

An Early Miocene long-snouted marine platanistid dolphin (Mammalia, Cetacea, Odontoceti) from the Korneuburg Basin (Austria)

by

Lawrence G. BARNES*

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Abstract

The dolphin family Platanistidae is represented by relatively common fossils from Miocene marine deposits of the Northern Hemisphere, but is today represented only by the living dolphins called the susus, members of the genus *Platanista* WAGLER, 1830, which live in fresh water environments of southeast Asia. A new genus and species of marine long-snouted platanistid dolphin, *Prepomatodelphis korneuburgensis*, is represented by a well-preserved skull from the Karpatian (latest Early Miocene) of Teiritzberg in the Korneuburg Basin, Austria. This dolphin shares with other members of the family Platanistidae such cranial characters as the lateral lamina of the pterygoid bone in the ventromedial part of the orbit, a long and slender rostrum with an anteroposteriorly aligned groove on either side following the maxilla/premaxilla suture, and a dorsoventrally expanded zygomatic process of the squamosal which has an enlarged and medially-directed glenoid fossa. Its closest relationships are with members of the extinct Miocene platanistid genera *Pomatodelphis* ALLEN, 1921, and *Zarhachis* COPE, 1868, with whom it shares a dorsoventrally flattened rostrum and dorsoventrally flattened symphyseal portion of the mandible, but from whom it differs by lacking a thickened supraorbital process and by having a thickened border on its lambdoidal crest.

Two subfamilies can now be recognized within the family Platanistidae. The new subfamily Pomatodelphininae includes the Northern Hemisphere genera *Prepomatodelphis*, new genus (Early Miocene, Austria), *Pomatodelphis* (Middle and Late Miocene, France, Florida), and *Zarhachis* (Middle Miocene, Maryland). Members of the subfamily Pomatodelphininae can be identified by their dorsoventrally flattened rostra and symphyseal portions of their mandibles. The subfamily Platanistinae, used here in a new context, includes only the Recent genus *Platanista*. It shares with members of the subfamily Pomatodelphininae an elongate and pointed anterior process on the tympanic bulla, a lateral lamina of the pterygoid bone in the orbit, and other characters that define the fa-

mily Platanistidae. Unique characters that define the subfamily Platanistinae include an anteroposteriorly lengthened zygomatic process of the squamosal, transversely flattened rostrum and symphyseal portion of the mandible, a large pneumaticized supraorbital crest, and numerous other derived characters.

Zusammenfassung

Fossile Delphine aus der Familie der Platanistidae sind in miozänen marinen Sedimenten der nördlichen Hemisphäre relativ häufig. Rezent existiert jedoch nur mehr eine ausschließlich im Süßwasser lebende Gattung, der Ganges-Delphin (*Platanista* WAGLER, 1830), der in Südostasien beheimatet ist. Eine neue Gattung und Art eines marinen platanistiden Delphins aus dem Karpatium (Untermiozän) des Korneuburger Beckens (Teiritzberg; Österreich), die durch einen gut erhaltenen Schädel belegt ist, wird im folgenden beschrieben. Zu den nächsten Verwandten zählen die ausgestorbenen miozänen Gattungen *Pomatodelphis* ALLEN, 1921 und *Zarhachis* COPE, 1868, die ebenfalls ein dorsoventral abgeflachtes Rostrum und einen dorsoventral abgeflachten symphysealen Bereich der Mandibel aufweisen. Im Gegensatz zu den beiden genannten Gattungen fehlt bei dem Fund aus dem Korneuburger Becken unter anderem der verdickte supraorbitale Fortsatz.

Innerhalb der Familie der Platanistidae können zwei Unterfamilien unterschieden werden: Die neu eingeführte Unterfamilie Pomatodelphininae umfaßt die in der nördlichen Hemisphäre verbreiteten Gattungen *Prepomatodelphis* (Untermiozän, Österreich), *Pomatodelphis* (Mittelmiozän und Obermiozän; Frankreich, Florida) und *Zarhachis* (Mittelmiozän, Maryland). Die Unterfamilie Platanistinae wird neu definiert und umfaßt nur mehr die rezente Gattung *Platanista*.

Schlüsselwörter

Cetacea – Platanistidae – Pomatodelphininae – *Prepomatodelphis korneuburgensis*, neue Gattung und neue Art – Karpatium – Untermiozän – Korneuburger Becken – Österreich

* Anschrift d. Verf.: Curator of Vertebrate Paleontology, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007, U. S. A.

Key words

Cetacea – Platanistidae – Pomatodelphininae – Korneuburg Basin – Austria – Miocene – *Prepomatodelphis korneuburgensis* – new genus and species

Introduction

The Odontoceti are the clade of echolocating toothed whales. Several different lineages of long-snouted, dolphin-like odontocetes evolved during the Middle and Late Tertiary (BARNES et al., 1985), and their fossils are relatively common and widespread in various parts of the world, especially in Miocene marine deposits. Ironically, such long-snouted dolphins, which are among some of the earliest cetacean fossils to have been studied by paleontologists, continue to confront researchers with many problems relating to their identification and relationships. Some of these long-snouted dolphins are members of the odontocete family Platanistidae, and their fossils have been reported from Europe and from North America.

The family Platanistidae is classified in a higher category of Odontoceti, the superfamily Platanistoidea, within which are also included other families of early and relatively primitive odontocetes that represent several clades of diverse dolphin-like animals. Known from the Late Oligocene to the Recent, platanistoid odontocetes have the same geochronologic range as do the typical, modern, pelagic delphinoid dolphins that are classified within such families as the Kentriodontidae, Albireonidae, Delphinidae, Phocoenidae, and Monodontidae (BARNES, 1977, 1984, 1997; FORDYCE and BARNES, 1994; FORDYCE et al., 1995).

The superfamily Delphinoidea increased in abundance and taxonomic diversity during middle and later Cenozoic time, in both marine and fresh water environments. Conversely, the superfamily Platanistoidea, which also originated in marine environments and approximately at the same time, decreased in abundance and diversity through the later Cenozoic. Platanistoids survive now only as one relict fresh water genus, *Platanista* WAGLER, 1830, which includes the Recent, but extremely imperiled, Ganges River dolphin, *Platanista gangetica* (ROXBURGH, 1801) of India and Pakistan (see HERSHKOVITZ, 1966). Fossil platanistoids have not yet been reported from any strictly fresh water deposits.

Extremely long-snouted fossil Platanistidae, for example species of the genera *Pomatodelphis* ALLEN, 1921, and *Zarhachis* COPE, 1868, are characteristic of Miocene sedimentary marine deposits in Europe and on the east coast of North America. The taxonomy of these fossil dolphins has not been precisely established, and few recent publications deal with the subject. MUIZON (1987, 1988a, 1994), FORDYCE (1994), and MORGAN (1994) dealt with some aspects of fossil platanistoid relationships and taxonomy.

A relatively complete skull of a long-snouted platanistoid dolphin was found in the latest Early Miocene Central Paratethyan Karpatian stage (early MN5, Chron C5Cn3n between 16,5 and 16,7 Million years) at Teiritzberg 001/I/1-2-3-4/1989 in the Korneuburg Basin, Austria (a detailed description of the locality was given by SOVIS,

1998). The cranium of this specimen demonstrates the diagnostic characteristics of the family Platanistidae, and its completeness allows a confident identification of the specimen. It is the purpose of this paper to report on this new skull of a platanistid dolphin, to identify it and name it as a new taxon, to comment on its relationships, and to make some new observations of the morphology and some changes in the systematics of the platanistid odontocetes to which it is related. The geology of the area in which the specimen was found has been documented by WESSELY (1998).

Material and Methods

Institutional abbreviations are as follows:

CAS	Division of Birds and Mammals, California Academy of Sciences, San Francisco, California, U. S. A.
MCZ	Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts, U. S. A.
NHMW	Natural History Museum, Vienna, Austria.
UMMP	Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, U. S. A.
USNM	Department of Paleobiology, United States National Museum of Natural History, Smithsonian Institution, Washington D. C., U. S. A.

Millions of years ago is abbreviated Ma. Illustrations of the skull were made with the axis of the rostrum in a horizontal or vertical plane in all views to achieve standard orientation.

The comparisons made in this study were based on the following specimens and sources:

The holotype of the Middle Miocene (Helvetian correlative) *Pomatodelphis stenorhynchus* (HOLL, 1829), from France (which in some publications was referred to and illustrated under its junior synonym *Delphinus renovi* LAURILLARD, 1844), is the proximal rostral part of the right maxilla and premaxilla. It was illustrated by VAN BENEDEEN and GERVAIS (1874-1880), and I observed it in the Muséum Nationale d'Histoire Naturelle in Paris. No other specimens can be confidently referred to this taxon at this time.

For comparisons with *Pomatodelphis inaequalis* ALLEN, 1921, I relied on the holotype and referred specimens as indicated by ALLEN (1921), and on the referred specimen (MCZ 4433) that was described by KELLOGG (1959). All are from the Bone Valley Formation of Florida, U. S. A., and are of late Middle Miocene age, approximately 10,5 to 11,5 Ma, correlative with the early part of the Clarendonian North American Land Mammal Age (MORGAN, 1994: 251-252).

The holotype specimen (UMMP 15117) of *Pomatodelphis bobengi* (CASE, 1934) is from the same deposits as the specimens mentioned above of *Pomatodelphis inaequalis*. Information about the cranial characters of *Zarhachis flagellator* COPE, 1868, is based on USNM 10485, a partial skeleton that includes the rostral portion of a skull and a

periotic, referred to this species and described by KELLOGG (1924); on USNM 10911, which is another partial skull that was described by KELLOGG (1926); and on USNM 13768, an unpublished referred specimen. All of these are from the lower part of the Calvert Formation in Maryland, U. S. A., and are of middle Middle Miocene age (GOTTFRIED et al., 1994: 233), correlative with the Barstovian North American Land Mammal Age, approximately 13 to 15 Ma. The holotype of *Zarhachis flagellator* is a vertebra (COPE, 1868) from the same formation. For comparisons with Recent *Platanista gangetica* (ROXBURGH, 1801) I used CAS 16340, a cranium, mandible, and skeleton of an adult female from Sind, Pakistan.

Systematic Paleontology

Class Mammalia LINNAEUS, 1758

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1864

Superfamily Platanistoidea (GRAY, 1863) SIMPSON, 1945

Included families. Squalodontidae BRANDT, 1872; Waipatiidae FORDYCE, 1994; Squalodelphinidae DALPIAZ, 1916; possibly the Acrodelphinidae ABEL, 1905; Dalpiaziniidae MUIZON, 1988a; and the Platanistidae (GRAY, 1863).

Comments. The superfamily Platanistoidea takes its identity from the family Platanistidae. Following the conclusions of MUIZON (1987, 1988a, 1994), and FORDYCE (1994), the superfamily Platanistoidea now includes a diversity of related odontocetes: members of the archaic shark-toothed dolphin family Squalodontidae, the heterodont and symmetrical-skulled Waipatiidae, the Squalodelphinidae which have very thick supraorbital processes, the diminutive Dalpiaziniidae, possibly the long-snouted Acrodelphinidae, and the modern fresh-water Platanistidae. The majority of the taxa in these families are of Oligocene and Miocene age (MUIZON, 1988b, 1994; BARNES, 1977, 1997; BARNES et al., 1985; FORDYCE, 1994; FORDYCE and BARNES, 1994; FORDYCE et al., 1995).

MUIZON (1987, 1988a, 1994) expanded the previous concepts (*sensu* SIMPSON, 1945) of the superfamily Platanistoidea by including in it, as well as other family-level groups, the large-toothed primitive odontocetes of the family Squalodontidae. MUIZON (1988a) 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 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 the 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, 1971.

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 are addressed in the following text.

Family Platanistidae (GRAY, 1863)

Emended diagnosis of family. Members of the superfamily Platanistoidea having cranium with elongate and narrow rostrum, premaxillae and maxillae both reaching the anterior rostral extremity, premaxillae and maxillae fused distally, anteroposteriorly elongated groove present on the lateral side of the rostrum approximately following the maxilla/premaxilla suture, posterior maxillary foramen very close to the posterior end of the premaxilla (positioned at the posterior margin of the premaxilla, and in some taxa overhung by the margin of that bone), lateral lamina of the pterygoid present (formed as an outer lamina or bony plate of the pterygoid within the orbit that extends posteriorly from the palate and contacts with the styliiform process of the squamosal), peg present on ridge on articular process of periotic, tympanic bulla with an elongate and pointed anterior process or spine, tympanic bulla with a thin outer lip that is smoothly overarching and high relative to the transverse width of the bulla; symphyseal portion of mandible narrow and anteroposteriorly elongated, mandibular symphysis anteroposteriorly elongate and firmly ankylosed; and all teeth single-rooted.

Type genus. *Platanista* WAGLER, 1830.

Included subfamilies. Pomatodelphininae, new subfamily; and Platanistinae (GRAY, 1863), new context.

Comments. The diagnosis of the family Platanistidae provided above is more detailed and more taxonomically restrictive than those that have been previously provided. It employs osteological characters that can be compared between fossil and Recent taxa. Some of these characters, principally those of the periotic and tympanic bulla, were among those that were listed in the character analysis by FORDYCE (1994).

All known fossil and Recent members of the family Platanistidae have an elongate and narrow rostrum and symphyseal portion of the mandible. A long and narrow rostrum has evolved independently in various clades of Odontoceti (for example among the members of the families Eurhinodelphinidae, Pontoporiidae, Iniidae, Kentriodontidae, and Delphinidae), and it has evolved at various times in various clades. Nonetheless, I include the long and narrow rostrum as one of the diagnostic characters of the family Platanistidae.

Contradictory to FORDYCE (1994), I do not include the presence of a supraorbital crest among the diagnostic characters of the family Platanistidae. Such a crest is not demonstrably present in all specimens, nor in all taxa of Platanistidae, and it might have evolved convergently more than once within the family.

Distribution. Early to Late Miocene, in the North Atlantic realm and the North Pacific Ocean (CROWLEY et al., 1999); Recent in freshwater habitats of southeast Asia (HERSHKOVITZ, 1966).

Subfamily Platanistinae (GRAY, 1863), new context

Emended diagnosis of subfamily. A subfamily of the family Platanistidae that includes animals having cranium with transversely flattened rostrum, posterior end of premaxilla tapered (not expanded transversely), enlarged and anteriorly extended zygomatic process of squamosal, atrophied eye, extreme development of left-skew asymmetry of the cranial vertex, reduced nasal bones, greatly enlarged supraorbital crests (formed by maxillary bones and pneumaticized by extensions from the middle ear air sinus system), reduced lambdoidal crests, secondarily thickened zygomatic process of the jugal; transversely flattened symphyseal portion of mandible; and secondary heterodonty (crowns of anterior teeth greatly elongated apically, crowns of posterior teeth widened transversely).

Type genus. *Platanista* WAGLER, 1830.

Included genera. *Platanista* WAGLER, 1830.

Comments. The subfamily Platanistinae has its basis in taxonomy from the genus *Platanista* WAGLER, 1830, whose type species is the living, endangered, *Platanista gangetica* (ROXBURGH, 1801), the fresh water Ganges River dolphin (or susu) of the Ganges, Bramaputra and Meghna river systems of Nepal, Bangladesh, and India (see HERSHKOVITZ, 1966). The other living species in this genus is *Platanista minor* OWEN, 1853, the Indus dolphin of the Indus River system of Pakistan and India. *Platanista indi* BLYTH, 1859, is a junior synonym of *P. minor*. Here I use the subfamily Platanistinae in a restricted sense, and at the present writing I include in it only the living genus *Platanista*. Some un-named fossil taxa will in the future be assigned to the subfamily Platanistinae, some of these being from the North Pacific Basin (CROWLEY et al., 1999; BARNES, 1977).

The establishment here of this new context for the subfamily Platanistinae serves to distinguish this clade from a separate clade of fossil Platanistidae, which is recognized below as a different subfamily, the Pomatodelphininae. The subfamily Platanistinae includes the most highly derived species of Platanistidae, and pedomorphism may have been involved in the development of some of the derived characters of the group. When fossil taxa are added to this subfamily, it will undoubtedly become necessary to transfer from the subfamily diagnosis to a generic diagnosis some of the derived characters of *Platanista* that are related to the adaptations to muddy fresh waters. Establishment of the new context for the subfamily Platanistinae allows for a more precise taxonomic placement of the new taxon of platanistid from the Korneuburg Basin, which is described in the following text.

Subfamily Pomatodelphininae, new subfamily

Diagnosis of subfamily. A subfamily of the family Platanistidae that includes animals differing from members of the subfamily Platanistinae by having cranium with dorsoventrally (rather than transversely) flattened rostrum, posterior end of premaxilla transversely expanded (rather than narrow and tapered), enlarged and dorsoventrally expanded zygomatic process of squamosal, eye and bony orbit of normal size (not atrophied), lacking extreme degree of left-skew asymmetry of the cranial vertex, nasal bones not reduced in size, supraorbital crest absent, or when present, never pneumaticized by extensions from the middle ear air sinus system, lambdoidal crests enlarged and prominent; dorsoventrally (rather than transversely) flattened symphyseal portion of mandible; and crowns of all teeth simple, conical, and of similar shape (absence of secondary heterodonty).

Type genus. *Pomatodelphis* ALLEN, 1921.

Included genera. *Prepomatodelphis*, new genus; *Pomatodelphis* ALLEN, 1921; and *Zarhachis* COPE, 1868.

Comments. MORGAN (1994), in a review of fossil Cetacea from Florida, clarified the identities of some problematic Miocene platanistids that I assign to the subfamily Pomatodelphininae, and I have incorporated his conclusions in the following observations.

Pomatodelphis ALLEN, 1921, is a platanistid genus whose species have dorsoventrally flattened rostra and whose mandibular symphyses are likewise dorsoventrally flattened. The type species of this genus is *Pomatodelphis inaequalis* ALLEN, 1921, which is known from the late Middle Miocene Agricola Fauna that is derived from the Bone Valley Formation in central Florida. Fossil land mammals that are mixed with the marine mammals in this fauna provide a correlation with the early part of the Clarendonian North American Land Mammal Age, and an age of approximately 10,5 to 11,5 Ma. When ALLEN (1921) named *Pomatodelphis inaequalis*, he designated as its holotype (MCZ 15750) a fragment of the proximal part of the right maxilla, representing the posterior part of the rostrum. However, he referred to the species a much more complete specimen (Florida Geological Survey 2343), which consists of the rostrum and other cranial parts of one individual.

KELLOGG (1959) later referred a nearly complete skull (MCZ 4433) to this species. Many additional specimens of *Pomatodelphis inaequalis* have subsequently been found, the species has become relatively well known, and MORGAN (1994: 252) reported that it is the most abundant cetacean in the Agricola Fauna of the Bone Valley Formation in central Florida.

MORGAN (1994: 251) declared *Pomatodelphis inaequalis* to be the senior synonym of *Schizodelphis depressus* ALLEN, 1921, another platanistid species that MILLER described in the same publication and from the same deposit. Although *Schizodelphis depressus* has page priority over *P. inaequalis*, it was based on a rostral fragment that possibly

is not diagnostic at the species level, and *P. inaequalis* is the better known and more thoroughly described species. CASE (1934) described another, larger species of platanistid, *Schizodelphis bobengi*, based on a skull with associated mandibles and ear bones (UMMP 15117) from the same phosphate deposits of Florida that yielded the specimens that were used by ALLEN (1921) to describe *Schizodelphis depressus* and *Pomatodelphis inaequalis*. MORGAN (1994) transferred this species to *Pomatodelphis*, thus creating the new binomen *Pomatodelphis bobengi*. The genus *Pomatodelphis* includes another referred species (see ALLEN, 1921), which is *P. stenorhynchus* (HOLL, 1829), of Middle Miocene age from France. The holotype of *Pomatodelphis stenorhynchus* is the proximal rostral part of the right maxilla and premaxilla. The specimen is sufficiently complete to demonstrate that the rostrum is dorsoventrally flattened, and that it is thus assignable to the subfamily Pomatodelphininae. Immediately anterior to the antorbital notch, the lateral margin of the maxilla is thickened and laterally expanded, and this same character is also present in the North American Miocene pomatodelphinine platanistids *Zarhachis flagellator*, *Pomatodelphis bobengi*, and *Pomatodelphis inaequalis*. However, although *P. stenorhynchus* can be confidently referred to the subfamily Pomatodelphininae, because the holotype of this species lacks preserved characters of the braincase that are useful in distinguishing species, it might prove difficult to objectively determine its generic or specific relationships.

Zarhachis COPE, 1868, is another long-snouted Miocene genus whose members have dorsoventrally flattened rostra and dorsoventrally flattened symphyseal portions of the mandibles. The type species, *Zarhachis flagellator* COPE, 1868, was based on a caudal vertebra from the Middle Miocene Calvert Formation of Maryland, which is the holotype, and on three other vertebrae. When he named *Zarhachis*, COPE (1868) had also named *Zarhachis velox* and *Z. tysonii*. KELLOGG (1924) assigned to *Zarhachis flagellator* a skull lacking the brain case, and (1924: 3) restricted the genus *Zarhachis* to the species *Z. flagellator*. When KELLOGG (1924) referred a partial skeleton (USNM 10485) to *Zarhachis flagellator*, he noted (KELLOGG, 1924b:4) that the vertebral position that is represented by the holotype caudal vertebra of *Zarhachis flagellator* is not represented in this subsequently referred partial skeleton. Therefore, the referred specimens, which include skulls (KELLOGG, 1924, 1926), and upon which all subsequent determinations of the relationships of *Zarhachis flagellator* have been based, are not directly comparable with the holotype material. Furthermore, the genus and species have their basis in one vertebra.

Of the three genera that I refer to the new subfamily Pomatodelphininae, I have selected *Pomatodelphis* ALLEN, 1921, to be the type genus because its type species, *Pomatodelphis inaequalis* ALLEN, 1921, is based upon and is known by the most complete and diagnostic cranial material of any taxon in this group. This is in contrast to the situation with *Zarhachis flagellator*, a species to which wonderfully complete cranial material has been subsequently referred, but which, as noted above, might poten-

tially have problematic typology. There remains the possibility that revision of this taxon could raise questions about the taxonomic utility of its holotype material. The holotype skull of *Prepomatodelphis korneuburgensis*, new genus and species, is not as complete as are skulls that have been referred to either *Pomatodelphis inaequalis* or *Zarhachis flagellator*, and for this reason I chose not to base the new subfamily on *Prepomatodelphis*, new genus.

Prepomatodelphis, new genus

Diagnosis of genus. A genus of the subfamily Pomatodelphininae differing from *Zarhachis* and *Pomatodelphis* by being smaller; by having cranium with surface of the premaxillary sac fossa undulating, having in its mid-part a sulcus bounded both medially and laterally by a ridge, and sloping ventrally at both its medial and lateral margins; zygomatic process of squamosal very deep dorsoventrally in the posterior part; and a thick and rounded lambdoidal crest where it forms the posterior margin of the temporal fossa; by lacking dorsoventrally thickened supraorbital process; and by having a thinner nuchal crest; and differing further from *Zarhachis* by having a relatively larger and deeper posterolateral premaxillary sulcus, a relatively wider posterior termination of premaxilla, and by having posterior termination of premaxilla bifurcated, with the bifurcation containing an exposed wedge of the maxillary bone.

Type species. *Prepomatodelphis korneuburgensis*, new species.

Included species. *Prepomatodelphis korneuburgensis*, new species only.

Etymology. The generic name reflects the primitive nature of this taxon, which has morphological characters that could be antecedent to those of *Pomatodelphis*

Distribution. Karpatian (latest Early Miocene; early MN5), Korneuburg Basin, Austria.

Prepomatodelphis korneuburgensis, new species

Figures 1a-c, 2a-c

Diagnosis of species. Because the genus *Prepomatodelphis* is at present monotypic, the diagnosis of the genus and species shall remain identical until further species are described in the genus.

Holotype. NHMW 2002z0001/0000, cranium lacking part of the left side of the braincase and rostrum, collected by Dr. Reinhard ROETZEL (Geologische Bundesanstalt Wien) and Dr. Wolfgang SOVIS, 22 October 1989.

Type locality. Teiritzberg 001/I/1-2-3-4/1989, on the Teiritzberg / Korneuburg, Lower Austria. The locality was given by SOVIS in "Das Karpat des Korneuburger Beckens. Teil 1" (1998).

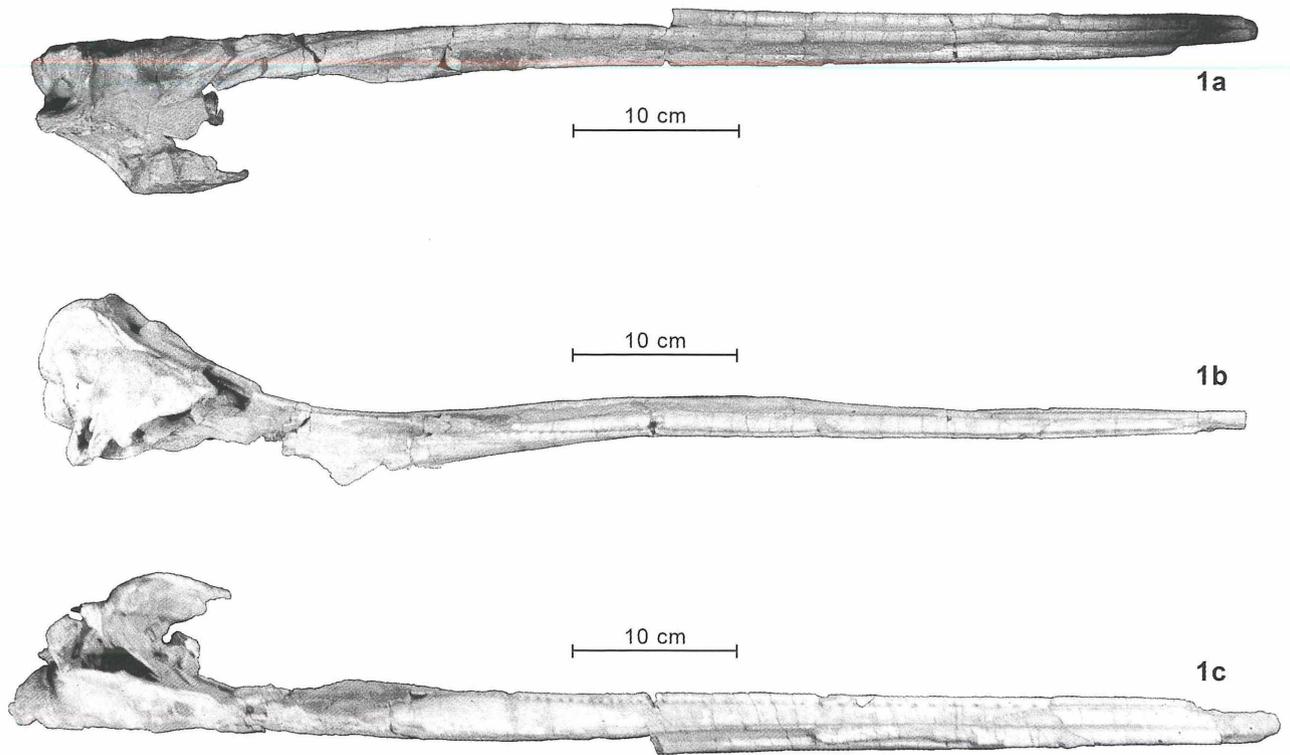


Fig. 1: *Prepomatodelphis korneuburgensis*, new genus and species, holotype skull, NHMW 2002z0001/0000; 1a: dorsal view; 1b: right lateral view; 1c: ventral view.

Etymology. The species name calls attention to its distribution which, as presently known, is limited to the Korneuburg Basin of Austria.

Description and comparisons. The holotype specimen is comprised of a nearly complete cranium. The cranium is represented for essentially its total original length as preserved, from near the anterior rostral extremity to the occipital condyles (Fig. 1). On the left side, the braincase and the posterior part of the rostrum have been cut away by machinery. The rostral extremity, the lateral part of the right supraorbital process, and the lateral border of the rostrum immediately anterior to it were eroded away before final deposition and fossilization. Neither a periotic nor a tympanic bulla are associated with the cranium. The specimen represents an individual that was mature at the time of its death, because the articular surfaces in the glenoid fossa and on the occipital condyle are smooth and dense, the lambdoidal crest is large, and the cranial sutures are closed. It was not an old individual, however, because the cranial sutures were not obliterated from fusion. This is an extremely long-snouted dolphin skull. Although the exact original length of the rostrum cannot be determined for the holotype specimen, the rostrum comprises approximately 75% of the original total skull length. The braincase is relatively small, but it has relatively large zygomatic processes of the squamosals, large occipital condyles, and a relatively small supraorbital process.

As in species of *Zarhachis* and *Pomatodelphis*, the rostrum is compressed (flattened) dorsoventrally, and it is

expanded transversely. These features are especially noticeable in the anterior part of the rostrum (Fig. 1c). Although the rostral extremity was eroded away prior to final fossilization, it appears that the rostrum is nearly complete and is missing no more than 10 or 20 mm from its anterior extremity. In its anterior half, the rostrum is markedly compressed dorsoventrally, being wider than it is high. Beginning in the middle of the rostrum, the premaxillae arch dorsally, and their flatness is less extreme in this part of the rostrum. Approaching the facial region, the rostrum is deeper, and this is emphasized by the depth of the ventral part of the rostrum in this area. The anterior parts of both maxillae, both on the palatal and the lateral surfaces of the rostrum, were broken off prior to fossilization, so neither maxilla reaches as far as the preserved anterior extremities of the premaxillae. Judging by the degree of taper of both of the maxillae, however, it appears that in life they both extended as far as the anterior extremities of the premaxillae. This is the case in skulls of other related Platanistidae, such as in *Zarhachis flagellator* (see KELLOGG, 1924: pl. 1) and in *Pomatodelphis inaequalis* (see KELLOGG, 1959: pl. 6).

The rostral portions of the premaxillae are composed of dense bone, whose surface is faintly striated. Only the anterior half of the left premaxilla is preserved, the remainder having been broken away by human activity after fossilization. The preserved part of the left premaxilla demonstrates that for more than half the rostral length, the right and left premaxillae met at the midline and that they roofed over the mesorostral groove (Fig. 1a). The curvature of the medial border of the preserved right premaxil-

la indicates that when the skull was complete, the mesorostral groove was similarly closed over dorsally for the entire rostral length, except for that part which is immediately anterior to the facial region.

No teeth are present in the holotype, so inferences about the nature of the rostral dentition are derived from the empty dental alveoli that remain. Neither rostral alveolar row is completely preserved, but the right row is more complete than the left although, due to breakage and erosion, it has several gaps and is missing its anterior part. The right rostral alveolar row now has approximately 58 alveoli, and when complete, it probably had nearly 75 teeth. The uncertainty in both of these counts results from some missing bone where alveoli were present. As is typical of other members of the subfamily Pomatodelphininae, the rostral teeth are relatively widely separated. The anterior teeth are relatively more widely separated and have larger diameter roots than the posterior teeth. The roots of the posterior teeth were shorter and of smaller diameter than those of the anterior teeth, and are more closely spaced. None were crowded together, however.

At the posterior end of the rostral alveolar row, the lateral margin of the right maxilla is thickened dorsoventrally and spreads laterally. Immediately anterior to the antorbital notch, the right maxilla is broken away, but the parts surrounding this area indicate that this specimen had a thick, flared, lateral part of the maxilla anterior to the antorbital notch. This feature is present in all other species of the Pomatodelphininae.

Approaching the posterior portion of the rostrum, immediately anterior to the narial passages, the right and left premaxillae diverge. At this place, there is a triangular-shaped, rough area on the dorsal surface of the premaxilla that marks the attachment in life of the nasal plug retractor muscle (Fig. 2a). In the middle of this rough area was the premaxillary foramen. A depression where the foramen was located is present on the right premaxilla, but the foramen itself is no longer preserved on the holotype specimen. On the right premaxilla, the indistinct anteromedial premaxillary sulcus extends anteriorly from this point. A relatively large and deep posterolateral premaxillary sulcus is present, and it traverses obliquely posterolaterally across the dorsal surface of the premaxilla, reaching the lateral margin of the premaxilla in the area dorsal to the posterior part of the orbit (Fig. 2a). In its depth and size, this posterolateral sulcus exceeds the posterolateral sulcus in the more primitive Late Oligocene waipatiid platanistoid, *Waipatia maerewhenua* (see FORDYCE, 1994: figs. 4a, 5a). The area on the holotype skull of *Prepomatodelphis korneuburgensis* where the right posteromedial premaxillary sulcus would have been is not preserved.

The posterior-most part of the preserved right premaxilla is very wide adjacent to the narial passage, having a maximum width of at least 31 mm at this place. This wide part of the premaxilla is dense and smooth, and it marks the location in life of the premaxillary sac. The premaxillary sac of an odontocete is a diverticulum from the lateral wall of each dorsal narial passage. These sacs lie clo-

sely upon the dorsal surface of the skull, each sac being closely appressed to its corresponding premaxillary bone on the lateral side of each bony dorsal narial opening of the cranium (MEAD, 1975). The former locations and approximate shapes in life of these sacs can be determined on skulls of Recent and fossil Odontoceti by the presence of a widened and smooth area where the sac was appressed to the dorsal surface of each premaxillary bone. The premaxillary sacs of the Odontoceti are apparently involved in the movement of air that is involved in the production of sounds that are used by these cetaceans for echolocation. Odontocetes also have other cranial modifications that allow for the reception of reflected sounds. The propagation of sounds into the environment by an odontocete, and the reception by the animal of reflected sounds, perform the function of organic echolocation (NORRIS, 1968; BRILL et al., 1988; CRANFORD et al., 1996; MEAD, 1975; WOOD and EVANS, 1980).

The premaxillary sac fossa of *Prepomatodelphis korneuburgensis* is not nearly so flat, however, as it typically is in most Odontoceti. Instead, in the holotype skull, the premaxillary sac fossa is undulating, having in its mid-part a sulcus bounded both medially and laterally by a ridge, and sloping ventrally at both its medial and lateral margins.

The posterior termination of the premaxilla is very wide transversely. This exceptional width of the posterior end of the premaxilla is a derived character. By contrast, in both *Waipatia maerewhenua* and Recent *Platanista gangetica* the posterior end of the premaxilla tapers to a narrow end. In *Prepomatodelphis korneuburgensis* the posterior end of the premaxilla bifurcates, and within this bifurcation there is an exposed wedge of the maxillary bone. This exposure of the maxillary bone is located in the lateral part of the posterior premaxillary termination. Similarly the much more narrow posterior end of the premaxilla in *Waipatia maerewhenua* is likewise bifurcated, although not so deeply as in *Prepomatodelphis korneuburgensis*, and within the gap in the premaxilla there is an exposure of the maxilla. The less prominent bifurcation of the posterior end of the premaxilla in Recent *Platanista gangetica* is undoubtedly a derived character state, resulting from reduction of the bifurcation.

The right supraorbital process of the holotype of *Prepomatodelphis korneuburgensis* is not complete, but it is partially preserved. Enough of the horizontally projecting parts of the maxilla and the supraorbital process of the frontal are present to indicate that the species did not have a dorsoventrally thickened supraorbital process. The combined thickness of the preserved parts of the maxilla and frontal over the orbit is only approximately 2 to 3 mm. All other known platanistids for which the supraorbital process is preserved have some type of derived condition. In *Pomatodelphis inaequalis*, the supraorbital process is dorsoventrally thickened and elevated. In *Zarhachis flagellator* it is also thickened, but in addition to this, at the lateral border of the orbit, the lateral margins of the frontal and maxilla are elevated, extended dorsally, and re-curved medially. In Recent *Platanista*, the supraorbital

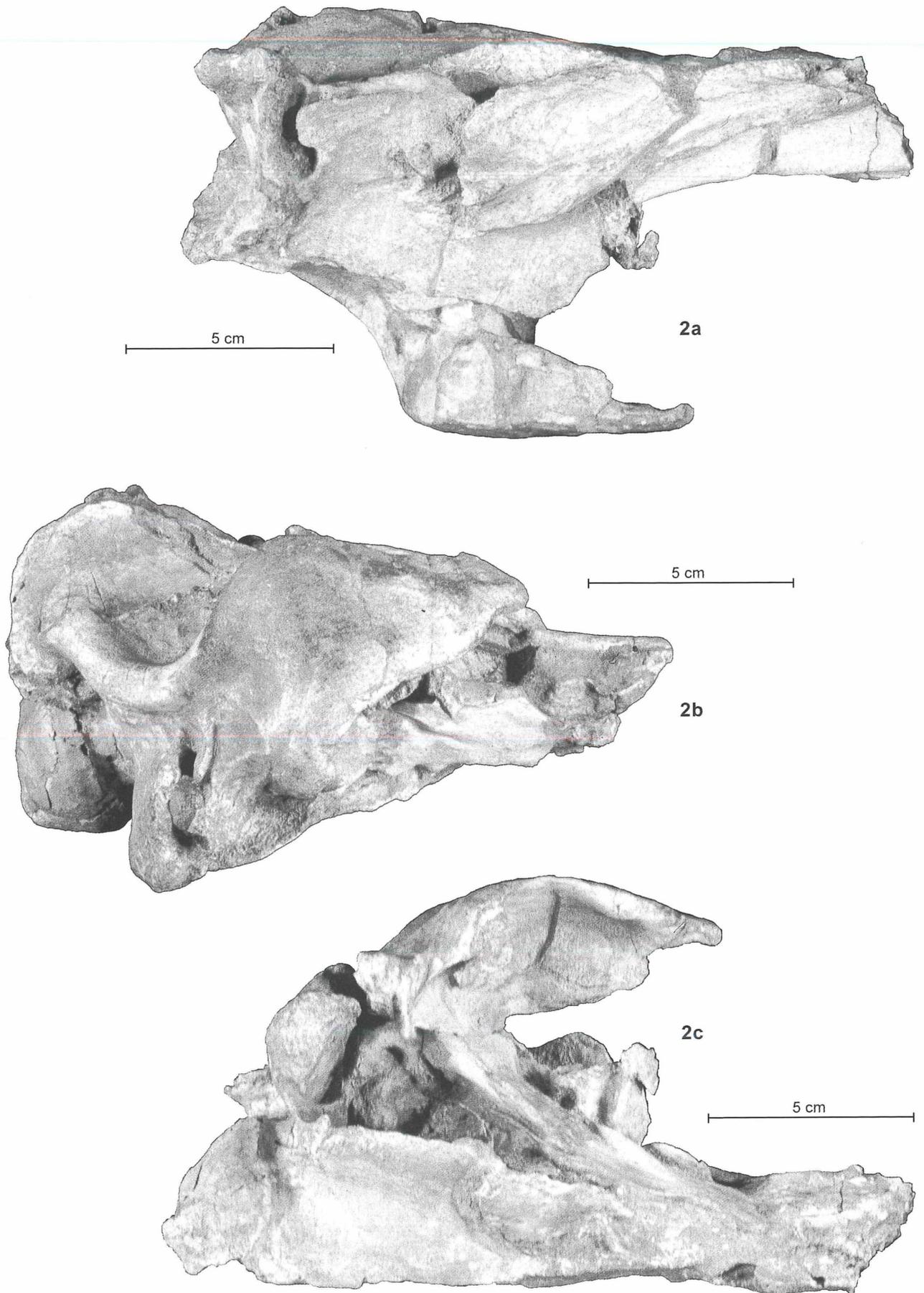


Fig. 2: *Prepomatodelphis korneuburgensis*, new genus and species, enlarged views of the braincase of the holotype, NHMW 2002z0001/0000; 2a: dorsal view; 2b: right lateral view; 2c: ventral view.

crest is thin, very extensive dorsally, posteriorly and anteriorly, and is penetrated by numerous passages that contain pneumatic tissue. The structure of the supraorbital process in *Prepomatodelphis korneuburgensis* is the most primitive of any known platanistid skull, and it is constructed as it is in “typical” generalized odontocetes. This is consistent with the other primitive characters of this species. Only the right margin of the right narial passage is preserved, so the sizes and shapes of the dorsal nares cannot be determined in *Prepomatodelphis korneuburgensis*. Based on the preserved bone (see Fig. 2a), however, it appears that the nares were relatively small and tapered anteriorly. In both *Pomatodelphis inaequalis* and *Zarhachis flagellator* the dorsal nares are proportionally larger and are oval in shape.

Likewise, it is not possible, based on the holotype specimen of *Prepomatodelphis korneuburgensis*, to determine if its cranial vertex was symmetrical or asymmetrical. The bones that would be involved in cranial asymmetry, the nasals, frontals, and the apex of the nuchal crest, are not preserved. For an odontocete, the temporal fossa of *Prepomatodelphis korneuburgensis* is relatively large in relation to the size of the braincase. There has been considerable distortion of the temporal fossa as a result of breakage, offset, and geologic compression at the squamosal/parietal suture, but it is possible to estimate the original size of the opening of the temporal fossa. By subtracting 11 mm from the measurement to account for anteroposterior offset, it can be estimated that the temporal fossa originally measured approximately 53 mm anteroposteriorly. By adding 17 mm to the measurement to account for dorsoventral compression, it can be estimated that the temporal fossa originally measured approximately 62 mm dorsoventrally. The temporal fossa opens posteriorly where the lambdoidal crest wraps around the posterolateral corner of the braincase at its mid-height. The posterodorsal part of the temporal fossa is slightly over-hung by the parietal and the maxilla. In its anterior part, the temporal fossa is roofed over by a horizontal extension of the posterior part of the supraorbital process. The temporal fossa is bordered posteroventrally by a thick, projecting, and rounded lateral part of the lambdoidal crest. The thickening of this crest is an autapomorphy of *Prepomatodelphis korneuburgensis*. In other generalized Odontoceti and in other Platanistidae this crest is narrow and sharp, and that is the primitive condition.

The right zygomatic process of the squamosal is virtually complete on the holotype skull of *Prepomatodelphis korneuburgensis*. It is enlarged, and it is expanded dorsoventrally, especially so in its posterior part (Fig. 2b). This dorsoventral expansion of the posterior part of the zygomatic process of the squamosal is more extensive than in *Pomatodelphis inaequalis* and *Zarhachis flagellator*, and this is another autapomorphy of *Prepomatodelphis korneuburgensis*. Its shape is similar to that of the zygomatic process of Recent *Platanista*, which is also expanded dorsoventrally, although in that genus the expansion is more prominent in the medial and anterior parts, and the zygomatic process is more elongate anteroposteriorly. The

dorsoventral expansion of the zygomatic process of *Prepomatodelphis korneuburgensis* results in an enlarged, vertically expanded glenoid fossa, which faces medially, toward the lateral wall of the braincase, rather than anteroventrally; the latter being the primitive character state that is present in most Odontoceti. This derived character state is likewise present in *Platanista*. Both the dorsal and ventral margins of the zygomatic process of *Prepomatodelphis korneuburgensis* are transversely narrow and smoothly rounded.

The lateral surface of the zygomatic process of *Prepomatodelphis korneuburgensis* is nearly a vertical and featureless surface. Just ventral to its mid-part, it is very slightly concave near the anterior end, and also near the posterior end, at which point the lateral surface curves medially into the muscle fossa. There is a small notch in the ventral margin of the process at its anteroventral corner (Fig. 2b), near the presumed point of attachment of the posterior end of the zygomatic process of the jugal. Toward the posterior end of the zygomatic process of the squamosal, the ventral margin curves medially and becomes confluent with a strongly re-curved postglenoid process. The ventral extremity of the postglenoid process is so prominently bent that it projects almost horizontally in an anterior direction (Fig. 2c). This anterior projection lies ventral to a greatly excavated posterior part of the glenoid fossa. The actual surface of the glenoid fossa measures 55 mm anteroposteriorly and 33 mm dorsoventrally in its greatest dimensions, and it occupies most of the medial side of the zygomatic process. At the anterior part of the zygomatic process there is only a small triangular area on the medial surface that is not occupied by the glenoid fossa. The posteromedial margin of the glenoid fossa is clearly marked by a thin, raised lip of bone that ascends vertically from the postglenoid process. This raised lip of bone curves dorsolaterally toward the dorsal margin of the zygomatic process. This lip also defines the lateral margin of the fossa for the middle sinus (see FRASER and PURVES, 1960, for terminology) ventrally, and this middle sinus fossa occupies a wide concavity between the glenoid fossa and the ear region.

The basicranium of *Prepomatodelphis korneuburgensis* is very similar to that of both *Pomatodelphis inaequalis* and *Zarhachis flagellator*, but is more lightly constructed. A prominent feature of the basicranium is the well-developed lateral lamina of the pterygoid bone (Fig. 2c). In the typical platanistid manner, this lateral lamina is formed as a posterior extension of the pterygoid, extending posterolaterally from the posterolateral corner of the palate. This lateral lamina passes along the lateral side of the internal narial passage, through the ventromedial part of the orbit, and connects, via an interdigitating suture (see Fig. 2b), to the ventrally-projecting styliiform process of the squamosal. The lateral surface of the lateral lamina is faintly undulating. The lateral lamina of the pterygoid thus encloses the anterior part of the cranial hiatus, making its anterior part very narrow where it encloses part of the fossa for the pterygoid sinus. Due to breakage, the anterior extent of the pterygoid sinus fossa cannot be determined.

The basioccipital crests diverge slightly posteriorly from the sagittal plane, and thus are not so parallel as they are in either *Pomatodelphis inaequalis* or *Zarhachis flagellator*. These crests in *Prepomatodelphis korneuburgensis* are more slender than they are in the two former species, and in this regard *P. korneuburgensis* is the more primitive of the three species.

The median lacerate foramen (Fig. 2c) is large and distinct, and it is surrounded by thick bone that lies dorsal to the periotic. The external acoustic meatus is marked by a narrow, transversely-oriented sulcus in the ventral surface of the squamosal posterior to the postglenoid process. As in other species of Pomatodelphininae, there is a prominent vertical cleft separating the external acoustic meatus from the paroccipital process. The paroccipital process is obliquely oriented, rather than transversely oriented as it is in *Pomatodelphis inaequalis* and *Zarhachis flagellator*. The paroccipital process is relatively thick anteroposteriorly in *Prepomatodelphis korneuburgensis*, and it is proportionally thicker than it is in the latter two species. This is an apomorphy of *Prepomatodelphis korneuburgensis*.

Only the right occipital condyle is preserved on the holotype specimen of *Prepomatodelphis korneuburgensis*. The occipital condyle is very convex posteriorly, relatively large, and protrudes prominently from the occipital shield. As an indication of the relatively large size of the condyles, when the skull was complete, in posterior view the condyles would have occupied approximately 1/4 of the area of the occipital shield. The dorsal margin of the right occipital condyle is nearly continuous with the plane of the posterior surface of the supraoccipital bone; there does not appear to have been a prominent supracondylar fossa as is present in some Odontoceti. The lateral margin of the right occipital condyle is prolonged laterally at mid-height toward the posterior margin of the temporal fossa. The condyle is also positioned at the lowest part of the occipital shield, and the articular surface extends ventrolaterally farther than the occipital shield. The margin of the articular surface of the condyle in this area is clearly defined and slightly raised. In its ventral part, the articular surface of the right condyle curves posteriorly, so it appears that the ventral parts of the right and left occipital condyles were not confluent when they were complete. The medial margin of the right occipital condyle is nearly straight in a dorsoventral plane, and is slightly protruded posteriorly. The relative size, position, and prominent convexity of the occipital condyles resemble the same structures in *Zarhachis flagellator* and *Pomatodelphis inaequalis*.

Classification

The following classification of the Platanistidae is derived in part from classifications by FORDYCE (1994), FORDYCE and BARNES (1994), and FORDYCE et al. (1995), and was modified on the basis of the morphological observations and characters that are discussed in this study. This revised classification places *Prepomatodelphis korneu-*

burgensis in taxonomic context with the other platanistoids. 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, 1863) SIMPSON, 1945

Family Squalodontidae BRANDT, 1872

Family Waipatiidae FORDYCE, 1994

Family Squalodelphinidae (DAL PIAZ, 1916) RICE, 1998

Family Dalpiaziniidae (MUIZON, 1988a) MUIZON, 1994

?Family Acrodelphinidae (ABEL, 1905) RICE, 1998

Family Platanistidae (GRAY, 1863)

Subfamily Pomatodelphininae, new subfamily

Prepomatodelphis, new genus

Prepomatodelphis korneuburgensis, new species

Pomatodelphis ALLEN, 1921

Pomatodelphis stenorhynchus (HOLL, 1829)

Pomatodelphis inaequalis ALLEN, 1921

Pomatodelphis bobengi (CASE, 1934)

Zarhachis COPE, 1868

Zarhachis flagellator COPE, 1868

Subfamily Platanistinae

Platanista WAGLER, 1830

Platanista gangetica (ROXBURGH, 1801)

Platanista minor OWEN, 1853

Conclusions

1. *Prepomatodelphis korneuburgensis*, a new genus and species of odontocete cetacean in the family Platanistidae, is based on a nearly complete skull from the Karpatian (latest Early Miocene) in the Korneuburg Basin, Austria.
2. This is the most primitive known member of the family Platanistidae, as demonstrated by its small size, and non-thickened, non-elevated supraorbital process. Among its autapomorphies are: dorsoventrally very deep posterior part of the zygomatic process of the squamosal, thick paroccipital process, and a thick and rounded lateral part of the lambdoidal crest posterior to the temporal fossa.
3. The paleontological record demonstrates that members of the family Platanistidae were much more widespread in the past than they are now. Unlike the living *Platanista* of India, Bangladesh, and Pakistan, which is exclusively fresh water in distribution, all of the known fossil platanistid dolphins are from marine, or at least partly marine deposits, in the Northern Hemisphere.
4. All fossil and Recent members of the family Platanistidae have exceptionally long and narrow rostra and symphyseal portions of their mandibles.
5. The described Platanistidae can be classified in two subfamilies: the new fossil subfamily Pomatodelphininae, and the subfamily Platanistinae, which is used here in an emended context.

6. The new subfamily Pomatodelphininae includes all of the named fossil Platanistidae: members of the extinct genera *Prepomatodelphis*, new genus; *Zarhachis* COPE, 1868; and *Pomatodelphis* ALLEN, 1921. These dolphins are Middle and Late Miocene in age, and are known only from the North Atlantic realm - from marine deposits in Europe and from the eastern margin of North America. Unique derived characters of the Pomatodelphininae include a wide posterior end of the premaxilla, dorsoventrally flattened rostrum and symphyseal portions of the mandible, and the development in the derived taxa of a dorsoventrally thickened supraorbital process.
5. The subfamily Platanistinae, employed here in a new context, presently includes only the living genus *Platanista* WAGLER, 1830. Its Recent species include the fresh water susus of southeastern Asia, *Platanista gangetica* (ROXBURGH, 1801), and *Platanista minor* OWEN, 1853. The Platanistinae are comparatively high derived odontocete taxa. Among their unique derived characters are: small size, enlarged and anteriorly extended zygomatic process of squamosal, atrophied eye, extreme left-skew asymmetry of the cranial vertex, reduced nasal bones, greatly enlarged supraorbital crests (formed by maxillary bones and pneumaticized by extensions from the middle ear air sinus system), reduced lambdoidal crests, secondarily thickened zygomatic process of the jugal, transversely flattened rostrum and symphyseal part of the mandible, secondary heterodonty (crowns of anterior teeth greatly elongated, crowns of posterior teeth widened), and pedomorphism (which accounts for some of the derived characters).

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