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Dead ossicones, and other characters describing Palaeotraginae (Giraffidae; Mammalia) based on new material from Gansu, Central China

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Abstract

While the identity and validity of the extant families of ruminants are undoubted, there are significant problems with the determination of the interrelationships among the families, notably within the families of the Pecora, or horned ruminants. The morphological features used to construct ruminant phylogeny have been a source of controversy: many features used over the past century have been shown to be highly homoplastic and related to functional similarities. Ruminants evolved in the context of the later Cenozoic climatic changes, and many lineages adopted functional morphological adaptations related to feeding on more abrasive diets (resulting in the parallel evolution of a greater extent of loph development in the molars and, in some lineages, hypsodonty) and locomotion in open habitats (resulting in the parallel evolution of fused metapodials and reduction and/or loss of lateral digits). The fact that the molecular phylogeny shows a very different pattern from the currently accepted morphological one is of particular cause for concern, especially as molecular data are of no use for understanding the relationships of extinct lineages. Here we review the morphological data used in ruminant phylogenetics, and show even many of the less obviously functional features (e.g., number and position of the lacrimal orifices) are subject to homoplasy and variation, especially when fossil taxa are included. In addition, many morphological features treated as independent traits in phylogenetics are correlated (e.g., cranial morphology associated with hypsodonty). Some potentially reliable features are identified, but these do not help to sort out relationships within the Pecora. We advocate for the investigation into better morphological features, possibly derived from basicranial and ear region characters (although these features are not without their own issues of homoplasy), and for caution in character consideration in performing phylogenetic analyses.

Key words: Ruminants, systematics, phylogenetics, morphology, Pecora, traguline, bovoid, cervoid, giraffoids, moschid.

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1. Introduction

During the Early Miocene, the record of Giraffidae is scarce except for a few localities in France, Pakistan, Libya, and Kenya (Hamilton 1973, Geraads 1986, Barry et al. 2005, Grossman & Solounias in review). In these regions, there is a notable diversity in species that still needs to be explored. In Africa (Libya: Gebel Zelten, Kenya: Moruorot Hill and Kalodirr) and Asia (Pakistan: lower Siwaliks) Giraffidae are represented by Canthumeryx and Progiraffa during the Early to Middle Miocene. During the Late Miocene, there was a notable adaptive radiation of Giraffidae and their record is much more widespread and diverse. Most Late Miocene giraffids are large animals, which are comparable to the size of modern deer Cervus and Alces or even larger. These giraffid species are an important component of many Late Miocene faunas, e.g. in Gansu and Shanxi in China,

in the Siwaliks and in south Europe (Spain, Italy, and Greece), Ukraine, Turkey, and Iran (Geraads 1977, 1986, 1989; Solounias 2007). Among these, palaeotragines are common in Eurasia but absent from sub-Saharan Africa. So far, they have been defined in a rather limited way using the morphology of the lower p4 (Hamilton 1978) with detailed descriptions of teeth and ossicones of palaeotragine giraffids by Godina (1979), Geraads (1977, 1979, 1986), Solounias (2007), and Kostopoulos (2009) being informative. It seems the subfamily is based on this single tooth character (Hamilton 1978). Hence, despite these descriptions, it is not clear if the Palaeotraginae is a valid subfamily (with respect to the strength of the uniting characters) and which taxa are included and which are excluded. Currently, the p4 with posterior cuspids enlarged and directed mesiodistally is used as a significant shared derived character (Hamilton 1978). Samotheriinae are distinguished

from Palaeotraginae based on the morphology of p4 with reduced posterior cuspids, which are directed obliquely (Hamilton 1978) and the larger body size. We feel this is not sufficient to distinguish these two families. In the present study we re-affirm the validity of Palaeotraginae and bring forward a more focused definition based on ossicones. We propose to suppress Samotheriinae as a subfamily and include the samothere taxa in Palaeotraginae. The central new character is the distally dead ossicones in adults. In addition, we investigate occipitals and premaxillae which also clarify specific issues with *Alcicephalus* and *Palaeotragus*. *Alcicephalus*, unlike all other Palaeotraginae, has a broad occipital. In Palaeotragus, we find the premaxilla to have an inner shelf, unlike other ruminants. The new observations would not have been possible utilizing the material from the classic localities such as Axios Valley, Pikermi, Samos and Maragheh because the material is too fragmentary for a more in-depth examination. Ossicones from these sites are few, lack apices and commonly are not found with the skulls, as the skulls are often fragmented. New material from Gansu, China is notably more complete, so that new morphological features and patterns are discernible. To demonstrate this, we have selected for this study complete skulls, which were identified by one of the authors (Solounias). There is certainly more material from Gansu to be integrated in the future. This material is utilized for the observations, which can be added to the understanding of Palaeotraginae, but presently, we do not review all of the other characters from the literature. Materials from the following institutions were used in this study: HPM Hezheng Paleozoological Museum, Hezheng; MNHNP Muséum National d'Histoire Naturelle Paris; NHM Natural History Museum, London; PIU Paleontological Institute of Uppsala; SMF Senckenberg Naturmuseum und Forschungsinstitut, Frankfurt; BSPG Bayerische Staatssammlung für für Paläontologie und Geologie, München; KNM National Museums of Kenya; NHMW Naturhistorisches Museum Wien.

2. Material

Complete skulls from Gansu and Shanxi, China:

- *Samotherium boissieri*; HPM NS 56, HMV 1929;
- *Samotherium sinense*; HPM NS 1 HMV 1930;
- *Alcicephalus neumayr*; HPM NS 8 HMV 0947, NS 20 HMV 0948;
- *Schansitherium tafel*; HPM NS 54 HMV 1931, NS 46 HMV 1932, NS 54 HMV 1934;
- *Palaeotragus rouenii*; HPM HMV 1316;
- *Palaeotragus* sp.; HPM NS 22 HMV 1570;
- *Palaeotragus coelophrys*; HPM NS 21 HMV 0951.

Complete skulls:

- *Palaeotragus rouenii* (*microdon*); PIU M 3961; Gansu (China) Locality 116;
- *Samotherium major*; SMF M 3600; Samos (Greece) (specific locality unknown).

Partial specimens:

- *Palaeotragus coelophrys*; HPM NS 5 HMV 1933 frontlet; Gansu (China) (specific locality unknown);
- *Palaeotragus rouenii* (*microdon*); PIU 608 frontlet; Shanxi (China) Locality 108;
- *Alcicephalus neumayri*; NHMW 4960 holotype face with maxilla and complete upper dentition Maragheh (Iran) (specific locality unknown);
- *Alcicephalus neumayri*; BSPG 1973 XXI 49 atlas; Kerjabad near Maragheh (Iran) Locality K2;
- *Alcicephalus neumayri*; MNHNP 651 damaged cranium; MNHNP 1329, 1330 ossicones; Maragheh (Iran) (specific locality unknown);
- *Canthumeryx sp.*, KNM-WK 17089, ossicone; Kalodirr (Kenya);
- *Samotherium boissieri*, NHM M Forsyth Major catalogue #207, atlas; Samos (Greece) (specific locality unknown).

Extant specimens:

- *Giraffa camelopardalis*; AMNH 14135, AMNH 24290; cranial skeleton; Botswana;
- *Okapia johnstoni*; AMNH 51251; cranial and postcranial skeleton; Zaire;
- *Boselaphus tragocamelus;* AMNH 35520, 54476; cranial skeletons, horn sheaths, postcranial skeletons; India.

3. Results

The results address the occipitals, the position of the ossicones, the presence of wear facets, which are distinct from apical polish, and the premaxillae. We begin with the occipitals because this is a novel character that distinguishes *Alcicephalus* from *Samotherium*.

3.1 *Alcicephalus neumayri*

The occipitals of *Samotherium* and *Palaeotragus* are hour-glass shaped with a constriction in the center (Fig. 1b, d). This relates to the shape of obliquus capitis and semispinalis captitis muscles. The central constriction forms an abrupt separation from the mastoid bone. Thus the mastoid above the auditory meatus is much more anteriorly positioned and in another plane from the rest of the occipital. In other words, it does not contribute to the edge of the hourglass shape of the occipital. In *Canthumeryx sirtensis,* this condition is similar to that of the hour-glass observed in *Samotherium* and in *Palaeotragus*. The occipital of *Alcicephalus*, however, does not form a protruding backward shelf which is present in *Samotherium*. It must be noted here, that the type specimen of *Alcicephalus neumayri* comprises only a face with the upper dentition (Rodler & Weithofer 1890, plate 1), but a braincase (MNHNP 681) from Maragheh, although damaged, appears also to have a wide occipital and the non-protruding shelf. An atlas from Maragheh (BSPG 1973 XXI 49) is different from the atlas of *Samotherium boissieri* (NHM M Forsyth Major catalogue #207) in that the lamina is very short and a dorsal tubercle is lacking. In Gansu, *Alcicephalus neumayri* is also rare and only two skulls have been identified as this species based on the
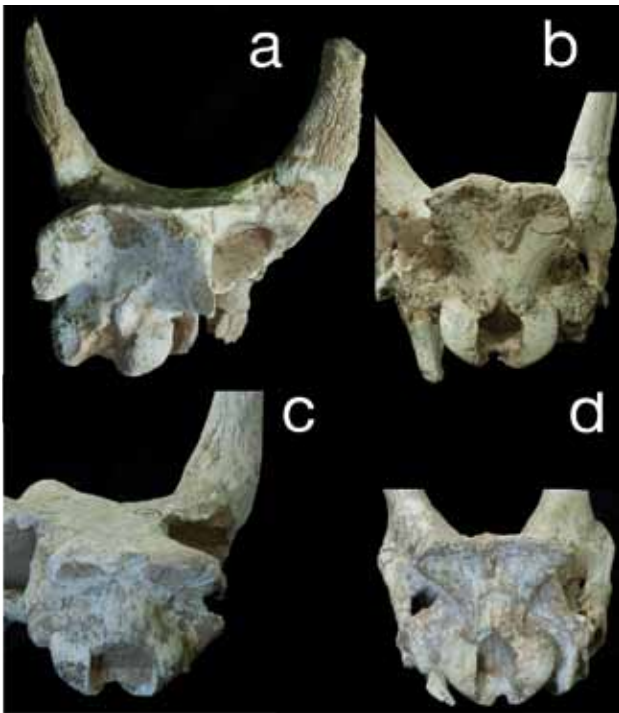
Figure 1: Two types of occipitals; **(a)** and **(c)** show the broad occipitals, **(b)** and **(d)** show the more typical hour-glass shaped occipitals . **(a)** *Alcicephalus neumayri* NS 20 HMV 0948. **(b)** *Samotherium boissieri* NS 56 –HMV 1929. **(c)** *Alcicephalus neumayri* NS 8 HMV 0947. **(d)** *Palaeotragus coelophrys* NS 21 HMV 0951.

small masseteric fossa (NS 8 HMV 0947 and NS 20 HMV 0948). These skulls differ from *Samotherium* by a contribution of the mastoid bone to the edge of the hour-glass morphology in the occipital (Fig. 1 a, c) so that the occiput resembles that of cervids. In one of these skulls (NS 20 HMV 0948, Fig. 1a), the occipital is concave and forms a large inverted U. In the other skull (NS 8 HMV 0947, Fig. 1c), the occipital is very wide at the dorsal lateral edge but less concave. The occipital is flattened in both specimens and there is no protruding shelf. These two Gansu skulls resemble the type of *Alcicephalus neumayri* from Maragheh (NHMW 4960) in that the masseteric fossa of the maxilla is small, while in *Samotherium boissieri* the masseteric fossa is larger. The Gansu skulls possess ossicones that are similar to those of *Samotherium*. They curve inward, having a curvature similar to that of two other *Alcicephalus* specimens from Maragheh (MNHNP 1329 and 1330). Using this character, there is agreement with the type material of *Alcicephalus neumayri* from Maragheh. In addition, the rest of the Gansu skulls and dentition strongly resembles that of *Samotherium boissieri*. Because of the small masseteric fossa, the inwardly curved ossicone and especially the occipital we place the two skulls from Gansu in *Alcicephalus neumayri* (Fig. 1).

3.2 Position of ossicones

Giraffidae possess ossicones (Lankester 1907a, 1907b; Bohlin 1926; Davis et al. 2011). The ossicones of *Samotherium* are positioned at the edge of the

supraorbital rim, forming a continuous surface with that rim (Solounias 2007). Thus there is no discernible area of frontal bone margin separating the orbit from the ossicone. In *Palaeotragus,* the ossicones are more medial and leave the supraorbital rims free (Godina 1979; Kostopoulos 2009) so that while the supraorbital edge is thin, it is distinct from the ossicone base. The base of the ossicones in Palaeotraginae has no expansions of flanges as in sivatheres and in *Giraffokeryx*. *Giraffa*, *Bohlinia*, and other species do not have flanges.

3.3 Wear at the apices of ossicones

Bohlin 1926 first noted the wear facets on the ossicones of *Palaeotragus rouenii* (*microdon*). The ossicones of the Palaeotraginae display apical beveled wear facets in all species but not all individuals, and it appears that in younger individuals, the ossicones are without apical wear. No other taxon outside Palaeotraginae has such beveled wear facets (Fig. 2), while the only other taxon with exposed apices is *Okapia*. *Okapia* ossicones display surfaces where fragments have been broken off and/or contain polished facets but never have large, beveled wear facets. Thus the structure of the skin-free apices of *Okapia* is different from the wear observed in Palaeotraginae (Fig. 3). Fig. 3 shows polish around the entire apex in *Okapia*, small apical bump like growths, and a narrow groove below separating the apex from the ossicone shaft (Solounias 2007). Breaks and/or polish on the ossicone is seen in most adult *Okapia*, but are absent in young adults and juveniles. The apical polish of Palaeotraginae is not common, but when present, it is minimal and is found on the apex more distally to (above) the wear facets. So far minimal polish has been observed in *Samotherium* and *Schansitherium* (Fig. 4a) but not in *Palaeotragus*. *Samotherium* and *Schansitherium* never show the small bumps and growths with a groove below which is the typical morphology in *Okapia* (Solounias 2007).

One exceptional *Samotherium major* specimen is SMF M 3600 from Samos. This is an adult skull where the left ossicone never formed or if it had, it has fallen off as the animal grew into an adult. In this specimen, the right ossicone is normal, large and straight as in other individuals of *S. major*. It shows substantial polish on the lateral surface and no beveled facet (Fig. 4b). This data can be used in the future to understand the paleobiology and behavior resulting in such surfaces.

3.4 Premaxilla

The premaxilla is a rather conservative structure in ruminants and the premaxillae of *Giraffa* and *Okapia* are typical (Fig. 5a, 6a). We have not found any premaxillae of extinct giraffid specimens in the European museums. The premaxilla is a very delicate struc-

ture that is easily broken or displaced from the skull, which happens in both extant and fossil specimens. One exception is the type of *Samotherium boissieri* from Samos NHM M 4215, a complete crushed skull. The premaxilla on this specimen is intact but not prepared (the jaw adheres to it by sediment) (Solounias et al. 1988). This premaxilla is fairly typical in morphology and resembles that of grazer ruminants. In contrast, there are several premaxillae of most species from Gansu. One of the best is that of *Samotherium sinense* NS 1 HMV 1930 (Fig. 5b). Like *S. boissieri* and others, it shows a rather simple and conservative structure; similar to that of *Okapia* and *Giraffa*.

The premaxillae of *Palaeotragus* differ from those of *Samotherium* and *Giraffa* by the presence of smaller incisive foramina (*Palaeotragus rouenii* HMV 1316). In *Palaeotragus*, the left and right maxillary processes of the premaxilla are anteriorly broad (Fig. 5b). Such a broadening relates to the "inner premaxillary shelf" structure of the *Palaeotragus* premaxilla (see below).

There are four premaxillae of *Palaeotragus* from Gansu that are not typical of other ruminants. On these premaxillae, the inner side forms a shelf and the median region displays a fusion anterior to the nasal cavity (Fig. 5c, d). The fusion is between the left and right sides of the anterior most aspect of the premaxilla, and this fusion is absent in other ruminants. These specimens are also lacking the anterior notch at the tip of the premaxilla that is typically present in mammals. The oral aspect (underside) is also atypical. It shows overlapping of the maxilla in the median plane and a large anterior development of the maxilla at the region of the incisive foramina (Fig. 6b). The incisive foramina are small and the shelf of premaxilla is discernible on the oral aspect. This atypical morphology is found in *P. rouenii, Palaeotragus* sp. and *P. coelophrys* and in a new genus to be described and named (Fig. 5d).

3.5 Lower 4th premolar

There are two types of lower 4th premolars known in *Palaeotragus and Samotherium*. So far this character seems to be a uniting factor of the species of *Palaeotragus* versus the species of *Samotherium* (Hamilton 1978). There is a preliminary phylogenetic analysis that links these two species (Solounias 2007). In *Palaeotragus* the posterior cuspids are enlarged and directed mesiodistally. In *Samotherium* the posterior cuspids are small and directed more lingually. It appears from the fossil records that the oblique is more primitive than the mesiodistal (Hamilton 1978 figs 4, 5, 6).

4. Discussion

In this study, based on the results described abo-

Figure 2: Ossicone apical wear facets. **(a)** *Schansitherium tafeli* NS 54 HMV 1931. **(b)** *Schansitherium tafeli* NS 46 HMV 1932. **(c)** *Palaeotragus rouenii* (*microdon*) PIU M 3931 complete skull. **(d)** *Palaeotragus coelophrys* NS 5 HMV 1933 frontlet. **(e)** *Palaeotragus rouenii* (*microdon*) PIU M 608 frontlet.

ve we are re-establishing the genus *Alcicelaphus* as a valid genus. Rodler & Weithofer (1890) erect and mention the new genus *Alcicephalus* with *neumayri* first (page priority) but use this genus with two species *neumayri* and *coelophrys*. Therefore, since the genus is valid, it should be based on the specimen
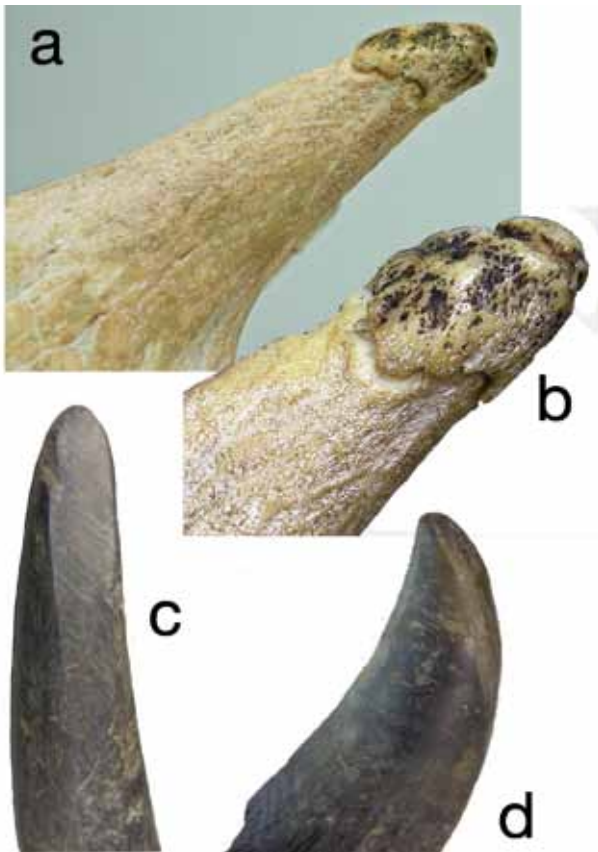
Figure 3: **(a)** *Okapia johnstoni* left ossicone with apical polish, apical growth bumps and a groove. **(b)** AMNH 51215 (same specimen enlarged). **(c)** *Boselaphus tragocamelus* AMNH 35520. Similar wear facets of the nilgai horn sheath to *Palaeotragus* (see Fig. 2). **(d)** Second nilgai horn sheath AMNH 54476.

The ossicones of *Samotherium* are positioned at the edge of the supraorbital rim. This character is plesiomorphic since the ossicones of *Canthumeryx sirtensis,* the most primitive giraffid, are in this position. In *Palaeotragus* the ossicones are more medial. In *Palaeotragus*, the rims are separate from the ossicones and are composed of thin bone without sinuses as in most ruminants. Hence, in terms of the ossicone morphology of Giraffidae, *Palaeotragus* is more specialized than *Samotherium*. This observation suggests a polarity from which *Samotherium* can be seen as ancestral to *Palaeotragus*. *Palaeotragus* is smaller and definitely a derived taxon.

The holotype of Palaeotragus is *Palaeotragus rouenii* from Pikermi. Our anatomical observations that *Palaeotragus* is more specialized than *Samotherium* allow us to interpret the relative age of Pikermi in relation to Samos. There is no *Samotherium* found in Pikermi, while in Samos there is both *Palaeotragus* and *Samotherium*. With these data, one may be able to develop biostratigraphic observations. These observations support the proposal of Solounias et al. (2010) that Pikermi may be younger than Samos (average date 7.4 Ma).
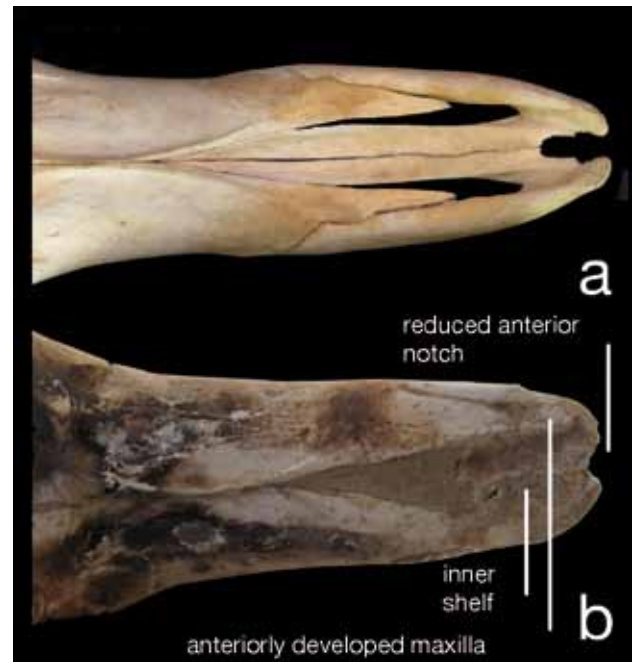
of *neumayri*. We find that *Alcicephalus* is a distinct genus from *Samotherium.* The recognition of *Alcicephalus* as a distinct genus from *Samotherium* raises issues in understanding the differences. So far five differences stand out. (a) The broad flattened occipital is different from that of *Samotherium,* in which the center of the occipital protrudes posteriorly, forming an hour-glass central shape. (b) The dorso-median aspect of the occipital does not protrude to from a backward shelf and in that it is different from that of *Samotherium* where it does protrude. (c) In addition, an atlas from Maragheh at BSPG 1973 XXI 49 is substantially different from that of *Samotherium*. The difference is that the atlas of *Alcicelaphus* has no dorsal tubercle, and the lamina is very short. In *Samotherium*, the dorsal tubercle is present and posteriorly positioned, and the lamina is broad. This makes sense since the atlas is next to the occipital; both regions interconnecting with muscles. (d) The ossicones of *Alcicephalus* curve inward unlike those of *Samotherium.* In *Samotherium*, the ossicones are positioned more laterally and tend to either be straight or curve posteriorly (*S. major* versus *S. boissieri*). (e) The masseteric fossa is notably smaller in *Alcicephalus*. Thus it appears that *Alcicephalus* and *Samotherium* are close in morphology and size and it would be impossible to separate their dentitions and postcranials.

Figure 4: Ossicone apical polish. **(a)** *Schansitherium tafeli* HMV 1934. **(b)** *Samotherium major* SMF M 3600 complete skull. The left ossicone of this specimen was not developed or fell off early in life.
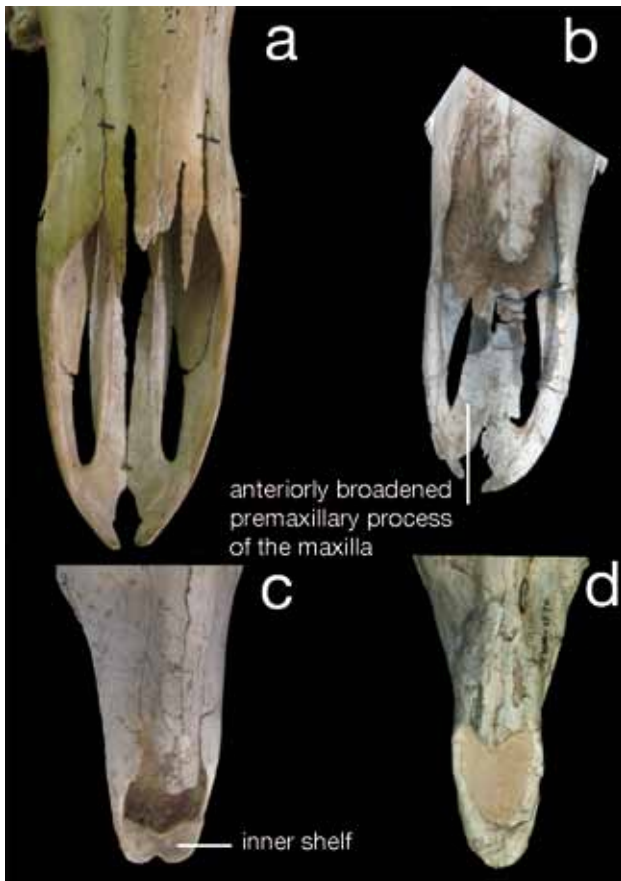
Figure 5: Premaxillae, dorsal surface. **(a)** *Giraffa camelopardalis* AMNH 14135. **(b)** *Samotherium sinense* NS 1 HMV 1930. **(c)** *Palaeotragus rouenii* HMV 1316. **(d)** *Palaeotragus* sp. HMV 1570.

Figure 6: Premaxillae, oral surface. **(a)** *Giraffa camelopardalis* AMNH 14135. **(b)** *Palaeotragus rouenii* HMV 1316.

It is known that bone is a live tissue that would bleed and become infected if exposed to air. Therefore, giraffids are exceptional in that several species have exposed bone without overlying integument. This is well-known from the permanent ossicones of *Okapia*. In cervids, the antler is also exposed temporarily, but it is shed and replaced annually. Using *Okapia* as a model, we are able to better understand the fossils in question. One ossicone attributed to *Canthumeryx* from Kalodirr in Kenya may have an exposed apex (Grossman & Solounias this volume, KNM-WK 17089). The ossicones of the Palaeotraginae display beveled apical ossicone wear facets in adults. For these taxa, beveled wear facets at the apices imply that the ossicone was at least distally dead and it is possible the entire ossicone was dead down to the base. As such there was probably a specific biological mechanism for the ossicone bone to die in adults. No other species besides those of Palaeotraginae have this feature. Thus it is reasonable to use such a feature in uniting the subfamily. *Okapia* is a problematic taxon in that it is both similar to and different from other giraffids (Colbert 1938, Bohlin 1926). We know from observations that the ossicone apices are also exposed in *Okapia* (Lankester 1907b) and one of the authors (Solounias) has observed live adult okapis with ossicones exposing the apices at the White

Oaks Conservation Center in Florida. The bone is exposed and the skin around the exposed area digs into a groove and the skin appears thin and dry. The bare ossicones of *Okapia* do not bleed. The apex is probably dead and future studies of the histology may reveal to what extent the whole ossicone is dead (Solounias 2007). The integument adheres well at the shaft. It is possible that the integument is primarily vascularized in all giraffids from surficial supraorbital vessels and less internally from the bony ossicone (Ganey et al. 1990). The common occurrence of multiple supraorbital foramina in giraffids suggests high vascularization from that region. Another similarity of Palaeotraginae and Okapiinae ossicones is that their surface is relatively smooth, with little secondary bone growth and small bony bumps. Unlike these two subfamilies, Sivatheriinae, Bohlininae and Giraffidae display irregular ossicone surfaces. This is due to the secondary bone growth. Spinage (1968) has described this growth for *Giraffa* where it is extreme. Observations such as these can be used for better understanding the relationships within Giraffidae. They suggest a dichotomy in Giraffidae ossicone structures with two types of ossicones: those with surficial small bumps and irregular streaks of secondary bone growths and those that are almost smooth. The first is that of Giraffidae, Bohlininae and Sivatheriinae; the second is that of Palaeotraginae and Okapiinae. In *Okapia* the ossicone apical polish is pervasive and no wear facets have been observed, although we have only been able to examine six specimens at the AMNH and larger samples are needed. Figures by Fraipont (1907) and Lankester (1910) confirm our observations. In a few specimens, direct transverse breaks are observed. In Palaeotraginae there is minimal

apical polish, but usually the large beveled wear facets is the main distinguishing character.

Apical wear facets are rare in other species of ruminants. In cervids, there is not sufficient time for wear and polish as they shed the antlers every year. In bovids, wear would occur on the keratinous horn sheaths, however, we are not aware of any specimens except for the nilgai. The nilgai, *Boselaphus tragocamelus* (Boselaphinae), has apical wear which is very similar to that of Palaeotraginae (Fig. 3b, c). However, this wear is convergent as they wear the horn sheaths. The behavior causing these facets may be similar to that of Palaeotraginae.

Schansitherium tafeli needs to be studied in more detail. The skull and dentition is similar to that of *Samotherium boissieri*. However, there are four ossicones, which merge at the base. The posterior pair is similar to *Samotherium boissieri* in that it is polished at the apex (Fig. 2a, b; 4a). The anterior ossicones are complicated and are currently being investigated in a separate study.

All Giraffidae possess ossicones (Solounias 1988) and a more in-depth study of their formation is necessary. The peculiar *Okapia* ossicones and the secondary bone growth in many taxa are problems to be analyzed further. We also believe that new technologies and histology will help in explaining the formation and death of ossicones.

The three-dimensional anatomy of premaxillae and associated soft tissue of ruminants have not been extensively studied. The premaxilla is devoid of incisor teeth and is used to crop vegetation. Shapes of premaxillae have been related to browsing versus grazing diets (Solounias et al. 1988, Solounias & Moelleken 1993). In structure, however, most appear to be very similar to one another. Even in the bovids, *Madoqua*, *Saiga* and *Litocranius* which are browsing specialists, a conservative structural pattern is present. In *Palaeotragus*, we find an atypical inner morphology on the floor of the premaxilla. The flat anterior inner shelf is unusual and reminiscent of the premaxillae of tapirs. Small nostril and or lip muscles are present in the medal narial area, which attach at the very base of the premaxilla. These muscles may be larger in *Palaeotragus* to affect a flexible upper lip. The undersides of the premaxillae in the oral cavity of *Palaeotragus* are also different. The inner shelf is discernible in the oral aspect, with a larger contribution of the maxilla covering the smaller incisive foramina. At the median plane one side of the premaxilla slightly overrides the other. In other words, they appear to be asymmetrical. These are specializations possibly relating to the anterior buccinator muscles and to the upper lip. In *Samotherium sinense* the premaxilla is typical of other ruminants but the anterior side of the premaxillary process is enlarged, suggesting the close systematic affinity to *Palaeotragus*. We know this from a specimen in the Hezheng Paleozoological Museum (*Samotherium sinense* NS 1 HMV 1930).

As mentioned above, previous studies have shown that *Palaeotragus* species possess large posterior cuspids on the lower p4, which are directed mesio-distally. In *Samotherium* species the cuspids are smaller and directed more lingually (Hamilton 1978). This is a more primitive morphology in accordance to other extinct Giraffoidea. Hamilton (1978) erected a different subfamily on the basis of p4 for the samotheres: the Samotheriinae. The p4 data need to be investigated further as it is only one character. It seems other premolars resemble the samothere and the *Palaeotragus* morphs. Convergence is likely in some of these cases and even Hamilton has suggested this. We believe that the few characters that separate samotheres from palaeotragines are not sufficient to create a new subfamily. However, the differentiating characters between *Samotherium* and *Palaeotragus* are sufficient for generic distinction. They include the position of ossicones, larger body size, shorter metapodials and the morphology of the p4. Hamilton 1978 fig. 9 provided a cladistic analysis of Giraffoidea. In that analysis, the clades of *Palaeotragus* and *Samotherium* are intermixed, which further supports that these two subfamilies should be reunited. We are inclined to propose one subfamily for the following Miocene species. Palaeotraginae Pilgrim, 1911 has priority as a name.

In conclusion we have developed the following classification and list some localities where taxa occur (more localities are definitely possible):

• Palaeotraginae Pilgrim, 1911, (a subfamily united by the partially dead ossicones);
• *Samotherium* sp. (to be named, a rather primitive species from Gansu);
• *Samotherium bossieri* Major, 1888 – Samos, Gansu;
• *Samotherium major* Bohlin, 1926 – Samos (Bohlin suggesting it as a variety of *S. boissieri*);
• *Samotherium sinense* Bohlin, 1926 – Gansu, Shanxi;
• *Alcicephalus neumayri* Rodler & Weithofer, 1890 – Maragheh, Gansu;
• *Schansitherium tafeli* Killgus, 1922 – Gansu;
• *Schansitherium decipiens* (Bohlin, 1926) – Shanxi;
• *Schansitherium quadricornis* (Bohlin, 1926) – Samos;
• *Palaeotragus coelophrys* (Rodler & Weithofer, 1890) – Samos, Maragheh, Gansu, Shanxi;
• *Palaeotragus rouenii* (*microdon*) Gaudry, 1861 – Pikermi, Samos, Maragheh, Shanxi, Gansu.

Notes:

- *Palaeotragus primaevus* and *Samotherium africanum* are placed into *Giraffokeryx primaevus* Harris et al., 2010.

- *Palaeotragus eminens* Alexjew (or Alexeyev), 1916 and *Palaeotragus expectans* Borissiak, 1914 are from Ukraine and Moldavia and are not well known.

Acknowledgements

5. References

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