



Metaxytherium serresii (Mammalia: Sirenia): new pre-Pliocene record, and implications for Mediterranean paleoecology before and after the Messinian Salinity Crisis

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KEY WORDS - *Metaxytherium serresii*, Mammalia, Sirenia, Osteology, Phylogeny, Late Miocene, Tortonian, Calabria, Southern Italy.

ABSTRACT - The osteology of the halitheriine dugongid sirenian *Metaxytherium serresii* is summarized and knowledge of its phylogenetic character states is updated, based on the fossil specimens from Montpellier, France; Sahabi, Libya; and a new record from Calabria, Italy. Specimens from Calabria are illustrated. This new Calabrian record is the earliest known occurrence of the species, dating to the Late Miocene (latest Tortonian; 7.3-7.6 Ma), whereas the previously known specimens are younger (latest Miocene-Early Pliocene; Messinian-Zanclean). Nevertheless, the Calabrian specimens differ in no important way from the younger ones, displaying both mid-sized tusks and reduced body size, in contrast to their ancestor, the Middle Miocene *M. medium*. Their reduction in body size is hypothesized to represent ecophenotypic dwarfism due to disruption of Mediterranean marine ecology and seagrass resources by the Tortonian and Messinian Salinity Crises (MSC). This hypothesis is supported by the fact that the dwarfing is observed in fossils of the species dating from both before (Calabria, Sahabi) and after (Montpellier) the MSC.

RIASSUNTO - [*Metaxytherium serresii* (Mammalia: Sirenia): nuovi ritrovamenti pre-pliocenici, e implicazioni per la paleoecologia del Mediterraneo prima e dopo la crisi di salinità messiniana] - Viene riassunta l'osteologia del *Metaxytherium serresii* (Sirenia, Dugongidae, Halitheriinae) ed aggiornata la conoscenza dei caratteri filogenetici stabiliti sulla base degli esemplari fossili di Montpellier (Francia), Sahabi (Libia) e di nuovi reperti della Calabria. Questi nuovi resti, qui illustrati, sono i più antichi conosciuti della specie, riferibili al Miocene superiore (Tortoniano terminale; 7,3-7,6 Ma), mentre gli esemplari precedentemente conosciuti sono più recenti (Miocene finale-Pliocene inferiore; Messiniano-Zancleano). Il nuovo materiale ci consente altresì di ampliare la gamma delle variazioni morfologiche nel *Metaxytherium serresii* e di estendere stratigraficamente la conoscenza della specie al di sotto del Tortoniano terminale. I nuovi fossili provengono infatti da un orizzonte più antico del Messiniano, ma più giovane rispetto alla (meno estrema) crisi di salinità tortoniana, datata a circa 7,8-7,6 Ma e quindi dalle fasi iniziali dell'alterazione generale di salinità del Miocene superiore.

Gli esemplari calabresi, pur non differendo in maniera rilevante dai precedenti, mostrando sia zanne di media dimensione che un corpo ridotto, ampliano il campo di variazione morfologica intraspecifica e rappresentano il più antico ritrovamento della specie. Questo aumento dell'estensione temporale riveste una notevole importanza per la paleoecologia del Mediterraneo. È ipotizzabile che la riduzione corporea rappresenti un nanismo ecofenotipico dovuto allo sconvolgimento dell'ecologia marina del Mediterraneo e delle praterie marine a causa della crisi di salinità del Tortoniano e del Messiniano. Tale ipotesi è supportata dal fatto che il nanismo è stato osservato sia sugli esemplari antecedenti la crisi di salinità (Calabria, Sahabi) che nei successivi (Montpellier).

INTRODUCTION

Fossils of the extinct herbivorous marine mammals included in the genus *Metaxytherium* de Christol (= *Felsinotherium* Capellini; Order Sirenia, Family Dugongidae, Subfamily Halitheriinae) have been collected from Neogene rocks of Mediterranean lands for almost 200 years (Domning & Thomas, 1987). This genus makes its appearance in Europe (possibly as an immigrant from the New World) in the Early Miocene, and persists in the European fossil record until the mid-Pliocene as an anagenetically-evolving lineage, currently divided into four chronospecies (Domning & Thomas, 1987; Canocchi, 1987, recognizes a fifth). From the Middle Miocene onward, these species appear to have been the only sirenians surviving in the Mediterranean and Paratethyan region out of what had been a more diverse Paleogene sirenian fauna.

In a revision of this lineage, Domning & Thomas (1987) noted the very slight morphological change

exhibited by the Early and Middle Miocene species (*Metaxytherium krahuletzii* and *M. medium*, respectively). This near-stasis (documented in more detail by Domning & Pervesler, 2001) was followed by two conspicuous changes.

One was increase in tusk size (in the Early Pliocene *Metaxytherium serresii* and culminating in *M. subapenninum*, the last species of the lineage). Enlarged tusks are interpreted as adaptations to feeding on the rhizomes of the larger kinds of seagrasses, which are storage organs for carbohydrates and therefore nutritionally valuable (Domning, 2001).

The other morphological change seen in the sirenians was reduction in overall body size in *Metaxytherium serresii*, followed by a return in *M. subapenninum* (= "*Felsinotherium*" *forestii*, = "*F.*" *gervaisi*, = "*F.*" *gastaldi*) to the original and even larger size. Domning (1981; Domning & Thomas, 1987) interpreted this size reduction as ecophenotypic dwarfing coincident with the Messinian Salinity Crisis (MSC), speculating that

	Site	Stage	N.	Skeletal Element	Coll.	Number
1	Cessaniti (VV)	Upper Tortonian	1	Right rib 1	GPT	1(ces)VM7
			2	Incomplete right humerus	GPT	8(ces)VM7
			3	Cervical vertebrae 3 & 4	GPT	9(ces)VM7a,b
			4	Several vertebrae and rib fragments	GPT	14(ces)VM6
			5	Partial adult skeleton (vertebrae, ribs, sternum; left scapula, left humerus, and left radius-ulna; partial metacarpal)	GPT	15(ces)VM5
			6	Adult mandible with M ₃₋₃ (CARONE 1997)	GPT	18(ces)VM7
			7	Several vertebrae and rib fragments	GPT	27(ces)VM6
			8	Several vertebrae and rib fragments	GPT	29(ces)VM5
			9	Skull roof lacking left frontal	GPT	31(ces)VM5
			10	Right squamosal	GPT	32(ces)VM7
			11	Partial left scapula	GPT	38(ces)VM7
			12	Juvenile right radius	GPT	39(ces)VM7
			13	Caudal vertebra	GPT	40(ces)VM7
			14	Cervical vertebra 6	GPT	41(ces)VM7
			15	Immature right frontal	GPT	42(ces)VM6
			16	Left half of skullcap	GPT	43(ces)VM6
			17	Right radius-ulna	GPT	44(ces)VM6
			18	Juvenile right frontal	GPT	45(ces)VM7
			19	Rib	GPT	46(ces)VM5
			20	Tusk	GPT	47(ces)VM7
			21	Tympanic, malleus	GPT	48(ces)VM7a,b
			22	Sphenoid	GPT	49(ces)VM7
			23	Supraoccipital	GPT	50(ces)VM5
			24	Right M ₂	GPT	52(ces)VM7
			25	Right M ₃	GPT	54(ces)VM7
			26	Right DP ₃	GPT	55(ces)VM6
			27	Mandibles with M ₂₋₃	DSTC	CMS 21
			28	Adult skull lacking the zygomatic arches, lacrimals, and most of the rostrum	GPT	MBC 001
			29	Cervical vertebra 6	GPT	MBC 002
			30	Skull lacking maxilla, premaxilla and palatal region	GPT	MBC 003
			31	5 vertebrae and 12 ribs	GPT	MBC 004
			32	Immature mandible with M ₃	GPT	MBC 005
			33	Premaxillary rostrum with tusks (VAZZANA 1988a)	GPT	MBC 032
			34	4 vertebrae, Ribs, Cranial fragments	MAUL	143/1; 161/1; 167/1
			35	Rib fragments	MPMPN	MN05
2	Zungri (VV)	Upper Tortonian	36	Immature left scapula	GPT	7(zun)VM2
			37	Partial thorax of juvenile (vertebrae, ribs)	GPT	16(zun)VM2
3	Papaglionti (VV)	Upper Tortonian	38	2 caudal vertebrae	GPT	10(pap)VM2
			39	Cervical vertebra 7	GPT	36(pap)VM3
			40	Thoracic incomplete	GPT	37(pap)VM3
			41	Right M ₂	GPT	51(pap)VM3
			42	Left M ₂	GPT	53(pap)VM1
4	Zaccanopoli (VV)	Upper Tortonian	43	Adult skull lacking entire dorsal side and zygomatic arches	DSTC	"Cranio C"
5	Caria (VV)	Upper Tortonian	44	Rib fragment (DEL CAMPANA 1924)	MGPF	-
			45	Supraoccipital and fragment of parietal	MPMPN	MN01
			46	Incomplete thoracic vertebra	MPMPN	MN06
6	Rombiolo (VV)	Upper Tortonian	47	Xiphisternum	MPMPN	MN04
Metaxytherium medium						
7	Santa Domenica (VV)	Upper Tortonian	48	Skull, mandible, vertebrae, ribs, scapulae, humerus, radius-ulnae (MONCHARMONT ZEI & MONCHARMONT 1987)	MSNUN	M18403
8	Fitili (VV)	Upper Tortonian	49	Atlas, 9 ribs (probably same individual) (<i>partim</i> VAZZANA 1988a)	GPT	MBC 010
Metaxytherium cf. medium						
9	Caccuri (CS)	Miocene	50	Manubrium and ribs	DSTC	CMS 12
10	Catanzaro (CZ)	Tortonian?	51	Rib fragments (NEVIANI 1886a)	MGPB	--
			52	Rib fragments (NEVIANI 1886a)	MPC	--
			53	2 tusks (NEVIANI 1887)	?	--
11	Crichi (CZ)	Middle Miocene	54	Tusk (NEVIANI 1886a)	?	--
			55	Rib fragments (NEVIANI 1886a)	?	--

Tab. 1 - Sirenian localities in Calabria, age and all known material.

degradation of the near-shore habitat and food resources (seagrasses) on which these animals depended was reflected in stunted growth.

This explanation implied that the reduction in body size should have first occurred near the onset of the MSC, and should have been reversed after its end (or whenever adequate seagrass resources again became available) for those sirenian populations that survived the crisis or (more likely) recolonized the Mediterranean afterward. The Pliocene record was consistent with this prediction, but a Late Miocene, immediately pre-Messinian sirenian record was lacking in the region (the Sahabi specimens of *M. serresii* then being considered Pliocene in age). Thus it remained uncertain whether the size reduction began well before the MSC, perhaps for reasons unrelated to it; or coincided with the onset of Mediterranean desiccation; or was only manifested after the end of the MSC.

Here we report recent discoveries of Late Miocene (upper Tortonian) *Metaxytherium serresii* in Calabria, southern Italy, which establish that both tusk enlargement and reduction in body size occurred prior to the Messinian. These fossils demonstrate that the dwarfing in this lineage was indeed “peri-Messinian”, i.e., manifested before as well as after the MSC (Bianucci et al., 2004 and in press).

The first reports of fossil Sirenia in the Miocene deposits of Calabria date from 1886, when Prof. Antonio Neviani, in a study of fossils marine mammals, mentioned fragmentary remains brought to light by a chance find on the outskirts of the city of Catanzaro. In 1924, Del Campana reported a partial rib from the environs of Caria, in the province of Vibo Valentia. In 1970 the Tortonian sands of Santa Domenica di Ricadi, a few kilometers from Tropea, yielded most of a skeleton of *Metaxytherium medium* that was described by Moncharmont Zei & Moncharmont (1987). This specimen is preserved in the Museum of Paleontology of the Museo delle Scienze Naturali dell’Università “Federico II” di Napoli, with the number MSNUN M18403. More recently, Vazzana (1988) and Carone (1996, 1997) reported (also under the name *M. medium*) various skeletal elements, including a mandible with two molars, from localities between Tropea and Cessaniti.

The sand quarries near Cessaniti have since produced more complete and diagnostic material, which we describe here. These new specimens allow us to establish that the Cessaniti sirenians, which are stratigraphically higher than the skeleton from S. Domenica di Ricadi, represent not *M. medium* but its direct descendant *M. serresii*, previously known only from France and Libya and previously thought to be exclusively Pliocene in age.

MATERIALS AND METHODS

This study is based on the fossil materials from the Cessaniti area listed below as Newly Referred Material (Tab. 1), together with previously-studied topotypic material from Montpellier in French and Swiss collections (not all of which we have had the opportunity to study), and material from Sahabi in the collection of the International Sahabi Research Project, Garyounis University, Benghazi, Libya.

Institutional abbreviations: DSTC, Dipartimento di Scienze della Terra, Università della Calabria, Cosenza, Italy; FSL, Faculté des Sciences, Muséum des Sciences Naturelles, Lyon, France; FSM, Faculté des Sciences, Université de Montpellier, France; GPT, collection of the Gruppo Paleontologico Tropeano, Tropea, Italy; MAUL, Museo dell’Ambiente dell’Università di Lecce, Italy; MGPB, Museo di Geologia e Paleontologia “G. Capellini”, Bologna, Italy; MGPF, Museo di Geologia e Paleontologia di Firenze, Italy; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MPC, Museo Provinciale di Catanzaro, Italy; MPMPN, Museo Provinciale di Mineralogia e Petrografia di Nicotera, Italy; MSNUN, Museo delle Scienze Naturali dell’Università “Federico II” di Napoli, Italy; NHMB, Naturhistorisches Museum, Basel, Switzerland.

Specimens in the collection of the Gruppo Paleontologico Tropeano are numbered as follows. In the designation of (for example) specimen 15(ces)VM5, 15 denotes the fifteenth specimen collected, (ces) denotes the general locality of Cessaniti, V and M stand respectively for “vertebrate” and “marine”, and 5 refers to level 5 of the stratigraphic sequence exposed at Cessaniti (cf. Fig. 3). The locality of Papaglionti is indicated by (pap), and that of Zungri by (zun); the initial MBC denotes the specimen in the collection of the member Mario Bagnato.

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

GEOLOGICAL AND PALEONTOLOGICAL SETTING

In the Monte Poro Area (Fig. 1), in particular in the northeastern and southwestern parts (I.G.M. Sheets: n. 245, I NE Spilinga; n. 245, I NE bis Tropea; n. 246, IV NW Mileto), from which the studied finds come (Fig. 2), the Calabrian crystalline basement (made up of intrusive acidic rocks and crystalline schists) is overlain by a transgressive sedimentary series. This series seems to date back to the Tortonian age, and it is mainly made up of organogenic-alluvial parts. It comprises several sedimentary cycles, starting with the Tortonian transgression and ending with the Messinian regression. The deposits (Fig. 3) generally consist of sands (both fine- and coarse-grained) and clay. This sedimentation cycle ended with a period of desiccation and formation of evaporites. The end of the Miocene cycle of sedimentation was characterized by a series of conglomerates produced by rapid erosion and deposition following the terminal Miocene and its tectonic activity (Nicotera, 1959).

The landscape shows the typical morphology of a plateau, with a sometimes rather hilly and sometimes quite level aspect. The structure of the plateau seems to progress seaward through a series of wide terraces, crossed by radially-placed valleys and river cuts. From the highest point (710 meters above sea level), these terraces slope down to the seaside beaches, which are characterized by the presence of high, retreating cliffs. Along the river cuts, the typical rocky formations of the area crop out, and, due to their visibility, it is possible

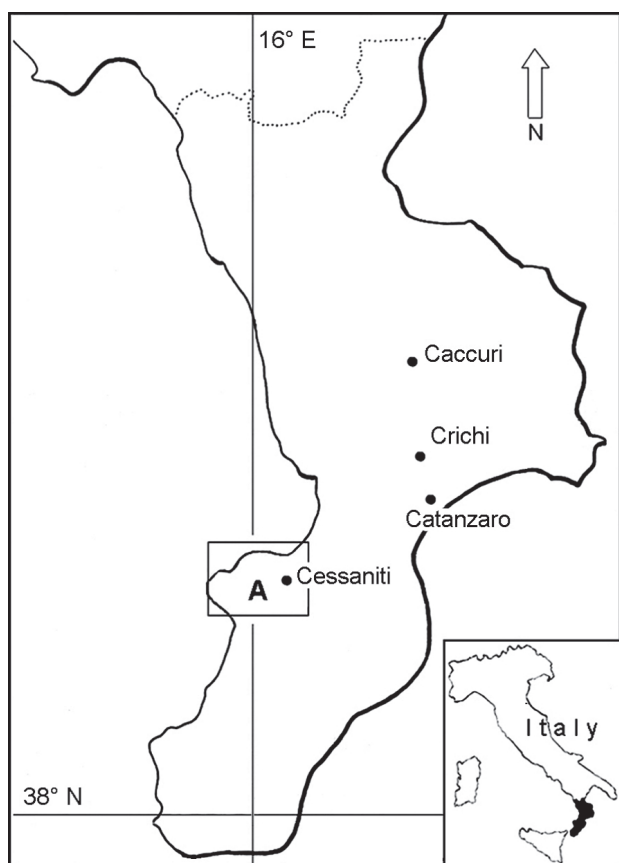


Fig. 1 - Geographic locations of Calabria where the sirenian specimens reported here were collected. A - Monte Poro area with Cessaniti, Catanzaro, Cricchi, Caccuri.

to reconstruct rather easily the several stratigraphic units of the sedimentary structure, and to examine the variations of the facies. The Monte Poro Area has been studied by Seguenza (1880), Cortese (1895), and Checchia Rispoli (1925), and, in the last 50 years, it has been carefully described and illustrated by Nicotera (1959), Ogniben (1973), and Barbera & Tavernier (1990b).

The crystalline basement in the Monte Poro area is made of various granitic rocks and crystalline-schistose rocks: the granitic rocks are the most widely distributed, while the others are found mainly in the eastern part of the area.

Upon the eroded crystalline substratum lies a transgressive sedimentary carpet made up of chemical and organogenic debris. These sediments range in age from Late Miocene (Tortonian) to Quaternary, and can be divided into several sedimentary cycles. The first cycle is the most important; it starts with a Tortonian transgression and ends with a Messinian regression. The second cycle, shorter than the first, is entirely Lower Pliocene. The following cycles are Quaternary, which are harder to date because they are extremely uniform sediments, and because they lack fossils.

The environments of deposition of the Tortonian units change from transitional (supralittoral, lagoonal,

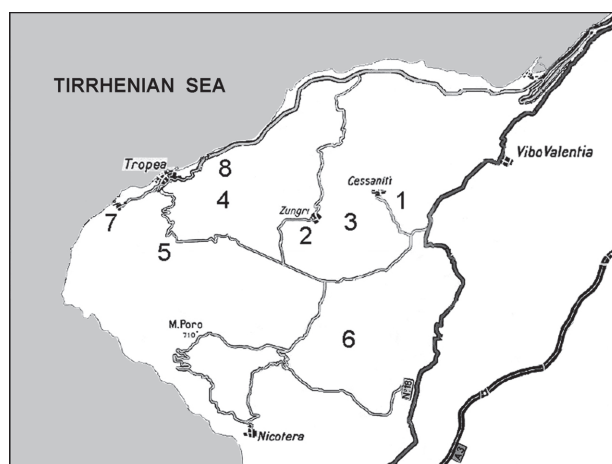


Fig. 2 - Monte Poro area, sirenian localities: 1 - Cessaniti; 2 - Zungri; 3 - Papaglionti; 4 - Zaccanopoli; 5 - Caria; 6 - Rombiolo, 7 - Santa Domenica, 8 - Fitili.

and perhaps also estuarine and deltaic) to infralittoral and circalittoral at the outer limit of the platform. Also present, intercalated in the series of normal marine deposits, are a number of examples of euxinic facies (Barbera & Tavernier, 1990a).

Up to now, all the Calabrian finds of Sirenia have come from a certain number of sites that have not been methodically excavated, and due to this all the finds lack taphonomic data.

All the specimens, which are kept in the DSTC and by a local society of avocational collectors (the Gruppo Paleontologico Tropeano, GPT), come from a series of nearby sand quarries. The bones were salvaged from the mining activities in these quarries, and have been preserved by the members of the GPT.

Cessaniti is the starting point for the description of the stratigraphic sections of the area, and this choice is not fortuitous: indeed, the area near this little town is the most famous and the most studied, as well as where most of the sirenian finds come from.

Close to the village of Cessaniti, near the Luigi Razza Military Heliport, some open sand quarries show the whole Tortonian sedimentary series (Fig. 3). The sediments consist of conglomerates (Level 1), black clays with molluscs (Level 2), barren greyish-yellow sands (Level 3), grey-blue medium- to fine-grained sands, with molluscs, marine and terrestrial vertebrates, and abundant *Clypeaster* (Levels 4-7), and greyish-yellow medium- and fine-grained sands with *Heterostegina papyracea*, gastropods and other molluscs (Level 8).

Levels 4-8 have been described by Nicotera (1959, p. 54) as "Arenarie giallastre o grigiastre semicoerenti, a grana variabile, in grossi banchi alternati a strati di medio spessore di arenarie ben cementate e riccamente fossilifere a *Clipeastri*, *Terebratulæ*, *Pettinidi* ed *Heterostegine*. Calcarei detritico-organogeni." ("Semi-coherent yellowish or grey sandstones, with variable particle size, localized in thick reefs in which they alternate with well-cemented sandstone strata of medium

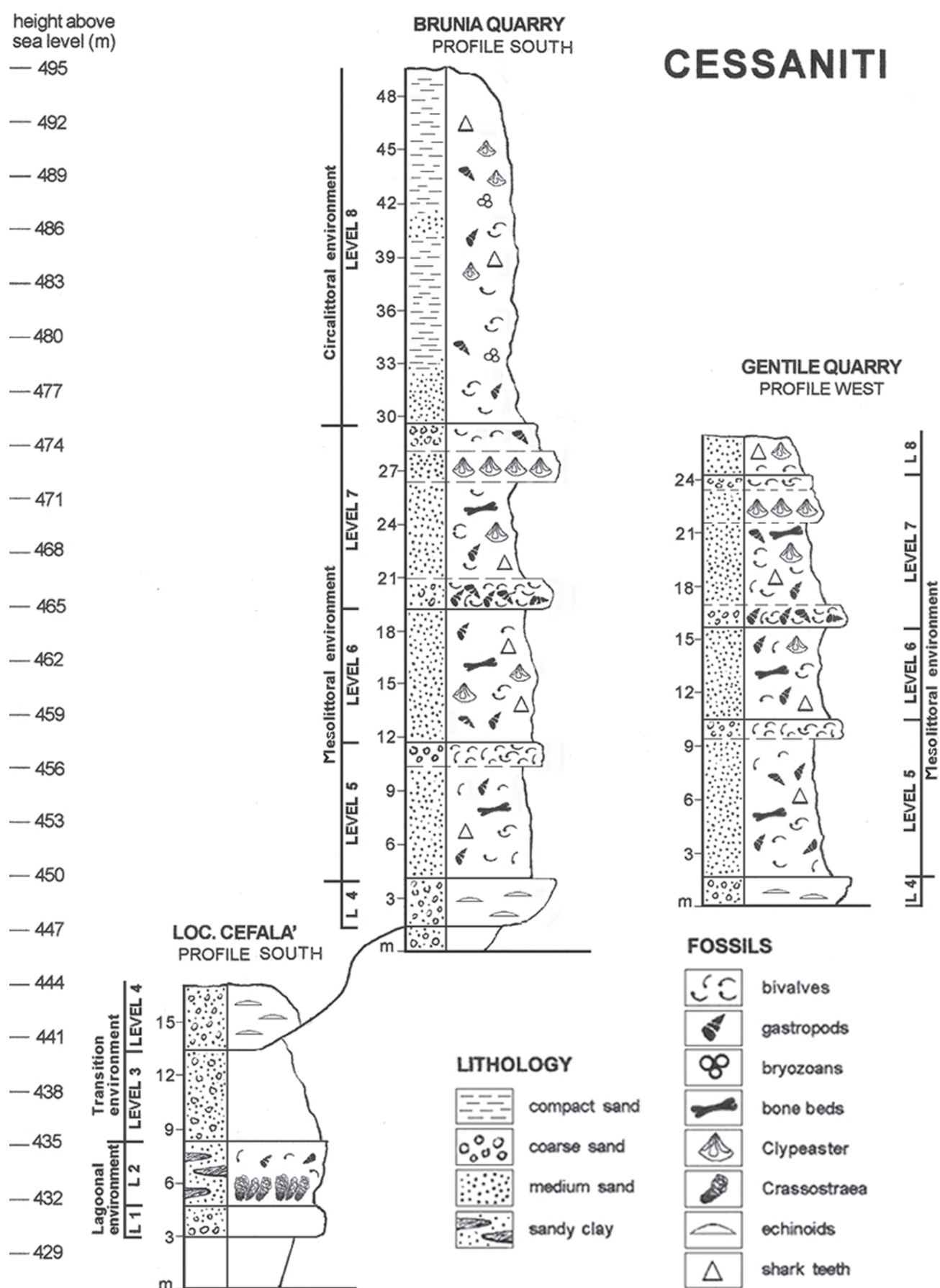


Fig. 3 - Stratigraphic section of the Cessaniti sandpits.

thickness, rich in *Clypeaster*, *Terebratula*, bivalves, and *Heterostegina*. Detrital and organogenic limestones.”).

This complex, widely outcropping in the whole province of Vibo Valentia, with a thickness of 150 meters in some places, needs to be subdivided due to its variety of environments of deposition.

Level 1 - In the overall Cessaniti area, the formation often begins with conglomerates alternating with slightly clayey sands, which are characterized by finer grain farther away from the substratum. Here the clayey strata are represented by grey-greenish sands and clays, lacking in foraminifera (Nicotera, 1959, pp. 50-51).

Level 2 - This layer is characterized by black clay with *Crassostrea gryphoides* and *Cerithium lignitarum*. It has variable thickness (1-3 m), and is lenticular. Lignite beds and thin chalky crusts are present. The oyster shells in this stratum are notably large (averaging about 25 cm thick), and are all in life position, arranged vertically and leaning against each other. There is no *post mortem* displacement or transport of shells, which could mean that a sudden influx of sandy material caused the death of the whole shoal by sudden burial (Barbera & Tavernier, 1990a, p. 416).

Level 3 - This unit is typified by poorly coherent greyish or yellowish fine sands and by unconsolidated arkosic sands with variable grain size. The characteristic of this sandstone level is the rarity of fossils, while the following levels abound in them. Nicotera (1959, p. 53) does not regard this formation as a distinct horizon, but as a transitional facies from a lagoonal or marshy coastal environment to a distinctly marine one. Its thickness is about 5 m.

Level 4 - In the Brunia quarry at Cessaniti, this stratum is a conglomerate a few centimeters thick, made up of mostly granodioritic pebbles together with numerous remains of *Amphiope bauriculata*. Nearby in the Gentile quarry, this stratum forms the base of the sandpit, and it crops out for about 5 m.

Level 5 - This layer is made up of grey-blue medium-grained sands, in which are found abundant internal casts of gastropods, oysters, fragments of carapaces of *Trionyx*, and remains of terrestrial and marine mammals.

Level 6 - Soft white medium- and fine-grained sands form this stratum, and contain numerous *Clypeaster*, fish teeth, and marine mammals.

Level 7 - The sandstones of this layer are not much different from the previous ones: their color is just a little bluer, and they are completely unconsolidated. This layer has been described by Barbera & Tavernier (1990b, p. 238) as “full of huge *Clypeaster*”; indeed, among the macrofossils, it is usual to find *Clypeaster insignis*, *C. redii*, and *C. franchi*. This level also yielded the greatest

number of skeletal remains and isolated bones of *Metaxytherium serresii*, dolphins, and whales.

Level 8 - This is the concluding layer of the Tortonian sedimentary cycle. It is made up of greyish-yellow medium- and fine-grained sandstones, with *Terebratula sinuosa*, bivalves, *Heterostegina papyracea* (named *H. complanata* by Ferretti et al., 2003), and *Clypeaster portentosus*. It is also the horizon that yielded, some 4 m below the *Heterostegina* level in the Brunia quarry, a specimen of the proboscidean *Stegotetabelodon syrticus* (Ferretti et al., 2003). Papazzoni & Sirotti (1999), in a biometric study of a population of *Heterostegina papyracea* from this level, refer the samples from the Cessaniti area to the terminal Tortonian, and argue (based on the *Stegotetabelodon* occurrence) that this might be correlative with the MN 13 Mammal Zone. However, the latest Tortonian is more usually considered equivalent to MN12 (Steininger et al., 1996). Ferretti et al. (2003) regarded the Cessaniti *Stegotetabelodon syrticus* as comparable in age to the type material from Sahabi, or possibly slightly earlier, but late Tortonian in any event.

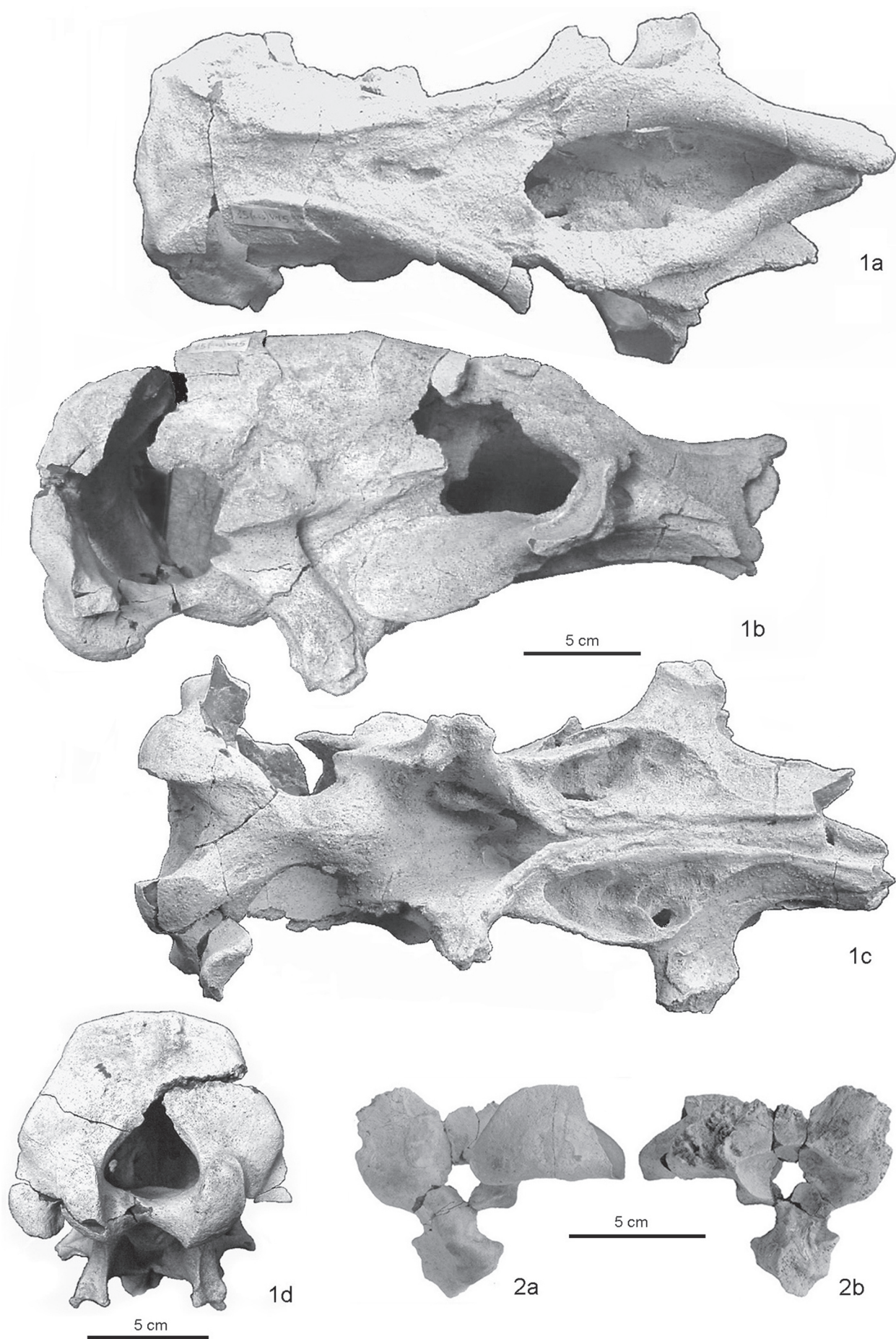
Conclusions drawn from the Miocene sedimentary associations of the Cessaniti area depend on the horizon being considered. Indeed, the associations go from a coastal lagoon (Level 2) to a fairly deep, near-shore environment (Level 8). The black sandy clay with *Crassostrea gryphoides* and *Cerithium lignitarum* testifies to the presence of a relatively hyposaline lagoonal environment, with rather unstable sedimentary conditions (Barbera & Tavernier, 1990b).

The “reefs” of *Crassostrea* can be attributed to “string reef associations”. This kind of “reef” is characteristic of brackish environments, and acts as a bar separating this environment from the sea. Later, in this lagoonal environment, different environmental conditions became established: the progressive reduction of the clay component was followed by the increase of sand grain size and by the deposition of sands containing *Clypeaster*. All these elements bear witness to a marine environment (Barbera & Tavernier, 1990b). The grey-blue sands with abundant *Clypeaster* and gastropod internal casts indicate a lagoonal environment. The presence of brachiopods, concomitant with the reduction in echinoids (Level 8), indicates a deeper environment, probably an open sea environment.

In the highest layers of the succession, Papazzoni & Sirotti (1999) detected the slight predominance of *Elphidium craticulatum*, which is characteristic of the euphotic zone (0-50 m; Murray, 1991).

EXPLANATION OF PLATE 1

- figs. 1-2 - *Metaxytherium serresii*.
 1 - Skull MBC 001. Dorsal (a), lateral (b), ventral (c) and posterior (d) views.
 2 - Right squamosal 32(ces)VM7. Lateral (a) and medial views.



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 serresii (Gervais, 1847) Depéret,
 1895

- 1832 *Halicore Cuvierii* - CHRISTOL, [partim], p. 244.
 1838 *Halicore medius* (Desmarest) - SERRES, p. 286. [Note that this new combination was misapplied to material specifically distinct from the original "*Hippopotamus*" *medius* of Desmarest (= *Metaxytherium medium*).]
 1841 "*Metaxytherium* de Montpellier" - CHRISTOL, p. 332; pl. 7: figs. 2-3, 6.
 1844 *M[anatus]. Cuvieri* (Christol) - BLAINVILLE, [partim], p. 122.
 1844 *M[etaxytherium]. Cuvieri* (Christol) - CHRISTOL IN BLAINVILLE, p. 130. [This and the previous name are *nomina oblita* as applied to Montpellier specimens.]
 1847 *Halitherium Serresii* - GERVAIS, p. 221.
 1878 *Felsinothierium Serresii* (Gervais) - ZIGNO, p. 941.
 1883 *Halitherium minor* - COPE, p. 52.
 1895 *M[etaxytherium]. Serresi* (Gervais) - DEPÉRET, p. 409.
 1997 *Metaxytherium medium* (Desmarest) - CARONE, p. 91; figs. 2-6.

Type - No type specimens of this species have ever been designated.

Type Locality - Montpellier, France.

Type Formation - Sables à *Gryphaea virleti*.

Age - Early Pliocene (lower Zanclean, MN 14).

Newly Referred Material - Listed in Tab. 1.

Locality, Formation, and Age of Newly Referred Material - Sandpits near Cessaniti, Vibo Valentia, Calabria, southern Italy; sandstones with *Clypeaster*, *Heterostegina*, and pectinids; Late Miocene (latest Tortonian, MN 12).

Range - Late Miocene (latest Tortonian, MN 12) to Early Pliocene (early Zanclean, MN 14), Mediterranean basin. Specimens have been recorded from Montpellier, France; Sahabi, Libya; and Calabria, Italy. A skullcap fragment and a lower second molar from the Pliocene of Dar bel Hamri, Morocco, were doubtfully referred to this species by Ennouchi (1954). An Early Miocene mandible from Benken, Switzerland, referred to *M. serresii* by Pilleri (1987, pp. 78-84), should instead be attributed to an earlier species of *Metaxytherium* (Domning & Pervesler, 2001, p. 40).

DESCRIPTION

Specimens of *Metaxytherium serresii* from Montpellier have been described at length by Gervais (1859), Depéret & Roman (1920), Thomas (1970), and Pilleri (1987, pp. 84-85; 1988). The sample from Sahabi was described by Domning & Thomas (1987). Here we supplement these sources with a redescription of

the species, emphasizing the new Calabrian material, in a format comparable to the redescrptions already published for *Metaxytherium floridanum* by Domning (1988) and *M. krahuletzii* by Domning & Pervesler (2001).

SKULL (Tabs. 2-3; Pls. 1-3, 5-6)

Premaxilla - Rostrum large [c. 3(1)]; dorsal keel thin and sharp anteriorly, broadens posteriorly into a convex surface; posterior end of rostrum upraised to form a boss in lateral view [c. 10(1)]. Lateral edges thin, not flaring much anteriorly; sides of anterior half of symphysis slightly convex where swollen by tusk alveolus. Symphysis long (13.5-17 cm or more in adults). Palatal surface rugose, deeply concave; right and left halves form angle of about 100-125°. Incisive foramen widens and shallows forward, its anterior end undefined. Nasopalatine canal subcircular to somewhat flattened dorsoventrally. Masticating surface of rostrum slightly trapezoidal in outline. Medium-sized incisors present; alveoli extend about half length of symphysis in adults [c. 140(1)]; for example, in MNHN I1789, with a premaxillary symphysis 153 mm long, alveolus has a depth of about 7 cm. Opening of premaxillary canal lies posteroventral to incisor alveolus. Nasal process long [c. 7(0)] and thin [c. 6(0)], contacts lacrimal and frontal [c. 9(1)] and abuts against nasal; ventrally it lies in groove in maxilla. Anterior end of mesorostral fossa constricted very slightly by bulge on medial side of premaxilla in Montpellier but not Calabrian specimens. Rostral deflection 50-55° in three Montpellier specimens, 73° in DSTC Cranio C.

Nasal - Large, thick and massive, set in socket in anterior margin of frontal. Nasals separated in midline of skull roof by processes of frontals in MBC 001, MBC 003, and MNHN I1829, but evidently in contact in FSM SM10 and possibly in MNHN I1789 [c. 31(0 or 1), scored as (1); see discussion below]. Dorsal exposure of nasal small [c. 32(1)] and variable in shape: parallelogram-shaped in MNHN I1829, but with convex medial border and anterolateral depression for nasal process of premaxilla in four other specimens including MBC 001 and MBC 003.

Ethmoidal Region - Poorly preserved.

Vomer - Not preserved.

Lacrimal - In NHMB MP994, lacrimal is 54 mm long, 25 mm wide, and 19 mm thick ventrally; bears a thin longitudinal flange at its ventral end, about 1 cm long and broad and protruding laterad; jugal does not appear to have overlapped lateral side of lacrimal.

Frontal - Supraorbital process moderately to well developed (as in MBC 003, Pl. 3, fig. 1), not inclined strongly ventrolateral [c. 43(0)]; variable in shape [c. 36(1)], generally broad mediolaterally with a laterally jutting posterolateral corner; in MNHN I1789 it is blunt anteriorly with a more distinct posterolateral corner. Lateral margin of supraorbital process not divided by deep groove(s) [c. 44(0)]. Orbicular apophyses are never present. Medial wall of temporal fossa formed by thin lamina orbitalis of frontal [c. 38(0)], whose falciform anterior edge may extend slightly forward of posterolateral corner of supraorbital process. A crista intratemporalis is weak or absent, but the lower part of the temporal wall may be slightly recessed. Internasal

process dorsally flat in midline; nasal incisure small or absent [c. 37(0)]. Median portion of frontal roof flat or slightly convex [c. 42(0)]. Lateral crests of frontals overhang in two of 9 specimens (FSM SM10, MBC 003). Anterior end of fronto-parietal suture lies 2.5 cm or less abaft nasals.

Parietal - Cranial vault more or less trapezoidal in coronal section anteriorly; 1.5-2.4 cm thick in anterior

midline in adults. Posterolateral corners of roof indented by squamosals. Roof flat or slightly convex anteroposteriorly. Temporal crests lyriform, variable in development: sometimes low, confined to lateral edges of a nearly flat roof and producing a nearly rectangular vault (type A; 8 specimens out of 17); or at lateral edges of, but upraised above, a markedly concave roof (type B; 6/17); or smoothly rounded and separated by about

		MBC 001	MBC 003	"Cranio C"
AB	Condylbasal length	-	-	390e
ab	Height of jugal below orbit	-	-	-
AH	Length of premaxillary symphysis	-	-	140*
BI	Rear of occipital condyles to anterior of interfrontal suture	205e	183	-
CC'	Zygomatic breadth	-	-	-
cc'	Breadth accross exoccipitals	132	-	133
de	Top of supraoccipital to ventral sides of occipital condyles	117	120	-
F	Length of frontals, level of tips of supraorbital processes to frontoparietal suture	108e	135	-
FF'	Breadth across supraorbital processes	120e	155	-
ff'	Breadth across occipital condyles	84	-	86
GG'	Breadth of cranium at frontoparietal suture	58	48	-
gg'	Width of foramen magnum	43	-	39
HI	Length of mesorostral fossa	115e	-	-
hi	Height of foramen magnum	46	57	41
JJ'	Width of mesorostral fossa	40e	-	-
KL	Maximum height of rostrum	63e	-	-
MM'	Posterior breadth of rostral masticating surface	-	-	74
no	Anteroposterior length of zygomatic-orbital bridge of maxilla	35	-	46
OP	Length of zygomatic process of squamosal	-	138	-
OT	Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen	-	175	-
P	Length of parietals, frontoparietal suture to rear of external occipital protuberance	89	75*	-
pq	Length of row of tooth alveoli	71	-	85
QR	Anteroposterior length of root of zygomatic process of squamosal	-	51	-
rr'	Maximum width between labial edges of left and right alveoli	83	-	79
ST	Length of cranial portion of squamosal	-	93	-
ss'	Breadth across sigmoid ridges of squamosals	-	-	-
T	Dorsoventral thickness of zygomatic-orbital bridge	8e	-	11
tt'	Anterior breadth of rostral masticating surface	-	-	50
UV	Height of posterior part of cranial portion of squamosal	-	92*	-
WX	Dorsoventral breadth of zygomatic process	-	40	-
yy'	Maximum width between pterygoid processes	48	-	42
YZ	Length of jugal	-	-	-
LFr	Length of frontal in midline	82e	88	-
HSo	Height of supraoccipital	59	50	-
WSo	Width of supraoccipital	90	84	-
PaW	Width of parietal roof between indentations made by squamosals	72	70	71
RD	Deflection of masticating surface of rostrum from occlusal plane (degees)	-	-	73°

Tab. 2 - Measurements (in mm) of skulls of *Metaxytherium serresii* from Cessaniti and Zaccanopoli. Letters at left in this and following tables denote measurements used by Domning (1978 and subsequent publications). e = estimated; * = broken

		31(ces)VM5	43(ces)VM6	50(ces)VM5	MN01	32(ces)VM7	42(ces)VM6	45(ces)VM7	MBC 003
QR	Anteroposterior length of root of zygomatic process of squamosal	-	-	-	-	43	-	-	-
ST	Length of cranial portion of squamosal	-	-	-	-	79	-	-	-
UV	Height of posterior part of cranial portion of squamosal	-	-	-	-	86	-	-	-
WX	Dorsoventral breadth of zygomatic process	-	-	-	-	34	-	-	-
F	Length of frontals, level of tips of supraorbital processes to frontoparietal suture	-	-	-	-	-	112	75	-
FF'	Breadth across supraorbital processes	-	-	-	-	-	120e	86	-
GG'	Breadth of cranium at frontoparietal suture	-	-	-	-	-	66e	58e	-
LFr	Length of frontal in midline	-	-	-	-	-	70e	52	-
HSo	Height of supraoccipital	58	50	40	51	-	-	-	-
WSo	Width of supraoccipital	87	74e	76	87	-	-	-	-
PaW	Width of parietal roof between indentations made by squamosals	71	-	-	66	-	-	-	-
cc'	Breadth across exoccipitals	-	-	-	-	-	-	-	142
ff'	Breadth across occipital condyles	-	-	-	-	-	-	-	100
gg'	Width of foramen magnum	-	-	-	-	-	-	-	48
yy'	Maximum width between pterygoid processes	-	-	-	-	-	-	-	51

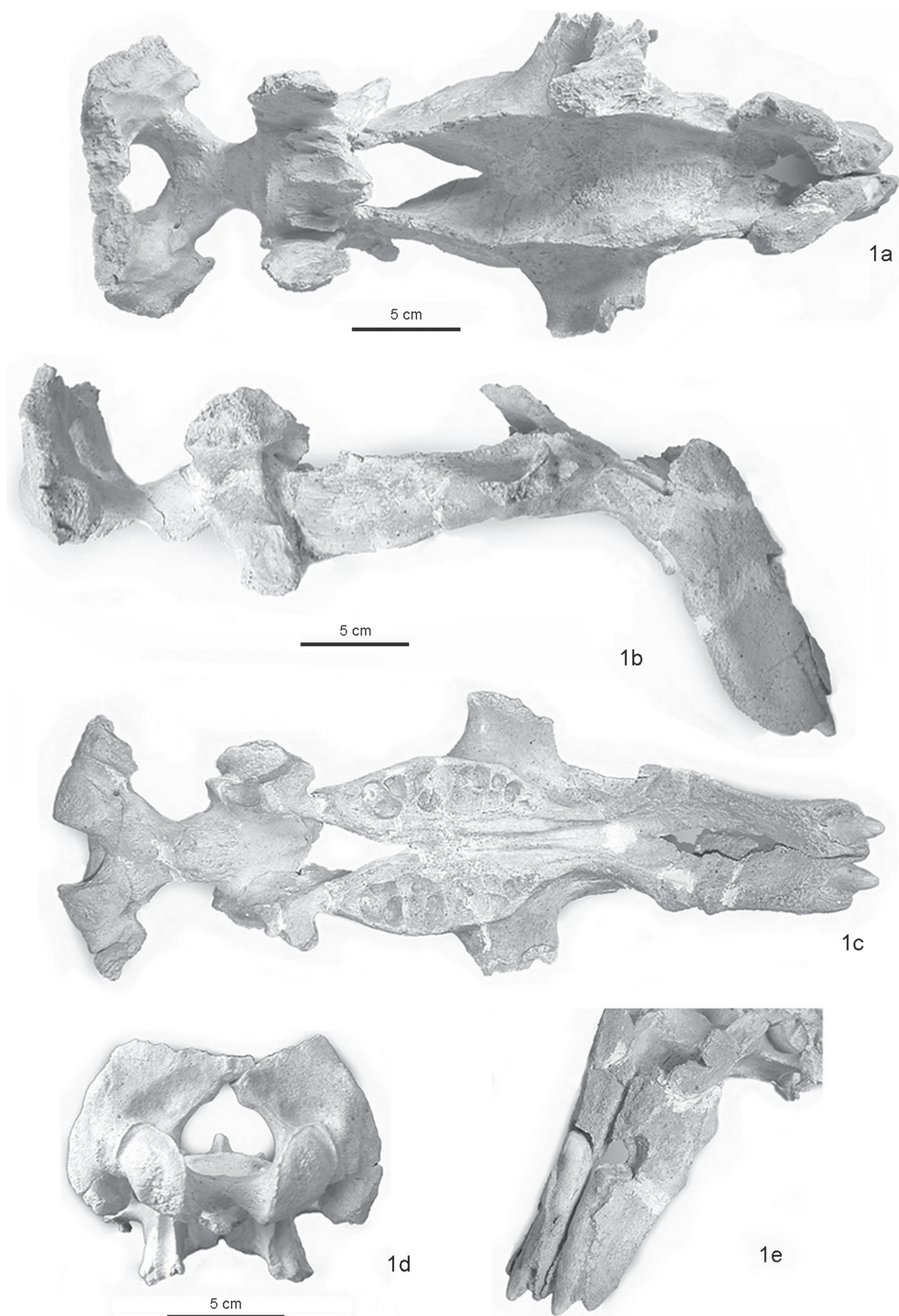
Tab. 3 - Measurements (in mm) of squamosal, frontals, parietal-supraoccipital skullcaps, and basicranium of *Metaxytherium serresii* from Cessaniti and Caria. e = estimated

2 cm, with a distinctly concave roof (type C; 2/17); or with distinct, sharp medial edges separated by >2 cm (type D; 1/17). (Types A, B, C, and D are represented in Calabria.) Internal occipital protuberance distinct, sometimes (5/17; both MBC 003 and MN 01) sharply pointed; tentorium a straight but often (8/17; only in

MBC 003) indistinct transverse ridge; transverse sulcus more or less shallow, usually (13/17) without distinct lateral pits. Bony falx may remain sharp as far as frontoparietal suture (6/16), or become low and rounded (7/16; MBC 003) or almost flat and indistinct anteriorly (3/16); the first two conditions are

EXPLANATION OF PLATE 2

fig. 1 - *Metaxytherium serresii*. skull DSTC "Cranio C". Dorsal (a), lateral (b), ventral (c), posterior (d) views, and detail of rostrum and tusks, in anterolateral view (e).



represented in Calabria. An emissary foramen is present in only one specimen (and that one from Calabria), but a small, low median bump just in front of the external occipital protuberance is usually seen (13/16).

Supraoccipital - Pentagonal or hexagonal in outline, with more or less rounded dorsolateral corners. Forms angle of about 100°-124° with after part of parietals (N = 19). External occipital protuberance usually rises above plane of parietal roof (13/19); median ridge below it always distinct. Nuchal crest usually not distinct at its lateral ends near squamosals (12/19). Areas of insertion for semispinalis capitis muscles typically are flattish, oval, rugose, and face posterodorsal, usually markedly concave (12/19) and with sharply defined ventromedial edges (16/19); extend no more than halfway to ventral end of supraoccipital. Lower part of supraoccipital more or less concave in midline and convex laterally below semispinalis insertions. Lateral borders of supraoccipital thick and rounded, usually sloping outward at bottom, and without overhanging upper corners. Ratio of width to height of supraoccipital varies from 1.24 to 2.04 (N = 19). Sutural surfaces for exoccipitals distinctly separated in midline in nearly all cases (16/18), sometimes (4/18) by a notch.

Exoccipitals - Never fuse to supraoccipital and usually (4/5) do not meet in dorsal midline; in Cranio C, however, they are fused along a suture about 11 mm long (Pl. 2, fig. 1d) [c. 66(0 or 1, scored as 1)]. In MBC 001, the exoccipitals almost meet, but are separated by a downward projection of the supraoccipital (Pl. 1, fig. 1d). Foramen magnum has acute dorsal peak. Dorsolateral border of exoccipital has more or less smoothly rounded posterior edge [c. 70(0)]. In adults this border sometimes forms a more or less flat surface (facing laterally) which is broadest (about 1.5 cm) at level of top of supracondylar fossa. Fossa usually reduced to only moderate depth (4/5), but primitively deep in the immature specimen MBC 003 (Pl. 3, fig. 6) [c. 67(2 or 3, scored as 3)]. Arc of condylar articular surface subtends angle of about 96°-120° (N = 6). Condylod foramen single. Condyle extends ventrally to about same level as tip of paroccipital process.

Basioccipital - As in other dugongids, bears pair of rugosities for longus capitis muscles. Posterior slope steeper than anterior.

Basisphenoid - Sella turcica shallow; region of tuberculum sellae nearly flat (2/5) or bearing a sharp transverse ridge (3/5).

Presphenoid - No elevated shelf (orbitosphenoidal crest) overhangs chiasmatic grooves, nor are distinct grooves present.

Orbitosphenoid - Optic foramen lies at level of dorsal side of sphenorbital foramen. Bony wall lateral to optic foramen does not bear a distinct pointed process.

Alisphenoid - Lateral side of pterygoid process usually sculptured to some degree. A slight convexity continues forward edge of zygomatic root anteriorly in about half of cases.

Pterygoid - Pterygoid fossa fairly broad and well-developed, extending above level of roof of internal nares [c. 102(1)]; lateral and medial edges usually meet dorsally in a well-defined intersection. Medial edge of fossa projects farther aft than lateral edge. Ventral tips of alisphenoid and pterygoid enclose end of palatine in slot between them anteromedially.

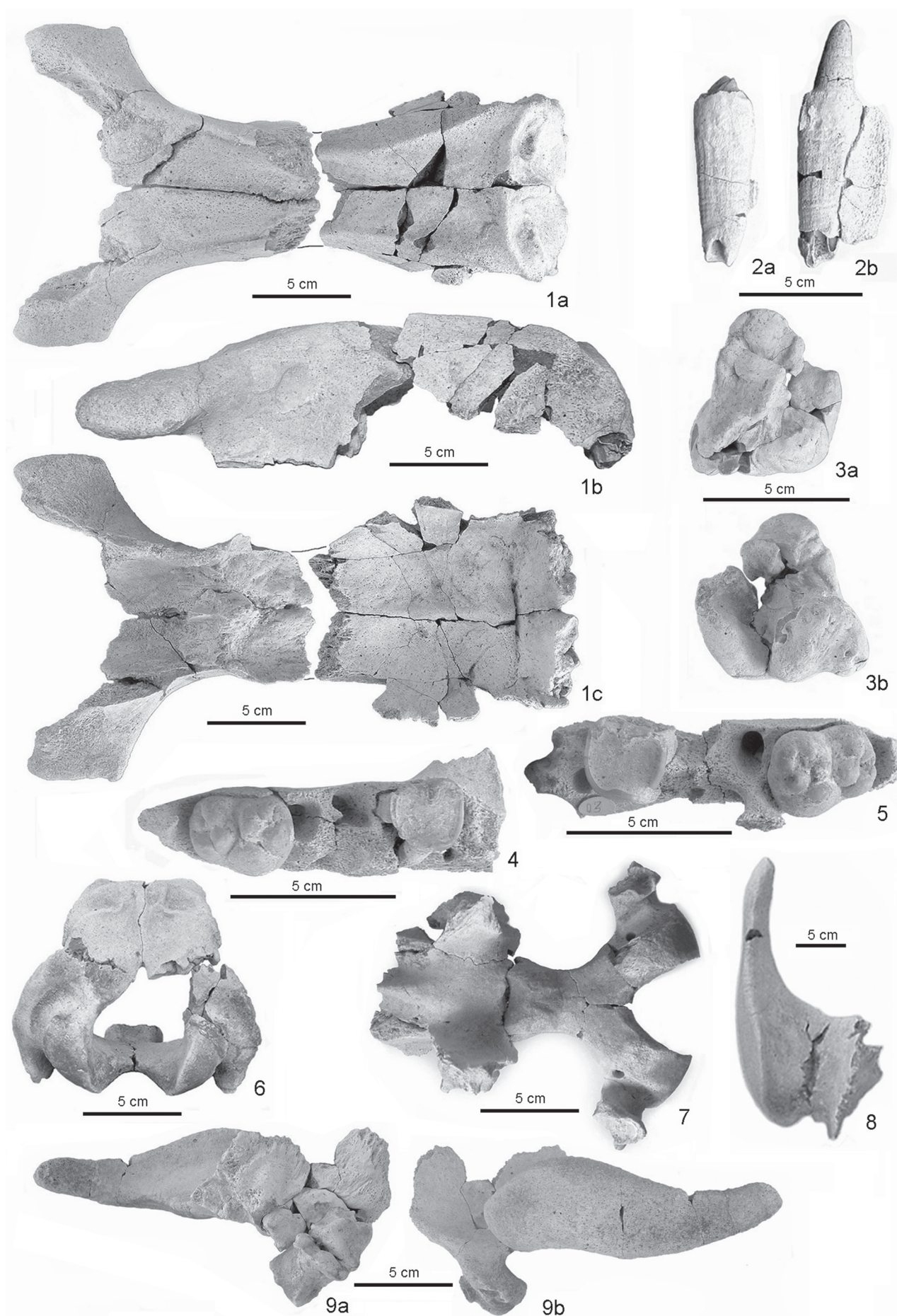
Palatine - Forms anteromedial side and (together with alisphenoid) smooth, rounded (not bladelikey) anterolateral extremity of pterygoid process. Palate <1 cm thick at level of M² [c. 16(0)]. Palatal incisure reaches posterior edge of M² alveoli in Cranio C (Pl. 2, fig. 1c), reaches about middle of M³ alveoli in MBC 001 (Pl. 1, fig. 1c). Anterior end of palatine probably lies at or just behind posterior edge of zygomatic-orbital bridge [c. 99(1?)].

Maxilla - Alveolar portion heavy and massive. Edges of palatal surface lyriiform; surface narrows rapidly forward of molars, becomes narrowest just forward of anterior edge of zygomatic-orbital bridge, then widens at posterior end of rostral masticating surface. Palatal gutter fairly deep, with rounded edges. Palatal and rostral surfaces meet in smooth but abrupt curve; anterior part of palate (between toothrow and strongly deflected premaxillary portion of rostrum) is downturned about 25-40° from occlusal plane. Zygomatic-orbital bridge elevated ≥ 1 cm above alveolar margin [c. 11(1)]. Bridge long anteroposteriorly [c. 14(0)], with thin forward edge and thick, rounded after edge. Posterior opening of maxillopremaxillary canal 5-8 mm in diameter.

Squamosal (Tab. 3; Pl. 1, fig. 2; Pl. 3, figs. 8-9) - Dorsally in contact with squared posterior part of parietal roof [c. 76(1)]. Sigmoid ridge prominent [c.

EXPLANATION OF PLATE 3

- figs. 1-9 - *Metaxytherium serresii*. Cranial elements MBC 003.
- 1 - Skull roof; dorsal (a), lateral (b) and ventral (c) views.
 - 2 - Left tusk (a) and right tusk (b); lateral views.
 - 3 - Right periotic; dorsomedial (a) and ventrolateral (b) views.
 - 4 - Right maxilla fragment with M¹ and M³ and alveoli, in occlusal view.
 - 5 - Left maxilla fragment with M¹ and M³ and alveoli, in occlusal view.
 - 6 - Supraoccipital, exoccipitals and basioccipital, in posterior view.
 - 7 - Basicranium (exoccipitals, basioccipital, basisphenoid, presphenoid, alisphenoid, pterygoid), in ventral view.
 - 8 - Left squamosal, in dorsal view.
 - 9 - Right squamosal with periotic *in situ*, in medial (a) and in lateral (b) views.



		18(ces)VM7	MBC 005	CMS 21
AB	Total length	-	217	213*
AG	Anterior tip to front of ascending ramus	-	158	167*
AP	Anterior tip to rear of mental foramen	-	79	67*
AQ	Anterior tip to front of mandibular foramen	-	-	145*
AS	Length of symphysis	-	-	77*
BG	Posterior extremity to front of ascending ramus	73*	78	79
BQ	Posterior extremity to front of mandibular foramen	-	-	87
CD	Height at coronoid process	134*	-	-
DF	Distance between anterior and posterior ventral extremities	110*	-	-
DK	Height at mandibular notch	-	-	-
DL	Height at condyle	-	-	-
EF	Height at deflection point of horizontal ramus	104	103*	112e
EU	Deflection point to rear of alveolar row	97	98*	105e
GH	Minimum anteroposterior breadth of ascending ramus	-	66	67
GP	Front of ascending ramus to rear of mental foramen	98	-	93
IJ	Maximum anteroposterior breadth of dorsal part of ascending ramus	-	-	71*
MN	Top of ventral curvature of horizontal ramus to line connecting ventral extremities	27*	-	-
MO	Minimum dorsoventral breadth of horizontal ramus	66	59e	59
RR'	Maximum breadth of masticating surface	69	46	57
SQ	Rear of symphysis to front of mandibular foramen	71	-	77
TU	Length of alveolar row	65	76e	80
VV'	Maximum width between labial edges of left and right alveoli	85	-	-
WW'	Minimum width between angles	77e	-	61e
XX'	Minimum width between condyles	-	-	147e
MD	Deflection of symphyseal surface from occlusal plane (degrees)	70°e	69°	73°e

Tab. 4 - Measurements (in mm) of mandibles of *Metaxytherium serresii* from Cessaniti. e = estimated, * = broken.

74(0)], usually with strongly bent dorsal shoulder. Mastoid indentation usually deep. External auditory meatus <1 cm long mediolaterally [c. 75(1)], and about as wide anteroposteriorly as high [c. 82(1)]. Surface of cranial portion dorsal to zygomatic root may be slightly inflated or bulging. Postglenoid process and postarticular fossa distinct and well-developed. Temporal condyle irregularly oval with more or less well-defined edges. Processus retroversus moderately inflected [c. 77(1)], does not project below squamosal's line of suture with jugal, and is not turned inward ventrally to a noticeable degree; its posterior end lacks distinct dorsal and ventral protuberances or terminations. Zygomatic process broader posteriorly than anteriorly. Posterodorsal edge of process straight or convex in outline and more or less convex laterad.

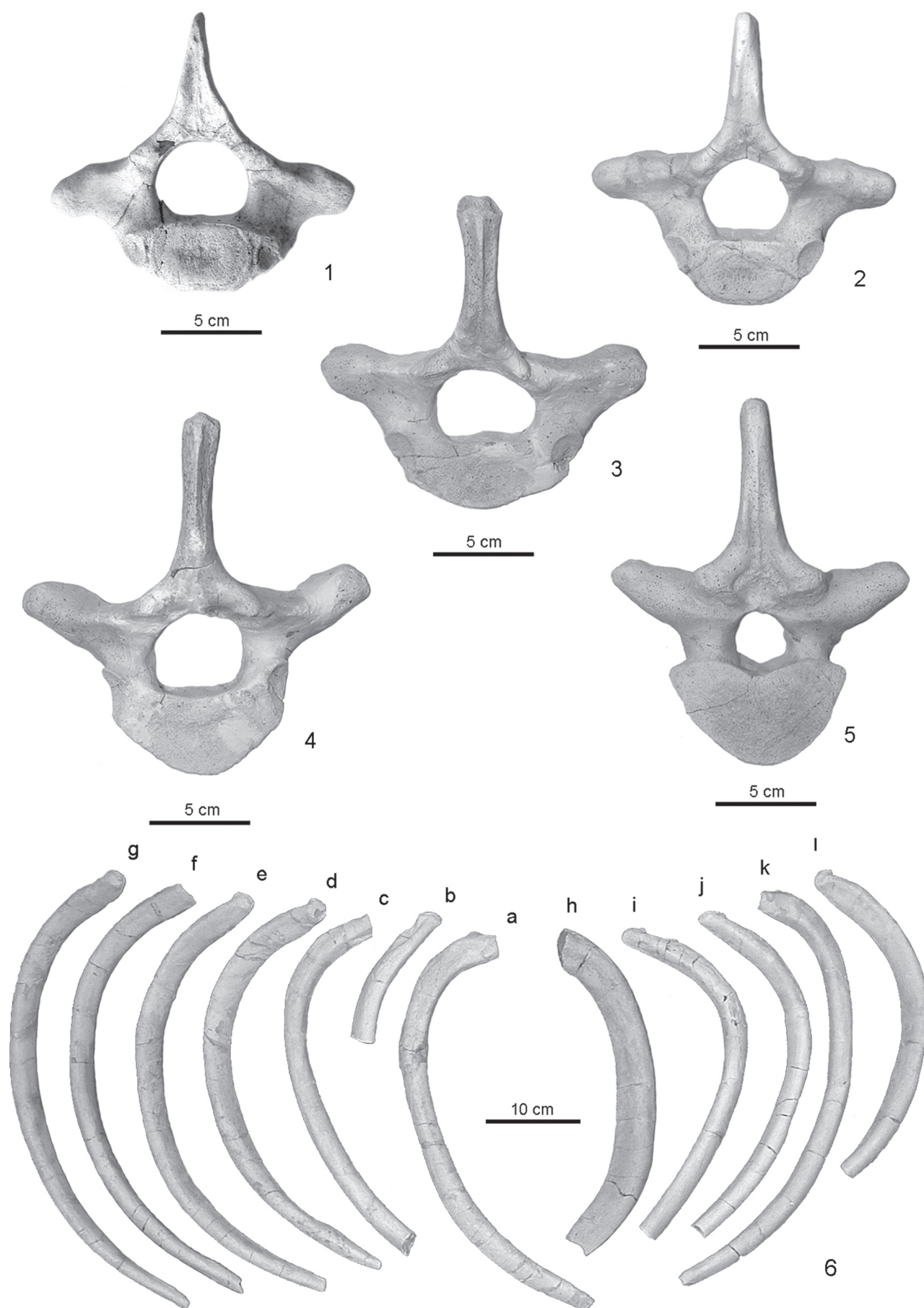
Jugal - Jugal does not contact premaxilla [c. 87(0)]. Preorbital process relatively flat and thin [c. 88(0)]. Ventralmost point of jugal lies under posterior part of orbit [c. 85(2)]. Ventral tip not thickened; border behind it generally smooth, and variably concave in outline. Ventral margin of orbit not overhanging lateral surface of jugal [c. 90(0)]. Raised postorbital process not present in front of tip of squamosal. Posterior process longer than diameter of orbit [c. 89(0)]; posteroventral edge concave in outline. Zygomatic process probably extends just beyond level of front edge of temporal condyle.

Ear Region - See also Thomas (1970).

Tympanic - Left tympanic 48(ces)VM7a (Pl. 5, fig. 7a) has V-shaped distal border, rounded in outline with more or less irregular blunt tip. Posterodistal edge slightly concave. External side smooth and somewhat

EXPLANATION OF PLATE 4

- figs. 1-6 - *Metaxytherium serresii*, MBC 004.
- 1 - First thoracic vertebra, in posterior view.
 - 2 - Second thoracic vertebra, in posterior view.
 - 3 - Third thoracic vertebra, in posterior view.
 - 4 - Fourth thoracic vertebra, in posterior view.
 - 5 - Seventh? thoracic vertebra, in posterior view.
 - 6 - Twelve ribs; left (a-g) and right (h-l) ribs, in posterior view.



	47(ces)VM7	MBC 003		MBC 032	
		Left	Right	Left	Right
Total length	80	73*	94	91	92
Length of crown	36	--	27	31	29
Diameter at base of crown	16 x 20	--	16 x 21	18 x 19	18 x 19
Diameter at midsection of crown	11 x 12	--	11	11 x 12	12 x 13
Diameters of the root	17.5 x 24	18 x 25,5	18,5 x 26	15,5 x 28	15 x 27

Tab. 5 - Measurements (in mm) of tusks of *Metaxytherium serresii* from Cessaniti. * = broken.

convex; inner part presents a slight convexity, with shallow grooves and ridges on proximal edge. Branches not preserved. Bone structure entirely osteosclerotic.

Malleus - On the associated left malleus 48(ces)VM7b (Pl. 5, fig. 7b), posterior end of orbicular apophysis convex. Processus muscularis massive, swollen, and elliptical in outline. Manubrium not preserved. Two facets (connected ventrally by small fold of bone) articulate with incus: anterior facet larger (5+ mm wide), forming somewhat flat plate raised above body of malleus; posterior smaller and saddle-shaped; axes of the two facets form angle of about 66°.

Mandible (Tab. 4; Pl. 6) - Condyle somewhat elliptical (nearly round in NHMB MP 145); overhangs laterally. Mandibular notch usually deep (but wide and shallow in NHMB MP 145 [Pilleri, 1988, pl. 2] and MP 188); coronoid process well developed, with backward-pointing tip; anterior border of process extends slightly anterior to base [c. 126(1)]. Posteromedial edge of condylar process thin and sharp. Notch in rear of mandible below condyle smooth in outline, not distinctly stepped at its lower end [c. 125(2)]. Edge of angle thickened. Angle convex in outline with crenulated edges. Internal and external pterygoid fossae large; medial side of angle is flat area 2-3 cm wide separating internal pterygoid fossa from ventral tip. Coronoid canal and dental capsule as in other *Metaxytherium* and *Dusisiren*. Shelf lateral to M_3 in immature specimens (e.g., NHMB MP 145) may be concave dorsally, reminiscent of condition reached by *D. jordani* in old age. Horizontal ramus short though not very deep [c. 128(1)], with strongly concave ventral border [c. 122(3)] that is not tangent to mandibular angle [c. 129(1)]; posterior part of ventral edge not especially sharp; dorsal edge thin anterior to toothrow. Mental

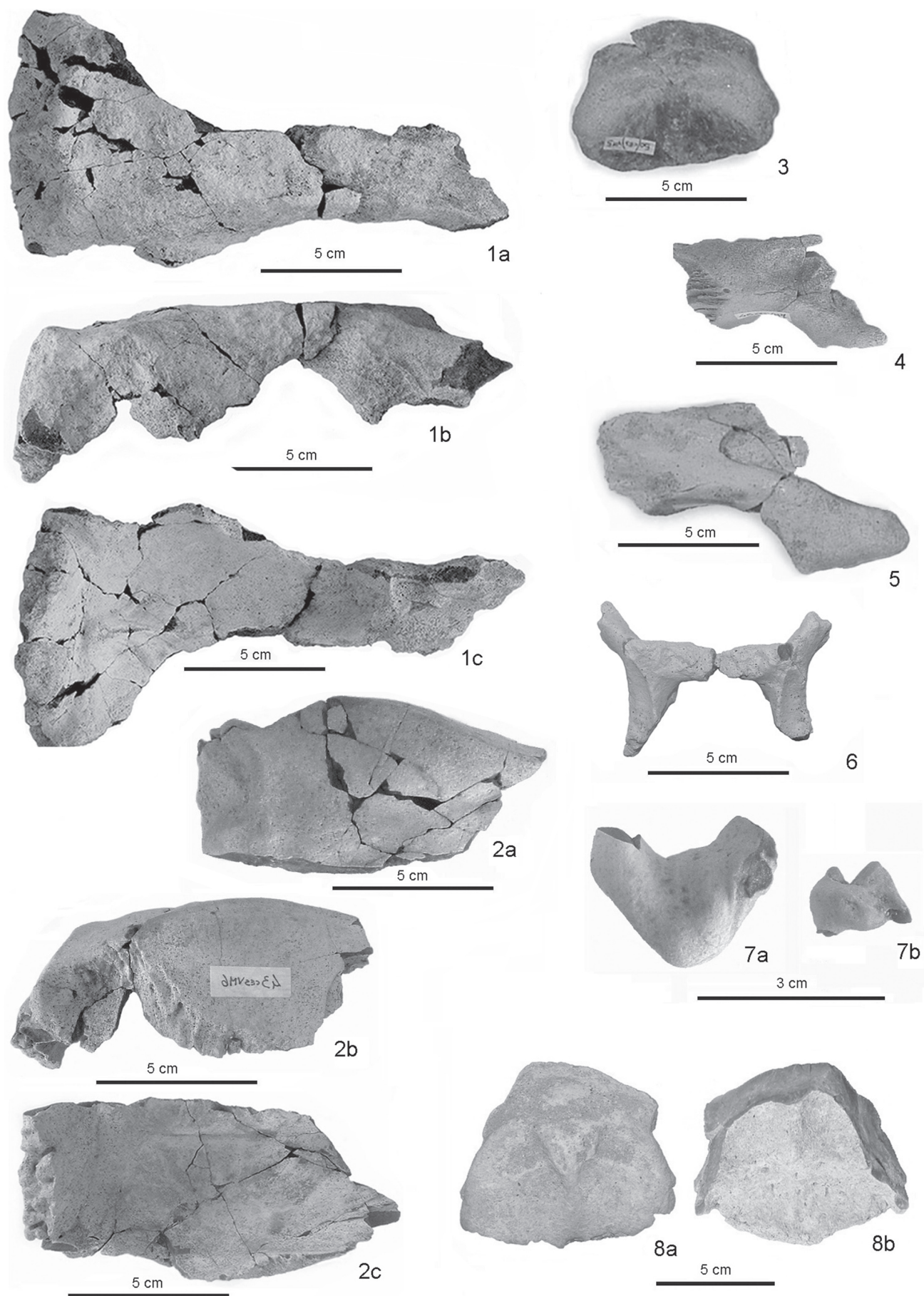
foramen lies at or just behind level of deflection of dorsal edge of ramus; foramen very large and almost always single [c. 123(1)]. In DSTC CMS 21 (Pl. 6, fig. 3a), however, there was on both sides (but now broken) a complete bridge about 8 mm wide across the anterior part of the mental gutter, which closed off the large mental foramen about 3 cm from its posterior edge. Anterodorsal margin of mental foramen may be formed by sharp ridge(s). Dorsal side of mandibular canal pierced by much smaller anterodorsal-directed canals. Deflection of masticating surface abrupt, about 56-75°. Masticating surface broad [c. 121(1)], deeply notched posteriorly, bears two rows of vestigial incisor alveoli (sometimes indistinct) that did not contain teeth; surface constricted anteriorly, narrow part bears one pair of vestigial alveoli, as in other *Metaxytherium*, *Halitherium*, and *Dugong*; lateral edges of masticating surface convex, thin, overhanging. Posteroventral side of symphysis flat or concave; anteroventral side broadly convex transversely, slightly concave anteroposteriorly. Symphyseal suture may remain unfused, even in adults.

Dentition (Tabs. 5-7) - Lifetime dental formula presumed to be I 1/0, C 0/0, DP 3/3, M 3/3, as in other *Metaxytherium*. We interpret the deciduous premolars, by analogy with *Dusisiren* Domning, *Prototherium* Zigno, and *Trichechus* (see Domning, 1978, pp. 16-17; 1982, p. 608; Domning et al., 1982, p. 59), as DP3-5.

The cheek teeth erupt sequentially throughout the animal's growth to maturity. The most anterior teeth are worn out and shed as new ones erupt at the rear, and the empty alveoli are eventually obliterated by mesial drift of the posterior teeth. (This process, however, should not be likened to horizontal tooth replacement in manatees, which produce unlimited numbers of

EXPLANATION OF PLATE 5

- figs. 1-8 - *Metaxytherium serresii*. Cranial elements.
- 1 - 31(ces)VM5, skull roof; dorsal (a), lateral (b) and ventral (c) views.
 - 2 - 43(ces)VM6, skull roof; dorsal (a), lateral (reversed - b) and ventral (c) views.
 - 3 - 50(ces)VM5, supraoccipital; posterior view.
 - 4 - 45(ces)VM7, juvenile right frontal; dorsal view.
 - 5 - 42(ces)VM6, immature right frontal; dorsal view.
 - 6 - 49(ces)VM7, sphenoid; posterior view.
 - 7 - 48(ces)VM7, left tympanic (a) and malleus (b); medial views.
 - 8 - MN01, supraoccipital; posterior (a) and anterior (b) views.



		Crown length	Anterior width	Posterior width
MBC 003	M ¹ (l)	20.2	19.8	18.1
	M ¹ (r)	20.4	19.6	-
	M ³ (l)	30.5	25.1	20.3
	M ³ (r)	29.8	24.6	19.8
GPT 18(ces)VM7	M ₃ (l)	26.1	18.2	18.1
	M ₃ (r)	25.5	18.3	18.4
DSTC CMS21	M ₂ (l)	21.1	17.8	17.7
	M ₂ (r)	21.0	-	-
	M ₃ (l)	27.2	19.3e	19.7e
	M ₃ (r)	25.9e	-	-

Tab. 6 - Linear dimensions (in mm) of cheek teeth in associated dentitions of *Metaxytherium serresii* from Cessaniti. e = estimated.

supernumerary molars; Domning & Hayek, 1984.) In adult *Metaxytherium*, the cheek dentition is typically reduced to DP5-M3 or M1-3; and of these, M1 and frequently M2 are so heavily worn that no enamel pattern remains. In old age, even the anterior molars may be lost. The distance between M₃ and the rear of the coronoid canal increases with age; in an old adult *M. serresii* from Sahabi (3P66A) this distance is about 14 mm.

Molars of *Metaxytherium* spp. show considerable individual variation in size, complexity, and cusp arrangement, and most of this variation is not of value for systematics. For more detailed descriptions, measurements, and/or illustrations of molars of *M. serresii*, see Gervais (1859), Depéret & Roman (1920), Thomas (1970), Pilleri (1987, 1988), and Domning & Thomas (1987).

I¹ (Pls. 2-3, 6): Tusk present [c. 139(0)], straight [c. 138(0)], of medium size, with an alveolus extending about half the length of the premaxillary symphysis [c. 140(1)]. Enamel crown complete, subconical, with suboval or subelliptical cross section [c. 136(0), 137(0), 141(0), 142(0)]. Enamel irregularly wrinkled; unworn crowns often have a slight transverse ridge at tip. Root mediolaterally compressed, marked by growth rings and sometimes by a few narrow (1 mm) longitudinal grooves along whole root and base of crown; widely open at first and increasing in diameter away from

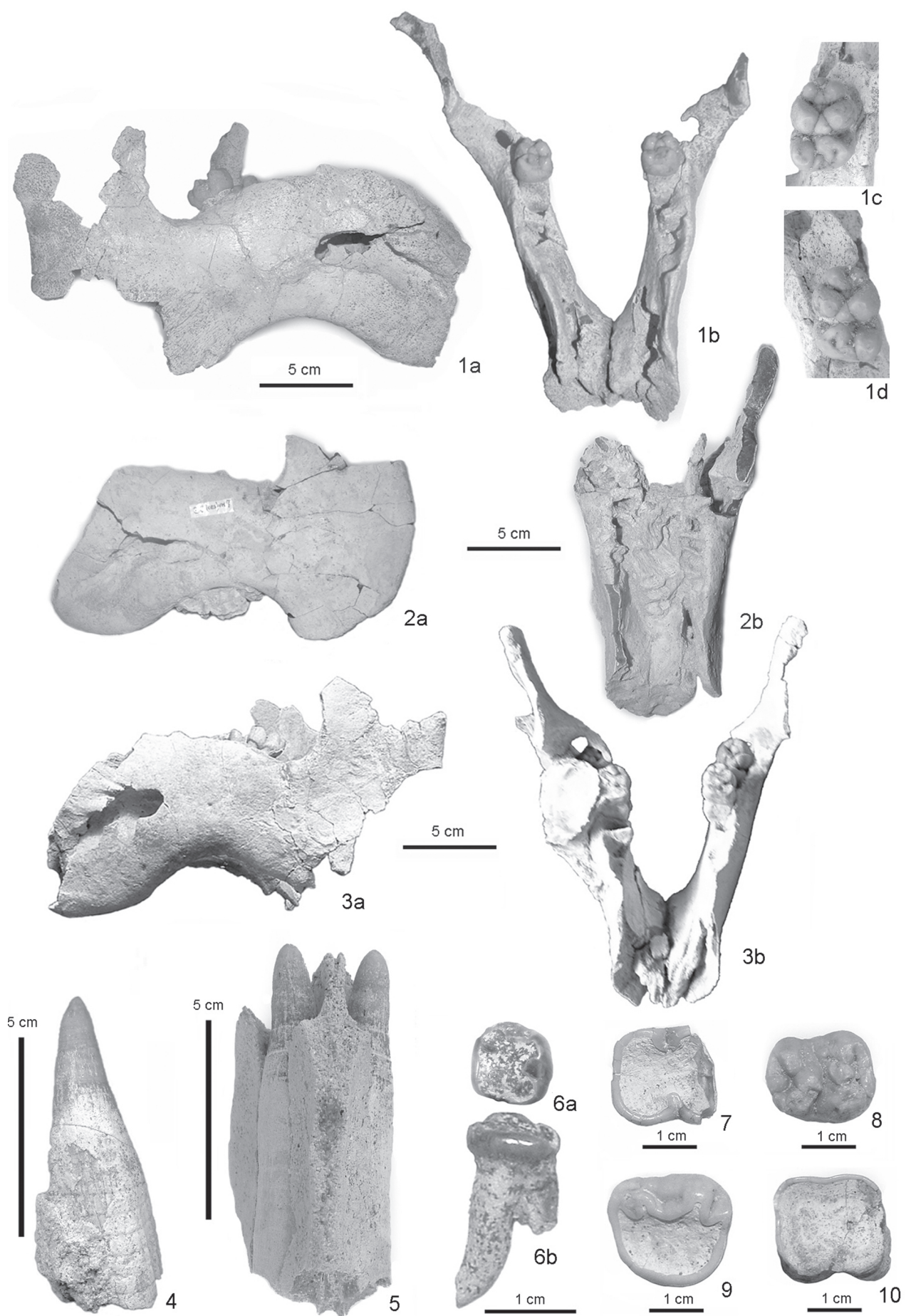
crown. With increasing maturity, root lengthens and closes, tapering toward root apex and taking on a somewhat contorted form as pulp canal becomes more constricted. At the same time, cement is deposited on root and increasingly overlaps base of crown. Total length of tusk about 7-11 cm; crown initially up to 56 mm in height before it starts to be covered by cement. Maximum diameters at base of crown 27 x 17.5 mm. Eruption of tusk beyond tip of premaxilla can reach 1-3 cm by the time M³ is fully erupted; correlation of tusk growth, tusk eruption, and molar eruption seems to be variable. Most tusks show little or no wear, perhaps because few represent mature animals.

A specimen from Montpellier (FSM SM 10) requires comment. The skull was described and illustrated by Depéret & Roman (1920), but without mention of any associated tusk. When it was observed by one of us (Domning, pers. obs., 1983), however, a tusk had been inserted into the right alveolus. (The curator of the collection now informs us that it is no longer present.) This tusk was the same size and shape as the roots of isolated tusks of *M. serresii*, and had similar growth rings. Its diameters were 27 mm dorsoventrally and 18 mm mediolaterally; as inserted, it extended about 28 mm outside the alveolus. (The tusk alveoli of this skull are about 76 mm deep, and form larger bulges on the sides of the premaxillae than in other specimens.) In contrast to other tusks of this species, nothing

EXPLANATION OF PLATE 6

figs. 1-10 - *Metaxytherium serresii*.

- 1 - 18(ces)VM7, mandible with M₃₋₃; lateral (a) and dorsal (b) views; details of left M₃ (c) and right M₃ (d), occlusal views.
- 2 - MBC 005, immature mandible with right unerupted M₃; lateral (a) and dorsal (b) views.
- 3 - CMS 21, mandible with right and left M₂₋₃; a cluster of oysters is attached to the lateral surface of the right mandible; lateral (a) and dorsal (b) views.
- 4 - 47(ces)VM7, right isolated tusk; lateral view.
- 5 - MBC 032, premaxillary rostrum with tusks; anterodorsal view.
- 6 - 55(ces)VM6, right DP₃; occlusal (a) and lateral (b) views.
- 7 - 52(ces)VM7, right M₂; occlusal view.
- 8 - 54(ces)VM7, right M₃; occlusal view.
- 9 - 51(pap)VM3, right M₂; occlusal view.
- 10 - 53(pap)VM1, left M₂; occlusal view.



	Crown length	Anterior width	Posterior width
M1/ GPT 51(pap)VM3 (r)	22.1	19.9	19.5
M3/ GPT 54(ces)VM7 (r)	21.9	17.5e	17.9
DP3/ GPT 55(ces)VM6 (r)	8.5w	7.9	8.2
M2/ GPT 52(ces)VM7 (r) GPT 53(pap)VM1 (r)	20e 20.1w	18.4 17.9w	-- 17.5e

Tab. 7 - Linear dimensions (in mm) of isolated cheek teeth of *Metaxytherium serresii* from Papaglionti and Cessaniti. e = estimated; r = right; w = dimension reduced by wear.

remained of the enamel crown; instead the tip was worn, with an anterior and a (larger) posteromedial wear facet.

DP³: Not preserved. In *M. floridanum*, DP³ has two roots that are fused near the crown (Domning, 1988, p. 409). It is possible that in some *Metaxytherium* individuals this tooth may have only a single root.

DP⁴: Not preserved. In related species, this tooth is three-rooted and submolariform, being slightly more elongate than fully molariform teeth and narrower anteriorly than posteriorly.

DP⁵: Three-rooted, fully molariform; heavily worn in the known specimens.

M¹ (Pl. 3, figs. 4, 5): Three-rooted. Shows the standard *Metaxytherium* cusp pattern, with two transverse rows of three cusps, in addition to pre- and postcingula connected lingually to the main loph. Precingulum typically consists of a crenulated ridge, thickened lingually into a transversely-elongated cuspule. Anterior cingular valley closed labially. Cusps of protoloph distinct; slopes deeply furrowed. Transverse valley may be partly blocked by spurs of anterior cusps at either end and by metaconule, which is advanced only slightly forward of metacone and hypocone. Metacone stands slightly apart from linked hypocone and metaconule. Postcingulum forms a crenulated ridge descending posterolabial from hypocone. Posterior cingular valley somewhat constricted labially.

M² (Pl. 6, fig. 9): Three-rooted; differs from DP⁵ and M¹ primarily in its larger size.

M³ (Pl. 3, figs. 4, 5; Pl. 6, fig. 8): In *Metaxytherium* generally, M³ is not reliably distinguishable from M² by overall size, but is usually narrower posteriorly, and has a larger and more posteriorly-directed posterior root than the other upper molars. Metacone may be small or absent.

DP₃: (55[ces]VM6; Pl. 6, fig. 6) (Right) Double-rooted; anterior root broken, posterior root curves backward apically and has pulp cavity exposed on anterior side. Crown premolariform, almost circular in outline, rather heavily worn (more on labial side and on anterior surface); appears to have 3 large subequal cusps and one smaller (hypoconid). Protoconid enlarged (perhaps by fusion with an anterior cingular cusp); metaconid well circumscribed and displaced forward; protoconid, entoconid and hypoconid smaller. Transverse valley mostly obliterated by wear. Low posterior cingulum (hypoconulid lophule?) bears three small conules, the central one more evident. Both lingual and labial sides of crown slope gently forward.

DP₄₋₅: The Sahabi mandible 45P15A preserves three sets of alveoli for two-rooted teeth anterior to M₁. NHMB MP 145 also displays an alveolus about 7 mm long for a possibly two-rooted tooth anterior to DP₅.

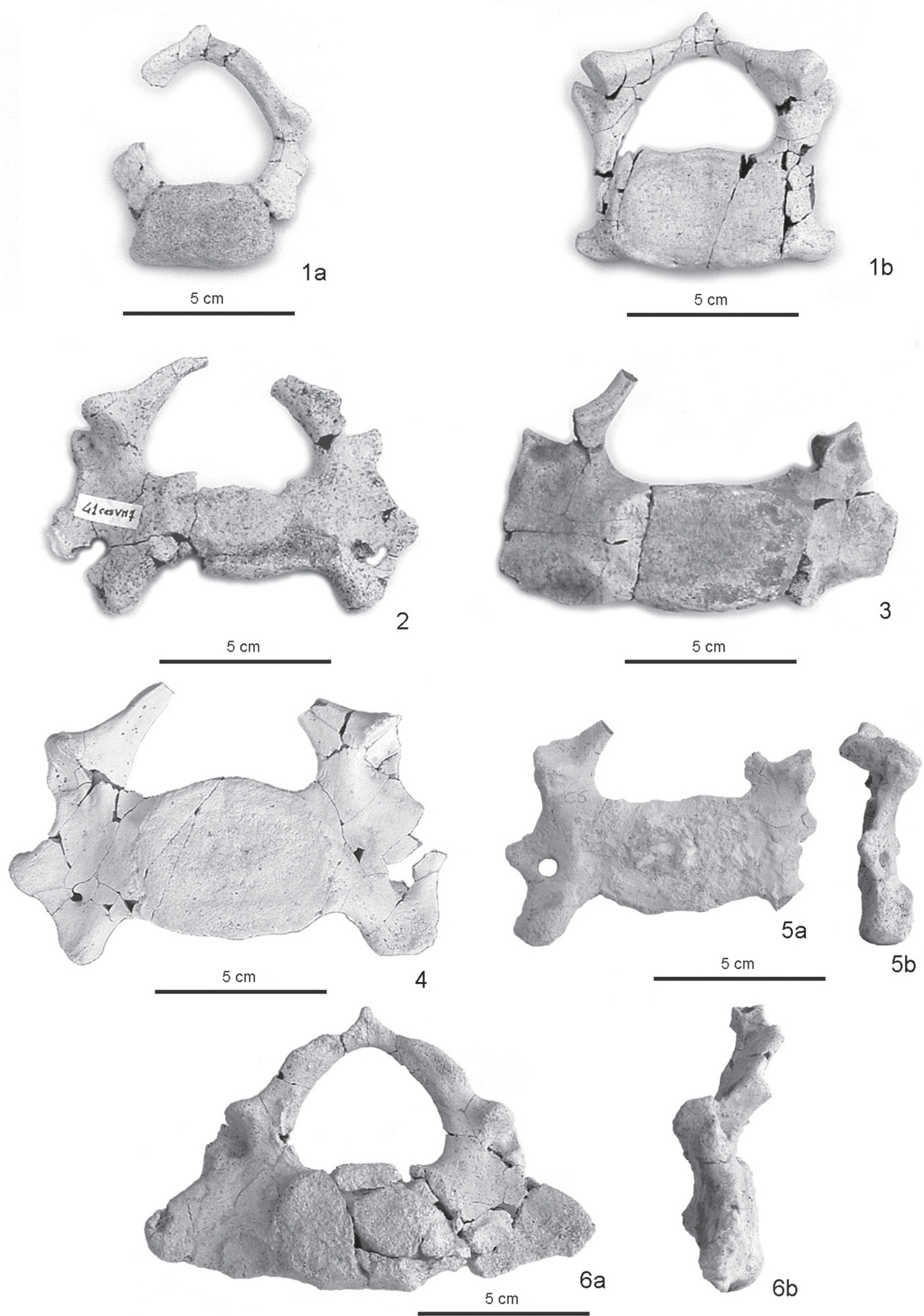
M₁: Has two anteroposteriorly-compressed roots; crown heavily worn in most specimens.

M₂ (Pl. 6, figs. 3, 7, 10): A rectangular tooth with two anteroposteriorly-compressed roots and the standard lower molar pattern of the genus: two nearly transverse, anteriorly-convex lophids and a Y-shaped hypoconulid. A slight indentation ("vorderes Basalband")

EXPLANATION OF PLATE 7

figs. 1-6 - *Metaxytherium serresii*.

- 1 - 9(ces)VM7b. Third cervical (a) and Fourth cervical (b) vertebrae; posterior view.
- 2 - 41(ces)VM7. Sixth cervical vertebra; posterior view.
- 3 - 36(pap)VM3. Seventh cervical vertebra; posterior view.
- 4 - MBC 002. Sixth cervical vertebra; posterior view.
- 5 - 15(ces)VM5. Sixth cervical vertebra; anterior (a) and right lateral (b) views.
- 6 - 15(ces)VM5. Seventh cervical vertebra; posterior (a) and left lateral (b) views.



	Vertebra	Total height	Breadth across transverse processes	Posterior breadth of centrum	Height & thickness of centrum in midline		Width & height of neural canal		Height of neural spine	Max. length, front to rear of zygapophyses	Breadth across post-zygapophyses
9(ces)VM7	C3	76	-	38	25	13	41	39	13	-	-
	C4	78	80	53	36	14	-	30	14	27	72
10(pap)VM2	Ca4?	-	-	72	51	46	18	17	-	34	-
	Ca5?	-	-	68	50	42	16	12	-	-	-
15(ces)VM5	C6	-	-	59	37	13	49	-	-	26	85
	C7	84*	137	57	37	17	46	34	11*	26	87
	T1	132	145	47	33	27	41	29	69	43	67
	T2	170	156	57	39	35	38	32	103	54	62
	T3	168	156	62e	37	38	56	29	107	61	66
	T4	169	153	-	36	37	27	26e	109	56	68
	T5	167	150	-	39	45	28e	21	103	66	68
	T6	161	141	76	36	43	27	20	99	73	64
	T7?	186	135	85	53‡	42	28	22	108	68	63
	T8?	189	132	93	61‡	48	29	17	113	70	63
	T9?	181	132	86	57	48	30	17	107	69	57
	T10?	189	134	94	60	51	38e	17	112	79	49
	T11?	190	133	91	61	51	29	17	112	72	62
	T12?	176	140	88	49	47	24e	18	105	75	65
	T13?	193	137	97	67‡	46	34e	12	112	72	67
	T18	186	129	91	58	53	31	18	110	73	50
	T19	192	125	92	62	47	37	19	112	77	41
	T20	183	127*	98	57	47	39	18	110	83	35
	L1	-	-	-	-	-	-	-	-	-	-
	L2	171	373	99	61	55	-	12e	100e	77	27
	L3	-	365	93	57	55	-	13	-	73	25e
	S	166	330	89	60	54	27	-	98	64	19
	Ca1	161	283*	87	57	51	-	15	-	66	17
	Ca2	149	271	91e	59	52	23	13	91	67	17
	Ca3	148	227*	84	57	51	21	12	88	53*	16
	Ca4	137	208*	83	58	53	21	11	82	NA	NA
	Ca5	129	192	85	56	50	20	10	76	NA	NA
	Ca6	122	176	80	58	49	17	6	68	NA	NA
	Ca7	-	159	73	57	49	17e	8	-	NA	NA
	Ca8?	117	140	75	57	49	15e	11	65	NA	NA
	CaX	94	111	66	56	39	14	9	47	NA	NA
	CaY	58	118e	51e	41	32	7	4	14	NA	NA
	CaZ	39	132e	43	27	28	4	2	7	NA	NA
36(pap)VM3	C7	-	-	62	38	14	-	-	-	-	-
37(pap)VM3	T3?	-	-	-	-	-	-	-	88	57	47
40(ces)VM7	Ca5?	-	-	66	50	38	22	16	-	-	-
41(ces)VM7	C6	-	113	52	29	9	54	-	-	24	-
MPMPN MN04	T9?	-	-	65	40	36	-	-	-	-	-
MBC 002	C6	-	133	56	45	14	55	-	-	31	91
MBC 004	T1	126	114	46	31	24	45	39	56	23	52
	T2	141	147	49	32	23	43	41	70	29	56
	T4	145	157	54	35	29	50	41	91	36	57e
	T?	160	164	58	39	36	46	44	90	47	55
	T?	156	36	70	42	45	27	29	94	61	66

Tab. 8 - Measurements (in mm) of vertebrae of *Metaxytherium serresii* from Cessaniti, Papaglionti and Rombiolo. e = estimated; NA = not applicable; * = broken; ‡ = includes keel on bottom of centrum.

	Rib	Total length (straight-line)		Tip of capitulum to lateral edge of tuberculum		Mid-shaft diameters	
		L	R	L	R	L	R
15(ces)VM5	1	197	192	45	51	25 x 20	27 x 24
	2	268(*)	255	--	60	55 x 38	52 x 37
	3	319	317	73	75	55 x 37	55 x 36
	4	348	354	53	--	50 x 41	52 x 40
	5	398	392	80	80	52 x 41	50 x 39
	6	425	420	82	85	49 x 38	50 x 38
	7	433	445	79	85	49 x 39	52 x 36
	8 ?	400(°)	450	--	78	52 x 37	50 x 34
	9 ?	453(+)	442(+)	80	73	50 x 37	51 x 34
	10 ?	473	465	75	75	52 x 34	51 x 35
	11 ?	450(+)	465(+)	69	64	51 x 30	49 x 30
	12 ?	446	455(+)	65	69	50 x 32	50 x 29
	13 ?	453	453	57	52	51 x 30	50 x 30
	14 ?	446(°)	397(**)	--	50	51 x 30	52 x 30
	15 ?	454	435	50	52	50 x 31	50 x 29
	16	413(+)	450	43	50	51 x 29	49 x 30
	17	415	417	45	45	50 x 31	49 x 32
	18	412	422(+)	49	51	53 x 33	49 x 34
	19	416	426	46	46	57 x 34	55 x 35
	20	385(°)	355	--	43	52 x 32	50 x 34
1(ces)VM7	1		135		40		20 x 16
46(ces)VM5	19?	378		28		50 x 31	

Tab. 9 - Measurements (in mm) of ribs of *Metaxytherium serresii* from Cessaniti. L, left; R, right. (*) = from distal end to tuberculum; (°) = lacking proximal end; (+) = distal portion incomplete; (**) = lacking distal portion.

of Abel, 1904) may be present on anterolabial side of protolophid. Protolophid weakly G-shaped (cf. Domning, 1988, p. 412), or D-shaped and enclosing an anterior basin. Transverse valley more or less obstructed by contact of protoconid spur and crista obliqua, and sometimes by a labial cuspule. Hypolophid with two major cusps and two accessory cusps internal to them (the labial of these forms the crista obliqua; alternatively, these two may be replaced by a single large cusp); a low median ridge crossing (or a central cusp nearly filling) the talonid basin; and labial and lingual hypoconulid cuspules, forming (together with the median ridge) an incipient but indistinct Y-shaped hypoconulid, which may enclose a small posterior basin.

M₃ (Pl. 6, figs. 1-3): Usually distinguishable from M₂ because posterior root is typically enlarged and labiolingually rather than anteroposteriorly compressed (having a triangular, oval, or round cross section contrasting with the flattened anterior root), and hypoconulid is usually larger, making crown more elongate. Protolophid and hypolophid identical to those of M₂; “vorderes Basalband” sometimes present. Hypoconulid usually Y-shaped but quite variable, and sometimes composed of only a single large cusp.

POSTCRANIAL SKELETON

Hyoid Apparatus - Not preserved.

Vertebral Column (Tab. 8; Pls. 4, 7-8, 10) - Complete column not preserved in any specimen, but comprised 7 cervicals, 19-20 thoracics, 3 lumbers, 1 sacral, and an unknown number of caudals. The following observations pertain to 15(ces)VM5 where not otherwise stated. Of the skeleton 15(ces)VM5 there were recovered in all

33 vertebrae: 2 cervicals, 16 thoracics, 2 lumbers + both transverse processes of the third, 1 sacral, and 11 caudals. All the vertebrae are generally similar to those of other dugongids.

Cervical Vertebrae - Atlas, Axis: See Depéret & Roman (1920).

Cervicals 3, 4 (Pl. 7, fig. 1; Depéret & Roman, 1920, pl. 4, fig. 4): A C3, 9(ces)VM7a, lacks its transverse processes. Neural lamina thin with weakly developed zygapophyses. The associated C4, 9(ces)VM7b, has only small remnants of transverse processes which extend anteriorly with rounded protuberances, and very elongated postzygapophyses.

Cervical 5: Not preserved.

Cervicals 6, 7: In 15(ces)VM5 (Pl. 7, fig. 5), ventral parts of transverse processes on C6 swollen and extend 1 cm below centrum. Vertebrarterial canal round, 6+ mm in diameter. Arch of C7 (Pl. 7, fig. 6) has median keel whose apex is broken. Transverse processes triangular, fairly thin, and without vertebrarterial canals; ventrolateral facets for costal articulation present (more prominent on right). An isolated C6, 41(ces)VM7 (Pl. 7, fig. 2), has asymmetrical vertebrarterial canals, right canal smaller than left. An isolated C7, 36(pap)VM3 (Pl. 7, fig. 3), did not have vertebrarterial canals; ventrolaterally it displays two shallow costal facets.

Thoracic Vertebrae (Tab. 8; Pls. 4, 8, 10; Depéret & Roman, 1920, pl. 6, figs. 1-5) - Of 20 thoracic vertebrae originally present in 15(ces)VM5, 16 were recovered. T1 (Pl. 8, fig. 1) is quite different from the T1 of Depéret and Roman (1920, pl. 6, fig. 1); the latter specimen from Montpellier may be anomalous. The Cessaniti specimen conforms better to the pattern

	Rib	Total length (straight-line)		Tip of capitulum to lateral edge of tuberculum		Mid-shaft diameters	
		L	R	L	R	L	R
MBC 004	(u)	L	R	L	R	L	R
	A	420(°)		--		38 X 25	
	B	--		42		--	
	C	362(°°)		--		40 X 26	
	D	405		31		39 X 26	
	E	438		32		38 X 24	
	F	455(#)		--		39 X 24	
	G	482		41		42 X 22	
	H		342(#)		--		45 X 32
	I		326(**)		40		42 X 24
	J		342(**)		39		38 X 23
	K		425(++)		--		37 X 26
	L		323(**)		NA		40 X 26

Tab. 10 - Measurements (in mm) of ribs of *Metaxytherium serresii* from Cessaniti. L, left; R, right. (u): uncertain sequence; (°): lacking proximal end; (°°): lacking distal portion and proximal end; (#): lacking proximal end and distal portion incomplete; (**): lacking distal portion; (++): distal portion and proximal end incomplete; NA: not applicable due to wear.

of *M. krahuletzii* (Domning & Pervesler, 2001, pl. 8, fig. 2a).

Neural spines reach their greatest height on the more posterior vertebrae, in particular on T13?. (Depéret & Roman, 1920, indicate the highest point of the neural spines to be on T13 in the skeleton of *M. serresii* from Montpellier.) The thickest spine is on T3. On all thoracics, neural spine extends somewhat behind body, but less so on more posterior vertebrae. Most spines have thin anterior edge and rounded posterior edge; on T19-20 posterior edge also thin. From T7, tip of spine tilts slightly to left; on T12? spine is almost curved; and on T19 and T20 the tilting affects the entire spine. From T2, tip of spine shows irregular swellings on the sides; on T1 the tip is instead a bit pointed. Transverse processes massive, thick, and directed upward on T2-5; thereafter they become horizontal, and diminish in prominence on T18-20. T1-4 have anterior and posterior articular demifacets for ribs. From T5 onward, only anterior facet remains; it progressively enlarges up to last thoracic. Vertebral bodies become progressively thicker up to T18 and thereafter diminish on T19-20. (In the skeleton described by Depéret & Roman, 1920, the bodies of the vertebrae progressively become thicker until T13, and thereafter remain constant.) The bodies

maintain a rectangular sagittal section and are composed of spongy bone, while neural arches and spines consist mainly of compact bone. Neural canal becomes progressively flattened dorsoventrally from first thoracic to last. T13?-20 have more or less pronounced midventral keels.

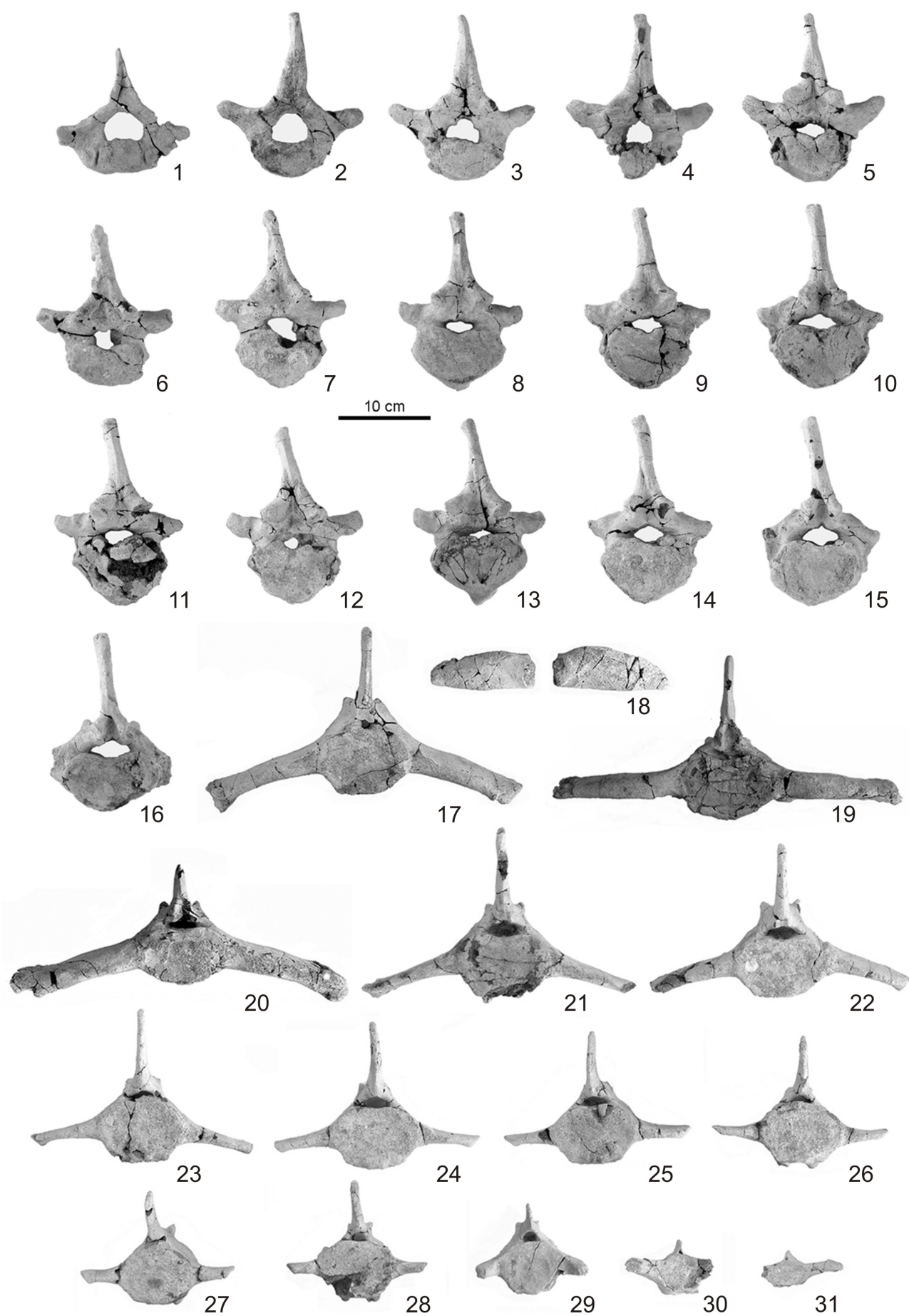
Lumbar Vertebrae (Pl. 8, figs. 18-20; Depéret & Roman, 1920, pl. 5, figs. 1-2) - From L1, only unfused transverse processes are preserved (cf. the more riblike "appendice costiforme" of the Montpellier skeleton; Depéret & Roman, 1920, 16, pl. 5, fig. 1a, b): right process 11.9 cm long, left 12.8 cm; in their proximal extremities, right process 3.5 cm wide and 1.6 cm thick, left 3.8 cm wide and 1.6 cm thick. L2-3 have thinner neural arches compared to posterior thoracics, and neural canal more flattened. L2 neural spine more slender than in T20; L3 spine damaged. Both spines essentially vertical, anteroposteriorly broad in proximal half, sharp on anterior and posterior edges. L2 transverse processes horizontal, taper at ends; L3 transverse processes wider and incline downward with mild torsion, terminal parts slightly expanded.

Sacral Vertebra (Pl. 8, fig. 17; Depéret & Roman, 1920, pl. 5, fig. 3) - Transverse processes reduced and thinner than in lumbar, tending to become bent

EXPLANATION OF PLATE 8

figs. 1-31 - *Metaxytherium serresii*, vertebrae, 15(ces)VM5 (adult), posterior views except fig. 18.

- 1-6 - Thoracic vertebrae (T1 to T6);
- 7-13 - Thoracic vertebrae (T7? to T13?);
- 14-16 - Thoracic vertebrae (T18 to T20);
- 17 - Sacral (S) vertebra;
- 18 - Lumbar (L1) vertebra; dorsal views of the transverse processes;
- 19-20 - Lumbar (L2 and L3) vertebrae;
- 21-31 - Caudal vertebrae (Ca1 to Ca8, X, Y, and Z);



downward, with distal ends expanded and swollen ventrolaterally. Ventral side of centrum lacks keel.

Caudal Vertebrae (Pl. 8, figs. 21-31; Depéret & Roman, 1920, pl. 5, figs. 4-5): The caudals of skeleton 15(ces)VM5 constitute the most complete associated series of caudal vertebrae known up to now for *Metaxytherium serresii* (and perhaps for the entire genus). Centra hexagonal or elliptical in outline, with a series of double pairs of demifacets for chevron bones on ventral side. Neural arches decrease in size posteriorly. Neural spines tilt backward and have sharp anterior and posterior edges. Only Ca1-2 have postzygapophyses, and those only weakly developed. Transverse processes gradually diminish in size. On Ca1-5 transverse processes still straight, but from Ca6 onwards they are directed towards the back. Ca8? and CaX represent peduncle region of tail; CaY and CaZ represent fluke region and lack zygapophyses.

Chevron Bones - Not preserved.

Ribs (Tabs. 9-10; Pls. 4, 9-10; Depéret & Roman, 1920, pl. 1; pl. 4, figs. 6-10) - Two complete adult ribcages have been collected. These comprise 19 (Montpellier specimen, Depéret & Roman, 1920) to 20 pairs (Cessaniti specimen, 15(ces)VM5), of which probably 3-4 pairs were connected to the sternum. The following description is based on an essentially complete ribcage of an adult (15[ces]VM5; Pl. 9) composed of 20 pairs of ribs, of which 3 pairs were connected to the sternum, as indicated by the number of costal cartilage attachments present on the associated sternum (Pl. 11, fig. 1). This skeleton was salvaged from impending quarry operations, and fragments of some ribs were lost. Due to partial disarticulation of the skeleton, there is also some question as to the proper sequence of the ribs from the middle part of the thorax. All ribs show the characteristic pachyosteosclerotic structure, except for some cancellous bone in heads and distal ends.

R1: Tuberculum and capitulum very prominent and extend up above level of neck; capitulum has two facets, articulating with vertebrae C7 and T1. Large anteriorly-protuberant process for m. longus capitis is present on ventral side of neck. Shaft has flat profile, constricted at middle (especially on left), then widening in distal half and tending to turn inward. Proximal curvature (angle) prominent. Middle of shaft bears thick longitudinal ridge on posterior edge. Distal end rough, slightly concave for cartilage attachment, with small protuberance at its center.

An isolated juvenile rib, 1(ces)VM7, has a body on the whole like that of 15(ces)VM5. Tuberculum and capitulum little developed; ventral process weakly developed and concave on tip. Proximal curvature (angle) prominent. Middle of shaft bears thick longitudinal ridge on posterior edge. Distal end rough for cartilage

attachment, with small central protuberance, less marked than in 15(ces)VM5.

R2-6: Distal part strongly curved inward on R3; this is less accentuated on following ribs. Distal end rough and truncated.

R4-9: Capitulum and tuberculum tend gradually to become more widely separated. Tuberculum well developed and tends to enlarge and become lower, almost disappearing on last rib. On R5, distal end tends to turn towards back; this becomes more evident from R9 onwards.

R6-18: Articular part reduced to capitulum and not very prominent tuberculum, and an almost indistinct ventral process (much smaller than the process on R1 for m. longus capitis) which diminishes in size posteriorly until it disappears. Ribs as far back as approximately R9 or 10 bear two distinct demifacets; following ribs probably articulate with only one vertebra. Shaft tends to become thinner mediolaterally, forming elliptical cross-section that tends to become round in distal part; it reaches its minimum thickness (2 cm on R12) at level of proximal curvature and becomes thicker in distal third. This thinning just proximal to midshaft caused by distinct, broad concavity for m. iliocostalis on lateral side just distal to angle.

R19-20: Proximal part of shaft wide and flat, neck very short. Upper distal portion very thick; distal part quickly becomes spindle-shaped. R19 has swelling in upper distal part, more pronounced on left.

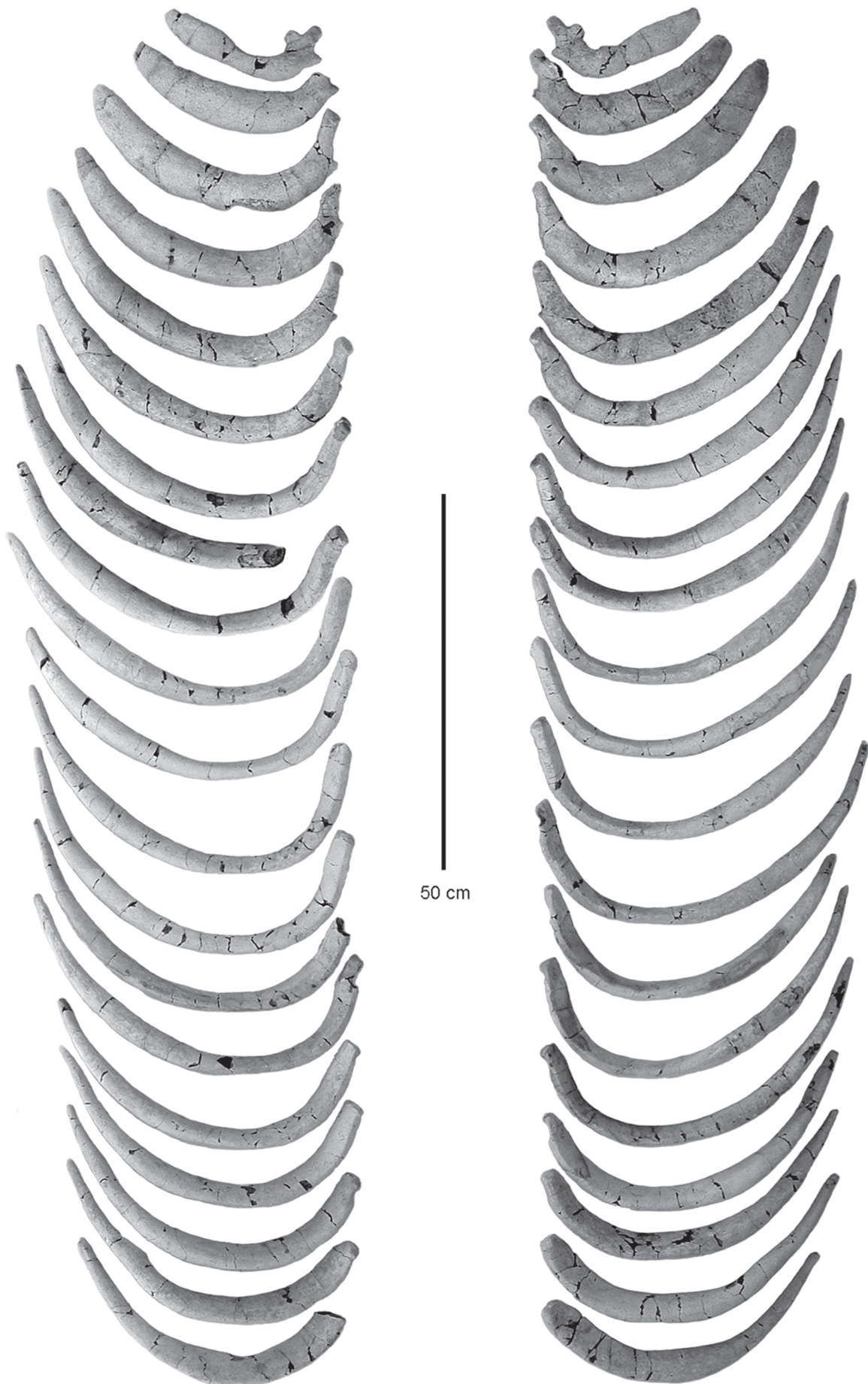
Proximal part of shaft of an isolated rib, 46(ces)VM5 (R19?), broad and flat. Capitulum and tuberculum almost indistinct. Upper distal part considerably thickened; distally shaft tapers rapidly.

Also available is a fragmentary thorax of a juvenile animal, 16(zun)VM2 (Pl. 10, fig. 4). It comprises parts of about 8 thoracic vertebrae (neural arches only, not fused with centra) and about 16 ribs. Maximum breadth across transverse processes of a complete neural arch = 86 mm. Minimum diameters of a rib = 19 x 17 mm.

Sternum (Tab. 11; Pl. 11, figs. 1-2; Depéret & Roman, 1920, pl. 3, fig. 5; Domning & Thomas, 1987, fig. 5) - Comprises only two separate elements, as in *Metaxytherium medium* but in contrast to the apparently more primitive condition of three elements seen in *M. krahuletzii*. These can be fused in adults and show varying degrees of asymmetry. Sternum as a whole gently concave dorsally. Manubrium notably broader than in *M. krahuletzii*; anterior process spatulate, about as broad as body of sternum, with variably pronounced, sometimes asymmetrical ventral keel. Anterior pair of costal cartilage attachments (large lateral protuberances with irregular, often concave surfaces) is the best developed; sternum broader at level of these anterior attachments than farther aft. Second costal attachment located at

EXPLANATION OF PLATE 9

Metaxytherium serresii, 15(ces)VM5 (adult), left ribs 1-20 and right ribs 1-20, anterior views.



	15(ces)VM5	MN 04	CMS 12
Length overall	264*	-	-
MANUBRIUM			
Length	136	-	184*
Maximum breadth (at anterior rib articulations)	78	-	88
Breadth of anterior process near middle of its length	56	-	35e
Length of anterior process in midline	57	-	95e
Posterior thickness	21	-	21‡
Anterior rib articulation to posterior end	53	-	-
Breadth of anterior end	59	-	55e
Maximum thickness at keel	22	-	17
XIPHISTERNUM			
Length	128*	130*	-
Maximum breadth anteriorly	48*	45	-
Minimum breadth	44	22	-
Maximum breadth posteriorly	74*	37*	-
Anterior thickness	17*	23	-
Posterior thickness	9e	11	-

Tab. 11 - Measurements (in mm) of sterna of *Metaxytherium serresii* from Cessaniti, Rombiolo and of *Metaxytherium* cf. *medium* from Caccuri (CMS 12). e = estimated; * = broken; ‡ = at level of rib articulation 2.

junction of manubrium and xiphisternum, third costal attachment just behind this on xiphisternum. Behind last costal attachment, xiphisternum narrows slightly, then broadens posteriorly, thins, and often bifurcates. Xiphisternum strongly convex ventrally just abaft rib attachments, but much flatter farther aft and lacking a keel. The xiphisternum MN 04 (Pl. 11, fig. 2), broken at the posterior end, is 13 cm long as preserved; its minimum breadth is 22 mm, maximum breadth anteriorly (at rib articulation) 45 mm, maximum breadth posteriorly where broken 37 mm, anterior thickness 23 mm, and posterior thickness 11 mm.

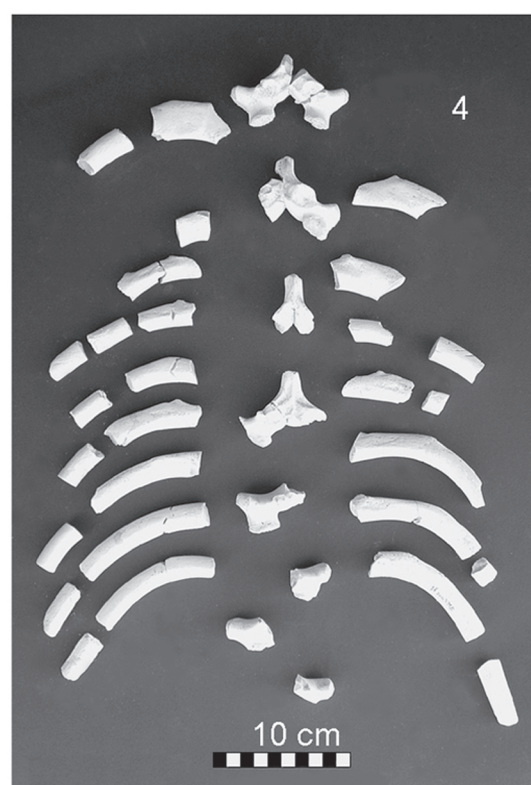
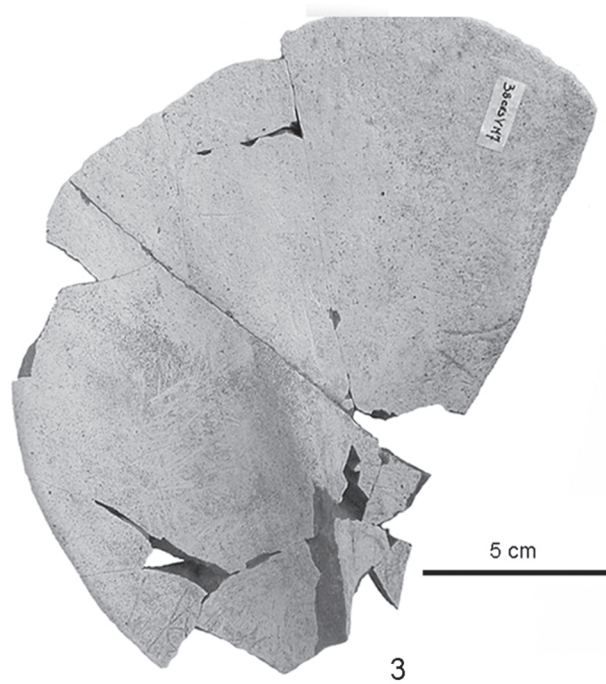
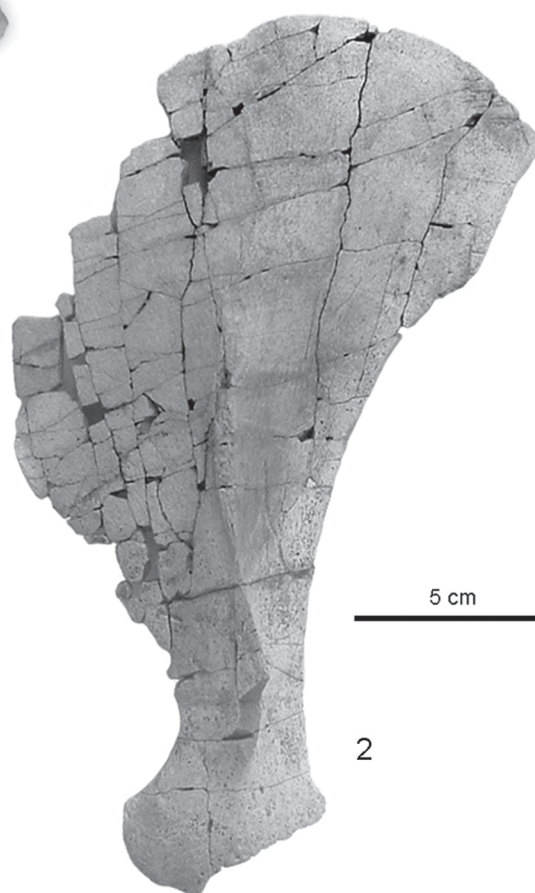
Scapula (Tab. 12; Pl. 10, figs. 1-3; Depéret & Roman, 1920, pl. 3, fig. 2; pl. 6, fig. 6; Domning & Thomas, 1987, fig. 6) - Does not differ from those of other *Metaxytherium*. Supraspinous fossa broad; anterior edge variably convex in outline. Spine moderately high, distal part overhanging posteriorly. Acromion small, protrudes laterally and posteriorly. In some specimens (7[zun]VM2, 15[ces]VM5), acromion separated from dorsal part of spine by a more or less abrupt indentation or notch. Neck narrow; coracoid process prominent and inflected medially. Glenoid fossa deep and ovoid, usually broader posteriorly.

Humerus (Tab. 13; Pl. 11, figs. 3-4; Depéret & Roman, 1920, pl. 3, fig. 3; Domning & Thomas, 1987, fig. 7) - Resembles those of other *Metaxytherium*: robust and dumbbell-shaped, with large tubercles, deep bicipital groove, and slightly elliptical, obliquely-oriented head; but with a proportionately shorter shaft than in *M. krahuletsi*. Greater tubercle extends well proximal of head, has a large anteromedial flange, and bears large supraspinatus and infraspinatus muscle scars. Lesser tubercle somewhat elongated proximodistally, reaching nearly as far distally as deltoid crest, unlike *M. krahuletsi*. Tubercles diverge at angle of about 85°. Deltoid crest prominent and recurved, continued by deltopectoral crest, which ends distally in a more or less pronounced swelling where m. pectoralis major inserted. Trochlea canted obliquely to shaft at angle of about 70-80°. Trochlear articular surface has deep, widely-open notch in posterolateral side for attachment of a humeroulnar ligament. Olecranon and coronoid fossae shallow.

Radius and Ulna (Tab. 14; Pl. 12; Depéret & Roman, 1920, pl. 3, fig. 4; Domning & Thomas, 1987, fig. 8) - Resemble those of other *Metaxytherium*; fused to each other with considerable torsion. Anterior side of olecranon process tilted back at angle of about 55° to

EXPLANATION OF PLATE 10

- figs. 1-4 - *Metaxytherium serresii*; scapulae and partial thorax of juvenile.
 1 - 15(ces)VM5 (adult), left scapula, lateral view.
 2 - 7(zun)VM2 (immature) left scapula, lateral view.
 3 - 38(ces)VM7 (adult), partial left scapula, lateral view.
 4 - 16(zun)VM2, (juvenile) partial thorax in posterior view.



		7(zun)VM2 (left)	15(ces)VM5 (left)	38(ces)VM7 (left)
AB	Max. length, vertebral border to border of glenoid fossa	245	310	-
BI	Mediolateral width of glenoid fossa	34	43	-
BJ	Lateral border of glenoid fossa to inside of concave distal end of spine	27e	37e	-
CD	Max. breadth of blade dorsally	153e	222	180e
EF	Minimum anteroposterior breadth of neck	34	44	-
GH	Max. anteroposterior breadth of distal end	56e	65	-
KL	Summit of spine to medial side of blade, measured parallel to plane tangent to posterior edges of spine and neck	-	-	-
MN	Anteroposterior length of glenoid fossa	44e	46	-
TMO	Length of teres major origin from teres protuberance to posterior corner of blade	45	74e	60e

Tab. 12 - Measurements (in mm) of scapulae of *Metaxytherium serresii* from Zungri and Cessaniti. e = estimated.

		15(ces)VM5 (left)	8(ces)VM7 (right)
AB	Maximum length, greater tubercle to distal end	-	-
CD	Maximum breadth, greater to lesser tubercle	72e	80
EF	Maximum breadth, ectepicondyle to entepicondyle	-	64
GH	Maximum thickness, posterior side of head to anterior side of greater tubercle	74	76
IJ	Maximum thickness, posterior to anterior ends of medial rim of trochlea	-	27
KL	Maximum (proximolateral-mediodistal) breadth of head	44	49
MN	Minimum (proximolateral-mediodistal) breadth of head	-	40
OP	Breadth of anterior side of trochlea	-	42
QR	Length, saddle between head and greater tubercle to saddle of trochlea	-	-
	Maximum mediolateral diameter perpendicular to lateral surface, midshaft	-	24

Tab. 13 - Measurements (in mm) of humeri of *Metaxytherium serresii* from Cessaniti, Italy.

axis of ulnar shaft. Lateral side of semilunar notch deeply indented. Lateral sides of distal ends of radius and ulna and their epiphyses bear distinct grooves for extensor tendons. Distal articular surfaces as in other *Metaxytherium*.

Manus - Only metacarpals known; see Domning & Thomas (1987).

Innominate - See Depéret & Roman (1920); Domning & Thomas (1987).

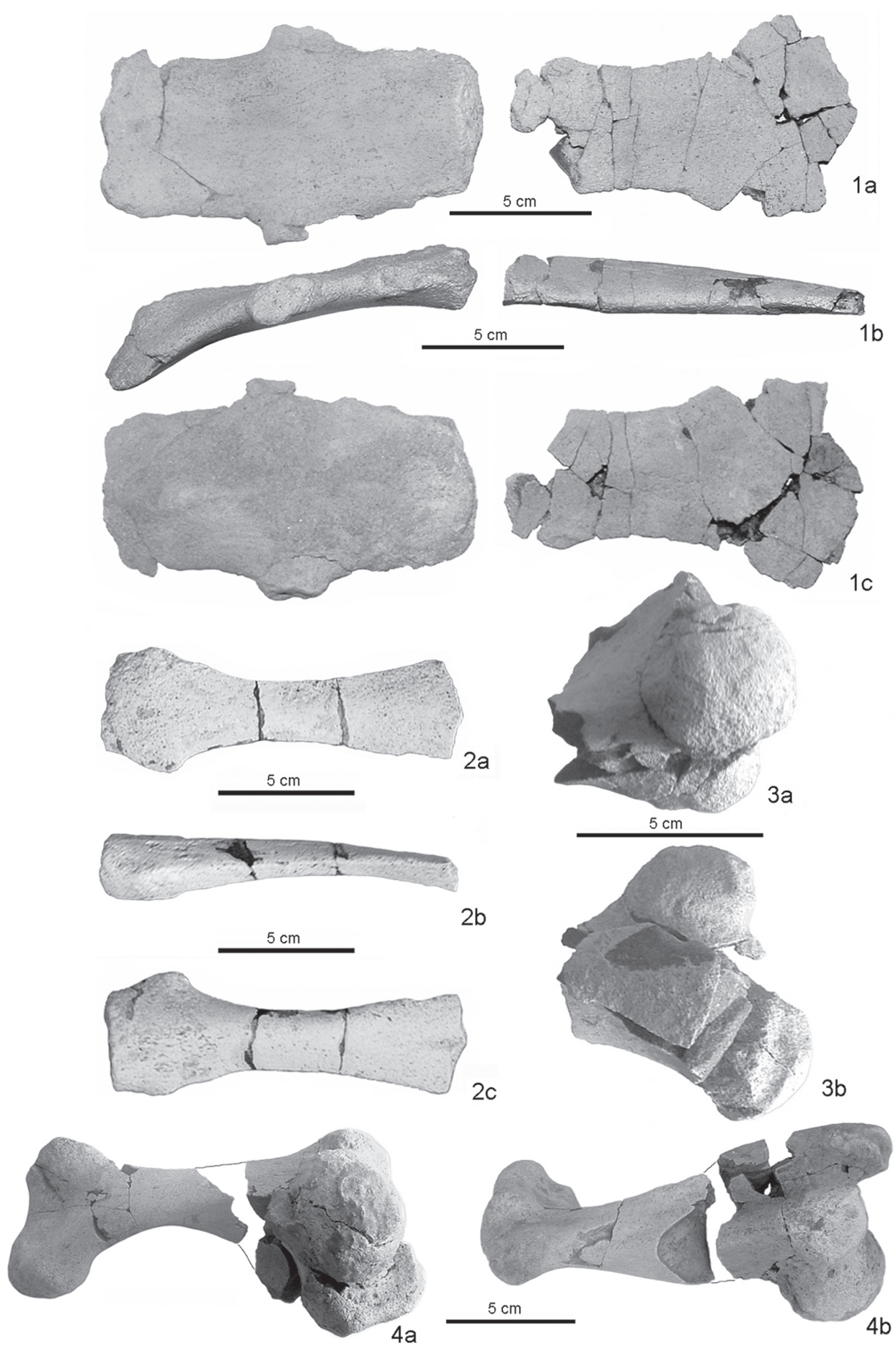
COMPARISONS

With the following possible exceptions, none of the Calabrian specimens differs in any important way from the topotypic specimens of *Metaxytherium serresii* from Montpellier, France, or from the sample from Sahabi, Libya.

Cranio C (Pl. 2, fig. 1b) has a rostral deflection of 73°, in contrast to deflections of 50-55° measured on three Montpellier specimens, and 55-59° estimated in three from Sahabi. The total observed range in seven *M. serresii* is therefore 23°. Estimated deflections in two *M. medium* are 50-58+°, and in three *M. subapenninum* are 60-63°. Six *M. floridanum*, however, vary over a range of 17°, from 64° to 81°, and deflections in 78 Recent *Trichechus manatus* vary from 29° to 52°, a range of 23° (Domning & Hayek, 1986, Tab. 1), showing that this much variation can occur in a single sirenian species. Alternatively, ranking the *M. serresii* samples in chronological order (Calabria-Sahabi-Montpellier) suggests a diminution in rostral deflection over the period of the MSC. If larger samples substantiate this, it might have interesting paleoecological implications.

EXPLANATION OF PLATE 11

- figs. 1-4 - *Metaxytherium serresii*, sterna, humeri.
 1 - 15(ces)VM5, manubrium and xiphisternum; dorsal (a), right lateral (ventral side up, b), and ventral (c) views.
 2 - MN 04, xiphisternum (anterior end at left); ventral (a), left lateral (b), and dorsal (c) views.
 3 - 15(ces)VM5, left proximal humerus; posterior (a) and lateral (b) views.
 4 - 8(ces)MV7, right humerus; posterior (a) and medial (b) views.



		15(ces)VM5 (left)	39(ces)VM7 (right)	44(ces)VM6 (right)
AB	Total length of ulna	201	-	-
CD	Total length of radius, anterior lip of semilunar notch to distal end	159	110*	-
EC	Height of semilunar notch, anterior tip of olecranon to anterior radial lip of notch	27	-	29
EF	Thickness of olecranon, anterior tip to posterior side	34	-	34
GH	Distal thickness, anterior side of radius to posterior side of ulna	60	-	-
IJ	Maximum mediolateral breadth, radial portion of semilunar notch	49	31	53
KL	Maximum mediolateral breadth, ulnar portion of semilunar notch	25	-	26
MN	Minimum mediolateral breadth of semilunar notch at its midsection	25	-	24
OP	Minimum thickness of olecranon, posterior side to semilunar notch	24	-	23

Tab. 14 - Measurements (in mm) of radii and ulnae of *Metaxytherium serresii* from Cessaniti. * = lacks distal epiphysis.

	External height	Internal height	Total breadth	Width between tips of processes for transverse ligament	Breadth across anterior cotyles	Breadth across posterior cotyles	Length in dorsal midline	Length in ventral midline
MBC 010	101	67	154	39	112	89	32	26

Tab. 15 - Measurements (in mm) of atlas of *Metaxytherium medium* from Filiti.

In the present slightly enlarged sample of *M. serresii*, the nasals are separated in the midline in at least three of five specimens, rather than one of three. This removes the incongruence of this polymorphism as defined by Domning (1994, p. 184), and improves the support for the character scoring of c. 31(1).

The exoccipitals of Cranio C are fused to each other in a suture about 11 mm long (Pl. 2, fig. 1d). This results in a newly documented polymorphism for *M. serresii*: c. 66(0 or 1); but the same polymorphism also occurs in *M. krahuletzii* and *M. subapenninum*, showing that variation in this character persisted throughout the entire Neogene history of this lineage.

The exoccipital of MBC 003 (Pl. 3, fig. 6) has a deep supracondylar fossa, in contrast to the other Calabrian skulls and ones from Sahabi and Montpellier, in which it is only moderately deep. This constitutes another newly documented polymorphism for this species: c. 67(2 or 3). *M. floridanum* is also polymorphic for this character, varying from deep to shallow. The presence of 67(2) as a minority state in the Calabrian sample is arguably a primitive trait of the population, in contrast to other, later *M. serresii* and *M. subapenninum*.

Both MBC 001 (Pl. 1, fig. 1b) and Cranio C (Pl. 2, fig. 1b) display a slight convexity of the alisphenoid continuing anteriorly the forward edge of the zygomatic root, in contrast to three Montpellier specimens. This feature probably has no taxonomic significance.

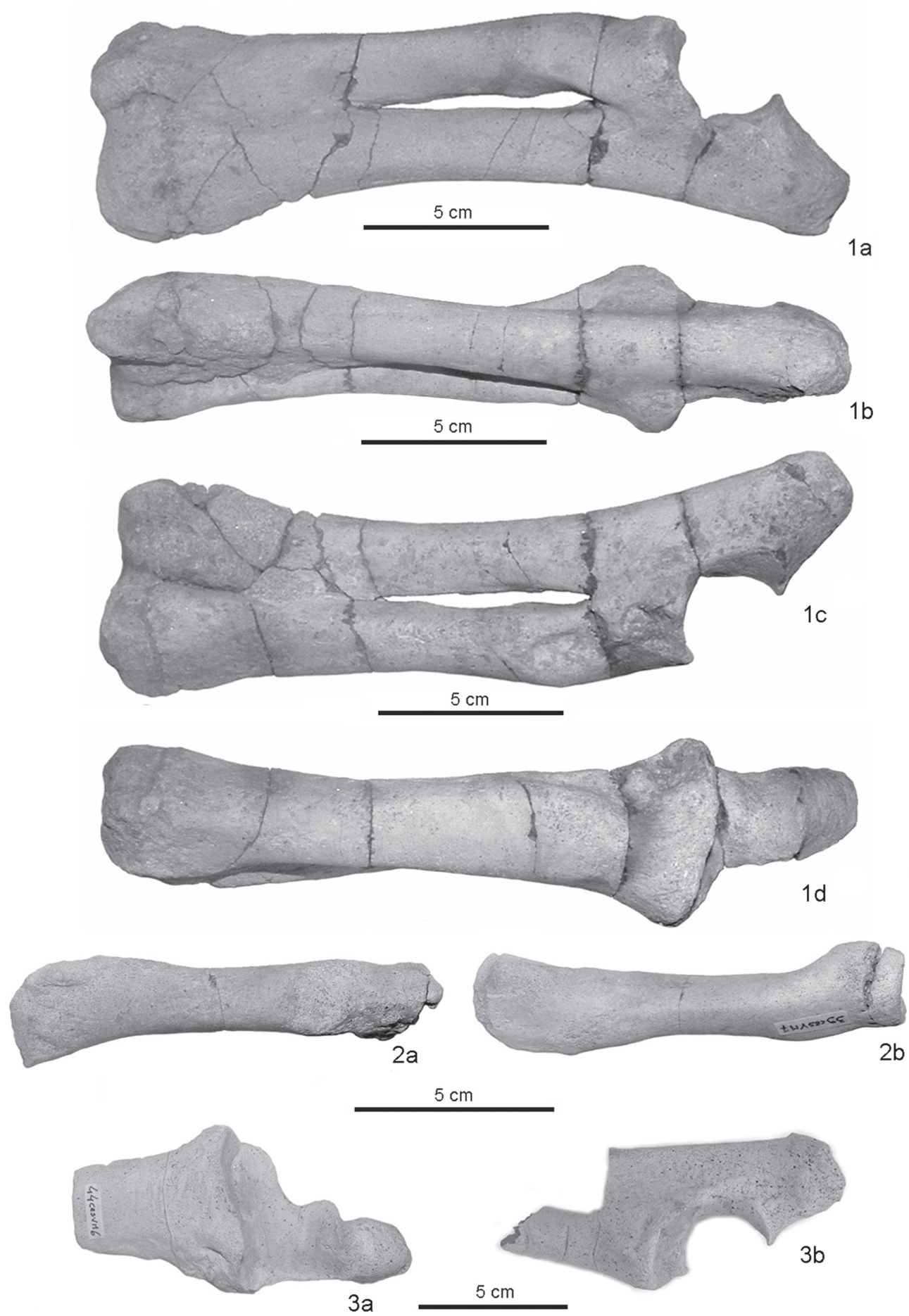
With the minor emendations noted above, comparison of the *M. serresii* sample as a whole with other sirenians is adequately provided in the cladistic analysis of Domning (1994). The results of that analysis, and of the present study, are consistent with the interpretation of *M. krahuletzii*, *M. medium*, *M. serresii*, and *M. subapenninum* as a single anagenetic lineage (Domning & Thomas, 1987).

The specimens from Calabria referable to *Metaxytherium medium* differ only trivially if at all from other members of the species, and hence do not alter this conclusion. For example, the skeleton from Santa Domenica di Ricadi, described by Moncharmont Zei & Moncharmont (1987), has an anteriorly pointed, mediolaterally broad supraorbital process with a laterally-jutting posterolateral corner. This condition has not been observed in *M. krahuletzii* or other *M. medium*, but is the most common condition in *M. serresii*. As the latest representative of its species, the S. Domenica specimen could therefore be seen as foreshadowing *M. serresii* in this regard. However, the high intraspecific variability in shape of this process in other *Metaxytherium* species (Domning, 1988; Domning & Pervesler, 2001), and the small samples of each species available, caution us against drawing firm conclusions from such minor and probably nonfunctional osteological details.

An atlas referred to *M. medium* (MBC 010; Tab. 15; Pl. 13, fig. 1) likewise closely resembles those of

EXPLANATION OF PLATE 12

- figs. 1-3 - *Metaxytherium serresii*; radius-ulnae.
 1 - 15(ces)VM5, left radius-ulna; lateral (a), posterior (b), medial (c) and anterior (d) views.
 2 - 39(ces)VM7, juvenile right radius; lateral (a) and medial (b) views.
 3 - 44(ces)VM6, proximal right radius-ulna; anterior (a) and medial (b) views.



	Rib	Total length (straight-line)		Tip of capitulum to lateral edge of tuberculum		Mid-shaft diameters	
		L	R	L	R	L	R
MBC 010	(u) A		--		62		39 x 26
	B	315(**)		40		35 x 19	
	C	347(**)		23		33 x 16	
	D	381		21		37 x 20	
	E	333(**)		39		36 x 20	
	F	390		56		35 x 24	
	G	461		63		34 x 22	
	H	432		58		33 x 20	
	I	386(°)		--		36 x 19	

Tab. 16 - Measurements (in mm) of ribs of *Metaxytherium medium* from Fitili. L: left; R: right; (u): uncertain sequence; (**): lacking distal portion; (°): lacking proximal end..

congeneric species (cf. *M. krahuletsi*, Domning & Pervesler, 2001, p. 27, pl. 7, fig. 1; *M. serresii*, Depéret & Roman, 1920, pl. 4, figs. 1-2; *M. floridanum*, Domning, 1988, p. 412) but differs in minor details. The ventral part of the vertebral foramen is narrower than the dorsal. Internally, the ventral arch bears a concave articular surface (fossa dentis) that receives the odontoid process. The ventral tubercle has two small posterior processes. The posterior side of the dorsal arch bears a prominent keel where it contacted the neural spine of the axis. The passage above the anterior cotyle for the first cervical nerve is a closed foramen. The transverse process is knoblike, extending horizontally outward. The vertebralarterial canal is open ventrally. These features vary individually and are unlikely to have taxonomic significance.

Finally, a sternum of *Metaxytherium* cf. *medium* (DSTC CMS 12; Tab. 11; Pl. 13, fig. 3) appears to consist of a fused manubrium and xiphisternum, unlike a Calabrian specimen of *M. serresii* (15[ces]VM5; Pl. 11, fig. 1), which has two separate elements as described above. The anterior process of the manubrium is narrower than the body of the sternum but is broadened at its anterior end, with markedly concave lateral borders and a weak, asymmetrically-placed keel. The first costal cartilage attachments are pronounced; the second and third are close together; the bone is broken behind the third. Fusion of the manubrium and xiphisternum occurs often in mature *Metaxytherium* (Domning, 1988, p. 413; fig. 10A; Domning & Pervesler, 2001, p. 30, 44; pl. 14, figs. 2-3), and has been reported in *M. serresii* from Sahabi

(Domning & Thomas, 1987, p. 215; fig. 5b); so this does not constitute a taxonomic distinction.

On the whole, *Metaxytherium serresii* is distinguished from *M. medium* by reduced depth of the supracondylar fossa [c. 67(3)] and greater length of the tusk [c. 140(1)]. *M. subapenninum* is distinguished from *M. serresii* by still greater length of the tusk [c. 140(2)]. *M. serresii* is also notably smaller than these other species, but we regard this as an ecophenotypic difference.

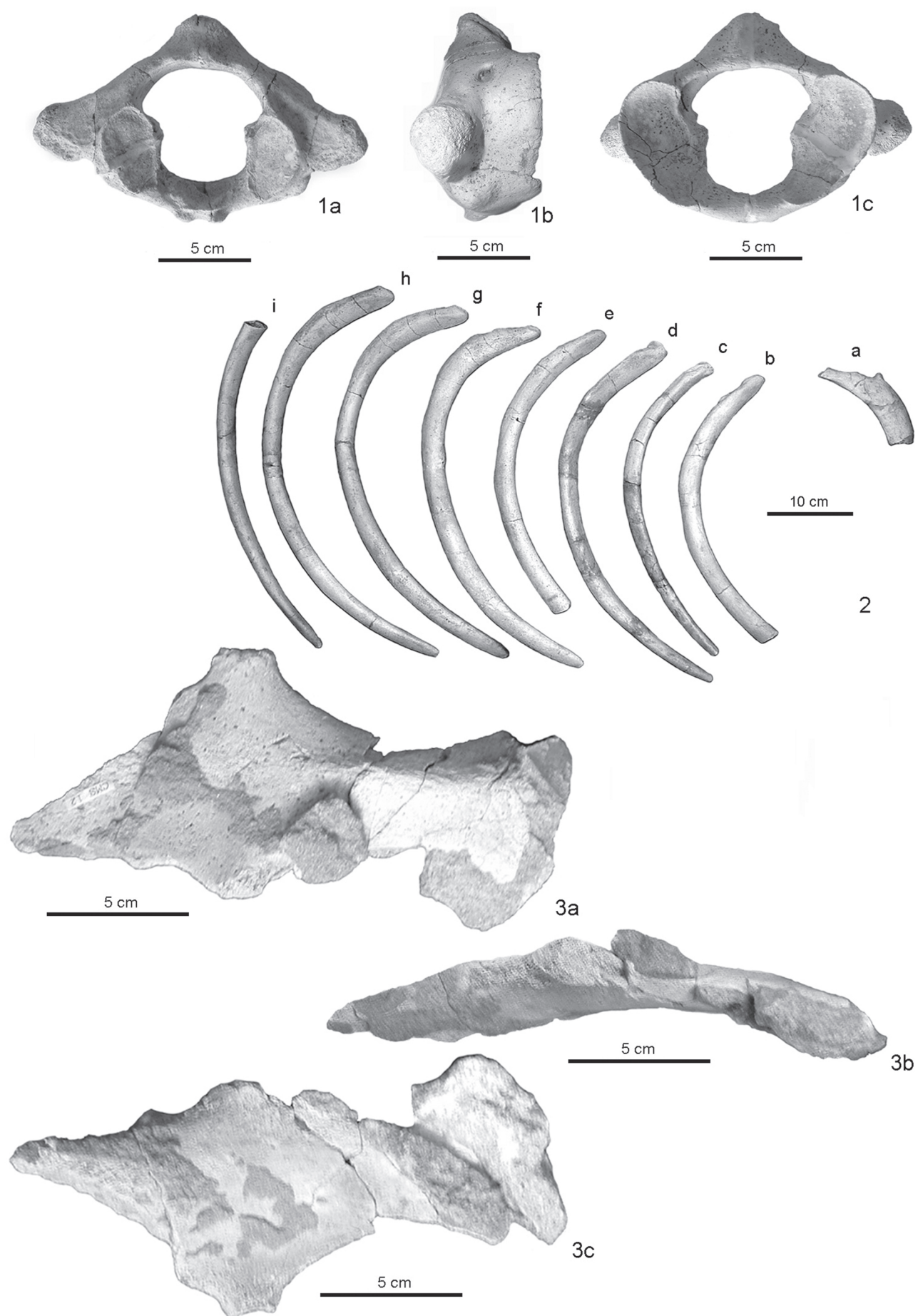
DISCUSSION

The new material from Calabria enlarges somewhat the known range of morphological variation within *Metaxytherium serresii*. Much more importantly, it extends the available sample of this species downward stratigraphically into the uppermost Tortonian. Its known chronological range is now from European Mammal Zone MN12 (7.6-7.3 Ma; Tortonian, Late Miocene; Calabria) through MN13 (ca. 6.8 Ma; Messinian, latest Miocene; Sahabi) to MN14 (5.3-4 Ma?; Zanclean, Early Pliocene; Montpellier) (Bianucci et al., 2004 and in press). The significance of this temporal range extension lies in its confirmation of a prediction made by Domning & Thomas (1987), and the implications of this for Mediterranean paleoecology.

The latter authors concluded that all the European *Metaxytherium* constitute a single anagenetically-evolving Miocene and Pliocene lineage. This implied that the small body size of *M. serresii* relative to both earlier and later species might represent ecophenotypic

EXPLANATION OF PLATE 13

- figs. 1-2 - *Metaxytherium medium*, MBC 010,
 1 - Atlas; posterior (a), right lateral (b) and anterior (c) views.
 2 - Left (a) and right (b-i) ribs; anterior views.
- fig. 3 - *Metaxytherium* cf. *medium*, DSTC CSM 12,
 fused manubrium and xiphisternum (anterior end at right; dark areas are adherent matrix); ventral (a), left lateral (b) and dorsal (c) views.



dwarfism. This episode of dwarfism appeared to be connected with the MSC, because both of the then-known samples of *M. serresii* (Montpellier and Sahabi) were dated as immediately post-Messinian (Sahabi has since been re-dated as possibly early Messinian; Boaz et al., 2004). Domning & Thomas (1987, p. 230) therefore conjectured that the Messinian disturbances of salinity and sea level reduced the quality, quantity, and/or diversity of the seagrass forage on which the sirenians depended, and that this was reflected in the temporarily reduced body size of the seacows. This hypothesis, in turn, predicted that such dwarfism should be observed immediately before as well as immediately after the salinity crisis - that is, while Mediterranean desiccation was just beginning as well as while conditions were returning to normal. However, no immediately pre-Messinian samples of Mediterranean *Metaxytherium* were then available to test this prediction.

This changed with the discovery of the sirenian fossils in the Cessaniti area. These came, fortuitously, from horizons older than the Messinian, but younger than a less extreme Tortonian salinity crisis dated at about 7.8-7.6 Ma (Kouwenhoven et al., 2003), and hence within the early stages of the overall late Miocene salinity disturbances. And they proved to be as small as, or even smaller than, the other specimens of *M. serresii*, confirming the original prediction of "peri-Messinian" dwarfing (Bianucci et al., 2004 and in press). This confirmation, in turn, tends to support the ground of the original inference, namely that the dwarfing of the sirenians resulted from poor habitat. This case now stands alone in showing how Mediterranean desiccation affected the morphology of a lineage of vertebrates, before and after the MSC itself.

The second-most obvious morphological pattern observed in European/Mediterranean *Metaxytherium* is increase in tusk size, from small in the Early and Middle Miocene (*M. krahuletsi*, *M. medium*) to medium in the Late Miocene and Early Pliocene (*M. serresii*) and finally to large in the Middle Pliocene (*M. subapenninum*). These tusks (especially medium and large ones) are thought to play an important role in feeding on seagrass rhizomes (Domning, 2001). Bianucci et al. (in press) propose a scenario in which the small-tusked *Metaxytherium* would have fed on seagrass leaves and small- to medium-sized rhizomes, but would not have had access to the rhizomes of the largest seagrasses such as *Posidonia oceanica*. This species, however, is a climax form that is very sensitive to changes in salinity or temperature, and would presumably have succumbed to the late Miocene salinity crises. Mediterranean seagrass communities, reduced in areal extent and biomass, would then have become dominated by more eurybiontic pioneer species of *Cymodocea* and *Zostera*, with rhizomes of medium size. The nutritionally-stressed, dwarfed sirenians of this period might have had to shift to a diet richer in nutritious rhizomes, especially these newly-dominant, medium-sized ones. The predicted evolutionary result (according to the model of Domning, 2001) would have been an increase in tusk size to the "medium" dimensions observed in *M. serresii*.

Return of normal marine conditions in the Pliocene restored the dominance of *Posidonia*, but climatic cooling at this time subjected the sirenians to a different source of metabolic stress. Rather than return to a diet of seagrasses with only small and medium rhizomes - now once more diminished in abundance by competition with *Posidonia* - they might have obtained a greater energy yield by adapting to feed on rhizomes of the latter. This may be the reason for the increase in tusk (and body) size seen in the Pliocene *Metaxytherium* up to their demise, which coincided with the acceleration of climatic cooling after 3 Ma (Capozzi & Picotti, 2003).

There is some evidence that *Metaxytherium subapenninum* was sexually dimorphic in size and wear of the tusks, at least in its latest evolutionary stage (middle Pliocene, MN 15; Bianucci et al., in preparation). It is therefore intriguing that the latest sample of *M. serresii* (that from Montpellier) has yielded one skull (FSM SM 10) with pronounced premaxillary bulges for tusk alveoli. Whether or not the peculiarly- and heavily-worn (though not enlarged) tusk that was once inserted into it was properly associated with it, these bulges are suggestive of unusual tusk morphology in this specimen. Sexual dimorphism of tusks or tusk use in this species is not otherwise apparent; but this specimen could be interpreted as a male and pointed to as a first piece of evidence of incipient evolution in such a direction within this lineage.

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