

New record of *Metaxytherium* (Mammalia, Sirenia) from the lower Miocene of Manosque (Provence, France)

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ABSTRACT

A new specimen of *Metaxytherium* (Mammalia, Sirenia) consisting of a skull with associated thoracic vertebrae and ribs from the lower Miocene "Molasse calcaire et sablo-marneuse Formation" of Manosque (Provence, France) is described. The specimen is referred to *Metaxytherium* cf. *krabuletzki* on the basis of geological age, but its anatomical characters, size and proportions are also consistent with *Metaxytherium medium*. The difficulty of separating these two species is confirmed. The species of the genus *Metaxytherium* show morphological stasis over a period of more than 10 million years. This new specimen, however, provides new information about the continuity of the Miocene Old World *Metaxytherium* record.

KEY WORDS

Mammalia,
Sirenia,
Metaxytherium,
Miocene,
Mediterranean domain,
France.

RÉSUMÉ

Un nouveau *Metaxytherium* (Mammalia, Sirenia) dans le Miocène inférieur de Manosque (Provence, France).

Un nouveau spécimen du genre *Metaxytherium* (Mammalia, Sirenia) est décrit d'après un crâne et une mandibule, associés à plusieurs vertèbres thoraciques et des côtes. Il provient de la formation de Molasse calcaire et sablo-marneuse du Miocène inférieur de Manosque (Provence, France). Il est attribué à *Metaxytherium* cf. *krabuletzki* d'après l'âge des dépôts, mais ses caractères anatomiques, sa taille et ses proportions sont également compatibles avec *Metaxytherium medium*. La difficulté à différencier morphologiquement ces deux espèces est avérée. Les espèces du genre *Metaxytherium* manifesteraient une sorte de stase morphologique pendant plus de 10 millions d'années. Mais ce nouveau spécimen donne des nouveaux renseignements sur la continuité de l'enregistrement fossile de ce genre dans le domaine méditerranéen et paratéthysien du Miocène.

MOTS CLÉS

Mammalia,
Sirenia,
Metaxytherium,
Miocène,
domaine méditerranéen,
France.

INTRODUCTION

Metaxytherium de Christol, 1840 is an extinct halitheriine dugongid sirenian genus with a wide geographical and biostratigraphical distribution. *Metaxytherium* remains have been collected in several Miocene localities of the Mediterranean and Paratethyan region (e.g., Domning & Thomas 1987; Domning & Pervesler 2001; Bianucci *et al.* 2004; Carone & Domning 2007), northeastern Atlantic (e.g., Cottreau 1928; Estevens 2003a, b), southeastern Pacific (Muizon & Domning 1985), northeastern Pacific (Aranda-Manteca *et al.* 1994) and western Atlantic-Caribbean region (Domning 1988; Toledo & Domning 1991), and also in Pliocene sediments of the Mediterranean Basin (e.g., Domning & Thomas 1987; Pilleri 1988; Sendra *et al.* 1999; Bianucci *et al.* 2004; Carone & Domning 2007).

In the Old World (Mediterranean Basin, Paratethys and northeastern Atlantic coasts) most of the *Metaxytherium* species seem to represent a single evolutionary lineage from early Miocene to middle Pliocene currently divided into four species: *M. krahuletzki* Deperét, 1895 (Burdigalian); *M. medium* (Desmarest, 1822) (Langhian to Tortonian); *M. serresii* (Gervais, 1847) (uppermost Tortonian to early Zanclean); and *M. subapenninum* (Bruno, 1839) (Zanclean to Piacenzian) (Domning & Thomas 1987; Domning & Pervesler 2001; Bianucci *et al.* 2004; Carone & Domning 2007). The exception is *M. petersi* Abel, 1904 which apparently evolved in isolation in the Carpathian Basin during the middle Miocene as a short-lived and localized offshoot of the *M. krahuletzki*-*M. medium* stem (Domning pers. comm.).

Metaxytherium krahuletzki is considered the oldest securely dated *Metaxytherium* species, apart from one unpublished Late Oligocene occurrence in the USA (Domning, unpublished data), and it appears to be the sister group and direct ancestor of all the other Old World *Metaxytherium* (Domning & Pervesler 2001). *Metaxytherium krahuletzki* has been recently revised by Domning & Pervesler (2001). They recorded the species with confidence only from the Burdigalian Central Paratethys deposits of Austria and Switzerland and maybe also from Horné-

Strháre (Slovakia) and Léognan (France). Moreover, they cited some specimens from Klattau (Bohemia, Czech Republic) referred by Pia & Sickenberg (1934) to *M. krahuletzki*; two skull fragments from the Burdigalian of Gebel Zelten (Libya) described as *Metaxytherium* sp. indet. by Heal (1973), which might be referable to *M. krahuletzki*; and in particular a skeleton, now lost, from the Burdigalian of Beaucaire (France) named *M. beaumontii* by Christol in Blainville (1844) and supposed to represent *M. krahuletzki* by Depéret & Roman (1920: 31). This skeleton was found in the Burdigalian deposits of the Rhodanian region such as the new specimen (MPNRL-MAN2000) here described.

The exact relationships of *M. krahuletzki* to its assumed predecessor *Halitherium christolii* Fitzinger, 1842, to the Oligocene and Miocene *Metaxytherium* of the New World, and to *Caribosiren turneri* Reinhart, 1959 and the Dugonginae, all of which seem to share a common ancestry in the Oligocene, are still unclear. Also in need of clarification is the extent of the differences between *M. krahuletzki* and *M. medium*, which appear to be successive species, and between *M. medium* and the contemporaneous *M. floridanum* Hay, 1922 from the Caribbean region (Domning 1988; Domning & Pervesler 2001).

This difficulty of separation reflects the fact, unique among all known sirenians, that the Miocene species of *Metaxytherium* in both Europe and eastern North America display near morphological stasis over a period of more than 10 million years (Domning & Pervesler 2001).

The new fossil specimen of *Metaxytherium* described in this paper provides new information about the continuity of Miocene Old World *Metaxytherium* records and about this near morphological stasis.

MATERIAL AND METHODS

SPECIMEN

The fossil specimen described in this paper was collected in 1988 from the lower Miocene "Molasse calcaire et sablo-marneuse" Formation at La Rochette (Manosque, Provence, South of France) (Fig. 1).

The specimen was extracted and prepared by Christian Lary and now is housed in the Maison

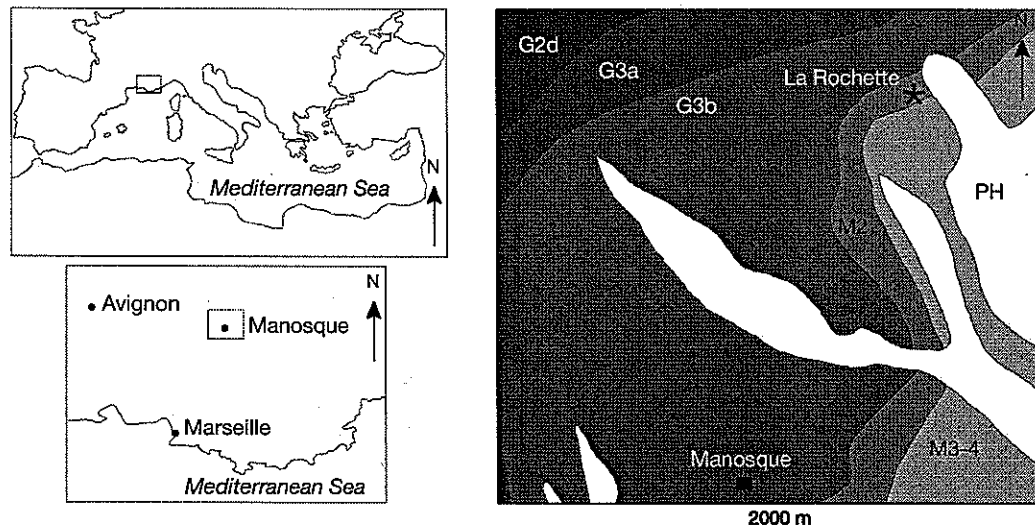


FIG. 1. — Situation and geologic maps of Manosque. The black star indicates the site where the specimen MPNRL-MAN2000 of *Metaxytherium* cf. *krahuletz* Depéret, 1895 was collected (modified from SIG service of Parc naturel régional du Luberon). Oligocene: **G2d**, "marnes de Viens"; **G3a**, "calcaires de Reillanne"; **G3b**, "marnes de la Tuilerie"; Miocene: **M2**, "molasse calcaire et sablo-marneuse"; **M3-4**, "sables et molasse"; Pleistocene-Holocene: **PH**, Pleistocene-Holocène deposits.

du Parc Naturel Régional du Luberon (Apt) with the catalogue number: MPNRL-MAN2000.

TERMINOLOGY

Anatomical terminology and measurements follow Domning & Pervesler (2001).

ABBREVIATIONS

- KME Krahuletz-Museum, Eggenburg, Austria;
 MPNRL Maison du Parc naturel régional du Luberon, France;
 c. character state as described and numbered by Domning (1994) or Bajpai & Domning (1997); e.g., c. 3(1) refers to state one of character three.

GEOLOGICAL SETTING AND AGE

La Rochette, where the specimen was collected, belongs to the Rhodanian region (Provence, South of France). In this locality is exposed the "Molasse calcaire et sablo-marneuse" Formation (Fig. 1). This formation crops out in several other areas of the Rhodanian region (Ménerbes, Lacoste, Bonnieux,

Apt, Saignon, St-Martin-de-Castillon, Viens, Case-neuve, Reillanne, Montjustin, Vachères, Manosque) (SIG service of Parc naturel régional du Luberon); it is considered a local variation of the "Marnes bleues" Formation and is referable to the late Burdigalian (early Miocene) and to an age interval between 16.5 and 17.5 Ma (Wallez *et al.* 1986: tab. 2).

The "Marnes bleues" Formation and its local variations are interpreted as poorly consolidated shallow-marine deposits influenced by calcareous paleoreliefs of a subtropical marine environment with normal salinity and temperature, like those of the present-day South Mediterranean Sea (Pouyet *et al.* 1984). These conditions agree with the typical natural habitats of sirenians.

SYSTEMATIC PALEONTOLOGY

- Class MAMMALIA Linnaeus, 1758
 Order SIRENIA Illiger, 1811
 Family DUGONGIDAE Gray, 1821
 Subfamily HALITHERIINAE Abel, 1913
 Genus *Metaxytherium* de Christol, 1840

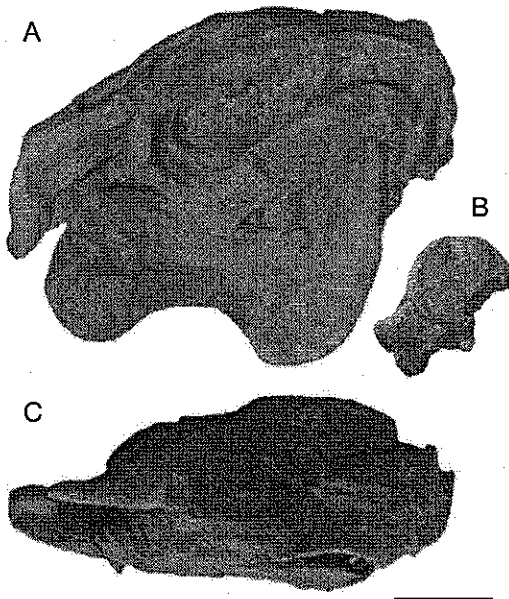


FIG. 2. — Skull of *Metaxytherium* cf. *krahuletzki* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France): A, left lateral view; B, posterior view; C, dorsal view. Scale bar: 10 cm.

Metaxytherium cf. *krahuletzki* Depéret, 1895
(Figs 2-5; Tables 1-4)

SYNONYMY. — See Domning & Pervesler 2001: 17.

REFERRED NEW SPECIMEN. — One additional specimen: MPNRL-MAN2000 skull, thoracic vertebrae and ribs.

LOCALITY. — La Rochette, Manosque (Provence, France).

AGE AND STRATIGRAPHIC OCCURRENCE. — Early Miocene, late Burdigalian, 16.5-17.5 Ma. "Molasse calcaire et sablo-marneuse" Formation.

DESCRIPTION

Preservation state

The cranium and the mandible are in anatomic connection, so the ventral side of the cranium and the dorsal side of the mandible are not visible. They are deformed, mediolaterally flattened with the right side still partially embedded in the molasse, and the posterior portion incomplete (lacking the right exoccipital and the basioccipital).

The rib cage is also embedded in the hard sandstone matrix; the left ribs are more or less in anatomic position, the right ones are posteriorly inclined, the vertebrae are crushed, lying on the right side, but more or less in anatomic connection.

The exoccipital-supraoccipital and the inter-premaxillary sutures completely fused, and the M_3 is completely erupted, which indicates that the specimen was an adult.

The state of preservation and the incomplete preparation do not permit scoring of all the morphological characters used by Domning (1994) and Bajpai & Domning (1997). However, the features visible include those most critical for taxonomic determination in this case; the difficulty in making a specific identification does not result from incomplete preparation.

Premaxilla

The rostrum is incomplete and compressed, but long enough to be supposed enlarged relative to the cranium [c. 3(1?)]. Only the dorsal portion is preserved, but the dorsal keel is damaged so that the dorsal surface of the premaxillary symphysis appears to be concave. The posterior end of the rostrum seems to be upraised to form a slight boss in lateral view [c. 10(1?)]. The lateral edges are thin, not flaring. The tusks and the alveoli are not preserved, but, judging from the development of the rostrum, they were probably small, extending less than half the length of the symphysis [c. 140(0)].

The nasal process is long [c. 7(0)] and thin at its posterior end [c. 6(0)]. It contacts the frontal [c. 9(1)], the lacrimal, and abuts against the nasal, but the sutures with these bones are unclear. The premaxillary-maxillary suture is partially visible and its anterior end is estimated to be about 5 mm posterior to the dorsal tip of the symphysis. The contact with frontal and lacrimal appears to be about 86 mm long.

The mesorostral fossa is long and narrow and the external nares appear to be retracted and enlarged beyond the level of the anterior margin of the orbit [c. 8(1)], but these characters could be accentuated by compression and deformation. A nasal incisure at posterior end of mesorostral fossa is absent [c. 37(0)]. The rostral deflection is uncertain; probably c. 60°.

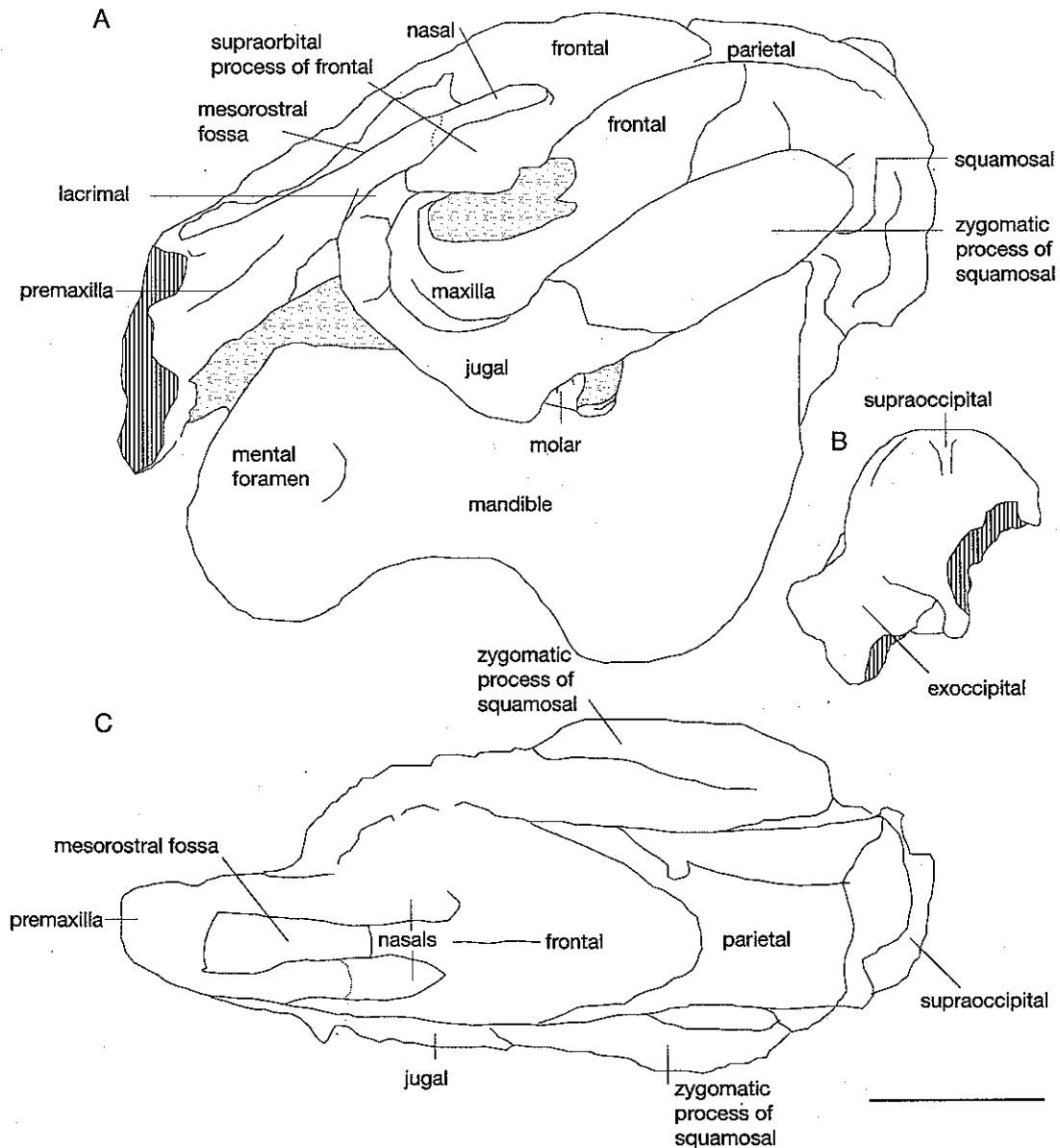


FIG. 3. — Line drawings of the skull of *Metaxytherium* cf. *krauletzki* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France): A, left lateral view; B, posterior view; C, dorsal view. Scale bar: 10 cm.

Nasal

The nasal region is abraded and incomplete, so the dorsal exposure of the nasal cannot be clearly delineated, but processes of the frontals seem to separate the nasals in the midline [c. 31(1?)].

Lacrimal

The lacrimal is about 5 cm long and has a prominent ridge, 3 cm long, on its lower lateral surface. It abuts posterodorsally against the supraorbital process of the frontal and is anteromedially in contact with

TABLE 1. — Measurements (in mm) of the cranium of *Metaxytherium* cf. *krahuletzii* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France). Abbreviation: e, estimated.

Condylbasal length	460e
Height of jugal below orbit	56
Length of premaxillary symphysis	165e
Rear of occipital condyles to anterior end of interfrontal suture	284
Top of supraoccipital to ventral sides of occipital condyles	151
Length of frontals, level of tips of supraorbital processes to frontoparietal suture	187
Breadth across supraorbital processes	72 × 2e
Breadth of cranium at frontoparietal suture	88
Length of mesorostral fossa	110e
Maximum height of rostrum	58e
Length of zygomatic process of squamosal	160
Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen	174
Length of parietals, frontoparietal suture to rear of external occipital protuberance	74
Height of posterior part of cranial portion of squamosal	118
Dorsoventral breadth of zygomatic process	59
Length of jugal	170e
Length of frontals in midline	133e
Height of supraoccipital	76e
Width of supraoccipital	46 × 2e
Deflection of masticating surface of rostrum from occlusal plane (degrees)	60°
Parietal-supraoccipital angle (degrees)	125°

the jugal. The contact with the maxilla is unclear. A nasolacrimal canal is absent [c. 91(1)].

Frontal

The supraorbital process is well developed, about 2 cm thick dorsoventrally with a long, acute anterior point and a small posterolateral corner [c. 36(1)], flattened in the horizontal plane, with a dorsal surface inclined relatively gently ventrolaterad [c. 43(0)]; not divided by deep dorsoventral grooves indenting its lateral margin [c. 44(0)]. A large orbicular apophysis is present on each side. The lateral crests are not significantly overhanging. The medial wall of the temporal fossa is formed by a thin lamina orbitalis of the frontal [c. 38(0)] and the crista orbitotemporalis is present. The median portion of the frontal roof is convex [c. 42(0)] with a low longitudinal crest. The anterior portion is not well preserved and the contacts with nasal and premaxilla are not visible. The interfrontal sutural surface is fused.

Parietal

The parietal is 74 mm long in the midline and 119 mm long laterally. The interparietal suture is fused. The fronto-parietal suture is concave in

shape. The frontal process of the parietal is about 65 mm long. The posterolateral corners of the roof are indented by the squamosals. The roof is nearly rectangular, posteriorly flat and anteriorly slightly concave. The temporal crests are lyriiform, low, broad, confined to the lateral edges; minimum external distance between crests 74 mm, minimum internal distance 37 mm (Type B of Domning 1988). A median bump is present just in front of the external occipital protuberance.

Supraoccipital

The right ventral portion of the supraoccipital is lacking. The supraoccipital is hexagonal in outline with rounded dorsolateral corners; it forms an angle of 125° with the posterior part of the parietals. The parietal-supraoccipital suture is fused. The external occipital protuberance is very large and thick anteroposteriorly; it rises above the plane of the parietal roof, and the median ridge below it is present but short, the nuchal crest is distinct at its lateral ends near the squamosals, and the lateral border is thick, rounded and not overhanging. The areas of insertion for semispinalis capitis muscles are flattish, face posterodorsad, and extend about

TABLE 2. — Measurements (in mm) of the mandible of *Metaxytherium* cf. *krahuletzii* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France). Abbreviation: e, estimated.

Total length	302
Anterior tip to front of ascending ramus	207
Anterior tip to rear of mental foramen	83
Length of symphysis	106e
Posterior extremity to front of ascending ramus	103
Distance between anterior and posterior ventral extremities	183
Height at condyle	226
Height at deflection point of horizontal ramus	133
Deflection point to rear of alveolar row	78e
Minimum anteroposterior breadth of ascending ramus	95
Front of ascending ramus to rear of mental foramen	131
Top of ventral curvature of horizontal ramus to line connecting ventral extremities	48
Minimum dorsoventral breadth of horizontal ramus	82
Length of alveolar row	60e
Deflection of symphyseal surface from occlusal plane (degrees)	64°
M ₃	
Crown height	15
Crown length	19

TABLE 3. — Measurements (in mm) of the thoracic vertebrae of *Metaxytherium* cf. *krahuletzii* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France). Abbreviations: e, estimated; T, thoracic vertebrae.

	Ta	Tb	Tc	Td	Te	Tf	Tg	Th	Ti	Tj	Tk	Tl	Tm
Height of neural spine	105e	100e	95	90	85	85	80e	76e	89e	84			
Length of neural spine at apex		50e	40	58	52	63	55	59	61	60	46		
Length of transverse process at the base	40e					85	86					79	

TABLE 4. — Measurements (in mm) of the ribs of *Metaxytherium* cf. *krahuletzii* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France). Abbreviation: R, ribs.

	Ra	Rb	Rc	Rd	Re	Rf	Rg	Rh	Ri	R1j	Rk	Rl
Left side												
Length in straight line	365	420	480	525	580	605	>330	>245	>180	>175		
Mid-shaft maximum diameter	56	58	60	58	50	52	53	52	52	53		
Right side												
Length in straight line					>191	>164	>84		>420	>250	>182	>81
Mid-shaft maximum diameter					51	53	52		55	54	54	54

halfway to the ventral end of the bone. The lower part of the supraoccipital is convex laterally below the semispinalis insertions. The sutural surfaces for the exoccipitals are not distinct. The ratio of width to height is *c.* 1.21.

Exoccipitals

Only the dorsal portion on the left side of exoccipital is preserved. The bone appears to be fused with the supraoccipital. The dorsolateral border is

rounded, smooth and not flange-like [*c.* 70(0)]. The supracondylar fossa is deep and extends across the entire width of the occipital condyle [*c.* 67(2)].

Maxilla

Only a small dorsal portion of maxilla is visible laterally. The ventral side and the zygomatic-orbital bridge are concealed by matrix. The infraorbital foramen is not visible in anterior view because of the compression.

Squamosal

The squamosal is dorsally in contact with the squared posterior part of the parietal roof [c. 76(1)]. The sigmoid ridge is prominent [c. 74(0)], dorsally slightly sharp and ventrally more rounded. The surface of the cranial portion dorsal to the zygomatic root is nearly flat. The postglenoid process and the postarticular fossa are distinct and well developed. The processus retroversus is present, moderately inflected [c. 77(1)], and does not project below the line of the suture with the jugal; its posterior end is incomplete, but distinct dorsal and ventral protuberances are present. The temporal condyle is not visible. The zygomatic process is 160 mm long, narrow throughout its length [new character]. The posterodorsal edge of the process is almost straight (slightly concave) in outline and convex laterad. The external auditory meatus is partly obscured, but seems to be about as wide anteroposteriorly as high [c. 82(1?)].

Jugal

The preorbital process is relatively flat and thin [c. 88(0)], but with a protuberance on the posterior side. It presumably does not contact the premaxilla [c. 87(0?)]. The ventralmost point of the jugal lies clearly under the orbit itself [c. 85(2)], as mentioned by Domning & Pervesler (2001: 43). The ventral tip is thick and rounded; the border behind is smooth. The ventral margin of the orbit is concave, smooth, large but not overhanging [c. 90(0)]. There is a raised postorbital process against which the squamosal abuts. The posterior process is incomplete, but seems to be as long as the diameter of the orbit [c. 89(0?)], tapering rapidly in outline with a longitudinal low sulcus on the lateral side.

Mandible

Left and right dentaries are preserved, but they are mediolaterally flattened. The left is exposed, but the right is enclosed in the matrix. The mandible is in anatomic position and the dorsal extremity of the ascending ramus is therefore covered by the zygomatic arch. The condyle, partially exposed, is elliptic and laterally overhanging. The mandibular notch and coronoid process are not exposed. The base of the anterior border of the coronoid process is exposed and extends slightly anterior to the base

of the process [c. 126(1)]. The posterior border is thick and rounded. It has no distinct processus angularis superior, but has a broadly convex outline beginning well below the condyle [c. 125(2)]. Lateral to M_3 there is a shelf that slopes steeply. The horizontal ramus is deep and short [c. 128(1)], with a strongly concave ventral border [c. 122(3)] that is not tangent to the mandibular angle [c. 129(1)]. The ventral border is thickened and rounded anteriorly, tapering posteriorly. Only one large mental foramen is present [c. 123(1)], and it lies at the level of deflection of the dorsal edge of the ramus. The deflection of the masticating surface is abrupt, about 64° (60° according to Domning & Pervesler 2001: 44). The masticating surface is incomplete and mediolaterally compressed. The lateral edge is thin and overhanging. The posteroventral side of the symphysis is concave and the anteroventral side is convex transversely. The symphyseal suture is not well preserved, but appears to be fused. The labial side of M_3 is visible. The distance between M_3 and the coronoid process is about 25 mm.

Vertebrae

The cervical and the most anterior vertebrae are missing. Twelve thoracic vertebrae and a very small fragment representing a thirteenth thoracic vertebra are preserved in anatomic sequence (Ta-m). They are crushed, fragmented and lying on the right side. The centra seem to be collapsed and only the left sides of the neural spines and the left transverse processes are exposed. The neural spines are better preserved than the transverse processes. The first vertebrae are partially overlapping. The overlapping diminishes from the first to the seventh vertebra and the following vertebrae are in anatomic position.

The neural spines are laterally flattened with a slight backward slope. Their full height is around 100 mm. The posterior side of each spine has a rounded protuberance; posteriorly this protuberance gradually becomes confined to the lower part of each spine. The posterolateral edge of each spine is notched just above the postzygapophysis, the notch seems to become less developed from the eighth vertebra. The summit of each spine is expanded (mediolateral width about 20-25 mm; anteroposterior width around 60 mm), flattened,

with anterior and posterior corners rounded. The transverse processes are massive and thick. Their mediolateral length is about 25 mm, anteroposterior length about 42 mm, and dorsoventral thickness about 10 mm. They are deformed, but seem to be horizontal and anterior to their neural spines. The zygapophyseal articular planes are nearly horizontal on anterior vertebrae and seem to slope inward beginning with the seventh vertebra.

Ribs

Ten ribs in anatomic sequence (Ra-j) and a small fragment (R?) are preserved on the left side; seven ribs posteriorly inclined are preserved on the right side (Re-j; Ri-l). Their contacts with the vertebrae are not visible. The ribs are massive and thick, smooth with a low ridge (iliocostalis tendon insertion) on the posterior edge; this ridge becomes longer on the posterior ribs. The shafts are elliptical in cross section and maintain their diameters for most of their length. The distal ends are flattened, swept back, and taper in the last 10-20 cm.

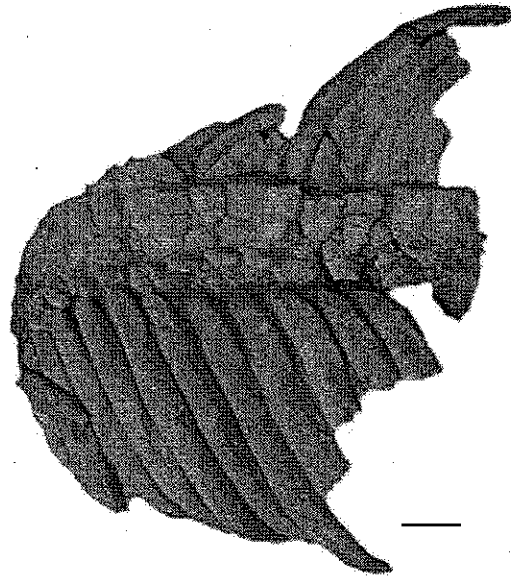


FIG. 4. — Ribs and thoracic vertebrae of *Metaxytherium* cf. *krahuletzii* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France) in dorsal view. Scale bar: 10 cm.

COMPARISONS

The sirenian specimen here described (MPNRL-MAN2000) comes from the upper Burdigalian of Manosque (Provence, France); therefore the most critical species for comparison are the other Euro-North African upper Oligocene to middle Miocene sirenian species: the trichechids *Anomotherium langewieschei* Siegfried, 1965 from the upper Chattian of Germany (Siegfried 1965) and *Miosiren* spp. from the lower Miocene of Belgium and England (Dollo 1889; Sickenberg 1934); the dugongines "*Halitherium*" *bellunense* Zigno, 1875 from the Chattian (pers. obs.) of North Italy (Zigno 1875; Dugonginae incertae sedis Domning 1996 and pers. obs.) and *Rytiodus* spp. from the lower Miocene of France and Libya (Lartet 1866; Heal 1973); and the halitheriine nominal species: *Halitherium christolii* Fitzinger, 1842 from the Chattian of Germany and Austria (Fitzinger 1842), *Metaxytherium krahuletzii* from the Burdigalian of Europe (Domning & Perverler 2001), *M. aquitaniae* Pilleri, 1987 from the Aquitanian of northern France (Pilleri 1987),

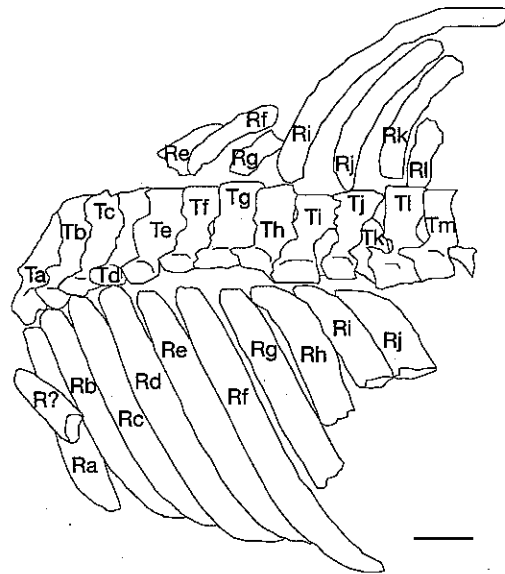


FIG. 5. — Line drawings of the ribs and the thoracic vertebrae of *Metaxytherium* cf. *krahuletzii* Depéret, 1895 (MPNRL-MAN2000) from Manosque (Provence, France). Abbreviations: R, ribs; T, thoracic vertebrae. Scale bar: 10 cm.

M. catalaunicum Pilleri, Biosca & Via, 1989 from the late lower Miocene of Spain (Pilleri *et al.* 1989), *Metaxytherium petersi* Abel, 1904 from the middle Miocene of Austria (Sickenberg 1928; Domning pers. comm.), and *M. medium* from the middle to upper Miocene of Europe (e.g., Cottreau 1928; Moncharmont Zei & Moncharmont 1987; Bianucci & Landini 2003).

MPNRL-MAN2000 differs from the Trichechidae in having a large estimated rostral deflection (about 60° for the premaxilla and 64° for the mandible); an enlarged rostrum [c. 3(1)]; a squamosal with a processus retroversus [c. 77(1)]; a supposed deeply rounded external auditory meatus [c. 82(1?)] and a mandible with a deep and short horizontal ramus [c. 128(1)] and a strongly concave ventral border [c. 122(3)]. Moreover it differs from *Anomotherium langewieschei* and *Miosiren* spp. in having a thin lamina orbitalis of the frontal [c. 38(0)] and processes of the frontals which seem to separate the nasals in the midline [c. 31(1?)] and it particularly differs from *Miosiren* spp. in having supposed small I¹ alveoli [c. 140(0?)].

MPNRL-MAN2000 differs from the Dugonginae in having the supraorbital process of the frontal flattened in the horizontal plane, with a dorsal surface inclined relatively gently ventrolaterad [c. 43(0)], the preorbital process of the jugal relatively flat and thin [c. 88(0)], and the ventral margin of the orbit not overhanging [c. 90(0)].

Moreover it differs from "*Halitherium*" *bellunense* and *Rytiodus* spp. in having the nasal process of the premaxilla thin at its posterior end [c. 6(0)] and a long nasal process of the premaxilla [c. 7(0)]. In particular it differs from *Rytiodus* spp. in having supposed small I¹ alveoli [c. 140(0?)], and a convex median portion of the frontal roof [c. 42(0)]; and from "*Halitherium*" *bellunense* in having a squamosal extending to the temporal crest [c. 76(1)].

All the morphological characters identified for MPNRL-MAN2000 are consistent with the Halitheriinae species.

MPNRL-MAN2000 differs from *Halitherium christolii* in having the supraorbital process of the frontal dorsoventrally thickened with a posterolateral corner [c. 36(1)]. This character is scored as derived in all the Old World Neogene Halitheriinae

(Domning 1994: tab. 1), therefore MPNRL-MAN2000 appears to be closer to the Old World Neogene Halitheriinae. Among them *M. aquitaniae* is represented only by a few fragmentary specimens; its status and affinities are considered uncertain by Domning (1996) and it is probably a synonym of *M. krabuletzki* (pers. obs.); *M. catalaunicum* is considered a synonym of *M. medium* by Domning 1996, but it could also be referred to *M. krabuletzki* (pers. obs.); and *M. petersi* is considered a species having evolved in isolation in the Carpathian Basin (Domning pers. comm.).

Therefore the only Old World early to middle Miocene halitheriine species recognized and widespread are *M. krabuletzki* and *M. medium*. Domning & Pervesler (2001) pointed out the difficulty for separating *M. krabuletzki* and *M. medium* and this situation makes a specific attribution of MPNRL-MAN2000 difficult.

MPNRL-MAN2000 appears to be primitive among the *Metaxytherium* species in retaining the following characters: nasal incisure at posterior end of mesorostral fossa absent [c. 37(0)] and zygomatic process of squamosal narrow throughout its length [new character].

Character 37 is scored as primitive in *M. krabuletzki* and in *M. catalaunicum*, while in *M. medium* and *M. floridanum* a nasal incisure at posterior end of mesorostral fossa is usually present [c. 37(1)] and it separates the nasals.

The zygomatic process is narrow throughout its length in most *M. krabuletzki* specimens (Domning & Pervesler 2001: 22) and in MV 1210; while it is narrow throughout its length or lozenge-shaped, broader posteriorly than anteriorly in *M. floridanum* (Domning 1988), and lozenge-shaped in *M. medium*, *M. serresii*, and *M. subapenninum* (pers. obs.).

On the other hand MPNRL-MAN2000 has a dorsoventrally broad horizontal ramus of the mandible, with a ratio of minimum height of horizontal ramus (MO) to total length of mandible (AB) of 0.27, and with a mandibular deflection of about 64°.

The MO/AB ratio appears to be higher than the typical ratio in *M. krabuletzki* mandibles graphed by Domning & Pervesler (2001: fig. 10). The mandibular deflection also appears to be greater than those observed in *M. krabuletzki* (53–63°, after

Domning & Pervesler 2001). In *M. catalaunicum* it is about 66°, in the *M. medium* specimen MPUN 18403 it is about 65° and in the *M. medium* specimen MNHN 1921-10 it seems to be 75°, but the anterior end is damaged and this renders the datum questionable.

DISCUSSION AND CONCLUSIONS

The description and comparison of this new *Metaxytherium* specimen (MPNRL-MAN2000) do not permit a certain specific attribution, since all the systematic characters identified for MPNRL-MAN2000 are consistent with both the early and middle Miocene Old World *Metaxytherium* species.

This fact confirms the difficulty of separation between *M. krahuletzki* and *M. medium* documented by Domning & Pervesler (2001). These authors showed that the available sample of *M. medium* is too poor to permit this species to be distinguished unambiguously from *M. krahuletzki*, but they maintained the established usage of recognizing both nominal species as valid. This difficulty of separation reflects the fact that, alone among all known sirenians, the Miocene species of *Metaxytherium* in both Europe and eastern North America display a near morphological stasis over a period or more than 10 million years (Domning & Pervesler 2001).

Chronostratigraphically, MPNRL-MAN2000 is late Burdigalian in age (16.5-17.5 Ma), so it appears to be slightly younger than *M. krahuletzki* (early to middle Burdigalian), but older than *M. medium* (Langhian to Tortonian).

In conclusion, I refer MPNRL-MAN2000 to *M. cf. krahuletzki*. MPNRL-MAN2000 could represent a late form of *M. krahuletzki* with a slightly greater mandibular deflection and a slightly greater ratio of minimum height of horizontal ramus (MO) to total length of mandible (AB).

Moreover, the late Burdigalian age of MPNRL-MAN2000 gives new information about the continuity of the *Metaxytherium* record in the Old World during the early to middle Miocene, since this specimen is slightly younger than *M. krahuletzki* (early to middle Burdigalian), but older than *M. medium* (Langhian to Tortonian).

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REFERENCES

- ARANDA-MANTECA F. J., DOMNING D. P. & BARNES L. G. 1994. — A new middle Miocene sirenian of the genus *Metaxytherium* from Baja California and California: relationships and paleobiogeographic implications, in BERTA A. & DEMÉRE T. A. (eds), Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr. *Proceedings of the San Diego Society of Natural History* 29: 191-204.
- BAJPAI S. & DOMNING D. P. 1997. — A new dugongine sirenian from the early Miocene of India. *Journal of Vertebrate Paleontology* 17 (1): 219-228.
- BIANUCCI G. & LANDINI W. 2003. — *Metaxytherium medium* (Mammalia: Sirenia) from upper Miocene sediments of the Arenaria di Ponsano Formation (Tuscany, Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 109 (3): 567-573.
- BIANUCCI G., CARONE G., DOMNING D. P., LANDINI W. & ROOK L. 2004. — Peri-Messinian dwarfing in Mediterranean *Metaxytherium* (Mammalia: Sirenia): evidence of habitat degradation related to Mediterranean desiccation. *Abstracts, Third Symposium on Geology of East Libya*, Benghazi, Nov. 21-23: 21.
- BLAINVILLE H. M. D. DE 1844. — Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie, in BERTRAND A. (ed.), *Des lamantins (Buffon), (Manatus, Scopoli), ou gravigrades aquatiques*. J. B. Baillièrre & Fils, Paris, 140 p.
- CARONE G. & DOMNING D. P. 2007. — *Metaxytherium serresii* (Mammalia: Sirenia): new pre-Pliocene record, and implications for Mediterranean paleoecology before and after the Messinian Salinity Crisis. *Bollettino della Società Paleontologica Italiana* 46 (1): 55-92.
- COTTREAU J. 1928. — Le *Metaxytherium cuvieri* du Golfe

- de la Loire. *Annales de Paléontologie* 17: 1-20.
- DEPÉRET C. & ROMAN F. 1920. — *Felsinotherium serresi* des sables Pliocènes de Montpellier et les rameaux phylétiques des Siréniens fossiles de l'Ancien Monde. *Archives du Musée d'Histoire naturelle de Lyon* 12: 1-56.
- DOLLO L. 1889. — Première note sur les siréniens de Boom (résumé). *Société belge de Géologie, Paléontologie et Hydrologie* 3: 415-421.
- DOMNING D. P. 1988. — Fossil Sirenia of the West Atlantic and Caribbean region. I — *Metaxytherium floridanum* Hay, 1922. *Journal of Vertebrate Paleontology* 8 (4): 395-426.
- DOMNING D. P. 1994. — A phylogenetic analysis of the Sirenia, in BERTA A. & DEMÉRE T. A. (eds), Contributions in marine mammal Paleontology honoring Frank C. Whitmore, Jr. *Proceedings of the San Diego Society of Natural History* 29: 177-189.
- DOMNING D. P. 1996. — Bibliography and index of the Sirenia and Desmostylia. *Smithsonian Contributions to Paleobiology* 80: 1-611.
- DOMNING D. P. & THOMAS H. 1987. — *Metaxytherium serresii* (Mammalia: Sirenia) from the Early Pliocene of Libya and France: a reevaluation of its morphology, phyletic position, and biostratigraphic and paleoecological significance, in BOAZ H., EL-ARNAUTI A., GAZIRY A. W., HEINZELIN J. DE & BOAZ D. (eds), *Neogene Paleontology and Geology of Sababi*. Alan R. Liss, New York: 205-232.
- DOMNING D. P. & PERVESLER P. 2001. — The osteology and relationships of *Metaxytherium krahuletzki* Depéret, 1895 (Mammalia: Sirenia). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 553: 1-89.
- ESTEVENS M. 2003a. — Mamíferos marinhos do Miocénico da península de Setúbal. *Ciências da Terra* esp-5: 60-63.
- ESTEVENS M. 2003b. — Mamíferos marinhos do Miocénico de Lisboa. *Ciências da Terra* esp-5: 64-67.
- FITZINGER L. J. 1842. — Bericht über die in dem Sandlagern von Linz aufgefundenen fossilen Reste eines urweltlichen Säugers, (*Halitherium Christolii*). *Bericht Museum Franco-Carolinum*, Linz 6: 61-72.
- HEAL G. J. 1973. — *Contributions to the Study of Sirenian Evolution*. PhD thesis, University of Bristol, UK, 285 p.
- LARTET É. 1866. — Note sur deux nouveaux siréniens fossiles des terrains tertiaires du bassin de la Garonne. *Bulletin de la Société géologique de France* 23 (2): 673-686.
- MONCHARMONT ZEI M. & MONCHARMONT U. 1987. — Il *Metaxytherium medium* (Desmarest) 1822 (Sirenia, Mammalia) delle arenarie tortoniane (Miocene sup.) di S. Domenica di Ricadi (Catanzaro, Italia). *Memorie di Scienze Geologiche* 39: 285-341.
- MUIZON C. DE & DOMNING D. P. 1985. — The first records of fossil sirenians in the southeastern Pacific Ocean. *Bulletin du Muséum national d'Histoire naturelle*, section C, 7 (3): 189-213.
- PIA J. VON & SICKENBERG O. 1934. — Katalog der in den österreichischen Sammlungen befindlichen Säugetierreste des Jungtertiärs Österreichs und der Randgebiete. *Denkschriften Naturhistorisches Museum Wien, Geologische-Paléontologische Reihe* 4: 1-544.
- PILLERI G. 1987. — *The Sirenia of the Swiss Molasse with a Descriptive Catalogue of the Fossil Sirenia Preserved in Swiss collections*. Brain Anatomy Institute, Ostermundigen, 114 p.
- PILLERI G. 1988. — The Pliocene Sirenia of the Po Basin (*Metaxytherium subapenninum* (Bruno) 1839), in PILLERI G. (ed.), *Contributions to the Paleontology of some Tethyan Cetacea and Sirenia (Mammalia)*. Brain Anatomy Institute, Ostermundigen: 45-103.
- PILLERI G., BIOSCA J. & VIA L. 1989. — *The Tertiary Sirenia of Catalonia*. Brain Anatomy Institute, Ostermundigen, 98 p.
- POUYET S., DAVID L., DEMARCO G., LATREILLE G., CARBONNEL G., PRIEUR A., PHILIPPE M., LAURAIN M., PAJAUD D., CAPPETTA H., BARBILLAT R. & CHEVALIER J.-P. 1984. — Le faciès « Marnes bleues » du Burdigalien du bassin de Faucon-Mollans-Malauçène (Sud-Est de la France): essai de synthèse paléocécologique et paléogéographique. *Géologie de la France* 1-2: 123-130.
- SENDRA J., MONTOYA P. & BELINCHÓN M. 1999. — Un cráneo de sirenio en el Plioceno de Pilar de la Horadada (Alicante, España). *Temas Geológico-Mineros* 26: 350-355.
- SICKENBERG O. 1928. — Eine Sirene aus dem Leithakalk des Burgenlandes. *Denkschriften der Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftliche Klasse* 101: 293-323.
- SICKENBERG O. 1934. — Beiträge zur Kenntnis tertiärer Sirenen. *Mémoires du Musée royal d'Histoire naturelle de Belgique* 63: 1-352.
- SIEGFRIED P. 1965. — *Anomotherium langewieschei* n. g. n. sp. (Sirenia) aus dem Ober-Oligozän des Dobergs bei Bünde (Westfalen). *Palaeontographica* A 124: 116-150.
- TOLEDO P. M. DE & DOMNING D. P. 1991. — Fossil Sirenia (Mammalia: Dugongidae) from the Pirabas Formation (Early Miocene), northern Brazil. *Boletim do Museu Paraense Emílio Goeldi, Série Ciências da Terra* 1 (2): 119-146.
- WALLEZ M.-J., MAGNE J., GOURINARD Y. & DEMARCO G. 1986. — Nouvelles grade-datations de sédiments burdigaliens des régions rhodaniennes. *Géologie méditerranéenne* 12-13 (1-2): 59-63.
- ZIGNO A. DE 1875. — Sireni fossili trovati nel Veneto. *Memorie Istituto Veneto di Scienze, Lettere ed Arti* 18 (3): 427-456.

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