New finds of *Metaxytherium serresii* (Gervais, 1847) (Mammalia: Sirenia) from the Upper Miocene of Monte Poro (Calabria, Italy)

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KEY WORDS - Metaxytherium serresii, Sirenia, Osteology, Phylogeny, Tortonian, Southern Italy.

ABSTRACT - We summarize the osteology, update phylogenetic characters and document variability and biometrics of the species *Metaxytherium serresii* Gervais, 1847 (Sirenia, Dugongidae, Halitheriinae), by providing new cranial and postcranial remains from the Miocene of Monte Poro (Vibo Valente, Calabria, Italy). The new data confirm the marked polymorphism within the genus *Metaxytherium*, which was already noted.

The characters and measurements of the new specimens confirm the reduction in the body size that the species underwent, probably as an ecophenotypic adaptation to changes preceding the Messinian Salinity Crisis of the Mediterranean.

The new fossil material, while not differing significantly from the finds already known, demonstrates a broader range of intraspecific morphological variability of the species *M. serresii*.

RIASSUNTO - [Nuovi rinvenimenti di *Metaxytherium serresii* Gervais, 1847 (Mammalia: Sirenia) del Miocene Superiore del Monte Poro (Calabria, Italia)] - Viene descritta l’osteologia, aggiornati i caratteri filogenetici e ampliato il range di variabilità morfologica e biometrica della specie *Metaxytherium serresii* Gervais, 1847 (Sirenia, Dugongidae, Halitheriinae), disponendo di nuovi resti diagnostici craniali e post craniali provenienti dal Miocene del Monte Poro (Vibo Valente, Calabria, Italia). I dati che si ricavano provano lo spiccato polimorfismo del genere, già segnalato in letteratura.

I caratteri morfologici osservabili nei nuovi esemplari e le misure espresse confermano il trend di riduzione della taglia corporea che la specie ha subito, probabilmente a causa di un adattamento ecophenotipico dovuto ai cambiamenti ambientali precedenti la Crisi di Salinità Messiniana nel bacino del Mediterraneo rispetto alla probabile specie ancestrale *M. medium* Desmarest, 1822 ed alla specie possibile derivata M. subappenninum (Sorbi et al., 2012), nonché ad un aumento degli incisivi (zanne) rispetto alla specie ancestrale.

Il nuovo materiale fossile, costituito da elementi scheletrici inediti databili al Tortoniano finale, ci consente di ampliare il range cronologico della specie, rappresentando il dato più antico finora registrato, e di ampliare il campo di variabilità morfologica intraspecifica di alcuni caratteri della specie *M. serresii*.

INTRODUCTION

Sirenian bones and teeth are quite common fossils in the Upper Miocene sandstones of the Monte Poro-Capo Vaticano area, from the sites of Cessaniti, Zungri, Zaccanopoli and Caria (Vibo Valente, Calabria; Fig. 1). The site most often mentioned in scientific literature is that of Cessaniti; it yielded most of the fossils and it exposes the most representative stratigraphic section in the area (Carone & Domning, 2007; Gramigna et al., 2008).

A skeleton of *Metaxytherium medium* Desmarest, 1822 was excavated from the Tortonian sandstones of Santa Domenica di Ricàdi and described by Montchamont Zei & Montchamont (1987); while a great number of specimens of *Metaxytherium serresii* Gervais, 1847 were collected by members of the Gruppo Paleontologico Tropeano (GPT) in the last twenty-five years from several localities (Cessaniti, Zungri, Papagliantoni, Zaccanopoli, Caria), in layers stratigraphically higher in the Tortonian than the site of Santa Domenica di Ricàdi.

The description of bones of *M. serresii* from these younger sites by Carone & Domning (2007) significantly increased the knowledge of the species. First of all, the stratigraphically higher records from Calabria demonstrated that *M. serresii*, formerly considered a Pliocene species, was already present in the Late Miocene, before the Messinian Salinity Crisis (MSC). The species has a reduced body size with respect to its ancestor *M. medium* and, before the finds from Calabria, a dwarfing related to the environmental deterioration that occurred during the MSC had been inferred (Domning, 1981; Domning & Thomas, 1987). The age of *M. serresii* from Cessaniti indicates that dwarfing processes evolved during the early ecological changes prior to the MSC. In contrast to the dwarfism of the body, the species has enlarged tusks, interpreted by Domning (2001) as an adaptation to feeding on the rhizomes of seagrasses, and by Sorbi (2007) as an adaptation for territorial fights among males. The record from Monte Poro-Capo Vaticano provides evidence that the “peri-Messinian” dwarfing hypothesized by Bianucci et al. (2008) occurred after the Tortonian salinity crisis (7.8-7.3 Ma, according to Kouwenhoven et al., 2003) and before the MSC, probably in its early stages (Carone & Domning, 2007). Therefore, the specimens from Monte Poro-Capo Vaticano support the hypothesis that the dwarfing process started coincidentally with the habitat impoverishment prior to the MSC.
The material studied by Carone & Domning (2007) significantly enlarged the known range of morphological variation within *M. serresii*. The new finds studied here fall within the body size range previously documented for the species and they display a similar morphology; however, some characters present a variability broader than measured so far.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

The Neogene succession of the Monte Poro-Capo Vaticano area rests on the Paleozoic crystalline substratum. The succession encompasses a transgressive (Tortonian) - regressive (Messinian) cycle. The units recently described by Gramigna et al. (2008) at Cessaniti (as well as those previously described by Nicotera in 1959, for the northern sector of Monte Poro) crop out over the whole Monte Poro-Capo Vaticano area, with differences in thickness and lateral variations in lithology, as supported also by the findings in the northern sector of Monte Poro (Nicotera, 1959).

According to Gramigna et al. (2008), four units can be distinguished at Cessaniti, from the bottom to the top:

Unit 1: dark gray-shales alternating with gray coarse sandstones, with abundant specimens of the gastropod *Cerithium* spp. and ostreid bivalves (marginal lagoon deposits). The unit corresponds to “Level 5” of Carone & Domning (2007) with a thickness from a few meters to 10-15 m.

Unit 2: gray sandstones separated from the previous unit by a sharp erosional contact. These sandstones contain a fully marine fauna, with extremely abundant echinoids, mainly *Clypeaster*, deposited in lower shoreface conditions, and point to the onset of marine conditions. The unit corresponds to “Levels 6 and 7” of Carone & Domning (2007) with a thickness from about 20 meters to 50 meters.

Unit 3: yellowish poorly cemented sandstones, showing a depositional style similar to Unit 2 (fully marine deposits). The presence of a great number of benthic foraminifera, mainly *Heterostegina papyracea* Papazzoni & Sirotti, 1999, indicates open marine conditions. The unit corresponds to “Level 8” of Carone & Domning (2007) with a thickness of about 20 meters.

Unit 4: thin-bedded blue marls, rich in planktonic foraminifers (hemipelagic deposits), known as “Marne ad Orbulina” (this unit is poorly exposed at Cessaniti). Unit 2, with a thickness reaching 50 m at some places, yielded most of the fossil mammals recovered so far in the Monte Poro-Capo Vaticano area. *M. serresii* is the best-represented taxon, but terrestrial mammals are also preserved (Marra et al., 2011), represented by a boselaphine bovid, a hexaprotodontid hippopotamus, the giraffids *Samotherium* *cf.* *boissieri* Forsyth Mayor, 1888 and *Bohlina* *cf.* *attica* Gaudry & Lartet, 1856, a rhinoceros, and the elephantid *Sextotetrabelodon syrticus* Petrocchi, 1941. The co-occurrence of two taxa typical for the Pikermian biome (*S.* *cf.* *boissieri* and *B.* *cf.* *attica*), together with a definitely Afro-Arabian species (*S. syrticus*), indicates a land connection between the Cessaniti area and North Africa (Marra et al., 2011).

The occurrence of *Heterostegina complanata* Meneghini, 1857 in the level capping Unit 2 is an ante quem term, this species being present, although rare, in the Mediterranean until the late Tortonian (Papazzoni & Sirotti, 1999).

Guido et al. (2011) analysed the microstructure and preservation state of sirenian ribs collected at Cessaniti in Unit 2, and observed that dissolution/recrystallization processes are absent or very low. The paleohistologic structures are preserved, while the external layer of the bones is usually absent or thickened and deeply micritized. According to Guido et al. (2011), except for the external layer, post-burial processes did not significantly affect the micromorphological and biogeochemical features of the bones.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758  
Order Sirenia Illiger, 1811  
Family Dugongidae Gray, 1821  
Subfamily Halitherinae (Carus, 1868) emend Abel, 1913  
Genus Metaxytherium Christol, 1840
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Metaxytherium serresii (Gervais, 1847) Depéret, 1895 (Figs 2-4)

Type - No type specimens of this species have ever been formally designated. The species name was introduced by Gervais (1847) referring generically to materials from Montpellier, without indicating type specimens. Specimens were later described and figured by Gervais (1859) (Tav. 4, figs 1-3; Tav. 5, figs 1-3; Tav. 6, figs 1-5 e Tav. 41, fig. 3).

Type locality - Montpellier, France.

Formation - Sables à Gryphaea virleti.

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

New material - Eight skulls: 56(ces)VM5, 62(ces)VM6, 82(ces)VM5, 87(ces)VM5, 91(ces)VM5, 65(pap)VM2, 89(zac)VM, 66(car)VM1; three mandibles: 70(ces)VM7, 81(ces)VM6, 92(ces)VM5; two isolated teeth: 85(ces)VM5, 90(ces)VM5; one xiphisternum: 84(zac)VM; vertebrae and ribs: 57(ces)VM7, 58(ces)VM7, 59(ces)VM5, 60(ces)VM6 64(ces)VM6, 77(ces)VM6, 83(ces)VM7, 88(ces)VM6. The specimens are stored with temporary inventory numbers in the collections of the “Civico Museo Paleontologico” of Ricadi (VV), still under construction, listed in Tab. 1.

Locality, formation, and age of newly referred material - Sandpits near Cessaniti, Zungri, Zaccanopoli and Caria, province of Vibo Valentia, Calabria, southern Italy; sandstones with Clypeaster, Heterostegina, and pectinids; Late Miocene (uppermost Tortonian, MN 12).

Range - Late Miocene (uppermost Tortonian, MN 12) to Early Pliocene (lower Zanclean, MN 14), Mediterranean basin. Specimens have been reliably recorded only from Montpellier (France), Sahabi (Libya), and Calabria, Italy.

Emended diagnosis - Metaxytherium in which the supracondylar fossa of the exoccipital is usually reduced to only moderate depth or less (c. 67[3]; occasionally deeper = 67[2]), and the tusk alveolus is lengthened to roughly one-half the length of the premaxillary symphysis (c. 140[1]); contrasts with M. medium, which has a deeper supracondylar fossa (c. 67[2]) and a smaller tusk alveolus (c. 140[0]); contrasts with M. subapenninum, in which the supracondylar fossa is shallow or lost (c. 67[3]) and the tusk alveolus is longer (c. 140[2]).

Description - Topotypical specimens of M. serresii from the Zanclean (MN 14) of Montpellier, France, have been described at length by Gervais (1859), Depéret & Roman (1920), Thomas (1970), and Pilleri (1987, 1988). The sample from the ?Messinian (MN 13?) of Sahabi, Libya, was described by Domning & Thomas (1987). The previous specimens from Calabria (uppermost Tortonian, MN 12) were described by Carone & Domning (2007). Here we supplement these sources with a description of the new Calabrian material (Tab. 1), with emphasis on elements exhibiting morphological variation or new distinctive features. The organization of the descriptions is comparable to that of the descriptions already published.

<table>
<thead>
<tr>
<th>Site</th>
<th>N.</th>
<th>Skeletal elements</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cessaniti</td>
<td>1</td>
<td>Frontal and occipital</td>
<td>56(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Immature rib</td>
<td>57(ces)VM7</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Immature left scapula</td>
<td>58(ces)VM7</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Postcranial skeleton with 12 vertebrae, 10 ribs, left scapula and left humerus</td>
<td>59(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Vertebræ and ribs fragmented</td>
<td>60(ces)VM6</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Skull with right DP5-M3 and left DP5-M2</td>
<td>62(ces)VM6</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Several vertebrae and ribs</td>
<td>64(ces)VM6</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Right mandubular fragment with M3</td>
<td>70(ces)VM7</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Incomplete skeleton with left exoccipital, 21 ribs and 4 vertebrae</td>
<td>77(ces)VM6</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>Mandible with right and left DP5-M3 and 2 lumbar vertebrae</td>
<td>81(ces)VM6</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>Skull with left M3</td>
<td>82(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>Immature rib</td>
<td>83(ces)VM7</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Right M1</td>
<td>85(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>Left frontal</td>
<td>87(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>Proximal end of scapula</td>
<td>88(ces)VM6</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>Left M1</td>
<td>90(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>Fragment of right maxilla with DP5 and M1</td>
<td>91(ces)VM5</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>Fragmentary mandible</td>
<td>92(ces)VM5</td>
</tr>
<tr>
<td>Zungri</td>
<td>19</td>
<td>Skull with right DP5-M2 and left M1-M3</td>
<td>65(pap)VM2</td>
</tr>
<tr>
<td>Zaccanopoli</td>
<td>20</td>
<td>Distal end of xiphisternum</td>
<td>84(zac)VM</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>Immature left premaxilla</td>
<td>89(zac)VM</td>
</tr>
<tr>
<td>Caria</td>
<td>22</td>
<td>Skull with right M3 and left M1-M3</td>
<td>86(car)VM1</td>
</tr>
</tbody>
</table>

Tab. 1 - List of new Monte Poro upper Tortonian specimens collected by the Gruppo Paleontologico Tropeano and referred to Metaxytherium serresii (Gervais, 1847).
for *Metaxytherium floridanum* Hay, 1922 (see Domning, 1988), *M. krahuletzi* Dépèret, 1895 (see Domning & Pervesler, 2001), *M. medium* (see Domning & Pervesler, 2013), and *M. subapenninum* (Bruno, 1839) (see Sorbi et al., 2012).

Fractions (e.g., 3/3) denote the number of specimens exhibiting the stated condition out of all the specimens newly reported here that preserve the structure in question; c. = character state (according to Vélez-Juarbe & Domning, in press); e.g., c. 3(1) refers to state one of character three. Numbering of states of c. 3 and 74 have been revised. For conditions in previously-reported specimens of the species, see Carone & Domning (2007).

**Skull (Figs 2 and 4, Tab. 2)**

Premaxilla - rostrum large (c. 3[2])(3/3); posterior end of rostrum upraised to form a boss in lateral view (c. 10[1])(3/3, but less pronounced in two of the specimens compared to specimens from Montpellier). Palatal surface rugose and concave; right and left halves form angle of about 90-120° (3/3). Incisors not preserved in any of these specimens. Nasal process long (c. 7[0]) and thin (c. 6[0]), contacts lacrimal and frontal (c. 9[1]) and abuts against nasal. Also, 2/3 of the new Calabrian specimens (Tab. 1), unlike all the previous ones described by Carone & Domning (2007), but like the toputypical specimens from Montpellier, exhibit a slight constriction of the anterior part of the mesorostral fossa created by a protuberance on the medial side of the premaxilla. Rostral deflection is 65° in 86(car)VM1, 73° in DSTC Cranio C, and 50-55° in three Montpellier specimens (Carone & Domning, 2007).

Nasal - In all four specimens, nasals are separated at midline of the skull roof by processes of frontals (c. 31[1]) and have a dorsal exposure that is small (c. 32[1]) and variable in shape: almond-shaped in 65(pap)VM2, deltoid in 82(ces)VM5. In 62(ces)VM6, both nasals are lost, leaving vacant cavities.

**Ethmoidal region:** Usually poorly preserved, but well preserved in 65(pap)VM2 (Fig. 4). The nasal bones lie just above the dorsal concha in such a way that the medial side of the nasal is in contact with the dorsomedial surface of the concha. The three conchae are parallel to each other with different sizes and shapes. The middle concha is the smallest. The surface for attachment of the septal cartilage is wide and extends ventrally below the roof of the narial passage. The perpendicular plate has a thickness of seven mm.

**Vomer** - Well preserved only in 65(pap)VM2; it is in contact with the maxillae. The part preserved is broken off at the center of the mesorostral fossa. Its inner part forms the sulcus septalis.

**Lacrimal** - Irregular in shape. Preserved on right side of 65(pap)VM2, where it has a teardrop form. In 82(ces) VM5 it is more cylindrical. The jugal does not appear to have overlapped the lateral side of the lacrimal (c. 91[1]).

**Frontal** - The supraorbital process is well developed in 65(pap)VM2 and 56(ces)VM5, moderately developed in
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82(ces)VM5 and 87(ces)VM5, and not inclined strongly ventrolateral (c. 43°); it is variable in shape (c. 36°), generally broad mediolaterally with a laterally jutting posterolateral corner. The nasal incisure is small in 82(ces)VM5, absent in 65(pap)VM2 (c. 37°); in the latter, the median portion of the frontal roof has a considerable degree of convexity. The lateral (temporal) crests of the frontals overhang in the three specimens (62(ces)VM6, 65(pap)VM2, 82(ces)VM5); the crests are low in 87(ces)VM5 and 56(ces)VM5.

**Parietal** - The cranial vault is more or less trapezoidal in coronal section anteriorly. The temporal crests are lyriform (3/3), with variable morphology: type A (low, confined to

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Measurements</th>
<th>56(ces)VM5</th>
<th>62(ces)VM6</th>
<th>65(pap)VM2</th>
<th>82(ces)VM5</th>
<th>86(car)VM1</th>
<th>87(ces)VM5</th>
</tr>
</thead>
<tbody>
<tr>
<td>AB</td>
<td>Condylobasal length</td>
<td>- 370r</td>
<td>- 394</td>
<td>394</td>
<td>220</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>ab</td>
<td>Height of jugal below orbit</td>
<td>-</td>
<td>- 50</td>
<td>40</td>
<td>30</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>AH</td>
<td>Length of premaxillary symphysis</td>
<td>-</td>
<td>-</td>
<td>121r</td>
<td>95</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>BI</td>
<td>Rear of occipital condyles to anterior of interfrontal suture</td>
<td>- 170</td>
<td>184</td>
<td>160</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CC'</td>
<td>Zygomatic breadth</td>
<td>-</td>
<td>- 229</td>
<td>198</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>cc'</td>
<td>Breadth across exoccipitals</td>
<td>- 130e</td>
<td>140</td>
<td>118</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>de</td>
<td>Top of supraoccipital to ventral sides of occipital condyles</td>
<td>- 106</td>
<td>115</td>
<td>125</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>Length of frontals, level of tips of supraorbital processes to frontoparietal suture</td>
<td>128</td>
<td>-</td>
<td>175r</td>
<td>120</td>
<td>-</td>
<td>122</td>
</tr>
<tr>
<td>FF'</td>
<td>Breadth across supraorbital processes</td>
<td>70x2 = 140e</td>
<td>-</td>
<td>80x2 = 160</td>
<td>129</td>
<td>-</td>
<td>55x2 = 110</td>
</tr>
<tr>
<td>f'</td>
<td>Breadth across occipital condyles</td>
<td>- 90e</td>
<td>94</td>
<td>101</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>GG'</td>
<td>Breadth of cranium at frontoparietal suture</td>
<td>-</td>
<td>- 30</td>
<td>54</td>
<td>-</td>
<td>3x2 = 6</td>
<td></td>
</tr>
<tr>
<td>gg'</td>
<td>Width of foramen magnum</td>
<td>-</td>
<td>- 45</td>
<td>55</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hl</td>
<td>Length of mesorostral fossa</td>
<td>- 136</td>
<td>-</td>
<td>123</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>hi</td>
<td>Height of foramen magnum</td>
<td>-</td>
<td>- 38</td>
<td>51</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>JJ'</td>
<td>Width of mesorostral fossa</td>
<td>- 56</td>
<td>36x2 = 72</td>
<td>55</td>
<td>54</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>KL</td>
<td>Maximum height of rostrum</td>
<td>- 45</td>
<td>-</td>
<td>50</td>
<td>48</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>MM'</td>
<td>Posterior breadth of rostral masticating surface</td>
<td>- 45</td>
<td>-</td>
<td>60e</td>
<td>60</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>no</td>
<td>Anteroposterior length of zygomatic-orbital bridge of maxilla</td>
<td>- 31</td>
<td>39</td>
<td>28e</td>
<td>36</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>OP</td>
<td>Length of zygomatic process of squamosal</td>
<td>-</td>
<td>- 137</td>
<td>127</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>OT</td>
<td>Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen</td>
<td>-</td>
<td>-</td>
<td>156</td>
<td>154</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>Length of parietals, frontoparietal suture to rear of external occipital protuberance</td>
<td>- 75</td>
<td>75</td>
<td>80</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pq</td>
<td>Length of row of tooth alveoli</td>
<td>- 91</td>
<td>74</td>
<td>-</td>
<td>89</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>QR</td>
<td>Anteroposterior length of root of zygomatic process of squamosal</td>
<td>-</td>
<td>-</td>
<td>53</td>
<td>52</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>r'</td>
<td>Maximum width between labial edges of left and right alveoli</td>
<td>- 65r</td>
<td>78</td>
<td>-</td>
<td>60</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>ST</td>
<td>Length of cranial portion of squamosal</td>
<td>-</td>
<td>- 86</td>
<td>88</td>
<td>-</td>
<td></td>
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<tr>
<td>ss'</td>
<td>Breadth across sigmoid ridges of squamosals</td>
<td>-</td>
<td>- 158</td>
<td>168</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>Dorsoventral thickness of zygomatic-orbital bridge</td>
<td>- 13</td>
<td>16</td>
<td>13</td>
<td>12</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>t'</td>
<td>Anterior breadth of rostral masticating surface</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>UV</td>
<td>Height of posterior part of cranial portion of squamosal</td>
<td>-</td>
<td>- 97</td>
<td>98</td>
<td>-</td>
<td></td>
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<tr>
<td>WX</td>
<td>Dorsoventral breadth of zygomatic process</td>
<td>-</td>
<td>- 42</td>
<td>38</td>
<td>-</td>
<td></td>
<td></td>
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<tr>
<td>yy'</td>
<td>Maximum width between pterygoid processes</td>
<td>- 33</td>
<td>44</td>
<td>45</td>
<td>-</td>
<td></td>
<td></td>
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<tr>
<td>YZ</td>
<td>Length of jugal</td>
<td>-</td>
<td>- 154</td>
<td>-</td>
<td>110e</td>
<td>-</td>
<td></td>
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<tr>
<td>LFr</td>
<td>Length of frontal in midline</td>
<td>85r</td>
<td>80</td>
<td>112</td>
<td>79</td>
<td>-</td>
<td>60e</td>
</tr>
<tr>
<td>HSo</td>
<td>Height of supraoccipital</td>
<td>60</td>
<td>44</td>
<td>62</td>
<td>56</td>
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<td></td>
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<tr>
<td>WSo</td>
<td>Width of supraoccipital</td>
<td>41x2 = 82e</td>
<td>92</td>
<td>91</td>
<td>86</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>PaW</td>
<td>Width of parietal roof between indentations made by squamosals</td>
<td>- 71</td>
<td>66</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RD</td>
<td>Deflection of masticating surface of rostrum from occusal plane (degrees)</td>
<td>-</td>
<td>-</td>
<td>65°</td>
<td>79°</td>
<td>-</td>
<td></td>
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<tr>
<td>TTC</td>
<td>Type of temporal crests</td>
<td>-</td>
<td>A</td>
<td>C</td>
<td>B</td>
<td>-</td>
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Tab. 2 - Measurements (in mm) of crania of Metaxytherium serresii (Gervais, 1847) from Monte Poro: e, estimated measurements; r, broken.
lateral edges of a nearly flat roof and producing a nearly rectangular vault) in 62(ces)VM6; type B (at lateral edges of, but upraised above, a markedly concave roof) in 82(ces)VM5; type C (smoothly rounded and about two cm apart, with a distinctly concave roof) in 65(pap)VM2. In skulls 62(ces)VM6 and 82(ces)VM5 the internal occipital protuberance is distinct and rounded, the tentorium is straight, and the transverse sulcus is shallow. Distinct lateral pits are observed in 62(ces)VM6 and 56(ces)VM5. The bony falx is low and rounded. No emissary foramen is present in front of the external occipital protuberance, except for a small one in 82(ces)VM5.

Supraoccipital - Pentagonal or hexagonal in outline, with more or less rounded dorsolateral corners; wider ventrally than dorsally (c. 64[1]). In the three specimens preserving this bone it forms an angle of about 109-123° with the parietal roof. The external occipital protuberance rises above the plane of the parietal roof (4/4); the median ridge below it, is always distinct. The nuchal crest is not distinct at its lateral ends near squamosals. Areas of insertion for semispinalis capitis muscles are flat, oval, rugose, and concave with sharply defined ventromedial edges (4/4); none extends more than halfway to the ventral end of the supraoccipital. In 65(pap)VM2, the lateral border of the supraoccipital is very thick and rounded. Ratio of width to height of supraoccipital varies from 1.46 to 2.09 (N = 3).

Exoccipital - Exoccipitals never fuse to supraoccipital and never meet in dorsal midline (c. 66[1]) (3/3, including 77[ces]VM6). The foramen magnum has an acute dorsal peak. The dorsolateral border of the exoccipital has a more or less smoothly rounded posterior edge (c. 70[0]). The supracondylar fossa is reduced to only moderate depth (c. 67[3]) (4/4). The condyloid (= hypoglossal) foramen is single. The condyle extends ventrally to about the same level as the tip of the paroccipital process.

Basioccipital - In all specimens, it bears marked rugosities for longus capitis muscles. Its posterior slope is steeper than the anterior one.

Basisphenoid - The region of the tuberculum sellae is nearly flat (only observed in 65[pap]VM2).

Presphenoid - No distinct chiasmatic grooves are present.
Length of symphysis
Minimum width between angles
Anterior tip to front of ascending ramus
Length of alveolar row
Total length
Minimum anteroposterior breadth of ramus
Maximum breadth of masticating surface
Posterior extremity to front of mandibular foramen
Posterior extremity to front of ascending ramus
Deflection point to rear of alveolar row
34° - 64°
Deflection of symphyseal surface from occlusal plane (degrees)
3° 55°
Measurements
135
52
65 (DP5-M3)
70
140 - 154
2
142
65 (at the M3)
Rear of symphysis to front of mandibular foramen
126
Anterior tip to rear of mental foramen
121
Anterior tip to front of mandibular foramen
71
Distance between anterior and posterior ventral extremities
126
Height at mandibular notch
116
Height at condyle
123
Height at deflection point of horizontal ramus
140
Deflection point to rear of alveolar row
95
Minimum anteroposterior breadth of ascending ramus
64
Front of ascending ramus to rear of mental foramen
106
Maximum anteroposterior breadth of dorsal part of ascending ramus
71
Top of ventral curvature of horizontal ramus to line connecting ventral extremities
34
Minimum dorsoventral breadth of horizontal ramus
70
Maximum breadth of masticating surface
57
Rear of symphysis to front of mandibular foramen
71
Length of alveolar row
65 (DP5-M3)
Maximum width between labial edges of left and right alveoli
64 (at the M3)
Minimum width between condyles
-
Deflection of symphyseal surface from occlusal plane (degrees)
55°

Tab. 3 - Measurements (in mm) of mandible 81(ces)VM6 of *Metaxytherium serresii* (Gervais, 1847) from Monte Poro.

**Orbitosphenoid** - Not preserved.

**Alisphenoid** - In 65(pap)VM2, there is a suture between alisphenoid and pterygoid.

**Pterygoid** - The pterygoid fossa is fairly broad and well-developed, extending above the level of the roof of the internal nares (c. 102[1]) (3/3). Ventral tips of alisphenoid and pterygoid enclose the end of the palatine.

**Palatine** - In skull 65(pap)VM2, the palatine is less than one cm thick at the level of M² (c. 16[0]). The anterior end of the palatine probably lies just behind the posterior edge of the zygomatic-orbital bridge (c. 99[1]). The palatal incisure reaches the front part of M² (c. 97[1]).

**Maxilla** - The alveolar portion is heavy and massive. The palatal surface (including the areas of the tooth alveoli) narrows rapidly forward of the molars, becomes narrowest just forward of the anterior edge of the zygomatic-orbital bridge, then widens at the posterior end of the rostral masticating surface (c. 23[0]). The palatal gutter is very deep in 65(pap)VM2. The zygomatic-orbital bridge is elongated anteroposteriorly (c. 14[0]).

**Squamosal** - Dorsally in contact with the squared posterior part of the parietal roof (c. 76[1]). The sigmoid ridge is very prominent in 82(ces)VM5 (c. 4[1]). The mastoid indentation is very deep (2/2). The external auditory meatus is as wide anteroposteriorly as high (c. 82[1]). The postglenoid process is well-developed (2/2). The processus retroversus is moderately inflected (c. 77[1]) (2/2). The zygomatic process is broader posteriorly than anteriorly. The posterodorsal edge of the zygomatic process is straight or convex in outline.

**Jugal** - The jugal does not contact the premaxilla (c. 87[0]) (4/4). The preorbital process is relatively flat and thin (c. 88[0]) (4/4). The ventralmost point of the jugal lies under the posterior part of the orbit (c. 85[2]) (3/3). In 65(pap)VM2, the border behind the ventral tip is strongly concave in outline. A raised postorbital process is not present in front of the tip of the squamosal (3/3). The zygomatic process is longer than the diameter of the orbit (c. 89[0]), and extends just beyond the level of the front edge of the temporal condyle (2/2).

**Ear region** - Intact in 65(pap)VM2; intentionally left covered by matrix, with tympanic and malleus in view.

**Mandible** - The mandible 81(ces)VM6 (Tab. 3, Fig. 3) is relatively complete and well preserved. The condyle is almost triangular (20x19 mm), not ovoid or elliptical as previously observed, and projecting laterally. The mandibular notch is shallow, as previously observed in NHMB MP 145 (Pilleri, 1988, pl. 2) and NHMB MP 188 (Carone & Domning, 2007). The coronoid process has an unusual form, with the anterior border extending slightly anterior to the base (c. 126[1]). The posteromedial edge of the condylar process is thin and sharp. The notch in the rear edge of the mandible below the condyle is smooth in outline, not distinctly stepped at its lower end (c. 125[2]). The internal pterygoid fossa on the medial side of the mandible is nearly absent; the external pterygoid fossa dorsal to it is more pronounced. The edge of the mandibular angle is thickened; the angle is convex in outline, and has crenulated edges. The retromolar fossa (coronoid canal) is prominent. The shelf lateral to the incompletely erupted M₃ of this immature specimen is concave dorsally. The horizontal ramus is deep dorso-ventrally (c. 128[1]), with a strongly concave ventral border (c. 122[3]) that is not tangent to the mandibular angle (c. 129[1]). On each side, three mental foramina are present; two of them are large. This condition resembles that seen in DSTC CMS 21 (Carone & Domning, 2007; p. 70; pl. 6, fig. 3A) and also in the Late Oligocene “*Halitherium abeli*” Spillmann, 1959 (= *H. christolii* Domning & Thomas, 1987) from Austria (Spillmann, 1959; fig. 25). In these cases, it seems better (most phylogenetically congruent) to interpret the most posterior foramen as the “principal” mental foramen, because of its position just behind the deflection point of the dorsal edge of
the ramus. Therefore these specimens should all be scored as c. 123(1). The masticating surface is broad (c. 121[1]), with a deflection of about 55°. As usual in Neogene sirenians, the mandible bears two rows of vestigial incisor alveoli that did not contain teeth; however, in this case these are unusually deep. The lateral edges of the masticating surface are thin and prominent. The posteroventral side of the symphysis is slightly concave transversely; the symphysis is unfused. The young adult specimen 81(ves)VM6 exceptionally preserves eight teeth, making it the jaw with the most complete lower dental series so far known for the species.

**Dentition** - The lifetime dental formula is presumed to be I 1/0, C 0/0, DP 3/3, M 3/3, as in other *Metaxytherium* species. We interpret the deciduous premolars, by analogy with *Dusisiren* Domning, 1978, *Prototherium* Zigno, 1887, and *Trichechus* Linnaeus, 1758 (see Domning, 1978, pp. 16-17; Domning, 1982, p. 608; Domning et al., 1982, p. 59; Carone & Domning, 2007; pp. 70-74), as DP3-5. Molars of *Metaxytherium* spp. show considerable individual variation in size, complexity, and cusp arrangement, and we consider most of this variation as not of value for systematics. Unfortunately no tusk was found in the new sample, but the alveolus has a depth of about half the length of the premaxillary symphysis (c. 140[1]).

**DP3, DP4:** Not preserved in the new specimens.

**DP5:** Three-rooted, fully molariform; heavily worn in all the new specimens.

**M1:** Three-rooted. All specimens display the standard *Metaxytherium* cusps pattern, with two transverse rows of three cusps, in addition to pre- and postcingula connected lingually to the main loths. Judging from its lack of wear, the tooth 90(ves)VM5 belonged to a very young specimen (cf. *Dusisiren jordani* Domning, 1978 UCMP102635, in Domning, 1978: fig. 13b). The precingulum is composed of four separate cuspsules that show a slight degree of wear. The anterior cingular valley (anterior basin) is closed on both the buccal and lingual sides. Protocone, protocuneole and paracone are arranged transversely. The transverse valley is open and unobstructed so as to divide the tooth into two halves. The metacone is well developed due to the presence of two endocuspules very close to each other. Hypocone and metaconule are very closely united. The posterior cingular valley (posterior basin) is closed and the postcingulum consists of two cingular cusps located postlingually.

**M2:** Three-rooted; differs from DP5 and M1 primarily in its larger size and lesser degree of wear.

**M3:** In all specimens, M3 is narrower posteriorly than M2. In 62(ves)VM6 and 65(pap)VM2, the metacone is smaller than in other specimens.

**DP5, DP6:** Not preserved in the new specimens.

**DP7:** Two-rooted; preserved on both the left and right sides of 81(ves)VM6; heavily worn.

**M7:** Two-rooted, rectangular, fully molariform, and heavily worn.

**M8:** Rectangular, larger than M1, and moderately worn.

**M9:** Larger than the previous teeth. In 81(ves)VM6, it is not fully erupted; therefore, it has only slight wear on the protoconid. The hypoconulid is formed by four cusps.

**Postcranial skeleton**

No complete vertebral column is known for *M. serresii*, but two complete adult rib cages have been collected and comprise 19 (Montpellier: Depéret & Roman, 1920) to 20 pairs of ribs (Cessaniti, 15[ves]VM5; Carone & Domning, 2007).

The new finds (Tab. 1) include three incomplete postcranial skeletons: 59(ves)VM5, 64(ves)VM6, and 77(ves)VM6; as well as a fragmentary xiphisternum, 84[zac]VM. Vertebrae, ribs, and appendicular elements fall within the morphology of specimens from Cessaniti described by Carone & Domning (2007).

The xiphisternum (84[zac]VM) consists of the anterior portion near the lost distal bifurcation. It has a sharp profile around the entire perimeter. The rear portion narrows and then flattens out. The xiphisternum is strongly convex on the ventral side and flat on the dorsal side.

The scapula of 59(ves)VM5 presents a wide supraspinous fossa and a narrower infraspinous fossa. The spine is moderately high. The neck is narrow, and the glenoid fossa is deep.

In the humerus of 59(ves)VM5, the large tubercles diverge at an angle of approximately 83°. The intertubercular groove has a circular cross section with a diameter of about 19 mm. The greater tubercle has an extension at its top that turns toward the head. The lesser tubercle is rather long in the proximo-distal direction. The deltoid crest is prominent and recurved, and the deltopectoral crest has a prominent bulge. The trochea is inclined obliquely to the shaft at an angle of approximately 72°. The groove for the humeroulnar ligament is very evident, and extends across about half of the articular surface of the trochea. The coronoid fossa and olecranon fossa are deep.

**DISCUSSION AND CONCLUSIONS**

The new specimens of *M. serresii* from the Cessaniti area are valuable in that they are of good quality and improve the knowledge of the species. Since most fossil sirenian species are represented by fewer than a dozen individuals (Domning, 1994: tab. 1), the range of individual variation in the cranial and dental characters used for phylogenetic analyses is inadequately known for most. This introduces uncertainties into estimates of their cladistic relationships (Domning, 1994).

The main improvements in our knowledge of the species *M. serresii* revealed by this study (compare to Carone & Domning, 2007) are: the character scorings c. 23(0), 64(1), and 97(1) are newly recorded here; the rostral deflection can extend up to 78°; separation of nasals (c. 31[1]) occurs in 7/9 of the known specimens of the species from all localities rather than just 3/5; separation of exoccipitals (c. 66[1]) occurs in 7/8 rather than 4/5; the supracondylar fossa is only moderately deep (c. 67[3]) in 8/9 rather than 4/5; and scoring of the anterior extent of the palatine (c. 99[1]) is better supported.

For the last four characters, the new specimens raise the level of confidence we can have in their scorings, bringing one of them (c. 67[3]) above the lower 95% confidence limit for the first time. As explained by Domning (1994), the minimum proportion of a sample which permits 95% confidence that a character state occurred at a frequency of ≥ 0.50 in the original population is (for sample sizes from six to nine) 6/6, 7/7, 8/8, and 8/9, respectively. For a
sample of only five specimens or fewer, one cannot have 95% confidence that a state was present in even as many as half of the sampled population, not even if the entire sample exhibits that state. Therefore, in the case of c. 67, an occurrence of 8/9 provides that 95% confidence, whereas the previously known proportion of only 4/5 did not. For c. 31(1) and 66(1), the proportions in the present sample of 7/9 and 7/8, respectively, still fall short of that level of confidence, but they do bring us closer to it.

This kind of improvement in our knowledge makes our phylogenetic conclusions more robust in the face of “noise” introduced into the dataset by seemingly noncongruent character states. For example, c. 31 was already known to be intraspecifically variable in *M. serresii* in the early analysis of Domning & Thomas (1987: fig. 12; character XII), where this lessened the confidence placed on this character. Similar variability of c. 66 and 67 in *M. subapenninum* Bruno, 1839 (= “*M. forestii*” Capellini, 1872) had a similar effect (Domning & Thomas, 1987: fig. 12; characters XI and IX, respectively). Such spurious “noise” might cause a character to be omitted from an analysis. But with only a slightly larger sample it could be demonstrated statistically that each character provides useful phylogenetic information, justifying their use (e.g., c. 67 in Sorbi et al., 2012: fig. 12). The pervasive biological reality of polymorphism can thereby be dealt with in a biologically justifiable fashion (by means of an objective rationale for disregarding it below a certain level) without need for the kind of convoluted and arbitrary procedure devised by Domning (1994). But this requires larger sample sizes, such as those partially provided here.

These new specimens also corroborate the lack of variability in other, intraspecifically constant characters, such as the size of the tusk (c. 140[1]). They thereby add to the support for the conclusion that *M. serresii* was a chronospecies in a single, anagenetically-evolving lineage of Mediterranean sirenians, as follows: *M. krahaluetzi*, Burdigalian (MN 3-4?); *M. medium*, Langhian-Tortonian (MN 5-12); *M. serresii*, uppermost Tortonian-lower Zanclean (MN 12-14); *M. subapenninum*, upper Zanclean-lower Piacenzian (MN 14?-15) (Bianucci et al., 2008; Sorbi et al., 2012). The small dimensions of these new specimens, in comparison with measurements in Bianucci et al. (2008), further corroborate the phenomenon of peri-Messinian dwarfing in *M. serresii*.

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