PALÆO VERTEBRATA

ARTICLE

Revision of the historical collections of Pliocene-Pleistocene large mammals from Le Rièg e and Saint-Palais localities, near Pézenas (Southern France)

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Abstract: Numerous "Quaternary" large-mammal fossils have been collected since the 1830s along the Le Rièg e stream, near Pézenas (Southern France). More than 120 specimens are stored in the collections of the *Université de Montpellier* (UM) under the name "Le Rièg e". A major operation aiming at relocating the palaeontological collections of the University has made it possible to group together all the specimens of interest and launch their systematic revision for the first time. The fossils belong to the Reboul (1839; 51 samples) and de Christol (1865; 18 samples) Collections and 17 samples compose the Crochet & Ivorra Collection (1998). The remaining 38 samples have no mention about the exact time and location of their finding. We provide a critical inventory with literal transcription of inscriptions on specimens and historical labels. This revision confirms the presence of two distinct faunal assemblages under the name of "Le Rièg e": Saint-Palais (Early Pliocene, MN14–15) and Le Rièg e *sensu stricto* (late Early Pleistocene, most likely MNQ19). The former assemblage, with coastal affinities, is composed of the ruminants *Alephis* sp. and *Procapreolus* cf. *pyrenaicus*, the rhinocerotid *Pliorhinus megarhinus*, the gomphotheriid *Anancus arvernensis* and marine mammals, all emblematic taxa for the Early Pliocene of Montpellier and Perpignan. The latter assemblage documents a late Early Pleistocene fluvio-volcanic sequence, yielding the bovid *Bison* (*Eobison*) spp., the cervid *Eucladoceros* cf. *giulii*, the hippopotamid *Hippopotamus antiquus*, the rhinocerotid *Stephanorhinus etruscus*, the equid *Equus* cf. *altidens*, and the elephantid *Mammuthus* cf. *meridionalis*, plus a few specimens of uncertain taxonomic affinities. This revision underscores the interest of revisiting historical collections and further provides a starting point for future research.

Keywords: Mammalia, Neogene, Quaternary, Languedoc, Hérault

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INTRODUCTION

Since the 19th century, large-mammal fossils have been collected from various localities along the Le Rièg e stream, near the town of Pézenas, between the Tourbes and Alignan-du-Vent Municipalities (Hérault, Southern France). The first paleontological study was conducted by the local naturalist and paleontologist Henri Reboul in the early 1830s (Reboul, 1834). This important scholar, gathering a huge collection (here called "Reboul 1839"), reported the discovery of deer, rhinoceros, hippopotamus and proboscidean remains along the Le Rièg e stream, near the Domaine de Peyrat, located at that time on his own land. However, no chronological distinction has been reported by Reboul among the fossils themselves (although here considered as Pliocene-Pleistocene mixed taxa). The surroundings of the Le Rièg e stream were cited as a fossil vertebrate-yielding area also by Boué (1832), as well as by de Christol (1835), who gathered a small collection (here named "de Christol 1865"). Later, other large-mammal remains from the Le Rièg e stream area were described and illustrated by the famous scholar Paul Gervais (1859). Then, Gaudry (1868) claimed that, along the Le Rièg e stream, the fauna near Saint-Martial was older than the Pliocene fauna from the nearby site of Saint-Palais, situated further to the northeast (Fig. 1). At the end of the 19th century, however, this chronological interpretation was denied by Depéret (1897). Thanks to detailed stratigraphical descriptions of the rock sequences, cropping out in the Hérault valley near Pézenas, Depéret (1897) proposed the opposite chronological interpretation. He stated that the fauna near Saint-Martial would document Upper Pliocene fluvio-volcanic sequences (nowadays Early Pleistocene in age). Later on, during the 20th century, the paleontological localities along the Le Rièg e stream were cited and discussed in a few studies, such as those by Guérin (1980) and Faure (1985) on rhinocerotids and artiodactyls, respectively. Yet, to our knowledge, none concluded unambiguously to the existence of two distinct faunas or depicted thoroughly the older one. The most recent published paleontological study about the fauna from the Le Rièg e stream was conducted by Ambert *et al*. (1996). Among other Pleistocene mammals, these authors described a partial bovid skull from Saint-Martial, collected slightly before. They assigned it to an early *Bison* (*Eobison*),

without illustrating it. They proposed that this Pleistocene fauna would document the Mammal Neogene-Quaternary zone 20 (MNQ20; Mein, 1975a, b), which nowadays corresponds to the Epivillafranchian, within the Calabrian standard age (late Early Pleistocene; Bellucci *et al*., 2015). Finally, at the end of the last century, Jean-Yves Crochet and Jérôme Ivorra gathered a new small collection (here called "Crochet and Ivorra 1998"), which includes details about the specific localities from where the remains were found along the Riège stream.

Almost thirty years after the most recent study, here we provide a critical inventory and give a revision of the paleontological record from Le Riège stream surroundings. Here, we describe and discuss more than one hundred large-mammal fossils, collected in different epochs and for which more specific geographical and stratigraphical data are mostly lacking. Accordingly, to avoid misunderstandings, we will refer to the area crossed by the Le Riège stream, between the Tourbes and Alignan-du-Vent Municipalities, simply as "Le Riège" (see Fig. 1). The fossils described herein are stored in the collections of the *Université de Montpellier* (UM), and we further provide tentative biochronological ages for the corresponding assemblages.

GEOLOGICAL FRAMEWORK

In Southern France, the Hérault department is the central portion of the Languedoc region (Occitanie), between the French Massif Central and the Mediterranean Sea (Fig. 1). In this area, the Pliocene sedimentary sequences consist of coastal deposits. Near Le Riège locality (Pézenas), Saint-Palais is an important historical Zanclean paleosite where gravels of lacustrine setting crop out (Ambert *et al*. 1998). Upon these Lower Pliocene deposits, a fluvial-volcanic sequence represents phreato-magmatic eruptive events over a period spanning between 2.0 and 0.68 Ma (Dautria *et al*., 2010). Numerous maars have been identified along NE-SW direction. This alignment seems to be determined by the prolongation of the Cévennes fault in Languedoc (Dautria *et al*., 2010). On both sides of this main axis, some volcanoes have been dated from the Early Pleistocene with radiometric methods. For example, a dating was conducted on a basaltic outflow at Valros, 3 km to the southwest of Le Riège, and the age results about 1.4 Ma (e.g., Bandet, 1983). At the nearby Bois-de-Riquet archeological-paleontological site (Lézignan-la-Cèbe), a basaltic eruption event dates back to 1.57 Ma (Bourguignon *et al*., 2016), whereas the corresponding vertebrate fauna originates from a secondary infilling, late Early Pleistocene in age (1–0.9 Ma; Lozano-Fernández *et al*., 2019). At Le Riège site, a double maar has been recognized (Ambert *et al*., 1996) (Fig. 2). Radiometric dating has not yet been conducted, especially because of the alteration. The Pleistocene fauna comes both from tuff-ring and contemporaneous lacustrine infilling (Depéret, 1897: fig. 5; Ambert *et al*., 1996: fig. 3, 2).

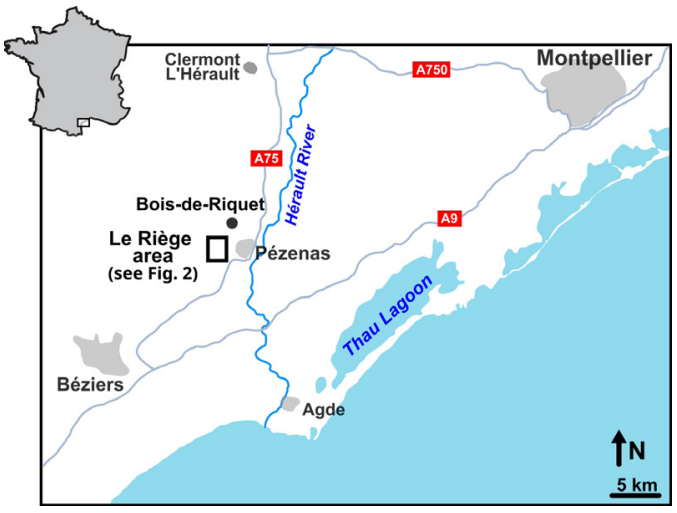

Figure 1. Location map of Le Riège area (rectangle) and Bois-de-Riquet Pleistocene locality (black dot), in Southern France (see Fig. 2 for a detailed map of Pliocene–Pleistocene localities of interest).

MATERIALS AND METHODS

Most identifiable fossils originate from the historical collections of Reboul and de Christol, deposited in the UM collections in 1839 and 1865, respectively. Another part of the collection originates from a field work season led in 1998 by two of us (J-YC and JI). Other remains are labeled without any further information about the date of their arrival in the UM collections. Among the fossils we recognized two different faunas: one is from Lower Pliocene gravels, and the other one is from the late Early Pleistocene fluvio-volcanic sequences.

Materials. The Pliocene–Pleistocene large-mammal fossils from Le Riège (Hérault, France) consist of 123 specimens in total. They are currently housed in the paleontological collections of the *Institut des Sciences de l'Évolution de Montpellier* (ISEM), and they are part of the *Université de Montpellier* collections (Montpellier, France). The fossils have

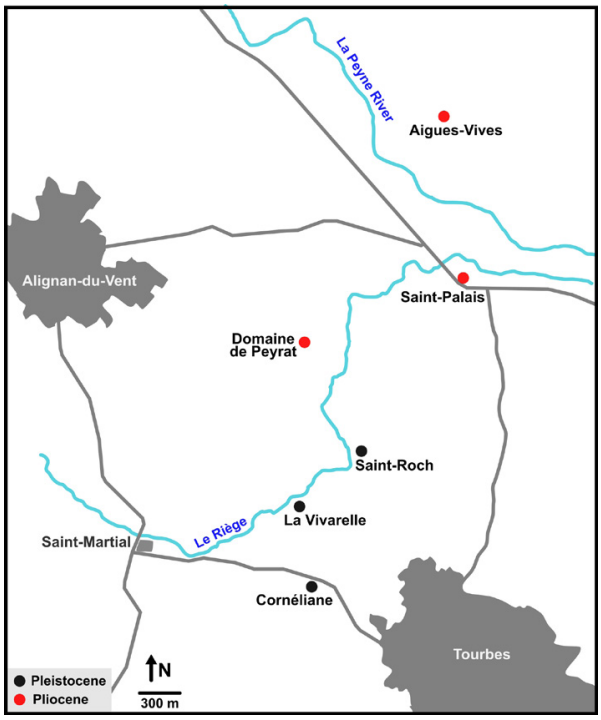

Figure 2. Location map of the main fossil-yielding localities near Le Riège stream (see Fig. 1 for a general geographical context). Red and black dots denote Pliocene and Pleistocene localities, respectively. Saint-Roch, La Vivarelle, and Cornéliane are toponyms corresponding to collects of Pleistocene "Le Riège" fossils, notably by J.-Y. Crochet and J. Ivorra in 1998.

been divided in distinct collections, based upon tags and code numbers: "Reboul 1839"; "de Christol 1865"; "Crochet and Ivorra 1998"; "anonymous Collection". The "Reboul 1839" collection is composed of 51 fossil specimens. Each sample has a tag "H. Reboul 1839 n° *number*" and another more recent code number is present, "UM-PEZ-*number*" (UM-PEZ = *Université de Montpellier* Pézenas). The complete code number, with which the samples will be listed, is: "Reboul 1839, n° *number*, UM-PEZ-*number*". The Reboul collection's fossils will be listed following the historical number written on the tag, among the same taxonomic group. The samples of this collection, both from Pliocene (cervids, rhinoceroses, proboscideans, and bovids) and Pleistocene (cervids, rhinoceroses, proboscideans, equids, bovids, hippopotamuses, and unidentified), are stored in three boxes. The "de Christol 1865" collection consists of 18 specimens, which have "Fac. Sc. Montpellier. COLL^{on} DE CHRISTOL. 1865." written on a tag and a recent code number, "UM-PEZ-*number*". The complete code number, with which the samples will be listed, is: "de Christol 1865, UM-PEZ-*number*". The fossils are stored in one box, with both Pliocene (rhinoceroses) and Pleistocene large mammals (cervids, bovids, and hippopotamuses). The "Crochet and Ivorra 1998" collection comprises 17 Pleistocene specimens (cervids, proboscideans, equids, and bovids), stored in a box (the original one). The concerned collectors have left two papers: one shows where fossil specimens were found on a geographic map on 29th October 1998 (Le Riège locality, Tourbes, near Pézenas; Montpellier). The other paper contains information about each sample: where they were found, the "UM-PEZ-*number*" code, which bony elements are a preliminary taxonomy determination. The fossils from "Crochet and Ivorra 1998" collection are composed of Pleistocene cervids, proboscideans, equids, bovids and modern fauna. The remaining fossils belong to an anonymous collection: 29 specimens have a code number, "UM-PEZ-*number*", and nine specimens do not have a code number. The collection is composed by specimens of Pliocene proboscidean and marine mammals and Pleistocene fauna. Among the collections, the figured specimens in the literature had been marked by a circular green sticker. On most specimens are inscribed historical words. Here, we will provide a tentative transcription of the concerned text in a dedicated table (Supplementary Data).

Methods. Measurements of the fossil specimens were taken with a manual metric caliper (0.02 mm accuracy). The osteological identification/comparison was performed by direct examination of articulated skeletons from the UM collections and through anatomical atlases (e.g., Barone, 1995). Regarding taxonomic assignments, Depéret and Donnezan (1890), Guérin (1980), Dong (1996), Alberdi and Palombo (2013), van der Made *et al*. (2017), Croitor (2018), Mecozzi *et al*. (2023) and Sorbelli *et al*. (2023) were among the most useful sources. Some specimens from Montpellier historical collections (Montpellier, Sables Marins Littoraux (Hérault); MN14), stored at the ISEM, were studied for comparison. The studies of de Bruijn *et al*. (1992), Guérin (2007) and Palombo and Valli (2004) were consulted on biochronological purpose.

For this revision, we considered each collection separately (i.e., Reboul Collection [RC], de Christol Collection [CC], Crochet and Ivorra Collection [CIC], and "Unlabelled Le Riège UM Collection" [RUM]). We then produced a synthesis of the whole taxonomic information in order to provide separate faunal lists for Pliocene and Pleistocene assemblages, respectively (Supplementary Data).

RESULTS

Systematic Paleontology

Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Family Bovidae Gray, 1821
Genus *Alephis* Gromolard, 1980
Alephis sp.
Fig. 3A

Illustrated samples. "Reboul Collection 1839" - Right lower jaw fragment bearing p2 (n°11, UM-PEZ-4333) (Fig. 3A).

Biochronological range. Ruscinian – Lower Villafranchian (MN14–MN16a) (e.g., de Bruijn *et al*., 1992; Bianucci *et al*., 2001; Palombo and Valli, 2004; Montoya *et al*., 2006; Guérin, 2007; van der Made *et al*., 2010; Konidaris and Kostopoulos, 2024).

Remarks. Pliocene bovids from the Montpellier area have been always referred to *Parabos cordieri* (*Antilope cordieri*, Gervais, 1859: pp. 139–140, Pl. I, figs. 14, 15, Pl. VII, figs. 3–11; Gaudry, 1868: p. 954; *Palaeoryx cordieri*, Depéret, 1897: pp. 647–649; Gromolard, 1980: pp. 767–772, Pl. I; Gromolard and Guérin, 1980: pp. 741–755, Pl. I). When compared to specimens from "Sables De Montpellier (de Christol, 1832) collection" (SM 331, SM 330, SM 321), the sample from Le Riège is different from second premolars of *Parabos cordieri*, which are longer and more elongated. In addition, the latter have an anterior stylid and both posterior and back valleys. In *P. cordieri*, the lower jaw (SM 321) is slenderer than the specimen from Le Riège. Therefore, it may not be referred to *Parabos*. It has morphology and dimensions comparable with those of *Alephis lyrix* from Roussillon (Depéret and Donnezan, 1890: Pl. VII, figs. 2, 3; Gromolard, 1980: Pl. I, fig. 3). Considering the few published studies about *Alephis* (e.g., *Alephis lyrix* from Val di Pugna, Italy, Bianucci *et al*., 2001; *Alephis boodon* from Alcoy, Spain, Montoya *et al*., 2006; *Alephis* sp. from Milia, Greece, Crégut-Bonnoure and Tsoukala, 2017; *Alephis tigneresi* from Camp dels Ninots, Spain, Gómez de Soler *et al*., 2012) and due to the lack of comprehensive comparison, the lower jaw fragment preserving p2 from Le Riège is referred to an indeterminate species of *Alephis* genus.

Genus *Leptobos*? Rütimeyer, 1877–1878
Fig. 3B

Illustrated samples. "Reboul Collection 1839" **-** Distal fragment of right tibia (n°39, UM-PEZ-4352) (Fig. 3B).

Biochronological range. Lower Villafranchian – Late Villafranchian (MN16a–MNQ19) (e.g., Palombo and Valli, 2004; Sorbelli *et al.,* 2023).

Remarks. The specimen UM-PEZ-4352 has higher dimensions than Zanclean bovids (Crégut-Bonnoure and Tsoukala, 2017: table 17). The size is more similar to what is observed in *Leptobos* than in *Bison* (Sorbelli *et al*., 2023: table S19). Its morphology differs from that of the distal fragment of tibia assigned to *Bison* (UM-PEZ-18) of Le Riège *sensu stricto* from "Crochet and Ivorra 1998" collection. Morphological characters (e.g., cochlea, obliquity and depth of articular

facets) closely resemble those of *Leptobos etruscus* from the Upper Valdarno as illustrated by Cherin *et al*. (2019: fig. 14c).

Genus *Bison* Hamilton Smith, 1827

Subgenus *Eobison* Flevor, 1972

Bison (*Eobison*) spp.

Fig. 3C–F; Fig. 4; Fig. 5

Illustrated samples. "Reboul Collection 1839" - Fragment of horn-core (n°3, UM-PEZ-4331) (Fig. 3C); distal fragment of left humerus (n°13, UM-PEZ-4376) (Fig. 3D); left II phalanx (n°14, UM-PEZ-4346) (Fig. 3E); distal fragment of right humerus (n°15, UM-PEZ-4363) (Fig. 3F); proximal fragment of right tibia (n°34, UM-PEZ-4364) (Fig. 4A); distal fragment of right femur (n°35, UM-PEZ-4362) (Fig. 4B); right astragalus (n°38, UM-PEZ-4283) (Fig. 4C). "de Christol Collection 1865" - Proximal fragment of left radio-ulna (UM-PEZ-4292) (Fig. 4D); proximal fragment of left scapula (UM-PEZ-4325) (Fig. 4E); proximal fragment of left humerus (UM-PEZ-4365) (Fig. 4F). "Crochet and Ivorra Collection 1998" - Distal fragment of right femur (UM-PEZ-3) (Fig. 5A); left upper molar (M3?) (UM-PEZ-9) (Fig. 5B); distal fragment of right tibia (UM-PEZ-18) (Fig. 5C). "Unlabelled Le Rièg UM Collection" - Back skull with left horn-core (UM-PEZ-51) (Fig. 5D); left horn-core with pedicle (UM-PEZ-4304) (Fig. 5E); left m3 (UM-PEZ-4329) (Fig. 5F).

Other referred specimens. "Reboul Collection 1839" - Last cervical vertebra (n°4, UM-PEZ-4315); lumbar vertebra (n°7, UM-PEZ-4310); fragment of right mandible with condyle (n°9, UM-PEZ-4297); fragment of right maxilla bearing P2-M3 in alveoli (n°12, UM-PEZ-4311); proximal fragment of right scapula (n°15, UM-PEZ-4290); distal fragment of left tibia (n°32, UM-PEZ-4330); distal fragment of right radio-ulna (n°61 UM-PEZ-4358). "Crochet and Ivorra Collection 1998" - Fragment of cervical vertebra (UM-PEZ-2); fragment of lower molar (UM-PEZ-11). "Unlabelled Le Rièg UM Collection" - Lumbar vertebrae (UM-PEZ-34, 4294); proximal fragment of right ulna (UM-PEZ-4326).

Biochronological range. Late Villafranchian (MNQ18–MNQ19) (e.g., Sorbelli *et al*., 2023).

Figure 3. Pliocene–Pleistocene bovids from "Le Rièg" localities (near Pézenas, Southern France). ***Alephis* sp.**: "Reboul Collection 1839" - (A) Right lower jaw fragment bearing p2 (n°11, UM-PEZ-4333) in lingual view. ***Leptobos*?**: "Reboul Collection 1839" - (B) Distal fragment of right tibia (n°39, UM-PEZ-4352) in distal view. ***Bison* (*Eobison*) spp.**: "Reboul Collection 1839" - (C) Fragment of horn-core (n°3, UM-PEZ-4331); (D) distal fragment of left humerus (n°13, UM-PEZ-4376) in anterior view; (E) left II phalanx (n°14, UM-PEZ-4346) in distal view; (F) distal fragment of right humerus (n°15, UM-PEZ-4363) in anterior view. Scale bars= 20 mm.

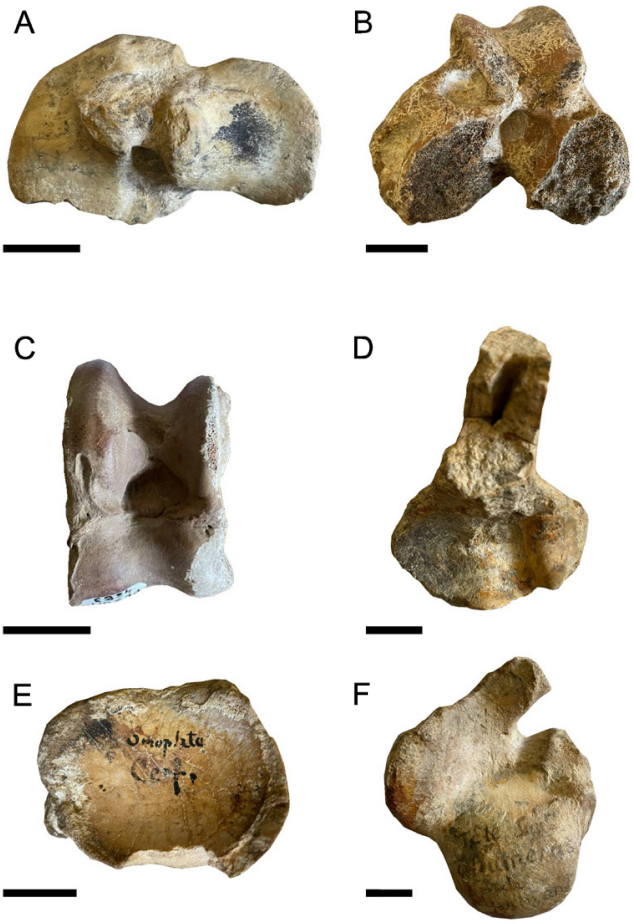

Figure 4. Pleistocene bovids from "Le Rièg" localities (near Pézenas, Southern France). ***Bison* (*Eobison*) spp.**: "Reboul Collection 1839" - (A) Proximal fragment of right tibia (n°34, UM-PEZ-4364) in proximal view; (B) distal fragment of right femur (n°35, UM-PEZ-4362) in distal view; (C) right astragalus (n°38, UM-PEZ-4283) in dorsal view. "de Christol Collection 1865" - (D) Proximal fragment of left radio-ulna (UM-PEZ-4292) in proximal view; (E) proximal fragment of left scapula (UM-PEZ-4325) in proximal view; (F) proximal fragment of left humerus (UM-PEZ-4365) in proximal view. Scale bars= 20 mm.

Remarks. Some samples were historically referred to deer fossils. For example, Gervais (1859) affirmed that the right astragalus (Reboul 1839, n°38, UM-PEZ-4283) belongs to *Cervus martialis* (large Pleistocene deer) and he illustrated it (Gervais, 1859: plate XXI, figs. 7, 7[a]). Also, proximal fragment of right scapula (Reboul 1839, n°15, UM-PEZ-4290) is referred historically to a deer because the mention "*Omoplate de grand Cerf*" ("large deer scapula") is written upon the fossil itself. Among the diagnostic samples, the fragment of horn-core from Reboul Collection (n°3, UM-PEZ-4331) has a morphology similar to the horn-core of *Bison* cf. *degiulii* from Apollonia (Kostopoulos *et al*., 2018: fig. 6c) and especially of *Bison* (*Eobison*) *degiulii* from Pietrafitta (Sorbelli *et al*., 2023: fig. 3). In the diagram reported by Sorbelli *et al*. (2023: fig. 6), the size of the sample from Le Riège locality falls in the range of *Bison* (*Eobison*) *degiulii* from different sites of Italy. The left II phalanx (Reboul 1839, n°14, UM-PEZ-4346) is similar in morphology and size to that in *Bison* (*Eobison*) sp. (anterior part) from Moldova (Croitor, 2016: fig. 1). Its morphology is exactly the same as *Bison* (*Eobison*) *degiulii* from Pietrafitta (Sorbelli *et al*., 2023: fig. S6d). The distal fragment of left humerus (Reboul 1839, n°13, UM-PEZ-4376) and the distal fragment of right humerus (Reboul 1839, n°15, UM-PEZ-4363) have dimensions very similar to those of *Bison* (*Eobison*) *degiulii* (Sorbelli *et al*., 2023: table S10), but the morphology is quite different (notably a more inclined trochlea).

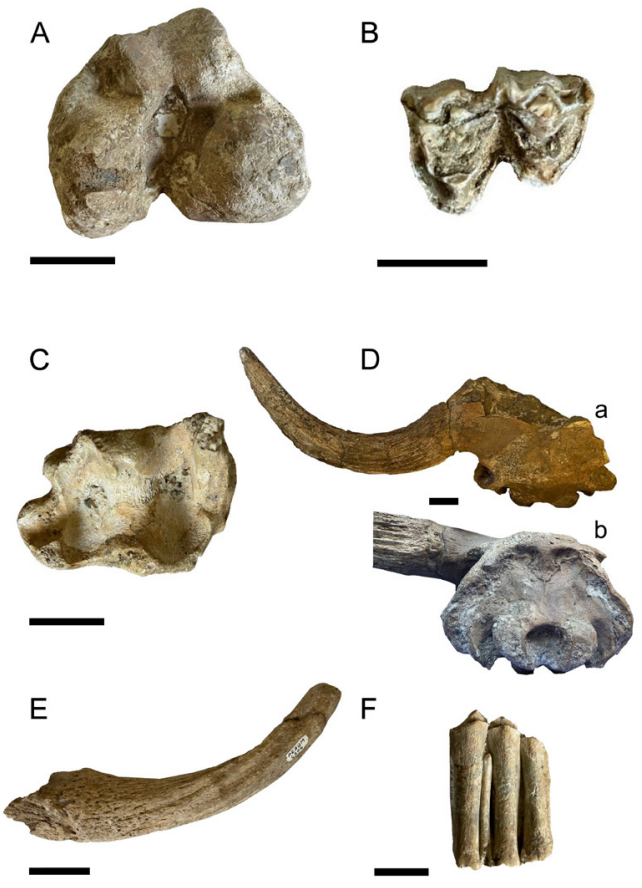

Figure 5. Pleistocene bovids from "Le Riège" localities (near Pézenas, Southern France). ***Bison* (*Eobison*) spp.**: "Crochet & Ivorra Collection 1998" - (A) Distal fragment of right femur (UM-PEZ-3) in distal view; (B) left upper molar (M3?) (UM-PEZ-9) in occlusal view; (C) distal fragment of right tibia (UM-PEZ-18) in distal view. "Unlabelled Le Riège UM Collection" - (D) Back skull with left horn-core (UM-PEZ-51) in a. dorsal-occipital view, b. occipital view; (E) left horn-core with pedicle (UM-PEZ-4304) in medial-ventral view; (F) left m3 (UM-PEZ-4329) in lingual view. Scale bars= 20 mm.

In the de Christol Collection (1865), the proximal fragment of radio-ulna (UM-PEZ-4292) is very similar to *Bison* (*Eobison*) sp. from Venta Micena (Spain) in terms of dimensions, and smaller than that of *Bison* (*Eobison*) *degiulii* (Sorbelli *et al*., 2023: table S12). The proximal fragment of left scapula (UM-PEZ-4325) has the same morphology as a fragment of scapula from Reboul Collection (n°15, UM-PEZ-4290).

Crochet and Ivorra recognized the osteology of the fossils from Le Riège area (Tourbes, Pézenas) and proposed a preliminary determination: unidentified bovid (similar to *Leptobos*) for UM-PEZ-2; unidentified bovid (similar to *Bison*) for UM-PEZ-3; unidentified bovid for UM-PEZ-9 and UM-PEZ-11; *Leptobos*? for UM-PEZ-18. The distal fragment of right femur UM-PEZ-3 and the same bony element from Reboul Collection (UM-PEZ-4362) have the same morphology and size, which are further compatible with *Bison (Eobison) degiulii* as illustrated by Sorbelli et al. (2023: fig. S4), peculiarly regarding the position of the notches. Samples UM-PEZ-9 and UM-PEZ-11 were collected from the same place. About UM-PEZ-9, we cannot write so much, because the tooth is particularly worn, and the specimen has not been fully prepared. The general dimensions and morphology are comparable with those of *Bison* (*Eobison*) *degiulii* (Kostopoulos *et al*., 2018; Sorbelli *et al*., 2023). Sample UM-PEZ-18 was referred to *Leptobos* with doubts by the collectors. However, it has a morphology more similar to *Bison* (*Eobison*) (Sorbelli et al., 2023: fig. S4) than *Leptobos* (Duvernois 1990: fig. 36). The dimensions fall within the range of different species in table S19 by Sorbelli et al. (2023) and they are the same as those of *Bison* (*Eobison*) *degiulii* from Pirro Nord.

Within the "Unlabelled Le Riège UM Collection", the sample UM-PEZ-51 has a horn-core clearly distinct from those of all species of *Leptobos* (Masini *et al*., 2013: figs. 3-7), regarding both morphology and insertion position. These features are comparable instead to what is known in *Bison* (*Eobison*) (Masini *et al*., 2013). Using diagnostic morphological characters as synthesized by Sorbelli *et al*. (2023: table 7), UM-PEZ-51 has more in common with *Bison* (*Eobison*), especially as for horn-core shape, horn-core position, occipital squama and intertemporal bridge. Concerning the dimensions, UM-PEZ-51 has values much more like *Bison* (*Eobison*) than *Leptobos* (Kostopoulos *et al*., 2018: tables 2, 5). Kostopoulos *et al*. (2018) described a skull from Greece assigned to *Bison* (*Eobison*) cf. *degiulii* and in both specimens, the cranial roof is flat to slightly concave until the back of the horn-cores and slightly convex at the parietal region. The horn-core is inserted caudo-laterally and it bends immediately downwards without rising above the frontal level. The horn-core curves quickly upwards and taper rapidly. The lowermost preserved point of the ventral surface of the horn-core is at the level of the lower edge of the external occipital protuberance. The pedicle is short, with slightly inflated dorsal profile. The greater rostro-caudal axis of the horn-core base is trending parallel to the frontals. The intertemporal bridge is narrow (intertemporal bridge heigh (IBH)= 35 mm) and the occipital surface has a roughly trapezoidal outline and is moderately undulated. However, the Le Riège horn-core is rather smaller compared to the cranium size of *B. (E.) degiulii* and in UM-PEZ-51 the base of the horn-core is more circular (basal dorsoventral diameter of horn-core (HDV)/basal anteroposterior diameter

of horn-core (HAP)= 97 mm; instead, 83–89 mm in *B*. (*E*.) *degiulii*). Sorbelli *et al*. (2023) figured different cranial remains of *Bison* (*Eobison*) *degiulii*, belonging both to male and female specimens, whose horn-cores are stockier than the specimen n°51 (similar to fig. 10d2). The specimen from Le Riège locality may be an early *Bison* (*Eobison*), a "transitional form" between *Leptobos* and *Bison*, because comparing its occipital view with fig. 11c by Sorbelli *et al*. (2023), there are a lot in common with *Bison* (*Eobison*) (short pedicle that emerges laterally and similar horn-core), but the intertemporal bridge is higher, and the frontals are lower (more archaic features). Ambert *et al*. (1996) reached the same conclusion studying an uncomplete skull from Le Riège (unfortunately unfigured). UM-PEZ-51 and the specimen described by Ambert *et al*. (1996) share a median swelling on the frontal between the horn-cores, which denotes the highest point of the skull; a wide and low occipital of triangular shape; a long and relatively thin basioccipital with a tightening just behind the posterior tuberosities; temporal fossae going as far back as the occipital plane, which give a narrow and thick nuchal crest; a smooth keel on the postero-basal side of horn-core with thin furrows covering the entire surface; small-sized horn-cores with sub-circular cross section. They are not swollen or flattened and taper out gradually. They curve gradually, backward with a slight twist. The specimen UM-PEZ-51 has a horn core different from the specimen Reboul 1839, n°3, UM-PEZ-4331 in being slender. The horn-core with pedicle (UM-PEZ-4304) is completely different from the other ones, similar to what was assigned to *Bison (Bison)* cf. *sivalensis* from Pakistan by Khan *et al*. (2010: fig. 2). The lower m3 (UM-PEZ-4329) has dimensions matching those of different species of bovids, especially in *Bison* (*Eobison*) (Sorbelli *et al*., 2023: table 4) and a morphology compatible with this latter (even if the worn stages are different). It falls near *Bison* from Mygdonia Basin (Kostopoulos *et al*., 2018: fig. 14).

With caution, we consider a referral to *Bison* (*Eobison*) for all these large bovid specimens and suspect the potential presence of different species of this subgenus in the available samples. A certain diachronism might occur between the concerned localities (compare Reboul 1839, n°3, UM-PEZ-4331 with de Christol 1865, UM-PEZ-51 and UM-PEZ-4304 from "Unlabelled Le Riège UM Collection").

Family Cervidae Goldfuss, 1820

Cervidae indet.

Figs. 6A, B

Illustrated samples. "Reboul Collection 1839" - Antler fragment (n°26, UM-PEZ-4300) (Fig. 6A). "Crochet and Ivorra 1998" - Distal fragment of left humerus (UM-PEZ-8) (Fig. 6B).

Other referred specimens. "Crochet and Ivorra 1998" - Proximal fragment of left ulna (UM-PEZ-16). "Unlabelled Le Riège UM Collection" - proximal fragment of right astragalus (no code).

Remarks. The specimen n°26, UM-PEZ-4300 from Reboul Collection 1839 is a basal fragment of antler with a subcircular-ovoid burr. The shaft bends, with a nodule (?). Due to its poor state of preservation, a taxonomic determination is not possible, even if it has some features in common with the antler of *Praeelaphus* (Croitor, 2018: pp. 59–66). Crochet and Ivorra recognized the osteology of UM-PEZ-8, but not of UM-PEZ-16 (they wrote "indet."). They proposed a preliminary determination: "unidentified bovid" for UM-PEZ-8 and for UM-PEZ-16. The distal fragment of humerus (UM-PEZ-8) is similar to the same bony element from "de Christol 1865" collection (UM-PEZ-4296). They are compatible with a large Pleistocene deer (Pfeiffer-Deml, 2016; Tong and Zhang, 2019).

Genus *Procapreolus* Schlosser, 1924

Procapreolus cf. *pyrenaicus* Depéret, 1890

Figs. 6C, D

Illustrated samples. "Reboul Collection 1839" - Antler fragments (n°20, UM-PEZ-4323; n°29, UM-PEZ-4351) (Figs. 6C, D).

Biochronological range. Ruscinian (MN15) (for *P. pyrenaicus*) (e.g., de Bruijn *et al*., 1992; Palombo and Valli, 2004; Guérin, 2007).

Remarks. *Procapreolus*, a small-medium size deer, was abundant during the time interval ranging from the Late

Figure 6. Pliocene–Pleistocene deers from "Le Riège" localities (near Pézenas, Southern France). **Cervidae indet.**: "Reboul Collection 1839" - (A) Antler fragment (n°26, UM-PEZ-4300). "Crochet & Ivorra Collection 1998" - (B) Distal fragment of left humerus (UM-PEZ-8) in anterior view. ***Procapreolus* cf. *pyrenaicus***: "Reboul Collection 1839" - (C) Antler fragment (n°20, UM-PEZ-4323); (D) antler fragment (n°29, UM-PEZ-4351). ***Eucladoceros* cf. *giulii***: "Reboul Collection 1839" - (E) Left lower jaw fragment with alveoli (n°5, UM-PEZ-4305) in buccal view; (F) left lower jaw bearing m3 (n°10, UM-PEZ-4285-4319) in buccal view. Scale bars= 20 mm.

Miocene to the Early Pleistocene in Eurasia. It has a three-pointed lyre-shaped antler with deep external ornamentation (Valli, 2010; Croitor, 2018, 2022). The specimens from Le Rièges locality share the same morphological features. The most complete specimen (Reboul 1839, n°20, UM-PEZ-4323), a bit eroded, preserves the first bifurcation with a smaller cylindrical branch and a bigger flattened branch. The second bifurcation is not complete. The sample differs from antlers of *P. loczyi* (Zapfe, 1997), *P. vesti*, *P. moldavicus* and *P. cusanus* (Valli, 2010; Croitor, 2018: fig. 3) in having a curved shaft, a more U-shaped first bifurcation, a longer and cylindrical first tine (except for *P. loczyi*), and in being curved inward with a convex outer margin after the first bifurcation. The other specimen (Reboul 1839, n°29, UM-PEZ-4351) is a fragment of basal antler, with the burr and partially preserved first bifurcation. Upon the sample historical words, "*Bois de Cerf*" and "*Chevreuil*", are written ("deer antler" and "roe deer", respectively). Both specimens seem to be similar to *"Cervus" pyrenaicus* antlers from the Pliocene of Roussillon in France (*Cervus ramosus,* Depéret and Donnezan, 1890: pp. 99–103, Pl. VIII, figs. 1–3; Dong, 1996: pp. 149–153, Pl. II, figs. 4–5). *"Cervus" pyrenaicus* antlers from "Sables De Montpellier (de Christol 1832) collection" are very few and fragmentary, indeed the comparisons with these historical samples are not possible. Therefore, both samples belong surely to *Procapreolus* and they are confrontable to "*Cervus*" *pyrenaicus*, which Croitor (2018) assigned to *Procapreolus*.

Genus *Eucladoceros* Falconer, 1868

Eucladoceros cf. *giulii* Kahlke, 1997

Figs. 6E, F; Fig. 7; Fig. 8; Fig. 9; Fig. 10

Illustrated samples. "Reboul Collection 1839" - Left lower jaw fragment with alveoli (n°5, UM-PEZ-4305) (Fig. 6E); left lower jaw bearing m3 (n°10, UM-PEZ-4285-4319) (Fig. 6F); antler fragments (n°18, UM-PEZ-4284; n°19, UM-PEZ-4356; n°21, UM-PEZ-4322) (Figs. 7A–C); left mandible fragment preserving dp4 (n°21, UM-PEZ-4342) (Fig. 7D); antler fragments (n°22, UM-PEZ-4282; n°25, UM-PEZ-4318; n°28, UM-PEZ-4301-4302) (Fig. 7E; Figs. 8A, B); proximal fragment of left metacarpal (n°33, UM-PEZ-4281) (Fig. 8C). "de Christol Collection 1865" - Distal epiphysis of right humerus (UM-PEZ-4296) (Fig. 8D); distal fragment of right tibia (UM-PEZ-4304) (Fig. 8E); skull fragment with pedicle (UM-PEZ-4324) (Fig. 8F); antler fragment (UM-PEZ-4335) (Fig. 9A); antler fragments (UM-PEZ-4344; UM-PEZ-4355; UM-PEZ-4363) (Figs. 9B–D). "Unlabelled Le Rièges UM Collection" - Right lower jaw fragment bearing dp2-dp4 (UM-PEZ-4309) (Fig. 9E); right lower jaw fragment preserving m3 (UM-PEZ-4343) (Fig. 10A); antler fragments (UM-PEZ-4367(x2)-4368-no code; UM-PEZ-4368) (Figs. 10B, C).

Not illustrated samples. "Reboul Collection 1839" - Proximal fragment of II phalanx (n°13, UM-PEZ-4360); antler fragments (n°23, UM-PEZ-4308; n°27, UM-PEZ-4336; n°27, UM-PEZ-4349); proximal fragment of left tibia (n°36, UM-PEZ-4295); distal fragment of left tibia (n°37, UM-PEZ-4291); fragment of left tibia (n°40, UM-PEZ-4375). "de Christol Collection 1865" - Antler fragments (UM-PEZ-4334; UM-PEZ-4340; UM-PEZ-4341; UM-PEZ-4366); back skull fragment (UM-PEZ-4337); distal fragment of femur without epiphysis (UM-PEZ-4354). "Unlabelled Le Rièges UM Collection" - Axis (UM-PEZ-4307); antler fragment (4317); left navicular-cuboid (UM-PEZ-4350); antler fragment (no code).

Biochronological range. Late Villafranchian – early Galerian (MNQ19–MNQ21) (for *E. giulii*) (e.g., Kahlke, 2009; van der Made *et al*., 2017).

Remarks. Historical scholars (Gervais, 1859; Gaudry, 1868; Depéret, 1897) referred to Pleistocene large deer specimens from Le Rièges as *Cervus martialis*. Formally, this species is no longer accepted (NOW – New and Old Worlds – Database of fossil mammals). Croitor (2018) assigned some samples of *Cervus martialis* from Le Rièges (here from the Reboul Collection n°22, UM-PEZ-4282 and n°28, UM-PEZ-4301-4302), figured by Gervais (1859: plate XXI, figs. 2–5), to *Eucladoceros dicranios*, a large late Early Pleistocene deer with "brush-like" antler. However, most of specimens from the UM collections differ from what is known of *E. dicranios*. Among the mandibles, the sample preserving m3 from Reboul Collection (n°10, UM-PEZ-4285-4319), figured by Gervais (1859: plate XXI, fig. 1), has a length-premolar/molar ratio higher than *E. dicranios* values (Croitor, 2018: table 3) and closer to *E. giulii*, an elusive Late Villafranchian deer (Croitor and Kostopoulos, 2004: fig. 11). A similar specimen from "Unlabelled Le Rièges UM Collection" **(**UM-PEZ-4343) has a m3 the size of which matches those of *E. giulii* (see van der Made *et al*., 2017: fig. 10). From the de Chistol Collection, the skull fragment with pedicle (UM-PEZ-4324) closely resembles

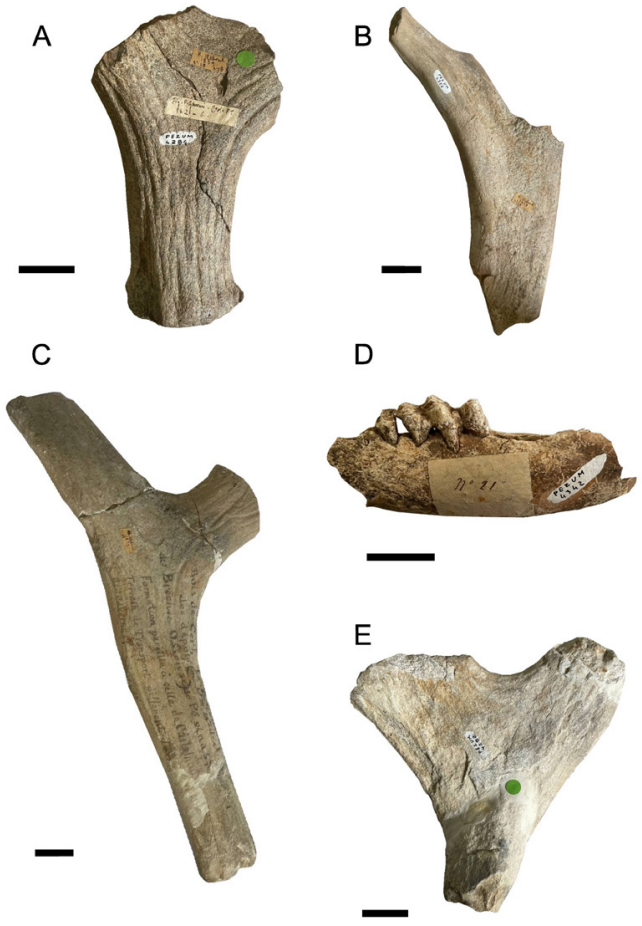

Figure 7. Pleistocene deers from "Le Rièges" localities (near Pézenas, Southern France). ***Eucladoceros* cf. *giulii***: "Reboul Collection 1839" - (A) Antler fragment (n°18, UM-PEZ-4284); (B) antler fragment (n°19, UM-PEZ-4356); (C) antler fragment (n°21, UM-PEZ-4322); (D) left mandible fragment preserving dp4 (n°21, UM-PEZ-4342) in buccal view; (E) antler fragment (n°22, UM-PEZ-4282). Scale bars= 20 mm.

that of *E. giulii* from Saint-Prest (Guérin *et al*., 2003; Croitor, 2018), even if in the sample from Le Rièg̀e, the pedicles point more sideward and backward.

The most diagnostic fossils, however, are the antler fragments. The distance between the burr and the first bifurcation in the samples from Le Rièg̀e (for example, around 187 mm in Reboul 1839, n°18, UM-PEZ-4284) is higher than in *E. dicranios* antler (e.g., de Vos *et al*., 1995; Baygusheva and Titov, 2013; Rook *et al*., 2013; Croitor, 2018). From the "Reboul Collection" the sample n°18, UM-PEZ-4284 (figured by Gervais, 1859: plate XXI, fig. 6) and from the "Christol Collection" UM-PEZ-4355 and UM-PEZ-4366 has a similar morphology and size to *E. giulii* antler fragment from Atapuerca (van der Made, 1999: fig. 13). Among the paleontological collections from Le Rièg̀e, UM-PEZ-4367(x2)-4368-no code from "Unlabelled Le Rièg̀e UM Collection" is the most complete antler, belonging to an adult specimen. It is composed from the base to the top by the following samples: from burr to first bifurcation (4368); lower main beam (4367); second bifurcation (no code); upper main beam and third bifurcation (4367). This antler is clearly distinct from "brush-like" antler of *Eucladoceros dicranios*, instead it has similar antler structure of *Eucladoceros giulii* (van der Made *et al*., 2017: fig. 10; Breda *et al*., 2020).

For all these reasons, we propose to assign these large deer remains from Le Rièg̀e to *Eucladoceros* cf. *giulii*, further considering they originate from Lower Pleistocene deposits.

Suborder Cetancodonta Arnason *et al*., 2000

Infraorder Cetacea Brisson, 1762

Cetacea indet.

Unillustrated sample. "Unlabelled Le Rièg̀e UM Collection" - Cranial bone fragment (jugal/squamosal) (UM-PEZ-4312).

Remarks. This very dense bone clearly belongs to a large-bodied marine mammal. Marine mammals, such as cetaceans and sirenians, are recorded in the Lower Pliocene faunas from the Sables De Montpellier (e.g., de Bruijn *et al*., 1992) and Roussillon (Depéret and Donnezan, 1890). In contrast and to our knowledge, there exists no mention of Pleistocene marine mammals from any Hérault Valley locality.

Family Hippopotamidae Gray, 1821

Hippopotamidae indet.

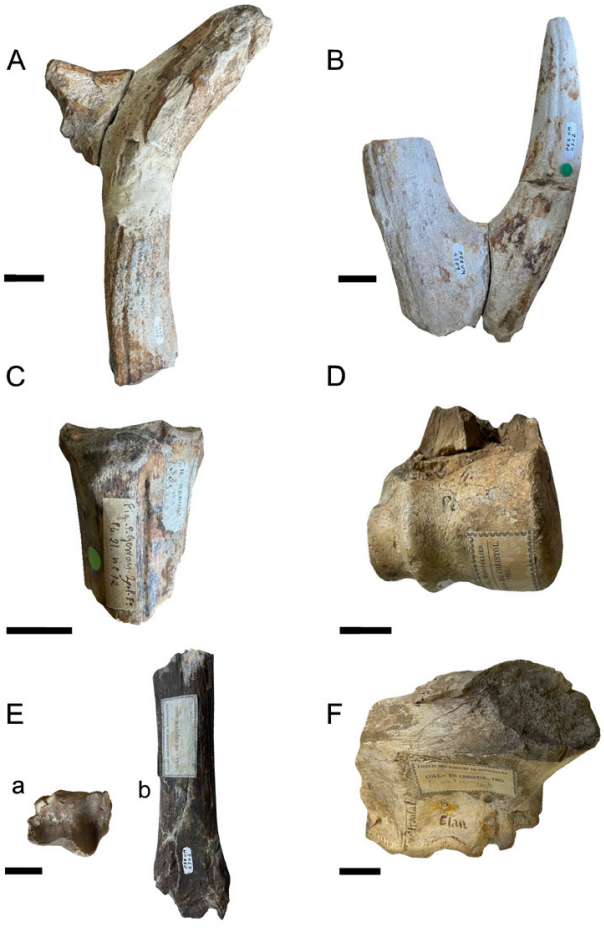

Figure 8. Pleistocene deers from "Le Rièg̀e" localities (near Pézenas, Southern France). ***Eucladoceros* cf. *giulii***: "Reboul Collection 1839" - (A) antler fragment (n°25, UM-PEZ-4318); (B) antler fragment (n°28, UM-PEZ-4301-4302); (C) proximal fragment of left metacarpal (n°33, UM-PEZ-4281) in dorsal view. "de Christol Collection 1865" - (D) Distal epiphysis of right humerus (UM-PEZ-4296) in anterior view; (E) distal fragment of right tibia (UM-PEZ-4304) in a. distal view, b. anterior view; (F) skull fragment with pedicle (UM-PEZ-4324) in dorsal view. Scale bars= 20 mm.

Figure 9. Pleistocene deers from "Le Rièg̀e"Le Rièg̀e localities (near Pézenas, Southern France). ***Eucladoceros* cf. *giulii***: "de Christol Collection 1865" - (A) Antler fragment (UM-PEZ-4335); (B) antler fragment (UM-PEZ-4344); (C) antler fragment (UM-PEZ-4355); (D) antler fragment (UM-PEZ-4363). "Unlabelled Le Rièg̀e UM Collection" - (E) Right lower jaw fragment bearing dp2-dp4 (UM-PEZ-4309) in buccal view. Scale bars= 20 mm.

Unillustrated samples. "de Christol Collection 1865" - Thoracic vertebra (UM-PEZ-4332).

Remarks. The sample, a robust thoracic vertebra (fourth or fifth?), seems to belong to a juvenile individual due to the lack of epiphyses. Given its large size, this vertebra cannot be referred to a bovid, a deer or a horse. The shape and size of the transverse process (stocky, short, and without additional apophyses), of the posterior face of the centrum (heart-shaped but dorso-ventrally compressed), of the neural canal (narrow and elliptical), and of the postzygapophyses (elliptical, nearly horizontal), allow to refer the specimen to Hippopotamidae instead of Rhinocerotidae and Proboscidea.

Genus *Hippopotamus* Linnaeus, 1758

Hippopotamus antiquus Desmarest, 1822

Fig. 11

Illustrated samples. "Reboul Collection 1839" - Left mandible fragment with m2 and m3 (n°49, UM-PEZ-4286) (Fig. 11A); uncomplete skull (n°60; UM-PEZ-4369) (Fig. 11B). "Unlabelled Le Riège UM Collection" - Palate bearing right P4-M3 and left M1-M3 (UM-PEZ-4370) (Fig. 11C).

Unillustrated samples. "Reboul Collection 1839" - Mandible fragment bearing p2-m2 in alveoli (n°51; UM-PEZ-4313); fragment of rib (n°54, UM-PEZ-4327). "Unlabelled Le Riège UM Collection" - Distal lower jaw fragment (UM-PEZ-4371).

Biochronological range. Late Villafranchian – Early Aurelian (MNQ18–MNQ24) (e.g., Martino and Pandolfi, 2021; Fidalgo *et al*., 2023).

Remarks. The molars of the mandible fragment from the Reboul Collection (n°49, UM-PEZ-4286) are illustrated by Gervais (Pl. XXI, figs. 11, 11[a]) in occlusal and buccal views. This author wrote that they are into the alveoli of a big mandible of *Hippopotamus major* (nowadays *H. antiquus*). The dimensions of m3 fall in the ranges of different taxa of *Hippopotamus* reported by Martino *et al*. (2023: tables 1, 2), even they are closer to mean values of *H. antiquus*. However, the dental dimensions do not seem to be diagnostic at the species level, as the ranges of the European Pleistocene hippopotamuses, *H. antiquus* and *H. amphibius*, highly overlap to each other (Mazza, 1995; Athanassiou *et al*., 2018). The uncomplete skull (Reboul 1839, n°60; UM-PEZ-4369) has the following features comparable to *H. antiquus* (Mazza, 1995; Fidalgo *et al*., 2023; Mecozzi *et al*., 2023): flat dorsal margin of the occipital bone; obtuse angle between the dorsal margin and the lateral ones of the occipital bone; vertical occipital; extended condyles with

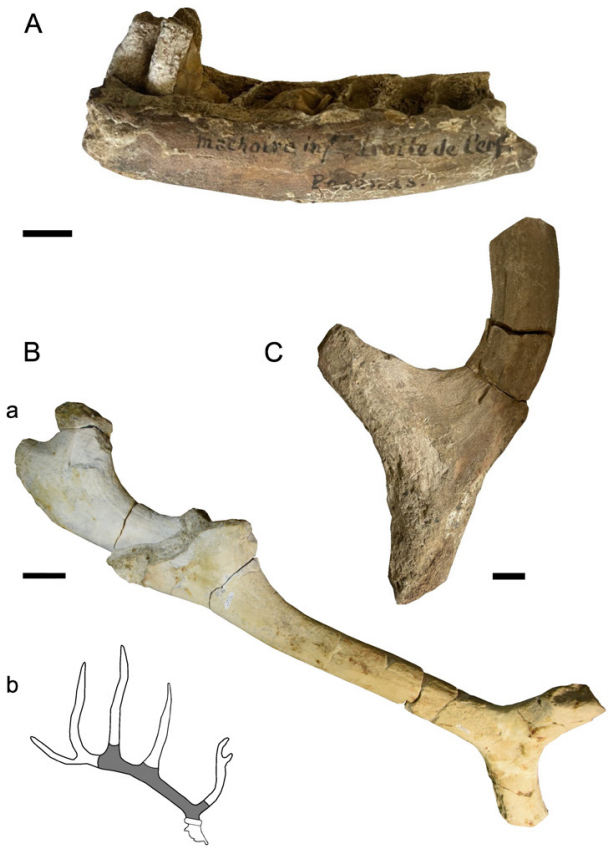

Figure 10. Pleistocene deers from "Le Riège" localities (near Pézenas, Southern France). ***Eucladoceros* cf. *giulii***: "Unlabelled Le Riège UM Collection" - (A) Right lower jaw fragment preserving m3 (UM-PEZ-4343); (B) antler fragment (UM-PEZ-4367(x2)-4368-no code): a. fossil from studied locality; b. fossil from studied locality (dark grey) in the reconstruction of *Eucladoceros giulii* antler (after Kahlke, 1997); (C) antler fragment (UM-PEZ-4368). Scale bars= 20 mm.

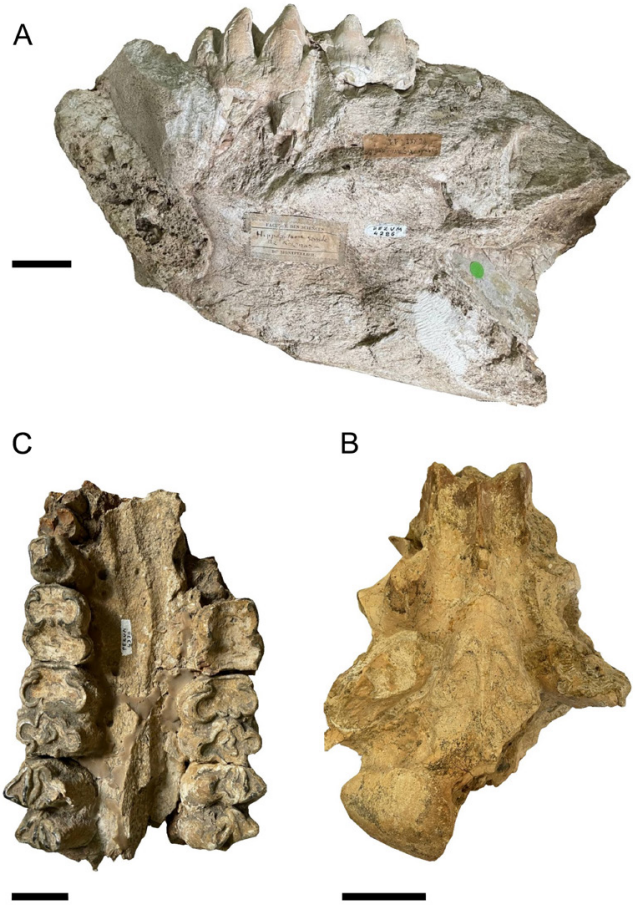

Figure 11. Pleistocene hippopotamuses from "Le Riège" localities (near Pézenas, Southern France). ***Hippopotamus antiquus***: "Reboul Collection 1839" - (A) Left mandible fragment with m2 and m3 (n°49, UM-PEZ-4286) in lingual view; (B) uncomplete skull (n°60; UM-PEZ-4369) in ventral view. "Unlabelled Le Riège UM Collection" - (C) Palate bearing right P4-M3 and left M1-M3 (UM-PEZ-4370) in occlusal view. Scale bars= 30 mm.

triangular shape (see Pandolfi and Petronio, 2015: fig. 3a); comparable sulci and morphological elements in relief in the occipital bone. The specimen UM-PEZ-4370 is much more similar in size to *H. antiquus* than to *H. amphibius*, as observed in Mazza (1995: table 4) and Mecozzi *et al*. (2023: table 1).

Hence, we consider that the complete hippopotamus collection from Le Riège, except for the thoracic vertebra UM-PEZ-4332, documents *Hippopotamus antiquus* and is Early Pleistocene in age.

Order Perissodactyla Owen, 1848

Suborder Tapiromorpha Haeckel, 1873

Family Rhinocerotidae Gray, 1821

Genus *Pliorhinus* Pandolfi *et al*., 2021

Pliorhinus megarhinus (de Christol, 1834)

Figs. 12A, B

Illustrated samples. "Reboul Collection 1839" - Right III metatarsal (n°55, UM-PEZ-4348) (Fig. 12A). "de Christol Collection 1865" - Distal fragment of right II metacarpal (UM-PEZ-4357) (Fig. 12B).

Figure 12. Rhinoceroses from "Le Riège" localities (near Pézenas, Southern France). ***Pliorhinus megarhinus***: "Reboul Collection 1839" - (A) Right III metatarsal (n°55, UM-PEZ-4348) in dorsal view. "de Christol Collection 1865" - (B) Distal fragment of right II metacarpal (UM-PEZ-4357) in dorsal view. ***Stephanorhinus etruscus***: "Reboul Collection 1839" - (C) Proximal fragment of right ulna (n°28, UM-PEZ-4306) in medial view; (D) proximal fragment of right humerus (n°30, UM-PEZ-4338) in proximal view. Scale bars= 30 mm.

Biochronological range. Late Turolian-Ruscinian (MN13–MN15) (e.g., de Bruijn *et al*., 1992; Palombo and Valli, 2004; Guérin, 2007; Pandolfi *et al.,* 2021; Pandolfi *et al.,* 2025).

Remarks. The third metatarsal has the same size as that of *Pliorhinus megarhinus* from France reported by Guérin (1980: pp. 549–554). The proximal epiphysis is comparable with that of *Pliorhinus megarhinus* even if some elements are not preserved in the sample. The section of diaphysis is the same as in this species, with a slightly convex dorsal surface and a flat-concave plantar surface, with medial side shorter than the lateral side. The second metacarpal fragment has also dimension and morphology compatible with *Pliorhinus megarhinus* from France reported by Guérin (1980: pp. 502–507). Both perfectly match the corresponding specimens identified as *P. megarhinus* and originating from the Lower Pliocene Sables de Montpellier housed in the UM collection.

Accordingly, we consider that these metapodials document *Pliorhinus megarhinus*, a conspicuous element of the Sables de Montpellier and Roussillon faunas (see Pandolfi *et al*., 2021). They are further assigned an Early Pliocene age (MN14–15).

Genus *Stephanorhinus* Kretzoi, 1942

Stephanorhinus etruscus Falconer, 1868

Figs. 12C, D

Illustrated samples. "Reboul Collection 1839" **-** Proximal fragment of right ulna (n°28, UM-PEZ-4306) (Fig. 12C); proximal fragment of right humerus (n°30, UM-PEZ-4338) (Fig. 12D).

Biochronological range. Early Villafranchian–Epivillafranchian (MN16a–MNQ20) (e.g., Palombo and Valli, 2004; Bourguignon *et al*., 2016; Pandolfi *et al.,* 2017; Pandolfi, 2023).

Remarks. Ambert *et al*. (1996) wrote that Guérin (1980) reported the presence of *Dicerorhinus etruscus brachycephalus* (= *Stephanorhinus hundsheimensis*) among the Pleistocene fauna from Le Riège. The proximal fragment of ulna (Reboul 1839, n°28, UM-PEZ-4306) and humerus (Reboul 1839, n°30, UM-PEZ-4338) have dimensions and morphology closer to the small-sized and slender-limbed *Stephanorhinus etruscus* than to any other Pliocene–Pleistocene rhinocerotine documented in Western Europe. Dimensions further match those reported by Guérin (1980) and Fortelius *et al*. (1993) for the Etruscan rhinoceros.

Accordingly, contrary to the taxonomic assignment proposed by Guérin (1980), these two postcranial specimens are here considered as documenting *Stephanorhinus etruscus*. This species was the most conspicuous rhinocerotine in Lower Pleistocene deposits across Europe (Pandolfi, 2023), so we can confidently assign a Pleistocene age to these postcranial bones.

Suborder Hippomorpha Ferrusquia-Villafranca, 1969

Family Equidae Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus sp.

Unillustrated samples. "Unlabelled Le Riège UM Collection" **-** Distal fragment of right humerus (UM-PEZ-4303); proximal fragment of left scapula (UM-PEZ-4314).

Remarks. In terms of general morphology, these fossils are

compatible with *Equus* and they are further likely to match those of *E*. cf. *altidens* from the other collection (see below) as for their dimensions. However, their fragmentary state discards any refined taxonomic identification. We assign them to an unidentified species of *Equus*.

Genus *Equus* Linnaeus, 1758

Equus cf. *altidens* von Reichenau, 1915

Fig. 13

Illustrated samples. "Reboul Collection 1839" - Proximal fragment of left metacarpal (n°43, UM-PEZ-4287) (Fig. 13A); distal fragment of left metacarpal (n°43, UM-PEZ-4353) (Fig. 13B); distal fragment of left metatarsal (n°44, UM-PEZ-4328) (Fig. 13C); distal fragment of right humerus (n°45, UM-PEZ-4316) (Fig. 13D). "Crochet and Ivorra 1998" - Upper molar fragment (UM-PEZ-6) (Fig. 13E).

Biochronological range. Late Villafranchian–Epivillafranchian (MNQ19–MNQ21) (e.g., Boulbes and Asperen, 2019).

Remarks. The proximal fragment of left metacarpal (n°43; UM-PEZ-4287) is described and illustrated by Gervais (1859: pp. 79, 80; Pl. XXI, figs. 9, 9[a]). This author referred to the sample as *Equus piscenensis,* a species that is no longer accepted (NOW – New and Old Worlds – Database of fossil mammals). The fragments of metacarpal (n°43; UM-PEZ-4287; n°43, UM-PEZ-4353) and humerus (n°45, UM-PEZ-4316) have dimensions perfectly matching those of *Equus altidens*, and they are smaller than those of *E. suessenbornensis* (Eisenmann - Official Website; Piñero and Alberdi, 2012-2014; Cirilli *et al.,* 2023). Both species are common during the Villafranchian–Galerian transition in Europe, considering also the presence (scanty record) of other three taxa (*E. stenonis*, *E. wuesti*, and *E. apolloninensis*). In their field notes, Crochet and Ivorra identified the specimen UM-PEZ-6 as an upper molar fragment and referred it as to *Equus*. The tooth closely resembles those of *E. altidens* and it is far less compatible with *E. suessenbornensis* molars, which have a more complex morphology (Boulbes and Asperen, 2019: fig. 3). In the specimen from Le Riège, the protocone has an external straight external margin as in *E. altidens* (Alberdi and Palombo, 2013: fig. 8), contrary to *E. suessenbornensis,* in which a lingual groove is present (Cirilli *et al*., 2023: fig. 2), although the variability of these morphological characters could be considered.

The specimens available in the studied collection are not fully diagnostic. Accordingly, we prefer to consider them as documenting *Equus* cf. *altidens*.

Order Sirenia Illiger, 1811

Family Dugongidae Gray, 1821

Dugongidae indet.

Unillustrated sample. "Unlabelled Le Riège UM Collection" - Rib fragment (UM-PEZ-4320-4361).

Remarks. This rib fragment is both pachyostotic and osteosclerotic (no medulla). The circular cross section and the curvature are compatible with a rib of a dugongid. Dugongids, such as *Metaxytherium serresi*, have been long reported in the Early Pliocene Sables de Montpellier (e.g., Bianucci *et al*., 2008). Due to its fragmentary condition and undiagnostic generic/specific features, we assign this specimen to an unidentified dugongid.

Order Proboscidea Illiger, 1811

Family Gomphotheriidae Hay, 1922

Genus *Anancus* Aymard, 1855

Anancus arvernensis (Croizet and Jobert, 1828)

Figs. 14A–C

Illustrated samples. "Reboul Collection 1839" - Tusk fragment (tip of an early permanent?) (n°50, UM-PEZ-4321) (Fig. 14A). "Unlabelled Le Riège UM Collection" - Molar fragments (UM-PEZ-25; UM-PEZ-4377) (Figs. 14B, C).

Biochronological range. Late Turolian – Middle Villafranchian (MN13–MNQ17a) (e.g., de Bruijn *et al*., 1992; Palombo and Valli, 2004; Guérin, 2007).

Remarks. The tusk tip is flat, with median grooves and sagittally oriented crenulations. This pattern matches that of gomphotheriids and, among them, *Anancus*. In contrast, it is

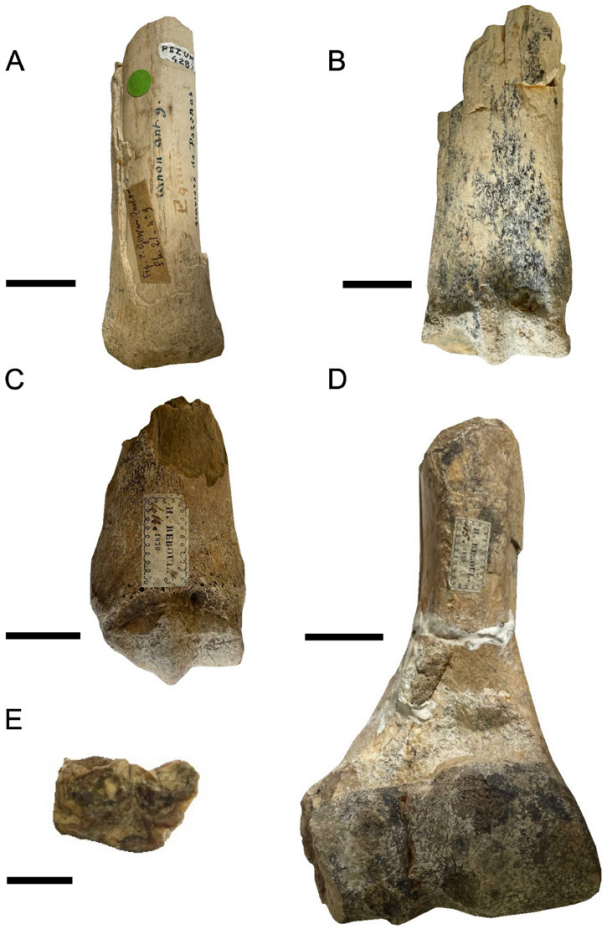

Figure 13. Pleistocene equids from "Le Riège" localities (near Pézenas, Southern France). ***Equus* cf. *altidens***: "Reboul Collection 1839" - (A) Proximal fragment of left metacarpal (n°43, UM-PEZ-4287) in dorsal view; (B) distal fragment of left metacarpal (n°43, UM-PEZ-4353) in plantar view; (C) distal fragment of left metatarsal (n°44, UM-PEZ-4328) in dorsal view; (D) distal fragment of right humerus (n°45, UM-PEZ-4316) in anterior view. "Crochet and Ivorra 1998" - (E) Upper molar fragment (UM-PEZ-6) in occlusal view. Scale bars= 20 mm.

not compatible with those of Pleistocene elephantids, such as *Mammuthus* (e.g., Mol *et al*., 2018). An enamel cap with grooves covered part of the tusk fragment. For this reason, it could be an early permanent tusk (cf. Depéret and Donnezan, 1890: Pl. V, fig. 1; Mol *et al*., 2008: fig. 7; Rountrey *et al*., 2012). Along the broken surface, it is possible to discern the engine-turning ivory pattern and the "Schreger pattern" with acute angles, compatible with values reported for *Anancus* (Reolid *et al*., 2021). The specimen UM-PEZ-25 was previously identified as a left upper M3 (written in a recent tag). Indeed, it is similar in morphology and dimension to the posterior part of the left lower m3 in the mandible of *Anancus arvernensis* from Greece described by Athanassiou (2016: fig. 4). The sample UM-PEZ-4377 may be a portion of lower molar fragment (m3?). It can relate to a more advanced *Anancus arvernensis* than specimens from "Sables Marins Littoraux" of the Montpellier collection for having more aligned cusps. However, we cannot refer the two molar fragments to a specific molar locus without any doubts.

In any case, both the size and morphological patterns of the corresponding specimens match those of *Anancus arvernensis*, a common element of Early Pliocene faunas of Montpellier and Roussillon. We consider these specimens as documenting unambiguously this species.

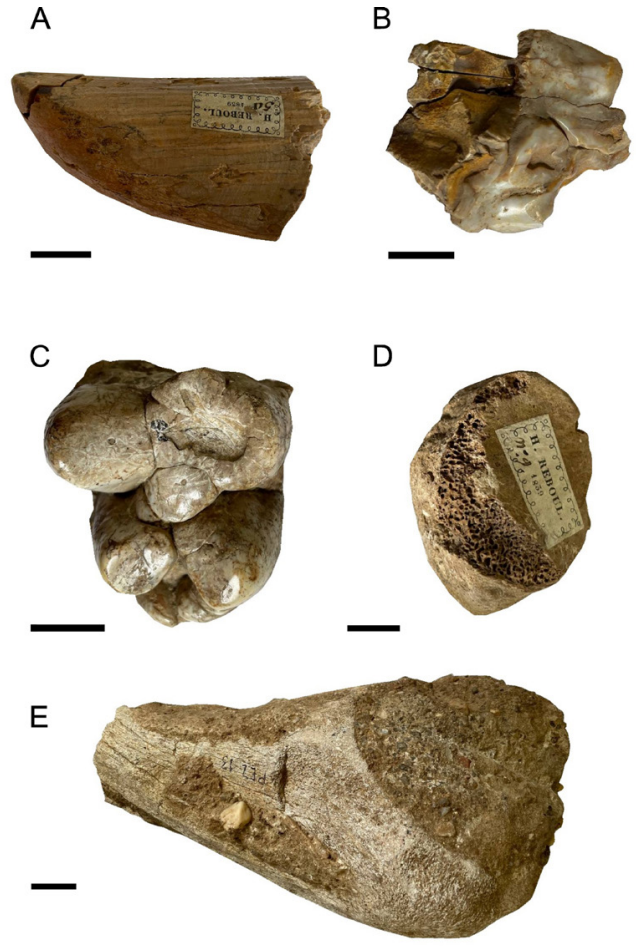

Figure 14. Pliocene–Pleistocene proboscideans from "Le Riège" localities (near Pézenas, Southern France). ***Anancus arvernensis***: "Reboul Collection 1839" - (A) Tusk fragment (tip of an early permanent?) (n°50, UM-PEZ-4321) in medial view. "Unlabelled Le Riège UM Collection" - (B) Molar fragment (UM-PEZ-25) in occlusal view; (C) molar fragment (UM-PEZ-4377) in occlusal view. **Elephantidae indet.**: "Reboul Collection (1839)" - (D) Sesamoid (n°9, UM-PEZ-4359). "Crochet and Ivorra 1998" - (E) Fragment of left pelvis (UM-PEZ-13). Scale bars= 20 mm.

Family Elephantidae Gray, 1821

Elephantidae indet.

Figs. 14D, E

Illustrated samples. "Reboul Collection 1839" - Sesamoid (n°9, UM-PEZ-4359) (Fig. 14D). "Crochet and Ivorra 1998" - Fragment of left pelvis (UM-PEZ-13) (Fig. 14E).

Remarks. It was not possible to compare directly the sesamoid with those of other proboscideans. However, its large size (5.3 x 3.8 mm) allows for discarding the gomphotheriid *Anancus arvernensis* and to consider it as documenting a huge elephantid instead (such as *Mammuthus meridionalis*) according to other remains of Pleistocene proboscideans. Crochet and Ivorra labeled the sample UM-PEZ-13 as a very large indeterminate bone, without further taxonomic identification. The fossil is compatible with an elephantid pelvis fragment (cf. Petrova, 2009; Rabinovich and Lister, 2017), which would therefore point to *Mammuthus meridionalis*, given the local context.

We prefer, however, to consider these specimens as documenting an unidentified elephantoid, most likely Pleistocene in age.

Genus *Mammuthus* Brookes, 1828

Mammuthus cf. *meridionalis* (Nesti, 1825)

Fig. 15

Illustrated samples. "Unlabelled Le Riège UM Collection" - Tooth fragment (right lower molar?) (UM-PEZ-4378) (Fig. 15A); right astragalus (no code) (Fig. 15B).

Unillustrated samples. "Unlabelled Le Riège UM Collection" - Two metapodial bones (no code).

Biochronological range. Middle Villafanchian – Epivillafranchian (MNQ17a–MNQ20) (for *M. meridionalis*) (e.g., Palombo and Valli, 2004; Konidaris *et al.,* 2020).

Remarks. The sample UM-PEZ-4378 might be a right lower molar fragment because its morphology and size match those

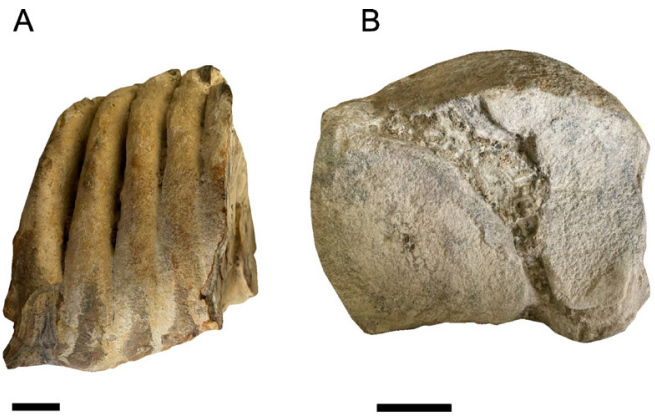

Figure 15. Pleistocene proboscideans from "Le Riège" localities (near Pézenas, Southern France). ***Mammuthus* cf. *meridionalis***: "Unlabelled Le Riège UM Collection" - (A) Tooth fragment (right lower molar?) (UM-PEZ-4378) in buccal view; (B) right astragalus (no code) in plantar view. Scale bars= 20 mm.

of a *Mammuthus* sp. lower molar from Greece (Athanassiou *et al*., 2022: fig. 8, p. 358). They have diagnostic characteristics (UM-PEZ-4378 sample: hypsodont index (HI)=1.3; laminar frequency (LF)= 5.5) of an early species of *Mammuthus*, such as *M. meridionalis* (see van Essen, 2003; Agostini *et al*., 2012; Ros-Montoya *et al*., 2012). The tips are not so worn; therefore, the specimen may be considered an early adult. The huge-sized astragalus (no code; 20 x 16 x 5 cm), upon which "*Éléphant. Astragale d'éléphant de Pézénas*" ("Elephant. Astragalus of Pézénas elephant") is written, clearly belongs to an elephantid (see Chen and Tong, 2017).

Due to their fragmentary state (lower molar) and restricted comparison sample (astragalus), these specimens are referred to as *Mammuthus* cf. *meridionalis*. They are assigned an Early Pleistocene age.

Mammalia indet.

Unillustrated samples. "Reboul Collection 1839" - Bone fragment (pelvis?) (n°16, UM-PEZ-4347); vertebra fragment (spinal process) (n°17, UM-PEZ-4345). "Crochet and Ivorra 1998" - Fragments of rib (UM-PEZ-4, 5); bone fragments (UM-PEZ-7, 17). "Unlabelled Le Riège UM Collection" - bone fragments (UM-PEZ-4293; UM-PEZ-4298; UM-PEZ-4299; no code); rib fragment (UM-PEZ-4339); (Proboscidea?) uncomplete rib (no code); vertebral fragments (no code); bone fragments (no code); pelvis fragment (no code).

Other specimens (Recent mammals)

Unillustrated samples. "Crochet and Ivorra 1998" - Distal fragment of left tibia of artiodactyl (roe deer) (UM-PEZ-10); left astragalus of artiodactyl (roe deer) (UM-PEZ-14); caudal vertebra of unidentified small-sized artiodactyl (UM-PEZ-15).

Remarks. Due to their color and patina, these specimens most likely belong to recent artiodactyls, and most likely roe deers (*Capreolus capreolus*), given their size and morphological pattern.

DISCUSSION

The fossils from Le Riège locality (Montpellier, France), stored at the ISEM, have been studied and collected since the 1830s (e.g., Reboul, 1834; de Christol, 1835; Gervais, 1859; Ambert *et al*., 1996). The oldest paleontological collection stored in the *Université de Montpellier* is the "Reboul (1839) Collection", followed by the "de Christol (1865) Collection". In contrast, the "Crochet and Ivorra (1998) Collection" was assembled with a different study methodology, giving importance to the places of discoveries. Other fossils lack any information about the circumstances of their discovery and some of them were found in the last years.

The paleontological record from Le Riège, as available in the UM collections, is composed by mixed Pliocene and Pleistocene taxa (Fig. 16). According to this new systematic

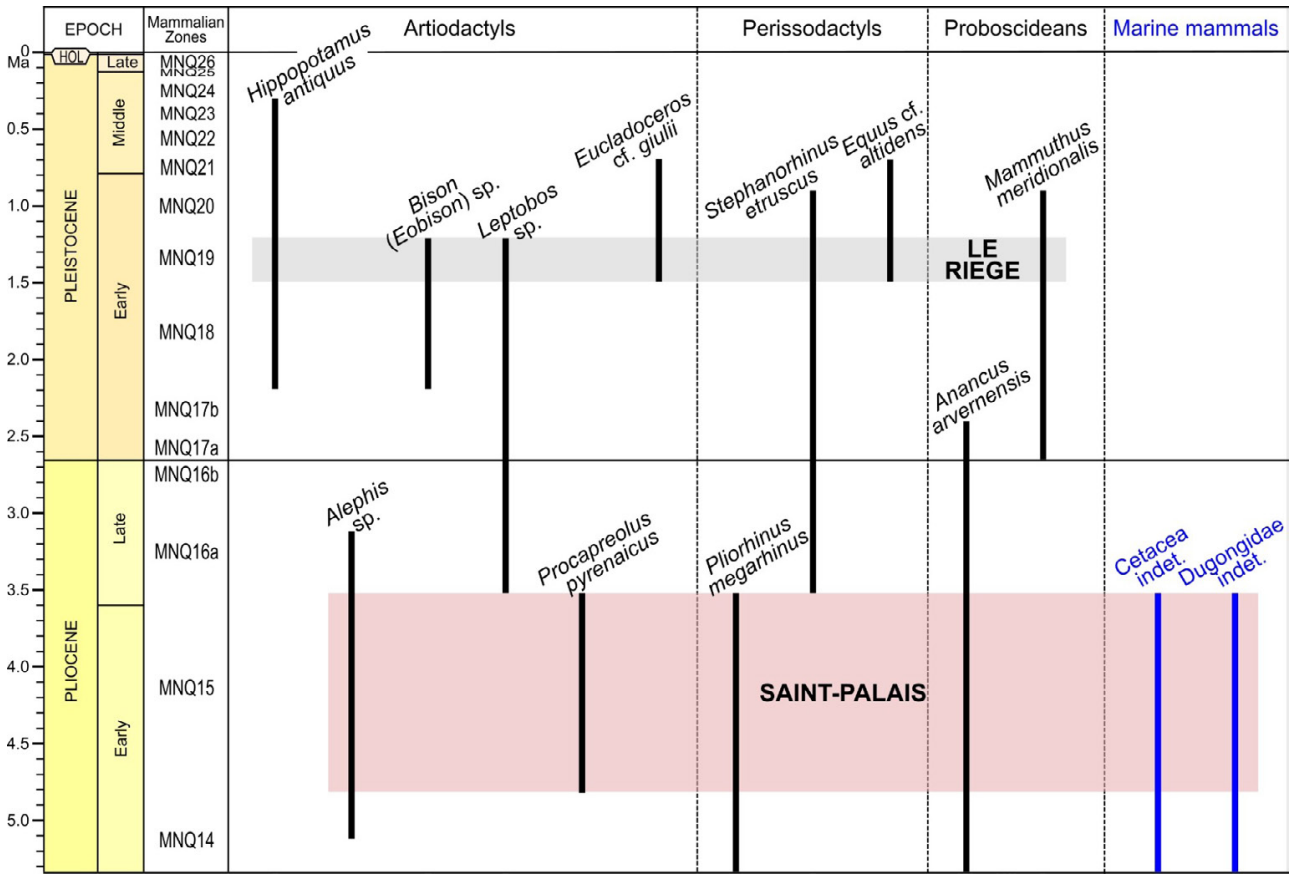

Figure 16. Biostratigraphical chart of the Pliocene–Pleistocene large mammals from "Le Riège" localities, pointing to the presence of two distinct assemblages along the Riège stream, namely Saint-Palais (MN15, Early Pliocene), with littoral affinities (yielding marine mammals), and Le Riège (MNQ19, Early Pleistocene). See the discussion for the ages of each taxon. The timeline is based on Pandolfi *et al.* (2017, 2021).

review, Pliocene specimens belong to *Alephis* sp., *Procapreolus* cf. *pyrenaicus*, *Pliorhinus megarhinus*, *Anancus arvernensis* and marine mammals (a cetacean and a dugongid sirenian). The biochronological distribution of these taxa (de Bruijn *et al*., 1992; Palombo and Valli, 2004; Guérin, 2007) points unambiguously to a Ruscinian age (MN14–MN15). This assemblage is likely to be slightly younger than the early Ruscinian Montpellier Faunal Unit (Sables Marins Littoraux, Hérault; MN14) and documenting the MN15 instead, notably based on the advanced shape of *Procapreolus* antlers. Considering the presence of both terrestrial and marine mammals, the paleoenvironmental context was probably a coastal setting, ranging from fluvial to shallow water environments, as documented conspicuously over Pliocene times in the Mediterranean Basin (e.g., Bianucci *et al*., 2001; Dumitru *et al*., 2019). In contrast, the Pleistocene fauna was fully continental and of terrestrial affinities, deposited in a maar setting (fluvio-volcanic sequence; Ambert *et al*. 1996). Characterized by the bulk of fossils from Le Riège, it is composed by *Equus* sp., *Equus* cf. *altidens,* Elephantidae indet.*, Mammuthus* cf. *meridionalis,* Cervidae indet., *Eucladoceros* cf. *giulii, Bison* (*Eobison*) spp., Hippopotamidae indet.*, Hippopotamus antiquus*, and *Stephanorhinus etruscus* (Fig. 16). According to the biochronological distribution of these taxa (e.g., Palombo and Valli, 2004; Bourguignon *et al*., 2016; van der Made *et al*., 2017; Boulbes and Asperen, 2019; Sorbelli *et al*., 2023), the fauna documents the late Early Pleistocene, more precisely the late Villafranchian to Epivillafranchian (most likely MNQ19). This biochronological interpretation refines the time interval proposed by Ambert *et al*. (1996), i.e. 1.5–1.1 Ma (MNQ19–MNQ20), slightly older than the nearby Bois-de-Riquet paleontological locality (1.0 to 0.8 Ma depending on the fossil levels concerned; Bourguignon *et al*., 2016; Lozano-Fernández *et al.,* 2019). The biochronological distribution of Cervidae indet. (Reboul 1839, n°26, UM-PEZ-4300) from the Le Riège, however, remains uncertain.

CONCLUSIONS AND PERSPECTIVES

The large-mammal fauna from Le Riège (Hérault, Southern France) is a classical end Neogene-Quaternary paleontological site in Languedoc. Almost thirty years after the most recent studies, we proposed here a revision of the large-mammal paleontological record from Le Riège "locality", housed at the *Université de Montpellier*. The concerned fossils, stored at the ISEM, consist of 123 specimens, originating from both remarkable historical collections and more recent collects. Half of the specimens comprise the important "Reboul Collection" from 1839 (51 specimens) and the "de Christol Collection" from 1865 (18 specimens). The "Crochet and Ivorra Collection", assembled in 1998, consists of 17 specimens with information about the place of discoveries. There is neither provenance nor any other information regarding the remaining 38 fossils, probably belonging to a more recent anonymous collection. From a taxonomic and biochronological perspective, two distinct faunas are recognized. Cranio-dental, mandibular and postcranial remains of *Alephis* sp., *Procapreolus* cf. *pyrenaicus*, *Pliorhinus megarhinus*, *Anancus arvernensis*, plus marine mammals (indeterminate cetacean and dugongid sirenian) were identified. These taxa are common in lowland and coastal Mediterranean environments during Early Pliocene times (Ruscinian Mammal Age, MN14–15). This assemblage might further document an intermediate time interval between Montpellier and Roussillon local faunas, which nevertheless needs to be confirmed. The other assemblage is composed of *Equus* sp., *Equus* cf. *altidens,* Elephantidae indet.*, Mammuthus* cf. *meridionalis,* Cervidae indet., *Eucladoceros* cf. *giulii, Bison* (*Eobison*) spp., Hippopotamidae indet.*, Hippopotamus antiquus*, and *Stephanorhinus etruscus.* This faunal association is typical of late Early Pleistocene times (most likely MNQ19), in agreement with previous studies, and the fossils were deposited in fluvio-volcanic settings. These new systematic and biochronological interpretations have allowed us to enhance the value of the concerned paleontological heritage, and to provide a starting point for future researches and a solid foundation for more detailed studies.

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