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Revision of the genus *Pachyacanthus* Brandt, 1871 (Mammalia: Cetacea: Odontoceti)

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(With 1 figure, 3 plates and 2 tables)

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Abstract

The Middle Miocene genus *Pachyacanthus* Brandt, 1871 is represented by three incomplete skeletons from Nussdorf-Heiligenstadt, Vienna, and several isolated skeletal elements from other localities in Vienna and the Vienna Basin (Austria). A few disarticulated vertebrae and limb elements from three Miocene localities in Hungary are referred to *Pachyacanthus* here for the first time.

Of the six nominal species of *Pachyacanthus*, only the type species, *P. suessii* Brandt, 1871 is now recognized. The scapula of *P. suessii* lacks a coracoid process and a supraspinous fossa, and the acromion process is located on the anterior margin of the scapula. The scapular morphology of *P. suessii* points to phylogenetic relationship with members of the superfamily Platanistoidea. The presumably elongated and narrow rostrum of the lectotype specimen indicates that *P. suessii* is probably a member of the family Platanistidae Gray, 1846, but in the lack of more cranial evidence this allocation remains hypothetical.

All occurrences of *Pachyacanthus suessii* are of Sarmatian age (late Serravallian, Middle Miocene). There are no records of *P. suessii* from outside the area of the ancient Central and Eastern Paratethys.

Keywords: *Pachyacanthus*, Odontoceti, Cetacea, Paratethys, taxonomy.

Zusammenfassung

Der Genus *Pachyacanthus* Brandt, 1871 aus dem Sarmatium (Mittel-Miozän) ist von drei unvollständigen Skeletten aus Nussdorf-Heiligenstadt, Wien, sowie von zahlreichen nicht-artikulierten Knochen aus verschiedenen Fundstellen in Wien und im Wiener Becken bekannt. Einige Wirbel und Knochen des Vordergliedes aus drei Fundstellen aus dem Miozän von Ungarn werden hier erstmals der Gattung *Pachyacanthus* zugeordnet.

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Von den sechs beschriebenen Arten der Gattung *Pachyacanthus* wird hier nur die Typusart, *P. suessii* Brandt, 1871 anerkannt. Das Schulterblatt von *P. suessii* hat kein Processus coracoideus und keine Fossa supraspinata. Das Acromion ist auf die Vorderkante der Scapula verlagert. Die Morphologie der Scapula deutet darauf hin, dass *P. suessii* phylogenetische Verwandtschaft mit den Vertretern der Superfamilia Platanistoidea hat. Die erhaltengebliebenen Reste des Maxilla und Praemaxilla weisen auf ein langes, dünnes Rostrum hin, was eine Mitgliedschaft in der Familie Platanistidae Gray, 1846 wahrscheinlich macht, allerdings reicht das Material nicht aus, um diese Hypothese zu prüfen.

Das Vorkommen von *Pachyacanthus suessii* ist auf das Sarmat (spätes Mittel-Miozän) beschränkt. Von außerhalb des Gebietes des ehemaligen Zentralen und Östlichen Paratethys sind keine Funde bekannt.

Schlüsselwörter: *Pachyacanthus*, Odontoceti, Cetacea, Paratethys, Taxonomie.

Introduction

During the main construction period of the city of Vienna (Austria) in the 19th century, three postcranial skeletons and several isolated skeletal elements of an enigmatic marine mammal were excavated from Sarmatian (Middle Miocene) Tegel deposits of Nussdorf-Heiligenstadt near Vienna (today in the 17th district of the city of Vienna). The most peculiar characteristic of the fossil was the highly pachyosteotic thickening of the vertebral spines, for which Brandt (1871a, 1871b, 1872a, 1872b, 1873) described the remains under the name *Pachyacanthus*. Similarly to sirenians (Domning & Buffrénil 1991), the increase in cross-sectional area ("pachyostosis") of the vertebral spines seemingly goes together with the replacement of cancellous with compact bone ("osteosclerosis"). Nevertheless, the histological investigation of the bone tissue of *Pachyacanthus* was beyond the scope of the present study. The functional significance of pachyostosis and pachyosteosclerosis in various fossil and recent aquatic tetrapods has been discussed by Kaiser (1960), Domning & Buffrénil (1991), and Taylor (2000).

Because, except for a few fragments of a rostrum and two fragmentary tympanic bullae, there were no skulls associated with the skeletons, the new genus experienced an unusually broad range of taxonomical allocations. Brandt (1871a, 1871b, 1872a, 1872b, 1873) placed *Pachyacanthus* in the Mysticeti. Van Beneden (1875) suggested that the limb elements and the sternum were of an odontocete cetacean, and the ribs and vertebrae represented a sirenian. Capellini (1877) concluded that the atlas of *Pachyacanthus* cannot possibly be referred to a mysticete or a sirenian but most closely resembles that of a river dolphin (Platanistidae sensu lato). Gervais (in: Van Beneden & Gervais 1880) regarded *Pachyacanthus* as a pathologically deformed platanistid odontocete, and pointed to the osteological resemblance of *Pachyacanthus* to *Inia* and to "*Champsodelphis*" *letochae* Brandt, 1873, another poorly-known cetacean from the Sarmatian of Vienna.

Following Van Beneden (1875), Abel (1899: p. 853, 870) was convinced that the three skeletons of *Pachyacanthus* were constructed from different specimens of a sirenian and

of a small dolphin representing the genus *Champsodelphis* Gervais, 1848. However, Abel (1912, 1919) later regarded *Pachyacanthus* as an extremely specialized, pathological representative of the mysticete *Cetotherium* Brandt, 1843. Dombrovskij (1927) likewise placed *Pachyacanthus* among the Mysticeti. In their fossil mammal catalog Pia & Sickenberg (1934) listed the remains of *Pachyacanthus* as of "Balaenopteridae (Mysticeti)".

Based on the study of the morphology of vascular depressions in the posterior lumbar and of the caudal vertebrae, Slijper (1936: 366-370) concluded that *Pachyacanthus* is a representative of the Platanistidae, and shows greatest resemblance to modern *Platanista gangetica* (Roxburgh, 1801). Slijper noted (1936) that the bones of the forelimb of *Pachyacanthus* can be morphologically related to the species of the recent Platanistidae (sensu lato). This was also the opinion of Pia (1937: 413-416), who payed much attention to the morphology of the ulna and the atlas. In the recent literature *Pachyacanthus* is listed as an Odontoceti incertae sedis (McKenna & Bell 1997). Fordyce & Muizon (2001) placed *Pachyacanthus* in the Delphinida.

Up to the present day no further cranial material has been found of *Pachyacanthus*. In the lack of knowledge on the morphology of the skull, the definition of this cetacean species remains incomplete. Yet, two factors shed more light onto the phylogenetic position of *Pachyacanthus*. Firstly, the modern definition of the Platanistoidea (Muizon 1987, 1990, 1994; Fordyce 1994) includes characters of the scapula, which is well-preserved in *Pachyacanthus*. Secondly, in the original description given by Brandt (1873), the fragmentary tympanic bones preserved with the lectotype of *P. suessii* were not mentioned. Tympanic bullae are considered to bear significant taxonomic information (Kasuya 1973), and the morphology of the tympanic bulla of *Pachyacanthus* is considered here for the first time.

The aim of the present paper is (1) a taxonomic revision of the genus *Pachyacanthus*, with an attempt (2) to list all specimens referable to the genus from institutional collections; (3) the redescription of the skeletal elements that are relevant for the phylogenetic position of *Pachyacanthus*; (4) to document the recently found material referable to *Pachyacanthus* from three Miocene localities in Hungary, where the presence of *Pachyacanthus* is demonstrated here for the first time; and (5) a summary of data on the palaeobiogeography of *Pachyacanthus*.

Study Area

The fossil remains discussed in this paper come from seven Middle Miocene localities in Austria (Vienna Basin and Leitha Mountains) and Hungary (Fig. 1). Two isolated vertebrae and three other skeletal fragments are of unknown Vienna Basin localities of Sarmatian age. In the following, a short resume is given on the geological background of the localities, listed in order of geographical position from West towards the East. The stratigraphic correlation follows Rögl (1998) and Harzhauser & Piller (2004, 2005).

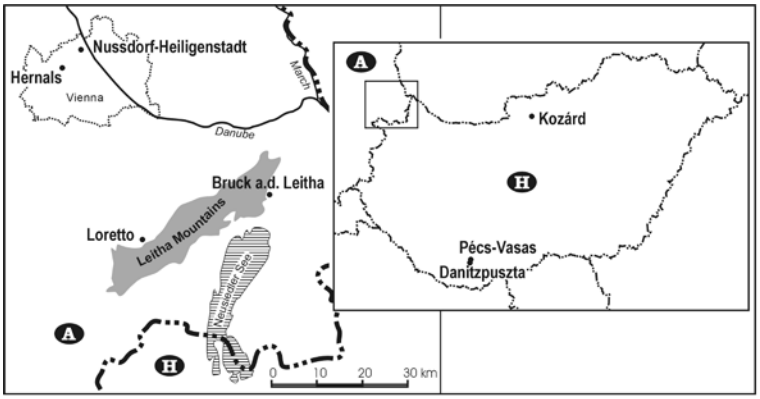

Fig. 1. Geographical setting of the localities with record of *Pachyacanthus suessii* Brandt, 1871 in the Central Paratethys. The main map shows the new localities in Hungary. The small box in the main map indicates the area enlarged (left; Austrian localities).

***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 1934; Schmid 1974; Schmid 1989). Because the quarries of Nussdorf and Heiligenstadt were only a few kilometers apart, the exact finding place 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 blue marls of the Vienna Basin. Stratigraphically, Hernals and Nussdorf-Heiligenstadt belong to the *Mohrensternia* Zone (Papp 1956; Schmid 1974). A single caudal vertebra (NHMW 1823/0027/0105) is labelled as from Vienna, without further information on the exact locality. It most probably came from one of the quarries producing the "Hernalser Tegel".

***Loretto* (*Burgenland*, *Austria*)**: The quarry of Loretto was opened in 1872. It produced pale yellow limestone of Sarmatian age (late Serravallian) (Telegdi-Róth 1903; Schafarzik 1904), and belongs to the *Mohrensternia* Zone (M. Harzhauser pers. comm. 2004).

***Bruck an der Leitha* (*Niederösterreich*, *Austria*)**: The former quarries of Bruck an der Leitha that yielded the material in the NHMW collection have long been closed down. Vertebrate material, among others cetaceans, has recently been found in sediments at a small pond NW of Parndorf (Kazár 2006; Nagel et al. 2007). The deposits are correlated with the upper *Ervilia* Zone where the marine vertebrates were reworked from the Lower Sarmatian (Harzhauser & Piller 2004; Nagel et al. 2007).

***Danitzpuszta* (*Baranya County*, *Hungary*)**: The Pannonian (Late Miocene) sands of Danitzpuszta contain the bones of fluvial-terrestrial Late Miocene vertebrates. The marine fossils are reworked from the Sarmatian (Kazár et al. 2001; Koretsky 2001). The locality is a still active sand pit, where fossils continue to be found.

***Pécs-Vasas* (*Baranya County*, *Hungary*)**: Fossils were found in the early 20th century, probably south of the road no. 6, where a former sand pit exposed Pannonian (Late Miocene) sands. The marine vertebrate fossils were reworked, probably from the Sarmatian (L. KORDOS pers. comm. 2001).

***Kozárd* (*Nógrád County*, *Hungary*)**: The geological section of the Kozárd locality is given in BODA (1974). The exact locality of the single vertebra discussed in the present paper is unknown. According to the inventory documentation it was collected from Sarmatian deposits.

Material and Methods

Institutional abbreviations – KTGy, Komlói Természettudományi Gyűjtemény (Natural History Collection of Komló); MÁFI, Magyar Állami Földtani Intézet (Geological Institute of Hungary), Budapest; MTM, Magyar Természettudományi Múzeum (Natural History Museum of Hungary), Budapest; NHMW, Naturhistorisches Museum Wien (Vienna); PIUW, Paläontologisches Institut Universität Wien (Vienna); USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.

The skeletal elements in private ownership are labeled as follows: Ch-, ex. coll. C. Chefdeville; Dp., ex. coll. F. Cserpák; LC140-, ex. coll. Z. Evanics; OZ-, ex. coll. Z. Orbán; SL-, ex. coll. L. Sövér.

The following specimens are inventoried casts of the private originals in parentheses:

MÁFI V.24200 (Ch-86); MÁFI V.24190 (Ch-121); MÁFI V.24195 (Ch-199); MÁFI V.06.284.1 (Ch-198); MÁFI V.06.280.1 (LC140-4448); MÁFI V.06.279.1 (LC140-4449); MÁFI V.06.278.1 (LC140-4450); MÁFI V.06.275.1 (LC140-4451); MÁFI V.06.276.1 (LC140-4452); MÁFI V.06.277.1 (LC140-4453); MÁFI V.06.281.1 (LC140-4454); MÁFI V.06.282.1 (LC140-5027); MÁFI V.06.274.1 (LC140-5038); MÁFI V.24189 (OZ-136); MÁFI V.06.273.1 (OZ-154); MÁFI V.24174 (SL-8); MÁFI V.06.283.1 (original in private collection without number); MÁFI V.24213 (Dp.4779); MÁFI V.24214 (Dp.4780); MÁFI V.24215 (Dp.1816); MÁFI V.09.326.1 (Dp.6849); MÁFI V.09.325.1 (Dp.4536); MÁFI V.09.329.1 (Dp.5667); MÁFI V.09.327.1 (Dp.2700); MÁFI V.09.324.1 (Dp.5330); MÁFI V.09.328.1 (Dp.5968). Measurements and photographs were taken on the original specimens.

Direct comparisons were made with *Prepomatodelphis korneuburgensis* BARNES, 2002 (NHMW 2002z0001/0000, holotype), and postcranial skeletons of the recent *Platanista gangetica*. All measurements were made with the same measuring caliper. Tympanic bullar terminology was derived from KASUYA (1973) and FORDYCE (1994).

Systematic Palaeontology

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Platanistoidea Simpson, 1945

Family ?Platanistidae Gray, 1846

Pachyacanthus Brandt, 1871

Diagnosis: Platanistoid with pachyostosis in the spinous processes of the postcervical vertebrae.

The present diagnosis follows Brandt (1871a: 564, 1871b: 216) who defined the genus by the "odd thickening of the upper neural spines of its thoracic, lumbar, and caudal vertebrae".

Type and only included species: *Pachyacanthus suessii* Brandt, 1871a, p. 564.

Discussion: There are six nominal species of *Pachyacanthus*: *Pachyacanthus suessii* Brandt, 1871 (lectotype, NHMW 1860/0016/0081 to …/0083, …/0085, …/0086, …/0088 to …/0102); *P. letochae* Brandt, 1873 (holotype, PIUW 1556); *P. ambiguus* (Brandt, 1872) (holotype, NHMW 1859/0005/0106); *P. trachyspondylus* Brandt, 1873 (holotype probably lost); *P. andrussovi* Dombrovskij, 1927 (p. 39, figs 6-9); and *P. bajarunasi* Dombrovskij, 1927 (p. 39, figs 10-11).

Pachyacanthus suessii is the first named and type species of the genus (Brandt 1871a, 1871b, 1872b). Brandt (1873: 188, pl. 14: figs 17-21, pl. 15, pl. 16: figs 4-8, pl. 17: fig. 12) questionably defined *P. letochae* Brandt, 1873 on the basis of a larger skeleton with more pronounced pachyostosis of the vertebral processes (PIUW 1556). Because the holotype of this species is simultaneously part of the type series of *Pachyacanthus suessii*, *P. letochae* is a junior synonym of *P. suessii*.

Pachyacanthus ambiguus (Brandt, 1872) was based on a single caudal vertebra from Nussdorf-Heiligenstadt and originally placed in the mysticete genus *Cetotherium* by Brandt (1872a: 4, 1873: 138; holotype: NHMW 1859/0005/0106). Pia (1937: 399-400) referred two isolated caudal vertebrae from the Leitha Mountains and Loretto to the same species and placed *C. ambiguum* in the genus *Pachyacanthus*.

The first mention of the species *P. trachyspondylus* Brandt, 1873 is a nomen nudum (Brandt 1871a, 1871b), because the diagnosis of the species is given two years later by

Brandt (1873: 187-188). The species was based on cervical vertebrae, which I did not find in the collection of the NHMW. Van Beneden (1875: 6) and Pia (1937: 418) regarded *P. trachyspondylus* as a junior synonym of *P. suessii*.

The type material of *P. andrussovi* Dombrovskij, 1927 consists of two vertebrae, a vertebral process, fragments of ribs, and a single metacarpal (Dombrovskij 1927, p. 39, figs 6-9). *Pachyacanthus bajarunasi* Dombrovskij, 1927 was defined on the basis a vertebral fragment and a rib fragment (Dombrovskij 1927, p. 39, figs 10-11).

The known fossil material referrable to *Pachyacanthus* is insufficient to decide whether the difference in size and degree of pachyostosis of the vertebral processes in the preserved three partial skeletons are indicative of two different species, or they are within the range of the intraspecific variation in *P. suessii* (see also Pia 1937; Brandt 1874). Pilleri & Gihr (1970) reported a body length difference almost as large as 100% between individuals of the modern *Platanista gangetica* gathered from two different rivers, nevertheless the smaller specimens from the Brahmaputra River were probably subadults. Many authors recognize the populations of the Indus and Ganges rivers as two species (for a review, see Rice 1998). Geisler & Sanders (2003) recognizes the much larger size of the females compared to the males as being one character supporting a clade that includes *Platanista* Wagler, 1830 and *Zarhachis* Cope, 1868. This implies that the fossil *Pachyacanthus* might have been as well sexually dimorphic.

There is no significant morphological difference between the individuals of *P. suessi* and those of the nominal species *P. letochae* Brandt, 1873. The greater pachyostosis of the vertebral processes of the skeletons traditionally referred to *P. letochae* is probably related to the greater body size of these individuals. I hereby refer all specimens of *Pachyacanthus letochae* to the species *P. suessii*. All other named species of *Pachyacanthus* are likewise junior synonyms of *P. suessii*.

Pachyacanthus suessii Brandt, 1871

*	1871a	*Pachyacanthus Suessii* – Brandt: p. 564.
	1871b	*Pachyacanthus Suessii* – Brandt: p. 216.
	1872a	*Cetotherium ambiguum* – Brandt: p. 4.
	1873	*Pachyacanthus Suessii* J. F. Brdt. – Brandt: pp. 169-186, taf. XIV-XVII.
	1873	?*Cetotherium ambiguum* Brdt. – Brandt: p. 138, taf. XIV: figs 1-5.
	1873	?*Pachyacanthus trachyspondylus* – Brandt: pp. 187-188, taf. XVIII: figs 1-4A-F.
	1873	*Pachyacanthus Letochae* – Brandt: p. 188, taf. XIV: figs 17-21; taf. XV; taf. XVI: figs 4-8; taf. XVII: fig. 12A.
	1874	*Pachyacanthus Letochae* – Brandt: p. 11.
	1927	*Pachyacanthus Andrussovi* n. sp. – Dombrovskij: p. 39, tab. I, tab. II: figs 6-9.
	1927	*Pachyacanthus Bajarunasi* n. sp. – Dombrovskij: p. 39, tab. II: figs 10-11.
	1937	*Pachyacanthus*(?) *ambiguus* – Pia: p. 401.
	1937	*Pachyacanthus trachyspondylus* – Pia: p. 418.

1937 *Pachyacanthus suessi* – Pia: pp. 418-420.
1937 *Pachyacanthus letochae* – Pia: pp. 418-420.

Emended diagnosis of species: As of the genus *Pachyacanthus*.

Lectotype: designated here (following the suggestion of Pia 1937, p. 420): NHMW 1860/0016/0081 to …/0083, …/0085, …/0086, …/0088 to …/0102, (so-called "skeleton b" or "Individuum b" (Brandt 1873; Pia & Sickenberg 1934: SK [= Säugetierkatalog No.] 193; Pia 1937)), partial skeleton including fragments of the rostral maxilla and premaxilla, incomplete left and right tympanic bullae, manubrium of sternum, incomplete atlas, neural arch of axis, fragments of the other five cervical vertebrae, 34 postcervical vertebrae, several ribs and rib fragments corresponding to probably 11 pairs of ribs, incomplete left and right scapular blades, left and right humeri, left and right radii and ulnae, and four metacarpals from Nussdorf-Heiligenstadt (Vienna), Sarmatian deposits (late Serravallian, Middle Miocene).

Remarks: Brandt (1871a, 1871b) did not designate a holotype specimen. The description was based on three skeletons (Brandt 1873: 169-186, Pls 14-17, Pl 18: Figs 1-4), which are therefore syntypes. These are the so called "skeleton a" (today: NHMW 2008z0173/0002), the so called "skeleton b" (NHMW 1860/0016/0081 to .../0083, .../0085, .../0086, .../0088 to .../0102), and the skeleton from the "Letocha collection" (PIUW 1556). When Brandt (1873: 188) questionably named a new species, *Pachyacanthus letochae*, he based its description on the PIUW 1556 skeleton. The NHMW 1860/0016/0081 to .../0083, .../0085, .../0086, .../0088 to .../0102 specimen is designated here as being the lectotype of *P. suessii*, because this is the best-preserved partial skeleton including cranial fragments and tympanic bullae. This designation is in accordance with Pia (1937: 419-420) who noted that the NHMW 2008z0173/0002 skeleton is more similar in size to the PIUW 1556 specimen.

The catalogue number above is given as of Pia & Sickenberg (1934). In the old catalogue the lectotype includes the numbers NHMW 1860/0016/0080, …/0084, …/0087, …/0103 as well. These numbers, however, refer to skeletal elements that obviously do not belong to the lectotype skeleton, such as fragments of mandibles (…/0080), clavicula (…/0084), phalanges (…/0087), and diverse bones from a different species of a cetacean (…/0103).

The sternum is not listed in the old catalogue as being part of the lectotype skeleton. It has a light brownish color, versus the dark grey of the rest of the lectotype skeleton. Its morphology is markedly different from the sterni preserved with the referred skeletons, suggesting that it was subsequently placed in the same box and does not belong to the lectotype or other representative of *Pachyacanthus* (see also Brandt 1873: 179-180).

Referred specimens: Below are listed all specimens of *Pachyacanthus suessii* in institutional collections that I have personally seen. Not listed are a few others, e.g. NHMW 1853/0002/0010, which were mentioned by Pia & Sickenberg (1934) but which I have not been able to relocate in the collections of the NHMW and PIUW.

Specimens from localities in the Vienna Basin:

Bruck a.d. Leitha: NHMW 1841/0013/0030 (Pia & Sickenberg 1934: SK 232), caudal vertebra

Hernals: NHMW 1886/0017/0046 (Pia & Sickenberg 1934: SK 261), right humerus

Nussdorf-Heiligenstadt: NHMW 2008z0173/0002 (so called "skeleton a" or "Individuum a"; Brandt 1873; Pia & Sickenberg 1934: SK 203; Pia 1937: 419-420, Figs 51-52), partial skeleton including two fragments of sternum, both humeri, left ulna, left and right scapulae, atlas, axis, 28 postaxial vertebrae, approx. 25 ribs or rib fragments corresponding to about 11 pairs of ribs; PIUW 1556, partial skeleton (individual from the collection of Letocha; Brandt 1873; Pia 1937) including atlas, fragmented axis, 36 postaxial vertebrae, left and right incomplete scapulae, both thyrohyals, one stylohyal, fragment of manubrium of sternum, left and right humeri, left and right radii and ulnae, 8 carpals, 4 metacarpals, 11 digits; NHMW 1859/0005/0106 c.3 (Brandt 1873: Pl 14: Figs 1-5; Pia & Sickenberg 1934: SK 228 as *P. ambiguus*), caudal vertebra; NHMW 1859/0005/0109.c.28, right humerus; NHMW 2008z0172/0009, ulna; NHMW 2008z0172/0010, metacarpal; NHMW 1860/0016/0103, (Pia & Sickenberg 1934: SK 217), atlas; NHMW 1871/0026/0002 (Pia & Sickenberg 1934: SK 3496), lumbar vertebra; NHMW 1871/0026/0003, (Pia & Sickenberg 1934: SK 3496), two lumbar and two caudal vertebrae; NHMW 1871/0026/0005 (Pia & Sickenberg 1934: SK 225), two thoracic vertebrae; NHMW 1871/0026/0004 and NHMW 1871/0026/0006, three thoracic vertebrae in the same box; NHMW 1871/0026/0008 (Pia & Sickenberg 1934: SK 262), scapula; NHMW 1871/0026/0009 (Pia & Sickenberg 1934: SK 264, SK 265), left and right humeri of probably the same individual; NHMW 1871/0026/00010 (Pia & Sickenberg 1934: SK 253), fragments of ribs; NHMW 2008z0172/0008 (Pia & Sickenberg 1934: SK 209), fragments of skull; NHMW 1888/0012/0032, lumbar vertebra; NHMW 1888/0012/0095, fragment of rib; NHMW 2008z0172/0007 (Pia & Sickenberg 1934: SK 219), lumbar vertebra; NHMW 2008z0172/0004, caudal vertebra; NHMW 2008z0173/0003, lumbar vertebra; NHMW 2008z0172/0001, rib fragments; NHMW 2008z0172/0002 to …/0003, two spinous processes of vertebrae; NHMW 2008z0172/0004, caudal vertebra; NHMW 2008z0173/0001, fragments of ribs, vertebrae, and sternum; NHMW 2008z0173/0003, lumbar vertebra; PIUW 3941, caudal vertebra; PIUW 3942, manubrium sterni; PIUW 4303, caudal vertebra; NHMW 2008z0172/0006, left humerus probably from Nussdorf-Heiligenstadt

unknown locality of Sarmatian age in Vienna: NHMW 1823/0027/0105 (Pia & Sickenberg 1934: SK 579), caudal vertebra

unknown locality or localities of Sarmatian age from the Leithagebirge: NHMW 1896/0002/0018 (Pia & Sickenberg 1934: SK 224 as *P. ambiguus*), caudal vertebra; NHMW 2008z0171/0001, spinous process of vertebra; NHMW 2008z0171/0002, transverse process of vertebra; NHMW 2008z0171/0003, proximal fragment of left humerus

Loretto: NHMW 2008z0171/0004 (Pia & Sickenberg 1934: SK 223; Pia 1937: fig. 53a, as *P. ambiguus*), caudal vertebra

Specimens from localities in Hungary:

Kozárd: MTM V.72.36, caudal vertebra

Pécs-Vasas: MÁFI V.18383, left humerus

Danitzpuszta: KTGy 2006.175.376, vertebral process; MÁFI V.21677, proximal fragment of right humerus; MÁFI V.21678, spinous process of lumbar vertebra; MÁFI V.24200, caudal vertebra; MÁFI V.24190, left humerus; MÁFI V.24195, caudal vertebra; MÁFI V.06.284.1 (MÁFI V.24519), vertebra lacking both epiphyses; MÁFI V.06.280.1 (MÁFI V.24515), spinous process of caudal vertebra; MÁFI V.06.279.1 (MÁFI V.24514), spinous process of caudal vertebra; MÁFI V.06.278.1 (MÁFI V.24513), spinous process of lumbar vertebra; MÁFI V.06.275.1 (MÁFI V.24510), spinous process of caudal vertebra; MÁFI V.06.276.1 (MÁFI V.24511), spinous process of lumbar vertebra; MÁFI V.06.277.1 (MÁFI V.24512), spinous process of caudal vertebra; MÁFI V.06.281.1 (MÁFI V.24516), spinous process of ?lumbar vertebra; MÁFI V.06.282.1 (MÁFI V.24517), caudal vertebra; MÁFI V.06.274.1 (MÁFI V.24509), caudal vertebra; MÁFI V.24189, left humerus; MÁFI V.06.273.1 (MÁFI V.24508), caudal vertebra; MÁFI V.24174, proximal fragment of left humerus; MÁFI V.06.283.1 (MÁFI V.24518), caudal vertebra; MÁFI V.24213, distal fragment of left humerus; MÁFI V.24214, ulna; MÁFI V.24215, metacarpal; MÁFI V.09.326.1 (MÁFI V.28775), spinous process of caudal vertebra; MÁFI V.09.325.1 (MÁFI V.28774), spinous process of caudal(?) vertebra; MÁFI V.09.329.1 (MÁFI V.28778), caudal vertebra; MÁFI V.09.327.1 (MÁFI V.28776), lumbar vertebra; MÁFI V.09.324.1 (MÁFI V.28773), caudal vertebra; MÁFI V.09.324.1 (MÁFI V.28777), caudal vertebra

Description and comparison: The description given by Brandt (1873: 166-186) is supplemented here with the redescription of the skeletal elements that are relevant for the phylogenetical position of the species. The description of the cranial material is based on the lectotype specimen, NHMW 1860/0016/0084. With the postcranial skeletal elements all preserved specimens from the classical Vienna material were considered.

Maxilla and praemaxilla (Pl. 1, figs 1a, 1b) – Seven fragments of the rostrum are preserved with the lectotype specimen of *P. suessii*. Of these, only two fragments (1 and 2) are identifiable. Fragment no. 1 is an approximately 176 mm long fragment of the right maxilla-praemaxilla, and probably represents the segment of the rostrum just posterior to the mid-length. Fragment no. 2 is the approximately 92 mm long terminal extremity of the right maxilla, with the dorsal part broken off.

The total length of the rostrum is unknown. It is rectilinear throughout the preserved fragments, and very gracile. The greatest unilateral mediolateral extension is 20.6 mm at the end of the fragment 1 and 18.4 mm at about the middle of the preserved fragment 1 across the maxilla and praemaxilla. The rostrum depth at the same positions is estimated at about 13.3 mm and 11.6 mm, respectively.

The rostrum appears to be compressed dorso-ventrally and slightly expanded transversely. The exact morphology of the rostrum is unknown in every part, because the palatal sur-

face is not preserved. Compared to the rostrum of *Prepomatodelphis korneuburgensis*, the dorso-ventral compression and medio-lateral expansion is most similar to the section, which is about in the second quarter of the rostrum from posterior. In cross section, the praemaxilla has a flat dorsal surface, a rectangular dorso-lateral profile where it turns into the maxillary suture, and the maxilla has a convex lateral profile. This morphology is similar to the cross section of the rostrum of *P. korneuburgensis*.

Posteriorly, the preserved fraction of the praemaxilla is slightly expanded medio-laterally. The maxilla is at any position narrower than the praemaxilla in dorsal view.

Over the entire length of the preserved fragment, there is a deep, well-defined longitudinal groove of the maxilla along its suture with the praemaxilla. It becomes slightly more shallow posteriorly. This suture is everywhere narrower than in *P. korneuburgensis*, however, the rostrum of *P. suessii* is generally much smaller and more gracile than that of *P. korneuburgensis*.

There are no foramina in fragment 1. There are numerous fine, irregular striae on the praemaxilla. The maxilla has a slightly spongious bone surface. Although the ventral surface of the bone is largely eroded away, in the middle part of the fragment two small areas of paler color can be recognized. They possibly correspond to two dental alveoli(?). They have an anteroposteriorly elongated oval shape of about 4.2x2 mm, and are approx. 2.5 mm apart. There is no rostral alveolar row preserved in fragment 1.

Fragment 2 is the ventral surface of the terminal extremity of the right maxilla. Its greatest width is 11.3 mm. It is unknown if the maxilla reached the apex of the praemaxilla. There is a deep alveolar groove close to the lateral margin of the bone, which has an anterior section of 26 mm where alveoli were not separated by septa. Anteriorly it turns medially and becomes broader (1.2 mm wide posteriorly, 3.8 mm wide at the anterior extremity). Posterior to this section of the alveolar row there is a distinct dental alveolus (5.2 mm long and 1.5 mm wide). The next dental alveolus has broken off with the rest of the maxilla.

The terminal maxillary fragment differs from *Pomatodelphis inaequalis* Allen, 1921 in the lack of individual dental alveoli and in its smaller size. The largest preserved fragment of the right praemaxilla and maxilla is significantly smaller than the same part of the rostrum in *P. korneuburgensis*. It is similar to all species referred to the Pomatodelphininae in the dorso-ventral flattening of the rostrum (Kellogg 1959; Barnes 2002; Lambert 2006), which condition is a synapomorphy of the subfamily as defined by Barnes (2002, 2006).

Tympanic bulla (Plate 1: 2a-2c, 3) – Both tympanic bullae of the lectotype specimen of *P. suessii* are preserved. The description is a composite of both bullae. Of the left one, only the involucrum and the base of the posterior process are preserved. The right tympanic has the posterior part of the involucrum, both incomplete posterior prominences, parts of the lateral wall, and the base of the posterior process.

The measurements of the tympanic bulla are as follows: Total length as preserved (right tympanic; from preserved tip of the outer posterior prominence to the preserved anterior-most part of the lateral wall): 36.8 mm; width across both posterior prominences: 20.8 mm; greatest dorso-ventral extension of tympanic in lateral view: 22.2 mm; mediolateral thickness of the medial lobe: 9.7 mm, medio-lateral thickness of the lateral lobe: approx. 9.0 mm.

The ventral contour of the tympanic bulla is convex in lateral view. The involucrum is elevated dorso-ventrally, but not as much as in *Pomatodelphis* Allen, 1921. Its surface is striated. The medial contour of the involucrum is more or less straight in dorsal view. Anteriorly, the inner area of the bulla is filled with bone tissue, more so in the left tympanic than in the right one. The medial lobe is slightly thicker than the lateral lobe. The medial lobe is slightly shorter posteriorly than the lateral lobe. The extent of length reduction is probably smaller than in *Pomatodelphis* and *Zarhachis* (Muizon 1987, figs 17d, 17e), nevertheless, the tip of the lateral lobe is missing.

The interprominential notch is deep. There is a shallow ventral groove extending from the interprominential notch anteriorly. It is obscured by the spongy tissue anteriorly at the presumed midlength of the tympanic.

The outer lip of the tympanic is convex and slightly inflated in its posterior part, but not as much as in *Pomatodelphis*. As in *Pomatodelphis*, the inflated posterior area of the outer lip terminates with a distinct depression anteriorly. A lateral furrow is not visible, however, much of the lateral wall is broken away in both specimens. The anterior apex of the tympanic is missing, and the presence or absence of an anterior spine is unknown.

Scapula (Plate 1: 4a, 4b) – The right scapula of the lectotype specimen is best-preserved, with only two fragments of the dorsal part and of the posterior edge of the blade missing. In the right scapula of the NHMW 2008z0173/0002 the distal part of the acromion process is broken off; a large, triangular dorsal fragment and a small posterior fragment are missing. Both incomplete scapulae are preserved with the PIUW 1556 specimen.

Measurements were taken on the right scapula of the lectotype specimen (NHMW 1860/0016/0082): greatest anteroposterior extension as preserved: 108 mm (estimated: 110 mm); estimated dorsoventral height of the scapula: approx. 84 mm; length of acromion process as preserved: 42.5 mm; greatest width of acromion process: 19.2 mm; anteroposterior length of glenoid cavity: 23.7 mm; mediolateral width of glenoid cavity: 18.3 mm.

The scapula is not pachyostotic. The scapular blade is small and fan-shaped. The acromion process is placed at the anterior margin of the scapula, there is no supraspinous fossa. The anterior margin above the acromion process is shallowly concave. The glenoid cavity is markedly concave both anteroposteriorly and mediolaterally. The glenoid cavity is slightly elongated anteroposteriorly in the lectotype scapula, and circular in NHMW 2008z0173/0002. The scapular neck is long, comparable to *Platanista*, *Notocetus vanbenedeni* Moreno, 1892, a platanistoid from Venezuela (Sánchez-Villagra et al. 2001),

and a newly described, unnamed platanistoid from Japan (Kimura et al. 2009). There is no coracoid process.

The acromion process is moderately flattened mediolaterally, its cross-section being elliptical. The acromion process is long, and it does not broaden distally as in *Squalodon* Grateloup, 1840. Instead, the dorsal and ventral margins of the acromion process are nearly parallel, it gets narrower only at the apex. The apex is rectangular rather than rounded. The relative width of the acromion process is comparable to *Notocetus vanbenedeni* and the recent *Platanista*. The acromion process projects ventrally rather than anteriorly, reducing the space between the scapular neck and the acromion process to a deep, narrow notch. In this respect, *P. suessii* differs from all known members of the Platanistoidea sensu Muizon (1987, 1994).

Humerus, radius, and ulna (Plate 2: 1-6, Tables 1, 2) – Both humeri are preserved with the lectotype skeleton of *P. suessii*. The left humerus is almost complete, with only a fragment of the anterior margin missing. The right humerus has a large fracture across

Table 1. *Pachyacanthus suessii* Brandt, 1871, measurements of the humeri. (a): total length between the top of the caput and the crista distalis; (b) mediolateral width of proximal epiphysis; (c) anteroposterior length of distal epiphysis; (d) mediolateral width of distal epiphysis; (e) anteroposterior length of facies for attachment of radius. All measurements in mm (±0.5 mm); x: missing data; e: estimated value.

Humerus, left/right	**a**	**b**	**c**	**d**	**e**
NHMW 1860/0016/0084 (lectotype), left	72.5	35.5	x	21.0	26.0
NHMW 2008z0173/0002, right	88.5	44.0	51.5	23.5	30.5
NHMW 2008z0173/0002, left	89.0	41.0	49.0	22.5	28.0
NHMW 1859/0005/0109.c.28, left	77.0	35.0	43.0	20.5	27.5
NHMW 1871/0026/0009, right	88.0	38.5	49.0	23.0	30.5
NHMW 1871/0026/00099, left	87.0	42.0	47.5	24.0	27.0
NHMW 1886/0017/0046, right	76.5	36.5	47.5	20.5	30.0
NHMW 2008z0172/0006 (NHMW 246/1957), left	77.0	37.0	48.5	19.5	29.5
PIUW 1556, left	87.0	45.0	47.0	22.5	28.0
PIUW 1556, right	86.0	43.0	47.0	22.5	30.5
MÁFI V.24190, left	81.0	33.5	38.0	20.0	23.5
MÁFI V.24189, left	89.5	x	44.0	21.0	27.0
MÁFI V.18383, left	84.0	e39.0	44.5	21.0	27.5

the body, and has larger fragments missing anterolaterally and posteriorly. Complete left and right humeri are associated with the NHMW 2008z0173/0002 and the PIUW 1556 skeletons. Five other humeri are referred to *Pachyacanthus suessii* from different Vienna Basin localities, a single humerus from Pécs-Vasas, all well-preserved, and a few worn or fragmented specimens from Danitzpuszta.

The lectotype humeri are among the smallest humeri known for the species. In lateral view, the narrowest point of the humerus is at the midlength, well below the caput. From here, the anterior and posterior margins are diverging anteroventrally and posteroventrally. On the anterior margin, there is no distinct deltoid tuberosity, but a small ridge of rugose bone forms a keel along the entire length of the anterior margin.

The caput is small and circular in lateral view, rounded in anterior view. The infraspinous fossa is small, but well expressed. It is placed anteriorly to the long axis of the humerus in all specimens, and in NHMW 2008z0173/0002 it is shifted more to the anterior margin. The posterior tuberosity is either indistinct (lectotype and NHMW 2008z0173/0002), or it is a small, rugose area posterodistally to the infraspinous fossa (PIUW 1556, NHMW 1871/0026/0009).

In anterior view, the humerus is narrow, the proximal epiphysis being only slightly broader, and the distal epiphysis only slightly narrower than the rest of the bone.

On the proximal epiphysis the greater tubercule can not be distinguished from the lesser tubercle. The lesser tubercle is compressed transversely. It projects dorsally beyond the highest level of the caput in all specimens. The distal epiphysis has a larger attachment site for the radius, a shorter for the ulna, and there is no fovea for the olecranon.

The lectotype specimen of *Pachyacanthus suessii* has both pairs of radii and ulnae preserved. The PIUW 1556 specimen has left and right radii and ulnae and the NHMW 2008z0173/0002 has a left(?) ulna preserved. An isolated ulna (NHMW 1859/0005/0110c6) is also known.

The lower arm bones are always shorter than the humerus in *Pachyacanthus*, where the lower arm is about 60% of the length of the humerus. The radius and the ulna are thick. The radius is anteroposteriorly broader than the ulna as measured at midlength and at the proximal epiphysis of the bones. Both bones widen distally so that the flippers must have been broad distally. The radius and the ulna are attached via a large dorsal, and a small ventral attachment site. Between the two attachment sites, there is a small, almost circular gap between the radius and the ulna. The ulna bears no olecranon process.

Description of the most important specimens from the new localities Kozárd, Danitzpuszta, and Pécs-Vasas (Hungary) (Plate 2: 7-11, Plate 3: 1-4, Tables 1, 2)

From Pécs-Vasas a well preserved left humerus (MÁFI V.18383) is referred to *P. suessii*. It has small fractures broken off from the distal edge of the posterior margin, from the anterior margin, and posteriorly from the caput and the lesser tubercle. There is some white or pale yellow matrix attached to parts of the medial and lateral surfaces of the bone.

The morphology of the humerus agrees with that of the Vienna specimens, except for the almost complete lack of an anterior crest. There is only a faint keel at the distalmost part of the anterior margin. The fossa for the radius is considerably longer than the one for the ulna. The MÁFI V.18383 humerus is intermediate in size between the humeri of the lectotype and the larger PIUW 1556 specimen.

MÁFI V.24189 is a left humerus. Its anterior margin is particularly worn. The humerus has sandy matrix attached to its surface. The posterior and medial parts of the distal epiphysis are broken. The surface of the bone eroded at some parts of the caput. At these sites, a spongious (not osteosclerotic) bony tissue is exposed. The morphology, as far as preserved, is identical with that of MÁFI V.18383. MÁFI V.24190 is a left humerus. It is worn and has large fractures on the medial and lateral sides of the humeral shaft, probably caused by taphonomic processes. It is smaller than the other two humeri and as it is preserved, it has a less constricted central part of the shaft in lateral view.

The Danitzpuszta material contains a left(?) ulna of *P. suessii* (MÁFI V.24214). It is worn throughout, particularly on the presumed lateral surface. In morphology it agrees with the ulnae of the articulated skeletons from Vienna, but it is proximo-distally shorter. One metacarpal (MÁFI V.24215) shows the same morphology as do some of the metacarpals preserved with the PIUW 1556 skeleton. The identification of MÁFI V.24215 among the metacarpals is unknown. It is moderately flattened, thick, being broad proximally and getting narrow distally. The proximal articulating surface (toward the carpals) is spongious and uneven. The distal epiphysis was fully ossified. Greatest proximodostal length: 36.6

Table 2: *Pachyacanthus suessii* BRANDT, 1871, measurements of the radii and ulnae. (a): proximo-distal length between the midpoints of the proximal and distal epiphyses; (b): anteroposterior width measured in the midlength of the bone; (c): greatest anteroposterior extension of the proximal epiphysis. All measurements in mm (±0.5 mm); x: missing data.

	radius			ulna		
Specimen, left/right	**a**	**b**	**c**	**a**	**b**	**c**
NHMW 1860/0016/0086 (lectotype), left	47.0	29.5	28.0	50.5	29.0	21.0
NHMW 1860/0016/0085 (lectotype), right	47.5	30.0	27.5	50.0	30.0	22.5
PIUW 1556, left	57.0	31.5	32.5	55.5	28.0	24.0
PIUW 1556, right	60.0	33.0	32.5	56.5	29.5	26.0
NHMW 1859/0005/0110.c6	x	x	x	53.5	30.0	22.5
NHMW 2008z0173/0002	x	x	x	55.5	30.5	25.0
MÁFI V.24214	x	x	x	47.0	28.5	23.0

mm, greatest anteroposterior extension at proximal end: 28.9 mm, greatest anteroposterior extension at distal end:17.0 mm, mediolateral depth at midlength: 12.6 mm.

All other fossil remains referable to *P. suessii* from Danitzpuszta are vertebrae or vertebral fragments. MÁFI V.21678 is a spinous process of a lumbar vertebra. Posteriorly the base of the neural arch is preserved. The process is anteroposteriorly longer than high, and it is tilted anteriorly. The anterior margin is slightly convex, whereas the dorsal and posterior margins are united in a confluent, rounded (almost semicircular) contour. The preserved fragment of this vertebra is moderately pachyostotic. Revealed from its proportions, it corresponds to the 20th vertebra of the lectotype skeleton and it is one of the last vertebrae in the lumbar series. Greatest antero-posterior length: 55.7 mm, greatest dorso-ventral height as preserved: 47.4 mm.

MÁFI V.24200 is a caudal vertebra from the posterior part of the pre-fluke caudal series (plate 3.1). Compared to the vertebral series of the lectotype of *P. suessii*, it is the 28th vertebra of a vertebral column. MÁFI V.06.283.1 (MÁFI V.24518) is a caudal vertebra with a preceeding position (27th vertebra) of a similarly sized individual. Both have circular anterior and posterior epiphyses, where the anterior epiphysis is slightly concave. The neural canal is closed by bone, and the neural spine is low in both specimens, but lower in the MÁFI V.06.283.1. The neural spine has a straight anterior and a convex dorsal contour. The posterior margin is tiny and straight. The neural arch is without pachyostosis.

MÁFI V.24195 is a completely preserved but strongly worn caudal vertebra. The spinous and lateral processes are pachyostotic. The neural spine is slightly higher than long. The neural canal is dorso-ventrally compressed anteriorly, and it is completely closed posteriorly. The anterior and posterior epiphyses are circular. The transverse processes are short and project ventro-laterally. Its proportions suggest it is the first caudal vertebra.

MÁFI V.24508 (plate 3, 3a-b) is a large caudal vertebra, most probably of the same position as MÁFI V.24195 (plate 3, 2a-b). The neural canal is open anteriorly and closed by bone posteriorly.

A single caudal vertebral fragment of *P. suessii* is from the Kozárd locality (MTM V.72.36) (plate 3, 4a-b). Most of the vertebral body is broken away, but the neural spine, the neural arch, and the prezygapophyses are almost intact. It is a small vertebra (greatest anteroposterior extension of neural spine: 37.0 mm, width across prezygapophyses: 34.1 mm). The neural canal is almost closed by bone: it is only a dorsoventrally compressed narrow slit. The prezygapophyses are short, pachyostotic, and have a convex lateral contour in the dorsal view. The neural spine is only very slightly pachyostotic. It is approximately as long as it is high, and it has a straight anterior, dorsal, and posterior margins.

D i s c u s s i o n : The small relative size and the anteroposterior rather than a dorsoventral elongation of the scapular blade makes *Pachyacanthus* unlikely to be a mysticete. The lack of a ventral keel of the tympanic bulla indicates that *Pachyacanthus* is an odontocete cetacean.

Pachyacanthus suessii is hereby recognized as a member of the superfamily Platanistoidea on the basis of its scapular morphology.

The scapula lacking a coracoid process and the acromion process being placed on the anterior edge of the scapula, which lacks a supraspinous fossa, are the key synapomorphies of the superfamily Platanistoidea as defined by Muizon (1987, 1994). This concept includes the Late Oligocene to Middle Miocene family Squalodontidae and the Late Oligocene Waipatiidae Fordyce, 1994; of the "river dolphins" only the Platanistidae are included, whereas *Inia*, *Lipotes*, *Pontoporia*, and their fossil relatives are excluded. This phylogeny is widely accepted in recent literature (Fordyce & Muizon 2001; Fordyce 1994; Barnes 2002, 2006; Sánchez-Villagra et al. 2001; Kimura et al. 2009) and it is supported by molecular studies (Cassens et al. 2000; Nikaido et al. 2001).

According to Fordyce (1994), some squalodontid species, and hence, some of the supposed Platanistoidea do possess a coracoid process and a conspicuous supraspinous fossa. Geisler & Sanders (2003) critically investigated paraphyly versus monophyly of the river dolphins and returned to the original concept of the Platanistoidea by Simpson (1945).

One of the synapomorphies by Geisler & Sanders (2003) that supports a clade of all extant river dolphins to the exclusion of all other extant Cetacea is the absence of the olecranon process of the ulna. *Pachyacanthus suessii* also lacks an olecranon process of the ulna. Of note, the delphinoid *Atocetus iquensis* Muizon, 1988a of the Oligocene to Miocene family Kentriodontidae likewise has no olecranon process.

The morphology of the scapula alone is not sufficient to assign *Pachyacanthus* to any of the included families of the superfamily Platanistoidea as defined by Muizon (1994), Fordyce (1994), and Barnes (2006), because the lack of a coracoid process is a synapomorphy of the Platanistoidea. *Pachyacanthus suessii* is possibly a member of the family Platanistidae as defined by Barnes (2006), because it has an elongated and narrow rostrum.

The morphology of the tympanic bulla is insufficiently known in *P. suessii*. The preserved fragments show similarities with other platanistoids, particularly the elevated involucrum and the inflated lateral wall. A shared character of the tympanic bulla of all Platanistoidea is the reduction in length and transverse thickness of the medial lobe (Muizon 1987). In *Pachyacanthus suessii*, the medial lobe has about the same thickness as the lateral one, and the length reduction of the medial lobe is probably less pronounced than in *Pomatodelphis* and *Zarhachis*.

The synapomorphies of the tympanic bulla that define the family Platanistidae, such as the presence of an anterior spine (Fordyce 1994; Barnes 2006) and the greater elevation of the lateral wall (Muizon 1987; Barnes 2006), cannot be determined in *Pachyacanthus*.

Within the superfamily Platanistoidea the morphology of the humerus and the fore-arm is only known in the Squalodontidae and in the recent *Platanista* of the Platanistidae. The humeral morphology of *Pachyacanthus suessii* is markedly different from that of *Squalodon* whereas it is very close to the recent *Platanista*. In particular, they are similar

in the medial constriction of the humeral shaft in lateral view, in the loss of the greater tubercle, and in the reduction of the deltoid tuberosity.

The tendency to a reduction of the length of the radius and the ulna can be observed in various groups of odontocetes. Besides the Squalodontidae (Kellogg 1923; Dooley 2003; Kazár & Bohaska 2008), *Schizodelphis* Gervais, 1861 (sensu Muizon 1988b) of the Eurhinodelphinidae, all modern river dolphins (*Platanista*, *Lipotes* Miller, 1918, *Inia* d'Orbigny, 1834), *Pontoporia* Gray, 1846 of the Pontoporiidae, and the delphinoid *Albireo whistleri* Barnes, 1984 possess radii and ulnae that are shorter than the humerus.

Palaeobiogeography and Phylogeny

Fossil remains referable to *Pachyacanthus suessii* have been reported from the Sarmatian (late Serravallian, Middle Miocene) of Nussdorf, Heiligenstadt, and Hernals in Vienna; from Loretto, Bruck an der Leitha, and the Leitha Mountains in the Vienna Basin (Brandt 1871a, 1871b, 1873; Pia & Sickenberg 1934; Pia 1937). The species has been identified from the Sarmatian of three localities in Hungary (present paper): from Kozárd, Pécs-Vasas, and Danitzpuszta.

All of these occurrences are from the area of the ancient Central Paratethys Sea.

The presence of *Pachyacanthus suessii* in the Eastern Paratethys is shown by a few vertebrae and rib fragments from the Miocene of the Caucasus (Dombrovskij 1927).

No records of *Pachyacanthus* are known from localities outside the Paratethys. Capellini (1877) described a single atlas from the Miocene of Galatone (Italy), which he referred to *Pachyacanthus*. The vertebra in his figures (Capellini 1877: Pl 3, Figs 1-3) is up to 10-25% larger than the four known atlas vertebrae of *Pachyacanthus* from Vienna. The cervical vertebrae of *Pachyacanthus* are not characterized by pachyostosis and an identification of the genus based on a single cervical vertebra is problematic.

There are no records of the family Platanistidae from the Eastern and Central Paratethys. *Platanista croatica* Gorjanovic-Kramberger, 1892 from the Sarmatian of Podsused, Croatia, is based on a rostrum fragment with teeth. Kellogg (1925) indicated closer morphological relationships to "*Heterodelphis*" *leiodontus* Papp, 1905, which was demonstrated to be a representative of the family Kentriodontidae by Kazár (2006).

Platanistid fossils have important occurrences in the area of the ancient Western Paratethys sea. Barnes (2002) described *Prepomatodelphis korneuburgensis* from the Karpathian (Early Miocene) of Korneuburg, Austria, which he placed in a newly erected subfamily, the Pomatodelphininae Barnes, 2002. Bianucci & Landini (2002) referred two isolated periotics from Early to Middle Miocene (Burdigalian-Langhian) deposits of Baltringen, South Germany, to *Zarhachis* and *Pomatodelphis*.

The Early Miocene platanistid occurrences in the Western Paratethys on the one hand, and the Sarmatian (Middle Miocene) record of *Pachyacanthus* in the Central and Eastern

Paratethys on the other raise the possibility of an evolutionary connection between the older and the younger forms. However, a phylogenetical continuity between the older Badenian (Langhian – early Serravallian) and the younger Sarmatian (late Serravallian) odontocete faunas of the Central Paratethys sea could not be demonstrated (KAZÁR 2006). GRIGORESCU & KAZÁR (2005) suggested that a new marine mammal invasion occurred in the Central Paratethys in the Sarmatian.

Conclusions

(1) *Pachyacanthus suessii* BRANDT, 1871 is the type and only species of the genus *Pachyacanthus* BRANDT, 1871. *Pachyacanthus letochae* BRANDT, 1873, *P. ambiguus* (BRANDT, 1872), *P. trachyspondylus* BRANDT, 1873, *P. andrussovi* DOMBROVSKIJ, 1927, and *P. bajarunasi* DOMBROVSKIJ, 1927 are junior synonyms.

(2) The revision of the classical Vienna and Vienna Basin material in the collections of the NHMW and PIUW resulted in the confirmation of 38 items. A further 29 isolated postcranial skeletal elements from the collections of the KTGy, the MTM, and the MÁFI have been recognized as representatives of the species *P. suessii*.

(3) The redescription of the scapula revealed that *P. suessii* is a species of the Platanistoidea as defined by MUIZON (1987, 1994), FORDYCE (1994), and BARNES (2006). The preserved rostral fragments of the lectotype specimen of *P. suessii* indicate a close relationship with the family Platanistidae, but in the lack of knowledge of the cranial morphology an inclusion in the family remains hypothetical. The bones of the arm and manus indicate morphological affinities with the modern *Platanista*.

(4) The palaeogeographical distribution of *P. suessii* is extended by three Middle Miocene localities in Hungary: Kozárd, Pécs-Vasas, and Danitzpuszta.

(5) The occurrences of *P. suessii* indicate that this species was restricted to the Central and Eastern Paratethys in the Sarmatian (late Serravallian, Middle Miocene). No records of the species from older or younger deposits are known.

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Plate 1

Pachyacanthus suessii Brandt, 1871, lectotype (NHMW 1860/0016/0081 to .../0083, .../0085, .../0086, .../0088 to .../0102) from Nussdorf-Heiligenstadt, Vienna (Austria)

Fig. 1a: rostral fragment no. 1 in dorsal view

Fig. 1b: rostral fragment no. 1 in lateral view

Fig. 2a: right tympanic bulla in lateral view

Fig. 2b: right tympanic bulla in dorsal view

Fig. 2c: right tympanic bulla in ventral view

Fig. 3: left tympanic bulla in medial view

Fig. 4a: right scapula in lateral view

Fig. 4b: right scapula in medial view

Arrow head indicates the missing apex of the lateral lobe.

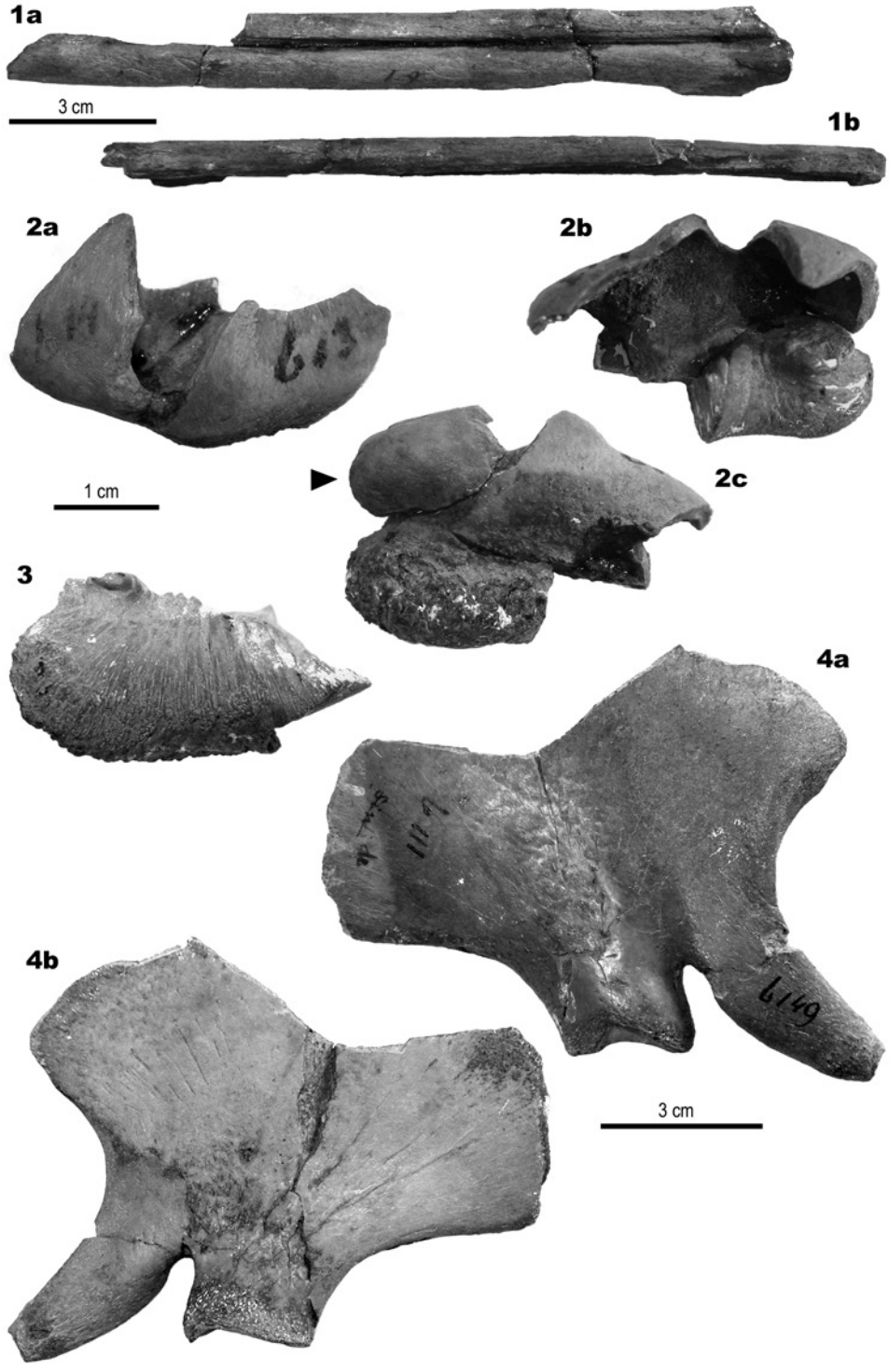

1a
3 cm
1b
2a
2b
1 cm
2c
3
4a
4b
3 cm

Plate 2

Pachyacanthus suessii Brandt, 1871, bones of the arm and manus.

Figs 1, 3, 5: lectotype (NHMW 1860/0016/0084, .../86) from Nussdorf-Heiligenstadt, Vienna (Austria); 1: Left humerus in lateral view; 3: left radius in lateral view; 5: left ulna in lateral view

Figs 2, 4, 6: specimen (PIUW 1556) from Nussdorf-Heiligenstadt, Vienna (Austria); 2: right humerus in lateral view; 4: right radius in lateral view; 6: right ulna in lateral view

Fig. 7: left humerus (MÁFI V.18383) from Pécs-Vasas (Hungary); 7a: in lateral view; 7b: in anterior view

Fig. 8: left humerus in lateral view (MÁFI V.24189) from Danitzpuszta

Fig. 9: left humerus in lateral view (MÁFI V.24190) from Danitzpuszta

Fig. 10: left(?) ulna in medial view (MÁFI V.24214) from Danitzpuszta

Fig. 11: metacarpal (MÁFI V.24215) from Danitzpuszta

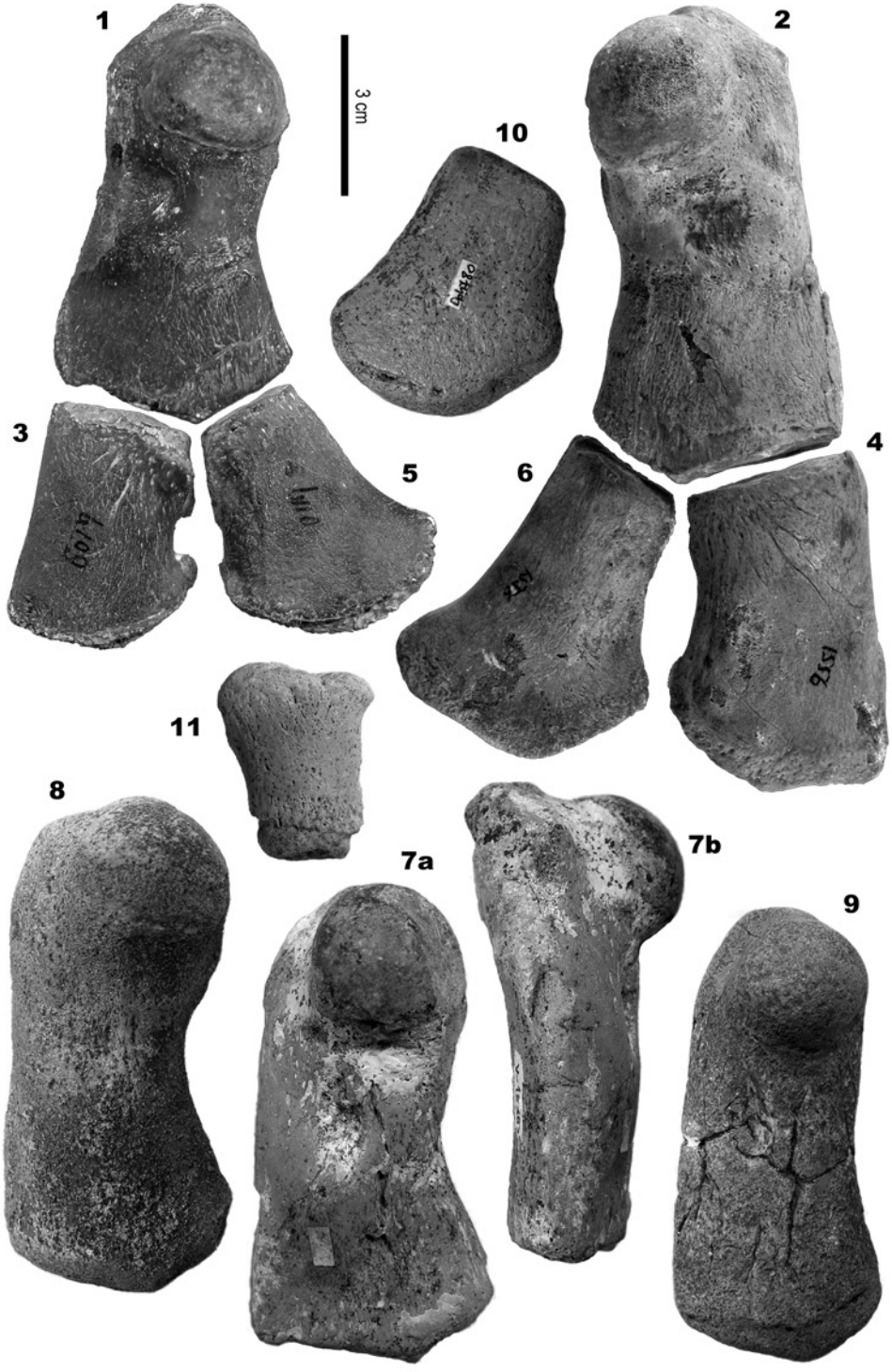

1
3 cm
10
2
3
5
6
4
11
8
7a
7b
9

Plate 3

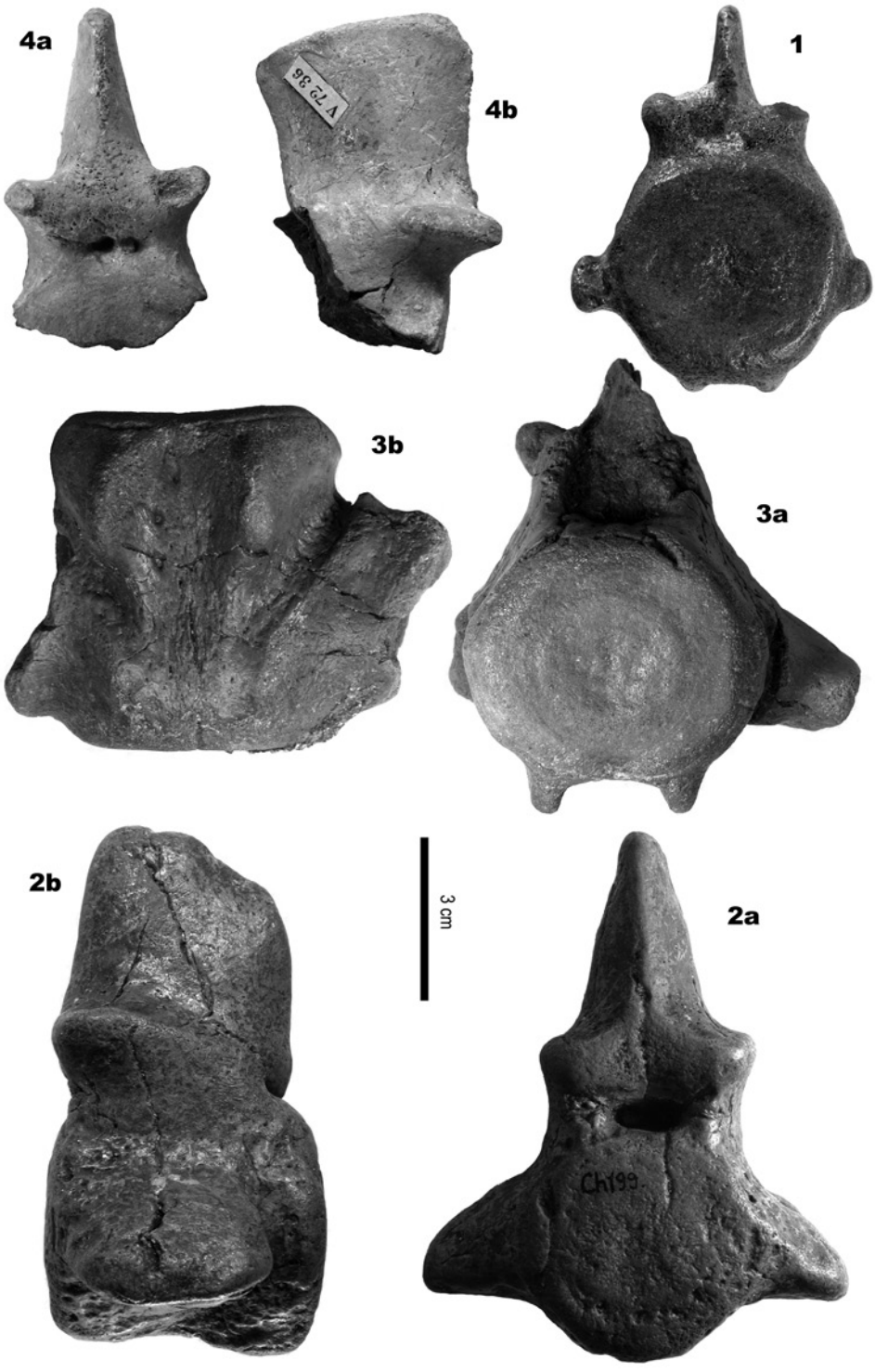
Pachyacanthus suessii Brandt, 1871, vertebrae.

Fig. 1: caudal vertebra in anterior view (MÁFI V.24200) from Danitzpuszta

Figs 2a-2b: caudal vertebra in anterior and lateral views (MÁFI V.24195) from Danitzpuszta

Figs 3a-3b: caudal vertebra in anterior and ventral views (MÁFI V.06.273.1) from Danitzpuszta

Figs 4a-4b: fragment of caudal vertebra in anterior and lateral views (MTM V.72.36) from Kozárd


4a
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4b
1
3b
3a
2b
3 cm
2a
Ch199