The sirenian Metaxytherium (Mammalia: Dugongidae) in the Badenian (Middle Miocene) of Central Europe

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Abstract

The fossil record of sirenians in the Middle Miocene (Badenian; Langhian-early Serravallian) of the Central Paratethys region (principally eastern Austria) is reviewed, and new specimens are described from the localities of Gainfarn, Baden/Rauchstallbrunngraben, ?St. Margarethen, and Retznei (Austria) and Fazekasboda (Hungary). All these are referred to *Metaxytherium medium* (Desmarest, 1822) Hooijer, 1952, which is the only sirenian here recognized in the Middle Miocene of the Central Paratethys. *Thalattosiren petersi* (Abel, 1904) Sickenberg, 1928 is considered a synonym of *Metaxytherium medium*. This conclusion extends the known geographic range of *M. medium*, and is consistent with the hypothesis that European and North African Miocene and Pliocene *Metaxytherium* formed a single, anagenetically-evolving lineage. Although the area in which "*Thalattosiren petersi*" was thought to occur (mainly the Vienna Basin) was progressively cut off from other marine basins during the course of the Badenian, and could conceivably have supported an endemic sirenian taxon isolated on the northeastern margin of the range of *M. medium*, the few diagnostic specimens available do not appear to support this scenario. *Metaxytherium medium* is considered an ecological generalist among sirenians, inhabiting tropical to warm temperate shallow marine waters and feeding on seagrasses. Its fossil record in the Central Paratethys ends with the Badenian, but its lineage continued in the Mediterranean into the Late Pliocene.

Der Fossilbestand der Sirenen im Mittleren Miozän (Badenium; Langhium-frühes Serravallium) der Zentralen Paratethys (im Prinzip Ostösterreich) wird revidiert und neue Exemplare aus den Lokalitäten Gainfarn, Baden/Rauchstallbrunngraben, ?St. Margarethen, und Retznei (in Österreich) und Fazekasboda (in Ungarn) werden beschrieben. Sie alle sind dem *Metaxytherium medium* (Desmarest, 1822) Hooijer, 1952, der einzigen Seekuh des Mittleren Miozäns in der Zentralen Paratethys, zugeordnet. *Thalattosiren petersi* (Abel, 1904) Sickenberg, 1928 wird als Synonym von *Metaxytherium medium* betrachtet. Diese Schlussfolgerung erweitert die bisher bekannte geographische Verbreitung des *M. medium* und stimmt auch mit der Hypothese überein, dass europäische und nordafrikanische, miozäne und pliozäne Metaxytherien eine einzige, sich anagenetisch entwickelnde Linie repräsentieren. Obwohl das vermutete Verbreitungsgebiet von "*Thalattosiren petersi*" (vor allem das Wiener Becken) im Laufe des Badenium zunehmend von anderen marinen Becken abgeschnitten wurde und so die Bildung eines endemischen Taxons am nordöstlichen Rand des Verbreitungsgebietes von *M. medium* möglich gewesen wäre, geben die wenigen diagnostischen Exemplare keinen Hinweis darauf. *Metaxytherium medium* kann als Generalist unter den Sirenen betrachtet werden, der tropische, warm temperierte, flachmarine Gewässer bewohnt und dort Seegräser beweidet. Der fossile Nachweis in der Zentralen Paratethys endet mit dem Badenium, im Mediterran setzt sich die Linie bis in das Pliozän fort.
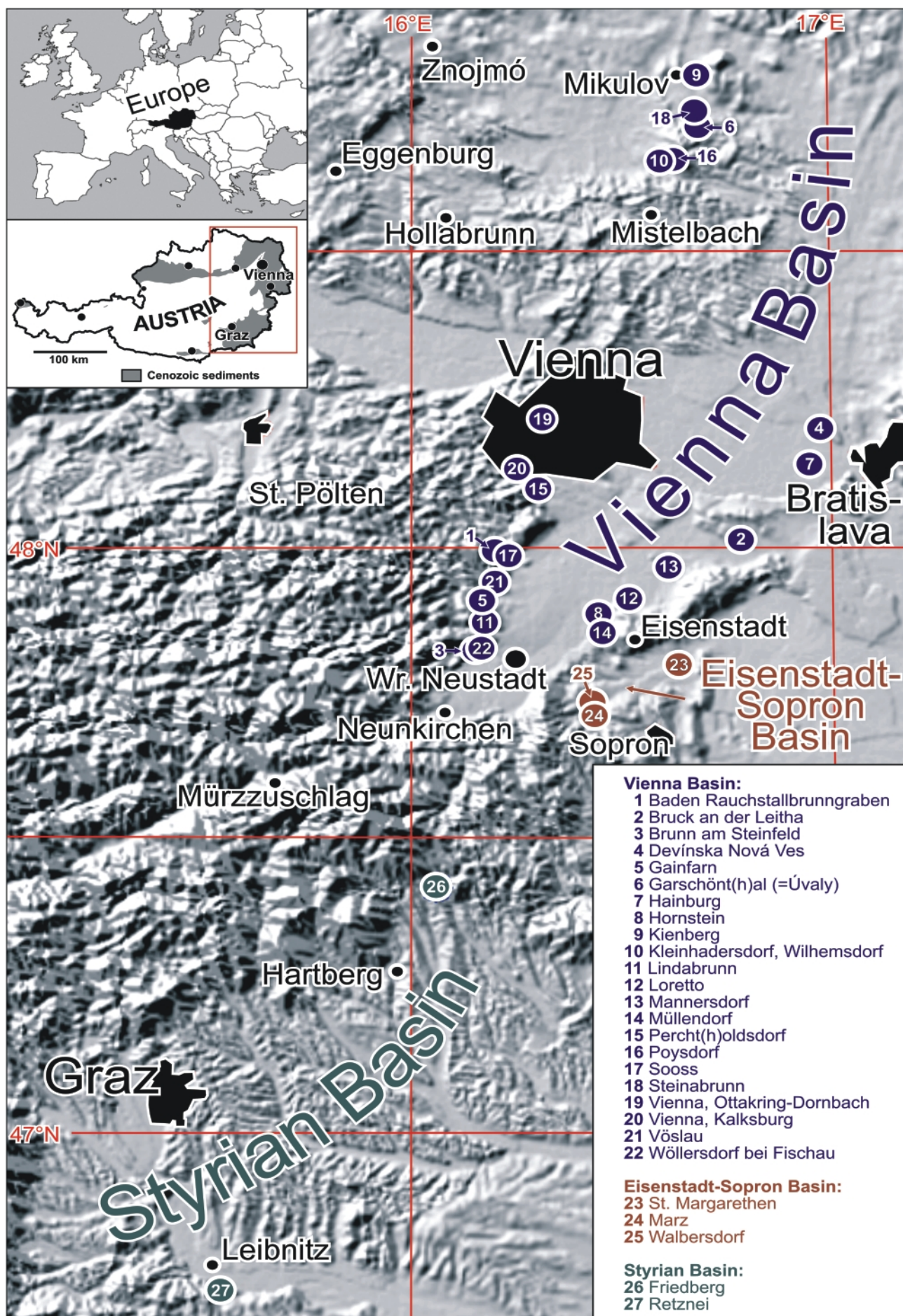
1. Introduction

The Miocene fossil record of sirenians in Central Europe is somewhat limited, but it has been studied for more than a century and a half and has occasioned a substantial body of descriptive literature. This literature, unfortunately, applies to the fossils a confusing and largely outdated array of taxonomic names, and presents little coherent paleozoogeographic, phylogenetic, or evolutionary pattern. In this paper we report a new occurrence of sirenian fossils in the Vienna Basin, describe additional unpublished material, revise earlier records from this and surrounding areas, and attempt to clarify the Middle Miocene distribution and evolutionary history of sirenians in the central Paratethys.

In an earlier paper Domning and Pervesler (2001) reviewed Central European sirenian records from the later Early Miocene (Eggenburgian-Ottnangian), showing that all could be referred to the single species *Metaxytherium krahuletzi* Depéret,

1895 (Dugongidae: Halitheriinae), which was originally described and is still best known from Austria. This species is the earliest Old World representative of *Metaxytherium* Christol, 1840, and the progenitor of a Miocene-Pliocene series of chronospecies distributed from Europe to North Africa (Domning and Thomas, 1987; Carone and Domning, 2007; Bianucci et al., 2008; Sorbi et al., 2012), which also comprises almost all of the Neogene sirenians known from that region.

In 2006 a partial skeleton of *Metaxytherium* was discovered in Middle Miocene (Badenian) deposits at Gainfarn in the Vienna Basin of Austria. The description of this specimen gives us the opportunity to extend our earlier study into the Middle Miocene, by reviewing the fossil record of other sirenians of that age in the same general region of Europe, and addressing the unresolved question of the validity of the nominal taxon *Thalattosiren petersi* (Abel, 1904) Sickenberg, 1928.

Vienna Basin:
1 Baden Rauchstallbrunngraben
2 Bruck an der Leitha
3 Brunn am Steinfeld
4 Devínska Nová Ves
5 Gainfarn
6 Garschönt(h)al (=Úvaly)
7 Hainburg
8 Hornstein
9 Kienberg
10 Kleinhadersdorf, Wilhemsdorf
11 Lindabrunn
12 Loretto
13 Mannersdorf
14 Müllendorf
15 Percht(h)oldsdorf
16 Poysdorf
17 Sooss
18 Steinabrunn
19 Vienna, Ottakring-Dornbach
20 Vienna, Kalksburg
21 Vöslau
22 Wöllersdorf bei Fischau

Eisenstadt-Sopron Basin:
23 St. Margarethen
24 Marz
25 Walbersdorf

Styrian Basin:
26 Friedberg
27 Retznei

Abbreviations: BLLM = Burgenlandisches Landesmuseum, Eisenstadt, Austria; BMNH = Natural History Museum, London, UK; GBAW = Geologische Bundesanstalt, Vienna, Austria; GITUW = Geologisches Institut, Technische Universität (formerly Technische Hochschule), Vienna, Austria; IPUW = Institut für Paläontologie, University of Vienna, Austria; IPUWRG = Ritter-Gulder collection in IPUW; IPUWWF = Weinfurter collection in IPUW; IPUWZA = Zapfe collection in IPUW; KÜH = collection from Kühnring in the Krahuletz-Museum, Eggenburg, Austria (KÜH 88 is on indefinite loan for display at the Steinmetzhaus Zogelsdorf, Zogelsdorf, Austria), LPB = Laboratoire de Paléontologie, Université de Bretagne Occidentale, Brest, France; MAFI = Hungarian Geological Institute, Budapest, Hungary; MNHN = Muséum National d'Histoire Naturelle, Paris, France; MPUN = Museo di Paleontologia dell'Università di Napoli, Italy; NHMBs = Natural History Museum, Basel, Switzerland; NHMW = Naturhistorisches Museum, Vienna, Austria; NOELM = Niederösterreichisches Landesmuseum, St. Pölten, Lower Austria; PS = specimen listed by Pia and Sickenberg (1934); SK = S. Karrer collection in NHMW; STMBV = Stadtmuseum Bad Vöslau, Lower Austria; TH = Technische Hochschuhle, Wien; USNM = U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

In reference to cheek teeth: L = crown length, AW = anterior width, PW = posterior width, W = total width.

In reference to morphological character states: c. = character state as described and numbered by Domning (1994a), Bajpai and Domning (1997), or Domning and Aguilera (2008); e.g., c. 3(1) refers to state one of character three.

2. Geological Setting

2.1 Vienna Basin

The Vienna Basin (Fig. 1) constitutes a classical area of geological and palaeontological investigations of Miocene strata. The basin comprises a structurally complex pull-apart basin at the junction of the Eastern Alps and the Western Carpathians (e.g. Wessely, 1988; Decker and Peresson, 1996; Hamilton et al., 2000; Sabol and Kováč, 2006). The structural evolution of the Vienna Basin is characterized by successive phases of compression, strike-slip movements and extension, related to compression and lateral extrusion within the Eastern Alps (Ratschbacher et al., 1991; Decker and Peresson, 1996; Strauss et al., 2006).

In general, the evolution of the Vienna Basin started during the Early Miocene (Eggenburgian-Ottnangian-Karpatian) with the development of a partly non-marine piggyback basin on top of Alpine thrusts to the northeast of Vienna (Kováč et al., 1999; Hamilton et al., 2000). Sinistral transtension during the Early and Middle Miocene led to the formation of small-scale, rapidly subsiding lows and relatively stable highs during the

Figure 1: Relief map of eastern Austria showing the Vienna Basin, Styrian Basin and Eisenstadt-Sopron Basin with the distribution of Badenian seacow localities.

Badenian and Sarmatian. A renewed marine transgression started in the early Badenian and reached the southern part of the basin. Up to 3000 m-thick successions of marls and sandstones characterize the central parts of the basin, whereas delta sands and carbonates were deposited at the basin margins or at shallow depths (Sauer et al., 1992; Weissenbäck, 1996; Seifert, 1996). During Sarmatian and Pannonian times, salinity oscillated and finally decreased, leading to limnic-fluvial deposits (Harzhauser and Piller, 2004a, 2004b).

The western margin of the southern Vienna Basin shows large normal or oblique faults that displace marginal sediments such as deltaic deposits and shallow-marine limestone (Leithakalk) against fine-grained basin strata ("Tegel"). In the old Sooss brickyard, faults have been visible that displace Badenian against Sarmatian strata (Rögl et al., 2008).

Due to the lack of good outcrops, detailed sedimentological and palaeontological investigations are restricted to a few natural outcrops and a handful of active pits and exploration drillings.

The oil industry (mainly OMV) and several research projects (e.g. Decker et al., 2005; Hinsch et al., 2005) gathered a wealth of data for the Vienna Basin. The Sooss scientific borehole (FWF project P13743-BIO) penetrated a succession of early Badenian (Langhian, Middle Miocene) sediments, starting from the type section of the Badenian, the old Baden-Sooss brickyard near Baden (Hohenegger et al., 2008, 2009; Pervesler et al., 2008; Wagreich et al., 2008). Papp et al. (1978) published detailed descriptions of the Badenian stratotype.

The beginning of the Paratethyan Badenian stage approximately coincides with the beginning of the Langhian stage (Fig. 2; Hohenegger and Wagreich, 2012). The subdivision of the Badenian into the Moravian (lower Badenian), Wielician (middle Badenian) and Kosovian (upper Badenian) reflects the subdivision in the Vienna Basin based on benthic foraminifera into the "Lagenidae Zone", the "*Spiroplectammina* Zone" and the "*Bulimina/Bolivina* Zone". Most characteristic are the widespread evaporites of the Wielician in the Carpathian Foredeep and the Transylvanian Basin. According to this subdivision, the beginning of the Kosovian coincides with the Serravallian stage.

The lithostratigraphic division of the Badenian sediments in the Austrian part of the basin is still under debate. The recent lithostratigraphic chart of Austria (Piller et al., 2004) places these deposits of the classical "Badener Tegel" into the Baden Group, which can be subdivided into the Jakubov Formation and the Lanžhot Formation in the Slovakian part of the basin. The lower part of the Badenian with the Sooss borehole correlates to the Lanžhot Formation (e.g. Kováč et al., 2004).

Based on biostratigraphic data, the succession at the Sooss brickyard can be correlated to the lowermost sequence of the Badenian, sequence VB 5 or Ba1, which is dated as Lower Lagenid Zone and parts of the Upper Lagenid Zone (Kováč et al., 2004; Strauss et al., 2006). The top of this sea-level cycle has been correlated to the global 14.2 Ma hiatus (Strauss et al., 2006) and is associated with a major sealevel drop through-

out the Vienna Basin (e.g. Weissenbäck, 1996).

2.2 Eisenstadt-Sopron (Sub-)Basin

This small basin (Fig. 1), nearly in the shape of an equilateral triangle with side lengths of about 20 km, is a sub-basin of the Vienna Basin. In the north it is limited by the NE-SW trending Leitha Mountains and the associated SE-dipping Eisenstadt fault (Rasser and Harzhauser, 2008). In the east, the basin is limited by the N-S trending Rust faults. The Rust Mountains separate the basin from the Danube Basin in the east. The southern margin in E-W orientation from the Brennberg to the Rosalia Mountains is defined by a crystalline ridge, now covered by Lower Miocene gravel. Tectonically and palaeogeographically this relief separates the Eisenstadt-Sopron Basin from the Styrian Basin complex.

During the Early Miocene (Ottnangian, Karpatian), terrestrial, lacustrine and fluvial sediments related to the fluvial systems of the southern Vienna Basin were deposited in the Eisenstadt-Sopron Basin. During the Early Badenian the first marine ingression reached the area. Offshore shoal areas with coral carpets and corallinacean growth developed during periods of high sea level in the Middle and late Badenian, as the Leitha Mountains were covered by the sea.

A marine seaway between the Eisenstadt-Sopron Basin and the southern Vienna Basin can be supposed in the area of Wiener Neustadt.

2.3 Styrian Basin

The Styrian Basin (Fig. 1), which is part of the western Pannonian Basin system, was subdivided by swells into different sub-basins. The main structure, the Middle Styrian Swell, separates the Western from the Eastern Styrian Basin. The basement is formed by the Austroalpine nappe system. Subsidence of the basin, which started during the early Miocene, probably during the Ottnangian, was connected with the lateral extrusions of crustal wedges along strike-slip faults towards the Pannonian Basin (Decker and Peresson, 1996; Frisch et al., 2000). A combination of block rotation, subsidence and uplift formed the different sub-basins. Large areas were covered by lava flows during extensive volcanic activity. Extended lignite
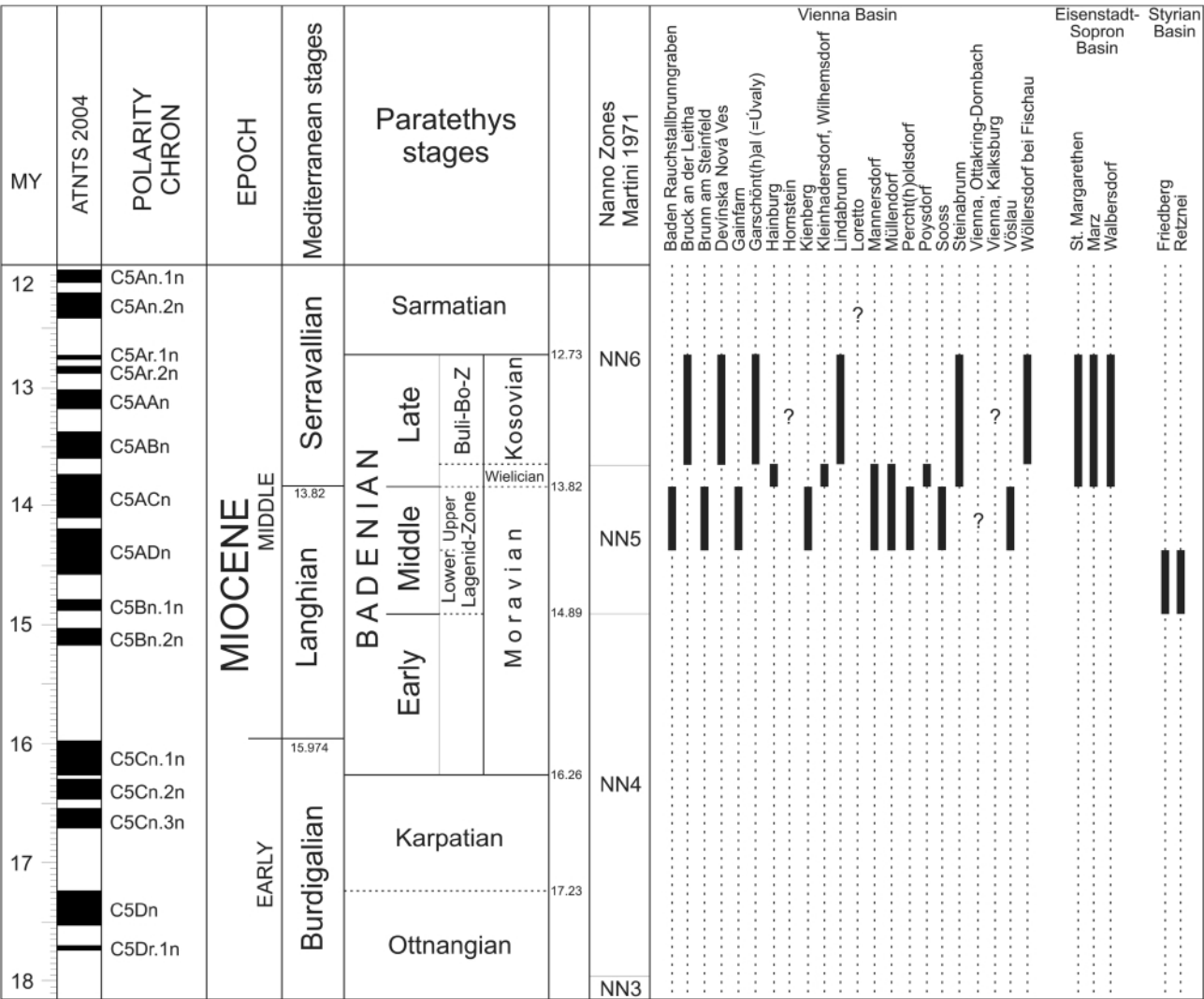

Figure 2: Correlation chart of Early and Middle Miocene stratigraphic units (modified after Hohenegger et al., 2011); range of seacow occurrences in the Vienna Basin, Eisenstadt-Sopron Basin and Styrian Basin.

Site # (Fig.1)	Site	Stage	Collection and Catalogue Number	Skeletal Elements	References
Vienna Basin					
1	Baden Rauchstallbrunngraben	late Middle Badenian	NHMW 2007z0106/0001 (cast in USNM)	juvenile skull	This paper
2	Bruck an der Leitha	Late Badenian	Staedt. Mus. Bruck a. d. Leitha (PS 3364)	lower molar fragment	Pia and Sickenberg, 1934
			Staedt. Mus. Bruck a. d. Leitha (PS 3407)	2 rib fragments	Pia and Sickenberg, 1934
3	Brunn am Steinfeld	late Middle Badenian	Staedt. Mus. Wiener Neustadt (PS 3337)	skullcap, endocast, scapula & vertebra fragments, ribs	Pia and Sickenberg, 1934
4	Devínska Nová Ves (=Neudorf an der March)	Late Badenian	NHMW 1857 (PS 3347)	cranial & other fragments	Pia and Sickenberg, 1934
			NHMW 1865 I 1180 (PS 3354)	upper molar fragment	Pia and Sickenberg, 1934
			GBAW (PS 3355)	upper molar fragment	Pia and Sickenberg, 1934
			NHMW 1850 XVI 21 (PS 3360)	left m2 or m3	Peters, 1867: pl. 7, fig. 2; Abel, 1904: pl. 1, fig. 18
			NHMW 1865 I 1181 (PS 3362)	right m3	Peters, 1867: pl. 7, fig. 1
			NHMW 1868 VIII 3 (PS 3365)	lower molar	Pia and Sickenberg, 1934
			NHMW (PS 3375)	vertebra fragment	Pia and Sickenberg, 1934
			GBAW (PS 3378)	"sternum" (misidentified?), vertebra & rib fragments	Pia and Sickenberg, 1934
			NHMW 1906, 1898, & unnum. (PS 3408-3410)	3 rib fragments	Pia and Sickenberg, 1934
			NHMW 1859 V 126, 1854 (PS 3432-3433)	2 juvenile ulnae	Pia and Sickenberg, 1934
			IPUWZA(PS 3717)	caudal vertebra	Pia and Sickenberg, 1934
			IPUWWF (PS 3725)	rib fragment	Pia and Sickenberg, 1934
			IPUWZA (PS 3726)	right humerus	Thenius, 1952: fig. 68
			IPUWZA	stapes, vertebra fragment, left m2, molar fragment	
			IPUW	left m1	
			IPUWRG	left scapula	Thenius, 1952: fig. 69
			NHMW 2012/0156/0001 (Theben-Neudorf; coll. Kornhuber from the TH WIEN)	left M2	
			GBAW 2006/18/1, 2355 [in part]	partial skull roof of juvenile	Abel, 1904: 107-108
			NHMW 1997z0178/1984 (PS 3717?)	2 caudal vertebrae	Pia and Sickenberg, 1934
			IPUWWF	juvenile thoracic neural arch	
			NHMW 1997z0178/1983, 1985	stapes, vertebra fragment, left m2, molar fragment	
			NHMW 862, 1868 VIII 3, and unnum. (PS 1778-1779?)	tooth fragments; same as the "Suide indet." molar fragments listed by Pia and Sickenberg, 1934?	PS 1778-1779 referred to Sirenia by Thenius, 1952: 109
5	Gainfarn	late Middle Badenian	STMBV/Met/0001	partial skeleton	This paper
6	Garschönt(h)al or Garschental (Úvaly)*	Late Badenian	NHMW 1859 I 13 (PS 3363)	lower molar	Abel, 1904: 110
7	Hainburg an der Donau	early Late Badenian	GBAW Inv. Nr. 2006/18/1 -6 (PS 3331) **(holotype of *Metaxytherium petersi* Abel, 1904)**	skeleton lacking skull; now lost and probably destroyed in World War II except for distal epiphysis of a radius, 2 carpals, 1 metacarpal, 1 phalanx, left innominate, & a cervical vertebra	Peters, 1867: 309-314; pl. 7, figs. 4-8); Abel, 1904: 107-137; figs. 3, 4, 6, 7, 10, 11, 12; pl. 2, fig. 6; pl. 7, fig. 2
			NHMW (PS 3352)	upper incisor [not seen; questionably referred]	Pia and Sickenberg, 1934
8	Hornstein	?Late Badenian, ?Sarmatian	NHMW 1970/1396/911 (Fürst Collection #558)	rib fragment	
9	Kienberg (= Kienberk)	late Middle Badenian	GBAW (PS 3421-2)	3 rib fragments	Pia and Sickenberg, 1934
10	Kleinhadersdorf – Wilhelmsdorf	early Late Badenian	IPUWWF	3 rib fragments	
11	Lindabrunn	Late Badenian	Niederöst. Landesmus. St. Pölten (F 5412)	ribs & vertebrae (on exhibition)	
12	Loretto	Sarmatian	NHMW 1890 XX 6 (PS 3412-3413); NHMW I. a. d, V.A, 18 (PS 3720); NHMW unnumbered	rib fragments	Pia and Sickenberg, 1934
13	Mannersdorf	Late Badenian	NHMW 1850 XXVI 20 (PS 3361)	right m3	Peters, 1867: pl. 7, fig. 3; Abel, 1904: pl. 1, fig. 19
14	Müllendorf	Late Badenian	IPUW	right M2, left m2	
			NHMW 1952/37	left mandible fragment with m3	
			NHMW 1970/1396/910 (Fürst Collection #554)	right rib	
			Gerhard Wanzenböck collection, Gainfarn	fragments of skull, scapula, vertebrae, and ribs of juvenile	This paper
15	Percht(h)oldsdorf	late Middle Badenian	NHMW 1883, C.6123, A2945	3 rib fragments	
			NHMW 1904 (PS 3341)	scapula, humerus, & rib fragments	Pia and Sickenberg, 1934
			NHMW 1886 XVII 48 (PS 3405?)	2 ribs	Pia and Sickenberg, 1934
16	Poysdorf (Poisdorf)	early Late Badenian	GBAW (PS 3403)	rib fragments	Pia and Sickenberg, 1934
17	Sooss	late Middle Badenian	IPUWWF	2 rib fragments	
18	Steinabrunn (=Steinebrunn)	Late Badenian	NHMW 1851 XIII 59 (PS 3398?)	rib	Pia and Sickenberg, 1934
			GBAW (PS 3399)	rib fragments	Pia and Sickenberg, 1934
			NHMW 1851 XIII 60 (PS 3400)	proximal rib fragment	Pia and Sickenberg, 1934

TABLE 1 : Fossil sirenian specimens recorded from Middle Miocene (Badenian) deposits of the Vienna Basin and adjacent regions (Central Paratethys).

Site # (Fig.1)	Site	Stage	Collection and Catalogue Number	Skeletal Elements	References
Vienna Basin					
19	Vienna, Ottakring-Dornbach	late Middle Badenian	NHMW 1885 (PS, 3367)	subadult skeleton comprising the "mounted skeleton" (sternum, 12 vertebrae, 32 pairs of ribs) (Wolf sandpit)	Abel, 1904: 108, 131-133
			NHMW 1885 (PS 3350, 3368)	immature skeleton comprising right mandible with ?m2, vertebrae & 23 ribs (Baumann sandpit)	Abel, 1904: 133
			NHMW 1908 103 (PS 3374)	caudal vertebra ("Sandstaette in der Kipflingstrasse")	Pia and Sickenberg, 1934
20	Vienna, Kalksburg	?Late Badenian	IPUW (PS 3342)	partial skeleton, including humerus, partial radius, & ribs	Abel, 1904: 121, pl. 4, fig. 5
			IPUW (PS 3370)	thoracic vertebra & lumbar vertebra	Pia and Sickenberg, 1934
			IPUWWF	rib fragments	
			GITUW (PS 3406)	rib fragments	Pia and Sickenberg, 1934
			NHMW; IPUW?	vertebrae & ribs	Abel, 1904: 106-107
			NHMW 1935 II 54, SK 4874	rib	
21	Vöslau	late Middle Badenian	?	thoracic vertebra	Abel, 1904: 105
			K.F.J. Mus. Baden (PS 3415)	rib fragments	Pia and Sickenberg, 1934
			IPUWZA (PS 3724)	rib fragment	Pia and Sickenberg, 1934
22	Wöllersdorf bei Fischau	Late Badenian	NHMW 1897 (PS 3358)	left m3	Abel, 1904: pl. 1, fig. 17
Eisenstadt-Sopron Basin					
23	St. Margarethen	Late Badenian	BLLM 32816 (Inv. Nr. 3972 - 3983, 4570, 7309, 7310) (PS 3332)	nearly complete skull with scapula, vertebrae including atlas, & ribs of an immature animal	Sickenberg, 1928: 293-323; figs. 1-6; pls. 1-2
			BLLM 32815 (locality uncertain)	adult braincase	This paper
24	Marz (= Márczfalva–Péherko-bánya)	early Late Badenian	MAFI Ob-3036, Ob-3995-3996, Ob-3037, Ob-3039, Ob-3040	left & right humeri, right radius-ulna, 2 metacarpals, right m3 (all seem to have represented the same individual, of which the skullcap, other molars, 6 vertebrae, & some ribs were apparently also collected)	Schréter, 1917
25	Walbersdorf	early Late Badenian	NHMW 1938 No. 38, SK 4879	2 rib fragments	
Styrian Basin					
26	Friedberg	?Early to Middle Badenian	GBAW Inv. Nr. 1927/01/7 -8 (PS 3338)	skullcap fragment & 5 rib fragments	Ehrenberg, 1927: 105
27	Retznei	early Middle Badenian	Gerhard Wanzenböck collection, Gainfarn	skullcap with frontals & supraoccipital	This paper
Pannonian Basin					
	Fazekasboda, Hungary	Late Badenian	MAFI unnumbered	juvenile partial skull, right mandible, left DP4-M1, right dp4-m1, partial atlas, 5 or more thoracic neural arches, & 10 or more ribs	This paper

Table 1 continued

formation occurred in the Western Styrian Basin during the Early and early Middle Miocene, on top of coarse-grained fan deposits. The Paratethys Sea flooded the Western Styrian Basin during the Karpatian (Hohenegger et al., 2009). The Karpatian/Badenian boundary is marked by angular unconformities and sedimentation gaps (Styrian Unconformity). A series of marine transgressions of the Badenian Sea followed on top of the Karpatian deep-water sediments (the Steirischer Schlier). In the Styrian Basin, the transgressions reached their greatest extent in the Early Badenian. The correlation of calcareous nannoplankton and planktonic foraminiferal events between the Styrian Basin and the Mediterranean demonstrates similarities caused by marine connections (Hohenegger et al., 2009).

3. Selected Sirenian localities of Badenian (Langhian and Early Serravallian) age in the Vienna, Eisenstadt-Sopron and Styrian Basins: Stratigraphy, age, environmental characteristics and taphonomy.

Numerous specimens of seacow fossils were collected in a period of intensified construction activities in the final years of the Austro-Hungarian Empire. Growing urban centers required

construction material like stones and bricks; new railways needed tunnels and cuttings. Need of water supply for growing cities caused the creation of aqueducts. Human power was an important factor in this period and fossils were not always destroyed by mechanical excavation. Countless fossil-bearing localities got lost in the last 100 years and the reconstruction of their coordinates is sometimes only an approximation based on old literature.

In the following description of localities, some of which are indicated in Figs. 1 and 2, three marine basins of Badenian (Middle Miocene) age, inhabited by the seacow *Metaxytherium*, are distinguished. The sirenian remains recorded from these localities are listed in Table 1.

3.1 Vienna Basin

3.1.1 Baden Rauchstallbrunngraben, Lower Austria

Quarries SSW of Baden; 16°11.94´E, 47°59.94´N (Fig. 1, #1) (Baden Group, Leitha limestone, Baden conglomerate, late Middle Badenian).

South of the road from Baden to the "Gasthof Jägerhaus", two levels of abandoned quarries can still be visited, although

they are becoming more and more overgrown by trees. Within the 60 meters of sediments exposed in these outcrops, a variety of near-shore deposits are developed. The sediments are time equivalents of the pelitic facies in the center of the Vienna Basin.

In the deeper quarry, the "Bryozoenmergel" represents a quieter environment of deposition with not too much wave or current energy. The upper quarries with medium sandstones, fine conglomerates, and coarse sandy limestone with irregular sea urchins (*Clypeaster*) and the trace fossil *Teredolites* represent a higher-energy environment. The following 250 cm-thick bioturbated layer of fine sand and sandy marl contains foraminifers (*Ammonia beccarii* and *Elphidium crispum*), ostracods and clypeasterids. From this layer originates the skull of a juvenile *Metaxytherium*.

The section continues with 5 meters of cross-bedded conglomerates (deltaic sedimentation) inclined toward the center of the basin. The section finishes with marly coralline limestone (Piller and Vávra, 1991).

3.1.2 Bruck an der Leitha, Lower Austria

Two quarries on the northern flank of the Spittelberg (=Spitalberg), 0.5 km south of train station Bruck an der Leitha; 16°46.961´E, 48°0.794´N (Fig. 1, #2)

(Baden Group, Leitha limestone, ?late Badenian)

3.1.3 Devínska Nová Ves (=Neudorf an der March), Slovakia

Sandberg locality; 16°58.66´E, 48°12.084´N (Fig. 1, #4)

(Baden Group, Sandberg Member, late Badenian)

Mesozoic limestone (layer 1 in Švagrovský, 1978) is covered by Neogene coarse quartz sand with intercalated gravel horizons (layer 3). The following cross-laminated fine sand layer contains vertebrate fossils (layer 4). The top of the section is formed by further coarser sand layers, carbonate sandstone rich in molluscs and coralline algae (layers 5 and 6). The section is covered by alluvial gravel.

The vertebrate fauna is dominated by teeth, fin rays, vertebrae and otoliths of fishes. Reptiles like sea turtles (*Psephophorus polygonus*) are rare. Several examples of seal and seacow remains are reported from this section. Many of the seacow bones seem to have gotten abraded during taphonomic processes. Wind erosion was proposed by Thenius (1952), but similar appearance of bone shapes was found in specimens of *Metaxytherium krahuletzi* from the Eggenburgian area deposited under water cover (Pervesler et al., 1995; Pervesler et al., 1996; Pervesler et al., 1998; Domning and Pervesler, 2001), and in sirenian specimens from several other parts of the world (Domning, unpublished).

Sedimentology and faunal composition support a near-shore interpretation with periods of higher hydrodynamic energy. That
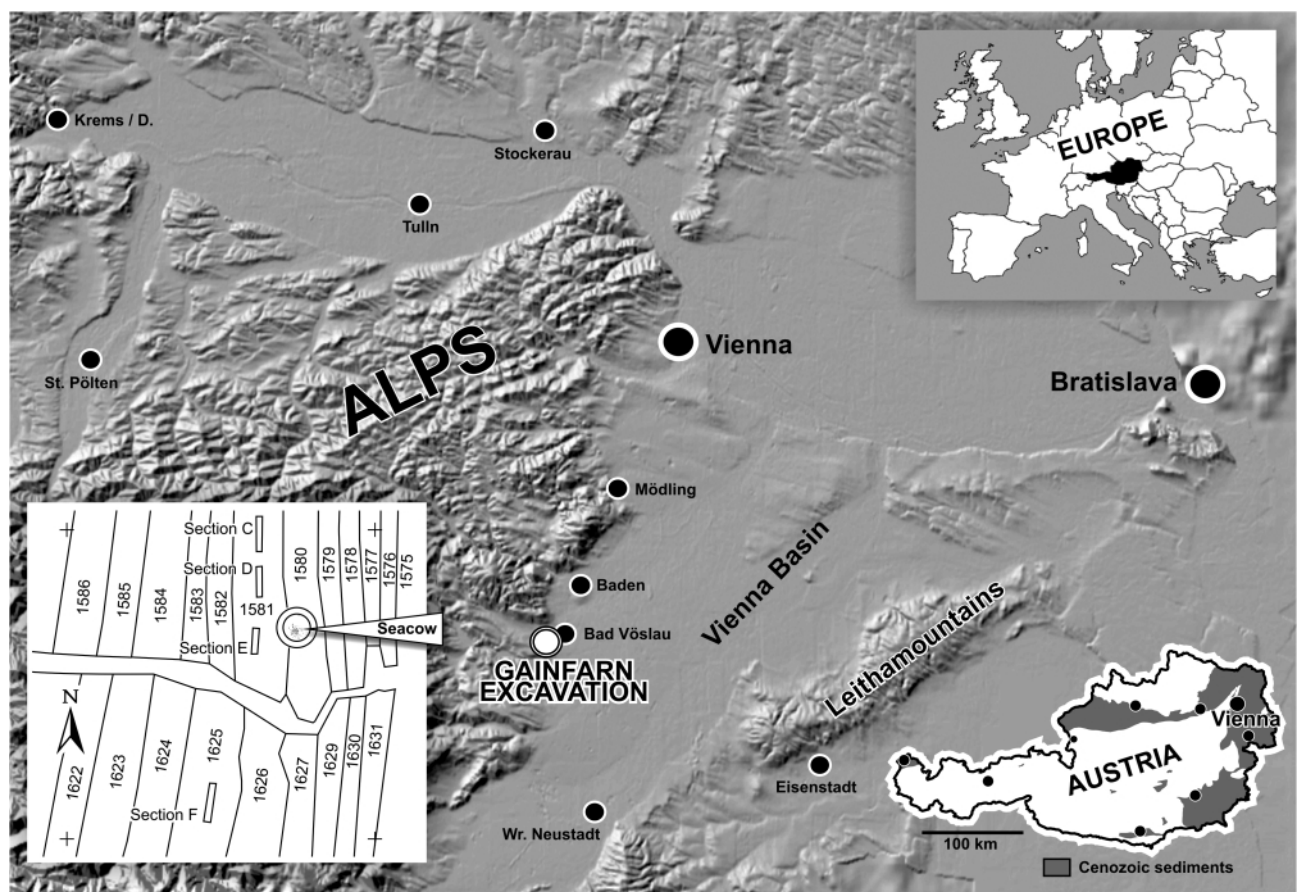

FIGURE 3: Location of the excavation area near Gainfarn (Vienna Basin) with the position of skeletal parts shown in the cadastral map. Sections C, D, E and F correspond to Zuschin et al., 2007.

01-rib
02-rib
003A-vertebra thoracic
03B-vertebra thoracic
04-?
05-neural arch
06-neural arch
07-vertebra cervical
08-vertebra cervical neural arch
    fragment [glued to 7]
09-vertebra thoracic
10-innominate R
11-?femur R
12-transverse process lumbar?
13-humerus R
14-squamosal L
15-radius-ulna R
16-tooth m3 L
17-bone indet.
18-tooth M1 R
19-vertebra thoracic
20-humerus L
21-?
22-rib
23-jugal L
24-scapula L
25-scapula R
26-rib?
27-rib
28-rib
29-rib
30-rib
31 -vertebra
32-?
33 -rib
34-rib
35-rib
36-rib?
37-mandibles L & R,
    vertebrae cervical &
    thoracic, ribs, etc.
38-vertebra cervical 2 (axis)
39-manubrium, rib L1
40-rib
41-?
42-vertebra thoracic
43-rib
44-rib
45-rib?
46-rib
47-rib
48-rib
49-rib
50-rib
51-rib
52-rib
53-rib
54-vertebra thoracic
55-rib R3?
56-neural arch
57-vertebra
    thoracic;
    3 rib sections
58-rib R
59-rib L
60-vertebra
61-rib
62-rib
63-rib
64-xiphisternum
65-rib
66-rib
67-rib
68-rib
69-vertebra thoracic
70-vertebra

71-rib L
72-neural arch
73-transverse
    process lumbar?
74-rib?
75-?
76-neural spine
77-vertebra caudal
78-vertebra sacral
79-?
80-neural arch
81-vertebra caudal
82-vertebra caudal
83-vertebra caudal
84-vertebra caudal
85-bone fragments + S12
86-vertebra thoracic
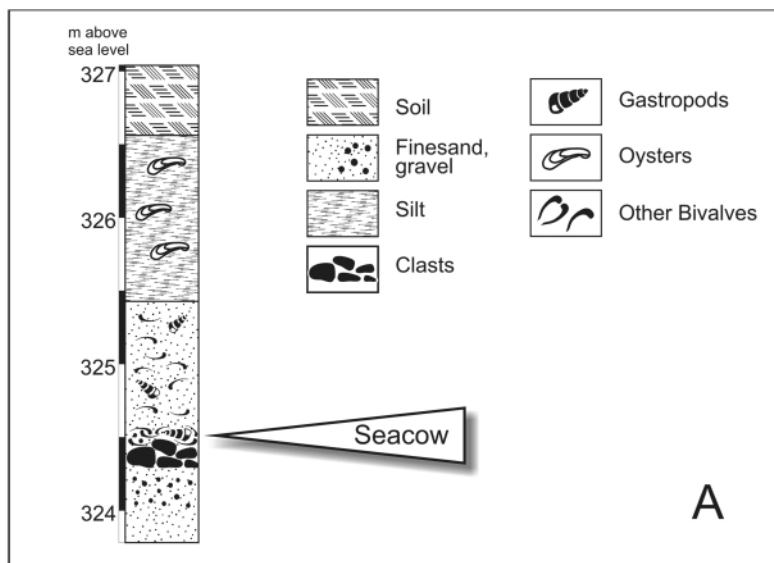87-vertebra lumbar
88-braincase
89 -squamosal R

Figure 4: A: Sedimentary profile with position of the seacow skeleton (STMBV/Met/0001) on top of a clast layer. B: Distribution of associated skeletal parts deposited in a supine position.

could also explain the generally disarticulated or dissociated occurrence of vertebrate remains.

3.1.4 Gainfarn, Lower Austria

Excavation area in farmland on the north slope of the "Veitinger Gebirge" south of the village of Gainfarn; 16°11´E, 47°56.72´N (Fig. 1, #5)

(Baden Group, late Middle Badenian)

Seven trenches were excavated in the farmland about 1.3 km south of the village of Gainfarn (Fig. 3) during a university field course in the year 2000. The purpose was the study of fine-scale palaeocommunity dynamics (Zuschin et al., 2007). The first evidence of fossil seacows in Gainfarn was a scapula (IPUW 1007) found in section D approximately 321 meters above sea level.

In 2006 the private collector Gerhard Wanzenböck from Gainfarn made an important seacow discovery. The subsequent scientific excavation by the Department of Palaeontology of the University of Vienna yielded an associated but disarticulated, rather complete skeleton of a mature seacow positio-

ned on top of a clast layer (sampling level E2 in Zuschin et al., 2007) at around 326 meters above sea level (Figs. 4, 5). The stratigraphic position of the seacow layer is late Langhian (late Middle Badenian). The sequence stratigraphic framework of the section is made up of three fully marine depositional units, which consist of siliciclastic, pelitic, and sandy to gravelly shallow-water deposits. The marine benthic faunas in this succession primarily occur as autochthonous and storm-influenced, level-bottom assemblages (Zuschin et al., 2007).

The skeleton (STMBV/Met/0001, described below) was found in supine position, dispersed over an area of more than 16 m². Cervical vertebrae, a great number of thoracic vertebrae, the sacral vertebra and some caudal vertebrae, most of the ribs, fragments of sternum and shoulder blades, both humeri, both forearms, pelvis, femur, and the mandibles were located within this bone cluster. The isolated skull was found at a distance of around 4 meters from the center of the bone accumulation (Fig. 4B).

The skeleton is on exhibition in the Museum of Bad Vöslau.

3.1.5 Garschönthal = Garschenthal

(= Úvaly, Czech Republic), 4 km W of Feldsberg (= Valtice, Czech Republic)

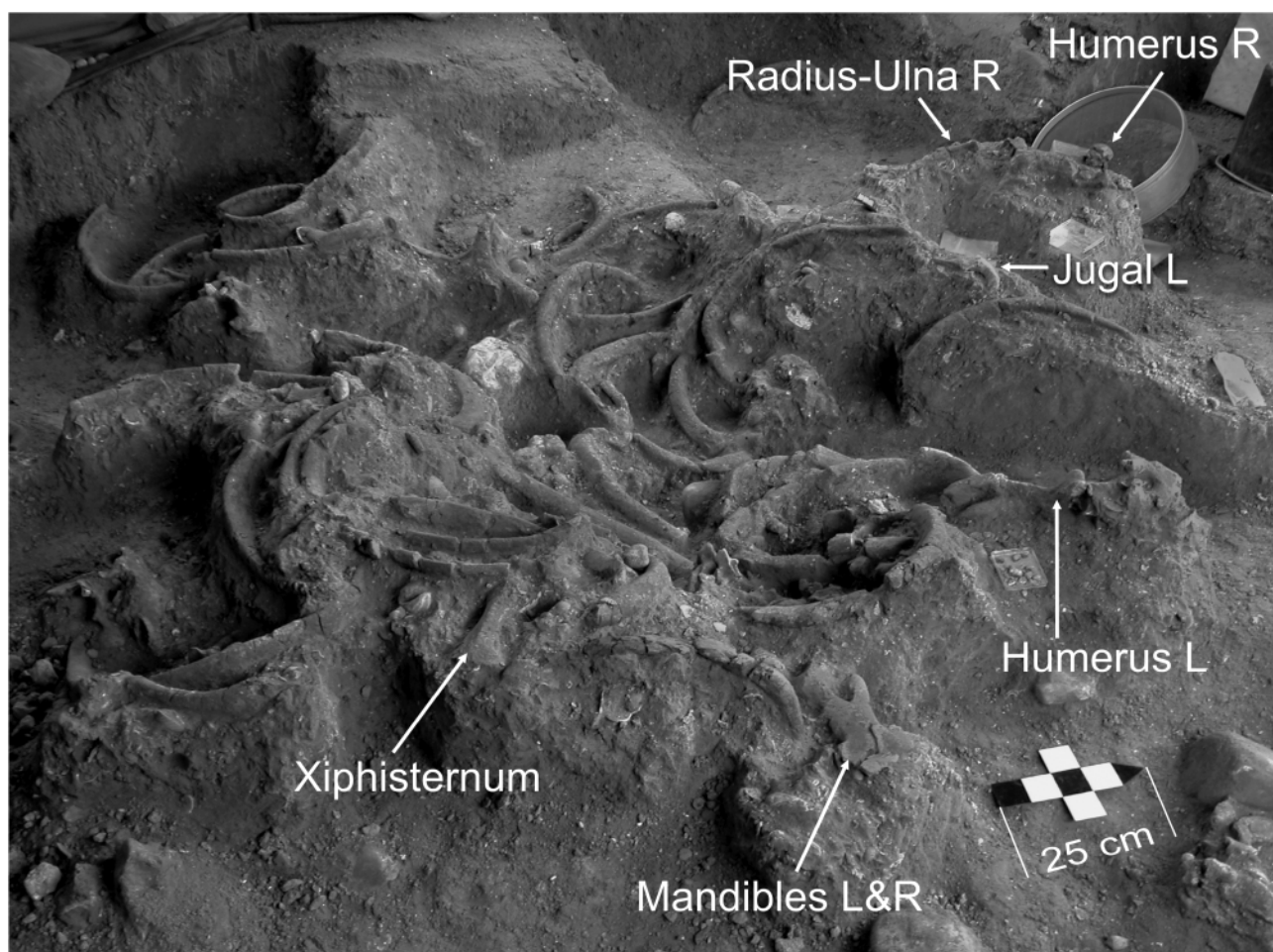Quarry; ?16°40.832′E, 48°44.837′N (Fig. 1, #6)

Figure 5: View of seacow skeleton (Gainfarn specimen, STMBV/Met/0001) in the course of excavation.

(Baden Group, Leitha limestone, late Badenian)

Moritz Hörnes (1848) mentions fossils collected by Joseph Poppelack (architect of Prince Liechtenstein in Feldsberg) from the Leitha limestone of Garschenthal (between Feldsberg and Steinabrunn): "A tooth of *Halianassa collinii*, Meyer (remains of which have hitherto been found only in the tertiary sand of Linz and in the millstone-molasse of Wallsee), teeth of *Oxyrhina xyphodon*, Ag., *O. desorii*, Ag., *Galeus aduncus*, Ag., *Lamna elegans*, Ag. and *Myliobates haidingeri*, Münster".

Several quarries in the Leitha limestone still are recognizable in a N-S oriented low mountain ridge now situated at the Austria-Czech border (Veitsberg). These localities lie more or less halfway between Steinebrunn (= Steinabrunn) and Garschenthal (= Garschönthal = Úvaly). The exact locality of the *Metaxytherium petersi* tooth mentioned by Abel (1904): "The k.k. Naturhistorische Hofmuseum in Vienna has in its possession an anterior left molar from the lower jaw of *Metaxytherium* from Garschenthal near Feldsberg in Lower Austria", cannot be determined.

3.1.6 Hainburg an der Donau, Lower Austria

Former sandpit; 16° 56.685´E, 48° 8.509´N (Fig. 1, #7)

(Baden Group, late Badenian).

A nearly complete seacow skeleton lacking the skull was found at the end of the 19th century in a quarry close to the "Kadettenschule" of Hainburg. Stache (1867) described the section of the quarry to the west of the castle hill of Hainburg. The skeleton was stored in the "k.k. Geologischen Reichsanstalt" (Survey) and destroyed to a large extent by bombing in World War II. It is still possible to determine the location of the quarry despite the houses built in its area (houses Steinbruchweg 6 and 12, southwest of the Schlossberg). It is also possible to recognize Stache´s description in the field, with sands and sandstones at the base of the section followed by coarser conglomeratic sandstones and the rock face composed of quartz conglomerate behind the grave of Juliana von Schickler (Stache's "Grab der Engländerin"). The locality of the seacow may be slightly below the lowermost outcropping sandstone layers.

The skeleton was found embedded supine in a sandstone layer with its vertebral column, ribs and most of the other bones sticking up into the overlying layer of loose sand. The skull was possibly lost during work in the quarry, or isolated by taphonomic processes before deposition of the skeleton (Hauer, 1867; Stache, 1867; Abel, 1904). It became the holotype of *Metaxytherium petersi* Abel, 1904.

3.1.7 Lindabrunn, Lower Austria

Quarries in conglomerate; 16°9.873´E, 47°54.895´N (Fig. 1, #11)

(Baden Group, Lindabrunn conglomerate, late Badenian)

Two quarries located southwest of the village of Enzesfeld at the western margin of the southern Vienna Basin show two coarsening-upward sequences containing silty arenites to coarse-grained conglomerates (Rabeder, 2001).

Sedimentary structures as well as biofacies and lithofacies point to a transition from marine-dominated environments in the lower part of the outcrops to brackish and fluviatile environments in the upper part. The Lindabrunn Conglomerate can be described as a fan delta with delta plain, delta front and prodelta. The sandy parts of the outcrops contain foraminifera, bivalves, spines of sea urchins and trace fossils (*Ophiomorpha*); the conglomerates contain tusks of proboscideans and bones of seacows (*Metaxytherium*).

3.1.8 Mannersdorf, Lower Austria

Quarries; 16°36.639´E, 47°58.085´N (Fig. 1, #13)

(Baden Group, Leitha limestone, late Middle Badenian).

A recently published paper (Wiedl et al., 2012) on the Mannersdorf quarries at the northeastern edge of the Leitha Mountains (Lower Austria) concentrates on the tectonic phases of this Badenian carbonate platform in the Vienna Basin. At the beginning stands a marine transgression with the development of a coastal slope scree and subsequent prograding of a Gilbert-type fan delta, overlain by very heterogeneous corallinacean limestones. Corallinacean limestones indicate shallow-water environments (i.e., seagrass meadows).

Other parts of the quarry area show a rapid facies change from relatively deeper environments (i.e., indicated by the abundance of the bivalve *Pholadomya* in-situ) to shallow waters (indicated by corals). Corals are generally rare in the limestones of the Mannersdorf quarries, which represent mostly deeper environments with conspicuous differences in faunal associations.

3.1.9 Müllendorf, Burgenland, Austria

(till 1921 Szárazvám, Hungary)

Chalk quarry; 16°27.175´E, 47°51.511´N (Fig. 1, #14)

(Baden Group, Leitha limestone, late Middle Badenian)

Several quarries at the western margin of the Leitha Mountains (Fig.1, #14) exploited Leitha limestone since around 1870. In the beginning the quarries produced stones, later up to 10 quarries produced quicklime and chalk and covered an extensive area (Tollmann, 1955). The origin of the chalk is weathered Leitha limestone with destruction of fossils to a large extent (Dullo, 1983). Digging of the soft chalk is now done by strip mining; observation of vertical successions is therefore difficult (Piller and Vávra, 1991). Well-preserved oysters and sea urchins as well as strongly weathered corals (*Tarbellastrea reussiana* with diameters of up to 1 meter) are very common. The corals were bored by bivalves such as *Lithophaga* and *Gastrochaena* and by barnacles (*Pyrgoma costatum* [Abel, 1928]).

3.1.10 Steinabrunn (=Steinebrunn), Lower Austria

Quarries; 16°40.705´E, 48°44.821´N (Fig. 1, #18)

(Baden Group, Leitha limestone, late Badenian)

Several quarries in the Leitha limestone in the N-S oriented low mountain ridge already mentioned in the paragraph on

Garschenthal (= Garschönthal = Úvaly). Now they are situated at the Austria-Czech border (Veitsberg). Fragments of red algae, bryozoans and echinoderms are the main components of this biodetritic packstone to grainstone.

3.1.11 Vienna, Ottakring, Hernals, Dornbach

Wolf sandpit, Baumann sandpit, ?Kipflingstrasse sandpit (Fig. 1, #19)

(Baden Group, ?Late Middle Badenian)

The k.k. Naturhistorische Hofmuseum excavated 12 vertebrae, 32 ribs, and the sternum of an adult "*Halitherium*" in the Josef Wolf sandpit west of the Dornbacher Strasse (Hauer, 1886: 28). In the neighboring sandpit owned by the jurist Dr. Moritz Baumann, ribs, vertebrae and a right mandible of a juvenile seacow were excavated in the same year from a sand layer higher in position than the Wolf specimen. Both skeletons lacked skulls and limbs (Hauer, 1886: 28). Some confusion concerning these skeletons was introduced by Pia and Sickenberg (1934), who assigned the number PS 3350 to the mandible but mistakenly attributed it to the adult skeleton including the sternum (PS 3367). PS 3350 should have been associated with the immature skeleton PS 3368.

3.1.12 Vienna, Kalksburg

Quarries in Leitha conglomerate and breccia. ?16°14.888´E, 48°8.287´N (Fig. 1, #20)

(Baden Group, ?late Badenian)

Kalksburg was formerly an independent village, but in 1938 it was integrated into Vienna. It belongs now to the 23rd district at the southwestern margin of Vienna (Liesing).

Fuchs (1869) mentions a quarry east of Kalksburg, possibly quarry 1 (= Steinbruch 1 in Karrer, 1877) with "Leytha-Conglomerat" (ca. 300 meters east from the parish church in Kalksburg). The quarry had a thickness of around 13 meters (= 42 Fuss) and from base to top was composed of coarse and fine-grained conglomerates, fine sand with *Teredo* and plant fossils, sandstone, hard conglomerate with molluscs and clayey sand. The author lists the fossil content in a table with the categories echinoderms, bivalves, gastropods, foraminifers and "varia" which includes also bones of seacows ("Knochenreste von *Halitherium*"). Already Karrer (1877) notes abandonment of the quarry due to construction of houses nearby.

Abel (1904) mentions seacow remains from Kalksburg discovered by quarry workers in 1896. Probably they came from another quarry around 80 meters further to the east (Quarry 2 in Karrer, 1877). Regrettably, only a humerus and a fragment of the forearm reached the University collection.

3.2 Eisenstadt-Sopron Basin

3.2.1 St. Margarethen, Burgenland, Austria

Quarries; 16°38.084´E, 47°48.194´N (Fig. 1, #23)

(Baden Group, Leitha limestone, late Badenian)

The location of the quarry named "Steinbruch St. Margare-

then" is not well defined. The coordinates given above describe the center of a vast quarry area between St. Margarethen and the town of Rust, exploited since the first century AD by the Romans. Sickenberg (1927, 1928) describes remains of a seacow found by quarrymen after blasting in the St. Margarethen quarry. No exact information on the position of the discovery or the section is given. The sediment, characterized as calcareous sandstone with a matrix of fragmented calcareous red algae ("Lithothamnienknollen"), contains fragments of oysters, pectinids, and shells of sea urchins. Only cavities and endocasts indicate the existence of aragonitic shells of bivalves like *Glycymeris* and several gastropods. The color of the sediment varies from white to yellowish and brownish near skeletal remains.

Sickenberg restored and studied a relatively complete skeleton after extracting the bones from eight hard calcareous sandstone blocks, which were moved to the Burgenländisches Landesmuseum in Eisenstadt. He found the nearly complete skull (unfortunately the occipital region was damaged), a fragment of the atlas, parts of several other vertebrae, many rib fragments, the left shoulder blade, and other bone fragments.

A braincase (BLLM 32815) was mentioned by Bianucci et al. (2008) as *Metaxytherium* sp. ("BLLM 22816") from Mannersdorf. However, this provenance is apparently incorrect: it is now believed to have come from St. Margarethen, but no other details of its discovery are available. Its gray color differs from that of Sickenberg's specimen (BLLM 32816), which is yellow-brown, indicating a different locality in the St. Margarethen complex. The sandy matrix of BLLM 32815 did not yield any microfossils.

3.2.2 Marz, Burgenland, Austria

(= Márczfalva–Péherkő-bánya, Sopron County, Hungary). Brickyard; 16°26.148´E, 47°43.2´N (Fig. 1, #24)

(Baden Group, late Badenian)

This locality yielded a partial skeleton of a *Metaxytherium* (Schréter, 1917), of which only limb bones and a tooth now remain.

3.2.3 Walbersdorf, Burgenland, Austria

Brickyard; 16° 25.40´E, 47° 44.34´N (Fig. 1, #25)

(Baden Group, late Badenian)

3.3 Styrian Basin

3.3.1 Friedberg, Styria, Austria

Hochstraßtunnel; from 16°3.494´E, 47°25.652´N to 16°3.916´E, 47°25.675´N (Fig. 1, #26)

(Tauchen Formation, Karpatian, ?early to Middle Badenian)

During construction of the "Hochstrasstunnel" south of Friedberg (NE Styria), J. Winkler did geological studies between 1924 and 1925 (Winkler, 1927). He reports a clayey bone layer uncovered during tunneling for the railway, which contained marine mammals together with marine bivalves indicating shallow marine deposition. Ehrenberg (1927) identified remains of

rhinoceros, stag, leopard and seacow (*Metaxytherium*).

Recent environmental interpretations of deltaic environments in the Bay of Friedberg-Pinkafeld (Nebert, 1985) do not conflict with the old descriptions.

3.3.2 Retznei, Styria, Austria

Quarry of cement plant; 15°33.532´E, 46°44.388´N (Fig. 1, #27) (Baden Group, Weissenegg Formation, Lower Lagenidae Zone, early Middle Badenian)

The Lafarge cement quarry of Retznei (southern Styria) comprises Upper Karpatian and Lower Badenian sediments. Only a small 4 m-high outcrop in the middle part of the quarry exhibits the erosive top of the Karpatian overlain by Badenian limestones. The Karpatian sediments ("*Steirischer Schlier*") consist of dark-gray silty marls with sparse pebbles ("*Geröll-mergel*") from the crystalline basement (Spezzaferri et al., 2002). It contains some mollusc and echinoid debris, and a rich foraminiferal and ostracod fauna. Another pebble layer, containing also large clasts bored by bivalves, forms the base of a huge carbonate buildup.

This buildup starts in the old quarry (cf. Friebe, 1988, 1990) with a small coral reef and extends into corallinacean limestones of the Weissenegg Formation (Leithakalk). Towards the southeast the limestones show a basinward transition into reworked material of the slope facies. At the top of the buildup, marly sands with tuffitic intercalations terminate the carbonate sedimentation.

Several meters below the tuffitic layer (14.39 ± 0.12 Ma, Handler et al., 2006), a skull roof of a seacow with frontals and supraoccipital was found in early Middle Badenian sediments by the private collector Gerhard Wanzenböck (collection stored in Gainfarn).

4. Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Order SIRENIA Illiger, 1811
Family DUGONGIDAE Gray, 1821
Subfamily HALITHERIINAE (Carus, 1868) Abel, 1913
Genus *Metaxytherium* Christol, 1840

Metaxytherium Christol, 1840, L'Institut Vol. 8, Sect. 1, No. 352: 323. [Type, by subsequent designation (Depéret and Roman, 1920): *Metaxytherium cuvieri* Christol (= *Hippopotamus medius* Desmarest).

Thalattosiren Sickenberg, 1928, Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 101: 293. [Type, by monotypy: *Metaxytherium petersi* Abel].

For other synonyms, see Domning (1996, 2010).

Emended Diagnosis. – A paraphyletic genus of dugongids that differs from most other halitheriines by possession of the following apomorphies: permanent premolars 1-4 lost [c. 157 (2)]; supraorbital process of frontal reduced and dorsoventrally thickened [c. 36(1)]; posterior part of zygomatic-orbital bridge of maxilla usually elevated >1 cm above alveolar margin [c. 11(1)]; nasals usually separated in midline [c. 31(1)];

supraoccipital wider ventrally than dorsally; exoccipitals usually not meeting in a midline suture above foramen magnum [c. 66(1)]; and ventral border of horizontal ramus of mandible strongly concave [c. 122(3)]; differs from hydrodamalines by lack of the following apomorphies: processus retroversus of squamosal uninflected [c. 77(2)]; lacrimal reduced [c. 91(2)]; ventral border of horizontal ramus of mandible moderately concave [c. 122(2)]; horizontal ramus of mandible slender [c. 128(0)]; first upper incisor vestigial or absent [c. 139(1)] (J. Vélez-Juarbe and D. P. Domning, in preparation).

Metaxytherium medium (Desmarest, 1822) Hooijer, 1952
Hippopotamus medius Desmarest, 1822, Mammalogie: 388.
M[etaxytherium] Cuvierii (Christol) Christol in Blainville, 1844, Ostéogr., Genre Manatus: 130.
Halitherium cordieri Christol, sensu Peters, 1867, Jb. Geol. Reichsanst. Wien 17(2): 309.
Metaxytherium petersi Abel, 1904, Abh. K.-K. Geol. Reichsanst. Wien 19(2): 15, 107, June 1904. [Holotype: GBAW Inv. Nr. 2006/18/1-6, skeleton lacking skull; described by Peters (1867: pl. 7, figs. 4-8) and Abel (1904: figs. 3, 4, 6, 7, 10, 11, 12; pl. 2, fig. 6; pl. 7, fig. 2), termed "Typusexemplar" by Pia and Sickenberg (1934: 403, no. 3331); probably destroyed in World War II except for the distal epiphysis of a radius, two carpals, one metacarpal, one phalanx, the left innominate, and a cervical vertebra (GBAW Inv. Nr. 2006/18/1-6, 2350-2355). The radial epiphysis (2354) was not mentioned by Peters (1867), but was briefly described by Abel (1904:122). Abel (1904:133) explained that several elements of the skeleton, including the body of the axis, another cervical vertebra (C3?), and a number of chevron bones, were prepared subsequent to Peters' 1867 publication, although the C3? actually appears in Peters' (1867) plate 7, fig. 4. Of these, only the C3? (2355) survives today. Bearing the same number as this vertebra (2355) is a skullcap fragment, mistakenly associated with this specimen; it is actually from Neudorf an der March and was described by Abel (1904:107-108). Type locality: Hainburg an der Donau, Lower Austria; "Zweite Mediterranstufe"; Baden Group, *Spiroplectammina* Zone [pers. communication, G. Wessely]; Late Badenian.] NEW SYNONYMY.
Thalattosiren petersi (Abel) Sickenberg, 1928, Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 101: 293.
Metaxytherium medium (Desmarest) Hooijer, 1952, Osiris 10: 114.
Metaxytherium catalaunicum Pilleri in Pilleri, Biosca, and Via, 1989, Tert. Sir. Catalonia: 68. [Holotype: Mus. Vilafranca del Penedès (Barcelona) no. 1210, skull, mandible, and postcranial remains. Type locality: Olèrdola, Catalonia, Spain; upper Burdigalian-Langhian.] Synonymized by Domning, 1996, Smithson. Contr. Paleobiol. 80: 387.
For other synonyms, see Abel (1904: 13-14) and Domning (1996, 2010).
Emended Diagnosis. – *Metaxytherium* differing from *M. krahuletzi* by ventral extremity of jugal usually lying fully ventral to orbit [c. 85(2)]; differs from later European species (*M. serresii,*
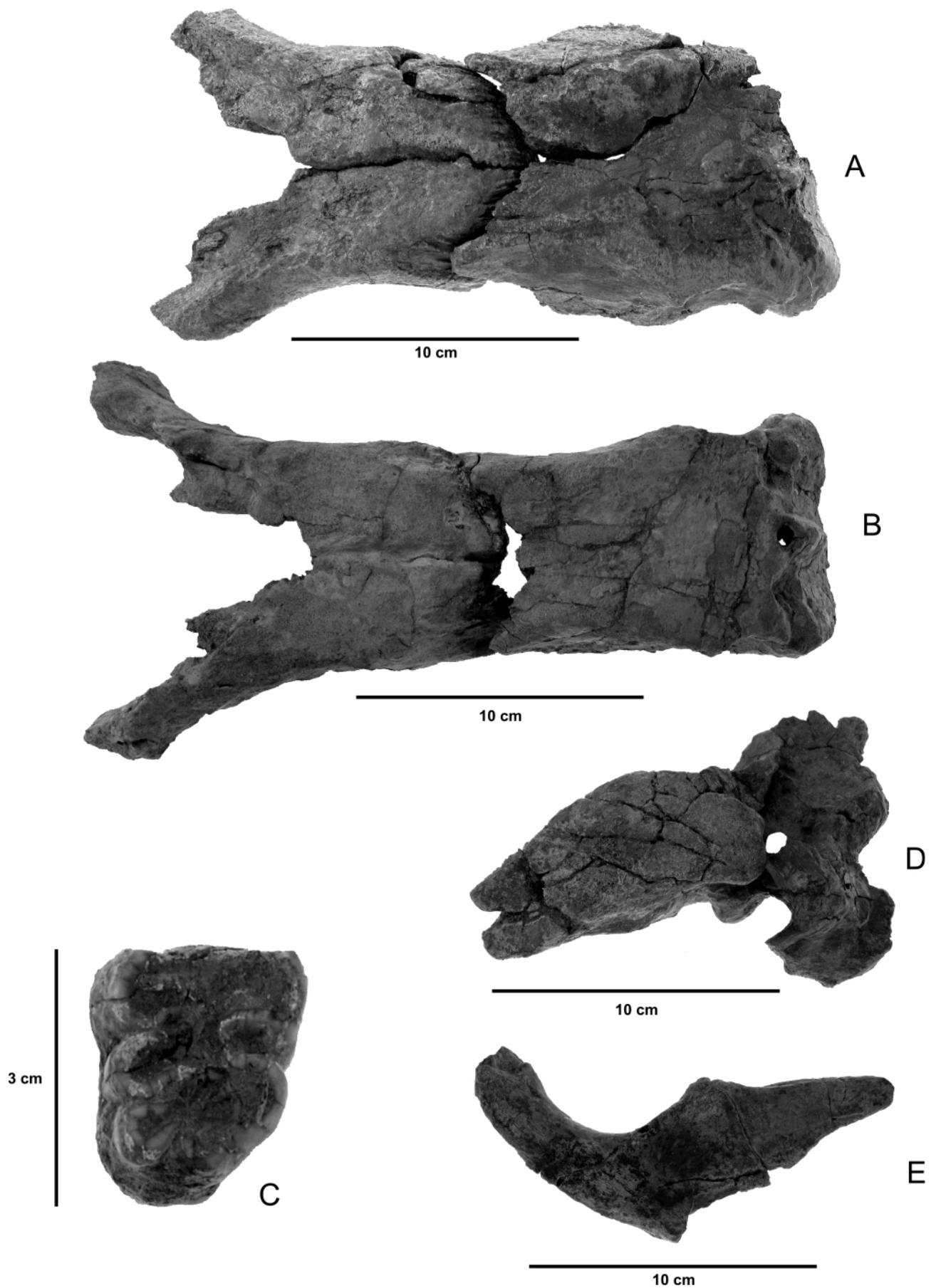
Figure 6: *Metaxytherium medium*. A: Braincase (frontals, nasals, parietal, supraoccipital) from the Gainfarn specimen (STMBV/Met/0001), dorsal view (Fig. 4, #88). B: Braincase (frontals, parietal, supraoccipital) from the Retznei specimen, dorsal view. C: left m3 of STMBV/Met/0001, occlusal view (Fig. 4, #16). D: Left squamosal of STMBV/Met/0001, lateral view (Fig. 4, #14). E: Left jugal of STMBV/Met/0001, lateral view (Fig. 4, #23).

ab	Height of jugal below orbit
AH	Length of premaxillary symphysis
BI	Rear of occipital condyles to anterior end of interfrontal suture
CC'	Zygomatic breadth
cc'	Breadth across exoccipitals
de	Top of supraoccipital to ventral sides of occipital condyles
F	Length of frontals, level of tips of supraorbital processes to frontoparietal suture
FF'	Breadth across supraorbital processes
ff'	Breadth across occipital condyles
GG'	Breadth of cranium at frontoparietal suture
gg'	Width of foramen magnum
HI	Length of mesorostral fossa
hi	Height of foramen magnum
KL	Maximum height of rostrum
MM'	Posterior breadth of rostral masticating surface
no	Anteroposterior length of zygomatic-orbital bridge of maxilla
OP	Length of zygomatic process of squamosal
OT	Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen
P	Length of parietals, frontoparietal suture to rear of external occipital protuberance
QR	Anteroposterior length of root of zygomatic process of squamosal
rr'	Maximum width between labial edges of left and right alveoli
ss'	Breadth across sigmoid ridges of squamosals
ST	Length of cranial portion of squamosal
T	Dorsoventral thickness of zygomatic-orbital bridge
tt'	Anterior breadth of rostral masticating surface
UV	Height of posterior part of cranial portion of squamosal
WX	Dorsoventral breadth of zygomatic process
yy'	Maximum width between pterygoid processes
YZ	Length of jugal
LFr	Length of frontals in midline
LSR	Length of skull roof from anterior end of interfrontal suture to posterior side of external occipital protuberance
LPt	Dorsoventral length of pterygoid process, measured from roof of internal nares
WPI	Minimum width of palate just anterior to tooth row
HSo	Height of supraoccipital
WSo	Width of supraoccipital
RD	Deflection of masticating surface of rostrum from occlusal plane (degrees)

Dimension	Müllendorf (juvenile)	MAFI unnum. [Fazekasboda] (juvenile)	NHMW 2007z0106/ 0001 (juvenile)	BLLM 32816 (juvenile)	BLLM 32815 (adult)	Retznei (adult)	STMBV Met/0001 [Gainfarn] (old adult)
ab	--	--	--	44	--	--	--
AH	--	--	72+	108+	--	--	--
BI	--	--	--	---	206+	--	--
CC'	--	--	--	187	215	--	--
cc'	--	--	--	--	144	--	--
de	--	--	--	--	121	--	--
F	--	--	--	120e	--	145e	--
FF'	--	--	105	130	100+	145e	--
ff'	--	--	--	--	107	--	--
GG'	55	72e	75	81	68e	70	76
gg'	--	--	--	--	49	--	--
HI	--	--	108e	117e	--	--	--
hi	--	--	--	--	45	--	--
JJ'	--	--	49e	56	--	--	--
KL	--	--	50	68	--	--	--
MM'	--	--	46	46e	--	--	--
no	--	--	23+	--	--	--	32
OP	--	74	--	109e	118+	--	--
OT	--	--	--	--	156+	--	--
P	75	76	--	90	100	105	94
QR	--	38	--	50	62	--	46e
rr'	--	--	--	70	--	--	--
ss'	--	--	--	--	193	--	--
ST	--	--	--	--	101	--	104
T	--	--	7e	9e	--	--	13
tt'	--	--	30e	--	--	--	--
UV	--	--	--	--	96	--	102
WX	--	30	--	41	42	--	49
yy'	--	--	48e	65e	--	--	55e
YZ	--	--	--	137e	--	--	149+
LFr	47e	--	--	64	63+	80e	74
LSR	--	--	--	153*	160+	190e	170e
LPt	--	--	40e	40e	--	--	62+
WPI	--	--	36e	16e	--	--	--
HSo	--	44	--	53	56	56	59
WSo	71	83	--	86	96	86+	90e
RD	--	--	48+	55e	--	--	--

* 165 mm from anterior end of internasal suture.

M. subapenninum) by having a tusk alveolus much less than half the length of the premaxillary symphysis [c. 140(0)].

Holotype. – MNHN Fs 2706, partial left mandible with M2-3 and roots of M1 (the "Moyen hippopotame" of Cuvier, 1821).

Type Locality. – Saint-Michel en Chaisine, Maine-et-Loire, France.

Formation. – Calcareous tuff.

Age. – Middle or Late Miocene (Serravallian-Tortonian).

Range. – Europe and probably North Africa, with reports from Portugal, Spain, France, The Netherlands, Italy, Austria, Slovakia, Hungary, and Mediterranean islands including Sardinia and Crete. Middle to Late Miocene; Langhian to late (but not latest) Tortonian, approximately MN 5 to MN 11, since only *M. serresii* is recorded from MN 12 (Carone and Domning, 2007).

Newly Referred Specimens. – The following previously-undescribed specimens from the Central Parathys/ Vienna Basin are here referred to *M. medium*. The other specimens listed in Table 1 (many of them rib or other fragments not individually diagnostic at the specific or even generic level) may also be presumed to represent this species, in the absence of evidence that another sirenian species is present in these deposits.

Baden, Rauchstallbrunngraben quarry, Lower Austria: NHMW 2007z0106/ 0001, juvenile skull.

Gainfarn, Lower Austria: STMBV/Met/ 0001/#1 - #89, partial skeleton.

St. Margarethen (?), Burgenland, Austria: BLLM 32815, braincase. Mentioned by Bianucci et al. (2008) as *Metaxytherium* sp. ("BLLM 22816"), supposedly from Mannersdorf.

TABLE 2: Measurements (in mm) of skulls of Badenian *Metaxytherium medium* from the Central Parathys. Measurements designated by letters are modified from Domning (1988) and earlier works. e = estimated; nm = not measured; + = measurement on incomplete element.

Müllendorf, Burgenland, Austria: Wanzenböck collection, juvenile skull fragments and partial skeleton.

Retznei, Styria: Wanzenböck collection, adult skull roof.

Fazekasboda, Hungary: MAFI unnum., juvenile partial skull, right mandible, left DP4-M1, right dp4-m1, partial atlas, 5 or more thoracic neural arches, and 10 or more ribs.

5. Description of Gainfarn Specimen

(Tables 2-3, 5-10; Figs. 6A, C-E, 7, 8)

The skeleton excavated at Gainfarn in 2006 (STMBV/Met/0001/#1-#89) is that of an old adult (m1 probably lost, m3 moderately to heavily worn) and, judging from the morphology of the pelvis, probably a female. Most parts of the skull, mandibles, and appendicular elements (excepting the manus) are represented, together with at least some vertebrae from each region of the column and many ribs. Also collected at the same site in 2000, a few meters away but at a lower horizon, was an isolated left scapula (Table 7; Zuschin et al., 2007).

The following descriptions also mention for convenience some contrasts with the most complete skull from this region, the juvenile specimen BLLM 32816 (Sickenberg, 1928). For other labeled sketches of the cranial anatomy of *Metaxytherium* and related dugongids, see also Domning (1978:fig. 7) and Sorbi et al. (2012:figs. 5-6).

Premaxilla, Ethmoid, Vomer, Lacrimal, Palatine, Tympanic, Auditory Ossicles, Hyoid Apparatus, Carpals, Metacarpals, Phalanges
-- Not preserved.

Nasal – Large, thick, and massive, bordering the retracted external nares [c. 8(1)]; set in socket in anterior margin of frontal and exposed dorsally. The posterior end of the nasal is slightly recessed below the surface of the frontal roof, causing the nasal-frontal suture to be well mar-

AB	Total length
AG	Anterior tip to front of ascending ramus
AP	Anterior tip to rear of principal mental foramen
AQ	Anterior tip to front of mandibular foramen
AS	Length of symphysis
BG	Posterior extremity to front of ascending ramus
BQ	Posterior extremity to front of mandibular foramen
DF	Distance between anterior and posterior ventral extremities
DK	Height at mandibular notch
DL	Height at condyle
EF	Height at deflection point of horizontal ramus
EU	Deflection point to rear of alveolar row
GH	Minimum anteroposterior breadth of ascending ramus
GP	Front of ascending ramus to rear of principal mental foramen
MN	Top of ventral curvature of horizontal ramus to line connecting ventral extremities
MO	Minimum dorsoventral breadth of horizontal ramus
RR'	Maximum breadth of masticating surface
SQ	Rear of symphysis to front of mandibular foramen
TU	Length of alveolar row
XX'	Minimum width between condyles
MD	Mandibular deflection (degrees)

Dimension	MAFI unnum. [Fazekasboda] (juvenile)	NHMW 1885 [PS3350] [Ottakring] (juvenile)	STMBV Met/0001 [Gainfarn] (old adult) (left)	STMBV Met/0001 [Gainfarn] (old adult) (right)
AB	--	190	260e	--
AG	--	144	--	215e
AP	51	68	--	120e
AQ	--	nm	--	135e
AS	54e	nm	--	75e
BG	62e	65	85e	--
BQ	53e	--	--	--
DF	--	100e	--	130e
DK	--	111e	--	--
DL	--	121e	--	--
EF	--	--	113e +?	--
EU	--	--	127	--
GH	--	54	74	--
GP	--	77	107	107
MN	--	21e	--	32e
MO	--	49	83	81
RR'	30e	--	--	44e
SQ	--	--	--	64e
TU	--	--	67	67e
MD	--	60e	56e	62e

Table 3: Measurements (in mm) of mandibles of Badenian *Metaxytherium medium* from the Central Paratethys. Measurements designated by letters are modified from Domning (1988) and earlier works. e = estimated; nm = not measured; + = measurement on incomplete element.

ked. Anteriorly, the surface of the nasal is transversely concave for reception of the premaxilla. The nasals are separated in the midline by a nasal incisure and (at the posterior end) by processes of the frontals [c. 31(1), 32(1)]. (In BLLM 32816 the nasals are in contact; see discussion below.) The dorsal width of the nasal cavity between the nasals is ~22 mm.

Frontal – The supraorbital processes are broken off at their bases. Orbicular apophyses are absent. A thin lamina orbitalis [c. 38(0)] forms the medial wall of the temporal fossa and the lateral wall of a large hollow, open anteriorly, whose medial wall was formed by the ethmoid. A crista intratemporalis is absent, and the ventral part of the wall of the temporal fossa is not recessed. The internasal processes are broken, but do not seem to have extended very far anteriorly between the nasals (perhaps only 1-2 cm beyond the rear end of the nasal). The frontal border surely lay well posterior to the posterior corner of the supraorbital process (though still at the level of the base of the process); thus the posterior border of the mesorostral fossa may have been incised to some extent [c. 37(1?)]. The same is true of the skull roof from Retznei (see below); and also of skulls of *M. medium* from France (Chazé-Henri specimen MNHN Fs 5001, Moncharmont Zei and Moncharmont, 1987: pl. 3, fig. 1; unpublished skull LPB 16001) and Italy (MPUN M18403, Moncharmont Zei and Moncharmont, 1987), *M. "calvertense"* (= *crataegense*) from Peru (MNHN PRU 7, Muizon and Domning, 1985), a skull fragment of *Metaxytherium* sp. from Libya (BMNH M82421; Heal, 1973), some specimens of *M. floridanum* (Domning, 1988; e.g., USNM 359670, 359748), a cf. *Metaxytherium* from Brazil (Toledo and Domning, 1991), and the holotype of *M. arctodites* (Aranda-Manteca et al., 1994). In short, this condition occurs widely, at least as a polymorphism, in Middle Miocene *Metaxytherium*, though not in earlier or later species of the genus (Domning and Pervesler, 2001; Carone and Domning, 2007; Sorbi et al., 2012). The median portion of the frontal roof is slightly convex [c. 42(0)]. The temporal crests are weakly developed. The anterior end of the fronto-parietal suture lies 3 cm behind the nasal. The intracranial surface formed by the frontals is 3 cm in length in the midline.

Parietal – The parietal roof is 24 mm thick in the anterior midline, flat anteroposteriorly, and strongly concave between thick, rounded, lyriform temporal crests separated by ~2 cm (type C of Domning, 1988; in BLLM 32816 they are of type B: upraised on the lateral edges of a markedly concave roof). The posterolateral corners of the roof are indented by the squamosals; the minimum width between these indentations is ~78 mm (74 mm in BLLM 32816). A small bump is present anterior to the external occipital protuberance. The internal occipital protuberance is distinct but blunt; the tentorium forms a straight transverse ridge; and the transverse sulcus is narrow and distinct throughout its length, with distinct but not very deep lateral pits. (In BLLM 32816 the tentorium is indistinct and the sulcus has no pits.) The bony falx cerebri is distinct as far as the fronto-parietal suture, and only slightly rounded at its anterior end. No emissary foramina are evident.

Supraoccipital – Pentagonal in outline, with rounded dorsola-

teral corners. Forms angle of ~114° with the posterior parietal roof. The external occipital protuberance rises slightly above the plane of the parietal roof; the median ridge below it is weakly developed. The nuchal crest is strongly convex anterad but indistinct at its lateral end (distinct laterally in BLLM 32816). The area of insertion for the semispinalis capitis muscle is trapezoidal, shallowly concave, and faces more dorsally than posteriorly; it extends halfway to the ventral margin of the supraoccipital, and its ventromedial edge is well defined. The lower part of the supraoccipital is strongly concave medially and convex laterally. Its lateral border is thick and rounded, sloping outward at the bottom, with only a slightly overhanging upper corner. The ratio of width to height of the supraoccipital is 1.53. The sutural surfaces for the exoccipitals do not appear to be separated in the midline, although the exoccipitals themselves are.

Exoccipital – Do not meet dorsally in a median suture [c. 66(1)]. The foramen magnum has an acute dorsal peak. The dorsolateral border of the bone is smoothly rounded [c. 70(0)] and has a flat surface, facing laterad and slightly anterad, which is broadest (18 mm) at the level of the top of the supracondylar fossa. The fossa is moderately deep [c. 67(2)].

Basioccipital – As in other dugongids, the basioccipital bears a pair of rugosities (here separated by a deep keel) for the longus capitis muscles. Its posterior slope is steeper than the anterior.

Basisphenoid – The sella turcica is shallow; the region of the tuberculum sellae bears an abraded ridge.

Presphenoid – No elevated shelf (orbitosphenoidal crest) overhangs the area of the optic chiasm, nor are distinct chiasmatic grooves present.

Orbitosphenoid – The optic foramen lies at the level of the dorsal side of the sphenorbital foramen.

Alisphenoid – The lateral side of the pterygoid process is smooth, with little sculpture.

Pterygoid – The pterygoid fossa is well developed, ~1 cm wide, extending above the level of the roof of the internal nares [c. 102(1)]. Its lateral and medial edges converge dorsally but do not have a well-defined intersection; the lateral edge forms a projecting flange at its top end, whereas the medial edge becomes indistinct. The medial edge of the fossa projects farther posteriorly than the lateral edge.

Maxilla – The alveolar portion is heavy and massive; its dorsal edge helped form the wall of the temporal fossa. The edges of the palatal surface were presumably lyriform, but the anterior portion of the bone is fragmented. No part of the intermaxillary suture remains. The zygomatic-orbital bridge is elevated only ~6 mm above the alveolar margin [c. 11(0)]. The bridge is short anteroposteriorly [c. 14(1)], with a thin anterior edge and a thick, rounded posterior edge. The infraorbital foramen is not preserved.

Squamosal – Only the left squamosal is preserved (Fig. 6D), except for the posttympanic portion of the right squamosal. Its broad and rounded posterodorsal margin reached the level of the parietal roof [c. 76(1)]. Its posterior margin is slightly not-

ched above the sigmoid ridge, and below that it has a deep mastoid indentation. The sigmoid ridge is prominent [c. 74(0)], and broad in its midsection. The external auditory meatus is ~13 mm long mediolaterally [c. 75(0)], a seemingly atavistic variation from the condition 75(1) that is usual in *Metaxytherium* but resembling one specimen of *M. krahuletzi* (Domning and Pervesler, 2001: 22). The meatus is semicircular in lateral view, about as wide anteroposteriorly as high [c. 82(1)]. The postglenoid process and postarticular fossa are well developed; the temporal condyle has an irregularly oval outline. The processus retroversus is moderately inflected [c. 77(1)], does not project below the line of suture with the jugal, and is turned in ventrally; its posterior end has distinct dorsal and ventral terminations, the dorsal one being a continuation of the zygomatic root. The zygomatic process is broader posteriorly than anteriorly; its posterodorsal edge is convex in outline (concave in BLLM 32816) and also convex laterad. Its medial side is relatively flat [c. 84(1)].

Jugal – Only the left jugal is preserved (Fig. 6E). The preorbital process is flattened [c. 88(0)], and presumably did not contact the premaxilla [c. 87(0?)]. The ventralmost point of the bone is missing, but lay approximately below the rear edge of the orbit [c. 85(1?)] (in BLLM 32816 it lies below the posterior half of the orbit). The border behind it is smooth and concave in outline. The ventral margin of the orbit does not overhang the bone's lateral surface [c. 90(0)]. There is a slightly raised postorbital process, behind which the initially broad and concave surface in contact with the squamosal tapers posteriorly. The posterior process lacks its termination, but was longer than the diameter of the orbit [c. 89(0)].

Periotic – Not fused with other bones, but set in a socket of the squamosal [c. 115(1)]. The lateral surfaces are smooth; a slight groove partly demarcates the pars temporalis from the pars mastoideus. The anteroventral notch between these two portions is broad and V-shaped. The anteromedial end of the pars temporalis is tapering. The pars mastoideus bears a slightly raised processus fonticulus that fits into the mastoid foramen. The posterolateral edge of the pars mastoideus is relatively sharp. The pars petrosa is broken.

Mandible – The left and right dentaries (Table 3; Fig. 7) were found in articulation, compressed together. The condyle and coronoid process are missing from both. The notch in the rear margin below the condyle is smooth in outline, not stepped at its lower end [c. 125(2)]. The medial side of the angle is a flat area 1.5 cm wide, lateral to which the lower end of the internal pterygoid fossa is deeply excavated. In this old adult, the coronoid arch is narrow (9 mm) dorsoventrally; the dental capsule is enclosed within the mandible [c. 127(1)] and is degenerate, indicating maturity; and the m3 alveolus is separated by 28 mm from the rear of the coronoid canal. Lateral to m3, the bone surface slopes steeply downward without formation of a shelf. The horizontal ramus is short though not very deep [c. 128(1)]. Its ventral border is strongly concave [c. 122(3)] in its posterior portion, and apparently not tangent to the angle [c. 129(1?)]; but anteriorly, this curvature diminishes and the

outline of the ramus even appears slightly convex. This, however, may partly be an artifact of abrasion on the ventral side of the symphysis, the amount of which is unclear. The posterior part of the ventral edge is sharper than the anterior part. The dorsal edge of the ramus is thin anterior to the tooth row. The single mental foramen [c. 123(1)] is proportionately larger than in other *Metaxytherium*. It extends back to the level of m1. Its anterodorsal margin is rounded rather than sharp; in this region large nutrient canals pierce the roof of the mandibular canal. Deflection of the masticating surface is abrupt, ~60°. The masticating surface is damaged but was broad [c. 121(1)]; on the right side are visible the remains of two or three circular pits ~1 cm in diameter (vestigial incisor alveoli). The edges of this surface were convex, thin, and overhanging. The symphyseal suture is unfused posteroventrally and displays weak vertical interdigitations, but is apparently ankylosed anteriorly and dorsally.

Dentition – Owing to loss of the premaxillae, nothing can be said about presence or morphology of an I1 tusk. As is normal for an old adult *Metaxytherium*, the cheek dentition is reduced to M1-3/m1-3 [c. 150(0), 151(0), 157(2), 158(0)]. Even

Tooth and Dimension	MAFI unnum. [Fazekasboda] (juvenile) (left uppers, right lowers)	BLLM 32816 (juvenile) (left)	MAFI V.10973 (subadult) (left)
DP4 L	17.8	15.3w	--
DP4 AW	14	13.7	--
DP4 PW	14.6	13	--
DP5 L	20	17e	--
DP5 AW	18.5	18.4	--
DP5 PW	17.8	15.8	--
M1 L	21.5	20e	--
M1 AW	24.2	21.8	--
M1 PW	17.1	18.2	--
M2 L	--	25e	--
M2 AW	--	22	--
M2 PW	--	nm	--
M3 L	--	--	--
M3 AW	--	--	--
M3 PW	--	--	--
dp4 L	18.6	--	9
dp4 AW	11.9	--	--
dp4 PW	13.2	--	--
dp5 L	18e	--	14
dp5 AW	16.5e	--	--
dp5 PW	16.3e	--	--
m1 L	24.4	--	20
m1 AW	16+	--	--
m1 PW	17.4	--	--
m2 L	--	--	31.8
m2 AW	--	--	24.7
m2 PW	--	--	22.9
m3 L	--	--	32.3
m3 AW	--	--	--
m3 PW	--	--	23.9

TABLE 4: Linear dimensions (in mm) of associated cheek dentitions of Badenian *Metaxytherium medium* and *Haplosiren leganyii* (holotype: MAFI V.10973) from the Central Paratethys. L = crown length; AW = anterior width; PW = posterior width; e = estimated; nm = not measured; w = dimension reduced by wear; + = measurement on damaged tooth. Measurements in parentheses refer to empty alveoli.
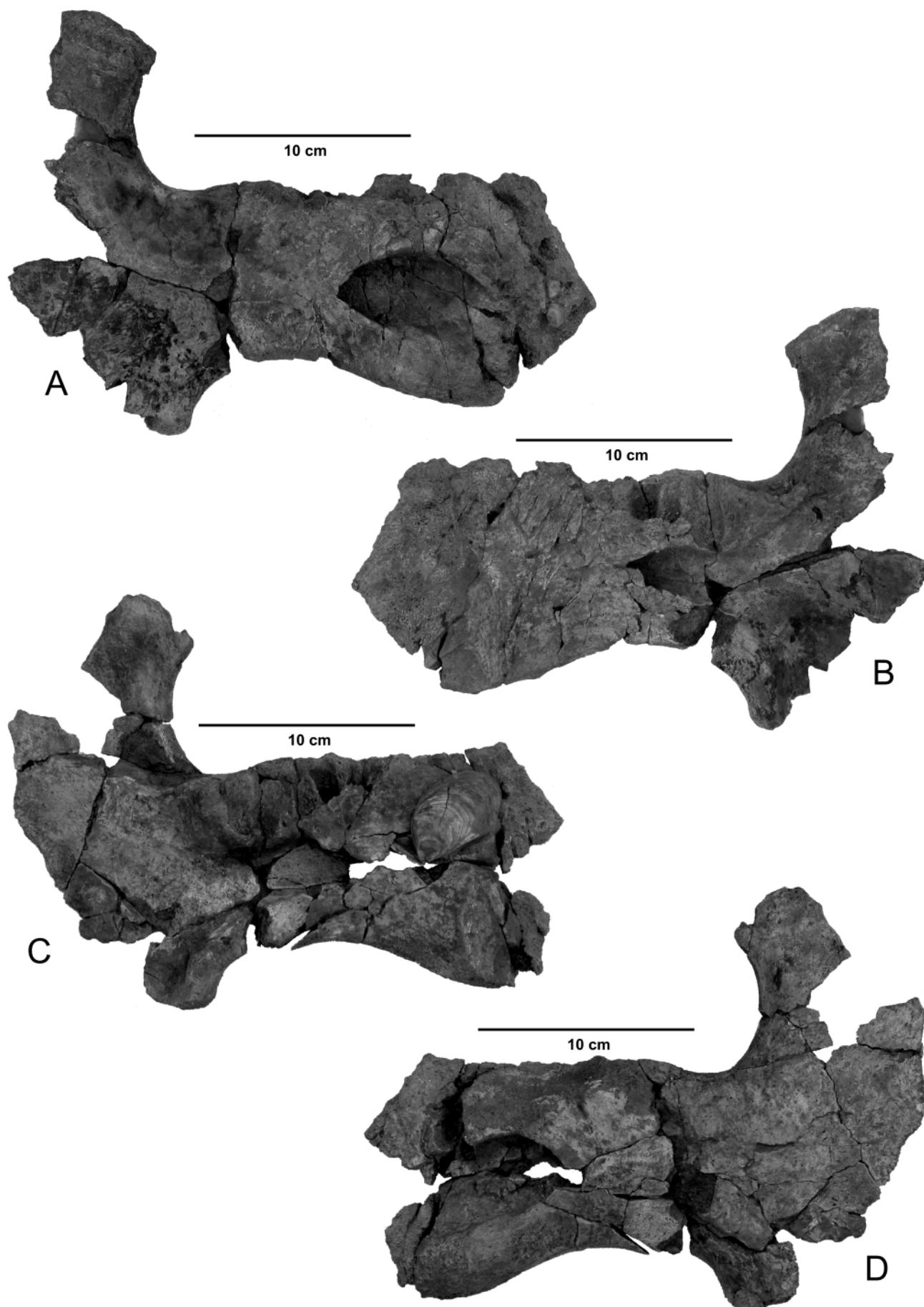
Figure 7: *Metaxytherium medium*, Gainfarn specimen (STMBV/Met/0001). A: Right mandible, lateral view (Fig. 3, #37). B: Right mandible, medial view (Fig. 3, #37). C: Left mandible, medial view (Fig. 3, #37). D: Left mandible, lateral view (Fig. 3, #37).

the left and right m1 were probably lost before death, as their alveoli are already reduced in size and were probably being resorbed. As noted above, the m3 alveolus is separated by 28 mm from the rear of the co-ronoid canal, also a sign of advanced age.

One very heavily worn upper tooth, probably the right M1, is preserved; its width is reduced by wear to 23.5 mm, and its crown length is reduced by interdental wear even more, to only 19.1 mm. Fragments of another tooth, possibly m2, are present; but the only tooth relatively well preserved is the left m3 (Table 5; Fig. 6C). The posterior root is large and triangular in cross section, in contrast to the more anteroposteriorly-

	Tooth	L	AW	PW
NHMW 2007z0106/0001 [Rauchstallbrunngraben]	Left DP5?	16.5	17.9	16.7
NHMW 2012/0156/0001 [Theben-Neudorf]	Left M2	25.9w	25.3	22.0e
IPUW unnum. [Müllendorf]	Right M2?	20.3	23.1	20
IPUW unnum. [Müllendorf]	Left m2?	22.2	--	18.8
IPUW unnum. [Neudorf/March]	Left m2?	21.4	18	17.3
NHMW 1859.I.13 [PS3363] [Garschöntal] (Abel, 1904: 110)	Left m2?	23.5	--	18.6+
NHMW 1850.XVI.21 [PS3360] [Neudorf] (Peters, 1867: pl. 7, fig. 2; Abel, 1904: pl. 1, fig. 18))	Left m2	23.3	19.5e	19.0e
NHMW 1997z0178/1983 [Neudorf]	Left m2	21.7	17.7	18.2
NHMW [PS3358] [?Wöllersdorf-Fischau] (Abel, 1904: pl. 1, fig.17)	Left m3	29.8	21.7	20
NHMW 1850.XXVI.20 [PS3361] [Mannersdorf] (Peters, 1867: pl. 7, fig. 3; Abel, 1904: pl. 1, fig. 19)	Right m3?	26.1	18.9	19.2
NHMW 1865.I.1181 [PS3362] [Neudorf] (Peters, 1867: pl. 7, fig. 1)	Right m3	31.3w	24.3	22.6
NHMW 1952/37 [Müllendorf]	Left m3	32	20.9	20.4
STMBV Met/0001 [Gainfarn]	Left m3	30.0w	24.7	21.4
MAFI Ob-3040 [Marz (Márczfalva–Péherko-bánya)]	Right m3	27.8w	21.6w	18.1w

TABLE 5: Linear dimensions (in mm) of isolated cheek teeth of Badenian *Metaxytherium medium* from the Central Paratethys. L = crown length; AW = anterior width; PW = posterior width; e = estimated; w = dimension reduced by wear; + = measurement on damaged tooth.

flattened anterior root. The occlusal surface is moderately to heavily worn; interdental wear has also removed a significant portion of the mesial surface. Three lophids were present; the large protolophid and the smaller hypolophid are reduced to lakes of dentine, connected at the midline of the crown. The large hypoconulid has only a labial lobe and a posterior central lobe still distinct; these are coalesced with the hypolophid, but probably constituted an originally Y-shaped form (cf. Domning, 1988: 412) as in many other *Metaxytherium*.

Vertebrae, Ribs – Show no apparent differences from *M. krahuletzi.*

Sternum – Of the three separate elements observed in young *Metaxytherium krahuletzi* (and all fused in older ones), the anterior two are here fused, with the xiphisternum remaining separate (Table 6; Fig. 8A). The manubrium + central element are slightly asymmetrical, and concave dorsally. The manubrium lacks its anterior tip; the spatulate anterior process is not expanded, but is comparable in breadth to the body of the sternum. On the ventral side the manubrium has a low keel. The anterior pair of rib attachments are prominent; the second pair are asymmetrically placed, being located more anteriorly on the left side. The third and last pair are again symmetrical and coincided with the joint between the central element and xiphisternum. Behind this, the xiphisternum narrows slightly, then broadens markedly, thins, and bifurcates, with a narrow median notch separating the left and right cartilage attachments along the nearly straight posterior margin. The xiphisternum is more convex on the presumed ventral side. On the whole, this sternum does not differ significantly from that of *M. krahuletzi.*

Scapula (Table 7) – The supraspinous fossa is broad, and its anterior edge is turned somewhat laterally. The spine is high and overhangs posteriorly, without a tuber spinae. The acromion is not preserved. The coracoid process is broken but was inflected medially. The glenoid fossa is deep and elliptical. The

posterodorsal corner of the blade is missing; but on the fragmentary scapula (IPUW 1007) collected at Gainfarn in 2000 (which is comparable in size to that of the 2006 specimen), the teres major origin is 89 mm long, with a prominent teres protuberance.

Humerus (Table 8; Fig. 8B,C,D) – Robust and dumbbell-shaped, with large tubercles, deep bicipital groove, and a nearly circular head. The curvature of the head is much flatter both

Dimension	NHMW 1885 [PS 3367] [Ottakring]	STMBV Met/0001 [Gainfarn]
Total length	285+	310+
MANUBRIUM		
Length	nm*	nm**
Breadth at anterior rib articulations	69	64
Breadth of anterior process near middle of its length	nm	42
Length of anterior process in midline	70e	64+
Posterior thickness	15	nm*
Breadth of anterior end	73	41+
Maximum thickness at keel	18	25
CENTRAL ELEMENT		
Length	nm*	nm**
Posterior thickness	nm*	25
XIPHISTERNUM		
Length	115+	153
Anterior breadth	nm*	49
Minimum breadth	38e	33
Maximum breadth posteriorly	--	90e
Anterior thickness	nm	26
Posterior thickness	10e	7

* Elements of sternum fused; boundaries not distinguishable.
** Combined length of manubrium and central element = 60+ mm.

TABLE 6: Measurements (mm) of sterna of *Metaxytherium medium* from the Central Paratethys; e = estimated; nm = not measured; + = measurement on damaged bone.
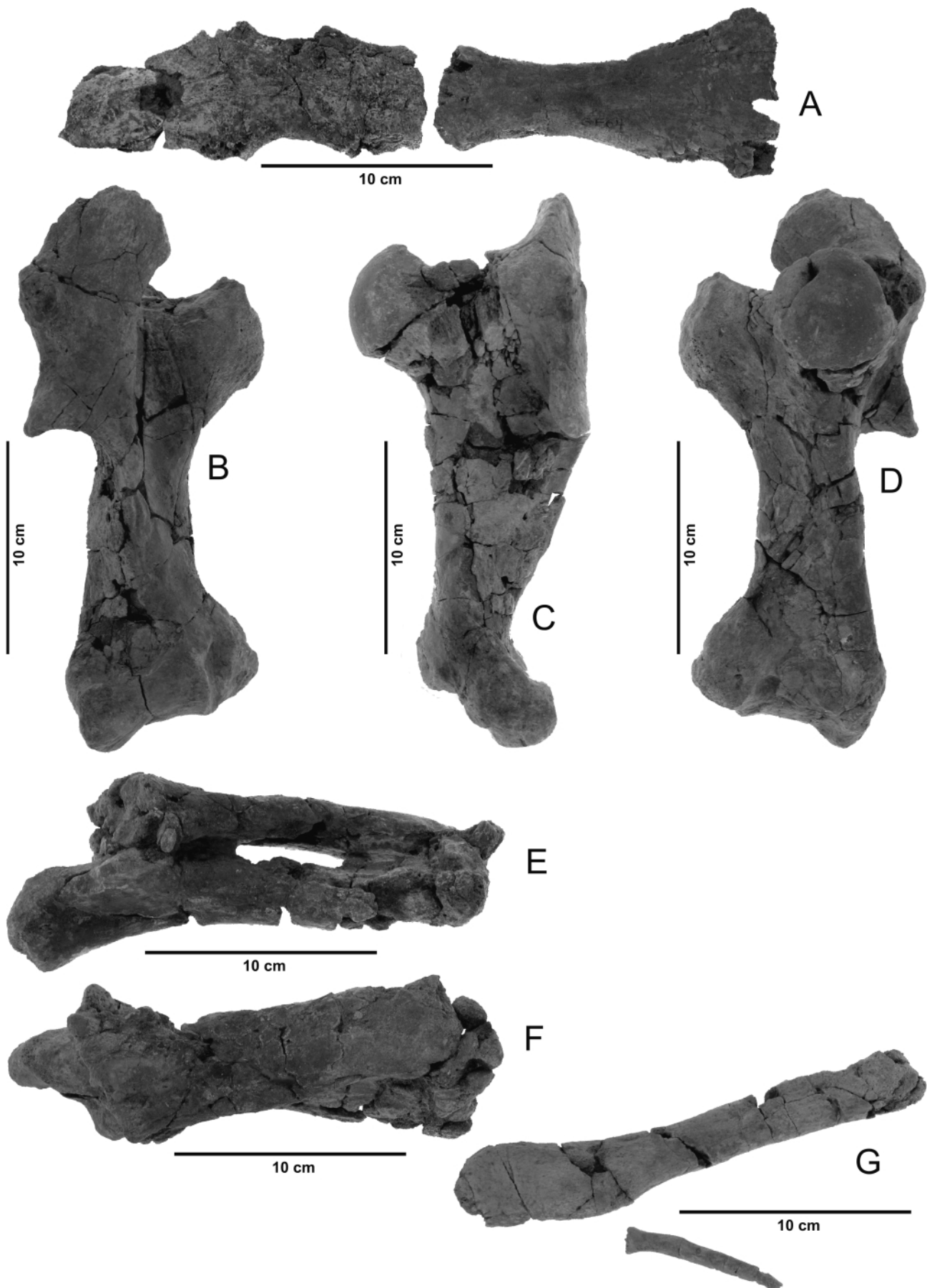
Figure 8: *Metaxytherium medium*, Gainfarn specimen (STMBV/Met/0001). A: Sternum, anterior end at left, ventral view (xiphisternum: Fig. 4, #64). B: Right humerus, anterior view (Fig. 4, #13). C: Right humerus, lateral view (Fig. 4, #13). D: Right humerus, posterior view (Fig. 4, #13). E: Right radius-ulna, lateral view (Fig. 4, #15). F: Right radius-ulna, anterior view (Fig. 4, #15). G: Right innominate with ?femur, lateral views (Fig. 4, #10, #11).

longitudinally and mediolaterally than in *M. krahuletzi*, in part because the proximal margin of the articular surface does not extend as far anteriorly. The greater tubercle extends well proximad of the head, has a large anteromedial flange, and bears distinct supraspinatus and infraspinatus muscle scars. The lesser tubercle is perhaps slightly more elongated distally than in *M. krahuletzi*. There is a weak triangular protuberance on the lateral side of the neck. The tubercles diverge at an angle of ~80º as seen in proximal view. The deltoid crest is prominent and recurved, and is continued by the deltopectoral crest, which is slightly roughened at its distal end for insertion of m. pectoralis major. Posterior and distal to this insertion on the medial side is a longitudinal pit ~2 cm long, probably for another muscle insertion. The shaft is relatively thick, corresponding to the stockier morph of Middle Miocene *Metaxytherium* (cf. Domning and Pervesler, 2001: 36). The trochlea is canted obliquely to the shaft at an angle of ~75º-80º. The trochlear articular surface has a barely discernible notch in its posterolateral side for a humeroulnar ligament. The olecranon fossa is well defined. The coronoid fossa has a large lateral pit, and a medial pit that is much larger on the right humerus than on the left.

Radius-ulna (Table 9; Fig. 8E,F) – Fused to each other with pronounced torsion. The anterior side of the olecranon process is tilted back at a sharp angle (60*-70*) to the ulnar shaft. The semilunar articular surface is notched on its medial side; on the lateral side at the same level, there may also be a notch in the articular surface, and lateral to it there is a pronounced shoulder on the ulna. The Gainfarn specimen is chiefly remarkable for the proportionately great mediolateral breadth of the humeroradial articular surface, its steep inclination (deviating some 25*-30* from perpendicular to the long axis of the ulna), and the overhanging lip at the lateral edge of the surface. This lip gives the appearance of arthritic pathology, but the left and right bones are nearly symmetrical and the humeri show no corresponding pathology. The pit on the medial side of the radioulnar junction for the biceps tendon is very large and deep. As is typical in *Metaxytherium*, the shaft of the radius is compressed anteroposteriorly, while

that of the ulna is more nearly triangular in cross section. In the Gainfarn specimen, the posterior border of the ulna is low and rounded for most of its length rather than sharp. The distal end, though present on the right side, is badly damaged; more informative are the separated distal epiphysis of the right radius (holotype of *M. petersi*, Hainburg) and the complete distal radius-ulna from Kalksburg (Abel, 1904: 121-122). The former differs from the latter in that the entire anteromedial half of its articular surface is strongly and evenly convex, rather than just the portion within 1 cm of the anteromedial margin; also, in that the posterolateral edge of the articular surface, adjacent to the ulna, is distinctly raised. Furthermore, in the Hainburg specimen there is a narrow, shallow nonarticular area (possibly for attachment of a ligament) extending onto the articular surface for a distance of ~1 cm posterolate-

Dimension	IPUW 1007 ["Gainfarn 2000"] (left)	STMBV Met/0001 [Gainfarn] (left)	STMBV Met/0001 [Gainfarn] (right)
Maximum length, vertebral border to border of glenoid fossa (AB)	--	--	310e
Mediolateral width of glenoid fossa (BI)	--	51e	--
Lateral border of glenoid fossa to inside of concave distal end of spine (BJ)	--	53e	--
Maximum breadth of blade dorsally (CD)	--	--	--
Minimum anteroposterior breadth of neck (EF)	--	--	--
Maximum anteroposterior breadth of distal end (GH)	--	--	--
Summit of spine to medial side of blade, measured parallel to plane tangent to posterior edges of spine and neck (KL)	--	--	60
Anteroposterior length of glenoid fossa (MN)	--	60e	--
Length of teres major origin from teres protuberance to posterior corner of blade (TMO)	89	--	--

TABLE 7: Measurements (mm) of scapulae of *Metaxytherium medium* from the Central Paratethys; e = estimated.

	Marz (Márczfalva–Péherkő-bánya)		IPUW unnum.	STMBV Met/0001 [Gainfarn]	STMBV Met/0001 [Gainfarn]
	MAFI Ob-3036 (left)	MAFI Ob-3995/6 (right)	[PS 3342] [Kalksburg] (left)	(left)	(right)
Maximum length, greater tubercle to distal end (AB)	232	--	248	255	263
Maximum breadth, greater to lesser tubercle (CD)	110e	--	106	113	116
Maximum breadth, ectepicondyle to entepicondyle (EF)	88	--	86	94	99
Maximum thickness, posterior side of head to anterior side of greater tubercle (GH)	99	99	98	108	111
Maximum thickness, posterior to anterior ends of medial rim of trochlea (IJ)	29	31	33	34	38
Maximum (proximolateral-mediodistal) breadth of head (KL)	54+	55	46e	58	57
Minimum (proximomedial-distolateral) breadth of head (MN)	63	63	56e	55	56
Breadth of anterior side of trochlea (OP)	58	56	60	60	64
Length, saddle between head and greater tubercle to saddle of trochlea (QR)	195	--	218	208	210
Maximum mediolateral diameter perpendicular to lateral surface, midshaft (MLD)	49e	--	42e	43	43

TABLE 8: Measurements (mm) of humeri of *Metaxytherium medium* from the Central Paratethys; e = estimated; + = measurement on damaged bone.

rally from the anterior extremity.

Innominate (Table 10, Fig. 8G) – The proximal (iliac) end is not noticeably inflected, but it bears on its dorsomedial side a broad, slightly roughened concavity extending 5 cm along the shaft. The shaft is straight with an oval cross section. The acetabulum is very shallow, and its rim is incomplete posteroventrally. The ventral and posterior edges of the bone are damaged, so the size of the pubis (if any) and the distal ischial margin cannot be judged. This damage admittedly biases the assessment of gender towards the female; but despite the advanced osteological maturity of this individual, nothing about the pelvis gives the impression of male morphology. In particular, where a portion of the ventral margin of the ischium is preserved (~4 cm behind the acetabulum), the bone was no more than 4 cm wide dorsoventrally – a degree of ischial expansion too slight to suggest a male (cf. *M. krahuletzi*, Domning and Pervesler, 2001: pls. 19-20). In the holotype of *M. petersi* (Abel, 1904: pl. 7, fig. 2), the acetabulum is much deeper and more distinct than in the Gainfarn specimen, and the pubis is distinct; but such differences are within the range of intraspecific variation.

?Femur – A slender bone found near the right innominate is apparently the right femur (Fig. 8G). Its proximal end is flat, subtriangular or trapezoidal, 11 x 13 mm, and rugose, having evidently had a proximal epiphysis. The nearly straight, subcylindrical shaft is 10 mm in diameter; it tapers distally to 7 mm diameter, and apart from a slight bend 2 cm from the proximal end it has no distinct muscle attachments. There is no expansion at the distal end, which was probably blunt though is now damaged. At the distal end the bone has a cancellous core but a denser cortex. Its total length is 73 mm.

6. Descriptions of Other Newly Referred Specimens

The following descriptions emphasize features that differ from most other *Metaxytherium*.

6.1 Rauchstallbrunngraben Skull

This juvenile skull (NHMW 2007z0106/0001; Tables 2, 5; Fig. 9), mentioned in a field trip guide by Piller et al. (1996: 16), is incompletely prepared and lacks the right premaxilla, occipital bones, and zygomatic arches. A natural endocranial cast is present, together with the left tympanic, periotic, and auditory ossicles.

Premaxilla – Anterior surface convex, without a distinct keel. There is no sign of tusk alveoli, though the premaxillary canal is visible close to the anterior end, which is damaged at the tip. The posterior end of the symphysis forms an upraised boss [c. 10(1)]. The rostral deflection was greater than 50°.

Nasal, Ethmoid, Vomer, Lacrimal – Not discernible or not preserved.

Frontal – Lateral side of supraorbital process long anteroposteriorly (~38 mm); the process is a maximum of 23 mm thick dorsoventrally on its medial side, with a thin (~7 mm) posterolateral corner [c. 36(1)]. Orbicular apophyses are absent. A nasal incisure is absent [c. 37(0)]. The median portion of the roof is slightly convex, with no distinct boss [c. 42(0)]. No crista intratemporalis is present, and the lower part of the temporal surface is not recessed.

Parietal – The temporal crests are of type C (Domning, 1988): smoothly rounded, separated by a concavity ~2 cm wide.

Basisphenoid – Sutural surface for basioccipital ~25 mm wide.

Alisphenoid – The lateral surface of the pterygoid process is smooth; length of process ~40 mm. The con-

Dimension	MAFI Ob-3037 [Marz] (right)	STMBV Met/0001 [Gainfarn] (left)	STMBV Met/0001 [Gainfarn] (right)
Total length of ulna (AB)	--	--	205e
Total length of radius, anterior lip of semilunar notch to distal end (CD)	--	--	180e
Height of semilunar notch, anterior tip of olecranon to anterior radial lip of notch (EC)	43	39	38e
Thickness of olecranon, anterior tip to posterior side (EF)	--	47	45e
Distal thickness, anterior side of radius to posterior side of ulna (GH)	--	--	74e
Maximum mediolateral breadth, radial portion of semilunar notch (IJ)	60	70	74e
Maximum mediolateral breadth, ulnar portion of semilunar notch (KL)	30	33e	32e
Minimum mediolateral breadth of semilunar notch at its midsection (MN)	28	36	32e
Minimum thickness of olecranon, posterior side to semilunar notch (OP)	31	37	37

Table 9: Measurements (mm) of radii and ulnae of *Metaxytherium medium* from the Central Paratethys; e = estimated.

Dimension	GBAW Inv. Nr. 2006/18/1, #2350 [Hainburg] (left)	STMBV Met/0001 [Gainfarn] (right; old female?)
Total length	200+	218+
Dorsoventral breadth, proximal end	33	29
Mediolateral thickness, proximal end	16	21
Minimum dorsoventral thickness of ilium	22	25
Minimum mediolateral thickness of ilium	15	18
Proximal end of ilium to acetabular area	141	150
Mediolateral thickness at acetabular area	23	23
Anteroposterior diameter of acetabulum	nm	17
Dorsoventral breadth at pubis	45	34+
Maximum dorsoventral breadth of ischium	46+	36+
Mediolateral thickness of distal end	--	15+

Table 10: Measurements (mm) of innominates of *Metaxytherium medium* from the Central Paratethys; e = estimated; nm = not measured; + = measurement on damaged bone.
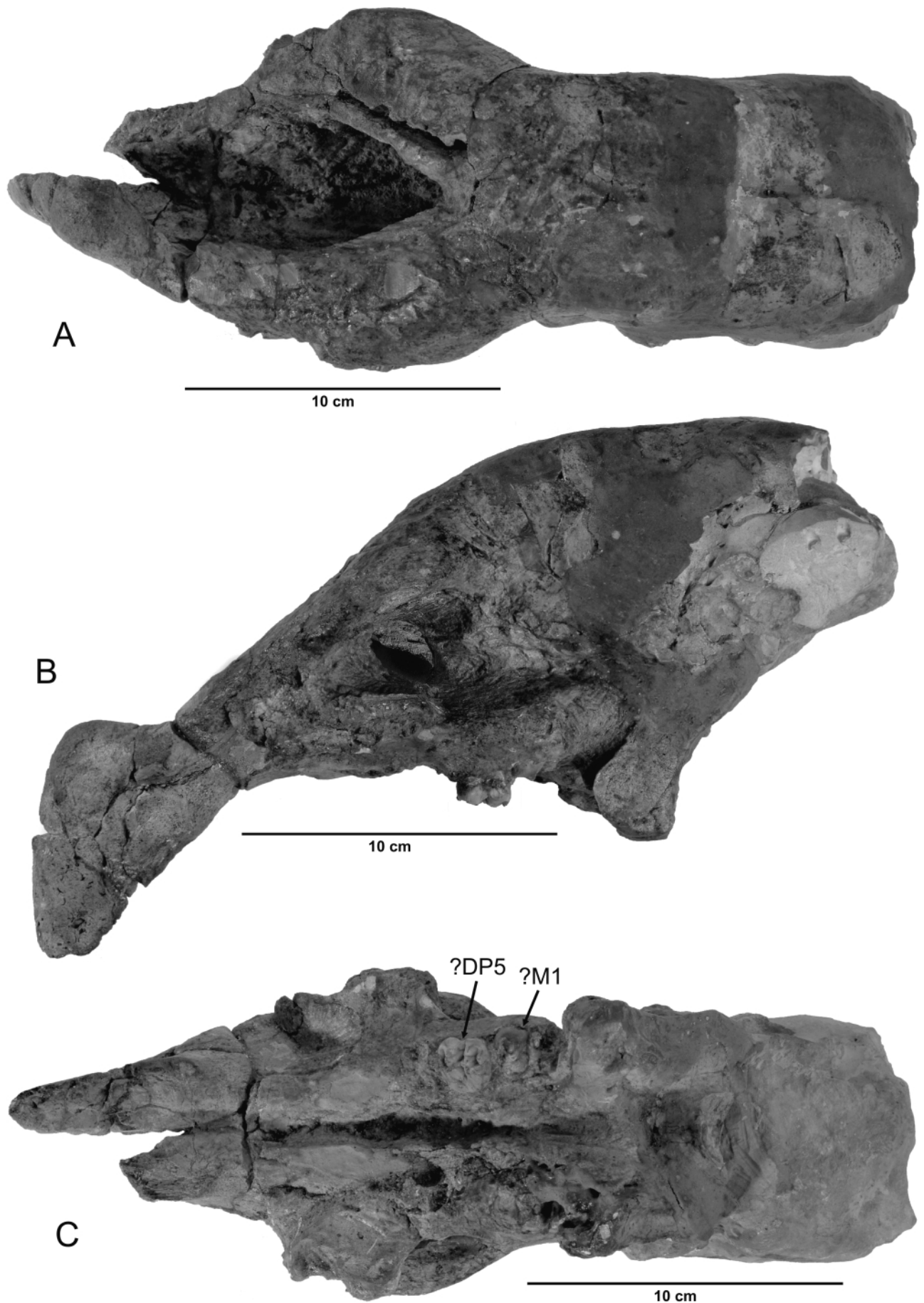
Figure 9: *Metaxytherium medium*, Rauchstallbrunngraben specimen (NHMW 2007z0106/0001), juvenile skull with left ?DP5 and unerupted ?M1. A: dorsal view. B: left lateral view. C: ventral view.

vexity anterior to the zygomatic root is almost negligible.

Pterygoid – The pterygoid fossa is well developed. The posterior width across the tops of the pterygoid processes is ~70 mm (~64 mm in BLLM 32816).

Palatine – The extent of the palatines and palatal incisure is unclear [c. 97(?), 99(?)].

Maxilla – The palatal gutter is deep. The palatal and rostral surfaces meet in a smooth but abrupt curve. The zygomatic-orbital bridge is elevated ~9 mm above the alveolar margin [c. 11(0)] and has a thick, rounded posterior edge.

Dentition – Alveoli are present for a 3-rooted ?DP4. The almost unworn left ?DP5 is preserved (L = 16.5 mm, AW = 17.9 mm, PW = 16.7 mm). An unerupted tooth (M1?) is preserved on each side. The cusp patterns resemble those of BLLM 32816 described by Sickenberg (1928).

6.2 ?St. Margarethen Braincase

This adult specimen (BLLM 32815; Table 2; Fig. 10) displays erosion resembling sandblasting (cf. Thenius, 1952: 109-111) on its supraorbital, pterygoid, and zygomatic processes. The entire rostral and palatal portions, jugals, and ear bones are missing.

Ethmoid – The perpendicular plate is 15 mm thick. Several conchae are visible in cross section, but are not fully prepared.

Nasal – The nasals are large, set in sockets in the anterior margins of the frontals, and separated in the midline by ~32 mm [c. 31(1), 32(1)]. The right nasal is missing.

Frontal – Orbicular apophyses are absent. No nasal incisure extends abaft the nasals [c. 37(0)]. The frontal roof is flat with a median groove [c. 42(0)], not overhanging laterally. The anterior end of the frontoparietal suture lies ~4.5 cm abaft the nasals. Endocranially, the length of the frontals exposed in the midline between the mesethmoid and the parietals is approximately 22 mm, slightly more than in BLLM 32816.

Parietal – Maximum width = 84 mm; minimum width of roof at squamosal sutures = 72 mm; thickness in anterior midline ~20 mm. The temporal crests are of type A (Domning, 1988): low, at edges of a nearly flat roof; cranial vault nearly rectangular. No emissary foramen is present. Endocranially, the bony falx cerebri is low and rounded at the frontoparietal suture. The pits at the lateral ends of the transverse sulcus are not very deep.

Supraoccipital – Forms an angle of 107° with the after part of the parietals. The dorsal portions of the lateral borders do not overhang, in contrast to BLLM 32816 which here displays (as an individual peculiarity?) a state more primitive than is seen in other Metaxytherium. The external occipital protuberance does not rise above the plane of the parietal roof; below it is a distinct median ridge. The exoccipital sutures meet at an angle of ~135° and are separated in the midline by a slight notch. The semispinalis insertions extend less than halfway to the ventral border. The nuchal ridge is indistinct near the squamosal sutures.

Exoccipital – The exoccipitals do not meet in the dorsal midline [c. 66(1)]. The dorsolateral border is 18 mm thick, smoothly rounded, and not overhanging posteriorly. The supracondylar fossa is moderately deep. The hypoglossal (= condyloid) foramen is single. The paroccipital processes extend ~2 mm lower than the condyles. Arc of condylar articular surface ~116°.

Basioccipital – Fused with basisphenoid, indicating adulthood. Width at suture = 40 mm.

Basisphenoid – The sella turcica is shallow; the region of the tuberculum sellae is rugose.

Presphenoid – No elevated shelf overhangs chiasmatic grooves.

Orbitosphenoid – The optic foramen lies at the level of the dorsal side of the sphenorbital fissure.

Alisphenoid – The lateral surface of the pterygoid process is smooth where preserved. No convexity is present anterior to the zygomatic root.

Pterygoid – The pterygoid fossa is mostly obliterated by erosion. Posterior width across tops of pterygoid processes = 69 mm.

Squamosal – Dorsally in contact with the squared posterior part of the parietal roof [c. 76(1)], but does not have a narrow posterodorsal process as in some Metaxytherium krahuletzi or Halitherium christolii (cf. Domning and Pervesler, 2001: 22). The sigmoid ridge is prominent, its dorsal shoulder strongly bent. The external auditory meatus is 14 mm long mediolaterally, as is the case aberrantly in some M. krahuletzi (Domning and Pervesler, 2001: 22) [c. 75(0) rather than (1) as would be expected]. The surface of the cranial portion dorsal to the zygomatic root is not inflated. The processus retroversus is distinctly double, protruding below the zygomatic root, but not turned in ventrally to a noticeable degree; medial to it, the bone is deeply concave. The posterodorsal edge of the zygomatic process is slightly concave in outline, and very slightly convex laterad.

6.3 Müllendorf Skeleton

This juvenile specimen comprises the skull roof, squamosals, right periotic, right scapula fragment, several unfused neural arches of vertebrae, and numerous ribs. Cranial measurements are included in Table 2.

Parietal – The temporal crests are of type A, but weakly developed. The minimum width of the roof at the squamosal sutures is 59 mm. There is no emissary foramen or median bump on the posterior part of the roof.

6.4 Retznei Skull Roof

This adult specimen comprises the frontals, parietals, supraoccipital, and a natural endocranial cast (Table 2; Fig. 6B).

Nasal – The nasals were probably separated in the midline [c. 31(1), 32(1)].

Frontal – A small orbicular apophysis is present on the right side. The anterior end of the frontoparietal suture lies ~4 cm abaft the nasals. The midline length of the endocranial surface is ~32 mm.

Parietal – The parietal roof is convex anteroposteriorly, and 21 mm thick in the anterior midline; the temporal crests are of type B. The minimum width of the roof at the squamosal sutures is 69 mm. There is a low median bump on the posterior
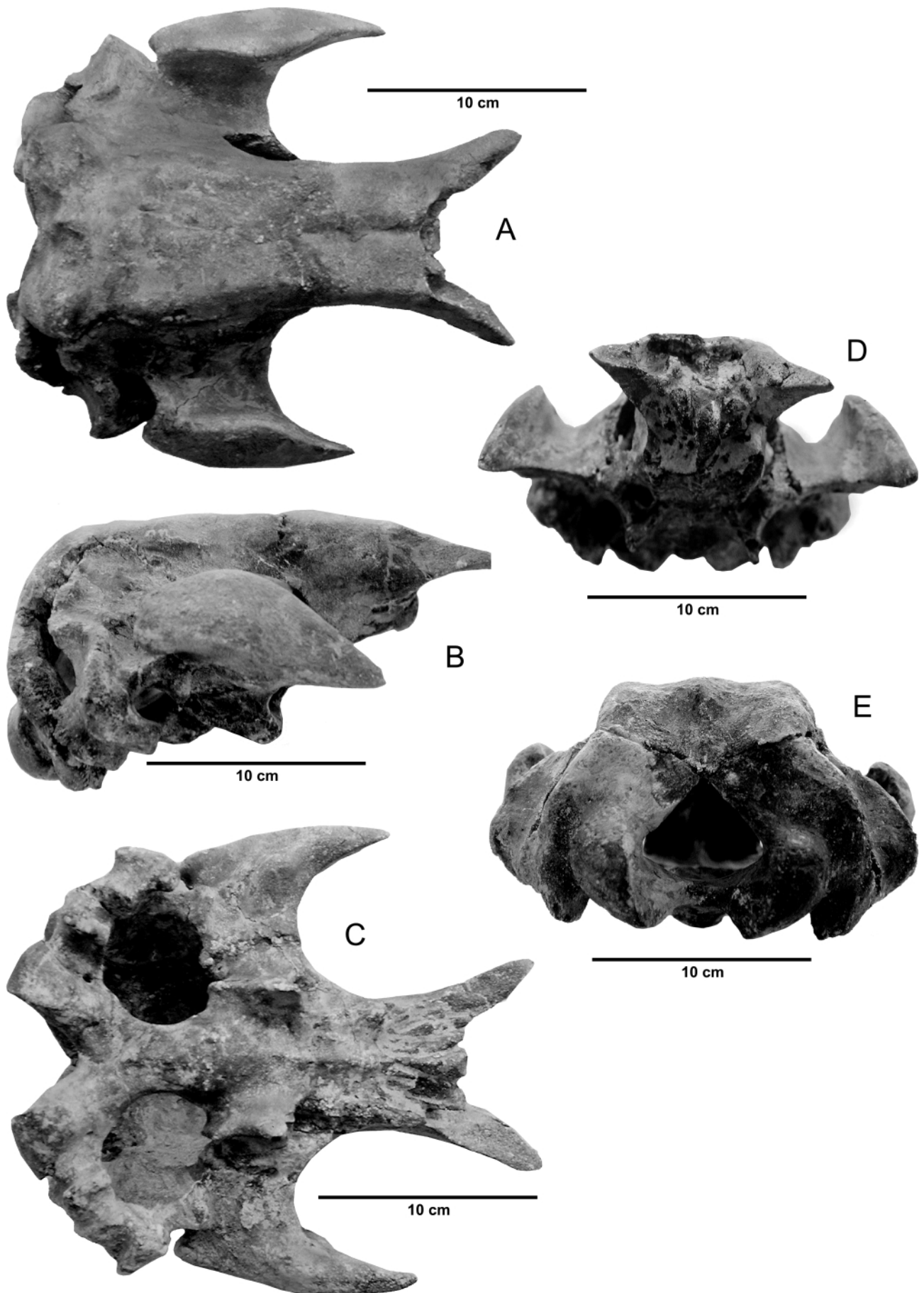
Figure 10: *Metaxytherium medium*, ?St. Margarethen specimen (BLLM 32815), adult braincase. A: dorsal view. B: right lateral view. C: ventral view. D: anterior view. E: posterior view.

part of the roof. Behind it, a very large emissary foramen ~5 mm in diameter extends from the top of the external occipital protuberance to the transverse sulcus. The dorsoventral thickness of the bone at the sulcus is 33 mm. Endocranially, no pits are present at the ends of the sulcus, and the bony falx cerebri is flat at the frontoparietal suture.

Supraoccipital – The median crest is very strong. No notch separates the exoccipital sutures.

6.5 Fazekasboda Skeleton

This juvenile specimen in the MAFI collection includes the parietal-supraoccipital skullcap, right squamosal, ear bones, partial mandible, left DP4-M1 and right dp4-m1, in addition to vertebrae and ribs (Tables 2-4).

Parietal – Maximum width = 86 mm; minimum width of roof at squamosal sutures = 76 mm; thickness in anterior midline = 12 mm. The temporal crests may be of type C but have very little relief. Endocranially, the internal occipital protuberance, tentorium, and transverse sulcus are very weak; the bony falx cerebri is relatively sharp at the frontoparietal suture.The dorsoventral thickness at the transverse sulcus is 22 mm. Emissary foramina are absent. A low median bump is present on the posterior part of the roof.

Supraoccipital – Forms an angle of 127° with the after part of the parietals. The nuchal ridge distinctly extends to the squamosal sutures. The external occipital protuberance does not rise above the plane of the parietal roof; below it is a distinct median ridge. The semispinalis insertions are only faintly marked. The exoccipital sutures are separated in the midline, possibly by a notch.

Squamosal – The surface dorsal to the zygomatic root is not inflated. A prominent foramen or canal deeply notches the dorsal edge of the cranial portion. The zygomatic process is much broader posteriorly than anteriorly, thick and massive, and sigmoid in lateral view (as is typical for juveniles; cf. *Dusisiren jordani*, Domning, 1978: pl. 4, figs. a,b). The posterodorsal edge is concave in outline, and convex laterad. The processus retroversus is distinctly double, and turned in ventrally. The medial and lateral edges of the anterior tip are about equally blunt.

Mandible – The anteroventral outline of the symphysis is convex anteroposteriorly.

Dentition – The fourth deciduous premolars are erupted; DP4 is unworn, dp4 slightly worn. DP5 and dp5 are beginning to erupt, and are unworn. M1 and m1 are unerupted. The enamel is not wrinkled. DP4 probably has three roots like DP5. The cusp patterns resemble those of other *Metaxytherium*. M1 has a lingual cleft between the precingulum and protocone. The semimolariform dp4 has three lophids; the anterior one is joined to the protolophid by a spur labial to the midline; the transverse valley is open; the hypolophid is joined to the middle cuspule of the postcingulum by a spur lingual to the midline. Of the three postcingular cuspules, the middle is largest and the lingual smallest. On dp5, the hypoconulid lophule lacks distinct cuspules or a median ridge forming a Y-shape

(cf. Domning, 1988: 412). On m1, the "Y" is fairly distinct, but the "G" shape of the protolophid is indistinct.

Rib 1 (left) – A process for m. longus capitis is present on the underside of the neck. Total length = 120 mm; tip of capitulum to lateral edge of tuberculum = 37 mm; mid-shaft diameters = 23 x 16 mm.

7. Comparisons and Reconsiderations of Phyletic Relationships

The Miocene and Pliocene *Metaxytherium* of Europe and North Africa form a single lineage of four chronospecies (Domning and Thomas, 1987; Sorbi et al., 2012): *M. krahuletzi* (Burdigalian; Eggenburgian-Ottnangian), *M. medium* (Langhian-Tortonian), *M. serresii* (latest Tortonian-Zanclean), and *M. subapeninnum* (Zanclean-Piacenzian) (Pilleri, 1988; Domning and Pervesler 2001; Carone and Domning, 2007; Bianucci et al., 2008; Sorbi et al., 2012). All these species are assumed to have lived throughout the contiguous, shallow marine waters of the Mediterranean-Paratethyan realm. However, except for *M. krahuletzi*, which is best known from Austria, this lineage is best documented from western Europe, Mediterranean islands, and North Africa, especially France, Spain, Italy, and Libya. Moreover, apart from the Early Miocene (Aquitanian-Burdigalian) dugongine *Rytiodus* (Domning and Sorbi, 2011) and the miosirenines *Miosiren* (Burdigalian) and *Prohalicore* (Serravallian) (Sorbi, 2008a), no other Neogene sirenians are definitely known to have inhabited the Mediterranean-Paratethyan region.

The fossil record of Central Europe, therefore, presents an apparent anomaly in that the sirenians of this area, as hitherto interpreted, do not fit the simple pattern of a single, anagenetically-evolving halitheriine lineage: one or more additional species or genera reportedly occur in the Middle Miocene (Badenian) of the Vienna Basin and neighboring areas, and the expected species *Metaxytherium medium* has hitherto not even been recognized there. Instead, workers as far back as Abel (1904) described the Vienna Basin sirenians as a separate species (*M. petersi*), later given its own genus *Thalattosiren* by Sickenberg (1928). Subsequently, Kretzoi (1951) named yet another new genus and species (*Haplosiren leganyii*) from "Tortonian" deposits in Hungary (this presumably reflects not the western European but the older, Paratethyan sense of the term "Tortonian", which is approximately equivalent to the Badenian in present usage).

These Paratethyan depositional basins were connected to each other and to the Mediterranean from the Early Miocene up through the middle Badenian, though by the late Badenian the Mediterranean connection had been lost and a marine connection with the Eastern Paratethys and Indopacific (interrupted in the Ottnangian-Karpatian and middle Badenian) had been re-established (Rögl and Steininger, 1983; Rögl, 1998, 1999, Meulenkamp and Sissingh, 2003; Bianucci et al. 2011).

Thus it is possible that distinct taxa of sirenians (Indopacific immigrants, and/or endemics that evolved in the Paratethys in isolation from Mediterranean forms) might have appeared there

during or after the late Badenian, but evolution of Parathethyan endemics is unlikely to have occurred earlier. So how are the reportedly distinct taxa to be understood?

7.1 Distribution of "*Metaxytherium petersi*"

Material from other parts of Europe, and even America, has occasionally been referred to *M. petersi* or *Thalattosiren*, but these referrals are not convincing:

- A humerus from the Middle Miocene of Portugal was described by Zbyszewski (1944) as an *M. petersi* resembling in its dimensions the specimen from Kalksburg – particularly in the 80° angle of divergence of the tubercles. However, this aspect of the specimen was not illustrated, and it is not clear how the measurement was made. The shaft of the bone is extremely long and parallel-sided, more so even than in *M. krahuletzi*, in which the divergence of the tubercles can be as great as 85°. Therefore, the taxonomic assignment of the Portuguese humerus remains uncertain.
- Depéret and Roman (1920: 29-30, pl. 7, fig. 4) referred to "*M.* aff. *petersi*" a braincase from the "Vindobonian molasse" of Mont-de-Marsan, Landes, France, primarily on the basis of the form and degree of separation of its temporal crests (apparently of type A) in contrast to those of *M. medium* from the Loire Basin. However, although the latter sample has a notably high incidence of closely-spaced crests (type E) (Domning, 1988: 418), the form of the temporal crests is notoriously variable in *Metaxytherium*, and some other French *M. medium* also exhibit crests of types A, B, or C. Therefore this referral cannot be considered well founded.
- Sirenian remains from the Badenian limestones near Pińczów, southern Poland, have also been cited as *Thalattosiren* sp. (Czyżewska and Radwański, 1991; Wolsan, 1991), but without any morphological justification being offered. This name may have been used simply because the Vienna Basin sirenians were closer geographically and stratigraphically (and hence presumably taxonomically) to the Polish ones than any others.
- Similarly, Šuklje (1938) reported sirenian remains from "Mediterranean sandstone" near Zagreb and Samobor, Croatia, said to be "most probably identical" with *M. petersi* from the Vienna Basin. These included isolated teeth, a radius, vertebrae, and ribs. Although a partial molar was illustrated, it does not suffice for a specific identification.
- Pilleri (1987: 31-33) identified a Burdigalian humerus from Othmarsingen, Switzerland, as *M.* cf. *petersi*, based on its resemblance to one referred to that species by Abel (1904). However, no particular traits were adduced that support this species assignment to the exclusion of the more chronostratigraphically probable *M. krahuletzi*.
- VanderHoof (1941) identified a Middle Miocene skull and skeleton from Santa Cruz, California, as *M. petersi*. It is now regarded as *Dusisiren jordani* (Domning, 1978: 21).

In summary, "*M. petersi*" has not been reliably recorded outside of Austria. It remains to be determined whether it can be regarded as a distinct species even within our study area.

7.2 Validity of "*Metaxytherium petersi*"

The distinctiveness of *Metaxytherium* (or *Thalattosiren*) *petersi* has been defended by several authors. Abel (1904), who originally named *M. petersi* and regarded it as representing a lineage distinct from other *Metaxytherium*, unfortunately had little but isolated teeth and postcranial elements of this species to study, and these were mostly referred specimens; the holotype from Hainburg lacked the skull and was of little diagnostic use. He compared them almost exclusively with *M. krahuletzi*, and in the few instances where he was able to make the more relevant comparisons with the coeval *M. medium* (his "*M. cuvieri*") he found practically no differences. Neither did he give an explicit diagnosis of *M. petersi*, but for the most part merely pointed out contrasts with other species in the course of his description. Among these, the following distinctions from other Miocene *Metaxytherium* seem to have struck him as most important:

- Lower molars more quadratic, with more numerous secondary cuspules but (on m3) a less developed hypoconulid than in *M. krahuletzi*
- Scapula with ridge extending from dorsal end of spine to anterodorsal corner of scapula; blade narrower, with broadest portion of supraspinous fossa located more distally than in *M. krahuletzi*, and spine reaching closer to glenoid
- Tubercles of humerus larger relative to head than in *M. krahuletzi*; head with flatter curvature; greater and lesser tubercles in proximal view form angle of 80°, compared with 55° in *M. krahuletzi* and 85°-90° in *M. medium*; greater tubercle reaching higher (i.e., farther proximally) than head (unlike *M. krahuletzi* but like *M. medium*); entepicondyle "lies [anteroposteriorly] closer to the [distal] joint surface" than in *M. krahuletzi*; diaphysis strongly constricted just above anterior border of trochlea
- Posterior edge of distal part of ulna rounded, not sharp as in *M. krahuletzi*; torsion between radius and ulna less than in either *M. krahuletzi* or *M. medium*

Sickenberg (1927; 1928: 320-321), having at last a good skull to study, still did not give a formal diagnosis, but mentioned the following characters as distinctive, emphasizing "the unusual combination of relative simplicity of the tooth structure and high specialization of the skull" as justifying the erection of the new genus *Thalattosiren*:

- Braincase broadened, shortened
- Rostral deflection strong
- Well-developed nasal bones retained
- Molars simple, relatively lophodont

Later, however, Sickenberg (in Pia and Sickenberg, 1934: 403) abandoned the name *Thalattosiren* and explicitly returned to consistent use of the combination *Metaxytherium petersi*, though without giving reasons. Thenius (1952: 109-110) surmised that Sickenberg had simply come to a more inclusive concept of the genus *Metaxytherium*, taking into account its observed variability (although Thenius himself evidently did

not agree, since he continued to use *Thalattosiren*). Thenius (1952: 112) then went on to list explicitly the chief characters that for him distinguished *Thalattosiren* from *Metaxytherium*:

- Braincase broader, more shortened
- Rostral deflection stronger
- Nasal bones well developed
- Molars simpler, lophodont
- Incisor tusks possibly lacking

We shall consider these alleged differences individually:

- Stronger rostral deflection: The rostral deflection of the St. Margarethen "*Thalattosiren*" skull (BLLM 32816) is 55°, which is comparable to or less than the deflections seen in *Metaxytherium*: e.g., *M.* cf. *krahuletzi*, estimated 60° (Sorbi, 2008b); *M. medium*, ca. 50° (as seen in "*M. catalaunicum*" of Pilleri et al., 1989, and the specimen of Moncharmont-Zei and Moncharmont, 1987, measured by Domning); *M. serresii*, 50°-73° (Carone and Domning, 2007); *M. subapenninum*, 57°-63° (Sorbi et al., 2012); *M. floridanum*, 64°-81° (Domning, 1988; Carone and Domning, 2007); *M. arctodites*, 71° (Aranda-Manteca et al., 1994). Therefore, the view of Sickenberg (1928) and Thenius (1952) that *Metaxytherium* characteristically has a less deflected snout than *Thalattosiren* was a mistaken impression occasioned by their lack of data on well-preserved skulls of *Metaxytherium*. The rostral deflection of the St. Margarethen specimen is probably not outside the range of variation to be expected in *M. medium*.

- Possible lack of incisor tusks: No trace of tusk alveoli is visible in BLLM 32816 or NHMW 2007z0106/0001, but in each case an unknown length is missing from the tip of the rostrum. If tusks were present, they were at least as small as in other Early and Middle Miocene *Metaxytherium*, and absence of tusks cannot be ruled out. Both skulls are juvenile (see below), so the tusks (if present) would have consisted of little but the developing and unerupted crown (cf. *M. floridanum*, Domning, 1988: 409). The Gainfarn specimen lacks the premaxillae and sheds no new light.

- Well-developed nasal bones: The nasals of BLLM 32816 are indeed very large compared to known *Metaxytherium*, and are in contact in the midline for a length greater than 1 cm [c. 31(0)], whereas in most *Metaxytherium* they are completely separated in the midline [c. 31(1)]. However, there are exceptions: the nasals were possibly in midline contact in some *M. krahuletzi* (Domning and Pervesler, 2001), and were in contact in one or two out of five *M. serresii* (Carone and Domning, 2007). Pilleri, in describing his nominal species "*M. catalaunicum*", illustrated it (in Pilleri et al., 1989: fig. 33b) as questionably having large, conjoined nasals, though he did not comment on this feature (and we have not seen the specimen). Even in the Recent and much more derived dugongid *Hydrodamalis gigas*, vestigial but nonetheless conjoined nasals can occur (Brandt, 1868: pl. 1, fig. 5). Therefore it seems possible that, in a species with otherwise reduced and separated nasals such as *M. medium*, occasional atavistic individuals with much larger

and consequently conjoined nasals might occur. Furthermore, no Neogene dugongid taxon other than "*Thalattosiren*" is known to have had large, conjoined nasals; and this makes the existence of a Middle Miocene genus with this characteristic unexpected and doubtful a *priori*.

- Broader, more shortened braincase: This is the most visually-striking distinction between BLLM 32816 and other *Metaxytherium*. However, it is a characteristic of juvenile mammals in general; and BLLM 32816 is clearly immature, as shown by its open basioccipital-basisphenoid suture; DP2 alveolus, DP3-5, and M1 present; and M2 unerupted (Dp3-M2 were respectively identified as P³, d4, and M¹⁻³ by Sickenberg, 1928). NHMW 2007z0106/0001 is an even younger juvenile, with an open basioccipital-basisphenoid suture and spacious dental capsules for still-forming molars, in addition to being much smaller than BLLM 32816 and similar in size and proportions to a juvenile *M. krahuletzi* (KÜH 88; Domning and Pervesler, 2001). The still smaller MAFI juvenile from Fazekasboda (Table 2) has the shortest parietals relative to their width of any of these specimens. However, the Müllendorf skull, with the smallest dimensions of all, has a narrower, more rectangular parietal roof like more mature specimens. Hence individual variation may be a confounding factor here.

- Molars lophodont, simpler: The dental comparisons of previous workers were hampered by small samples and faulty understanding of dental homologies. Sickenberg (1928), followed by Thenius (1952), misinterpreted the dentition of the St. Margarethen skull. The first four teeth in its upper toothrow in fact correspond to those of a juvenile *M. floridanum* (Domning, 1988: fig. 8A); i.e., DP3-5 and M1. The latter do not differ materially from the Austrian form in complexity of cusp pattern or degree of lophodonty; thus there is no basis in these features for a generic distinction. Sickenberg's belief that M1-2 of his specimen were instead M2-3 may have led him to think they should have more complex patterns if they were to represent *Metaxytherium*. M3 is often larger and more complex in other *Metaxytherium*, but not always, and the homology was mistaken in any case.

- Lower molars more quadratic, with more numerous secondary cuspules but a less developed m3 hypoconulid than in *M. krahuletzi*: Having only isolated teeth of *M. krahuletzi* and "*M. petersi*" to work with, Abel (1904: 112) called particular attention to an unworn specimen (Peters, 1867: pl. 7, fig. 2; Abel, 1904: pl. 1, fig. 18) that clearly is more quadratic and with a smaller hypoconulid than the worn m3 of *M. krahuletzi* shown in his pl. 1, fig. 20. However, the former is not m3 (as is clear from its lack of an enlarged posterior root; Abel, 1904: 111) but a more anterior molar, which accounts for the difference in shape; and its unworn condition could account for the numerous secondary cuspules (whose distinctness would be obscured by moderate wear like that of the latter tooth).

- Scapula with ridge from dorsal end of spine to anterodorsal

corner: This peculiarity of the holotype of *M. petersi* is unique among known sirenians, and is not observed in the 2006 Gainfarn specimen. Without corroboration it is not advisable to base a taxonomic distinction on it, as it may be just an individual anomaly of the m. supraspinatus attachment. In fact, it bears a distinct resemblance to an elevated area at the dorsal end of the spine in a scapula of *M. subapenninum* (= "*Felsinotherium Forestii*"; compare Abel, 1904: pl. 2, figs. 6 and 7).

- Supraspinous fossa differently shaped, with scapular spine reaching closer to glenoid: The better sample of *M. krahuletzi* available today shows that the differences from the Hainburg specimen noted by Abel are merely individual ones. In fact, his two forms of the supraspinous fossa are almost matched on the two sides of a single specimen (Domning and Pervesler, 2001: pl. 15)! In a specimen of *M. medium* (Moncharmont Zei and Moncharmont, 1987: pl. 12), the fossa is intermediate but closer in shape to that of the Hainburg scapula. (The scapula of the St. Margarethen specimen BLLM 32816 was not described by Sickenberg, but its outline, preserved as an impression in matrix, resembles that of the Hainburg scapula.) As for the location of the distal end of the spine, it is difficult to discern any difference between the nominal species, even in Abel's own illustrations.

- Humeral tubercles larger relative to head; greater tubercle reaching farther proximally: Of the specimens studied by Abel (1904: pl. 4), the tubercles and other parts of the humerus he assigned to *M. petersi* are indeed more robust; however, the present sample of *M. krahuletzi* includes similarly robust forms (Domning and Pervesler, 2001: pls. 16-17), as does *M. medium*. The greater tubercle in *M. krahuletzi* usually extends well proximad of the head (Domning and Pervesler, 2001: 36, pl. 16), and this is also the norm in *M. medium* (e.g., Moncharmont Zei and Moncharmont, 1987: pl. 13) and other species of the genus, including the Gainfarn specimen.

- Greater and lesser tubercles of humerus more nearly perpendicular: This seems to characterize later species of *Metaxytherium* more than earlier ones, but is variable in those that have been adequately sampled: for example, the angle between the axes of the tubercles is approximately 60°-85° in the Early Miocene *M. krahuletzi* (Domning and Pervesler, 2001), and 75°-90° in the late Middle Miocene *M. floridanum* (Domning, 1988). Three Middle Miocene *M. medium* from France measure approximately 78°-95° (Domning, unpublished data). The value reported for "*M. petersi*" (Abel, 1904: 119) and that of the Gainfarn specimen are both 80°; that of the Marz specimen MAFI Ob-3036 is ~90°. Therefore, even if a trend toward greater values exists, it is of scant use in identifying individual specimens or distinguishing species.

- Humeral head with flatter curvature: This is true of the Gainfarn specimen. However, in contrast to the Kalksburg specimen described by Abel (1904: pl. 4, fig. 5b,c), the holo-

type of *M. petersi* does not have a flatter curvature (Peters, 1867: pl. 7, fig. 6a,c); hence this trait, evidently varying among individuals, does not reliably characterize the species.

- Humerus with entepicondyle closer to trochlea, and diaphysis more constricted above trochlea: Based on larger samples than were available to Abel (1904), these features likewise appear to be individually variable.

- Ulna with less sharp posterior edge; less torsion between ulna and radius: The former distinction is true of the Gainfarn specimen, but the latter is not. The degree of torsion is variable in *M. krahuletzi* (Domning and Pervesler, 2001: 36-37); Abel (1904: 175) says only that in *M. petersi* it is "still less" than in the latter, which in turn shows less torsion than *M. medium* (= *cuvieri*). Since this observation was based only on a distal radius-ulna from Kalksburg, of which the ulnar part had apparently been lost by the time of Pia and Sickenberg (1934: no. 3342), no corroboration or quantification can now be provided. It is probable that these features of "*M. petersi*" would fall within the range of variation of *M. medium* and other species.

In summary, we conclude that when individual and ontogenetic variation are taken fully into account, there remains no convincing basis for separating the *Metaxytherium* of the Vienna and neighboring basins from the contemporary Western European and Mediterranean *M. medium* at the specific, let alone the generic level. Certainly there is no reliable basis for a differential diagnosis of *M. petersi*, let alone *Thalattosiren*. The holotype of *M. petersi* was inadequately diagnostic even before parts of it were lost; hence we have had to base our conclusions on broadly "topotypic" specimens (i.e., the entire sample of Badenian age from the Vienna and neighboring basins). Neither individually nor collectively do these show evidence of distinction from *M. medium*. We therefore formally synonymize *M. petersi* Abel with *M. medium* (Desmarest).

7.3 Validity of Haplosiren leganyii

One more nominal taxon from the Badenian of the Central Paratethys is *Haplosiren leganyii* from Hungary, described by Kretzoi (1951) but not illustrated (Thenius [1952] considered it a nomen nudum). The sole specimen is a fragment of an immature left mandible containing m2-3 and the roots of dp4-5 and m1 (Fig. 11). It is very large, its molars being within the size range of *Metaxytherium subapenninum* or (in the case of m2) even larger. It is also larger than the dugongine *Rytiodus heali* (Domning and Sorbi, 2011), and has no special resemblance to it that would suggest *Haplosiren* is other than a halitheriine. The m2 is moderately worn; m3 is unworn and just beginning to erupt. Its posterior root is not elongated anteroposteriorly, but has a longitudinal ridge on its posterior surface (as m2 may have also). The cusp pattern is typical of *Metaxytherium*, and surprisingly simple, as Kretzoi noted and the name *Haplosiren* denotes. The hypolophids each have two cuspules placed anteriorly toward the midline of the tooth. Each molar has a single large hypoconulid cusp; on m2 this has a small cuspule on its anterior side. Otherwise there are
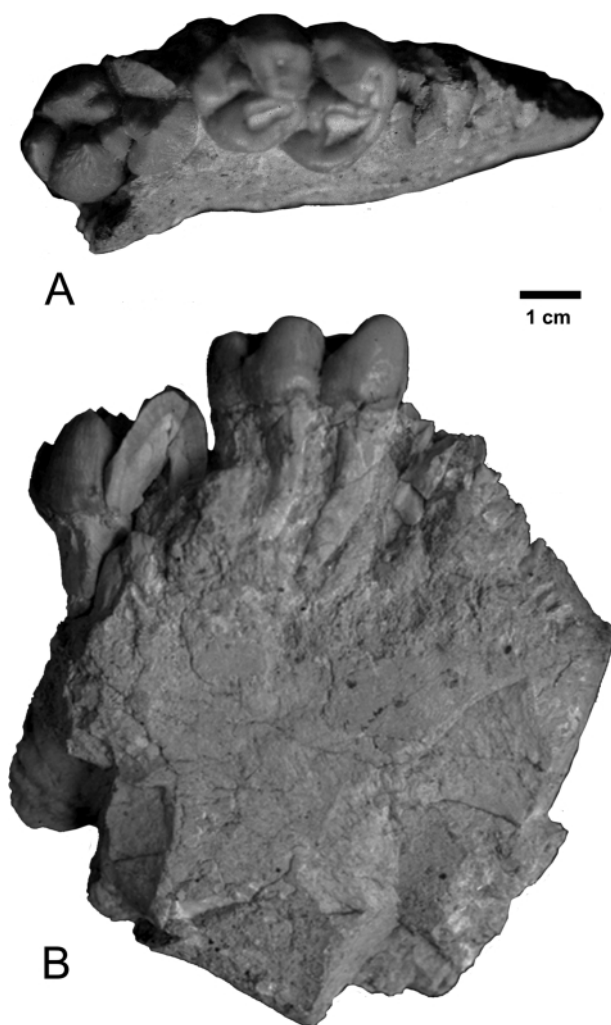
Figure 11: (MAFI V.10973), left mandibular fragment with m2-3. A: dorsal (occlusal) view. B: medial view.

no accessory cuspules. The unworn cusps have sharp tips, and the enamel (which is up to 3 mm thick near a cusp apex) is wrinkled where not worn smooth. A "vorderes Basalband" (sensu Abel, 1904) is present on the anterolabial corner of m2.

In comparison with *Metaxytherium* from the Central Paratethys, the teeth of *Haplosiren leganyii* are only slightly larger than some isolated m3s from the Vienna Basin, although none of the m2s yet collected from there match the Hungarian specimen in size (Tables 4, 5). It is possible for even very large m3s of *Metaxytherium* to have a single-cusped hypoconulid, as shown by *M. floridanum* (Domning, 1988: fig. 8H; crown length of USNM 359703 = 31.9 mm). The wrinkled enamel on m3 of the Hungarian form, however, is a peculiarity not previously noted in a dugongid.

Domning and Thomas (1987) tentatively regarded *Haplosiren leganyii* as a synonym of *Metaxytherium medium*. Despite its unusual size, simple molars, and wrinkled enamel, this is still a possible interpretation of this possibly aberrant individual. A conceivable alternative would be the late Badenian immigration of a different taxon, possibly even a dugongine, from the Indopacific. (An analogous Mediterranean-Indopacific connection in the late Oligocene was cited to explain the distribution of

some fossil cetaceans by Bianucci et al., 2011.) However the Indopacific sirenians of the late Badenian still remain unknown.

7.3 Implications of Recognition of Central Paratethyan *Metaxytherium medium*

These conclusions expand the known geographic range of *M. medium*, and also the species' known morphological sample. This is of particular interest in regard to the sternum, an element hitherto not well represented in this species, but possibly useful in distinguishing *M. medium* from *M. krahuletzi* (Domning and Pervesler, 2001: 44, pl. 14). The latter species has a long sternum with three parts (a primitive condition); these fuse in the adult, and are all about equally narrow. At least some later species, including *M. serresii* and *M. floridanum*, have shorter sterna that are broader in their middle and sometimes anterior portions, and comprise no more than two elements. Evidence concerning *M. medium*, however, is scanty and ambiguous. The Gainfarn sternum (Fig. 8A), the best-preserved example to date, is scarcely wider than in *M. krahuletzi*; and although its fusion of the two anterior elements can be seen as a resemblance to *M. medium*, this condition would hardly be surprising if found in *M. krahuletzi*, given the great individual variability customarily seen in sirenian sterna. On the whole, the Gainfarn specimen seems to indicate that *M. medium* and *M. krahuletzi* shared the same sternal morphology.

As for the stratigraphic range of *M. medium*, this is regarded as extending from approximately the beginning of the Langhian into the late Tortonian (Sorbi et al., 2012:fig. 12B). The Badenian correlates with the Langhian and the early part of the Serravallian; therefore the specimens reported here (the earliest of which is "?early to middle Badenian"; Table 1) do not extend the known chronological range of the species. Neither do they provide a more precise datum for the first appearance of the species – especially since they are mostly fragmentary, and the distinction between *M. krahuletzi* and *M. medium* is problematical even given good material (Domning and Pervesler, 2001:43-45). Bianucci et al. (2003:table 1) provide a table of *Metaxytherium* records from the Miocene (Burdigalian-Tortonian) of the Mediterranean basin; these are mostly not determined to species, but with the addition of the present evidence, they justify the conclusion of Bianucci et al. (2003) that *M. medium* had a very wide distribution in Europe, stratigraphical as well as geographical.

The synonymization of *M. petersi* with *M. medium* further corroborates the hypothesis (e.g., Sorbi et al., 2012) that the Old World *Metaxytherium* comprise an unbranched anagenetic series of chronospecies. Interestingly, this tends to support a comment of Abel (in Sickenberg, 1927: 106, concerning the discovery of the St. Margarethen skull) that in the case of the Sirenia we are able – sometimes, at least – to observe the evolutionary stages in a direct line of descent, "and not, as usual, just side branches"!

8. Paleozoogeography and Paleoecology

Although we conclude that taxonomic separation of these

Paratethyan animals from their contemporary *Metaxytherium medium* is not justified, the fact that they have been so separated in the past draws attention to their peculiar zoogeographic circumstances, which are in fact such that taxonomic differentiation would not have been surprising. During the course of the Badenian, the portion of Paratethys that included the Vienna, Eisenstadt-Sopron, and Styrian Basins became sporadically but progressively cut off from the Indopacific and/or Mediterranean Sea, respectively to the southeast and southwest, until by the late Badenian and Sarmatian they formed a virtually landlocked sea (Rögl and Steininger, 1983; Rögl, 1999; Meulenkamp and Sissingh, 2003; Bianucci et al. 2011). Their sirenian inhabitants would then have been reproductively isolated from other populations of *M. medium*, and given enough time, this marginal isolate could well have evolved into a separate species. At the least, considering the basin's environmental changes, we might expect some genetic and morphological peculiarities to have appeared in it, which could possibly account for the unusual features of a form like *Haplosiren leganyii*. If such differences never attained the level of taxonomic differentiation, it may be because this isolated population soon went extinct – if by Sarmatian time the Vienna and Pannonian Basins became too low in salinity (Harzhauser and Piller, 2007) for the seacows (or the seagrasses they depended on) to tolerate.

The data on the Central Paratethyan *Metaxytherium medium* presented above permit some inferences about its mode of life. As with the Eggenburgian *M. krahuletzi* (compare Domning and Pervesler, 2001), relationships and gross similarities to the Recent dugongids *Dugong* and *Hydrodamalis* suggest that, like them, the seacows of Badenian age from the Vienna, Styrian, and Eisenstadt-Sopron Basins dwelt exclusively in shallow marine waters. The co-occurrence of diagnostic shallow marine faunas points to a transition from humid, tropical shallow subtidal biotopes in the early early Badenian (16.26-14.89 Myr) to a subtropical climate in the Middle Badenian (14.89-13.82 Myr) to warm temperate climate during late Badenian (13.82-12.73 Myr) (Hohenegger et al., 2008). Such reasoning points to tropical to warm temperate climatic tolerances and a diet of seagrasses (cf. Domning, 2001), the presence of which at Gainfarn was inferred by Zuschin et al. (2007).

The rostral deflection from the occlusal plane of the St. Margarethen skull (BLLM 32816) is 55º, which is comparable to or less than the deflections seen in other *Metaxytherium* (see above) but less than that of the bottom-feeding *Dugong* (circa 70°). Probably *M. medium* was an obligate consumer of benthic plants (Domning, 2001) like most halitheriines and dugongines.

The presence of tusks cannot be proven; no trace of tusk alveoli is preserved in BLLM 32816 or NHMW 2007z0106/0001. Small tusks were, however, possessed by other *M. medium*, and they were presumably present in these Central European populations as well. The effect on feeding strategies of lacking larger tusks might have been the avoidance of large and tough seagrass rhizomes. Presumably the Badenian seacows ate seagrass leaves, shoots, and the more delicate and less deeply buried rhizomes, as the tuskless manatees (*Trichechus*) do today (e.g., Packard, 1984). In contrast to the large-tusked dugongines like *Rytiodus*, the more common though seemingly less diverse halitheriines like *Metaxytherium* with smaller tusks were probably ecological generalists.

On the other hand, the fact that *M. medium* had large, complex, well-enameled molariform teeth shows that it was not restricted to the most delicate, least fibrous seagrasses, as the modern *Dugong* (with its degenerate cheek teeth that lack functional enamel crowns) largely is (Lanyon, 1991).

In conclusion, *Metaxytherium medium* was a halitheriine dugongid distributed throughout the marine waters of the Central Paratethys, other parts of Europe, and presumably North Africa during the Middle Miocene. It was an ecological generalist that probably fed on the leaves and rhizomes of small and medium-sized benthic seagrasses. Its fossil record in the Central Paratethys ends with the Badenian, but its lineage continued in the Mediterranean into the late Pliocene.

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