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Carcharopsis prototypus and the adaptations of single crystallite enameloid in cutting dentitions

CHRISTOPHER J. DUFFIN[1] & GILLES CUNY[2]

[1]*146, Church Hill Road, Sutton, Surrey SM3 8NF, England. E-mail: cduffin@blueyonder.co.uk*
[2]*Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen K, Denmark. E-mail: gilles@snm.ku.dk*

ABSTRACT:

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Carcharopsis is a Palaeozoic shark comprising an enameloid-covered cutting dentition comprising serrated teeth. The enameloid ultrastructure of the teeth of *C. prototypus* is examined for the first time and consists of a 35 µm thick layer of tightly compacted apatite crystallites with a maximum individual length of 0.1 µm. The crystallites are randomly-oriented toward the base of the enameloid layer, but assume a roughly parallel orientation higher up in the enameloid, with their long axes arranged normal to the tooth surface. The enameloid of typical hybodonts comprises a compact outer crystallite layer and a looser, bundled inner layer. The Cretaceous hybodonts, *Priohybodus arambourgi* and *Thaiodus ruchae*, by contrast, have a compact, less differentiated enameloid very similar to that of *C. prototypus*. This suggests that crystallite compaction is a corollary of the evolution of serrated dentitions possessing single crystallite enameloids.

Key words: *Carcharopsis, Priohybodus, Thaiodus,* Carboniferous, Enameloid ultrastructure.

INTRODUCTION

Neoselachian sharks have independently developed cutting or cutting-clutching dentitions with serrated teeth in a number of lineages: e.g., the Carcharhinidae, Lamnidae, Anacoracidae and Dalatiidae (CAPPETTA 1987). However, such dentitions are much rarer among more primitive sharks. Within the Hybodontiformes, for example, dentitions with serrated teeth are known in only three species: *Priohybodus arambourgi, Pororhiza molimbaensis,* and *Thaiodus ruchae* (CAPPETTA 1987, CAPPETTA & *al.* 1990, DUFFIN 2001, CUNY 2006). As non-batoid neoselachians (Synechodontiformes, Galea and Squalea) are characterized by a triple-layered enameloid, a feature otherwise unknown in other chondrichthyan lineages, the rarity of such serrated teeth in non-neoselachian chondrichthyan dentitions may be linked to enameloid microstructure. Indeed, the neoselachian parallel-bundled enameloid (PBE, CUNY & *al.* 2001) is particularly resistant to tensile stresses (PREUSCHOFT & *al.* 1974).

Some xenacanthiform sharks (*Dicentrodus, Lebachacanthus* and *Orthacanthus*; HAMPE 2003), while possessing serrated lateral cusp margins, possess no enameloid covering to the orthodentine crown. We accordingly describe here the enameloid microstructure of another Palaeozoic shark known to have developed serrated teeth, *Carcharopsis prototypus,* and we compare it with that of the Mesozoic hybodonts, *Priohybodus arambourgi* and *Thaiodus ruchae,* to see if these teeth share a similar enameloid microstructure that can be linked to the development of a cutting dentition.

CARCHAROPSIS AGASSIZ, 1843

The genus has a complex nomenclatural history which will be reviewed elsewhere (GINTER, HAMPE & DUFFIN, in preparation). The generic name was originally cited in the synoptic table of the third volume of Louis Agassiz's *Recherches sur les Poissons Fossiles* (AGASSIZ 1843, p. 313), with a footnote indicating his intention to give more detailed treatment in the *Feuilleton*. Although no formal description, diagnosis or figure were presented by Agassiz, it is obvious that he intended the holotype to be NHM P.5445, an isolated crown from the Carboniferous Limestone of Pateley Bridge, Yorkshire, U.K (Text-fig. 1A). The validity of *Carcharopsis* has been accepted by LUND & MAPES (1984), whose work forms the most recent review of the genus.

In addition to the holotype, *C. prototypus* is also known from a partial articulated dentition collected from the Millstone Grit shales of Crimple Beck, Yorkshire (NHM P.24804, Text-fig. 1B). Recent processing of an impersistent red wayboard clay (possibly a decomposed hyaloclastite) from the Eyam Limestone Formation (P_2 zone, Brigantian, late Dinantian) of Coleshill Quarry (The National Stone Centre, SK 28785503, near Matlock, Derbyshire) for microvertebrates has further yielded a number of isolated teeth suitable for histological analysis. In this quarry, the Carboniferous Limestone is represented by a number of mound-like carbonate mud ”reef knolls” surrounded by crinoid-rich grainstones. Deposited under marine subtidal conditions, the mound crests often show impersistent calcretes and caliches indicating periods of sub-aerial exposure. The Eyam Limestone deposits are generally draped over the mounds with syn-depositional dips to the south.

The teeth of *C. prototypus* are quite robust and may measure up to 25 mm in height. Asymmetrical in shape, the labio-lingually compressed crown possesses a single well developed central cusp, flanked by up to two pairs of lateral cusplets. The central cusp and lateral cusplets have prominent cutting edges which are strongly denticulated. Each serration has a base which is 1mm in length, and their long axes are normal to the cusp margin. The serrations decrease in height basally and apically from the middle of the cutting edge. The largest denticles are 0.9 mm high. Each is well separated from its neighbour by a deep cleft and has a base which is subcircular in cross section. A series of smaller denticles is present on the cutting edges of each individual denticle.

A series of very coarse, non-bifurcating vertical ridges is present on the labial face of the lateral cusplets and the mesial and distal flanks of the central cusp base. Each ridge has a coarse, upturned accessory cusplet developed at its base.

The very shallow root makes up only 5% of the total tooth height at the central cusp. Slightly reniform in outline, the root has anaulacorhize vascularisation and is projected lingually.

MATERIAL AND METHOD

Only natural breakages in the enameloid were examined in this study. Each tooth was first etched for 5 seconds in 10% HCl and studied using a Scanning Electron Microscope (SEM). If no microstructure was visible, the teeth were further acid-etched, several times if needed, until the microstructure was properly revealed. One broken tooth of *Carcharopsis prototypus* from Coleshill quarry was etched for 35 seconds in 10% HCl. Its microstructure was compared with that of the enameloid in teeth of *Thaiodus ruchae* (Khok Pha Suam, Ubon Ratchathani Province, Thailand, Khok Kruat Formation, Cretaceous, Aptian/Albian (CAPPETTA & *al.* 2006), etched for 1 minute 35 seconds) and *Priohybodus arambourgi* (one tooth from Jebel Boulouha, southern Tunisia, Douiret Formation, Aptian; ANDERSON & *al.* 2007, CUNY & *al.* 2004), etched for 5 seconds, and two teeth from Nalut, northwestern Libya, Chicla Formation, Aptian/Albian (DUFFIN 2001), etched for 1 minute and 1 minute 35 seconds respectively).

The teeth of *Priohybodus arambourgi* are large, measuring up to 35 mm long and around 40 mm high, with a labio-lingually compressed, triangular central cusp flanked by up to 3 pairs of lateral cusplets. The cutting edges of the cusps are strongly serrated. The root, which has a flat basal surface, is angled at around 10^o lingually away from the crown underside, and forms just less than half the total tooth height.

The teeth of *Thaiodus ruchae* are also large (up to around 30 mm long) but, unlike the teeth of *Carcharopsis* and *Priohybodus*, possess a relatively low crown. The strong, serrated cutting edge runs the length of the crown, passing through the apices of a slightly off-centre, low median cusp and its flanking series of marginal denticles.

DESCRIPTION

The enameloid is 35 µm thick in the tooth of *Carcharopsis prototypus* and is made of tightly packed, short crystallites which never exceed 0.1 µm in length

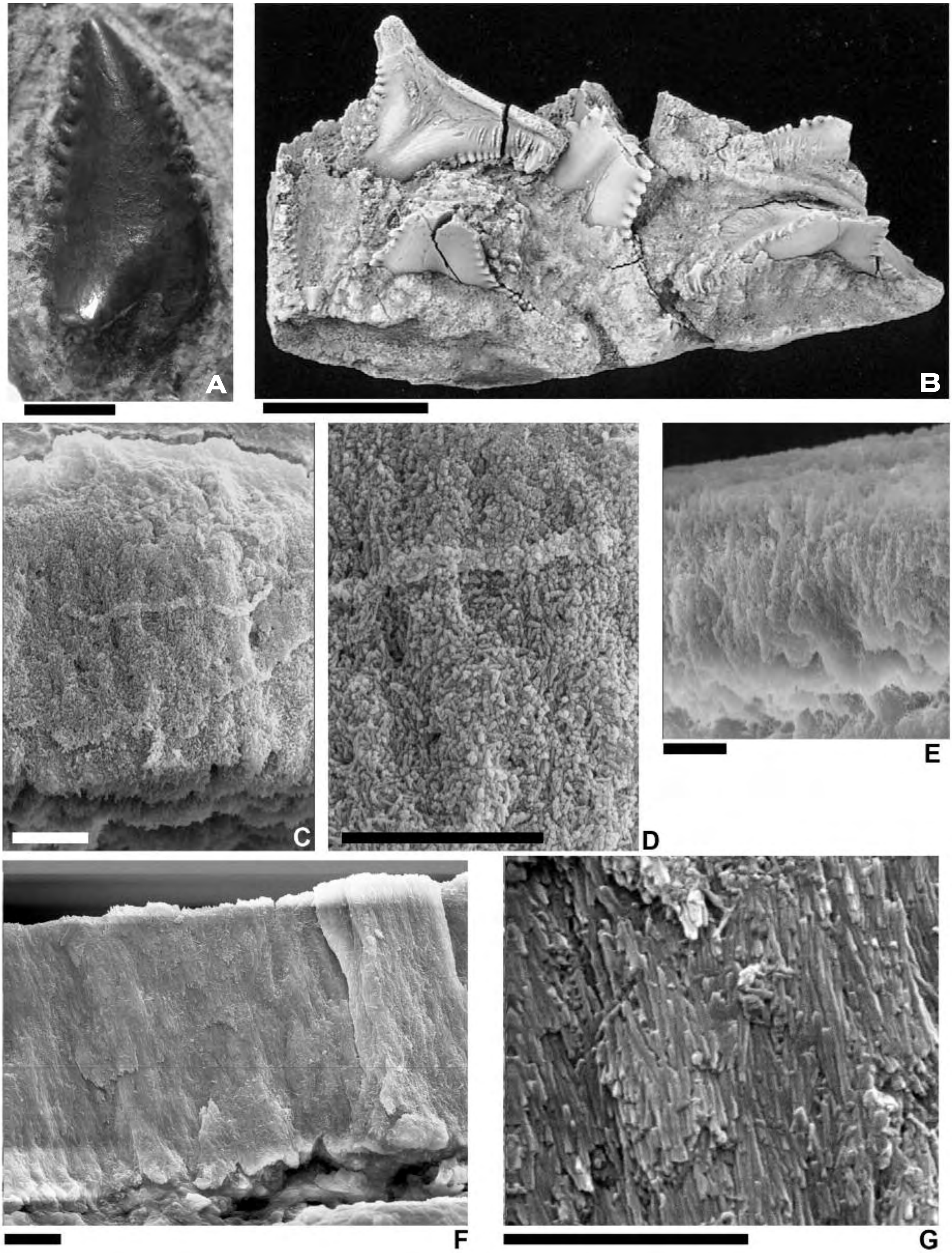

Fig. 1. A – *Carcharopsis prototypus,* NHM P.5445, holotype from Pateley Bridge, B – *Carcharopsis prototypus,* NHM P.24804, partial articulated dentition from Crimple Beck, C-D – *Carcharopsis prototypus* from Coleshill Quarry (Dinantian), tooth etched 35 s in 10% HCl, C – Natural fracture of the enameloid, D – Same area at higher magnification, E – *Thaiodus ruchae* from Khok Pha Suam (Aptian/Albian), tooth etched 1 mn 35 s in 10% HCl, natural fracture of the enameloid, F-G – *Priohybodus arambourgi* from Jebel Boulouha (Aptian), tooth etched 5 s in 10% HCl, F – Natural fracture of the enameloid, G – Same area at higher magnification. Scale bars: A – 5 mm; B – 20 mm; C-F – 10 µm; G – 5 µm

(Text-fig. 1C-D). This gives the enameloid a very compact appearance. Near the top of the enameloid layer, the crystallites are arranged roughly parallel to each other and orientated perpendicular to the oral surface of the tooth, whereas near the contact with the underlying dentine, the crystallites are more randomly orientated.

COMPARISONS AND DISCUSSION

The enameloid of *Carcharopsis prototypus* appears to be very compact when compared with that of the Hybodontiformes. Amongst the latter, teeth normally have an enameloid made of two layers: a compact outer layer and a looser, bundled inner layer (CUNY & *al.* 2001). This contrasts with the enameloid as developed in hybodonts with serrated cutting dentitions. The teeth of neither *Thaiodus ruchae* nor *Priohybodus arambourgi* possess the inner bundled layer otherwise typical of hybodont enameloids (Text-fig. 1E-G). Instead, the enameloid in both hybodonts shows a microstructure very similar to that of *C. prototypus,* except that the individual rod-shaped crystallites are more elongated, reaching 2 µm in length in *P. arambourgi*. This convergence suggests that, in the absence of a triple-layered structure, the development of a cutting dentition necessitates compaction of the crystallites building up the enameloid in order to resist the tensile stresses induced by this mode of feeding.

The teeth of *P. arambourgi* are the highest and most labio-lingually compressed, and also possess the most compact enameloid, suggesting that the two conditions might be correlated. The necessity of compacting a single-layered enameloid might partly explain the rarity of this tooth design among non-neoselachian sharks, although more studies are required before a definite conclusion can be reached.

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