A new Middle Miocene odontocete (Mammalia: Cetacea) locality and the Sarmatian Marine Mammal Event in the Central Paratethys

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ABSTRACT – A few disarticulated odontocete (Cetacea: Odontoceti) fossils have been found at Comăneşti in western Romania. The locality had hitherto yielded only brackish mollusks and terrestrial micromammals. The entire stratigraphic section was divided by Radulescu & Samson (in Feru et al., 1980) into two local biostratigraphic units: Comăneşti-1 (Sarmatian) and Comăneşti-2 (Pannonian). On the basis of micromammals of the same deposits, these two authors assigned Comăneşti-1 to the MN8 zone of the Mediterranean Neogene. This can be correlated with the upper Volhynian of the Eastern Paratethys, possibly including also the base of the Bessarabian.
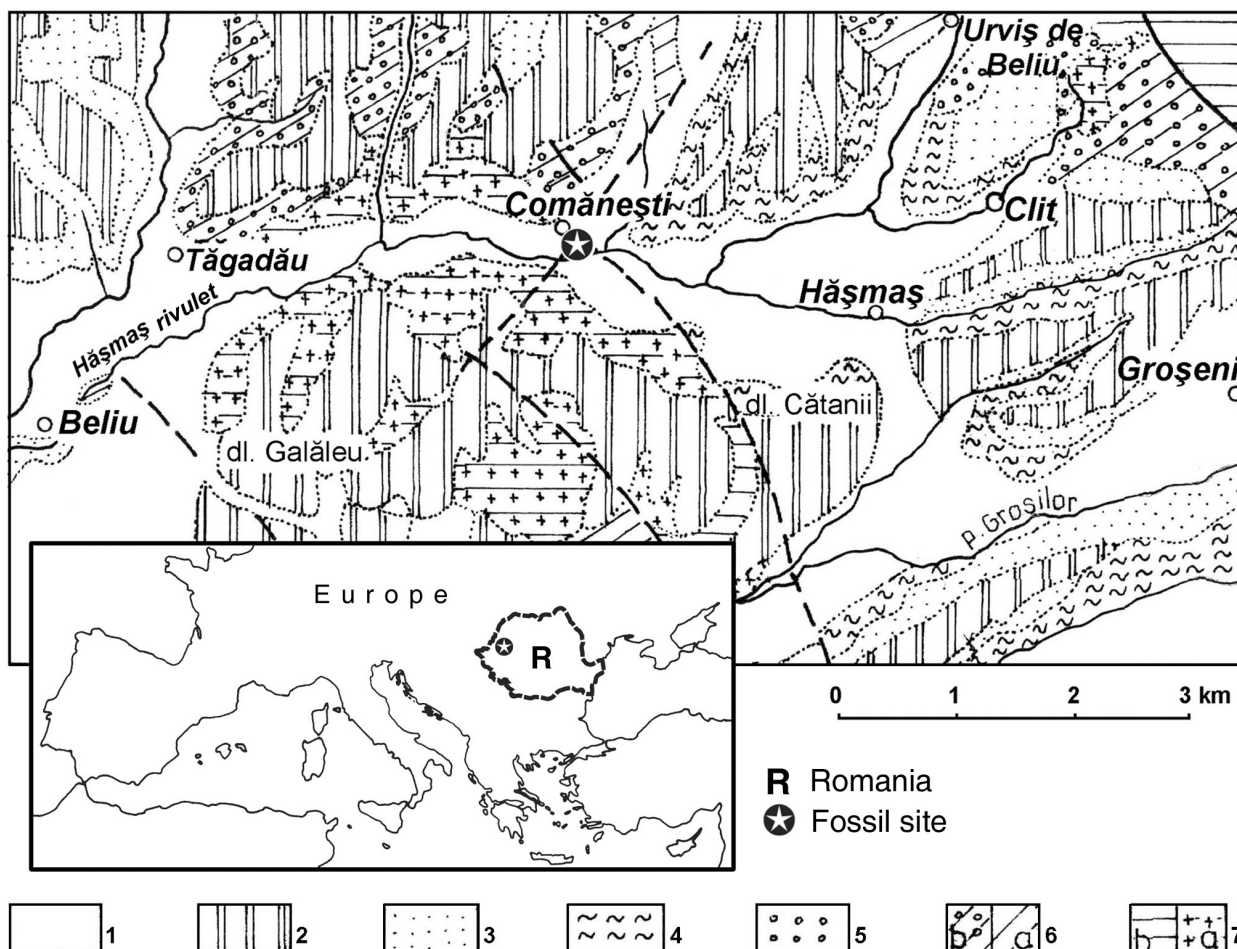The fossils are assigned to *"Champsodelphis" fuchsii* Brandt, 1873, a species already known from six other localities in the Carpathian Basin, specifically from the Vienna Basin of Austria, south Hungary, and western Romania. Several other late Middle Miocene odontocete localities are known from the Carpathian Basin as well. In all cases where zonation was possible, the stratigraphic position of the occurrences is lower Sarmatian, including the upper *Ervilia* Zone (ca. 12 Ma). This correlation suggests that there was a 'marine mammal event' in the Central Paratethys at that chronostratigraphic level, which was the re-appearance of small odontocetes, mysticetes, and phocid seals from the Eastern Paratethys. The Sarmatian 'Marine Mammal Event' followed the marine regression of the late Badenian (ca. 13 Ma), which caused the apparent disappearance of marine mammals in this area. Sperm whales and sirenians, all well-documented from the Middle Badenian, failed to invade the Central Paratethys again.

Key words: Miocene, Sarmatian, Central Paratethys, Romania, Odontoceti

Une nouvelle localité à Odontocètes (Mammalia: Cetacea) du Miocène Moyen et «l'Événement Mammifère Marin» du Sarmatien dans la Paratethys Centrale – Quelques os désarticulés rapportés au dauphin *Atocetus*(?) *fuchsii* (Brandt, 1873) sont décrits en provenance de Comăneşti, dans l'ouest de la Roumanie. La localité était jusqu'alors connue seulement par des assemblages de mollusques d'eau saumâtre et de micromammifères terrestres. La section stratigraphique a été divisée par Radulescu et Samson (in Feru et al., 1980) en deux unités biostratigraphiques locales: Comăneşti-1 (Sarmatien) et Comăneşti-2 (Pannonien). Sur la base des micromammifères trouvés dans les mêmes dépôts que les restes de dauphin, les deux auteurs ont placé Comăneşti-1 dans la zone MN8 du Neogène Mediterranéen qui correspond au Volhynien final, voire même au début du Bessarabien.
Les fossiles sont attribués à *"Champsodelphis" fuchsii,* qui est déjà connu dans six autres localités du Bassin des Carpates, notamment dans le Bassin de Vienne en Autriche, dans le sud de la Hongrie et dans l'ouest de la Roumanie. D'autres localités du Miocène moyen-terminal contenant des odontocètes sont connues dans le Bassin de Carpates, en incluant la partie supérieure du *Ervilia* zone (ca 12 Ma). Dans tous les cas où une zonation a été possible, la position stratigraphique des découvertes se situe dans le Sarmatien inférieur (~12 Ma). Cette corrélation suggère la présence d'un «événement mammifère marin» dans la Paratethys Centrale à ce niveau chronostratigraphique qui correspond à l'arrivée depuis la Paratethys Orientale des odontocètes de petite taille, ainsi que des mysticètes et des phoques. Cet «événement mammifère marin» a suivi la régression marine dans la Paratethys Centrale à la fin du Badenian (~13 Ma) qui a causé l'apparente disparition des mammifères marins dans cette région. Les cachalots et les siréniens, tous très bien documentés dans le Badenien moyen, n'ont pas envahi à nouveau la Paratethys Centrale.

Mots clés: Miocène, Sarmatien, Paratethys, Roumanie, Odontoceti

INTRODUCTION

During search for micromammals in the Miocene deposits of the Crisul alb Basin (Western Romania), a few isolated odontocete skeletal remains were found by Costin Radulescu and Petru Samson near the village Comăneşti in the late 1970s. The odontocete bones were not mentioned in the publication that followed (Feru et al., 1980), nor in any other paper. The fossil remains, consisting of a periotic and a tympanic, two humeri, and three vertebrae, were handed over to the senior author of the present paper who recorded them in the Catalogue of the Laboratory of Paleontology/ Faculty of Geology and Geophysics, University of Bucharest (UBFG) as *Acrodelphis* sp.

Based on the micromammals, Radulescu and Samson divided the entire stratigraphic section of Comăneşti in two parts: Comăneşti-1 (Sarmatian) and Comăneşti-2 (Pannonian). The micromammal assemblage of Comăneşti-1, which also yielded the odontocete remains, was assigned to the MN8 zone of the Mediterranean Neogene by Radulescu & Samson (in Feru et al., 1980).

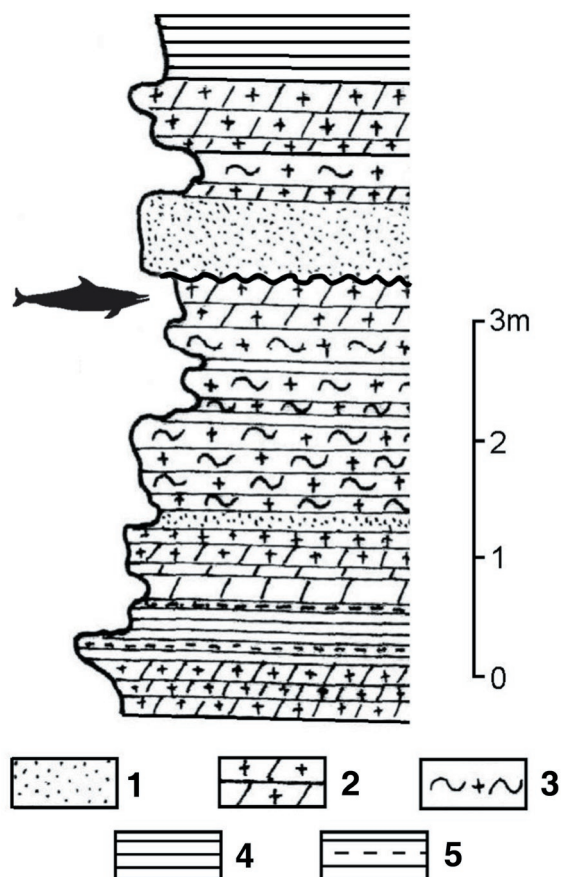The significance of the isolated odontocete bones is that no cetaceans have been reported from the locality before. On the other hand, the species identified at Comăneşti-1 is known from a number of other Carpathian Basin localities (Brandt, 1873; Kazár, 2003; Kazár et al., 2004). The aim of the present publication is to document the odontocete remains from Comăneşti-1, to discuss the paleobiogeographic evidence of the species they represent, and finally, to investigate the patterns of Miocene marine mammal occurrences in the territory of the Central Paratethys Sea.

The odontocete remains from Comăneşti-1 were compared with specimens of the collections of the Geological Museum of Hungary, Geological Institute of Hungary, Budapest (MÁFI), the Musée "Bassin de Transylvanie", Université "Babeş-Bolyai", Cluj-Napoca (MBT), the Muséum national d'Histoire naturelle, Paris (MNHN), the Naturhistorisches Museum Wien (NHMW), the Paläontologisches Institut der Universität Wien (UW), and the United States National Museum of Natural History of the Smithsonian Institution, Washington, D.C. (USNM).

In the anatomical description of the fossil remains we mainly followed Flower (1870) and Rommel (1990); terminology of the ear bones is derived from Kasuya (1973), Barnes & Mitchell (1984), and Luo & Marsh (1996). We use the vernacular name "dolphin" as a general term for small odontocetes, and do not imply affinities with the family

Figure 1 (left) – Geological map of the Crişul alb Basin around Comăneşti (after Istocescu, 1971) and the location of the fossil site within Europe (inserted map). *Legend*–1: Holocene; 2: Pleistocene; 3: upper Pannonian; 4: lower Pannonian; 5: upper Sarmatian; 6: lower Sarmatian; a: lower, tuffitic–diatomitic bed; b: lacustrine/volcanogenic bed; 7: Badenian; a: volcanoclastic facies, b: marly facies.

Figure 2 (right) – Lithological sequence of the fossil site on the right bank of the Hăşmaş Valley at Comăneşti (after Istocescu, 1971). *Legend*–1: sands; 2: tuffitic marls; 3: tuffitic claystones; 4: diatomite and diatomitic shales; 5: bioaccumulated marls with *Cardium vindobonense*. Symbol of dolphin: the level where the odontocete remains came from, as indicated by Radulescu.

Delphinidae.

The Central Paratethyan stage name Sarmatian has been used for deposits of the Eastern Paratethys as well (for a more comprehensive discussion see Harzhauser & Piller, 2004). Recently, Harzhauser & Piller (2004) recommended to abandon the term Sarmatian for the Eastern Paratethys and urged the usage of the regional stage names Volhynian, Bessarabian, and Khersonian instead. In the following, we will use the term Sarmatian sensu lato, when citing literature in which Sarmatian stands for Eastern Paratethyan deposits.

GEOLOGIC SETTING

According to Radulescu and Samson (personal communication to D.G.), the odontocete bones were collected from a lens-like bed of tuffaceous marls of maximum 12 cm thickness, intercalated in a 11 m thick vertical section on the right side of the Hăşmaş rivulet at the eastern end of the village Comăneşti (N46°29'08.1" and E22°3'58"; Fig. 1). The small pits on the surface of some of the bones still preserve the fine whitish embedding matrix.

The entire lithological section belongs to the "tuffitic–diatomitic complex" separated by Istocescu (1971) and afterwards by Istocescu & Istocescu (1974), representing the lower part of the Sarmatian (late Middle Miocene) from the Crisul alb Basin (Fig. 2). According to these authors, the lithostratigraphic column of the Sarmatian from the region is completed by two parts that overlie the lower one, namely "the middle complex: lacustrine or volcanogen" and "the upper complex, biogenetic and epiclastic". Based on mollusk assemblages, the lower and the middle parts are assigned to the Volhynian, while the upper one is reported to be Bessarabian (Istocescu, 1971).

Although Comăneşti is located in the territory of the Central Paratethys, Istocescu (1971), Istocescu & Istocescu (1974), and Radulescu & Samson (in Feru et al., 1980) used the Eastern Paratethyan stage names Volhynian and Bessarabian. In our paper, we apply these terms for Central Paratethyan localities as citations.

(1) The lower, "tuffitic-diatomitic" part consists of thin beds, usually less than 10 cm thick, of alternating sandy tuffite, tuffitic marls and diatomitic shales. The layer from the base of the section is rich in mollusk shells and shell debris, among which the following taxa were recognized: *Cardium vindobonense vindobonense* (Partsch), *Ervilia dissita podoloca* (Eichwald), *Trochus pictus* Eichwald. These are characteristic of the lower Volhynian. (2) The lens-like

tuffitic sands that provided the odontocete bones, lie 2.5 m above the shelly bed, and also include numerous fragments of mollusk shells, especially of the genus *Cardium*. (3) The sandy layers that overlie the tuffitic bed provided an assemblage of terrestrial micromammals including *Galerix socialis* (Meyer), *Hispanomys* cf. *lavocati* (Freudenthal), *Megacricetodon* gr. *similis* (Fahlbusch), *Democricetodon* gr. *gaillardi* (Schaub), *Peridyromys* gr. *hamadryas* (Major), *Myoglis meini* (de Bruijn), *Prolagus oeningensis* (König), together with fragments of turtles and fishes. Radulescu & Samson (in Feru et al., 1980: 187) assigned this assemblage to the upper part of the MN8 biozone of the Mediterranean Neogene, the upper limit of which probably coincides with the uppermost Volhynian of the Eastern Paratethys, possibly including the base of the Bessarabian (Feru et al., 1980). Steininger et al. (1996) assigned Comăneşti-1 to the Central Paratethyan lower Sarmatian.

Sedimentologically, the sequence that outcrops on the right side of the Hăşmaş rivulet near Comăneşti, corresponds to a shallow marine episode in a calm, lagoon or bay type of basin, in which the main sediment supply was the eroded clastic sediments carried in by the rivers from the continent. These sediments carried the fine products of the volcanic eruptions of the region and the micromammal remains. The silica resulted from the eruptions and dissolved in the brackish water of the basin. It was then incorporated by the tiny skeletons of the planktonic diatoms that formed the diatomite and the diatomitic shale, a major component of the lithostratigraphic section of Comăneşti-1.

Description of the odontocete remains from Comăneşti

Cetacea BRISSON, 1762
Odontoceti FLOWER, 1867
Odontoceti indet.

UBFG.221/1, caudal vertebra of adult (Fig. 3: 1) – This is a vertebra from the middle part of the caudal series. Both epiphyses are ankylosed to the centrum. The vertebral body is not foreshortened but elongated, the epiphyses are nearly circular (depth at anterior epiphysis: 25.0 mm, width at anterior epiphysis: 27.5 mm, length of vertebral body: 37.5 mm). In lateral view, the centrum faces are gently convex anteriorly and posteriorly. On the ventral surface the vertebra has distinct processes for the chevron bones both anteriorly and posteriorly, but the posterior ones are larger. The transverse processes are now broken away. Their bases are set posteriorly on the vertebral body, and they were relatively narrow. On either side, a large arterial foramen passes through the vertebral body near the insertion of the transverse processes. The foramen on the right side is larger and opens slightly more anteriorly than the left one. The neural arch is positioned anteriorly on the vertebral body, and the neural canal is narrow.

UBFG.221/2, caudal vertebra of juvenile (Fig. 3: 2) – This

is a small vertebra from the posterior part of the vertebral column. Both epiphyses are missing. The vertebral body is higher than long and laterally compressed (depth: 19.5 mm, width: 17.0 mm, length: 17.5 mm). The spine is low and triangular, the neural canal is closed. The transverse processes are completely reduced. One small arterial foramen opens dorsally on either side of the vertebral body posterior to midlength.
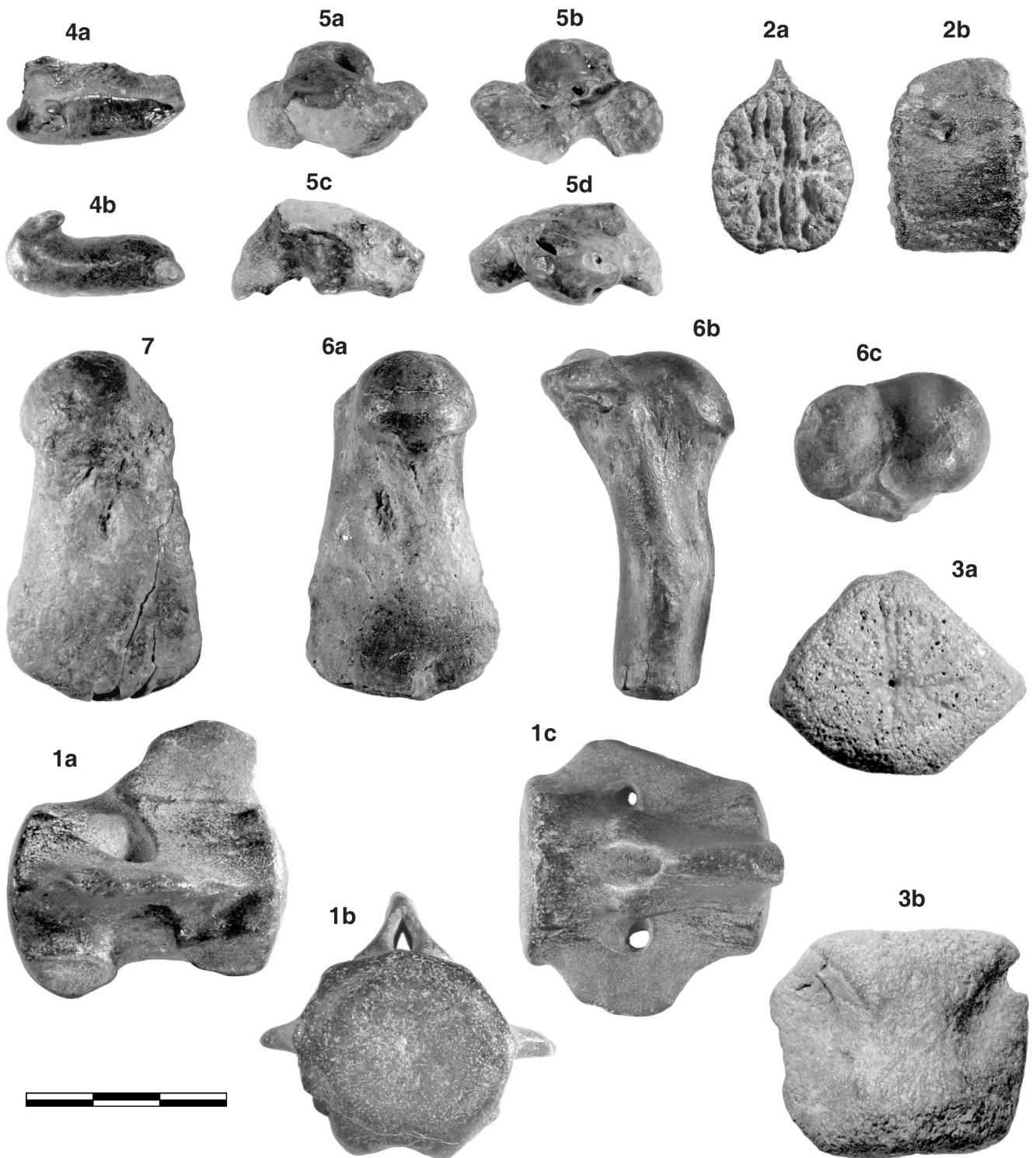
UBFG.224, lumbar(?) vertebra (Fig. 3: 3) – This vertebra with somewhat eroded surfaces originates either from the lumbar region, as concluded from the arterial depressions forming a V-shape on the ventral surface of the bone, or from the caudal series, as indicated by the strongly eroded eminences on the ventral aspect of the vertebra that could be the attachment sites of the chevron bones. The vertebral body is slightly elongated and the epiphyses are somewhat wider than high (depth: ca. 23.5 mm, width: ca. 26.0 mm, length: 30.5 mm). The faint ridges on the anterior aspect of the vertebra may indicate a missing epiphysis. The neural canal was extremely narrow if open at all, and there is no arterial opening on the centrum.

Discussion – The Odontoceti indet. remains from Comăneşti-1 belonged to at least two individuals, because a caudal vertebra from the peduncle region (UBFG.221/2) lacks both epiphyses, indicative of juvenile ontogenetic stage, whereas a more anterior caudal vertebra (UBFG.221/1) has fused anterior and posterior epiphyses. It is well known that ankylosis of the vertebral epiphyses to the centra begins at both ends of the vertebral column and progresses to the middle in cetaceans.

A systematic identification of the vertebrae within the Odontoceti is not possible. The lateral compression of UBFG.221/2 is typical of the peduncle region of cetaceans (Buchholtz & Schur, 2004). The elongated form of UBFG.221/1 is regarded as primitive (Muizon, 1988a; Buchholtz, 2001), as contrasted by the foreshortened caudal vertebrae of the Middle to Late Miocene *Atocetus* (Barnes, 1985; Muizon, 1988b). The elongated body and the convex centrum faces of the UBFG.221/1 vertebra are indicative of rotation with high displacement of the neighboring vertebrae during locomotion as pointed out by Buchholtz & Schur (2004).

Delphinida MUIZON, 1984
Delphinoidea GRAY, 1821
Delphinoidea indet.

UBFG.225, left tympanic (Fig. 3: 4) – The tympanic is fragmentary; only the involucrum and the inner posterior prominence has been preserved with the base of the posterior process and a medial fragment of the outer posterior prominence. The involucrum has a smooth dorsal surface and a delicately sinusoid dorsal contour. The inner posterior prominence is narrow. There is a broad median furrow between the inner and outer posterior prominences that

Figure 3 – Odontocete remains from Comăneşti, Romania. 1: UBFG.221/1, caudal vertebra in right lateral view (a); in posterior view (b); and in dorsal view (c). 2: UBFG.221/2, caudal vertebra in anterior view (a) and in right lateral view (b). 3: UBFG.224, lumbar(?) vertebra in anterior view (a) and in ventral view (b). 4: UBFG.225, left tympanic bulla in dorsal view (a) and in medial view (b). 5: UBFG.222, right periotic in dorsal view (a); in ventral view (b); in lateral view (c); and in medial view (d). 6: UBFG.223/1, left humerus in lateral view (a); in anterior view (b); and in dorsal view (c). 7: UBFG.223/2, right humerus in lateral view. Scale bar: 3 cm throughout Figure 3.

Total length from anterior tip of anterior process to posterior tip of posterior process	26.0
Width across cochlear part and ventrolateral tuberosity	16.0
Width across base of cochlear part	12.3
Distance between internal auditory meatus and perilymphatic foramen	2.6
Distance between internal auditory meatus and endolymphatic foramen	4.6
Distance between endolymphatic and perilymphatic foramina	4.8

Table 1 – Measurements of the periotic of *"Champsodelphis" fuchsii* Brandt, 1873 from Comăneşti-1, Romania (UBFG.222; in mm).

becomes progressively shallower anteriorly. The anterior lip of the bulla is obtuse and there was no anterior bullar spine. The total length of the tympanic bulla (measured from the anterior lip to the inner posterior prominence) is 26.1mm.

Discussion–The sinusoid dorsal contour and the lack of an anterior spine of the tympanic bulla are typical of species in the Delphinoidea (Muizon, 1988a). In the lack of more diagnostic features, the specimen can not be assigned to any known delphinoid taxa.

Kentriodontidae SLIJPER, 1936
Kentriodontidae incertae sedis:
"Champsodelphis" fuchsii Brandt, 1873

UBFG.222, right periotic (Fig. 3: 5) – The periotic is elongate with the anterior process projecting slightly antero-medially and the posterior process bending slightly postero-laterally. The cochlear part is mediolaterally small, attaches broadly to the body, and is not tilted anteriorly. The internal auditory meatus is narrow, almost slit-like. It is separated anteriorly from the internal facial foramen by a bony bridge so that the latter foramen opens outside the internal auditory meatus. There is no crest on the posteromedial margin of the internal auditory meatus. The perilymphatic and endolymphatic foramina are widely separated from each other and from the fundus of the internal auditory meatus. Between the fenestra rotunda and the foramen perilymphaticus a prominent eminence can be observed.

The dorsal surface of the periotic is flat in lateral view and slightly convex in anterior view. The anterior process is short but not reduced. 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 terminates in a tiny, conical process that gives the anterior process a rectangular profile, and this conus is positioned anterior to the ventral angle.

In the ventral aspect of the periotic, the fossa for the head of the malleus is moderately large and elliptical, the ventrolateral tuberosity is strong. A distinct cleft separates the cochlear part and the anterior process, which can be observed both in the ventral and dorsal views.

The posterior process has a pentagonal articular surface without an elongated postero-lateral tip. In lateral view, the posterior process has a slightly convex dorsal margin, which closes at a wide angle with the dorsal surface of the periotic. Measurements are given in Table 1.

UBFG.223/1, left humerus (Fig. 3: 6) – Complete humerus in good preservational state.

The left humerus from Comăneşti-1 is a slender bone. In lateral view the shaft is broad distally as compared to the neck region. The neck of the humerus is long, so that the infraspinous fossa is set at a considerable distance from the humeral head. The humeral head is small and is not shifted laterally. The greater tubercle forms a small, distinct plateau on the anterior margin of the proximal epiphysis. The lesser tubercle is broad, and has an elevated area in its posterior part. The infraspinous fossa is small and shallow, and it is placed closer to the anterior margin than to the posterior margin of the bone in lateral view. The posterior tuberosity is a low eminence posterior and distal to the infraspinous fossa. The area distal to the infraspinous fossa and the posterior tuberosity, which was presumably the attachment area of the deltoid muscle, is large, and slightly broader than long. The deltoid tuberosity is not prominent, but is a small rugose area on the anterior margin of the bone. It is positioned rather distally, but not reaching the distal epiphysis of the humerus. Posteriorly, the distal epiphysis of the humerus bears a small but distinct attachment site for the olecranon process of the ulna.

UBFG.223/2, right humerus (Fig. 3: 7) – Somewhat eroded humerus with fractures.

The overall shape of the humerus is similar to the UBFG.223/1 specimen, but the whole bone is more massive, and the neck is shorter so that the infraspinous fossa is close to the distal margin of the humeral head. The infraspinous fossa is a small and shallow depression. The head is small and it is shifted slightly laterally. In lateral view, the narrowest point of the shaft is the neck just distal to the humeral head, and from here the humerus becomes progressively broader distally. The attachment site for the deltoid muscle is broader than long. The deltoid tuberosity is indistinct and is placed distally on the anterior margin of the humerus, but it does not contact the distal epiphysis. The articulating surface for the olecranon process of the ulna is well-marked and

	UBFG.223/1, left	UBFG.223/2, right
Total length of humerus	51.0	51.5
Anteroposterior diameter of humeral head	18.0	(19.5)
Dorsoventral diameter of humeral head	20.0	20.5
Mediolateral width of proximal epiphysis	28.0	30.0
Anteroposterior width of proximal epiphysis	20.0	22.5
Mediolateral width of humeral neck	16.5	17.5
Anteroposterior width of humeral neck	19.5	20.0
Mediolateral width of distal epiphysis	13.0	15.5
Anteroposterior width of distal epiphysis	28.0	29.0
Distance between infraspinous fossa and crista distalis	24.0	24.0

Table 2 – Measurements of the humeri of *"Champsodelphis" fuchsii* Brandt, 1873 from Comăneşti-1, Romania (in mm; +/- 0,5 mm; parentheses indicate estimated value).

vertical. The greater tubercle is a small but distinct eminence anteriorly on the proximal epiphysis. The dorsal surface of the lesser tubercle is a nearly circular plateau with a slightly elevated posterior part.

Discussion – The periotic from Comăneşti-1 shows the characteristic rounded apex and mediolateral flattening of the anterior process of the Delphinoidea as discussed by Muizon (1988a). It shows marked resemblance to species of two kentriodontid genera, *Kentriodon* Kellogg, 1927 and *Atocetus* Muizon, 1988b.

The relative size and shape, and the rectangular profile of the anterior process is nearly identical in UBFG.222 and in the holotype of *Kentriodon pernix* Kellogg, 1927 (USNM 8060). Nevertheless, the dorsal angle of the anterior process bears a tiny eminence in the Comăneşti periotic, absent in *K. pernix*, which causes the dorsal angle being situated more anteriorly than the ventral angle of the anterior process (Fig. 3: 5c). In this respect, the Romanian periotic resembles *Atocetus iquensis* Muizon, 1988b. Muizon (1988b) regarded the more anterior position of the dorsal angle of the anterior process as a synapomorphy of the genus *Atocetus*, but a cf. *Kentriodon* sp. periotic from the Miocene Sharktooth Hill Bonebed of California also shows this feature (Barnes & Mitchell, 1984: fig. 11). The anterior process of the UBFG.222 periotic is markedly different from the almost rode-like anterior process of *A. iquensis* and *A. nasalis* (Barnes, 1985).

The posterior process of UBFG.222 has a pentagonal articulating surface, which is more circular than that of *Atocetus* and *Kentriodon*. The posterior process of the Romanian periotic is bent more laterally than in *Atocetus*, and is similar to *K. pernix* and *K. obscurus* (Kellogg, 1931). In the holotype of *K. pernix*, the posterior process closes with the dorsal surface of the periotic nearly at a right angle, whereas in *A. iquensis* there is a wide angle between these two structures. In this respect, UBFG.222 is intermediate
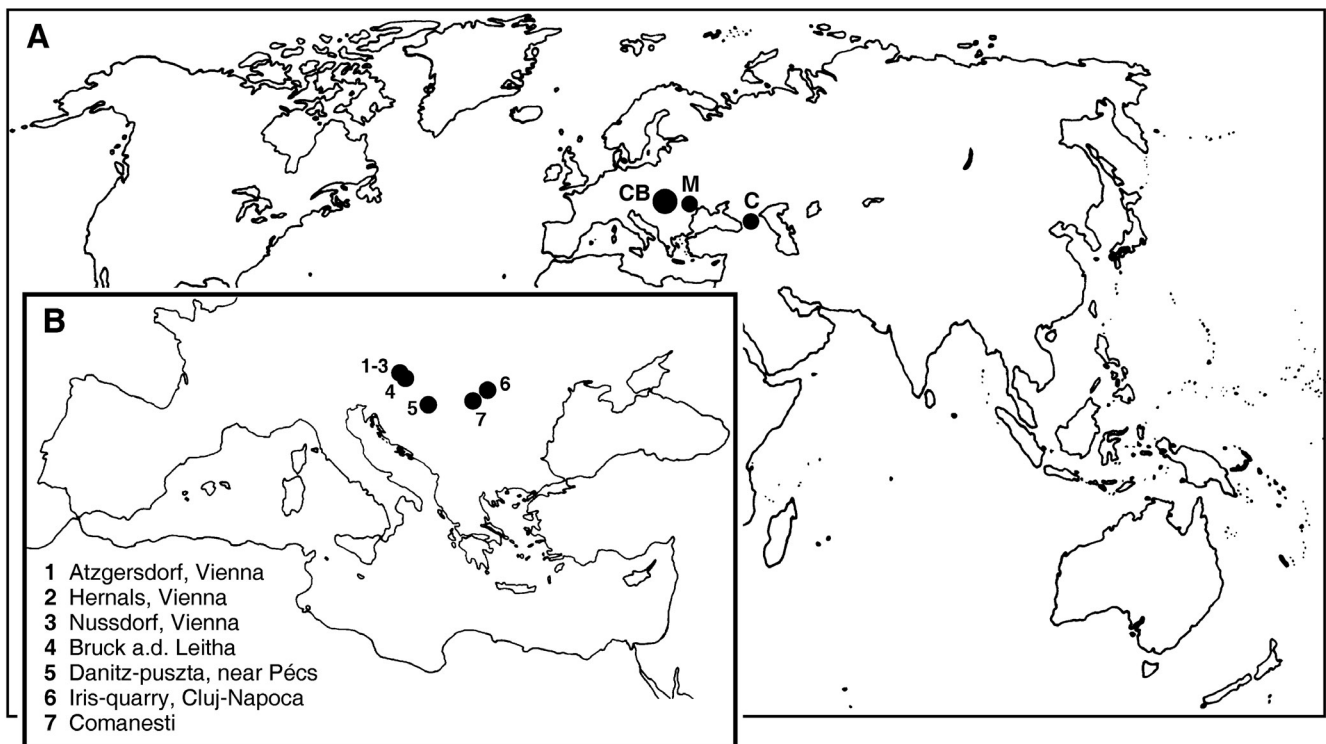
between *Kentriodon* and *Atocetus*.

The cochlear part of the Romanian periotic is similar to the same structure of *Atocetus* in that it is joined to the body with a broad base. It is not as circular and not as deep medially as in the holotype of *K. pernix* (USNM 8060), in the holotype and referred specimens of *K. obscurus* (see Barnes & Mitchell, 1984: figs. 8, 9), and in the holotype of *Delphinodon dividum* True, 1912 (USNM 7278). In contrast to *Atocetus*, however, in UBFG.222 the pars cochlearis is not flattened anteriorly.

The UBFG.222 periotic from Comăneşti-1 is identical in morphology to several periotics from other Carpathian Basin localities, which were assigned to the species *"Champsodelphis" fuchsii* Brandt, 1873, on the basis of two incomplete skeletons including ear bones and humeri but not skull, from the Iris Quarry at Cluj-Napoca (Romania), by Kazár (2003) and Kazár et al. (2004). The morphological and metric variation of these periotics is discussed in the same papers.

Discussion – Although UBFG.223 is a left and a right humerus, their somewhat different morphology indicates that they belonged to two individuals. The UBFG.223/1 humerus has a more elongated neck region where the infraspinous fossa is at a considerably greater distance from the distal border of the humeral head. Also, the humeral head appears smaller than in the other specimen, as a consequence of the complete lack of lateral shifting of the humeral head in UBFG.223/1.

The two isolated humeri from Comăneşti-1 most probably represent a delphinoid species, because they do not show characteristics of the humeri in non-delphinoid groups (for more detail on recent groups see Benke, 1993; and on many fossil groups Kazár & Bohaska, in press), and because of the distal shift of the deltoid tuberosity, which is a general tendency in the Delphinoidea (see Muizon, 1988a). Known representatives of the Odobenocetopsidae

Figure 4 – Geographical distribution of the records of *"Champsodelphis" fuchsii* Brandt, 1873. A, Main areas of occurrence as indicated by the black dots; *C:* Caucasus, *CB:* Carpathian Basin, *M:* Moldavia. B, The Carpathian Basin localities (Austria, Hungary, Romania). For more detail see the text.

and the Monodontidae have much larger, more robust, and more elongated humeri; the Albireonidae is characterized by anteroposteriorly expanded limb elements; and in the known Phocoenidae and Delphinidae the deltoid tuberosity reaches the distal epiphysis of the humerus distally (Barnes, 1984; Muizon, 1988a; Muizon & Domning, 2002). The Kentriodontidae is a morphologically diverse group of Late Oligocene to Late Miocene delphinoids, which is phylogenetically probably paraphyletic (e.g. Muizon, 1984, 1988a).

The known humeri of kentriodontid species often have a more or less elongated shaft, which does not get wide distally; the humeral head can be moderately shifted laterally; the greater and lesser tubercles are well-marked; and the deltoid tuberosity is usually situated centrodistally on the anterior margin (for a short overview see Kazár & Venczel, 2003). In contrast to this general morphology, the humerus of *Atocetus iquensis* is relatively shorter, has a laterally shifted humeral head, and the reduced deltoid tuberosity nearly reaches the distal end of the anterior margin (MNHN PPI 114; Muizon, 1988b). A small delphinoid from Oradea (Romania) has an even smaller and more compact humerus, with well-marked muscle attachment sites (Kentriodontidae indet., unnamed n. sp. of Kazár & Venczel, 2003).
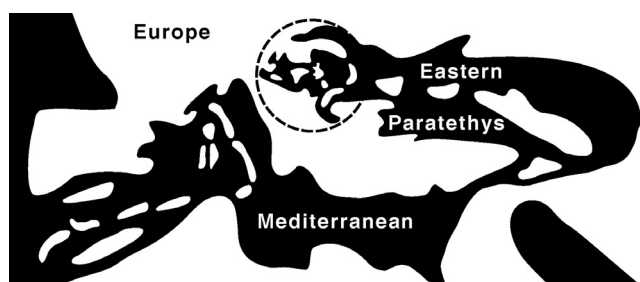
The Comăneşti-1 humeri are very close in morphology to both *A. iquensis* and the unnamed kentriodontid of Kazár & Venczel (2003). UBFG.223/1

differs from *A. iquensis* in the lack of lateral shifting of the humeral head, and in having a more elongated neck. Both humeri from Comăneşti-1 differ from the Peruvian species in the presence of an articular facet for the olecranon process of the ulna. They differ from the humerus of the Kentriodontidae n. sp. of Kazár & Venczel (2003) in their greater size, and relatively more elongated shafts.

The UBFG.223/1 and 223/2 humeri from Comăneşti-1 belong to a morphotype that was described on the basis of several hundreds of isolated humeri from Danitz-puszta, Hungary, as well as from humeri attached to partial skeletons from Vienna Basin localities (preliminary description and discussion of the morphological variation in Kazár, 2003). Because the holotype partial skeleton of *"Champsodelphis" fuchsii* (NHMW 1859.XXVII.6.m) contains a humerus of the same morphotype, all isolated humeri were assigned to this species by Kazár (2003).

"Champsodelphis" fuchsii was described on the basis of a partial skeleton from the so called "Hernalser Tegel" deposit (Suess, 1862) of Nussdorf-Heiligenstadt, Vienna, and questionably referred to the genus *Champsodelphis* by Brandt (1873). For a more detailed discussion on the taxonomy of the species see Kazár et al. (2004: 183). The type species of *Champsodelphis* Gervais, 1848 is *C. macrogenius* (=*macrognathus*) Gervais, 1848, which is based on a mandible fragment. Because this is insufficient material for diagnosing an odontocete, Muzion

Figure 5 – The Paratethys and the Mediterranean seas during the early Sarmatian sensu stricto (late Middle Miocene). Redrawn after Rögl (1998). Encircled area: Central Paratethys.

(1988c) regarded *Champsodelphis* as an Odontoceti incertae sedis, restricted to its type species.

The periotics and humeri referred to *"C." fuchsii* above and elsewhere (Kazár, 2003; Kazár et al., 2004) show that this species is a member of the Delphinoidea, and can be included in the grade family Kentriodontidae. The periotic of *"C." fuchsii* is close in morphology to *Kentriodon* and *Atocetus*, and the humerus shows marked similarities to *Atocetus iquensis*. However, the morphological resemblance of the humerus of *"C." fuchsii* to *A. fuchsii* does not necessarily indicate phylogenetic relationship, as limb bones can be subjected to homoplasy. Kazár et al. (2004) questionably transferred *"Champsodelphis" fuchsii* to the genus *Atocetus*, but in the present concept, in the lack of more diagnostic cranial material, we retain the species name *"Champsodelphis" fuchsii*.

Paleobiogeography

As mentioned above, the holotype of *"Champsodelphis" fuchsii* comes from the Sarmatian of Nußdorf-Heiligenstadt, Vienna. On the basis of ear bones and humeri, this species was recognized at a number of other Sarmatian localities in the Carpathian Basin: Atzgersdorf and Hernals in Vienna; Bruck an der Leitha in the Vienna Basin; Danitz-puszta near Pécs, south Hungary; the Iris-quarry in Cluj-Napoca, Romania (Kazár, 2003; Kazár et al., 2004); as well as Comăneşti-1 in Romania (present paper).

Besides the above mentioned localities, *"Champsodelphis" fuchsii* has also been reported from outside the Carpathian Basin: from Moldavia and the Caucasus. Macarovici & Oescu (1942) and Ionesi & Galan (1988) identified the species from Chişinău (=Kishinev) and Darabani, respectively, whereas Macarovici & Zaharia (1967) mentioned the occurrence of *"Champsodelphis"* cf. *fuchsii* from three further Sarmatian sensu lato localities of the Moldavian Platform. From the middle Sarmatian sensu lato of Armavir, Northern Caucasus, Mchedlidze (1960, 1964) described several postcranial elements of an odontocete that he referred to as *Champsodelphis* cf. *fuchsii*.

Figure 4 shows the occurrences of *"Champsodelphis" fuchsii* including the above mentioned records. It must be noted, however, that the Moldavian reports were based on vertebrae only (Macarovici & Oescu, 1942; Macarovici & Zaharia, 1967; Ionesi & Galan, 1988), which are not highly diagnostic in cetaceans (Fordyce & Muizon, 2001).

The Central European occurrences of *"Champsodelphis" fuchsii* are from the Carpathian Basin (including the Vienna Basin), which is the territory of the Early to Late Miocene Central Paratethys Sea (Fig. 5). The Moldavian and Caucasian records indicate that the same species inhabited the Eastern Paratethys as well, suggesting that these two seas formed a single zoogeographical unit during the Sarmatian.

The Sarmatian Marine Mammal Event

Marine mammals in the Central Paratethys – Cetaceans in the Central Paratethys Sea had three main invasion events. Squalodontid odontocetes, primitive sperm whales, and possible eurhinodelphinid remains have been reported from a few Eggenburgian (Early Miocene, ca. 20.5-18.3 Ma according to Rögl, 1998) localities in north Hungary and south Slovakia (Böckh, 1899; Koch, 1903, 1904; Holec et al., 1995; Kazár, 2003). A completely new cetacean fauna including baleen whales, sperm whales, and kentriodontid dolphins appeared in the middle Badenian (early Middle Miocene, ca. 14.7-13.6 Ma, Rögl et al., 2002; Harzhauser et al., 2003) of Austria and Hungary (Kadić, 1904; Papp, 1905; Kazár, 2002, 2003). Finally, a large number of Sarmatian (late Middle Miocene) localities yielded numerous remains of mysticetes and odontocetes (e.g. Brandt, 1873; Kellogg, 1925; Kazár, 2003; and Table 3).

The earliest phocid seals in the Central Paratethys are from the Badenian (14.8 Ma; early Middle Miocene) of the Bonanza and Sandberg localities at Devinská Nová Ves (Zapfe, 1937; Holec et al., 1987; Fejfar, 1990; Koretsky & Holec, 2002). A somewhat larger number of phocid fossils originate from lower and middle Sarmatian localities of the Central Paratethys, and represent a taxonomically different fauna from that of the Badenian (Brühl, 1860; Toula, 1898; Kretzoi, 1941a). The Danitz-puszta locality in south Hungary yielded marine mammals of Sarmatian, possibly also of Badenian age (Kazár, 2001, 2003). The phocids of this locality are probably of the Sarmatian (Koretsky, 2001).

Sirenians were in the Central Paratethys during the Eocene, as represented by the numerous localities in the Trans-Danubian Central Mountain, north Hungary and in the Transylvanian Basin. Sea cows have recorded occurrences from the Oligocene as well (Kretzoi, 1941b; for an overview of Eocene finds see Kordos, 2002). A new sirenian fauna appeared in the Central Paratethys during the early to middle Badenian (Kretzoi, 1951; Kordos, 1985, 1992). No sirenians

Name of locality	Stratigraphy	Source
Atzgersdorf, Vienna (Austria)	upper Ervilia Zone	Papp (1956)
Hernals, Vienna (Austria)	Mohrensternia Zone	Schmid (1974)
Nussdorf-Heiligenstadt, Vienna (Austria)	Mohrensternia Zone	Papp (1956)
Bruck a.d. Leitha, Vienna Basin (Austria)	Mohrensternia Zone	Papp (1956)
Bruckneudorf, Vienna Basin (Austria)	lower Sarmatian	Harzhauser, pers. comm. (2004)
Loretto, Vienna Basin (Austria)	Mohrensternia Zone	Harzhauser, pers. comm. (2004)
Bad Sauerbrunn, Vienna Basin (Austria)	upper Ervilia Zone	Steininger & Thenius (1964)
Holic (Slovakia)	Holic Formation; lower Sarmatian	Vass (2002)
Kovácsszénája, Mecsek Mt. (Hungary)	lower Sarmatian	Kazár (2003)
Kozárd, Nógrád County (Hungary)	Kozárd Formation; lower Sarmatian	Hámor (1998)
Iris Quarry, Cluj-Napoca (Romania)	upper Volhynian; lower Sarmatian	Mészáros et al. (1991)
Tăşad-2, Oradea (Romania)	Volhynian (MN7); lower Sarmatian	Hír et al. (2001); Kazár & Venczel (2003)
Comăneşti-1 (Romania)	upper Volhynian; lower Sarmatian	Istocescu (1971); Istocescu & Istocescu (1974); Steininger et al. (1996)

Table 3 – Stratigraphy of the Sarmatian odontocete localities of the Carpathian Basin, including the Vienna Basin. For a stratigraphic correlation, see Fig. 6. A number of other Carpathian Basin localities yielded odontocete remains of Sarmatian age, but their exact stratigraphic position is unknown. These are as follows: Budafok, Budapest-Kőbánya, Danitz-puszta, Pécs-Vasas, Hird, Pécsvárad, Hímesháza, Radoboj, Podsused, Daruvar, and Pakrac.

are known from younger deposits in the Central Paratethys (Kordos, 1985).

Marine mammals in the Eastern Paratethys – The known record of Miocene Cetacea of the Eastern Paratethys mainly derives from Sarmatian sensu lato (Volhynian, Bessarabian, and Khersonian) localities of northern Caucasus, Azerbajdzhan, western Gorgia, Mangyshlak, and Moldavia. To mention only the most important finds, the holotype skull of *Microphocoena podolica* Kudrin & Tatarinov, 1965 was found in Sarmatian sensu lato deposits of western Ukraina. The incomplete holotype skull of *Sarmatodelphis moldavicus* Kirpichnikov, 1954 of Moldavia is of Bessarabian age (Macarovici & Oescu, 1942; Simionescu, 1943), whereas the single known specimen of *Leptodelphis stavropolitanus* Kirpichnikov, 1954 is from the middle Sarmatian sensu lato of Stavropol, south Russia. *Imerodelphis thabaga*rii Mchedlidze, 1959 is a badly preserved articulated skeleton from the lower Sarmatian sensu lato of the Caucasus.

Isolated cetacean material is known from the Sarmatian sensu lato of Moldavia (Macarovici & Oescu, 1942; Macarovici & Zaharia, 1967; Ionesi & Galan, 1988) and the Caucasus (Dombrovskij, 1927; Mchedlidze, 1960, 1964). Importantly, some of the species of the Carpathian Basin are represented in the Caucasus as well. Notably *Pachyacanthus* spp., *Acrodelphis letochae* (Brandt, 1873), and *"Champsodelphis" fuchsii*, all three described from the Vienna Basin and reported from several other Austrian and

Hungarian localities (Kazár, 2003; Kazár et al., 2004; for a discussion on the taxonomic status of *Acrodelphis letochae* see Kazár, 2003: 91-92), were reported from the Caucasus as well (Dombrovskij, 1927; Mchedlidze, 1960, 1964; Pilleri, 1986: 30-31).

A large number of Eastern Parathethyan localities yielded the remains of phocid seals from Romania, Moldavia, Russia, Ukraina, Azerbajdzhan, and Kazakhstan. The age of the localities covers the entire Sarmatian sensu lato of the Eastern Paratethys (Simionescu, 1925; Grigorescu, 1976; Ray, 1976; Repenning et al., 1979; Koretsky, 2001; Koretsky & Grigorescu, 2002).

Of the Sirenia, a few rib fragments from the Paleogene of Romania were described by Grigorescu (1967). The taxonomic position of *"Manatus maeoticus"* Eichwald, 1850 from the Sarmatian of Kerch, Moldavia, is questionable (Koretsky, 2001). No other sirenian remains are known from the Eastern Paratethys to date (Domning, 1996).

The Sarmatian Marine Mammal Event (Fig. 6) – The lack of faunal continuity between the Badenian and Sarmatian marine mammals points to two independent invasions of the Central Paratethys. The first occurred during the early or middle Badenian, and the second during the Sarmatian. This is also supported by the fact that the Badenian forms are not known from Sarmatian localities (Brandt, 1873; Gorjanović-Kramberger, 1892; Abel, 1899; Pia & Sickenberg, 1934; Simionescu, 1931; Grigorescu, 1976; Koretsky, 2001).

During the early Badenian, the Central Paratethys

| Time (Ma) | Epoch | Standard Stages | Central Paratethyan | | | Eastern Paratethyan Stages |
| | | | Regional Stages | Biozones | | |
				Mollusca	Foraminifera	
11	Late Mioc.	Tortonian	Pannonian	*Mytilopsis hoernesi* Zone		Sarmatian — Bessarabian
				Mytilopsis ornithopsis Zone		
	Middle Miocene	Serravallian		"pauperization"	*Porosononion granosum* Zone	
				Mactra Zone		
12			**Sarmatian**	upper *Ervilia* Zone		Volhynian
				lower *Ervilia* Zone	*Elphidium hauerinum* Z.	
				Mohrensternia Zone	*Elphidium reginum* Zone	
13			Badenian	*Flabellipecten besseri* Zone	*Bulimina Bolivina* Zone	Konkian
						Karaganian
						Tshokrakian

Figure 6 − The Sarmatian Marine Mammal Event (SMME). The high number of marine mammal remains from lower Sarmatian localities in the Carpathian Basin (including the Vienna Basin) and the Eastern Paratethys indicate a marine mammal event during the Sarmatian (black area). This invasion of various phocid seals, mysticetes, and odontocetes followed the disappearance of marine mammals in the Central Paratethys in the late Badenian, and covers the *Mohrensternia* Zone, the lower and upper *Ervilia* Zones of the Central Paratethys. The symbols to the right represent the invasion of phocid seals, odontocetes, and mysticetes from the east. The stratigraphic correlation is derived from Harzhauser & Piller (2004).

Sea maintained a southwest passage from the Mediterranean (Rögl, 1999). The general Serravallian regression of the Mediterranean may have caused the closure of the Mediterranean–Central Paratethyan connection by the end of the Badenian, and thereby the so called Middle Miocene Paratethys "salinity crisis" (Rögl et al., 1978). Most stenohaline-marine mollusk species became extinct in the Central Paratethys, in spite of the broad connection between the Eastern Paratethys and the Indopacific Ocean at that time (Rögl, 1998). Although the "Trans-Tethyan Trench Corridor" in Slovenia has never re-established, in the early Sarmatian the Central Paratethys gained connection to the World Ocean through the Eastern Paratethys again, the latter being connected to the Mediterranean through narrow marine straits in present-day Anatolia (Rögl, 1998).

By the end of the Badenian, marine mammals became largely or entirely extinct in the Central Paratethys. Their absence might be due to the incompleteness of the fossil record in general. This can be explained by the lack of proper conditions for fossilization during the late Badenian, or by subsequent erosion of the deposits. Nevertheless, the complete replacement of Badeian taxa in the Sarmatian suggests that the late Badenian changes in salinity and circulation patterns did have a major impact on the abundance of marine mammals. The new pinnipedian and cetacean fauna invaded the Carpathian Basin through the Eastern Paratethys, but their origin is probably Atlanto-Mediterranean. The great abundance of taxa and individuals of the newly appearing marine mammals of the Central Paratethys, particularly small odontocetes, leads to the recognition of a Sarmatian Marine Mammal Event (SMME). The SMME covers the *Mohrensternia* Zone, and the lower and upper *Ervilia* Zones of the Central Paratethys. This can be correlated with the Volhynian of the Eastern Paratethys (Fig. 6).

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