

The shark *Carcharhinus* sp. from the Middle Eocene of Jamaica and the Eocene record of *Carcharhinus*

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ABSTRACT. An upper tooth of a previously unrecorded species of the shark *Carcharhinus* was recovered from the Middle Eocene of Jamaica. This represents one of the oldest examples of the genus, which today is one of the dominant groups of predators within a variety of tropical environments. This is also the oldest record of a carcharhinid shark from marginal marine facies and confirms that the early radiation of *Carcharhinus* occurred within Tethyan regions

Key words: Eocene, Shark, *Carcharhinus*, Jamaica, Guys Hill Formation.

1. INTRODUCTION

The Carcharhinidae are one of the most diverse shark families, including species of maximum lengths of less than one metre to over six metres in length, and being very significant components of a large proportion of tropical and subtropical marine ecosystems. Within the Carcharhinidae, the genus *Carcharhinus* (s.l.) is both speciose and widely distributed; whilst the majority of species occur in tropical shelf seas, others are present in the open ocean, temperate shelf areas and, in the case of the bull shark, *Carcharhinus leucas*, entering freshwater. There is some degree of variation in the overall anatomy between species of *Carcharhinus*, which also demonstrates a great diversity in tooth morphology. Although it is likely that the species traditionally placed in *Carcharhinus* (s.l.) should be regarded as members of a number of closely related, but separate, genera there is no consensus as to how the nominal genus should be divided. Whilst many species of *Carcharhinus* (s.l.) have blade-like upper teeth with strong serrations with rather more slender lower teeth, some species have a more homodont dentition of slender teeth, although these are still typically serrated.

2. THE EARLY FOSSIL RECORD OF CARCHARHINUS

Despite the importance of the carcharhinid sharks, the group evolved relatively recently in comparison to most other living shark clades. Teeth of small members of the Carcharhinidae are first recorded from the Late Cretaceous (Underwood and Ward, 2008), but the family does not become abundant or diverse until the Paleocene.

Paleogene teeth that have been referred to

Carcharhinus fall into several distinct morphologies. Slender teeth that lack distinct serrations and have a low, smooth lateral part of the crown have been referred to in the literature as *Carcharhinus*, *Negaprion* and *Aprionodon*. *Negaprion* is an extant carcharhinid genus related to *Carcharhinus*, and possibly forming a basal sister taxon to it (e.g., Human et al., 2006). *Aprionodon* is based on the extant species *Carcharhinus isodon*, which was synonymised with *Carcharhinus* by Garrick (1985). Despite this, teeth of *C. isodon* are distinct in being slender and lacking any serrations (being very similar to teeth of *Negaprion*) and it is possible that *Aprionodon* should be considered as valid. Paleogene teeth of this morphology are here referred to as *Negaprion* following Underwood et al. (2011). A second morphology of teeth, also variously referred to *Carcharhinus*, *Negaprion* or *Aprionodon*, is similar but with a somewhat more compressed and wider cusp in some (upper) teeth and a distinct notch at the base of the cusp with the lateral parts of the crown being blade-like with various degrees of incipient to weak serration. These teeth are here referred to as cf. *Negaprion* due to their similarities to teeth of larger individuals of the extant *N. brevirostris*, but further study may suggest that a separate genus should be erected for teeth of this general form. Teeth of a similar general morphology but with regular serrations on much of the upper teeth (as in the extant *C. limbatus* and *C. brevipinna*) appear to be absent in the Paleogene. Other teeth of taxa referred to *Carcharhinus* show strong dignathic heterodonty, with broad and serrated upper teeth and more slender lower teeth. There is great variation in the profile of the upper teeth and form of the serrations in modern species of *Carcharhinus*, and so all of the teeth of this

general morphology are here referred to *Carcharhinus*, although it is acknowledged that further work on extant species of the genus may result in the erection of new genera, some of which may be present in the Paleogene.

The earliest known occurrence of teeth referred to *Carcharhinus* (s.l.) is in rocks of basal Middle Eocene (basal Lutetian) age of Morocco (*Negaprion marcaisi* (Arambourg, 1952)) and Lutetian of Seymour island Antarctica (Kriwet, 2005). *N. frequens* (Dames, 1883) is very common in the late Bartonian and Priabonian of Egypt (e.g., Underwood et al., 2011). Note that study of material from the type locality of *N. frequens* (pers. obs.) revealed that Underwood et al. (2011) were in error due to the poor quality of figures in the original description, and the small species they refer to as *N. sp.* is *N. frequens*, and not the larger species that they refer to *N. frequens* in the publication. Teeth of cf. *Negaprion amekiensis* (White, 1926) were considered to have come from the Middle Eocene of Nigeria, but the rocks are likely to be Late Eocene in age (King, pers. comm.). These may then be of a similar age to cf. *Negaprion* sp. from the mid to late Priabonian of Egypt (e.g., Underwood et al., 2011, as *Negaprion frequens*, Adnet et al., 2011, as *Carcharhinus* sp. or *Negaprion* sp.) and Morocco (Adnet et al., 2010). Teeth of cf. *N. gilmorei* (Leriche, 1942) were originally considered to have come from the Ypresian of Alabama, but this species is present in the Priabonian (Cicimurri and Knight, 2009) and so the type material is considered to be incorrectly dated. Manning (2006) recorded cf. *N. gilmorei* in the Late Eocene and Early Oligocene of the Gulf Coastal Plain, USA. Additional Early Oligocene species of cf. *Negaprion* include cf. *N. gibbesii* (Woodward, 1889) (the Late Eocene age stated for the type material was considered in error by Cicimurri and Knight, 2009), cf. *N. elongatus* (Leriche, 1910) and two species from Pakistan (as *Carcharhinus* sp. 1 and 2, Adnet et al., 2007).

Teeth from a heterodont *Carcharhinus*-like taxon are known from the mid Lutetian of southern England (e.g., Kemp et al., 1990), but these are small and not typical for extant members of *Carcharhinus*, with the upper teeth being only partially serrated. In Egypt, the first *Carcharhinus* s.s. teeth are in rocks of latest Bartonian age with rare specimens of a finely serrated species (Underwood et al., 2011) and do not become common until the mid Priabonian when a more coarsely serrated species becomes common; this species is also present in Morocco (Adnet et al., 2010, as *Carcharhinus* sp.) in rocks that are probably of similar age. Reports of this species (as

Carcharhinus sp. 1) in the Gehannam Formation (latest Bartonian to lower Priabonian) by Case and Cappetta (1990) are almost certainly in error. A tooth of *Carcharhinus* sp. (as *Galeocerdo* sp, Bajpai and Thewissin, 2002, fig. 2f) supposedly from the Ypresian of India is almost certainly incorrectly dated, as evidenced by presence of *Galeocerdo eaglesomi* (Bajpai and Thewissin, 2002, fig. 2g), which is elsewhere restricted to the late Lutetian to Priabonian. This *Carcharhinus* may be synonymous with *C. balochensis* (Adnet et al., 2007) from the Priabonian of Pakistan. Early Oligocene examples of *Carcharhinus* include *C. perseus* (Adnet et al., 2007) from Pakistan and an unnamed species (figured as a lamniform) from non marine facies in Egypt (Murray, 2004); it is possible this is a specimen of *C. balochensis*.

As well as published occurrences of Eocene *Carcharhinus*, teeth of a coarsely serrated species are common in the Bartonian of Little Stave Creek, Alabama (David Ward, pers. comm.). In addition, specimens in the Natural History Museum, London, labelled as "*Carcharhinus songoensis*" represent material of a supposed Eocene species from Sierra Leone that was never published. Several species of carcharhinids are also present near the Eocene-Oligocene boundary in Baja California, Mexico (pers. obs.) but have yet to be described.

Some other early occurrences of *Carcharhinus* appear to be in error. *Carcharhinus* cf. *macloti* was recorded (but not figured) by Hulbert et al. (1998) from the basal Bartonian of Georgia, although there are no other records of *Carcharhinus* in similar aged rocks of that region and this record is probably in error. Material described as *Negaprion kraussi* Probst, 1878, by Case and Borodin (2000), from the Middle Eocene of North Carolina appears to be based on *Physogaleus* or *Abdounia*. The type material of *Aprionodon woodwardi* Leriche, 1905, from the Lutetian of Belgium is considered by Cappetta (2006) to represent a tooth of *Physogaleus*.

3. GEOLOGICAL SETTING

A single upper lateral tooth embedded in a matrix of ferruginous sandstone was recovered during a field excursion hosted by the Petroleum Corporation of Jamaica (August 9th-11th, 2011) which sought to highlight the petroleum potential of the island. The tooth was recovered in place from a fossiliferous bed within the Guys Hill Formation of the Yellow Limestone Group exposed at Broomwell (**Figure 1**). The Guys Hill Formation (formerly the Guys Hill Member of Burke et al., 1969) consists of a succession of quartz-rich fine- to medium-grained

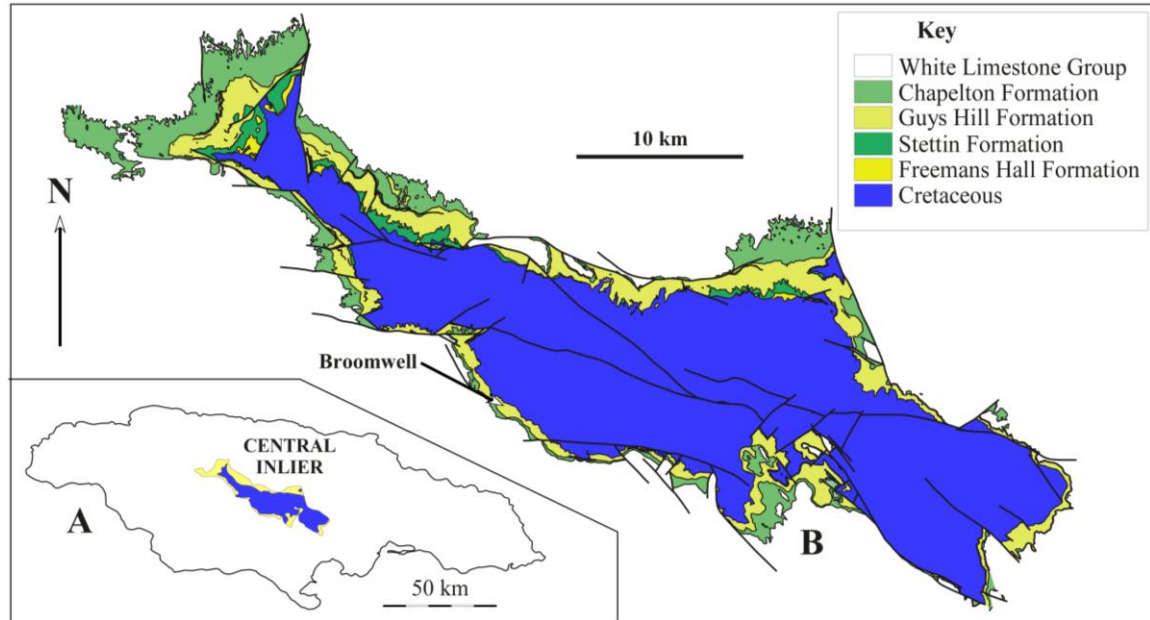


Figure 1. Locality map showing location of Central Inlier in Jamaica (A) and location of the Broomwell locality near the Central Inlier (B). Modified from Mitchell (2003).

siliciclastic sandstones and fine-grained conglomerates exposed on the margins of the Benbow and Central inliers (Robinson and Mitchell, 1999). The cross-bedded sandstones are associated with mudstones which locally contain lignitic or bituminous shales (Robinson, 1996; Matchette-Downes and Mitchell, 2005) and the succession has been interpreted as a tide-dominated estuarine complex (Maharaj and Mitchell, 2000). The small scale of the exposure prevented the exact stratigraphic context of the site being recorded.

Although the sands of the Guys Hill Formation are generally unfossiliferous, an irregularly developed limestone (Dump Member of Robinson and Mitchell, 1999) contains an ostreid-rich fauna with a distinctive larger benthic foraminiferal assemblage (Assemblage 3 of Robinson and Mitchell, 1999, comprising *Yaberinella hottingeri*, *Pellatispirella* & *Eulinderina subplana*). Robinson and Mitchell (1999) have interpreted that assemblage as being indicative of the lower part of Zone 2A of Robinson (1993), which is Lutetian in age. Based on the presence of ostreid fragments within the horizon from the specimen site, the horizon could represent the lateral equivalent of one of the many limestones exposed in the Broomwell area. Some workers consider the specimen locality to be lower than the Dump Member (R. Coutou and S. Mitchell, pers. com. Dec. 2012) and a definitive correlation of the many limestone exposures found around Broomwell will have to await further detailed study. If this tooth is from a horizon equivalent to, or lower than, the

Dump Member, it would represent the oldest occurrence of a true *Carcharhinus*.

4. SHARK TOOTH

Order Carcharhiniformes
 Family Carcharhinidae
 Genus *Carcharhinus* s.l.

Carcharhinus sp. (Figure 2)

Description. Only the labial face of the tooth is exposed. The tooth is 12 mm high and 13 mm wide and comprises a wide and oblique cusp above a relatively low root. The cusp is not clearly demarcated from the rest of the crown, but the width of the base of the cusp is about half of the total tooth width, with the cusp being somewhat longer than wide. The tooth is strongly labio-lingually compressed, with a weakly convex labial crown face. The cusp is distally inclined, with the tip reaching close to above the distal edge of the tooth. A well-developed cutting edge is present along the mesial edge of the tooth crown, from the mesial edge of the tooth to the cusp apex. The profile of this edge is weakly sigmoidal, being concave close to the cusp base and convex on the cusp. Well-developed but irregularly sized serrations are present along this mesial edge, being largest on the lower part of the crown and decreasing in size towards the apex. The serrations have rounded terminations and there are typically three to four serrations per millimetre. The distal edge of the

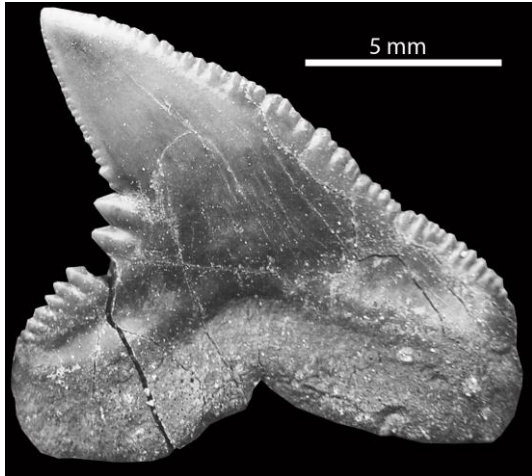


Figure 2. Labial view of upper tooth of *Carcharhinus* sp. (University of the West Indies Geological Museum UWIGM 2012.03.01)

cusps are faintly convex and have very small and regular serrations with about 12 serrations per millimetre. At the distal base of the cusp is a sharp angle after which the distal part of the crown slopes towards the tooth edge. Along this distal crown are nine large and regular serrations (one missing) that are triangular in profile and decreasing in size distally. The base of the crown on the labial tooth face is slightly swollen and weakly overhangs the root. The basal crown edge is somewhat 'V'-shaped, being highest near the centre of the tooth. The root is divided into two poorly defined lobes, with the base of the root paralleling the basal edge of the crown. The mesial and distal edges of the root are rounded.

Discussion. Fossil fish are relatively rare components of the Jamaican fossil record, even from horizons which are otherwise highly fossiliferous (Donovan and Gunter, 2001; Underwood and Mitchell, 2004). Only the Late Pliocene Bowden shell bed, from which a diverse collection of otoliths has been recorded, stands out as an exception (Stringer, 1998). This report represents the first well-documented fossil shark find from the Eocene of Jamaica as the earlier report of *Carcharias* sp., postulated to have been from the Chapleton Formation, was based on a single UWI Geology Museum specimen of unknown locality (Donovan and Gunter, 2001).

No other described species of *Carcharhinus* from the Eocene or Early Oligocene has the overall tooth shape, continuous and irregular serrations and large distal serrations seen in this species, and it is therefore clearly a species that has not previously been named. Upper teeth of the undescribed species from Little Stave Creek most closely resemble the

specimen here, but these have more regular serrations and lack the greatly enlarged distal serrations. Undescribed teeth from the British Lutetian (Kemp et al., 1990) are also similar to the Jamaican specimen in overall form, but differ in being smaller, more gracile and being incompletely serrated. The serration pattern is similar to that seen in some Paleogene species of *Galeocerdo* (many of which are probably best not considered as congeneric with the extant *G. cuvier*), but the overall tooth and root profile are rather different from any *Galeocerdo*, whilst the serrations of *G. cuvier* and related forms are compound, unlike the serrations seen here.

5. PALAEOBIOLOGY AND DISTRIBUTION OF EARLY *CARCHARHINUS*

The majority of Eocene records of *Carcharhinus*, *Negaprion* and cf. *Negaprion* are from Tethyan regions (Jamaica, Morocco, Egypt, India, Pakistan, Mexico, southern USA), despite the high level of study of rocks of this age from boreal Europe and North America. It therefore appears that the initial radiation of the larger carcharhinids was within the Tethyan realm, to some extent mirroring their Recent occurrence, which is centred on tropical and subtropical areas. The majority of modern species of *Carcharhinus* are inshore to mid shelf neritic or coastal pelagic, with several species being strongly reef associated (e.g., Compagno, 1988; Musick et al., 2004). There are a small number of oceanic pelagic taxa, and only one species of *Carcharhinus*, in addition of several species of the related genus *Glyphis*, that enter marginal marine to freshwater environments. Despite the small number of species of carcharhinids inhabiting marginal marine habitats today, several of the Paleogene examples, including the specimen described here come from shallow inshore to restricted marine facies (Underwood et al., 2011), or from facies with high degrees of fluvial influence (Murray, 2004; Murray et al., 2010). Where Paleogene carcharhinids are present within rocks deposited in inshore to marginal palaeoenvironments, they are typically more abundant and diverse than lamniform sharks, which typically dominate in more offshore facies of this age (e.g., Underwood et al., 2011). It is therefore possible that the initial radiation of *Carcharhinus* and related larger carcharhinids (such as *Negaprion*, cf. *Negaprion* and *Misrichthys*) occurred within Tethyan regions, with their propensity to colonise shallow and even brackish water allowing them to colonise environments where lamniforms with similar cutting dentitions were largely absent (lamniforms inhabiting inshore environments

apparently being largely restricted to taxa with clutching-type dentitions living in boreal regions).

6. CONCLUSIONS

Whilst the material described here represents only a single tooth, this gives clear evidence of one of the earliest occurrences of the shark genus *Carcharhinus*. This presence of this specimen reinforces the idea that *Carcharhinus* and related genera arose as a dominantly Tethyan clade, several members of which inhabited shallow to marginal marine environments. Critical review of previous reports of *Carcharhinus* remains in the

Eocene suggests that many reports of the genus have been either incorrectly dated or based on misidentification of other genera.

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