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DOLPHIN REMAINS (CETACEA: ODONTOCETI) FROM THE MIDDLE MIOCENE OF CLUJ-NAPOCA, ROMANIA

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Abstract – Two incomplete dolphin skeletons and four ear bones from Sarmatian layers (Late Volhynian) of the Iris Quarry in Cluj-Napoca were investigated. The fossil remains represent three individuals of the same species. The humeri of both partial skeletons match the morphology of the holotype humerus of *Champsodelphis fuchsii* BRANDT, 1873, a species in need of further taxonomic reconsideration. On the basis of the petrosal morphology of the new material, Brandt's species is tentatively placed in the genus *Atocetus* MUIZON, 1988, family Kentriodontidae (Delphinoidea, Odontoceti). Our results show that *Atocetus*, hitherto known from the eastern shoreline of the Pacific Ocean only, had Paratethyan occurrences as well.

Key words – Miocene, Sarmatian, Kentriodontidae, *Atocetus*, *Champsodelphis fuchsii*, Romania

INTRODUCTION

The fossil dolphin remains described in the present paper were collected in the Iris Quarry of Cluj-Napoca by Prof. J. A. P. Maxim in 1960-1965 and are being held in the Muzeul "Bazinul Transilvaniei" (MBT) of the University Babeş-Bolyai in Cluj-Napoca, Romania. The MBT 14943 and the MBT 15029 specimens are partial skeletons of two individuals, whereas the MBT 15001 consists of an isolated left periotic and left tympanic, and a right tympano-periotic complex. The latter elements were described and assigned to as "Delphinoidea *incertae sedis* (?Kentriodontidae)" by Codrea (1995), the skeletons were preliminarily described and evaluated by Kazár (2003).

The Iris Quarry is located in the northern part of Cluj-Napoca, at the road leading to the village Chinteni. Mészáros et al. (1991) presented a detailed description of the geologic section exposed in the quarry. The dolphin remains came from a layer of calcareous marl above a thick layer of tuffs. The age of the marls is Lower Sarmatian (Volhynian Stage, Middle Miocene, NN 8; Mészáros et al., 1991).

MATERIAL & METHODS

In the present paper we describe the fossil remains of three dolphin specimens of the MBT. Comparisons were made with the holotypes and referred specimens of several Miocene kentriodontid species, but reference is given to the phylogenetically closely related *Atocetus nasalis* (BARNES, 1985) and *Atocetus iquensis* MUIZON, 1988 only. In the anatomical descriptions of the ear bones we follow Fraser & Purves (1960), Kasuya (1973), Barnes & Mitchell (1984), Muizon (1987) and Luo & Marsh (1996). Terminology for the other elements is mainly derived from Flower (1870), and Rommel (1990). The measuring points of the arm bones are figured in Kazár (2003) and Kazár & Venczel (2003). All measurements were taken with the same digital caliper.

Institutional abbreviations

MBT, Muzeul "Bazinul Transilvaniei", University "Babeş-Bolyai", Cluj-Napoca; **MNHN,** Muséum national d'Histoire naturelle, Paris; **NHMW,** Naturhistorisches Museum Wien.

SYSTEMATIC PALEONTOLOGY

Cetacea BRISSON, 1762
Odontoceti FLOWER, 1869

Delphinida MUIZON, 1984
Delphinoidea GRAY, 1821
Kentriodontidae SLIJPER, 1936
Pithanodelphinae BARNES, 1985
Atocetus MUIZON, 1988

Atocetus(?) *fuchsii* (BRANDT, 1873)

1873a ?*Champsodelphis Fuchsii* J. F. Brandt – Brandt: pp. 269-276, pl. 29.
1873a *Delphinus Fuchsii* –Brandt: p. 275.
1873b *Champsodelphis fuchsii* –Brandt: p. 195.
1880 ?*Champsodelphis Fuchsii* –Van Beneden & Gervais: p. 496.
1899 ?*Acrodelphis Fuchsii* Brandt sp.–Abel: p. 853.
1934 *Acrodelphis fuchsii* Brandt - Pia & Sickenberg: p. 37, SK 287.
1937 *Acrodelphis fuchsii* – Pia: p. 403.
2003 *Atocetus fuchsii* (BRANDT, 1873) – Kazár: pp. 181-189.

Holotype – NHMW 1859.XXVII.6.m, several vertebrae, sternum, fragment of scapula, humerus (Brandt, 1873a: pl. XXIX: figs. 1-7A).

Type locality and age – The holotype material was found in the "3. Ziegelgrube" in Nussdorf, Vienna in 1859 (Brandt, 1873a). Brick quarries in Nussdorf exposed clays of Sarmatian age (upper Middle Miocene; *e.g.* Suess, 1862; Schmid, 1974).

Referred specimens from the Iris Quarry of Cluj-Napoca, Romania – MBT 14943, partial skeleton of eight thoracic vertebrae, both humeri, left radius and ulna with almost complete manus, two

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inassociated carpals and one phalanx, left scapula, fragments of ribs and some unidentifyable fragments; MBT 15001a, left periotic; MBT 15001b, left tympanic; MBT 15001c, right tympano-periotic complex of the same individual (Codrea, 1995); MBT 15029, partial skeleton containing right tympano-periotic complex, fragments of mandible, atlas, axis, the 7th and at least two other cervical vertebrae, seven thoracic and two lumbar vertebrae, fragment of left humerus, scapula and sternum.

Formation and age – Early Sarmatian (Volhynian Stage, NN 8) according to Mészáros et al. (1991).

Description of the Iris Quarry dolphin material

Skull and mandible – Possible skull fragments are preserved with the MBT 14943 skeleton, but their anatomical identification is difficult. The MBT 15029 specimen contains a mandible fragment. It was not removed from the slab, now it exposes the lateral surface of the postsymphyseal fragment of perhaps the right ramus. The greatest depth (ca. 39 mm) was measured at the posterior end of the preserved fragment. Here, a slight concavity demarcates the coronoid crest.

Periotic – The description of the petrosal bone is based on the best preserved, from the tympanic detached, MBT 15001/a periotic except where noted. The overall shape of the periotic is elongate. The cochlear part is low, it is tilted slightly anteriorly and attaches to the body with a broad base. The internal auditory meatus is narrow and continues anterolaterally in a narrow slit. In the MBT 15001/b periotic there is a low crest on the posteromedial margin of the internal auditory meatus, the same crest is absent in the MBT 15001/a and in the MBT 15029 periotics. Lateral to the internal auditory meatus a dorsal flat area can be seen, which gives a flat dorsal contour of the periotic in lateral view. The perilymphatic foramen is situated at a relatively great distance to the opening of the internal auditory meatus and to the endolymphatic foramen. A prominent eminence is present between the fenestra rotunda and the foramen perilymphaticus. In the ventral aspect of the periotic, the fossa for the head of the malleus is large and medio-laterally elongated; the ventrolateral tuberosity is strong.

The anterior process is short but not reduced in size. In dorsal view it is triangular with a rounded tip, projecting more anteriorly than medially. In medial view, the dorsal angle of the anterior process reaches farther anteriorly than the ventral angle in the MBT 15001/b and the MBT 15029 periotics (the dorsal angle is broken away in the MBT 15001/a specimen). The posterior process is long with a pentagonal articular surface, the tip of which can be elongated in presumably old specimens (as in MBT 15001/a). In lateral view, the posterior process has a straight dorsal margin, which closes at a wide angle with the dorsal surface of the periotic. Measurements of the MBT periotics are given in Table 1.

TABLE 1

Measurements of the periotics and tympanic bullae of *Atocetus* (?) *fuchsii* (BRANDT, 1873) from the Iris Quarry of Cluj-Napoca, Romania (in mm; e: estimated value; ?: missing data).

	MBT 15001/a (left)	MBT 15001/b (right)	MBT 15001/c (left)	MBT 15029 (right)
periotic: total length from anterior tip of anterior process to posterior tip of posterior process	27.5	29.3		25.5e
periotic: width across coxhlear part and ventrolateral tuberosity	16.7	16.3		16.5
periotic: width across base of cochlear part	12.5	13.1		12.5
periotic: distance between IAM and perilymphatic foramen	3.5	3.9		3.2
periotic: distance between endolymphatic and perilymphatic foramen	4.0	5.1		4.8
tympanic: length from anterior tip to posterior end of inner posterior prominence		26.7	26.8	26.5e
tympanic: length from anterior tip to posterior end of outer posterior prominence		28.8	28.6	28.5e
tympanic: depth between ventral margin and top of sigmoid process		16.3	?	16.6

Tympanic – The description presented here is a composite of the characteristics of all three preserved tympanic bullae of the MBT material. All are fragmentary; the lateral walls and the adjoining structures are crushed in the MBT 15001/b and in the MBT 15029 tympanics, and of the MBT 15001/c only the involucrum and both posterior eminences are preserved.

The involucrum is flattened and almost completely smooth dorsally, with a sinusoid dorsal contour. The inner and outer posterior prominences are narrow, the inner being even more narrowed. The outer posterior prominence projects farther posteriorly than the inner. The median furrow is deep and broad, it reaches to almost mid-length of the ventral aspect of the tympanic bulla. The anterior lip of the bulla is obtuse and there is no anterior spine. The lateral wall of the bulla is relatively low; the sigmoid process is bulbous and erect. The presence or absence of the lateral furrow is unknown due to the preservation state of all three specimens. For measurements see Table 1.

Cervicals – Fragments of the atlas, axis and some of the postaxial cervical vertebrae are preserved with the MBT 15029 skeleton, whereas the centrum of the 7th cervical vertebra of the MBT 14943 can be studied.

The atlas has broad triangular anterior articular facets. The ventral lamina of the transverse process is short, rounded off and it projects posterolaterally. The neural canal is wider than that of *Atocetus iquensis*. The axis has broad anterior articular facets. The odontoid process is reduced, as is usual in the Delphinoidea.

TABLE 2

Measurements of the 7th cervical and the preserved thoracic vertebrae of *Atocetus*(?) *fuchsii* from the Iris Quarry of Cluj-Napoca (in mm; ±0.5 mm; e: estimated value; ?: missing data. Ce: cervical vertebra; Th: thoracic vertebra). 1. length of vertebral body; 2. width of vertebral body; 3. height of vertebral body.

	MBT 14943			MBT 15029		
	1.	2.	3.	1.	2.	3.
Ce. 7th	6.0	24.0e	20.0	5.5	23.0	17.0
Th. 1st	8.0	30.0	18.5	5.5	20.5	16.0
Th. 2nd	10.0	23.5	18.0	7.5	19.5	14.0
Th. 3rd	14.0	22.5	20.0	16.5	16.5	15.0
Th. 4th	17.5	21.5	18.5	18.5	16.5	15.0
Th. 5th	?	?	?	21.0	?	?
Th. 6th	21.0	19.5	17.5	?	?	?
Th. 7th	24.5	20.0	18.5	26.5	17.0	16.0
Th. 8th	27.5	21.0	18.0	?	?	?
Th. 9th	?	?	?	?	?	?
Th. 10th	31.0	20.5	19.0	?	?	?

Thoracics – Of the thoracic region, vertebrae 1-4, 6-8 and 10 are preserved with the MBT 14943 skeleton. All of their processes are broken away. The pedicles of the neural arches tilt anteriorly and are positioned anteriorly on the centra. The vertebral bodies are shortened in thoracic vertebrae 1 through 4, the 6th thoracic is cuboid, whereas the following ones have slightly elongated centra. The vertebral epiphyses are horizontally elliptical in the 1st thoracic, triangular in the 2nd through 4th, and semicircular in the rest.

The MBT 15029 has thoracic vertebrae 1 through 7 preserved. They are basically similar to the thoracics of the other skeleton. The 1st and 2nd thoracics have horizontally elliptical epiphyses, the following ones have semicircular epiphyses. The spine of the second thoracic vertebra is partially preserved; it is narrow and moderately tall, slightly inclined posteriorly. The neural canal is wider than high. Measurements of the thoracic vertebrae are shown in Table 2.

Lumbars – Two incomplete lumbar vertebrae are preserved with the MBT 15029 specimen, the description is based on the better preserved one. The vertebral body is slightly elongated (centrum length: 26.5 mm; centrum width: 20.5 mm; centrum height: 19.5 mm). The vertebral epiphyses are circular, and in lateral view they are deflected from the vertical plane. The lumbar arteries left a broad, posteriorly opening V-shaped depression on the ventral side of the lumbar vertebra, the ventral keel is pronounced. The transverse process is long (43 mm) and broad throughout its length, with a posterior (and possibly anterior) extension from about midlength to tip. This extension, however, is not triangular as in *A. iquensis* but smoothly arched. The tip of the transverse process is rounded off in ventral view.

Ribs – The preserved rib fragments of the MBT 15029 agree with the genral morphology of ribs in delphinoids in their delicate, narrow and flattened appearance.

Sternum – The sternum of MBT 15029 is exposed with its dorsal side upward. Thus, the ventral surface is unknown. The manubrium is incomplete with the anterior processes and the lateral margins missing, but the mesosternum is almost complete (Fig. 1). A hollow area on the anterolateral part of the manubrium indicates the attachment site of the first pair of sternal ribs on either side. The mesosternum is composed of two sternebrae. The first sternebra almost equals the manubrium in length, whereas the second is much shorter. The posterior margin of the latter is hollowed out, forming a wide and relatively deep posteior notch. The length of the sternum between the deepest point of the anterior notch and

the posterior notch is 68 mm. Minimal width across the first sternebra is 29 mm, that of the second is 32 mm. The number of sternal ribs was probably 4 pairs.

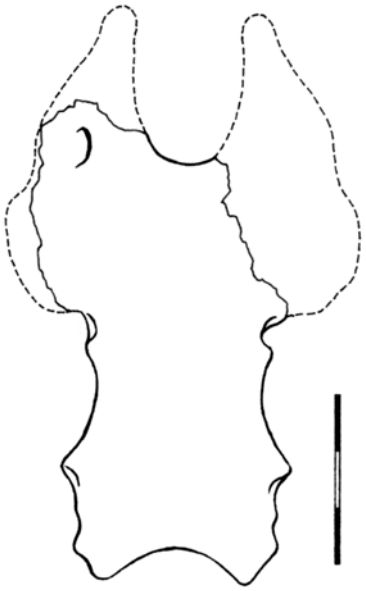

Figure 1. Sternum of the MBT 15029 specimen of *Atocetus*(?) *fuchsii* (BRANDT, 1873) from the Iris Quarry of Cluj-Napoca in dorsal view. Scale bar: in cm. Restoration (dotted line) is based on the holotype.

Scapula – An incomplete scapula is preserved with both skeletons from the Iris Quarry. The scapula of the MBT 14943 could be better prepared and hence, the description is based on this. In the present state of preservation, the medial aspect of the left scapula can be studied. The anterior margin and the acromion are not preserved, and the anterior part of the dorsal margin is covered by other elements. The distance between the dorsal margin and the posterior corner of the glenoid cavity is ca. 98 mm; the width of the neck as preserved is 30 mm, and the length of the glenoid cavity is 20.5 mm. The preserved base of the coracoid process indicates that it was a gracile process pointing anteriorly, similar to the same element of *A. iquensis*. The posterior and the dorsal margins close at an angle of about 60º or less, which is very similar to *A. iquensis*.

Humerus – A distal fragment of the left humerus is preserved with the MBT 15029, and both humeri of MBT 14943. The description is based on the best preserved left humerus of the MBT 14943 skeleton. Comparative measurements are presented in Table 3.

The humerus of *Atocetus*(?) *fuchsii* is reduced in length in comparison with other Miocene kentriodontids such as *Delphinodon dividum* TRUE, 1912 and *Incacetus broggii* COLBERT, 1944, but not as compact and stout as in members of the Delphinidae. There is a distinct neck region, which is the narrowest portion of the bone in lateral view. Distally the shaft extends anteroposteriorly, indicating large attachment site for the deltoid muscle. The deltoid tuberosity is distinct but not prominent, and it occupies the distal half of the anterior margo. Nevertheless, it does not reach the distal epiphysis. The infraspinous fossa is moderately large, shallow and it sits just below the caput, anterior to the main axis of the shaft in lateral view. The caput is relatively small (its dorsoventral depth takes up about one-third of the humerus length) and is slightly shifted laterally. The greater tubercule forms a small but distinct plateau on the top of the anterior margin of the humerus. The lesser tubercule is mediolaterally broad with an elevated posterior area. In anterior and posterior views the humerus is not very robust but rather flat, where the lesser tubercule extends medially from the main axis of the bone. On the posterior margo, a large articular surface indicates the presence of a well-developed olecranon process of the ulna.

Radius and ulna –The lower arm is slightly longer than the humerus. The radius is broader than the ulna, and both lower arm bones are mediolaterally flattened. The anterior margin of the radius is convex, its posterior margin is slightly concave. The ulna has straight anterior and posterior margins, so that the narrow gap between the radius and ulna has a semilunar outline. The radius and ulna attach at their proximal and distals ends, but a small articular facet for their attachment is found at their proximal ends only. The olecranon process of the ulna is well-defined, flag-like.

Manus – The carpals are ordered in two distinct rows. In the more proximal row, the scaphoid and the cuneiform are relatively small and pentagonal, whereas the lunar is very large and has a trapezoid form. A small trapezium opens the second row at the radial margin. This is followed by the pentagonal trapezoid, which interdigitates with the scaphoid and the lunar. The next carpal, which interdigitates with the lunar and the cuneiform, is probably the unciform. This means that there is no magnum. The metacarpal I is small and gracile, whereas the metacarpals II-V are elongated, ca. 2-2.5 times longer than wide. The proportions of the preserved phalanges are similar to those of the metacarpals. The number of phalanges is not clear, their probable arrangement is 1-6-5-3-1.

TABLE 3

Measurements of the humerus, radius and ulna of Atocetus(?) fuchsii from the Iris Quarry of Cluj-Napoca (in mm; ±0.5 mm; ?: missing data).

	MBT 14943, left	MBT 15029, left
Length of the humerus	54.0	?
Anteroposterior diameter of the head of the humerus	19.5	?
Dorsoventral diameter of the head of the humerus	22.5	?
Mediolateral width of proximal epiphysis	30.0	?
Anteroposterior extension of the humerus neck	21.0	?
Mediolateral extension of the humerus neck	18.0	?
Anteroposterior extension of the distal epiphysis of the humerus	33.0	26.5
Mediolateral extension of the distal epiphysis of the humerus	14.5	12.5
Length of the radius	60.0	?
Anteroposterior extension of the proximal end of the radius	23.5	?
Anteroposterior extension of the distal end of the radius	29.5	?
Length of the ulna	53.5	?
Anteroposterior extension of the distal end of the ulna	28.0	?

DISCUSSION

In his monograph on the Vienna Basin fossil Cetacea, Brandt (1873a) introduced a new species that he questionnably assigned to the genus *Champsodelphis* GERVAIS, 1848. *Champsodelphis fuchsii* BRANDT, 1873 was based on postcranial material that came from a brick quarry of Vienna in 1859 (Brandt, 1873a). Brandt (1873a: p. 269) included in the species 13 other vertebrae from the Sarmatian of Kishinev (Moldavia), which had been described previously by Nordmann (1860) as *Delphinus fossilis bessarabicus*. Van Beneden & Gervais (1880) already noted that Brandt's species is a synonym of the latter. However, the type material of *D. fossilis bessarabicus* is even less diagnostic than that of *C. fuchsii*, and thus the complete taxonomic review of *C. fuchsii* is problematic. The re-investigation of the holotype material of *D. fossilis bessarabicus* is beyond the scope of the present study and thus, we use the species name *"C." fuchsii* here.

The Romanian skeletons are assigned to the species *"Champsodelphis" fuchsii* on the basis of their humerus morphology. It is often stated that the morphology of the postcranial elements including the humerus provides little phylogenetic information in the Odontoceti (e.g. Fordyce & Muizon, 2001). Yet, the likely number of odontocete species in the Carpathian Basin late Middle Miocene is known, and moreover it has been surveyed mainly on the basis of the humerus morphology (Kazár, 2003). Hence, the morphologic agreement between the humeri of the Iris Quarry specimens and the holotype of *"C." fuchsii* is regarded here as taxonomically reliable.

The possibility to phylogenetically revise *"C." fuchsii* arose by studying the dolphin material of the Iris Quarry in Cluj-Napoca.

Although the herein described material contains in large part the same postcranial elements as does the holotype (cervical and lumbar vertebrae, sternum, scapular fragment and humerus), the tympanic bullae and especially, the periotics of the MBT material extend our knowledge about the phylogenetic relations of the species. The periotic associated with the MBT 15029 skeleton and the MBT 15001 periotics undoubtedly show affinities with members of the family Kentriodontidae. The elongated form of the periotic, the low pars cochlearis, the narrow, almost slit-like internal auditory meatus and especially, the placement of the dorsal angle vs. the ventral angle on the anterior process indicate close phylogenetic relations with *Atocetus* spp.

In diagnosing the genus *Atocetus*, Muizon (1988a) emphasised that the dorsal angle of the anterior process of the periotic is always situated anterior to the ventral angle in medial view. Two of the three periotics from the Iris Quarry display this character state (in MBT 15001/a the corresponding part of the periotic is broken away), for which it seems reasonable to questionnably include *"Champsodelphis" fuchsii* in the genus *Atocetus*. There are other features of the periotic that show close relationships to *Atocetus*. Barnes (1985) gives a list of peculiarities of the periotic of *A. nasalis*, which include the presence of a prominent crest on the posteromedial margin of the internal auditory meatus and the eminence between the fenestra rotunda and the perilymphatic foramen. The former can be observed with one periotic of the Iris Quarry material, the latter eminence is prominent in all three periotics of *A.*(?) *fuchsii*. The only important

difference between the periotics of *A.*(?) *fuchsii* vs. *A. nasalis* and *A. iquensis* is the morphology of the anterior process, which is larger and has a pointed tip in Brandt's species.

More dramatic are the differences of the tympanic bullae between the Iris Quarry finds and those of *A. nasalis* and *A. iquensis*. The narrowed inner posterior prominence and the low involucrum of *A.*(?) *fuchsii* is in sharp contrast with the robust bullae and the bulbous posterior parts of the involucrum in the North and South American species. It is unknown whether the different tympanic morphology of *A.*(?) *fuchsii* reflects difference in the hearing abilities of the species. Studies focusing on the hearing of odontocetes equivocally indicate that the cochlear structure is directly connected with hearing (e.g. Fraser & Purves, 1960; Fleischer, 1976; Ketten, 1992; Luo & Eastman, 1995; Luo & Marsh, 1996), but little information exists on the differences in the tympanic morphology of odontocetes on lower taxonomic level as related to differences in function. Nummela et al. (1999) concluded that the tympanic bullae are functionally similar in extant odontocete taxa in spite of the differences in their morphologies. If this holds true for the Miocene species of *Atocetus*, then different habitats can not account for the contrast in tympanic morphology between *A.*(?) *fuchsii* and the other two species of the genus.

The humerus morphology varies considerably between species of the Kentriodontidae (for a short overview see Kazár & Venczel, 2003). *Atocetus iquensis* and *A.*(?) *fuchsii* have remarkably similar humerus morphologies in that their shafts are extending distally in lateral view. The deltoid tuberosity is not very prominent but it occupies a large part of the radial margin, and it almost reaches the distal epiphysis of the bone in both species. The only known Middle Miocene form with a similar morphology is another Carpathian Basin kentriodontid (unnamed n. sp. of Kazár & Venczel, 2003). The humerus of *A.*(?) *fuchsii* differs from *A. iquensis* in the presence of the fovea olecranica. In the Peruvian species, a complete reduction of the olecranon process of the ulna can be observed (Muizon, 1988a). Muizon (1988a) regarded this feature diagnostic for the genus *Atocetus*, but in the light of the newly described material of *A.*(?) *fuchsii* it seems more likely that the reduction of the olecranon took place only in *A. iquensis*.

TAPHONOMY

The dolphin material from the Iris Quarry of Cluj was collected in the 1960s, without taphonomic data collection. Luckily, during the excavation and subsequent preparations, most of the skeletal elements were not removed from the matrix. Figure 9 and 10 of Plate 1 show the skeletal elements of the MBT 14943 and MBT 15029 specimens in the calcareous marl slabs. The MBT 15001 ear bones were found *ex situ*, washed out from the section close to the site where the skeletons were excavated (oral communication from Prof. Şuraru Nicolae to V. Codrea). The left periotic and tympanic, and the right tympano-periotic complex most likely belonged to a single individual, indicating that a third skeleton might have been preserved in the dolphin-bearing layer.

The preserved vertebrae, and most bones of the left flipper of the MBT 14943 specimen remained in anatomical articulations. Only the cuneiform of the carpals is somewhat dislocated, and the distal phalanges of some fingers are lost. The scapula lies in its presumed original position, however, the whole flipper is shifted to close at a smaller than physiologically normal angle with the main axis of the scapula. The left flipper is exposed with its medial surface upward. A few more carpals and phalanges lie in the vicinity of the left elbow joint, these are most likely disarticulated elements of the right flipper, just like the fragmentary right humerus and radius. The latter elements were found between the arch of the vertebral column and the left scapula. From the placement of the flipper elements it can be concluded that the carcass was lying on its left side when buried, and that the soft tissues of the chest and the left flipper completed decomposition after burial. The right flipper, on the other hand, probably hung out from the sediment and so its elements became disarticulated and displaced before burial. The two possible cranial fragments indicate that the skull undervent fossilization with the other elements.

The MBT 15029 shows a somewhat different scenario. Here, all elements are disarticulated and displaced from their original anatomical positions. Nevertheless, both tympano-periotic complexes were preserved in the vicinity of the mandible, the atlas, axis and the subsequent cervical and thoracic vertebrae are approximately in anatomical sequence. Also, the scapula and the sternum are partially overlapping, pointing to only slight displacement of the elements. While the left periotic and tympanic were probably lost after excavation (their impressions were clear in the unprepared slab), the skull is altogether missing and was possibly not fossilized. In conclusion, the carcass of the MBT 15029 specimen probably had became already incomplete before it sunk to the bottom (? with its skull and posterior parts of the vertebral column already lost) in a fashion described by Schäfer (1962). The possibly slow burial must have followed the decomposition of the soft tissues.]

PALEOBIOLOGY

Both skeletons (MBT 14943 and MBT 15029) have completely fused vertebral centra, and the epiphyses of the preserved arm bones are likewise ankylosed to the shafts. Thus, both specimens are considered physically mature. A comparison of the

elements preserved with both skeletons, notably, the humeri and some of the thoracic vertebrae, reveals that the humerus of the MBT 14943 individual was considerably (20-25%) larger than that of the MBT 15029 (Table 3). The vertebral measures, on the other hand, do not draw such a clear picture (Table 2). The width and height of the vertebrae are generally larger in the MBT 14943 specimen, whereas the centrum lengths are more or less the same in both specimens or slightly larger in the MBT 15029. These data suggest that in *Atocetus*(?) *fuchsii* either significant intraspecific variation in body size or sexual dimorphism must be presumed. In a sexually dimorphic population of the recent bottlenose dolphin (*Tursiops truncatus*) the males possess allometrically larger propulsion features and weapons (flippers and flukes), which may help them to coerce females as part of their mating strategy (Tolley et al., 1995; Connor et al., 2000).

The length reduction of the vertebral centra accompanied by an increase in the vertebral count is a tendency of phylogenetic significance, which is directly correlated with column stability and swimming style (Howell, 1930; Slijper, 1936; Buchholtz, 2001). *Atocetus*(?) *fuchsii* had slightly elongated lumbar and posterior thoracic vertebrae, whereas the contemporaneous *A. iquensis* (late Middle to early Late Miocene; Muizon, 1988a) and the geologically younger *A. nasalis* (Late Miocene; Barnes, 1985) had shortened bodies of the thoracic and lumbar vertebrae. Both *A. iquensis* and *A. nasalis* were more derived in this respect than *A*.(?) *fuchsii*.

The flipper of *A*.(?) *fuchsii* shows the general outline of modern delphinids, however, a number of differences suggest that the Middle Miocene species was less specialized (Fig. 2). The humerus, although progressive among Miocene kentriodontids in its reduced length and in the distal broadening of the shaft, is much less robust and compact than the humerus of present-day delphinids. The gap between the radius and ulna indicates the remnant of the antebrachial muscles. The number and overall morphology of the carpals is the same as in modern dolphins, but their size, and especially, that of the lunar is larger than in *Tursiops* and *Stenella*. The carpalia, as a whole, occupy more of the flipper area than in present-day delphinids. Likewise, the metacarpals and the phalanges are more elongated in *A*.(?) *fuchsii*. Although the exact number of phalanges of the fingers II-IV is uncertain, it appears that hyperphalangy of the fingers II-III was less pronounced in *A*.(?) *fuchsii* than in modern delphinids such as *Tursiops truncatus*, whereas the fingers IV and V were not as reduced in length.

The flipper of *Atocetus*(?) *fuchsii* was wider at the level of the carpals, and probably shorter and less rigid than the pelvic limb of the pelagic, fast-moving dolphins of recent days.

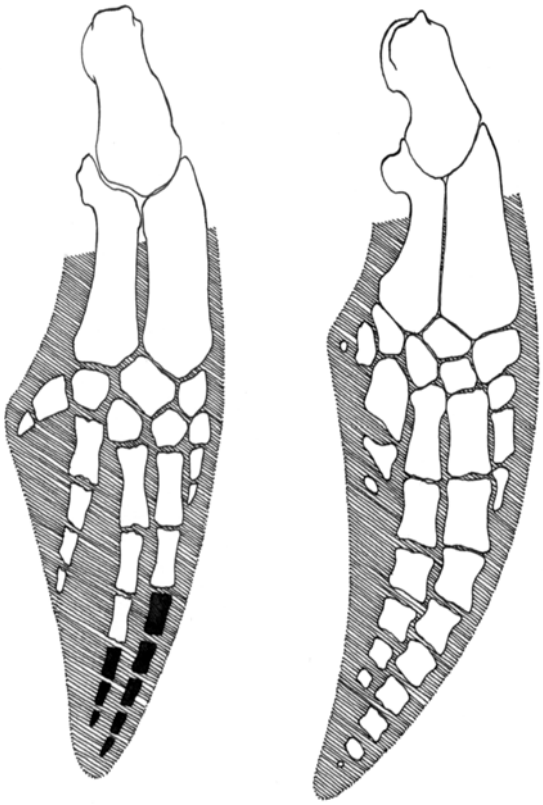

Figure 2. Comparison of the forelimbs of the Middle Miocene *Atocetus*(?) *fuchsii* (to the left; based on the MBT 14943 specimen) and the recent *Stenella attenuata* (to the right; skeletal parts redrawn after Perrin, 1975). Drawn are the left forelimbs in medial view. Not to scale. Shaded area: Supposed outline of the flippers. Black filling: reconstructed elements. The exact number of phalanges of fingers II and III of *A*.(?) *fuchsii* is unknown and thus, the outline of its flipper is hypothetical. The supposed phalanges 2 and 3 of finger IV were dislocated in the MBT 14943 specimen, their exact orientation is reconstructed.

PALEOBIOGEOGRAPHY

Besides the type locality and the Iris Quarry in Cluj-Napoca, Romania, *Atocetus*(?) *fuchsii* has been reported from a few other localities in the Vienna Basin and in Hungary (Brandt, 1873a; Kazár, 2003). However, future taxonomic revision of the species may possibly extend the fossil record of *A*.(?) *fuchsii* in the Paratethys region. In spite of recent advances in the study of old and new Miocene delphinoid material (e.g. Bianucci et al., 1994; Bianucci & Varola, 1995; Bianucci, 2001; Brocard, 2000), there is no indication of the species in the Mediterranean and the Atlantic coasts of Europe. Other members of the subfamily Pithanodelphinae in Europe are *Pithanodelphis cornutus* DU BUS, 1872 from the Miocene of Antwerp, Belgium (Du Bus, 1872), and *Leptodelphis stavropolitanus* KIRPICHNIKOV, 1954 from the Middle Miocene of Moldavia (Kirpichnikov, 1954; Muizon, 1988b). Barnes (1978) suggested that the Moldavian species *Sarmatodelphis moldavicus*

KIRPICHNIKOV, 1954 may be another member of the subfamily. The latter two species, however, are based on fragmented skulls and are in need of a taxonomic review.

The closest relatives of *A.*(?) *fuchsii*, members of the genus *Atocetus* have recorded occurrences from the Pisco Formation of Peru (Muizon, 1988a) and from Orange County, California (Barnes, 1985, 1988). More recently, a new species of *Atocetus* has been discovered from the Late Miocene of the Chino Hills, California (Barnes et al., 2003). All these species were found at the eastern shoreline of the Pacific Ocean in the north and south hemispheres. The remains of *Atocetus*(?) *fuchsii* in Central Europe show that the genus was represented in the ancient sea Paratethys as well, and it must be assumed that a related species inhabited the Atlantic Ocean and the Mediterranean, through which the ancestors of *A.*(?) *fuchsii* could enter the Paratethys.

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PLATE I

Fig. 1 – MBT 15001/a, left periotic in dorsal view (a) and in ventral view (b). Scale bar for Figs. 1, 2 and 3 equals 1 cm.

Fig. 2 – MBT 15001/b, right tympano-periotic complex in lateral view.

Fig. 3 – MBT 15001/c, left tympanic bulla in medial view (a) and in ventral view (b).

Fig. 4 – MBT 15029, atlas from anterior and slightly dorsal. Scale bar for Figs. 4-7 equals 1.5 cm.

Fig. 5 – MBT 15029, 7th cervical vertebra.

Fig. 6 – MBT 15029, thoracic vertebrae in ? anterior view.

Fig. 7 – MBT 15029, lumbar vertebra in ventral view. Posterior: upwards.

Fig. 8 – MBT 14943, left humerus in anterior view (a) and in lateral view (b). Scale bar: 3 cm.

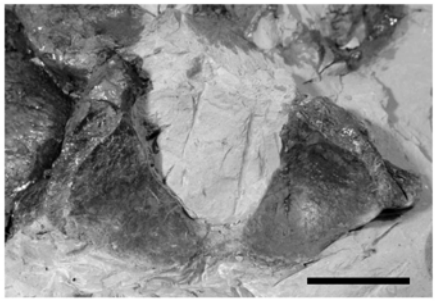
Fig. 9 – MBT 14943, all preserved skeletal elements in situ. The 10th thoracic vertebra is erroneously placed in the place of the (missing) 9th thoracic vertebra in the photograph. Diameter of the Nikon lense cap is 5.5 cm.

Fig. 10 – MBT 15029, all preserved skeletal elements in situ. Scale bar: 3 cm.

3a

3b

2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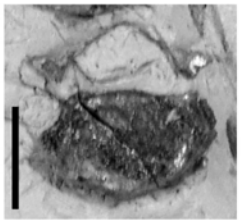
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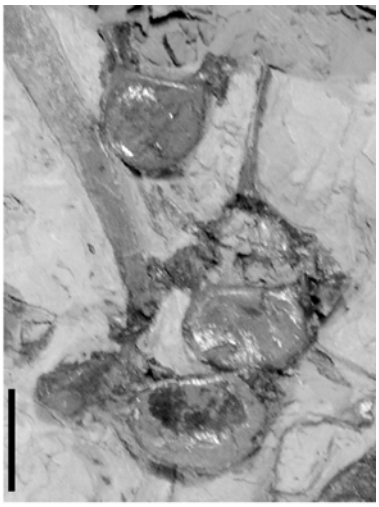
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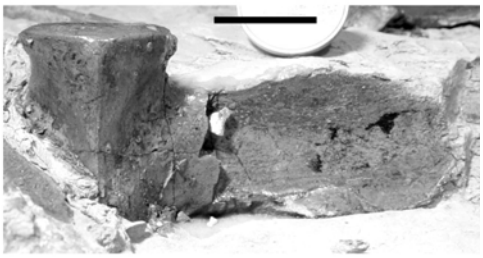
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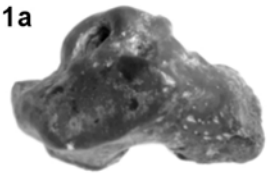
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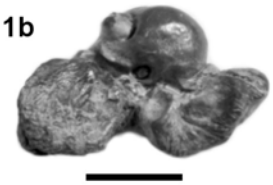
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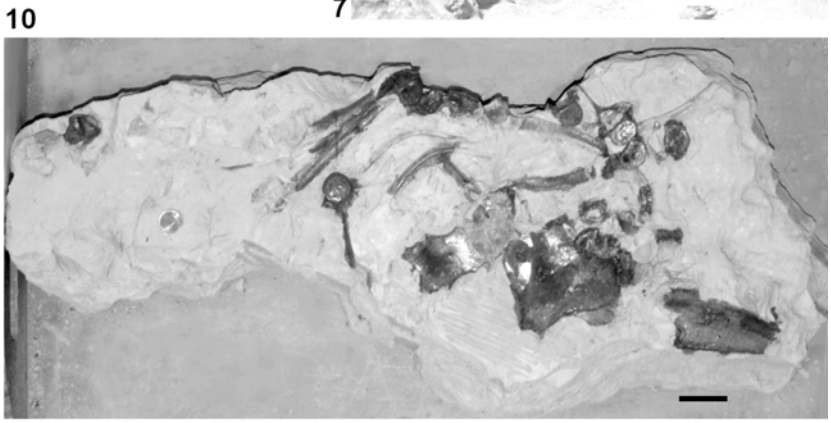
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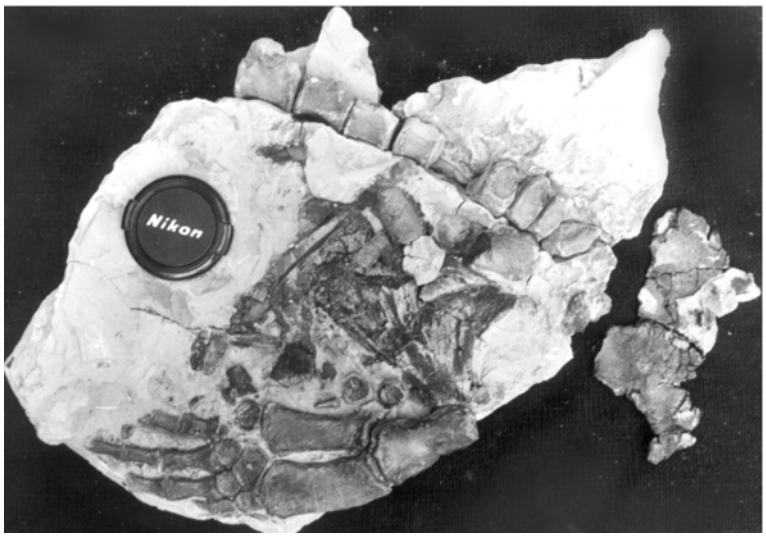
Nikon
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8a
8b