei n. subsp.; Polšak and Mamužić, p. 239.

Hippurites (O.) lapeirousei Goldfuß; Sladić-Tričunović, text-fig. 13b [cop. Goldfuß 1840].

Hippurites (Orbignya) cf. lapeirousei Goldfuß; Sladić-Tričunović, pp. 131, 147, pl. 11, fig. 1; pl. 12, fig. 1; text-fig. 14a.

Hippurites (Orbignya) lapeirousei Goldfuß; Slišković, pp. 15, 18.

Hippurites lapeirousei Goldfuß; Lupu, p. 222, pl. 4, fig. 10.

Hippurites (Orbignya) lapeirousei Goldfuß; Pleničar, pp. 87, 107, pl; 1, fig. 1; text-fig. 2.

Hippurites (O.) lapeirousei; Slišković, p. 139.

Hippurites (Orbignya) lapeirousei Goldfuß; Sladić-Tričunović, p. 258.

Hippurites lapeirousei; Sladić-Tričunović, pp. 428, 440.

H. lapeirousei; Laviano and Sirna, p. 69.

Hippurites (O.) lapeirousei Goldfuß; Sladić-Tričunović, p. 293.

Hippuriella lapeirousei (Goldfuß); Sánchez, p. 10 [with synonymy].

Hippuriella lapeirousei Gold.; Bilotte, p. 1020.

Hippuriella lapeirousei Gold.; Bilotte, p. 111.

H. lapeirousei; Czabaly, pp. 44, 81, pl. 24, fig. 1.

Hippurites (Orbignya) lapeirousei Goldfuß; Polšak et al., text-fig. 3.

Hippuriella lapeirousei (Goldfuß); Pons, tab. 3.

H. lapeirousei; Czabaly, text-fig. 3.

Hippuriella lapeirousei; Gallemi et al., tab. 3.

Hippurites (Orbignya) cf. lapeirousei Goldfuß; Özer, p. 18, pl. 3, fig. 3.

Hippuriella cf. lapeirousei Gold.; Philip, p. 90, fig. 4.

H. lapeirousei; Philip and Bilotte, tab. 2.

Hippurites lapeirousei; Sladić-Tričunović, tab. 1.

Hippurites (O.) lapeirousei; Slišković, p. 12.

Hippuriella lapeirousei (Goldf.); Bilotte, pl. 39, fig. 9.

Hippurites (Orbignya) lapeirousei Goldfuß; Slišković, p. 215.


Hippurites (Orbignya) lapeirousei (Goldfuß); Polšak, pp. 4, 17.

Hippuriella espaillacianna espaillacianna (d'Orbigny); Pamouktchev, p. 100, pl. 2, figs 1–3 [cop. d'Orbigny 1847], figs 4–5 [cop. Toucas 1903], fig. 6 [cop. Douvillé 1895].
Hippuritella espaillaciana toucasí subsp. n. Pamoukchiev, p. 101, pl. 1, figs 4–5 [cop. Toucas 1903].

1986b *Hippurites* lapeiroseui Goldfuss; Pamoukchiev, p. 98, pl. 1, fig. 1 [cop. Goldfuss 1840], figs 2–3 [cop. Douvillé 1895].

1988b *H. lapeiroseui*; Özer, p. 49.

1989 *Hippurites* lapeiroseui; Accordi et al., p. 165.

1989 *Hippuritella lapeiroseui* (Goldf.); Pascual et al., p. 225, text-fig. 3.

1989 *H. lapeiroseui* Goldfuss; Sladić-Trifunović, p. 149.

1990 *Hippurites* lapeiroseui; Gušić and Jelaska, text-fig. 11.

1991 *Hippurites* (H. lapeiroseui; Floquet, text-fig. 286.

1992b *Hippurites* lapeiroseui Goldfuss; Özer, p. 133.

1992 *Hippuritella lapeiroseui* (Goldfuss); Swinburne et al., text-fig. 2.

1992 *Hippuritella lapeiroseui* (Goldfuss); Vicens, p. 125, pl. 1, figs 16–20; text-figs 4f, 8a–c.

1993b *Hippurites* lapeiroseui Goldfuss; Steuber, p. 47.

1993 *Hippurites* lapeiroseui Goldfuss; Steuber et al., text-fig. 11.

1993 *Hippurites* lapeiroseui Goldfuss; Swinburne and Noacco, p. 33.

1995a *Hippuritella lapeiroseui* (Goldfuss); Caffau, p. 124, pl. 1.

1995b *Hippuritella lapeiroseui* (Goldfuss); Caffau and Plemenčar, text-fig. 2b [cop. Vicens 1992], 2d [cop. Douvillé 1895].

1997 *Hippurites* aff. lapeiroseui Goldfuss; Morris and Skelton, p. 292, pl. 5, figs 1–2.

1997 *Hippuritella lapeiroseui* (Goldfuss); Höfling, pl. 17, figs 5–6.

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


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. lapeiroseui*. 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. lapeiroseui*.

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.

1993a *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 (1892a), plate 5, figure 9, 9a.

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

Description. See Steuber (1993a).

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].
v1892a Hippurites variabilis Munier-Chalmas; Douvillé, p. 50, pl. 7, fig. 17.
v1910 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.
1946a 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.
1965a Hippurites (Hippuritella) variabilis Munier-Chalmas; Polšak, p. 337.
1965b Hippurites (Hippuritella) variabilis Munier-Chalmas; Slošković, p. 373.
1966 Hippurites variabilis Munier-Chalmas; Todiria-Mihăilescu, p. 72, pl. 48, fig. 6.
1968 Hippurites variabilis Mun.-Chalm.; Bogdanović, p. 76.
1968a Hippurites (Hippuritella) variabilis Munier-Chalmas; Slošković, 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); Pankouktchiev, 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.; Bilote, text-fig. 2.
1981b Hippurites variabilis variabilis (Munier-Chalmas); Pankouktchiev, 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.; Bilote, p. 111.
1982 Hippurites variabilis Munier-Chalmas; Czabaley, pp. 44, 80, pl. 25, figs 3–5; text-fig. 23.
1982 Hippurites (Hippuritella) variabilis Munier-Chalm.; Polšak et al., text-fig. 3.
1982 Hippuritella variabilis (Mun.-Chalm.); Pons, tab. 2.
1983 Ha. variabilis; Philip and Bilote, tab. 1.
1983 Hippurites (Hippuritella) variabilis Munier-Chalmas; Slišković, pp. 3, 12.
1984 Hippurites variabilis (Munier-Chalmas); Busulini et al., p. 251, text-fig. 1.
1984b Hippuritella variabilis Munier-Chalmas; Slišković, p. 214.
1987 Hippuritella variabilis; Accorő et al., p. 140.
1989 Hippurites nabrescensis 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 1892a], figs 11–15; text-fig. 7.
1993 Hippurites (Hippuritella) variabilis; Camoin, p. 157.
1993b 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 (1892a), 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 Keratovoune Hill. Munier-Chalmas gave the original material of *H. variabilis* from Leychert to Douvillé, who provided a detailed description in 1892. Later, a badly preserved, squashed RV from the Munier-Chalmas collection from Keratovoune Hill was figured as *Hippurites maestrei* Vidal, 1878 (Douvillé 1897a, pl. 32, fig. 7). I did not find *H. maestrei*, *H. 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 wp' 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 CANALICULATUS Rolland du Roquan, p. 50, pl. 3, figs 2–4; pl. 7, fig. 2.
1893 HIPPURITES CANALICULATUS Rolland du Roquan; Douville, p. 61, pl. 8, figs 6–10.
1893 HIPPURITES CRASSICOSTATUS n. sp. Douville, p. 63, pl. 8, figs 11–13; pl. 9, fig. 1; text-fig. 45.
1895 HIPPURITES CANALICULATUS Rolland du Roquan; Douville, p. 173, pl. 26, figs 8a, 9a.
1932 HIPPURITES (Orbignya) CANALICULATUS Rolland du Roquan; Kühn, p. 40 [with synonymy].
1932 HIPPURITES (Orbignya) CRASSICOSTATUS Douville; Kühn, p. 45 [with synonymy].
1936 O. CANALICULATUS Roll. du Roq.; Antonini, p. 120.
1937 HIPPURITES (Orbignya) CANALICULATUS Rolland du Roquan; Oosterbaan, p. 103, pl. 2, figs 19–21.
1938 O. CANALICULATUS Rolland du Roquan; Antonini, p. 172.
1950 ORBIGNYA CANALICULATUS Rolland du Roquan; Rengarten, p. 47, pl. 8, figs 2a–b; text-fig. 20.
1965 H. (O.) CANALICULATUS Rollaand du Roquan; Manužič, p. 344.
1969 HIPPURITES (Orbignya) CANALICULATUS Rolland du Roquan; Polšak and Manužič, p. 239.
1981 H. (H.) CRASSICOSTATUS Douv.; Bilotte, text-fig. 2.
1981 HIPPURITES CANALICULATUS Rolland du Roquan; Sánchez, p. 16 [with synonymy].
1981 HIPPURITES CRASSICOSTATUS Douville; Sánchez, p. 17 [with synonymy].
1983 H. CANALICULATUS; Philip and Bilotte, tab. 1.
1984 HIPPURITES (Hippurites) CANALICULATUS Rolland du Roquan; Billette, pl. 38, fig. 5.
1989 H. CANALICULATUS Roll. du Roq.; Pascual et al., p. 224, text-fig. 3.
1992 HIPPURITES CANALICULATUS Rolland du Roquan; Vicens, p. 131, pl. 4, figs 1–3 [cop. Douville 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 Deprance, 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.
1897a *Hippurites colliciatus* Woodward; Douvillé, p. 221, pl. 32, fig. 8 [cop. Woodward 1855].
v.1897a *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.
1937 *H. (Orbignya) colliciatus* Woodward; Milovanović, p. 128.
1937 *Hippurites (Orb.) colliciatus* Woodward; Žapfe, p. 76, text-fig. 3.
1944b *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 1944b].

1946b *Hipp. (Orb.) colliciatus* Woodward; Stchépinsky, p. 354.
1959 *Hippurites colliciatus* Woodward; Aubouin, p. 152, pl. 16, fig. 2a.
1959 *Hippurites colliciatus* Woodward; Petkovski 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* Woodward; Cetlet, pl. 6, fig. 2a–b.
1962 *Hippurites exaratus* Zittel; Kaumanns, p. 303, text-fig. 5.
1963 *Hippurites colliciatus* Woodward; Ambrosetti, p. 213.
1965 *Hippurites (Orbignya) colliciatus* Woodward; Benkö-Czabalay, p. 402.
1969 *Hippurites (Orbignya) colliciatus* Woodward; Polšak and Mamuzić, p. 240.
1974 *Hippurites (Orbignya) colliciatus* Woodward; Slišković, p. 133.
1975d *H. (O.) colliciatus*; Slišković, p. 139.
1978 *Hippurites colliciatus* Woodward; Sladić-Trifunović, pp. 435, 443, fig. 8/1 [cop. Woodward 1855], fig. 8/2 [cop. Douvillé 1897a], 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.
1981b *Hippurites colliciatus* Woodward; Pamouktchiév, 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); Plenčar 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  

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 Radić, 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.

1989a  
*Hippurites colliciatus* Woodward; Cestari and Sirna, p. 135, tab. 1, pl. 3, fig. 3.

1989b  
*Hippurites colliciatus* (Woodward); Cestari and Sirna, p. 19, pl. 1, fig. 1, tab. 1.

1989  
*Hippurites colliciatus*; Luperto Sini 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.

1992b  
*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 (1897a), 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 1989b; Reali 1992).

Hippurites cornucopiae Defrance, 1821

Text-figure 46A–C, E–F

*1821 Hippurites cornucopiae Defrance, p. 196.
1824 Hippurite, corne d’abondance; Defrance, Cahier 31, pl. 20, fig. 1, 1a–c [?non fig. 1, teste Douvillé 1897a].
v1897a Hippurites cornucopiae Defrance; Douvillé, p. 223, pl. 32, fig. 12.
v1910 Hippurites (Hippuritella) cornucopiae Defrance; Douvillé, p. 79, pl. 7, figs 3–4.
1932 Hippurites (Hippuritella) cornucopiae Defrance; Kühn, p. 43 [with synonymy].
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 Mažić, 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 Hippurites 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.
1992a 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 Hippurites 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 71, 1a–c.

Material. More than 20 sections of RVs in compact limestones from Akrafion (H259, H261, H264–H267, H337,
H573–H574), together with Hippuritella la peerousei (Goldfuß, 1840); other material from Gökdag, east of Tuz Gölu, 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 Gölu is more complete and shows the arrangement of the myocardial elements (Text-fig. 46b): 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 (1897a), 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 la peerousei (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 cornu vaccinum Bronn, 1831.

**Vaccinites archiaci** (Douvillé, 1892a)

Plate 23, figure 1; Text-figure 48A–C

*1892a Hippurites archiaci* Munier Chalmas; Douvillé, p. 45, pl. 5, figs 1–2, text-figs 30–33.

**v**1892a 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-Czabaly, 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 Mamuzić, p. 239.
TEXT-FIG. 48. *Vaccinites archiaci* (Douville, 1892a) from Grammatiko, Vermion Mountains. RV sections; A, H465; B, H532; C, H466. Scale bar represents 30 mm.

1971 *Vacc. archiaci* (Douv.); Vogel, p. 65.
1975 *Hippurites (Vaccinites) archiaci* Munier-Chalmas, *manuscr.*; Plemenar, pp. 95, 110, pl. 8, figs 1–2; pl. 9, fig. 1.
1976 *Hippurites archiaci* (Munier-Chalmas); Kühn, in Andrusov, 14.
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 *Vaccinites archiaci* Munier-Chalmas; Sánchez, p. 37 [with synonymy].
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.
1982 *Vaccinites chalmsi* (Douville); Czabalay, pp. 36, 75, pl. 13; pl. 15, figs 4, 7.
1982 *Vaccinites archiaci* (Mun.-Chal.); 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; Plemenar and Premru, p. 194.
1984 *Vaccinites archiaci* Munier-Chalmas; Bilotte, pl. 41, fig. 7.
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.
1992 *V. archiaci* Munier-Chalmas; Plemenar and Šribar, p. 305.
1992 *Vaccinites archiaci* Munier-Chalmas; Swinburne *et al.*, text-fig. 2.
1992 *Vaccinites archiaci* (Douville); Vicens, p. 139, pl. 6, fig. 7 [cop. Douville 1892a], 8–13, text-fig. 4a., tabs 9–10.

**Syntypes.** Douville (1892a) 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*’ (Douville 1892a, 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 (Douville, 1892a).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H532</td>
<td>60</td>
<td>224</td>
<td>30</td>
<td>98</td>
<td>1.6</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>H466</td>
<td>62</td>
<td>245</td>
<td>30</td>
<td>104</td>
<td>1.4</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td>H465</td>
<td>59</td>
<td>250</td>
<td>28</td>
<td>107</td>
<td>1.0</td>
<td>0.5</td>
<td>0.5</td>
</tr>
</tbody>
</table>

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/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* (Douville, 1897a)

Text-figures 49D, G–H (cf.), J (cf.), K, 82A–B (cf.)

---

*1897a Hoppirites Boehmi* Douville, p. 197, pl. 30, figs 1–2; pl. 34, fig. 7.

*1897a* Hoppirites *Chalmasi* nov. sp. Douville, p. 210, pl. 34, figs 3–4.

1932 *Hoppirites* (Vaccinites) *boehmi* Douville; Kühn, p. 39 [with synonymy].

1932 *Hoppirites* (Vaccinites) *chalmasi* Douville; Kühn, p. 41 [with synonymy].

1933a *Hoppirites* (Vaccinites) *chalmasi* Douville; Kühn, p. 153.

1937 *H. boehmi* Douv.; Zapfe, p. 75.

1939 *Hoppirites* (Vaccinites) *boehmi* Douville; Klinghardt, p. 137, pl. 3, fig. 4, 4a.

1942 *Hoppirites* boehmi Douville; Kühn and Andrusov, p. 458.

1947 *H. boehmi* Douv.; Kühn, p. 185.

1947 *Hoppirites* (Vaccinites) *boehmi* Douville pars; Müllerried, p. 390, text-figs 20–25.

1954 *H. (V.) boehmi* Douville; Milovanović, p. 164.


1959 *Hipp. (Vacc.) boehmi* Douville; Petković et al., p. 287.

1960 *V. chalmasi* Douv.; Aubouin et al., p. 462.


1961a *Hoppirites* (V.) boehmi Douville; Polšak, p. 422.

1961b *Hoppirites* (Vaccinites) *boehmi* Douville- Polšak, p. 442, pl. 2, fig. 2.

1964 *H.(V.) boehmi* Douville; Polšak, p. 67.


1968 *Hoppirites* boehmi Douville; Kennedy and Taylor, p. 326, text-fig. 1.

1968a *Hoppirites* (Vaccinites) boehmi Douville; Slišković, p. 39.

1969 *Hoppirites* (Vaccinites) boehmi Douville; Polšak and Mamičić, p. 239.

1974 *Hoppirites* (Vaccinites) *boehmi* Douville; Lupu, p. 63, pl. 5, fig. 20, 20a–b.


1974 *Hoppirites* (Vaccinites) *boehmi* Douville; Slišković, p. 133.

1974 *Hoppirites* (Vaccinites) *boehmi* n. subsp.; Slišković, p. 133.

1975a *H. (V.) boehmi* Douville; 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 Douville; Carbone and Sirna, p. 436, text-figs 4b, 6.
TEXT-FIG. 49. A–B, F, I, Vaccinites praesulcatus (Douville, 1897a); c, Vaccinites sp.; E, V. sulcatus (Defrance, 1821); D, k, V. boehmi (Douville, 1897a); G–H, J, V. cf. boehmi (Douville, 1897a); 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.

1981b Vaccinites chalmasi (Douville); Pamouktchiev, p. 171, pl. 85, figs 1–2.
1981 Vaccinites boehmi (Douville); Sánchez, p. 39 [with synonymy].
1981 Vaccinites chalmasi (Douville); Sánchez, p. 40 [with synonymy].
non 1982 Vaccinites chalmasi (Douville); Czabalay, pp. 36, 75, pl. 13, fig. 9; pl. 15, figs 4, 7.
1982 Hippurites (Vaccinites) boehmi Douville; Polšak et al., text-fig. 3.
1985 Vaccinites boehmi Douville; Lupu, in Kollmann et al., p. 129, pl. 4, figs 15–20.
1985 H. (V.) boehmi Douville; Slišković, p. 17.
?1989b Vaccinites boehmi (Douville); Cestari and Sirna, p. 19, tab. 1, pl. 1, fig. 2.
1989 Vaccinites boehmi Douville; Merighis, 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 (1897a), 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, 1897a); 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/P0–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, 1897a).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P22</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H392</td>
<td>46</td>
<td>163</td>
<td>33</td>
<td>78</td>
<td>0.9</td>
<td>0.7</td>
<td>0.8</td>
</tr>
<tr>
<td>H419</td>
<td>43</td>
<td>179</td>
<td>32</td>
<td>96</td>
<td>1.1</td>
<td>0.9</td>
<td>0.8</td>
</tr>
<tr>
<td>H426</td>
<td>46</td>
<td>195</td>
<td>38</td>
<td>114</td>
<td>1.1</td>
<td>0.7</td>
<td>0.7</td>
</tr>
</tbody>
</table>

**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, 1897a) has been considered to be a synonym of *V. boehmi* by Toucas (1904) and Parona (1926). Kühn (1932, 1933a) 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, 1892a).

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


*Vaccinites chaperi* (Douvillé, 1897a)

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

?1865 *Hippurites Taburnii* v. sp. Guiscardi, p. 2, pl. 1, fig. 1.

v*1897a* *Hippurites Chaperi* nov. sp. Douvillé, p. 214, pl. 30, fig. 7.

*Vnon* 1897a *Hippurites Chaperi* nov. sp. Douvillé, p. 214, pl. 30, fig. 6.

v·1897a *Hippurites Taburnii*? Guiscardi; Douvillé, p. 216, pl. 30, fig. 8.

1899 *Hippurites Taburnii* Guiscard.; 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 Ktanas, p. 698, 1 text-fig.

non 1911b 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 Ktanas; Kühn, p. 38.
p1932 Hippurites (Vaccinites) chaperi Douvillé; Kühn, p. 41.
p1932 Hippurites (Vaccinites) taburni Guiscardi; Kühn, p. 70.
1932 Vaccinites Taburni Guiscardi; Milovanović, p. 51, pl. 2, fig. 2.
1934 Hippurites (Vaccinites) chaperi Douvillé; Milovanović, p. 199, text-figs 4–5.
1934 Hippurites (Vaccinites) atheniensis Ktanas; Milovanović, p. 202, text-fig. 6 [cop. Ktanas 1907], 7–13.
1948 Hippurites (Vaccinites) atheniensis Ktanas; 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 Ktanas; Milovanović, p. 164.
1954 H. (V.) atheniensis Ktanas var. serbicus nov.var. Milovanović, p. 165, text-figs 1–2.
1954 H. (V.) chaperi Douville; Milovanović, p. 164.
1957 Hippurites (Vaccinites) atheniensis Ktanas; Pašić, p. 119, pl. 35, fig. 1; pl. 37, fig. 1; text-fig. 60.
1957 Hippurites (Vaccinites) atheniensis Ktanas; Pejović, p. 95, pl. 24, fig. 1; pl. 25, fig. 1; pl. 26, fig. 1; pl. 27, fig. 1.
1959 Hippurites atheniensis Ktanas; Kühn and Pejović, p. 981.
1959 Hipp. (Vacc.) atheniensis Ktanas; Petković et al., p. 282.
1959 Hipp. (Vacc.) chaperi Douvillé; Petković et al., p. 287.
p1959 Hippurites (Vaccinites) atheniensis Ktanas; Polšak, pp. 58, 73, pl. 1, figs 1–3; pl. 2, fig. 2; pl. 3, fig. 1; text-fig. 1.
1960 Vaccinites atheniensis Ktanas; Aubouin et al., p. 458.
1960 Hippurites chaperi Mun.-Chal.; Aubouin et al., p. 459.
1960 Hippurites atheniensis Ktanas; Kühn, p. 48.
1960 Hippurites atheniensis Ktanas; Milovanović, p. 367.

1962 Hippurites atheniensis Ktanas; Kaumanns, p. 296.
1962 Hippurites (Vacc.) atheniensis Ktanas; Slišković et al., p. 130.

?1963b Hippurites (Vaccinites) atheniensis Ktanas; Slišković, p. 8, pl. 1, fig. 1.
1964 Hippurites (Vaccinites) atheniensis Ktanas; Polšak, p. 67.
1965 Hippurites (Vaccinites) atheniensis Ktanas; Benkő-Czabaly, p. 402.
1965 H. (V.) atheniensis Ktanas; Mamužić, p. 344.
1967 Hippurites (Vaccinites) atheniensis Ktanas; Plenčar and Buser, p. 156, pl. 7, fig. 1.
1967b Hippurites (Vaccinites) atheniensis Ktanas; Polšak, pp. 118, 210, pl. 73, figs 1–2; text-fig. 39.

EXPLANATION OF PLATE 21

Fig. 1. Vaccinites chaperi (Douvillé, 1897a); H531, Moukharemi Hill (Verkuijun Mountains); × 1.
Fig. 2, 4–5. Vaccinites curtuvaccinum (Brom, 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.
TEXT-FIG. 50. Pseudocolony with (a) *Vaccinates* cf. *boehmi* (Douvillé, 1897a) and (b–f) *V. praesulcatus* (Douvillé, 1897a) from Paleokastron Hill. RV sections; H563. Scale bar represents 30 mm.


1967 *Hippurites atheniensis serbicu* Milovanović; Sladić-Trifunović, pp. 277, 282, text-fig. 22 [cop. Milovanović 1954].

1967 *Hippurites (Vaccinates) 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 (Vaccinates) atheniensis* Ktenas; Slišković, p. 38.

1968a *Hippurites (Vaccinates) chaperi* Douvillé; Slišković, p. 38.

1969 *Hippurites (Vaccinates) atheniensis* Ktenas; Polšak and Mamužić, p. 239.

1969 *Hippurites (Vaccinates) chaperi* Douvillé; Polšak and Mamužić, p. 239.

1970 *Hippurites atheniensis* (Ktenas); Benkö-Czabalay, p. 277.

1971a *Hippurites (Vaccinates) atheniensis* Ktenas; Slišković, p. 40.

1971a *Hippurites (Vaccinates) chaperi* Douvillé; Slišković, p. 40.

1973 *Vaccinates atheniensis* Ktenas; Mercier, p. 311, pl. 1, fig. 1.

1973 *Hippurites (Vaccinates) atheniensis* Ktenas; Sakellariou-Mané, p. 399, pl. 4, figs 1–2.

1974 *Vac. chaperi* (Douv.); Philip, p. 112.

1975 *Hippurites (Vaccinates) chaperi* Douvillé; Pleničar, pp. 98, 111, pl. 13, fig. 1; pl. 14, figs 1–2.

1976 *Vaccinates chaperi* Douvillé; Lupu, p. 116, pl. 5, fig. 3; pl. 37, fig. 4.

1978 *Vaccinates atheniensis* Ktenas; Pamouktchiev, p. 238, tab. 1.

1978a *Vaccinates 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 *Vaccinates atheniensis* (Ktenas); Combes et al., p. 353.

TEXT-FIG. 51. *Vaccinates chaperi* (Douvillé, 1897a). RV sections; A, holotype; B, D–G, RVs from Moukharem; 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.
non 1981b Vaccinítes atheniensis (Ktenas); Pamoukchíev, p. 177, pl. 86, fig. 3.
1981 H. (V.) atheniensis Ktenas; Polšák, p. 454.
1981 Vaccinítes atheniensis (Ktenas); Sánchez, p. 38 [with synonymy].
1981 Vaccinítes atheniensis grubici (Sladić-Trifunović); Sánchez, p. 38 [with synonymy].
1981 Vaccinítes chaperi (Douville); Sánchez, p. 41 [with synonymy].
1982 Vaccinítes atheniensis (Ktenas); Accordi et al., p. 770, pl. 4, figs 2, 6.
1982c Pseudovaccinítes chaperi Douv.; Bilotte, p. 112.
1982 Vaccinítes atheniensis Ktenas; Czabalay, pp. 34, 74, pl. 11, fig. 3; pl. 12, fig. 1; text-fig. 13.
1982 Hippurítes (Vaccinítes) atheniensis Ktenas; Polšák et al., text-fig. 3.
1982 Vaccinítes chaperi (Douville); Pons, tab. 1.
1983 Vaccinítes atheniensis (Ktenas); Czabalay, p. 187.
1983 Vaccinítes chaperi; Gallemi et al., tab. 3.
1983 H. (Vacc.) atheniensis Ktenas; Plenčar and Premru, p. 192.
1983 Vaccinítes atheniensis; Sladić-Trifunović, tab. 1.
?1985 Vaccinítes atheniensis (Ktenas); Caminiti, p. 133, pl. 30, fig. 1.
1987 Vaccinítes atheniensis; Accordi et al., p. 139.
1987 Vaccinítes gaudryi (Munier-Chalmas); Konertz, pl. 1, fig. 4.
1987 Vaccinítes atheniensis (Ktenas); Pejović and Radićić, p. 126, tab. 2.
1989b Vaccinítes atheniensis Ktenas; Philip et al., p. 1382.
1990 Vaccinítes atheniensis; Gušić and Jelaska, text-figs 8, 11.
1991 Hippurítes (Vaccinítes) atheniensis Ktenas; Širbar and Plenčar, p. 179.
1991 H. (Vacc.) Douville; Širbar and Plenčar, p. 179.
1992a V. atheniensis (Ktenas); Peza, p. 87.
1992a V. chaperi Douville; Peza, p. 87.
1992 Vaccinítes atheniensis Ktenas; Swinburne et al., text-fig. 2.
1993 Vaccinítes atheniensis (Ktenas); Cherchi et al., p. 95, pl. 5, fig. 1.
?1993 Vaccinítes taburni (Guiscardi); Cherchi et al., p. 95, pl. 5, fig. 4.
1993 Vaccinítes chaperi (Douville); Gill, tab. 1.
1993b Vaccinítes cf. chaperi (Douville); Steuber, p. 44.
1993b Vaccinítes atheniensis (Ktenas); Steuber, p. 46.
1993 Vaccinítes atheniensis (Ktenas); Steuber et al., p. 260, text-fig. 9.
1994 Vaccinítes atheniensis; Jeričić et al., text-fig. 2.
1996 Vaccinítes fortissi (Catullo); Cestari et al., p. 171, text-figs 1, 2a–n, 30–z.
1996 Vaccinítes atheniensis; Sanders, p. 852.

Holotype. Douville (1897a), plate 30, figure 7.

Material. Six RVs from the top of Paleovouna Mountain, Helicon range, (H257–H258, H259), one from Kiriaki village (H528), two from the quarry at Tsouka Hill (H497, H556) and 21 from the Vermion Mountains (Moukharem, 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(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 ‘Vaccinítes atheniensis grubici (Sladić-Trifunović, 1967b)’. Accessory cavity shallow and
TEXT-FIG. 52. *Vaccinates chaperi* (Douville, 1897a) from Vermion Mountains. RV sections; A–C, H560; Moucharemi; different growth stages of one valve; D, H531; E, H557; F, H3; Moucharemi. 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 *Vaccinates chaperi* (Douville, 1897a). The intraspecific variability within a few generations of the species is demonstrated by numerous specimens that have been collected from a single horizon at Moucharemi Hill (Vermion Mountains) where the shells are preserved
TABLE 9. Measurements (mm) of RVs of *Vaccinites chaperi* (Douville, 1897a).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>holotype</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douv. 1897a, pl. 30, fig. 8</td>
<td>92</td>
<td>406</td>
<td>28</td>
<td>160</td>
<td>1.6</td>
<td>0.9</td>
<td>0.6</td>
</tr>
<tr>
<td>Vermion (n = 7)</td>
<td>114</td>
<td>556</td>
<td>42</td>
<td>269</td>
<td>1.1</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>min.</td>
<td>70</td>
<td>314</td>
<td>24</td>
<td>130</td>
<td>1.3</td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>max.</td>
<td>106</td>
<td>546</td>
<td>38</td>
<td>270</td>
<td>1.9</td>
<td>1.0</td>
<td>0.6</td>
</tr>
<tr>
<td>mean</td>
<td>92</td>
<td>430</td>
<td>31</td>
<td>190</td>
<td>1.5</td>
<td>0.7</td>
<td>0.5</td>
</tr>
</tbody>
</table>

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

EXPLANATION OF PLATE 22

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

Figs 2, 4. *Vaccinites chaperi* (Douville, 1897a); Moukharemi Hill (Vermion Mountains); sub-polygonal pores of LV. 2, H581; × 7.7. 4, H558; × 7.1.

Figs 3, 5–6. *Vaccinites cornuvaccinum* (Bonn, 1831); Keratovouno Hill; sub-polygonal, partly denticulate pores of LVs. 3, H69; 5, H580; 6, H476. All × 7.3.
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 (1897a, pl. 30, fig. 6) figured, together with the holotype and under the same name, a RV of *Vaccinites cornuvaccinum* (Bonn, 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* (Bonn, 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, 1897a) from Vermion Mountains (dots), the holotype (flag) and in ‘Hippurites Taburnii’ (+, after Douvillé 1897a, 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 (Brown, 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, 1892a) 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. cornu-vaccinum* (Bonn, 1831).

**Vaccinites cornu-vaccinum** (Bonn, 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 *Hippurites cornu-vaccinum* n. s. Bronn, p. 374.
1832 *Hippurites cornu vaccinum* n. sp. Bronn, p. 172.
1838 *Hippurites cornu-vaccinum*; Bronn, p. 634, pl. 31, fig. 2a–b.
1840 *Hippurites Cornu vaccinum*; Bronn; Goldfuß, p. 302, pl. 165, fig. 1.
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.
1851 *Hippurites cornu-vaccinum*; Cambon; d’Orbigny, p. 162, pl. 526, fig. 1.
1855 *Hippurites cornu-vaccinum*; Woodward, p. 43, pl. 4, figs 2–3, text-fig. 8.
1857 *Hippurites cornu-vaccinum*; Bayle, p. 665, pl. 15, figs 1–3.
1857 *Hippurites cornu-vaccinum*; Coquand, p. 501.
1858 *Hippurites cornu-vaccinum*; Zittel, p. 135, pl. 21, figs 1–7 (text Douvillé 1891, Kühn 1932).
1863 *Hippurites costulatus*; Goldfuß, p. 288, pl. 165, fig. 2a.
1865 *H. cornu-vaccinum*; Guiscardi, p. 2.
1866 *Hippurites cornu-vaccinum*; Bronn; Vaillant, p. 280 [text Kühn 1932].
1866 *Hippurites cornu-vaccinum*; Coquand, p. 501.
1868 *Hippurites cornu-vaccinum* Bronn; Zittel, p. 141, pl. 23, fig. 6 (= *Hippurites alpinus* teste Douvillé 1897a).
1866 *Hippurites Touciusianus* d’Orb.; Zittel, p. 140, pl. 23, fig. 5 (= *Hippurites alpinus* teste Douvillé 1897a).
1867 *Hippurites cornu-vaccinum*; Hébert, p. 364.
1867 *Hippurites Gaudryi* Munier Chalmas; Munier-Chalmas, in Gaudry, p. 390.
1868 *Hippurites cornu-vaccinum*; Quenstedt, p. 818, pl. 64, figs 22–23; text-fig. 305.
1880 *Hippurites cornu vaccinum*; Bonn; Bittner, p. 40.
1881 *Hippurites cornu-vaccinum*; Bonn; Boehm, p. 548.
1885 *Hippurites cornu-vaccinum*; Bonn; Peron, p. 263.
1888 *Hippurites Gaudryi* M.-Ch.; Munier-Chalmas, p. 819.
1891 *Hippurites cornu-vaccinum*; Bronn; Douvillé, p. 6, pl. 1, figs 1 [cop. Bronn 1838], 2 [cop. Goldfuß 1840], 3 [cop. Woodward 1855].
1891 *Hippurites cornu-vaccinum*; Douvillé, p. 6, pl. 1, fig. 4.
1892a *Hippurites gaudryi* Munier Chalmas; Douvillé, p. 48, pl. 7, fig. 2; text-fig. 34.
1892a *Hippurites gaudryi* Munier Chalmas; Douvillé, p. 48, pl. 7, figs 1, 3.
1897a *Hippurites alpinus* nov. sp. Douvillé, p. 217, pl. 34, fig. 5.
1897a *Hippurites alpinus*?; Douvillé, p. 217, pl. 32, figs 1–2.
1897a *Hippurites Chaperi* nov. sp. Douvillé, p. 214, pl. 30, fig. 6.
1897a *Hippurites cornu-vaccinum*; Bronn; Douvillé, p. 212, pl. 31, fig. 2.
1897a *Hippurites cornu-vaccinum*; Bronn; Douvillé, p. 212, pl. 31, figs 3–4.
1897a *Hippurites Gaudryi* Munier-Chalmas; Douvillé, p. 213, pl. 31, figs 5–6; pl. 34, figs 1–2.
1897a *Hippurites Gaudryi* Munier-Chalmas; Toucas, p. 99, figs 1–2.
1897a *Hippurites cornu-vaccinum*; Deprat, p. 238.
1897a *Hippurites Gaudryi*; Deprat, p. 238.
1901 *Hippurites vaccinum*; Toucas, p. 100, text-fig. 157.

**Text-fig. 57. Vaccinites cornu-vaccinum** (Bonn, 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.
1904 Hippurites (Vaccinites) cornu-vaccinicum Bronn; Toucas, p. 100, text-fig. 158.
1908b Hippurites (Vaccinites) Chaperi Douv.; Parona, p. 147, text-fig. 6.
1908b Hippurites (Vaccinites) Gaudryi Mun.-Chalm.; Parona, p. 148, text-fig. 8.
non 1910 Hippurites cornu-vaccinicum (Goldf.); Fraas, p. 158, text-fig. 99a–b (= Hippurites (Vaccinites) gosaviensis (Douville, 1890) teste Kühn 1932).

v. p1910 Hippurites (Vaccinites) Taburni Guiscardi; Douvillé, p. 41, pl. 2, figs 1, 2, 2a.
1914 H. cornu-vaccinicum; 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 cornu-vaccinicum Matheron; Klinghardt, p. 63
1922 Hippurites (Vaccinites) cornu-vaccinicum 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) cornu-vaccinicum Bronn; Klinghardt, p. 35, pl. 3, figs 10–11; text-fig. 9.
1932 Hippurites (Vaccinites) alpinus Douvillé; Kühn, p. 37.
1932 Hippurites (Vaccinites) cornu-vaccinicum 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-vaccinicum Bronn; Milovanović, p. 215, text-fig. 16.
1937 Hippurites (Vacc.) cornu-vaccinicum Bronn; Zapfe, p. 74.
1939 Hippurites (Vaccinites) alpinus Douvillé; Klinghardt, p. 135.
?1939 Hippurites (Vaccinites) cornu-vaccinicum Bronn; Klinghardt, p. 137.
1939 Hippurites (Vaccinites) cornu-vaccinicum Bronn, var. crassa Klinghardt; Klinghardt, p. 135.
1939 Hippurites (Vaccinites) gaudryi Munier-Chalmas; Klinghardt, pp. 133, 135.
1941 Hippurites (Vacc.) gaudryi Munier-Chalmas; Montagne, p. 61, pl. 4, fig. 4.
?1941 Hippurites cornu-vaccinicum Bronn; Stchépinsky, p. 17.
?1941 Hippurites cornu-vaccinicum Bronn; Tromp, p. 608.

non 1942 Hippurites cornu-vaccinicum Bronn; Stchépinsky, p. 53, pl. 7, fig. 14.
1943 Hippurites (Vaccinites) gaudryi Munier-Chalmas; Klinghardt, p. 128, pl. 8, fig. 9.
1943 Hippurites (Vaccinites) cornu-vaccinicum Bronn, text-fig. 5.
1944 Hippurites (Vaccinites) alpinus Douv.; Klinghardt, p. 201, pl. 4, fig. 4.
1944 Hippurites (Vaccinites) gaudryi Munier-Chalmas; Klinghardt, pl. 201, pl. 4, figs 6–7.
non 1946a Hippurites cornu-vaccinicum Bronn; Stchépinsky, p. 125, pl. 16, fig. 7 [cop. Stchépinsky 1942].
?1946b Hippurites cornu-vaccinicum Bronn; Stchépinsky, p. 353.
1948 Hippurites (Vaccinites) cornu-vaccinicum Bronn, var. gaudryi (Mun.-Ch.) Kühn; Kühn, p. 180, pl. 27, fig. 1; text-figs 8–11.
1948 Hippurites (Vaccinites) cornu-vaccinicum Bronn, var. gaudryi (Mun.-Ch.) Kühn; Kühn, p. 180, pl. 27, fig. 1; text-figs 8–11.
1948 Hippurites (Vaccinites) cornu-vaccinicum Bronn, var. gaudryi (Mun.-Ch.) Kühn; Kühn, p. 180, pl. 27, fig. 1; text-figs 8–11.
1951 Hippurites (Vaccinites) fortisi Catullo; Kühn, p. 177, text-fig. 5 [cop. Parona 1908b].
1954 Hippurites (Vaccinites) klinghardtii 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) cornu-vaccinicum Bronn, var. gaudryi (Mun.-Ch.) Kühn; Pašić, p. 123, text-fig. 62.
1957 Hippurites (Vaccinites) taburni Guiscardi; Pašić, p. 130, pl. 37, fig. 2.

TEXT-FIG. 58. Vaccinites cornu-vaccinicum (Bonn, 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.
1959 Vaccinítes gaudryi Mun. Chal.; Auboin, p. 62, pl. 1, fig. 1a.

1959 Hippurítes (Vaccinítes) cornuvaccínium gaudryi (Mun.-Chalm.) Kühn; Polšák, pp. 64, 74, pl. 5, figs 1–3; pl. 6, figs 1–2; text-fig. 2.

1960 Vaccinítes gaudryi Mun.-Chal.; Auboin et al., p. 458.

1960 Hippurítes cornuvaccínium Bronn; Kühn, p. 48.


1960 Hippurítes (Vaccinítes) archiári Mun. Chalmas Form B; Lupu and Lupu, p. 246, pl. 2, fig. 39; text-fig. 11.

1960 H. cornuvaccínium Bronn; Milovanović, p. 367.

1960 H. gaudryi; Milovanović, p. 367.

1960 H. cornuvaccínium Bronn var. gaudryi (Mun.-Ch.); Milovanović, p. 367.

1960 Hippurítes cornuvaccínium Bronn; Pejović and Kühn, p. 137.

1961 Hippurítes (Vaccinítes) cornuvaccínium Bronn var. gaudryi (Mun.-Ch.) Kühn; Pleničar, p. 54, text-figs 11–12.

1961 Hippurítes (Vaccinítes) cornuvaccínium Bronn var. gaudryi (Mun.-Ch.) Kühn; Pleničar, p. 56, pls 10–11, 14.

1961a Hippurítes (V.) cornuvaccínium Bronn; Polšák, pp. 422, 432.

1961a Hippurítes (V.) cornuvaccínium Bronn; Polšák, pp. 422, 432.

1961b Hippurítes (Vaccinítes) cornuvaccínium Bronn; Polšák, pp. 436, 451, pl. 1, figs 1–2.

1961b Hippurítes (Vaccinítes) cornuvaccínium Bronn; Polšák, pp. 438, 451, pl. 2, fig. 1.

1962 Vaccinítes cf. gaudryi M. Ch.; Celet, pl. 13, fig. 1.

1962 Hippurítes cornuvaccínium Bronn; Kaumanns, p. 300, text-fig. 3.

1962 Hippurítes cornuvaccínium gaudryi (Mun.-Ch.) Kühn; Kaumanns, p. 302, text-fig. 4.

1962 H. cornuvaccínium Bronn; Pleničar, p. 42.

1962 Hippurítes (Vacc.) cornuvaccínium Bronn; Śliškóvić et al., p. 131.

1962 Hippurítes (Vacc.) cornuvaccínium Gaudry (Mun. Chalm.) Kühn; Śliškóvić et al., p. 131.

1962 Vaccinítes gaudryi M. Ch.; Sornay, in Celet, p. 187, pl. 6, fig. 3a–b; pl. 7, fig. 4a–b.

1963b Hippurítes (Vaccinítes) cornuvaccínium Bronn; Śliškóvić, p. 9, pl. 2, fig. 1.

1963b Hippurítes (Vaccinítes) cornuvaccínium gaudryi (Mun.-Chalmas) Kühn; Śliškóvić, p. 10, pl. 2, fig. 2; pl. 3, fig. 1.

1964 Vaccinítes gaudryi Mun.-Chal.; Dercourt, p. 197.

1964 H. (V.) cornuvaccínium Bronn; Polšák, p. 67.

1965 Hippurítes (Vaccinítes) cornuvaccínium Bronn; Benkő-Czabálay, p. 402.

1965 Hippurítes (Vaccinítes) cornuvaccínium Bronn; Mamužić, p. 344.

1965 H. (V.) cornuvaccínium gaudryi (Mun.-Chalm.); Mamužić, p. 344.

1965b Hippurítes (Vaccinítes) cornuvaccínium Bronn; Polšák, p. 451.

1966 Vaccinítes cornuvaccínium gaudryi (Munier-Chalmas); Panoukhtchiev, p. 26, pl. 3, fig. 1.

1966 Hippurítes (Vaccinítes) cornuvaccínium Bronn var. gaudryi (Munier-Chalmas) Kühn; Todiria-Mihăilescu, p. 73, pls 23–24.

1967b Hippurítes (Vaccinítes) cornuvaccínium Bronn; Polšák, pp. 120, 211, text-fig. 41.


1968a Hippurítes (Vaccinítes) cornuvaccínium Bronn; Śliškóvić, p. 38.

1968a Hippurítes (Vaccinítes) cornuvaccínium gaudryi Kühn; Śliškóvić, p. 38.

1969 Hippurítes (Vaccinítes) cornuvaccínium Bronn; Polšák and Mamužić, p. 239.

1969 Hippurítes (Vaccinítes) cornuvaccínium gaudryi (Munier-Chalmas); Polšák and Mamužić, p. 239.

1969 H. cornuvaccínium Bronn; Sladić-Trifunović, text-figs 23 [cop. Bronn 1838], 24 [cop. Milovanović 1934].

1970 H. gaudryi Munier-Chalmas; Benkő-Czabálay, p. 283.

1971a Hippurítes (Vaccinítes) cornuvaccínium Bronn; Śliškóvić, p. 40.

1971a Hippurítes (Vaccinítes) cornuvaccínium gaudryi Kühn; Śliškóvić, p. 40.

1971 Vacc. cornuvaccínium (Bronn); Vogel, p. 65.


1974 Hippurítes (Vaccinítes) cornuvaccínium cornuvaccínium Bronn; Lupu, p. 59, pl. 4, fig. 15, text-fig. 7.

1974 Hippurítes (Vaccinítes) cornuvaccínium gaudryi Munier-Chalmas; Lupu, p. 60, pl. 4, fig. 16, text-fig. 8.


Text-fig. 59. Vaccinítes cornuvaccínium (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.
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 (Bonn); 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 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 gaudryi Munier-Chalmas; 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 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 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 (Douville); 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.
1982 Vaccinites cornuvaccinum gaudryi (Munier-Chalmas); Czabanay, pp. 35, 74, pl. 10, fig. 1.
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 (Douville); Pons, tab. 1.
1982 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 V. 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. cornuvaccinum gaudryi Mun.-Chalm.; Lupu, p. 22.
1985 Vaccinites cornuvaccinum gaudryi Munier-Chalmas; Lupu, in Kollmann et al., p. 129, pl. 1, fig. 1.
1987 Vaccinites gaudryi (Munier-Chalmas); Konertz, pl. 1, fig. 4.
1989b Vaccinites taburni (Guiscardi); Cestari and Sirna, p. 20, tab. 1, pls 4–6.
1989 Vaccinites sulcatus Deffrance; Ózer, pl. 337, p. 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.
1992a Vaccinites cornuvaccinum gaudryi (Mun.-Chalmas) Kühn; Chkhi-Aouimeur, p. 174, pl. 4.
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. *Vaccinies cornuvaccinum* (Brom, 1831). RV sections; A–G, from Pavlos; H, from Makroastron; A, H495; B, H480; C, H494; D, H481; E, H489; F, H490; G, H585; H, H166. Scale bar represents 30 mm.

1992 *V. cornuvaccinum* Brom; Peza, p. 87.
1993 *Vaccinies taburni* Guiscardi; Carannante *et al*., p. 28, text-fig. 2a.
1993 *Vaccinies gaudryi* Munier-Chalmas; Cherchi *et al*., p. 95, text-fig. 2.
1993 *Vaccinies 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 Kalamas Hill. RV sections; a, H241; b, H234; c, H232; d, H230; e, H236. Scale bar represents 30 mm.

1993b Vaccinites alpinus (Douville); Steuber, p. 44, pl. 1, fig. 7.
1993b Vaccinites cornuvaccinum (Munier-Chalmas); Steuber, p. 44, pl. 1, fig. 5.
1993b Vaccinites gaudryi (Munier-Chalmas); Steuber, p. 44, pl. 1, fig. 6.
1993b Vaccinites cf. boehni (Douville); Steuber, p. 46, pl. 1, fig. 4.
1993 V. aff. boehni (Douville); Steuber et al., text-fig. 8.
1993 Vaccinites alpinus (Douville); 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.
1996b 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.

Additional material. The specimen figured by Goldfuß (1840, pl. 165, fig. 1); the holotype of Vaccinities alpinus (Douville, 1897a), several figured originals and topotypes from the collection of the Ecole des Mines (Lyon), and another topotype (MNHB-KC 8015).

Remarks. Douville (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 (Douville 1892a, 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 (Douville 1897a); 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. cornuvacinum and Vaccinities taburnii (Guiscardi, 1865) have been addressed frequently (e.g. ChikhAli-Aouimeur 1992a, 1992b). 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 1989b), while others consider its rounded termination as a characteristic feature (ChikhAli-Aouimeur 1992a). V. gaudryi has been considered a variety (Kühn 1948), subsequently a subspecies (Polshak 1959) of V. cornuvacinum, and was finally regarded to be...
indistinguishable from *V. cornuwacccimum* (Höfling 1985). In respect of this taxonomic confusion it seems useful to define *Vaccinites cornuwacccimum* 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 toptotypic, 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 0.3-0.5 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 6-7 mm over the tip of P0.

Transverse section 23 mm below commissure: General morphology of pillars unchanged, but diagenetic thinning of P0 is more pronounced. (1) separates anterioventral 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/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, 1897a) 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

**EXPLANATION OF PLATE 24**

Figs 1-6. *Vaccinites cornuwacccimum* (Bonn, 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.
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 IP0 and IP2 (Text-fig. 66). P2 almost generally longer than P0 or P1. LP0/IP1 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, posterovertrally 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, 1897a). Boxes, P1 with parallel sides; dots, P1 with pinched base; +, P1 with peduncled base.

Systematic position. Douvillé (1892a) 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
recognition of a truncated P0 in *V. cornuvaccinum* (Douville 1897a), 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* (Douville, 1897a). Despite their similarity, both species were maintained, even though Douville (1897a, 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.
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 (1892a) 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 (1892a, p. 48; 1897a, 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 1897a). 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 (1992b) and are caused by an insufficient knowledge of the holotype. The drawing
(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 IP0 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, 1897a) 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/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 IP0/IP1 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 (Brönn, 1831) and (+, asterisk = holotype) V. chaperi (Douvillé, 1897a). Ontogenetic stages of individual valves are connected by lines, respectively. See Text-figure 11 for measurements.

P1. Therefore, low IP0/IP1 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 (1897a) 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 *Vaccinites cornuvaccinum* (Broml, 1831).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>neotype:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adult</td>
<td>98</td>
<td>247</td>
<td>21</td>
<td>158</td>
<td>1.4</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td>juvenile</td>
<td>69</td>
<td>272</td>
<td>22</td>
<td>100</td>
<td>1.5</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td>toptotypes:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douv. 1891, pl. 1, fig. 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adult</td>
<td>105</td>
<td>432</td>
<td>30</td>
<td>161</td>
<td>1.4</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td>juvenile</td>
<td>81</td>
<td>321</td>
<td>29</td>
<td>117</td>
<td>1.5</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>Douv. 1897a, pl. 31, fig. 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adult</td>
<td>92</td>
<td>390</td>
<td>33</td>
<td>158</td>
<td>1.4</td>
<td>0.8</td>
<td>0.6</td>
</tr>
<tr>
<td>juvenile</td>
<td>81</td>
<td>336</td>
<td>31</td>
<td>130</td>
<td>1.6</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>Douv. 1897a, pl. 31, fig. 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Keratovouno (n = 14)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>min.</td>
<td>44</td>
<td>159</td>
<td>17</td>
<td>62</td>
<td>1.2</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>max.</td>
<td>57</td>
<td>232</td>
<td>25</td>
<td>99</td>
<td>1.5</td>
<td>0.8</td>
<td>0.7</td>
</tr>
<tr>
<td>mean</td>
<td>50</td>
<td>204</td>
<td>21</td>
<td>81</td>
<td>1.3</td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Anthochorion (n = 14)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>min.</td>
<td>50</td>
<td>217</td>
<td>16</td>
<td>84</td>
<td>1.0</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>max.</td>
<td>75</td>
<td>381</td>
<td>30</td>
<td>157</td>
<td>1.8</td>
<td>1.0</td>
<td>0.7</td>
</tr>
<tr>
<td>mean</td>
<td>66</td>
<td>280</td>
<td>22</td>
<td>107</td>
<td>1.4</td>
<td>0.8</td>
<td>0.6</td>
</tr>
<tr>
<td>Dionysos (n = 17)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>min.</td>
<td>46</td>
<td>188</td>
<td>14</td>
<td>76</td>
<td>1.0</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>max.</td>
<td>69</td>
<td>312</td>
<td>26</td>
<td>125</td>
<td>1.6</td>
<td>0.9</td>
<td>0.7</td>
</tr>
<tr>
<td>mean</td>
<td>59</td>
<td>248</td>
<td>21</td>
<td>99</td>
<td>1.3</td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Kalamos (n=4)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>min.</td>
<td>52</td>
<td>198</td>
<td>16</td>
<td>72</td>
<td>1.0</td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>max.</td>
<td>69</td>
<td>283</td>
<td>26</td>
<td>116</td>
<td>1.4</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td>mean</td>
<td>59</td>
<td>241</td>
<td>21</td>
<td>97</td>
<td>1.2</td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Pavlos (n = 16)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>min.</td>
<td>45</td>
<td>164</td>
<td>17</td>
<td>63</td>
<td>0.9</td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>max.</td>
<td>75</td>
<td>339</td>
<td>32</td>
<td>148</td>
<td>1.4</td>
<td>0.8</td>
<td>0.6</td>
</tr>
<tr>
<td>mean</td>
<td>60</td>
<td>239</td>
<td>25</td>
<td>106</td>
<td>1.2</td>
<td>0.6</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Inner termination of P0 of the juvenile shell in one specimen is truncated, in adult specimens it is rounded or tapering. Unfortunately, the figures (Polšák 1959, pl. 5, figs 1–3) do not reveal whether the ligament was actually ontogenetically atrophied, but the pedunculate P2 of this RV from Rakičev 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 1968a; Polšák 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 1897a, 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* (Bonn, 1831) and (dots, asterisk = holotype) *V. chaperi* (Douville, 1897a). See Text-figure 11 for measurements.

p. 254) repeatedly mentioned the occurrence of both species from the Gosau and the Bakony Mountains (*'athenienis-gaudryi-' or *'athenienis-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* (Douville, 1892a) 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.
TEXT-FIG. 72. A–D, *Vaccinites* aff. *cornuvaccinum* (Bronn, 1831) from Paleokastron Hill; E–F, *V. chaperi* (Douville, 1897a) 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, IP1/IP1 plotted against U in (dots; flag = neotype; asterisks = topotypes) *Vaccinites cornuvaccinum* (Bronn, 1831) and (+) *V. chaperi* (Douville, 1897a) 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* (Douville, 1897a), material from Boeotia, Vermion Mountains, collection Ecole des Mines, and after Kienas (1907); Milovanović (1934); Kühn (1948); Milovanović (1954); Polšak (1967b); Sličić-Trifunović (1967b); Slišković (1967); Lupu (1976); arrow to the right indicates value of holotype.
TABLE 11. Measurements (mm) of RVs of *Vaccinites aff. cornuvaccinum* (Bonn, 1831).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P₀ – P₂</th>
<th>P₀ – P₂ cont</th>
<th>IP₀/IP₁</th>
<th>IP₀/IP₂</th>
<th>IP₁/IP₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>H413</td>
<td>84</td>
<td>380</td>
<td>41</td>
<td>171</td>
<td>1.3</td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>H537</td>
<td>70</td>
<td>331</td>
<td>30</td>
<td>142</td>
<td>1.9</td>
<td>1.1</td>
<td>0.6</td>
</tr>
<tr>
<td>H550</td>
<td>80</td>
<td>361</td>
<td>30</td>
<td>153</td>
<td>1.5</td>
<td>0.9</td>
<td>0.6</td>
</tr>
<tr>
<td>H551</td>
<td>68</td>
<td>398</td>
<td>34</td>
<td>134</td>
<td>1.6</td>
<td>1.0</td>
<td>0.6</td>
</tr>
</tbody>
</table>

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 (1908b) and assigned to *V. chaperi* (Douville, 1897a). 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 (1961b) 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* (Douville, 1897a), *V. gaudryi* (Munier-Chalmas, 1867) and *V. taburnii* (Guiscard, 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* (Douville, 1892a) and (boxes) *V. aff. cornuvaccinum* (Bonn, 1831). Bold lines delimit the intraspecific variation of *V. cornuvaccinum* (cf. Text-fig. 64). See Text-figure 11 for measurements.
knowledge of the type specimen of *V. forti*si. 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 forti*si (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 (1989b). The occurrence of *V. cornuvaccinum* (or *V. alpinus*) in the Pyrenees (Klinghardt 1931; Gallema et al. 1983; Bilotte 1984) is controversial (Vicens 1992, p. 140).
**TEXT-FIG. 75.** A–B, *Vaccinates giganteus* (d’Hombres-Firmas, 1838) from Paleokastro Hill; C–G, I, *V. vredenburgi* (Kühn, 1933a) from Paleokastro 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.

**Vaccinates aff. cornuvaccinum** (Bronn, 1831)

Plate 23, figure 4; Text-figure 72A–D

**Material.** Seven RVs from Paleokastro 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 at a varying extent, P2 is strongly pinched, straight or curved anteriorly and oval to sickle-shaped. U/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/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).

<table>
<thead>
<tr>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H415</td>
<td>68</td>
<td>334</td>
<td>42</td>
<td>180</td>
<td>0.9</td>
<td>0.8</td>
</tr>
<tr>
<td>H420</td>
<td>80</td>
<td>370</td>
<td>53</td>
<td>184</td>
<td>0.9</td>
<td>0.7</td>
</tr>
</tbody>
</table>

(Text-fig. 73), and P0 is longer in relation to IP1 and IP2 (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.
*1891* Hippurites giganteus d’Hombres-Firmas; Douville, p. 19, pl. 3, fig. 5; text-fig. 7.
*1895* Hippurites giganteus d’Hombres Firmas; Douville, p. 152, pl. 22, fig. 1.
*1904* 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; Mählerried, p. 270.
*1935* Hipp. giganteus var. major; Klinghardt, p. 30.
*1936* Vaccinites giganteus d’Hombres-Firmas var. major Toucas; Mählerried, 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.
*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 medulminus n. subsp. Polšak, p. 67 [nomen nudum].
*1966b* H. (V.) giganteus medulminus Polšak; Slišković, p. 373 [nomen nudum].
*1967b* Hippurites (Vaccinites) giganteus medulminus 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 medulminus 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.
*1975* Hippurites (Vaccinites) giganteus medulminus 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. vesiculosis (Woodward, 1855); diamonds, V. giganteus (d'Hombres-Firmas, 1838); asterisks, V. vredenburgi (Kühn, 1933a); dots, V. praesulcatus (Douvillé, 1897a); black boxes, Vaccinites sp.; white triangles, V. boehmi (Douvillé, 1897a); black triangle, V. sulcatus (Deffrance, 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.
1979b 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, Paleostron Hill.
Fig. 2. Hippurites colliciatus Woodward, 1855; H416, Paleostron Hill.
Fig. 3. Vaccinites vredenburgi (Kühn, 1933a); H545, Paleostron Hill.
All transverse sections of RVs; × 1.
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 Bilotta, tab. 1.
1983 V. giganteus-major; Philip and Bilotta, 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.
1989b Vaccinites giganteus (d'Hombres-Firmas); Cestari and Sirna, p. 19, tab. 1, pl. 2, fig. 1.
1989 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.
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 P. 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 (Douville 1891) was based on para- and toptotypes.

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/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. M1’ 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, 1933a).
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 (Polšák et al. 1982). Specimens from the Campanian of Apulia (Laviano and Guarnieri 1989) that have been determined as *V. vredenburgi* (Kühn, 1933a) do not differ substantially from *V. giganteus.*
TEXT-FIG. 78. A–C, ontogeny of a RV of Vaccinates inaequicostatus (Münster, in Goldfuß, 1840) from Paleokastron Hill; H424. Scale bar represents 30 mm.

**Vaccinates** cf. **grossouvrei** (Douville, 1894)

*1894*  
*Hippurites Grossouvrei* n. sp. Douville, p. 118, pl. 18, figs 1–4.

1993a  
**Vaccinates** cf. **grossouvrei** (Douville); Steuber, p. 40 [with synonymy and description].

1993  
**Vaccinates** cf. **grossouvrei** (Douville); Steuber et al., p. 259.

**Holotype.** Douville (1894), plate 18, figure 1.

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

**Description.** See Steuber (1993a).

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

**Vaccinates inaequicostatus** (Münster, in Goldfuß 1840)

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

*1840*  
**Hippurites inaequicostatus** Münster, in Goldfuß, p. 303, pl. 165, fig. 4.

1897a  
**Hippurites inaequicostatus** Munster; Douillé, p. 199, pl. 30, fig. 3.

1897a  
**Hippurites inaequicostatus** Munster; Douillé, p. 199, pl. 30, fig. 5; pl. 33, figs 2–3.

1899  
**Hippurites inaequicostatus** Münst.; de Alessandri, p. 181, pl. 14, fig. 5; pl. 16, figs 2, 4–6.

1932  
**Hippurites (Vaccinates) inaequicostatus** Münster; Kühn, p. 52 [with synonymy].

1937  
**Vaccinates inaequicostatus** macgillavryi (Palmer); Mac Gillavry, p. 111, pl. 4, figs 1–8; pl. 10, fig. 2.

1937  
**Vaccinates inaequicostatus** vermuti n. sbssp. Mac Gillavry, p. 118, pl. 5, fig. 2.

1937  
**H. inaequicostatus** Münst.; Zapfe, p. 88.

1939  
**Hippurites (Vaccinates) inaequicostatus** Douville; 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, 1933a) 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.
?1946a *Hippurites (Vaccinites) inaequicostatus* Münster; Stchépinsky, p. 126, pl. 17, fig. 5.
?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.


*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.


1965 *H. (V.) inaequicostatus* Münster; Slišković, p. 373.
TABLE 13. Measurements (mm) of five RVs from Boeotia and the holotype of Vaccinutes inaequicostatus (Münster, in Goldfuß, 1840).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>min.</td>
<td>58</td>
<td>236</td>
<td>46</td>
<td>118</td>
<td>1.5</td>
<td>1.1</td>
<td>0.7</td>
</tr>
<tr>
<td>max.</td>
<td>83</td>
<td>356</td>
<td>52</td>
<td>177</td>
<td>1.7</td>
<td>1.4</td>
<td>0.9</td>
</tr>
<tr>
<td>mean</td>
<td>74</td>
<td>315</td>
<td>50</td>
<td>156</td>
<td>1.6</td>
<td>1.3</td>
<td>0.8</td>
</tr>
<tr>
<td>holotype</td>
<td>41</td>
<td>166</td>
<td>30</td>
<td>87</td>
<td>1.3</td>
<td>1.0</td>
<td>0.8</td>
</tr>
</tbody>
</table>

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

Holotype. Münster, in Goldfuß (1840), plate 165, figure 4; Douville 1897a, 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’). Douville’s (1897a) 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’ (Douville 1897a, 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).


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 IP1 and IP2, 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 (1967a); Slisković (1968c); Laviano and Gallo Maresca (1992), and Text-figure 85A, F of this study; (black flag = holotype) *V. inaequicoostatus* (Münster, *in* Goldfuß, 1840), specimens from Paleokastron Hill (dots) and the southern Alps (asterisks, after Douville 1897a); *V. macgillavyi* Palmer, 1933 from Somalia (diamonds, after Pons *et al.* 1992); *V. inaequicoostatus macgillavyi* Palmer, 1933 from Cuba (boxes, after Mac Gillavry 1937); *V. inaequicoostatus vrmunti* Mac Gillavry, 1937 from Cuba (triangle, after Mac Gillavry 1937). See Text-figure 11 for measurements.

sections. U/P0—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 inaequicoostatus* from the Mediterranean region and similar forms of the group around *V. inaequicoostatus macgillavyi* (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 IP0/IP2-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, 1897a) and V. cornuvaccinum (Brown, 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 Örmen (Philip and Plate 1996). Santonian–Campanian of the Apennines, Slovak 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.

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>min.</td>
<td>23</td>
<td>79</td>
<td>18</td>
<td>39</td>
<td>0.6</td>
<td>0.4</td>
<td>0.5</td>
</tr>
<tr>
<td>max.</td>
<td>40</td>
<td>154</td>
<td>29</td>
<td>72</td>
<td>1.5</td>
<td>1.1</td>
<td>0.9</td>
</tr>
<tr>
<td>mean.</td>
<td>32</td>
<td>123</td>
<td>24</td>
<td>60</td>
<td>1.1</td>
<td>0.8</td>
<td>0.7</td>
</tr>
</tbody>
</table>

**Vaccinites inferus** (Douvillé, 1891)

Plate 22, figure 1

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

Distribution. Middle–Upper Turonian of the Mediterranean region, Turonian–Coniacian of Caucasus.
TEXT-FIG. 81. *Vaccinities kühni* (Pejović, 1957) from Kefallinia. RV sections; A, H402; B, H403. Scale bar represents 30 mm.

*Vaccinities kühni* (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.
1967b *Hippurites (Vaccinities) kühni* Pejović; Polšak, pp. 124, 212, pl. 79, fig. 3.
1967b *Hippurites (Vaccinities) cf. kühni* Pejović; Polšak, p. 125, pl. 79, fig. 1.
1968a *Hippurites (Vaccinities) kühni* Pejović; Slišković, p. 39.
1981 *Vaccinities kühni* (Pejović); Sánchez, p. 49.
1982 *Hippurites (Vaccinities) 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. kühni* differs from *V. vredenburgii* (Kühn 1933a) by the lost ligament. *V. giganteus* (d'Hombres-Firmaus, 1838) has a longer P0, and P1 and P2 insert farther dorsally. A safe distinction from *V. vredenburgii*, however, is difficult, as only a few RVs of *V. kühni* from Istria and Serbia have been described and figured, and the LV is unknown.

Distribution. Santonian–Campanian of Serbia and Istria.

*Vaccinities ljalintzensis* Pamoukchiew, 1975

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

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

Material. Two fragments of RVs from Marmeko quarry (H251a, H310).
Description. See Steuber (1993a).

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.
1993a Vaccinites praegiganteus (Toucas); Steuber, p. 46, text-figs 6a–h, 8/6, 8/8 [with synonymy and description].
1993a Vaccinites praegiganteus (Toucas) var. glaensis; Steuber, p. 46, text-figs 6g–h, 8.
1993b 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 1897a, pl. 32, fig. 7) V. praesulcatus (Douvillé, 1897a); (diamonds, flag = holotype) V. boehmi (Douvillé, 1897a), and (box) the holotype of ‘V. chalmasi (Douvillé, 1897a)’. 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 (1993a).

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.
1993a *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 (1993a).

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

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>min.</td>
<td>52</td>
<td>216</td>
<td>27</td>
<td>94</td>
<td>0.8</td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>max.</td>
<td>73</td>
<td>293</td>
<td>42</td>
<td>137</td>
<td>1.4</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>mean</td>
<td>61</td>
<td>254</td>
<td>33</td>
<td>112</td>
<td>1.1</td>
<td>0.8</td>
<td>0.7</td>
</tr>
</tbody>
</table>

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

*Vaccinites praesulcatus* (Douville, 1897a)

Text-figures 49A–B, F, I, 50, 82A–C

*1897a Hippurites praesulcatus* nov. sp. Douville, p. 209, pl. 32, fig. 7, 7a.
1932 *Hippurites (Vaccinites) praesulcatus* Douville; Kühn, p. 62 [with synonymy].
1937 *H. praesulcatus* Douv.; Zapfe, p. 75.
1939 *Hippurites (Vaccinites) praesulcatus* Douville; Klinghardt, p. 133.
1941 *Hippurites (Vacc.) sulcatus* Defrance; Montagne, p. 62, pl. 4, fig. 5.

**non 1941 Hippurites (Vacc.) praesulcatus** Douville; Montagne, p. 62, pl. 4, fig. 6.

?1944 *Hippurites (Vaccinites) praesulcatus* Douv.; Klinghardt, p. 198, pl. 4, fig. 5.
1959 *Hipp. (Vacc.) praesulcatus* Douville; Petković et al., p. 282.
1959 *Vaccinites praesulcatus* Douv.; Rengarten, p. 256.
1961a *Hippurites (V.) praesulcatus* Douville; Polšak, pp. 422, 432.
1968a *Hippurites (Vaccinites) praesulcatus* Douville; Sliškovič, p. 36.
1969 *Hippurites (Vaccinites) praesulcatus* Douville; Polšak and Mamanžič, p. 239.
1975 *Hippurites (Vaccinites) praesulcatus* Douville; Plenčar, pp. 91, 109, pl. 2, figs 5–6; pl. 3, figs 1–2.
1981 *Vaccinites praesulcatus* (Douville); Sánchez, p. 54 [with synonymy].

**non 1982 Vaccinites praesulcatus** (Douville); Czabaj, pp. 31, 71, pl. 15, fig. 3.
1983 *Vaccinites praesulcatus*; Sladić-Trifunović, tab. 1.
1985 *Vaccinites praesulcatus* Douville; Lupu in Kollmann et al., p. 126, pl. 1, fig. 2.

?1989 *Vaccinites praesulcatus* Douville; 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* (Douville, 1897a).**

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>min.</td>
<td>49</td>
<td>186</td>
<td>34</td>
<td>94</td>
<td>0.5</td>
<td>0.4</td>
<td>0.7</td>
</tr>
<tr>
<td>max.</td>
<td>69</td>
<td>272</td>
<td>55</td>
<td>152</td>
<td>0.9</td>
<td>0.6</td>
<td>1.0</td>
</tr>
<tr>
<td>mean</td>
<td>58</td>
<td>233</td>
<td>45</td>
<td>127</td>
<td>0.7</td>
<td>0.5</td>
<td>0.8</td>
</tr>
</tbody>
</table>
TEXT-FIG. 84. Vaccinites salopekii (Pošlák, 1967b), Paleokastron Hill. RV section; H434. Scale bar represents 30 mm.

1989b Vaccinites praesulcatus Douvillé; Philip et al., p. 1381.
1997 Vaccinites praesulcatus (Douvillé); Steuber et al., p. 179, text-fig. 3f–g.

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

Material. Eighteen RVs from Paleokastron Hill, most of them in pseudocolonies with Vaccinites boehmi (Douvillé, 1897a) 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 49f, 82a). U/P0–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., 1989b).

Vaccinites ptoonensis Steuber, 1993a

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

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

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

Description. See Steuber (1993a).

Distribution. Middle Turonian–?Coniacian of Marmeko quarry (Boeotia).
Vaccinipes salopeki (Polšak, 1967b)

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].
*1967b Hippurites (Vaccinipes) salopeki n. sp. Polšak, pp. 112, 208, pl. 80, figs 1–3, 5; text-figs 34–35.
1968a Hippurites (Vaccinipes) salopeki Polšak; Sliškovič, p. 39.
1969 Hippurites (Vaccinipes) salopeki Polšak; Polšak and Maňužič, p. 239.
1974 Hippurites (Vaccinipes) salopeki Polšak; Lupa, pp. 66, pl. 3, fig. 14; text-fig. 15.
1974 Hippurites (Vaccinipes) salopeki Polšak; Sliškovič, p. 133.
1975 Hippurites (Vaccinipes) salopeki Polšak; Pleničar, pp. 96, 110, pl. 9, figs 2–3.
1981 Vaccinipes salopeki (Polšak); Sánchez, p. 55.
1982 Hippurites (Vaccinipes) salopeki Polšak; Polšak et al., text-fig. 3.
1985 H. (V.) salopeki Polšak; Sliškovič, p. 17.

Holotype. Polšak (1967b), 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 (Lupa 1974).

Vaccinipes sulcatus (Defrance, 1821)

Text-figure 49e

*1821 Hippurites sulcatus Defrance, p. 196.
1824 Hippurite sillonnée; Defrance, Cahier 31, pl. 20, fig. 3.
1892a Hippurites sulcatus Defrance; Douvillé, p. 43, pl. 5, figs 4–5 [cop. Defrance 1821].
v.1892a Hippurites sulcatus Defrance; Douvillé, p. 43, pl. 5, figs 6–8.
v.1895 Hippurites sulcatus Defrance; Douvillé, p. 159, pl. 23, fig. 2.
v.1897a Hippurites sulcatus Defrance; Douvillé, p. 207, pl. 32, figs 4–6.
1932 Hippurites (Vaccinipes) sulcatus Defrance; Kühn, p. 68 [with synonymy].
1935 Hipp. (Vaccin.) sulcatus var. maastrichtiensis Kühn; Klinghardt, p. 23.
1937 Hippurites sulcatus Defr.; Zapfe, p. 74, text-figs 2, 7, 10/4.
1941 Hippurites (Vacc.) prae.sulcatus Douvillé; Montagne, p. 62, pl. 4, fig. 6.
1941 Hippurites (Vacc.) sulcatus Defrance; Montagne, p. 62, pl. 4, fig. 5.
1954 H. (V.) sulcatus Defrance; Milovanović, p. 164.
1957a Vaccinipes sulcatus Defr.; Astre, p. 194.
1959 Hipp. (Vacc.) sulcatus Defrance; Petković et al., p. 282.
1960 Hippurites (Vaccinipes) 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; Polšák, p. 67.
1966b *Hippurites (Vaccinites) sulcatus* Defrance; Todiřič-Mihăilescu, p. 73, pl. 26, figs 1–2.
1969 *Hippurites (Vaccinites) sulcatus* Defrance; Polšák and Mamužić, p. 239.
1970 *H. (V.) sulcatus* Defrance; Benkö-Czabalay, p. 283.
1972b *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.
1975 *Hippurites (Vaccinites) sulcatus* Defrance; Plenčar, pp. 92, 109, pl. 3, figs 3–5.
1978 *Vaccinites sulcatus* (Defrance); Pamouktchiev, p. 235, tab. 1.
1978 *H. (V.) sulcatus* Defrance; Polšák et al., p. 190.
1979 *H. (V.) sulcatus* Defrance; Polšák, p. 205.
1981 *Ps. sulcatus* Defr.; Bilotte, text-fig. 2.
1981a *Vaccinites sulcatus* Defrance; Carbone and Sirna, p. 437, text-fig. 6.
1981b *Vaccinites sulcatus* Defrance; Pamouktchiev, p. 405, text-fig. 1.
1981c *Vaccinites sulcatus* Defrance; Pamouktchiev, p. 173, pl. 85, figs 6–7.
1981 *H. (V.) sulcatus* Defrance; Polšák, p. 454.
1981 *Vaccinites sulcatus* Defrance; Sánchez, p. 55 [with synonym].
1981c *Vaccinites sulcatus* Defrance; Bilotte, p. 111.
1982 *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; Polšák et al., text-fig. 3.
1982 *Vaccinites sulcatus* (Defrance); Pons, tab. 2.
1983 *Vaccinites sulcatus*; Babín et al., tab. 3.
1983 *V. sulcatus* (Defr.); Czabalay, p. 187.
1983 *V. sulcatus*; Philip and Bilotte, tab. 1.
1983 *H. (Vac.) sulcatus* Defrance; Plenčar and Premr, p. 192.
1983 *Vaccinites sulcatus*; Šaldač-Třifunović, 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 *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.
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. (Vac.) sulcatus* Defrance; Šrbar and Plenčar, p. 178.
1992 *V. sulcatus* (Defrance); Cestari et al., p. 366.
1992a *V. sulcatus* Defrance; Peza, p. 87.
1992b *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. Douville 1892a], figs 2–6.
1996 *Vaccinites sulcatus*; Sanders, p. 852.
1997 *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 (Douville 1892a). The syntype was obviously not available to Douville.
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, Bocotia. 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/P0–P2 is 4:6 (Text-fig. 76).

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

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H436</td>
<td>34</td>
<td>133</td>
<td>29</td>
<td>66</td>
<td>1·1</td>
<td>0·8</td>
<td>0·8</td>
</tr>
</tbody>
</table>
Remarks. *Vaccinites praesulcatus* (Douville, 1897a) 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 (Polšák et al. 1982), Upper Santonian–Lower Campanian of the Pyrenees, of southern France, the Gossau, Apennines, Hungary, Romania (Sánchez 1981), the Slovak 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.
1897a *Hippurites vesiculosus* Woodward; Douville, p. 201, pl. 29, fig. 7.
1897* Hippurites vesiculosus* Woodward; Douville, p. 201, pl. 29, fig. 8a–b; text-fig. 71.
1927 *Hippurites vesiculosus* Woodward; Böhm, p. 208, pl. 17, fig. 5.
1932 *Hippurites (Vaccinite) vesiculosus* Woodward; Kühn, p. 73 [with synonymy].
1933a *Hippurites bithynicus* nov. spec.; Kühn, p. 169.
1941 *Hippurites vesiculosus* Woodward; Tromp, p. 609.
1944a *H. vesiculosus* Woodward; Schépinsky, p. 97.
1944b *Hippurites (Vaccinite) vesiculosus* Woodward; Schépinsky, p. 237, pl. 3, fig. 1; pl. 4, figs 1, 5; pl. 5, figs 1, 3; pl. 7, fig. 3.
1946a *Hippurites (Vaccinite) vesiculosus* Woodward; Schépinsky, p. 129, pl. 20, fig. 1a–b [cop. Schépinsky 1944b].
1946b *Hippurites (Vaccinite) vesiculosus* Woodward; Schépinsky, p. 354.
1949 *Vaccinites vesiculosus* Woodward; Erentöz, p. 22, pl. 1, figs 3–4.
1951 *Hippurites (Vaccinite) inaequicoastus* Münster; Pejović, p. 95, pl. 2, fig. 1.
1968a *Hippurites (Vaccinite) bracieni* Sladić-Trifunović; Slišković, p. 43.
1969 *Hippurites (Vaccinite) bracieni* Sladić-Trifunović; Polšák and Manužić, p. 240.
1975 *Hippurites (Vaccinite) bracieni* Sladić-Trifunović; Plenčićar, pp. 103, 112, pl. 22, fig. 2; pl. 23, fig. 1.
1975d *H. (V.) bracieni*; Slišković, p. 139.
1976 *Vaccinites bracieni* Sladić-Trifunović; Karacakbey-Öztemür, p. 75, pl. 4, fig. 2; pl. 5, figs 1, 3–4.
1978 *Hippurites (Vaccinite) bracieni* Sladić-Trifunović; Polšák et al., p. 190.
1979 *Hippurites (Vaccinite) giganteus* d'Hombres-Firmas; Polšák, pp. 205, 224, pl. 9, fig. 7.
1979 *Hippurites (Vaccinite) inaequicoastus* Münster; Polšák, pp. 205, 224, pl. 9, figs 5–6.
1981 *Hippurites (Vaccinite) giganteus* d'Hombres-Firmas; Polšák, p. 454, text-fig. 8d [cop. Polšák 1979].
1981 *Hippurites (Vaccinite) inaequicoastus* Münster; Polšák, p. 454, text-fig. 8b–c [cop. Polšák 1979].
1981 *Vaccinites bracieni* [sic] (Sladić); Sánchez, p. 40 [with synonymy].
1981 *Vaccinites vesiculosus* (Woodward); Sánchez, p. 57 [with synonymy].
1982 *Hippurites (Vaccinite) bracieni* Sladić-Trifunović; Polšák et al., text-fig. 3.
1983 *V. bracieni* (Sladić-Trifunović); Czabalay, p. 187.
1983 *H. (Vac.) bracieni* Sladić-Trifunović; Plenčićar and Premru, pp. 192, 194.
1983 *Vaccinites bracieni*; Sladić-Trifunović, tab. 1.
1984b *Hippurites (Vaccinite) bracieni* Sladić-Trifunović; Slišković, p. 214.
1985 *Vaccinites bracieni* Sladić-Trifunović; Cazzinini, p. 135, pl. 30, fig. 4.
1986 *Vaccinites bracieni* Sladić-Trifunović; Negra and Philip, p. 51, pl. 1, fig. 1.
1986 *Vaccinites bracieni* Sladić-Trifunović; Özer, p. 101, pl. 1, figs 3–4; text-fig. 2.
1987 *Vaccinites vesiculosus*; Pejović and Radičić, tab. 2.
TABLE 18. Measurements (mm) of RVs of *Vaccinites vesiculosus* (Woodward, 1855) from Bayburt, Anatolia (H44) and Analipsis, Boeotia (H500).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0—P2</th>
<th>P0—P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H44 adult</td>
<td>114</td>
<td>535</td>
<td>100</td>
<td>279</td>
<td>1:3</td>
<td>0:9</td>
<td>0:7</td>
</tr>
<tr>
<td>H44 juvenile</td>
<td>52</td>
<td>232</td>
<td>49</td>
<td>119</td>
<td>1:3</td>
<td>0:6</td>
<td>0:5</td>
</tr>
<tr>
<td>H500</td>
<td>64</td>
<td>297</td>
<td>54</td>
<td>161</td>
<td>0:9</td>
<td>0:7</td>
<td>0:7</td>
</tr>
</tbody>
</table>

1987 *Vaccinites braciensis* (Sladić-Trifunović); Pejović and Radić, p. 132, tab. 2.
1988b *V. braciensis*; Özer, p. 49.
1989 *Vaccinites braciensis* [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. 9b.
1991 *Vaccinites vesiculosus* (Woodward); Skelton and Gili, pl. 1, fig. 3.
1991 *H. (Vacc.) braciensis*; Šribar and Plenčar, p. 182.
1992 *Vaccinites vesiculosus* (Woodward); Laviano and Gallo Maresca, p. 49, text-figs 2–9 [with synonymy].
1992 *V. braciensis* Sladić-Trifunović; Plenčar 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 (1897a), 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 IP0 and IP2 variable (Text-fig. 80). U/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, 1967a) are considerably larger. In these shells, the formation of peduncles is more pronounced even in juvenile growth stages (Text-fig. 85). 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, 1933a).

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H538</td>
<td>108</td>
<td>481</td>
<td>57</td>
<td>224</td>
<td>1.2</td>
<td>1.0</td>
<td>0.8</td>
</tr>
<tr>
<td>H542</td>
<td>85</td>
<td>430</td>
<td>56</td>
<td>230</td>
<td>0.8</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td>H544</td>
<td>98</td>
<td>508</td>
<td>61</td>
<td>281</td>
<td>0.7</td>
<td>0.6</td>
<td>0.9</td>
</tr>
</tbody>
</table>

*Distribution.* Campanian–Maastrichtian (Polšák 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 sulcataoides* (Douville, 1892a), *Vaccinites ultimus* (Milovanović, 1935).

*Vaccinites vredenburgi* (Kühn, 1933a)

Plate 25, figure 3; Text-figure 75C-1

1932 *Hippurites (Vaccinites) vredenburgi* Kühn, p. 73 [with synonymy, nomen nudum].

*1933a* *Hippurites (Vaccinites) vredenburgi* sp. nov. Kühn, p. 156, text-figs 1–2.

1938b *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 Grubič, p. 950, text-fig. 4.

1959 *Hippurites vredenburgi* Kühn; Pejović *et al.*, p. 287.


1960 *Vaccinites vredenburgi* Kühn; Vogel, p. 280.

1961a *Hippurites (Vaccinites) vredenburgi* Kühn; Polšák, pp. 422, 432.

1962 *Hippurites vredenburgi* Kühn; Grubič, p. 108, text-figs 1–12.


1962 *Hippurites (Vaccinites) vredenburgi* Kühn; Slišković *et al.*, p. 130.

1964 *H. (V.) vredenburgi* Kühn; Polšák, p. 67.


1965 *H. (V.) vredenburgi* Kühn; Slišković, p. 373.

1967b *Hippurites (Vaccinites) taburni* Guiscardi; Polšák, pp. 119, 211, pl. 74, figs 1–3; text-fig. 40.

1968a *Hippurites (Vaccinites) vredenburgi* Kühn; Slišković, p. 38.

1969 *Hippurites (Vaccinites) vredenburgi* Kühn; Polšák and Mamužić, p. 239.

1974 *Hippurites (Vaccinites) vredenburgi* Kühn; Slišković, p. 133.


1975 *Hippurites nazemi* n. sp. Grubič, p. 146, pl. 2.

1975 *Hippurites Polskí* n. sp. Grubič, 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) bacievicensis* n. sp. Sladić-Trifunović, pp. 258, 266, pl. 1, figs 1–2; text-fig. 1.

1978 *Vaccinites vredenburgi* Kühn; Pamouktchiev, p. 238, tab. 1.


1979 *Hippurites (Vaccinites) vredenburgi* Kühn; Polšák, pp. 205, 224, pl. 9, fig. 4.

1981 *Vaccinites vredenburgi* Kühn; Pamouktchiev, p. 176, pl. 86, fig. 2.

1981 *Hippurites (Vaccinites) vredenburgi* Kühn; Polšák, p. 454, text-fig. 8a [cop. Polšák 1979].

1981 *Vaccinites vredenburgi* (Kühn); Sánchez, p. 57 [with synonymy].

1981 *Vaccinites vredenburgi nazemi* (Grubič); Sánchez, p. 57 [with synonymy].

1981 *Vaccinites vredenburgi occidentalis* (Grubič); Sánchez, p. 58 [with synonymy].

1981 *Vaccinites vredenburgi persicus* (Grubič); Sánchez, p. 58 [with synonymy].

?1982 *Vaccinites vredenburgi* (Kühn); Czabalay, pp. 31, 72, pl. 10, fig. 4; pl. 25, fig. 2.
Vaccinites gosaviensis (Douvillé; Czabały, pp. 33, 72, pl. 17, figs 2–3).
1982 Vaccinites vredenburgi Kühn; Pamukitchiev, p. 223, pl. 9, fig. 3.
1982 Hippurites (Vaccinites) vredenburgii Kühn; Pošák et al., text-fig. 3.
1983 H. (Vacc.) vredenburgii Kühn; Plenčíčar and Premru, p. 192.
1983 Vaccinites bacevicensis; Sladić-Trifunović, tab. 1.

non
1989 Vaccinites vredenburgii Kühn; Laviano and Guarneri, p. 80, pl. 1, figs 1–3; 6; text-figs 2–3.
1989 Vaccinites vredenburgii Kühn; Mermighis, p. 80, pl. 22, fig. 8; text-fig. 24.
1989 Vaccinites vredenburgii hellenica nov. subsp. Mermighis, p. 83, pl. 22, fig. 6; text-fig. 28.
1989b V. vredenburgii Kühn; Philip et al., p. 1382.
1989 V. vredenburgii; Pieri and Laviano, p. 352.
1990 Vaccinites vredenburgii; Gušić and Jelaska, text-figs 8, 11.
1991 Hippurites vredenburgii; Caffau and Plenčíčar, p. 209.
1992 Vaccinites vredenburgii Kühn; Swinburne et al., text-fig. 2.
1992 V. vredenburgii Kühn; Cherchi et al., p. 95, pl. 6, fig. 4.
1994 Vaccinites vredenburgii (Kühn); Platel et al., p. 156.
1996 Vaccinites vredenburgii Kühn; Philip and Platel, p. 262, pl. 1, fig. 6.
1997 Vaccinites vredenburgii (Kühn); Steuber et al., p. 179, text-fig. 3b–c.

Holotype. Kühn (1933a), 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 denticate 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/P0–P2 ranges from 7.6 to 8.5 (Text-fig. 76). The myocardial elements are preserved in one shell only (Text-fig. 75): (1') anterior to P0; (3') posterior to P0, outline long-elliptically and radially aligned. Axis (1')–(3') inclined at 40° with respect to P0. M' aligned parallel to (3'), shifted posteroventrally and distally extended.

Remarks. The problematical definitions of V. vredenburgi, V. giganteus (d’Hombres-Fírmans, 1838) and V. gosaviensis (Douville, 1890) have been discussed by Laviano and Guarneri (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 m 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 1933a). 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 Keratocholeous 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, 1933a). 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 1967b; Pleničar 1975) because of the sickle-shaped and anteriorly inflected P2. RVs that were figured by Polšak (1967b) as V. taburni (Guiscardi, 1865) and V. vredenburgi co-occur at several localities, and are considered to delineate the inospecific 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 (Grubič 1962). This is supported by the stratigraphical position of the rudist beds at Paleokastron which are not younger than early Campanian.

**Distribution.** Santonian–Campanian (Grubič 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 (Douville, 1897a); H410, H428.
TABLE 20. Measurements (mm) of RVs of *Vaccinites* sp.

<table>
<thead>
<tr>
<th></th>
<th>Dmax</th>
<th>U</th>
<th>P0–P2</th>
<th>P0–P2 cont</th>
<th>IP0/IP1</th>
<th>IP0/IP2</th>
<th>IP1/IP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H428/1</td>
<td>49</td>
<td>207</td>
<td>33</td>
<td>110</td>
<td>0·8</td>
<td>0·7</td>
<td>0·8</td>
</tr>
<tr>
<td>H428/2</td>
<td>51</td>
<td>201</td>
<td>32</td>
<td>110</td>
<td>0·8</td>
<td>0·8</td>
<td>1·0</td>
</tr>
</tbody>
</table>

_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 1897a) 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.
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 Büttner (1880). It is the type locality of *Hippurites gaudryi* Munier-Chalmes and *Plagioptychus boeoticus* Munier-Chalmes, and Dousis (1892a, 1895, 1897a) 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-bededded, up to 0.4 m thick limestone beds 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 thrust against these clastics. A Lower Cretaceous microflora (Steuber 1993b) 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 conformably 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-beded limestones contains only a few redepotted 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 (1897a, 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* Polsak 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 *Blastoechozetes 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 serpentinitized 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* (Brönns). *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* (Brönns) 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.
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. Deposited 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 hippocritid 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 hippocritid 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
environment. The associated calcareous microfaunas of this unit are exceptionally poor both near Dionysos and at Keratovouno Hill.

The corresponding high energy deposits at Kalamas 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 monotinous in all three sections. This is also expressed in rather constant compositions of principal components (Text-figs 86–88). Biointrinsicites 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. *Dicyclyna 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 δ¹⁸O as well as δ¹³C of whole rock samples of these mud-and wackestones indicate sporadic hypersaline 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 δ¹³C 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 1996a) was apparently best-adapted to elevated turbulence and rapidly accumulating or unstable sediments. Dense associations and the concurrent high CaCO₃ production (Steuber 1996c) 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 (Bromi). 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 reclinata, 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 1979b), 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 Vaccinities 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 postmortem 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 Vaccinities cornuvaccinum managed to prevent infestation of the shell by bioerosers 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 Vaccinities 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 Vaccinities, 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 Vaccinities are not a simple, elongated, well-balanced cone (Text-fig. 90), but the ventral shell margin expanded disproportionately 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 Vaccinities (Text-figs 12–13; Steuber 1993a), 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 Vaccinities 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 Vaccinities 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 1996b) 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 1996a, 1996b, 1996c, 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 spiroygrate 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. cornu vaccinum 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 1996b, 1997), delineate a lagoonal environment with low mean annual sedimentation (<5 mm/year) during the formation of the V. cornu vaccinum 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. cornu vaccinum 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 1996b). 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. cornu vaccinum 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 Gornjanovicia banks at Keratovouno Hill (Text-fig. 89).

The morphotypes of V. cornu vaccinum 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 1996a). 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 subradius 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 1992b), 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, Macedonía; Aubouin 1959, northern Greece; Célet 1962, Parnassus Mountains; Mercier 1973, central Macedonía) 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. 1989b; 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>
<thead>
<tr>
<th>TABLE 21. Compilation of rudist species known from Greece.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aptian</strong></td>
</tr>
<tr>
<td><em>Eoradiolites plicatus</em> (Conrad)</td>
</tr>
<tr>
<td><em>Horiopleura cf. baylei</em> (Coquand)</td>
</tr>
<tr>
<td><em>Horiopleura</em> sp. nov.</td>
</tr>
<tr>
<td><em>Offneria italica</em> Masse</td>
</tr>
<tr>
<td><em>O. nicolai</em> (Mainelli)</td>
</tr>
<tr>
<td><em>Pachytraga paradoxa</em> (Pictet and Campiche)</td>
</tr>
<tr>
<td><em>Polyconites distefanoi</em> Parona</td>
</tr>
<tr>
<td><em>Requienia ammonia</em> (Goldfiß)</td>
</tr>
<tr>
<td><em>Toucasia carinata</em> (Matheron)</td>
</tr>
<tr>
<td><em><em>Sphaerulites foliaceous</em> Lamarck</em>*</td>
</tr>
<tr>
<td>middle Turonian–?Coniacian</td>
</tr>
<tr>
<td><em>Biradiolites angulosus</em> d’Orbigny</td>
</tr>
<tr>
<td><em>Distefanella montagnai</em> Slišković</td>
</tr>
<tr>
<td><em>D. raricostata</em> Slišković</td>
</tr>
<tr>
<td><em>D. cf. lombricalis</em> (d’Orbigny)</td>
</tr>
<tr>
<td><em>Durania martelli</em> Parona</td>
</tr>
<tr>
<td><em>D. cf. montisferrati</em> Astre</td>
</tr>
<tr>
<td><em>Lapeirousella amulensis</em> Douvillé</td>
</tr>
<tr>
<td><em>Praeapulianus</em> sp. nov.</td>
</tr>
<tr>
<td><em>Praeradiolites ponsianus</em> d’Archiac</td>
</tr>
<tr>
<td><em>P. cf. arnalis</em> Astre</td>
</tr>
<tr>
<td><em>Radianolites lusitanicus</em> (Bayle)</td>
</tr>
<tr>
<td><em>Radiolites peroni</em> (Choffat)</td>
</tr>
<tr>
<td><em>Radiolites praegalloprovincialis</em> Toucas</td>
</tr>
<tr>
<td><em>Radiolites sauvesi</em> (d’Hombres-Firmas)</td>
</tr>
<tr>
<td><em>Hippuriella resecta</em> (Defrance)</td>
</tr>
<tr>
<td><em>Vaccinites grossoureet</em> (Douvillé)</td>
</tr>
<tr>
<td>V. <em>inferus</em> (Douvillé)</td>
</tr>
<tr>
<td>V. <em>ljalintzensis</em> Pamouktchiev</td>
</tr>
<tr>
<td>V. <em>narentanus</em> Slišković</td>
</tr>
<tr>
<td>V. <em>praegiganteus</em> Toucas</td>
</tr>
<tr>
<td>Species</td>
</tr>
<tr>
<td>------------------------------------------------------------------------</td>
</tr>
<tr>
<td><em>Neocaprina gigantea</em> Plenčićar</td>
</tr>
<tr>
<td><em>Neocaprina nanos</em> Plenčićar</td>
</tr>
<tr>
<td><em>Orthoptychus striatus</em> Futterer</td>
</tr>
<tr>
<td><em>Schiosia carinatoformis</em> Polšak</td>
</tr>
<tr>
<td><em>Sphaerucaprina woodwardi</em> Gemmellaro</td>
</tr>
<tr>
<td><em>Ichthyosarcolithes bicornatus</em> Gemmellaro</td>
</tr>
<tr>
<td><em>I. triangularis</em> (Desmarest)</td>
</tr>
<tr>
<td><em>Distefanelia douvillei</em> Parona</td>
</tr>
<tr>
<td><em>Neoradiolites epidavricus</em> Mermighis</td>
</tr>
<tr>
<td><em>N. helladensis</em> Mermighis</td>
</tr>
<tr>
<td><em>N. kosjerici</em> Pašić</td>
</tr>
<tr>
<td><em>N. majdanensis</em> Pašić</td>
</tr>
<tr>
<td><em>N. pelagoniensis</em> Mermighis</td>
</tr>
<tr>
<td><em>N. peloponnesiacus</em> Mermighis</td>
</tr>
<tr>
<td><em>N. piadiensis</em> Mermighis</td>
</tr>
<tr>
<td><em>N. scapensis</em> Pašić</td>
</tr>
<tr>
<td><em>N. turoensis</em> Pašić</td>
</tr>
<tr>
<td><em>Radiolites cremai</em> Parona</td>
</tr>
<tr>
<td><em>R. radius d'Orbigny</em></td>
</tr>
<tr>
<td><em>Sauvagesia nicaisi</em> (Coquand)</td>
</tr>
<tr>
<td><em>S. praesharpei</em> Toucas</td>
</tr>
<tr>
<td><em>S. sharpei</em> (Bayle)</td>
</tr>
<tr>
<td><em>S. vellei</em> (Toucas)</td>
</tr>
<tr>
<td><em>G. lipparini</em> Polšak</td>
</tr>
<tr>
<td><em>Lapeirousia zitelli</em> Douville</td>
</tr>
<tr>
<td><em>Medeaella zignana</em> (Pirona)</td>
</tr>
<tr>
<td><em>Petkovicii? veraianca</em> Slišković</td>
</tr>
<tr>
<td><em>Praeradiolites echennensis</em> Astre</td>
</tr>
<tr>
<td><em>Pseudopolyconites laskarevi</em> Milovanović and Sladić</td>
</tr>
<tr>
<td><em>Ps. ovalis apulienisis</em> Sladić-Trifunović and Campobasso</td>
</tr>
<tr>
<td><em>Radiolites angeoïdès</em> (Lapeirouse)</td>
</tr>
<tr>
<td><em>Radiolites galloprovincialis</em> Matheron</td>
</tr>
<tr>
<td><em>Radiolites styriacus</em> (Zittel)</td>
</tr>
<tr>
<td><em>Radiolites subradius</em> Toucas</td>
</tr>
<tr>
<td><em>Rajka spinosa</em> Milovanović</td>
</tr>
<tr>
<td><em>Sauvagesia meneghiniana</em> (Pirona)</td>
</tr>
<tr>
<td><em>Sauvagesia tenuicostata</em> Polšak</td>
</tr>
<tr>
<td><em>Hippuritella variabilis</em> (Munier-Chalmas)</td>
</tr>
<tr>
<td><em>Hippurites cf. canaliculatus</em> Rolland du Roquan</td>
</tr>
<tr>
<td><em>H. collicatus</em> Woodward</td>
</tr>
<tr>
<td><em>H. heritschi</em> Kühn</td>
</tr>
<tr>
<td><em>H. socialis</em> Douvíllé</td>
</tr>
<tr>
<td><em>Pseudopironaea hellenica</em> Lupu</td>
</tr>
<tr>
<td><em>Tetravaccinites macedoniensis</em> Lupu</td>
</tr>
<tr>
<td><em>Vaccinites archaiaci</em> (Douvillé)</td>
</tr>
<tr>
<td><em>V. boehmi</em> (Douvillé)</td>
</tr>
<tr>
<td><em>V. chaperi</em> (Douvillé)</td>
</tr>
<tr>
<td><em>V. cornuvaccinum</em> (Bronn)</td>
</tr>
<tr>
<td><em>V. douvillei</em> (de Alessandri)</td>
</tr>
<tr>
<td><em>V. giganteus</em> (d’Hombres-Firmas)</td>
</tr>
<tr>
<td><em>V. gosaviensis</em> (Douvillé)</td>
</tr>
<tr>
<td><em>V. praepetrocoriensis</em> (Toucas)</td>
</tr>
<tr>
<td><em>V. praeasulcatus</em> (Douvillé)</td>
</tr>
<tr>
<td><em>V. ptooonensis</em> Steuber</td>
</tr>
<tr>
<td><em>Mitrocaprina bayani</em> (Douvillé)</td>
</tr>
<tr>
<td><em>M. boeotica</em> (Munier-Chalmas)</td>
</tr>
<tr>
<td><em>Plagioptychus aquilloni</em> (d’Orbigny)</td>
</tr>
<tr>
<td><em>Sabinia aniensis</em> Parona</td>
</tr>
<tr>
<td><em>Biradiolites angulosissimus</em> Toucas</td>
</tr>
<tr>
<td><em>Bournonia africanana</em> Douvillé</td>
</tr>
<tr>
<td><em>B. fourtaui</em> Douvillé</td>
</tr>
<tr>
<td><em>B. wiontzei</em> Pejović</td>
</tr>
<tr>
<td><em>Durania katzeri</em> (Slišković)</td>
</tr>
<tr>
<td><em>Durania martelii</em> Parona</td>
</tr>
<tr>
<td><em>Fossilites dionysii</em> Steuber</td>
</tr>
<tr>
<td><em>Gorjanovicia boeotica</em> Steuber</td>
</tr>
<tr>
<td><em>G. costata</em> Polšak</td>
</tr>
<tr>
<td><em>G. gracilis</em> (Wiontzeck)</td>
</tr>
<tr>
<td><em>G. kayae</em> Özer</td>
</tr>
<tr>
<td><em>V. inaequicostatus</em> (Münster)</td>
</tr>
<tr>
<td><em>V. kuegni</em> (Pejović)</td>
</tr>
<tr>
<td><em>V. appellii</em> Douvillé</td>
</tr>
<tr>
<td><em>V. praeasulcatus</em> (Douvillé)</td>
</tr>
<tr>
<td><em>V. salopeki</em> (Polšak)</td>
</tr>
<tr>
<td><em>V. sulcatus</em> (Defrance)</td>
</tr>
<tr>
<td><em>V. vesiculosus</em> (Woodward)</td>
</tr>
<tr>
<td><em>V. vredenburgi</em> (Kühn)</td>
</tr>
<tr>
<td><em>Maastrichtian</em></td>
</tr>
<tr>
<td><em>Mitrocaprina bulgarica</em> Tzankov</td>
</tr>
<tr>
<td><em>Sabinia aniensis</em> Parona</td>
</tr>
<tr>
<td><em>Bournonia dinarica</em> Slišković</td>
</tr>
<tr>
<td><em>B. wiontzei</em> Pejović</td>
</tr>
<tr>
<td><em>Durania apala</em> (Parona)</td>
</tr>
<tr>
<td><em>Joufa reticulata</em> Boehm</td>
</tr>
<tr>
<td><em>Pseudopolyconites laskarevi</em> Milovanović and Sladić</td>
</tr>
<tr>
<td><em>Ps. ovalis apulienisis</em> Sladić-Trifunović and Milovanović</td>
</tr>
<tr>
<td><em>Radiolitella mastrichtianena</em> Pejović</td>
</tr>
<tr>
<td><em>Radiolites angeoïdès</em> (Lapeirouse)</td>
</tr>
<tr>
<td><em>Rajka spinosa</em> Milovanović</td>
</tr>
<tr>
<td><em>Hippuritella lapeirousei</em> (Goldfuß)</td>
</tr>
<tr>
<td><em>Hippurites cornucopiae</em> Defrance</td>
</tr>
<tr>
<td><em>H. collicatus</em> Woodward</td>
</tr>
<tr>
<td><em>H. heritschi</em> Kühn</td>
</tr>
<tr>
<td><em>H. socialis</em> Douvíllé</td>
</tr>
</tbody>
</table>
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 *Amphitriteculeus* 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 1900b; 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), *Retta* sp. (Combes et al. 1981), *Monopleura* sp. and *Himeraellites* 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 endemicism began to take shape during the Cenomanian (Philip 1982a).

In contrast with Boeotia (Table 2), the associations of the external Helemids, Parnassus platform and of Argolis are remarkably diverse (Table 21), and can be divided into three groups: *Caprina reversa*
d’Orbigny, *Ichthyosarcolites* Desmarest, *Radiolites radiosus* Lamarck, *Sauvagesia* Choffat and *Sphaerulites* Lamarck were widely distributed in the Mediterranean Tethys. *Orthoptychus striatus* Putterer and *Sphaerocrapina* Gemellaro are known only from the circum-Adriatic regions while *Caprina baylei* (Gemellaro) and *Neocaprina* Plenčar occur also in the Taurid Mountains (Özer 1988a). *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 Aïraud-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. 1989b). 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. 1989b). 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* (Douville), *Vaccinites giganteus* (d’Hombres-Firmas), *Hippuritella variabilis* (Munier-Chalmas), *Hippurites cf. canaliculatus* Rolland du Roquan in Boeotia, and *V. archiaci* (Douville) 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. 1989b). It is also widely distributed in the Alps as well as in the external and internal Dinarids (Milošanović 1934, 1960; Pašić 1957; Polšak 1967b) 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 cornuaccinum* (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 Sirma 1992). On the other hand, typical central Mediterranean species occurred in southern Spain (*Pironaea Meneghini*, *Vaccinites ultimus* (Milošanović)), 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-Trifanović 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* Milošanović 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. 1989b) 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. Engelken for her help with the photography. Dr P. W. Skelton and Dr J.-P. Masse provided valuable comments on the manuscript.

REFERENCES


PUGLIESE, N. and PLENICAR, M. 1996. The development of the mollusc fauna in the Cenomanian of the stratigraphic sequence of Visogliano (Karst of Trieste, Italy). *Geologija*, 37/38, 87–121, pls 1–11.


LAPEIROUSE, P. de 1781. *Description de plusieurs nouvelles espèces d’Orthocératites et d’Ostracidés*. Wolfgang Walther, Erlangen, 48 pp., 13 pls.


**Pechintsev, V. F.** 1959. [Rudists from the Mesozoic of Crimea.] Geologicheskij Muzej Imeni A.P. Karpinski, Akademiï Nauk SSR, Serija monograficheskaje, Moscow, 178 pp., 43 pls. [In Russian].


**Petković, K., Pejović, D. and Pašić, M.** 1959. Le développement biostratigraphique et la disposition paléogéographiques


PLENIČAR, M. 1961. The stratigraphic development of Cretaceous beds in Southern Primorska (Slovene Littoral) and Notranjska (inner Carniola). Geologija, 6, 22–145.
1962. Situation of the Cretaceous beds from southern Slovenia in the mediterranean geosyncline (Summary). Geologija, 7, 41-42.


RENGARTEN, V. P. 1950. [Cretaceous rudist facies of Transcaucasia.] Trudy Instituta Geologicheskich Nauk, Akademija Nauk SSR, 130, 1–92, pls 1–16. [In Russian].

1959. [Stratigraphy of Cretaceous deposits from Caucasus and their correlation with western European standard sections.] Congreso Geologico Internacional, Mexico City, XX sesión, El sistema Cretácico, Vol. 2, 245–262. [In Russian].


ROLLAND DU ROQUAN, O. 1841. Description des coquilles fossiles de la famille des rudistes qui se trouvent dans le terrain créacé des Corbières. L. Pomiès-Gardel, Carcassonne, 69 pp., 8 pls.


THOMAS STEUBER
Institut für Geologie und Mineralogie
Universität Erlangen-Nürnberg
Schloßgarten 5
91054 Erlangen
e-mail steuber@geol.uni-erlangen.de

Typescript received 10 April 1997
Revised typescript received 7 September 1998