The Fossil Record of Giraffes (Mammalia: Giraffidae) in Greece

George Iliopoulos and Socrates Roussiakis

1 Introduction

Giraffidae consist a group of medium- to large-sized ruminant cetartiodactyl mammals which as typical pecorans are characterized by the presence of cranial appendages and more specifically by the presence of ossicones in the males of some taxa and in both males and females in some other taxa. Ossicones are epiphyseal osseous protuberances found either paired on the dorsal part of the frontoparietal suture, or paired or unpaired on the frontonasal of giraffid skulls (Churcher 1990) but their structure and development is completely distinct from that of horns and antlers. As epiphyseal growths they are deriving from the ossification of cartilage during the gradual development of the animal (Lankester 1907; Janis and Scott 1987; Solounias 1988; Prothero and Schoch 2002). At early stages, the ossicone cartilage is not attached to the skull, but gradually as the ossicones develop and get ossified, they are fused to the skull (Solounias 1988; Prothero and Schoch 2002). In addition, unlike horns and antlers, ossicones are permanently covered by skin and fur (Harris et al. 2010). Another typical feature of the giraffids is their bilobed lower canine (Hamilton 1978) in which, compared to Climacoceridae, the second lobe is notably enlarged (Solounias 2007; Harris et al. 2010). The elongation of the neck, typical for long necked giraffes, seems to be a general trait that can be seen in most giraffids (Danowitz et al. 2015), as it is the elongated skull as well. Similarly, another feature seen in most giraffids is the elongation of their limb bones (Solounias 2007).

G. Iliopoulos (✉)
Department of Geology, University of Patras, Rio Patras, Greece
e-mail: iliopoulosg@upatras.gr

S. Roussiakis
Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Athens, Greece
e-mail: srousiak@geol.uoa.gr

E. Vlachos (ed.), *Fossil Vertebrates of Greece Vol. 2*,
https://doi.org/10.1007/978-3-030-68442-6_10

Giraffids appear for the first time in the early Miocene of Africa and more specifically at Gebel Zelten, Libya (Churcher 1978) with *Canthumeryx sirtensis* as the first representative of the family. During the middle Miocene they migrate to Eurasia, and since then they consist a common faunal element in African and Eurasian faunas until the Early Pleistocene and particularly during the late Miocene when they present their maximum diversity with several species. Despite their significant contribution in the Neogene faunas of Eurasia, the last Eurasian giraffes became extinct in the interval 1.3–1.1 Ma (Lebatard et al. 2014). Until recently, two giraffid species were supposed to survive in Africa, *Okapia johstoni* and *Giraffa camelopardalis*, that belong to the subfamilies Palaeotraginae and Giraffinae, respectively. Concerning the latter species, a recent study by Fennessy et al. (2016) which applied multi-locus population genetic analyses on the genetic material of the 9 *G. camelopardalis* subspecies, indicated that notably four distinct giraffe species should be considered instead of one, namely *G. camelopardalis, G. tippelskirchi, G. giraffa*, and *G. reticulata*. However, two new studies that were only published this year using multiple methods of multi-locus DNA sequence analysis on genetic material from the different subspecies (Petzold and Hassanin 2020) and mitochondrial sequences from old museum specimens (Petzold et al. 2020), suggested that there are 10 extant subspecies of *Giraffa*, which belong to three different species, namely *G. camelopardalis, G. tippelskirchi,* and *G. giraffa*.

The Greek giraffid fossil record is fairly rich, containing 14 species ranging from the middle Miocene to the Early Pleistocene, of which 10 have been named based on material from Greek type localities. To date, more than 50 localities, mainly in the eastern and northern part of mainland Greece have revealed giraffid findings, nevertheless a number of these localities is found on islands of the Eastern Aegean Sea such as Lesvos, Chios, Samos, and Rhodes and surprisingly there is an additional report for a giraffid astragalus found on the island of Antikythera (Verikiou-Papaspyridakou 1986). Most of the localities as well as most of the species (11) are found in late Miocene deposits. The stratigraphically oldest Greek finding is *Georgiomeryx georgalasi* from the middle Miocene of Thymiana, Chios, whereas 7 localities bear the Plio-Pleistocene (Villafranchian) taxon *Palaeotragus inexspectatus*. The Greek late Miocene record includes the species *Helladotherium duvernoyi, Samotherium boissieri, Samotherium major, Palaeotragus rouenii, Palaeotragus coelophrys, Palaeotragus quadricornis, Palaeotragus* aff. *berislavicus, Palaeogiraffa macedoniae, Palaeogiraffa pamiri, Palaeogiraffa major, Bohlinia attica*, and *Bohlinia nikitiae*.

2 Historical Overview

In 1854, M. Chaeretis sent to the Natural History Museum in Paris fossil bones from Pikermi which in the same year were studied and published by Duvernoy (1854); in that paper, two alleged giraffid species, one "giraffe" and one large species of giraffe are mentioned. This was the first report of giraffid fossil material from Greece.

Since then, several giraffid findings, mainly of Late Miocene age, have been discovered in the Greek Peninsula. The most important findings and the most eminent giraffid workers will be reported herein.

Two years later, Gaudry and Lartet (1856) studied the "Chaeretis" material, as well as new material from excavations they contacted that year at Pikermi and described two new species: *Camelopardalis attica* and *Camelopardalis duvernoyi*. In 1860, Gaudry, after studying additional material from the excavations at Pikermi, proposed a new generic name for the robust giraffid, *Helladotherium duvernoyi*. A year later he (Gaudry 1861) erected the species *Palaeotragus rouenii,* a small and gracile giraffid, which he at first considered to be a large bovid. On the same year, Wagner (1861), after studying material also from Pikermi, described the taxon *Giraffa vetusta*, which today is considered as an invalid taxon. Before the end of the nineteenth century, Forsyth Major conducted excavations at the locality Mytilinii on Samos Island, where he collected bones that belonged to a large giraffid. He originally described this material as *H. duvernoyi*, but later he established a new species, *Samotherium boissieri* (Forsyth Major 1888). Four decades later, Bohlin (1926) after studying material from Samos considered that the large-sized *Samotherium* material presented certain different characters from the typical *S. boissieri* and thus he described it as *Samotherium boissieri* var. *major*. Weithofer (1888), after studying material from Pikermi, erected the new species *Giraffa parva*, which today is also considered as an invalid taxon. Despite the fact that in the following decades major excavation projects took place in Pikermi and Samos, no significant data concerning giraffids have been produced, except for the new findings from Axios valley reported by Arambourg and Piveteau in 1929. The next important giraffid finding came in 1940 by Paraskevaidis who described a mandibular fragment with P2–3 from the middle Miocene locality Thymiana in Chios which belonged to a primitive giraffid and which he named *Georgiomeryx georgalasi*. Sickenberg (1967) reported from the Villafranchian deposits of Volax the giraffid taxon *Macedonitherium martini*. Athanassiou (2014) in his study on the giraffid material from Sesklo, considered that this material as well as all Greek and Eurasian Villafranchian giraffid material belongs to *Palaeotragus inexspectatus*. In the early 1970s, Denis Geraads (1974) working on his PhD project studied the giraffid skeletal material that had been collected from the late Miocene localities of Axios Valley. In the years to come he published a number of papers on this material (Geraads 1978, 1979, 1989) and in one of them (1989) he erected the species *Decenatherium macedoniae* from the Vallesian locality of Pentalophos 1, which later Bonis and Bouvrain (2003) revised. They erected the new genus *Palaeogiraffa*, to accommodate *P. macedoniae* and determined material from the locality of Xirochori 1 as a second different species of the same genus, *P. pamiri*, and raised a third new species as well, *P. major*, from the Vallesian locality of Ravin de la Pluie.

Solounias is another important worker that reported giraffid material from Samos (Solounias 1981), and also has done among others a lot and significant work in determining the feeding and dietary habits of giraffids found in Greek localities and defining their paleoecological adaptations (e.g., Solounias et al. 2000, 2010). Kostopoulos et al. (1996) studied the giraffids from the localities of Nikiti and erected a new species of *Bohlinia*, *B. nikitiae*. Iliopoulos (2003) studied for his thesis the giraffid material from the different sites of the late Miocene locality of Kerassia. Kostopoulos and Koufos (2006) described the giraffid taxa that have been determined in the late Miocene locality of Perivolaki. Kostopoulos (2009) provided a detailed account on the giraffid findings from the late Miocene localities of Samos Island. A new generation of Greek vertebrate paleontologists in the last few years has added new data to the Greek giraffid record. Lazaridis (2015) for his thesis reported giraffid taxa from Kryopigi and Kassandra, Xafis et al. (2019) from Thermopigi and recently Laskos (2020) for his MSc thesis revised old *Palaeotragus* material from Vallesian localities of Macedonia, reporting for the first time the presence of *Palaeotragus* aff. *berislavicus* from Nikiti 1.

3 Phylogenetic Relationships

Giraffidae as ruminants are cetartiodactyl pecorans having ossicones as cranial appendages. Ruminants with ossicones located above the orbits have been placed to the clade Giraffomorpha, which includes two superfamilies, Palaeomerycoidea and Giraffoidea (Solounias 2007; Sánchez et al. 2015; Rios et al. 2017). According to Janis and Scott (1987), Giraffoidea consist a monophyletic group that originated from Gelocidae before the early Miocene. The main synapomorphies of the Giraffoidea that support their monophyly are: the bilobed lower canine (Hamilton 1978) and the lacking of first premolars (Harris et al. 2010). Two families are included in the Giraffoidea, Climacoceratidae, and Giraffidae. Climacoceratidae present a small accessory lobe and a plesiomorphic ruminant-like P4 (Hamilton 1978). The synapomorphies that characterize the Giraffidae are, on the other hand, mainly the large size of the second lobe of the bilobed lower canine (Hamilton 1978) (Fig. 1), the long slender limbs, the large body size, and the narrow occipital (Solounias 2007), indicating that Giraffidae consist a monophyletic clade.

Solounias (2007) based on metacarpal morphology proposed that the family consists of eight subfamilies: Canthumerycinae, Bohlininae, Okapiinae, Giraffokerycinae, Sivatheriinae, Samotheriinae, Palaeotraginae, and Giraffinae. Nevertheless, as the phylogeny of this group is still not very clear, herein a more conservative approach will be followed, taking under consideration what is widely accepted and more specifically that four subfamilies should be included in the family, Canthumerycinae (Hamilton 1978), Sivatheriinae, Palaeotraginae, and Giraffinae (Merceron et al. 2018). Recent phylogenetic analysis (Rios et al. 2017) has shown that Sivatheriinae and Giraffinae are monophyletic groups, whereas Palaeotraginae is paraphyletic.

The Greek fossil record contains giraffid fossils from all four subfamilies, such as the Canthumerycinae *Georgiomeryx georgalasi* from the middle Miocene, the Sivatheriinae *Helladotherium duvernoyi* from the late Miocene, the Giraffinae *Bohlinia attica* and *Bohlinia nikitiae* from the late Miocene as well, and the fairly diverse Palaeotraginae represented by *Samotherium boissieri, Samotherium major,*

Fig. 1 The left bilobed canine of *Giraffa camelopardalis* (lingual view) presenting the large-sized second lobe, a typical feature of the Giraffidae. Scale bar equals 10 mm

Palaeotragus rouenii, Palaeotragus coelophrys, Palaeotragus quadricornis, Palaeotragus aff. *berislavicus, Palaeogiraffa macedoniae, Palaeogiraffa pamiri* and *Palaeogiraffa major* from the late Miocene, and *Palaeotragus inexspectatus* from the Early Pleistocene.

4 Distribution

Taking in mind literature, as well as the most recent reports on the fossil giraffid findings of the Greek Peninsula, 56 localities bearing giraffid remains have been recorded until now (see Fig. 2 and Appendix). These localities are mainly found in the eastern and northern part of the peninsula, as well as on islands of the Eastern and South Aegean Sea such as Lesvos, Chios, Samos, Rhodes, Crete, and Antikythera (see Appendix). The two oldest localities are Thymiana B from the late Orleanian (MN5) of Chios Island (40), the type locality of *Georgiomeryx georgalasi* (Paraskevaidis 1940), and Melampes from the Astarachian (MN6 or MN7–8) of South Rethymnon on Crete (39), reported herein for the first time.

The latter consists mainly of a few long bone parts belonging possibly to a Palaeotraginae and which were collected in 1975 by Kuss (now stored in the collections of the Natural History Museum of Crete). Giraffids from the Vallesian and mainly from MN10 have been found in localities from Axios Valley (localities 35, 36, 38) and Chalkidiki (34, 37), represented by *Palaeogiraffa* spp., robust *Palaeotragus* species (*P. coelophrys, P.* aff. *berislavicus), Bohlinia* spp. (*B. attica, B. nikitiae*), and *Helladotherium duvernoyi*. Giraffids during the Turolian were more widespread expanding in the eastern and northern part of the peninsula, and have been found in several localities at Samos Island (14), as well as in Rhodes Island (10) (Appendix). More specifically, early Turolian (MN11) giraffids have been found in localities at Axios Valley (32), Chalkidiki (33), and Samos (14). The

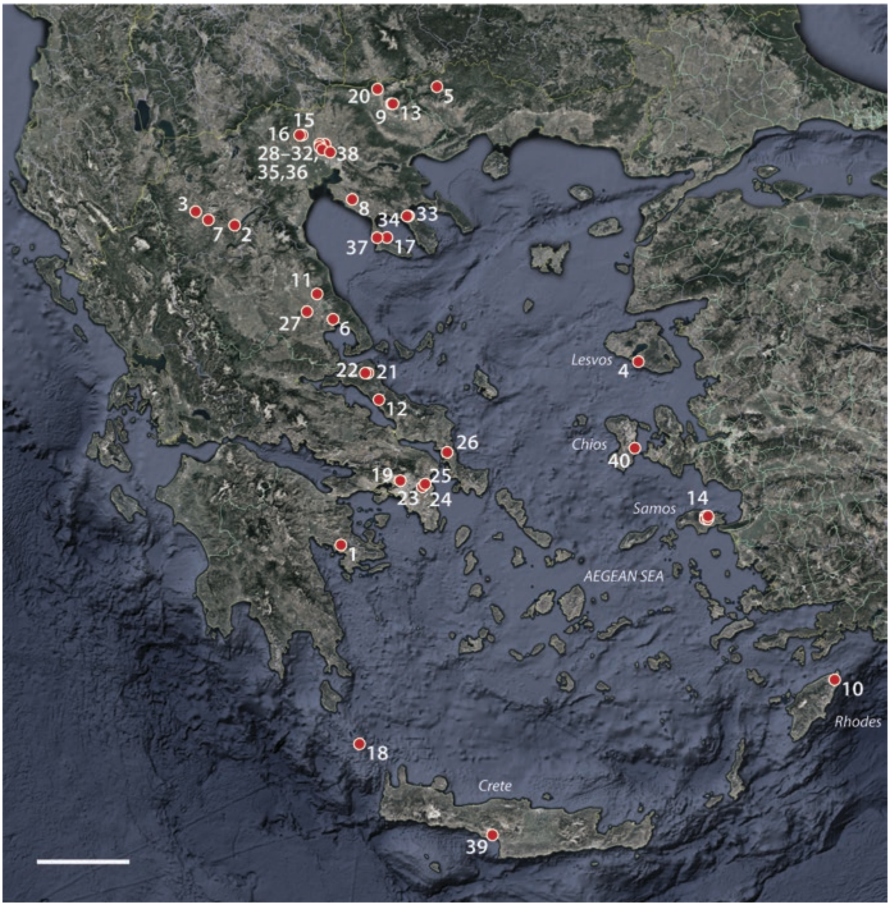

Fig. 2 Map of the occurrences of fossil giraffes from Greece. See Appendix for further information. **Pleistocene**: **1**, Karnezeika; **2**, Haliakmon; **3**, Libakos; **4**, Vatera-F; **5**, Volax; **6**, Sesklon; **7**, Dafnero. **Pliocene/Miocene**: **8**, Nea Silata; **9**, Maramena. **Miocene**: **10**, Rhodes Island; **11**, Alifakas; **12**, Drazi; **13**, Ano Metochi; **14**, various localities in Mytilinii basin on Samos Island; **15**, Dytiko 2; **16**, Dytiko 1; **17**, Kryopigi; **18**, Kamarella; **19**, Pyrgos Vassilissis; **20**, Thermopigi; **21**, Kerassia 1; **22**, Kerassia 3 and 4; **23**, Pikermi Valley 1; **24**, Pikermi; **25**, Chomateri; **26**, Halmyropotamos; **27**, Perivolaki; **28**, Ravin X; **29**, Prochoma; **30**, Vathylakkos 3; **31**, Vathylakkos 2; **32**, Ravin des Zouaves; **33**, Nikiti 2; **34**, Nikiti 1; **35**, Xirochori 1; **36**, Ravin de la Pluie; **37**, Fourka; **38**, Pentalophos 1; **39**, Melambes; **40**, Thymiana B. Data from the Paleobiology Database (PBDB). Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/Copernicus. Scale bar equals 80 Km, north faces upward

Early Turolian localities of Samos are the only Greek sites where *Samotherium boissieri* has been found. Furthermore, *H. duvernoyi, Palaeotragus rouenii, P. coelophrys,* and *B. attica* are also common early Turolian giraffids. The majority of the Greek late Miocene localities come from the late Turolian (MN12–13) and these localities are situated in Axios Valley (15, 16, 28, 29, 30, 31), Chalkidiki (8, 17), Strymon Valley (9, 13, 20) Euboea Island (12, 21, 22, 26), Attiki (19, 23, 24, 25), Samos (14), and Rhodes Island (10). The late Turolian giraffid fauna is characterized by the presence of *H. duvernoyi, Samotherium major, P. rouenii, P. coelophrys, Palaeotragus quadricornis*, and *B. attica*. *P. quadricornis* has been only reported from Samos Island. Finally, early Pleistocene giraffids have been discovered in the Haliakmon Valley (2, 3, 7), Drama (5), Magnesia (6), Lesvos Island (4), and Argolida (Karnezeika) (1), represented by the Villafranchian taxon *Palaeotragus inexspectatus*. The latter locality is reported for the first time herein (Sianis pers. comm.).

5 Systematic Paleontology

Giraffidae Gray, 1821

Type Genus *Giraffa* Brisson, 1762.

Canthumerycinae Hamilton, 1978

★***Georgiomeryx* Paraskevaidis,** 1940

Type Species *Georgiomeryx georgalasi* Paraskevaidis, 1940.

Distribution Middle Miocene (MN5) of Chios Island, Greece (Bonis et al. 1997).

Comments Primitive giraffid consisting probably the oldest European giraffid taxon.

★***Georgiomeryx georgalasi* Paraskevaidis**, 1940

Type Material Mandibular part with p2–3, Athens Museum of Paleontology and Geology, National and Kapodistrian University of Athens (figs. 4–5, pl. 13 in Paraskevaidis 1940).

Type Locality Thymiana B, Chios Island, Greece, late Orleanian, MN5.

Distribution Known only from the type locality.

Taxonomic Remarks *Georgiomeryx georgalasi* is a medium size primitive canthumerycine giraffid and, as a basal form, presents primitive features, such as the flat and wide roof of the skull, and a pair of flattened ossicones projecting laterally just above the orbits (Fig. 3). It presents a typical brachyodont giraffid dentition. Upper fourth premolars and molars have a clear and strong lingual cingulum. Upper P3 and P4 have clearly different shape and morphology (heteromorphic). *G. georg-*

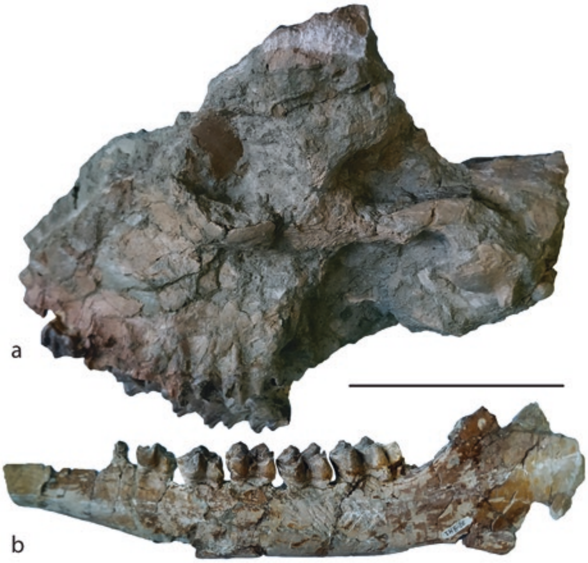

Fig. 3 Left lateral view of the cranium (THB 30) (**a**) and left mandible (THB 16) (**b**) of *Georgiomeryx georgalasi* from Thymiana B, Chios Island. Scale bar equals 10 cm (photos provided by DS Kostopoulos)

alasi as a canthumericine differs from Climacoceratidae in the shorter and more molarized lower P2 and P3. Nevertheless, its lower premolars are less molarized than *Canthumeryx*. Compared with *Injanatherium*, it is missing the small triangular anterior pair of ossicones found in front of the orbit and also the posterior pair projects laterally just above the orbits and not posteriorly behind the orbits, and its dentition is more brachyodont with stronger cingulums in the upper teeth (Bonis et al. 1997). *Giraffokeryx* also possessed two pairs of ossicones; however, the anterior one was placed anteriorly to the orbit above the frontals and the posterior one behind the orbits at the frontoparietal region (Bonis et al. 1997).

Comments When Paraskevaidis (1940) raised the new species for the first time, he considered that it belonged to Cervidae.

Palaeotraginae Pilgrim, 1911

★*Palaeotragus* Gaudry, 1861

Type Species *Palaeotragus rouenii* Gaudry, 1861.

Included Taxa 17 species are included in *Palaeotragus*: *Palaeotragus rouenii*; *Palaeotragus microdon* (Koken, 1885); *Palaeotragus pavlowae* Pavlow, 1913; *Palaeotragus coelophrys* (Rodler and Weithofer, 1890); *Palaeotragus quadricornis*

Bohlin, 1926; *Palaeotragus expectans* Borissiak, 1914; *Palaeotragus borissiaki* Alexeiev, 1930; *Palaeotragus hoffstetteri* Ozansoy, 1965; *Palaeotragus berislavicus* Korotkevich, 1957; *Palaeotragus moldavicus* Godina, 1979; *Palaeotragus asiaticus* Godina, 1975; *Palaeotragus tungurensis* Colbert, 1936; *Palaeotragus inexspectatus* (Samson and Radulesco, 1966); *Palaeotragus progressus* Tang and Ji, 1983; *Palaeotragus germaini* Arambourg, 1959; *Palaeotragus lavocati* Heintz, 1976; *Palaeotragus robinsoni* Crusafont-Pairó, 1979.

Distribution Middle Miocene of North Africa, Mongolia and China; late Miocene of North and East Africa, and Eurasia; late Pliocene and Early Pleistocene of Eurasia (Laskos 2020; Athanassiou 2014).

Comments This genus includes small- to middle-sized palaeotragines. Based on their relative size, the late Miocene species of *Palaeotragus* are separated into two groups: small and large (Geraads 1974, 1986; Kostopoulos et al. 1996; Iliopoulos 2003; Kostopoulos and Saraç 2005; Kostopoulos 2009). *P. rouenii*, *P. microdon,* and *P. pavlowae* are members of the small-sized group ("*P. rouenii*" group), which is characterized by slender and quite elongated limb bones. *P. coelophrys*, *P. expectans*, *P. borissiaki*, *P. hoffstetteri*, *P. moldavicus*, *P. asiaticus,* and *P. berislavicus* on the other hand are included in the large-sized group ("*P. coelophrys*" group), having shorter but more robust limb bones.

★*Palaeotragus rouenii* Gaudry, 1861

Type Material MNHN.F.PIK1670 (Fig. 4), almost complete skull with dentition, Muséum national d'Histoire naturelle, Paris (Pl. 1, Tabs. 1–5 in Gaudry 1861).

Type Locality Pikermi, Attiki, Greece, late Miocene, Turolian, MN12.

Distribution Late Miocene (Turolian, MN11–13) of Greece, Republic of North Macedonia, Bulgaria, Turkey, Moldova, Ukraine, and Afghanistan. In Greece, it has been found in Turolian (MN11–13) localities of Axios Valley (Ravin des Zouaves 5, Dytiko 2), Kryopigi (Chaldidiki), Thermopigi (Strymon valley), Perivolaki (Magnesia), Kerassia (Euboea Island), Pikermi and Chomateri (Attica), and Samos Island (Q1, Q2, QA, MGLS Stefana hill, MGLS Andrianos ravine, Mytilinii 4 MLN, Mytilinii-1A MTLA, Mytilinii-1B MTLB) (Fig. 2).

Taxonomic Remarks Small-sized palaeotragines with ossicones that are located above the orbits and are absent in females (Fig. 4), and slender and quite elongated postcranial elements (Fig. 5). Fourth lower premolar is molarized. It differs from *Palaeotragus microdon* in the shape of the ossicones, which are curved in *P. rouenii* but straight in *P. microdon*, and the presence of weak ossicones in the females in *P. microdon* (Bohlin 1926; Geraads 1974). The more robust representatives of the genus, the "*P. coelophrys*" group, have shorter but more robust elements and their teeth are significantly larger. In *B. attica,* the teeth and the toothrows are also slightly larger. The external tubercles and the stylids of the upper premolars are not so fully developed as in *B. attica* and in addition, their parastyle is not bifurcated.

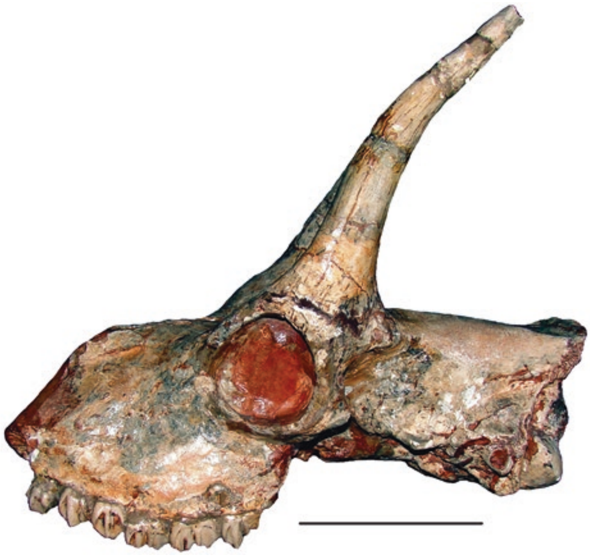

Fig. 4 Left lateral view of *Palaeotragus rouenii* cranium (MNHN.F.PIK1670) from Pikermi. Scale bar equals 10 cm

Fig. 5 Dorsal view of metacarpal bones of different Giraffidae taxa from Greek localities. (**a**) Extant *Giraffa reticulata* (NHMW 26429), (**b**) *Bohlinia attica* from Pikermi (AMPG(V) PA1923/91), (**c**) *Palaeotragus rouenii* from Pikermi (MNHN.F.PIK1692), (**d**) *Palaeotragus inexpectatus* from Volax (AMPG(V) 981), (**e**) *Helladotherium duvernoyi* from Pikermi (AMPG(V) PA1457/91), (**f**) *Samotherium major* from Samos (Andrianos) (MGL S535). Scale bar equals 10 cm

Comments *P. rouenii* is a very widespread palaeotragine in western Eurasia during the late Miocene. Based on masticatory morphology and tooth microwear, *P. rouenii* has been interpreted as a seasonal mixed feeder (Solounias et al. 1999, 2000, 2010; Merceron et al. 2018).

Palaeotragus coelophrys (Rodler and Weithofer, 1890)

Nomenclatural and Taxonomical History *Alcicephalus coelophrys* in Rodler and Weithofer 1890 (new species); *Achtiaria coelophrys* in de Mecquenem 1924 (new combination); *Palaeotragus coelophrys* in Bohlin 1926 (new combination).

Type Material Right cranium part with orbit and dentition, Naturhistorisches Museum Wien (Pl. 1, fig. 2 in Rodler and Weithofer 1890).

Type Locality Maragheh, Iran, late Miocene, Turolian, MN11.

Distribution Late Miocene (Vallesian and Turolian, MN9–13) of Turkey, Ukraine, Iraq, Iran, Georgia, and China. In Greece, it has been found in the Vallesian (MN9–10) of Axios Valley (Pentalophos 1, Ravin de la Pluie) and in the Turolian (MN11–12) of Samos Island (Qx, Q1, MGLS Andrianos ravine) (Fig. 2).

Taxonomic Remarks *P. coelophrys* is a medium-sized palaeotragine. Ossicones are absent in female skulls. The crowns of the teeth are relatively low compared to the type species (Fig. 6). Its long bones are slightly elongated and relatively robust. The morphology and the dimensions of the skull and the dentitions are quite similar with *P. expectans, P. borissiaki,* and *P. hoffstetteri* (Bohlin 1926; Alexeiev 1930; Geraads 1986). The long bones are less elongated and more robust than *P. rouenii* and *P. microdon*, and the teeth are significantly larger. On the other hand, the dimensions of its skeletal elements are clearly smaller than *S. boissieri*, which consists a much larger giraffid.

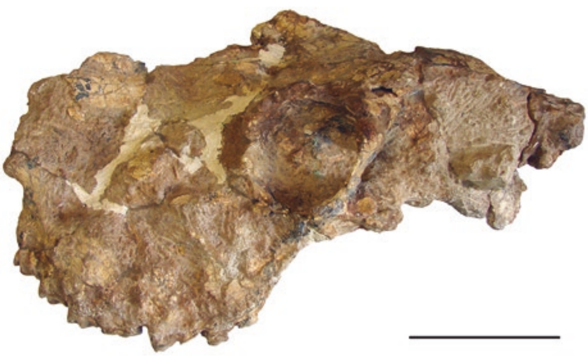

Fig. 6 Left lateral view of a female *Palaeotragus coelophrys* cranium (R.Pl 91) from Ravin de la Pluie. Scale bar equals 10 cm (photo provided by DS Kostopoulos)

Comments Geraads (1974, 1986) stated that the differences between *P. coelophrys, P. expectans, P. borissiaki*, and *P. hoffstetteri* are not significant and considered them all as synonyms of *P. coelophrys*. Tooth microwear analysis consistently showed that *P. coelophrys* was a grazer (Solounias and Moelleken 1993; Solounias et al. 1999, 2000) although more recent analyses have indicated browsing and mixed feeding diets (Danowitz et al. 2016; Merceron et al. 2018).

★*Palaeotragus quadricornis* Bohlin, 1926

Type Material No catalog number, part of cranium with dentition and ossicone and related right mandible with dentition, Bayerische Staatssammlung für Paläontologie und historische Geologie-München (BSPM) (figs. 53–57 in Bohlin 1926)—permanently lost during World War II (Kostopoulos 2009).

Type Locality Samos, Greece, late Miocene, Turolian, MN12.

Distribution Besides its type locality (MN11–12), it has been found in the Turolian of Iran (MN11–13).

Taxonomic Remarks A medium-sized palaeotragine, with ossicones present in female skulls being small in size, conical, and straight. Male skulls have a subquadrangular orbit located behind the third molar, and their ossicones are long and slightly curved caudally found just above the orbit. Toothrows of *P. quadricornis* are longer than *P. coelophrys*, while ossicones are absent from the female skulls of *P. coelophrys*. The orbit of *P. coelophrys* is located in a more anterior position than *P. quadricornis*, found above M2–3 (Kostopoulos 2009). The slight but notable bilobation of P3 and P4 in *P. quadricornis* and *P. hoffstetteri* is not observed in *P. coelophrys and P. expectans*. Also, the first two species have a P2 with a paracone that differs from *P. coelophrys* and *P. expectans* in having a flat posterior flange and a reduced parastyle than a concave one.

Comments The available material is scarce and fragmentary coming from different localities of Samos—with uncertain stratigraphic affinities. Bohlin (1926) erected this species based on his observation that the taxon possessed an extra anterior pair of ossicones on the anterior margin of the orbits, characterizing as ossicone an osseous protuberance of the frontal sinuses. Several authors in the past have synonymized *P. quadricornis* with *P. coelophrys* (Bosscha-Erdbrink 1977; Geraads 1986; Gentry and Heizmann 1996). Nevertheless, Kostopoulos (2009), after studying the available material of *P. quadricornis* and *P. coelophrys*, considered that despite the fact that the two species present several common features, there are certain cranial and dental features that are different. Hence, herein we agree with his view that the two species should be considered as distinct until more suitable material is available. Tooth microwear analysis showed that *P. quadricornis* was a grazer (Solounias et al. 1999, 2000).

Palaeotragus aff. *berislavicus* Korotkevitch, 1957

Nomenclatural and Taxonomical History *Palaeotragus* cf. *rouenii* in Kostopoulos 1996 (initial identification).

Distribution Late Miocene (Vallesian, MN10) of Greece and Ukraine. In Greece it has been found in the Vallesian (MN10) of Nikiti 1 in Chalkidiki (Fig. 2).

Taxonomic Remarks *P. berislavicus* is a medium-sized palaeotragine, slightly smaller than *P. coelophrys* and *P. expectans* with a large dentition though. The diastema between the canine and p2 is short, less than the length of p2–m3. The teeth are brachyodont. Long bones are elongated and rather slender. It has a size in between *P. rouenii and P. coelophrys*, having slender metapodials with a length in between *P. rouenii and P. coelophrys* and a large skull (Laskos 2020). The skeletal elements of *P. berislavicus* are smaller than *P. expectans* (Korotkevich 1957). The length of the dentition is close to *P. coelophrys*, *P. expectans,* and *P. borissiaki*.

Comments The only locality that *P. berislavicus* had been described until recently was the Vallesian site of Berislav in Ukraine (Korotkevich 1957). Recently, Laskos (2020) studied *Palaeotragus* material from Nikiti 1 that Kostopoulos et al. (1996) had previously described as *P.* cf. *rouenii*, and assigned it to *P.* aff. *berislavicus,* based on morphological as well as metrical differences. Concerning the latter, he identified that the length of the metapodials is in between *P. rouenii* and *P. coelophrys* with values that fitted *P. berislavicus*. So he considered that the material belonged to a taxon of intermediate size. Thus, he proposed the presence of a third distinct late Miocene *Palaeotragus* group with dimensions of the limb bones in between *P. rouenii and P. coelophrys* and included *P. asiaticus* and *P. berislavicus*. Iliopoulos (2003) reported *Palaeotragus* sp. from Kerassia 4 and Xafis et al. (2019) *Palaeotragus* sp. from Thermopigi. Both agreed that the studied material belonged to a large-sized *Palaeotragus* that presented differences though from the typical *P. coelophrys*. Nevertheless, this material from both localities could possibly belong to the intermediate-sized group and could be affiliated to *P. berislavicus* as well.

Palaeotragus inexspectatus (Samson and Radulesco, 1966)

Nomenclatural and Taxonomical History *Mitilanotherium inexspectatum* Samson and Radulesco 1966 (new species); *Palaeotragus inexspectatus* Athanassiou 2014 (new combination). Considered as the senior synonym of *Macedonitherium martini* Sickenberg, 1967, *Sogdianotherium kuruksaense* Sharapov, 1974, and *Palaeotragus (Yuorlovia) priasovicus* Godina and Bajgusheva, 1985.

Type Material No 5227, ISERB, distal part of left lower M3**,** Institute of Speleology "Emil Racoviţă," Bucharest (Pl. 1–2 in Samson and Radulesco 1966).

Type Locality Fîntîna lui Mitilan, Oltenia, Romania, Early Pleistocene, Villafranchian, MN17.

Distribution Late Pliocene–Early Pleistocene (Villafranchian, MN16–MNQ19) of Eurasia. In Greece, it has been found in the middle Villafranchian (MN17–MNQ19) of Volax (Drama), Haliakmon Valley (Dafnero, Libakos, Haliakmon) Sesklo (Magnesia), Vatera (Lesbos Island), and Karnezeika (Argolida) (Fig. 2).

Taxonomic Remarks *P. inexspectatus* is a medium-sized and moderately brachyodont palaeotragine. It possesses simple, long and parallel ossicones, rostrally inclined and located above the orbit (Fig. 7). The orbit is found behind the M3. The parietal crests are developed. The premolar rows are relatively reduced. Its limb bones are slightly elongated and relatively robust (Fig. 5). Concerning its size this is comparable to that of the large "*P. coelophrys*" group. Unlike the typical representatives of the palaeotragines, the ossicones of which are inclined backward, in *P. inexspectatus* they are inclined rostrally (Athanassiou 2014).

Comments Athanassiou (2014) suggested that all the post-Miocene palaeotragines found in Western Eurasia belong to the genus *Palaeotragus* and more specifically should be attributed to *Palaeotragus inexspectatus*. This taxon represents the last member of the family in western Eurasia.

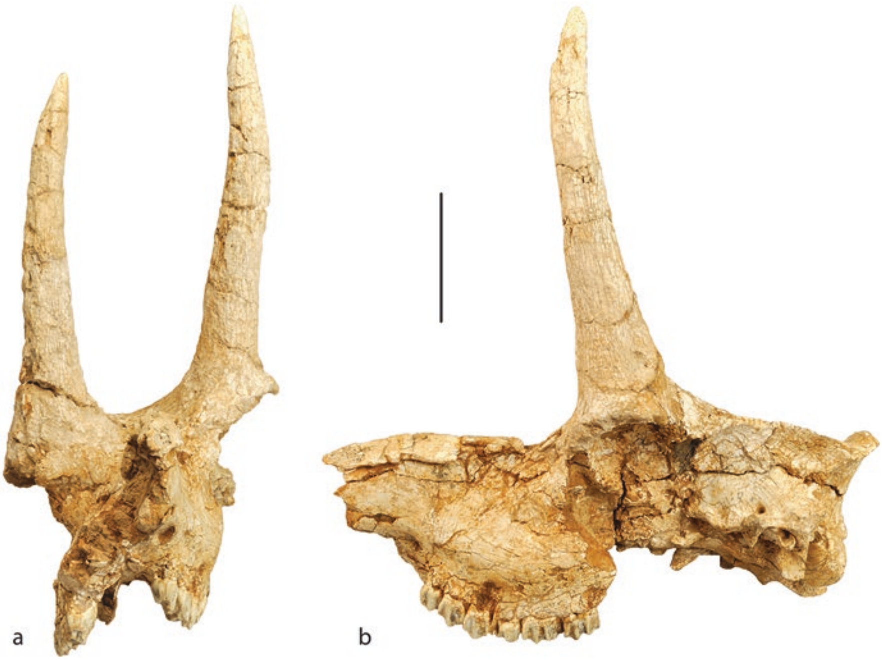

Fig. 7 Cranium of *Palaeotragus inexspectatus* (AMPG SE3–31) from Sésklo. (**a**) Rostral view, (**b**) left lateral view. Scale bar equals 10 cm (photos provided by A Athanassiou)

★*Palaeogiraffa* Bonis and Bouvrain, 2003

Type Species *Decennatherium macedoniae* Geraads, 1989.

Included Taxa *Palaeogiraffa macedoniae* (Geraads, 1989) Bonis and Bouvrain 2003; *Palaeogiraffa pamiri* (Ozansoy, 1965); *Palaeogiraffa major* Bonis and Bouvrain, 2003.

Distribution Late Miocene (Vallesian) of Greece and Turkey (Kostopoulos and Sen 2016).

Comments *Palaeogiraffa* is a genus with a very restricted distribution. Until now, the three species that have been included in the genus have been reported only from three localities in the Axios valley (Pentalophos 1, Xirochori, and Ravin de la Pluie) and two localities in Turkey (Yassiören and Sinap). Rios et al. (2016) in their phylogenetic analysis linked *Palaeogiraffa* with the samothere clade and thus herein we include this taxon in the Palaeotraginae subfamily.

★*Palaeogiraffa macedoniae* (Geraads, 1989)

Nomenclatural and Taxonomical History *Decennatherium macedoniae* Geraads, 1989 (new species); *Palaeogiraffa macedoniae* in Bonis and Bouvrain 2003 (new combination).

Type Material PNT 111, mandible, Museum of Geology, Paleontology, Palaeoanthropology, Univ. of Thessaloniki, Greece (Pl. II, fig. 1, 3 in Geraads 1989).

Type Locality Pentalophos 1, Axios Valley, Greece, late Miocene, Vallesian, MN9–10.

Distribution Besides its type locality, it is found in Turkey (Vallesian, MN9–10).

Taxonomic Remarks It is small in size, and relatively hypsodont *Palaeogiraffa*. The P3 and P4 have a sub-rectangular shape with enlarged lingual sides (Fig. 8). The styles in both molars and premolars are strong and prominent and particularly the metastyle of P3 that projects occlusally. The p4 is molarized with a continuous lingual wall. The posterior part of p3 forms a clear lobe. The canines are slightly bilobed. The limb bones are moderately elongated. Compared to the other two *Palaeogiraffa* species it is the smallest one in size. The short diastema differentiates it from other giraffids. *Samotherium* differentiates from *Palaeogiraffa* in having brachyodont teeth, a relatively long diastema, the shape of the incisors and the canines, the clearly different ulna and radius, the presence of acromion in the scapula (Geraads 1989). The morphology of p3 and particularly the non-isolated and strong mesolingual conid clearly differentiates *P. macedoniae* from *Decenatherium* and *Birgerbohlinia* (Geraads 1989; Rios et al. 2016).

Comments Geraads (1989) identified the differences between *Decenatherium* and the material from Pentalophos 1 and despite the fact that he affiliated the new spe-

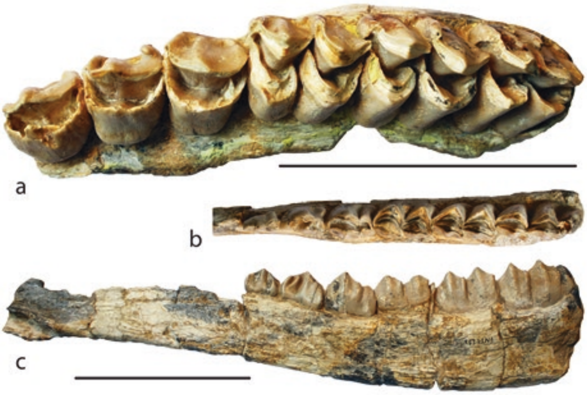

Fig. 8 *Palaeogiraffa macedoniae*: (**a**) Occlusal view of left maxilla with P2–M3 (PNT 145), (**b**) Occlusal view of right mandible with p2–m3 (PNT 111, holotype), (**c**) Lingual view of right mandible with p2–m3 (PNT 111, holotype). Scale bars equal 10 cm

cies he erected to *Decenatherium,* he suggested that the material certainly deserves the erection of a new generic name. *P. macedoniae* was a browser that included also herbaceous monocotyledons in its diet as tooth microwear analysis has shown (Merceron et al. 2018).

Palaeogiraffa pamiri (Ozansoy, 1965)

Nomenclatural and Taxonomical History *Samotherium pamiri* Ozansoy, 1965 (new species); *Palaeogiraffa pamiri* in Bonis and Bouvrain (2003) (new combination).

Type Material MNHN.F.TRQ1031, Maxilla, Muséum national d'Histoire naturelle, Paris (France) (Plate VII, fig. 1 in Ozansoy 1965).

Type Locality Yassiören, Sinap, Turkey, late Miocene, Vallesian.

Distribution Late Miocene (Vallesian, MN10) of Greece and Turkey. In Greece, it has been found in the Vallesian (MN10) of Xirochori (Fig. 2).

Taxonomic Remarks A large-sized giraffid which is considered as relatively medium in size species of *Palaeogiraffa*, having very strong styles. It is larger than *P. macedoniae* and smaller than *P. major*. The lingual cingulum in the upper molars is weak or absent. The lingual wall of DP2 is not bilobed, whereas in DP3 the two lobes are not symmetrical with the anterior lobe being elongated (Fig. 9). A rounded fossa found on the posterior flange of the hypocone of the upper M2 is a feature shared by both *P. pamiri* and *P. major* and which is not present in *P. macedoniae*. The presence of a continuous eocristid in p4 differentiates *P. pamiri* from *Decenatherium* (Kostopoulos and Sen 2016). *Bohlinia attica* is smaller in size than *P. pamiri* having weaker styles and pillars in the upper molars (Bonis and Bouvrain 2003).

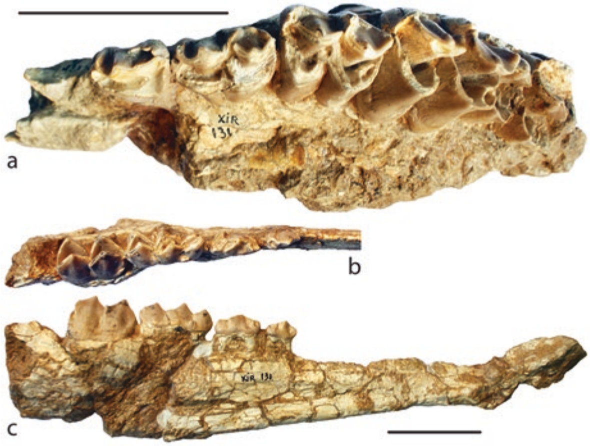

Fig. 9 *Palaeogiraffa pamiri*: (**a**) Occlusal view of left maxilla with DP2–M2 (XIR 131), (**b**) Occlusal view of left mandible with dp2–m1 (XIR 131), (**c**) Lingual view of left mandible with dp2–m1 (XIR 131). Scale bar equals 10 cm

Comments The *P. pamiri* material from Xirochori is rather scarce and consists of juvenile cranial material having the milk molars still attached. Tooth microwear analysis has shown that *P. pamiri* could be identified as a browser (Merceron et al. 2018).

★*Palaeogiraffa major* Bonis and Bouvrain, 2003

Nomenclatural and Taxonomical History *Decennatherium* cf. *pachecoi* Geraads 1979; *Palaeogiraffa major* in Bonis and Bouvrain 2003 (new species).

Type Material RPl 733, right Maxilla with DP2–M1, Museum of Geology, Paleontology & Palaeoanthropology of Thessaloniki University (Greece) (Plate 4 in Bonis and Bouvrain 2003).

Type Locality Ravin de la Pluie, Axios Valley, Greece, late Miocene, Vallesian, MN10.

Distribution Late Miocene (Vallesian, MN10) of Greece (Fig. 2).

Taxonomic Remarks A large-sized giraffid, being the largest of the three species of *Palaeogiraffa*, being even larger than *P. pamiri*. It possesses strong styles both in molars and milk molars. The lingual wall of DP2 is bilobed, whereas in DP3 the two lobes are not symmetrical with the anterior lobe fairly enlarged (Fig. 10). Except for its larger size, *P. major* differs from *P. pamiri* in having a bilobed DP2, a DP3 with a larger anterior lobe, low cingulums, molars that are higher, and the first lobe of dp4 is larger and more symmetrical (Bonis and Bouvrain 2003). The morphology of p3 and particularly the non-isolated and strong mesolingual conid clearly differenti-

Fig. 10 *Palaeogiraffa major*: (**a**) Occlusal view of right maxilla with DP2-M1 (RPL 733), (**b**) Buccal view of left mandible with dp3–m3 (RPL 734, holotype). Scale bar equals 10 cm

ates *P. major* from *Decenatherium* and *Birgerbohlinia* (Geraads 1989; Rios et al. 2016). *P. major* presents a larger second lobe in the deciduous canines than *Decenatherium pachecoi* (Bonis and Bouvrain 2003). *Samotherium* species possess more derived deciduous molars than the *Palaeogiraffa* species, having a much shorter DP3 and a more molarized dp3 (Bonis and Bouvrain 2003). The members of the large "*P. coelophrys*" group differentiate from *Palaeogiraffa* in having weaker styles and stylids in their upper and lower molars and deciduous molars (Bonis and Bouvrain 2003).

Comments The material is scarce and represents mainly subadult individuals. The absence of limb bones makes comparisons with other giraffid taxa rather difficult. Geraads (1979) described this material from Ravin de la Pluie as *Decennatherium* cf. *pachecoi*. Tooth microwear analysis has shown that *P. major* was a browser that included also herbaceous monocotyledons in its diet (Merceron et al. 2018).

★*Samotherium* Forsyth Major, 1888

Type Species *Samotherium boissieri* Forsyth Major, 1888.

Included Taxa *Samotherium boissieri* Forsyth Major, 1888; *Samotherium major* Bohlin, 1926; *Samotherium neumayri* (Rodler and Weithofer, 1890); *Samotherium sinense* (Schlosser, 1903); *Samotherium africanum* Churcher, 1970; *Samotherium eminens* (Alexejev, 1916) Bohlin 1926; *Samotherium mongoliense* Godina, 1954; *Samotherium maeoticum* Korotkevitch, 1978; *Samotherium borissiaki* Godina, 2002; *Samotherium irtyshense* Godina, 1962; *Samotherium korotkevichae* Godina, 2002.

Distribution Late Miocene (Vallesian and Turolian) of Algeria, Libya, Kenya, Greece, Turkey, Moldova, Ukraine, Georgia, Iran, Iraq, Kazakhstan, Kyrgyzstan, Tajikistan, Thailand, and China (NOW database).

Comments The genus includes large-sized palaeotragines.

★***Samotherium boissieri*** **Forsyth Major**, 1888

Type Material M4215, cranium with mandible, Natural History Museum of London (NHML) (fig. 1, p. 318 in Forsyth-Major 1891).

Type Locality MGLS Stefana Hill Samos, Greece, late Miocene, Turolian, MN11.

Distribution Late Miocene (Turolian, MN11–12) of Greece, Turkey, Moldova, and Iraq. In Greece, it has been found in the Turolian (MN11–12) of Samos Island (Qx, Q2, MGLS Stefana hill, Vrysoula, Mytilinii-4 MLN) (Fig. 2).

Taxonomic Remarks *S. boissieri* is a large-sized palaeotragine, nevertheless it can be considered as a medium-sized *Samotherium*. Ossicones are absent from females and which are long and curved caudally in males, located above the orbit (Fig. 11). The orbit is placed rather high above the middle of M3. It has a relatively brachyodont dentition, nevertheless the molars have a relatively higher crown with narrow but well-marked styles. The premolars compared to the molars are smaller in size. The p3 presents a low degree of molarization. The limb bones are weakly elongated. *S. boissieri* is smaller in size than *S. major* and *S. sinense*. According to Geraads (1974), the differences of *S. boissieri* with *S. neumayri* are not quite significant, nevertheless the latter species is considered for the moment a separate taxon. *B. attica* has relatively longer premolar rows and lower tooth crowns and far longer limb bones (Geraads 1974). *Palaeotragus* has shorter premolar rows and except for size differences and the more brachyodont teeth, usually in the upper premolars the paracone is separated from the metacone (Geraads 1974).

Comments Based on tooth microwear, *S. boissieri* has been identified as a seasonal mixed feeder that included herbaceous monocotyledons in its diet (Solounias et al. 2000; Merceron et al. 2018).

Fig. 11 Right lateral view of *Samotherium boissieri* cranium (M4215, holotype) from MGLAS Stefana Hill Samos. Scale bar equals 10 cm (photo provided by DS Kostopoulos)

★***Samotherium major* Bohlin**, 1926

Type Material S90 and S87, Incomplete cranium and left mandible, Senckenbergisches Naturhistorisches Museum-Frankfurt (text fig. 140, Pl. IX, figs. 8–11 in Bohlin 1926).

Type Locality Andrianos ravine Samos, Greece, late Miocene, Turolian, MN12.

Distribution Late Miocene (Turolian, MN12) of Greece and Turkey. In Greece, it has been found in the Turolian (MN12) of Samos (Mytilinii-1B, Mytilinii-1 BC, Mytilinii-3, Mytilinii-6, Q1, Q4, MGLS Andrianos ravine), Axios valley (Vathylakkos 3), Thermopigi (Strymon valley), and Kerassia 1, 3 and 4 (Euboea Island) (Fig. 2).

Taxonomic Remarks *S. major* is a *Samotherium* of great size with long and robust long bones (Fig. 5) but less robust than *H. duvernoyi* and shorter than *S. sinense*. Ossicones are absent from females and are long and inclined caudally in males at different angles, located above the posterior part of the orbit. The orbit is located behind the M3. The p3 is always molarized resembling p4 (Iliopoulos 2003) (Fig. 12). *S. major* was an intermediate-necked giraffid (Danowitz et al. 2015). The always molarized p3 of *S. major* differentiates it clearly from *S. boissieri* and *H. duvernoyi* (Geraads 1994). The fairly larger third lobe of m3 is a character that indicates *H. duvernoyi*. The postcranial elements of *S. sinense* are generally longer than *S. major* (Geraads 1994), while the upper and lower toothrows are evidently longer

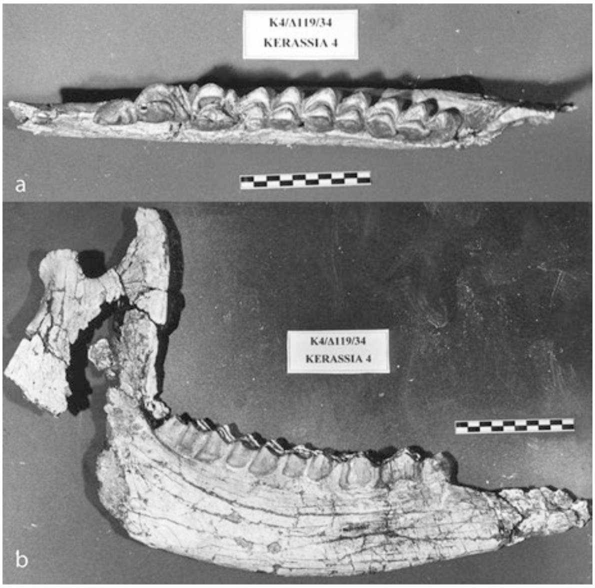

Fig. 12 Occlusal view (**a**) and buccal view (**b**) of a right mandible of *Samotherium major* (K4/Δ119/34) from Kerassia K4. Scale bar equals 10 cm

in *S. major*, as well as the diastema. *S. major* is clearly larger in size and more robust than *S. boissieri* and *S. neumayri*.

Comments *S. major* is a species with a very restricted distribution in Western Eurasia as it has been reported until now only from localities in Greece and Turkey. Both dental mesowear and tooth microwear analysis clearly indicated that *S. major* was a mixed feeder (Solounias et al. 2010; Danowitz et al. 2016).

Sivatheriinae Zittel, 1893

★*Helladotherium* Gaudry, 1860

Type Species *Camelopardalis duvernoyi* Gaudry and Lartet, 1856.

Included Taxa *Helladotherium duvernoyi*; *Helladotherium gaudryi* de Mecquenem, 1924.

Distribution Late Miocene (Vallesian and Turolian) of Greece, Turkey, Bulgaria, Republic of North Macedonia, Hungary, Moldova, Ukraine, Georgia, Iran (The NOW Community 2020), Italy, and France.

★*Helladotherium duvernoyi* (Gaudry and Lartet 1856)

Nomenclatural and Taxonomical History *Camelopardalis duvernoyi* Gaudry and Lartet, 1856 (new species); *Helladotherium duvernoyi* in Gaudry 1860 (new combination).

Type Material MNHN.F.PIK1500 (lectotype), cranium with dentition, Muséum national d'Histoire naturelle, Paris (Pl. XL, fig. 1, Pl. XLII fig. 1 in Gaudry 1862–67).

Type Locality Pikermi, Attiki, Greece, late Miocene, Turolian, MN12.

Distribution Late Miocene (Vallesian, MN10, and Turolian, MN11–13) of Greece, Turkey, Bulgaria, Republic of N. Macedonia, Hungary, Moldova, Ukraine, Georgia, Iran, and France. In Greece, it has been found in the Vallesian (MN10) of Nikiti 1 (Chalkidiki) and in the Turolian (MN11–13) of Samos, Axios valley (Ravin des Zouaves 5, Prochoma, Ravin X), Nikiti 2, Kryopigi (Chalkidiki), Ano Metochi, Thermopigi (Strymon valley), Perivolaki, Alifakas (Magnesia), Pikermi (Attiki), Halmyropotamos, Kerassia (Euboea Island) and Rhodes (Fig. 2).

Taxonomic Remarks *H. duvernoyi* is a large-sized sivatherine having long and fairly robust long bones (Fig. 5). It is a typically brachyodont taxon with relatively long premolar rows (Fig. 13). Styles and pillars of the teeth are fairly strong. The skull is fairly long and the presence of ossicones is still unknown as the only complete skull found until now in Pikermi, belonging presumably to a female individual, has no ossicones. The p3 is always not molarized. It is a very robust animal and

Fig. 13 Occlusal view of a *Helladotherium duvernoyi* cranium (MNHN.F.PIK1501) from Pikermi with P2–M3 on the right maxilla and P3–M3 on the left. Scale bar equals 10 cm

compared to *S. major*, an almost similar in size taxon, its postcranial elements clearly indicate a far more robust giraffid.

Comments *H. duvernoyi* is one of the most common giraffid representatives in the late Miocene faunas of western Eurasia. Postcranial elements show clear sexual dimorphism (Roussiakis and Iliopoulos 2004). Based on tooth microwear analysis *H. duvernoyi* has been identified as a browser (Solounias et al. 2000; Merceron et al. 2018).

Giraffinae Zittel, 1893

★*Bohlinia* Matthew, 1929

Type Species *Camelopardalis attica* Gaudry and Lartet, 1856.

Included Taxa *Bohlinia attica*; *Bohlinia nikitiae* Kostopoulos et al., 1996.

Distribution Late Miocene (Vallesian and Turolian) of Greece, Turkey, Bulgaria, Republic of North Macedonia, Iraq and Iran (The NOW Community 2020).

★*Bohlinia attica* (Gaudry and Lartet, 1856)

Nomenclatural and Taxonomical History *Camelopardalis attica* Gaudry and Lartet, 1856 (new species); *Orasius atticus* in Bohlin 1929 (new combination); *Bohlinia attica* in Geraads 1974 (new combination).

Type Material MNHN.F.PIK2757 (lectotype), almost complete left hind limb, Muséum national d'Histoire naturelle, Paris (France) (Plate XL, fig. 1 left, 5, 6, 8 in Gaudry 1862–67). Lectotype was designated by Geraads in 1979 (p. 378); however, Gentry (2003) commented that the selected specimen was not part of the 1856 type series as it was collected years later, after 1860, therefore the above mentioned lectotype should be reconsidered as a neotype.

Type Locality Pikermi, Attiki, Greece, late Miocene, Turolian, MN12.

Distribution Late Miocene (Vallesian, MN10, and Turolian, MN11–13) of Greece, Turkey, Bulgaria, Republic of North Macedonia, Iraq, and Iran. In Greece, it has been found in the Vallesian (MN10) of Nikiti 1 (Chalkidiki) and Ravin de la Pluie (Axios valley) and in the Turolian (MN11–13) of Axios valley (Ravin des Zouaves 5, Vathylakkos 2, Vathylakkos 3, Dytiko 1, Dytiko 2), Pikermi, Pikermi Valley, Pyrgos Vassilissis (Attiki), and Kerassia 1 (Euboea Island) (Fig. 2).

Taxonomic Remarks *B. attica* is a giraffine of large size with a long neck and very long but slender long bones (Fig. 5). The orbit is placed above the middle of M3. At least the skulls of the males bear a pair of robust ossicones with a wide base, found above the posterior half of the orbits and extending up to the parietals (Fig. 14a). They are slightly curved and inclined caudally. Pneumatization of the frontal bone is observed which extends up to the parietal bones. The profile of the nasal bones is convex. It is a typically brachyodont taxon with comparatively small in size teeth having a low crown. The parastyle of the upper premolars is bifurcated, and the upper molars are wider than long having a weak eperon hypoconal. The upper deciduous molars are long with primitive features. In *Honnanotherium*, the ossicones are straight and rather vertical to the roof of the skull (Kostopoulos et al. 1996).

Comments Postcranial elements of *B. attica* present clearly sexual dimorphism (Roussiakis and Iliopoulos 2004). *B. attica* was characterized as a browser based on its masticatory morphology and tooth microwear analysis (Solounias et al. 1999, 2000; Merceron et al. 2018). A maxilla (CM458) from Samos that has been recently determined as *B. attica* by Parizad et al. (2019) consists probably an erroneous determination. The specimen depicted in their fig. 5 (page 28) most likely belongs to *Palaeotragus*.

★*Bohlinia nikitiae* Kostopoulos, Koliadimou and Koufos, 1996

Type Material NKT-147, cranium part with maxilla and both toothrows, Museum of Geology, Paleontology, Palaeoanthropology, Univ. of Thessaloniki, Greece (fig. 13 in Kostopoulos et al. 1996).

Type Locality Nikiti 1, Chalkidiki, late Miocene, Vallesian, MN10.

Distribution Late Miocene (Vallesian, MN10) of Greece.

Taxonomic Remarks *B. nikitiae* has a skull relatively shorter than *B. attica*. The orbit is found high far from the alveolar level. The ossicones are robust located behind the orbit toward the parietals (Fig. 14b). They are inclined and curved caudally having an elliptical to rounded transverse section, and present strong and deep

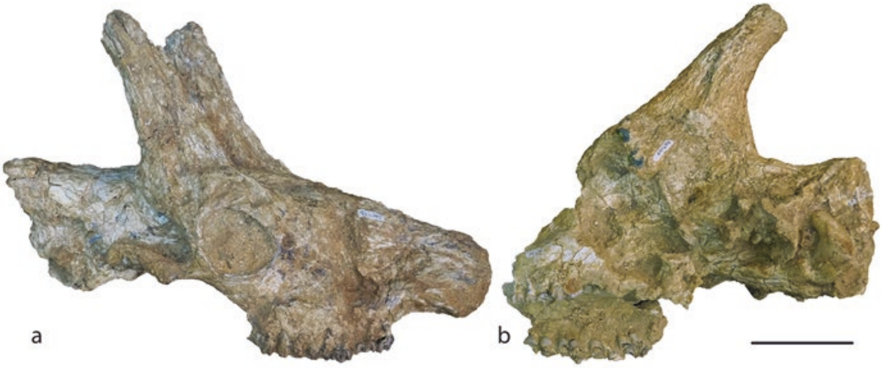

Fig. 14 (**a**) Right lateral view of a *Bohlinia attica* cranium (NKT-148) from Nikiti 1, (**b**) Left lateral view of a *Bohlinia nikitiae* cranium (NKT-147, holotype) from Nikiti 1. Scale bar equals 10 cm

grooves along the external surface. The anterior and posterior carines of the ossicones are weak. Compared to the skull the toothrow is considered long, having rather short premolars relative to the molars. According to Kostopoulos et al. (1996), *B. nikitiae* differs from *B. attica* in the position of the orbit which is placed higher above the alveolar level, the shape of the ossicones' transverse section which is elliptical at the base for *B. nikitiae* and rhomboid for *B. attica*, which becomes in the middle rounded and squarish respectively, the flat posterior end and fine and shallow grooves on the ossicones of *B. attica*, and the relatively short toothrow accompanied by a moderate to long premolar row of *B. attica*. Kostopoulos et al. (1996) observed similarities in the dentition between *B. nikitiae* and the female skull of *P.* cf. *coelophrys* from Ravin de la Pluie.

Comments *B. nikitiae* to date is known only from Nikiti 1. The material referred to this taxon consists a skull and a proximal part of a metacarpal bone. The skull presents a certain degree of damage, being distorted, the front part of the maxilla is broken, the left toothrow is incomplete and a number of teeth of the right one are broken. We believe that more material is needed, including postcranial material, to verify the attribution of this material to *B. nikitiae*, nevertheless we believe that for the time being, *B. nikitiae* should be considered a valid species.

Giraffidae indet.

Except for the determined material that has been assigned to all the taxa mentioned above, there are still a number of giraffid findings from six localities (Melampes, Fourka, Nikiti 2, Kamarella, Drazi, and Nea Silata) that has not been possible to be determined to the species or even to the genus level. Nevertheless, since this is the first comprehensive review of the Greek Giraffidae, it is considered important to discuss these findings further.

The giraffid material that was collected by Kuss in 1975 from the middle Miocene (Astaracian MN6 or MN7–8) locality of Melampes from south Crete Island consists of 5 hindlimb bone parts and a few bone fragments, including a rather well preserved diaphysis and lower epiphysis of a left metatarsal. The long bone parts are elongated and slender indicative of a small-sized giraffid that shows affinities with Palaeotraginae, and taking in mind the age of the locality this giraffid can be considered as a very primitive representative of this group. The material is reported for the first time herein and due to its fragmentary nature it is determined as Palaeotraginae indet.

Lazaridis (2015) in his PhD thesis described giraffid remains from the late Miocene (Vallesian) locality Fourka in Chalkidiki. The studied material consists of two large ossicones, a lower second molar and three long bone parts. The dimensions of the postcranial material are comparable to *S. boissieri* and smaller than those of *H. duvernoyi*. Nevertheless, the morphology of the ossicones indicates similarity with the ossicones of Sivatherinae. As no ossicones of the common west Eurasian *H. duvernoyi* have been found until now, the similarities with the uncommon sivatherine for western Eurasia *Bramatherium*, and the small number of specimens of the studied material, Lazaridis (2015) suggested that Sivatherinae indet. should be considered a suitable assignment for the time being.

Among the giraffid material from the late Miocene (Turolian MN11) locality Nikiti 2 in Chalkidiki, two parts of first phalanges and two juvenile second phalanges have been referred by Kostopoulos (2016) as Palaeotraginae indet., as they are larger than *P. rouenii*, with dimensions similar to *B. attica*, but with a morphology resembling the phalanges of palaeotragines.

Verikiou-Papaspyridakou (1986) in her PhD thesis reported the presence of a left incomplete astragalus belonging to a large giraffid, which she found in a karstic cavity located in Paleocene limestones at the locality Kamarella in Antikythera Island. Verikiou-Papaspyridakou (1986) suggests that this astragalus has been reworked from older deposits. The specimen had been originally determined by E. Thenius as *Camelopardalis* sp. or its synonym *Giraffa* sp. Herein, as the specimen is only known to us by a photograph of the anterior view of the astragalus as it is presented in the PhD thesis of Verikiou-Papaspyridakou (1986), we consider that the specimen should be referred as Giraffidae indet.

In 1947, Mitzopoulos presented in his study on the localities of Euboea Island with Pikermian fauna, fossil mammal bones from the late Miocene (Turolian MN11–13) locality of Drazi that had been collected by A.S.Woodward in 1901. Among the material there were some giraffid remains which Woodward suggested that they should belong to a form related to *Samotherium*. However, due to the fragmented character of the material we consider that this material should be referred as Giraffidae indet. as well.

In 2006, Koufos described a distal part of a metacarpal bone with only the internal condyle still attached on from the latest Miocene (Miocene/Pliocene boundary, late Turolian–early Ruscinian, MN13–14) locality of Nea Silata in Chalkidiki. Koufos (2006) compared the specimen with *Helladotherium* and *Samotherium* metacarpals and he suggested that metrically it could belong either to a *Helladotherium* or a *Samotherium*. Therefore, we consider more appropriate for the specimen to be referred as a large Giraffidae indet.

Acknowledgments We would like to thank Dimitris Kostopoulos and Athanassios Athanassiou for providing the photographs for some of the species mentioned in the text. We would like to thank A. Xafis for valuable comments that helped improving this manuscript.

Appendix

Table with a detail list of the occurrences of giraffid fossils in Greece. Type localities are marked with bold. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB)

Localities[PBDB No]	Age (MN)	Taxon
Karnezeika[202122]	Early Pleistocene, Villafranchian (MN17–MNQ18)	*Palaeotragus inexspectatus*[a]
Haliakmon	Early Pleistocene, Villafranchian (MN17)	*Palaeotragus inexspectatus*[1,2]
Libakos[34764]	Early Pleistocene, Villafranchian (MN17–MNQ19)	*Palaeotragus inexspectatus*[1,2]
Vatera F[183341]	Early Pleistocene, Villafranchian (MN17)	*Palaeotragus inexspectatus*[3,2]
Volax[34593]	Early Pleistocene, Villafranchian (MN17)	*Palaeotragus inexspectatus*[4,2]
Sesklon[34614]	Early Pleistocene, Villafranchian (MN17)	*Palaeotragus inexspectatus*[2]
Dafnero[34594]	Early Pleistocene, Villafranchian (MN17)	*Palaeotragus inexspectatus*[5]
Nea Silata[191612]	Late Miocene, Late Turolian–Early Ruscinian (MN13/14)	Large Giraffidae indet.[6]
Maramena[32189]	Late Miocene, Late Turolian–Early Ruscinian (MN13/14)	*Samotherium* sp.[7]
Rhodes	Late Miocene, Turolian (MN9–13)	*Helladotherium duvernoyi*[8,9]
Alifakas[207134]	Late Miocene, Turolian (MN11–13)	*Helladotherium duvernoyi*[10]
Drazi, Euboea	Late Miocene, Turolian (MN11–13)	Giraffidae indet.[11]
Ano Metochi-2[31924], 3[31928]	Late Miocene, Turolian (MN13)	*Helladotherium* cf. *duvernoyi*[12]
Samos Q5[95690]	Late Miocene, Turolian (MN13)	*Palaeotragus rouenii*[13], *Samotherium major*[13], *Helladotherium duvernoyi*[13]
Dytiko 2[32375]	Late Miocene, Turolian (MN13)	*Palaeotragus rouenii*[14,15] *Bohlinia attica*[14,15]
Dytiko 1[32374]	Late Miocene, Turolian (MN13)	*Bohlinia attica*[15]
Kryopigi[157582]	Late Miocene, Turolian (MN12–13)	*Palaeotragus rouenii*[16], *Helladotherium duvernoyi*[16]
Kamarella, Antikythera	Late Miocene, Turolian	Giraffidae indet.[17]

(continued)

Localities[PBDB No]	Age (MN)	Taxon
Pyrgos Vassilissis[195555]	Late Miocene, Turolian (MN12)	cf. *Palaeotragus* sp.[18], *Bohlinia attica*[18]
Thermopigi[73553]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[19], *Palaeotragus* sp.[19], *Samotherium major*[19], *Helladotherium duvernoyi*[19]
Kerassia 1 Upper[195432]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[20], *Samotherium major*[20], *Helladotherium duvernoyi*[20], *Bohlinia attica*[20]
Kerassia 3[195434], 4 Lower[195435]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[20], *Palaeotragus* sp.[20], *Samotherium major*[20], *Helladotherium duvernoyi*[20]
Pikermi Valley (PV1) [202630]	Late Miocene, Turolian (MN12)	*Bohlinia* cf. *attica*[21]
Pikermi[182754]	Late Miocene, Turolian (MN12)	***Palaeotragus rouenii*[23,24], *Helladotherium duvernoyi*[22], *Bohlinia attica*[22]**
Chomateri[195562]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[25]
Halmyropotamos[202213]	Late Miocene, Turolian (MN12)	*Helladotherium duvernoyi*[26]
Perivolaki[194879]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[27], *Helladotherium duvernoyi*[27]
Samos[207137]	Late Miocene, Turolian (MN12)	***Palaeotragus quadricornis*[28,13]**
MGLS Andrianos ravine, Samos	Late Miocene, Turolian (MN12)	*Palaeotragus coelophrys*[13], *Palaeotragus rouenii*[13], ***Samotherium major*[28]**, *Helladotherium duvernoyi*[13]
Samos Q4[95689]	Late Miocene, Turolian (MN12)	*Samotherium major*[13]
Samos QA[206462]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[13]
Samos Q1[95691]	Late Miocene, Turolian (MN12)	*Palaeotragus coelophrys*[13], *Palaeotragus rouenii*[13], *Samotherium major*[13], *Helladotherium duvernoyi*[13]
Mytilinii 1C[202217]	Late Miocene, Turolian (MN12)	*Samotherium major*[13]
Mytilinii 1B[202216]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[13] *Palaeotragus* sp.[13], *Samotherium major*[13]
Mytilinii 1A[202215]	Late Miocene, Turolian (MN12)	*Palaeotragus rouenii*[13], *Samotherium major*[13], *Helladotherium duvernoyi*[13]
Mytilinii 6	Late Miocene, Turolian (MN12)	*Samotherium major*[13]
Mytilinii 3[202218]	Late Miocene, Turolian (MN12)	*Samotherium major*[13]
Mytilinii 4[202219]	Late Miocene, Turolian (MN12)	*Palaeotragus* sp.[13], *Palaeotragus rouenii*[13], *Samotherium boissieri*[13]
Ravin X[182745]	Late Miocene, Turolian (MN12)	? *Helladotherium duvernoyi*[29]
Prochoma[202222]	Late Miocene, Turolian (MN12)	*Helladotherium duvernoyi*[30]

(continued)

Localities[PBDB No]	Age (MN)	Taxon
Vathylakkos 3[182750]	Late Miocene, Turolian (MN12)	*Samotherium major*[14,15], *Bohlinia attica*[14,15]
Vathylakkos 2[202703]	Late Miocene, Turolian (MN12)	*Bohlinia attica*[15]
Vrysoula, Samos	Late Miocene, Turolian (MN11)	*Samotherium boissieri*[13]
MGLS Stefana hill, Samos	Late Miocene, Turolian (MN11)	*Palaeotragus rouenii*[13], ***Samotherium boissieri***[31,13]
Samos Q2[206460]	Late Miocene, Turolian (MN11)	*Palaeotragus rouenii*[13], *Samotherium boissieri*[13]
Samos Q6[206462]	Late Miocene, Turolian (MN11)	*Samotherium* sp.[32]
Samos Qx[211913]	Late Miocene, Turolian (MN11)	*Samotherium boissieri*[13,32], *Palaeotragus coelophrys*[13,32], *Palaeotragus* sp.[13,32]
Ravin des Zouaves 5[195489]	Late Miocene, Turolian (MN11)	*Palaeotragus rouenii*[33], *Helladotherium duvernoyi*[33], *Bohlinia attica*[33]
Nikiti 2[73869]	Late Miocene, Turolian (MN11)	*Helladotherium duvernoyi*[34], *Palaeotragus rouenii*[34], Palaeotraginae indet.[34]
Nikiti 1[202729]	Late Miocene, Vallesian (MN10)	*Palaeotragus* aff. *berislavicus*[36], *Helladotherium duvernoyi*[35,36], *Bohlinia attica*[35,36], ***Bohlinia nikitiae***[35,36]
Xirochori 1[195490]	Late Miocene, Vallesian (MN10)	*Palaeotragus* sp.[36,37], *Palaeogiraffa pamiri*[36,37]
Ravin de la Pluie[191070]	Late Miocene, Vallesian (MN10)	*Palaeotragus coelophrys*[14,15,37], ***Palaeogiraffa major***[14,15,37], *Bohlinia attica*[14,15,37]
Fourka[202330]	Late Miocene, Vallesian	Sivatherinae indet.[16]
Pentalophos 1[202119]	Late Miocene, Vallesian (MN9–10)	*Palaeotragus coelophrys*[36,38], ***Palaeogiraffa macedoniae***[36,38]
Melampes[208183]	Middle Miocene, Astaracian (MN6 or MN7–8)	Palaeotraginae indet[b]
Thymiana B[202728]	Middle Miocene, Late Orleanian (MN5)	***Georgiomeryx georgalasi***[39,40]

MN Mammal Neogene

[1]Steensma (1988), [2]Athanassiou (2014), [3]de Vos et al. (2002), [4]Sickenberg (1967), [5]Kostopoulos (1996), [6]Koufos 2006, [7]Köhler et al. (1995), [8]Boni (1943), [9]de Bruijn (1976), [10]Melentis and Schneider (1966), [11]Mitzopoulos (1947), [12]de Bruijn (1989), [13]Kostopoulos (2009), [14]Geraads (1978), [15]Geraads (1979), [16]Lazaridis (2015), [17]Verikiou-Papaspyridakou (Verikiou-Papaspyridakou 1986), [18]Böhme et al. (2017), [19]Xafis et al. (2019), [20]Iliopoulos (2003), [21]Theodorou et al. (2010), [22]Gaudry and Lartet (1856), [23]Gaudry (1860), [24]Gaudry (1861), [25]de Bruijn et al. (1999), [26]Melentis (1970), [27]Kostopoulos and Koufos (2006), [28]Bohlin (1926), [29]Arambourg and Piveteau (1929), [30]Bonis et al. (1988), [31]Forsyth Major (1888), [32]Solounias (1981), [33]Koufos (2006), [34]Kostopoulos (2016), [35]Kostopoulos et al. (1996), [36]Laskos (2020), [37]Bonis and Bouvrain (2003), [38]Geraads (1989), [39]Paraskevaidis (1940), [40]Bonis et al. (1997)

[a]Sianis pers. com

[b]This study

References

Alexeiev A (1930) Die obersarmatische Fauna von Eldar. I. *Achtiaria borissiaki* nov. sp. Trav Mus Geol Acad Sci URSS 8:167–204
Alexejev A (1916) Animaux fossiles du village Novo-Elizavetovka. Tipografiya "Technik". pp 453
Arambourg C (1959) Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Mém Serv Carte Géol Algérie, (n.s.). Paléontology 4:1–161
Arambourg C, Piveteau J (1929) Les Vertébrés du Pontien de Salonique. Ann Paléontol 18:59–138
Athanassiou A (2014) New giraffid (Artiodactyla) material from the lower Pleistocene locality of Sésklo (SE Thessaly, Greece): evidence for an extension of the genus *Palaeotragus* into the Pleistocene. Zitteliana B 32:71–89
Bohlin B (1926) Die Familie Giraffidae. Palaeontologica Sinica, Series C 4:178
Böhme M, Spassov N, Ebner M, Geraads D, Hristova L, Kirscher U, Kötter S, Linnemann U, Prieto J, Roussiakis S, Theodorou G, Uhlig G, Winklhofer M (2017) Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe. PLoS One 12(5):e0177347
Boni A (1943) Fauna di *Hipparion* a Rodi. Palaeontographia It 41:23–36
Bonis LD, Bouvrain G (2003) Nouveaux Giraffidae du Miocène supérieur de Macédoine (Grèce). In: Petculescu A, Stiuca E (eds) Advances in vertebrate paleontology "hen to Panta". Romanian Academy, Bucharest, pp 5–16
Bonis LD, Bouvrain G, Koufos GD (1988) Late Miocene mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphical significance. Modern Geol 13:141–147
Bonis LD, Koufos GD, Sen S (1997) A giraffid from the middle Miocene of the island of Chios, Greece. Palaeontology 40:121–134
Borissiak A (1914) Mammifères fossiles de Sébastopol. I: Mem Com Géol 87:105–154
Bosscha-Erdbrink DP (1977) On the distribution in time and space of three giraffid genera with Turolian representatives at Maragheh in N.W. Iran. Proc K Neder Akad Weten B 80(5):337–355
Brisson MJ (1762) Regnum animale, in classes IX distributum sive synopsis methodical. Theodorum Haak, Leiden, 294 pp
Churcher CS (1970) Two new upper Miocene giraffids from fort Ternan, Kenya, East Africa: *Palaeotragus primaevus* n sp and *Samotherium africanum* n sp. Fossil Vertebrates of Africa 2:1–106
Churcher CS (1978) Giraffidae. In: Maglio VJ, Cooke HBS (eds) Evolution of African Mammals. Princeton, Princeton University Press, pp 509–535
Churcher CS (1990) Cranial appendages of Giraffoidea. In: Bubenik GA, Bubenik AB (eds) Horns, pronghorns, and antlers: evolution, morphology, physiology, and social significance. Springer, New York, pp 180–196
Colbert EH (1936) *Palaeotragus* from the Tung Gur formation of Mongolia. Am Mus Novit 874:1–17
Crusafont-Pairó M (1979) Les Girafidés des gisements du Bled Douarah (W. de Gafsa, Tunisie). Not Service Geol 44:7–75
Danowitz M, Domalski R, Solounias N (2015) The cervical anatomy of *Samotherium*, an intermediate-necked giraffid. R Soc Open Sci 2(11):150521
Danowitz M, Sukuan H, Mihlbachler M, Hastings V, Solounias N (2016) A combined-mesowear analysis of late Miocene giraffids from north Chinese and Greek localities of the Pikermian biome. Palaeogeogr Palaeoclimatol Palaeoecol 449:194–204
de Bruijn H (1976) Vallesian and Turolian rodents from Biotia, Attica and Rhodes (Greece) I and II. Proc K Neder Akad Weten, Ser B 79:361–384
de Bruijn H (1989) Smaller mammals from the upper Miocene and lower Pliocene of the Strimon basin, Greece. Rodentia and Lagomorpha. Boll Soc Paleontol It 28:189–195
de Bruijn H, Saraç G, van den Hoek Ostende LW, Roussiakis S (1999) The status of the genus name *Parapodemus* Schaub, 1938; new data bearing on an old controversy. DEINSEA 7:95–112
de Mecquenem R (1924) Contribution à l'étude des fossiles de Maragha. Ann Paléontol 13:135–160

de Vos J, van der Made J, Athanassiou A, Lyras G, Sondaar P, Dermitzakis M (2002) Preliminary note on the late Pliocene fauna from Vatera (Lesvos, Greece). Ann Géol Pays Helléniques 39:37–69
Duvernoy M (1854) Sur des ossements de mammifères fossiles découverts à Pikermi, village près d'Athènes, au pied du mont Pentélique. C R Acad Sci, Paris 38:251–257
Fennessy J, Bidon T, Reuss F, Kumar V, Elkan P, Nilsson MA, Vamberger M, Fritz U, Janke A (2016) Multi-locus analyses reveal four giraffe species instead of one. Curr Biol 26(18):2543–2549
Forsyth Major CI (1888) Sur un gisement d'ossements fossiles dans l'ile de Samos, contemporain de l'âge de Pikermi. C R Acad Sci, Paris 107:1178–1182
Forsyth-Major CJ (1891) On the fossil remains of species of the family Giraffidae. Proc Zool Soc London 59:315–326
Gaudry A (1860) Résultats des fouilles exécutées en Grèce sous les auspices de l'Académie. C R Acad Sci, Paris 51:802–804
Gaudry A (1861) Note sur la Girafe et l' Helladotherium trouvés à Pikermi (Grèce). Bull Soc Géol Fr, Ser. 2 18:587–598
Gaudry A (1862–67) Animaux Fossiles et Géologie de l'Attique. Recherches faites en 1855–1856, 1860. Savy F, Paris
Gaudry A, Lartet E (1856) Sur les résultats de recherches paléontologiques entreprises dans l'Attique sous les auspices de l' Académie. C R Acad Sci, Paris 43:271–274
Gentry AW (2003) Ruminantia (Artiodactyla). In: Fortelius M, Kappelman J, Sen S, Bernor RL (eds) Geology and paleontology of the Miocene Sinap formation, Turkey. Columbia University Press, New York, pp 332–379
Gentry A, Heizmann EPJ (1996) Miocene ruminants of the central and eastern Tethys and Paratethys. In: Bernor RL, Fahlbusch V, Mittmann HW (eds) The evolution of Western Eurasian Neogene mammal faunas. Columbia University Press, New York, pp 378–391
Geraads D (1974) Les giraffidés du Miocène Supérieur de la région de Thessalonique (Grece) [PhD thesis]; Université de Paris VI, Paris
Geraads D (1978) Les Palaeotraginae (Giraffidae, Mammalia) du Miocène supérieur de la région de Thessalonique (Grèce). Géol Méditerranéenne 5:269–276
Geraads D (1979) Le Giraffinae (Artiodactyla, Mammalia) du Miocène supérieur de la région de Thessalonique (Grèce). Bull Mus National d'Hist Nat Paris 4e ser C 1(4):377–389
Geraads D (1986) Remarques sur la systématique et la phylogénie des Giraffidae (Artiodactyla, Mammalia). Geobios 19(4):465–477
Geraads D (1989) Un nouveau giraffidé du Miocène supérieur de Macédoine (Grèce). Bull Mus National d'Hist Nat Paris 4e Ser 11:189–199
Geraads D (1994) Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie. VIII: Giraffidae. Bull Mus National d'Hist Nat Paris 4e Ser C 16(1):159–173
Godina AY (1954) A new extinct giraffe from Mongolia. Tr Paleontol Inst (Moscow) 47:172–180
Godina AY (1962) A new *Samotherium* species from Kazakhstan. Paleontol Zh 1:131–139
Godina AY (1975) *Palaeotragus* from Neogene deposits of Mongolia and middle Asia. In: Academia Nauk USSR (ed) The fossilized fauna and flora of Mongolia. Transactions of unified Soviet-Mongolian Palaeontology, vol 2, pp 67–76
Godina AY (1979) History of fossil giraffes of the genus *Palaeotragus*. Trudy Paleontol Inst Akad Nauk USSR 177
Godina AY (2002) On the taxonomy and evolution of *Samotherium* (Giraffidae, Artiodactyla). Paleontol J 36:395–402
Godina AY, Bajgusheva VS (1985) A new *Palaeotragus* species from the late Pliocene of the peri-Azov region. Paleontol Zh 3:84–89
Gray JE (1821) On the natural arrangement of vertebrate animals. London Medical Repository 15:296–310
Hamilton WR (1978) Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. Phil Trans R Soc London B 283:165–229

Harris J, Solounias N, Geraads D (2010) Giraffoidea. In: Werdelin L, Sanders WJ (eds) Cenozoic mammals of Africa. University of California Press, Berkley, CA, pp 797–811
Heintz E (1976) Les Giraffidae (Artiodactyla, Mammalia) du Miocène de Beni Mellal, Marocco. Geologie Méditerranéenne 3:91–104
Iliopoulos G (2003, Published 2015) the Giraffidae (Mammalia, Artiodactyla) and the study of the histology and chemistry of fossil mammal bone from the late Miocene of Kerassia (Euboea Island, Greece). University of Leicester, UK. ProQuest LLC, UMI195587, Ann Arbor
Janis CM, Scott KM (1987) The interrelationships of higher ruminant families: with special emphasis on the members of the Cervoidea. Am Mus Novit 2893:1–85
Köhler M, Moyà-Solà S, Morales J (1995) The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene), 15. Bovidae and Giraffidae (Artiodactyla, Mammalia). Münch Geowiss Abh A Geol Paläontol 28:167–180
Koken E (1885) Über fossile Saugetiere aus China. Paläeontologische Abhand Bd III 2:85
Korotkevich EL (1957) Giraffes in Hipparion fauna of Berislav. Trudy. Zool Inst Acad Nauk USSR 14:129–140
Korotkevitch EL (1978) A new *Samotherium* species from the Meotian of the northern part of the Black Sea region. Vestnik Zoologii 4:9–18
Kostopoulos DS (1996) The Plio-Pleistocene Artiodactyls of Macedonia (N. Greece). Systematics, Palaeoecology, Biochronology, Biostratigraphy. Unpublished PhD Thesis, Aristotle University of Thessaloniki, Greece
Kostopoulos DS (2009) The late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: new collection: 13. Giraffidae. In: Koufos GD, Nagel D (eds) the late Miocene mammal faunas of Samos. Beit Paläontol 31:299–343
Kostopoulos DS (2016) Artiodactyla. In: Koufos GD, Kostopoulos DS (eds) Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki peninsula, Macedonia, Greece). Geobios 49(1–2):119–134
Kostopoulos DS, Koufos GD (2006) The late Miocene vertebrate fauna from Perivolaki (Thessaly, Greece). 8. Giraffidae. Palaeontographica, Abt A 276:135–149
Kostopoulos DS, Saraç G (2005) The late Miocene mammal locality of Akkaşdaği (Central Anatolia, Turkey). Giraffidae Geodiversitas 27(4):735–745
Kostopoulos DS, Sen S (2016) Suidae, Tragulidae, Giraffidae, and Bovidae, in Sen S. (ed.), late Miocene mam-mal locality of Küçükçekmece, European Turkey. Geodiversitas 38(2):273–298
Kostopoulos DS, Koliadimou K, Koufos GD (1996) The Giraffids (Mammalia, Artiodactyla) from the late Miocene mammalian localities of Nikiti (Macedonia, Greece). Palaeontographica Abt A 239:61–88
Koufos GD (2006) The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. Hellenic J Geosci 41:183–214
Lankester ER (1907) The origin of the lateral horns of the giraffe in foetal life on the area of the parietal bones. Proc Zool Soc London 1907:100–115
Laskos K (2020) The Vallesian large-sized *Palaeotragus* (Giraffidae, Mammalia) from northern Greece. Master thesis, interinstitutional program of postgraduate studies in Palaeontology-Geobiology. School of Geology, Aristotle University of Thessaloniki
Lazaridis G (2015) Study of the Late Miocene Vertebrate Locality of Kryopigi and Other Localities of Kassandra Peninsula, Chalkidiki (Greece). Systematics, Taphonomy, Paleoecology, Biochronology. PhD Thesis, Aristotle University of Thessaloniki. Scientific Annals of the School of Geology 174:350
Lebatard AE, Alçiçek MC, Rochette P, Khatib S, Vialet A, Boulbes N, Bourlès DL, Demory F, Guipert G, Mayda S, Titov VV, Vidal L, de Lumley H (2014) Dating the *Homo erectus* bearing travertine from Kocabaş (Denizli, Turkey) at least 1.1 ma. Earth Planet Sci Lett 390:8–18
Matthew WD (1929) Critical observations upon Siwalik mammals. Bull Am Mus Nat Hist 56:437–560
Melentis JK (1970) Die Pikermifauna von Halmyropotamos (Euböa, Griechenland)—1. Teil: Odontologie und Kraniologie. Ann Géol Pays Helléniques 24:283–411

Melentis JK, Schneider H (1966) Eine neue Pikermifauna in der Niihe der Ortschaft Alifaka in Thessalien. Ann Géol Pays Helléniques 17:267–288
Merceron G, Colyn M, Geraads D (2018) Browsing and non-browsing extant and extinct giraffids: evidence from dental microwear textural analysis. Palaeogeogr Palaeoclimat Palaeoecol 505:128–139
Mitzopoulos MK (1947) Die Verbreitung der Pikermistufe auf der Insel Euboea. Ann Géol. Pays Helléniques 12:209–216
Ozansoy F (1965) Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie. Mem Soc Géol. Fr N Ser 44:1–92
Paraskevaidis I (1940) Eine obermiocäne Fauna von Chios. N Jahrb Mineral Geol Paläontol 83:363–442
Parizad E, Ataabadi MM, Mashkour M, Solounias N (2019) First giraffid skulls (*Bohlinia attica*) from the late Miocene Maragheh fauna, Northwest Iran. Geobios 53:23–34
Pavlow M (1913) Mammifères tertiaires de la Nouvelle Russie. 1re partie. N Mem Soc imp Nat Moscou 17(3):1–72
Petzold A, Hassanin A (2020) A comparative approach for species delimitation based on multiple methods of multi-locus DNA sequence analysis: a case study of the genus Giraffa (Mammalia, Cetartiodactyla). PLoS One 15(2):e0217956
Petzold A, Magnant AS, Edderai D, Chardonnet B, Rigoulet J, Saint-Jalme M, Hassanin A (2020) First insights into past biodiversity of giraffes based on mitochondrial sequences from museum specimens. Eur J Taxon 703:1–33
Pilgrim GE (1911) The fossil Giraffidae of India. Memoirs of the Geological Survey of India 4:1–29
Prothero DR, Schoch RM (2002) Horns, tusks, and flippers: the evolution of hoofed mammals. The Johns Hopkins University Press, Baltimore, MD
Rios M, Sanchez IM, Morales J (2016) Comparative anatomy, phylogeny, and systematics of the Miocene giraffid Decennatheriumpachecoi Crusafont, 1952 (Mammalia, Ruminantia, Pecora): state of the art. J Vertebr Paleontol 36(5):e1187624
Rios M, Sanchez IM, Morales J (2017) A new giraffid (Mammalia, Ruminantia, Pecora) from the late Miocene of Spain, and the evolution of the sivathere-samothere lineage. PLoS One 12(11):e0185139
Rodler A, Weithofer KA (1890) Die Wiederkäuer der Fauna von Maragha. Denks Math Naturwissen Cl K Akad Wissen 57:753–771
Roussiakis S, Iliopoulos G (2004) Preliminary observations on the metrical variation of *Helladotherium duvernoyi* and *Bohlinia attica*. In: 5th International Symposium on Eastern Mediterranean Geology, Thessaloniki, pp 343–346
Samson P, Radulesco C (1966) Sur la présence des Girafidés dans le Villafranchien supérieur de Roumanie. N Jahrb Geol Paläontol Monats 10:588–594
Sánchez IM, Cantalapiedra JL, Ríos M, Quiralte V, Morales J (2015) Systematics and evolution of the Miocene three-horned palaeomerycid ruminants (Mammalia, Cetartiodactyla). PLoS One 10(12):e0143034
Schlosser M (1903) Die fossilen Säugetiere Chinas nebst einer odontographie der rezenten Antilopens. Abh Bayer Akad Wiss Math-Phys Kl 22:220 pp
Sharapov S (1974) *Sogdianotherium*—a new genus of the family Giraffidae from the upper Pliocene of Tadzhikistan. Paleontol J 8(4):517–521
Sickenberg O (1967) Die unterpleistozäne Fauna von Wolaks (Griech.-Mazedonien): I. Eine neue Giraffe (*Macedonitherium martinii* nov. gen. nov. spec.) aus dem Unteren Pleistozän von Griechenland. Ann Géol Pays Helléniques 18:314–330
Solounias N (1981) The Turolian fauna from the island of Samos, Greece, with special emphasis on the Hyaenids and the Bovids. Contributions to Vertebrate Evolution 6:1–232
Solounias N (1988) Prevalence of ossicones in Giraffidae (Artiodactyla, Mammalia). J Mammal 69:845–848

Solounias N (2007) Family Giraffidae. In: Prothero DR, Foss SE (eds) The evolution of artiodactyls. Johns Hopkins University Press, Baltimore, MD, pp 257–277

Solounias N, Moelleken SMC (1993) Dietary adaptation of some extinct ruminants determined by premaxillary shape. J Mammal 74:1059–1074

Solounias N, Plavcan JM, Quade J, Witmer L (1999) The paleoecology of the Pikermian biome and the savanna myth. In: Agusti J, Rook L, Andrews P (eds) The evolution of Neogene terrestrial ecosystems in Europe. Hominoid evolution and climatic change in Europe, vol 1. Cambridge, Cambridge University Press, pp 436–453

Solounias N, McGraw WS, Hayek LAC, Werdelin L (2000) The paleodiet of the Giraffidae. In: Vrba ES, Schaller GB (eds) Antelopes, deer, and relatives. Yale University Press, New Haven, CT, pp 84–95

Solounias N, Rivals F, Semprebon GM (2010) Dietary interpretation and paleoecology of herbivores from Pikermi and Samos (late Miocene of Greece). Paleobiol 36:113–136

Steensma KJ (1988) Plio-/Pleistozäne Großsäugetiere (Mammalia) aus dem Becken von Kastoria/Grevena, südlich von Neapolis—NW Griechenland. Inaugural-Dissertation, Technische Universität Clausthal

Tang Y, Ji H (1983) A Pliocene–Pleistocene transitional fauna from Yuxian, northern Hebei. Vertebrata PalAsiatica 21(3):245–254

The NOW Community (2020) New and Old Worlds Database of Fossil Mammals (NOW). Licensed under CC BY 4.0. Release [09/2017]. http://www.helsinki.fi/science/now/. Accessed 16 Jun 2020

Theodorou GE, Roussiakis S, Athanassiou A, Filippidi A (2010) Mammalian remains from a new site near the classical locality of Pikermi (Attica, Greece). In: Proceedings of the XIX CBGA congress, Thessaloniki, Greece. Scientific Annals, School of Geology, Aristotle University of Thessaloniki, vol 99, pp 109–119

Verikiou-Papaspyridakou E (1986) Geomorphological study of the area of Maleas Cape-Kythera-Antikythera-Gramboussa. Unpublished PhD Thesis, National and Kapodistrian Univ Athens, Greece

Wagner R (1861) Nachträge zur Kenntniss der fossilen Hufthier-Ueberreste von Pikermi. Sitzunberichte Bayer Akad Wiss 2:78–82

Weithofer A (1888) Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. Beit Paläontol Oesterreich-Ungarns 6(3):225–292

Xafis A, Tsoukala E, Solounias N, Mandic O, Harzhauser M, Grimsson F, Nagel D (2019) Fossil Giraffidae (Mammalia, Artiodactyla) from the late Miocene of Thermopigi (Macedonia, Greece). Palaeontol Electronica 22(3.68):1–38

Zittel KA (1893) Handbuch der Paläontologie. Vertebrata (Mammalia), vol 4. R. Oldenbourg, Munich and Leipzig