A Miocene ocean sunfish (Tetraodontiformes, Molidae) from the Pietra Leccese formation of Southern Italy

(Running title: **Miocene Molidae from Southern Italy**)

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With 4 figures

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Abstract: The ocean sunfishes of the family Molidae comprise one of the tetraodontiform clades with the least known fossil record. Here, we report on what appears to be an isolated paraxial ossicle likely pertaining to the Molidae from a widely known marine vertebrate-bearing deposit of Southern Italy, i.e., the Miocene Pietra Leccese formation of Apulia. Thus far, paraxial ossicles are exclusively known from the genus *Mola*; however, the possibility that some extinct species of *Ranzania* or *Masturus* developed paraxial ossicles cannot be definitively ruled out, hence the attribution of the fossil described herein to an indeterminate taxon of the family Molidae. A careful scrutiny of palaeoichthyological literature reveals that, besides contributing to the meagre Mediterranean and global fossil record of the Molidae, the Apulian ossicle may be regarded as the best candidate to represent the first fossil find of the genus *Mola* from the Mediterranean Basin. In light of the environmental preferences of extant molids, the occurrence of an ocean sunfish in the Pietra Leccese matches well the warm-water, highly productive, outer neritic setting witnessed by this sedimentary unit and its fossil content. Considering also that the Miocene has been recognised as a time span of increased abundance and diversity of ocean sunfishes worldwide, our find should encourage the quest for new, hopefully articulated specimens of molids in this celebrated fossiliferous limestone.

Key words: clavus, dermal plate, Mediterranean Basin, *Masturus*, *Mola*, palaeobiogeography, palaeoecology, palaeoichthyology, paraxial ossicle, *Ranzania*

1. Introduction

The ocean sunfishes, also known as molas (family Molidae), comprise five species arranged in three genera (*Mola*, *Masturus* and *Ranzania*) of large-sized, highly idiosyncratic gymnodont fishes. Broadly known as oceanodromous, tropical to warm-temperate, pelagic-oceanic representatives of the charismatic marine megafauna (Leis et al. 2015; Liu et al. 2015a, b; Nyegaard 2018), molids can reach titanic sizes, up to a length of over 3 m and a weight of more than 2000 kg, which makes them among the heaviest living teleost fishes (e.g., Santini & Tyler 2003; Watanabe & Sato 2008). The general morphology of ocean sunfishes is also remarkable, resembling a "half fish" whose posterior portion has been cut off abruptly (McCann 1961). This is due to the disappearance of the caudal fin, which is functionally replaced by a deep and greatly shortened tail region, i.e., the clavus (sensu Fraser-Brunner 1951) (Johnson & Britz 2005; Nakae & Sasaki 2006). Several autapomorphies identified in the skeletal structure and soft anatomy define the molids, including a rigid and abbreviated vertebral column, loss of the gas bladder in physically mature individuals, and an extreme reduction of axial musculature (Fraser-Brunner 1951; Tyler 1980; Weems 1985; Santini & Tyler 2002; Carnevale et al. 2020). Molids are also characterised by poorly mineralised, cartilage-rich, spongy and/or fibrous bones, and their skeletal remains are rarely preserved as fossils (Carnevale et al. 2021). Anyway, molids possess thickened beak-like jaws as well as a sort of exoskeleton constituted by a continuous cover of scale plates (Tyler 1980; Weems 1985; Katayama & Matsuura 2016). Furthermore, adult individuals of certain species also exhibit additional dermal plates on the chin, mouth and clavus, all of these being well ossified, and as such, characterised by a relatively high fossilisation potential (Leriche 1926; Fraser-Brunner 1951; Tyler 1980; Weems 1985; Carnevale et al. 2021). As a consequence of the peculiar anatomy of molids,

the fossil record of ocean sunfishes is fragmentary, and mostly consists of jaw bones and dermal plates from Eocene to Holocene deposits of the Northern Hemisphere and Argentina (CARNEVALE et al. 2021, and references therein).

Here, we describe a new putative find of molid material from the Miocene Pietra Leccese formation of southern Italy. We address the systematic affinities of this fossil specimen and briefly discuss its palaeontological significance.

2. Material and methods

As many other vertebrate fossils from the Pietra Leccese, the putative molid specimen described herein was collected in the 1980s by ANGELO VAROLA in the framework of the palaeontological field activities of the Dipartimento di Scienze della Terra dell'Università di Pisa. This fossil is currently housed in the Museo di Storia Naturale dell'Università di Pisa (=MSNUP, Calci, Pisa Province, Italy) with accession number MSNUP I-16953.

Measurements of MSNUP I-16953 were obtained using a standard analog caliper. Photographs were taken using a Sony a6000 digital camera equipped with a Sony 50 mm F1.8 lens. A 3D model of the specimen was created by aligning 321 photos through the photogrammetric software Agisoft Metashape v1.70. The 3D model is freely available via figshare at the following internet address: https://figshare.com/s/fb0fa0078463231e5688.

3. Geological and palaeontological framework

The Pietra Leccese (namely, “Lecce stone”) is an informal calcareous formation that extensively crops out in the Salento peninsula of Apulia, southern Italy (Fig. 1). Spanning chronostratigraphically between the upper Burdigalian and the lower Messinian, this informal sedimentary unit consists mostly of foraminiferal biomicrites and biosparites (e.g., MAZZEI

1994; Foresi et al. 2002; Bossio et al. 2005, 2006; Calia et al. 2014; Mazzei et al. 2009). Although the Pietra Leccese records a ~11-My-long depositional history (Bossio et al. 2006), its thickness is limited to a few tens of metres (Foresi et al. 2002), possibly due to the occurrence of several hiatuses that reflect erosional events and are marked by glauconite-rich horizons (Foresi et al. 2002; Bossio et al. 2005). For over a century and a half, quarrying activities have provided palaeontologists with an impressive amount of marine vertebrate fossils entombed in the Pietra Leccese limestone, including turtles, crocodiles, bony and cartilaginous fishes, sirenians, cetaceans, and their coprolites and gastroliths (Costa 1853, 1856, 1865; Capellini 1878; Vigliarolo 1891; Misuri 1910; Bassani 1911, 1915; Moncharmont Zei 1950, 1956; Menesini & Tavani 1968; Menesini 1969; Tavani 1973; Varola et al. 1988; Bianucci et al. 1992, 1994a, b, 2004, 2016; Bianucci 2001; Bianucci & Landini 2002, 2006; Carnevale et al. 2002; Bisconti & Varola 2000; 2006; Chesi et al. 2007; Collareta et al. 2019; Peri et al. 2019, 2020). Palaeontological and sedimentological observations concur to suggest an outer neritic depositional environment for most of the Pietra Leccese exposures, though shallower settings are witnessed by parts of the Tortonian portion of this formation (e.g., Bossio et al. 2005, 2006).

Although the provenance of MSNUP I-16953 from the Pietra Leccese strata is ascertained, the exact stratigraphic position of this fossil is unfortunately uncertain. The reddish colouration of MSNUP I-16953 and the presence of dark brownish remains of the entombing matrix attached to it suggest an origin from the so-called Terra rossa (namely, “Red earth”) that is thought to represent a product of local alteration of the Pietra Leccese limestone (Menesini 1969).

4. Systematic palaeontology

Actinopterygii COPE, 1887

Tetraodontiformes REGAN, 1929

Molidae RANZANI, 1839

Molidae gen. et sp. indet.

(Figure 2)

Referred material: MSNUP I-16953, an isolated medial paraxial ossicle.

Occurrence: Miocene (upper Burdigalian – lower Messinian) Pietra Leccese formation of southern Apulia, southern Italy.

Description and indentification: MSNUP I-16953 is a drop-like, oblong, roughly ellipsoidal mass of hyperostotic bone (Fig. 2). One of the extremities of MSNUP I-16953 along its main axis appears to be gently keeled (Fig. 2c, d), while the opposite one displays what appears to be a broken (or otherwise irregularly interrupted) surface (Fig. 2b, c); across the latter, the bone appears as osteosclerotic and exhibits a radial-fibrous aspect. On one side of the specimen, a broad and shallow sulcus runs parallel to the main axis of the bone for about half of its length (Fig. 2a). The maximum length of MSNUP I-16953, measured along its main axis, is 99 mm; its transverse width, measured perpendicular to the main axis and the aforementioned sulcus, is 64 mm; and its thickness, measured orthogonal to the above directions, is 59 mm. The external surface of MSNUP I-16953 is mostly rugous and coarsely pitted, but smoother areas are locally also observed.

The overall configuration of MSNUP I-16953 is consistent with that of the dermal plates that are found along the posterior margin of the clavus of extant adult individuals of *Mola* spp. (Fig. 3), i.e., the paraxial ossicles (sensu FRASER-BRUNNER 1951), by virtue of the

following combination of characters: i) irregularly ellipsoidal outline; ii) presence of an anteriorly facing longitudinal furrow for the allocation of the membrane that connects the supporting rays of the clavus; iii) external surface mostly rough and rugous; iv) bone tissue hyperostotic, organised with a radial-fibrous pattern (e.g., LERICHE 1926; FRASER-BRUNNER 1951; TYLER 1980; PORCASI & ANDREWS 2001; CARNEVALE et al. 2021). In light of its remarkable size (total length approaching 10 cm, vs a maximum length of slightly more than 8 cm as reported from the subfossil material studied by PORCASI & ANDREWS 2001) and stout rather than elongate overall morphology, MSNUP I-16953 likely originates from the median portion of the clavus of a large-sized, aged individual (see also LERICHE 1926; CARNEVALE et al. 2021; THYS et al. 2021).

Besides the paraxial ossicles, in the living species *Mola alexandrini* and *Mola mola*, two additional ossicles – the so-called nasal and jugular plates – are observed above and below the mouth (SAWAI et al. 2018, and references therein); according to FRASER-BRUNNER (1951), these ossifications may represent the remains of postlarval skin spines. Fossil paraxial ossicles of the Molidae have been collected in association with material referred to extant and extinct species of *Mola*, including nasal and jugular plates, from a few localities worldwide (LERICHE 1926; DEINSE 1953, VAN DEN BOSCH et al. 1975; PORCASI & ANDREWS 2001). Thus far, paraxial ossicles are not known from molid genera other than *Mola*; however, detailed studies on the dermal plates of the extant Molidae would be desirable. In addition, at least a single extinct molid species assigned to *Ranzania* (i.e., *Ranzania grahami* from the middle Miocene of the Chesapeake Group, Maryland and Virginia) developed nasal and jugular plates that are remarkably similar to those of *Mola* (WEEMS 1985; CARNEVALE & GODFREY 2018). Consequently, the possibility that some extinct species of *Ranzania* or *Masturus* developed *Mola*-like paraxial ossicles cannot be definitively ruled out. In light of these

considerations, here we prefer to refer to MSNUP I-16953 as Molidae gen. et sp. indet., pending a better understanding of the variability and taxonomic value of dermal plates across the three extant molid genera.

5. Discussion and perspectives

As already mentioned, the global fossil record of ocean sunfishes is relatively poor (CARNEVALE et al. 2021); therefore, the discovery of even largely incomplete fossil remains pertaining to this lineage is of interest. Thus far, as regards the Mediterranean Basin and the peri-Mediterranean areas, fossils of molids were limited to four Miocene occurrences from Algeria, Austria, France and Italy, respectively (Fig. 4). The Algerian record is comprised of an incomplete anal fin that has been attributed to *Ranzania* sp. and takes its place in Messinian deposits of the Chelif Basin (CARNEVALE & SANTINI 2007). The Austrian occurrence consists of three partially complete skeletons (including the type series) of *Austromola angheroferi* from the lower Miocene (Aquitanian) of the North Alpine Foreland Basin of Central Paratethys (GREGOROVA et al. 2009). The French record takes its place in the Rhône Basin, in deposits that likely date to the middle Miocene (BRISSWALTER 2009); it consists of two dermal plates figured by GERVAIS (1859: pl. 68, figs. 34, 35) as indeterminate fish bones ("ossements de diverse Poissons") and re-attributed by LERICHE (1907) to *Orthagoriscus* (=*Mola*). LERICHE (1907) refrained from assigning these specimens, which he did not observe in person, to the species-level; however, he noted their smaller size compared to the Belgian molid remains described by VAN BENEDEN (1881, 1883), which he regarded as all belonging to *Orthagoriscus pileatus* (=*Mola pileata*). Considering that nasal plates that strongly recall those of extant *Mola mola* seemingly occur in at least one Miocene member of *Ranzania* (WEEMS 1985; CARNEVALE & GODFREY 2018), the specimens figured by GERVAIS

(1859) may not be positively assigned to either *Mola* or *Ranzania*. The Italian occurrence consists of the holotype and only known specimen of *Ranzania zappai* from the middle Miocene (Serravallian) of Torricella Peligna, Abruzzo; it comprises some fragments of the carapace (CARNEVALE 2007). In light of these data, and considering also that the occurrence of paraxial ossicles has never been verified in molids other than *Mola* spp., our new specimen could be regarded as the best candidate to represent the first fossil find of this genus of the family Molidae from the Mediterranean Basin and the adjacent regions.

As the stratigraphic whereabouts of MSNUP I-16953 are unknown, its palaeoecological significance is unfortunately very limited. One may just notice that the oceanodromous, pelagic-oceanic habits of living molids (e.g., LEIS et al. 2015; LIU et al. 2015a, b, and references therein) fit well the outer neritic setting witnessed by most of the Pietra Leccese outcrops. Furthermore, the environmental preferences of extant ocean sunfishes match the overall palaeoenvironmental signature of the best known fish assemblage from the Pietra Leccese, i.e., that from the Tortonian strata of Cisterna quarry (MARGIOTTA & SANSÒ 2017). This fossil ichthyofauna mostly comprises large epipelagic inhabitants of the outer and inner shelf, including various specimens of billfish, namely, the marlin *Makaira* cf. *nigricans* (CARNEVALE et al. 2002). Interestingly, the common mola *Mola mola* comprised some 70–93% of the total fish catch in Spanish drift gillnet fisheries targeting a close ally of *Makaira* (i.e., the broadbill *Xiphias gladius*) on the Mediterranean side of the Strait of Gibraltar between 1992 and 1994 (SILVANI et al. 1999).

The Italian fossil finds of *Mola* and *Ranzania* come from the Eastern (i.e., Adriatic) side of the Apennine chain. Nowadays, both *M. mola* and the slender sunfish *Ranzania laevis* frequent the Mediterranean Sea, although they are sighted only rarely (PSOMADAKIS et al. 2012; LIU 2015a, b; SANTIN et al. 2021); these molid species are rather infrequent off Italy,

being relatively more common (though still rare) in the Adriatic Sea (DULČIĆ et al. 2007; PASTORE 2009). In this semi-enclosed sea region, sightings of *M. mola* over more than two centuries of observations correlate with high seawater temperatures; on the other hand, sightings of *R. laevis* seemingly couple with periods of great availability of zooplankton and small pelagic fishes (the target prey of slender molas), which in turn result from phases of increased primary productivity (DULČIĆ et al. 2007). Similar mechanisms may have controlled the presence and abundance of molids in central Mediterranean waters in deep time. During the Miocene, the Mediterranean seawater temperatures were significantly higher than that of toady (e.g., PRISTA et al. 2015, and references therein), and conditions of high nutrient availability off the Italian coasts are hypothesised on the basis of the widespread occurrence of phosphate- and glauconite-rich intervals in the Pietra Leccese and other marine deposits of Italy and Malta (FÖLLMI et al. 2008, 2015; VESCOGNI et al. 2018; PERI et al. 2020). Taking into account the neritic depositional environment of the Pietra Leccese, and considering also that the Miocene has been recognised as a time span of increased abundance and diversity of ocean sunfishes worldwide (CARNEVALE et al. 2021), our find should encourage the quest for new remains of molids in this celebrated fossiliferous limestone of Southern Italy. New finds of articulated molid skeletons from Miocene strata may help in answering prominent open questions regarding the fossil history of ocean sunfishes, including the skeletal anatomy of the widespread Neogene species *Mola pileata* and of the extinct species of *Ranzania* that are only known from isolated jaw bones and dermal plates.

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Figure captions

[*Possible positions for the three figures: Fig. 1 between lines ... and ...; Fig. 2 between lines ... and ...; Fig. 3 between lines ... and ...; Fig. 4 between lines ... and ...*]

Fig. 1. Schematic geological map of the Salento peninsula (Apulia, southern Italy). Grey-shaded areas indicate the exposures of the Pietra Leccese, the Miocene limestone from which the fossil specimen MSNUP I-17604 originates. Redrawn and modified after the original illustration by CALIA et al. (2014).

Fig. 2. MSNUP I-16953, an isolated medial paraxial ossicle of Molidae gen. et sp. indet. from the Miocene Pietra Leccese of Southern Italy, in (a) anterior, (b) posterior and (c,d) lateral views. A digital 3D model of the specimen is freely available via figshare at the following internet address: https://figshare.com/s/fb0fa0078463231e5688.

Fig. 3. Location of the paraxial ossicles (black arrows) along the posterior portion of the clavus of a 600-mm-long extant specimen of *Mola mola*. Modified after FRASER-BRUNNER (1951: fig. 16).

Fig. 4. Distribution of fossil remains of the family Molidae in the Mediterranean Basin and the adjacent regions. See the main text for further information.

Figures

Figure 1

Figure 2

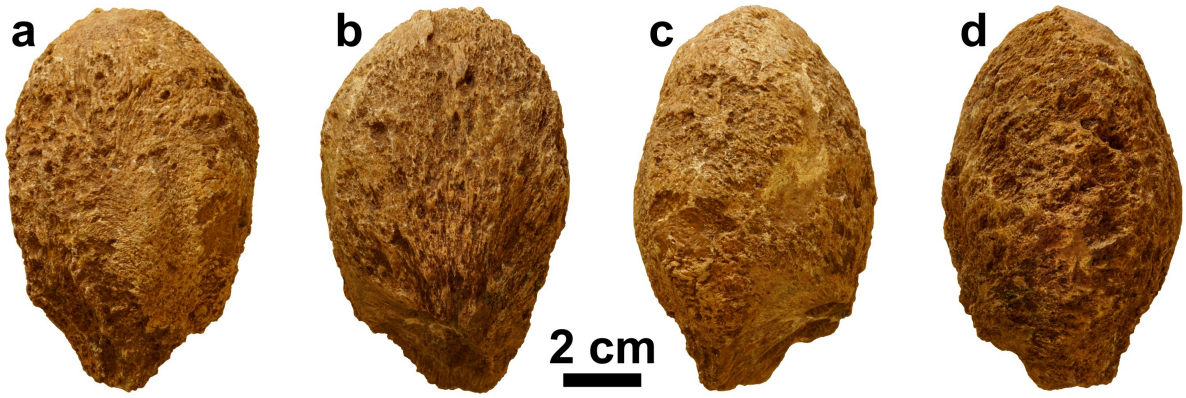

Figure 3

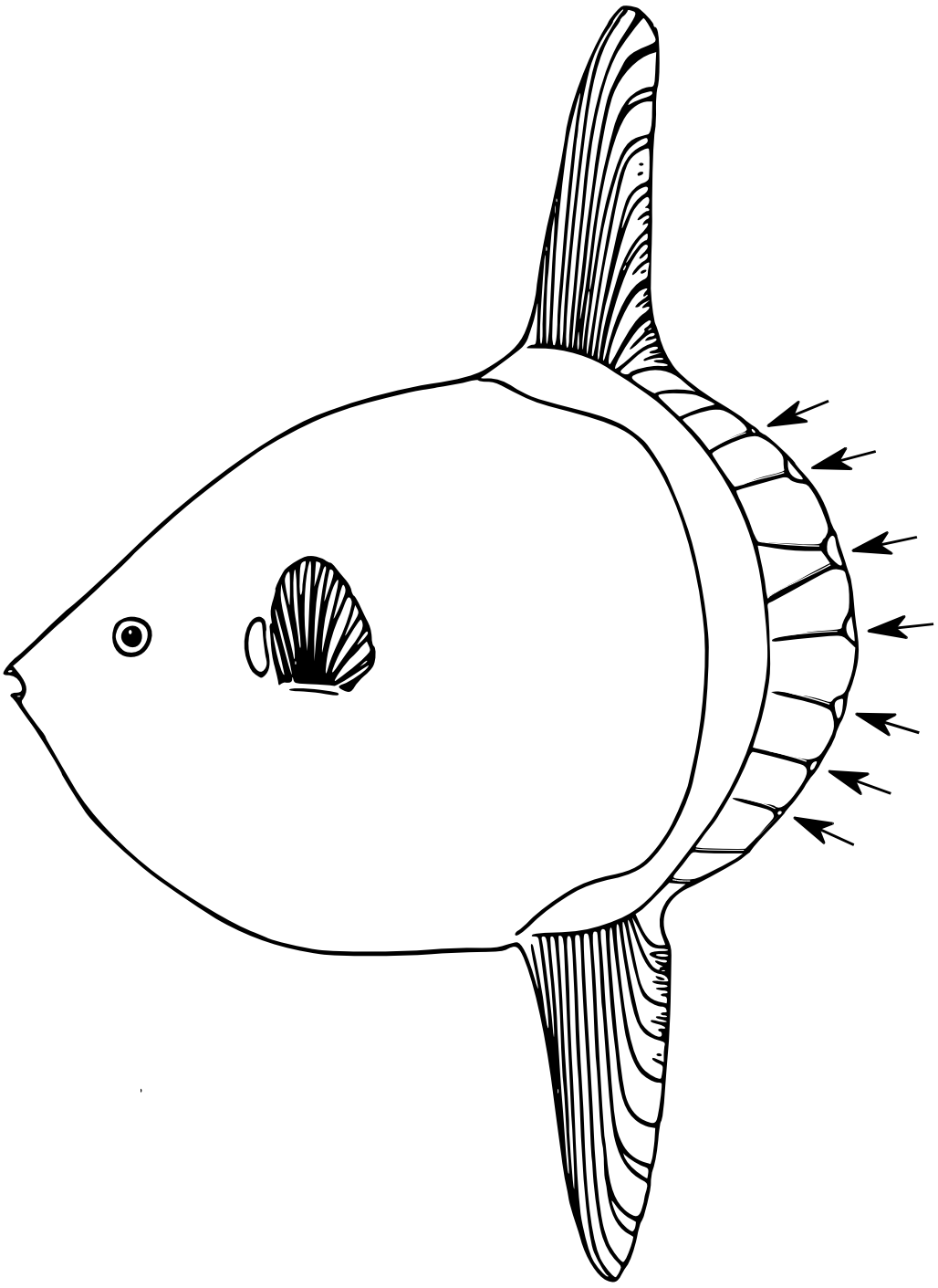

Figure 4


Molidae gen. et sp. indet.
middle Miocene?
(Leriche 1907; this work)
Austromola angerhoferi
Aquitanian
(Gregorova et al. 2009)
Ranzania zappai
Serravallian
(Carnevale 2007)
Molidae gen. et sp. indet.
Miocene
(this work)
Ranzania sp.
Messinian
(Carnevale & Santini 2007)