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

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Abstract

The peri-Mediterranean and western Asian Plio-Pleistocene faunas are characterised by the sporadic presence of a palaeotragine taxon with a complex nomenclatural history, usually referred to the genus *Mitilanotherium*. Due to its rarity, its morphological characters are incompletely known. Recently excavated giraffid material in the Lower Pleistocene locality of Sésklo (Thessaly, Greece) includes an almost complete skull that provides a better knowledge of the taxon's morphology. The skull is long with a proportionally elongate postorbital part. Dorsally it is very wide, and has a markedly flat cranial roof. The long ossicones emerge supraorbitally and are widely separated. The dentition is brachyodont with short premolar section with regard to other palaeotragines. A stratigraphically associated atlas is very large and robust, implying a very powerful neck.

As indicated by the comparisons based on the new material, the samples previously referred to *Mitilanotherium* and related genera form a homogeneous conspecific group, similar to the Late Miocene palaeotragine species, especially those of the genus *Palaeotragus*. The main common features include the presence of simple supraorbital cranial appendages, the long postorbital part of the skull, and the long and slender metapodials. The implied close phylogenetic relationship between *Mitilanotherium* and *Palaeotragus* points to the synonymy between them, extending the stratigraphic range of *Palaeotragus* into the Pleistocene. *Palaeotragus* is a long lived, morphologically conservative genus spanning from about 10–11 to almost 1 million years ago. The Plio-Pleistocene species, *P. inexspectatus*, was adapted to open and dry habitats of the peri-Mediterranean and SW Asian region.

Key words: Giraffidae, *Palaeotragus*, *Mitilanotherium*, cranial morphology, biochronology, Early Pleistocene, Villafranchian, Greece.

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1. Introduction

An impoverished family in recent times, represented by only two genera —*Giraffa* Linnaeus, 1758 and *Okapia* Lankester, 1902— and confined to sub-Saharan Africa, Giraffidae exhibited a rich taxonomic diversity during the Neogene, across a much wider biogeographic range in the Old World. The family is united by a single synapomorphy, the bilobed structure of the lower canines, the crown of which consists of a larger mesial and a smaller distal lobe (Bohlin 1926; Hamilton 1978; Geraads 1986a; Solounias 2007). Other characters that most giraffids have in common are the large body size, the presence of permanent, unbranched cranial appendages of dermal origin (ossicones), the brachyodont dentition with very long diastema and relatively long premolar section, the long neck and limbs, and a distinct metatarsal morphology (low and flat articular facet for the cubonavicular, distally open groove along the dorsal face, concave plantar face, strongly reduced lateral metatarsals) (Bohlin 1926; Hamilton 1978; Geraads 1986a; Janis & Scott 1987; Solounias 2007).

The origins of Giraffidae remain rather obscure, though a descent from an African, *Gelocus*-like form is probable (Janis & Scott 1987; Gentry 1994). The first fossils referred to this family were recovered from Lower Miocene deposits in the North and East Africa (Churcher 1978; Gentry et al. 1999; Harris et al. 2010). By the Middle Miocene, the giraffids were already established in southern Europe, having considerably expanded their geographic range (Godina 1979). The migration to new environments brought about an increase in taxonomic diversity, which reached its peak during the Late Miocene. Genera like *Bohlinia*, *Helladotherium*, *Bramatherium*, *Samotherium* and *Palaeotragus* are known from numerous localities in North Africa and southern Eurasia, constituting a significant faunal element of that age. Nevertheless, giraffids are generally less abundant

in the fossil record compared to other non-giraffid ruminant genera. After the end of the Miocene, however, they experienced a dramatic loss in taxonomic diversity, and until recently Ruscinian (Early Pliocene) and Villafranchian (Late Pliocene to Early Pleistocene) giraffids were largely unknown or only scarcely present in Eurasian and N. African fossil faunas, mostly from fragmentary material.

The currently available finds from post-Miocene localities of this geographic region are separated in two groups, mainly based on size: A larger-sized group is metrically similar to *Giraffa* and is found in Middle East and North Africa (Textfig. 1). The available samples are scanty in most cases and are tentatively referred to *G. pomeli* Arambourg, 1979 (in N. African and Middle East localities) and to *G. jumae* Leakey, 1965 (in Çalta, Turkey) (Geraads 1981, 1998). A smaller-sized and more homogenous group of palaeotragine affinities is known under various generic and specific names in the Northern Mediterranean and peri-Pontic regions, as well as in Central Asia (Textfig. 1). In the most recent studies this latter group is usually referred to the genus *Mitilanotherium* Samson & Radulesco, 1966 (Kostopoulos & Athanassiou 2005; Garrido & Arribas 2008; van der Made & Morales 2011), with an implied or clearly expressed suggestion that it also belongs to the same species, *M. inexspectatum* Samson & Radulesco, 1966 (Kostopoulos & Athanassiou 2005; van der Made & Morales 2011). A new cranial specimen presented here among other finds strengthens this view. Moreover, the new material suggests a further synonymy of *Mitilanotherium* with *Palaeotragus*, as

there are no sufficient differences to justify a taxonomic distinction at the genus level.

1.1 Post-Miocene Palaeotraginae

A palaeotragine giraffid was first recognized in Eurasian Villafranchian deposits by Samson & Radulesco (1966), who restudied dental and postcranial material from Fîntîna lui Mitilan and Valea Grăunceanului (Oltenia, SW Romania), previously erroneously referred to the bovid species *Pliotragus ardeus*. They erected a new genus and species, *Mitilanotherium inexspectatum* Samson & Radulesco, 1966, based on these finds. Almost concurrently, and apparently unaware of Samson & Radulesco's publication, Sickenberg (1967) erected another new giraffid taxon, *Macedonitherium martinii*, on cranial and postcranial material from Vólax (Macedonia, N. Greece). Later on, Sharapov (1974) based a third new genus and species, *Sogdianotherium kuruksaense*, on a fairly complete skull from Kuruksay, Tajikistan. Some other finds from the European and Asian territories of the former Soviet Union, notably those from Liventsovka (Sea of Azov region, Russia), were described as *Palaeotragus (Yuorlovia) priasovicus* Godina & Bajgusheva, 1985, or referred to as *Palaeotragus* sp., assuming a close phylogenetic relationship with the Miocene *Palaeotragus* species (Godina 1979, 1981; Godina & Bajgusheva 1985; Bajgusheva & Titov 2002; Titov 2008).

The giraffid samples collected during the last decades in Villafranchian localities of Greece and

Textfigure 1: Geographic distribution of post-Miocene giraffid-bearing localities of North Africa and W. Eurasia: 1: Huélago, 2: Fonelas, 3: Ternifine, 4: Ain Hanech, 5: Ain Brimba, 6: Fîntîna lui Mitilan, 7: Valea Grăunceanului, 8: Libákos, 9: Haliákmon Q-Profil, 10: Dafneró, 11: Sésklo, 12: Vólax, 13: Vaterá, 14: Kocabaş, 15: Gülyazı, 16: Etulia, 17: Çalta, 18: 'Ubeidiya, 19: Liventsovka, 20: Dmanisi, 21: Kuruksay, 22: Esekartkan. At least two additional Pliocene sites with *Palaeotragus* sp. are located further east, in Transbaikalia and Mongolia (Godina 1981, cited in Vislobokova 2008), and are not included in the map. Localities marked black have yielded samples of the large-sized group, while the white marks denote the palaeotragine-bearing sites. Data according to Haas (1966), Samson & Radulesco (1966), Sickenberg (1967), Sharapov (1974), Sickenberg (1975), Arambourg (1979), Geraads (1981), Godina & Bajgusheva (1985), Geraads (1986b), Steensma (1988), Kostopoulos (1996), David (1997), Geraads (1998), Arribas et al. (2001), Bajgusheva & Titov (2002), de Vos et al. (2002), Vekua et al. (2008), Vislobokova (2008), van der Made & Morales (2011) and Boulbes et al. (2014). Graphical scale: 500 km. Composite satellite image source: Google Maps.

Turkey (notably Libákos, Dafneró, Sésklo and Vaterá) were usually identified with Sickenberg's species (Sickenberg 1975; Sickenberg & Tobien 1977; Steensma 1988; van der Meulen & van Kolfschoten 1988; Athanassiou 1996; Kostopoulos 1996), except for the Vaterá sample, which was tentatively attributed to *M. inexspectatum* (see de Vos et al. 2002). In a subsequent revision of the Plio-Pleistocene giraffids from Greece Kostopoulos & Athanassiou (2005) included all above species in the genus *Mitilanotherium*, but they were hesitant to accept a species-level synonymy implied by the comparison of the available samples, pending new fossil discoveries.

Given the eastern European and Asian distribution of the above mentioned localities, the discovery of a very similar giraffid, preliminarily referred to as *Mitilanotherium* sp., in the Spanish locality of Fonelas was quite surprising (Arribas et al. 2001). A more detailed study of the findings corroborated this taxonomic attribution (Garrido 2006; Garrido & Arribas 2008), while more recently *M. inexspectatum* was identified on dental material from another Spanish site, Huélago (van der Made & Morales 2011).

1.2 The Sésklo locality and fossil fauna

The locality of Sésklo (Magnesia, Thessaly, Greece, 39.368°N, 22.851°E, Textfig. 2) is a clay quarry employed by *Heracles General Cement Company* as a raw material source. It is located in a basin of the Mesozoic metamorphic basement filled with fluvio-lacustrine clayey sediments with sporadic coarser clastic material intercalations (channel deposits). Since 1971 numerous mammal fossils have come to light during the quarrying works, particularly during a large-scale collection in 1982. Subsequent excavations and fossil collections have yielded a diverse

Table 1: Faunal list of the Early Pleistocene locality of Sésklo (Thessaly, Greece), according to Symeonidis (1992), Athanassiou (1996, 2002a,b), more recent unpublished research data, and the present study.

Aves
    Struthio sp.
Rodentia
    cf. *Hystrix*
Carnivora
    Ursus etruscus Cuvier, 1823
    Nyctereutes megamastoides (Pomel, 1843)
    Vulpes alopecoides Forsyth Major, 1875
    Pliocrocuta perrieri (Croizet & Jobert, 1828)
    Homotherium crenatidens (Fabrini, 1890)
Proboscidea
    Anancus arvernensis (Croizet & Jobert, 1828)
    Mammuthus meridionalis (Nesti, 1825)
Perissodactyla
    Equus stenonis Cocchi, 1867
    Stephanorhinus sp.
Artiodactyla
    Croizetoceros ramosus (Croizet & Jobert, 1828)
    cf. *Dama rhenana* (Dubois, 1904)
    Eucladoceros sp.
    Palaeotragus inexspectatus (Samson & Radulesco, 1966)
    Gazella borbonica Depéret, 1884
    Gazella bouvrainae Kostopoulos, 1996
    Gazella aegaea Athanassiou, 2002
    Gazellospira torticornis (Aymard, 1854)
    Gallogoral meneghinii sickenbergii Kostopoulos, 1997
    Euthyceros thessalicus Athanassiou, 2002
    Antilopinae indet.
    Bovidae indet.
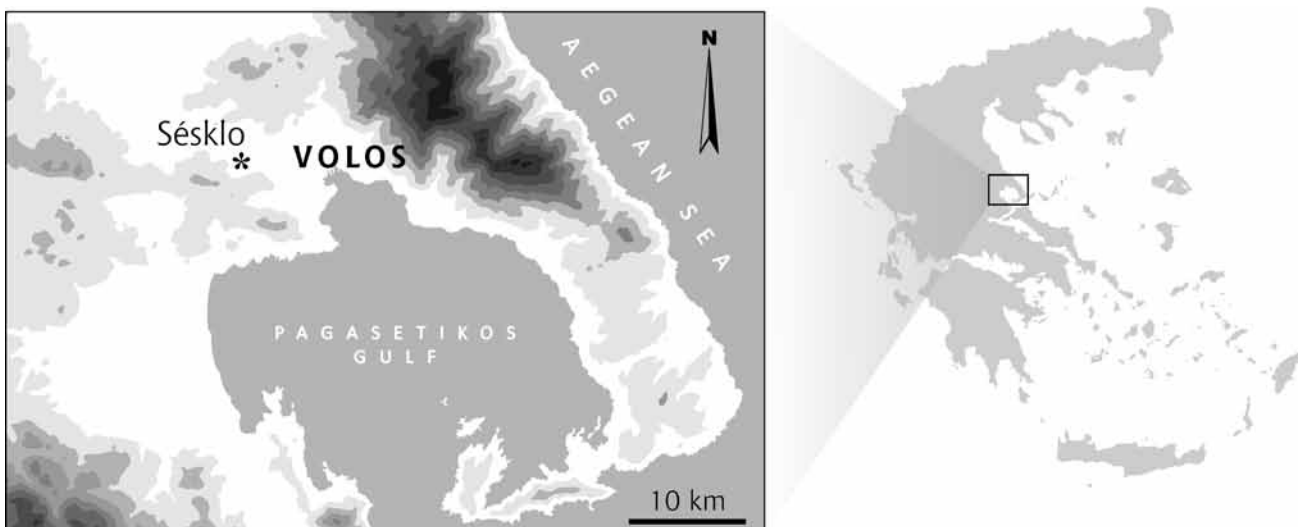
Textfigure 2: Map of Greece, indicating the geographic location of the Sésklo locality (asterisk), NE of the homonymous village, W of the Magnesia's capital city Vólos. Locality coordinates: 39.368°N, 22.851°E (WGS84 datum). Contour interval: 200 m.

Early Pleistocene mammal fauna, biochronologically dated in the lower part of European Land Mammal Zone MN17 as defined by Mein (1990), or in MNQ17 as defined by Guérin (1990) (Athanassiou 1996). The faunal list, according to Symeonidis (1992), Athanassiou (1996, 2002a,b) and as revised by more recent data and the present study, is given in Tab. 1. A small part of the fauna that includes the proboscidean and the avian fossils comes from different, possibly stratigraphically lower sites in the same quarry than the rest of the fauna and may be slightly older. The Sésklo fauna is dominated by horses (*Equus stenonis*) and exhibits a high diversity of antelopes. The faunal composition, as well as ecomorphological and palaeodietary studies, indicate a generally open and dry environment, punctuated by open woodland or thickets (Athanassiou 1996; Rivals & Athanassiou 2008).

2. Material and methods

A recent excavation carried out in April and May 2009 in the Sésklo quarry revealed a heterogeneous accumulation of tightly packed fossil skeletal elements in a clayey matrix. The fine matrix material and the prevailing orientation of the long bones indicate that the fossils accumulated by a low-energy water stream of N-S direction. The association comprises mainly horse remains, but fine specimens belonging to antelopes and carnivores (hyenas, a machairodont and a fox) also exist. The new site in the quarry is topographically very close, and quite probably at a closely adjacent stratigraphical level, with respect to the main site exploited in 1982, the stratigraphic level of which is not precisely known. Given the continuous and fairly rapid sedimentation in the fluvial basin, it is unlikely that the new material differs biochronologically from that collected in 1982.

A prominent specimen among the new finds is an almost complete giraffid skull, which is the main subject of the present study. The skull is associated with two other giraffid skeletal remains, an atlas and a metatarsal fragment. All three specimens belong to the collections of the Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, as does the rest of the Sésklo material. The skull is the first virtually complete giraffid cranial specimen from the Pleistocene of Europe, and offers new data on the morphology of this rare taxon.

The description of the finds is based on standard anatomical terminology (König & Liebich 2004; I.C.V.G.A.N. 2005). The cranial appendages are conventionally called "ossicones", although it is still unresolved if their anatomy, ontogeny and use were similar to the true ossicones of the extant giraffids (Geraads 1986a, 1991; Solounias 1988; see also Section 3.2).

All measurements are in mm with an accuracy of up to one decimal digit, when possible. The use of parentheses in the tables denotes an inaccurate or estimated measurement because of specimen distortion or incomplete preservation. To avoid ambiguities about the cited sources, citations to figures, plates, tables etc. of referenced publications are given in lowercase (e.g. pl. 1, fig.1), while citations to figures etc. of the present paper are given with a capital first letter (e.g. Textfig. 1, Pl. 1, Fig. 1, Tab. 1).

Institutional abbreviations: AMPG: Museum of Palaeontology and Geology, National and Kapodistrian University of Athens; ISERB: Institute of Speleology "Emil Racoviţă", Bucharest; LGPUT: Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki; MGL: Geological Museum, Lausanne; MSU: Moscow State University; NHML: Natural History Museum, London; NHMW: Natural History Museum, Vienna; MNHNP: National Natural History Museum, Paris.

3. Systematic palaeontology

Family Giraffidae Gray, 1821
Subfamily Palaeotraginae Pilgrim, 1911
Genus *Palaeotragus* Gaudry, 1861
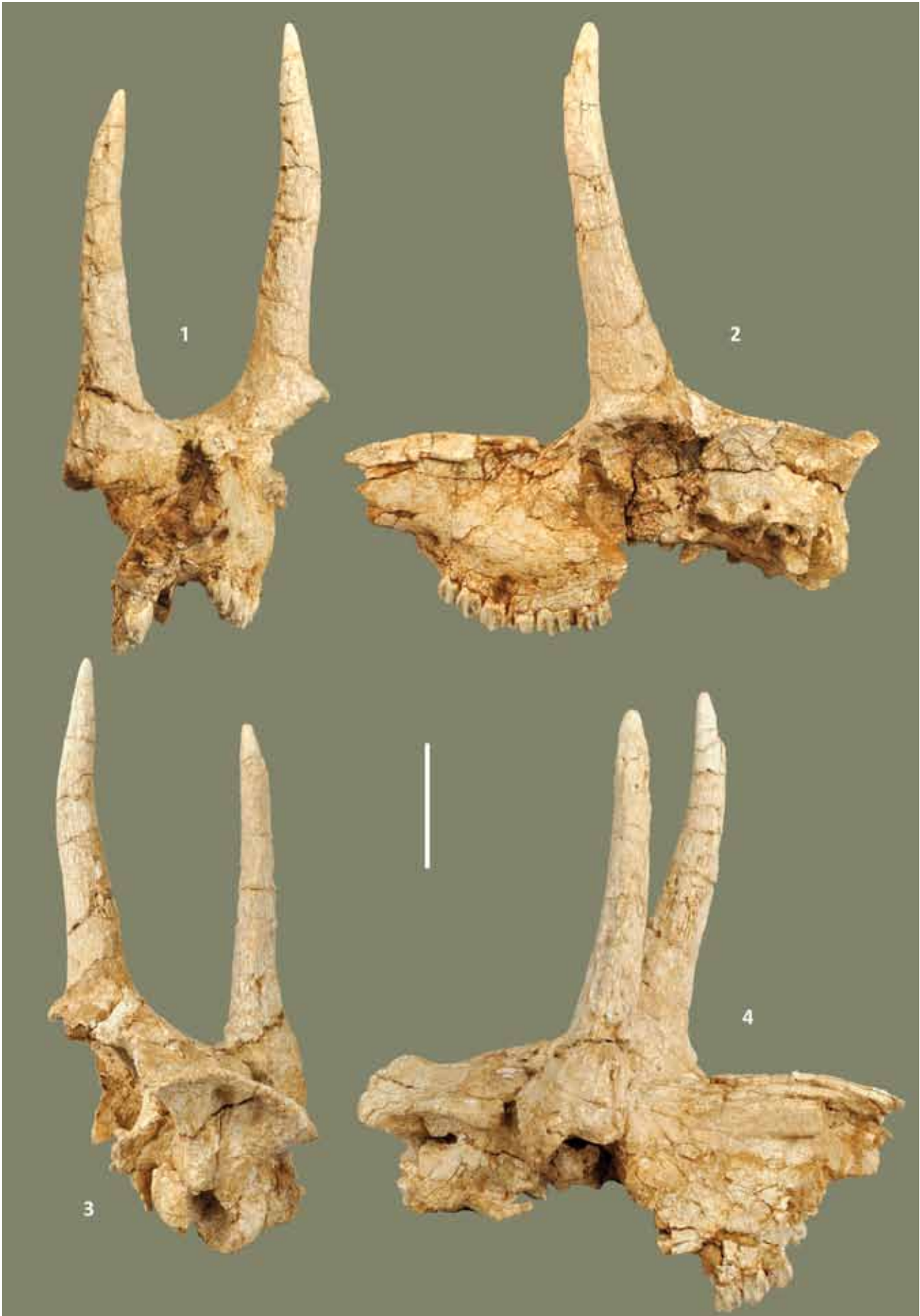
Type species: *Palaeotragus rouenii* Gaudry, 1861

Genus diagnosis (based on Geraads 1974 and Churcher 1978): Giraffids of small to medium size. Skull wide with long postorbital cranial part. Ossicones simple, paired, upright, subparallel to each other, pointed, slightly curved and widely separated, borne on frontals in supraorbital position. Frontals concave between the ossicones. Diastema long; dentition brachyodont, premolar section proportionally long. Metapodials elongate with concave palmar/plantar faces.

Palaeotragus inexspectatus
(Samson & Radulesco, 1966)
(Plates 1–2)

Holotype: distal part of left m3 (№ 5227, ISERB).

Synonymy:
1965   *Pliotragus ardeus* (Depéret) pro parte — Bolomey: p. 319, figs 5–8.
1966   *Mitilanotherium inexspectatum* n. gen. n. sp. — Samson & Radulesco: p. 589, fig. 1.
1967   *Macedonitherium martinii* n. gen. n. sp. — Sickenberg: p. 314, pl. 1, fig.1, pl. 2, figs 1–5.
1971   *Macedonitherium* sp. — Sickenberg & Tobien: p. 60.
1974   *Sogdianotherium kuruksaense* n. gen. n. sp. — Sharapov: p. 517, figs 1–2.
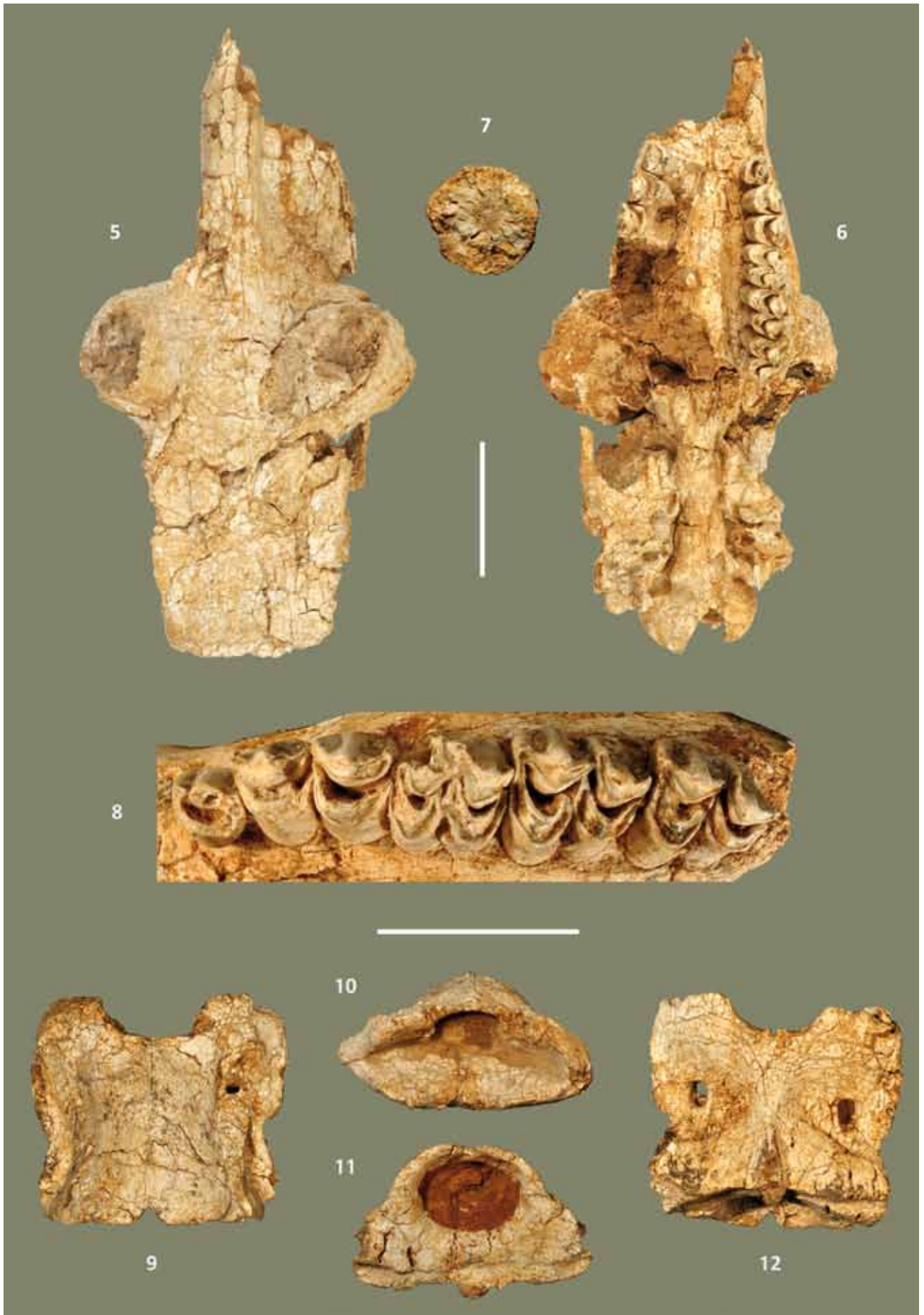1975   *Macedonitherium martinii* — Becker-Platen, Sickenberg & Tobien: p. 43.

Plate 1: *Palaeotragus inexspectatus*, skull SE3-31, Sésklo, AMPG: **(1)** rostral view; **(2)** left lateral view; **(3)** caudal view; **(4)** right rostrolateral view. Graphical scale: 10 cm.

Table 2: Cranial measurements (in mm) of *Palaeotragus inexspectatus* from Sésklo, SE3-31, AMPG, compared to those of cranial specimens from Vólax (AMPG 980), Kuruksay (according to Sharapov 1974) and Liventsovka (according to Bajgusheva & Titov 2002; Titov 2008). Parentheses indicate inaccurate or estimated values; the asterisk indicates a similar, but not indubitably identical measurement method. The maximal preserved lengths of the Sésklo and Kuruksay specimens are not comparable because the preserved cranial parts are different in each specimen.

	Sésklo	Vólax	Kuruksay	Liventsovka
maximal preserved length (rostral nasal end – nuchal crest)	448	—	424	—
mesial margin of P2 – caudal margin of occipital condyles	348	—	—	—
mesial margin of P2 –middle of the nuchal crest (measured parallel to the skull's longitudinal axis)	355	—	344	—
distal margin of M3 – caudal margin of occipital condyles	208	—	—	—
rostral margin of choanae – caudal margin of occipital condyles	239	—	—	—
postorbital length (midpoint between the ossicone bases – middle of the nuchal crest)	199	—	200	—
width of the maxilla at the level of P4 / M1	>107	—	—	—
maximal width (at the lateral orbital rims)	(237)	—	—	—
width at the lateral margins of the ossicone bases	(197)	204	159	—
dorsal width at the level of the caudal orbital margin	(152)	—	142	—
width at the nuchal crest	123	—	—	—
width at the mastoid processes	149	—	—	—
width of the occipital condyles	(91)	—	—	106
width at the lateral margins of the jugular processes	112	—	—	138*
praeorbital height (teeth excluded)	136	—	—	—
postorbital height	96	—	—	99.1
occipital height	130	—	—	115
left ossicone height	302	204	—	—
right ossicone height	295	202	260*	—
left ossicone basal minimal diameter	49	50	—	—
right ossicone basal minimal diameter	49	50	46	—
dental series length (P2–M3)	141	—	139	—

Plate 2: *Palaeotragus inexspectatus*, skull SE3-31, Sésklo, AMPG: (**5**) dorsal view, ossicones removed along postdepositional fracture surfaces; (**6**) ventral view. Graphical scale: 10 cm. (**7**) ossicone cross section, at the ossicone's apical third. Graphical scale: 5 cm. (**8**) left dental series, occlusal view. Graphical scale: 5 cm. *Palaeotragus inexspectatus*, atlas SE3-68, Sésklo, AMPG: (**9**) dorsal view (cranial side is at the top); (**10**) cranial view; (**11**) caudal view; (**12**) ventral view (cranial side is at the top). Graphical scale: 10 cm.

1977   *Macedonitherium martinii* Sickenberg, 1967 — Sickenberg & Tobien: p. 32.

1985   *Macedonotherium martini* — Alexejeva & Motuzko: p. 109.

1985   *Palaeotragus priasovicus* n. sp. — Godina & Bajgusheva: p. 84, fig. 1.

1988   *Macedonitherium martinii* Sickenberg, 1967 — van der Meulen & van Kolfschoten: fig. 3.

1988   *Macedonitherium martinii* Sickenberg, 1967 — Steensma: p. 228, pl. 10, figs 1–3.

1988   Palaeotraginae gen. et sp. indet. — Steensma: p. 231, pl. 10, fig. 4.

1988   Giraffidae gen. et sp. indet. — Steensma: p. 233, pl. 10, fig. 5.

1996   *Mitilanotherium martinii* (Sickenberg, 1967) — Kostopoulos: p. 44, pl. 2.

1996   cf. *Macedonitherium martinii* Sickenberg, 1967 — Athanassiou: p. 95, fig. 43, pl. 4, figs 4–5.

2001   Giraffidae cf. *Mitilanotherium* sp. — Arribas et al.: pp. 17, 22, pl. 2, fig. 2.

2002   *Mitilanotherium* cf. *inexpectatum* Samson & Radulesco, 1966 — de Vos et al.: p. 45.

2002   *Palaeotragus (Yuorlovia) priasovicus* — Bajgusheva & Titov: p. 360, figs 1–2.

2004   *Mitilanotherium* nov. sp. aff. *M. martinii* — Arribas et al.: p. 573, tab. 1, fig. 3E.

2004   *Mitilanotherium* Samson y Radulesco, 1966 — Garrido & Arribas: p. 77.

2005   *Mitilanotherium martinii* (Sickenberg, 1967) — Kostopoulos & Athanassiou: p. 186, figs 8–9, pl. 4, figs 4–5.

2006   *Mitilanotherium* sp. — Garrido: p. 406, figs 100–103, 107.

2008   *Mitilanotherium* sp. — Garrido & Arribas: p. 400, figs 1–4, 7.

2008   *Palaeotragus (Yuorlovia) priasovicus* Godina & Bajgusheva, 1985 — Titov: pp. 147, 229, figs 66–67, pls 10–11.

2008   *Palaeotragus rouenii* Gaudry, 1861 — Vekua et al.: p. 104, figs 1–4.

2009   *Mitilanotherium* sp. — Arribas et al.: fig. 5.

2011   *Mitilanotherium inexspectatum* Samson & Radulesco, 1966 — van der Made & Morales: p. 617, fig. 3.

2014   *Palaeotragus* sp. — Boulbes et al.: p. 62, fig. 2n.

Note that in many publications the species name *M. inexspectatum* is erroneously spelled as *M. inexpectatum*. The spelling of *Macedonitherium martinii* also varies, particularly in the Russian literature.

Referred specimens: skull, SE3-31; atlas, SE3-68; metatarsal III-IV shaft, SE3-44.

3.1. Description

3.1.1. Skull

The studied skull (Pl. 1; Pl. 2, Figs 5–8) is nearly complete. Although it has undergone postdepositional distortion and fracturing, it preserves some easily breakable anatomical parts as the ossicones and the basicranial processes, but lacks its rostral part (praemaxillae and parts of the maxilla and the nasals), both zygomatic arches (except for the right zygomatic process of the temporal bone) and the right molars. It was deposited lying on its left side and has suffered a certain degree of lateral compression, particularly at its rostral part, as a result of the overlying sediment pressure. It is also distorted in a direction subparallel to the sagittal plane, the right side having been shifted ventrally; this is more evident in the praeorbital part. It is probable that it remained at least partly exposed for a certain period of time, as the right (upper) side has signs of weathering and seriously damaged toothrow.

The specimen is dolichocephalic with long, narrow praeorbital and very long postorbital part. As it was observed in postdepositionally fractured surfaces, the frontal area is moderately pneumatised with numerous sinuses, which, however, do not result in an inflation of the frontals, as it is the case in the recent *Giraffa*. The sinuses extend well into the bases of the ossicones (Pl. 2, Fig. 5).

In lateral view (Pl. 1, Figs 2, 4) the skull exhibits an almost straight dorsal profile; its praeorbital and postorbital parts form an extremely obtuse angle of more than 160°. The nasal profile is slightly convex dorsally and almost parallel to the toothrow. There is no conspicuous ethmoidal fissure. The maxilla is very high at the dental region, but tapers abruptly rostrally, becoming slender rostrally of P2. The dental alveoli series forms a markedly convex arc, so that the central teeth (e.g. M1) are positioned considerably more ventrally than the anterior and posterior ones. A large infraorbital foramen opens in front of P2. The orbits are positioned centrally, with their rostral end situated just above the mesial lobe of M3; their dorsal wall is completely covered by the ossicones. The zygomatic arch was quite slender, as inferred by the preserved zygomatic process of the temporal bone. Caudally to the ossicones the dorsal profile is markedly straight, delineated by the strongly laterally protruding parietal crests, and ending in a prominent nuchal crest. The temporal fossa is long rostrocaudally and moderately concave. The jugular processes extend ventrally below the ventral condylar margin.

In rostral view (Pl. 1, Fig. 1) the most striking character is the extreme lateral position of the ossicones on the laterally protruding orbital roofs, slightly medially to the lateral orbital rims. Their bases are located essentially more laterally than the dentition. The frontal area between the ossicones is concave.

In dorsal view (Pl. 2, Fig. 5) the skull exhibits a relatively narrow praeorbital part, and then broadens abruptly at the level of the orbits. At this point the skull attains its maximal breadth. The laterally positioned ossicone bases occupy most of the central dorsal area. The noticeably flat postorbital dorsal surface is trapezoid in shape, delineated laterally by the prominent, straight parietal crests, and becoming gradually narrower toward the nuchal crest. Its caudal area becomes slightly concave before rising again to form the nuchal crest.

In ventral view (Pl. 2, Fig. 6) the palate appears rostrally narrow, widening progressively till the level of M1. The choanae reach the level of the M2/M3 contact. The basioccipital is very wide caudally, because of the massiveness of the occipital condyles,

but its rostral part narrows progressively. A sagittal groove runs along its ventral surface and ends caudally between the condyles. The basioccipital separates from the temporal bone by a very deep petro-occipital fissure that merges caudally with the ventral condylar fossa. The auditory bullae are not preserved; it seems that they were well separated from the paroccipital processes.

In caudal view (Pl. 1, Fig. 3), the occipital region is dorsally broad and fan shaped. It is constricted at mid level, and then broadens again at the level of the large occipital condyles. The squamous part of the occipital is marked by a pair of deep fossae for the attachment of the nuchal ligaments, situated medially, on either side of the median sagittal plane, under the nuchal crest. The paroccipital processes are long and mediolaterally flattened. Their apices extend ventrally more than the ventral margin of the condyles. The cranial dimensions are given in Tab. 2.
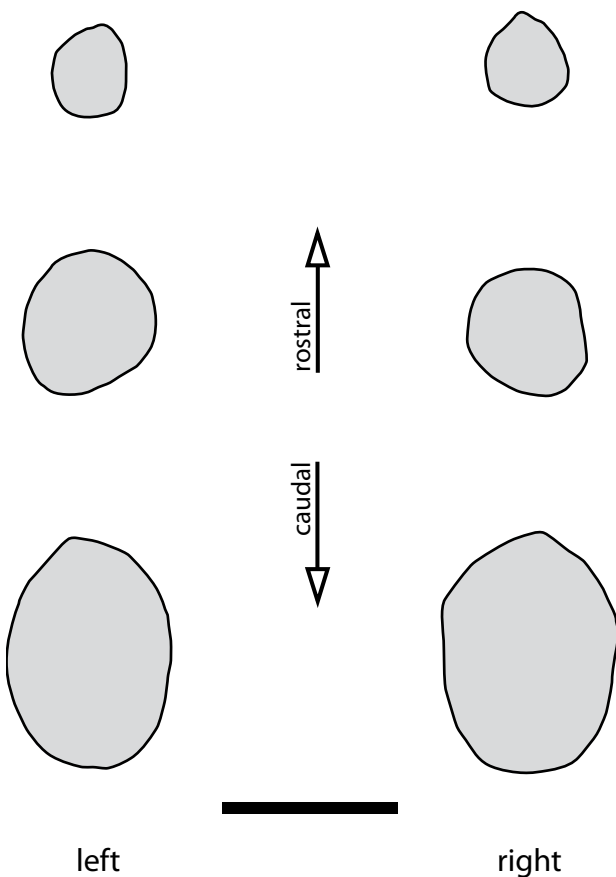
Textfigure 3: Ossicone cross-sectional morphology of the *Palaeotragus inexspectatus* cranial specimen SE3-31 from Sésklo (AMPG). The sections were taken near the base, at the middle, and near the apex of each ossicone. Graphical scale: 50 mm.

3.1.2. Ossicones

The ossicones are very long and of large diameter, indicating that the specimen belongs to a male individual (assuming a sexual dimorphism similar to that observed in other palaeotragines). They are in-

serted right above the orbits and in extreme lateral position, their lateral side almost concurring with the dorsolateral orbital rim (Pl. 1, Figs 1, 3). Their bases extend strongly caudally, lowering progressively till they reach the neurocranial dorsal surface. Basally they are almost straight, subparallel to each other and rostrally inclined, but their apical part exhibits a weak caudomedial curve. Their surface is in general moderately rugose (in certain lateral regions more deeply grooved) except for the apices, which are smooth. This morphology is very similar to the one observed in the recent *Okapia*, where the lower rugose part is covered with skin, while the skinless apical part is polished due to wear (Lankester 1907). However, unlike *Okapia*, there is no transverse constriction under the apex. The ossicone cross section is elliptical near the base to almost circular towards the apex (Textfig. 3), its long axis directing caudomedially–rostrolaterally. The lateral side is flatter than the medial one, while there is a subtle "keel" on the rostral side. The ossicone bone is dense, particularly near the outer surface, but it is penetrated by the frontal sinuses near the ossicone base (Pl. 2, Fig. 5). Above the base it becomes much more compact (Pl. 2, Fig. 7). The ossicone dimensions are given in Tab. 2.

3.1.3. Dentition

The dentition (Pl. 2, Fig. 8) is moderately brachyodont, as the unworn molars' height is estimated to have been clearly smaller than their maximal length (mesiodistal diameter) or maximal width (linguolabial diameter). The premolar series is rather short for a giraffid: it makes up 42% of the dentition, while the premolar/molar ratio is 0.68. The enamel is finely rugose, particularly on the lingual sides of the teeth. There are extensive cement deposits, mainly on the labial walls. All teeth have prominent labial styles and paracone and metacone ribs on their labial wall, which weaken progressively towards the base of the crown. In labial view, the occlusal relief is high and the cusps rounded (characterisation according to Fortelius & Solounias 2000: fig. 1).

The premolars are large. The lingual and labial crescents do not fuse to each other in P3 and P4. The distal flange of the lingual crescent is flat lingually, resulting in a trapezium-shaped occlusal surface, particularly in P2 and P4, with almost parallel lingual and labial sides. This indicates that there is an incipient separation of the lingual crescent into two cusps, a mesial and a distal one. The left P3, but not the right one, has a medial pointed enamel fold projecting into the distal part of the central fossette.

The molars are preserved only on the left side. All, even the more worn M1, exhibit generally unfused lingual and labial crescents on the occlusal surface; only the mesial wall of all molars is closed, while the same is true for the distal wall of M1. There is a very weak mesiolingual cingulum in all molars, as well as

a weak lingual one that forms a small entostyle between the molar lobes. The lingual cusps tend to be rather pointed lingually, but become blunt near the base of the crown. The labial wall is markedly uneven, because of the presence of prominent styles and cusp ribs; the paracone ribs are always much more salient than the metacone ones. In occlusal view the distal lobes of M2 and M3 are oblique, that is somewhat rotated clockwise, in relation to the mesial lobe. The dental dimensions of SE3-31 are given in Tab. 3.

Table 3: Dental measurements (in mm) of *Palaeotragus inexspectatus* from Sésklo, SE3-31, AMPG. *Length* stands for the mesiodistal maximal diameter, *width* for the linguolabial maximal one. Parentheses indicate an inaccurate value.

		left	right
P2	length	18.0	18.4
	width	19.4	19.8
P3	length	20.8	20.1
	width	24.2	25.1
P4	length	18.9	19.5
	width	26.6	—
M1	length	(27.4)	—
	width	—	—
M2	length	31.8	—
	width	31.3	—
M3	length	30.5	—
	width	31.5	—
dental series length (P2–M3)		141.0	—
premolar series length (P2–P4)		59.5	62.2
molar series length (M1–M3)		87.4	—
premolar/molar ratio		0.68	—

3.1.4. Atlas

A giraffid atlas (SE3-68) found about 40 cm east of the skull's caudal end belongs certainly to the same species, and quite possibly to the same individual. The latter cannot be confirmed, however, as the two specimens are distorted in different directions and their articular faces could not match each other anymore. The atlas is almost complete (Pl. 2, Figs 9–12), lacking only the caudolateral processes at the caudal ends of the wings (*alae atlantis*). It is a massive bone, having approximately the shape of a flattened cylinder, without any prominent processes. The dorsal arc is markedly convex, while the ventral one is almost flat, particularly caudally (Pl. 2, Fig. 11). The tube-shaped vertebral foramen is situated in the

dorsal half of the bone. The cranial side appears low and flattened because of a dorsoventral distortion (Pl. 2, Fig. 10). The very wide articular surfaces for the occipital condyles are separated dorsally by a rather thin bony arc and ventrally by a narrow median groove. The dorsal tubercle has the form of a weak sagittal crest, which disappears gradually towards the caudal end of the bone. The lateral wings are weak with concave lateral margins. The alar foramina are small; there are no transverse foramina, as in other ruminants. The ventral face (Pl. 2, Fig. 12) is laterally concave, forming deep fossae that open laterally. Between them there is a median ridge that ends caudally to a sagittally elongated ventral tubercle; the latter is broken, but does not seem to have been strong. The caudal face (Pl. 2, Fig. 11) is flat and subtriangular in shape. The ventral arc is massive, extending laterally. The dorsal one remains thin and has a median incision at its apex. The maximal preserved length is 118 mm, the maximal width is 128 mm at the cranial end and >118 mm at the caudal end, and the dorsoventral diameter (height) is about 81 mm (inaccurate, measured caudally).

SE3-68 is clearly larger, but morphologically very similar to S-1149 (MGL) from Samos (Adrianos) referred to *Palaeotragus rouenii*. The latter is less symmetrical craniocaudally, having more prominent wings and carrying a large dorsal tubercle at its cranial end. Otherwise the two specimens do not differ, being particularly similar in the morphology of the cranial and caudal faces. SE3-68 appears to be larger than an atlas described by Sharapov (1974) as *Sogdianotherium kuruksaense*, who measured it at 80 mm long and 89 mm wide, but these metrical data may be inaccurate since the accompanying sketch (Sharapov 1974: fig. 2c) figures a damaged specimen. A specimen described by Bohlin (1926: p. 56–57, textfigs 67, 68) and referred to *Samotherium sinense* is wider but shorter than SE3-68, having a less elongated shape, has a much more slender ventral arc and a larger vertebral foramen. The same author (Bohlin 1926: p. 85) gives additional measurements for three specimens attributed to *S. boissieri*; SE3-68 is metrically closer to the largest of them. Geraads (1974: tab. VI) gives measurements of atlas specimens from Maragheh referred to *S. neumayri*, all of which are somewhat larger than SE3-68. The same holds for two atlases from Maragheh (site K2) referred to as *S. boissieri sinense* (Bosscha Erdbrink 1978: fig. 1, tab. 2). In comparison to two atlases from Samos assigned to *S. major* (Kostopoulos 2009: p. 320–321, pl. 2, fig. 1) the studied specimen is more elongate but more robust, it is lower dorsoventrally, and has similar or somewhat smaller width. It also differs in the shape of the median incision at the caudal end of the dorsal arc, which is much deeper and more open in the figured specimen from Samos (Kostopoulos 2009: pl. 2, fig. 1). The large dimensions of the Sésklo atlas are mainly a result of its thick arcs (especially the massive ventral one)

and imply a very robust neck and are consistent with the strong occipital and prominent parietal crests of the skull.

3.1.5. Metatarsal

A 335-mm-long metatarsal part that was found under the skull has a typical giraffid morphology, that is large dimensions, slenderness, and the presence of a fairly deep trough along its plantar face. The specimen lacks both articular ends, preserving most of the bone shaft. The cross-section dimensions are fairly constant; at about the middle of the bone they measure 39 mm (dorsoplantar diameter) and 38 mm (mediolateral diameter) respectively. These are somewhat larger than the corresponding dimensions of the six already known specimens (three from Romania, one from Dafneró, one from Fonelas and another one from Sésklo) all of which have a minimal shaft width of about 33–36 mm (Samson & Radulesco 1966; Athanassiou 1996; Kostopoulos 1996; Garrido 2006).

3.2. Comparisons

The studied skull with its flat dorsal surface and the supraorbital, laterally positioned ossicones is characterised by a typical palaeotragine morphology (Geraads 1986a; Harris et al. 2010). It differs from the extant *Giraffa* mainly in the absence of advanced frontal pneumatisation, the position, shape and number of the ossicones, the laterally protruding orbits, and its somewhat smaller size. It is larger than *Okapia*, the latter also having more rostrally positioned orbits (with regard to the dentition), pronounced frontal inflation and more caudally positioned ossicones. Further, the ossicones of SE3-31 differ in structure from the recent ones, being overall less dense, particularly near the ossicone's axis. They may also had different development patterns, as it is questioned whether the palaeotragine ossicones ossified from a dermal cartilage and then fused to the skull in a later ontogenetic stage (as in extant *Giraffa* and *Okapia*), or are mere frontal bone outgrowths (see Geraads 1986a, 1991 and Solounias 1988 for arguments from both sides).

Compared to extinct genera, it is readily distinguished from large-sized giraffids, such as the sivatheres (e.g. *Sivatherium*, *Bramatherium*, *Helladotherium*) by its much smaller size, as well as by its very different, simple ossicones. *Bohlinia* Matthew, 1929, a Late Miocene genus morphologically close to *Giraffa*, has a less elongated postorbital cranial region, somewhat narrower skull and conical ossicones, unlike SE3-31. *Giraffokeryx* Pilgrim, 1910, a genus that has been frequently considered as a palaeotragine, has two pairs of ossicones, one praeorbital and one postorbital, a significant difference from the ossicone arrangement seen in the studied specimen. Ano-

ther rare four-horned form, *Schansitherium* Killgus, 1922, has a different ossicone configuration, featuring a supraorbital pair, quite probably homologous to that of *Palaeotragus* and *Samotherium*, another pair on the rostral end of the frontals, as well as a median bony protuberance on the parietal (Killgus 1922; Bohlin 1926: p. 80–81). Although its cranial and dental morphology is otherwise palaeotragine, it differs markedly in these characters from the studied skull, which is also smaller.

The subfamily Palaeotraginae commonly comprises two Late Miocene genera, which count among the best known fossil giraffids: *Palaeotragus* Gaudry, 1861 and *Samotherium* Forsyth Major, 1888. Both comprise several named species across the Old World. *Samotherium* includes the large-sized members of the subfamily, being also distinguished from *Palaeotragus* by its reduced postorbital cranial region, increased hypsodonty and proportionally shorter premolar section (Geraads 1974: p. 23, 1986a). The best known *Samotherium* species (*S. boissieri*, *S. major*, *S. neumayri*, *S. sinense*) are significantly larger than SE3-31 in dental dimensions (Textfig. 4), but they have comparable premolar/molar ratios: the average ratio of the *S. boissieri* sample is 0.69 (based on metrical data in Bohlin 1926; Iliopoulos 2003; Kostopoulos 2009), almost equal to 0.68 of the Sésklo skull.

Compared to *Palaeotragus*, SE3-31 is larger than the smaller species, including the type species *P. rouenii*, being dimensionally closer to the larger *coelophrys–quadricornis* group (Textfig. 4). It differs from most samples of both groups, however, in having a shorter premolar section with regard to the molar one. Indeed, most published *Palaeotragus* upper dentitions have premolar/molar ratios higher than 0.72 (Bohlin 1926; Geraads 1978; Iliopoulos 2003; Kostopoulos 2009), but samples with lower ratios also occur: Geraads (1974: p. 39) assigns to *Palaeotragus* a premolar/molar ratio range of 0.67–0.81, while a single specimen referred to *P. coelophrys* has very similar tooth measurements to those of SE3-31 (Textfig. 4; Bohlin 1926: p. 27). This means that SE3-31 has proportionally shorter premolars than the average Late Miocene *Palaeotragus* and falls close to the minimum of the genus' range.

In terms of general cranial morphology, SE3-31 shares with both genera, *Palaeotragus* and *Samotherium*, the same configuration of a broad and dorsally flat skull, with simple, supraorbital, parallel to each other ossicones. Its size and proportions are though closer to *Palaeotragus*, because *Samotherium* is larger and has a less elongated postorbital region (Textfig. 5). A difference from Late Miocene forms is found in the relative development of the parietal crests, which are very strong and protrude laterally in the study specimen. This character, together with the enlarged atlas, may be related to the large ossicones, which are stronger than in most Late Miocene palaeotragines. In comparison
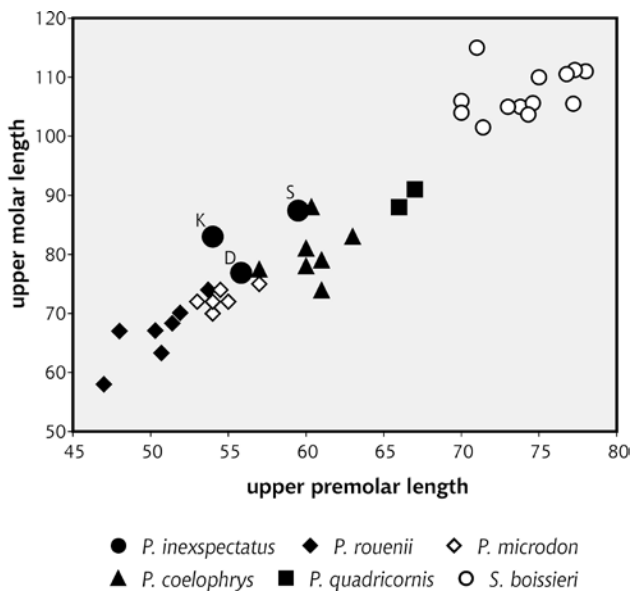
Textfigure 4: Scatter diagram of the premolar to molar series length (in mm) of the palaeotragine species *Palaeotragus rouenii* (Pikermi, Samos, Dytikó – Bohlin 1926; Geraads 1978; Iliopoulos 2003; Kostopoulos 2009), *P. microdon* (China – Bohlin 1926), *P. coelophrys* (China, Maragheh, Ravin de la Pluie – Bohlin 1926; Geraads 1978), *P. quadricornis* (Maragheh – Bohlin 1926), and *Samotherium boissieri* (Samos – Bohlin 1926; Iliopoulos 2003) in comparison to *P. inexspectatus* from Kuruksay (K) (Sharapov 1974), Dmanisi (D) (Vekua et al. 2008) and Sésklo (S) (SE3-31, AMPG). The Kuruksay data are inaccurate, as the corresponding specimen has incompletely preserved dentition.

to *Palaeotragus* specimens, such as those referred to *P. rouenii*, SE3-31 has somewhat more caudally positioned orbit with regard to the molar series position. Yet the most noticeable difference constitutes the ossicone direction: in SE3-31 the ossicones are inserted with a rostral inclination, in contrast to the caudally-inclined ossicones of *Palaeotragus* and *Samotherium* (Textfig. 5). It seems, however, that there is a considerable variation in this character, the various known *Palaeotragus* specimens exhibiting a certain degree of variation in ossicone inclination, curvature and relative development (Textfig. 5D–G), including a rostrally inclined ossicone variant (see Bohlin 1926: p. 9).

The available post-Miocene palaeotragine cranial specimens are very few, the most important being the almost complete skull from Kuruksay (holotype of *Sogdianotherium kuruksaense*; Sharapov 1974). According to Sharapov's short description and outline sketches (unfortunately the author does not provide any photographic documentation) this specimen is morphologically and metrically very similar to the Sésklo skull in all cranial characters, including the rostral ossicone inclination and the prominent parietal crests (Textfig. 5; Tab. 2). The only appreciable difference is found in its shorter ossicones, although their basal diameters are similar. Another cranial specimen, the frontlet AMPG 980 from Vólax (holotype of *Macedonitherium martinii*; Sickenberg 1967) carries

even shorter ossicones, again having essentially the same basal diameter (Textfig. 5; Tab. 2).

Two more cranial specimens were found at Liventsovka (Sea of Azov region, Russia) and referred to *Palaeotragus priasovicus* by Bajgusheva & Titov (2002) and Titov (2008). One preserves the caudal part of the skull, the other the ossicone and part of the orbit. The skull fragment (ОП-1887; Bajgusheva & Titov 2002: fig. 1; Titov 2008: pl. X) is remarkably similar to SE3-31, exhibiting a very wide and flat cranial roof, protruding parietal crests and very strong occipital region with prominent nuchal crest. The metrical differences (Tab. 2) are very small and are mostly due to the distortion of the Sésklo specimen. The Liventsovka ossicone (MSU 186; Bajgusheva & Titov 2002: fig. 2; Titov 2008: fig. 66) preserves its basal half and part of the orbital wall. Since the authors identify it as a right one, it must be rostrally inclined, as the Kuruksay, Vólax and Sésklo specimens. Bajgusheva & Titov (2002) and Titov (2008) estimate its length to 200 mm (similar to the Vólax find) and give an unoriented basal diameter of 60 mm, noting that the basal cross section is subtriangular rather than elliptical. This is cited as the main distinguishing character between the Liventsovka ossicone and those from Vólax and Kuruksay, and it seems that it also distinguishes it from SE3-31, although the actual difference may be subtle.

The famous palaeoanthropological locality of Dmanisi, Georgia, has also yielded giraffid remains usually referred to as *Palaeotragus* sp. in faunal lists and papers dealing with the human fossils of the site. In a publication describing the available specimens (an upper dentition, two ossicones, and four partly preserved metapodials) Vekua et al. (2008) assigned them to the Turolian species *Palaeotragus rouenii*, despite the Early Pleistocene age of the site. According to the authors' metrical data, the dentition is 10% smaller than the SE3-31 one, also having proportionally longer premolar section (the premolar/molar ratio is 0.73; see also Textfig. 4). Its size is comparable to that of the maxilla part DFN-28 from Dafneró (LGPUT; Kostopoulos 1996: fig. 2-6; Kostopoulos & Athanassiou 2005: p. 187). The rest of the finds are very similar dimensionally to the corresponding material from Sésklo: The ossicones have a transverse basal diameter of 49–50 mm, as is the case in the Sésklo and Vólax specimens, and a total measurable length of 217 and 256 mm, being intermediate between the specimens from the aforementioned Greek localities. The metapodials are larger than those of the Turolian *P. rouenii* and metrically close to those referred to *P. inexspectatus* (Textfig. 6). Taking into account the metrical comparisons, as well as the age and geographic location of Dmanisi, the giraffid material from this locality is better assigned to *P. inexspectatus*.

A single ossicone specimen from Denisli, W. Turkey, described very recently and referred to *Palaeotragus* sp. (Boulbes et al. 2014), preserves its apical
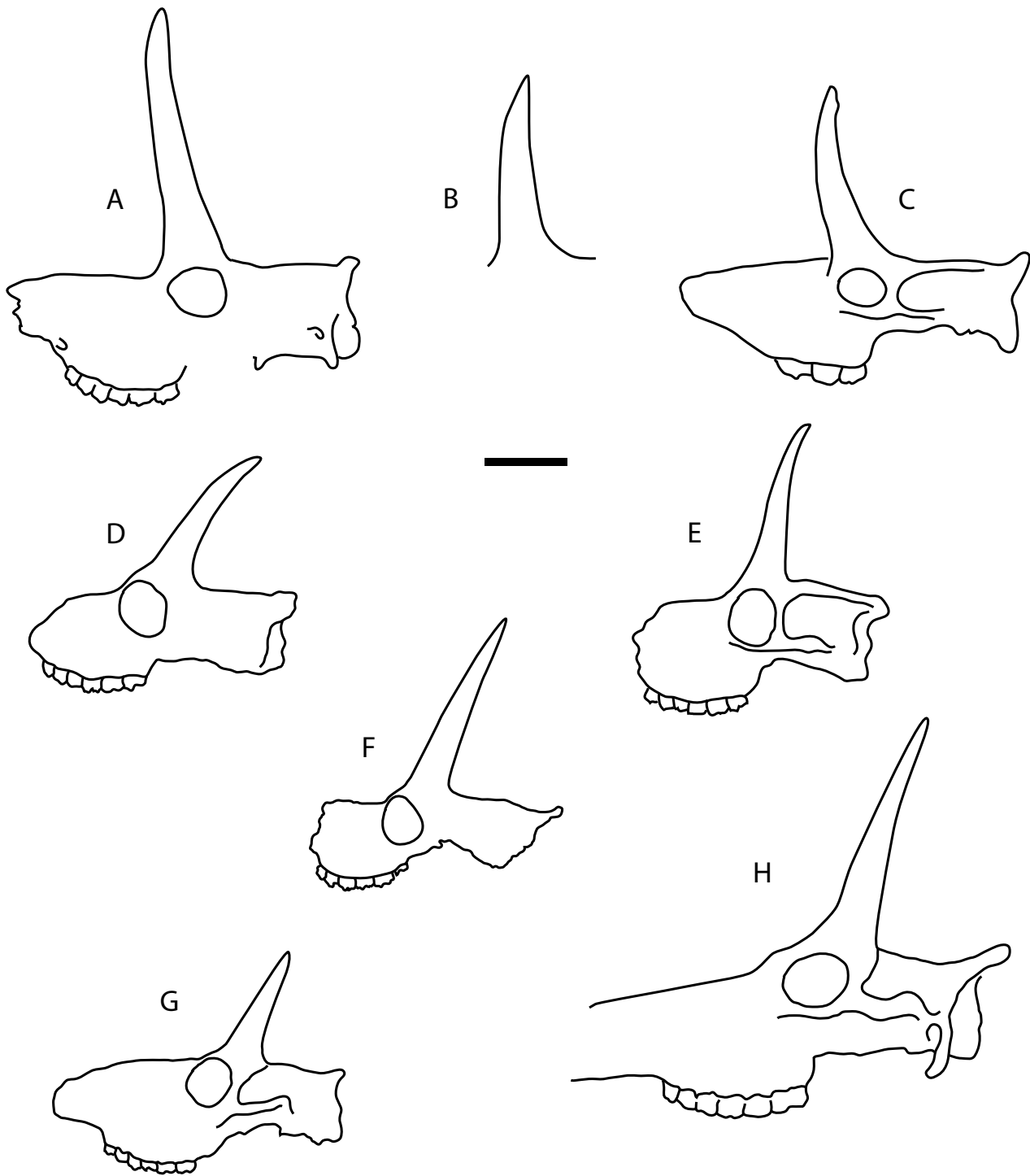
Textfigure 5: Outline comparison of *Palaeotragus* and *Samotherium* cranial specimens: **A**, *P. inexspectatus*, Sésklo, AMPG SE3-31; **B**, *P. inexspectatus*, Vólax, AMPG 980; **C**, *P. inexspectatus*, Kuruksay (holotype of *Sogdianotherium kuruksaense*); **D**, *P. rouenii*, Pikermi, holotype MNHNP PIK-1670; **E**, *P. rouenii*, Samos, NHMW A476; **F**, *P. rouenii*, Ciobruciu; **G**, *P. microdon*, Locality 116, specimen III, China; **H**, *S. boissieri*, Samos, NHML M4215. Graphical scale: 10 cm. Figure A is slightly corrected for specimen's distortion. Figures C, F, G and H according to Sharapov (1974: fig. 1), Pavlow (1913: pl. I, fig. 3a), Bohlin (1926: pl. I, fig. 1) and Bohlin (1926: textfig. 135) respectively. Note the consistent rostral inclination of the ossicones in *P. inexspectatus*, despite their considerably variant length, as well as the differences in ossicone direction and morphology in the *P. rouenii–microdon* group specimens from Pikermi, Samos, Ciobruciu and Loc. 116.

part and, though incomplete, it is morphologically and metrically comparable to the Sésklo ossicones. The authors consider it as similar to *Mitilanotherium inexspectatum* and *Palaeotragus priasovicus*; indeed its identity with the peri-Mediterranean Villafranchian palaeotragine is quite plausible.

The presence of Plio-Pleistocene giraffids is mentioned in a few more Eurasian localities, usually based on scanty finds, without detailed descriptions. David (1997) briefly reported the discovery of a giraffid pha-
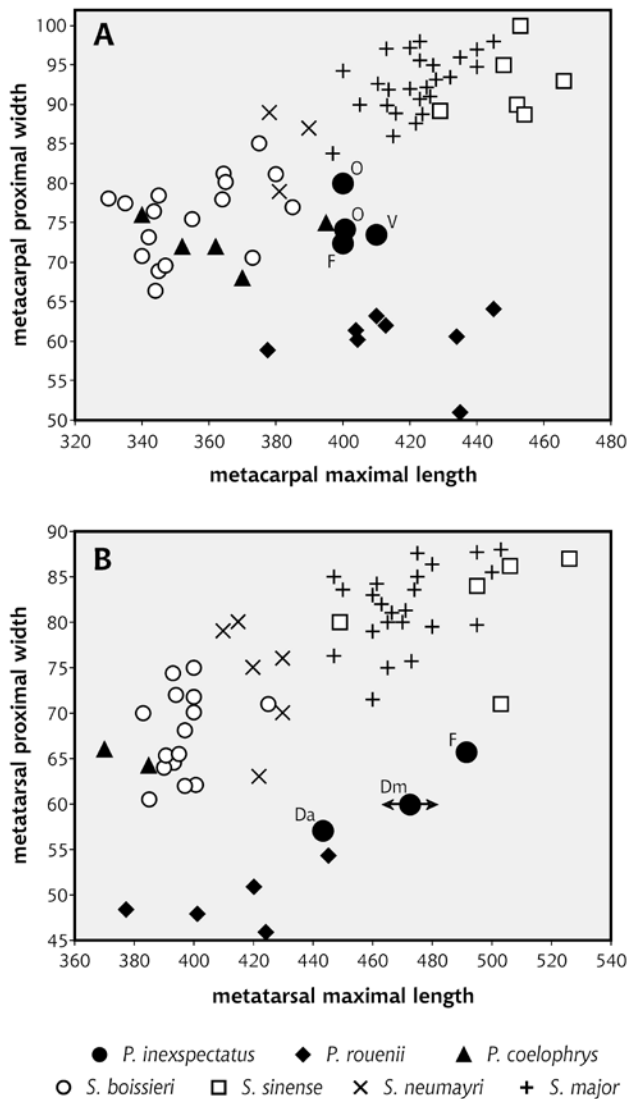
Textfigure 6: Scatter diagrams of metapodial length to proximal width (in mm) of the palaeotragine species *Palaeotragus rouenii* (Pikermi, Samos, Kemiklitepe, Nikiti, Kerassiá – Bohlin 1926; Geraads 1974, 1994; Kostopoulos et al. 1996; Iliopoulos 2003; Kostopoulos 2009), *P. coelophrys* (Maragheh – Rodler & Weithofer 1890; Geraads 1974), *Samotherium boissieri* (Samos – Bohlin 1926; Kostopoulos 2009), *S. sinense* (China – Bohlin 1926), *S. neumayri* (Maragheh – Rodler & Weithofer 1890; Geraads 1974; Gaziry 1987) and *S. major* (Samos – Kostopoulos 2009) in comparison to *P. inexspectatus* from Oltenia (O) (Samson & Radulesco 1966), Vólax (V) (Sickenberg 1967), Dafneró (Da) (Kostopoulos 1996), Fonelas (F) (Garrido 2006) and Dmanisi (Dm) (Vekua et al. 2008). **A**, metacarpal III-IV; **B**, metatarsal III-IV. The lengths of the two Oltenian and the one Spanish metacarpal plotted here to 400 mm are inaccurate (estimated by Samson & Radulesco 1966 and Garrido 2006 respectively). The same is true for the metatarsal from Dmanisi whose length is given as >460 mm (Vekua et al. 2008). Some overlapping points have been shifted slightly to improve legibility.

lanx at Etulia, as well as an astragalus and a carpal bone at Salcia (both localities in Moldova), without providing descriptions or illustrations. The phalanx is larger than the corresponding specimen from Vólax (AMPG 974; Sickenberg 1967) and comparable to the two phalanges from Fonelas (Garrido 2006:

tab. 45). Based on the metrical data the Etulia form may be related to *P. inexspectatus*. The astragalus from Salcia is clearly larger than Σ-1124 from Sésklo (AMPG; Athanassiou 1996) and the three astragali from Oltenia (Samson & Radulesco 1966), having the size of a large *Samotherium* or *Helladotherium*. According to Vislobokova (2008) both localities are correlated to the Ruscinian, MN15, but Nadachowski et al. (2006) present a more complex stratigraphy: In Etulia they also mention the presence of a more recent horizon (Etulia 3) correlated with MN17. The same authors cite faunal lists of the Salcia locality comprising taxa as divergent biochronologically as *Deinotherium* and *Equus stenonis*, or *Hipparion* and *Bison*, and point to the fact that the older fossils are redeposited. It is very probable that the Salcia specimens come in fact from a lower stratigraphic level, which is consistent with their large dimensions.

Central Asian localities with Plio-Pleistocene *Palaeotragus* sp. include Beregovaya (Transbaikalia) and Esekartkan (Kazakhstan) (Vislobokova 2008); these forms may be related to *P. inexspectatus*, but there are no available morphological or metrical data. The Chinese fossil record includes the allegedly Early Pleistocene *Palaeotragus progressus* Tang & Ji, 1983, a species erected on an incomplete upper dental series. The holotype is about 5–10% larger than the SE3-31 dentition. The type locality Yuxian (Hebei) is placed in the post-Olduvai Matuyama chron (Liu et al. 2012), but its age is uncertain, particularly when considering the apparently mixed faunal association listed by Tang & Ji (1983).

4. Discussion

Previously published data and the comparisons in the preceding section strongly suggest that the West Asian and European Villafranchian palaeotragines form a homogeneous conspecific group. The older complex taxonomic scheme comprising in total three genera and four species was the result of the scarcity of the material in the various localities which did not allow for detailed comparisons among the existing samples. Another reason was the frequent disregard of intraspecific variation, though metrical and morphological variation may be higher in larger mammals (see e.g. Owen-Smith 1988: p. 175 for a relevant discussion). The new finds accumulated during the last decade show that this splitting should not be accepted anymore, as all these taxa were based on very similar samples, both in morphology and dimensions (Kostopoulos & Athanassiou 2005; van der Made & Morales 2011). Their main characters are the medium size (similar to that of *P. coelophrys* but more long limbed), the proportionally short premolar section, the forward inclined ossicones, the long and very wide dorsally neurocranium, and the slender metapodials. A peculiar feature is the high variation observed in the ossicone length:

the longest is almost 50 % longer than the shortest one. Despite its size, this difference is attributed here to intraspecific variation for the reason that the localities with maximal and minimal ossicone lengths (Sésklo and Vólax, respectively) are roughly contemporary, have yielded very similar faunal associations and are situated quite close to each other (about 300 km). Therefore, it is very unlikely that they comprised two ecologically similar, sympatric species, which were hardly distinguishable from each other except for their ossicone length. The intermediate lengths of the Dmanisi ossicones also support this view. A case of sexual dimorphism can also be rejected, as all available ossicone samples have comparable crosssectional shape and size, and can be assigned to male individuals.

The Villafranchian palaeotragine samples are morphologically and metrically intermediate between *Palaeotragus* and *Samotherium*, though they are much closer to the former genus. They resemble *Palaeotragus* in cranial morphology because of their long postorbital cranial part (Textfig. 5) and the small dentition size (Textfig. 4), but their proportionally shorter premolar series is more like *Samotherium* (though still inside the *Palaeotragus* range). The metapodials (especially the metatarsals) from all localities are slender (Textfig. 6) and thus unlike *Samotherium* (including the less robust *S. sinense*). They are more robust than those of the extremely gracile *P. rouenii* but generally more slender than those of *P. coelophrys* (the metacarpal slenderness difference with *P. coelophrys* is subtle, but this might be an artefact of an underestimated length of incompletely preserved specimens — see Textfig. 6 caption).

The character that differentiates the Pleistocene from the Late Miocene palaeotragines most strongly is the formers' forward inclined ossicones, which is constant in all four specimens (Vólax, Kuruksay, Liventsovka and Sésklo) that preserve at least a small part of the frontal bone. However, it seems that this feature existed already in the Miocene *Palaeotragus* stock, as Bohlin (1926: p. 9) mentions at least one case of rostrally inclined ossicones in *P. microdon*. Bohlin considered it as possibly abnormal, but it might be a rare variant demonstrating a considerable degree of plasticity in ossicone direction and shape (see also Textfig. 5D–G). It is quite plausible that this morphology became fixed sometime during the Pliocene and was retained by the Pleistocene populations. Therefore, the ossicone orientation is not considered sufficient to separate the Villafranchian palaeotragines at the generic level, and consequently *Mitilanotherium* (together with *Macedonitherium* and *Sogdianotherium*) is regarded as a junior synonym of *Palaeotragus*. This is definitely not a novel idea and it was expressed previously by certain authors (Geraads 1986a; van der Made & Morales 2011), while in the Russian literature the genus name *Palaeotragus* is used almost exclusively for the Pleistocene forms (e.g. Godina 1979; Alexejeva & Motuzko 1985; Godi-

na & Bajgusheva 1985; Bajgusheva & Titov 2002; Titov 2008; Vislobokova 2008). The very close affinity to *Palaeotragus* is also acknowledged by Sickenberg (1967), who finally erected his new genus *Macedonitherium* on alleged postcranial differences.

Palaeotragus has been considered as a genus of primitive morphology (Janis & Scott 1987). As its main characters have been regarded as plesiomorphic, its validity in phylogenetic terms has been seriously questioned and it has been considered as paraphyletic or polyphyletic (Hamilton 1978). Another important reason for this issue is that *Palaeotragus* has frequently been used as a convenient "waste basket" taxon to include several fragmentary specimens of "primitive" morphology, otherwise undeterminable to the genus level. Nevertheless, at least the Eurasian cranial samples currently referred to the genus are morphologically homogeneous, according to the genus' current diagnosis, and despite lacking a synapomorphy, they may well constitute a monophyletic group and belong to a single genus (see also Geraads 1981: p. 50). *Palaeotragus inexspectatus* is regarded as a relict species that survived in post-Neogene ecosystems, descending from a *P. rouenii*-like ancestor, and following an evolutionary path similar to that of other Neogene palaeotragines: increase in body size, acquisition of more hypsodont dentition, shortening of the premolar section, and development of less slender limbs.
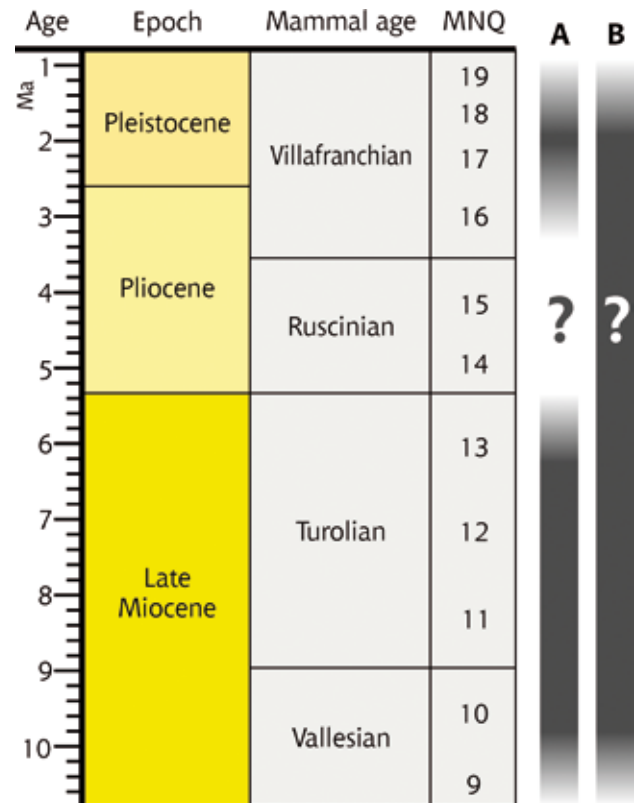
5. Biochronology

Most of Plio-Pleistocene *Palaeotragus*-bearing localities, which have also so far yielded the best available material, are dated to the Early Pleistocene, European Land Mammal Zone MN17: Huélago, Fonelas, Valea Grăunceanului, Dafneró, Vólax, Sésklo, Vaterá, Liventsovka, Kuruksay (Sotnikova et al. 1997; Radulescu et al. 2003; Kostopoulos & Athanassiou 2005; Garrido & Arribas 2008; Titov 2008; van der Made & Morales 2011). This may reflect a true abundance and distribution peak of this rare animal in MN17, but most likely is an artefact of the better representation of the MN17 faunas in the fossil record. Older localities, dated in MN16, include Gülyazı (Sickenberg & Tobien 1977; van der Meulen & van Kolfschoten 1988) and possibly Esekartkan (Tleuberdina 1982, cited in Vislobokova 2008), where *Palaeotragus* sp. is potentially conspecific with *P. inexspectatus*. The latter site may be older, however, as Sotnikova et al. (1997), though emphasising its Villafranchian faunal character, place it magnetostratigraphically in terminal Gilbert (i.e. at least 3.6 Ma). Another potentially early fauna with a giraffid very similar to *P. inexspectatus*, Etulia, is correlated to Ruscinian (MN15) by Vislobokova (2008), but note that Nadachowski et al. (2006) report the presence of a MN17-equivalent level in the same locality. The upper limit of the species' biostratigraphic range might

be placed in the MNQ19, as indicated by the faunal association in Libákos (Steensma 1988). The recently revised *Homo*-bearing fauna of Kocabaş, W. Turkey, which includes a giraffid ossicone referable to *P. inexspectatus* (see section 3.2), is radiometrically / palaeomagnetically dated in the interval 1.1–1.3 Ma, and placed biochronologically in the late Villafranchian, late MNQ19 (Boulbes et al. 2014; Lebatard et al. 2014). No *Palaeotragus*-like fossils are known after the end of Villafranchian, though there are several well-sampled Galerian sites in the palaeobiogeographic area of *P. inexspectatus*. In conclusion, the biochronologic range of *P. inexspectatus* is from MN16 to MNQ19, that is the entire Villafranchian, with a possible extension to the Ruscinian (MN15).

The synonymy of the various Plio-Pleistocene palaeotragine genera (*Mitilanotherium*, *Macedonitherium*, *Sogdianotherium*) with *Palaeotragus*, as suggested here, has implications for the biochronology of the latter genus, as its range extends for at least four million years. According to the available evidence the genus *Palaeotragus* appears in the fossil record in the early Late Miocene (older African material referred to this genus is scanty and rather insufficient for a genus-level determination) and disappears from Eastern Europe and Western Asia at the end of the Miocene (late MN13) (Koufos 2003; Vangengeim & Tesakov 2013: p. 531). Yet the genus may have survived in the peri-Mediterranean area during the Pliocene, remaining cryptic in the currently poorly known Ruscinian faunas. This possibility is similar to the case of the Plio-Pleistocene species *P. inexspectatus*, which remained unknown for many decades, despite the comparatively much better sampling of the Villafranchian faunas in comparison to the Ruscinian ones. Another possibility is the regional extinction of the genus in Europe and West Asia at the end of Miocene and the subsequent re-colonisation of the region in the Late Pliocene by populations of central Asian provenance, where *Palaeotragus* is reported to have persisted during the Pliocene (Kazakhstan, Kyrgyzstan, Transbaikalia, Mongolia and China – Godina 1979; Vislobokova 2008). Currently there are insufficient data to indicate which of the two possible scenarios is the most plausible. Both imply, however, a quite long biochronologic range for *Palaeotragus*, which may have lived in Eurasia for more than nine million years (Textfig. 7). This may seem long for a ruminant genus, but *Palaeotragus* includes highly conservative species that retained the same general morphology, changing modestly across the time.

6. Palaeoecology

Palaeotragus inexspectatus seems to have spread to areas where open and dry environments predominated. All European localities are confined to the Mediterranean South (Textfig. 1), while the western

Textfigure 7: Biochronologic chart (based on Rook & Martínez-Navarro 2010 and Hilgen et al. 2012: fig. 29.9, partly modified to accommodate the Villafranchian mammal age) figuring two possible hypotheses about the presence of *Palaeotragus* in S. Europe and W. Asia since its appearance in the Vallesian: **A**, *Palaeotragus* goes extinct in this region at about the end of the Turolian, is absent during the Ruscinian, and recolonises the region following a migration from a Central or East Asian core area; **B**, the genus has a continuous presence in the region, but is yet cryptic during the Ruscinian.

Asian ones are also located in low geographic latitudes. Even in the northernmost locality, Liventsovka (at 47° N), the environment was steppe-like with patches of woodland, and the climate was warm and relatively dry, as indicated by palaeobotanical and mineralogical data (summarised in Titov 2008). Godina (1979) also assumed the woodland steppes to be the most common habitat of *Palaeotragus*. In the case of the Pleistocene faunas this is also indicated by their taxonomic composition: most localities are dominated by grazing stenonid horses, in terms of number of individuals represented in the available material, which is a common indicator of open environments. A similar environment has been suggested for Sésklo for the same reason, additionally supported by the high antelope diversity (Athanassiou 1996), as well as by the microwear and mesowear study of the ungulate dentitions (Rivals & Athanassiou 2008). In contrast to most taxa of the fauna, the brachyodont dentition, the high occlusal relief and the cusp morphology of *P. inexspectatus* indicate that the species' palaeoecological role in Sésklo and contemporary palaeoecosystems was probably that of a browser (at least predominately), feeding in the

woodland that punctuated the open landscapes. The proportionally shorter premolar section in comparison to other giraffids may indicate that grasses might contribute to the species' diet, but this assumption has to be corroborated by a better statistical sample, as well as by a future microwear study.

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