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Odontocete periotics (Mammalia: Cetacea) from the Carpathian Basin, Middle Miocene (Badenian and Sarmatian Stages), including the Vienna Basin, Austria

by

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Abstract

The present paper describes Middle Miocene (Badenian and Sarmatian Stages) periotics of odontocetes (Mammalia: Cetacea) from the Carpathian Basin, the area of the ancient Central Paratethys Sea. Nine odontocete taxa are recognized; five of these are new to the Middle Miocene odontocete assemblage of the Central Paratethys. With the exception of two taxa (Odontoceti indet., Delphinoidea indet.), all other periotics are representatives of the grade family Kentriodontidae SLIJPER, 1936. *"Heterodelphis" leiodontus* PAPP, 1905 is a kentriodontid, but its phylogenetic affinities within the family remain unknown. This species does not belong in the genus *Heterodelphis* BRANDT, 1873, which is an Odontoceti incertae sedis, restricted to its type species, *H. klinderi* BRANDT, 1873. The genus *Kentriodon* has recorded occurrences in the Carpathian Basin Middle Miocene, as evidenced by the periotics assigned to *Kentriodon* (= *Champsodelphis*) *fuchsii* (BRANDT, 1873). The ?pithanodelphinine *Sophianaecetus commenticius* (KAZÁR, 2005) has a new record from Bruck Neudorf, which is the first evidence for the presence of the species in the Vienna Basin. Four periotics in two taxa (Kentriodontidae indet. 2, ?*Loxolithax* sp.) bear a longitudinal dorsal crista (= crista dorsalis; new term) on their cerebral surface. The function of the crista dorsalis in hearing is unknown, and it probably does not have taxonomical significance.

Keywords: Miocene, Parathethys, Odentoceti, Kentriodontidae, taxonomy, periotic

Zusammenfassung

Der vorliegende Artikel beschreibt Zahnwal-Periotika (Mammalia: Cetacea: Odontoceti) des mittleren Miozäns (Badenien und Sarmatien) aus dem Karpathenbecken, dem Gebiet des früheren Zentralen Paratethys. Es wurden neun Taxa identifiziert, fünf davon sind neu in der mittleren miozänen Zahnwalfauna des Zentralen Paratethys. Mit Ausnahme von zwei Taxa (Odontoceti indet., Delphinoidea indet.), sind alle anderen Periotika Vertreter der Familie Kentriodontidae SLIJPER, 1936. *"Heterodelphis" leiodontus* PAPP, 1905 ist ein Kentriodontide; seine phylogenetischen Beziehungen innerhalb der Familie bleiben ungeklärt. Diese Art gehört nicht zur Gattung *Heterodelphis* BRANDT, 1873. Letztere wird als Odontoceti incertae sedis angesehen, beschränkt auf die Typusart der Gattung, *H. klinderi* BRANDT, 1873. Die Gattung *Kentriodon* KELLOGG, 1927 ist im mittleren Miozän des Karpathenbeckens nachgewiesen anhand der Periotika, die zur Art *Kentriodon* (= *Champsodelphis*) *fuchsii* (BRANDT, 1873) zugeordnet sind. Der ?pithanodelphinine Zahnwal *Sophianaecetus commenticius* (KAZÁR, 2005) hat ein neues Vorkommen in Bruck Neudorf, und dies ist der erste Beweis, daß die Art auch im Wiener Becken vorkam. Vier Periotika in zwei Taxa (Kentriodontidae indet. 2, ?*Loxolithax* sp.) tragen einen longitudinalen Kamm (Crista dorsalis, neuer Terminus) auf der dorsalen Oberfläche des Periotikums. Es ist unbekannt, welche Funktion das Crista dorsalis für das Hören gehabt hat, und es hat wahrscheinlich keine taxonomische Bedeutung.

1. Introduction

The Carpathian Basin (including the Vienna Basin in Austria, the southern part of the Slovakian Republic, Transsylvania in Romania, the northern part of Croatia, and Hungary) is generally rich in cetacean remains (BRANDT, 1873; GORJANOVIĆ-KRAMBERGER, 1892; ABEL, 1899; KOCH, 1904; KADIĆ, 1904; PAPP, 1905; PIA, 1937; KORDOS & SOLT, 1984; CODREA, 1995; HOLEC et al., 1995). However, due to the local sedimentological characteristics, most localities yield only non-associated skeletal elements. A few exceptions exist, such as the so called "Hernalser Tegel" in Vienna, the calcareous marls in Kovácsszénája (Hungary), in Tăşad and Cluj-Napoca (Romania), all Sarmatian in age, as well as the Badenian corallinaceous limestone in St. Margarethen, and the marine sands of Stotzing (Austria). Even in these deposits, articulated cetacean skeletons are extremely rare, and the only ones including well-preserved

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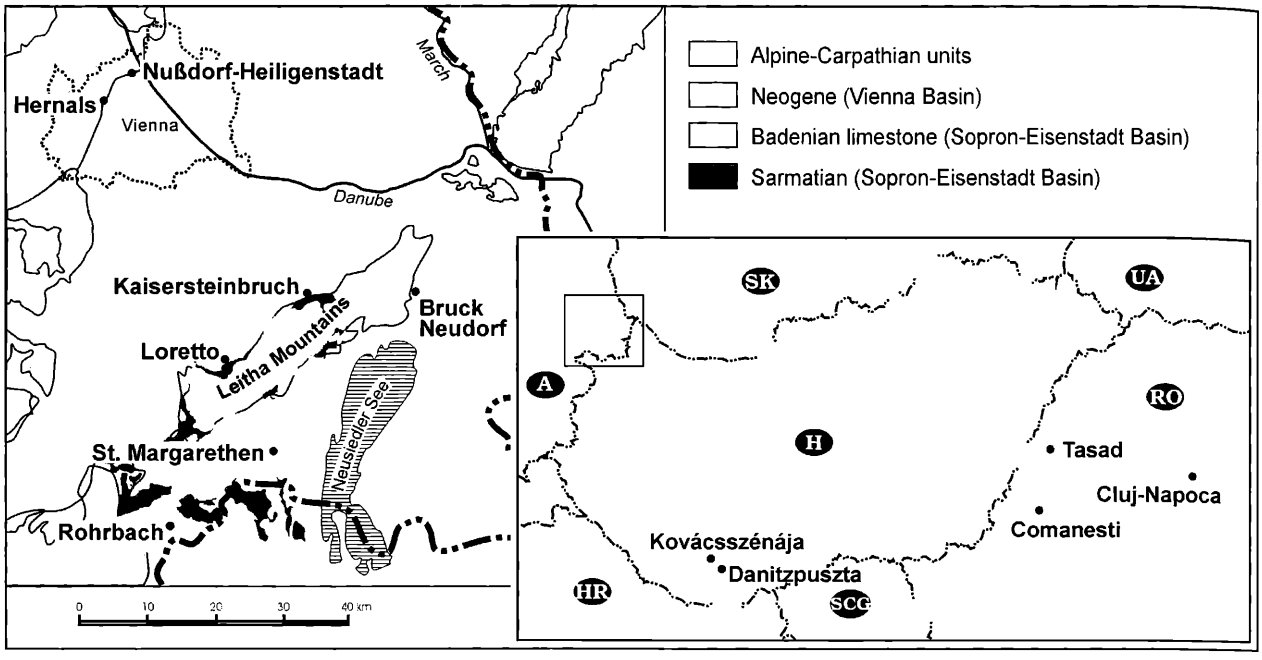

Figure 1: Geographic setting of Middle Miocene odontocete periotic localities in the Carpathian Basin. The box in the main map indicates the place of the enlarged area on the left (Austrian localities). The geology of the Vienna Basin and the Eisenstadt-Sopron Basin is derived from HARZHAUSER & PILLER (2004) and HARZHAUSER et al. (2004).

skulls are the holotype of *Sophianaecetus commenticius* (KAZÁR, 2005) from Kovácsszénája and a physeterid from Stotzing (KAZÁR, 2002, 2005).

In order to obtain a better idea of the cetacean assemblages of the ancient Central Paratethys Sea, which covered the entire territory of the present-day Carpathian Basin during Middle Miocene time, isolated elements must be investigated as well. Of these, the periotics or petrosal bones are the most promising, because they bear a considerable amount of phylogenetic and taxonomic information (KASUYA, 1973; LUO & MARSH, 1996). Due to their great density, periotics also tend to fossilize well, and can be found in relatively large numbers in sediments that do not preserve skulls.

Cetacean ear bones were collected together with other skeletal elements in the 19th century Vienna. The first periotic of an odontocete was inventoried in 1867; more specimens were collected during the main construction period of the city of Vienna in the 1870s-1890s, and the last ones of the classical collections were inventoried in 1906 (PIA & SICKENBERG, 1934). Yet, the study of cetacean petrosals does not have a long history in the Carpathian Basin. The catalogue of PIA & SICKENBERG (1934) listed odontocete "Gehörapparate", and PIA (1937:391) briefly commented on the "platanistid" periotics from Kaisersteinbruch and Rohrbach. In the other parts of the Carpathian Basin, no cetacean finds of the 19th century included periotics (e.g., GORJANOVIĆ-KRAMBERGER, 1892; KOCH, 1904; KADIĆ, 1904; PAPP, 1905).

In recent years, CODREA (1995) was the first to describe and illustrate tympano-periotic complexes of a cetacean from the Central Paratethys. During the past 15 to 20 years, the south Hungarian sand pit Danitzpuszta attracted a myriad of amateur collectors, whose findings sometimes included odontocete periotics. These, along with a few new discoveries of odontocete skeletons, gave a new impetus to the study of odontocete periotics in the Carpathian Basin (KAZÁR, 2003; KAZÁR & VENCZEL, 2003; KAZÁR et al., 2004; GRIGORESCU & KAZÁR, 2006).

The aim of the present paper is a comprehensive overview on the periotic morphologies of the odontocete assemblages of the Central Paratethyan Middle Miocene. It contains the description of the periotics of all Badenian and Sarmatian Carpatian Basin odontocete localities known to date. Older material (Eggenburgian, Early Miocene) is not included in the present work, because it represents a completely different cetacean fauna (HOLEC et al., 1995; KAZÁR, 2003).

Abbreviations: MÁFI, Magyar Állami Földtani Intézet, Budapest (Geological Institute of Hungary); MBT, Musée "Bassin de Transsylvanie", Université "Babeş-Bolyai" (Cluj-Napoca, Romania); MTC, Museul Ţării Crişurilor (Oradea, Romania); MTM, Magyar Természettudományi Múzeum, Budapest (Natural History Museum of Hungary); NHMW, Naturhistorisches Museum in Wien (Vienna); PIUW, Paläontologisches Institut Universität Wien (Vienna); UBFG, Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

2. Material and methods

It has been attempted to include all Central Paratethyan odontocete periotic bones stored in institutional collections, and the best-preserved or most important specimens in private collections. Of the latter, Gerhard Wanzenböck owns significant material from Bruck Neudorf, Zoltán Evanics and Roland Molnár have important specimens

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from Danitzpuszta. The periotics in private ownership are labeled as follows: LC140-, ex. coll. Z. Evanics; M00R, ex. coll. R. Molnár; W., ex. coll. G. Wanzenböck.

Ferenc Cserpák has kindly donated many excellent specimens from Danitzpuszta to the MÁFI, these are inventoried accordingly (MÁFI V.23118, V.23119, V.23124, V.23125, V.23231, V.23232, V.23233). The following specimens are inventoried casts of the private originals in parentheses: MÁFI V.23098 (M32R), V.23099 (M34R), V.23101 (M261R), V.23102 (LC140-4514), V.23106 (M5R), V.23107 (M6R), V.23108 (LC140-4519), V.23109 (M23R), V.23110 (LC140-4516), V.23111 (LC140-4518), V.23112 (M19R), V.23113 (M35R), V.23114 (M37R), V.23115 (M38R), V.23234 (M27R), V.23235 (M25R), V.24557 (W.2), V.24558 (W.3), V.24559 (W.4), V.24560 (W.5), V.24561 (W.6), V.24562 (W.7), V.24563 (W.8), V.24564 (W.9), V.24565 (W.10), V.24566 (W.11), V.24567 (W.12), V.24568 (W.13), V.24569 (W.14), V.24570 (W.15), V.24571 (W.16), V.24572 (W.17), V.24573 (W.18), V.24574 (W.19), V.24575 (W.20), V.24576 (W.21), V.24577 (W.22), V.24578 (W.23), V.24579 (W.24), V.24580 (W.25), V.24581 (W.26). Measurements were taken on the original periotics, except MÁFI V.24236, which is a cast of a specimen in the private collection of László Kanizsai. No measurements were possible on the referred specimen of "*Heterodelphis*" *leiodontus* PAPP, 1905 in the private collection of G. Wanzenböck, because the periotic of this specimen is only partially prepared and largely obscured by a rib.

Petrosal terminology was derived from KASUYA (1973), FORDYCE (1983, 1994), and LUO & MARSH (1996). All periotics were measured with the same measuring caliper. The following measurements were taken: 1. Total length of periotic; from tip of anterior process to posterior end of posterior process; 2. Width of periotic across pars cochlearis and ventrolateral tuberosity; 3. Least distance from rim of internal auditory meatus to endolymphatic foramen; 4. Least distance from rim of internal auditory meatus to perilymphatic foramen; 5. Least distance between endolymphatic and perilymphatic foramina; 6. Length of pars cochlearis at base.

3. The localities

Twelve Middle Miocene localities yielded periotics of odontocetes in the Carpathian Basin. Seven of these are in Austria (Vienna Basin and Sopron-Eisenstadt Basin) (Fig. 1). In the following, a short resume is given on the geological background of the localities, starting with the older ones, listed in order of geographic position from West towards East. The stratigraphic correlation follows RÖGL (1998) and HARZHAUSER & PILLER (2004, 2005).

Rohrbach (Burgenland, Austria) – A few odontocete teeth and the periotic discussed in the present paper were found in the Badenian marls (Langhian – early Serravallian) of the brick quarry in Rohrbach (PIA, 1937).

St. Margarethen (Burgenland, Austria) – The middle Badenian (Langhian – early Serravallian) corallinacean limestone of St. Margarethen has been extensively studied (e.g., FUCHS, 1965; DULLO, 1983; BELLWOOD & SCHULTZ, 1991; SCHMID et al., 2000). The holotype of "*Heterodelphis*" *leiodontus* came from the Roman Quarry. New discoveries by amateur collectors, among these a partial skeleton of "*H.*" *leiodontus*, were collected in the Kummer Quarry (KAZÁR & LANTOS, 2001; KAZÁR, 2003).

Kaisersteinbruch (Burgenland, Austria) – PIA (1937:391) already mentioned the occurrence of odontocete periotics from the middle Badenian (Langhian – early Serravallian) corallinacean limestone of Kaisersteinbruch. Two periotics of the NHMW are known from this locality (SCHULTZ, 1998: pl. 61, fig. 4). The fundus of the internal auditory meatus of both is filled with sediment, possibly corallinacean limestone. Other marine vertebrate remains came from the Badenian transgressive breccia (ZAPFE, 1984). However, in the vicinity of Kaisersteinbruch Sarmatian deposits also occur, and SCHULTZ (1998) indicated that the periotics are of ?Sarmatian age (late Serravallian).

Hernals and **Nußdorf-Heiligenstadt** (Vienna, Austria) – Former quarries producing the so called "Hernalser Tegel" lie in the 17th district of Vienna, and are mentioned in the literature under the names Hernals, Heiligenstadt, and Nußdorf (PIA, 1937; SCHMID, 1974; SCHMID, 1989). Because the quarries of Nußdorf and Heiligenstadt lay only a few kilometers apart, the exact collecting locality of the fossils is not always clear (many are inventoried as of Nußdorf-Heiligenstadt). Hence, these two sites are united here as a single locality, Nußdorf-Heiligenstadt. The term "Hernalser Tegel" was introduced by SUESS (1862) for the Sarmatian (late Serravallian) blue marls of the Vienna Basin. Stratigraphically, Hernals and Nußdorf-Heiligenstadt belong to the *Mohrensternia* Zone (PAPP, 1956; SCHMID, 1974).

Loretto (Burgenland, Austria) – The quarry of Loretto, opened in 1872, produced pale yellow limestone of Sarmatian age (late Serravallian) (TELEGDI-RÓTH, 1903; SCHAFARZIK, 1904), which belongs to the Mohrensternia Zone (M. HARZHAUSER, pers. comm. 2004).

Bruck Neudorf (Burgenland, Austria) – Recently acquired material (all of the periotics in the private collection of G. Wanzenböck, and probably also NHMW 1982/74/1) were collected in Sarmatian age clay, which became exposed during the establishment of an artificial lake near Bruck Neudorf. The classic material of the NHMW, however, probably comes from the neighbouring Bruck a.d. Leitha (Niederösterreich), from quarries that had long been closed down and built over. PAPP (1956) places Bruck a.d. Leitha in the *Mohrensternia* Zone, and Bruck Neudorf is likewise of lower Sarmatian age, late Serravallian (M. HARZHAUSER, pers. comm. 2004).

Kovácsszénája (Baranya County, Hungary) – The calcareous marl exposed at the type locality of *Sophianaecetus commenticius* (KAZÁR, 2005) is of lower Sarmatian age, late Serravallian (BOHN-HAVAS, 2001; SZUROMI-KORECZ & SZEGŐ, 2001; BARABÁS, 2001; KAZÁR, 2003, 2005).

Danitzpuszta (Baranya County, Hungary) – The Pannonian (Late Miocene) sands of Danitzpuszta contain the bones of fluviatile-terrestrial Late Miocene vertebrates as well as reworked marine fossils of probably Sarmatian age

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	1.	2.	3.	4.	5.	6.
Odontoceti indet.						
NHMW 1939.I.31	33.2	20.1	1.2	2.3	3.2	15.2
Kentriodontidae indet. 1						
MÁFI V.21679/1	24.4	16.5	3.1	2.4	4.0	12.1
MTC 22404	24.3	16.7	3.3	2.2	4.2	12.6
?*Loxolithax* sp.						
PIUW 3128/9	24.9	16.1	2.7	2.5	4.0	13.6
"*Heterodelphis*" *leiodontus* PAPP, 1905						
MÁFI Ob. 580	28.0	17.8	3.1	2.3	4.0	13.8
?*Kentriodon* sp.						
NHMW 1906/1	24.6	15.3	2.1	1.1	3.1	12.1
NHMW 1906/2	25.5	17.0	?	2.0	?	12.1

Table 1: Measurements of the periotics of the Odontoceti indet., Kentriodontidae indet. 1, ?*Loxolithax* sp., "*Heterodelphis*" *leiodontus*, and ?*Kentriodon* sp. from the Carpathian Basin (in mm). ?: missing data. The measuring points (1-6) are defined in the Material and Methods

(KAZÁR, 2001; KAZÁR et al., 2001; KORETSKY, 2001, review of the geology of Danitzpuszta in KAZÁR, 2003:81-83).

Tăşad (Bihor County, Romania) – An incomplete odontocete skeleton was found in Sarmatian (late Serravallian) calcareous marls at the Tăşad-2 locality, which was correlated with the MN 7/8 zone (HÍR et al., 2001; KAZÁR & VENCZEL, 2003).

Comăneşti (Arad County, Romania) – The odontocete bones were collected from a lens-like bed of tuffaceous marls at the Comăneşti-1 locality (GRIGORESCU & KAZÁR, 2006). The lithological section has been correlated with the MN 7/8 zone of the Mammalian Neogene (lower Sarmatian, late Serravallian; ISTOCESCU, 1971; FERU et al., 1980).

Cluj-Napoca (Cluj County, Romania) – Odontocete fossils were found in a calcareous clayey layer in the Iris Quarry (KAZÁR et al., 2004). The entire section was correlated with the Eastern Paratethyan Volhynian Stage (NN 8, early Sarmatian) by MÉSZÁROS et al. (1991).

4. Results

4.1. Systematic paleontology

Ordo Cetacea BRISSON, 1762
Subordo Odontoceti FLOWER, 1869

Odontoceti indet.

1937 ?*Schizodelphis* sp. – PIA:391-392.
2003 Eurhinodelphidae gen. et sp. indet. – KAZÁR:139-143.

Referred specimen: NHMW 1939.I.31, left periotic from Rohrbach.

Description (Table 1, Fig. 2): The anterior process is large, slightly swollen, and elongate. It is slightly compressed mediolaterally. An anterior keel is not present; instead, the anterior surface of the anterior process is smooth and convex. The apex of the anterior process (the homologue of the anteroventral angle; FORDYCE, 1983) is directed anteroventrally, and terminates in a large but indistinct tuberosity. The homologue of the anterodorsal angle is a faint eminence in the centre of the dorsal surface. A U-shaped anteroexternal sulcus is present posteriorly on the lateral surface of the anterior process: it has a short dorsal part, which is convex, and a longer ventral part, which is straight and runs parallel to the ventral margin of the anterior process. In dorsal and ventral views of the periotic, a deep notch formed by the anteroexternal sulcus is apparent. The anterior bullar facet is a strongly concave and elongate groove, but is not as long and narrow as in *Eurhinodelphis cocheteuxi* DU BUS, 1867 (figured in LAMBERT, 2005). Posterointernal to the bullar facet, the fovea epitubaria is short and deep: it is rather a V-shaped notch in lateral view than a well-defined fossa.

The mallear fossa is oval and opens posteromedially. The ventrolateral tuberosity (lateral tuberosity of BARNES, 1978) is prominent. The ventral foramen of the facial canal lies about in the level of the mid-point of the pars cochlearis; the fenestra ovalis is situated slightly posteriorly to that. The stapedial muscle fossa is deep and wide. The posterolateral part of the pars cochlearis and the medial margin of the posterior process are only somewhat recurved over the stapedial muscle fossa.

The dorsal surface of the periotic is smooth and convex; there is no dorsal crest as defined by FORDYCE (1994). The superior process is elevated. The short posterior process closes at a sharp angle with this part of the dorsal surface.

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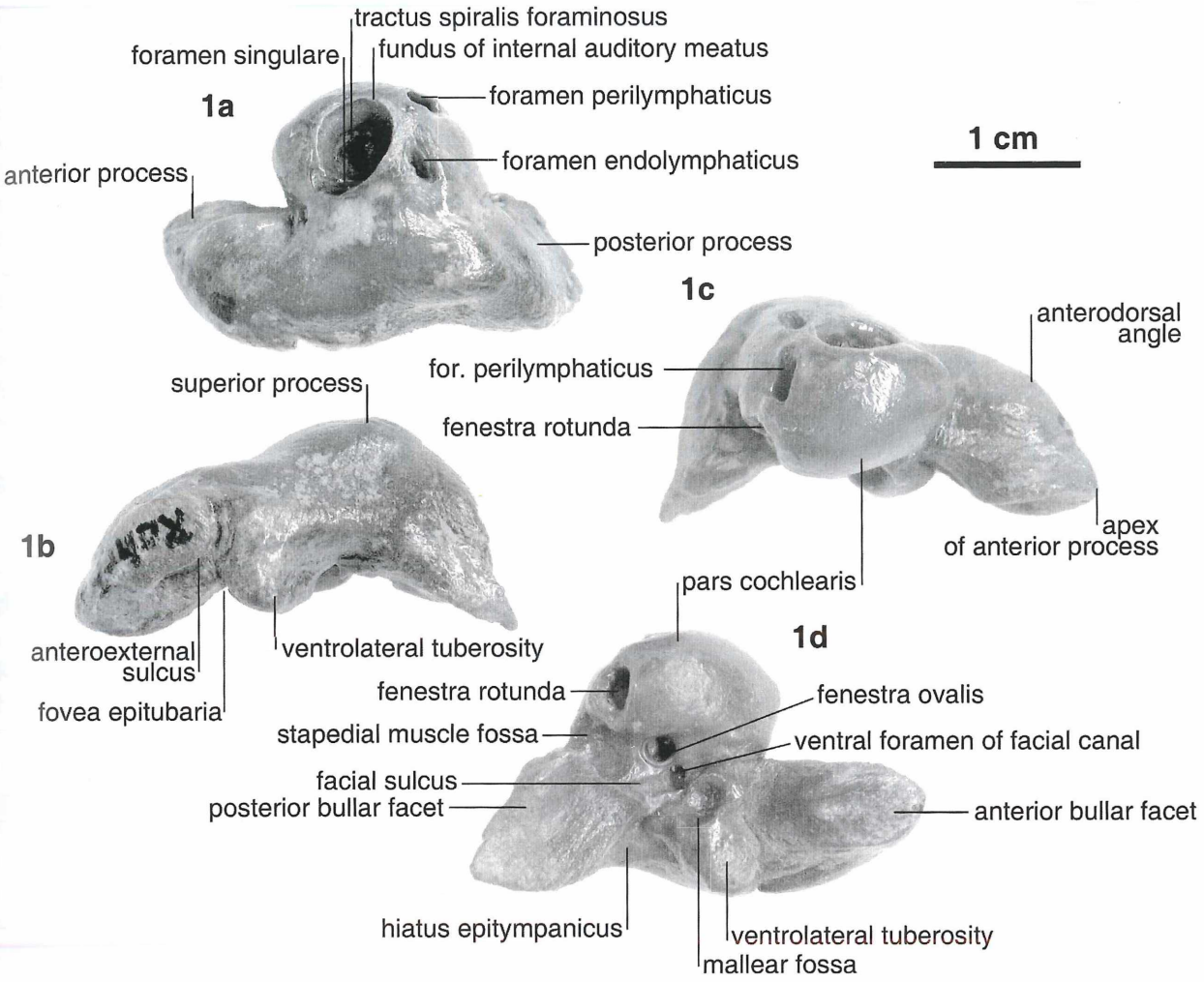

Figure 2: Odontoceti indet., NHMW 1939.I.31 from Rohrbach, Austria. Left periotic in 1a, dorsal; 1b, lateral; 1c, medial; and 1d, ventral views.

The dorsal surface of the posterior process wears fine rugosities, more towards the apex of the process. The posterior process is slightly flattened mediolaterally, but a prominent keel is not present. The lateral surface of the posterior process is featureless. The posterior bullar facet is almost completely smooth, elongate, and roughly rhomboidal.

The pars cochlearis is not broadly joined to the body of the periotic. It is squared in dorsal view, as a consequence of the rim of the perilymphatic foramen and the thickening of the anteromedial surface of the pars cochlearis. Its ventral surface is flattened in the medial view, and the posterior part of the pars cochlearis is slightly inflated. The fenestra rotunda is large and elliptical. The area dorsomedial to the fenestra ovalis is finely excavated, and forms a relatively sharp edge to the rest of the pars cochlearis. The fundus of the internal auditory meatus is deep and nearly circular. The tractus is also circular. The foramen singulare and the internal aperture of the Fallopian aquaeduct are only slightly placed anterolaterally, and are separated from the tractus by a low septum. A tiny foramen (?opening of the internal aperture of the Fallopian aquaeduct) is about 2 mm anterolateral to the fundus. The relatively large and elliptical endolymphatic foramen is close to the fundus of the internal auditory meatus; the perilymphatic foramen opens posteromedially.

Discussion: PIA (1937:391-392) briefly discussed a periotic from Rohrbach, in all probability the one described in the present paper, and stated that it was very similar to a periotic of *Cyrtodelphis sulcatus* (GERVAIS, 1853) figured by DAL PIAZ (1903: figs. 8, 9, pl. 31: fig. 4). PIA (1937) concluded that the Rohrbach specimen might belong to the genus *Schizodelphis* GERVAIS, 1861. The odontocete figured by DAL PIAZ (1903) was assigned to the genus *Eoplatanista* DAL PIAZ, 1916 by MUIZON (1988c). The Rohrbach periotic differs from *Eoplatanista* as defined by MUIZON (1988c) in having a longer and more robust anterior process, and a less reduced fovea epitubaria.

The elongate, cylindrical anterior process, the well-excavated anterior bullar facet, and the presence of an anteroexternal sulcus are generally typical of eurhinodelphinid periotics (FORDYCE, 1983). The NHMW 1939.I.31 periotic differs from specimens of the genera *Eurhinodelphis* DU BUS, 1867, and *Schizodelphis* sensu MUIZON (1988c) and LAMBERT (2004, 2005) in having a stronger anterior process, a shorter anterior bullar facet, and a less pronounced fovea epitubaria. Also, the relatively broad posterior bullar facet and the almost fundus-like internal auditory meatus

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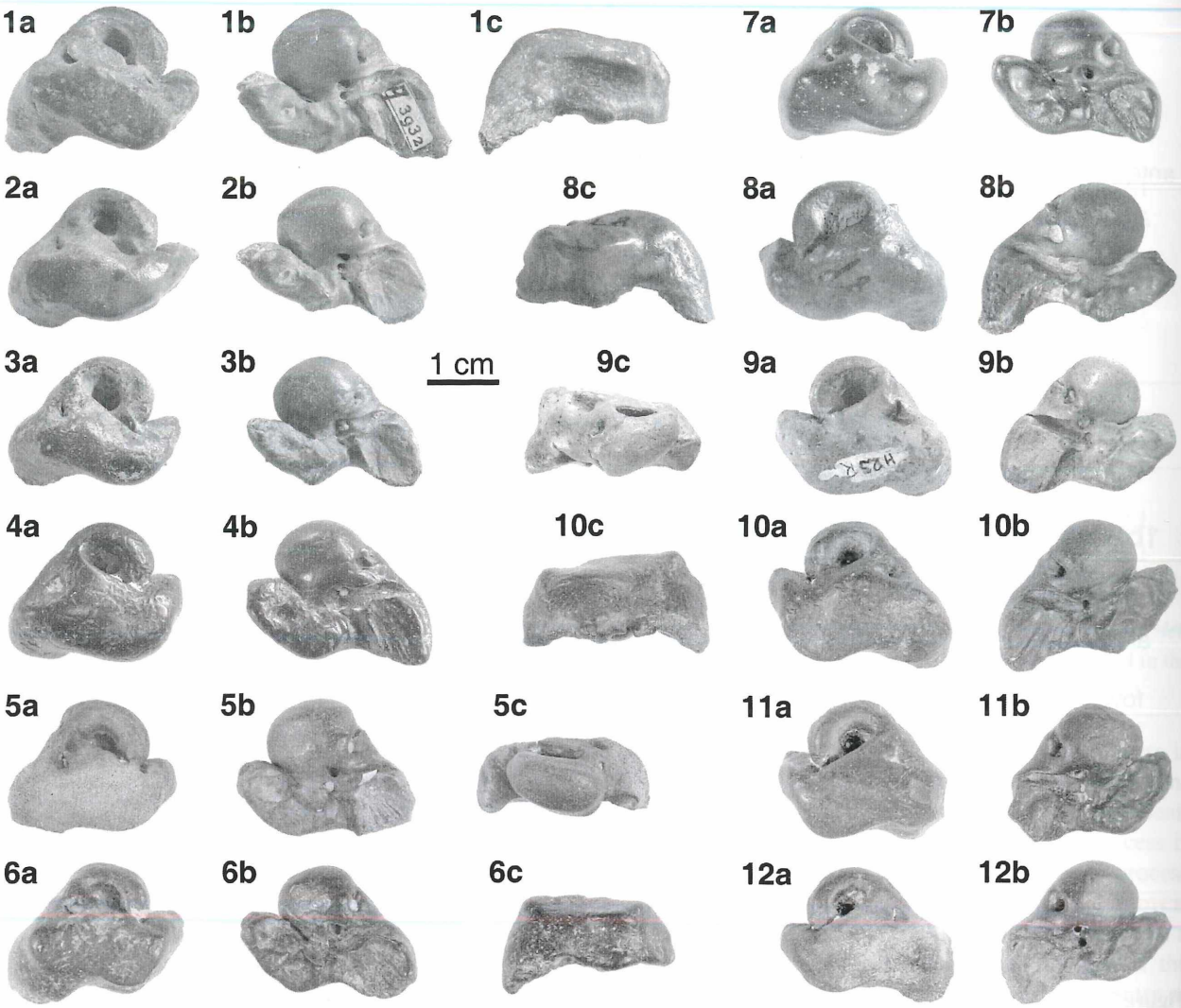

Figure 3: Delphinoidea indet. from Nußdorf-Heiligenstadt, Bruck Neudorf and Danitzpuszta. 1–NHMW 1891/1, right periotic in (a) dorsal, (b) ventral, and (c) lateral views. 2–NHMW 1906/30, right periotic in (a) dorsal and (b) ventral views. 3–NHMW 1890/121, right periotic in (a) dorsal and (b) ventral views. 4–NHMW 1982/74/1, right periotic in (a) dorsal and (b) ventral views. 5–W.3, original to MÁFI V.24558, right periotic in (a) dorsal, (b) ventral, and (c) medial views. 6–W.4, original to MÁFI V.24559, right periotic in (a) dorsal, (b) ventral, and (c) lateral views. 7–W.5, original to MÁFI V.24560, right periotic in (a) dorsal and (b) ventral views. 8–NHMW 2006z0195/0001, left periotic in (a) dorsal, (b) ventral, and (c) lateral views. 9–M23R, original to MÁFI V.23109, left periotic in (a) dorsal, (b) ventral, and (c) medial views. 10–W.9, original to MÁFI V.24564, left periotic in (a) dorsal, (b) ventral, and (c) lateral views. 11–W.7, original to MÁFI V.24562, left periotic in (a) dorsal and (b) ventral views. 12–W.8, original to MÁFI V.24563, left periotic in (a) dorsal and (b) ventral views.

of the Rohrbach periotic are not typical in the Eurhinodelphinidae (see FORDYCE, 1983).

The anteroexternal sulcus is also present in *Platanista* WAGLER, 1830, *Zarhachis* COPE, 1868, *Notocetus* MORENO, 1892 and *Waipatia* FORDYCE, 1994. The Rohrbach periotic resembles *Notocetus*, *Phocageneus*, and *Squalodelphis* in its squared pars cochlearis, and in having a relatively closed, deep internal auditory meatus. It differs from *Notocetus* in the more elevated superior process, from species of the Squalodelphinidae and Platanistidae sensu FORDYCE & MUIZON (2001) and FORDYCE (1994), from *Waipatia* and probably from *Schizodelphis morckhoviensis* (DU BUS, 1872) in the lack of an articular rim of the posterior process (LAMBERT, 2004; articular rim defined by MUIZON, 1987). The articular rim was proposed as a squalodontid-platanistoid synapomorphy (MUIZON, 1987, 1994; see also FORDYCE, 1994; FORDYCE & MUIZON, 2001), whereas LUO & MARSH (1996) suggested that the lack of a sutural contact between the periotic and the squamosal is the derived condition. The squared pars cochlearis is a synapomorphy of the Squalodelphinidae sensu MUIZON (1987), along with the perilymphatic foramen being large, and opening dorsally. However, the pars cochlearis is also squared in *Dalpiazina* MUIZON, 1988 as noted by MUIZON (1988c). The Rohrbach periotic does not have an articular rim or a homologue structure, but has a squared pars cochlearis, where the perilymphatic foramen opens posteriorly rather than dorsally.

Besides the shape of the pars cochlearis, the Rohrbach periotic resembles *Dalpiazina ombonii* (LONGHI, 1898) in having a swollen anterior process with a delicately convex dorsal contour and a faint apical tubercle in medial view;

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a narrow fovea epitubaria; a high superior process; and a prominent ventrolateral tuberosity. The apical tubercle and the smoothly convex dorsal surface of the anterior process are also typical of the Squalodontidae as discussed by MUIZON (1988c) and FORDYCE (1994). In contrast to squalodontids and *Dalpiazina*, however, the Austrian periotic has an anteroexternal sulcus, and the mallear fossa opens posteromedially, not ventrally.

In summary, the NHMW 1939.I.31 periotic shows morphological similarities with the families Dalpiazinidae, Squalodontidae, and Eurhinodelphinidae. In the lack of more diagnostic material, however, the single periotic from Rohrbach can not be assigned with certainty to any of the known families.

Superfamilia Delphinoidea GRAY, 1821

Delphinoidea indet.

2003 Delphinoidea gen. et sp. indet. – KAZÁR:145-149, pl. 13.

Referred specimens: NHMW 1867, NHMW 1890/121, NHMW 1891/1 (3932), NHMW 1906/30, NHMW 2006z0195/0001 from Nußdorf-Heiligenstadt; NHMW V.23109, MÁFI V.24558-24564 (7 specimens) from Bruck Neudorf; MÁFI V.23109, MÁFI V. 23124 from Danitzpuszta.

Description (Table 2, Fig. 3): These periotics show an overall sinuosity, which is, the anterior process is bent medially and the posterior process is bent laterally in both dorsal and ventral view. The pars cochlearis is broadly joined to the body of the periotic and it is tilted anteriorly. The anterior process is short and mediolaterally flattened. The apex of the anterior process lies ventrally, and in well-preserved specimens there is a small rugosity on the apex. The dorsal surface of the anterior process is rounded in medial or lateral view. The cleft between the pars cochlearis and the anterior process is narrow, and it does not bear a crease in any of the specimens. The internal auditory meatus has the shape of a semi-circle, and continues anterolaterally in a small groove to include the internal facial foramen. In some periotics, however, a strip of bone occludes the groove and the internal facial foramen opens outside the internal auditory meatus (NHMW 1891/1). In some specimens the ventral surface of the pars cochlearis is flattened thereby forming an edge or

Delphinoidea indet.	**Measurement (number)**	**Observed range**	**Mean**	**Standard deviation**
	1. (11)	24.4-29.4	26.0	1.6
	2. (14)	17.1-21.0	18.8	1.0
	3. (14)	3.3-5.0	4.1	0.6
	4. (15)	2.0-3.0	2.5	0.3
	5. (14)	3.0-5.2	4.1	0.6
	6. (13)	14.2-16.5	15.2	0.7
Kentriodontidae indet. 2				
	1. (6)	21.6-24.1	22.9	0.9
	2. (6)	15.1-15.9	15.5	0.3
	3. (6)	3.1-3.9	3.4	0.3
	4. (6)	1.7-3.0	2.3	0.4
	5. (6)	3.6-4.4	4.0	0.3
	6. (6)	12.6-14.3	13.3	0.6
Kentriodon fuchsii (BRANDT, 1873)				
	1. (49)	23.5-31.2	26.4	1.5
	2. (46)	15.6-20.0	17.1	1.0
	3. (49)	2.2-5.4	3.9	0.7
	4. (48)	1.7-3.9	2.6	0.4
	5. (48)	3.0-6.2	4.8	0.6
	6. (48)	11.7-14.2	13.0	0.7
Sophianaecetus commenticius (KAZÁR, 2005)				
	1. (7)	28.6-32.9	30.3	1.7
	2. (6)	20.5-23.5	21.6	1.1
	3. (6)	2.8-4.6	3.5	0.6
	4. (6)	2.1-2.8	2.6	0.3
	5. (6)	3.3-5.1	4.0	0.6
	6. (7)	18.0-20.5	18.8	1.0

Table 2: Delphinoidea indet., Kentriodontidae indet. 2, *Kentriodon fuchsii* (BRANDT, 1873), and *Sophianaecetus commenticius* (KAZÁR, 2005) of the Carpathian Basin. Measurements of periotics (in mm). The measuring points (1-6) are defined in the Material and Methods.

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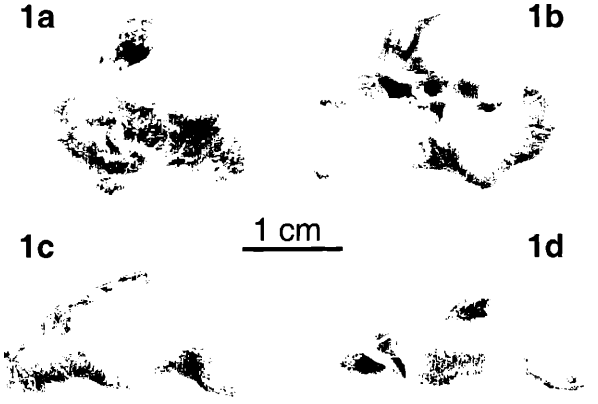

Figure 4: Kentriodontidae indet. 1, MÁFI V.21679/1 from Tăşad (Romania). Left periotic in 1a, dorsal; 1b, ventral; 1c, lateral; and 1d, medial views.

a faint ridge with the more globular medial surface of the pars cochlearis in some specimens. The posterior process is short, and its shape is elongate rhomboidal in ventral view. The posterior bullar facet is concave and either completely smooth or finely striated on its posterolateral part. The posterior process is bent ventrally at a sharp angle from the body of the periotic, forming a sharp angle on the posterior part of the dorsal surface (particularly sharp in MÁFI V.24564). In NHMW 1891/1, and in all specimens which are worn, the same area is rounded off. The cerebral surface of the periotic is sometimes convex mediolaterally (NHMW 1891/121), but typically there is a prominent flat area, which protrudes anterolaterally. In lateral view, this results in a groove between the protruding plateau of the cerebral surface and the ventrolateral tuberosity (particularly excavated in MÁFI V.24564). The endolymphatic foramen is situated relatively far from the internal auditory meatus, and in well-preserved specimens it is a "half-moon" or "quarter moon"-shaped slit. The groove for the head of the malleus is elliptical. The hiatus epitympanicus is moderately wide.

Discussion: A total of 15 periotics represents this species in the Carpathian Basin. They come from three localities, two of which are in the Vienna Basin. All are isolated periotics. Because no other elements are known, the taxonomic identity of this odontocete is unknown. I refer the species to the Delphinoidea, because the short and mediolaterally slightly compressed anterior process with a squared apex and without an anterior bullar facet is diagnostic of the Delphinoidea as defined by Muizon (1988a).

The periotics from the Carpathian Basin referred here as Delphinoidea indet. show morphological similarities to species of modern delphinoid groups. Specifically, the relatively large and anteriorly inclined pars cochlearis (e.g., Fig. 3, 1a-b) resembles the latest Miocene monodontid *Denebola brachycephala* Barnes, 1984. The Carpathian Basin delphinoid periotics differ from *D. brachycephala* in having a larger anterior process and a medially less extended pars cochlearis. Likewise, the Carpathian Basin delphinoid shows marked similarities to the Late Miocene phocoenid *Piscolithax boreios* Barnes, 1984 in the size and medial bending of the anterior process, in the size, shape and lateral bending of the posterior bullar facet, and, particularly, in the anterior tilting of the pars cochlearis (see Barnes, 1984). However, in the Carpathian Basin periotics the internal auditory meatus closes at a smaller angle with the body of the periotic than in the holotype periotic of *P. boreios*, and the mallear fossa is larger.

All 15 specimens reported here as Delphinoidea indet. clearly represent a single morphology. The differences in the relative size and medial bending of the anterior process, in the relative size and anterior tilting of the pars cochlearis, point to a moderate intraspecific variation.

Familia Kentriodontidae Slijper, 1936

Kentriodontidae indet. 1

2003 "*Heterodelphis*"(?) n. sp. – Kazár:159-168, pl. 15.
2003 Kentriodontidae indet. (unnamed n. sp.) – Kazár & Venczel:55.

Referred specimen: MÁFI V.21679/1, left periotic and MTC 22404, right periotic of the same individual from Tăşad.

Description (Table 1, Fig. 4): A detailed description of this specimen is given by Kazár & Venczel (2003). The periotic is slightly smaller than the holotype periotic of *Kentriodon pernix* Kellogg, 1927. The anterior process is small but not reduced; longer than the same structure in the Delphinoidea indet. periotic, and nearly as long as in "*Heterodelphis*" *leiodontus*. It is slightly bent medially. In dorsal view the anterior process has a conical tip, and there is a small crease on the cleft between the anterior process and the pars cochlearis. The dorsoventral depth of the anterior process is small, and in medial view it has an obtuse end. The apex of the anterior process (anteroventral angle) bears a tiny rugosity. The dorsal surface of the anterior process is convex.

The pars cochlearis is small and broadly joined to the body of the periotic. A small but distinct tuberosity between the perilymphatic foramen and the fenestra rotunda makes the pars cochlearis appear elongate anteroposteriorly. The cerebral surface of the periotic is mediolaterally convex, and posteriorly, there is a sharp peak on the cerebral surface caused by the ventral bending of the posterior process. The posterior process is bent laterally to the same amount as in the holotype of *Kentriodon pernix*. The posterior bullar facet is broadly pentagonal, concave, and finely striated. The stapedial muscle fossa is broad. The facet for the head of the malleus is circular, and faces ventrally. The ventrolateral tuberosity bears a small lateral eminence.

Discussion: The odontocete skeleton from Tăşad was referred to the Kentriodontidae by Kazár & Venczel (2003), among others because its periotic shows a morphology typically observed in members of this family: relatively small anterior and posterior processes; the sinuosity caused by the medial bending of the anterior process and the lateral bending of the posterior process; a small pars cochlearis, which is often broadly joined to the body of the periotic.

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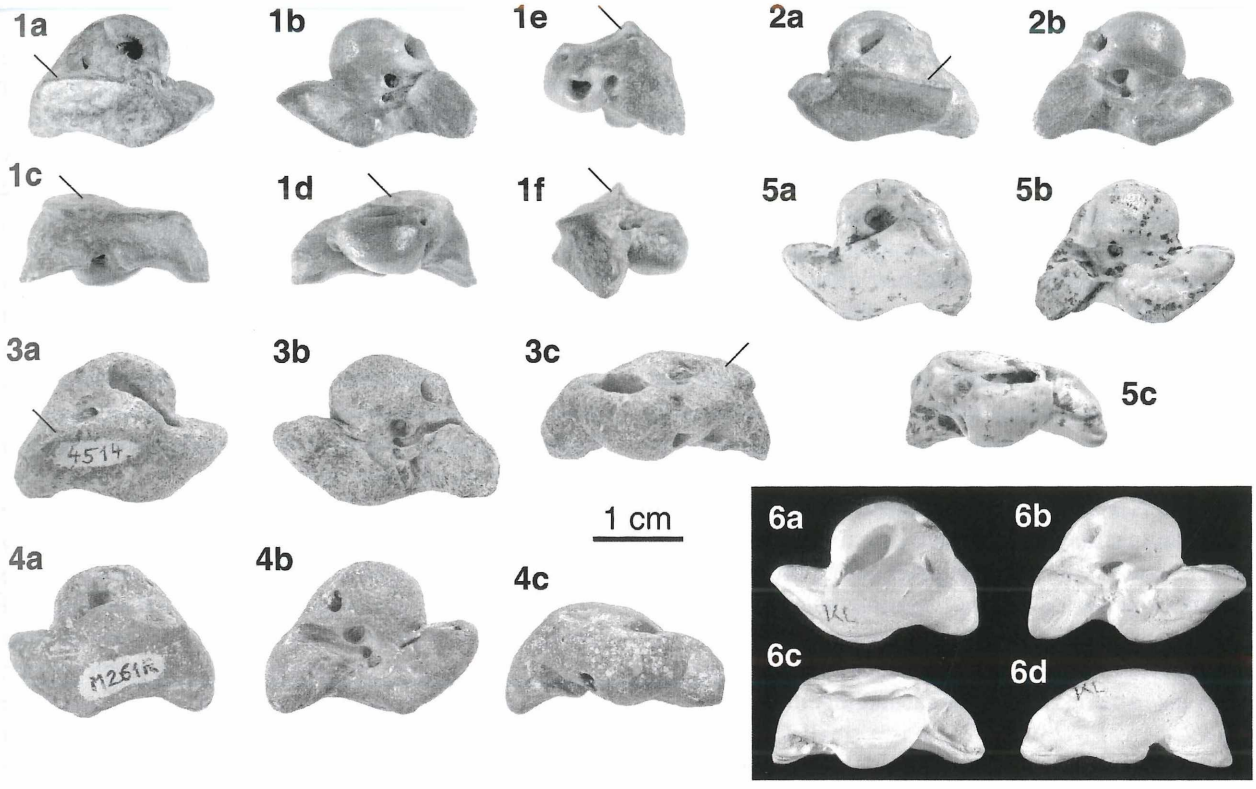

Figure 5: Kentriodontidae indet. 2 from Nußdorf-Heiligenstadt and Danitzpuszta. 1–PIUW 3128/2, right periotic in (a) dorsal, (b) ventral, (c) lateral, (d) medial, (e) posterior, and (f) anterior views. 2–PIUW 3128/1, left periotic in (a) dorsal and (b) ventral views. 3–LC140-4514, original to MÁFI V.23102, right periotic in (a) dorsal, (b) ventral, and (c) medial views; 4–M261R, original to MÁFI V.23101, left periotic in (a) dorsal, (b) ventral, and (c) medial views; 5–MÁFI V.23125, left periotic in (a) dorsal, (b) ventral, and (c) medial views; 6–MÁFI V.24236 (cast), left periotic in (a) dorsal, (b) ventral, (c) medial, and (d) lateral views. The crista dorsalis is marked with slash.

The periotic of the Tăşad dolphin differs in morphology from all named kentriodontid species and from all other odontocete periotics of the Carpathian Basin. Its size is close to that of "*Heterodelphis*" *leiodontus* and the Kentriodontidae indet. 2 of this paper. It differs from the latter in the smaller pars cochlearis and in the shape of the posterior bullar facet, which is pentagonal in the Romanian odontocete and oval in the Kentriodontidae indet. 2 periotics. The shape of the posterior bullar facet separates the Tăşad kentriodontid from "*Heterodelphis*" *leiodontus*, *Kentriodon pernix* and *K. obscurus* (KELLOGG, 1931), where it is diamond-shaped and more elongate. The periotic of the unnamed kentriodontid from Tăşad also has an anterior process with smaller dorsoventral depth, a smaller pars cochlearis, a distinct lateral eminence on the ventrolateral tuberosity, and a larger tuberosity between the perilymphatic foramen and the fenestra rotunda than the periotics of *K. pernix* and *K. obscurus*. A more extensive comparison of the Kentriodontidae indet. 1 periotic from Tăşad with other kentriodontid species is given in KAZÁR & VENCZEL (2003).

Kentriodontidae indet. 2

2003 cf. "*Heterodelphis*"(?) n. sp. – KAZÁR:168-170.

Referred specimens: PIUW 3128/1-2, left and right periotics, in all probability of the same individual from Nußdorf-Heiligenstadt; MÁFI V.23101, MÁFI V.23102, MÁFI V.23125, and MÁFI V.24236 from Danitzpuszta.

Description (Table 2, Fig. 5): The periotic of this species is small, MÁFI V. 23125 being the smallest known periotic from the Carpathian Basin Middle Miocene. The anterior process is bent medially, more so in the MÁFI V.23125 specimen, with the apex pointing anteriorly, giving the anterior process the shape of the pouring of a watering can in ventral view (Fig. 5:1b, 2b, 6b). In dorsal view it is triangular with a conical tip. In medial view, its dorsal contour is convex. The anterior process is mediolaterally compressed, and in well-preserved specimens its dorsal surface bears a rugose anterior keel. The apex of the anterior process (the anteroventral angle) has a tiny anterior protuberance, which is worn away on the MÁFI V.23101 and MÁFI V.23102 specimens. The relative length of the anterior process is somewhat variable: it is relatively longer in MÁFI V.23125 and MÁFI V.24236, whereas short and stout in PIUW 3128/1, 2, and in MÁFI V.23101. The cleft between the anterior process and the pars cochlearis bears a small crease in most specimens, but not in MÁFI V.23125 and MÁFI V.24236.

The posterior process is likewise short and it is bent laterally. The posterior process is bent ventrally at a sharp angle from the body of the periotic, thus giving a rectangular profile of the posterior part of the periotic in lateral view. The posterior bullar facet is small, finely striated, and its shape is narrowly oval. It is strongly concave mediolater-

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ally in most specimens, but in MÁFI V.23125 and MÁFI V.24236 it is almost flat. The stapedial muscle fossa is deep. It is wide in some specimens (Fig. 5:1b-3b), whereas it is largely obscured by the overhanging medial edge of the posterior process and the recurved posterolateral part of the pars cochlearis in others (Fig. 5:4b-6b). The mallear fossa is relatively small and oval. The hiatus epitympanicus is wide. The ventrolateral tuberosity is generally small.

The pars cochlearis is large but not inflated, and broadly joined to the body of the periotic. The internal auditory meatus is narrowly elliptical, its axis closes at a sharp angle with the body of the periotic. The fundus of the internal auditory meatus occupies only the anterior part of the pars cochlearis, whereas a large, triangular area posterior to the internal auditory meatus includes the endolymphatic foramen. Nevertheless, in the MÁFI V.23125 and MÁFI V.24236 specimens the tractus spiralis foraminosus is more circular, and the fundus of the internal auditory meatus occupies a larger area. The internal facial foramen either opens in a short anterior slit of the fundus of the internal auditory meatus (MÁFI V.23102, 24236), or there is a tiny hole anterior to the internal auditory meatus (PIUW 3218/2, MÁFI V.23125). There is a small eminence between the perilymphatic foramen and the fenestra rotunda, wich is prominent in some specimens (PIUW 3128/1, 2, MÁFI V.23102), indistinct in others.

The most conspicuous feature of the periotic of this odontocete is the morphology of the cerebral surface. A ridge runs longitudinally from the junction of the pars cochlearis and the anterior process towards the posterior margin of the periotic, which attains height posteriorly. Posteriorly it terminates in a small, rounded tuberosity, which is visible even in worn specimens such as MÁFI V.23102. This structure is hereby termed crista dorsalis (dorsal crista). Medial to the crista dorsalis, the surrounding area of the endolymphatic foramen is concave; lateral to the crista dorsalis the cerebral surface of the periotic is strongly excavated: the laterally sloping lateral wall of the crista dorsalis turns into a medially sloping lateral plateau. Thus, a wide, shallow fossa is formed between the keel of the crista dorsalis and the lateral margin of the cerebral surface of the periotic. The lateral plateau of the cerebral surface closes at a right angle with the lateral side of the anterior process, thus giving a rectangular profile of this part of the periotic in anterior view (Fig. 5:1f).

The crista dorsalis is less prominent in MÁFI V.23102, and completely lacking in MÁFI V.23101, 23125, 24236. The MÁFI V.23102 and MÁFI V.23125 specimens are slightly eroded, the MÁFI V.23101 is strongly worn, as seen by the rounded edges of the posterior processes. The posterior tuberosity of the crista dorsalis is visible in this latter specimen, and hence it is likely that the MÁFI V.23101 periotic also had a crista dorsalis. On the other hand, the lack of the the crista dorsalis in the MÁFI V.23125 and MÁFI V.24236 specimens are in all probability not due to wear, as the dorsal surface of these periotics seems to be intact. The cerebral surface of the periotic is mediolaterally convex and anteroposteriorly flat in the MÁFI V.23125 periotic. In the MÁFI V.24236, the cerebral surface is divided longitudinally into a flat medial and a slightly concave lateral areas, which close at a right angle in the anterior and posterior views of the periotic. The place of the division corresponds to the position of the crista dorsalis of the other specimens, and posteriorly, there is a tiny rugosity, which resembles the posterior termination of the crista dorsalis. However, a crista dorsalis is not present, although the specimen is well-preserved and not worn.

Discussion: The species represented by the six periotics from Nußdorf-Heiligenstadt and Danitzpuszta has short and mediolaterally compressed anterior process, which is typical of the Delphinoidea as defined by MUIZON (1988a). The six periotics are hereby referred to the family Kentriodontidae, because they show the general sinuosity usually observed with members of this family.

The MÁFI V.23125 and MÁFI V.24236 specimens are somewhat similar to a periotic of *Liolithax* sp. figured by BARNES (1978: fig. 3) in the shape and relative length of the anterior process, in the shape of the pars cochlearis and the internal auditory meatus. However, the Danitzpuszta periotics are significantly smaller than the Californian periotic, and the endolymphatic and perilymphatic foramina are more widely spaced. They also resemble *Nannolithax gracilis* KELLOGG, 1931 in general morphology and in the shape of the posterior bullar facet, but the anterior process is shorter in the Hungarian specimens, and there is no crease on the medial surface of the anterior process at the junction with the pars cochlearis.

The Kentriodontidae indet. 2 periotics of the Carpathian Basin differ from all known odontocete periotics in the presence of the crista dorsalis. The crista dorsalis is possibly homologueous with the small longitudinal keel observed on the cerebral surface of the holotype periotic of "*Heterodelphis*" *leiodontus* and on a few others referred to *Kentriodon fuchsii* (BRANDT, 1873) in this paper, but it is much more prominent and it terminates posteriorly in a tuberosity. Nothing is known on the importance and function of the crista dorsalis. Its taxonomic significance is weakened by the following observations: (1) a similar structure is sometimes but not always present in periotics referred to the species *Kentriodon fuchsii* (BRANDT, 1873) in this paper; (2) two well-preserved specimens (MÁFI V.23125, MÁFI V.24236) of the Kentriodontidae indet.2 are completely lacking a crista dorsalis; and (3) the crista dorsalis is present in a single periotic referred to a different species (?*Loxolithax* sp., see below).

It must be noted, however, that the MÁFI V.23125 and MÁFI V.24236 specimens are a little different from the other periotics referred to as Kentriodontidae indet. 2. In particular, the internal auditory meatus is more circular in the latter two periotics, the anterior process is bent slightly more medially, there is no crease on the cleft between the anterior process and the pars cochlearis, the posterior process is bent more laterally, and the posterior bullar facet is not concave but flat in MÁFI V.23125 and MÁFI V.24236. It is not clear if the above mentioned differences are strong enough to exclude conspecificy, and if the presence or absence of the crista dorsalis is diagnostic. In the present concept, the MÁFI V.23125 and MÁFI V.24236

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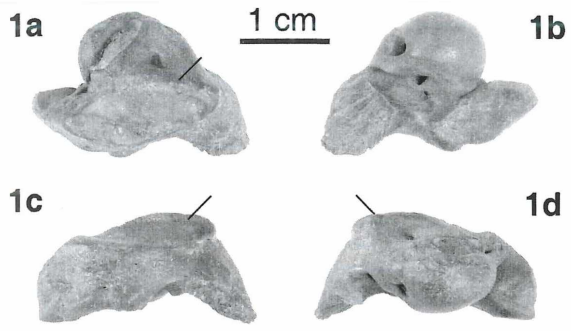

Figure 6: ?*Loxolithax* sp. from Nußdorf-Heiligenstadt (Austria). 1–PIUW 3128/9, left periotic in (a) dorsal, (b) ventral, (c) lateral, (d) medial views. The crista dorsalis is marked with slash.

specimens are regarded as conspecific with the other four periotics from Nußdorf-Heiligenstadt and Danitzpuszta, but in the lack of more diagnostic cranial material I can not exclude the possibility that they represent a different species, or even a different genus.

Moreover, the ?*Loxolithax* sp., as discussed below, is very close in morphology to the Kentriodontidae indet. 2 periotics. It is treated here as a separate taxon, but again, more material is needed to reach a final conclusion. As long as these taxonomic questions can not be answered, the diagnostic significance of the crista dorsalis remains unresolved. It is possible that the development of the crista dorsalis had a yet unknown functional significance for these small odontocetes of the Central Paratethys, perhaps in a response to special environmental conditions.

?*Loxolithax* sp.

Referred specimen: PIUW 3128/9 from Nußdorf-Heiligenstadt.

Description (Table 1, Fig. 6): This species has a small periotic with short anterior and posterior processes, while the anterior process is bent medially. In dorsal view it has a triangular shape and a conical tip. Nevertheless the anterior process is straight in ventral view, unlike in the Kentriodontidae indet. 2 periotics. In medial view, the anterior process has a convex dorsal contour, where the apex is situated ventrally, forming a small protuberance, similarly to the periotics of the Kentriodontidae indet. 2. The anterior process is compressed mediolaterally. Its lateral surface bears a shallow longitudinal groove or depression, as a consequence of the lateral expansion of the dorsal surface of the periotic.

The posterior process is short, but slightly longer than that of the Kentriodontidae indet. 2. It is bent ventrally at a sharp angle. Its posterior bullar facet is finely striated, and has a pentagonal outline. The stapedial muscle fossa is deep and wide. The cleft between the anterior process and the pars cochlearis bears a small crease. The mallear fossa is narrowly oval, the hiatus epitympanicus is wide. The ventrolateral tuberosity is small but prominent.

The pars cochlearis is relatively large, as compared to other kentriodontid periotics discussed in the present paper, and it is broadly joined to the body of the periotic. As with the Kentriodontidae indet. 2 periotics, the internal auditory meatus has a narrow fundus, which occupies only the anterior part of the pars cochlearis. It continues anteriorly in a narrow slit. The cerebral surface of this periotic is dominated by a crista dorsalis (definition see above). The morphology of the crista dorsalis and the surrounding area of the dorsal surface of the periotic agrees with that of the PIUW 3128/1, PIUW 3128/2 specimens of the Kentriodontidae indet. 2, and is not repeated here. The eminence between the perilymphatic foramen and the fenestra rotunda is weakly developed.

Discussion: The PIUW 3128/9 specimen is very close in morphology to the above discussed Kentriodontidae indet. 2 periotics. Most obviously, both forms are characterized by a prominent crista dorsalis. Nevertheless, the taxonomic significance of this structure is doubtful (see discussion above). The PIUW 3128/9 periotic differs from the Kentriodontidae indet. 2 in its slightly greater size (Tables 1, 2), in having a relatively longer and more elongate anterior process, a longer posterior process, and in the greater width of the posterior bullar facet, which is narrowly pentagonal rather than oval in outline.

An isolated periotic from the Miocene of Apulia, Italy, referred to as *Lamprolithax*? sp. by BIANUCCI & VAROLA (1995:fig. 2: 2) has similar overall size and general morphology to the Austrian specimen. However, the PIUW 3128/9 periotic differs from the Italian *Lamprolithax*? sp. in the shape of the posterior bullar facet, which is broadly pentagonal in the Apulian periotic.

The PIUW 3128/9 specimen is close in morphology to *Loxolithax sinuosa* KELLOGG, 1931, a species based on two isolated periotics from the Middle Miocene Temblor Formation of California (KELLOGG, 1931). The PIUW 3128/9 periotic is somewhat smaller than the holotype and paratype specimens of *Loxolithax sinuosa* as measured by KELLOGG (1931:393). It resembles the holotype of *L. sinuosa* in the general shape of the periotic, in the relative length and morphology of the anterior and posterior processes, in the shape of the posterior bullar facet, and in the size and form of the pars cochlearis. It differs from the Californian species in the following features: the fundus of the internal auditory meatus is narrower, the stapedial muscle fossa is broader in the Austrian periotic, and the endolymphatic foramen is situated farther medially (that is, closer to the rim of the internal auditory meatus).

BARNES & MITCHELL (1984) noted that *L. sinuosa* differs from *Kentriodon* among others by being flatter dorsoventrally, having a larger pars cochlearis, having a groove on the lateral surface of the anterior process, and by lacking any flattening of the cerebral surface. The PIUW 3128/9 periotic differs from the holotype of *K. pernix* in the same ways, except that the presence of the crista dorsalis affects the morphology of the cerebral surface of the periotic. Thus, the dorsoventral depth of the periotic of ?*Loxolithax* sp. from Nußdorf-Heiligenstadt is not apparently smaller than that of *K. pernix*, and the cerebral surface lateral of the crista dorsalis is flattened.

Because of the great morphological similarity of the PIUW

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3128/9 specimen to the paratype and, especially, to the holotype of *Loxolithax sinuosa*, I questionnably refer the single periotic from Nußdorf-Heiligenstadt to the genus *Loxolithax*. KELLOGG (1931) described *Loxolithax sinuosa* as a species of Delphinidae, but the general morphology of the type periotics agrees with that of many kentriodontid species.

Familia Kentriodontidae SLIJPER, 1936

Genus "*Heterodelphis*" BRANDT, 1873

"*Heterodelphis*" *leiodontus* (PAPP, 1905)

1905 *Heterodelphis leiodontus* nova forma – PAPP:30.
2003 "*Heterodelphis*" *leiodontus* – KAZÁR:150-159.

Holotype: MÁFI Ob.580, nearly complete skeleton, including skull, split longitudinally and preserved on two limestone slabs, from St. Margarethen, Roman Quarry. The preserved right periotic and tympanic are incomplete: the dorsal surface of the posterior process of the periotic is broken away, and of the tympanic only the involucrum and the inner posterior prominence are preserved.

Referred specimen: Without inventory number in the private collection of G. Wanzenböck from the Kummer Quarry of St. Margarethen: left periotic, teeth, axis, fragments of other vertebrae and ribs, right humerus, radius, ulna of the same individual preserved in a block of corallinaceous limestone. The periotic is partially prepared, with only the dorsal surface of pars cochlearis, anterior process and cerebral surface being visible.

Emended diagnosis of species: A kentriodontid having smaller pars cochlearis and less rounded internal auditory meatus of periotic than *Kentriodon pernix* and *K. obscurus*; having small, conical teeth with smooth enamel; having short humerus which does not widen distally; deltoid tuberosity of humerus is centrally positioned on the anterior margin; radius and ulna slightly longer than humerus and having only a narrow space between the two bones; ulna bearing a flag-like olecranon process. (The arm bones are illustrated in PAPP, 1905: figs. 5, 6, pls. 5, 6 and in KAZÁR, 2003: fig. 5.6, pl. 14. The skull and postcrania are described by PAPP, 1905.)

Description of periotic (Table 1, Fig. 7): The description is based on the right periotic of the holotype specimen, MÁFI Ob.580. It is largely complete, but the dorsal and posterior parts of the posterior process are missing.

The size of the periotic is basically identical to the holotype periotic of *Kentriodon pernix* (USNM 8060). The anterior process is short, mediolaterally flattened, and it is moderately bent medially. The apex is conical in dorsal view. In medial or lateral view, the apex is situated dorsally, whereas the ventral contour of the anterior process is convex. In the terminology of MUIZON (1988b), the dorsal angle projects more anteriorly than the ventral angle. The posterior process bends ventrally at a sharp angle from the body of the periotic, and thus forms a peak on the dorsal surface of the periotic posteriorly. The posterior bullar facet, as far as preserved, is rhomboidal or narrowly pentagonal, and bears a few fine striae. The stapedial muscle fossa is narrow, largely obscured from posterolateral by the posterior bullar facet. The ventrolateral tuberosity is pronounced and laterally it has a sharp peak, which gives the anterior part of the periotic a triangular appearance in ventral view. The mallear fossa is large and almost circular. The hiatus epitympanicus is narrow. The pars cochlearis is small but broadly joined to the body of the periotic. The internal auditory meatus is narrow and roofed over by bone tissue from lateral. As a consequence, the endolymphatic foramen is far from the rim of the internal auditory meatus. The cerebral surface of the periotic does not form a plateau-like dorsal area: the triangular area around the endolymphatic foramen is separated from the laterally sloping cerebral surface by a weak, longitudinal keel. It is not clear if this longitudinal keel is homologueous with the dorsal crest defined by FORDYCE (1994). The dorsal crest of FORDYCE (1994) extends anteriorly from the vertex of the cerebral surface and continues in the anterior keel of the anterior process in *Waipatia* FORDYCE, 1994. In the MÁFI Ob.580 periotic, the longitudinal keel does not extend anteriorly on the dorsal surface of the anterior process, but terminates at the junction between the pars cochlearis and the anterior process. The cleft between the anterior process and the pars cochlearis has a broad crease.

The referred periotic of "*Heterodelphis*" *leiodontus* is similar in size to the holotype. The relative size and shape of the pars cochlearis and of the internal auditory meatus is likewise similar to the holotype, but the anterior process seems to be more robust and less compressed mediolaterally. The longitudinal keel on the cerebral surface of the periotic is possibly present, but this part of the periotic is largely obscured by a rib fragment.

Discussion: The type species of the genus *Heterodelphis* BRANDT, 1873 is *H. klinderi* BRANDT, 1873. This species was based on mandibular and rostral fragments, a tympanic bulla, a few teeth and ribs, a scapula, a sternum, a humerus, and several vertebrae of a juvenile specimen (BRANDT, 1873:249-253, pls. 25, 26). Besides *H. klinderi* and "*H.*" *leiodontus*, a third species has been included in the genus *Heterodelphis*: GORJANOVIĆ-KRAMBERGER (1884) referred to a rostrum fragment with attached teeth of an odontocete from Podsused as ?*Heterodelphis* sp. He later (GORJANOVIĆ-KRAMBERGER, 1892) described the material as a new species and named it *Platanista croatica*.

The systematic position of the genus *Heterodelphis* is unresolved. TRUE (1912) included it in the Delphinidae, WINGE (1921) assumed that it was closely related to *Schizodelphis*. KELLOGG (1925, 1927) mentioned *Heterodelphis klinderi* and "*H.*" *leiodontus* when comparing these with the teeth of *Kentriodon pernix*, and shortly thereafter he listed *Heterodelphis* as a member of the Delphinidae (KELLOGG, 1928). BARNES (1978) stated that in the lack of the skull it is impossible to refer the genus to any of the odontocete families, and MCKENNA & BELL (1997) listed the genus as Odontoceti incertae sedis. MUIZON (1988a, c) and FORDYCE & MUIZON (2001) regarded the genus as a possible member of the Delphinida.

A systematic revision of the genus *Heterodelphis* is not

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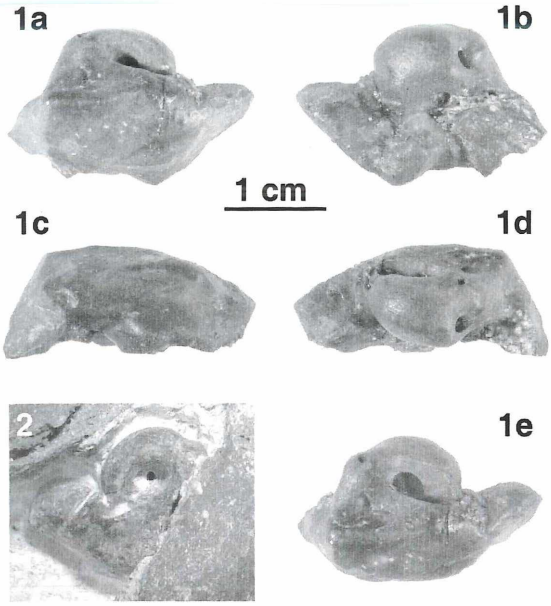

Figure 7: *"Heterodelphis" leiodontus* (PAPP, 1905) from St. Margarethen (Austria). 1–MÁFI Ob.580, holotype, right periotic in (a) dorsal, (b) ventral, (c) lateral, (d) medial, and (e) dorso-medial views. 2–specimen without inventory number in the private collection of G. Wanzenböck (Bad Vöslau, Austria), left periotic in dorso-medial view.

possible, partly because the holotype of the type species does not include a well preserved skull, only non-diagnostic cranial fragments, and also because the type material is probably lost. BRANDT (1873) indicated that the material was sent to Vienna in 1865; up to the present day, I was not able to find it in the collections of the NHMW and PIUW. MUIZON (1988c) suggested that the morphology of the tympanic bulla, of the atlas [correctly: the axis] and that of the transverse processes of the lumbar vertebrae indicate a relationship with the Delphinida.

In addition, the rostral fragments are of a long-snouted, homodont species with circular, closely spaced dental alveoli. The scapula bears a short, thin, rod-like coracoid process; a large acromion, which is not shifted to the anterior border of the scapular blade but borders the supraspinatus fossa from lateral (BRANDT, 1873: pl. 26, fig. 25). The humerus is gracile and elongate, with a small caput, a shallow infraspinous fossa and a faint posterior tuberosity. It probably lacks a distinct greater tubercle and an olecranon facet, and there is no deltoid tuberosity (BRANDT, 1873: pl. 26, fig. 26). The humeral morphology of the holotype of *Heterodelphis klinderi* as figured by BRANDT (1873) most closely resembles the recent *Platanista*, but because this is of a juvenil (proximal and distal epiphyses are not completely fused), the humeral characters must be treated cautiously. The scapula with its small but not reduced coracoid process and the presence of the supraspinatus fossa is similar to the eurhinodelphinid *Eurhinodelphis* and *Schizodelphis* sensu MUIZON (1988c), and the kentriodontid *Atocetus iquensis* MUIZON, 1988.

In conclusion, *Heterodelphis klinderi* is probably a species of the Delphinida as suggested by MUIZON (1988c), but in the lack of evidence it is more adequate to regard the genus *Heterodelphis* as Odontoceti incertae sedis, as proposed by BARNES (1978) and MCKENNA & BELL (1997).

"Heterodelphis" leiodontus was described on the basis of a distorted skeleton, which is lying on a slab of corallinaceous limestone split longitudinally (PAPP, 1905). In the description of the species PAPP (1905) included a right humerus, radius, ulna of a single specimen, and six vertebrae from Borbolya (today: Walbersdorf, Austria). Unfortunately, the holotype skeleton including the skull is so badly preserved that basically no characters can be observed (see PAPP, 1905: pls. 5, 6). Of the skull, only a number of teeth were preserved well. PAPP (1905) assigned his newly described species to the genus *Heterodelphis* mainly on the basis of the dental morphology: the teeth of *"H." leiodontus* are indeed very similar to those of *H. klinderi* in their smooth enamel, long and conical crowns, and delicately recurved roots.

However, in *"Heterodelphis" leiodontus* the coracoid process of the scapula is large and flag-like as is common in delphinoid species (PAPP, 1905: pl. 5). The humerus is robust, proximo-distally shortened. It has a well-defined greater tubercle, and the lesser tubercle is a more or less circular plateau. The humerus has a large deltoid tuberosity in the middle of the anterior margin (PAPP, 1905). Although PAPP (1905) stated that the species probably had long mandibles and rostrum, the exact length of these structures is actually unknown, because the anterior part of the skull is lost. The preserved part of the rostrum is 190 mm long, and has 31-33 dental alveoli. The mandible as preserved is 246 mm long (estimated; the posterior end of the mandible is fragmentary) and contains 25 teeth. Of these, 12 are situated in the preserved fragment of the symphyseal part (68 mm). The postsymphyseal part of the tooth row measures 68 mm with 13 alveoli.

In 2001, L. Kordos, head of the Geological Museum of Hungary of the MÁFI prepared the otic region of the exposed right side of the skull further and managed to free the ear bones of the holotype. Of the tympanic, only the involucrum and the inner posterior prominence is preserved. Based on the development of the involucrum of the tympanic bulla (KAZÁR, 2003), *"Heterodelphis" leiodontus* is a member of the Delphinida as defined by MUIZON (1988a). The humerus is morphologically similar to kentriodontid species (for a comparison see KAZÁR & VENCZEL, 2003: fig. 6), and the periotic shows an overall morphology typical of the grade family Kentriodontidae.

The periotic of *"Heterodelphis" leiodontus* is similar to the holotype of *Kentriodon pernix* in size, in overall morphology, and in the relative size and morphology of the anterior process (fig. 7). *"Heterodelphis" leiodontus* differs from species of *Kentriodon* in having a smaller pars cochlearis, where the internal auditory meatus is less circular. All other described genera of the Kentriodontidae have markedly different periotic morphologies.

The differences in the scapular and humeral morphology between *H. klinderi* and *"H." leiodontus* indicate that these two species are not congeneric. Thus, the genus *Heterodelphis* should be restricted to its type species, *H. klinderi*

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BRANDT, 1873. Because "*Heterodelphis*" *leiodontus* is not a member of the genus *Heterodelphis* BRANDT, 1873, to which *H. klinderi* BRANDT, 1873 is the type species, "*Heterodelphis*" *leiodontus* deserves a new genus. However, with the exception of the holotype periotic, the available material does not include diagnostic cranial elements and is thus not sufficient to define a new odontocete taxon. For this reason, the generic name *Heterodelphis* is used here in quotation marks.

Kentriodon fuchsii (BRANDT, 1873), new combination

1873 ?*Champsodelphis Fuchsii* – BRANDT:269-276, pl. 29.
1873 *Delphinus Fuchsii* – BRANDT:275.
1899 ?*Acrodelphis Fuchsii* BRANDT sp. – ABEL:853.
1934 *Acrodelphis fuchsii* BRANDT – PIA & SICKENBERG:37.
1937 *Acrodelphis fuchsii* – PIA:403.
1995 Delphinoidea inc. sed. (?Kentriodontidae) – CODREA:94.
2003 *Atocetus fuchsii* (BRANDT, 1873) – KAZÁR:181-189.
2004 ?*Atocetus fuchsii* – KAZÁR et al.:179.
2006 "*Champsodelphis*" *fuchsii* – GRIGORESCU & KAZÁR:36.

Holotype: NHMW 1859.XXVII.6m, several vertebrae, sternum, fragment of scapula, left humerus from Nußdorf-Heiligenstadt.

Referred specimens: NHMW 2006z0194/0001 from Hernals; NHMW 1891/2 (A 3932), NHMW 4/905, PIUW 3128/3 (1874/IIII/8), PIUW 3128/4, PIUW 3128/5, PIUW 3128/6, PIUW 3128/8 from Nußdorf-Heiligenstadt; NHMW 1887/vi/19 from Loretto; NHMW 1982/74/2 and MÁFI V.24565-24581 (17 specimens) from Bruck Neudorf; M17R, M22R, MÁFI V.23098, MÁFI V.23099, MÁFI V.23110-23119 (10 specimens), MÁFI V.23122, and MÁFI V.23231-23235 (5 specimens) from Danitzpuszta; UBFG.222 from Comăneşti; MBT 15001/a, MBT 15001/b, MBT 15029 from Cluj-Napoca.

Description (Table 2, Figs. 8, 9, 10): Some of the periotics that I hereby refer to *K. fuchsii* have been already described in detail by KAZÁR (2003), KAZÁR et al. (2004), and GRIGORESCU & KAZÁR (2006). Since KAZÁR (2003) was finished, a few other periotics of the same species were collected. All periotics referred to *K. fuchsii* are characterized by (1) an overall sinuosity in dorsal view caused by the medial bending of the anterior process and the lateral bending of the posterior process; (2) a short anterior process which is slightly compressed mediolaterally; (3) a short posterior process with a pentagonal posterior bullar facet; (4) a small pars cochlearis which is joined broadly to the body of the periotic; (5) a strong ventrolateral tuberosity; (6) a strong eminence between the perilymphatic foramen and the fenestra rotunda (this character can not be seen on worn specimens); (7) a narrow hiatus epitympanicus; (8) an almost circular mallear fossa; (9) the posterior process is bent ventrally at a sharp angle thus forming a sharp peak on the posterior part of the dorsal surface of the periotic.

The morphology of the anterior process is somewhat variable: in medial or lateral view the anterior process typically has an anterodorsal protuberance, which projects more anteriorly than does the anteroventral termination of the anterior process. This gives the anterior process a rectangular appearance, similarly to *Kentriodon pernix* and *Atocetus iquensis*. A few periotics, however, have their apex in anteroventral position with a small rugosity, and a rounded, convex anterodorsal surface of the anterior process (PIUW 3128/8). The degree at which the anterior process is bent medially is similar in all specimens, but the mediolateral compression of the anterior process is variably expressed. Some have an anterior process with a conical apex in dorsal view, others are more robust and have a rounded tip. A few periotics (NHMW 1891/2) have a faint anterior keel on the anterior process, similarly to the holotype periotic of *K. pernix*, but the majority of the periotics referred to *K. fuchsii* have a smooth dorsal surface of the anterior process with a convex contour in medial view. The dorsoventral thickness of the anterior end of the anterior process is likewise variable.

Differences exist among the periotics referred to *K. fuchsii* in the morphology of the cerebral surface: some have a dorsal surface that is both mediolaterally and anteroposteriorly convex (MÁFI V.23235, V.23110), others have an oval, flat area on the cerebral surface (UBFG.222, MBT 15001a). Very few periotics (MÁFI V.24569, V.24573) have a faint longitudinal keel at the medial part of the cerebral surface of the periotic, similarly to the holotype periotic of "*H.*" *leiodontus*.

The morphology of the periotics of *Kentriodon fuchsii* as discussed above is very close to those of *K. pernix* and *K. obscurus*. In *K. fuchsii*, the ventrolateral tuberosity is stronger, the pars cochlearis is smaller and the internal auditory meatus is narrower than in *K. pernix*. The tuberosity between the perilymphatic foramen and the fenestra rotunda is stronger on many specimens of *K. fuchsii* than on the holotype periotic of *K. pernix* and most periotics referred to *K. obscurus* by BARNES & MITCHELL (1984: fig. 9, 10). The angle at which the posterior process closes with the body of the periotic is wide in *K. fuchsii*, whereas it is close to a right angle in *K. pernix*.

Discussion: BRANDT (1873:269) described a new species of odontocete from Vienna, and questionnably referred it to the genus *Champsodelphis* GERVAIS, 1848. Based on the description and figures of BRANDT (1873:269-277, pl. 29, figs. 1-7a), the material inventoried as NHMW 1859. XVII.6m must be regarded as the holotype of *Champsodelphis fuchsii* (PIA, 1937:403; SK 287 in the catalogue of PIA & SICKENBERG, 1934). In the following over 130 years, several inassociated vertebrae, forelimb elements and skeletal fragments have been referred to the same species from different localities in the territory of the ancient Paratethys Sea (MACAROVICI & OESCU, 1942; MCHEDLIDZE, 1960, 1964; MACAROVICI & ZAHARIA, 1967; IONESI & GALAN, 1988; KAZÁR, 2003; KAZÁR et al. 2004; GRIGORESCU & KAZÁR, 2006).

As discussed by KAZÁR et al. (2004), the taxonomy of *Champsodelphis fuchsii* is fairly complicated, because BRANDT (1873) included in the species 13 vertebrae that had been previously described by NORDMANN (1860) as *Delphinus fossilis bessarabicus* and thus, Brandt's spe-

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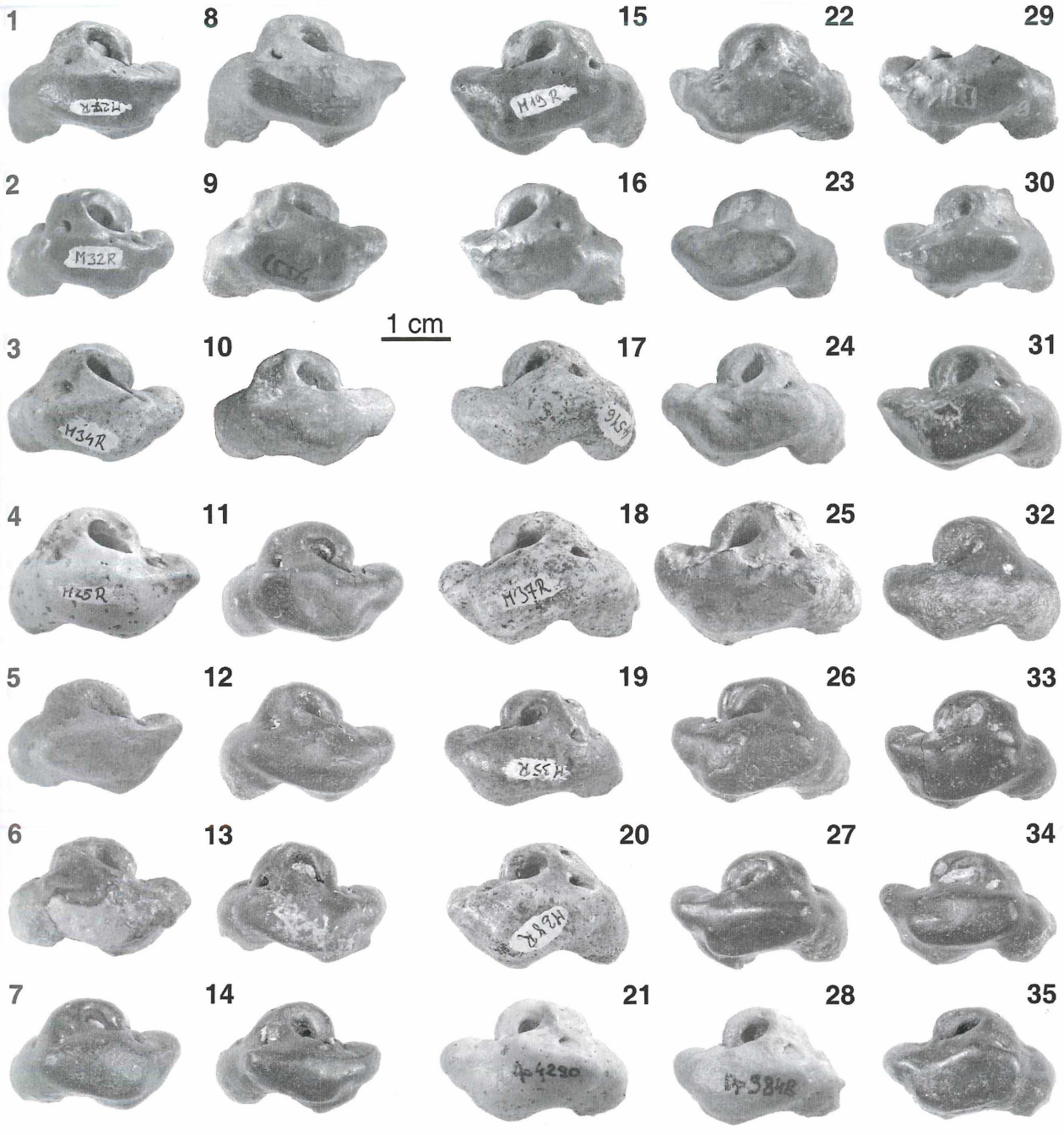

Figure 8: *Kentriodon fuchsii* (BRANDT, 1873) from Hernals, Nußdorf-Heiligenstadt, Loretto, Bruck Neudorf, Danitzpuszta, Comăneşti, and Cluj-Napoca. 1-14, right periotics, 15-35, left periotics in dorsal view. 1–M27R, original to MÁFI V.23234; 2–M32R, original to MÁFI V.23098; 3–M34R, original to MÁFI V.23099; 4–M25R, original to MÁFI V.23235; 5–MÁFI V.23117; 6–UBFG.222; 7–W.24, original to MÁFI V.24579; 8–NHMW 1891/2; 9–PIUW 3128/8; 10–NHMW 1887/6/19; 11–W.16, original to MÁFI V.24571; 12–W.19, original to MÁFI V.24574; 13–W.22, original to MÁFI V.24577; 14–W.26, original to MÁFI V.24581; 15–M19R, original to MÁFI V.23112; 16–PIUW 3128/4; 17–LC140-4516, original to MÁFI V.23110; 18–M37R, original to MÁFI V.23114; 19–M35R, original to MÁFI V.23113; 20–M38R, original to MÁFI V.23115; 21–MÁFI V.23232; 22–MBT 15001/a; 23–PIUW 3128/5; 24–NHMW 4/905; 25–NHMW 2006z0194/0001; 26–W.12, original to MÁFI V.24567; 27–W.18, original to MÁFI V.24573; 28–MÁFI V.23233; 29–PIUW 3128/3; 30–PIUW 3128/6; 31–NHMW 1982/74/2; 32–W.10, original to MÁFI V.24565; 33–W.17, original to MÁFI V.24572; 34–W.23, original to MÁFI V.24578; 35–W.25, original to MÁFI V.24580.

cies is possibly a junior synonym of the latter. Until more diagnostic material can be assigned to *D. fossilis bessarabicus*, however, it is reasonable to continue to use the specific name *fuchsii*, as proposed by KAZÁR et al. (2004). The value of the genus *Champsodelphis* is likewise problematic, because the type species was based on a mandible fragment. MUIZON (1988c) regarded *Champsodelphis* as a genus restricted to its type species.

The holotype of "*Champsodelphis*" *fuchsii* does not contain cranial material. The morphology of the holotype humerus and sternum were identified in two partial skeletons from Cluj-Napoca, which do not have skulls

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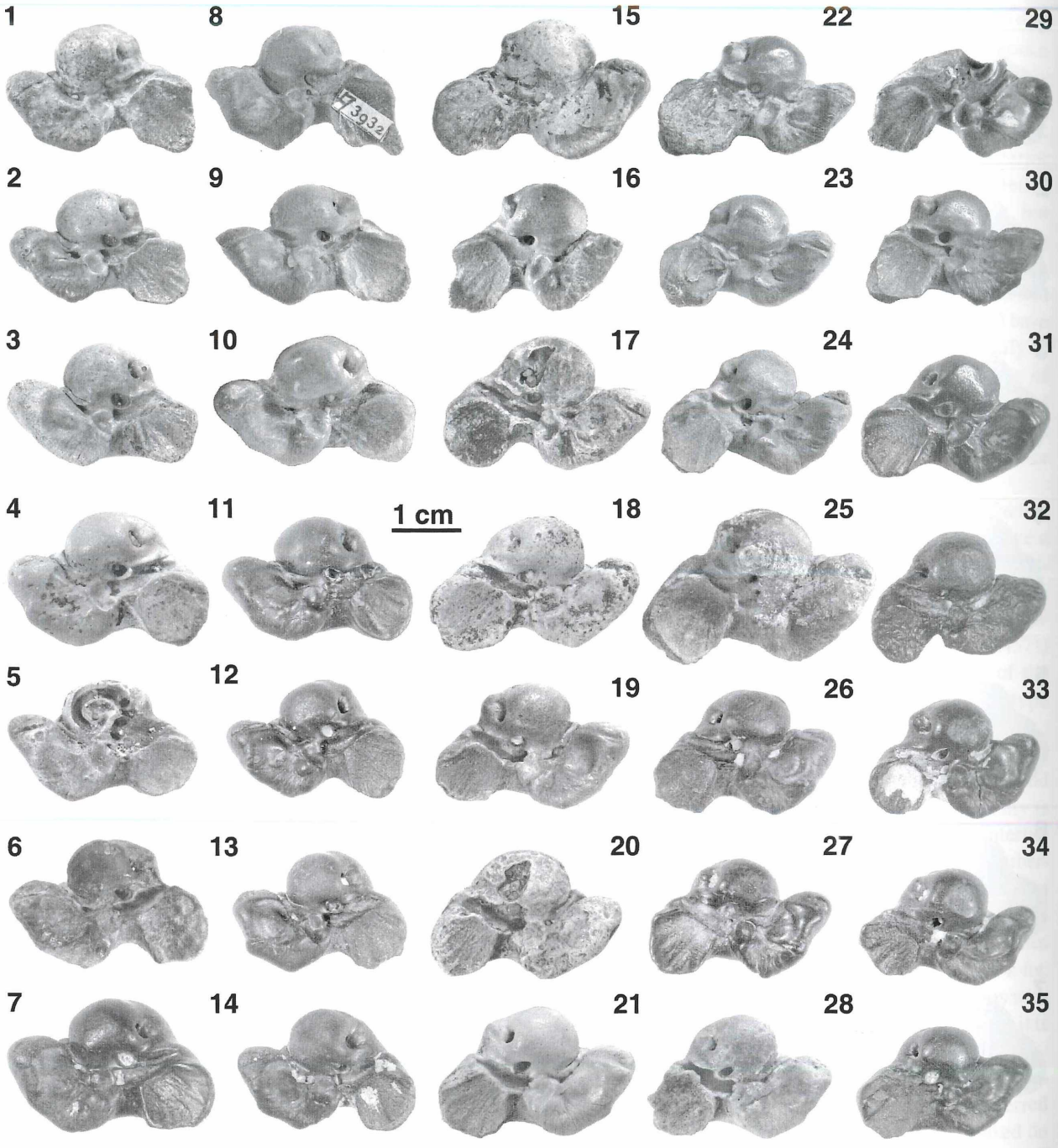

Figure 9: *Kentriodon fuchsii* (BRANDT, 1873) from Hernals, Nußdorf-Heiligenstadt, Loretto, Bruck Neudorf, Danitzpuszta, Comăneşti, and Cluj-Napoca. 1-14, right periotics, 15-35, left periotics in ventral view. 1–M27R, original to MÁFI V.23234; 2–M32R, original to MÁFI V.23098; 3–M34R, original to MÁFI V.23099; 4–M25R, original to MÁFI V.23235; 5–MÁFI V.23117; 6–UBFG.222; 7–W.24, original to MÁFI V.24579; 8–NHMW 1891/2; 9–PIUW 3128/8; 10–NHMW 1887/6/19; 11–W.16, original to MÁFI V.24571; 12–W.19, original to MÁFI V.24574; 13–W.22, original to MÁFI V.24577; 14–W.26, original to MÁFI V.24581; 15–M19R, original to MÁFI V.23112; 16–PIUW 3128/4; 17–LC140-4516, original to MÁFI V.23110; 18–M37R, original to MÁFI V.23114; 19–M35R, original to MÁFI V.23113; 20–M38R, original to MÁFI V.23115; 21–MÁFI V.23232; 22–MBT 15001/a; 23–PIUW 3128/5; 24–NHMW 4/905; 25–NHMW 2006z0194/0001; 26–W.12, original to MÁFI V.24567; 27–W.18, original to MÁFI V.24573; 28–MÁFI V.23233; 29–PIUW 3128/3; 30–PIUW 3128/6; 31–NHMW 1982/74/2; 32–W.10, original to MÁFI V.24565; 33–W.17, original to MÁFI V.24572; 34–W.23, original to MÁFI V.24578; 35–W.25, original to MÁFI V.24580.

preserved, but include ear bones (KAZÁR et al., 2004). On the basis of the comparable postcranial material, KAZÁR et al. (2004) regarded these skeletons as representatives of the species "*C.*" *fuchsii*. The periotics described above and elsewhere (KAZÁR, 2003; GRIGORESCU & KAZÁR, 2006) are of the same species as the two partial skeletons from Cluj-Napoca, and are thus regarded conspecific with "*Champsodelphis*" *fuchsii*.

Because postcranial elements are reported to bear little diagnostic information (e.g., FORDYCE & MUIZON, 2001),

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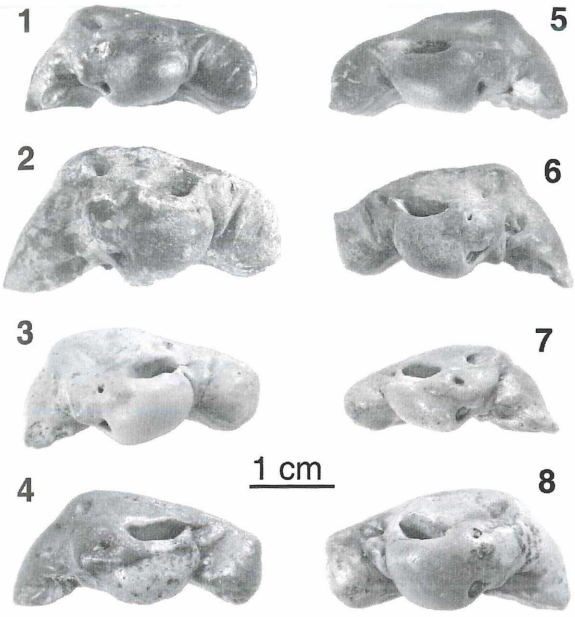

Figure 10: *Kentriodon fuchsii* (BRANDT, 1873) from Hernals, Nußdorf-Heiligenstadt (Austria), and Danitzpuszta (Hungary). 1-4, left periotics, 5-8, right periotics in medial view. 1–PIUW 3128/6; 2–NHMW (2006z0194/0001); 3–MÁFI V.23232; 4–M19R, original to MÁFI V.23112; 5–PIUW 3128/8; 6–NHMW 1891/2; 7–M32R, original to MÁFI V.23098; 8–M25R, original to MÁFI V.23235.

the above procedure is disputable. Alternatively, the partial skeletons and periotics from Cluj-Napoca could be regarded as a new species of odontocetes, and "*Champsodelphis*" *fuchsii* would be restricted to its type specimen. Nevertheless, this would result in an additional nominal species, which would probably be a junior synonym of "*C.*" *fuchsii*. New discoveries of more complete specimens are needed to justify or to reject the phylosophy followed here.

On the basis of the periotic morphology of "*C.*" *fuchsii* as defined above, KAZÁR (2003) and KAZÁR et al. (2004) indicated close relationship with the genus *Atocetus* MUIZON, 1988. However, the periotic of "*C.*" *fuchsii* is markedly different from *Atocetus*. Instead, it has close morphological agreement with that of *Kentriodon pernix* and *K. obscurus*. For this reason, I hereby transfer "*Champsodelphis*" *fuchsii* to the genus *Kentriodon*.

?*Kentriodon* sp.

2003 aff. *Delphinodon* sp. – KAZÁR:175.

Referred specimens: NHMW 1906/1, NHMW 1906/2 from Kaisersteinbruch.

Description and discussion (Table 1, Fig. 11; SCHULTZ, 1998: pl. 61, fig. 4): Both periotics are worn. The fundus of the internal auditory meatus is filled with sediment. The morphology of these periotics, as far as it can be seen, is very similar to those referred to *Kentriodon fuchsii*. The only signifact differences between *K. fuchsii* and the periotics of Kaisersteinbruch are that in the latters, the cleft between the pars cochlearis and the anterior process is wide, and the anterior process is more deflected medially. All other differences (the lack of a strong eminence between the perilymphatic foramen and the fenestra rotunda, the circular shape of the posterior bullar facet) are probably due to wear. It is also possible that the two periotics from Kaisersteinbruch represent the species "*Heterodelphis*" *leiodontus*. However, the periotic morphology of "*H.*" *leiodontus* is only known from two specimens and therefore the morphological variation in this species is inproperly known.

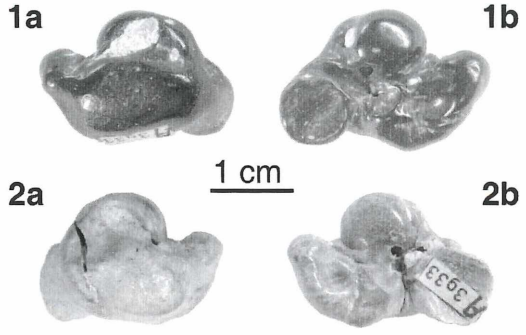

Figure 11: ?*Kentriodon* sp. from Kaisersteinbruch (Austria). 1–NHMW 1906/1, left periotic in (a) dorsal and (b) ventral views; 2–NHMW 1906/2, right periotic in (a) dorsal and (b) ventral views.

Subfamilia ?Pithanodelphininae BARNES, 1985

Genus *Sophianaecetus* KAZÁR, 2006

Sophianaecetus commenticius (KAZÁR, 2005)

2003 N. gen. n. spec. – KAZÁR:190-199, pls. 18-21.
2005 *Mediocris commenticius* n. sp. – KAZÁR:55.

Holotype: MTM V.93.2, nearly complete skeleton including skull, both tympanic bullae, and right periotic, and MÁFI V.21681, left periotic; all from the same individual from Kovácsszénája.

Referred specimens: MÁFI V.24557 from Bruck Neudorf; MÁFI V.23106, MÁFI V.23107, MÁFI V.23108, MÁFI V.23123 from Danitzpuszta.

Description (Table 2, Fig. 12): As described by KAZÁR (2005), the periotic of this species has a compact appearance with short anterior and posterior processes, and a broad cerebral surface. The dorsal surface is slightly convex in the holotype specimen, whereas almost flat in some of the referred specimens (MÁFI V.23107, V.24557), and it slopes laterally. The pars cochlearis is small mediolaterally, and it is broadly joined to the body of the periotic. The posterior bullar facet is pentagonal, shallowly concave, and typically has a few striae (but it is almost completely smooth in the left periotic of the holotype, MÁFI V.21681). The form of the anterior process in medial view is somewhat variable: the dorsal surface of the anterior process either has a convex contour (e.g. MÁFI

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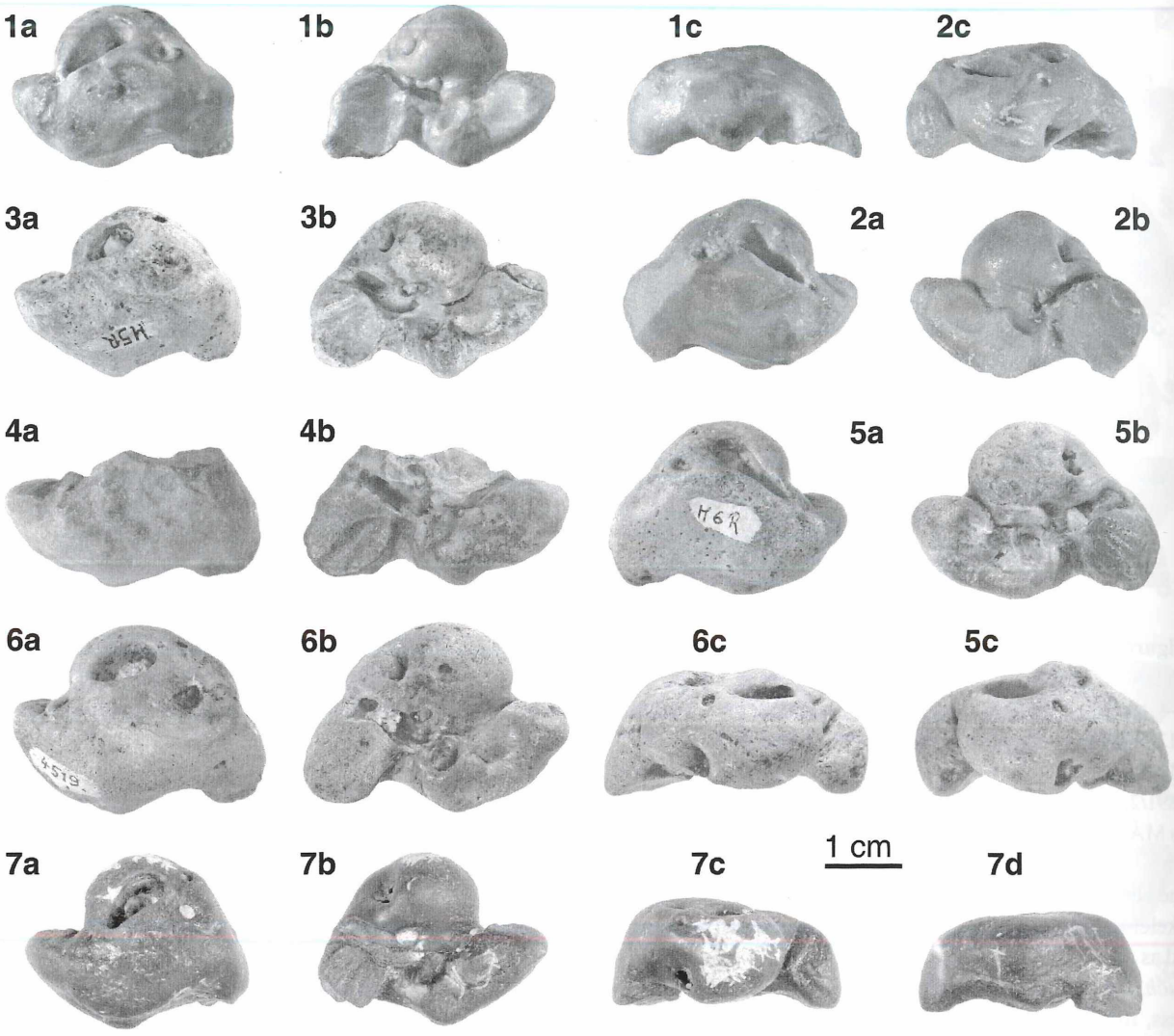

Figure 12: *Sophianaecetus commenticius* (KAZÁR, 2005) from Bruck Neudorf (Austria), Kovácsszénája and Danitzpuszta (Hungary). 1–MTM V.93.2, holotype, left periotic in (a) dorsal, (b) ventral, and (c) lateral views. 2–MÁFI V.21681, holotype, right periotic in (a) dorsal, (b) ventral, and (c) medial views. 3–M5R, original to MÁFI V.23106, left periotic in (a) dorsal and (b) ventral views. 4–MÁFI V.23123, left periotic in (a) dorsal and (b) ventral views. 5–M6R, original to MÁFI V.23107, right periotic in (a) dorsal, (b) ventral, and (c) medial views. 6–LC140-4519, original to MÁFI V.23108, left periotic in (a) dorsal, (b) ventral, and (c) medial views. 7–W.2 original to MÁFI V.24557, left periotic in (a) dorsal, (b) ventral, (c) medial, and (d) lateral views.

V.21681), or it is obtuse with a more or less sharp angle on the dorsal surface (?homologue of the anterodorsal angle; MÁFI V.23106). The fundus of the internal auditory meatus is deep, narrowly elliptical. Usually an anterior slit is present to include the internal facial foramen, but in V.23106 the internal auditory meatus is oval, without an anterior slit. The cleft between the anterior process and the pars cochlearis does not bear a crease.

Discussion: *Sophianaecetus commenticius*, originally described as *Mediocris commenticius* but the generic name was a homonym (UHEN, 2006; KAZÁR, 2006), was tentatively placed in the subfamily Pithanodelphininae by KAZÁR (2005) on the basis of characters of the skull. Among the species referred to this subfamily (BARNES, 1985; MUIZON, 1988b; FORDYCE & MUIZON, 2001; KAZÁR & GRIGORESCU, 2005), only species of the genus *Atocetus* are known from periotics. Both *A. iquensis* and *A. nasalis* (BARNES, 1985) have periotics with a less compact appearance, where the anterior process has a more conical tip in dorsal view. The lateral bending of the posterior process is stronger in *S. commenticius*, the pars cochlearis is relatively larger, and the ventrolateral tuberosity of the periotic is less pronounced than in *Atocetus*.

5. Discussion

5.1. Taxonomic diversity and relative abundance of the Central Paratethyan odontocete periotics

An evaluation of the complete odontocete taxonomic composition of the Middle Miocene Central Paratethys is beyond the scope of the present work. Periotics from

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Taxon	No.	Localities	Geologic age
Delphinoidea indet.	15	Nußdorf-Heiligenstadt, Bruck Neudorf, Danitzpuszta	Sarmatian
Kentriodontidae indet. 1	1 (2)	Tăşad	Sarmatian
Kentriodontidae indet. 2	5 (6)	Nußdorf-Heiligenstadt, Danitzpuszta	Sarmatian
?*Loxolithax* sp.	1	Nußdorf-Heiligenstadt	Sarmatian
Kentriodon fuchsii	50 (51)	Hernals, Nußdorf-Heiligenstadt, Loretto, Bruck Neudorf, Danitzpuszta, Comăneşti, Cluj-Napoca	Sarmatian
Sophianaecetus commenticius	6 (7)	Bruck Neudorf, Kovácsszénája, Danitzpuszta	Sarmatian
?*Kentriodon* sp.	2	Kaisersteinbruch	Badenian/Sarmatian
"Heterodelphis" leiodontus	2	St. Margarethen	Badenian
Odontoceti indet.	1	Rohrbach	Badenian

Table 3: Odontocete periotics in the Carpathian Basin, Middle Miocene – summary of results. No.: Number of individuals; in parentheses: total number of periotics (if different).

Middle Miocene localities in the Carpathian Basin reveal nine different odontocete taxa (Table 3). Four of these are known from other skeletal elements (Kentriodontidae indet. 1, *„Heterodelphis" leiodontus*, *Kentriodon fuchsii*, *Sophianaecetus commenticius*), which have been described elsewhere (BRANDT, 1873; PAPP, 1905; KAZÁR & VENCZEL, 2003; KAZÁR, 2005). The other five (Odontoceti indet., Delphinoidea indet., Kentriodontidae indet. 2, ?*Loxolithax* sp., ?*Kentriodon* sp.) are only known from the herein described periotics.

As can be deduced from Table 3, *K. fuchsii* has the greatest relative abundance among the taxa, in terms of number of specimens. On the other extreme, the Odontoceti indet., the Kentriodontidae indet.1, and ?*Loxolithax* sp. are only represented by a single individual each. If the number of localities is considered, periotics of *K. fuchsii* are known from seven different fossil sites, the Delphinoidea indet. and *S. commenticius* have occurrences at three localities. The ?*Loxolithax* sp. is known from Nußdorf-Heiligenstadt only, the Kentriodontidae indet. 1 from Tăşad. This can be due to the overall small abundance of these species, as the latter two forms are known from 1-2 individuals only. In general, the relative abundance of each species seems to correlate with the number of localities they were found (and vica versa), and are perhaps not informative of the palaeobiogeographic distribution of the species within the Central Paratethys. *Sophianaecetus commenticius* was for many years only known from around Pécs in south Hungary: from Kovácsszénája and Danitzpuszta (KAZÁR, 2003, where all skeletal elements were investigated), and KAZÁR (2005) suggested that the species did not live in the embayment of the Central Paratethys Sea known today as the Vienna Basin. However, a single periotic from Bruck Neudorf was found recently (MÁFI V.24557), providing first evidence for the occurrence of this species in the Vienna Basin as well.

If we compare the taxonomic composition of the Sarmatian odontocete periotic localities of the Vienna Basin (Hernals, Nußdorf-Heiligenstadt, Loretto, Bruck Neudorf) with that of Danitzpuszta, it is clear that all but one species that occur at the Vienna Basin have records at Danitzpuszta as well. There is one form (?*Loxolithax* sp.) that is known from Nußdorf-Heiligenstadt but not from Danitzpuszta. It can be therefore concluded that, based on odontocete periotics, the entire Carpathian Basin including the Vienna Basin formed a single zoogeographic unit, and the lack of species at some localities is probably a bias caused by the local taphonomical and sedimentological characteristics, or by the small relative abundance of some of the species. The Badenian finds to date are unfortunately so scarce that hardly any conclusion is possible on the abundance and taxonomic diversity of the odontocete fauna at that time.

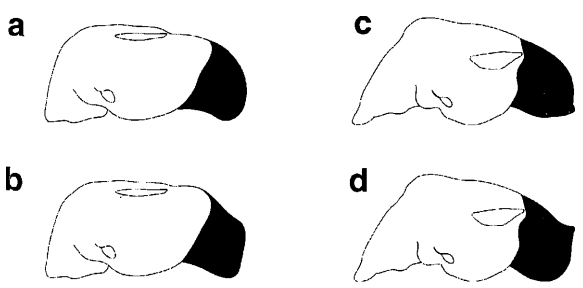

Figure 13: Morphology of the anterior process in *S. commenticius* (a-b) and *K. fuchsii* (c-d). Medial views; without scale; based on several specimens.

5.2. Intraspecific variation of morphological characters of the periotics

Four of the nine odontocete taxa identified in the Carpathian Basin are represented by more than 1-2 periotics (*Kentriodon fuchsii*: 51, Delphinoidea indet.: 15, *Sophianaecetus commenticius*: 7, Kentriodontidae indet. 2: 6). Among the periotics referred to these species, some of the characters are variable.

1. Morphology of the cerebral surface: In *Kentriodon fuchsii* and in the Delphinoidea indet., the cerebral surface of the periotic is either rounded, convex, or there is a flat, plateau-like area. The variability of this character was also observed by BARNES & MITCHELL (1984) in *K. obscurus*. The flat cerebral surface is regarded as the derived condition within the Delphinoidea (WHITMORE, 1987). The degree of convexity of the cerebral surface is

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slightly variable in *S. commenticius*, but in this species the flat dorsal area never forms a distinct plateau.

The cerebral surface of the periotics of Kentriodontidae indet. 2 and that of the single specimen referred to as *?Loxolithax* sp. is dominated by the crista dorsalis (except MÁFI V.23101, where the crista dorsalis is probably worn away, as well as MÁFI V.23125 and MÁFI V.24236). It is likely that the presence of the crista dorsalis is not taxonomically significant, but more material is needed to clarify this assumption.

In the periotics of *Kentriodon fuchsii*, sometimes a faint longitudinal keel is present lateral to the endolymphatic foramen, which runs from the level of the posterior junction between the pars cochlearis and the posterior process towards the anterior junction of the same structures. The longitudinal keel is also present in the holotype periotic of "*Heterodelphis*" *leiodontus*, and in some of the periotics of *K. obscurus* figured by BARNES & MITCHELL (1984). The majority of the periotics of *K. fuchsii*, however, lacks a longitudinal keel, and the dorsal area lateral to the pars cochlearis is smooth.

2. Morphology of the anterior process: The mediolateral compression of the anterior process is variously expressed in the periotics, and a faint anterior keel is sometimes present on the anterodorsal surface of the anterior process in *Kentriodon fuchsii* and in the Kentriodontidae indet. 2, but not in *Sophianaecetus commenticius*. In medial view, the shape of the anterior process is strongly variable in *K. fuchsii* and, to a lesser degree, in *S. commenticius*, but it has a different pattern in both species. In *S. commenticius* the apex is always rounded and never bears a rugosity. The dorsal contour of the anterior process is variable: it is either smoothly convex (Fig. 13: a), or there is a sharp angle anterodorsally (Fig. 13: b). In *K. fuchsii* the apex is situated ventrally, it is either rounded (Fig. 13: d), or it is peaked with a small anterior tuberosity (Fig. 13: c). The dorsal surface of the anterior process varies between two extremes: (a) anterodorsally it bears a tuberosity, which projects anteriorly farther than the ventral apex (Fig. 13: d); (b) it is smooth and rounded, and the ventral apex projects farther anteriorly (Fig. 13: c). Thus, in some but not all specimens, the anterior process is rectangular in medial view, similarly to the holotype of *K. pernix* and *Atocetus iquensis*.

3. Morphology of the posterior process: In the Carpathian Basin periotics, the relative length of the bullar facet is variable: some of the specimens of the Delphinoidea indet., *Kentriodon fuchsii* and *Sophianaecetus commenticius* have a posterolateral elongation of the bullar facet (e.g. NHMW 1891/1; NHMW 1891/2, MÁFI 21681), whereas other periotics of the same species do not have it (NHMW 1906/30; NHMW 4/905). It is known that the absolute length of the posterior process is a figure of the ontogenetic age, and the apex of the posterior process attains a postero-laterally pointing, spongy process in older animals (KASUYA, 1973; BARNES & MITCHELL, 1984). The basic shape of the bullar facet, on the other hand, seems to be largely constant within a species. Among the delphinoid periotics of the Carpathian Basin, two main forms of the posterior bullar facet occur: (a) the Delphinoidea indet., the Kentriodontidae indet. 1, *K. fuchsii*, the *?Kentriodon* sp. periotics, and *S. commenticius* have posterior bullar facets of pentagonal shape. In presumably older specimens, where the posterior process is posteriorly elongated, the form of the bullar facet appears diamond-shaped (rhomboidal). (b) The Kentriodontidae indet. 2 periotics have a rounded, narrowly elliptical posterior bullar facet. The single periotic of *?Loxolithax* sp. and probably "*Heterodelphis*" *leiodontus* have an intermediate morphology: the posterior bullar facet is pentagonal, but narrower than in the first group.

The exact ornamentation of the posterior bullar facet is probably individually variable, because it is almost smooth in the left periotic of the holotype specimen of *Sophianacetus commenticius*, whereas shallowly striated in the right periotic of the same individual. The degree of rugosity of the posterior bullar facet is also variable in *K. obscurus* (see BARNES & MITCHELL, 1984). All species of the studied material have either smooth or finely striated posterior bullar facets, none have deeply grooved ones. The smooth surface of the posterior bullar facet is regarded as a derived condition (LUO & MARSH, 1996).

4. Other characters of the periotic: The anterior margin of the fundus of the internal auditory meatus continues in a narrow groove, which includes the internal opening of the facial nerve canal in all Carpathian Basin species. Similarly to *Kentriodon obscurus* (see BARNES & MITCHELL, 1984), the length of this groove is variable. In some specimens of the Delphinoidea indet., the Kentriodontidae indet. 2, and *S. commenticius*, the groove is obscured by bone tissue so that an additional opening (?of the facial nerve canal) emerges anterolateral to the internal auditory meatus.

As in *K. obscurus* (see BARNES & MITCHELL, 1984), the development of a tuberosity on the posterior surface of the pars cochlearis between the perilymphatic foramen and the fenestra rotunda is variable in the periotics of the Kentriodontidae indet. 2 and *K. fuchsii* (basically absent in the Delphinoidea indet. and *S. commenticius*).

The characters that are variable in the periotics of the Delphinoidea indet., the Kentriodontidae indet. 2, *Kentriodon fuchsii*, and *Sophianaecetus commenticius* of the Central Paratethys are variable in *Kentriodon obscurus* as well (see BARNES & MITCHELL, 1984:16), and it is possible that the same characters are variable in the Miocene Kentriodontidae or Delphinoidea in general.

6. Conclusions

1. A total of 87 odontocete periotics were investigated from twelve Middle Miocene (Badenian and Sarmatian) Carpathian Basin fossil sites. Nine taxa were identified; five of these (Odontoceti indet., Delphinoidea indet., Kentriodontidae indet. 2, *?Loxolithax* sp., *?Kentriodon* sp.) are only known from the herein described ear bones.

2. A morphologically primitive odontocete periotic from the Badenian (Langhian – early Serravallian) of Rohrbach

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shares characters with the Dalpiazinidae, Squalodontidae, and Eurhinodelphinidae, but can not be referred to any of these families.

3. The description of the periotic of "*Heterodelphis*" *leiodontus* PAPP, 1905 is presented here for the first time. "*Heterodelphis*" *leiodontus* is a kentriodontid species, and it does not belong in the genus *Heterodelphis* BRANDT, 1873. The latter genus is an Odontoceti incertae sedis restricted to its type species, *H. klinderi* BRANDT, 1873.

4. Based on the morphology of 51 periotics, "*Champsodelphis*" *fuchsii* BRANDT, 1873 belongs in the genus *Kentriodon*.

5. A new character of the periotic, the crista dorsalis is defined to describe the cerebral surface of the periotics of the Kentriodontidae indet. 2 and ?*Loxolithax* sp. The crista dorsalis is probably homologueous with the faint longitudinal keel sometimes present on periotics of *Kentriodon* spp. Its significance and function is unknown.

6. *Kentriodon fuchsii* is the most abundant species among the Carpathian Basin odontocetes, as represented by the greatest number of individuals (51) and localities (7). The Delphinoidea indet. is the second-most abundant species with 15 periotics from three localities. All other species are represented by 1 to 7 specimens.

7. The intraspecific variation of the Central Paratethyan delphinoid periotics shows that the morphology of the cerebral surface, the dorsal surface of the anterior process, and a few other characters may vary individually within a species, and do not bear taxonomic significance. These results are in accordance with the observations of BARNES & MITCHELL (1984) on *Kentriodon obscurus*.

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