Evolution of Aquatic Tetrapods

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EAT Conference organized by:
J.G.M. “Hans” Thewissen, Northeastern Ohio Universities College of Medicine, Rootstown OH
Sandra I. Madar, Hiram College, Hiram, OH
Frank Fish, West Chester University, West Chester, PA
Mark D. Uhen, Cranbrook Institute of Science, Bloomfield Hills, MI

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CONTENTS

EVOLUTION OF THE CARNIVOROUS MARINE MAMMAL FEEDING GUILD: A PRELIMINARY OVERVIEW.

PETER J. ADAM; University of California, Los Angeles, Department of Ecology and Evolutionary Biology

All marine mammals, with the exception of herbivorous sirenians and (arguably) desmostylians, prey on other animals ranging in size and diversity from copepods to fish and squid to other marine mammals. Owing to their predatory habits, cetaceans, pinnipeds, and sea otters can be grouped together into a marine mammal carnivore guild (MMG). Guilds provide a useful paradigm from which to examine interspecific competition for resources and its effects. I present preliminary results of an examination of global MMG evolution through the Cenozoic. Better-known fossil taxa were classified into four general feeding categories based on functional characteristics of the skull and teeth established from analogy with extant forms (e.g., Adam and Berta. 2002): 1) masticatory, 2) pierce, 3) suction, 4) and filter feeders. Suction feeders are further divisible into pelagic (primarily teuthophagous) and benthic (primarily molluscivorous) feeders based on rostrum length, size of pterygoid hamuli, and patterns of tooth loss. Filter feeders are divisible into those feeding on microscopic prey (e.g. balaenids, with a highly arched and narrow rostrum and hinge-like jaw joint) and those preying on krill-sized or larger prey (e.g., balaenopterids, with moderately arched rostra, spherical jaw joint, and laterally displaced coronoid processes; and crabeater seals, *Lobodon carcinophaga*, with interdigitating lattice-like postcanine teeth and post-dental ridges). Extant pierce feeding species (most cetaceans and pinnipeds) can be separated into small-, medium-, and large-prey strategists. Although measures of rostrum length and width, tooth size, and tooth density are useful in defining different pierce strategies, establishment of these subcategories also required: 1) characterization of diet in extant taxa, 2) analysis of body and prey body size relationships in extant species, and 3) founding of accurate methods for estimating body size in fossil taxa. Width across paired occipital condyles proved to be the best indicator of body length in all marine mammals (n=72 spp., 698 specimens; Fig. A), although regression coefficients and slopes differed for odontocete ($r^2=0.877$), phocid ($r^2=0.747$), and otariid ($r^2=0.624$) lineages. A positive correlation was found to exist between prey and predator (odontocete) body sizes (Fig. B; $r^2=0.610$, n=20 spp.), allowing extrapolation of prey size in fossil forms.

Temporal and spatial distributions of fossil taxa were determined from the literature. These data, coupled with inferences of feeding strategy and palaeoceanographic data, allow for a detailed (but preliminary) analysis of the Cenozoic MMG. The earliest pinnipeds and all sea otters were masticatory feeders, while most early (pre-Miocene) cetaceans were relatively unspecialized small- to medium-prey pierce feeders. In the Late Miocene, all carnivorous marine mammal lineages experienced a sudden burst in both taxonomic and morphologic diversity. Opening of Drake Passage and partial emergence of the Panamanian Isthmus likely contributed to this diversification by establishing latitudinal stratification of the oceans, resulting in increased equatorial and coastal upwelling. Morphological diversification included establishment of specialized (suction and filter) feeding strategists, in addition to greater numbers of medium- and large-prey pierce strategists. Several instances of competitive and passive replacement are also evidenced, most notably among benthic suction feeding pinnipeds in the north Pacific and medium- and large-prey pierce feeding strategists throughout most of the world's oceans.

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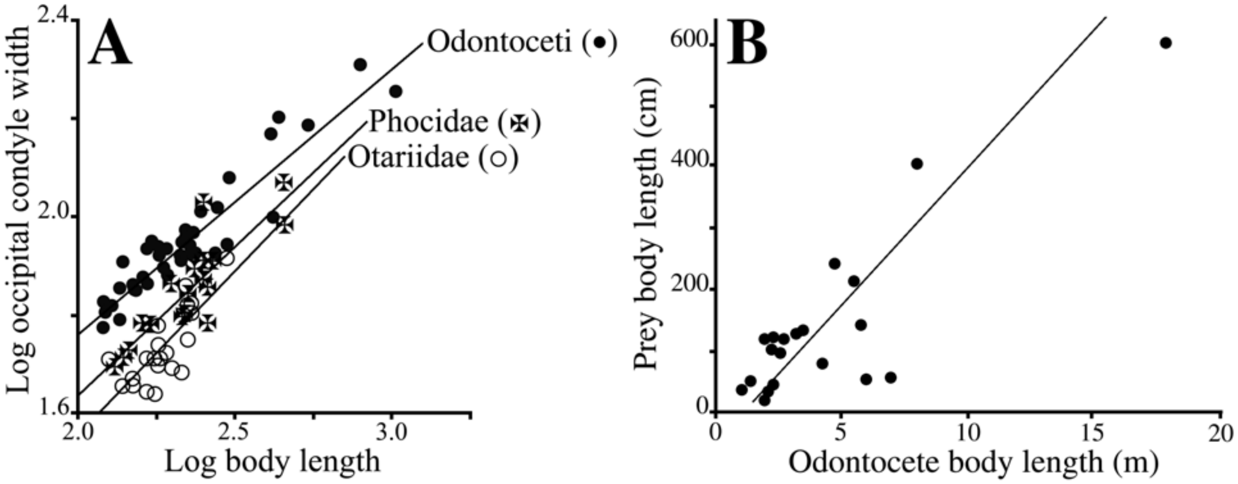

AGES OF THE WHALE-BEARING STRATA IN THE EOCENE OF INDIA: TIMING OF THE ORIGIN OF WHALES

SUNIL BAJPAI, Department of Earth Sciences, Indian Institute of Technology, Roorkee, India; J. G. M. THEWISSEN, Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, OH

In India, there are at least six intervals that yield archaeocete remains and the precise age of these intervals is crucial to our understanding of the timing of terrestrial-aquatic transition and of the early evolution of whales.

The oldest whale-bearing strata occur in the marine, lower part of the Subathu Formation in the type locality near Subathu, District Solan, in the northwestern Himalayan state of Himachal Pradesh. Although mammals are extremely rare, this level (hard, pelletal, oyster-bearing limestone) is potentially important in producing some of the oldest Cenozoic mammals in the Indian subcontinent. The only known whale fossil from this level is the type mandible of *Himalayacetus subathuensis*, characterized by fairly derived molars. Additional material is needed to work out the familial affinities (pakicetid/ambulocetid) of this important taxon. The age of this stratigraphically oldest known whale is constrained by associated benthic foraminifera belonging to Shallow Benthic Zone SB 8 of middle Ypresian age, approximately 53 million years old. It is important to note that possible Ypresian artiodactyls (Khirtharia horizon of Rangarao and Misra 1981) are also known to occur in the same area, in green foraminiferal shales stratigraphically above the *Himalayacetus*-yielding level, but still much (100s of meters) below the classic middle Eocene land mammal fauna of Kalakot (Jammu & Kashmir State).

Younger whales of early middle Eocene or Lutetian age (approximately 48 million years old) in the Subathu Formation come from two stratigraphic levels in the upper part of the formation. Of particular interest is a horizon near the top of the formation near Kalakot (District, Rajauri, Jammu & Kashmir State, northern India) that yields isolated teeth of pakicetids in association with a variety of artiodactyls including the endemic raoellids to which the cetacean ancestry may be closely tied.

The best-known record of Eocene whales in India is from the Kachchh (Kutch) region of western India. Apart from the long known whale-bearing Harudi Formation of middle Eocene age, fragmentary cetacean remains (Remingtonocetidae) have been recently recovered from mudstones correlatable stratigraphically with the Naredi Formation which is well dated at early Eocene (Ypresian) on the basis of larger Foraminifera. Interestingly, the Naredi whales occur in a shallow marine depositional setting, in association with a marine fauna. This fauna is currently under study.

The best-known archaeocete fauna from India comes from the Harudi Formation of Kachchh. Recent field work has yielded a much more diverse assemblage than was previously recognized, comprising at least three but possibly four families: Remingtonocetidae, Protocetidae, Basilosauridae and Dorudontidae. The age of the Harudi Formation is best estimated at mid-late Lutetian rather than Bartonian, based on an evaluation of the published microfossil record from near the top of the Harudi and the overlying Fulra Limestone. It is important to note that the nannofloral assemblage recorded from the Harudi Formation includes the marker species *Sphenolithus spiniger*, characterizing the calcareous nannoplankton zones NP 13-NP 15, well within the Lutetian (approximately 45 million years old).

EVOLUTIONARY PATTERNS AMONG THE OTARIOID PINNIPEDS (MAMMALIA: CARNIVORA).

LAWRENCE G. BARNES, Natural History Museum of Los Angeles County, Los Angeles, CA

The superfamily Otarioidea (sea lions, fur seals, walruses, and extinct relatives) are secondarily aquatically-adapted mammals in the order Carnivora. The otarioid pinnipeds are a monophyletic clade that first appeared in the North Pacific in Late Oligocene time. Otarioids underwent four major and sequential evolutionary diversifications, each one replacing a previous one. Stem members of each otarioid radiation were small in body size, piscivorous judging by their dentitions, and retained the “ursid loop” of the internal carotid artery situated within an embayment in the basioccipital bone. The first otarioid diversification was the primitive Late Oligocene to Middle Miocene subfamily Enaliarctinae of the family Otariidae. Small by comparison with most later otarioids, enaliarctines retained vestigial carnassial cheek teeth, traces of their terrestrial ursoid carnivoran ancestry. The late Early Miocene to Late Miocene Desmatophocidae comprise the second radiation of otarioids. The family Desmatphocidae includes the earlier and less specialized subfamily Desmatophocinae, and the later-appearing, larger, deep-diving, and enormous-eyed members of the subfamily Allodesminae. Desmatophocids might have been specialized squid-feeders. The third otarioid radiation is the family Odobenidae, which in the latest Miocene and Pliocene were the most diverse otarioids, and only the later members of which have tusks. Stem odobenids are early Middle Miocene Imagotariinae which are small piscivores with unmistakable odobenid basicranial and limb features. Through the Late Miocene, imagotariines retained their basic body plan, and some became very large, probably resembling the living South American sea lion, *Otaria*. From the imagotariines evolved the Late Miocene “pseudo-walruses” of the odobenid subfamily Dusignathinae, whose later members had multiple pairs of tusks, the various late Miocene and Pliocene “hyper-walruses” such as *Valenictus*, which had osteosclerotic and pachyostotic limb bones, and the last-appearing Pliocene to Recent true walruses of the subfamily Odobeninae, represented now only by the relict *Odobenus*. The fourth radiation of otarioids is the sea lions and fur seals of the otariid subfamily Otariinae. Clearly derived from the Enaliarctinae, they apparently have an Early and Middle Miocene ghost lineage. Otariines first appear in Late Miocene time (*Pithanotaria*), diversified during the Pliocene and Pleistocene, and appear to be now at their maximum diversity, represented by the many species of fur seals and sea lions. With the exception of the Enaliarctinae, each evolutionary radiation of Otarioidea was characterized by increasing body size and specialization of feeding methods. The most successful otarioid adaptations include the development of homodont but non-specialized dentitions that have allowed feeding on a variety of prey items (fishes, cephalopods, arthropods). This undoubtedly explains the persistence of the relatively generalized living Otariinae subsequent to the extinctions of the more specialized desmatophocines, allodesmines, dusignathines, valenictines, and odobenines.

MIDDLE MIOCENE MARINE ECOSYSTEMS AND CETACEAN DIVERSITY AS EXEMPLIFIED BY THE SHARKTOOTH HILL BONEBED, CALIFORNIA, USA

LAWRENCE G. BARNES, Natural History Museum of Los Angeles County, Los Angeles, CA; NICHOLAS D. PYENSON, University of California, Berkeley, CA; SAMUEL A. MCLEOD, Natural History Museum of Los Angeles County, Los Angeles, CA

Miocene marine ecosystems, especially those of Middle Miocene age (16-13 Ma), show high diversity and abundance in marine mammal, seabird, and planktonic taxa (Lipps and Mitchell, 1976). Both mysticete and odontocete cetaceans also show high taxonomic richness during the Middle Miocene, which also marks the first appearance of several extant cetacean clades. The abundance and diversity of cetaceans at this time is best documented by the Sharktooth Hill Local Fauna (STHLF) in California, which is derived from a dense bonebed in near shore marine sediments of the Round Mountain Silt (Barstovian NALMA correlative). The STHLF, intensively collected for nearly a century, contains a fossil cetacean assemblage whose diversity and richness are unique in the North Pacific Basin. If the Middle Miocene time represents a peak in cetacean taxonomic richness (Barnes 1977), then assemblages like the STHLF are useful for evaluating community structure, taxonomic diversity, and morphologic diversity within and among fossil cetacean assemblages.

The STHLF cetaceans include some associated skeletons and many isolated bones. Although Kellogg (e.g., 1931) originally named the odontocetes and most of the mysticetes on the basis of isolated petrosals, sufficient specimens are now available to assess taxonomic diversity based on crania. We have identified the STHLF cetaceans represented by crania in three different collections, and list these species in the order of decreasing abundance: the small sperm whale *Aulophyseter morricei*; the long-snouted kentriodontid *Lamprolithax simulans*; the large platanistid “*Squalodon*” *errabundus*; the small cetotheriid *Parietobalaena securis*; an apparently un-named small delphinid; the broad-headed cetotheriid *Peripolocetus vexillifer*; the slender-headed cetotheriid *Tiphyocetus temblorensis*; an un-named large kentriodontid; the thick-snouted kentriodontid *Loxolithax sinuosa*; a large cetotheriid that resembles *Aglaocetus*; a large kentriodontid with large nasal bones; the primitive kentriodontid *Kentriodon obscurus*; an unidentified species of herpetocetine cetotheriid; and a sperm whale of the form-genus “*Scaldicetus*”.

The STHLF differs from other Miocene cetacean assemblages by the abundance of sperm whales and platanistids, and by the first occurrence of true delphinids. The STHLF, however, compares favorably with other Middle Miocene assemblages with a similar richness of odontocetes (principally Kentriodontidae) and mysticetes (principally Cetotheriidae sensu lato). The high taxonomic richness of the STHLF cetaceans might be an artifact caused by the apparent lengthy duration of deposition of the Sharktooth Hill Bonebed. The vertically compressed deposit might include taxa that evolved and/or migrated through the area for a million years or more. In the future we hope to calculate the relative abundances of the STHLF cetacean species based on isolated petrosals, and evaluate collecting or preservational biases. The STHLF merits careful comparison with the Calvert Formation in the North Atlantic Basin, because several genera appear to be shared in common by the two deposits. We therefore propose a rigorous re-examination of the identities of the cetaceans in both deposits, as well as explicit quantitative analyses of the relative abundance of the various taxa. Such analyses will better demonstrate faunal similarities and differences between Atlantic and Pacific marine Miocene ecosystems.

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Kellogg, R. 1931. Pelagic mammals from the Temblor Formation of the Kern River region, California. *Proceedings of the California Academy of Sciences*, Ser. 4, 19(12):217-397.

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DENTAL MICROWEAR IN AQUATIC VERTEBRATES: CONSTRAINTS, OPPORTUNITIES AND PRELIMINARY RESULTS FOR SELECTED MARINE MAMMALS

BRIAN LEE BEATTY, University of Kansas Natural History Museum & Biodiversity Research Center

Dental microwear has proved to be a fruitful avenue of research of terrestrial mammals, though nothing of this sort has yet been done among the aquatic vertebrates. Here I discuss the theoretical constraints and opportunities of this endeavor and present some of the preliminary results concerning these constraints now being examined in a variety of pinnipeds, sirenians, and desmostylians. Potential anatomical factors in wear are the functional consequences of dental materials, dental implantation (mechanics of gomphoses), cranial kinesis, material properties of mouthparts, material properties of food items, bite forces, and jaw motions (mastication, suction feeding, etc). Ecological parameters that can affect microwear signals include dietary preferences, the environmental details of the prey species (pelagic, carbonate versus siliclastic substrates, etc), and preservational environment bias. Ongoing current studies include differentiating the wear features associated with diet, substrate, jaw motions, and lingual movements in suction feeding. Light and scanning electron microscopy methods are presented with regard to their efficacy in these studies and the magnification level at which important features are found.

PHYLOGENETIC RELATIONSHIPS AMONG THE DIVERSE TOOTHED MYSTICETE CLADE THE AETIOCETIDAE AND RECONSIDERATION OF THE FILTER FEEDING NICHE

ANNALISA BERTA, Department of Biology, San Diego State University, San Diego CA; THOMAS A. DEMÉRÉ, Department of Paleontology, San Diego Natural History Museum, San Diego, CA

Aetiocetids are the most taxonomically and morphologically diverse clade of toothed mysticetes known from the late Oligocene of the eastern and western North Pacific. The holotype of *Aetiocetus weltoni* has been further prepared and new anatomical details revealed. An emended diagnosis for *Aetiocetus* clarifies the differences between it and other aetiocetid genera. Although previous work has identified four aetiocetid genera, only three are likely valid *Aetiocetus*, *Chonecetus* and *Morawanocetus*. We recognize two species in the genus *Aetiocetus*, *A. polydentatus* and *A. cotylalveus*; *A. weltoni* and *A. tomitai* are junior synonyms of *A. cotylalveus*. We report several additional skulls and a partial skeleton that can now be referred to *A. cotylalveus*. Aetiocetids can be distinguished from other toothed mysticetes by the following unequivocal synapomorphies: lobate or triangular parietal-frontal suture; zygomatic process of squamosal expanded near anterior end; “window” in the palate exposing vomer; short, broad extension of the palatine that overlaps the pterygoid; and exoccipital developed ventrally as an anteriorly directed posterior sinus. Cladistic analysis of 25 cranial and dental characters supports monophyly of the Aetiocetidae. Among other toothed mysticetes, *Llanocetus* and *Mammalodon* are successive sister taxa to aetiocetids.

The presence of palatal nutrient foramina associated with the upper teeth in all aetiocetids suggests that these toothed mysticetes had already evolved some type of baleen. The form and function of this rudimentary baleen is currently unknown, but the fact that these archaic mysticetes also possessed procumbent anterior teeth, broad diastemata, and posterior teeth with sharply pointed cusps, accessory denticles, and longitudinal enamel ridges suggests development of a specialized type of filter feeding differing from that of other toothed and edentulous mysticetes.

PHYLOGENETIC IMPLICATIONS OF SKULL STRUCTURE AND FEEDING BEHAVIOUR IN BALAENOPTERIDAE (CETACEA, MYSTICETI).

VIRGINIE BOUETEL, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, Paris, France.

Balaenopteridae actively feed by engulfment. They swim rapidly at their prey (40-50 km/h), their mouth open and their lower jaw is pulled wide open at a 90° angle. Their mouth and ventral pouch engulf up to 60 m3 of water, then the mouth closes and food is swallowed after the expulsion of water through the baleen. These highly specialized feeding mechanisms are associated with a developed ascending process of the maxilla and a hook-like and outwardly bent coronoid process of the dentary. These features participate in the strengthening of the architecture of the skull and jaw.

Although all fossil baleen mysticetes bear a developed coronoid process, only 6 taxa (*Piscobalaena nana*, *Cetotherium rathkei*, *Herpetocetus sendaicus*, *Metopocetus durinasus*, *Mixocetus elysius* and *Nannocetus eremus*) have a posteromedially expanded ascending process of the maxilla.

Feeding strategies and mechanisms of each extant family of baleen whales are compared and correlated with the associated skull and dentary features. This correlation suggests a phylogeny of the mysticetes and a new definition of the Cetotheriidae sensu stricto (*Piscobalaena nana*, *Cetotherium rathkei*, *Herpetocetus sendaicus*, *Metopocetus durinasus*, *Mixocetus elysius* and *Nannocetus eremus*).

COMPLEXITY IN DELPHINOID EVOLUTION

EMILY A. BUCHHOLTZ, Wellesley College; ELIZABETH M. WOLKOVICH, Dartmouth College.

Darwin (1859) noted an “ill-defined sentiment, felt by many paleontologists, that organization on the whole has progressed” over geological time, but few tests of that sentiment have been made. The radical reorganization of terrestrial morphology in cetaceans offers an opportunity to test whether evolutionary changes within the group represent increases in complexity. As a discrete structure with countable units, the vertebral column is particularly amenable to such a study.

McShea (1993) defined the complexity of biological series as being “some function of the number of different parts [the series] has, or the degree of differentiation among parts, and of the irregularity of their arrangement.” He (1992, 1993) defined range, irregularity, and polarization metrics to address the possibility that the mammalian vertebral column has increased in complexity over evolutionary time.

In 1914 Williston suggested that count and differentiation are inversely correlated. This assertion is particularly interesting because it links an increase in one aspect of complexity (number of parts) to a decrease in another (differentiation among those parts). It runs counter to McShea’s (1992) suggestion that selection may favor increases in count because high counts allow more specialization and internal division of labor among parts.

We evaluated the complexity of five parameters of vertebral column morphology in a single dolphin species, the Atlantic White-sided dolphin *Lagenorhynchus acutus*, at different body sizes to test for ontogenetic changes in complexity. We then compared complexity of the adult *L. acutus* column to that of 18 comparative delphinoid taxa of different vertebral counts to test Williston’s prediction.

We find that complexity in the *L. acutus* vertebral column is dependent on the context of the comparison (Fig. 1). In intraspecific comparisons, centrum length (but not other vertebral parameters) shows statistically significant changes in complexity with ontogeny. Increases in range, irregularity, and polarization reflect variable growth of centrum length in different column regions. Lumbar and prefluke caudal vertebrae grow at rates more than three times that of thoracics and more than eight times that of fluke and cervical vertebrae. Such changes suggest increased column regionalization with increase in size, an interpretation supported by graphic representation of incremental contributions to cumulative complexity values.

In interspecific comparisons, *L. acutus* is neither more complex nor less complex than other delphinoids, but rather complex in a different way. As a species with a very high vertebral count, it lies at the high end of a complexity continuum with respect to number of parts, but these numerous parts show less differentiation, and therefore lower complexity, than do those of animals of smaller count. These results support the prediction Williston made more than 90 years ago.

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HISTOLOGY OF TOOTH ATTACHMENT AND TOOTH REPLACEMENT PATTERNS IN MOSASAURS: WHAT IS THECODONTY ANYHOW?

MICHAEL W. CALDWELL, Department of Earth and Atmospheric Sciences, and Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Recently published data on the tooth attachment histology of the Late Cretaceous marine lizard *Platecarpus* (Mosasauridae) noted the presence of all currently recognized thecodont attachment tissues. In mosasaurs, a woven-fiber bone matrix forms the margins and floor of the tooth alveolus and is identified as alveolar bone based on its histologic and topologic similarities to archosaurian and mammalian alveolar bone. Mosasaurs also appear to possess a cribriform-plate like structure in the alveolus, which is consistent with histologic evidence indicating the presence of a periodontal ligament. Evidence of the periodontal ligament includes parallel fibers present in multiple, non-resorbed generations of alveolar bone that are similar to mineralized collagen fiber bundles known in thecodonts as Sharpey's fibers. The mosasaur tooth also possesses a dentine root around which is a thin layer of acellular cementum which itself is surrounded by a massive amount of cellular cementum. This latter tissue completely fills the alveolar space, increasing in size during tooth replacement. The cementum mass is composed of two histologically distinct tissues: 1) a loosely organized cellular cementum ground matrix; 2) a laminar form surrounding the vascularization. The growth of the complete suite of tooth tissues is mapped into discrete phases of tooth replacement. The enamel tip of the tooth crown develops in the dental lamina, posterior and lingual to the tooth position it will later occupy. The crown develops within the lamina in a vertical position and not horizontally as has been recently suggested. Utilizing a mechanism not currently understood, the developing crown and its dental papilla migrate to the posterolingual margin of the tooth position where the lamina and papilla appear to initiate resorption of the cementum mass at the base of the crown; it is important to note that in mosasaurs the enamel of the crown never shows etching linked to resorption. As the resorption pit grows in size, the crown, papilla, and presumably the dental lamina, descend into the pit. Once the resorption pit has achieved a dimension equal to the size of the adult tooth crown, crown growth is truncated, and cementum begins to develop around the non-enameled portion of the tooth. The resorption pit expands to include generalized resorption of the cementum and alveolar bone contact throughout the alveolus. Growth of cementum tissues appears to be rapid as the mineralized component thickens from the bottom down. The effect is to erupt the tooth vertically in the alveolus; the replaced tooth likely is removed mechanically during feeding as the replacement tooth rises into the alveolus. The mosasaur form of tooth attachment is certainly thecodont and raises intriguing questions about the evolution of pleurodonty and acrodonty within lepidosauromorphs. Likewise, the pattern of tooth replacement in mosasaurs appears to be unique among squamates specifically, and among thecodont amniotes generally. The conclusion that mosasaurs possess the attachment tissues used to diagnose thecodont ankylosis are explored further here, and examined in the context of a reassessment of the pattern of mosasaur tooth replacement.

MIDDLE EAR ANATOMY IN UPPER CRETACEOUS MOSASAURS (SQUAMATA): FROM IMPEDANCE MATCHING TO UNDERWATER HEARING

MICHAEL W. CALDWELL, Department of Earth and Atmospheric Sciences, and Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada; ALEXANDER DUTCHAK and TAKUYA KONISHI, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

The anatomical constituents of the mosasaurid middle ear are seldom preserved in their entirety in any one mosasaur specimen as the elements are represented by three skeletal types: 1) ossified endochondral elements; 2) non-ossified/non-calcified cartilaginous elements; 3) calcified cartilage elements. However, by study of many different mosasaur specimens from around the globe, preserved in a variety of sediments and affected by a variety of taphonomic conditions, we have collected sufficient data to reconstruct the middle ear skeleton in its entirety. Beginning externally, we identify a massive, plate-like element laying across the expanse of the quadrate conch, with a short, internally trifurcating process that extends towards the stapedial opening, as the expanded and fused pars superior, pars inferior and processus posteriorus of the extracolumella. In this regard, we agree in large part with previous identifications as given by Camp (1942). This element has traditionally been identified, even since Camp, as an ossified tympanum, a myth, which has persisted for nearly one hundred years, but is dispelled here. We differ from Camp (1942) in our identification of the elements internal to the stapedial foramen, medial to the quadrate. As the extracolumella passes through the stapedial foramen, the shaft does not articulate with the processus internus, but rather is fused to it so that the processus internus appears to be a middle ear bifurcation of the extracolumellar shaft. The head of the processus internus inserts into the characteristic mosasaurid stapedial pit. The length of the fused calcified cartilaginous shaft of the processus internus + extracolumella is extremely long, tapering medially as it approaches the very delicate, ossified, columella. Our new reconstruction of the middle ear anatomy of mosasaurs necessitates two major considerations: 1) re-evaluation of anatomical nomenclature as applied to the process internus; 2) re-evaluation of the acoustic capacity of mosasaurs as it is not clear if they retained any capacity for impedance-matching hearing in such a massive middle ear skeleton. The phylogenetic implications of this anatomy will be discussed by comparison to more basal mosasauroids, snakes, and other lizards.

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A RETURN TO THE ANCESTRAL FEEDING MODE IN AQUATIC FROGS

CARRIE A. CARRENO, Northern Arizona University; KIISA C. NISHIKAWA, Northern Arizona University

The family Pipidae is a basal lineage of frogs known from the early Cretaceous, but these frogs are now highly derived, exhibiting unusual morphology and behavior. Unlike most frogs, pipids are strictly aquatic and are well adapted for their aquatic lifestyle. They are dorso-ventrally compressed, have large webbed feet, and a lateral line system. Most frogs feed by flipping their tongue out of their mouth. However, frogs of the family Pipidae have secondarily lost their tongues thereby necessitating an alternate method of prey capture. Most aquatic vertebrates use suction to capture prey. To create suction, rapid buccal expansion drops the internal buccal pressure below ambient pressure. Water is then drawn into the mouth, as is the prey item. Based on their aquatic habit and tonguelessness, we hypothesize that pipid frogs use suction to capture prey underwater.

We examined aquatic feeding in pipid frogs using high-speed image analysis (500 fps), pressure recordings (1000 Hz), and anatomical measurements. We examined species from each of the four pipid genera (*Pipa*, *Xenopus*, *Hymenochirus* & *Pseudhymeochirus*). All pipids examined were found to generate suction during prey capture. The magnitude of the pressure drop was greatest during prey capture (*P. pipa* mean ñ0.8 kPa, max ñ2.6 kPa; *X. laevis* mean -1.7 kPa, max. -8.7 kPa) and decreased subsequently during prey manipulation and transport. The mean rate of pressure change was ñ20.7 kPa s-1 in *P. pipa* and ñ57.8 kPa s-1 in *X. laevis*. The buccal cavity of pipid frogs is greatly enlarged and was found to expand to 12-30% of total body volume, far more than terrestrial frogs (4%). Both the sternum and hyoid of pipids are expanded and modified, likely providing additional attachment sites for muscles used during buccal expansion.

STABLE ISOTOPE EVIDENCE OF DIETARY DIVERSIFICATION, SPECIALIZATION, AND STASIS WITHIN THE SIRENIA

MARK CLEMENTZ, Smithsonian Marine Station at Fort Pierce, FL; PAUL KOCH, University of California, Santa Cruz; DARYL DOMNING, Howard University, Washington, DC; LAWRENCE BARNES, Natural History Museum of Los Angeles County, CA; BRIAN BEATTY, University of Kansas, Lawrence, KS

The record of morphological change associated with the adaptation of sirenians to the aquatic environment is well documented by recent fossil discoveries, but how these changes relate to ecological transitions within this group remains unclear. Application of a coupled carbon and oxygen isotope analysis can provide new insight into how and when the diet and habitat preferences of sirenians changed during the transition from terrestrial to marine ecosystems. The carbon isotope ($\delta^{13}C$) values of enamel are controlled by diet and are labeled by the $\delta^{13}C$ composition of primary producers at the base of the food web. Because mean $\delta^{13}C$ values for aquatic and terrestrial vegetation differ significantly, enamel $\delta^{13}C$ values can be used to discriminate among freshwater herbivores (low $\delta^{13}C$), terrestrial herbivores (intermediate ($\delta^{13}C$), marine algal consumers (intermediate to high $\delta^{13}C$), and seagrass consumers (very high $\delta^{13}C$). Likewise, habitat information can be interpreted from mean enamel oxygen isotope ($\delta^{18}O$) values, which reflect the $\delta^{18}O$ composition of environmental waters, and thereby distinguish marine (high $\delta^{18}O$) and freshwater (low $\delta^{18}O$) taxa. However, physiological and dietary differences also influence enamel $\delta^{18}O$ values, which complicates interpretation of mean values. An alternative is to look first at differences in $\delta^{18}O$ variance among populations, which can differentiate between aquatic (low variance) and terrestrial (high variance) fauna, and then use mean $\delta^{18}O$ values to interpret habitat preferences. In combination, $\delta^{13}C$ and $\delta^{18}O$ values provide a powerful tool for gathering ecological information from fossil sirenians that is completely independent of morphology.

To examine changes in feeding and habitat preferences of sirenians through time, we analyzed the carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope composition of tooth enamel from several sirenian species found in three regions: the West Atlantic – Caribbean; Tethys – Mediterranean; and Eastern Pacific. In the West Atlantic – Caribbean, fossil material from the earliest family of sirenians, the Prorastomidae, were sampled from the early Middle Eocene. Because these taxa were capable of terrestrial locomotion, the prorastomids were not limited to aquatic resources and may have also consumed terrestrial vegetation. High enamel $\delta^{13}C$ and $\delta^{18}O$ values, however, indicate that these early taxa were consuming mostly seagrasses and were spending a significant amount of time within marine waters. Later protosirenids and dugongids sampled from this region and the Tethys-Mediterranean had similarly high $\delta^{13}C$ and $\delta^{18}O$ values, which suggest these groups were seagrass specialists throughout the Cenozoic. Only with the appearance of the Trichechidae in the West Atlantic – Caribbean and the Hydrodamalinae in the Eastern Pacific does this pattern change. Early trichechids (i.e., *Potamosiren*) from the Middle Miocene have extremely low $\delta^{13}C$ and $\delta^{18}O$ values, which are indicative of a diet composed largely of freshwater vegetation. Enamel $\delta^{13}C$ and $\delta^{18}O$ values of later trichechids sampled from Florida, however, rose significantly in the Pleistocene and indicate increased consumption of marine seagrasses. In the Eastern Pacific, Middle Miocene hydrodamalines (i.e., *Dusisiren*) had high mean $\delta^{18}O$values and intermediate $\delta^{13}C$ values, suggesting a diet composed mostly of marine algae and very little, if any, seagrass. Unlike trichechids, later hydrodamalines show consistent mean $\delta^{13}C$ values all the way into Holocene, signifying that these sirenians were specialized algivores and not dietary generalists.

GETTING LEGLESS: DEVELOPMENTAL MECHANISMS OF VERTEBRATE LIMB EVOLUTION

MARTIN J. COHN, Department of Zoology, University of Florida, Gainesville, FL

The origin of the vertebrate limb skeleton involved induction of a new distal axis of outgrowth as well as a new tissue type, cartilage, in the lateral plate mesoderm. Over the past few years, our understanding of the evolutionary history of limbs has been improved by important new discoveries in the fossil record. Additionally, rapid progress has been made in identifying molecular basis of vertebrate limb development. It is now possible to integrate these two areas of research in order to identify the molecular developmental mechanisms underlying the origin and subsequent evolution of paired appendages in vertebrates. After the origin of paired appendages, several vertebrate lineages reduced or eliminated fins and limbs and returned to the limbless condition. Examples include cetaceans, snakes, eels, caecilians, and skinks. Analyses of fossil and extant vertebrates show that evolution of limblessness frequently occurred together with elongation of the trunk and loss of clear morphological boundaries in the vertebral column. This may be suggestive of a common developmental mechanism linking these two processes. This talk will address these questions at the interface of development and evolution of the postcranial skeleton, and describe how they are being addressed with developmental tools in a phylogenetic context.

EVOLUTION OF THE CETACEAN MANUS: PATTERNS OF REDUCTION, HYPERPHALANGY, AND POLYDACTYLY

LISA N. COOPER, Department of Anatomy, Northeastern Ohio Universities College of Medicine, 4209 State Route 44, Rootstown, OH 44272-0095 and ANNALISA BERTA, Department of Biology, San Diego State University, 5500 Campanile Dr., San Diego, CA 92182

Among secondarily aquatic tetrapods, extinct marine reptiles and extant cetaceans have independently acquired similar patterns of digit elongation and reduction. The objectives of this study were to conduct a survey of cetacean digit and phalanx counts, trace the evolution of hyperphalangy in a phylogenetic context, test previously published digit loss hypotheses, and comment on the broad patterns of convergence in the reptilian and cetacean manus. In cetaceans and marine reptiles the manus is elongated by increased numbers of phalanges (hyperphalangy) beyond the plesiomorphic condition of 2/3/4/5/4 for reptiles and 2/3/3/3/3 for mammals. Marine reptiles may exhibit hyperphalangy in all digits, while it is restricted to a few digits in cetaceans. Some marine reptile and cetacean groups have also lost a digit. Some ichthyopterygian marine reptiles (i.e *Stenopterygius*) are reported to have lost either digit I or V, and a similar uncertainty surrounds three families of mysticete cetaceans (Balaenopteridae, Neobalaenidae, and Eschrichtiidae), with the missing digit identified as digit I, III, or V by various authors. Data come from published descriptions, dissections, and examination of osteological specimens and radiographs. Regarding hyperphalangy, odontocetes exhibit hyperphalangy in digits II and III, while digits III and IV display hyperphalangy in mysticetes. Furthermore, the first ossified supernumary digit in a mysticete manus is reported and compared to previously published reports of cetacean and fossil marine reptilian anomalous digits.

ACOUSTIC ADAPTATIONS FOR DEEP DIVING IN ODONTOCETES

TED W. CRANFORD, MEGAN F. MCKENNA, BRIDGETT KNOWLES, AND ANNALISA BERTA, Department of Biology, San Diego State University, San Diego, CA

A recent spate of whale deaths has been associated with exposure to high intensity sound. These events have provided an impetus to study the anatomic geometry of the most effected, yet little-known group of cetaceans, the beaked whales (Family: Ziphiidae). Decades of research have provided significant understanding of the anatomy of acoustic transmission and reception in adult dolphins (Family: Delphinidae). Comparisons between the cephalic anatomy of an adult Cuvier's beaked whale (*Ziphius cavirostris*) and an adult bottlenose dolphin (*Tursiops truncatus*), as shown by CT scans, yield numerous acoustically relevant similarities and differences. Chief among the anatomic differences is that *Ziphius* has a broad band of dense connective tissue that wraps around its melon in an arch that is anchored to the skull and forms part of the beam formation apparatus. The deep diving odontocetes, primarily sperm whales and beaked whales, have a pair of pterygoid sinuses with a surprisingly large air capacity. All odontocetes possess pterygoid sinuses that narrow posteriorly before they ramify to form a series of pockets on the medial aspect of each bony hearing complex (tympanoperiotic). These diverticula are inflated through the Eustachian tube and are juxtaposed to an extensive fibrous venous plexus. These anatomic anomalies within specific groups of the odontocetes may indicate different strategies for the deepest divers among them. The tendency is for deep diving species to use dense connective tissue boundaries where other species might use air as an acoustic reflector. At the same time, the deep divers apparently reserve most of their air volume, which decreases with depth, as a means to isolate the hearing complexes acoustically and maintain directional hearing. Other morphological relationships, like those between the mandibular fat bodies and the bony hearing apparatus, the internal structure of the melon, and the bilateral structure of the phonic lips are, overall similar across the entire suborder. These unprecedented comparisons of anatomic geometry have also spawned novel perspectives on transmission beam formation and the mechanism of hearing in odontocetes.

PALATE VASCULARIZATION IN AN OLIGOCENE TOOTHED MYSTICETE (CETACEA: MYSTICETI: AETIOCETIDAE); IMPLICATIONS FOR THE EVOLUTION OF BALEEN

THOMAS A. DEMÉRÉ, Department of Paleontology, San Diego Natural History Museum, San Diego, CA

Additional preparation of the palate of the holotype of *Aetiocetus weltoni*, a late Oligocene toothed mysticete from the Yaquina Formation of Oregon, USA, has revealed a series of delicate foramina on the lateral half of the maxillae. Each foramen occurs at the rear of a shallow sulcus and is closely positioned within 3 to 9 mm of the lingual margin of the adjacent tooth. The longitudinal orientation of the sulci relative to the sagittal plane varies from back to front (i.e., 40º at M2, 60º and 25º at M1, 20º at P4, 10º at P3, 2º at P2, and 0º at P1. These lateral palatal foramina may be homologous with the prominent baleen nutrient foramina in edentulous mysticetes.

The palates of adult mysticete cetaceans are marked by numerous foramina and associated sulci. A general distinction can be made between foramina positioned near and parallel to the midline and foramina more laterally placed and often radially arranged. The latter foramina provide passage of the rich blood supply to the baleen racks. In fetal specimens of modern mysticetes the lateral foramina have not yet formed and instead there is a distinct open alveolar groove running along the lateral margin of the flat palate. Embryologically, this alveolar groove is the site of the developing temporary dentition, which passes through the bud, cap, and bell stages of development before degradation and resorption of the deciduous tooth buds begins. Dermal papillae of the rudimentary baleen plates begin to develop coincident with tooth bud degradation. At the same time the open alveolar groove starts to fill with bone until finally the distinct lateral nutrient foramina begin to form. This progressive ossification also involves a widening of the palatal region above the developing baleen racks.

Given the close association between tooth and baleen development observed in modern mysticetes it is plausible that we are seeing an ancient ontogeny played out in *Aetiocetus*. The form of this early baleen system of *Aetiocetus* is currently unknown, but perhaps it consisted of small bundles of keratinized tubules similar to those occurring at the front and rear of the main baleen racks of modern balaenopterids. In *Aetiocetus* such bundles could have formed a rudimentary filter between the widely spaced teeth of the upper dentition.

EVOLUTION OF THE VOMERONASAL SYSTEM IN AQUATIC VERTEBRATES

HEATHER EISTHEN, Michigan State University, East Lansing, MI

The vomeronasal system is an accessory olfactory system in vertebrates that is evolutionarily newer than the main olfactory system. Vomeronasal receptor neurons are located in a specialized epithelium that is physically separate and anatomically distinct from the main olfactory epithelium. Olfactory and vomeronasal receptor neurons express different classes of G-protein-coupled receptors, and their axons project to the main and accessory olfactory bulbs, respectively.

The vomeronasal organ and accessory olfactory bulb are generally present in tetrapods, and have not been found in any of the fishes that have been examined. Although the function of the vomeronasal system is unclear, it may function to detect large molecules of biological origin that are of sufficiently high molecular weight that they do not become airborne and cannot contact the olfactory receptor epithelium; in mammals, these large molecules include some pheromones. Because of both its anatomical distribution and its presumptive function, the vomeronasal system has been suggested to have arisen when vertebrates became terrestrial.

I have examined the anatomy of the nasal cavities and olfactory bulbs in larvae or unmetamorphosed adults, or both, from five families of salamanders: sirenids, amphiumids, proteids, salamandrids, and ambystomids. These data indicate that the vomeronasal system is present in most larval and aquatic adult salamanders, and is lost in the proteid family. Given that a vomeronasal organ also seems to be present in embryonic and larval frogs, these data suggest that the system is present throughout life in amphibians and does not develop at metamorphosis, as one might expect for a feature that arose as an adaptation to terrestrial life. Further, because the vomeronasal system is generally present in extant amniotes as well as extant amphibians, it must have been present in the last common ancestor. Paleontological evidence suggests that this common ancestor was fully aquatic, indicating that the vomeronasal system could not have arisen when vertebrates became terrestrial.

What is the function of the vomeronasal system in aquatic amphibians? We are currently working on this problem in my lab using electrophysiological recordings from the olfactory and vomeronasal epithelia of axolotls (*Ambystoma mexicanum*), a nonmetamorphosing salamander. To date, we have found few consistent differences in responsiveness of olfactory and vomeronasal epithelia to a wide range of odorants, including whole-body odorants from male and female conspecifics, axolotl bile acids, odorants from food pellets, amino acids, and volatile odorants.

DYNAMICS OF THE AERIAL MANEUVERS OF SPINNER DOLPHINS: ASSOCIATION OF MECHANICS WITH EXTREME PERFORMANCE

FRANK FISH, West Chester University; ANTHONY NICASTRO, West Chester University; DANIEL WEIHS, Technion, Israel Institute of Technology

The spinner dolphin (*Stenella longirostris*) performs spectacular leaps from the water while rotating around its longitudinal axis up to seven times. Although twisting of the body while airborne has been proposed as the mechanism to effect the spin, the morphology of the dolphin and basic physics precludes the spinning maneuver. A mathematical model was developed that demonstrates that angular momentum to induce the spin was generated underwater, prior to the leap. Subsurface corkscrewing motion represents a balance between drive torques generated by the flukes and by hydrodynamic forces at the pectoral fins, and resistive torques, induced by the drag forces acting on the rotating control surfaces. As the dolphin leaps clear of the water, this balance no longer is maintained and a net drive torque remains, which permits the dolphin's rotation speed to increase by as much as a factor of four for a typical specimen. The model indicates that the high rotation rates and orientation of the dolphin's body during re-entry into the water could dislodge hydrodynamically-parasitic remoras.

THE MYOLOGY OF THE PYGMY HIPPOPOTAMUS (*CHOEROPSIS LIBERIENSIS*): MUSCLES OF THE FORE AND HIND LIMB

REBECCA E. FISHER, Midwestern University (Arizona College of Osteopathic Medicine); KATHLEEN M. SCOTT, Rutgers University; VIRGINIA L. NAPLES, Northern Illinois University

There are two extant species of hippopotami, the common hippo (*Hippopotamus amphibious*) and the pygmy hippo (*Choeropsis liberiensis*). Based on morphological analyses, hippos have traditionally been classified as Suiformes, along with pigs and peccaries. However, molecular studies indicate hippos and cetaceans are sister taxa. Hippos are the only semi-aquatic artiodactyls, and show marked morphological adaptations for this lifestyle. However, the two extant species of hippo differ in their degree of aquatic specialization and size, making them ideal subjects for the comparative study of limb morphology. In this study, we document muscle origins and insertions in the pygmy hippo fore and hind limb. Dissections were conducted on two specimens received from the National Zoo. Observations were recorded via detailed muscle descriptions, digital photographs, and muscle maps for all postcranial elements. In addition, moment arm, muscle weight, fiber length, and fiber angle were measured for each muscle. Dissections revealed that pectoralis superficialis, pectoralis profundus, supraspinatus, infraspinatus, and gluteus medius are characterized by broad sites of origin in the pygmy hippo, compared to other artiodactyls. Published descriptions of these muscles in the common hippo also indicate extensive origins. Thus, muscles responsible for supporting the trunk, fixing the forelimb, and retracting the fore and hind limb are especially well-developed in hippopotami. Dissections also demonstrated a full complement of interossei muscles (two per digit), and a well-developed lumbrical muscle in both the manus and pes. The presence of additional digital adductors would function to prevent abduction of the toes in hippos. This arrangement would be particularly advantageous in an animal walking on soft, muddy terrain. In addition, the long flexor tendons serve each of the digits, reflecting the fact that all toes are weight-bearing in hippos. Finally, based on our pygmy hippo dissections and published accounts of common hippos, hippopotami are unique among artiodactyls in having a palmaris longus, flexor digitorum brevis, articularis coxae, and a well-developed obturator internus. These findings support the hypothesis that hippos are the product of an evolutionary trajectory distinct from other artiodactyls. Additional studies of facial and trunk muscles may help determine whether this trajectory was one more closely allied to that of Cetacea.

TOOTHED MYSTICETES (MAMMALIA: CETACEA) FROM THE LATE OLIGOCENE OF AUSTRALIA

ERICH M. G. FITZGERALD, School of Geosciences, Monash University, and Geosciences, Museum Victoria, Melbourne, Victoria, Australia

The first toothed baleen whale (Cetacea: Mysticeti) known to science, *Mammalodon colliveri* Pritchard 1939, was discovered in Australia in 1932. However, very little new information on the morphology and phylogeny of Australian toothed mysticetes has come to light since that time. *M. colliveri* (Museum Victoria Palaeontology-NMV P-199986) is now known to be one taxon amongst a hitherto unrecognized diversity of Late Oligocene SW Pacific toothed mysticetes. These archaic, small (max. CBL <60 cm) baleen whales were all derived from the Upper Oligocene (Chattian; planktonic foram zone P22; 24-27 Ma) Jan Juc Marl, and its lateral equivalent the Point Addis Limestone, in coastal Victoria, SE Australia.

Mammalodontidae Mitchell 1989 is represented by *Mammalodon colliveri*, a new species of *Mammalodon* (NMV P48794), an incomplete skeleton (NMV P199587) referred to Mammalodontidae genus and species indet., and several isolated periotics. Possible synapomorphies of Mammalodontidae include: foreshortened, rounded rostrum; atrophied and delicate premaxilla bearing only 1-2 incisors; ascending process of maxilla is tongue-shaped with concave dorsal surface; on periotic, dorsal facial foramen is separated from rest of internal acoustic meatus by salient crista transversa, and lateral rim of internal acoustic meatus is elongated towards cranial cavity forming a longitudinal ridge. Two other specimens, NMV P216928 and P216929 represent two new species, in at least one new genus, within a new family of toothed Mysticeti. NMV P216929 is the most complete Paleogene cetacean discovered in Australia. NMV P216929 is brevirostral, like *Mammalodon*, but possesses a distinct suite of primitive and derived features: prognathous incisors; robust apical premaxillae; mesorostral groove is closed anteriorly; double-rooted cheek teeth with well-developed accessory denticles and ornamentation on crown; last upper molar is M2; ascending process of premaxilla terminates anterior to posterior margin of nasal; inflated zygomatic process of squamosal; low sagittal crest; and posterolaterally flared nuchal crests.

These fossils indicate that at least four, and perhaps as many as five, species of toothed mysticete inhabited the seas around southeast Australia during the Late Oligocene. These taxa belong in two distinct families. Thus, Late Oligocene SW Pacific toothed mysticete faunas seem to have been markedly different to those of the North Pacific, which were apparently dominated by one family, the diverse Aetiocetidae. None of the Australian toothed mysticetes appear closely related to North Pacific aetiocetids. Morphological disparity amongst the SW Pacific, N Pacific, and NW Atlantic, toothed mysticetes suggests that toothed Mysticeti may have employed a wider range of feeding methods than previously thought. Furthermore, Australian fossils, with those from elsewhere, indicate that at least five distinct families of toothed Mysticeti existed during the Oligocene.

MIOCENE ZIPHIIDS (CETACEA: ODONTOCETI) FROM THE CHESAPEAKE GROUP OF CALVERT CLIFFS, MARYLAND, U.S.A.

ANNA J. FULLER, Calvert Marine Museum; STEPHEN J. GODFREY, Calvert Marine Museum.

More than 600 species have been identified from Miocene sediments along Calvert Cliffs, Maryland including a diverse assemblage of approximately 30 extinct species of cetaceans (both odontocetes and mysticetes). In terms of vertebrate remains, those of cetaceans are second only to the number of chondrichthian teeth that erode from the length of Calvert Cliffs and their extensions out under the waters of the Chesapeake Bay.

However, fossil ziphiids from Calvert Cliffs are exceedingly rare and to date, are known by only two specimens: CMM-V-3138 and USNM 476359. Previous reports of ziphiid remains from Calvert Cliffs were erroneous. CMM-V-3138 consists of a partial rostrum derived from the St. Marys Formation. It shares with *Messapicetus longirostris*, from South Italy, unique features of the rostrum. Both this specimen and the Italian form are from the lower Upper Miocene Tortonian Stage.

USNM 476359 consists of the prenarial region of a cranium including a nearly complete rostrum. It was dredged offshore by oyster fishermen and is likely derived from the Choptank Formation (Middle Miocene Serravallian Stage). The configuration of the mesorostral canal, premaxillae, and maxillae affiliate USNM 476359 with *Choneziphius*. *Choneziphius* has been reported from Miocene and/or Pliocene deposits in England, Italy, and Belgium, as well as more locally from South Carolina, U.S.A.

If these Miocene ziphiids preferentially inhabited deep-water marine environments, as do their living relatives, then, that ziphiid remains are so scarce within the Chesapeake Group is potentially a paleoenvironmental artifact. This we attribute to the relatively shallow water within the Miocene epicontinental Salisbury Embayment, rather than their absolute rarity within the Miocene western North Atlantic.

USING SIMULTANEOUS ANALYSES OF MOLECULAR AND MORPHOLOGICAL DATA TO RESOLVE DELPHINIDAN PHYLOGENY

JONATHAN H. GEISLER, Museum and Dept. of Geology and Geography, Georgia Southern University; JOHN GATESY, Dept. of Biology, University of California, Riverside

We report preliminary results of our study on the phylogeny of Delphinida, which includes the living cetacean families of Delphinidae, Phocoenidae, Mondontidae, Iniidae, Pontoporiidae, and Lipotidae as well as the wholly extinct families of Albireonidae, Kentriodontidae, and Odobenocetopsidae. To resolve delphinidan phylogeny, we gathered new morphological and molecular data and concatenated it with published data sets to create a matrix of 65 taxa (of which 40 are extinct) scored for 328 morphological characters, 25 transposon characters, and 945 informative nucleotide characters distributed across 7.4 kilobases. A parsimony analysis of this dataset found 78 most parsimonious trees each 6,796 steps in length. The strict consensus of the trees had 83% of the nodes resolved. As in several previous studies, we found a monophyletic Delphinoidea, a sister-group relationship between Monodontidae and Phocoenidae, and *Inia* and *Pontoporia* to be sister-groups. The extinct delphinidan *Parapontoporia* grouped with the Yangtze River dolphin, *Lipotes*, to form Lipotidae, which we found to be the most basal delphinidan clade. Perhaps the most surprising result concerned the paraphyletic family Kentriodontidae. The two species we sampled, *Kentriodon pernix* and *Liolithax pappus*, were excluded from Delphinida and instead were successive sister-taxa to the clade including Delphinida + Platanistoidea.

We optimized several morphological characters found in all or most extant species of river dolphins onto our most parsimonious trees. Previous authors had speculated that these characters were convergent and reflect adaptations to similar habitats, but our results suggest that most of these characters are symplesiomorphies. Given the disparate distribution of extant river dolphins, many have presumed that their ancestors were marine and the current distribution reflects three separate invasions of river systems. If only the distributions of extant taxa are mapped onto our trees; however, it is equally parsimonious to infer a freshwater ancestor for *Inia*, *Pontoporia*, *Platanista*, and *Lipotes*. When fossils from marine deposits are included in analysis, the hypothesis that each of the extant river dolphins evolved independently from different marine ancestors is favored.

SEMICIRCULAR CANAL SHAPE IN TERRESTRIAL AND AQUATIC NON-SYNAPSID VERTEBRATES

JUSTIN A GEORGI, Stony Brook University; JUSTIN SIPLA, Stony Brook University.

The vertebrate vestibular system is stimulated by movements of the head. Linear accelerations are sensed by the utricular system and rotational accelerations are sensed by the semicircular canals. Synthesis of this sensory information into a 3-dimensional representation of head movement is required for precise control of the spinal, cervical and extraocular musculature which stabilize the head and eyes. Such stability ensures that a consistent image falls upon the retina and reduces blurred vision during head movements. This relationship between the vestibular system and head movement has spawned a family of hypotheses relating the specific morphology of the vestibular system to specific modes of locomotion employed by different organisms. This study examines the changes in vestibular morphology as they relate to transitions from terrestrial to aquatic locomotion.

Here we present data on the shape of the semicircular canals of select non-synapsid vertebrates, focusing on specific groups that encompass both aquatic and terrestrial taxa. Via elliptical fourier analysis, the aspect ratio of the anterior semicircular canal is shown to correlate with the range of aquatic and terrestrial behaviors in the crocodylomorph clade. Low aspect ratio canals are found in the aquatic fossil crocodylomorphs *Metriorhynchus* and *Rhabdognathus* as well as the more aquatic extant crocodilians such as Gavialis. Fossil crocodylomorphs with possible fully terrestrial lifestyles such as *Araripesuchus*, *Simosuchus* and the newly described *Jungarrsuchus* have anterior canals with high aspect ratios. Extant crocodilians with semiaquatic locomotor capacity show an intermediate canal aspect ratio.

The canal morphologies of the same locomotor categories are then examined in varanoids and testudines to broaden our survey of aquatic adaptations of the vestibular system. This is the first step of a larger study investigating vestibular morphology across amniotes and its relationship with many aspects of the distinct morphologies associated with aquatic behavior.

SINKERS NOT SWIMMERS: THE HISTOLOGICAL ANALYSIS OF BONE FROM EARLY CETACEA AND TETHYTHERIA.

NOEL-MARIE GRAY, Hiram College Biology; S. I. MADAR, Hiram College Biology.

Previous analyses have shown that the several Eocene archaeocetes (e.g. *Ambulocetus*, *Basilosaurus*) exhibit microstructural changes in bone associated with aquatic lifestyle similar to that of modern sirenians and other secondarily aquatic tetrapods. Here we study the bone histology of early cetaceans, including members of the Pakicetidae, Ambulocetidae, Protocetidae, Remingtonocetidae, and Basilosauridae, representing the first ten million years of their evolutionary transition to obligate aquatic habitats. Each taxon shows signs of secondary osteological specialization, thought to be attributed to development of a complex buoyancy control system. In addition, several tethytherians (sirenians and proboscidean anthracobunids) found at the same localities as early cetaceans are examined histologically for similar osteological signs of aquatic adaptations. We describe the patterns of osseous adaptations in the earliest cetacean lineages, and then examine whether the tethytherians and cetaceans achieve their osteological specializations in the same manner. We will also attempt to understand the mechanism of bone development in these mammals via a comparison to a range of modern aquatic and terrestrial mammals. While little outward skeletal aquatic specialization is seen, histological analysis clearly shows increased bone density that is dependent on an aquatic environment in all early whales as well as several early members of the Tethytheria.

A COMPARISON BETWEEN THE HEARING ORGANS OF THE HARP SEAL (*PHOCA GROENLANDICA*) AND THE HARBOR PORPOISE (*PHOCOENA PHOCOENA*) USING ULTRA-HIGH RESOLUTION CT-DATASETS.

JOHANNES HARBERING, University of Frankfurt, Germany; LARS KOSSATZ, University of Frankfurt, Germany; MICHAEL KNAUTH, University of Goettingen, Germany; CHRISTIAN DULLIN, University of Goettingen, Germany; CHRISTIAN LYDERSEN, Norwegian Polar Institute, Tromso, Norway; KIT KOVACS, Norwegian Polar Institute, Tromso, Norway; HELMUT A. OELSCHLÄGER, University of Frankfurt, Germany

Aim of study: Using ultra-high resolved isotropic CT-datasets, we evaluate the anatomy of the hearing organs of the harp seal and harbor porpoise in order to compare two lines of evolutionary and functional adaptations to aquatic life.

Methods: We scanned two juvenile heads of each species using a flat-panel-detector Volume-CT-Scanner (General Electrics). Volume-CT creates datasets with an isotropic spatial resolution in the order of 0.1 mm, which is about five times higher than that of the most advanced multislice-CT-scanners. To show the position of the ear bones with respect to the rest of the skull we documented the heads with an isotropic resolution of 0.095 mm to achieve optimal raw data for 3D reconstructions. Multiplanar and 3D reconstruction were performed using the VITREA 2 (Toshiba/Vital Images, Neuss, Germany) and Amira Graphics™ software running on commercially available workstations.

Results and Discussion: With ultra-high resolution CT-scanning (Volume-CT) isotropic resolutions in the range of 0.1 mm can be achieved, allowing the minute depiction of osseous structures as fine as the crura of the stapes or the spiral lamina of the cochlea. All relevant morphological details of the hearing organs in the harbor porpoise and harp seal were visualized with multiplanar and 3D reconstructions. Volume-CT-datasets with an isotropic resolution can be resliced in any direction and even curved reconstructions or transparent 3D reconstructions can be calculated.

Potential morphological adaptations to aquatic life are much more obvious in harbor porpoises than in harp seals. The main difference lies in the fact that in the porpoise the ear bones are detached from the skull as a functional unit (tympano-periotic complex) in order to achieve acoustic isolation of the hearing organ, which is thought to be a prerequisite for echolocation. This complex is in osseous contact with the squamosal bone only and suspended from the rest of the skull by ligaments. In the rostral direction, the tympano-periotic complex touches the “acoustic fat body” of the mandibular (alveolar) canal. In contrast, the hearing organ of harp seals very much resembles that of terrestrial mammals, e.g., in morphology of the ossicular chain and the inner ear structures. In comparison with porpoises, harp seals have a much better vision and sense of touch (vibrissae around nose and mouth). These systems are essential for the seal´s hunting strategy, whereas the harbor porpoise uses echolocation for prey detection, localization and pursuit. The partially striking deviations in the anatomy of the ears in harp seals and harbor porpoises mirror differences in hunting behavior and represent two morphological and functional trends in the “acoustic” adaptation of these mammals to their underwater environment.

On the other hand the seal depends on hearing on shore to identify its own pup while breeding. Pups´ calls have a major frequency component at about 1 kHz with overtones as high as 12 kHz. Adult individuals communicate at a frequency range from about 0.8 kHz (main component) to 6 kHz (overtones). Amazingly, underwater audiograms of harp seals show a frequency spectrum up to about 80 kHz. The obvious ability of hearing such high frequency sounds poses the question which middle ear structures had to change for reaching this aim.

EVOLUTIONARY TRANSFORMATIONS OF THE EARS OF SECONDARILY AQUATIC AMPHIBIANS, REPTILES, AND BIRDS.

THOMAS E. HETHERINGTON, Ohio State University.

Most amphibians and reptiles, and all birds, have auditory systems adapted for hearing aerial sound. Several lineages within these groups have become secondarily aquatic, providing opportunities to examine the evolutionary transformation of terrestrial ears into aquatic ears adapted for detecting underwater sound. Although the ears of amphibians and reptiles/birds share many similarities, significant differences exist between them, suggesting an independent origin of their terrestrial auditory systems. Study of the ears of secondarily aquatic members of these groups therefore allows a comparison of evolutionary transformations from different morphological and physiological starting points. Patterns of change in external, middle, and inner ear structures during this terrestrial-to-aquatic transition will be examined by comparison of several aquatic lineages (both extant and fossil) with their terrestrial sistergroups. Although many lineages of amphibians, reptiles, and birds have become secondarily aquatic, most have evolved an amphibious lifestyle, spending considerable time on land or at the air/water interface. These groups typically have ears that retain most features of a terrestrial auditory system, suggesting a functional emphasis on airborne sound reception. For example, certain specialized features, such as peripheral tissues that prevent water from entering the external ear canal of crocodilians and many aquatic birds, are adaptations to facilitate hearing in air rather than in water. Of more interest are the transformations of the ears of true aquatic specialists that appear to have auditory systems adapted for underwater hearing (e.g., pipid frogs, sea turtles, mosasaurs, etc.) These lineages typically show dramatic modification of the external and middle ear and will be examined in detail.

CEPHALIC VASCULAR ANATOMY OF THE CARIBBEAN FLAMINGO (*PHOENICOPTERUS RUBER*) USING HIGH-RESOLUTION CT IMAGING AND DIGITAL SOFT-TISSUE RECONSTRUCTION

CASEY HOLLIDAY, Ohio University; RYAN RIDGELY; LAWRENCE WITMER; Ohio University; AMY BALANOFF, University of Texas

The head of a Caribbean Flamingo (*Phoenicopterus ruber*) was subjected to differential-contrast dual-vascular injection (DCDVI), a new technique developed in the lab allowing discrimination of arteries and veins in CT imagery. Vessels were cannulated and injected with an injection medium consisting of two different concentrations of barium sulfate and latex: 40% barium/red latex for arteries and 20% barium/blue latex for veins. The specimen was scanned at the high resolution X-ray CT facility at the University of Texas, Austin. Vessels were digitally segmented via 3D reconstruction using Amira (v 3.1) software to facilitate topographical visualization, and the specimen subsequently was dissected. These anatomical and digital postprocessing techniques enabled the identification of a relatively complete vascular skeleton, a previously undescribed, bilateral, paralingual cavernous sinus as well as numerous arteriovenous vascular devices. The paralingual vascular sinus is intimately associated with the hyolingual vasculature and musculature as well as the medial aspects of the jaw muscles. Other notable vascular devices include the ophthalmic rete, palatal plexus, and suborbital plexus. Techniques such as these greatly enhance our ability to discern anatomical patterns between the bony and vascular skeleton prior to destructive techniques. Additional imagery can be seen at www.digimorph.org.

MAMMALIAN TEETH, DEVELOPMENTAL MODELS AND SEALS

AAPO T. KANGAS, University of Helsinki; JUKKA JERNVALL, University of Helsinki

Shaping teeth during development requires many molecular signaling factors. Modifying existing developmental molecular interactions is in the core of organic evolution. This co-option and reorganization takes place both in reshaping of existing organs as well as in creation of novelties. A telltale fact is that the signaling factors (and the genes encoding them) are shared by practically all organs. This also suggests that convergent evolution of tooth cusps, for example, is likely to involve tinkering with the same molecular interactions. Mammals of different lineages have frequently evolved similar tooth morphologies. Frequent convergence can be a problem for phylogenetic work relying largely on dental characters. An example of convergent evolution of dental form in aquatic mammals can be found in Phocid seals whose teeth resemble that of early whales. Explanations for these convergent tooth morphologies have been suggested from the facts that they both are aquatic groups with a trend of morphological simplification of tooth shape in response to similar changes in diet. An additional hypothesis that we would like to explore here is that, due to the way teeth are made during development, simplification of tooth shape may in itself predispose to convergent evolution. We first determined the tooth shape and its variation in different populations of ringed seals (*Phoca hispida*). Next we examined whether population size and genetic variation affect the amount of morphological variation. We then reproduced the variation found in seal tooth shapes by using a computer based simulation on tooth development. This model links a simple gene-network model with tissue growth and enables us to determine how many developmental parameters and how large changes in parameters are needed to simulate the morphological variation found in seal teeth. Finally, we tested whether the model parameters reproducing variation in seal teeth might correspond to genes implicated in causing simplification of tooth cusp patterns in experimental mice.

DEPOSITIONAL ENVIRONMENTS OF THE EOCENE WHALE-BEARING STRATA OF INDIA: INFERENCES ABOUT PALEOECOLOGY

VIVESH V. KAPUR, Department of Earth Sciences, Indian Institute of Technology, Roorkee, India

Depositional environments of the early Tertiary sedimentary sequences producing archaeocetes provide the much- needed information on the physical context of early whale evolution. In India, sediments yielding fossil whales are exposed primarily in three areas. The best known occurrences are in Kachchh region of the western Indian state of Gujarat, where fossil whales are found in the early Eocene Naredi Formation and the overlying middle Eocene Harudi Formation. The Naredi whales are found in beds that are stratigraphically adjacent to thick lignitic deposits (e.g. Panandhro Mine). These beds (grey siltsones/shales) indicate backswamp/coastal marsh depositional conditions in a humid tropical climate. Associated with whales is a typical shallow marine fauna including abundant shark and ray teeth, catfishes, aquatic snakes, turtles and crocodiles. Land animals are rare. Whale remains are much more common in the Harudi sediments and come mainly from two levels: a coquina bearing abundant molluscs (Chocolate Limestone) representing a littoral environment, and the overlying gypsified shales that suggest low-energy lagoonal conditions. The associated Harudi fauna is entirely marine. It is important to note that both the Naredi and Harudi whales are dominated by the long and narrow-snouted remingtonocetids. Recent work on the middle ear and semicircular canals of some of the Harudi whales indicate their adaptation to a marine environment, consistent with the depositional setting and with the oxygen isotope data indicating their independence from freshwater. Limited data on the long bones limb and vertebral column, however, suggest that remingtonocetids may have been amphibious and probably similar to modern freshwater otters in their swimming behavior.

In the Himalyan realm, a fossil whale (*Himalayacetus subathusensis*) as old as middle Ypresian (ca. 53 Ma) is known from the lowermost part of the type Subathu Formation (equivalent to the basal black-grey facies of Sahni et al. 1981) exposed along the Kuthar Nala near Subathu, Himachal Pradesh. Here, the whale-bearing lithology comprises a hard, grey limestone with oyster bands, occurring in association with foraminiferal shales. *Himalayacetus* is still poorly known and its taxonomic affinities are in dispute, but the available information (based on morphology of the type dentary and the oxygen isotope values of the tooth phosphate) is not inconsistent with the depositional environments of the lower Subathu. The discovery of this geologically oldest whale in a typically shallow marine deposit does suggest that at least some of the whales had become amphibious/aquatic quite early in the cetacean history.

Younger (Lutetian) whales in the Subathu Formation occur in purple and red shales and siltstones (red beds) representing fluvio-deltaic environments near the top of the formation transitional with the overlying continental Murree sediments. The best known localities are near Kalakot (Jammu & Kashmir State), where isolated teeth of pakicetids are found in association with artiodactyls, perissodactyls, anthracobunids and abundant rodents.

AN OUTLINE OF THE CETOTHERES OF JAPAN

TOSHIYUKI KIMURA, Gunma Museum of Natural History; YOSHIKAZU HASEGAWA, Gunma Museum of Natural History

During the past decade, many cetothere fossils have been found from Japan. These specimens show a diverse cetothere fauna of the western North Pacific. The "Cetotheriidae" is an extinct, edentulous mysticete family ranging from the late Oligocene to the early Pliocene. They are regarded as a paraphyletic group which includes the lineage of ancestor of the Balaenopteridae and the Eschrichtiidae. They exhibit the greatest diversity during the Miocene. Forty-two cetotheres have been reported from Japan, with 22 specimens from the Miocene. Focusing particularly on the Miocene cetotheres, we present an outline of the cetotheres of Japan.

Four specimens of cetothere have been found from the late early Miocene of central Japan. *Isanacetus laticephalus* is a relatively small-sized cetothere (skull length: ca. 1 m). Relatively large-sized cetothere (length of mandible: ca. 1.8 m) has also been reported and described as Cetotheriidae gen. et sp. indet. Based on the apomorphic characters of the mandible, this specimen is regarded as a primitive engulfment feeder (Kimura, 2002).

The most abundant and diversified cetothere fossils have been found from the early middle Miocene. These fossils suggest that at least four genera (*Aglaocetus*?, *Diorocetus*, *Parietobalaena* and *Pelocetus*?) were distributed in the western North Pacific. In contrast to this, only a limited number of specimens have been reported from the late middle to late Miocene. Two cetothere specimens have been found from the late middle Miocene Haraichi Formation, Tomioka Group, one with a nearly complete skull. A balaenopterid has also been reported from the Tomioka Group.

The "Cetotheriidae" can be subdivided into two groups based on the mode of dorsal rostral telescoping. Although many cetothere fossils have been reported from Japan, none belong to the *Cetotherium*-group, which is characterized by having a rostrum posteriorly wedged in a deep V-shaped pattern. During the late early - early middle Miocene, they reached their highest diversity and at least 5 genera have been reported from Japan (*Isanacetus*, *Aglaocetus*?, *Diorocetus*, *Parietobalaena* and *Pelocetus*?), giving a diversity as high as that for present-day mysticetes in waters near Japan. This cetothere fauna roughly corresponds with that of North America.

CLOSURE AND TIMING OF CLOSURE OF THE FORAMEN OVALE IN BEARDED, RINGED & HARP SEALS: AN ADAPTATION TO DIVING?

MICHAEL KNAUTH, University of Göttingen, Germany; KIT KOVACS, Norwegian Polar Institute, Tromsö, Norway; STEFAN RIES , Neurologische Gemeinschaftspraxis, Erbach, Germany; MIKE O'HAMMILL, Department of Fisheries and Oceans, Mont-Joli, Canada; CHRISTIAN LYDERSEN, Norwegian Polar Institute, Tromsö, Norway

Introduction: The aim of our study was to determine, whether the closure and the timing of closure of the Foramen ovale in the hearts of semi-aquatic marine mammals is an adaptation to the diving performed by these animals.

Methods: This study consists of three parts. (1) and (2): We used a Doppler ultrasonic device, in combination with a sonographic contrast medium, to test whether free-living bearded seal (*Erignathus barbatus*) pups and harp seal (*Pagophilus groenlandicus*) pups have a closed (anatomically or functionally) foramen ovale (FO). These parts of the study were performed in Svalbard, Norway and in the Gulf of St. Lawrence, Canada. (3) Heart specimens of adult harp seals (n=16) and ringed seals (n=112) were dissected to determine the closure status of the Foramen ovale.

Results: (1) Bearded seals pups: A total of 17 examinations were performed on 12 bearded seal pups with a body mass range of 29–103 kg (0–21 days old). These examinations showed that young bearded seal pups dive with a patent foramen ovale (PFO), and that this structure closes, at least functionally, during the 2nd week of life. The majority of individuals older than 1 week of age had a closed FO. (2) Harp Seals pups: A total of 34 examinations were performed on 34 harp seal pups with a body mass range of 9.5-37.5 kg (0–13 days old). Harp seals do not dive during the first weeks of life. We found a closed FO in only 6 pups (18%) and even in the weight group above 30kg only 2 pups (17%) had a closed FO. Thus, harp seal pups do not seem to be in a hurry to close their FO. (3) In the adult (harp and ringed) seals all Foramina ovalia were closed, which is in contrast to the data obtained from terrestric mammals (e.g. man), in which a certain proportion of Foramina ovalia remain open even in adult life (man: 20-30%).

Conclusion: Bearded seals dive during their first week of live. The primary function of this early diving is to avoid surface predation and only moderate diving ability is sufficient to achieve this goal. However, some of the diving performed by bearded seal pups with a PFO would likely be sufficient to create intravenous bubble formation during breathhold diving in humans and after one week of life the majority of individuals have a closed PFO. In contrast, harp seals do not dive during their first weeks of life and the Foramen ovale was closed in only a minority of even the oldest animals.

Thus, early diving seems do be associated with a faster closure of the Foramen ovale. This (early) closure of the FO is probably one of several adaptations (e.g. collapsible lungs, diving with minimal lung air volume) of these marine mammals to diving. This conclusion is further endorsed by our finding, that in contrast to terrestric mammals in adult (ringed and harp) seals all Foramina ovalia were closed.

EVOLUTION OF SPECIAL TOOTH REPLACEMENTS AND DISPLACEMENTS IN THE DESMOSTYLIA AS REVEALED BY HIGH-RESOLUTION X-RAY CT.

NAOKI KOHNO, National Science Museum Japan

The enigmatic Miocene North Pacific tethythere, *Desmostylus* is often characterized by the specialized teeth. The peculiarity of the teeth in this genus is the columnar “desmostylodont” cheek teeth with “elephant-like” sequential eruption and horizontal drifts of molars during life.

Examinations of more than 10 cranial material, represented by the individuals of juveniles, sub-adults, adults, and sexually both males and females, using high-resolution X-ray CT, reveal the patterns of tooth replacements and displacements during their life. The substantial peculiarity in *Desmostylus* is the unreduced second-generation teeth with sequential displacements of almost all these teeth including incisors, canines, and premolars as well as molars. For instance, the lower second incisor is displaced sequentially by the lower third incisor, and the lower third incisor is also displaced sequentially by the lower canine during life.

These peculiar displacements of second-generation teeth during life led misinterpretation on the pattern of their cheek tooth displacements as “intermediate stage toward the horizontal cheek tooth replacements”. In the case of *Desmostylus*, the second-generation teeth are not reduced in trend in contrast to the strong reduction of such teeth in proboscideans. The pattern of the tooth displacements represented by the second-generation teeth in *Desmostylus* must, therefore, be a result of different feeding adaptation, in other words, it might correspond to a different trend toward the reinforcement of defense against the tooth wear, probably not only by food items but also by other items on and in substrata, during their long life.

EAR MORPHOLOGY AS A CRITERION FOR RELATIONSHIP AMONG RIVER DOLPHINS: AN INVESTIGATION WITH COMPUTER TOMOGRAPHY (CT)

LARS S. KOSSATZ, Department of Anatomy III; MARTINA DRIESKE, Department of Diagnostic and Interventional Radiology; THOMAS J. VOGL, Department of Diagnostic and Interventional Radiology; HELMUT A. OELSCHLÄGER, Department of Anatomy III

We investigated the ear region of the Indus river dolphin (*Platanista minor*), the La Plata dolphin (*Pontoporia blainvillei*) and the Amazon dolphin (*Inia geoffrensis*) with computer tomography. The heads were scanned with a Siemens Somatom Plus 4 Volume Zoom in the coronal plane. Detailed images were obtained with the following protocol settings (InnerEarSpi 0.75 U30u: slice thickness 0,75mm, image size 512*512, KVP: 120, Exposure time 1000, X-ray tube current: 250, convolution kernel U30u). The CT datasets were segmented manually to perform realistic surface reconstruction using the Amira Graphics™ software solution by Mercury Computer Systems, Inc.

Our aim was to detect the exact topographical relationships of ear bones (tympanic, periotic) to the skull, the ossicles (malleus, incus, stapes) and the bony cavities of the inner ear (cochlea, vestibular organ) as well as the vestibulocochlear and facial nerves. Due to the high resolution of the scans it was possible to reconstruct all these details in the three species except the vestibular organ which could only be detected in *Platanista*.

An interesting phenomenon in odontocetes is the uncoupling of the tympanoperiotic complex. In *Platanista*, the complex is well-fixed within the skull whereas *Pontoporia* and particulary *Inia* have an advanced condition with a ligamentous suspension of the ear bones from neighboring skeletal elements. In *Platanista*, the periotic bone is large and heavy and exhibits a well-developed anterior process. Moreover, this species retains an internal auditory meatus. In the other two species, the periotic is smaller, particularly its anterior process: here, again, Inia shows an extreme. In *Pontoporia*, and a little less in *Inia*, the internal auditory meatus is reduced to insignificance, i.e. the vestibulocochlear and facial nerves enter the periotic separately. The tympanic bone is particularly prominent in *Platanista* and has a funnel with a pointed opening into the eustachian tube. In the other two species, it looks more like a rounded shell with a blunt end towards this tube. The tympanic bone is big in *Platanista* and its absolute size is smaller in *Inia* and even more in *Pontoporia*. Interestingly, the inner lip of the tympanic bulla is very thick in both *Platanista* and *Inia*; whether this could be an adaptation to hearing in fresh water habitats is an open question. In *Pontoporia*, in contrast, a coastal and estuarine species, the inner lip is thin. The last structure showing differences between the three species is the malleus. *Platanista* has the biggest malleus, with the subregions caput, manubrium and an anterior and lateral process. In contrast, *Pontoporia* has a rather small spherical malleus, and *Inia* shows an intermediate situation.

Our data from the ear region of the three odontocete species imply that the Indus river dolphin does not have a close relationship with either of the two other species. This result corresponds with former studies (e.g. de Muizon 2002) but more evidence is needed for a substantial analysis, including ecological aspects.

De Muizon, C. (2002) River dolphins, evolutionary history. In *Encyclopedia of Marine Mammals* (eds. Perrin, W.F., Würsig, B., Thewissen J.G.M.), pp. 1043-1050.

EYE DESIGN AND FUNCTION IN SECONDARILY AQUATIC TETRAPODS

RONALD H. H. KRÖGER, Lund University, Dept. of Cell and Organism Biology

I. Physical constraints

Terrestrial and aquatic habitats are considerably different with respect to the physical environment. With regard to vision, the difference in refractive index is most conspicuous. The refractive index of air is 1.0003, while the index of water is about 1.33. This means that substantial refractive power may reside in the cornea in air, but not in water. Aquatic eyes therefore have powerful lenses capable of creating well-focused images without any additional refractive power residing in the cornea. The power of the cornea is added if an aquatic eye is used in air, and lost if a terrestrial eye is used in water. In both cases, the images are severely blurred, unless there are efficient compensatory mechanisms.

Because of the absorption and scattering of light by water molecules as well as dissolved substances and suspended particles, aquatic habitats are generally dimmer and poorer in visual contrast as well as the spectral range of light being available. Scattering also limits visual range, which even in clear-blue ocean water is limited to 40 meters at maximum. The density of water causes further constraints. Static pressure, however, is a minor problem for the water-filled eye, because water is almost incompressible. Dynamic pressure caused by fast swimming, on the other hand, is an important factor, because it may deform the eye.

II. Adaptations

There are secondarily aquatic species among reptiles, birds, and mammals on all levels of aquatic life-style, from occasional visits to watery habitats to completion of the entire life-cycle in water. Here I only consider species spending most or all of their time in water and briefly present a selection of evolutionary changes.

Almost all species having returned to a life in water have well developed eyes. In fact, secondarily aquatic ichthyosaurs had the largest eyes known to have ever existed (264 mm in diameter). The eyes are reduced only in a few species living in very turbid waters (e.g. some river dolphins). In all other species, the eyes and entire visual systems have been changed and refined to cope with the demands of the new environment. Different evolutionary backgrounds as well as different ecological niches being populated have led to a large number of sophisticated adaptations, of which many are still poorly understood.

Surprisingly, many secondarily aquatic animals can use their eyes in both water and air (amphibious vision). Lizards and birds started the evolutionary journey with eyes having bi-directional accommodative mechanisms. The aquatic species can usually compensate for the difference in refractive index between air and water by powerful accommodation. Mammals have simpler, uni-directional accommodation and have found other ways, such as flat corneas acting as diving (or rather surfacing) goggles in seals. There have been numerous attempts to explain the cetacean capability of amphibious vision. However, so far none of the proposed mechanisms could be verified experimentally. The eyes of snakes are aberrant in many ways. It has recently been suggested that the group may be primarily aquatic.

Warm-blooded aquatic animals frequently return to the surface for breathing. On a sunny day, this exposes the eyes of deep-diving species to vastly different light levels in rapid succession. Extreme pupillary constriction and fast dark adaptation have been observed in pinnipeds and may also be present in other groups.

SOLUTION OF THE RORQUAL PARADOX AND ITS EVOLUTIONARY IMPLICATIONS

RICHARD H. LAMBERTSEN, Ecosystems International, Inc., Newtown Square, PA

Rorquals (Balaenopteridae) are second only to humans in their ability to project power. Individual capacity for work in these whales derives from the kinetic energy of a massive, fleet body. However, the hydrodynamic equation for lift predicts that evolutionary maximization of Ek body should be limited by the finite strength of the muscles that elevate the jaw. Dynamical loads arising from flow asymmetries eventually should cause loss of control of the mouth and involuntary deployment of that high impedance system.

Here I resolve hard evidence that this hypothetical constraint actually controlled evolutionary diversification. A special theory is formulated that predicts canalization of head shape toward four stable forms when both Ek body and life span are maximized. Blue, bowhead and sperm whales are found to confirm the differential phylogenetic occurrence of three of the four head shapes predicted. The fourth clearly is maladaptive and, in fact, does not exist.

This same theory, nevertheless, fails to assign correctly the head shapes predicted to the calculable global maxima for Ek body. It suggests instead that a blue whale should either move more slowly than a bowhead or sperm whale (if of the same mass) or be less massive (if the same speed) because hydrodynamic lift, as a first approximation, loads the horizontal area of the mouth. But blue whales which have very broad rostrums in fact do attain greater swimming speeds and greater masses than any reported bowhead or sperm whale. This is The Rorqual Paradox.

In a search for a solution to The Rorqual Paradox, complex surfaces of the mandibles and crania of 4 minke whales, *Balaenoptera acutorostrata*, were plotted by close-range photogrammetry. Photogrammetric data sets representing naturally opposed borders of the mandible and maxilla were used to determine 3-D conformal coordinate transformations. These allowed creation of precise 3-D computer models of skulls in which the strongly bowed mandibles were closely opposed along their entire length to the curved lateral borders of the rostrum. This simulated mouth closure. Subsequent internal measurements demonstrated an anatomical specialization heretofore unknown in the class Mammalia -- a maxillomandibular cam articulation. Imparting to the rorqual's craniomandibular system the mechanical advantage of the screw, the cam articulation discovered would operate in the final stage of mouth closure in conjunction with the rorqual's highly derived temporomandibular joints. At speed, a major function would be to counter torques on the mandibles generated by downward pressure loads, or negative lift, acting on the ventral surface of the head (Lambertsen and Hintz, 2004).

Discovery of this morphological innovation in the smallest and genetically least differentiated balaenopterid notably solves The Rorqual Paradox. Its novel occurrence probably was the root enabling cause of the adaptive radiation of Balaenopteridae (ibid). Its existence allows initial interpretation of both the very narrow rostrums of Balaenidae (right whales) and the very narrow lower jaws of many Odontoceti (toothed whales) as primitive locomotor adaptations. Like the maxillomandibular articulation discovered, those skull configurations would enhance craniomandibular stability, as required for effective forward movement.

This discovery notably also allows an extension of the aforementioned special theory. One may now reasonably purport that the ultimate constraint on body size in organic evolution is imposed by planetary dimensions (more precisely interphasic topologies), not the oft-conjectured “problem” of dissipating body heat. Straightforward theoretical equations imply that the final constraint on body mass would be the finiteness of the freedom to move in a buoyant fluid space. The interhemispheric size dimorphism of *Balaenoptera* races and the seemingly paradoxical pectoral flippers of *Megaptera* provide two empirical confirmations of this proposition.

Lambertsen, R. H. and R. J. Hintz, 2004. Maxillomandibular cam articulation discovered in North Atlantic minke whale. *Journal of Mammalogy* 85:446-452.

MORPHOLOGICAL MODELING AND BODY MASS ESTIMATION IN EOCENE CETACEANS

TERRY E. LANCASTER, Kent State University/NEOUCOM

The body mass of an animal is important in the physiological study of fossil mammals; however, estimating the body mass of transitional fossil species, such as the Eocene cetaceans, is difficult. Selecting an extant mammalian model for the Eocene cetaceans is problematic for several reasons. Not only are the Eocene cetaceans morphologically different from modern cetaceans, but also the size range of the Eocene whales is large in magnitude and there is great variation in body shape. Finally, many Eocene cetacean skeletons are incomplete, though in the absence of a complete skeleton, simple regression equations can still be used to estimate body mass from available material.

I estimated the body mass for representatives of each of the following families of Eocene cetaceans: Pakicetidae, Ambulocetidae, Protocetidae, and Remingtonocetidae. I measured the skulls, vertebrae and limbs of extant carnivores and artiodactyls. I used Principal Component Analysis (PCA) to categorize the extant mammals into specific morphological categories. For each morphological category, I developed a series of equations to estimate body mass using simple and multiple linear regression analysis. I then placed each fossil whale specimen into a morphological category and calculated its body mass using the regression equations generated for that category.

AQUATIC SPECIALIZATION IN MARSUPIALS FROM THE LATE CRETACEOUS OF NORTH AMERICA

NICK LONGRICH, University of Calgary

Following the end-Cretaceous mass extinction, a wide range of mammals became adapted to life in water, including marsupials, xenarthrans, artiodactyls, rodents, and carnivores. No strong evidence, however, is known for aquatic mammals during the Mesozoic.

Recently, a series of unusual, large (1.4-2.6 cm) mammalian caudal vertebrae were identified from the Upper Cretaceous (Campanian) Judith River group of Alberta. These caudals are broad, flattened, and bear large transverse processes; their resemblance to platypus (*Ornithorhynchus*) and beaver(*Castor*) suggests an oarlike tail used for steering underwater. The vertebrae do not seem to pertain to multituberculates; of the remaining mammals in the fauna, only the stagodont marsupials *Eodelphis browni* and *E. cutleri* are large enough to account for them.

As in river otters (*Lutra canadensis*) and mink (*Mustela vison*), *Eodelphis* displays unusually heavy tooth wear, suggesting a diet of fish and shellfish. The Maastrichtian *Didelphodon* (including *D. vorax*, *D. padanicus*, and *D. coyi*) is a large, highly specialized stagodont, which has previously been interpreted as a durophage. It may have preyed on the diverse gastropods and bivalves of the Hell Creek and Lance formations: *Didelphodon* possesses short, robust mandibles with bulbous premolar teeth resembling those of the sea otter, *Enhydra*. The large wear facets likewise resemble those of *Enhydra*, and the teeth are frequently worn down to the roots.

The large size of stagodonts, and their occurrence alongside a diverse freshwater biota, are consistent with semiaquatic habits. A semiaquatic lifestyle also predicts heavy bones to decrease buoyancy during dives; the jaws of *Eodelphis* and *Didelphodon* have massively thickened cortices. Finally, stable isotopes differ between semiaquatic and terrestrial mammals: tooth enamel should exhibit low variance in 18 O levels compared to contemporary terrestrial mammals. Future studies will test this prediction.

Stagodonts therefore appear to represent the earliest known aquatic mammals, and with half a dozen species, they formed a diverse and successful radiation. The largest mammals in Late Cretaceous North America were aquatic, underscoring the extent to which dinosaurs constrained mammalian diversification, yet stagodonts also hint at an unappreciated ecological diversity among Mesozoic mammals.

SIGNIFICANCE OF BODY PROPORTIONS IN THE TRANSITION TO DORSOVENTRAL UNDULATORY MODES OF SWIMMING IN ARCHAEOCETE WHALES.

AMY MAAS, Hiram College Biology; S. I. MADAR, Hiram College Biology

We expand upon the efforts of P.D. Gingerich (2003) to examine skeletal proportions and locomotor modes of modern semi-aquatic mammals, as a means of understanding locomotion in early whales. Utilizing the same taxonomic sample of modern semi-aquatic mammals as Gingerich, we have been able to expand the morphological scope of the data set to include eight additional metrics from the neck, sacrum and tail, using newly described fossil material from several archaeocete families. As modern cetacean locomotion is powered by muscular forces generated by the lumbar and caudal spinal segments, we seek to test the assertion that there were two stages in evolutionary transition to oscillatory swimming modes in early whales: hindlimb followed by tail domination. Newly described axial skeletal material from several early whale taxa permits this effort. Like Gingerich, we make use of a Principal Components Analysis to examine 22 linear postcranial measurements from 52 taxa. We have included the more primitive Eocene artiodactyl *Diacodexis* in addition to the anthracothere *Elomeryx*, and added *Pakicetus* to the original archaeocete sample that previously included *Ambulocetus*, *Rodhocetus* and *Dorudon*. Results emphasizing the long lumbus and tail vertebrae in early whales and modern dorsoventral undulators suggests that a specific stage of hindlimb dominance did not occur in early cetaceans.

Gingerich, P. D. 2003. Land-to-sea transition in early whales: evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals. *Paleobiology* 23:429-454.

TOOTHED WHALE ECHOLOCATION: SIGNALS, USE AND EVOLUTIONARY SCENARIOS

PETER T. MADSEN, Woods Hole Oceanographic Institution

Toothed whales (Cetacea, Odontoceti) encompasses some 70 species of large aquatic predators that navigate and find food by means of active echolocation, also called biosonar. Dolphins in trained settings can locate small steel spheres at ranges in excess of 100 meters, and have acute discrimination capabilities of acoustic targets. Target detection in biosonars is maximized by high source sound pressure levels at frequencies with little background noise and by directionality in both the transmitting and receiving systems to minimize clutter and masking noise.

The sonar signals of toothed whale are generated pneumatically in a complicated nasal system of air sacs, connective tissue and fats dorso-anterior of the bony nares. Clicks are generated by actuating a single or paired set of phonic lips with pressurized air by which an ultrasonic sound pulse propagates into the water column via the fatty melon. Echoes from ensonified objects or sounds from the environment are received by fats in the lower jaw that channel the acoustic energy to the oval window of the cochlea via the ossicular chain. Auditory inputs are processed in an auditory system spanning 10-12 octaves up to 150 kHz, with acute angular and temporal resolution. Research in recent years on free ranging toothed whales echolocating during foraging has revealed that they employ a vocal behavior that in functional convergence with echolocating bats (Microchiroptera) involves a search phase with slow, regular emission of sonar signals and a capture phase with a high repetition rate click train, a so-called buzz. The overall acoustic behavior of echolocating bats and toothed whales is therefore quite similar irrespective whether it is a 3 gram bat in a tropical rainforest or a 1000 kg whale at 800 meter depth off the continental shelf. Contrary to bats, there is less divergence in sonar signal types of toothed whales. The signal types of the latter can be divided into four different groups: 1) High frequency, narrow band signals above 100 kHz produced by mainly porpoises, 2) broad band, short duration signals from 30 to 150 kHz produced by a wide range of dolphins, 3) Narrow band, long duration signals around 40 kHz produced by beaked whales, and 4) short duration, high powered, low frequency signals around 15 kHz produced by the sperm whale. It seems that size is the overall most important scaling factor in toothed whale sonar signals in that frequency drops and source level increases with size. The most extreme species in this context is the sperm whale that generates the highest sound pressure levels ever measured from any animal with sound producing nasal structures that may take of 1/3 of their body length. These high-powered sonar signals at low frequencies are well suited for use in a long-range sonar system in the open ocean where the sperm whale forages. At the other end of the spectrum are small toothed whales such as porpoises that produce low output, high frequency signals that can only be used for short range echolocation.

The following scenario may be envisioned for the evolution of a biosonar system during the secondary adaptation to life in water of archaeocetes. A prerequisite for biosonar is directional hearing that enables the listening animal to locate the direction to a sound source. It is therefore argued that as cetacean ancestors became aquatic, their ears, which were initially adapted to airborne sounds, became adapted to the impedance of water so that they could use underwater hearing to locate passive sound sources such as calling conspecifics, predators and prey. Sound producing systems with air recycling and impedance matching to the aquatic medium may have evolved to produce low frequency sounds to serve a communicative function, and from there to a coarse echolocation system for navigation as seen in echolocating oilbirds and fruit eating bats. The coevolution of sound producing structures that could generate ultrasonic pulses and auditory systems that could receive and process such may gradually have evolved to detect and discriminate prey items in aquatic environments where visual cues were impeded.

ENCEPHALIZATION IN ODONTOCETES: WHAT'S BEING AQUATIC GOT TO DO WITH IT?

LORI MARINO, Neuroscience and Behavioral Biology Program, Emory University, Atlanta, GA.; MARK D. UHEN, Cranbrook Institute of Science, Bloomfield Hills, MI.; DANIEL W. MCSHEA, Department of Biology, Duke University, Durham, NC

Cetaceans have very large brains when measured both absolutely and with reference to body size. The toothed whales (Order Cetacea: Suborder Odontoceti) in particular are highly encephalized, possessing brains that are significantly larger than expected for their body sizes. Not only are modern odontocetes the most highly encephalized fully aquatic taxon to have evolved but they are also significantly more encephalized than any terrestrial mammals with the exception of modern humans. How did the large brains of odontocetes evolve? Did adaptation to a fully aquatic environment have anything to do with it? To begin to investigate this question we quantified and averaged estimates of brain and body size for thirty-six fossil cetacean species using Computed Tomography and analyzed these data along with those for modern odontocetes. We provide the first description and statistical tests of the pattern of change in brain size relative to body size in cetaceans over 47 million years. We show that brain size increased significantly in two critical phases in the evolution of odontocetes. The first increase occurred with the origin of odontocetes from the ancestral group Archaeoceti near the Eocene-Oligocene boundary and was accompanied by a decrease in body size. The second occurred only in the origin of Delphinoidea by 15 million years ago. This dataset can be used to identify and eventually test specific hypotheses about how and why odontocete encephalization occurred, eventually converging on the general question of whether any selective factors specific to the fully aquatic regime played a role in this process.

COMPARATIVE MORPHOLOGY OF THE FOREHEAD OF ODONTOCETES: INSIGHTS ON THE EVOLUTION OF ECHOLOCATION

MEGAN F. MCKENNA, San Diego State University; TED W. CRANFORD, San Diego State University; ANNNALISA BERTA, San Diego State University

Odontocetes (toothed whales) emit directional and high intensity sounds and use the information from the returning echoes to sense the surrounding environment and to locate food; a complex behavior defined as echolocation. The evolution of echolocation in odontocetes is a possible key feature associated with diversification of various lineages of odontocetes. The fossil record shows a major radiation of toothed whales in the early Oligocene and late to middle Miocene, perhaps largely as a result of the acquisition of echolocation, allowing them to utilize previously unexploited food resources and marine habitats. The ability to echolocate can be divided into two main functional units: sound production and reception. This study investigates the morphological changes associated with the sound production component of echolocation in fossil and extant odontocetes. Our two main research questions are: (1) When did the morphologies associated with sound production originate? (2) Are the modifications in extant odontocete morphology related to ecological factors? The ingroup includes 13 extant and 11 fossil odontocetes representing a broad taxonomic range. Both soft tissue and bony characters were defined and traced on several recent cetacean phylogenies. The evidence suggests that the ability to produce echolocation clicks is unique to odontocetes and evolved in their common ancestor. Therefore, the ability to echolocate does not directly correlate with the origin of fully aquatic hearing capabilities. Modifications in the signal generators and melon among extant lineages suggest specializations for specific habitats, not necessarily dependant on evolutionary history (e.g. both phocoenids and physeterids produce a narrow band echolocation clicks). The present study provides the first comprehensive description and reconstruction of the morphological changes associated with the production of echolocation clicks and enables inference on the evolution of echolocation.

HEARING IN AQUATIC MAMMALS

SIRPA NUMMELA; J. G. M. THEWISSEN, Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, OH

Acoustically, air and water are very different environments. However, in both media hearing is initiated by setting the inner ear fluid in the cochlea into motion. This can be accomplished using three different mechanisms: terrestrial mammal hearing mechanism, bone-conducted hearing and the modern odontocete hearing mechanism.

In terrestrial mammals air-borne sound travels along the external auditory meatus, sets the tympanic membrane and the middle ear ossicles into vibration, which moves the inner ear fluid in the cochlea. This mechanism is also used by pinnipeds while on land. Unlike otariids, phocids and odobenids have large, inflated ossicles. Due to this additional mass in the ossicles, their hearing range is shifted towards lower frequencies, and their sensitivity is also impaired. In the earliest whales, pakicetids, the sound path to the inner ear passed through the external auditory meatus to the tympanic membrane and the ossicular chain. This represents the terrestrial mammal type and allows pakicetids to hear in air.

In bone-conducted hearing, sound sets the whole head into vibration, and this vibration directly reaches the cochlea. Bone conduction requires that the head stays in contact with a sound conductor (e.g. the surrounding medium, water or soil, which has a density close to that of the head). Bone conduction takes place in any animals when their head is submerged, making this mechanism often the first and most simple underwater hearing mechanism, preceding later evolutionary adaptations to aquatic life. Pinnipeds use this mechanism underwater. In phocids and odobenids the inflated middle ear ossicles help to make bone conduction more efficient (this adaptation also occurs in fossorial mammals). Bone-conducted hearing was also used for underwater hearing by the earliest whales, pakicetids, where the periotic bone still had a bony connection to the skull, but the tympanic bulla already had a thick involucrum medially and a thin tympanic plate laterally. The hearing mechanism of desmostylians and sirenians is currently not known, but it is likely that they used bone-conducted hearing to some extent.

In modern odontocetes, waterborne sound is received and guided forward by the lower jaw and its fat body in the mandibular canal, reaching the tympanic plate, the lateral wall of the tympano-periotic complex. Unlike in land mammals, this whole complex is acoustically isolated from the skull by air sinuses. Hence, although bone-conducted sound underwater causes vibration of the head, these vibrations don't reach the cochlea. Among mammals, whales have undergone the most radical evolutionary changes in their ear morphology. For instance, the malleus is synostosed to the tympanic plate, and the ossicular chain transmits sound to the inner ear. The tympanic membrane is an elongated ligament attached to the malleus, mainly functional in equalizing pressure in the middle ear cavity. This mechanism developed early in the evolutionary history of cetaceans, and was present already in remingtonocetids and protocetids. Directional hearing was not very sophisticated, due to partial connections between the ear and the skull, and Eocene whales did not echolocate.

EVOLUTIONARY ADAPTATIONS OF SENSORY SYSTEMS AND THE BRAIN IN TOOTHED WHALES

HELMUT A. OELSCHLÄGER, LARS SV KOSSATZ, CHRISTIAN FUNG, CLEMENS POTH, JOHANNES HARBERING, Dept. of Anatomy, Univ. Frankfurt a.M.; STEFAN HUGGENBERGER, Dept. of Biochemistry and Biology, Univ. Potsdam; ONUR GÜNTÜRKÜN, Dept. of Biopsychology, Univ. Bochum, Germany; SAM H. RIDGWAY, Univ. California, San Diego, CA

This is a synopsis on evolutionary research in our lab during the last few years and in international cooperation with other groups of morphologists focusing on the nose, ear, and the brain. The history of early whales and their ancestors has been studied in detail by a number of authors. Much less is known on the soft tissues, which normally do not fossilize.

Hearing in odontocetes is correlated with acoustic isolation and pachyosteosclerosis of the ear bones and ossicles, which show different adaptations in various species (Kossatz et al., Harbering et al.; this volume). Another important phenomenon is mandibular hearing via the mandibular fat body located in the wide alveolar canal. Traces of this configuration are already seen in archaeocetes and it is well developed in early fetal stages of extant odontocetes.

The efferent part of the extant sonar system appeared in the early odontocetes in correlation with a total reconstruction of the nose. Today, the nasal structures dedicated to sound generation and emission are integrated topographically and functionally in the so-called “epicranial complex“ (Cranford et al. 1996, Huggenberger 2003), a genuine synapomorphy for the suborder Odontoceti. Concomitantly, the facial nerve is well developed because it supplies the blowhole musculature, which may be used in echolocation as well as in communication (“acoustic facial expression“?).

Many of these facts and thoughts are supported by the morphology of the brain and the size of its components dedicated to the relevant biological tasks. The auditory pathway is very well developed and the primary auditory cortex widely expanded already in the generalized La Plata dolphin (*Pontoporia*) whereas the vestibular system seems to be drastically reduced.

The size of the dolphin brain is outstanding in both absolute and relative terms, as is the degree of corticalization and gyrification (cf. Oelschläger and Oelschläger 2002). However, the cortex is very thin and both its layering and arealization are indistinct. The number of neurons per neocortical unit is comparatively low. The hippocampus seems to be much reduced in cetaceans with respect to their (artiodactyl) relatives. The very large size of the cerebellum might be explained with well-developed acousticomotor pathways and three-dimensional locomotion.

Although our knowledge has significantly increased during the last few years, particularly the enigmatic structure of the neocortex and the very small size of the hippocampus are challenges for further investigations.

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PHYLOGENY OF WHALES BY USING SINES

NORIHIRO OKADA, Department of Bioscience and Biotechnology, Tokyo Institute of Technology

Baleen whales (suborder Mysticeti) comprise eleven extant species that are classified into four families. Although several phylogenetic hypotheses about these taxa have been proposed, their phylogenetic relationships still remain confusing. SINE (short interspersed repetitive element) insertion data are now regarded as almost ideal shared derived characters at the molecular level, and we have applied this method to this problem. Here, we successfully reconstruct the phylogenetic relationships of these whales by characterizing 40 informative SINE loci. One of the intriguing conclusions is that balaenopterids and eschrichtiids radiated very rapidly during a very short evolutionary period. During this period, when newly inserted SINE loci retained ancestral polymorphisms, speciation occurred and these SINEs were sorted incompletely into each lineage, thus resulting in inconsistencies regarding the presence or absence of the SINE. This is in sharp contrast to the phylogeny of toothed whales, for which no SINE inconsistencies have been found. Furthermore, we found monophyletic groupings between humpback and fin whales, and also between (sei + Bryde's) and blue whales, both of which have not previously been recognized. The comprehensive SINE insertion data, together with the mitochondrial DNA phylogeny that was recently completed (Sasaki et al., 2005), provide a nearly complete picture of the evolutionary history of baleen whales.

On the other hand, a trichotomy of sperm whales, dolphins, and baleen whales, namely, the monophyly or paraphyly of toothed whales had been a great issue of debates for many years. Previously, our group succeeded in characterizing independent three loci, where the SINE insertions were shared among dolphins and sperm whales, thus supported a traditional hypothesis of toothed whales monophyly. However, when we elucidate the phylogeny of rapidly radiated taxa based on SINE insertions, there are two major problems, which should not be dismissed. The first is the ascertainment bias on choosing the taxa for genome screening. The second is lineage sorting effect, which sometimes led to the inconsistent SINE patterns among each locus. To resolve the trichotomy of these three lineages, whose split is prospected to be rapid, we should examine all the possible topologies of them by collecting SINE loci from all major three lineages; dolphins, sperm whales, and baleen whales. This might eliminate the possible ascertainment biases, and make it possible to check the presence or absence of inconsistent SINE patterns among these groups. In the present study, we collected SINE loci from the genomes of sperm whales, dolphins and baleen whales. The analyses of 19 independent SINE loci, together with the previous data strongly support a monophyly of tooted whales with no inconsistency. Our conclusion suggests that the lineage splitting of dolphins, sperm whales, and baleen whales has occurred in the absence of ancestral polymorphisms. We also succeeded in eliminating the possibility of the ascertainment biases, which sometimes might affect the data by the SINE method.

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STRAIGHTENING OUT THE STORY OF ODONTOCETE SKULL ASYMMETRY EVOLUTION

JOSHUA D. OLSON, University of California, Los Angeles; KRISTIN N. JETT, University of California, Los Angeles; PETER J. ADAM, University of California, Los Angeles

The skulls of most mammalian species are relatively symmetrical, this is not the case in toothed whales. Odontocetes have enlarged bones of the right side of their skulls, resulting in leftward skew in the topology of certain landmarks. This asymmetry is not a new observation and it is generally recognized that different species have differences in the expression of asymmetry. Although some workers have given detailed descriptions of the asymmetry and some have tried to explain why it exists, there has only been a single previous attempt to quantify asymmetry and postulate why it exists and varies among taxa (Ness, 1967). Methods used in Ness' study include establishing a midline axis of the skull from which orthogonal deviations of two landmarks (scaled to skull length) were used to establish an index of asymmetry. These methods may be useful in intraspecific studies, but may be inappropriate for comparisons among species as asymmetrical features cannot be accurately summarized by only two landmarks. In addition, establishing a midline on an asymmetric object is fraught with problems.

We adapted Procrustes analysis, previously used to compare left and right wings in insects and shells in ostracods, to obtain indices of asymmetry from 42 extant and 25 fossil odontocete species. The skulls of at least 4 individuals per species (2 of each sex) were examined where possible. Larger sample sizes (>20) were obtained for more common species: *Delphinus delphis*, *Kogia breviceps*, *Phocoena phocoena*, *Pontoporia blainvillei*, and *Tursiops truncatus*. Digital photographs were taken of skulls in dorsal view. We scored (x, y) coordinates of 15 bilateral landmarks and 2 "midline" landmarks on the left side of original pictures and from the right side on digitally reflected pictures. We used Procrustes software to rotate and translate left and right coordinate data sets for optimal fit (excluding "midline" points). Relative distances between landmarks were calculated. We then used these distances as a quantitative description of asymmetry, and explored three hypothetical correlates with asymmetry: body size (Ness, 1967), skull apex height (Heyning and Mead, 1990), and phylogeny (new postulate). Our results indicate that asymmetry is not related to body size or apex height among species. There is, however, a significant phylogenetic signal in degree of skull asymmetry.

With few exceptions, basal odontocetes (Ziphiidae, Physeteridae) have the most asymmetric skulls, while more derived odontocetes (Delphinidae, Phocoenidae), despite having marked asymmetry in the facial foramina, antorbital notch and processes, and posterior maxilla, have relatively symmetrical skulls. Quantification of multiple landmarks reveals that asymmetry is not a single character that simply increases or decreases within this lineage. We recognized three separate steps in the evolution of asymmetry within odontocetes: 1) basal odontocetes have strong narial asymmetry (reduced in phocoenids and delphinids), 2) asymmetry of the posterior maxillae and rostral deflection characterize all but the most basal odontocete families (Physeteridae and Ziphiidae), and 3) asymmetry of the antorbital region is pronounced in the monodontids, phocoenids, and delphinids.

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CRANIAL MORPHOLOGY OF THE OLFACTORY ORGAN IN AQUATIC AND SEMI-AQUATIC MAMMALS

HENRY PIHLSTRÖM, University of Helsinki

Much less is known about olfaction than about vision and hearing. The present study describes the current state of knowledge regarding the morphology of the olfactory organs of aquatic and semi-aquatic mammals. Certain groups of mammals, such as semi-aquatic insectivores, have been relatively well studied with regards to their olfactory organs. Other taxa, however, have received little or no attention. Despite this lack of actual data, it is frequently stated in the literature that aquatic and semi-aquatic mammals have reduced olfactory organs. As far as olfactory bulb volume is concerned, this assertion is indeed correct as most of the aquatic mammals studied to date have relatively smaller olfactory bulbs than their terrestrial relatives.

Cranial material can also be used to measure olfactory organ size. The perforated area of the ethmoid bone, i.e. the part of the endocranial wall through which the olfactory nerves reach the olfactory bulb, is an important part of the mammalian olfactory system. Existing data for 18 species of mammals show that ethmoid bone area is directly proportional to olfactory epithelium area, and thus the ethmoid bone can be used as an indicator of olfactory organ size. Measurements of the ethmoid bone areas of 150 species of mammals (Pihlström et al, in press) show that the size relation between ethmoid bone area and total skull area is more or less isometric. Excepting haplorhine primates, the only deviations from this pattern are the sirenians, which have small ethmoid bone areas, and the cetaceans and the platypus, which lack ethmoid bones altogether. By contrast, seals and sea lions have ethmoid bone areas of similar relative size as terrestrial carnivores. Apparently, the reduction of the olfactory organs has proceeded furthest in the most ancient aquatic mammal lineages.

THE POTENTIAL OF CT DATA FOR REVEALING DETAILS OF THE PTERYGOID SINUS COMPLEX IN EXTANT AND EXTINCT PHOCOENIDS

RACHEL RACICOT, San Diego State University, ANNALISA BERTA, San Diego State University, THOMAS A. DEMÉRÉ, San Diego Natural History Museum, TED CRANFORD, San Diego State University

The anatomical structure of the air-filled pterygoid sinus system in the head of extant and fossil porpoises provides phylogenetic and functional data that has previously been unattainable by traditional methods of dissection and osteological examination. The pterygoid sinus is an air-filled sac extending from the middle ear into the pterygoid bones in cetaceans. The pterygoid sinus complex is found in archaeocetes and mysticetes, although it is much smaller and less specialized than in odontocetes. Within odontocetes, more basal taxa have smaller, simpler pterygoid sinuses than later diverging lineages. Phocoenids, in particular, appear to have a more derived pterygoid sinus system than other odontocetes. High resolution X-ray computed tomography (HRXCT), a non-destructive, non-invasive procedure that allows visualization of the interior of opaque objects, reveals details of the pterygoid sinus system of a fossil porpoise. Digital endocasts, which represent casts of cavities, of the pterygoid sinuses were extracted from within the fossil skull by manually filling the spaces that they once occupied. Information provided by these endocasts allows interpretation of variation in this structure within and among phocoenids. For example, details about the extent to which the diverticula of the pterygoid sinuses extend into the frontals, indicating a more derived character state in porpoises, can be obtained. Comparisons of the anatomy of a fossil porpoise specimen and extant odontocetes provide insight into the evolution of the pterygoid sinus complex among phocoenids. In addition to their phylogenetic significance, volumetric and linear comparisons of the pterygoid sinuses point to functional differences such as biosonar capabilities, and limits on diving ability. These results demonstrate the utility of HRXCT for interpreting the internal cranial anatomy of both extant and fossil cetaceans.

THE GREAT COVER-UP: TRACING THE EVOLUTION OF LARYNGEAL PROTECTION IN AQUATIC TETRAPODS

JOY S. REIDENBERG AND JEFFREY T. LAITMAN, Center for Anatomy and Functional Morphology, Mount Sinai School of Medicine, New York, NY

The larynx evolved in air breathing animals as a protective cover to the entrance of the lower respiratory tract. It initially arose as a regulator of the gas filled swim bladder in fish. Re-entering the aquatic habitat as an air breather introduced a new hazard: water potentially flooding the lungs. In this study, we test the hypothesis that constraints of aquatic life would result in convergent evolution of aquatic-specific laryngeal protection. Larynges were dissected post mortem in specimens representing 2 genera of aquatic amphibians, 4 of aquatic reptiles, 10 of non-cetacean aquatic mammals, 3 of mysticetes, 15 of odontocetes, and 43 of terrestrial mammals. Results show a wide range of laryngeal phenotypes among aquatic animals. The larynx in amphibians and reptiles is a simple valve with no secondary protective structures, such as an epiglottis. The larynx of most non-cetacean aquatic mammals resembles that of terrestrial mammals, having an epiglottis that overlaps the soft palate and a lateral barrier called the aryepiglottic fold. The hippopotamus larynx resembles that of terrestrial artiodactyls with both rostral and caudal protective elevations of the larynx. Mysticetes also retain the artiodactyl configuration with some epiglottic and corniculate elongation and palatal expansion. Odontocetes exaggerate the elongated epiglottic and corniculate cartilages of the artiodactyl pattern. Their epiglottis is expanded at its tip to interlock with an encircling palatopharyngeal sphincter. Our findings indicate that secondary mechanisms of laryngeal protection are not unique among aquatic animals. Rostral and lateral barriers (epiglottis, aryepiglottic folds) and expansion of the palatal arch (soft palate-epiglottic overlap) arose in terrestrial mammals as well, probably to protect airflow for olfaction while feeding. Caudal protection of the larynx from a corniculate-pharyngeal interlock is similarly not an aquatic adaptation, but rather a protective feature that probably arose initially in long necked ungulates in response to head-down feeding, and was further exaggerated in artiodactyls to facilitate rumination. Maintenance or elaboration of these terrestrial laryngeal protections, however, may enable some aquatic mammals to keep a patent airway (e.g., for vocalization) while performing open-mouthed behaviors underwater. The degree of protection in aquatic animals does not, however, correspond with the amount of time spent in the water (e.g., manatees have less protection than hippopotami; seals have more protection than sea turtles). The nature of an animal's diet also does not correspond with degree of laryngeal protection. Sea turtles consume soft prey while alligators consume hard prey, yet both have similar larynges. Bulky food is consumed by both sea lions and toothed whales, yet their larynges show marked differences. Manatees feed face down underwater while sea otters feed face up above the water, yet they both have epiglottic-soft palate overlap. Hippopotami are herbivores and mysticetes are carnivores, yet they both have epiglottic and corniculate elongation. Thus, our hypothesis is not supported as the differing degrees of laryngeal protection observed appear dependent upon evolutionary relationships, rather than the similar constraints of an aquatic habitat.

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VISUAL PIGMENTS AND RETINAL GANGLION CELLS IN TERRESTRIAL AND AQUATIC TETRAPODS.

TOM REUTER, University of Helsinki; LEO PEICHL, Max-Planck-Institut fur Hirnforschung, Frankfurt

Tetrapod vision in water calls for distinct adaptations in eye optics, independent of the depth of diving. The retina, however, needs no dramatic adaptations for aquatic vision close to the surface, and under bright and spectrally broad illumination. Thus day-active amphibious tetrapods like freshwater turtles and diving petrels and shearwaters have elaborate retinae with four cone visual pigments, colored cone oil droplets and high ganglion cell densities, comparable to those of terrestrial tortoises and birds. However, the cone visual pigments of at least one deep-diving penguin, *Spheniscus humboldti*, show a clear adaptation to the bluish light dominating the ocean depths.

Specialized deep-diving mammals like many whales and seals show drastic retinal adaptations to the faint bluish light penetrating down to mesopelagic depths, 150-1000 meters under the surface. Their rod visual pigments are "blue-shifted" from the 500 nm absorption maximum characterizing rod visual pigments of terrestrial tetrapods, to 480-490 nm, the exact blue-shift being a function of their typical foraging depth. The blue-shift seems to increase sensitivity through two mechanisms. Firstly, the shifted absorption spectrum improves the match between the pigment and the available light, and secondly, visual pigments absorbing shorter wavelengths seem to produce less thermal noise, the latter factor being crucial when the photon flux becomes very sparse below 300 meters. The amino acid substitutions producing rhodopsin blue-shifts in whales are similar to those seen in deep-sea marine fish and in deep-water Lake Baikal cottid fish, thus exemplifying evolutionary convergence on the molecular level.

Surprisingly, seals and whales have lost functional genes coding for blue-sensitive cone pigments, and thus they seem to have lost the efficient dichromatic color vision system characterizing most diurnal and crepuscular mammals. The evolutionary background to this deprivation is not fully understood, especially as similarly deep-diving penguins seem to retain good color vision.

The retinal ganglion cells of whales, and to some degree also those of seals, show several characteristics typical for mammals evolutionarily adapted to low light levels. They are very large and sparsely distributed, i.e. the visual scenery is sampled with a low "pixel" density and a large "pixel" size. Thus the ganglion cell topography favors high light sensitivity by a high convergence of photoreceptors to ganglion cells, but seems not to be designed for high spatial resolution (acuity).

DEVELOPMENT OF THE FLIPPERS AND TAIL FLUKES IN THE SPOTTED DOLPHIN

MICHAEL K. RICHARDSON, OLIVER BECKMANN, Institute of Biology, Leiden University, 2311 GP Leiden, The Netherlands; IRMGARD KIRSCHENBAUER, and HELMUT A. OELSCHLÄGER, Institute for Anatomy III (Dr. Senckenbergische Anatomie) J. W. Goethe University Frankfurt am Main, 60590 Frankfurt am Main, Germany

The forelimb of whales and dolphins is a flipper that shows hyperphalangy (numerous finger bones). The developmental basis of hyperphalangy is unclear. We have prepared a series of whole mounted and serially sectioned embryonic flipper buds of the spotted dolphin *Stenella attenuata*. This cetacean shows marked hyperphalangy on digits II and III. We confirm previous reports that the proximodistal laying down of phalanges is prolonged in digits II and III. Histology showed that the apical ectoderm was thickened into a cap. There was a weak ridge-like structure in some embryos. The cap or ridge formed part of a bud-like mass that persisted on digits II and III at stages when it had disappeared from other digits. Thus the dolphin differs from other mammals in showing a second period of limb outgrowth during which localized hyperphalangy develops. New phalanges only formed at the tip of the digits. These findings are consistent with a model in which heterochrony leads to the terminal addition of new phalanges. Examination of the developing tail flukes showed that they develop significantly later than the limbs, and do not possess and AER-like thickening. Flukes may therefore be a developmental novelty.

TURNING PERFORMANCE OF AQUATIC FRESHWATER TURTLES

GABRIEL RIVERA, Clemson University; RICHARD W. BLOB, Clemson University

For aquatic vertebrates, the ability to move through water is an important aspect of function that is strongly influenced by the combination of body shape and the structure and movement of propulsors. Recently, considerable interest has been directed at examining the impact of body stiffness on aquatic turning performance. Descriptions of turning performance can be separated into two primary components, maneuverability and agility. Maneuverability refers to the space required to execute a turn, and is most commonly measured as the minimum length-specific radius of an organism's turning path (rpath/L). Agility is the rate of a turn, and is measured as the angular velocity about the center-of-rotation.

Flexibility of the body has a substantial impact on swimming performance in aquatic vertebrates. In general, rigid bodies are expected to incur less drag and are inherently more stable during rectilinear locomotion than flexible bodies. However, this enhanced stability is often derived at the expense of maneuverability and agility, in part by requiring rigid-bodied animals to rely on appendages (fins or limbs), rather than bending of the body axis.

The rarity of completely rigid body designs among aquatic vertebrates suggests that such a design may impose substantial constraints on performance. Such organisms, therefore, provide a unique opportunity to examine how a particular design affects function. However, evaluations of maneuverability and stability in rigid-bodied vertebrates have focused primarily on fishes. As a result, the effects of a rigid body design on turning performance have not been examined for a wide range of vertebrate body shapes.

Semi-aquatic freshwater turtles, in which the vertebrae are fused dorsally with a bony carapace, represent the largest group of aquatic rigid-bodied vertebrates (>100 species). As a result of their immobilized axial skeleton, thrust in swimming turtles is generated exclusively by the movements of fore- and hindlimbs. Analyses of morphological data indicate that the body shapes of distantly related freshwater turtles have converged toward an “aquatic form”, suggesting that natural selection has yielded a shape well suited for movement through aquatic habitats. Although the swimming performance of freshwater turtles has received little previous study, we believe that freshwater turtles provide an ideal system in which to evaluate the effects of body shape and the use of different propulsors (e.g., jointed limbs versus fins) on the aquatic turning performance of animals constrained by rigid bodies.

To begin evaluating the aquatic turning performance of turtles, we examined agility and maneuverability for hatchling and juvenile red-eared sliders (*Trachemys scripta*). Turning maneuvers were recorded simultaneously in lateral and ventral views using two synchronized digital high-speed video cameras. Videos were recorded at 100-250 Hz, but were analyzed to yield effective framing rates of 50 Hz. Turns were either routine maneuvers around obstacles placed into the glass test arena, or were made while pursuing fish. In general, the maximum and average angular velocities of routine turns made by turtles were lower than those recorded from turns executed during predatory encounters. However, the slower routine turns resulted in smaller length-specific turning radii (rpath/L). Still, boxfish require less space (rspace/L) to perform routine turns than turtles performing the same behaviors. In addition to the data collected on turning performance, we identified three different patterns of limb movements used to execute turns. Each pattern produces a distinct kinematic profile, and appears to be differentially employed to balance the speed entering a turn with the space required to make the turn (rspace/L).

MOLECULAR CHARACTERIZATION OF ROD AND CONE BASED VISION IN AQUATIC MAMMALS

PHYLLIS R. ROBINSON, JEFFRY I. FASICK, LUCY A. NEWMAN, Department of Biological Sciences, University of Maryland, Baltimore County

It has long been hypothesized that the visual systems of animals are evolutionarily adapted to their visual environment. The entrance many millions of years ago of mammals into the sea gave these new aquatic mammals completely novel visual surroundings with respect to light availability and predominant wavelengths. This study examines both the rod and cone opsins of marine mammals, and observes that the visual pigments of deep-foraging marine mammals have adapted to the dark monochromatic ocean environment. The visual pigments of deep-foraging mammals are blue-shifted in terms of their wavelength of maximal absorbance when compared to analogous pigments from terrestrial mammals. In addition, the evolutionary pressure to maintain dichromacy appears to be relaxed in these animals. Short-wavelength sensitive (SWS) , long-wavelength sensitive (LWS) cone opsin genes and rod opsin genes (rhodopsin) from two orders (Cetacea and Sirenia) and an additional suborder (Pinnipedia) of aquatic mammals were amplified from genomic DNA (for SWS) and cDNA (for LWS and rhodopsin) by PCR, cloned and sequenced. All animals studied from the order Cetacea have SWS pseudogenes, whereas a representative from the order Sirenia has an intact SWS gene, for which the corresponding mRNA was found in the retina. One of the pinnipeds studied (harp seal) had a SWS pseudogene, while another species (harbor seal) appeared to have an intact SWS gene. However, upon further examination, no SWS cone opsin mRNA was found in the harbor seal retina, suggesting a promoter or splice site mutation preventing transcription of the gene. The LWS opsins and rod opsins were expressed and maximal absorption wavelengths were determined for each. The deeper dwelling Cetacean species had blue shifted maximal absorption wavelength values compared to shallower dwelling aquatic species. The mechanisms underling these blue-shifted pigments were also elucidated and depend on three amino acids in rhodopsin and only one amino acid in LWS pigments. Taken together, these findings support the hypothesis that in the monochromatic oceanic habitat, the pressure to maintain color vision is removed, and mutations are retained in the SWS genes, resulting in pseudogenes. Additionally, LWS and opsins are retained in the retina and, in deeper-dwelling animals, are blue-shifted in maximal absorption wavelengths.

COMPARATIVE MORPHOLOGY OF THE EPIDURAL CIRCULATION IN SEALS, DOLPHINS, AND MANATEES

SENTIEL ROMMEL, Florida Fish & Wildlife Conservation Commission, ALEXANDER COSTIDIS, Florida Fish & Wildlife Conservation Commission

The morphology of epidural arterial and venous structures in the harbor seal (*Phoca vitulina*), bottlenose dolphin (*Tursiops truncatus*), and Florida manatee (*Trichechus manatus*) are described. In these diving mammals, relatively large epidural vascular masses are juxtaposed to the spinal cord, yet the spinal cord diameters are approximately the same as those of similarly sized terrestrial mammals. Thus, in contrast to terrestrial mammals, the neural canals of seals, dolphins, and manatees are substantially more voluminous than the spinal cord to accommodate this extensive vasculature (and in manatees, fat).

Seal brains are supplied by internal carotid, vertebral, and spinal arteries. Dolphin brains are supplied by epidural retia, which are fed by thoracic retia; the lateral margins of the thoracic retia are supplied by bilaterally paired supreme intercostal arteries. Additionally, the mediocaudal margins of the cervical retia anastomose with the epidural retia. Manatee brains are supplied by internal carotid arteries and by epidural retia. Epidural retia anastomose with cervical and thoracic retia. Manatee cervical retia are supplied by vertebral arteries; manatee thoracic retia are supplied by supreme intercostal arteries.

Venous return is more variable than arterial supply and the walls of veins are typically thinner than those of arteries. Thus, venous patterns are not as well studied as those of arteries.

In cetaceans and seals, the epidural veins may anastomose with more peripheral vascular complexes (reservoirs of blood at potentially different temperatures) via intervertebral foramina of the vertebral column at each level of the spinal cord. This topography suggests potential for unique temperature distributions via regulated exchange of blood masses.

The wall thicknesses of the epidural vessels may preclude direct exchange of O_2 but heat transfer could readily occur if temperature differences exist between the vascular mass and the spinal cord. In seals and cetaceans the epidural vessels represent relatively large thermal masses when compared with adjacent spinal cord tissues. In manatees the epidural veins are substantial but relatively smaller than those of seals and dolphins.

It has been suggested that the epidural veins contribute the major venous return from the abdomen in axial locomotors because vessels in the neural canal are not subject to the biomechanical pressures known to collapse the venae cavae. In all mammal species the epidural veins are without valves so blood flow direction is dependent upon local pressure distributions. Thus, substantial quantities of venous blood can flow to or from the head along the spinal cord in species that have enlarged epidural veins. If this blood were supplied at least in part by cooled veins from the skin surface, considerable temperature regulation of the spinal cord could be achieved. To compliment the valveless epidural system, we introduce a novel non-cardiac pump mechanism in the neck of the seal, which may produce flow from the post-capillary brain into the epidural veins.

IN VIVO SKULL FUNCTION IN AN AQUATIC TETRAPOD, *ALLIGATOR MISSISSIPPIENSIS*

CALLUM F. ROSS, University of Chicago; KEITH A. METZGER, Stony Brook University

Skull morphology in aquatic tetrapods reflects the conflicting demands of various behaviors, including locomotion, acquisition of prey, and resisting the forces generating during feeding. How are the conflicting design requirements of these different behaviors accommodated? Busbey (1995) suggested that the flat snout of platyrostral crocodilians improved their ability to capture prey during lateral snapping by reducing drag, but at the cost of strength during biting. He argued that flat snouts are not optimal for resisting bending and twisting moments, and that the fused palatal shelves and overlapping scarf joints characterizing crocodilian snouts function to compensate for the deficiency of overall cross-sectional geometry. If this hypothesis is correct, it suggests that the performance demands of prey acquisition in water have precedence over those for resisting the forces generated during feeding. In vivo strain data from the skull of alligators during biting and feeding are relevant to these questions.

In vivo bone strain data were collected from the snouts of two alligators during unilateral biting on a force transducer at different points around the toothrow. Strain data were collected from the maxillary, frontal, zygomatic and prefrontal bones using rosette strain gauges. The strain orientations and magnitudes were compared with those predicted for an elliptical beam under bending and torsion. Strain magnitude data were also compared with strain data from the mandibles of the same animals and from a wide variety of vertebrates reported in the literature.

Strain orientation data confirm that the rostrum is bent upwards and twisted about the long axis during unilateral biting. The frontal bone is primarily subjected to bending stress during biting at all bite points, whereas the snout is subjected to a combination of bending and twisting, depending on bite point and gauge position. Strain magnitudes are generally higher in the skull than those reported for the postcranium (Blob & Biewener, 1999), and higher than those reported from comparable places on the skulls of primates.

The observation that the alligator rostrum is bent dorsally and twisted about a rostrocaudal axis during biting corroborates Busbey's hypothesis that the cross-sectional geometry of the rostrum is not optimized for the loading regimes experienced during feeding. It suggests that the functional demands associated with prey acquisition (i.e., reducing drag during snapping behavior) are more important for determining overall snout shape than those associate with prey processing.

The morphology of the primate middle and upper face has also been shown to not be optimally designed for resisting feeding forces, where optimality is defined as maximum strength with minimum material (Hylander et al., 1991; Ravosa et al., 2000; Ross, 2001). Together, these results suggest that in performing the many functions required in the head, the cranium may often be strong enough (i.e., over-designed) for resisting the forces generated during feeding.

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MOSASAUR ASCENDING: THE PHYLOGENY OF BENDS.

BRUCE M. ROTHSCHILD, Carnegie Museum of Natural History; LARRY D. MARTIN, University of Kansas.

Recognition of decompression syndrome-related pathology (in the form of avascular necrosis) reveals diving behavior in mosasaurs. Macroscopic and radiologic examination was performed to identify linear bone death characteristic of avascular necrosis in vertebrae from the major North American and European collections. This survey of mosasaurs extends throughout most of their geographic and stratigraphic range and including examples across their diversity.

Avascular necrosis was invariably present in *Platycarpus corphaeus* and *P. ictericus*, *Tylosaurus proriger*, *Mosasaurus lemonnnieri* and *M. conodon*, *Plioplatecarpus houzeaui*, *P. primaeus* and *P. primaevus*, *Prognathodon giganteus*, *Hainosaurus bernardi* and the as yet unnamed Antarctic mosasaur. The frequency of occurrence in a given genera was independent of geography, present equally in European and North American and in the Niobrara and Selma Chalk. It was invariably absent from *Clidastes propython*, *C. liodontus*, *C. tortor* and *C. westii*, *Ectenosaurus*, *Halisaurus* and *Plotosaurus*.

The bone pathology, avascular necrosis, has a characteristic distribution in 7 genera and 13 species of mosasaurs and is absent in 5 genera and 9 species. It segregated according to diving habits, uniformly present in supposed deep divers and uniformly absent in the shallow habitat group. This correlates with findings in plesiosaurs, ichthyosaurs and cetaceans.

CONNECTIVE-TISSUE FIBER REINFORCEMENT IN “PADDLE” OF BEAVER TAIL (*CASTOR CANADENSIS*)

NATALIA RYBCZYNSKI, Canadian Museum of Nature; ANN PABST and BILL MCLELLAN, University of North Carolina at Wilmington

The beaver, *Castor*, is more specialized for swimming than any other living rodent. Characteristics associated with swimming include a streamlined body, valvular nostrils and ears, a cloaca, webbed hind feet, and a highly specialized tail. In the water the tail is used to control body movements, and sometimes as a propulsive structure (Fish 2000, pers. obs.). The tail’s capacity to function in swimming depends in part on the properties of its “paddle”. The paddle is dorsoventrally flattened with a scaled surface. It is largely made up of soft tissues, including a thick fatty core, and appears “rubbery”. Results from this study suggest that the mechanical behavior of the whole paddle is at least partly attributable to structural fiber reinforcement of the fatty component.

The aim of this preliminary study was to examine the connective tissue within the fatty component in order to assess whether it might provide a supportive function. Three *Castor canadensis* carcasses were used in this study. The paddle of each was each divided into three parts: proximal, middle and distal. From each part, cross sectional, parasagittal and transverse sections were removed using a razor. Several samples of each section type were recovered from each sample site. Sections ranged from 1 to 2 millimeters in thickness. The sections were dehydrated using acetone, and cleared in methylsalicylate. Birefringant structural fibers were viewed through a polarizing light microscope.

The patterns of structural fibers within the fat component of the tail were qualitatively similar for each of the three parts of the tail. Fibers were found attached to both the transverse processes and bodies of the vertebrae as well as the dermis. In cross-sectional samples the fibers were relatively thin and generally dorsoventrally oriented except in the vicinity of the vertebral elements where they were oriented more diagonally. In the transverse sections the fibers were thin and tended to cross, forming a woven pattern. Parasagittal sections were characterized by the presence of thickened fibrous bands, diagonally crossing, and oriented roughly between 40° to 60° degrees from the long axis of the tail.

The pattern of connective tissue fiber orientation and attachment suggest a supportive function. Similar to the structural fibers observed in the keel blubber in the harbor porpoise (*Phocoena phocoena*) (Hamilton et al. 2004), the fiber in the fatty tissue of Castor’s paddle may act as tensile stays, maintaining the shape of the paddle. The presence of diagonally crossing fibers would function to limit deformation, increasing stiffness (Hamilton et al. 2004; Johnsen & Kier 1993). Future work will examine the relationship between the connective tissue structure and mechanical properties of the paddle.

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GEOMETRIC MORPHOMETRIC ANALYSIS AND COMPARISON OF SKULL SHAPE IN SEMI-AQUATIC RODENTS

JOSHUA X. SAMUELS, University of California, Los Angeles

Adaptations to a semi-aquatic way of life are seen in numerous extant species of rodents from several highly diverse families. Many postcranial skeletal adaptations related to swimming behavior have been studied in these rodents (Stein 1988), but little attention has been paid to adaptive modifications of the skull. The relative dorsal placements of external features (nostrils, eyes, and ears) on the heads of some semi-aquatic mammals allow them to more easily breathe, see, and hear while remaining predominantly submerged (Howell 1930). These external features are robustly linked with osteological characteristics of the skull, although the extent of these adaptations in rodents has not previously been quantified. This study uses a geometric morphometric approach to examine 3-dimensional skull characteristics associated with semi-aquatic habits in rodents. Dorsal, ventral, and lateral digital photos were taken of skulls of 4 semi-aquatic and 9 terrestrial rodent genera, relatively closely related to the sampled semi-aquatic genera. Coordinates of a set of 37 easily recognized cranial landmarks were scored from images of each skull. The Procrustes procedure was used to scale, align, and transform data for analyses. Relative warp and thin-plate spline methods were used to characterize the skull shape in these species. Preliminary results show several differences in the shape of skulls from species with semi-aquatic habits. Compared to confamilial rodents with terrestrial or arboreal habits, some semi-aquatic species show more dorsal and medial positioning of the orbits, elevation of the nares relative to the rostrum, and a dorsal orientation of the external auditory meatus. However, these results require further scrutiny, as the extent to which fossorial, subterranean, or other habits can lead to similar osteological features is unknown. Further application of this method could ultimately be used as a quantitative method to infer the behavior and evolutionary trends in extinct rodent species, particularly those known from cranial remains but with poorly represented postcranial elements. Application of this method to several extinct beaver genera (*Dipoides*, *Castoroides*, and *Palaeocastor* from the family Castoridae) suggests that the evolution of adaptations in the skull parallel adaptations in the postcranial skeleton associated with semi-aquatic habits.

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THE BALEEN OF MYSTICETES GROWS ON THE ALVEOLAR PROCESS OF MAXILLA: COMPARATIVE ANATOMY OF THE FETUS OF THE MINKE WHALE

HIROSHI SAWAMURA, Ashoro Museum of Paleontology; HIROTO ICHISHIMA, Fukui Prefectural Dinosaur Museum; HARUKA ITO, National Research Institute of Fisheries Science; HAJIME ISHIKAWA, Institute of Cetacean Research

Whales are one of the most typical aquatic tetrapods. In the Mysticeti evolution the origin of baleen, which has no precursor in their evolutionary process, is a key assignment.

Toothed-mysticetes would stand high in the study of the evolutionary process of the baleen. The most diverse toothed mysticetes Aetiocetidae, which are the most derived group of the toothed mysticetes and are known from the Late Oligocene of the both sides of the north pacific region, is considerable for the resolution of the baleen origin.

After Barnes et al. (1995), some new specimens of the Aetiocetidae occurred from Morawan site in Hokkaido, Japan and they could show to have not only teeth but also baleen. To get characters related to the baleen we investigated the extant Minke whale fetus rostrum anatomically and young individual skulls osteologically.

RESULTS: The foramen alare appears immediately under the oral mucosa and is very close to the opening of the optical canal at the back of the orbit. The foramen alare opens forward a special space which extends under the anterior part of the supraorbital process of the frontal bone, over the infraorbital process of the maxilla and laterally to the perpendicular lamina of the palatine bone, temporally named the Fossa frontomaxillaris, which may correspond to the pterygopalatine fossa in the human skull. Crossing in the frontomaxillary fossa the maxillary nerve divides into three branches and they run distally in their respective ways.

Medial branch, the greater palatine nerve, run forward along the lateral margin of the palatine bone, turns on the dorsal surface of the palatine bone, and then appears at the palatinomaxillary suture, distally in the greater palatine grooves on medial half of the oral surface of the maxilla, that is on the palatine process of the maxilla.

Intermediate branch, the infraorbital nerve, divides into two sub branches. The medial sub branch enters the infraorbital canal and re-divided into some rami. The nasal rami emerges onto the face through the postero-medial infraorbital foramina and the anterior labial rami through the anterior foramina. The lateral sub branch, the inferior palpebral rami and the posterior labial rami penetrates slantingly laterally and emerges through the lateral infraorbital foramina.

Lateral branch, the superior alveolar nerves, is divides into small rami. They pierce the floor of the fossa frontomaxillaris, that is the dorsal surface of the infraorbital process of the maxilla, and link up together forming the superior "dental" plexus in the infraorbital process and in the lateral half of the maxilla, then emerge through many small foramina in the basin of the oral surface of maxilla.

DISCUSSION: Our results introduce the general mammalian morphology is applicable to Mysticeti. The homology of the nerve supply shows that the rostrum of Mysticeti consist of two processes of the maxilla, that is the palatine process and the alveolar process. The former is the medial convex area in the oral surface of the maxilla and accept the greater palatine nerve. The latter is looks the basin lying in the lateral area of the oral surface of the maxilla and accept the superior alveolar nerve.

In whales the general morphology of the mammalian skull is often obscure by the extreme modification so called telescoping. Senior researchers confused in the rostrum anatomy of Mysticeti and misconstrued the origin or the homology of the baleen. The generally accepted theory that the baleen of Mysticeti derived from the transverse ridges present on the palates of many terrestrial mammals might be reviewed.

The baleen grows on the alveolar process of maxilla and accepts the nerve supply from the dental tissue nerve, the superior alveolar nerve of the maxillary nerve. It shows that the baleen is homologous to the periodontal tissue, the gingiva.

THE SEMICIRCULAR CANAL SYSTEM AND MAMMALIAN AQUATIC BEHAVIOUR

FRED SPOOR, Evolutionary Anatomy Unit, Department of Anatomy and Developmental Biology, University College London, U.K.; J. G. M. THEWISSEN, Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, OH

The semicircular canal system, part of the sensory organ of balance in the inner ear, contributes to the coordination of body movements during locomotion through the vestibular reflexes. Particularly well understood is the sensory input into the vestibulo-ocular and vestibulo-collic reflexes which stabilize the head and eyes. Comparative studies indicate that the arc size of the semicircular canals reflects an animal's locomotor behavior (see reviews in Spoor and Zonneveld, 1998; Spoor, 2003). The canals of agile species are larger than those of slow-moving species. The larger arc increases a canal's sensitivity, and thus the ability to resolve small changes in angular head motion. For animals showing fast and highly maneuverable locomotion such accurate sensory information is vital to maintain body coordination. Importantly, the canals of such species can be sensitive, without the risk of constant overstimulation, because they are part of a feedback system. The canals supply the vestibulo-collic reflex, which stabilizes the head by compensatory neck movements, thus keeping the input signal of the canals within limits.

Aquatic locomotion in mammals offers a good opportunity to study the functional relationship between the semicircular canal system and behavior. It is marked by distinct locomotor requirements, and has occurred in several orders, and to a variable degree, from obligatory aquatic to partially amphibious. In a broad review we used computed tomography to examine the semicircular canals of cetaceans, artiodactyls, carnivores, rodents, and sirenians, comparing species showing forms of aquatic locomotion with others that are fully terrestrial.

Of all mammals, the cetaceans show the most dramatic evolutionary change in semicircular canal morphology (Spoor et al., 2002). A three-fold reduction in canal size occurred as soon as they invaded the seas, and well before they looked like modern whales or dolphins. This canal morphology, and the associated decrease in sensitivity, appears to be linked with their highly acrobatic aquatic behavior, in combination with very limited neck motility, which renders reflex stabilization of the head ineffective. On the other hand, the canal sizes of those amphibious and aquatic, non-cetacean mammals investigated thus far are within the range of terrestrial species. This is expected, as none of these combine great aquatic agility with lack of neck motility.

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DIGITAL LIBRARY OF DOLPHIN DEVELOPMENT

J. G. M. THEWISSEN, Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, OH

The Digital Library of Dolphin Development aims to document dolphin development on the World Wide Web (www.neoucom.edu/DLDD), by given access to a large collection of digitized microscopic sections. In general, the database will resemble the Visible Human Project, although there are differences.

At the base of this library stand more than 50 embryos and fetuses of the Spotted Dolphin (*Stenella attenuata*). The smallest of these embryos is approximately 4 mm long (approximate age 3 weeks), while the largest are full-term fetuses. This embryological series documents the complete development of all major organs in this mammal. These embryos are being sectioned and each slice will be mounted on microscope slides. Photos and drawings are posted on the WWW, and these will document the external morphology of all embryos. Digitized images of all individual slices of each dolphin are being posted as downloadable (JPG and TIFF) files. For small embryos, there are approximately 100 imaged slices, but for large embryos there could be thousands of 1000 slices.

This will be the only web-based embryological series for any cetacean, and one of only a few among mammals. This collection will be unique: it is extremely hard to acquire a complete ontogenetic series for any whale or dolphin, and none are available in North America. The best collection of embryos of cetaceans in at the Senckenbergische Anatomie in Frankfurt, Germany, but this collection is not web accessible. Housing this series on the Web will make it possible for any interested person to study embryology using real specimens.

This digital library can be used in at least three ways.

1. High school and college biology teachers can give their students access to real embryological data and not the abstractions of the real data that are found in textbooks. The files can easily be downloaded, and even a single file is rich in data and easy to interpret. Development of most organs (e.g., heart, brain) is very standardized in mammals, and this collection of dolphin embryos is an excellent model for study of these organs in any mammal, including humans.

2. Researchers can now study the development of any organ that they are interested in by downloading files reducing wear-and-tear on the original collection of microscope slides, and reducing the time and money that they need to spend on such projects.

3. Whales and dolphins speak to the public’s imagination, and researchers in these fields receive regularly requests for information from the public. This library will give easy access to anyone interested in seeing a dolphin embryo with hind limbs, or one with hair.

4. Whales and dolphins are one of the text book examples of evolution, and the science of embryology stands as one of the basal pillars of that Evolutionary Theory. However, dolphin embryology is a poorly studied subject because embryos are hard to collect. This digital library will remedy the problem.

HIND LIMBS IN CETACEANS: EVOLUTION AND DEVELOPMENT

J. G. M. THEWISSEN, Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, Ohio; M. J. COHN, Department of Zoology, University of Florida, Gainesville; JOHN HEYNING, Los Angeles Museum of Natural History; SUNIL BAJPAI, Department of Earth Sciences, Indian Institute of Technology, Roorkee, Uttaranchal, India; L. S. STEVENS, Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, Ohio; W. E. HORTON, Jr., Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, Ohio

One of the most exciting areas of modern evolutionary studies is the rapidly growing field that studies the interaction of regulatory genes and evolving organ systems. Although there is a plethora of studies pointing out the potential evolutionary importance of such processes, it is only rarely that developmental patterns can be shown to match actual (fossil-documented) transitions. One of these rare examples is limb loss in snakes, for which developmental mechanisms as well as paleontological patterns are well understood (Cohn and Tickle, 1999).

At present, the evolutionary pattern leading to the absence of limbs in cetaceans is well understood (reviewed by Thewissen and Williams, 2001). The descriptive embryology of the hind limbs in whales is also well known (Sedmera et al., 1997). However, direct experimental tests of developmental mechanisms in cetacean embryos are highly impractical, and illegal in many countries. In order to study the relation between paleontological and developmental patterns, we acquired preserved dolphin embryos. We used immunohistochemistry to determine gene expression patterns in cetacean limb development. At present, we have data for the expression in the limb bud of Shh, Fgf-8, dHand and Myosin.

Our goal is to integrate the developmental data into a comprehensive theory about the evolution of cetacean locomotion. Fish (e.g, 1996) developed an explicit theory for cetacean locomotor evolution based on hydrodynamic and kinematic data on modern swimming mammals. Thewissen and Fish (1997) used modern mammalian swimmers to identify morphological correlates of each swimming mode and tested Fish's model by comparing these predicted morphologies to those of fossil cetaceans. Fish's hypothesis suggests that selection for enhanced swimming efficiency drove the reduction of the postcranial skeleton. Our developmental evidence is consistent with this suggestion, and adds that early development of hind limbs was not affected until after limbs had lost their locomotor function.

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THE EVOLUTION OF HIGH ENCEPHALIZATION IN ODONTOCETES IN RELATION TO THE ORIGIN OF ECHOLOCATION

MARK D. UHEN, Cranbrook Institute of Science, Bloomfield Hills, MI; LORI MARINO, Neuroscience and Behavioral Biology Program, Emory University, Atlanta, GA

Second only to humans in relative brain size, dolphins and whales possess large and highly elaborated brains (Marino, 1998). The present study asks the question: How did the large brains of dolphins evolve? To investigate this question we collected and measured estimates of brain and body size for 36 fossil dolphin and whale species using Computed Tomography and analyzed these data along with those for modern species. Here we demonstrate the pattern of change in brain size relative to body size in cetaceans over 47 million years. We show that brain size increased significantly in two phases in their evolution. The first phase occurred near the Eocene-Oligocene boundary (~ 33 Ma) and the second occurred within one group only, Delphinoidea, by the mid-Miocene (~15 Ma).

One hypothesis about cetacean encephalization which has drawn a great deal of consideration is that cetaceans developed high encephalization due to the emergence and elaboration of the ability to process high frequency acoustic information. Several theorists postulate that either echolocation per se or its elaboration into a complex perceptual system may underlie an increase in brain size in the suborder Odontoceti and precursors. Fleischer (1976) noted that the periotic (ear bone) structure of Oligocene and early to mid Miocene squalodontoids was very similar to that of echolocating modern dolphins. Luo and Marsh (1996) suggested that squalodontoid periotic structure had not yet reached the modern range of high frequency processing capability observed in later Pliocene groups, e.g., Kogiine whales.

We collected new morphological information from the periotics of ten additional fossil taxa ranging in age from late Eocene to Pliocene. These data were collected from high resolution CT scans made at the University of Texas High-Resolution X-ray CT Facility. The slice thicknesses were 0.0622, with a field of view of 29 mm, allowing for sub-millimeter measurements of periotic structures to be taken. Fleischer (1976) used the basilar gap along the length of the cochlea to separate mysticetes, which lack high-frequency sound perception, from odontocetes, which have high-frequency sound perception. Reliably measurements of these structures proved difficult to obtain to due poor resolution from infilling sediment and breakage. Ketten (1992) used more gross anatomical structures to distinguish different types of cetacean cochlea, and to separate echolocating cetaceans from non-echolocating cetaceans. Using these parameters, we can also separate these two groups. Archaeocetes and mysticetes are clearly separated from the echolocating odontocetes. Fossil odontocetes from modern groups known to echolocate, as well as other odontocetes from extinct groups have gross anatomical features that indicate they too were able to perceive high-frequency sounds, and at least potentially to echolocate.

The earliest odontocetes in our study are from the late Oligocene, as are the earliest odontocetes demonstrating an increase in encephalization over their archaeocete ancestors. The association of evidence for high frequency hearing in taxa that display increased encephalization is consistent with the hypothesis that at least the initial increase in odontocete encephalization is related to the increased demand for neural processing of echolocation signals. Further study is under way to determine if the facial structure of these early odontocetes is also indicative of the ability to produce echolocation signals, which would further support this hypothesis.

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REINTERPRETATION OF THE AUDITORY STRUCTURE IN *DESMOSTYLUS HESPERUS* (MAMMALIA: DESMOSTYLIA): NEW EVIDENCE FROM THE MIDDLE MIOCENE TACHIKARAUSHINAI FORMATION, HOKKAIDO, JAPAN

HIKARU UNO, National Institution for Environmental Studies

A new specimen of *Desmostylus hesperus* Marsh, 1888, from the upper Middle Miocene Tachikaraushinai Formation, Utanobori, Hokkaido, northern Japan provides important data related to desmostylian auditory structure. The specimen consists of a nearly complete skull and mandible, but the posterior halves of the left side are broken away. It was a juvenile individual that retained a heavily-worn fourth deciduous molar (dm4) in the right upper jaw. There have been two different interpretations regarding the position of the external acoustic meatus of *Desmostylus*. The interior of the cranium of the new specimen reveals, unequivocally, that the position of the meatus should be identified as being the foramen immediately posterior to the zygomatic root of the squamosal. The position and structure of the external acoustic meatus suggests a peculiar (possibly aquatic) adaptation for hearing and is apparently comparable to that of early proboscideans but sirenians, among the Tethytheria. However, it will remain unclear whether the condition of the auditory structure in desmostylians and proboscideans is homologous or analogous until the skull of a neonate desmostylians can be obtained.

THE CEPHALIC ANATOMY OF THE FLORIDA MANATEE (*TRICHECHUS MANATUS*), AS REVEALED BY VIRTUAL DISSECTION WITH COMPUTED TOMOGRAPHY (CT), DIFFERENTIAL-CONTRAST DUAL-VASCULAR INJECTION, AND 3D VISUALIZATION

LAWRENCE WITMER, RYAN RIDGELY, PATRICK O'CONNOR, CASEY HOLLIDAY, TOBIN HIERONYMUS, JOSEPH DANIEL, ERIN RASMUSSON, JUSTIN TICKHILL, Ohio University; ANDREW CLIFFORD, Brown University

An anatomical study of the head region of the Florida manatee was conducted using computed tomography (CT) and a novel vascular injection technique. Heads of a large and small individual of *Trichechus manatus* were obtained from the Marine Mammal Pathobiology Laboratory of the Florida EPA through the courtesy of S. A. Rommel. Each head was scanned using a GE multislice CT scanner at O'Bleness Memorial Hospital (Athens, OH) at a slice thickness of 1mm and using a bone algorithm. Specimens were subsequently subjected to differential-contrast dual-vascular injection (DCDVI), a new technique developed in the lab allowing discrimination of arteries and veins on CT. Vessels were cannulated and injected with an injection medium consisting of two different concentrations of barium sulfate and latex: 40% barium for arteries and 20% barium for veins. The injected heads were CTed again using the same scan parameters. Arteries and veins could be distinguished on CT by the differing gray values resulting from using injection media of different densities. Vascular elements were segmented using Amira 3.1, allowing them to be visualized in 3D. Vascular injection using radio-opaque contrast, however, comes at the cost of diminished resolution of other structures due to the streaking artifact ("beam hardening") caused by the steep gradients of x-ray attenuation. Streaking artifacts were ameliorated by registering and merging the pre- and post-injection datasets using a landmark-based approach. Thus, the vascular data extracted (segmented) from the DCDVI dataset could be digitally "inserted" into the pristine uninjected dataset to evaluate the relationships of vessels to bony and soft-tissue structures. Using Amira, various head muscles were relatively easily segmented and visualized due to the clear fat planes of lower density separating the higher density muscles. Other segmented structures included the skull, brain cavity, nasal airway, fat, and skin. All of these structural elements, including the vessels, could be visualized in isolation or in any combination using 3D visualization tools. Thus, virtual dissection is an invaluable tool for studying such rare and endangered species prior to more traditional, and ultimately destructive, techniques.