

A new kentriodontine dolphin from the middle Miocene of Portugal

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A nearly complete skull, a partial left scapula, five lumbar vertebrae, and some fragments of ribs of a medium-sized kentriodontid dolphin (Cetacea, Odontoceti) discovered in the middle Miocene of Setúbal Peninsula, Lower Tagus Basin, Portugal, are herein assigned to a new genus and species, *Tagicetus joneti*. Within the grade-level family Kentriodontidae, the new taxon is referred to the specifically and ecologically diversified subfamily Kentriodontinae, essentially defined by a well-developed posterolateral projection of the nasal. The elongated rostrum, the constriction of the asymmetric premaxillae at the base of the rostrum, the anteriorly elongated palatines, and the elevated vertex of *T. joneti* suggest closer affinities with the larger, more derived *Macrokentriodon morani*, from the middle Miocene of Maryland (USA). Among other features, *T. joneti* differs from the latter in having more numerous maxillary teeth and shorter zygomatic processes of the squamosals. Besides providing additional indications about the evolutionary trends within the Kentriodontinae, this occurrence constitutes the first record of the subfamily from the east coast of the North Atlantic based on a nearly complete skull. Considering their morphological diversity and wide geographic range, the Kentriodontinae may have constituted one of the dominant groups of Miocene oceanic dolphins.

Key words: Cetacea, Odontoceti, Kentriodontidae, Miocene, Lower Tagus Basin, Portugal.

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Introduction

The grade-level family Kentriodontidae is a diversified group of small to moderately large-sized dolphins recorded mostly from the Miocene of numerous regions of the world (for a review, see Ichishima et al. 1994). Three subfamilies are currently distinguished within the family: Kentriodontinae Slijper, 1936, Pithanodelphininae Barnes, 1985, and Lophocetinae Barnes, 1978 (Dawson 1996a; Fordyce and Muizon 2001). The kentriodontines are the most diversified taxonomically, with four to five genera based on well-preserved cranial material (True 1912; Kellogg 1927; Barnes and Mitchell 1984; Ichishima 1994; Dawson 1996b; Bianucci 2001).

Fossil odontocetes from the Atlantic-facing Lower Tagus Basin, in Portugal, have been mentioned several times, but rarely described in detail (review in Estevens 2000). Among these, the well-preserved skull and associated vertebrae found in the Miocene of Penedo and preliminarily referred to *Eurhinodelphis* cf. *cristatus* (du Bus, 1872) by Mata (1962–63) belong instead to a new lophocetine kentriodontid (Estevens 2003a; Lambert 2004). The periotics and associated fragmentary remains from the Miocene of Costa de Caparica originally reported as a eurhinodelphinid by Jonet (1980–81) also show affinities with the kentriodontids (Estevens 2003a), namely with *Kentriodon* Kellogg, 1927. Both of

these occurrences are currently being reviewed by one of us (ME). More recently, Estevens and Antunes (2002, 2004) reported a few fragmentary remains of odontocetes from the Miocene of the Lower Tagus Basin, among which there were some rostral and mandibular fragments, as well as isolated teeth, tentatively assigned to kentriodontids (cf. *Rudicetus* sp., cf. *Macrokentriodon* sp. and an undetermined lophocetine). Finally, Estevens (2003a, b) summarized the occurrence of these and other kentriodontid specimens in the Miocene of Setúbal Peninsula and Lisbon Region (both within the Lower Tagus Basin area), also alluding briefly to the specimen formally described in this paper.

The new specimen was discovered by RS at Penedo Norte, Setúbal Peninsula, Lower Tagus Basin, Portugal in July 1977. It comprises a nearly complete skull, a partial left scapula, five lumbar vertebrae, and some fragments of ribs (all assigned to one animal), which constitute the holotype of a new genus and species of kentriodontine dolphin.

Material and methods

Preparation of the specimen.—Prior to the preparation, a large portion of the skull and most of the postcranial elements were

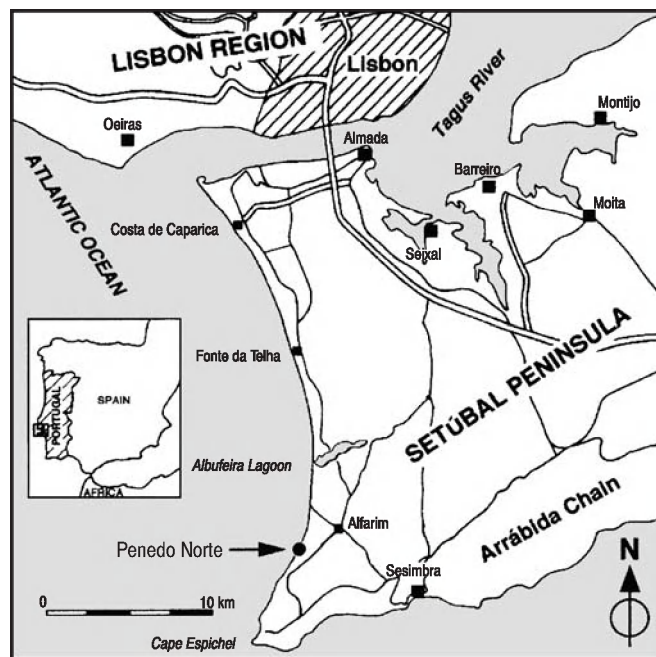


Fig. 1. Geographic location of the type locality Penedo Norte, Setúbal Peninsula, Lower Tagus Basin, Portugal (modified from Antunes et al. 1997).

surrounded by hardened sediment, constituted mostly of medium to coarse sand grains mixed with poorly-rounded, isolated fine gravel elements, in a light gray to white, slightly glauconitic, clayey matrix. The specimen was prepared by OL using mostly mechanical clearing (mainly with a pneumatic pen), and was also subjected to several water immersions to remove part of the thinner matrix. One vertebra, the scapula, and several fragments of vertebral apophyses and ribs were thus detached from the block, but other postcranial elements could not be separated from the skull, to which they remain attached, partially hiding the right lambdoidal crest.

Institutional abbreviations.—CMM, Calvert Marine Museum, Solomons, Maryland, USA; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; M, Fossil mammals collection of types and figured specimens of IRSNB; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Systematic palaeontology

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Delphinoidea Gray, 1821 *sensu* Flower, 1864

Family Kentriodontidae Slijper, 1936 *sensu* Barnes, 1978

Subfamily Kentriodontinae Slijper, 1936

Included genera: *Delphinodon* Leidy, 1869; *Kentriodon* Kellogg, 1927;

Kampholophos Rensberger, 1969; *Macrokentriodon* Dawson, 1996b; *Rudicetus* Bianucci, 2001; and *Tagicetus* gen. nov.

Remarks.—While the best known members of the Kentriodontinae show obvious similarities at the level of the face, the diagnosis of this subfamily is generally based on characters for which the polarity is difficult to determine (e.g., Barnes 1978; Muizon 1988a; and discussion below). More detailed data about the basicranium and the ear bones in a greater number of species supposed to belong in this subfamily would probably restrict the diagnosis of this taxon. From the previously published diagnoses cited above, only one character might be considered as a synapomorphy of the group, namely the posterolateral projection of the nasal between the frontal and the maxilla, first proposed by Muizon (1988a). However, the intraspecific variability of this character in *Macrokentriodon morani* Dawson, 1996b may weaken its value as a synapomorphy. A revision of the phylogenetic relationships between taxa within the Kentriodontinae and/or Kentriodontidae is beyond the scope of this paper though.

The kentriodontid genera *Belonodelphis* Muizon, 1988b and *Incacetus* Colbert, 1944 were also referred by Fordyce and Muizon (2001) to the subfamily Kentriodontinae. The low level of information about the vertex of these two taxa makes that attribution questionable though, for which they are not included in the differential diagnosis of the new genus and species presented below.

Genus *Tagicetus* nov.

Etymology: From *Tagus*, the Latin name of the river with the same English spelling (in allusion to the Lower Tagus Basin as the area of provenance of the holotype); and *cetus*, the Latin word for whale.

Diagnosis.—Same as for the type and only known species.

Tagicetus joneti gen. et sp. nov.

Figs. 2–7, Tables 1, 2.

Holotype and only known specimen: IRSNB M.1892, a nearly complete skull missing the apex of the rostrum, all teeth, the left supraorbital process, the left lambdoidal crest, the left squamosal, the lateral laminae and hamular processes of the pterygoids, some other thin fragments of the basicranium, and the earbones. The anterior part of the rostrum is transversely crushed, precluding width measurements from a level 100 mm anterior to the antorbital notches. The skull is associated to five lumbar vertebrae (four of which still attached to the right posterolateral region of the skull), two fragments of ribs, and a partial left scapula.

Type locality: Known as Penedo Norte in recent literature, corresponds to the northern section of the coastal cliffs at Bicas beach (38°27'N, 9°11'W), located some 30 km SW of Lisbon in southwestern Setúbal Peninsula, Lower Tagus Basin, Portugal (Fig. 1).

Type horizon: Judging from the adhering matrix, this specimen probably came from bed 8 or 9 of the section published by Antunes et al. (1997) for the type locality. According to these authors, these beds were ⁸⁷Sr/⁸⁶Sr dated at 13–11.5 Ma and consequently correlated with the N12–N13 planktonic foraminifera zones of Blow; they may thus correspond to the depositional sequence S2 of Antunes et al. (2000), which ranges from 12.7 to 11.6 Ma, late Serravallian, middle Miocene. The same beds constitute a condensed section that accumulated abundant vertebrate remains ranging in age from the late Burdigalian–Langhian to the Serravallian (N9–N13 of Blow), among which are included sev-

eral odontocetes, but also some mysticetes and even scarce sirenians and phocids (Estevens 2003a).

Taphonomy: The skull was extracted from the outcrop with five lumbar vertebrae and several fragments of ribs piled up against the right posterolaterodorsal side of the cranium. All vertebral apophyses and neural spines were still connected to the centra, except for one apophysis, slightly shifted from its original position. The left scapula was wedged between the paroccipital process of the right exoccipital and the corresponding basioccipital crest.

Etymology: Dedicated to the late Simon Jonet (13.11.1902–29.01.1987), a Belgian palaeontologist who lived in Portugal during the 1960s–1980s, having then published mostly on the Miocene fish faunas of that country (but likewise on fossil cetaceans), and who introduced RS to the outcrops of the Penedo area.

Generic and specific diagnosis.—*Tagicetus joneti* gen. et sp. nov. is a moderate-sized kentriodontine with a cranium length close to *Rudicetus*, differing from *Delphinodon*, *Kampholophos*, *Kentriodon*, *Macrokentriodon*, and *Rudicetus* by the long and wide posterolateral projection of the nasal on the vertex; from *Delphinodon*, *Kampholophos*, *Kentriodon*, and *Rudicetus* by the premaxilla distinctly wider than the maxilla in the rostrum (anterior to a constriction at the level of the antorbital notch) and the elevated vertex (with anterior surface of the premaxilla reaching a slope of 65 degrees); from *Delphinodon*, *Kampholophos*, *Macrokentriodon*, and *Rudicetus* by the shortened zygomatic process of the squamosal (in which the dorsoventrally thick apex ends abruptly); from *Delphinodon*, *Kentriodon*, and *Rudicetus* in that the rostrum is more than twice as long as the neurocranium; and by the elongated fossa for the hamular lobe of the pterygoid sinus reaching significantly beyond the antorbital notches anteriorly; from *Delphinodon* and *Kentriodon* by the lower number of alveoli by length unit; and from *Macrokentriodon* by the considerably smaller size and the less prominent and more laterally located lambdoidal crests.

Description and comparisons

Skull

The skull has a total preserved length of 442 mm; the missing distalmost part of the rostrum, probably corresponding to the premaxillary portion, is estimated at about 15–25 mm, thus giving the rostrum a total estimated length of 327–337 mm (Figs. 2, 3). The rostrum is therefore more than 2.3 times longer than the cranium, and the ratio between the width of the skull at the level of the preorbital process and the length of the rostrum is less than 0.43 (see Table 1). The rostrum is thus proportionately much longer than in *Delphinodon divi-dum* True, 1912, distinctly longer than in *Kentriodon pernix* Kellogg, 1927 and *Rudicetus squalodontoides* (Capellini, 1878), and somewhat closer to the length in *Macrokentriodon morani* Dawson, 1996b.

Premaxilla.—The premaxillae flatten and widen rapidly in the region immediately anterior to the antorbital notches,

Table 1. Measurements (in mm) on the holotype skull IRSNB M.1892 of *Tagicetus joneti* gen. et sp. nov. from the middle Miocene of Portugal; e, estimated measurement.

	IRSNB M.1892
total length of the skull as preserved	442
length of the rostrum as preserved	312
length of the orbit	53
longitudinal distance between occipital condyles and preorbital processes	e140
longitudinal distance between posterior of bony nares and preorbital processes	79
longitudinal distance between anterior of supraoccipital and posterior of bony nares	22
maximal length of the frontals on the vertex	14
width of the rostrum at its base	e2x46 = 92
maximal width of the premaxillae at the rostrum base	47
width of the skull across the preorbital processes	e2x71 = 142
width of the skull across the postorbital processes	e2x83 = 166
maximal width of the right premaxillary sac fossa	28
width of the bony nares	27
width of the premaxillae at the posterior margin of the nasals	57
width of the nasals	42
minimal distance between maxillae across the vertex	37
length of the squamosal from zygomatic to post-glenoid process	39
distance between ventromedian margins of paroccipital processes of exoccipitals	77
width across the occipital condyles	61
width of the foramen magnum	32
height of the foramen magnum	32
maximal height of the cranium	134

reaching their maximal width at a level 20 mm anterior to the notches. Here, the right and left premaxillae are asymmetrical and present respective widths of 22 and 18 mm. The lateral margin of the better preserved right premaxilla is constricted anterior to the premaxillary foramen in a way similar to, but not as pronounced as, *Macrokentriodon*, and otherwise deeper than in *Kentriodon pernix* (USNM 10670) and *K. hobetsu* Ichishima, 1994 (condition stressed in the holotype of the latter by the convex lateral margin of the premaxillary sac fossae). The flat premaxillary sac fossae are anterolaterally margined by a shallow posterolateral sulcus and medially limited by a low ridge that runs along the anterior part of the bony nares. The ascent of the premaxillae towards the vertex is relatively abrupt; the slope reaches ca. 65 degrees, as in *Macrokentriodon*, and is steeper than in the other kentriodontines. Posterior to a weak constriction at the level of the bony nares, the premaxillae widen and thicken dorsolaterally, forming knob-like lateral projections at their proximal ends (similar to the ones seen in *Macrokentriodon* and *Rudicetus*). The premaxillae contact the anterolateral

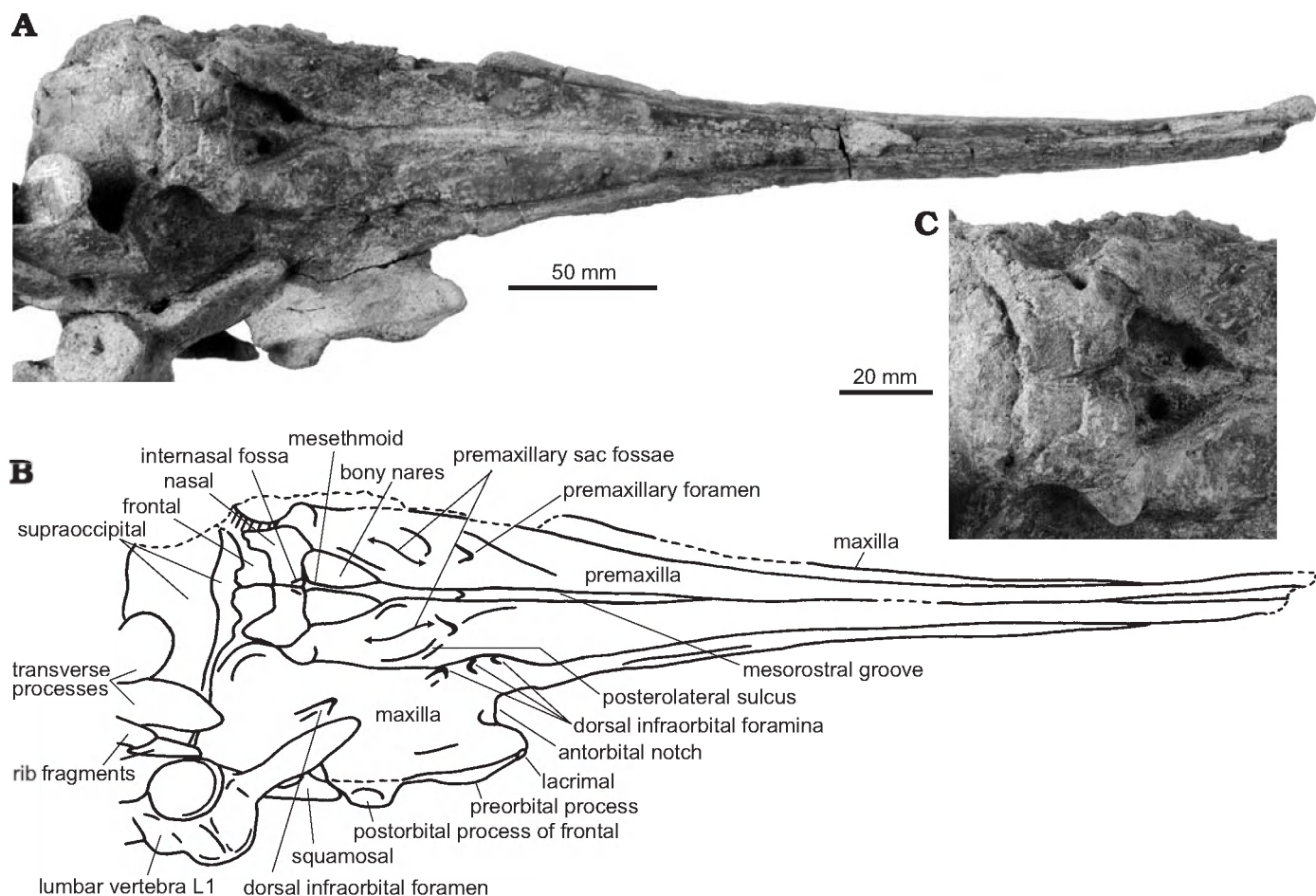


Fig. 2. *Tagicetus joneti* gen. et sp. nov., IRSNB M.1892, holotype, Middle Miocene of Portugal. **A.** Dorsal view of the skull. **B.** The explanatory drawing of the same; not to scale. **C.** Detail of the vertex in dorsal view.

corners of the nasals and taper towards the posterior end at about mid-length of each nasal.

Maxilla.—The preserved rostral portion of the right maxilla, probably nearly complete, bears about 22 alveoli in a 240 mm long alveolar row (Fig. 3). In its posterior portion, there are ca. 10 alveoli in a length of 100 mm, a number much lower than in *Kentriodon pernix* (18–22/100 mm), *K. obscurus* Barnes and Mitchell, 1984 (8/32 mm, Barnes and Mitchell 1984), and *Delphinodon dividum* (15/100 mm), closer instead to the ratio estimated by Bianucci (2001) for *Rudicetus squalodontoides* (30/280 mm = 10.7/100 mm). Most of the alveoli are worn and poorly delimited; the 8th, 9th and 10th from the posteriormost have a diameter of 5–5.5 mm and intervening septa of 6–6.5 mm; the length of these septa does not increase significantly towards the anterior end, reaching only about 7–8 mm apically. The alveoli are ventrolaterally directed and follow the lateral margin of the rostrum up to the posterior end of the alveolar row, where that margin thickens, becomes roughly square-shaped, and raises dorsally towards the deep, anterolaterally opened antorbital notch. Concomitantly with a rather narrow and pointed preorbital process, the antorbital notches are wide and overall squared-off. The maxillae are always nar-

rower than the premaxillae on the dorsal surface of the rostrum, especially some centimetres anterior to the antorbital notches, where the right maxilla is only 6 mm wide. At the level of the premaxillary constriction, the right maxilla is pierced by three dorsal infraorbital foramina, and a larger foramen also pierces the right supraorbital process of the maxilla further posteriorly (10 mm laterally to the premaxillary sac fossa). The posteromedial plate of the maxilla along the vertex is slightly concave, with a posterior margin that reaches only 12 mm beyond the level of the anteriormost margin of the supraoccipital.

Nasal.—The essentially symmetrical nasals occupy most of the vertex area, sending a wide posterolateral projection between the frontal and the maxilla, which is only 4 mm apart from the supraoccipital on the left side (Fig. 2). This projection is longer and/or wider than in all other kentriodontines in which this area is known. It bends the anterolateral corner of the otherwise transversely straight nasal-frontal suture almost at right angles. On the subhorizontal dorsal surface of the vertex, the nasals are slightly higher than the frontals (Fig. 3), and their anteromedial corners are excavated to form a distinct internasal fossa, more pronounced than in *Kentrio-*

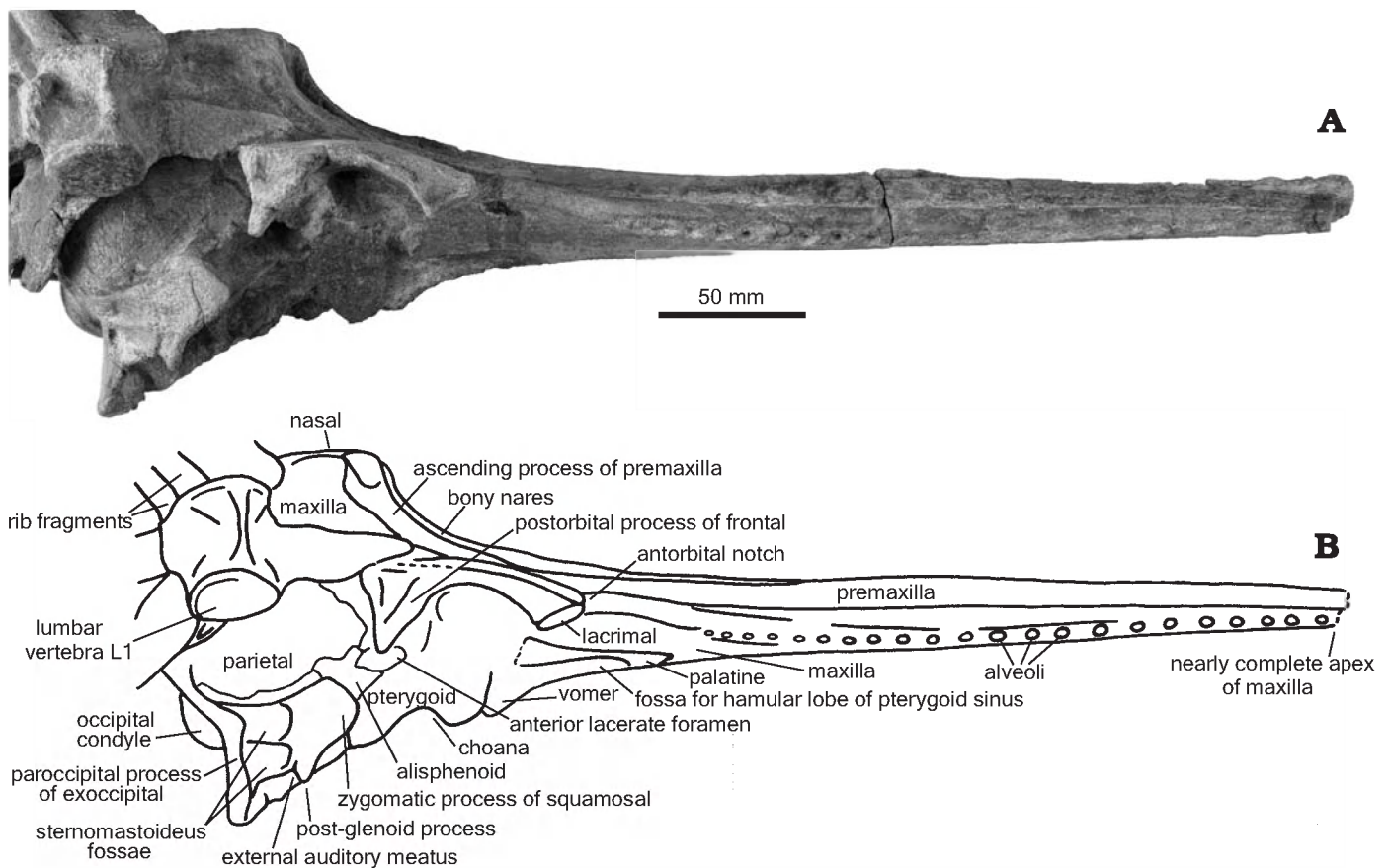


Fig. 3. *Tagicetus joneti* gen. et sp. nov., IRSNB M.1892, holotype, middle Miocene of Portugal. **A.** Right lateral view of the skull. **B.** The explanatory drawing of the same; not to scale.

don pernix and *Delphinodon dividum*. The anterior margin of the combined nasals is weakly concave anteriorly and the vertical notch is shallower than in *Kentriodon pernix* and *Delphinodon dividum*, and more similar to *Rudicetus* and *Macrokentriodon*.

Mesethmoid.—The posterior plate of the mesethmoid extends dorsally up to 10 mm below the dorsal surface of the nasals, at the anteromedial bottom of the internasal fossa. The keel of the mesethmoid separates two slightly asymmetrical bony nares (left is 2 mm wider than the right). At its anterior end, the mesethmoid is ossified at least until the level of the premaxillary foramina.

Frontal.—The maximal length occupied by the frontals at the vertex is 14 mm, measured along the mid-line. The contact with the thickened anterior margin of the supraoccipital on the vertex is irregular. The arched roof of the orbit is limited posteriorly by a relatively long (27 mm) and strong postorbital process (Fig. 3). In ventral view, the lateral margin of the frontal on the orbit is strongly concave (Fig. 4). The flat aspect of the ventral surface of the supraorbital process of the frontal in the area usually marked by the postorbital ridge (e.g., in *Kentriodon* and *Delphinodon*), and the anterior shift of the more median portion of that ridge,

might suggest a particularly developed postorbital lobe of the pterygoid sinus.

Supraoccipital.—After a distinct step, the supraoccipital shield is regularly convex towards the occipital condyles. As in other smaller kentriodontines, the lateral lambdoidal crests are low and, compared to the same element in the larger *Macrokentriodon* and *Kampholophos*, laterally displaced in dorsal view.

Occipital condyle.—The narrow and dorsally diverging occipital condyles protrude weakly from the posterior of the cranium, in a way similar to *Kentriodon pernix*. The foramen magnum has a pointed dorsal margin.

Lacrimal-jugal.—In lateral view, the lacrimal is exposed for a length of 19 mm anteroventrally to the preorbital process of the frontal. Ventrally, the lacrimal is partially fused with the jugal. The ventral surface of the jugal is hollowed out by a shallow fossa posterior to the antorbital notch, which might correspond to the preorbital lobe of the pterygoid sinus (Fig. 4).

Palatine.—The palatines are considerably elongated anteriorly, reaching 47 mm beyond the level of the antorbital notches, where the relatively pointed apices of these bones are

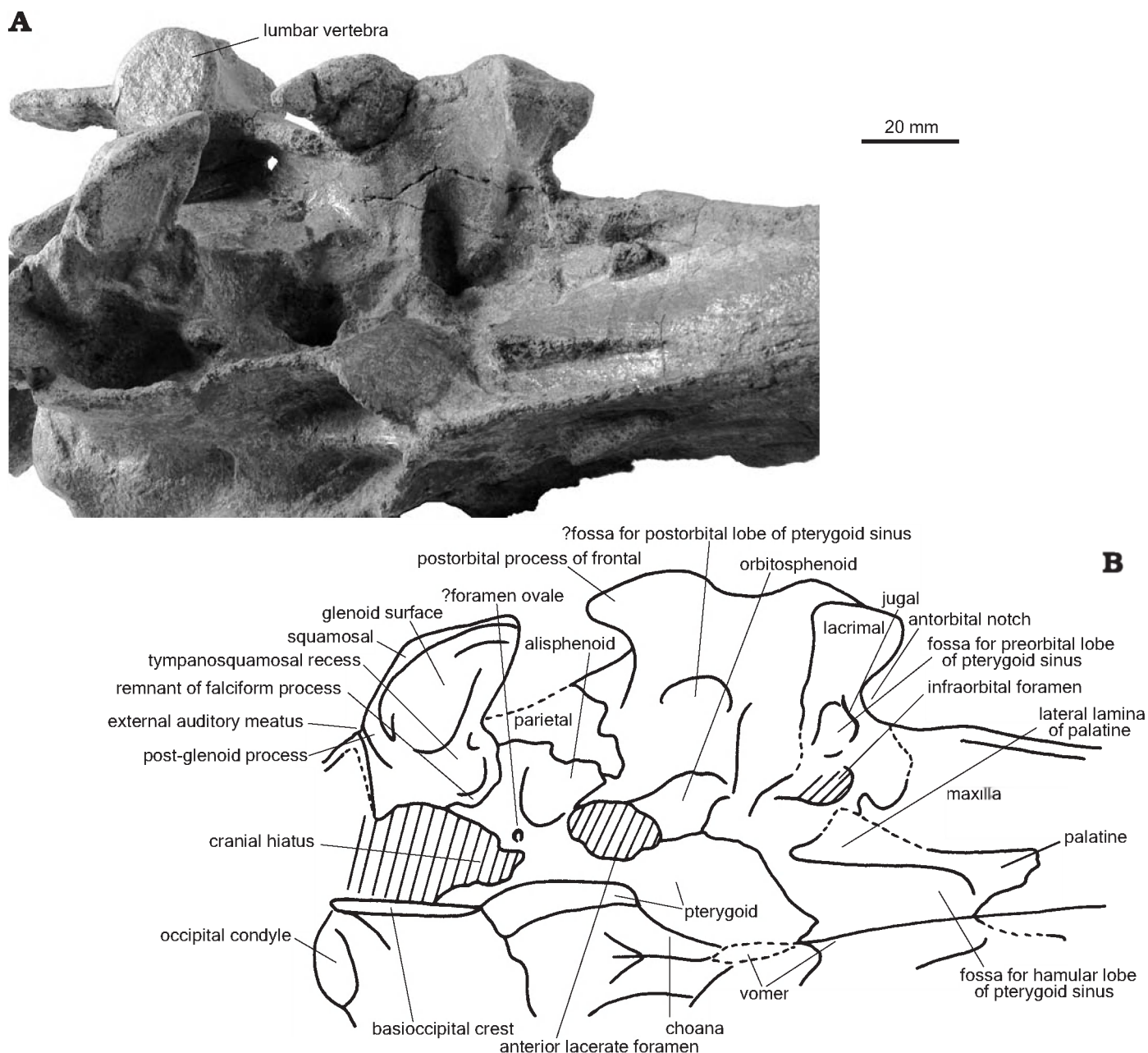


Fig. 4. *Tagicetus joneti* gen. et sp. nov., IRSNB M.1892, holotype, middle Miocene of Portugal. **A.** Ventrolateral view of the right part of the cranium. **B.** The explanatory drawing of the same; not to scale. The broken lines indicate missing elements or hidden sutures between bones.

separated by ca. 19 mm. The fossae for the hamular lobes of the pterygoid sinus deeply excavate the palatines, resulting in distinctive lateral laminae, which extend posteriorly until the level of the anterior margin of the infraorbital foramen (Fig. 4). The apex of the right pterygoid sinus fossa is located more than 33 mm anterior to the antorbital notch; it is longer than in *Rudicetus*, *Delphinodon dividum*, *Kentriodon pernix*, and *K. hobetsu*, and otherwise more similar to *Macrokentriodon* and *Kentriodon obscurus*.

Squamosal.—The zygomatic process of the right squamosal is short, laterally compressed, with a blunt anterior corner

separated by 15 mm from the postorbital process of the frontal (Fig. 3). The zygomatic processes of *Delphinodon dividum*, *Kampholophos*, *Macrokentriodon*, *Rudicetus*, *Kentriodon hobetsu*, and, in a lesser extent, those of *K. pernix* are comparatively more elongated anterodorsally. The tympanosquamosal recess is deeper close to the short, antero-posteriorly flattened post-glenoid process, and constitutes the medial margin of the glenoid surface for the whole length of the latter. The external auditory meatus is narrow. Although broken at its base, the falciform process was probably narrow and thin, a condition that suggests the absence of a contact between the squamosal and the non-preserved lateral lamina

of the pterygoid. The posterolaterally exposed sternomastoid fossae are long and high.

Alisphenoid.—The limits of the foramen ovale are difficult to distinguish and the loss of some of the thin bones from the basicranium (mainly the parietal) have artificially connected it to the likewise enlarged cranial hiatus (Fig. 4).

Orbitosphenoid.—The surface of the orbitosphenoid is only slightly concave towards the anterior lacerate foramen. The margins of the latter, made of very thin bone, are probably not complete (Fig. 4).

Postcranial elements

Lumbar vertebrae (Figs. 5, 6).—The ratio between posterior width and length of the centrum ranges from 0.71 to 0.81 (Table 2), values close to the first lumbar of *Kentriodon pernix* and the last of *Kampholophos*, but lower than in other kentriodontids such as *Belonodelphis peruanus* Muizon, 1988b and *Atocetus iquensis* Muizon, 1988b.

The neural arch is relatively low as compared to the high and anterodorsally bent neural spine. In fact, the distal part of the neural spine is more anteriorly projected (Fig. 6) than in the known lumbar of *Kentriodon pernix* and *Belonodelphis peruanus*. The metapophyses are well-developed; the transverse processes are long and wide, presenting an antero-posterior development at approximately two-thirds of their length. A somewhat similar condition is observed at the posterior lumbar of *Atocetus iquensis* (Muizon 1988b: fig. 90) and some of the anterior lumbar of the extant monodontid *Monodon* Linnaeus, 1758.

All preserved epiphyses are fused to the centra. At least in two vertebrae, the ankylosis is not complete and the suture with the centrum is still visible (state C according to Galatius and Kinze 2003). These authors found that the epiphyseal ankylosis of *Phocoena phocoena* (Linnaeus, 1758) started among the cervical vertebrae, then proceeded in the caudal region, and finally ended in the thoracics and lumbar (following approximately the same pattern as in other studied cetacean species). However, the timing of the process appears to vary widely: in *P. phocoena*, for example, the complete

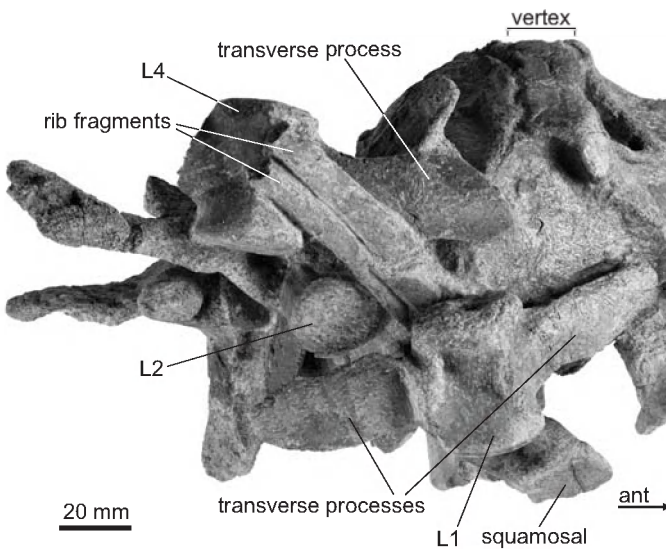


Fig. 5. *Tagicetus joneti* gen. et sp. nov., IRSNB M.1892, holotype, Middle Miocene of Portugal. Back of the cranium in posterolaterodorsal view, with attached lumbar vertebrae and rib fragments. The numbers of the lumbar do not necessarily correspond to their position, exact and relative, on the vertebral column.

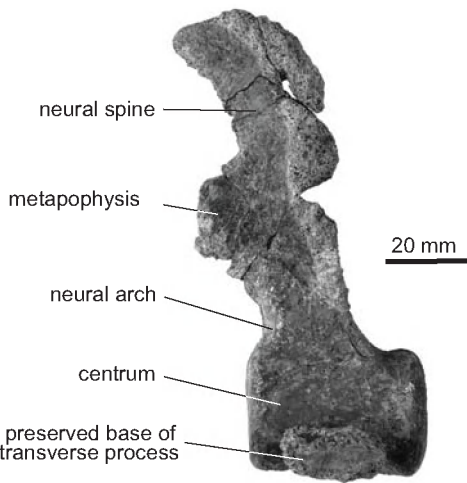


Fig. 6. *Tagicetus joneti* gen. et sp. nov., IRSNB M.1892, holotype, Middle Miocene of Portugal. Detached lumbar vertebra in left lateral view (L5 in Table 2).

Table 2. Measurements (in mm) on the holotype lumbar vertebrae IRSNB M.1892 of *Tagicetus joneti* gen. et sp. nov. from the Middle Miocene of Portugal; i. incomplete measurement; e. estimated measurement.

	L1	L2	L3	L4	L5
length of centrum	i36	–	i39	41	42
anterior width of the centrum	30	–	–	29	32
anterior height of the centrum	e31	–	–	i28	e31
posterior width of the centrum	–	e30	–	29	34
posterior height of the centrum	–	–	–	–	31
length of the transverse process	e51	58	–	58	–
maximal anteroposterior width of the transverse process	–	23	–	26	–

ankylosis is found in some 6-year-old specimens, while other 22-year-old specimens do not show that condition. The lumbar vertebrae of IRSNB M.1892 reveal that this individual was not fully physically mature in the sense of Galatius and Kinze (2003), although it could have been already adult.

Scapula.—The scapula has a deep supraspinous fossa laterally margined by the well-developed acromion, of which only the wide and thin base is preserved (Fig. 7). The broken coracoid process is less continuous with the margins of the 22 mm long glenoid fossa than in *Delphinodon dividum*, presenting instead a more distinct angle as in *Kentriodon* and *Atocetus* Muizon, 1988b (see Muizon 1988b: 180). The cur-

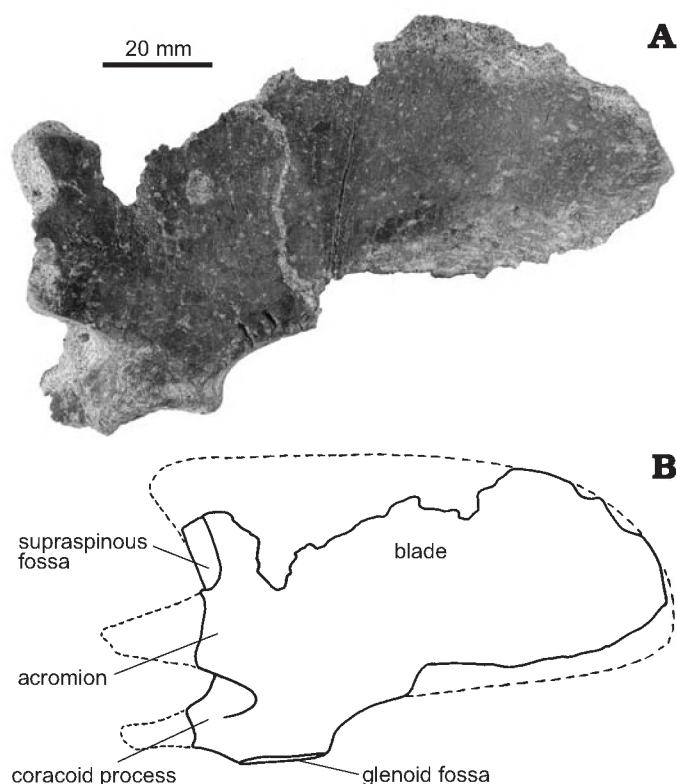


Fig. 7. *Tagicetus joneti* gen. et sp. nov., IRSNB M.1892, holotype, Middle Miocene of Portugal. **A.** Left scapula in lateral view. **B.** Reconstruction of the left scapula in lateral view, not to scale, with broken line indicating missing elements reconstructed on the basis of *Kentriodon* and *Delphinodon*.

vature of the posteroventral margin of the blade is strong; that margin becomes nearly parallel to the margins of the glenoid fossa as in *Squalodon* Grateloup, 1840 and *Notocetus* Moreno, 1892 (see Muizon 1987: fig. 13). This condition differs from the other known kentriodontid scapulae [*Atocetus*, *Delphinodon*, *Kentriodon*, and *Liolithax pappus* (Kellogg, 1955)], which show a less pronounced curvature; among extant delphinoids, it is closer to *Delphinapterus* Lacépède, 1804, *Orcaella* Gray, 1866, and *Pseudorca* Reinhardt, 1862.

Discussion

The presence of an internasal fossa is the most frequently observed character in members of the grade family Kentriodontidae (Muizon 1988a), which is otherwise only rarely encountered in other odontocete families (e.g., the extant ziphiids *Mesoplodon* and *Hyperoodon*). The internasal fossa is weakly pronounced in *Delphinodon* and *Kentriodon*, and totally absent in the holotypes of *Macrokentriodon morani* and *Rudicetus squalodontoides*, but the observation of that feature in *Tagicetus joneti*, added to the wide, knob-like posterior extremities of the premaxillae and the likely loss of a contact between the falciform process of the squamosal and

the lateral lamina of the pterygoid, suggests kentriodontid affinities for this species.

The essentially symmetrical skull is also often recognized as characterizing kentriodontid genera (Barnes 1978; Ichishima 1994; Bianucci 2001). That condition, however, is very likely a symplesiomorphy, not definitely recorded in all forms within this family (e.g., pithanodelphinines with asymmetric premaxillae, Barnes 1985). Whilst the left premaxillary sac fossa is only partially preserved on the holotype of *Tagicetus joneti*, the right premaxilla is notably wider than the left in the basal area of the rostrum. That feature, also observed in *Macrokentriodon* and *Hadrodelphis* Kellogg, 1966, is associated here with a flattening of both premaxillae. When observing the soft anatomy of the forehead of extant delphinids (e.g., x-ray tomography of *Delphinus* Linnaeus, 1758 and *Tursiops* Gervais, 1855 in Cranford et al. 1996: figs. 3a, 4a), the melon is closely fitted to the dorsal surface of the premaxillae at the rostrum base. Therefore, the flattening described in *Tagicetus joneti* is likewise supposed to be an accommodation feature for the melon. It is well-known that the asymmetry of the bony structures in the odontocete face is related to the asymmetry of the overlying soft structures, which are themselves linked to the production of high frequency sounds for echolocation (review in Mead 1975; Heyning 1989; Cranford et al. 1996). Heyning (1989: fig. 13) showed that even the melon may be asymmetric; in a specimen of *Mesoplodon bidens* (Sowerby, 1804), this structure was distinctly offset to the right at the level of the antorbital notches. It is therefore supposed that the wider right premaxilla in *Tagicetus joneti* would likewise reflect a right offset of the melon. Analogously, the widened right premaxillary sac fossa of *Ziphius cavirostris* Cuvier, 1823 is closely related to the greater development of the nasal plug lying on it (Heyning 1989).

The holotype of *Macrokentriodon morani* lacks the posterolateral projection of the nasals that confers a curved or angular shape to the nasal-frontal suture, a feature previously thought to define the Kentriodontinae (Muizon 1988a). However, the skull USNM 517874, clearly referable to *Macrokentriodon morani*, shows a pronounced posterolateral projection of the nasal. Even if this character is intraspecifically variable (e.g., among *Kentriodon pernix* skulls, the projection is longer in USNM 10670 than in the holotype), its great development in *Tagicetus joneti* points definitely to its inclusion in the Kentriodontinae. The general morphology of the vertex, flat and wide, is also similar to other kentriodontines. Previously used to refer taxa to this subfamily (Dawson 1996b; Bianucci 2001), that character may in fact be primitive, as more archaic odontocetes such as *Waipatia* Fordyce, 1994 or *Squalodon* Grateloup, 1840 have a somewhat similar vertex.

Within the subfamily, *Tagicetus joneti* has a cranium size relatively close to those of *Delphinodon dividum* and *Rudicetus squalodontoides*. Its rostrum is much longer than the former though and slightly longer than the latter; whilst its vertex is also more elevated. Those two characters (added to the constriction of the premaxillae at the level of the ant-

orbital notches associated with an obvious widening anteriorly and the elongated palatines and pterygoid sinus fossae) make it resemble instead the much bigger *Macrokentriodon morani*. Apart from its size, *Tagicetus joneti* differs from *Macrokentriodon morani* in having narrower frontals on the vertex, more numerous maxillary teeth, and a much shorter zygomatic process of the squamosal. The prominent lambdoidal crests of *Macrokentriodon morani* may be related to its larger size (cf., the well-developed crests of the equally large lophocetine kentriodontid *Hadrodelphis calvertense* Kellogg, 1966).

The relatively elevated vertex, the wide and long postero-lateral projections of the nasals, and the anterior elongation of the palatines and the pterygoid sinus fossae are features that place *Tagicetus joneti* as one of the most specialized kentriodontines. It could be thought that the anterior extension of the palatines is related to a lengthening of the rostrum, but *Rudicetus squalodontoides* has an equally long rostrum and conversely short palatines. The elevation of the vertex in *Tagicetus joneti* and *Macrokentriodon morani*, not associated to a transverse pinching (as in some lophocetines), supports the idea of a lineage distinct from that leading to *Hadrodelphis calvertense*.

Conclusions

The description of *Tagicetus joneti* from a rather complete specimen reasserts the Kentriodontinae as the best-known subfamily within the Kentriodontidae. Differing from similar-sized kentriodontines by, among other characters, its elongated rostrum, *T. joneti* further supports the substantial ecological diversity within the subfamily, a feature already stressed by the large size of *Macrokentriodon morani* (Dawson 1996b). This diversity, together with the wide geographic range of the kentriodontines, might place them as one of the dominant groups of Miocene oceanic dolphins, with a pattern close to extant delphinids. Such a pattern will probably lead to the description of other kentriodontine taxa in less extensively studied areas of the world.

So far, the described Portuguese kentriodontid record derives mostly from middle Miocene sediments (Estevens and Antunes 2004; this paper), and may provide an eastern North Atlantic complement to the rich record long known from the east coast of North America (Ichishima et al. 1994; Dawson 1996b).

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