

A partial skull of *Dremotherium feignouxi* from the Aquitanian of France (MN2, Saint-Gérard-le-Puy, Allier)

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AGEOS Nekompletná lebka *Dremotherium feignouxi* z Aquitánu Francúzska (MN2, Saint-Gérard-le-Puy, Allier)

Abstract: An unpublished skull of the Late Oligocene–Early Miocene antlerless ruminant *Dremotherium* is described. It brings complementary information on the skull anatomy of this abundant but rather poorly known genus. It is confirmed that *Dremotherium feignouxi* had the combination of a single lacrimal orifice together with a lacrimal fossa. This particular configuration, not very common in fossil or recent ruminants is discussed. The ear region of *Dremotherium feignouxi* is well-preserved on the skull described here. It shows a tympanohyal vagina which is laterally enclosed by a strong lamina vaginalis. The tympanohyal vagina is not centrally placed like on *Hispanomeryx*. And together with the moderately inflated bulla, the overall shape of the ear region recalls that of cervids or moschids rather than that of bovids. After the study of this skull, the phylogenetic affinities of *Dremotherium feignouxi* are still difficult to establish, but future analysis of internal characteristics, beyond the scope of this contribution, should help to tackle this question.

Key words: Ruminantia, Miocene, *Dremotherium*, systematics, France

1. INTRODUCTION

Dremotherium GEOFFROY SAINT-HILAIRE, 1833 is a classical small antlerless ruminant genus of the European, and to a lesser extent Asian, Late Oligocene–Early Miocene faunas (Vislobokova, 1997; Gentry et al., 1999). *Dremotherium feignouxi*, the type species described by Geoffroy Saint-Hilaire (1833), is a species mostly found in French localities. This genus is often mentioned in the literature because it almost always occurs in association with another small antlerless ruminant, *Amphitragulus*, and because both taxa proved to be difficult to identify from one another with certainty or ascribe to a specific ruminant family (Geoffroy Saint-Hilaire, 1833; Pomel, 1846, 1853; Gervais, 1848–1852; Filhol, 1880; Rüttimeyer, 1881, 1883; Viret, 1929; Richard, 1946; Sigogneau, 1968; Webb & Taylor, 1980; Jehenne, 1985; Janis & Scott, 1987). Four species of *Amphitragulus* were described in the Early Miocene of the French set of localities known as Saint-Gérard-le-Puy: *A. elegans*, *A. lemanensis*, *A. boulangeri* and *A. gracilis*, the two later being now included in genus *Pomelomeryx* and *A. lemanensis* being tentatively ascribed to genus *Hydropotopsis* by Jehenne (1985) in an unpublished PhD thesis. In contrast, *Dremotherium* from Saint-Gérard-le-Puy always was represented by a single species and stayed a valid genus.

As reminded by Sigogneau (1968), the type specimen of the species was lost and a skull stored at the Muséum National d'Histoire Naturelle, Paris (hereafter MNHN; skull MNHN SG. 4304) was raised as neotype and described in details by Sigogneau (1968). She compared it with material ascribed to *Amphitragulus*, found differences but also found them hard to

separate. She eventually came to the ambiguous conclusion that both genera might well not be different, but also that if the variability she could grasp would indicate two different structural types, they would certainly sign differences above the genus level.

The antlerless *Dremotherium* has a long history of systematic ascriptions to various ruminant families but was almost always consistently considered as belonging in the “Cervoidea” (see Janis & Scott, 1987 for a review). It was long ascribed to the musk deer family Moschidae because of the absence of antlers, presence of enlarged *Moschus*-like canines, a single lacrimal orifice, and presence of other traits found in early and/or recent cervoids (e.g., *Palaeomeryx*-fold, closed metatarsal gully, entostyle on upper molars) such as in the living genus *Moschus pro parte*. This would be tempting if other characters pertaining to *Dremotherium*, such as the presence of a lacrimal fossa, would not tend to raise doubts on this ascription. However the taxonomic value of either the lacrimal fossa or of the number of lacrimal orifices alone is by far not evident (see Janis & Scott, 1987 for a review).

In this context, undescribed material of *Dremotherium* is always welcome to enrich previous observations. The Centre de Conservation et d'études des collections in Lyon and the MNHN have important and historical collections of the Allier Basin and particularly of the area surrounding Saint-Gérard-le-Puy. These collections hold a number of cranial specimens of the above mentioned ruminant that were figured by Filhol (1880) or Viret (1929) and a relatively well-preserved skull from Lyon that appears not to have been published before was recently found. The skull from Lyon shows interesting characters of the facial

and orbital regions that help to better constrain the morphology of *Dremotherium*.

2. LOCALITY AND GEOLOGICAL SETTING

The fossil site of Saint-Gérard-Le-Puy is known in several museum collections; it is actually composed of several quarries in the vicinity of the villages of Saint-Gérard-Le-Puy itself and Montaigu-le-Blin in Central France, in the Allier administrative department. Old collections in various museums (including Basel, Lyon and Paris for instance) were gathered more than a hundred years ago and the exact provenance of the fossils together with their sedimentological context are often unknown. Attempts to understand the geological context of the famous palaeontological finds were undertaken in the last 30 years and Donsimoni (1975), Bucher et al. (1985) and later Wattine et al. (2003) described the geology of the largest quarry of the area at Montaigu-le-Blin or the formation of the lacustrine calcareous deposits. In summary these works point out that large amounts of lacustrine limestones were deposited in the fluvio-lacustrine context of the Limagne sedimentary Basin which was highly subsident during the Oligocene and which saw the development of lakes in the Early Miocene. Stromatolitic bioconstructions also flourished in these lakes. The fossils often come from marly sediments trapped within the bioconstructions and transported through small scale mud flows (Bucher et al., 1985).

3. MATERIAL AND METHODS

Museums' Abbreviations. NMB: Naturhistorisches Museum Basel; MNHN: Muséum d'Histoire Naturelle Paris; NHM: Natural History Museum London; CCEC: Centre de Conservation et d'Etudes des Collections Lyon; SMNS: Staatliches Museum für Naturkunde Stuttgart.

The unpublished skull numbered StG. 548 from the CCEC is described here. A number of skulls or partial skulls of *Dremotherium feignouxi* from the collections of the MNHN and of the CCEC were also studied in the framework of the present work (in MNHN: MNHN SG. 4304 already published in Filhol, 1880; Viret, 1929; Sigogneau, 1968 and Jehenne, 1985; MNHN SG. 12000 published in Filhol, 1880 and Sigogneau, 1968; and unpublished partial skulls MNHN SG. 9660 [mentioned without collection number as "*Dremotherium III*" in Sigogneau, 1968] and MNHN SG. 9661; and in CCEC: StG. 3052 published in Filhol, 1880). Other skulls and partial skulls of other fossil ruminant species were seen, including *Amphitragulus* sp. (StG. 620, M.A. 7804 in CCEC, MNHN SG. 12002 published in Sigogneau, 1968), *Amphitragulus elegans* (MNHN SG. 4303), and *Amphitragulus lemanensis* (StG. 600bis published in Viret, 1929; NMB Ph. 3107 published in Sigogneau, 1968; Jehenne, 1985 and Janis & Scott, 1987). Skulls and partial skulls of *Amphitragulus* were mentioned in Filhol (1880) and Viret (1929) but correspondence between this material and the material studied here was difficult to recognize from old illustrations without collection numbers. Besides this

material, skulls of Early to Middle Miocene ruminants were used in the comparative study: *Amphimoschus* sp. (unpublished skull SMNS 40693 from Langenau, Germany, Early Miocene, European Land Mammal Zone MN4), *Micromeryx flourensianus*, *Euprox furcatus* and *Heteroprox larteti* (unpublished skulls NMB Sth. 833, NMB Sth. 222, SMNS 43320, respectively, from Steinheim, Germany, Middle Miocene, European Land Mammal Zone MN7/8). Comparisons with recent species were also necessary and a number of skulls from various institutions were used: *Hydropotes inermis* (NHM BM 7.7.3.32, NHM BM 8.11.14.8, and NMB 9853); *Moschus moschiferus* (NHM BM 91.8.7.221, NHM BM 30.1.2.57, NMB 8874, and NMB 5110); *Hyemoschus aquaticus* (NMB 8699). Finally the extensive collections of recent ruminants of the NMB and MNHN were used for comparative material of various bovid and cervid genera. Besides the specimens drawn here on figure 2, the collection of the NHM further served as comparative material for *Moschus moschiferus* and *Hydropotes inermis*.

Cranial osteological nomenclature follows Barone (1999) and tooth nomenclature is from Gentry et al. (1999).

4. SYSTEMATIC PALAEOLOGY

Mammalia LINNAEUS, 1758

Cetartiodactyla MONTGELARD ET AL., 1997

Family indet.

Dremotherium GEOFFROY SAINT-HILAIRE, 1833

Type species: *Dremotherium feignouxi* GEOFFROY SAINT-HILAIRE, 1833

Neotype: Skull MNHN SG. 4304, Muséum d'Histoire Naturelle Paris.

Type locality: Saint-Gérard-le-Puy, France, Early Miocene, Aquitanian, European Land Mammal Zone MN2.

Dremotherium feignouxi GEOFFROY SAINT-HILAIRE, 1833

Repository: Centre de Conservation et d'Etudes des Collections Lyon.

Material, locality and age: incomplete skull, number StG. 548, Saint-Gérard-le-Puy, France, Early Miocene, Aquitanian, European Land Mammal Zone MN2.

Description

The skull lacks its facial part, so that no observation on the relative length of this part or on the presence of enlarged upper canines can be made. The left part of the skull containing the maxillary, lacrimal and orbital areas is also missing as well as most of the basicranium. The right part is better preserved and a single tooth, the right upper fully erupted and unworn third molar is still in place. The temporal and occipital parts of the skull, although fractured, are preserved and both tympanic bullae are available, the right one being displaced and rather badly preserved.

The distal part of the right maxillary bone bearing the M3 is there and surmounted rostral of the orbit by a caudal piece of the lacrimal bone that confirms the presence of a lacrimal fossa in *D. feignouxi* (Fig. 1c; another partial unpublished skull [SG.

9660] from the MNHN also bears a deep fossa); its depth and extent cannot be firmly stated because of the caudal deformation of the bone. The preserved remains of the right lacrimal bone let assume a deep fossa but not as deep as on MNHN SG. 4304, the neotype of *D. feignouxi*. The maxillary tuberosity is rather strong compared to *Moschus* or *Hydropotes* and its dorsal development towards the zygomatic bone nonetheless slightly recalls that of *Moschus*.

The right orbit is rather quadrangular in shape (Fig. 1c) reminding that of the living antlerless Chinese water deer *Hydropotes inermis* or tufted deer *Elaphodus cephalophus* and is not as rounded as in the skulls ascribed to his contemporaneous *Amphitragulus* (Sigogneau, 1968; Jehenne, 1985; Janis & Scott, 1987). Its rostral border reaches the level of the contact between M2 and M3 (Fig. 1c), in contrast to *Amphitragulus*, whose orbits

reach the level of M2's first lobe (Janis & Scott, 1987, and pers. obs.). A single lacrimal foramen is visible inside the orbit just as on the neotype MNHN SG. 4304.

The frontal bones are wide above the orbits and largely spread laterally (Fig. 1a and Fig. 2e), yielding a strong post-orbital constriction; this is also the case in *Amphitragulus* and in *Moschus*; in the latter the roof between the orbits is much flatter than in the living moschid, which is also the case for *Hydropotes*. The supraorbital right groove (the left one lacks) is large and looks rather short rostrally, like on *Hydropotes*, *Moschus*, *Amphitragulus* or other *Dremotherium* specimens (Fig. 1a and Fig. 2), although the skull is broken and prevents further comment on this; it originates from a single supraorbital foramen. On the neotype MNHN SG. 4304 the groove is also large above the orbit but ends rostrally at the level of the rostral part of the orbit in a fine

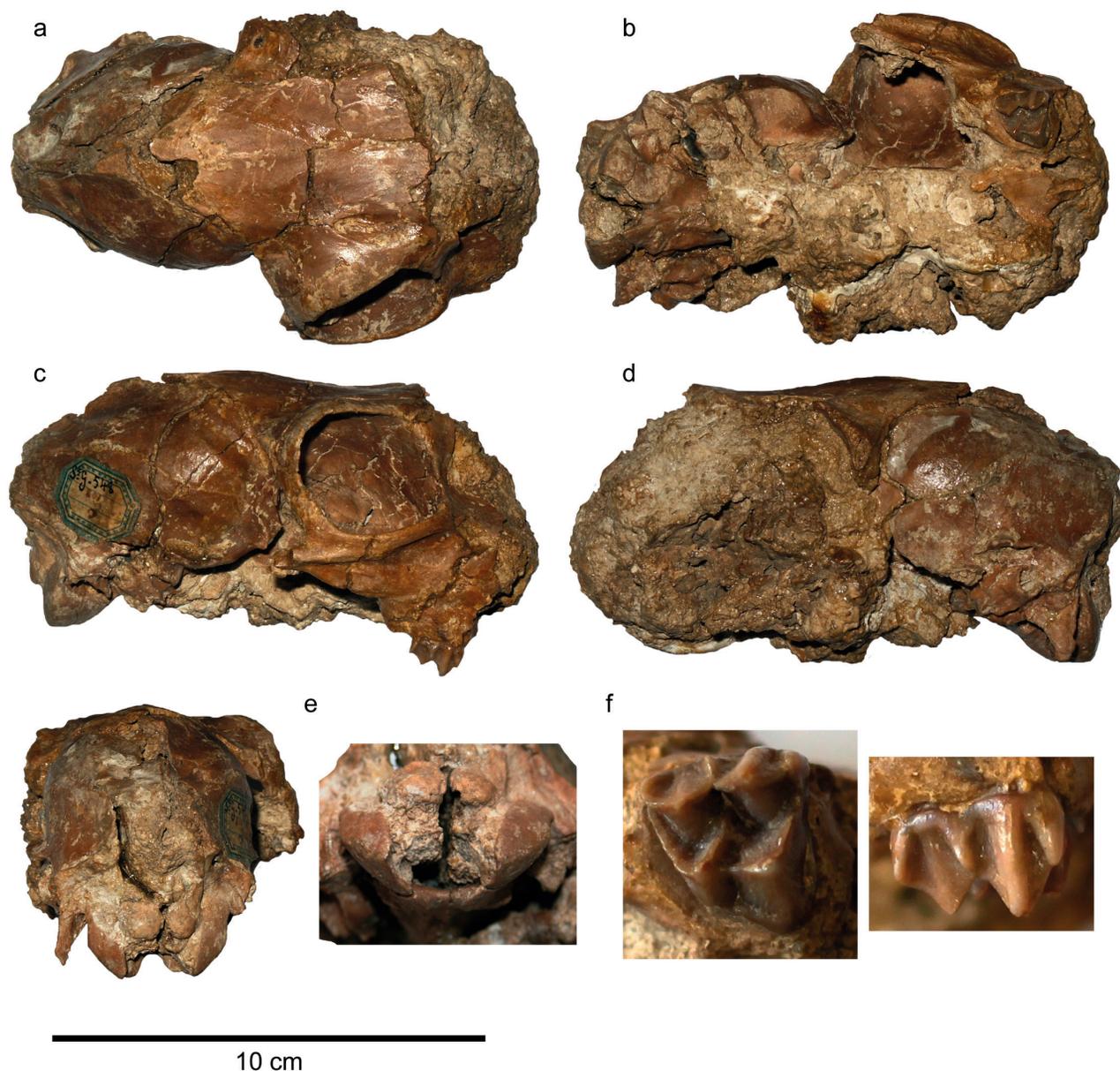


Fig. 1. Skull StG. 548. a) dorsal view; b) palatine view; c) right lateral view; d) left lateral view; e) occipital view and close-up on *foramen magnum*; f) close-up of the upper third molar (left: occlusal view and right: labial view). Scale bar for a-e. Size of tooth is given in text.

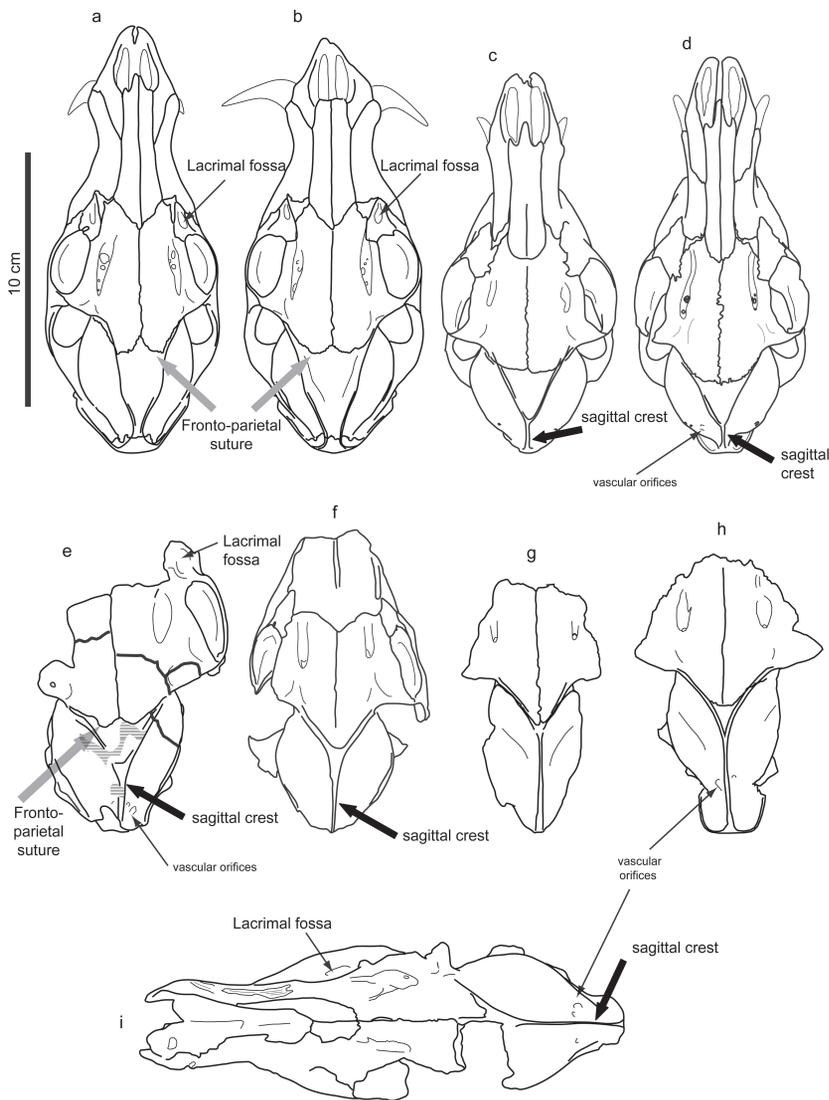


Fig. 2. Sketches of the dorsal view of skulls of recent and fossil ruminants. a) *Hydropotes inermis* NHM BM 7.7.3.32; b) *Hydropotes inermis*, NMH BM 8.11.14.8; c) *Moschus moschiferus* NHM BM 91.8.7.221; d) *Moschus moschiferus* NHM BM 30.1.2.57; e) *Dremotherium feignouxi* StG. 548; f) *Amphitragulus lemanensis* NMB Ph. 3107; g) *Amphitragulus* sp. M.A. 7804; h) *Dremotherium feignouxi* StG. 3052; i) *Dremotherium feignouxi* MNHN SG. 4304. Scale bar for a-i.

gully (Fig. 2i). As this character seems highly variable in living or extinct ruminant species (Sigogneau, 1968, and pers. obs.), it bears alone no real taxonomical value.

The zygomatic arch is not preserved but its ventral and dorsal origins show it could have been close in morphology to that of *Hydropotes* or *Moschus*, although it is slightly different on both genera with its temporal contribution joining the temporal bones more proximally on *Moschus* than on *Hydropotes* where a slightly stronger bony projection of the temporal crest runs above the external auditory meatus. This caudal area of the zygomatic process of skull StG. 548 looks more like that of *Hydropotes* than that of *Moschus* in the less concave temporal crest above the external auditory meatus and running above the retroarticular foramen. The temporal lines are not well preserved but were present and probably rather strong, they converge caudally and merge into a strong sagittal crest (Fig. 1a and Fig. 2e), which is also broken. We can infer that the length of the sagittal crest should have occupied about half of the length of the globular braincase, which is much more than for *Moschus* when this crest exists (e.g., BM 91.8.7.221, BM 30.1.2.57, Fig. 2c, d), and recalls the condition seen in the tragulid *Hyemoschus*

(pers. obs. on NMB 8699) or in *Amphitragulus* (NMB Ph. 3107, Fig. 2f). The neotype of *D. feignouxi* confirms this situation (Fig. 2i). The parietal bones present 2 large vascular orifices just left and right of the sagittal crest, but rather caudally (Fig. 2e). The same condition is seen on the neotype and on StG. 3052 (Fig. 2h). Both orifices are much stronger than on *Amphitragulus* from the same locality (Sigogneau, 1968, and pers. obs., Fig. 2f, i). They are placed at about the same position as in *Moschus* (Fig. 2d); when they exist, they are placed further away from the sagittal crest or midline of the skull roof in other ruminants such as *Hydropotes*.

The suture between the frontal and the parietal bones draws a wide and obtuse W-shape, common in antlered or horned living ruminants (pers. obs.); this pattern is rarer but still exists in the hornless or antlerless species, some specimens of *Hydropotes inermis* exhibit this W-shape (e.g. BM 7.7.3.32, BM 8.11.14.8, or Fig. 2a, b). Another skull roof attributable to *Dremotherium* (StG. 3052, Fig. 2h) does not show this W-shape, the suture is here rounded.

The occipital region is partly broken but the ventral part is visible. The *foramen magnum* looks rather quadrangular in shape

in caudal view (Fig. 1e), more like *Hydropotes* than *Moschus* (although variation also exists: skull NMB 5110 of *Moschus moschiferus* has an almost quadrangular *foramen magnum* in caudal view, pers. obs.). The occipital condyles do not join on the ventral side in the basal part of the occipital bone and are separated by a large gully running ventrally towards the basioccipital (Fig. 1b). This gully, when present in *Moschus*, is not that large; it seems larger in extant cervids or bovids (pers. obs.). Above all, the basal part of the *foramen magnum* constituted by the walls of the occipital condyles is not rounded and makes a rather acute V-like angle much like in *Hydropotes* or *Elaphodus*, whereas this angle looks more obtuse and the basal part of the foramen more rounded in *Moschus* or some bovids (*Cephalophus*, *Litocranius*, *Alcelaphus*, *Rupicapra*, but not in *Capra ibex* where it is also V-shaped, pers. obs.). The articular facets with the atlas are rather large, more like in *Hydropotes* than in *Moschus* where they seem relatively narrower.

The left bulla of StG. 548 is well-preserved (Fig. 3), it is small and not as inflated as in *Hydropotes*, it resembles more the condition seen in *Moschus* or cervids like *Elaphodus* (pers. obs.). The external auditory meatus is large and circular. The tympanohyal vagina is only laterally enclosed by a strong and projecting

lamina vaginalis and thus is not ensheathed as it is in *Moschus* (Fig. 3); it is also slightly more caudally placed than in *Moschus* and than in *Hispanomeryx* although the only known skull of the latter preserving this part seems quite crushed (Sánchez et al., 2010). Overall the situation recalls that seen in *Micromeryx* and *Amphitragulus* (Fig. 3). There's no contact between the tympanohyal vagina and the mastoid process since the bulla is quite inflated. The postglenoid process, although partly crushed on StG. 548 but preserved on the neotype, does not come into too close contact with the external auditory meatus leaving the temporal canal visible such as, though to a lesser extent, in *Moschus*, *Hydropotes* or *Amphitragulus*.

The upper right M3 is preserved (Fig. 1f); it is a simple tooth with a reduced hypocone. It is a selenodont tooth very moderately hypsodont compared to other pecoran ruminants from the Early Miocene. There is an anterior, a lingual and a slight posterior cingulum. No real entostyle is visible at the weak lingual cingulum being only stronger on the posterior wall of the protocone. The parastyle and the labial rib of the paracone are very strong, the mesostyle and the metastyle are well developed and there is almost no labial rib of the metacone. The postprotocrista is almost parallel to the lingual side of the tooth. There

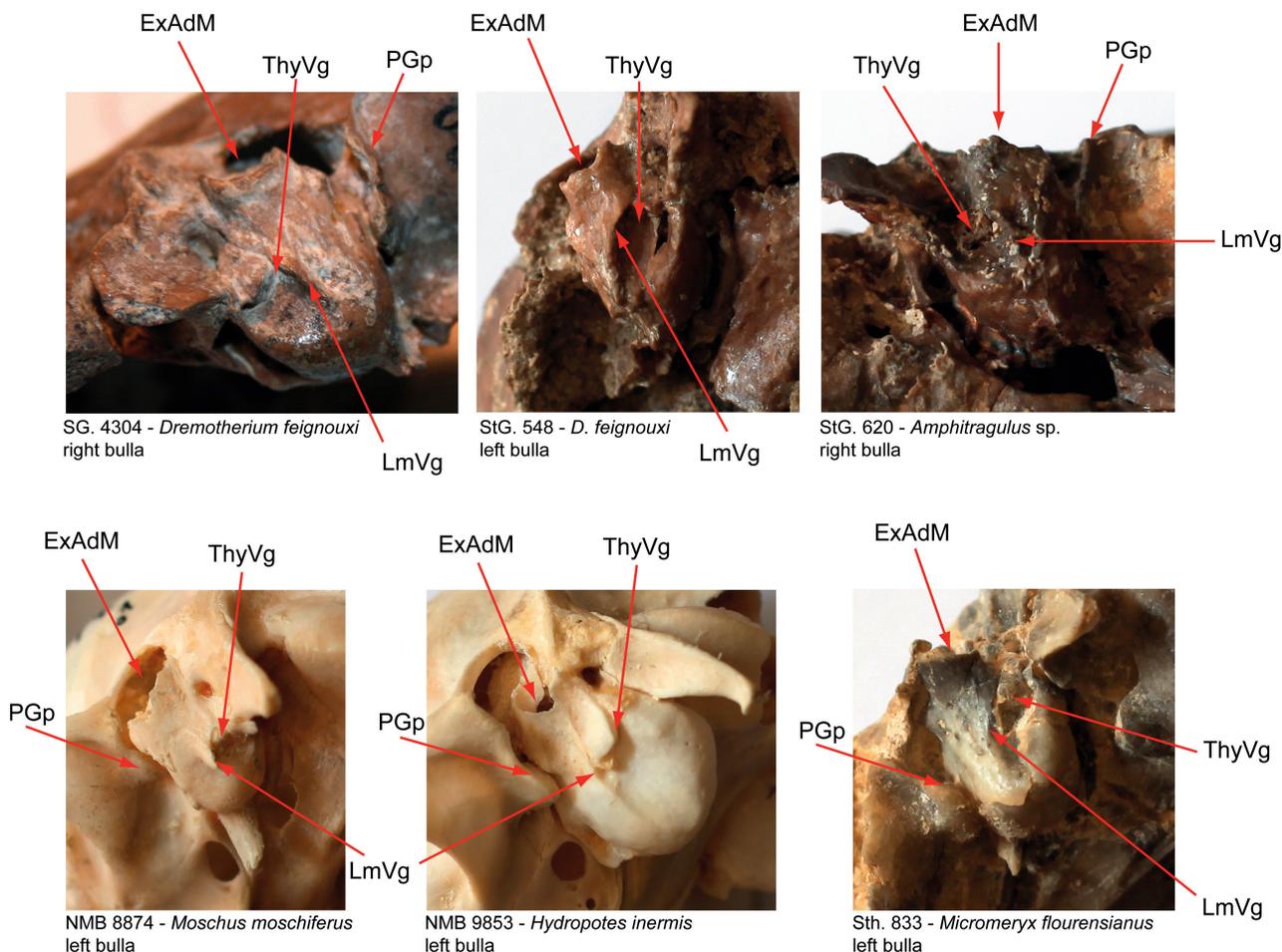


Fig. 3. Ear region of *Dremotherium feignouxi* compared to other fossil (*Amphitragulus* from Saint-Gérand-le-Puy, *Micromeryx* from Steinheim) or recent ruminants (*Moschus moschiferus* and *Hydropotes inermis*). Abbreviations follow Sánchez et al. (2010). ExAdM: External Auditory Meatus; LmVg: Lamina vaginalis; PGp: Postglenoid Process; ThyVg: Tympanohyal Vagina. The bullae are not to scale.

is a slight bulge indicating the presence of a possible neocrista arising from the postprotocrista. The latter goes straight into the prehypocrista, which itself is divided in two small cristae at its end. There's no spur on the posthypocrista in the posterior fossa. The dimensions of the tooth are: length: 11.5 mm, width (base of crown): 12.7 mm.

5. DISCUSSION

Dremotherium feignouxi was long studied in comparison to *Amphitragulus*, a common antlerless ruminant often found in association with it. Albeit Viret (1961) stated that both genera were quite easy to differentiate, *Dremotherium* having a much longer facial region, and thus much longer diastema on the lower mandibles together with more molarised lower premolars and no p1, several authors concluded that both taxa could well be the same (Sigogneau, 1968; Jehenne, 1985). This is also probably because of the poor definition of the two species of genus *Amphitragulus*, *A. elegans* and *A. lemanensis*, for which no analysis of the morphological variability was ever fully undertaken (this is now in progress). The single difference between the diastema of both genera is largely sufficient to substantiate both of them, since such a variability never occurs inside a single genus of any other ruminant. Skulls of *Dremotherium* are known from Saint-Gérand-le-Puy (France) and Ulm-Westtangente (Germany, pers. obs.) both dated to Land Mammal Zone MN2 in the Aquitanian of Western Europe (Heizmann et al., 1989; Huguene, 1997). Although the skull of the neotype MNHN SG4304 looks more slender probably because of its age status (a young adult with upper canines only erupting and no sign of dental wear), the other partial skulls including the one described here are rather broad and massive with raised frontals above the orbits and strong post-orbital constrictions. These characteristics seem to be traits of the species. All the skulls attributed to *D. feignouxi* where the lacrimal bone is preserved also bear a quite deep lacrimal fossa; this is the case on StG. 548. The lacrimal fossae bear the preorbital glands that produce pheromones serving at many occasions for chemical communication such as territory scent markings, or visual stimuli such as signals of calf satiety or encounters between males or females (Anderson, 1979; Bartos et al., 2005). This ecological feature related to social behaviours is, when present, morphologically very variable in size and in the bones concerned. In cervids, where all species have a fossa, it can be deep and wide (e.g., *Hydropotes inermis* or *Cervus elaphus*, pers. obs. at MNHN), or shallow and small (e.g., some specimens of *Capreolus capreolus* from the MNHN, pers. obs.). A maxillary contribution to the fossa is not always achieved (e.g., *Capreolus capreolus*) and thus sometimes only the lacrimal bone encloses this feature. It is also highly variable in bovids, where it can be absent (e.g., *Tragelaphus scriptus*, *Capra ibex*, *Rupicapra rupicapra* or *Kobus kob*, pers. obs. MNHN and Leinders & Heintz, 1980) or very deeply impressed (e.g., *Ovis ammon* or *Sylvicapra grimmia*, pers. obs. MNHN and NMB, respectively) sometimes largely perforating the lacrimal bone (e.g., *Tetracerus quadricornis*, pers. obs. NMB). Living moschids do not show this particular feature, but males have other specific glands included in chemical com-

munication (e.g., musk glands) and located close to their genitales. As reminded by Janis & Scott (1987) the presence of a lacrimal fossa alone may not be phylogenetically very informative although its significance in combination with other traits is of relevance. For *D. feignouxi*, it is associated with a single lacrimal foramen such as on StG. 548 and on the neotype MNHN SG. 4304. Specimens attributed to genus *Amphitragulus* seem to have a single lacrimal orifice (pers. obs. on MNHN SG. 4303, ascribed to species *A. elegans*) and others have two orifices in a rather cervid-like position (Sigogneau, 1968; Janis & Scott, 1987 and pers. obs. on NMB Ph. 3107). This distinction is significant and might sign two different structural types such as postulated by Jehenne (1985) who invented a new genus, *Hydropotopsis*, for the 2-orifice-bearing skull NMB Ph. 3107, previously ascribed to *Amphitragulus lemanensis*. Other early Miocene ruminants showing the *Dremotherium*-type configuration are rare, since they often show either a single orifice without lacrimal fossa (e.g., *Micromeryx*, pers. obs. and Sánchez & Morales, 2008 for the lack of lacrimal fossa; or *Amphimoschus*, pers. comm. B. Mennecart), or 2 orifices without lacrimal fossa (e.g., *A. lemanensis*, skull NMB Ph. 3107), or with unknown condition of the lacrimal fossa (e.g., *Procervulus*, Rössner, 1995). Skulls of the Cervidae *Euprox furcatus* and *Heteroprox larteti* from Steinheim (NMB Sth. 222 and SMNS 43320, respectively) show a deep lacrimal fossa, but poor preservation of the orbits prevents to see the number of lacrimal foramina. Early bovids such as *Eotragus* share this condition of a fossa (although much larger than in *Dremotherium* or in the cervids) but the condition of the number of orifices is unknown (a reconstruction given by Solounias & Moelleken, 1992 seems to imply the presence of a single orifice but no complete skull is known); the same seems also to be true for the Chinese purported giraffoid *Palaeomeryx tricornis* (Qiu et al., 1985) but Janis & Scott (1987) refute this observation that does not fit in their phylogenetic scheme and postulate that *Palaeomeryx* may have 2 lacrimal orifices, which along with other characteristics would put it closer to cervoids. A single lacrimal foramen in association with a lacrimal fossa is thus a rather peculiar condition in a fossil hornless or antlerless ruminants. Some living bovids do show this condition (e.g., *Tetracerus quadricornis*, *Ovis ammon*, *Capra caucasica*, *Sylvicapra grimmia*, *Litocranius walleri*, *Naemorhedus sumatrensis* or *Alcelaphus buselaphus*... pers. obs. at MNHN and NMB) but many others don't (Leinders & Heintz, 1980). While antlers are the only character typifying living cervids (except for the secondary loss in *Hydropotes*), the possession of a fossa together with 2 lacrimal orifices in a specific position (the dorsal orifice inside the orbit and the ventral one on or slightly external to the rim) is also a suite of characters found in living cervids and is part of the suite defining the family and more largely cervoids (Janis & Scott, 1987). Living moschids most often show a single orifice inside the orbit, and no lacrimal fossa, and are allied to cervoids by many authors on the basis of postcranial characters (the closed metatarsal gully among others, but *contra* Sánchez et al., 2010). This is a variable association as, although no lacrimal fossa was ever found on a living moschid, 2 orifices can actually although very rarely be identified (e.g., skull NMB 5111, with 2 orifices in a typical cervid position). This would reinforce the proximity of moschids with cervids, although it cannot be ruled

out that this character (2 orifices in cervid position) might have arisen in parallel in both lineages (see Janis & Scott, 1987 for discussion). Thus the condition of the lacrimal fossa and/or of the lacrimal foramina seem variable inside these families and the possession of a *Dremotherium*-like association is also found in primitive members of the Bovidae (e.g., the boselaphini *Tetracerus*) as well as in more derived members (e.g., *Naemorhedus*). This makes the association of both character states a rather poor phylogenetic marker such as already mentioned by Janis & Scott (1987). However, the same authors do mention their utility within the suite of characters typifying ruminant families. The ear region plays a crucial role in phylogenetic analyses and is often of critical importance for the phylogeny of ruminants (Webb & Taylor, 1980; Sánchez et al., 2010). The left ear region is well preserved on StG. 548 and the combination of characters shows its proximity with *Amphitragulus*, *Moschus* or *Micromeryx* as the tympanohyal vagina is subcentral to slightly caudal and not at all central like in *Hispanomeryx* (Sánchez et al., 2010). The tympanohyal vagina is only partly enclosed by a strong lamina vaginalis, a very different situation than in *Moschus* where it is fully enclosed. Several bovids have the tympanohyal vagina quite centrally placed (e.g., *Sylvicapra*, *Alcelaphus*, *Litocranius*, pers. obs.) while others may have it more caudally placed (e.g., *Rupicapra*, pers. obs.). In this respect and in the inflation of the bulla itself, *Dremotherium* looks more “cervoid” like (*sensu* Janis & Scott, 1987).

Assigning *Dremotherium* to a ruminant family seems much more problematical. Although *Dremotherium* was often supposed to be close to moschids, no character seems to ally it firmly to this family, except maybe the enlarged moschid-shaped upper canine which has evidently evolved in parallel in various pecoran families (*Hydropotes* shows more or less the same kind of morphology) and which is actually a primitive character of the cervoids (e.g., Janis & Scott, 1987). Sánchez et al. (2010) reject *Dremotherium* from the moschid family because of the absence of derived cranial characters, and further indicate that moschid-like canines are widespread in several extinct and extant pecorans and as such do not constitute a strong character linking these animals to cervids or even cervoids. Janis & Scott (1987) ally *Dremotherium* to moschids following the observations of Webb & Taylor (1980) on the ear region and put this group in a clade Cervoidea. Gentry (1994) considers *Dremotherium* to be a plesion of Cervoidea themselves constituted by cervids and palaeomerycids; Hassanin & Douzery (2003) further exclude moschids from Cervoidea because their DNA analyses regard them closer to bovids. It is to be noted that a recent supertree built from various sources (morphological, ethological and molecular) considers moschids closer to cervids (Hernández-Fernández & Vrba, 2005).

Finally, Janis & Scott (1987) consider the presence of the entostyle on upper molars to be phylogenetically significant linking bovids to cervoids. But this character must be used with caution regarding its highly variable development in fossil species such as *D. feignouxi* or *Amphitragulus elegans* (pers. obs.) within one individual where size varies from the M1 to the M3 and where an internal cingulum might only grow stronger without forming a fully developed entostyle such as here on StG. 548.

Dremotherium feignouxi is probably a cervoid characterized by its enlarged upper canine, a lacrimal fossa and a single lacrimal foramen, the presence of a *Palaeomeryx*-fold on the lower molars (character shared with other primitive ruminants), and although no skeleton was ever found in connexion, all the metatarsal bones from the fossil collections of Saint-Gérard-le-Puy show the typical cervoid closed metatarsal gully. The lacrimal condition in *Dremotherium* (1 lacrimal foramen and a lacrimal fossa) seems not to be diagnostic at the genus level since it has evolved several times in ruminants; it is found in fossil and extant bovids (e.g., *Eotragus* or *Tetracerus*) and in other pecoran ruminants (e.g., *Palaeomeryx* tentatively considered as a giraffoid, see Qiu et al., 1985). As such the combination could indicate proximity between *Dremotherium* and early bovids, but other post-cranial characteristics such as the cervoid closed metatarsal gully contradict the picture. Although Ginsburg & Heintz (1966) proposed the family Dremotheriidae to include *Dremotherium* and related other Palaeogene antlerless pecorans, it seems premature to classify *Dremotherium* to a particular family. The presence of several well-preserved skulls will allow non destructive analyses of internal structures which will undoubtedly help to better understand the affinities of *Dremotherium* and other Early Miocene antlerless ruminants.

6. CONCLUSIONS

 The new cranial material StG. 548 of the antlerless ruminant *Dremotherium feignouxi* from the French locality Saint-Gérard-le-Puy tackles the question of the phylogenetic importance of cranial characters such as the lacrimal foramen and fossa. The skull confirms the presence of a single lacrimal foramen, inside the orbit (the plesiomorphic pecoran state) associated to a rather deep lacrimal fossa; this combination is shared by a number of fossil and extant ruminants found in the Bovidae and Palaeomerycidae. All known recent cervids have a lacrimal fossa and two lacrimal foramina; the condition for the fossa in fossil species, especially in the Miocene is mostly unknown while preserved skulls often show two foramina. True moschids (*Moschus* or *Micromeryx*) have one to occasionally two lacrimal orifices but have no fossa. Other characteristics of *Dremotherium* (closed metatarsal gully, *Palaeomeryx* fold, enlarged upper canine) being often considered as cervoid, a *Dremotherium*-like lacrimal combination is likely to have arisen in parallel in various pecoran lineages. Alone the association of both character states is phylogenetically rather weak although they help in a suite of characters. The description of new skull material of *D. feignouxi* further shows that the species had a rather massive skull with a strong post-orbital constriction and possessed a long sagittal crest. These two characteristics are shared by other early Miocene antlerless ruminants such as *Amphitragulus*, which nonetheless displays a more primitive skull shape. The affinities of these two taxa are still problematic but the availability of material in public collections opens new possibilities to investigate internal skull structures (ear region) of higher phylogenetic importance.

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