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ARIMIDELPHIS SORBINII A NEW SMALL KILLER WHALE-LIKE DOLPHIN FROM THE PLIOCENE OF MARECCHIA RIVER (CENTRAL EASTERN ITALY) AND A PHYLOGENETIC ANALYSIS OF THE ORCININAE (CETACEA: ODONTOCETI)

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Abstract. *Arimidelphis sorbinii* is a new genus and a new species of Delphinidae (Cetacea, Odontoceti) based on an incomplete skull with right ear bones, mandible, teeth and left forelimb, all from one animal, from the Late Pliocene sediments of Marecchia river (Central Eastern Italy). This specimen had previously been wrongly referred to the fossil species *Tursiops osennae*.

Arimidelphis shows some affinities with killer whale (*Orcinus*), as the short rostrum, the very strong preorbital process with circular lateral outline, and the very elevated coronoid crest of the mandible.

A cladistic phylogenetic analysis points out the belonging of *Arimidelphis* to Orcininae and particularly to a clade also including the fossil genus *Hemisyntrachelus*, *Orcinus* and *Pseudorca.* The strong rostrum and mandible indicate a trophic adaptation similar to that of the last two genera. Other results of this cladistic analysis are the placement of *Orcaella* outside the Orcininae, and the position of *Grampus* near *Globicephala,* clearly inside the Orcininae. *Tursiops* and *Delphinus* (two genera of Delphininae) appear strongly distinct from Orcininae.

This new genus confirms the high radiation of delphinids in the Pliocene of the Mediterranean, probably related to the recolonization of this basin after the Messinian salinity crisis.

Riassunto. *Arimidelphis sorbinii* è un nuovo genere e una nuova specie di Delphinidae (Cetacea, Odontoceti) basato su un cranio incompleto, ossa uditive destre, mandibola, denti e arto anteriore sinistro, appartenenti ad un unico animale e provenienti dai sedimenti pliocenici del fiume Marecchia (Italia centro-orientale). Questo reperto era stato in precedenza erroneamente attribuito alla specie fossile *Tursiops osennae*.

Arimidelphis è affine all'orca (*Orcinus*) per il corto rostro, per il processo preorbitale molto robusto e con contorno circolare in veduta laterale e per la cresta coronoidea della mandibola molto elevata.

Un'analisi filogenetica cladistica ha messo in risalto l'appartenenza di *Arimidelphis* agli Orcininae ed in particolare ad un clade rappresentato anche dal genere fossile *Hemisyntrachelus* e da *Orcinus* e *Pseudorca*. In tutti i casi, il rostro e la mandibola robusti indicano un adattamento trofico simile a quello di questi ultimi due generi. Altri risultati di questa analisi cladistica sono l'esclusione di *Orcaella* dagli Orcininae e la posizione di *Grampus* vicina a *Globicephala*, chiaramente all'interno degli Orcininae. Invece *Tursiops* e *Delphinus* (due generi dei Delphininae) risultano non appartenere agli Orcininae.

Questo nuovo genere conferma la grande radiazione dei delfinidi nel Mediterraneo durante il Pliocene, probabilmente da mettere in relazione alla ricolonizzazione di questo bacino dopo la crisi di salinità messiniana.

Introduction

The Pliocene odontocete fauna from Mediterranean shows a great affinity with the extant fauna in respect to that of the Miocene, for the appearance of the modern delphinids and the disappearance of some extinct families, such as the eurhinodelphinids and the squalodontids. This change in the odontocete association may be due in part to a global renewal observed from the Middle Miocene to the Pliocene (Fordyce & Barnes 1994; Fordyce 1996; Bianucci & Landini 2002) and in part it may be related to the extinction of the Miocene fauna during the Messinian closure of the Mediterranean and the following Atlantic repopulation. So far, no delphinid records are know in the late Miocene of the Mediterranean (Bianucci & Landini 2002), while findings of this family are common in Pliocene sediments with specimens collected in several localities from northern and central Italy since the XVIII century. These Pliocene records have been recently reviewed (Bianucci 1996) and referred to some living and extinct genera. A relatively high diversity and the

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relevant presence of extinct taxa characterize this delphinid association. This datum is confirmed here by the description of a new delphinid genus and species based on one specimen from Marecchia river (Central Eastern Italy) previously referred to *Tursiops osennae* Simonelli, 1911 by Pilleri (1985). The supposed affinities of this specimen with *Tursiops osennae* (Simonelli 1911; Bianucci 1996) are not founded considering that it has many characters differing from this species, such as a stronger and shorter rostrum, wider premaxillae in the anterior portion of rostrum, sturdy antorbital process with circular outline in lateral view and more elongated anterior and posterior processes of the periotic.

The new systematic assessment has been supported by a better preparation of the fossil and by the use of computer tomography (CT) scans which also allowed the discovery of the right ear bones covered by the mandible.

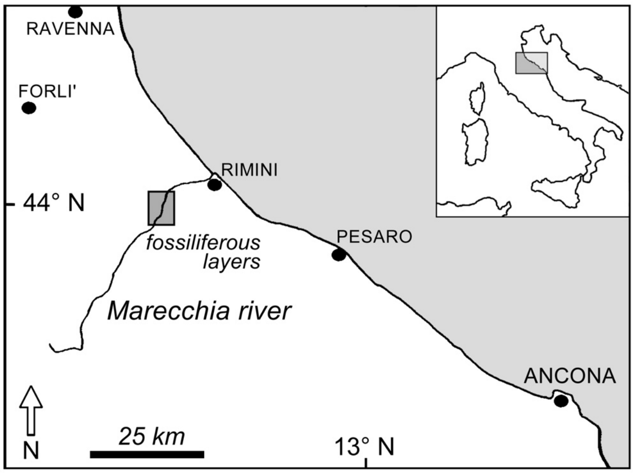


Fig. 1 - Geographic location of the Marecchia river fossilferous deposits.

Geological and taphonomic setting

The fossil delphinid here examined was collected in the about 2 km thick Pliocene sedimentary succession outcropping on the banks of Marecchia river (Rimini province, Central Eastern Italy, Fig. 1). These beds were exposed in seventies by active fluvial erosion (Colalongo et al. 1982). The delphinid here described was collected in bioturbated and homogeneous marly-silty clays of the upper 450 m of this section (Rio et al. 1997) which indicate a deep-water (600-1000 m) and hemipelagic environmemts. These clays are intercalated with 15 m thick, laminated sapropels that contain a rich ichthyofauna (37 families and 48 genera) studied by Sorbini L. (1982, 1988). Recently Chanet & Sorbini C. (2001) reported the presence of an extant species of flatfish (*Bothus podas*) from these sediments. Deep-sea stagnation cycles associated with eutrophication of the water may be the cause of the mass-mortality of the fish fauna observed in the laminated organic pelites (Colalongo et al. 1982). Paleontological evidences (fishes, cephalopods, insects, frogs and terrestrial plants) suggest a deep water basin not far from the coast (Sorbini L. 1988).

Based on biostratigraphic and magnetostratigraphic correlations the Marecchia section has been dated to a time interval between the Piacenzian and the Gelasian (Middle - Late Pliocene) ranging from 3.1 to 2.2 Ma (Rio et al. 1997).

The examined fossil bones are included in a single block of silty claystone about 60x45 cm (Pl. 1, fig. 1). The incompleteness of the skeleton may be due to the partial recovery of an entirely preserved specimen. The bones are disarticulated but still associated (Beherensmeyer 1991) and consist of part of the skull, incomplete right mandibular body, teeth in situ both on the skull and on the mandible, right ear bones, hyoid bones, and left limb lacking the manus. Except humerus, ulna and radius, the bones are partially overlapped or very approximated, and appear not to have suffered strong displacement. Humerus, ulna and radius are about 15 cm from the other preserved bones but they are very close one to each other, although not in anatomical connection. There is no evidence of bioturbation, scavenging or predation on the exposed surface of the bones.

A hypothetical taphonomic history is based on the disposition and preservation of the bones. No data are available concerning the cause of death of the animal. The unworn teeth indicate a young adult but the lack of pathological evidences or shark bits on the preserved bones suggest that predation was not responsible for its immature death (Deméré & Cerutti 1982; Cigala Fulgosi 1990). Furthermore, no shark teeth have been collected near the fossil bones as indication of a possible feeding interaction with these predators, unlike some other cases quoted in bibliography (Bianucci et al. 2002). Judging from the disposition of the skull and hyoid bones, the carcass deposited on the bottom dorsally. The relatively deep water environment of deposition (600-1000 m) may have prevented the carcass flotation during decomposition (Allison et al. 1991). The left forelimb probably detached from the body before the complete decomposition of soft parts because its bones fossilized separately from the others but in close connection one to another. After the complete soft-part decomposition, the right ear bones (not articulated with the squamosal in the delphinids) dropped to the bottom by gravity, without disarticulating. The mandibular bodies, forced by the weight of the skull, separated and rotated along their axis of 90 degrees. The right mandible overlapped the ear bones previously separated from the skull. The mandibular teeth suffered a little dislocation during rotation. The hyoid bones are preserved near their original position, ventral to the mandible and the skull. The scapula sank in the still soft sediment and the humerus, radius and ulna suffered small shifts in their reciprocal original anatomical position.

Absence or weakness of bottom currents and bioturbation and/or fast burial are supposed considering the small shift suffered by the bones and particularly by the teeth very close to their original position (a very small apical tooth is preserved in close proximity to the preserved anterior portion of the mandibular body).

Systematic description

Class **Mammalia** Linnaeus, 1758
Order **Cetacea** Brisson, 1762
Suborder **Odontoceti** Flower, 1867
Superfamily Delphinoidea Gray, 1821
Family Delphinidae Slijper, 1936
Subfamily Orcininae Wagner, 1846

Emended diagnosis. A subfamily of Delphinidae characterized by relatively short rostrum (< 55 % skull length), by lateral margins of premaxillae parallel or anteriorly diverging at apex of rostrum, and by antorbital process globose and robust.

Genus *Arimidelphis* gen. n.

Diagnosis. Small sized odontocete with strong and probably short rostrum, at least 17 teeth for each tooth row and high postalveolar body of the mandible. Referred to Delphinoidea because the periotic has a short anterior process (without anterior bullar facet) and a rectangular section. Referred to Delphinidae because the posterior bullar facet of the periotic is strongly ridged and posterolaterally directed and the coracoid process and acromion of the scapula widen distally. Similar to *Orcinus* by having short rostrum, very strong preorbital process with circular lateral outline, and very elevated coronoid crest of the mandible. Different from *Orcinus* by having smaller size, more numerous and smaller teeth without lateral compression, not inflated periotic and narrower tympanic bulla in ventral view, smaller basihyal and more elongated thyrohyal, scapula with larger coracoid process and acromion and smaller supraspinous fossa, more gracile humerus and radius and ulna not distally widened.

Type and only included species. *Arimidelphis sorbinii* n. sp.

Etymology. The genus name is from *Ariminus*, ancient Latin name of the Marecchia river, flowing near the locality where the holotype of this species was collected, and *delphis*, Latin for dolphin. Gender masculine.

Arimidelphis sorbinii n. sp.

(Fig. 2-5; Pl. 1, 2; Tab. 1)

1985 *Tursiops osennae* - Pilleri, p. 13-15, pl. 1, 2.
1997a New Genus - Bianucci, p. 81, fig. 7.

Holotype and only referred specimen. S.A.E. 39756, kept in the Museo Civico di Storia Naturale di Verona and consisting of a skull lacking almost all the left side, the anterior portion of the rostrum, the vertex and all the posterior portion of braincase; right ear bones; maxillary teeth preserved in their alveoli; right mandibular body lacking its anterior portion, with some teeth in their alveoli and others near the body; thyrohyals and basihyal; left scapula; left humerus, ulna and incomplete radius; all from the same animal.

Horizon and Locality. Piacenzian - Gelasian (Pliocene) clays outcropping along the bed of Marecchia river, near Poggio Berni locality, Rimini Province (Central Eastern Italy) (Fig. 1). The age ranges from 3.1 to 2.2 Ma (Rio et al. 1997).

Etymology. The species is named in honor of Lorenzo Sorbini, outstanding paleontologist who dedicated his researches mainly to the marine fish faunae of Italy and was the first to study the Marecchia river fossil fishes. He organized and directed the excavations in the Marecchia river fossiliferous deposits, in which the only specimen of this species was collected.

Description

Skull. The skull is relatively small (the condylobasal length may be estimated about 45 cm). The rostrum is strong and, considering that the lateral outline of the anterior preserved portion of rostrum, in dorsal view, is medially bent, we can suppose that it was also relatively short (Fig. 2A). In dorsal view, the rostrum exhibits an abrupt widening about four centimeters from the base, and consequently the lateral outline shows a weak concavity anterior to this widening. The antorbital notches are wide and very deep.

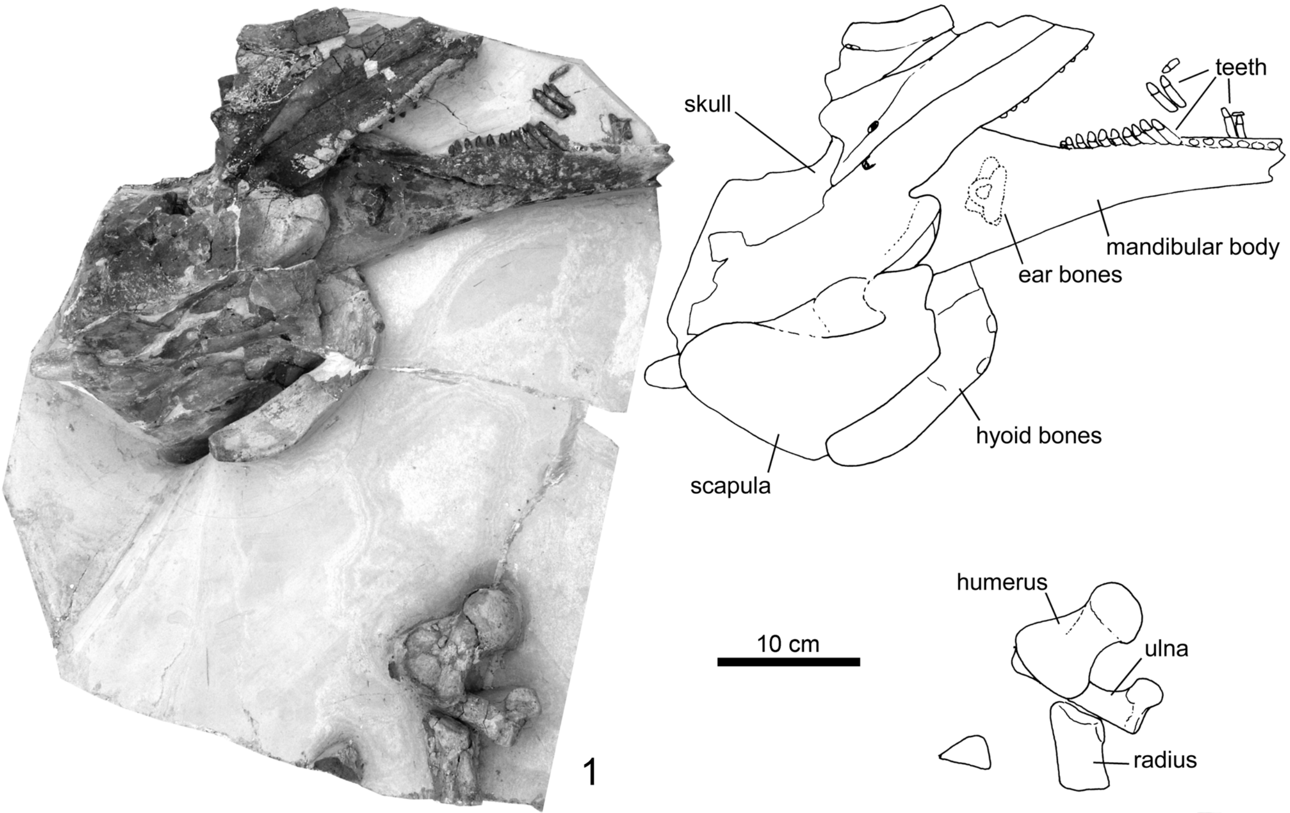
A portion of right premaxilla (ca. 20 cm) and one of the left premaxilla (ca. 10 cm) are preserved in the posterior part of the rostrum. About four centimeters anteriorly to the base of the rostrum, the premaxillae show a weak constriction; more anteriorly, their width remain more or less constant for all the preserved portion of the rostrum. The premaxillary foramina are located in the anterior sulci and the left is more anterior than the right.

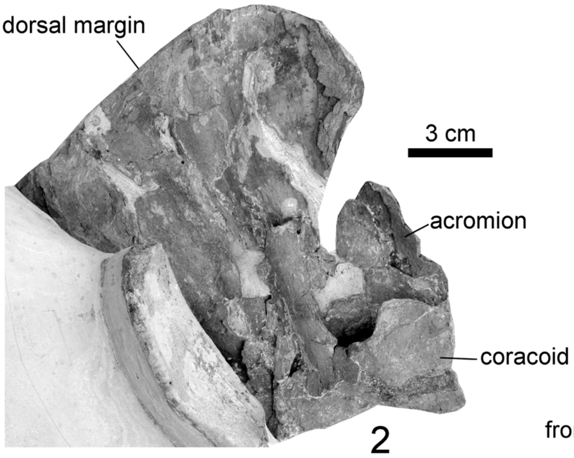
Only the incomplete right maxilla is preserved. Its minimum width (2.3 cm) is located in the anterior part of the preserved portion of rostrum. The dorsal surface of the maxilla on the rostrum bents lateroventrally and near the lateral margin it is almost vertical. A relatively large maxillary foramen is located near the premaxilla immediately posterior to the base of the rostrum. A distinct maxillary crest marks the dorsal surface of the

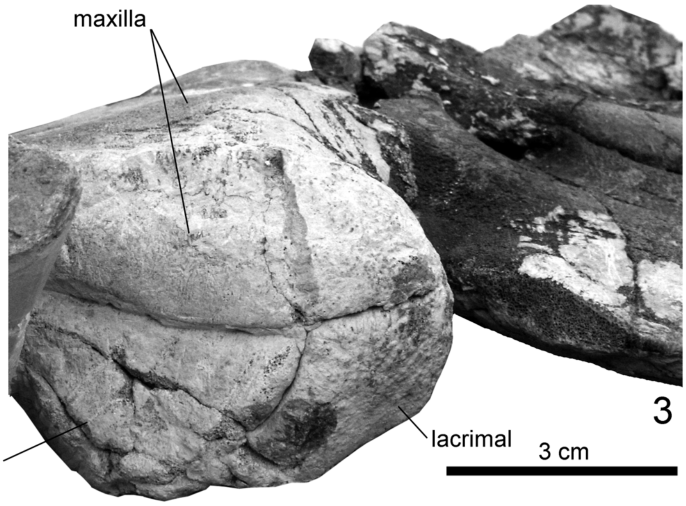
PLATE 1

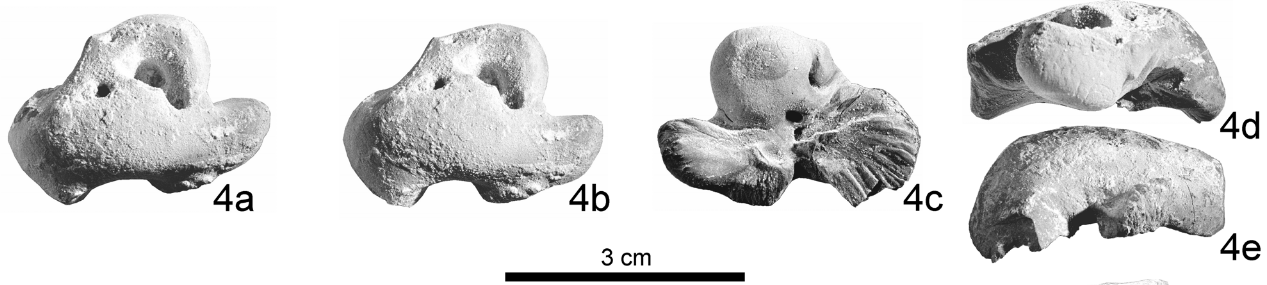
Arimidelphis sorbinii, holotype from the Pliocene of Marecchia river

Fig. 1 - all preserved bones with their geometrical disposition; Fig. 2 - left scapula in medial view; Fig. 3 - right antorbital process in lateral view; Fig. 4 - right periotic in dorsal (a), dorsolateral (b), ventral (c), medial (d) and lateral (e) views; Fig. 5 - right tympanic bulla in ventral (a), lateral (b) and medial (c) views; Fig. 6 - right periotic and tympanic bulla in posterior view.


skull
teeth
mandibular body
ear bones
hyoid bones
scapula
humerus
ulna
radius
10 cm
1


dorsal margin
3 cm
acromion
coracoid
2


maxilla
frontal
lacrimal
3 cm
3


4a
4b
4c
4d
4e
3 cm


5a
5b
5c


6

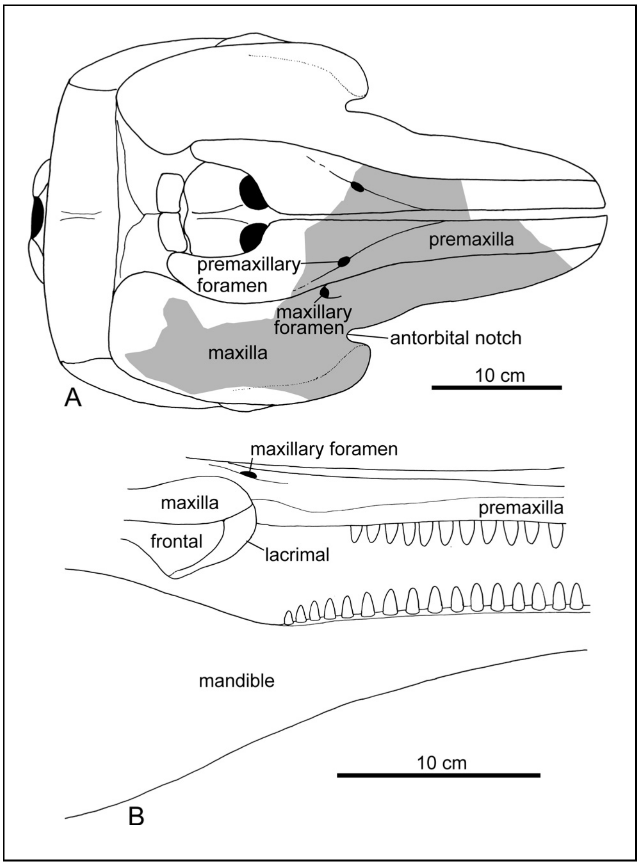


Fig. 2 - Reconstruction of skull and mandible of *Arimidelphis sorbinii*. A, skull in dorsal view (gray indicates preserved dorsal surface; the restoration of lacking part is based on related extant delphinid genera); B, antorbital process and preserved portions of rostrum and mandible in lateral view.

antorbital process. The CT scan of the rostrum shows a curved right tooth row 12 cm long, bearing 14 teeth (Fig. 3). The posteriormost tooth is located about 3 cm from the basis of the rostrum.

The antorbital process is strong and projects further beyond the rostrum basis. In lateral view, the antorbital process is dorsoventrally thick and shows a circular outline (Pl. 1, fig. 3). Its dorsal half is formed by the maxilla, while ventrally a sturdy triangular apex of the frontal wedges penetrates between the maxilla and the lacrimal.

Ear bones. The anterior process of the periotic (Fig. 4A-E; Pl. 1, fig. 4a-e) is relatively slender and elongated for a delphinid. It is mediolaterally compressed with a rectangular section, and exhibits an anterior keel on its dorsomedial surface. The anteroventral angle is anterior to the anterodorsal angle and both angles are rounded. The fovea epitubaria is anteroposteriorly elongated and laterally margined by a sturdy parabullary ridge, particularly in its posterior portion. A small but distinct lateral tuberosity posteriorly delimits the anterior process. A deep hiatus epitympanicus separates the anterior process from the posterior process. The latter is relatively short and exhibits a ridged posterior bullar facet, slightly concave, and parallel to the plane of the periotic body. The ventral point of the posterior bullar facet is lost but it may be reconstructed with the help of the posterior process of the tympanic bulla which indicates that the posterior bullar facet was

Skull	
Width of rostrum at base (3)	150*
Width of premaxillae at base of rostrum (4)	90*
Width of rostrum 60 mm anterior to base (5)	62
Greatest preorbital width (12)	250*
Length of antorbital process of lacrimal (23)	43
Ear bones	
Greatest length of periotic (1)	34.8
Greatest width of periotic (2)	23.4
Width of periotic at level of upper tympanic aperture (3)	21.2
Greatest thickness of periotic (4)	14.6
Thickness of periotic at level of upper tympanic aperture (5)	12.7
Length of pars cochlearis (6)	12.5
Thickness of pars cochlearis (7)	10.6
Length of anterior process of periotic (8)	18.6
Length of posterior process of periotic (9)	14.4
Length of ventral tuberosity+ventral swelling of periotic (10)	16.5
Greatest length of tympanic (11)	35.2
Greatest width of tympanic (12)	20.0
Length of lateral lobe of tympanic (13)	35.4
Length of medial lobe of tympanic (14)	32.7
Hyoid bones	
Length of fused basihyal and thyrohyals (A)	105*
Width of fused basihyal and thyrohyals (B)	190*
External width between articulations for the keratohyal cartilages (C)	50
Internal width between articulations for the keratohyal cartilages (I)	16
Anterior width of basihyal (E)	81
Posterior width of basihyal (F)	43
Length of thyrohyal (I)	95
Width of thyrohyal (H)	37

Scapula	
From anterior angle to glenoid fossa (A)	135
From dorsal margin to glenoid fossa (B)	160
Coracoid length (F)	45
Distal width of coracoid (G)	+52
Acromion length (H)	55*
Distal width of acromion (I)	64
Humerus	
Length	93
Anteroposterior diameter of head	44
Distal anteroposterior diameter	58
Distal transverse diameter	22
Ulna	
Length	104
Proximal transverse diameter	21
Proximal anteroposterior diameter	46
Radius	
Proximal transverse diameter	34

Asterisk indicates estimated measurement.
For numbers and letters within parentheses and explanation of relative measurements see:
Bianucci (1996, fig. 3) for skull;
Bianucci (1996, fig. 2) for ear bones;
Nishiwaki et al. (1965, p. 80) for hyoid bones;
Nishiwaki et al. (1965, p. 79) for scapula.

Tab. 1 - Measurements of *Arimidelphis sorbinii* holotype (in mm).

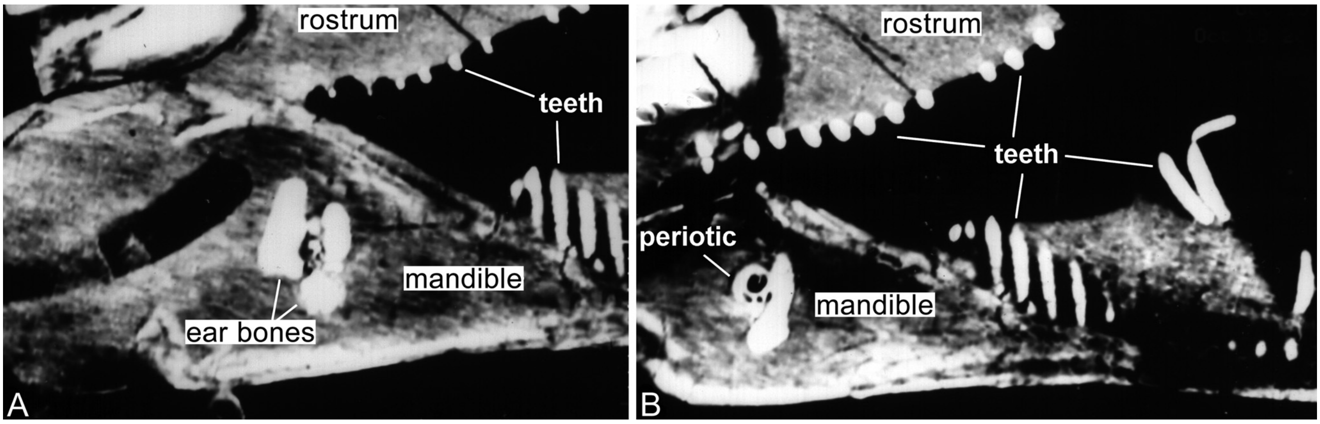


Fig. 3 - CT scan of mandible and portion of rostrum of *Arimidelphis sorbinii* holotype showing the elevated coronoid crest (A), the curved tooth row (B) and the straight teeth (A, B) and the ear bones, under the mandible, before their extraction (A, B).

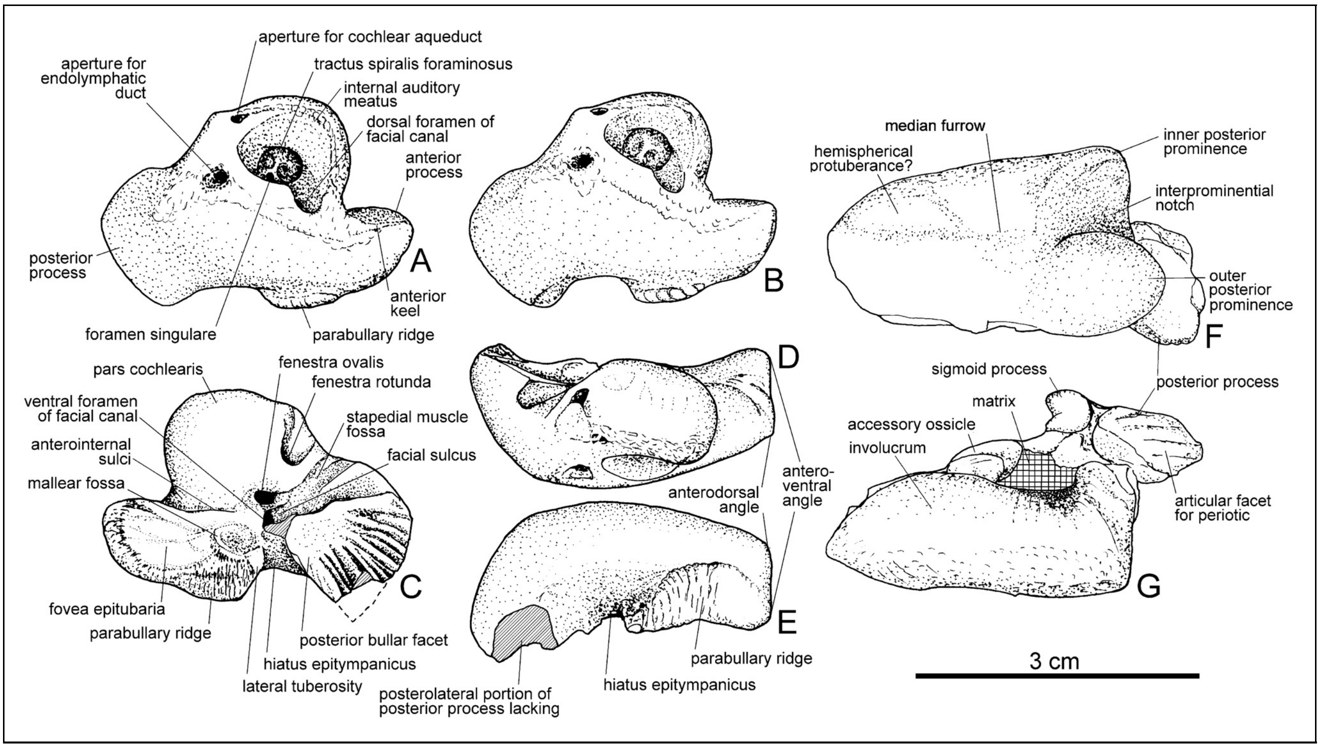


Fig. 4 - Right periotic (A-E) and tympanic bulla (F-G) of *Arimidelphis sorbinii* holotype. A, dorsal view; B, dorsolateral view; C, ventral view; D, medial view; E, lateral view; F, ventral view; G, medial view.

originally trapezoidal in shape. The major axis of the posterior bullar facet is posterolaterally directed. In dorsal view, the pars cochlearis is high with an almost vertical anterior margin and an inclined posterior margin. The internal auditory meatus is separated anterolaterally from the dorsal foramen of the facial canal by a low crista transversa. The tractus spiralis foraminosus and the foramen singulare are located deeply. The aperture for cochlear aqueduct and the aperture for endolymphatic duct open both dorsally in a flat area posterior to the internal auditory meatus. The fenestra rotunda is large and semicircular. The fenestra ovalis is elliptical with the major axis anterposteriorly oriented. The dorsal surface of the periotic body (superior process) is narrow and lacks a lateral keel.

The tympanic bulla (Fig. 4F,G; Pl. 1, fig. 5a-c) is rather damaged: the posterior process, the sigmoid process and the accessory ossicle are partially displaced, while the lateral surface is badly preserved. In ventral view, the inner posterior prominence is narrow and separated by a very deep and wide interprominential notch from a hemispherical outer posterior prominence. The latter extends posteriorly more than the inner one. The inner prominence exhibits a narrow rugose longitudinal area (longitudinal keel of Kasuya 1973) and an anterior low convexity (hemispherical prominence of

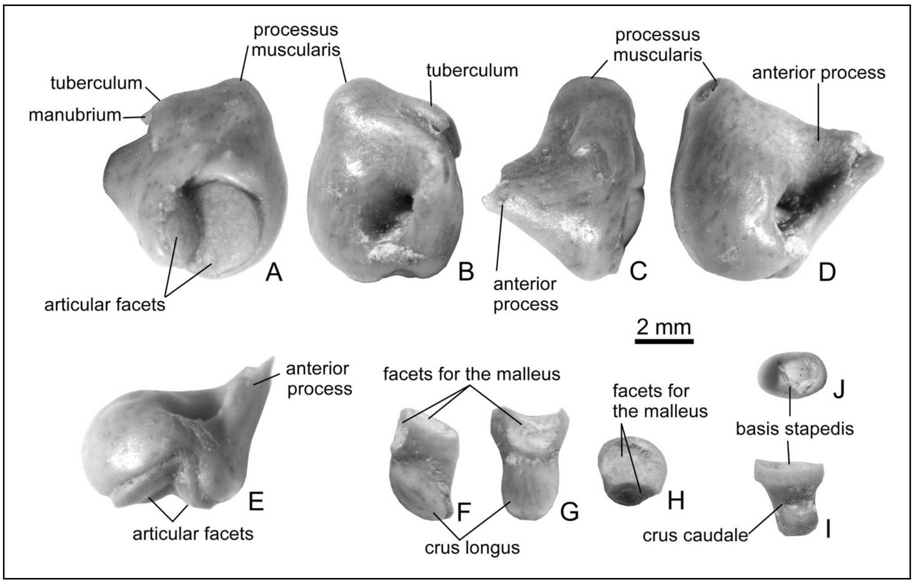


Fig. 5 - Right malleus (A-E), incus (F-H) and stapes (I-J) of *Arimidelphis sorbinii* holotype. A, posterior view; B, anterior view; C, medial view; D, lateral view; E, ventral view; F, dorsal view; G, medial view, H, anterior view; I, medial view; J, ventral view.

Kasuya 1973). The median furrow is shallow and the anterior spine is absent. In medial view, the involucrum shows a right posteroventral angle and a sigmoid dorsal margin. In lateral view, the tympanic bulla is anteroventrally bent; consequently its ventral margin is concave. The sigmoid process is L-shaped and the medial furrow is absent. The elliptical foramen is apparently absent but this aperture may have been closed by the diagenetic compression and the partial dislocation of the posterior process.

The malleus (Fig. 5A-E) is relatively globose and has a low tuberculum and a developed processus muscularis with a small fossa for the tendon of the tensor tympani. The manubrium is small and pointed. As in the other Delphinida, in posteromedial view (Fig. 5A), the processsus muscularis is distinctly higher than the manubrium. The great facet for the incus is large and circular while the other facet is smaller. The robust anterior process lacks the apex.

The incus (Fig. 5F-H) has two facets for the malleus that are semicircular, slightly concave and forming an angle of 90 degrees between them. The crus breve is missing and the crus longum is relatively robust and curved; it terminates with a pointed processus lenticularis with a small facet for the stapes.

The stapes (Fig. 5I-J) exhibits a relatively large basis stapedis that articulates with the fenestra ovalis of the periotic. The crus caudale is short, compressed and terminates with a narrow caput stapedis with the articulation for incus.

Hyoid bones. The thyrohyoid and basihyoid bones are fused and relatively slender. They are not regularly arched but bent to form an obtuse angle (Pl. 2, fig. 3). The basihyal is slightly wider than high and it exhibits low and widely separeted articulations for the keratohyal cartilages. The thyrohyal exhibits a relatively wide and slightly concave dorsal surface, where the sternohyoid muscle inserted, and a distinctly convex lateral margin.

Mandible. Only the right body of the mandible lacking its anterior portion is preserved (Fig. 2B; Pl. 2, fig. 2). The posterior portion of posteralveolar branch is covered by the skull but its outline may be reconstructed looking at the CT scans (Fig. 3). In lateral view, the height of the body increases progressively posteriorly; posterior to the alveolar row, the dorsal margin raises abruptly forming an high coronoid crest; the ventral margin is gently and regularly concave. On the whole, the body has a triangular outline and a very elevated posteralveolar branch. The preserved alveolar part is 15 cm long and bears 16 alveoli. The symphyseal portion is not preserved.

Teeth. The teeth diameter ranges between 4 and 7 mm and their length varies between 17 and 32 mm, with the exception of a very small tooth (diameter: 2.5 mm, length: 10 mm) which probably represents an anteriormost tooth (Pl. 2, fig. 2). The crown is relatively small, slightly medially bent at the apex and with a circular cross section; the enamel lacks striation and keels, and there are not accessory denticles. The root of mandibular teeth is cylindrical, without lateral compression and straight.

Forelimb. The preserved left scapula is still partially embedded in the matrix and only the anterior half medial surface is visible (Pl. 1, fig. 2). The dorsal margin is almost straight. The acromion is very large and dorsally expanded. The coracoid process is short, and strongly widened distally. The supraspinous fossa is reduced.

The humerus is short; it exhibits a large hemispherical head, a sturdy diaphysis with a distal location of the deltopectoral tuberosity. It distal epiphysis is anteroposteriorly expanded and transversely flattened (Pl. 2, fig. 4).

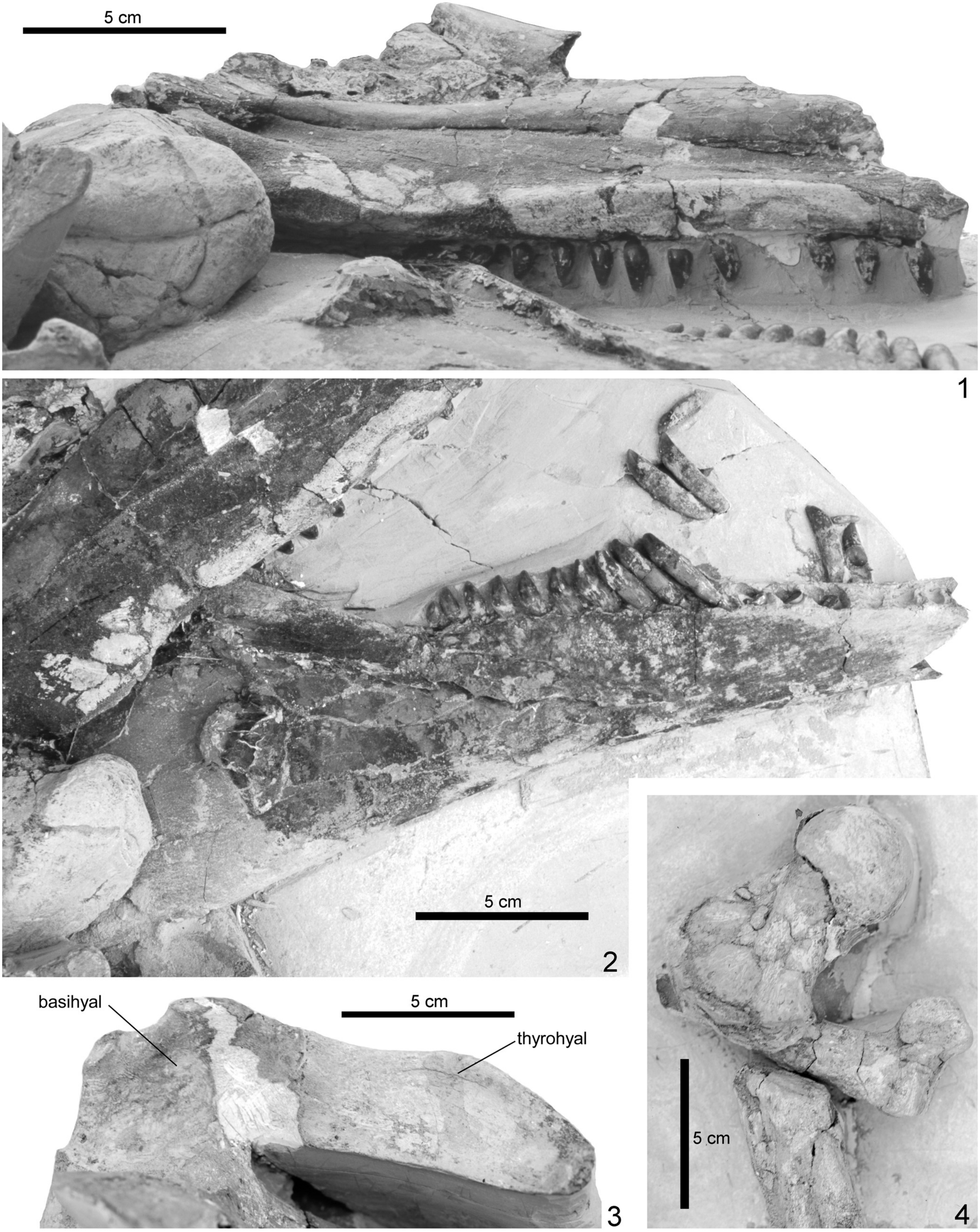


PLATE 2

Arimidelphis sorbinii, holotype from the Pliocene of Marecchia river

Fig. 1 - antorbital process and preserved portion of rostrum in lateral view; Fig. 2 - portion of skull in dorsal view and teeth and right mandible in lateral view; Fig. 3 - basihyal, right thyrohyal and portion of left thyrohyal; Fig. 4 - left humerus, ulna and incomplete radius.

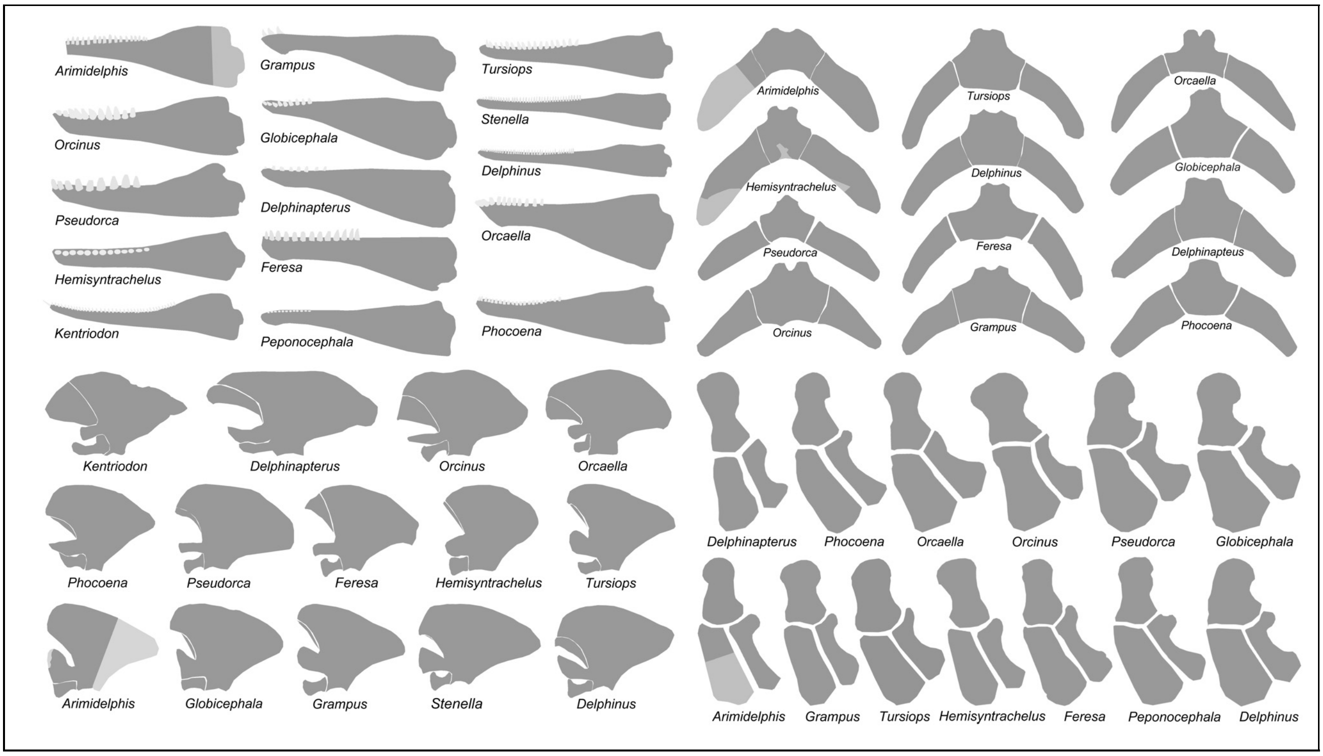


Fig. 6 - Comparison of mandible (top left), thyrohyals and basihyal bones (top right), scapula (bottom left) and humerus, radius and ulna (bottom right) of *Arimidelphis* and other delphinoid genera.

The ulna is slender and relatively elongated with sturdy olecranon process.

The preserved proximal portion of the radius is not anteroposteriorly expanded.

Comparison. The assignation of *Arimidelphis* to delphinids is based on some characters of the ear bones and scapula because other apomorphies of this family regard parts of the skull either not preserved in the fossil specimen (e.g.: the asymmetry of the proximal end of the premaxilla) or probably preserved but still included in the matrix (e.g.: the pterygoid sinus complex). In any case, the preserved osteological portions of *Arimidelphis* are well in accordance with some delphinids as explained below.

The strong rostrum, relatively short and with the premaxilla not narrowing anteriorly is observed in all the Globicephalinae (sensu Muizon 1988). The rostrum of *Arimidelphis* is particularly similar in shape, size, elongation, extension of the premaxillae, to *Peponocephala* and *Feresa*, while it differs from *Globicephala* and the supposed Delphininae *Grampus* in narrower base and a weaker widening of the premaxillae. The rostrum of *Arimidelphis* is apparently shorter than in the fossil genus *Hemisyntrachelus*.

The antorbital process is very similar to that of *Orcinus* in lateral view for its sturdy and circular outline. I also observed a rather strong antorbital process in some skulls of *Pseudorca*, *Globicephala*, *Feresa*, *Grampus* and *Hemisyntrachelus,* but without the characteristic circular outline of *Orcinus* and *Arimidelphis*.

The ear bones exhibit the odontocete derived characters emphasized by Luo & Gingerich (1999) which are: the position of the hiatus fallopii on the medial side of the pars cochlearis of periotic (dorsal foramen of the facial canal); the lack of contact between the anterior process and the entoglenoid part of the squamosal; the presence in the tympanic bulla of an accessory ossicle articulating with the anterior process of periotic; and the well extended median furrow on the ventral surface of the tympanic bulla.

The lack of articulation of the posterior process of the tympanic bulla with the squamosal is an apomorphy shared with the Eurhinodelphinoidea-Delphinida clade (Muizon 1991; Fordyce 1994).

The periotic is similar to that of other delphinoids for the short anterior process without anterior bullar facet and with a rectangular section. It is similar to that of other delphinids in having the posterior bullar facet strongly rough and posterolaterally directed. In particular, the periotic of *Arimidelphis* shows great affinities with that of *Hemisyntrachelus*, differing essentially in the higher pars cochlearis and the deeper hiatus epitympanicus. Among the extant delphinids, this periotic shows some affinities with *Tursiops* from which it differs essentially in having the anterodorsal angle of the anterior process rounded, in the anteroventral angle more advanced than the anterodorsal one, in the circular and larger internal auditory meatus, and in the dorsal opening of the aperture for cochlear aqueduct.

The tympanic bulla shows the typical sigmoid dorsal margin of the involucrum in medial view that has been observed in all Delphinida (Muizon 1988). The tympanic bulla does not exhibit the strong transverse compression observed by Kasuya (1973) in *Grampus*, *Globicephala*, and *Feresa*.

The malleus shows a strong processus muscularis as observed by Muizon (1988) in all the Delphinida.

The mandible is similar to that of *Orcinus* and *Pseudorca* in the strong elevation of the dorsal margin of the posteroalveolar branch and, for this character, drastically differs from *Grampus, Globicephala,* and *Feresa,* which have an almost horizontal dorsal margin (Fig. 6, top left). *Hemisyntrachelus,* shows an intermediate condition between *Arimidelphis* and *Tursiops*, which has a moderate elevation of the posteroalveolar branch. The ventral margin of the mandibular body of *Arimidelphis* slopes abruptly posteriorly more that in *Orcinus* and *Hemisyntrachelus,* and for this character, it is similar to *Globicephala*, *Grampus*, *Peponocephala*, *Feresa,* and *Orcaella*. The mandibular ventral margin of *Pseudorca* is instead almost rectilinear. A supposed rectilinear ventral margin is described by Bianucci (1996) for the mandibular body of *Hemisyntrachelus pisanus*. Nevertheless my re-examination of the holotype and only known specimen of this species suggests that the straight rectilinear ventral margin is an artefact due to the original bad restoration of the specimen. In this new context, the validity of the species *H. pisanus* should be re-discussed.

The size and probably a number of teeth of *Arimidelphis* is similar to that of *Tursiops*; it differs from *Hemisyntrachelus*, *Orcinus*, *Globicephala, Pseudorca, Feresa* and *Grampus,* which show a progressive (from *Hemisyntrachelus* to *Grampus*) increase in tooth-size and/or decrease in number of teeth. An opposite trend (decrease in tooth-size and increase in number of teeth) is observed in *Peponocephala*.

The fused thyrohyals and basihyal are relatively slender as in other delphinids, differing from the wide and sturdy hyoid bones of ziphiids and physeterids. Among the delphinids, they differ from those of *Hemisyntrachelus*, *Tursiops* and most other genera of this family in having not prominent and relatively distant articulations for the keratohyal cartilages (Fig. 6, top right). Besides, I observed some differences in the proportion between the length of thyrohyals and basihyal in *Arimidelphis* compared with *Orcinus* and *Grampus* (which have relatively larger basihyal) and *Hemisyntrachelus* (which has relatively smaller basihyodal bones). On the whole these bones are similar to those of *Hemisyntrachelus*, *Pseudorca* and *Orcinus* for their angular shape; they differ from the arched bones of other delphinids (even if in *Orcinus* this character is partially obliterated by the shortening of the thyrohyal). In any case, some caution is necessary when using these characters as diagnostic because of the poor knowledge of their intraspecific variability.

The scapula is similar to that of other delphinids for the distal widening of acromion and coracoid process (Fig. 6, bottom left). In particular, the coracoid process widely expanded, even more than in *Stenella, Delphinus,* and *Feresa*, the extant genera in which this character is the most emphasized. Moreover, the acromion is triangular because of the dorsal dilatation of its apex as observed in *Tursiops*, *Grampus* and particularly in *Delphinus*, *Stenella,* and *Globicephala*. The only known scapula of *Hemisyntrachelus* has a wide acromion, but not triangular in shape (Sacco 1893, tab. 2, fig. 12) and a coracoid process similar in robustness to that of *Arimidelphis*, but again without the characteristic very accentuated distal widening. The preserved anterior margin of the scapula of *Arimidelphis* shows an inclination similar to that of other delphinids except *Orcaella* and *Orcinus* which have an almost horizontal anterior margin as a result of the larger extension of the supraspinous fossa.

The humerus is similar to that of other delphinids in having a short and sturdy diaphysis and a distally located deltopectoral tuberosity (Fig. 6, bottom right). In particular, the humerus of *Arimidelphis* shows strong affinities with *Tursiops*, *Grampus*, *Hemisyntrachelus*, *Feresa* and *Peponocephala* while it differs from those, even more robust and shorter, of *Orcinus*, *Pseudorca*, *Globicephala*, *Delphinus,* and *Stenella*.

The ulna exhibits a sturdy and prominent olecranon process as in other delphinids excepted *Orcaella* and *Orcinus*. The ulna and the radius do not show the proximal widening observed in *Orcaella*, *Globicephala*, *Orcinus,* and *Pseudorca*.

Phylogenetic analysis

Previous analyses. A cladistic phylogenetic analysis within the delphinids, based on the osteological characters, was proposed for the fist time by Muizon (1988) who distinguished three clades (Delphininae, Globicephalinae and Cephalorhynchinae only including *Cephalorynchus*). Barnes (1990) suggested five subfamilies (Cephalorhynchinae, Delphininae, Globicephalinae, Lissodelphininae and Steninae) in a cladogram showing the relationships between *Tursiops* and other cetacean groups. Bianucci (1996) considered the relationships of the fossil genus *Hemisyntrachelus* within the Globicephalinae and the Delphininae, and of the fossil genus *Astadelphis* within the Steninae. In their study on the affinities of *Orcaella,* Arnold & Heinsohn (1996) proposed for the first time a computer assisted cladistic analysis for the delphinids and related groups. Messenger & McGuire (1998) considered a group of selected species of delphinids in their phylogenetic analysis of cetacean using combined morphological and molecular data. LeDuc et al. (1999) analyzed the delphinid phylogenesis using mitochondrial DNA of the full cytochrome b sequences; they recognized five subfamilies (Delphininae, Globicephalinae, Lissodelphininae, Orcininae and Stenoninae). This last research disarranged the traditional assessment of the systematic of delphinids; in particular, *Grampus* was placed within the subfamily Orcininae, and *Orcinus* was removed from this group and placed in the Orcininae with *Orcaella*. Finally, Fordyce etal. (2002) described the new delphinid genus *Australodelphis* without presenting a phylogenetic analysis.

Methods. With the aim to clarify the relationships of *Arimidelphis* within the Delphinidae and particularly with the short-rostrum delphinids traditionally placed in the Globicehalinae and Orcininae, a cladistic analysis is here proposed, using the computer software PAUP version 4.0 b10 (Swofford 1998). The computer analysis was performed using the heuristic search option, considering all characters as ordered and unweighted. This analysis must be considered as an attempt of computer assisted phylogenetic treatment of delphinid characters despite the difficulties to discern significant morphological apomorphies among this family. In fact, as already pointed out by some authors (Perrin 1975; Bianucci 1996; LeDuc et al. 1999), the delphinids exhibit a large evolutionary plasticity (particularly for the characters associated to feeding adaptation); that plasticity might have favored the appearance of homoplasies. However, I considered in this analysis not only the characters associated to feeding apparatus (rostrum, teeth, and mandible) but also some features of the braincase considered as more conservative, such as those related to ventral sinuses and ear bones (LeDuc et al. 1999). Additionally, postcranial characters are considered.

This analysis resulted in a matrix of 40 characters coded as binary or multistate (Tab. 2). Morphological characters used in this analysis are partially taken from the works of Arnold & Heinsohn (1996), Barnes (1990), Bianucci (1996), Fraser & Purves (1960), Kasuya (1973), Mead (1975), and Muizon (1988). While some of these characters have been previously considered by other authors (as those relative to the ear sinuses of the ventral surface of the skull, observed by Fraser & Purves (1960) and already used by Muizon (1988) in his phylogenetic analysis). Other characters, as the length of the rostrum, widening of premaxillae at the apex of the rostrum and number of vertebrae, even if previously considered by other authors, have been reformulated in the present analysis. Finally, some supposed apomorphies, as those relative to the hyoid bones and the scapula, are considered for the first time. All the characters considered for the first time or reformulated and part of those previously used are preferentially directly examined in specimens from various European museums, with the exception of *Kentriodon* (the outgoup), for which the data are extracted from the figures and descriptions in Kellogg (1927). The data relative to *Hemisyntrachelus* are personal observations in Italian collections, in part already published (Bianucci 1996, 1997a, 1997b). In any case, bibliographical data (descriptions, measurements, drawings, and figures) have been useful for the characters state determinations: mainly Marsh et al. (1989) and Arnol & Heinsohn (1995) for *Orcaella*; Dahlhein & Heyning (1999) for *Orcinus*; Purves & Pilleri (1978) and Odell & McClune (1999) for *Pseudorca*; Nishiwaki & Norris (1966) and Perryman et al. (1994) for *Peponocephala*; Nishiwaki et al. (1965), Yamada (1954), Pryor et al. (1965) and Cadenat (1958) for *Feresa;* Bernard & Reilly (1999) for *Globicephala*; Kruse et al. (1999) for *Gram-*

Taxa	Characters																																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Kentriodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orcaella	2	1	1	0	0	0	1	1	1	0	0	0	0	1	2	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	1	1
Arimidelphis	2	1	1	1	1	0	1	?	?	?	?	?	?	?	1	0	0	0	1	1	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	?	?	?
Hemisyntrachelus	1	1	1	1	0	0	1	1	1	?	?	?	0	1	1	0	0	0	1	1	0	0	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	0
Orcinus	2	1	1	1	1	0	1	1	1	0	0	0	0	1	2	0	0	0	1	1	0	0	0	1	1	1	0	2	0	2	0	0	1	0	1	1	0	1	0	0
Feresa	2	1	1	1	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	0	1	3	2	0	2	1	1	1	0	1	1	1	1	2	1
Peponocephala	2	1	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	?	1	2	0	1	0	?	?	?	?	1	1	1	1	2	1
Globicephala	2	2	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	1	1	0	0	1	1	0	1	3	2	0	2	1	1	1	1	1	1	1	1	1	1
Grampus	2	2	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1	3	2	0	2	1	1	1	1	1	1	1	1	2	1
Pseudorca	2	1	1	1	1	0	1	1	1	0	0	0	0	1	2	0	0	0	1	1	0	0	0	1	1	1	0	2	0	2	1	0	1	0	1	1	1	1	0	0
Tursiops	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	2	0	0	0	1	1	1	1	1	1	1	1	2	1
Delphinus	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	0	1	2	0	1	0	1	1	1	1	1	1	1	1	2	1

Tab. 2 - Character-taxon matrix used in cladistic analysis of *Arimidelphis*. 0, ancestral state; 1-3, derived states;? = missing data.

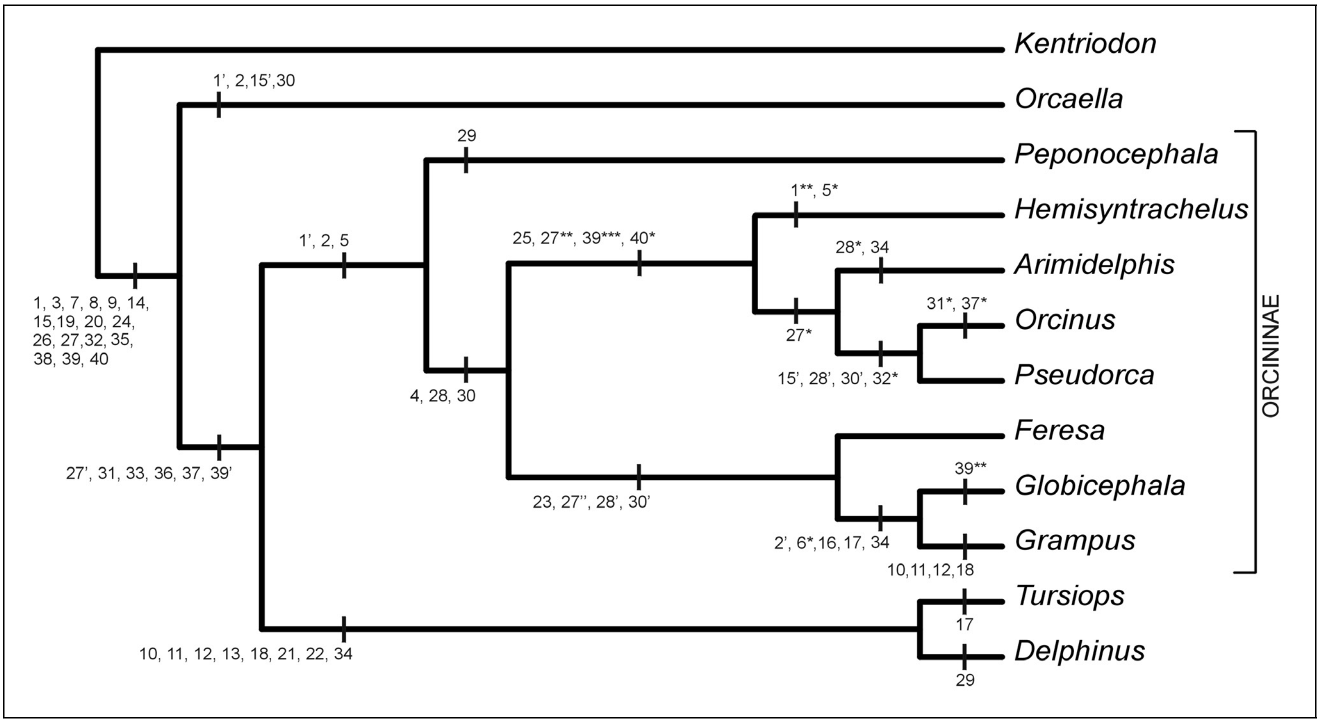


Fig. 7 - Cladogram of relationships of *Arimidelphis* with Orcininae and other related genera. For numbers see Tab. 2 and the list of character-states on the text.
' = change from state 1 to state 2; " = change from state 2 to state 3; * = reversal from state 1 to state 0; ** = reversal from state 2 to state 1; *** = reversal from state 2 to state 0.

pus; Rommel (1990), Wells & Scott (1999) and Ross (1977) for *Tursiops*; Heyning & Perrin (1994) for *Delphinus*.

List of characters and character-states

Rostrum

1. Length of rostrum: (0) very elongated (> 60 % skull length); (1) elongated (60-55 %); (2) short (< 55 %).
2. Premaxillae at apex of rostrum: (0) narrowing; (1) with lateral margins parallel or weakly diverging; (2) strong widening of premaxillae and flattening dorsal surface of the anterior portion of rostrum.
3. Lateral margin of the rostrum: (0) concave; (1) convex (Bianucci 2001).

Neurocranium

4. Antorbital process: (0) triangular and slender; (1) globose and robust.
5. Deep and wide antorbital notch: (0) no; (1) yes.
6. Widening of cerebral skull: (0) no; (1) yes.
7. Cranial vertex skewed asymmetrically to left side (Barnes 1990): (0) no; (1) yes.
8. Posterior end of left premaxilla always narrower and shorter than right and anteriorly retracted away from anterolateral corner of left nasal (Barnes 1990): (0) no; (1) yes.
9. Development of a mesethmoid plate overhanging narial fossae and consequent anteroposterior squashing of nasals (Muizon 1988; Barnes 1990): (0) no; (1) yes.

Ventral sinus

10. Widening of apices of pre- and postorbital lobe of pterygoid sinus with tendency to fuse together and to insert optic nerve in a canal (Muizon 1988): (0) no; (1) yes.
11. Middle sinus apex lobulated and decked edged (Muizon 1988): (0) no; (1) yes.
12. Supplementary expansion of pterygoid sinus in the sphenoidal region (Muizon 1988): (0) no; (1) yes.
13. Enlargement of the anterior sinus (Muizon 1988): (0) no; (1) yes.
14. Keel affecting the ventral surface of hamular processes (Muizon 1988): (0) no; 1, yes.

Ear bones

15. Parabullary ridge of periotic: (0) thin; (1) sturdy; (2) very sturdy.
16. Parabullary ridge of periotic: (0) not sturdy posteriorly; (1) sturdy posteriorly.
17. Anterior process of periotic: (0) anterodorsal angle rounded; (1) pointed.
18. Anterior process of periotic: (0) in the same plane as the body of periotic; (1) ventrally bent.
19. Posterior process of periotic: (0) ventrally bent; (1) in the same plane as the body of periotic.
20. Posterior bullar facet of periotic: (0) without striation; (1) with striation.
21. Internal auditory meatus of periotic: (0) circular; (1) elliptical.
22. Aperture for cochlear aqueduct of periotic: (0) dorsally open; (1) dorsomedially or medially open.
23. Tympanic bulla laterally compressed (Kasuya 1973): (0) no; (1) yes.
24. Loss of lateral groove of tympanic bulla (Muizon 1988): (0) no; (1) yes.

Hyoid bones

25. Fused thyrohyal and basihyal: (0) arched; (1) angle shaped.

Mandible

26. Length of mandibular symphysis. (percentage value of symphysis length in respect to total length of mandible): (0) elongated (> 20 %); (1) short (< 20 %).

27. Elevation of coronoid crest: (0) very marked; (1) marked; (2) low; (3) absent.

Teeth

28. Increase in the size of teeth: (0) no; (1) moderate; (2) marked
29. Decrease in the size of teeth: (0) no; (1) yes;
30. Number of teeth in each tooth row: (0) > 18; (1) 18-13; (2) <13.

Anterior limb

31. Anterior angle of scapula: (0) strongly expanded anteriorly producing the large supraspinous fossa; (1) weakly expanded anteriorly.
32. Posterior angle of scapula: (0) strongly extended posteriorly; (1) weakly extended posteriorly.
33. Coronoid process of scapula: (0) not expanded distally; (1) expanded distally.
34. Acromion of scapula: (0) narrow and not expanded distally; (1) triangular due to its dorsodistal expansion.
35. Distal migration of deltopectoral tuberosity of humerus (Muizon 1988): (0) no; (1) yes.
36. Head of humerus enlarged and spherical (Barnes 1990): (0) no; (1) yes.
37. Olecranon process of ulna: (0) very low; (1) sturdy.

Vertebrae

38. Loss of triangular morphology of the transverse apophysis of lumbar vertebrae (Muizon 1988): (0) no; (1) yes.
39. Number of lumbar vertebrae: (0) 9-11; (1) 12-14; (2) 14-19.
40. Number of caudal vertebrae: (0) 21-24; (1) 25-44

Results. The output of PAUP analysis was a single cladogram of 74 steps with a consistency index (CI) of 0.6486 (reduced to 0.5873 after excluding uninformative characters), and retention index (RI) of 0.6941 (Fig. 7). Within this cladogram *Arimidelphis* is placed within a wide clade also including *Hemisyntrachelus*, *Orcinus*, *Pseudorca*, *Feresa*, *Globicephala*, *Grampus* and *Peponocephala*. The apomorphies of this clade are: the short rostrum, the lateral margins of premaxillae parallel or anteriorly diverging at apex of rostrum, and the antorbital process globose and robust. This clade, including genera previously referred to both Orcininae Wagner, 1846 and Globicephalinae Gray, 1850, is here all referred to Orcininae, the firstly named subfamily. Within the Orcininae, *Peponocephala* is the sister group of all other genera characterized by: a deep and wide antorbital notch and 18-30 large teeth in each tooth row. Even if placed within this clade, *Arimidelphis* does not show the derived condition of the teeth; while the antorbital process it very robust, as already emphasized above. The angular shape of the fused hyoid bones and the elevation of the coronoid process of the mandible (interpreted as reversion) place *Arimidelphis* in the same clade as *Hemisyntrachelus*, *Orcinus* and *Pseudorca*. These three last genera also exhibit the plesiomorphic conditions of low number of lumbar and caudal vertebrae, two characters not observed in *Arimidelphis* (vertebrae missing on the only known specimen). *Arimidelphis*, *Orcinus* and *Pseudorca* show a more pronounced elevation of the coronoid process relatively to *Hemisyntrachelus,* and for this character are considered as a more derived group. Considering the reversals of the *Hemisyntrachelus-Arimidelphis-Orcinus-Pseudorca* clade, the lack of two Orcininae apomorphies in *Hemisyntrachelus* (the short rostrum and the deep and wide antorbital notch) and the primitive scapula of *Pseudorca* and *Orcinus*, it is possible that a more detailed research of characters and/or new fossil specimens might give these genera a more basal position within the delphinids.

Other results of this cladistic analysis are the placement of *Orcaella* outside the Orcininae, despite some similarities with *Orcinus*, and the position of *Grampus* near *Globicephala,* clearly inside the Orcininae. These two last genera share with *Feresa* the strong lateral compression of the tympanic bulla (Kasuya 1973), the low coronoid process of the mandible and the further increase in size and decrease in number for the teeth. *Tursiops* and *Delphinus* (two genera of Delphininae) appear clearly distinct from Orcininae and mainly characterized by apomorphies concerning the ventral sinuses and the ear bones.

Conclusion

The performed phylogenetic analysis places *Arimidelphis* in the same clade as the extinct genus *Hemisyntrachelus* and the living *Orcinus* and *Pseudorca*. Concerning the feeding apparatus, *Arimidelphis* appears more specialized than *Hemisyntrachelus* for the shorter rostrum and the more robust mandible. These characters are shared with the living *Orcinus* and *Pseudorca*; as these two genera, *Arimidelphis* probably had a strong bite for seizing relatively large preys. The presence of relatively slender hyoid bones, that might exclude suction feeding, could corroborate this shark-like feeding hypothesis. Thick and wide basihyal and thyrohyal, as observed in ziphiids and physeterids, were interpreted as adaptations for suction feeding (Heyning & Mead 1996; Werth 2000). Nevertheless, I observed slender hyoid bones in *Grampus*, *Globicephala,* and *Feresa,* three living delphinids with low coronoid process of mandible and strong reduction of number of teeth, features probably related to a certain degree of suction feeding.

Arimidelphis confirms the high diversification of the delphinids in the Mediterranean during the Pliocene: in addition to *Arimidelphis*, at least six delphinid genera and height species based on significant cranial remains have been identified (Bianucci 1996). The recorded genera are: the living *Orcinus*, *Tursiops*, *Stenella*, and possibly *Globicephala* and the fossil *Hemisyntrachelus* and *Astadelphis*. An even more diversified delphinid fauna is actually indicated by numerous isolated periotics collected from Tuscany (Central Italy). This high Pliocene delphinid diversification may be a consequence of the complete recolonization of the Mediterranean after the Messinian salinity crisis. Delphinids probably of Atlantic origin may have rapidly occupied the trophic niches available after the extinction of the Miocene fauna. This condition may have favored a fast diversification of the modern delphinids in the Mediterranean. However, because of the fragmentary and poorly studied delphinid remains of the extramediterranean area, it is not possible now to delineate an exhaustive picture of Pliocene delphinid distribution and the possible role of the Mediterranean in their speciation and radiation.

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