

***Metailurus major* Zdansky, 1924 (Carnivora, Mammalia) from the classical locality of Pikermi (Attica, Greece)**

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Abstract — The species *Metailurus major* has a large geographical extension and is known from localities spread out from West Europe to China. In Greece it is known from the Late Miocene locality of Halmyropotamos in Euboea, while some authors mention it also in Pikermi and Samos in faunal lists only. Two specimens from Pikermi prove its existence in this classical locality. © 2001 Éditions scientifiques et médicales Elsevier SAS

Mammalia / Felidae / Late Miocene / Greece / Pikermi

Résumé — *Metailurus major* Zdansky, 1924 (Carnivores, Mammifères) de la localité classique de Pikermi (Attique, Grèce). L'espèce *Metailurus major* a une vaste extension géographique, d'Europe occidentale jusqu'en Chine. En Grèce elle est connue dans le Miocène supérieur de Halmyropotamos en Eubée, et citée par certains auteurs dans quelques listes fauniques de Pikermi et Samos, sans documentation suffisante. Deux spécimens démontrent son existence dans la localité classique de Pikermi. © 2001 Éditions scientifiques et médicales Elsevier SAS

Mammifères / Felidae / Miocène supérieur / Grèce / Pikermi

INTRODUCTION

The species *M. major* Zdansky, 1924, became known for the first time from Tai-Chia-Kou (Loc. 30) in China [29]. New findings of that species from China are

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mentioned also by Zdansky [30] and Teilhard de Chardin & Leroy [26], while Chang & Liu [7] mention some more specimens from China as *Metailurus* cf. *major*.

In Europe this species is known from the Middle Turolian (MN 12) of Spain and the localities of Concud [2, 10, 17], Ademuz [10] and Cerro de la Garita [1], from the Late Turolian (MN 13) of Italy and the locality V3 of Baccinelo [21], as well as from the Late Turolian (MN 13) of Polgardi in Hungary [12].

In Greece *M. major* is known from the locality of Halmyropotamos in Euboea [16]. Solounias [24: table 4] reports its occurrence in Samos and Pikermi, but he does not make clear which specimens he has been based on. It is mentioned also in Pikermi and with some reservations in Samos by Bernor et al. [5]. Its occurrence in Samos has been based on a fragment of a lower jaw found by Solounias (pers. com.) in the collections of the AMNH New York, but no specimens from Samos or Pikermi have been described until now.

SYSTEMATICS

Genus *METAILURUS* Zdansky, 1924

Diagnosis: Felinae with P1, P2 absent, P3 large, P4 with prominent protocone and well developed parastyle; p2 if present very reduced; short diastemata between I3-C and C-P3; mastoid process slightly more developed than in recent Felinae; carotid and jugular foramen confluent, condylar foramen situated slightly more posteriorly.

Type species: *Metailurus major* Zdansky, 1924.

Metailurus major Zdansky, 1924

Diagnosis: *Metailurus* of large size, P3 relatively wide in front, with strong posterior accessory cusp, anterior accessory cusp smaller and situated slightly lingually; M1 relatively large.

DESCRIPTION

Material

P.A. 1257/91: Almost complete skull, in good state of preservation but compressed from above. Partly broken are the zygomatic arcs, the sagittal crest and part of the skull in front of the left P3. In position are the right P3, P4 and M1, while the right C is broken at its base. In front of this canine part of the alveole of I3 is preserved. On the left side only P3, M1 and the protocone of P4 are preserved.

P.G. 95/1532: Left portion of a skull, laterally compressed. Preserved are the maxilla bone, part of the zygomatic and the nasal. The only tooth intact is the P4. The canine is broken at its base, as well as the P3. The alveole of M1 is visible.

Both specimens were found in the pikermian collections of the Palaeontological and Geological Museum of Athens and come from old excavations. The specimen P.A. 1257/91 was also described by Roussiakis [22].

Description of the skull

In lateral view and with the alveolar border horizontal, the highest point of the skull lies at the frontal region. Oriented in the same way, the infraorbital foramen is situated above and slightly before the contact between P3 and P4 (*figure 1a*).

On P.A. 1257/91 the premaxillary bones are not in contact with the frontals. The nasals are slightly deformed but most probably retain the same width all over their length. The same characters are also present on the type specimen [29]. On the specimen of *M. major* from Halmyropotamos (No 1967/1) the frontals are not in contact with the premaxillary bones, but the nasals seem slightly wider at their anterior part.

The palatine fissures are extended posteriorly to the posterior part of the canines (*figures 1b, 4b*). On the hard palate there are two ridges that converge anteriorly towards the palatine fissures. The anterior openings of the palatine foramina open opposite of the protocones of P4, laterally of the palatine ridges and slightly behind the palatine suture. The anterior limit of that suture is opposite of the posterior part of P3 (*figure 4b*). On the palatine and medially of the metastyle of P4 there is a depression. The choana opens slightly behind the posterior limit of M1 (*figures 1b, 4b*). The perpendicular blades of the palatine (lamina perpendicularis) converge posteriorly, thus the interpterygoid fossa narrows posteriorly (*figure 1b*), which is also observable on the holotype of *M. major* [29: plate 29, figure 2]. On the specimen of *M. parvulus* from Chomateri [25: plate 1] as well as in "*M. minor*" (= *M. parvulus*, after Thenius [27]) from China [29: plate 30, figure 2] the interpterygoid fossa retains almost the same width all over its length. The specimen of *M. parvulus* from Halmyropotamos [No 1967/5, 16: plate 30, figure 2] is deformed, however the interpterygoid fossa appears narrow posteriorly.

The orbital region starts above the front part of P4. The lachrymal canal opens at the anterior margin of the orbit. Inside the orbit opens the posterior opening of the palatine foramen and more posteriorly the spheno-palatine foramen. The optic foramen, the orbital fissure and the foramen rotundum are arranged on an oblique line that slopes ventrally and posteriorly, as is usual in the Felinae. There is no alisphenoid canal.

With the skull in lateral view, the glenoid cavity is almost on the same level with the external auditory meatus (*figure 1a*). On the same level is also the hard palate. The postglenoid process is curved forwards and situated far from the auditory bulla (*figures 1-3*). On the available skull specimen from Pikermi there is no postglenoid

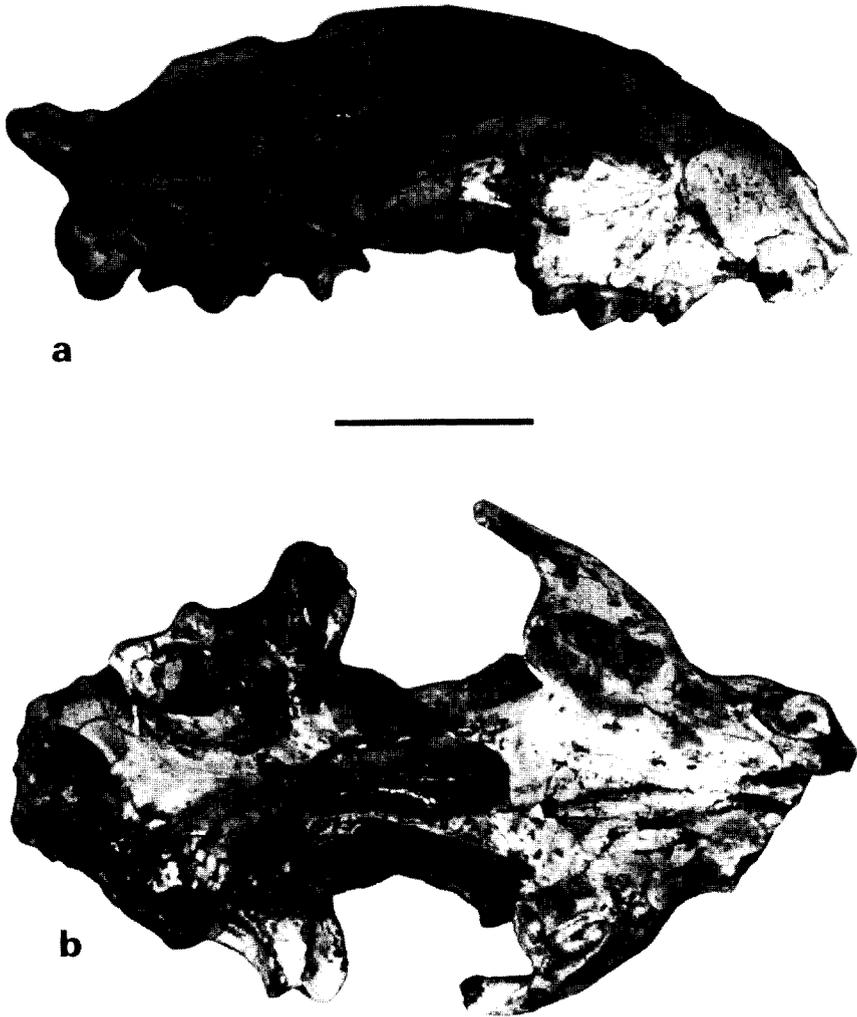


Figure 1. *M. major*. Skull (P.A. 1257/91). a, lateral view; b, ventral view. Scale bar 50 mm. Pikermi.

Figure 1. *M. major*. Crâne (P.A. 1257/91). a, vue latérale ; b, vue ventrale. Échelle : 50 mm. Pikermi.

foramen. After additional preparation of the specimen of *M. major* from Halmyropotamos (No 1967/1) it was possible to observe that there are postglenoid foramina. These foramina however are so small that can hardly be observed with bare eyes. On specimens of recent Felinae, stored in the Museum of Palaeontology and Geology of Athens, the postglenoid foramen sometimes is present only on one side of the skull, while in other cases where it is present on both sides its development or position varies. The foramen ovale is situated on the axis of the glenoid cavity but slightly higher.

The mastoid process is almost vertical and does not overlap the external auditory meatus. The auditory bulla is compressed, but the mastoid process does not seem to pass ventrally the lower level of the bulla. The paroccipital process stops higher and faces backwards. The mastoid process lies closer to the paroccipital process than to the postglenoid one (*figures 2, 3*).

The auditory bulla has on its ventral surface a characteristic ridge that starts from the antero-medial corner of the bulla and stops in front of the stylomastoid foramen (*figures 2, 3*). Most probably this ridge corresponds to the trace of the septum (*septum bullae*) that in the Felidae separates the acoustic bulla into two chambers, the external or acoustic one and the internal or posterior one. It is not certain whether this septum is homologue to that of other Felidae. Piveteau [19] mentions that the development of the acoustic chamber in relation to the posterior one varies from species to species. According to that author, in tropical species the acoustic chamber is small and the posterior one is larger, whereas in other species these two portions of the bulla are almost equally developed. On the present skull specimen the acoustic chamber is smaller than the posterior one. The same septum can also be observed at the broken auditory bulla of the specimen 1967/1 from Halmyropotamos.

The arrangement of the foramina at the basal region of the skull is similar to that of the recent Felinae (*figure 2*). In front of the acoustic bulla opens the lacerate foramen, medially of that the Eustachian opening (*sulcus tubae auditivae*) and laterally the small canal of Huguier. In front of the Eustachian opening there is a delicate groove that most probably corresponds to the opening for the Vidian nerve (*sulcus n. canalis pterygoideus*). The jugular foramen and the carotid canal are confluent while the condylar foramen opens more posterior and is clearly separated from these. The same disposition is also visible on the specimen from Halmyropotamos. Piveteau [19] mentions that in the Felinae the condylar canal and the jugular foramen open in the same depression. Ewer [9] however, is not in complete accord and mentions that a wide separation between the condylar and the jugular foramen is certainly primitive, whereas in modern cats these two foramina open usually, but not always, in a common depression. Ewer [9] mentions also that there is a considerable individual variation. According to Bonis [6] in the lion or the tiger these two foramina are more separated than in the medium or the small sized felids. Stock (1934, in [23]) mentions that in *Metailurus* the condylar foramen and the carotid canal are closely connected with the jugular foramen. That arrangement however, cannot be seen on the type specimen of *M. major* [29: plate 29, figure 2] which is also the genotype of *Metailurus*, since the corresponding portion of the skull is missing. On the specimen of "*M. minor*" (= *M. parvulus*) figured by Zdansky [29: plate 30, figures 1–2] as well as on the specimen of *M. parvulus* from Chomateri the arrangement of these foramina is similar to the skull of *M. major* from Pikermi.

The basioccipital has a faint median ridge and the muscular tuberosities (which are the areas of insertion of the muscle longus capitis) are poorly developed (*figure 3*).

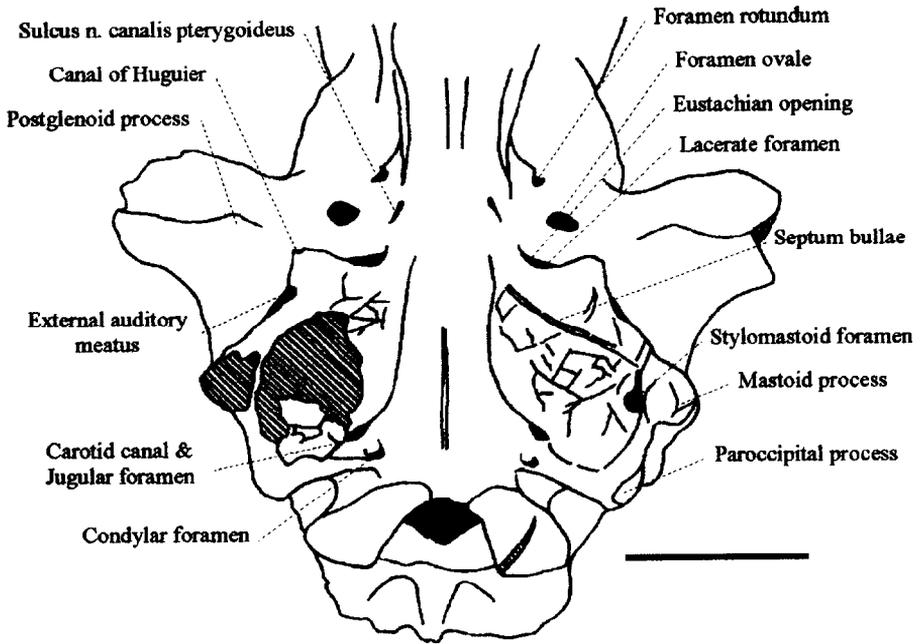


Figure 2. *M. major*. Basicranial region of the skull (P.A. 1257/91). Scale bar 30 mm. Pikermi.

Figure 2. *M. major*. Région basale du crâne (P.A. 1257/91). Échelle : 30 mm. Pikermi.

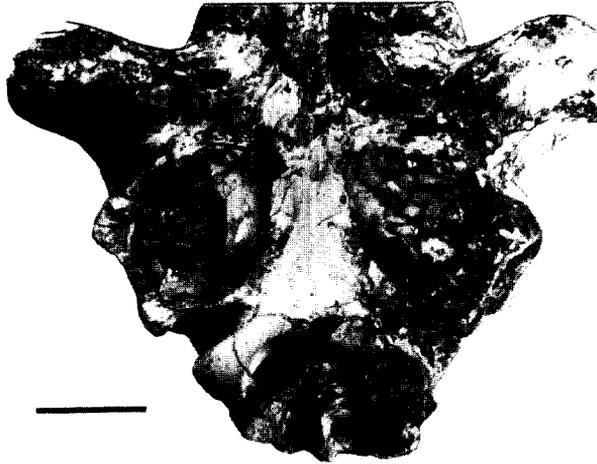


Figure 3. *M. major*. Basicranial region of the skull (P.A. 1257/91). Scale bar 20 mm. Pikermi.

Figure 3. *M. major*. Région basale du crâne (P.A. 1257/91). Échelle : 20 mm. Pikermi.

Table I. Skull measurements (mm).

Tableau I. Dimensions (en mm) crâniennes.

| | <i>M. major</i> P.A. 1257/91 Pikermi | <i>M. major</i> 1967/1, Halmyropotamos after the author |
|--|--|---|
| total length from inion to prosthion | (210) | 219 |
| length from inion to bregma | 85 | 91 |
| length from bregma to nasion | (72) | (70) |
| length from basion to prosthion | (179) | (178) |
| length from basion to palatine spine | 96 | (95) |
| length from palatine spine to prosthion | (84) | (87) |
| length from nasion to nasal notch | (48) | (47) |
| maximum width at the buccal walls of the canines alveoles | (53) | 59 |
| maximum width at the buccal walls of the carnassials | (83) | (86) |
| minimum width at the orbits | (52) | (51) |
| width at the zygomatic processes of the frontals | (75) | (66) |
| minimum width behind the zygomatic processes | 47 | 41 |
| distance between the tips of the postglenoid processes | 70 | 67 |
| width between the inner margins of the infraorbital foramina | 51 | 55 |
| width at the mastoid processes | 83 | 79 |
| maximum width of the occipital condyles | 46 | 47 |
| maximum width of the foramen magnum | 25 | 25 |
| maximum height of the foramen magnum | — | (20) |

Behind these are the depressions for the muscle rectus capitis ventralis. These depressions are not especially marked and together with the small development of the muscular tuberosities may indicate the small importance of the corresponding muscles which flex the atlanto-occipital joint and draw the head downwards. The auditory bullae are not widely separated. Compared to the smaller *M. parvulus* from Chomateri [unnumbered, 25: plate 1] or "*M. minor*" (= *M. parvulus*) from China [29: plate 30, figure 2] the auditory bullae are relatively closer to each other. The lambdoidal ridge extends to about 1,5 cm behind the occipital condyles.

The dimensions of the skull P.A. 1257/91 are comparable to those of the specimen 1967/1 from Halmyropotamos (*table I*).

Description of the upper dentition

On both the available specimens from Pikermi the canines are broken just below the crown (*figures 4a, b*). The outline of the canines on that level shows a lateral side stronger curved than the lingual one, a posterior edge, and an anterior edge on a slightly lingual position. These edges must correspond to the positions of the anterior and posterior keels of the canine. The canine is separated from the alveole of I3 by a short diastema of about 5 mm. Judging from the size of the alveole of I3, that incisor must have been large. No alveoles for P1 and P2 are visible and the distance that separates the alveole of C from the alveole of P3 (on P.A. 1257/91) is about 7,6 mm. The length C-P4 measures 74,0 mm on P.A. 1257/91 and 74,8 mm on P.G. 95/1532. The length P3-P4 measures 47,5 mm (P.A. 1257/91).

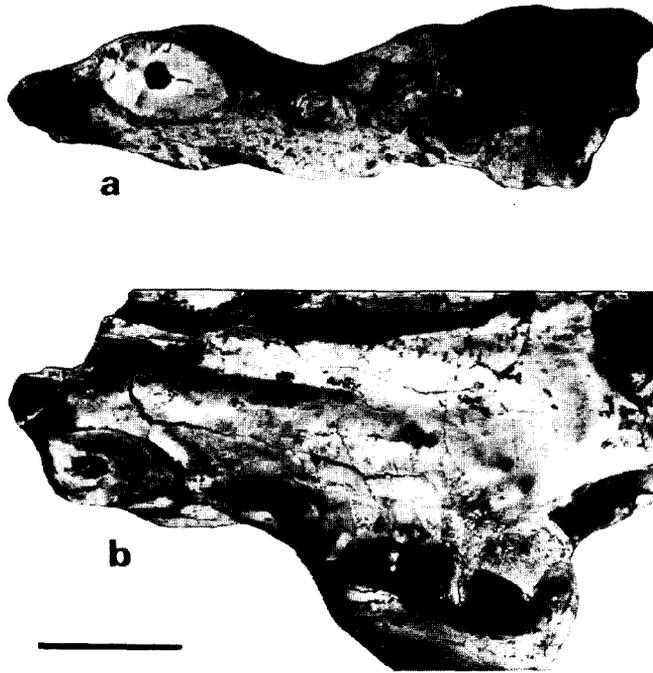


Figure 4. *M. major*. **a**, Left maxilla (P.G. 95/1532) with P4 and parts of C and P3, occlusal view; **b**, Right portion of the skull P.A. 1257/91 with P3-M1 and part of the C, occlusal view. Scale bar 20 mm. Pikermi.

Figure 4. *M. major*. **a**, Maxillaire gauche (P.G. 95/1532) avec P4 et parties de C et P3, vue occlusale ; **b**, Portion droite de crâne P.A. 1257/91 avec P3-M1 et partie de C, vue occlusale. Échelle : 20 mm. Pikermi.

P3 (*figure 4b*) has two roots and a strong posterior accessory cusp, while the anterior one is less developed. The anterior accessory cusp is situated lingually in relation to the main cusp of the tooth. On the specimen of *M. major* from Halmyropotamos (No 1967/1) the anterior accessory cusp is in the same position but less developed. The greatest width of the tooth lies on the posterior part, at the region of the posterior accessory cusp. The anterior part of the tooth however, is not narrow but relatively wide. Because of these, the lingual outline of the tooth appears concave.

The protocone of P4 (*figures 4a, b*) is situated behind the front limit of the parastyle. A crest connects the lingual side of the paracone to the protocone. Between the protocone and the parastyle there is a depression that receives the posterior part of p4. Such a character is common in the Felinae and *T. diastemata* [19] as well as in *Stenailurus teilhardi* and *Metailurus* [8].

M1 (*figure 4b*) is transversally elongated with a length-width ratio smaller than 0,5 (*table II*). On P.G. 95/1532 the dimensions of M1 (given on *table II*) were taken at the alveole of the tooth. The specimens P.G. 95/1532 from Pikermi and 1967/1 from Halmyropotamos show that M1 has two roots.

Table II. Dimensions of upper teeth (mm).

Tableau II. Dimensions (en mm) des dents supérieures.

| | | LC | WC | LP3 | WP3 | LP4 | WP4 | LM1 | WM1 |
|---|-------|--------|--------|------|--------|--------|--------|-------|--------|
| <i>M. major</i> | sin. | — | — | 19,0 | 9,7 | — | — | 5,5 | 12,0 |
| P.A. 1257/91, Pikermi | dext. | (16,7) | (10,8) | 18,8 | 9,6 | 29,7 | 14,1 | 5,9 | 12,5 |
| <i>M. major</i> , P.G. 95/1532, Pikermi | | (18,1) | (10,9) | — | — | 28,9 | 14,9 | (4,9) | (12,2) |
| <i>M. major</i> , China, [29] | | 18,7 | 11,5 | 20,2 | 8,9 | 31,2 | 14,0 | 5,5 | 11,9 |
| <i>M. major</i> , China, [30] | | — | — | 17,0 | 8,5 | — | — | — | — |
| <i>M. major</i> , China, [26] | | 19,5 | 11,5 | 20,0 | 10,0 | 32,0 | 16,0 | — | — |
| <i>M. major</i> , no 1967/1 | sin. | 20,6 | 12,2 | 19,0 | (10,2) | (28,8) | (13,8) | — | — |
| Halmhyropotamos, [author] | dext. | 20,3 | 11,9 | 18,8 | (9,7) | — | 14,5 | — | — |
| <i>M. major</i> , Spain, [17] | | 19,0 | 12,1 | — | — | — | — | — | — |
| <i>M. cf. major</i> , China, [7] | | 18,5 | 11,5 | 16,3 | 8,5 | 29,0 | 12,5 | 5,0 | 8,5 |
| <i>S. teilhardi</i> , Spain, [8] | | 17,0 | 9,6 | 18,5 | 8,5 | — | 11,6 | — | — |
| <i>F. acerensis</i> , Spain, [20] | sin. | — | — | 19,7 | (9,0) | 30,8 | 14,3 | — | — |
| | dext. | (17,9) | 8,9 | 19,9 | 8,7 | — | 14,2 | — | — |
| <i>P. orientalis</i> , Maragha, [14] | | 17,0 | 9,6 | 15,0 | — | 28,0 | — | — | — |
| <i>P. orientalis</i> , Maragha, [18] | | — | — | — | — | 28,5 | 14,0 | — | — |

DISCUSSION

The morphology of the skull previously described shows great similarity with that of the Felinae. The skull is high on the frontals as in the Felinae, while in the machairodonts the highest point of the skull lies on the occipital region [19]. Some species however, such as *Therailurus diastemata* and *T. piveteaui*, have an intermediate position since the frontals and the occipital are in the same level [9, 19]. The alisphenoid canal is absent as in *T. diastemata* [19] and *T. pivetaui* [9]. That canal however is present in *Pseudailurus* [19]. The glenoid cavity is almost at the same level with the external auditory meatus as in *Felis* while in the “machairodonts” the glenoid cavity is situated far below the external auditory meatus [19]. The postglenoid process is situated far from the auditory bulla as in the Felinae, while in the “machairodonts” the postglenoid process tends be in contact with the auditory bulla [19]. The postglenoid foramen is absent as in *T. piveteaui* [9] and *T. diastemata* [19]. That foramen is usually absent or very small in recent Felinae. Some characters of *M. major* however, show development towards a “machairodont” type. Such a character is the slightly larger, than the common situation in the Felinae, mastoid process, but in any case that process does not attain the extreme development found in the “machairodonts”. The distance that separates the mastoid from the paroccipital process is significantly smaller than that that separates the mastoid process from the postglenoid one, as in the Felinae [19]. The opposite is observable in *T. piveteaui* [9: figure 2], while in *T. diastemata* [19: figure 8] these two intervals are almost equal. Characters as the afore mentioned are typical in the Felinae and show that *M. major* does not achieve the structural-functional level of the “machairodonts”.

Table III. Teeth indexes.

Tableau III. Indices dentaires.

| | | (W.C/L.C) × 100 | (W.P3/L.P3) × 100 | (W.P4/L.P4) × 100 | (L.P3/L.P4) × 100 |
|---|-------|--------------------|----------------------|----------------------|----------------------|
| <i>M. major</i> | sin. | — | 51,1 | — | — |
| P.A. 1257/91, Pikermi | dext. | (64,7) | 51,1 | 47,5 | 63,3 |
| <i>M. major</i> , P.G. 95/1532, Pikermi | | (60,2) | — | 51,6 | — |
| <i>M. major</i> , China, [29] | | 61,5 | 44,1 | 44,9 | 64,7 |
| <i>M. major</i> , China, [30] | | — | 50,0 | — | — |
| <i>M. major</i> , China, [26] | | 59,0 | 50,0 | 50,0 | 62,5 |
| <i>M. major</i> 1967/1 | sin. | 59,2 | (53,7) | (47,9) | (66,0) |
| after the author, Halmhyropotamos | dext. | 58,6 | 51,6 | — | — |
| <i>M. major</i> , Spain, [17] | | 63,7 | — | — | — |
| <i>M. cf. major</i> , China, [7] | | 62,2 | 52,1 | 43,1 | 56,2 |
| <i>S. teilhardi</i> , Spain, [8] | | 56,5 | 45,9 | — | — |
| <i>F. acerensis</i> , Spain, [20] | sin. | — | (45,7) | 46,4 | 64,0 |
| | dext. | (49,7) | 43,7 | — | — |
| <i>P. orientalis</i> , Maragha, [14] | | 56,5 | — | — | 53,6 |
| <i>P. orientalis</i> , Maragha, [18] | | — | — | 49,1 | — |

In comparison with the type specimen of *M. major* [29: plate 29, figures 1–2] the specimen P.A. 1257/91 shows a less compressed canine (table III). The length of the canine seems smaller than that of other specimens of *M. major* (table II) but one must keep in mind that the canine of that specimen is broken and no accurate measurements can be given. Moreover a canine from Spain [17] has an index of compression similar to that of P.A. 1257/91 (table III).

Compared with other specimens of *M. major*, the type specimen has relatively narrower P3 and P4 (table III). P.A. 1257/91 has wider P3 and P4 than the type specimen of *M. major* but comparable with other specimens attributed in that species. These differences are considered acceptable, since, for example, in the living leopard the compression index of P4 varies from 46,0 to 57,1 [15]. As most important is regarded the index $(L.P3/L.P4) \times 100$, since it shows the development of the third premolar relative to the carnassial. That index shows small variation on the specimens attributed in *M. major*, but is smaller on the specimen referred as *M. cf. major* by Chang & Liu [7], which shows a P3 reduced relative to P4 (tables II, III). That specimen shows also a smaller M1 (table II, figure 5).

The species *M. major* differs from *Paramachairodus orientalis* (Kittl, 1887) in the morphology of P4 and P3, their relative sizes, and the compression of the upper canine. The P4 of *P. orientalis* shows a less developed protocone and presents a small ectoparastyle [14: plate 14, figure 3]. The P4 of *M. major* and *P. orientalis* have comparable lengths, but the P3 of *P. orientalis* is considerably smaller (table II, figure 5). That is clearly visible from the ratio $(L.P3/L.P4) \times 100$ (table III). Moreover, the maximum width of P3 in *P. orientalis* lies on its middle, its outline is convex lingually [14: plate 14, figure 3] and does not have an anterior accessory cusp. In *M. major* the maximum width of that tooth lies at the region of the posterior

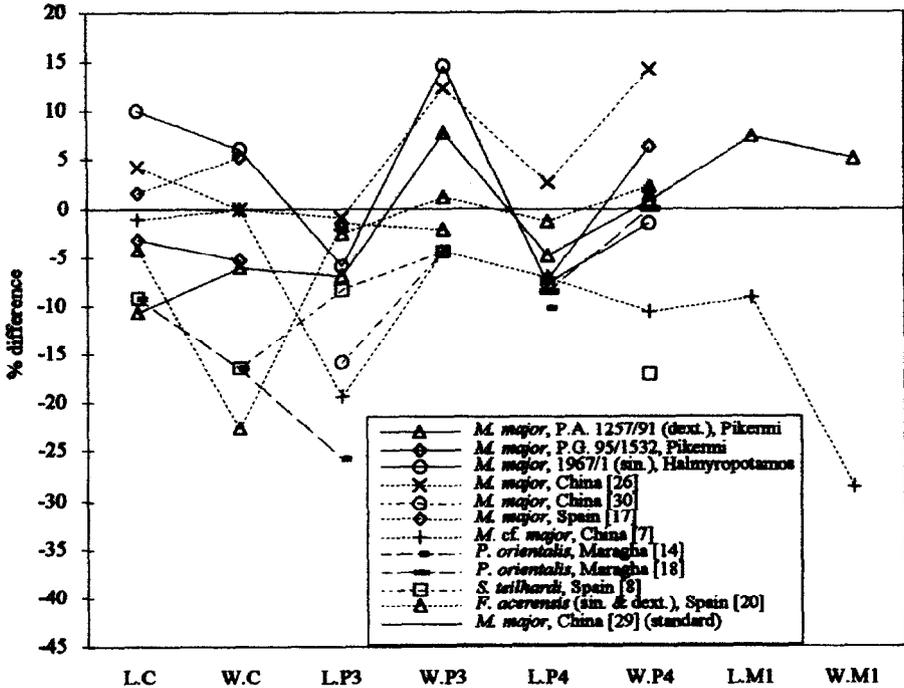


Figure 5. Comparison diagram of the upper teeth of *M. major*, *P. orientalis*, *S. teilhardi* and *F. acerensis*.
 Figure 5. Diagramme de comparaison des dents supérieures chez *M. major*, *P. orientalis*, *S. teilhardi* et *F. acerensis*.

accessory cusp, the lingual outline is concave and there is an anterior accessory cusp. The upper canine of *P. orientalis* is slightly more compressed than that of *M. major* (table III). The shortened P3 and the more compressed canines of *P. orientalis* may indicate an evolution towards a more “machairodont” type. The skull of *P. orientalis* is partly known from the holotype. On that specimen the choana is partly broken but seems equally wide anteriorly and posteriorly [14: plate 14, figure 3], while on the present skull specimen it narrows posteriorly. The mandibles from Pikermi mentioned by Weithofer [28: plate 11, figures 3–5] as *Machairodus schlosseri* have teeth comparable in size to the lower teeth of *M. major*. These specimens however are characterised by a mental crest as is common in the “machairodonts”, while the mandible of *M. major* [29: plate 29, figures 3–4] is not unlike that of the Felinae. *Machairodus schlosseri* has been considered a synonym of *P. orientalis* by Pilgrim [18] and Beaumont [4] but any comparison is difficult since *P. orientalis* is known from its typical locality (Maragha) from upper teeth only, whereas *M. schlosseri* from lower ones from Pikermi. Pilgrim [18] mentions that in the Woodward collections from Pikermi stored in the British Museum (Natural History) there are two mandibles almost identical with those mentioned by Weithofer [28] as *M. schlosseri*.

He also mentions that there is a P4 and a mandible with the m1 from Maragha. According to Pilgrim [18] the P4 is not different from that of *P. orientalis*, while the m1 is identical to that of *M. schlosseri*. Based on these observations Pilgrim [18] considers that *M. schlosseri* is a synonym of *P. orientalis*. Beaumont [4] is in accordance with that opinion and states also that the size and degree of specialisation of the lower mandible of *M. schlosseri* are in accordance with those of *P. orientalis*. The same author also mentions that the astragalus figured by Kittl [14: plate 14, figure 5] – as *P. orientalis*? – has similarities to that figured by Gaudry [11: plate 17, figure 3]. In the pikermian collections of the Palaeontological and Geological Museum in Athens, a mandible was found which shows significant resemblance in morphology and dimensions to that of “*M. schlosseri*”. This specimen however, is fragmentary and preserves only part of the canine, part of the m1, the alveoles of p3 and p4, as well as a minute one root alveole, possibly for the p2. This mandible is slightly small compared to the present skull portions of *M. major* and shows clearly a mental crest, character absent on the mandible of *M. major*.

The species *Stenailurus teilhardi* Crusafont-Pairó & Aguirre, 1972, is known from the Early Turolian (MN 11) locality of Piera in Spain. This species has a more compressed upper canine and significantly smaller width on P4 (*table II, figure 5*). Moreover in this species the protocone of P4 is situated more anteriorly than the parastyle and the anterior and posterior crests of the canine are opposite to each other [8]. The last character cannot be evaluated precisely on the available specimens, since no complete canines are preserved, but judging from the outline of their bases the anterior crest is situated more lingually. Furthermore, *S. teilhardi* retains the alveole of P2 [8], which has never been observed in *M. major* and is absent on the present specimens.

Fortunicis acerensis Pons-Moyà, 1987, is known from the Middle Turolian (MN 12) of Casa del Acero (Spain). Pons-Moyà [20] reported also its occurrence in the Late Turolian (MN 13) locality of El Arquillo de la Fontana (Spain). Compared with the present specimens or other specimens of *M. major*, *F. acerensis* has a stronger compressed canine (*table III*). P3 and P4 have similar dimensions and proportions (*tables II, III*) to those of *M. major* but P3 has lost its anterior accessory cusp and the parastyle of P4 is laterally compressed. Moreover the mandible of that species shows a mental crest [20: plate 1, figure 5].

CONCLUSIONS

The two available specimens of *M. major* from Pikermi, exhibit great resemblance, both in morphology and dimensions, to other specimens of that species. The existing size differences of the teeth are not statistically important and within the

expected intraspecific variation. The occurrence of *M. major* in Pikermi, as well as in Samos, has been mentioned earlier by Solounias [24] and Bernor et al. [5], but the two described specimens from Pikermi are the first to be studied. The morphology of the available skull shows many Felinae characters. Some characters towards a more machairodont-type functional level are not especially developed. Following Beaumont [3] it is preferable to consider *M. major* member of the tribe Metailurini within the subfamily Felinae.

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