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## New bovid remains from the Early Pleistocene of Umbria (Italy) and a reappraisal of *Leptobos merlai* --Manuscript Draft--

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<b>Corresponding Author:</b>	Marco Cherin, PhD Università di Perugia Perugia, ITALY
<b>Corresponding Author Secondary Information:</b>	
<b>Corresponding Author's Institution:</b>	Università di Perugia
<b>Corresponding Author's Secondary Institution:</b>	
<b>First Author:</b>	Marco Cherin, Ph.D.
<b>First Author Secondary Information:</b>	
<b>Order of Authors:</b>	Marco Cherin, Ph.D. Vittorio D'Allestro, M.Sc. Federico Masini, Ph.D.
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<b>Abstract:</b>	<p>The extinct bovid <i>Leptobos</i> is one of the most characteristic elements of Eurasian faunal assemblages during most of the Villafranchian Land Mammal Age (i.e., from the late Pliocene to most of the Early Pleistocene). Several species of this genus have been established since the end of XIX Century, but their taxonomic status and phylogenetic relationships remain unclear due to the fact that most of them are described on the basis of scanty material. European species are divided into two groups or lineages. The first includes <i>L. stenometopon</i>, <i>L. merlai</i>, and the poorly known <i>L. furtivus</i>, the second <i>L. etruscus</i> and <i>L. vallisarni</i>. While the latter two species are well documented in the Italian Early Pleistocene fossil record, very little is known on the <i>L. stenometopon-merlai-furtivus</i> group and especially on <i>L. merlai</i>, whose richest sample is from the French locality of Saint Vallier.</p> <p>Here we describe new material of <i>L. merlai</i> from the early late Villafranchian of Umbria (central Italy), including a nearly complete female cranium and a male neurocranium with horn cores. These remains constitute the best-preserved and complete sample of <i>L. merlai</i> in the Italian Peninsula and bring new consistency to the fossil record of this species. In addition, they serve to confirm the extension of the spatial distribution of <i>L. merlai</i> to the south and of the chronological distribution of this taxon from the middle to the early late Villafranchian. Finally, we offer critical remarks on some not well defined <i>Leptobos</i> species.</p>

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## New bovid remains from the Early Pleistocene of Umbria (Italy) and a reappraisal of

### *Leptobos merlai*

Marco Cherin, Vittorio D'Allestro and Federico Masini

M. Cherin, Dipartimento di Fisica e Geologia, Università di Perugia, Via A. Pascoli, 06123 Perugia, Italy; (+39)0755852626; marco.cherin@unipg.it; corresponding author

V. D'Allestro, Via M. Buonarroti 46F, 06073 Corciano (PG), Italy; vidall@libero.it

F. Masini, Dipartimento di Scienze della Terra e del Mare, Università di Palermo, Via Archirafi 22, 90123 Palermo, Italy; federico.masini@unipa.it; senior author

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## Abstract

1 The extinct bovid *Leptobos* is one of the most characteristic elements of Eurasian faunal  
2 assemblages during most of the Villafranchian Land Mammal Age (i.e., from the late  
3 Pliocene to most of the Early Pleistocene). Several species of this genus have been  
4 established since the end of XIX Century, but their taxonomic status and phylogenetic  
5 relationships remain unclear due to the fact that most of them are described on the basis of  
6 scanty material. European species are divided into two groups or lineages. The first includes  
7 *L. stenometopon*, *L. merlai*, and the poorly known *L. furtivus*, the second *L. etruscus* and *L.*  
8 *vallisarni*. While the latter two species are well documented in the Italian Early Pleistocene  
9 fossil record, very little is known on the *L. stenometopon-merlai-furtivus* group and especially  
10 on *L. merlai*, whose richest sample is from the French locality of Saint Vallier.

11 Here we describe new material of *L. merlai* from the early late Villafranchian of Umbria  
12 (central Italy), including a nearly complete female cranium and a male neurocranium with  
13 horn cores. These remains constitute the best-preserved and complete sample of *L. merlai*  
14 in the Italian Peninsula and bring new consistency to the fossil record of this species. In  
15 addition, they serve to confirm the extension of the spatial distribution of *L. merlai* to the  
16 south and of the chronological distribution of this taxon from the middle to the early late  
17 Villafranchian. Finally, we offer critical remarks on some not well defined *Leptobos* species.

## Keywords

18 *Leptobos*, Bovidae, Early Pleistocene, Villafranchian, Italy

## Introduction

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4 The extinct genus *Leptobos* belongs to the tribe Bovini, the group of large-sized bovids  
5 that today includes buffaloes, bison, and cattle, among others. Stem Bovini represented by  
6 *Selenoportax vexillarius* occurred in the Siwaliks (southern Asia) by the upper Miocene  
7 (about 10 Ma) (Bibi et al. 2009; Bibi 2013). This is roughly in agreement with molecular data,  
8 according to which the origin of the clade should be placed about 12–11 Ma (Bibi 2013).  
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10 From 8–7 Ma, bovines spread to Africa and later to Eurasia (Bibi 2013), but the time and  
11 place of origin of the crown group are still not clear.  
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21 *Leptobos* is reported from several Eurasian localities from Spain to China, spanning  
22 biochronologically for most of the Villafranchian Mammal Age (i.e., from the late Pliocene to  
23 most of the Early Pleistocene). The northernmost—although scanty and questionable—  
24 record of *Leptobos* is in the British Isles (Breda et al. 2010). The taxon is often considered  
25 as close to the ancestry of *Bison* (Sala 1986; Duvernois and Guérin 1989; Geraads 1992;  
26 Martínez-Navarro et al. 2007; Mead et al. 2014, among others).  
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35 Characters of the cranium, especially the horn cores (absent in females), have been  
36 normally used to describe different species of *Leptobos*. Nevertheless, problems related to  
37 possible intraspecific variability including sexual dimorphism, to low sample richness in  
38 various localities, and to the difficulty of identifying diagnostic characters especially in the  
39 postcranial skeleton have hampered clarification of the systematics and phylogenetic  
40 relationships within the genus. Isolated teeth are often common in Plio-Pleistocene  
41 paleontological assemblages, but these elements have proved to be poorly suitable for  
42 species-level identification because of their high variability.  
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54 The type species *L. falconeri* was described on cranial remains from the Early  
55 Pleistocene Pinjor Stage of the upper Siwaliks (Pakistan) (Rütimeyer 1877–1878). In China,  
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57 *Leptobos* occurs for the whole Early Pleistocene, with the earliest record at Longdan (2.55–  
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2.16 Ma) and the latest at Yunxian Man Site (0.8 Ma) (Mead et al. 2014). *Leptobos brevicornis* (Hu and Qi 1978; includes *L. amplifrontalis* and *L. laochihensis* of Chi 1975) shows relatively short, nearly straight, and caudally-oriented horn cores and wide parietal, frontal and nasal areas (Qiu et al. 2004). On the contrary, the large-sized *L. crassus* (Jia and Wang 1978) has longer horn cores inclined dorsocaudally (Dong 2008). *Leptobos vallisarni* from the Early Pleistocene of Gonghe (Zheng et al. 1985; Tong et al. 2017) is the only species shared with the European region (see below).

In Europe, several species have been described in early to late Villafranchian mammal assemblages. Masini (1989) and Masini et al. (2013) recognized two different groups or lineages. The first includes *L. stenometopon*-*L. merlai*-*L. furtivus*, the second *L. etruscus*-*L. vallisarni*. Duvernois (1990, 1992) established for the above groups the two subgenera *Leptobos* (*Leptobos*) and *Leptobos* (*Smertiobos*), respectively (the author also referred to the latter subgenus the species *L. bravardi*). However, these subgenera are poorly adopted in the literature and affected by formal inconsistencies. In fact, the subgenus *Leptobos* (*Smertiobos*)—according to the original diagnosis (“Ce sous-genre correspond a *L. etruscus*, forme dont la courbure des chevilles est simple et dont les dents sont plus hypsodontes que pour le sous-genre nominal”; Duvernois 1990: 28; 1992: 6)—should also include the Indian species *L. falconeri*. Nevertheless, as the latter is the type species of the genus *Leptobos*, it should more properly be included within the nominal subgenus (Masini et al. 2013). For these reasons, here we refer to the informal evolutionary taxonomy of Masini (1989) and Masini et al. (2013).

The European documentation of the aforementioned *Leptobos* species is particularly rich in Villafranchian localities of France and Italy. Recent reviews of the Italian record (Masini and Gentili 2005; Masini et al. 2013) show that most of the paleontological sites are concentrated in the central-western part of the Peninsula, with some spots in northern Italy (Masini et al. 2013: fig. 2).

1 *Leptobos stenometopon* is a small and primitive form characterized by long and spiral-  
2 shaped horn cores and rather brachyodont teeth defined on material from Dusino  
3 (Piedmont, Italy) and quoted also from Montopoli (early and early middle Villafranchian,  
4 respectively) (Merla 1949). Duvernois and Guérin (1989) and Duvernois (1990, 1992)  
5 considered *L. stenometopon* as younger synonym of *L. elatus*. Nevertheless, the validity of  
6 the latter species (and consequently of the proposed synonymy) is questionable. *Leptobos*  
7 *elatus* was established on the basis of cranial material from Les Étouaires (Pomel 1853;  
8 Depéret 1884), but this material seems no longer available, at least in part (Viret 1954;  
9 Masini 1989). Therefore, Duvernois and Guérin (1989) and Duvernois (1990, 1992) re-  
10 defined *L. elatus* only on the basis of dental and postcranial material, offering also a  
11 description of the (unavailable) cranial material assuming that it might be comparable to that  
12 from Dusino (Masini et al. 2013). In addition, some dental and postcranial characters of *L.*  
13 *stenometopon* and *L. elatus* show significant differences (Masini et al. 2013) therefore, here  
14 we support the validity of the former taxon and the inconsistency of the synonymy with *L.*  
15 *elatus*.

16 *Leptobos merlai* is a large bovine morphologically and phylogenetically close to *L.*  
17 *stenometopon*. The species has been reported in Italy by fragmentary remains from Upper  
18 Valdarno and Castel Viscardo (Merla 1949; Masini 1989; Masini et al. 2013), whereas is  
19 well known from the French middle Villafranchian locality of Saint Vallier, whose material  
20 was originally referred first to *L. elatus* (Viret 1949), then to *L. stenometopon* (Viret 1954).  
21 De Giuli (1987) recognized significant differences between the remains from Dusino and  
22 those from Saint Vallier and proposed the name *L. merlai* for the latter. Masini (1989) gave  
23 the revised diagnosis and description of this species. *Leptobos merlai* was regarded by  
24 Duvernois and Guérin (1989) and Duvernois (1990, 1992) as a subspecies of *L. elatus* (= *L.*  
25 *stenometopon*, in their opinion), namely "*L. elatus merlai*," according to presumed

1 morphological differences “of subspecific order” between the Dusino and Saint Vallier  
2 specimens. Again, here we consider *L. merlai* as a valid species.

3 *Leptobos furtivus* is a poorly known species based on fragmentary material from  
4 Senèze, France (Duvernois and Guérin 1989). Unfortunately, the description of this small-  
5 sized form given by Duvernois and Guérin (1989) and Duvernois (1990) is based only on a  
6 single horn core, maxillary, mandible, some teeth, and postcranial elements. In Italy, the  
7 species may be present in early late Villafranchian assemblages of Tuscany (Olivola-Tasso  
8 Faunal Units; FUs) (Masini 1989; Duvernois 1990; Gentili and Masini 2005). *Leptobos* aff.  
9 *L. furtivus* is also reported from Carsoli (Masini 1989; Segre Naldini and Valli 2004; Gentili  
10 and Masini 2005). However, “this species is really difficult to be detected in the osteological  
11 collections, just as is suggested by its name (furtive, secret, stealthy)” (Masini et al. 2013:  
12 50) and the material requires new detailed studies to be properly classified.

13 *Leptobos etruscus* and *L. vallisarni* are morphologically similar and possibly strictly  
14 related. The first species is common in early late Villafranchian (Olivola-Tasso FUs) mammal  
15 assemblages of Italy (as well as in some European sites). *Leptobos etruscus* is the largest  
16 European leptobovine (estimated average weight of 350 kg; Masini et al. 2013), comparable  
17 in size to *L. crassus* from China (Mead et al. 2014). The horn cores are long, slender, shaped  
18 as a half crescent moon, and lie on the same level of the frontal area. *Leptobos vallisarni* is  
19 a large and stout species with grazing behavior (Masini et al. 2013), which occurs in the late  
20 Villafranchian (Tasso-Farneta FUs) of Italy. It is also reported from the Chinese locality of  
21 Gonghe by a complete skull (mid Early Pleistocene; Zheng et al. 1985; Tong et al. 2017),  
22 likely representing a clue to its wide Euro-Asian distribution. It differs from *L. etruscus* in  
23 having shorter and stouter horn cores, a shorter parietal roof, stronger temporal and occipital  
24 ridges and deeper and narrower temporal fossae (Masini 1989; Masini et al. 2013). The type  
25 material from the Upper Valdarno (Merla 1949), the skull from Gonghe, and the abundant  
26 collection from Pietrafitta referred to as *Leptobos* aff. *L. vallisarni* (Masini 1989; Gentili and  
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Masini 2005) are definitely different from the equivalent skeletal elements of *L. etruscus*, thus disproving the hypothesis of synonymy between the two species proposed by Duvernois (1990).

Despite the relative abundance of fossils of *L. etruscus* and *L. vallisarni* in Italy, to date very little is known on the *L. stenometopon-merlai-furtivus* group. In particular, findings referred to *L. merlai* appear to be concentrated at the locality of Saint Vallier in France. This species is represented in Italy only by a fragmented male neurocranium from the Upper Valdarno (lacking more precise stratigraphic indications) and two isolated horn cores belonging to the same individual from Castel Viscardo (Umbria), also devoid of stratigraphic information (Merla 1949; Masini 1989; Masini et al. 2013). Furthermore, the female crania from Saint Vallier, in spite of their good preservation, lack the parietal-occipital portion, which therefore was virtually unknown before this work. In this scenario, the Umbrian material described herein is of crucial importance because it represents the best-preserved and complete sample of *L. merlai* in the Italian Peninsula, and offers a unique opportunity to deepen our knowledge on this bovine's anatomy, specially on the female cranium.

## Materials and methods

The *Leptobos* sample analyzed in this work includes a female cranium (SBAU 337644), a maxillary fragment with teeth (SBAU 337650), two fragmented tibiae (SBAU 167342, 167354) from Pantalla, and a male cranium (SBAU 266661) from an unknown Umbrian site. This material was compared with the equivalent skeletal elements of European *Leptobos* stored in various museums and institutions. Specimens included in our comparative study are listed in Table 1.



1 Additional morphological and morphometric data were taken from the literature  
2 (Duvernois 1989, 1990, 1992; Duvernois and Guérin 1989; Masini 1989; Masini et al. 2013;  
3 Crégut-Bonnoure and Valli 2004; Gentili and Masini 2005).  
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5 The anatomical terminology used in this paper are mostly from Masini (1989).  
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7 Morphometric measurements are according to those adopted by Masini (1989), and  
8 were recorded to the nearest 0.1 mm with a digital caliper. Measurements taken on the  
9 cranium, teeth, and tibia are reported in Fig. 1 and Tables 2, 3, 5, 6.  
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15 All data generated or analyzed during this study are included in this published article  
16 and its supplementary information files.  
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18 *Institutional abbreviations*—IGF: Museo di Storia Naturale, Sezione di Geologia e  
19 Paleontologia, Università di Firenze; MCL: Musée des Confluences, Lyon; MGCB: Museo  
20 Geologico “Giovanni Capellini,” Bologna; MNHN: Muséum National d’Histoire Naturelle,  
21 Paris; NHMB: Natural History Museum of Basel; SBAU: Soprintendenza per i Beni  
22 Archeologici dell’Umbria, Perugia.  
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## 37 **Systematic Paleontology**

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42 Class MAMMALIA Linnaeus, 1758

43 Order ARTIODACTYLA Owen, 1848

44 Family BOVIDAE Gray, 1821

45 Subfamily BOVINAЕ Gray, 1821

46 Tribe BOVINI Gray, 1821

47 Genus *Leptobos* Rüttimeyer, 1877-1878  
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59 *Leptobos merlai* De Giuli, 1987  
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- 1 *Leptobos elatus*, Viret 1949  
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3 *Leptobos stenometopon*, Viret 1954 (partim)  
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5 *Leptobos stenometopon merlai* Duvernois in Duvernois and Guérin 1989  
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8 *Leptobos (Leptobos) elatus merlai* Duvernois 1990  
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10 *Leptobos (Leptobos) elatus merlai* Duvernois 1992  
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12 *Leptobos stenometopon*, Geraads 1992  
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15 *Leptobos (Leptobos) elatus merlai* Valli 2001  
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18 *Leptobos (Leptobos) elatus merlai* Crégut-Bonnoure and Valli 2004  
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21 *Leptobos stenometopon*, Qiu et al. 2004  
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23 *Leptobos elatus merlai* Dong 2008  
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25  
26 *Leptobos elatus merlai* Mead et al. 2014  
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#### 30 Type specimen

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32 Male cranium MCL 20.162182 (ex QSV-982), described by Viret (1954: 127–130, plate 19,  
33 fig. 2) as *L. stenometopon*.  
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#### 40 Stratigraphic and geographic range

41  
42 Middle to early late Villafranchian (“Saint Vallier” to Olivola/(Tasso?) FUs; biozones  
43 MNQ17a to MNQ18) of France and Italy.  
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#### 50 Additional new material

- 51  
52 SBAU 337644: complete female cranium with damaged nasal portion (Fig. 2a–d)  
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54 SBAU 337650: fragment of right maxilla with dP2–M1 (Fig. 2e–f)  
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57 SBAU 167342: distal fragment of left tibia (Fig. 2g–h)  
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59 SBAU 167354: distal portion of left tibia, crushed and fragmented (Fig. 2i)  
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1 SBAU 266661: male neurocranium with horn cores broken posteriorly to the orbits (Fig. 3a–  
2 g).

3 The first four specimens come from the site of Pantalla (Umbria, Italy), the fifth from an  
4 unknown Umbrian locality. Morphometric data of the five specimens are reported in Tables  
5 1–3, 5–6 and Appendices 1 and 2.  
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### 10 Geographical and geological framework

11 The site of Pantalla is located about 30 km south to Perugia (Italy; 42°52'46.79"N,  
12 12°24'23.26"E; Fig. 4). The mammal assemblage was recovered from a 15 m-thick  
13 stratigraphic succession referred to the Early Pleistocene Santa Maria di Ciciliano Unit  
14 (Gentili et al. 1997). Fossils were found in two different levels in the middle-upper portion of  
15 the succession: fluvial silty sands below, interpreted as crevasse-splay deposits; silty clays  
16 above, interpreted as a drained paleosol (Gentili et al. 1997). SBAU 337644, 337650, and  
17 167342 come from the first level, while the tibia SBAU 167354 comes from the second.  
18 Besides the bovid described in this paper, the mammal assemblage includes *Apodemus* cf.  
19 *A. dominans*, *Canis etruscus*, *Vulpes* sp., *Lynx issiodorensis valdarnensis*, *Acinonyx*  
20 *pardinensis*, *Lutraeximia umbra*, *Sus strozzi*, *Pseudodama nestii*, *Equus* sp., and  
21 *Mammuthus* cf. *M. meridionalis* (Cherin et al. 2013a, 2013b, 2014a, 2014b, 2016). From a  
22 biochronological point of view, the assemblage can be referred to the Olivola/(Tasso?) FUs  
23 (Gentili et al. 1997), in a time interval ranging approximately between 2.1 and 1.9 Ma  
24 (Nomade et al. 2014).  
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49 Unfortunately, we do not have precise information on the discovery location of the male  
50 cranium SBAU 266661, which is part of the historical “Bellucci Collection.” Giuseppe Bellucci  
51 (1844–1921) was University Chancellor, chemist, ethnographer, historian, and  
52 paleontologist in Perugia. The core of his paleontological collection (including the specimen  
53 described therein) was collected in the “surroundings of Perugia.” The fine yellow-ochre  
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1 sediment that fills the cranium is very similar to that forming the lower fossiliferous level at  
2 Pantalla (see above) and is compatible with the fluvial silty sand layers attributed to the  
3 Santa Maria di Ciciliano Unit, outcropping along most of the southwestern branch of the  
4 Tiber Basin (Fig. 4) (Basilici 1997).  
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#### 10 Revised diagnosis

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12 A middle- to large-sized *Leptobos*. Narrow forehead extending caudally. Very thick and  
13 pneumatized frontals. High and narrow intertemporal bridge. Wide nasals, small ethmoidal  
14 fissure. Supraorbital foramina located in a deep groove and placed posterior to the caudal  
15 margin of the orbits. Wide and dorsocaudally opened temporal fossae, with a horizontal  
16 furrow in the median part, both in males and females. Weak temporal crest, lying above the  
17 parietal roof. High and narrow neurocranium, tapering dorsally. Bell-shaped occipital  
18 squama, with prominent mastoid region. Well-developed external occipital protuberance.  
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20 Horn cores absent in females. In males, horn cores long, inserted caudally and dorsally with  
21 respect to the orbits, close to each other. Horn cores directed initially posteriorly then forming  
22 a wide spiral curve projecting laterally and finally frontally and slightly upwards. The  
23 caudolateral side of the horn cores shows deep parallel grooves that determine the  
24 occurrence of two keels. The horn core section is oval close to base, then becoming sub-  
25 rounded-squarish due to the occurrence of the keels. Moderately hypsodont cheek teeth.  
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27 Central cavities of the upper molars relatively simple. P4 shows incipient molarization.  
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29 Postcranial skeleton rather robust, not particularly different in proportions with respect to  
30 that of the other *Leptobos* species.  
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#### 54 Description

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57 *Cranium SBAU 337644* The cranium belongs to an adult-aged female individual as  
58 can be inferred by the wear stage of the cheek teeth and by the ossified sutures. As normally  
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1 occur in *Leptobos* (Masini 1989), females do not bear horn cores. The cranium lacks the  
2 premaxillary and nasal bones, thus preventing measurement of its total length. In the  
3 occipital region, the paraoccipital processes are missing. The collection of morphological  
4 and morphometric data was also made difficult by the ossification and/or the diagenetic  
5 obliteration of cranial sutures. Diagenetic stresses have slightly deformed the cranium,  
6 which appears dorsoventrally compressed. The frontal region is flattened and the original  
7 outline of the orbits is altered. In rostral view, the anterior part of the cranium is slightly  
8 shifted on the left side. The deformation is minimal in the occipital and ventral areas.  
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10  
11 In lateral view (Fig. 2a), the postorbital bar and the zygomatic arch are stout. The orbits  
12 are defined ventrally by a prominent facial crest and show a very pronounced posterior  
13 lacrimal process, which is included between two deep notches. The temporal fossae are  
14 long and caudally very broad, extending also on the dorsocaudal surface of the parietal roof  
15 and showing here a rounded outline. A deep horizontal furrow is present on the median part  
16 of each fossa.  
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19 In dorsal view (Fig. 2b), the nasal processes of the frontals run out very rostrally, up to  
20 the mesostyle of M2. The frontoparietal suture is not visible, while a sagittal groove crossing  
21 the line of the interfrontal suture is very clear. The frontal bosses are pronounced and  
22 located caudal to the orbits. The supraorbital foramina are placed into deep grooves located  
23 between the orbit and the frontal bosses. The parietal roof is short and delimited posteriorly  
24 by a large, rounded protuberance. The parietal crests are short, strong, and straight; they  
25 form an angle, marked by a small spur, with the ridge delimiting the temporal fossa in the  
26 frontal postorbital region, then taper running towards the external occipital protuberance,  
27 finally prolonging and curving to delimit the sides of the intertemporal bridge.  
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31 In caudal view (Figs. 2c and 5), the nuchal crest is thin and very prominent. The  
32 intertemporal bridge is very high and narrow. It is delimited laterally by the curved portion of  
33 the parietal crests. It is inclined at a wide angle to the parietal roof and at a right angle to the  
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1 occipital region. The latter is characterized dorsally by a triangular and sharp external  
2 occipital protuberance. Ventral to the protuberance develops the external occipital crest,  
3 which is wide but low. Two deep grooves are bounded medially by the external occipital  
4 crest and laterally by two subvertical convex areas (Fig. 5). The occipital squama is wide  
5 but low, semicircular in shape, and very concave. The occipital condyles are massive and  
6 projected caudally.  
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12 In ventral view (Fig. 2d), the basioccipital has a marked anterior constriction, thus  
13 showing a wedge shape. Both the occipital muscular tubercles and the pterygoid processes  
14 are slender and diverge laterally. The basioccipital is inclined at a 45° angle to the  
15 basisphenoid. Such feature, however, might be partially the result of the compression of the  
16 cranium. The pterygopalatine fossae are placed anteriorly, beyond the level of the posterior  
17 margin of M3. The palatine foramina are not visible.  
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27 The upper dentition is complete except the right P2. The teeth are moderately  
28 hypsodont and show a medium to high degree of wear.  
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32 In occlusal view (Fig. 6a), the molars show an angular and prismatic lingual outline,  
33 due to the mesiodistal constriction of lingual lobes. Styles are sharp and projecting labially.  
34 The parastyle is more developed than the meta- and (even more so) the mesostyle, with the  
35 exception of M3, in which the metastyle is as thick as the parastyle and is directed  
36 distolabially. In addition, the metastyle is delimited by a vertical furrow on the distal surface  
37 of M3, giving rise to a characteristic vertical distolingual pillar. The labial cusps of the molars  
38 are always less prominent than the styles, and the paracone fold is deeper than the  
39 metacone one. The entostyle is present in all the molars. It has a simple occlusal outline  
40 and is rather low (the entostyle of M3 is not still fused with the posterior surface of the  
41 protocone despite the advanced wear). The central cavities have a simple outline and little  
42 cement. A little spur—"bubaline fold" after Masini (1989)—is visible on the distal margin of  
43 the central cavity of the distal lobe of M3, whereas it is represented by a faint prominence in  
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1 M2 (which is more worn than M3). This indicates that the spurs are more developed in the  
2 higher part of the cavities.

3 The P4 is the largest premolar and shows a squared occlusal outline. Its appearance  
4 is strong and stout on the whole. The parastyle is much more prominent than the metastyle.  
5 The former is oriented mesiolabially, the latter distolabially. The paracone fold is wide and  
6 flattened, and separated from the parastyle by a vertical furrow. The lingual lobe is shifted  
7 mesially and exhibits an incipient molarization, being present a weak vertical furrow that  
8 separates the lobe in a mesial and a smaller distal part. The central cavity shows a very  
9 marked mesiodistal constriction and a complex outline, especially in the distal part. Some  
10 isolated enamel circles are present distolingually to the central cavity.

11 In P3 the parastyle is less projecting than that of P4. The paracone fold is oblique in  
12 labial view, shifted mesially and placed against the parastyle. A deep and narrow notch  
13 separates the paracone and the parastyle. The metastyle is very reduced and oblique in  
14 labial view. The occlusal outline of the central cavity is simpler than that of P4. This premolar  
15 does not show any trace of incipient molarization of the lingual wall.

16 The P2 is the smallest and narrowest premolar. In occlusal view, the labial outline is  
17 straight because of the "migration" of the parastyle and the paracone lobe to a mesial  
18 position. The notch separating parastyle and paracone is shallower than those of P3 and  
19 P4. The metastyle is virtually indistinct. The occlusal surface is very worn. An isolated  
20 enamel circle is visible in the mesial part of the tooth.

21 *Maxilla SBAU 337650* The maxillary fragment (Fig. 2e–f) belongs to a juvenile/subadult  
22 individual. Deciduous premolars (dP2–dP3–dP4) and the first permanent molar (M1) are  
23 preserved. The teeth show a decreasing degree of wear proceeding from dP2 to M1, with  
24 the latter almost unworn.

1 The dP2 is bilobed. In occlusal view, the mesial lobe has a sub-rounded outline, only  
2 interrupted by the pointed shape of the paracone. The distal lobe is wider than the mesial  
3 one and has a trapezoidal outline, with a rather indistinct metacone and a large and pointed  
4 metastyle. In dP3, the widths of the mesial and distal lobes are closer to each other than in  
5 dP2. The former lobe is narrower and more elongated than the distal one, with a pointed  
6 shape in mesial direction. Labially, cones and styles are compressed mesiodistally and have  
7 approximately the same height. Lingually, the mesial lobe is straight, while the distal lobe is  
8 mesiodistally compressed and pointed inwards, very similar to the homologous lobe of an  
9 upper permanent molar. The pillar of the paracone is strong and pointed. The dP4 also has  
10 two lobes and is very similar to the M1, being less hypsodont and somewhat more lightly  
11 built. The lingual cusps are compressed and acute; between them a low, small, and  
12 mesiodistally flattened entostyle occurs. The labial styles are strong; the mesostyle projects  
13 labially more than the two other styles. The central cavities are wide and simple. The lightly  
14 worn M1 is larger and more hypsodont than the dP4 and bears a low and small entostyle,  
15 being just erupted. The distal side of the central cavities of the anterior and posterior lobes  
16 shows a short spur, which likely is confined to the higher part of the crown. The parastyle is  
17 the strongest style.

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42 *Cranium SBAU 266661* The cranium belongs to an adult male. The horn cores and the  
43 neurocranium broken caudally to the orbits are preserved. The left horn core can be  
44 connected to the cranium, while the right one lacks the basal portion.

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49 In cranial view (Fig. 3b), it is evident that the base of the horn cores and the intercornual  
50 region are placed very dorsally on the braincase.

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54 In dorsal view (Fig. 3a), the forehead is narrow and elongated, and the horn cores are  
55 inserted very caudally. The intercornual area is markedly concave, with a medial swelling.  
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57 The parietal roof is short and narrow, inclined with respect to the frontal surface.  
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Dorsocaudally, the intertemporal bridge is long and narrow, delimited dorsally by a bulging tuberosity.

In caudal view (Fig. 3d), the occipital squama is bell shaped, characterized by a marked enlargement of the mastoid areas. The nuchal crest is damaged but seems very strong and protruding. The external occipital protuberance is not prominent and triangular in shape. The external occipital crest is sharp and high. Deep furrows are present laterally to the external occipital crest and in the jugular area. The occipital condyles are missing.

In lateral view (Fig. 3e), the temporal fossae are broad, especially in the caudal portion where they extend over the dorsocaudal part of the braincase. A horizontal furrow is visible on the median part of each fossa.

In ventral view (Fig. 3c), the basioccipital shows a marked anterior constriction. The occipital muscular tubercles and the pterygoid processes are strong and diverge laterally. The basioccipital and the basisphenoid are not inclined to each other.

The horn cores (Fig. 3f–g) emerge in caudal position, very close to each other. They are directed caudally and laterally to the base, then they turn laterally and cranially and rise on the frontal plane. The spiralization culminates in the tip, which is further oriented dorsally. The section is dorsoventrally flattened in the proximal third, sub-rectangular in the middle, and sub-circular in the distal third. The dorsocaudal surface is carved by a deep groove. A second, shallower groove develops below the first, without reaching half of the caudal surface. The two grooves are separated by a strong keel and another one develops dorsal to the main groove. The entire surface, especially in the caudal part, is crossed by smaller grooves parallel to the main one.

*Tibiae SBAU 167342-167545* Both the fossils are distal fragments of the left tibia, but SBAU 167545 (Fig. 2i) is very fragmented and crushed, so the morphological description of the distal articular area is based primarily on SBAU 167342 (Fig. 2g–h). In distal view, the

1 medial articular groove is more elongated craniocaudally than the lateral one. The caudal  
2 and distal extremities of the medial groove are markedly pointed. The medial malleolus is  
3 not very pronounced, while the lateral one is quite large, with rounded edges. The cranial  
4 fibular facet is smaller than the caudal one and the two are separated by a deep transversal  
5 groove.  
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10 In cranial view, the medial malleolus is thin and extends distally below the triangular  
11 process separating the two articular grooves. The surface immediately above the medial  
12 malleolus is a raised tubercle. The caudolateral margin is very inclined and runs steeply  
13 from the caudal fibular facet to the triangular process between the articular grooves. In  
14 caudal view, a distinct and deep groove begins caudally to the medial malleolus and runs  
15 vertically up the shaft.  
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## 32 **Comparative analysis**

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### 37 **Cranium**

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40 The fossil material from Umbria described herein was compared with a large sample  
41 of *Leptobos* remains kept in various European museums and institutions. Most of the  
42 comparisons were made directly by analyzing the fossils, rarely referring to bibliographic  
43 information (Table 1).  
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49 The first step was to refer the new Umbrian material to one of the two groups in which  
50 the genus *Leptobos* is divided, i.e., *L. stenometopon-merlai-furtivus* and *L. etruscus-*  
51 *vallisarni*. For this reason, focusing on the skeletal elements of interest (i.e., cranium, teeth,  
52 and distal tibia), we reviewed the anatomy of the taxa referred to the two groups, in order to  
53 identify diagnostic characters for taxonomic purposes.  
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1 The distinction of horn cores and male crania of the two groups is relatively easy, while  
2 that of female crania is more difficult. Our comparative analyses of the cranium confirm the  
3 high diagnostic value of the intertemporal region to distinguish the two *Leptobos* groups  
4 (Masini 1989; Masini et al. 2013). *Leptobos stenometopon* and especially *L. merlai* (no  
5 cranium of *L. furtivus* is known to date) are characterized by a high and narrow intertemporal  
6 bridge, delimited craniomedially by a large, rounded protuberance (see also the description  
7 of *L. merlai* from Saint Vallier in Masini 1989). Conversely, in *L. etruscus* and *L. vallisarni*  
8 the parietal roof is broader and the intertemporal bridge is flat, short, and broad. The two  
9 crania SBAU 337644 and SBAU 266661 clearly show the first condition (Figs. 7 and 8). This  
10 is supported by morphometric data (Appendix 1) reported in Fig. 9, which shows the  
11 relationship between height and breadth of the intertemporal bridge. Cranial specimens  
12 referred to *L. etruscus* and *L. vallisarni* are located in the lower part of the scatter plot, with  
13 height of the intertemporal bridge less than about 40 mm. The two new Italian finds occupy  
14 the highest positions in the graph, with values close to those of *L. stenometopon* and *L.*  
15 *merlai*. The only specimen attributed to *L. bravardi* is in the right lower part of the graph.  
16 This specimen consists of a fragmented and deformed neurocranium stored in the MNHN  
17 without catalogue number, cited by Viret (1954) as “Mus. Nat. Paris 137” and selected by  
18 Duvernois (1989) as holotype of the species. Morphometric measurements of this specimen  
19 are from Masini (1989), who actually referred the cranium to *L. elatus*.

20 Most of the other morphological differences between the two groups are concentrated  
21 in the dorsocaudal part of the cranium. In caudal view (Figs. 7a, c and 8), the external  
22 occipital protuberance is relatively more developed in *L. etruscus-vallisarni* than in *L. merlai*  
23 (the occipital region is missing in the type cranium of *L. stenometopon* from Dusino). On the  
24 contrary, the nuchal crest is much stronger in *L. merlai* than in *L. etruscus-vallisarni*, so that  
25 in lateral view, the crest hides the occipital squama in the former species (see female crania  
26 in Fig. 7b, d). The parietal crests are almost straight (or slightly concave) in *L. stenometopon-*

1 *merlai* and slightly convex in *L. etruscus-vallisarni* (Fig. 7a, c). The occipital squama is bell-  
2 shaped in males of *L. merlai* (Fig. 3d) while it is more rounded in *L. etruscus*. The specimens  
3 from Umbria fit the condition found in *L. stenometopon-merlai* for all the considered  
4 characters.  
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8 Differences between the two *Leptobos* groups are even more dramatic in the  
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10 intercornual and cornual areas. In *L. stenometopon-merlai* the horn cores are close to each  
11 other and emerge relatively posteriorly compared to the orbits and in a higher position  
12 relative to the plane of the braincase (Fig. 8). In female individuals, such as SBAU 337644  
13 and MCL 20.162182, these characters are reflected in the presence of two swollen frontal  
14 bosses placed far behind the orbits (Fig. 7a). This raised morphology of the frontals  
15 corresponds internally to an extensive development of the frontal sinuses, at least in males  
16 (Masini 1989). The horn cores of *L. stenometopon* emerge in caudolateral direction, then  
17 bend cranially, and rear up markedly on the frontal plane; finally, the tips curve sagittally  
18 moving closer to each other. The surface of the horn cores is carved by deep grooves,  
19 especially in the caudal part. The morphology of the horn cores in *L. merlai* is similar, and  
20 they differ from those of *L. stenometopon* in the larger dimensions, the more marked caudal  
21 grooves, delimiting one or two main keels, and the more markedly dorsoventrally flattened  
22 section. The horn cores of *L. furtivus* (NHMB Se202) seem morphologically similar, but  
23 smaller, than those of *L. merlai* from Saint Vallier. All the above characters are clearly visible  
24 in the male cranium SBAU 266661 from Umbria (Fig. 3a–b, f–g). Conversely, the  
25 morphology of the horn cores is completely different in *L. etruscus* and *L. vallisarni*. In these  
26 species, the intercornual area is almost flat and placed slightly over the parietal roof. The  
27 horn cores emerge immediately behind the orbits and lie on the frontal plane. *Leptobos*  
28 *etruscus* has very long slender and half-moon-shaped horn cores, while in *L. vallisarni* they  
29 are shorter and stout.  
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1 In lateral view, the most significant difference concerns the temporal fossa. In *L. merlai*  
2 and in the two crania from Umbria, the dorsocaudal margin of the fossa is rounded and  
3 expands over the dorsal part of the neurocranium, while in *L. etruscus-vallisarni*, the caudal  
4 end of the temporal fossa is more pointed and not dorsally enlarged (see the comparison  
5 between female crania in Fig. 7b, d–e). Additionally, *L. merlai* shows a characteristic  
6 horizontal furrow in the middle of the temporal fossa, which is also present in SBAU 337644  
7 and SBAU 266661 (Figs. 3e and 7b).

8 In dorsal view, *L. merlai* shows supraorbital foramina lying in deep grooves and located  
9 behind the orbits. The same can be seen in SBAU 337644 (Fig. 7a), while this part is  
10 fractured in SBAU 266661 and the supraorbital foramina are not distinguishable. *Leptobos*  
11 *etruscus*, on the other hand, generally has foramina housed in shallow sulci and placed at  
12 the height of the caudal margin of the orbits (Fig. 7c). Although fragmented, the  
13 splanchnocranium of SBAU 337644 shares with *L. merlai* a relatively wide preorbital  
14 constriction and enlarged caudal margin of nasals (both narrower in *L. etruscus-vallisarni*).  
15 Furthermore, females of *L. etruscus* (NHMB Se1736 and NHMB VA605) show very large  
16 and long ethmoidal fissures (Fig. 7d), whereas they are significantly smaller and shorter in  
17 *L. merlai* (MCL 20.162182) (Fig. 7e). Unfortunately, SBAU 337644 is fragmented right at the  
18 caudal end of nasals; however, no large and caudally-placed ethmoidal fissures appear to  
19 be present. Finally, SBAU 337644 agrees morphologically with *L. merlai* from Saint Vallier  
20 in also having a strong and pointed posterior lacrimal process on the cranial margin of the  
21 orbit.

22 From the morphometric point of view, apart from the size of the intertemporal bridge  
23 shown in Fig. 9, the analyzed sample is very heterogeneous (i.e., each species is  
24 characterized by a high degree of intraspecific variability) and dimensional characters useful  
25 in taxonomic order were not identified (Appendix 1).

## Permanent teeth

1           The detection of diagnostic characters in the cheek teeth is very difficult given their  
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3 morphological variability within the genus *Leptobos*. This also applies to the morphometric  
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5 data. Table 3 and Fig. 10 show the comparison between the tooth measurements of SBAU  
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7 337644 and the average values for *L. merlai*, *L. furtivus*, *L. elatus*, and *L. etruscus* (data  
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9 from Duvernois 1990) (morphometric data of some individual specimens are reported in  
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11 Appendix 2). As evident in Fig. 10, the measures roughly follow the same trend. Noteworthy  
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13 is only the large relative size of the first two premolars in SBAU 337644, which indeed may  
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15 be related to the wear stage.  
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20           Nevertheless, our comparative analysis allowed to recognize many morphological  
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22 similarities between the upper teeth of SBAU 337644 and those of the considered  
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24 specimens of *L. merlai* and *L. furtivus*. Table 4 summarizes these results, showing also the  
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26 differences with the teeth of *L. etruscus* and *L. vallisarni*. Many of the characters taken into  
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28 account are partially modified from Masini (1989) and Duvernois (1990). The most peculiar  
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30 tooth in the Pantalla specimen is the P4, which is characterized by a very stout and  
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32 quadrangular appearance in occlusal view (Fig. 6a). Similar teeth were not observed in any  
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34 other of the analyzed specimens, although the P4 of *L. merlai-furtivus* (Fig. 6b–c) appears  
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36 generally more squared than those of *L. etruscus-vallisarni*, which are normally shorter than  
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38 wider (Fig. 6d). The incipient molarization of this tooth observed in SBAU 337644 was also  
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40 recognized—although to a lesser degree—in some *L. merlai* specimens such as the female  
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42 MCL 20.162182 (Fig. 6b).  
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## Deciduous teeth

52           Also for deciduous teeth, the morphometric comparison (Table 5) between the  
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54 specimen from Pantalla (SBAU 337650) and those from other European sites did not allow  
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56 detecting any dimensional peculiarity of the first nor significant similarities and/or differences  
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with the examined taxa. As for permanent teeth, Fig. 11 shows that the considered measurements approximately follow the same trend in the comparative sample.

On the other hand, we recognized the following morphological characters that differentiate SBAU 337650 from *L. etruscus*, while match it with the morphology of *L. merlai* (Fig. 12):

- The dP2 is relatively stouter than in *L. etruscus*, in which it is narrow, elongated, and tapered;
- The shape of the mesial lobe of the dP3 in occlusal view is different from *L. etruscus*. In the latter species, the mesial lobe is mesially more squarish and is overall narrower than the distal lobe;
- The entostyle of dP4 is normally larger and with a more complex occlusal outline in *L. etruscus* than in *L. merlai* and SBAU 337650.

The analyzed specimens of *L. stenometopon* (IGF 2178 and IGF 3232) show a general morphology very similar to that of *L. merlai*. The only exception is the presence of a small enamel fold at the mesiolingual corner of dP3, which was found also in some *L. etruscus* specimens (e.g., NHMB VA1209). Nevertheless, the recognition of this feature may be related to the wear stage. On the whole, the morphology of the upper deciduous teeth from Pantalla are perfectly comparable with the specimen NHMB StV452 from Saint Vallier, referred to *L. merlai*.

## Tibia

The distal mediolateral diameter (DMLD) and distal craniocaudal diameter (DCCD) of the fragmented tibiae from Pantalla (SBAU 167342 and SBAU 167354) and of the comparative sample (*L. merlai*, *L. elatus*, *L. etruscus*) are almost comparable (Table 6). The average value and standard deviation of the DCCD/DMLD ratio are  $0.82 \pm 0.04$  (n=15), highlighting the overall similarity in size of the analyzed specimens. Conversely, Fig. 13

1 points to some stable morphological characters of the tibial distal epiphysis that allow to  
2 easily distinguish *L. etruscus* and *L. merlai*. In distal view, the former species shows a  
3 moderate convexity of the medial malleolus (more convex and even angular in *L. merlai*);  
4 the presence of a marked step at the caudal end of the medial malleolus (absent in *L.*  
5 *merlai*); a small difference in the relative development of the caudal margins of the articular  
6 grooves (in *L. merlai*, the caudal edge of the medial groove is point-shaped and is longer  
7 and narrower than the lateral groove); the notch separating the articular facets for the fibula  
8 in the lateral malleolus is narrow, deep, and U-shaped (wider and shallower in *L. merlai*).  
9 The distal epiphysis of *L. elatus* (NHMB Prr333) shows intermediate features between *L.*  
10 *merlai* and *L. etruscus*, while those of SBAU 167342 and SBAU 167354 fit the morphology  
11 of *L. merlai* from Saint Vallier.  
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### 30 **Additional material from Italy**

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35 In the framework of our reappraisal of the *L. stenometopon-merlai-furtivus* group in  
36 Italy we re-examined the two specimens previously described by Masini (1989), cited by  
37 Gentili and Masini (2005), figured by Masini et al. (2013), and referred by these authors to  
38 *L. merlai*.  
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45 The two horn cores from Castel Viscardo (southern Umbria; MGCB no num.) (Fig. 3h–  
46 i) are broken just near the tip. They are very long, robust, dorsoventrally flattened, and show  
47 the overall forward orientation and the morphology described above for *L. stenometopon-*  
48 *merlai-furtivus*. The caudoventral and especially the caudal keels are high and strong. The  
49 size of the horn cores (total length of about 40 cm; 66 cm following the caudal margin)  
50 suggests that the body size of this individual was remarkable, even more of the large male  
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1 MCL 20.162182 from Saint Vallier (Fig. 8c). Unfortunately, we do not have precise  
2 information on the geological context and age of the horn cores from Castel Viscardo.

3 The fragmented neurocranium of *L. merlai* MGCB 202 was collected in an unknown  
4 location of the Upper Valdarno basin (Tuscany). It shows the typical morphological features  
5 of the male crania of *L. merlai* (Fig. 8d). The frontals are elevated above the cranial roof and  
6 are carved by very large frontal sinuses; the forehead is narrow; the bases of the horn cores  
7 are close to each other and are placed very caudally; the intertemporal bridge is long and  
8 narrow, delimited cranially by a broad, triangular median protuberance; the occipital squama  
9 is bell shaped; the temporal fossae are wide and dorsocaudally enlarging over the  
10 braincase.  
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## 27 **Discussion**

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32 Our comparative analysis allows to refer the new material from Umbria (female  
33 cranium SBAU 337644, male cranium SBAU 266661, juvenile right maxilla SBAU 337650  
34 and distal tibiae SBAU 167342 and SBAU 167354) to *L. merlai*. The cranium SBAU 337644  
35 belongs to a large-sized female, which is larger than the females from Saint Vallier (see  
36 Table 2). This material adds to the horn cores from Castel Viscardo (MGCB no num.) and  
37 the neurocranium from Upper Valdarno (MGCB 202) referred to *L. merlai* by Masini (1989),  
38 and reported and figured in Masini et al (2013). The specimen SBAU 337644 is the first  
39 female skull of *L. merlai* with a preserved complete neurocranium and therefore it allows to  
40 complete the diagnosis and the description of this species, which were previously based  
41 mainly on male crania and horn cores.  
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56 These new reports are also very important from a paleobiogeographic perspective  
57 because they fully confirm the southern extension of the spatial distribution of *L. merlai*. The  
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1 type locality of Saint Vallier is referred to the biozone MN17a (Guérin et al. 2004), which  
2 corresponds to the early/middle part of the middle Villafranchian Mammal Age (Masini and  
3 Sala 2007). Nomade et al. (2014) attributed an age of about 2.5 Ma to the Saint Vallier FU,  
4 while it is considered slightly younger by Masini and Sala (2007) and Rook and Martínez-  
5 Navarro (2010). The new material from Pantalla can be instead referred to the early late  
6 Villafranchian (Olivola/(Tasso?) FUs; about 2.1–1.9 Ma), thus extending forward the last  
7 occurrence of *L. merlai* in Europe.  
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However, the difficulty in identifying diagnostic characters for taxonomic purposes in our sample leads to speculation that other remains of *L. merlai* can be “hidden” in some other European collection and have been mistakenly attributed to other species of *Leptobos*. The Italian finds definitely refresh the *L. merlai* species. Our analysis, however, opens several questions on *Leptobos* taxonomy.

Actually, a number of species erected or redefined by French scholars are based on scanty fossil record. This is the case of *L. bravardi*, *L. furtivus*, and even *L. elatus*. *Leptobos bravardi* was established by Duvernois (1989) on the basis of some material from Perrier-Les Étouaires, where also *L. elatus* is reported. Different from the latter species, *L. bravardi* has larger size and cranium with “an opened frontoparietal angle, thick temporal and mastoid crests and broad nuchal crest; horn cores, badly preserved, seem strong, tilted upwards and backwards; teeth are more hypsodont” (Duvernois 1989: 770). As well as in Perrier-Les Étouaires, Duvernois reported the co-occurrence of *L. bravardi* and *L. elatus* also in the Spanish site of Villarroya, of comparable age (MNQ 16b; early Villafranchian). However, Andrés et al. (2010) compared the humeri of *L. elatus* and *L. bravardi* from Villarroya and hypothesized that the two species are synonyms (*L. elatus* would precede) and that the size differences observed in the humerus may be related to sexual dimorphism. Consequently, Andrés et al. also questioned the subgeneric division of *Leptobos* proposed by Duvernois (1990, 1992), as also advocated by Masini et al. (2013).

Duvernois (1990) attributed, albeit with same caution, *L. bravardi* to the subgenus *Leptobos* (*Smertiobos*), i.e., taxonomically and phylogenetically close to *L. etruscus*. Leptobovines of this subgenus are diagnosed only by simple curvature of the horn cores and teeth more hypsodont than the nominal subgenus (Duvernois 1990: 28). We agree that the material referred to as *L. bravardi* might represent a good species. However, even though the measurements of the intertemporal bridge would suggest that *L. bravardi* could belong to the *L. etruscus-vallisarni* group (Fig. 9), we believe that the available material is too fragmentary to support the reliability of such a relationship.

*Leptobos elatus* is another enigmatic taxon. As anticipated in the introduction, the species was erected by Pomel (1853) and revised by Depéret (1884) on the basis of cranial material from Les Étouaires, which apparently has been lost (see also Viret 1954). Duvernois (1989) considered as lectotype an incomplete right mandible with m1–m3 (MCL FSL211219). The neodiagnosis published by Duvernois (1989: 772) describes *L. elatus* as a small-sized *Leptobos*, whose cranium is characterized by strong parietal crests, narrow intertemporal bridge, shallow temporal fossae, caudal part of the cranium slightly extending behind the pedicles, horn cores with double curvature (slightly ventral at the base, then dorsal and cranial), dorsoventral compression and longitudinal grooves, and a major dorsocaudal groove. Unfortunately, this diagnosis is very difficult to test because of the scarce cranial material available from the type locality. The neurocranium NHMB Prr431 is so damaged as to prevent the identification of significant morphological characters. Two horn cores stored at the MNHN without catalog number are attributed to *L. elatus* by Deperet (1884) and described and figured by Masini (1989). They do not present spiralization and are massive and very short (about 20 cm). The very simple morphology differentiates these horn cores from those of *L. stenometopon-merlai* as well as those of *L. etruscus* (Masini 1989), and does not fit the neodiagnosis of *L. elatus* by Duvernois (1989). Masini (1989) also described and figured a partial juvenile cranium from Roca-Neyra (MCL FSL211278).

1 The preserved part of the left horn core shows a morphology that resembles *L. merlai*, but  
2 it differs in the non-flattened section and the absence of caudal keels. This cranium shares  
3 some similarities with the holotype of *L. bravardi* such as the wide and short intertemporal  
4 bridge, the horn cores inserted laterally, the high temporal fossae, etc., but the possible  
5 attribution of the two specimens to the same taxon needs further analyses. For further  
6 discussion on the validity of the species *L. elatus* see also Masini et al. (2013: 48). According  
7 to the original descriptions of the fossils from Les Étouaires (Pomel 1853; Depéret 1884), *L.*  
8 *elatus* would seem similar to *L. stenometopon*, but the scarcity of available material does  
9 not allow confirmation of this hypothesis. Additional analyses that are beyond the objectives  
10 of this paper are needed to clarify the taxonomic status of *L. elatus* and its possible  
11 relationships with the *L. stenometopon-merlai-furtivus* group.  
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25 The validity of *L. furtivus* as a good species has been questioned by Garrido (2008).  
26 In her description of *Leptobos* material from Fonelas P-1 (Spain), she emphasized that the  
27 tooth sample shows intermediate features between *L. etruscus* and *L. furtivus*, suggesting  
28 that the latter species may be considered a younger synonym of *L. etruscus*. As a matter of  
29 fact, *L. furtivus* is represented in Europe only by few remains from Senèze (Duvernois and  
30 Guérin 1989). Masini (1989), Duvernois (1990), and Gentili and Masini (2005) also reported  
31 the occurrence of teeth and postcranial remains of *L. furtivus* in some early late  
32 Villafranchian local faunas from Tuscany, but the recognition of this material compared to  
33 that of the coeval *L. etruscus* was based partly on the smaller dimensions of the former.  
34 Actually, the absence of cranial material prevented the authors from reaching a definitive  
35 conclusion. On the basis of the descriptions of the type material from Senèze (Duvernois  
36 and Guérin 1989; Duvernois 1990), it is clear that *L. furtivus* shows affinities with *L. merlai*.  
37 In the light of all this, it is currently difficult to determine whether *L. furtivus* is a good species  
38 phylogenetically related to *L. merlai*—as suggested by Masini et al. (2013)—or a small-sized  
39 variant of the latter.  
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The description and revision of the Italian material bring new consistency to the fossil record of *L. merlai*. Actually, after being a somewhat phantom species, it is now the second best documented *Leptobos* in Italy (after *L. etruscus*), at least for what concerns the cranial material. We hope that this work may be the starting point for a reappraisal of other *Leptobos* samples, starting with those from Umbria and Tuscany (e.g., Pazzaglia et al. 2013; Rook et al. 2013, respectively) and then expanding the study to France and beyond, including Eastern Europe and eventually the Indian subcontinent and the Chinese Far East, which already yielded promising common species with the rest of Eurasia.

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## TABLE AND FIGURE CAPTIONS

**Table 1** *Leptobos* specimens analyzed for the comparative analysis

**Table 2** Cranial measurements (mm) of *Leptobos merlai* from Pantalla (SBAU 337644) and the Perugia area (SBAU 266661). Values in italics are estimated

**Table 3** Measurements (mm) of the permanent upper teeth of *Leptobos merlai* from Pantalla (SBAU 337644) compared with the minimum-maximum range (left) and average values (right) of other *Leptobos* species (sample size in brackets). Comparative data are from Duvernois (1990). The occurrence of *L. furtivus* in the Upper Valdarno needs to be confirmed (see text)

**Table 4** Comparison of selected morphological characters of the upper cheek teeth between *L. merlai-furtivus* and *L. etruscus-vallisarni*, modified from Duvernois (1990)

**Table 5** Measurements (mm) of the upper deciduous premolar and permanent first molar of *Leptobos merlai* from Pantalla (SBAU 337650) and other *Leptobos* species. Values in bold refer to erupted permanent teeth

**Table 6** Measurements (mm) of the distal tibia of *Leptobos merlai* from Pantalla (SBAU 167342 and 167354) and other *Leptobos* species

**Fig. 1** Measurements (mm) taken on the cranium (**a–e**) and on the distal epiphysis of the tibia (**f**). Measurement abbreviations are explained in Tables 2 (cranium) and 6 (tibia). A, Akrokranium; B, Basion; Br, Bregma; C, Horn core base; Ect, Ectorbitale; Ent, Entorbitale; If, Infraorbitale; N, Nasion; O, Opisthion; Ot, Otion; P, Prosthion; Pd, Postdentale; Pi, Caudal end of intertemporal bridge; Pm, Premolare; Po, Palatinorale; Rh, Rhinion; Sup, Midpoint of the line connecting the caudal end of the supraorbital foramina.

**Fig. 2** *Leptobos merlai* from Pantalla (Italy): **a–d** cranium SBAU 337644 in (**a**) lateral, (**b**) dorsal, (**c**) caudal and (**d**) ventral views; **e–f** maxilla SBAU 337650 in (**e**) labial and (**f**) occlusal views; **g–h** tibia SBAU 167342 in (**g**) distal and (**h**) cranial views; **i** tibia SBAU 167354 in distal view (black arrows indicate unremoved sediment)

1 **Fig. 3 a–e** Cranium of *Leptobos merlai* SBAU 266661 from the surroundings of Perugia  
2 (Italy) in (a) dorsal, (b) cranial, (c) ventral, (d) caudal and (e) lateral views; **f–g** horn cores  
3 of SBAU 266661 in (f) caudal and (g) cranial views; **h–i** horn cores of *Leptobos merlai*  
4 MGCB no number from Castel Viscardo (Italy) in caudal (h) and cranial (i) views  
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9 **Fig. 4** Location of the paleontological site of Pantalla (Italy). The intermontane Tiber Basin  
10 is highlighted in light grey along the middle part of the region Umbria  
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14 **Fig. 5** *Leptobos merlai* from Pantalla (Italy) in caudal view with indication of the main  
15 anatomical features  
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19 **Fig. 6** Occlusal views of the left cheek teeth of (a) *Leptobos merlai* SBAU 337644 from  
20 Pantalla; (b) *L. merlai* MCL 20.162182 from Saint Vallier; (c) *L. furtivus* MCL FSL210825  
21 (type) from Senèze (modified from Duvernois 1990); (d) *L. etruscus* NHMB Se1736 from  
22 Senèze  
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27 **Fig. 7** Cranium of female adult individuals of (a–b) *Leptobos merlai* SBAU 337644 from  
28 Pantalla; (c–d) *L. etruscus* NHMB Se1736 from Senèze; and (e) *L. merlai* MCL 20.162181  
29 from Saint Vallier. a, c dorsocaudal views (intertemporal bridge highlighted in red); b, d, e  
30 lateral views (dorsocaudal margin of temporal fossa highlighted in yellow)  
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38 **Fig. 8** Cranium of male individuals of (a) *Leptobos merlai* SBAU 266661 from the  
39 surroundings of Perugia; (b) *L. etruscus* NHMB Se792 from Senèze; (c) *L. merlai* MCL  
40 20.162182 from Saint Vallier; and (d) *L. merlai* MGCB 202 from Upper Valdarno. The  
41 intertemporal bridge is highlighted in red; the dorsal profile of the intercornual area is  
42 highlighted in yellow  
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49 **Fig. 9** Scatter plot showing the relationship between breadth and height of the intertemporal  
50 bridge in some *Leptobos* species and in the two crania described in this paper.  
51 Morphometric data used to build the chart are in Appendix 1  
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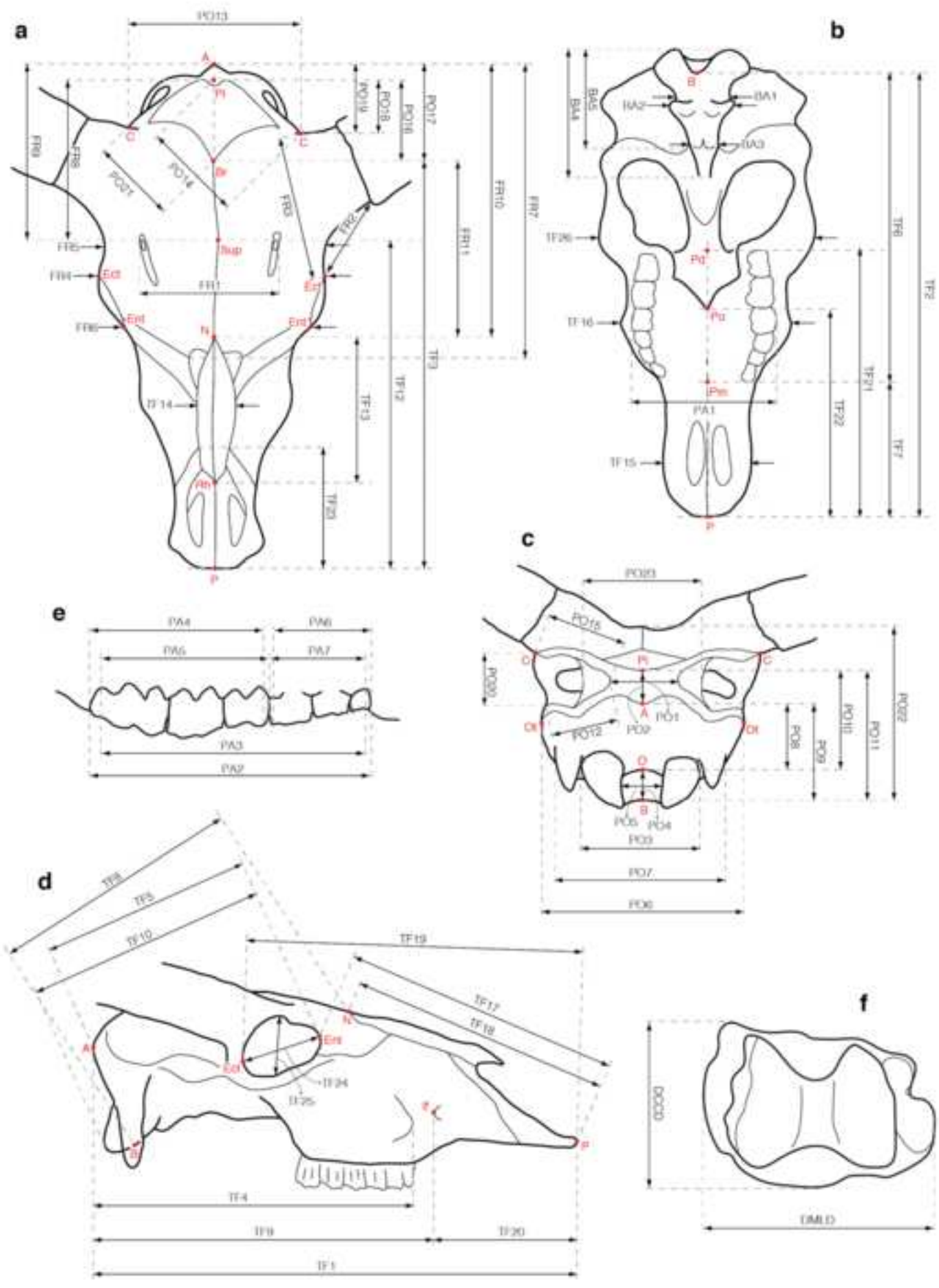
57 **Fig. 10** Logarithmic ratio diagram comparing the permanent cheek teeth of SBAU 337644  
58 with the average values of different *Leptobos* species. Log differences are on the vertical  
59 axis. Standard of comparison ( $y=0$ ) is the primitive bison *Bison menneri* from Untermassfeld  
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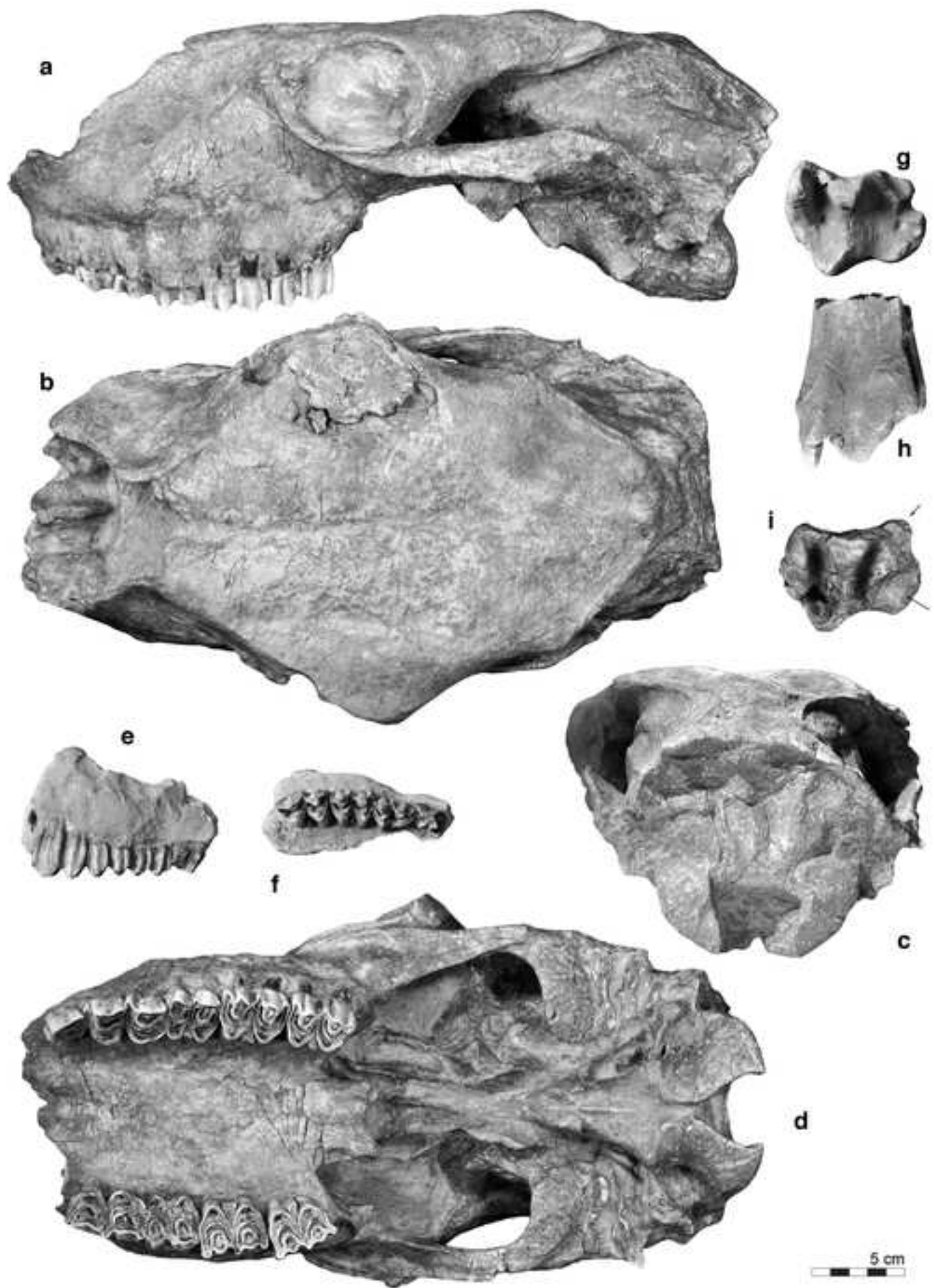
(Germany; about 1 Ma). Morphometric data on *Leptobos* used to build the chart are in Table 3. Data on *B. menneri* are from Sher (1997)

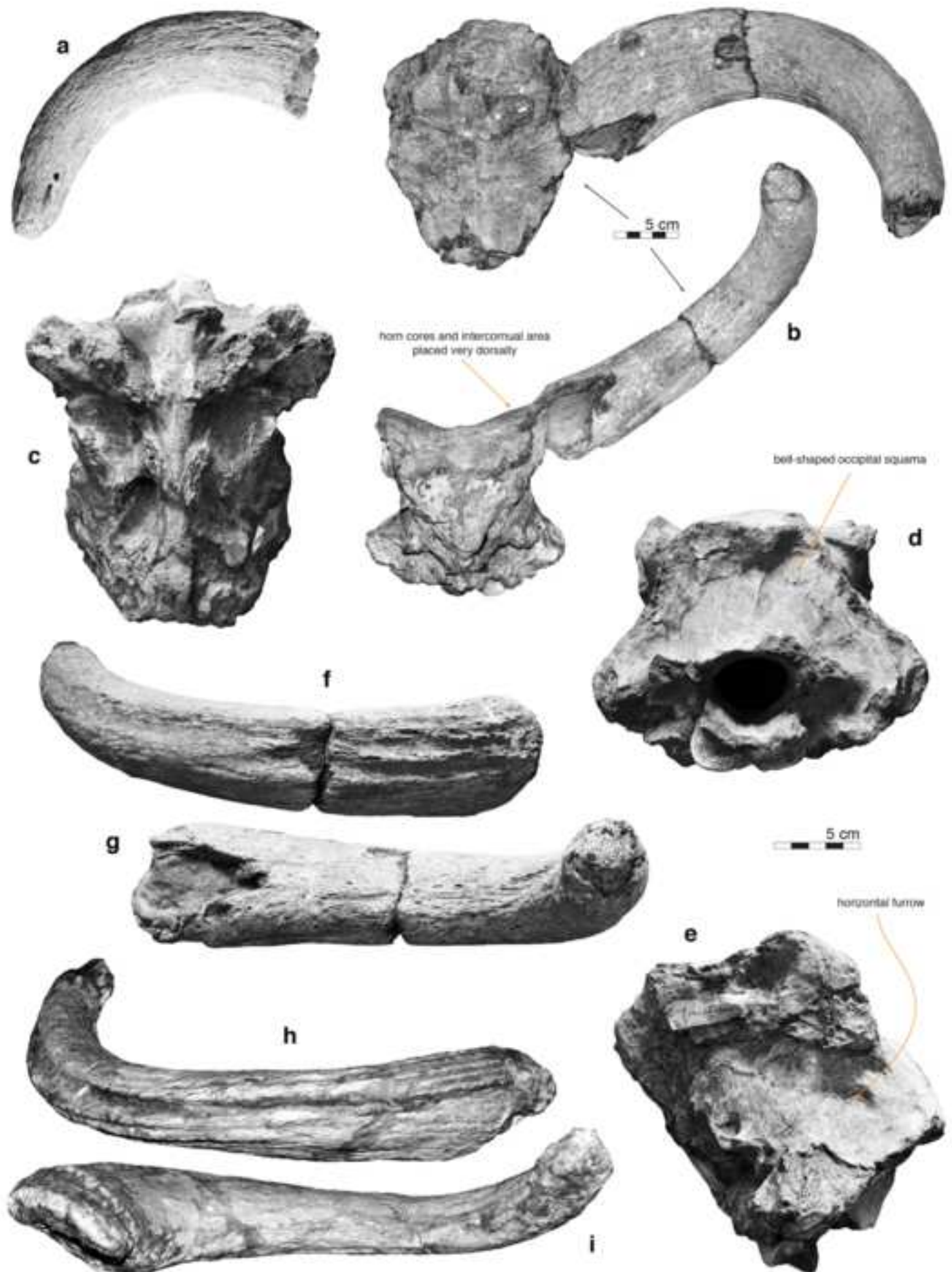
**Fig. 11** Logarithmic ratio diagram comparing the deciduous teeth of SBAU 337650 with those of individual specimens referred to different *Leptobos* species. Log differences are on the vertical axis. Standard of comparison ( $y=0$ ) is the primitive bison *Bison menneri* from Untermassfeld (Germany; about 1 Ma). Morphometric data on *Leptobos* used to build the chart are in Table 5. Data on *B. menneri* are from Sher (1997)

**Fig. 12** Occlusal views of the right deciduous teeth of (a) *Leptobos merlai* SBAU 337650 from Pantalla; (b) *L. merlai* NHMB StV452 from Saint Vallier; and (c) *L. etruscus* NHMB VA258 from Upper Valdarno

**Fig. 13** Distal views of the left tibia of (a) *Leptobos merlai* SBAU 167342 from Pantalla; (b) *L. merlai* MCL FSL496282 from Saint Vallier; and (c) *L. etruscus* IGF 2597 from Upper Valdarno. The medial margin of the medial malleolus and the notch separating the articular facets for the fibula in the lateral malleolus are highlighted in red. The caudal margin of the articulation is highlighted in yellow. The black arrow indicates the step at the caudal end of the medial malleolus in *L. etruscus*

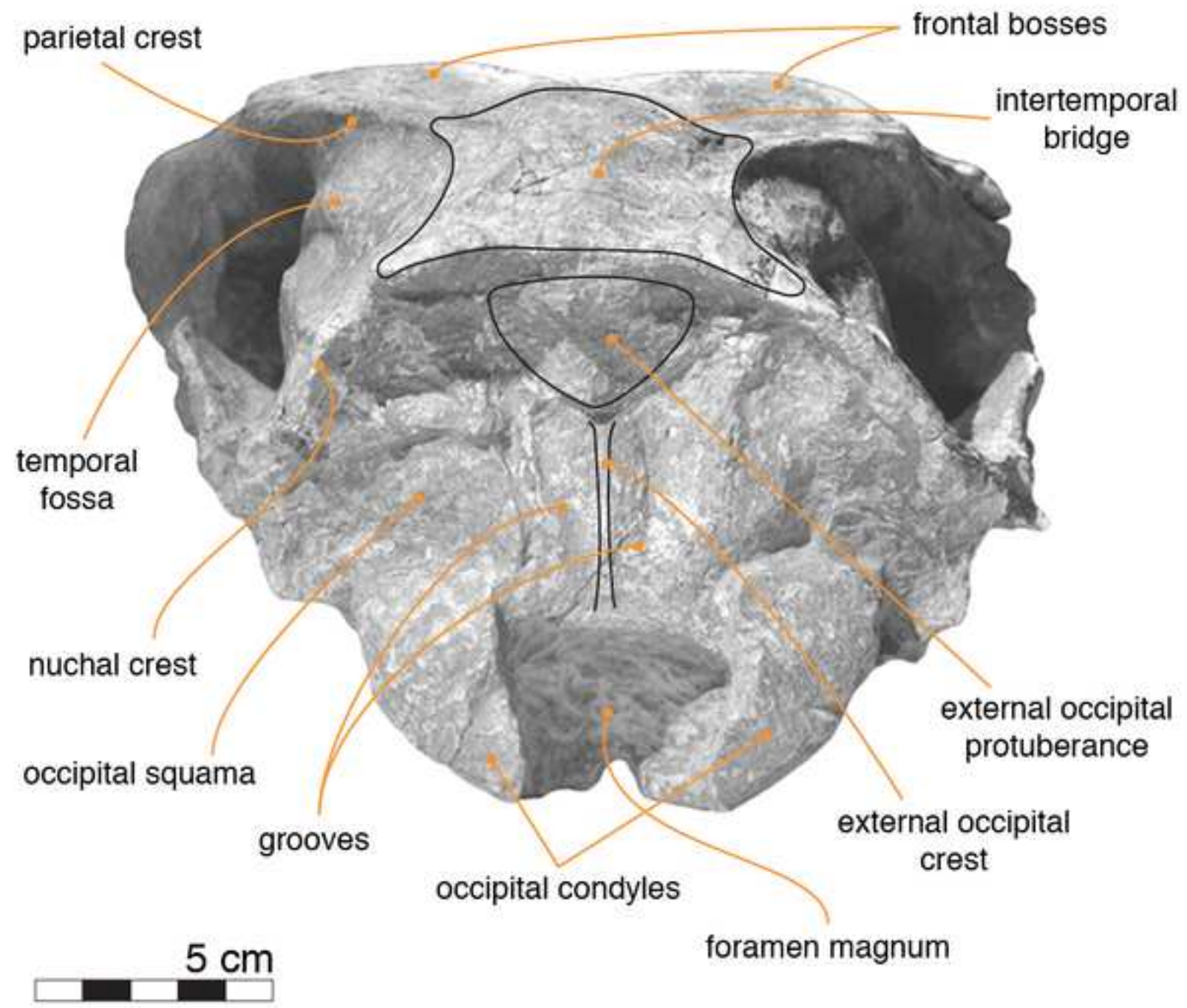


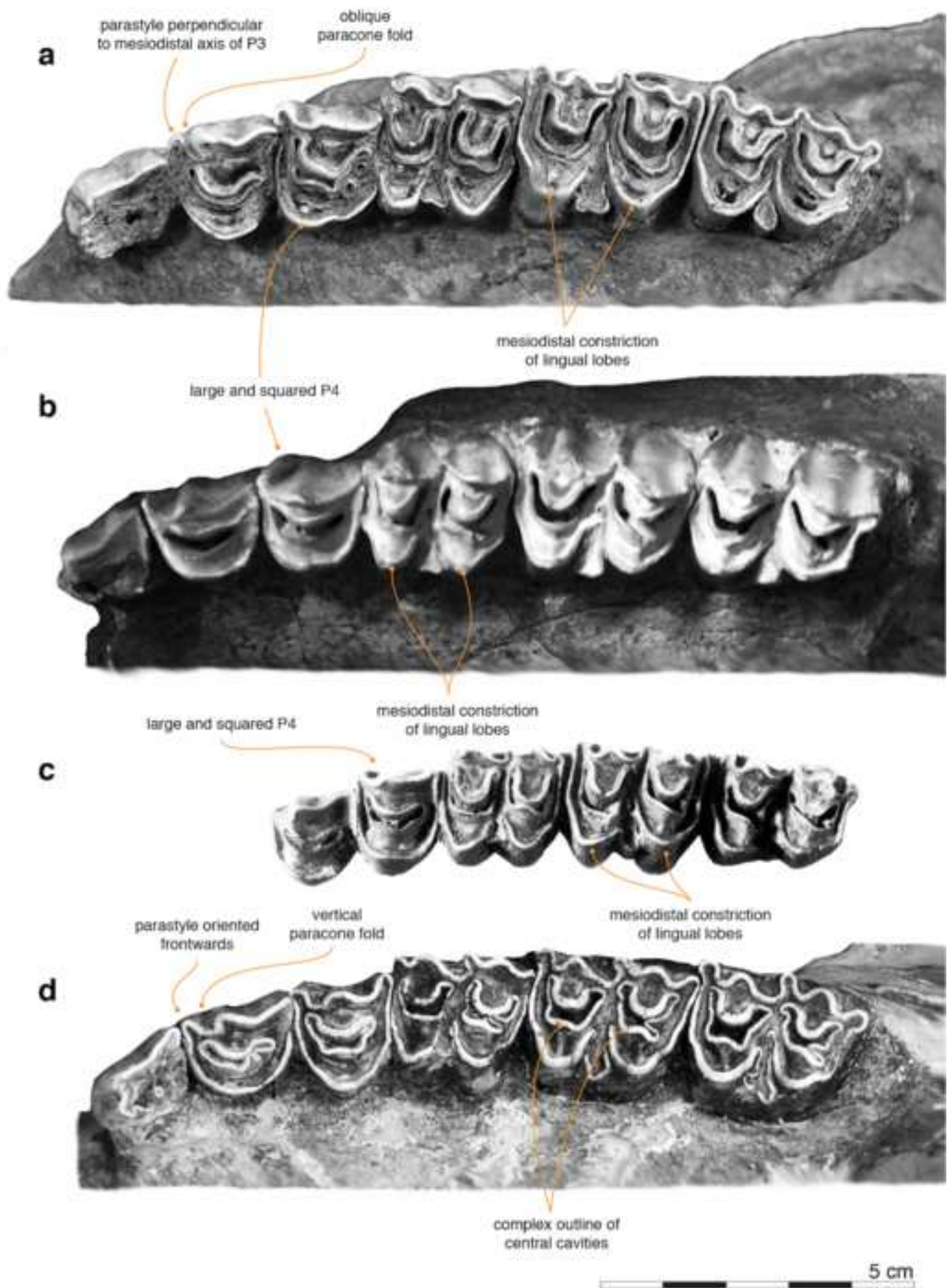


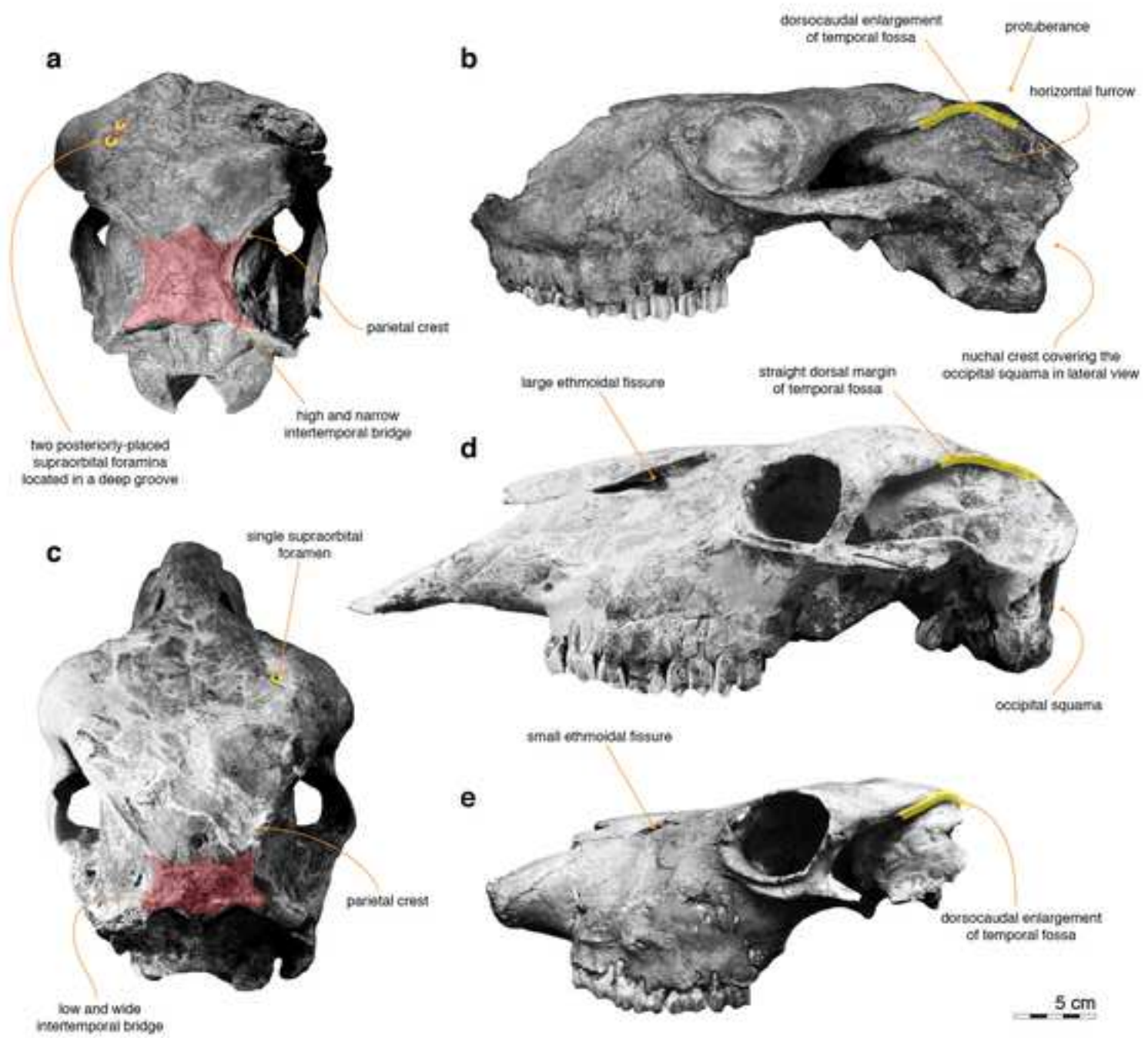


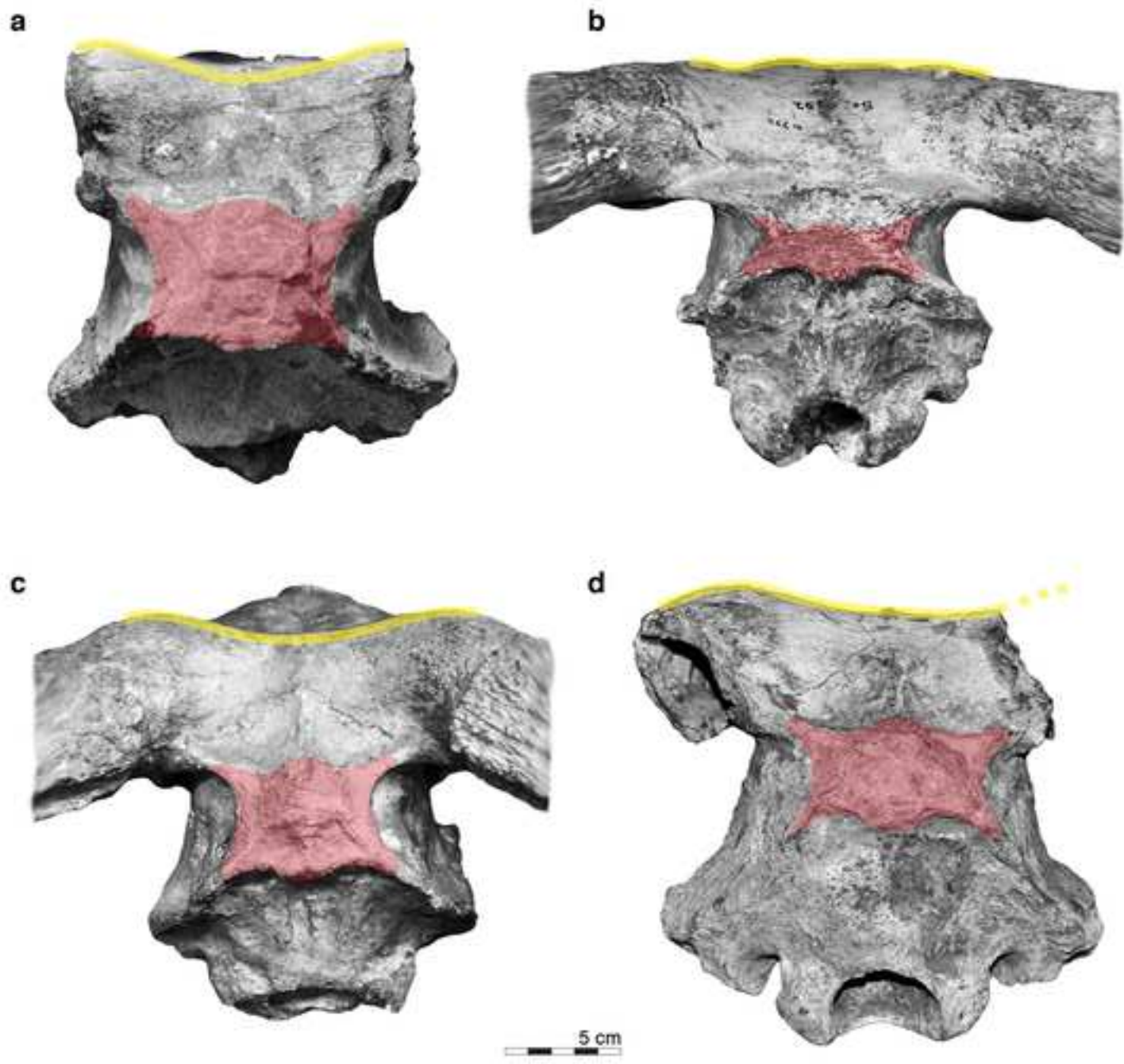




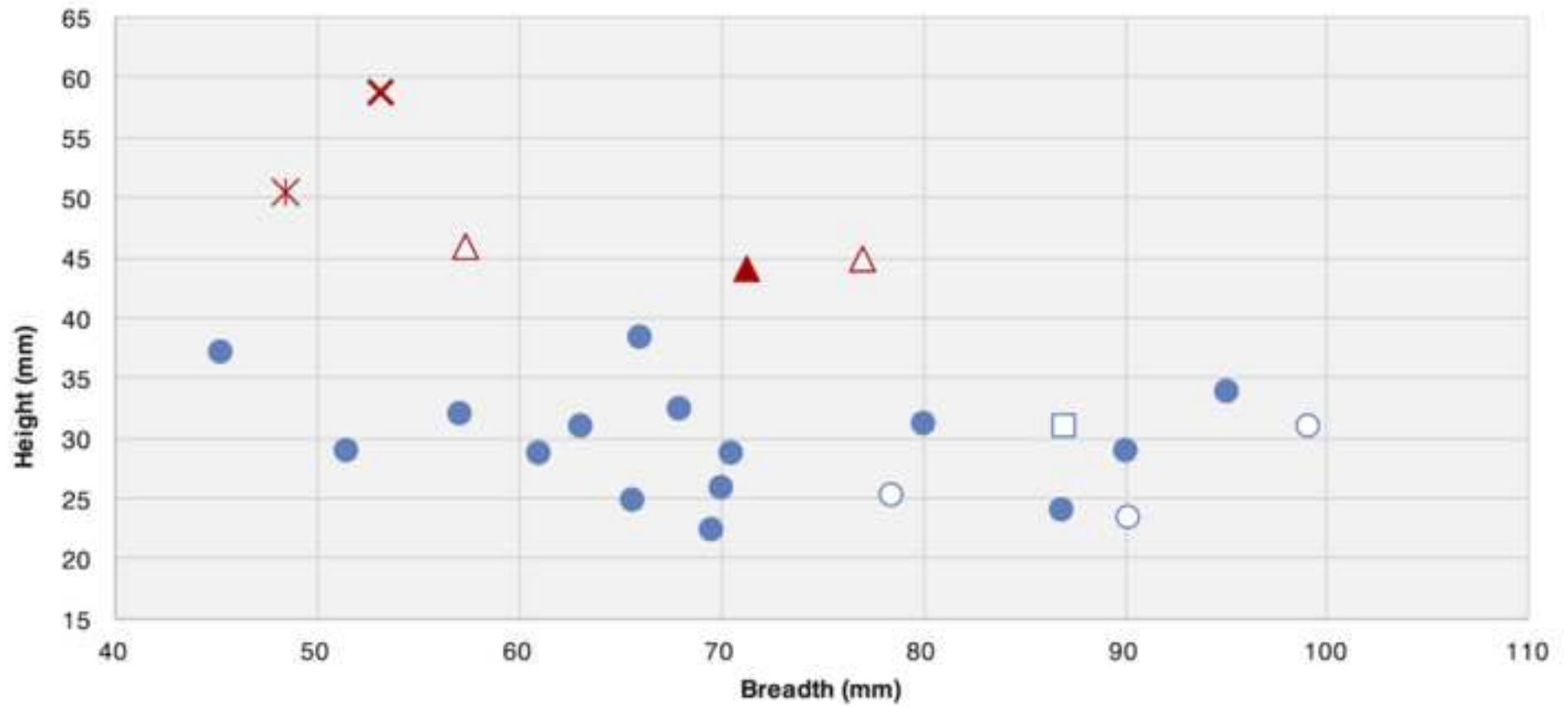






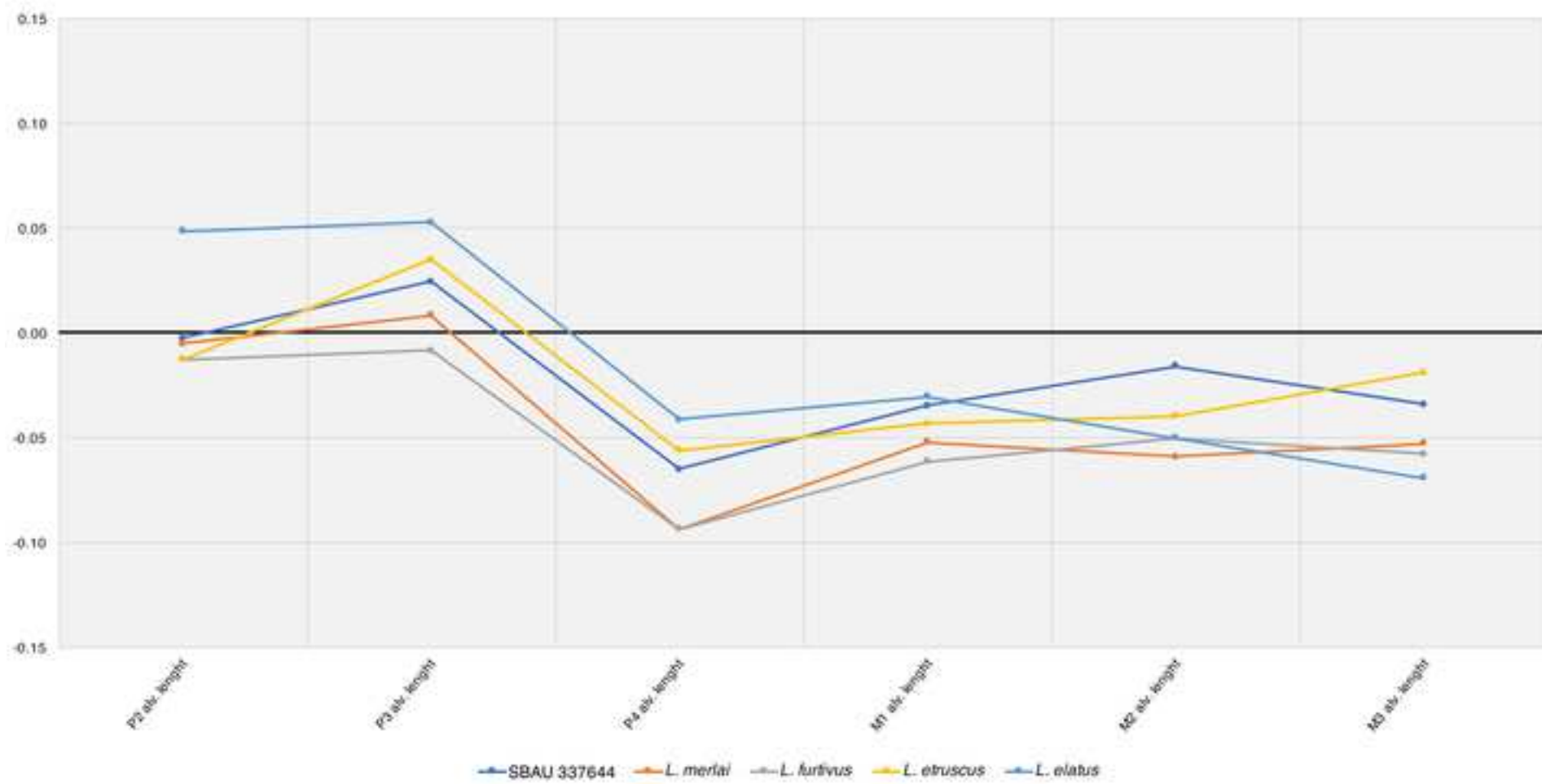


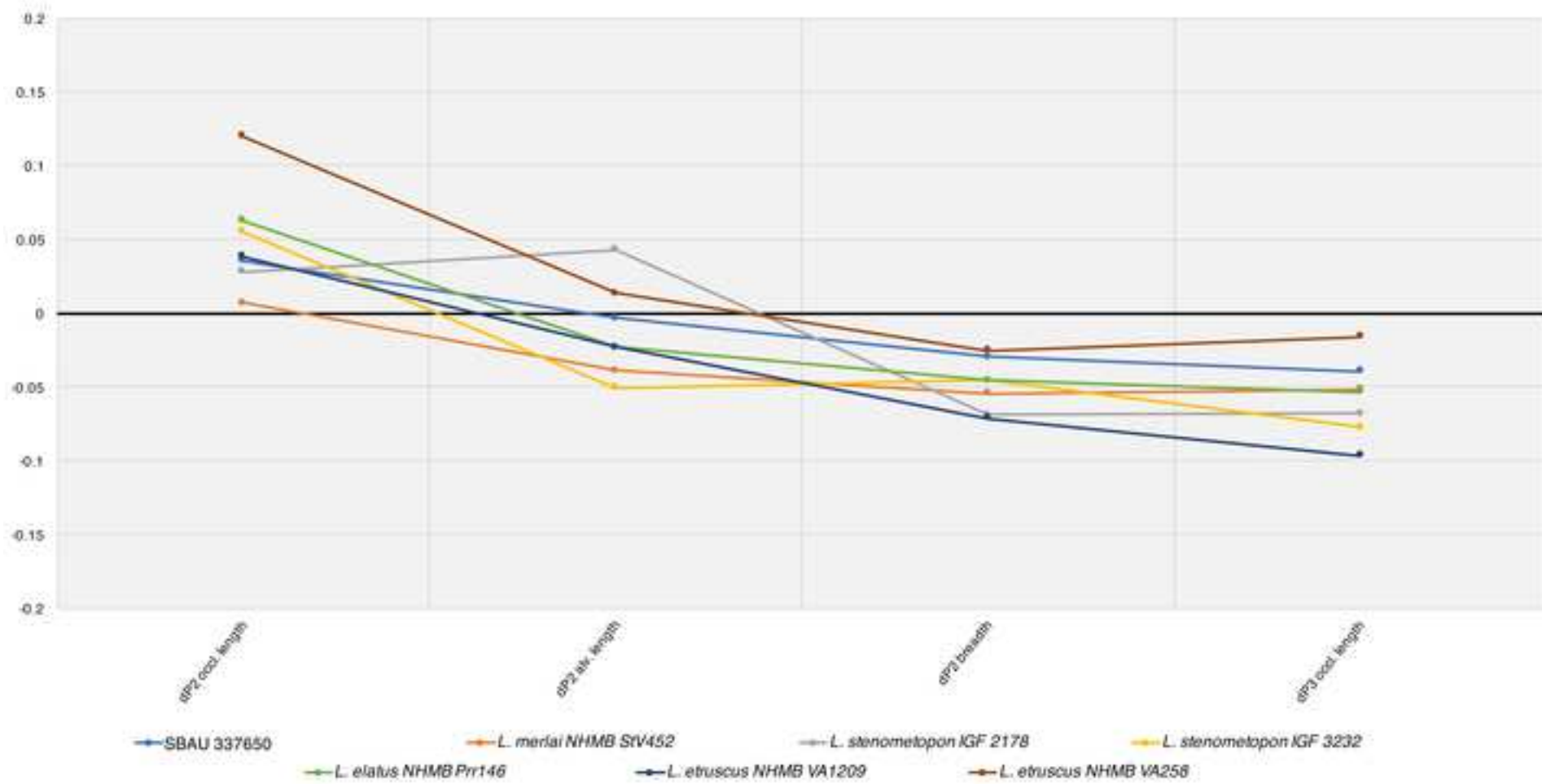
## Intertemporal bridge



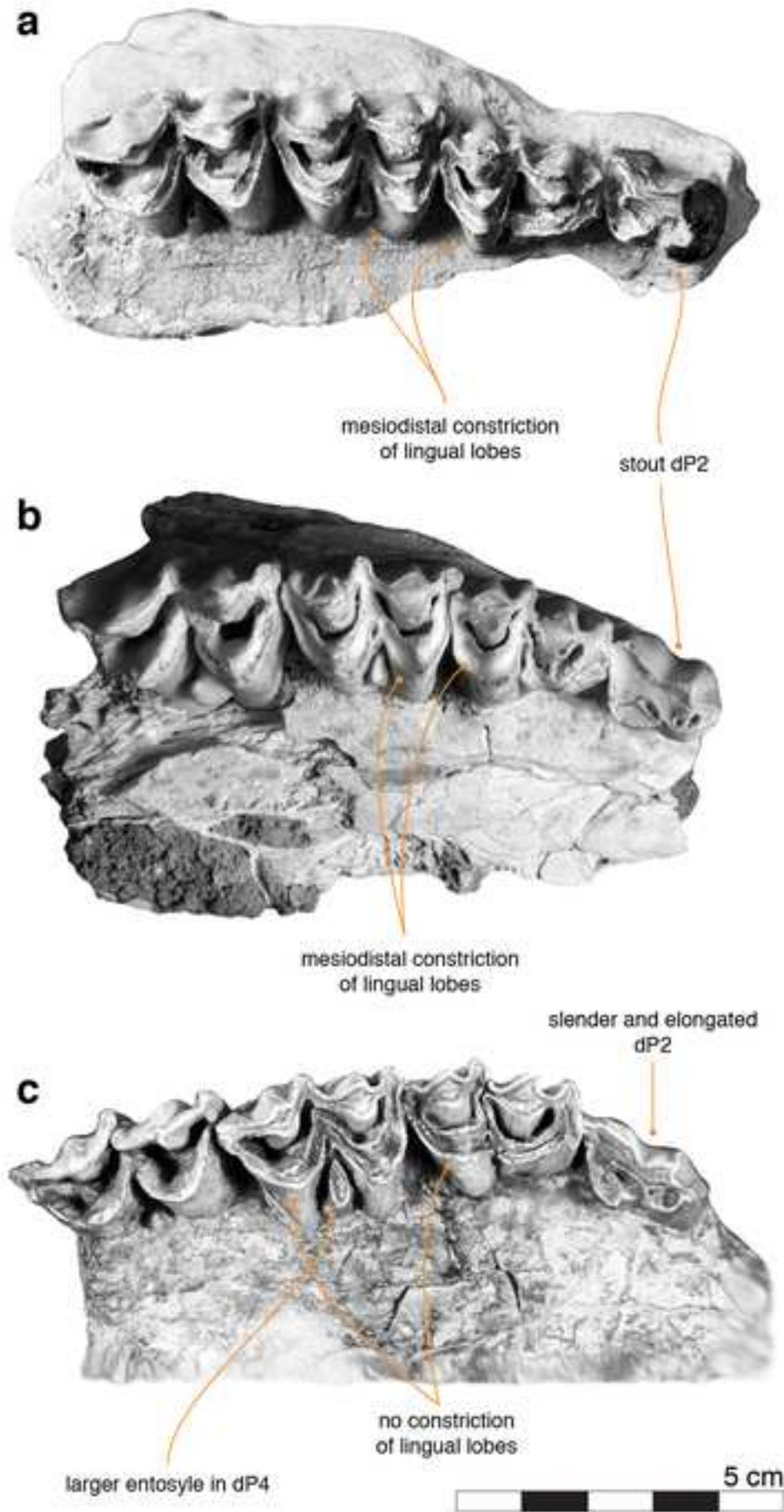
□ *L. bravardi* ● *L. etruscus* ○ *L. vallisami* ▲ *L. stenometopon* △ *L. merlai* ✕ SBAU 266661 ✕ SBAU 337644

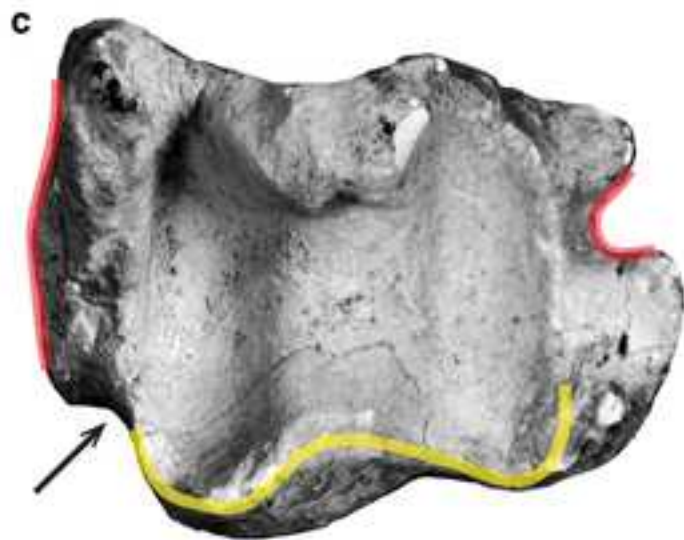
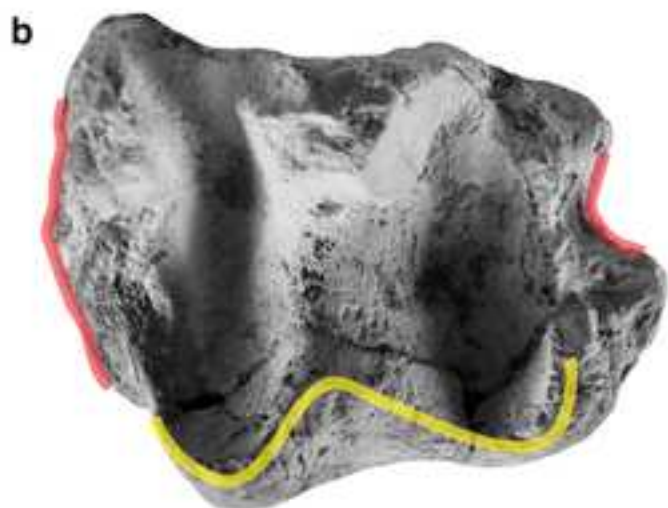
Figure 10











Taxon	Coll.	ID	Locality	Element	Sex/Age	Source of data
<i>L. bravardi</i>	MNHN	no num.	Les Étouaires	Neurocranium	♂	Duvernois (1989), Masini (1989)
<i>L. bravardi</i>	MNHN	no num.	Les Étouaires	Mandible with p3–m3, left	?	Duvernois (1989)
<i>L. elatus</i>	NHMB	Prr-146	Les Étouaires	Maxillae with dP2–M1	juv	This study
<i>L. elatus</i>	NHMB	Prr-149	Les Étouaires	Tibia, left	?	This study
<i>L. elatus</i>	NHMB	Prr-178	Les Étouaires	Tibia, left	?	This study
<i>L. elatus</i>	NHMB	Prr-332	Les Étouaires	Tibia, left	?	This study
<i>L. elatus</i>	NHMB	Prr-333	Les Étouaires	Tibia, left	?	This study
<i>L. elatus</i>	NHMB	Prr-431	Les Étouaires	Cranium	♂	This study
<i>L. elatus</i>	MNHN	no num.	Les Étouaires	Horn cores	♂	Masini (1989)
<i>L. elatus</i>	MCL	FSL-211278	Roca-Neyra	Neurocranium	♂ juv	Masini (1989)
<i>L. etruscus</i>	IGF	485	Upper Valdarno	Tibia, left	?	This study
<i>L. etruscus</i>	IGF	486	Upper Valdarno	Tibia, left	?	This study
<i>L. etruscus</i>	IGF	589	Upper Valdarno	Neurocranium	?	This study
<i>L. etruscus</i>	IGF	597	Upper Valdarno	Horn core, left	♂	This study
<i>L. etruscus</i>	IGF	599	Upper Valdarno	Cranium	♀	This study
<i>L. etruscus</i>	IGF	600	Upper Valdarno	Horn core, right	♂	This study
<i>L. etruscus</i>	IGF	602	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	IGF	604	Upper Valdarno	Horn core, left	♂	This study
<i>L. etruscus</i>	IGF	606	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	IGF	608	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	IGF	609	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	IGF	610	Upper Valdarno	Horn core, left	♂	This study
<i>L. etruscus</i>	IGF	612	Upper Valdarno	Cranium	♂	This study
<i>L. etruscus</i>	IGF	617	Upper Valdarno	Horn cores	♂	This study
<i>L. etruscus</i>	IGF	2173	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	IGF	2174	Upper Valdarno	Cranium	♀	This study
<i>L. etruscus</i>	IGF	2344	Olivola	Cranium	♀	This study
<i>L. etruscus</i>	IGF	2597	Olivola	Tibia, left	?	This study
<i>L. etruscus</i>	IGF	2599	Olivola	Tibia, left	?	This study
<i>L. etruscus</i>	IGF	2608	Olivola	Tibia, left	?	This study
<i>L. etruscus</i>	IGF	11611	Upper Valdarno	Cranium	?	This study
<i>L. etruscus</i>	IGF	16323	Olivola	Cranium	♀	This study
<i>L. etruscus</i>	IGF	16326	Olivola	Maxillae	?	This study
<i>L. etruscus</i>	IGF	16327	Olivola	Neurocranium	♂	This study

<i>L. etruscus</i>	IGF	4068V	Upper Valdarno	Tibia, right	?	This study
<i>L. etruscus</i>	IGF	4069V	Upper Valdarno	Tibia, left	?	This study
<i>L. etruscus</i>	IGF	no num.	Upper Valdarno	Tibia, left	?	This study
<i>L. etruscus</i>	NHMB	OL-11	Olivola	Maxilla with P2–M3, left	juv	This study
<i>L. etruscus</i>	NHMB	Se-1476	Senéze	Maxilla with P2–M3 and mandible with p3–m3, left	?	This study
<i>L. etruscus</i>	NHMB	Se-1736	Senéze	Cranium	♀	This study
<i>L. etruscus</i>	NHMB	Se-792	Senéze	Neurocranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-1042	Upper Valdarno	P3, right	?	This study
<i>L. etruscus</i>	NHMB	VA-1209	Upper Valdarno	Maxillae with dP2–M2 and mandible with dp2–m2, left	juv	This study
<i>L. etruscus</i>	NHMB	VA-1404	Upper Valdarno	P2–M1, right and M2–M3, left	?	This study
<i>L. etruscus</i>	NHMB	VA-1490	Upper Valdarno	M3, right	?	This study
<i>L. etruscus</i>	NHMB	VA-1712	Upper Valdarno	P2–M2, right and M1–M3, left	?	This study
<i>L. etruscus</i>	NHMB	VA-1732	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-1740	Upper Valdarno	M2, left?	?	This study
<i>L. etruscus</i>	NHMB	VA-1741	Upper Valdarno	P4, left	?	This study
<i>L. etruscus</i>	NHMB	VA-1875	Upper Valdarno	Cranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-1876	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-1880	Upper Valdarno	M1–M3, right	?	This study
<i>L. etruscus</i>	NHMB	VA-2023	Upper Valdarno	Maxilla with P4–M3, right	?	This study
<i>L. etruscus</i>	NHMB	VA-2222-3	Upper Valdarno	M2-M3, right	?	This study
<i>L. etruscus</i>	NHMB	VA-2533	Upper Valdarno	Cranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-2534	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-258	Upper Valdarno	Maxillae with dP2–M1	juv	This study
<i>L. etruscus</i>	NHMB	VA-2594	Upper Valdarno	Maxilla with dP4–M2	juv	This study
<i>L. etruscus</i>	NHMB	VA-2672	Upper Valdarno	M1/2, right	?	This study
<i>L. etruscus</i>	NHMB	VA-320	Upper Valdarno	P4, right	?	This study
<i>L. etruscus</i>	NHMB	VA-605	Upper Valdarno	Cranium	♀	This study
<i>L. etruscus</i>	NHMB	VA-608	Upper Valdarno	Splanchnocranium	juv	This study
<i>L. etruscus</i>	NHMB	VA-647	Upper Valdarno	Cranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-859	Upper Valdarno	Neurocranium	♂	This study
<i>L. etruscus</i>	NHMB	VA-974	Upper Valdarno	M2-M3, left	?	This study
<i>L. etruscus</i>	MCL	FSL-90136	Senéze	Cranium	♂	Masini (1989)
<i>L. furtivus</i>	NHMB	Se-202	Senéze	Horn core, left	♂	This study
<i>L. merlai</i>	MCL	20.162114	Saint Vallier	Cranium	?	This study
<i>L. merlai</i>	MCL	20.162180 (ex QSV-980)	Saint Vallier	Cranium	♂	This study

<i>L. merlai</i>	MCL	20.162181 (ex QSV-981)	Saint Vallier	Cranium	♀	This study
<i>L. merlai</i>	MCL	20.162182 (ex QSV-982)	Saint Vallier	Cranium	♂	This study
<i>L. merlai</i>	MCL	20.162186	Saint Vallier	Cranium	♀	This study
<i>L. merlai</i>	MCL	20.162189	Saint Vallier	Tibia, right	?	This study
<i>L. merlai</i>	MCL	FSL-495015	Saint Vallier	Tibia, right	?	This study
<i>L. merlai</i>	MCL	FSL-496282	Saint Vallier	Tibia, right	?	This study
<i>L. merlai</i>	MCL	FSL-496725	Saint Vallier	Tibia, left	?	This study
<i>L. merlai</i>	MCL	FSL-496873	Saint Vallier	Tibia, left	?	This study
<i>L. merlai</i>	MCL	FSL-497762	Saint Vallier	Tibia, right	?	This study
<i>L. merlai</i>	MGCB	220	Upper Valdarno	Neurocranium	♂	This study
<i>L. merlai</i>	MGCB	no num.	Castel Viscardo	Horn cores	♂	This study
<i>L. merlai</i>	NHMB	StV-221	Saint Vallier	Tibia, left	juv	This study
<i>L. merlai</i>	NHMB	StV-452	Saint Vallier	Maxilla with dP2–M1, right	juv	This study
<i>L. stenometopon</i>	IGF	2178	Montopoli	Maxilla with dP2–M1, left	juv	This study
<i>L. stenometopon</i>	IGF	3232	Montopoli	Maxillae with dP2–M2	juv	This study
<i>L. stenometopon</i>	NHMB	FP-18	Dusino	Neurocranium (cast)	♂	This study
<i>L. vallisarni</i>	IGF	603	Upper Valdarno	Neurocranium	♂	This study
<i>L. vallisarni</i>	IGF	622	Upper Valdarno	Cranium	♂	This study
<i>L. vallisarni</i>	IGF	16331	Val di Chiana	Neurocranium	♂	This study
<i>L. vallisarni</i>	IGF	2796V	Val di Chiana	Horn core, left	♂	This study

Abbrev.	Measurement	Pantalla	Perugia area
		SBAU 337644	SBAU 266661
		♀	♂
PO1	Breadth of the intertemporal bridge	48.4	53.1
PO2	Height of the intertemporal bridge (A-Pi)	50.4	58.8
PO3	Greatest breadth of the occipital condyles	89.6	-
PO4	Height of the foramen magnum (B-O)	31.1	39.0
PO5	Breadth of the foramen magnum	37.5	43.0
PO6	Greatest mastoid breadth (Ot-Ot)	131.9	163.0
PO7	Greatest breadth at the base of paraoccipital processes	118.0	112.0
PO8	Height of the occipital squama (A-O)	64.6	61.8
PO9	Akrokranion-Basion (A-B)	91.5	101.0
PO10	Height from the occipital squama to the parietal roof (Pi-O)	96.8	97.7
PO11	Height from the occipital squama to the Basion (Pi-B)	125.8	131.0
PO12	Length of the temporal crest	83.8	97.9
PO13	Posterior breadth between the horncore bases (C-C)	127.9	94.1
PO14	Distance between the horncore base and the midpoint of the dorsal margin of the intertemporal bridge (C-Pi)	73.3	43.1
PO15	Length of the parietal crest	76.8	-
PO16	Length of the parietal roof (Br-Pi)	43.7	48.4
PO17	Length of the parietal roof (intertemporal bridge included) (Br-A)	85.5	99.0
PO18	Length of the parietal roof behind the horncore bases (Pi-midpoint C-C)	-	6.0
PO19	Length of the parietal roof behind the horncore bases (intertemporal bridge included) (A-midpoint C-C)	-	61.7
PO20	Height of the temporal fossa	64.5	73.5
PO21	Length of the frontoparietal suture (Br-C)	-	64.0
PO22	Height of the neurocranium	129.2	133.9
PO23	Breadth of the braincase	109.9	93.3
BA1	Breadth at the caudal constriction	47.7	50.2
BA2	Breadth at the occipital muscular tubercles	50.3	55.3
BA3	Breadth at the pterygoid processes	25.9	24.8
BA4	Distance between the condyles and the sphenoid suture	107.4	-
BA5	Distance between the condyles and the pterygoid processes	97.1	-
FR1	Max breadth between the supraorbital foramina	93.9	-
FR2	Distance between the horncore rostral base and the orbit	-	-
FR3	Distance between the horncore caudal base and the orbit	85.0	-
FR4	Max orbital breadth (Ect-Ect)	194.5	-
FR5	Breadth of the postorbital constriction	132.3	-
FR6	Min orbital breadth (Ent-Ent)	133.5	-
FR7	Max length of the frontoparietal plane (A-oral border of the frontals)	264.6	-
FR8	Distance between the aboral border of supraorbital foramina and the Pi point (Sup-Pi)	94.9	-
FR9	Distance between the aboral border of supraorbital foramina and the Akrokranion (Sup-A)	133.6	-
FR10	Frontoparietal length (N-A)	231.2	-
FR11	Frontal length (N-Br)	137.4	-
TF1	Total length (P-A)	-	-
TF2	Basal length (B-P)	-	-
TF3	Frontofacial length (P-Br)	-	-

<b>TF4</b>	Distance between the Akrokranium and the maxillary tuberosity	307.4	-
<b>TF5</b>	Distance between the Akrokranium and the oral margin of the orbit (A-Ent)	227.0	-
<b>TF6</b>	Basion - Premolare (B-Pm)	285.9	-
<b>TF7</b>	Premolare - Prosthion (Pm-P)	-	-
<b>TF8</b>	Neurocranium length (N-B)	271.5	-
<b>TF9</b>	Infraorbitale - Akrokranium (If-A)	333.9	-
<b>TF10</b>	Distance between the aboral border of the condyle and the Entorbitale of the same side	229.9	-
<b>TF11</b>	Distance between the aboral border of the condyle and the Infraorbitale of the same side	321.0	-
<b>TF12</b>	Distance between the aboral border of supraorbital foramina and the Prosthion (Sup-P)	-	-
<b>TF13</b>	Nasal length (N-Rh)	-	-
<b>TF14</b>	Max nasal breadth	-	-
<b>TF15</b>	Max premaxillary breadth	-	-
<b>TF16</b>	Max palatal breadth (measured across the molar tuberosities)	136.8	-
<b>TF17</b>	Min lateral facial length (P-Ent)	-	-
<b>TF18</b>	Splanchnocranium length (P-N)	-	-
<b>TF19</b>	Max lateral facial length (P-Ect)	-	-
<b>TF20</b>	Infraorbitale - Prosthion (If-P)	-	-
<b>TF21</b>	Dental length (Pd-P)	-	-
<b>TF22</b>	Oral palatal length (Po-P)	-	-
<b>TF23</b>	Premaxillary length	-	-
<b>TF24</b>	Max inner length of the orbit (Ect-Ent)	58.2	-
<b>TF25</b>	Max inner height of the orbit	42.4	-
<b>TF26</b>	Zygomatic breadth	174.8	-
<b>PA1</b>	Palatal breadth measured across the outer borders of the alveoli	129.1	-
<b>PA2</b>	Occlusal length of the cheektooth row	131.3	-
<b>PA3</b>	Alveolar length of the cheektooth row	129.9	-
<b>PA4</b>	Occlusal length of the premolar row	53.9	-
<b>PA5</b>	Alveolar length of the premolar row	49.2	-
<b>PA6</b>	Occlusal length of the molar row	80.2	-
<b>PA7</b>	Alveolar length of the molar row	79.4	-

Measurement	SBAU 337644		<i>L. merlai</i>		<i>L. furtivus</i>		<i>L. elatus</i>		<i>L. etruscus</i>	
	Pantalla		St. Vallier		Senéze/Valdarno		Les Étouaires		Senéze/Valdarno	
	sn	dx	-		-		dx		-	
<b>P2</b> alv. length	16.9	-	15.5-18.5	16.8 (3)	15.5-18.0	16.5 (5)	-	19.0 (1)	13.5-20.0	16.5 (18)
<b>P2</b> occl. length	18.9	-	16.0-18.0	17.0 (3)	15.5-18.0	17.2 (5)	-	16.5 (1)	13.5-19.0	15.9 (17)
<b>P2</b> breadth	16.0	-	13.5-15.5	14.5 (3)	12.5-14.0	13.1 (5)	-	14.5 (1)	12.0-14.5	13.0 (16)
<b>P3</b> alv. length	16.4	17.6	14.0-17.5	15.8 (3)	14.0-16.5	15.2 (8)	-	17.5 (1)	15.0-18.5	16.8 (21)
<b>P3</b> occl. length	18.8	17.6	16.5-19.5	17.7 (3)	15.0-19.0	16.7 (8)	-	17.0 (1)	15.5-20.0	18.1 (22)
<b>P3</b> breadth	19.8	19.5	16.0-18.0	16.7 (3)	14.5-18.0	16.5 (8)	-	18.0 (1)	15.0-18.0	16.1 (19)
<b>P4</b> alv. length	14.2	14.5	12.5-14.0	13.3 (3)	12.0-14.5	13.3 (8)	-	15.0 (1)	12.5-16.5	14.5 (26)
<b>P4</b> occl. length	17.7	17.9	15.5-17.5	16.2 (3)	13.5-19.0	15.9 (8)	-	16.0 (1)	13.5-19.0	16.9 (27)
<b>P4</b> breadth	20.4	21.3	18.0-20.0	19.0 (4)	16.5-22.5	19.5 (8)	-	22.0 (1)	16.5-22.5	19.9 (28)
<b>M1</b> alv. length	20.3	21.1	18.0-20.5	19.5 (4)	18.0-20.0	19.1 (7)	-	20.5 (1)	17.0-23.0	19.9 (26)
<b>M1</b> occl. length	23.0	23.0	18.0-23.5	21.2 (4)	18.5-24.5	21.8 (6)	-	23.5 (1)	19.5-27.5	23.3 (27)
<b>M1</b> mes. breadth	23.3	23.4	21.0-24.5	22.9 (4)	21.5-24.0	22.4 (7)	-	23.0 (1)	18.5-24.5	21.6 (26)
<b>M1</b> dist. breadth	23.5	24.2	21.0-25.5	23.4 (4)	22.5-25.5	23.4 (7)	-	23.0 (1)	17.5-27.0	23.2 (29)
<b>M2</b> alv. length	27.3	26.6	22.0-26.0	24.0 (4)	20.5-28.0	24.5 (7)	-	24.5 (1)	20.0-28.0	25.1 (30)
<b>M2</b> occl. length	28.9	28.4	25.0-27.5	26.6 (4)	22.5-28.5	25.5 (7)	-	27.0 (1)	24.0-31.5	27.3 (29)
<b>M2</b> mes. breadth	24.4	25.6	24.0-27.0	25.6 (4)	21.5-26.0	23.9 (7)	-	25.5 (1)	28.5-28.0	23.5 (30)
<b>M2</b> dist. breadth	23.5	25.6	24.5-28.0	25.6 (4)	20.0-26.5	23.4 (7)	-	25.5 (1)	16.0-28.5	23.5 (30)
<b>M3</b> alv. length	28.2	28.2	25.5-29.0	27.0 (4)	24.0-30.0	26.7 (7)	-	26.0 (1)	25.0-34.0	29.2 (27)
<b>M3</b> occl. length	28.8	28.5	27.5-30.0	28.4 (4)	26.0-29.0	27.1 (7)	-	26.5 (1)	25.0-33.5	29.3 (25)
<b>M3</b> mes. breadth	22.0	24.0	24.0-26.5	24.9 (4)	19.5-25.0	22.1 (7)	-	25.0 (1)	18.5-28.0	23.5 (27)
<b>M3</b> dist. breadth	21.3	21.8	21.0-24.5	23.1 (4)	18.5-24.5	21.3 (7)	-	22.5 (1)	17.0-27.5	22.2 (26)



Character		<i>L. merlai-furtivus</i>	<i>L. etruscus-vallisarni</i>
<b>P3</b>	Orientation of the parastyle relative to the mesiodistal axis	Perpendicular	Frontwards
	Notch between parastyle and paracone	Wide	Narrow
	Paracone fold in labial view	Oblique	Vertical
	Metastyle in labial view	More oblique than the paracone fold	Vertical
	Metastyle in occlusal view	No orientation	Oriented distolabially
	Central cavity	In the middle	Shifted forward
<b>P4</b>	Paracone fold	Marked	Low
	Lingual lobe	Shifted forward	In the middle
	Molarization	Incipient	Absent
<b>Molars</b>	Constriction of lingual lobes	Low	Marked
	Infoldings in the central cavities	Rare and shallow	Frequent and deep
	Mesostyle near the neck	Decreasing progressively	Decreasing abruptly
	Margin of entostyle in occlusal view	Generally simple, rounded or drop-shaped	Complex, with many infoldings
	Distal margin of M3 in occlusal view	Vertical distolingual pillar	Rounded

Measurement	Pantalla	<i>L. merlai</i>	<i>L. stenometopon</i>	<i>L. stenometopon</i>	<i>L. elatus</i>	<i>L. etruscus</i>	<i>L. etruscus</i>	<i>L. etruscus</i>	<i>L. etruscus</i>
		St. Vallier	Montopoli	Montopoli	Les Étouaires	Valdarno	Valdarno	Valdarno	Valdarno
	SBAU 337644	NHMB StV452	IGF 2178	IGF 3232	NHMB Prr146	NHMB VA1209	NHMB VA258	NHMB VA2594	NHMB VA608
	dx	dx	sn	dx	sn	dx	dx	dx	dx
<b>dP2</b> occl. length	15.9	17.0	18.1	13.1	16.5	17.7	18.1	-	-
<b>dP2</b> alv. length	17.3	16.2	17.0	18.1	18.4	17.4	21.0	-	-
<b>dP2</b> breadth	11.8	12.0	11.8	13.5	13.0	10.1	10.9	-	-
<b>dP3</b> occl. length	23.0	21.5	19.5	20.3	21.8	19.9	24.2	-	21.9
<b>dP3</b> alv. length	20.4	18.8	22.7	18.3	19.5	19.5	21.2	-	20.4
<b>dP3</b> mes. breadth	13.1	11.8	12.8	12.5	12.5	12.0	12.1	-	13.7
<b>dP3</b> dist. breadth	18.1	15.8	18.1	16.6	17.2	16.2	16.8	-	18.6
<b>dP4</b> occl. length	22.7	22.9	22.2	19.5	23.0	21.0	24.7	19.0	21.6
<b>dP4</b> alv. length	19.8	18.7	18.1	19.1	19.1	18.0	20.0	15.8	19.6
<b>dP4</b> mes. breadth	19.2	18.4	19.7	19.6	19.5	19.2	17.3	18.6	21.1
<b>dP4</b> dist. breadth	19.2	17.6	19.6	19.1	17.9	19.4	18.0	18.6	22.0
<b>M1</b> occl. length	26.4	28.0	26.2	26.1	25.6	25.6	29.6	26.0	28.5
<b>M1</b> alv. length	25.3	24.6	23.7	23.2	24.5	22.2	26.7	20.0	25.3
<b>M1</b> mes. breadth	18.6	19.9	17.7	20.2	18.5	17.0	14.8	17.3	23.2
<b>M1</b> dist. breadth	17.4	20.3	15.5	19.4	17.4	15.5	14.4	15.9	22.9

Taxon and site		ID	side	DMLD	DCCD
				Distal mediolateral diameter	Distal craniocaudal diameter
Pantalla		SBAU 167342	sn	63.0	54.1
Pantalla		SBAU 167354	sn	69.1	57.0
<i>L. elatus</i>	Les Étouaires	MNHB Prr333	sn	64.7	54.5
<i>L. elatus</i>	Les Étouaires	NHMB Prr149	sn	64.8	56.4
<i>L. elatus</i>	Les Étouaires	NHMB Prr178	sn	65.4	56.0
<i>L. elatus</i>	Les Étouaires	NHMB Prr332	sn	68.0	58.2
<i>L. merlai</i>	St. Vallier	NHMB StV221	dx	64.8	-
<i>L. merlai</i>	St. Vallier	MCL FSL492282	dx	66.0	54.5
<i>L. etruscus</i>	Valdarno	IGF 485	sn	65.0	53.4
<i>L. etruscus</i>	Valdarno	IGF 486	sn	63.6	55.0
<i>L. etruscus</i>	Valdarno	IGF 4068V	dx	64.6	48.1
<i>L. etruscus</i>	Valdarno	IGF no num.	sn	67.1	53.0
<i>L. etruscus</i>	Valdarno	IGF 4069V	sn	68.8	55.8
<i>L. etruscus</i>	Olivola	IGF 2597	sn	70.0	53.2
<i>L. etruscus</i>	Olivola	IGF 2608	sn	66.0	55.3
<i>L. etruscus</i>	Olivola	IGF 2599	sn	66.3	52.4



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