The Affinities of *Notocetus vanbenedeni,* an Early Miocene Platanistoid (Cetacea, Mammalia) from Patagonia, Southern Argentina

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ABSTRACT

The study of previously undescribed material of the Early Miocene Odontocete Cetacean *Notocetus vanbenedeni* allows a new interpretation of its relationships, and a reevaluation of the taxon Platanistoidea. The new specimen consists of a well preserved auditory region (periotic, tympanic, malleus, stapes, squamosal, and partial occipital) associated with several teeth and some postcranial elements (scapula, vertebrae, and rib fragments). The presence of an articular rim on the periotic and the morphology of the tympanic demonstrate the close relationship of *Notocetus* with the Platanistidae. *Notocetus* is referable to the family Squalodelphidae, which also includes the genera *Squalodelphis* and *Phocageneus.* This family is the sister-group of the Platanistidae, which consists of the genera *Platanista, Zarachis,* and *Pomatodelphis.* Platanistidae and Squalodelphidae are regarded as the sister-groups of the Squalodontidae on the basis of two synapomorphies of the scapula:

the loss of the coracoid process and the acromion located on the anterior edge. These three families (Platanistidae, Squalodelphidae, and Squalodontidae) constitute the Platanistoidea. The Squalodontidae, however, may be poly- or paraphyletic as they are defined by symplesiomorphies only; they are not analyzed here and the group is tentatively regarded as monophyletic. The phylogenetic relationships of this family will be considered elsewhere. The ziphiid affinities of *Notocetus vanbenedeni,* assumed by some previous workers, are rejected. The Ziphiidae could, however, have their origin in some squalodont-like odontocetes, a statement which favors a possible polyphyletism of the Squalodontidae.

Notocetus is an Argentinian genus, but the occurrence of a periotic and a partial tympanic from the Calvert Formation of Maryland extends the distribution of the genus to the Middle Miocene of North America.

INTRODUCTION

Notocetus vanbenedeni was first described under that name by Moreno (1892) on the basis of a well preserved skull and associated mandible. Later, True (1910) described a new specimen consisting of a nearly complete skull, mandible, some ribs, and vertebrae. Both skulls lack the periotics, while a tympanic bone is associated with the specimen

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described by True. The collections of the American Museum of Natural History include a specimen (AMNH 29026) here referred to *Notocetus vanbenedeni* that consists of a partial right squamosal and occipital, complete tympanic, periotic and malleus, several teeth, a scapula, and some incomplete vertebrae and rib fragments. I here describe the most important parts of this specimen, which allows a new interpretation of the phylogenetic relationships of *Notocetus vanbenedeni,* a species here classified among the Platanistoidea (sensu de Muizon, 1984).

Ameghino (1894: 43) regarded the genus *Notocetus* Moreno (1892) as preoccupied by *Notiocetus* Ameghino (1891) because the names differed by one letter only, and proposed the new name *Diochoticus.* The same year, apparently ignorant of Ameghino's (1894) study, Lydekker (1894: 12) proposed, for the same reason, the name *Argyrodelphis.* True (1910: 19), Kellogg (1928), and Colbert (1944) followed Ameghino's designation which is two months older than Lydekker's. In fact, it is a recommendation of the International Code of Zoological Nomenclature to avoid the creation of names which differ by only one letter and which may result in confusion to other workers, but once such names are established they must strictly follow the law of priority. It is for this reason that Cabrera (1926), Simpson (1945), and Romer (1969) recognized the genus name *Notocetus* as valid and regarded the name *Diochotichus* Ameghino (1894), used by True (1910), as a junior synonym of *Notocetus.* This opinion is followed here.

ACKNOWLEDGMENTS

ABBREVIATIONS

Institutional

AMNH   American Museum of Natural History, New York, USA
IGUP   Instituto di Geologia del l'Universita di Padova, Italy
MLP   Museo de La Plata, Argentina
MNHN   Muséum National d'Histoire Naturelle, Paris, France
USNM   Smithsonian Institution, United States National Museum of Natural History, Washington, D.C., USA

Abbreviations in illustrations

ACR   acromion
AES   anteroexternal sulcus
AFI   articular facet for incus
AFP   articular facet for periotic
AFT   articular facet for tympanic
AHM   articular head of malleus
ALCT   anterolateral convexity of tympanic
ALNT   anterolateral notch of tympanic
APP   anterior process of periotic
ARP   articular rim of periotic
AST   anterior spine of tympanic
AZS   articular zone for squamosal
AZT   articular zone for tympanic
CGL   glenoid cavity of the squamosal
COP   coracoid process
CPT   conical process of tympanic
DOCA   dorsal opening of cochlear aqueduct
DOFA   dorsal opening of Fallopian aqueduct
DOVA   dorsal opening of vestibular aqueduct
DTPP   dorsal tuberosity of posterior process of periotic
EAM   external auditory meatus
ETF   epitubarian fossa
EXO   exoccipital
FCM   fossa capitis mallei
FMS   fossa for medium sinus
FPOS   fossa for posterior sinus
FPS   falcate process of squamosal
FSG   foramen singulare
HAPP   hooklike articular process of periotic
IAM   internal auditory meatus
IAW   internal auditory window

IV	involucrum
LFT	lateral furrow of tympanic
LLT	lateral lobe of tympanic
MLT	medial lobe of tympanic
MNM	manubrium of malleus
MPM	processus muscularis of malleus
MX	maxillary
PA	palatine
PCP	pars cochlearis of periotic
PEO	periotic
PGP	postglenoid process
PMP	postmeatal process
POP	paroccipital process
PPP	posterior process of periotic
PPT	posterior process of tympanic
PTT	processus tubarius of tympanic
PT	pterygoid
RAP	relictual articular pit
RW	round window
SPP	superior process of periotic
SPS	spiny process of squamosal
SPT	sigmoid process of tympanic
ST	stapes
STF	fossa for stapedial muscle
STMF	sternomastoid fossa
TBM	tuberculum of malleus
UPN	notch for unciform process of tympanic
UPT	unciform process of tympanic
VGT	ventral groove of tympanic
VOFA	ventral opening of Fallopian aqueduct
VTP	ventral tuberosity of periotic
ZPS	zygomatic process of squamosal

LOCALITY AND AGE OF THE SPECIMEN

The specimen AMNH 29026 was collected in 1933 by the J. H. Scarritt Expedition, near Cerro Castillo opposite Trelew in Patagonia. It was discovered in bed g of Simpson's section of the south wall of the Chubut Valley (Simpson, 1935: fig. 1). The sediment is a "thick bedded, pale, yellowish tuff," with *Ostrea hatcheri*, numerous sharks, rays, cetaceans, and penguins. This bed is commonly recorded as Patagonian and according to Simpson, is 35 m thick. Below the fossiliferous marine Patagonian level is a gray tuff with abundant land mammals (bed e). According to Simpson (1935: 11): "this fauna is manifestly of Colhué-Huapi or Santa Cruz age or intermediate between the two." No land mammals are recorded by Simpson above the bed g of his section 1.

Frenguelli (1927) mentioned the occurrence of some land mammal remains in the Patagonian beds. However, Simpson (1935: 11) stated that Frenguelli's Patagonian land mammals probably come from his bed e and, if they are actually from marine beds, this author sees no evidence against the possibility of an intermediate age between Colhué-Huapi and Santa Cruz. Since no land mammals have been found in beds right above the Patagonian, it may be assumed, pending further discoveries, that the Patagonian marine mammals have a Colhué-Huapi to Santa Cruz age, i.e., Early Miocene (Marshall et al., 1983, 1986; MacFadden et al., 1985).

DESCRIPTION OF THE SPECIMEN

The dentition of *Notocetus vanbenedeni* shows slight but obvious heterodonty. The teeth are all single-rooted, differing from the posterior teeth of the Squalodontidae and the Agorophiidae which are double-rooted (fig. 1). The anterior teeth of *N. vanbenedeni* have a conical and elevated crown which is slightly recurved posteriorly and lingually. In shape they resemble typical delphinoid teeth. They show a slight anterior keel, the bases of which sometimes bear one or two tiny cingular cusps. A posterior keel is hardly discernible and often absent. No distinct cingulum can be observed at the base of the crown. The enamel is roughly rugose, approaching in this respect the morphology observed in *Steno* and *Inia*. The posterior teeth have a low triangular crown; they are approximately triangular in cross section, and the posteriormost teeth are generally as long as high. Their crown possesses well marked anterior and posterior keels; the posterior keel bears one, two, or three notable accessory cusps, the highest sometimes reaching the apical third of the keel. A chain of small cingular cusps rise at approximately half the height of the anterior keel obliquely joining the centrolingual base of the crown, forming an anterolingual cingulum. This cingulum sometimes extends posteriorly to the base of the posterior keel. In general aspect, the teeth of *N. vanbenedeni* are very similar to those of *Squalodelphis fabianii* and *Phocageneus venustus,* differing only in the occurrence of accessory cusps which seem to be consistently absent in those two latter species.

The squamosal of AMNH 29026 is partially preserved, and the zygomatic process and articular region of the auditory region are in good condition.
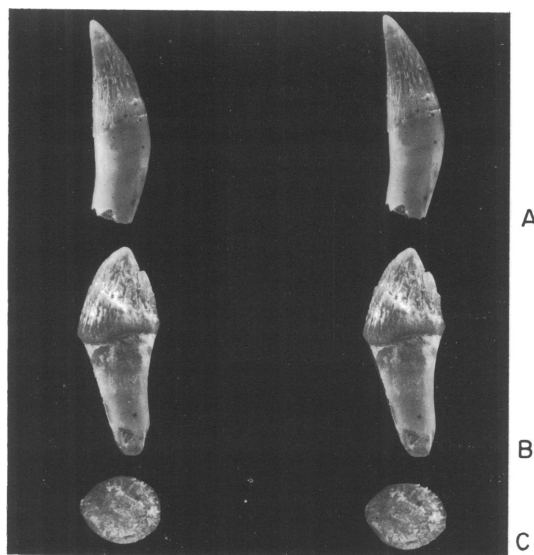
Fig. 1. Stereophotographs of teeth of *Notocetus vanbenedeni* (AMNH 29026). (A) Anterior tooth in medial view, (B) posterior tooth in lingual view, (C) the same in occlusal view. Scale ×2.6.

The zygomatic process is large and stout, and resembles True's specimen more than Moreno's in being slightly recurved ventrally (fig. 2). Its external face shows a well marked fossa for the probable insertion of the m. splenius and part of the m. illiocostalis capitis and m. sternomastoideus. Posterior to the postglenoid process is a wide external auditory meatus, the posterior wall of which is formed by a large postmeatal apophysis. This portion of the squamosal is made of spongy and squamous bone, and articulates with the anterolateral edge of the paroccipital process; the medial face of the postmeatal process of the squamosal articulates with both the tympanic bulla and periotic. On the lateral side of the process were probably inserted the m. brachiocephalicus and the m. sternomastoideus, the latter apparently being also partially inserted on the apex of the posterior process of the tympanic (see below).

A large external auditory meatus and a well developed postmeatal process of the squamosal are found also in *Platanista, Zarachis, Squalodelphis,* and *Squalodon* but they are always much more reduced in the Delphinida (sensu de Muizon, 1984).

The medial side of the postglenoid process shows a fossa for the middle sinus which is
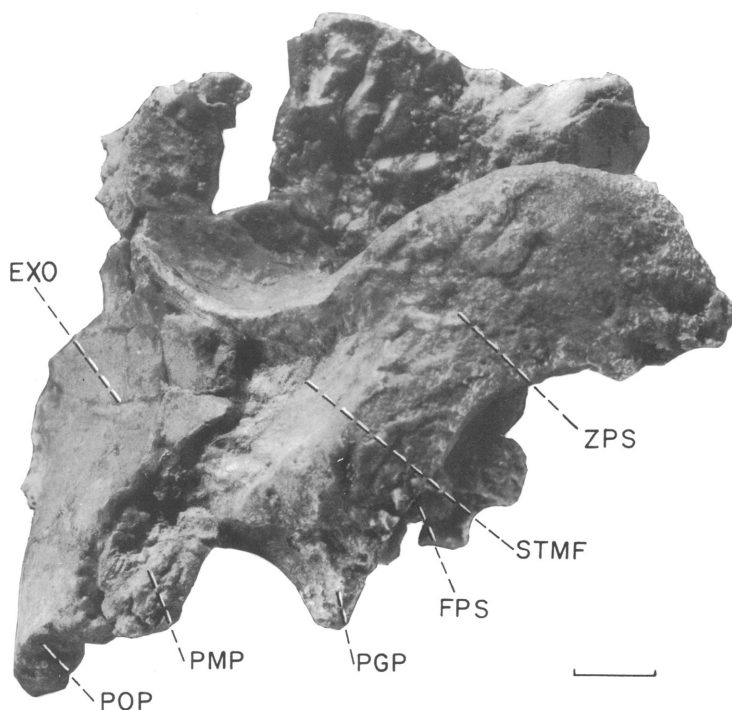

Fig. 2. *Notocetus vanbenedeni* (AMNH 29026). Lateral view of the squamosal and paroccipital process. For abbreviations see text. Scale = 1 cm.
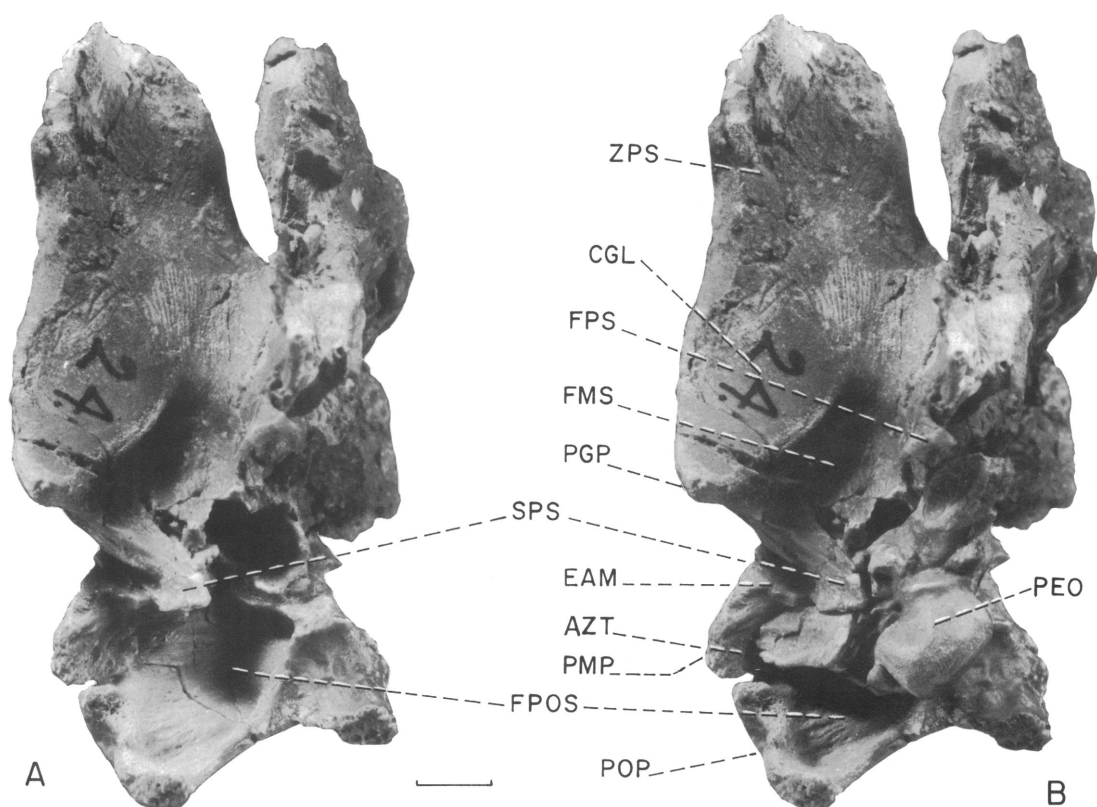
Fig. 3.   *Notocetus vanbenedeni* (AMNH 29026). Ventromedial view of the auditory region. (**A**) Tympanic and periotic removed, (**B**) tympanic removed, periotic in situ. For abbreviations see text. Scale = 1 cm.

much shallower and smaller than in *Platanista* but is similar in shape. The postglenoid process is smaller and more acute than in *Platanista*. From its posterior wall slopes a dorsomedially oriented crest which reaches the internal base of the postmeatal process and there develops a spiny process which imbricates with the ventral side of the periotic, between the posterior process and the ventral tuberosity (fig. 3).

Dorsal to this spiny process and above the periotic is a deep subcircular fossa which is approximately 15 mm long, 9 mm wide, and 8 mm deep in its center. This fossa is also present in *Squalodelphis* (IGUP 26378), *Pomatodelphis* (USNM 187414), *Zarachis* (USNM 10911), and *Platanista* but is not found to such an extent in any other odontocete (although more reduced in this genus). The function of this structure has not been elucidated, although it could represent a simple extension of the peribulary sinus which

partially surrounds the periotic and the tympanic. Nevertheless, this feature is so rare among the odontocetes that it is regarded here as a synapomorphy of the family Platanistidae + Squalodelphidae. Between the spiny process and the subcircular fossa, the squamosal is crushed but it is possible to see what was probably a small fossa. In *Platanista, Zarachis,* and *Pomatodelphis* a similar fossa is seen in the same position, at the base of the postmeatal process; it receives the hook-like articular process which connects the periotic and the squamosal (see below). In *Notocetus* the process is smaller (articular rim — see below) and was probably lodged in this fossa. Anterior to the periotic and abutting it is the falcate process of the squamosal. (The term *falcate process* is employed here for this apophysis of the squamosal following Fraser and Purves [1960]. This term is often used to designate the basioccipital crests which will be termed here processus alaris or alar pro-
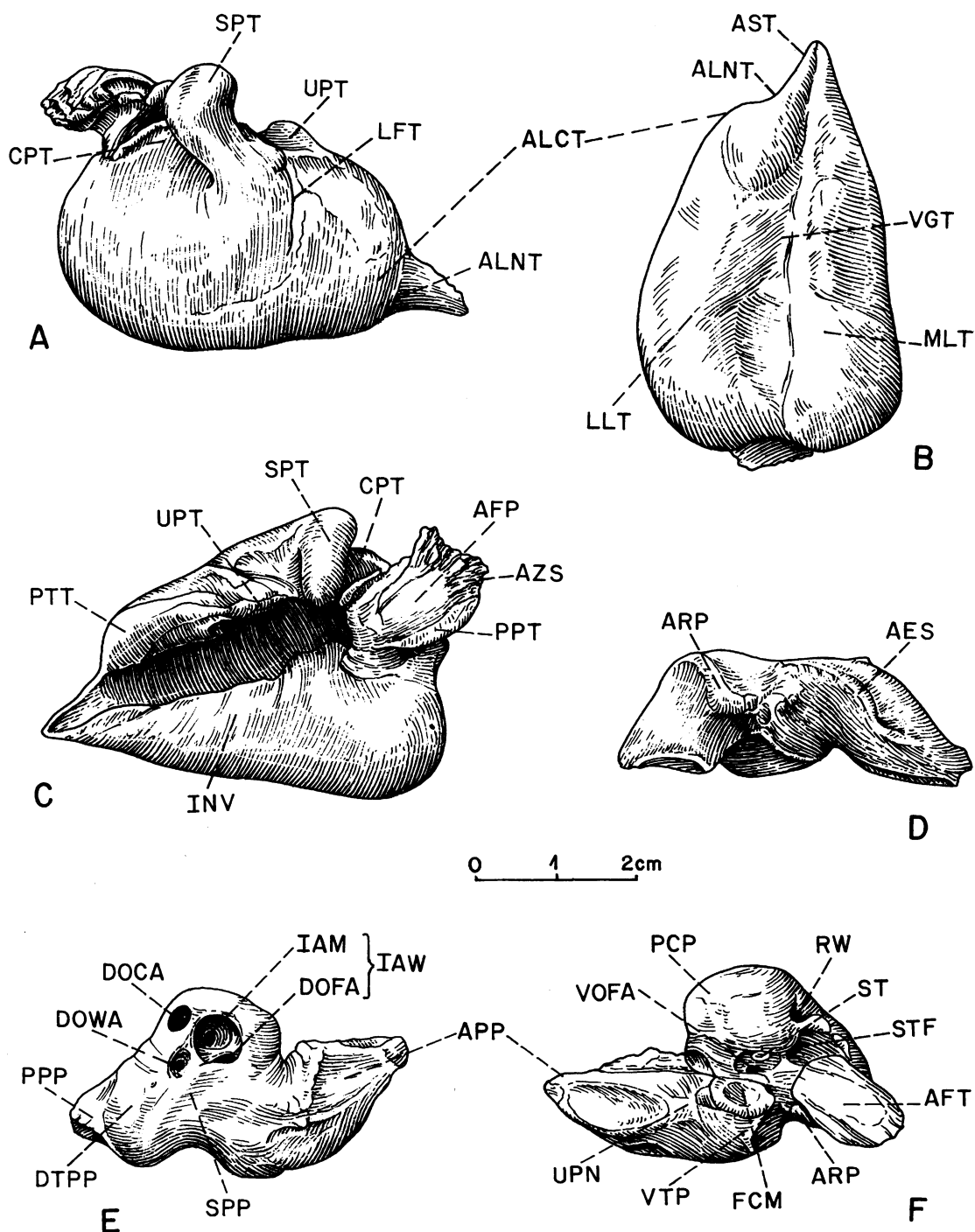
Fig. 4. *Notocetus vanbenedeni* (AMNH 29026). Right tympanic: (A) lateral view, (B) ventral view, (C) medial view. Right periotic: (D) lateral view, (E) dorsal view, (F) ventral view. For abbreviations see text.

cess.) It is slightly damaged but it is possible to note that, as in *Zarachis,* it was much broader than that of *Platanista.*

On the anterior border of the falcate process are some fragments of the lateral lamina of the pterygoid which most probably formed

a continuous bridge from the squamosal to the palatine. This condition is clearly seen on the skull described by True (1910) but also exists in *Squalodelphis,* in the Squalodontidae, and in the Platanistidae.

The periotic and the tympanic of AMNH 29026 are exceptionally well preserved (fig. 4). The terminology employed for the description of these bones is that used by de Muizon (1984) which partially follows Kasuya (1973) and Fordyce (1983).

The periotic of *Notocetus vanbenedeni* (fig. 5) is mainly characterized by the large size of its anterior and posterior processes. The anterior process is much longer and more slender than in *Platanista* although it has the same robust aspect in ventral view. In its length, it could approach the condition found in some rhabdosteids but it is always thicker and more swollen, mainly in ventral view. This side of the process shows a regularly curved lateral edge from the fossa capitis mallei to the apex. There is no distinct ventral rim as can be seen in the Delphinida, but the ventral tuberosity, whose medial side bears the fossa capitis mallei, is more pronounced than in *Platanista* and *Squalodon,* but it is similar to that in *Zarachis* and *Pomatodelphis.* The epitubarian fossa which receives the processus tubarius of the tympanic is long and deep, and covers half the length of the ventral side of the anterior process. It is much longer than in any Platanistidae and Squalodontidae, a feature even more emphasized in USNM 206286 (see below); however, it approaches the condition found in some Rhabdosteidae.

Posterior to the epitubarian fossa is a deep transverse notch which received the unciform process of the tympanic. This notch is less emphasized than in *Platanista* but, considering the variation shown by this structure, it is close in size to that of *Zarachis, Pomatodelphis,* and *Squalodon.* The lateral side of the anterior process presents a well marked anterolateral sulcus; it is V-shaped and opens anteriorly. Its ventral part is narrow and deep, whereas its dorsal part is wide and shallow. Such a groove is generally well marked in fossil platanistids like *Zarachis* and *Pomatodelphis* and in some rhabdosteids; it is hardly visible in squalodonts and strongly attenuated by the hyperostosis of the anterior process in *Platanista.* The apex of the anterior process is pointed and sharp re-
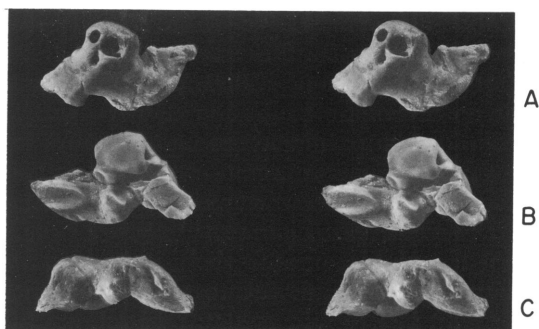

Fig. 5. *Notocetus vanbenedeni* (AMNH 29026). Stereophotographs of right periotic: **(A)** dorsal view, **(B)** ventral view, **(C)** lateral view. Scale ×0.50.

sembling in this respect that of the rhabdosteids and differing from that of the platanistids.

The posterior process of the periotic is well developed; posterolateral to the dorsal opening of the vestibular aqueduct it bears a salient dorsal tuberosity which is separated from the articular part of the process by an abrupt narrowing. This condition is clearly visible in posterolateral view. A slightly curved crest joins the top of the tuberosity and the apex of the posterior process. From the anterolateral border of the tuberosity, a short rounded crest (3.5 mm wide and 8 mm long), which is termed the articular rim, is directed anteroventrally into the deep notch which separates the ventral tuberosity and the articular facet of the tympanic. This notch receives the spiny process of the squamosal which passes ventrally to the articular rim. The latter is lodged in the small fossa of the squamosal, mentioned above, dorsal to the postmeatal process.

An almost identical condition is found in *Phocageneus venustus* and in *Squalodelphis fabianii* where the articular rim is emphasized as a small apophysis. However, the development of this structure in *Notocetus* shows some variation; as in *P. venustus* (USNM 21039) the right periotic bears a small apophysis similar to that of *S. fabianii,* while the left periotic only has an articular rim close to that of *N. vanbenedeni.* The configuration found in the Squalodelphidae is also very similar to that found in some Platanistidae, although it is always more specialized in this family. In *Pomatodelphis* and *Zarachis* the

Fig. 6.   *Zarachis* cf. *flagellator* (USNM 13768). Stereophotograph of the right periotic in lateral view, showing joint occurrence of the hooklike articular process and the articular peg. Scale ×0.53.

articular rim has developed laterally and posteriorly into a hooklike articular apophysis which enters a corresponding fossa in the squamosal at the base of the postmeatal process. The periotic and the squamosal are interlocked in such a way that it is impossible to separate them without breaking either the articular process or the fossa. In *Platanista* the condition is even more specialized as the tuberosity of the posterior process is much higher, the articular part much reduced, and the groove between it and the hooklike articular process is much narrower. The periotic of *Platanista* is hence even more difficult to remove from the skull. This condition is highly derived and must be regarded as a synapomorphy of *Notocetus, Phocageneus, Squalodelphis,* and the Platanistidae. The articular process must not be confused with a small articular peg which is found at the same position in some rhabdosteids. This peg is a relict of an ancestral articulation between periotic and squamosal which may reappear sporadically, as an indication of individual variation. It has a typical laminated structure which strongly differs from the pachyostotic bone of the articular process. The fact that both articular peg and hooklike articular process are sometimes found together in *Zarachis* supports this observation (fig. 6).

The articular facet for the posterior process of the tympanic is smooth, gently concave, and longer than wide; it is similar in shape to that of *Zarachis, Pomatodelphis,* and *Phocageneus* but much wider than that of *Platanista.*

The anterior extremity of the articular facet is slightly damaged. However, it is possible to note the absence of a distinct fossa crus breve incudis. A similar condition also exists in *Phocageneus* and *Platanista,* but a shallow fossa is generally found in *Zarachis, Pomatodelphis,* and in squalodonts.

The superior process is like that in other platanistids, being more excavated than salient. In fact, as I have already expressed (de Muizon, 1984), the term is not very appropriate for this structure, as it is more often a flat zone than a process and its posterior extremity is very rarely distinguishable from the posterior process. In AMNH 29026 and in some Platanistidae, there is a distinct slit posterolateral to the dorsal opening of the vestibular aqueduct which separates both processes. However, the presence of this slit is variable within platanistids.

The pars cochlearis has a square-shaped outline as in *Phocageneus* and *Squalodelphis.* This condition is found sometimes in *Zarachis* and *Pomatodelphis,* although in these two genera this feature is never as obvious as in *Notocetus vanbenedeni.* The cochlea is not square-shaped in *Platanista* nor in any other Neogene odontocetes. The cochlea of *Notocetus vanbenedeni* shows an anterodorsal projection of the anteromediodorsal angle of the pars cochlearis. The *Notocetus* condition is common, and sometimes much more emphasized, in the Platanistidae, some Squalodontidae, and some Rhabdosteidae. It is probably a plesiomorphic character which recalls the primitive flat condition of the pars cochlearis and an ancestral hypothetical contact with the alisphenoid. However, it is noteworthy that this feature can be accentuated in some groups (i.e., ziphiids, platanistids).

On the dorsal side of the pars cochlearis, the internal auditory window (comprising the internal auditory meatus + foramen singulare + dorsal aperture of Fallopian aqueduct; see de Muizon, 1984) is almost circular as in *Platanista* while it is generally pyriform in the other platanistids. The foramen singulare is small and almost assimilated to the dorsal aperture of Fallopian aqueduct. In this respect *Notocetus vanbenedeni* resembles *Platanista* and *Phocageneus* but differs from *Zarachis* and *Pomatodelphis.*

The dorsal aperture of the cochlear aqueduct is very close to the edge of the internal auditory meatus; it is large with very thin edges and faces almost dorsally. In this respect, it differs from the condition found in most platanistids, squalodontids, and rhabdosteids, where it is generally small, and has thick edges. Among the platanistoids it is al-

most identical to that of *Phocageneus* and *Squalodelphis.* However, in this latter genus the foramen is slightly smaller and its edges are not as thin as in the two other genera. The dorsal aperture of vestibular aqueduct is similar to that found in Platanistidae.

On the ventral side of the pars cochlearis just lateral to the fossa capitis mallei is a longitudinal crest. This crest is found sometimes in *Zarachis* and some squalodonts, but it is always less developed in these taxa. The oval window is located in the bottom of a distinct pit posterior to which is found a large fossa for the m. stapedius. This fossa is clearly separable from the round window fossa by a distinct transverse crest, a condition very well marked in *Phocageneus* and squalodonts; the crest is sometimes present, but less developed, in some rhabdosteids. The condition is never present in Platanistidae and could represent a plesiomorphic feature.

The tympanic (fig. 7) is the bone which allows reference of AMNH 29026 to *Notocetus vanbenedeni* as it is almost identical to that figured by True (1910) and associated with the skull AMNH 9485.

The outer lip of the tympanic is very high, as in *Phocageneus, Squalodelphis,* and to a larger extent the Platanistidae. This condition seems unique among Miocene odontocetes, but could not be observed in the Squalodontidae because of the lack of complete tympanic available for this study. The outer lip of the tympanic of *Notocetus vanbenedeni* is very convex and inflated, particularly on its anterior extremity posterolateral to the anterior spine; this anterolateral convexity is, in fact, an extension of the processus tubarius on the dorsal edge of the lateral lip. It is separated from the anterior spine by a smooth notch. The same condition is found in *Zarachis, Phocageneus,* and *Squalodelphis.* The processus tubarius is much less developed in *Platanista* but more pronounced in *Pomatodelphis* (USNM 187414 and MNHN FS 2342). Posteriorly, on the lateral lip of the tympanic, is a very fine slit which seems to be homologous to the deep lateral furrow found in *Zarachis, Pomatodelphis,* and *Platanista.* The conditions in *Phocageneus* and *Squalodelphis* are apparently intermediate between that of the Platanistidae and that of *Notocetus vanbenedeni.*
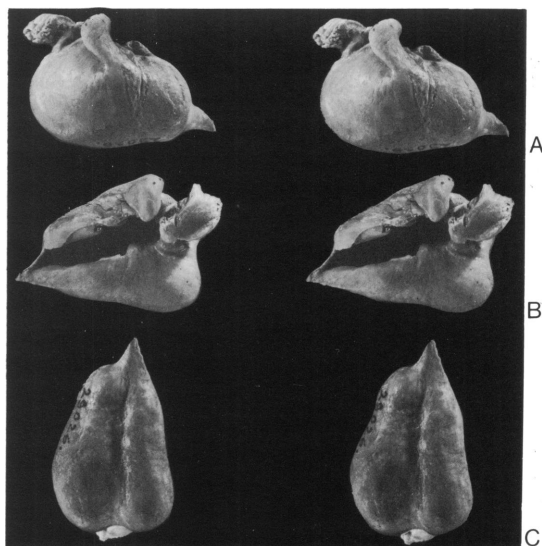
Fig. 7. *Notocetus vanbenedeni* (AMNH 29026). Stereophotographs of right tympanic: (A) ventral view, (B) lateral view, (C) medial view. Scale ×0.50.

The sigmoid process is roughly square-shaped anteriorly and is oriented more posterodorsally than dorsally, as it is in *Platanista.* The conical process is moderately developed as in *Zarachis* and *Pomatodelphis* but it is smaller than in *Platanista.* Its posterolateral side presents a small crest which reaches the base of the lateral pedicle of the posterior process. The latter is posterolaterally oriented and bears the articular facet with the periotic. Posterior to the facet is a zone of laminate bone which articulates with the postmeatal process of the squamosal in such a way that the apex of the process extends slightly lateroventrally, and the process probably received some fibers of the m. sternomastoideus and/or the m. mastohumeralis.

On the anterolateral edge of the posterior process is a deep groove which receives the ventral crest of the spiny process of the squamosal. The posterior process of the tympanic of *Notocetus vanbenedeni* has therefore a double articulation with the periotic and the squamosal. This condition has been demonstrated to be plesiomorphic (de Muizon, 1984) and the loss of the tympanic-squamosal articulation has been regarded as a synapomorphy of the Rhabdostoidea + Inioidea + Delphinoidea (de Muizon, 1984: 68).
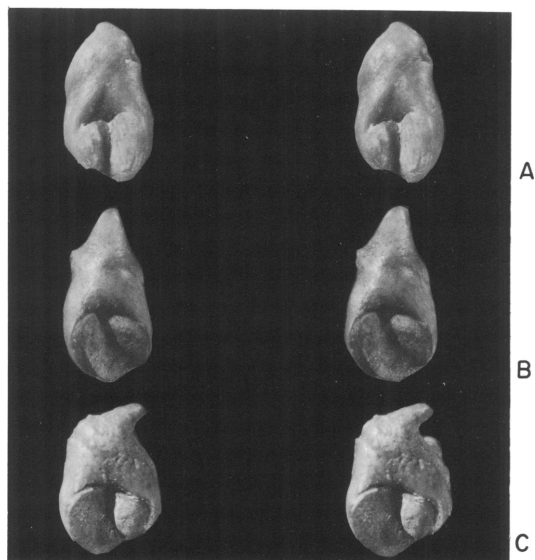
Fig. 8. Stereophotographs of posteromedial view of the malleus of (A) *Notocetus vanbenedeni* (AMNH 29026), (B) *Phocageneus venustus* (USNM 21039), (C) *Pomatodelphis* cf. *inaequalis* (USNM 187414). Scale ×2.6.

It is also probable that the posteroapical angle of the process had a contact with the paroccipital process.

The posterior process of AMNH 29026 is shorter than that of AMNH 9485; they both strongly resemble that of *Phocageneus* although the former is slightly shorter. The condition in *Platanista* is different because the lateral groove is absent, the articulation with the squamosal has moved anterolaterally, and the process is not so elongate as in *N. vanbenedeni*. The posterior process of *Zarachis* is unknown, but in *Pomatodelphis* (USNM 187414) and squalodonts, the condition is similar to that of *Notocetus*. The posterior process is attached to the bulla by two pedicles and a transversely elongate, elliptical foramen is seen in posterior view of the tympanic. In this view, the ventral side being horizontal, the involucrum is strongly protruding medially, as in *Phocageneus, Prosqualodon,* and (to a lesser extent) in the Platanistidae. (Because of the transverse posterior compression of the tympanic in platanistids, the involucrum is less prominent.)

A different condition is found in the Rhabdosteidae and in all groups of modern Odontocete. On the medial side of the tympanic,

the involucrum is stout, straight, and conical at its anterior extremity. It differs from the more dorsoventrally inflated involucrum of *Pomatodelphis* and *Zarachis* and from that of *Platanista* whose height is reduced markedly at its anterior extremity. The involucrum of *Phocageneus* seems to be closer to that of *Zarachis* than to that of *Notocetus,* but in *Prosqualodon* the involucrum is fairly similar to that of *N. vanbenedeni* in being little inflated dorsoventrally.

The ventral side of the tympanic shows a distinct longitudinal groove continuous from the anterior spine to the posterior notch, which separates the lateral and medial lobes. This groove also reaches the anterior spine in *Phocageneus* and *Squalodelphis* but it stops anterior to it in *Squalodon, Prosqualodon, Zarachis, Platanista,* and *Pomatodelphis*. The ventral groove of *Notocetus* is not filled with a spine of spongy bone as is found in *Platanista* and *Pomatodelphis*. There is no spine in *Zarachis* or in *Phocageneus,* but the bottom of the groove exposes some spongy bone as in some rhabdosteids. A similar condition is observed in *Notocetus vanbenedeni* and *Squalodelphis fabianii*. Both lobes have the same length posteriorly and their posterior extremities have approximately the same thickness. The *Notocetus* condition is also found in *Phocageneus, Squalodelphis,* and squalodonts.

In Platanistidae and Rhabdosteidae the medial lobe is generally shorter and thinner than the lateral one. The anterolateral convexity and notch are very clearly seen in that view and show strong similarities with *Phocageneus* and *Squalodelphis,* as mentioned above. The anterior spine is well developed as in the Platanistidae and the other Squalodelphidae.

The malleus (figs. 8, 9) is well preserved and its similarity to that of Platanistidae was mentioned by de Muizon (1985: fig. 1). In that paper (de Muizon, 1985), the specimen USNM 187414 was erroneously referred to *Zarachis,* but, on the basis of the skull and the tympanic, it must be assigned to *Pomatodelphis*. The malleus of *Notocetus* shows a strong development of the tuberculum relative to that in *Pomatodelphis*. In this respect, it resembles *Phocageneus* and *Squalodelphis,* but also the delphinid condition, and clearly
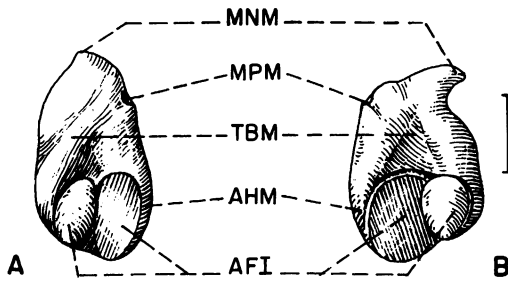
Fig. 9. Posteromedial view of the malleus of (A) *Notocetus vanbenedeni* (AMNH 29026), (B) *Pomatodelphis* cf. *inaequalis* (USNM 187414). For abbreviations see text. Scale ×3.4.

Fig. 10. *Notocetus vanbenedeni* (AMNH 29026). Lateral view of the scapula. Scale = 2 cm.

differs from rhabdosteids. The posteromedial aspect of the malleus is the most relevant and will be described with its mediolateral axis in vertical position. The articular head bears the articular facets for articulation of the incus; they are similar to those of *Pomatodelphis*. The tuberculum bears the manubrium and the processus muscularis. The manubrium in *Pomatodelphis* is hook-shaped and presents on its ventral side a groove for the insertion of the tympanic ligament. In *Notocetus* the manubrium is smaller, much less recurved, more expanded apically, and the groove is longer than in *Pomatodelphis*. The condition in *Phocageneus* and *Squalodelphis* is closer to that in *Notocetus* than to that in *Pomatodelphis*. The apical extension of the manubrium is not found in the Platanistidae and could be a synapomorphy of the Squalodelphidae.

On the dorsal side of the tuberculum is a distinct pit for the insertion of the tendon for the tensor tympani. The processus muscularis which bears that insertion is lower than the apex of the manubrium, resembling therefore the primitive condition found in mysticetes and platanistids. As has been stated (de Muizon, 1985), the Delphinida are defined, in part, by an apical increase in size of the processus muscularis and by a reduction of the manubrium which, in posteromedial view, is lower than the processus muscularis. In this respect, *Notocetus vanbenedeni* resembles *Pomatodelphis, Phocageneus,* and *Squalodelphis* and clearly differs from the Delphinida.

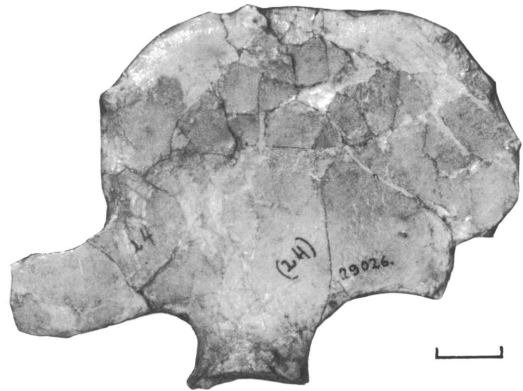The incus is not preserved in AMNH 29026 and only the basal part of the stapes is pre-

served in situ on the periotic. Although this latter bone is incomplete, it is noteworthy that the stapes does not have a stapedial foramen. The Squalodontidae, Platanistidae, and *Phocageneus* also lack this foramen, but it is present in rhabdosteids and delphinoids.

The occipital has a well developed paroccipital process which shows on its anterior surface a large fossa for the posterior sinus (fig. 3). The fossa is more pronounced near the dorsal end of the process where it forms a deep hollow. The depth of the fossa, however, is not related to the size of the posterior sinus. In *Stenella* and *Tursiops,* where the fossa is very shallow, the sinus is large.

The processus alaris of the basioccipital is thick, a primitive condition found in Platanistidae and Squalodontidae and also in Pontoporiidae and Rhabdostoidea. The base of the lateral face of the alisphenoid shows a well developed carotid foramen.

Among the postcranial elements preserved in AMNH 29026, the most significant bone is the scapula (fig. 10). The specimen is not very complete but shows two essential features of phylogenetic significance. First, the coracoid process, which is always long in odontocetes and in such primitive groups as archaeocetes, is absent in *Notocetus*. As observed by de Muizon (1984), it is also absent in *Platanista* and Squalodontidae and it is always present in the Delphinida (see de Muizon, 1984), Rhabdostoidea, Ziphioidea, and Physeteroidea. (In *Zarachis, Pomatodelphis, Phocageneus,* and *Squalodelphis,* the scapula has not yet been found.) Second, the acromion is located exactly on the anterior edge

TABLE 1

Measurements of Squamosal, Periotic, Tympanic, and Malleus of *Notocetus vanbenedeni*
(AMNH 29026) in mm

Length of zygomatic process of squamosal	
from the bottom of the external auditory meatus to apex	70.2
Length of periotic	43.6
Maximum width of periotic	24.6
Maximum length of the pars cochlearis	15.3
Maximum length of the ventral side of tympanic	50.0
Maximum width of the ventral side of tympanic	32.2
Maximum length of tympanic (with posterior process)	52.3
Height of the posteromedial face of malleus	7.1
Width of the posteromedial face of malleus	4.6

of the scapula, probably as a result of the total absence of the supraspinous fossa. This condition is also found in *Platanista* and in all the Squalodontidae (where the scapula is preserved enough to enable the observation). All the other odontocetes and all the archaeocetes have a supraspinous fossa, although it is small in the most specialized forms. These two characters, which could be functionally related, are so unique among cetaceans that they can be considered as good synapomorphies of Platanistidae, Squalodelphidae, and Squalodontidae (de Muizon, 1984).

OTHER MATERIAL REFERRED
TO *NOTOCETUS*

The collection of the La Plata Museum (Argentina) contains several specimens that are referable to *Notocetus vanbenedeni*.

1. MLP 5-5 is the holotype.

2. MLP 5-10 is a partial skull with associated mandible, designated in the collection as paratype. Most of the posterior part of the skull is missing and the skull mainly consists of a rostrum with the right supraorbital region and anterior part of the pterygoid region. Most of the teeth are well preserved.

3. MLP 76-X-2-5 is a right periotic, whose posterior process has lost its articular region. The characteristic shape of the anterior process of the lateral side of the posterior process, the square-shaped cochlea, and the large, thin-edged dorsal opening of the cochlear aqueduct, cast little doubt about its identity.

4. MLP 76-IX-2-11 and 76-IX-2-12 are tympanics that are also referable to *N. vanbenedeni*.

All these specimens come from the "Pata-

gonian Fm." of the Trelew region in Chubut Province (Argentina).

The collection of the U.S. National Museum of the Smithsonian Institution in Washington contains a periotic which, if not associated with a tympanic, could be referable to *Notocetus vanbenedeni* (fig. 11). The specimen (USNM 206286) comes from the Middle Miocene age Calvert Formation of Maryland. It presents a long and laterally inflated anterior process with an acute apex, a square-shaped cochlea with a wide, thin-edged dorsal aperture of the cochlear aqueduct, a deep fossa for the stapedial muscle, an articular rim born from the dorsal tuberosity of the posterior process, and a narrow crest joining the tuberosity to the apex of the process. All these features are found in *Notocetus vanbenedeni*. USNM 206826 differs from *Phocageneus* essentially by the length and the thickness of its anterior process. However, USNM 206286 also differs from *Notocetus vanbenedeni* in its longer and less swollen anterior process, its less developed ventral tuberosity, its smaller articular facet for the tympanic, and its more salient articular rim. Nevertheless, considering the scarcity of the specimens referred to *Notocetus*, these features could represent individual variation.

Associated with the USNM periotic is a partial tympanic in which are preserved the involucrum and the median part of the ventral groove. In ventral view, the medial lobe is slightly different from that of *Notocetus vanbenedeni* in being narrower and more concave in its median part (it is almost straight in both specimens of *Notocetus vanbenedeni*). In True's specimen (AMNH 9485), however,

there is a very weak medial concavity and the median part of the medial lobe is narrower than in AMNH 29026. In medial view, the anterior part of the involucrum is relatively more swollen than in *N. vanbenedeni,* and shows a distinct convexity in its posterior part. In these features, the condition of True's specimen is intermediate between AMNH 29026 and USNM 206286 although closer to the other Patagonian specimen (AMNH 29026). Despite the important similarities existing between the periotics of the Argentinian and North American specimens, the latter should be referred to another species of the genus *Notocetus,* a conclusion that takes into account the differences existing between the anterior processes of the periotics of both species.

Fig. 11. *Notocetus* sp. (USNM 206286). Stereophotographs of right periotic: (**A**) dorsal view, (**B**) ventral view, (**C**) lateral view. Scale ×0.50.

DISCUSSION

PLATANISTOID CLASSIFICATION

Traditionally (Simpson, 1945; Bourdelle and Grassé, 1955), the taxon Platanistoidea was defined to include the four genera of living river dolphins and related fossil forms. Hershkovitz (1966) used the term Susuidae (=Platanistidae) but assigned to it the same set of taxa as did Simpson. Rice (1968) also followed Simpson (1945). Zhou (1982) included each of the four living genera in a separate family: Pontoporiidae, Iniidae, Lipotidae, and Platanistidae. Recently, Barnes et al. (1985) used the same classification, but included the family Acrodelphidae, a fossil group they regarded as including *Schizodelphis, Pomatodelphis,* and probably *Zarachis.* de Muizon (1984, 1985) suggested a new interpretation of the phylogeny of the river dolphins as a polyphyletic assemblage. The family Platanistidae was recognized to include only the living genus *Platanista* while the three other living genera were related to the Delphinoidea and, with that superfamily, were included in the infraorder Delphinida (de Muizon, 1984). The following classification was proposed:

Superfamily Platanistoidea
    Family Platanistidae (*Platanista,* †*Zarachis,* †*Pomatodelphis,* †*Phocageneus,* †*Areodelphis*)
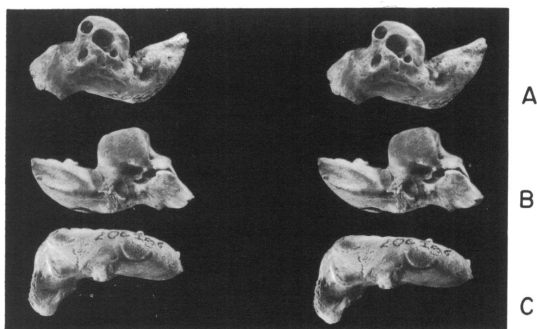   Family Squalodelphidae (†*Squalodelphis,* †*Notocetus*)

Family Squalodontidae (among others, †*Squalodon,* †*Prosqualodon,* †*Neosqualodon,* †*Phoeberodon*)

The classification adopted here is very similar except for some minor changes (see fig. 12).

Areodelphis, regarded (de Muizon, 1984) as a possible Platanistidae, is known only by a rostrum and a referred vertebral column. As no auditory region of this form can be associated to the type specimen it must be considered as incertae sedis.

Phocageneus is not a Platanistidae but a Squalodelphidae because of its auditory region morphology.

In the Squalodontidae should also be included the following genera: *Eosqualodon, Australosqualodon, Kelloggia, Microcetus, Parasqualodon,* and *Tangaroasaurus.* However, the abundance of incertae sedis taxa in the classification given by Whitmore and Sanders (1977: 305) is an indication of the crucial need for revision of the squalodonts and other related primitive cetaceans. Such a revision may possibly result in elevation of this family to the rank of superfamily.

Therefore, the classification proposed here is as follow:

Superfamily Platanistoidea
    Family Platanistidae (*Platanista,* †*Zarachis,* †*Pomatodelphis*)
    Family Squalodelphidae (†*Notocetus,* †*Squalodelphis,* †*Phocageneus,* possibly †*"Champsodelphis"* [*"C."* *tetragorhinus*])
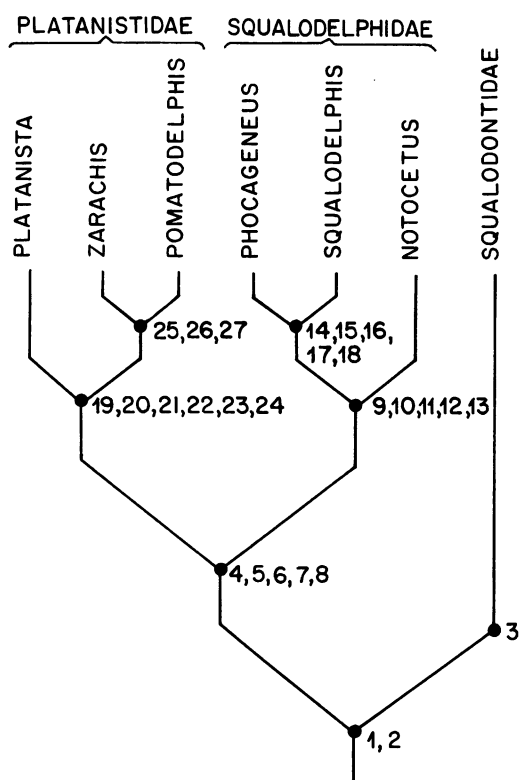   Family Squalodontidae (†*Australosqualo-*

Fig. 12. Assumed phylogenetic relationships of the Platanistoidea:

1. acromion located on the anterior edge of the scapula and loss of supraspinous fossa;
2. loss of the coracoid process of the scapula;
3. the phylogeny of the squalodonts is not considered here and the group is tentatively regarded as monophyletic, although *Sulakocetus* should perhaps be excluded from the family (see text);
4. development of a supplementary articular mechanism with the squamosal on the lateral edge of the periotic (articular rim);
5. development of a long, narrow, sharp anterior spine on the tympanic with salient anterolateral convexity separated from the spine by prominent notch;
6. loss of double rootness;
7. tendency toward thickening of the supraorbital process;
8. deep subcircular fossa dorsal to the spiny process of the squamosal;
9. square-shaped pars cochlearis of the periotic;
10. large, thin-edged dorsal opening of the cochlear aqueduct, which faces dorsally;
11. ventral groove of the tympanic affecting the whole length of the bone including the anterior spine;

don, †*Eosqualodon*, †*Kelloggia*, †*Microcetus*, †*Neosqualodon*, †*Parasqualodon*, †*Phoeberodon*, †*Prosqualodon*, †*Squalodon*, †*Sulakocetus* (?), †*Tangarosaurus*)

PLATANISTOID PHYLOGENY (FIG. 12)

Platanistoidea

The Platanistoidea bear two important shared derived characters on the scapula. As discussed above, the platanistoid scapula has lost its coracoid process while it is very large in all other odontocetes and in archaeocetes (fig. 13). Moreover, the acromion is always situated on the anterior edge of the scapula and there is no supraspinous fossa, while this fossa is always present in the other odontocetes and in the archaeocetes. As stated in the preceding description, these two features are probably related, but no satisfactory functional explanation was found. Hence, they are

12. apical extension of the manubrium of the malleus;
13. very strong development of dorsal transverse process of the atlas and extreme reduction of the ventral process;
14. loss of accessory cusps of the posterior teeth;
15. anterior spine longer than in *Notocetus*;
16. lateral furrow of the tympanic better marked than in *Notocetus*;
17. occurrence of a small longitudinal elevation in the ventral groove of the tympanic lacking in *Notocetus*;
18. articular rim more developed than in *Notocetus*;
19. development of very high maxillary crests on the supraorbital region of the skull;
20. dorsolateral migration of the palatine bones, which are separated from each other;
21. reduction in length and transverse thickness of the medial lobe of the tympanic;
22. greater elevation of the lateral wall of the tympanic;
23. transformation of the articular rim of the Squalodelphidae into a hooklike articular process;
24. shortening and transverse thickening of the anterior process of the periotic;
25. frontal associated with the maxillary to form a supracranial frontomaxillary crest;
26. involucrum more elevated than in *Platanista*;
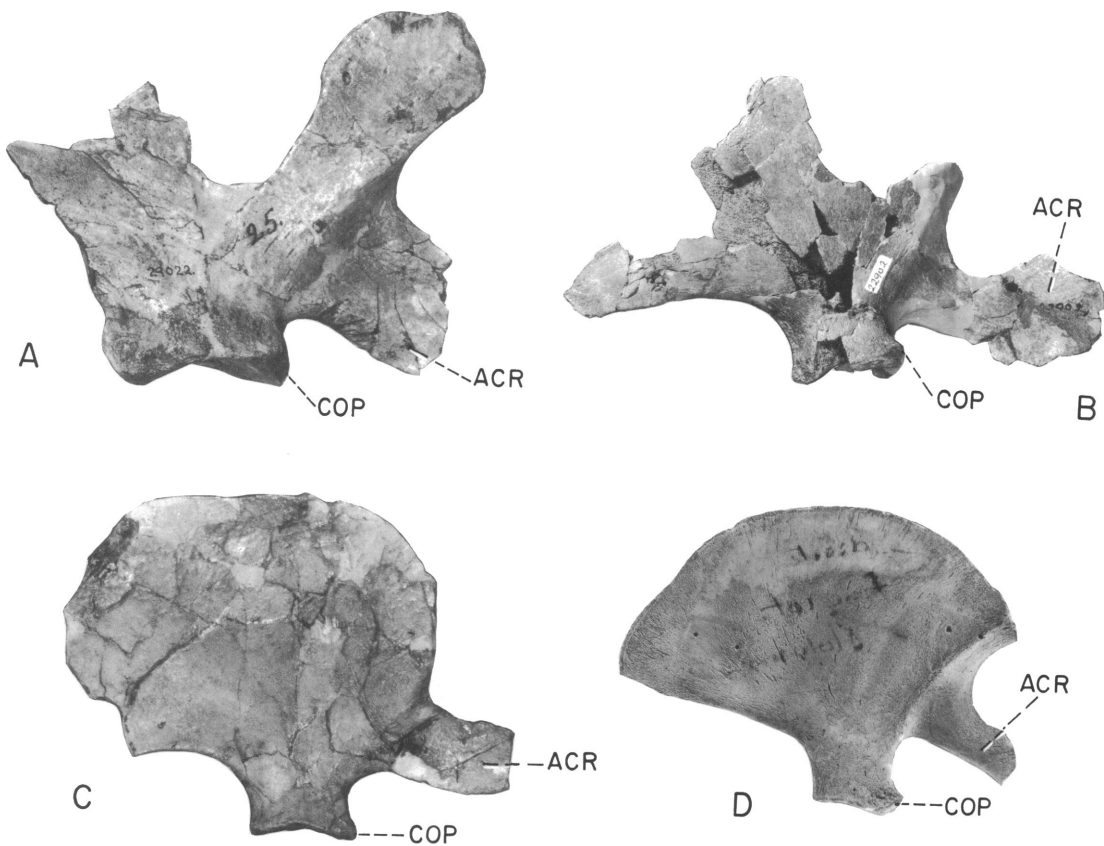27. dorsoventral thickening of the anterior process of the periotic.

Fig. 13. Scapulae of Platanistoidea in medial view. (**A**) *Prosqualodon* (AMNH 29022), (**B**) *Squalodon* (USNM 22902), (**C**) *Notocetus* (AMNH 29060), (**D**) *Platanista* (MNHN 1870-79). For abbreviations see text. Not to scale.

tentatively maintained as independent synapomorphies of the Platanistoidea. However, it is noteworthy that the scapula of *Sulakocetus* figured by Mchedlize (1984: pl. XVI) seems to have a well developed coracoid process and that author mentions a "coracoid process narrow but apparently long" (Mchedlize, 1984: 43). Nevertheless, the acromion seems to show the platanistoid condition described above. Therefore, it is possible that *Sulakocetus* could represent the sister-group of all other Platanistoidea which can then be defined only by the loss of the coracoid process. The superfamily Platanistoidea (incl. *Sulakocetus*) would thus be defined by the anterior position of the acromion and the loss of the supraspinous fossa.

The scapula of *Sulakocetus* is very poorly preserved and a better specimen is needed to be certain of its condition. The skull figured by Mchedlize (1976: pl. XIII) seems to be fairly primitive, but it apparently shows a maxilla contacting the occipital, a condition which makes it different from the primitive *Agorophius* or *Xenorophus* or even from the less primitive *Patriocetus* (a genus related to the Squalodontidae by Rothausen, 1968), where the bones are always separated. *Sulakocetus* should perhaps be regarded as a primitive squalodont-like platanistoid, but it is clear that a more detailed analysis of the skull and especially the auditory region of this form is necessary for identification of its phylogenetic position. The synapomorphies of the Platanistoidea must be assumed to exist in *Squalodelphis, Phocageneus, Zarachis,* and *Pomatodelphis* as the scapulae of these genera are unknown. However, these taxa bear other synapomorphies which relate them to the Platanistidae and Squalodelphidae and it is

plausible that they also possessed the platanistoid synapomorphies of the scapulae.

Squalodontidae

In the following discussion the Squalodontidae are regarded as a possible monophyletic group, as it is not the purpose of this paper to reanalyze this family. However, one must be aware that, until now, the Squalodontidae are "defined" only by symplesiomorphies, such as heterodont dentition, double-rooted posterior teeth, low vertex, and narrow occipital shield. Consequently, this group may be demonstrated to be nonmonophyletic. Furthermore, few squalodonts are known by complete skulls with associated periotics, tympanics, and auditory ossicles, elements regarded here as important phylogenetically. The type skull of *Squalodon* (=*Rhizoprion*) *bariense* (Jourdan, 1861), whose ventral side is still embedded in matrix, and which still retains these bones in good condition, is being reprepared and restudied by the author and will perhaps shed more light on the problem of squalodont phylogeny.

Squalodelphidae + Platanistidae

The Platanistoidea were defined (de Muizon, 1984: 68) by the presence of a hooklike articular process on the lateral side of the periotic between the ventral tuberosity and the articular part of the posterior process. As noted above and elsewhere (de Muizon, 1984), this condition is very clear in the Platanistidae; it is present but less developed (forming only an articular rim) in the Squalodelphidae. I have stated (de Muizon, 1984: 67) that the condition of the Squalodontidae shows some variation and is not very obvious in *Prosqualodon*. In fact, as noted above, the condition of Squalodontidae seems to be a holdover of an ancestral articulation of the periotic with the spiny process of the squamosal, where spongy and laminated bone that characterizes cranial articulations is present. The squalodont condition may be found occasionally in rhabdosteids and monodontids as the retention of a plesiomorphic character. The fact that it may be observed in some Platanistidae like *Zarachis* between the posterior process and the hooklike articular pro-

cess demonstrates the novel formation of the latter and, therefore, its apomorphic status. Consequently, the presence of an articular process on the lateral side of the periotic, even incipiently developed as is the articular rim of some Squalodelphidae, is regarded here as a synapomorphy of the Platanistidae and the Squalodelphidae (fig. 14). All the genera of both families show a large subcircular fossa. This structure is unknown in all the other odontocetes, and is also regarded here as a synapomorphy of the Squalodelphidae + Platanistidae (see above). The fossa is only inferred to be present in *Phocageneus* since the skull of this form is unknown. Moreover, the supraorbital process of both families is clearly more developed than in the other odontocetes. In the Squalodelphidae, the process is strongly thickened, this character being more pronounced in *Squalodelphis* than in *Notocetus*. In *Phocageneus,* however, it is only assumed to be present since the skull of this genus is unknown. In the Platanistidae, the thickening turns into a real supraorbitory crest (see below). Both families are also defined, relative to squalodonts, by the lack of double-rootness and by the acquisition of a long, narrow, and sharp anterior spine of the tympanic with an anterolateral notch and convexity. These are sometimes less emphasized in *Platanista* but, as noted in the description, they are always strongly marked in *Pomatodelphis.* This condition of the tympanic in Squalodelphidae and Platanistidae is either absent or very little developed in primitive odontocetes like squalodonts, agorophiids (undescribed material, USNM), and archaeocetes. The development of an anterior spine to the tympanic also occurs through parallel evolution in some rhabdosteids, some delphinids (*Globicephala*), and in *Lipotes,* but in these forms the anterior spine is more conical, wider, and less acute.

Squalodelphidae

Until now, the periotic and malleus of *Squalodelphis fabianii* were unknown since the tympanic is in situ in the holotype and does not allow any observation of these bones (Dal Piaz, 1916b: pl. 3). The skull portion with attached periotic (IGUP 26377) illustrated by Pilleri (1985: pl. 29) and referred
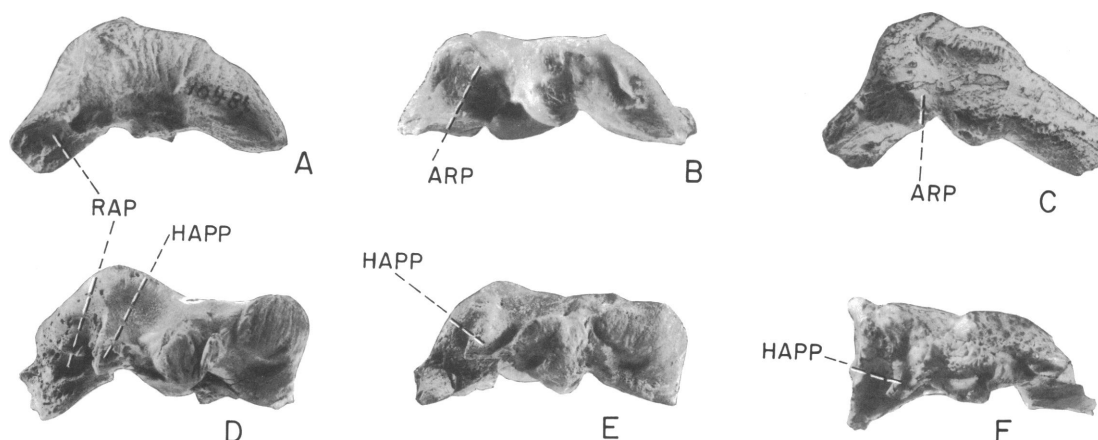
Fig. 14. Periotics of Platanistoidea in lateral view. (A) *Squalodon* (cast of USNM 10484), (B) *Notocetus* (AMNH 29060), (C) *Phocageneus* (cast of USMN 21039), (D) *Zarachis* (USNM 13768), (E) *Pomatodelphis* (USNM 187414), (F) *Platanista* (MNHN 1870-79). For abbreviations see text. Scale ×0.46.

to *Squalodelphis* does not belong to this genus. This skull and its periotic (which I have prepared) are probably those of a rhabdosteid or a primitive ziphid, but definitely not that of a squalodelphid. The specimen IGUP 26378 illustrated by Pilleri (1985: pl. 30) has a tympanic which is identical to that of the holotype of *S. fabianii*; furthermore, its skull base perfectly matches that of *S. fabianii* to which it may reasonably be referred. I had the opportunity to prepare the periotic and the malleus of IGUP 26377 (fig. 15 and 16), and the references made to the periotic and malleus of *Squalodelphis* in the above description are based on this specimen.

As stated above, the periotic of *Squalodelphis* shows the typical synapomorphy of the Platanistidae + Squalodelphidae. The synapomorphies of the Squalodelphidae are mainly based upon characters of the auditory region since other areas of the skull of *Phocageneus* are unknown. The three genera included in the family share two characters of the periotic which seem to be fairly uniform among the odontocetes: the typical square-shaped pars cochlearis and the large, thin-edged dorsal aperture of the cochlear aqueduct which faces directly dorsally. The square-shaped cochlea is found sometimes in *Zarachis* and *Pomatodelphis* but to a much lesser extent than in the Squalodelphidae.

The malleus of the Squalodelphidae shows an apomorphic apical extension of the manu-

brium that is lacking in *Pomatodelphis* and *Platanista* (figs. 8, 9, and 16).

The tympanics of the three Squalodelphidae are very similar; they show the anterior spine and the anterolateral notch and convexity that are absent or little developed in Squalodontidae. The tympanics also have ventral lobes equally long and equally thick posteriorly as in squalodonts, which contrast with Platanistidae where there is always a reduced medial lobe. These features are symplesiomorphies only (fig. 17). Nevertheless, the tympanics of the three known genera of Squalodelphidae show the same ventral groove that is continuous up to the anterior
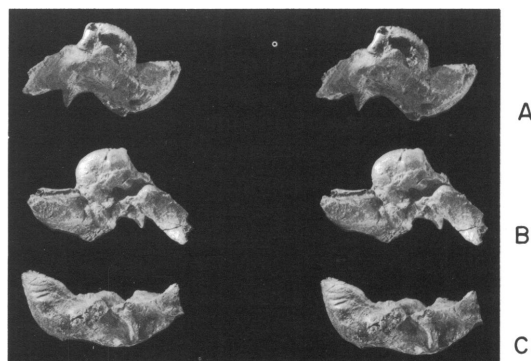

Fig. 15. *Squalodelphis fabianii* (IGUP 26378). Stereophotographs of right periotic: (A) dorsal view, (B) ventral view, (C) lateral view. Scale ×0.50.
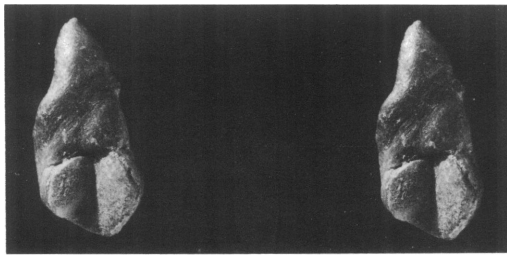
Fig. 16. *Squalodelphis fabianii* (IGUP 26378); stereophotographs of right malleus in postero-medial view. Scale ×3.

extremity and where it reaches the anterior spine. This condition is absent in all the other odontocetes where the groove stops before the anterior extremity of the tympanic (fig. 17). This apparently unique feature could be a synapomorphy of the Squalodelphidae.

Furthermore, the atlas of *Notocetus* and *Phocageneus* have a very well developed dorsal transverse process whereas the ventral process is very reduced. This condition does not exist in the Squalodontidae and in the Platanistidae where the atlas is known, and is tentatively considered as a synapomorphy of the Squalodelphidae. The atlas of *Squalodelphis* is unknown, and this feature is only inferred to be present in that genus.

Among the Squalodelphidae, *Squalodelphis* and *Phocageneus* are more specialized than *Notocetus* in several respects. The posterior teeth of *Phocageneus* and *Squalodelphis* resemble each other in lacking one or several accessory cups on their posterior edge, whereas these are present in *Notocetus*. The loss of posterior accessory cups is a character derived from a primitive squalodont-like ancestral tooth morphology and could be regarded as a synapomorphy of both genera.
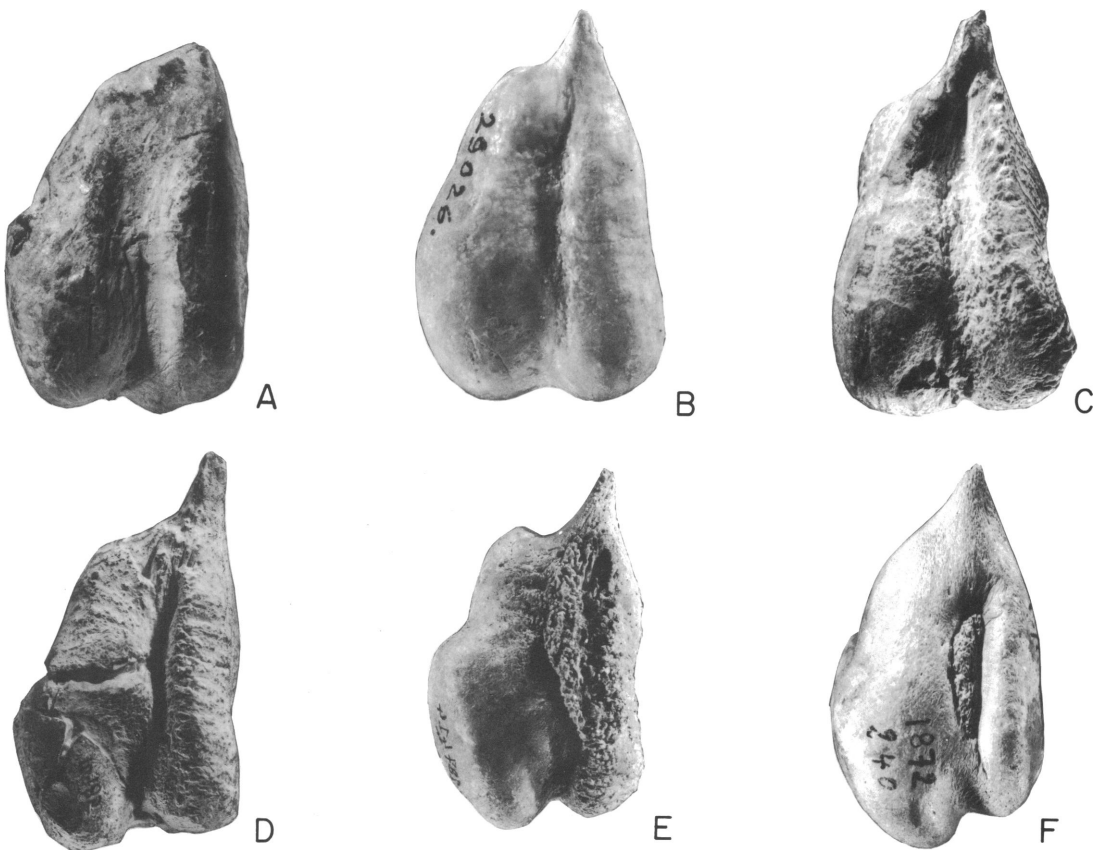

Fig. 17. Tympanics of Platanistoidea in ventral view. (A) *Prosqualodon* (AMNH 29022), (B) *Notocetus* (AMNH 29026); (C) *Phocageneus* (cast of USNM 21039), (D) *Zarachis* (cast of USNM 10485), (E) *Pomatodelphis* (USNM 187414), (F) *Platanista* (MNHN 1870-79). Scale ×0.51.
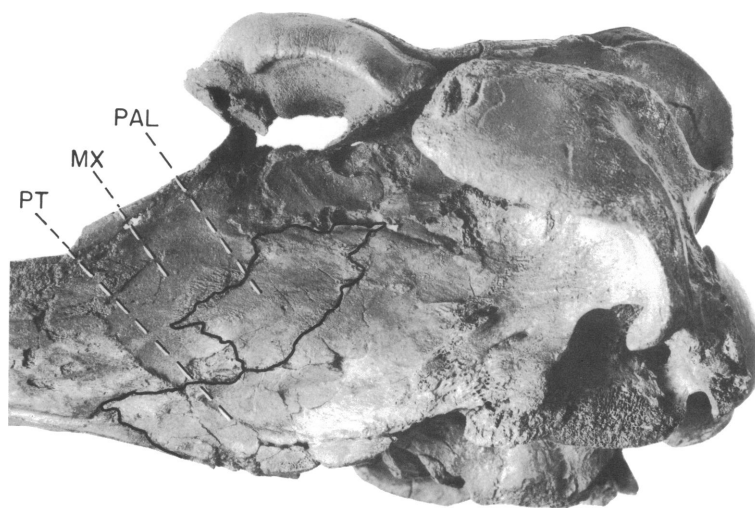
Fig. 18. Lateral view of the skull of *Pomatodelphis* cf. *inaequalis* (USNM 187414). For abbreviations see text. Scale ×0.33. (The maxillary–pterygoid–palatine suture has been outlined to enhance the position of the palatine.)

Furthermore, the articular rim is more developed in *Phocageneus* and *Squalodelphis* than in *Notocetus*; it is, in fact, a small apophysis which foreshadows the development of a hooklike articular process of the Platanistidae. In other respects, the tympanics of *Phocageneus* and *Squalodelphis* resemble each other more than they do *Notocetus,* essentially in the greater length of the anterior spine. (The lateral furrow is more distinct than in *Notocetus* and the small longitudinal elevation in the ventral groove recalls the ventral spine of *Platanista* and is absent in both tympanics known for *Notocetus.*) These features in *Phocageneus* and *Squalodelphis* are derived when compared to the condition in *Notocetus.* Considering these synapomorphies, *Phocageneus* and *Squalodelphis* are regarded here as sister-genera and both constitute the sister-group of *Notocetus.* It should be also mentioned that the condition of the supraorbital process of *Squalodelphis,* which is thicker and hence more specialized than that in *Notocetus,* is anticipated for as yet unknown skulls of *Phocageneus.*

Platanistidae

The Platanistidae are essentially defined by the appearance of very high and large maxillary or frontomaxillary crests. Similar structures may be found in some other odonto-

cetes (Iniidae and Pontoporiidae) but they are always much smaller than in the Platanistidae. Pilleri and Ghir (1979) reconstructed large maxillary crests in *Ischyrorhynchus vanbenedeni* mainly inspired by the morphology of *Platanista.* Their interpretation may be correct, but one could very well imagine a much less developed crest approaching the condition observed in *Inia.* Nevertheless, a more complete skull with complete maxillary crest and associated auditory region and scapula is necessary to decide whether *I. vanbenedeni* is related to the Platanistidae (sensu de Muizon, 1984). If the large maxillary crests are actually present in *Ischyrorhynchus vanbenedeni,* this condition could also represent a parallelism with the platanistid anatomy instead of an indication of close phylogenetic relationship. However, in the absence of an associated auditory region with a skull, the assignation of *I. vanbenedeni* to the Inioidea remains uncertain (de Muizon, 1984: 75).

Another synapomorphy of the Platanistidae is represented by the structure of the palatine bones. The palatine bones of the Platanistidae are not articulated medially. In contrast to their usual position in the other odontocetes, they show a clear dorsolateral migration. The condition observed in *Platanista* is even more specialized as the palatine is completely overlapped laterally by the
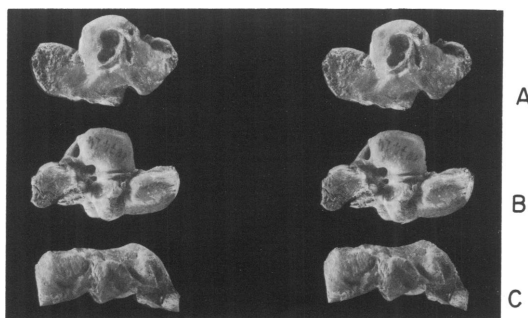
Fig. 19. *Pomatodelphis* cf. *inaequalis* (USNM 187414). Stereophotographs of left periotic: (**A**) dorsal view, (**B**) ventral view, (**C**) lateral view. Scale ×0.50.

pterygoid. The relationship of the platanistid palatine bones is unique among the odontocetes and is regarded here as one of the major synapomorphies of the family Platanistidae (fig. 18).

The Platanistidae are also defined by the reduction in length and transverse thickness of the medial lobe of the tympanic, by the greater elevation of the lateral wall of the tympanic, by the transformation of the periotic articular rim of the Squalodelphidae into a hooklike articular process, and by the shortening and thickening of the anterior process of the periotic.

Among the Platanistidae, *Zarachis* and *Pomatodelphis* resemble each other more than they resemble *Platanista,* but precise synapomorphies are not easy to define, and most of the similarities are symplesiomorphies. The supracranial crests are frontomaxillary in *Zarachis* and *Pomatodelphis* while they are maxillary only in *Platanista.* Apparently, the frontomaxillary crests could be apomorphic as compared to the maxillary crests of *Platanista.* However, the condition in that genus could also be the result of a secondary regression of the frontal part of the crest, a possible consequence of the great enlargement of the maxillary crest. On the periotic, the apex of the anterior process is dorsoventrally thicker in *Zarachis* and *Pomatodelphis* than in *Platanista.* In some specimens the apex is even square-shaped while it is more rounded in others, representing possible sexual dimorphism. Moreover, on the tympanic of *Pomatodelphis* and *Zarachis,* the medial aspect of the involucrum is much more elevated than

in *Platanista.* Although restrictions could be made concerning some of these features, they are tentatively regarded as synapomorphies of *Zarachis* and *Pomatodelphis* (figs. 19, 20).

Platanista is often regarded as a very primitive odontocete and sometimes as the most primitive among the living forms. However, as mentioned by Barnes et al. (1985), this genus shows many highly specialized features. Some characters commonly regarded as primitive could very well be due to reversals. The typical autapomorphic characters of *Platanista* are:

1. extreme development of the maxillary crests;
2. increase in the size of the zygomatic process of the squamosal and the correlative reduction of the orbit;
3. well marked asymmetry of the vertex, which is almost absent in the other Platanistidae;
4. narrowness of the rostrum;
5. position of the palatines, covered ventrally by the pterygoids;
6. reduction of the articular portion of the posterior process of the periotic;
7. development of the unciform process of the tympanic;
8. round internal auditory window;
9. development of a well differentiated spine of spongy bone in the ventral groove of the tympanic;
10. increase in length of the crown of anterior teeth.

However, some features are obviously plesiomorphic:

1. notable heterodonty;
2. lateral lamina of the pterygoid, which contacts the falciform process of the squamosal, therefore forming a continuous lateral bony wall for the pterygoid sinus (see de Muizon, 1984: 39);
3. double articulation of the tympanic with the squamosal and the periotic (see de Muizon, 1984);
4. small size of the mandibular foramen and of the internal fossa for the fatty body of the mandible;
5. unfused cervical vertebrae which have a longer centrum than in any other living cetaceans.

In other respects some features of *Platanista* seem to be apparently plesiomorphic but are tentatively regarded here as reversals:

1. lambdoidal crests inflected medially to a much greater extent than in any other Platanistoidea; this morphology is a probable consequence of the development of very large maxillary crests and the zygomatic process of the squamosal;

2. elevation of the dorsal tuberosity of the posterior process of the periotic (absent in all the other Platanistoidea), which imbricates in the angle formed at the squamosal-occipital suture. This structure is probably related to the necessity for strengthening the attachment of the periotic to the skull in the Platanistidae, a function accomplished in the other Platanistidae and in Squalodelphidae by the development of either an articular process (as in *Platanista*) or an articular rim.

PREVIOUS ASSIGNMENTS OF
NOTOCETUS VANBENEDENI

In the original description of *N. vanbenedeni,* Moreno (1892) did not make a precise assignation of his specimen but compared it to *Pontoporia, Inia,* and *Squalodon.* Ameghino (1894) and Lydekker (1894) referred Moreno's specimen to the Platanistidae and Lydekker regarded *Notocetus vanbenedeni* as a primitive platanistid with squalodont features. True (1910: 31) definitely related *Notocetus vanbenedeni* to the Squalodontidae although he recognized that the species was not "so distantly related" to the ziphiids (True, 1910: 21). Dal Piaz (1916b) created the family Squalodelphidae which included the genera *Squalodelphis* (established in the same paper) and *Argyrodelphis* (=*Notocetus*). He concluded that there was a close affinity between the Squalodontidae and Squalodelphidae.

Subsequently, Winge (1918, 1921), Cabrera (1926), Kellogg (1928), and Simpson (1945) referred *Notocetus* to the Ziphiidae. However, one of the typical ziphiid characters given by Cabrera (1926: 392) (i.e., the inflation of the posterolateral part of the dentaries) is also found in *Squalodelphis, Squalodon,* and some Rhabdostoidea. Moreover, this part of the mandible is very fragile and is often distorted by fossilization. The asym-
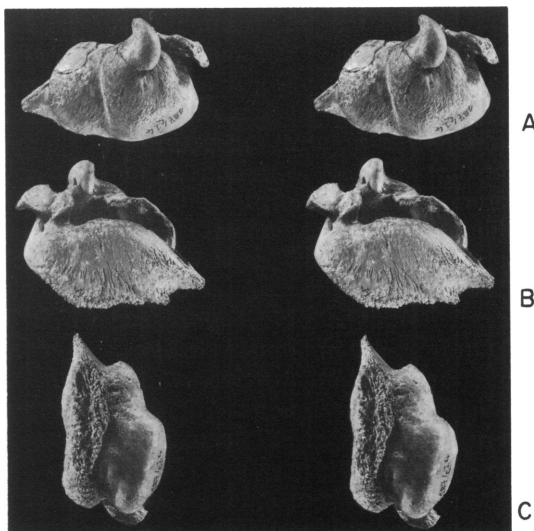

Fig. 20.   *Pomatodelphis* cf. *inaequalis* (USNM 187414). Stereophotographs of left tympanic: (**A**) lateral view, (**B**) medial view, (**C**) ventral view. Scale ×0.50.

metry of the vertex of *N. vanbenedeni* was also regarded by Cabrera as a ziphiid character. Nonetheless, the same asymmetry is found in *Squalodelphis* and is more emphasized in *Platanista,* but is much less developed on True's specimen. In fact, this feature reflects a general tendency of the Odontocetes, which is most pronounced in the Physeterida (Physeteroidea + Ziphioidea). The shallow facial depression, which according to Cabrera is a ziphiid character, is much more reduced than in the ziphiids and is similar to that in *Squalodon, Pomatodelphis,* and *Zarachis.* In fact, none of the characters cited by Cabrera are fully satisfactory and they are either symplesiomorphies or features which are easily attained through parallelism. Kellogg (1928: 58) did not comment much on the ziphiid features of *Notocetus,* but he did find several similarities of this genus with *Squalodon.* Among these is the stoutness of the zygomatic process of the squamosal, which is also found in the Platanistidae (*Platanista, Zarachis,* and *Pomatodelphis*) and *Squalodelphis.* The similarity was also noted by Winge (1921: 38).

The vertebrae of *Notocetus vanbenedeni* have often been regarded as typically ziphioid (True, 1910; Winge, 1921; Cabrera, 1926; Kellogg, 1928). However, the ziphioid fea-

tures noted by True (1910) and Cabrera (1926) are also present in the squalodonts described by Dal Piaz (1916a). Moreover, the transverse processes of the atlas of *Notocetus* is distinct from the ziphiid condition. The primitive condition is found in *Squalodon, Eurhinodelphis,* or *Zarachis* where both dorsal and ventral transverse processes (resulting from the opening of the transverse foramen) are approximately the same size. In the Delphinoidea and Physeterida the dorsal transverse process almost completely disappears and the ventral one is well developed. The Inioidea (sensu de Muizon, 1985) have a much reduced ventral transverse process while the dorsal is only a little longer. In *Notocetus vanbenedeni* the dorsal process is much longer than the ventral and this condition is therefore closer to that of the Inioidea than to that of the Ziphioidea. The condition in *Phocageneus* is the same as that in *Notocetus.* In fact, the dorsal transverse processes of *Notocetus* and *Phocageneus* are much larger than in the Inioidea, and considering that it is perhaps one of the few characters that could relate the Squalodelphidae to the Inioidea, it is here regarded as a result of parallel evolution.

In conclusion, the similarities of *Notocetus* with both the Ziphiidae and Squalodontidae indicate that some relationships could exist between Ziphiidae and Squalodontidae. This idea is not new; it has already been expressed by Abel (1905) and Kellogg (1928). This statement also suggests polyphyletic or paraphyletic nature of the Squalodontidae. In fact, it is possible that the Ziphioidea and Physeteroidea have their origin in some squalodont-like odontocete. Most of the Squalodontidae bear the synapomorphies of the scapula identified above. However, we have seen that *Sulakocetus* still retains a coracoid process, whereas it is lost in the other Platanistoidea. At the same time, *Sulakocetus* appears to have an acromion located on the anterior edge of the bone. In this respect, this bone would differ from the scapula of the Physeterida where the supraspinous fossa is sometimes nearly absent but where the base of the acromion is lateral to the anterior edge of the bone. However, the scapula of the holotype of *Sulakocetus* is very poorly preserved and it is not easy to determine precisely the scapular condition in this genus. If

this character was absent from *Sulakocetus,* this form would approach somehow the morphology of an hypothetical squalodont-like ancestor of the Ziphioidea and Physeteroidea.

After Kellogg (1928), few references were made about *Notocetus vanbenedeni.* Colbert (1944), Simpson (1945), Dechaseaux (1961), Romer (1969), and Mead (1975) accepted the assignment to the Ziphiidae without much criticism. Recently, Barnes et al. (1985) have proposed a phylogeny of cetaceans in which the family Squalodelphidae is recognized as an early derivation of the Squalodontidae. Although the genus *Notocetus* is not discussed in the text, it is apparently related to that family and the ziphiid affinities are rejected. In this respect I agree with the phylogeny given by Barnes et al. (1985) which, in other respects, strongly differs from the platanistoid phylogeny proposed here. Those authors accept the monophyly of the Platanistoidea (sensu Simpson, 1945) and the family Acrodelphidae is regarded as closely related to the Pontoporiidae. The Acrodelphidae are considered by these authors to include such genera as *Pomatodelhis, Zarachis,* and *Schizodelphis.* However, Barnes et al. (1985: 20) mention that "for the sake of the present discussion, we leave the family in the Platanistoidea, but it needs serious reevaluation," a statement I regard as very reasonable.

NOTES ON THE ACRODELPHIDAE AND RHABDOSTOIDEA

In a recent publication (de Muizon, 1984), I related the Acrodelphidae to the Rhabdostoidea. The Acrodelphidae were thought to include the genera *Acrodelphis, Schizodelphis, Eoplatanista,* and *Champsodelphis.* As I stated, the monophyly of the Rhabdostoidea and that of the Acrodelphidae have yet to be demonstrated by synapomorphies. Furthermore, the genera *Schizodelphis, Acrodelphis,* and *Champsodelphis* have to be reconsidered. Here I briefly expose the major problems concerning these taxa which will be analyzed in detail elsewhere (de Muizon, in prep.).

The type specimen of *Schizodelphis sulcatus* (Gervais, 1848–52) is an incomplete

skull (MNHN RL12) from Cournonsec (Department of Hérault, France) which has lost both its periotics and tympanics during fossilization, and whose vertex and occipital region were destroyed during excavation. Abel (1900) and Dal Piaz (1903) referred skulls from the Vienna basin and from Belluno (Italy) to Gervais' species but assigned them a new genus name: *Cyrtodelphis* Abel 1900. This latter name is a junior synonym of *Schizodelphis* Gervais 1861 (Eastmann, 1907; Winge, 1921; Kellogg, 1928; Simpson, 1945; Romer, 1969; Pilleri, 1985). In other respects, the holotype of *Schizodelphis sulcatus* (with further preparation) is generically different from the specimens figured by Abel (1900), Dal Piaz (1903), and Pilleri (1985) and shows greater similarities to the Rhabdosteidae; it resembles some *Rhabdosteus* specimens from the Calvert formation of Maryland (USA) revised by Myrick (1979). Furthermore, *Eoplatanista italica* Dal Piaz (1916c) shows striking similarities with the specimens referred by Abel, Dal Piaz, and Pilleri to *Cyrtodelphis sulcatus* or to *Schizodelphis sulcatus*. The auditory regions are identical and the skulls are otherwise morphologically very similar. I consider Abel's, Dal Piaz's, and Pilleri's specimens to belong to the genus *Eoplatanista,* and I regard the species of *Schizodelphis brachycephalus* Pilleri 1985 as a junior synonym of *Eoplatanista italica* Dal Piaz 1916c (this conclusion will be further developed in a work in preparation).

Two other remarks are noteworthy. First, it is true that the illustration given by Abel (1900: pl. 3, figs. 2–4) for the tympanic he refers to *Schizodelphis* (=*Cyrtodelphis*) *sulcatus* indicates obvious squalodelphid affinities. However, Dal Piaz (1903: 204), who studied the specimen, mentions that Abel's illustrations are not accurate and that a comparison of the Eggenburg tympanic with the Belluno tympanic shows strong morphological affinities. Second, Van Beneden and Gervais (1880: pl. 57, fig. 8) illustrated an auditory region of an odontocete (MNHN RL11) from the Castries shales (Department of Hérault, France) and they referred the specimen to *Schizodelphis sulcatus* without explanation. In fact, this specimen is very similar to the periotic and tympanic of *Rhabdosteus* and

its malleus is identical to that of *Eurhinodelphis.* In other respects, it is different from the auditory region illustrated by Dal Piaz (1903) and therefore the malleus of MNHN RL11 that I figured elsewhere (de Muizon, 1985: fig. 1) is not that of an Acrodelphidae but that of a Rhabdosteidae.

Consequently, *Schizodelphis* is a possible rhabdosteid distinct from *Eoplatanista,* which is related to the Acrodelphidae. The lack of information on the vertex and the auditory region of the holotype of *Schizodelphis sulcatus* perhaps requires one to consider this species as an incertae sedis taxon.

Among the Acrodelphidae, the genus *Acrodelphis* was established by Abel (1900) for several species of the genus *Champsodelphis.* No type species was formally named by Abel, and so one must consequently choose the oldest species referred by that author to *Acrodelphis*: *A. macrognathus* (Brandt, 1873). This species was originally referred by Brandt to the genus *Champsodelphis* Gervais 1848–52. However, this species is a junior synonym of *Champsodelphis macrogenius* (Laurillard, 1844). The latter species name was created by Laurillard for both specimens recorded by Cuvier (1823) as "Dauphin à longue symphyse" which are a portion of mandible with part of the symphysis (Cuvier, 1823: pl. 23, figs. 4, 5) and a portion of rostrum (Cuvier, 1823: pl. 23, figs. 9–11). Because Cuvier's name makes reference to the mandible and Laurillard mentions the mandible first in his formal designation of "*Delphinus*" *macrogenius,* the lower jaw must therefore be regarded as the lectotype of that species. *Champsodelphis macrognathus* Brandt 1873, based on this specimen, is therefore a junior synonym of *Champsodelphis macrogenius* (Laurillard, 1844). The genus *Acrodelphis* Abel 1900 is consequently a junior synonym of *Champsodelphis* Gervais (1848–52) as both genera have the same type species. The family Acrodelphidae should have the same fate as its type genus, but, as it is not the purpose of this paper to revise this group of odontocetes, the family is provisionally retained here in the sense of de Muizon (1984). *Acrodelphis ombonii* (Longhi, 1898) is based on a partial skull with associated auditory region, and must be given a new genus name (de Muizon, in prep.); its auditory region,

illustrated by Dal Piaz (1977) and Pilleri (1985), seems to indicate some affinities with the Squalodelphidae but a detailed study of this form is needed to settle that point.

The type specimen of the type species of the genus *Champsodelphis* (i.e., the lectotype of *C. macrogenius* designated above) is a portion of mandible which is regarded as totally inadequate to define an odontocete cetacean. Consequently, the genus *Champsodelphis* and the species *C. macrogenius* must be regarded either as nomina vana or as incertae sedis restricted to the type specimen. Given that the skull described by Delfortrie (1875) as *C. tetragorhinus* cannot be seriously referred to *Champsodelphis*, "*C.*" *tetragorhinus*, which is known by a fairly complete skull but without an associated auditory region, must therefore be given a new genus name. The squamosal morphology and the thickened supraorbital process of that species strongly suggest squalodelphid affinities. As the original specimen was not observed during this study, "*C.*" *tetragorhinus* will not be taken into account here, although it could be tentatively classified in the Squalodelphidae. The Acrodelphidae therefore include two well defined genera only: "*Acrodelphis*" ("*A.*" *ombonii*) and *Eoplatanista*; however, as stated above, the monophyly of that family still remains to be established by synapomorphies.

Rhabdosteidae is defined by an important shortening of the mandible relative to the rostrum and the concurrent loss of its corresponding anterior teeth. This feature is absent in *Eoplatanista*. Rhabdostoidea (Rhabdosteidae + Acrodelphidae), whose monophyly has still to be demonstrated, has been related to the Delphinidae on the basis of two synapomophies (de Muizon, 1984): (1) the palatine bones are slightly in contact with the anterior extremity of the pterygoid sinus but no palatine lateral lamina is present and (2) the articulation of the squamosal and tympanic is lost.

With the exception of some of the generic affinities, the platanistoid phylogeny presented here is in general agreement with what I have proposed elsewhere (de Muizon, 1984, 1985).

SUMMARY AND CONCLUSIONS

Notocetus vanbenedeni is an early Miocene odontocete from Patagonia, southern Argentina. The first detailed description of its auditory region and scapula indicates the presence of synapomorphies which relate the species to the superfamily Platanistoidea and to the family Squalodelphidae. This hypothesis disagrees with the long-believed affinity of *Notocetus* to the Ziphiidae but acknowledges the similarities of this genus with the Squalodontidae recognized by all authors since the original description by Moreno (1892). As a matter of fact, Squalodontidae is regarded here as the sister-group of the monophyletic assemblage formed by the Squalodelphidae and the Platanistidae. The three families are considered to constitute the monophyletic superfamily Platanistoidea (sensu de Muizon, 1984, 1985).

Notocetus vanbenedeni shows synapomorphies of the Platanistoidea:

1. loss of the coracoid process of the scapula;
2. loss of the supraspinous fossa with the acromion located on the anterior edge of the bone.

N. vanbenedeni shows synapomorphies of the Platanistidae-Squalodelphidae group:

1. development of a supplementary articulation on the lateral side of the posterior process of the periotic (this structure is a thick and salient articular rim which will transform into a hooklike process in the Platanistidae);
2. occurrence of a large subcircular fossa dorsal to the spiny process of the squamosal;
3. development of an anterior spine on the tympanic with a well marked anterolateral convexity, separated from the spine by a notable notch; and
4. single-rooted teeth.

N. vanbenedeni shows features tentatively regarded as synapomorphies of the Squalodelphidae:

1. square-shaped cochlea of the periotic;
2. wide and thin-edged dorsal opening of the cochlear aqueduct;
3. apical extension of the manubrium of the malleus;
4. development of the dorsal transverse process of the atlas and reduction of the ventral process.

Among the Squalodelphidae, the genus *Notocetus* is the sister-group of the group

Squalodelphis + *Phocageneus* which is related by the loss of accessory cusps of the posterior teeth, the more developed articular rim, the greater length of the anterior spine of the tympanic, the better marked lateral furrow, and the occurrence of a small longitudinal elevation in the ventral groove of the tympanic.

The Squalodelphidae include the following genera: *Notocetus* (the most primitive) from the Early Miocene of Patagonia, *Squalodelphis* from the Middle Miocene of Italy, and *Phocageneus* from the Middle Miocene of the Calvert Formation (Maryland, USA). Another form of Squalodelphidae is from the Middle Miocene of the Pungo River Formation at Lee Creek Mine in North Carolina; it is known from periotics and tympanics and is under study by F. C. Witmore. A probably new species of *Notocetus* is reported from the Middle Miocene of the Calvert Formation, thus extending the range of that genus to the Middle Miocene of the Northern Hemisphere.

The Platanistidae are mainly defined by the acquisition of strongly developed maxillary or frontomaxillary crests on the supraorbital regions of the skull. This structure is never found with such an extension in any other cetacean. The Platanistidae are also defined by synapomorphies relating to the periotic and tympanic. This family includes: the living genus *Platanista* and the Middle Miocene genera, *Zarachis* and *Pomatodelphis* from the Calvert Formation and for the latter also (Middle to late Miocene) from the lower Bone Valley Formation of Florida.

No synapomorphy is given to define the Squalodontidae, an apparently conservative group. This family is "defined" only by symplesiomorphies, and could well be a paraphyletic or even polyphyletic taxon. Most of the Squalodontidae are referred to the Platanistoidea because of synapomorphies of the scapula. *Sulakocetus* could, however, be excluded from that superfamily (see above). Moreover, the striking similarities between the Squalodontidae and the Ziphiidae seem to indicate a squalodont-like morphology for the ancestors of that family and probably of the Physeteroidea. The platanistoid affinities of the squalodonts have been documented here, but it is noteworthy that this group shows some similarities with the Rhabdostoidea

which probably represent symplesiomorphies. Also, similarities with the Oligocene forms like *Patriocetus, Agorophius,* or *Xenorophus* are obvious. It is therefore clear that the squalodonts are perhaps the odontocete group in most need of a serious revision. Such a study would certainly shed light on the understanding of the evolution of early odontocetes and on the origin of the living groups.

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