

Osteological Associations With Unique Tooth Development in Manatees (Trichechidae, Sirenia): A Detailed Look at Modern *Trichechus* and a Review of the Fossil Record

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ABSTRACT

Modern manatees have a unique type of tooth development, continually forming identical new molars in the posterior end of each quadrant of their mouths, and then progressively moving teeth anteriorly, only to reabsorb roots and spit out worn crowns. This process is not only developmentally complex, but requires space in the oral cavity that imposes its own limitations on other uses of that space. To gain a clearer understanding of the anatomical constraints on the evolution of this unique developmental process, we identified the specialized craniodental features in modern *Trichechus* that permit this specialization using visual observation and CT. Furthermore, to better understand the evolution of these traits, we review the fossil record of trichechids for these traits, including CT analysis of the skull of *Miosiren kocki*, a possible early member of the family from the Early Miocene of Belgium. *Anat Rec*, 295:1504–1512, 2012. © 2012 Wiley Periodicals, Inc.

Key words: Sirenia; Trichechidae; polyphyodonty; tooth development; *Trichechus*; *Miosiren*

Manatees (*Trichechus*) are unusual animals in many ways, including having pachyosteosclerotic skeletons (Domning and Buffrénil, 1991) and vascular corneas (Harper et al., 2005). Unlike any other modern mammal, perhaps except for the wallaby *Peradorcas concinna* and the chisel-tooth rodent *Heliophobius* (Gomes Rodrigues et al., in press), *Trichechus* has an unusual way of continuously developing new molars. This has been termed “horizontal tooth replacement” (Domning and Hayek, 1984), though a more technical way to describe this would be as a sort of polyphyodonty, such as continuous distomesial tooth replacement. Delayed dental eruption like that seen in modern Proboscidea (Roth and Shoshani, 1988) and *Dugong dugon* (Mitchell, 1973; Marsh, 1980) is a different sort altogether, primarily because the same normal set of premolars and molars develop in proboscideans, but innumerable nearly identical molars develop in manatees. The development of supplementary replacement molars

in *Peradorcas concinna* is not well understood, but as many as nine molars may erupt successively in each quadrant (Thomas, 1904). In contrast the system found in *Trichechus* may encompass the development of >30 molars in each quadrant (Domning and Hayek, 1984), totaling ~120+ teeth in a lifetime. In each quadrant of the mouth, new molars are developed in the posterior-most portion of the jaw in a continuously active and

Grant sponsor: National Science Foundation; Grant number: DEB 0309369.

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Received 10 February 2012; Accepted 18 May 2012.

DOI 10.1002/ar.22525

Published online 7 July 2012 in Wiley Online Library (wileyonlinelibrary.com).

developing crypt. These molars (molars 1–3 plus numerous supernumerary molars) are morphologically identical to the one preceding it except for the initial three deciduous teeth (Domning, 1982), and move at a rate ranging between 0.052 and 0.028 mm per day (Domning and Hayek, 1984). These teeth move by virtue of the constant absorption and deposition of alveolar bone, moving the roots anteriorly. This happens until they reach the most anterior portion of the tooth row, at which stage the roots are absorbed, the crown falls out and the alveolus closes. This process occurs continuously, and each tooth after tooth III can only be generically considered a molar, but not ascribed to any specific number or position as is done with the dentition of other mammals (Domning and Hayek, 1984; Hillson, 2005). Subtle variations in size and/or cusp morphology may change throughout life, but this has not been studied in detail yet.

How this unique dental development originated is still a mystery. The family Trichechidae has a scarce fossil record, with all known fossils of “true” manatees (Subfamily Trichechinae) found in South America with a possible exception from the southeastern US (Domning, 1982). Aside from the Middle Miocene taxon *Potamosiren* from the Amazon Basin of Columbia, all trichechines, including the Late Miocene *Ribodon* and Pleistocene to Recent *Trichechus* appear to have had the horizontal tooth replacement like that found in modern manatees (Domning, 1982, 2005).

The ecological context of the emergence of this specialization is also unclear. This was hypothesized to have been an adaptive response to the highly abrasive diets of river plants (Domning, 1982), which include grasses, though no studies have examined the abrasives of Amazonian aquatic plants. It is increasingly questioned whether phytoliths in grasses can cause dental wear (Sansom et al., 2007), and recent studies have shown that sediment interactions in manatees and dugongs may have more impact on dental wear than any other factor (Beatty, 2007; Beatty and Muhlbachler, 2010; Beatty et al., 2011). There is debate whether the Amazon Basin was a rainforest or a seasonally flooded savanna during the Pleistocene (Webb and Rancy, 1996), and consequently it is unclear whether the influence of siliclastic sediments from the growing and eroding Andes (Hoorn et al., 1995) or the dispersal of phytoliths from the spread of grasslands in the Late Miocene of South America had more impact as a source of abrasives. Unlike the North American record of paleosols and vertebrate faunas for which the evolution and spread of phytoliths and C4 grasses has been decoupled from the spread of “grazing taxa” (Stromberg, 2005), much of the existing understanding of the spread of grasslands in South America is based on the spread of mammal herbivores that are interpreted as grazers (Ortiz-Jaureguizar and Cladera, 2006) or the isotopic signature of C4 plants in the paleosols or fossil mammal teeth (Cerling et al., 1997; Latorre et al., 1997). But in aquatic ecosystems it is becoming abundantly clear that much of the Amazon Basin went through repeated marine transgressions as sea level rose and fell, causing some portions of the basin to become estuarine or marine. This is especially evident in the portions of the early western Amazon Basin’s paleo-Orinoco River in the area now within the borders of Peru, Venezuela, and Colombia (Hoorn, 2006). This may have not only enabled populations of marine seacows to get into the shallows of the Amazon Basin and eventually evolve into trichechines,

but growing evidence shows that plants came and went with these transgressions, including mangroves (Hoorn, 2006), which form a common habitat for manatees today (Castelblanco-Martínez et al., 2011). The uncertainty about whether the spread of phytolith sources in South America tracked the spread of C4 grasses, coupled with the increased sources of siliclastic sediment exposure at the time of the evolution of trichechines in South America, make it difficult to know which factor had the greatest influence on the evolution of this unusual tooth replacement system.

Nonetheless, the evolution of continuous distomesial tooth replacement only makes sense as a means of increasing the amount of tooth material that can be worn away during the lifetime of the animal, akin to the way some mammals, like equids, evolved hypsodonty to increase the wear life of their teeth (Muhlbachler et al., 2011).

Two bizarre taxa of sirenians, *Anomotherium* (Siegfried, 1965) and *Miosiren* (Dollo, 1889; Sickenberg, 1934), from the Late Oligocene of Germany and Early Miocene of Belgium respectively, comprise the subfamily Miosireninae (Domning, 1994), presumably derived from the Eocene family Protosirenidae. The Miosireninae are considered the sister group to the Trichechinae based on two cranial features, the lamina orbitalis of the frontal and the size of the nasals. These two features may or may not conclusively ally *Miosiren* and *Anomotherium* with trichechids, though at present all existing evidence suggests it is most prudent to assume so. Because protosirenids are known from both sides of the Eocene Atlantic basin (Domning et al., 1982; Zalmout et al., 2003; Beatty and Geisler, 2010), it is possible that the Miosireninae evolved from protosirenids of the Tethys region and the Trichechidae evolved from protosirenids of the Americas. Though *Miosiren* and *Anomotherium* were suggested to have been mollusk-eating durophages because of their robust dentition (Sickenberg, 1934; Domning, 2001), the Paratethys seas were dominated by less seagrass and more algae in the Late Oligocene and Early Miocene this time (Diedrich, 2008) and it is possible that they continued to eat aquatic plants like other Sirenia. The exact nature of the plants they may have eaten is still uncertain.

To better assess the anatomical and spatial constraints on the evolution of this unique developmental process so that we can recognize it in fossil trichechids, we investigated modern *Trichechus* more thoroughly and compared it with fossil trichechids. We did this by means of visual observation, as well as visualization and measurement of internal structures not visible from external observation using CT scans of *Trichechus senegalensis*. We identified the specialized craniodental features in modern *Trichechus* that permit this increased number of teeth to develop during an individual manatee’s lifetime, and its associated management of space. Finally, we reviewed the fossil record of trichechids for these traits, including CT analysis of the skull of *Miosiren kocki*, and outline a prospectus for what features need to be identified in fossil taxa to identify the origins of continuous distomesial tooth replacement. We hope that this might set the stage for careful interpretation of new fossils of trichechids as they are found in the future, as well as further studies of tooth development and how it ties into cranial development and maturity of the earliest sirenians.

Institutional abbreviations—AMNH, American Museum of Natural History, New York, NY, USA; FLMNH, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA; NHM, Natural History Museum, London, UK; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA.

Anatomical abbreviations—CAE, closing anterior alveolus; CryptB, crypt bone; HoBC, homogenous bilophodont cusps; j, jugal; MaFBr, mandibular foramen bridged; MaTCEX, mandibular tooth capsule extension; mx, maxilla; MxTCEX, maxillary tooth capsule extension; sphc, sphenorbital canal; SpiRotOS, spiraling rotation of occlusal surface.

MATERIALS AND METHODS

Modern *Trichechus* specimens are numerous in collections, and though many specimens from the AMNH, USNM, and FLMNH were investigated for confirming the morphology of the developing dentition, only specimens key to understanding the ontogeny and variations of morphology of this unique mode of tooth replacement are listed and/or figured. Specimens of fossil trichechids are rare, with the possible exception of the Pleistocene subspecies *Trichechus manatus bakerorum* (Domning, 2005), so sampling of these taxa is exhaustive and small. Fossil taxa of trichechids other than *Trichechus* are also rare. Originals and casts of specimens of *Ribodon limbatus* (NHM M7073) and *Potamosiren* were observed at the USNM and NHM. The only known specimens of *Anomotherium langewieschei* and *Miosiren kocki* are the holotypes, and though *A. langewieschei* was only observable via published images, the holotype (IRSNB M.136) of *M. kocki* was studied. The holotype of *A. langewieschei* (Siegfried, 1965) does not include a mandible or palate, thus it is impossible to determine whether this taxon has any of the features of specialized tooth replacement identified in *Trichechus*, except for the nature of the postcanine teeth and external indicators of any spiraling rotation of the occlusal surface (SpiRotOS). Considering that all other features of this taxon seem to indicate an affinity to *Miosiren* (Domning, 1994), it is most likely that the tooth replacement of *Anomotherium* is similar to that of *Miosiren*.

In addition to visual observation and measurement of these taxa, CT scans of *Trichechus senegalensis* (AMNH 53939) and *Miosiren kocki* (RBINS M.136) were studied. The skull of *T. senegalensis* was imaged at the University of Texas High-Resolution X-ray CT facility (Austin, TX) and imagery of this specimen is available on the Internet at http://www.digimorph.org/specimens/Trichechus_senegalensis/. The skull of *Miosiren kocki* was scanned with a hospital scanner (Siemens Sensation 64), at Universitair Ziekenhuis Gasthuisberg, in Leuven (Belgium), by W. Coudyser.

The analysis of the CT images included virtual tooth volume reconstructions created using Amira 2005 (Visage Imaging). Developing posterior-most molars surrounded by a capsule were clearly visualized in both the mandibular and maxillary sets of teeth of *T. senegalensis*. Three-dimensional renderings of teeth and capsules were reconstructed using different colors to differentiate the structures from one another. Superimposing the teeth on

a translucent 3D rendering of the skull demonstrates the spatial relationship of the developing molars to the more anterior teeth. A simple solid volume reconstruction shows that the crypts are open behind the posterior-most molars.

The teeth of *Miosiren* were well preserved with the exception of one molar that is missing. Vertical cracks were visible but did not affect the reconstruction. The apex of the roots of the posterior-most molars were not clearly demarcated from the surrounding alveolar bone on either side because the densities of bone and root were too similar.

Features related to continuous distomesial tooth replacement found in *Trichechus* via visual observation and CT were then compared to those of other fossil trichechids and put in a phylogenetic context.

RESULTS

Modern *Trichechus* CT Data

Morphologically the fully developed molars are nearly identical, with all uppers looking alike and all lowers looking alike. The upper ones have one large lingual root and two buccal roots (mesial and distal), whereas the lower molars have only two roots (mesial and distal). Upper molar occlusal surfaces face almost ventrally, with a slight inclination medially. Lower molar occlusal surfaces face dorsally with a slight inclination laterally.

Tooth development starts distally, far inside the crypts. The upper crypts are located in a tooth capsule that osteologically perforates the cranial cavity, extending dorsally over the pterygoid plates of the sphenoid in a broadened opening, the sphenorbital fissure, which is formed by the fused superior and inferior orbital fissures and foramen rotundum (Fig. 1). Inside the crypt, before roots form, the upper teeth are oriented on the tooth row such that their occlusal surfaces face ventrolaterally. Then, as they move mesially, the teeth rotate such that the occlusal surfaces ultimately face ventrally with a slight inclination medially, a total rotation of $\sim 90^\circ$.

The lower crypts are located in a tooth capsule in the enlarged mandibular canal (Fig. 2). The mandibular foramen is large in *Trichechus*, with a bridge of bone found crossing it in most individuals of *T. senegalensis*, but rarely in *T. manatus* and never in *T. inunguis* (Domning and Hayek, 1986). Inside the crypt the lower teeth are oriented on the tooth row such that their occlusal surfaces face nearly medially. Then, as they move mesially, the teeth rotate such that the occlusal surfaces ultimately face dorsally with a slight inclination laterally, a total rotation of $\sim 100^\circ$.

The developing molar grows inside of a bony encasement which anteriorly is a continuation of the maxillary alveolar bone in the upper tooth row and the mandibular alveolar bone in the lower tooth row. Progressing posteriorly this bone continues independently of the maxilla or mandible (Fig. 1D), presumably surrounded by soft tissues of the tooth capsule in life. When viewed from the posterior aspect it appears like a floating structure. The maxillary capsular bone is thickest dorsally and the mandibular capsular bone is thickest ventrally; in both cases the bone is thickest at the pole of the developing tooth closest to where the roots will be. Both sets of capsular bone are open distally, so that no bone separates

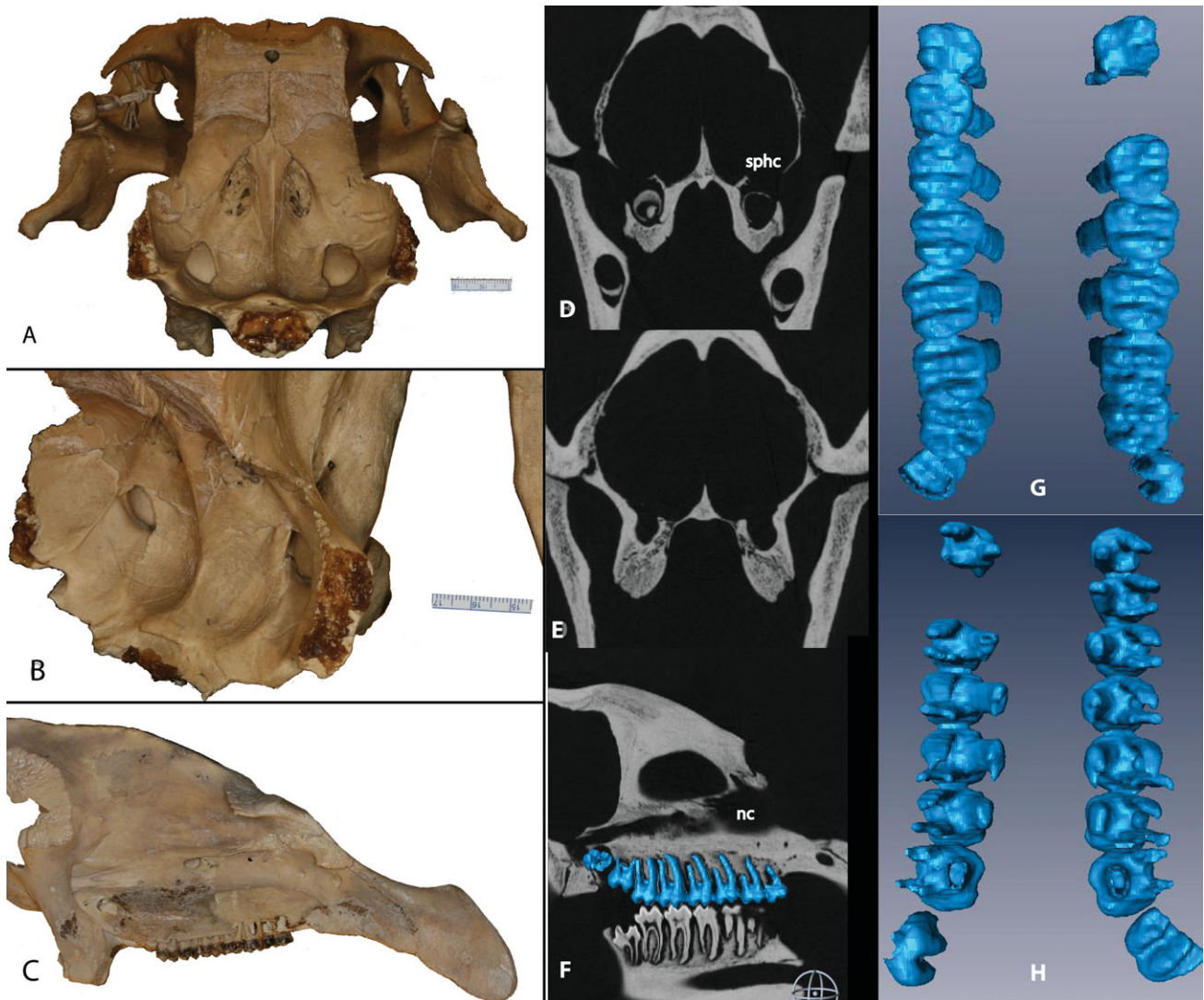


Fig. 1. **A–C:** Dental capsule of *Trichechus manatus* seen in posterior (A) and oblique (B) views of partial skull (AMNH), and lateral view of skull missing the zygomatic arch (AMNH 92530). **D, E:** CT slices of cross sections of *T. senegalensis* (AMNH 53939). **F:** Sagittal section of

CT of *T. senegalensis* (AMNH 53939) with superimposed 3D reconstructions of upper dentition. **G, H:** 3D reconstructions of upper teeth of *T. senegalensis* (AMNH 53939) from CT, in occlusal (G) and dorsal (H) views.

the dental capsule in the back of the sphenorbital fissure or mandibular foramen.

Ultimately these molars, both upper and lower, move mesially until they reach the diastema (Figs. 1 and 2). Both upper and lower diastemata have a continuation of the same bony edge that is similar to the alveolar bone surrounding the roots, but it is much narrower and forms a thin ridge, presumably because there is no tooth in it. It is unknown how this region retains this ridge of bone but lacks teeth that could also continue to move mesially into it. The transition from a tooth-bearing region full of premolars to a thin edentulous ridge may be inferred from the thinning of this ridge of bone and loss of some premolars and incisors found along it as seen in some Eocene fossil Sirenia, especially species of *Protosiren* (Domning and Gingerich, 1994; Gingerich et al., 1994; Zalmout et al., 2003).

The evolutionary origins of the osteological features associated with the continuous distomesial tooth replacement found in *Trichechus* are versions of normal dental anatomy that are slightly modified to accommodate the extra space and unusual orientation needed for the distally developing supernumerary molars. These osteological features can be considered maxillary and mandibular features, as well as general features of the developing tooth. The primary maxillary feature is that the tooth capsule extends into the sphenorbital fissure (MxTCEx) (Fig. 1). The primary mandibular feature is that the tooth capsule extends posteriorly into an enlarged mandibular canal (MaTCEx) (Fig. 2A–C), and the mandibular foramen is broad and sometimes bridged (MaFBr). Features shared between the upper and lower dentition are more numerous. The loss of the most anterior molars in *Trichechus* usually leads to the presence

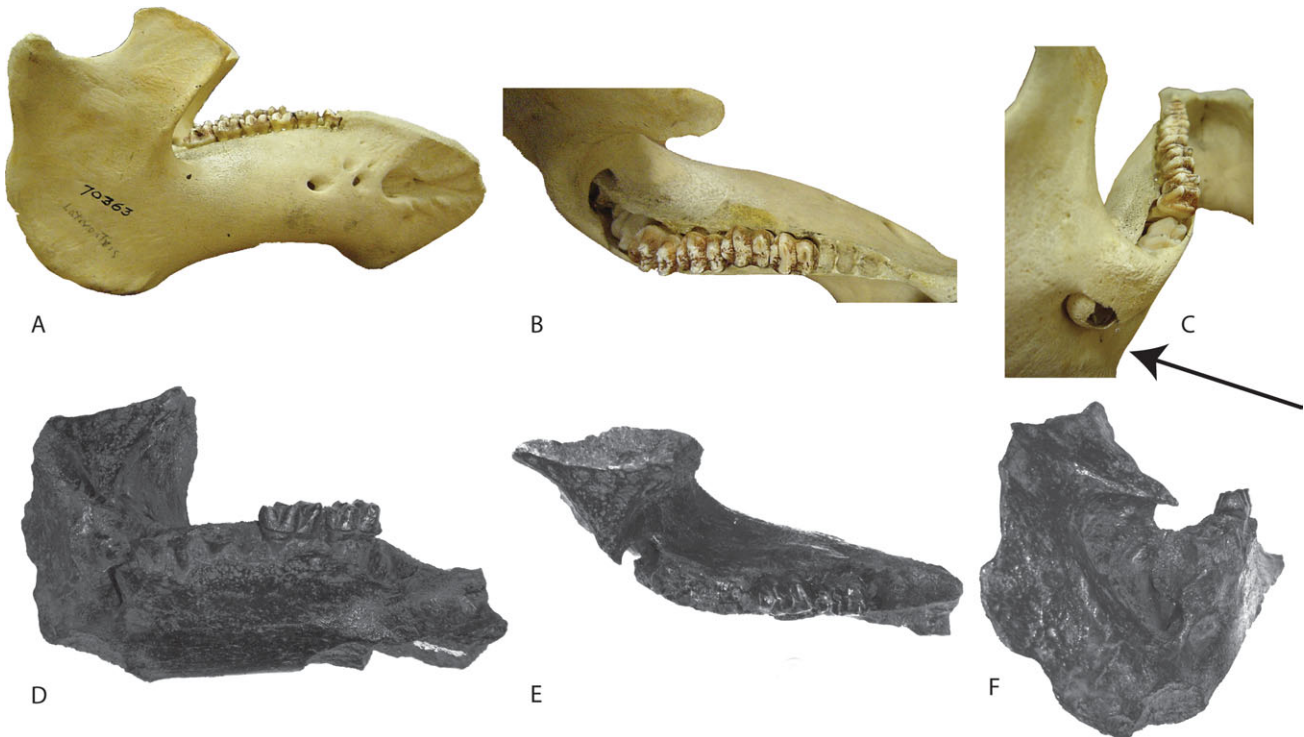


Fig. 2. Mandibles of *T. manatus latirostris* (AMNH 70363) (A–C) and *Ribodon limbatus* (NHM M7073) (D–F) in lateral (A, D), occlusal (B, E), and posterior/oblique (C, F) views. Arrow in C points at the enlarged mandibular canal with visible crypt bone protruding from it.

of an open alveolus partly filled with bone growing back until closure, here referred to as a closing anterior alveolus (CAE) (Fig. 2B). General features of the developing teeth include molars that all resemble a homogenous bilophodont cusp morphology (HoBC) (Figs. 1G,H, 2B), a spiraling rotation of the occlusal surface (SpiRotOS) along the long axis of the toothrow (in opposite directions for upper and lower teeth), and the maintenance of a thin shelf of bone in the crypt (CryptB) sitting along the base of the area where the roots of the new tooth will develop (Figs. 1A–C, 2C). This capsular bone is an extra flange of bone cupping the base of the developing roots, and appears to be an extension of the dentary or maxilla itself.

Fossil Taxa

Maxillary features. Based on published accounts and external inspection of specimens of Eocene and Oligocene prorastomids (Savage et al., 1994), protosirenids (Gingerich et al., 1994), and dugongids (Andrews, 1906; Domning et al., 1994), there seems to be no evidence of crania having dental capsules that extend into the sphenorbital fissure (MxTCEx) like is seen in *Trichechus*. The same can be said for *Prototherium*, which is the taxon most closely aligned with the divergence between the Trichechidae and Dugongidae (Zigno, 1887; Bizzotto, 1983).

In the publication including the detailed description of the holotype of *Miosiren kocki* (Sickenberg, 1934) it can be seen that the palate contains a clearly heterodont set

of teeth, with three complex molars that bear a greater resemblance to dugongids (Fig. 3A) and three sets of single-cusped, globular premolars. This appears to be a fully-erupted set of adult teeth, and CT scans of this specimen show that the upper molar crypts are not open to the cranial cavity dorsally, and no tooth is seen in any stage of development inside the maxilla (Fig. 3). The teeth present do not resemble the homogenous bilophodont cusp morphology (HoBC).

Mandibular features. The mandibular foramen appears to be normal (not enlarged dorsally or mediolaterally) in nontrichechid Eocene taxa, except for a specimen referred to *Protosiren fraasi*, CGM 42297 (Gingerich et al., 1994). This specimen is a mandible not found with the holotype, and it has what appears to be a slightly enlarged mandibular foramen (MaTCEx?) that is not bridged (no MaFBr). However, the most posterior molar in this specimen has a hypoconulid unlike the other teeth, which suggests it is a normal lower third molar, and not a modern *Trichechus* type molar (HoBC). A slightly larger mandibular foramen could simply be for the inferior alveolar neurovascular structures, serving the teeth or structures anterior to them, such as tactile receptors on the lower lip.

The mandibular canal is also found to be bridged in *Prorastomus sirenooides* (Savage et al., 1994), suggesting it may be a primitive feature of sirenians generally (Domning and Hayek 1986).

There is no mandible known for *Miosiren kocki*, so it is unknown whether it had an enlarged mandibular foramen

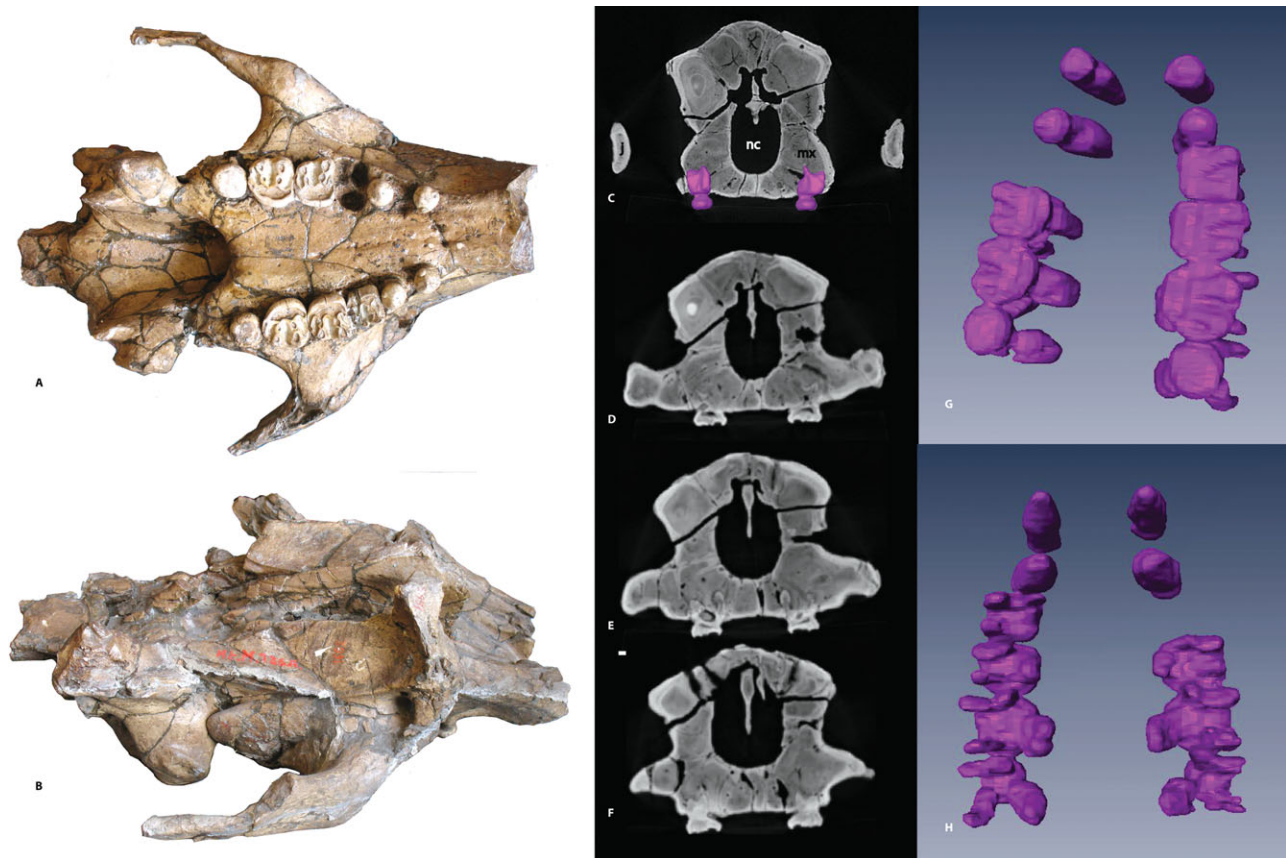


Fig. 3. **A,B:** Skull of *Miosiren kocki* (IRSNB M.136) seen in occlusal (A) and dorsal (B) views. **C–F:** CT slices of cross sections of *Miosiren*. **G,H:** 3D reconstructions of upper teeth from CT, in occlusal (G) and dorsal (H) views.

(MaTCEx) and canal to host continuous distomesial tooth replacement, or whether this mandibular foramen was bridged (MaFBr).

The few mandibles of *Ribodon* that exist are very similar to those of *Trichechus* (Fig. 2D–F) and seem to have a large open mandibular foramen and signs of closing anterior alveoli like those seen in all *Trichechus*. Like *T. senegalensis*, the mandibular foramen is bridged in *Ribodon* (Domning and Hayek 1986).

Features shared between upper and lower teeth. *Closing anterior alveolus (CAE).* The partial loss of anterior dentition (all incisors and canines besides the first upper incisor tusk) in nontrichechid sirenians seems to have occurred early in the evolution of dugongids, as the earliest dugongids had their dentition reduced to I1/i0, M1-3/m1-3 by the Oligocene (Owen, 1875; Sickenberg, 1934; Gingerich, 1992; Domning et al., 1994). In most dugongids (including modern *Dugong dugon*) there are signs of the alveoli of the anterior dentition remaining underneath the horny pad of the mandibular symphysis (Lanyon and Sanson, 2005), but these do not close or contain tooth tissues except for a vestigial mandibular tusk occasionally observed in *Dugong dugon* (Reinhart, 1976). Closing anterior alveoli (CAE) are not observed in any nontrichechid sirenian. Very few specimens of *Potamosi-*

ren are known, and most are isolated postcanine teeth, though there is one reported mandible in which CAE is not present (Domning, 1997). As stated above, *Ribodon* mandibles have signs of CAE akin to those of *Trichechus* mandibles (Pascual, 1953).

Homogenous bilophodont cusp morphology (HoBC). *Miosiren* lacks the homogeneous bilophodont cusp morphology (HoBC) typical of *Trichechus*. The isolated teeth allow us to see that already in *Potamosiren* the homogeneous bilophodont cusp morphology had evolved (HoBC). Many specimens of *Ribodon* are single teeth (Ameghino, 1883; Frailey, 1986), only recognized as Sirenia because of their homogeneous bilophodont cusp morphology (HoBC).

Spiraling rotation of the occlusal surface (SpiRotOS). A small degree of spiraling rotation of the occlusal surface (SpiRotOS) along the long axis of the tooth row is natural in most mammalian dentitions, and can be seen even in the earliest Sirenia such as protosirenids (Gingerich et al., 1994). In *Miosiren kocki* all the teeth are erupted and in occlusion, but it does not appear that any of them are oriented such that the occlusal surfaces spiraled around the longitudinal axis (SpiRotOS). Because the teeth are fully developed and CT scans show no open crypt, it cannot be determined whether the teeth had crypt bone (CryptB) when

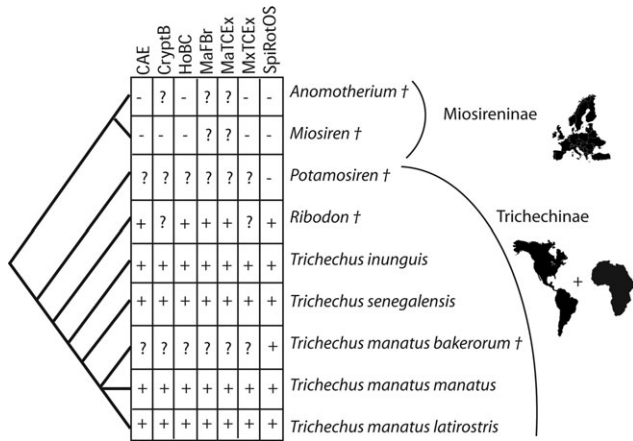


Fig. 4. Phylogeny of the Trichechidae (modified from Domning, 1994, 2005), with mapping of tooth development features identified in this work. + = feature present, - = feature absent, ? = unknown. Note subfamily designations and geographic locations of these groups as illustrated by map silhouettes.

developing, though the mere fact that no teeth continue to develop indicates that this taxon lacked continuous distomesial tooth replacement. But the degree of rotation seen in *Trichechus* is not found in *Potamosiren* and *Miosiren*; it can only be seen in *Ribodon* and *Trichechus*.

No specimens of nontrichechid sirenian taxa have any thin shelf of bone in the crypt (CryptB) sitting along the base of where the roots will develop. Without CT of more fossils this cannot be conclusively considered absent in these taxa, though those specimens with mandibular foramina and canals devoid of matrix have no visible remains of such bone. The possibility that this bone was present but damaged during diagenesis is real, though it is unlikely and requires further CT imaging of fossil taxa to confirm.

CONCLUSION

Ultimately, the general conclusion that the continuous distomesial tooth replacement found in modern *Trichechus* did not evolve until Late Miocene taxa, such as *Ribodon*, is the same as what was concluded previously by Domning (1982). What this study demonstrates, however, is that there is a set of anatomical specializations for the unique tooth replacement pattern of trichechids that evolved partly in tandem, and that many of the details and timing of the emergence of this anatomy is still unknown. This can be seen most clearly when these features are mapped onto the existing cladogram of trichechids (Domning, 1994, 2005) (Fig. 4).

Regarding the Miosireninae, it is interesting to note that paleoecological details remain elusive for identifying the context in which they retain a simple tooth development pattern like other non-trichechid sirenians. Based solely on the presence of geological signs of the presence of algae in the facies from which *Anomotherium* was found, it has been argued that this is what this taxon ate (Diedrich, 2008). Note, however, that algae are the dominant plant life in areas where the modern sea otter, *Enhydra*, is found, yet algae is not part of its diet (Kenyon, 1969). Stable isotopic studies of

Miosiren cannot conclusively differentiate whether *Miosiren*'s diet included benthic invertebrates or algae (Clementz et al., 2009). Ultimately many interpret the thick palate and globular premolars of *Miosiren* as indicative of a hard-object diet (Domning, 2001; Clementz et al., 2009). Hard-object feeders tend to thicken their enamel to minimize tooth fracture and maintain tooth shapes necessary for fracturing hard foods (Lucas et al., 2009). Such animals tend to avoid abrasives because of the changes to tooth shape they cause by wear, so the specialization of making expendable teeth seen in *Trichechus* may not be the best pattern of tooth development for a hard-object feeder like a miosirenine may have been. But we cannot be certain of *Miosiren*'s dietary habits with the data currently available, as they have only narrowed it to algae or benthic invertebrates. Coupled with a better understanding of the lithology of the sediment in which *Miosiren* was feeding, gross dental wear and dental microwear studies like those done for other sirenians may allow us to determine which of these it ate (Beatty, 2007; Beatty and Muhlbachler, 2010; Beatty et al., 2011).

One notable observation from the CT imagery of *Miosiren* is that it has considerably thicker bones in the skull (Fig. 3) in comparison to *Trichechus*. It is outside the scope of this study to determine the functional role of such thick bone, and finite element analyses as well as bone histology are needed to better understand whether this condition strengthened the skull for durophagy or made it potentially too brittle for it. It has been hypothesized that other fossil Sirenia structurally reinforced their skulls to deal with increased cranial stresses associated with using enlarged tusks (Domning, 1989, 1990; Domning and Beatty, 2007). However, *Miosiren*'s tusks are not specialized in the same ways as *Corystosiren* or *Xenosiren*, and it is still unclear whether skull features of *Corystosiren* and *Xenosiren* are similar to the thickening seen in *Miosiren*.

Interestingly, the extension of the maxillary dental capsule into the sphenorbital fissure had not been noted before in the literature, and is not seen in any other mammal. Further work is needed to confirm the histological details of how far this capsule extends, particularly if it has influence on the way that the trigeminal nerve divides, how the processus ascendens and/or lamina ascendens form, or has contact with any portions of the cavernous sinus or parts of the dura mater. It is unlikely that any dura mater would contact the dental capsule, as it is not a neurocranial bone (Starck, 1967; Presley, 1993), though only observation can confirm this.

Finally, what is ultimately understood from this study is that a number of previously unrecognized osteological correlates are associated with the evolution of continuous distomesial tooth replacement in manatees and that some, but not all, of these features are recognized in the existing fossil record of this group. The geographic gaps between the European Miosireninae and largely neotropical Trichechinae indicate a large gap in the fossil record of this group, one that probably contains many of the anatomical transitions identified here. It is likely that these questions will be best answered by finds of more complete cranial fossils of Miocene trichechids from the ancient Amazon Basin and paleo-Orinoco River, particularly in Peru and Colombia.

ACKNOWLEDGEMENTS

The authors thank the Dept. of Anatomy for allowing T. Vitkovski to utilize the dedicated Amira computer for the purposes of this study. Thanks are also due to W. Coudyser (Universitair Ziekenhuis Gasthuisberg Leuven) for his help during the scanning of the skull of *Miosiren kocki*, and to A. Folie and E. Steurbaut (IRSNB) for making the specimen available for the analysis. J. Velez-Juarbe provided initial productive feedback on earlier versions of this work.

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