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Original Article

New Miocene fossil Allodelphinidae (Cetacea, Odontoceti, Platanistoidea) from the North Pacific Ocean

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Abstract: Species in the extinct platanistoid family Allodelphinidae are dolphin-like odontocete (echolocating) cetaceans known by fossils from early and middle Miocene marine deposits around the eastern and western margins of the North Pacific Ocean. Allodelphinids were relatively large animals, having estimated adult total body lengths of approximately 3 to 5 meters, a long rostrum, the mandible extending to the end of the rostrum with a fused mandibular symphysis, large and anteroposteriorly elongated cervical vertebrae, and elongated humerus. The previously named allodelphinid species, all from California, are early Miocene *Allodelphis pratti* Wilson, 1935, and A. *woodburnei* Barnes and Reynolds, 2009, and middle Miocene *Zarhinocetus errabundus* (Kellogg, 1931). Additional new species belonging in the family are *Goedertius oregonensis* Barnes and Kimura, new genus and new species, from the early Miocene Nye Mudstone in Lincoln County, Oregon, U.S.A.; *Ninjadelphis ujiharai* Kimura, new genus and new species, from the early Miocene Awa Group in Mie Prefecture, Japan; and *Zarhinocetus donnamatsonae* Barnes, new species, from the late early Miocene to early middle Miocene Astoria Formation in Grays Harbor County, Washington State, U.S.A. *Goedertius oregonensis* is more derived than the species of *Allodelphis*. *Ninjadelphis ujiharai* is more derived than *Goedertius oregonensis* and has anteriorly retracted posterior ends of its premaxillae. Species of *Zarhinocetus* Barnes and Reynolds, 2009, have a maxillary tuberosity on each side of the base of the rostrum and a maxillary crest over the orbit. *Zarhinocetus donnamatsonae* is more derived than *N. ujiharai*, but more primitive than *Zarhinocetus errabundus*, which is the most derived species in the family. Contrary to the general evolutionary trend in cetaceans, allodelphinids evolved secondarily enlarged and anteroposteriorly elongated cervical vertebrae, and all cervical vertebrae remained un-fused to one another. Their elongated necks, combined with a large occipital shield and thick nuchal crest on the cranium, indicate that allodelphinids had well-developed muscles for movements of the head. Their extremely long and slender rostra may have allowed either raptorial or benthic feeding, and niche partitioning can explain the diversity that is now being documented within the family. Their swimming methods likely favored maneuverability but not speed.

Key words: Miocene fossil Cetacea, Platanistoidea, Allodelphinidae, *Allodelphis*, *Goedertius*, *Ninjadelphis*, *Zarhinocetus*, odontocete benthic feeding, odontocete swimming methods

INTRODUCTION

The odontocete superfamily Platanistoidea is currently understood to include five families (Figure 1) of small to medium-sized dolphin-like species: Squalodontidae (Figure 2), Allodelphinidae, Waipatiidae, Squalodelphinidae, and Platanistidae (see Barnes et al., 2010). Several relatively lesser understood species of the genera *Prosqualodon* Lydekker, 1892, *Phoberodon* Cabrera, 1926, and *Dalpiazina* Muizon, 1988, have also been considered as belonging to the Platanistoidea (Muizon, 1994, 2009; Fordyce and Muizon, 2001; Barnes, 2006; Barnes et al., 2010). Recently, Tanaka and Fordyce (2014) and Aguirre-Fernandez and Fordyce (2014) have questioned the position and characterization of basal platanistoids among odontocetes, however. Phylogenetic analyses have shown the Allodelphinidae to be a basal branch of the Platanistoidea (Barnes, 2006; Barnes and Reynolds, 2009; Barnes et al., 2010; Figure 1 herein).

The only living platanistoids are the species of *Platanista* Wagler, 1830, (Figure 3) in India and Pakistan: *P. gangetica gangetica* (Roxburgh, 1801) in the Ganges, Brahmaputra, and Karnaphuli river systems, and *P. g. minor* Owen, 1853, in the Indus River and its tributaries (Jefferson et al., 1993). The fossil record of the Platanistoidea demonstrates that this group was much more widely distributed in the past, and that these were relatively diverse odontocetes during late Oligocene and early Miocene time (Fordyce, 1994; Fordyce and Barnes, 1994; Fordyce et al., 1995; Fordyce and Muizon, 2001; Barnes et al., 2010).

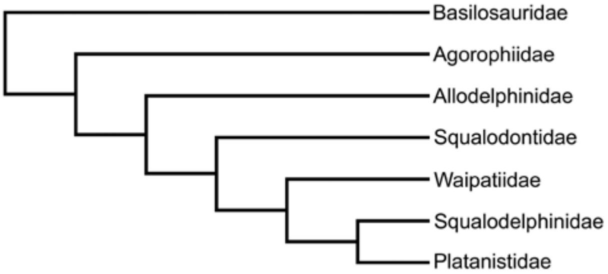

Figure 1. Tree showing postulated phylogenetic relationships between the family Allodelphinidae, more primitive cetacean families (Basilosauridae and Agorophiidae), and other currently recognized families within the superfamily Platanistoidea: the Squalodontidae, Waipatiidae, Squalodelphinidae, and Platanistidae. This tree is based on the analyses that have been presented by Barnes (2006:fig. 9), Barnes and Reynolds (2009:fig. 1), and Barnes et al. (2010:fig. 12). The analyses used 64 characters among nine taxa of fossil Cetacea, including some described members of the superfamily Platanistoidea for which reasonably complete crania were available. The derived late Eocene archaeocete, *Zygorhiza kochii* (Reichenbach, 1847) from Alabama, U.S.A., was used to root the tree, and the primitive odontocete, *Agorophius pygmaeus* (Müller, 1849), probably of late Oligocene age and from South Carolina, U. S. A., was used as the out-group for the Platanistoidea. This was the only resulting tree, having a tree length of 84, a Consistency Index of 0.76, a Retention Index of 0.75, and was obtained by manipulating a character matrix with MacClade Version 3.01 (Maddison and Maddison, 1992), and using the Branch and Bound search option of PAUP Version 3.1.1.

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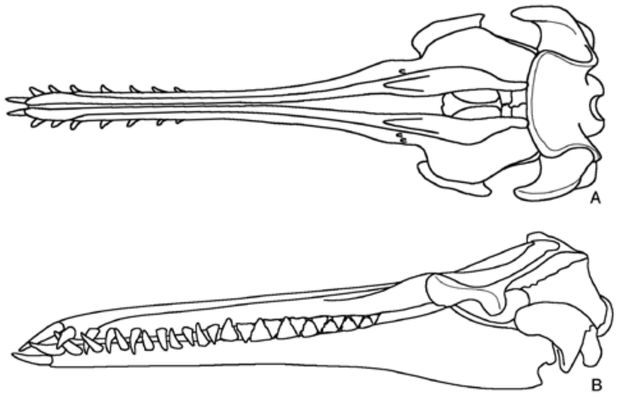

Figure 2. Crania of two species of North Atlantic species in the genus *Squalodon*. **A**, *Squalodon calvertensis* Kellogg, 1923, middle Miocene, Maryland, U.S.A., dorsal view; **B**, *Squalodon bariensis* (Jourdan, 1861), middle Miocene, France, left lateral view. Modified from Kellogg (1928:figs. 5, 6).

Allodelphis Wilson, 1935, was originally assigned to the family Delphinidae. Later, Barnes (1977) assigned this genus to the Platanistidae, and subsequently (Barnes, 2006) he re-assigned it, as the type genus, to the new platanistoid family Allodelphinidae. This family now includes three named species: *Allodelphis pratti* Wilson, 1935 (early Miocene, central California); *A. woodburnei* Barnes and Reynolds, 2009 (early Miocene, southern California); and *Zarhinocetus errabundus* (Kellogg, 1931) (middle middle Miocene, central California); as well as several other un-named North Pacific species from Japan and the Pacific coast of North America.

All known fossils of allodelphinids have been recovered from early to middle Miocene age marine deposits. These large dolphin-like cetaceans had estimated adult body lengths of approximately 3 to 5 meters. Phylogenetic analyses have shown the Allodelphinidae to be a basal branch of the Platanistoidea (Barnes, 2006; Barnes and Reynolds, 2009; Barnes et al., 2010; Figure 1 herein).

The purpose of this study is to review the previously named species of the family Allodelphinidae, to report some additional specimens of those species, to name two new genera and three new species in the family based upon specimens from Japan, Oregon, and Washington, and to discuss the possible swimming and feeding behaviors of allodelphinids.

MATERIAL AND METHODS

For anatomical terminology we generally follow Mead and Fordyce (2009). The measurements were made following the methods of Perrin (1975). Some species of the Allodelphinidae, similar to the Pontoporiidae, have anteriorly converging supraorbital processes; thus the antorbital process is narrower than the distance across orbits. Perrin's (1975) measurements were established for species of *Stenella* which, like most other species of the family Delphinidae, have large and wide antorbital processes. In those species, the least interorbital width is usually approximately at the center of the supraorbital arch. To be consistent among different families of Odontoceti, we recommend making the measurement of the least interorbital width at the center of the margin of the orbit, across the supraorbital process of the frontal, even if, as in some that species we report here, this distance is wider than the antorbital width.

Institutional abbreviations are: **CAS** – California Academy of Sciences, San Francisco, California, U.S.A; **GMNH** – Gunma Museum of Natural History, Tomioka, Gunma Prefecture, Japan; **LACM** – Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; **SBCM** – San Bernardino County Museum, Redlands, California, U.S.A.; **UCMP** – University of California Museum of Paleontology, Berkeley, California, U.S.A.; **USNM** – United States National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.; **YPM** – Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Cetacea Brisson, 1762
Suborder Odontoceti (Flower, 1864) Flower, 1867
Superfamily Platanistoidea (Gray, 1846) Simpson, 1945

Platanistina Gray, 1846:45.

Susuoidea Gray. 1868:4; the only included family was Platanistidae, based on *Susu* Lesson, 1828, which is a rejected senior synonym of *Platanista*, see Hershkovitz, 1961:555.

Platanistoidea Simpson, 1945:100; as a new superfamily of Odontoceti, to include the family Platanistidae, which included three subfamilies — Platanistinae, Iniinae, and Stenodelphininae.

Type genus. *Platanista* Wagler, 1830; type by tautonymy.

Included families. Allodelphinidae Barnes, 2006; Prosqualodontidae Cozzuol, 1996; Squalodontidae Brandt, 1872; Waipatiidae Fordyce, 1994; Squalodelphinidae (Dal Piaz, 1916) Rice, 1998; and Platanistidae (Gray, 1846) Gray, 1863.

Comments. Our use here of the superfamily Platanistoidea is not the same as that of Simpson (1945), which included only one family, the Platanistidae, whose contents were not then the same as are recognized in this study.

Muizon (1987, 1988, 1994) expanded the previous concepts (*sensu* Simpson, 1945) of the superfamily Platanistoidea by including within it, as well as other family-level groups, the large-toothed primitive odontocetes of the family Squalodontidae. Muizon (1988) named the new genus *Dalpiazina* to include only *Champsodelphis ombonii*, and established for it the new family Dalpiaziniidae. Fordyce (1994:170) further discussed the monotypic family Dalpiaziniidae in regards to its relationships to the superfamily Platanistoidea.

Fordyce (1994) established the family Waipatiidae to include the late Oligocene *Waipatia maerewhenua* Fordyce, 1994, from New Zealand. He further expanded the concepts of superfamily Platanistoidea, and of the family Waipatiidae, by provisionally assigning to the Waipatiidae such enigmatic previously described, late Oligocene taxa as *Sulakocetus dagestanicus* Mchedlidze, 1984, and *Sachalinocetus cholmicus* Dubrovo, 1970, in Siryk and Dubrovo, 1970.

Fordyce (1994) provided characters that are useful in defining the superfamily Platanistoidea and presented a cladistic analysis of the group. His study did not deal with the finer details of the interrelationships of fossil and Recent members of the family Platanistidae. Some of those issues were addressed by Barnes (2006), who presented a revised phylogenetic analysis of the superfamily Platanistoidea. The monophyly of the Platanistoidea has been suggested in some but not all previous studies (for example, Geisler and Sanders, 2003; Lambert, 2005a; Geisler et al., 2011; Murakami et al., 2012a,b; Aguirre-Fernández and Fordyce, 2014; Geisler et al., 2014; Lambert et al., 2014; Murakami et al., 2014b; Tanaka and Fordyce, 2014).

The coracoid process of the scapula is absent in all fossil platanistoid specimens for which a scapula is known, and its loss has been interpreted as a synapomorphy of the superfamily. However, this character has not been unequivocally demonstrated in all fossil platanistoid taxa, simply because scapulae are not known for many of them. We do, nonetheless, accept the absence of the coracoid process of the scapula as a diagnostic character of the entire superfamily Platanistoidea.

Family Allodelphinidae Barnes, 2006

Barnes, 2006:30; as a family of the superfamily Platanistoidea.

Barnes and Reynolds, 2009:487; Barnes, Kimura, and

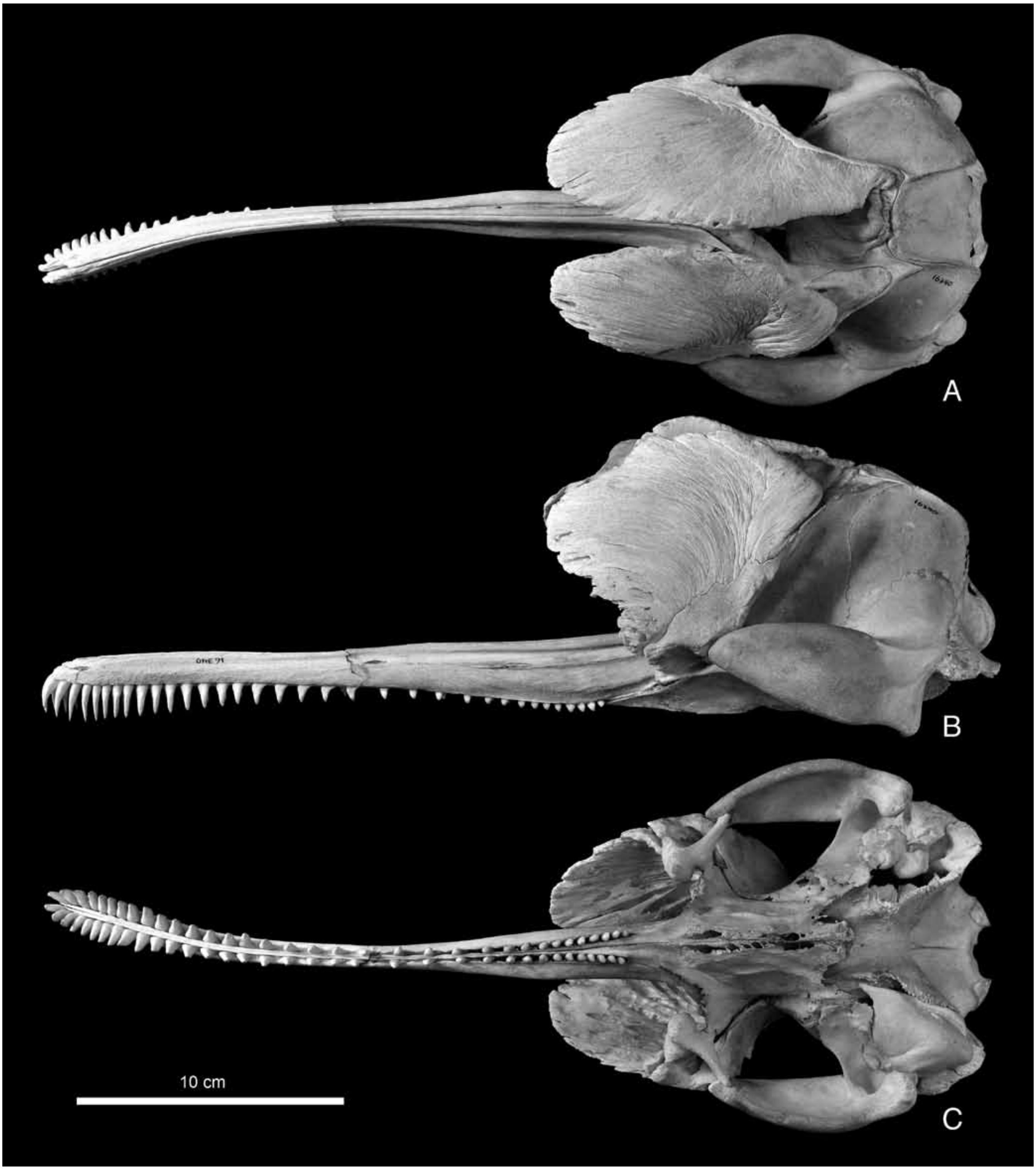

Figure 3. Cranium of the only living species of the superfamily Platanistoidea, *Platanista gangetica* (Roxburgh, 1801), adult female individual, CAS 16340, from Sind, Pakistan. **A**, dorsal view; **B**, left lateral view; **C**, ventral view. Scale bar equals 10 cm. The rostral curvature is not natural and is the result of unequal drying of the bone. After Barnes and Reynolds (2009).

Godfrey, 2010:450; Thomas and Barnes, 2015:21.

Type genus. *Allodelphis* Wilson, 1935.
Included genera. *Allodelphis* Wilson, 1935; *Goedertius* Barnes and Kimura, new genus; *Ninjadelphis* Kimura, new genus; and *Zarhinocetus* Barnes and Reynolds, 2009.
Emended diagnosis of family. A family of the odontocete superfamily Platanistoidea including relatively large dolphin-like odontocetes having estimated adult total body lengths of approximately three to five meters, cranial lengths of approximately one meter, having cranium with elongate and narrow rostrum, rostral length approximately four times braincase length, premaxillae and maxillae both reaching anterior rostral extremity, premaxillae and maxillae fused together distally, mesorostral canal open dorsally only in posterior part of rostrum, anteroposteriorly elongated groove present on lateral side of rostrum approximately following maxilla-premaxilla suture, posterior maxillary foramen located posterolateral to dorsal naris and not close to posterior end of premaxilla, posterolateral sulcus and posteromedial sulcus on

premaxilla shallow or absent, posterior ends of premaxillae separating from lateral sides of corresponding nasal bones, posterior ends of premaxillae relatively thin dorsoventrally and narrow (not expanded transversely), nasal bones small and narrow transversely, nuchal crest thick anteroposteriorly, lateral lamina of pterygoid forming bony plate extending posteriorly from palate and contacting anterior falciform process of squamosal, palatine bone extending posteriorly from palate dorsal to lateral lamina of pterygoid, forming part of bony plate within orbit, and also contacting anterior falciform process of squamosal, preorbital lobe of pterygoid sinus absent, postorbital lobe of pterygoid sinus absent, posterior sinus not present in anterior surface of paroccipital process; internal acoustic meatus of the petrosal opening anteromedially, superior process of the petrosal wide, smooth and almost flattened, posterior process of the petrosal atrophied; tympanic bulla with elongated and pointed anterior process, outer lip inflated and with smooth ventral surface; mandible with transversely narrow symphyseal portion, anteroposteriorly elongated and somewhat compressed dorsoventrally, mandibular symphysis very long and firmly ankylosed, elongate sulcus present on lateral surface of symphyseal part of dentary; all teeth single rooted, crowns tall and slender; neck relatively long with cervical vertebrae proportionally large and with anteroposteriorly elongated centra, atlas vertebra bearing separate dorsal and ventral transverse processes, axis vertebra with relatively large odontoid process; caudal vertebrae enlarged; humerus with diaphysis proximodistally elongated and oval in cross section, humeral head proportionally large; propensity for distal trochlea of humerus to fuse to olecranon process of ulna; radius and ulna equal to or less than length of humerus.

Geographic and geochronologic ranges. Early and middle Miocene; North Pacific Ocean coasts of present day central and southern California, Oregon, Washington, and Japan.

Allodelphis Wilson, 1935

Allodelphis Wilson, 1935:13; as a genus in the delphinoid family Delphinidae.

Allodelphis Wilson, 1935. Barnes, 1977:325, table 2; as a genus in the family Platanistidae; Barnes, 2006:31-32, as the type genus of the platanistoid family Allodelphinidae; Barnes and Reynolds, 2009:487; Barnes, Kimura and Godfrey, 2010.

Emended diagnosis of genus: A genus of the family Allodelphinidae differing from *Ninjadelphis*, new genus, and *Zarhinocetus* by having cranium with wider dorsal opening of mesorostral canal anterior to dorsal nares, posterior part of rostrum anterior to dorsal nares not depressed, posterior ends of premaxillae less irregular and digitated, posterior ends of premaxillae extending posteriorly beyond level of posterior margins of corresponding nasal bones, nasal bones elevated anteriorly rather than tilting anteroventrally into posterior part of dorsal nares, nasal bones expanded in width anteriorly rather than narrow anteriorly, nasal bones not fused to each other at midline or to underlying frontal bones, instead having margins defined clearly by sutures, nasal bones and dorsal exposures of frontal bones at cranial vertex symmetrical, with mid-line sutures on mid-sagittal plane rather than skewed asymmetrically to left side, right and left halves of nuchal crest symmetrical and having approximately equal widths and curvatures, and nuchal crest nearly straight transversely rather than curved anteriorly near cranial vertex; tympanic bulla with less inflated outer lip, and smaller and more posteriorly directed sigmoid process; atlas vertebra having dorsal transverse process tapered and not expanded dorsoventrally; differing further from *Goedertius*, new genus, by having posterior ends of premaxillae less irregular and digitated, nasal bones elevated anteriorly rather than tilting anteroventrally into posterior part of dorsal nares, nasal bones expanded in width anteriorly rather than narrow anteriorly; differing further from *Ninjadelphis* by having cranium with laterally-flaring margin of maxilla anterior to antorbital notch expanded and flaring laterally equally on both right and left sides rather than being smaller on right side, postglenoid process of squamosal oriented transversely and not expanded on posterolateral side of glenoid fossa (articular surface for mandibular condyle facing anteroventrally rather than anteromedially); petrosal with larger cochlear portion, shorter and more robust anterior process, shorter posterior process, articular facet for tympanic bulla oval shaped and furrowed rather than elongate and smooth, articular facet for bulla not divided into two articular surfaces; tympanic bulla with shorter posterior process, and smaller facet for articulation with petrosal; and atlas vertebra with ventral transverse process shorter; differing further from *Zarhinocetus* by having cranium lacking maxillary tuberosity on lateral edge of maxilla immediately anterior to antorbital notch, lacking supraorbital crest of maxilla on dorsal surface of supraorbital process, mesethmoid bone between dorsal nares rising dorsally above level of margins of nares, supraorbital process of frontal thinner dorsoventrally, temporal crest more prominent and flaring posterolaterally, occipital shield not so high dorsoventrally, external occipital protuberance developed as vertically-oriented crest near apex of occipital shield, occipital condyles smaller; petrosal less robust, with cochlear portion more elongate anteroposteriorly, anterior process more slender, posterior process longer, and facet on posterior process for articulation with bulla larger and not bent laterally; atlas vertebra relatively smaller; humerus relatively smaller, rather than being enlarged and lengthened to approximately 25% of total cranium length; radius and ulna approximately same lengths as humerus.

Type species. *Allodelphis pratti* Wilson, 1935; type by original designation by Wilson (1935:13).

Included species. *Allodelphis pratti* Wilson, 1935; and *Allodelphis woodburnei* Barnes and Reynolds, 2009.

Geographic and geochronologic ranges. Early Miocene; eastern North Pacific Ocean coast of present-day central and southern California.

Allodelphis pratti Wilson, 1935

Figures 4-8, 9B, 37A, 38A, 39A, 40C,D, Table 1, 2

Allodelphis pratti Wilson, 1935:14, figs. 1-3, pl. 1, figs, a-b; Horikawa, 1977:109; Barnes, 1977:325, table 2; Barnes, 2006: 26-27, 31-32, figs. 1-3; Barnes and Reynolds, 2009:491, figs. 5, 6C, 10A, 11A, table 1; Barnes, Godfrey and Kimura, 2010:450, fig. 1.

Emended diagnosis of species. A species of the genus *Allodelphis*, differing from *A. woodburnei* by having cranium with larger and transversely wider dorsal nares, posterior ends of premaxillae extending farther posteriorly toward nuchal crest, nasal bones longer anteroposteriorly, anterior edges of nasal bones located farther posteriorly, relatively smaller fossa present on each side of vertically-oriented sagittal crest in dorsal part of occipital shield, dorsal part of temporal crest smaller and less prominently flaring, anterior end of zygomatic process of squamosal smaller and more tapered rather than robust and lobate, glenoid fossa of squamosal facing more anteroventrally, occipital condyles relatively and absolutely of larger size.

Holotype. YPM 13408, a partial skeleton of one individual, including cranium that lacks the rostrum, with broken parts of the right dentary adhering to both the dorsal and ventral sides of the right supraorbital process, the right petrosal (which has been removed from the cranium), the atlas vertebra (which still adheres by sediment to the occipital condyles), approximately thirty other vertebrae, and some ribs; collected by Charles A. Pracht in the Autumn of 1928, and additional parts of the same individual collected after that date by Charles A. Pracht and Leslie E. Wilson.

Note about the collector. In the publication by Wilson (1935:9, 13, 15), Charles A. Pratt is identified as a student during the years 1928 and 1929 at Bakersfield Junior College, which is now called

Bakersfield College, and is located in the eastern part of the city of Bakersfield, California. On the original specimen label that is curated with the holotype specimen, YPM 13408, written lightly with a lead pencil is the annotation, "Collector's name is Chas. A. Pracht" . It is probable that the last name, Pratt, that appears in Wilson's (1935) publication, and forms the species patronym, was an Anglicization of the original German surname Pracht.

Type Locality. YPM locality 4940, approximately 8 km southwest of the small town of Woody, on the south side of a hill having an elevation of 1240 feet, in the SW 1/4 of Sec. 12, T. 26 S., R 28 W., Mt. Diablo Base and Meridian, Woody Quadrangle, United States Geological Survey, Kern County, California, U.S.A. This locality is shown as locality "A" on a map published by Mitchell and Tedford (1973:fig. 1).

Referred Specimen. UCMP 83791, a partial skeleton of one individual, excavated near the type locality of *A. pratti*, including left tympanic bulla, hyoid bones, atlas vertebra and two other cervical vertebrae, four thoracic vertebrae, parts of at least six ribs, manubrium, left humerus fused to left ulna, of one individual, collected by Lawrence G. Barnes, 18 May 1969 (see Barnes, 2006; Barnes and Reynolds, 2009).

Formation and age. The specimens of *A. pratti* are from a near shore marine rock unit that was identified by Wilson (1935) as the Jewett Sand, but which has been mapped more recently as sediments that are not differentiated between being the Freeman Silt and the Jewett Sand (*fide* Addicott. 1972), early Miocene in age, approximately 21 to 22 million years old, correlated with the Vaqueros provisional marine stage of Addicott (1972) and the Arikareean North American Land Mammal Age (Mitchell and Tedford, 1973:216, 265-275; Barnes, 1977:324-325, table 2; Tedford et al., 1987:156, 201, fig. 6.2 (chart in pocket); Tedford et al., 2004:fig. 6.2; Barnes, 2006). The holotype (YPM 13408) and referred specimen (UCMP 83791) are from the Woody Local Fauna, named and characterized by Mitchell and Tedford (1973), and this local fauna is from strata that stratigraphically overlie and are chronologically younger than, the Pyramid Hill Local Fauna (named by Mitchell and Tedford, 1973).

Geographic and geochronologic ranges. Early Miocene, North Pacific coast of present-day central California.

Comments. *Allodelphis pratti* Wilson, 1935, is a taxonomically and historically important species of North Pacific fossil cetacean. It is one of the earlier named fossil cetaceans from California. It is the type species of the genus *Allodelphis* Wilson, 1935, and that genus is the type genus of the family Allodelphinidae (Barnes, 2006). *Allodelphis pratti* is the most primitive named platanistoid from the North Pacific realm, and for many years it remained poorly known and was rarely mentioned in the scientific literature.

Wilson (1935) originally assigned *A. pratti* to the delphinoid family Delphinidae. Barnes later (1977:325) re-identified *A. pratti* as a platanistid, having affinities with the North Atlantic Miocene platanistid *Zarhachis flagellator* Cope, 1868. Subsequently Barnes (2006) designated *Allodelphis* as the type genus of the new platanistoid family Allodelphinidae. Barnes (2006:figs. 1-3), Barnes and Reynolds (2009), and Barnes et al. (2010) published additional images of the holotype cranium, which supplement the original outline drawings of the same specimen that were presented by Wilson (1935:figs. 1-3). We provide here additional images of the holotype and referred specimen to facilitate comparisons with the other allodelphinids.

Supplemental description.

Cranium. *Allodelphis pratti* has a non-enlarged and arc-shaped zygomatic process of the squamosal, relatively wide exposures of the palatine bones on the posterior part of the palate between the maxilla and the pterygoid, a relatively small glenoid fossa that faces anteroventrally, a wide dorsal opening of the mesorostral canal (rather than being closed over dorsally), and lacks an anteroposteriorly aligned crest on the dorsal surface of the supraorbital process of the maxilla.

The posterior ends of the premaxillae are irregularly formed (Figures 4A, 37A), being somewhat digitated, relatively narrow, parallel-sided, and extend posteriorly on the cranium to beyond the posterior margins of the nasal bones. The premaxillae do not make wide contact with the lateral edges of the nasal bones, but this is not clear in the images provided by Wilson (1935). On the right side of the holotype the premaxilla is close to the lateral edge of the right nasal, but it is not in full contact with it (Barnes and Reynolds, 2009:fig. 10; Figure 37A). On the left side of the holotype there is a wider gap of approximately 1 mm between the medial side of the posterior end of the premaxilla and the adjacent nasal bone, and this gap has sediment in it (Barnes and Reynolds, 2009:fig. 10; Figure 37A). On each side of the cranium it is the underlying maxilla, rather than the premaxilla, that makes contact with the lateral side of the nasal bone.

Among odontocetes, the primitive state is for the posterior ends of the premaxillae to be transversely wider, and for each premaxilla to have an anteroposteriorly elongate and clear sutural contact with the lateral side of the adjacent nasal bone. This condition exists, for example, in the primitive odontocete *Agorophius pygmaeus* (Müller, 1849) (see Fordyce, 1981:fig 2b). The condition in the holotype of *A. pratti* appears to represent the beginning stages of a progressive separation of the posterior end of the premaxilla from the adjacent nasal bone. This progressive separation culminates in the more derived species *Ninjadelphis ujiharai* Kimura, new genus and new species, *Zarhinocetus donnamatsonae*, new genus and new species, and *Zarhinocetus errabundus*, in which the premaxillae are retracted anteriorly onto the facial region, leaving the maxillae contacting the lateral edges of the nasal bones.

The cranial vertex is essentially symmetrical (Figure 37A), not skewed to the left side as is the case in *Ninjadelphis ujiharai* Kimura, new genus and new species, *Zarhinocetus donnamatsonae*, new species, and *Zarhinocetus errabundus*. The posterior ends of the maxillary bones are expanded medially toward the cranial vertex, squeezing between them the nasal bones and the dorsal exposures of the frontal bones. The nasal bones of *A. pratti* are thus relatively small and transversely narrow compared to those of most primitive Odontoceti, but nonetheless larger and wider than in any other species of Allodelphinidae.

The lateral lamina of each pterygoid bone extends posteriorly within the orbit, forming a vertical wall between the orbit and the narial passage. The lateral lamina extends posteriorly so far that it makes a wide contact with the anterior falciform process of the squamosal.

The palatine bone also extends posteriorly from the posterolateral corner of the palate, thus forming a thin plate of bone that also is part of the wall of bone in the medial part of the orbit. This plate of the palatine is attached to the lateral lamina of the pterygoid along its dorsal margin, and it also makes contact with the anterior falciform process of the squamosal.

Petrosal. The right petrosal was found adhering by sediment (see Wilson, 1935:21) to the mandibular fragment that is still attached to the holotype cranium of *A. pratti* (Wilson, 1935:fig. 3; pl.1, figs, a, b; Figure 5 herein). This petrosal is of the correct size to articulate with the tympanic bulla of the referred specimen, UCMP 83791, described in following text, thus contributing to evidence that these two specimens do represent the same species. The petrosal of *A. pratti* is relatively uninflated, and has relatively small anterior and posterior processes, but has a relatively large cochlear portion. The cochlear portion is elongated anteroposteriorly, contrasting with that of *Ninjadelphis ujiharai* Kimura, new genus and new species (Figure 21), which is smaller and not elongated in this fashion, and with that of *Zarhinocetus errabundus* (Figure 33), which is more bulbous and more enlarged mediolaterally. It has a very prominent lateral tuberosity. The anterior process is not as elongated as that of *N. ujiharai*, but it is deeper dorsoventrally. The anterior process of *A. pratti* is not as deep dorsoventrally as it is in *Z. errabundus*. The posterior process is deeper dorsoventrally and not elongated posteriorly compared to that of *N. ujiharai*, and it has a much larger articular facet for the tympanic bulla. Its articular facet is

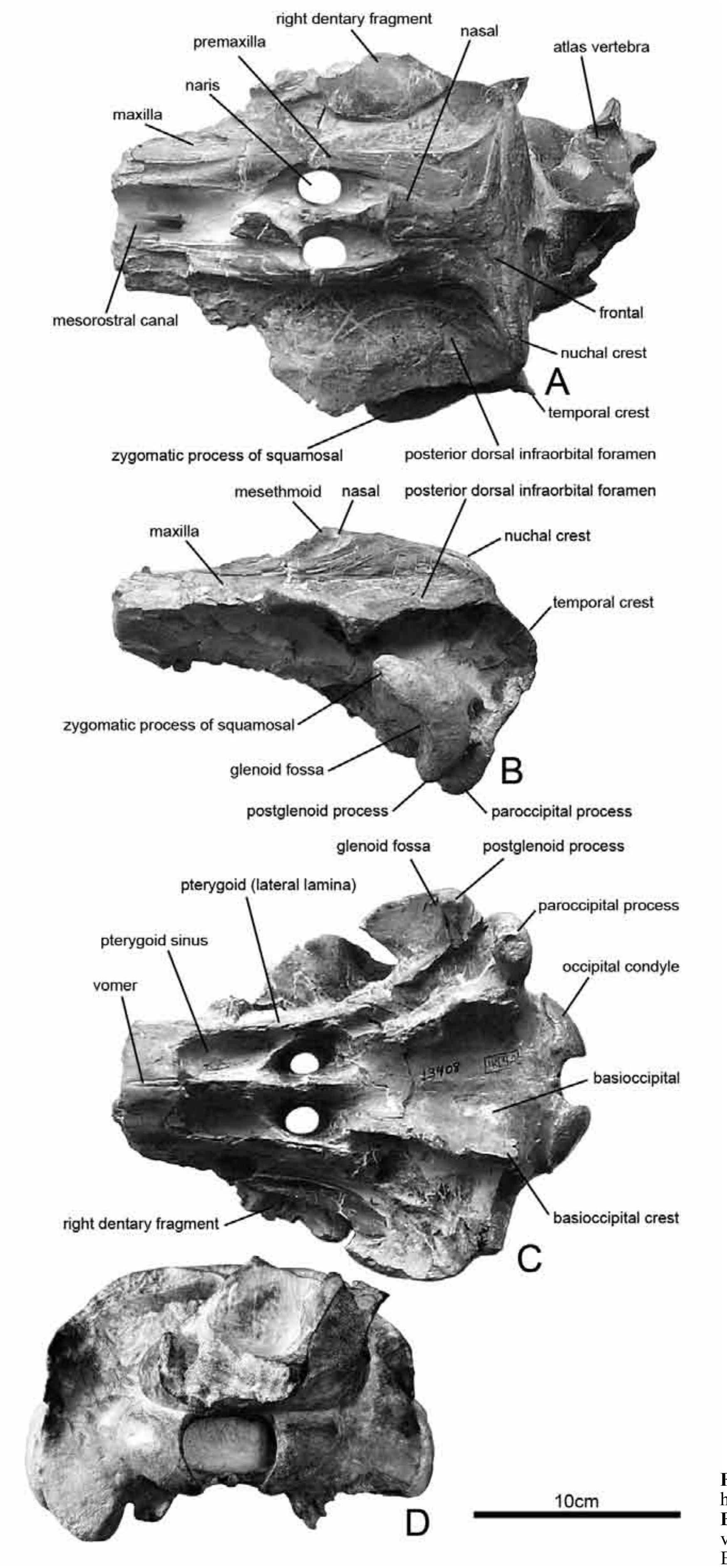

Figure 4. *Allodelphis pratti* Wilson, 1935, holotype cranium, YPM 13408. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, posterior view. Scale bar equals 10 cm. Modified from Barnes and Reynolds (2009).

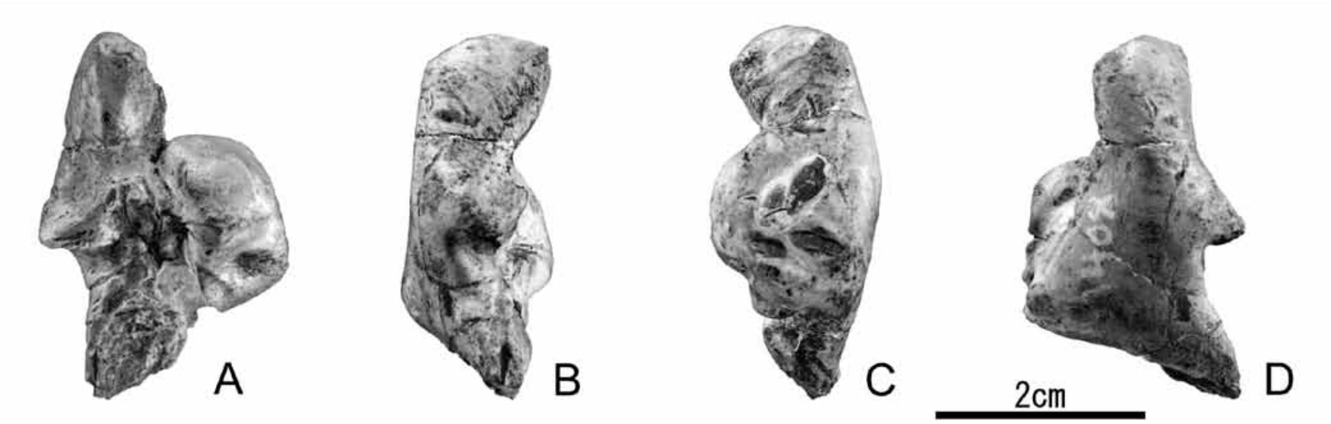

Figure 5. *Allodelphis pratti* Wilson, 1935, holotype right petrosal, YPM 13408. **A**, ventral view; **B**, lateral view; **C**, medial view; **D**, dorsal view. Scale bar equals 2 cm.

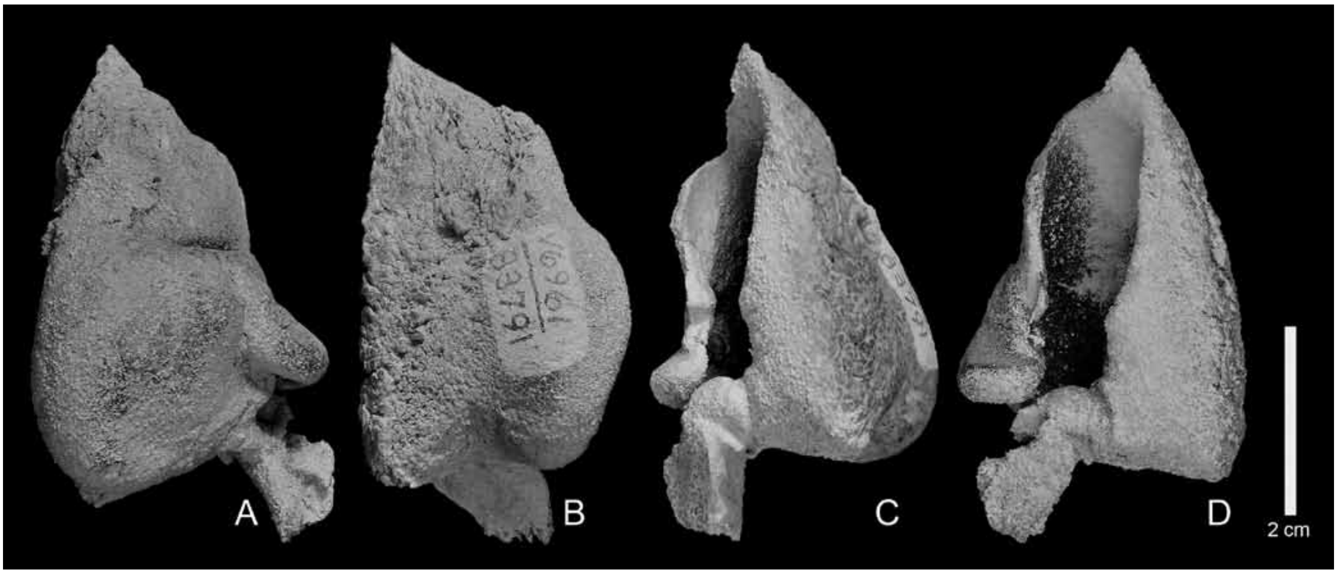

Figure 6. *Allodelphis pratti* Wilson, 1935, left tympanic bulla of referred partial skeleton, UCMP 83791. **A**, lateral view; **B**, ventral view; **C**, medial view; **D**, dorsal view. Scale bar equals 2 cm.

elliptical in shape and has a furrowed surface, unlike the smooth articular facet of *N. ujiharai* that is divided into two differently oriented surfaces. The posterior process of *A. pratti* differs from that of *Z. errabundus* by being larger, not bent so much laterally (see Figure 33C), and by having a rugose rather than smooth articular surface for the tympanic bulla.

Tympanic bulla. The complete left tympanic bulla is preserved with the referred specimen (UCMP 83791, Figure 6, anteroposterior length: 50 mm) of *A. pratti*. Like that of other species of Allodelphinidae, it is relatively large, and it has a large and pointed anterior spine. Presence of such a spine has been considered to be diagnostic for species in the superfamily Platanistoidea (Kellogg, 1924; Muizon, 1987, 1994; Fordyce, 1994; Barnes, 2002, 2006).

The ventral surface of the bulla is very rugose, being more rugose than the bullae of both *N. ujiharai* and *Z. errabundus*. The outer lip of the bulla is less inflated than in both of those species (Figures 23, 34), and in the sequence *A. pratti* ➡ *N. ujiharai* ➡ *Z. errabundus* the outer lips of the bullae are progressively more inflated. The sigmoid process is directed posterolaterally rather than laterally as it is in both *N. ujiharai* and *Z. errabundus*. The posterior process is smaller than that of *N. ujiharai*, commensurate with the different sizes of the posterior processes of the petrosals of these two species. The posterior processes are broken off of the known bullae of *Z. errabundus*, making comparison of that structure impossible.

Mandible. Broken parts of the mandible adhere by dense matrix to the holotype cranium. Most of these are small and relatively uninformative, some of them obscuring areas of anatomy of the cranium. Part of the posterior end of what apparently is the right dentary, however, adheres to the dorsal surface of the right supraorbital process, and its convex lateral surface is facing away from the cranium. This is a part of the very thin area of the ascending ramus that is excavated on its medial side by the mandibular fossa. This fragment demonstrates that *A. pratti* has on its dentary the area that is termed the acoustic window (Norris, 1968:298, 308-312; Mead and Fordyce, 2009:42, fig. 15), and the presence of this structure indicates that the species was capable of receiving sounds that could be used in echolocation.

Atlas. The atlas vertebra is present both with the holotype, YPM 23408 (Figures 4A, D), and the referred specimen, UCMP 83791 (Figure 7). The similarities between these two bones are part of the evidence for assigning specimen UCMP 83791 to the species *Allodelphis pratti*. The holotype atlas is firmly attached by sediment to the occipital shield of the holotype cranium (Wilson, 1935:figs. 1, 2; Figure 4A herein). The vertebra is badly broken, missing much of its posterior part and the transverse processes. The referred atlas is essentially complete.

The holotype and referred atlas vertebrae are nearly identical in size. The holotype atlas measures 104 mm in maximum transverse width across the anterior articular surfaces, and the referred atlas measures 103 mm. Both are 68 mm in overall

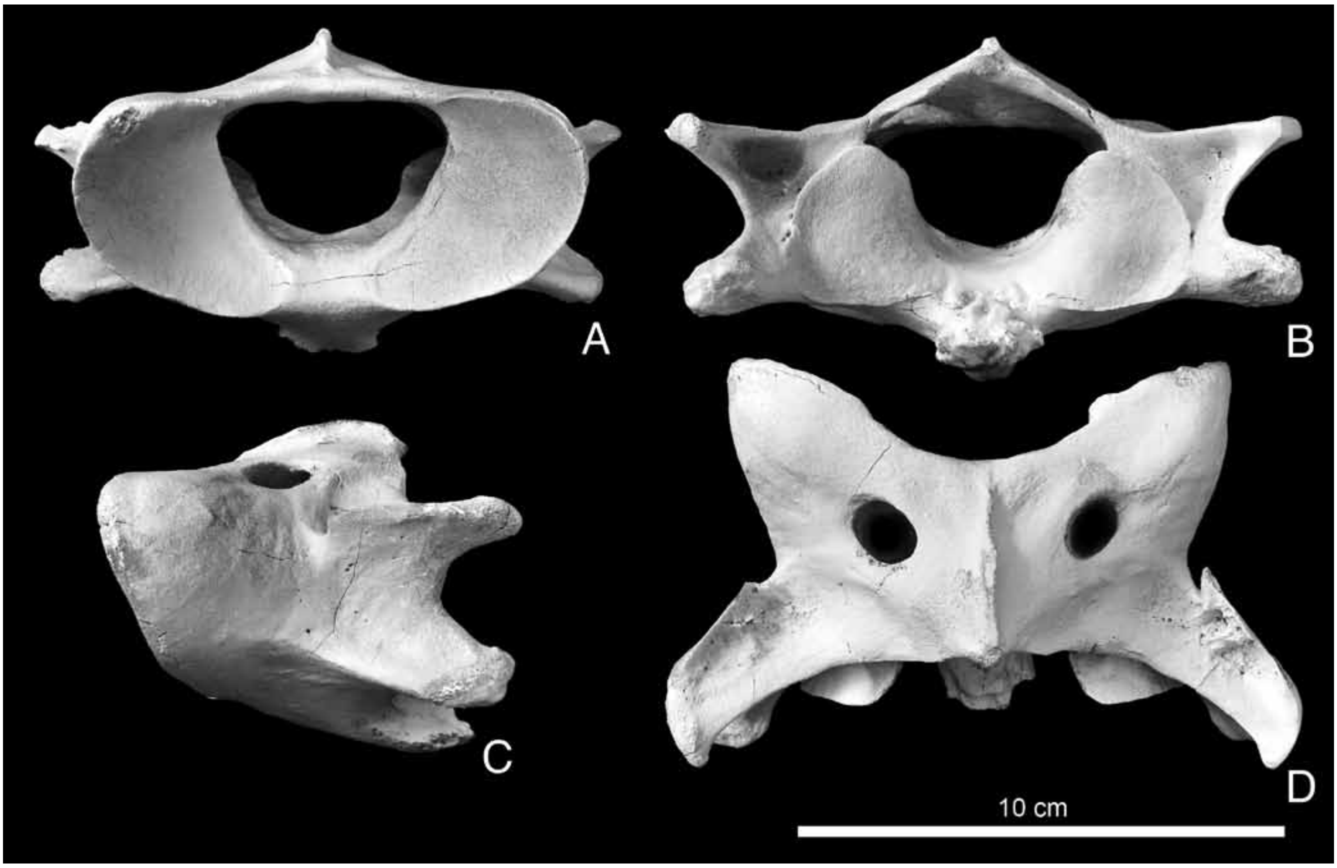

Figure 7. *Allodelphis pratti* Wilson, 1935, referred atlas vertebra, part of associated skeleton, UCMP 83791. **A**, anterior view; **B**, posterior view; **C**, left lateral view; **D**, dorsal view. Scale bar equals 10 cm.

height (measured at the center of the vertebra to the apex of the neural process), and 48 mm in maximum width of the posterior opening of the neural canal.

The referred atlas differs from that of the holotype by having a slightly lower neural arch, by this arch being highest in its posterior part instead of its anterior part, and by the dorsally facing transverse foramina being larger. The referred atlas has a large and tapered dorsal transverse process that bends posterolaterally and hooks medially at its end. The ventral transverse process is thicker, shorter, flattened dorsoventrally, and has a bulbous and rugose distal end.

The atlas of *A. pratti* differs from that of *N. ujiharai* by having a smaller spinous process, a smaller and more slender dorsal transverse process that is not expanded dorsoventrally, and a much shorter ventral transverse process.

The atlas of *A. pratti* differs from that of *Z. errabundus* by being relatively and absolutely smaller, less robust, more compressed dorsoventrally, and by having smaller dorsal and ventral transverse processes.

Manubrium. The anterior part of the manubrium is preserved with the referred specimen, UCMP 83791, of *Allodelphis pratti* (Figure 8); it is broken off approximately at its mid-length. It closely resembles the same bone of *Ninjadelphis ujiharai* Kimura, new genus and new species, by being relatively massive, elongate anteroposteriorly, having a blunt anterior end, and relatively large and rugose facets for cartilaginous attachments of the sternal ribs. These facets are located at the anterolateral corner and at mid-length on each side of the bone. The ventral surface (Figure 8A) is convex, and at its mid-length bears a large and rugose tubercle. At this latter location on the manubrium of *N. ujiharai* there is a relatively smooth crest, not a tubercle. The elongation of the manubrium and wide spacing between the sternal rib facets reflects the length of the thoracic vertebrae and the concomitantly wide spacing between the ribs that are attached to those vertebrae. Elongation of the manubrium is also consistent with *A. pratti* being relatively primitive.

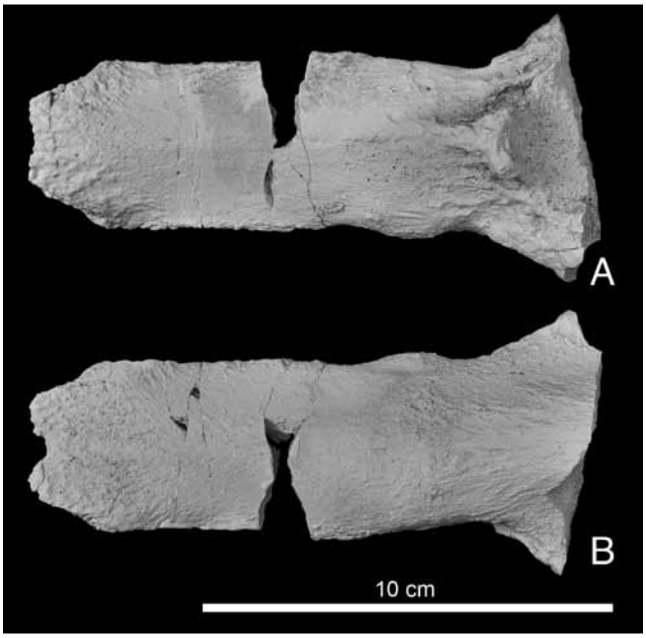

Figure 8. *Allodelphis pratti* Wilson, 1935, referred manubrium, part of associated skeleton, UCMP 83791. **A**, ventral view; **B**, dorsal view. Scale bar equals 10 cm.

Humerus. An odontocete right humerus (Figure 9A; Barnes and Reynolds, 2009:fig. 2A) was originally incorrectly catalogued with the holotype of *A. pratti*, YPM 13408, and it was referred to this species by Wilson (1935:26). This humerus is from a different individual fossil, and it most probably represents a

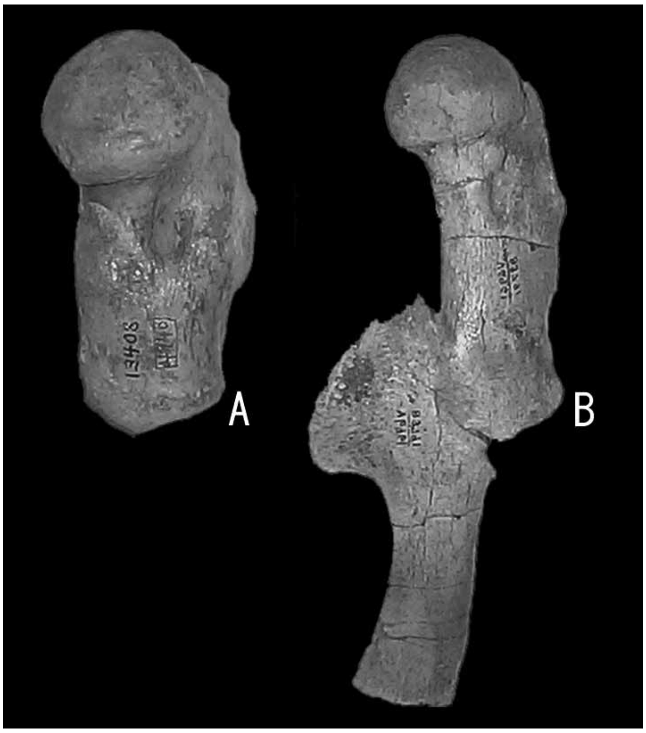

Figure 9. A, right humerus catalogued with holotype (YPM 13408) of *Allodelphis pratti* Wilson, 1935, re-identified by Barnes and Reynolds (2009) as an unidentified species of Eurhinodelphinidae. **B**, left humerus and ulna of *Allodelphis pratti* Wilson, 1935, part of associated skeleton, UCMP 83791, image reversed). Not to scale.

species in the somewhat distantly related odontocete family Eurhinodelphinidae (see Barnes, 2006:26). Several species of Eurhinodelphinidae occur in the deposit that yielded the holotype of *A. pratti* (see Wilson, 1935; Barnes, 1977), and at the present time it is not possible to identify this humerus more definitively than as family Eurhinodelphinidae, genus and species undetermined. It should not be considered as being part of the holotype (YPM 13408) of *Allodelphis pratti*.

The correct humerus of *A. pratti* is represented by that with the partial skeleton referred to this species, UCMP 83791 (Figure 9B) by Barnes and Reynolds, 2009). In Figure 9B these bones are shown reversed photographically to facilitate comparison. This humerus differs from the one that Wilson referred to the holotype of *A. pratti* (compare Figures 9 A and 9B) by being longer, and by having a diaphysis that is straighter, more slender, and nearly circular in cross section (rather than flattened transversely), a smaller deltopectoral crest, a smaller and more spherical head, and a smaller distal end.

The referred humerus, UCMP 83791, is very similar to that with the holotype of *A. woodburnei*, (compare Figures 39A and 39B), from which it differs by having a slightly thicker diaphysis, larger deltopectoral crest, and by being fused to the ulna.

The humerus of *A. pratti* also resembles the one here referred to *Zarhinocetus errabundus* (LACM 21031, Figure 39E) by having an elongate and relatively slender diaphysis and a narrow distal end. It differs from that humerus by being smaller, but by having a proportionally larger humeral head and a larger deltopectoral crest. The humeri of *A. pratti*, *Ninjadelphis ujiharai* Kimura, new genus and new species, and *Z. errabundus* all are fused to their corresponding ulna. The area of fusion is at the proximal part of the olecranon process of the ulna. Such fusion occurs randomly in cetaceans, and it was reported in the holotype of the late Miocene fossil phocoenid, *Piscolithax tedfordi* Barnes, 1984, from Mexico (see Thomas et al., 2008). However, because it occurs in all reported specimens of the Allodelphinidae except for the holotype of *A. woodburnei*, this fusion may prove to be a diagnostic character of some species in the family.

Ulna. The left ulna, as mentioned above, is fused to the left humerus. The overall length of the ulna is essentially the same as the overall length of the humerus. These are the same proportions as in species of the basilosaurid Archaeoceti (Kellogg, 1936; Uhen, 2004), and this is therefore assumed to be the plesiomorphic state. Typically in the Mysticeti, however, the distal forelimb bones are longer than the humerus, and in the Odontoceti they are shorter than the humerus (see Sanders and Barnes, 2002).

The diaphysis of the ulna is relatively stout, being nearly the same width craniocaudally as that of the articulated humerus. The diaphysis curves caudally toward its distal end. The distal epiphysis was not fused to the diaphysis in life, and had become separated during deposition and was not found with the specimen. The semilunar notch is not divided as distinctly into two facets as it is in most species of Odontoceti. The olecranon process is relatively large and, considering the similarly large size of this process on the ulnae of archaeocetes (Kellogg, 1936; Uhen, 2004), this is most likely a plesiomorphic condition. The caudal border of the olecranon process forms a broad arc.

The ulna of *A. pratti* resembles that of *Zarhinocetus errabundus* (LACM 21031, Figure 39E) in its general shape, but it differs markedly by being proportionally larger and by having a much larger olecranon process.

Allodelphis woodburnei **Barnes and Reynolds, 2009**

Figures 10, 37B, 39B, Table 1

"…long-snouted member of the archaic superfamily Platanistoidea." Barnes and Reynolds, 2007:107.

Allodelphis woodburnei Barnes and Reynolds, 2009:494, figs. 6B, 8, 9, 10B, 11B, 12, table 1.

Emended Diagnosis of Species. A species of the genus *Allodelphis* differing from *A. pratti* by having cranium with mesorostral canal more closed over in its posterior part by slightly closer approximation of medial margins of right and left premaxillae, medial margins of premaxillae sloping medially anterior to dorsal nares rather than being horizontal, premaxillae lateral to dorsal nares having elevated lateral margins that overhang adjacent maxillae, premaxillae wider adjacent to dorsal nares, dorsal nares of smaller diameter, zygomatic process of squamosal shorter anteroposteriorly, more bulbous, and more steeply inclined anteriorly causing glenoid fossa for articulation with mandibular condyle to face more anteriorly, basisphenoid and basioccipital more arched on midline of basicranium; and by having humerus relatively and absolutely larger compared to body size, with relatively larger humeral head.

Holotype. SBCM L3210-1, the partial skeleton of one individual, including the cranium and the articulated mandible which is missing the posterior ends of both dentaries, at least five teeth on the left side, parts of the left tympanic bulla, two posterior cervical vertebrae, at least 11 thoracic vertebrae, 12 lumbar vertebrae, four caudal vertebrae, major parts of at least 17 ribs, the manubrium, distal part of the right scapula, and the right humerus; collected by Robert E. Reynolds, Tom Greer, Quinton Lake, and other SBCM volunteers from 1973 to 1975.

Type Locality. SBCM locality, 1.103.77, weathering from a northeast-facing cliff on the southwest side of a northwest-trending intermittent stream drainage, approximately 1 mile southwest of Cajon Junction, west of U.S. Interstate Highway 15, and south of California State Route 138, at 3,320 feet elevation, in the NE 1/4 of Section 34, Township 3 North, Range 6 West, U.S.G.S. Cajon 7,5" Quadrangle, 1956, in Cajon Pass, San Bernardino County, California, U.S.A. (Barnes and Reynolds, 2009: figs. 4-6).

Formation and Age. Vaqueros Formation, early Miocene, correlative with the Arikareean North American Land Mammal Age, and the Vaqueros provisional mega-invertebrate stage of Addicott (1972), approximately 22 million years old (Barnes and Reynolds, 2009:495-496).

Geographic and geochronologic ranges. Early Miocene; eastern North Pacific Ocean coast of present-day southern California.

Supplemental description.

The holotype is from an adult specimen because the epiphyses of all of the preserved vertebrae (cervical, thoracic, or caudal) are fused to their centra, and both the proximal and distal epiphyses are fused to the diaphysis of the humerus (Ogden et al., 1981; Galatius et al., 2006; Moran et al., 2015). The sex of the individual cannot be determined with currently available information.

Cranium. The cranium and mandible remain joined together by sediment (Barnes and Reynolds, 2009:fig. 8). The rostrum is essentially complete to the anterior extremity and is very long, relatively narrow, and very slightly compressed dorsoventrally (Figure 10). The suture between the maxilla and the premaxilla is distinct, except for a section measuring approximately 50 mm from the anterior tip of the rostrum where the two bones appear to have been in life fused together. Such fusion of the maxilla to the corresponding premaxilla at the distal end of the rostrum is a character of species in both the families Platanistidae and Allodelphinidae. An anteroposteriorly elongate sulcus on the lateral side of the rostrum follows the line of the suture between the maxilla and the premaxilla. In approximately the anterior half of the rostrum, the mesorostral canal is closed over by the right and left premaxillae, the premaxillae being in contact at the midline. The mesorostral canal is open widely in the posterior half of the rostrum, and is approximately 20 mm wide at the posterior end, in the area between the antorbital notches. The section of the mesorostral canal that is open at the posterior part of the rostrum is longer anteroposteriorly than in *Zarhinocetus errabundus*.

On the posterior part of the rostrum the dorsal surfaces of the premaxillae slope medially toward the mesorostral canal. However, the lateral edge of each premaxilla is elevated along its lateral margin to the extent that it forms an elongate crest that is the highest part of the rostrum.

The posterior ends of the premaxillae resemble those of *A. pratti* by being relatively narrow for an odontocete, nearly parallel-sided rather than lobate, and having irregularly shaped posterior terminations (Figures 37A, B). As in *A. pratti* the premaxillae extend posteriorly beyond the posterior margins of the nasal bones, but they do not extend so far posteriorly, terminating farther from the nuchal crest. In this latter condition

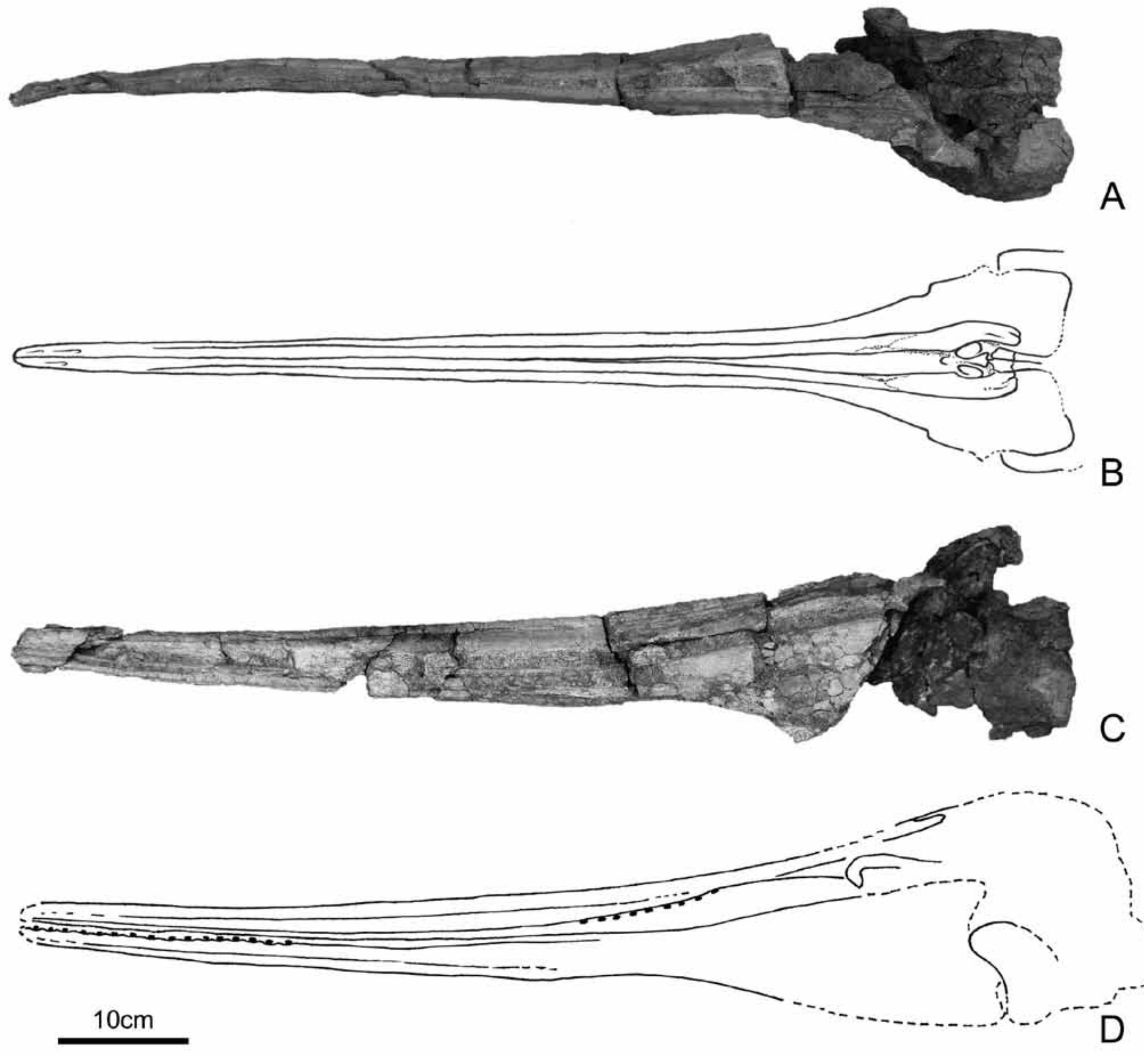

Figure 10. *Allodelphis woodburnei* Barnes and Reynolds, 2009, holotype cranium, SBCM L3210-1. **A**, dorsal view; **B**, partial restoration of dorsal view; **C**, left lateral view; **D**, partial restoration of left lateral view. Scale bar equals 10 cm. Modified from Barnes and Reynolds (2009).

A. woodburnei is more derived than *A. pratti*.

Similar to the condition in *A. pratti*, the posterior ends of the premaxillae do not make actual contact with the lateral edges of the corresponding nasal bones. On the right side of the holotype there is a gap of approximately 2 to 3 mm between the posterior end of the premaxilla and the adjacent nasal bone (Barnes and Reynolds, 2009:fig. 10; Figure 37B). On the left side of the holotype the premaxilla is close to the lateral edge of the left nasal, but it is not in contact with it (Barnes and Reynolds, 2009:fig. 10; Figure 37B), there being a gap of approximately 1 mm. The underlying maxillary bone contacts the nasal bone within this gap.

This separation between the premaxillae and nasals on the holotype of *A. woodburnei* is a more derived state than that exemplified by *A. pratti*. This progressive separation could be viewed as transitional to the more derived state in *Ninjadelphis ujiharai* Kimura, new genus and new species, *Zarhinocetus donnamatsonae* Barnes, new species, and *Z. errabundus*, in which the premaxillae are retracted much farther anteriorly on the facial surface.

In the proximal part of the rostrum, immediately anterior to the antorbital notch, the lateral edge of the rostral maxillary is developed into a thin, relatively sharp-edged shelf, and this shelf extends laterally. The dorsal surface of the maxilla here slopes ventrolaterally relative to the plane of the rostrum. A similar lateral expansion of the maxilla in the proximal part of the rostrum is characteristic of various primitive species of Oligocene Odontoceti such as *Agorophius pygmaeus* (see Fordyce, 1981); *Waipatia maerewhenua* Fordyce, 1994; and *Xenorophus sloanii* Kellogg, 1923 (and see Whitmore and Sanders, 1977). There is a similar lateral expansion of the proximal part of the maxilla in *Allodelphis pratti*. In species of *Zarhinocetus*, however, the same laterally projecting area of the maxilla has an oval-shaped tubercle of bone on its dorsal surface (Figure 32), and this is an autapomorphy of those taxa.

Each known species of allodelphinid has a differently shaped zygomatic process of the squamosal. The zygomatic process of *A. woodburnei* is thick and arched like that of *A. pratti* (Figure 4B), but is thicker, shorter, and more inclined anterodorsally, causing the glenoid fossa for articulation with the mandibular condyle to face more anteriorly (Barnes and Reynolds, 2009:fig. 11), rather than anteroventrally. *Allodelphis woodburnei* differs from *Ninjadelphis ujiharai* Kimura, new genus and new species, (Figure 18B, C) by having a shorter zygomatic process and by lacking a lateral expansion of the postglenoid process that forms a buttress, causing the glenoid fossa of the latter to face anteromedially. The zygomatic arch of *A. woodburnei* differs from those of species of *Zarhinocetus* by not being rectangular in lateral view and by not extending so far anteriorly (Figure 32B).

The anterior half of the left supraorbital process of the frontal is preserved on the holotype of *A. woodburnei*, demonstrating that this process is relatively small, and is not thickened dorsoventrally. The relatively thin supraorbital process is a primitive character state that *A. woodburnei* shares with *Allodelphis pratti*. Both of these species differ from species of *Zarhinocetus*, which have larger and more dorsoventrally thickened supraorbital processes of their frontals.

Tympanic bulla. Only the posterior part of the left tympanic bulla of the holotype of *A. woodburnei* is preserved, so the presence of an anterior bullar spine cannot be proven unequivocally for the species. The bulla is relatively large for the size of the cranium and, as in *Allodelphis pratti* and *Zarhinocetus errabundus*, it has a large and inflated outer lip.

Mandible. The dentary of *A. woodburnei* is in its anterior part very slender and relatively delicate. Posteriorly it is dorsoventrally deeper: the left dentary is 27.7 mm deep at the posterior end of the symphysis, and it increases to a depth of at least 82 mm dorsoventrally where it is broken off ventral to the antorbital notch. This abrupt deepening of the dentary posteriorly also occurs in the mandible of the referred specimen, LACM 149588, of *Zarhinocetus errabundus* (Figure 35B). The ascending ramus of the left dentary of the holotype is preserved far enough posteriorly (Barnes and Reynolds, 2009:fig. 8) to indicate that *A. woodburnei* has the thin posterior part of the dentary that is termed the acoustic window. This is the structure that allows transmission of sound to the ear during echolocation.

The right and left dentaries of the holotype of *A. woodburnei* are firmly ankylosed along the mandibular symphysis. The location of the fused symphyseal suture is marked on the ventral surface of the mandible by a fine line that extends for the entire length of the symphysis. As in *Ninjadelphis ujiharai* Kimura, new genus and new species, (Figure 24E) and *Zarhinocetus errabundus* (Figure 35D), the symphyseal portion of the mandible is slightly flattened dorsoventrally. The symphyseal portion of the mandible of *A. woodburnei* at its mid-length measures 42.1 mm in width and 27.7 mm dorsoventrally.

The anterior end of the mandible of *A. woodburnei* curves slightly dorsally, conforming to a similar curvature of the rostrum (Barnes and Reynolds, 2009:fig. 8B). The mandible of *Z. errabundus* also curves dorsally in this manner (Figure 35B). The mandibular fragments with the holotype of *A. pratti*, are too small to determine this feature, and the anterior end of the mandible of *Ninjadelphis ujiharai* Kimura, new genus and new species, is missing.

In *A. woodburnei* the anterior extremity of the mandible unequivocally reaches to the distal extremity of the long rostrum (Barnes and Reynolds, 2009:fig. 8B), and the same is true for *Z. errabundus* (Thomas and Barnes, 2015:fig. 17). As noted above, the specimens of *Ninjadelphis ujiharai* Kimura, new genus and new species, and *A. pratti*, do not include the distal end of the mandible, but it is likely that in those species the mandible also extended to the anterior extremity of the rostrum.

Not all species of Odontoceti have mandibles and rostra that are of the same length, however. For example, while this is the case in extant *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844) and *Platanista gangetica*, in some species of the family Delphinidae the mandible extends slightly farther anteriorly than the tip of the rostrum. An extreme of this is found in *Semirostrum ceruttii* Racicot, Deméré, Beatty, and Boessenecker, 2015).

The opposite is the case in species of the family Eurhinodelphinidae, in which the mandible typically is significantly shorter than the rostrum (see Abel, 1905). These different relative lengths of mandibles and rostra are certainly related to differences in feeding behavior.

On the lateral side of the dentary of *A. woodburnei* there is an elongate sulcus that extends the entire length of the symphyseal part of the mandible. This sulcus is near the ventral edge of the dentary at the anterior end of the mandible, and progressing posteriorly it ascends to be just below the mid-height of the dentary. This sulcus extends posteriorly to beyond the level of the posterior end of the symphysis, where it widens and diminishes on the side of the ascending ramus. This sulcus is relatively shallow, and this shallowness is likely a primitive character of *A. woodburnei* compared to the deeper sulci that exist in *Ninjadelphis ujiharai* Kimura, new genus and new species (Figures 24D-F), and *Zarhinocetus errabundus*. (Figures 35B-D). Correlated with the shallowness of these sulci in *A. woodburnei*, the ventral surface of the symphyseal part of the mandible is more deeply keeled, or "V" -shaped in cross-section. In *N. ujiharai* and *Z. errabundus* the sulci are deeper and the ventral surface of the dentary between them is wider and flatter.

Teeth. With the holotype of *A. woodburnei* at least five teeth are exposed in matrix that fills the left side of the oral cavity. The anterior teeth have tall and slender crowns, one of which has a crown measuring at least 10 mm tall and 1.5 mm wide at its base, and the posterior teeth have shorter and stouter crowns. These teeth are similar to those of *Ninjadelphis ujiharai* Kimura, new genus and new species (Figure 24G). No teeth have yet been identified for *A. pratti*, *Z. donnamatsonae*, new species, or *Z. errabundus*.

Judging by the dental alveoli in the rostrum of *A. woodburnei*, the anterior teeth are of relatively large diameter, and the openings of their alveoli are elliptical, expanded in an anteroposter direction. These anterior alveoli measure approximately 7 mm in diameter anteroposteriorly, and are spaced approximately 15 to 17 mm on center. In contrast, the more posterior dental alveoli on the rostrum are more nearly circular at their alveolar rims, and are relatively smaller, measuring approximately 5 mm in diameter, and they are spaced approximately 7 mm on center. This is similar to the spacing and sizes of alveoli in the holotype mandible of *Ninjadelphis ujiharai* Kimura, new genus and new species (Figure 24C), but differs from the situation in *Z. errabundus*, in which the alveoli in the rostrum and mandible are closer together in the anterior and posterior parts of the tooth row, but farther apart in the middle part of the tooth row (Figure 31C).

Goedertius Barnes and Kimura, new genus

Diagnosis of genus. A genus of Allodelphinidae having depression on dorsal surface of posterior part of rostrum, wide dorsal opening of mesorostral canal anterior to nares, premaxillae extending posteriorly to position of nasal bones, premaxillae curving medially to constrict posterior ends of nasals, cranial vertex symmetrical, nuchal crest not greatly elevated or thickened, zygomatic process of squamosal relatively large and arc-shaped, and temporal fossa relatively small and tapered anteriorly; differing from *Allodelphis* by having depression on basal part of rostrum anterior to nares, nasal bones smaller and greatly compressed transversely between posterior ends of premaxillae, and smaller temporal fossa; differing further from *Ninjadelphis*, new genus, by having shallower depression anterior to nares, small anteroposteriorly aligned maxillary crest dorsal to orbit, posterior ends of nasal bones more constricted transversely, postorbital process of frontal shorter, temporal fossa smaller and more tapered anteriorly, shorter and more curved zygomatic process of squamosal, dorsal exposures of frontals at cranial vertex smaller, mesethmoid septum between posterior parts of nares shorter, posterior maxillary foramen positioned more anteriorly, occipital condyles more protruding posteriorly; and differing further from *Zarhinocetus* by lacking tuberosity on each maxilla anterior to antorbital notch, and by having wider dorsal opening of mesorostral canal on posterior part of rostrum, shallower basin on dorsal surface of rostrum anterior to nares, posterior ends of premaxillae extending posteriorly and ending lateral to nasal bones rather than being retracted anteriorly and terminating lateral to dorsal nares, nasal bones larger, exposures of frontals on cranial vertex smaller, cranial vertex symmetrical rather than displaced to left side, nuchal crest narrower and lower, and zygomatic process of squamosal short and very curved in lateral view rather than elongate and rectangular.

Type and only included species. *Goedertius oregonensis* Barnes and Kimura, new species.

Etymology. The genus name is patronymic, honoring James L. Goedert and Gail H. Goedert, two of the collectors of the holotype of the type species of this genus. Mr. And Mrs. Goedert have been instrumental for decades in collecting, preserving, and interpreting fossils from the Pacific Northwest.

Geographic and geochronologic ranges. Early Miocene; eastern North Pacific Ocean coast of present day Oregon.

Goedertius oregonensis Barnes and Kimura, new species

Figures 11-15, 38C, 39D, Table 1

Diagnosis of species. Because the genus *Goedertius* is presently monotypic, the diagnosis of the species shall remain identical to that of the genus until further species are described in the genus.

Holotype. LACM 123887, partial skeleton of one individual, including complete cranium and mandible, 23 loose teeth, both petrosals and both tympanic bullae still in place, hyoid bones, atlas vertebra, axis vertebra, fourth through sixth cervical vertebrae, four thoracic vertebrae, part of the manubrium, right and left first ribs, and right humerus; collected by James L. Goedert, Gail H. Goedert, and the late Donald J. Martel, 9 and 12 May 1982, field number J. L. Goedert 39. The specimen was discovered by James Goedert and Gail Goedert as it was being uncovered by erosion in the intertidal zone on the wave-cut beach terrace. The anterior extremity of the rostrum was exposed, and they removed a section of rock that contained the anterior part of the rostrum and some of the cervical vertebrae. Upon preliminary cleaning, they realized the significance of the specimen, and returned to the site on 12 May 1982, found the ocean tide to be at a higher level, and labored to excavate under water the remainder of the specimen.

Type locality. LACM Locality 5057, in the intertidal zone on the beach at the mouth of Moore Creek, Lincoln County, Oregon, U.S.A.

Formation and age. The holotype is from the Nye Mudstone, and is early Miocene in age.

The strata at this site are dipping steeply, and because the specimen was on a bedding plane, the rostrum extended up-slope and was exposed. The brain case was more deeply buried.

The Nye Mudstone is correlative with the Pacific Northwest Pillarian Provincial Molluscan Stage (Addicott, 1976:102; Moore and Addicott, 1987). It overlies the late Oligocene Yaquina Formation, and underlies the late early Miocene to early middle Miocene Astoria Formation. The base of the overlying Astoria Formation has been indicated to be approximately 19.2 to 20.7 million years old based on magnetostratigraphic methods (Prothero et al., 2001). Thus, the holotype of *Goedertius oregonensis* is older than approximately 20 million years, and is understood here to be approximately 20 to 21 million years old.

Etymology. The species name, *oregonensis*, is in reference to the geographic occurrence of the holotype on the Pacific Ocean coast of Oregon, and is neutral in gender.

Geographic and geochronologic ranges. Early Miocene, eastern North Pacific Ocean coast in the region of present day Oregon.

Description. The holotype is from a subadult specimen because, although it appears to have attained its adult size and adult rostral length, the epiphyses of the cervical and thoracic vertebrae are not fused to their centra, and the proximal and distal epiphyses are not fused to the diaphysis of the humerus (Ogden et al., 1981; Galatius et al., 2006; Moran et al., 2015). The sex of the individual cannot be determined with currently available information.

Cranium. The cranium and mandible remain joined together by sediment, closely articulated, almost in the life position. The rostrum is essentially complete to the anterior extremity, but is missing probably 3 to 5 mm from its anterior tip due to erosion. There is an oblique fracture in the anterior one-third of the rostrum resulting from geologic distortion and, judging by the amount of offset in the left upper alveolar row, the rostrum as it is now preserved, is approximately 2 to 3 mm shorter than it was originally.

The rostrum is very long, relatively narrow, curved dorsally toward the distal end, and very slightly compressed dorsoventrally (Figure 11). The distal end of each premaxilla has on its dorsolateral surface an anteriorly facing foramen, which has an aperture approximately 1 mm in diameter that is continuous with an elongate, anteriorly extending sulcus. The suture between the maxilla and the premaxilla is distinct, except for a section toward the anterior end of the rostrum where the two bones are fused together. As stated before, such fusion of the maxilla to the corresponding premaxilla at the distal end of the rostrum is a character of species in both the families Platanistidae and Allodelphinidae. An anteroposteriorly elongate sulcus on the lateral side of the rostrum follows the line of the suture between the maxilla and the premaxilla. In approximately the anterior two-thirds of the rostrum, the mesorostral canal is closed over by the right and left premaxillae, the premaxillae being in contact at the midline. The mesorostral canal is open widely in the

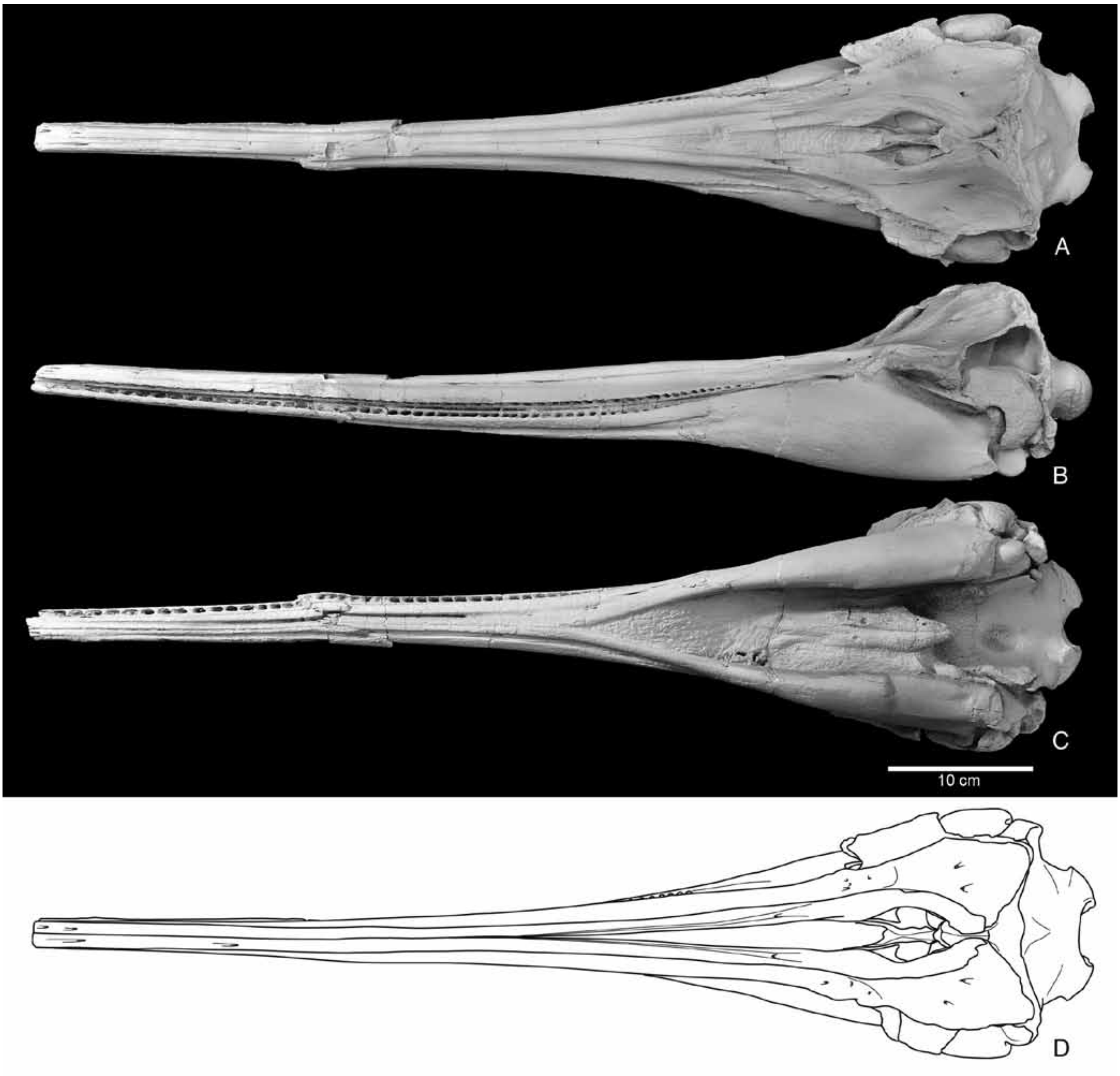

Figure 11. *Goedertius oregonensis* Barnes and Kimura, new genus and new species, holotype cranium, LACM 123887. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, dorsal view, line drawing. Scale bar equals 10 cm.

posterior one-third of the rostrum. The section of the mesorostral canal that is open at the posterior part of the rostrum is longer anteroposteriorly than in species of *Zarhinocetus*.

The right premaxillary foramen is open dorsally and is elongate anteroposteriorly. The left premaxillary foramen is partly roofed over by premaxillary bone and opens facing more posteriorly. Such variability of these foramina is typical among species of Allodelphinidae. On both premaxillae there is an anteromedial sulcus on the dorsal surface that defines the prenarial triangle, and a posterolateral sulcus that extends posteriorly onto the central part of the premaxilla, but does not curve toward the lateral side of the bone. As in *N. ujiharai* and the species of *Zarhinocetus* there is no posteromedial sulcus emanating from the premaxillary foramen.On the posterior part of the rostrum the dorsal surfaces of the premaxillae slope slightly medially toward the mesorostral canal, but then are elevated along the medial margin, forming an elongate crest adjacent to the mesorostral canal.

The posterior ends of the premaxillae resemble those of species of *Allodelphis* by being relatively narrow, and having irregularly shaped posterior terminations (Figure 12A). The premaxillae extend posteriorly to the posterior ends of the nasal bones, but they terminate farther from the nuchal crest than in *A. pratti*, in this respect being more like the condition in *A. woodburnei*.

Unlike the condition in both species of *Allodelphis* the posterior ends of the premaxillae make broad contact with the lateral edges of the corresponding nasal bones; they are not separated from the nasals. This is a primitive character state, because it is shared with most primitive odontocetes.

In the proximal part of the rostrum, immediately anterior to the antorbital notch, the lateral edge of the maxilla protrudes laterally, forming a shelf that slopes ventrolaterally. This is similar to the lateral expansion of the maxilla in the species of *Allodelphis*, and it is the same part of the maxilla that is developed into a tubercle in the species of *Zarhinocetus*. The maxilla is exposed in the posterior part of the mesorostral canal anterior to the naris, and medial to the premaxilla. It forms a blocky triangular area of exposed bone.At the posterior end of the mesorostral canal, the mesethmoid has an anteriorly facing cavity where the un-ossified vomer cartilage was inserted in life. This part of the mesorostral canal is widely open, and thus is different from the more closed-over canal in this area in species of *Zarhinocetus*.

The dorsal nares are oval in shape, tapered and convergent posteriorly. The mesethmoid septum between them is thick, and rises dorsally posteriorly toward the contact with the nasal bones, as it does also in *Ninjadelphis ujiharai* Kimura, new genus and new species. An olfactory foramen perforates the posterior wall of each naris, forming a dorsoventrally expanded, crescent-shaped opening that measures approximately 17.5 mm dorsoventrally and 3 mm transversely.The anterior part of the right supraorbital process is complete, and is comprised of relatively thin maxilla overlying frontal, with the lacrimal exposed on, and forming, the posterior side of the antorbital notch. The lachrymal bone is oriented obliquely, anterolaterally to posteromedially, and is not fused to the jugal bone.

The zygomatic process of the jugal is present and complete on the holotype (Figure 12B), and this is a rarity in the fossil record. This rather delicate bone of odontocetes is usually destroyed before fossilization or during weathering processes. The body of the jugal is wedged between the lacrimal (to which it is not fused) and the frontal, expands laterally, and narrows medially. On the right side of the holotype the broken base of the zygomatic process of the jugal is still attached to the body of the jugal, showing that the zygomatic arch of the jugal departed from the posterior side of the antorbital notch. The main part of the zygomatic arch of the jugal, however, is broken and displaced, although it is complete. It is long and slender, and of uniformly very small diameter (1 mm) for most of its length. The zygomatic arch of the jugal has an expanded, flared posterior end that articulated with a flat pad on the anteroventral corner of the zygomatic process of the squamosal. The right zygomatic process of the jugal is complete and measures 76 mm long.

Compared to the antorbital process of species of *Zarhinocetus*, it is relatively small, and is not thickened dorsoventrally. The relatively thin supraorbital process is a primitive character state shared with species of *Allodelphis*. On both sides of the holotype the maxilla has been eroded away along the margin of the orbit.

The sutures defining the nasal bones are clearly discernible: on the mid-line between the right and left nasals, between the nasals and the mesethmoid anteriorly, and between the nasals and the frontals posteriorly. The mid-line suture between the right and left nasals is very fine, and bends toward the right side anteriorly. Each nasal bone expands both anteriorly and posteriorly, and is compressed at mid-length between the posterior ends of the right and left premaxillae. The combined nasal bones contact the mesethmoid in a fan-like arc that curves posteriorly at the lateral edges. In their mid-parts, the nasals are pinched between the posterior ends of the premaxillae, being only 2 to 3 mm wide, combined. They widen posteriorly where they abut the frontal bones. A very narrow posterior extension of each nasal extends posteriorly, and is inserted between the right and left frontals where they are exposed on the cranial vertex. The nasal bones are much smaller than they are in species of *Allodelphis*, although not as small as they are in species of *Zarhinocetus*.

On the posterior facial surface of each maxilla there are two posterior maxillary foramina. The larger of these is closer to the posterior end of the premaxilla, being approximately 8 to 9 mm from it. The more laterally positioned foramen is smaller, and is located closer to the postorbital process of the frontal. Maxilla extends onto the cranial vertex, expanding medially, curving posterior to the end of each premaxilla, and abuts the lateral side of the posterior end of the corresponding nasal bone.

Each frontal has a triangular area of exposure on the cranial vertex. A small area of frontal is exposed on the lateral side of each nasal, and a larger area of each frontal extends laterally between the supraoccipital and the maxilla, and thus contributes to the apex of the nuchal crest. The exposed areas of frontal are asymmetrical right to left, but there is no skew of the mid-line suture to the left side as there is in species of *Zarhinocetus*.

The zygomatic process of the squamosal is thick, strongly arched, and inclined anterodorsally, like that of *A. woodburnei*, and the glenoid fossa for articulation with the mandibular condyle faces anteriorly rather than anteromedially as it does in *Ninjadelphis ujiharai* Kimura, new genus and new species. The zygomatic arch differs from those of species of *Zarhinocetus* by not being rectangular in lateral view and by not extending so far anteriorly.

The sternomastoid fossa is compressed anteroposteriorly because the zygomatic process of the squamosal is displaced posteriorly toward the paroccipital process. Because of the anteroposterior compression in this area, the sternomastoid fossa is expanded dorsoventrally.

The occipital shield is smaller than that of species of *Zarhinocetus*, and its top is arched transversely (Figure 12D), rather than squared. The occipital condyles are relatively small for an allodelphinid, but they project very far posteriorly (Figure 12A), outward, from the occipital shield. Dorsal to each condyle is a supracondyloid fossa.

The basioccipital crests (Figure 12C) are relatively small, and not so far apart and widely divergent posteriorly as they are in species of *Zarhinocetus*.

On the palate, each pterygoid tapers anteriorly to a point, and a long, tapered extension of each palatine bone extends posteriorly between the right and left pterygoids. The pterygoid sinus fossa is large and elongate anteroposteriorly. Each sinus has a large opening that is expansive anteroposteriorly and faces laterally. The sinus fossa does not extend into the pterygoid hamulus, which is solid bone. The hamular process, as it is also in *Z. donnamatsonae*, new species, is relatively large, solid, and projects, finger-like, posteriorly (Figure 12C), ventral to the internal naris. This process is rarely preserved in fossils of odontocetes, including most specimens of Allodelphinidae.

As in other species of Allodelphinidae, the lateral lamina of the pterygoid extends posteriorly to contact the anterior falciform process of the squamosal, and a posteriorly-extending plate of the palatine is dorsal to the lateral lamina of the pterygoid within the medial part of the orbit. On the left side of the holotype the lateral lamina of the pterygoid is preserved, extending posteriorly toward its connection with the squamosal, not all of which can be seen because of the presence of the articulated mandible. The lateral and medial laminae of the pterygoid are only one mm apart lateral to the ventral naris.

Tympanic bulla. Both tympanic bullae of the holotype are complete and remain articulated in their correct anatomical positions (Figure 12C). Each bulla has an enlarged and pointed anterior spine, a diagnostic character of the superfamily Platanistoidea. The sigmoid process is large and has a curved lateral side. Similar to bullae of other species of allodelphinids, the posterior end of the bulla is bilobed. The large and globose outer posterior prominence is separated from the smaller and rugose inner posterior prominence by an interprominential notch. The inner posterior prominence extends farther posteriorly than the outer posterior prominence. The medial furrow extends from the interprominential notch anteriorly for essentially the length of the bulla. The involucrum is nearly straight, conforming to the lateral side of the basioccipital crest, and the outer lip is smooth and inflated. The posterior process is relatively small and extends in a posterolateral direction.

The right tympanic bulla is 47 mm in total length from the anterior spine to a line across the posterior tuberosities, and 28.9 mm transversely across the posterior tuberosities.

Mandible. The mandible of the holotype is complete. Probably 3 to 5 mm of bone is missing from the anterior tip of the mandible due to erosion. It curves dorsally in its anterior part, conforming to the similar dorsal curvature of the rostrum (Figure 12B). The anterior tip of the mandible reaches to the anterior tip of the rostrum. It is very slender and relatively delicate anteriorly, and is dorsoventrally very deep in the posterior part. This abrupt

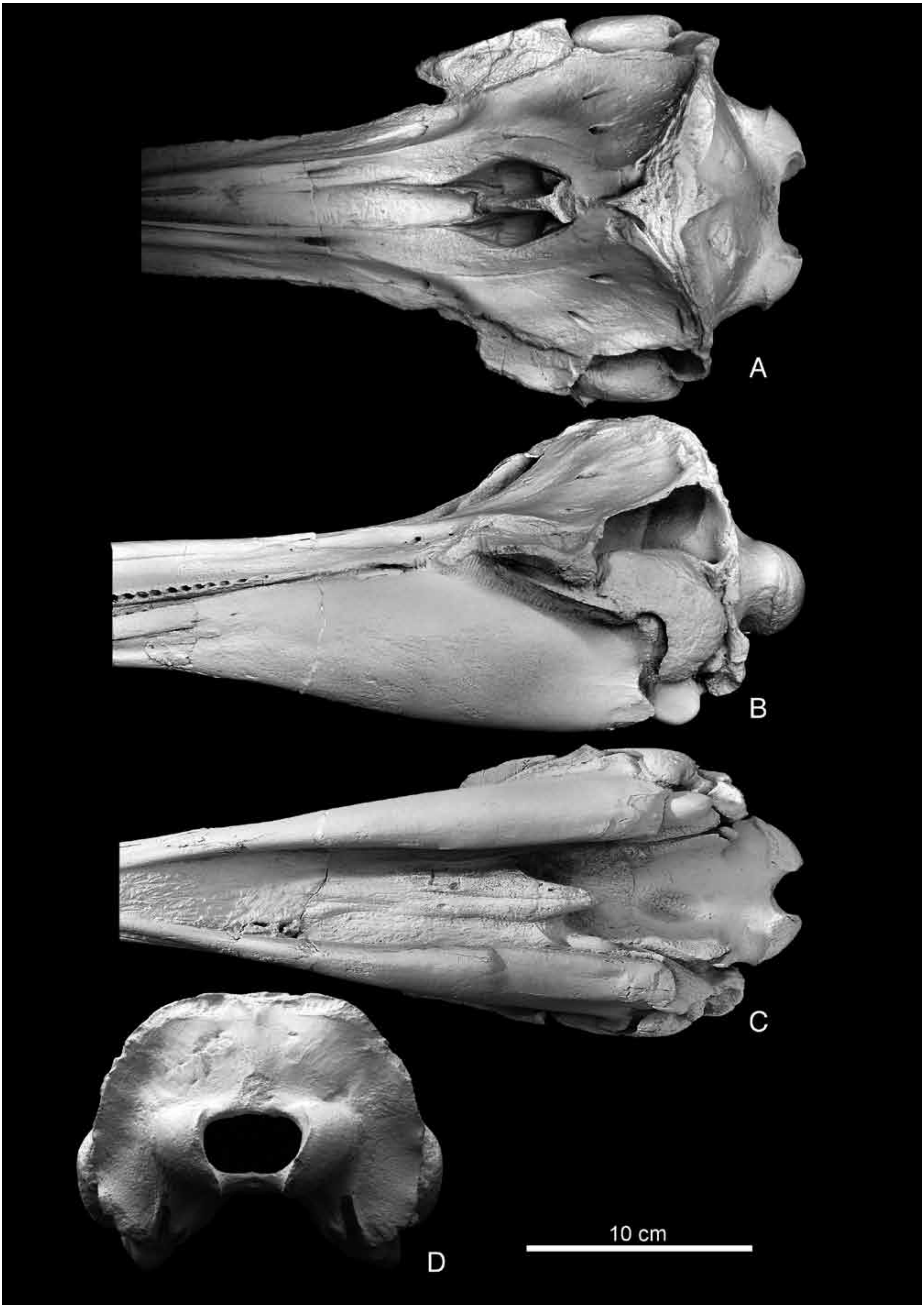

Figure 12. *Goedertius oregonensis* Barnes and Kimura, new genus and new species, holotype, enlargement of cranium, LACM 123887. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, posterior view. Scale bar equals 10 cm.

deepening of the dentary posteriorly exists also in the holotype of *A. woodburnei* and the referred specimen (LACM 149588) of *Zarhinocetus errabundus*. The ascending ramus has the acoustic window, the structure that allows transmission of sound to the ear during echolocation.

The right and left dentaries are firmly fused along the mandibular symphysis, which occupies slightly more than half of the length of the mandible. The fused symphyseal suture can be traced on the ventral surface of the mandible (Figure 11C) by a fine line extending the entire length of the symphysis. As in *A. woodburnei*, *N. ujiharai*, new genus and new species, and *Zarhinocetus errabundus*, the symphyseal portion of the mandible is slightly flattened dorsoventrally.

The ascending ramus is very deep dorsoventrally. The angle of the dentary is very large, and it extends in a lobate shape posteriorly ventral to the postglenoid process of the squamosal (Figure 12B). The mandibular condyle is large and expanded transversely.

On the lateral side of the dentary is an elongate sulcus, extending the entire length of the symphyseal part of the mandible. This sulcus is on the ventral surface of the dentary anteriorly, and progressing posteriorly it ascends to mid-height on the lateral side of the dentary, where it widens and diminishes onto the side of the ascending ramus. This sulcus is relatively deep, which is most likely the derived character state, compared to the shallow sulcus of *A. woodburnei*.

Dentition. The dental formula of *G. oregonensis* is 57 to 59/53 to 54, and the dentition is polydont and has vestiges of heterodonty.

Loose in the sediment surrounding the holotype of *G. oregonensis*, 32 loose teeth were found scattered among the bones. These teeth have tall and slender crowns that curve medially (lingually), and the enamel on the crowns is smooth, lacking any wrinkles or accessory cusps. Most of these teeth are approximately 18 mm long, and have crowns that are approximately 7 mm tall and 2 mm in diameter at the enamel base. Each tooth has a single elongate and slender root, approximately 11 mm long, that curves posteriorly at its end. These are similar to the teeth with the holotypes of *A. woodburnei* and *Ninjadelphis ujiharai* Kimura, new genus and new species. No teeth have yet been identified for *A. pratti*, *Z. donnamatsonae*, new species, or *Z. errabundus*.

The loose teeth with the holotype of *G. oregonensis*, being 2 mm in diameter at the bases of their crowns, appear to be too small to properly fit into the alveoli that are 8 to 9 mm in diameter at their rims. However, one tooth is in situ in the specimen, in the sixteenth upper (maxillary) alveolus from the anterior end, and it clearly demonstrates that these small teeth do fit in these larger alveoli. Possibly periodontal ligaments, or longitudinal bands of such material along the tooth row helped to hold the teeth in place.

All of the preserved upper dental alveoli in the holotype are in the maxillary bones. No alveoli are known to be in the premaxillae, whose anterior tips, as noted above, are both eroded off. The upper right tooth row contains 57 preserved maxillary alveoli, and probably there were originally one or two more alveoli present in the missing rostral extremity. The upper left tooth row has 56 preserved alveoli, and probably one or two more alveoli were present in the missing rostral extremity. Thus, the upper tooth count was approximately 57 to 59.

The anterior alveoli in the upper tooth row are large, measure approximately 8 to 9 mm in anteroposterior diameter, their alveolar rims are oval-shaped anteroposteriorly, and they open facing anteroventrally. The alveoli in the middle of the tooth row are similarly oval-shaped anteroposterioly, measure approximately 8 to 9 mm in anteroposterior diameter at the alveolar rims, and they open facing ventrally. The posterior-most upper teeth were much smaller, their alveoli being approximately 4 mm in diameter anteroposteriorly at their alveolar rims, round, and project facing laterally.

The upper tooth rows extend father posteriorly than the lower tooth rows in the articulated mandible. Thus, six upper right posterior teeth and five upper left posterior teeth were unopposed by lower teeth.

Each dentary of the mandible has 53 alveoli, and probably one alveolus was present in the missing anterior end of each. The alveoli in the anterior part of the dentary are elliptical, elongate anteroposteriorly at their rims, measure approximately 8 to 9 mm in anteroposterior diameter at the alveolar rims, and open facing anterodorsally. Those in the middle part of the dentary measure approximately 8 to 9 mm in anteroposterior diameter at their alveolar rims, and face dorsolaterally. The posterior alveoli are small, measure 3 to 4 mm at their alveolar rims, and open facing dorsally.

The spacing and sizes of the alveoli in *G. oregonensis* are similar to those of the holotype mandibles of *Allodelphis woodburnei* and *Ninjadelphis ujiharai* Kimura, new genus and new species, but differs from the situation in *Z. errabundus*, in which the alveoli are closer together in the anterior and posterior parts of the tooth rows, but larger and farther apart in the middle parts of the tooth rows.

Vertebrae. Nine vertebrae are present with the holotype. None of them were found articulated, and they were scattered in the sediment around the skull. They probably became lodged against the skull by current action, and the missing vertebrae were apparently displaced farther from the main bone concentration. No analog exists for allodelphinid cervical vertebrae among modern cetaceans, but the Amazon River dolphin, *Inia geoffrensis* (Blainville, 1817), has cervical vertebrae that are similarly not fused to one another, that are relatively large, and have large processes. Using a Recent specimen of *I. geoffrensis* (LACM Mammalogy Department No. 19591) the vertebrae of the holotype of *G. oregonensis* can be identified as cervicals one (atlas), two (axis), three, four, and six, thoracic one, and possible thoracics three, five, and six. The atlas and axis are unequivocal. The other cervicals are identified based on the sizes and shapes of their transverse processes. The thoracics were identified based on the pattern of progressively narrower centra and neural canals and taller neural processes proceeding posteriorly within the anterior part of the thorax.

Atlas vertebra. The atlas vertebra (Figure 13), as in other species of allodelphinids is proportionally very large, much expanded in the anteroposterior dimension, and has relatively large dorsal and ventral transverse processes. The atlas vertebra measures approximately 96 mm across the incomplete but restored anterior articular facets, 111 mm across the incomplete but restored dorsal transverse processes, 122 mm across the incomplete but restored ventral articular processes, and is 72 mm tall from the ventral surface to the apex of the dorsal spine. The other cervical vertebrae are also large, elongated anteroposteriorly, and have large prezygapophyses and postzygapophysis. The neck of this species is secondarily elongated, as it is in all other known species of the Allodelphinidae. The thoracic vertebrae are large, have elongated centra, and large fovea for articulation with the head of the ribs.

Axis vertebra. The axis is relatively large, elongated anteroposteriorly, and has a large and stout odontoid process, widely spaced anterior articular facets, a large neural canal that is peaked at its center, thin pedicles, small but well-formed postzygapophyses, and a large hatchet-shaped, anteroposteriorly expanded neural spine.

Its centrum has an anteroposterior length of 61 mm as preserved, but this length originally would have been approximately 66.5 mm, when adding approximately 4 mm for the missing anterior tip of the odontoid process, and 1.5 mm for the thickness of the missing epiphysis. The dorsoventral height of the axis is approximately 87 mm, and when complete this dimension would have been approximately 91 mm when adding approximately 4 mm for the missing posterior tip of the neural process, and for some bone that has eroded from the ventral surface of the centrum.

Third cervical vertebra. This vertebra resembles the third

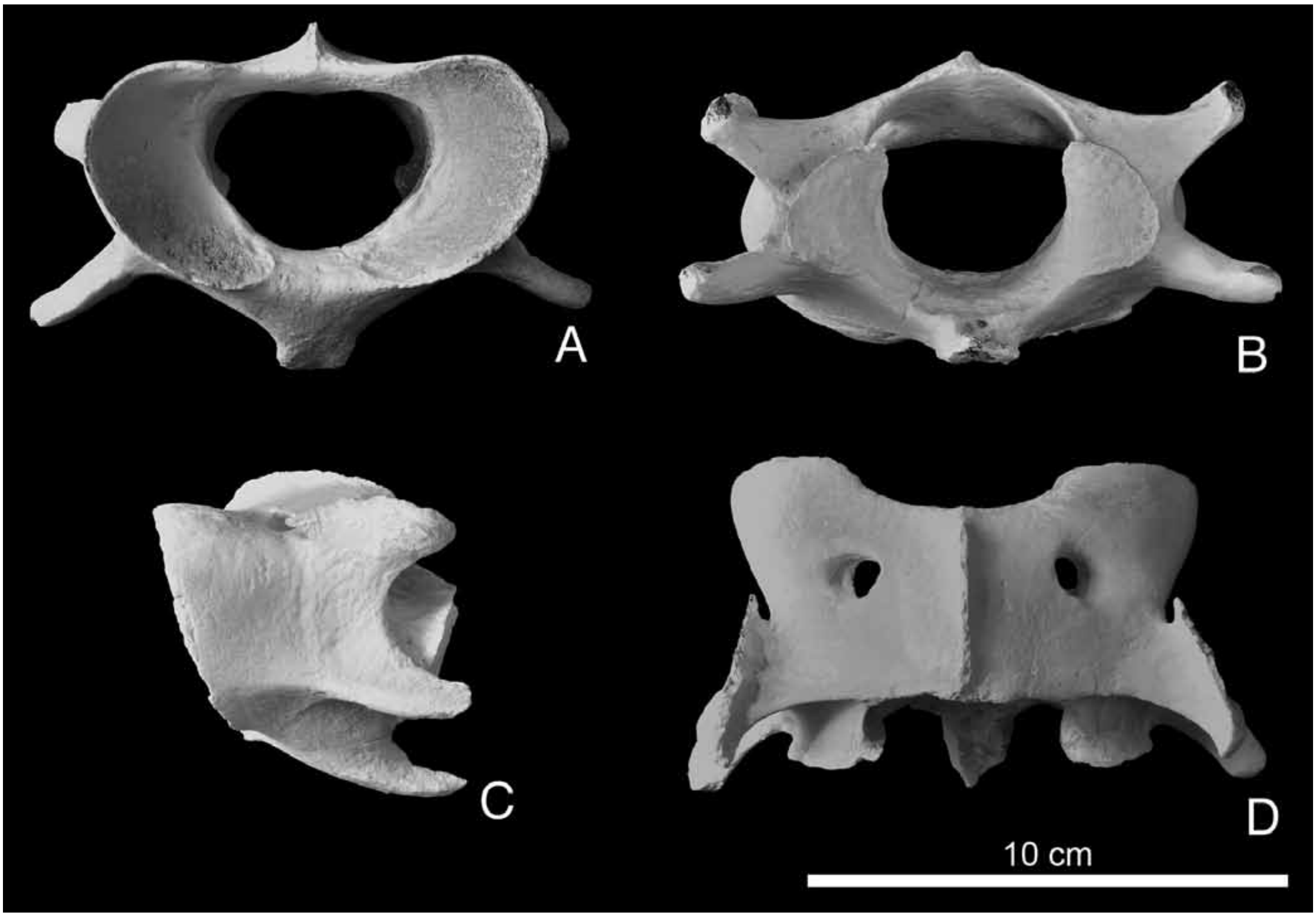

Figure 13. *Goedertius oregonensis* Barnes and Kimura, new genus and new species, holotype atlas, LACM 123887. **A**, anterior view; **B**, posterior view; **C**, left lateral view; **D**, dorsal view. Scale bar equals 10 cm.

cervical vertebrae of *Ninjadelphis ujiharai* Kimura, new genus and new species, and of the Recent *Inia geoffrensis* (Amazon River dolphin) by having a large, blade-like ventral projection on the transverse process, and by lacking a laterally projecting process originating from the transverse process.

The anterior epiphysis of this vertebra is attached, but the posterior one has become separated and is missing. Both of the epiphyses were un-fused to the centrum at the time of death. The vertebra has an elongate, barrel shaped centrum with a sharp, mid-line keel on its ventral surface, relatively delicate transverse processes, a large and vertically expanded transverse foramen, and a large and transversely wide neural canal. Its transverse process has a large keel-like ventral branch, which has on its anterior side two smaller processes. One of these is positioned dorsally, and is near the centrum. The other process is anteriorly directed, and located at the anteroventral corner of the transverse process. Near the posterior corner of the transverse process is a posteriorly directed process, and ventral to this is a smaller process. There is no lateral process projecting outward from the transverse process.

The prezygapophyses are both broken and missing. The postzygapophyses are relatively short, similar to those on the following fourth cervical vertebra, and have relatively small, ventrally facing articular facets. The neural process is broken off, but it appears to have been originally very short, probably extending only approximately 12 mm dorsally, measured from inside the neural canal. The remaining base of the neural process is 22.7 mm long, measured anteroposteriorly, rectangular in lateral view, and apparently originally was erect, not sloping posteriorly.

The centrum measures 39.5 mm long as preserved, and originally would have been approximately 41 mm long when adding approximately 1.5 mm for the thickness of the missing posterior epiphysis. The dorsoventral height of this vertebra originally (as now accurately restored) would have been approximately 76.2 mm. The original overall transverse width, measured across the tips of the transverse processes (estimated by doubling half of the width because part of the left transverse process is broken), would have been approximately 94.4 mm.

Fourth cervical vertebra. This is demonstrably the fourth cervical vertebra because it articulates correctly with the third, described above. It is very similar to the fourth cervical of *Ninjadelphis ujiharai* Kimura, new genus and new species, and resembles the same vertebra of *Inia geoffrensis* in the shapes of its transverse processes and neural spine. It has an elongate, barrel-shaped centrum, lacking both epiphyses, which had not fused at the time of death. The centrum has on its ventral mid-line a sharp keel. The neural canal is large and widened transversely. The transverse processes are relatively delicate, and each has a large transverse foramen. Each transverse process has a ventral branch, and a prominent posterolaterally directed lateral process.

The prezygapophyses are elongate, and each has a relatively small, oval-shaped articular facet. The postzygapophyses are smaller and shorter than the prezygapophyses. The completely preserved neural process is 28.2 mm tall, measured from inside the neural canal, 27 mm long at it base, measured anteroposteriorly, triangular in shape, and erect, not sloping posteriorly.

The centrum is 36.3 mm long, and originally would have been approximately 39.3 mm long when adding approximately 1.5 mm for the estimated thickness of each of the two missing vertebral epiphyses. The total height of the vertebra, as completely preserved, is 90.7 mm. The overall width across the transverse processes is estimated to have originally been approximately 103 mm, this measurement being twice the half width, because part of the left transverse process is broken off.

Sixth cervical vertebra. This is identified as the sixth cervical vertebra because it does not articulate correctly with the fourth cervical, described above, is very similar to the sixth cervical of *Ninjadelphis ujiharai* Kimura, new genus and new species, and resembles that one, as well as the sixth cervical of *Inia geoffrensis*, by having a large and elongate ventral branch of the transverse process and a lateral process. A loose tooth of this individual remains adhering to the anterior epiphyseal surface. This vertebra has an elongate, barrel-shaped centrum, and lacks both epiphyses, which became separated because they had not fused at the time of death. The centrum has on its ventral mid-line a sharp keel, which is not as prominent as the same keel on either the third or fourth cervicals. The neural canal is large, transversely wider than that of the fourth cervical, and peaked dorsally, forming a triangular shape. The transverse processes are large, relatively delicate, and each one has a large, nearly circular, transverse foramen that measures 18.0 mm dorsoventrally and 19.1 mm transversely. Each transverse process has a large, laterally projecting process, and a very large, ventrally projecting, keel-like ventral branch, which expands distally, and has on its anterior side a process near its ventral corner. On both sides of the vertebra the posteroventral part of this ventral branch of the transverse process is broken off.

The prezygapophyses are elongated and slender, each with an elongated, oval shaped articular facet. As on the fourth cervical, the postzygapophyses are smaller and shorter. The completely preserved neural process is tall and erect, not sloping posteriorly, and has a lobate dorsal tip. It is 41.7 mm tall, measured from inside neural canal, and is 24.5 mm long at its base, measured anteroposteriorly.

The centrum measures 39.2 mm long, as preserved, and originally would have been approximately 42.2 mm long when adding approximately 1.5 mm each for the estimated thicknesses of the two missing epiphyses. The total height of this complete vertebra is 106.5 mm, and the width across its complete transverse processes is 124.3 mm.

First thoracic vertebra. This vertebra is undoubtedly the first thoracic because the centrum, like the entire vertebra, is transversely broad and dorsoventrally compressed, in this regard resembling the first thoracic vertebra of *Inia geoffrensis*. There is no transverse foramen, indicating that it is not a cervical. The neural canal is broad and triangular in shape. The transverse process has a single lateral projection that bears a facet for articulation with the large, flat-tipped tuberculum of the first rib, and a secondary small ventrolaterally projecting process on the side of the centrum for articulation with the tiny head of that rib. Both the anterior and posterior epiphysis were loose and are missing. The elongate, barrel-shaped centrum is widened transversely, and it does not have a prominent ventral mid-line keel such as that on the cervicals, only a smoothly rounded surface. This vertebra has large transverse processes, and large, widely spaced prezygapophyses with large, oval-shaped articular facets. The postzygapophysis are less widely spaced than the prezygapophyses, shorter, and have ventrolaterally facing articular facets. The neural process is broken off, and is 22.2 mm long anteroposteriorly at its base.

The centrum measures 39.1 mm long anteroposteriorly, and it originally would have been approximately 42.1 mm long when adding approximately 1.5 mm thickness for each of the two missing epiphyses. The total preserved height of the vertebra, to the broken part of the neural process, is 80.1 mm, and the width across the complete transverse processes is 116.6 mm.

Possible third thoracic vertebra. This is not a second thoracic vertebra because it is too narrow to articulate correctly with the first thoracic vertebra described above. It is not the fourth thoracic because it is too wide to articulate correctly with the possible fifth thoracic described below. This is most likely a third thoracic vertebra because the centrum is dorsoventrally taller and narrower than the first thoracic. It generally resembles the third thoracic of *Inia geoffrensis*, by being transversely narrower and taller than the first thoracic, but it is relatively longer anteroposteriorly, and has proportionally larger processes and articular facets. The impression of a carbonized dicot leaf has been purposely left in some sediment that still adheres to the posterior side of the left pedicle.

The anterior and posterior vertebral epiphyses were un-fused to the centrum in life, became loose during fossilization, and are missing. The centrum is anteroposteriorly elongated, somewhat dorsoventrally flattened, and slightly widened transversely. Along the ventral mid-line of the centrum there is no sharp keel, only a gently rounded surface. The neural canal is peaked dorsally, thus triangular shaped.

The large transverse process has no transverse foramen. It has a single lateral projection, which has on it a large facet for articulation with the tuberculum of the corresponding rib. There is a small laterally projecting process on the side of the centrum, anteriorly, with a facet on it for articulation with the head of the same rib. A small ridge is on the lateral side of the centrum, posterior to the facet for attachment of the head of the rib.

The prezygapophyses originate from the anterior sides of the pedicles, are widely spaced, and each has a large, oval-shaped, and dorsomedially facing articular facet. The postzygapophyses are less widely spaced, and their articular facets are smaller and face ventrally. The neural process is broken off at what appears to be its mid-height. The base of this process shows that it was clearly large, wide anteroposteriorly, and sloped posteriorly. This process is 43.3 mm long, anteroposteriorly, at its base, and 46.8 mm tall, measured from inside the neural canal to where it is broken off.

The centrum is 42.8 mm long, and originally would have been approximately 45.8 mm long when adding approximately 1.5 mm for the thickness of each of the two missing epiphyses. The total height of the vertebra, to where the neural process is broken off, is 111.6 mm. The estimated original transverse width of the vertebra across the transverse processes is 101.8 mm. The right transverse process is broken off, and this estimated width is twice the preserved half width.

Possible fifth thoracic vertebra. This is an essentially complete thoracic vertebra. Its anterior and posterior epiphyses were both un-fused to the centrum, became separated, and are now missing. A loose tooth of the holotype individual adheres by matrix to the posterior epiphyseal surface, and seven loose teeth are preserved in the sediment that was purposely left around the right transverse process.

This is not a fourth thoracic vertebra because it does not articulate correctly with the possible third thoracic vertebra that is described above. In its general shape it resembles the fifth thoracic vertebra of Recent *Inia geoffrensis*, by being narrow and relatively tall, but it is more robust and has relatively larger processes. Its centrum is dorsoventrally higher and transversely narrower than that of the possible third thoracic. Its neural canal is tall and oval shaped. The transverse process has a single lateral projection, which has a facet for articulation with the large tuberculum of the corresponding rib. A small, laterally projecting process at the anterior end of the centrum is for articulation with the head of the same rib.

The elongate, barrel-shaped centrum is only slightly widened transversely. The vertebra has large transverse processes without transverse foramina. The widely spaced prezygapophyses are large, located on the anterior sides of the pedicles, and have oval-shaped articular facets. The postzygapophyses are less widely spaced, smaller, and have ventrally facing articular facets. The ventral mid-line of the centrum has no keel, only a rounded surface. The neural process is broken off at what appears to have been its mid-height. When complete, this process clearly was large, wide anteroposteriorly, and sloped posteriorly. The base of the neural process is 50.5 mm long, measured anteroposteriorly, and is approximately 32 mm tall where it is broken off.

The centrum measures 45.1 mm long, anteroposteriorly, and when complete would have been approximately 48.1 mm long, when adding approximatley 1.5 mm of length for each for the

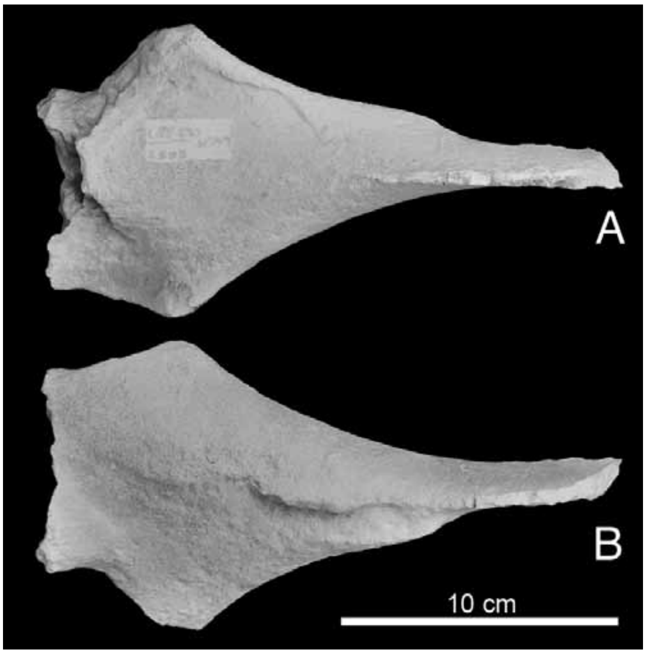

Figure 14. *Goedertius oregonensis* Barnes and Kimura, new genus and new species, holotype manubrium, LACM 123887. **A**, ventral view; **B**, dorsal view. Scale bar equals 10 cm.

two missing epiphyses. The total height of the vertebra to its broken neural process is 96.7 mm. Its width, across the complete transverse processes, is 85.4 mm.

Possible sixth thoracic vertebra. A partial vertebral centrum with the holotype is part of a broken thoracic vertebra. It is possibly the sixth thoracic because it has a transversely narrow centrum, measuring 53.2 mm wide transversely.

The centrum measures 46.2 mm anteroposteriorly, and originally was approximately 49.2 mm long, when adding approximately 1.5 mm for each of its missing, un-fused epiphyses. This centrum is nearly U-shaped in cross section, and it lacks an anteroposteriorly-aligned keel on its ventral midline.

Ribs. The first ribs on both the right and left sides are preserved with the holotype. Similar to the first ribs of Recent *Platanista gangetica*, the strange first ribs of *G. oregonensis* are relatively short, wide medio-laterally, flattened anteroposteriorly, and have a very small (reduced) capitulum, but a very large tuberculum.

The right first rib has a total curvilinear length along its lateral surface of 79 mm. Its very small capitulum projects only 7.2 mm beyond the body of the tuberculum. The left first rib has a completely preserved tuberculum that is large, and has a large, oval shaped, articular facet for the vertebra that measures 25.1 mm by 14.3 mm. This rib at its mid-length measures in cross section 23.3 mm by 8.3 mm, and at its distal end measures 31.1 mm by 14.8 mm.

Manubrium. The posterior end of the manubrium is present with the holotype. Like that of *Allodelphis pratti* and *Ninjadelphis ujiharai* Kimura, new genus and new species, it is relatively large and elongated anteroposteriorly. Its narrow posterior end is twisted, making it asymmetrical (Figure 14).

Humerus. The right humerus (Figure 15) is present with the holotype, and is complete. Its un-fused and loose distal epiphysis remains held on to the diaphysis only by sediment. At the time of death, the proximal epiphysis had only partly fused to the diaphysis, owing to the relatively young ontogenetic age of the individual. Similar to the humeri of *A. pratti*, *A. woodburnei*, *Ninjadelphis ujiharai* Kimura, new genus and new species, and *Zarhinocetus errabundus*, the humeral head is spherical and relatively small, the diaphysis is elongate proximo-distally and nearly circular in cross section, and the distal articular facets are relatively small. The greater tuberosity does not extend farther proximally than the proximal surface of the head. The lesser tuberosity is located on the anterior side of the greater tuberosity, from which it is separated by a deep notch. The deltopectoral crest is rugose, but the diaphysis is otherwise smooth.

Figure 15. *Goedertius oregonensis* Barnes and Kimura, new genus and new species, holotype right humerus, LACM 123887. **A**, anterior view; **B**, lateral view; **C**, posterior view; **D**, medial view. Scale bar equals 10 cm.

The proximal part of the facet for articulation with the olecranon process of the ulna is relatively large. It has rugosities around its margins indicating that it had begun to fuse with the olecranon process of the ulna. Fusion of the humerus and ulna occurs in the other allodelphinids (except *A. woodburnei*) for which these bones are known.

The oval-shaped head of the humerus measures 42.2 mm transversely and 44.6 mm anteroposteriorly. The total length of the humerus is 138.4 mm. The diaphysis at its mid-length measures 44.4 mm anteroposteriorly and 23.4 mm mediolaterally. The humerus of *G. oregonensis* is relatively small, compared to the size of the cranium (and by inference the size of the body), and this contrasts with the proportionally larger humeri of *Allodelphis pratti*, *A. woodburnei*, and *Z. errabundus*.

***Ninjadelphis*, new genus**

Platanistoidea. Kimura and Ozawa, 2001:92.
Allodelphinidae··· Japan. Barnes and Reynolds, 2009:484.
“···an unnamed taxon of the family Allodelphinidae". Barnes, Kimura and Godfrey, 2010:450.
“···new taxon is represented by a partial skeleton ···". Kimura, Barnes and Rivin, 2011:44.
Allodelphinidae. Kimura, 2015:22.

Diagnosis of genus. A genus of Allodelphinidae differing from *Allodelphis*, *Goedertius* and *Zarhinocetus* by having cranium with trapezoidal shaped exposure of frontals on cranial vertex, postglenoid process of squamosal enlarged at posterolateral corner of glenoid fossa, glenoid fossa for articulation with mandibular condyle facing anteromedially rather than anteroventrally, nuchal crest partly overhanging posterior end of maxilla, basioccipital wider, basioccipital crests widely diverging posteriorly, paroccipital process enlarged; differing further from *Allodelphis* and *Zarhinocetus* by having petrosal with smaller cochlear portion, longer anterior process, longer and transversely compressed posterior process, articular facet for tympanic bulla on posterior process divided into two articular surfaces, forming ventral and posteromedial surfaces; differing further from *Allodelphis* by having cranium with cranial vertex asymmetrical and skewed slightly to left side, medial margins of premaxillae closer together over mesorostral canal anterior to dorsal nares, premaxillary foramen recessed in sulcus on dorsal surface of premaxilla, medial part of dorsal surface of posterior part of rostrum depressed, posterior ends of premaxillae retracted anteriorly to location opposite centers of dorsal nares, area where posterior end of premaxilla formerly existed, forming premaxillary sac fossa, formed of smooth, convex, and dense maxillary bone, and right and left nasal bones fused together at midline and fused to the underlying and adjacent mesethmoid and frontal bones; petrosal with articular facet for tympanic bulla smoother, lacking furrows; tympanic bulla with more inflated outer lip, longer posterior process, and larger and more laterally directed sigmoid process; and atlas vertebra with dorsal transverse process more expanded dorsoventrally, and ventral transverse process longer; differing further from *Goedertius* by having posterior end of premaxilla anteriorly retracted rather than extending posteriorly to posterior ends of nasal bones, deeper depression anterior to nares, larger dorsal exposure of frontals at cranial vertex, larger temporal fossa, longer zygomatic process of squamosal, mesethmoid septum between posterior parts of nares extending farther dorsally, posterior maxillary foramen positioned more posteriorly, occipital condyles less protruding posteriorly; and differing further from *Zarhinocetus* by having cranium with posterior end of premaxilla extending to position opposite centers of dorsal nares rather than terminating farther anterior at point anterolateral to dorsal nares, facial region narrower and not projecting as far laterally over temporal fossa, temporal fossa more anteroposteriorly elongated, occipital shield not so high dorsoventrally, occipital condyles smaller, and by lacking swollen tubercle of bone on lateral part of rostral maxilla anterior to antorbital notch; petrosal less robust, with longer and more slender anterior process, longer and more tapered posterior process; tympanic bulla with less inflated outer lip; and atlas vertebra relatively smaller and less robust, with dorsal transverse process smaller and less expanded dorsoventrally, and ventral transverse process more slender but longer.

Type and only included species. *Ninjadelphis ujiharai*, new species.

Etymology. The generic name is derived from Ninja, which is the name given to Japanese warrior, combined with *delphis*, which is the Greek word for dolphin. Iga, the city in Japan where the holotype of the type species was found, is famous historically for Ninja warriors who resided there.

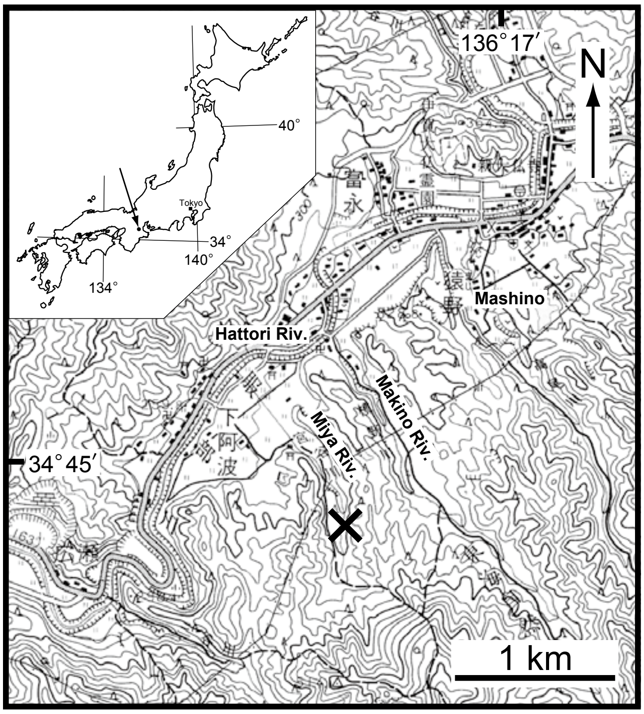

Figure 16. Map showing the type locality of *Ninjadelphis ujiharai* Kimura, new genus and new species. The base map is from the "Tsu-seibu" 1:50,000 topographic map published by the Geospatial Information Authority of Japan.

Geographic and geochronologic ranges. Late early Miocene; western North Pacific Ocean around present day Japan.

***Ninjadelphis ujiharai*, new species**

Figures 17-29, 37C, 38B, 39C, 40A, B, Tables 1, 2

Platanistoidea. Kimura and Ozawa, 2001:92.
Allodelphinidae··· Japan. Barnes and Reynolds, 2009:484.
“···an unnamed taxon of the family Allodelphinidae". Barnes, Kimura, and Godfrey, 2010:450.
“···new taxon is represented by a partial skeleton ···". Kimura, Barnes and Rivin, 2011:44.
Allodelphinidae. Kimura, 2015:22

Diagnosis of species. Because the genus *Ninjadelphis* is presently monotypic, the diagnosis of the type species shall remain identical to that of the genus until additional species are described in the genus.

Holotype. GMNH-PV-2570, partial skeleton of a single individual, including the cranium, both petrosals, tympanic bulla, partial mandible, isolated teeth, manubrium, scapula, humerus, radius, ulna, carpal bones, metacarpal bone, phalanx, vertebrae (four cervical, two thoracic, and one caudal), and ribs; discovered by Atsushi Ujihara in June 1998.

Type locality. The holotype was found in sediments that were exposed by erosion in the bed of the Miya River (Figure 16), at Iga City (formerly Ohyamada-mura, and subsequently merged with Iga City in 2004), Mie Prefecture, Japan; latitude 34º44'57" N, longitude 136º16'11"E.

Formation and age. The holotype was collected from the Hiramatsu Formation of the Awa Group, and is late early Miocene in age, correlated to Zone N7 of Blow (1969) and NPB2B of Yanagisawa and Akira (1998), and is approximately 17 million years old (Yoshida, 1987, 1991; Fujiwara et al., 2005).

Etymology. The species name, *ujiharai*, is a patronym honoring

Figure 17. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype cranium with isolated rostral fragment, GMNH-PV-2570, dorsal view, from the early Miocene Awa Group at Iga, Mie Prefecture, Japan. Scale bar equals 10 cm.

Dr. Atsushi Ujihara of Nagoya University, Japan, who found the holotype specimen. The species name is masculine in gender.

Geographic and geochronologic ranges. Late early Miocene; western North Pacific Ocean around present day Japan.

Description. The holotype is from an adult specimen because the epiphyses of all of the preserved vertebrae, whether cervical, thoracic, or caudal, are fused to their centra, both the proximal and distal epiphyses are fused to the diaphysis of the humerus, the proximal epiphyses are fused to the diaphyses of the radius and ulna, and some of the carpal bones are fused to one another. The individual was not an old adult because the distal epiphyses of the radius and ulna are not fused to their respective diaphyses (Ogden et al., 1981; Galatius et al., 2006; Moran et al., 2015). The sex of the individual cannot be determined with currently available information.

Ninjadelphis ujiharai shares with other species of the family Allodelphinidae a long and slender rostrum and symphyseal part of the mandible, posteriorly expanded lateral laminae of the pterygoids medial to the orbits, internal acoustic meatus of the petrosal opening anteromedially, superior process of the petrosal wide, smooth, and almost flattened, posterior process of the petrosal atrophied, enlarged cervical vertebrae with anteroposteriorly elongated centra, and distal end of the humerus fused to the olecranon process of the ulna.

Cranium. The cranium is well preserved, but it lacks part of the base of the rostrum and fragments of the maxillae and premaxillae (Figures 17-20). The facial region of the cranium is nearly rectangular-shaped in dorsal view, and the rostrum was very long and slender. The maxilla and frontal fully roof over the temporal fossa dorsally. The cranial vertex is skewed slightly asymmetrically to the left side of the cranial midline.

The rostrum is attenuated anteriorly, and the preserved parts of the maxillae and premaxillae are narrow, confirming that the specimen originally had a slender and very long rostrum (Figure 17).

Each antorbital notch is deep and opens facing anteriorly. The right antorbital notch is U-shaped in dorsal view, and it is slightly wider than the left one, which is more V-shaped in dorsal view. A small tubercle and a well-defined ridge are formed on the lateral part of the rostral maxilla anterior to the left antorbital notch. This tubercle and ridge are unclear on the right maxilla. At the base of the rostrum, the dorsal surface of the cranium is notably concave, and in lateral view the rostral margin of the maxilla is deep dorsoventrally. The proximal part of the rostrum is relatively very deep dorsoventrally. The mesorostral canal is open dorsally in the mid-part of the rostrum, but is narrower both anteriorly and posteriorly. This is in contrast with other species of Allodelphinidae, in which the posterior part of the mesorostral canal is more widely open dorsally. At least 20 dental alveoli are preserved on the fragment of the right maxilla, but the total dental formula cannot be determined for the species based on the holotype.

The premaxilla is widest at a point immediately anterior to the narial openings (Figure 18A), at the site of the premaxillary sac fossa, which is expanded transversely. A single premaxillary foramen is present in each premaxilla. Anterior to the premaxillary foramen the premaxillary bone is thick, its dorsal surface is convex, and it becomes narrower in width progressing more anteriorly. The anteromedial and posterolateral sulci, extending from the premaxillary foramen, are shallow but distinct. The posteromedial sulcus, which is usually present in odontocetes, is not present on the specimen. The posterior end of the premaxilla is thin dorsoventrally, irregular, and can best be described as being atrophied. The posterior termination of each premaxilla is retracted anteriorly, being located lateral to the center of the narial openings. Posterior to the end of each premaxilla the area where the premaxillary bone formerly existed is now formed of smooth and convex maxillary bone (Figures 18A, 19A) that imitates the texture and shape of the premaxillary bone that was previously in this area. This condition is similar to that in the species of *Zarhinocetus*, in which the posterior end of the premaxilla is retracted further anteriorly, and the raised border of the maxilla is instead present adjacent to the narial opening.

In contrast, the posterior ends of the premaxillae in species of *Allodelphis* and *Goedertius* are not atrophied, and they extend posteriorly onto the facial surface beyond the ends of the nasals, and this is the primitive character state for Odontoceti.

Although the premaxillae of *N. ujiharai* ceased to underlie the entire premaxillary sac fossae, and now maxillary bone underlies much of the area where each sac was positioned in life, we continue to identify this flat area on the facial surface of the cranium as the premaxillary sac fossa.

The maxilla covers most of the supraorbital process of the frontal, except for that portion that borders the lateral margin of the orbit. In lateral view, the orbital margin of the supraorbital process is slightly arched dorsally. The antorbital and postorbital processes are both relatively small.

Posteriorly, the maxilla rises abruptly where it contacts the supraoccipital, thus forming a thickened and prominent nuchal crest. Part of the posterior end of each maxilla is slightly overhung by this well-developed nuchal crest. The posteromedial corner of each maxilla contacts the adjacent frontal bones. Three dorsal infraorbital foramina are present in each maxilla. The largest one, which is the posterior dorsal infraorbital foramen, is located posterolateral to the external nares, and is not close to the posterior end of the premaxilla. In species of the family Platanistidae a derived character state exists in which the posterior dorsal infraorbital foramen is located very close to the posterior end of the premaxilla, and in some species and individuals this foramen is essentially covered by the lateral edge of that bone. In *N. ujiharai* the two anterior dorsal infraorbital foramina on each side are located medial to the respective antorbital notches.

On the cranial vertex the frontal is exposed in an area that is trapezoidal in shape. The dorsal surface of the frontal in this exposure is very rugose. The anterior edges of the frontals are fused to the nasals and there are no visible sutures between these bones.

The nasal bones are small, and abut both the mesethmoid bone anteriorly and the frontal bones posteriorly. The right and

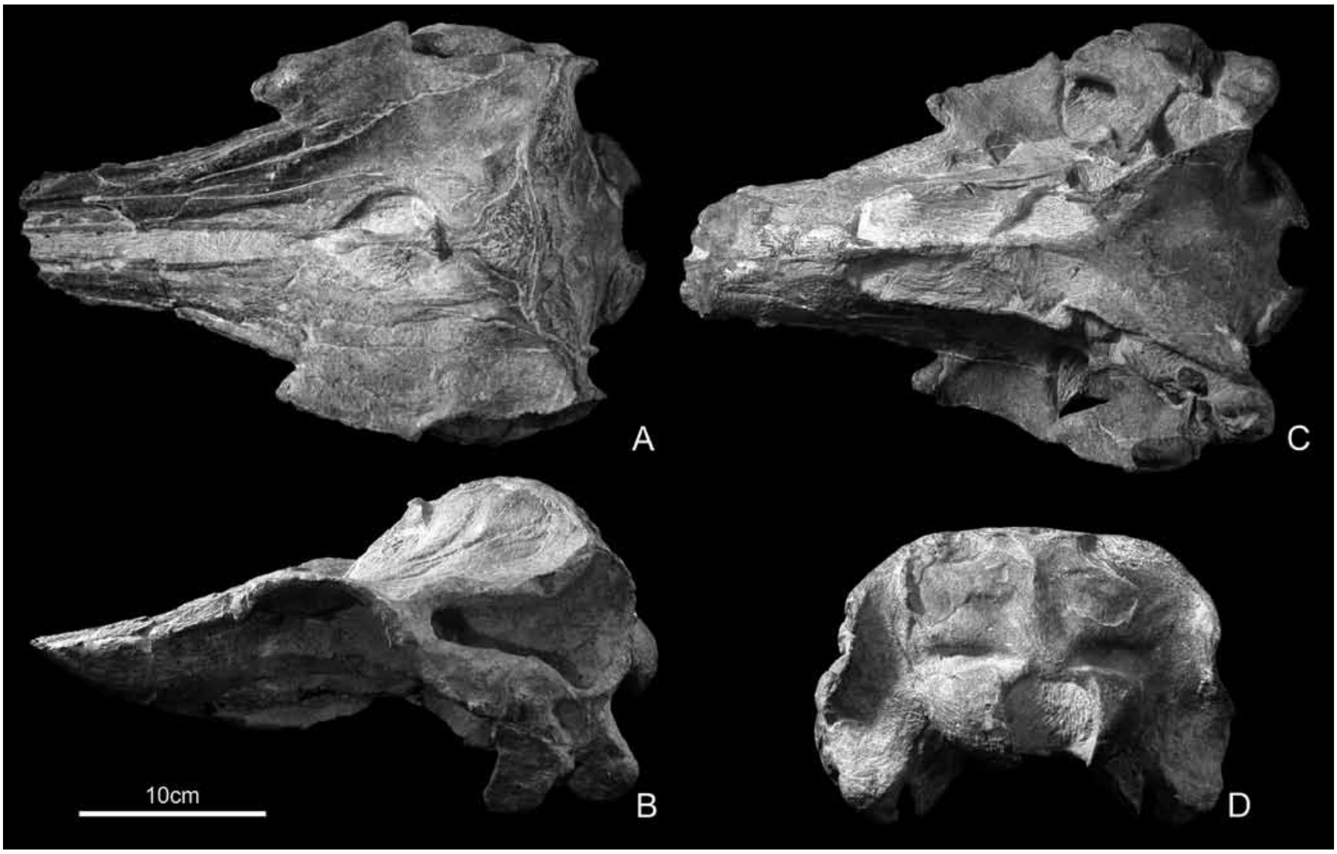

Figure 18. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype cranium, GMNH-PV-2570. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, posterior view. Scale bar equals 10 cm.

left nasal bones are firmly fused to each other at the midline, and they are also fused to the underlying and adjacent mesethmoid and frontal bones. This fusion in part obscures the exact shape of each of the nasal bones. At their anterior borders the nasal bones do not overhang the posterior parts of the nares.

The mesethmoid bone forms the inter-narial septum, and this septum is elevated between the right and left nares, not recessed as is common among odontocete species, and as in the species of *Zarhinocetus*. The posterior end of the mesethmoid is elevated dorsally, and in this manner forms dorsally projecting process between the posterior parts of the dorsal narial openings. An ethmoturbinate bone is present, located on each side of the mesethmoid in the posterior part of each naris. As in some archaic odontocetes (e.g., Hoch, 2000; Godfrey, 2013), a crescentic foramen is present on the posterior wall of each naris. Each foramen has an aperture that is curved laterally, is located between the ethmoturbinate and mesethmoid, and is at least 3 mm wide.

Both the right and left lacrimals are preserved on the holotype. On each side the lacrimal is appressed to the anterior edge of the antorbital process of the frontal, and the lacrimal bone forms the lateral side of the antorbital notch. The right lacrimal is slightly larger than the left one, thus contributing to the asymmetry that was noted above between the shapes of the right and left antorbital notches.

The parietals form most of the lateral walls of the braincase. Ventrally, the parietal bone is exposed medial to the squamosal (Figure 20A). It separates the cranial foramen ovale from the posterior lacerate foramen. The parietals probably have a narrow exposure on the cranial vertex between the frontals and the supraoccipital, as is the case in *A. pratti*, but it is not possible to discern any sutures between these bones.

The thick and robust zygomatic process of the squamosal is directed anterodorsally. Differing from the condition in species of Platanistidae, the zygomatic process is not excavated on its medial surface, nor is it compressed transversely. The anterior tip of the process extends anteriorly to approximately the level of the nasal bone, and it does not contact the postorbital process of the frontal. Its lateral surface, dorsal to the external auditory meatus, has a deep and large fossa, which is the area for the insertion of muscles such as the sternomastoideus.

The postglenoid process extends so far anterolaterally that it is aligned with the lateral edge of the cranium. The glenoid fossa faces anteromedially, not anteroventrally as it does in species of *Zarhinocetus*. On the ventral surface of the squamosal, a relatively shallow and small fossa for the middle sinus is present medial to the postglenoid process. A ventral crest is well developed on the ventral surface of the spiny process. When the tympanic bulla is in place, this ventral crest rests in the groove on the anterolateral edge of the posterior process of the bulla. The bony recess that housed the external auditory meatus is narrow, oriented mediolaterally, and it is closely appressed to the posterior side of the postglenoid process. A postmeatal apophysis is present but is small.

On the palate, the palatine bones are anteroposteriorly elongated, and the right and left palatines contact each other on the mid-line of the palate. Each palatine is contacted by the maxilla anteriorly and dorsally, by the pterygoid posteriorly, and extends posteriorly within the medial part of the orbit as a thin plate of bone to contact the anterior falciform process of the squamosal (Figure 20).

Although most parts of both of the pterygoids are missing, the parts that remain indicate that the pterygoid is elongate anteroposteriorly, and that the very thin lateral lamina of each pterygoid extends posteriorly to contact the anterior falciform process of the squamosal. The pterygoid sinus fossa is relatively large, and is expanded anteroposteriorly. The anterior falciform process of the squamosal on each side of the basicranium is in contact with the posterior extensions of both the palatine and the lateral lamina of the pterygoid. On the left squamosal of the

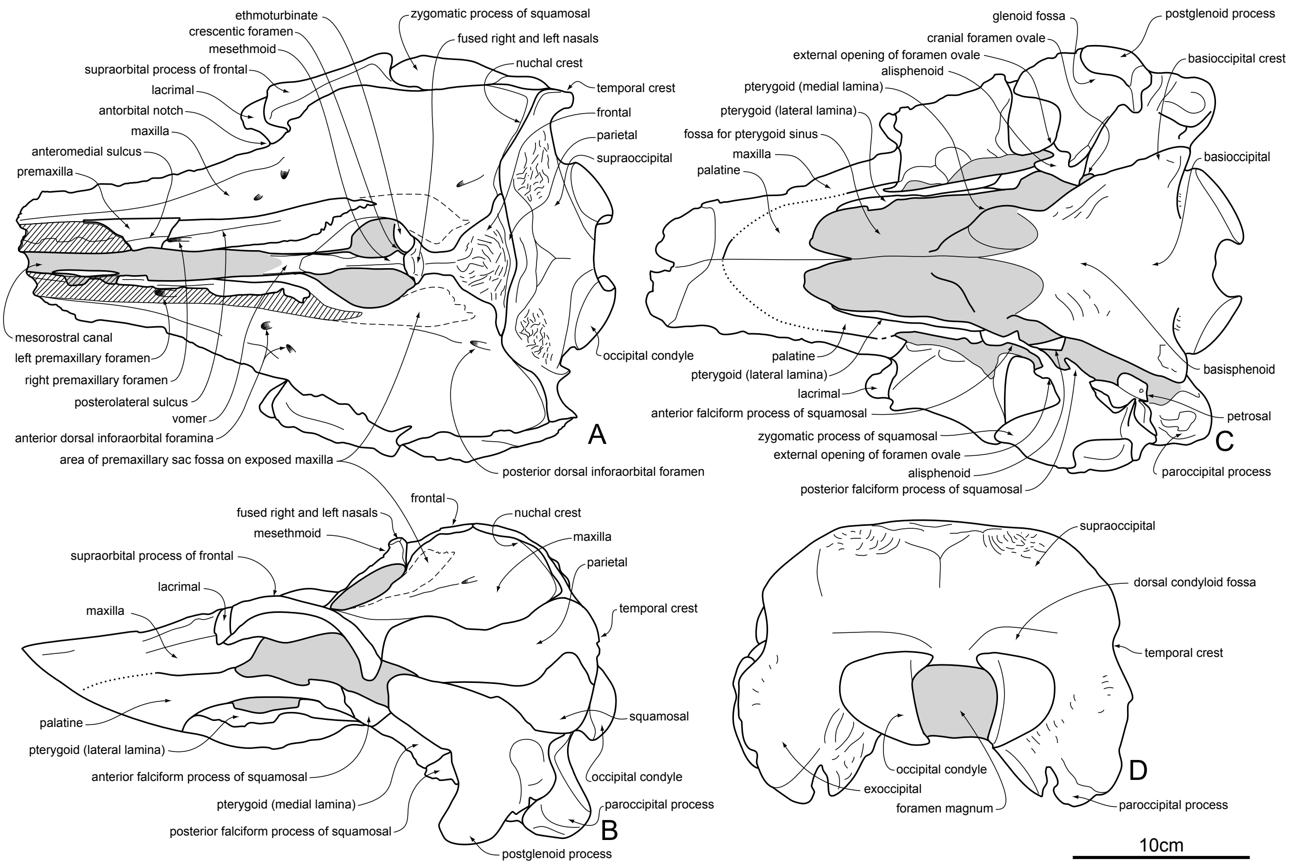

Figure 19. *Ninjadelphis ujiharai* Kimura, new genus and new species, line drawings of holotype cranium, GMNH-PV-2570. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, posterior view. Gray indicates areas covered by matrix, hatched lines represent areas of missing premaxilla, dashed lines indicate the area of the premaxillary sac fossa, and dotted lines indicate estimated sutures. Scale bar equals 10 cm.

holotype, the anterior part of the falcate process is broken off, and the alisphenoid bone is exposed on the ventral surface of the cranium. The cranial foramen ovale (*sensu* Mead and Fordyce, 2009) opens on the posterior edge of the alisphenoid bone, and in life the mandibular nerve passed through this foramen (Figure 20). From the cranial foramen ovale, the mandibular nerve ran externally in a groove, and exited through the external opening of the foramen ovale (*sensu* Mead and Fordyce, 2009; the foramen pseudo-ovale of Fordyce, 1994).

The occipital shield is transversely relatively wide, and it is nearly rectangular in shape in posterior view. It is nearly vertically oriented, being inclined only slightly anteriorly. The nuchal crest is thickened anteroposteriorly, and elevated above the posterior part of the facial surface of the cranium. At the dorsal extremity of the supraoccipital, a tabular-shaped surface is present on each side of the nuchal crest (labeled 1 in Figure 40B). Lateral to this tabular surface, the surface of the supraoccipital is very rugose (labeled 2 in Figure 40B). There is a low external occipital crest near the apex of the supraoccipital. On each side the temporal crest flares posterolaterally. The occipital condyles are relatively large, and they protrude prominently posteriorly. Above each condyle is a large and deep dorsal condyloid fossa.

The basioccipital is relatively broad transversely. The

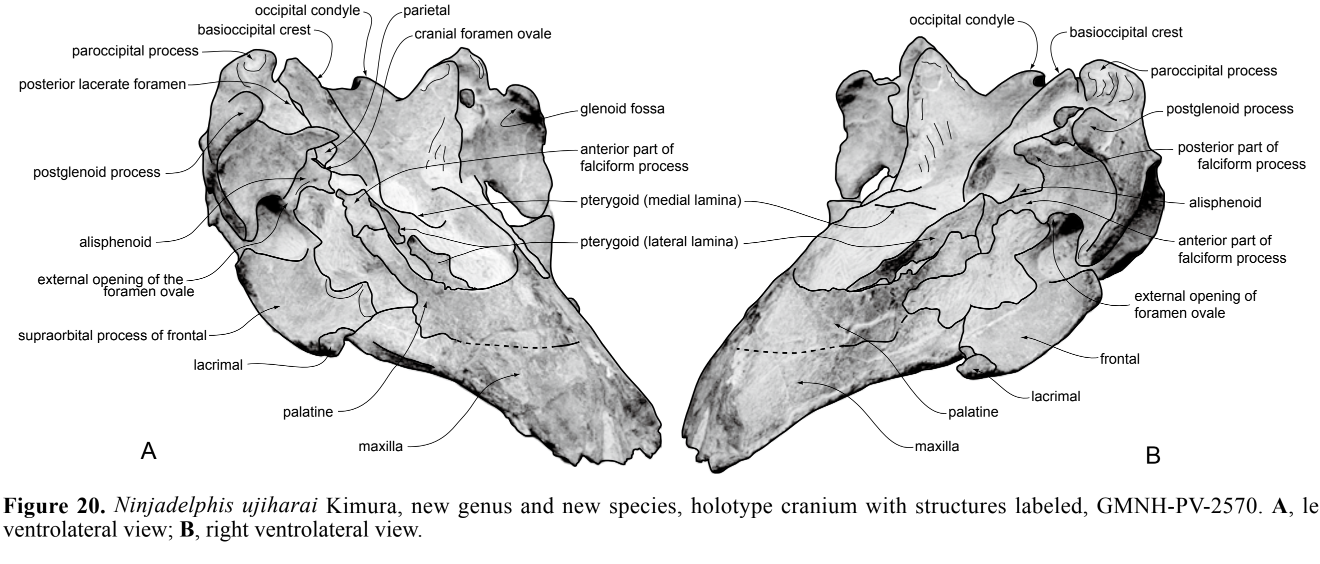

Figure 20. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype cranium with structures labeled, GMNH-PV-2570. **A**, left ventrolateral view; **B**, right ventrolateral view.

basioccipital crests are relatively large, and they diverge from the mid-line posteriorly. The paroccipital process is prominent, and the ventrolateral surface of this process bears an unidentified fossa and groove. There is no fossa for a posterior sinus developed in the anterior surface of the paroccipital process.

Petrosal. Both petrosals are preserved with the holotype. The left one is detached from the cranium (Figure 21), and the right one is still in situ. The anterior process of the petrosal is slender and elongated anteriorly, and is more robust than this same process is in species of Eurhinodelphinidae (see Abel, 1905; Lambert, 2005b; Whitmore and Kaltenbach, 2007). The dorsal part of the anterior process is deflected laterally. A relatively deep and U-shaped anteroexternal sulcus is present on the lateral surface of the anterior process. The ventral part of this sulcus is slightly deeper and wider than its dorsal part. Because the dorsal part of the anterior process is deflected laterally, the anteroexternal sulcus is visible in the ventral view of this bone. The apex of the anterior process is bluntly pointed and directed anteroventrally. The anterior keel is transversely rounded. A small tubercle is developed on the medial surface of the anterior process. The anterior bullar facet (*sensu* Fordyce, 1994; the epitubarian fossa of Muizon, 1987), which receives the processus tubarius of the tympanic bulla, is not distinct. A broken fragment of the accessory ossicle of the tympanic bulla is attached to the ventral surface of the anterior process.

The pars cochlearis is nearly square in ventral view. It is smaller than the same structure in *A. pratti* and *Z. errabundus*. There is an indistinct shallow groove on the medial face of the pars cochlearis, and this groove may be a medial promontorial groove. The small fenestra rotunda opens onto the posterior side of the pars cochlearis. The internal acoustic meatus opens facing anteromedially. It is slightly compressed dorsoventrally and is pyriform in outline. The foramen singulare is relatively large, and it is not incorporated within the endocranial opening of the facial canal. The aperture for the cochlear aqueduct and the aperture for the endolymphatic duct are both relatively small. Both apertures open on the posteromedial surface of the pars cochlearis, and are located near the edge of the internal acoustic meatus. The superior process is transversely wide, smooth, and almost flattened.

The cochlear canal of the petrosal of *N. ujiharai* has 1.75 turns (Figure 22). The first (basal) and second (apical) turns are not coaxial, and the first turn is offset and separated from the second turn. The secondary bony lamina is developed in the first 3/4 turn of the cochlear canal. The axial pitch and basal ratio (*sensu* Ketten and Wartzok, 1990) are 2.08 and 0.55, respectively. The three semicircular canals of *N. ujiharai* are relatively large for odontocetes. Extremely small semicircular canals relative to the size of cochlea have been noted in some extant odontocetes (Boenninghaus, 1903; Yamada, 1953, 1960; Yamada and Yoshizaki, 1959; Ketten, 1992; Spoor et al., 2002). The living platanistid, *Platanista gangetica*, however, has an exceptionally large semicircular canal for the size of its cochlea (Anderson, 1878; Purves and Pilleri, 1974). The relative size of the semicircular canals compared to the cochlea in *N. ujiharai* is similar to that of modern and fossil platanistoids (Anderson, 1878; Luo and Eastman, 1995).

The mallear fossa is large and deep, whereas the fossa incudis is not well defined. Lateral to the mallear fossa, the lateral tuberosity is integral with the parabullary ridge, and it is transversely elongated. A wide epitympanic hiatus is present posterior to the lateral tuberosity. It is wider and deeper than that of *Zarhinocetus errabundus*. It receives the spiny process of the squamosal. The distal opening of the facial canal is relatively small. The fenestra ovalis is anterolateral to the foramen. The anterior part of the facial sulcus is unclear. The stapedial muscle fossa is large and deep.

In contrast to the relatively short posterior process of the petrosal in both *A. pratti* and *Z. errabundus*, the posterior process is more slender, and it is dorsoventrally compressed. Its

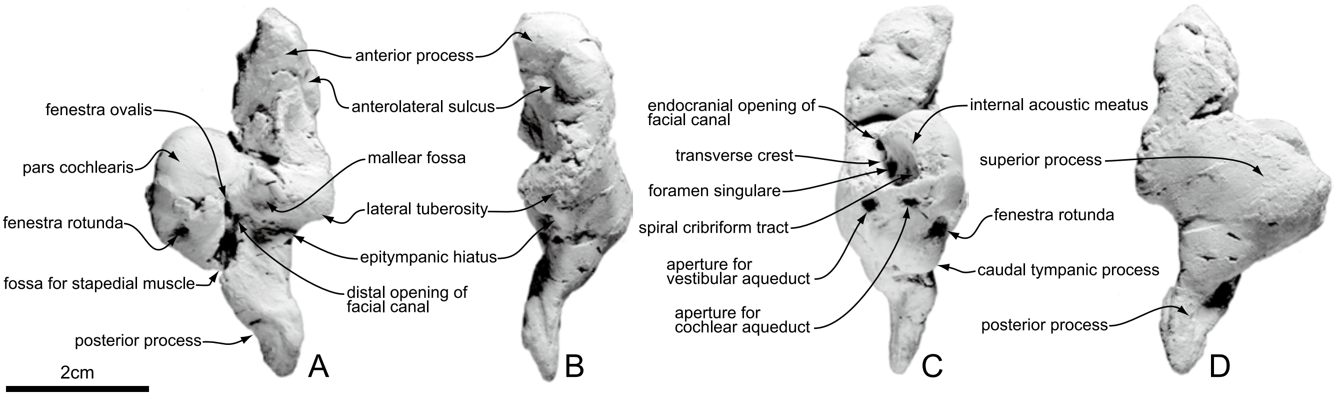

Figure 21. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype left petrosal, GMNH-PV-2570. **A**, ventral view; **B**, lateral view; **C**, medial view; **D**, dorsal view. Scale bar equals 2 cm.

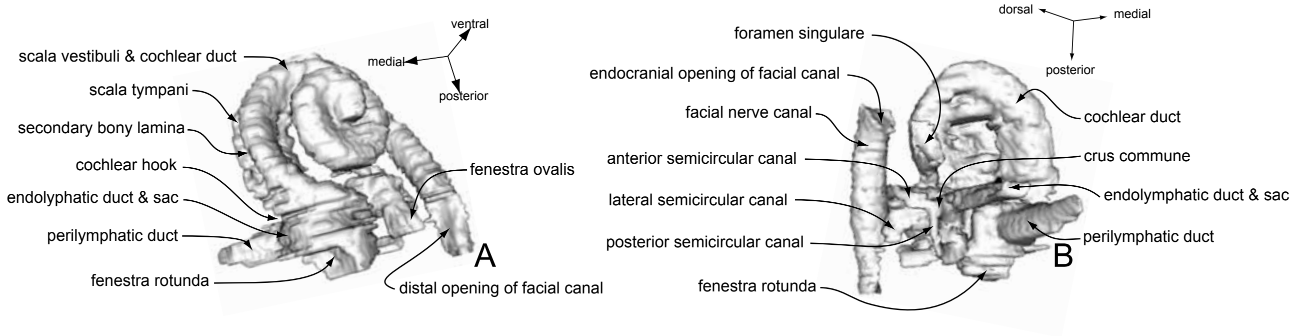

Figure 22. *Ninjadelphis ujiharai* Kimura, new genus and new species, bony labyrinth, holotype left petrosal, GMNH-PV-2570. **A**. dorsomedial view; **B**, ventromedial view. CT scan was performed at the National Museum of Nature and Science, Tokyo, with an X-ray micro-focus CT system (TESCT TXS320-ACTIS), under experimental conditions of 312 kV and 200 μA. The resolution of the square slice CT was 48 mm per 512 pixels, and the spacing between each CT slice was 0.2 mm. Analysis and surface rendering were performed using the software OsiriX version 1.6.4.

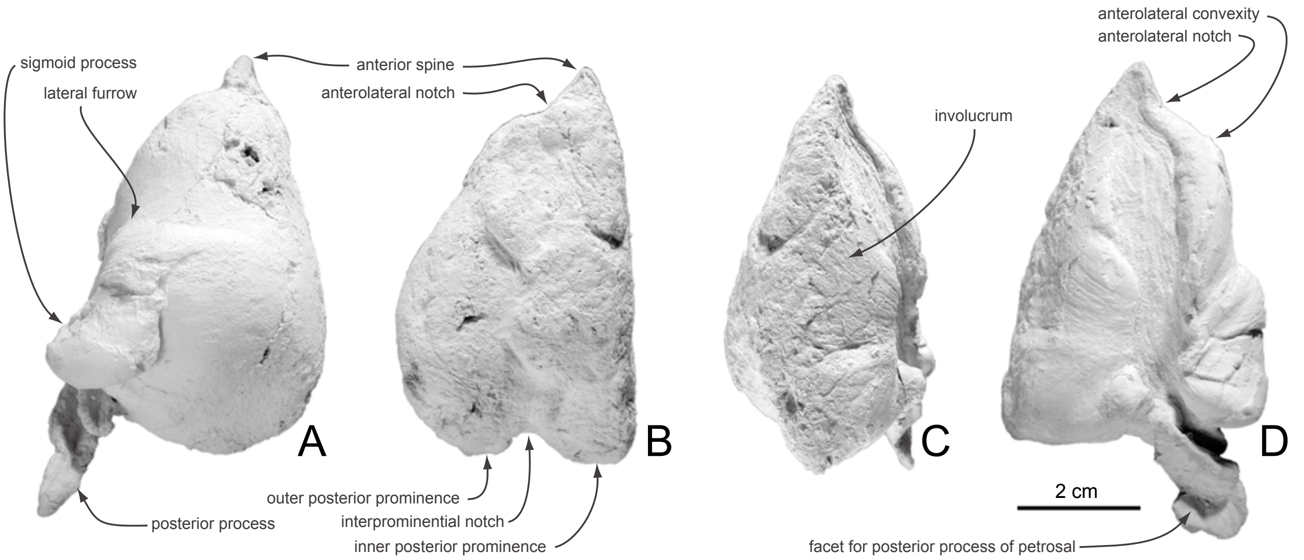

Figure 23. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype right tympanic bulla, GMNH-PV-2570. **A**, lateral view; **B**, ventral view; **C**, medial view; **D**, dorsal view. Scale bar equals 2 cm.

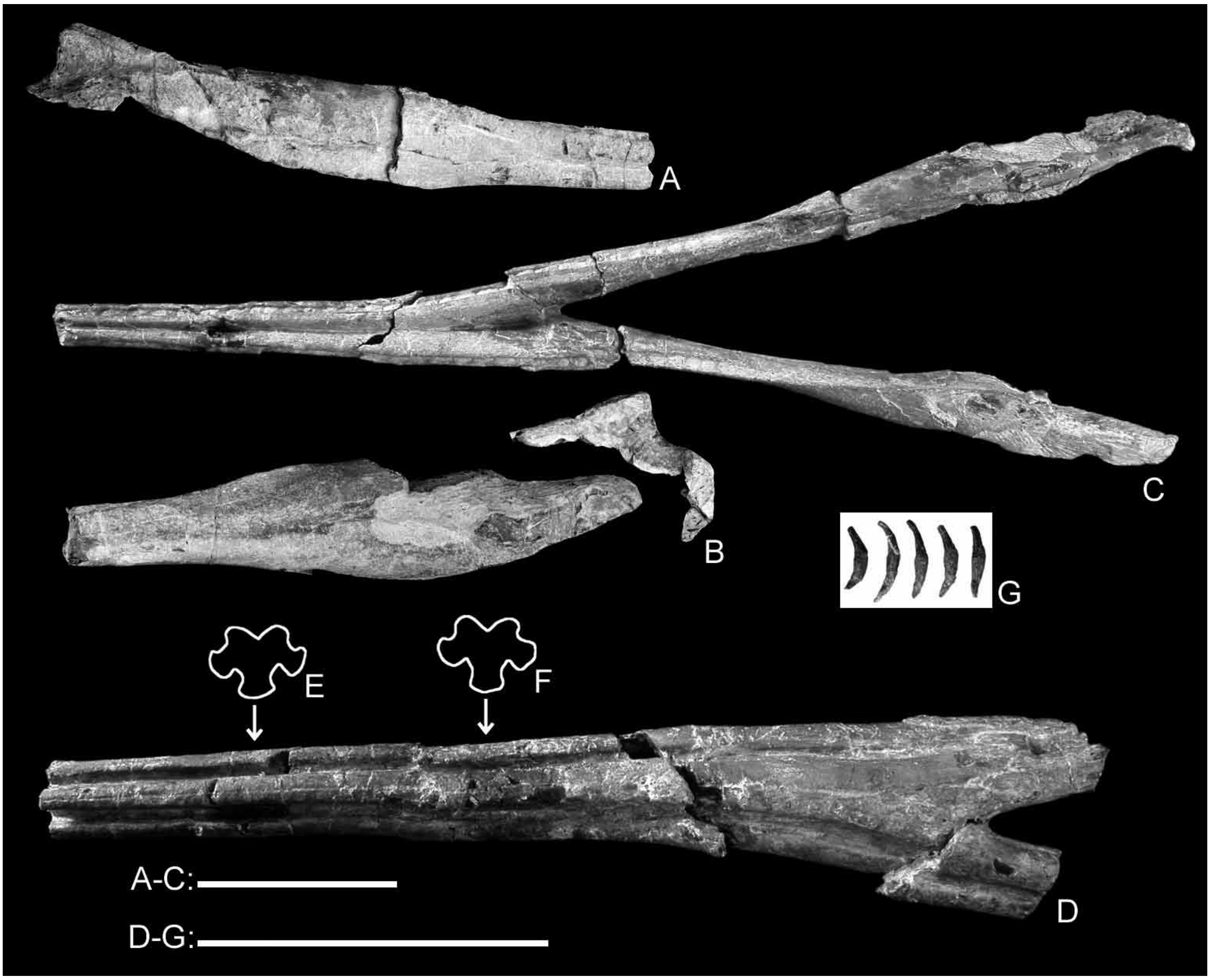

Figure 24. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype mandible and isolated teeth, GMNH-PV-2570. **A**, posterior part of right dentary in lateral view; **B**, posterior part of left dentary in lateral view; **C**, dorsal view of mandible; **D**, ventral view of symphyseal part of mandible; **E**,**F**, cross sectional views of symphyseal part of mandible; **G**, isolated teeth. Scale bars equal 10 cm.

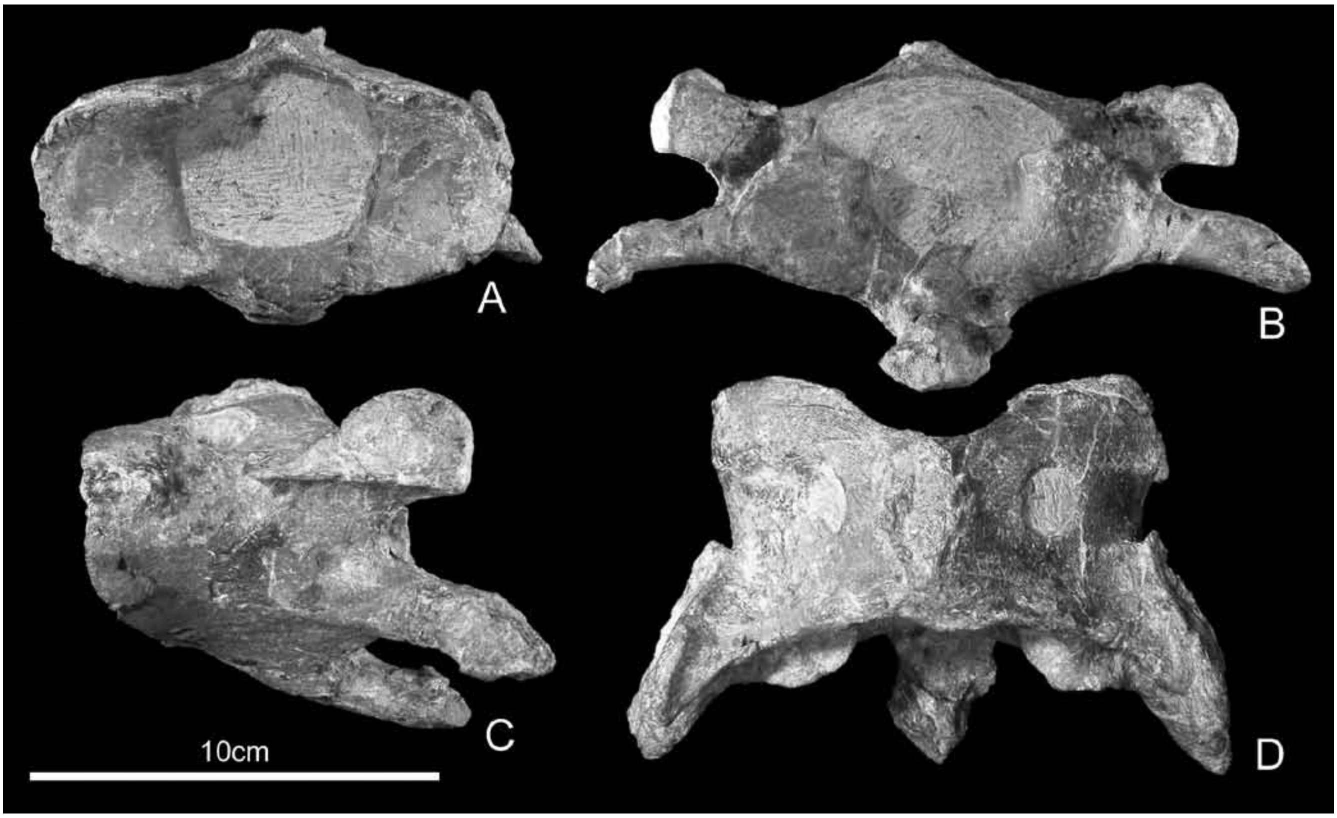

Figure 25. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype atlas, GMNH-PV-2570. **A**, anterior view; **B**, posterior view; **C**, left lateral view; **D**, dorsal view. Scale bar equals 10 cm.

end is oriented posterolaterally. The facet for the tympanic bulla on the posterior process is relatively narrow, and it is parallel-sided. This facet extends dorsally onto the posteromedial face of the posterior process, so that the posterior process of the petrosal has two articular surfaces with the posterior process of the tympanic bulla (i.e., one part of the posterior bulla facet faces ventrally, and the other faces posteromedially). On the anterior border of the articular facet for the tympanic bulla, the petrosal has a groove, oriented anteromedially to posterolaterally, which receives the spiny process of the squamosal.

Tympanic bulla. The right tympanic bulla of the holotype is nearly complete (Figure 23). This bulla has an enlarged and pointed anterior spine. Posterolateral to the spine is a salient anterolateral convexity on the outer lip of the bulla. This convexity is separated from the anterior spine by the anterolateral notch. This notch is more obvious than it is on the bulla of *Z. errabundus* (for example the referred specimen, LACM 149588), and on the bulla referred to *A. pratti* (UCMP 83791). The sigmoid process is large and approximately square. It is oriented posterodorsally, but it is slightly broken and deformed. The lateral furrow is shallow. The conical process is obscured by the deformed sigmoid process.

The tympanic bulla has a bilobed posterior surface. The outer posterior prominence is separated from the inner posterior prominence by the interprominential notch. The outer posterior prominence is more inflated than is the inner posterior prominence. The inner posterior prominence protrudes slightly more posteriorly than does the outer one. In ventral view, the medial furrow extends from the interprominential notch anteriorly to approximately level with the sigmoid process. The involucrum is straight, and its dorsomedial surface is nearly flat. In medial view, there is a notch at the middle of the dorsomedial face of the involucrum.

The posterior process is narrow and directed posterolaterally. A deep groove on the anterolateral edge of the posterior process receives the ventral crest of the spiny process of the squamosal. Therefore, the posterior process of tympanic bulla has a double articulation: one with the petrosal and the other with the squamosal. The facet for the posterior process of the petrosal is concave, and is divided into two articular surfaces. The proximal surface has a smooth surface and articulates with the ventral surface of the posterior process of the petrosal (Figure 23D). The distal surface articulates with the posterolateral surface of the posterior process of the petrosal. On this articular surface of the posterior process of the bulla there are several shallow grooves, and these mesh tightly with the grooved surface of the corresponding part of the petrosal. Although the posterior process is secondarily separated from the inner posterior pedicle, the posterior process was attached to the bulla by two pedicles, and an elliptical foramen can be seen in posterior view.

Mandible. The dorsal shape of the mandible forms a Y-shape, with an elongated symphysis and the diverging rami (Figure 24). At least 33 dental alveoli are preserved in the right dentary and 32 in the left. Progressing anteriorly, the alveoli shift in their orientations, according to the curvature of the dentary, from being directed vertically to more dorsolaterally. In the right dentary the posterior-most alveolus is located 227 mm anterior to the apex of the coronoid process.

In the symphyseal region of the mandible, the medial part of each dentary slopes medially, forming a longitudinal groove along the mid-line of the symphysis. This groove becomes deeper posteriorly. In the symphyseal region, the dorsal and ventral borders of the body of each dentary are nearly parallel. The body of the dentary becomes slightly deeper posterior to the end of the symphysis, and becomes more abruptly deeper farther posterior, at the level of the posterior-most alveoli. A deep longitudinal groove is present on the ventral part of the lateral surface of the symphyseal portion of the dentary. Because this groove is quite deep, the cross-sectional shape of the symphyseal part of the mandible forms an inverted clover shape (Figure 24E, F). This groove is deepest in the anterior part of the preserved mandible, and it becomes shallower and wider posterior to the end of the symphysis. Similar grooves are also present on mandibles of other long-snouted odontocetes: *Zarhachis*

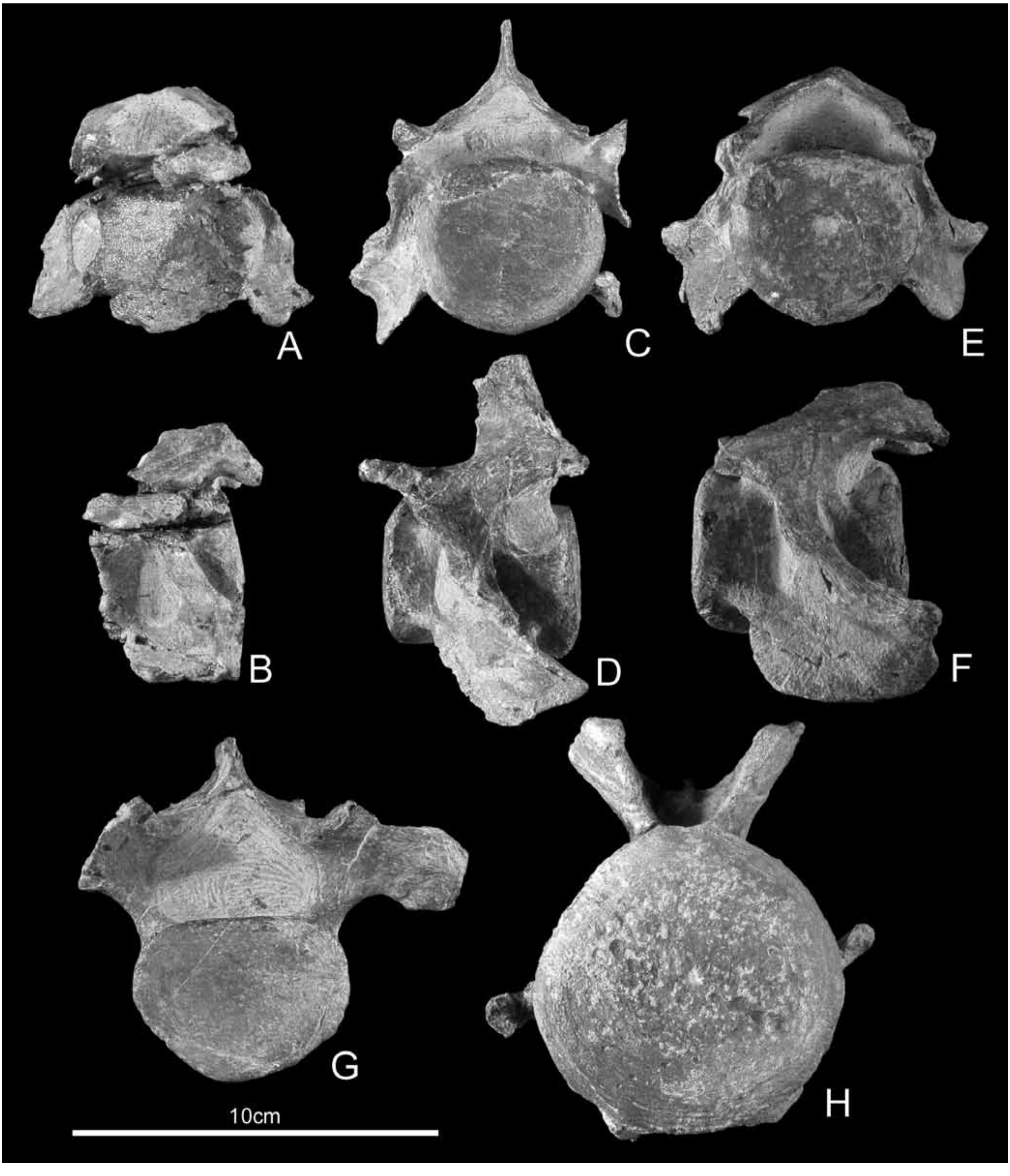

Figure 26. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype vertebrae, GMNH-PV-2570. **A**, **B**, third cervical vertebra in anterior (A) and left lateral (B) views; **C**, **D**, fifth cervical vertebra in anterior (C) and right lateral (D, image reversed) views; **E**, **F**, sixth cervical vertebra in anterior (E) and left lateral (F) views; **G**, anterior view of thoracic vertebra (possibly thoracic two or three); **H**, anterior view of caudal vertebra. Scale bar equals 10 cm.

flagellator, *Platanista gangetica*, *Pontoporia blainvillei*, and within the family Allodelphinidae, in *Allodelphis woodburnei*, *Goedertius oregonensis*, and *Zarhinocetus errabundus*. This groove apparently functions to strengthen a very elongated mandible by adding surface area, creating sort of an "I-beam" shape.

The coronoid crest, preserved on the right dentary anterior to the coronoid process, is smooth and rounded. A longitudinal crest is present, extending from 146 mm anterior to the apex of the coronoid process anteriorly toward the body of the dentary. Part of this crest is also preserved on the left dentary. The coronoid process is relatively low, is directed dorsally, and its apex bends slightly laterally. The dorsal margin of the coronoid process is thickened transversely, and its lateral and medial margins form a longitudinal ridge (Figure 24A). The mandibular condyle is directed posteriorly, and a mandibular notch is located between it and the coronoid process.

Teeth. Forty-one isolated teeth are preserved with the holotype of *Ninjadelphis ujiharai*, and they indicate that the species is polydont and nearly homodont. All of these teeth have slender crowns covered by smooth enamel, and single roots that are long and curved posteriorly at their ends (Figure 24G).

Vertebrae. Seven vertebrae (four cervical, two thoracic, and one caudal) were recovered with the holotype. The epiphyses are firmly fused to the centra of all of these vertebrae. As in the other allodelphinids, *Allodelphis pratti*, *Goedertius oregonensis*, and *Zarhinocetus errabundus*, *Ninjadelphis ujiharai* has enlarged cervical vertebrae that have anteroposteriorly elongated centra, and none of the cervical vertebrae are fused to one another.

Atlas. The atlas vertebra (Figure 25) is large and relatively elongated anteroposteriorly. The greatest length of the lateral face is approximately two-thirds of the greatest width of the anterior articular facets for the occipital condyles. The vertebra is also compressed dorsoventrally, the greatest height of anterior articular surface being less than half of the greatest width of the anterior articular facets. It is not so compressed dorsoventrally as is the atlas of *A. pratti*, however. The anterior articular facets are deeply concave, and each facet has the shape of a half-ellipse. The two facets are widely separated from each other. The neural arch is not very arched, and a large, elliptical-shaped vertebrarterial canal is present on each side of the neurapophysis. A low and blunt neural spine is preserved, and although partly eroded, it was probably short as is the same spine in *A. pratti*, *G. oregonensis*, and *Z. errabundus*. In anterior view, the opening of the neural canal has the shape of a rounded quadrangle, and its height is approximately equal to the transverse width.

The atlas has both dorsal and ventral transverse processes, and these are large and project posterolaterally. The dorsal transverse process is much expanded dorsoventrally and wide at its distal end. The lateral surface of the dorsal transverse process is flattened, and its dorsal and ventral margins have salient margins. The ventral transverse process is more slender and slightly longer than dorsal one. The posterior articular facets for the axis are slightly convex, and each one has the shape of a half-ellipse. The hypophyseal process is long, robust, and irregularly roughened on its dorsal surface.

The atlas of *N. ujiharai* resembles in its general morphology the ones with the holotype and referred specimen (Figure 7) of *A. pratti*. It differs from them by not being so compressed dorsoventrally, and by having its dorsal transverse process much more expanded dorsoventrally, the ventral transverse process nearly twice as long, more slender, and bent medially at its distal end. Enlargement of the dorsal and ventral transverse processes in *N. ujiharai* are interpreted here as being derived character states.

Compared to that of *Z. errabundus* (Figure 36), the atlas of *N. ujiharai* is smaller, less massive, has a smaller dorsal transverse process, but a larger and longer ventral transverse process.

The atlas of *N. ujiharai* also resembles that of a referred specimen, USNM 11231 (see Kellogg, 1924) of the pomatodelphinine platanistid *Zarhachis flagellator* by being relatively large and having enlarged dorsal and ventral transverse processes, but differs from it by being wider transversely, more compressed dorsoventrally, by having a larger dorsal transverse process, the dorsal and ventral transverse processes closer together, and both the anterior and posterior articular surfaces wider transversely.

Other cervical vertebrae. The other three cervical vertebrae of the holotype of *N. ujiharai* are tentatively identified as cervicals three, five, and six, of which the possible cervical three is badly damaged (Figure 26). Each of these cervical vertebrae has a centrum that is anteroposteriorly elongated, has round anterior and posterior epiphyseal surfaces, and an anteroposteriorly-aligned ridge on both its dorsal and ventral surface. The neural canal of each of these is wider than high. On the possible cervical five the large and tall neural spine is directed anterodorsally. The neural spine is broken off of the possible cervicals three and six. The transverse processes of these vertebrae are relatively large and directed posterolaterally, and each of these processes has a large arterial canal near its base. The prezygapophyses of these vertebrae are slender and elongate anteriorly, projecting beyond the anterior faces of the centra. The prezygapophysial facets slope steeply from the external toward the internal margins. The postzygapophysial articular facets are elongate.

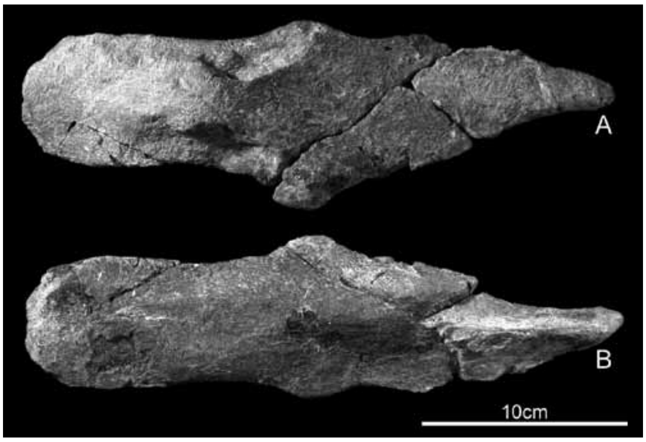

Figure 27. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype manubrium, GMNH-PV-2570. **A**, ventral view; **B**, dorsal view. Scale bar equals 10 cm.

Thoracic vertebrae. A thoracic vertebra of uncertain position is preserved with the holotype specimen and is tentatively identified as being either thoracic two or three (Figure 26G). It is relatively large, and the anterior face of its centrum is ovoid in outline. The centrum has no anteroposteriorly aligned ridge on either its dorsal or ventral surface. Each of its transverse processes bears an articular facet for a rib. Another thoracic vertebra that is preserved with the holotype is closely attached with sediment to the scapula (Figure 28A, B).

Caudal vertebra. The caudal vertebra has the largest centrum of any vertebra found with the holotype of *N. ujiharai* (Figure 26H). This caudal vertebra has circular anterior and posterior epiphyseal surfaces on the centrum, and on each side a relatively small transverse process.

Manubrium. The manubrium of *N. ujiharai* (Figure 27) resembles that of the referred specimen of *A. pratti* (UCMP 83791, Figure 8) by being relatively large, elongate anteroposteriorly, and having well defined facets for the cartilaginous attachments of the sternal ribs. It has a slightly concave dorsal surface, a convex ventral surface, an elongate and somewhat rectangular-shaped anterior end, and a narrow and twisted posterior end that has an asymmetrical raised crest on its dorsal surface. The manubrium of *G. oregonensis* likewise has a twisted posterior end. On each side of the bone there is a facet at the anterolateral corner and anterior to the mid-length for attachment of the cartilaginous ends of the sternal ribs. The surfaces of these facets are rugose and they face anterodorsolaterally. The dorsal surface of the posterior end (Figure 27B) has an anteroposteriorly elongate crest that has a rounded apex. In *A. pratti* the anterior end of this same crest is more elevated and rugose.

Scapula. The left scapula with the holotype of *N. ujiharai* is nearly complete, missing only small parts of its posterior (caudal) margin. This is the only described scapula of any allodelphinid species. It is large and relatively wide, being expanded cranio-caudally (Figure 28A). It measures more than 400 mm cranio-caudally, and approximately 226 mm proximo-distally. It is distinguished from the scapulae of other platanistoids by being relatively wider cranio-caudally. The vertebral border of the scapula is nearly straight, in this way differing from that of Recent *Platanista gangetica*, in which the vertebral border is more convex. The straight vertebral border of *N. ujiharai* is similar to that of a referred specimen, USNM 11867, of the

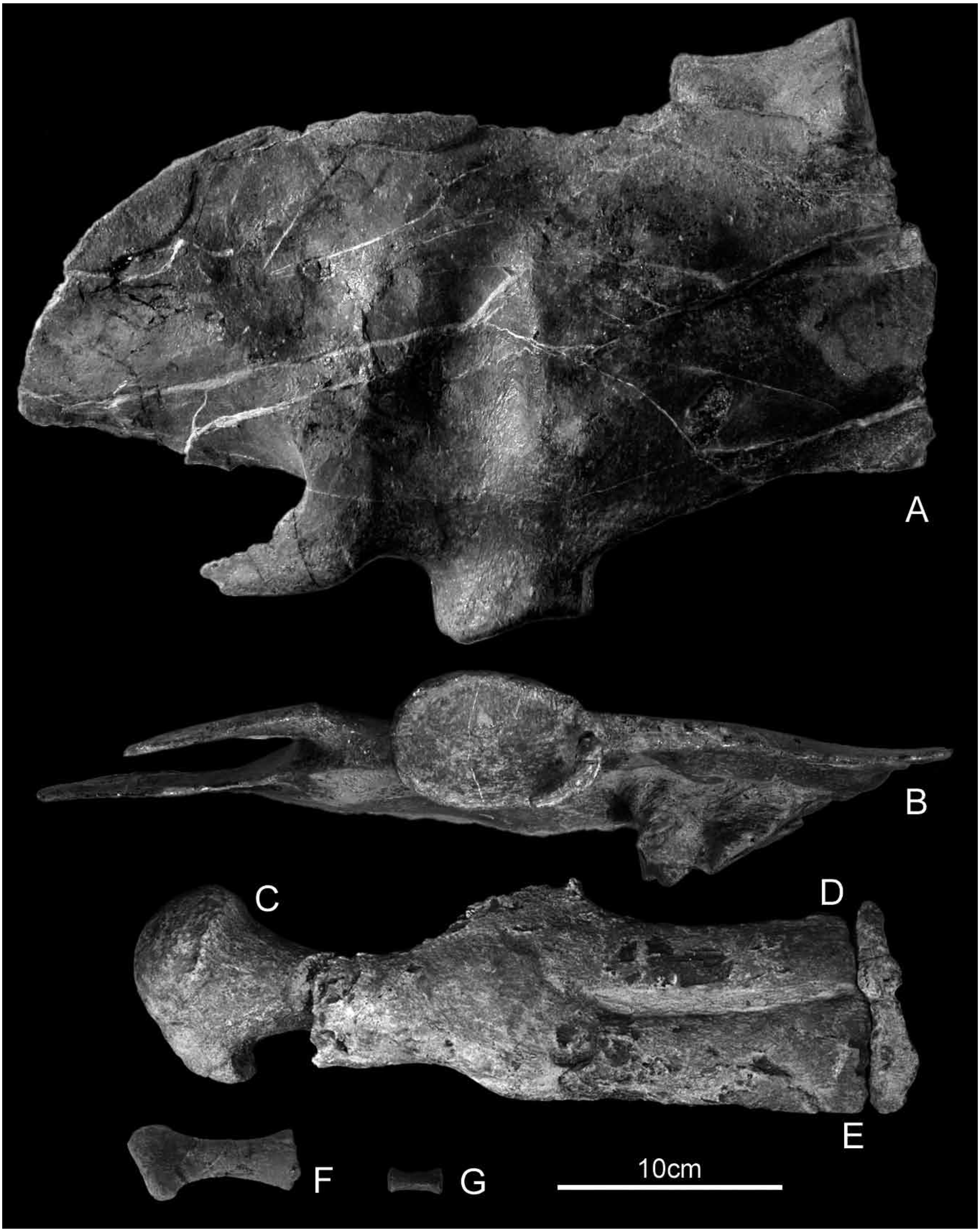

Figure 28. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype, GMNH-PV-2570. **A**, **B**, scapula in lateral (A) and ventral (B) views; **C**-**E**, lateral views of left humerus (C), ulna (D), and radius (E) with isolated distal epiphysis of ulna and radius; **F**, metacarpal bone; **G**, phalanx in lateral view. Scale bar equals 10 cm. A thoracic vertebra is attached to the dorsoposterior angle of the scapula.

middle Miocene eurhinodelphinid *Xiphiacetus bossi* (Kellogg, 1925) from the Calvert Formation in Maryland, U.S.A.

On the holotype scapula of *N. ujiharai* the coracoid process is entirely absent. Absence of this process is reputedly a synapomorphy of species in the superfamily Platanistoidea (Muizon, 1994), although Tanaka and Fordyce (1914) in describing the late Oligocene platanistoid, *Otekaikea marplesi* (Dickson, 1964) from New Zealand, suggested that some basal platanistoids retained a reduced coracoid process. The acromion process of *N. ujiharai* is located on the lateral side of the anterior margin of the scapula. It projects anteriorly, bends slightly medially, and is slender and attenuated anteriorly. The supraspinatus fossa is present and occupies a considerable part of the lateral surface of the scapula. The glenoid fossa is deeply concave, elliptical in shape, and measures 71 mm anteroposteriorly and 48 mm transversely. The anterior and posterior margins of the scapular blade are slightly concave. The scapular blade is thickened along its anterior margin medial to the acromion process and along its posterior margin near the glenoid fossa. The angle between the anterior and posterior margins of the scapular blade is approximately 120º. There is a large concavity in the center of the lateral surface of the scapular blade, and there are no ridges in this area. Two broad ridges are present, however, on the medial surface of the scapula.

Humerus. The left humerus of the holotype of *N. ujiharai* is well preserved, but it is broken into separate proximal and distal parts (Figure 28C). The diaphysis of the humerus is elongate proximodistally, nearly cylindrical in shape, and slightly expanded distally. Both the proximal and distal epiphyses are completely fused to the diaphysis, adding to other indications that the animal was mature. The head of the humerus is relatively large, hemispherical in shape, and is oriented facing slightly caudally. The distal trochlea of the humerus is fused with the olecranon process of the ulna. The humerus and ulna are similarly fused in specimens referred here to *A. pratti* and *Z. errabundus*.

Radius. The left radius is preserved with the holotype. At its proximal end its ulnar process is firmly fused to the ulna. The diaphysis of the radius is relatively slender, elongated proximodistally, and slightly expanded cranio-caudally at its distal end. The cranial border of the diaphysis is nearly straight, whereas the caudal border is slightly concave. The caudal border is thicker than the cranial border. A low tuberosity is present on the cranial border of the proximal part of the diaphysis, and this tuberosity has on it a small concavity. The separate distal epiphysis of the radius is present with the specimen, indicating that at the time of death of the individual it had not yet become fused to the diaphysis (see Figures 28E, 29).

Ulna. The left ulna is preserved with the holotype and, as noted above, its olecranon process is fused to the humerus. Such fusion also occurs between the ulna and the humerus in *A. pratti* and *Z. errabundus*. The diaphysis of the ulna of *N. ujiharai* is more slender than that of the radius. Its cranial margin is slightly convex, and the caudal margin is slightly concave. The olecranon process is incompletely preserved, but appears to have originally been large and rather crescent-shaped as it is in *A. pratti* (see Figure 39). The distal epiphysis of the ulna is present with the holotype and, similar to the situation for the radius, at the time of death of the individual it had not yet become fused to the diaphysis (see Figures 28D, 29). The ulna is slightly shorter than the humerus, but not as short proportionally as that of *Z. errabundus*. In *A. pratti* the ulna and humerus are essentially of the same length.

Carpal bones. The right carpal bones are preserved with the holotype; these bones are rarely recovered or described with fossil cetacean specimens. Unlike the arrangement of the carpals of most species of the Odontoceti, except for species in the families Ziphiidae and Pontoporiidae, the carpal bones of *N. ujiharai* are arranged in two parallel rows (Figure 29).

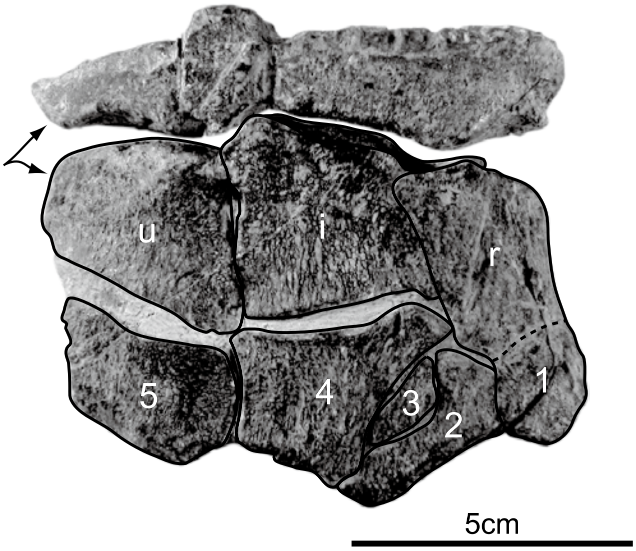

Figure 29. *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype right carpal bones and distal epiphysis of the ulna and radius in lateral view, GMNH-PV-2570. Arrows indicate the facet for the accessory carpal bone (pisiform). Scale bar equals 10 cm. Abbreviations: i, intermediate carpal bone; r, radial carpal bone; u, ulnar carpal bone; 1-5, first-fifth carpal bones. Scale bar indicates 5 cm.

The radial carpal bone (labeled r in Figure 29) is small and is fused with the first carpal bone (labeled 1 in Figure 29), a condition that is also present in Recent *Platanista gangetica* (see Turner, 1910; Pilleri and Gihr, 1976; Gihr et al., 1982; *contra* Anderson, 1878). The suture line between the radial carpal bone and first carpal bone is distinct on its lateral surface but it is not clear on the medial surface. The intermediate carpal bone (labeled i in Figure 29) is large, and it articulates proximally with the distal ends of both the radius and the ulna, distally with the fourth carpal bone, cranially with the radial carpal bone, and caudally with ulnar carpal bone. The ulnar carpal bone (labeled u in Figure 29) articulates proximally with the ulna, and distally with the fourth and fifth carpal bones, although the facet for its contact with the fourth carpal bone is very small.

Although the accessory carpal bone, the pisiform, is not preserved with the holotype, it was clearly present in this species because the facet for its articulation is present on the caudal surface of the ulnar carpal bone and on the caudal surface of the distal epiphysis of the ulna (indicated by arrows in Figure 29).

The fourth carpal bone (labeled 4 in Figure 29) is one of the largest of the carpals. It is fused with both the second and third carpal bones, and the sutures between these bones are visible on their lateral surfaces, although they are completely obliterated by fusion on their medial surfaces.

The fifth carpal bone (labeled 5 in Figure 29) articulates proximally with the ulnar carpal bone, and cranially with the fourth carpal bone.

One metacarpal (Figure 28F) and one phalanx (Figure 28G) are also present with the holotype, but their original positions within the manus cannot be determined.

Zarhinocetus Barnes and Reynolds, 2009

Squalodon (part). Kellogg, 1931:373, for *Squalodon errabundus* Kellogg, 1931.

"*Squalodon*". Barnes, 1977:327, table 3, for *Squalodon errabundus* Kellogg, 1931, as a taxon of the platanistoid family Platanistidae; Barnes, 2006:31-34, [part], for *Squalodon errabundus* Kellogg, 1931, as a taxon of the platanistoid family Allodelphinidae.

Zarhinocetus Barnes and Reynolds, 2009:488; new genus for "*Squalodon*" *errabundus* Kellogg, 1931.

Zarhinocetus Barnes and Reynolds, 2009. Barnes, Godfrey, and Kimura, 2010:452; Thomas and Barnes, 2015:21.

Emended diagnosis of genus: A genus of the family

Allodelphinidae differing from *Allodelphis*, *Goedertius*, and *Ninjadelphis* by having cranium with more depressed medial part of dorsal surface of proximal part of rostrum, enlarged tubercle present on dorsolateral surface of maxilla anterior to antorbital notch, supraorbital process of frontal thicker dorsoventrally, anteroposteriorly-oriented crest present on dorsal surface of supraorbital process of maxilla, bony orbit of larger diameter, dorsal exposures of frontals on cranial vertex asymmetrical with midline suture located to left of cranial midline, zygomatic process of squamosal nearly rectangular in lateral view rather than arc shaped, nuchal crest curving anteriorly at apex posterior to cranial vertex, occipital shield larger and more vertically oriented, occipital condyles proportionally larger; petrosal more massive, with anterior process more robust, posterior process shorter, posterior articular facet for tympanic bulla smaller; tympanic bulla with outer lip more inflated; atlas vertebra relatively larger and more massive; humerus proportionally larger in relation to body size, with more stout diaphysis and relatively larger humeral head; and radius and ulna shorter than humerus; differing further from *Allodelphis* and *Goedertius* by having cranium with posterior end of premaxilla retracted anteriorly from proximity of nasal bone, terminating on lateral side of dorsal nares, area where posterior end of premaxilla formerly existed, forming premaxillary sac fossa, instead formed of smooth, convex, and dense maxilla, nasal bones smaller, narrower anteriorly, fused to each other along midline suture, and fused to underlying frontals; petrosal with relatively larger cochlear portion; atlas vertebra with dorsal transverse process expanded dorsoventrally; and differing further from *Goedertius* by having cranium with smaller nasal bones, nasal bones nearly unrecognizable because of fusion to each other and to underlying frontal bones; differing further from *Ninjadelphis* by having petrosal with posterior articular facet for tympanic bulla not divided into two surfaces; mandible more flattened dorsoventrally in posterior part of symphyseal region; atlas vertebra relatively larger and more robust, with dorsal transverse process larger and more expanded dorsoventrally, and ventral transverse process more massive and shorter.

Type species. *Squalodon errabundus* Kellogg, 1931; type by original designation by Barnes and Reynolds, 2009.

Included species. *Zarhinocetus donnamatsonae* Barnes, new species; and *Zarhinocetus errabundus* (Kellogg, 1931).

Geographic and geochronologic ranges. Late early Miocene to middle middle Miocene; eastern North Pacific Ocean coast of present-day California and Washington (and presumably of Oregon).

Zarhinocetus donnamatsonae Barnes, new species

Figure 30, Table 1

Diagnosis of species. A species of the genus *Zarhinocetus*, differing from *Z. errabundus* by being smaller as adult, and by having cranium with dorsal opening of mesorostral canal transversely wider in posterior part of rostrum anterior to nares, tuberosity on maxilla anterior to antorbital notch smaller, crest on dorsal surface of supraorbital process of maxilla smaller, fossa medial to this crest deeper, facial surface narrower transversely with frontal and parietal not extending so far laterally over temporal fossa, fossa in dorsal surface of maxilla lateral to cranial vertex deeper, narial opening widened (expanded) posterolaterally rather than narrowing, mesethmoid septum between narial passages extending farther dorsally so that its posterior part is above margin of nares, mesethmoid septum between posterior parts of nares at anterior edge of nasal bones wider and spreading posterolaterally onto anterior surfaces of nasals, rather than narrow and below anterior edges of nasals, nasal bones wider transversely, postorbital process of frontal larger with ventral extremity more pointed, zygomatic process of squamosal dorsoventrally narrower, more elongated anteroposteriorly, and not so inflated, nuchal crest lower and less prominent, occipital shield relatively smaller with less prominent dorsolateral corners, occipital condyles relatively and absolutely of smaller size, basioccipital crests proportionally smaller and transversely narrower.

Holotype. UCMP 86139, a partial cranium lacking approximately the distal two-thirds of the rostrum, with the right and left petrosals and tympanic bullae in place, and part of presumably the right dentary in matrix within the right orbit, associated with a vertebra and other fragments; collected in 1930.

Type Locality. UCMP locality V69171, in the area of the Chehalis River, near Elma, Grays Harbor County, western Washington State, U.S.A.

Formation and age. The holotype specimen of *Zarhinocetus donnamatsonae* (Figure 30) was found in a concretion of fine grained gray sandstone derived from an undetermined level of the Astoria Formation. The Astoria Formation in western Washington is a thick, marine, near shore, relatively shallow water shelf deposit that overlies the Lincoln Creek Formation and underlies the Montesano Formation. It represents a considerable period of geologic time, and has been correlated with the Pillarian and Newportian molluscan stages, with the Saucesian Foraminiferal Stage, is approximately correlative with the late part of the Arikareean and the Hemingfordian North American Land Mammal Ages, and its possible age spans from late early Miocene to early middle Miocene. Because it is uncertain from what horizon within the Astoria Formation the holotype was derived, its age can only be stated as being approximately between 20 and 15 million years old (Etherington, 1931; Moore, 1964, 1984:1; Wolfe and McKee, 1968; Addicott, 1976:101; Moore and Addicott, 1987; Barnes, 1977:324-325, table 2; Barnes, 1987:6; Tedford et al., 1987:156, 201, fig. 6.2 (chart in pocket); Berglund and Goedert, 1992; Tedford et al., 2004:fig. 6.2). Parts of the Astoria Formation in western Washington are apparently older than the well-known fossil-bearing sediments that have been referred to the Astoria Formation and are exposed farther south along the Pacific Ocean coast in Lincoln County, Oregon (Moore, 1964; Moore and Addicott, 1987; Barnes, 1987:4; Moore and Moore, 2002). Other species of marine vertebrates that have been reported from the Astoria Formation in western Washington State include bony fishes and the desmatophocine otarioid pinniped *Desmatophoca brachycephala* Barnes, 1987.

Etymology. The species name, *donnamatsonae*, is patronymic, and honors the late Donna Marie Matson (deceased 18 July 2015) of Los Angeles, California. Ms. Matson was a long-time friend of Lawrence G. Barnes, and was a world traveler, photographer, teacher, and producer of educational films. Ms. Matson was fascinated with marine mammals, particularly with dolphins, and she swam with bottlenose dolphins even in the years just prior to her death. She supported research at the Natural History Museum of Los Angeles County, and was a benefactor to the Museum's Fossil Marine Mammal Research Account, which supported this research project.

Geographic and geochronologic ranges. Late early Miocene or early middle Miocene, eastern North Pacific coast in the area of present-day Washington.

Description. The holotype cranium was found in a sandstone concretion, and the rostrum was broken off by erosion prior to its discovery. Much of the enclosing sediment was removed using power tools and a dilute formic acid solution with water. The specimen is from a mature individual because the cranial sutures are closed and the cranial tuberosities and crests are fully developed. The sex of the individual cannot be determined with currently available information.

Cranium. Presumably, as in the other species of Allodelphinidae, the rostrum when complete was originally very long, thus the cranial length originally was approximately one meter. At the place where it is broken off, the rostrum is flattened dorsoventrally. In the mid-part of the rostrum the medial margins of the premaxillae are elevated adjacent to the mesorostral canal. More posteriorly, where the dorsal surface of

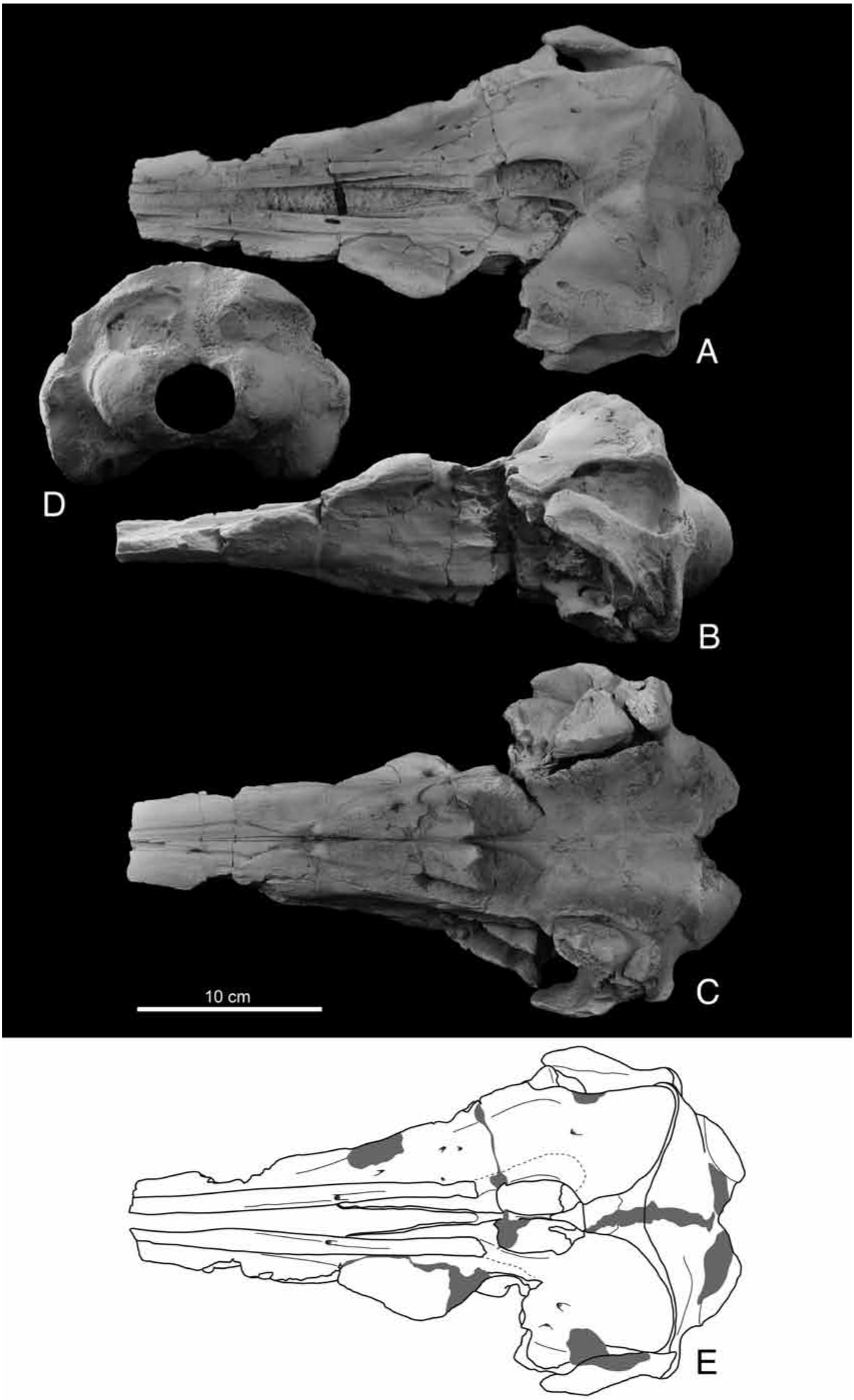

Figure 30. *Zarhinocetus donnamatsonae* Barnes, new species, holotype cranium, UCMP 86139. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, posterior view; **E**, dosal view, line drawing. Gray indicates areas restored and/or damaged. Dashed lines indicate the area of the premaxillary sac fossa. Scale bar equals 10 cm.

the rostrum is depressed, the dorsal surfaces of the premaxillae slope medially toward the mesorostral canal, forming a deep fossa on the midline of the rostrum anterior to the nares (Fig. 30A). The lateral edge of each premaxilla is elevated along its lateral margin to the extent that it forms an elongate crest. In the area where the rostral surface is depressed, the mesorostral canal is widest and, presumably because of bone atrophy related to formation of this depression, the narrow lateral edge of the mesorostral part of the vomer is exposed dorsally, along the medial margin of the adjacent premaxilla.

Each premaxilla has a single, anteroposteriorly elongate, premaxillary foramen, which is continuous with a faint anteromedial sulcus and a deeper posterolateral sulcus. As in *N. ujiharai* there is no posteromedial sulcus. Such a sulcus is typically present in many species of Odontoceti (Barnes, 1978; Mead and Fordyce, 2009).

The posterior ends of the premaxillae are atrophied, retracted anteriorly, and they terminate at a location anterior to the naris. The left premaxilla at this location is completely preserved, and its posterior end is thin, has vacuities, and is irregularly digitated. In the place where in more primitive species of Allodelphinidae, such as *Allodelphis pratti* and *Goedertius oregonensis*, the premaxillae curve around the lateral sides of the nares, there is in *Z. donnamatsonae* only the exposed dorsal surfaces of the maxillae. These surfaces of the maxillae surrounding the nares form smooth and slightly elevated surfaces that held the premaxillary sacs on either side of the nares. This is the same derived character that exists in *N. ujiharai* and *Z. errabundus*.

At the place where the rostrum is broken off, the medial margin of the maxilla is elevated adjacent to the premaxilla, its mid-part is depressed, and along the lateral margin, dorsal to the alveolar row, the maxilla is elevated and thickened. More posteriorly, where as previously mentioned, the mid-part of the rostrum is depressed, the dorsal surface of the maxilla slopes medially toward the adjacent premaxilla.

Immediately anterior to the antorbital process each maxilla has an elevated tubercle of bone that is elliptical anteroposteriorly, and porous on its dorsolateral surface. Among the described species of Allodelphinidae, such tubercles are known to exist only in *Z. errabundus*. The medial surfaces of these tubercles are denser bone than are the lateral surfaces. The left tubercle on the holotype is complete, and the right one is partly broken off, however, it is clear that these tubercles were asymmetrical (Fig. 30A), the right one originally being smaller than the left one. These same tubercles are similarly asymmetrical (but larger) in the more derived allodelphinid, *Z. errabundus*.

Similar asymmetrical development is present in the laterally-flaring margins of the maxillae anterior to the antorbital notches in *Ninjadelphis ujiharai*; the right maxillary margin is smaller than the left margin. In *N. ujiharai*, however, neither of these flared margins of the rostrum is developed into a tubercle as in the species of *Zarhinocetus*. Combining information from the preserved parts of both sides of the holotype, in *Z. donnamatsonae* there are apparently four anterior dorsal infraorbital foramina, all of them positioned on the medial side of each of the maxillary tubercles.

On the facial surface of the cranium, each maxilla spreads posteriorly and laterally, forming the lateral side of the dorsal naris, contacting the nasal bone (where the retracted premaxilla is not present), contacting the frontal bone at the cranial vertex, meeting the supraoccipital to participate in forming the prominent nuchal crest, and spreading laterally over the orbit and the temporal fossa.

Dorsal to the orbit, the dorsal surface of the maxilla has an anteroposteriorly-aligned crest that slightly diverges posteriorly from the sagittal plane, and is approximately 40 mm long. The height of this crest is accentuated by the presence of a fossa in the dorsal surface of the maxilla medial to it. Compared to the same structures in *Z. errabundus*, this crest in *Z. donnamatsonae* is lower, but the fossa medial to it is deeper.

The posterior dorsal infraorbital foramen is located in the middle portion of the postorbital part of the maxilla, located approximately equidistant between the margin of the naris and the edge of the temporal fossa. This differs from the autapomorphic condition that exists in species of Platanistidae (see Barnes, 2006), in which the posterior maxillary foramen is located very close to the posterolateral corner of the premaxilla. The maxilla does not extend to the lateral edge of the supraorbital process, and the frontal bone is thus exposed over the margin of the orbit. Lateral to the cranial vertex, the posterolateral part of each maxilla has a broad and shallow fossa. Such a fossa also exists in *Z. errabundus*, but in that species it is broader but shallower.

Most of the left supraorbital process and the right antorbital process are broken off and lost. The preserved parts on the right side demonstrate that the frontal was not so widely exposed beyond the lateral edge of the maxilla as it is in *Z. errabundus*. The orbital margin, formed by the frontal, is concave as in *N. ujiharai*, and not convex as it is in *Z. errabundus*.

The narial openings are elongate oval in shape when viewed dorsally. They are separated by the tall and thin mesethmoid septum, which posteriorly extends dorsally to above the level of the adjacent maxillae, and which is increasingly thicker transversely and higher posteriorly approaching the anterior edges of the nasal bones. The posterior wall of each narial passage has an irregular and convex exposure of the ectethmoid, which on each side is perforated by a small vestige of the olfactory foramen. On the posterior wall of each naris is a protuberance, lateral to the olfactory foramen, which is homologous to the turbinate bone as occurs in *N. ujiharai*. Anterior to the nares, the mesethmoid facing into the mesorostral canal is a solid mass of bone that in life abutted the mesethmoid cartilage.

The nasal bones are irregularly shaped, concave across their anterior sides where they abut the arcuate posterior end of the mesethmoid, and become slightly wider posteriorly. They have indistinct sutures posteriorly where they contact the frontal bones, to which the nasals are fused. The nasals peak at their midlines, so that the dorsal surface of each nasal bone slopes laterally.

Frontals form the apex of the cranial vertex, being exposed posterior to the nasals, between the right and left maxillae, and anterior to the supraoccipital, and are exposed in broad arcs where they contribute to the nuchal crest. The cranial vertex is asymmetrical, the mid-line suture between the right and left frontals being displaced laterally to the anatomical left side of the cranium, as is typical of many, but not all, species of Odontoceti. The sagittal suture between the frontals is located 5 mm to the anatomical left side of the mid-line of the cranium.

Although it is somewhat eroded, the nuchal crest is prominent, but clearly not as thick, nor as elevated, as is that of *Z. errabundus*. The crest is somewhat V-shaped, being indented anteriorly immediately posterior to the cranial vertex. This is similar to the condition in *Z. errabundus*, and differs from the condition in species of *Allodelphis*, *Goedertius*, and *Ninjadelphis*, in which the nuchal crest protrudes posteriorly at the cranial vertex. In *Z. donnamatsonae* there is an anterior indentation in the left half of the nuchal crest that is related to the asymmetrical displacement of the cranial vertex to the left side.

The temporal fossa is relatively small in relation to the size of the cranium, and in lateral view is approximately triangular in outline, being narrowest anteriorly (Fig. 30B). The maxilla, frontal, and parietal form a shelf that projects prominently laterally over each temporal fossa, but these bones do not extend so far over the temporal fossae as they do in *Z. errabundus*. In this regard, *Z. donnamatsonae* more resembles *N. ujiharai* by having a convex margin of the facial region dorsal to the temporal fossa.

Compared to the short and blunt postorbital process of the frontal of *Z. errabundus*, in *Z. donnamatsonae* the same process is deeper dorsoventrally and nearly triangular in lateral view.

The lambdoidal crest projects prominently laterally where it encloses the posterior margin of the temporal fossa. The parietal-squamosal suture arches across the lateral wall of the braincase, and is very irregular. A well-defined squamosal fossa is present in the surface of the squamosal at the base of the temporal fossa. The zygomatic process is inclined anterodorsally, and is somewhat rectangular in lateral view, with a nearly square anterior end.

The occipital shield is relatively large, as in *Z. errabundus*, but its dorsal margin forms an arch, similar to the condition in *N. ujiharai*, and is therefore not so squared, and straight across its dorsal edge, in posterior view (Fig. 30D) as it is in *Z. errabundus*. As in *Z. errabundus* the occipital condyles are relatively large, widely spaced, and are separated by wide notches both ventrally and dorsally.

The posterior part of the palate is relatively deep dorsoventrally, and its ventral surface is convex. The palatal parts of the pterygoids are nearly complete; such good preservation is exceptional among reported specimens of allodelphinids. Each pterygoid has a relatively large surface area, and has an anteroposteriorly elongate exposure on the palate, tapering to a point anteriorly (Fig. 30C). In contrast, in *N. ujiharai* the anterior ends of the pterygoids are rounded and not tapered to a point. As in *N. ujiharai*, in *Z. donnamatsonae* a small wedge of each palatine bone extends posteriorly between the anterior ends of the pterygoids. The ventral surface (floor) of the pterygoid sinus is completely enclosed by the pterygoid bone, and the pterygoid sinus fossa opens facing both laterally and posteriorly. Projecting posteriorly from the medial side of each pterygoid is the somewhat cylindrical, and solid, hamular process. These can be seen to be solid where each is broken off, and there is no excavation of the process by the pterygoid sinus. For an odontocete, this process is relatively large and thick. This is probably a primitive character state. On each side the fully ossified and dorsoventrally deep lateral lamina of the pterygoid, less than 1 mm thick, extends posteriorly, separating the orbit from the narial passages, and connecting with the anterior falciform process of the squamosal. As in the other allodelphinids, the palatine bone also forms a thin plate of bone, less than 1 mm thick, lying dorsal to the lateral lamina of the pterygoid, that extends posteriorly to contact the anterior falciform process of the squamosal.

On the ventral surface of the supraorbital process there are no bony fossae present that would have held either an antorbital lobe or a postorbital lobe of the pterygoid sinus. There is also no fossa present in the anterior face of the paroccipital process that would have held a posterior sinus. The paroccipital process is relatively large, blocky, and has a rugose concavity in its ventral surface.

Typical of species of Allodelphinidae, the basioccipital is relatively wide. The basioccipital crests are prominent and they diverge slightly from the mid-line of the cranium posteriorly. They are thinner transversely than are the same crests in *Z. errabundus*.

Tympanic bulla. Both tympanic bullae are in situ in the holotype cranium, and their ventral surfaces are visible (Fig. 30C). The bulla of *Z. donnamatsonae* resembles those of all other described species of the Allodelphinidae by being relatively large, having an inflated outer lip that has a relatively smooth ventral surface, and an elongated and pointed anterior process.

The large, globose outer posterior prominence is separated from the smaller and rugose inner posterior prominence by an interprominential notch. The inner posterior prominence extends farther posterior than does the outer posterior prominence. The medial furrow extends anteriorly from the interprominential notch for the length of the bulla. The involucrum is nearly straight, being aligned with the lateral side of the basioccipital crest, and the outer lip of the bulla is smooth and inflated.

Zarhinocetus errabundus **(Kellogg, 1931)**

Figures 31-36, 37D, 38D, 39E, Table 1

Squalodon errabundus Kellogg, 1931:373; as a species of Squalodontidae. Mitchell and Tedford, 1973:270.

"*Squalodon*" *errabundus* Kellogg, 1931. Barnes, 1977:327, table 3; as a species of Platanistidae.

"*Squalodon*" *errabundus* Kellogg, 1931. Barnes, 2006:31-34; as a species of Allodelphinidae.

Zarhinocetus errabundus (Kellogg, 1931). Barnes and Reynolds, 2009:488, fig. 4, new combination; Barnes, Godfrey, and Kimura, 2010:450, 452, 463, figs. 2, 3; Thomas and Barnes, 2015:21, figs. 17, 18.

Emended diagnosis of species. A species of the genus *Zarhinocetus*, differing from *Z. donnamatsonae* by being larger as adult, and by having cranium with dorsal opening of mesorostral canal transversely narrower in posterior part of rostrum anterior to nares, fossa in dorsal surface of base of rostrum deeper, tuberosity on maxilla anterior to antorbital notch larger, crest on dorsal surface of supraorbital process of maxilla more prominent, facial surfaces wider transversely, dorsal nares narrower transversely, mesethmoid septum between narial passages lower and not extending dorsally above margin of nares, posterior end of mesethmoid septum between nares narrower approaching nares, not flaring laterally, tubercles of bone representing remnants of turbinate bones adjacent to olfactory foramina smaller, nasal bones narrower transversely, postorbital process of frontal smaller, fossa in posterior part of maxilla lateral to cranial vertex deeper and wider, zygomatic process of squamosal dorsoventrally thicker, shorter, and more inflated, nuchal crest thicker and more prominent, occipital shield larger with prominent dorsolateral corners, occipital condyles relatively and absolutely of larger size, basioccipital crests proportionally larger and transversely thicker.

Holotype. USNM 11573, isolated left petrosal, collected by Charles Morrice in 1924.

Type locality. CAS locality 905, in the Sharktooth Hill Bonebed "on a hill west of Round Mountain, locally known as one of the Shark Tooth Hills. Near latitude 35° 28' North, and longitude 119° 27' West, about 6.5 miles northeast of Bakersfield, 4 miles east of the Kern River Oil Field and 0.5 miles north of Kern River, Kern County, California. Section 25, Township 28 South, Range 28 East, Caliente Quadrangle, United States Geological Survey" (quoted directly from CAS locality catalog).

Referred specimens. USNM 11574, left petrosal collected by Charles Morrice in 1924 at CAS locality 905; LACM 13981, atlas vertebra collected by William Harold Barnes in April 1965 at LACM locality 1625 (field number LG Barnes locality 15); LACM 21031, fused left humerus and ulna collected by Edward D. Mitchell and Camm C. Swift, 19 to 20 August 1963 at LACM locality 1625; LACM 21258, braincase with left petrosal and right tympanic bulla collected by Edward D. Mitchell, Jr., on 8 September 1963 at LACM locality 1625; LACM 119370, atlas vertebra (pathologic) collected by William Hawes, Jr., in January 1977 at LACM locality 3499; LACM 149588, cranium and mandible with associated right petrosal and left tympanic bulla collected by Gregory Art in 1976 at LACM locality 4314 (field number LG Barnes 1818).

Formation and age. All known specimens of *Zarhinocetus errabundus*, including the holotype, are from the middle middle Miocene age Sharktooth Hill Bonebed (named by Barnes, 1977:326–327), a relatively thin stratum with densely packed fossils in the upper part of the Round Mountain Silt, a marine near-shore shelf deposit that crops out to the northeast of Bakersfield, in Kern County, central California, U.S.A. This bonebed is approximately between 14.5 and 16.1 million years old, and is correlated with the Temblor Provisional Provincial mega-invertebrate stage of Addicott (1972), the Relizian and/or Luisian foraminiferal stages, and the later part of the Barstovian North American Land Mammal Age (Barnes, 1977; Barnes and

Mitchell, 1984; Tedford et al., 1987:156, 201, fig. 6.2 (chart in pocket); Barnes et al., 2010; Tedford et al., 2004:172, fig. 6.2; Prothero et al., 2008a, 2008b; Pyenson et al., 2009). The Sharktooth Hill Local Fauna (named by Mitchell and Tedford, 1973:fig. 3) is derived from the Sharktooth Hill Bonebed, and is a global standard of comparison for fossil marine vertebrates of its age (Mitchell, 1965:iii; and see Barnes, 1977:326-327; 2006),

Geographic and geochronologic ranges. Middle middle Miocene, eastern North Pacific coast in the area of present-day central California.

Comments. This species was originally named *Squalodon errabundus* by Kellogg (1931) on the basis of two isolated petrosals, USNM 11573 (the holotype, Figure 33A, B), and USNM 11574 (a referred specimen), belonging to two different individuals, both from the Sharktooth Hill Bonebed. Kellogg (1931) stated that *Squalodon errabundus* was the first documented fossil occurrence of a squalodontid from the Pacific coast of North America. Unquestioned squalodontids are known from the North Pacific. Two occurrences include teeth (LACM 17033, 17034) from the earliest Miocene Pyramid Hill Sand in Kern County, California, U.S.A. (Mitchell and Tedford, 1973:270), which is from a lower stratigraphic unit that is exposed farther east than where *Squalodon errabundus* occurs in the Sharktooth Hill Bonebed.

Subsequent to Kellogg’s (1931) publication, a complete cranium and mandible (LACM 149588, Figures 31, 32), and a braincase (LACM 21258) have been collected from the Sharktooth Hill Bonebed. Each of these was found with a petrosal lying adjacent to its basicranium. These petrosals (Figures 33C-J) are both conspecific with the holotype, USNM 11573, of *Squalodon errabundus*. However, the crania are unquestionably those of allodelphinid platanistoids, not of squalodontids.

Therefore, *Squalodon errabundus* Kellogg, 1931, clearly does not belong in the genus *Squalodon* (see specimens of Squalodontidae in Figure 2 herein; and Kellogg, 1923; Whitmore and Sanders, 1977; Dooley, 2005). For this reason the generic name *Squalodon* has been used in quotation marks when the species *Squalodon errabundus* has been referred to in some previous publications (e.g. Barnes, 1977, 2002, 2006).

No genus had been proposed that was appropriate for this species, and for this reason the new genus *Zarhinocetus* was

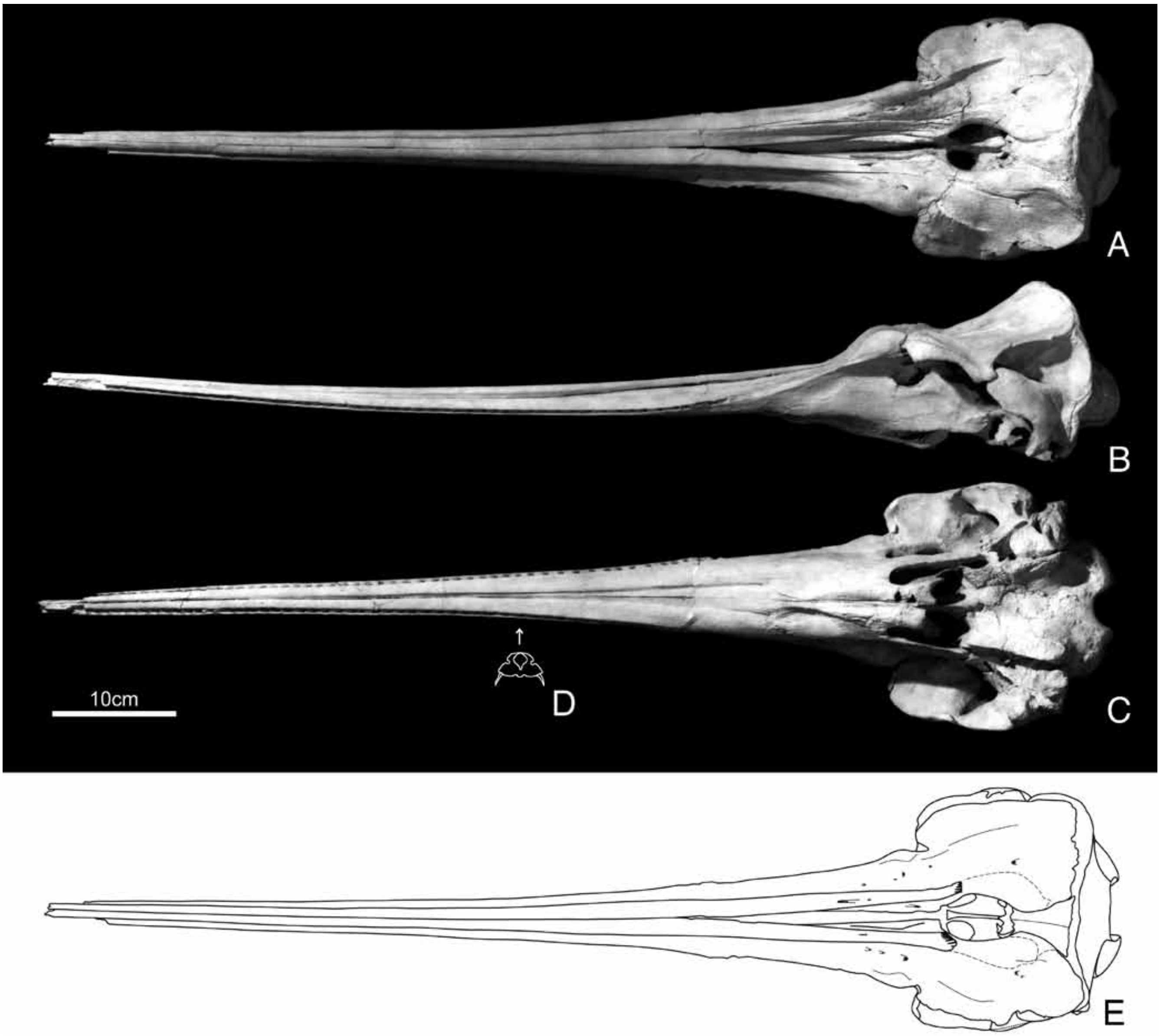

Figure 31. *Zarhinocetus errabundus* (Kellogg, 1931), referred cranium, LACM 149588. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, cross section at mid-length of the tooth row, orientations of teeth are generalized and restored from teeth preserved with the holotypes of *Allodelphis woodburnei* Barnes and Reynolds, 2009, and *Ninjadelphis ujiharai* Kimura, new genus and new species; D, dorsal view, line drawing. Dashed lines indicate the area of the premaxillary sac fossa. Scale bar equals 10 cm. Modified from Barnes and Reynolds (2009).

proposed for it by Barnes and Reynolds (2009), yielding the new combination *Zarhinocetus errabundus* (Kellogg, 1931). Barnes and Reynolds (2009) assigned this species to the extinct platanistoid family Allodelphinidae (and see Barnes et al., 2010). *Zarhinocetus errabundus* is the only species of platanistoid that has been reported from the Sharktooth Hill Local Fauna, and fossils of the species have thus far been reported only from the Sharktooth Hill Bonebed. In contrast to the other species of Allodelphinidae, several specimens of *Z. errabundus* are now known. Thomas and Barnes (2015:fig. 17) presented an image of the articulated cranium and mandible (LACM 149588) of this species, and assigned two atlas vertebrae to it (Thomas and Barnes, 2015:21, fig. 18).

Supplemental description.

Cranium. The partial cranium of the old adult individual, LACM 21258, which lacks its rostrum, shares with the referred complete cranium of the young adult, LACM 149588 (Figures 31, 32) the following species-diagnostic characters: a wide facial surface, large and nearly vertically oriented occipital shield, asymmetrical cranial vertex, oval dorsal nares, very small nasal bones that are fused to the underlying frontal bones, narrow exposures of the frontal bones on the cranial vertex, anteroposteriorly aligned supraorbital maxillary crests, posterior ends of the premaxillae retracted anteriorly to a location anterolateral to the nares, dorsal surface of each premaxilla depressed anterior to the nares, lateral side of the rostrum expanded laterally anterior to the antorbital notch and bearing a hemispherical tuberosity, zygomatic process of the squamosal nearly rectangular in lateral view, glenoid fossa facing anteroventrally, posterior part of the palatal surface convex.

The rostrum of LACM 149588 is essentially complete to its anterior-most extremity, is long, relatively narrow, and slightly dorsoventrally compressed. The suture between the maxilla and the premaxilla is fused for a distance of approximately 50 mm at the anterior tip of the rostrum. An anteroposteriorly elongate sulcus on the lateral side of the rostrum follows the line of the suture between the maxilla and the premaxilla. In approximately the anterior three-fourths of the rostrum, the mesorostral canal is closed over by the right and left premaxillae, with the premaxillae therefore in contact at the midline. The mesorostral canal is open dorsally only in its posterior one-fourth. In this species the mesorostral canal is more closed over dorsally than in any other allodelphinid. In the posterior part of the rostrum the surface is deeply depressed, forming a fossa that is deeper than that of *Z. donnamatsonae*. Because of this fossa, the dorsal surfaces of the premaxillae slope very steeply medially toward the mesorostral canal. The lateral edge of each premaxilla is elevated along its lateral margin to the extent that it forms an elongate crest.

As in *N. ujiharai* and *Z. donnamatsonae* the posterior ends of the premaxillae are retracted anteriorly, away from the cranial vertex, and they have thin and irregular posterior ends. In *N. ujiharai* each premaxilla terminates lateral to the dorsal naris; in *Z. errabundus* each premaxilla terminates farther anteriorly, at a point more near the anterolateral corner of the naris. The premaxillary foramen is very small and is concealed in a furrow in the dorsal surface of the premaxilla. A narrow anteromedial sulcus emanates from the foramen. Because the dorsal surface of the posterior end of the premaxilla has been greatly modified, the posterolateral and posteromedial sulci no longer exist. Other species of allodelphinids retain the posterolateral sulci but have lost the posteromedial sulci.

Anteromedial to the antorbital notch, where the dorsal surface of the maxilla is depressed, there are several scattered anterior dorsal infraorbital foramina. In the proximal part of the rostrum, immediately anterior to the antorbital notch, the lateral edge of the rostral maxillary is formed as a thin, relatively sharp-edged shelf, and this shelf extends laterally. The dorsal surface of the maxilla here slopes ventrolaterally relative to the plane of the rostrum. A similar lateral expansion of the maxilla at the basal part of the rostrum is characteristic of such primitive Oligocene odontocetes as *Agorophius pygmaeus*, see Fordyce, 1981; *Waipatia maerewhenua* Fordyce, 1994; and *Xenorophus sloanii*, see Whitmore and Sanders, 1977). There is a similar lateral expansion of the maxilla in *Allodelphis pratti*. In *Z. errabundus*, however, the same laterally projecting shelf of the maxilla has in addition the enlarged, oval-shaped tubercle of bone on its dorsal surface (Figures 31B, 32A, B), and this is an autapomorphy that this species shares, among the Allodelphinidae, only with *Z. donnamatsonae*.

The supraorbital process of the frontal is prominent and thickened dorsoventrally, in contrast to the more primitive character state of other species of Allodelphinidae, which have a dorsoventrally relatively thin supraorbital process. In *Z. errabundus* the lateral margins of the supraorbital processes do not converge anteriorly as much as they do in *A. pratti*, *A. woodburnei*, *G. oregonensis*, and *N. ujiharai*, but are more nearly parallel to one another. Thus, *Z. errabundus* has a rather prominent antorbital process.

The diameter of the bony orbit of *Z. errabundus* is relatively large, larger than it is in the other species of Allodelphinidae. The orbit is more inclined anteriorly than it is in other allodelphinids. The antorbital process of the frontal is thick. The postorbital process of the frontal is short and broad, and overlaps the lateral side of the anterior end of the zygomatic process of the squamosal.

The cranial vertex is much modified. It is asymmetrical, being skewed to the left side, with the sutures between the right and left frontals being on the left side of the mid-line of the cranium. The right and left halves of the nuchal crest are asymmetrical. The right half of the crest is wider than the left. The left half of the crest curves more anteriorly onto the facial surface than does the right. The dorsal exposures of the frontal bones are slightly convex and relatively smooth. The maxillae curve toward the vertex on each side, forming a broad arc where they contact the frontals.

The nasal bones are fused to the frontals, making it difficult to determine their exact borders. They are very small, rugose, constricted mediolaterally and, unlike other allodelphinids, they descend into the posterior side of the dorsal nares.

The dorsal nares are oval shaped, taper posteriorly, and the left naris is slightly larger than the right.

The lacrimal bone is relatively large. It is exposed in dorsal view in a small, obliquely oriented area at the anterior corner of the supraorbital process. This dorsal exposure of the lacrimal is smaller than in *N. ujiharai*. On its ventral side is the base of the zygomatic process of the jugal, fused to the lacrimal at the posterolateral side of the antorbital notch. There is no fossa on the ventral side of the supraorbital process of the frontal, thus no osteological indication of the presence of an antorbital lobe of the pterygoid sinus. The tract for the optic nerve is not very distinct; it does not occupy a well-defined groove as is typical of most odontocetes. There is no fossa posterior to the optic nerve tract that would have housed a postorbital lobe of the pterygoid sinus.

The palatal surfaces of the maxillae on the rostrum are essentially flat transversely, with a deep channel on the mid-line separating them. This channel widens posteriorly, and at its posterior end, where the maxillae meet the palatines, there is on each side a posterior palatine foramen that opens into the channel. There is no exposure of vomer bone on the mid-line of the palate. The posterior part of the palate is broad and convex, particularly where the rostrum deepens and the posterior ends of the tooth rows curve dorsally.

Each palatine bone has a broad, arcuate anterior border that has an irregular suture where it laps onto the corresponding maxilla. Each palatine has a long, slender posterior process on the mid-line between the pterygoids, and this extension extends approximately half of the palatal exposure of the pterygoid. The central part of the palatal exposure of the palatine has a broad and shallow fossa.

The palatal surface of the pterygoid has an anterior extension

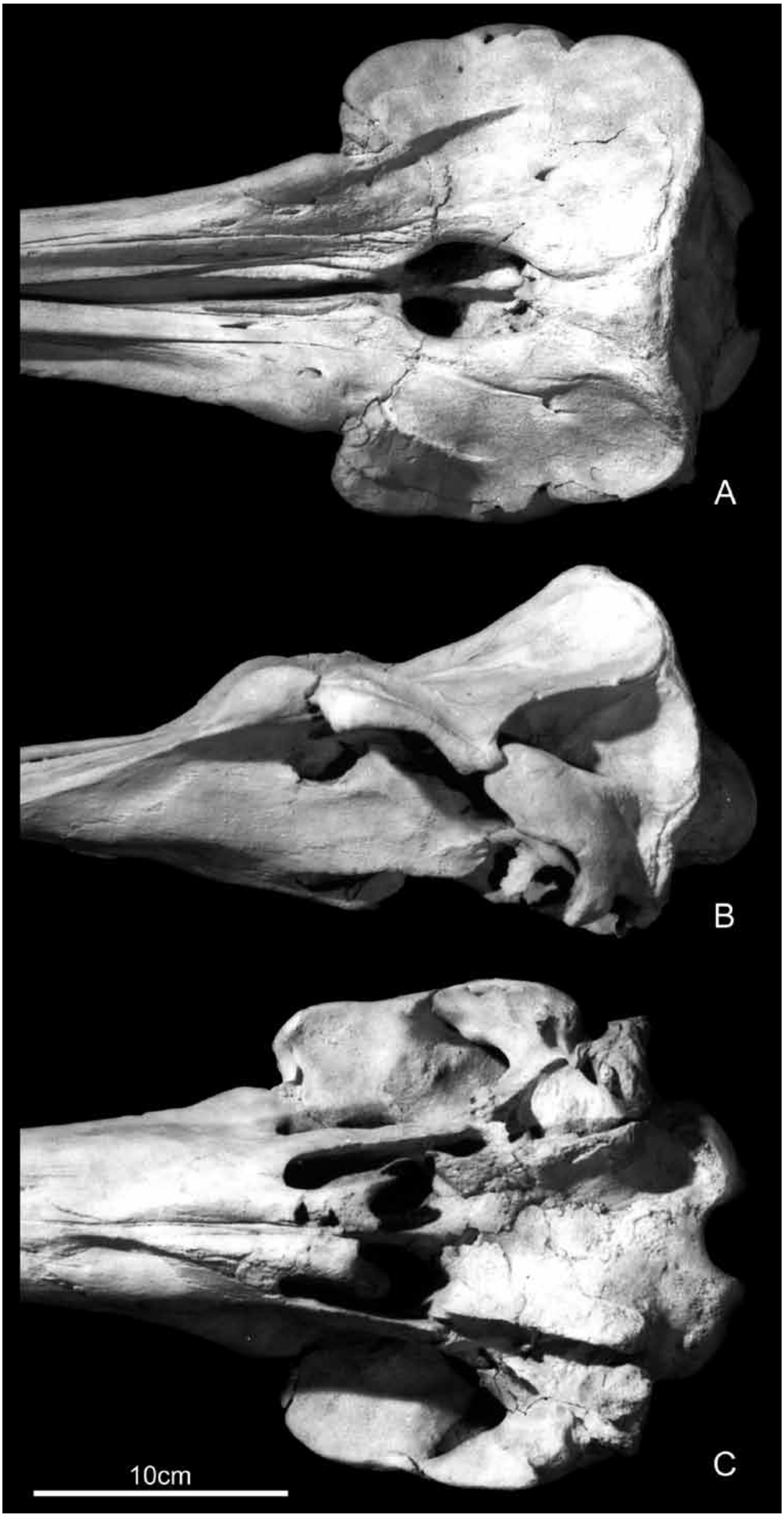

Figure 32. *Zarhinocetus errabundus* (Kellogg, 1931), referred cranium in detail with rostrum omitted, LACM 149588. **A**, dorsal view; **B**, left lateral view; **C**, ventral view. Scale bar equals 10 cm. After Barnes et al. (2010).

toward the palatine, and houses an anteroposteriorly elongate and dorsoventrally deep pterygoid sinus fossa. This fossa has a broad, U-shaped opening that faces ventrolaterally. The hamular process is broken on the right side, but essentially complete on the left side, missing perhaps one mm of bone from its tip. Like that of *Z. donnamatsonae*, it is located on the medial part of the pterygoid, adjacent to the mid-line, and is solid, finger-like in shape, and arises from a solid part of the pterygoid that is not excavated by the pterygoid sinus. The hamulus differs from that of *Z. donnamatsonae* by being shorter and directed posteromedially rather than posteriorly. As in other allodelphinids, the lateral lamina of the pterygoid is a thin membrane of bone, less than 1 mm thick, that extends from the palate posteriorly, forming a wall of bone spanning between the orbit and the naris, and connecting broadly with the anterior falciform process of the squamosal. Approximately mid-length in this span, its lateral exposure, facing toward the orbit, measures approximately 13 mm dorsoventrally.

Also, as in other allodelphinids, a posterior extension of the palatine bone into the medial part of the orbit forms a thin, vertically expanded lamina, approximately 1 mm thick, and is approximately more than twice the dorsoventral height of the lateral lamina of the pterygoid. This plate of the palatine bone overlaps, and is connected to, the dorsal edge of the pterygoid. It terminates in the posterior part of the orbit, where it has a digitated suture upon the lateral lamina of the pterygoid, and it does not extend far enough posteriorly to contact the anterior falciform process of the squamosal.

The zygomatic process of the squamosal is relatively large. The anterior part of this process is nearly rectangular in lateral view, and is inclined anteriorly, in this way differing from the arc-shaped process of *A. woodburnei*, *N. ujiharai*, or *G. oregonensis*. The glenoid fossa faces anteroventrally, as it does in *A. pratti*, rather than facing anteriorly as it does in *A. woodburnei* or anteromedially as it does in *N. ujiharai*. The tympanosquamosal recess is very shallow and has a smooth surface. The temporal fossa is relatively small, and narrows anteriorly. The lateral edge of the maxilla arches dorsally over it, and the temporal crest at its posterior side is slightly curved posteriorly.

The occipital shield is nearly vertical in its orientation and relatively smooth. The occipital condyles are proportionally very large, and they project straight out posteriorly from the occipital shield. The paroccipital processes are relatively smaller than in *N. ujiharai*. As in *A. pratti*, *G. oregonensis*, and *N. ujiharai*, there is no fossa for a posterior sinus in the anterior face of the

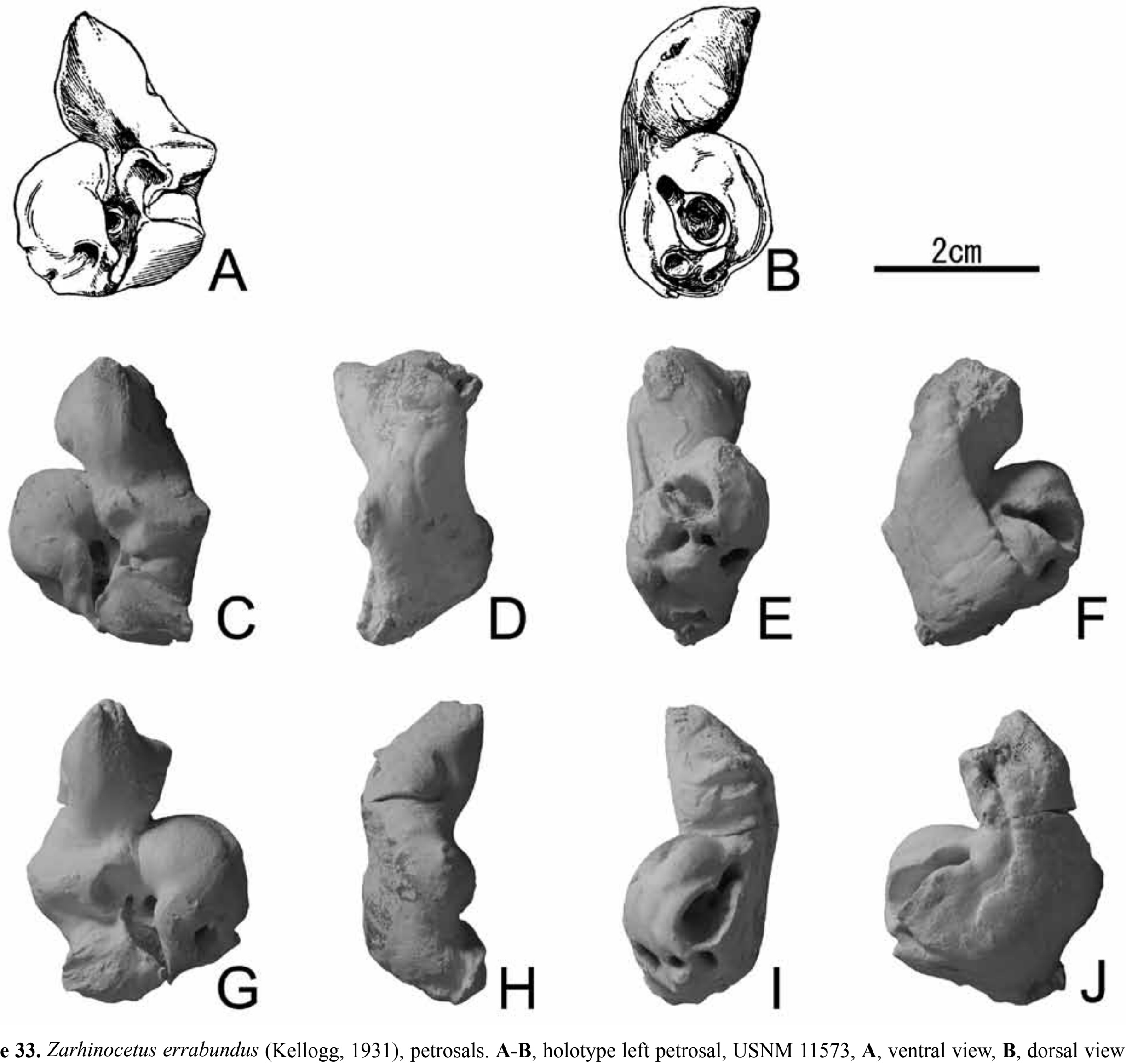

Figure 33. *Zarhinocetus errabundus* (Kellogg, 1931), petrosals. **A-B**, holotype left petrosal, USNM 11573, **A**, ventral view, **B**, dorsal view; **C-J**, petrosals found associated with referred crania LACM 21258 and 149588. **C-F**, LACM 21258, left petrosal, **C**, ventral view; **D**, lateral view; **E**, medial view; **F**, dorsal view; **G-J**, LACM 149588, right petrosal, **G**, ventral view; **H**, lateral view; **I**, medial view; **J**, dorsal view. Scale bar equals 2 cm; A and B from Kellogg (1931:figs. 113-114).

paroccipital process. The ventral extremity of the paroccipital process is not as thick as that of *Z. donnamatsonae*.

Dentition. Damage to the distal end of the rostrum of LACM 149588 prevents determining the exact number of dental alveoli, but a composite between the right and left sides indicates that originally there were approximately 57 alveoli present on each side of the rostrum. The alveoli are closer together near the anterior and posterior ends of the tooth rows, and farther apart in the middle section. No teeth have been found associated with any specimens of *Z. errabundus*, and no isolated teeth from the Sharktooth Hill Bonebed have yet been identified as belonging to this species.

Petrosal. The species *Squalodon errabundus* Kellogg, 1931, was originally based by Kellogg (1931) on the holotype isolated left petrosal, USNM 11573, and a referred partial isolated left petrosal, USNM 11574, both of which were collected from the same locality in the Sharktooth Hill Bonebed. Kellogg (1931:373) explained his referral of this new species to the genus *Squalodon* by writing: "The two ear bones hereinafter described are referred to the genus *Squalodon*, for reasons which are almost indefinable, and yet all known squalodonts have similar peculiarly shaped periotics. The subtle characters that distinguish the periotics of squalodonts from those of other porpoises are apparent to anyone who has studied these bones, although it is difficult to point out any tangible feature which will invariably identify them."

The characters resembling *Squalodon* that Kellogg observed in the periotics when he named *Squalodon errabundus* are primitive characters that are shared by various other species of the superfamily Platanistoidea, the group that is now interpreted as including the family Squalodontidae.

A left petrosal (Figures 33C-F) was found adjacent to the basicranium of the referred cranium of LACM 21258. A right petrosal (Figures 33G-J) was found adjacent to the basicranium of the referred cranium LACM 149588. Although neither of these petrosals was located in the correct anatomical position within the cranial hiatus, each of them is concluded to belong to the closely associated cranium. These two petrosals share with the holotype left petrosal, USNM 11573 (Figures 33A-B) an enlarged, obliquely oriented cochlear portion, an enlarged anterior process that has a pointed distal end and is curved medially, a small posterior process with a small and smooth articular facet for the tympanic bulla, a wide cerebral surface lateral to the internal acoustic meatus, and similar sizes and locations of all major foramina.

Kellogg (1931:373) described the holotype (USNM 11573) as having lost the posterior process. The two referred specimens demonstrate that the posterior process of this species is unusually small, and the articular facet for the bulla is also small and relatively smooth, and devoid of grooves and ridges. If the posterior process of USNM 11573 is incomplete as Kellogg wrote, then it is missing only a very small part of its articular surface.

Each of these petrosals of *Z. errabundus* differs from that with the holotype of *Allodelphis pratti* by having a more bulbous anterior process that is curved medially, a larger and more inflated cochlear portion, a smaller posterior process on which the articular facet is directed more laterally, and a broader and more massive lateral tuberosity. The petrosal associated with the old adult cranium, LACM 21258, has a large rugose anterodorsal process on its anterior process that apparently is an age-related feature that is not present on either the holotype or the petrosal that is associated with the young adult cranium, LACM 149588.

Tympanic bulla. Neither tympanic bulla of this species is completely preserved. The left bulla (Figures 34E-H) associated with the young adult cranium, LACM 149588, is the more complete of the two, but lacks the edge of the outer lip and the posterior process. The right bulla (Figures 34A-D) that was found associated with the referred old adult cranium, LACM 21258, is less complete.

These bullae, like those of other species of Allodelphinidae, are relatively large, and have a pointed anterior spine and a large

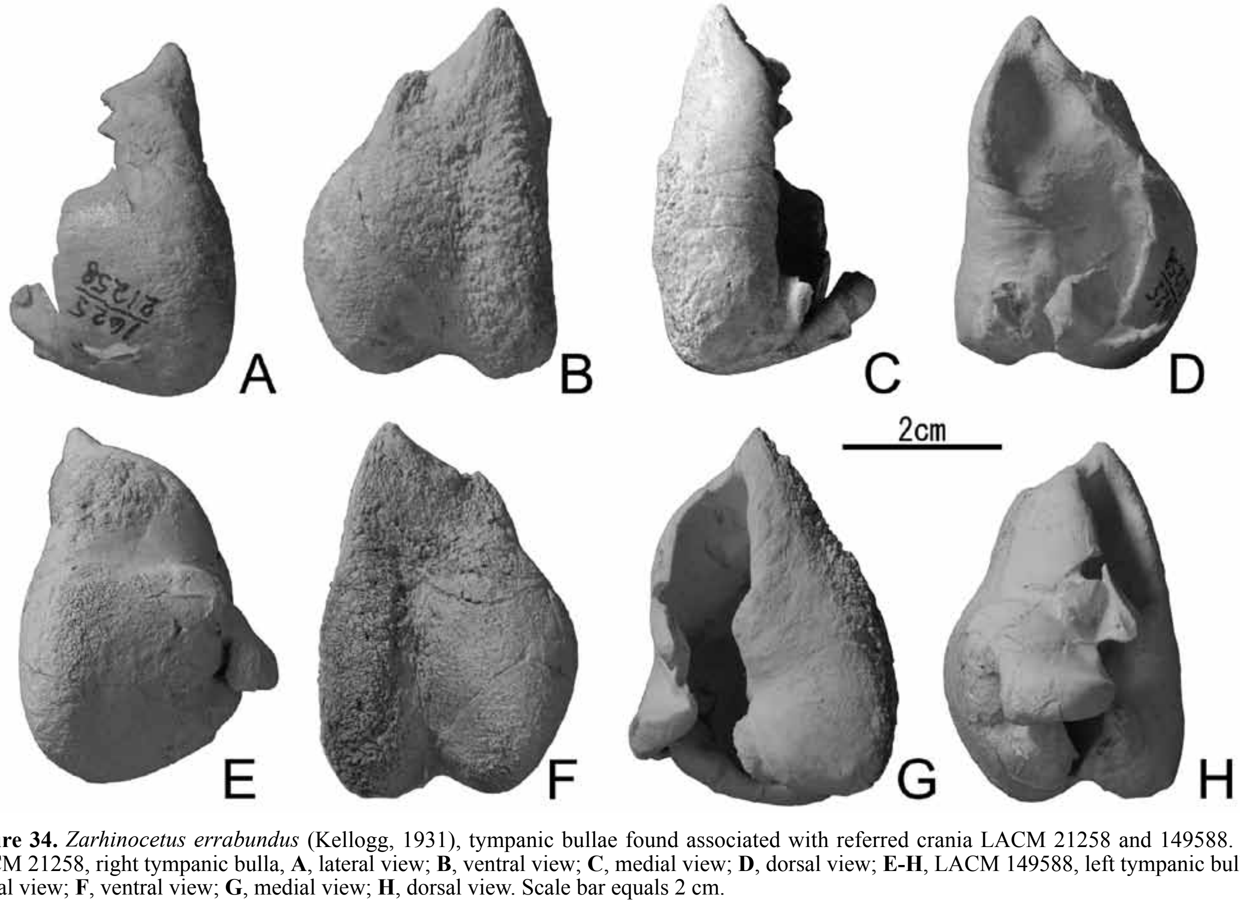

Figure 34. *Zarhinocetus errabundus* (Kellogg, 1931), tympanic bullae found associated with referred crania LACM 21258 and 149588. **A-D**, LACM 21258, right tympanic bulla, **A**, lateral view; **B**, ventral view; **C**, medial view; **D**, dorsal view; **E-H**, LACM 149588, left tympanic bulla, **E**, lateral view; **F**, ventral view; **G**, medial view; **H**, dorsal view. Scale bar equals 2 cm.

outer lip. The anterior spine is blunt like that of *N. ujiharai*, not sharp like that of *A. pratti*. The ventral surface of the bulla is less rugose than in both *N. ujiharai* and *Z. errabundus*. The outer lip is more inflated than in both of those species (Figures 23, 34), and in the sequence *A. pratti* ➡ *N. ujiharai* ➡ *Z. errabundus* the outer lips of the bullae are progressively more inflated. The sigmoid process is directed laterally, as it is in *N. ujiharai*, rather than posterolaterally, as it is in *A. pratti*. The posterior processes are broken off of both bullae of *Z. errabundus*, but because the posterior process of the petrosal is small in this species, the posterior process of the bulla was probably similarly small and short.

Mandible. The nearly complete mandible (Figure 35) was found with the referred cranium, LACM 149588, of *Z. errabundus*. The fused right and left dentaries are firmly ankylosed along the mandibular symphysis, but the location of the symphyseal suture remains visible as a narrow line on the mid-line of the ventral surface of the mandible and as a slight ridge in a sulcus along the midline of the dorsal surface of the symphysis. This line marking the symphyseal suture is clearly visible for its entire length.

The symphyseal portion of the mandible is slightly flattened dorsoventrally (Figure 35D), and it curves slightly dorsally in its anterior part, conforming to a slight dorsal curvature of the distal part of the rostrum. The anterior extremity of the mandible is broken off, but when complete it certainly reached to the anterior end of the rostrum. It was likely not shorter than the rostrum, as is the case in members of the family Eurhinodelphinidae (see Abel, 1905).

The dentary is comparatively slender and delicate anteriorly, and this contrasts with its dorsoventral depth posteriorly. On the lateral side of the dentary is an elongate sulcus that extends the full length of the symphyseal part of the mandible. This sulcus is positioned toward the ventral margin of the dentary, and it extends posteriorly to slightly beyond the level of the posterior end of the symphysis, where it expands and fades out onto the lateral side of the ascending ramus of the dentary. This sulcus is relatively deep, as it is in *N. ujiharai*, and contrasts with the shallower sulcus of *A. woodburnei*.

The ascending ramus is very deep dorsoventrally, and thin transversely, forming the area that is termed the acoustic window. The medial side is excavated by a large mandibular fossa. This thin area of the dentary allows transmission of sound to the ear during echolocation.

The ventral border of the ascending ramus is slightly convex. The angle of the dentary is deep, and nearly square in lateral view. The dorsal margin of the coronoid crest is sharp and slightly convex. There is a depression in the dorsal margin anterior to the thickened apex of the coronoid process. The mandibular condyle is prominent and directed posteriorly, and the articular surface is large and nearly hemispherical.

The right dentary has at least 49 dental alveoli preserved, and the left has at least 51. It appears that two to four alveoli were present in the now missing anterior end of the right dentary, and that one to three more were present in the broken anterior end of the left dentary. Thus, the lower tooth count may have been 51 to 54 teeth per side. The alveoli are closer together near the anterior and posterior ends of the tooth rows, and farther apart in the middle section.

Atlas. Thomas and Barnes (2015:21, fig. 18) assigned two isolated atlas vertebrae to *Z. errabundus*: an atlas of an old adult, LACM 13981; and a pathologic atlas of a younger individual, LACM 119370. These were the first postcranial bones to be

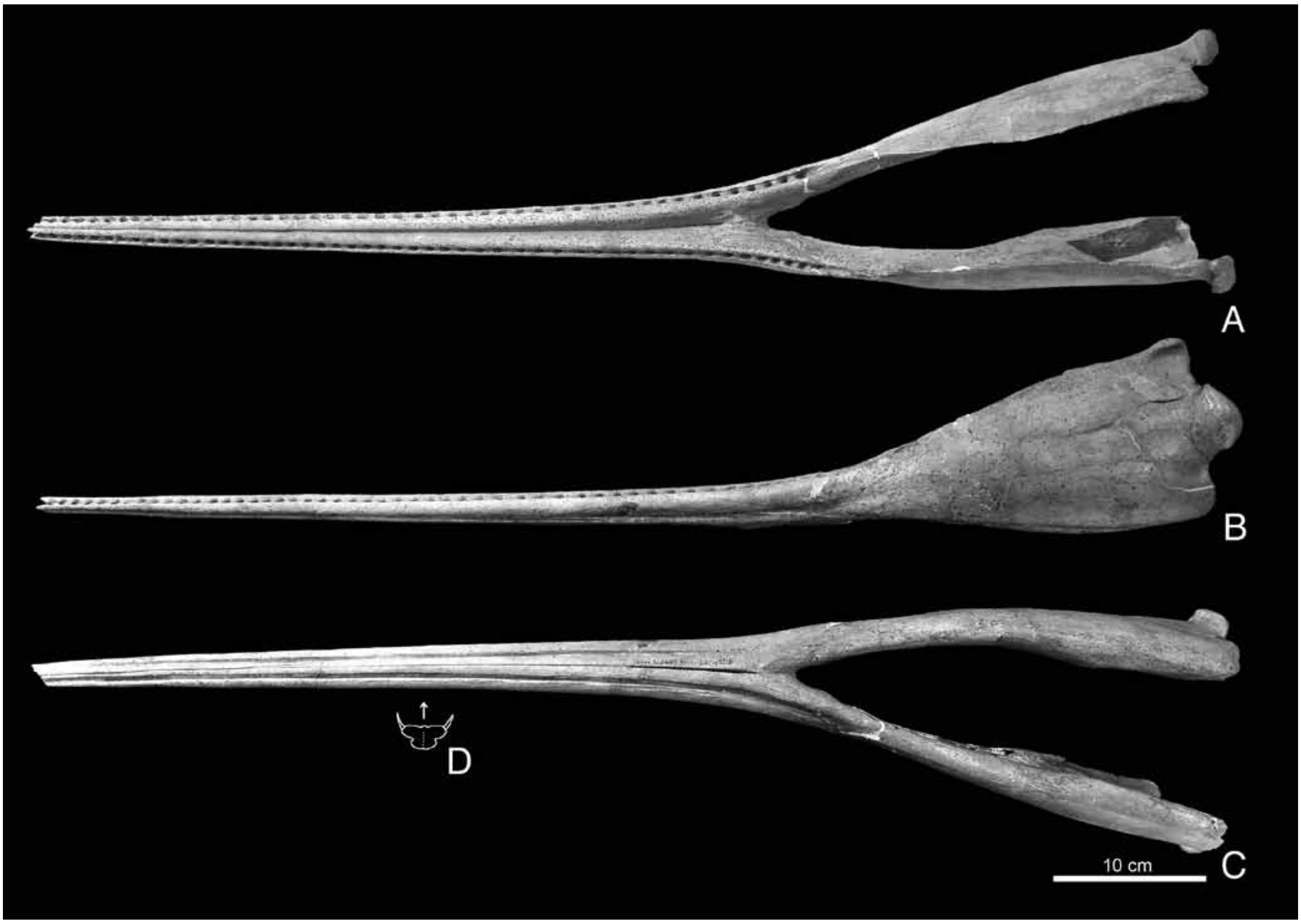

Figure 35. *Zarhinocetus errabundus* (Kellogg, 1931), mandible, LACM 149588. **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, cross section at mid-length of the symphyseal region, orientations of missing teeth are generalized and restored from teeth preserved with the holotype of *Allodelphis woodburnei* Barnes and Reynolds, 2009, and *Ninjadelphis ujiharai* Kimura, new genus and new species. Scale bar equals 10 cm.

referred to this species,

The identification of the cranium, LACM 21258, as belonging to an old adult of *Z. errabundus* allowed assignment to this species of atlas vertebra, LACM 13981 (Thomas and Barnes, 2015: figs. 18 A, C-D), which is also of an old adult individual. This atlas articulates correctly with the occipital condyles of cranium LACM 21258, and it is possible that the two belong to the same individual, because they were fossilized relatively near one another, being excavated only a few meters apart in the Sharktooth Hill Bonebed.

This atlas measures 121 mm across the anterior articular surfaces, approximately 149 mm across the ventral transverse processes, both of which are incomplete at their apices, and 178 mm in maximum anteroposterior dimension across the articular facets.

The smaller atlas, LACM 119370, is extensively remodeled because of its pathologies, but it shares with the atlas LACM 13981 such characters as separate and enlarged dorsal and ventral transverse processes, relatively large and widely-spaced anterior articular facets for the occipital condyles that have prominent and flaring lateral margins, a large fovea to accommodate the relatively large odontoid process of the axis vertebra, and large transverse foramina. This pathologic atlas differs from the normal one by being smaller overall and relatively shorter anteroposteriorly. Its transverse processes are broken off, and their original sizes thus cannot be determined. It likely belonged to a subadult individual of the species.

The atlas of *Z. errabundus* shares with those of *A. pratti*, *G. oregonensis*, and *N. ujiharai* proportionally large size compared to the cranium, unusual anteroposterior length, dorsoventral compression resulting in a transversely wider neural canal, presence of separate dorsal and ventral transverse processes, posterolaterally flaring dorsal transverse process, a large fovea for reception of the odontoid process of the axis, anteroposteriorly wide pedicles, each of which bears a large-diameter vertebrarterial foramen, and an anteroposteriorly long but very low spinous process.

The atlas of *Z. errabundus* differs from that of *A. pratti* by being absolutely and relatively larger, by having a larger and more dorsoventrally expanded dorsal transverse process, and by having the vertebrarterial foramen opening more laterally rather than facing dorsally. In these differences *Z. errabundus* is likely more derived.

The atlas of *Z. errabundus* differs from that of *N. ujiharai*, in addition to also being absolutely and relatively larger, by having a shorter ventral transverse process. The latter is likely a plesiomorphic character of *Z. errabundus*.

Humerus. The left humerus (LACM 21031) of *Z. errabundus* is shown in Figure 39E. It is referred to *Z. errabundus* because of similarities it shares with the humeri of *Allodelphis pratti*, *A. woodburnei*, and *Ninjadelphis ujiharai*: relatively large size in proportion to the cranial length, relatively small and spheroid head that is directed caudally from the diaphysis, greater tuberosity that does not extend proximal to the head, elongate diaphysis that is oval in cross rather than flattened medio-laterally, absence of an enlarged deltopectoral tuberosity, and distal articular facet for the ulna not distinctly divided into two facets.

This humerus measures 214 mm in maximum proximodistal length, 43 mm in transverse (medio-lateral) thickness of the diaphysis at mid-shaft, and 61 mm in the cranio-caudal (anteroposterior) width of the diaphysis at the mid-shaft. Its proximal epiphysis is fused to the diaphysis on the medial side of the bone, but at the time of death had not become entirely

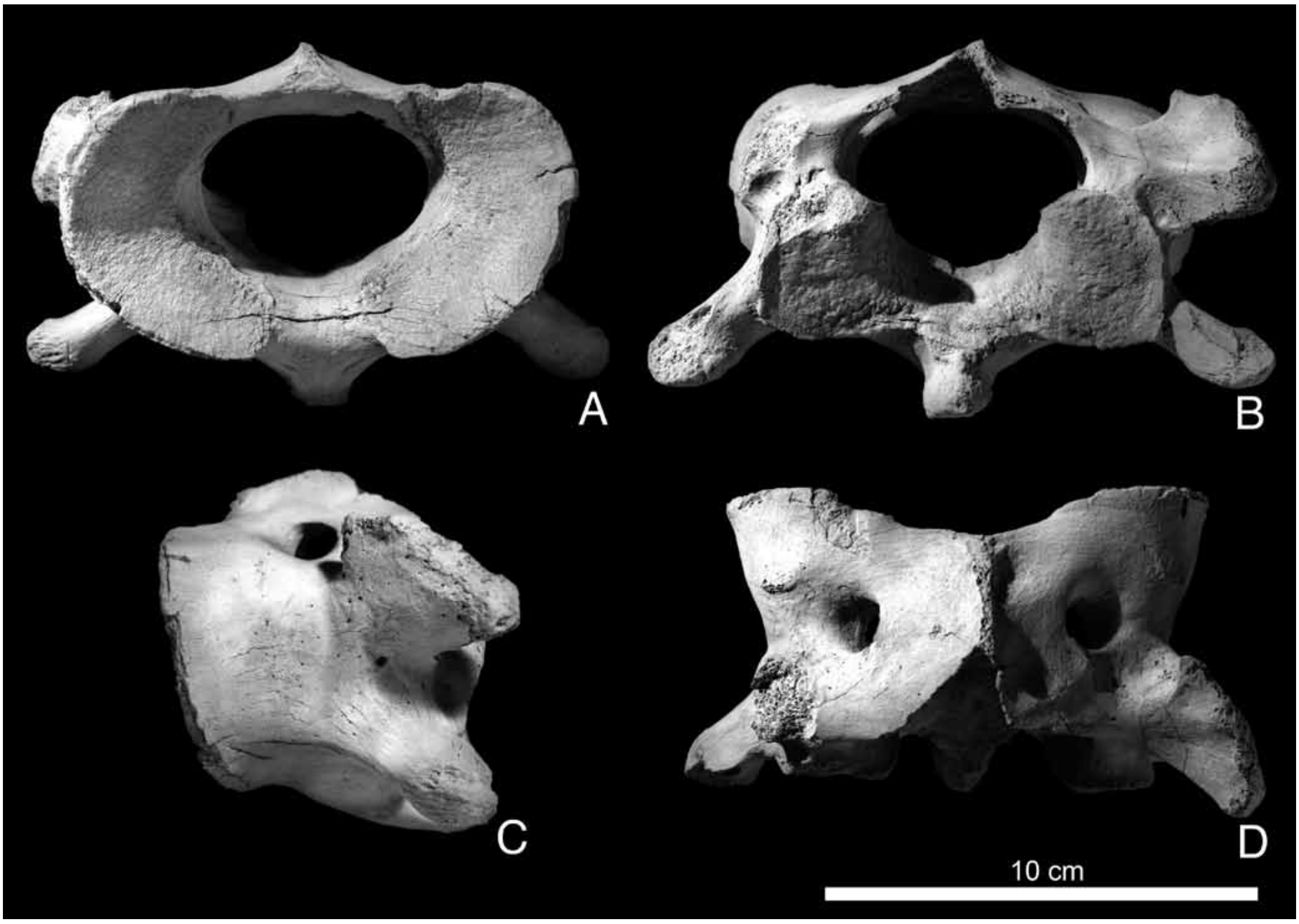

Figure 36. *Zarhinocetus errabundus* (Kellogg, 1931), referred atlas vertebra, LACM 13981. **A**, anterior view; **B**, posterior view; **C**, left lateral view; **D**, dorsal view. Scale bar equals 10 cm.

fused on the lateral side, and the distal epiphyses are both fused to the diaphysis, thus indicating the individual had reached adulthood but was not an old adult. The diaphysis is proximodistally relatively elongate for a cetacean. The fossa that exists in most cetaceans on the anterior part of the diaphysis, located proximal to its mid-length, is nearly indistinct on this humerus, being represented only a slight depression.

On the referred humerus of *Allodelphis pratti*, UCMP 83791 (Figure 39A), this same fossa is much deeper, indicating that reduction of this fossa is apomorphic for *Z. errabundus*. The distal trochlear surface for articulation with the ulna is abruptly inclined proximally, and it has only a very slight separation into two facets. This is unlike the condition in species of the superfamily Delphinoidea, in which a prominent transverse ridge exists, which divides the trochlea for the ulna into two distinct planes or articular facets.

The humeral head is slightly ovoid anteroposteriorly, measuring 61 mm mediolaterally and 69 mm anteroposteriorly, and its posterior margin projects beyond the posterior border of the diaphysis. The proximal surface of the greater tuberosity is approximately 25 mm lower than the proximal surface of the humeral head.

Ulna. An ulna was collected from the same locality as the humerus, LACM 21031, which is described above. It was excavated near the humerus, but it was given a separate field number when it was found. Later, during curation of the collection, it was noticed by Barnes that the two bones fit together by virtue of a subsequently broken area that had become fused in life. Therefore, in the LACM collection the humerus and ulna are now glued together and have the same specimen catalog number.

When this ulna and its corresponding humerus are thus joined (Figure 39E), they are very similar to the fused referred humerus and ulna of *Allodelphis pratti* (UCMP 83791) (Figure 39A). When compared to the forelimb of *A. pratti*, the ulna of *Z. errabundus* is notably much shorter than the humerus. Its maximum proximo-distal length is approximately 155 mm, taking into consideration that it is missing the distal epiphysis and the olecranon process is fused to the humerus. The proximal end of the olecranon process of the ulna is so firmly fused to the humerus that when the two bones broke apart, part of the olecranon process remained attached to the humerus (Figure 39E).

The diaphysis of the ulna is ovoid in cross section, and in this regard is not so flattened transversely as are the ulnae of delphinoids. Its caudal margin is narrower than its cranial (radial) border. There is a large, rugose, and transversely wide proximal radial facet on the anterior border of the ulna. The olecranon process is relatively small, but thick mediolaterally, and has a convex posterior margin. The olecranon notch is inclined proximally, and the facet for articulation with the humerus is not so markedly divided into two surfaces, as is the case with most odontocetes.

This ulna of *Z. errabundus* differs from that of *A. pratti* (Figure 39A) by having a smaller olecranon process and by being proportionally smaller and shorter proximo-distally in proportion to the humerus. The ulna of the referred specimen, UCMP 83791, of *A. pratti* is nearly equal to the length of its corresponding humerus, whereas the ulna of *Z. errabundus* is approximately 75% of the length of its corresponding humerus. This suggests that through the evolutionary history of the Allodelphinidae, even though the humerus was becoming relatively longer, the

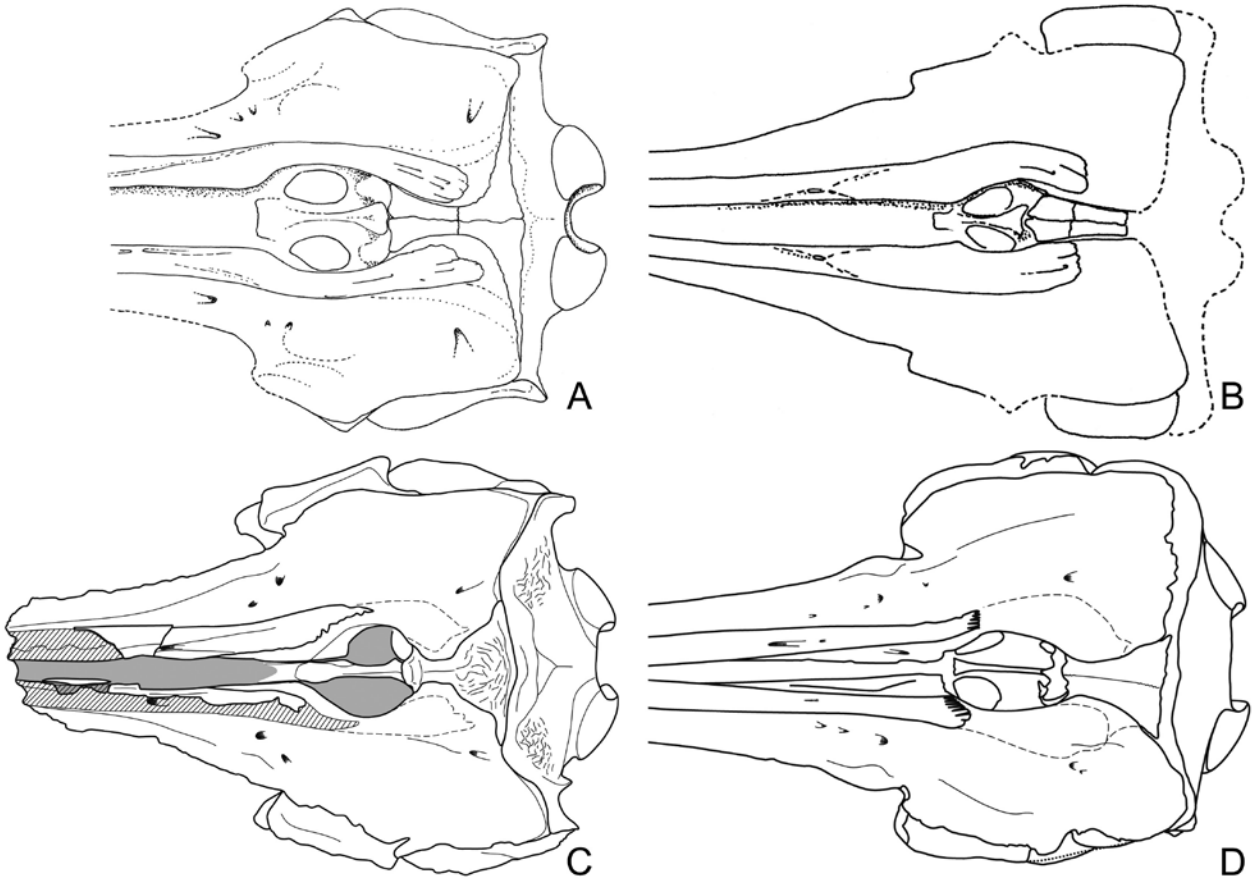

Figure 37. Crania of four species of Allodelphinidae in dorsal views. **A**, *Allodelphis pratti* Wilson, 1935, holotype, YPM 13408; **B**, *Allodelphis woodburnei* Barnes and Reynolds, 2009, holotype, SBCM L3210-1; **C**, *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype, GMNH-PV-2570; **D**, *Zarhinocetus errabundus* (Kellogg, 1931), referred specimen, LACM 149588. All images reduced to the same zygomatic width; A and B after Barnes and Reynolds (2009).

distal part of the forelimb was becoming progressively shorter. The ulna of *Z. errabundus* differs further from that of *A. pratti* by having a more slender diaphysis, a smaller olecranon process, and less curvature of its caudal border.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of the family Allodelphinidae and its position within the superfamily Platanistoidea have been discussed by Barnes (2006), Barnes and Reynolds (2009), and Barnes et al. (2010). Compared to other groups of platanistoids, the allodelphinids possess a suite of very unusual apomorphies, some of them unexpected: very elongated and slender rostrum and mandible, polydonty, near homodonty, progressive reduction of the nasal bones and their ultimate fusion to the frontal bones, progressive anterior retraction of the posterior ends of the premaxillae with development of the premaxillary sac fossa on the maxillary bone, enlargement and anteroposterior lengthening of the cervical vertebrae, enlargement of dorsal and ventral transverse processes on the atlas vertebra, enlargement of the humerus, and fusion of the ulna to the distal end of the humerus. Despite these unusual apomorphies, the Allodelphinidae, are in general relatively primitive and generalized compared to some of the other groups of platanistoids, as demonstrated by the relatively primitive characters of their basicrania, ear bones, and thoracic vertebrae.

The same year that Barnes (2006) presented a cladistic analysis of the Platanistoidea, Fordyce (2006:fig.3, and see p. 764) also provided a tree that was based on other previous analyses. These two authors independently concurred in their recognition of the monophyly of the superfamily Platanistoidea, the monophyly of each of its included families, the placement of the family Squalodontidae, the more crown-ward placement of the family Waipatiidae, the sister relationship between the families Squalodelphinidae and Platanistidae, and interpretation of the extant family Platanistidae as being the crown group.

In the analyses by Barnes (2006) and Barnes et al. (2010), the Allodelphinidae appeared near the base of the tree because of their possession of a relatively primitive braincase, on which the relatively small nares are positioned relatively anteriorly, and the nasal bones are elongate anteroposteriorly and transversely narrow. The members of the family Squalodontidae, while being dentally the most primitive platanistoids, share with the more crown-ward families Waipatiidae, Squalodelphinidae, and Platanistidae, a more telescoped (*sensu* Miller, 1923) cranium on which the nares are enlarged and the nasal bones have become anteroposteriorly shortened and transversely widened.

The families Squalodontidae, Waipatiidae, and Squalodelphinidae demonstrate, in that sequence, progressive simplification of the dentition, reduction in size of the anterior teeth, and coalescing of the roots of the premolars and molars. The families Squalodelphinidae and Platanistidae share such derived characters as a tuberosity or crest on the maxilla over the orbit, the location of the posterior maxillary foramen very close to the posterolateral corner of the ascending process of the premaxilla, and the medial excavation and transverse compression of the zygomatic process of the squamosal. The members of the family Platanistidae have extensions of the pterygoid air sinus into the supraorbital process of the frontal bone. The clade that is represented by the subfamily Pomatodelphininae of the family Platanistidae is notable by dorsoventral compression of the rostrum and the symphyseal part of the mandible, and the clade that is represented by the subfamily Platanistinae of the family Platanistidae is characterized by transverse compression of the rostrum and the symphyseal part of the mandible.

The postulated relationships between the family Allodelphinidae and other cetaceans are represented by the phylogenetic tree that is shown here in Figure 1. The

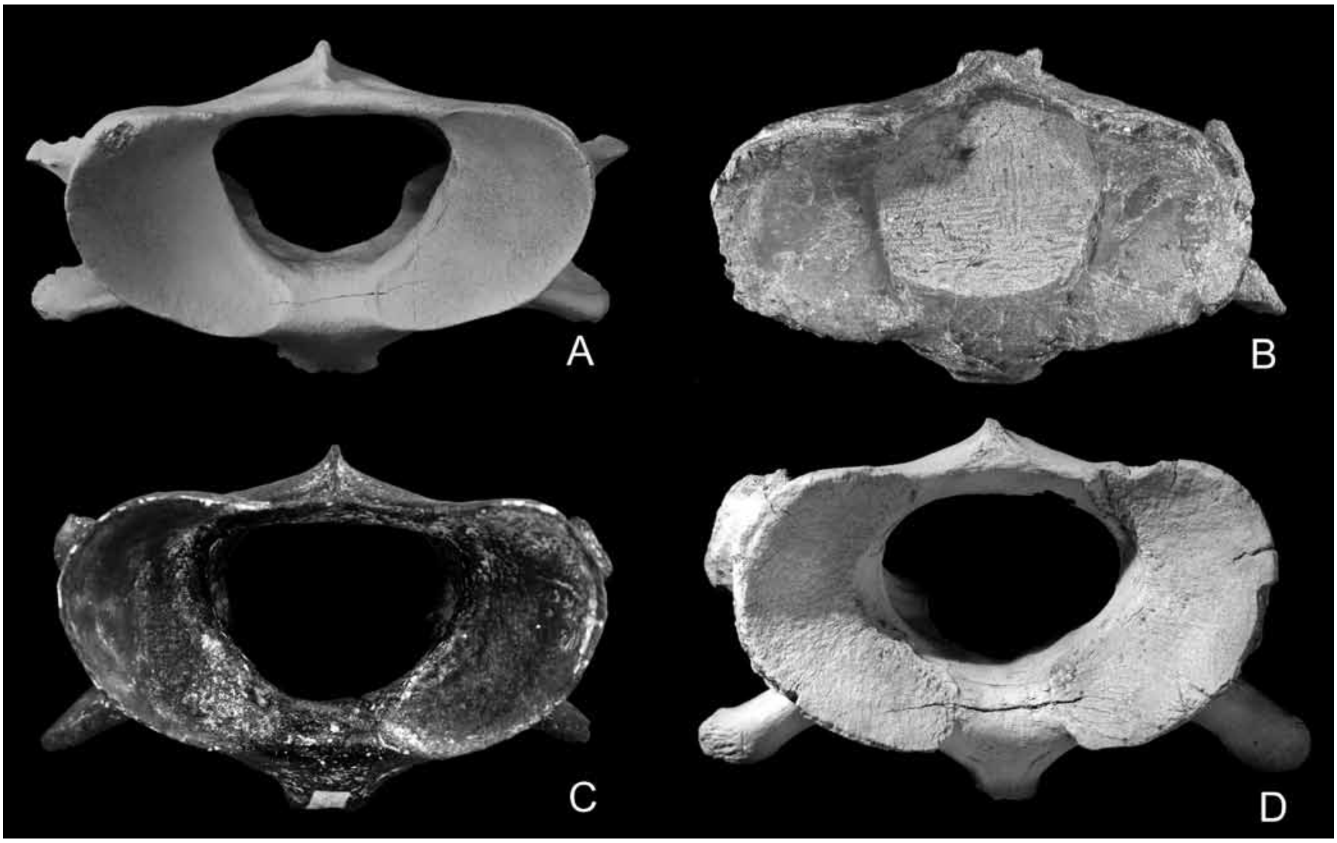

Figure 38. Anterior views of atlantes of species of Allodelphinidae. **A**, *Allodelphis pratti* Wilson, 1935, referred, UCMP 83791; **B**, *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype, GMNH-PV-2570; **C**, *Goedertius oregonensis* Barnes and Kimura, new genus and new species, holotype, LACM 123887; **D**, *Zarhinocetus errabundus* (Kellogg, 1931), referred, LACM 21031. Not to scale.

more primitive cetacean families, the Basilosauridae among the Archaeoceti and Agorophiidae among the Odontoceti, are included, and the postulated relationships are shown with the other currently recognized families within the superfamily Platanistoidea: the Squalodontidae, Waipatiidae, Squalodelphinidae, and Platanistidae.

It is not the intention of this study to undertake an analysis of the phylogenetic relationships between the named species currently assigned to the family Allodelphinidae. It is apparent from the morphological descriptions that are presented in this study, however, that the species that are now known in the genera *Allodelphis* and *Goedertius* are basal allodelphinids. They are more primitive than the later-occurring species in the genera *Ninjadelphis* and *Zarhinocetus* by having relatively smaller adult body size, symmetrical cranial vertices rather than having the vertex skewed asymmetrically to the left side, relatively larger nasal bones that are not fused to the adjacent frontal bones, posterior ends of the premaxillae remaining adjacent to the nasal bones, and smaller nuchal crests.

Of the two currently named species of *Allodelphis*, *A. woodburnei* is more derived than its congener, *A. pratti*, by having the mesorostral canal on the posterior part of the rostrum more closed over by the medial margins of the right and left premaxillae, the dorsal surfaces of the premaxillae depressed anterior to the nares rather than being flat, the premaxillae where they form the premaxillary sac fossae lateral to the nares transversely wider, dorsal narial openings that are smaller in diameter and more elliptically shaped anteroposteriorly, a larger zygomatic process of the squamosal that is more steeply inclined anteriorly causing the glenoid fossa for articulation with the mandibular condyle to face more anteriorly, and by having a humerus that is both relatively and absolutely larger compared to the body size, and which has a larger head and proportionally a more stout diaphysis (Barnes and Reynolds, 2009).

Goedertius oregonensis is more derived than the species of *Allodelphis* by having a depression on the basal part of the rostrum anterior to the nares, narrower premaxillary sac fossae around the narial openings, transversely narrower and thinner posterior ends of the premaxillae, smaller nasal bones that are compressed transversely between the posterior ends of the premaxillae, and more protruding occipital condyles.

Ninjadelphis ujiharai is more derived than both species of *Allodelphis* and *G. oregonensis* by having its cranial vertex asymmetrically skewed slightly to the left side, the exposed areas of the frontal bones on the cranial vertex having a trapezoidal shape and being rugose, the glenoid fossa of the squamosal facing anteromedially rather than anteriorly, the nuchal crest enlarged and partly overhanging the posterior part of the facial surface of the cranium, a wider basioccipital with the basioccipital crests more widely diverging posteriorly, the paroccipital processes larger, the articular facets between the posterior processes of the petrosal and tympanic bulla having two differently-oriented surfaces, the medial margins of premaxillae closer together over the mesorostral canal immediately anterior to the narial openings, the dorsal surface of the proximal part of rostrum depressed, the posterior ends of the premaxillae not extending posteriorly to the position of the nasal bones, but instead retracted anteriorly to a location that is opposite the centers of the dorsal narial openings, the area where the posterior end of the premaxilla formerly existed around the nares formed of smooth, convex, and dense maxillary bone, smaller nasal bones that are fused together at the midline and to the underlying and adjacent frontal bones, and enlarged dorsal and ventral transverse processes on the atlas vertebra.

The species of *Zarhinocetus* are more derived than both species of *Allodelphis* and *Goedertius oregonensis* by having an asymmetrical cranial vertex that is skewed to the left side, smaller nasal bones that are fused to the adjacent frontal bones and, similar to the condition in *N. ujiharai*, the posterior end of each premaxilla retracted anteriorly from the primitive position

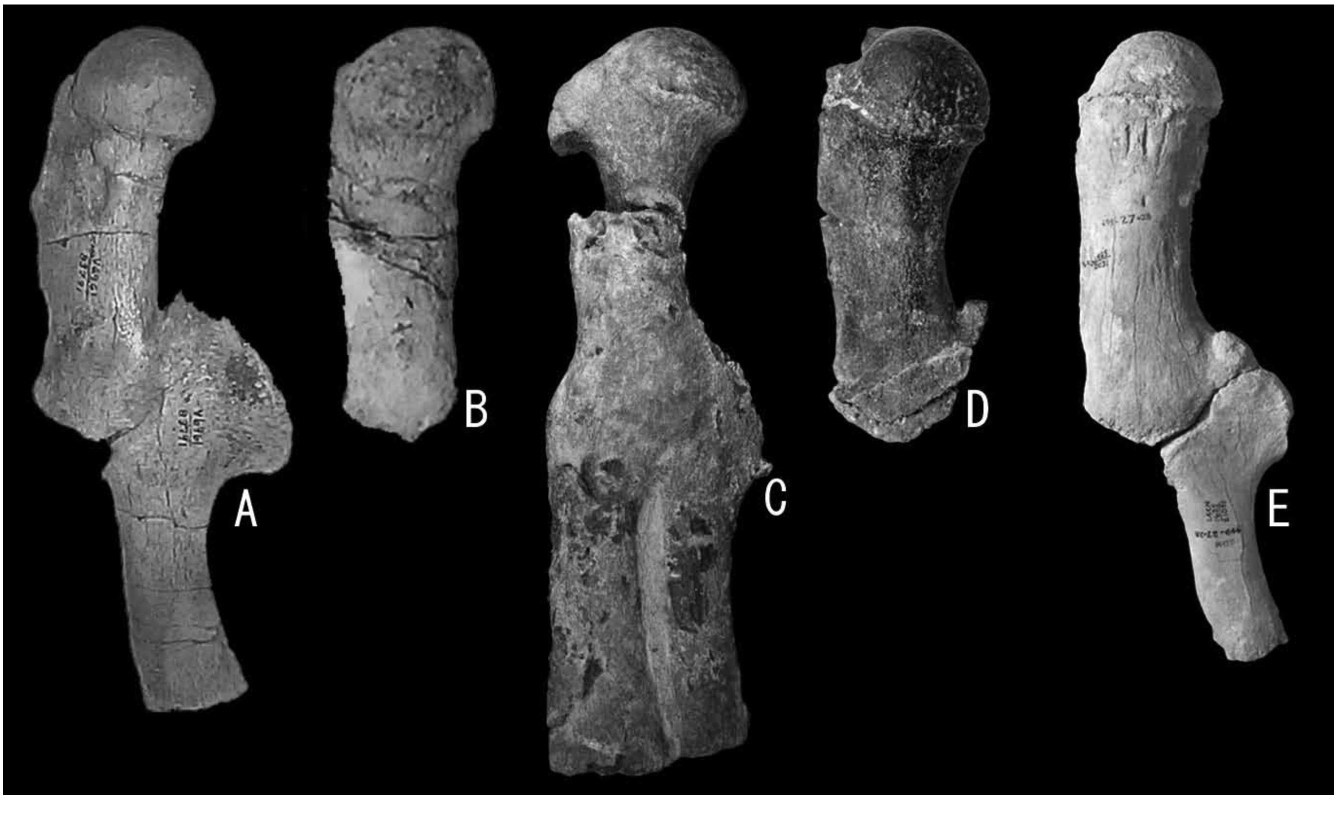

Figure 39. Humeri of species of Allodelphinidae. **A**, *Allodelphis pratti* Wilson, 1935, referred left humerus and ulna (UCMP 83791); **B**, *Allodelphis woodburnei* Barnes and Reynolds, 2009, holotype right humerus (SBCM L3210-1), image reversed; **C**, *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype left humerus, ulna and radius (GMNH-PV-2570); **D**, *Goedertius oregonensis*, new genus and new species, holotype right humerus (LACM 123887), image reversed, **E**, *Zarhinocetus errabundus* (Kellogg, 1931), referred left humerus and ulna (LACM 21031). Modified in part from Barnes and Reynolds (2009). Not to scale.

adjacent to the respective nasal bone.

Species of *Zarhinocetus* differ from all other allodelphinids by having a depression or basin on the dorsal surface of the proximal part of the rostrum, a large tuberosity on the lateral side of each maxilla anterior to the antorbital notch, an anteroposteriorly-aligned crest on each supraorbital process of the maxilla, anterior curvature of the apex of the nuchal crest, and anterodorsally inclined and rectangular shaped zygomatic process of the squamosal. They retain a primitively shaped zygomatic process, on which the glenoid fossa for articulation with the mandibular condyle faces anteroventrally rather than anteromedially, as it does in *Ninjadelphis ujiharai*.

Zarhinocetus donnamatsonae is in some ways intermediate morphologically between the more primitive *Ninjadelphis ujiharai* and the more derived *Zarhinocetus errabundus*. It shares with *N. ujiharai* such primitive characters as the wider dorsal opening of the posterior part of the mesorostral canal, concave margin of the facial region dorsal to the temporal fossa, relatively larger postorbital process of the frontal, and rounded rather than squared occipital shield.

Zarhinocetus donnamatsonae indicates that the clade that includes the later-occurring (middle middle Miocene) allodelphinid *Zarhinocetus errabundus* had a relatively early origin, and that the derived characters of this clade appeared among North Pacific allodelphinids that were contemporaneous with structurally more primitive species of the genera *Goedertius* and *Ninjadelphis*.

Zarhinocetus errabundus is more derived than all other known allodelphinids by being larger, and by having the posterior ends of the premaxillae more anteriorly-retracted, smaller nasal bones that are rendered in most specimens indistinct by virtue of their having fused to the frontals, a more massive nuchal crest, larger occipital condyles, a larger atlas vertebra that has smaller and shorter ventral transverse processes, a humerus that is both relatively and absolutely larger and has a larger head and a proportionally more stout diaphysis, and shortened radius and ulna.

Notably, the six named species of the Allodelphinidae are in many of their structures progressively more derived in approximately the same sequence that they appear geochronologically in the fossil record.

CLASSIFICATION OF THE FAMILY ALLODELPHINIDAE

The following classification of the family Allodelphinidae is derived in part from the classifications and phylogenetic analyses that have been proposed by Barnes (2006) and Barnes et al. (2010), and on the morphological observations presented in this study. It includes the new genera and species, shown in bold text, that are described herein for the first time, and it places them in taxonomic context with the other species of the family. Parentheses indicate names that originally were proposed by authors at different ranks than they are used here, followed by the name of the reviser and the date of publication of that revision.

- Order Cetacea Brisson, 1762
  - Suborder Odontoceti Flower, 1864
    - Superfamily Platanistoidea (Gray, 1846) Simpson, 1945 (including Squalodontoidea (Brandt, 1873) Simpson, 1945
      - Family Allodelphinidae Barnes, 2006
        - *Allodelphis* Wilson, 1935
          - *Allodelphis pratti* Wilson, 1935 (early Miocene, California, U.S.A.)
          - *Allodelphis woodburnei* Barnes and Reynolds, 2009 (early Miocene, California, U.S.A.)
        - ***Goedertius*** **Barnes and Kimura, new genus**
          - ***Goedertius oregonensis*** **Barnes and Kimura, new species** (early Miocene, Oregon, U.S.A.)
        - ***Ninjadelphis*** **Kimura, new genus**
          - ***Ninjadelphis ujiharai*** **Kimura, new species** (late early Miocene, Mie Prefecture, Japan)
        - *Zarhinocetus* Barnes and Reynolds, 2009
          - ***Zarhinocetus donnamatsonae*** **Barnes, new species** (late early Miocene and/or early middle Miocene, Washington State, U.S.A.)
          - *Zarhinocetus errabundus* (Kellogg, 1931) (middle middle Miocene, California, U.S.A.)

ECHOLOCATION ABILITIES

Among cetaceans, the species of Odontoceti are distinguished by the ability to echolocate during navigation and feeding by generating high frequency sounds with the facial muscle complex and the nasal apparatus, and receiving those reflected sounds in the ear by way of the mandible (Norris, 1968; Mead, 1975; Wood and Evans, 1980; Barnes; 1990; Fordce and Barnes, 1994; Au, 2002).

All of the described species of the family Allodelphinidae have a premaxillary foramen in each premaxilla in the proximal part of the rostrum. The premaxillary foramen is an important and diagnostic structure of the Odontoceti (Barnes, 1990; Fordyce and Barnes, 1994; Fordyce et al., 1995; Au, 2002; Mead and Fordyce, 2009:81), and it transmits branches of the infraorbital nerve complex to the muscles of the facial region.

In most odontocete species the premaxillary foramen is approximately centered in the dorsal surface of the premaxilla in the posterior part of the rostrum (Mead and Fordyce, 2009). This foramen is located relatively anteriorly on the rostrum in primitive species (Fordyce, 1981), and farther posteriorly in more derived species (Barnes, 1990) whose crania are more telescoped (Miller, 1923). For example, in extant bottlenose dolphins (*Tursiops truncatus*) it is located just anterior to level of the antorbital notches (Mead and Fordyce, 2009:fig. 1), but in the lophocetine kentriodontid delphinoid *Lophocetus repenningi* Barnes, 1978, it is located posterior to the level of the antorbital notches (Barnes, 1978:fig. 5).

In all four named species of Allodelphinidae the premaxillary foramina are located relatively anteriorly on the rostrum, anterior to the antorbital notches, and this is a primitive character state. These foramina are well defined in species of *Allodelphis*, also a primitive character state. In *N. ujiharai* and *Z. errabundus*, however, they are smaller, and are located within anteroposteriorly aligned fissures in the dorsal surfaces of the premaxillae, and in some specimens partly obscured by bone.

In most odontocetes three sulci emanate from each premaxillary foramen: the anteromedial sulcus, the posterolateral sulcus, and the posteromedial sulcus (Barnes, 1978; Mead and Fordyce, 2009:81). In some species, however, one, two, or all three of these sulci may be shallow, or even absent.

The extent of development of these sulci varies in different species of allodelphinids. In both species of *Allodelphis*, all three of the sulci are present, and this is the primitive character state. In *N. ujiharai* and *G. oregonensis*, however, the posteromedial sulcus is absent, and in *Z. errabundus* both the posterolateral and posteromedial sulci are absent. The loss of the posterior sulci in the latter two species is probably related to the atrophy of the posterior ends of their premaxillae. In *Z. errabundus* the part of the premaxilla that would have had these foramina is atrophied, thin, and digitated.

All of the described species of the family Allodelphinidae also have osteological evidence that in life they had another diagnostic structure of the Odontoceti: the premaxillary sac (Barnes, 1990; Fordyce and Barnes, 1994; Fordyce et al., 1995). The premaxillary sacs are pocket-like lateral diverticula from each of the dorsal narial passages, and they are involved in producing sounds used in echolocation (Au, 2002). The locations of these sacs can be determined in cleaned osteological specimens by the presence of a flat, smooth, and in most species, relatively dense area of the premaxillary bone immediately lateral to each dorsal narial opening. This bony impression of the premaxillary sac is called the premaxillary sac fossa (Mead and

Table 1. Species of Allodelphinidae, measurements of crania and mandibles. Abbreviations: *, 2X the half width; +, less than true value.

	Allodelphis pratti	*Allodelphis woodburnei*	*Goedertius oregonensis*	*Ninjadelphis ujiharai*	*Zarhinocetus donnamatsonae*	*Zarhinocetus errabundus*	
	YPM13408	SBCM L3210-1	LACM123887	GMNH-PV-2570	UCMP86139	LACM149588	LACM21258
Cranium							
Condylobasal length	——	——	743 mm	——	——	853 mm	——
Length of rostrum	——	707 mm	585 mm	——	——	680 mm	——
Length of tooth row	——	610 mm	516 mm	——	——	548 mm	——
Width of rostrum at base	103 mm	101 mm	100 mm	126 mm	104 mm *	107 mm	122 mm
Width of rostrum at mid-length	——	32.4 mm	34.5mm	——	——	33.8 mm	——
Width of premaxillae at rostral mid-length	——	——	17.0 mm	——	——	——	——
Distance from tip of rostrum to nares	——	——	596 mm	——	——	——	——
Greatest preorbital width	138 mm *	——	130 mm *	185 mm	——	181 mm	187 mm
Greatest postorbital width	170 mm	172 mm *	167 mm	220 mm	168 mm *	192 mm	205 mm
Least supraorbital width	160 mm*	147 mm *	134 mm *	198 mm	134 mm *	186 mm	195 mm
Width of nasals at anterior end	26.0 mm	23.6 mm	19.5 mm	——	15.8 mm	16.2 mm	7.0 mm
Width of nasals at mid-length	13.0 mm	13.5 mm	2.3 mm	12.0 mm	24.4 mm	17.8 mm	16.1 mm
Width of nasals at posterior end	11.0 mm	13.5 mm	12.9 mm	——	19.2 mm	25.0 mm	19.9 mm
Length of nasals on inter-nasal suture	36.7 mm	29.1 mm	40.5 mm	9.8 mm	21.1 mm	28.0 mm	27.2 mm
Greatest width of dorsal nares	43.5 mm	43.8 mm	36.0 mm	52.4 mm	37.2 mm	37.6 mm	35.0 mm
Greatest width of ventral nares	——	——	48.0 mm *	58.0 mm *	56.2 mm *	——	——
Greatest width across posterior parts of premaxillae (where it is retracted)	——	——	60.0 mm	73.2 mm *	47.4 mm	——	——
Zygomatic width	194 mm	194 mm	175 mm	226 mm	197 mm	198 mm	210 mm
Greatest parietal width, within temporal fossae	136 mm	——	124 mm	174 mm	144 mm	168 mm	165 mm
Width across occipital condyles	97.1 mm	——	91.6 mm	105 mm	120 mm	111 mm	115 mm
Height of occipital condyles	——	——	40.5 mm	44.1 mm	60.5 mm	53.2 mm	60.0 mm
Width of foramen magnum	——	——	42.6 mm	39.2 mm	43.6 mm	——	——
Height of foramen magnum	——	——	27.1 mm	33.7 mm	41.5 mm	——	——
Vertical external height of braincase	——	——	100 mm	145 mm	116 mm	——	——
Anteroposterior length of temporal fossa	83.5 mm	83.8 mm	59.5 mm	94.9 mm	67.3 mm	68.7 mm	71.4 mm
Dorsoventral height of temporal fossa	——	——	38.1 mm	57.1 mm	44.4 mm	——	——
Anteroposterior length of bony orbit	37.5 mm	41.7 mm	55.3 mm	64.6 mm	——	45.8 mm	53.0 mm
Greatest length of pterygoid	——	——	105 mm (left)	96.8+ mm (left)	111 mm (right)	——	——
Mandible							
Mandible length	——	——	609 mm (add 3 to 5 mm)	——	——	783 mm	——
Length of symphysis	——	467 mm	385 mm	——	——	488 mm	——
Length of tooth row	——	609 mm	464 mm	——	——	526 mm	——
Width of mandible at mid-length	——	——	34.5 mm	——	——	——	——
Height of mandible at apex of coronoid process	——	——	90.0 mm	——	——	——	——

Fordyce, 2009:81. figs. 20a, d). The size and shape of the fossa reflects the location, size, and shape of the ventral side of the premaxillary sac in life. While the presence of premaxillary sacs defines the Odontoceti, the sacs may be modified in some groups (especially the sperm whales, family Physeteridae).

In the species of *Allodelphis* the premaxilla lateral to the dorsal nares is narrower than it is in most odontocetes, and the premaxillary sac fossa does not have the characteristic crescentic shape that is present in most species of odontocetes (e.g. *Tursiops truncatus*, Mead and Fordyce, 2009:fig. 1). Instead, in species of *Allodelphis* the premaxillary sac fossa is a poorly defined, relatively narrow, and anteroposteriorly elongated area of the premaxilla that is slightly convex, rather than having the more characteristic flat or concave surface (as it is, for example, in most species of the Delphinidae, and even in extent *Platanista gangetica*. The premaxillary sac fossa is very elevated in extant *Pontoporia blainvillei* (see Flower, 1867), but it is none-the-less still well defined and crescentic in shape.

Ninjadelphis ujiharai, *Zarhinocetus donnamatsonae*, and *Z. errabundus* all have premaxillary sac fossae, but these fossae are constructed in a manner that is unique among the odontocetes. In these species the posterior ends of both premaxillae are atrophied and retracted anteriorly. In *N. ujiharai* and *Z. donnamatsonae* each premaxilla terminates lateral to the middle of the dorsal naris, and in *Z. errabundus* it terminates at the anterolateral corner of the naris. In all of these species the posterior end of the premaxilla is irregularly digitated. Posterior to the end of the premaxilla, the maxilla that is in primitive species covered by the premaxilla now has the shape of the premaxillary sac fossa: crescentic, slightly elevated, and with a dense surface. Therefore, in these species, the premaxillary bone no longer underlies all of the premaxillary sac, and the fossa for the sac is developed partly on the remaining posterior end of the premaxilla, and mostly on the exposed dorsal surface of the maxilla. Because the premaxillary sac necessarily retained its anatomical position lateral to the coresponding narial passage, its location remained the same in these animals, even while the underlying premaxillary bones became re-configured.

Odontocetes have elaborate extensions of the pterygoid air sinus system in the basicranium around the ear bones, and in some species extending into the orbit and onto the posterior part of the palate (Fraser and Purves, 1960; Au, 2002). In various species these sinuses are developed in different ways, and they invade different parts of the cranium. In most cases the positions of these sinuses in life are indicated by the presence of fossae in the bones, usually clearly visible in both fossil and modern specimens.

In odontocetes, mysticetes, and the higher archaeocetes the peribullary sinus surrounds the petrosal and bulla (Fraser and Purves, 1960), and serves to isolate them from the surrounding cranial bones. In odontocetes, to varying degrees and in varying ways, depending on the species, the pterygoid sinus extends anteriorly, adjacent to the naris, and toward the palate, and invades the pterygoid hamulus. In some species the pterygoid sinus develops a postorbital lobe adjacent to the posterodorsal side of the tract for the optic nerve, a preorbital lobe anterodorsal to the tract for the optic nerve, and an anterior sinus on the palate that lies external to the pterygoid sinus in the pterygoid hamulus. In many species of odontocetes a middle sinus extends laterally from the peribulary sinus toward the tympanosquamosal recess (Fraser and Purves, 1960) medial to the glenoid fossa in the squamosal. In some species there is a posterior sinus that extends from the peribullary sinus into a fossa in the anterior face of the paroccipital process. Many species of the family Delphinidae have all of these sinuses.

No known species of allodelphinid has osteological evidence for the presence of all of these sinuses. All species of allodelphinids do have space around the petrosal and bulla that certainly held the peribullary sinus. All allodelphinids also have osteological evidence for a large and extensive pterygoid sinus that extended anteriorly from the peribullary sinus, to occupy the area medial to the orbit, between the plate of bone that is formed by the combined lateral lamina of the pterygoid and the posterior extension of the palatine, and extending from there further anteriorly into the pterygoid bone to occupy a fossa at the posterior end of the palate.

No species of allodelphinid has an antorbital fossa on the ventral surface of the supraorbital process. This fossa is present in species of Delphinidae (see Mead and Fordyce, 2009:fig. 2), and it holds the preorbital lobe of the pterygoid sinus (Fraser and Purves, 1960). Thus, there is no osteological evidence in any known allodelphinid for the existence of a preorbital lobe of the pterygoid sinus.

Similarly, there is no distinct fossa located on the posterior side of the tract for the optic nerve in any allodelphinid, and thus, there is no osteological evidence for the existence of a postorbital lobe (Fraser and Purves, 1960) of the pterygoid sinus.

Significantly, in allodelphinids there is no evidence of the extension of any sinuses into the supraorbital process of the frontal. Extensive invasion of the supraorbital process of the frontal by sinuses is a remarkable character of extant *Platanista gangetica* (Figure 3; and see Fraser and Purves, 1960:pl. 17).

Species of Delphinoidea typically have a very well defined and often rugose tympanosquamosal recess that holds the middle sinus (Fraser and Purves, 1960). *Platanista gangetica* has a relatively deep, smooth, and pocket-like fossa in the tympanosquamosal recess (Figure 3C), and this fossa holds a middle sinus (see Fraser and Purves, 1960:pls, 17, 18 (structure labeled TSQR)). Compared to the anatomy of delphinids and platanistids, allodelphinids have a relatively very shallow and poorly defined tympanosquamosal recess: for *A. pratti* see Figure 4C, *N. ujiharai* see Figures 19 and 20, and *Z. errabundus* see Figure 32C. Thus, allodelphinids may have had a middle sinus, but the osteological evidence for its presence is equivocal.

A posterior sinus is present in diverse odontocetes, but it is absent in others. Among extant odontocetes, this sinus is present in a delphinid, the long-finned pilot whale, *Globicephala melas* (traill, 1809) (see Fraser and Purves, 1960:pl. 34), but absent in some other species of the family. It is present in the phocoenids *Phocoena phocoena* (Linnaeus, 1758), the harbor porpoise, and in *Neophocaena phocaenoides* (G. Cuvier, 1829), the finless porpoise (see Fraser and Purves, 1960:pls. 27 and 28), in the pontoporiid *Pontoporia blainvillei* (see Fraser and Purves, 1960:pls, 19-20), in the iniid *Inia geoffrensis* (see Fraser and Purves, 1960:pls. 21-22), and in the lipotid *Lipotes vexillifer* Miller, 1918, the baiji or Yangtze River dolphin (see Fraser and Purves, 1960:pl. 23). It is absent, however, in extant species of the Ziphiidae.

No known allodelphinid has osteological evidence of having had a posterior sinus. If such a sinus had been present it would have occupied a deep recess in the anterior side of the paroccipital process, facing toward the tympanic bulla. Such a deep fossa is present in *P. gangetica*, (Figure 3C), and this fossa does hold a large posterior sinus (see Fraser and Purves, 1960:pl. 17). In contrast, in all known allodelphinid specimens the anterior side of the paroccipital process is flat and there is no fossa present. The fact that the posterior sinus is absent in the allodelphinids, but present in the crown taxon *Platanista gangetica*, and also present in various other extant groups of odontocetes and absent in others, suggests that the structure probably was acquired independently in different lineages. Its acquisition may well prove to be a useful character for future phyogenetic analyses within family-level clades.

In odontocetes the medial side of the thin posterior end of the dentary contains a large mandibular fossa (Mead and Fordyce, 2009:fig. 15) that in life is filled with a fat body. This structure has been implicated in the process of echolocation. Sounds generated by the individual are reflected off of prey or other objects in the water, received via this thin area on the horizontal ramus of the dentary, and thence transmitted to the ear region (Norris, 1968; Wood and Evans, 1980). The middle part of this thin area of the mandible is termed the acoustic window. Among the Allodelphinidae, this characteristic thin part of the dentary is preserved on specimens of four named species. Therefore, allodelphinids have the acoustic window in the mandible.

In summary, members of the Allodelphinidae have osteological features indicating that they possessed the same types of soft anatomical structures of the cranium and mandible that in extant groups of odontoceti are understood to faciitate the production and reception of sounds that are utilized for echolocation in navigation and feeding. These structures include the premaxillary foramen, premaxillary sac, peribullary sinus, pterygoid sinus, and possibly the middle sinus. Among the allodelphinids the details of these structures, their relative sizes, and their distribution within the head are unique to this group, and these differences help to define the clade.

Notable among the allodelphinids is the absence of any bony evidence for the existence of both a preorbital lobe and a postorbital lobe of the pterygoid sinus, and of a posterior sinus. In the more derived allodelphinid species of the genera *Ninjadelphis* and *Zarhinocetus*, anterior retraction of the posterior end of the premaxilla resulted in reduction of the posterolateral sulcus and loss of the posteromedial sulcus emanating from the premaxillary foramen. In these species, following the retraction of the premaxilla from part of the area lateral to the naris, the premaxillary sac remained at this location, connected with the latral side of each narial passage. With the disappearance of the premaxillary bone in this area of the cranium, the distinctive impression of the prexmaillary sac, the premaxillary sac fossa, was developed on the exposed dorsal surface of the maxilla, which became dense and smooth, as the dorsal surface of the premaxilla had been in the same location.

POSTULATED SWIMMING METHODS OF THE ALLODELPHINIDAE

In general, during their evolutionary history, cetaceans have undergone anteroposterior shortening of the neck region, which was an adaptation to enhance hydrodynamics. This shortening of the neck has been accomplished by reduction of the anteroposterior length of the centra of the cervical vertebrae. Fusion of adjacent cervical vertebrae occurs convergently in several lineages of cetaceans, both mysticetes and odontocetes, and in some species, cervical vertebrae two through seven are fused into a single unit. Such shortening of the centra of the cervical vertebrae developed as early as in some Eocene species of the Archaeoceti (e.g. *Basilosaurus cetoides* (Owen, 1839), *Zygorhiza kochii* (Reichenbach, 1847), and *Dorudon atrox* (Andrews, 1906)) (see Buchholtz, 2001a; Uhen, 2004).

In contrast to this general trend, a relatively unexpected and bizarre characteristic of all known species of Allodelphinidae is an elongated neck. Allodelphinids through time developed progressively larger cervical vertebrae with anteroposteriorly lengthened centra, and these vertebrae remained un-fused to one another. The centrum of each cervical vertebra is longer than its height or width in *Allodelphis pratti* (referred specimen, UCMP 83791, Table 2), *Goedertius oregonensis*, and *Ninjadelphis ujiharai* (Table 2). Their cervical vertebrae are more elongate anteroposteriorly than even those of archaeocetes (Buchholtz, 2001a; Uhen, 2004).

Buchholtz (2001a) compared the general shapes of cetacean vertebrae based on an index of the relative centrum length, which she defined as being the centrum length divided by the average of the centrum transverse width and dorsoventral height. The relative centrum lengths of the cervical vertebrae of *Ninjadelphis ujiharai* and other allodelphinids are always more than 1.0.

Buchholtz (2001a) showed that in extant marine mammals there is a positive correlation between shortening of cervical vertebra centrum length and the degree of aquatic adaptation. Contrary to these correlations, in the Allodelphinidae the index of cervical vertebral centrum length is not within the range of any group of extant cetaceans but, rather, it is within the range of the extant walrus, *Odobenus rosmarus* (Linnaeus, 1758). Thus, the long necks of the allodelphinids suggest that they had unique swimming and/or feeding strategies that are completely different from those of any other cetaceans, either fossil or extant.

Table 2. Allodelphinidae, measurements of cervical vertebra centra (in mm). Abbreviations: AH, anterior height; AW, anterior width; L, anteroposterior length of centrum; RCL, relative centrum length (Buchholtz, 2001a); *, posterior face of the centrum; +, less than true value.

	Ninjadelphis ujiharai			*Allodelphis pratti*	
	3rd	5th	6th	UCMP83791	
AH	61*	56	57	45	48
AW	63*	61	59	48	50
L	54+	68	65	51	52
RCL	0.87+	1.16	1.12	1.10	1.06

In cetaceans, elongated cervical vertebrae can serve to enhance mobility of the neck (Buchholtz, 2001a, b; Buchholtz et al., 2005), whereas shortened cervical vertebrae serve to make the body more hydrodynamic and thus to stabilize the head (e.g. Fish, 1997). Achieving a hydrodynamic shape would not be enhanced with the development of a long and flexible neck. A long and flexible neck would enhance maneuverability at slow swimming speeds, but would decrease stability at faster swimming speeds (Fish, 2002; Lambert et al., 2013). This suggests that the Allodelphinidae were slow but maneuverable swimmers.

The few thoracic vertebrae that have been found of Allodelphinidae are also proportionally large, and their centra are not anteroposteriorly compressed. These vertebrae appear not to have become secondarily elongated, as the cervical vertebrae were, but to simply have retained the primitive proportions. Cetaceans with dorsal vertebrae having proportions similar to those of the allodelphinids include the archaeocetes, many mysticetes, and many of the Oligocene odontocetes. Extant Ganges dolphins (*Platanista gangetica*) and Amazon River dolphins (*Inia geoffrensis*) have relatively few, but relatively elongate dorsal vertebrae, yet these are not so large and elongate as those of the Allodelphinidae.

The pectoral limbs of allodelphinids were also relatively large and elongate (the one exception being apparently *Goedertius oregonensis*). Extant odontocetes that have relatively large pectoral flippers and few dorsal vertebrae with relatively elongate centra generally are slow swimmers with flexible bodies, and those with small pectoral flippers and increased numbers of vertebrae with anteroposteriorly shortened centra are generally fast swimmers with torpedo-shaped bodies (Benke 1993; Buchholtz and Schur, 2004; Woodward et al., 2006; Sanchez and Berta, 2010). A helpful comparison in this respect is between the fast-swimming Dall's porpoise (*Phocoenoides dalli* (True, 1885)) and the slow-swimming Amazon River dolphin (*Inia geoffrensis*).

The mobility of the flipper is greater among slow-swimming and highly maneuverable odontocetes than among fast-swimming odontocetes (Howell, 1930; Pilleri et al., 1976; Fish, 2002). Presence of a large scapula and humerus in the allodelphinids implies a high development of the shoulder musculature, also related to a mobile flipper. This is supporting evidence for enhanced maneuverability but slow swimming speed by allodelphinids. Thus, in their swimming methods, the allodelphinids apparently compromised speed for maneuverability.

MUSCLES RELATED TO HEAD AND NECK MOVEMENTS IN ALLODELPHINIDAE

Structures of the cranium and the cervical vertebrae of the allodelphinids indicate that they had large neck and head muscles

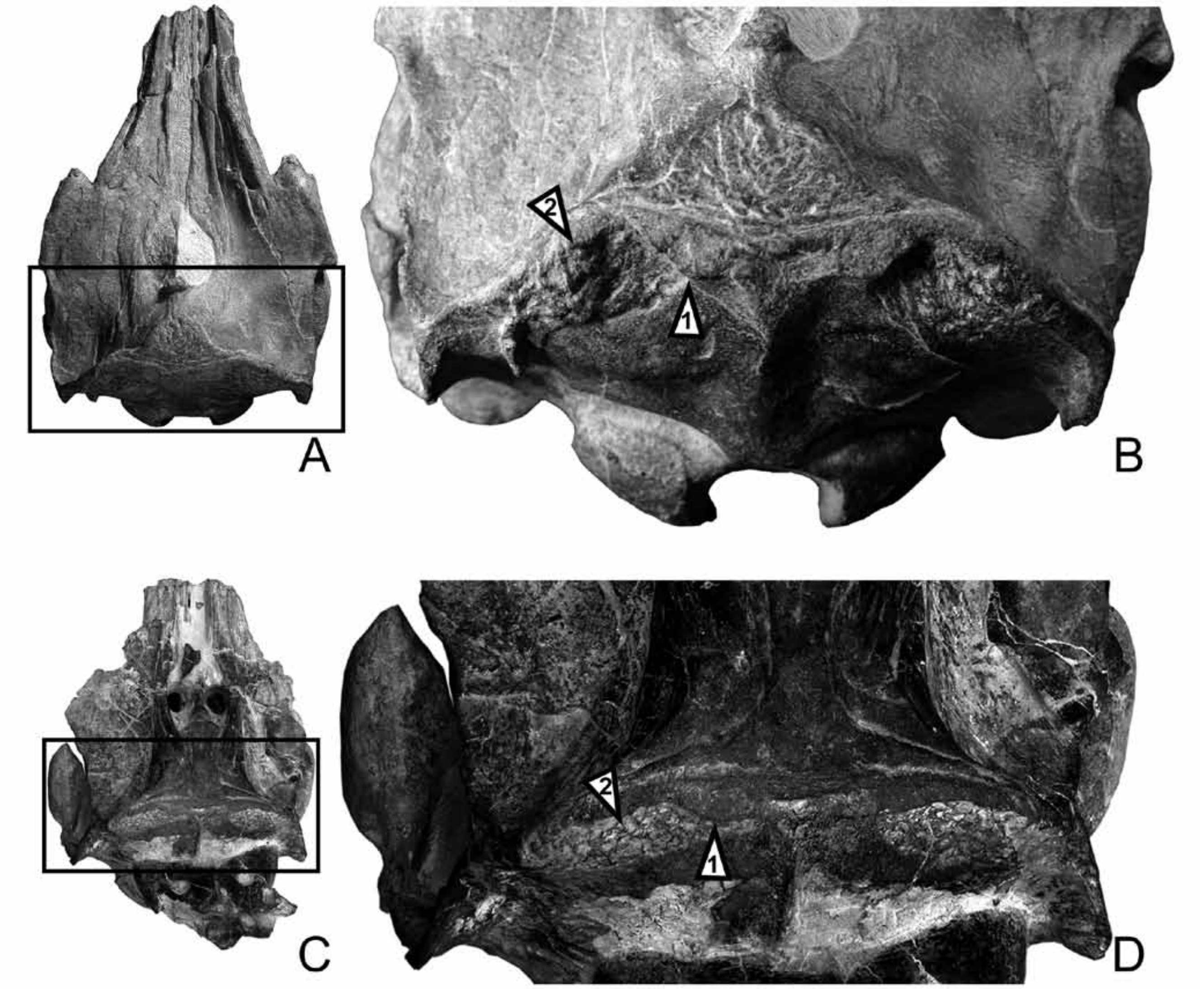

Figure 40. Details of the dorsal surfaces of crania of two species of Allodelphinidae showing structures related to insertion of massive neck muscles. **A** and **B**, *Ninjadelphis ujiharai* Kimura, new genus and new species, holotype, GMNH-PV-2570; **A**, photograph of cranium as preserved; **B**, structures labeled; **C** and **D**, *Allodelphis pratti* Wilson, 1935, holotype, YPM 13408; **C**, photograph of cranium as preserved; **D**, structures labeled. Labels "1" and "2" indicate the tabular crest and the rugose area of the supraoccipital, respectively.

that would have facilitated powerful and flexible head and neck movements. Thus, allodelphinids make an interesting contrast to virtually all of the living cetaceans (Howell, 1927, 1930; Stickler, 1980; Pabst, 1990). Allodelphinids have an enlarged, elevated, and anteroposteriorly thickened nuchal crest. Stickler (1980) demonstrated that in extant *Pontoporia blainvillei* the rectus capitis posterior major muscle attaches onto the nuchal crest and onto much of the supraoccipital bone adjacent to the crest. He also described the rectus capitis posterior minor muscle combining with the rectus capitis posterior major cranially, and inserting along with it onto the supraoccipital. The semispinalis cervicis muscle also attaches onto the nuchal crest and the interparietal region (Stickler, 1980; Pabst, 1990).

The thickened nuchal crest of the Allodelphinidae, therefore, would suggest great development of the rectus capitis posterior major, the rectus capitis posterior minor, and the semispinalis cervicis. This would have been especially true in the case of *Ninjadelphis ujiharai*, in which species the nuchal crest is very prominent and has a wide tabular area at the apex of the supraoccipital (labeled 1 in Figure 40B). Lateral to this tabular area, the surface of the supraoccipital bone is very rugose (labeled 2 in Figure 40B). At the cranial vertex, anterior to the nuchal crest, there is a relatively large, triangular-shaped dorsal exposure of the frontal bone that is also very rugose. These rugose surfaces of the frontal and the supraoccipital imply great development of the semispinalis cervicis and rectus capitis posterior in *N. ujiharai*. A similar tabular nuchal crest and rugose surface of the supraoccipital also exist in *Allodelphis pratti* (Figure 40D).

Ninjadelphis ujiharai also has larger basioccipital crests than do *Allodelphis pratti*, *Goedertius oregonensis*, or *Zarhinocetus errabundus*, and in *N. ujiharai* the posterior part of the basioccipital crest has a rugose surface. In extant cetaceans the ventral division of the scalenus muscle inserts on the basioccipital crest (Howell, 1927, 1930). The enhanced structure of the basioccipital crest in *N. ujiharai* suggests that in this species the ventral division of scalenus muscle was more developed than among the other species of Allodelphinidae.

The atlas vertebra of allodelphinids is relatively large and anteroposteriorly elongated, its neural arch is anteroposteriorly long, the transverse processes are enlarged, and the hypophyseal process is relatively large. In cetaceans, muscles involved in neck and head movements, such as the longus colli and longus capitis insert onto the ventral surface of the atlas (Howell, 1927, 1930; Uhen, 2004). Specifically, most of the cranial fibers of the longus colli muscle insert onto the hypophyseal process of the atlas (Uhen, 2004). The enlargement of the atlas and of its hypophyseal process in allodelphinids would have enlarged the areas of attachment of these muscles.

The dorsal side of the neural arch of the atlas is the area of origin of the rectus capitis posterior minor (Stickler, 1980), and this enlarged area in allodelphinids likely provided a large area for the origin of that muscle.

The transverse process of the atlas is the area of insertion of such muscles as the dorsal division of the scalenus and the cervical ventral intertransversarii (Howell, 1927, 1930; Uhen, 2004). The obliquus capitis superior and the obliquus capitis inferior also attach to the transverse processes of the atlas (Stickler, 1980). Compared to most other cetaceans, the allodelphinids have exceptionally large transverse processes on the atlas, and the lateral surface of the dorsal transverse process forms a large and flattened area with a salient edge. This provides a very large area for attachment of these muscles. Each of the four species for which the atlas vertebra has been documented has different-sized and different-shaped dorsal and ventral transverse processes. While all of them clearly had enlarged neck musculature, in each species different muscles were more enhanced.

In allodelphinids all of the cervical vertebrae posterior to the axis have anteroposteriorly elongated centra, and each has a prominent keel on its ventral surface, large transverse processes, anteroposteriorly wide neural arches, and tall and large spinous processes. The ventral surfaces of the centra of the cervical vertebrae are the areas of insertion of the cervical portion of the longus collii muscle (Uhen, 2004). The long and prominent ventral keels on the post-axis cervical vertebrae in allodelphinids would have been large areas for attachment of this muscle.

The transverse processes of the post-axis cervical vertebrae are areas of attachment of muscles for head and neck movements such as the longus colli, the dorsal division of scalenus, and the cervical ventral intertransversarii (Howell, 1927, 1930; Uhen, 2004). The large transverse processes of these cervical vertebrae in allodelphinids would provide large areas for the origins for these muscles.

The multifidus muscle attaches to the neural arches and neural spines of the cervical vertebrae caudal to the axis (Howell, 1930; Stickler, 1980; Pabst, 1990), and the semispicalis cervicis also arises from the neural arches of the anterior cervical vertebrae (Stickler, 1980). The spinous processes of the post-axis cervical vertebrae of allodelphinids are relatively tall, and would have provided increased areas for the attachment of these muscles. Additionally, these tall neural spines would have placed the areas for insertion of these muscles relatively dorsally in the neck, thereby increasing the distance from the force application to the centrum, and increasing the moment arm of these neck muscles. The anterodorsal orientations of the spinous processes, and the lengthening of the vertebral centra, would have reduced interference between the processes of adjacent vertebrae during any hyperextension of the neck.

In summary, the morphology of the cranium and cervical vertebrae of allodelphinids indicates that they had well-developed muscles for controlling movements of the head and neck. Allodelphinids would have had longer and more slender necks that any known cetaceans, fossil or extant, and they have no modern analogs (Figure 41). Among the known allodelphinids, *Ninjadelphis ujiharai* has the most prominent nuchal crest, the largest basioccipital crests, and the longest transverse processes of the atlas vertebra. These differences suggest that it was capable of more active and powerful movements of the head and neck than even the other species of the Allodelphinidae.

POSSIBLE FEEDING METHODS OF ALLODELPHINIDAE

The feeding strategies of marine mammals can be divided into four categories: grazers, filter feeders, suction feeders, and raptorial feeders (see Werth 2000a). Grazing is not applicable to the odontocetes. There is no morphological evidence for filter feeding by allodelphinids; they lack short rostra, wide palates, and deep throat regions that exist in suction feeding odontocetes of the families Delphinidae, Phocoenidae, Monodontidae, Physeteridae, and Ziphiidae (Werth 2000a). Species of cetaceans that suction feed generate a negative pressure in the oral cavity for drawing in the prey items, along with some surrounding water, by expanding the oral cavity. This is accomplished by rapid, piston-like retraction and depression of the tongue (Werth, 1992; Heyning and Mead, 1996). Hyolingual musculature that retracts the tongue and hyoid apparatus is characteristically well-developed in suction feeding cetaceans (Werth, 1992, 2000b, 2007; Heyning and Mead, 1996; Bloodworth and Marshall, 2007: Fitzgerald, 2010). The muscles for depression and retraction of the tongue (e.g. hyoglossus, genioglossus, and geniohyoid) attach onto the mandible posterior to the symphysis (Werth, 1992).

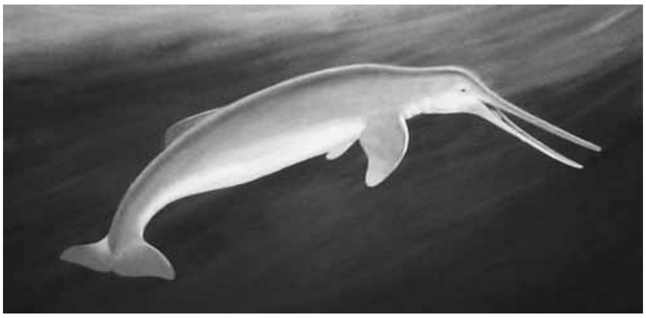

Figure 41. Suggested in-life appearance of an allodelphinid odontocete, generalized concept based on the morphologies of *Allodelphis pratti* Wilson, 1935; *Allodelphis woodburnei* Barnes and Reynolds, 2009; *Ninjadelphis ujiharai*, new genus and new species; and *Zarhinocetus errabundus* (Kellogg, 1931). From an original watercolor painting by Mary Butler.

Cetaceans that employ suction feeding typically have a short and wide rostrum, short lower jaw, short mandibular symphysis, blunt head, wide mouth, and a limited lateral gape (Werth, 2006a). Head shape is therefore a fundamental determinant of suction generation. Werth (2006a) experimentally showed that the types of negative oral pressures that are necessary for suction feeding significantly decrease among species that have elongate and slender jaws. All species of the Allodelphinidae have an extremely long and slender rostrum and a long mandibular symphysis. This type of mouth is ill suited for suction feeding. The closest modern analogs for allodelphinids are the Ganges dolphin (*Platanista gangetica*), Amazon River dolphin (*Inia geoffrensis*), and the Franciscana (*Pontoporia blainvillei*). These odontocetes are not suction feeders; they capture individual prey with their long beaks and numerous pointed teeth.

Beaked whales are known to be suction feeders. Although their rostra are relatively slender they are not at all comparable to the extremely long rostra and mandibular symphyses of the Allodelphinidae. Ziphiids are capable of generating the necessary negative pressures within the oral cavity because their mandibular symphyses are short and they have well-developed gular musculature (Heyning and Mead, 1996).

Suction feeding is also employed by extant sperm whales, *Physeter macrocephalus* Linnaeus, 1758 (see Werth, 2006a, b) which, in contrast to other suction feeding cetaceans, have a long, slender rostrum, and a long mandibular symphysis that occupies more than half the length of the mandible (Werth, 2004). They have an extremely wide gape that plays an important role in their ability to suction feed. Werth (2004) suggested that they accomplish this by creating a round opening by exposing their circular oropharyngeal opening and ingesting prey directly into the oropharynx. There is no indication that allodelphinids had a wide gape, thus they would not have employed the feeding method that is used by sperm whales.

Therefore, allodelphinids most likely were raptorial feeders, and could have caught either swimming or benthic animals, or those living on or near the substrate, with a sweeping and biting

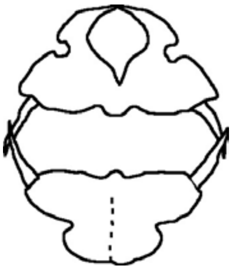

Figure 42. Allodelphinidae, generalized cross-section through the rostrum and mandible at mid-length, showing pattern of inter-meshing of tooth crowns and transverse spread of teeth. Rostrum and mandible are based on a referred specimen (LACM 149588) of *Zarhinocetus errabundus* (Kellogg, 1931), and the teeth are based on the holotype (SBCM L3210-1) of *Allodelphis woodburnei* Barnes and Reynolds, 2009, and holotype (GMNH-PV-2570) of *Ninjadelphis ujiharai* Kimura, new genus and new species.

action (Figure 42). Raptorial feeding has been considered to be the primitive feeding strategy of cetaceans (Werth, 2000a; *contra* Johnston and Berta, 2011), and it has been suggested that archaeocetes were raptorial feeders (Swift and Barnes, 1996; Werth, 1992, 2006; Uhen, 2004). The only living species in the Platanistoidea, *Platanista gangetica*, also employs this type of feeding method (Pilleri et al., 1970, 1976). These dolphins have flexible cervical vertebrae and a long rostrum and mandible with numerous sharp teeth (Figure 3), and they catch prey items by rapidly opening their pincer-like jaws, followed by a very quick snap (Pilleri et al., 1970, 1976).

In a dolphin with a long rostrum, movements of the neck will increase the speed of movement and the sweep of the distal end of the rostrum (Taylor, 1987). Lengthening of the rostrum serves to increase the range of feeding access by placing the tooth-bearing rostral tip in a wider radius of sweep, and this will be further enhanced by a long and flexible neck. The allodelphinid body morphology was ill suited for high speed pursuit of prey items, but the ability to make quick movements of the head and neck would have compensated for the lack of swimming speed.

The dorsal condyloid fossa on the occipital shield allows space for movement of the atlas vertebra adjacent to the cranium (Mead and Fordyce, 2009), *Ninjadelphis ujiharai* has a larger and deeper dorsal condyloid fossa than other allodelphinids, suggesting that it had a wider range of extension of the head, allowing unusual dorsoventral flexibility, for an odontocete.

To move prey items thorough the mouth and into the gullet allodelphinids might have utilized the force of gravity (for gravity feeding see Taylor, 1987). Importantly, extant *Platanista gangetica* is the only side-swimming cetacean that captures prey items by lateral sweeps of the head, accompanied by bobbing of the head to help move food down the throat (Herald et al., 1969).

In allodelphinids, the expanded range of flexion and extension of the neck might be an adaptation for the *Platanista*-style of head-bobbing movement while capturing prey. This conclusion should be viewed with caution, because the dorsal condyloid fossa of *Platanista gangetica* is smaller than that of *Ninjadelphis ujiharai*.

Certain anatomical structures of allodelphinids suggest that they may have been specialists on benthic prey. Their relatively large and posteriorly-protruding occipital condyles would have allowed for greater flexion between the head and neck, and enhanced head movement in cetaceans has been hypothesized as a benthic feeding adaptation (Muizon and Domning, 2002; Fitzgerald, 2010). The deep and large dorsal condyloid fossa of allodelphinids also correlates with enhanced head movement. The orbits of allodelphinids are directed more anterolaterally than is usual for most cetaceans, and this might have allowed some degree of binocular vision. Benthic feeding among marine mammals is usually accompanied by binocular vision (Fay, 1982; Werth, 2000a; Muizon and Domning, 2002; Muizon et al., 2002; Fitzgerald, 2010).

Because many living odontocetes employ more than one feeding method, and opportunistically utilize them (Werth, 2006a), the allodelphinids might have utilized different types of raptorial feeding methods. Differences in the structure of the cranium and the atlas vertebra suggest that *N. ujiharai* used more powerful and active movements of its head and neck compared with the other allodelphinids.

Raptorial feeders sometimes grasp swimming prey with rapid lateral movements of the head (Werth, 2000a). Such lateral movement in cetaceans having an extremely long rostrum could produce substantial drag, and the enhanced musculature of the necks of allodelphinids might have been a compensation for this.

Compared to the other allodelphinids, in *Ninjadelphis ujiharai*, the postglenoid process of the squamosal is rotated more anterolaterally, and the glenoid fossa faces more anteromedially. This changes the way in which the mandibular condyle articulates with the glenoid fossa: having an articulation that is more buttressed on its lateral side. This modified articulation between the mandible and cranium in *N. ujiharai* may have been an adaptation that served to stabilize the mandible and reduce lateral slip at the mandible-squamosal articulation that would have been created by drag during lateral movements of the head.

The osteology of *Goedertius oregonensis*, *Zarhinocetus donnamatsonae* and *Zarhinocetus errabundus* suggests that their muscles related to head and neck movement were less developed than those of *Ninjadelphis ujiharai*. These other species do have most of the adaptations for benthic feeding that we have discussed here, and their large and posteriorly protruding occipital condyles may indicate that they were more adapted to benthic feeding, while *Ninjadelphis ujiharai* might have been more adapted to raptorial feeding.

Species of the family Eurhinodelphinidae also have extremely long and slender rostra, but their cervical vertebrae are shortened anteroposteriorly, and *Xiphiacetus bossi* (Kellogg, 1925) has vertebral proportions similar to those of the kentriodontid delphinoids (Abel, 1931; Buchholtz, 2001a). This suggests that although eurhinodelphinids and allodelphinids have extremely long and slender rostra, their feeding and/or swimming strategies were markedly different. This also suggests that elongation of the cervical vertebrae in the allodelphinids was not simply related to the functional and/or physical requirements of having evolved an extremely long and slender rostrum.

SUMMARY AND CONCLUSIONS

1. The superfamily Platanistoidea is a clade of Odontoceti that was taxonomically diverse during Oligocene and Miocene time, and subsequently declined in diversity. Presently only the family Platanistidae survives, represented by *Platanista gangetica*, which lives in rivers of south Asia. Fossils of the family Platanistidae are known from marine, estuarine, and fresh water deposits.

2. Five extinct families are currently recognized in the superfamily Platanistoidea: Allodelphinidae (Miocene), Squalodontidae (Oligocene and Miocene), Prosqualodontidae (Oligocene and Miocene), Waipatiidae (Oligocene), and Squalodelphinidae (Miocene).

3. Fossils of the extinct platanistoid family Allodelphinidae Barnes, 2006, are relatively rare and are known only from marine sedimentary deposits around the margin of the North Pacific Ocean; from California, Oregon, Washington, and Japan. The presently known geochronologic range of the family Allodelphinidae, currently represented by four named genera and six named species, is from the earliest Miocene, approximately 22 million years ago, to the middle Miocene, approximately 15 million years ago.

4. Despite their rarity as fossils, all of the named species of Allodelphinidae are known by crania, and four of them are

known by informative partial skeletons. These partial skeletons begin to provide considerable information about the osteology of the group by virtue of their directly comparable parts.

5. Diagnostic osteological characters of the Allodelphinidae include cranium with very long rostrum, dorsal aperture of the posterior maxillary foramen not located close to the posterolateral end of the premaxilla, small and transversely narrow nasal bones, posterior ends of the premaxillae progressively losing contact with the lateral margins of the nasal bones, no invasion of the supraorbital process by the pterygoid sinus, relatively small temporal fossae, well-ossified lateral lamina of the pterygoid bone which, accompanied by a posterior extension of the palatine, forms a vertical wall in the medial part of the orbit that extends posteriorly to contact the anterior falciform process of the squamosal, petrosal with a groove on the ventral surface of the anterior process, tympanic bulla with a large anterior spine, mandible extending to the anterior end of the rostrum, atlas vertebra with separate enlarged dorsal and ventral transverse processes, axis vertebra with a large odontoid process, enlarged cervical vertebrae with anteroposteriorly elongated centra, a large and anteroposteriorly elongated manubrium, scapula lacking the acromion process, humerus relatively long with a nearly circular cross section of the diaphysis, radius and ulna the same length as the humerus or shorter, and distal trochlea of the humerus usually fused to the olecranon process of the ulna. This latter fusion appears to be evolutionarily significant and not pathological.

6. Currently recognized genera in the family Allodelphinidae, in order from the most primitive to most highly derived, are *Allodelphis* Wilson, 1935, *Goedertius* Barnes and Kimura, new genus, *Ninjadelphis* Kimura, new genus, and *Zarhinocetus* Barnes and Reynolds, 2009.

7. *Allodelphis* Wilson, 1935, is the type genus of the family Allodelphinidae, and includes two named species from the eastern North Pacific Ocean: *Allodelphis pratti* Wilson, 1935; and *A. woodburnei* Barnes and Reynolds, 2009. Species of *Allodelphis* possess a symmetrical cranial vertex, dorsoventrally thin but laterally expanded margin of the maxilla anterior to the antorbital notch, posterior part of the mesorostral canal widely open dorsally, mesethmoid bone between narial passages elevated as far dorsally as the nasal bones, and posterior ends of the premaxillae extending posteriorly beyond the posterior margins of the nasal bones.

8. *Allodelphis pratti* Wilson, 1935, the type species of the genus *Allodelphis*, is known only from near-shore marine sediments that are undifferentiated between the Freeman Silt and the Jewett Sand that crop out in the foothills of the Sierra Nevada in Kern County, central California, U.S.A. The species is early Miocene in age, approximately 21 to 22 million years old, and is part of the Woody Local Fauna. It is known by the holotype, which includes a cranium, petrosal, mandible parts, vertebrae, and ribs, and a referred specimen from the same deposit that includes the tympanic bulla, hyoid bones, vertebrae, ribs, manubrium, humerus, and ulna.

9. *Allodelphis woodburnei* Barnes and Reynolds, 2009, is known only from shallow water marine sediments of the Vaqueros Formation exposed in the Cajon Pass, San Bernardino County, California, U.S.A. The species is early Miocene in age, and approximately 22 million years old. It is known by the holotype partial skeleton that includes the cranium, mandible, teeth, vertebrae, ribs, and forelimb bones. It is more derived than *A. pratti*, from which it differs by having the posterior part of its mesorostral canal more closed dorsally, the dorsal surface of the rostrum anterior to the dorsal nares depressed, smaller dorsal narial openings, a more massive zygomatic process of the squamosal that is more inclined anterodorsally so that the glenoid fossa for articulation with the mandibular condyle faces more anteriorly, and a larger humerus that has a proportionally larger humeral head.

10. *Goedertius* Barnes and Kimura, new genus, currently includes only the type species, *Goedertius oregonensis* Barnes and Kimura, new species, which is from the eastern North Pacific.

11. *Goedertius oregonensis* Barnes and Kimura, new species, is the type species of the genus *Goedertius*. It is known only from near-shore coastal marine shelf deposits of the Nye Mudstone in Lincoln County, Oregon, U.S.A. The species is early Miocene in age, and is approximately 20 to 21 million years old. It is known by the holotype partial skeleton that includes the cranium, petrosals, bullae, mandible, teeth, vertebrae, ribs, and humerus. It is more derived than either species of *Allodelphis*, from which it differs by having narrower premaxillary sac fossae around the narial openings, posterior ends of the premaxillae narrower transversely, thinner, and making full contact with the lateral sides of the nasal bones. Its small nasal bones are constricted transversely by the posterior ends of the premaxillae that extend medially toward the sagittal plane of the cranium. *Goedertius oregonensis* differs from other allodelphinids by not having the tendency for retraction of the premaxillae from contact with the nasals, and thus has undergone no retraction anteriorly in the area of the premaxillary sac fossa as occurs in species of *Ninjadelphis* and *Zarhinocetus*. It also has an exceptionally massive and curved zygomatic process of the squamosal, and its occipital condyles project prominently posteriorly from the occipital shield. The ways in which it differs from other allodelphinids suggest that it may have been affected by paedomorphism.

12. *Ninjadelphis* Kimura, new genus, currently includes only the type species, *Ninjadelphis ujiharai* Kimura, new species, which is from the western North Pacific.

13. *Ninjadelphis ujiharai* Kimura, new species, is known only from shallow water marine sediments of the Hiramatsu Member of the Awa Group, from Iga (formerly Oyamada-mura), Mie Prefecture, Japan, The species is late early Miocene in age, and is approximately 17 million years old. It is known by the holotype partial skeleton that includes the cranium, petrosal, bulla, parts of the mandible, teeth, vertebrae, ribs, manubrium, scapula, humerus, radius, ulna, and part of the manus. It is more derived than the species of *Allodelphis* and *Goedertius*, from which it differs by having asymmetrical reduction in the size of the laterally expanded margin of the right maxilla anterior to the antorbital notch, a slightly lower septum of the mesethmoid bone between the dorsal nares, wider premaxillary sac fossae around the narial openings, posterior ends of the premaxillae retracted anteriorly to a point lateral to mid-parts of the dorsal nares, right and left nasal bones fused together at the midline and to the underlying mesethmoid and frontal bones, more anteromedially facing glenoid fossa for articulation with the mandible, and larger dorsal transverse process and longer and more slender ventral transverse process of the atlas vertebra.

14. The holotype of *Ninjadelphis ujiharai* includes the first reported complete scapula of an allodelphinid, and this important specimen demonstrates that the species had lost the coracoid process of the scapula, that the acromion process is located on the lateral side of the anterior margin of the scapula, and that the supraspinatus fossa was present. This adds to previous conclusions that these derived characters unite at least the more crown-ward members of the Platanistoidea.

15. *Zarhinocetus* Barnes and Reynolds, 2009, has as its type species *Squalodon errabundus* Kellogg, 1931, which was subsequently transferred by Barnes and Reynolds (2009) from the family Squalodontidae to the family Allodelphinidae and

placed in the genus *Zarhinocetus*. *Zarhinocetus errabundus* (Kellogg, 1931), which is from the eastern North Pacific.

16. *Zarhinocetus donnamatsonae* Barnes, new species, is known from an unspecified level within marine continental shelf deposits of the Astoria Formation in the area of the Chehalis River, near Elma, Grays Harbor County, western Washington State, U.S.A. The geochronologic age of the holotype can only be stated as late early Miocene to early middle Miocene, and thus approximately between 20 and 15 million years old. It is known only by the holotype cranium that lacks the distal part of the rostrum. It shares some plesiomorphic characters with *Ninjadelphis ujiharai*, but shares with *Z. errabundus* a depression on the dorsal surface of the base of the rostrum, a maxillary tubercle anterior to each antorbital notch asymmetrically developed with the left side larger than the right, mesethmoid bone between nares retracted to a more ventral position between the narial passages, posterior ends of the premaxillae retracted anteriorly to the anterolateral borders of the dorsal nares and with irregular and digitated posterior ends, a maxillary crest over the orbit, and an asymmetrical cranial vertex with the midline sutures between the nasal bones and the dorsal exposures of the frontal bones skewed to the left side of the mid-line of the cranium, an elevated and thickened nuchal crest, and the zygomatic process of the squamosal rectangular in lateral view rather than being arc-shaped,

17. *Zarhinocetus errabundus* (Kellogg, 1931) is known only from marine continental shelf deposits in the upper part of the Round Mountain Silt that crop out in the hills northeast of Bakersfield, Kern County, California, U.S.A. The species is middle middle Miocene in age, between approximately 16.1 and 14.5 million years old, only known from the Sharktooth Hill Bonebed, and is part of the Sharktooth Hill Local Fauna. It is known by the holotype isolated petrosal and by referred petrosals, two crania with associated petrosals and bullae, atlas vertebrae, humerus, and ulna. It is the geochronologically youngest and most derived described species of the family Allodelphinidae, and the largest species at maturity, and has an enlarged atlas vertebra with enlarged dorsal and ventral transverse processes, an enlarged humerus, and shortened radius and ulna.

18. Allodelphinids probably attained adult body lengths ranging from between three and four meters to as much as five meters, had skulls approximately one meter long, very long and slender rostra, lower jaws reaching the same length as the rostrum, many small and single-rooted teeth, unusually elongated cervical vertebrae that were not fused to one another, relatively normally-proportioned (primitive) thoracic vertebrae, proximo-distally relatively long humeri, radii and ulnae the same length as the humerus, or shorter.

19. General evolutionary trends among the Allodelphinidae include increase in body size, loss of contact between the posterior end of the premaxilla and the lateral edge of the adjoining nasal bone, progressive retraction anteriorly of the posterior end of the premaxilla (except for *Goedertius oregonensis*), development of a crest on the supraorbital process of the maxilla, development of left-skew asymmetry of the cranial vertex, development of a basin on the dorsal surface of the posterior part of the rostrum, reduction in size of the nasal bones, fusion of the nasal bones to the underlying frontal and mesethmoid bones, retraction of the mesethmoid between the nares, enlargement and asymmetrical development of the nuchal crest, enlargement of the occipital condyles, increase in size of the petrosal, enlargement of the dorsal and ventral transverse processes of the atlas vertebra, anteroposterior elongation and enlargement of the cervical vertebrae, increase in size of the humerus (except for *Goedertius oregonensis*), and shortening of the radius and ulna.

20. Allodelphinids have osteological evidence for structures that are linked to echolocation abilities in extant odontocetes: premaxillary foramina on the facial surface to innervate muscles involved with a melon, a wide facial disk to support such a melon, a premaxillary sac fossa on the lateral side of each narial passage, a pterygoid sinus extending from the peribullary sinus into the orbital region and the posterior part of the palate, an acoustic window in the ascending ramus of the dentary, and petrosal and tympanic bulla joined tightly together and isolated from surrounding cranial bones within a peribullary sinus. Allodelphinids may have had a middle sinus, but their tympanosquamosal recess is not particularly deep and has no pocket-like fossa indicating its presence. Allodelphinids also show no osteological evidence for the presence of a preorbital lobe of the pterygoid sinus, a postorbital lobe of the pterygoid sinus, or a posterior sinus.

21. With their long rostra, very long and flexible necks, and large and elongate pectoral flippers, allodelphinids have no morphological or behavioral analogs among extant cetaceans. It is postulated here that they were capable of navigating and feeding using echolocation, were slow swimmers but were very maneuverable, could make powerful and rapid sweeping movements of the head and rostrum in both dorsal-ventral and side-to-side directions, and were raptorial feeders, taking their prey using rapid biting actions, and fed either in the water column or near the substrate. The diversity of members of the family, some of which were quasi-contemporaneous, may indicate that there was niche partitioning.

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REFERENCES

Abel, O. (1905): Les Odontocètes du Boldérien (Miocène Supérieur) d' Anvers. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 3:1-155.

Abel, O. (1931): Das Skelett der Eurhinodelphiden aus dem oberen Miozaen von Antwerpen. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, (48):191-334.

Addicott, W. O. (1972): Provincial middle and late Tertiary molluscan stages, Temblor Range, California. *In* Stinemeyer, E. H. (ed.) Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium. Society of Economic Paleontologists and Mineralogists, Bakersfield, California, p. 1-26.

Aguirre-Fernández, G. and Fordyce, R. E. (2014): *Papahu taitapu*, gen. et sp. nov., an Early Miocene stem odontocete (Cetacea) from New Zealand. *Journal of Vertebrate Paleontology*, 34:195-210.

Allen, G. M. (1921): A new fossil cetacean. *Bulletin of the Museum of Comparative Zoology*, 65:1-14.

Ameghino, F. (1892): Énumération synoptique des espèces de Mammifères fossils des foramations éocènes de Patagonie. *Boletin de la Academia Nacional de Ciencias en Cordoba (Republica Argentina)*, 13:259-455.

Anderson, J. (1878): Anatomical and zoological researches: comprising an account of the zoological results of two expeditions to western Yunnan in 1868 and 1875; and a monography of the two cetacean genera, *Platanista* and *Orcaella*. Bernard Quaritch, London, 984 pp.

Au, W. W. L. (2002): Echolocation. *In* Perrin, W. F., Thewissen, H. and Wursig, B. (eds.) Encyclopedia of Marine Mammals. Academic Press, Inc., San Diego, p. 358-367.

Barnes, L. G. (1977): Outline of eastern North Pacific fossil cetacean assemblages. *Systematic Zoology*, 25:321-343. [This is the volume for December 1976, but was published in January 1977.]

Barnes, L. G. (1978): A review of *Lophocetus* and *Liolithax* and their relationships to the delphinoid family Kentriodontidae (Cetacea: Odontoceti). *Natural History Museum of Los Angeles County Science Bulletin*, (28):1-35.

Barnes, L. G. (1987): An Early Miocene pinniped of the genus *Desmatophoca* (Mammalia: Otariidae) from Washington. *Contributions in Science, Natural History Museum of Los Angeles County*, (382):1-20.

Barnes, L. G. (1990): The fossil record and evolutionary relationships of the genus *Tursiops*. *In* Leatherwood, S. and Reeves, R. R. (eds.) The Bottlenose Dolphin. Academic Press, San Diego, California, p. 3-26.

Barnes, L. G. (2002): An Early Miocene long-snouted marine platanistid dolphin (Mammalia, Cetacea, Odontoceti) from the Korneuburg Basin (Austria). *Beitrage zur Paläontologie*, 27:407-418.

Barnes, L. G. (2006): A phylogenetic analysis of the superfamily Platanistoidea (Mammalia, Cetacea, Odontoceti). *Beiträge zur Paläontologie*, 30:25-42.

Barnes, L. G., Kimura, T. and Godfrey, S. G. (2010): The evolutionary history and phylogenetic relationships of the superfamily Platanistoidea. *In* Ruiz-Garcia, M. and Shostell, J. M. (eds.) Biology, Evolution and Conservation of River Dolphins within South America and Asia. Nova Publishers, New York, p. 445-488.

Barnes, L. G. and Reynolds, R. E. (2009): A new species of Early Miocene allodelphinid dolphin (Cetacea, Odontoceti, Platanistoidea) from Cajon Pass, southern California, U.S.A. *Museum of Northern Arizona Bulletin*, 65:483-507.

Benke, H. (1993): Investigations on the osteology and the functional morphology of the flipper of whales and dolphins (Cetacea). *Investigations on Cetacea*, 24:9-252.

Berglund, R. E. and Goedert, J. L. (1992): A new species of *Cancer* (Decapoda: Brachyura) from the Miocene Astoria Formation in Washington. *Burke Museum Contributions in Anthropology and Natural History*, 9:1-11.

Bloodworth, B. E. and Marshall, C. D. (2007): A functional comparison of the hyolingual complex in pygmy and dwarf sperm whale (*Kogia breviceps* and *K. sima*), and bottlenose dolphins (*Tursiops truncatus*). *Journal of Anatomy*, 211:78-91.

Blow, W. H. (1969): Late middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In* Brönnimann, P. and Renz, H. H. (eds.) Proceedings of the First International Conference on Planktonic Microfossils. E. J. Brill, Leiden, p. 199-422.

Boenninghaus G. (1903). Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung. Zoologische Jahrbücher. *Abteilung für Anatomie und Ontogenie der Tiere Abteilung für Anatomie und Ontogenie der Tiere*, 19:189–360.

Bohaska, D. J., Barnes, L. G. and Godfrey, S. J. (2007): *Araeodelphis natator* Kellogg, 1957, the most primitive known member of the Platanistidae (Odontoceti, Cetacea) and a review of the Platanistidae from Calvert Cliffs (Miocene, Chesapeake Croup), Maryland, USA. *In* Geological Society of Australia, Abstracts, Number 85, 11th Conference on Australasian Vertebrate Evolution, Palaeontology, and Systematics, Programme Abstracts. Melbourne, Australia, p. 61-62.

Brandt, J. F. (1872): Bericht über den bereits vollendeten, druckfertigen Theil seiner Untersuchungen über die fossilen and subfossilen Cetaceen Europas. *Compte rendu de l'Académie impériale des Sciences de St. Petersbourg*, 17:407–408.

Brandt, J. F. (1873): Untersuchungen über die fossilen und subfossilen cetaceen Europa's. *Mémoires de L'Académie Impériale des Sciences de Saint-Petersbourg, Series* 7, 20:1-372.

Brisson, A. D. (1762): Regnum animale in classes IX Distributum, sive synopsis methodica. Lugdum Batarorum, apud. Theodorum Haak, Leiden, Holland, 296 pp.

Buchholtz, E. A. (2001a): Vertebral osteology and swimming style in living and fossil whales (Order Cetacea). *Journal of Zoology*, 253:175-190.

Buchholtz, E. A. (2001b): Swimming styles in Jurassic ichthyosaurs. *Journal of Vertebrate Paleontology*, 21:61-73.

Buchholtz, E. A. and Schur, S. A. (2004): Vertebral osteology in Delphinidae (Cetacea). *Zoological Journal of the Linnean Society*, 140:383-401.

Buchholtz, E. A., Wolkovich, E. M. and Cleary, R. J. (2005): Vertebral osteology and complexity in *Lagenorhynchus acutus* (Delphinidae) with comparison to other delphinoid genera. *Marine Mammal Science*, 21:411-428.

Case, E. C. (1934): A specimen of a long-nosed dolphin from the Bone Valley Gravels of Polk County, Florida. *Contributions from the Museum of Paleontology, University of Michigan*, 4:105-113.

Cope, E. D. (1868): Second contribution to the history of the Vertebrata of the Miocene period of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20:184-194.

Cozzuol, M. A. (1996): The record of aquatic mammals in southern South America. *Munchner Geowissenshaftliche Abhandlungen. A, Geoligie und Palaontologie*, 30:321-342.

Dal Piaz, G. (1917): Gli Odontoceti del Miocene bellunese, Parte Terza. *Squalodelphis fabiannii. Memorie dell' Instituto Geologico della R. Universita di Padova*, 5:1-28.

Delfortrie, E. (1875): Un daupin d'espece nouvell dans les faluns du sud-ouest. *Actes de la Societe Linneenne de Bordeaux*, 30:177-181.

Dickson, M. R. (1964): The skull and other remains of *Prosqualodon marplesi*, a new species of fossil whale. *New Zealand Journal of Geology and Geophysics*, 7:626-635.

Dooley, A. C., Jr. (2005): A new species of *Squalodon* (Mammalia, Cetacea) from the Middle Miocene of Virginia. *Virginia Museum of Natural History Memoir*, (8):1-43.

Duncan, F. M., Waterhouse, F. H. and Peavot, H. (1937): On the dates of publication of the Society's Proceedings, 1830-1858, compiled by the late F. H. Waterhouse, and of the Transactions, by the late Henry Peavot, originally published in P.Z.S. 1893, 1913. *In* Proceedings of the Zoological Society of London for the year1937, p. 71-81.

Etherington, T. J. (1931): Stratigraphy and fauna of the Astoria Miocene of southwest Washington. *University of California Department of Geological Sciences Bulletin*, 20:31-142.

Fay, F. H. (1982): Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North American Fauna*, 74:1-279.

Ferry-Graham, L. A., Wainwright, P. C. and Bellwood, D. R. (2001): Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits. *Journal of Experimental Marine Biology and Ecology*, 256:167-184.

Fish, F. E. (1997): Biological designs for enhanced maneuverability: Analysis of marine mammal performance. *In* Proceedings of the Special Session on Bio-Engineering Research Related to Autonomous Underwater Vehicles,. Autonomous Undersea Systems Institute, p. 109-117

Fish, F. E. (2002): Balancing requirements for stability and maneuverability in cetaceans. *Integrative and Comparative Biology*, 42:85-93.

Fitzgerald, E. M. G. (2010): The morphology and systematics of *Mammalodon colliveri* (Cetacea: Mysticeti), a toothed mysticete from the Oligocene of Australia. *Zoological Journal of the Linnaean Society*, 158:367-476.

Flower, W. H. (1864): Notes on the skeletons of whales in the principal museums of Holland and Belgium, with descriptions of two species apparently new to science. *In* Proceedings of the Zoological Society of London for theyear 1864, p. 384–420.

Flower, W. H. (1867): Description of the skeleton of *Inia geoffrensis* and of the skull of *Pontoporia blainvillei*, with remarks on the systematic position of these animals in the order Cetacea. *Transactions of the Zoological Society of London*, 6(3):87–116. [This paper was "Read November 22nd, 1866"; the title page of Volume 6 is dated 1869, but Part 3 of Volume 6 was issued during 1867, according to contemporary sources — Duncan et al. (1937) from Rice (1998:175).]

Fordyce, R. E. (1981): Systematics of the odontocete *Agorophius pygmaeus* and the family Agorophiidae (Mammalia: Cetacea). *Journal of Paleontology*, 55:1028-1045.

Fordyce, R. E. (1994): *Waipatia maerewhenua*, new genus and new species (Waipatiidae, new family), an archaic late Oligocene dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. *Proceedings of the San Diego Society of Natural History*, (29):147-176.

Fordyce, R. E. (2006): A southern perspective on Cetacean evolution and zoogeography. *In*, Merrick, J., Archer, M., Hickey, G. M. and Lee, M. S. Y. (eds.) Evolution and Biogeography of Australasian Vertebrates. Australian Scientific Publishing, Oatlands, New South Wales, Australia, p. 755-778.

Fordyce, R. E. and Barnes, L. G. (1994): The evolutionary history of whales and dolphins. *Annual Review of Earth and Planetary Sciences*, 22:419-455.

Fordyce, R. E., Barnes, L. G. and Miyazaki, N. (1995): General aspects of the evolutionary history of whales and dolphins. *The Island Arc*, 3:373-391 [for 1994].

Fordyce, R. E. and Muizon, C. de (2001): Evolutionary history of cetaceans: a review. *In*, Mazin, J.-M. and Buffrénil, V. de (eds.) Secondary Adaptation of Tetrapods to Life in Water. Verlag Dr. Friedrich Pfeil, München, Germany, p. 169-233.

Fraser, F. C. and Purves, P. E. (1960): Hearing in cetaceans: evolution of the accessory air sacs and the structure of the outer and middle ear in Recent cetaceans. *Bulletin of the British Museum (Natural History), Zoology*, 7:1-140.

Fujiwara, Y., Irizuki, T., Hayashi, H., Tanaka, Y., Watanabe, M. and Shimizu, K. (2005): Stratigraphy and age of the Miocene Awa Group, eastern Iga City, Mie Prefecture, central Japan. *Journal of Geological Society of Japan*, 111:779-791. (in Japanese with English abstract)

Galatius, A., Andersen, M.-B. E. R., Haugan, B., Langhoff, H. E., and Jespersen, Å. (2006): Timing of epiphyseal development in the flipper skeleton of the harbour porpoise (*Phocoena phocoena*) as an indicator of paedomorphosis. *Acta Zoologica*, 87:77-82.

Geisler, J. H., Colbert, M. W. and Carew, J. L. (2014): A new fossil species supports an early origin for toothed whale echolocation. *Nature*, 508:383-386.

Geisler, J. H., McGowen, M. R., Yang, G. and Gatesy, J. (2011): A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. *BMC Evolutionary Biology*, 11:112-145.

Geisler, J. H. and Sanders, A. E. (2003): Morphological evidence for the phylogeny of Cetacea. *Journal of Mammalian Evolution*, 10:23-129.

Gihr, M., Kraus, C. and Pilleri, G. (1982): The manus of *Pseudorca crassidens* (Owen): a study of variability. *Investigations on Cetacea*, 13:101-124.

Godfrey, S. J. (2013): On the oflactory apparatus in the Miocene odontocete *Squalodon* sp. (Squalodontidae). *Comptes Rendus Palevol*, 12:519-530.

Godfrey, S. J., Barnes, L. G. and Bohaska, D. J. (2006): *Araeodelphis natator* Kellogg, 1957, the most primitive known member of the Platanistidae (Odontoceti, Cetacea), and relationships to other clades within the Platanistoidea. *Journal of Vertebrate Paleontology*, 26: 68A.

Grateloup, J. P. S. (1840): Description d'un fragment de machoire fossile, d'un genre nouveau de reptile (saurien). *Actes de l'Academie Nationale des Sciences Belles-Letres et Arts de Bordeaux*, 2:201-210.

Gray, J. E. (1846): On the cetaceous animals. *In* Richardson, J. and Gray, J. E. (eds.) The zoology of the voyage of H.M.S. Erebus and Terror, under the command of captain Sir James Clark Ross during the years 1839 to 1843. Volume 1: Mammalia, Birds. E. W. Janson, London, p.13-53.

Gray, J. E. (1863): On the arrangement of the cetaceans. *Proceedings of the Scientific Meetings of the Zoological Society of London*, 31:197-202.

Gray, J. E. (1868): Synopsis of the species of whales and dolphins in the collection of the British Museum. Bernard Quaritch, London, 10 pp.

Herald, E. S., Brownell, R. L., Frye, F. L., Morris, E. J., Evans, W. E. and Scott, A. B. (1969): Blind river dolphin: first side-swimming cetacean. *Science*, 166:1408-1410.

Hershkovitz, P. (1961): On the nomenclature of certain whales. *Fieldiana Zoology*, 39:547-565.

Heyning, J. E. and Mead, J. G. (1996): Suction feeding in beaked whales: morphological and observational evidence. *Contributions in Science, Natural History Museum of Los Angeles County*, (464):1-12.

Hoch, E. (2000): Olfaction in whales: evidence from a young odontocete of the Late Oligocene North Sea. *Historical Biology*, 14:67-89.

Holl, F. (1829): Handbuch der Petrefactenkunde, mit einer Einleitung über die Vorwelt der organischen Wesen auf der Erde von Dr. Ludwig Choulant. *P. G. Hilscher'sche Buchhandlung, Dresden*, 1:1-115.

Howell, A. B. (1927): Contribution to the anatomy of the Chinese finless porpoise, *Neomeris phocaenoides*. *Proceedings of the United States National Museum*, 70:1-43.

Howell, A. B. (1930): Myology of the narwhal (*Monodon monoceros*). *The American Journal of Anatomy*, 46:187-215.

Jefferson, T. A., Leatherwood, S. and Webber, M. A. (1993): FAO species identification guide. *Marine mammals of the world*. Food and Agriculture Organization of the United Nations, Rome, 320 pp.

Johnston, C. and Berta, A. (2011): Comparative anatomy and evolutionary history of suction feeding in cetaceans. *Marine Mammal Science*, 27:493-513.

Jourdan, C. (1861): Description de restes fossiles de deux grands mammifères constituant deux genres, l'un le genre Rhizoprion de l'ordre des Cétecés et du groupe des Delphinoides; l'autre le genre Dynocyon de l'ordre des Carnassiers et de la familie des Canidés. *Annales des Sciences Naturelles*, 16:369-374.

Kellogg, A. R. (1923): Description of two squalodonts recently discovered in the Calvert Cliffs, Maryland; and notes on the shark-toothed cetaceans. *Proceedings of the United States National Museum*, 62:1-69.

Kellogg, A. R. (1924): A fossil porpoise from the Calvert Formation of Maryland. *Proceedings of the United States National Museum*, 63:1-39.

Kellogg, A. R. (1925): On the occurrence of remains of fossil porpoises of the genus Eurhinodelphis in North America. *Proceedings of the United States National Museum*, 66:1-40.

Kellogg, A. R. (1926): Supplementary observations on the skull of the fossil porpoise *Zarhachis flagellator* Cope. *Proceedings of the United States National Museum*, 67:1-18.

Kellogg, R. E. (1928): The history of whales - their adaptation to life in the water. *Quarterly Review of Biology*, 3:29-76, 174-208.

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

Kellogg, A. R. (1936): A review of the Archaeoceti. *Carnegie Institution of Washington Publication*, (482):1-366.

Kellogg, R. E. (1957): Two additional Miocene porpoises from the Calvert Cliffs Maryland. *Proceedings of the United States National Museum*, 107:279-337.

Ketten, D. R. (1992): The cetacean ear: Form, frequency, and evolution. *In* Thomas, J. A., Kastelein, R. A. and Supin, A. Y. (eds.) Marine mammal Sensory Sestems. Plenum Press, New York, p. 53-75.

Ketten, D. R. and Wartzok, D. (1990): Three-dimensional reconstruction of the dolphin ear. *In* Thomas, J. and Kastelein, R. (eds.) Sensory Abilities of Cetaceans. Plenum Press, New York, p. 81-105.

Kimura, T. (2015): A new allodelphinid from Japan, and the swimming and feeding strategies of the Allodelphinidae. *In* Abstracts of the 164th Regular Meeting of the Paleontological Society of Japan, p. 22. (in Japanese)

Kimura, T., Barnes, L. G. and Rivin, M. A. (2011): The platanistoid family Allodelphinidae, and a new early Miocene species from central Japan. *In* Abstracts of the Sixth Triennial Conference on Secondary Adaptation of Tetrapods to Life in Water, p.44-45.

Kimura, T. and Ozawa, T. (2001): An Early Miocene odontocete from the Awa Group, central Japan. *In* Abstracts of the 150th Regular Meeting of the Palaeontological Society of Japan, p. 92. (in Japanese)

Lambert, O. (2005a): Phylogenetic affinities of the long-snouted dolphin

Eurhinodelphis (Cetacea, Odontoceti) from the Miocene of Antwerp, Belgium. *Palaeontology*, 48:653-679.

Lambert, O. (2005b): Review of the long-snouted dolphin *Priscodelphinus cristatus* du bus, 1872 (Cetacea, Odontoceti) and phylogeny among eurhinodelphinids. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 75:211-235.

Lambert, O., Bianucci, G. and Urbina, M. (2014): *Huaridelphis raimondii*, a new early Miocene Squalodelphinidae (Cetacea, Odontoceti) from the Chilcatay Formation, Peru. *Journal of Vertebrate Paleontology*, 34:987-1004.

Lambert, O., Muizon, C. de and Bianucci, G. (2013): The most basal beaked whale *Ninoziphius platyrostris* Muizon, 1983: clues on the evolutionary history of the family Ziphiidae (Cetacea: Odontoceti). *Zoological Journal of the Linnaean Society*, 167:569-598.

Leidy, J. (1869): The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences, Philadelphia*, 2:1-472.

Lesson, R. P. (1828): Cétacés. *Complément des oeuvres de Buffon ou Histoire Naturelle des animaux rares découverts par les naturalistes et les voyageurs depuis la mort de Buffon*. 1:1-442.

Linnaeus, C. (1758): Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Laurentii Salvii, Holmiae, Stockholm, 823 pp.

Luo, Z. and Eastman, E. R. (1995): Petrosal and inner ear of a squalodontid whale: Implicationsfor evolution of hearing in odontocetes. *Journal of Vertebrate Paleontology*, 15:431-442.

Lydekker, R. (1892): On zeuglodont and other cetacean remains from the Tertiary of the Caucasus. *In* Proceedings of the Zoological Society of London for the year 1892, p. 558-564.

Maddison, W. P. and Maddison, D. R. (1992): MacClade, Version 3.01. Sinauer Associates, Inc., Sunderland, Massachusetts , 404 pp.

Mchedlidze, G. A. (1984): Fossilized Whale from the Miocene Deposits in the Environs of the Village of Otradnaya (Northern Caucasus). "Metsniereba" Press, Tbilisi, 64 pp.

Mead, J. G. (1975): Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). *Smithsonian Contributions to Zoology*, (207):1-72.

Mead, J. G. (1989): Bottlenose whales - *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* Flower, 1882. *In*, Ridgway, S. H. and Harrison, R. (eds.) Handbook of Marine Mammals. Volume 4: River dolphins and the larger toothed whales. Academic Press, San Diego, p. 321-348.

Mead, J. G. and Fordyce, R. E. (2009): The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology*,(627):1-248.

Miller, G. S. (1923): The telescoping of the cetacean skull. *Smithsonian Miscellaneous Collections*, 76:1-70.

Mitchell, E. D. (1965): History of research at Sharktooth Hill, Kern County, California. *In* Special Publication of the Kern County Historical Society, p.1-45

Mitchell, E. D. and R. H. Tedford. (1973). The Enaliarctinae. A new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bulletin of the American Museum of Natural History*, 151:201-284.

Moore, E. J. (1964): Miocene marine mollusks from the Astoria Formation in Oregon. *United States Geological Survey Professional Paper*, 419:1-109. [for 1963, published in 1964]

Moore, E. J. and Addicott, W. O. (1987): The Miocene Pillarian and Newportian (Molluscan) stages of Washington and Oregon and their usefulness in correlations from Alaska to California. United States Geological Survey Bulletin, 1664:A1-A13.

Moore, E. J. and Moore, G. W. (2002): Miocene molluscan fossils and stratigraphy, Newport, Oregon. *Field Guide to Geologic Processes in Cascadia, Oregon Department of Geology and Mineral Industries, Special Paper*, (369):187-200.

Moran, M., Bajpai, S., George, J. C., Suydam, R., Usip, S., and Thewissen, J. G. M. (2015): Intervertebral and epiphyseal fusion in the postnatal ontogeny of cetaceans and terrestrial mammals. *Journal of Mammalian Evolution*, 22:93-109.

Moreno, F. P. (1892): Lijeros apuntes sobre dos generos de cetaceos fosiles de la Republica Argentina. *Revista del Museo de La Plata*, 3:393-400.

Morgan, G. S. (1994): Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of central Florida. *Proceedings of the San Diego Society of Natural History*, (29):239-268.

Muizon, C. de (1987): The affinities of *Notocetus vanbenedeni*, an Early Miocene platanistoid (Cetacea, Mammalia) from Patagonia, southern Argentina. *American Museum Novitates*, (2904):1-27.

Muizon, C. de (1988): Le polyphylétisme des Acrodelphidae, odontocètes longirostres des Miocène européen. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Sciences de la Terre, Série 4*, 10:31-88.

Muizon, C. de (1994): Are the squalodonts related to the platanistoids? *Proceedings of the San Diego Society of Natural History*, (29):135-146.

Muizon, C. de (2009): River dolphins, evolutionary history and affinities. *In* Perrin, W. F., Würsig, B. W. and Thewissen, J. G. M. (eds.) Encyclopedia of Marine Mammals. 2nd edition. Academic Press, San Diego, p. 979-986.

Muizon, C. de and Domning, D. P. (2002): The anatomy of *Odobenocetops* (Delphinoidea, Mammalia), the walrus-like dolphin from the Pliocene of Peru and its palaeobiological implications. *Zoological Journal of the Linnaean Society*, 134:423-452.

Muizon, C. de, Domning, D. P. and Ketten, D. R. (2002): *Odobenocetops peruvianus*, the walrus-convergent delphinoid (Mammalia: Cetacea) from the early Pliocene of Peru. *Smithsonian Contributions to Paleobiology*, (93):223-261.

Müller, J. (1849): Über die fossilen Reste der Zeuglodonten von Nordamerica, mit Rücksicht auf die europäischen Reste aus dieser Familie. Verlag von G. Reimer, Berlin, 38 pp.

Murakami, M., Shimada, C., Hikida, Y. and Hirano, H. (2012a): A new basal porpoise,*Pterophocaena nishinoi*(Cetacea, Odontoceti, Delphinoidea), from the upper Miocene of Japan and its phylogenetic relationships. *Journal of Vertebrate Paleontology*, 32:1157-1171.

Murakami, M., Shimada, C., Hikida, Y. and Hirano, H. (2012b): Two new extinct basal phocoenids (Cetacea, Odontoceti, Delphinoidea), from the upper Miocene Koetoi Formation of Japan and their phylogenetic significance. *Journal of Vertebrate Paleontology*, 32:1172-1185.

Murakami, M., Shimada, C., Hikida, Y. and Hirano, H. (2014a): Asymmetrical Basal Delphinoid Skull from the Upper Lower Miocene Yamato Formation of Hokkaido, Northern Japan: Implications on Evolution of Cranial Asymmetry and Symmetry in Odontoceti. *Paleontological Research*, 18:134-149.

Murakami, M., Shimada, C., Hikida, Y., Soeda, Y. and Hirano, H. (2014b): *Eodelphis kabatensis*, a new name for the oldest true dolphin Stenella kabatensis Horikawa, 1977 (Cetacea, Odontoceti, Delphinidae), from the upper Miocene of Japan, and the phylogeny and paleobiogeography of Delphinoidea. *Journal of Vertebrate Paleontology*, 34:491-511.

Norris, K. S. (1968): The evolution of acoustic mechanisms in odontocete cetaceans. *In* Drake, E. T. (ed.) Evolution and environment: a symposium presented on the occasion of the one hundredth anniversary of the foundation of the Peabody Museum of Natural History at Yale University. Yale University Press, New Haven, Connecticut, p. 297-324.

Ogden, J. A., Conlogue, G. J., and Rhodin, A. G. J. (1981): Roentgenographic indicators of skeletal maturity in marine mammals (Cetacea). *Skeletal Radiology*, 7:119-123.

Owen, R. (1853): Order Cetacea. *In* Descriptive catalogue of the osteological series contained in the Museum of the Royal College of Surgeons of England, Volume 2. Taylor and Francis, London, p.439-458.

Pabst, D. A. (1990): Axial muscles and connective tissues of the bottlenose dolphin. *In* Leatherwood, S. and Reeves, R. R. (eds.) The Bottlenose Dolphin. Academic Press, San Diego, California, p. 51-67.

Perrin, W. F. (1975): Variation of spotted and spinner porpoise (genus *Stenella*) in the Eastern Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography*, 21:1-206.

Pilleri, G. and Gihr, M. (1976): The function and osteology of the manus of *Platanista gangetica* and *Platanista indi. Investigations on Cetacea*, 7:109-118.

Pilleri, G., Gihr, M. and Kraus, C. (1970): Feeding behaviour of the Gangetic dolphin, *Platanista gangetica*, in captivity. *Investigations on Cetacea*, 2:69-73.

Pilleri, G., Gihr, M., Purves, P. E., Zbinden, K. and Kraus, C. (1976): On the behaviour, bioacoustics and functional morphology of the Indus River dolphin (*Platanista indi* Blyth, 1859). *Investigations on Cetacea*, 6:11-137.

Prothero, D. R., Bitboul, C. Z., Moore, G. W. and Moore, E. J. (2001): Magnetic stratigraphy of the lower and middle Miocene Astoria Formation, Lincoln County, Oregon. *In* Prothero, D.R. (ed.) Magnetic Stratigraphy of the Pacific Coast Cenozoic. Pacific Section. Society of Economic Paleontologists and Mineralogists, Society for Sedimentary Geology, Book 91, p. 272-283.

Prothero, D. R., Liter, M. R., Barnes, L. G., Wang, X., Mitchell, E. D., McLeod, S. A., Whistler, D. P., Tedford, R. H. and Ray, C. E. (2008): Land mammals from the Middle Miocene Sharktooth Hill Bonebed, Kern County, California. *Bulletin of the New Mexico Museum of Natural History and Science*, (44):299-314.

Prothero, D. R., Sanchez, F. and Denke, L. L. (2008): Magnetic stratigraphy of the Early to Middle Miocene Olcese Sand and Round Mountain

Silt, Kern County, California. *Neogene Mammals, Bulletin of the New Mexico Museum of Natural History and Science*, (44):357-363.

Purves, P. and Pilleri, G. (1975): Observations on the ear, nose, throat and eye of *Platanista indi*. *Investigations on Cetacea*, 5:13-57.

Pyenson, N. D., Irmis, R. B., Lipps, J. H., Barnes, L. G., Mitchell, E. D. and McLeod, S. A. (2009): The origin of a widespread marine bonebed deposited during the Middle Miocene climatic optimum. *Geology*, 37:519-522.

Racicot, R. A., Deméré, T. A., Beatty, B. L. and Boessenecker, R. W. (2014): Unique feeding morphology in a new prognathous extinct porpoise from the Pliocene of California. *Current biology*, 24:774-779.

Reichenbach, H. G. L. (1847): Systematisches. *In* Carus, C. G. (ed.) Resultate geologischer, anatomischer und zoologischer Untersuchungen über das unter dem Namen Hydrarchos von Dr. A. C. Koch zuerst nach Europa gebrachte und in Dresden angestellte grosse fossile Skelett. Arnoldische Buchlandlung, Dresden and Leipzig, p. 13-15.

Rice, D. W. (1998): Marine mammals of the world. Systematics and distribution. *The Society for Marine Mammalogy, Special Publication*, (4):1-231.

Roxburgh, W. (1801): An account of a new species of *Delphinus*, an inhabitant of the Ganges. *Asiatic Researches (Calcutta)*, 7:170-174.

Sanchez, J. A. and Berta, A. (2010): Comparative anatomy and evolution of the odontocete forelimb. *Marine Mammal Science*, 26:140-160.

Sanders, A. E. and Barnes, L. G. (2002): Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina. 3: Eomysticetidae, a new family of primitive mysticetes (Mammalia: Cetacea). *Smithsonian Contributions to Paleobiology*, (93):313-356.

Simpson, G. G. (1945): The principles of classification, and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85:1–350.

Spoor, F., Bajpai, S., Hussain, S. T., Kumar, K. and Thewissen, J. G. M. (2002): Vestibular evidence for the evolution of aquatic behaviour in ealy cetaceans. *Nature*, 417:163-166.

Strickler, T. L. (1980): The axial musculature of *Pontoporia blainvillei*, with comments on the organization of this system and its effect on fluke-stroke dynamics in the Cetacea. *American Journal of Anatomy*, 157:49-59.

Swift, C. C. and Barnes, L. G. (1996). Stomach contents of *Basilosaurus cetoides*: implications for the evolution of cetacean feeding behavior and evidence for vertebrate fauna of epicontinental Eocene seas. *Abstracts of Papers, Sixth North American Paleontological Convention. The Paleontological Society, Special Publication*, (8):380.

Tanaka, Y. and Fordyce, R. E. (2014): Fossil dolphin *Otekaikea marplesi* (latest Oligocene, New Zealand) expands the morphological and axonomic diversity of Oligocene cetaceans. *PloS ONE*, :9(9): e107972.

Taylor, M. A. (1987): How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnaean Society*, 91:171-195.

Tedford, R. H., Skinner, M. F., Fields, R. W., Rensberger, J. M., Whistler, D. P., Galusha, T., Taylor, B. E., Macdonald, J. R. and Webb, S. D. (1987): Faunal succession and biochronology of the Arikareean through Hemphillian interval (Late Oligocene through earliest Pliocene epochs) in North America. *In* Woodburne, M. O. (ed.) Cenozoic Mammals of North America. Geocrhonology and Biostratigraphy. University of California Press, Berkeley, Los Angeles, p.153-210.

Tedford, R. H., Albright, L. B., III, Barnosky, A. D., Ferrusquía-Villafranca, I., Hunt, R. M., Jr., Storer, J. E., Swisher, C. C., III, Voorhies, M. R., Webb, S. D. and Whistler, D. P. (2004): Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Early Pliocene epochs. *In* Woodburne, M. O. (ed.) Late Cretaceous and Cenozoic Mammals of North America. Biostratigraphy and Geochronology. Columbia University Press, New York, p.169-231.

Thomas, H. W. and Barnes, L. G. (2015): The bone joint pathology osteochondrosis in extant and fossil marine mammals. *Contributions in Science, Natural History Museum of Los Angeles County*, (523):1-35.

Thomas, H. W., Barnes, L. G., Klein, J. E. and McLeod, S. A. (2008): Examples of paleopathologies in some fossil Cetacea from the North Pacific realm. *Science Series, Natural History Museum of Los Angeles County*, (41):153-179.

Turner, W. (1910): The morphology of the manus in *Platanista gangetica*, the dolphin of the Ganges. *Proceedings of the Royal Society of Edinburgh*, 30:508-514.

Uhen, M. D. (2004): Form, function and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an archaeocete from the Middle to Late Eocene of Egypt. *University of Michigan, Papers on Paleontology*, (34):1-222.

Van Beneden, P. J. (1861): Un mammifere nouveau du Ccrag d'Anvers. *Bulletins de L'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 12:22-28.

Van Beneden, P. J. (1865): Recheres sur les ossements provenant du crag d'Anvers. Les Squalodons. *Memoires de L'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 35:1-80.

Wagler, J. G. (1830): Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur vergleichenden Zoologie. J.G. Cotta'schen Buchhandlung, München, 354 pp.

Werth, A. J. (1992): Anatomy and evolution of odontocete suction feeding. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts, 313 pp.

Werth, A. J. (2000a): Feeding in marine mammals. *In* Schwenk, K. (ed.) Feeding Form, Function, and Evolution in Tetrapod Vertebrates. Academic Press, San Diego, p. 475-514.

Werth, A. J. (2000b): A kinematic study of suction feeding and associated behavior in the long-finned pilot whale, *Globicephala melas* (Traill). *Marine Mammal Science*, 16:299-314.

Werth, A. J. (2004): Functional morphology of the sperm whale (*Physeter macrocephalus*) tongue, with reference to suction feeding. *Aquatic Mammals*, 30:405-418.

Werth, A. J. (2006a): Odontocete suction feeding: experimental analysis of water flow and head shape. *Journal of Morphology*, 267:1415-1428.

Werth, A. J. (2006b): Mandibular and dental variation and the evolution of suction feeding in Odontoceti. *Journal of Mammalogy*, 87:579-588.

Werth, A. J. (2007): Adaptations of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation. *Anatomical Record*, 290:546-568.

Whitmore, F. C., Jr. and Kaltenbach, J. A. (2007): Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. *Special Publication of the Virginia Museum of Natural History*, (14):181-269.

Whitmore, F. C., Jr. and Sanders, A. E. (1977): Review of the Oligocene Cetacea. *Systematic Zoology*, 25:304-320.

Wilson, L. E. (1935): Miocene marine mammals from the Bakersfield region, California. *Bulletin of the Peabody Museum of Natural History*, (4):1-143.

Wolfe, E. W. and McKee, E. H. (1968): Geology of the Grays River Quadrangle, Wahkiakum and Pacific counties, Washington. *Washington State Department of Natural Resources, Division of Mines and Geology*, Geologic Map GM-4.

Wood, F. G. and Evans, W. E. (1980): Adaptiveness and ecology of echolocation in toothed whales. *In* Busnel, R. G. and Fish, F. J. (eds.) Animal Sonar Systems. Plenum Press, New York, p. 381-425.

Woodward, B. L., Winn, J. P. and Fish, F. E. (2006): Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology*, 267:1284-1294.

Yamada, M. (1953): Contribution to the anatomy of the organ of hearing of whales. *The Scientific Reports of the Whales Research Institute (Tokyo)*, (8):1-79.

Yamada, M. (1960): On the hearing organ of cetacea, with special reference to the problems of dispute of its structural characteristics. *Journal of the Juzen Medical Society* , 66:1-15.

Yamada, M. and Yoshizaki, F. (1959): Osseous labyrinth of Cetacea. *The Scientific Reports of the Whale Research Institute (Tokyo)*, (14):291-304.

Yanagisawa, Y. and Akiba, F. (1998): Refined Neogene diatom biostratigraphy for the northwest Pacific around Japan, with an introduction of code numbers for selected diatom biohorizons. *Journal of the Geological Society of Japan*, 104:395-414.

Yoshida, F. (1987): Planktonic foraminifera from the Miocene Awa Group, Mie Prefecture, central Japan. *Bulletin of the Geological Survey of Japan*, 38:473–483. (in Japanese with English abstract)

Yoshida, F. (1991): Planktonic Foraminifera from the Ichishi, Fujiwara, and Morozaki groups in the eastern Setouchi Geologic Province, central Japan. *Bulletin of the Mizunami Fossil Museum*, (18): 19-31.

北太平洋の中新統より産出した新たなアロデルフィス科クジラ類（クジラ目ハクジラ亜目ガンジスカワイルカ上科）

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要旨：アロデルフィス科はハクジラ亜目ガンジスカワイルカ上科の絶滅科であり，これまで北太平洋沿岸の下部－中部中新統の海成層より産出が知られている．彼らは体長およそ3－5メートルに達すると推定される比較的大型のハクジラ類で，長い吻部，癒合した下顎結合を持ち吻部前端まで達する下顎骨，大きくて前後に長い頚椎，長い上腕骨を持つ．既知のアロデルフィス類は下部中新統産の*Allodelphis pratti* Wilson, 1935および*A. woodburnei* Barnes and Reynolds, 2009, 中部中新統産の*Zarhinocetus errabundus* (Kellogg, 1931)で，いずれもカリフォルニア産である．本論文では新たに以下のアロデルフィス類を報告する：*Goedertius oregonensis* Barnes and Kimura, new genus and new species,（前期中新世，Nye泥岩，アメリカ合衆国オレゴン州Lincoln郡産）, *Ninjadelphis ujiharai* Kimura, new genus and new species,（前期中新世, 阿波層群, 三重県伊賀市産）, *Zarhinocetus donnamatsonae* Barnes, new species,（前期中新世後期/中期中新世前期，アストリア累層，アメリカ合衆国ワシントン州Grays Harbor郡産）．*Goedertius oregonensis*は*Allodelphis*属のいずれの種よりも派生的な形質を持つ．*Ninjadelphis ujiharai*は*Goedertius oregonensis*に比べて前上顎骨の後端が前方に位置するなど，より派生的な形質を獲得している．*Zarhinocetus*属のいずれの種も吻部基部の上顎骨背面には隆起が発達するとともに眼窩背側の上顎骨背面には前後方向の稜が発達する．*Zarhinocetus donnamatsonae*は*N. ujiharai*よりも更に派生的な形質により特徴付けられるが，アロデルフィス科において最も派生的な形質を持つ*Zarhinocetus errabundus*に比較すると祖先的な形質を持つ．

クジラ類の一般的な進化傾向とは逆にアロデルフィス類では前後に長い頚椎の椎体を獲得しており，頚椎間の癒合は発達しない．アロデルフィス類では非常に長い頚部や大きな後頭骨，厚い項稜などを持つことから，頚部および頭部の運動に関する筋が非常に発達していたことが示唆される．彼らはきわめて細長い吻部を用いて底生あるいは遊泳する餌生物を捕食する噛み付き摂餌者(raptorial feeder)であったと考えられる．さらにアロデルフィス科内に見られる形態変異はアロデルフィス科内におけるニッチ分化の存在を示している可能性がある．また彼らは高速遊泳というよりは低速で遊泳し，操縦性の高い遊泳戦略であったと考えられる．

キーワード：中新世クジラ類化石，カワイルカ上科，アロデルフィス科，*Allodelphis*，*Goedertius*，*Ninjadelphis*，*Zarhinocetus*，底生生物捕食者，遊泳戦略