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Manuscript Draft

Manuscript Number:

Title: A functional symphyseal odontoid in the dentary of the Early Cretaceous istiodactylid pterosaur *Istiodactylus latidens*

Article Type: Full Length Original Article

Keywords: Pterosauria; Ornithocheiroidea; Cretaceous; Wealden Supergroup; Dentition; Odontoid.

Corresponding Author: Dr. David Martill, Ph.D.

Corresponding Author's Institution:

First Author: David Martill, Ph.D.

Order of Authors: David Martill, Ph.D.; David M Martill, BSc PhD

Abstract: ABSTRACT

The Early Cretaceous ornithocheiroid pterosaur *Istiodactylus latidens* (Pterosauria, Archosauria, Reptilia) from the Wealden Supergroup of the Isle of Wight, southern England, has a triangular osseous projection at the dentary symphysis that occluded into a similarly shaped diastema between the first tooth of the left and right premaxillae and functioned as an odontoid (pseudotooth). The possession of an odontoid at the dentary symphysis for *Istiodactylus latidens* appears to be unique among the Pterosauria. An odontoid has not been noted in other members of the Istiodactylidae and may be autapomorphic for the species *I. latidens*, although its non-recognition in other istiodactylid taxa may be a consequence of poor preservation compared with the Isle of Wight material.

Highlights

1. Istiodactylus has a closely spaced, arcuate isodont dentition that could be used to remove a chunk of flesh.
2. A paired isodont dentition would however, leave an unopposed gap during any bite.
3. Istiodactylus overcame this by producing a bony symphyseal structure that operated as a pseudotooth.
4. This is the first time such a structure has been observed in pterosaurs.

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8 Cretaceous istiodactylid pterosaur *Istiodactylus latidens*
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14 David M. Martill
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21 Palaeobiology Research Group, School of Earth and Environmental Sciences, University of
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23 Portsmouth, Portsmouth PO1 2 QL UK david.martill@port.ac.uk
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18 David M. Martill
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23 Palaeobiology Research Group, School of Earth and Environmental Sciences, University of
24
25 Portsmouth, Portsmouth PO1 2 QL UK. david.martill@port.ac.uk
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29
30 ABSTRACT
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32 The Early Cretaceous ornithocheiroid pterosaur *Istiodactylus latidens* (Pterosauria,
33 Archosauria, Reptilia) from the Wealden Supergroup of the Isle of Wight, southern
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59 *Keywords:*
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Pterosauria

Pterosauria; Ornithocheiroidea; Cretaceous; Wealden Supergroup; Dentition;

Odontoid.

1. Introduction

A tooth-like morphology on the dental border of bones comprising the dentary, prementary, premaxilla and maxilla occurs in a number of disparate groups where a single or multiple bony protuberances appear to function as teeth. Such protuberances, often referred to as pseudoteeth or odontoids, are exceptionally developed in the toothless, extinct avian clade Pelagornithidae, a group of birds that flourished around the world from the Late Palaeocene to Late Pliocene (Mayr, 2008; McKee, 1985; Walsh and Hume, 2001); in the prementary of certain early Cretaceous iguanodontian dinosaurs (e.g. Naish and Martill, 2001, pl.12); in some Recent turtles, and in Tusked Frogs (Katsikaros and Shine, 1997), among tetrapods. The placoderms of the Palaeozoic also possessed jaws that lack teeth, and instead have jaw bones with sharp shearing surfaces and tooth-like processes (Ørvig, 1980).

Here I describe the dentition and report on the occurrence of a pseudotooth located in the symphysis of the dentary of the istiodactylid pterosaur *Istiodactylus latidens* (Seeley, 1901) from the Lower Cretaceous Wealden Supergroup of the Isle of Wight, southern England. The following museum abbreviations are used: LPM, Liaoning Palaeontological Museum, Western Liaoning Institute of Mesozoic Paleontology, Shenyang Normal University, Shenyang, China; NHMUK, Natural History Museum, London, UK; IWCM, Isle of Wight County Museum Service, Sandown, Isle of Wight, UK.

2. Description

Istiodactylus is an early Cretaceous (Barremian) ornithocheiroid pterosaur included in the clade Istiodactylidae, that is considered to be a sister taxon to the Euornithocheira (Ornithocheiridae + Pterodontidae + *Nyctosaurus*) (Unwin 2003, Sweetman and Martill 2010). Its skull is characterised by an expanded nasoantorbital fenestra and a rounded terminal rostrum with a near uniform dentition concentrated in the anterior rostrum (premaxilla and anterior most portion of maxilla and anterior dentary). There is a slight upturn of the dental border of the premaxilla (but no equivalent downturn of the dental border of the dentary) resulting in a slight terminal gape during full occlusion of the jaws (Fig. 1). Teeth are present in the jaws from the anterior margin of the nasoantorbital fenestra to the dentary and premaxillary symphyses with twelve tooth pairs in both the upper and lower jaws. The first tooth crown is as large as the last. The teeth bear triangular crowns with a single enamel ridge on the labial surface (Sweetman and Martill 2010), the largest of which has a crown height of 11 mm (right premaxilla alveolus four). The tooth crown of dentary alveolus twelve is 7 mm high, suggesting a gradual reduction of crown height caudally of around one third. The crowns of adjacent teeth abut at their base resulting in a near continuous dentition lacking inter-alveolar spaces in the anterior most part of the dental series, but tooth pairs 10-12 are slightly wider spaced and have slightly raised alveolar borders (Fig. 3). Several of the tooth crowns bear wear facets on their apico-lateral surfaces. The roots of the teeth are cone-like and appear to be somewhat longer than the crown height (Fig. 4).

1 The dental border of the dentary is more or less straight where teeth are present
2 anteriorly, but is developed into a sharp process at the dentary symphysis between
3 mandibular tooth pair one. This process is interpreted here as a pseudotooth (odontoid
4 of some authors). It lacks enamel, and is raised to a height approximately half that of
5 the adjacent tooth crowns (Fig. 2A). In a restored dentition with artificially occluded
6 jaw a gap remains between the pseudotooth and the superior pair of true teeth (Fig.
7 2D) suggesting that the pseudotooth was encased in a thickened rhamphotheca-like
8 envelope against which the true teeth occluded. This appears to be the first occurrence
9 of a pseudotooth in the Pterosauria.
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27 **3. Comparisons**

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32 Until relatively recently istiodactylids had only been recorded from the Wealden
33 Supergroup of the type locality of the Isle of Wight. Subsequently, istiodactylids were
34 reported from the Lower Cretaceous Yixian Formation of China, where the genera
35 *Istiodactylus*, *Liaoxipterus*, *Longchepterus* and *Nurhachius* were described (Dong and
36 Lü, 2005; Wang et al., 2005; Andres and Ji, 2006; Wang et al., 2006). The Chinese
37 istiodactylids are often more complete than the Isle of Wight specimens, but they are
38 highly compacted with all bones severely crushed and shattered. Nevertheless, despite
39 the compacted preservation, a number of specimens reveal detail of the jaw tips. In
40 particular, the holotype of *Longchepterus zhaoi* Wang et al., 2006 (specimen number
41 LPM 00023) exposes the distal dentary in occlusal view (Lü et al., 2006, fig. 3.45)
42 revealing a pseudotooth located medially at the tip of the dentary. It appears to be
43 directed anteriorly, and is somewhat longer and more slender than that of
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1 *Istiodactylus latidens*, but it cannot be ruled out that the severe compaction of the
2 specimen may have exaggerated the degree of forward projection somewhat.
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4 Illustrations of the dentary of *Istiodactylus sinensis* Andres and Ji, 2006 are of
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6 insufficient clarity to reveal a pseudotooth and illustrations of the dentary of
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8 *Nurhachius ignaciobrito* Wang et al., 2005 do not show a pseudotooth on the dentary.
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12 Neither is a pseudotooth indicated for the dentary symphysis of *Liaoxipterus*
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14 *brachyognathus* (Lü et al. 2008).
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19 Pseudoteeth appear to be rare in other groups of pterosaurs too. Some dsungaripterids,
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21 notably *Phobetor* and *Domeykodactylus* (Martill et al. 2000) have elevated alveolar
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23 borders that, if teeth were reduced in height, or absent, may have functioned as
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25 pseudoteeth, and raised alveolar borders also occur in lonchidectids, but in these
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27 forms the teeth are prominent, and erupt well above the alveolar margin
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36 **4. Function and evolution**

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42 The presence of an odontoid in a medial location on the dentary in some istiodactylids
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44 appears to be unique for the Pterosauria and requires explanation. Istiodactylids are
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46 found to form a sister clade to Ornithocheiridae and Pterandodontidae on account of
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48 similarities of their humeral morphology (Unwin, 2003) and together forming the
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50 Ornithocheiroidea (a similar relationship is found by Andres and Ji (2008) but the
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52 clade terminology differs). Ignoring momentarily the edentulous pteranodontids, the
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54 anterior-most teeth of Ornithocheiridae are elongate, gently recurved (fang-like) with
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56 circular or nearly circular cross-sections, and often bear fine striae, or even
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1 occasionally ribs on the enamel (Unwin and Martill 2007). The teeth are not crowded
2 in the jaw with some considerable space between adjacent teeth. Furthermore, there is
3
4 marked size heterodonty with some teeth being extremely long while others perhaps
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6 have only half the crown height of an adjacent tooth. More caudally located teeth are
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8 small and widely spaced. By contrast, the dentition of *Istiodactylus latidens* is isodont
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10 and the tooth crowns are labio-lingually compressed and sub-triangular in outline.
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13 Adjacent teeth appear to be in contact at their base and the labial surface bears a feint
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15 vertical ridge, well developed in *Longchepterus zhaoui*, but only incipient in *I. latidens*.
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18 The teeth of *Istiodactylus* are restricted to that part of the rostrum anterior of the
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20 nasoantorbital fenestra, whereas in tooth-bearing euornithocheirids the teeth, albeit
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22 small and well-spaced, extend almost to the orbit in many (most) taxa. The restricted
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24 dental distribution in *Istiodactylus* presumably reflects their presence in only the more
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26 robust parts of the rostrum where the relatively deep root required for a cutting tooth
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28 can be accommodated.
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34 The presence of a pseudotooth in *Istiodactylus* while surprising, is easily explained in
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36 functional terms: it filled a space where a tooth was unable to. A dentition producing a
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38 complete arc-like bite in order to sever a morsel must have a complete cutting arcade.
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42 A symmetrical dentition of paired teeth will require one additional tooth to fill a gap
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44 at the symphysis. Without the pseudotooth present in *Istiodactylus* any bitten piece of
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46 flesh would have remained attached by a thread. Some large predatory sharks such as
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48 *Hexanchus* overcame this problem with the development of symmetrical symphyisial
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50 teeth (Adnet 2006) and are able to remove a single piece of flesh with one bite. The
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52 symphyisial tooth is unknown in higher tetrapods. Mammals overcame this problem
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1 by developing an overbite of closely spaced incisors while *Istiodactylus* developed a
2 bony pseudotooth to fill an embarrassing gap.
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7 Edentulous pterosaurs of the clades Azhdarchidae, Pteranodontidae and
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9 Nyctosauridae are not known to have developed pseudoteeth on their dental borders,
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11 although the presence of tooth-like structures developed on keratinous rhamphothecae
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13 (as in sawbill ducks like the red-breasted merganser *Mergus serratus*) cannot be ruled
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24 **Acknowledgements**

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29 At NHM UK Lorna Steel and Sandra Chapman are thanked for their tolerance as well
30
31 as access to specimens in their care. Many thanks also to the photographic team at
32
33 NHM for images of *I. latidens*. Dino Frey, Mick Green, Steve Hutt, Darren Naish,
34
35 Steve Sweetman, Dave Unwin, Steve Vidovic and Mark Witton and are thanked for
36
37 discussions on IoW pterosaurs.
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western Liaoning. *Geological Bulletin of China* 25, 737-740.

FIGURE CAPTIONS

Fig. 1. *Istiodactylus latidens* (Seeley, 1901), NHMUK R3877, from the Vectis Formation of the Wealden Supergroup of the Isle of Wight. Left, in rostral view, right in left lateral view. Arrow indicates location of pseudotooth. Scalebar = 10 mm.

Fig. 2. *Istiodactylus latidens* (Seeley, 1901), NHMUK R3877. A, detail of premaxillary dentition centred on pseudotooth. B, line drawing distinguishing teeth and bone (in all drawings bone is shaded 30% black while teeth are shaded 70% black), matrix uncoloured. C, restoration of the premaxillary dentition in rostral view. D, restoration of premaxillary dentition in rostral view as if in full occlusion.

Fig. 3. *Istiodactylus latidens* (Seeley, 1901), NHMUK R3877. Rostrum in right lateral view with tooth positions numbered. Scale bar = 10 mm.

Fig. 4. *Istiodactylus* sp. referred specimen IWCMS 2003.40. Probably a juvenile example missing the three posterior most alveolar pairs. Lack of alveolar pairs at rostral symphysis suggests this is a dentary fragment. This specimen is preserved as a pyritised internal mould, with the outer bone compacta missing. Notice the triangular alveolae now filled with pyritised sediment. Scale bar = 10 mm.

Figure 1
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Figure 2
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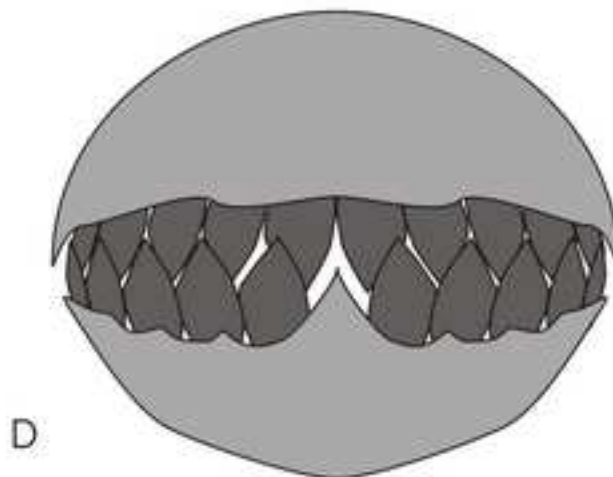
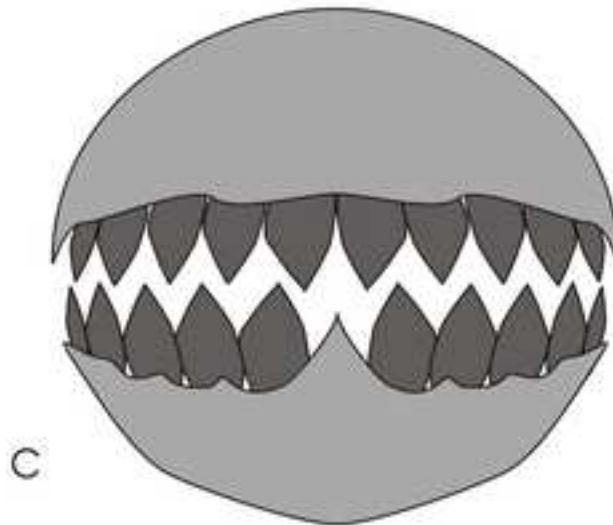
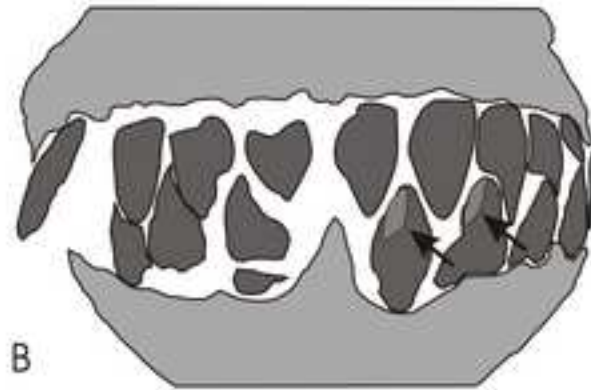


Figure 3
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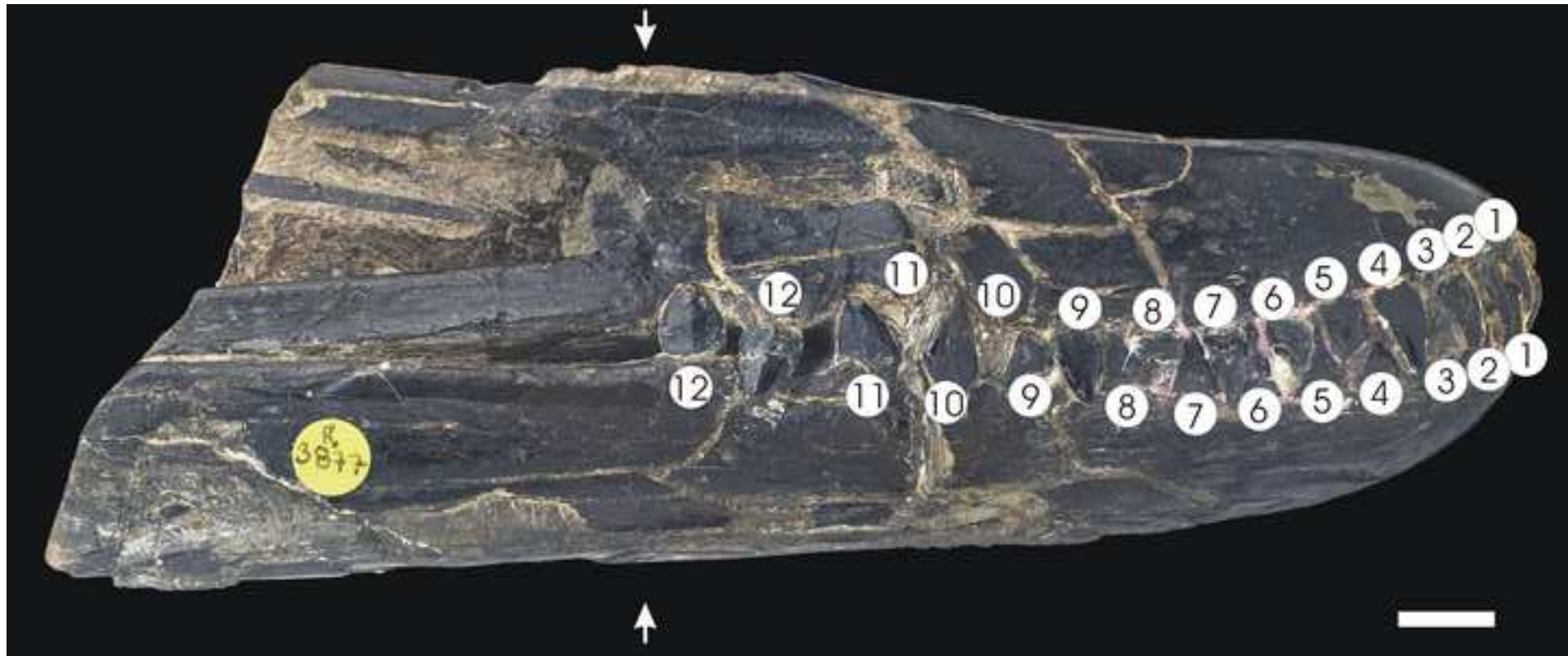


Figure 4
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