

## NOTA BREVE - SHORT NOTE

**KOGIA PUSILLA FROM THE MIDDLE PLIOCENE OF TUSCANY (ITALY)  
AND A PHYLOGENETIC ANALYSIS OF THE FAMILY KOGIIDAE  
(ODONTOCETI, CETACEA)**

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*Riassunto.* Viene preso in esame un cranio quasi completo di cetaceo odontoceto proveniente dai sedimenti del Pliocene medio di Monte Voltraio (provincia di Pisa, Toscana). Tale esemplare, in passato erroneamente attribuito alla famiglia Ziphiidae e descritto come olotipo della specie *Hyperoodon pusillus*, viene qui riferito al genere *Kogia* (famiglia Kogiidae). La specie *Kogia pusilla* è ridescritta e messa a confronto con le specie attuali *K. breviceps* e *K. simus*.

Da un punto di vista filogenetico, viene ipotizzata una separazione antica (almeno nel Miocene inferiore) dei Kogiidae e Physeteridae (Physeteroidea). Il mancato ritrovamento di reperti attribuibili con sicurezza alla famiglia dei Kogiidae in sedimenti più antichi del Miocene superiore è probabilmente dovuto alla rarità di questi cetacei. L'analisi delle relazioni filetiche tra i Kogiidae è stata condotta prendendo in esame supposte apomorfie relative alla morfologia e/o estensione del bacino sopraccraniale che alloggia le sacche aeree e l'organo dello spermaceti.

*Abstract.* A partial skull of an odontocete cetacean from Middle Pliocene sediments of Monte Voltraio (Pisa Province, Tuscany, Italy) is examined. This fossil, erroneously referred to the family Ziphiidae and described in the past as holotype of the species *Hyperoodon pusillus*, is assigned here to the genus *Kogia* (family Kogiidae). The species *Kogia pusilla* is redescribed and compared to the living species *K. breviceps* and *K. simus*.

Phylogenetically, an old separation (at least in the Lower Miocene) of Kogiidae and Physeteridae is suggested. The lack of substantiated kogiid records until the Upper Miocene is probably due to the rarity of these cetaceans. Phyletic analysis within the Kogiidae is undertaken and supposed apomorphies in the morphology and/or the extension of the supracranial basin that houses the large air sacs and the spermaceti organ are considered.

### Introduction.

The Kogiidae are a family of small odontocetes (Cetacea) similar and closely related to the extant sperm whale (Physeteridae). Well-preserved records of Kogi-

idae are very rare: only two almost complete skulls from late Miocene sediments of Mexico (Barnes, 1973, 1984) and Peru (Muizon, 1988) have been described previously. Those specimens are the holotype of the extinct genera and species *Praekogia cedrosensis* and *Scaphokogia cochlearis*, respectively. Other presumed records of kogiids are fragmentary and consist essentially of mandibular fragments (Kellogg, 1929), isolated teeth (Matsumoto, 1927) and/or auditory bones (Pilleri, 1986a, 1986b, 1987, 1988; Pilleri et al., 1989).

The skull from the Pliocene of Tuscany described here represents the third known significant record of this family. This specimen was referred erroneously to the Ziphiidae in the past. Capellini (1893) assigned it to *Placoziphius* and Pilleri (1987) described it as holotype of the species *Hyperoodon pusillus*. This fossil skull, already referred to the genus *Kogia* by Bianucci (1997) and Bianucci et al. (1998), is redescribed in detail in this paper. *Kogia pusilla* represents the ancestor of *Kogia breviceps* and *K. simus*, the only two living species of this family.

### Systematic description.

Class M a m m a l i a Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily P h y s e t e r o i d e a (Gray, 1821)

Gill, 1872

Family K o g i i d a e (Gill, 1871) Miller, 1923

Genus *Kogia* Gray, 1846

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**Kogia pusilla** (Pilleri, 1987)

(Fig. 1-4a)

1893 *Placoziphius*, V. Beneden - Capellini, pp. 287-288.1987 *Hyperoodon pusillus* Pilleri, pp. 35-36, fig. 11, pl. 13.1997 *Kogia pusilla* (Pilleri) - Bianucci, pp. 172-173, fig. 6b.1998 *Kogia pusilla* (Pilleri) - Bianucci et al., pp. 124, 126, 127, figs.3a<sub>1</sub>, a<sub>2</sub>.

**Emended diagnosis of species.** A species of the genus *Kogia* that differs from *K. simus* and *K. breviceps* in having a more elongated rostrum, a less anteriorly extended antorbital process, a smaller lacrimal, a slightly more pronounced dorsal asymmetry, and a lesser elevation of the posterior region of the neurocranium. It differs from *K. breviceps* in its smaller size and in having a more narrow sagittal crest.

**Holotype.** IGF1540V: distorted and incomplete skull, lacking part of the right side and of the ventral portion of the braincase. Auditory bones, teeth, mandible and postcranial skeleton are not preserved. The specimen was donated by Lawley in 1877 to the Museo di Paleontologia of the University of Florence, where it is preserved today.

**Type locality.** La Rocca locality in Monte Voltraio hill, near Volterra, province of Pisa, Tuscany (Italy).

**Age.** Middle Pliocene: *Globorotalia crassaformis crassaformis* subzone of Iaccarino & Salvatorini (1982), approximately between 3 MA and 2.6 MA (Bianucci et al., 1998).

**Description.** The condylobasal length of the only known but incomplete skull is estimated to be about 270 mm. This skull size is similar to that of *Kogia simus* and it is slightly smaller than that of an adult of *Kogia breviceps*. In fact, according to Ross (1979), the condylobasal length of 24 skulls of *Kogia simus* range between 201 mm and 323 mm while the condylobasal length of 22 skulls of *K. breviceps* range between 237 mm and 467 mm (less than 300 mm are young animals).

Compared to the living species, the rostrum has a similar triangular shape from a dorsal view, but differs in being more elongate (Fig. 4). Moreover, it has a well-developed dorsal concavity and a ventral convexity that we have not observed in extant species. Post mortem deformation may have accentuated these last characters in the fossil specimen.

The cerebral skull has a semicircular outline in dorsal view. In this respect the skull is similar to that of *K. breviceps* and *K. simus* but differs from the antero-posteriorly elongated skulls of both *Praekogia* and *Scaphokogia*. Nevertheless, this skull differs from those of extant *Kogia* spp. in having a more pronounced dorsal asymmetry (due to the displacement of the external nares toward the left side and to the displacement of the sagittal crest toward the right side), and in having smaller elevation of the posterior region of the neurocranium. The first of these two features may have been emphasized by *post mortem* deformation of the skull.

In dorsal view (Figs. 1a<sub>1</sub>, 1a<sub>2</sub>) the premaxillae, the maxillae and probably the vomer (covered by matrix) extend as far as the apex of the rostrum, as in living species. A similar extension of the rostral bones was observed also in *Scaphokogia* by Muizon (1988). Muizon (1991) considered this feature an apomorphy of the Kogiidae.

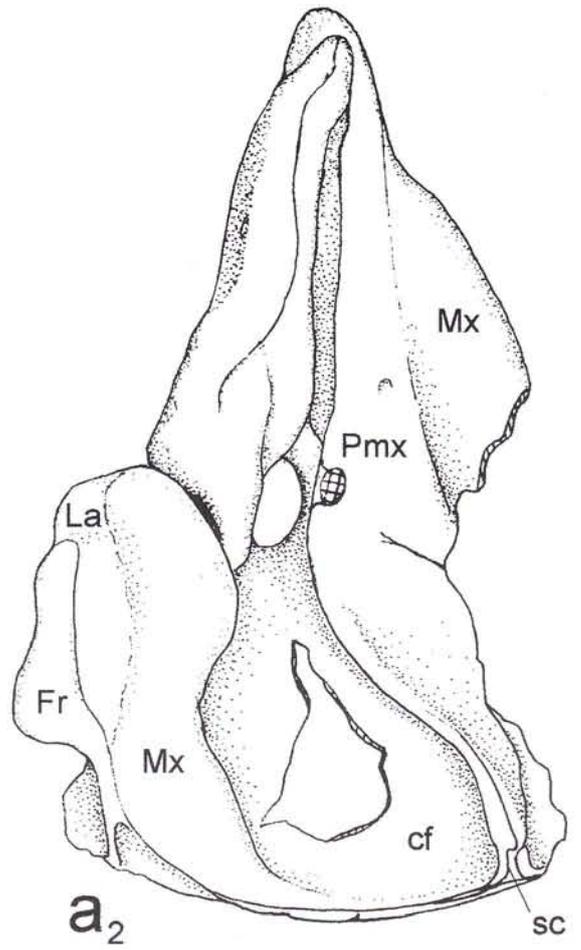
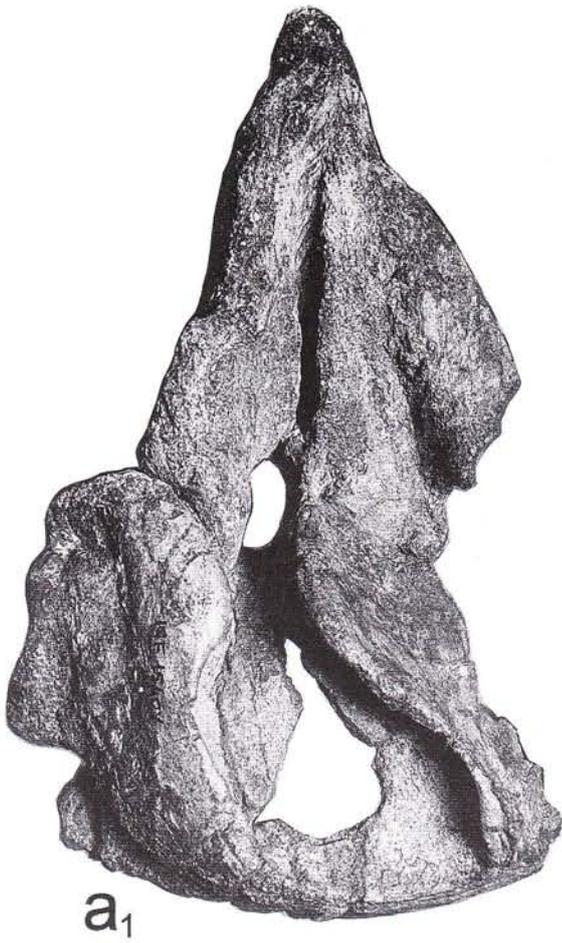
Two asymmetrical superior nares are present at the base of the rostrum as in all Physeteroidea (Physeteridae and Kogiidae). In particular, the left naris is 14 mm wide and 10 mm long while the right is 6 mm wide and 10 mm long. The nasals are missing, as in the other Kogiidae.

The left premaxilla extends posteriorly as far as the postero-dorsal margin of the skull and its medial margin joins the right maxilla to form a very prominent sagittal crest, as in living species. This crest is bent left in its anterior portion. It is delimited by vertical walls and is very narrow at the vertex (width: 13.3 mm), as in *K. simus*. The width of the sagittal crest is a diagnostic character for the distinction of the two living species (Handley, 1966). Ross (1979) observed that in 26 skulls of *K. simus* the minimum width of this crest ranges from 5 to 20.5 mm while in 22 skulls of *K. breviceps* this width ranges from 14.5 to 49 mm (from 23 to 49 mm excluding five young specimens).

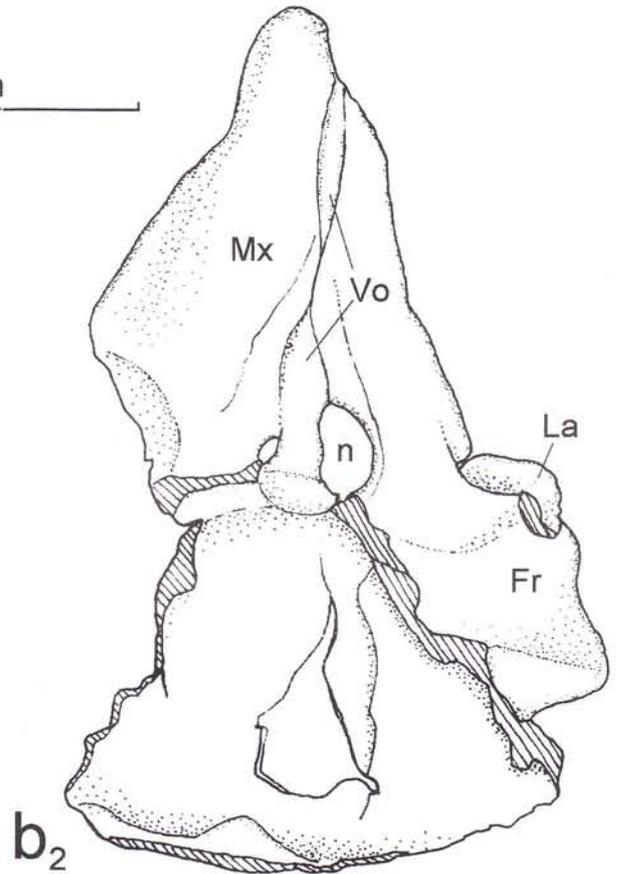
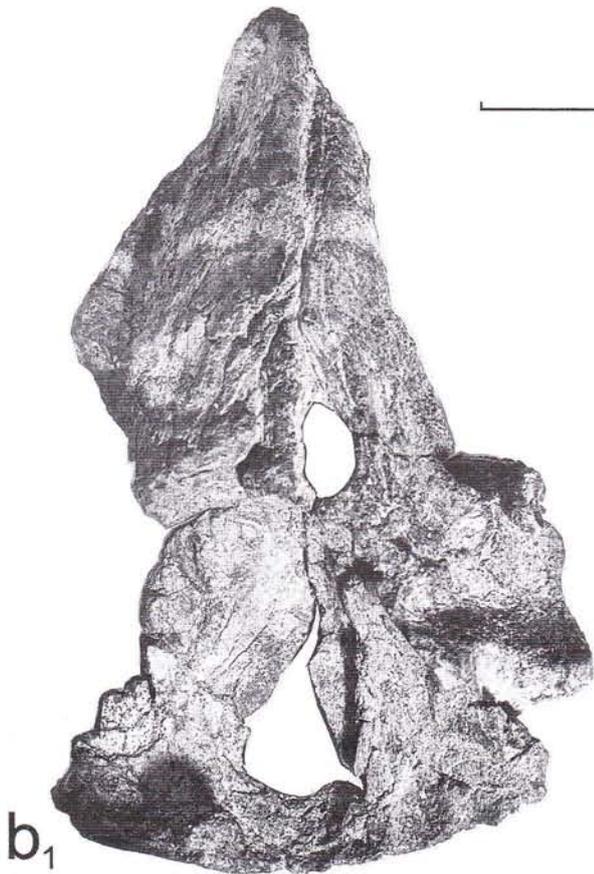
The right premaxilla forms a small elevated basin on the neurocranium, extending from the sagittal crest on the left and to its lateral margin on the right. A similar depression is present in the living species of *Kogia* where the spermaceti organ (Kernan & Shulte, 1918; Raven & Gregory, 1933; Schenckan & Purves, 1973) resides. In contrast, in *Praekogia*, the lateral margin of the right premaxilla is not protuberant and the right maxilla and the right premaxilla form a single cranial fossa that probably resulted in a more developed spermaceti organ than in *Kogia*. *Scaphokogia* shows an even more dissimilar dorsal cranial architecture than *Kogia*. In fact, the skull of *Scaphokogia* has no sagittal crest at all (the facial crest is displaced near the left margin of the neurocranium) and consequently it is likely that the spermaceti organ also invaded the left side of cerebral skull (Muizon, 1988).

The antorbital notches penetrate the supracranial basin as in living species of *Kogia* and in *Praekogia*, but not in *Scaphokogia* and in the other Physeteroidea. This character is considered by Muizon (1988) to be an apomorphy of the Kogiinae (*Kogia* and *Praekogia*) related to the large antero-lateral development of the supracranial basin.

Fig. 1 - *Kogia pusilla* (Pilleri, 1987) holotype; La Rocca locality, Monte Voltraio (province of Pisa, Tuscany). Almost complete skull (IGF1540V). a<sub>1</sub>, a<sub>2</sub>, dorsal view; b<sub>1</sub>, b<sub>2</sub>, ventral view. cf, cranial fossa; Fr, frontal; La, lacrimal; Mx, maxilla; n, naris; Pmx, premaxillae; sc, sagittal crest; Vo, vomer.



10 cm



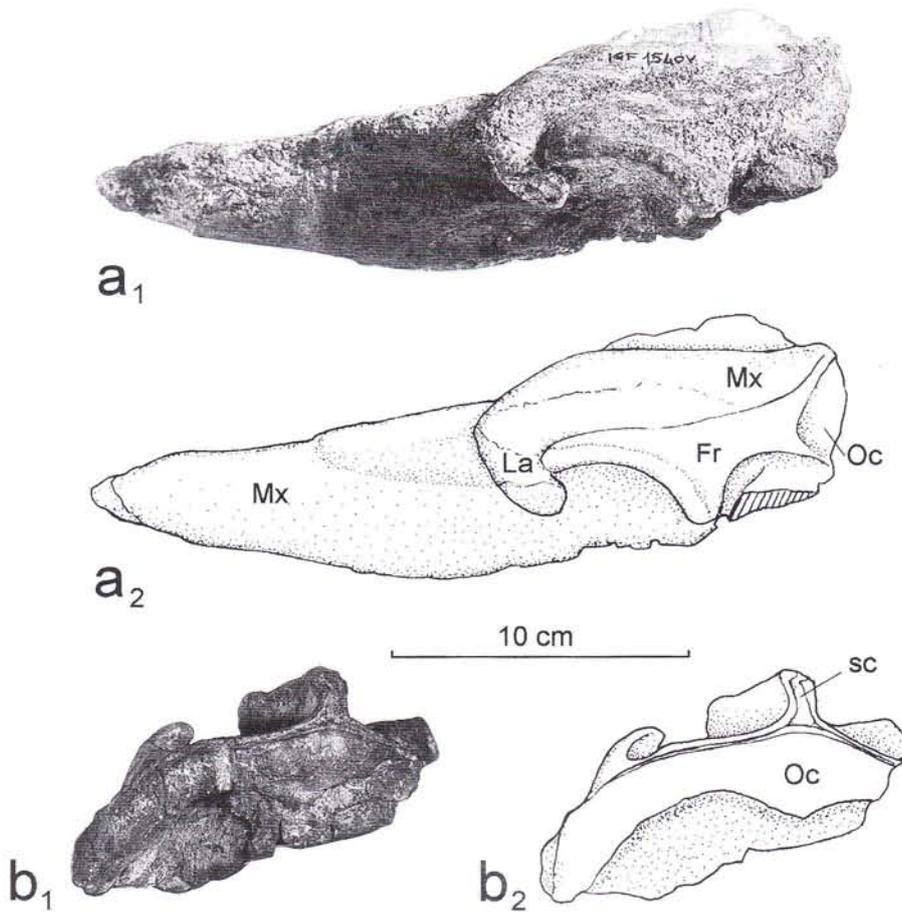


Fig. 2 - *Kogia pusilla* (Pilleri, 1987) holotype; La Rocca locality, Monte Voltraio (province of Pisa, Tuscany). Almost complete skull (IGF1540V). a<sub>1</sub>, a<sub>2</sub>, lateral view; b<sub>1</sub>, b<sub>2</sub>, posterior view. Fr, frontal; La, lacrimal; Mx, maxilla; Oc, occipital; sc, sagittal crest.

The antorbital process is narrower than in living species and does not extend anteriorly on the proximal portion of the rostrum. As a consequence, the cranial fossae (antero-laterally delimited by the antorbital processes) are less developed antero-posteriorly in this fossil species.

The anterior portion of left cranial fossa is almost completely covered dorsally by the lateral and sagittal crests, both being bent towards the fossa. Posteriorly, the cranial fossae are slightly more elevated than in *K. breviceps*. This feature makes *K. pusilla* very different from *K. simus*, in which the posterior part of the cranial fossae rises strongly (Handley, 1966; Ross, 1979).

The lateral view (Figs. 2a<sub>1</sub>, 2a<sub>2</sub>) shows a larger antero-posterior exposure of the rostrum than in the living species. This condition is due to both the greater elongation of the rostrum and the smaller anterior extension of the antorbital processes (in *K. breviceps* and *K. simus* the antorbital processes cover the proximal part of the rostrum).

The anterior portion of the lacrimal is smaller than in the living species and is comma-shaped as in the Physeteridae, whereas it is triangular in the other Kogiidae. There is no evident lacrimal-maxilla suture. Figs. 2a<sub>2</sub> and 3 present the probable course of this suture: the postero-dorsal process of the lacrimal is large and posteri-

orly extended, to a greater extent than in the other Kogiidae. Muizon (1988) noted that the postero-dorsal process of the lacrimal is not present in the Physeteridae except in a young specimen of *Aulophyseter*, and the presence of this process in the Kogiidae is considered as a plesiomorphic character.

The supraorbital process is thinner than in both living species and *Praekogia*.

The lateral view shows also an elevation of the posterior portion of the cranium, smaller than in living species and in *Praekogia*.

In posterior view (Figs. 2b<sub>1</sub>, 2b<sub>2</sub>) the sagittal crest is high, narrow and delimited laterally by vertical walls.

In ventral view (Figs. 1b<sub>1</sub>, 1b<sub>2</sub>) the skull is badly damaged and most of the ventral surface of the neurocranium is not preserved. In particular, only the left frontal, the left lacrimal and a small portion of the left squamosal are preserved. The medial groove of the rostrum allows the vomer to be observed. Along the right preserved margin of the rostrum is a small deep furrow but without distinct alveoli. In this respect *K. pusilla* is similar to the living species and differs from *Scaphokogia* (with distinct but shallow alveoli).

Comparisons. A peculiar kogiid feature of the only skull known of *Kogia pusilla* is the lack of both nasals. The presence of a supracranial basin and the strong

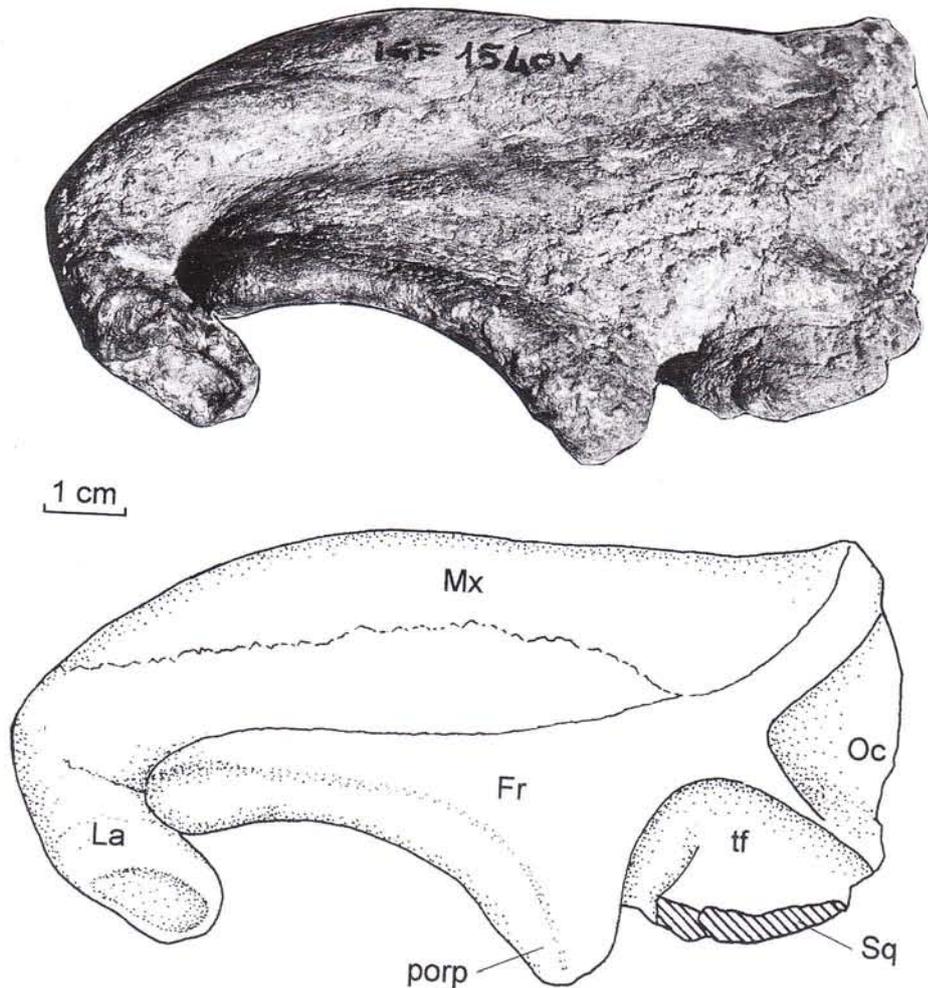


Fig. 3 - *Kogia pusilla* (Pilleri, 1987) holotype; La Rocca locality, Monte Voltraio (province of Pisa, Tuscany). Neurocranium in lateral view of skull (IGF1540V). Fr, frontal; La, lacrimal; Mx, maxilla; Oc, occipital; porp, postorbital process; Sq, squamosal; tf, temporal fossa.

asymmetry of the skull are other characters typical of all the Physeterida (Kogiidae and Physeteridae). *Kogia pusilla* is similar to *K. breviceps* and *K. simus* in the peculiar outline of the skull in dorsal view (the cranium is semicircular and the rostrum is triangular), and in having a vertical sagittal crest on the cranium (Fig. 4).

Moreover, as the extant species, *K. pusilla* shows a small basin on the cerebral portion of the right premaxilla that extends as far as the postero-dorsal margin of the skull. *K. pusilla* is more similar to *K. simus* than *K. breviceps* in the relatively small size of the skull and in the narrow sagittal crest at the vertex.

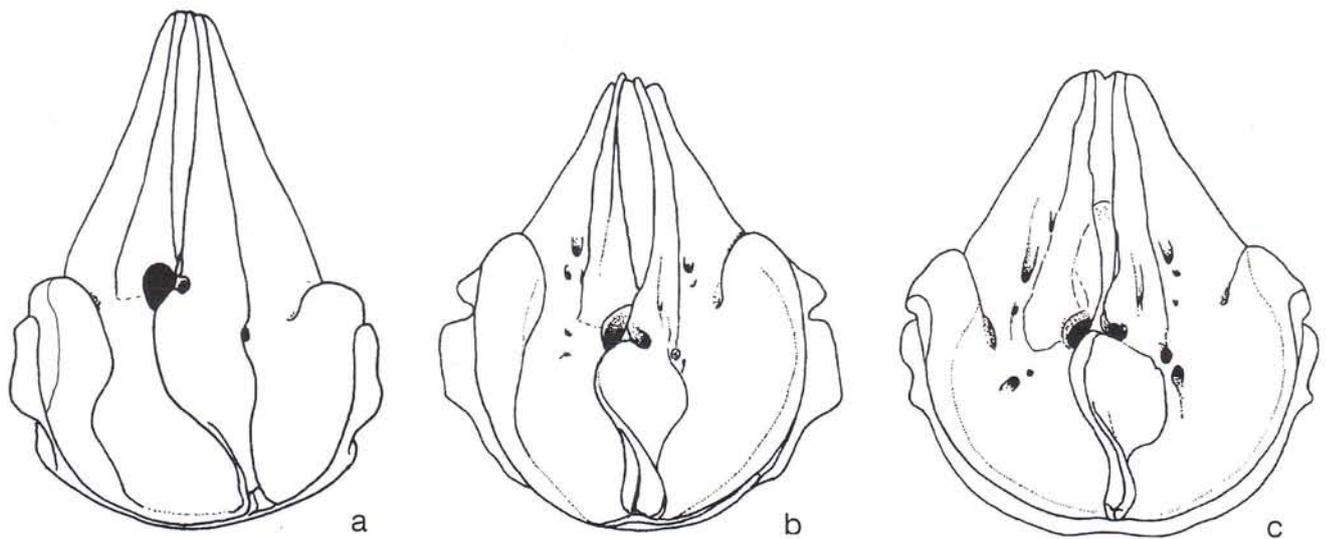


Fig. 4 - Comparisons of the skull in dorsal view of: a, *Kogia pusilla* (restoration of the skull based on holotype, IGF 1540V); b, *Kogia breviceps* (Laboratoire de Anatomie Comparée de Paris, 1883-483); c, *Kogia simus* (Accademia dei Fisiocritici di Siena).

*K. pusilla* differs from both *K. breviceps* and *K. simus* in its longer rostrum, smaller lacrimal and perhaps greater asymmetry of its skull in dorsal view.

**Phylogenetic relationships.**

The genus *Kogia* shows evident affinities with *Physeter*. Common apomorphies of these two genera concern particularly the facial anatomy (Heyning, 1989) and the concave shape of the dorsal surface of the skull (scaphidiomorphy) for housing the large air sacs and the spermaceti organ. Consequently, the single bones of the skull suffered large modifications, in particular, a marked asymmetry and the reduction of the right external nares.

Even if there is consensus on the close affinities of *Kogia* and *Physeter*, precise systematic relationships between these two genera are debated. Some authors (Caldwell & Caldwell, 1989; Fraser & Purves, 1960;

Handley, 1966; Heyning, 1989; Simpson, 1945) consider that *Kogia* and *Physeter* belong to the same family Physeteridae. Others (Barnes, 1973; Kasuya, 1973; Miller, 1923; Muizon, 1991) think these two genera have such distinctive characters that their separation in two families (Kogiidae and Physeteridae) is justified. This last hypothesis was strengthened by recent studies on cetacean mitochondrial DNA (Árnason et al., 1993; Milinkovitch et al., 1994) that confirm a large divergence between *Physeter* and *Kogia*.

We believe that the fossil and phylogenetic evidence reveal that the separation of these two groups may be relatively old. In particular, all fossil skulls of Physeteridae show a marked enlargement of the posterior portion of the right premaxilla, an apomorphy absent in *Kogia* and in fossil taxa related to this genus. As observed by Muizon (1991) this feature is relatively less emphasized in living *Physeter* than in fossil physeterids. This derived character is also present in the most ancient known skull of physeterid, assigned to *Diaphorocetus*

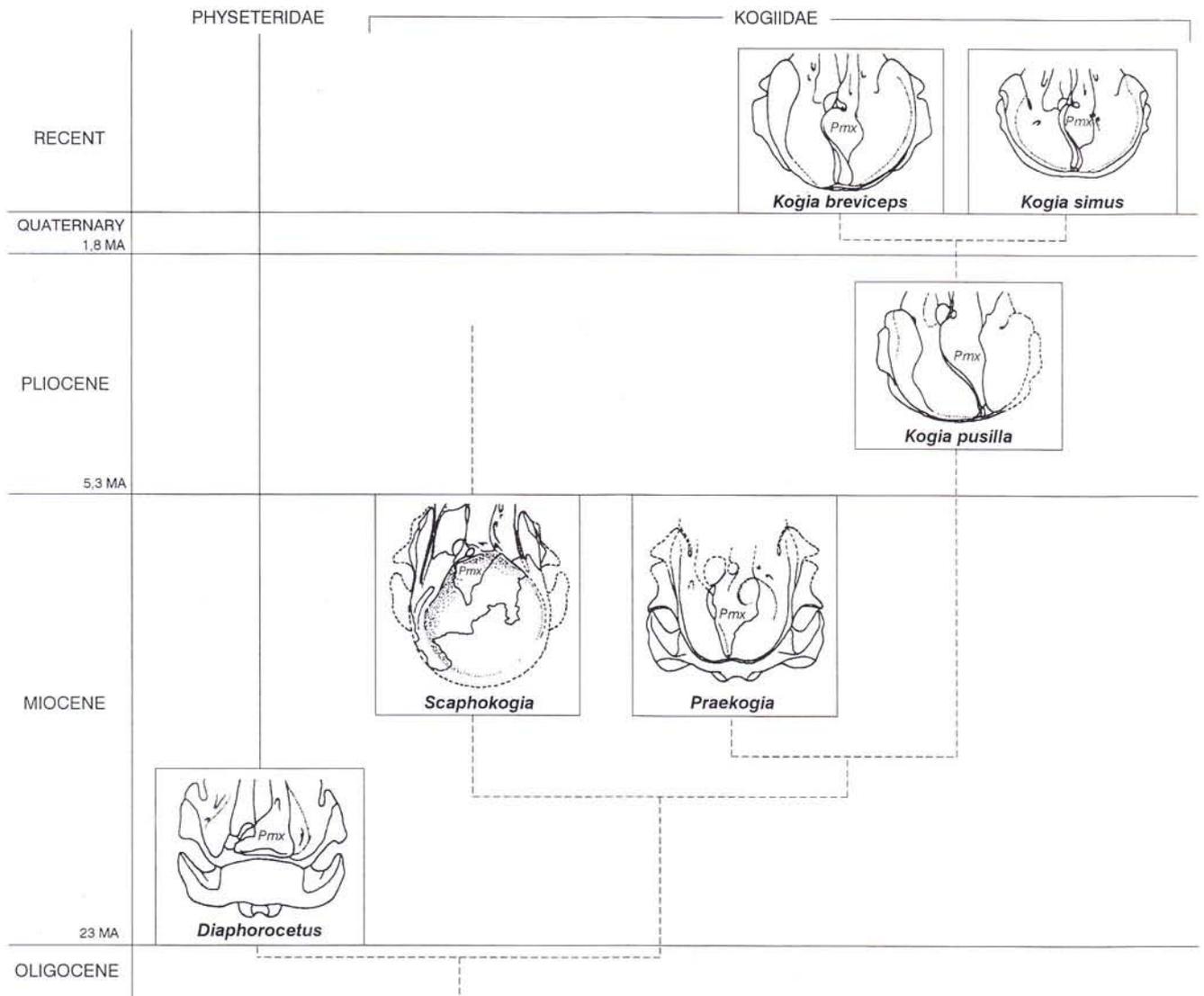


Fig. 5 - Phylogeny of the Kogiidae. Dotted lines indicate no fossil or fragmentary record.

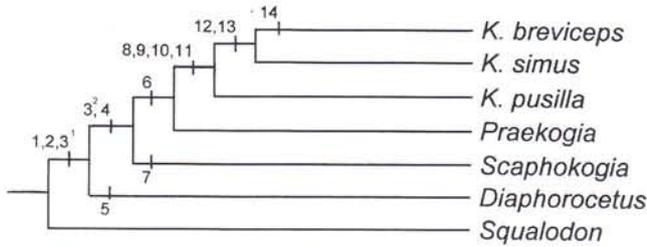


Fig. 6 - Maximun-parsimony cladogram (cosistency index = 100) computed from the data in Tab. 1 using Henning 86, version 1.5 (Farris, 1988).

*poucheti* (Early Miocene from Argentine; Moreno, 1892; Lydekker, 1894)

The primitive state of Kogiidae, regarding the shape of right premaxillae, suggests their origin is no younger than the beginning of the Miocene (Fig. 5). The lack of kogiid records prior to the Late Miocene may be due to their low frequency in the ancient sea. However, some isolated auditory bones and teeth from the Lower Miocene of Piedmont (North Italy) and Baltringhen (Austria) and Middle Miocene of Visiano (North Italy) were referred to this family by Pilleri (1986b, 1988) and Pilleri et al. (1989). Nevertheless, because these elements (periotics and teeth) are the only remains of kogiids found in the sediments, their conclusion must be viewed with caution. As in *Kogia*, some periotics show an articular surface for the tympanic flat and parallel to the general plane of the periotic and not ventrally oriented; nevertheless, on the whole they differ substantially from *Kogia* periotics and show also affinities with those of some fossil physeterids. The distinction of the two families on the basis of these structures is problematic, considering also that skulls of fossil physeterid and kogiid genera with preserved auditory bones are rare. The isolated teeth are referred to *Mioko-*

*gia elongata* (emended of *Miokogia elongatum*), a genus and species created on the basis of three teeth from Baltringen (Pilleri, 1986b). In fact, all teeth referred to this presumed kogiid are similar in shape and size to those of the physeterid *Scaldicetus bellunensis* from the Early Miocene of Belluno (North Italy) (Dal Piaz, 1977). In accordance with other authors (Barnes, 1976; Muizon, 1988) we attribute a low systematic value to isolated teeth and therefore consider *nomina dubia* both genus and species names of *Miokogia elongata*.

Considering other described kogiid fossils, only two skulls were referred correctly to this family. One, from the Late Miocene of Mexico (Barnes, 1973, 1984), was named *Praekogia cedrosensis*, and the other, from the Late Miocene of Peru (Muizon, 1988) was named *Scaphokogia cochlearis*. *Praekogia* and *Scaphokogia* share with *Kogia* the loss of nasal bones, an apomorphy of the family Kogiidae. Nevertheless, the two fossil genera differ from *Kogia* by having a different architecture of the supracranial basin. In particular, in *Praekogia* the basin for the spermaceti organ extends to the entire right portion of the dorsal surface of the cerebral skull that is formed by the premaxilla and maxilla. As observed by Barnes (1973), this genus lacks a distinct right maxillary fossa that is present in *Kogia*. The basin for the spermaceti organ in *Scaphokogia* takes up the entire dorsal surface of neurocranium and only a large cranial fossa is present. Because of this peculiar shape of the supracranial basin and other peculiar characters, *Scaphokogia* was assigned to the subfamily Scaphokogiinae by Muizon (1988). Apparently *Scaphokogia* shows affinities with *Physeter* in having a large cranial basin for the spermaceti organ. Nevertheless, the cranial basin of *Scaphokogia* does not extend on the rostrum as in *Physeter*. A cranial basin more anteriorly extended than in *Scaphokogia* is present also in *Kogia* and *Praekogia*, both having the dorsal depression that exceeds the external nares. More-

Taxon	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Squalodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diaphorocetus</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	0
<i>Scaphokogia</i>	1	1	2	1	0	0	1	0	0	0	0	0	0	0
<i>Praekogia</i>	1	1	2	*	0	1	0	0	*	0	0	*	*	0
<i>Kogia pusilla</i>	1	1	2	0	0	1	0	1	1	1	1	0	0	0
<i>Kogia simus</i>	1	1	2	0	0	1	0	1	1	1	1	1	1	0
<i>Kogia breviceps</i>	1	1	2	0	0	1	0	1	1	1	1	1	1	1

Tab. 1 - Data matrix used in the cladistic analysis. \*= missing characters. Character states: 1) Supracranial basin: 0, no; 1, yes; 2) Strong asymmetry: 0, no; 1, yes; 3) Lack of nasals: 0, two nasals; 1, one nasal; 2, nasals absent; 4) Vomer, premaxillae and maxillae reach the apex of rostrum; 5) Enlargement of posterior portion of right premaxillae: 0, no; 1, yes; 6) Antorbital notch penetrating the cranial fossae: 0, no; 1, yes; 7) Supracranial basin formed by only one hemispherical depression posteriorly developed and anteriorly closed (see Muizon, 1988, 1991, for more detail on the bone modifications): 0, no; 1, yes; 8) Cranium half-circle shaped: 0, no; 1, yes; 9) Rostrum triangular: 0, no; 1, yes; 10) Small basin on the cerebral portion of right premaxilla: 0, no; 1, yes; 11) Very prominent sagittal crest: 0, no; 1, yes; 12) Very large antorbital process and lacrimal; 0, no; 1, yes; 13) Rostrum very short: 0, no; 1, yes; 14) Relatively broad sagittal crest: 0, no; 1, yes.

over, in these last two genera, the cranial basin takes up the antorbital processes and consequently the antorbital notches penetrate the cranial fossae. This last character was considered as an apomorphy of the Kogiinae (*Kogia* and *Praekogia*) by Muizon (1988).

Considering interrelationships among the three species of the genus *Kogia*, apparently *K. breviceps* and *K. simus* are more derived than *K. pusilla* in having more anteriorly extended antorbital processes (and consequently more elongated cranial fossae) and a shorter rostrum. A parsimonious interpretation would suggest that the wide sagittal crest of *K. breviceps* is an apomorphy, considering the primitive status of the narrow crest observed in *K. pusilla* and *K. simus*.

The characters discussed below are used to create a maximum-parsimony cladogram of the relationships of *Kogia pusilla* using Henning 86, version 1.5 (Farris, 1988) (Tab. 1, Fig. 6).

Regarding other fossils referred to the family Kogiidae in the past, we agree with Barnes (1973) and Muizon (1988) on the attribution of *Kogiopsis floridanus* from the Miocene of Florida (Kellogg, 1929) as a probable physeterid and in considering the name of the species *Kogia prisca* (Miocene?, from Japan; Matsumoto, 1927) a *nomen dubium*.

Pilleri (1986a, 1987) identifies the living species *Kogia simus* and *K. breviceps* in the Pliocene of Tuscany on the basis of isolated teeth and periotics. We consider these fossils and other unpublished specimens as belonging to the Kogiidae and most probably to the genus *Kogia*. Nevertheless, we do not agree with Pilleri in referring these fossils to the two living species because the periotics show different characters and the teeth are not diagnostics at this systematic level. It is possible that most of these specimens belong to the fossil species *Kogia pusilla*.

Fossil kogiids were reported recently from Pliocene sediments of the Yorktown Formation (Whitmore, 1994) and northern Apennines (Cigala Fulgosi, 1996), but they were not described in detail.

### Conclusions.

The assignation of the specimen examined here to the Kogiidae confirms the presence of this family in the Pliocene of Tuscany, already documented by Pilleri (1986a) on the basis of isolated teeth and periotics. Other auditory bones from these sediments are under study by the authors.

*K. pusilla* is a primitive species of the genus *Kogia* that differs significantly from living *K. breviceps* and *K. simus* in having a smaller antorbital process and a more elongated rostrum.

The phyletic relationships between the Kogiidae and the *Physeteridae* were examined and an origin of the

Kogiidae older (at least Early Miocene) than that suggested by the paleontological data (Late Miocene) is suggested.

In accordance with Muizon (1988, 1991), the Kogiidae are separated into two subfamilies on the basis of different architecture of the supracranial basin: the Kogiinae (*Kogia* and *Praekogia*) and the Scaphokogiinae (*Scaphokogia*). The morphology of the supracranial basin of *Kogia pusilla* is similar to that of *K. breviceps* and *K. simus* even if the basin of the fossil species differs in having a smaller anterior extension.

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