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RAPID COMMUNICATION

A ctenochasmatid pterosaur from the Stonesfield Slate (Bathonian, Middle Jurassic) of Oxfordshire, England

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Abstract

The anterior end of a lower jaw bearing long slender teeth, from the Bathonian Stonesfield Slate of Oxfordshire, was hitherto referred to the crocodilian *Teleosaurus*. It is reinterpreted as belonging to a ctenochasmatid pterosaur reminiscent of *Gnathosaurus*. It is the earliest known representative of the Ctenochasmatidae, and one of the earliest known pterodactyloids. The diversity of pterosaurs from the Stonesfield Slate is higher than previously recognized, comprising at least three taxa.

Keywords: Jurassic, Bathonian, England, Stonesfield Slate, Pterosauria, Ctenochasmatidae.

1. Introduction: the pterosaurs from the Stonesfield Slate

Pterosaurs have been known from the Bathonian Stonesfield Slate of Oxfordshire since the early nineteenth century. As early as 1829, Buckland noted that, following a suggestion made in 1823 by Mr I. S. Miller from Bristol, he now considered that the bones from Stonesfield hitherto referred to birds in fact belonged to flying reptiles of 'the genus Pterodactyle' (Buckland, 1829, p. 219). Meyer (1832) coined the name *Pterodactylus bucklandi* for the Stonesfield pterosaur, without a description or diagnosis. Subsequently, a number of specimens were reported from the Stonesfield Slate and more or less coeval Bathonian formations, notably by Huxley (1859), who referred them to the genus *Rhamphorhynchus* (as *R. bucklandi* and *R. depressirostris*), an identification followed by Phillips (1871). Owen (1874) erected three distinct species of *Pterodactylus* on the basis of wing phalanges from the Stonesfield Slate. Seeley (1880) erected the new genus *Rhamphocephalus* for pterosaur material from the Middle Bathonian Cotswold Slate (*Rhamphocephalus sedgwicki*) and Stonesfield Slate. Lydekker (1888) recognized two species of *Rhamphocephalus*, *R. bucklandi* and *R. depressirostris*. Seeley (1901) gave a general account of *Rhamphocephalus* at the generic level. In a review of the pterosaurs from the Stonesfield Slate, Unwin (1996, p. 293) concluded that 'only a single genus, and species, *Rhamphocephalus bucklandi* seems to be present'. In addition, he also noted that the skull material on which Seeley (1880) erected the species *Rhamphocephalus sedgwicki* does not belong to a pterosaur, but very probably to a crocodilian (Unwin, 1996). As *R. sedgwicki* is the only species mentioned by Seeley in the 1880 paper in which he erected the generic name *Rhamphocephalus*, the validity of the latter name for a pterosaur taxon may be open to question. Be that as it may, the jaw material included by Unwin (1996) in *Rhamphocephalus bucklandi* clearly indicates a rhamphorhynchid pterosaur with a relatively short symphysis and proportionately large teeth. Steel (2010) noted that the pterosaur collection from Stonesfield in the Natural History Museum (London) includes material having affinities with recently described pterosaurs from China, which implies that a second pterosaur taxon, in addition to *Rhamphocephalus*, is present at Stonesfield.

A recent examination of material from Stonesfield in the Oxford University Museum of Natural History has revealed that a specimen (OUM J.01419) hitherto considered as belonging to a teleosaurid crocodilian actually belongs to a pterosaur taxon clearly different from previously reported forms and apparently representing the earliest known representative of the family Ctenochasmatidae, as described below.

2. History of previous research and taxonomic remarks on *Teleosaurus subulidens*

Phillips (1871) erected a new species of the crocodilian genus *Teleosaurus* Geoffroy Saint-Hilaire, 1825, *T. subulidens*, for two incomplete lower jaws from the Stonesfield Slate (including the dentary fragment OUM J.01419 redescribed in the present paper, and a more complete lower jaw, OUM J.01414). However, he did not designate a type specimen. Lydekker (1888, p. 121) noted that 'it will be convenient to take as the type the mandible represented in Phillips's "Geology of Oxford", p. 195, fig. 55', thereby designating a lectotype. This specimen, OUM J.01414, is clearly crocodilian. Woodward & Sherborn (1890) cited Lydekker (1888) but simply mentioned that the type was a mandibular symphysis in the Oxford Museum. Kuhn (1936) considered the taxon as invalid. In his revision of the Teleosauridae in the Oxford University Museum, Phizackerley (1951) considered that OUM J.01419 had to be referred to *Teleosaurus cadomensis* (a taxon Phizackerley incorrectly attributed to Geoffroy Saint-Hilaire, 1825; the real author is Lamouroux, 1820, as *Crocodilus cadomensis*). In addition, he referred OUM J.01414 to *Steneosaurus megistorhynchus* Eudes-Deslongchamps, 1866. As a result, apparently oblivious of Lydekker's designation of a lectotype, he concluded (Phizackerley, 1951, p. 1173): 'As both Phillips' types of *T. subulidens* are thus referred to other species,

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T. subulidens is now a synonym'. Phizackerley's conclusions were not accepted by Steel (1973), who listed *Teleosaurus subulidens* as a separate species represented by a mandibular symphysis and an incomplete lower jaw (i.e. OUM J.01419 and J. J.01414, respectively). Benton & Spencer (1995) also listed *Teleosaurus subulidens* as a valid taxon, with OUM J.01419 as type specimen. Following Phizackerley, Powell (2005, p. 35) figured OUM J.01419 as 'part of the jaw of a small crocodile, *Teleosaurus cadomensis*'. Jouve (2009) also considered *Teleosaurus subulidens*, represented by Phillips' fig. 54 (viz. OUM J.01419), as a junior synonym of *Teleosaurus cadomensis*.

To sum up, following Lydekker's designation, the lectotype of *Teleosaurus subulidens* is the incomplete lower jaw OUM J.01414, irrespective of whether this particular specimen belongs to *Steneosaurus megistorhynchus*, as suggested by Phizackerley (1951), or not. OUM J.01419, which, as shown below, is a pterosaur, clearly does not belong to the same taxon as OUM J.01414, which is definitely a crocodilian. Therefore, the name *Teleosaurus subulidens* cannot be applied to OUM J.01419, which currently has no valid Linnaean name.

3. Geographical and geological setting

Specimen OUM J.01419 comes from the so-called 'Stonesfield Slate' at Stonesfield, Oxfordshire. The Stonesfield Slate, actually a sedimentary calcareous sandstone (Powell, 2005) or tilestone, was formerly mined from three levels within the Taynton Limestone Formation (Boneham & Wyatt, 1993), which is considered Middle Bathonian in age. The Stonesfield Slate has long been well known for its abundant flora and fauna (Benton & Spencer, 1995; Powell, 2005). The earliest descriptions of Stonesfield fossils were published in the seventeenth century (Benton & Spencer, 1995).

The Stonesfield Slate is of limited outcrop, probably extending no more than a kilometre around the village (Aston, 1974; Boneham & Wyatt, 1993), and is nowhere visible at surface outcrop today. Former workings consisting of shafts and adits exist, but access is difficult. The term 'Stonesfield Slate' derives from this unmetamorphosed fissile calcarenite's widespread use as a roofing material within the district.

Within the workings, exploitable horizons existed at different levels around the village (Aston, 1974; Boneham & Wyatt, 1993). Typical Stonesfield Slate as used for roofing purposes is a laminated, calcareous-cemented, poorly sorted detrital quartz silty sandstone. Fossil-bearing matrices are more variable, and include more or less shelly, sandy limestones or sandy marls, which may contain significant quantities of discrete ooliths, which tend to be somewhat polished or worn suggesting they were derived from pre-existing sediments.

The Taynton Limestone Formation of Stonesfield is highly fossiliferous throughout and contains an uncommonly diverse assemblage clearly derived from a range of terrestrial, fluvio-deltaic and marine regimes. Marine molluscs abound, alongside brachiopods, echinoids, asteroids and crustaceans plus fish, turtles and crocodiles; alongside these are land plants, insects, dinosaurs, pterosaurs and mammals, suggesting deposition in a near-shore marine environment with significant fluvial input.

Fossils were collected during the active period of the tilestone's exploitation, deriving from 'close work by men on the stone over a very long time' (Aston, 1974); it is likely that tilestone miners made a little extra income from the sale of interesting items to scientists or dealers.

Figure 1. (Colour online) Ventral view of anterior end of lower jaw of cf. *Gnathosaurus*, OUM J.01419, Stonesfield Slate, Bathonian, Stonesfield, Oxfordshire. Scale bar: 10 mm.

4. Systematic palaeontology

Order PTEROSAURIA Kaup, 1834
Superfamily PTERODACTYLOIDEA Plieninger, 1901
Family CTENOCHASMATIDAE Nopcsa, 1928
Genus cf. *Gnathosaurus* Meyer, 1834

Description. OUM J.01419, originally described and figured by Phillips (1871, p. 194, diagram LIV), is the anterior end of a lower jaw, visible in ventral view on a slab of Stonesfield Slate (Fig. 1). It is formed by the fused dentaries and several well-preserved teeth. Five teeth are visible on the left side and eight on the right side, showing various degrees of completeness and insertion in the jaw. The 97 mm long specimen has undergone some dorsoventral compression, but probably was originally rather shallow. It shows a moderate anterior expansion, its maximum width, in the anterior part, being 20 mm. The anterior end of the jaw is thus spatula-shaped. Whereas the bone surface is poorly preserved and cracked, many of the teeth are well preserved and several of them show the complete crown. The teeth were very close set, as can be seen in the posterior region of the jaw where several successive teeth are visible. In that area, there are about two teeth per 5 mm, and the spaces between the teeth are so short that interlocking with teeth in the upper jaw may have been limited. Although this has probably been exaggerated by compression, the teeth apparently projected laterally and slightly anteriorly. It is difficult to assess how much they projected dorsally.

The teeth (Fig. 2) have a long tubular root. The crown is long and slender, recurved and slightly compressed. Enamel covers most of the crown and bears fine longitudinal striations. No carinae are present. The limit between the enamelled and non-enamelled parts of the teeth is curved, being concave towards the root. The length of the teeth, as preserved, appears relatively constant, with a crown length of about 13 mm and a diameter at the base of the crown of about 2 mm.

Discussion. The identification as a crocodilian by Phillips (1871), which has hitherto been generally accepted, was mainly based on comparison with the teleosaurid *Teleosaurus cadomensis* from the Middle Bathonian Pierre de Caen of the Caen area of Normandy. As described notably by Eudes-Deslongchamps (1870), *Teleosaurus cadomensis* does show a large number of slender teeth inserted in the jaws in a fashion that is reminiscent of the condition seen in OUM J.01419, although the interdental spaces appear to be somewhat longer in *Teleosaurus cadomensis*. However, details of tooth morphology separate OUM J.01419 from

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Figure 2. (Colour online) Close-up of teeth on the right side of lower jaw of cf. *Gnathosaurus* from Stonesfield, OUM J.01419, showing details of enamel pattern. Scale bar: 10 mm.

Teleosaurus cadomensis. In the latter, teeth show a double curvature and a carina (see Eudes-Deslongchamps, 1870, pl. II, fig. 9), which do not occur in the specimen from Stonesfield. In addition, in teeth of *Teleosaurus cadomensis* the slightly inflated root appears to be shorter and less tubular.

The teeth of OUM J.01419 show various characters that are pterosaur-like rather than crocodile-like. These include the lack of carinae and the compression of the crown, and the particular enamel pattern, with the concave boundary between the enamelled and non-enamelled parts of the tooth. In addition, the pulp cavity extends into the crown, as shown by a broken tooth at the posterior end of the jaw fragment, as in at least some pterosaurs (see below), but unlike the condition in crocodilians. OUM J.01419 is clearly different from *Rhamphocephalus bucklandi*, in which the mandibular symphysis is short and the teeth are fewer in number and more robust (see Unwin, 1996). The teeth of OUM J.01419 are very reminiscent of those of pterosaurs with long slender teeth, in particular ctenochasmatids, and what can be seen of jaw morphology is also in agreement with referral to a ctenochasmatid pterosaur. Among ctenochasmatids (see review by Martill *et al*. 2006), the Stonesfield specimen differs from forms with extremely long and slender teeth such as *Pterodaustro*. It can be distinguished from *Ctenochasma*, from the Late Jurassic of Germany and France, by its relatively shorter teeth and by the expansion of its proximal end; in *Ctenochasma*, there is no such expansion, the lower jaw remaining parallel-sided all the way to its anterior tip (Wellnhofer, 1970; Bennett, 2007). Conversely, in *Plataleorhynchus streptophorodon*, from the Purbeck of England, the anterior expansion is much more marked than in OUM J.01419, forming a spoon-shaped rosette (Howse & Milner, 1995). The closest outline of the anterior tip of the lower jaw among Jurassic ctenochasmatids is apparently found in *Gnathosaurus subulatus* Meyer, 1834 from the Tithonian of Bavaria (Wellnhofer, 1970, 1991) and in *Gnathosaurus macrurus* (Seeley, 1869) from the Berriasian of England (Howse & Milner, 1995), in which the anterior spatula is moderately expanded. Interestingly, like OUM J.01419, *Gnathosaurus* also was originally considered as a crocodilian (Münster, 1832; see Wellnhofer, 1970 for historical details). The type specimen of *Gnathosaurus subulatus*, an incomplete lower jaw (Fig. 3) bearing a number of teeth (Meyer, 1834; Wellnhofer, 1970, 1991), is generally similar to OUM J.01419, the main differences being that in *Gnathosaurus* the teeth seem to be slightly more widely spaced than on the Oxford specimen. As in OUM J.01419, in *Gnathosaurus* the teeth sometimes bear fine striations and the pulp cavity extends into the crown (Wellnhofer, 1970). However, OUM J.01419 is too incomplete to warrant a precise identification, notably because it shows only a relatively small number of teeth, so that no estimate of total tooth count can be provided. Moreover, the anteriormost teeth are not preserved, so that it cannot be decided whether they were greatly elongate as in *Gnathosaurus subulatus*. For these reasons, OUM J.01419 is here referred to as cf. *Gnathosaurus*. More complete material will be needed to assess its position within the Ctenochasmatidae.

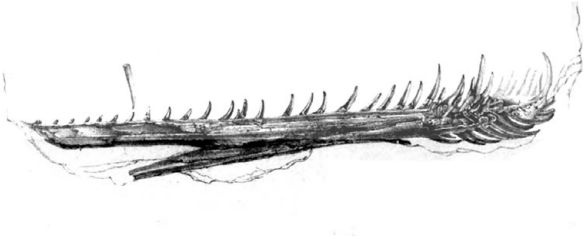

Figure 3. Holotype of *Gnathosaurus subulatus* Meyer, 1834 from the Tithonian of Bavaria for comparison. After Meyer (1834).

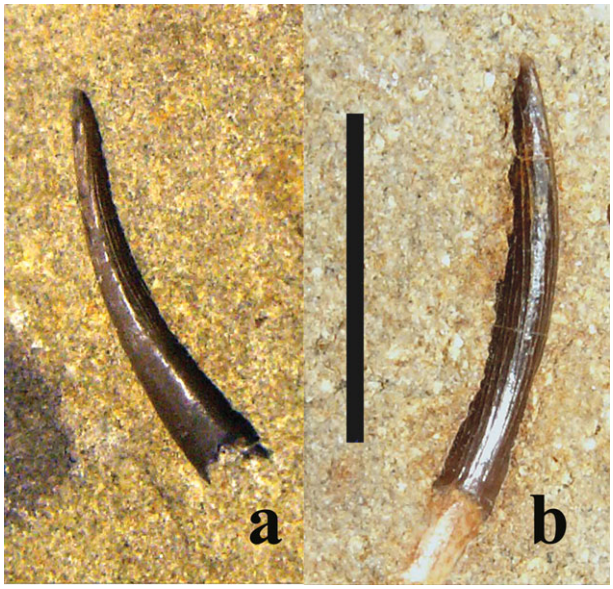

Figure 4. (Colour online) Isolated ctenochasmatid teeth from the Stonesfield Slate, OUM J.028418 (a) and OUM J.028421 (b). Scale bar: 10 mm.

It should be noted that a number of isolated teeth in the Oxford collection show the same characters as those still present on OUM J.01419 (Fig. 4). Ctenochasmatid remains are therefore not uncommon in the Stonesfield Slate.

5. Conclusion

The identification of a *Gnathosaurus*-like ctenochasmatid in the Stonesfield Slate shows that, contrary to previous

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conclusions (Unwin, 1996), more than one pterosaur taxon is present in this formation. The form resembling Chinese specimens mentioned by Steel (2010) probably represents a third taxon, as no pterosaur closely resembling *Gnathosaurus* is currently known from China.

The *Gnathosaurus*-like pterosaur from Stonesfield appears to be the earliest known ctenochasmatid, and also one of the earliest known pterodactyloids. Its occurrence in rocks of Bathonian age points to an early differentiation among this superfamily, with forms possessing a highly derived comb-like dentition appearing as early as Middle Jurassic time. Hitherto reported Middle Jurassic pterosaurs (Barrett *et al*. 2008), belonged mostly to non-pterodactyloid or 'transitional' forms including the peculiar taxa *Darwinopterus* (Lü *et al*. 2010) and *Wukongopterus* (Wang *et al*. 2009) from the Tiaojishan Formation of NE China. The specimen from Stonesfield suggests that the chronological pattern of pterosaur evolution prior to Late Jurassic time was more complex than usually recognized, with relatively derived forms such as ctenochasmatids appearing at an early date.

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