

*Prodeinotherium bavaricum* (Proboscidea, Mammalia) from  
Lesvos island, Greece; the appearance of deinotheres  
in the Eastern Mediterranean

*Prodeinotherium bavaricum* (Proboscidea, Mammalia) de l'île de Lesvos,  
Grèce ; apparition des déinothères en mer Méditerranée orientale

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**Abstract**

The island of Lesvos, eastern Aegean, Greece is well known for the Neogene Petrified Forest of Sigri, situated in the southeastern part of island. The Miocene mammals were hitherto unknown in the island and the deinotheres studied herein is the first evidence of their presence. The material was found near the village Gavathas in strongly silicified lacustrine marls. The morphological characters of the studied teeth and their dimensions indicate that they belong to a primitive form of *Prodeinotherium bavaricum*. This fact together with the available radiometric ages of the volcanic rocks of the area suggests a minimum age of 18.4 Ma corresponding to the upper part of early Miocene or to late MN 3. The arrival and the dispersion of the deinotheres in Eurasia are also discussed and the Lesvos material represents the first known appearance of deinotheres in Europe. They arrived at the end of MN 3 (18.0–19.0 Ma) and they rapidly dispersed into Europe as their first occurrence in France and Spain is dated at the early MN 4 (18.0). Their first appearance in Asia seems to be earlier as they were traced in the Bugti fauna (Pakistan) dated at 20.5 Ma. This suggests an early connection of Africa and Asia before the final closure of the Tethyan Seaway.

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**Résumé**

L'île de Lesvos (Mer Égée, Grèce) est bien connue par la présence de la forêt pétrifiée néogène à Sigri au bord sud-est de l'île. Jusqu'à aujourd'hui les mammifères du Miocène sont absolument inconnus dans la région. Les restes des déinothères étudiés ici constituent la première évidence de leur présence à Lesvos. Les restes sont trouvés à proximité de Gavathas dans les dépôts lacustres silicifiés. Les caractères morphologiques des dents et leurs dimensions permettent leur attribution à l'espèce *Prodeinotherium bavaricum*. Un âge minimum de 18.4 Ma peut être supposé selon les estimations radiométriques de roches volcaniques dans lesquelles les fossiles ont été découverts. Cet âge absolu indique la partie supérieure du Miocène inférieur (limite MN 3). La dispersion eurasiatique de déinothères est aussi discutée. La forme de Lesvos représente la première apparition de déinothères en Europe. Les déinothères arrivent en Europe de l'est avant 18.0–19.0 Ma et sont rapidement dispersés vers l'ouest où ils sont justement présentés à la MN 4 (France, Espagne). En ce qui concerne l'Asie, les déinothères apparus dans la faune de Bugti, Pakistan, sont datés à 20.5 Ma.

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**Keywords:** Mammalia; *Prodeinotherium*; Early Miocene; Greece; Biochronology

**Mots clés :** Mammifère ; *Prodeinotherium* ; Miocène inférieur ; Grèce ; Biochronologie

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## 1. Introduction

The material presented in this article was found in the island of Lesvos, east Aegean Sea, Greece. The Miocene deposits of Lesvos are mainly volcanic including a rich flora with entire trees (Petrified Forest of Sigri) but mammals from that time were hitherto unknown. The studied deinother is the first evidence of the presence of Miocene mammals in Lesvos. The other mammalian fauna known in Lesvos is from Vatera, dated to the end of Pliocene (Dermitzakis et al., 1990, de Vos et al., 2002). Deinotheres are well known in Greece especially in the late Miocene. Until now their earliest appearance in Greece was recorded in the locality of Thymiana, Chios Island (Paraskevaidis, 1940), dated to MN 5 and more precisely at 15.5 Ma (Bonis and Koufos, 1999). Some deinotherian remains are also known from Psara island, near to Chios, probably of similar age (Besenecker and Symeonidis, 1974). Deinotheres are well known in the late

Miocene faunas of Greece (Pikermi, Axios Valley, Samos, etc.) and they are also known in the Pliocene. The new findings from Lesvos are the oldest known in Greece and the eastern Mediterranean corresponding to the first appearance of the family in Eurasia. They were found near the village of Gavathas, northwestern Lesvos (Fig. 1). Unfortunately, our efforts to find more material were unsuccessful. Search is very difficult because the fossils are included in an extremely hard-silicified marl and even with mechanical tools it is difficult to dig. To obtain the studied fossils, we were working 3 days with a big mechanical hammer (compressor) and two mechanical cutters. The preparation of the fossils was continued for more than 2 months.

## 2. Geological setting

According to the available data, the geological structure of Lesvos island consists of the alpine basement, including

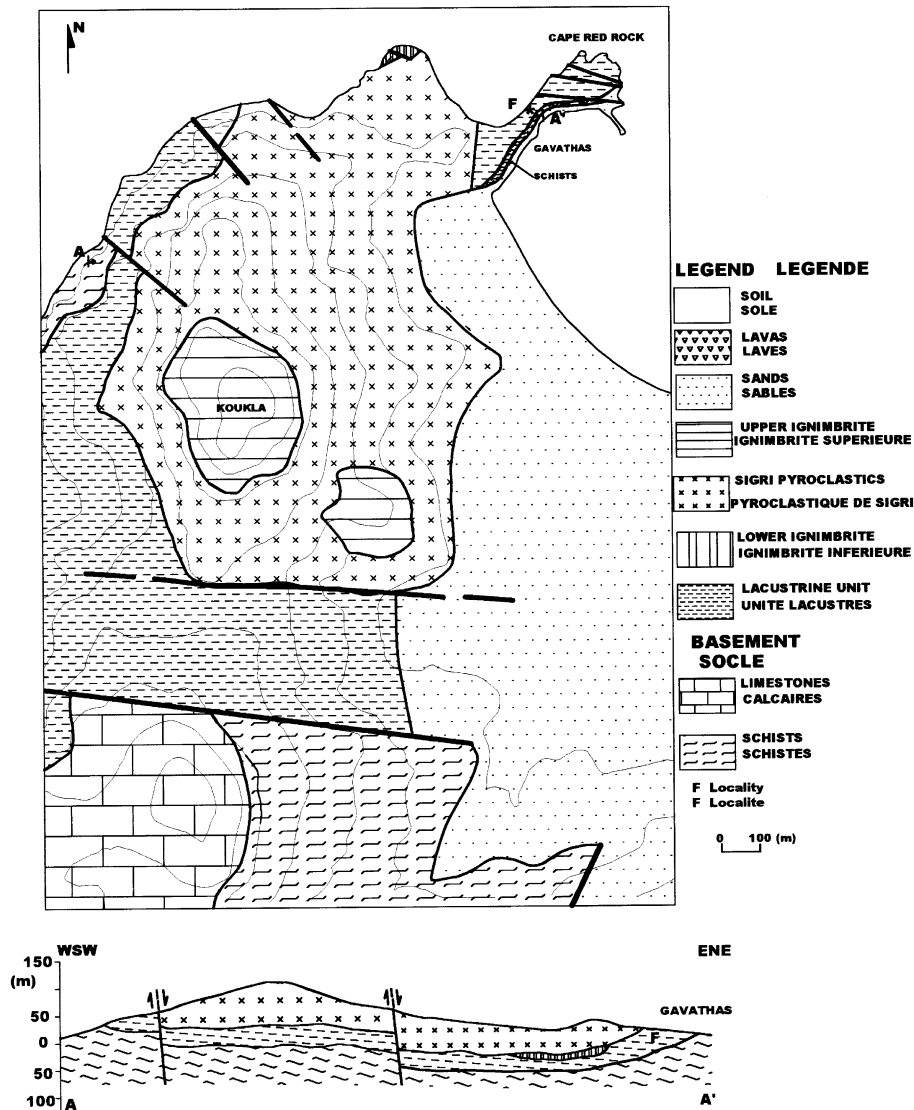


Fig. 1. Geological map of the Gavathas area indicated the position of the fossiliferous site.

Fig. 1. Carte géologique de la région de Gavathas et position du site fossilifère.

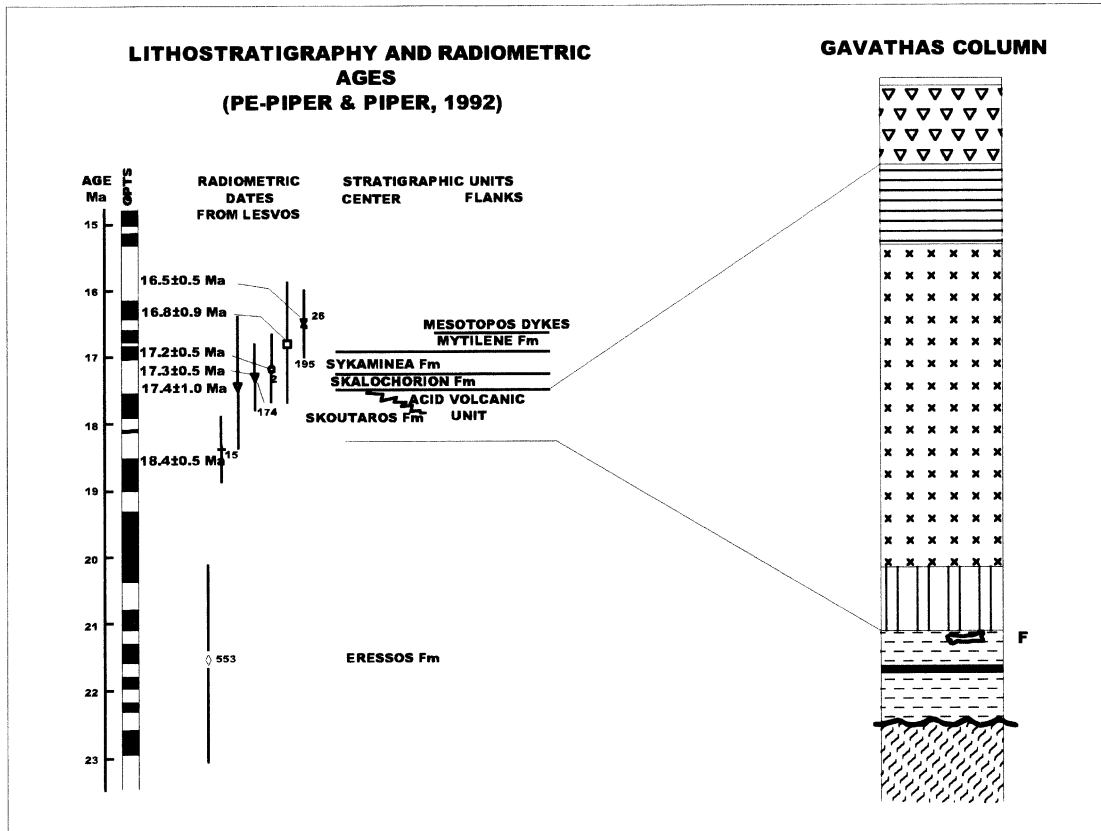


Fig. 2. Stratigraphic column of the Gavathas area and its correlation with the Neogene volcanic and pyroclastic deposits of Lesvos. Symbols as in Fig. 1.  
 Fig. 2. Colonne stratigraphique de la région de Gavathas et corrélations avec les dépôts volcaniques et pyroclastiques de Lesvos. Symboles, voir Fig. 1.

schists and crystalline carbonates, overthrust by a Tethyan ophiolitic nappe, Neogene volcanic rocks and lacustrine deposits, as well as Tertiary marine and lacustrine deposits.

The volcanic rocks are widely distributed and of varied thickness in the area (Hecht, 1974; Pe-Piper, 1978). Neogene volcanic rocks dominate the central western part of the island. They overlie the alpine rocks and comprise andesites, rhyolites and various other lava types, pyroclastic tuffs and volcanic ashes. The following lithostratigraphy has been proposed for them (Pe-Piper and Piper, 1992) from oldest to the youngest: (1) Eressos Formation (andesites and agglomerates); (2) Skoutaros Formation (pyroxene andesite lavas)/Acid Volcanic Unit (Sigri pyroclastics); (3) Polychnitos Ignimbrite; (4) Skalochorion Formation; (5) Sykaminea Formation; (6) Mytilene Formation (basalts), and (7) Mesotopos Dykes.

In the area of Gavathas, where the fossils were found the following lithostratigraphic units can be recognized (Mouroukidou, 2001):

- The Basement consists mainly of various schists and limestones (Fig. 2) of Neopaleozoic age (Katsikatsos et al., 1993).
- The Lacustrine Unit, situated unconformably on the basement, corresponds to the first Neogene deposits (Fig. 2). The unit consists of alternating marly limestones and marls with tiny lignitic intercalations of about 1 m thickness. In the base of the unit there are more

marly limestones, while in the upper part marls are more common. This unit is strongly silicified because of the younger volcanic action in the area. The fossils were found in the upper levels of the Lacustrine Unit (Fig. 2).

- The Pyroclastic Unit overlies the Lacustrine Unit and is known in the area as the “Sigri pyroclastics”. In the Gavathas area the unit consists of: (a) the lower ignimbrite comprising small lava conglomerates and volcanic ashes, (b) the pyroclastic deposits consisting of debris flow in the upper part and of mud flow in the base, and (c) the upper ignimbrite consisting of black glassy lavas.
- The Lava Unit consists of dacites and dakito-andesites.

The pyroclastic formations of the Gavathas area (Fig. 2) correspond to the Acid Volcanics Unit, which is correlated with the Skoutaros Formation. The various pyroclastics and lavas have been dated radiometrically but their age will be discussed together with the biochronological data in order to obtain an idea of the age of the fossils.

### 3. Palaeontology

Order: PROBOSCIDEA Illinger, 1811  
 Suborder: DEINOTHERIOIDEA Osborn, 1921  
 Family: DEINOTHERIIDAE Bonaparte, 1845  
 Genus: *Prodeinotherium* EHIK, 1930  
*Prodeinotherium bavaricum* (v. MEYER, 1831)

**Material:** Right lower tooth row with P<sub>3</sub>-M<sub>3</sub> in situ and left lower tooth row with P<sub>3</sub>-M<sub>3</sub> in situ of the same individual, GVT-1

**Locality:** Gavathas, Lesvos island, Greece

**Age:** Early Miocene, MN 3

**Measurements:**

	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	P <sub>3</sub> -M <sub>3</sub>	P <sub>2</sub> -P <sub>4</sub>	M <sub>1</sub> -M <sub>3</sub>
DAP	38.8	50.6	58.8	59.1	68.4	259.2	80.7	181.5
DT <sub>ant.</sub> sin	22.6+	40.2	42.2	52.1+	55.5	—	—	—
DT <sub>post.</sub>	27.2+	42.2	43.0	51.4+	48.6	—	—	—
DAP	36+	50.2	60.0	59.2	—	—	80.5	—
DT <sub>ant.</sub> dex	24+	29.5	40+	52.0	52.5++	—	—	—
DT <sub>post.</sub>	28.5+	41.4	42.0	51+	—	—	—	—

**Description:** The dentition is very worn, the cuspids are heavily worn and the lophids are connected. In M<sub>3</sub>, the inner cuspids are slightly worn, and still separated (Fig. 3). The right M<sub>3</sub> is broken and preserves only the mesial lophid (metalophid according to Gräf, 1957). The enamel of the teeth was damaged in several corners postmortem.

- **P<sub>3</sub>.** The right P<sub>3</sub> is partly broken and worn in its inner part. However, the left one is better preserved but both inner and outer surfaces are worn and the enamel has disappeared. The mesial lophid (metalophid) is high and subdivided into two cuspids by a shallow groove in its mesial and distal surface. In the mesial border of the tooth, there is a small mesial projection clearly observed in the left P<sub>3</sub> (Fig. 3b). It is slightly broken anteriorly but it is possible to distinguish a small cuspid situated lingually and the trace of another one. The distal lophid (hypolophid) consists of two cuspids separated by a valley. The labial cuspid is stronger and higher than the lingual one and it is connected with the anterior lingual cuspid by a shallow crest. The metalophid is separated from the hypolophid by a deep valley, which is open lingually.
- **P<sub>4</sub>.** The distolabial surface of both available teeth is very worn and the enamel is absent; in the left tooth, it is broken. The mesial lophid consists of two cuspids, the metaconid and the protoconid. The protoconid is weaker than the metaconid. In the distal lophid, the entoconid is stronger than the hypoconid. The mesial lophid is separated from the distal one by two valleys, a labial and a lingual one; both are deep and open labially and lingually, respectively. The paraconid is well expressed and it is separated from the mesial lophid by a shallow valley open lingually. The hypoconulid is stronger than the paraconid, it is wider and also separated from the distal lophid by a shallow valley which opens lingually.
- **M<sub>1</sub>.** It is elongated with three lophids separated by deep valleys. The tooth is heavily worn and its morphology is not very clear. The third lophid is narrower than the other two.
- **M<sub>2</sub>.** It is wider than M<sub>1</sub> with two lophids and a reduced hypoconulid preserving a cuspid situated labially. The hypoconulid is separated from the distal lophid by a

shallow valley open lingually. The protoconid and hypoconid are stronger than the metaconid and entoconid, respectively.

- **M<sub>3</sub>.** It is like M<sub>2</sub> but it has a stronger and triangular hypoconulid, which is separated as a lophid having a cuspid situated labially and directed backwards. The valley separating the hypoconulid from the distal lophid is deep and divided into two parts (labial and lingual) by a small crest in the middle of the valley. This gives it a morphology similar of the typical valley separating the mesial from the distal lophid in the molars.

**Discussion:** The taxonomy of the European deinotheres has a long history and the known material has been classified in various species with several synonymy (Osborn, 1936; Gräf, 1957; Bergounioux and Crouzel, 1962). The genus *Prodeinotherium* was erected by Ehik (1930) who described a new species from Hungary under the name *Prodeinotherium hungaricum*. Later, it was synonymized with *Deinotherium* (Gräf, 1957; Bergounioux and Crouzel, 1962), while Harris (1973, 1978) considered this as a separate genus including the small-sized deinotheres and recently it was again transferred to the genus *Deinotherium* (Ginsburg and Chevrier, 2001). Besides *P. hungaricum* four other species, *P. bavaricum*, *P. cuvieri*, *P. pentapotamiae*, *P. hobleyi* and *P. (?) orlovii* are also known, while several synonymy between them are known (Gräf, 1957; Sahni and Tripathi, 1957; Bergounioux and Crouzel, 1962; Ginsburg and Chevrier, 2001). The systematics of the deinotheres needs a complete study of the known material and certainly it is out of the aim of this article. As we are dealing with a small-sized deinotheres, the name *Prodeinotherium* will be used.

*P. hungaricum* has been synonymized with *P. bavaricum* (Bergounioux and Crouzel, 1962). The main difference between the two species is the position of the labial posterior cuspid of P<sub>3</sub>. In *P. hungaricum* it lies inside the cingulum, while in *P. cuvieri* and *P. hobleyi* it is connected with the lingual one by the cingulum (Ehik, 1930). Such a position of the labial posterior cuspid inside the cingulum is also present in one P<sub>3</sub> of *P. bavaricum* from Chevilly, France (Bergounioux and Crouzel, 1962) and cannot be used as a distinctive character. The position of the mental foramina between P<sub>3</sub> and P<sub>4</sub> is also used for the distinction of the Hungarian specimen (Ehik, 1930). However, such a position of the mental foramina between P<sub>3</sub> and P<sub>4</sub> is also observed in *P. bavaricum* and *D. giganteum* (Bergounioux and Crouzel, 1962). In 1908, Mayet described the new species "*Deinotherium*" *cuvieri* from the early Miocene deposits of Sables de l'Orléanais, France. Its slightly smaller size than *P. bavaricum* was used for this distinction. However, there is a great size variation in *P. bavaricum* and *D. giganteum*. "*D.*" *cuvieri* is considered to be a synonym of *P. bavaricum* (Gräf, 1957; Bergounioux and Crouzel, 1962). *P. hobleyi* is a small-sized African deinotheres, which has been synonymized with *P. bavaricum* (Gräf, 1957), but Harris (1978) considers this as an independent species. It differs from *P. bavaricum* by: (a) the more distinct separation of the two cuspids in the



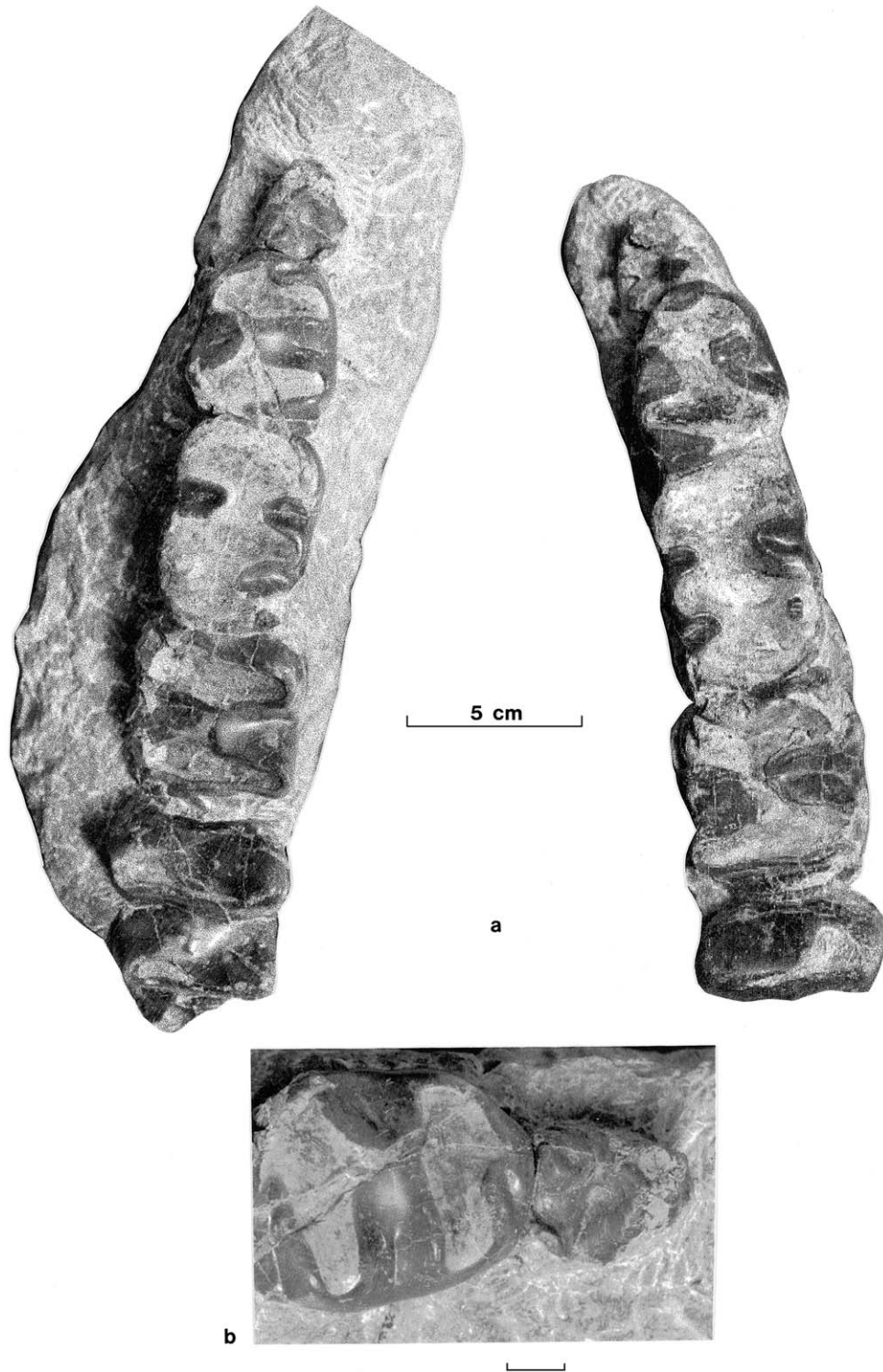


Fig. 3. *Prodeinotherium bavaricum*, GVT-1, Gavathas, Lesvos island, Greece. a. Right and left lower tooth row, occlusal view. b. Left  $P_3$ .  
 Fig. 3. *Prodeinotherium bavaricum*, GVT-1, Gavathas, île de Lesvos, Grèce. Rangées dentaires inférieures gauche et droite, vues occlusales.

anterior lophid of  $P_3$ , (b) the relatively shorter  $P_4$  compared to its breadth, and (c) the more distinct and independently developed labial cuspid of the talonid in  $M_3$  (Harris, 1978). *P. pentapotamiae* is known from Indian sub-continent, and it was described by Lydekker (Osborn, 1936). It is a small-sized deinothere similar to *P. bavaricum* and *P. hobleyi* and it

is included in the synonymy list with *P. bavaricum* (Gräf, 1957).

*P. bavaricum* is accepted as the common European small-sized deinothere (Gräf, 1957; Bergounioux and Crouzel, 1962). According to Gräf (1957), the main characters of the species are:

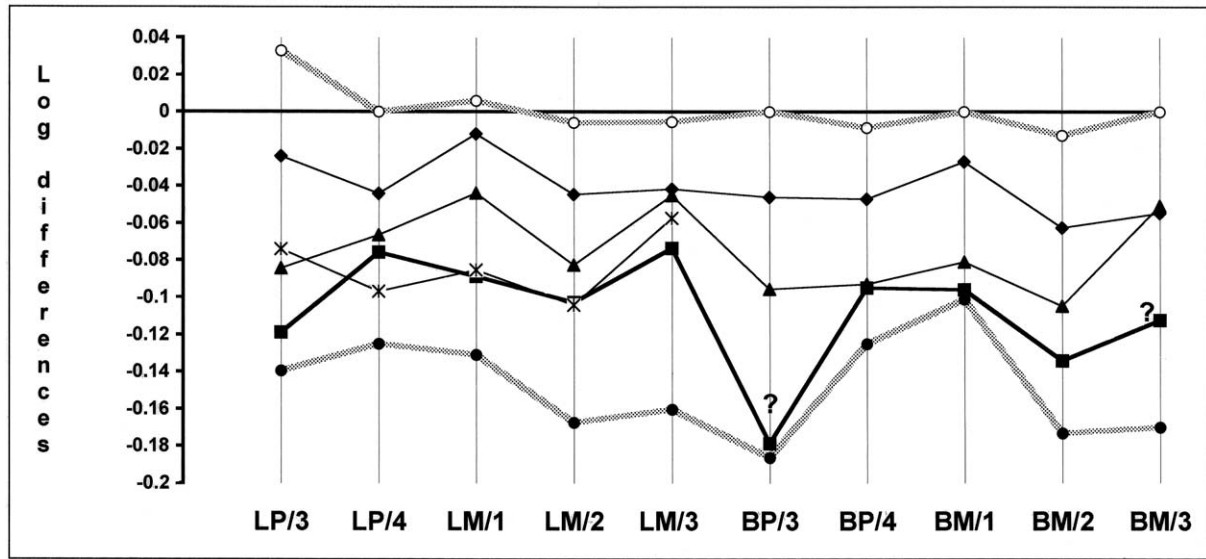


Fig. 4. Logarithmic ratio diagram comparing the studied teeth with those of *Prodeinotherium bavaricum* from various localities. Standard: *P. hobleyi*, Africa,  $n = 3-6$  (Harris, 1978). ■, GVT-1; ◆, *P. bavaricum*, Dinotheriumsande,  $n = 7-12$  (Gräf, 1957); ▲, *P. bavaricum*, Breitenbronn,  $n = 1$  (Malez and Sliskovis, 1965); ✱, *P. bavaricum*, Sables de l'Orléanais,  $n = 1$  (Osborn, 1936); ●, *P. bavaricum*, minimum values for Europe (Bergounioux and Crouzel, 1962); ○, *P. bavaricum*, maximum values for Europe (Bergounioux and Crouzel, 1962).

Fig. 4. Diagrammes de Simpson comprenant le matériel étudié avec *Prodeinotherium bavaricum* de différentes localités. Standard: *P. hobleyi*, Africa,  $n = 3-6$  (Harris, 1978). ■, GVT-1; ◆, *P. bavaricum*, Dinotheriumsande,  $n = 7-12$  (Gräf, 1957); ▲, *P. bavaricum*, Breitenbronn,  $n = 1$  (Malez et Sliskovis, 1965); ✱, *P. bavaricum*, Sables de l'Orléanais,  $n = 1$  (Osborn, 1936); ●, *P. bavaricum*, valeurs minimales pour l'Europe (Bergounioux et Crouzel, 1962); ○, *P. bavaricum*, valeurs maximales pour l'Europe (Bergounioux et Crouzel, 1962).

- the mesial lophid of  $P_3$  is well separated into two cuspids,
- the mesial projection of  $P_3$  is well developed and often bicuspid, and
- the base of the protoconid in  $P_3$  is longer than that of the metaconid.

According to Bergounioux and Crouzel (1962), *P. bavaricum* has:

- small size,
- generally simple dental structure,
- less enamel plication and crenulation and thus the valleys of the premolars are well separated,
- slender teeth,
- bicuspid mesial lophid in  $P_3$  (the cuspids are distinct but more compressed against each other than in *P. hobleyi*), and
- clear mesial projection ("preprotolophide") in  $P_3$ ; sometimes is bicuspid.

Taking into account all the above mentioned two small-sized deinotheres can be recognized, the African *P. hobleyi* and the European *P. bavaricum* (Gräf, 1957; Bergounioux and Crouzel, 1962; Harris, 1978). The studied material belongs to the small-sized deinotheres. Its dental dimensions are into the ranges of variation for *P. bavaricum* of Europe (Fig. 4), while they are smaller than those of *D. levius* and *D. giganteum* of Europe (Fig. 5). Thus, a morphological comparison with the two known small-sized species of *Prodeinotherium* will help to the attribution of the material.

One of the distinctive characters between *P. bavaricum* and *P. hobleyi* is the morphology of the  $P_3$ . In *P. hobleyi*, the

mesial lophid is bicuspid (metaconid and protoconid) with well-separated cuspids. In the  $P_3$  of the mandible 6404:13 from Gebel Zelten (Harris, 1973: Pl. 5, Fig. 5a), the two cuspids of the mesial lophid are separated by a clear and deep valley developed in its mesial and distal surface. The separation of the two cuspids in *P. bavaricum* is not so clearly established (Bergounioux and Crouzel, 1962). In the Lesvos material, the mesial lophid of the  $P_3$  is bicuspid but the cuspids are separated by a shallow groove and they are more compressed against each other. This morphology seems to be closer to that of *P. bavaricum*. The morphology of the mesial projection ("preprotolophide" of Bergounioux and Crouzel, 1962) is another distinctive character. In *P. hobleyi*, it is stronger and higher (Harris, 1973: Pl. 5, Fig. 5a) than in *P. bavaricum*. In the studied specimen, it seems to be closer to that of *P. bavaricum*. The relative proportions of the  $P_4$  are also used for the distinction of *P. hobleyi* from *P. bavaricum*. The previous species has shorter  $P_4$  compared to its breadth (Harris, 1978). In the studied specimen, the index **Length**  $\times$  **100/Breadth** for the  $P_4$  is 120, vs. 115 for *P. hobleyi* (data from Harris, 1978), 115–117 for *P. bavaricum* of Europe (data from Bergounioux and Crouzel, 1962) and 116 for *P. bavaricum* of Dinotheriumsande (data from Gräf, 1957). These values suggest that there are no clear differences in the proportions of  $P_4$  between the two species. However, the mean values for the European *P. bavaricum* indicate somewhat longer  $P_4$  compared to its breadth. The third difference of *P. hobleyi* and *P. bavaricum* is referred to the more distinct and independent buccal cuspid in the talonid of  $M_3$  (Harris, 1978). The value of this difference cannot be confirmed, as it

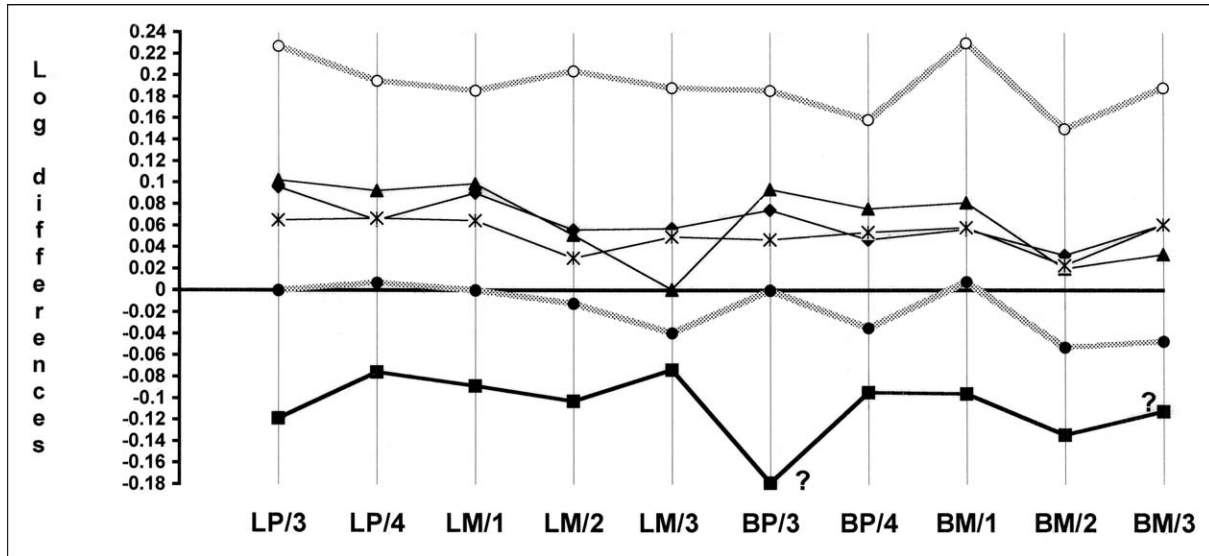


Fig. 5. Logarithmic ratio diagram comparing the studied teeth with those of *Deinotherium* from various localities. Standard: *P. hobleyi*, Africa,  $n = 3-6$  (Harris, 1978). ■, GVT-1; \*, *D. levius*, Dinotheriumsande,  $n = 5-10$  (Gräf, 1957); ◆, *D. giganteum*, Dinotheriumsande,  $n = 9-12$  (Gräf, 1957); ▲, *D. giganteum*, Montredon,  $n = 5-13$  (Tobien, 1988); ●, *D. giganteum*, minimum values for Europe (Bergounioux and Crouzel, 1962); ○, *D. giganteum*, maximum values for Europe (Bergounioux and Crouzel, 1962).

Fig. 5. Diagrammes de Simpson comprenant le matériel étudié avec *Prodeinotherium* de différentes localités. Standard: *P. hobleyi*, Africa,  $n = 3-6$  (Harris, 1978). ■, GVT-1; \*, *D. levius*, Dinotheriumsande,  $n = 5-10$  (Gräf, 1957); ◆, *D. giganteum*, Dinotheriumsande,  $n = 9-12$  (Gräf, 1957); ▲, *D. giganteum*, Montredon,  $n = 5-13$  (Tobien, 1988); ●, *D. giganteum*, valeurs minimales pour l'Europe (Bergounioux et Crouzel, 1962); ○, *D. giganteum*, valeurs maximales pour l'Europe (Bergounioux et Crouzel, 1962).

is necessary to see all the known material. However, comparing the studied specimen with the  $M_3$  of the mandible 6412:10 from Gebel Zelten (Harris, 1973: Pl. 4, Fig. 4a), the latter seems to have more distally projected cuspid than the studied one. Moreover, the well-defined and distinguished valleys and the simple dental structure of the studied specimen are characters of *P. bavaricum* (Bergounioux and Crouzel, 1962). The base of the protoconid in  $P_3$  is longer and in this feature the studied material is closer to *P. bavaricum* (Bergounioux and Crouzel, 1962).

Two large-sized species *D. giganteum* and *D. levius*, as well as one very large deinothere *D. gigantissimum* are known from Europe. The extremely large size of the latter species compared to that of the studied teeth distinguish them from it. The former two species are referred to either separately (Gräf, 1957) or are synonymized (Bergounioux and Crouzel, 1962). *D. giganteum* is characterized by large size, complicated dental structure with more plications and crenulations, more massive dentition, two well separated cuspids in the mesial lophid of  $P_3$  and decreasing or absent mesial projection in  $P_3$  (Bergounioux and Crouzel, 1962). The larger size, the different structure of the mesial lophid of  $P_3$  with less clearly separated cuspids and the lingual one more inclined backwards, as well as the weaker or absent mesial projection in  $P_3$  distinguish *D. giganteum* from *P. bavaricum* (Gräf, 1957).

*D. levius* has no clear distinctive characters from the other species but it occupies a morphologically and metrically intermediate position between *P. bavaricum* and *D. giganteum*, e.g., the mesial lophid of  $P_3$  has two cuspids separated at the top and connected at the base or the mesial projection is

weaker than that of *P. bavaricum* and stronger than that of *D. giganteum* (Gräf, 1957). Moreover, its dimensions are larger than *P. bavaricum* and slightly smaller than or close to those of *D. giganteum* (Fig. 4).

The dimensions of the Lesvos dentition indicate a small-sized deinothere. The available teeth are compared with the small-sized *P. bavaricum* (Fig. 4) from various localities. The studied teeth are close to the sample from Dinotheriumsande (Germany), Breitenbronn (Germany) and Sables de l'Orléanais (France). Moreover, they are within the ranges of variation for *P. bavaricum* of Europe as it was referred by Bergounioux and Crouzel (1962), and more exactly very close to the minimum values (Fig. 4). The breadth of  $P_3$  and  $M_3$  in the studied teeth is estimated (see measurements) and for this reason their points in the diagrams are accompanied by question mark (Figs. 4 and 5). The other two European deinotheres *D. giganteum* and *D. levius* have larger teeth (Fig. 5). All the above-mentioned comparisons suggest that the Lesvos deinothere can be determined to *P. bavaricum*.

#### 4. Biochronology–Palaeobiogeography

The sole known specimen of *P. bavaricum* from the locality of Gavathas, Lesvos and the great stratigraphic distribution of the species in Eurasia, spanning the middle-late Miocene (MN 4–10), cannot allow a certain age determination. However, the combination of the morphological characters of the studied specimen with the local stratigraphy and the absolute dating of the volcanic sediments of the area can lead to an age determination. The development of the mesial



projection of  $P_3$  can give an idea about its age. Usually, this projection has 2–1 cuspids in *P. bavaricum*, while in *D. giganteum* it is reduced or absent (Bergounioux and Crouzel, 1962). In *P. hoblelyi*, from Gebel Zelten, Libya there is a well-developed and bicuspid mesial projection in  $P_3$  (Harris, 1973: Pl. 4, Fig. a; Pl. 5, Fig. 5a). The Gebel Zelten fauna has been dated to early Miocene (Harris, 1973) but recently it is considered as middle Miocene between 17–16 Ma (Pickford, 1991). In the description of the middle Miocene *P. "hungaricum"*, there is no reference to the morphology of the mesial projection of  $P_3$ . However, in the illustrations it is clear that the projection exists, it is large and probably bicuspid (Ehik, 1930: Pl. 1, Figs. 4, 7, 7a). The  $P_3$  of *P. bavaricum* from Dinotheriumsande, Germany, dated to the late Miocene, has a smaller and monocuspid mesial projection, while *D. giganteum* from the same locality has a reduced mesial projection without cuspids (Gräf, 1957: p. 157, abb. 11; p. 141, abb. 5). Thus, a decrease in size of the mesial projection of  $P_3$  as well as in the number and development of the cuspids is clear from the older to the younger forms of *Prodeinotherium* and deinotheres generally. The studied  $P_3$  with well developed, large and bicuspid mesial projection is closer to the most primitive early/middle Miocene forms of the genus. Moreover, the size of the studied  $P_3$  is very small and closer to the primitive forms confirming the above assumption (Fig. 6).

The Lesvos material was found below a series of pyroclastic deposits, known as Acid Volcanics Unit (Sigri pyroclastics) correlated to Skoutaros Fm (Fig. 2). These pyroclastics extend in the wider area and there are several radiometric ages for them. The Skoutaros Fm is dated at  $18.4 \pm 0.5$  Ma by K/Ar, while the Acid Volcanics Unit (Polychnitos ignimbrite which is correlated to the upper ignimbrite of Gavathas area) at  $17.2 \pm 0.5$  Ma (Borsi et al., 1972; Pe-Piper and Piper,

1993). Taking into account these ages and the stratigraphic position of the fossiliferous site the age of the studied deinotheres must be older than 18.4 Ma. This age fits quite well with its evolutionary stage and corresponds to the upper part of early Miocene (late MN 3). The Lesvos specimen represents the earliest record of deinotheres in Europe and it is one of the oldest known mammalian fossils in Greece.

During middle Burdigalian (middle Orlanian), about 18.0–19.0 Ma, the African and Arabian plates collided providing a land bridge between Africa and Eurasia (Fig. 7). This land bridge is known as "*Gomphotherium* land bridge" and allowed the first migrations between both continents since the early Palaeogene (Rögl, 1999a). Among the first migrated mammals were the gomphotheres and the deinotheres.

The genus *Prodeinotherium* is known from several African localities. For some of them there are radiometric ages such as those of Bukwa (Uganda) dated to 22.0 Ma, as well as of Karungu and Koru (Kenya) dated to 22.5 and 19.5 Ma, respectively (Harris, 1978). More recent datations suggest that the Bukwa fauna is dated at 17 Ma (Pickford, in press) while those of Karungu and Koru are considered as >17.9 and 19.5 Ma, respectively (Pickford, 1991; Drake et al., 1988). During the upper part of early Miocene (19.0–18.0 Ma) when the "*Gomphotherium* land bridge" formed, the deinotheres rapidly migrated to Eurasia. Despite the great number of localities and the huge amount of fossils recovered from China deinotheres are unknown in northern Asia. The reasons are probably ecological as deinotheres are considered to be forest living animals, which survived in relatively, closed environments (Tassy, 1990). Such closed environment existed in Lesvos island as proved by the Petrified Forest of Sigri including several big trees (Table 1). The fossilized

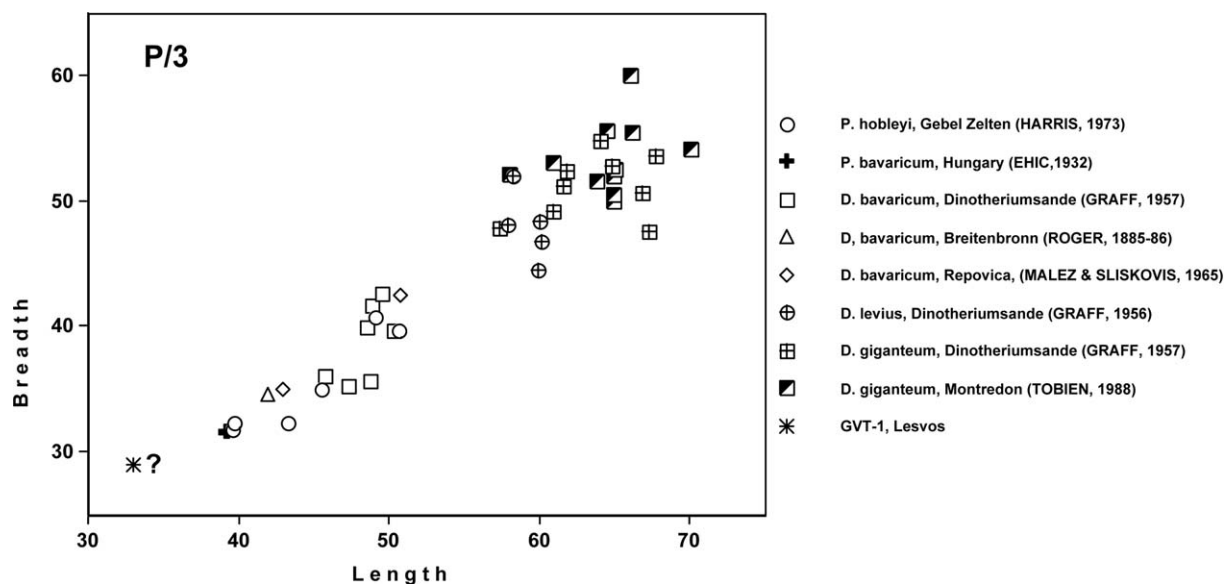


Fig. 6. Scatter diagram comparing the  $P_3$  size in various deinotheres. The question marks in the symbols for the studied specimens indicate that their dimensions are the measured ones, which are slightly smaller than the real ones as the teeth are broken (see measurements).

Diagramme de dispersion comparant les dimensions des  $P_3$  de différents déinotheres. Le point d'interrogation pour les spécimens étudiés indique que les dimensions sont sous-évaluées du fait de l'état incomplet des dents (voir dimensions).



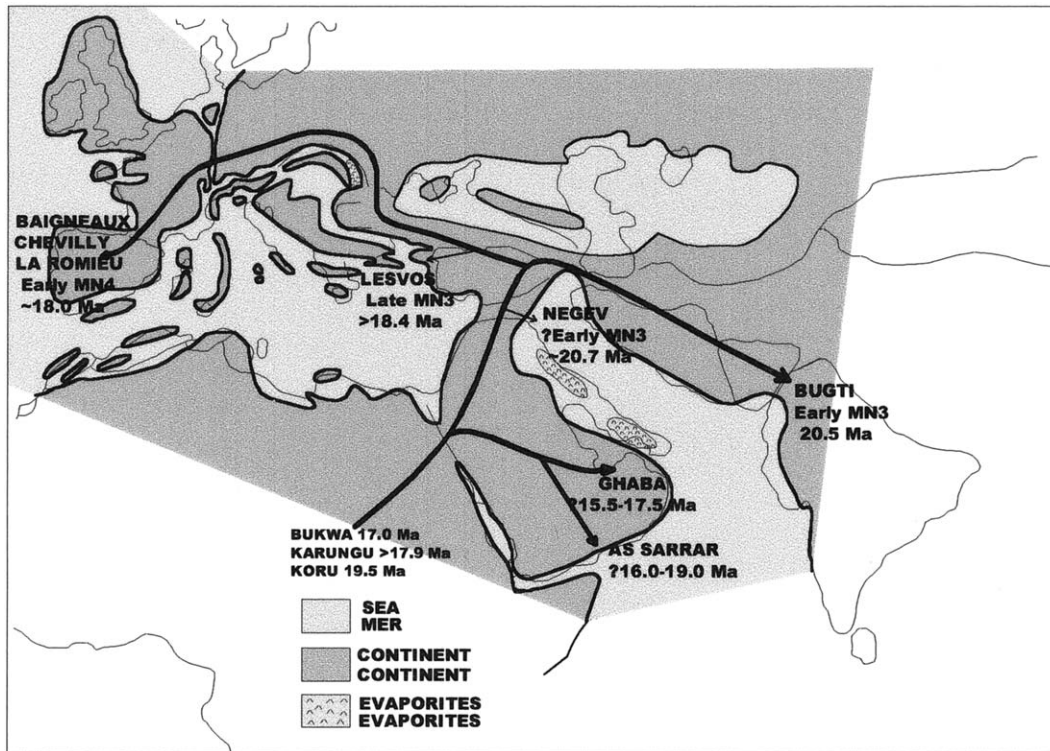


Fig. 7. Origin and geographic distribution of *Prodeinotherium* in Old World. The palaeogeography is based on the map of Rögl (1999b).  
 Fig. 7. Origine et distribution géographique de *Prodeinotherium* dans l'Ancien Monde. La paléogéographie est basée sur Rögl (1999b).

trees were found in the pyroclastic unit or in the Sigri pyroclastics. This means that during the early Miocene there was an extensive forest in the area provided an ideal habitat for the deinotheres.

The connection of Africa and Eurasia allowed a rapid dispersion of diverse mammals into Eurasia from Africa. However, an opposite directed migration from Eurasia was also took place. The Negev fauna in the Hatzeva Formation, Israel reflects this two-way migration. The fauna includes African elements like *Prodeinotherium*, *Gomphotherium*, *Dorcatherium*, *Megapedetes*, *Kenyalagomys*, as well as Asian elements such as *Eotragus*, Rhinocerotidae. The deposits could be correlated with the lower part of MN 3 (Tchernov et al., 1987). Absolute dating of the base of the Hatzeva Fm including the fauna gave an age of 20.7 Ma (Rögl, 1999b). In Asia, the first deinotheres are known from the Bugti fauna, Pakistan, dated to the end of MN 3 and more precisely at about 18.3 Ma (Barry et al., 1985). Recent investigations in the Bugti Hills dated the first appearance of *Prodeinotherium* at the beginning of Burdigalian (Welcomme et al., 2001). According to Steininger et al. (1999), the Aquitanian/Burdigalian boundary is dated at 20.5 Ma. Thus, *Prodeinotherium* appeared in the Indian subcontinent at ~20.5 Ma. This age fits with the age of the Negev fauna (20.7 Ma) and indicates a short-time early connection of Africa and Asia. During that time, a migration wave between the two continents gave the faunas of Negev and Bugti.

The oldest record of deinotheres in Arabian Peninsula is at the locality of As Sarrar, Saudi Arabia, dated to the lower part of the middle Miocene (?16.0–19.0 Ma), from where cf. *Prodeinotherium* is referred. A certain appearance of *Prodeinotherium* in Arabian peninsula is from the locality of Ghaba (Sultanate of Oman) dated to middle Miocene 15.5–17.5 Ma (Thomas et al., 1982, 1999). There is an indication for a simultaneous appearance of deinotheres in Arabian Peninsula (Loc. As Sarrar) and Eurasia but their certain appearance seems to be somewhat younger. Rögl (1999b) considered that the high trans-Jordanian mountains in the east and the southward extended Mediterranean gulf in the west prevented the migration of the deinotheres to the Arabian peninsula. But, if the As Sarrar fauna includes *Prodeinotherium* and belongs to early Miocene then the deinotheres arrived in Arabia at the same time.

The Lesvos specimen with its primitive dental morphology and with a minimum age of 18.4 Ma represents the earliest known deinotheres in southeastern Europe. It also means that the deinotheres as they passed “*Gomphotherium* land bridge” immediately dispersed to Europe and Asia. In western Europe (France, Spain), the first deinotheres are recorded from the localities of Baigneaux, Chevilly, La Romieu dating to the beginning of MN 4 (Tassy, 1990) which means an age ~18.0 Ma. The above-mentioned data suggest:

- a rapid migration of *Prodeinotherium* from Africa to the whole Eurasia except the far north,

Table 1

List of plant species identified in the Petrified Forest of Lesvos. According to Velitzelos and Zouros (1997, 1998)

Tableau 1

Liste des espèces de plantes identifiées dans la Forêt Pétrifiée de Lesvos (d'après Velitzelos et Zouros (1997, 1998))

Pteridophytes	Angiosperms
1. <i>Pronofrium striacum</i>	1. <i>Cinnamomum polymorphum</i> HEER sensu GRANGEON
<b>Gymnosperms–conifers</b>	2. <i>Laurus</i> sp.
1. <i>Pinoxylon paradoxum</i> SUSS and VELITZELOS	3. <i>Laurus primigenia</i> HEER
2. <i>Pinoxylon pseudoparadoxum</i> SUSS and VELITZELOS	4. <i>Litsea primigenia</i> (UNG.) TAKHT.
3. <i>Pinoxylon</i> sp.	5. <i>Lindera ovate</i> KOLAK.
4. <i>Pinus</i> sp.	6. <i>Oreodaphne heeri</i> GAUD.
5. <i>Taxaceoxylon biseriatum</i> SUSS and VELITZELOS	7. <i>Quercus apocynophyllum</i> ETT.
6. <i>Taxodioxylon gypsaceum</i> (GOPPERT) KRAUSEL	8. <i>Quercus crutiatum</i> (AL. BR.) WILDE
7. <i>Taxodioxylon albertense</i> (PENHALLOW) SCHIMAKURA	9. <i>Pungiphyllum crutiatum</i> (AL. BR.) WILDE
8. <i>Cunnighamia miocenica</i> ETTINGS HAUSEN	10. <i>Carpinus pliofaurei</i> RATIANI forma helladae n.f.
9. <i>Sequoia abietina</i> (BRONG.) KNOBLOCH	11. <i>Carpinus uniserata</i> (KOLAKOVSKI) RATIANI (?)
10. <i>Tetraklinis salicornoides</i>	12. <i>Alnus cycladum</i> UNGER fo parvifolia n.f.
<b>Monocotyledons</b>	13. <i>Populus balsamoides</i> GOEPP.
1. <i>Phoenix</i> sp.	14. <i>Populus</i> sp.
2. <i>Palmoxylon</i> sp.	15. <i>Tilia</i> sp.
	16. <i>Diospyros brachysepala</i> AL. BR.
	17. <i>Daphnogene polymorpha</i> AL. BR.
	18. <i>Engelhardia orsbergensis</i>
	19. <i>Myrsinites</i> sp.
	20. <i>Rhus</i> sp.
	21. <i>Platanus</i> sp.
	22. <i>Acer</i> sp.

- the palaeoecological conditions in Europe and southern Asia were similar and more or less forested, allowing the dispersion of deinotheres, and
- the studied specimen represents the first appearance of deinotheres in Europe.

## 5. Conclusions

The morphological and metric analysis of the studied mandibular remains from Lesvos indicate that they belong to *Prodeinotherium bavaricum* a small-sized deinotheres of Eurasia. The morphology of P<sub>3</sub> suggests that it belongs to the primitive early/middle Miocene forms of the species. A more precise age for it can be estimated using the available radiometric ages of the overlying volcanic deposits of the area. The studied deinotheres was found below a series of pyroclastics dated to 18.4 ± 0.5 Ma and thus an age older than 18.4 Ma is possible for it. This age fits quite well with its dental morphology and evolutionary stage, as well as with the arrival time of the deinotheres in Eurasia estimated at 19.0–18.0 Ma (Rögl, 1999a, b). The studied deinotheres represents the first immigrants of the family from Africa to the eastern

Mediterranean and it is one of the oldest known mammalian fossils from Greece. After their arrival in eastern Mediterranean the deinotheres rapidly migrated to central and western Europe as they are known in France and Spain at ~18.0 Ma. This rapid migration indicates similar palaeoecological conditions throughout Europe. As the deinotheres are forest dwellers the palaeoenvironment in Europe was close (forests). This is confirmed for Lesvos by the extensive petrified forest with big trees found in the area, where the deinotheres remains were located.

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