

A GIANT EARLY MIOCENE SUNFISH FROM THE NORTH ALPINE FORELAND BASIN (AUSTRIA) AND ITS IMPLICATION FOR MOLID PHYLOGENY

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ABSTRACT—Three extraordinarily well-preserved skeletons and skeleton parts of an Early Miocene sunfish are described. These unique fossils allow a precise osteological description of one of the largest if not the largest sunfish (320 cm) known so far and represent one of the largest teleost fossils of the Cenozoic Era. This new sunfish genus is the sister-taxon of the extant *Mola+Masturus* clade and, together with these two genera, forms the sister-clade of *Ranzania*. The radiation of modern-type sunfishes therefore already had occurred during Oligocene times. The finding from the earliest Miocene narrows the gap between the oldest known Eocene primitive sunfish and the Middle and Upper Miocene records, which are all referable to extant genera. *Austromola* is introduced as a new genus of the family Molidae; *Austromola angerhoferi* is described as a new species.

INTRODUCTION

The Molidae Ranzani, 1839 comprise the family of ocean sunfishes within the order Tetraodontiformes Berg, 1940 and represent the largest extant bony fishes, reaching lengths of over 3 m. All known Molidae are characterized by a stout, truncated shape, with a body that ends rather abruptly just behind the dorsal and anal fins. This morphology is also reflected by a strong reduction in the number of vertebrae (Tyler, 1980). They are epipelagic and are distributed worldwide in tropical to temperate seas. Extant Molidae prey on jellyfish but also feed on algae, crustaceans and fishes (Parenti, 2003). Due to their largely cartilaginous, weakly ossified and spongy skeleton, the fossil record of the Molidae is very poor compared with the records of the other modern families of Tetraodontiformes. Consequently, representatives of the family Molidae are mostly represented by isolated jaws and dermal scale plates (Tyler and Santini, 2002). Complete skeletons even of modern sunfishes are rare in museum collections and, unsurprisingly, no complete Molidae skeletons have been reported so far in the fossil record.

GEOGRAPHIC AND GEOLOGIC SETTING

Three Molidae skeletons were found by private collectors during construction work for a hydroelectric power plant near Pucking (Austria; N 48° 12' 22"; E 14° 13' 27") in spring 1980 (Fig. 1). The specimens were associated with a complete dolphin skeleton, numerous small teleost fishes and scattered lucinid bivalves along with a diverse algal and leaf flora (Kovar, 1982). The pelitic deposits are part of the Ebelsberg Formation (Krenmayr and Schnabel, 2006) and are dated as Aquitanian (lower part of nannoplankton Zone NN2, Martini, 1971) based on the presence of *Helicosphaera scissura* Miller and *Helicosphaera sellii* Bukry & Bramlette and the absence of *Helicosphaera ampliaptera* Bramlette & Wilcoxon (Fig. 2). In terms of regional stages, the deposits are part of the upper Egerian stage and are c. 22 Ma old

(Piller et al., 2007). During that time, the area was part of the Central Paratethys Sea, and the North Alpine Foreland Basin was covered by a deep sea (Rögl, 1998). The section was situated on the northern shelf of that sea within the outer neritic zone.

MATERIAL

Specimen 1 consists of more than 210 fragments which form 5 larger units. It is stored in the collection of the NHMW. The largest plate, measuring 69 x 70 cm (Inv. NHMW2003z0026/0892; Fig. 3) displays 8 caudal vertebrae (9th and 10th are missing) and a series of 14 dorsal basal pterygiophores. A counter plate is also present (Inv. NHMW2003z0026/0789). The other slabs represent an almost complete dorsal fin (Inv. NHMW2003z0026/0808–0812, 2003z0026/0868–0872, 2003z0026/0878–0886; Fig. 3), a fragment with gill filaments (nr. 2003z0026/0121; Fig. 4), a fragment of the biting edge (Inv. NHMW2003z0026/0792), isolated scale plates (nr. Inv. NHMW2003z0026/0832), and some undeterminable fragments (Inv. NHMW2003z0026/0443, 0553–0566, 0790–0791, 0793–0807, 0813–0831, 0833–0867, 0873–0877, 0887, 0890–0891). Estimated total length c. 150–170 cm.

Specimen 2 is a relatively complete specimen with plate and counter plate comprising the caudal area of the vertebral column, pectoral-fin girdles, as well as dorsal, anal, and pseudocaudal fins (Figs. 5, 6). Only centra of the 5 last abdominal vertebrae are preserved. The upper jaw (Inv. NHMW2008z0037/0001; Fig. 7) is well preserved, the lower one only fragmentally. One plate of this specimen is stored in the private collection of Dr. Bercht Angerhofer (Buchkirchen, Austria), whilst the counterplate is on loan to the NHMW. Estimated total length c. 320 cm.

Specimen 3 was destroyed by construction work before excavation. The photos, however, provide important ancillary information for the description (e.g., 8th vertebra with a well-developed haemal and a well-developed neural spine, Fig. 8). Estimated total length c. 240 cm.

In addition, several specimens of *Mola mola* (Linnaeus, 1758) have been investigated in the collections of the NHMW (skeleton: NHMW 95.125, SL 127 cm, TL 151 cm; dermoplastic speci-

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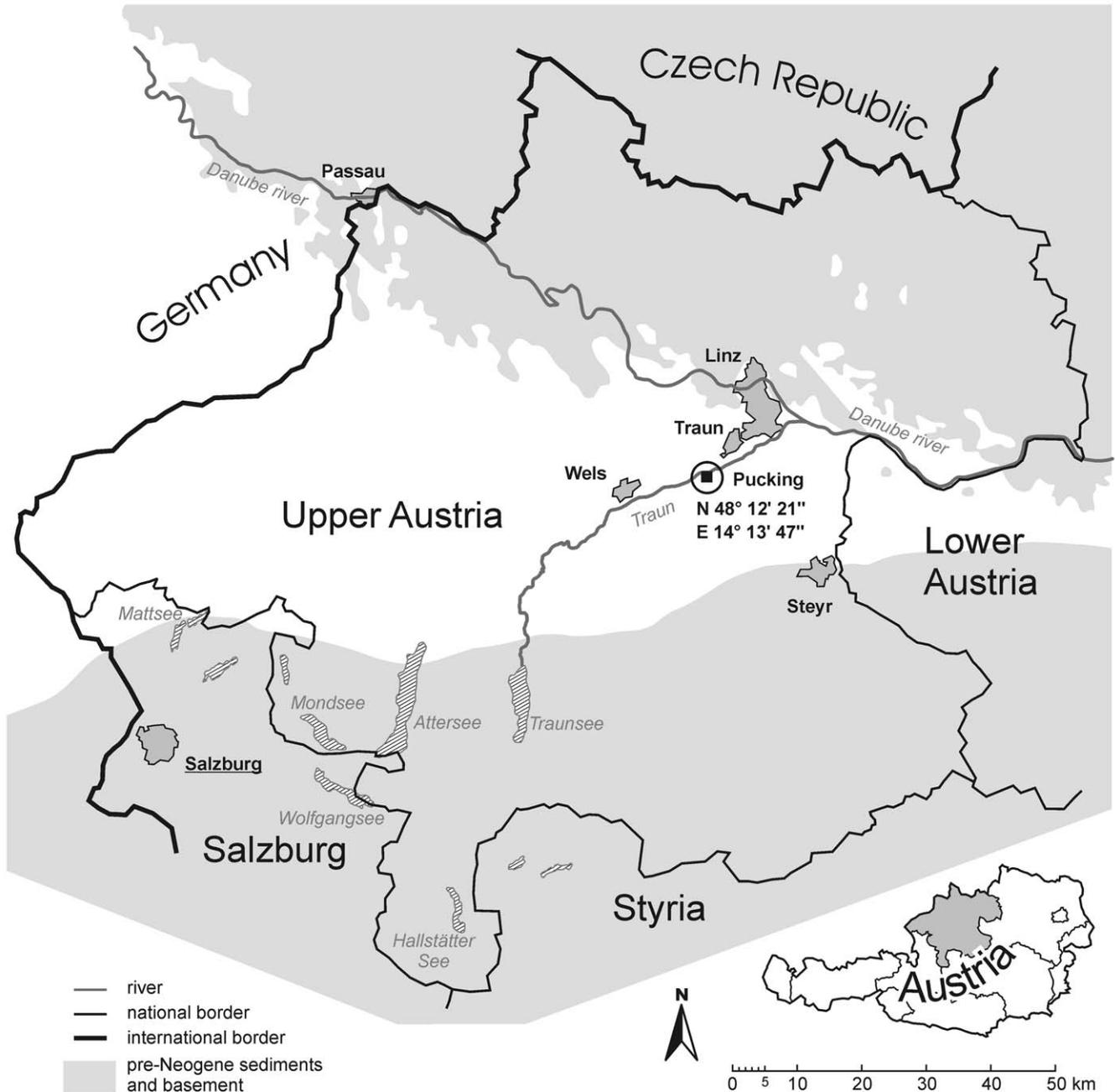


FIGURE 1. Geographic position of the locality Pucking in Upper Austria within the North Alpine Foreland Basin. The fish-bearing deposits are now covered by a hydro-electric power plant.

mens NHMW 95.123, TL 214 cm, NHMW 95.124, TL 116 cm), the Natural History Museum London (BMNH 1861.3.20:4 and three specimens without numbers), and the National Museum of Natural History, Washington, D.C. (USNM 111025, USNM 273214).

METHODS

The osteological analysis and identification of the bones is based on comparative material of *Mola mola*. The terminology follows Tyler (1980). Phylogenetic analysis was carried out using

the software packages PHYLIP vers. 3.6 (alpha3) (Felsenstein, 2002) and PAUP* 4.0b10 (PPC) (Swofford, 2002). Both branch and bound as well as heuristic search methods (with random additional replicates and TBR branch swapping) were used, yielding identical trees. Bootstrapping with 1000 replicates was carried out to test node support. Interestingly, analysis with PHYLIP (employing SEQBOOT, PARS and CONSENSE) always resulted in lower node support for one of the nodes (basal node of the Molidae). Bremer support values were calculated as well (Bremer, 1994). The analysis involved the three extant Molidae (*Mola*, *Masturus* and *Ranzania*), the new fossil molid

Age (Ma)	EPOCH	AGE	REGIONAL STAGE	Planktonic Foraminifera		Sequence Stratigraphy (3 rd order)	
				Calcareous	Nannoplankton		
20	Miocene	Burdigalian	Karpatian	M5	NN4	Bur4	
				M4		Bur3	
			Ottngian		NN3	Bur2	
						Aq3/Bur1	
		Eggenburgian	M2		Aq2		
				NN2	Ch4/Aq1		
		Aquitanian	M1				
				NN1			
		25	Oligocene	Egerian	P22		Ch3
						NP25	
Chattian					Ch2		
Kiscellian	P21	b	NP24				

FIGURE 2. Chronostratigraphy, biostratigraphy and sequence stratigraphy of the Central European late Oligocene and Miocene (see Piller et al. 2007 for details). Grey shading: stratigraphic position of the fish-bearing deposits of the Ebelsberg Formation.

(*Austromola*), as well as the two outgroups *Lagocephalus* and *Triodon*. The latter is a member of the Triodontidae, considered to be the most primitive living tetraodontid fish (Winterbottom, 1974; Tyler, 1980). *Lagocephalus* is a member of the Tetraodontoidea, the sister-group of the Molidae (Santini and Tyler, 2003). A total of 57 characters mainly based on skeletal morphology were scored. Most (48) of these were taken from Santini and Tyler (2002) and are indicated as such in the character list. All characters were treated as unordered and given equal weight. The full list of characters and the data matrix are given in appendices 1 and 2.

Abbreviations—**SL**, standard length; **TL**, total length, **BD**, body depth; **A**, anal fin; **D**, dorsal fin; **P**, pectoral fin; **PsC**, pseudocaudal fin; **NHMW**, Natural History Museum Vienna.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII Klein, 1885

Order TETRAODONTIFORMES Berg, 1940

Family MOLIDAE Ranzani, 1839

Genus *AUSTROMOLA* Gregorova, Schultz, Harzhauser and Kroh, gen. nov.

Type Species—*Austromola angerhoferi* Gregorova, Schultz, Harzhauser and Kroh, sp. nov.

Etymology—The generic epithet is from *Austro-* for Austria plus *-mola* referring to its relationship to the extant *Mola*.

Diagnosis—Differs from the three extant genera of the family Molidae and *Eomola* by combination of the following characters: Ten cartilaginous caudal vertebrae, the last one of which is a simple shaft ending with a flat surface posteriorly. The praemaxillae and its biting edge are indistinguishably fused along the midline. The pectoral fin is rounded and the basal pterygiophores of the anal fin are especially robust. No bony ossicles are developed on the distal ends of the basal pterygiophores of the

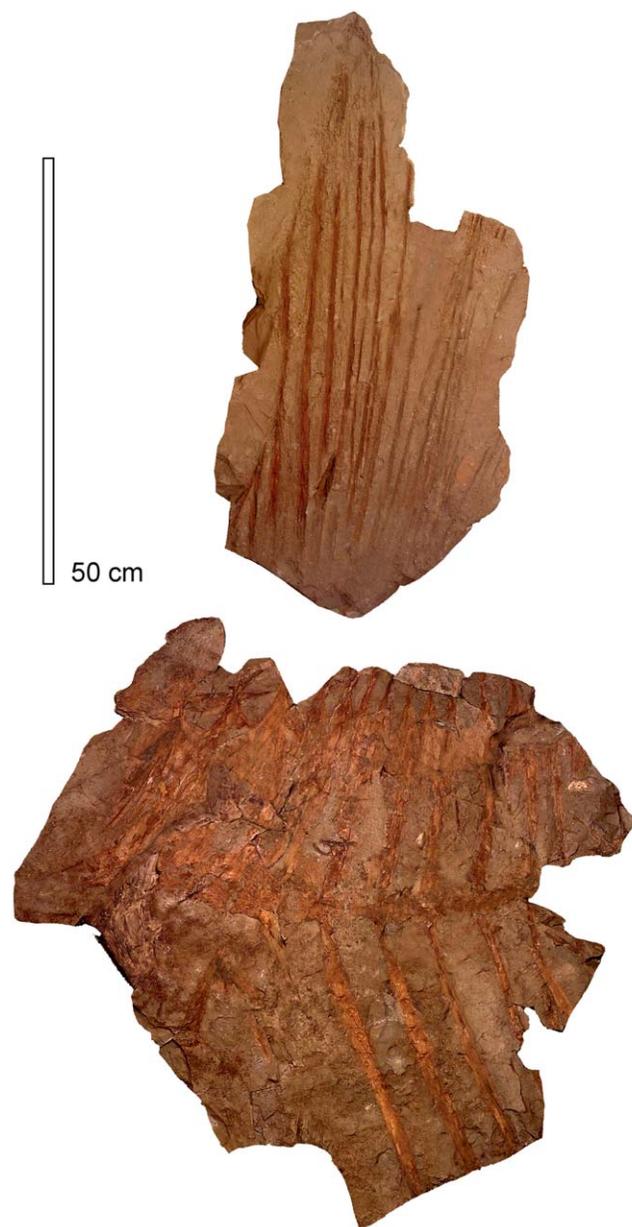


FIGURE 3. Holotype specimen of *Austromola angerhoferi* consisting of the caudal vertebrae (Inv. NHMW 2003z0026/0121) and the dorsal fin (Inv. NHMW2003z0026/0808–0812).

pseudocaudal fin. The basal pterygiophores of the anal part of the pseudocaudal fin are distinctly longer than those of the dorsal part. The caudal fin rays are unbranched. Scale plates are hexagonal or polygonal.

Occurrence—Lower Miocene (Aquitanian, = upper Egerian) pelites of the Ebelsberg Formation at Pucking in Upper Austria (Austria, Europe).

DISCUSSION OF GENERIC DIAGNOSTIC FEATURES

Caudal Vertebrae—*Austromola* has 10 caudal vertebrae, like the extant genus *Ranzania* (Fraser-Brunner, 1951). In contrast, *Mola* develops 9 and *Masturus* only 8 caudal vertebrae. The last vertebra is a simple shaft as in *Ranzania* and *Mola* (Tyler, 1980). Except for the different number of caudal vertebrae, the last and

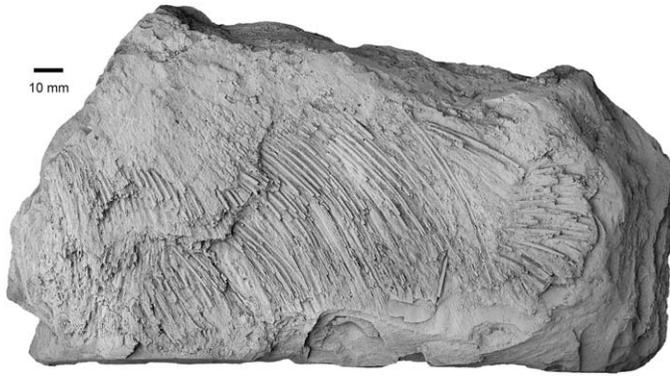


FIGURE 4. Gill filaments of *Austromola angerhoferi* (Holotype specimen, Inv. NHMW 2003z0026/0121).

the penultimate vertebrae are reminiscent only of those of *Mola*, whilst the 9th caudal vertebra of *Ranzania* bears a neural and a haemal spine. *Masturus* differs by its eight caudal vertebrae and by the haemal spine of the last caudal vertebra.

Jaws—In recent *Mola* jaws the premaxilla is gently curved downwards and has a beak-like distal end. In contrast, the dentary is relatively flat, without concavity, and lacks a beak-like termination. The well-preserved jaw of *Austromola* has a biting edge which corresponds fully to those of the premaxilla of *Mola* and is thus identified as an upper jaw. The left and the right premaxilla are indistinguishably fused in the midline. This character clearly distinguishes *Austromola* from *Eomola*, which has a twofold premaxilla and dentary, being divided along a midline into right and left parts.

Trituration plates are missing. Similarly, adult *Mola* lack trituration plates. These are only present in subadult *Mola* specimens under 1000 mm SL and are subsequently reduced during ontogeny (information by J. Tyler, 17 Jan. 2008, based on material in the Smithsonian collection).

Fins and Pterygiophores—The pectoral fin has a rounded outline like in *Mola* or in *Masturus*, thus differing clearly from the elongate shape in *Ranzania*. Especially the basal pterygiophores of the anal fin are robust in contrast to the extremely slender ones in *Ranzania*. The lack of bony ossicles on the distal ends of the basal pterygiophores of the pseudocaudal fin agrees with *Masturus* and *Ranzania*, whereas *Mola* develops bony ossicles. In *Mola* and *Masturus* the basal pterygiophores of the anal part of the pseudocaudal fin are longer than those of the dorsal part, whereas they are more or less equally sized or the dorsal basal pterygiophores are even slightly longer in *Ranzania*. This is a function of body shape: in *Masturus* and *Mola* the ventral part of the body is much deeper and the length of the pterygiophores is anatomically adapted to it. In *Austromola* the lowermost basal pterygiophores are up to three times longer than those of the dorsal part, while in *Mola* and *Masturus* this relation is only 1:2. Multibranching terminations of the rays of the pseudocaudal fin, as typical for *Ranzania*, are missing. The poor preservation of the distal part of the pseudocaudal fin, however, does not allow a clear description of that feature.

A tentative character is the relation of the dorsal and anal fins to their pterygiophores. The dorsal fin base in *Austromola* is very close to the distal ends of the dorsal pterygiophores (less than the length of one caudal vertebra), whereas the anal fin base is far removed from the anal pterygiophores (more than the length of two caudal vertebrae). In extant Molidae, in contrast, the relative depth of the cartilaginous band between the bases of the dorsal and anal fins is of approximately the same

depth at the dorsal and the anal fins. It is approximately about equal in depth to the length of a centrum in the caudal series of the vertebral column (Tyler, 1980).

Scales—The scale plates of *Austromola* are angular (hexagonal and polygonal) as in *Ranzania*, differing from the circular scales of *Mola* and *Masturus*.

AUSTROMOLA ANGERHOFERI Gregorova, Schultz, Harzhauser and Kroh gen. nov. et sp. nov.
(Figs. 3–8)

Diagnosis—as for genus.

Holotype—The specimen illustrated in Figure 3; Inv. NHMW 2003z0026/0892, stored in the collection of the Natural History Museum Vienna, estimated TL c. 150–170 cm.

Paratype—The specimen illustrated in Figure 4, on loan to the Natural History Museum Vienna by Dr. Bercht Angerhofer (upper jaw of Paratype: NHMW2008z0037/0001); estimated TL c. 320 cm, SL c. 269 cm.

Etymology—In honor of Dr. Bercht Angerhofer, who found and recovered the best preserved specimen and generously provided access to his material.

Occurrence—Lower Miocene (Aquitanian, = upper Egerian) pelites of the Ebelsberg Formation at Pucking in Upper Austria (Austria, Europe).

Description—The body has a characteristic mold outline. The caudal part is typically truncated; the caudal fin is absent and replaced by the pseudocaudal fin. Its soft rays are supported by seven dorsal and nine anal basal pterygiophores. The dorsal and the anal fin are widely branched and long; they represent together more than two-thirds of the depth of the whole animal. The upper jaw possesses edges with an angle of 90°; no teeth or trituration plates are preserved.

MEASUREMENTS

Paratype

Pectoral Fin—length of the 1st ray: 12 cm; 2nd ray: 20 cm; 3rd ray: 31 cm; the longest 6th: 32 cm.

Anal Fin—1st ray: 30 cm; 2nd ray: 53 cm; 3rd ray: 70 cm; 4th: 84 cm; 11th: 75 cm.

Dorsal Fin—length of the 1st ray: 28 cm; 2nd: 48 cm; 9th: 96 cm.

Pseudocaudal Fin—length of the basal anal pterygiophores 1st: 9 cm; 2nd: 9–10 cm; 5th: 40 or 35 cm; length of the caudal rays: 16.5, 18 and 17 cm.

Vertebrae—Length of the first caudal vertebra: 8.5 cm; length of the last caudal vertebra: 11 cm; length of the penultimate vertebra: 5.5 cm.

Distance between the extremities of the anal and dorsal (incomplete) fins—313 cm;

Body Depth—127 cm (= distance from the base of the anal fin to the base of the dorsal fin, measured perpendicularly to the vertebral column).

Body Size—total length: about 320 cm; distance between the tips of the dorsal and anal fins: >400 cm. This tentative estimation is based on linear extrapolation of morphometric parameters of recent *Mola mola* (Table 1). Hence, the relation between body depth (BD) and the length of the longest anal fin ray is 1:1.05 and 1:1.1 for the dorsal fin. It is 2.1 for the standard length and 2.5 for the total length. Claro (1994) reports the maximum size of *Mola mola* (Linnaeus, 1758) to be 333 cm. Thus, *Austromola* can be considered as one of the largest sunfishes.

Formule—Vertebrae ?+10; A17/10; D 18/15; PsC 7 (D) + 9 (A); a comparison of metric characters of *Austromola angerhoferi* with 3 extant Molidae species is presented in Table 2.



FIGURE 5. Near-complete specimen of *Austromola angerhoferi* (Paratype); major cracks in the slab have been digitally removed to enhance the quality. This specimen is the largest teleost fossil from the Cenozoic Era known so far.

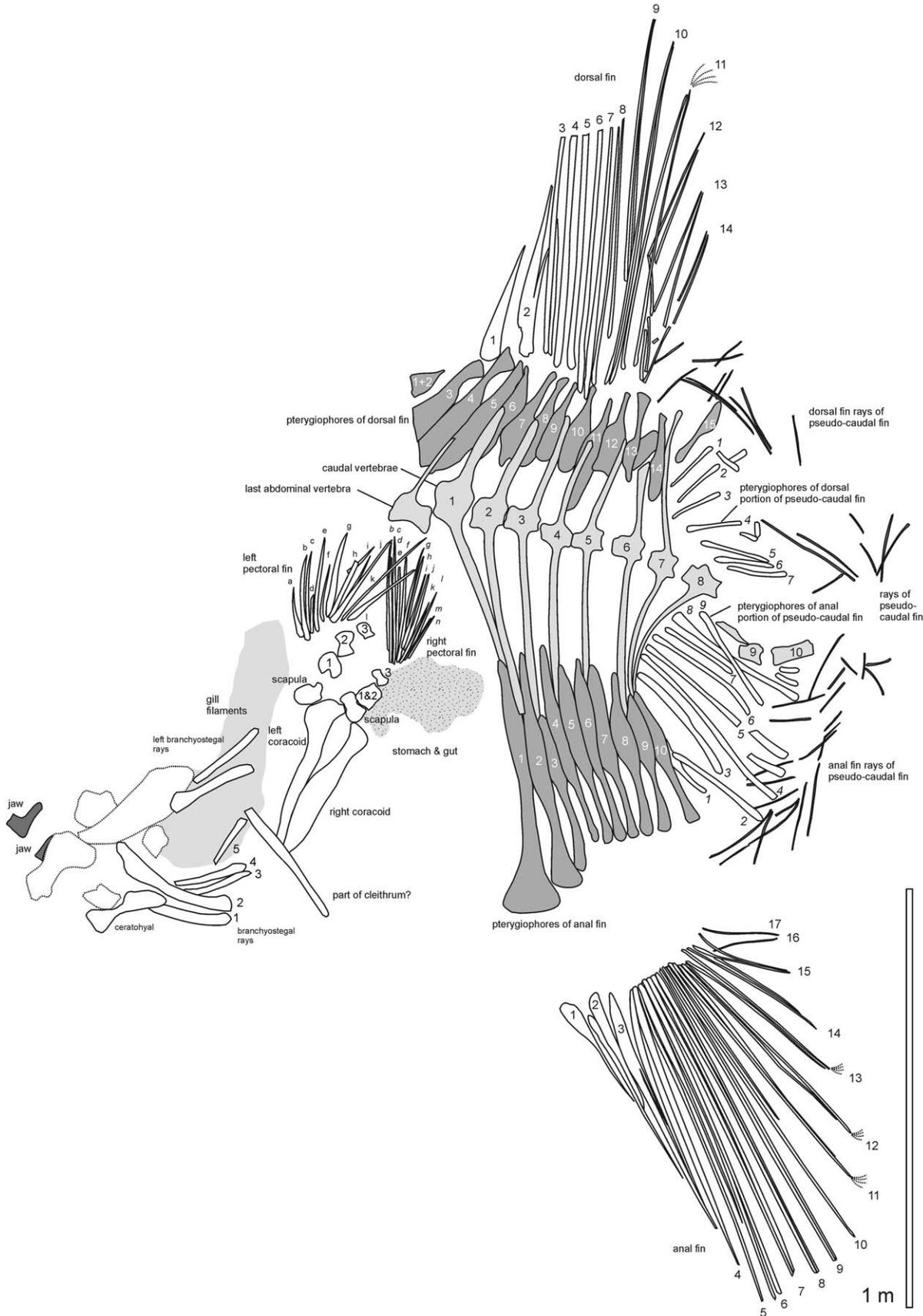


FIGURE 6. Skeleton reconstruction of *Austromola angerhoferi* based on the Paratype (Fig. 5).



FIGURE 7. Fused praemaxillae of *Austromola angerhoferi* (Inv. NHMW2008z0037/0001); this jaw element was isolated from the Paratype and replaced on the slab by a replica.

OSTEOLOGY

Skull—Only specimen 2 displays some skull bones. Four branchiostegal rays are more or less in situ and the ceratohyal from the hyoid arch lies close to them. Other branchiostegal rays are disarticulated and come from both sides of the head. The long gill filaments are disarticulated over large parts of the head. Only specimen 1 has a rather complete band of the gill filaments reaching a length of 6.8 cm.

Jaws—Aside from the premaxilla described above, an additional pointed jaw element is preserved, which is covered by a hard and shiny substance. This is considered to be an isolated biting edge of the lower jaw. In recent *Mola* the biting edge of the premaxillary and dentary is a hard and homogeneous substance, which is interpreted as fused teeth like in Diodontidae (Tyler, 1980).

Coracoid—In recent *Mola* the coracoid is a flattened plate throughout its length, except ventrally where it becomes more rounded and shaft-like. The dorsal end of the coracoid is expanded and dish-like. Its middle region is widened.

In *Austromola* both coracoids are preserved. On the left coracoid the dorsal rounded head is distinguishable and on the right coracoid the anterior extension in the middle region is visible. The osteologic interpretation is further supported by the position of both pectoral fins with the actinosts that are normally articulated with the coracoids.

Scapula and Actinosts—The roughly circular scapula is situated anterodorsally of the coracoid: the dorsal concave edge of the left coracoid articulates with the bases of the 3 actinosts, which decrease in size posteriorly in the series. The anteriormost actinost articulates with the scapula.

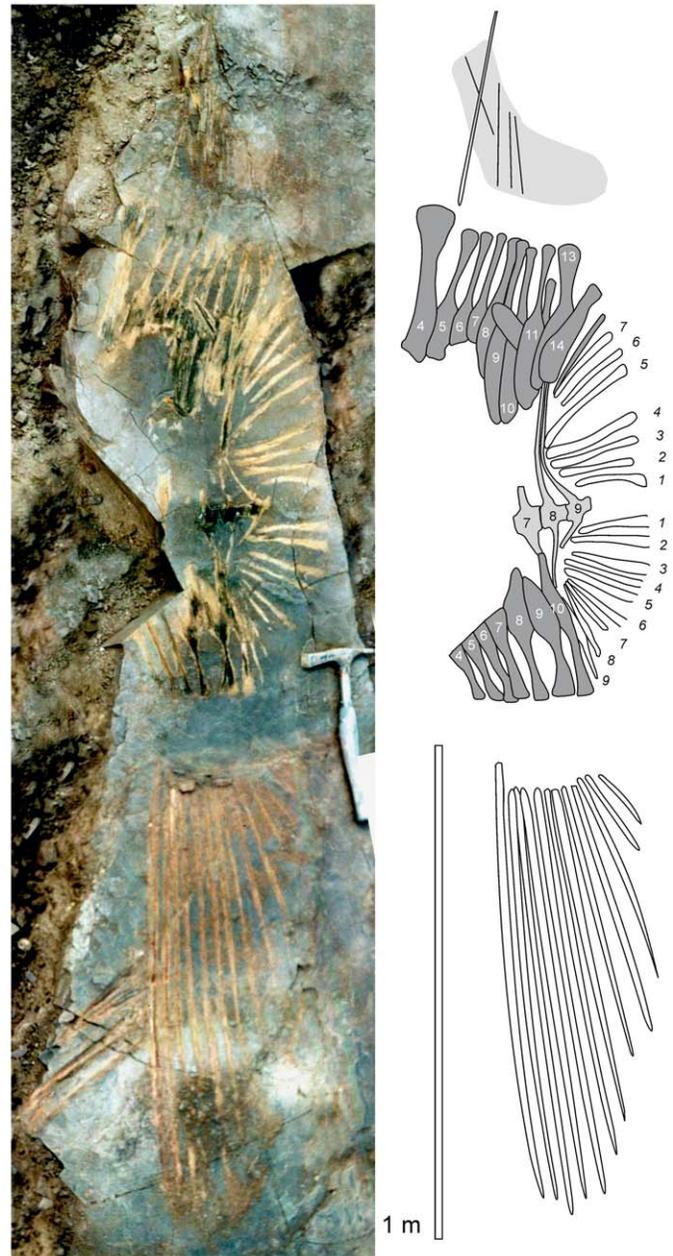


FIGURE 8. Photo and skeleton reconstruction of specimen 3. This specimen was completely destroyed during construction work. Nevertheless, it shows several details of the caudal part which is less well preserved in the other available specimens.

Fin Rays—Twelve fin rays are present in the rounded pectoral fins. The first 3 rays and the last ray are unbranched, whereas the others were probably extensively distally branched as in recent *Mola*. The medial and lateral halves of each fin ray are not closely apposed to one another except distally, where they are separated in the two halves for most of their lengths. The length of the first ray corresponds to about half of the second ray, the second ray represents two thirds of the third ray; the longest ray is 2.6 x longer than the first ray.

Vertebral Column—In specimen 2, only the last five centra of abdominal vertebrae are preserved, the last one has a neural arch inserted between the 4th and 5th basal pterygiophore of

TABLE 1. Morphometric characters of *Mola mola* (NHMW 95.125) and *Austromola angerhoferi* (paratype) for estimation of the TL, SL and distance between the distal ends of the dorsal and anal fins.

Species	TL	SL	BD	longest D	longest A	distance DA
<i>Mola mola</i>	151	127	60	66.5	63	196.5
<i>Austromola angerhoferi</i>	320*	269*	127	139.7	133.3	400*

*Estimations.

TABLE 2. Selected metric characters in species of the family Molidae based on Fahay (2007) and in *Austromola angerhoferi*

Species	V	DFR	AFR	PFR
<i>Masturus lanceolatus</i>	8+8	17–20	16–19	7–10
<i>Mola mola</i>	8+9	15–20	14–18	11–13
<i>Ranzania laevis</i>	8+10	18–19	18–19	13–14
<i>Austromola angerhoferi</i>	?+10	18	17	12

Abbreviations: V, vertebrae; DFR, dorsal fin rays; AFR, anal fin rays; PFR, pectoral fin rays; paratype.

the dorsal fin. The complete series of 10 caudal vertebrae is preserved. With the exception of the last two vertebrae, all of the caudal vertebrae have well-developed neural and haemal spines. The distal three-fourths of the haemal spines of the first and second caudal vertebrae articulate with one another, and the thick shaft is overlain laterally and anteriorly by the posterior surface of the enlarged basal pterygiophore of the first anal fin. The neural and haemal spines decrease slightly in stoutness, but not in length, posteriorly in the series. The neural spines of the 1st to the 7th caudal vertebrae support the more posterior basal pterygiophores of the dorsal fin. The posterior edge of the haemal spine of the 2nd caudal vertebra articulates with the anterior edge of the 2nd anal fin basal pterygiophore. The haemal spines of the 3rd to the 7th caudal vertebrae support the other anal fin basal pterygiophores. Between the 5th and 6th haemal spines lie the 7th and the 8th basal pterygiophores of the anal fin. The posterior-most pterygiophores of the dorsal and anal fins are inserted almost vertically to the body axis. Last vertebra (10th), penultimate (9th) and antepenultimate (8th) vertebrae are not in their natural position but are posteriorly displaced. The neural spine of the 8th vertebra is not completely preserved, but we suppose that it has the same length as the preceding spine. The 9th vertebra has only one spine preserved, but it remains uncertain whether it is a neural or a haemal spine because a disarticulation in this area of specimen 2 is certainly possible. In specimen 3 (Fig. 8) the neural and the haemal spines of the penultimate (9th) caudal vertebra curve interiorly and their distal ends articulate with the posterior edges of the neural spine and of the haemal spine of the antepenultimate (8th) caudal vertebra. All vertebrae have biconcave centra, except for the last (10th), which ends posteriorly with a relatively flat surface. In *Austromola* the penultimate (9th) vertebra is shorter than the preceding one (8th). In *Mola mola* the last (9th) vertebra is longest, the penultimate (8th) vertebra is shorter, of similar or slightly larger size as the antepenultimate (7th) vertebra.

Dorsal Fin—The dorsal fin is situated a short distance behind the middle of the body above the 1st and 2nd caudal vertebrae. It has 18 dorsal-fin rays anterior to the first dorsal-fin ray of the pseudocaudal fin. Fourteen of these rays are well preserved; the last 4 are disarticulated and fragmentary. In specimen 2 the first two rays are completely preserved; they are unbranched. The distal ends of the 3rd to 8th rays are not preserved, but the first 5 rays of specimen 1 are also unbranched (like in the recent *Mola* and *Masturus*). The 9th to 14th rays are extensively

branched as in the above-mentioned recent genera. The last 4 rays are disarticulated. As in the extant Molidae the right and the left halves of each ray are well-separated medially throughout their lengths, except distally where they begin to branch. These distal tips are extensively branched in specimen 1, as is typical for all known molids, where these rays are divided into up to 20 terminal segments (Tyler, 1980). The dorsal fin exhibits 15 basal pterygiophores. The 1st, 2nd, and 3rd dorsal fin basal pterygiophore are incompletely preserved and the basal region of some of the following is missing. The first two dorsal pterygiophores are better preserved in specimen 1, where the whole series is complete. The dorsal fin basal pterygiophores are flattened distally and narrow proximally, yielding a paddle shape.

The large cartilaginous plate that intervenes between the basal pterygiophores and the dorsal fin rays in recent *Mola* is not preserved and even the space for its insertion is missing. In extant Molidae the cartilaginous band is tough, fibrous, broad, strong, and just as strong as the weak bone. Therefore, considering the generally very good preservation, there is little reason to assume a selective preservational loss of this heavy cartilage band. Moreover, it is unlikely that the entire dorsal anal fins are detached and significantly displaced, as their middle and rear parts are only minimally degraded. This in-situ position is also indicated by the very long pterygiophores of the anal portion of the pseudocaudal fin. This is also valid for the dorsal region, where the pterygiophores of the dorsal portion of the pseudocaudal fin are shorter as an adaptation to the narrow space between the pterygiophores of the dorsal fin and the dorsal rays. If the fins are more or less in original position, this implies a very narrow space for a narrow cartilage band between the dorsal rays and their pterygiophores, and an exceptionally deep space (deep cartilage band) between the anal rays and their pterygiophores.

Anal Fin—originates between the 3rd and 4th caudal vertebrae. The bases of the two first rays are twice as large as those of the following rays. As in the recent *Mola*, 17 anal-fin rays are present anterior to the first anal fin ray of the pseudocaudal fin. This is supported by a modified basal pterygiophore posterior to the haemal spine of the 8th caudal vertebra. The first five anal-fin rays are unbranched (5th is perhaps not completely preserved), the 6th to 10th are not preserved in their whole length, and 11th and 15th are extensively branched as in the dorsal fins. The 16th and 17th anal-fin rays are much less branched than those anterior to them. Except for the anterior-most pterygiophore, the nine following anal fin basal pterygiophores are like those of the dorsal fin, but noticeably longer. The 1st anal fin basal pterygiophore partly overlies and articulates with the haemal spines of the first two caudal vertebrae. Distally, the first basal pterygiophore is enlarged; it is unclear if this enlargement represents the bifurcation as is in recent *Mola*. The anal-fin rays have the same structure as those of the dorsal fin and lack the plugs of calcified cartilage. The basal pterygiophores of the anal fin are very strongly developed. This contrasts with *Ranzania*, where these bones are very slender.

Pseudocaudal Fin—The caudal part of the body is somewhat disarticulated in specimen 2. This involves the last three vertebrae, basal pterygiophores and rays, which are important taxonomic characters in extant molids. Therefore, the reconstruction of the region is based partly on the photo of the destroyed specimen 3. In recent molids the fin rays of the pseudocaudal fin are continuous with those of the dorsal and anal fin series and are supported basally by the modified basal pterygiophores of the dorsal and anal fins. Only an arbitrary distinction can be made between the dorsal, pseudocaudal, and anal fins. The pseudocaudal fin, composed of posteromedially migrated dorsal and anal fin rays, is here considered to include all those fin rays supported by the modified basal pterygiophores posterior to the neural and haemal spines of the antepenultimate

vertebra. The relation between basal pterygiophores of the pseudocaudal fin and the last three caudal vertebrae is similar to that in recent *Mola*. Extant *Mola* develops seven modified dorsal fin basal pterygiophores posterior to the neural spine of the antepenultimate and penultimate vertebrae. The uppermost, or 1st, modified basal pterygiophore is at nearly a right angle to the vertebral column, but the 2nd to 7th ones are progressively more oblique, with the 7th being almost parallel to the column. In specimen 2 the position is slightly biased but generally still allows an estimation of the original situation. The exact relation between the missing neural spine and the proximal part of the modified basal pterygiophores is unknown due to the disarticulation of the last three caudal vertebrae. Nevertheless, the photo of destroyed specimen 3 documents an articulation of the neural spine of the penultimate vertebra with the 6th and the 7th basal pterygiophores; it also reveals a connection of the following five with the neural spine of the 8th vertebra. The haemal spine of the 9th vertebra articulates with the 9th to 7th basal pterygiophores, whereas the following five or six basal pterygiophores are articulated with the haemal spine of the 8th caudal vertebra.

The nine basal pterygiophores in the anal fin portion of the pseudocaudal fin have basically the same structure as those of the dorsal fin portion, but are much longer. Also in *Mola* and *Masturus* the basal pterygiophores of the anal part are longer relative to the dorsal part, while in *Ranzania* they are more or less equivalent or even shorter — as a function of the body outline. In *Masturus* and *Mola* the ventral part of the body is much deeper and pterygiophore length is therefore anatomically adapted to it. In *Austromola* the lowermost basal pterygiophores are up to three times longer than those of the dorsal part, whereas in *Mola* and *Masturus* this relation is only 1:2. The number of rays of the pseudocaudal fin is unknown due to disarticulation. Unfortunately, the distal endings of these rays are not preserved, but all rays are slender like in *Mola* or in *Masturus* and do not show multiple branching like in *Ranzania*.

Skin—Polygonal scale plates and skin-structure are still preserved, distinctly defining the former body outline. Scale plates are concentrated at the ventral part of the head, the bases of the dorsal and anal fins, and the base of the pseudocaudal fin, marking the body outline. In *Mola* and *Masturus* these plates rest upon a thick collagenous connective tissue and they have more or less circular scales. In contrast, scale plates in *Ranzania* are thicker and more angular and hexagonal, thus being reminiscent of *Austromola*. The head area bears a few dermal plates, which are interpreted as the displaced nasal and jugulaire plates.

DISCUSSION

The Fossil Record of the Molidae *Ranzani*, 1839

The Molidae have a long fossil record that dates back to the Eocene. Including the newly described *Austromola*, five Molidae genera are currently recorded. Of these, only three are still extant. The most basal representative is *Eomola* Tyler and Bannikov, 1992 with the single known species *Eomola bimaxillaria* Tyler and Bannikov, 1992. This comparatively small Molidae is documented from the Upper Eocene (Bartonian) Kumsky Horizon at the Psekkha River in the North Caucasus. The described material consists of the upper jaw of a single individual.

All other fossil records derive from the Neogene (Miocene and Pliocene) and are based on isolated jaws and dermal plates (Weems, 1985) or on very incomplete skeletons (Uyeno and Sakamoto, 1994; Carnevale and Santini, 2007). These specimens have been referred to the recent genera *Mola* and *Ranzania*. *Mola* Koelreuter, 1770 is represented in modern oceans by the near-cosmopolitan type species *Mola mola* (Linnaeus, 1758) and by *Mola ramsayi* (Giglioli, 1883), which is restricted to the South Indian Ocean and the Pacific (Weems, 1985; Bass et al., 2005). No fossils of the recent species are documented so far. Neverthe-

less, the genus *Mola* is traceable back to the Miocene. The oldest known representative is *Mola pileata* (van Beneden, 1881) from the Middle Miocene of the Rhône Basin (Leriche, 1907) and the Upper Miocene of Belgium and the Netherlands (Sables d'Anvers at Kessel in Belgium; Leriche, 1926; Groenlo and Delden, Netherlands; Deinse, 1953). *Pagurus torus* van Beneden, 1881 and *Orthogoriscus chelonopsis* van Beneden, 1883 have been described from the Miocene of Anvers (together with *Mola pileata*) and are synonyms of *Mola pileata* (Leriche, 1907). Therefore, the beaks from the Lower Pliocene (Zanclian) Yorktown Formation in North Carolina, USA, which have been described as *Mola chelonopsis* by Weems (1985) and as *Mola* cf. *chelonopsis* by Purdy et al. (2001), might either be the youngest records of *Mola pileata* or would require a new species name if they represent a distinct species.

The second extant molid genus with a fossil history is *Ranzania* Nardo, 1840 which is represented in modern oceans by the cosmopolitan species *Ranzania laevis* (Pennant, 1776) (Tortonese, 1986; Heemstra, 1986). Fossil *Ranzania* are documented so far only from the Middle and Late Miocene. The oldest records are *Ranzania grahmi* Weems, 1985 and *Ranzania tenneyorum* Weems, 1985 described from lower middle Miocene Calvert Formation of Virginia, USA. Their descriptions by Weems (1985) are based on the irregularly shaped polygonal scale plates (*Ranzania grahmi*) and the premaxillaries (*Ranzania tenneyorum*). *Ranzania zappai* Carnevale, 2007, from the Serravallian of Italy, is also only known from polygonal plates (Carnevale, 2007). The only known partly articulated skeleton of a fossil molid, aside from *Austromola*, represents *Ranzania ogaii* Uyeno and Sakamoto, 1994 from the Middle Miocene of Honshu in Japan. It displays closely attached, long neural spines of the caudal vertebrae and unique polygonal scale plates with a single prominent tubercle in the centre. A further unnamed *Ranzania* species is described from the Upper Miocene (Messinien) of Algeria (Carnevale and Santini, 2007) based on incomplete dorsal pterygiophores. Bass et al. (2005) mention fossils of *Ranzania* with an age of 35 Ma (Late Eocene), but do not provide any details or references.

Masturus Gill, 1884 is the only extant molid unknown from the fossil record. It is represented by the cosmopolitan species *Masturus lanceolatus* (Lienard, 1840) [synonym *Pseudomola lassarati* Cadenat, 1959] (Tyler, 1980; Tortonese, 1986; Heemstra, 1986).

This sparse fossil record suggests that the Molidae have been a rather poorly diverse group at the generic as well as species level, corresponding to the modern situation. After the rise of the group during the Eocene, a huge gap in the fossil record extends between *Eomola* and *Austromola*, spanning an interval from c. 41 Ma until 22 Ma.

A Phylogenetic Analysis and the Position of *Austromola*

Based on morphological data, *Austromola* is distinguished from the above-described Molidae genera by following characters: *Eomola* differs clearly from all other genera by its upper jaw which bears separate premaxillae and divided trituration plates, whereas all other molids develop completely fused premaxillary and dentary bones. *Mola* has nine vertebrae, bony ossicles at the distal ends of basal pterygiophores of the pseudocaudal fin and circular scale plates. *Ranzania* differs obviously in its elongate body outline and the strongly posteriorly displaced fins. It has ten caudal vertebrae, its 9th caudal vertebra bears a neural and a haemal spine, the basal pterygiophores of the pseudocaudal fin are similar in length, the rays of the pseudocaudal fin are distally broadening, and the pectoral fin is elongated. *Masturus* has only eight caudal vertebrae, large trituration plates, and the 8th caudal vertebra bears only a haemal spine. Despite these clear differences, *Austromola* shows several affinities with the extant genera. It has a body outline and rounded

pectoral fin which are reminiscent of *Mola* and *Masturus*. In contrast, the number of caudal vertebrae is identical to *Ranzania*, whereas the morphology of the caudal vertebrae is similar to that of *Mola*. *Ranzania*-like features are also found in the polygonal scale plates of *Austromola*.

Mola- and *Masturus*-like features of *Austromola* are the orientation of the haemal spines of the caudal vertebrae, the antero-posteriorly expanded and plate-like basal pterygiophores of the dorsal and anal fins, and the general configuration the pseudocaudal fin. Thus, the overall morphological features of *Austromola* suggest a closer affinity with *Mola* and *Masturus* than with *Ranzania*.

To clarify the phylogenetic position of *Austromola* in respect to other Molidae, a data matrix was compiled. The analysis of the combined matrix based on the characters in Tyler (1980) as interpreted by Santini, and Tyler (2002) plus a number of new characters yielded a single most parsimonious tree (Fig. 9) with a length of 71 steps, a retention index (RI) of 0.91, and a consistency index (CI) of 0.93. Node support obtained by bootstrapping was high, all nodes showing values above 80%, the basal node of the family Molidae occurring always. Bremer support is strong as well, except for the node joining *Mola* and *Masturus*, possibly reflecting the high number of unknown characters in *Austromola*. Tree topology is consistent with the results obtained by Santini, and Tyler (2002) and Bass et al. (2005). The placement of *Austromola* as sister the taxon to the clade formed by *Mola* and *Masturus* is not surprising and was expected based on the high osteological similarities and near-identical body shape. Characters shared between *Austromola* and *Ranzania*, in contrast, are few, being mainly related to their less reduced caudal spine (32 + 34) and lack of bony plates in the pseudocaudal fin (44, shared with *Masturus*). These are clearly the plesiomorphic states and thus phylogenetically uninformative.

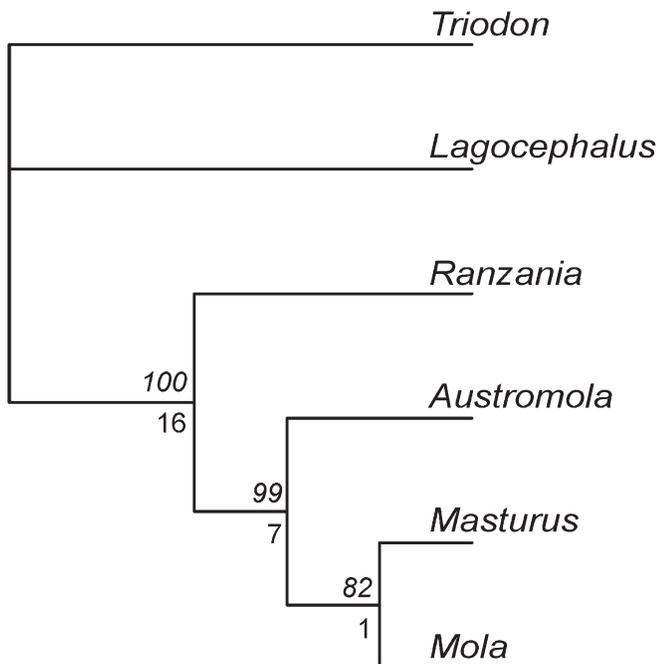


FIGURE 9. Placement of *Austromola* within the Molidae: Most parsimonious tree resulting from the phylogenetic analysis of the data matrix (see appendices 1 and 2). Numbers above branches represent bootstrap support (in italics) for the respective nodes (1000 replicates); numbers below are Bremer support values (normal font).

In the fourth shared character, the polygonal dermal scales (49), judgment between plesiomorphic and autapomorphic condition is less straightforward. It is likely, though, that the polygonal state is the ancestral one, based on the stratigraphic succession of the taxa.

The result of this analysis fits very well with the fossil record of the Molidae and implies only a small stratigraphic gap for the genus *Ranzania*, whose oldest known fossil comes from the early Mid-Miocene. Based on the tree, this genus is expected to appear before *Austromola*, possibly during the Late Oligocene or earlier. This agrees with the divergence estimates provided by Bass et al. (2005) based upon genetic differentiation in d-loop and cytochrome b mitochondrial genes of extant molids.

CONCLUSION

Austromola angerhoferi is the oldest known modern-type sunfish. A giant size of more than 320 cm body length and 400 cm maximum diameter can be calculated based on linear extrapolation of morphometric parameters of recent *Mola mola*. Thus, this early Miocene Molidae was one of the largest sunfish known so far.

Phylogenetic analysis shows that *Austromola* forms a sister-clade of *Ranzania* together with *Mola* and *Masturus*. Therefore, its Aquitanian age suggests an Oligocene age for the origin of *Ranzania* and an at least early Oligocene age for the last common ancestor of the extant Molidae. The radiation of the (*Austromola* (*Mola*+*Masturus*)) clade occurred soon thereafter during the Early Miocene and, consequently, the oldest *Mola* fossils are found in Middle Miocene deposits. The huge gap of c. 20 Ma between the basal molid *Eomola* and the giant *Austromola* and the lack of *Masturus*-fossils in Miocene to Pleistocene deposits emphasise the extremely spotty fossil record of the sunfishes, which usually are documented solely by isolated jaw elements or scale plates. Consequently, the three more or less complete skeletons from the deep water deposits of Upper Austria are an outstanding and unparalleled finding.

ACKNOWLEDGMENTS

We are very grateful that Dr. Bercht Angerhofer granted access to his collection and supported the research process. He collected the most complete of the skeletons together with his family and also saved the specimen from complete destruction during the construction work. Further, we thank Dr. Alexander Lukeneder, Anton Englert, Johann Preis, and Franz Topka (all NHMW) for their time-consuming work in reassembling the specimens from a multitude of fragments. Many thanks go to James C. Tyler and Sandra J. Raredon (National Museum of Natural History, Smithsonian Institution, Washington DC) for their support and help and to James MacLaine (Natural History Museum London) for providing access to extant specimens.

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Submitted July 3, 2008; accepted October 1, 2008.

APPENDIX 1. Description of characters used in phylogenetic analyses. All characters are treated as unordered. [Santini & Tyler #] = character number of Santini, and Tyler (2002).

Cranial characters

- (1) Basisphenoid: a small rod positioned far posteriorly in the interorbital septum and articulated with the anterior edge of the dorsal roof of the myodome (0); absent (1); present as a large plate in the interorbital septum (2). [Santini & Tyler 1]
- (2) Pterotic: only moderately prolonged posteriorly as a stout bone, about as long as wide (0); prominently prolonged posteriorly as a thinner bone, much longer (two times or more) than wide (1). [Santini & Tyler 2]
- (3) Epiotic: without any kind of posterodorsal prolongation (0); with a high dome-like or ribbon-like posterodorsal prolongation (1). [Santini & Tyler 3]
- (4) Exoccipitals: with condyles and in contact with the first vertebra, which articulates anteriorly with both the exoccipitals and the basioccipital, and the latter not prolonged dorsally behind the exoccipitals, the exoccipitals bordering all but the bottom edge of the foramen magnum (0); without condyles and not in contact with the first vertebra, which articulates anteriorly only with the basioccipital, and the latter greatly prolonged dorsally behind the exoccipitals to border the foramen magnum to the exclusion of the exoccipitals (1). [Santini & Tyler 4]
- (5) Basioccipitals: not prolonged dorsally to exclude the exoccipitals from bordering the foramen magnum (0); prolonged dorsally behind the exoccipitals to border the foramen magnum to the exclusion of the exoccipitals (1). [Santini & Tyler 5]
- (6) Supraoccipital crest: long, thin, projecting backward (0); short, stout, projecting upward (1). [Santini & Tyler 6]
- (7) Premaxillae: articulated to one another by interdigitation or by regular interlocking emarginations (0); fused (1). [Santini & Tyler 7]
- (8) Sesamoid articular: present (0); absent (1). [Santini & Tyler 8]

- (9) Teeth in biting edge of beak: retaining much of their individual identity (0); apparently indistinguishably incorporated into the bony matrix of the premaxillae and dentaries (1). [Santini & Tyler 9]
- (10) Trituration teeth in upper jaw: individual teeth small (0); individual teeth large (1). [Santini & Tyler 10]
- (11) Trituration teeth in lower jaw: individual teeth small (0); individual teeth absent (1); individual teeth large (2). [Santini & Tyler 11]
- (12) Mesopterygoid: large element, sometimes elongate, at least one-half the size of the ectopterygoid (0); small, squarish, much less than one-half the size of the ectopterygoid (1). [Santini & Tyler 12]
- (13) Mesopterygoid: not in contact with the metapterygoid (0); in contact with the metapterygoid (1). [Santini & Tyler 13]
- (14) Symplectic: long, extending posteriorly most of the length of the metapterygoid (0); small, extending posteriorly only about one-half the length of the metapterygoid (1). [Santini & Tyler 14]
- (15) Opercle and subopercle: of much greater complexity in structure and large lateral surface area (0); of greatly simplified structure and reduced lateral surface area (1). [Santini & Tyler 15]
- (16) Interopercle: with a ventral flange and posterior shaft-like portion extending at least a short distance posteriorly beyond the level of the epiphyal (0); absent as an ossification or present as a simple slender rod of bone without a ventral flange, and not extending posteriorly beyond the level of the epiphyal (1). [Santini & Tyler 16]
- (17) Gills: not greatly expanded dorsally (0); greatly expanded dorsally above and beyond the supporting arches (1). [Santini & Tyler 17]
- (18) Gills rakers along the anterior edge of the first gill slit: absent (0); present (1). [Santini & Tyler 18]
- (19) Ceratobranchials: not very deep-bodied (0); very deep-bodied (1). [Santini & Tyler 19]
- (20) Pharyngobranchials: with moderate to minute teeth (0); with extremely large teeth (1). [Santini & Tyler 20]

Pectoral fins

- (21) Cleithrum: greatly elongate anteriorly, strongly oblique to body axis at most posterior part and almost parallel at anterior end, reaching forward to at least the level of the middle of the ceratohyal (0); not elongate anteriorly, always strongly oblique to body axis, and reaching forward no further than beginning of the ceratohyal (1). [Santini & Tyler 21]
- (22) Postcleithrum: two pieces (0); one piece (1). [Santini & Tyler 22]
- (23) Postcleithrum: without an anteriorly directed process (0); with an anteriorly directed process toward or over the actinosts (1). [Santini & Tyler 23]
- (24) Postcleithrum: not expanded posteriorly (0); greatly expanded posteriorly as a flattened plate (1). [Santini & Tyler 24]
- (25) Supracleithrum: not very elongate, only its extreme proximate end articulated directly with the pterotic (0); extremely elongate, broadly articulated over the anterior one-third to one-half of its length with the pterotic (1). [Santini & Tyler 25]
- (26) Coracoid: short and wide, with a posterodorsal prong below the lower actinost always developed to some degree (0); long and slender, without a posterodorsal prong below the lower actinost (1). [Santini & Tyler 26]
- (27) Scapular foramen: complete, entirely enclosed by the scapula (0); incomplete, closed anteriorly by the cleithrum (1); a connective tissue sheet (2). [Santini & Tyler 27]
- (28) Actinosts: four (0); three (1). [Santini & Tyler 28]
- (29) Actinosts: not sutured to one another (0); sutured (1). [Santini & Tyler 29].

Vertebral column

- (30) Abdominal vertebrae: some centra with ventral or ventrolateral processes of some sort, whether or not forming complete haemal arches or zygapophyses (0); no ventral or ventrolateral processes, the ventral surface of the centra relatively smooth (1). [Santini & Tyler 30]
- (31) Caudal vertebrae: neural spines oriented from highly oblique (30% or less) to almost parallel to the body axis (0); neural spines oriented from almost perpendicular to slightly oblique (60% or more) to the body axis (1). [Santini & Tyler 31]
- (32) Number of caudal vertebrae: 8 (0); 9 (1); 10 (2); 11 (3).
- (33) 8th caudal vertebrae: neural & haemal spine present (0); only a haemal spine present (1); not present or very small (2).
- (34) 8th caudal vertebrae: haemal spine: flexed posteriorly (0); vertical (1); flexed anteriorly (2).

Median fins

- (35) First basal pterygiophore of dorsal fin: not in contact or only slightly in contact with the second pterygiophore (0); broadly in contact along one-half or more of its length with the second pterygiophore (1). [Santini & Tyler 32]
- (36) Most of basal pterygiophores of dorsal and anal fins: long slender rods (0); expanded and plate-like (1). [Santini & Tyler 33]
- (37) Dorsal-fin rays: not widely separated from their basal pterygial supports by a large block of cartilage (0); widely separated from their basal pterygial supports by a large block of cartilage (1). [modified from Santini & Tyler 34]
- (38) Anal-fin rays: not widely separated from their basal pterygial supports by a large block of cartilage (0); widely separated from their basal pterygial supports by a large block of cartilage (1). [modified from Santini & Tyler 34]
- (39) Dorsal-, anal-, and pectoral-fin rays: most fin rays less extensively branched but with a normal amount of cross-striations, these not confined to only the distal end of the rays (0); often extensively branched but with extremely few cross-striations, those present only at the extreme distal end of the rays (1). [modified from Santini & Tyler 35]
- (40) Pseudocaudal fin: rays branched: no (0); yes, up to three times (1); yes, multiple (more than 5 times) (2).
- (41) First basal pterygiophore of the anal fin, posterior surface of the proximal end of: not concave and does not enclose the distal end of the haemal spines of the first two caudal vertebrae (0); concave and does enclose the distal end of the haemal spines of the first two caudal vertebrae (1). [Santini & Tyler 36]
- (42) Posteriormost pterygiophores of dorsal and anal fins: inserted highly oblique to body axis (45° or less) (0); inserted almost vertical to body axis (60° or more) (1). [Santini & Tyler 37]
- (43) Caudal fin: relatively normal, with 9 to 12 rays supported by variously consolidated and fused but normal vertebral elements (0); aborted, either absent altogether or represented by only a few rays in the central region of the pseudocaudal fin formed by posteriorly migrated soft dorsal- and anal-fin rays and supported mostly by equally posteriorly migrated basal pterygiophores from the soft dorsal and anal fins (1). [Santini & Tyler 38]
- (44) Pseudocaudal fin: most rays terminating in bony plates: no (0); yes (1).
- (45) Pseudocaudal fin: basal pterygiophores of the anal part distinctly elongated in comparison to the dorsal part: no (0); yes (1).
- (46) Pectoral fin, outline: rounded (0); elongated to wedge-shaped, approximately twice as long as wide (1).

Miscellaneous

- (47) Body depth: at least two times longer than deep (0); one to one and a half times longer than deep (1). [Santini & Tyler 39]
- (48) Scales: small, elongate, with small spinules but no prickles or spines (0); large, the basal plates not forming a completely continuous covering over the entire body (no carapace), forming erectile prickles or spines (1); small, but the basal plates in more or less close contact and forming a relatively continuous covering over the entire body (collagenous or bony carapace), with none of the scales in the form of prominent prickles or spines (2). [Santini & Tyler 40]
- (49) Scale plates, shape: circular (0); polygonal (1).
- (50) Thick layer of collagenous tissue present under scales, if carapace present: absent (0); present (1). [Santini & Tyler 41]
- (51) Lateral line: present (0); either absent or extremely inconspicuous (1). [Santini & Tyler 42]
- (52) Air bladder: present and well developed (0); absent, at least in adults (1). [Santini & Tyler 43]
- (53) Bony canal for the nerves and blood vessels running from the orbit to the nasal region: incomplete, surrounded by the lateral ethmoid laterally, above, and below, but not medially (0); complete, entirely surrounded by the lateral ethmoid (1). [Santini & Tyler 44]
- (54) Nostrils: two moderate to large nostrils on each side in an upraised surface, or with flaps (0); two minute nostrils on each side, flush with surface [Santini & Tyler 45]
- (55) Gill rakers: not concealed in folds of skin (0); concealed in thick folds of skin (1). [Santini & Tyler 46]
- (56) Larvae: have no secondary post-metamorphosis (0); secondary post-metamorphosis present, with prominent spiny processes from the body (1). [Santini & Tyler 47]
- (57) Ossification: degree of ossification normal, bone relatively dense (0); bone weakly ossified, more spongy (1). [Santini & Tyler 48]

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis.

Character	1	111111112	222222223	333333334	444444445	5555555
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
<i>Triodon</i>	000000000	000000000	000000000	032000001	0000-100-0	0000000
<i>Lagocephalus</i>	100000000	101100000	0001001010	0300000001	0000-101-0	0000000
<i>Ranzania</i>	2111101111	2010111101	111112111	0200001112	0010010210	1111000
<i>Mola</i>	2111111111	2101111111	1110112101	1102111111	1111101201	1111111
<i>Masturus</i>	2111111111	2101111111	1110112101	1011111111	1110101201	1111111
<i>Austromola</i>	?????1?1?	?????1???	?????1?101	1200?10110	1110101211	?????1