A GIRAFFID FROM THE MIDDLE MIOCENE OF THE ISLAND OF CHIOS, GREECE

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ABSTRACT. A giraffid skull and mandible from the early Mid Miocene Keramaria Formation at Thymania (Island of Chios, Greece) has enabled revision of the genus *Georgiomeryx*. The new specimen is compared with *Canthumeryx syrtensis* from Libya and *Injanatherium* from Iraq and Arabia. It is concluded that all these genera, which have flat and laterally directed horns, belong, together with *Giraffokeryx*, to the subfamily Canthumerycinae. New palaeomagnetic data from Chios combined with the presence of the fossil mammals provide new evidence for dating the locality to chron C5Br or early MN5.

SINCE 1940, when Paraskevaidis described some mammalian remains from Chios, several opinions referring to the composition, the relationships and the age of the fauna have been expressed. The initial scanty and fragmentary material was not sufficient to provide firm conclusions. During the 1960s, a further collection was made in which the most significant discovery was a complete skull and mandible of a mastodont (Melentis and Tobien 1967; Tobien 1980). Other mammalian remains were very fragmentary and belong mainly to bovids and giraffids (Lehmann and Tobien in press) although their identifications are tentative. Some micromammalian remains were also noted in a preliminary faunal list (Tobien 1968), but they have never been described.

A new study of the bio- and magnetostratigraphy of the Neogene deposits of Chios has been carried out by a Hellenic-French team during 1991 and 1993. The material unearthed during this includes a rich micromammalian fauna and a few, quite complete macromammalian remains. The mammalian localities are in the Keramaria Formation, which consists of sands and silts alternating with siltstones and sandstones (for more details see Kondopoulou *et al.* 1993 and Koufos *et al.* 1995).

All the macromammalian remains were found in the level 'Thymiana B' (THB). They include a piece of skull and a left mandible with most of the cheek teeth of the same giraffid. The first remains of a giraffid from the Neogene deposits of Chios were described by Paraskevaidis (1940) under the new binomen *Georgiomeryx georgalasi* on the basis of a mandibular fragment with P2/–P3/ (Paraskevaidis 1940, pl. 13, figs 4–5). The comparison of such poor material with other taxa was very difficult, and for a long time its taxonomic position was unknown. The new material is more complete and increases our knowledge of the anatomy, the phylogenetic relationships and the systematics of this Miocene giraffid.

SYSTEMATIC PALAEONTOLOGY

Family GIRAFFIDAE Gray, 1821
Genus GEORGIOMERYX Paraskevaidis, 1940

Type-species. *G. georgalasi* Paraskevaidis, 1940.

Diagnosis. As for the type and only species.

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Georgiomeryx georgalasi Paraskevaidis, 1940

Text-figures 1–3, 4C

Holotype. Mandibular fragment with P/2–P/3 (Paraskevaidis 1940, pl. 13, figs 4–5) housed in the Paraskevaidis collection, Athens.

Paratype. Skull and left mandible (THB-30, 16), housed in the University of Thessaloniki, Laboratory of Geology and Paleontology.

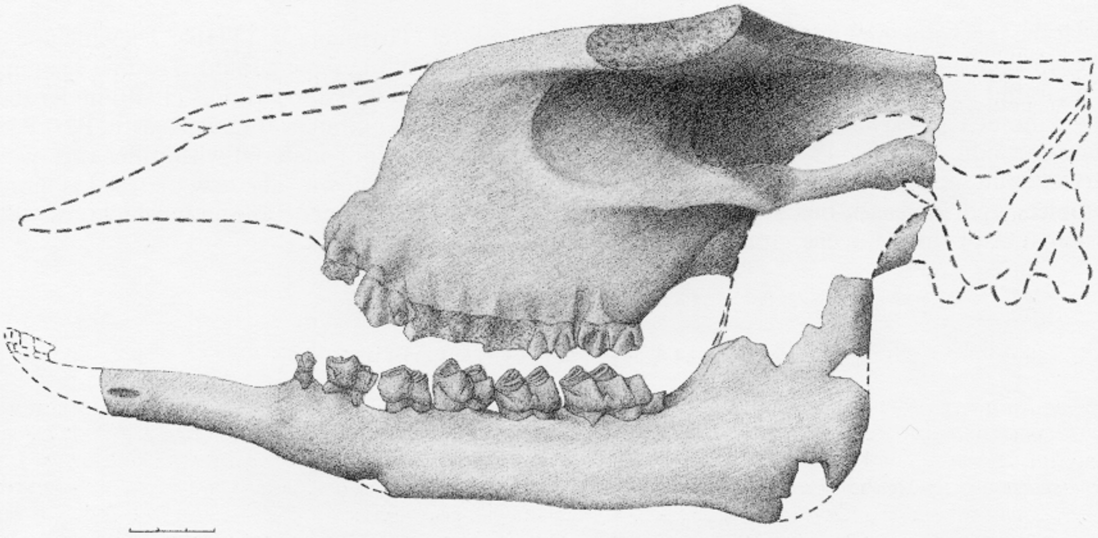
Locality and Horizon. Thymiana B, Chios, Greece. Keramaria Formation, Middle Miocene (MN 5).

Diagnosis. Primitive giraffid with a pair of flat and laterally oriented horns, situated just over the orbits. Brachyodont. Large upper premolar and molar cingulum. P3/ and P4/ heteromorphic. Differences between *Georgiomeryx georgalasi* and related genera are as follows. *Canthumeryx* differs from *G. georgalasi* by its less molarized lower premolars. *Injanatherium* differs from *G. georgalasi* by the presence of an anterior pair of horns, the second pair (posterior) situated back to the orbits, and in its more advanced dentition (lesser brachyodonty, weaker or absent upper cheek tooth cingulum). *Giraffokeryx* differs from *G. georgalasi* in the presence of an anterior pair of horns, a second pair situated back to the orbits, in the less lateral direction of the horns, and in the more advanced dentition (semi-hypsodonty, weaker or absent cingulum).

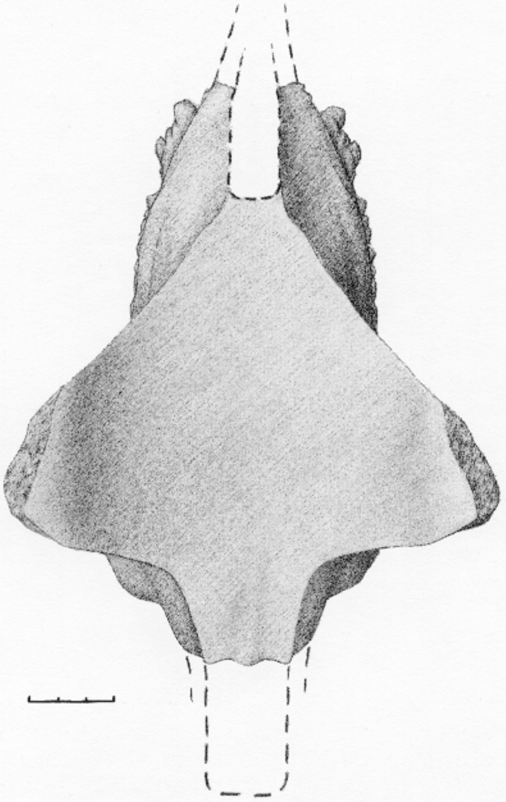
DESCRIPTION

Skull

The new skull is crushed, and both anterior and posterior portions are lacking. Its dimensions suggest a medium-sized giraffoid. The anterior part of the frontal is partially broken but there is no trace of an anterior pair of horns or ossicones, the remains of which would have been apparent as a bump on the frontal bone if they were present (as is the case for *Giraffokeryx*). On the left side of the skull, one of a posterior pair of horns is located exactly above the orbits and slightly posteriorly over the temporal fossa. The horn is flat and laterally oriented (Text-figs 1–2). A temporal crest starts from each horn on the parietal and passes toward the back of



TEXT-FIG. 1. *Georgiomeryx georgalasi* Paraskevaidis, 1940. Skull and mandible (THB 30) in lateral view; Thymiana, MN 5 (lower Middle Miocene), Chios, Greece, Scale bar represents 30 mm.



TEXT-FIG. 2. *Georgiomeryx georgalasi* Paraskevaidis, 1940. Skull (THB 16) in dorsal view; Thymiana, MN 5 (lower Middle Miocene), Chios, Greece. Scale bar represents 30 mm.

the skull which is lacking. Despite the crushing of the skull we can see that the maxilla is deep. The orbit is large, rounded, without any trace of a lacrimal foramen. The zygomatic arch, well preserved on the left side, is weak and not projected (Text-fig. 1). The palate is narrow in front of P2/ sockets and it widens posteriorly. The glenoid surfaces are widened laterally and they are more convex than in modern giraffes.

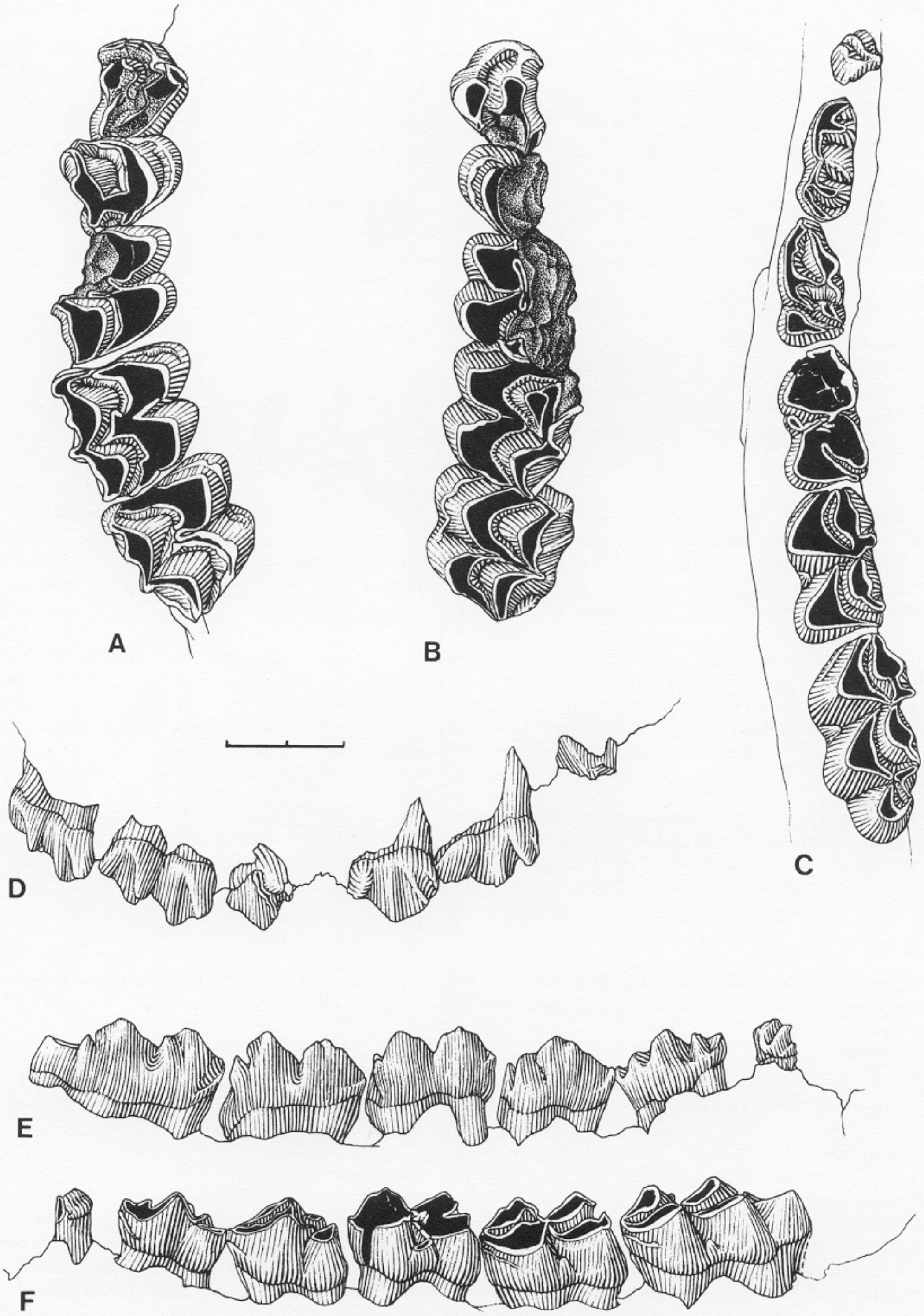
Mandible

The corpus is long and shallow especially forward of the dentition as in typical giraffes. The ramus is partially broken (Text-fig. 1).

Dentition

The dentition is characterized by the rugose structure of enamel, a giraffid characteristic.

Upper dentition (Text-fig. 3). All the teeth are very low. P2/ is missing on both sides. P3/ is widened posteriorly and has a triangular occlusal profile. The lingual cusp ('protocone') is elongated and crescentoid; it has an anterior vertical lingual groove and a well-marked spur on its buccal face. The buccal wall of the crown is clearly asymmetrical; the anterior part is smaller than the distal one and both are separated by a strong rib. The parastyle is sharp and well developed while the metastyle, also well developed, is more rounded. There is a slight lingual cingulum. P4/ is more symmetrical than P3/ and its length is smaller than its breadth. The external rib is central on the buccal wall. The buccal cusp (paracone) has also a vertical rib on its lingual face. There is a very large lingual cingulum which continues on the lingual part of the mesial face and on the entire



TEXT-FIG. 3. For caption see opposite.

TABLE 1. Measurements (in mm) of the upper teeth of *Georgiomeryx georgalasi*; Thymiana (Chios); Middle Miocene (MN5).

	LP3/	LP4/	LM1/	LM2/	LM3/	bP3/	bP4/	bM1/
THB-30	19·6	17·0	22·0	23·3	24·1	16·1	19·7	21·5
	bM2/	bM3/	b/L P3/	b/L P4/	b/L M1/	b/L M2/	b/L M3/	LM1/-M3/
	24·1	23·6	82·0	116·0	97·7	103·0	97·9	67·8

TABLE 2. Measurements (in mm) of the lower teeth of *Georgiomeryx georgalasi*; Thymiana (Chios); Middle Miocene (MN5).

	LP/3	LP/4	LM/1	LM/2	LM/3	bP/3	bP/4	bM/1
THB-16	19·2	21·0	21·3	22·2	31	9·2	11·0	12·7
	bM/2	bM/3	b/L P/3	b/L P/4	b/L M/1	b/L M/2	b/L M/3	LM/1-M/3
	14·5	14·8	47·11	52·0	60·4	65·3	47·7	76·7

distal face where the wear has caused a post-fossette. The size of the molars increases from M1/ to M3/ (Table 1). M1/ is broken on both sides of the maxilla but on the right side there is a weak metacone rib and a reduced metastyle. On M2/ and M3/ the styles are strong and there is a buccal cingulum and a paracone rib. The mesial and lingual cingulum is well marked, especially around the protocone of M3/. The distal part of the last molar is not reduced as in modern giraffes. There is no entostyle.

Lower dentition (Text-fig. 3). Like their upper counterparts, the lower cheek teeth are very low. All have relatively narrow and elongated crowns (Table 2). P/2 is broken. P/3 has five transverse crests and it is not molarized although the median crest is thickened on the lingual side, and the posterior valley is closed on the buccal side. P/4 is a typical giraffid premolar. The anterior valley is closed by a metaconid, the entoconid is well developed, the posterior valley is open on both buccal and lingual sides, hypoconid and posterior transverse crest are clearly separated from the rest of the crown.

On the molars, the metastylid and the entoconulid are weak on M/1 and more developed on M/2 and M/3. There is no lingual rib except a very weak one on M/3. The M/3 hypoconulid is very twisted toward the buccal side. An ectostylid is present on M/1, weakly developed on M/2 and even more so on M/3. There is no trace of any *Palaeomeryx*-fold.

COMPARISONS

Skull

Two characters of the Chios skull, absence of preorbital fossa and absence of lacrimal foramen, are currently considered as synapomorphies of Giraffidae and Giraffinae respectively, so we will restrict the comparisons to the giraffids.

Giraffokeryx. This genus was erected by Pilgrim (1910) for the species *G. punjabiensis*. The material, some fragmentary and scattered dentitions coming from the lower Siwaliks of the Salt Range and from localities near Chinji, was described and figured later (Pilgrim 1911). A skull unearthed from the middle Siwaliks of northern Punjab has been referred to *Giraffokeryx* (Colbert 1933). All these fossiliferous localities are of mid Miocene age (Pilgrim 1934). The skull of *Giraffokeryx* has two

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TEXT-FIG. 3. *Georgiomeryx georgalasi* Paraskevaidis, 1940. A, right upper cheek teeth in occlusal view; B, left upper cheek teeth in occlusal view; C, left lower cheek teeth in occlusal view; D, right upper cheek teeth in buccal view; E, left lower cheek teeth in lingual view; F, left lower cheek teeth in buccal view. Scale bar represents 20 mn.

pairs of horns. The anterior pair is situated on the anterior part of the frontal, clearly in front of the orbits 'above the first and second molars' and 'they are confluent at their bases'. The posterior horns arise 'directly back of the orbits', their bases being fronto-parietal. All these horns are directed upward, backward and laterally. This pattern does not correspond to the Chios skull, the horns of which arise directly over the orbits and are more laterally oriented.

Palaeotragus. The known skulls of *Palaeotragus* (e.g. Hamilton 1978; Geraads 1986) are characterized by a pair of simple supraorbital horns directed upwards, laterally and slightly backwards. These horns are, however, inclined slightly backwards. They have a rounded or oval basal section. This is the same for an isolated horn described under the name *Propalaeotragus actaensis* Godina, Vislobokova and Abdrachmanova, 1993 from the Miocene of Kazakhstan. The females can be hornless (Colbert 1936).

Canthumeryx (= Zarafa). An edentulous skull coming from the lower Miocene of Gebel Zelten (Libya), holotype of the species *Zarafa zelteni* (Hamilton, 1973), has been synonymized with *Canthumeryx syrtensis* Hamilton, 1973 which had been described from two mandibular fragments and an isolated M/3 from the same locality. Upper and lower teeth allocated to *Zarafa* are now identified also as *C. syrtensis.*

The *Canthumeryx* skull is broken anteriorly and posteriorly as is the Chios skull but the damage is far less on the North African skull. In dorsal view, the frontal is flat with a pair of laterally expanded flat horns with triangular bases very similar to that of Chios skull. These horns are also located just over the orbits and *Canthumeryx* is quite similar to the Chios skull.

Injanatherium. Erected for a toothless skull from late Miocene Gebel Hamrin layers (Iraq), type specimen of the species *I. hazimi* Heintz, Brunet and Sen, 1981, *Injanatherium* has been also found in Saudi Arabia in the mid Miocene Hofuf Formation near Al Jadidah (Morales *et al.* 1987) with *I. arabicum*. *Injanatherium* is characterized by laterally horizontally extended and relatively supraorbital horns. A large pair of robust horns is situated above or a little behind the orbits, over the temporal fossa. It is impossible to know whether *I. hazimi* had a second anterior pair of horns but a fragment of skull from Al Jadidah has a small horn in front of the orbit just posterior to the fronto-nasal suture. It has been suggested that a piece of skull identified as *Samotherium sinense* (Bohlin, 1926, text-fig. 137) could belong to the same group.

Injanatherium is similar to the Chios skull and *Canthumeryx* in its possession of lateral horizontal horns. However, the Al Jadidah remains show that there is an anterior pair of horns and that the posterior one is less flat, more elongated and set a little further back from the orbit without turning upwards.

Palaeomerycidae. The skull of *Palaeomeryx* is especially well known from specimens from the middle Miocene of China (Qiu *et al.* 1985), and that of *Triceromeryx* from fragmentary specimens from Spain (Crusafont-Pairo 1952; Astibia and Morales 1987). These two genera have an elongated skull with three horns. Two horns are over the orbits and the third, median, is on the occipital. They differ from the Chios skull in the shape of the orbital horns which are vertical and by the presence of a lacrimal foramen and a pre-orbital fossa.

Sivatheriinae. The species belonging to this group are characterized (Geraads 1986) by large size and by the cranial appendages behind the orbits, except in the females which can be hornless. These characters do not correspond to those of the Chios skull.

Dentition

Giraffokeryx. According to Pilgrim (1911), the first described specimens of *G. punjabiensis* come from 'one small spot near Phadial... which were remarkably free from the remains of any other animal except an antelope'; all the material can probably be referred to the same species. The upper cheek teeth differ from those of the Chios skull in the absence of a cingulum although P3/ and P4/ have the same general shape. The *Giraffokeryx* molars have a spur in the anterior fossette which is not present on Chios molars. The lower premolars, P/3 and P/4, have the same general pattern as have the Chios premolars but they are less narrow and more hypsodont, P/3 has a more pronounced buccal groove, its anterior portion is less elongated and the transverse crests are less oblique. P/4 has also a more reduced anterior portion. The lower molars, M/1 and M/2, have different proportions (Table 2). The metastylid of M/3 is less developed. The M/3 hypoconid is less twisted and the ectolophid is more developed. Like the premolars, the molars are also more hypsodont, even taking into account the dental wear. For Pilgrim (1911) the relative hypsodonty was one of the main characters of *Giraffokeryx*. The skull described by Colbert (1933) seems to have the same characters as Pilgrim's specimens.

The locality of Prebreza (Serbia) has yielded some dental remains identified as *Giraffokeryx* (Ciric and Thenius 1959; Pavlovic 1969). The upper tooth material consists of left and right maxillae with D3/–M1/, right P2/–P4/ belonging to an older individual and a broken piece with M2/. Compared with the Chios teeth, P3/ is more symmetrical, more giraffe-like, P4/ has a similar pattern but with a smaller breadth, a weaker buccal rib and absence of lingual cingulum. The upper molars seem to have a slightly higher degree of hypsodonty, a less marked paracone buccal rib and a weaker cingulum. The lower teeth are known from a piece of mandible with P/2–M/3 and two other ones with M/2–M/3. P/3 has the same pattern but the transverse crests are less oblique. The P/4 talonid breadth is larger and, perhaps due to differential wear, the posterior transverse crest is not isolated. The comparison of M/2–M/3 is more puzzling. They have the same degree of hypsodonty for one specimen (Pavlovic 1969, pl. 15) and a higher degree on the second one (Pavlovic 1969, pl. 16). M/3 has a better marked ectostylid and a weaker metastylid.

A few remains (P2/–P/4 and P/3–P/4) from the Upper Miocene of Nakali have been attributed to *Giraffokeryx* (Aguirre and Leakey 1974). These teeth are larger than the Chios teeth. P3/ is elongated but more symmetrical without any vertical lingual groove. The P4/ cingulum is weaker. P/3 is more evolved, more giraffe-like with a larger talonid.

A left mandibular corpus and several isolated teeth from the mid Miocene layers of Pasalar (Turkey) have been identified under the name *Giraffokeryx* aff. *punjabiensis* (Gentry 1990). The premolars display a large amount of variation. Thus two teeth are quite similar to the Chios P/3 (Gentry 1990, fig. 5g–h) but they are DP/3 and another one is more massive with a larger breadth (fig. 5f). P/4 could be very evolved (fig. 5d) or very primitive, *Palaeomeryx*-like (fig. 5c); it can have a large breadth (fig. 5a) or be narrow (fig. 5b). We consider the Pasalar material to be too scarce and incomplete to permit any precise identification. It may comprise more than one taxon.

Palaeotragus. This genus appears to have existed from the mid to the late Miocene but the different species allocated to it can display some significant differences, and it may prove to be paraphyletic (Hamilton 1978). Following Geraads (1986), all the palaeotragines could be included in the same genus except, we presume, *Canthumeryx* and *Giraffokeryx*. We consider here the middle Miocene species; the upper Miocene ones (*P. rouenii*, *P. coelophrys* and *P. germaini*) are larger and possess some derived characters lacking on the Chios material.

P. primaevus comes from the middle Miocene of Fort Ternan (Churcher 1970, 1978) and some other Kenyan localities (Hamilton 1978). P3/ has a primitive shape but the lingual cusp is more posteriorly situated; upper premolars and molars do not display any cingulum: M1/ and M2/ have a well-developed spur on the buccal face of the metaconule. The lower dentition is less brachyodont and the teeth are more robust (Table 2). P/3 has a small metaconid, a trend toward the crown molarization. P/4 is more giraffe-like with an anteriorly widened crown. The lingual surfaces of the lower cheek teeth are more flattened.

P. tungurensis Colbert, 1936 comes from the middle Miocene of Central Asia. The teeth differ by their degree of hypsodonty and the shorter premolars relative to the larger molars (Table 2). P3/ is primitive like that of *P. primaevus*. The upper molars have no cingulum, the mesostyle is higher *vis-à-vis* the paracone buccal wall and lower *vis-à-vis* the metacone buccal wall, and the paracone rib is weaker. P/3 is more molarized, the anterior portion of P/4 is widened and the third lobe (hypoconulid) of M/3 is more simple.

P. lavocati Heintz, 1976 was founded on scarce and fragmentary specimens from the middle Miocene of Beni Mellal (Morocco). It is difficult to characterize this species but the author concluded that the differences between *P. lavocati* and *P. tungurensis* are very slight. Most of the noted differences between Chios teeth and *P. tungurensis* are present in the Beni Mellal specimens.

Canthumeryx (= Zarafa). This genus is known from a single species from the lower middle Miocene of Gebel Zelten (Hamilton 1973) and other African localities (Hamilton 1978). *Canthumeryx* is brachyodont as is the Chios fossil. P3/ looks primitive with an asymmetrical crown and an antero-lingual groove. P4/ is quite similar to the Chios material but is a little less asymmetrical, wear facets being present on the two buccal crests of the paracone. The lingual cingulum is also a little less developed. M1/ and M2/ are also quite similar to that of the Chios fossil but the lingual cingulum is interrupted just in front of the cusps; the spur on the buccal face of the metaconule is very marked in some specimens (Hamilton 1973, pl. 5) and less marked on some other ones (Hamilton 1973, pl. 6). In a specimen from Muruorot (Hamilton 1978), P/3 does not differ a lot from the Chios P/3 but P/4 is far more primitive; a small elongated metaconid is present but the anterior valley is buccally open as in some specimens of *Palaeomeryx*. The few known lower molars do not differ significantly. We note that a lower molar on a piece of mandible (Hamilton 1973, pl. 5, figs 2–3) is larger than the other teeth identified as *C. syrtensis* or *Zarafa zelteni*. It differs also in possessing more wrinkled enamel, a higher crown relative to the length, the very weak ectostylid, the weak or absent lingual rib of the lingual cuspids and the less narrow buccal cuspids. This molar belongs certainly to another species of giraffid and may be a *Palaeotragus* sp.

Injanatherium. Some teeth have been allocated to this genus (Morales *et al.* 1987). P3/ is more symmetrical and the upper molars lack any lingual cingulum. The lower premolars, especially P/4, and the molars are quite similar but the degree of hypsodonty is a little higher.

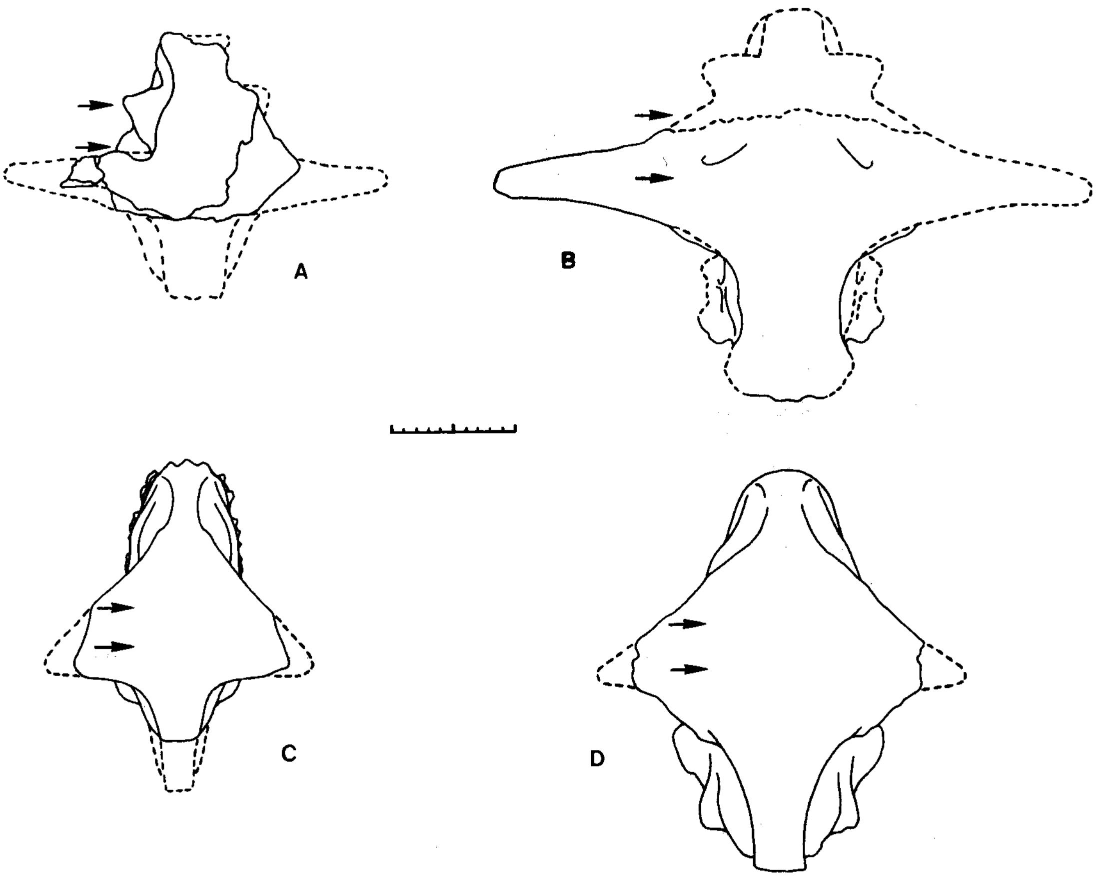
Palaeomerycidae. In this family, P3/ can be as primitive as is the Chios P3/. P4/ and the molars have a lingual cingulum. P/4 is primitive with a buccally open anterior valley but with a quite marked trend to close it, especially on some large specimens from Sansan (Astibia and Morales 1987). The trend toward the closure of the P/4 anterior valley can occur in some other genera which are probably linked to the giraffoids, for example *Hispanomeryx* (Moya-Sola 1986) or *Teruelia* (Moya-Sola 1987), or even in large cervids.

DISCUSSION

The use of horns and ossicones in giraffid taxonomy is accorded different significance by different authors. Bohlin (1926) perceived giraffid cranial appendages as highly variable and thus not giving any useful information on their relationships. As a result, he could put together in the same genus, or even the same species, skulls with upwardly or laterally directed appendages. However, although horns could be present or absent according to the sex in fossil giraffids, observation of recent species of giraffids leads us to consider horns or ossicones to be a good tool for specific or possibly generic taxonomy. Position and shape of ossicones do not display large variation in living species, so we prefer to hypothesize, as do most authors, that frontal appendage number, shape and position are significant in characterizing not only particular species but also genera or particular lineages.

Most recent and fossil giraffids, the latter including *Palaeotragus*, have upwardly and, sometimes, slightly backwardly or laterally directed frontal appendages. However, very few have purely laterally oriented ones with a flattened base. This pattern is found in *Canthumeryx* and *Injanatherium* although the latter genus has developed a second anterior pair of lateral horns

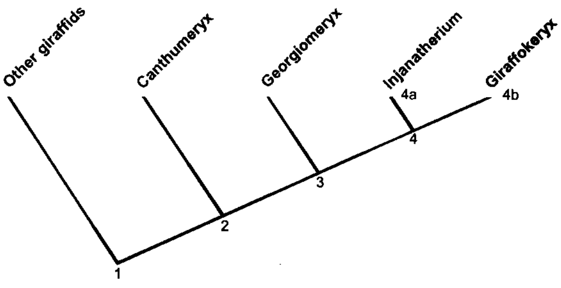
(Morales *et al.* 1987). Some authors (Morales *et al.* 1987; Gentry 1994) have supported the hypothesis that both could be put in a same genus, but the synonymy was not firmly established because of some differences. Most of the characters of the Chios skull correspond well with those of *Canthumeryx syrtensis*. Its frontal appendages have the same shape and are in a similar position just above and slightly behind the orbit. The two known skulls of *Injanatherium* display a slightly different pattern, with the horns emerging behind the orbits. There is also another difference, in the presence of an anterior second pair of horns situated between the anterior orbital rim and the fronto-nasal suture. This second pair is obviously absent in *Canthumeryx syrtensis* as well as in the Chios skull (Text-fig. 4). We consider that the appearance of a second pair of horns is a derived character. So, *Injanatherium* is more derived than *Canthumeryx* and the Chios skull, and we favour the opinion that the two sets must be placed in different genera.



TEXT-FIG. 4. Skulls of Canthumerycinae in dorsal view. A, *Injanatherium arabicum*; B, *Injanatherium hazimi*; C, *Georgiomeryx georgalasi*; D, *Canthumeryx syrtensis*. Scale bar represents 100 mm. Arrows indicate the anteroposterior extent of the orbits.

As shown above, the Chios and Gebel Zelten specimens match quite well in cranial characters but differ in their tooth morphology. Both are brachyodont but the *Canthumeryx* P/4 is more primitive and does not reach the 'giraffid stage' of evolution with a closed anterior valley and with a lingually open posterior valley. In this respect the Chios dentition is more derived (i.e. more giraffid-like) than that of *Canthumeryx*. If we consider the molarization of the premolars as a shared derived character of Giraffidae, we cannot include the Chios specimen and *Canthumeryx* in the same lineage, genus or family. However, on the other hand, it seems that premolar molarization is a general trend within giraffoids or even Pecora which can occur in Palaeomerycidae or in Cervidae as well, and which can have appeared several times in giraffid evolution. The horn shape, insertion, and orientation seem to be far more significant for giraffid phyletic and systematic assessments. The Chios and Gebel Zelten specimens could belong to the same lineage, in which the premolars follow the same general giraffid trend toward molarization. *Canthumeryx* is more primitive and the Chios giraffid more advanced in P/4 molarization. A further evolutionary step, unknown here, would have been P/3 molarization and the homomorphy of upper premolars P3/ and P4/. So, both forms must be included in genera different from *Injanatherium*. A generic name already exists for the Chios giraffid, namely *Georgiomeryx* Paraskevaidis, 1940. This genus was established on the species *G. georgalasi* Paraskevaidis, 1940, the type specimen of which is a fragment of mandible with P/2–P/3 from the same locality, Thymiana, where the new skull was collected. The premolars match those of the new specimen very closely and there is no doubt that both belong to the same species of brachyodont giraffid. Until now, it has been very difficult to compare *Georgiomeryx* remains with other giraffids because of the incomplete nature of the type specimen, but the new discoveries at the type locality permit the recognition of similarities to the Gebel Zelten material. Thus far, *Canthumeryx* Hamilton, 1973 could have been a junior synonym of *Georgiomeryx*, but if so, the species *Georgiomeryx georgalasi* would share some derived dental features (more molarized P/4) with other genera (*Injanatherium* and *Giraffokeryx*) and the genus *Georgiomeryx* would be paraphyletic.

Until now, *Georgiomeryx georgalasi* and *Canthumeryx syrtensis* have been known from Chios and Gebel Zelten from the type material of the two species. Some specimens from Muruarot (Kenya) have been also referred to *syrtensis* (Hamilton 1978). The two described species represent two successive evolutionary steps, *C. syrtensis* being the more primitive. *Injanatherium* is more derived with a second pair of lateral horns (anterior ones), the posterior horn back to the orbits, and the lesser degree of brachyodonty; *Giraffokeryx* is differently derived. All these genera constitute together an early offshoot of the family Giraffidae, an offshoot which requires subfamilial distinction (Text-fig. 5).



TEXT-FIG. 5. Cladogram of the sub-family Canthumerycinae. Character-states defining the nodes are as follows. 1. Bilobed lower canines; wrinkled enamel. 2. Flat and laterally directed supra-orbital horns. 3. Molarized P/4. 4. One pair of lateral horns slightly posterior to the orbits; one pair of anterior horns; P3/ relatively symmetrical; molarized P/3; relative hypsodonty. 4a. Very robust supra-orbital horns; 4b. Upwardly directed distal horns.

The Gebel Zelten locality, from which *C. syrtensis* was collected, has been dated to different geological or biochronological levels. It is attributed to the Burdigalian (upper Lower Miocene) by Arambourg and Magnier (1961) and Savage (*in* Selley 1969). Savage (1989) gives a more precise dating of MN3b. In East Africa, *C. syrtensis* occurs in Murourot (upper Lower Miocene, 'set II') and, with uncertainty, in set III (Pickford 1981). Nevertheless, the evolutionary level of some suids implies a later age for Gebel Zelten (Pickford 1987). Finally, if we try to correlate Gebel Zelten with European mammal zones, we can support a MN4 level. This locality has also yielded some rodents. Among them, the primitive murid *Potwarmus* sp. which looks quite similar to *P. primitivus* from Siwaliks of the Kamlial, northern Pakistan. *P. primitivus* has a time range between 14·3 and 18·0 Ma (Flynn *et al.* 1995). Almost the same conclusion is reached by Thomas (1979).

The locality of Thymiana in Chios can be dated to the middle Miocene, and more precisely MN5, based on the evolutionary stage of its rodents. Indeed, the rodent faunas collected from two levels, a few metres below and above the large mammal locality, contain several elements unknown in MN4 localities, such as ctenodactylids, five species of cricetids, the genus *Alloptox* (Ochotonidae, Lagomorpha). On the other hand, the stage of evolution of cricetids and glirids from Chios is much less progressive than those from MN6 localities.

The second argument for the age of the Chios faunas has been provided by magnetic stratigraphy. The mammalian localities are all included in a long reverse zone (Kondopoulou *et al.* 1993) which is preceded by an alternation of short normal and reverse polarities. The long normal zone including the fossiliferous levels is correlated tentatively with the Chron C5Br. According to Cande and Kent (1995), the time span of this chron is between 15·16 and 16·03 Ma. Such an age is in good agreement with the correlation suggested for the MN5 zone by Steininger *et al.* (1990, 1996).

Whatever the dating of the fossiliferous localities, both species *G. georgalasi* and *C. syrtensis* together with both species of *Injanatherium* and with *Giraffokeryx* constitute a morphological series, which may be a phyletic one, and which can be formalized as the subfamily Canthumericinae.

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