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A new caprin bovid (Mammalia) from the late Miocene of Morocco

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We describe here a bovid skull from the Upper Member of the Aït Kandoula Formation near Ouarzazate, Morocco, which can be dated by biostratigraphy to the late Miocene, Turolian-equivalent. We assign it to a new taxon, *Skouraia helicoides*, gen. nov., sp. nov. It has long horn-cores that are much inclined backwards, strongly spiralled in homonymous direction, very divergent, and have a strong anterolateral keel. The strong cranial flexure, broad basioccipital, and aegodont teeth demand inclusion of this new taxon within the tribe Caprini, a mostly Eurasian group with few African representatives. *Skouraia* must be an early offshoot of this tribe, but its highly derived cranial features suggest that the Caprini may have experienced, in the poorly known late Miocene of Africa, a broader morphological diversification than in Europe.

Keywords: Upper Miocene, Morocco, Africa, Bovidae, Caprinae, Caprini.

INTRODUCTION

With more than 70 living species, the Bovidae are by far the most diverse family of large mammals in Africa today. They include representatives of all major tribes except the Boselaphini, but most of them belong to tribes that are today endemic to the Afro-Arabian domain, namely the Tragelaphini, Cephalophini, Neotragini, Aepycerotini, Reduncini, Hippotragini and Alcelaphini. The Antilopini are also well represented, but they are mainly a Palearctic group. In the Pliocene and Pleistocene, evidence from the whole continent shows that the same groups dominated the bovid assemblages, although the proportions of the various tribes vary sharply with age and location. To these groups, Ethiopian in the terminology of modern faunal provinces, we must add the Bovini, more common and more diverse than today, the Boselaphini that went extinct in Africa by the earliest Pliocene (their last appearance is at Langebaanweg in South Africa, and in the Apak Member of Lothagam in Kenya), and the Caprini that were far less common than in Eurasia. It is likely that the differentiation of the African tribes took place in the Miocene, but it is only by the late Miocene, *c.* 7 Ma, at Sahabi in Libya, Lothagam in Kenya, and Toros Menalla in Chad, that we find fossils that can be unambiguously assigned to these modern endemic tribes (Lehmann & Thomas 1987; Harris 2003; Geraads *et al.* 2008; Bibi *et al.* 2009; Gentry 2010). At that time, the composition of the bovid assemblage is already fully African in character, with the exception of the last boselaphines.

Earlier late Miocene African bovid faunas are poorly known. The Beglia Formation of Tunisia, mostly, if not fully (Geraads 1989) of late Miocene age, yielded several bovids but only a few have been described (Robinson 1972, 1986); a few fragmentary specimens were described by Geraads (1989) from the slightly younger sites of Jebel Krechem in the same country; Bou Hanifia in Algeria yielded only the very poorly known *Damalavus boroccoi* Arambourg, 1959. It is noteworthy that none of the fossils from these localities foreshadow the later endemic African tribes. The greatest potential for improving our knowledge of bovids of the first part of the late Miocene (Vallesian – equivalent) in Africa probably rests in the Nakali and Samburu beds of Kenya, but these have not yet been published.

In this paper we describe the most complete known skull of a North African Miocene bovid, and assign it to a new taxon. It comes from the fluvial deposits (coarse sands and conglomerates) of the Upper Member of the Aït Kandoula Formation, near the village of Skoura, East of Ouarzazate, south of the High Atlas of Morocco (Fig. 1); these deposits have been dated to the late Miocene on a faunal basis (Zouhri *et al.* 2012).

SYSTEMATIC PALEONTOLOGY

In the descriptions, the tooth rows are supposed to be horizontal. Upper teeth are in upper case, lower teeth are in lower case.

Family Bovidae Gray, 1821
Subfamily Antilopinae Gray, 1821
Tribe Caprini Gray, 1821

Genus *Skouraia*, gen. nov.

Type species. Skouraia helicoides, new species.

Derivatio nominis. From Skoura, the village closest to the area of the type locality.

Diagnosis. That of the type-species.

Skouraia helicoides sp. nov., Fig. 2

Holotype. Almost complete cranium, bearing the complete right horn-core and a large part of the left one, with most of the teeth except the left P2 and all right premolars, but lacking most of the dorsal part of the face anterior to the orbit, and the premaxillae. It is unnumbered and preserved

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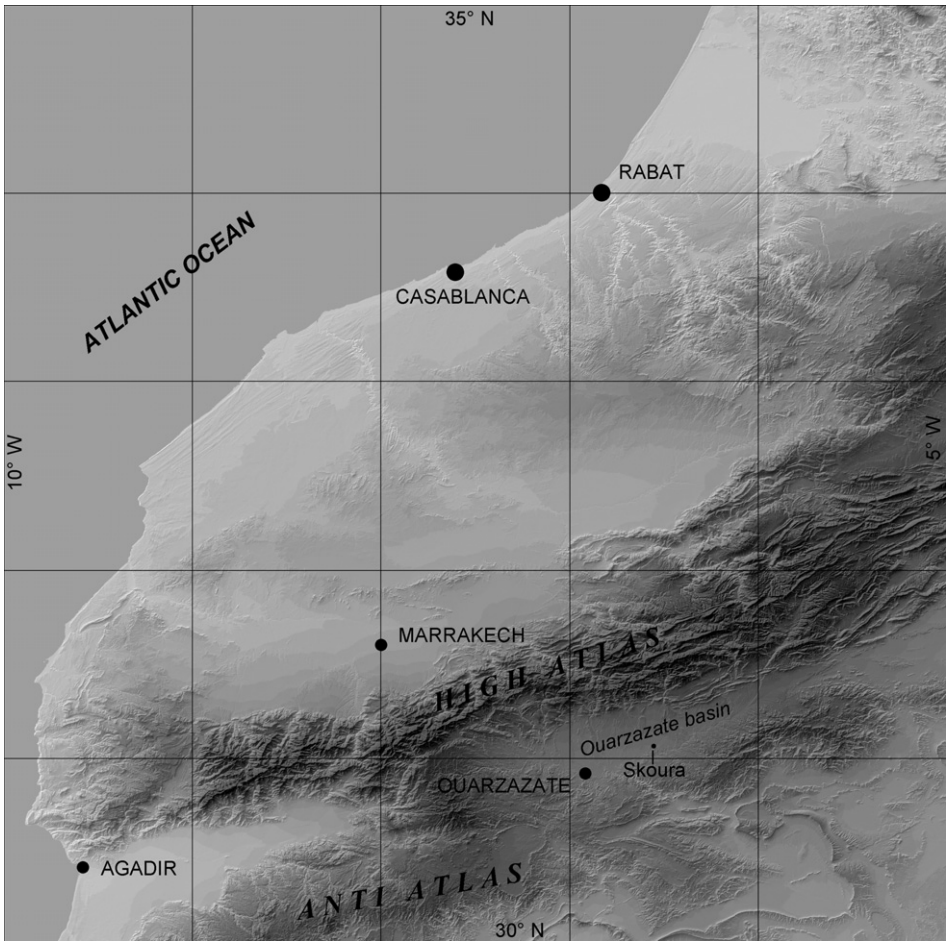


Figure 1. Map of Morocco with the location of Skoura in the Ouarzazate basin. Elevation data from http://hydrosheds.cr.usgs.gov/

in the private museum of Mr Brahim Tahiri in Erfoud, Morocco.

Diagnosis. A bovid with strong cranial flexure, early fusion of the bones of the braincase, low occipital, basioccipital broad and rather flat, with a narrow central groove. Horn-cores strongly divergent, much inclined posteriorly, with a virtually circular cross-section except for a strong antero-lateral keel, and describing a strong homonymous spiral. Upper teeth aegodont, with narrow styles, flat or poorly convex labial walls, and short premolars.

Type locality. The specimen was collected near Tizi N'Tadderht, in the Upper Member of the Aït Kandoula Formation of the Ouarzazate basin, Morocco, associated with a fauna dated by biostratigraphy to the youngest part of the late Miocene (equivalent to the European Turolian; Zouhri *et al*. 2012).

Derivatio nominis. Because the horn-cores are strongly spiralled.

Remarks. It is of course unfortunate that the holotype, and only known specimen, be kept in a private (albeit freely accessible as of November 2010) museum. Still, we believe that in spite of this shortcoming, the importance of this new taxon warrants description and formal naming.

Description. The skull is rather large for its geological age, comparable to that of European *Pachytragus* (measurements: Table 1). Its most obvious feature is the strong cranial flexure (Fig. 2A). The angle between the fronto-parietal profile, behind the horn-cores, and that of the (missing) dorsal profile of the face, can be estimated at about 100°; the angle between the basioccipital and the alveolar plane is about 50°. Correlated with this highly derived skull flexure, the orbit is located far behind the tooth row, and the frontals are strongly elevated between the horn-cores. The anterior part of the frontals, including the supra-orbital foramina, the nasals, the premaxillae, and most of the maxillae, are missing. There is a double postcornual fossa, which is in fact infracornual. All bones of the low, broad braincase are fused, and no suture is visible, but the parietal was certainly short; its dorsal profile is slightly concave. The angle between it and the plane of the occipital is about 130°. The occipital has a rounded outline, and is low and broad, with a central sagittal crest (Fig. 2G). The mastoid and auditory areas are

Table 1. Measurements (in mm) of holotype skull of *Skouraia helicoides*.

Length from occipital condyle to P2 (estimated)	193
Length from occipital condyle to M3	118
Minimum width of braincase	69
Width of occipital	82+
Height of occipital (from top of foramen)	39
Width of basioccipital	28.6
Bicondylar width	56
Width over M3s	75
Width over horn core pedicles	91
Antero-posterior diameter of horn-core	47.4
Transverse diameter of horn core	41.1
Length of right horn core	260+
Length M1-M3	55.8
Length P3-P4	21

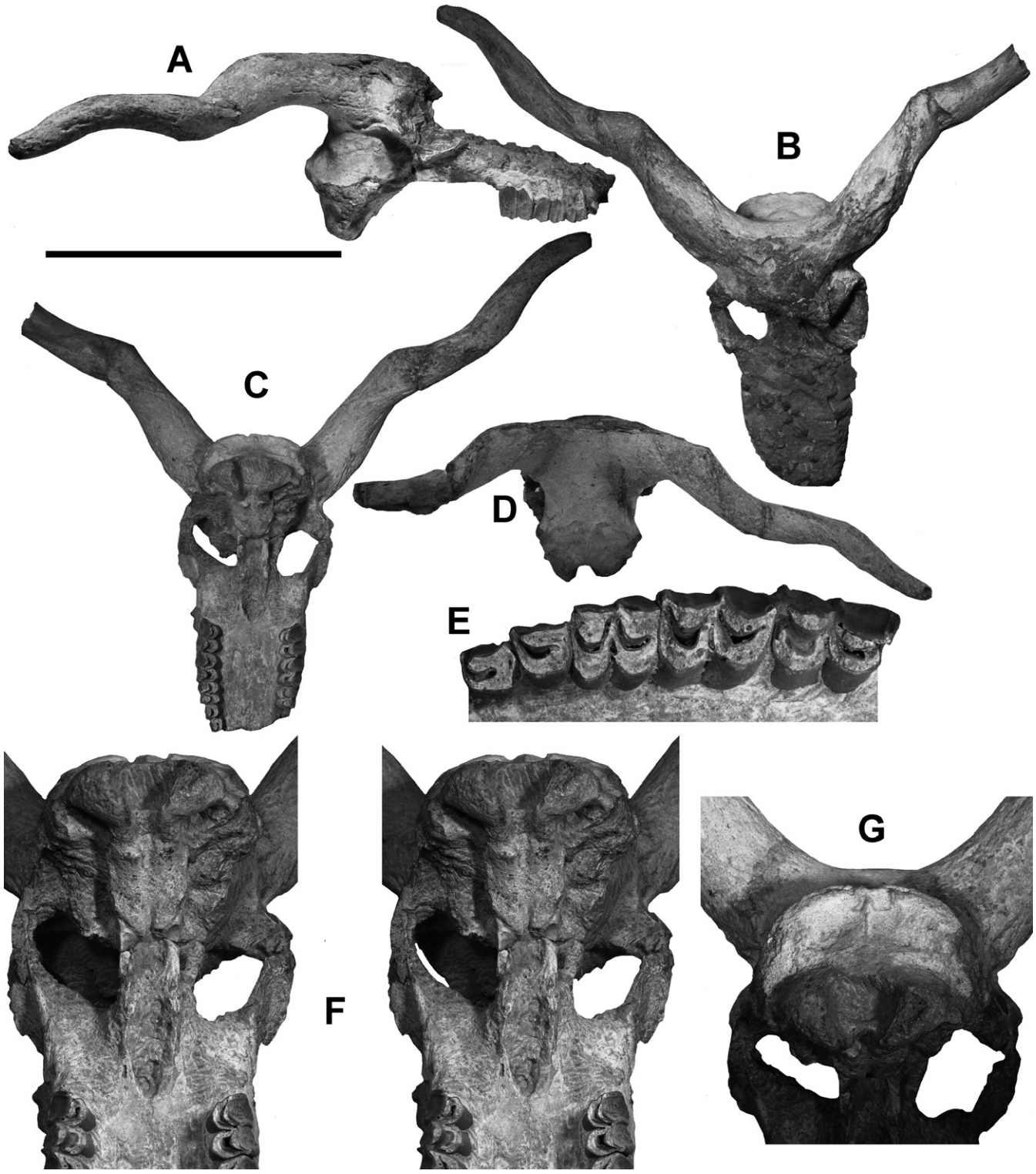


Figure 2. *Skouraia helicoides* sp. nov., holotype cranium. **A**, right lateral view; **B**, dorsal view; **C**, central view; **D**, posterior view; **E**, left tooth row P3–M3; **F**, stereo view of the cranial base; **G**, occipital view. Scale = 5 cm for Fig. E, 10 cm for Figs F, G, 20 cm for Figs A–D.

indistinct. On the basioccipital, the usual pairs of anterior and posterior tuberosities are hardly distinct; they are in fact little more than elevations above a pair of rectangular plateaus, only slightly narrower anteriorly than posteriorly, and separated by a long narrow groove in the midline (Fig. 2F); there are no accessory stop facets for the atlas. The choanae reach the level of the posterior border of M3, and the lateral indentations almost reach the same level (Fig. 2F).

The horn-cores are inserted above the orbits, and are strongly inclined backwards, as their basal part is parallel to the tooth row in lateral view, and their tips are more ventral than their base (Fig. 2A). Basal divergence is about 90°, and slightly increases towards the tips. They are strongly spiralled, but the axis of revolution of the horn core probably remains within the bone, thus forming a closed spiral. Torsion is homonymous, i.e. the right horn has a clockwise torsion (its is perhaps necessary to stress here that, although imperfectly preserved, the skull is wholly devoid of reconstruction, and therefore no error

can have occurred in fitting the horn-cores onto the skull). They have a strong anterolateral keel, which remains strong all the way to the tip, and a weaker anteromedial one; the anterior surface is almost flat between these keels, and the remaining part of the surface is rounded, with only a slight mediolateral compression. Owing to imperfect preservation of these parts, we do not know whether the base of the horn-cores and/or the frontal, were pneumatized.

The premolars are very short compared to the molars (Fig. 2E). The P4 has a rather square outline, being almost as long lingually as labially, and has a moderate, centrally placed, labial rib. This rib is much more mesially placed, and stronger, on P3, which is distinctly smaller than P4, making unlikely that the P2, now missing, was larger. Assuming that it was as large as P3, the index L P2-P4/L M1-M3 100 can be estimated at about 55, a very low value, comparable to that of modern *Capra*. The molars have no entostyles. The paracone has a weak labial rib, but there is none on the metacone, whose labial wall is a flat depressed surface between prominent styles; the metastyle of M3 is remarkably salient. On the whole, the dentition is therefore clearly of the aegodont type.

Comparisons. The most remarkable feature of this new bovid is the homonymous direction of horn torsion. Most spiral-horned bovids, living and fossil, instead have horns with heteronymous torsion, i.e. the right horn-core has an anticlockwise torsion. This is true, in particular, of those antelopes with the most conspicuously spiralled horns, the African Tragelaphini, but also of the modern *Antilope* (Antilopini) and *Addax* (Hippotragini), whose horns are markedly spiralled, and of *Kobus* (Reduncini), *Damaliscus* (Alcelaphini) and *Aepyceros*, where torsion is much weaker. Most of the abundant spiral-horned forms of the Palearctic late Miocene, such as *Palaeoreas, Prostrepsiceros, Protragelaphus*, and related genera, also have heteronymous torsion. Thus, their few representatives in Africa, such as *Prostrepsiceros libycus* Lehman & Thomas, 1987 from Sahabi (referred to *Dytikodorcas* by Bouvrain & Bonis, 2007), or the '*Palaeoreas*' from the Samburu Hills (Nakaya *et al*. 1987), can be readily excluded from the comparison.

A slight homonymous torsion can be found in many Alcelaphini, especially *Connochaetes*, *Megalotragus* and *Numidocapra*, but no member of this tribe has horns that are strongly spiralled, and they have a characteristic tooth morphology quite distinct from that of *Skouraia* (although they share the same premolar reduction). It is also detectable, but much weaker than in *Skouraia*, in some other African bovids that are clearly unconnected to genus, such as *Menelikia* and *Antidorcas*.

Bovids with a clear homonymous horn core torsion can be divided into four groups for convenience, and compared in the same order:

1) the *Oioceros* group, mostly of late Miocene age;
2) the *Sinotragus* group, also of late Miocene age, perhaps related to the next group, or to the *Pachytragus-Protoryx* group;
3) many modern Caprini, including the sheep and some goats;
4) a few fossils from northwestern Africa.

1) Among the informal *Oioceros* group, *Hispanodorcas* from Spain (Thomas *et al.* 1982; Alcalá & Morales 2006) and Greece (Bouvrain & Bonis 1988) has slender, almost straight horn-cores with weak torsion and no keels, which are uprightly inserted far from the occipital, and a rounded braincase. *Hispanodorcas* is clearly unrelated to *Skouraia*.

Pontoceros Verescagin *et al.*, 1971, from the Plio-Pleistocene of the Black Sea and Greece (Verescagin *et al.* 1971; Kostopoulos 1997) also has almost straight horn-cores, not spiralled like those of *Skouraia*, with a more triangular cross-section underlined by distinct furrows, and they are much less divergent.

Systematics of the late Miocene *Oioceros-Samotragus-Samodorcas* group is still debated, and its discussion is beyond the scope of this paper. '*Oioceros wegneri*' differs from *Oioceros sensu stricto*, and approaches *Skouraia*, in its stronger cranial flexure and larger size, but differs from *Skouraia* in several cranial features: the frontal is not strongly elevated between the horn-cores; even the largest '*O. wegneri*' remain of moderate size; the basioccipital has very strong anterior and posterior tuberosities; the occipital condyles are less broad relative to the occipital width. The horn-cores also offer clear distinguishing features between the *Oioceros* group and *Skouraia*. In the *Oioceros* group, the surface of the horn-cores is not smooth; instead, it is always marked by one or more longitudinal groove(s) and adjacent or intervening ridge(s) that may be acute and become keel-like, but these keels result from the depression of the areas adjacent to them, rather than from their own raising above the horn core surface, so that the cross-section is quite different; in *Oioceros sensu stricto*, it is often comma-shaped. *Oioceros* is also clearly unrelated to *Skouraia*.

2) *Prosinotragus* and *Sinotragus* from the Upper Miocene of China (Bohlin 1935), Samos (Solounias 1981), and Turkey (Geraads *et al.* 2002) have horn-cores that are short, only slightly divergent and close to each other at the base, with at most an incipient torsion, and with a keel that is anteromedial rather than anterolateral when present (in the Samos and Turkish forms). All these features differ from those of *Skouraia helicoides*.

The *Pachytragus-Protoryx* group has been revised by Kostopoulos (2009), who considered both names as synonymous and created the new genus *Skoufotragus*. This group, best known from the Turolian (Gentry 2003, and references therein), had long been placed among the Hippotragini, until Gentry (1971, 2000) convincingly argued that it is closer to the Caprini. Kostopoulos (2005, 2009) maintained that its affinities are still open to discussion because the i1 is larger than i2, unlike Caprini, but the size of i1 seems to be unrelated to phylogeny, and we suspect that its small size in modern Caprini is a consequence of its incipient hypsodonty, so that a moderately large i1 might just be primitive. Members of the *Pachytragus-Protoryx* group have a derived skull with a long face, a posteriorly located orbit, a strong cranial flexure, rather simple horn-cores variably curved backwards but without torsion, and an oval cross-section without keels.

Identification of the dentitions at species level is often difficult, but many of them resemble *Skouraia* in their aegodont pattern, with short premolars, and molars with weak labial ribs and flat metacone, prominent styles, no entostyles, and often a central fossette. *Pachytragus solignaci* Robinson, 1972, from the middle/late Miocene of Tunisia is the only African form; it resembles *Skouraia* in the slight spiralling of a horn-core figured by Robinson (1972, Fig. 3) but otherwise clearly differs in the strong transverse compression of the horn-cores. Horn-core morphology rules out any close connection between *Skouraia* and this group.

3) In many modern Caprini, such as *Capricornis, Naemorhedus, Oreamnos, Pseudois*, and *Rupicapra*, the horn-cores are short, conical, and lack keels and torsion, so that they differ completely from those of *Skouraia*; those of *Hemitragus* have keels but are also short and simple; those of the 'Ovibovini' *Ovibos* and *Budorcas* are very peculiar and completely different, although a clear homonymous torsion can be found in *Euceratherium*, an extinct relative of the musk-ox. *Ammotragus, Capra* and *Ovis* deserve greater attention. They have highly derived skulls with a long face and an orbit located posteriorly, and a strongly flexed cranium. Their horn-cores display a wide range of shapes; they are always curved, usually strongly so, and often show some spiralling. In *Capra* and *Ammotragus*, it is only incipient (except in *C. falconeri*, whose horn-cores are tightly twisted), and usually heteronymous, but some (especially domestic forms) may have a weak homonymous torsion. Many *Capra* (especially *C. falconeri* and domestic forms), as well as the probably related *Bouria* from the Ethiopian Pleistocene (Vrba 1997), have a strongly compressed cross-section with an anterior keel; *Capra wodaramoya* Bibi *et al.* 2012, from the early Pleistocene of Ethiopia is similar but without a clear anterior keel. Other *Capra*, and *Ammotragus*, have a more triangular cross-section, with rounded angles, and a tendency to form a flattened anterior face, limited by a poorly indicated anteromedial change of curvature, which may become a keel near the tip, and a better indicated anterolateral one, which may almost be a keel (e.g. in *C. sibirica*). In *Ovis*, the cross-section is similar but often less compressed and without true keels; however, the greater basal divergence that increases above the base and the strong homonymous torsion are resemblances with *Skouraia*. Thus, among living bovids, it is undoubtedly with the Caprini that we find any possible similarities with *Skouraia*.

4) In Northwestern Africa, *Parantidorcas latifrons* Arambourg, 1979 from the Pliocene of Aïn Brimba in Tunisia has horn-cores that have a weak but distinct heteronymous torsion, but this is a much smaller species that probably belongs to the Antilopini.

The northwestern African fossil form most similar to *Skouraia* is *Benicerus theobaldi* Heintz, 1973, from Beni Mellal in Morocco. This site has traditionally been assigned to the middle Miocene because it lacks hipparions, and Jaeger (1977) even concluded that it is not immediately anterior to the Vallesian because another site, Pataniak 6, is also ante-Vallesian but younger than Beni Mellal. However, Ginsburg (1977), followed by Werdelin & Peigné (2010), noted that its carnivore fauna is similar in composition to late Miocene ones; we estimate the age of Beni Mellal at *c.* 12 Ma.

The holotype, and only described specimen, of *B. theobaldi* is an incomplete left horn-core with most of the orbit (Heintz 1973, pl. 1); unfortunately, we could not locate it in the Muséum National d'Histoire Naturelle, Paris. From Heintz' description and figures, this horn-core is strongly curved posteriorly, moderately compressed transversely but with a compression that quickly increases above the base; it has a clear anticlockwise torsion, and a sharp anterior keel. It differs from the type of *S. helicoides* in its smaller size, shortness, more upright insertion, greater apical compression, and complete lack of an anteromedial keel and of an anterior surface. *Benicerus* is too poorly known for in-depth comparisons with *Skouraia*, but they are the only Miocene African bovids with distinctly homonymous torsion, and both are from Morocco.

There are two or three bovid species in the Upper Miocene of Jebel Krechem in Tunisia (Geraads 1989); some horn-cores could belong to a form close to *Prostrepsiceros*, but there are also some fragments of spiralled horn-cores whose direction of spiralling cannot be determined because they lack the base, but one of them looks so similar to the type of *B. theobaldi* that it is hard to believe that torsion was not homonymous, as in this species. The cross-section is ovoid, transversely compressed, with a keel that must have been anterior, and a hint of a posteromedial one. The presence of this second keel is the only difference with *B. theobaldi*, and we consider likely that a species close to that of Beni Mellal was also present at Jebel Krechem, whose age is probably equivalent to European MN10. Unfortunately, no spiral-horned bovid has been found in the Beglia Formation of Tunisia (Robinson 1986), which is of intermediate age, but it is conceivable that *Benicerus* survived into the late Miocene. How closely this genus is related to *Skouraia* is hard to tell; a *Benicerus theobaldi–Skouraia helicoides* lineage can be hypothesized, but unsubstantiated on the basis of the very poor record from Beni Mellal, and we prefer to propose *Skouraia* as a distinct genus.

Behaviour. The strong divergence of the horn-cores, and their strong inclination, with no part of them being dorsal to the frontal plane, strongly suggest that *Skouraia* performed some kind of the agonistic fighting behaviour known as ramming or Rammkampf, in which the opponents violently clash their heads after charging. It is best known in the Caprini *Ovis* and *Ammotragus*, in *Ovibos*, but also occurs in *Connochaetes* and some Bovini. Since *Skouraia* is obviously unrelated to any of the latter taxa, this inferred behaviour may be taken as supporting an assignment of this new taxon to the Caprini.

CONCLUSION

The most likely scenario is that *Skouraia* is an early, *Ovis*-like, offshoot of the Caprini, possibly related to *Benicerus*. Phylogenetic relationships between the living members of this tribe have recently been investigated, with limited consistency in the results (Schafer & Hall

2010; Bibi *et al.* 2012, and referencess therein). Molecular dating suggests that the early diversification within the tribe started in the late Miocene (Ropiquet & Hassanin 2005). The fact that *Myotragus*, which does not occupy a basal position in this group (Lalueza-Fox *et al.* 2005), must have reached the Balearics during the Messinian, implies that this is a minimum date, and if the shortened metapodials of *Aragoral mudejar*, of MN10 age, are indeed a synapomorphy with the Caprini (Alcalá & Morales 1997), the divergence of this tribe from the Hippotragini and Alcelaphini might go back to the middle Miocene (Bibi *et al.* 2009). It is therefore entirely possible that the North African latest Miocene witnessed an early diversification of the Caprini, which filled there a niche occupied in Eurasia by a variety of other antelopes. It is also likely that this group settled earlier and more deeply in Africa than hypothesized by Bibi *et al.* (2012), who regard its spotty record in this continent as mere successive waves of migrations from Eurasia.

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REFERENCES

ALCALÁ, L. & MORALES, J. 1997. A primitive caprine from the Upper Vallesian of La Roma 2 (Alfambra, Teruel, Aragon, Spain). *Comptes rendus de l'Académie des Sciences* **324**, 947–953.

ALCALÁ, L. & MORALES, J. 2006. Antilopinae (Bovidae, Mammalia) from the lower Pliocene of Teruel Basin (Spain). *Estudios Geológicos* **62**, 559–570.

ARAMBOURG, C. 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. *Publications du Service de la carte géologique de l'Algérie* (*N.S.*), *Paléontologie, Mémoire* **4**, 1–159.

ARAMBOURG, C. 1979. *Vertébrés villafranchiens d'Afrique du Nord* (*Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux*). Paris, Fondation Singer-Polignac.

BIBI, F., BUKHSIANIDZE, M., GENTRY, A.W., GERAADS, D., KOSTOPOULOS, D.S. & VRBA, E. 2009. The fossil record and evolution of Bovidae: State of the field. *Palaeontologia Electronica* **12**, 1–11.

BIBI, F., VRBA, E. & FACK, F. 2012. A new African fossil caprin and a combined molecular and morphological bayesian phylogenetic analysis of caprini (Mammalia: Bovidae). *Journal of Evolutionary Biology* **25**, 1843–1854.

BOHLIN, B. 1935. Cavicornier der Hipparion-Fauna Nord Chinas. *Palaeontologia Sinica* **9**, 1–166.

BOUVRAIN, G. & BONIS, L. DE. 1988. Découverte du genre *Hispanodorcas* (Bovidae, Mammalia) dans le Turolien de Grèce septentrionale. *Annales de Paléontologie* **74**, 97–112.

BOUVRAIN, G. & BONIS, L. DE. 2007. Ruminants (Mammalia, Artiodactyla: Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). *Annales de Paléontologie* **93**, 121–147.

GENTRY, A.W. 1971. The earliest goats and other antelopes from the Samos Hipparion fauna. *Bulletin of the British Museum* (*Natural History*) *– Geology* **20**, 231–296.

GENTRY, A.W. 2000. Caprinae and Hippotragini (Bovidae, Mammalia) in the Upper Miocene. **In**: Vrba, E.S. & Schaller, G.B. (eds), *Antelopes, Deer and Relatives*: *Fossil Record, Behavioral Ecology, Systematics and Conservation*, 65–83. New Haven, Yale University Press.

GENTRY, A.W. 2003. Ruminantia (Artiodactyla). **In**: Fortelius, M., Kappelman, J., Sen, S. & Bernor, R.L. (eds), *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, 332–379. New York, Columbia University Press.

GENTRY, A.W. 2010. 38 – Bovidae. **In**: Werdelin, L. & Sanders, W.J. (eds), *Cenozoic Mammals of Africa*, 741–796. Berkeley, University of California Press.

GERAADS, D. 1989. Vertébrés du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie centrale). Comparaisons biostratigraphiques. *Géobios* **22**, 777–801.

GERAADS, D., GÜLEÇ, E. & KAYA, T. 2002. *Sinotragus* (Bovidae, Mammalia) from Turkey and the late Miocene Middle Asiatic Province. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **8**, 477–489.

GERAADS, D., BLONDEL, C., LIKIUS, A., TAISSO MACKAYE, H., VIGNAUD, P. & BRUNET, M. 2008. New Hippotragini (Bovidae) from the late Miocene of Toros-Menalla, Chad. *Journal of Vertebrate Palaeontology* **28**, 231–242.

GINSBURG, L. 1977. Les carnivores du Miocène de Beni Mellal. *Géologie Méditerranéenne* **4**, 225–240.

GRAY, J.E. 1821. On the natural arrangment of vertebrose animals. *London Medical Repository* **15**, 296–310.

HARRIS, J.M. 2003. Bovidae from the Lothagam succession. **In**: Leakey M.G. & Harris J.M. (eds), *Lothagam – The Dawn of Humanity in Eastern Africa*, 531–582. New York, Columbia University Press.

HEINTZ, E. 1973. Un nouveau bovidé du Miocène de Beni Mellal, Maroc: *Benicerus theobaldi* n.g., n.sp. (Bovidae, Artiodactyla, Mammalia). *Annales Scientifiques de l'Université de Besançon* **18**, 245–248.

JAEGER, J.-J. 1977. Les rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata* **8**, 1–166.

KOSTOPOULOS, D.S. 1997. The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia. 1. The fossiliferous site 'Apollonia-1', Mygdonia basin of Greece. *Geodiversitas* **19**, 845–875.

KOSTOPOULOS, D.S. 2005. The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkasdağı, Turkey. *Geodiversitas* **27**, 747–791.

KOSTOPOULOS, D.S. 2009. The late Miocene Mammal faunas of the Mytilinii basin, Samos Island, Greece: new collection. 14. Bovidae. *Beiträge zur Paläontologie* **31**, 305–349.

LALUEZA-FOX, C., CASTRESANA, J., SAMPIETRO, L., MARQUES-BONET, T., ALCOVER, J.A. & BERTRANPETIT, J. 2005. Molecular dating of caprines using ancient DNA sequences of *Myotragus balearicus*, an extinct endemic Balearic mammal. *BMC Evolutionary Biology* **5**, 70.

LEHMANN, U. & THOMAS, H. 1987. Fossil Bovidae (Mammalia) from the Mio-Pliocene of Sahabi, Libya. **In**: Boaz, N.T., El-Arnauti, A., Gaziry, A.W., Heinzelin, J. de & Dechant Boaz, D. (eds), *Neogene Paleontology and Geology of Sahabi*, 323–335. New York, Alan R. Liss.

NAKAYA, H., PICKFORD, M., YASUI, K. & NAKANO, Y. 1987. Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *African Study Monographs* **5**, 79–129.

ROBINSON, P. 1972. *Pachytragus solignaci*, a new species of caprine bovid from the Late Miocene Beglia Formation of Tunisia. *Notes du Service Géologique de Tunisie* **37**, 73–94.

ROBINSON, P. 1986. Very hypsodont antelopes from the Beglia Formation (central Tunisia), with a discussion of the Rupicaprini. *Contributions to Geology, University of Wyoming Special Paper* **3**, 305–315.

ROPIQUET, A. & HASSANIN, A. 2005. Molecular phylogeny of caprines (Bovidae, Antilopinae): the question of their origin and diversification during the Miocene. *Journal of Zoological Systematics and Evolutionary Research* **43**, 49–60.

SCHAFER, A.B.A. & HALL, J.C. 2010. Placing the mountain goat: a total evidence approach to testing alternative hypotheses. *Molecular Phylogenetics and Evolution* **55**, 18–25.

SOLOUNIAS, N. 1981. The Turolian Fauna from the Island of Samos, Greece, with special emphasis on the hyaenids and the bovids. *Contributions to Vertebrate Evolution* **6**, 1–232.

THOMAS, H., MORALES, J. & HEINTZ, E. 1982. Un nouveau Bovidé (Artiodactyla, Mammalia), *Hispanodorcas torrubiae* n.g., n.sp., dans le Miocéne supérieur d'Espagne. *Bulletin du Muséum national d'Histoire naturelle* **4**, 209–222.

VERESCAGIN, N., ALEXEJEVA, L., DAVID, A., BAIGUSHEVA, V. 1971. [Tribe Tragelaphini Sokolov, 1953]. **In:** Nikiforova, K. (ed.), *Pleistocene of Tiraspol*, 165–170. Shtiintsa, Chisinau [in Russian].

VRBA, E.S. 1997. New fossils of Alcelaphini and Caprinae (Bovidae: Mammalia) from Awash, Ethiopia, and phylogenetic analysis of Alcelaphini. *Palaeontologia africana* **34**, 127–198.

WERDELIN, L. & PEIGNÉ, S. 2010. 32 – Carnivora. **In**: Werdelin, L. & Sanders, W.J. (eds), *Cenozoic Mammals of Africa*, 603–657. Berkeley, University of California Press.

ZOUHRI, S., GERAADS, D., EL BOUGHABI, S. & EL HARFI, A. 2012. Discovery of an Upper Miocene Vertebrate fauna near Tizi N'Tadderht, Skoura, Ouarzazate Basin (Central High atlas, Morocco). *Comptes-rendus Palevol* **11**, 455–461.