SHARKS, BONY FISHES AND ENDODENTAL BORINGS FROM THE MIOCENE MONTPELIER FORMATION (WHITE LIMESTONE GROUP) OF JAMAICA

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Bulk samples of Miocene carbonate sediments (deep-water chalks and shallow-water-derived calcarenites) from the Montpelier Formation (White Limestone Group) in Duncans Quarry, Jamaica, have yielded a small, but diverse, fauna of disassociated fish remains. Shark remains include the teeth of five species, four of which are squalids. A diverse, but taxonomically indeterminate, osteichthyan tooth assemblage is also present. A number of the teeth contain microborings of two ichnotaxa. The assemblage is considered to be typical of a deep-water continental slope fauna, and indicates an abrupt northern margin of the Miocene shallow-water carbonate platforms.

Key words – Montpelier Formation, White Limestone Group, fish faunas, Miocene.

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INTRODUCTION

Although fish comprise very important elements of the vast majority of marine ecosystems, their study has typically been extremely piecemeal. The bulk of well-described fossil fish assemblages comprise either unusually rich concentrations of chondrichthyan teeth (often at hiatal levels) or exceptionally well-preserved assemblages of bony fish preserved as largely complete skeletons (often within atypical depositional settings). Despite these biases within the described fossil fish record, isolated fish remains, especially teeth, are present within many fossiliferous marine sedimentary rocks and represent a significant component of fossil biotas.

Deep-water fish assemblages are poorly known and have rarely been described in detail. This is especially true of bony fish faunas, where little work has been carried out on the tooth morphologies present within the different taxonomic groups. Deep-water shark assemblages are known from several levels within the Neogene, such as the Miocene of southern France (Ledoux, 1972) and the Pliocene of northern Italy (Cigala-Fulgosi, 1986). These assemblages are typically dominated by diverse squaliformes and deep-water lamniformes, along with some pelagic taxa.

In this paper, a deep-water fish assemblage from the Miocene limestones of the Montpelier Formation (White Limestone Group) at Duncans Quarry is described. All specimens carry requisition numbers of the Florida Museum of Natural History, University of Florida, Gainesville (UF).

PREVIOUS WORK AND GEOLOGICAL SETTING

There has been relatively little work on the Neogene fish assemblages from Jamaica. Eyles (1958) recorded abundant, small fish teeth from a phosphate band at the base of the bauxite deposits, that rests on the shallow-water limestones of the White Limestone Group. Purdy *et* *al*. (1996) recorded shark teeth from the Pleistocene of Jamaica. Stringer (1998) described teleostean ootoliths from the Pliocene Bowden Shell Bed. Donovan and Gunter (2002) described several large teeth found in the Geology Museum at the University of the West Indies, but without locality or age data. The presence of a small, but diverse, assemblage of fish teeth from the Montpelier Formation, therefore, adds considerably to this dataset.

The Montpelier Formation (White Limestone Group) of Jamaica consists of deep-water chalks and calcarenites that contain bands of nodular chert and bentonite clay bands (Mitchell, 2003). The Montpelier Formation is well-exposed in Duncans Quarry, which is situated on the north coast of Jamaica some 5 km west of Duncans (Fig. 1). About 50 m of the Montpelier Formation is exposed in the quarry. The lower part consists of deep-water chalks with chert bands and thin bentonites, and the upper part, deep-water chalks with abundant graded calacrenite beds. The graded calcarenites contain sand-grade carbonate that includes faunal elements, such as larger benthic foraminifera, derived from the nearby platform carbonate successions of the Clarendon Block (Fig. 1). The deep-water sediments at Duncans Quarry are of Miocene age (Steineck, 1974; Donovan *et al.*, 1995). The fish assemblages described in this paper were picked from bulk samples collected by Roger Portell (Florida Museum of Natural History) from the upper part of the succession at Duncans.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880

Order Squaliformes Goodrich, 1909

Remarks – It is possible that the Order Squaliformes as defined by Compagno (1973) is paraphyletic (e.g., Shirai, 1996).

Genus *Deania* Jordan and Snyder, 1902

Type species – *Acanthidium calceum* Lowe, 1839; Recent.

Deania sp.

Plate 1, Figs 1-2

1972 *Deania calceus* (Lowe) – Ledoux, p. 149-153, figs 7-8.

Material – One lower tooth: UF206535.

Description – The tooth is somewhat higher than wide and strongly compressed. A large principal cusp is directed towards the posterior, the apical part overhanging a small distal heel. An elongate, but narrow labial apron reaches almost to the base of the root, and has large foramina on its anterior and posterior side. The lingual face of the root has a pair of well-developed foramina above a narrow anterio-basally directed groove. A large indentation is present on the posterior part of the root lingual face. A strongly compressed flange projects from the anterior side of the root.

Comparisons – This single lower tooth appears almost identical to teeth described as *Deania calceus* (Lowe) by Ledoux (1972). These teeth differ from those of extant *D. calcea* figured by Herman *et al.* (1989) in having a deeper root, less erect cusp with a more convex cutting edge and narrower labial apron. These teeth can be distinguished from those of *Centrophorus* in having clearly separated lingual foramina and no lingual protuberance.

Genus *Squaliolus* Smith and Radcliffe, 1912

Type species – *Squaliolus laticaudus* Smith and Radcliffe, 1912; Recent.

Squaliolus schaubi (Casier, 1958)

Plate 1, Figs 3-9

1958 *Centroscymnus schaubi* Casier – Casier, pl. 1, fig. 11.

1972 *Squaliolus schaubi* (Casier, 1958) – Ledoux, fig. 11.

Material – One partial and three near complete lower teeth: UF 206537, 206538, 206539, 206464.

Description – Although all of the teeth recorded of this taxon are from the lower dentition, there is some degree of variation due to differing positions on the jaw. The teeth are considerably higher than wide and very strongly compressed. The principal cusp is very low and short, with a strongly convex anterior edge. This cusp completely overhangs the small distal heel. The lingual face of the tooth is flat, but with a recessed posterior section below the distal heel. A very well-developed foramen is roughly in the centre of the lingual face, immediately below the lower edge of the enameloid crown. The labial face of the tooth has an extensive enameloid covering, other than within a recessed region comprising approximately the anterior third of the tooth, the upper edge of which forms a strongly arcuate anterobasal edge of the crown. A very well-developed foramen in the lower part of the labial face forms the upper limit of a distinct groove, which in turn forms a notch on the root basal edge. This foramen and groove are separated from the anterior recess by a narrow ridge of enameloid. Several small foramina are present posterior to the labial groove.

Comparisons – These teeth appear almost indistinguishable from lower teeth of *S. schaubi* figured by Ledoux (1972), although no associated upper teeth or more erect (?male) lower teeth, as noted by Ledoux (1972), were recorded in this study. These teeth may be separated from the extant Atlantic species of *Squaliolus, S. laticaudus* (Smith and Radcliffe) as figured by Herman *et al.* (1989), by the lower and shorted principal cusp and more rectangular overall shape. Teeth of this taxon may be separated from those of the closely related genus *Euprotomicrus* Gill by the presence of a better developed labial anterior recess and a narrower labial groove.

Squaliolus sp.

Pl. 1, Figs 10-11

Material – One lower tooth: UF206536

Description – This single lower tooth is very strongly compressed and has a basal edge at an angle to the anterior and posterior edges of the tooth, giving an overall rhombic shape with a distally directed root. There is a large and erect principal cusp with a straight anterior edge and a very small distal heel. The flat lingual face of the root has a very large central foramen and a posterior recessed region, which is somewhat narrower than the distal heel above it. The labial face of the tooth has narrow anterior recessed region, the upper edge of which forms a strongly notched anterobasal edge of the crown. A very well-developed foramen in the lower part of the labial face opens into a strong groove. This foramen and groove are separated from the anterior recess by a narrow ridge of enameloid. Two small, oval foramina are present posterior to the labial groove.

Comparisons – This tooth is larger that any known lower tooth of *S. schaubi*, and differs in having a far larger and more erect cusp. The narrow labial groove suggests an affinity with *Squaliolus* rather than *Euprotomicrus* or *Heteroscymnoides* Fowler.

Genus *Scymnodon* Bocage and Capello, 1864

Type species – Scymnodon ringens Bocage and Capello, 1864; Recent.

Scymnodon aff. **obscurus** (Vaillant, 1888)

Pl. 1, Figs 12-17

Material – Two upper teeth, one partial and one complete: UF206534, 206553.

Description – These teeth comprise a larger, if somewhat damaged, anterior tooth and a smaller lateral tooth. In the lateral tooth (where the crown is well-preserved), the single cusp is elongate, about four times as long as wide, and slightly posteriorly inclined. A cutting edge is present along both sides of the cusp, except for within a slightly constricted 'collar' at the base of the cusp. This cutting edge separates a fairly flat labial face from a strongly convex lingual face. The preserved part of the cusp of the anterior tooth is similar, differing only in the possession of two faint ridges on the basal part of the labial face and lacking posterior inclination. The root of both teeth is strongly bilobate, with a distinct notch on the basal edge. The lingual face is flat and has a pair of well developed foramina, one at the base of the cusp and one within the basal notch. The labial edge is more convex with several small marginal foramina. The root lobes of the anterior tooth are similar in size and oval in lingual view. There is strong asymmetry of the root lobes of the lateral tooth, with an anterior pointed lobe and a posterior lobe of almost rectangular lingual profile.

Comparisons – The upper teeth of heterodont squaliformes are very variable in form between species, and often bear little resemblance to the lower teeth of the same taxa. The teeth recorded here appear extremely similar to upper teeth of *Scymnodon obscurus* (Vaillant 1888) figured by Herman *et al*. (1993). The strongly bilobed root and rather oval root lobes separate upper teeth of this taxon from those of other species of *Scymnodon* (Herman *et al*., 1989, 1993). These teeth can be separated from the rather similar upper teeth of *Squaliolus*, *Euprotomicrus* and *Heteroscymnoides* by the presence of a constriction at the base of the cusp, pronounced notch between the root lobes and lack of a deep excavation at the base of the cusp on the labial face. These teeth do not therefore appear to be conspecific with any of the lower teeth recorded in this study, this not being unsurprising considering the low total number of specimens.

?Squaliforme indet.

Pl. 2, Figs 1-2

Material – One scale: UF206474.

Description – The roughly diamond-shaped face of this scale is ornamented with several longitudinal ridges. The scale is low with no well-defined neck, but somewhat concave lateral faces are ornamented with a very weak reticulate pattern.

Comparisons – Selachian scales are generally regarded as poorly diagnostic, but the scale recorded here is of typical squalid form, being similar to scales of many Recent and fossil (e.g., Cappetta, 1980; Ledoux, 1972) heterodont squalids.

Order Carcharhiniformes Compagno, 1973

Genus *Carcharhinus* Blainville, 1816

Type species – *Carcharias melanopterus* Quoy and Gaimard, 1825; Recent.

Carcharhinus sp.

Pl. 2, Fig. 3

Material – One partial upper tooth: UF206554.

Description – This single isolated cusp is triangular, being rather higher than wide, and robust. Both lingual and labial faces are convex and unornamented, being separated by a well-developed cutting edge. The cutting edge is lightly and irregularly serrated other than at the extreme apex.

Comparisons – The robust and serrated shape of the cusp suggests that this specimen represents an upper tooth. Although there is great variation in the dentition of different species of *Carcharhinus*, identification of different species is extremely difficult even when dealing with intact teeth (e.g., Purdy *et al.*, 2001). This specimen must therefore be regarded as indeterminate.

Class Osteichthyes Huxley, 1880

Remarks – Although some teeth of osteichthyans are highly characteristic, in general isolated dental remains of osteichthyans are probably best regarded as being of relatively little taxonomic use. This is especially true of deeper-water fishes, where strong convergence is seen within relatively simple teeth morphologies. The difficulty in applying standard taxonomic methodology to isolated dental material of deep water osteichthyans (ichthyoliths) has lead to the development of generic descriptive methods for this material (see Doyle and Riedel, 1985). This generic descriptive terminology is here regarded as clumbersome and is not followed within this study. Despite this general difficulty in assigning taxonomic position to the isolated osteichthyan teeth described here, it may be possible to tentatively assign the molariform teeth of Tooth type 8 of this study to the Sciaenidae.

Tooth type 1.

Pl. 2, Fig. 4

Material – One partial tooth: UF206540.

Description – Although missing the apex, this tooth is extremely elongate. It is gently curved and oval in cross section. A narrow and delicate cutting edge is present on the upper part of the posterior edge of the tooth

Tooth type 2.

Pl. 2, Fig. 5

Material – Several teeth including UF206541.

Description – These teeth are high and somewhat curved, sometimes faintly sigmoidally. The tooth is oval in cross section and hollow for a large proportion of its length. A small clear enamel tip is present, which is expanded posteriorly into a short cutting edge. This cutting edge takes up less than a third of the posterior edge, terminating sharply to form a distinct barb.

Tooth type 3.

Pl. 2, Fig. 6

Material – One tooth: UF206478.

Description – The tooth is elongate and somewhat laterally compressed. The anterior edge of the tooth is rounded for the lower two thirds, with a well-developed cutting edge in the upper part. The base of the anterior cutting edge is coincident with a slight posterior curvature. A well-developed cutting edge is present along the entire posterior edge.

Tooth type 4.

Pl. 2, Fig. 7

Material – Frequent teeth including UF206477.

Description – These high and triangular teeth are very strongly compressed. Well-developed cutting edges are present on both sides of these symmetrical teeth. The preserved part of these teeth is composed entirely of clear enamel, with a conical basal cavity being clearly visible.

Tooth type 5.

Pl. 2, Fig. 8

Material – One tooth: UF206542.

Description – The single tooth of this morphology is triangular and very strongly compressed. A weakly-developed cutting edge covers both the convex anterior edge and the concave posterior edge. The central part of the tooth is taken up with a large basal cavity. There is no obvious clear enamel cap.

Tooth type 6.

Pl. 2, Fig. 9

Material – Several teeth including UF206480.

Description – These somewhat elongate teeth are round in cross section and have slight curvature. A small conical clear enamel cap is present.

Tooth type 7.

Pl. 2, Fig. 10

Material – One tooth: UF206476.

Description – This conical tooth is elongate with no curvature. The apex has a small and blunt clear enamel cap. The basal region is faintly flared.

Tooth type 8.

Pl. 2, Figs 11, 12

Material – Several teeth including UF206475, UF206479.

Description – Although very variable in size, molariform teeth comprise a relatively small number of different morphologies. The bulk are circular to faintly oval in occlusal view and approximately hemispherical in overall shape. A weakly developed apical boss is sometimes present. Rare examples of oval teeth have the apical boss stretched out to form a poorly-developed occlusal crest. No clear enamel tip was observed on any teeth.

ENDODENTAL BORINGS

Borings are commonly present within fossil bone material, especially that deposited within a marine setting. In many cases this boring can occur with sufficient intensity to severely damage or destroy parts of the fossil. Despite the abundance of these endodental borings, they have rarely been described.

Circular borings (?attributable to *Oichnus* Bromley).

Pl. 2, Fig. 13

Material – Borings in three shark teeth including UF206534.

Description – Widely dispersed circular holes of between 30 and 50 μm are seen on the surface of several shark teeth. They usually penetrate the root, although at least two were seen cutting the lower part of the enameloid crown. It was not possible to see the morphology of the borings within the tooth, although it is evident that they are deep and are not straight.

Comparisons – It is unclear whether these borings are the same as the flask-shaped borings in osteichthyan teeth described by Underwood *et al.* (1999). Despite the similarities in the shape and general size of the entrance holes, the deep and curved shape of the borings recorded here do not seem to be very similar to the Cretaceous borings of Underwood *et al.* (1999).

Ichnogenus *Mycelites* Roux, 1887

Type species – Mycelites ossifragus Roux, 1887; Jurassic to Miocene.

Mycelites ossifragus Roux, 1887

Pl. 2, Figs 14-15

1887 *Mycelites ossifragus* Roux – Roux, pls. 14-15, figs 1-7.

1989 *Mycelites enameloides* Martill – Martill, pl. 1.

1999 *Mycelites ossifragus* Roux – Underwood *et al.*, fig.1b-h

Material – Borings in many teeth including UF206535.

Description – These borings are relatively tubular and are generally about 5μm in diameter. Bifurcate branching present, but relatively uncommon. They are present both within the tooth and embedded within the tooth surface. These borings are seen to form irregular radiating masses up to 400 μm across.

Comparisons – Although many of the examples of *Mycelites* show a clear radial form, this is far more irregular that that of *Abeliella riccioides* Mägdefrau, 1937.

PALAEOECOLOGY

Despite the relatively small sample size, the material described here has important implications as to the water depth at the time of deposition of the Montpelier Formation at Duncans Quarry. Tropical shelf seas are typically inhabited by a diverse suite of selachians, including orectolobids, triakids, carcharhinids, rhinobatids and dasyatids. The absence of teeth of these forms and the presence of a squalid-dominated assemblage is highly indicative of deeper water environments.

All three of the genera of Squaliformes recorded during this study are basically deep water forms (e.g., Compagno, 1984; Froese and Pauly, 2001). Extant species of both *Deania* and *Scymnodon* are essentially benthopelagic inhabitants of continental slopes, being rarely found in less than 200 m of water. Although the maximum depths of many species are poorly known, most living species have been recorded at depths of between 1000 and 2000 m. Extant *Squaliolus* species are bathypelagic with well-developed luminescent organs. They undergo vertical migration, rising to about 200 m during the night and returning to between 1000 and 2000 m depth during the day. They are typically commonest near oceanic islands.

The numerous living species of *Carcharhinus* are very variable in their habitat. Although many species are present in shallow water, others are truly oceanic, living in surface waters away from land. The presence of indeterminate *Carcharhinus* is, therefore, palaeoenvironmentally undiagnostic, although teeth of oceanic taxa are to be expected within offshore deposits.

The osteichthyan assemblage is not readily interpreted due to the inherent difficulties of working with isolated teeth. Despite this, the dominance of elongate 'grasping' teeth is highly suggestive of the presence of mesopelagic and bathypelagic predators as opposed to more trophically diverse shallow-water forms.

Consequently, the fish assemblage indicates that the chalks at Duncans were deposited in water depths of more than 200 m, and possibly significantly more. This is particularly significant, since Duncans Quarry is situated only a few km north of platform margin (Fig. 1). It indicates, therefore, that there was a well-defined, fault-bounded northern margin to the Miocene carbonate platforms, similar to that of the modern north coast of Jamaica.

The presence of borings within many of the teeth is highly suggestive of significant reworking of biogenic phosphate (Martill, 1989; Underwood *et al.*, 1999). It should be noted, however, that the intensity of boring is far lower than that commonly recorded within shelfal assemblages. The implications of this are unclear, as the nature of the organisms involved in endodental boring (but see Gouget and Locquin, 1979), and the controls on the growth of these organisms, are still very poorly known.

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Figure Captions

Figure 1. Location of Duncans Quarry and its relationship to the shallow-water platforms in the Miocene.

Plates Captions

Plate 1.

Figs 1, 2. *Deania* sp., UF206535; 1, labial view. 2, lingual view.

Figs 3-9. *Squaliolus schaubi* (Casier, 1958); 3-4, UF206537; 3, labial view. 4, lingual view. 5-6, UF206538; 5, labial view. 6, lingual view. 7-8, UF206539; 7, labial view. 8, lingual view. 9, UF206464, labial view.

Figs 10, 11. *Squaliolus* sp., UF206536; 10, labial view. 11, lingual view.

Figs 12-17. *Scymnodon* aff. *obscurus* (Vaillant, 1888); 12-14, UF206534; 12, labial view. 13, lingual view. 14, lateral view. 15-17, UF206553; 15, labial view. 16, lateral view.17, lingual view.

Plate 2.

Figs 1, 2. ?Squaliforme indet., UF206474; 1, oblique view. 2, surface view.

Fig. 3. *Carcharhinus* sp.,UF206554. ?labial view.

Fig. 4. Tooth type 1, UF206540.

Fig. 5. Tooth type 2, UF206541.

Fig. 6. Tooth type 3, UF206478.

Fig. 7. Tooth type 4, UF206477.

Fig. 8. Tooth type 5, UF206542.

Fig. 9. Tooth type 6, UF206480.

Fig. 10. Tooth type 7, UF206476.

Figs 11, 12. Tooth type 8., 11, UF206475; lateral view of oval tooth. 12, UF206479; occlusal view of rounded tooth.

Fig. 13. Circular boring, UF206534.

Figs 14, 15. *Mycelites ossifragus* Roux, 1887, UF206535; 14, large ramifying mass. 15, small ramifying mass.

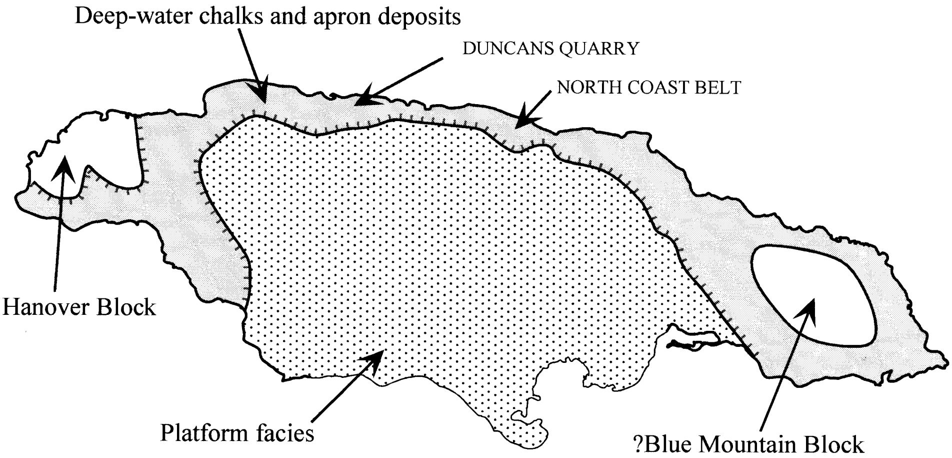
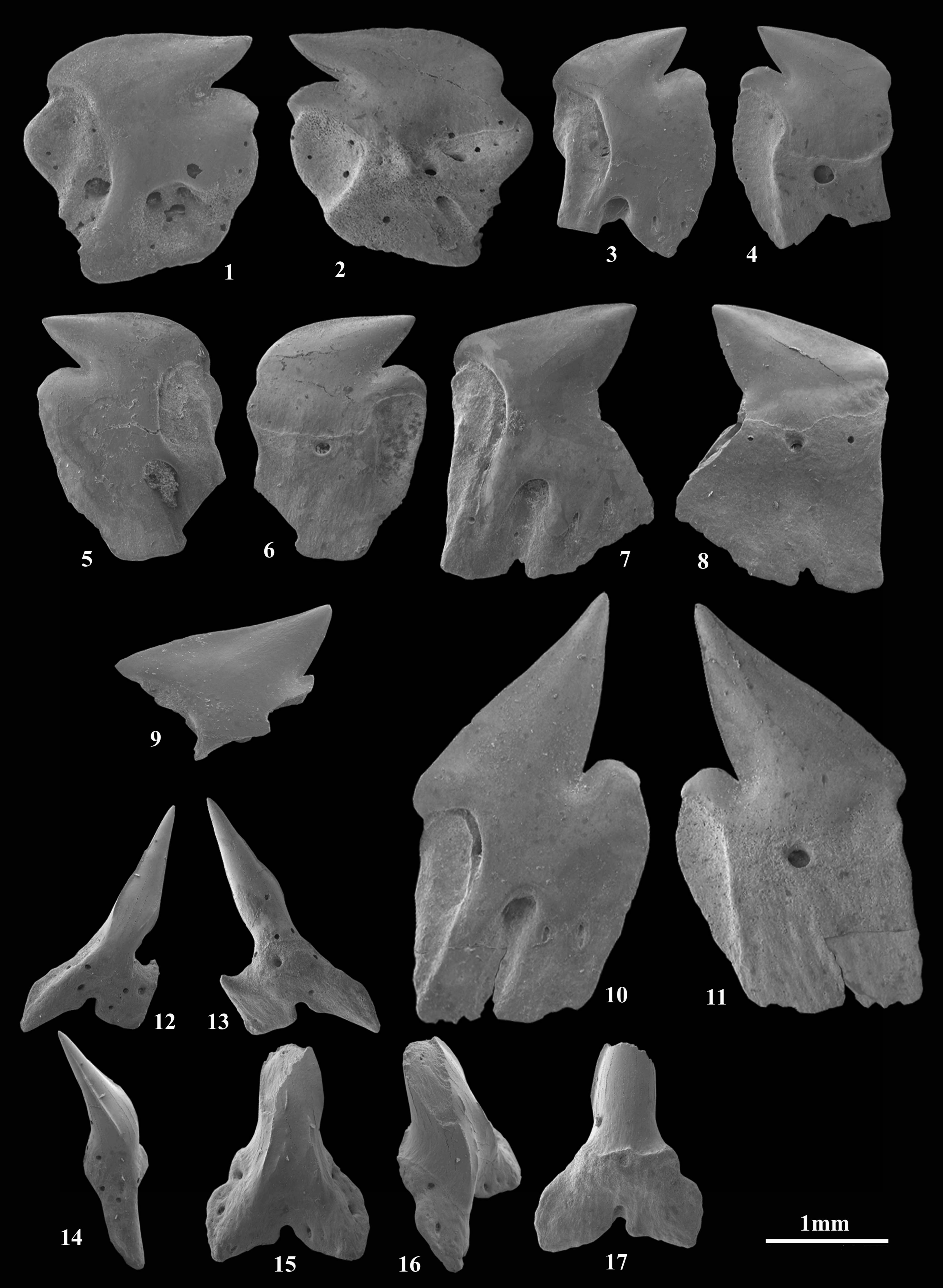


Figure 1. Location of Duncans Quarry and its relationship to the shallow-water platforms in the Miocene.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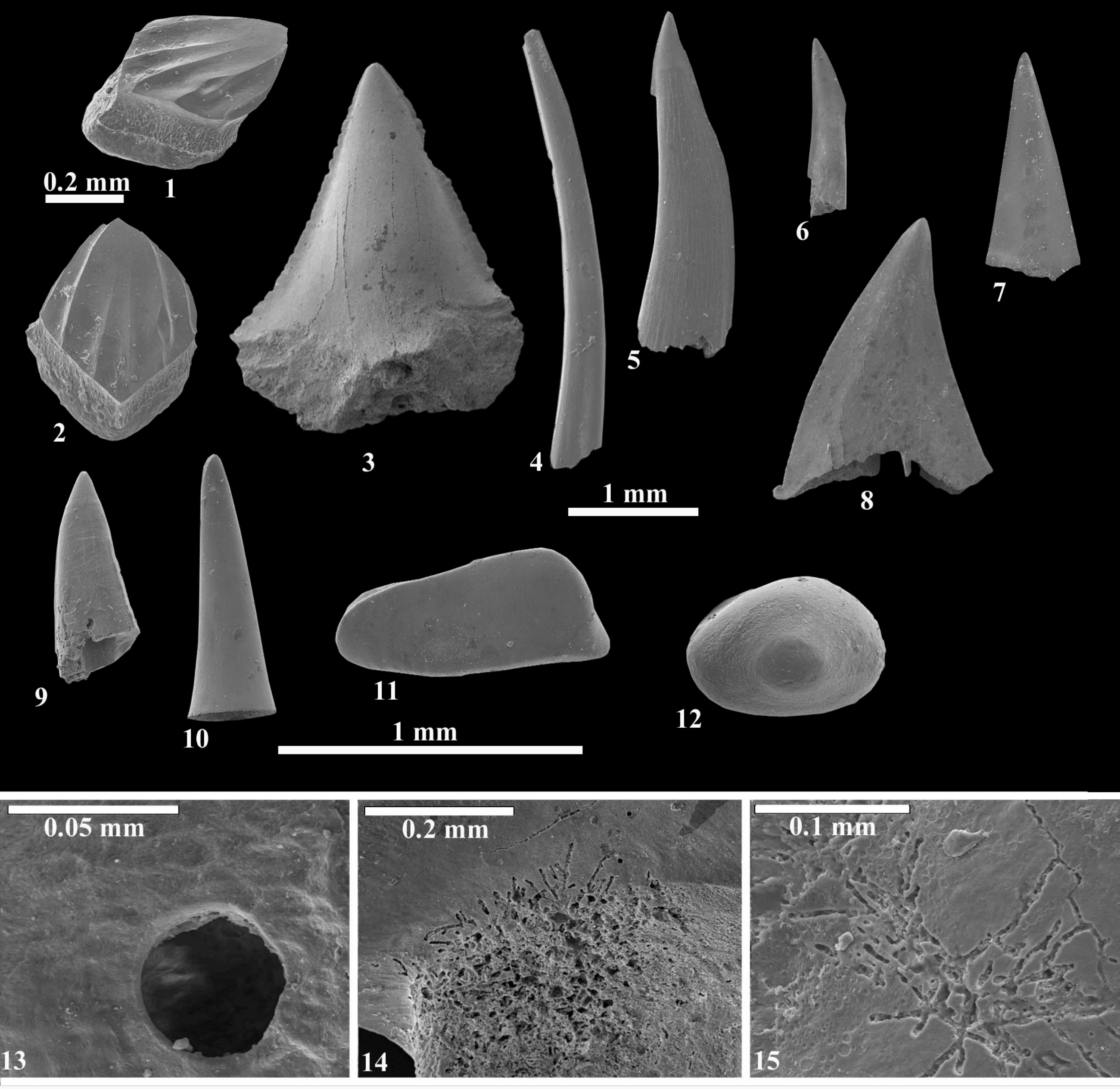
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