ASSOCIATED DENTITION OF THE CHIMAEROID FISH *BRACHYMYLUS ALTIDENS* FROM THE OXFORD CLAY

by D. J. WARD *and* K. J. MCNAMARA

ABSTRACT. The discovery of a well-preserved associated chimaeroid dentition in the Oxford Clay near Peterborough, England has permitted a revised description of the Jurassic chimaeroid *Brachymylus altidens* Woodward. It is assigned with *Pachymylus* and *Callorhinchus* to the family Callorhinchidae. The holotype of *B. minor* Woodward and lectotype of *B. altidens* Woodward are figured for the first time.

A COMPLETE set of associated dental plates of the chimaeroid fish *Brachymylus altidens* Woodward was found in 1972 in a disused Peterborough Oxford Clay Pit by one of the authors (K. J. M.). The part of the pit where the specimens were found consists of dumped mounds of non-bituminous clay which are thought to be from the *athleta* Zone of the Callovian stage which overlies the quarried bituminous lower zones. Weathering of the mounds results in fossil remains being exposed on the surface. One half of the left vomerine plate was visible, whereas the other half, along with the other five plates, was located below the surface close by. No dorsal fin spine was recovered. Associated with the plates was a large amount of fragmented lignite. No other macrofossils were found in the immediate vicinity, except for a specimen of *Gryphaea* associated with the right palatine plate.

Chimaeroids are cartilaginous fishes known in the Mesozoic and Tertiary eras, principally from their detached dental plates and fin spines, although skeletal remains have been found in the Kimmeridgian (Late Jurassic) and Chalk (Late Cretaceous). The first true chimaeroids, members of the suborder Chimaeroidei (Patterson 1965), appear in the Bathonian with the two closely related genera *Ischyodus* and *Ganodus*. In the Callovian and Oxfordian, *Ischyodus* is joined by *Pachymylus leedsi* Woodward and *B. altidens* Woodward. All these genera possess primitive, principally crushing, dentitions. *B. minor* Woodward and *Elasmodectes secans* Woodward, the earliest species with dentitions adapted for shearing as well as crushing, appear in the Kimmeridgian. *Ischyodus* and *Edaphodon*, genera with crushing dentitions, remained pre-eminent throughout the Cretaceous, then became extinct in the Tertiary. The Palaeogene saw the proliferation of a suite of more specialized forms, including *Chimaera* and *Amylodon*, heralding the modern fauna with small shearing dentitions.

Chimaeroid dentitions consist of three pairs of plates—mandibular, vomerine, and palatine. The palatine pair are larger than, and are positioned posterior to, the vomerine plates. In the absence of skeletal material, the taxonomy of fossil chimaeroids is based on the characteristics of the dental plates, particularly the number, size, and distribution of their raised biting surfaces known as tritors. The terminology is summarized in Ward (1973) based on Newton (1878), and Woodward (1891).

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SYSTEMATIC PALAEONTOLOGY

Class HOLOCEPHALI
Order CHIMAERIDA
Suborder CHIMAEROIDEI
Family CALLORHINCHIDAE
Genus BRACHYMYLUS Woodward, 1892

Type species. Brachymylus altidens Woodward, 1892, p. 15; from the Oxford Clay, Peterborough.

Revised diagnosis. Mandibular plate rhomboidal and laterally compressed. Oral surface with three tritoral areas all arising from a single body of tritoral dentine which forms the greater part of the plate. Post-oral margin parallel to the symphysial margin; oral margin excavated between the posterior-outer and symphysial tritors. Median tritor occupying the hinder half of the oral surface, not impinging on the oral margin. Inner surface excavated to expose the compact base of the tritoral dentine.

Brachymylus altidens Woodward, 1892

Plate 66, figs. 1–6; text-fig. 1A

*v**1892 *Brachymylus altidens* Woodward, p. 15.

Holotype. Incomplete corroded left mandibular plate P.6891, A. Leeds Collection.

Material. Holotype and P.57041*a–f*, an associated dentition of two mandibular, vomerine, and palatine plates.

Occurrence. Holotype: only recorded as 'Oxford Clay, Peterborough'; thus Callovian or Oxfordian. P.57041: ?*athleta* Zone, Callovian, near Peterborough, England (TL.167937).

Description. The mandibular plate (Pl. 66, figs. 1, 2) is rhomboidal, and laterally compressed, with a concave-oral and post-oral margin and prominent beak. The oral surface, which occupies half the outer surface, bears three tritoral areas. The large symphysial tritor runs the entire oral length of the symphysial margin and is medially truncated by an oblique wear facet. The ovoid median tritor is centrally placed and

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EXPLANATION OF PLATE 66

Brachymylus altidens Woodward ×1.

Fig. 1; P.57041b. Right mandibular plate; outer (oral) surface.
Fig. 2; P.57041b. Right mandibular plate; inner surface.
Fig. 3; P.57041c. Right palatine plate; inner surface.
Fig. 4; P.57041c. Right palatine plate; outer (oral) surface.
Fig. 5; P.57041f. Right vomerine plate; inner (lateral) surface.
Fig. 6; P.57041f. Right vomerine plate; outer (medial) surface.

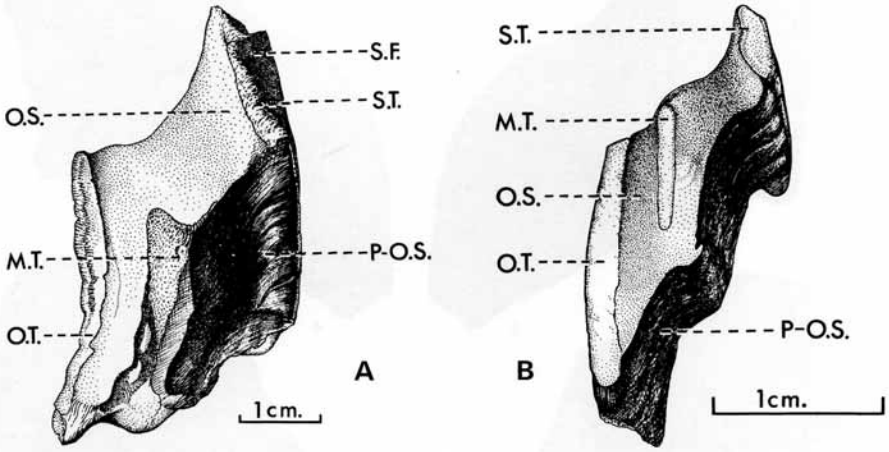
WARD and McNAMARA, Chimaeroid fish

occupies the posterior two-thirds of the length of the oral surface. The outer tritor is narrow and forms the lateral margin of the oral surface, but does not impinge anteriorly on the oral margin. The post-oral surface is covered with enameloid, which extends just over the symphysial and post-oral margins. The inner surface exposes the depressed-toughened base of the tritor, a series of fine lamellae running parallel to the post-oral margin, bounded antero-laterally by a band of enameloid-coated dentine covering the beak and running along the oral margin.

The vomerine plate (Pl. 66, figs. 5, 6) is quadrate, with a wide symphysial surface extending posteriorly to form a beak, and a prolonged maxillary articulation surface. The large oval tritor is placed medially in the oral surface. The inner and outer surfaces are covered with enameloid, except for the tip of the beak and the upper half of the inner surface, which have the same lamellar development as seen on the mandibular plate.

The palatine plate (Pl. 66, figs. 3, 4) is rounded anteriorly and has a laterally prominent post-oral wing. There are two oval tritoral areas, the inner tritor being slightly anterior to the larger median tritor. The post-oral surface is covered with enameloid, and the inner surface has the lamellar structure as on the mandibular plate, bounded antero-laterally by a band of enameloid-covered dentine. In both the palatine and mandibular plates the tritors arise from an unexposed mass of tritoral (pleromic) dentine which forms a substantial part of the plate.

All six plates are in an excellent state of preservation and are complete, with the exception of the left palatine plate, which is lacking a fragment of post-oral wing. The tritors are all corroded, a feature common to chimaeroids from aerobic sediments. The palatine and right mandibular plates are slightly crushed, a fragment of



TEXT-FIG. 1. A, *Brachymylus altidens* Woodward, holotype P.6891. Left mandibular plate, oral surface. Magnification approximately ×1·3. B, *B. minor* Woodward, lectotype P.4166a. Left mandibular plate, oral surface. Magnification approximately ×2·7. Abbreviations: O.S., outer surface; M.T., median tritor; O.T., outer tritor; S.F., symphysial tritor; P.-O.S., post-oral surface.

Gryphaea shell being embedded in the laminar tritor of the right palatine. The vomerines are virtually undistorted but have a number of dorso-ventral fissures.

The holotype, unfigured by Woodward (1892), is a small left mandibular plate (text-fig. 1A). The oral surface is worn, almost removing the median tritor and causing the outer tritor to impinge on the oral margin. The symphysial (wear) facet has obliterated all but a trace of the symphysial tritor. This degree of wear would suggest the individual died in senility. The inner surface is smooth, but not rolled, with no enameloid remaining and only traces of the laminae. The dentine is corroded and bears a large number of shallow multidirectional scratches. This is necessarily a post-mortem feature and suggests the plate was chewed and partially digested in the stomach of a marine predator or scavenger prior to fossilization. The tip of the beak is lacking but the break has sharp edges, suggesting that it occurred quite recently.

TABLE 1. A comparison of the mandibular dental plates of *Pachymylus leedsi*, *Brachymylus minor* and *B. altidens*.

Pachymylus leedsi	*Brachymylus minor*	*Brachymylus altidens*
Plate long	Plate short	Plate long
No symphysial tritor	Small symphysial tritor	Large symphysial tritor
Anteriorly positioned median tritor	Posteriorly positioned median tritor	Posteriorly positioned median tritor
Outer tritor three small punctate areas	Outer tritor large and convex	Outer tritor small and concave
Large symphysial facet	Small symphysial facet	Large symphysial facet
Symphysial margin longer than posterior outer margin	Symphysial margin shorter than posterior outer margin	Symphysial margin longer than posterior outer margin

DISCUSSION

Woodward's diagnosis of *Brachymylus* is understandably brief, since he had only the single worn *B. altidens* specimens and three diminutive examples of *B. minor*. The differences between *B. altidens* and *B. minor* are greater than could have been previously anticipated. Table 1 compares some aspects of their mandibular plates with those of *Pachymylus leedsi* Woodward, a species with which the dentition of *B. altidens* bears some functional similarities. Woodward also omitted to figure *B. minor*, nor did he specify a holotype. P.4166a is here designated the lectotype (text-fig. 1B).

It is difficult, when considering the dentition alone, to distinguish between features of varietal, specific, or generic significance. This problem is discussed in Newton (1878, p. 3) and acknowledged in Woodward (1912, p. 182) in relation to the recent *Chimaera colliei* Bennett. In spite of the differences between *B. altidens* and *B. minor*, their over-all similarities are considered sufficient to allow their inclusion in the same genus.

The presence of a single body of pleromic dentine, forming tritors on the oral surface and exhibiting laminar ornamentation on the inner surface, is a feature common to both *Brachymylus* and *Pachymylus*. In all other fossil genera, multiple

tritors are formed by longitudinally aligned tubes of pleromic dentine. Only in *Callorhinchus* is there a single body of pleromic dentine, which being fully exposed on the oral surface forms a single tritor. The base of the plate in both Recent and fossil species of *Callorhinchus* bears laminar ornament as in the Jurassic species. Patterson (1965), following Woodward (1891), conventionally assigns *Brachymylus* and *Pachymylus* to the Chimaeridae, along with *Elasmodus*, *Edaphodon*, *Ischyodus*, and *Chimaera* itself. *Brachymylus* appears more closely related to *Callorhinchus* than to *Chimaera*, and it is on this basis that it is assigned to the Callorhinchidae along with *Pachymylus*. The value of including extinct fossil genera in the present classification is questionable and is under review.

Associated dentitions are extremely rare. Where other skeletal remains are preserved, as, for instance, in the Chalk or Kimmeridgian, the plates are generally either crushed or impossible to free from the matrix without the destruction of the adjacent cartilage. The only comparable specimen known to the authors at present is an associated dentition of *Edaphodon mirificus* Leidy, from the Upper Cretaceous of New Jersey, U.S.A. (New Jersey State Museum registration no. 11301). A complete dentition of *E. sedgwicki* (Agassiz) from the Cambridge Greensand is on display in the Sedgwick Museum, Cambridge (S.M. B8802). It is, however, inferred from the account of Newton (1878, p. 8) and from their typical rolled and phosphatized condition, that the individual plates were not found in association and thus are unlikely to belong to a single individual.

Plaster replicas of P.57041a–f can be obtained through the senior author (D. W.).

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D. J. WARD
35 Addington Road
West Wickham
Kent

K. J. MCNAMARA
Department of Geology and Mineralogy
University of Queensland
St. Lucia 4067
Queensland
Australia

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