The polyphyly of Acrodelphidae, long-snouted odontocetes of the European Miocene

by Christian de Muizon*

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III. Acrodelphis

The genus *Acrodelphis* was created by ABEL (1900) in order to regroup several species of the genus *Champsodelphis* which have a pointed symphysial angle, whereas the forms with a rounded symphysial angle were regrouped under the generic name *Cyrtodelphis*. As previously stated, the precariousness of this feature casts doubt on ABEL’s generic subdivision.

ABEL (1900) did not formally designate a type species for his new genus and, as a result, I have proposed (MUIZON, 1987) to choose the earliest recognized species, and to refer it to this genus: *Acrodelphis macrognathus* BRANDT, 1873, a more recent synonym of *Champsodelphis macrogenius* (LAURILLARD, 1844).

A. The Problem of *Acrodelphis macrognathus* BRANDT, 1873

*Acrodelphis macrognathus* was initially referred by its author to the genus *Champsodelphis* GERVAIS, 1848-1852, and was established by BRANDT on an odontocete jaw with a large symphysial portion, from the village of Sort (Department of Landes, France). This specimen had already been described and illustrated by CUVIER (1823, pl. 23, figs. 4 and 5) under the designation “Dolphin with a long symphysis of the lower jaw.” This designation included, according to CUVIER, a second specimen, a portion of rostrum (CUVIER, 1823, pl. 23, figs. 9 to 11) from the same site. Contrary to what I stated (MUIZON, 1988: chap. 4), it is not LAURILLARD (1844) but FISCHER (1829) who regrouped the two specimens described by CUVIER (KELLOGG, 1925:5) under the name *Delphinus macrogenius*. However, as KELLOGG indicates (1925), doubt remains as to the validity of the species *Delphinus macrogenius*, since the same year, HOLL (1829) attributed the name *Delphinus bordae* to the same specimens. Since current usage has retained FISCHER’s (1829) designation, it will be retained in this work: the importance of this choice is, however, minor, as we will see shortly. FISCHER did not designate a type specimen, but taking into account the fact that CUVIER’s designation refers to the jaw, which is first studied in the description of FISCHER, the jaw illustrated by CUVIER (1823, pl. 23, fig. 4 et 5) should be chosen as the lectotype of *Delphinus macrogenius* Fischer, 1829. It is for this species that GERVAIS (1848-1852) created the genus *Champsodelphis*. As a result, *Champsodelphis macrognathus* Brandt, 1873, defined according to the same holotype as

Champsodelphis macrogenius, becomes synonymous with this species. For ABEL (1900), Champsodelphis macrogenius [= C. macrognathus] is referred to the genus Acrodelphis and constitutes the type species. Thus, the two genera Champsodelphis GERVAIS, 1848-1852, and Acrodelphis Abel, 1900 possess the same type specimen illustrated by CUvier (1823, figs. 4 and 5). Acrodelphis is thus a junior synonym of Champsodelphis, type genus of the family Acrodelphidae.

Furthermore, Champsodelphis macrogenius [= Champsodelphis macrognathus = Acrodelphis macrognathus] is defined based on a portion of jaw that is considered here as a totally inadequate specimen, because it is too incomplete to define a genus and a species of odontocete. As I have already suggested (MUIzon, 1987), the genus name Champsodelphis and the species C. macrogenius should be recognized either as nomina vana, or, and this seems preferable to me, seen as incertae sedis restricted to the lectotype. All of the other specimens referred to the genus Champsodelphis [=Acrodelphis] should thus be attributed to another genus. This is the case for “Acrodelphis” ombonii (LONGHI, 1898).

B. “Acrodelphis” ombonii (LONGHI, 1898)

This species was described by its author (LONGHI, 1898) under the name Champsodelphis [p. 63] ombonii for a portion of cranium attached to its jaw (incomplete), several isolated teeth, a tympanum, and a portion of occipital and squamosal to which an incomplete periotic is attached. The cranium, jaw, and tympanum come from the same block of sediment (#414; LONGHI, 1898: 323 and 349), whereas the occipital, squamosal, and periotic come from another (#416: LONGHI, 1898: 349). The author gives no indication of a possible association of the two blocks. The periotic (fig. 15), however, corresponds neither in size nor morphology to the tympanum (fig. 16). The periotic (LONGHI, 1898, pl. H, figs. A and E) has lost its anterior process, but it is possible to note its large size, the slight elevation, and the length of its pars cochlearis and the large axis of its internal auditory fenestra, slightly raised. By these three features, it strongly resembles the genus Squalodon to which it is referred here. The specimens coming from block #414 can belong neither to the jaw nor to the cranial fragment from block #416. Indeed, the teeth of this latter specimen are small, numerous, conical, uniradiculated, and fundamentally different from those of Squalodontidae, which are few, very large, triangular, and biradicated (these last two features are representative of the medial and posterior teeth).

Fig. 15. – Periotic attributed to Champsodelphis ombonii by LONGHI (1898), (IGUP 26 407a) from the Inferior Miocene of the Molasse of Belluno (Italy) and which, in fact, belongs to the genus Squalodon: a, dorsal view; b, ventral view. (Scale = 2 cm.)

The tympanum mentioned above was discovered by LONGHI (1898: 349) in the matrix surrounding the rostrum. It is apparently identical to that of Schizodelphis and shows great similarity to that attributed by VAN BENEDEN and GERVAIS (1880, pl. 57, fig. 15) to S. sulcatus. It probably belongs to a Eurhinodelphidae (fig. 16) and might be referred to forms such as Eurhinodelphis sigmoideus or “Eurhinodelphis” bellunensis whose teeth are much more slender than those of “Champsodelphis” ombonii (PILLERI, 1985); furthermore, it does not correspond very well to the periotic of individual A illustrated by DAL PIAZ (1977), the only specimen known for this form. Thus, there seem to be three forms in the series of syntypes of “Champsodelphis” ombonii, two of which are attributable to a squalodont and one to a possible Eurhinodelphidae.
Associations of this type are not infrequent in collections from the sandstone of Belluno or Bolzano. Actually, the fragmentation of specimens at the time of their extraction has probably facilitated the confusion and mix-ups, especially when the specimens were collected by workers who were not trained in paleontology and not made aware of the importance of the associations. ABEL (1900) referred the species *C. ombonii* to the genus *Acrodelphis* and DAL PIAZ (1977) referred several specimens (IGUP 26 172 to 26 181) to this genus, including some cranial pieces such as a rear-cranium and [p. 64] several auditory regions (individuals A, B, C). However, individual “B” of DAL PIAZ requires several remarks. This specimen includes a partial rostrum with some jaw elements, a periotic, a tympanum, and the first six cervical vertebrae (IGUP 26 175 to 26 180). The specimen IGUP 26 377 is the posterior portion of an odontocete cranium whose periotic (which I myself located) is evidently the symmetric of IGUP 26 176. This cranial fragment belongs to specimen B of *Acrodelphis ombonii* described by DAL PIAZ (1977). But then a contradiction arises because the posterior cranium of individual A of DAL PIAZ (1977), IGUP 26 480, has a temporal fossa, a much shallower orbit, and a much more slender zygomatic process, which show that specimens A and B cannot belong to the same genus. If we consider the features of the matrix and the preservation of the bone, the attribution to the same individual of the specimens composing individual B of DAL PIAZ (1977) is probable but not certain.

Fig. 16. - Tympanum attributed to *Champsodelphis ombonii* by LONGHI (1898) (IGUP 26 407b), from the Inferior Miocene molasse of Belluno (Italy); it could, in fact, be a Eurhinodelphidae: a, lateral view; b, ventral view. (Scale = 2 cm.).

Furthermore, taking into account the syntypic nature of the holotype of LONGHI (1898), it is important to designate a lectotype. In the present case, it seems that the attribution of individuals A and C of DAL PIAZ (1977) to the jaw from sediment block #414 of LONGHI (1898, pl. 1) is very probable. For this reason, for the sake of caution and in order not to multiply names in a group whose taxonomy is already sufficiently complex, I propose to choose specimen #IGUP 261405 from block #414 (LONGHI, 1898: 323) as the lectotype for “*Champsodelphis* ombonii.” This type thus includes an incomplete jaw and a portion of cranium. As a result of the two World Wars, the specimen was damaged and today is reduced to an incomplete jaw connected to a small portion of maxilla. We should now compare specimens A, B, and C described by DAL PIAZ (1977) in order to determine which ones can be referred to the lectotype designated above.

[p. 65] 1 – Relation between the lectotype and the specimens referred by DAL PIAZ (1977) to *Acrodelphis ombonii*.

The lectotype of “*Acrodelphis* ombonii” is, in its current state, a fairly incomplete specimen and, examined alone, it would be difficult not to consider it as *incertae sedis*. However, it shows great similarities to several other pieces described by DAL PIAZ (1977), particularly regarding the teeth. Furthermore, the specimens of LONGHI and DAL PIAZ from the same site (Burdigalian molasse from the Bolzano quarries near Belluno, Italy) belong to the same faunal group and are not representative of any other known form in this geological formation (fig. 17).

Fig. 17. – Holotype of *Dalpiazina ombonii* (LONGHI, 1898) (IGUP 26 405), Inferior Miocene molasse of Belluno (Italy). (Scale = 5 cm.)
The only known anatomical elements that would allow us to compare the lectotype of “Acrodelphis” ombonii with the specimens referred to this species by Dalpiaz are the teeth. Those of the lectotype “Acrodelphis” ombonii have a characteristic robustness that differentiates this species from Eurhinodelphis, Schizodelphis, Ziphiodelphis, and Eoplatanista. By their homodonty and smaller size, they are very different from those of Squalodontidae and likewise different from those of Squalodelphidae. The teeth of the lectotype and those of individuals A and C of Dalpiaz (1977) differ from those of individual B by their slightly smaller size and especially by the absence of anterior and posterior carina, as we clearly observe in individual B. Furthermore, the teeth of this latter specimen do not exhibit in such a marked way the slight bulging that characterizes the base of the crown of the teeth of the lectotype and individuals A and C. It thus seems that individuals A and C of Dalpiaz, rather than individual B, should be referred to the lectotype “Acrodelphis” ombonii. However, the differences between this specimen and the others remain slight and are perhaps due simply to the greater wear and tear in the first three specimens than in the latter. Furthermore, the morphology of the rostrum of specimen B is similar to that of the rostrum of individual A in its sturdiness and in the absence of a fissure on the maxillary-premaxillary suture. In this case, if we assume that the two rostrum fragments of specimen B are representative of “Acrodelphis” ombonii, one must assume that the structure to which they belong is formed by several individuals representing different genera because the periiotics, tympanum, and cranium that are connected with them belong to a form different from the cranium of specimen A. It is likewise possible that the association of pieces making up individual B is correct, and that the cranium and periiotic of individual A do not belong to the rostrum Dalpiaz associates them with. However, the fact that individual A was collected by the author himself (Dalpiaz, 1977:25) leads us to assume the correctness of the association with the pieces of individual A. If we assume this hypothesis, the association of the rostral elements of individual B with the cranial and vertebral pieces mentioned by Dalpiaz is possible but not proven. As a result, in the description that follows, we consider only individuals A and C as belonging to “A.” ombonii; while the rostral fragments of individual B could perhaps also belong to this species, to be on the safe side, they will not be referred to it.

2 – Systematics of “Acrodelphis” ombonii (Longhi, 1898)

Acrodelphis being a junior synonym of Champsodelphis, and this genus being an incertae sedis restricted to the type specimen of its type species, the lectotype of Longhi (1898), i.e. the connected jaw and rostral fragment, and individuals A and C of Dalpiaz (1977) should be attributed to another genus: Dalpiazina nov. gen. Furthermore, the type genus of the family, Champsodelphis [= Acrodelphis], being an incertae sedis restricted to the type specimen of its type species, the familial taxon Acrodelphidae likewise becomes an incertae sedis restricted to the type specimen of the type species of the type genus. Dalpiazina must then be referred to the new family Dalpiazinidae.

Diagnosis

A long-snouted odontocete whose maxillary-premaxillary suture does not reach the apex of the rostrum, which was formed exclusively by the premaxillae, as in Eurhinodelphidae and Squalodontidae and probably Squalodelphidae. The mandibular symphysis was probably of an identical length to that of the rostrum, which did not show a lateral groove as is found in
Eurhinodelphidae and *Eoplatanista*. The ventral side of the rostrum has a large vomerine fenestra as in Squalodontidae. The homodont teeth have more massive crowns than those of Eurhinodelphidae and have slightly wrinkled enamel; they are conical and do not have secondary cuspids. The posterior teeth, lower than the anterior, exhibit a wrinkled lingual bulging.

The cerebral cranium is massive, and its dorsal side not very concave. The vertex is lower than in Eurhinodelphidae but the occipital was more convex. The temporal fossa is low in a lateral view and narrow in a ventral view. The zygomatic process is narrow. The periotic has a very similar morphology to Squalodontidae. The jaw shows much development in the posterior region of the dentaries; these bones were evidently not knitted together to the symphysis.

Type species: *Dalpiazina ombonii* (LONGHI, 1898)

Derivatio nominis: In homage to Gorgio DAL PIAZ and his son Giambattista DAL PIAZ, with gratitude for their work in the paleontology of vertebrates of Italy, in particular for the special attention that they gave to the study of the odontocete fossils of the Belluno molasse.

Type locality: Bolzano quarries, near Belluno, southern Alps, Italy.

Geological formation and age: Molasse of Belluno, Burdigalian Age (CASON et al., 1981).

Type specimen: A jaw with the posterior region of the symphysis and a large part of the right dentary (IGUP 26 405), to which a portion of rostrum is still attached.

Hypodigm: The holotype as well as two of the three specimens referred by DAL PIAZ (1977) to *Acrodelphis ombonii*: specimen A: a posterior cranium (IGUP 26 480), a portion of connected rostrum and jaw (IGUP 26 172), a periotic (IGUP 26 173) and a sixth cervical vertebra (IGUP 26 174); specimen C: a fragment of dentary with ten teeth in place (IGUP 26 181).

Diagnosis: Identical to that of the genus.

Description

a – The teeth

On the lectotype, as on specimen A of DAL PIAZ (1977), IGUP 26 472, the teeth are all very slightly worn in a characteristic fashion, the worn facet perpendicular to the vertical axis of the crown; this type of wear facet is also often found on other specimens referred to *D. ombonii*. The teeth have a shorter and wider crown than those of *Eurhinodelphis* or *Ziphiodelphis* and show at their base a slight bulging that does not appear in these two genera. In addition, the teeth of *Dalpiazina ombonii* have an almost circular cross-section, and when they show a flattening, it is always transverse or slightly oriented toward a postero-labio-antero-lingual axis. In *Ziphiodelphis* [p. 68] and *Eurhinodelphis*, the flattening is always anteroposterior. The teeth of *Dalpiazina ombonii* are likewise very different from those of *Eoplatanista*, which are always lanceolate and are transversely flattened with anterior and posterior carinae and especially with the labial side showing a slight ectoflexus, an elongated depression affecting the crown over its entire top. When they are not worn, the teeth of *D. ombonii* show a slightly wavy enamel, and on their lingual side they exhibit a slight bulging at the base of their crown, from which several small folds of enamel emanate apically. Furthermore, they often have slight anterolabial and posterolingual carinae, but this is not a general feature. Generally speaking, these contours are more pronounced on the posterior teeth, which are lower and have a more triangular cross-section, than on the anterior teeth, which are higher, with a fairly circular cross-section. As in most Eurhinodelphidae and *Eoplatanista*, the roots of the teeth of *Dalpiazina ombonii* (IGUP 26
are clearly bulbous in their basal half. This feature is more pronounced in older individuals. For all the features just discussed, the teeth of the lectotype of *Dalpiazina ombonii* (IGUP 26 405) correspond perfectly to those of individuals A and C described and illustrated by DAL PIAZ (1977). Taking into account the similarities between the lectotype of *D. ombonii* and specimens A and C of DAL PIAZ (1977) concerning the teeth, and likewise taking into account the fact that the three individuals belong to the same faunal group, we can logically concur with the opinion of DAL PIAZ (1977) in associating them specifically. As previously stated, uncertainty exists about individual B whose cerebral cranium is very different from that of individual A but whose rostral elements and teeth are nevertheless very close.

b – The cranium (figs. 18 and 19)

The rostrum is poorly understood because it is incomplete on the two available specimens (IGUP 26 172 and IGUP 26 405). However, taking into account its relatively large cross-section at the apex of specimen IGUP 26 172, it is likely that it reached a length close to that observed in Eurhinodelphidae, if not shorter. On the lateral side of this specimen, we note a clear obliquity in the maxillary-premaxillary suture which certainly does not reach the apex of the rostrum as indicated by PILieri (1985: fig. 2). If we extended this suture along its axis, we observe that it intersects the alveolar edge at the anterior end of the specimen; the missing anterior portion of the rostrum was thus composed solely of the premaxillae. As far as this is concerned, *Dalpiazina* is similar to Squalodontidae and Eurhinodelphidae, where the apex of the rostrum is also composed only of the premaxillae. On the rostrum of *Dalpiazina*, in lateral view we note a clear diminution from back to front in the height of the maxilla, whereas that of the premaxilla increases, a condition existing in Eurhinodelphidae and Squalodontidae. The maxillary-premaxillary suture is sometimes knitted in older individuals, and it is this which caused KELLOGG (1925a) to deny the existence of such a trait in *Eurhinodelphis bossi*, whereas it was defended by ABEL (1901 and 1902) and DAL PIAZ (1935) based on the more recent specimens of *Eurhinodelphis cocheteuxi* from the Antwerp Basin (Belgium). However, the condition of *Dalpiazina ombonii* was probably different from that observed in Eurhinodelphidae. In these, the part of the premaxillae overflowing towards the front of the maxillae no longer has teeth and the jaw is shorter than the rostrum; in addition, the jaw is very narrow in its symphysial region, and its width is always clearly less than that of the rostrum. Table V shows the difference in width that exists between the rostrum and jaw in two species of Eurhinodelphidae compared to that measured in *Dalpiazina* (IGUP 26 172). We notice that for the two Eurhinodelphidae (*Ziphiodelphis abeli* and “*Eurhinodelphis*” *bellunensis*), the difference in diameter between the rostrum and the mandibular symphysis varies by 25–35% from the diameter of the rostrum, whereas it does not exceed 8% in *Dalpiazina ombonii*. This leads us to conclude that in *Dalpiazina*, the rostrum and mandibular symphysis had a similar width and that both probably had teeth at their apex. *Dalpiazina* would thus differ from Eurhinodelphidae but likewise from *Eoplatanista* whose maxillary-premaxillary suture reached the apex of the rostrum.

[p. 69] Fig. 18. – Cranium of *Dalpiazina ombonii* (LONGHI, 1898) (IGUP 26 480), Inferior Miocene molasse of Belluno (Italy): a, dorsal view; b, ventral view, c, lateral view; d, occipital view. (Scale = 5 cm.).

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Table V. – Comparison of cranial measurements between Dalpiazina ombonii and two species of Eurhinodelphidae.

| Classification / Anterior distance of the symphysial angle / Jaw width / Rostrum width / Difference in width |

We can likewise imagine a partial reduction in the number of premaxillary teeth, part of the premaxillary apex of the rostrum being toothless, and the mandibular symphysis extending toward the front up to the first premaxillary tooth. We would have a pre-Eurhinodelphidae arrangement (since in Eurhinodelphidae the premaxilla is toothless) where the apex of the jaw does not surpass or surpasses by very little the apex of the maxilla toward the front. However, this is a purely gratuitous supposition; it is for this reason that the first interpretation given here will be retained.

The rostrum of Dalpiazina does not show deep lateral fissures as we see in Eurhinodelphidae and Eoplanatista. The only fissure visible on the sides of the rostrum of Dalpiazina is a slight longitudinal depression due to the maxillary-premaxillary suture which is not very pronounced, as in Squalodon (especially Squalodon bariensis).

From dorsal view, the rostrum has a rostral groove closed dorsally by the premaxillae, as in Eurhinodelphidae and Eoplanatista but contrary to that seen in Squalodontidae, where it is always open dorsally (Fig. 19).

A characteristic feature of the premaxillae links Dalpiazina to Squalodontidae.

[p. 71] Fig. 19. – Rostrum of Dalpiazina ombonii (IGUP 26 172), Inferior Miocene molasse of Belluno (Italy): a, dorsal view, b, ventral view, c, lateral view (Scale = 5 cm.)

As in the latter, the width of the premaxillae in a dorsal view increases toward the apex of the rostrum. On IGUP 26 172, the curve is very clear, as the table below shows.

| Distance / Posterior region of the specimen / 3 cm in front / narrowest zone / 3 cm / 3 cm / anterior region of the specimen |

Maximum width of the premaxillaries in IGUP 26 172.

This arrangement is never seen in Eurhinodelphidae nor in Eoplanatista, whereas it is always seen in Squalodontidae, where it corresponds to an apomorphic widening of the apical region of the rostrum. The squalodont arrangement existed, perhaps a bit toned down, in Dalpiazina ombonii, and might constitute a fairly good synapomorphy of the Squalodontidae-Dalpiazina group. In this case, the scapula of Dalpiazina should show the two synapomorphies defining Platanistoidea: the loss of the coracoid process and the position of the acromion on the anterior edge of the bone, thus pushing back the supraspinous fossa into the medial position; however, this hypothesis cannot be verified because this bone was not found for Dalpiazina.

On the ventral side of the rostrum of specimen IGUP 26172, we see a very great development of the vomerine fenestra, which surpasses 15 mm in width. It is impossible to get an exact measurement of its maximum width because the jaw is very tightly attached to the rostrum and cannot be separated without taking great risks concerning the teeth. This great width of the vomerine fenestra is typical of Squalodontidae and differs from that of Eurhinodelphidae.
which is much narrower, and from Eurhinodelphidae and Eoplatalista. This width is found, on
the other hand, in Notocetus vanbenedeni of the Argentinean Miocene (MUIZON, 1987).

The cerebral cranium of Dalpiazina ombonii is known only from specimen IGUP 26
480. From a general view, it shows a fairly compact morphology, it differs in size from the much
larger Ziphiodelphis and Squalodon, but it is more like that of Eurhinodelphis and
Schizodelphis. Although the cerebral cranium is highly incomplete, the preservation of the
medial edge of the left preorbital indentation (the right having been totally destroyed) indicates
that it was probably approximately as long as wide, thus more closely resembling
Eurhinodelphis and Schizodelphis than Ziphiodelphis, whose cranium is wider than long. On
the dorsal side, the premaxillae have a width similar to that seen in Eurhinodelphis, but unlike
what we observe in this genus, the lateral edges of the premaxillae of Dalpiazina are slightly
convex and converge slightly toward the front. In Eurhinodelphis, as in Ziphiodelphis, their
edges are almost parallel or slightly concave. The spiracular plates of the premaxillae are
concave as in Eurhinodelphidae and Squalodontidae and, like these latter, reach the vertex in a
regular slope, whereas in Eurhinodelphis, Schizodelphis, and Ziphiodelphis this region of the
cranium is much more excavated, giving a more prominent appearance to the vertex. As far as
this is concerned, Dalpiazina likewise resembles Argyrocetus. Unlike what we see in
Squalodon, the premaxillae are contiguous in front of the nasal fossae and apparently do not
have the split/cleft fenestra that characterizes the rostral groove of Eurhinodelphidae at the base
of the rostrum and in the anterior region of the cerebral cranium. As far as this is concerned,
Dalpiazina ombonii resembles what we observe in Eoplatalista.

The vertex is wide but remains within the norms observed in Eurhinodelphis; it is, on the
other hand, much narrower than the vertex of Ziphiodelphis but shorter than that of Squalodon.
The frontals are trapezoidal and have a suture curving to the left; the right frontal is larger than
the left. This type of asymmetry corresponds to that seen most of the time in odontocetes. The
premaxillae are in contact with the lateral side of the frontals on the vertex, and fit into the corner
between the frontal and the maxillary without touching the occipital.

[p. 73] The anteromedial side of the frontals touches the two small triangular medial
bones joined in a diamond shape. These bones are not the nasals, as DAL PIAZ (1977) thought,
but probably detached parts of the frontals, sorts of interfrontals situated between the frontals and
the nasals. In Ziphiodelphis and Eurhinodelphis, the anteromedial edge of the frontals often has
a pointed morphology as if the small triangular medial bones observed in IGUP 26 480 were
knitted to the frontals. The nasals, detached at the time of fossilization of IGUP 26 480, were
lodged in the two dimples fitted into the front sides of the frontals. These dimples continue
laterally into the premaxilla. The morphology of the fronto-naso-premaxillary articulation is
similar to that seen in Eurhinodelphidae, and seems to indicate that Dalpiazina has nasals related
to those of Eurhinodelphis or Ziphiodelphis, wider than long, forming between them a V open
widely posteriorly, and their anteromedial angle projecting in a spur shape toward the front.

In the nasal fossae, the mesethmoid was not very ossified, and its posterior blade, which
fits over the nasals, was cartilaginous. This would explain that the nasals, no longer held in place
by the mesethmoid, fell off at the time of fossilization. On either side of the mesethmoid in the
nasal fossae, we can see two nasal dimples as are noted in Ziphiodelphis abeli and which
indicate good development of the olfactory bulbs in Dalpiazina ombonii.

The maxilla has a pronounced concavity in the lateral region of the vertex. The major part
of the supraorbital process is destroyed but we can nevertheless note a slight elevation in the
anteromedial region of the postorbital process, indicating a supraorbital thickening related to that of Eurhinodelphidae.

The lateral side of the maxilla is broken between the lambda and the supraorbital process. However, this accident has happened since the DAL PIAZ photo because this ridge is complete in the illustration he gives in 1977. According to this photo, it is clear that from dorsal view, the ceiling of the temporal fossa completely hid the zygomatic process of the squamosal, unlike Eurhinodelphidae and Squalodontidae.

The lateral view of the cranium confirms the slight straightening out of the premaxillae in reaching the vertex, which gives the impression of a less elevated cranium. This arrangement is primitive and indicates a lesser development of the melon and/or of the premaxillary sacks which are situated on the spiracular plates. The occipital condyles are destroyed and it is difficult to get an idea of the contour of the occipital region. However, if we reconstitute the rostrum in the extension of the slight curve of the premaxillae, we clearly see that if the occipital shield is more convex than in *Eurhinodelphis* and *Ziphiodelphis*, it is only slightly more sloping. As far as this is concerned, *Dalpiazina* is intermediate between what we see, on the one hand, in the two genera cited and, on the other hand, in *Argyrocoretus*, a form whose occipital is markedly oblique and whose occipital condyles are very pronounced toward the back, a more archaic condition than those of *Eurhinodelphis* and *Ziphiodelphis*. Let us note here that the cranium referred to the genus *Eurhinodelphis* by PILLERI (1985) under the species name *E. bellunensis* probably belongs to the genus *Argyrocoretus*.

The temporal fossa of *Dalpiazina ombonii* is relatively low, long, and oval. It differs in this regard from the fossae of *Eurhinodelphis* and *Ziphiodelphis* which are shorter, higher, and somewhat triangular, and those much larger of the Squalodontidae. The lambdoid ridge is oriented more posteriorly than laterally, as it is in *Eurhinodelphis* and *Ziphiodelphis*. Furthermore, the temporal fossa is much deeper than in other Eurhinodelphidae.

The zygomatic process, more slender than that of Eurhinodelphidae, is also much shorter and less raised than that of Squalodontidae. Its postglenoid process is thick and more developed than in *Eurhinodelphis sigmoideus* and *Ziphiodelphis abeli* but rather resembles the process of *Eurhinodelphis bellunensis*.

The essential feature of the ventral view of the cerebral cranium of *Dalpiazina ombonii* is the narrowness of the zygomatic process, and the shallowness of the temporal fossa and the front orbit compared to what we observe in Eurhinodelphidae and Squalodontidae. From the bulbous postglenoid process, a shallow fossa comes anteromedially, running medially alongside the glenoid cavity and housing the middle sinus. The medial side of this fossa is formed by the falciform process (*sensu* FRASER and PURVES, 1960), broken on IGUP 26 480. Between the falciform process and the ridge formed by the medial blade of the pterygoid on the one hand, and the alar process of the basioccipital on the other hand, is an elongated cavity, slightly uneven, that houses the pterygoid sinus. The hamulus processes of the pterygoid have disappeared, but we see the marks of the hamulus lobe of the pterygoid on the dorsal blade of the process, anterolateral to the choana. Anterolateral to this fossa, two small oblique ridges appear on the front end of the lateral blade of the pterygoid, destroyed on the specimen.

Generally speaking, the network of basicranial sinus does not differ fundamentally from that of Eurhinodelphidae. The pterygoid had a continuous lateral blade isolating these sinuses from the temporal fossa and the orbit, except perhaps on a small space in front of the groove for the optic nerve where, as in *E. sigmoideus*, it is possible that there was a passage for a small preorbital lobe. This passage was, however, clearly smaller than in *E. sigmoideus*. This anterior region of the
network of the pterygoid sinus was probably more massive than in *E. sigmoideus*, and certainly more compact anteroposteriorly. In *Dalpiazina ombonii*, the space between the optic groove and the front end of the lateral blade of the pterygoid barely exceeds 5 or 6 mm, whereas it is 30 mm in *E. sigmoideus*. In *Dalpiazina ombonii*, furthermore, this region is more upright than in *E. sigmoideus*, where it is very flat and where the front region of the lateral strip of the pterygoid, almost vertical in *D. ombonii*, is almost horizontal as in *Ziphodelphis abeli*. The auditory region of *Dalpiazina ombonii* is not well understood.

As we have seen above, the periotic and the tympanic shown by DALPIAZ (1977, pl. II, figs. 3 to 9) do not belong to this species. Moreover, the periotic referred to “*Champsodelphis* ombonii” by LONGHI (1898) is that of a *Squalodon*, and the tympanum illustrated by this author probably belongs to a Eurhinodelphidae close to *Schizodelphis*. A single periotic thus remains to be referred to *Dalpiazina ombonii* (fig. 20); if it indeed belongs to the same individual as the cranium of specimen A, the periotic shown by DALPIAZ (1977, pl. 1, figs. 5 and 6) might be the only known example of this species.

This periotic (IGUP 26173) is extremely similar to that of *Squalodon*. The principal differences that it has compared to *Squalodon* are in the morphology of the pars cochlearis. This is shorter and more raised (from a dorsal view) than in *Squalodon*. The anteromedial edge of the internal auditory fenestra is clearly thicker and gives the pars cochlearis a slightly more square morphology, as in Squalodelphidae and Platanistidae. The internal auditory fenestra has the [p. 75] classic piro-falciform morphology of odontocetes, but its major axis is clearly more upright than in *Squalodon*, as in Eurhinodelphidae. This condition of the pars cochlearis is more specialized than in *Squalodon*, and corresponds perfectly to the morphology of the rest of the cranium, which is itself also more specialized than in *Squalodon*. Furthermore, the front process is slightly more slender than that of *Squalodon*, and the dorsal edge of the round fenestra is not thickened as it is usually in Squalodontidae.

The rest of the periotic is very close to that of *Squalodon*. As in this genus, it shows in particular a wide dorsal process which has few contours, a dorsal office of the vestibular canal which is very medial and oriented more medially than dorsally, a bulbous front process with an epitubarian fossa with very blunt contours and a wide indentation for the unciiform process of the tympanum. As in *Squalodon*, the capitis mallei fossa is ventrally oriented, whereas it is posteroomedially oriented in Eurhinodelphidae, Squalodelphidae, and Platanistidae. The posterior process shows, as in *Squalodon*, a groove of spongy bones on the front edge of the articular surface with the tympanum that articulates with the rear edge of the thorny process of the squamosal.

Generally speaking, the periotic IGUP 26 173 is very similar to that of *Squalodon* and, considered alone, could belong to a form very close to this genus, indeed to a more specialized species of this genus. This proximity of the periotic of *Squalodon* and of IGUP 26 173 contrasts with the clear difference existing as far as the rest of the cranium is concerned and could put into doubt the association made by DALPIAZ. He (DALPIAZ, 1977:22) had already recognized the great similarity of this bone to that of *Squalodon* and, taking into account the fact that he himself
collected the specimens (DAL PIAZ, 1977:25), it is likely that the association is [p. 76] correct. In this case, the similarity between the periotics of Dalpiazina and Squalodon strongly suggests that they are related.

In occipital view, we note the strong convexity of the occipital, which differentiates Dalpiazina from Ziphiodelphis, Eurhinodelphis, and Schizodelphis. On the dorsolateral edges of the supraoccipital, we note the strong insertions of the complexus, as in Eurhinodelphidae and Eoplatanista; they are well marked, but we know that these insertions are very variable in development. The occipital view of the cranium of D. ombonii is higher and narrower than that of Eurhinodelphidae.

c – The jaw

The jaw of Dalpiazina ombonii is relatively well preserved in the lectotype (IGUP 26 405). It has several features reminiscent of Squalodontidae (fig. 17). The most evident feature of the dentary is the marked development of its posterior region. It is more raised than in Eurhinodelphidae, following the example of Squalodontidae. The jaw, is; however, more laterally convex, less high, and its coronoid ridge does not rise as abruptly as in Squalodon. Here again, this feature, absent in other odontocetes (except Physeteridae) might constitute a synapomorphy of the group Squalodontidae–Dalpiazina.

The jaw of Dalpiazina exhibits in the posterior region of the dental series a marked diminution in the height of the dentary, and in a fairly sudden way which is more similar to that which we saw in Eurhinodelphidae than in Squalodontidae. The mandibular symphysis was longer than in Squalodon but apparently, as in this genus, the two dentaries were not knitted together, even in older individuals, or at any rate very late. In effect, on the type specimen of LONGHI (1898) which, taking into account the wear and tear of the teeth, belonged to a relatively old animal, the two dentaries show a slight displacement in the height of the symphysial angle indicating the absence of synostosis.

The symphysis is, on the other hand, always knitted in adults of Eoplatanista and most often in Eurhinodelphidae. As in Squalodontidae and Eurhinodelphidae, the symphysis has a triangular cross-section. On the medial side of the dentary, the orifice of the mandibular canal which protected the fat mandibular body is much larger than that of Eurhinodelphidae but less raised than that of Squalodon (fig. 21).

**Fig. 21. – Medial view of the orifice of the mandibular canal in Dalpiazina ombonii, holotype (IGUP 26 405), Inferior Miocene molasse of Belluno (Italy). (Scale = 5 cm.)**

[p. 77] Dimensions (in mm): CRANIUM (IGUP 26 480): bizygomatic width, 102 x 2 = 204e; width of the zygomatic process from its apex to the apex of the postglenoid process, 93; width of the rostrum at its base, 64 x 2 = 128e; width of the temporal fossa, 98; height of the temporal fossa, 55. - PERIOTIC (IGUP 26 173): maximum length, 44; maximum width, 30.5; (e = estimated measure).

3 – Affinities of Dalpiazina ombonii

Dalpiazina ombonii shows numerous similarities to the genus Squalodon, many of which are considered here as synapomorphies; these are: the widening of the premaxillae toward the front of the rostrum; the width of the vomerine fenestra; the morphology of the dorsal process of
the periotic, wide, regularly concave, and showing few contours; the development of the posterior orifice of the mandibular canal.

Other similarities are evidently symplesiomorphies, as: the morphology of the maxillary-premaxillary suture, the absence of lateral fissure on the rostrum, the dentaries not knitted together at the symphysis.

In looking at certain features, *Dalpiazina ombonii* is more specialized than *Squalodon*: the homodonty, the reduction of the size of the teeth and the increase in their number; the greater height of the vertex, the marked convexity of the occipital and the greater development of the cranial box which results from this; the morphology of the pars cochlearis more developed medially (i.e. higher in a dorsal view) and shorter at its base; the thickening of the anterior edge of the internal auditory fenestra.

*Dalpiazina ombonii* is thus a long-snouted odontocete very different from *Eoplatanista*, a genus of which this species has traditionally been regarded as a neighbor; this is, at least, the interpretation that I gave in 1984. *Dalpiazina ombonii* is not related to *Eurhinodelphidae* either but, by certain features considered as apomorphies, can be regarded as phylogenetically close to *Squalodon* while being more specialized. The relationship suggested here is a working hypothesis which would be confirmed by the discovery of a complete cranium with its associated auditory region, as the material currently available is, after all, relatively unimportant.

IV. Affinities of “*Champsodelphis*” *tetrarohinus* (DELFORTRIE, 1875)

A. Familial affinities of “*Champsodelphis*” *tetrarohinus*

We have seen above that the genus *Champsodelphis*, an older synonym of *Acrodelphis*, was considered here as *incertae sedis* restricted to the type specimen of its type species, *C. macrogenius*. Among all the specimens referred to the genus *Champsodelphis*, the only relatively complete cranium is that of *C. tetrarohinus* (fig. 22). This species was created by DELFORTIE (1875) on a cranium of an odontocete from the Burdigalian of the ossiferous molasse of Saint-Medard-en-Jalles near Bordeaux (France), and not of Leognan, as VAN BENEDEN and GERVAIS (1868-1879) and ABEL (1900) incorrectly stated. Initially referred to the genus *Delphinus* by its author, this cranium was referred by VAN BENEDEN and GERVAIS to the genus *Champsodelphis*. All other specimens referred to this genus are fragments of rostrum or jaw, or teeth, elements that are judged inadequate for defining an odontocete.

Several features of the cranium of “*Champsodelphis*” *tetrarohinus* are representative of the Squalodelphidae–Platanistoidea group:

- The thickening of the preorbital process is greater than that observed in any other odontocete other than Platanistoidea or Squalodelphidae. In “*C.*” *tetrarohinus*, however, the thickening is close to that of *Notocetus* which, as in *Squalodelphis*, does not occur in the maxillary or fronto-maxillary ridge as in Platanistidae. The conditions of “*C.*” *tetrarohinus, Notocetus*, and *Squalodelphis* are plesiomorphic [?] compared to those of Platanistidae (figs. 23 and 25).
• A vast and deep subcircular fossa, situated dorsally to the thorny process of the squamosal which ventrally maintains the periotic, is present. This fossa is likewise dorsal to the dorsal process of the periotic (fig. 24).

• On the ventral edge of the fossa, i.e. on the dorsal side of the thorny process of the squamosal, we note a small elongated fossa that probably housed an articular fold of the periotic (MUizon, 1987). The presence of a well-defined articular fold is a synapomorphy of the Platanistidae–Squalodelphidae group (MUizon, 1984 and 1987). In Platanistidae, however, this structure increases because the articular fold is transformed into a veritable articular hook. The condition of Squalodelphis is intermediate between that of Platanistidae and those of Notocetus and Phocageneus; that of “C.” tetrarhorinus is evidently similar to that of these latter two genera.

• On the palate, at the anterior end of the hamulus fossae of the pterygoid sinus, we see two long and narrow articular zones of about 8–9 mm in width and 20–25 mm in length. They correspond to the articulation of the anterior ends of the pterygoids which evidently were articulated directly with the maxilla. No trace of palatine is observable in this zone. This condition is found in Platanistidae where the external surface of the palatine is pushed back posterolaterally (the palatine is even totally covered by the pterygoid in Platanista). In Squalodelphis, the poor preservation of this region in known specimens (IGUP 26 134 and 26 141) prevents observation of the sutures between the palatine and pterygoid. In Notocetus, observation of the sutures is likewise difficult but it seems, however, that the palatine-maxillary suture indicated on the specimen described by True (1910) is probably only the pterygoid-maxillary suture, as it can be observed in “C.” tetrarhorinus. It thus seems that the condition of this species relates it to Platanistidae and probably also Squalodelphidae. As a result, it seems that synapomorphy #20 of Platanistidae (MUizon, 1987, fig. 12) must be transformed into a synapomorphy of the group Platanistidae–Squalodelphidae.

• The large size of the zygomatic process of “C.” tetrarhorinus is symptomatic of Platanistidae and in a certain way of Squalodelphidae. Within this family, “C.” tetrarhorinus is closer to Notocetus than to Squalodelphis.

Of these four features, none has been used to define Squalodelphidae because the cranium of Phocageneus (one of the tree genera listed by MUizon, 1987) is only known by

[p. 80] Fig. 23. – Lateral view of a cast of the type Medocinia tetrarhorina showing the thickness of the preorbital process, which has disappeared on the original specimen (Scale = 5 cm.)
Plesiomorphies it is true, in common with Squalodelphidae and absent in Platanistidae. These
are: the simple thickening of the preorbital process which does not develop a ridge as in
Platanistidae, the tabular and square morphology of the frontals and nasals on the vertex, the
slight elevation of the vertex and slight concavity of the facial region, the probable presence of
an articular fold on the lateral edge of the periotic between the posterior process and the ventral
tubercle. Taking into account these features as well as those which link it to the
Squalodelphidae–Platanistidae group, “C.” tetragorhinus is here referred to the family
Squalodelphidae.

Within this family, two genera are known by their cranium: Notocetus and Squalodelphis. For
several features “C.” tetragorhinus differs from Notocetus and Squalodelphis:

- The morphology of the thickening of the supraorbital region is clearly different: in
  “Champsodelphis” tetragorhinus, only the preorbital process of the frontal is highly [p.
  82] developed and forms a sort of horn directed ventrally, whereas Notocetus and
  Squalodelphis show, on the contrary, a strong bulging of the maxilla.

- The mesethmoid of “C.” tetragorhinus is extremely thick in the nasal cavity and reaches
  its maximum development in its anterior region about 3–4 cm in front of the anterior
  edge of the bony nostril. In this region, it measures almost 30 mm in width at the end [?]
  and its thickness at the anterior edge of the nostril is about 20 mm. Such a morphology is
  not known in Notocetus and Squalodelphis.

- As a result of this width of the mesethmoid, the rostral groove is likewise extremely
  wide compared to that of the two other known crania of Squalodelphidae.

“C.” tetragorhinus does not match Phocageneus venustus either, whose teeth are
apparently very large. This comparison can be made because the jaw of P. venustus is known,
and taking into account the fact that the inferior and superior teeth of Squalodelphidae (like those
of numerous odontocetes) are very similar to each other.

As a result, “C.” tetragorhinus is not representative of any known genus of
Squalodelphidae and should thus be referred to a new genus: Medocinia nov. gen.

B – Systematics of the genus Medocinia

Diagnosis

Squalodelphidae differing from Notocetus and Squalodelphis by: 1) the morphology of its
supraorbital region: the preorbital process of the frontal, alone, is markedly thickened and forms
a well-defined, ventrally oriented, rounded hook; in Notocetus and Squalodelphis, the thickening
of the frontal is less but the maxilla is likewise markedly bulbous; 2) the great thickness of the
mesethmoid and the correlate width of the rostral groove which greatly exceeds that observed
in Notocetus and Squalodelphis.

Medocinia likewise differs from Phocageneus by the smaller size of its teeth. As all
Platanistoidea, Medocinia has a lateral blade of the pterygoid continuous from the squamosal to
the maxilla.

Type species: Medocinia tetragorhina (DELFORTRIE, 1875)

Derivatio nominis: From Médoc, name given to the region of France situated between the
left bank of the estuary of the Gironde and the Atlantic Ocean, and known for the quality of the
wines produced there.
**Medocinia tetragorhina** (DELFORTRIE, 1875)

Type locality: St. Medard-en-Jalles, near Bordeaux, Médoc region, Gironde, France.
Geologic formation and age: Molasse of Burdigalian age.

Fig. 25 – Reconstruction of the cranium of *Medocinia tetragorhina*: a, dorsal view; b, ventral view; c, lateral view. (Scale = 5 cm.)

**Type specimen:** A fairly complete but highly deformed cranium. The anterior end of the rostrum and the auditory region are missing (MNHB 174).

Hypodigm: The holotype is the only known specimen; the jaw referred to this species by VAN BENEDEN and GERVAIS (1868-1879) does not show any feature sufficiently characteristic to permit such a relationship, which is we will consider here as unfounded.

Diagnosis: Identical to that of the genus.

C – Affinities of *Medocinia tetragorhina* within Squalodelphidae

*Medocinia tetragorhina* cannot be positively linked to any of the other Squalodelphidae. It resembles *Notocetus* in the size of its teeth, smaller than those of *Squalodelphis* and *Phocageneus*, and in its supraorbital region which is less bulbous than that of the two genera. However, if the polarity of the first feature is not established, it is evident that the second is plesiomorphic.

If we assume the apomorphy of the reduction of the teeth in Cetacea, *Medocinia* should be referred to *Notocetus*. Although it remains to be proven and is certainly not as simple, we can as a first approximation consider *Medocinia* as the sister-group of *Notocetus*. The discovery of better-preserved specimens of *Medocinia tetragorhina* is, however, indispensable in order to confirm this hypothesis.

**GENERAL CONCLUSIONS**

The revision of the type specimens of *Schizodelphis sulcatus* (GERVAIS, 1853), *Rhabdosteus latiradix* COPE, 1868, *Eoplatanista italic*a DAL PIAZ, 1916, “*Acrodelphis*” ombonii (LONGHI, 1898), and “*Champsodelphis*” *tetragorhinus* (DELFORTRIE, 1875) lead to the following conclusions:

1. The type specimen of *Rhabdosteus latiradix* is too incomplete to define an odontocete and the taxa Rhabdosteidae and *Rhabdosteus latiradix* are incertae sedis restricted to the type specimen.
2. The specimens referred by MYRICK (1979) to the genus *Rhabdosteus* and by ABEL (1901) to *Eurhinodelphis longirostris* are congeneric with the holotype of *Schizodelphis sulcatus*.
3. The taxon Eurhinodelphidae is reestablished and includes the genera *Eurhinodelphis*, *Ziphiodelphis*, *Schizodelphis*, and *Argyroctenus*.
4. *S. sulcatus* is a different species from *S. longirostris*.
5. *S. longirostris* does not exist in the Calvert (MD, USA) Formation. The *Schizodelphis* from this formation are all representative of a single species with marked individual variations: *S. barnesi*.
6. *Schizodelphis brachycephalus* (sensu PILLERI, 1985) is a synonym of *Eoplatanista italic*a.
7. *Priscodelphinus squalodontoides* CAPELLINI, 1878, does not belong to the same genus as *Schizodelphis*? *squalodontoides capellinii* LONGHI, 1897. This subspecies, which is referred to the genus *Eoplatanista*, then becomes an entirely different species, *Eoplatanista capellinii*, whose type and only known specimen, too incomplete to determine a species of the genus *Eoplatanista*, is thus an incertae sedis restricted to its type specimen.

8. The specimens referred by PILLERI (1985) to *Schizodelphis sulcatus*, *S. yablokovi* and *S. gresalensis*, and the specimens referred by ABEL (1900) and DAL PIAZ (1903 and 1977) to *Cyrtodelphis sulcatus*, belong to the genus *Eoplatanista* and are referred to the species *Eoplatanista gresalensis* (DAL PIAZ, 1977).

9. The genus *Eoplatanista* belongs to the monogeneric family of the Eoplatanistidae which by itself constitutes the sister-group of the Eurhinodelphidae, a family with which it constitutes the superfamily of the Eurhinodelphoidea.

10. *Acrodelphis* ABEL, 1900 is a junior synonym of *Champsodelphis* GERVAIS, 1848-1852.

11. *Champsodelphis macrogenius* is considered as the type species of the genus, and its lectotype, designated here, is considered as totally insufficient to define an odontocete. Genus and species are here regarded as incertae sedis restricted to a single lectotype. *Champsodelphis* is the type genus of the family Acrodelphidae which is thus likewise an incertae sedis.

12. “*Acrodelphis* ombonii [= *Champsodelphis ombonii*] is referred to the new genus *Dalpiazina*, a form close to the genus *Squalodon* although clearly more specialized.

13. “*Champsodelphis*” tetragorhinus is attributed to the new genus: *Medocinia*; *Medocinia tetragorhnua* (DELFORTRIE, 1875) is a Squalodelphidae that could be the sister-genus of *Notocetus*.

This revision thus clearly shows that the family Acrodelphidae, which regrouped the genera *Acrodelphis*, *Schizodelphis*, *Eoplatanista*, and *Champsodelphis*, was polyphyletic in its traditional sense. *Schizodelphis* is a Eurhinodelphidae; *Acrodelphis* a junior synonym of *Champsodelphis* which is itself an incertae sedis restricted to the type specimen of its type species *Champsodelphis macrogenius*. *Acrodelphis ombonii* is referred to a new genus, *Dalpiazina*, related to the genus *Squalodon*, and *Champsodelphis tetragorhinus* is a Squalodelphidae referred to the new genus *Medocinia*. *Eoplatanista* is classed in the monogeneric family Eoplatanistidae and *Dalpiazini ombonii* in that of Dalpiazinidae. The family Acrodelphidae becomes a taxon incertae sedis restricted to the type specimen of the type species (*Champsodelphis macrogenius*) of the type genus (*Champsodelphis*).

Certain authors (BARNES et al., 1985) have placed the genera *Pomatodelphis* and perhaps *Zarhachis* among Acrodelphidae. In fact, these two genera show all the synapomorphies of Platanistidae, a family to which they should be referred (MUIZON, 1987).

The revision done in this work likewise underlines the important necessity of clarifying the taxonomy of odontocete fossils. In order to do this, it is indispensable to reanalyze all the type specimens and, if they are not sufficiently important to define an odontocete, we consider the taxon that they represent as an incertae sedis restricted to the single type specimen. Furthermore, the confusion introduced in the literature by authors describing new taxa on specimens such as isolated teeth or fragments of rostrum show, if it were necessary, the absolute necessity of
choosing holotypes including at least reasonably important cranial elements and, if possible, those associated with elements of the periotic and tympanum. Now that we recognize the intraspecific, interspecific, intergeneric, and even sometimes interfamilial variables of odontocete teeth, no further creation of a new taxon on isolated teeth is acceptable.

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