A new kentriodontine dolphin from the middle Miocene of Portugal

OLIVIER LAMBERT, MÁRIO ESTEVENS, and RICHARD SMITH


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 Esteves 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 (Esteves 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 (Esteves 2003a), namely with *Kentriodon* Kellogg, 1927. Both of these occurrences are currently being reviewed by one of us (ME). More recently, Esteves 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. *Radicetus* sp., cf. *Macrokentriodon* sp. and an undetermined lophocetine). Finally, Esteves (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...
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 Delphinoidae Gray, 1821 sensu Flower, 1864
Family Kentriodontidae Slijper, 1936 sensu Barnes, 1978
Subfamily Kentriodontinae Slijper, 1936

Included genera: Delphinodon Leidy, 1869; Kentriodon Kellogg, 1927; Tagicetus gen. nov.

Tagicetus Joneti gen. et sp. nov.

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

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. 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.

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 Macroentriodon 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.
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 postero-lateral dorsal 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 postero-lateral 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 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 divisum 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, 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, Delphinodon, Kentriodon, and other kentriodontines. Posterior to a weak constriction at the level of the bony nares, the premaxillae widen and thicken 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

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.

<table>
<thead>
<tr>
<th>Measurement Description</th>
<th>IRSNB M.1892</th>
</tr>
</thead>
<tbody>
<tr>
<td>total length of the skull as preserved</td>
<td>442</td>
</tr>
<tr>
<td>length of the rostrum as preserved</td>
<td>312</td>
</tr>
<tr>
<td>length of the orbit</td>
<td>53</td>
</tr>
<tr>
<td>longitudinal distance between occipital condyles and preorbital processes</td>
<td>e140</td>
</tr>
<tr>
<td>longitudinal distance between posterior of bony nares and preorbital processes</td>
<td>79</td>
</tr>
<tr>
<td>longitudinal distance between anterior of supraoccipital and posterior of bony nares</td>
<td>22</td>
</tr>
<tr>
<td>maximal length of the frontals on the vertex</td>
<td>14</td>
</tr>
<tr>
<td>width of the rostrum at its base</td>
<td>e2×46 = 92</td>
</tr>
<tr>
<td>maximal width of the premaxillae at the rostrum base</td>
<td>47</td>
</tr>
<tr>
<td>width of the skull across the preorbital processes</td>
<td>e2×71 = 142</td>
</tr>
<tr>
<td>width of the skull across the postorbital processes</td>
<td>e2×83 = 166</td>
</tr>
<tr>
<td>maximal width of the right premaxillary sac fossa</td>
<td>28</td>
</tr>
<tr>
<td>width of the bony nares</td>
<td>27</td>
</tr>
<tr>
<td>width of the premaxillae at the posterior margin of the nasals</td>
<td>57</td>
</tr>
<tr>
<td>width of the nasals</td>
<td>42</td>
</tr>
<tr>
<td>minimal distance between maxillae across the vertex</td>
<td>37</td>
</tr>
<tr>
<td>length of the squamosal from zygomatic to post-glenoid process</td>
<td>39</td>
</tr>
<tr>
<td>distance between ventromedian margins of paroccipital processes of exoccipitals</td>
<td>77</td>
</tr>
<tr>
<td>width across the occipital condyles</td>
<td>61</td>
</tr>
<tr>
<td>width of the foramen magnum</td>
<td>32</td>
</tr>
<tr>
<td>height of the foramen magnum</td>
<td>32</td>
</tr>
<tr>
<td>maximal height of the cranium</td>
<td>134</td>
</tr>
</tbody>
</table>

http://app.pan.pl/acta50/app50-239.pdf
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 narrower 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-
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 post-orbital 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

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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.
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*, *Kampholophos*, *Macrokentriodon*, *K. 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

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 sternomastoideus 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 lumbers 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 lumbars of *Kentriodon pernix* and *Belonodelphis peruanus*. The metapophyses are well-developed; the transverse processes are long and wide, presenting an anteroposterior development at approximately two-thirds of their length. A somewhat similar condition is observed at the posterior lumbars of *Atocetus iquensis* (Muizon 1988b: fig. 90) and some of the anterior lumbars 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 lumbars (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 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-

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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.

<table>
<thead>
<tr>
<th></th>
<th>L1</th>
<th>L2</th>
<th>L3</th>
<th>L4</th>
<th>L5</th>
</tr>
</thead>
<tbody>
<tr>
<td>length of centrum</td>
<td>i36</td>
<td>–</td>
<td>i39</td>
<td>41</td>
<td>42</td>
</tr>
<tr>
<td>anterior width of the centrum</td>
<td>30</td>
<td>–</td>
<td>–</td>
<td>29</td>
<td>32</td>
</tr>
<tr>
<td>anterior height of the centrum</td>
<td>e31</td>
<td>–</td>
<td>–</td>
<td>i28</td>
<td>e31</td>
</tr>
<tr>
<td>posterior width of the centrum</td>
<td>–</td>
<td>e30</td>
<td>–</td>
<td>29</td>
<td>34</td>
</tr>
<tr>
<td>posterior height of the centrum</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>31</td>
</tr>
<tr>
<td>length of the transverse process</td>
<td>e51</td>
<td>58</td>
<td>–</td>
<td>58</td>
<td>–</td>
</tr>
<tr>
<td>maximal anteroposterior width of the transverse process</td>
<td>–</td>
<td>23</td>
<td>–</td>
<td>26</td>
<td>–</td>
</tr>
</tbody>
</table>
Lacépède, among extant delphinoids, it is closer to Delphinodon (Kellogg, 1955), which show a less pronounced curvature; Delphinapterus, 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 extinct 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 anterio-
ry and the elongated palatines and pterygoid sinus fossae) make
it resemble instead the much bigger *Macrokenkiodont morani*.
Apart from its size, *Tagicetus joneti* differs from *Macrokenkiodont morani* in having narrower frontals on the
vertex, more numerous maxillary teeth, and a much shorter
zygomatic process of the squamosal. The prominent lambo-
doidal crests of *Macrokenkiodont morani* may be related to
its larger size (cf., the well-developed crests of the equally
large lophocetine kenriodontid *Hadrodelphis calvertense*

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
kenriodontines. It could be thought that the anterior exten-
sion 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 *Macrokenkiodont morani*, not associ-
ated to a transverse pinching (as in some lophocetes), 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 simi-
lar-sized kenriodontines 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 *Macrokenkiodont morani* (Daw-
son 1996b). This diversity, together with the wide geo-
graphic range of the kenriodontines, 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 kenriodontine taxa
in less extensively studied areas of the world.

So far, the described Portuguese kenriodontid record de-

erives 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).

**Acknowledgements**

The contribution of OL is part of a Ph.D. thesis at the Free University
of Brussels (ULB), granted by the “Fonds pour la Formation à la Recher-
che dans l’Industrie et dans l’Agriculture” (FRIA). The visit of OL to
the USNM and CMM collections was financed by a grant of the “Fonds
National de la Recherche Scientifique” (FNRS). ME participation was
supported by the Ph.D. scholarship BD 21741 granted by the “Fun-
dação para a Ciência e a Tecnologia” (FCT) under the PRAXIS XXI
Program. The authors wish to thank David Bohaska (USNM), Stephen
Godfrey (CMM), and Georges Lenglet (IRSNB) for providing access to
the collections under their care; Wilfried Misur (IRSNB) for taking the
photographs; Miguel Telles Antunes (Universidade Nova de Lisboa) and José
Vitorino de Pina Martins (Academia das Ciências de Lisboa) for kindly reviewing the manuscript. The comments and sug-
gestions of the two reviewers, Emese Kazár (Geological Institute of
Hungary, Budapest) and R. Ewan Fordyce (University of Otago, Dunedin), considerably improved a previous version of the manuscript.

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