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DESCRIPTION AND TAPHONOMIC INVESTIGATIONS
OF NEOGENE PROBOSCIDEA FROM RHODOS, GREECE*

by
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I. INTRODUCTION

Anancus arvernensis has been described from various Upper Pliocene localities in Greece (Fig. 1). In most earlier studies little stratigraphical information has been available in connection with the individual discoveries, but there has been broad agreement that *A. arvernensis* is generally limited to the Pliocene.

II. MATERIAL

Major road works were undertaken in 1992 and 1993 on the main road along the coast south of Apolakkia, involving the straightening out of bends and construction of some new branch roads. Several good sections through the delta plain and fluvial deposits of the Apolakkia Formation appeared in the new road cuttings, which could be up to 10-12 m high. Parts of two proboscidean skulls were found in two different fluvial deposits (Fig. 2). The best preserved skull, which was found by LAURITZEN & HANKEN (1992), was indentified as *Anancus arvernensis*; the genus of the other skull could not be determined because it was highly fragmented and lacked any clear diagnositc characteristics. Small and large fragments of various mammalian bones (long bones, ribs, pelvis) were also found at the same localities, but these had unfortunately been so badly damaged during the road construction that it proved impossible to achieve indentification even to the genus level, since they lacked every diagnostic feature (i.e. epiphyses, etc.). Their only real diagnostic character was their general shape and size, which clearly indicated a proboscidean. Several of the bones were found in the rock waste dumped beside the road. These pieces were clearly of no stratigraphical value even though their matrix showed that they came from the sandgravel facies. The fact that the bones derive from the channel fill has significant stratigraphical importance, as is discussed later. Some other remains, including Cervidae and Equidae, were found scattered on nearby scree slopes (area III in Fig. 2).

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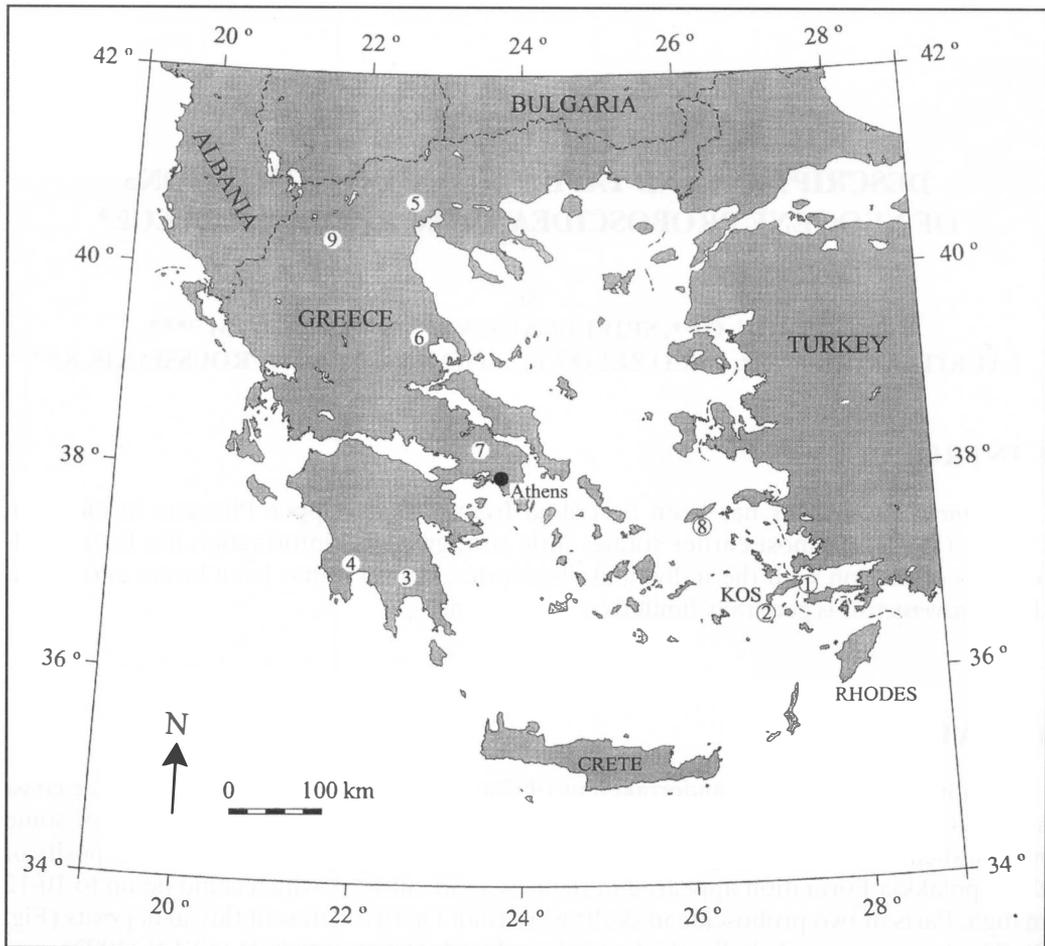
Fig. 1. Known occurrences of *A. arvernensis* in Greece. 1. *Mastodon arvernensis* at Antimachia on the island of Kos mentioned by FORSYTH MAJOR (1887). 2. *Mastodon arvernensis* in Villafranchian sediments on Kos (R. Almiri), mentioned by DESIO (1931, p. 210). KOTSAKIS *et al.* (1980) reported the same species from Kardamaena. 3. GEORGALAS (1941) described a lower M3 of *Anancus (Mastodon) arvernensis* from Skoura (near Sparta), South Peloponnese. It was found loose, giving no opportunity for discussion based on other fossils. 4. MITZOPOULOS (1965) reported a broken piece of *Anancus arvernensis* from the Astian sediments at Pylos (southwestern Peloponnese). The material consisted of a fragment of upper M2 (sin) 66 mm wide and 50 mm high (Ath. no. 1965/44). 5. SAKELLARIOU-MANÉ (1972) described *Anancus arvernensis* from the valley of Axios. KOUFOS (1977) described finds of *Anancus arvernensis* from Hag. Triada and Sani. He also mentioned that the species was known from Sparta, Pylos and Axios. Direct comparision with the Rhodes material is impossible (upper jaw). 6. ΣΥΜΕΩΝΙΔΗΣ & ΤΑΤΑΡΗΣ (1982) described a mandible of *Anancus arvernensis* from Sesklo in Thessaly, central Greece, said to be the best-preserved specimen in Greece. They concluded that it showed the sediments at Sesklo to be of Upper Pliocene age. ΑΘΑΝΑΣΙΟΥ (1996) studied a new *Anancus arvernensis* specimen (skull without dentition) from the same locality. Clearly there is no possibility for direct comparison with the Rhodes material. 7. GIDARAKOS (1938) mentioned the occurrence of Proboscidea remains in the village of Spaides, northeast of Thiva. No species name is given, but the photographs are good enough to see that the molars belonged to a mastodont with alternating mammilae. ΔΕΡΜΙΤΖΑΚΗΣ *et al.* (1982, p. 59) may have been referring to this specimen when they noted that *Anancus arvernensis* had been found at Thiva. 8. Some mastodont remains from the island of Ikaria (ΔΕΡΜΙΤΖΑΚΗΣ *et al.* 1982) may possibly belong to *Anancus*. 9. STEENSMA (1988, pp. 51, 274) mentioned the occurrence of *Anancus arvernensis* it W. Macedonia (Klima and Polylakkon). The material consisted of broken upper M3 from Klima and a dextral femur (*Anancus ?* sp. indet.) from Polylakkon. A Pliocene age was assumed.
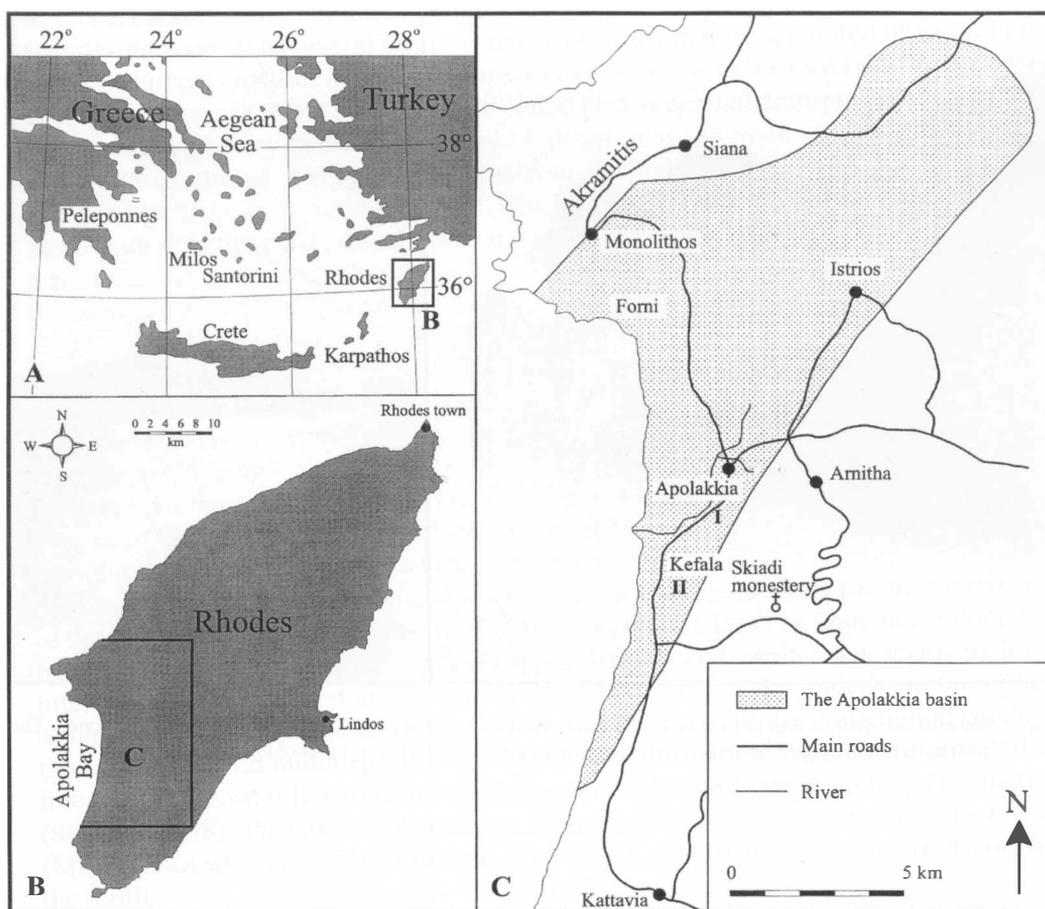
Fig. 2. A. Map of the southern Aegean area showing the location of the island of Rhodes. B. Map of Rhodes. C. Extent of the Apolakkia Basin. I, Apolakkia I locality where the *Anancus arvernensis* remains were found. The unidentified proboscidian was found at locality II. Area III shows where other vertebrate remains (including Cervidae and Equidae) were found on scree slopes.

III. THE APOLAKKIA BASIN

The Apolakkia Basin is situated on the southern side of Rhodes and is about 28 km long (N-S) and 11 km wide (E-W). The thickness of the exposed beds is more than 600 m. The first to mention the basin was HEDENBORG (1837), but the first real description of it was by BUKOWSKI (1899). The basin has later been mentioned by MUTTI *et al.* (1970), MEULENKAMP *et al.* (1972), WILLMANN (1981) and MOSTAFAWI (1989). A detailed description, with emphasis on the lignite deposits in the upper part of the Apolakkia Formation, was given by MARATOS & KOUKOUZAS (1966).

Like the other "Levantine" basins on Rhodes, it is cut by numerous small faults, especially along its margins. Much of the faulting took place either during sedimentation, or just after, when the sediments were soft and before the overlying beds were deposited. Along the steep margins it is difficult to discriminate between tectonic faulting and sliding in the rather unconsolidated sediments.
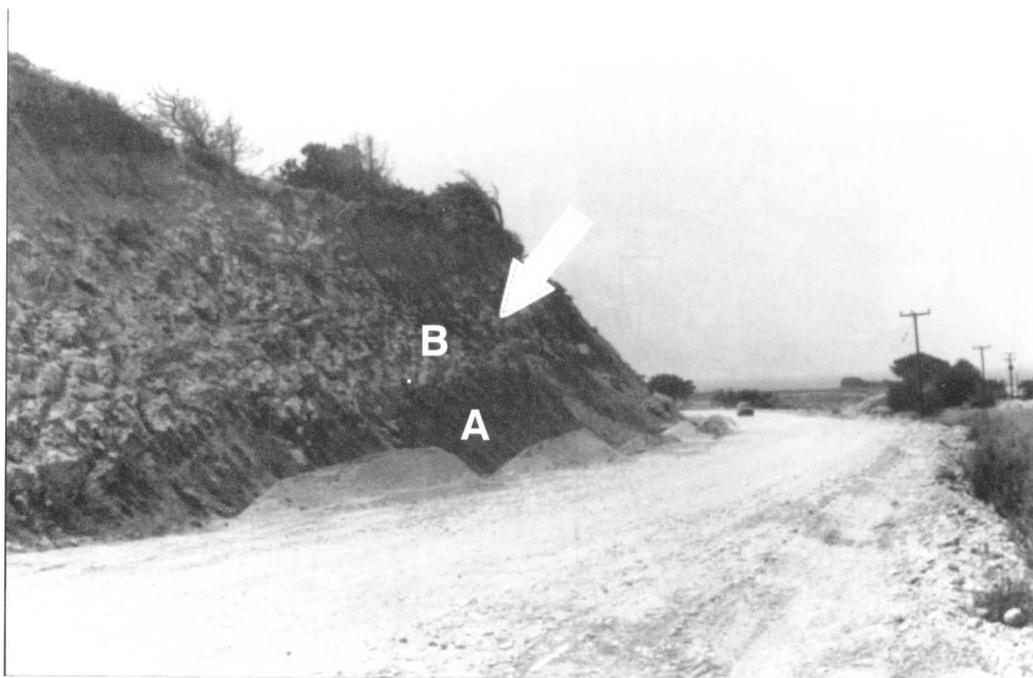
Fig. 3. View of the road section at locality I. The arrow shows where the skull of *Anancus arvernensis* was found. The section shown in figure 8 was measured at A (limnic deposits) and B (lower part of the fluvial deposits).

The dominating lithology is laminated clay/silt with a banding ranging from light grey to almost black. The darker bands, which are generally 5-38 cm thick, are separated by thicker light beds. When it weathers, the clay surface becomes jointed and breaks into approximately equidimensional angular blocks. This makes it difficult to find any plant fossils at the surface; it is necessary to dig into the unweathered parts of the succession to find well-preserved plant material. Calcareous fossils are locally very common on weathered surfaces, but the faunas are remarkably less diverse than in the other "Levantine" basins on Rhodes (especially the Salakos Basin). The dominating invertebrate fossils are *Theodoxus hellenica* Bukowski and various species of *Melanopsis*. Ostracods are common microfossils, with *Cyprideis* sp. as the dominating form. Oogonia of charophytes are also found. Other plant fossils (leaves, stems, wood and seeds) are common in sections where the weathered crust has been removed, but they have not been studied since their condition was very bad.

The clay/silt-dominated deposits also contain beds and/or lenses of sand and gravel. These are of two types. Some are thin beds (30-60 cm) which are often rather continuous over long distances and consist of more or less well-sorted sand and silt. They have conformable upper and lower boundaries and are interpreted as overbank desposits formed by river flooding. The other consists of fluvial desposits with a marked erosional base. The channel fill is often rather coarse (coarse sand to gravel) with scattered larger blocks. In some outcrops the channels are exposed laterally for several hundred metres. The biggest channels may attain a thickness of up to 8-10 m, but most are less than 5 m

thick (SPERRE 1998). The larger ones (such as that in which *Anancus arvernensis* was found) often consist of several layers or lenses of conglomerate separated by sandy beds.

Paleocurrent analyses indicate that the source area was to the east (MEULENKAMP *et al.* 1972). However, MUTTI *et al.* (1970) have also suggested transport from the south. Our own preliminary palaeocurrent data indicate that the main transport was towards south and southwest. There are few fossils in the conformable sandy beds; only a few corroded gastropods have been found. The river channel deposits often contain many gastropods, but their size, distribution and a distinct surface corrosion indicate that they were transported thence. There are also some other mammalian remains (additional to the *Anancus arvernensis* specimen), mostly worn fragments of bone and teeth.

The volume of sediments in the basin is large and the sediments seem to have been deposited rather rapidly under humid conditions. This led MEULENKAMP *et al.* (1972, p. 546) to assume that the clastic material came from the mainland (of which Rhodes was then a part). The gravelly material in the channels has a high percentage of ophiolitic material (see below), like many Plio-Pleistocene sediments on Rhodes. This seems to indicate that most, if not all, the clastic material in the basin is indigenous to the island, even if it was part of the mainland at the time, as indicated by the nature of the mammalian fauna (DERMITZAKIS & SONDAAR 1979).

The youngest part of the Apolakkia Formation is exposed along the west coast south of the limestones forming the Attaviros-Akrimites mountains. The sequence is dominated by alterations of thin-bedded clays, siltstones, lignites and lignitic clay seams with local intercalations of sand and gravel with erosional contacts to the underlying fine-grained sediments. This part of the succession, which was deposited under more humid conditions than the lower and middle parts of the Apolakkia Formation, has been interpreted as a flood-plain deposit originating in a landscape with lakes and swamps intersected by rivers (SPERRE 1998). Palaeocurrent analyses indicate that the source area was to the east (MEULENKAMP *et al.* 1972). However, MUTTI *et al.* (1970) also suggested transport from the south.

IV. GEOLOGICAL SETTING

Fig. 8 shows a profile through the part of the succession where the skull of *A. arvernensis* was found at locality I in the lower part of fluvial sequence that is at least 10 m thick and overlies limnic sediments.

The limnic sediments are characterised by fine-grained material (clay and fine silt). The deposits are well sorted and have a small content of terrigenous sand grains (normally less than 0.5%). Wet sieving of bulk samples also revealed scattered fragments of freshwater ostracods, gastropods and lamellibranchs.

Calcrete was found uppermost in the limnic sediments and in a horizon 0.5-1 m lower down. It results from cementation of calcium carbonate into soil profiles, in an arid or a semiarid, climate. Calcrete may assume various morphological forms, but in this case it consists of discrete hard concretions (up to 2 cm in diameter) of carbonate-cemented soil. According to the morphological classification proposed by WETTERBERG (1980), this type of calcrete can be termed as nodular calcrete. According to the classification of pedogenic calcrete based on stages of development (MACHETTE 1985), the nodules may be referred to stage 2, which is a fairly early stage in calcrete development. The rate of development of calcrete in a soil profile is highly variable (WRIGHT 1990), mainly depending on climate, Ca^{2+} and P_{CO_2}. However, under optimal conditions, the type of calcrete de-

scribed here may have been formed in less than 2000 years.

The lower part of the exposed limnic deposits contains a thick upward-coarsening sequence that is interpreted as a crevasse splay deposit, in other words material deposited by flooding of a nearby river. The primary lamination in the deposit has been somewhat damaged by bioturbation (*Planolites* isp. and *Taenidium* isp.).

The fluvial deposits are characterised by lenticular-shaped units consisting of poorly sorted gravel and sand. Scour and fill structures are common. Analysis of the clasts shows that these are dominated by ophiolite (serpentine and basalt) and metamorphic limestone with smaller quantities or red chert, sandstone and unconsolidated clay clasts. The clay clasts represent locally derived material torn loose from the river banks during floodings. A major propotion of the metamorphic limestone clasts may be derived from the Akrimites Limestone which covers large areas north of the Apolakkia Basin. The remainder of the clastic material is probably derived from the Koriati Conglomerate which occupies the eastern margin of the Apolakia Basin.

Gastropods are fairly common in the fluvial sediments. The gastropod fauna is dominated by *Theodoxus hellenicus hellenicus* (more than 90%) together with scattered specimens of *Melanopsis orientalis orientalis, Melanopsis tuberculata destafani* and *Planorbis* sp. The first three can tolerate low salinities, but the third is definitely a solely fresh-water form.

Nearly all the gastropods are worn, indicating transportation before final deposition. The *Theodoxus* specimens also show a good correlation between shell size and the grain size of the enclosing sediment in that large specimens dominate in coarse-grained deposits and smaller ones are relatively concentrated in more fine-grained deposits.

At locality II (Fig. 2), the fluvial deposits also overlie fossiliferous limnic sediments. In addition to a rich skeletal fauna (dominted by gastropods) the limnic deposits contain many plant fragments. The flora is dominated by leaves and vertical in situ stems (bamboo?). The boundary between the fluviatile and limnic sediments is sometimes considerably disturbed by loading, occasionally with the development of clay diapirs.

V. AGE

Parts of the Apolakkia Formation contain a very rich invertebrate fauna (see the fossil list in MUTTI *et al.* (1970). The age of the Apolakkia Basin has been taken to be Pliocene ("Levantine" of BUKOWSKI 1899) and early Pliocene by MEULENKAMP *et al.* (1972).

Based on the occurrence of gastropods of the genus *Corymbina*, WILLMANN (1981) believed that some of the beds could even be of late Miocene age. The single locality where *Corymbina* has been found (along the branch road to the Skiadhi Monastery) was described by BUKOWSKI (1899). The conditions there are not quite clear because the clay is visibly disturbed, possibly by landslinding, and rests on suspiciously fresh-looking gravel. Apart from the endemic *Corymbina*, macrofossils are lacking. No calcareous microfossils were found and the only pollen found was from *Pinus*. Hence, the occurrence of endemic *Corymbina* alone cannot be used for age determination.

The ostracods reported by MOSTAFAWI (1989) give no clue to the age as the identifications were made with many reservations. He suggested that the Apolakkia Basin may be older than the Salakos Basin because species of definite late Pliocene or Pleistocene age are found only in the latter basin. The ostracods found in the Apolakkia Basin do not exclude a late Pliocene age, but it must be concluded that there are some doubts about the real age of the beds, which must be resolved by further studies on both the mammalian

and invertebrate faunas. No marine incursions have been observed in the basin and this is taken to indicate that all of it belongs in the late Pliocene.

Preliminary studies of the sporomorph assemblages indicate a correlation with the Akça assemblage in the Turkish succession (BENDA 1971, BENDA & MEULENKAMP 1972).

A mammalian assemblage including *Hemihipparion dietrichi*, *Paleoryx pallasi*, etc. from the lowermost levels of the formation was described by BONI (1943). Later investigations by BENDA & MEULENKAMP (1972) indicated that the mammalian assemblage had a balanced character, suggesting that Rhodes was part of the Asiatic mainland. The fauna indicated an Upper Ruscinian age.

VAN DE WEERD *et al.* (1982) mentioned the occurrence of Proboscidea gen. et sp. indet. found by surface collection in the Apolakkia Formation. The same fossil list also mentions *Hipparion* aff. *crassum* and other large mammals and micromammals. Bones from the large mammals were found loose in weathered material derived from the Apolakkia Formation, whereas bones from micromammals were found by sieving unconsolidated sediments. Consequently, the material was collected from different stratigraphical levels, but unfortunately no mention was made of from which parts of the succession the individual finds were made. Based on the discoveries of *Hipparion* and *Cervus* it was assumed that the mammalian fauna indicated a Lower Pliocene age.

The mammalian fauna described by VAN DE WEERD *et al.* (1982) was also discussed by BENDA *et al.* (1977). The faunal composition raises a problem concerning the real age of the beds because it includes such forms as *Hipparion* which are referred to the older Pliocene (Ruscinian). The critical locality (APO 2A in Fig. 1 in BENDA *et al.* 1977) is rather close to where *Anancus arvernensis* was found. This specimen could not –because of its articulated preservation– have been resedimented. The other fossils reported by BENDA *et al.* (1977) may have been resedimented, but there is no direct evidence for this. None of the forms reported by them have been found in our, admittedly small and fragmentary, material from the other fluvial channels in the Apolakkia Basin.

RICHTER (1997) described a canine tooth from the sabretooth cat *Homotherium crenatidens* (?) from our locality II. *H. crenatidens* is a well known species from Eurasia in the late Pliocene.

TOBIEN (1978, p. 170-177) discussed the evolutionary and biostratigraphical position of *A. arvernensis*. This species was widespread in Europe and is also well known from the Ruscinian and Villafranchian in western Anatolia. *A. arvernensis* has so far not been found together with *Hipparion* which, according to available data, disappeared in Greece before the arrival of *Anancus*. This indicates that the mammalian fauna described by BENDA *et al.* (1977) and VAN DE WEERD *et al.* (1982) was collected from stratigraphically lower levels than our material. The preliminary study of the mammalian fauna in the Apolakkia Formation can thus suggest that the latter represents deposits from the Lower to the Upper Pliocene.

VI. METHODS

The fluvial sediments displayed large lateral and vertical variations in their degree of cementation. A few horizons may be virtually uncemented, but locally the primary porosity could be reduced by up to 80-90% as a consequence of calcite cementation. To extract the bone remains it was therefore necessary to use power drills and numerous small hand tools. Paraloid B72 and UHU diluted in acetone were available for hardening

purposes. Specialised speleological equipment was used for the safety of the excavators while working 5 m up on the section and to get the heavy finds safely down to road level.

The two tusks and the skull fragment at locality I were crudely conserved on site, the sediment above them being removed. The tusks lay perpendicular to the road cutting, almost parallel to an ancient erosional surface. They and the skull were fixed in plaster of Paris using gypsum bandages like those normally used for human bone fractures.

The entire sample was painstakingly undercut and simultaneously placed in a wooden crate prepared *in situ* by using screws and an electric screwdriver to avoid the vibrations that the hammering in of nails would have entailed. It was then taken to the Museum of Geology and Palaeontology at Athens University to be incorporated into its fossil vertebrate collection, in accordance with Greek law. Final preparation was undertaken in the museum laboratory by A. ATHANASSIOU and S. ROUSSIAKIS.

Thin sections of small bone fragments of *A. arvernensis* which were found loose at localities I and II were prepared. The samples had previously been vacuum impregnated with epofix glue to which a blue dye (oresol) had been added. This technique made it easy to indentify even extremely small pores using standard microscopy. All the thin sections were also studied by fluorescence microscopy and cathodoluminescence microscopy.

Fluorescence microscopy has mostly been used in carbonate petrography studies; the method was described by DRAVIES & YUREVICZ (1985). However, in this case it proved most suitable for studying the bioerosion of the skeletal material. A Leitz Aristoplan microscope equipped with incident light fluorescence was used.

Cathodoluminescence microscopy was used to study the calcite cement precipitated in primary cavities in the bones. The characteristic variation of the luminescence colours was used to deduce the composition of the pore fluids during crystal growth. The theoretical background for the method is well summarised by MARSHALL (1988). A Leitz Ortholux II pol-bk polarising microscope equipped with a Nuclide luminoscope was used. The studies were carried out using high voltage 14 kV, a power strength of 0.9-1.0 mA and a gas pressure in the vacuum chamber of around 110 millitor; the diameter of the electron beam was maintained at 20.

Fujicolor 800 was used for both fluorescence and cathodoluminescence photography. This film was chosen because it is very fine grained and has good colour reproduction because of its low Schwarzchild effect with long exposure times. Because of low intensity in emitted light, the exposure time could be about 1 minute.

VII. SYSTEMATIC DESCRIPTION

Order: Proboscidea ILLIGER, 1811
Suborder: Mastodontoidea OSBORN, 1921
Family: Tetralophodontidae VAUFREY, 1958
Subfamily: Anancinae HAY, 1922
Genus: *Anancus* AYMARD, 1855

Anancus arvernensis (CROIZET & JOBERT, 1828)

Locality: Apolakkia I

The material includes a large skull fragment, complete with the M^1 molars on both sides in the mandibular bone and the anterior parts of the M^2 molars on both sides. The

two complete tusks are *in situ*. The alveoli are broken and the roots of both tusks are missing. This is the first discovery of this species on Rhodes, although Proboscidean remains are known to have been found in the wider Apolakkia area. It is also one of the best preserved mastodont speciments in Greece and should consequently be described in detail.

The skull belongs to a juvenile animal. The two M^1 molars are only slightly worn, mainly on the anterior part of the masticate surface, and the two M^2 molars were in process of erupting. The tusks have not acquired their full length and the distance from the anterior part of the M^1 to the anterior tip of the tusks is 92.5 cm and 94.0 cm for the left and right sides, respectively. The bases of the tusks that were originally in the alveoli are partially broken, and the same is true for the alveolar bone. Both tusks have a maximum diameter of 65 mm about 60 cm from their tips.

The morphology of the masticate surface strongly resembles that described by SCHLESSINGER (1922, Plate XIII, Figure 1, and Plate XI, Figure 4), but the example shown in Plate XIII, Figure 1r, said to be M^2, is slightly more worn than our specimen. On the other hand, the molar in Plate XI Figure 4, which again is slightly worn, is M^1. The enamel shape is consequently more obvious. Each M^1 possesses four sets of cusplets, which are slightly alternating.

The dimensions of the M^2 molars in our material are very similar to those from the Arno Valley (WEITHOFER 1890, Plate XIV, Figure 5).

The references which we have been able to locate do not clearly specify any differences between M^1 and M^2 molars in *Anancus arvernensis*. However, M^2 are slightly longer than M^1, having a larger length/width index (Table 1), which is in keeping with M^3 molars of *Anancus arvernensis* being even longer than the M^2 molars.

Table 1 Measurements of M^1 molars of *Anancus arvernensis* from Apolakkia I, Rhodes, Greece

	sin.	dext.
Length	105	106
Heigth	41	41
Width	65	65
L/W ratio	1.615	1.630

All measurements are in mm.

Comparison of the Rhodes material with the data given by SCHLESSINGER (1922, p. 63) shows that the molar of the Rhodes mastodont is more similar to M^1 than M^2. The dimensions reported for M^2 molars of *Anancus arvernensis* by KOUFOS (1977, p. 110) also suggest that M^1 molars, which have the same number of tubercules as M^2, are slightly smaller than M^2 molars.

The material used by SCHLESSINGER (1921, p. 125) was thought to represent an intermediate form between *Mastodon longirostris* and *M. arvernensis* (cf. also Plate XVIII, Figure 1). Its M^2 molar was 122 mm long and 74 mm wide and was consequently significantly larger than the molar from Rhodes.

PIVETEAU (1958, p. 244) gives the dimensions of M^2 molars in *Anancus arvernensis* as length 120-174 mm and width 65-84 mm, which again exceed those of the Rhodes
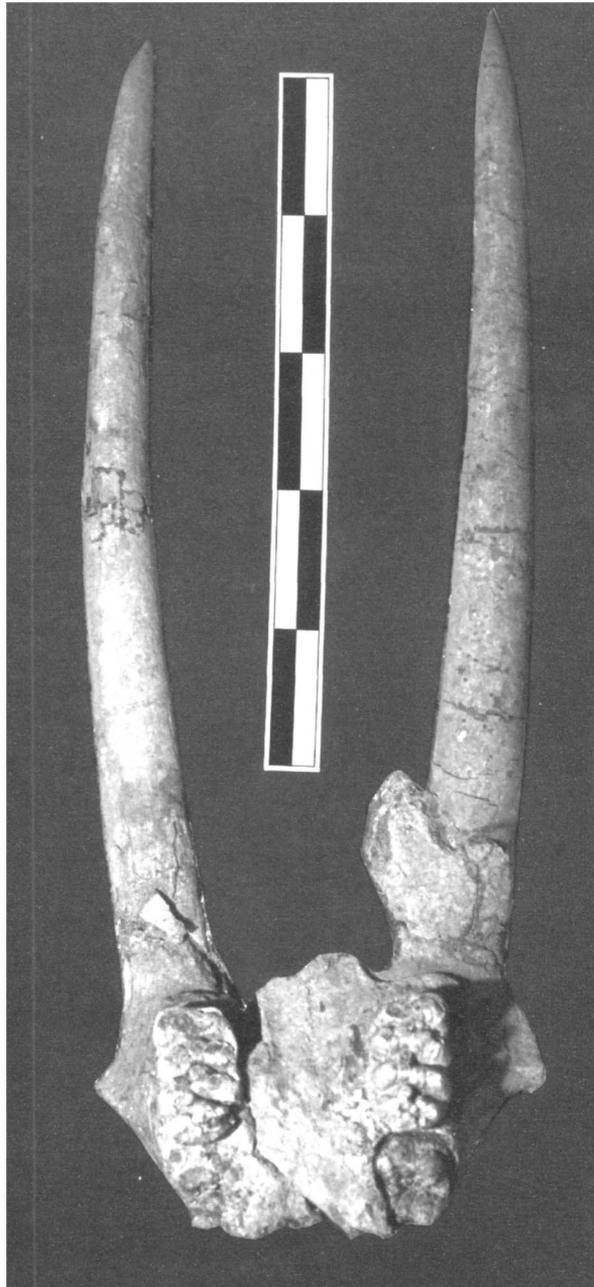
Fig. 4. *Anancus arvernensis* (CROIZET & JOBERT, 1828) from the Upper Pliocene of the Apolakkia Formation, Rhodes, Greece. Lingual view of the skull fragment after preparation. The tusks, though fractured in numerous places, were kept *in situ*. Scale: 50 cm.
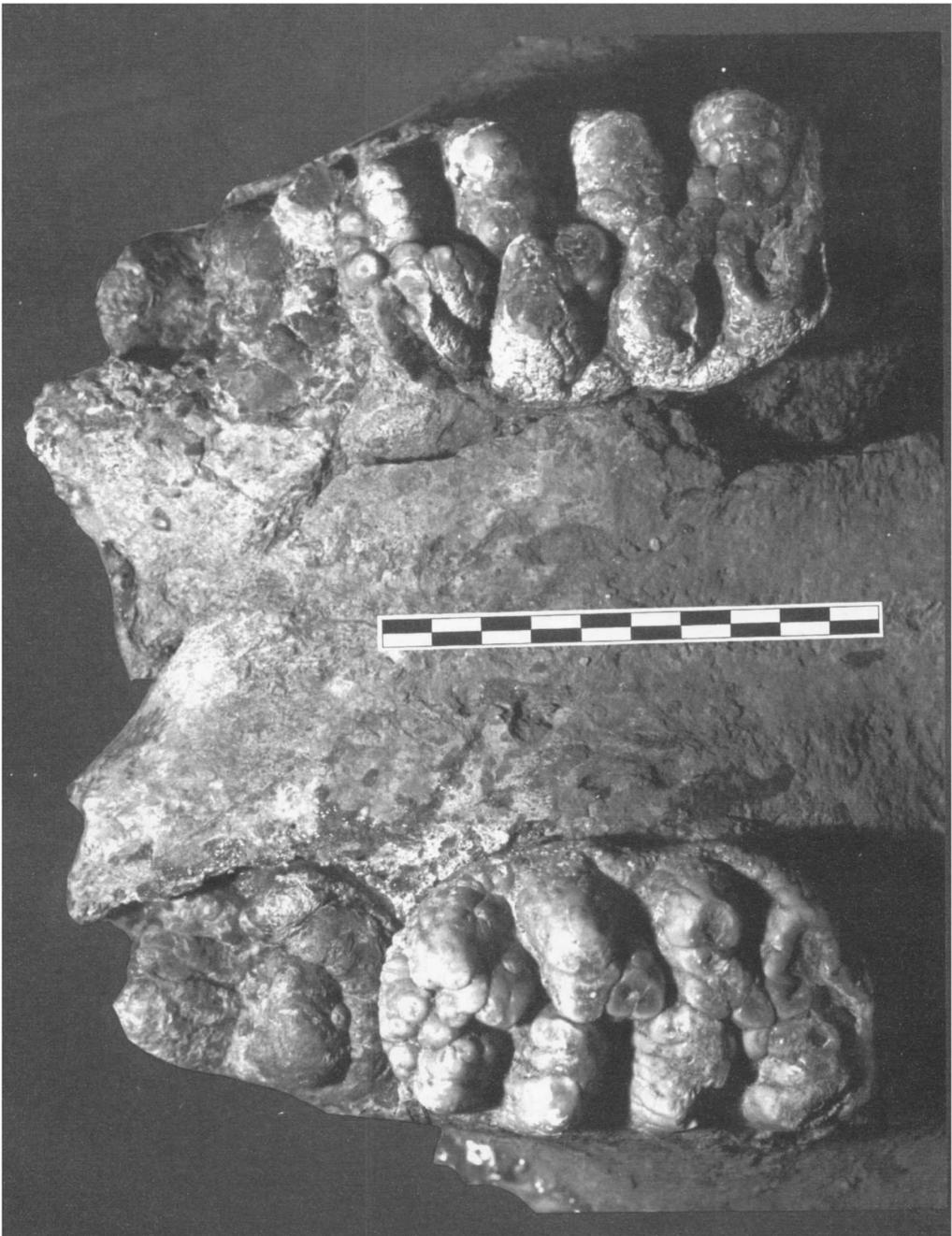
Fig. 5. *Anancus arvernensis* (CROIZET & JOBERT, 1828) from the Upper Pliocene of the Apolakkia Formation, Rhodes, Greece. Lingual view of the upper molars. The alternation of the cusplets and mammilae is obvious as is the existence of central intermediate cusplets. The M^1 molars are complete, but the M^2 molars are broken. Because the M^2 molars are erupting and wear is limited, the molars belong to a juvenile. Scale: 10 cm.

material. The dimensions of M^1 molars are not given.

BOEUF (1983) describes numerous remains of *Anancus arvernensis* from Chilhac, France. The dimensions of M^1 from Rhodes are quite comparable to those of M^1 from Chilhac (Table 3), although the former are somewhat wider.

Table 2 Data given by SCHLESSINGER (1922, p. 63)
(measurments in mm)

	Length	Width	L/W
M^1	100	60	1.67
M^2	128	74	1.73
M^1	116	72	1.61
M^2	145	79.8	1.82
M^2	140	81.5	1.72
M^2	142	81	1.75

Table 3 Data given by BOEUF (1983, p. 152)
(measurments in mm)

	Length	Width	L/W
M^1	104	59	1.76
M^1	103	59	1.75

According to these data, the Rhodes material is closer to M^1. In this material, the ridges consist of pairs of thick, high, conical mammilae (Mastodon cusplets). The inner and outer mammilae are alternating and not opposite each other as in *M. angustidens* and *M. longirostis*. The valleys between the ridges are interrupted by large accessory conical (intermediate tubercules) mammilae (cusplets) which on wear would unite with the lingual, main cusps to form a trifoil pattern. The anterior talon is not prominent, but the posterior one is obvious. A cingulum exists around the base of the tubercules (cusplets-mammilae) in certain parts of the molars. It is mainly found on the lingual (interior) side of the molars. The description given above for the Rhodes specimen is typical for *A. arvernensis*.

OSBORN (1936, p. 628) pointed out that in *Anancus* the tusks are straight and elongated and the intermediate molars have four ridge crests. The name *Mastodon arvernensis* CROIZET & JOBERT, 1828 was used well before the genus name of *Anancus* which has been widely used and accepted since the publication by OSBORN (1936, p. 630). However, it is beyond the scope of this paper to discuss or criticise Mastodon nomenclature.

While studying the Rhodes material we have tried to locate references dealing with skull material that includes both M^1 and M^2. So far we have not succeeded. Clearly, only by doing this could we exclude the possibility that some molars were wrongly accepted in old references as M^1 or M^2.

According to the description of *Anancus arvernensis* by MÜLLER (1970), Mastodon Proboscidea reached 2-2.9 m in height; *Tetralophodon* had a short rostrum and long, wide molars with alternating cusps which are not in series as in Tetralophodindae which had a
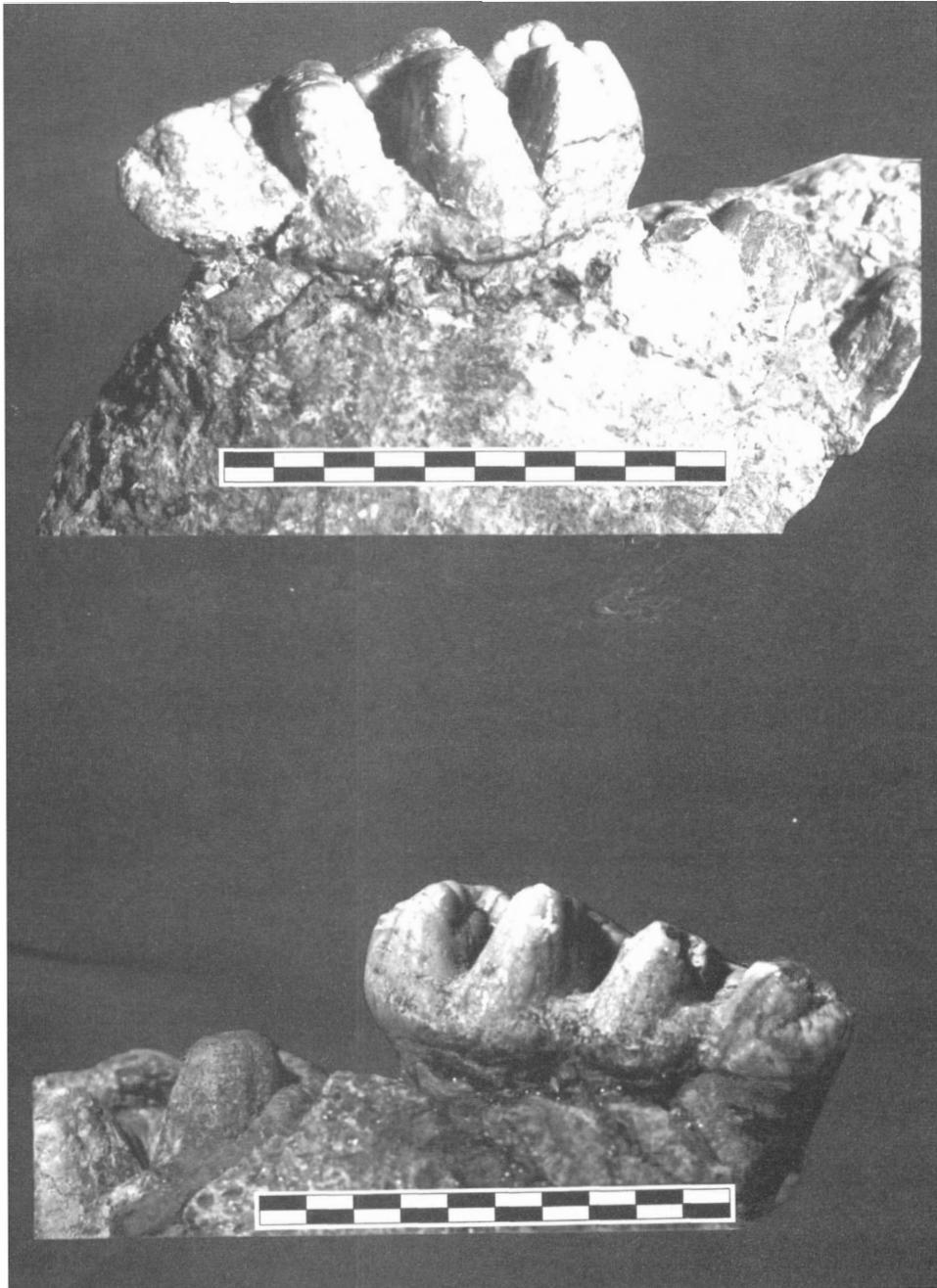
Fig. 6. *Anancus arvernensis* (CROIZET & JOBERT, 1828) from the Upper Pliocene of the Apolakkia Formation, Rhodes, Greece. Buccal view of the right M^1. M^2 is erupting. Scale: 10 cm.

Fig. 7. *Anancus arvernensis* (CROIZET & JOBERT, 1828) from the Upper Pliocene of the Apolakkia Formation, Rhodes, Greece. Buccal view of the left M^1. M^2 is erupting. Scale: 10 cm.
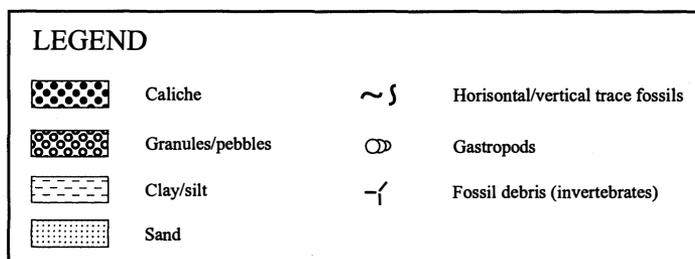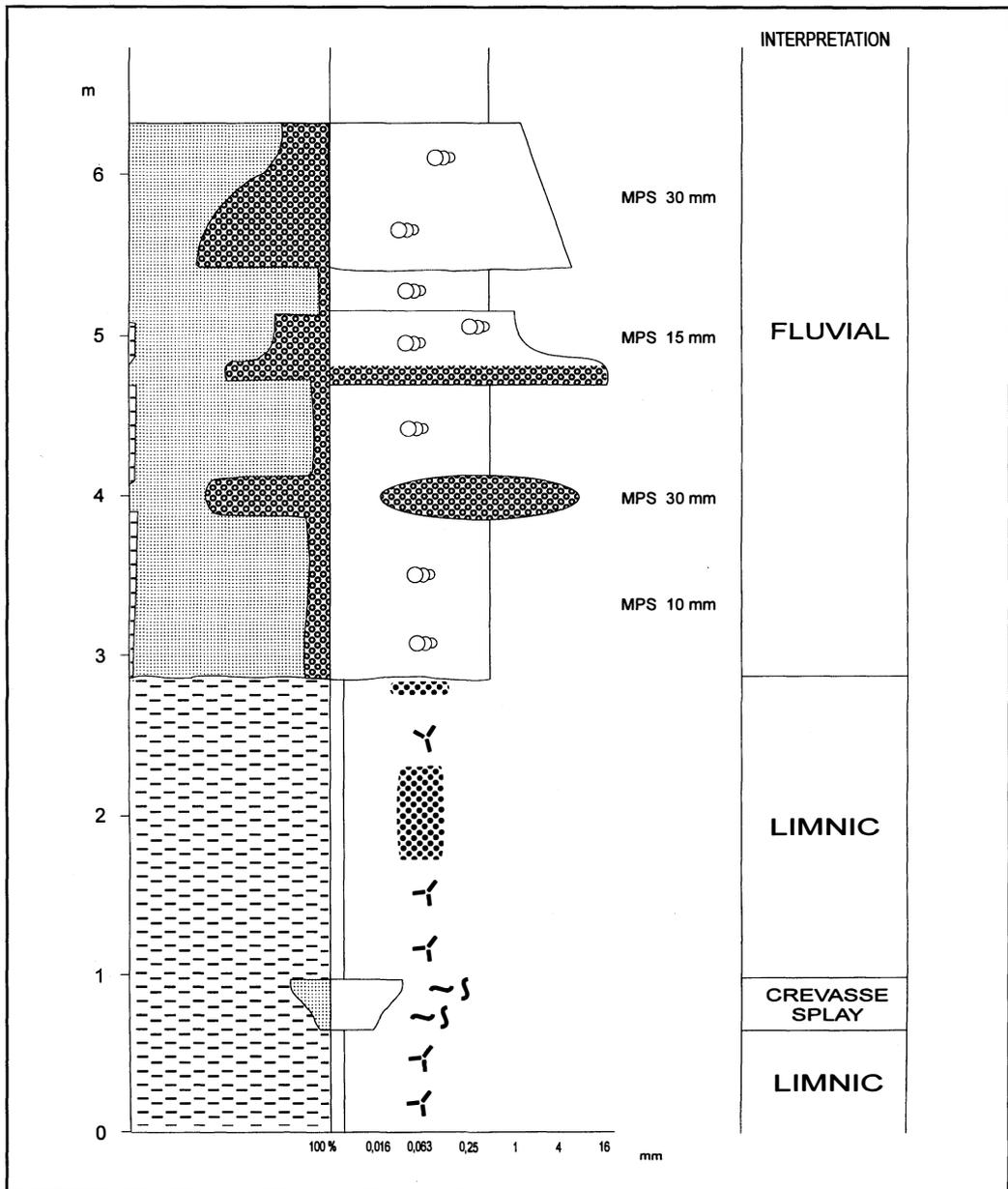
Fig. 8. Section at Apolakkia I. The skull fragment of *Anancus arvernensis* was found in the lower part of the sand/gravel unit just below the 5 m level MPS: MAXIMUM PEBBLE SIZE.

Fig. 9. View of the road section with fluvial deposits at locality II. After it was realized that the vertebrate bones were mostly found in the lower part of the channel fills, it became fairly easy to locate other vertebrate remains. Location of Vertebrate remains arrowed.

long rostrum; *Anancus arvernensis* only had tusks in its upper jaw and these reached about 3 m in length in adult animals; the enamel is only visible in juveniles.

Anancus arvernensis is regarded as being characteristic for the Upper Pliocene and "Villafranchian" in Europe. The geographical distribution of the species was reported by many authors during last century and by TOBIEN (1978). The latter could not *a priori* reject the possibility of subspecific differentiation (TOBIEN 1978, p. 169). In our opinion, this would only be possible if numerous samples that were favourable for biometrical purposes became available.

Our study did not put us in a position to correlate the sizes of M^1 and M^2 with those of tusks. The finding from Rhodes, if the documentation of M^1 is accepted, must be regarded as a normally sized specimen.

Locality: Apolakkia II

The remains of a skull belonging to a Proboscidian. Lack of diagnostic features hamper any closer identification.

VIII. BIOEROSION

To obtain more information about the taphonomy, thin sections were made from several of the loose bone fragments from localities I and II. Petrographical examination in ultraviolet light showed that some of the bone material was in part heavily bioeroded by endolithic cyanophytes (Fig. 10). The borings are elongate and have a rounded cross section. They are isodiametric and have a rounded cross section. The longest borings in particular tend to be orientated almost perpendicular to the surface.

The degree of bioerosion varies systematically from the inner to the outer parts of the bones, the inner parts being significantly less bioeroded (sometimes not at all) than the periphery which is sometimes strongly affected. The density and depth of the borings may also vary greatly over short spaces so that the bone substance around one and the same cavity may contain small areas that are significantly more bioeroded that the surrounding ones. Locally, the density of borings may be so high that it may be difficult to separate the individual borings from each other. Inwards from the outer zone, the number and density of borings decrease rapidly.

In some cases, the bioerosion may be so intensive that it has led to a distinct weakening of the mechanical strength of the bones. This weakening has led to these bones being easily abraded during fluvial transport. Hence, small, rounded bone fragments frequently show intensive bioerosion whereas only slightly abraded bones often show no or perhaps only minor bioerosion.
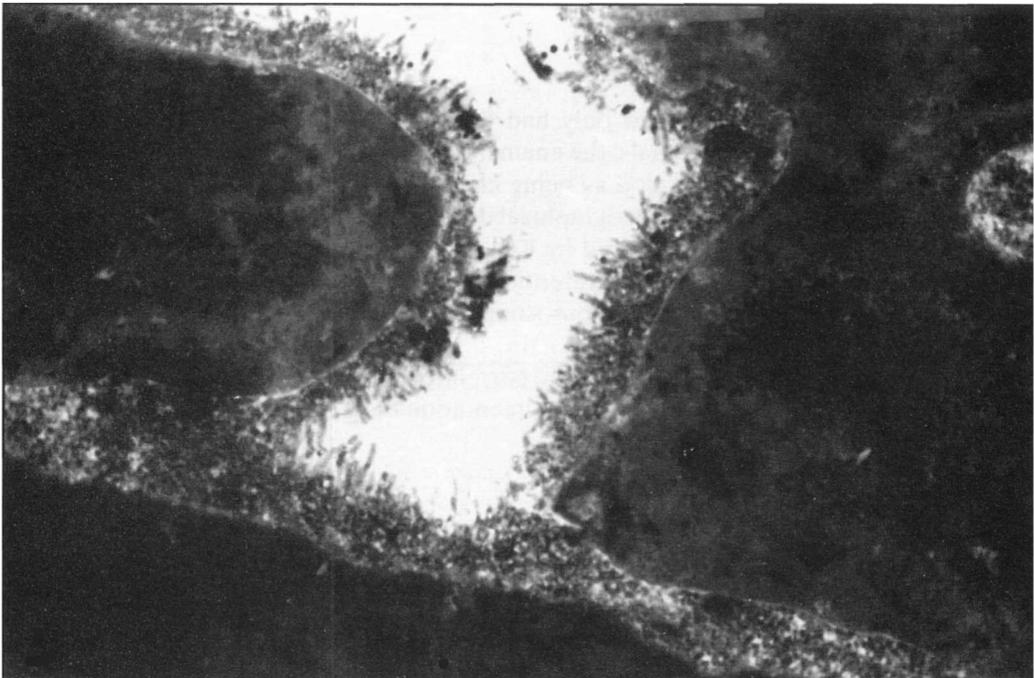

Fig. 10. Bone from locality I with borings made by endolithic cyanophytes. Thin section, ultraviolet light ≈ 80 x.

IX. CALCRETE

Petrographical studies of bone fragments show that the primary pores are often more or less cemented by a micritic mass (Fig. 11). The reduction of the primary pore volume is greatest in the pores close to the surface where these may be more or less entirely cemented. The volume of the micrite deposition decreases inwards towards the central part of the bone where the precipitation may constitute about 10% of the pore volume. The thickness of the micritic precipitations show substantial local variations, even within one and the same pore.

In some cases, the micritic precipitation is developed as a homogeneous micritic mass, but generally it has a peloidal structure (Fig. 11). The individual peloids have usually more or less amalgamated to form extremely irregular aggregates.

The micrite precipitation in the primary pores of the bones shows a substantial measure of agreement with calcrete that has a dense or nodular microstructure (see the description by WRIGHT 1990). This therefore suggests that the micrite-bearing bone fragments originally derived from a calcrete profile on land before their final deposition in a fluvial enninronment.
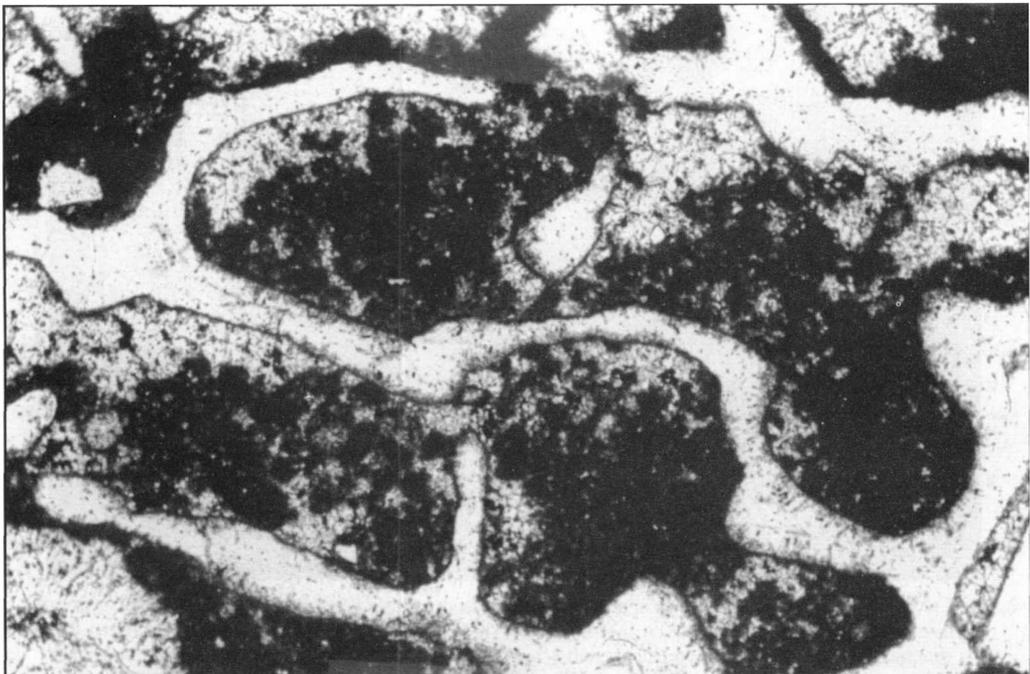
Fig. 11. Peloidal calcrete in primary cavities in a bone from locality I. Thin section, plane-polarised light ≈ 50 x.

X. CALCITE CEMENTATION

The bone material shows great variation with regard to calcite cementation. Thus, the bones from locality II were not calcite cemented, whereas some of those from locality I contained variable amounts of calcite cement in their primary pores. The calcite cementation could also vary greatly within one and the same bone. Usually, the peripheral parts of the bone were better cemented than the central part. This is a consequence of the passage of pore water, and therefore the supply of oversaturated pore water from which cement could be precipitated, was greater in the peripheral than the inner part of the bones.

Cathodoluminescence microscopy of the calcite cement showed that it is possible to distinguishe four distinct calcite generations on the basis of luminescence colours (Fig. 12). The first generation is thin and non-luminescent. This cement is not substrate selective and is precipitated directly, both as a lining on the exposed pore surfaces of the bones and directly on micritic precipitations after cyanobacteria where these have grown on the bones. The second cement generation is brightly luminescent and coats earlier non-luminescent cement as a thin layer. Its boundaries are sharply defined. The third
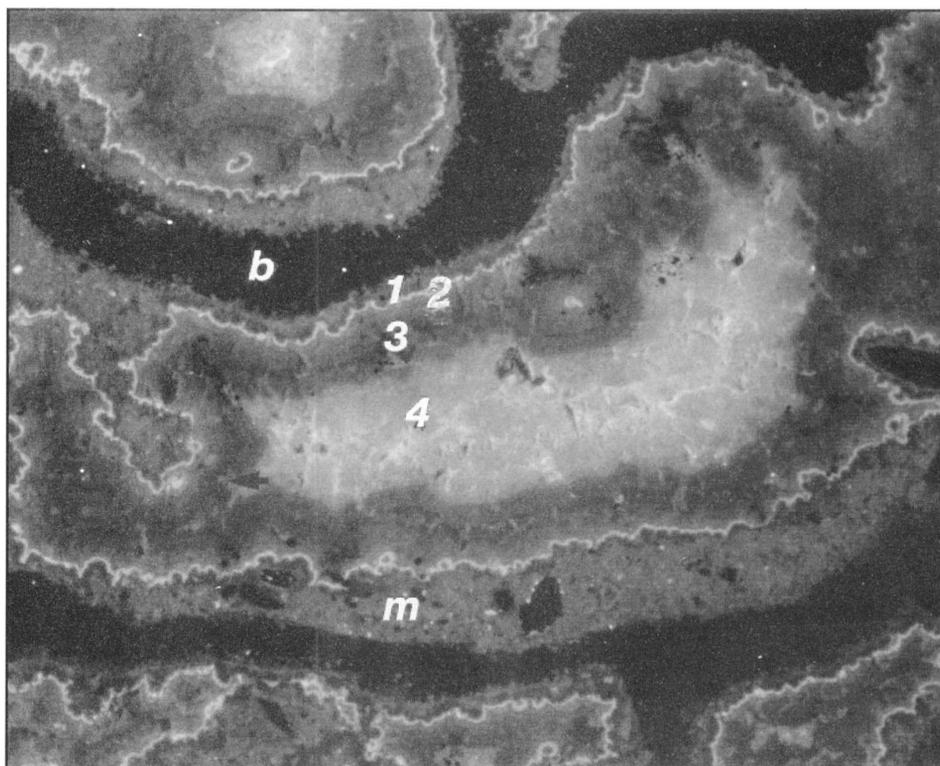

Fig. 12. Calcite cement in primary cavities in a bone fragment from locality I. b, bone substance; m, matrix in primary cavity. The cement generations in the primary cavities are numbered from 1 (first generation) to 4 (last generation). 1, dull/non-luminescent cement; 2, brightly luminescent cement; 3, dull/brown luminescent cement followed by a dissolution surface (arrow) which predates luminescent calcite cement (4). Thin section, cathodoluminescence.

generation is dark brown with alternating lighter and darker zones. This type of cement is volumetrically the most important type of cement and may in some cases result in complete cementation of the primary cavities. Partial dissolultion occurred after precipitation of the third cement generation. The dissolution surface cuts through growth layers in the third cement generation and led to partial solution along the intercrystalline boundaries. The fourth cement generation, which is only sporadically developed, has a characteristic reddish to orange luminescence.

The luminescing properties of calcite can be used to deduce the composition of the pore fluids during crystal growth (MEYERS 1974). The cathodoluminescence is attributed to the presence of Mn^{2+} as an activator ion whereas Fe^{2+} is believed to be the most important quencher ion (see summary by MARSHALL 1985).

In this investigation, the first three cement generations show the classical non-luminescent-bright-dull luninescent zonation which is related to increasing burial during crystal growth (see e.g. GROVER & READ 1983). The sequence is related to the increasingly reducing nature of pore fluids during burial (CARPENTER & OGLESBY 1976, FRANK *et al.* 1982). The early non-luminescent zone is precipitated from oxidising pore water in which Mn is the 4+ and Fe in the 3+ state. These ions are strongly excluded from the carbonate lattice and no cathodoluminescence is produced. The bright zone records the onset of permantelty reducing conditions when only Mn^{2+} is available whereas Fe remains in the 3+ state and is not incorporated in the calcite lattice. At deeper burial, the pore water becomes even more reducing. Unter these conditions, Mn and Fe are both in the 2+ state and can substitute for Ca, leading to dull, partly quenched cathodoluminescence.

XI. CONCLUSIONS

The mastodont skull remains from locality I belong to the Upper Pliocene *Anancus arvernensis*. The skull belongs to a not fully grown juvenile, as is clearly shown by the dentition and the wear state of the molars and tusks.

Petrographic studies of bone remains from locality I show some interesting variations, summarised in Fig. 13. The mixture of bioeroded and non-bioeroded fragments, with or without calcrete deposits, indicates that the bone remains have lain on land for a shorter or longer period prior to final deposition in a fluviatile environment. This also shows that they derive from several different individuals which have died near the river. Erosion of the river bank or flooding has then resulted in the bones falling into the river and being carried downstream for a shorter or longer distance prior to final deposition and burial in the fluvial deposits. Considerable variation in the length of transport is easy to deduce from the great variation in the degree of abrasion shown by the material. Sub-rounded bone fragments must thus have undergone significantly longer fluvial transport than well-preserved bones which scarcely show any sign of physical abrasion.

The concentration of bone fragments in the lower part of fluvial deposits is commonly encountered in other bone-bearing sites (BEHRENSMEYER & HILL 1980). More systematic investigation of the fluvial deposits of the Apolakkia Formation would therefore probably reveal much more vertebrate material than these preliminary investigations have succeeded in doing.
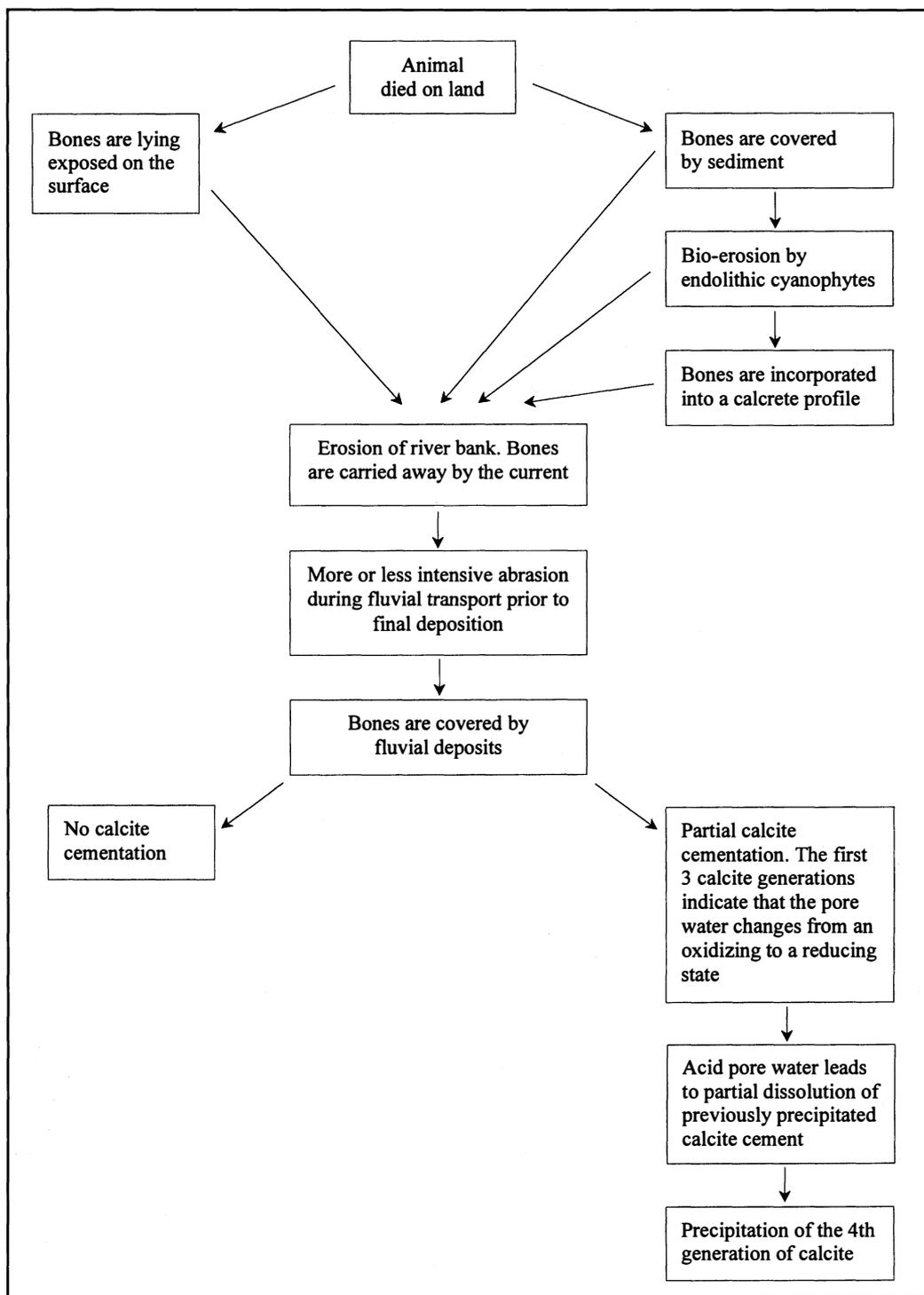
Fig. 13. Summary of taphonomic events, based on bone fragments from locality I.

SUMMARY

Remains of the skull and numerous smaller bone fragments of the mastodont *Anancus arvernensis* have been found for the first time on Rhodes in Greece. The biostratigraphy of the locality is discussed and correlated with plant remains and the endemic gastropod fauna from the same part of the sequence.

All the material was found in fluvial deposits in the Upper Pliocene Apolakkia Formation. The bone remains represent allochthonous material that has undergone various taphonomic processes prior to final deposition. Following burial, most of the bone fragments became partially cemented with calcite. Cathodoluminescence microscopy suggests the presence of an early precipitation of calcite from oxidised pore water which gradually became more reducing as the depth of burial increased.

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