PALÆO VERTEBRATA

ARTICLE

A partial skeleton of *Metaxytherium medium* from the middle Miocene of La Morfassière quarry (Indre-et-Loire, France)

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Abstract: Sirenians are among the common marine fossil remains found in the Faluns deposits of western France. We describe new material of a Dugongidae sirenian from the middle Miocene Savignean facies of La Morfassière quarry (Indre-et-Loire, northwestern France) that includes a well preserved and almost complete skull associated with its mandible, several vertebrae and ribs. The cranial remains exhibit features that allow to attribute them to *Metaxytherium medium*, a species recorded from the middle and early late Miocene of European and Mediterranean coasts. The discovery of an associated skull and mandible of this species is unusual in this area and deserves to be reported, mostly because its preservation contributes to a better knowledge of the variable structure of its skull and teeth anatomy. For the first time the body size and weight of *M. medium* can be assessed through regression equations based on skull measurements. The particularly good condition of the material can be explained by the calm and deep marine environment in which it was deposited.

Keywords: Sirenia, *Metaxytherium*, skull, mandible, postcranial, Miocene, Faluns, France

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INTRODUCTION

Modern sirenians are the only group of mammals adapted to feed exclusively on aquatic plants with only two living tropical genera (the dugong *Dugong* and the manatee *Trichechus*; Bertram and Bertram, 1973). The fossil sirenians are known since the Eocene and they have reached their most important diversity during the Miocene (Domning *et al*., 2010). Among fossil sirenians, *Metaxytherium* is a genus known from the late Oligocene (Vélez-Juarbe and Domning, 2014) to the late Pliocene (Sorbi *et al*., 2012), and its remains have a wide geographical distribution (west Atlantic, Caribbean, east and north Pacific, Europe and Mediterranean Bassin). It is also the most common sirenian in the Neogene fossil record of Europe (Domning and Pervesler, 2012). In France, *Metaxytherium medium* is a relatively abundant species in the Faluns of Anjou and Bretagne (Ginsburg and Janvier, 1971; Ginsburg and Mornand, 1986) and it is typically known from the middle Miocene to the base of the late Miocene (Ginsburg and Mornand, 1986 [MN5-MN9]; Carone, 1997: Bianucci and Landini, 2003; Sorbi, 2008a; Rateau *et al*., 2009; Sorbi *et al*., 2012; Domning and Pervesler, 2012; Gagnaison, 2013; Vélez-Juarbe and Domning, 2014). Several complete skeletons have been found (mostly during the 20th century) and are housed at the Muséum national d'Histoire Naturelle in Paris, at the Muséum des Sciences Naturelles in Angers (composite skeleton) and at the Muséum d'Histoire Naturelle in Tours (Ginsburg and Janvier, 1971; Rateau *et al*., 2009). In addition, numerous more fragmentary dental, cranial and postcranial remains have been recorded in western Europe (Germany, Netherlands, Austria, Italy, Greece, Spain, Portugal, Slovakia, Hungary, Mediterranean islands) and probably also in North Africa (Domning and Pervesler, 2012).

We report here a well-preserved and almost complete skull, associated with lower jaws in occlusion and several ribs and vertebrae attributed to *Metaxytherium medium* that have been collected from La Morfassière quarry in north-western France. However, they are not the first discovered in this area. A partial skeleton was collected in 1987 in the Savignean facies of Savigné-sur-Lathan and is now housed at the Muséum d'Histoire Naturelle in Tours but was never published, and several additional fragmentary dental remains have been reported (Rateau *et al*., 2009). It is very unusual to find a skull in connection with the lower jaws in the sediments of eastern Anjou and Touraine (Rateau *et al*., 2009), and the material described here thus represents one of the most complete individuals known so far in the areas of Savigné-sur-Lathan and Channay-sur-Lathan, and even from the Miocene of Anjou-Touraine Faluns.

GEOLOGICAL SETTING AND AGE

During the Miocene the transgressing sea in the Loire Valley deposited shelly and sandy sediments locally known as 'Faluns' (Dollfus and Dautzenberg, 1902) that yielded numerous marine and terrestrial faunal assemblages (for example, Ginsburg and Janvier, 1971; Pouit, 1982; Ginsburg and Mornand, 1986; Gantier *et al*., 2019). La Morfassière quarry is located about 60 km northwest of Tours between Savigné-sur-Lathan and Channay-sur-Lathan (Indre-et-Loire, northwestern France; Fig. 1A-B) and is exploited since the early 1980s (Lévêque, 1989).

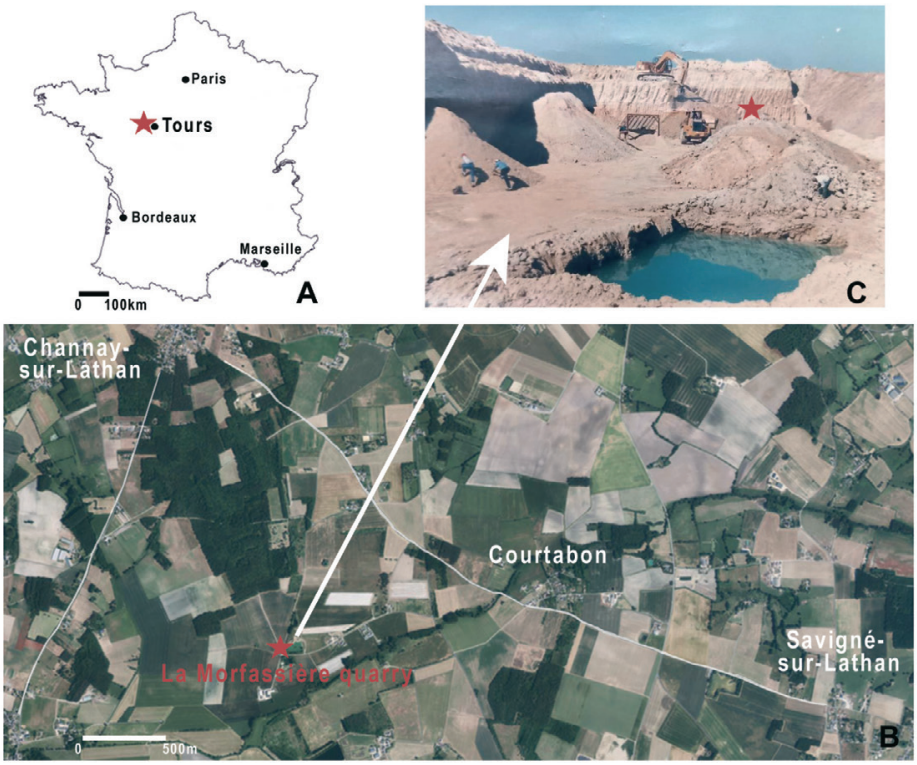

Figure 1. Location map of La Morfassière quarry. **A**, Map of the area where remains of *Metaxytherium medium* reported here were recovered in the Faluns (northwestern France). **B**, Location of La Morfassière quarry in the bassin of Savigné-sur-Lathan. **C**, View of La Morfassière quarry. The red star indicates the level where the material described here was collected. Photo by Patrice Raboeuf.

According to Gagnaison (2023), the 'Faluns' of La Morfassière included a shallow layer rich in bioclasts and slightly rolled mollusc shells. It displayed a lithology and a fossil record (mainly bryozoans, scaphopod molluscs, gasteropods and bivalves) equivalent to the Pontilevian facies (sandy bioclastic) of the 'Faluns' quarries from southern Touraine and of Loir-et-Cher. The Pontilevian facies represents a shallow sea with a beach environment and tidal currents (Ginsburg and Mornand, 1986; Lévêque, 1989). This facies is no more visible at La Morfassière due to the mining activities (Gagnaison, 2023). The Pontilevian facies is overlapped by a calcareous facies with bryozoans that deposited in a calm environment, i.e. the Savignean facies which is dated from the Langhian-Serravalian (middle Miocene; Gagnaison, 2023; Douteau, 2024). The Savignean facies corresponds to a deeper marine environment and is still visible at La Morfassière (Fig. 1C). The remains reported here have been collected from sediments corresponding to the Savignean facies.

MATERIAL AND METHODS

Fossil recovery and extraction. The material from La Morfassière consists of an almost complete skull associated with its mandible (Fig. 2), several ribs and vertebrae for which most of the apophyses are lacking. The remains were found in the 1980s by two quarry workers during excavations at La Morfassière quarry, and then rescued by J.-M. Sinturet. Careful extraction of the fossils was thus not performed under professional control and we do not know if the remains were in anatomical connection. However, we suspect that the fossil remains belong to a single individual. The skull and lower jaw were preserved into a consolidated matrix (Fig. 2) and they have been expertly separated, cleaned and prepared by F. Chevrier. The ribs and vertebrae have been prepared and cleaned at PALEVOPRIM Laboratory.

Fossil repository. The material is housed in the private Collection of J.-M. Sinturet in Saint-Cyr-sur-Loire. A cast of the skull (MOR-2024-001) and mandible (MOR-2024-002), as well as casts of the two better preserved vertebrae (MOR-2024-003 and MOR-2024-008) are housed in the Paleontological Collections of PALEVOPRIM (Poitiers). A CT-scan of the skull (pixel size of 89.6 x 89.6 µm) and a surface scan of the

Figure 2. Left lateral view of the skull and mandible of *Metaxytherium medium* from La Morfassière before preparation by F. Chevrier. Photo by F. Chevrier.

mandible have been performed and corresponding data are kept at PALEVOPRIM.

Dental nomenclature. We adopt here the dental nomenclature used by Sorbi *et al*. (2012).

Institutional Abbreviations. MOR, La Morfassière.

Anatomical Abbreviations. as, alisphenoid; bo, basioccipital; cp, coronoid process; dp, decidual lower premolar; DP, decidual upper premolar; eam, external auditory meatus; eo, exoccipital; fm, foramen magnum; fr, frontal; if, infraorbital foramen; la, lacrimal; mdf, mandibular foramen; mef, mental foramen; m, lower molar; M, upper molar; mf, mesorostral fossa; mx, maxilla; n, nasal; na, neural arch; np, nasal process; oa, orbicular apophysis; oc, occipital condyle; pa, parietal; pac, parietal crest; pgp, postglenoid process; pmx, premaxilla;, pp, paroccipital process; pt, pterygoid; ptp, posttympanic process; saf, superior articular facet; scf, superior costal facet; so, supraoccipital; sop, supraorbital process; sq, squamosal; sr, sigmoid ridge; tp, transverse process; ty, tympanic; vb, vertebral body; vo, vomer.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order SIRENIA Illiger, 1811

Family DUGONGIDAE Gray, 1821

Sub-Family HALITHERIINAE (Carus, 1868) Abel, 1913

Genus *Metaxytherium* Christol, 1840

Metaxytherium medium (Desmarest, 1822) Hooijer, 1952

Referred material: MOR-2024-001, almost complete skull with right DP5-M2 and left DP5-M3; MOR-2024-002, mandible with right m1-m3 and left dp5-m3; MOR-2024-003, cervical vertebra (C7); MOR-2024-004, thoracic vertebra (T1); MOR-2024-005, thoracic vertebra (T2 to T9); MOR-2024-006, thoracic vertebra (T2 to T9); MOR-2024-007, thoracic vertebra (T2 to T9); MOR-2024-008, thoracic vertebra (T2 to T9); MOR-2024-009, thoracic vertebra (T10 to T19); MOR-2024-010, thoracic vertebra (T10 to T19); MOR-2024-011, lumbar-sacral vertebra; MOR-2024-012, lumbar-sacral vertebra; MOR-2024-013, lumbar-sacral vertebra; MOR-2024-014, lumbar-sacral vertebra; MOR-2024-015, lumbar-sacral vertebra; MOR-2024-016, anterior caudal vertebra; MOR-2024-017, anterior caudal vertebra; MOR-2024-018, anterior caudal vertebra; MOR-2027-019, left first rib; MOR-2024-020, left anterior rib (R2 to R7); MOR-2024-021, left anterior rib (R2 to R7); MOR-2024-022; left anterior rib (R2 to R7); MOR-2024-023,

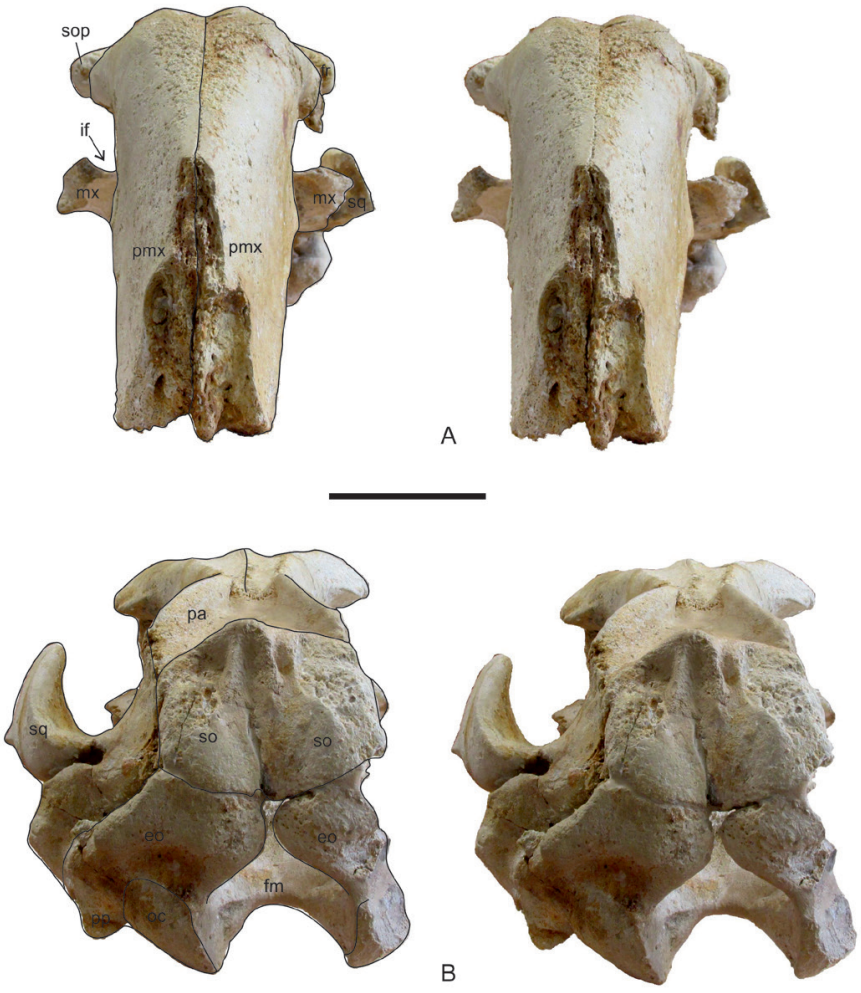

Figure 3. *Metaxytherium medium* from La Morfassière. **A**-**B**, MOR-2024-001, skull. **A**, Anterior view; **B**, Posterior view. Scale bar equals 5 cm.

left anterior rib (R2 to R7); MOR-2024-024, left posterior rib (R8 to R19); MOR-2024-025, left posterior rib (R8 to R19); MOR-2024-026, right first rib; MOR-2024-027, right anterior rib (R2 to R7); MOR-2024-028, right anterior rib (R2 to R7); MOR-2024-029, right anterior rib (R2 to R7).

Description

Skull (Fig. 3): The skull is well preserved but the right squamosal, part of the right parietal, jugals and the anterior end of premaxilla including the incisors are lacking. The left DP5-M3 and right DP5-M2 are present. Most of the skull structures in *Metaxytherium medium* have been described in details by several authors (Flot, 1886; Cottreau, 1928; Ginsburg and Janvier, 1971; Bianucci and Landini, 2003; Sorbi, 2008b; Domning and Pervesler, 2012) and their morphology correspond to what can be observed on the current specimen, so we will only provide here a general description (Table 1).

The anterior end of the premaxilla is damaged but it still displays two alveola for the missing incisors (Fig. 3A). The rostral deflection from the occlusal plane is about 50-55° (Fig. 4A, B). Anteriorly to the almond-shaped mesorostral fossa, the premaxillae form a bulge with a median slight groove corresponding to the suture between both premaxillae. Dorsally, those two bones are elongated, they line the mesorostral fossa and their distal ends (nasal processes) are in contact with the frontals, nasals (poorly preserved) and lacrimals that are

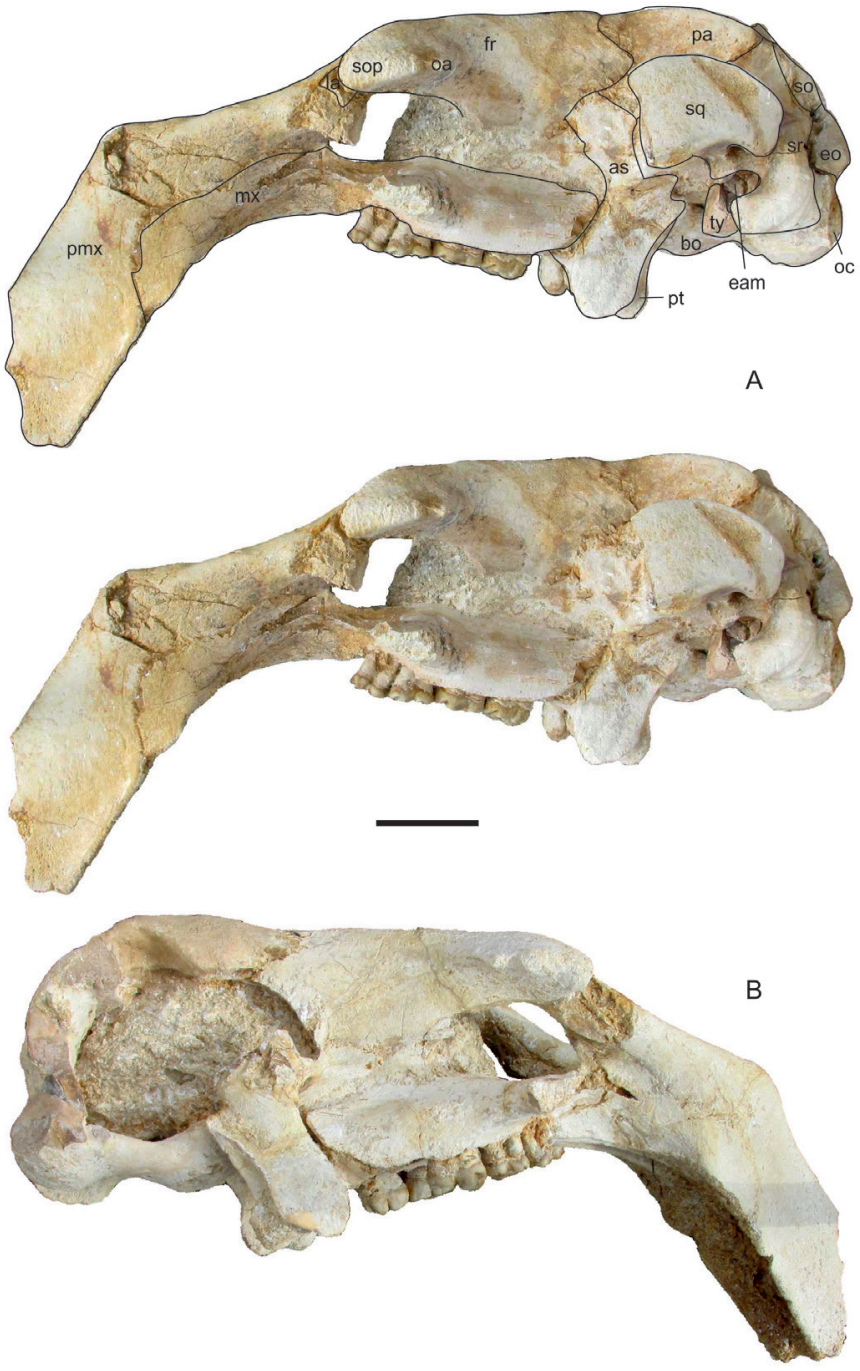

Figure 4. *Metaxytherium medium* from La Morfassière. **A**-**B**, MOR-2024-001, skull. **A**, Left lateral view; **B**, Right lateral view. Scale bar equals 5 cm.

damaged but present (Fig. 5A). Ventrally, the palatal surface of the premaxilla is concave but its preservation does not allow to observe an incisive foramen.

The nasals are only partly preserved, they are located above the orbital region, and posterior to the mesorostral fossa. They are in contact with the nasal processes of the premaxilla and the frontals (Fig. 5A).

In dorsal view, the opening of the mesorostral fossa allows to observe two parallel crests (nasal septum) on the anteroposteriorly slightly convex vomer (Fig. 5A). They are

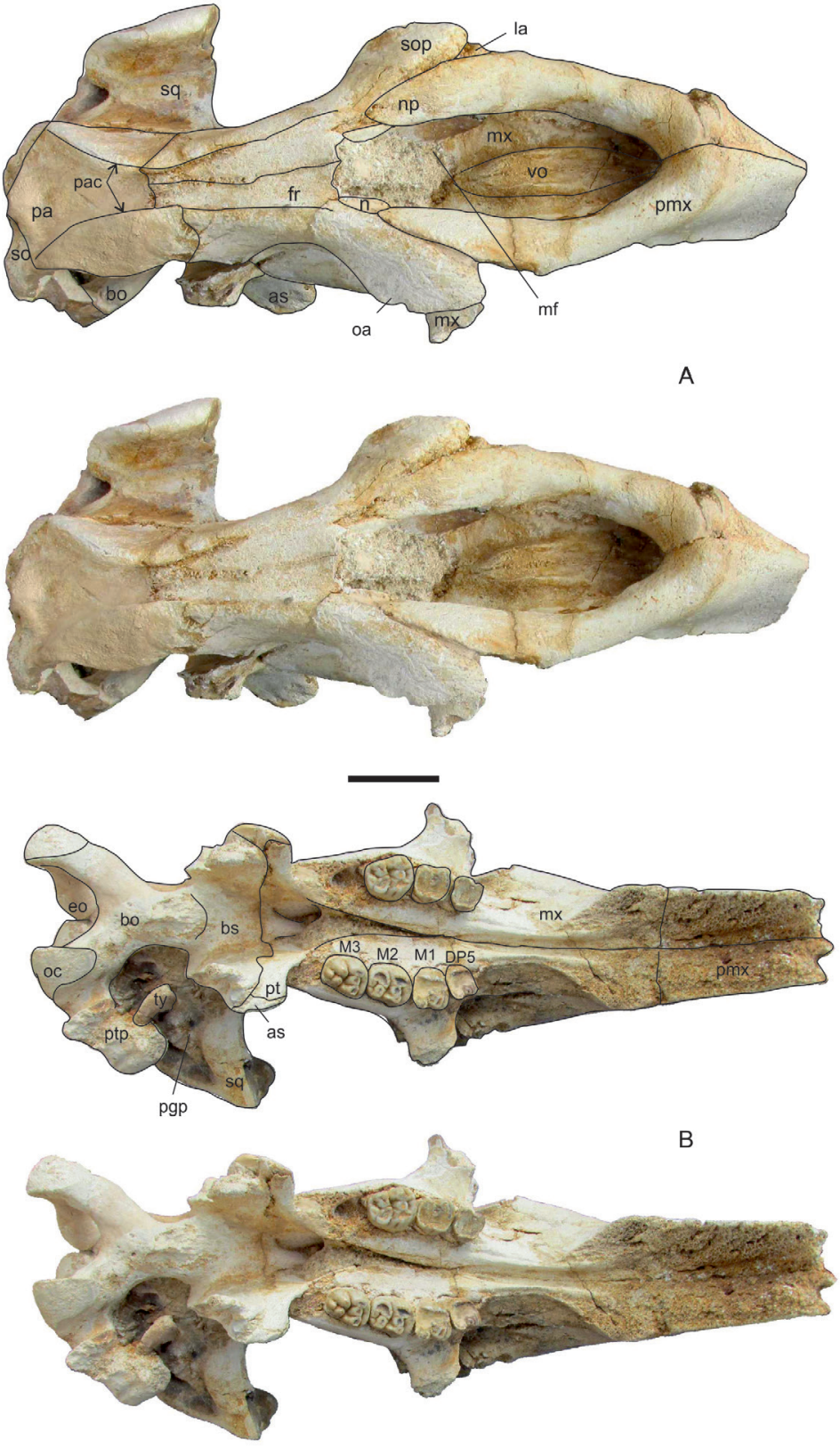

Figure 5. *Metaxytherium medium* from La Morfassière. **A**-**B**, MOR-2024-001, skull. **A**, Dorsal view; **B**, Ventral view. Scale bar equals 5 cm.

Table 1. Measurements (mm) of skull of *Metaxytherium medium* MOR-2024-001 (e: estimated measurements)

Total length	450
Length of mesorostral fossa	165e
Width of mesorostral fossa	58
Width between supraorbital processes	148
Minimum width at frontal level	65
Minimum distance between parietal crests	18
Height of zygomatic process of squamosal	52
Width of occipital condyles	115e
Foramen magnum width	51
Length of supraoccipital	88e
Maximum width of maxilla between tooth rows	45

about 60 mm long and 15 mm apart. This thin bone contacts the maxilla laterally and the septum extends slightly forward of middle of the mesorostral fossa.

The lacrymals are poorly preserved and only small bone fragments under the anterior end of the supraorbital processes can be observed (Fig. 4A, 5A).

The antero-lateral extensions of the frontals form the supraorbital processes that display a massive and ventral knoblike structure. Small orbicular apophyses are present behind the supraorbital processes (Fig. 4A, 5A). The anteromedian part of the frontals (internasal process) is lacking and their dorsal surface is roughly flat and laterally bordered by the weak anterior extension of the temporal crests (Fig. 5A). The frontoparietal suture is situated about 80 mm posteriorly to the nasals, and the interfrontal suture is still visible.

The dorsal part of the parietals is concave between the strongly developed parietal crests (their morphology is variable in *Metaxytherium* according to Domning, 1988) that diverge posteriorly (type D or E of Domning, 1988). Both crests are separated by about 18 mm in their narrowest area, above the anterior root of the zygomatic arch (Fig. 5A). No emissary foramen is visible and a small median bump is situated in front of the external occipital protuberance.

The supraoccipital is pentagonal in occipital view and forms an angle of about 120° with the posterior part of the parietal. The dorsal end of the supraoccipital rises above the plane of the parietal roof to form a strong external occipital protuberance. Two short median ridges extend downward from the occipital protuberance and are separated by a vertical groove. The medial and ventral parts of the supraoccipital are concave (Fig. 3B).

The exoccipitals are not fused to the supraoccipitals or to each other and they are dorsally separated by a groove. The foramen magnum is roughly triangular in outline. Only part of the left paroccipital process is preserved and its tip probably extended ventrally almost as much as the occipital condyle. The supracondylar fossa is distinct (Fig. 3B).

The structures of the basioccipital and basisphenoid are similar to those described by Flot (1886), Sorbi (2008b) and Domning and Pervesler (2012). The basioccipital and the basisphenoid are fused. On the basisphenoid, the *sella turcica* is nearly flat and shallow (Fig. 5B).

The pterygoid processes are well developed and lined by the alisphenoids on their anterolateral face. The pterygoid fossa is deep on the posterior face of the bone. The ventral ends of the pterygoid and alisphenoid line the posterior end of the palatine which is mostly lacking (Fig. 4, 5B). Ventrally, the suture between both maxillae forms a groove that is typical of *Metaxytherium*. This groove is rather deep with elevated and wide rims (which are sharper in *Dugong*), and it extends from the DP5 to the contact with the premaxilla (Fig. 5B).

The alveolar portion of the maxilla displays two slightly buccally convex tooth rows separated by a maximum width of about 40.5 mm (Fig. 5B). The palatal surface is much narrower in front of the molars, its edges are lyriform with a deep palatal groove (about 10 mm wide and 8 mm deep). The palatal surface makes an angle of about 30° with the rostral surface. Only the lower border (maxilla) of the infraorbital foramen is preserved, the jugal being absent, but the infraorbital foramen seems to be moderately large (about 30 mm dorsoventrally).

The squamosal contacts the parietal and jugal that is missing on both sides. It connects dorsally with the posterior end of the parietal crest. Only the strong posterior part of the longitudinal segment of the left zygomatic process is preserved and the round to oval external auditory meatus is visible beneath it (Fig. 4A). Ventrally, the preserved glenoid fossa is shallow and short, and the postglenoid apophysis forms a small tuberosity. The blunt sigmoid ridge can be observed on the distal part of the left squamosal, extending from the dorsal end of the mastoid foramen to the ventral end of the posttympanic process (Fig. 4A).

Posterointernally to the postglenoid apophysis the left V-shaped tympanic is preserved, but the periotic is entirely missing. The tympanic forms a triangular arch in lateral view with two anterior and posterior branches. The anterior one is massive whereas the ventral end of the posterior branch is laterally flattened (Fig. 4A, 5B).

Mandible (Fig. 6): It is almost complete except for the anterior end mesially to the large mental foramen, the angular apophyses and a part of the right coronoid apophysis and condyle. The right m1-m3 and left dp5-m3 are preserved (Fig. 6C). As other mandibles attributed to *M. medium*, the specimen from La Morfassière is robust, its ventral border is strongly curved and exhibits a marked concavity in lateral view (Fig. 6A, B). The horizontal ramus is deep (around 89.5 mm under m2, 88.3 mm under m3) and it exhibits a slight buccal transverse thickening beneath the tooth row. The dorsal edge of the horizontal ramus is blade-like anterior to the tooth row (Fig. 6C). The deflection of the symphyseal surface to the occlusal plane is about 55°. As described by Cottreau (1928), the anterior border of the wide coronoid process is slightly concave where it connects with the horizontal ramus. The tip of the sharp coronoid process is backwardly oriented about 30 mm above the mandibular condyle. The latter is located about 40 mm above the level of molar occlusal surface. Its surface is slightly concave in the middle. The single and large mental foramen opens mesioventrally as a large anterior groove beneath the posterior end of the mandibular symphysis. The symphyses are unfused in their ventral part. The mandibular foramina open medially about 35 mm below the distal wall of the m3 (Fig. 6D; Table 2).

Dentition (Fig. 7): The occlusal surface of the lower tooth row is mesio-distally slightly convex. Only the right three lower molars are present whereas the left dp5-m3 are preserved (Fig. 7A). There is no alveola mesially to the dp5 that might suggest that a dp4 was present, which is very uncommon in *Metaxytherium* (Sorbi, 2008b). However, the mesial wall of the left dp5 exhibits a small contact facet that testifies to

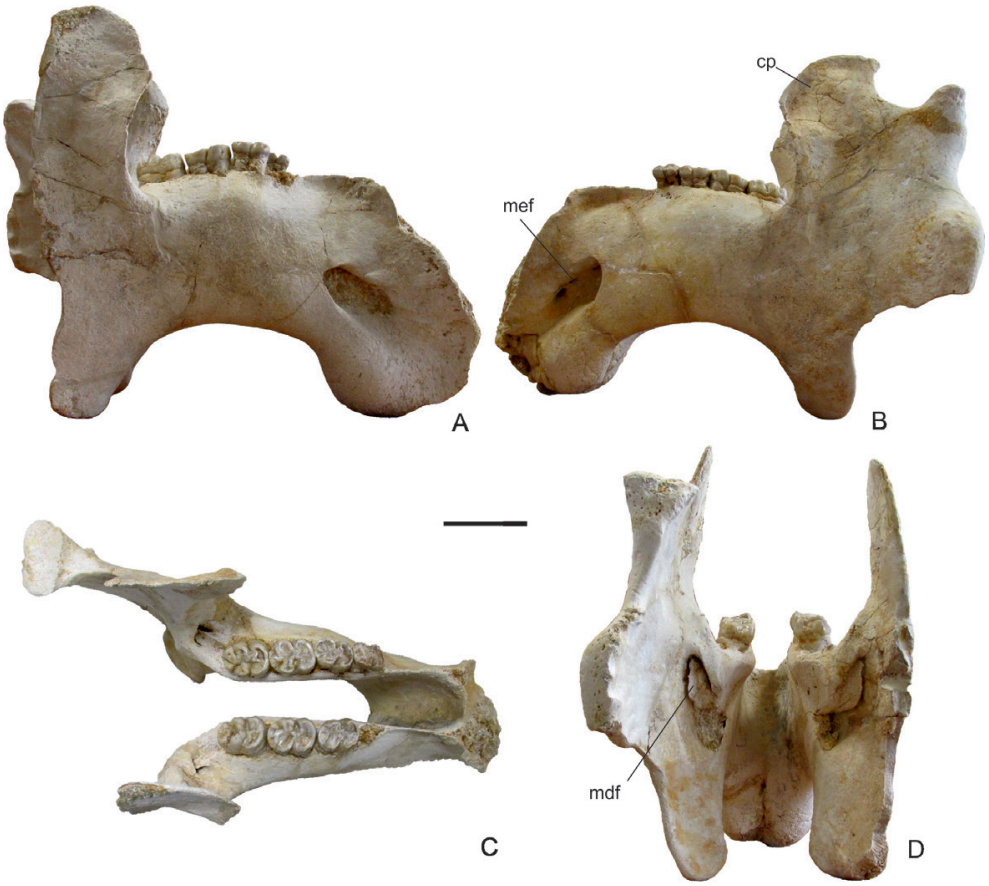

Figure 6. *Metaxytherium medium* from La Morfassière. **A-D**, MOR-2024-002, mandible. **A**, Right lateral view; **B**, Left lateral view; **C**, Occlusal view; **D**, Posterior view. Scale bar equal 5 cm.

the presence of a possible decidual tooth. The very narrow dorsal parts of the horizontal rami indicate that there was no anterior premolar. The dp5 and the three lower molars are rectangular in occlual outline and two-rooted, the lingual roots being fused with the buccal ones. All teeth are worn and their occlusal structure is mostly obliterated with the exception of the m3 talonid. The dp5 is very worn and only the remains of the four main cuspids can be seen. On the molars, two cuspids (protoconid and reduced metaconid) form the trigonid. A paraconid is not visible contrary to the descriptions of Ginsburg and Janvier (1971) and Carone (1997). Sorbi *et al*. (2012) rather observe anterior cingular cuspids mesially to the protoconid and metaconid. The occlusal wear of the two mesial cuspids forms a mesially convex lophid. A deep transverse valley separates this structure from the much more reduced hypoconid and entoconid that also form a lophid on the talonid. On m2 and m3, a distobuccal hypoconulid and a small lingual accessory cuspid occupy the distal part of the talonid. A small median accessory cuspid is distal to the protoconid and metaconid and is connected by a second accessory cuspid mesial to the hypoconid and entoconid. There is no cingulid on the teeth except a very short and narrow one mesiobuccally on molars.

The left DP5-M3 and right DP5-M2 are preserved (Fig. 7B). All premolars and molars have two buccal roots and one lingual root. The DP5 and M1 are square in occlusal outline (M1 is more elongated than DP5) and the M2 and M3 are more rectangular. The DP5 and M1 are heavily worn and their precise occlusal structure cannot be observed. On both teeth, a crest (referred to as the anterior cingular cusps or precingulum consisting of

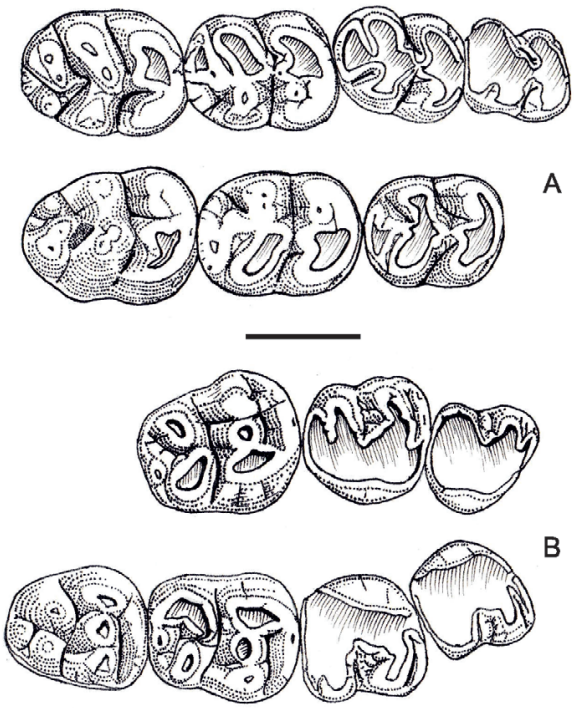

Figure 7. Tooth rows of *Metaxytherium medium* from La Morfassière. **A**, Left dp5-m3 (top) and right m1-m3 (bottom), MOR-2024-002; **B**, Right DP5-M2 (top) and left DP5-M3 (bottom), MOR-2024-001. Scale bar equals 2 cm. Drawings by F. Chevrier.

Table 2. Measurements (mm) of the mandible of *Metaxytherium medium* MOR-2024-002 (e: estimated measurement)

Total length	316
Total height	232
Length from end of premaxilla to root of ascending ramus	190
Length of symphysis	94e
Distance between anterior and posterior ventral extremities	130
Height of mandibular notch	57
Height of mandible above the mandibular notch	86
Height from mandibular dorsal edge to condyle	70
Length of ascending ramus	120
Deflection of symphyseal surface to occlusal plane (degrees)	55

four separate cuspules according to Sorbi *et al*., 2012) extends along the mesial face of the crown and ends mesiobuccally in front of the paracone. This crest is smooth and does not clearly show separate cuspules on MOR-2024-001. A sulcus separates that crest from the paracone and another valley can be observed buccally between the paracone and the metacone. The M2 and M3 are less worn. They exhibit three mesial cusps (a small paracone and a larger protocone connected to a protoconule) and three distal cusps (a small metacone connected to a smaller metaconule and a larger hypocone). The mesial and distal cusps tend to form lophs as they wear down. A small median cusp (posterior cingular cusp of Sorbi *et al*., 2012) is present on the distal face of the crown and an accessory distobuccal cusp is twinned with the distomedial cusp on the left M2 but not on the right one. The left M3 displays the same structure as the M2, but being less worn, the metaconule is not visible and the mesiobuccal crest of the hypocone invades the transverse valley. The tapering distal end of the crown bears only one small cusp. There is no cingulum on upper teeth. (Table 3). The specimen reported here is probably a young adult given the wear of the dp5/DP5 and anterior molars.

Postcranial material: The postcranial elements (vertebrae and ribs) have not been recovered in anatomical connection which makes their precise individual position difficult to assess. The recognizable vertebrae include one cervical vertebra, seven thoracic vertebrae, five lumbar-sacral vertebrae, and three caudal vertebrae (Fig. 8).

The only cervical vertebra (MOR-2024-003; probably the Ce7) is almost complete with the exception of the left transverse process (Fig. 8A-C). The body of the vertebra is circular, dorso-ventrally flattened and antero-posteriorly compressed, and its neural arch is complete. There is no transverse foramen on the preserved transverse process, as mentioned by Cottreau (1928).

Among the seven thoracic vertebrae that have been identified (Fig. 8A), the most complete ones are MOR-2024-004, a small T1 that preserves part of the body and the right transverse costal facet, and MOR-2024-008 (indeterminate position, T2-T9) that is complete with the body, the transverse processes, the backwardly slanted spinous process, and the superior articular and superior costal facets (Fig. 8D, E). The vertebral foramen is roughly heart-shaped. The morphology of this vertebra is similar to that described by Cottreau (1928). The other thoracic vertebrae are mainly represented by the body of the bone on which small parts of the transverse processes are sometimes preserved.

Five lumbar vertebrae have been recognized based on their kidney-shaped body in anterior view. All of them lack their processes, and it is thus not possible to determine their individual position within the vertebral column (Fig. 8F).

Table 3. Dental measurements (in mm) of MOR-2024-001 and MOR-2024-002.

	Tooth	Length	Width
MOR-2024-002	ldp5	18.4	17.0
	lm1	22.2	20.3
	lm2	26.9	21.7
	lm3	28.1	21.7
	rm1	23.3	18.6
	rm2	27.7	21.2
	rm3	28.6	21.5
MOR-2024-001	lDP5	20.1	21.1
	lM1	23.1	23.3
	lM2	27.2	23.2
	lM3	26.3	21.9
	rDP5	19.8	20.8
	rM1	22.5	22.4
	rM2	29.1	25.1

Finally, three caudal vertebrae are included in our material (Fig. 8G). They are characterized by their oval to hexagonal body in anterior view with two pairs of demi-facets for the hemal arches on their ventral face, flattened and short transverse processes. The most complete caudal vertebra (MOR-2024-018) also displays remnants of a small neural arch with a small oval vertebral foramen. This vertebra might be an anterior caudal because its transverse process is oriented laterally (Table 4). These vertebrae usually display a neural arch that becomes smaller backwardly.

Several ribs are present (8 left and 4 right). Their morphology is consistent with that of the material described in details by Cottreau (1928). The capitulum and tuberculum are preserved on most of them except on two right ribs and on the most anterior left rib. They are massive, pachyosteosclerotic, strongly curved in their anterior part and mediolaterally flattened. The first two ribs (R1) are shorter and less curved than the posterior ones. The most posterior ribs (R8 to R19) can be distinguished from the anterior ones by their shaft that progressively curves backwards (Fig. 9; Table 5).

COMPARISONS

The material from La Morfassière displays features that can be observed in dugongids (Domning, 1994; Sorbi, 2008b; Vélez-Juarbe and Domning, 2014) like the presence of the post-tympanic process and of the processus retroversus of the squamosal, and of a pterygoid fossa, the squamosal that extends to the temporal crests, the loss of the alisphenoid canal and of the permanent fifth premolar, the broad mandibular symphysis. Several other apomorphic characters also justify the attribution of the specimen to the paraphyletic genus *Metaxytherium* (Sorbi, 2008b; Domning and Pervesler, 2012) rather than to any other halitheriine: loss of permanent premolars, supraorbital process of frontals reduced and dorsoventrally thickened, supracondylar fossa present, supraoccipital wider ventrally than dorsally, exoccipital not meeting in a midline suture above the foramen magnum, and ventral border of the horizontal ramus of mandible strongly concave. The specific attribution of La Morfassière material is more challenging because contrary

to most other mammals, the teeth of *Metaxytherium* exhibit important variation in size and morphology and are therefore considered to be useless for taxonomic purpose (Sorbi, 2008b). A few non-autapomorphic characters listed by Sorbi (2008b) that define *M. medium* can however be observed on the material from La Morfassière: nasal process of premaxilla that contacts the lacrimal, infraorbital foramen moderately large, supracondylar fossa of exoccipital deep and not reduced. Unfortunately the jugals are not preserved which makes impossible to observe diagnostic features like their anterior extension or the morphology of the zygomatic-orbital bridge.

During the middle Miocene, only the genus *Metaxytherium* has been recorded in the Mediterranean Sea and the northeast Atlantic, and all specimens there have been referred to *M. medium* (Sorbi, 2008b). However, this species seems to be indistinguishable from *M. crataegense* and it is very similar to *M. floridanum*. *Metaxytherium crataegense* is known only in West Atlantic, Caribbean and east Pacific, whereas *M. floridanum* is restricted to Florida. We therefore refer the remains from La Morfassière to *M. medium*.

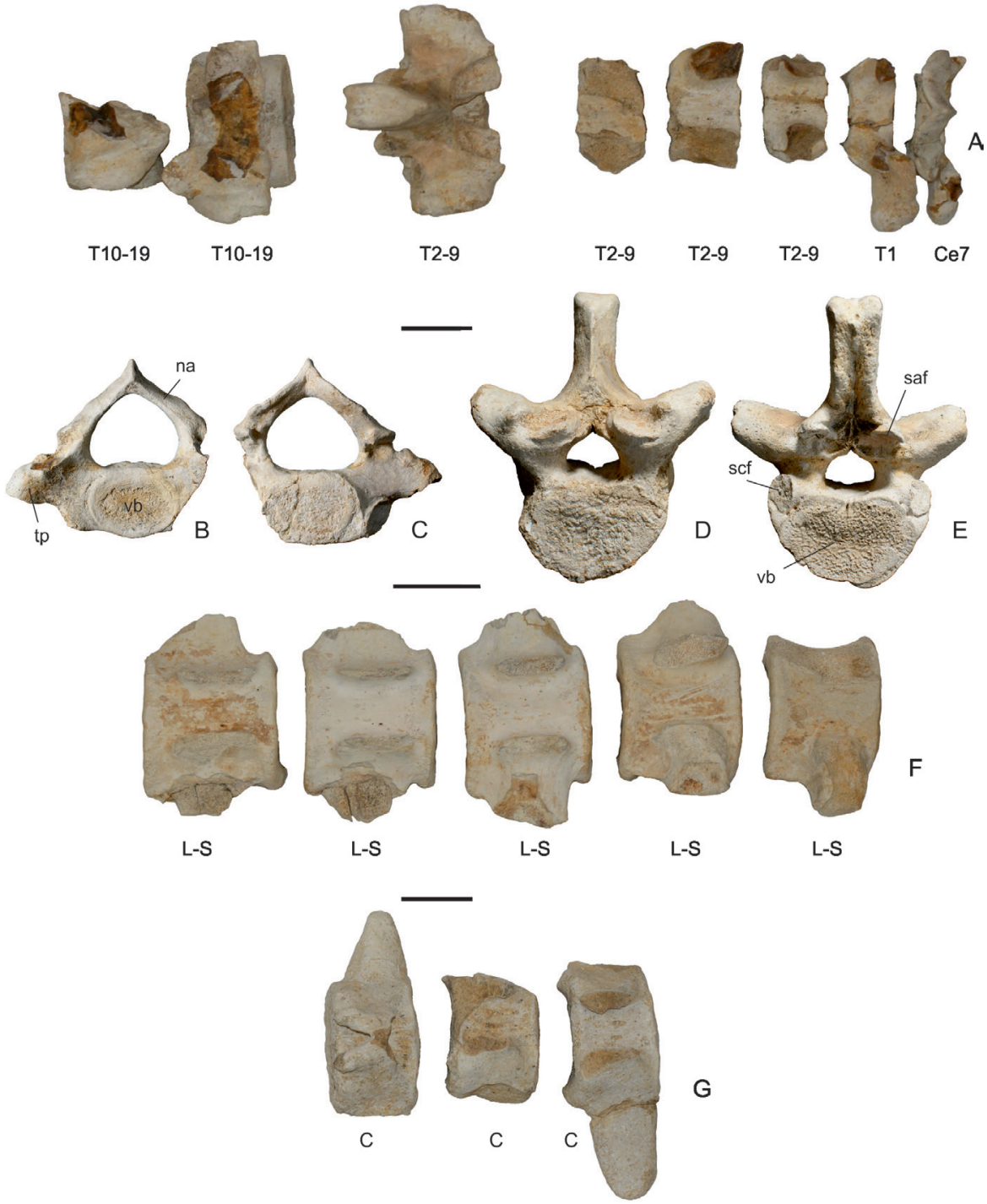

Figure 8. Elements of the axial skeleton of *Metaxytherium medium* from La Morfassière. **A**, Cervical (Ce7) and thoracic (T1-19) vertebrae in dorsal view; **B-C**, Cervical (Ce7) vertebra (MOR-2024-003); **B**, Anterior view; **C**, Posterior view; **D-E**, Thoracic (T2-9) vertebra (MOR-2024-008); **D**, Anterior view; **E**, Posterior view; **F**, Lumbar-sacral vertebrae in dorsal view; **G**, Caudal vertebrae in dorsal view. Scale bars equal 5 cm.

Table 4. Measurements (in mm) of vertebrae of *Metaxytherium medium* from La Morfassière. Ce: cervical vertebra; T: thoracic vertebra; L-S: lumbar-sacral vertebra; C: caudal vertebra; TH: total height; ABC: anterior breadth of centrum; PBC: posterior breadth of centrum; HC: Height of centrum; LC: length of centrum; BTP: breadth across transverse processes; WNC: width of neural canal; HNC: height of neural canal; e: estimated.

	Vertebra	TH	ABC	PBC	HC	LC	BTP	WNC	HNC
MOR-2024-003	Ce7	110.2	56.6	53.4	43.2	24.2	-	53.7	44
MOR-2024-004	T1	-	54.4	53.7	42.2	33.6	-	-	-
MOR-2024-005	T2 to 9	-	68.0	70.6	39.5	43.6	-	-	-
MOR-2024-006	T2 to 9	-	66.8	62.4	45.7	48.3	-	-	-
MOR-2024-007	T2 to 9	-	62.8	69.3	42.0	45.1	-	-	-
MOR-2024-008	T2 to 9	167	84.6	83.0	57.1	59.5	143.2	31.4	29.5
MOR-2024-009	T10 to 19	-	92.2	97.5	75.0	68.2	126e	-	-
MOR-2024-010	T10 to 19	-	-	-	65.4e	73.4	-	-	-
MOR-2024-011	L-S	-	105.4	108.0	88.7	82.7	-	-	-
MOR-2024-012	L-S	-	105.1	107.5	88.9	87.3	-	-	-
MOR-2024-013	L-S	-	103.4	111.8	90.4	93.3	-	-	-
MOR-2024-014	L-S	-	105.0	111.4	89.7	93.8	-	-	-
MOR-2024-015	L-S	-	103.7	112.3	88.7	98.8	-	-	-
MOR-2024-016	C	-	91.1	89.8	65.2	57.1	-	-	-
MOR-2024-017	C	-	-	84.0	62.0	58.8	-	-	-
MOR-2024-018	C	98e	86.2	85.2	62.6	56.4	-	23.5	16.7

The new material described here allows to list several skull and mandible features that seem to be variable in *M. medium*. On MOR-2024-01, the posterior end of the mesorostral fossa reaches the level of the posterior margin of the orbit (usually beyond the posterior margin of the orbit; Sorbi, 2008b). The rostral deflection of the occlusal plane (50-55°) is similar to the values given by Domning and Pervesler (2012) and by Sorbi (2008b) for *M. medium* (ca. 50° and 49°-66° respectively). Until now, the vomer was unknown in *M. medium* (Sorbi, 2008b) and very rarely preserved in *Metaxytherium*. It was shortly described in *M. albifontanum* (late Oligocene of eastern North America) by Vélez-Juarbe and Domning (2014). On MOR-2024-01, the vomer exhibits a shape similar to that observed in other sirenians but it seems to extends a little more forwardly than in *M. albifontanum*. On the frontals, small orbicular apophyses are present. The medial portion of the frontal is flat. The anterior end of the fronto-parietal suture is situated about 8 cm behind the nasals (about 3.5-5 cm according to Sorbi, 2008b), and the interfrontal suture is visible from the parietals to the anterior end of the frontals. On the parietal, temporal crests are of type D or E (Domning, 1988). No emissary foramen is visible, but a small median bump is present in front of the external occipital protuberance. Two parallel ridges about 3 cm long extend ventrally from the occipital protuberance, but they do not reach the ventral border of the supraoccipital. On the mandible MOR-2024-02, the buccal swelling that is usually present below m1 according to Sorbi (2008b) occurs below all molars. As described by Cottreau (1928), the anterior border of the wide coronoid apophysis is slightly concave where it connects with the horizontal ramus.

Although the dimensions of the upper and lower teeth of La Morfassière specimen (Table 3) are within the average measurements for those of *M. medium* published by Ginsburg and Janvier (1971), Carone (1997) and Domning and Pervesler (2012), the largest amount of variation is observed on the teeth. For example, on La Morfassière material the less worn upper molars exhibit an anterior cingular valley open buccally rather than lingually (Sorbi, 2008b) and a protoconule is present on M2 and M3. The anterior cingular crest also does not show distinct cuspules. On lower molars, the protolophid has a smooth rather than slightly crenulated mesial surface (Sorbi, 2008b), and a paraconid is not visible contrary to the description of Ginsburg and Janvier (1971) and Carone (1997).

DISCUSSION AND CONCLUSIONS

The discovery of the specimens in the Savignean facies (a deeper and calmer marine rather than a shallower and more agitated beach environment) might account for the association of the remarkably preserved skull with its mandible and several vertebrae and ribs which is unusual in this Faluns area. Although the skull and mandible are rather well preserved, most of the vertebrae have lost their processes, probably because these structures were more fragile and damaged during their extraction. However, the fossils of *Metaxytherium medium* found in Europe are very often fragmentary (Blainville, 1844; Flot, 1886; Mayet and Lecointre, 1909; Ginsburg and Janvier, 1971; Bianucci and Landini, 2003; Rateau *et al*., 2009; Domning and Pervesler, 2012), and the material from La Morfassière thus represents some of the most complete remains known for this species.

Modern dugongs are bottom feeders found in shallow coastal waters and usually inhabit broad bays and banks (Bertram and Bertram 1973; Berta *et al*., 2006). Rateau *et al*. (2009) suggested that *M. medium* lived in similar conditions. Bianucci and Landini (2003) also considered that this species lived in a tropical to sub-tropical and shallow marine environment, which is congruent with the discovery of the material from La Morfassière in the Savignean facies. According to Domning and Pervesler (2012), *M. medium* was probably a consumer of benthic plants (leaves and rhizomes of small and mid-sized seagrasses) and its complex teeth with thick enamel suggest that its diet was not restricted to delicate and soft seegrasses.

Numerous fossil remains have been discovered at La Morfassière over the years and the fossil record includes invertebrates (bryozoans, molluscs) and mainly dental remains of vertebrates (chondrichthyans, birds?, rodents, lagomorphs, primates, carnivores, proboscideans, artiodactyls, perissodactyls, cetaceans, sirenians; Ginsburg 2001; Gagnaison

Figure 9. Ribs of *Metaxytherium medium* from La Morfassière in dorsal view. Top, left ribs; Bottom, right ribs. Scale bar equals 10 cm.

Table 5. Measurements (in mm) of ribs of *Metaxytherium medium* from La Morfassière. (*): lacking proximal end.

	Rib	Length (along outside)	Mesiodistal width	Dorsoventral width
MOR-2024-019	1st left	320*	55.1	36.1
MOR-2024-020	2 to 7 left	615	63.5	32.0
MOR-2024-021	2 to 7 left	680	62.8	34.7
MOR-2024-022	2 to 7 left	780	61.8	34.2
MOR-2024-023	2 to 7 left	750	57.5	36.0
MOR-2024-024	8 to 19 left	770	55.8	35.4
MOR-2024-025	8 to 19 left	790	56.7	39.7
MOR-2024-026	1st right	275*	58.9	34.2
MOR-2024-027	2 to 7 right	610*	62.3	31.3
MOR-2024-028	2 to 7 right	760	53.8	36.2
MOR-2024-029	2 to 7 right	490	55.8	38.2

et al., 2009, 2020; Dubied *et al*., 2017; Gagnaison, 2020). The material of *Metaxytherium medium* described here is not the first one reported from La Morfassière, but it represents one of the most important association of particularly well-preserved cranial remains belonging to a single individual. The body size of *M. medium* has often been suggested in the litterature based on the succession of vertebrae or mounted of complete or composite skeletons (for example, Cottreau, 1926; Ginsburg and Janvier, 1971; Plusquellec and Racheboeuf, 1999; Sorbi, 2008b), but its estimated weight was always compared to that of the modern dugong. Sarko *et al*. (2010) have estimated body length and weight of fossil sirenians based on three cranial measurements (condylobasal skull length, foramen magnum width and occipital condyle width) and they concluded that the strongest predictor of body length and body weight is the condylobasal skull length. According to these authors, the body size for fossil dugongids might also be best predicted by regression equations derived from extant dugongs alone. Following this statement, the calculated estimations for body length and weight of *M. medium* from La Morfassière quarry are 3.41 m and 728 kg respectively. These values might have been slightly larger because the anterior-most end of the premaxilla is broken. These results are however congruents with calculated values for several species of *Metaxytherium* that have similar skull measurements (Sarko *et al*., 2010).

The partial skeleton of *Metaxytherium medium* from La Morfassière includes one of the best known preserved skull associated with its mandible for this species. Although some of its parts are not preserved (tusks, jugal, nasals, periotic, auditory ossicles), variations in size and morphology could be observed on others skull structures that provide additional information on the intraspecific variation of this species. In addition, the skull is well-preserved enough to provide further material suitable for endocranial and sensory systems investigations (see for example, Orihuela *et al*., 2019; Moore *et al*., 2021).

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