

Original Article

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Corresponding author:

Jonathan J.W. Wallaard,
Email: jj.w.wallaard@uu.nl

Ranzania tenneyorum (Weems, 1985) and *Mola pileata* (Van Beneden, 1881) (Molidae, Tetraodontiformes): highly specialised fishes from the Breda and Oosterhout formations at Mill-Langenboom, the Netherlands

Femke A. van der Sterren¹ and Jonathan J.W. Wallaard^{2,3}

¹Faculty of Science, Institute of Biology, Leiden University, Leiden, the Netherlands; ²Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands; ³Het Nationaal Oertijdmuseum, Boxtel, the Netherlands

Abstract

Research into faunal assemblages from the Upper Miocene and Lower Pliocene at Mill-Langenboom, province of Noord-Brabant, the Netherlands, has led to the recognition of premaxillary and dentary beaks of molid fishes (Molidae, Tetraodontiformes). These ex-situ finds, originating either from the Breda Formation or Oosterhout Formation, or both, are here assigned to two extinct taxa, namely, *Ranzania tenneyorum* and *Mola pileata*. *Mola pileata* has previously been recorded from the Middle Miocene of Belgium, the Netherlands, and the United States of America, while *R. tenneyorum* was up to now known only from the Lower-Middle Miocene Calvert Formation in Virginia (US). The present record thus extends the known geographical and stratigraphical ranges of *R. tenneyorum* to north-west Europe and the Middle-Miocene – Lower Pliocene.

Introduction and geological framework

At ‘De Kuilen’ (coordinates: 51° 41’ 59” N; 5° 44’ 59” E) is a man-made lake between the villages of Mill and Langenboom (Figure 1), in the province of Noord-Brabant (south-east Netherlands). Sand was excavated and suction dredged from mid-1990s until 2010. This marine sand was laid down in the southern North Sea Basin during the Miocene and Lower Pliocene, with the oldest interval at a depth of 18–16 metres below the water line dated as c. 11–8.7 Ma, and assigned to the Upper Miocene Breda Formation. High intervals of 15–12 metres [5.33–3.6 Ma] and of 12–17 metres [3.6–2.58 Ma] below the water line are referred to the Pliocene Oosterhout Formation. The level between 15 and 12 metres is characterised by the presence of common molluscan shells; these are not found in higher levels (18–16 m) as a result of poor carbonate preservation (Klomp maker & Wijnker, 2010). At ‘De Kuilen’ fossil assemblages were collected both *in situ* by scuba diving as well as *ex situ* on sand dumps at the site (Wijnker et al., 2008). Overlying the marine strata, between 7 and 6 metres below the water line are fluvial Quaternary deposits of the Breegden Formation (Wijnker et al., 2008; Zagwijn & Hager, 1987).

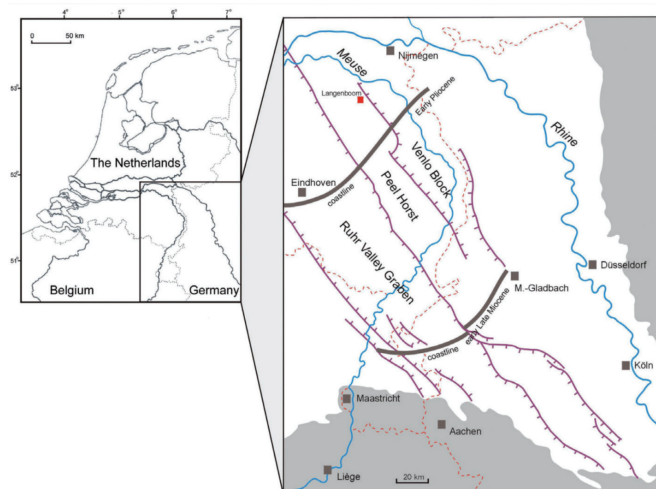


Figure 1. The former ‘De Kuilen’ sand pit at Mill-Langenboom location, and corresponding regional tectonic structures and reconstructed coastlines (from Wijnker et al., 2008, p. 166, Figure 1).

During the Upper Miocene and Lower Pliocene, the North Sea Basin was connected with the Norwegian and Greenland waters (Louwye & Laga, 2008). In the south, the maximum depth of this basin ranged between 130 and 400 metres (Cameron et al., 1993; Huuse, 2002; Kuhlmann et al., 2006). The present-day Mill-Langenboom was situated within this open-marine, near-coastal setting, with clear waters beneath the fair-weather wave base, and the paleoenvironment featured seagrass meadows (Louwye & De Schepper, 2010; Wesselingh et al., 2013; Wijnker et al., 2008).

The teleost fish remains studied herein, all collected *ex situ*, belong to oceanic sunfishes, or the tetraodontiform family Molidae. Representatives of this family inhabit the pelagic zones of both temperate and tropical waters (Carnevale et al., 2021; Carnevale & Santini, 2007; Collareta et al., 2021) and are characterised by a distinctive clavus instead of a normal caudal fin and by the development of a 'beak' by the merger of the contralateral premaxillae and dentaries along the sagittal plane (Santini & Tyler, 2002, 2003). Molids comprise the extant genera *Ranzania*, *Masturus* and *Mola*, as well as the extinct genera *Eomola* and *Austromola* (Bass et al., 2005; Carnevale et al., 2021; Gregorova et al., 2009; Tyler & Bannikov, 1992). Modern members of the family, such as *Mola mola*, occur in both hemispheres and display seasonal migration linked to ocean currents and prey abundance (Nakamura et al., 2015; Sims et al., 2009). They are generalist predators that utilise solar heat for warmth at the ocean surface prior to diving into deeper waters for hunting (Dewar et al., 2010; Nakamura et al., 2015; Sims et al., 2009).

A fossil representative of the genus *Mola* may be identified on the basis of its markedly reduced premaxillary and dentary beaks, either with only a few teeth or none at all. Additionally, its palatal tooth brace presumably consisted of cartilage, as seen in extant species. Consequently, this is missing in the beaks of extinct forms (Weems, 1985).

The extinct species, *Mola pileata*, lacks both teeth and a palatal tooth brace in its premaxillary beak. Additionally, the length of the latter exceeded the width (Gregorova et al., 2009; Nyegaard et al., 2018; Weems, 1985). To date, *Mola pileata* has been recorded from the Middle Miocene of the Netherlands (Van Deinse, 1953; Van den Bosch et al., 1975), and coeval levels in north-west Belgium (Antwerp Sands; Van Beneden, 1881), and Virginia (Calvert Formation; Carnevale et al., 2021; Weems, 1985). Material on record from the Antwerp Sands includes a pointed premaxillary beak (IRSNB P1129, Institut Royal des Sciences Naturelles de Belgique), a dentary beak (IRSNB P1128), a nasal plate, a jugular plate (IRSNB P1137), two medial paraxial ossicles (IRSNB P2960 and IRSNB P2960), as well as a dorsal/ventral paraxial ossicle (IRSNB P2961). Of note is that the premaxillary beak ends in a notably triangular shape on its ventral side, whereas the dorsal side of the dentary beak has a much more rounded edge (Carnevale et al., 2021, p. 6, Figure 3; Van Beneden, 1881). The specimen of *M. pileata* (USNM 265650, Smithsonian's National Museum of Natural History) finding from the Calvert formation also comprises a markedly triangular-shaped premaxillary beak (Weems, 1985, p. 432, Figure 6).

Until now, the other species, *Ranzania tenneyorum*, was known exclusively from the basal phosphatic horizon of the Calvert Formation at Gravett's Mill Pond (King William County, Virginia), in the form of premaxillary beaks with three pairs of tooth rows and distinct teeth (Weems, 1985).

The latter author noted that one of the specimens from the Upper Middle Miocene Antwerp Sands identified as *Mola chelonopsis* (= *M. pileata*) by Leriche (1926) in actual fact represented a specimen of *R. tenneyorum* (see also Carnevale et al., 2021).

Material and methods

Three specimens (MAB17193, MAB17194 and MAB17195; Figure 2, Table 1) from 'De Kuilen', Mill-Langenboom, province of Noord-Brabant, the Netherlands, are available for study. Measurements of the beak refer to beak width and length, plus total length, width and height, as preserved (Figure 3), thus following the methodology outlined by Weems (1985, p. 425, Figure 1) and Gouiric-Cavalli et al. (2021, p. 587, Figure 1).

In order to differentiate between dentary and premaxillary beaks, the curvature of the jaw and of any articulation surfaces on the jaw exterior were assessed. In lateral aspect, the ventral side of a dentary beak may appear more convex than that of a premaxillary beak, since the lower jaw (dentary) is separate from the skull, while the upper (premaxillary) is connected to the maxillaries, the ectopterygoids and the palatines (Tyler, 1980). In view of the fact that, in life, the dentary is exposed, there may also be an articulation surface visible to which tissue was attached. Additionally, the Mill-Langenboom material was compared in detail with previously published molid jaws.

After deciding if a certain specimen represented a dentary or premaxillary beak, the species involved was identified by using the key in Weems (1985) and with reference to more recently described taxa. The key involves several characteristics, including fused premaxillaries, well-visible fused edge, tooth morphology and the presence and number of tooth rows (see Figure 4) (compare Carnevale & Godfrey, 2018; Carnevale et al., 2021; Gregorova et al., 2009; Tyler, 1980; Weems, 1985).

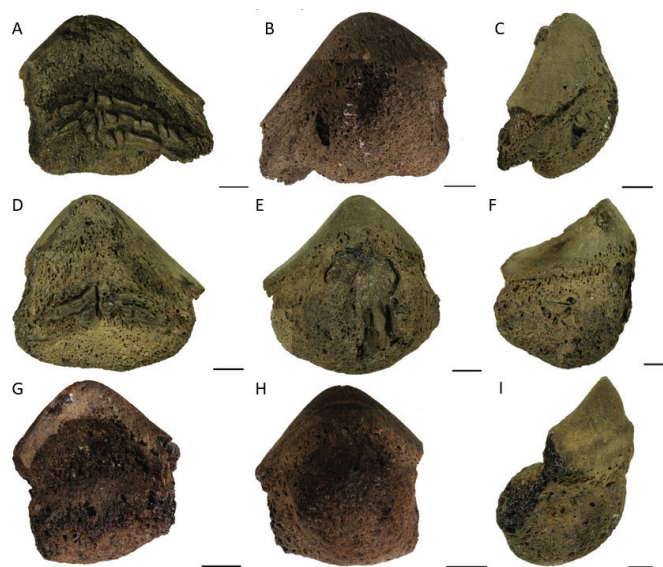
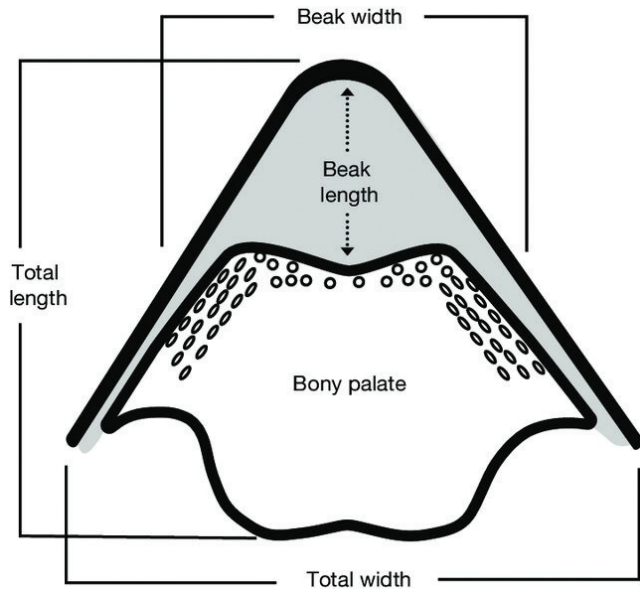


Figure 2. (A–C), *Ranzania tenneyorum*, premaxilla (MAB17193) in ventral, dorsal and lateral views, respectively. (D–F), *Ranzania tenneyorum*, premaxilla (MAB17194) in ventral, dorsal and lateral views, respectively. (G–I), *Mola pileata*, dentary (MAB17195) in dorsal, ventral and lateral views, respectively. Scale bars equal 5 mm.

Table 1. Measurements of mold fossils from Mill-Langenboom

Registration number	MAB17193	MAB17194	MAB17195
Species	<i>R. tenneyorum</i>	<i>R. tenneyorum</i>	<i>M. pileata</i>
Beak type	Premaxillary	Premaxillary	Dentary
Total width (mm)	27	28	20
Total length (mm)	26	27	21
Beak width (mm)	20	27	17
Beak Length (mm)	12	13	11
Total height (mm)	16	17	12.5

**Figure 3.** Measurements beaks of mold teleost fish. (after Gouiric-Cavalli et al., 2021, p. 587, Figure 1; originally based on Weems, 1985, p. 425, Figure 1).

Results

Order Tetraodontiformes (Berg, 1940)
 Family Molidae (Bonaparte, 1835)
 Genus *Mola* (Koelreuter, 1766)
 Species *Mola pileata* (Van Beneden, 1881)
 Figure 2G–I, Table 1

1881 *Orthogoriscus chelonopsis* – Van Beneden, pp. 116–126
 1907 *Orthogoriscus pileatus* – Leriche, pp. 367–472
 1985 *Mola chelonopsis* – Weems, pp. 431–433, Figures 6 and 7
 2021 *Mola pileata* – Carnevale et al., p. 6, Figure 3 (Shows specimens from Van Beneden, 1881)

Material: A single dentary, MAB17195.

Locality and stratigraphy: ‘De Kuilen’, Mill-Langenboom, province of Noord-Brabant, the Netherlands; Upper Miocene-Lower Pliocene (either Breda Formation or Oosterhout Formation).

Description (based solely on dentary): beak small, fused dentaries, entirely edentulate, with convex ventral side with a ridge located right below biting edge. Total width and length, as preserved, are 20 and 21 mm, respectively.

Remarks: This is a fused dentary with a clearly distinguishable biting edge, which places it near members of the genera

Masturus, *Mola* and *Ranzania*. It is here assigned to *M. pileata* purely on the basis of dentary features such as the lack of teeth. It should be noted that the identification key for mold beaks does not take into account the extensive ontogenetic changes in morphology that mold beaks and trituration teeth undergo (compare Carnevale et al., 2021; Collareta et al., 2025; Tyler, 1980; Tyler & Bannikov, 1992; Weems, 1985). In summary, the specific identification of MAB17195 is provisional.

Geographical and stratigraphical distribution: Middle Miocene, Upper Miocene and/or Lower Pliocene of the Netherlands (Van Deirse, 1953; Van den Bosch et al., 1975), Middle Miocene of north-west Belgium (Van Beneden, 1881) and Virginia, the United States of America (Weems, 1985).

Genus *Ranzania* (Nardo, 1840)
 Species *Ranzania tenneyorum* (Weems, 1985)
 Figure 2A–E, Table 1

1985 *Ranzania tenneyorum* – Weems, pp. 431 and 433, Figure 7

Material: Two premaxillaries MAB17193 and MAB17194.

Locality and stratigraphy: ‘De Kuilen’, Mill-Langenboom, Noord-Brabant, the Netherlands; Upper Miocene-Lower Pliocene (either Breda Formation or Oosterhout Formation).

Description (solely based on premaxillaries): fused premaxillaries with a clearly distinguishable biting edge and three pairs of well-defined tooth rows placed on the bony shelf of the palate. MAB17193 has a total width, as preserved, of 27 mm and a total length of 26 mm. In ventral aspect, the left side of the premaxillaries is missing, as are some teeth from the left side of the top and bottom tooth rows.

MAB17194 measures 28 mm in total width and 27 mm in total length and lacks a portion of the left side of the ventral view of the premaxillaries. On the left side it lacks teeth from the top and the bottom tooth rows, while on the right side teeth are lacking mainly in the top and median tooth rows.

Remarks: Fused premaxillaries with a distinguishable biting edge hint at placement in *Masturus*, *Mola* or *Ranzania*. On account of the presence of three paired rows of distinctive teeth, the material is here assigned to the genus *Ranzania*, and to *R. tenneyorum* in particular.

Geographical and stratigraphical distribution: Upper Miocene and/or Lower Pliocene of the Netherlands and Middle Miocene of Virginia, US (Weems, 1985).

Discussion

The present record of *Ranzania tenneyorum* from Mill-Langenboom significantly expands the known geographical distribution of this species. In view of the fact that the material was collected *ex situ*, its precise age cannot be established without doubt. The specimens studied originated either from the Breda Formation or the Oosterhout Formation, indicating a range between Upper Miocene and Lower Pliocene (Wijnker et al., 2008). Any potential future *in situ* finds from these units might pinpoint the level of provenance and yield data on the macrofaunal assemblage (and palaeoclimate proxies based on this) at present-day Mill-Langenboom. Despite these uncertainties, the stratigraphical range of *Ranzania tenneyorum* and *Mola pileata* may be expanded from the Middle

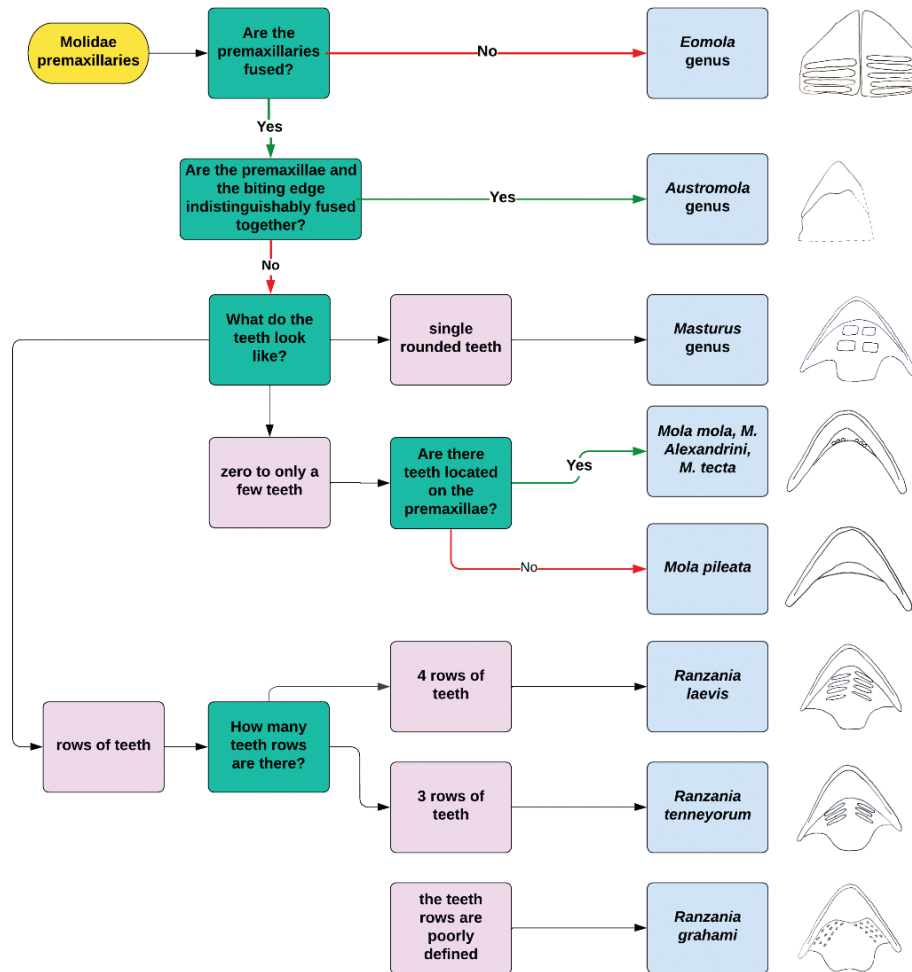


Figure 4. Identification key for premaxillary beaks of extant and extinct molid genera and species, based on data supplied by Tyler (1980), Weems (1985), Gregorova et al. (2009) and Carnevale & Godfrey (2018). The sketch of *Austromola* is based on Gregorova et al. (2009, p. 365, Figure 7), that of *Eomola* on Carnevale et al. (2021, p. 4, Figure 2) and those of *Masturus*, *Mola* and *Ranzania* on Weems (1985, p. 427, Figure 2).

Miocene to the Upper Miocene-Lower Pliocene, making the present specimens the youngest examples of these two species to date.

Around the globe, records of extinct molids are predominantly based on premaxillae, with dentaries representing a smaller proportion of finds. As a result of their general rarity and lack of (near-)complete skeletons, material for comparison (also with extant species such as *Mola mola*, *Ranzania laevis* and *Masturus lanceolatus*) and delineation of fossil species is altogether scanty. Making matters worse is the fact that certain extinct species the premaxillary is lacking, such as in Middle Miocene forms from Italy and Japan, while the sole bone available for others is exactly that premaxillary (e.g. *R. tenneyorum*) (see Carnevale, 2005; Uyeno & Sakamoto, 1994; Weems, 1985). One of the issues that only the finding of additional material can resolve is the question of whether or not *R. zappai* and *R. ogaii* constitute distinct species or rather are conspecific with *R. tenneyorum*.

Conclusion

The present material from Mill-Langenboom allows the geographical and/or stratigraphical ranges of the molids *Ranzania tenneyorum* and *Mola pileata* to be expanded to north-west Europe and into the Upper Miocene-Lower Pliocene.

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Competing interests

Competing interests: The authors declare none.

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