

Geo(im)pulse

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The first report of *Chelonioides* cf. *Ctenochelys* from the Late Cretaceous of the Maastrichtian type area

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Abstract

A mandible of a Late Cretaceous sea turtle with affinities to *Ctenochelys* is reported from the Maastrichtian type area of the Netherlands. The triangular mandible has a well-developed symphyseal ridge surrounded on both sides by large, concave areas on the triturating surface. It represents the first potential occurrence of *Ctenochelys* from the Maastrichtian type area. This finding increases the diversity of the turtle fauna known from the Maastrichtian type area.

Introduction

The late Maastrichtian type area (Jagt & Jagt-Yazykova, 2012; Vellekoop et al., 2022) (Late Cretaceous) is known for a high abundance of marine vertebrate fossils, especially mosasaurs, plesiosaurs, fishes and turtles (Mulder, 2003; Friedman, 2012; Schulp & Jagt, 2015; Miedema et al., 2019). This area represents a shallow (20–40 m), subtropical [19,7°C, as calculated by van Baal et al. (2013)] marine ecosystem, right before the K/Pg extinction event (Mulder, 2003; Vellekoop et al., 2022).

Currently, the turtle record from the Maastrichtian type area comprises the giant cheloniid sea turtle *Allopleuron hofmanni*, represented by several complete fossils (Mulder, 2003), and the much rarer *Glyptochelone suyckerbuyki*, represented only by carapacial material (Kruytzer, 1955). *Allopleuron hofmanni* was interpreted as a carnivore, based on $\delta^{13}\text{C}$ values comparable to that of extant carnivorous chelonioids (van Baal et al., 2013). It was a pelagic turtle, primarily represented by adult fossils with carapacial sizes between 1 and 2 m (Kruytzer, 1955; Janssen et al., 2011). Little is known about the ecology of *Glyptochelone*. Finally, *Platychelone emarginata* represents a single, large, undescribed carapace found in the Maastrichtian type area. It is considered a *nomen nudum* (Mulder, 2003, p. 160). This specimen was recently suggested to be a basal species of Dermochelyidae, but extensive formal description is still lacking (Hirayama et al., 2017). Several undescribed, fragmentary specimens from the Maastrichtian type area are tentatively assigned to *P. emarginata* (Nolis et al., 2018).

Here we describe an isolated dentary (MAB13689) from the ENCI-Heidelberg quarry of the type Maastrichtian area. The ENCI quarry is situated near Maastricht in the Netherlands (see Fig. 1). Strata exposed span the entire upper Maastrichtian and isolated fragments of the lower Maastrichtian (Jagt & Jagt-Yazykova, 2012; Vellekoop et al., 2022). The fossil is identified as cf. *Ctenochelys*, providing the first potential documentation of *Ctenochelys* from the Maastrichtian type area.

Ctenochelys (Zangerl, 1953), initially placed in Toxochelyidae, is now included in the family Ctenochelyidae, alongside *Asmodochelys*, *Prionochelys* and *Peritresius* (Gentry et al., 2019; Joyce et al., 2021). Placement of *Ctenochelys* with respect to crown-chelonioids remains contentious; several studies include this genus as a pan-cheloniid (e.g. Gentry, 2017; Evers et al., 2019), whereas other analyses recover it as a stem-chelonioid instead (e.g. Scavezzoni & Fischer, 2018; Gentry et al., 2019). Hirayama (1997) synonymised all species of *Ctenochelys* based on postcranial material. The new material reported here, however, that there might be more variation in the otherwise poorly documented mandible of the genus.

The genus *Ctenochelys* is known from the late Cretaceous (Campanian-Maastrichtian) of the USA (Zangerl, 1953; Nicholls & Russell, 1990; Matzke, 2007) and Germany (Karl & Nyhuis, 2012), and potentially from the Paleocene of Denmark (Myrvold et al., 2018). Two species are currently recognised within this genus (Hirayama, 1997): *C. acris* (Zangerl, 1953) and the holotype of the genus *C. stenoporus* (Hay, 1905). While *C. acris* occurs exclusively around the Western Interior seaway (Matzke, 2007), specimens of *C. stenoporus* including a lower jaw have been found in Germany (Karl & Nyhuis, 2012) and an isolated hyoplastron with a resemblance to *C. stenoporus* has been reported from the Paleocene of Denmark (Myrvold et al., 2018).



Fig. 1. The ENCI quarry south of Maastricht (the Netherlands) where MAB13689 was found. Adapted from Mulder *et al.* (1998).

The present specimen shares most resemblance with the dentary of *C. stenoporus* as described in Karl & Nyhuis (2012).

Institutional abbreviations

MAB: Oertijdmuseum, Boxtel, the Netherlands.

Systematic palaeontology

Order **Testudines** (Batsch, 1788)

Suborder **Cryptodira** (Cope, 1868)

Superfamily **Pan-Cheloniodea** (Joyce *et al.*, 2004)

Family **Ctenochelyidae** (Karl & Nyhuis, 2012)

Genus ***Ctenochelys*** (Zangerl, 1953)

Type species

Ctenochelys stenoporus (Hay, 1905)

cf. *Ctenochelys*

Material

An incomplete and fractured dentary (MAB13689) showing evidence of abrasion. An oblique anteroposterior fracture has displaced the right ramus over the triturating surface. The specimen was collected and prepared by Arno Savelkoul, who also donated it to the MAB collection.

Locality and stratigraphy

MAB13689 was found in the Emael member (Maastricht Formation) of the ENCI quarry (Fig. 1).

Description

In our description, we follow the updated anatomical nomenclature as defined by Evers *et al.* (2022). The ventral side of the dentary remains mostly embedded in the sediment, so that only the dorsal,

medial and part of the lateral sides are clearly exposed. This was done due to the fragility of the material. Anteriorly, there is material missing and part of the right ramus was fractured during collection (Fig. 2). Traces of abrasion are microscopically visible at several locations.

The two largely complete dentaries are tightly fused at the symphysis. The width of the intact half of the dentary is 19.7 mm (measured between the apex of the symphyseal ridge and posterolateral extremity), and it has a length of 34.5 mm (measured between the most anterior and posterior parts). No remnant of the foramen dentofaciale majus is visible on either the lateral or mediolateral surface of the dentary, suggesting that it is completely reduced, as in *Dermochelys* (Evers *et al.*, 2022). The dentaries bear a sharp symphyseal ridge, which ends posteriorly in a triangular elevation. Most of the symphyseal ridge has been heavily abraded, suggesting it was much higher than was preserved in the present specimen. The triturating surfaces are gently concave, forming a bowl-shaped dentary. The triturating surface extends posteriorly past the triangular elevation of the symphyseal ridge to form an oval shape. The labial ridge extends dorsally in the posterior end of the dentary, but is abraded on the anterior side. As preserved, the material suggests that the dentary had a bowl-shaped symphyseal area. A lingual ridge could not be identified. The anterior part of the symphyseal area is missing, but the orientation of the mandibular rami suggests that the dentary had a triangular shape overall. In contrast to chelonoids, the surangular in MAB13689 does not bear an anterior process as no suture scar on the posterolateral surface of the dentary could be discerned.

Discussion

MAB13689 has large concave areas on the triturating surface and a tall symphyseal ridge. Figure 3 shows a comparison of MAB13689 with closely matching genera, including *Argillochelys* (Lydekker, 1889), *Allopleuron*, *Procolpochelys* (Hay, 1908) and *Ctenochelys*. MAB13689 differs from *Argillochelys* in the fact that *Argillochelys* has labial ridges that curve upwards anteriorly forming a more pinched jaw (Moody, 1980; Tong & Hirayama, 2008; Zvonok *et al.*, 2015). *Allopleuron* also has a symphyseal ridge, but it is much shorter than in MAB13689 and the triangular elevation is much higher and longer (Mulder, 2003). It differs from *Procolpochelys* by having a much narrower triturating surface and in general a narrower dentary (Weems & Brown, 2017).

Two other turtle genera from the Maastrichtian deserve mentioning. The first is *Euclastes* (Cope, 1867), which is known from the Maastrichtian of North America, South America and Africa (Foster, 1980; Mateus *et al.*, 2012; Parham *et al.*, 2014). MAB13689 is easily differentiated from *Euclastes* by having a generally much narrower dentary and more prominent symphyseal ridge (Parham *et al.*, 2014; Ullmann *et al.*, 2018). The second genus is *Toxochelys* (Cope, 1873), where *T. latiremis* is described as having a narrow dentary, with a short symphysis and triturating surface of constant width across the dentary (Weems, 1988; Matzke, 2008). This also differs from MAB13689, which has a longer symphysis and triturating surface that narrows slightly across its length.

The fossil shares the most similarities with *Ctenochelys* (Matzke, 2007; Gentry, 2017), in having a well-developed symphyseal ridge and large concave areas on the triturating surface, which extend posteriorly. The dentary of *Ctenochelys* typically has a modest hook anteriorly, this cannot be detected in the present specimen, however, as most of the anterior material of the dentary

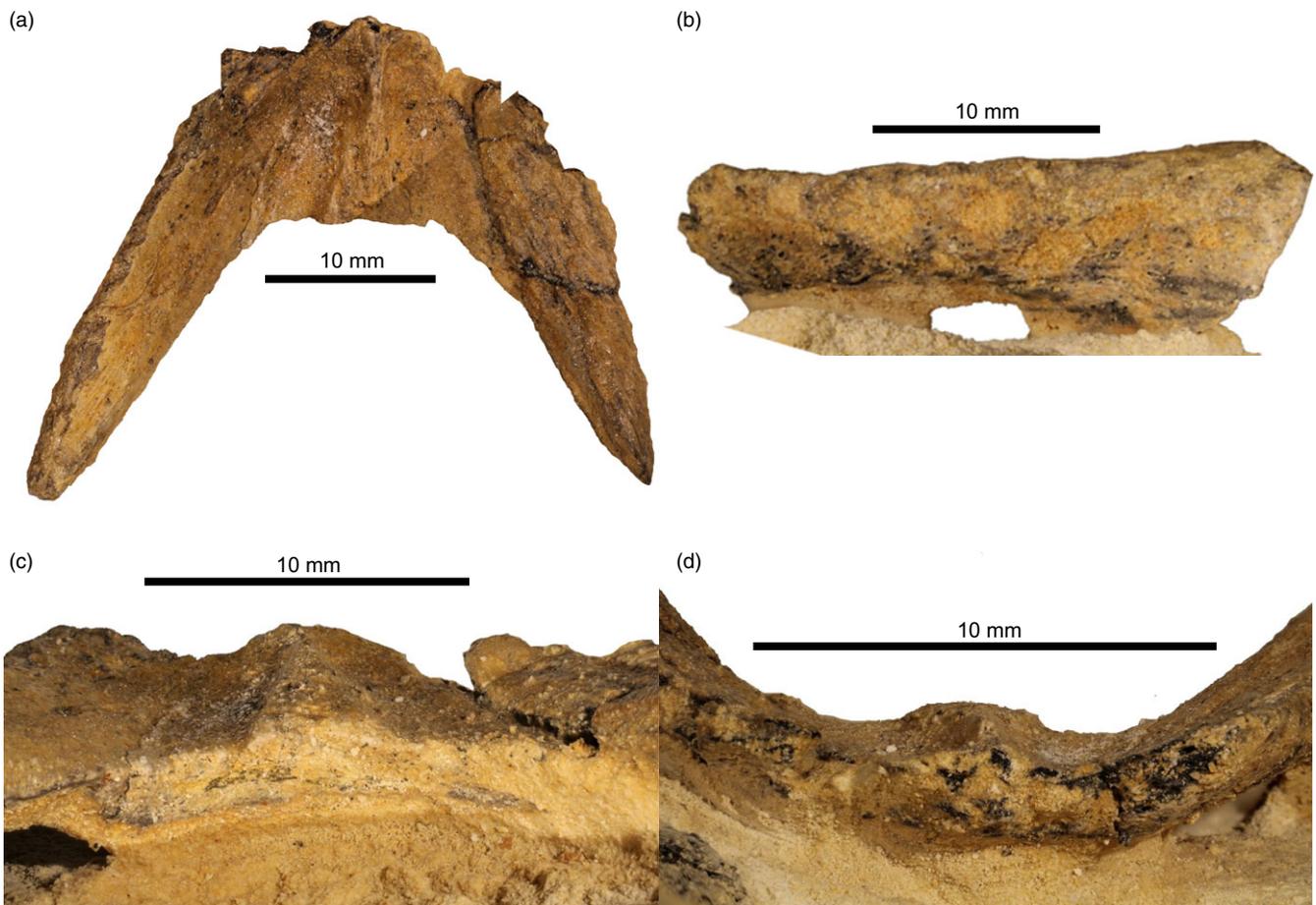


Fig. 2. (a) Dorsal view of MAB13689 (cf. *Ctenochelys*); (b) Left view of MAB13689; (c) Posterior view of the symphysis of MAB13689; (d) Anterior view of the symphysis of MAB13689.

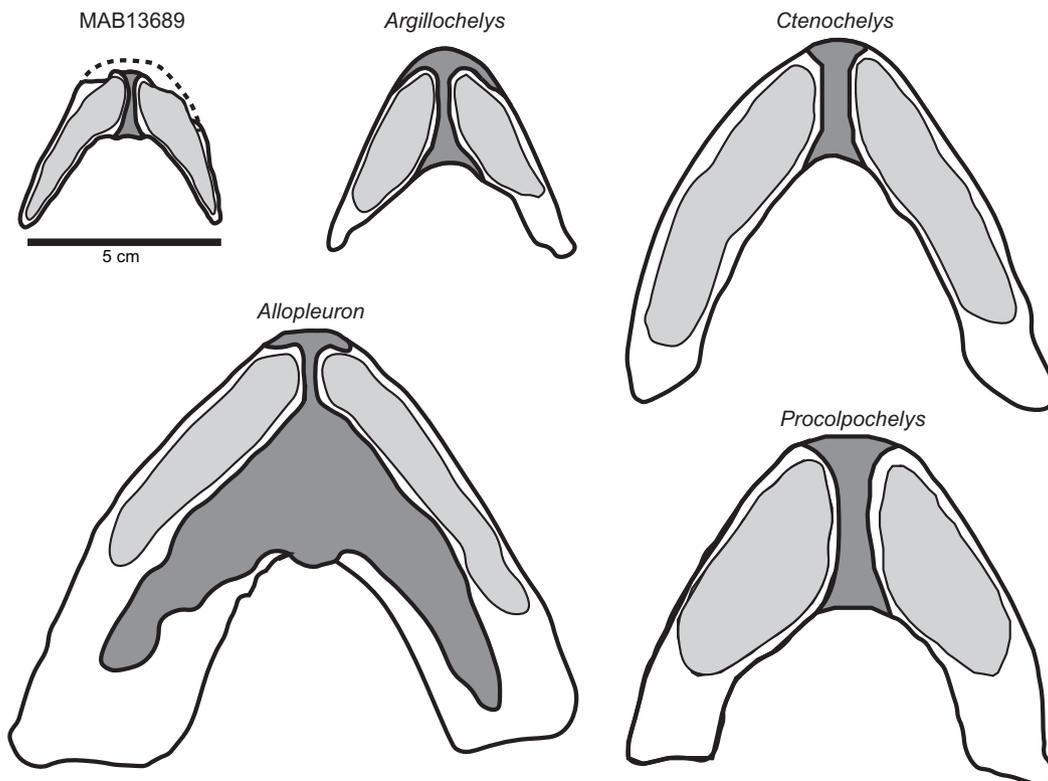


Fig. 3. Interpretative drawings of MAB13689 (cf. *Ctenochelys*) alongside dentaries of the genera that most closely resemble it (Mulder, 2003; Tong & Hirayama, 2008; Karl & Nyhuis, 2012; Weems & Brown, 2017). Dashed lines indicate missing material. Concavities and ridges on the tritulating surfaces are marked with light grey and dark grey coloring respectively.

is missing. Specifically, MAB13689 most resembles the dentary of *C. stenoporus* as described by Karl & Nyhuis (2012). An interesting note is that no remnants of the foramen dentofaciale could be identified in the present fossil, in contrast to the specimen described by Karl & Nyhuis (2012).

The size of the dentary is quite small when compared to described adult individuals of *Ctenochelys*, with a length of 34.5 mm and some material missing anteriorly. Matzke (2007) noted that the posteroventral part of the symphysis is visible in dorsal view in juvenile individuals of *C. stenoporus*. MAB13689 does not show this trait and is therefore not identified as a juvenile individual. There are no notable traits known in the dentary to identify subadult individuals of *Ctenochelys*.

Mandibular characters have received relatively little attention in most previous analyses of chelonioid phylogeny, and the placement of many basal taxa remains a topic of ongoing debate (e.g. Evers et al., 2019). The recent compendium of extant turtle mandibular anatomy by Evers et al. (2022) highlighted several synapomorphies for both Cheloniidae and Dermochelyidae, as well as Chelonioida as a whole, which may prove useful for distinguishing members of respective stem lineages. However, the mandibular characters present in *Ctenochelys* do not unambiguously favour any placement. First, the absence of an anterior process of the surangular supports a position outside of crown-Chelonioida. The reduced foramen dentofaciale majus in MAB13689 is more characteristic of *Dermochelys*, yet the hook development as described in other *Ctenochelys* specimens (Zangerl, 1953; Matzke, 2007; Karl and Nyhuis, 2012; Gentry, 2017) is modest compared to the prominent spike-like symphyseal hook in *Dermochelys* (Evers et al., 2022).

Conclusion

The dentary (MAB13689) found in the Emael Member of the ENCI quarry is identified as cf. *Ctenochelys* based on the shape of the dentary and traits such as the symphyseal ridge and a concave triturating surface. This specimen adds to the variation observed in mandibular anatomy within the genus *Ctenochelys*. Moreover, this provides the first potential occurrence of this genus from the Maastrichtian type area.

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