FOSSIL SIRENIA OF THE WEST ATLANTIC AND CARIBBEAN REGION. IX.

METAXYTHERIUM ALBIFONTANUM, SP. NOV.

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ABSTRACT—We describe a new species of the halitherine dugongid genus Metaxytherium from the late Oligocene of Florida and South Carolina. The new species is represented by cranial and postcranial material, including parts of the axial and appendicular skeleton. Metaxytherium albifontanum, sp. nov., differs from other species of Metaxytherium by the following unique combination of plesiomorphic and derived characters: posterior end of nasal process of premaxilla broad and flat relative to what is observed in most other members of the genus (somewhat resembling M. subapenninum); ventral extremity of jugal under posterior edge of orbit (character 85[1]) (shared with M. krahuletzi); exoccipitals separated in dorsal midline (character 66[1]) (shared with all other species in the genus, except some M. krahuletzi); and innominate with acetabulum (nearly lost or lost in M. crataegense, M. floridanum, M. serresii). This new species was sympatric with two dugongines, Crenatosiren olseni and Dioplotherium manigaulti. The small tusks and cranial morphology of M. albifontanum, sp. nov., indicate that it was likely a consumer of small seagrasses. Our phylogenetic analysis is consistent with previous ones in placing Hydrodamalinae within a paraphyletic Metaxytherium spp. and placing the Metaxytherium spp. + Hydrodamalinae clade as the sister group to Dugonginae. Metaxytherium albifontanum, sp. nov., is the oldest known member of its genus; this might indicate that the group originated in the West Atlantic and Caribbean region and later dispersed to the Old World Tethys region.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

INTRODUCTION

Dugongid sirenians of the genus Metaxytherium are commonly found in Neogene shallow marine deposits in the western Atlantic, Caribbean, eastern Pacific, and Mediterranean regions (Domning, 1996; 2010, and references therein). The geochronologically oldest and most plesiomorphic species currently referred to this genus is Metaxytherium krahuletzi Depéret, 1895, from the early Miocene of the north Tethys and western and central Paratethys regions (Domning, 1994; Domning and Pervesler, 2001; Sorbi, 2008). This has led authors to the conclusion that the genus originated in the Tethys region (Domning and Pervesler, 2001; Sorbi, 2008). The subsequent appearance of members of this genus in the late early Miocene of the Americas (Simpson, 1932; Kellogg, 1966; Varona, 1972; Muizon and Domning, 1985; Toledo and Domning, 1991) has seemed to support this view as well as call for an east-west trans-Atlantic dispersal of the group (Domning, 1988).

New material from the Oligocene of the West Atlantic and Caribbean region challenges these ideas. It is the aim of this paper to describe some of this material, which represents a new species of Metaxytherium from the late Oligocene of the east coast of North America. The material described includes well-preserved cranial and postcranial material. This new species was sympatric, at least in part of its range, with two other dugongids, Crenatosiren olseni (Reinhart, 1976) and Dioplotherium manigaulti Cope, 1883 (Domning, 1989a, 1989b, 1997; Velez-Juarbe et al., 2012).

Abbreviations—c., character state as described and numbered by Domning (1994), Bajpai and Domning (1997), Domning and Aguilera (2008), Bajpai et al. (2010), and/or Velez-Juarbe et al. (2012); e.g., (c. 6[0]) refers to state 0 of character 6; ChM PV, Charleston Museum, Charleston, South Carolina; M., muscle; SC, South Carolina State Museum, Columbia, South Carolina; UF, Florida Museum of Natural History, University of Florida, Gainesville, Florida; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order SIRENIA Illiger, 1811
Family DUGONGIDAE Gray, 1821
Subfamily HALITHERINI (Carus, 1868) Abel, 1913
METAXYTHERIUM Christol, 1840

Metaxytherium Christol, 1840:323, September 24, 1840.

Hesperosiren Simpson, 1932:426, September 6, 1932.

For additional synonyms based on Old World material, see Domning, 1996, 2010.

Type—Metaxytherium medium (Desmarest, 1822).

Included Species—Metaxytherium arctodites Aranda-Manteca, Domning, and Barnes, 1994; Metaxytherium crataegense (Simpson, 1932) Aranda-Manteca, Domning, and Barnes, 1994; Metaxytherium floridanum Hay, 1922; Metaxytherium krahuletzi Depéret, 1895; Metaxytherium medium (Desmarest, 1822) Hoogerwerf, 1952; Metaxytherium serresii (Gervais, 1847) Depéret, 1895; Metaxytherium subapenninum (Bruno, 1839) Fondi and Pacini, 1974; Metaxytherium albifontanum Vélez-Juarbe and Domning, sp. nov.
Range—Late Oligocene, southeastern United States; early-middle Miocene, Europe, North Africa, North and South America, and Caribbean; Pleistocene, Europe and North Africa.

**Emended Diagnosis**—Dugongidae based on loss of alisphe-noid canal (c. 101[1]), loss of permanent premaxilar 5 (c. 146[1]), squamosal reaching temporal crest (c. 76[1]), and open foramen ovale (c. 103[1]). ‘Halitheriinae’ based on retention of the following plesiomorphies: nasal process of premaxilla thin and tapering (c. 6[0]); tusks small (c. 140[0]); frontal skull roof convex to flat (c. 42[0]); and nasal incisure at posterior end of mesorostral fossa small or absent (c. 37[0]).

**Etymology**—Latin *albi* = white + *fontanus* = of a spring, in reference to the type locality near White Springs, Florida.

**Description**

**Skull**

Description of the skull is based on the holotype (UF 49051) (Figs. 1–5, 7; Table 1), which is a subadult individual (based on recently erupted M3 and unfused basioccipital/basisphenoid suture).

**Premaxilla**—An alveolus for a mediolaterally compressed tusk, about 20 × 8 mm in diameter, extends much less than half the length of the symphyseal part of each premaxilla (c. 140[0]).

**TABLE 1. Measurement of skulls (in mm) of *Metaxytherium albifontanum* sp. nov., following Domning (1978).**

| Dimension          | UF 49051 |
|--------------------|----------|
| AB                 | 374e     |
| AH                 | 39       |
| BI                 | 230e     |
| CC'                | 179e     |
| CC                  | 116      |
| CC'                 | 102      |
| F                  | 138      |
| FF'                | 115e     |
| ff'                | 84       |
| G                  | 39       |
| HI                 | 110e     |
| HI                  | 40       |
| JF                 | 48e      |
| KL                 | 59       |
| LFr                | 120e     |
| MM'                | 64       |
| no                 |         |
| OP                 | 120      |
| OT                 |         |
| P                  | 75       |
| pq                 | 85       |
| QR                 | 54e      |
| rr'                | 55       |
| rr'                 | 67c      |
| ST                 |         |
| ss'                |         |
| T                  |         |
| WX                 | 39       |
| YZ                 | 152      |
| HSo                | 52       |
| WSo                | 75       |
| RD                 | 60e      |

**Abbreviations:** e = estimate; l = left; r = right; + = measurement on incomplete element.
Each alveolus creates a slight bulge in the lateral surface of the bone. The dorsal and palatal sides of the rostrum are parallel in lateral view except anteriorly, where the dorsal outline abruptly becomes concave and then again convex at the tip of the snout (Fig. 3). The dorsal surface of the symphysis is slightly convex posteriorly, broad and flat more anteriorly, and narrows forward to a keel less than 7 mm thick above the tusks (c. 10°). The incisive foramen lacks a well-defined anterior end. The masticating surface of the rostrum is trapezoidal in outline and deeply concave (Fig. 2). Fractures and displacement of the bones prevent exact measurement of the rostral deflection, but it was approximately 60°. The anterior part of the mesorostral fossa is minimally constricted by a pair of small (∼1 cm in length) bumps about 3 cm posterior to its front end. The nasal process of the premaxilla is mediolaterally broad and relatively flat posteriorly (Fig. 1), a condition similar to that in *Metaxytherium subapenninum* (Sorbi et al., 2012), but scored as (c. 6[0]) because it does not approach the more derived conditions observed in dugongines (e.g., *Diplopootherium manigaulti* [Domning, 1989]). The part of it in contact with the lacrimal, nasal, and frontal extends less than half the length of the mesorostral fossa.

**Nasal**—The nasals are reduced (c. 32[1]); their dorsal exposure is about 35 mm long and 20 mm wide, broad anteriorly and narrowing posteriorly (Fig. 1). The nasals are separated in the midline by thin processes of the frontals (c. 31[1]), and together with these processes they form a dorsally convex arch. Anterolaterally, the nasals are overlapped by the premaxillae.
FIGURE 2. Ventral view of the holotype skull of *Metaxytherium albifontanum*, sp. nov. (UF 49051). **Abbreviations:** as, alisphenoid; bo, basioccipital; bs, basisphenoid; dP, deciduous upper premolar; eo, exoccipital; fm, foramen magnum; hf, hypoglossal foramen/canal; if, incisive foramen; ioc, infraorbital canal; j, jugal; M, upper molars; mx, maxilla; oc, occipital condyle; pgp, postglenoid process; pl, palatine; pmx, premaxilla; pp, paroccipital process; pr, processus retroversus; pt, pterygoid; ptp, posttympanic process; sq, squamosal; tc, temporal condyle; zpj, zygomatic process of the jugal.

**Ethmoidal Region**—A large (of about the same height as the nasal cavity) ethmoturbinal forms a thick vertical plate on either side of the dorsal part of the nasal cavity. Its rugose anterior end is about 2 cm high and 4 mm thick, and curves backward and inward ventrally as if to form a short, blunt hook. The remainder of the nasal cavity is still filled with matrix.

**Vomer**—Forms a delicate ‘V’-shaped trough as in other sireni-ans, and extends forward to about the middle of the mesorostral fossa.
**Lacrimal**—A large (extending for more than half of the length of the anterior orbital margin), somewhat crescentic bone measuring 30 mm dorsoventrally and 15 mm anteroposteriorly; a nasolacrimal foramen is absent (c. 91[1]). It is in contact with the premaxilla anterodorsally (c. 93[1]), the maxilla anteriorly and medially, and the jugal anteroventrally (Figs. 1, 3). Its ventral end projects laterad as a low knob.

**Frontal**—The supraorbital process has a blunt, rounded anterior end, a poorly developed postero lateral corner (c. 36[1]), no division in its lateral margin (c. 44[0]), and no orbicular apophysis (Figs. 1, 3). Its dorsal surface slopes laterally rather steeply, and is separated from the nearly horizontal frontal roof by a low but distinct temporal crest that extends straight forward across the base of the supraorbital process. The edges of the frontal roof do not overhang. The central portion of the roof, including the internasal processes, is gently convex (c. 42[0]) without knob-like bosses (c. 45[0]). The anterior border between the nasals is thin and broken but seems to have extended nearly the full length of the nasals, the nasal incisure thus being small or absent (c. 37[0]). The anterior extremity of the frontoparietal suture lies about 6 cm abaft the nasals. The temporal wall of the frontal is recessed ventral to the crista orbitotemporalis, which is a smooth ridge, indistinct anteriorly, that extends posteroventrad from the supraorbital process. The lamina orbitalis of the frontal, which forms this recessed part of the wall, is thin (c. 38[0]) and extends forward as a thin (<1 cm) plate to a level about 2 cm abaft the postero- lateral corner of the supraorbital process; its anterior border is falciform.

**Parietal**—The cranial vault is nearly rectangular in frontal section anteriorly. The roof is 13 mm thick in the anterior midline, and nearly flat; no sagittal crest is present (c. 51[1]) (Fig. 1). The posterolateral corner of the roof is slightly indented by
the squamosal. The temporal crests are low, barely rising above the level of the roof and confined to its lateral edges (temporal crest type A [Domning, 1988]). Endocranially, the internal occipital protuberance is conical and extends well below the rest of the internal surface. The tentorium and transverse sulus are distinct, but the latter is shallow and lacks deep lateral pits. The anterior end of the bony falk is flattened and indistinct.

**Supraoccipital**—Forms an angle of 112° with the posterior part of the parietales. The external occipital protuberance does not project above the parietal roof, and the median ridge below it
is only moderately developed, reaching a thickness of only a few millimeters (Fig. 4). The M. semispinalis insertions extend about halfway to the bone’s ventral border. The nuchal crest is damaged. The bone has a uniformly wide outline, without overhanging dorsolateral corners (c. 64°).

Exoccipital—The exoccipitals are separated in the dorsal midline by about 7 mm (c. 66°) (careful examination of the type by both of us confirms that this region has been restored erroneously in the holotype, giving the false impression that they were joined); the foramen magnum has an acute dorsal peak and reaches the supraoccipital (Fig. 1). The dorsolateral border of the exoccipital is rounded and about 10 mm thick, without any posteriorly projecting flange (c. 70°). The supracondylar fossa is fairly deep and wide (c. 67°). The hypoglossal foramen is single and surrounded by bone (c. 72°) (Fig. 2). The occipital condyle extends below the paramastoid process; its articular surface subtends an arc of about 120°.

Basioccipital—Bears a pair of convex rugosities for the longus capitis muscles. It had not yet fused with the basisphenoid (Fig. 2).

Basisphenoid—The sella turcica is deeper than the surrounding dorsal surface of the bone, with a strong, posteriorly overhanging tuberculum sellae.

Presphenoid—No elevated shelf (orbitosphenoidal crest) overhangs the chiasmatic grooves, nor are distinct grooves present.

Orbitosphenoid—The optic foramen lies at the level of the dorsal side of the sphenoidal foramen.

Alisphenoid—The lateral side of the pterygoid process is ridged ventrally (Fig. 3). A smooth horizontal ridge continues
the forward edge of the zygomatic root anteriorly, overhanging the anterior opening of the sphenorbital foramen. No alisphenoid canal is present (c. 101[1]).

Pterygoid—The pterygoid fossa is deep and broad, extending above the roof of the internal naris (c. 102[1]); its lateral and medial edges converge dorsally and intersect at a small protuberance (Figs. 2, 3). The medial edge projects farther aft than the lateral edge. The ventromedial tip is formed by a thickened, smooth trochlea (hamulus) for the M. tensor veli palatini tendon.

Palatine—Forms the rounded anteromedial side and ventral tip of the pterygoid process. Dorsally it forms part of the lateral wall of the internal naris, and anteriorly it reaches forward to the level of the rear edge of the zygomatic-orbital bridge (c. 99[0]).

The palatal incisure is very deep and narrow (c. 97[1]) (Fig. 2). The infraorbital foramen is poorly preserved, but seems to have been large (c. 13[1]). The infraorbital canal is unobstructed (c. 20[0]). A thin (<5 mm) plate ascends from the dorsal side of the massive alveolar process, helping to form the wall of the first canalis of the frontal, a prominent, thin, horizontal shelf is formed. The edge of this shelf bears a groove for the optic nerve.

Squamosal—The sigmoid ridge is prominent (projecting laterally ~1 cm), with a rugose surface, and almost semicircular in outline in posterior view (c. 74[2]) (Figs. 3, 4). The mastoid indentation is deep. The surface of the cranial portion dorsal to the zygomatic root is not inflated or bulging. The postglenoid process and postarticular fossa have well-defined edges. The temporal condyle is oval, with well-defined edges. The processus retroversus is not strongly turned in ventrally (c. 77[1]); it lacks distinct dorsal and ventral posterior terminations, in contrast to what is often observed in Metaxytherium floridanum (Domning, 1988). The zygomatic process is dorsoventrally narrow anteriorly and posteriorly, and broad in the middle; its posterodorsal edge is irregularly concave in outline and convex lateral; its medial surface is slightly concave (c. 84[0]). Its anterior portion has a sharper lateral than medial edge. The external auditory meatus is mediolaterally short (c. 75[1]) and about as high as it is wide (c. 82[1]). The posttemporal process projects anteromedially, bearing a facet for M. sternomastoideus (c. 73[0]) (Figs. 2, 3). The cranial portion of the squamosal reaches the temporal crest (c. 76[1]).

Jugal—The preorbital process contacts the maxilla and lacrimal (c. 87[0]) and is relatively flat and thin (c. 88[0]) (Fig. 3). The ventral rim of the orbit does not overhang the lateral surface (c. 90[0]). The ventral-most point lies beneath or just anterior to the rear edge of the orbit (c. 85[1]). This ventral tip is formed by a rounded process somewhat distinct from, and displaced slightly lateral from, the border behind it. The latter is somewhat irregularly ridged and beveled. The zygomatic process is long (c. 89[0]), and tapers to a dorsoventrally flattened tongue that reaches the level of the middle of the temporal condyle.

Periotic—The lateral surfaces are smooth; no clear boundary exists between the pars temporalis (= tegmen tympani) and pars mastoidea; the anteroventral notch at the intersection of these two parts is semicircular, as in Metaxytherium floridanum (Fig. 5A–D). The anteromedial end of the pars temporalis is prolonged, gradually tapering, and terminates in an abruptly downturned flange that appears to be curled laterally at its ventral edge. The raised area (processus foniculus) on the posteroconal surface of the pars mastoidea forms less of a triangular protuberance than a sharp, thick, vertical ridge that is inserted into the mastoid foramen. This ridge has a roughly semicircular outline in posterior view. The endolymphatic foramen is covered with sediment but seems to be narrow and slit-like. The cavity above the aerauductus vestibuli extends somewhat laterad over the medial shelf of the pars temporalis. The medial outline of the pars petrosa bears two convexities, the posterior much larger; its edges are fairly thin and sharp. The dorsal side of the pars petrosa is more or less flat; the ventral end of the promontory is bluntly pointed. The fossa muscularis minor for the origin of M. stapedius is distinct.

Tympanic—Bulbous, with anterior and posterior borders curving somewhat irregularly towards a sharp ventral point (Fig. 5E,
F). The sides are smooth, without marked irregularities except for a rough protruberance on the anteromedial surface where the M. tensor veli palatini probably took its origin. A faint, laterally positioned ridge may indicate the attachment of the posterior part of the tympanic membrane; no distinct sulcus tympanicus is present.

**Malleus**—Anteroposterior length = 13 mm. The posterior end (orbicular apophysis) is slightly convex. The processus muscularis is moderately large, and forms a distinct nipple-like protrusion on the medial side of the bone. The dorsolateral surface bears a rounded longitudinal ridge that does not connect with the external edge of the manubrium; they are instead separated by a broad, ‘U’-shaped valley. The external edge of the manubrium is 15 mm long, delicate, and strongly convex. The articulations with the incus are not prepared.

**Incus**—Not prepared.

**Stapes**—10 mm long, with a prominent stapedial foramen 1 mm in diameter located 4 mm above its base and close to the anterior side of the bone (Fig. 5G). The head end is flattened anteroposteriorly, the basal end dorsoventrally. The basal end is offset backward slightly; the basal facet is curved, its anterior part facing medially, its posterior part more ventromedially. A groove for the facial nerve is present.

**Mandible**—In the holotype (Fig. 6A, B; Table 2), the alveolar portion, coronoid process, and anterodorsal part of the symphysis are missing. The distance between its anterior and posterior ventral extremities (dimension DF) is 123 mm; the height of the ventral arch (dimension MN) is 41 mm. The ventral edge of the horizontal ramus is strongly concave in the holotype and in ChM PV4757 (c. 122[3]) (Figs. 6A, B, 14B). The mandible of the referred specimen (SC 89.115) (Fig. 6C–F) is unfused at the symphysis. It is smaller than the holotype and ChM PV4757 (Table 2). The symphyseal masticating surface is incompletely preserved in SC 89.115, but it seems to have been broad with a nearly rectangular outline, as it is in the other referred specimen (ChM PV4757) (c. 121[3]). In contrast to the holotype, the ventral border of the horizontal ramus of SC 89.115 is moderately and evenly concave (c. 122[2]) (Fig. 6C–F); the degree of concavity thus may vary individually and/or increase with life age (cf. M. krahrleitzi; Domning and Pervesler, 2001:pl. 5). The region of the mental foramen is mostly broken in both referred specimens, but it appears that there were no accessory foramina (c. 125[17]). In the holotype and SC 89.115, the mandibular condyle is elliptical in outline, its surface being convex to flat. In UF 49051, the pterygoid fossa has a rugose surface and well-delineated posteroventral border. The posterior border of the dentary descends smoothly from the condyle, becoming broadly convex beginning at the level of the tooth row (c. 125[2]). The anterior border of the ascending ramus is broken at the base in all specimens. The coronoid canal is oriented anterodorsally-posteroventrally, and the dental capsule is exposed posteroventrally (c. 127[1]). In the referred specimens, the horizontal ramus is dorsoventrally broad (c. 128[1]).

**Dentition**

UF 49051 (Figs. 2, 3, 7), a subadult individual, has a single empty alveolus, presumably for a root of DP4, at the front of the upper cheek tooth row. Four upper molariform teeth (DP5–M3), each three-rooted, are still present on each side, although the first two are worn out and the last has not quite come into wear. The adult upper dental formula would be I 1, C 0, DP 1 or 0, M 3 (c. 139[0]; 143[1]; 145[2]; 146[1]; 151[0]; 155[1]; 157[2]). In the referred mandible (SC 89.115) (Figs. 7C–F, 8), a heavily worn m2 and a lightly worn m3 are present, as well as empty alveoli for m1; hence, the adult mandibular dental formula is presumed to be i 0, c 0, dp 1 or 0, m 3. The alveolar region in ChM PV4757 is incompletely preserved.

**II**—The overall length of the tusk is 42 mm. The root is mediolaterally compressed. 13 × 8 mm in diameter, closed, and tapers toward the end. The root is intermediate in shape between the two specimens of *Metaxytherium floridanum* illustrated by Domning (1988:fig. 7); the posteroventral margin is uniformly convex; the apical end of the root curves slightly anterodorsally; closer to the crown, the anterodorsal margin of the root bears a distinct hump. The enameled crown is distinct from the root (c. 137[0]), virtually unworn, smooth, subconical, 11 mm high.

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**TABLE 2.** Measurement of mandible (in mm) of *Metaxytherium albifontanum* sp. nov., following Domning (1978).

| Dimension                  | UF 49051 | SC 89.115 | ChM PV4757 |
|----------------------------|----------|-----------|------------|
| AB Total length            | —        | 220+1)/225+1(r) | 288        |
| AG Anterior tip to front of ascending ramus | —        | 161+1(r)   | 220        |
| AP Anterior tip to rear of principal mental foramen | —        | 83+1(r)    | —          |
| AQ Anterior tip to front of mandibular foramen | —        | 138+1(r)   | —          |
| AS Length of symphysis     | —        | 55+1)/52+1(r) | 101        |
| BG Posterior extremity to front of ascending ramus | —        | 91(r)      | —          |
| BQ Posterior extremity to front of mandibular foramen | —        | 152+1(r)   | 100e       |
| CD Height at coronoid process | —        | —         | —          |
| DF Distance between anterior and posterior ventral extremities | 123      | 116+1)/117(r) | 141e       |
| DK Height at mandibular notch | —        | 140+1)/138(r) | —          |
| DL Height at condyle        | —        | 152+1)/151(r) | —          |
| EF Height at deflection point of mandible | —        | 101+1)/108(r) | 152       |
| EU Deflection point to rear of alveolar row | —        | 91+1)/94(r) | 99         |
| GH Minimum anteroposterior breadth of ascending ramus | —        | 64+1)/63(r) | 91         |
| GP Front of ascending ramus to rear of principal mental foramen | —        | 77(r)      | —          |
| IJ Maximum anteroposterior breadth of dorsal part of ascending ramus | —        | —         | —          |
| MN Top of ventral curvature of horizontal ramus to line connecting ventral extremities | 41       | 34+1)/35(r) | 48         |
| MO Minimum dorsoventral breadth of horizontal ramus | —        | 67(r)      | 77         |
| RR Maximum breadth of masticating surface | —        | 54e        | 67         |
| SQ Rear of symphysis to front of mandibular foramen | —        | 891(r)     | 110e       |
| WW Minimum width between angles | —        | 71e        | —          |
| XX Minimum width between condyles | —        | 116e       | —          |

**Abbreviations:** e, estimate; I, left; r, right. + = measurement on incomplete element.
and 8.3 × 6.3 mm in diameter at its base, which is suboval in cross-section (c. 141[0]). Incipient wear facets are developed on each tusk at and just posteroventral to its tip. This suggests there might have been a backward and downward movement of the tusk through the substrate while feeding, as inferred for other sirenian taxa (Domning and Beatty, 2007).

DP5, M1—Heavily worn, cusp patterns obliterated. DP5: length = 13 mm; anterior width = 15.1 mm; posterior width = 13.8 mm. M1: length = 16.0 mm; anterior width = 18.0 mm; posterior width = 14.3 mm.

M2—Moderately worn; displays the cusp pattern typical of Metaxytherium in its most basic form, without accessory cuspules. A smooth precingulum is connected lingually to the protocone but also closely appressed buccally to the paracone, thereby constricting or blocking the buccal end of the anterior cingular valley. The protoloph is straight. The transverse valley is open, impinged on only slightly by the centrally located metacone. The metacone and hypocone have become confluent through wear, and are continuous with a smooth postcingular ridge that descends buccally from the hypocone. The posterior cingular valley is open buccally. Length = 21.7 mm; anterior width = 19.2 mm; posterior width = 16.7 mm.

M3—Unworn; differs from M2 only in that the postcingulum consists of two small cuspsules rather than a smooth ridge, and the posterior cingular valley is occupied by a large cuspule. Length = 21.3 mm; anterior width = 17.6 mm; posterior width = 14.3 mm.

m2—Heavily worn, cusp patterns obliterated. Anterior and posterior roots mesiodistally compressed and recurved.

m3—Anterior interdental wear facet present; anterobuccal indentation on protolophid (‘vorderes Basalband’ of Abel, 1904) absent; protolophid crescentic in outline, metaconid and protoconid worn, forming a continuous lake of dentine. Transverse valley blocked by crista obliqua and hypoconid accessory cusp. Hypolophid crescentic; hypoconid with large accessory cusp near center of tooth, both well worn, forming a confluent lake of dentine; entoconid smaller than hypoconid, tip worn with some den-
**Atlas**—The odontoid process is circular in outline, ∼2 cm long, with an irregularly pointed tip in UF 49051. On the ventral surface of the odontoid process, near its base, there is an oval, flat surface for articulation with the corresponding facet on the atlas. The cotyles are triangular (SC 89.115) to kidney-shaped (UF 49051) in outline, with well-demarcated borders; their articular surfaces are convex to nearly flat. The vertebrarterial canals are open laterally and are bounded dorsally and ventrally by short, laterally directed processes. The posterior surface of the centrum is concave and kidney-shaped in outline. The pedicles are triangular in cross-section, with their lateral surfaces oriented anteromedial-posterolateral. The neural canal is nearly square in outline. The postzygapophyses are short and stout, with articular surfaces oriented ventrolaterad. The neural spine is incompletely preserved on UF 49051; in SC 89.115, it is robust, rounded, with convex anterior and dorsal surfaces and a flat posterior surface; no articular surface for the atlas is present on the neural spine; the midline suture is unfused in SC 89.115.

**Thoracics**—Only two anterior thoracics are preserved in UF 49051, of which only one is sufficiently preserved. The neural spine slopes strongly aft; the outline of its summit forms a straight line parallel to the body axis. Anterior and posterior costal demifacets are present; the anterior demifacets face anterolaterally, the posterior demifacets face posterolaterally and are larger. The transverse processes are robust and have ventrolaterally directed tubercular facets. Anterior to the postzygapophyses there are two mediolaterally elongate depressions that serve as attachment sites for the ligamentum flavum. The postzygapophyses are not separated from the laminae; therefore, they do not project farther aft than the transverse processes. The epiphyses of the centra are not fused.

At least 18 thoracic vertebrae are present in SC 89.115 (Table 5). With the exception of the first three and the last vertebrae, we are uncertain of their exact positions within the vertebral column; we have arranged them in as precise an order as possible based on comparisons with *Metaxytherium krahuletzi* (Domning and Pervesler, 2001) and *Dusisiren jordani* (Domning, 1978), and have assigned them letters a–l.

In T1–3, the spinous processes are inclined aft; their centra are subrectangular in outline. The prezygapophyses are antero-posteriorly short, with their articular surfaces facing dorsally; the
FIGURE 10. Elements of the axial skeleton of referred specimen (SC 89.115) of *Metaxytherium albifontanum*, sp. nov. First right rib in anterior (A) and posterior (B) views. First thoracic vertebra in anterior (C) view. Middle thoracic vertebrae in anterior (D, F) and right lateral (E, G) views. Posterior thoracic vertebra in anterior (H) and right lateral (I) views. Last thoracic vertebra (T18) in anterior (J) and right lateral (K) views. Second lumbar (L), sacral (M), and second and ninth caudal (N, O) vertebrae, in anterior views. Lumbar (L1–3), sacral (S1) and caudal (Ca1–13) series in dorsal (P) view.
TABLE 5. Measurements (in mm) of thoracic, lumbar, sacral, and caudal vertebrae of *Metaxytherium albifontanum* sp. nov. (SC 89.115) (based on Domning 1978).

| Vertebra | TH | BTP | ABC | PBC | HC | TC | WNC | HNC | ML |
|----------|----|-----|-----|-----|----|----|-----|-----|----|
| T1       | —  | —   | —   | —   | —  | —  | —   | —   | —  |
| T2       | 134| 123 | 49  | 57  | 36 | 37 | 29  | 29  | 53 |
| Ta       | —  | 111 | 52  | 61  | 38 | 42 | 28  | 28  | 32 |
| Tb       | 137| 128 | 45e | 54  | 36 | 37 | 27  | 27  | 55 |
| Tc       | —  | 101 | 55  | 69  | 44 | 42 | 24  | 24  | 63 |
| Td       | 139| 100 | 75  | 72  | 51 | 50 | 25  | 25  | 68 |
| Te       | 148| 101 | 55  | 69  | 42 | 44 | 27  | 27  | 65 |
| Tf       | 144| 99  | 62  | 67  | 48 | 48 | 30  | 30  | 35 |
| Th       | 140| 97  | 67  | 64+ | 47 | 47 | 29  | 29  | 67 |
| Tg       | 141| 95  | 65  | 72  | 49 | 49 | 27  | 27  | 69 |
| Th       | 138| 99  | 62  | 67  | 51 | 51 | 25  | 25  | 69 |
| L1       | 131| 260 | 71  | 78  | 52 | 52 | —   | —   | —  |
| L2       | —  | 71  | 71  | 72  | 51 | 51 | —   | —   | —  |
| L3       | —  | 68+ | 79  | 79  | 51 | 51 | —   | —   | —  |
| S        | —  | 75  | 75  | 75  | 53 | 53 | —   | —   | —  |
| Ca1      | —  | 175 | 65  | 70  | 50 | 50 | 24  | 24  | 69 |
| Ca2      | 107| 153 | 68  | 68  | 48 | 48 | 22  | 22  | 55 |
| Ca3      | —  | 136 | 64  | 64  | 47 | 47 | —   | —   | —  |
| Ca4      | 108| 119+| 64  | 65  | 47 | 47 | 15  | 15  | 53 |
| Ca5      | 88+| 61  | 61  | 61  | 45 | 45 | 18  | 18  | 50 |
| Ca6      | 69+| 91+ | 70  | 70  | 44 | 44 | 17  | 17  | 50 |
| Ca7      | —  | 68  | 68  | 68  | 41 | 41 | —   | —   | —  |
| Ca8      | —  | 55  | 55  | 55  | 40 | 40 | 16  | 16  | —  |
| Ca9      | —  | 88+ | 56  | 56  | 40 | 40 | 15  | 15  | —  |
| Ca10     | —  | 57  | 57  | 57  | 37 | 37 | 13  | 13  | —  |
| Ca11     | —  | 52  | 52  | 52  | 35 | 35 | 11  | 11  | —  |
| Ca12     | —  | 44  | 44  | 44  | 29 | 29 | 6   | 6   | —  |
| Ca13     | —  | 40  | 40  | 40  | 26 | 26 | 4   | 4   | —  |

**Abbreviations:** ABC, anterior breadth of centrum; BTP, breadth across transverse processes; HC, height of centrum; HNC, height of neural canal; ML, maximum length, front of prezygapophysis to rear of postzygapophysis; PBC, posterior breadth of centrum; TC, thickness of centrum in midline; TH, total height; WNC, width of neural canal; +, measurement taken on incomplete specimen.

postzygapophyses are not separated from the laminae and thus do not project posteriorly beyond the spinous processes, and their articular surfaces are oriented posteroverfully. In Ta–f (anterior thoracics), the outlines of the centra are dorsoventrally flattened, as in T2, but become more cardiform in outline posteriorly. Anterior and posterior costal demifacets are present, oriented anterolaterally and posterolaterally, respectively; demifacets are deep on the more anterior vertebrae, becoming shallow and nearly indistinct by Tf. The transverse processes are robust, with tubercular facets oriented ventrolaterally. Their prezygapophyses are anteroposteriorly short, with dorsally oriented articular surfaces in Ta and b, becoming more elongate with dorsomedially oriented articular surfaces on succeeding vertebrae. The postzygapophyses are anteroposteriorly elongated, with articular surfaces oriented ventrolaterally; anterior to the bases of the postzygapophyses there are semilunar depressions that served for the attachment of ligamenta flava. The spinous processes are nearly vertical with thickened ends; their anterior edges are sharp, and their posterior surfaces are concave with a midline ridge. The neural canals are nearly round in the more anterior thoracics, and become more acute dorsally in the more posterior ones.

Posterior thoracics (Tg–l, T18?) are overall similar to anterior thoracics. Faint indications of posterior costal demifacets are still visible on Tg and h. The centra are more triangular in outline than in the anterior thoracics, mostly due to the presence of a ventral keel. The transverse processes are shorter and less robust than in anterior thoracics and are greatly reduced in what is interpreted as the last thoracic (T18?). The costal facets on the transverse processes face laterally. The neural canals have an acute dorsal peak as in some of the anterior thoracics, but are more dorsoventrally compressed overall.

**Lumbars**—Three lumbar vertebrae are present in SC 89.115. The centrum of L1 has a ventral keel similar to posterior thoracic vertebrae. The transverse processes extend slightly posteriorly and are nearly uniform in anteroposterior width with nearly straight edges, tapering in their distal 3 cm. The distal ends of the transverse processes of L1 are rugose and dorsoventrally thickened. In L2, the neural spine is vertical, with its posterodorsal extremity thickened. The prezygapophyses are thick

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**FIGURE 11.** Sternum of referred specimen (SC 89.115) of *Metaxytherium albifontanum*, sp. nov., in dorsal (A) and ventral (B) views. **Abbreviations:** cf, costal facet; m, manubrium; s, intermediate sternebra; sf, sternal foramen; ssc, surface for sternal cartilage; x, xiphisternum.
and robust, with articular surfaces oriented dorsomedially; the postzygapophyses are more slender than the prezygapophyses and have articular surfaces oriented ventrolaterally. The anterior surface of the lamina, at the base of the prezygapophysis, is rugose and concave. The neural canal is wider than high, with a slit-like dorsal peak. The ventral surface of the centrum is keeled as in L1, but to a lesser degree; the posterior outline of the centrum is hexagonal. The transverse processes are oriented laterally, constricted anteroposteriorly proximally, widening towards midlength and tapering distally. The distal ends are similar to those of L1. The centrum of L3 has a hexagonal outline; its ventral surface is not keeled, being flat to concave overall. The transverse processes extend slightly posteriorly, with their anterior and posterior edges sigmoidal when viewed dorsally, being widest anteroposteriorly at about midlength; their distal ends are as in the other lumbar vertebrae.

**Sacral**—The centrum has a hexagonal outline, its ventral surface being concave as in L3. The transverse processes extend laterally and ventrally, with distal ends lower than the ventral surface of the centrum. The anterior edges of the transverse processes are straight, the posterior edges are convex; the distal ends are rugose and expanded dorsoventrally, more so than in the lumbar. The expanded ends of the transverse processes likely served for ligamentous attachment to the ilia.

**Caudals**—The neural spines are vertical in more anterior caudals (Ca2), becoming more posteriorly oriented distally (Ca4, Ca6). The transverse processes are oriented laterally on the first three caudals, and progressively become shorter and more posteriorly oriented caudally; by Ca9 the transverse processes extend beyond the posterior surface of the centrum. The transverse processes are dorsoventrally flattened up to Ca6, then become more triangular and almost rod-like in some of the more distal vertebra. The centra are hexagonal in outline, with their ventral surfaces bearing two pairs, one anterior and one posterior, of demifacets for the hemal arches; on each side the anterior and posterior demifacets are connected by a keel, with the surface between the keels being concave. The transverse processes on Ca12 and 13 seem to be more laterally oriented than the preceding ones, indicating the presence of a dugong-like fluke (Brandt, 1868; pl. 8, fig. 4; Domning, 1978; Zalmout and Gingerich, 2012) (Fig. 10P).

**Ribs**—Only the distal ends of 19 ribs are preserved in UF 49051. They are relatively slender, mediolaterally flattened, and pachyosteosclerotic; the largest has cross-sectional dimension of about 41 × 22 mm. In SC 89.115, there are about 15 right and 16 left ribs preserved; however, except for R1, we are uncertain of their individual positions within the ribcage.

**R1**—The capitulum and tuberculum lie dorsal to the neck (Fig. 10). On the ventral surface of the neck there is a prominent anteroventrally oriented process for M. longus capitis. The shaft is subtriangular in cross-section, becoming flatter distal to the angle. A low ridge extends along most of the length of the posterior surface of the shaft. The shaft is narrower at about midlength; anteriorly, just distal to this point, there is a protuberance for M. sternocostalis. The shaft tapers distally and turns inward; its end forms an oval rugose surface for attachment of cartilage.

The ribs are pachyosteosclerotic; only a small amount of cancellous bone is present at proximal and distal ends. Two distinct facets can be observed on the capitulum in more anterior ribs, whereas only one facet is present in posterior ones. The distance between the capitulum and the tuberculum diminishes posteriorly, but these never merge. The shafts are elliptical in cross-section; their distal ends taper and are turned inward and posteriorly. Nearly all ribs have a large, oval depression for M. iliopectoralis on the lateral surface distal to the angle.

**Sternal**—Not preserved in the holotype; the description is based on the sterna of SC 89.115 and ChM PV4757 (Figs. 11, 14C; Table 6). The sternal in SC 89.115 comprises three parts: manubrium, an intermediate sternbrea, and xiphisternum, whereas in ChM PV4757 only the xiphisternum is preserved. The anterior end of the manubrium is not preserved. The manubrium is flat, dorsally concave with a low, inconspicuous ventral keel. The anterolateral surface bears a rugose, flat, elongate surface for the sternal cartilage. The costal facets for rib 1 are oval and oriented dorsolaterally; they are asymmetrically located on the manubrium, with the left one more anterior than the right. The posterior surface of the manubrium is subrectangular in outline with a rugose surface. The single intermediate sternbrea is irregularly hexagonal in outline, dorsoventrally flat, and concave dorsally. The xiphisternum is straight overall, with convex dorsal and ventral surfaces. Anteriorly the xiphisternum is wide, becoming narrower posteriorly, then widening again where it bifurcates and becomes dorsoventrally flat. Only the left posterior extremity is completely preserved in SC 89.115; it is long and bowed laterally, with a length of ∼6.5 cm; a foramen is present at about its midlength with a posteromedial-antrolateral orientation; a shallow groove on the dorsal surface is continuous with the foramen. Both posterior extremities are incomplete in ChM PV4757, but it seems to have been similar to the other referred specimens.

**Scapula**—Not preserved in the holotype and poorly preserved in ChM PV4757; the description is based on the left scapula of SC 89.115 (Fig. 12; Table 7). The scapula is somewhat sickle-shaped, with a broad supraspinous fossa and shallower infraspinous fossa. Its medial surface is poorly preserved, anteroposteriorly convex and dorsoventrally concave. The vertebral border is mostly broken, but where preserved it is rugose for attachment of a scapular cartilage. The spine of the scapula is not preserved. The anterior border of the blade is thinner than the posterior border. Posteroventrally on the lateral surface of the blade, a low crest marks the origin of M. teres major. The neck of the scapula is long and narrow with a broad suprascapular notch. The surface on the posterior edge of the neck is rugose, marking the origin of the long head of M. triceps brachii. The coracoid process is medially inflected; its anteromedial surface is rugose, marking the origin of M. coracobrachialis. The glenoid is oval in outline, with its anterior end narrower than the posterior; the articular surface is concave, more so anteroposteriorly.

**Humerus**—Not preserved in the holotype; the description is based on the left humeri of SC 89.115 and ChM PV4757 (Figs. 12, 14D; Table 8). The proximal epiphysis is detached, indicating a young age for the specimens. The humerus is robust and dumbbell-shaped; the shaft is triangular in cross-section. The greater tubercle extends farther proximal than the humeral head.
facets for the infraspinatus mm. on the greater tuber-
cle are poorly defined. A flange of the greater tubercle ex-
tends anteromedially over the bicipital groove, which is deep and
narrow. The head is elliptical and oriented obliquely to the long
axis of the shaft. A subcylindrical groove area on the postero-
surface of the head marks the origin for the lateral head of M. tri-
 cepes brachii. The lesser tubercle does not rise above the humeral
head. The deltoid crest is prominent and recurved; distally, it is
continuous with the deltopectoral crest, ending in an elongated,
shallow, pitted depression, which marks the insertion of M. pec-
toralis major. Distally, the trochlea is canted obliquely to the long
axis of the shaft; a shallow circular notch subdivides the antero-
proximal surface. A shallow groove on the postero-lateral corner
of the trochlea marks the insertion of a humeral ligament.
The olecranon fossa is deep, with well-defined borders; the coro-
noid fossa is shallow. The entepicondyte extends distally as far as the
trochlea.

**Radius-Ulna**—Not preserved in the holotype; the description
is based on the left radii-ulnae of SC 89.115 and ChM PV4757
(Figs. 12, 14E; Table 9). The tip of the olecranon and the distal
epiphyseal of the ulna and radius are not preserved in SC 89.115.
The radius and ulna are fused proximally in SC 89.115, but
contact each other over a flat and rugose surface which would
have prevented pronation or supination; in ChM PV 4757, they
are fused proximally and unfused distally. The shafts are both
nearly straight, only slightly bowed anteriorly, with little torsion
between them. The olecranon is deflected posterolaterally ~50° from
the long axis of the shaft; the tip is oval in outline and rugose. An
elongate shallow depression, ~2.5 cm long, on the medial surface
of the olecranon posterior to the semilunar notch, possibly marks
the insertion of the long head of M. triceps brachii. An indenta-
tion on the lateral portion of the ulnar surface of the semilunar
notch marks the insertion of a humeral ligament. The cross-
section of the ulnar shaft is triangular, distally becoming more
ovoid and elongated anteroposteriorly. A shallow groove for the
tendon of M. extensor digiti quinti is located distally on the lat-
eral surface of the ulna. The proximal end of the radius has a
concave, mediolaterally elongate surface that forms part of the
semilunar notch. The radial tuberosity, located on the medial sur-
face about 2 cm distal to the proximal end, marks the insertion of
M. brachialis. The shaft of the radius is oval in cross-section, be-
coming triangular distally. Distally, there are two grooves on the
lateral surface of the shaft. The first, on the postero-lateral sur-
face, is a shallow groove for the M. extensor pollicis tendon; the
second, on the anterolateral surface, is shallow, but broader than
the other, and was likely for the M. extensor carpi radialis ten-
don. The distal epiphysis is partially unfused in ChM PV4757; the
distal articular surfaces do not differ from those of other species of *Metaxytherium*.

**Manus**

Not preserved in the holotype; the description is based on pre-
served elements of SC 89.115 (Fig. 12; Table 10), consisting of the
left scaphoid-lunar-centrale and metacarpals ?III and IV.

**Scaphoid-Lunar-Centrale**—The proximal articular surface is
roughly hourglass-shaped; the postero-medial one-fourth of its
surface is concave, the rest being flat to convex. The anterior
surface is convex. The posterior surface of the bone has a shal-
low median convexity. The medial half of the posterior surface
has a suboval facet and the lateral half has a smaller mediola-
terally elongated facet; these two facets are for articulation with
the cuneiform pisiform. The distal articular surface has two facets
for the trapezium-trapezoid-magnum; the anterior of these two
facets is mediolaterally elongated, oval, and flat; the posterior one
is concave, triangular in outline, with its apex pointed anteriorly.

**Metacarpal ?III**—The proximal articular surface is nearly
rectangular in outline; it has two articular surfaces, one
canted anteriorly and the other posteriorly, which are sep-
parated by a mediolaterally oriented ridge; the surfaces on
both facets are flat to slightly convex. Proximally, the ante-
rior, medial, and posterior surfaces of the shaft are
rugose; the postero-medial corner has a raised knob. The lateral
surface of the shaft is flat, whereas its medial surface has a low
ridge that extends proximodistally, beginning from the antero-
medial corner and going to the midline. The distal end of the shaft
is oval in outline, with its long axis oriented anteroposteriorly.
The distal epiphysis is not preserved.

**Metacarpal IV**—The proximal articular surface is trapezoidal
in outline and its surface is mediolaterally convex. Proximally,
the anterior, medial, and posterior surfaces of the shaft are rugose. The lateral surface of the shaft is flat and its medial surface is rounded. The distal end of the shaft is anteroposteriorly expanded, subtriangular in outline with its apex posterior. The distal epiphysis is not preserved.

Innominate—Not preserved in the holotype; the description is based on the left and right innominates of SC 89.115 (Fig. 13; Table 11). The ilium is long and rod-like; the cross-section of the shaft is oval. The proximal end of the ilium is flat mediolaterally and expanded dorsoventrally, with its dorsomedial surface rugose but not forming an auricular surface. This rugose surface was likely in contact with or, more likely, connected by ligaments to the expanded end of the transverse process of the sacral vertebra. An iliac spine is absent. The acetabulum is shallow, oriented posteroventrally, and oval in outline with no acetabular notch. The surface medial to the acetabulum is concave. A short pubis seems to have been present, but this area is broken on both innominates. The obturator foramen is absent. The ischium is mediolaterally flattened, with its distal end (ischial tuberosity) rugose and thicker posteroventrally, giving it a triangular cross-section. The ischium forms an angle of ∼129° with the long axis of the ilium. Based on the morphology of the innominate, it seems this specimen was a male (cf. Domning, 1991; Zalmout and Gingerich, 2012).

**PHYLOGENETIC ANALYSIS**

The choice of taxa used in the phylogenetic analysis follows that of Velez-Juarbe et al. (2012), with the addition of Halitherium christolii Fitzinger, 1842, and Metaxytherium subapenninum Bruno, 1839, and using Phosphatherium escuilliei Gheerbrant et al., 1996, and Cornwallius sookensis (Cornwall, 1922) as outgroup taxa representing Proboscidia and Desmostylia, respectively, for a total of 38 taxa. We chose Phosphatherium over Moeritherium (used in previous analyses, e.g., Domning, 1994) because it is now the basal-most proboscidean for which good comparative cranial material is known; character states were scored based on the description by Gheerbrant et al. (2005). We used Cornwallius as a representative of Desmostylia because it is one of the oldest members (late Oligocene) of the group that is known from good cranial material (see Beatty, 2009). Character states for Cornwallius were scored using Beatty (2009) and direct observations of the specimens referred to in that publication. Character states for sirenians were scored from direct observation of specimens by one or both of us.

TABLE 11. Measurements (in mm) of innominates of Metaxytherium albifontanum sp. nov. (SC 89.115) (based on Domning, 1978).

| Dimension                                      | SC 89.115 | ChM PV4757 |
|------------------------------------------------|-----------|------------|
| Total length of ulna                          | 147+      | 184        |
| Total length of radius, anterior lip of       | 126+      | 147        |
| semilunar notch to distal end                 |           |            |
| Height of semilunar notch, anterior tip of    | 27e       | 24         |
| oclearanon to anterior radial lip of notch    |           |            |
| Thickness of oclearanon, anterior to           | 31+       | 27         |
| posterior side                                |           |            |
| Distal thickness, anterior side of radius     | 58+       | 59         |
| to posterior side of ulna                     |           |            |
| Maximum mediolateral breadth, radial portion  | 36+       | 42         |
| of semilunar notch                           |           |            |
| Maximum mediolateral breadth, ulnar portion   | 30+       | 34         |
| of semilunar notch                           |           |            |
| Minimum mediolateral breadth of               | 19        | 21         |
| semilunar notch (at midsection)              |           |            |
| Minimum thickness of oclearanon,              | 13        | 24         |
| posterior side to semilunar notch             |           |            |

**Abbreviations:** e, estimated measurement; +, measurement based on incomplete element.

**FIGURE 13.** Lateral views of right (A) and left (B) innominates of referred specimen (SC 89.115) of Metaxytherium albifontanum, sp. nov. Abbreviations: ac, acetabulum; il, ilium; is, ischium; ist, ischial tuberosity; pu, pubis.

**TABLE 10.** Measurements (in mm) of left manus elements of Metaxytherium albifontanum sp. nov. (SC 89.115) (based on Domning, 1978).

| Scaphoid-lunar-centrale                     | 24 |
| Length (anteroposterior)                   | 22 |
| Breadth (medialateral)                     |   |
| Metacarpals                               |   |
| Total length (proximodistal)              |   |
| Length (anteroposterior), proximal end    |   |
| Breadth, proximal end                      |   |
| Length (anteroposterior), distal end       |   |
| Breadth, distal end                        |   |

**Abbreviation:** +, measurement on incomplete element.
algorithm with the following parameters: 1000 replicates and keeping 10 trees per replicate. This was followed by an analysis using the implied weight method (Goloboff, 1993; Goloboff et al., 2008b) set to \(K = 3.00\).

**Results**—The phylogenetic analysis resulted in 2205 most parsimonious trees (MPTs). 185 steps long with consistency index of (CI) \(= 0.5205\) and retention index (RI) \(= 0.7578\). The strict consensus was 271 steps but had very poor resolution. Analyzing those results using the implied weighting method resulted in one MPT, 187 steps long with CI \(= 0.5348\) and RI \(= 0.7521\) (Fig. 15). The topology of the tree is largely consistent with that of Vélez-Juarbe et al. (2012). Some of the main differences are that (1) the polytomies between an undescribed halitheriine (USNM 541417) and Caribosiren turneri as well as that among the different species of Metaxytherium have been resolved; and (2) Halitherium chris- toli is no longer the sister taxon to the Metaxytherium spp. + Hy- drodamalinae + Dugonginae clade (as in Domning, 1994). The position of Metaxytherium albifontanum among other species of Metaxytherium confirms its generic affinities.

**DISCUSSION**

**Comparisons**

Among species of Metaxytherium, UF 49051 is most similar, in size and overall morphology, to M. crataegense. However, M. albifontanum retains the plesiomorphic condition of having the ventral extremity of the jugal under the posterior edge of the orbit (c. 85[1]), a characteristic that it shares with M. krahuletzi, more basal halitherelines, and some basal dugongines (Fig. 3). M. albifontanum differs from some M. krahuletzi by having exoccipitals that do not meet in a suture dorsal to the foramen magnum (c. 66[1]) (Fig. 4; this area has been partially reconstructed in the holotype, giving the false impression that they did), a derived condition that is polymorphic in M. krahuletzi and present in all other Metaxytherium, hydrodamalines, and some dugongines. In this respect, UF 49051 seems to be a morphological intermediate between the more basal M. krahuletzi and other species within the genus, despite its earlier geological age.

The sternum gives a similar impression. M. krahuletzi and M. albifontanum (as well as M. arctoditates) retain the tripartite condition of the sternum seen in Halitherium schinzii (Lepsius, 1882:pl. 6, figs. 73–75; cf. Domning and Pervesler, 2001:pl. 14), whereas no other species of Metaxytherium for which the sternum is sufficiently known (M. floridanum, M. medium, M. serresii, M. sub- apenninum), nor any hydrodamaline, has been found to exhibit more than two separate elements, termed the manubrium and xiphisternum. A notable difference between M. krahuletzi and M. albifontanum, however, is the latter’s greater width of the manubrium relative to the posterior parts of the sternum. Three sterna of M. krahuletzi (a young adult and two mature adults) are quite uniform in their long, narrow shapes, with the manubrium not appreciably wider than the intermediate sternabra or the ante- rior part of the xiphisternum. None of these has the propor- tions seen in M. albifontanum. In the holotype of M. arctodites, the manubrium (not yet published) is intermediate in shape, being long relative to the rest of the sternum as in M. krahuletzi but expanded at its anterior end as in M. albifontanum.

Given the wide range of variation in sirenian sterna generally, and the inadequate sampling of individual and ontogenetic vari- ability of this element in the taxa at issue, it would be premature to conclude that these characters of the sternum are (or are not) of phylogenetic value. The evidence suggests patterns that are interesting, but too complex to decipher from the available data.

**Paleoecology**

Metaxytherium albifontanum lived sympatriically with Crenatosiren olsenii and Dioplotherium manigaultii (Domning, 1989b; Velez-Juarbe et al., 2012). These three species differed, most notably, in tusk size, which are hypothesized, together with other cranial characters, to serve as proxies for their feeding preferences. Metaxytherium albifontanum with its small

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**FIGURE 14.** Cranial and postcranial elements of referred specimen (ChM PV4757) of Metaxytherium albifontanum, sp. nov. Left zygomatic process of the squamosal in lateral view (A). Mandible in left lateral view (B). Xiphisternum in dorsal view (C). Left humerus in posterior view (D). Left radius-ulna in lateral view (E). Abbreviations: an, angle; h, head; mef, mental foramen; o, olecranon process; of, olecranon fossa; sln, semilunar notch.
tusks was most likely less well suited for uprooting larger seagrasses than the other two species. A much more detailed description of the paleoecology of *Metaxytherium albifontanum* was recently published by Vélez-Juarbe et al. (2012).

**Discussion**

The more basal position of *Metaxytherium krahuletzi* with respect to *M. albifontanum* (Fig. 15) indicates that the divergence between the two occurred prior to the late Oligocene. Indeed, the sister taxa to the *Metaxytherium + Hydrodamalinae* clade include two early Oligocene taxa from Puerto Rico, an undescribed genus and species of halitheriine (USNM 542417), and *Caribosiren turneri*. Of these, USNM 542417 is the most fitting, morphologically and chronologically, to be the ancestor of the *Metaxytherium + Hydrodamalinae* clade. *Caribosiren*, although the right age, shows derived features not seen in any of the later ‘halitheriines,’ such as extreme rostral deflection and possible loss of tusks. Previous assumptions for the origins of *Metaxytherium* have been in favor of either a European origin from *Halitherium christolii* or a New World origin (Domning, 1994). Based on our results, we argue in favor of a West Atlantic–Caribbean origin for *Metaxytherium* around the late early Oligocene. However, the more basal position of *M. krahuletzi* likely points to a more complicated history in this group.

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