A NEW BOVID, *ASOLETRAGUS GENTRYI* N. GEN. ET SP., FROM MONTE TUTTAVISTA (OROSEI, EASTERN SARDINIA, ITALY)

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Abstract. This work describes a new bovid, *Asoletragus gentryi* n. gen. et sp., from the Late Pliocene/Early Pleistocene fossiliferous fissure fillings (Cava VI, 3) in the karst network at Monte Tuttavista (Sardinia, Italy). It differs from other genera in its straight, almost conical, horn-cores, which diverge slightly from the sagittal plane, are very close together at their bases and slant strongly backwards (nearly parallel to the glenoid surface of the temporal bone). The very peculiar shape and position of these horn-cores render their phylogenetic relationship with other taxa from the Miocene of Europe and other circum-Mediterranean countries uncertain. Given the global features of the horn-cores and the absence of any alcelaphine-like tooth in the Monte Tuttavista samples, the hypothesis that *Asoletragus* belongs to an archaic "Caprinae" cannot be ruled out, despite the presence of quite a large frontal sinus rising through the pedicel and at least one-third of the horn-core proper. Pending the discovery of other fossils from this taxon, one may only hypothesize regarding its phylogeny.

Riassunto. Viene descritto un nuovo bovide, *Asoletragus gentryi* n. gen. et sp., proveniente dalla breccia ossifera della fessura carsica (Cava VI, 3) del Monte Tuttavista (Sardegna, Italia). Il nuovo taxon è caratterizzato dal peculiare impianto sul cranio dei cavicchi ossei, che sono diritti, conici e molti inclinati all'indietro (pressoché paralleli alla superficie temporale del temporale); le basi dei cavicchi sono molto ravvicinate medialmente, gli assi sono moderatamente divergenti. Questi peculiari tratti morfologici da un lato differenziano *Asoletragus* da tutti gli altri bovidi riconosciuti nel Neogene dell'area mediterranea, dall'altro rendono difficile ipotizzarne le possibili relazioni filogenetiche. Dato l'assetto dei cavicchi ossei e la mancanza di denti con caratteri alcelafini nel materiale fino ad ora recuperato nelle fessure di Monte Tuttavista, l'ipotesi che *Asoletragus* sia ascrivibile ad un taxon primitivo delle "Caprinae" non è da escludersi, malgrado la presenza di un largo seno frontale che penetra per almeno un terzo dell'altezza all'interno del cavicchio. Tuttavia, in attesa dell'acquisizione di nuovi dati, le relazioni filetiche di questo taxon permangono ipotetiche.

Introduction

Monte Tuttavista (Eastern Sardinia, Italy) is one of the major localities for Neogene-Quaternary fossil vertebrates in Sardinia. In 1995, some fossil remains were found in this area, after quarrying had led to the discovery of a number of fossiliferous deposits (Ginesu & Cordy 1997; Sondaar 2000; Abbazzi et al. 2004a) (Fig. 1). These remains yielded important information, opening up new perspectives on the biochronology of Sardinian fauna and the palaeobiogeography of the Mediterranean area.

Starting in 1998, the Ministry of Culture (Ministero per i Beni e le Attività Culturali) has sponsored research projects coordinated by experts from the Nuoro office of the Archaeological Service (Soprintendenza per i Beni Acheologici) whose constant supervision of quarrying activity has led to the discovery of a considerable number of fossiliferous cavities and fissures documenting the evolution of Sardinian fauna from at least the Late Pliocene to the Late Pleistocene or Holocene.

The most interesting area from a palaeontological standpoint extends for about 3 km² and is part of an

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Fig. 1   - Location map of the Monte Tuttavista area (dot in black).

imposing Mesozoic limestone massif (Dieni & Massari 1966; Dieni et al. 1966; Calvino et al. 1972) tending northeast/southwest and forming a line of mountains, the most prominent of which is Monte Tuttavista (836 m a.s.l.). These structural heights were affected by extensive karst activity producing characteristic karst surfaces such as karrens, cavities, cracks, niches, as well as vertically-oriented fissures of different shapes and sizes, created by intense limestone fracturing. Thus far, about twenty-three fossiliferous fissures containing abundant fossil vertebrate remains have been found within this vast karst network, and more than 85,000 fossil remains have been retrieved. Preliminary analysis has identified about 70 taxa: four fish species, four amphibians, ten reptiles, twenty-four birds and twenty-seven to twenty-nine mammals (one talpid, two soricids, one vespertilionid, two glirids, one gerbillid, two arvicolids, two murids, two ochotonids, one leporid, one cercopithecid, one hyaenid, three mustelids, one or two canids, one or two suids, two cervids and four bovids) (Abbazzi et al. 2004a, references therein and unpublished data).

More than 1500 bovid specimens have been collected from 6 fissures. There are very few well-preserved, complete bones, synsedimentary breakages and fractures are frequent, but there are also a few articulated bones.

The aim of the present paper is to describe a partial skull with highly peculiar features, found in the "Cava VI, 3 antica" fissure, in a LFA belonging to the "Capo Figari/Orosei 1 faunal sub-complex" (sensu Palombo, in press) (Fig. 2), along with *Talpa tyrrhenica, Nesiotites* sp. II, *Macaca* aff. *M. majori, Tyrrhenoglis* cf. *T. figariensis, Rhagamis minor, Prolagus* aff. *P. sardus, Oryctolagus* aff. *O. lacosti, Mustela* sp., *Pannonictis* sp., *Sus* cf. *S. sondaari, Nesogoral* sp. 1 cf. *N. melonii* and *Nesogoral* sp. 2 (Abbazzi et al. 2004a). The Monte Tuttavista specimen described here is completely different from all other bovids known to date in the Mediterranean region, and clearly belongs to a new taxon.

Systematic palaeontology

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Classe **Mammalia** Linnaeus, 1758

Order **Artiodactyla** Owen, 1848

Family Bovidae Gray, 1821

Genus *Asoletragus* gen. n.

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Derivatio nominis: from *Asole*, the surname of the person who retrieved and prepared the Monte Tuttavista specimen, and Τράγος, the Greek word for goat.

Species type: *Asoletragus gentryi.*

As the genus is monotypic, stratigraphical distribution, geographical distribution, and diagnosis are the same as for the species.

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Asoletragus gentryi n. sp.

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1904 - Caprinae nov. gen. nov. spec.: Rook et al., tab. 8, p. 22
2004 - Bovidae gen. et sp. nov.: Abbazzi et al. (2004a), p. 633

Derivatio nominis: dedicated to the English palaeontologist Alan W. Gentry, for his notable contributions to the study of fossil bovids.

Holotypus. Incomplete skull OR VI 1179 with horn-cores, part of the frontal bones and part of the base of the skull, with the glenoid articular surface for the mandibular condyle.

Depositorium. Soprintendenza ai Beni Archeologici delle Province di Sassari e Nuoro (Nuoro, Sardinia, Italy).

Locus typicus. Monte Tuttavista, Nuoro (Sardinia, Italy), Cave VI, fissurae "3 antica"

Stratigraphic distribution. Late Pliocene?-earliest Pleistocene?

Geographical distribution. Recorded only from Sardinia.

Diagnosis. Small-sized bovid with conical horn-cores (slightly flattened on posterolateral side), with no defined keels, transverse ridges or deep longitudinal grooves; horn-cores are straight (their axes have absolutely no torsion), strongly inclined backwards (their axes lie parallel to the glenoid articular surface for the mandibular condyle), slightly divergent from the sagittal plane and very close to each other at their base, where they are separated by a narrow "V"- shaped groove. Horn-cores are inserted on the posterior half of orbits: the pedicel is visible only on the medial side, while the curved anterior edge of the
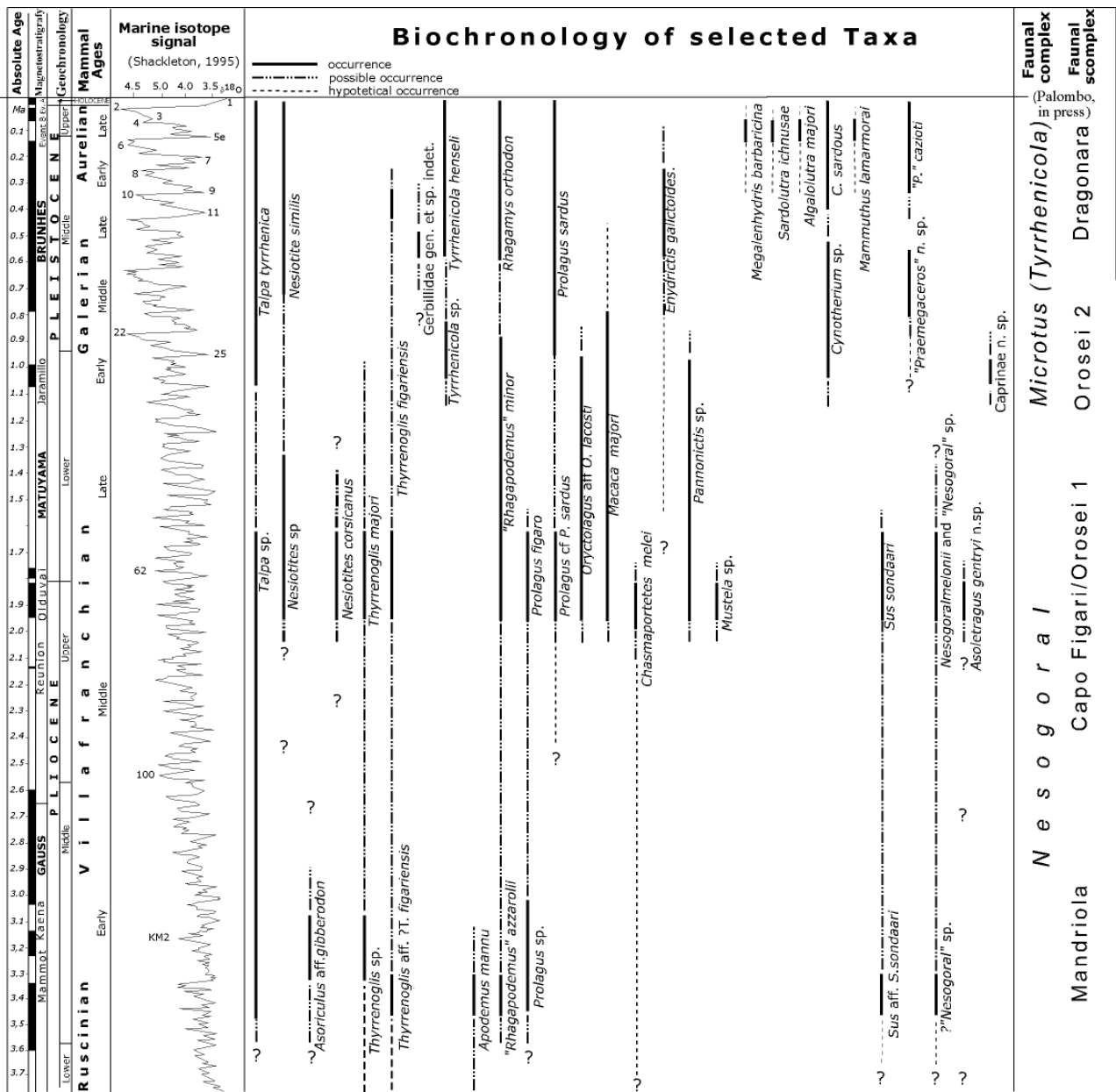
Fig. 2 - Biochronological scheme of the Plio-Pleistocene Sardinian mammalian faunas (Palombo in press, modified).

horn-core extends over the frontal bone, reaching the middle limit of the orbit. Frontal sinuses are well-developed, and quite a large sinus rises through the pedicel and at least one-third of the horn-core proper.

Description. The specimen consists of an incomplete skull, with horn-cores broken at the tips; the portion of the frontal bones posterior to the supraorbital foramina, small portions of the parietal, temporal and sphenoid bones and a partial natural endocast are preserved. The skull is slightly damaged but not deformed; the right side, with a rather complete horn-core, is the best-preserved portion (Fig. 3).

The most peculiar feature of this taxon is the orientation of the straight, conical, horn-cores, which are tilted backwards. On the posterior side, the base lies on

the parietal bones (Fig. 3b). In lateral view, the horn axes are almost parallel to the glenoid articular surface. In anterior view, the axes diverge slightly from the sagittal plane (Tab. 1). In addition, the basal medial edges of the horn-cores are very close together (Fig. 3a), and the point of minimal distance definitely lies behind the orbit. The pedicels are very reduced in size and restricted to the medial side of the horn-cores. The anterior edge of the right horn-core (the best preserved part) extends over the frontal bone, reaching the middle part of the orbit (Fig. 3).

This problematical horn-core inclination might be regarded as having derived from deformation forces during the fossilisation process, particularly taking into consideration the slight break between the back of the
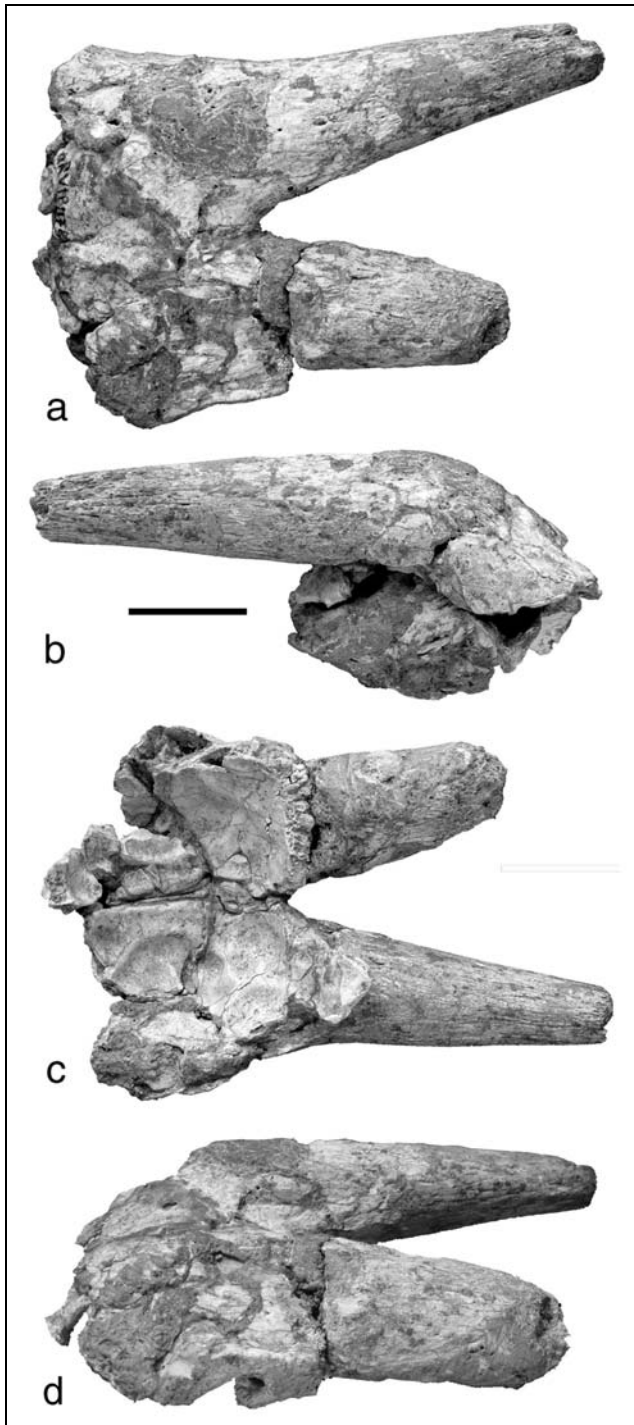
Fig. 3 - *Asoletragus gentryi* n. gen. et sp., Monte Tuttavista, Cava VI, 3: incomplete skull (OR VI 1179) in a) dorsal view; b) right lateral view; c) ventral view; d) left dorso-lateral view of the skullcap. Scale bar 2 cm.

Horn-cores	right	left
Horn-core height	> 61	> 43
Max TD at the base	25.0	20.4
Max APD at the base	26.8	19.2
TD at 1 cm from the base	22.5	18.5
APD at 1 cm from the base	21.2	19.0
TD at 2 cm from the base	19.5	18.2
APD at 2 cm from the base	20.3	19.5
TD at 3 cm from the base	17.0	16.4
APD at 3 cm from the base	17.4	18.6
TD at 4 cm from the base	14.7	13.6
APD at 4 cm from the base	-	-
TD at 5 cm from the base	12.5	-
APD at 5 cm from the base	12.0	-

Angle (measured on the right side)	
Horn-axis and frontal	21°
Horn-axis and parietal	48°
Horn-axis and saggittal plane	13°

Skull	
Min length of parietal bones	~ 54
External width at the base of the horns	58.4

Tab. 1 - *Asolotragus gentryi* n. gen. et sp.; horn-core and skull measurements (in mm). Measurements of the diameter of the horn-cores above the base are taken along their axis, starting from the posterior edge. TD = transverse diameter; APD = antero-posterior diameter.

verse break, and the huge internal sinus facilitated its compression. This section is relatively oval and its plane is steeply inclined backwards in relation to the right horn-core. There is no reason to believe that the orientation of the *Asoletragus'* right horn-core has undergone any further deformation or breakage, a view confirmed by the X-rays (Fig. 4), as well as by the preservational state of the braincase and endocranial roof (Fig. 3c and Fig. 5).

The particular features characterising the *Asoletragus* horn-cores, notably different from those already observed in *Nesogoral* specimens (see below), should be considered sufficient for the erection of a new genus, since they are not present as a group seen together in any extant or extinct bovid genera.

The horn-cores are rather large, stout (Tab. 1) and conical in shape. They taper regularly towards the apex, have elongated triangular longitudinal sections and a slender triangular profile, both in lateral and anterior views. The well-preserved right horn-core displays a nearly circular cross-section over its entire length (Fig.

horn base and the braincase roof. However, plastic deformation has never been observed on the fossil remains thus far retrieved from Cava VI, although many specimens found in the Monte Tuttavista karstic fillings have undergone synsedimentary breakages and fractures. In the present case, the left horn-core of the *Asoletragus* skull was broken (Fig. 3d), as indicated by the trans-
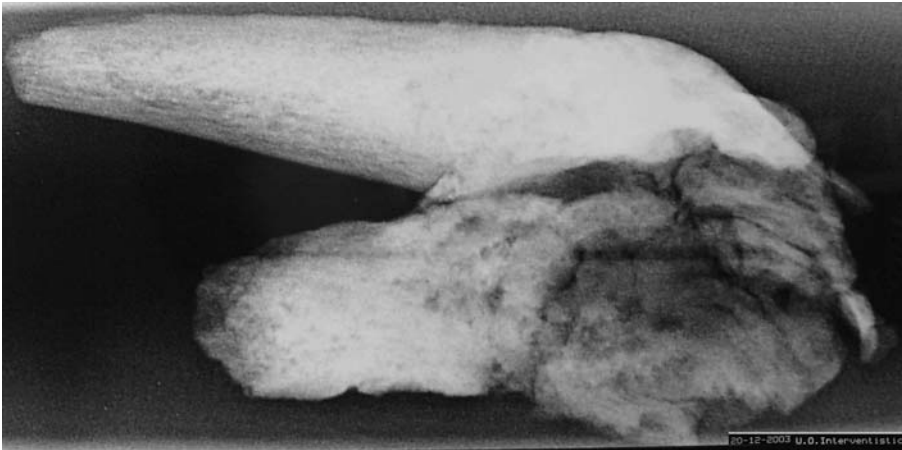
Fig. 4 - *Asoletragus gentryi* n. gen. et sp., Monte Tuttavista, Cava VI, 3. X-ray photographs of the incomplete skull (OR VI 1179): right-side lateral view.

6); only the posterior side is slightly flattened near the base. The horn-core surface is smooth, without grooves, transversal ridges or distinct keels; the inner structure of the horn-cores is made up of spongy tissue. A large sinus rises into and through the base of the horn-cores, occupying at least one-third of the core (as we can observe on the broken left one).

The horn-core has a simple base, with slightly inflated growth on its front portion. The pedicle clearly is visible only on the medial side. On the frontal bone, the curved front edge of the horn-core goes up to approximately the middle part of the orbit (Fig. 7).

The fronto-parietal suture apparently lies below the posterior base of the horn-cores (Fig. 3). Postcor-
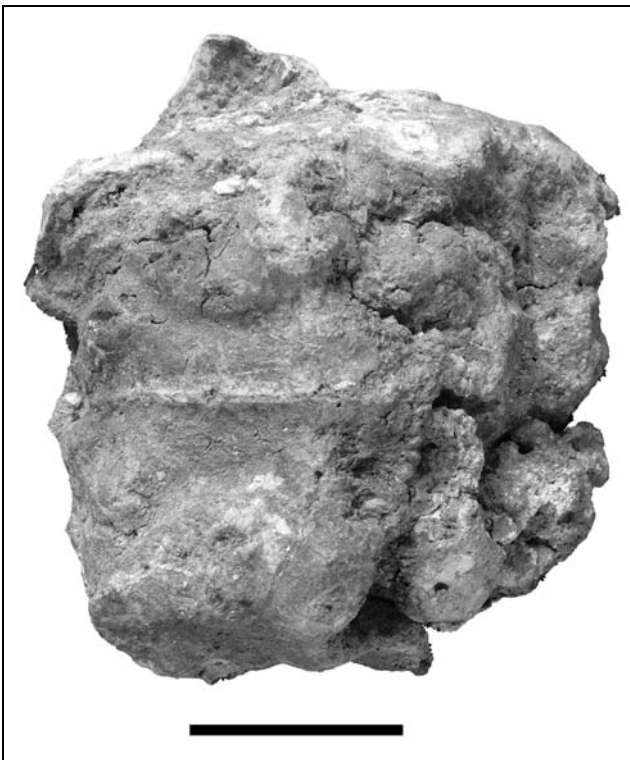

Fig. 5 - *Asoletragus gentryi* n. gen. et sp., Monte Tuttavista, Cava VI, 3. Endocranial natural cast of incomplete skull (OR VI 1179): dorsal view. Scale bar 2 cm.

nual fossae are not detectable on the rear side, due to the accentuated slope of the horn-core. Moreover, the incompletness of the skull makes it impossible to verify the presence of postcornual fossae on the lateral sides.

The frontal bones are thick, with a simple interfrontal suture. Small frontal sinuses are present at the orbits and sopraorbital foramina (Fig. 7), while more extensive ones occur on the lateral sides at the base of the horn-cores; one single large sinus rises quite far into the horn-core proper, although, judging by the X-rays, sinuses do not seem to extend deeply into it. Above its base, the horn consists of spongy tissue, and there does not seem to be a series of chambers (Fig. 5).

The glenoid articular surface for the mandibular condyle, though not complete, seems to be very large and flat. The foramina ovalia are small, and open laterally (Fig. 8). Judging by the neurocranial natural endocast, the cranial roof seems to be strongly inclined in back, which is considered an advanced character (Gentry 1992).

Comparison with the skull from the Early Pleistocene deposits at Capo Figari, a holotype of *Nesogoral melonii*, as well as with the specimens from Monte Tuttavista ascribed to *Nesogoral* sp. 1 cf. *N. melonii*, once more enable us to point out the peculiar features of *Asoletragus* horn-cores. According to Gliozzi & Malatesta's diagnosis (1980), the horn-cores of *Nesogoral melonii* are "almost straight.., extending backward on the same plane as the frontals, and very little diverging," with a frontal-horn-core angle of about 130 degrees. Moreover, we can note that, at their base, the medial sides of the *N. melonii* pedicels are separated by a flat or slightly concave surface, whose transverse extension nearly equals the transverse width of the horn-cores. It is worth noting that in the holotype of the species, as well as in Monte Tuttavista specimens, horn-cores are more slender than in *Asoletragus* (especially in the Monte Tuttavista skull from "Cava XI antilope", perhaps belonging to a female). They are also longer and less tapering than in *Asoletragus* (the diameter of their
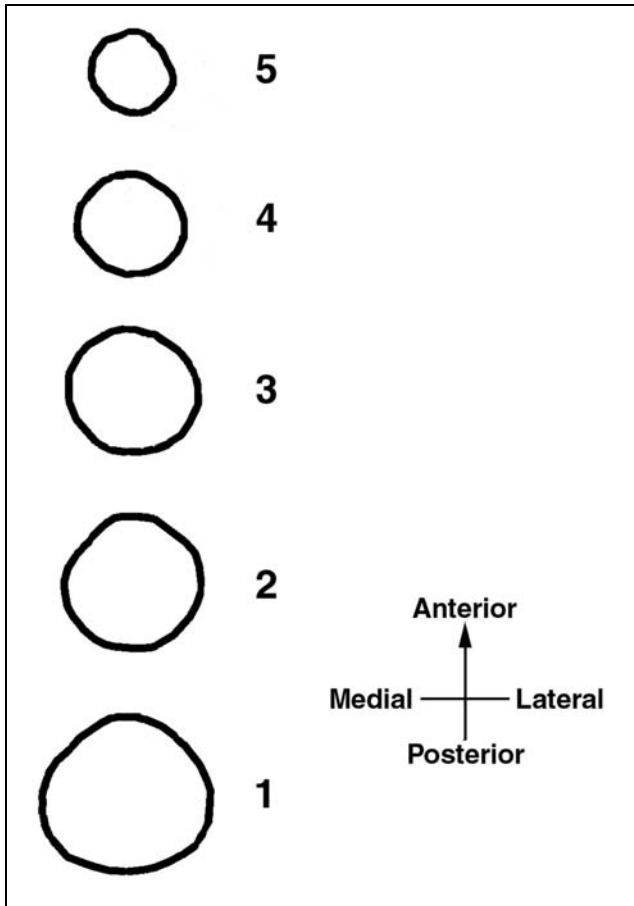
Fig. 6   - *Asoletragus gentryi* n. gen. et sp., Monte Tuttavista, Cava VI, 3. Cross-section of the right horn (OR VI 1179): 1) section at the base of the horn; 2) at 1 cm from the base; 3) at 2 cm from the base; 4) at 3 cm from the base; 5) at 4 cm from the base.
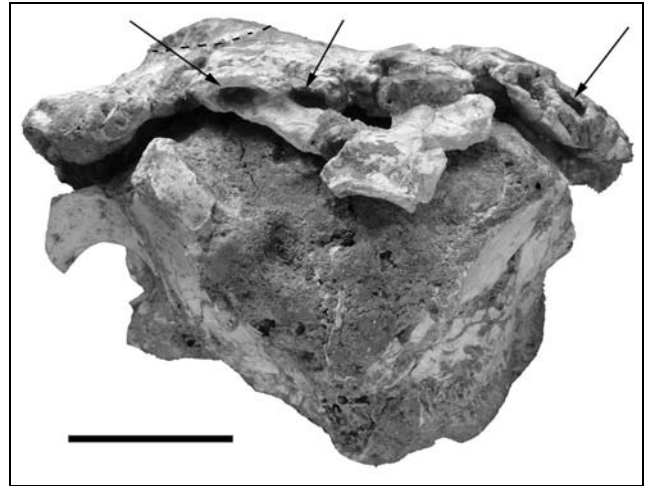

Fig. 7   - *Asoletragus gentryi* n. gen. et sp., Monte Tuttavista, Cava VI, 3. Incomplete skull (OR VI 1179) in anterior view. The dotted line indicates the anterior edges of the horn-cores; arrows show frontal sinuses. Scale bar 2 cm.

horn-cores decreases less quickly towards the tip), and thus the longitudinal triangular section appears more elongated. In addition, on the surface of the horn-cores ascribed to *Nesogoral* sp. 1 cf. *N. meloni*, more-or-less-deep grooves are evident. The pedicels are more highly developed than in *Asoletragus*, and the front edges of the horn-cores are clearly situated behind the orbits (Fig. 9).

Finally, we can observe that in the skull fragment from Monte Tuttavista (specimen n° SINuoro 1001, Or-VII-mustelide), probably belonging to a very old individual, the base of the horn-core is inflated and the horn-core itself partially re-absorbed, but the pedicel/horn-core transition is still evident and rather well marked along the whole horn-core circumference.

Discussion

The peculiar morphology of *Asoletragus* makes determining its phylogenetic relationships and envisaging its possible ancestor difficult.

Horn-cores are the most diagnostic features in bovid palaeontology, and in many extinct species only these parts have come down to us. However, *Asoletragus'* horn-cores show very peculiar features that make it difficult to distinguish plesiomorphic from apomorphic characters.

Horn-core characters in Bovidae

The occurrence of short, straight, simple (without keels or grooves) and uncompressed horn-cores is generally regarded as a plesiomorphic character in bovids. *Asoletragus* horn-cores are actually simple but rather long as compared with archaic bovids, and also stout, with very slight compression on the posterolateral side.

Moreover, the most archaic taxa are characterised by stumpy, fairly short, straight horn-cores inserted above the back of the orbit, widely separated and not divergent or only slightly so (Gentry 1992). Pedicels are more or less developed and the pedicle-horn core transition appears smooth or not well marked, but usually also visible on the anterior side. For instance, archaic bovids belonging to genus *Eotragus* have horn-cores which are triangular, straight, nearly parallel, slightly oval in cross-section and widely separated (*Eotragus sansaniensis*), but with a slight forward curvature near their tips (see *inter alios* Solounias & Moelleken 1992; Solounias et al. 1995; Ginsburg et al. 2001). Moreover, some Early or Middle Miocene *Eotragus*-like taxa from Libya (Hamilton 1973), Kenya (Gentry 1970) and Pakistan (Solounias & Moelleken 1992; Ginsburg et al. 2001) have horn-cores that show straight front and back profiles in the side view (see Solounias & Moelleken 1992 for a discussion). This primitive character is also present in several extant and extinct Cephalophini, along with

Fig. 8 - *Asoletragus gentryi* n. gen. et sp., Monte Tuttavista, Cava VI, 3. Skull (OR VI 1179) in ventral view. Scale bar 2 cm.
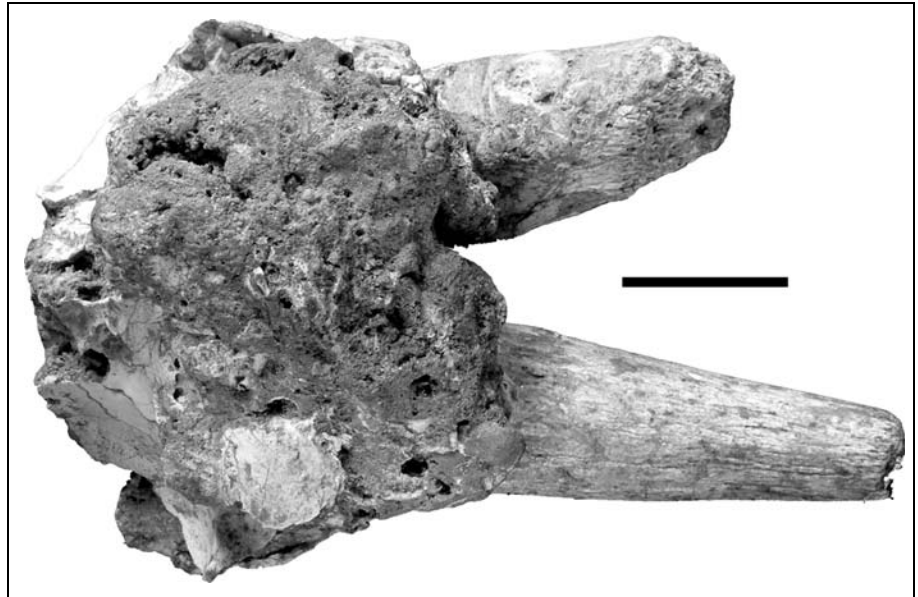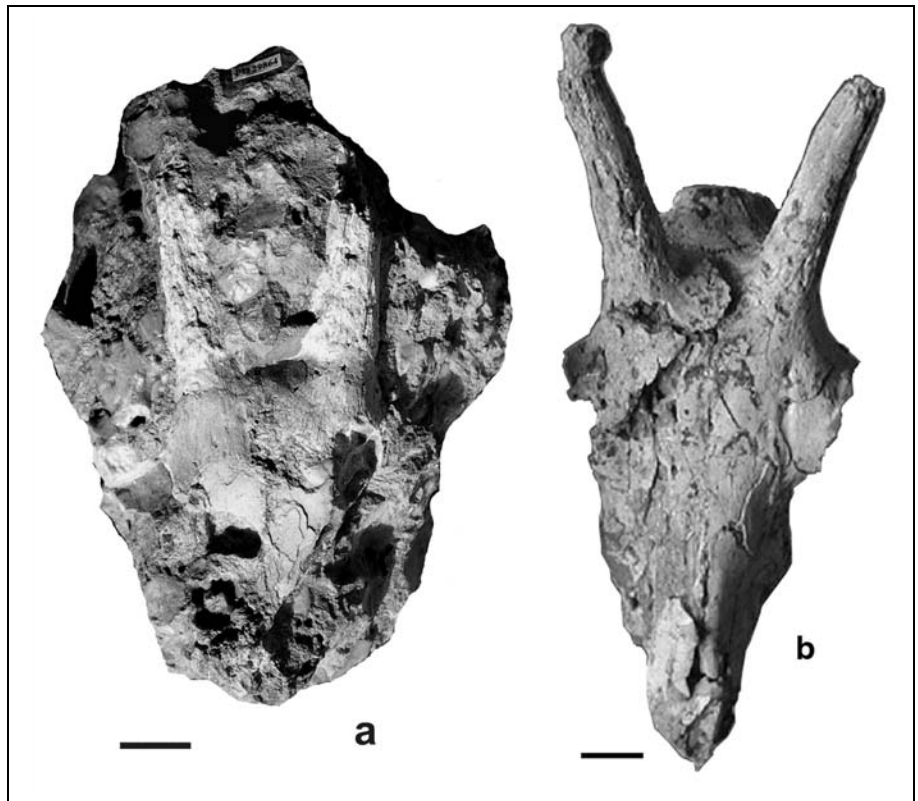

Fig. 9 - Skulls of *Nesogoral melonii* from Capo Figari (Holotype PU 29864; after the courtesy of Paleontological Museum of Department of Earth Science, Turin University) (a) and *Nesogoral* sp. 1 cf. *N. melonii* (OR XI ant 1) from Monte Tuttavista (Cava XI antilope) (b) in dorsal view. Scale bars 2 cm.

other primitive (e.g. small foramina ovalia) or advanced (e.g. insertion of horn-cores) features. *Namacerus garipensis,* a basal Middle Miocene bovid from Arrisdrift (Namibia), has short, conical horn-cores, quite similar to those of *Eotragus*. They are slightly compressed transversally, with a hint of a posterior keel (Morales et al. 2003).

In archaic bovids, triangularity is generally linked with shortness and straightness. *Asoletragus* has straight horn-cores with moderate enlargement at their posterior base (like the Middle Miocene species *Protragoceros*

chantrei, a possible Boselaphini, which has a broad horn-core base), from the side showing straight anterior and posterior profiles, although the horn-cores are shaped like a high, narrow triangle. Accordingly, the straightness and "triangular", albeit elongated, shape of *Asoletragus* horn-cores should be considered as a primitive, plesiomorphic character.

As far as the insertion of horn-cores is concerned, *Asoletragus* seems to be quite advanced in having horn-cores diverging from the sagittal plane, although closely-inserted. Accordingly, these features of the Sardi-

nian bovid should be regarded as apomorphic characters acquired in an insular environment.

Actually, large, closely-inserted and divergent horn-cores seem typical features of "Caprinae" (*sensu* Gentry 1992) [Recent molecular studies do not support the monophyly of tribal groups within the Caprinae, and some authors suggest that the whole group should be considered as a tribe (Caprini) within the Antilopinae subfamily (Hassanin & Douzery 1999; see also Hassanin et al. 1998; Gatesy et al. 1997; Mucci et al. 1998)].

Moreover, *Asoletragus* shares the reduction of the pedicel, especially on the lateral part (e.g. *Ovis*), with some representatives of this group. It is worth noting that in *Asoletragus,* on the best-preserved right side, the pedicle-horn core transition is not visible in anterior view, and it seems that the pedicle is overgrown by horn-core material except for the medial side, where the pedicle-horn core transition is quite abrupt. Most bovid taxa usually have a well-defined pedicle-horn core boundary, though some, such as *Palaeoryx* and some Alcelaphini, have a more gradual transition. Localised downgrowth over the front of the pedicel has been important in some Miocene boselaphines (Gentry, pers. Comm. to M.R.P. 2005), but an *Asoletragus*-Boselaphini relationship seems highly improbable. Horn-cores extending on the frontal bone towards the orbits are present in some taxa of the *Samotragus-Oioceros* group (Azanza et al. 1998, Fig. 1, p. 378), similar to *Asoletragus* in having horns inserted over the orbits and inclined backwards when viewed from the side, but whose section is elliptical at the base and more irregular in the distal half. In addition, some taxa in the *Samotragus-Oioceros* group, particularly *Oioceros,* differ from *Asoletragus* in the strong torsion of the horn-cores. As a result of this torsion, the anterior edge twists backwards when viewed from the side, while the posterior edge remains straight and the horns display a kind of groove that is clearly visible for half of their vertical length.

Another important feature distinguishing *Asoletragus* is the development of frontal sinuses and their extension through the base and the horn-core proper. Like "Caprinae", *Asoletragus* shows an extensive system of sinuses in the frontal area, reaching the base of horn-cores, but differs from more advanced and modern Caprini in the limited extension of sinuses into the horn-cores and the lack of a succession of chambers in the core itself. Moreover, a single large sinus that rises into and through the pedicel and then quite high into the basal part of the horn-core proper, as shown by *Asoletragus,* characterises some Alcelaphini (e.g. the extant species *Connochaetes taurinus, Damaliscus dorcas* or the extinct *Damalacra,* with sinuses well developed into the pedicels), Antilopini (e.g. *Antilope cervicapra*) and

Hippotragini (e.g *Hippotragus niger*) (Gentry 2000; Vrba & Schaller 2000).

Consequently, the typology of the sinuses in *Asoletragus* does not seem to be sufficient to clearly indicate "Caprine" affinities. On the other hand, moderately divergent horn-cores ("V"-shaped axes), more or less close at their bases, occur in extant and extinct bovids belonging to different groups. Accordingly, using horn-core morphology as the basic criterion, it is difficult to definitively and undoubtedly ascribe the Sardinian bovid to any of the Bovidae tribes, without the support of any post-cranial or dental characteristics. Unfortunately, none of the dental and post-cranial remains retrieved from the Monte Tuttavista quarries seems to fit with *Asoletragus,* mainly due to their larger size.

Phylogeny of Mediterranean island bovids: an unsolved issue

An initial hypothesis in the attempt to establish the phyletic relationships of *Asoletragus* might be that its ancestor lived in Sardinia during the Miocene. Indeed, in Sardinia, Miocene bovids have been found at Fiume Santo (Porto Torres, northwestern Sardinia) in a quite diversified but endemic fauna characterised by the occurrence of *Oreopithecus* (Cordy & Ginesu 1994; Cordy et al. 1995; Abbazzi et al. 2004b). "*Oreopithecus*" fauna from Fiume Santo shows that the Tusco-Sardinian palaeobioprovince came into existence as an isolated region during the late Miocene. Moreover, the occurrence of *Eumaioecherus* and *Agriotherium* in both Fiume Santo and Baccinello V2 (Tuscany) deposits suggests that Sardinia and Tuscany were connected during MN 12. Sardinia was possibly isolated from Tuscany before the Messinian, since the new immigrants from Europe recorded in the Baccinello V3 level (MN13) have not yet been found in Sardinia. On the other hand, *Oioceros occidentalis* from the late Messinian of Brisighella (Emilia Romagna, Italy) (Masini & Thomas 1989) is an improbable ancestor of *Asoletragus,* since it is characterised by twisted horn-cores. The bovids retrieved from Fiume Santo belong to the following taxa: *Tyrrhenotragus* cf. *T. gracillimus,* Neotragini gen. et sp. indet., a possible antelope, "*Etruria viallii*" and an unidentified bovid, whose teeth show "Caprinae" features (Abbazzi et al. 2004b), as well as the endemic alcelaphine *Maremmia* cf. *M. lorenzi,* the most abundant species. The small bovid *Tyrrhenotragus,* apparently a neotragine (Thomas 1984; Gentry et al. 1999), shares high-crowned teeth and a reduced premolar row with *Maremmia,* whereas "*Etruria*" shows less high-crowned teeth and a longer premolar row.

Like the majority of Neotragini, *Tyrrhenotragus* has quite simple horn-cores (Del Campana 1918, Tab. XIX, Fig. 13). They are straight, spike-like in shape,

very small (the antero-posterior and transverse diameters are respectively 10 and 9 mm) and are placed above the orbit, but in the posterior part and tilted backwards (lying on the fronto-nasal plane). The horn-core axes of Neotragini, and possibly *Tyrrhenotragus*, are more or less parallel to each other, and not divergent as in *Asoletragus*. Moreover, taking into consideration the small dimensions and high specialisation level of *Tyrrhenotragus*, this genus cannot be regarded as a possible forerunner of *Asoletragus*.

According to Thomas (1984) and Hürzeler (1983), *Maremmia* (specifically specimens found in lignite deposits cropping out in the Baccinello Basin, Tuscany) should be close to Alcelaphini or their ancestors. However, other authors believe (Moyà-Solà et al. 1999) that the African origin of Tuscan bovids, at least *Maremmia*, is only a hypothesis: the dental features utilised to support phylogenetic relationships with Alcelaphini might be shared, derived features or might reflect adaptation to the insular environment. Nevertheless, the horn-core features do not preclude origin from Alcelaphini stock. The spiral-horned *Maremmia* representatives are characterised by ever-growing incisors, very high-crowned teeth and a reduced premolar row. The presence of a single large sinus rising through the pedicel and quite high into the horn-core proper in both Alcelaphini and *Asoletragus* might suggest that *Maremmia* was the ancestor of *Asoletragus*. However, specialised features, as well as the spiralled horn-core morphology of *Maremmia*, seem to exclude any relationship with *Asoletragus*. On the other hand, we might suppose that the ancestor of *Asoletragus* (perhaps a "Caprinae", taking into account the close insertion of the horn-cores) may have acquired a single large sinus once it had become part of endemic island fauna.

Taking into account the teeth having "Caprinae" features recently identified at Fiume Santo, the hypothesis that the possible ancestor of *Asoletragus* was part of the Fiume Santo local faunal assemblage cannot be ruled out. Nevertheless, *Asoletragus* shows other morphological features, such as internally-solid and over-robust non-keeled horn-cores that seem to run counter to hypothesizing its "Caprinae" origin.

On the other hand, the hypothesis that the atypical horn-cores of *Asoletragus* could have been inherited directly from a Middle Miocene bovid seems difficult to prove, given the lack of any significant morphological affinities between *Asoletragus* and bovid taxa known to date in the Early and Middle Miocene of the Mediterranean area. Moreover, whether or not the "Caprinae" were part of the first radiation of Bovidae is still an open question (see *inter alio* Azanza & Morales 1994; Gentry 2000). For instance, the Middle Miocene Moroccan species *Beniceros theobaldi*, believed to belong to the "Caprinae" (Gentry 1978), shows counterclockwise torsion

(even if very limited) and a sharp anterior keel: its cross-section is not circular but pear-shaped (Heintz 1973; Chen 1988). According to Gentry (2000, p.76), the European and Turkish antelope "*Tethytragus* might be in Caprinae and close to the ancestry of the Caprini tribe." This genus differs from *Asoletragus* in having long, vertical, mediolaterally-compressed horn-cores; it seems less advanced due to to the fact that its horn-cores are more widely inserted and it has a less inclined cranial roof.

As it stands, it is reasonable to suppose that the ancestor of Sardinian endemic bovids belonging to the *Nesogoral* group did not descend from those of the Tusco-Sardinian palaeobioprovince, but arrived by means of later immigration during the Messinian, the same being true for the ancestor of *Asoletragus*. Indeed, in Sardinia, "Caprinae" have also been recorded from the Middle Pliocene Mandriola LFA on the basis of scanty tooth remains, ascribed to the endemic Sardinian genus *Nesogoral* (Van der Made 1999). The genus was recorded in Sardinia in the "*Nesogoral* faunal complex" (sensu Palombo, in press). Specimens belonging to the *Nesogoral* genus have been reported from Capo Figari (Dehaut 1911; Gliozzi & Malatesta 1980; Van der Made 1999 and references therein), Mandriola and the Campidano (Van der Made 1999, 2005) and from Capo Mannu (Carboni & Lecca 1995; Abbazzi et al., in press). The richest sample comes from Monte Tuttavista, where two different *Nesogoral* morphotypes (A and B) have recently been identified in the same fissure from which the *Asoletragus* skull was retrieved (Abbazzi et al. 2004a). Sardinian bovids belonging to the *Nesogoral* group have been regarded as "Caprinae" (Gliozzi & Malatesta 1980), like the highly-modified genus *Myotragus* from the Balearic Islands (Bover & Alcover 2000; Moyà-Solà & Pons-Moyà 1981; Moyà-Solà et al. 1999; Quetglas & Bover 1998; Palombo, in press; Palombo et al. in press). However, their ancestor(s) remains unknown. Indeed, these highly-modified taxa show numerous apomorphies obscuring their phyletic relationships. Nevertheless, as claimed by various authors, the forerunners of bovids belonging to the *Nesogoral* group probably entered Sardinia during the Messinian (see *inter alias* Van der Made 1999; Palombo et al. 2005 and references therein). Since bovids cannot swim or float, we may assume that the ancestor of *Asoletragus*, found together with such taxa, did not colonise Sardinia by water or by sweepstake dispersal, but possibly entered the island during the Messinian.

As mentioned above, some of the major shared features of "Caprinae" (straight, conical and nearly round horn-cores, slightly divergent from the sagittal plane) are also present in *Asoletragus*, whereas some other important features (such as the backwards slant

of the horn-cores) render *Asoletragus* different from both Sardinian and Balearic endemic "Caprinae".

As a result, the question remains: did the ancestor of *Asoletragus* enter Sardinia during the Messinian salinity crisis? If so, must the origin of such a peculiar endemic taxon be sought among Late Miocene continental taxa?

During the Late Miocene, several bovid taxa lived in the Mediterranean area and neighbouring regions (Gentry et al. 1999). Most of those identified come from the Greek-Iranian area (Bouvrain 1992, 1994; Bouvrain & de Bonis 1985, 1986, 1988; Bouvrain & Sen 1994; Bouvrain & Thomas 1992; Geraads 1999; Heintz 1963; Köhler 1987; Köhler et al. 1995; Kostopoulos & Koufos 1996, 1999; Roussiakis 2003) and the Iberian Peninsula (Alcalà & Morales 1997; Thomas et al. 1982), but they also dispersed towards islands and other continental regions in Europe (Alcover 1976; Bover & Alcover 1999; Gentry 1971; Masini & Thomas 1989; Romaggi 1987; Solounias 1981), as well as northern Africa (Gentry 1978; Robinson 1986; Thomas 1979).

Nonetheless, *Asoletragus*, even if it shares some features with Late Miocene bovids, acquired such peculiar characteristics during its isolation that it is difficult to recognise its possible ancestor among those bovids.

Conclusions

Despite the paucity of morphological features and biometric data available from only one incomplete specimen, *Asoletragus gentryi*, n. gen. et sp., is a well-typified taxon characterised by the peculiar shape of its horn-cores. These horn-cores present diverse features, among which it is difficult to distinguish plesiomorphic from apomorphic characters.

The horn-cores of *Asoletragus* are straight; assuming this to be a plesiomorphic characteristic, it seems that there is no relationship with spiral-horned taxa (e.g. *Oioceros*, *Protragelaphus* or *Nisidorcas*). Moreover, the general shape of the horns (with their triangular longitudinal section and surface without defined keels, transverse ridges or deep longitudinal grooves) might be a plesiomorphic characteristic (Gentry 1992, 2000; Vrba & Schaller 2000). However, horn-cores without keels, transverse ridges and deep longitudinal grooves are not of use in establishing subfamilial or tribal identity, as such features may be present or absent in several groups (e.g. Boselaphini or "Caprinae"). This is also true for extinct taxa, (among which Boselaphini *Graecoryx recticornis*, Köhler 1987), whereas *Tragoportax gaudryi* has

a differently-developed anterior keel (Moyà-Solà 1983). The horn-core of so-called "Rupicaprini" from the Beglia Formation (Robinson 1986) also has a smooth, finely-textured surface, lacking the strong groove characteristic of most bovids like *Gazella*, *Oioceros* and *Pachytragus*.

Moreover, an anterior position of the horn-core insertion, above the orbits, is a plesiomorphic feature in bovids (Robinson 1986; Gentry 1992) shared by some Late Miocene bovids belonging to different groups (e.g. *Turcoceros*, *Caprotragoides*, *Protoryx*, as well as *Gazella* II sp. by Köhler 1987). In *Asoletragus*, the insertion of the horn-cores is quite distinctive, since the anterior edge extends on the frontals to the inter-orbital line, but the medial insertion of the pedicels is clearly situated behind the orbits. Such an asymmetrical development of the visible part of the pedicels seems to be unusual among bovids. Therefore, the peculiar morphology of the horn-core base in *Asoletragus* should be regarded as an apomorphic character.

The presence of horn-cores that are closely inserted and divergent from the base, along with a frontal sinus reaching the horn-core base, leads to the conclusion that *Asoletragus* might belong to a primitive stock phylogenetically related to the "Caprinae". If this is correct, the overall shape of *Asoletragus* horns might be the result of an evolutionary process in an isolated environment, a process probably starting in the Messinian.

Considering the recent identification at Fiume Santo of teeth showing "Caprinae" features, the hypothesis that a possible ancestor of *Asoletragus* was already present before the Messinian in the Tusco-Sardinian bioprovince cannot be completely ruled out. Ongoing research will contribute to more clearly defining the colonisation time of the island and the systematic and phyletic relationships of this peculiar endemic bovid. *Asoletragus*' teeth or other parts of its skeleton are needed to clarify its phylogeny. Until they are found, all hypotheses remain highly speculative.

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