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ARTICLE

MARINE VERTEBRATES FROM THE ‘MIDDLE’ CRETACEOUS (EARLY CENOMANIAN) OF SOUTH INDIA

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ABSTRACT—Vertebrate fossils have been known from South India’s Cauvery Basin since the 1840s, but records of marine vertebrates from the late Albian to Turonian Karai Formation have been limited to a single set of ichthyosaur remains. Recent surface collecting and sieving of lower Cenomanian glauconitic mudstones has yielded the first ichthyosaur material reported in India over the last 140 years, as well as a diverse and previously unrecorded shark assemblage. The ichthyosaur material, including several teeth and vertebrae, is assigned to the sole described Cretaceous genus *Platypterygius* and to the species *P. indicus* (Lydekker, 1879). Eight species of shark (one squaliformes, two hexanchiformes, and five lamniformes) are recorded. A new hexanchiform genus *Gladioserratus* is erected, and two new species (*Gladioserratus magnus*, gen. et sp. nov., and *Dwardius sudindicus*, sp. nov.) are named. Many of the shark genera within this largely species-level endemic fauna are known from high paleolatitudes elsewhere, with many showing an antitropical distribution, but are absent in Tethyan areas. This first description of the Karai Formation marine fauna documents the previously unappreciated diversity and unique character of India’s Cretaceous marine vertebrates, and indicates a cool-water paleoenvironment for the marine vertebrate assemblage.

INTRODUCTION

Mesozoic fossils from the Indian subcontinent and their phylogenetic affinities have been of interest to paleontologists for well over a century (Lydekker, 1887; Sahni, 1984; Prasad and Sahni, 1988, 2009; Briggs, 1989; Thewissen and McKenna, 1992; Krause et al., 1997). Although the Indian subcontinent was united with the other Gondwanan continents throughout the early Mesozoic, the break-up of Gondwana in the Jurassic and Cretaceous periods sent India into a lengthy isolation from all other landmasses (Briggs, 2003). A united Indo-Madagascar began to separate from mainland Africa in the Jurassic; India separated from Australia and Antarctica in the Early Cretaceous, and finally from Madagascar in the early Late Cretaceous. Between the break-up of Gondwana and India’s collision with Asia in the late Paleocene–early Eocene, India traveled northward over 5000 km, experiencing a huge latitudinal gradient in a relatively short span of time. Mesozoic fossils from India are thus of interest to address a variety of questions, ranging from the dispersal patterns of major vertebrate clades to Gondwanan endemism. Some of the first Mesozoic fossils reported from India came from the Cauvery Basin (Egerton, 1845; Stoliczka, 1870–1871; Lydekker, 1879; Kossmat, 1895–1898), an immense basin of late Mesozoic to Paleogene continental and nearshore marine deposits in the south Indian state of Tamil Nadu (Blanford, 1862; Ramasamy and Banerji, 1991; Tewari et al., 1996; Sundaram et al., 2001). Although the continental Maastrichtian deposits in the Cauvery Basin have been extensively studied by vertebrate paleontologists for dinosaurian and other terrestrial vertebrate remains (Matley, 1929; Yadagiri and Ayyasami, 1987; Kohring et al., 1996; Gaffney et al., 2001), and the Lower and Upper Cretaceous marine deposits have been well studied by invertebrate paleontologists (Sastry et al., 1977; Ayyasami, 1990; Venkatachalapathy and Ragothaman, 1995; Gale et al., 2002) and paleobotanists (Venkatachala, 1977; Prasad and Pundeer, 2002), there has been little to no study of the Cretaceous marine vertebrate record of the Cauvery Basin, or elsewhere in India for that matter. The only descriptions of Cretaceous sharks from the Cauvery Basin are old and relatively inconclusive descriptions of poorly preserved material from the Upper Cretaceous (Campanian to Maastrichtian) beds of the Pondicherry region (Egerton, 1845). Here we describe a new marine vertebrate fauna from the early Cenomanian part of the late Albian to Turonian Karai Formation, including sharks and ichthyosaurs. These species expand the geographic ranges of several genera and provide the first ichthyosaur material reported from India in over a century.

GEOLOGICAL SETTING

The Cauvery Basin in Tamil Nadu, India, is a large basin of 25,000 km^2 containing late Mesozoic to Paleogene sediments deposited along India’s southeast coast (Blanford, 1862) that developed in passive margin systems following the separation of India from Australia and Antarctica during the Valanginian (137–132 Ma). Blanford (1862) divided the Cretaceous deposits of the Ariyalur region into three groups (Table 1): Uttatur, Trichinopoly, and Ariyalur. Here, we follow the terminology of the recent lithostratigraphic revision of Sundaram et al. (2001).

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TABLE 1. Cretaceous sequence of the Cauvery Basin, Tamil Nadu, India, following Sundaram et al. (2001).

Formation	Depositional environment	Age
Kallamedu Fm	Fluvial	late Maastrichtian
Kallankurichchi Fm	Shallow marine	early Maastrichtian
Sillakkudi Fm	Littoral	Campanian
Anaipadi Fm	Neritic	Turonian–Coniacian
Kulakkalnattam Fm	Shallow marine	Turonian
Karai Fm	Shallow marine	late Albian–early Turonian
Dalmiapurum Fm	Shallow marine	Albian
Arogyapurum Fm	Fluvial	Albian
Terani Fm	Fluvio-deltaic	Albian

The Uttatur Group represents a transgressive sequence of Albian to Turonian terrestrial to shallow marine deposits up to 820 m thick. The Albian deposits of the Uttatur Group include the fluvial and deltaic ‘Terani plant beds,’ the fluvial Arogyapurum Formation, and the shallow marine Dalmaipuram Formation. The Karai Formation ranges in age from late Albian to early Turonian and consists of mudstones and marls with interbedded siltstones and sandstones with local concentrations of belemnites and ammonites. The Karai Formation is divided into a lower Odiyam Member, containing the Albian-Cenomanian boundary, and an upper Kunnam Member, containing the Cenomanian-Turonian boundary. The depositional environment of the Karai Formation is interpreted as an offshore, highstand environment (Sundaram et al., 2001). The specimens reported here were surface collected from belemnite-rich mudstones of the Odiyam Member. The presence of the ammonite genera *Sharpeiceras* and *Mariella* (A. Gale, pers. comm., 2008) indicates an early Cenomanian age for the beds described here. The Karai Formation is uncomformably overlain by the shallow marine Kulakkalnattam Formation of the Trichinopoly Group. As the Kulakkalnattam Formation is of Turonian age, the unconformity probably represents a relatively small amount of time in the early Turonian (Sundaram et al., 2001).

MATERIALS AND METHODS

Surface collecting was carried out over several kilometres of Karai Formation exposures, located approximately 2.7 km northwest of Garudamanglam, Tamil Nadu, India (N11°05′01.9″; E078°55′14.1″). Vertebrate fossils were concentrated in a 0.01 km^2 area ranging from N11°05′47.9″ to N11°05′47.0″ and E078°53′58.0″ to E078°53′49.2″ (Fig. 1). The low dips and the limited exposures prevented the recording of detailed stratigraphic sections, but the fossils all originate from a glauconitic mudstone and are considered to be all from a single stratigraphic level. The majority of the fossils were recovered by surface collecting, although a few specimens were collected through screen-washing and limited excavation. Approximately 60 kg of matrix was collected and wet sieved in the field. The residues were sorted to 850 microns, with the high quantity of glauconite and ferruginous grains preventing sorting of finer fractions. Only three teeth (one of *Protosqualus*, and one each of ?*Eostriatolamia* and *Dwardius*) were collected by sieving, of which only *Protosqualus* may represent a taxon that was not pelagic. It is therefore likely that the lack of nectobenthic sharks and batoids in the fauna reflects the actual paleocommunity, and is related to an unsuitable paleoenvironment for such benthic taxa, rather than being the result of collection failure or bias.

Institutional Abbreviations—**DUGF**, Delhi University, Geology Department, Fossil Catalogue, Delhi, India; **NHMUK PV**, Department of Palaeontology, Natural History Museum, London, U.K.

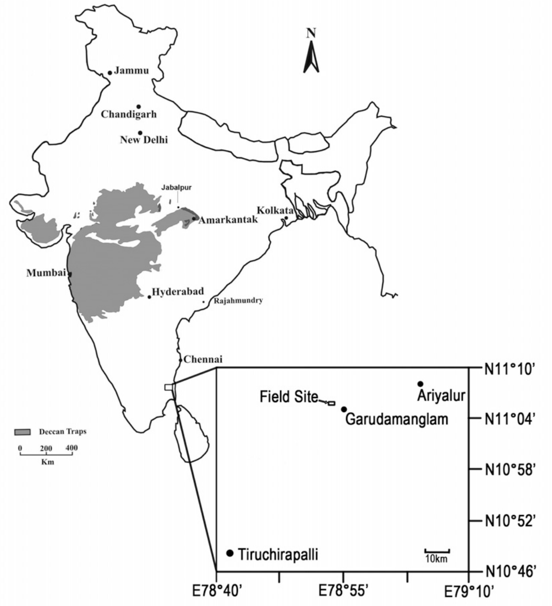

FIGURE 1. Map of India showing the location of marine vertebrate-yielding section of the Karai Formation.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order SQUALIFORMES Goodrich, 1909
Family SQUALIDAE Bonaparte, 1834
Genus *PROTOSQUALUS* Cappetta, 1977
PROTOSQUALUS sp.
(Fig. 2A, B)

Material—One incomplete tooth (DUGF/1).

Description—The single tooth recorded of this species is 2 mm wide. The crown is strongly compressed labiolingually and comprises a single highly inclined cusp that extends distally to strongly overhang the small distal heel. The mesial cutting edge of the cusp is straight for much of its length, but with a slight ‘hump’ above the point where the cusp separates from the body of the tooth. The cutting edge is weakly irregular to weakly serrated. The distal heel is rounded but also has a single weakly developed notch. The labial face of the crown is smooth and slightly convex. The labial basal edge of the crown is poorly preserved but a wide but very shallow apron is present, comprising the middle half of the tooth width. A strong crown overhang of the root is present near the distal end where preserved. The lingual face of the crown

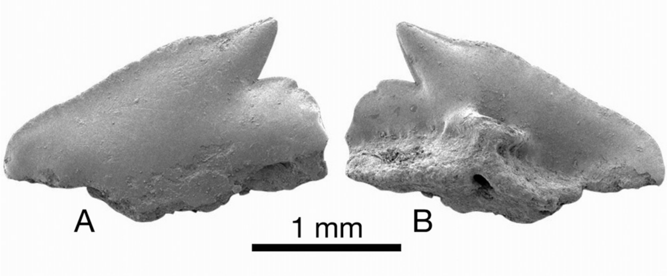

FIGURE 2. *Protosqualus* sp., DUGF/1. **A**, labial view; **B**, lingual view.

is weakly convex and somewhat indented at the contact with the root, except where the lingual bulge is present. The lingual bulge is narrow and low, but projects strongly lingually. The root is labiolingually wider than the crown and (from what can be observed in this incomplete specimen) low. The basal face is flat and there is a flared lip at the junction of the basal and lingual faces. A large infundibulum is present below the lingual bulge.

Discussion—The tooth is similar in overall size and shape to *Protosqualus sigei* Cappetta, 1977, and more closely resembles this species than any other recorded in the 'middle' Cretaceous globally. Despite this, the irregular cutting edge in this specimen is not seen in *P. sigei*, and the apron appears to be shallower than in that taxon. This specimen therefore probably represents a new species, but more material would be required prior to erecting a new taxon.

Several species of *Protosqualus* are known from the Albian and Cenomanian of northern Europe and Russia (e.g., Cappetta, 1977; Müller and Diedrich, 1991; Averianov, 1997; Underwood and Mitchell, 1999; Adnet et al*.,* 2008), but the genus is unknown from the Western Interior Seaway. It has also not been reported from tropical tethyan sites, but is present at several sites from the Albian (Kemp, 1991) and Upper Cretaceous (M. Siverson, pers. comm., 2010) of Australia. The presence of this genus in India therefore suggests an antitropical distribution pattern.

Order HEXANCHIFORMES de Buen, 1926
Family HEXANCHIDAE Gray, 1851
Genus *GLADIOSERRATUS*, gen. nov.

Etymology—From the overall serrated appearance of the tooth comprised of *gladius* (Latin for short sword)-like cusps.

Type Species—*Notidanus aptiensis* Pictet, 1865.

Diagnosis—Genus known only from isolated teeth. Moderate to strong dignathic heterodonty present and upper parasymphyseal teeth clearly differentiated. Roots of all teeth do not significantly exceed heights of crowns on labial sides. Roots of all teeth with flat labial faces and gently convex lingual faces, with a weak mesiodistal ridge just below base of crown. Root thickest and highest below base of first cusp, tapering distally, with rate of taper varying with tooth position. Upper teeth with one (in parasymphyseal teeth) to four cusps, each inclined and regularly decreasing in size distally, with first cusp more erect than successive cusps. Lower teeth with up to six cusps; first cusp in some specimens may be more erect in some specimens than in others (perhaps representing sexual dimorphism), but successive cusps decrease regularly in size distally. Cusps are biconvex, more strongly on lingual side, and with continuous cutting edge. Regular serrations of a consistent size on lower half of mesial edge of first cusp in lateral teeth of adults; serrations may be irregular or absent in upper parasymphyseal teeth and teeth of juveniles.

Age and Distribution—Cretaceous, Hauterivian to Cenomanian.

Discussion—*Gladioserratus* is erected here to encompass two species from the early and 'middle' Cretaceous that have previously been referred to the extant genus *Notorynchus* Ayeres, 1855. Although all Cretaceous specimens of *Notorynchus* described to date have been either of indefinite species assignment or placed in *N. aptiensis* (Pictet, 1865), which was referred to *Notorynchus* by Cappetta (1975) and Siverson (1997), it is possible that more than one species is present, but recognition of additional species has been hampered by the shortage of well-preserved specimens. *Notorynchus* is here considered to be well known from the Eocene (Ypresian) onwards. Two specimens from the Danian of Sweden (Siverson, 1995) have a root with a similar profile to that of *Gladioserratus*, but a crown more reminiscent of *Notorynchus.* It was noted that these teeth are "very compressed" relative to (other) species of *Notorynchus* (Siverson, 1995:5), unlike teeth of *Gladioserratus*, which are more robust and less compressed than extant or fossil *Notorynchus* teeth. These Danian teeth may be referable to an additional genus, but more material would be required for their affinity to be assessed with certainty.

Despite an overall superficial similarity, teeth of *Gladioserratus* differ from those of *Notorynchus* in several distinctive ways. Teeth of *Gladioserratus* have a lower root than those of *Notorynchus*, with the roots of teeth of the latter (other than in those from the last posterolateral position) being rectangular in profile (with only a very slight shallowing distally), and with an erect and straight mesial edge to the root, which possesses a concave notch in its upper part. The mesial edge of the root in *Gladioserratus* teeth is generally convex or with a very weak concavity. Rare teeth possessing a mesial edge to the root more similar to that of *Notorynchus* probably originate from the first lower file. Cusps of *Gladioserratus* teeth are more robust and erect than those of *Notorynchus*, and the serrations on the mesial edge of adult teeth of *Gladioserratus* are regular in size, orientation, and spacing, unlike those of *Notorynchus*, which gradually increase in size distally, with the last serration being the largest. Although no complete dentitions of *Gladioserratus* are known, it appears that the degree of dignathic heterodonty was less than in *Notorynchus*, with some teeth previously assigned to lower dentitions of *Gladioserratus* (= *Notorynchus*) *aptiensis* (e.g., Siverson, 1997; Fig. 2, I–J) being considered here to originate from the upper jaw. It is uncertain whether *Gladioserratus* was a direct ancestor or extremely close relative of *Notorynchus* (as used here) or whether the robust tooth morphology of the latter evolved convergently to facilitate the role of a more active predator in shallower water than is the case for other Hexanchiformes. The long gap in the fossil record between the two genera (from Cenomanian to Ypresian) may suggest that convergence is the more likely case.

GLADIOSERRATUS MAGNUS, sp. nov.
(Fig. 3A–J)

Etymology—*Magnus*, due to the large size of teeth relative to those of other species of the genus.

Holotype—Lower lateral tooth (DUGF/2).

Referred Specimens—Three additional virtually complete and one partial lower lateral teeth, one upper parasymphyseal tooth (DUGF/3–6).

Type Locality—Approximately 2.7 km northwest of the village of Garudamangalam, Tamil Nadu, India.

Diagnosis—In addition to generic diagnosis (above), lower lateral teeth moderately large (seen 13 to 19 mm wide) with up to six differentiated cusps. Cusps are all of similar shape and orientation and decrease in size distally, with the mesial (largest) cusp lower than root. In wider and lower teeth (maximum height half width), cusps are more broadly triangular than in narrower teeth. Mesial edge of root of all teeth, other than presumed first lower tooth, is gently convex. Mesial edge of first cusp straight or faintly convex, with six to nine serrations present on the lower half. Upper lateral teeth unknown.

Description—The upper parasymphyseal tooth is 8 mm high and comprises a narrow cusp that is curved lingually and distally rising from a massive root. The cusp is twice as high as wide, with a strongly convex lingual face and a moderately convex labial face. A weak but continuous cutting edge is present. The root has flat labial and linguobasal faces, with a curved upper edge on the linguobasal face of the root. Numerous small foramina are present on all of the surfaces of the root, most being rounded, but others becoming more elongate towards the mesiobasal edge of the labial face.

Of the lower teeth, one (the presumed first lower tooth) has a somewhat different morphology from the others. The presumed first lower tooth is 13 mm wide and the best preserved of the other teeth is 19 mm wide; the other two teeth have some damage to the root and cannot be reliably measured. All teeth are 8 to 10 mm high. Despite the difference in width to height, all teeth have six

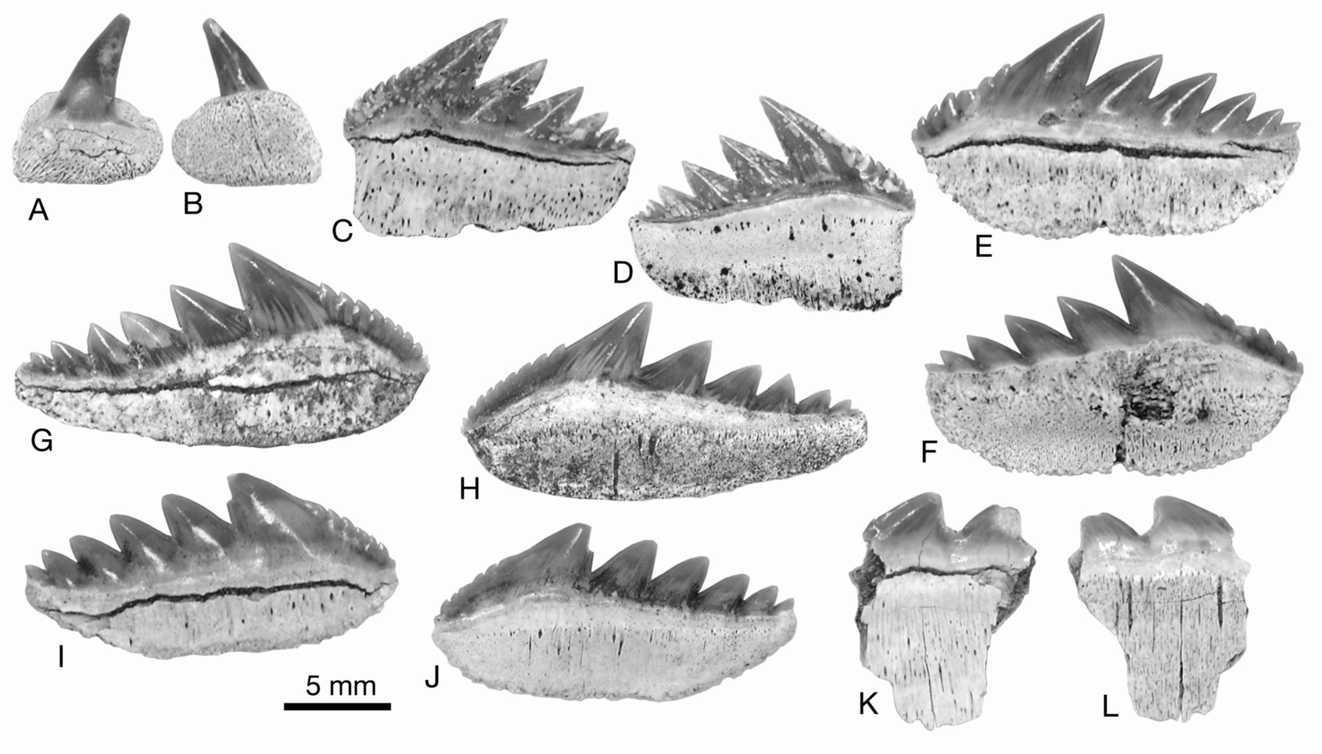

FIGURE 3. *Gladioserratus magnus* and ?*Notidanodon* sp. **A**–**J**, *Gladioserratus magnus*, gen. et sp. nov.; **A**–**B**, upper parasymphyseal tooth, DUGF/3; **A**, labial view; **B**, lingual view; **C**–**D**, presumed first lower tooth, DUGF/4; **C**, labial view; **D**, lingual view; **E**–**F**, lower lateral tooth, DUGF/5; **E**, labial view; **F**, lingual view; **G**–**H**, lower lateral tooth, DUGF/2, holotype; **G**, labial view; **H**, lingual view; **I**–**J**, lower lateral tooth, DUGF/6; **I**, labial view; **J**, lingual view; **K**–**L**, ?*Notidanodon* sp., partial tooth, DUGF/7; **K**, labial view; **L**, lingual view.

cusps, which are wider and lower in the wider teeth. Cusps of all teeth are of a similar shape and orientation and decrease in height regularly from the mesial (largest) cusp. In all teeth, the mesial edge of the first cusp is inclined at an angle of 30–35 degrees relative to the base of the root. All cusps have a quite strongly convex lingual face and a less convex labial face. There is no crown ornament, and a continuous cutting edge runs along the occlusal edge of the crown. The lower half of the mesial edge of the first cusp is straight to very gently convex, and has 6 to 10 serrations. These are evenly spaced and all of the same size and shape. Each serration comprises a convex mesial edge, the more distal part of which is parallel to the edge of the cusp, and a short distal edge that is oriented at about 90 degrees to the edge of the cusp. The serrations start at the anterobasal extremity of the crown. The basal edge of the crown is sharply defined on the lingual side, less so on the labial side, where the enameloid is thinner. The base of the crown slopes gently upwards to a point below the mesial cusp, and then slopes downwards forming a straight line to the distal end of the tooth. The roots of all teeth have a flat labial face and a more convex lingual face. Each root is thickest at a point below the base of the mesial cusp, but a weakly defined thickened ledge runs the length of the root along the lingual side. The roots of most of the teeth have a convex mesial edge and a weakly convex basal edge that slopes upwards to meet the distal end of the crown. Although this is a morphology commonly produced by damage to the root, these teeth show no damage sufficient to create this morphology. In the presumed first lower tooth the root is more angular, and the mesial edge is close to vertical and has a slight concavity near the top and forms a sharp angle with the root basal edge. The distal edge of the root arcs smoothly convexly to meet the distal edge of the crown. The roots of all teeth are strongly vascularized, although the degree of this varies between teeth. Generally there are more and smaller foramina on the lingual side of the root, most round or oval in outline, but some are very elongate and vertically orientated. Smaller numbers of vertically orientated oval foramina are present on the labial root face.

Discussion—Teeth assignable to *Gladioserratus magnus* have not been previously recognized within the array of forms formerly included within *Notorynchus*, and can be readily separated from teeth of its coeval relative, *G. aptiensis*. Relative to *G. magnus*, teeth of *G. aptiensis* have a smaller maximum size (the largest recorded being 12.9 mm; Siverson 1997), have a smaller number of cusps (four or five in lower teeth), and have cusps that in all lower teeth (other than the first file) are more elongate and gracile.

Although the type material of *Gladioserratus aptiensis* was collected from the Aptian of southern France (see Cappetta, 1975), all specimens from the Albian and Cenomanian are known from higher paleolatitudes of northern Europe (e.g., Ward and Thies, 1987; Underwood and Mitchell, 1999; Smart, 2001) or Western Australia (Siverson, 1997). It was noted by Underwood and Mitchell (1999) that *G.* (= '*N.*') *aptiensis* becomes more common in more northerly sites in England. The occurrence of a species of *Gladioserratus* in southern India in the 'middle' Cretaceous (at about 45°S during the time of deposition) is consistent with the genus inhabiting cooler paleoenvironments pertaining at this paleolatitude (given the distribution and inferred temperature preference for its close relative in northern latitudes).

Genus ?*NOTIDANODON* Cappetta, 1975

?*NOTIDANODON* sp.

(Fig. 3K, L)

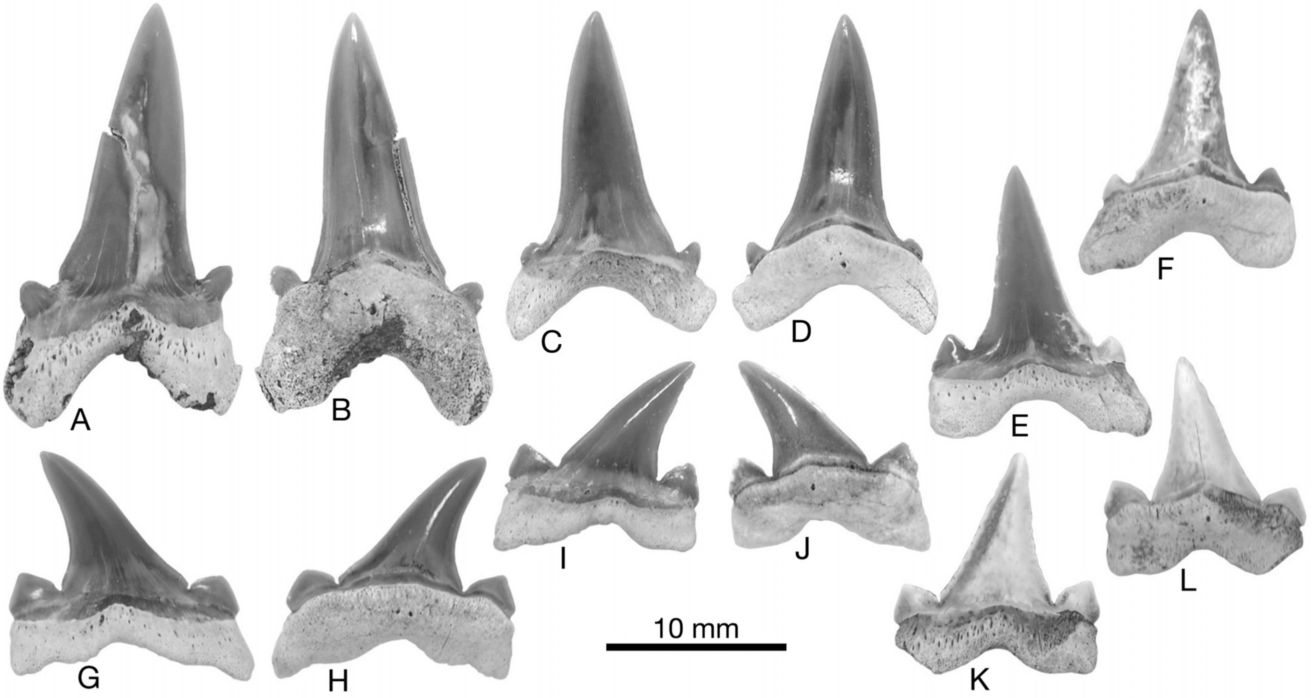

FIGURE 4. *Cretalamna appendiculata* Agassiz, 1843. **A**–**B**, ?first upper anterior tooth, DUGF/8; **A**, labial view; **B**, lingual view; **C**–**D**, ?third lower anterior tooth, DUGF/9; **C**, labial view; **D**, lingual view; **E**–**F**, ?first lower lateral tooth, DUGF/10; **E**, labial view; **F**, lingual view; **G**–**H**, upper lateral tooth, DUGF/11; **G**, labial view; **H**, lingual view; **I**–**J**, upper lateral tooth, DUGF/12; **I**, labial view; **J**, lingual view; **K**–**L**, lower lateral tooth, DUGF/13; **K**, labial view; **L**, lingual view.

Material—One tooth fragment (DUGF/7).

Description—The tooth fragment, probably from the distal part of a large lateral tooth, comprises two damaged cusps on a fragment of root and is 11 mm high. The cusps, although damaged, are wider than high and inclined distally, with the distal edge making an angle of about 90 degrees to the base of the root. The more distal cusp is somewhat smaller than the more mesial one. Both sides of the cusps are weakly convex, and there appears to be a continuous but weakly developed cutting edge. The cusps are gently inclined lingually. The root as preserved is twice as high as the crown and strongly compressed labiolingually. There is a slight ledge just below the base of the crown on the lingual side, but otherwise the lingual and labial root faces are flat. Narrow and elongate foramina are present on both sides of the root, but are more prominent and associated with numerous small rounded foramina on the lingual face.

Discussion—Although very poorly preserved, the relative size, shape, and orientation of the cusps and shape of the root suggest that this specimen represents *Notidanodon*. Teeth of Early to ‘middle’ Cretaceous *Notidanodon* specimens are known from northern Europe (e.g., Ward and Thies, 1987; Underwood et al., 1999) and California (Long et al., 1993), representing Boreal and probable oceanic upwelling environments respectively. Late Cretaceous (Campanian to Maastrichtian) examples of the genus are also known from California (e.g., Applegate, 1965) and British Columbia (D. Ward, pers. comm., 2010) as well as from high-paleolatitude sites in the southern hemisphere, including New Zealand (e.g., Woodward, 1886) and Antarctica (e.g., Grande and Chatterjee, 1987; Kriwet et al., 2006). It is evident, therefore, that *Notidanodon* was restricted to high latitudes or cooler water during the Cretaceous.

Order LAMNIFORMES Berg, 1958
Family OTODONTIDAE Glikman, 1964

Discussion—Otodontidae is a relatively poorly defined family but is here considered to be rather more inclusive than has previously been recognized, because it includes a number of Cretaceous genera in addition to the Cenozoic genera *Otodus* and *Carcharocles* (here taken to include *Megaloselachus*) typically referred to it. *Cretalamna* Glikman, 1958, has a number of derived dental characters in common with *Otodus* (well-developed lingual neck, clearly separated lateral cusplets, lack of developed nutritive groove, labiolingually compressed root lobes) and also appears to have had a similar dental formula (C. Underwood, pers. observ. of Moroccan *Otodus*, 2010), with three differentiated upper and lower anterior teeth, no upper intermediate teeth, and one or more lower parasymphyseal teeth (which are present but rarely recorded in *Otodus*; D. Ward, pers. comm., 2009). Although details may be debated, the general dentition of *Cretalamna* is recorded by Shimada (2007). *Dwardius* Siverson, 1999, has teeth that are morphologically similar to those of *Cretalamna* and *Otodus* and appear to have a similar dental formula, and likewise are here considered to belong within the Otodontidae.

Genus *CRETALAMNA* Glikman, 1958
CRETALAMNA APPENDICULATA (Agassiz, 1843)
(Fig. 4A–L)

Material—25 teeth, 9 of which are relatively well preserved (DUGF/8–16).

Description—Teeth of this species demonstrate strong heterodonty, with anterior teeth being larger and higher than lateral teeth, and upper teeth having a stronger distal inclination than lowers. All teeth possess an erect cusp and a single pair of lateral cusplets situated above a relatively low root with widely spaced root lobes. There is no ornamentation on any teeth. The main cusp varies in shape with tooth position; in anterior teeth the cusp is straight to faintly flexuous and 1.5 to 2 times as high as wide, whereas in lateral teeth the cusp is lower and broader based, being erect and triangular in lower lateral teeth but strongly curved distally in upper lateral teeth. There is no labiolingual curvature of the cusp other than a very slight labial inclination near the tip of some anterior teeth. The cusp lingual face is strongly convex, whereas the labial face is flat to faintly convex, especially in upper lateral teeth. Lateral cusplets are divergent and in the same plane as the main cusp in all teeth, but vary in size and shape with tooth position. In anterior teeth, lateral cusplets are small, especially so on the mesial side, and have a rounded apex. Lateral cusplets of lateral teeth are proportionally larger and somewhat wider than high with a triangular profile. A smooth and well-developed cutting edge is present across all cusps, but is weak or absent where the main and lateral cusps meet, giving the appearance of a small notch in some lateral teeth. The base of the crown only barely unites the main and lateral cusps on the lingual face, and there is a narrow but prominent neck at the base of the main cusp. The base of the crown extends onto the upper part of the labial face of the root, but does not extend down the root lobes. In upper lateral teeth, the entire crown is somewhat inclined labially relative to the root, but this is not the case with teeth from other positions. The root of anterior and lateral teeth is rather different in shape. The root of anterior teeth is 'V' shaped in lateral profile and comprises two similarly sized root lobes that are oval in cross-section. The labial face of the root lobes is gently convex, and passes without an edge to the lingual face, which may be convex or slightly labiolingually compressed depending on tooth position. There is a swollen protuberance below the main cusp on the lingual side, but this is not clearly differentiated. The ends of the root lobes are rounded to faintly angular. The root of the presumed third anterior tooth is intermediate in morphology between that of other anterior and lateral teeth. The root of lateral teeth is only weakly divided into root lobes, and is strongly labiolingually compressed. The distal edge of the root ends below the distal cusplet and has a square termination, but the mesial root edge extends somewhat beyond the edge of the crown and ends in a more sharply angled point. The labial face of the root is flat, and there is a clear edge where this meets the lingual root face. The root lingual face is also flat, but may be somewhat swollen to form a weak lingual protuberance that slopes upwards to form a narrow ledge at the base of the crown. The vascularization of all teeth is similar, with a prominent foramen at the apex of the lingual protuberance, and numerous, small foramina spread across the entire root, but being larger and more elongate on the labial face.

Discussion—*Cretalamna appendiculata* has been recorded from Albian to Ypresian deposits around the world. Despite this, many of the records are of teeth that are morphologically very different from those from the type area (Upper Cretaceous, probably Turonian, of Lewes, southern England), and it is considered here that *C. appendiculata* sensu lato should really be treated as a group of related species. Many published specimens from the Albian to Turonian appear similar to each other (e.g., Woodward, 1912; Welton and Farrish, 1993; Siverson, 1996, 1997, 1999), and may represent the same taxon or closely related species group. Most post-Turonian specimens, including the dentition figured by Shimada (2007), should be placed into other species because the tooth morphology is significantly different from that of the type material, in particular with regard to the anterior teeth.

Cretalamna appendiculata sensu stricto has been recorded very widely geographically, including from Australia (e.g., Siverson, 1996). It has not, however, been recorded from the southern margin of Tethys in North Africa (e.g., Werner, 1989), although later species are well known there (e.g., Arambourg, 1952).

Genus *DWARDIUS* Siverson, 1999
DWARDIUS SUDINDICUS, sp. nov.
(Fig. 5A–J)

Etymology—From the presence of the type material in southern India.

Holotype—DUGF/21.

Referred Specimens—128 teeth, many fragmentary but some very well preserved (DUGF/17–20, 22–30).

Type Locality—Approximately 2.7 km northwest of the village of Garudamangalam, Tamil Nadu, India.

Diagnosis—Lamniform with large teeth showing moderate monognathic and dignathic heterodonty. Parasymphyseal teeth variable in size, some relatively large. All teeth to some degree asymmetrical, with a degree of mesiodistal curvature of the main cusp of all teeth other than some upper anteriors and lower laterals. Upper and lower anterior teeth with lingual curvature of main cusp. Main cusp higher than wide in all teeth and flanked by a single pair of lateral cusplets, which are of similar size on both sides of tooth. Cusplets of similar height to width, triangular, sharply pointed, and divergent in all teeth. Additional incipient cusplets present only on large lower lateral teeth. Prominent neck present at the base of the lingual face of all teeth. No ornament on any teeth. Root robust and 'U'-shaped with rounded tips of root lobes. Lingual bulge present but not strongly protruding with one or more foramina but no groove.

Description—Teeth of this species are large, some specimens reaching 28 mm high. Lamniform monognathic and dignathic heterodonty is moderately developed. A rather small upper parasymphyseal tooth, probably equivalent to the first upper anterior tooth of Siverson (1999), is present. This tooth is somewhat asymmetrical, with an elongate main cusp having a distal curvature. A pair of poorly developed lateral cusplets is present, which is loosely connected to the main cusp by a narrow band of enameloid, and only reach to the level of the base of the main cusp. A well-developed cutting edge is continuous across all cusps and is the only ornamentation present on the tooth crown. The root is bulbous and divided into two root lobes, with the mesial and distal lobes having rounded and pointed terminations, respectively. The lingual root face is swollen and has a single, relatively small foramen at its apex. Small foramina are present across the remainder of the root. Other upper anterior teeth are larger, and generally close to symmetrical, with just slight curvature of the main cusp. Viewed labially, the main cusp constitutes about two thirds of the total tooth height, and is up to twice as high as wide. The sides of the cusp are faintly convex to (on the mesial side of a probable third tooth) faintly concave. The labial crown face is flat, but the lingual face is strongly convex, and the cusp is somewhat curved lingually. The main cusp is flanked by a single pair of short but robust lateral cusplets, which are triangular in lateral view, straight-edged, and strongly divergent. The three cusps are linked by enameloid on the labial side of the tooth, but this is thin and there is no enameloid overhang of the root. A narrow but well-developed neck is present at the lingual base of the main cusp. A well-developed and continuous cutting edge is present, but there is a complete lack of crown ornamentation. The root is robust and generally 'U'-shaped, with two well-separated root lobes. The root lobes are oval in cross-section and have rounded terminations, with the angle between the lobes being close to 90 degrees. There is a moderately well-developed lingual protuberance, with a single apical foramen or more rarely small cluster of foramina. Foramina are very small and uncommon elsewhere on the basal and lingual faces of the teeth, but are abundant on the labial face. Upper lateral teeth are similar in overall morphology to the anterior teeth, but have a main cusp that is distally inclined, or more commonly, has a strong distal curvature but is not significantly curved lingually. The overall proportions of the teeth vary between those in more anterior and posterior jaw positions, with

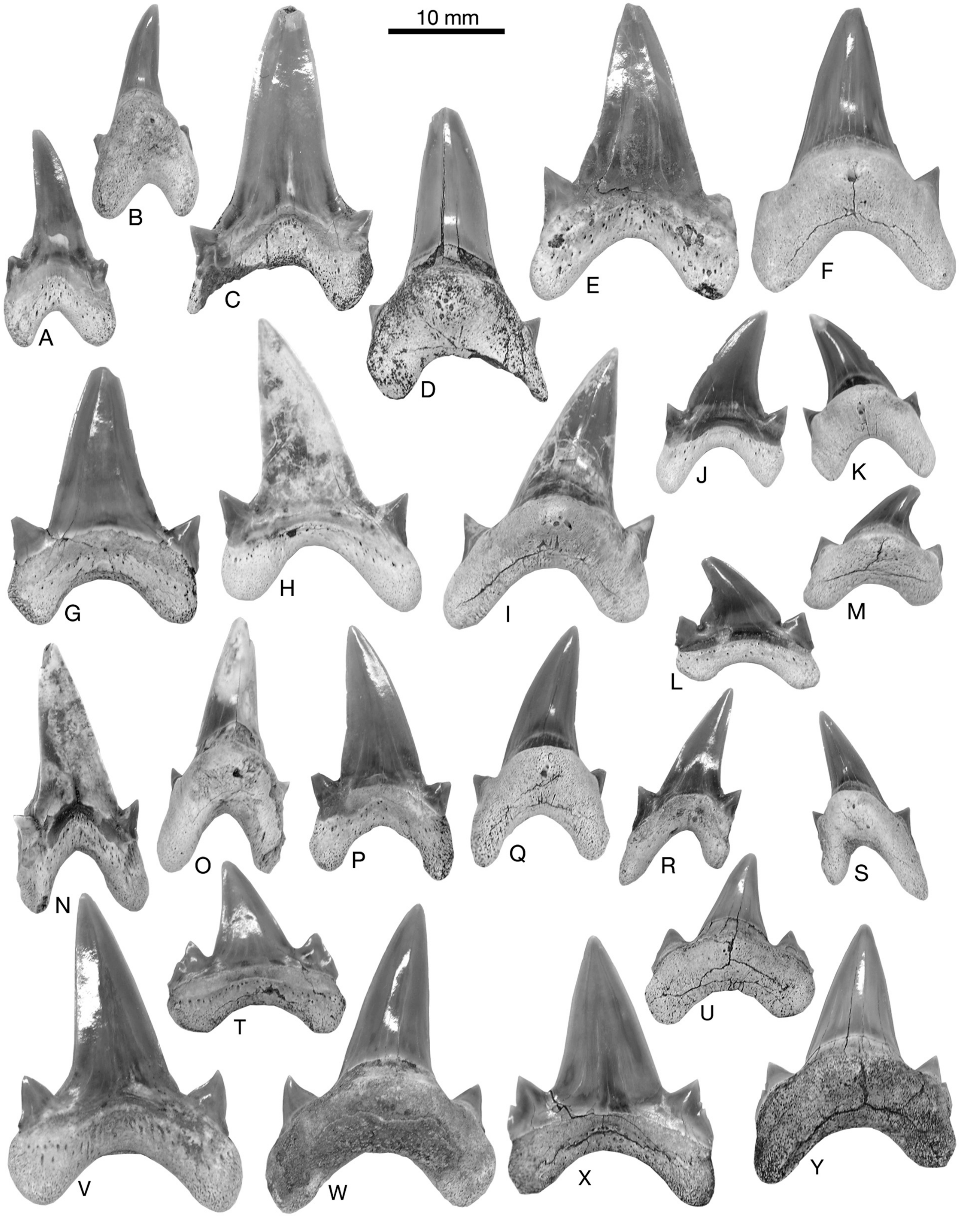

FIGURE 5. *Dwardius sudindicus*, sp. nov. **A**–**B**, upper parasymphyseal tooth, DUGF/17; **A**, labial view; **B**, lingual view; **C**–**D**, first anterior tooth, DUGF/18; **C**, labial view; **D**, lingual view; **E**–**F**, third upper anterior tooth, DUGF/19; **E**, labial view; **F**, lingual view; **G**, third upper anterior tooth, labial view, DUGF/20; **H**–**I**, first upper lateral tooth, DUGF/21, holotype; **H**, labial view; **I**, lingual view; **J**–**K**, upper lateral tooth, DUGF/22; **J**, labial view; **K**, lingual view; **L**–**M**, upper posterolateral tooth, DUGF/23; **L**, labial view; **M**, lingual view; **N**–**O**, first lower anterior tooth, DUGF/24; **N**, labial view; **O**, lingual view; **P**–**Q**, second lower anterior tooth, DUGF/25; **P**, labial view; **Q**, lingual view; **R**–**S**, third lower anterior tooth of juvenile, DUGF/26; **R**, labial view; **S**, lingual view; **T**–**U**, lower posterolateral tooth, DUGF/27; **T**, labial view; U, lingual view; **V**–**W**, ?first lower lateral tooth, DUGF/28; **V**, labial view; **W**, lingual view; **X**–**Y**, large lower lateral tooth, DUGF/29; **X**, labial view; **Y**, lingual view.

more posterior teeth becoming increasingly lower and wider, with more widely divergent root lobes.

Anterior lower teeth are similar in general shape to the upper anterior teeth, but are somewhat more mesiodistally compressed with a more slender main cusp, and in all but the first lower tooth, the main cusp has a gentle distal curvature. The root lobes are symmetrical, but with a more acute internal angle than in other teeth, other than in the third lower tooth in which the mesial root lobe is considerably longer than the distal one; this is also the only tooth position in which the root lobes have angular rather than rounded terminations. Lower lateral teeth are slightly more gracile than the upper laterals, and have a somewhat more flattened linguobasal root face. The main difference from the upper teeth is the orientation of the cusp, which is straight and only very faintly distally inclined. One of the lower lateral teeth (DUGF/29) is rather larger and more robust than the others, and possesses an incipient pair of additional cusplets.

Discussion—*Dwardius sudindicus* is the most common species within the fauna and is represented by teeth that vary somewhat in robustness. In some teeth this is clearly due to ontogenetic heterodonty, with juveniles possessing more gracile teeth, but also probably indicates sexual heterodonty. By analogy with modern sharks, it is likely that the more robust teeth are from mature females, with more gracile teeth being from males.

Dwardius sudindicus is one of a number of dentally similar, medium- to large-sized, ‘middle’ Cretaceous sharks. Teeth of the forms included in the genera *Archaeolamna* Siverson, 1992, *Cardabiodon* Siverson, 1999, larger forms of *Cretalamna* Glikman, 1958, *Cretodus* Sokolov, 1965, and cuspate forms of *Cretoxyrhina* Glikman, 1958, all can resemble those of *Dwardius*, and this has led to confusion in the past in differentiating among those taxa (e.g., see Siverson, 1999). Although most of these genera can be separated on morphology of the crown, root, and/or ornamentation, teeth of *Cardabiodon* and *Dwardius* cannot be so readily separated from each other. Although several criteria for distinguishing these genera were given by Siverson (1999), most relate to relative tooth size and therefore require an associated dentition or very large collection of isolated teeth. Separation of the genera based on differences in the degree of cusp curvature and lateral cusplet size requires anterior teeth of known position, and would probably be better considered as specific rather than as generic (or familial) level differences.

Cardabiodon was considered by Siverson (1999) to have a very different dental formula from other Cretaceous lamniforms, warranting a separate family. It could be argued, however, that this formula is an artifact of a large upper parasymphyseal tooth being considered as a first upper anterior within a rigidly defined dental formula and the incorporation of a poorly preserved first lower lateral tooth into the third lower anterior position; indeed, it could be suggested that within some less-derived lamniforms the differentiation of parasymphyseal and anterior teeth and between lower anterior and lateral teeth could be considered arbitrary. The dental formula of *Dwardius* has not yet been reconstructed, but it is clear that there were several teeth in parasymphyseal positions, some of which were relatively large.

The teeth here differ from the Cenomanian taxon *Cardabiodon ricki* Siverson, 1999, in a number of characters. All teeth of *Dwardius sudindicus*, including anteriors, have triangular and well-formed lateral cusplets without the distinct notch between the main cusp and lateral cusplets seen in *C. ricki*. In addition, the root lobes of anterior teeth are longer and narrower than in *C. ricki*, some of the lower teeth are more gracile than in the type set of *C. ricki*, and some anterior teeth are more laterally compressed than any of those in *C. ricki*. *Dwardius woodwardi* (Herman, 1977) is known primarily from two associated partial dentitions, of which the paratype tooth set (NHMUK PV P45; Woodward, 1911:fig. 64) is now completely removed from matrix. Although there are minor differences between these two specimens, with the teeth of the holotype being slightly larger and possibly more gracile, these differences are within the range that would be expected due to minor ontogenetic or sexual differences within an extant lamniform. *D. sudindicus* differs from *D. woodwardi* in several respects. The lower lateral teeth of *D. sudindicus* appear to be broader than upper laterals, unlike the situation in *D. woodwardi*. In addition, the root differs somewhat in shape, with the root lobes of *D. sudindicus* not being compressed as they are in *D. woodwardi*. *D. sudindicus* also lacks the projecting lingual protuberance that is evident in *D. woodwardi*. Published material, which is probably most similar to *D. sudindicus*, comprises two figured teeth. Both are poorly preserved with damaged roots and were assigned to *Pseudisurus siversoni* Zhelezko, 2000, but they have a morphology that instead suggests that they are referable to *Dwardius* (Siverson and Lindgren, 2005). Despite their poor preservation, teeth of *Dwardius siversoni* seem to differ from those of *D. sudindicus* in having a proportionally longer cusp and more erect lateral cusplets. This therefore suggests that the material described here belongs to a different species than any described previously, and the weight of evidence (in particular the overall tooth morphology and nature of cusplets of anterior teeth) suggest that it belongs within *Dwardius*.

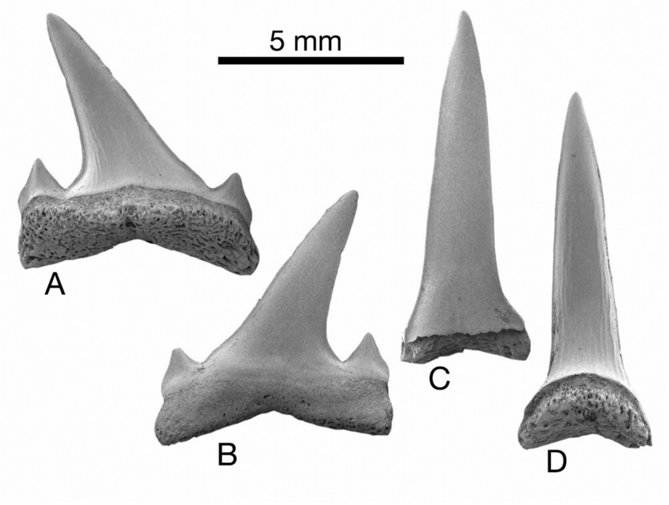

FIGURE 6. ?*Eostriatolamia* sp. **A**–**B**, upper lateral tooth, DUGF/31; **A**, labial view; **B**, lingual view; **C**–**D**, partial anterior tooth, DUGF/32; **C**, labial view; **D**, lingual view.

Dwardius is recorded from the Cenomanian of northern Europe, where it is also present in the Albian (C. Underwood, pers. observ.). It is also present in the Albian of Russia and Central Asia (D. Ward, pers. comm., 2010), but apparently is unrecorded elsewhere; specimens from Texas previously figured as *Dwardius woodwardi* (Welton and Farish, 1993) are not the same as the type species (Siverson, 1996, 1999) and instead represent a large species of *Cretalamna* (Underwood and Cumbaa, 2010).

Family ODONTASPIDAE sensu lato Müller and Henle, 1839
Genus ?*EOSTRIATOLAMIA* Glikman, 1980
?*EOSTRIATOLAMIA* sp.
(Fig. 6A–D)

Material—One upper lateral tooth (DUGF/31) and one cusp of an anterior tooth (DUGF/32).

Description—The anterior tooth of this species comprises an isolated cusp, which is 9 mm high, slender, and straight, with a faint sigmoidal labiolingual curvature. The labial face is very faintly convex, whereas the lingual face is strongly convex, giving

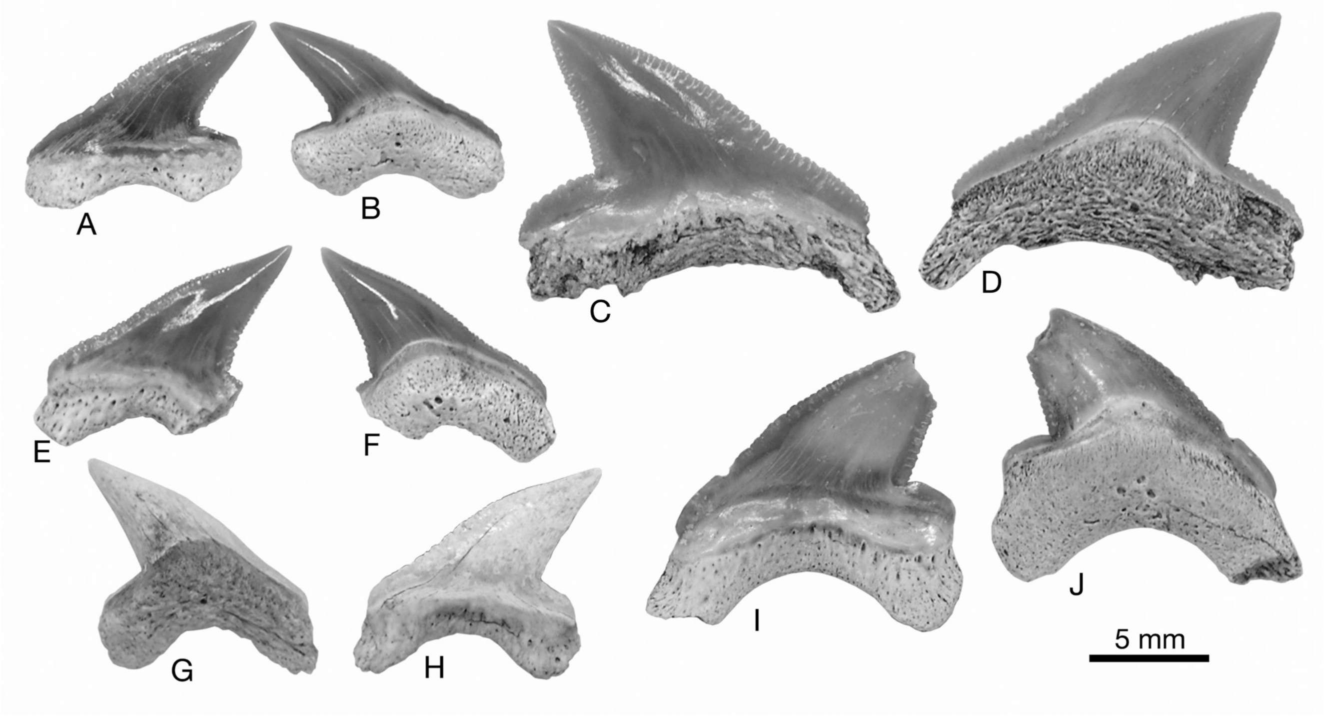

FIGURE 7. *Squalicorax* aff. *baharijensis*. **A**–**B**, lateral tooth of subadult, DUGF/33, holotype; **A**, labial view; **B**, lingual view; **C**–**D**, lateral tooth, DUGF/34; **C**, labial view; **D**, lingual view; **E**–**F**, lateral tooth of subadult, DUGF/35; **E**, labial view; **F**, lingual view; **G**–**H**, lateral tooth of subadult, DUGF/36; **G**, labial view; **H**, lingual view; **I**–**J**, anterior tooth, DUGF/37; **I**, labial view; **J**, lingual view.

the cusp a semicircular cross-section in its lower part. There is a weak but continuous cutting edge. The labial face is unornamented, but the lingual face has faint, flexuous, and rather irregular ridges that reach at least two thirds of the cusp height. The lateral tooth is 7 mm high and as high as wide. The main cusp is straight, distally inclined, and flanked by a single pair of lateral cusplets. The main cusp is higher than wide and has a straight mesial edge and slightly concave distal edge. The cusplets are erect, of a similar height and width, and have a sharply triangular profile. The labial side of all cusps is faintly convex, with a moderately convex lingual face. There is a well-developed cutting edge across all cusps. The labial face of the crown has no ornamentation, whereas fine and rather irregular striations are present on the lower half of the lingual face of the main cusp. The lingual base of the crown is immediately below the base of the cusps, sharply defined and lacking a neck. The base of the crown on the labial side is straight and does not extend onto the upper part of the root. The low root is similar in width to the crown and comprises very widely spaced root lobes. The ends of the root lobes are sharply angled, and there is an angled edge between the flat labial and lingual faces of the root. There is no lingual protuberance. A shallow nutritive groove is present between the root lobes and a relatively small foramen is present in its central part. There are almost no foramina on the labial face of the root, but foramina are very numerous on the lingual face.

Discussion—The upper lateral tooth is very similar in overall profile to that of species of *Eostriatolamia*, such as *E. striatula* (Dalinkevicius, 1935), with the short and angular root lobes and the triangular lateral cusplets being typical of the genus (e.g., Underwood and Cumbaa, 2010). Despite this, there are some differences that cause this taxon to be placed only tentatively in *Eostriatolamia*. Unlike other species of *Eostriatolamia*, the base of the crown on the labial side of the tooth is straight, does not extend along the top of the root lobes, and is not ornamented; indeed the lack of ornamentation on the tooth labial face is rare within *Eostriatolamia*. The shape of the root also separates this tooth from those of *Carcharias* sensu stricto and *Scapanorhynchus* sensu stricto (although both of these genera, sensu lato, have historically been used to accommodate taxa with a diversity of tooth types). The smooth labial crown face and straight crown base are similar to the morphology present in '*Odontaspis*' *subulata* Agassiz, 1843, but teeth of ?*Eostriatolamia* sp. appear to be more symmetrical and have more slender lateral cusplets.

Family ANACORACIDAE Casier, 1947
Genus *SQUALICORAX* Whitley, 1939
SQUALICORAX aff. *BAHARIJENSIS* (Stromer, 1927)
(Fig. 7A–J)

Material—Five teeth (DUGF/33; DUGF/14–37) and two fragmentary teeth.

Description—This species shows moderate monognathic heterodonty and dignathic and/or ontogenetic heterodonty. All teeth have a single cusp that is strongly inclined distally. The mesial (leading) edge of the cusp is longer than the total width of the tooth measured across the root, and is at an angle of 25 to 35 degrees from the base of the crown. The cusp mesial edge is straight overall in most teeth, or slightly convex in an anterior tooth, but there is a slight sigmoidal pattern, with a gentle concavity about one third of the way up toward the cusp apex, and a gentle convexity about two thirds of the way up. The cusp apex is sharp and makes a 20 to 30 degree angle. The distal edge of the cusp is straight to slightly concave. At its base there is a well-developed notch, and a low and flat-topped distal heel is present above the distal root lobe. A complete cutting edge is present. It is fully and regularly serrated across the cusp, other than close to the apex, with serrations usually being present on the distal heel, but irregular or absent on some teeth. The serrations, semicircular in profile, are at their largest about one third of the way up the cusp on the mesial side, but near the base on the distal side. The labial face of the crown is unornamented and gently convex, the lingual face is also unornamented but more strongly convex. The base of the crown on the lingual side is concave, with a moderately well-developed neck below the main cusp. The base of the crown on the labial side extends slightly onto the upper part of the root, and is somewhat swollen, to slightly overhang the top of the root. The root is low and relatively massive. The two root lobes are widely separated and quite short, with the mesial root lobe being slightly longer than the distal. The labial root face is low and somewhat convex, with no strong edge at the contact with the lingual face of the root. The lingual side of the root is divided into a relatively flat linguobasal (attachment) region and a short lingual face, with a rather rounded contact between the two. A relatively large main foramen is present on the lingual side of the root below the main cusp, and small foramina are present across the whole root. There is a concentration of foramina in the middle part of the labial face of the root, just below the base of the crown.

Discussion—Teeth of *Squalicorax* aff. *baharijensis* are very similar to those of *Squalicorax baharijensis* (Stromer, 1927) and *S.* aff. *baharijensis* of Siverson et al. (2007), and probably form a closely related group of species. Despite this, the quantity of well-preserved material prevents the naming of a new taxon. The cusp of *S.* aff. *baharijensis* of Siverson et al. (2007) is considerably more elongate and gracile than in other taxa, extending distally beyond the distal end of the root, especially in lateral teeth. In addition, the mesial edge of the cusp in lateral and anterolateral teeth is not strongly convex, and even in anterior teeth is only gently convex and lacks the 'hump backed' appearance of teeth of *S. baharijensis*. The distal edge of the cusp in the material described here is concave to straight, not convex as in many specimens of *S. baharijensis*, and overhangs a small distal heel that does not possess a convex upper edge.

Although teeth of *Squalicorax* are well known from the Cretaceous of the southern hemisphere (e.g., Siverson, 1996), teeth of the '*S. baharijensis* group,' which likely contains this new species, have previously been recorded only from areas with Tethyan influences in southern Europe (e.g., Vullo et al., 2007), southern Western Interior Seaway (e.g., Cappetta and Case, 1999; Siverson et al., 2007), and North Africa (e.g., Werner, 1989), apparently being absent either further south, in northern Europe, and in the northern Western Interior Seaway (e.g., Underwood and Cumbaa, 2010).

Family incertae sedis
Genus *CRETODUS* Solokov, 1965
CRETODUS LONGIPLICATUS Werner, 1989
(Fig. 8A–F)

Cretodus semiplicatus Münster in Agassiz, 1843; Antunes and Cappetta, 2002:pl. 10, 4–6.

Material—15 teeth, most fragmentary but 3 at least are half complete (DUGF/38–40).

Description—The more complete teeth of this species comprise a robust main cusp and a single (where preserved) pair of robust and triangular lateral cusplets. The main cusp is straight (in the anterior tooth) to distally inclined (in the lateral teeth). It has a moderately convex labial face and strongly convex lingual face. The main cusp is attached laterally to the lateral cusplets. These cusplets are proportionally large, at about one third of the length of the main cusp, and slightly divergent. A well-developed cutting edge is continuous across all cusps. All cusps are very strongly ornamented, with sharp-edged longitudinal ridges that reach almost to the base of the crown. Six to 10 ridges are present on the labial face of the main cusp, extending half way up the cusp in the anterior tooth, but further on the lateral teeth. Similar, but slightly weaker and more closely spaced, ridges are present in the cusp lingual face, where they reach slightly closer to the apex than on the labial side. Three to seven ridges are present on both sides of the lateral cusplets, almost reaching the apex. The base of the crown is close to the base of the cusps on the lingual side, where no neck is seen. On the labial face, the base of the crown extends a little way down the labial face of the root, but there is no significant overhang or extension onto the top of the root lobes. The roots are generally poorly preserved, but form a general 'U'-shape with a gentle basal curvature, and extend a similar distance laterally to the crown. The root is relatively massive compared to the size of the tooth, and the root lobe (where it is preserved) has a somewhat pointed apex. The labial face of the root is gently convex, whereas the lingual face of the root lobe is somewhat excavated on its lower part, widening upwards to a slight ledge below the lateral cusplet. There is a weakly developed lingual protuberance. Very small foramina are extremely abundant across the root, but the main lingual foramen, if present (the area is damaged), must have been small.

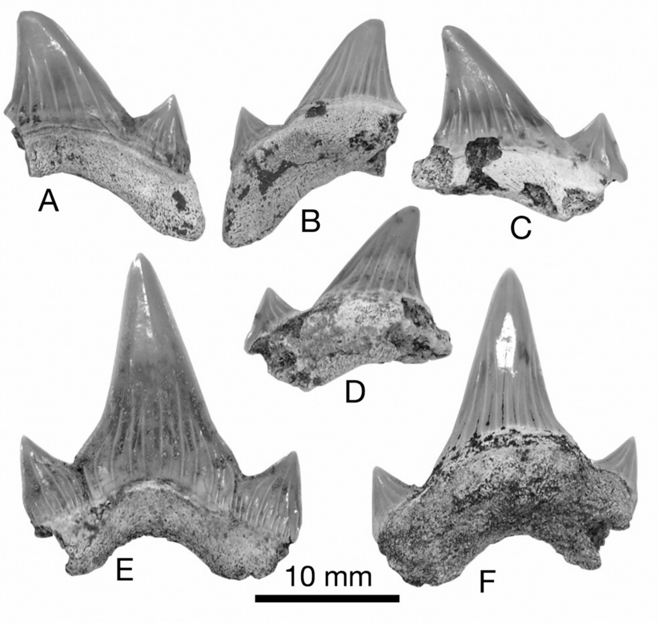

FIGURE 8. *Cretodus longiplicatus* Werner, 1989. **A**–**B**, partial upper lateral tooth, DUGF/38; **A**, labial view; **B**, lingual view; **C**–**D**, partial upper lateral tooth, DUGF/39; **C**, labial view; **D**, lingual view; **E**–**F**, partial anterior tooth, DUGF/40; **E**, labial view; **F**, lingual view.

Discussion—*Cretodus longiplicatus* was initially described based on relatively poor material from the Cenomanian of Egypt. Although synonymized with *C. semiplicatus* (Münster in Agassiz, 1843) by Cappetta and Case (1999), it is here considered to be a valid species. It differs from *C. crassidens* (Dixon, 1850) and *C. semiplicatus* (considered synonymous with each other by Schwimmer et al., 2002) in possessing long and very robust longitudinal ridges on both labial and lingual faces of the crown in all of the teeth described, both originally and here, and the presence of these ridges in teeth of all sizes suggests that this high degree of ornamentation was retained throughout ontogeny. Some partial teeth figured from the Cenomanian of Angola by Antunes and Cappetta (2002) appear to also represent this species. It is possible that *Cretodus longiplicatus* represents intraspecific variation within *C. semiplicatus*, but that is here considered unlikely due to the different stratigraphic distributions of the two forms, with *C. semiplicatus* not having been recorded in the Lower Cenomanian (M. Siverson, pers. comm., 2010). Although highly

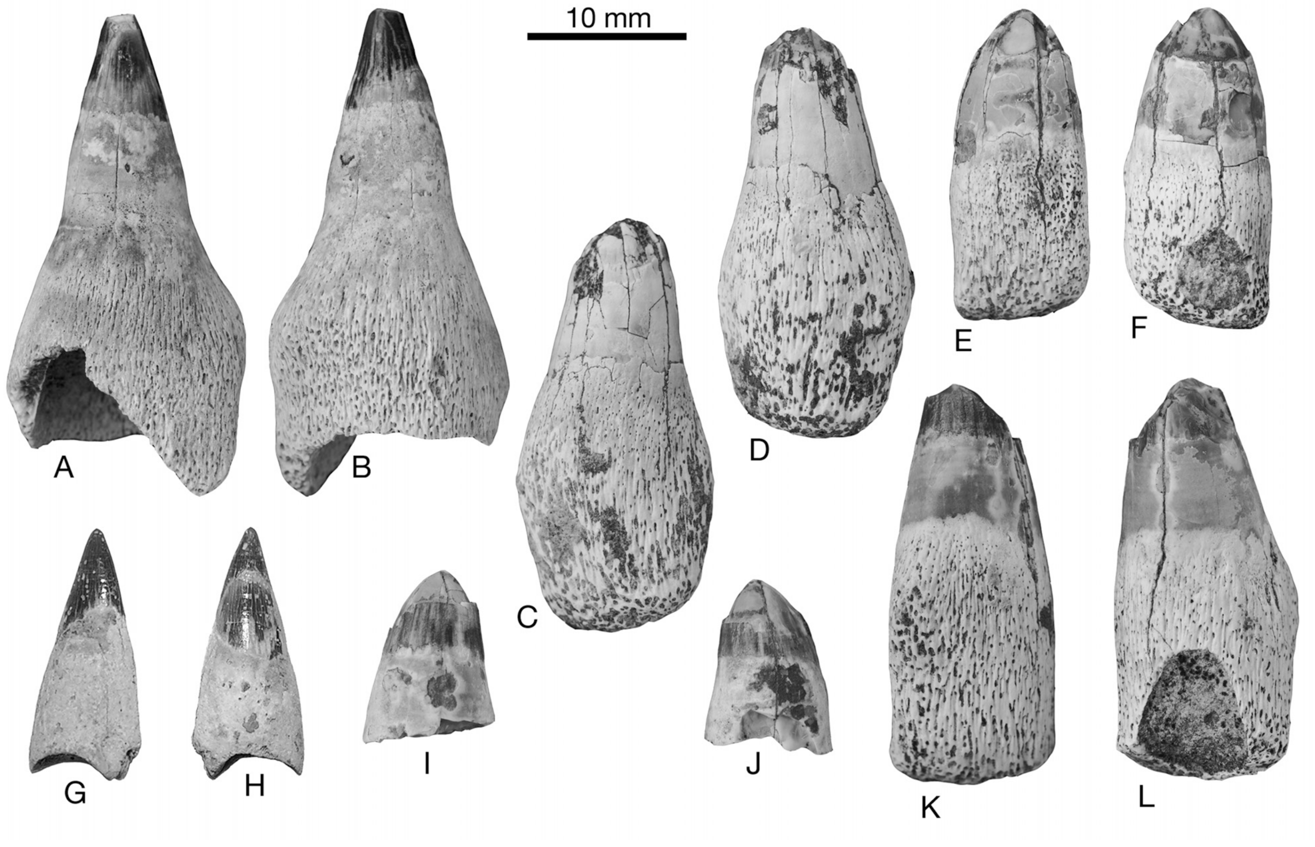

FIGURE 9. *Platypterygius indicus* Lydekker, 1879. **A**–**B**, complete tooth of adult, DUGF/41; **A**, lingual view; **B**, labial view; **C**–**D**, worn, broken adult tooth, DUGF/42; **C**, lingual view; **D**, labial view; **E**–**F**, worn, broken adult tooth, DUGF/43; **E**, lingual view; **F**, labial view; **I**–**J**, worn, broken adult tooth, DUGF/44; **I**, lingual view; **J**, labial view; **K**–**L**, worn, broken adult tooth, DUGF/45; **K**, lingual view; **L**, labial view; **G**–**H**, complete tooth of a juvenile, DUGF/46; **G**, lingual view; **H**, labial view.

ornamented teeth of *Cretodus* have been recorded in the Middle Cenomanian of Alberta (Cook et al., 2008), the figured specimen is small, and Cook et al. (2008:1190) note that "juveniles have more prominent lingual folds that extend further up the cusp." It is therefore possible that the different species of *Cretodus* represent chronospecies, with decrease in ornamentation and increase in maximum tooth size through time, with ontogenetic changes in tooth morphology possibly also being present. *Cretodus longiplicatus* is therefore probably present in three sites from south of Tethys (Egypt, Morocco, and southeastern India), but is apparently absent north of Tethys in either Eurasia or the Western Interior Seaway.

DIAPSIDA Osborn, 1903
ICHTHYOPTERYGIA Owen, 1840
ICHTHYOSAURIADE de Blainville, 1835
OPHTHALMOSAURIDAE Baur, 1887
PLATYPTERYGIUS von Huene, 1922
PLATYPTERYGIUS INDICUS? Lydekker, 1879
(Fig. 9A–L)

Material—Six adult teeth (DUGF/41–45), one juvenile tooth (DUGF/46), seven partial vertebrae.

Description—The adult teeth are conical, with three displaying slight curvature, two being relatively straight, and one incomplete and of uncertain curvature. All of the adult teeth display fine longitudinal ridges that do not reach the apex in the complete specimens. The enamel is worn at the apex of the complete teeth, with dentine visible at the apex and also at the base of the tooth. The roots are ovoid in cross-section and massive, equal to or slightly greater than the length of the crown. There is significant bulging near the top of the root, immediately below the crown. The juvenile tooth differs from the adult teeth in being highly laterally compressed, with no longitudinal ridges, no evidence of enamel wear, and no bulging of the root.

Remarks—*Platypterygius indicus* was originally described on the basis of a few complete and partial vertebrae collected in the Karai Formation of the Cauvery Basin (Lydekker, 1879), likely from the same or a nearby locality to the one reported on here. A new species was erected based on the observed greater concavity of the vertebrae. The partial vertebrae collected on this expedition do not contain sufficient information to evaluate the validity of Lydekker's (1879) designation of a distinct species, and therefore the materials described here are conservatively assigned tentatively to *P. indicus*, which may well be synonymized with other *Platypterygius* species after more detailed study of the genus. The morphology of the adult teeth is nearly identical to that presented in previous descriptions of dental morphology in species of *Platyptergyius*, such as for *P. longmani* from the Albian of Australia (Kear, 2005).

PALEOECOLOGY AND PALEOBIOGEOGRAPHY

The early Cenomanian vertebrate assemblage from the Karai Formation of southern India consists almost entirely of taxa that likely were medium- to large-bodied, active, pelagic or benthopelagic predators. Many of the more benthic vertebrates at the time, particularly chondrichthyans, were relatively small bodied (e.g., Cappetta and Case, 1999; Underwood and Mitchell, 1999) and unlikely to have been collected by surface collecting. Despite this, the absence of remains of benthic taxa in the sieved sample, which did yield some lamniform material (as described above in Materials and Methods), strongly suggests that the absence of these forms is real and not an artifact of collection failure. Thus the lack of smaller fish, including chondrichthyans, is probably due to a combination of paleoenvironmental and taphonomic factors.

Although the assemblage is almost completely composed of piscivorous taxa, the diversity of tooth size and morphology suggests that there was strong niche partitioning within the fauna, and a number of different feeding strategies, and presumably prey types, were utilized.

The ichthyosaur *Platypterygius* is cosmopolitan in the 'middle' Cretaceous, found on all continents apart from Antarctica during the Neocomian to Cenomanian (Kear, 2005). The shark fauna, however, provides several spatial range extensions that suggest an unusual paleobiogeographic pattern. *Gladioserratus* is known from the Aptian of southern France, but all Albian and Cenomanian records are restricted to high-latitude localities in both the northern (Europe) and southern (Western Australia) hemispheres. A similar pattern is shown by *Protosqualus*, being present in the 'middle' Cretaceous of both northern Europe and Australia (e.g., Kemp, 1991) as well as India. *Dwardius* has been reported from 'middle' Cretaceous sites in northern Europe, Russia, and Central Asia. This is the first published report of *Dwardius* from the southern hemisphere, but all records of this taxon are consistently from high-paleolatitude sites. *Notidanodon* is known from northern Europe and California in the 'middle' Cretaceous, with later Cretaceous records from high-paleolatitude sites in the northern and southern hemispheres, as well as California. The Californian localities have been described as oceanic upwelling zones, also suggesting a restriction to cooler waters for this taxon.

The remaining species in the Karai Formation chondrichthyan assemblage appear to tolerate wider temperatures ranges. *Cretalamna* is cosmopolitan in the 'middle' Cretaceous, whereas *Cretodus* has been reported from both equatorial (Egypt) and mid-latitude southern hemisphere (Angola) sites. This new southern Indian record thus expands its range to high paleolatitudes. Although *Squalicorax* is widely distributed, taxa of the '*S. baharijensis* group' (to which the new southern Indian material is ascribed) previously have been reported from only more equatorial and warm water sites in southern Europe, North Africa, and the southern region of the Western Interior Seaway. This, therefore, represents the first high-paleolatitude record for the *Squalicorax baharijensis* morphological group.

This combination of taxa suggests that although some Cretaceous sharks had cosmopolitan distributions and inhabited diverse climatic regimes, most of the species reported here from South India appear to be restricted to cooler water sites in both the northern and southern hemispheres. Such an antitropical distribution is observed today in many terrestrial and marine organisms, including several species of sharks, and a recent study demonstrated an antitropical distribution in another Cenomanian shark, *Cardabiodon ricki* (Cook et al., 2010). It is noteworthy that an antitropical distribution appears to be prevalent during the much warmer 'middle' Cretaceous, when sea surface temperatures may have been at record highs for the Phanerozoic and the latitudinal temperature gradient was likely flatter than it is today (Hart, 2001). An extensive review of 'middle' Cretaceous marine vertebrate paleobiogeography is beyond the scope of this paper, but these new records from a high-paleolatitude site in South India suggests that a detailed analysis of latitude, climate, and biodiversity would be a worthwhile avenue of research that could provide interesting data for modeling the effects of global warming on marine biodiversity.

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