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**KENTRIODONTID REMAINS
(CETACEA: ODONTOCETI)
FROM THE MIDDLE MIOCENE
OF BIHOR COUNTY, ROMANIA**

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Abstract. An incomplete dolphin skeleton was found and excavated in the Brusturilor Valley near the village Tășad (Bihor County, Romania) in 2000. The remains came from a layer of greenish clay that was deposited in the Early Sarmatian. The carcass was likely complete when it reached the sea floor, but the skeleton was slowly buried in a disturbed environment where the elements became unassociated and displaced. The dolphin from Tășad is a delphinoid, whose periotic closely resembles those of Miocene kentriodontids. A comparison of these elements to known kentriodontid species suggests that the dolphin of Tășad represents a new species. In the lack of the diagnostic features of the skull, however, its formal description must await the discovery of more complete material.

Introduction

During geological prospecting, a series of layers containing organogenic remains (“deltaic facies”) has been identified in the Brusturilor Valley (southwestern region of the Pădurea Craiului Mountains, Bihor County, Romania) (Istocescu et al., 1965; Istocescu & Istocescu, 1974). Cranial fragments of a rhinoceros were collected by D. Istocescu and assigned to *Lartetotherium sansaniensis* (LARTET) or *Gaindatherium* COL-

BERT by Codrea (2000). The Tășad-1 locality was discovered by the second author of this paper in 1999 and has been intensively sampled since then. The green clayey layer that yields a rich material of freshwater molluscs and terrestrial microvertebrates deposited during the Early Sarmatian (late Middle Miocene, Volhynian Substage, MN 7; Hir, 2002a, 2002b; Hir et al., 2001). When J. Hir and M. Venczel attempted to identify the same fossiliferous layer on the right side of the Brusturilor Valley in 2000, they struck upon teeth and vertebral fragments of a dolphin. Excavations in June and August of the same year by E. Kazár, L. Kordos and M. Venczel unearthed the incomplete skeleton of a small-sized dolphin. The aim of the present paper is to document the new odontocete locality (herein called the Tășad-2 locality) and to give an anatomical description of the new dolphin find. Although the incompleteness of the skeleton prevents a precise taxonomical allocation, the find provokes intriguing questions about odontocete history in the Miocene.

Institutional abbreviations – **CMM**: Calvert Marine Museum, Maryland, USA; **MÁFI**: Magyar Állami Földtani Intézet (Geological Institute of Hungary), Budapest, Hungary; **MNHN**: Muséum national d'Histoire naturelle, Paris, France; **MTC**: Muzeul Țării Crișurilor, Oradea, Romania; **MTM**: Magyar Természettudományi Múzeum (Hungarian Natural History Museum), Budapest, Hungary; **NHMW**: Naturhistorisches Museum Wien, Austria; **USNM**: National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Geological setting

Tășad is a village at the southwestern region of the Pădurea Craiului Mountains (Bihar County, Romania), ca. 20 km to the southeast of Oradea. The Tășad-2 locality lies ca. 1,5 km south of the village, on the right side of the Brusturilor Valley (**Figure 1**).

Around the village of Tășad, as in the marginal areas of the Beiuș Basin, the crystalline basement is covered by Neogene sediments. The Badenian deposits are tuffitic, calcareous, organoclastic, and lithothamnitic limestones and grey marls, overlain by brackish calcareous sandstones and marls. The Sarmatian sediments are conglomerates and limestones in the marginal areas; and white, tuffaceous marls, detrital limestones, and sandstones inwards the basin. The Middle Miocene deposits are overlain by the transgressive Pannonian sediments (Paucă, 1935; Ianovici et al., 1976).

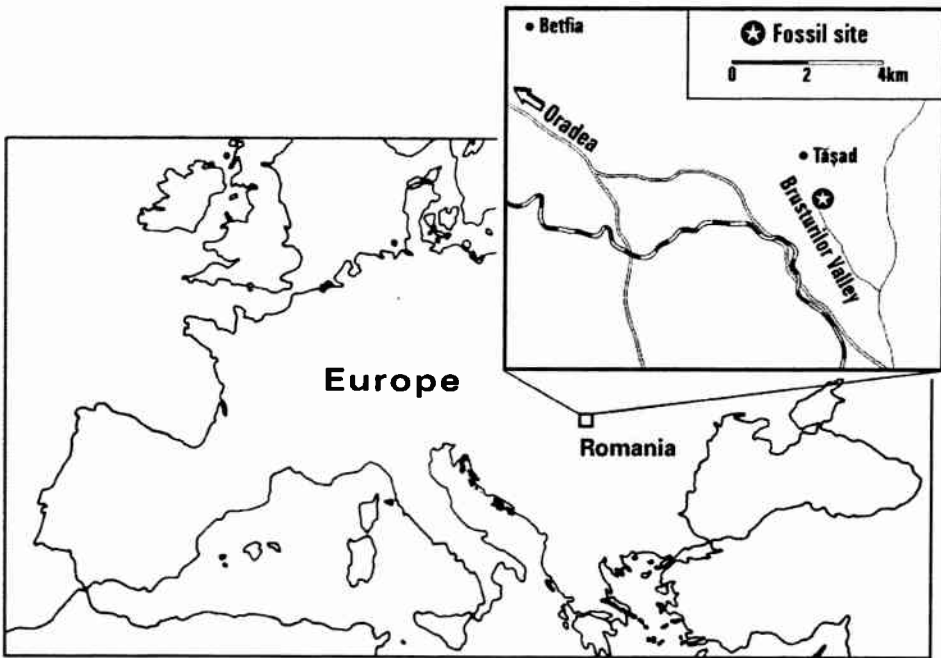


Figure 1. Geographic position of the Tășad-2 locality.

The section of Tășad-2 (GPS N 46°55'36" E 22°07'32") shows clay and marl below, calcareous sands and marl above (Figure 2). Underneath, at the level of the stream Cârpeștii Mici, hard, calcareous marl is exposed. This is underlain by a 7 cm deep, greenish-grey clay layer, which contained the dolphin skeleton and some bony fish remains. The fossiliferous layer of the Tășad-1 locality can be correlated with the grey clayey marl of Tășad-2, ca. 3,5 m above the dolphin skeleton. On the basis of the molluscs and the terrestrial microvertebrates, this layer was deposited during the Early Sarmatian (Volhynian, MN 7-8; Hir et al., 2002).

Material & Methods

All dolphin remains of the Tășad-2 locality belong to one individual. The incomplete skeleton consists of a mandible fragment; 28 teeth or tooth fragments; two fragments of the occipital region of the skull; left and right tympanic bullae; right periotic; right stylohyal; all seven cervical vertebrae; two thoracic and four caudal vertebrae; one chevron bone; several rib fragments; one scapular fragment; one radius; both ulnae; numerous car-

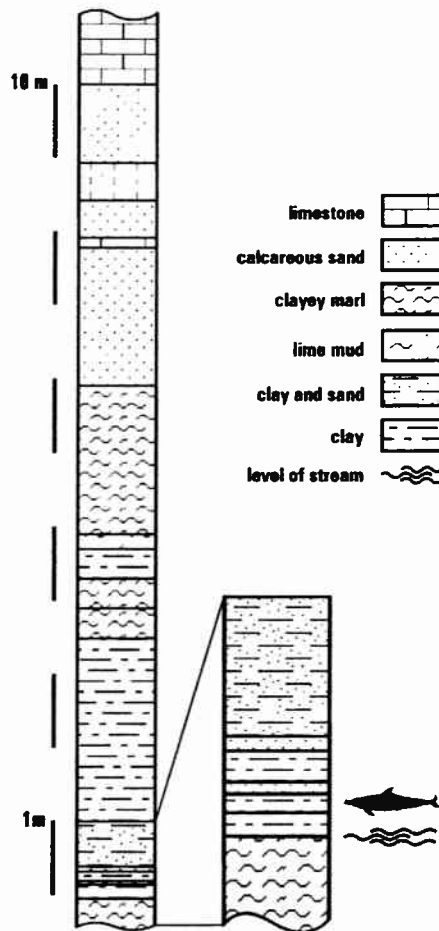


Figure 2. Geological profile of the Tășad-2 locality. The dolphin symbol points to the layer in which the skeleton was found.

pals, metacarpals, phalanges and a number of unidentifiable fragments (MTC 22404); left periotic and stapes (MÁFI V.21679/1-2); left humerus (MÁFI V.21680), and three more teeth (MÁFI V.21683/1-3).

In the terminology of the ear bones we follow Kellogg (1927), Fraser & Purves (1960), Kasuya (1973), Fordyce (1983), Barnes & Mitchell (1984), Muizon (1987) and Luo & Marsh (1996). Anatomical terminology for the other elements is mainly derived from Flower (1870), Abel (1931), Slijper (1936) and Rommel (1990). Relative centrum lengths were calculated with the method of Buchholtz (2001). All measurements were taken with the same digital caliper.

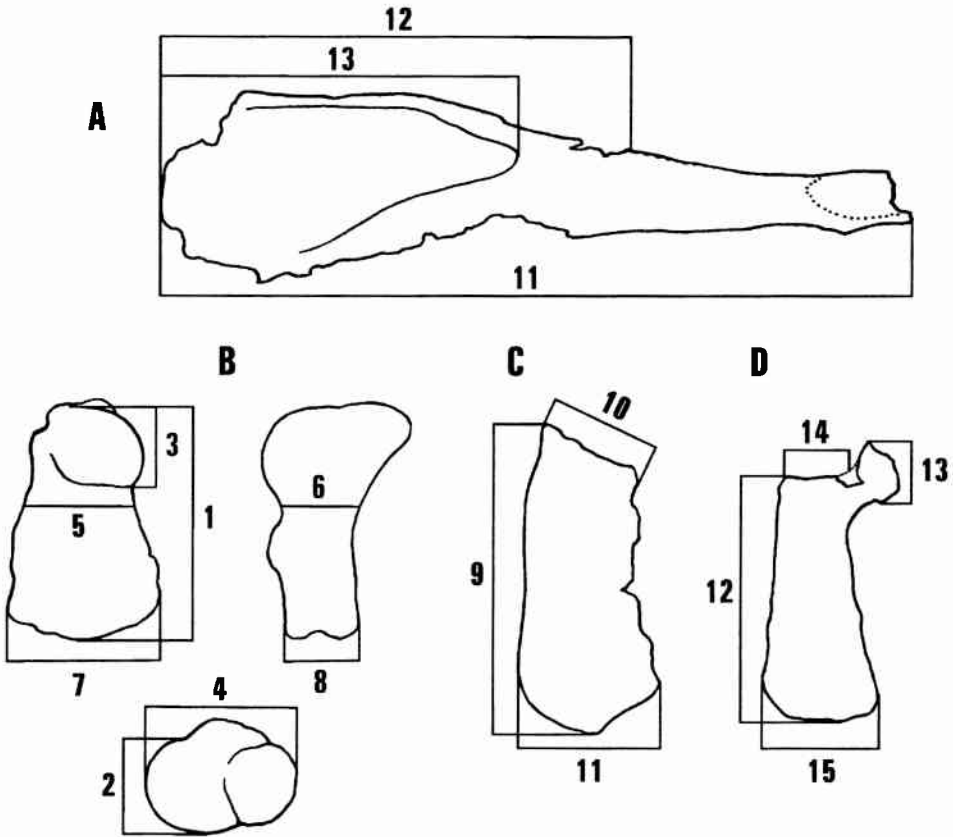


Figure 3. Measurements of the mandible (A), the humerus (B), the radius (C) and the ulna (D). The numbers refer to Table 1 (A) and Table 3 (B-D).

Description of the skeletal elements

Skull – Only two fragments of the occipital condyles and the adjacent exoccipitals could be unambiguously identified as skull remains. The condyles do not prominently protrude posteriorly from the exoccipitals. A few thin bony plates possibly represent other parts of the skull, but none bear diagnostic features.

Table 1

Kentriodontidae indet. (unnamed n. sp.) from Tășad (Bihor County, Romania). Measurements of the periotic, tympanic and mandible (in mm; with the mandible: ± 0.5 mm; e: estimated value; -: missing data).

	left	right
1. Length of periotic (from tip of anterior process to tip of posterior process)	24.4	24.3
2. Anteroposterior diameter of cochlear portion	12.1	12.6
3. Greatest transverse width of periotic	16.5	16.7
4. Greatest diameter of articular facet of posterior process	9.3	9.4
5. Least distance between the margin of fundus of internal auditory meatus and aperture of endolymphatic foramen	3.1	3.3
6. Least distance between the margin of fundus of internal auditory meatus and aperture of perilymphatic foramen	2.4	2.2
7. Length of tympanic (from anterior tip to posterior end of outer posterior prominence)	30e	29e
8. Distance between anterior tip and posterior end of inner posterior prominence	27e	27e
9. Greatest width of tympanic bulla	14.2	—
10. Width of tympanic bulla in the level of the sigmoid process	16.3	—
11. Length of mandible as preserved	184	—
12. Distance between last dental alveolus and preserved posterior end of mandible	113	—
13. Length of mandibular hiatus	91.5	—

Periotic (Plate 1a-d) – The periotic of the Tășad fossil dolphin is small. It shows the sinusoid shape characteristic of kentriodontids in general. The dorsal surface of the periotic is convex both in lateral and in anterior views. In other words, an elliptical dorsal plateau is absent in this periotic. The highest point of the bone in lateral view is the superior process. When viewed laterally, the dorsal margin of the periotic body closes at ca. 120° with the posterior process. In dorsolateral view, the hiatus epitympanicus forms a deep V-shaped notch between the ventrolateral tuberosity and the posterior process. The internal auditory meatus (IAM) is elongated, and it continues as a long, slit-like groove anterolaterally. The anterior process is slender, triangular, moderately long and slightly bent medially in dorsal view. It is not significantly constricted from the sides. A strong cleft separates the groove for the tensor tympani muscle from the anterior base of the pars cochlearis. The small cochlea is broadly joined to the body of the periotic and is rather low medially. It is only very

slightly bent toward the anterior process. In medial view, the pars cochlearis is slightly compressed dorsally. The perilymphatic foramen and the fenestra rotunda are separated by a prominent boss, which protrudes posteriorly. The perilymphatic foramen is a tiny opening, which lies approximately on the prolonged long axis of the internal auditory meatus, and it opens medially. The endolymphatic foramen opens dorsally as a slit in a depressed, triangular area medial to the superior process. In ventral aspect, the fossa for the head of the malleus is a shallow, almost circular depression. The fossa incudis starts at the posteromedial corner of the fossa for the head of the malleus. The fenestra ovalis has an elliptical shape and opens ventrolaterally. A bony rim separating the fenestra rotunda from the groove for the stapedial muscle overhangs the latter. The posterior process projects posterolaterally in ventral view. It has a pentagonal, concave posterior bullar facet, which bears a few fine striae.

Tympanic (Plate 1e-h) – The description is based on the better preserved left tympanic bulla. The posterior part of the lateral wall is fragmentary in the left tympanic bulla, and the conical and posterior processes and the accessory ossicle are either damaged or displaced.

As is usual with the Delphinida (sensu Muizon, 1988a), the involucrem has a sinusoid dorsal profile in medial view. This sinusoid shape, however, is not very pronounced because the anterior portion of the involucrem is only slightly above the dorsal margin of the posterior part. The involucrem is dorsoventrally compressed, its dorsal surface is smooth. No anterior spine is present. The transverse thickness of the lateral lobe is larger than that of the medial. The width across the posterior prominences is small; the tympanic is broadest at the center of the anteroposterior length of the bulla. The outer posterior prominence extends considerably farther posteriorly than the inner posterior prominence. Between both prominences a fairly deep interprominential notch is present, which continues ventrally in a short median furrow. The lateral wall is moderately high, the presence of a lateral furrow is questionable. The sigmoid process is slender and has an L-shape in lateral view, as is usual with the Delphinoidea. The articular facet of the posterior process is roughly triangular and finely striated medially, smooth elsewhere. The posterior process is directed posterolaterally in dorsal view. The elliptical foramen is wide open.

Stapes – The stapes is basically similar to the same bone of *Kentriodon pernix*. The foot plate is broad with a concave surface.

Mandible – The left mandible is preserved. Except for the last ca. 2 cm, the symphyseal part is lacking. Hence, the total length of the mandible is unknown. The preserved part of the symphysis shows a finely structured attachment site for the opposite mandibular ramus, indicating that the two

rami were not fused. The preserved posterior part is strongly damaged, lacking the angulus and the coronoid process. The condyle is ca. 20 mm deep and broad. Medially, there is a large, elongated mandibular hiatus. The pan-bone is thin. The overall shape of the mandible shows a strong S-curvature in lateral view, where the anterior part is arched dorsally, the posterior part ventrally (**Plate 2: 1a-b**). The preserved part of the mandible bears 17-20 small dental alveoli. The interalveolar septa are partially absorbed, resulting in a more or less continuous alveolar groove, as is common e.g. in the modern *Phocoena*.

Teeth (Fig. 4) – All thirty teeth found loose in the matrix are homodont and single rooted. Their total lengths vary between 8,0-8,7 mm, their greatest diameters are 1,7-1,9 mm. The crowns take up more than half of the total length, sometimes almost two-thirds of it. The crowns are slim, slightly curved and antero-posteriorly(?) compressed, linguo-labially(?) broadened, so that their form resembles a sickle. The enamel is smooth. The roots of most teeth are curved in a different plane than the crowns, so that the teeth are twisted along their long axes. The tooth necks are swollen as a result of cement deposition. Differences in the amount of the encircling swelling and in the degree of the curvature of the roots are most likely due to the different original positions of the preserved teeth in the mandible (or rostrum).



Figure 4. Two teeth of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (Bihor County, Romania). Left: anterior or posterior view. Right: approximately lingual view.

Scale bar: 5 mm.

Hyoid bone – The completely preserved right stylohyal has a slightly convex medial margin, a straight lateral margin, and a low ridge on the anterior surface. There is a distinct "neck" between the body and the proximal end. The proximal part, which articulates with the paroccipital process of the skull, has the shape of a fan in anterior view: it is antero-posteriorly flattened, medio-laterally expanded and the proximal margin is semicircular (**Plate 2: 2**).

Cervicals (Plate 2: 3a, 3b, 4a, 4b, 5) – All seven cervical vertebrae are preserved. The neural arch of the atlas is broken away, so is the ventral arch. Thus, orientation and relative position of the preserved left and right parts were reconstructed by fitting the corresponding elements to the anterior aspect of the epistropheus. Of the cervicals, the axis is best preserved, with only the tips of the transverse processes and the dorsal part of the neural arch missing. The presumed 4th and 5th cervicals are attached together by matrix and both are nearly complete. The other three are more seriously damaged.

All cervicals are free, together they measure ca. 4.5 cm antero-posteriorly (excluding the intervertebral discs). The anterior articular facet of the atlas is strongly concave with an upside-down pyriform shape. The long axis of the anterior articular facet lies at about 55° to the vertical. The posterior articular facet has a normally oriented pyriform shape, the long axis of which being nearly vertical. It is slightly convex ventrolaterally, and slightly concave on its narrower dorsal part. On each side, the posterior articular facet is elevated and divided by a distinct rim from the main "body" of the atlas. The foramen has an upside-down pyriform shape. The broader dorsal part is divided from the narrower ventral portion by the protruding medial margins of the anterior articular facets. The transverse processes are moderately long, dorsoventrally compressed, and they project posterolaterally.

The anterior articular facet of the axis is shallowly concave, oval, and it is inclined medially at about 15°. There is a large, nearly circular inferior articular process of the odontoid process for articulation with the atlas. In the centrum of the anterior surface of the odontoid process, a small aperture indicates where the embryonal chorda dorsalis entered the vertebra. The posterior epiphysis of the vertebra resembles the form of a horizontally elongated, idealized heart. The neural arch was high, the neural canal is wide at the base. The transverse process is short, and it projects posterolaterally.

The well-preserved 4th and 5th vertebrae have shortened bodies. The anterior epiphysis of the 4th cervical is triangular (**Plate 2: 5**), the posterior epiphysis of the presumed 5th is horizontally elliptical. The neural

canal is spacious, the neural arch is gracile, dorsoventrally compressed. There are small, ovoid prae- and postzygapophyses on either sides. The other cervicals have horizontally elliptical vertebral bodies. The 7th cervical has small, distinct concave articular facets for connection with the heads of the first ribs on either side.

Thoracics – Two thoracic vertebrae are preserved with the skeleton, both have epiphyses ankylosed to the centra. They lack the spines, but both have preserved one transverse process. The anterior and posterior epiphyses are vertical in lateral view, and semicircular in anterior and posterior views. There is no ventral keel. The one with more shortened body presumably was the 4th-6th thoracic vertebra (**Plate 2: 6a-c**), the other originated from a more posterior position. The former has a parapophysis posteriorly, showing that the corresponding rib had two attachment sites. The transverse process is short, slender and dorsoventrally thin. On its dorsal surface it bears a praezygapophysis medially and a short metapophysis laterally. The articular facet of the diapophysis is small. The other thoracic vertebra has a less shortened body (**Plate 2: 7a-b**). No parapophysis can be observed with this vertebra. The transverse process is short, the articular facet of the diapophysis is horizontally elliptical.

Caudals – Four caudal vertebrae are preserved. The two larger ones originate from the central part of the caudal series, as concluded from their large centra, reduced transverse processes and narrowed neural canals. Both have cuboid centra, where the length of the corpus is slightly greater than its depth. The anterior and posterior epiphyses are completely fused to the centra. They are vertical in lateral view and almost circular in posterior and anterior views. One of these caudals (**Plate 2: 8**) has the ventral crests for the articulation with the chevron bones (termed the caudapophyses by Abel, 1931) open in the middle. The base of the neural arch occupies the anterior half of the dorsal area of the vertebral corpus. The neural canal is narrow. A large hole bores through the base of the (broken) transverse process on both sides of the vertebra. The better preserved, almost complete caudal vertebra (**Plate 2: 9a-b**) had a more posterior position in the vertebral column. It has a low neural arch, which is limited to the anterior two-thirds of the dorsal surface of the vertebral body. The metapophyses are large, globular and project anteriorly well beyond the anterior epiphysis. The spinosus process is estimated to reach ca. 10 mm above the level of the metapophyses. The two other caudals are from the terminal (fluke) region, their form agrees with that of other delphinoids (**Plate 2: 10a-b, 11a-b**). The larger of these is the so-called "ball" vertebra located at the peduncle-fluke junction, as concluded from its convex anterior epiphysis (**Plate 2: 10b**). The other epiphysis is almost flat. Measurements are given in **Table 2**.

Table 2

Kentriodontidae indet. (unnamed n. sp.) from Tășad (Bihor County, Romania). Measurements of the vertebrae (in mm, ± 0.5 mm; e: estimation; .: not appropriate). The numbers indicate the presumed anatomical sequence and not exact positions in the vertebral column except with Ce. 1, Ce. 2 and Ce. 7, which are the first, second and seventh cervical vertebrae. Ce: Cervical vertebrae; Th: thoracic vertebrae; Ca: caudal vertebrae. 1. Length of vertebral body; 2. Height of vertebral body; 3. Width of vertebral body.

		1	2	3
Ce.	1	*	*	*
	2	13.0	15.5	21.5
	3	5.3	17.0e	20.5e
	4	3.5e	17.0	21.5
	5	4.5e	17.0	21.0
	6	5.0	17.0	20.5
	7	5.0	16.0	21.0
Th.	1	13.5	14.0	16.5
	2	18.0	14.0	16.0
Ca.	1	27.0	21.5	24.5
	2	28.0	21.5	22.5
	3	10.5	13.5	18.5
	4	8.0	10.0	14.5

Forelimb – Of the scapula, only a small posterior fragment is preserved. The glenoid fossa is a small, shallow concavity. There is no distinct neck on the scapula, but the posterior margin is rather vertical, it closes at about 70° with the plane defined by the fossa glenoidalis.

The left humerus is preserved (**Plate 2: 12a-c**). Both proximal and distal epiphyses are completely fused to the shaft. On the distal end of the bone, there are no signs of fusion between the humerus and the radius or the ulna, but sharp eaves overhanging the distal epiphysis distally indicate that the material represents an old individual. The humerus as a whole is stocky and remarkably small. The head is relatively small and flat rather than globular. The lesser tuberosity is a circular plateau projecting slightly above the head of the humerus. The greater tuberosity is a small but distinct rim on the anterior aspect of the proximal epiphysis. The anatomical collum does not appear as a neck, because of the shortness and robust-

ness of the bone. Nevertheless, the head is clearly separated from the neck by a distinct edge. In lateral view, the neck region has the least anteroposterior extension. Distally, the humerus broadens, so that the distal margin of the bone is of the greatest anteroposterior width. The fovea infraspinati is a small but distinct, circular cavity in the center of the lateral aspect of the humerus. The posterior tuberosity is an extremely well-developed, circular elevation providing strong attachment site for the deltoid muscle. Its center is positioned proximally from the distal margin of the fovea infraspinati. The well-developed deltoid tuberosity is a rugose area on the centrodistal part of the radial margin. Distally it does not reach the distal epiphysis but is separated from the latter by 8 mm. The articular facet for the radius is considerably longer anteroposteriorly than that of the ulna. There is a distinct articular facet for the olecranon process of the ulna, which runs parallel to the long axis of the humerus.

The lower arm bones slightly surpass the humerus in length (**Plate 2: 13, 14**; the illustrated ulna bears the number 17 in Figure 5). The radius is both anteroposteriorly and proximodistally longer than the ulna. The anterior margin of the radius is slightly convex, with an indistinct bump in the upper one-third of the anterior margin of the radius. The posterior margin is similarly concave. Because the anterior margin of the ulna is straight, however, the spatium interosseum between the two bones is a slim, half-moon-shaped area. The distal margin of the radius is sharply edged where it meets the carpals. Large articular facets for the other lower arm bone are present on the proximal part of the posterior and anterior margins of the radius and ulna, respectively. The proximal and distal epiphyses are completely fused to the shafts of both the radius and the ulna. The olecranon process is well-developed. Its posterodorsal margin has a sinusoid contour: convex below and concave above.

A number of carpals, metacarpals and phalanges were found. Most were disarticulated and scattered and hence, their exact identification and arrangement remain unclear.

Table 3

Kentriodontidae indet. (unnamed n. sp.) from Tășad (Bihor County, Romania). Measurements of the humerus, radius and ulna (in mm, ± 0.5 mm; e: estimated value).

1. Length of the humerus (from highest point of head to crista transversa)	41.5
2. Anteroposterior diameter of the head of the humerus	16
3. Dorsoventral diameter of the head of the humerus	17
4. Mediolateral width of proximal epiphysis	26.5
5. Anteroposterior extension of the humerus neck	20
6. Mediolateral extension of the humerus neck	14.5
7. Anteroposterior extension of the distal epiphysis of the humerus	26.5
8. Mediolateral extension of the distal epiphysis of the humerus	12
9. Length of the radius	57.5
10. Anteroposterior extension of the proximal end of the radius	20
11. Anteroposterior extension of the distal end of the radius	25.5
12. Length of the ulna	45.5
13. Height of the olecranon process	11
14. Anteroposterior extension of the articular facet of the ulna for the humerus	13e
15. Anteroposterior extension of the distal end of the ulna	21

Taphonomy

Figure 5 shows the skeletal elements of the Tășad dolphin as they were found in the site. The specimen was oriented such that the anterior end is toward the south-southwest, and the posterior end is toward the north-northeast. Nevertheless, one caudal vertebra was found together with the occipital condyles, the axis and two other cervical vertebrae. Elements of the flippers and teeth were distributed throughout the skeletal assemblage. With exception of both tympano-periotic complexes and two cervical vertebrae (presumably the 4th and 5th), all elements were disassociated. The majority of the bones were displaced from their original positions, but numerous elements of one manus were found in the vicinity of the right ulna. The presence of a number of bones at the edge of the present cutbank indicate that the missing elements of the skeleton had been removed by erosion and washed away by the stream prior to the excavations.

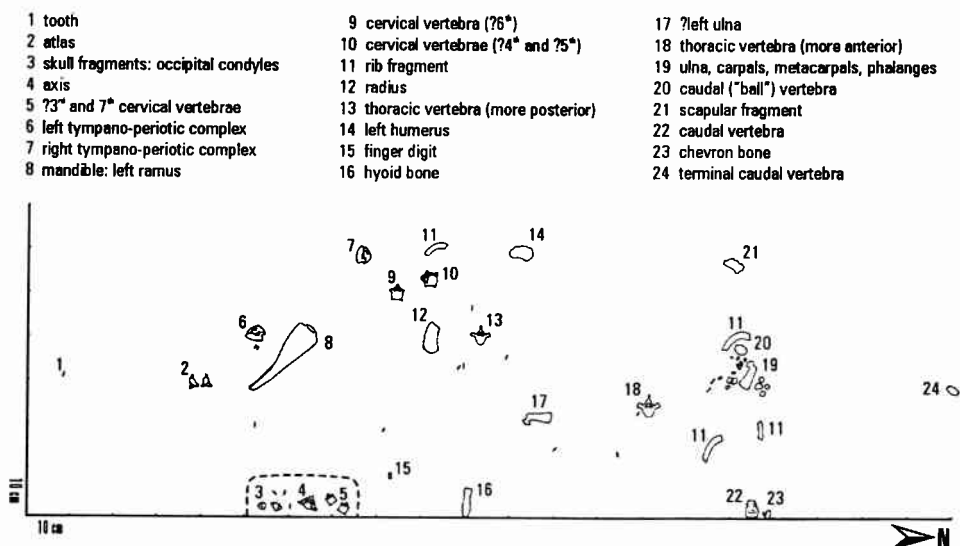


Figure 5. Diagram showing the skeletal elements of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (Bihar County, Romania) in the positions as they were found. The horizontal axis represents the margin of the present cutbank that borders the stream. The dotted line encircles the elements discovered and collected without coordinates by J. Hir and M.

Venczel early in 2000. Fourteen further teeth without coordinates were found around the mandible and are not illustrated. Only one of the illustrated teeth has a number (to the left). Unidentifiable fragments are not depicted.

Marine mammal carcasses usually drift on the surface before they sink to the sea floor. The sequence of decomposition and loss of skeletal elements during drifting is discussed by Schäfer (1962). According to his observations, the skull and mandibles are usually the first to become lost, often followed by the dangling flippers. The fossil assemblage of Tășad-2 includes the mandible, teeth, cranial fragments, bones of both flippers, and some caudal vertebrae. This means that the specimen must have reached the sea floor in a state where the integuments still held all skeletal elements together. Decomposition of the soft tissues progressed on the sea floor. The burial was slow, so that the individual elements could easily be displaced by water movements or scavengers. One exception may be the ?right lower arm and manus, the elements of which were found in close association (although not in anatomical positions). Perhaps the slowly decomposing connective tissues of the flipper held these elements together longer. It is not surprising that the tympano-periotics and two cervical vertebrae remained in articulation, because these elements are always in tight bone-to-bone contact in delphinoids. The complete lack of the lumbar vertebrae and the large number of missing thoracic and caudal vertebrae may indi-

cate scavenger activity or significant currents in the bottom waters, although removal of these elements by subsequent erosion is also possible. The majority of the bones were found poorly preserved. The fragments of vertebral processes show sediment between the clefts, indicating that the fractures occurred during or after burial.

Phylogenetic relations

In the taxonomy of odontocetes different groups and species are primarily distinguished by the morphological features of the skull. Ear-bones (periotic or petrosal and tympanic bulla) are also widely used so that Kasuya (1973) reconsidered the systematics of the recent Odontoceti on the basis of the tympanic and periotic bone morphology. Moreover, Kellogg (1931) based some of his new fossil taxa on isolated periotics. More recently Barnes (1976) discouraged authors to do so, because periotics may be the subject of convergent evolution resulting in similar morphology among not closely related species. Likewise, the flipper bones are thought to change their morphology rapidly, for which they are usually disregarded in phylogenetic analyses (Fordyce & Muizon, 2001), although when used cautiously, the phylogenetic signals of the humeri can aid in taxonomy (Kazár, 2003). Other skeletal elements including the vertebrae are only in a few cases diagnostic and can usually not be used in taxonomy and phylogenetic analyses.

Except for a few cranial fragments, there is no skull preserved with the dolphin remains from Tășad. We tried to learn more about the phylogenetic relations of the new find on the basis of the well-preserved ear bones, the teeth and the flipper bones.

Phylogenetic relations of the Tășad fossil on the basis of the ear bones

Based on the morphological similarity between the teeth and especially the petrosals of "*Heterodelphis*" *leiodontus* PAPP to those of the new find, Kazár (2003) postulated that the Tășad dolphin is a possible descendant of the Badenian (early Middle Miocene) "*H*". *leiodontus* and referred it to as "*Heterodelphis*"(?) n. sp. In spite of the overall similarity of the periotics of both species, however, there are two points where they do markedly differ. In medial or lateral view of the anterior process, the ventral angle is situated anteriorly to the dorsal angle (for definition of the dorsal angle see: Muizon, 1988b) in the new fossil, whereas the opposite

is the case with "*H.*" *leiodontus*. Secondly, the articulating surface of the posterior process is pentagonal in the Tășad specimen, whereas elliptical in "*H.*" *leiodontus*. These differences make a generic identity very unlikely. A third difference also exists: the periotic of "*H.*" *leiodontus* bears a low but well-defined longitudinal ridge on its otherwise flat dorsal surface (termed the dorsal ridge in Kazár [2003]), which is absent on the round dorsal surface of the Tășad kentriodontid. The diagnostic value and significance of the presence or absence of the dorsal ridge is unknown.

Barnes & Mitchell (1984) illustrate a large sample of periotics referred to the species *Kentriodon obscurus* KELLOGG. One of these (Barnes & Mitchell, 1984: fig. 9n) has marked morphological similarities to the periotic from Tășad, however, the latter is smaller, has a more elliptical internal auditory meatus and the endolymphatic and perilymphatic foramina are positioned at greater distances from each other. All other illustrated periotics of *K. obscurus* (in: Barnes & Mitchell, 1984) are considerably larger than the newly described periotic, and all have more circular cochlear parts.

The periotic of the Tășad dolphin is similar to the holotype periotic of *Belonodelphis peruanus* MUIZON (MNHN PPI 231) in the size, form and direction of the anterior process, in the position of the perilymphatic and endolymphatic foramina, and in having a convex cerebral surface. The new find, however, differs from the Peruvian species by having a smaller cochlea and a more slit-like internal auditory meatus. Also, the posterior process of the Tășad specimen has a broader, pentagonal articular surface in ventral view, it is bent less ventrally, and has a straight dorsal margin in lateral view.

All other described species of the family Kentriodontidae with a known periotic are markedly different from the Tășad specimen. The periotic of the new find resembles two unpublished possible kentriodontid specimens, the petrosal of the CMM-V-841 specimen and an isolated periotic (USNM 360007), both from the Calvert Formation, Maryland. The CMM-V-841 periotic, however, is larger than the Tășad periotic, and has a more elongated and more posteriorly pointing articular facet of its posterior process. The tympanic of the Tășad specimen differs from that of the Calvert dolphin by having a smaller width across the posterior prominences and by having the inner posterior prominence reduced in length. The total length (measured from apex of anterior process to apex of posterior process) of the USNM 360007 periotic is by a mm or so smaller than the Tășad specimen, and it has the anterior process more compressed from the sides. The Tășad specimen has a slightly longer anterior process with a more pointed apex, a more pronounced ventrolateral tuberosity, a more

compact form and a more slit-like internal auditory meatus. Both are similar in the presence of an eminence posterior to the fenestra rotunda and in the general appearance of the petrosals.

The periotic of the Tășad kentriodontid has some features in common with an isolated periotic from the Pietra leccese, Apulia, Italy, which was mentioned as *Lamprolithax?* sp. by Bianucci & Varola (1995, fig. 2: 2a-d). The new find resembles the Italian periotic in the form and size of the anterior process, but it projects more medially in the new find. Both have their posterior processes with a broad, pentagonal articular facet, which bears only a few fine striae. Also, the position of the perilymphatic foramen is the same in both specimens. On the other hand, the round cerebral surface of the Tășad periotic is clearly different from the flat superior process of the Italian find. The latter also has a larger, more globular pars cochlearis and a more circular internal auditory meatus. The hiatus epitympanicus is rather narrow in the Apulian periotic, whereas wide open in the new fossil. Probst (1888, pl. I, figs. 12-13) figured a periotic from Baltringen, Germany, which is also similar to the same element of the new dolphin find from Tășad in its small size and in the direction of the anterior process. Unfortunately, the illustrations do not allow a more throughout comparison.

In conclusion, the new fossil has a periotic morphology different from that of all nominal species of the Kentriodontidae. It shows more or less resemblance to the periotic of *Belonodelphis peruanus* as well as some isolated periotics, but the morphological differences are significant. For this reason it is highly probable that the dolphin of Tășad represents a new species of the Kentriodontidae.

The new fossil has a periotic morphology with a number of plesiomorphic character states mixed with some others that are thought to be derived. The relatively large, slightly anteromedially projecting anterior process is regarded as primitive. The anterior process is uncompressed from the sides and its anterior apex is not truncated, unlike in modern delphinids. The cochlear part is relatively small: it is neither globular nor inflated, nor does it prominently bend toward the anterior process as in more derived forms. Also, the convex cerebral surface of the periotic is probably primitive, as modern delphinids usually have a flat or slightly concave dorsal surface. The almost smooth articular facet of the posterior process is a plesiomorphic state of the new fossil from Tășad. On the other hand, the broadly joined cochlear part as well as the large angle at which the posterior process closes with the periotic body in dorsal or ventral view are derived features of the petrosal of the Kentriodontidae indet. (unnamed n. sp.) from Tășad. The tympanic bulla is primitive in that the sinusoid

shape of the involucrum is not particularly pronounced, and in the open elliptical foramen. On the other hand, the slender inner posterior prominence is perhaps a derived feature.

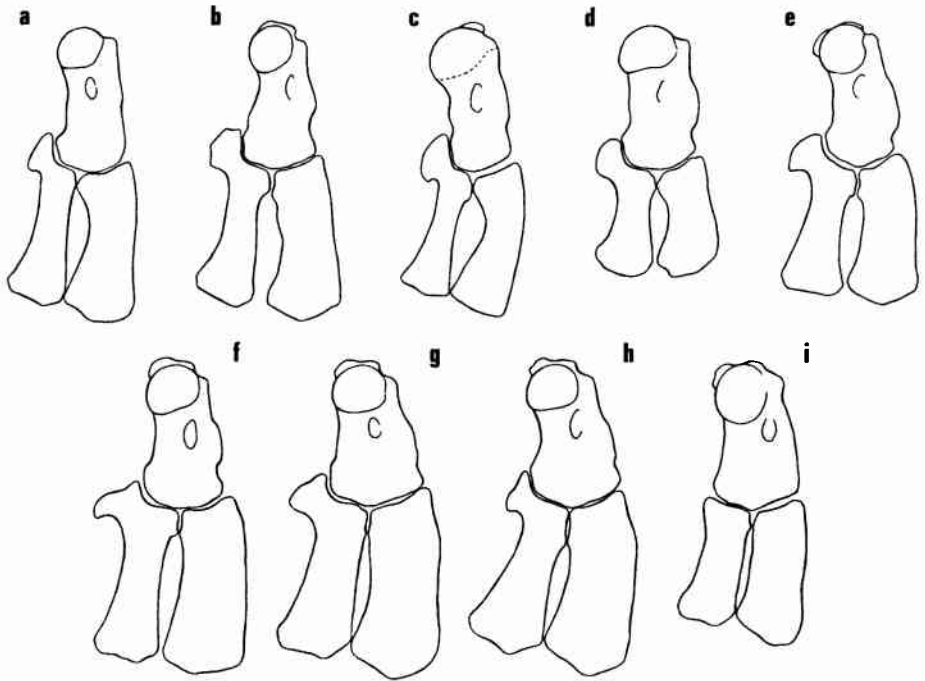


Figure 6. Morphology of the arm bones in the Kentriodontidae: *a* – *Incacetus broggi*, holotype (after Colbert, 1944: pl. 14 and Muizon, 1988b: fig. 128); *b* – a possible kentriodontid (CMM-V-841); *c* – *Delphinodon dividum*, holotype (USNM 7278; juvenile); *d* – *Hadrodelphis calvertense* (CMM-V-11); *e* – n. g. n. sp. (Kazár, in prep.), holotype (MTM V.93.2); *f* – “*Heterodelphis*” *leiodontus* (based on MÁFI Ob.2307 and Ob.258); *g* – Kentriodontidae indet. (unnamed n. sp.) from Tășad (MÁFI V.21680); *h* – “*Champsodelphis*” *fuchsii* (based on NHMW 1859.XXVII.6, NHMW 1883. C.6120 and NHMW 1859.66); *i* – *Atocetus iquensis* (MNHN PPI 114). For each species, humerus, radius and ulna are shown in lateral view. Missing parts reconstructed; drawings not to scale.

Morphology of the arm bones

There are only a few kentriodontid species with known flipper bones (Figure 6). Among these, two main types can be recognized. The holotypes of *Incacetus broggi*, *Delphinodon dividum*, the CMM-V-11 specimen of *Hadrodelphis calvertense* (Colbert, 1944; True, 1912; Dawson, 1996), the new genus and new species from Hungary (Kazár, in prep.) and the possible kentriodontid from Maryland (CMM-V-841) all have elongated humeri with a relatively small caput. The humerus does not significantly

widen distally because the distal part of the shaft is either equal to, or is smaller or only slightly wider anteroposteriorly than the same dimension of the humerus neck (**Figure 6: a-e**). This is the more primitive morphology among the kentriodontids. The head usually is situated on top of the shaft, with the exception of CMM-V-841 and the new species, which are more advanced in that their heads are shifted to the lateral side of the humerus body. The radius and the ulna are separated by a large spatium interosseum, indicating that the remnant of the antebrachial muscles was significant in these forms. The second type of arm bone is represented by "*Heterodelphis*" *leiodontus* PAPP, "*Champsodelphis*" *fuchsii* BRANDT, *Atocetus iquensis* MUIZON and the new find (**Figure 6: f-i**; for a taxonomic revision of "*Champsodelphis*" *fuchsii* see Kazár [2003]). These have a short and compact humerus. The shaft usually widens distally, as a consequence of the distal shift of the deltoid tuberosity and perhaps the more extensive development of the deltoid muscle (exception: "*H.*" *leiodontus*, which is primitive in this respect). The head can sit on top of the humeral body ("*H.*" *leiodontus*, "*C.*" *fuchsii* and the Tășad fossil) or be laterally shifted (*Atocetus iquensis*). The radius and ulna are not divided by a large gap, pointing to the more progressed reduction of the antebrachial muscles.

The humerus of the new kentriodontid from Tășad is an extreme case of the more derived second type of arm bone by its even more robust and compact appearance. Also, the deltoid tuberosity nearly reached the distal margin of the bone.

Comparison of the teeth

The Kentriodontidae indet. (unnamed n. sp.) from Tășad has remarkably small, homodont teeth. All have cement deposition around their necks to a greater or lesser extent. Cement deposition around the tooth necks is not a general phenomenon in the Delphinoidea. The recent *Pontoporia blainvillei*, the Miocene *Parapontoporia pacifica* BARNES, the Pliocene *Parapontoporia sternbergi* (GREGORY & KELLOGG) and the Pliocene *Pliopontios littoralis* MUIZON are similar to the new kentriodontid fossil in that their roots have cement deposition at the tooth necks, and in that the crowns are compressed anteroposteriorly. In *Pontoporia* the encircling swelling of the neck increases with ontogenetic age. As the mandible grows during the animal's life, but the number of teeth remains constant, the encircling cement deposition fills the increasing distance between the teeth, thus maintaining the stability of the mandibles (Flower, 1867; Muizon, 1984). In the mandible of the Tășad dolphin the teeth were not placed at great distances. On the contrary: the alveoles are tightly placed, and the interalveolar septa have largely disappeared. Thus, we suggest that the cement

deposition of the teeth in the Tășad fossil resulted from a different (unknown) mechanism than that of the *Pontoporia*, *Parapontoporia* and *Pliopontos*, which all have more widely spaced teeth. The morphological similarity of the teeth indicates convergent evolution instead of phylogenetic relations.

Paleobiology

Body size

The size of the dolphin skeleton of Tășad is remarkably small. The ankylosed epiphyses of all preserved vertebrae including some from the chest and peduncle, and the forelimb bones indicate that they belonged to a physically mature individual.

The type and only specimen of *Delphinopsis freyeri* MÜLLER, 1853 from the Miocene of Radoboj (Croatia) has deserved reputation by its small size (humerus length as preserved: ca. 3 cm; Müller, 1853, 1855; Meyer, 1863). Kellogg (1925) noted that *D. freyeri* is probably the smallest of the known Neogene dolphin species. However, the holotype humerus of *D. freyeri* is incomplete, the estimated length of the humerus must have been equal to or greater than that of the Kentriodontidae indet. (unnamed n. sp.) from Tășad.

One of the smallest living odontocete species is the vaquita, *Phocoena sinus* with total body lengths of 1,2-1,5 m (Noble & Fraser, 1971; Brownell, 1983). Given the smaller dimensions of the vertebral centra and the arm bones in the Tășad specimen, it is possible that the full-grown size of the Kentriodontidae indet. (unnamed n. sp.) was even smaller than that of the vaquita. However, a comparison based on the absolute measures of only few elements can only approximately indicate the total body length of the fossil species.

Implications for swimming performance

Although the dolphin of Tășad has unfused cervical vertebrae, the cervical vertebral centra are greatly reduced in length, indicating limited flexibility of the neck. The relative lengths of the postaxial cervical vertebrae vary between 0.18 and 0.28, in the range of living monodontids and the mysticete *Megaptera*; significantly shorter than those of river dolphins, and somewhat longer than those of recent delphinoids (definitions and comparative data: from Buchholtz, 1998, 2001). In modern, fast-moving delphinids the vertebrae of the caudal tail stock show lateral compression and increase in relative centrum length (Buchholtz, 2001). Two caudal

vertebrae of the Tășad dolphin originate from the peduncle region; their centra are slightly longer than wide or high, and they are wider than high (relative centrum lengths: 1.17 and 1.27). This points to the lack of a laterally compressed peduncle in the *Kentriodontidae* indet. (n. sp.). Unfortunately, none of the torso vertebrae are preserved that would enable a more detailed comparison with living cetacean species. The presence of the “ball” vertebra at the junction of the tail stock and the fluke, and the rectangular, laterally expanded, antero-posteriorly flattened terminal caudal vertebra on the other hand, signal the oscillatory movement of the fluke. The flipper was small and sickle-shaped as in the modern *Delphinidae*, indicating that it was used in a similar manner than in living delphinids. This idea is supported by the advanced reduction of the dorso-ventral length of the humerus.

These characteristics of the Middle Miocene *Kentriodontidae* indet. (n. sp.) from Tășad demarcate steps in the adaptation to a pelagic habitat where higher sustained speed swimming is of great advantage.

Paleobiogeography

During the Middle Miocene, the Carpathian Basin (including Hungary and the western part of Romania) was covered by the Central Paratethys Sea. By the Sarmatian (13-11.5 Ma according to Rögl, 1998), the Central Paratethys lost its connections with the Mediterranean but a broad seaway opened towards the Eastern Paratethys (Rögl, 1998, 1999; Kovàè et al., 1999; Hámor, 2001; Popov, 2001).

Due to the lack of the skull, the new fossil dolphin can only be identified in other localities from ear bones, teeth, or postcranials. Of these, the tympanic bulla is most often eroded to such an extent that only the involucrum is present. The tiny teeth are very unlikely to be found, unless a whole skeleton is discovered. The vertebrae are not diagnostic and hence, do not aid in searching for the presence of the newly described *Kentriodontidae* indet. (unnamed n. sp.) at other localities. Only the periotics and the humeri are helpful in this respect.

Kazár (2003) investigated the *Odontoceti* material of ca. 24 Sarmatian localities in the Carpathian Basin, but could not identify any petrosals referable to the *kentriodontid* species of Tășad. One humerus from Hernals, Wien (Vienna; NHMW 1891/43, left humerus) and fourteen humeri from Danitz-puszta (near Pécs, South Hungary; MÁFI V.21671, left humerus and LC140-4619, right humerus; LC140-4631, right humerus; LC140-4647, right humerus; M185R, right humerus; M205R, right humerus;

M304R, left humerus; M318R, right humerus; M366R, right humerus; M369R, right humerus; OZ-60, right humerus; OZ-68, right humerus; OZ-79, right humerus; and SL-6, left humerus in private collections) were unquestionably assigned to the Tășad species. A problem with this, however, is that the humerus morphology of the new fossil is remarkably similar to that of "*Champsodelphis fuchsii*", a species based on arm bones by Brandt (1873). Kazár (2003) used the anteroposterior position of the fovea infraspinati and the dorsoventral location of the posterior tuberosity to distinguish between the two species, but as she noted, this does not seem well-established until more specimens become available and the intraspecific variation of both species is better understood. It can be concluded that the species represented by the Tășad specimen does not have records from any other localities to date.

Conclusions

Tășad in Bihor County, Romania is a new late Middle Miocene cetacean locality. The new odontocete fossil is an incomplete skeleton of a remarkably small-sized dolphin. Despite the lack of diagnostic cranial characters the remains can be assigned to the family Kentriodontidae, because the tympanic and especially the periotic of the new fossil dolphin show all characters generally seen with Miocene delphinoids grouped in this family. Its periotic differs from all described species and thus, the fossil dolphin from Tășad should be regarded as a new species. Its formal description, however, is not possible until more cranial material becomes available.

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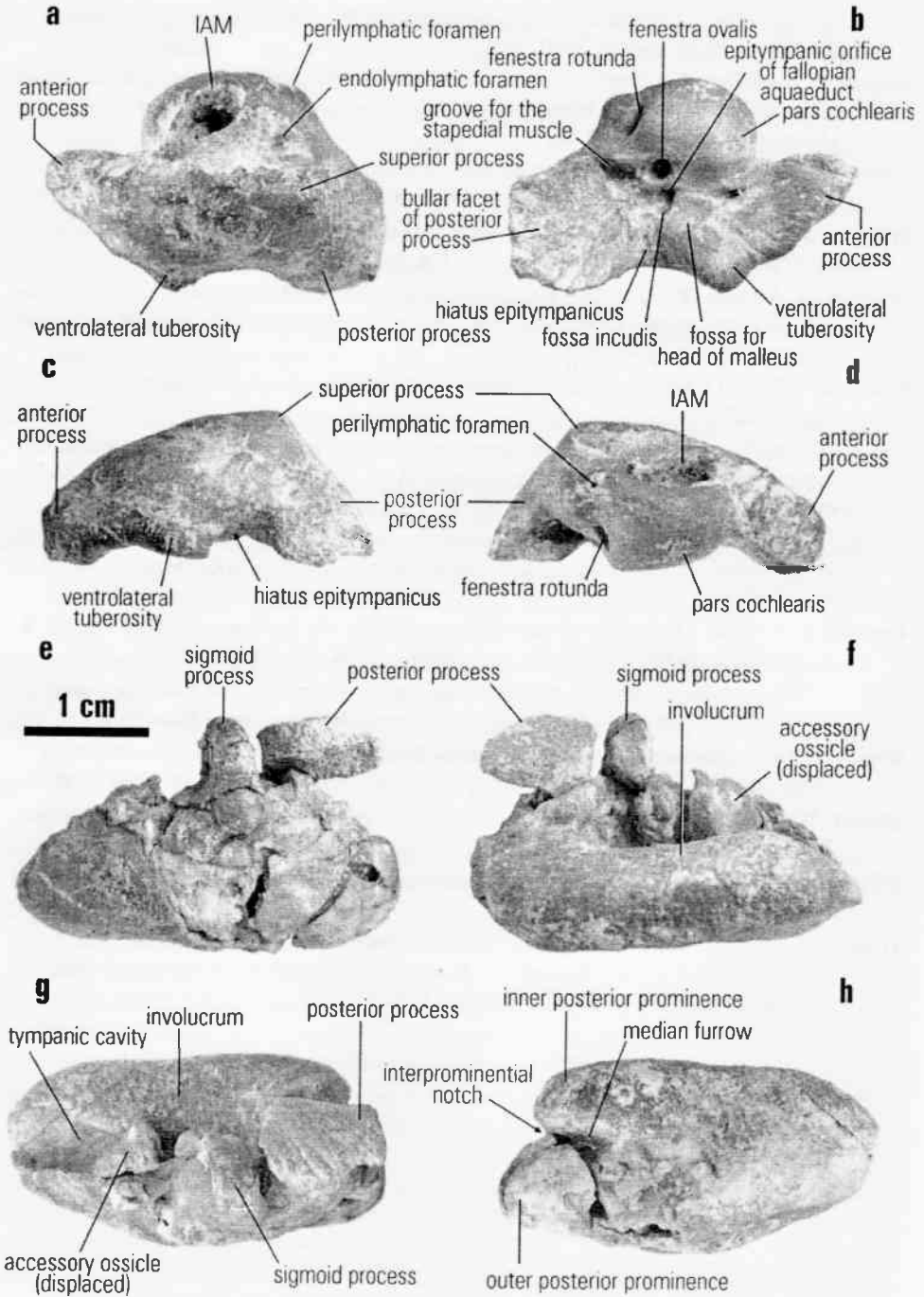


Plate 1.

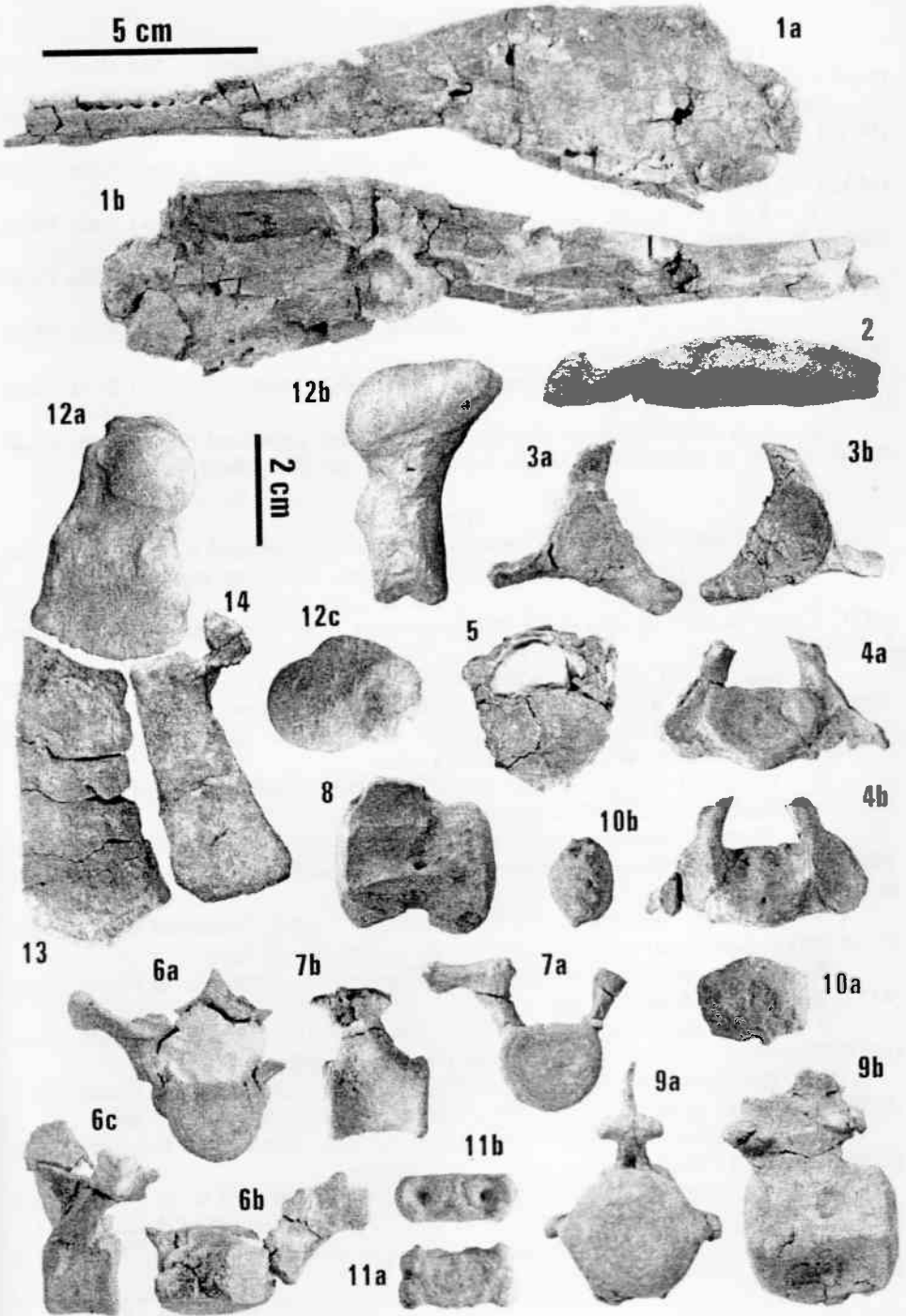


Plate 2.

Plate 1

- a** – Left periotic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MÁFI V.21679/1) in dorsal view.
- b** – Left periotic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MÁFI V.21679/1) in ventral view.
- c** – Left periotic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MÁFI V.21679/1) in lateral view.
- d** – Left periotic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MÁFI V.21679/1) in medial view.
- e** – Left tympanic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in lateral view.
- f** – Left tympanic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in medial view.
- g** – Left tympanic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in dorsal view.
- h** – Left tympanic of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in ventral view. Scale bar equals 1 cm throughout the plate.

Plate 2

- 1** – Left mandible of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in lateral view; (**b**) in medial view. Scale bar equals 5 cm.
- 2** – Right stylohyal of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in anterior view (proximal: to the left). Scale bar equals 3 cm in Figures 2 through 14.
- 3** – Left part of the atlas of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in posterior view; (**b**) in anterior view.
- 4** – Axis of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in posterior view; (**b**) in anterior view.
- 5** – Presumed 4th cervical vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in anterior view.
- 6** – Thoracic vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in anterior view; (**b**) in dorsal view (anterior: upward) and (**c**) in right lateral view.
- 7** – Thoracic vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in posterior view; (**b**) in left lateral view.
- 8** – Caudal vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in left lateral view.
- 9** – Caudal vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in anterior view; (**b**) in left lateral view.
- 10** – Caudal vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in anterior view; (**b**) in lateral view (anterior: to the left).
- 11** – Caudal vertebra of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) (**a**) in anterior view; (**b**) in dorsal view.
- 12** – Left humerus of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MÁFI V.21680) (**a**) in lateral view; (**b**) in posterior view and (**c**) in dorsal view.
- 13** – Radius of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in lateral view.
- 14** – Ulna of the Kentriodontidae indet. (unnamed n. sp.) from Tășad (MTC 22404) in lateral view.