LAMNIFORM SHARKS OF THE MID CRETACEOUS ALINGA FORMATION AND BEEDAGONG CLAYSTONE, WESTERN AUSTRALIA

by MIKAEL SIVERSON

ABSTRACT. The uppermost beds of the Alinga Formation and the basal part of the overlying Beedagong Claystone in the lower Murchison River area at the southern end of the Southern Carnarvon Basin, Western Australia, have yielded 15 species of lamniform sharks referred to ten genera, of which one genus and three species are new: *Cretoxyrhina mantelli*, *Archaeolamna* aff. *kopingensis*, *A. haigi* sp. nov., *Leptostyrax* sp., *Cretolamna appendiculata*, *C. gunsoni* sp. nov., *Pseudoisurus tomosus*, *Pseudoisurus*? sp., *Paranomotodon* sp., '*Anomotodon*' sp., *Johnlongia allocotodon* gen. et sp. nov., *Carcharias* sp. A, *C.* sp. B, *Squalicorax* ex gr. *curvatus*, and *S. volgensis*. Direct correlation with Germany and the Saratov Province of the Russian Platform, using cosmopolitan lamnoids, dates the basal part of the Beedagong Claystone in the studied area as early or mid Cenomanian. The top of the Alinga Formation is provisionally placed in the early Cenomanian. This contrasts with the most recent previous estimate which suggested an early Turonian age for the upper half of the Alinga Formation. The present account is the first comprehensive documentation of Cretaceous selachians from Australia. It demonstrates the great potential of the use of lamniform shark teeth in intercontinental correlation of mid Cretaceous marine deposits.

TOOTH morphology is an important character for taxonomists working on extant sharks (Bass 1973; Compagno 1984; Last and Stevens 1994). All living species of the order Lamniformes can be identified by their dentition alone (see Compagno 1984) and most of them have a very wide distribution, with reported occurrences in both the southern and northern hemispheres. In this paper, the uppermost beds of the Alinga Formation and the basal part of the overlying Beedagong Claystone are placed in an international stratigraphical framework on the basis of teeth of cosmopolitan lamnoid sharks, allowing direct correlation with north-west Germany and the Saratov Province of the Russian Platform.

As pointed out by Kemp (1991), little work has been done on Australian Cretaceous chondrichthyans. This is the first comprehensive description of Cretaceous sharks of Australia. One new genus and three new species are described: *Archaeolamna haigi* sp. nov. and *Cretolamna gunsoni* sp. nov. of the Cretoxyrhinidae Glikman, 1958 and *Johnlongia allocotodon* gen. et sp. nov., assigned to the Odontaspididae Müller and Henle, 1839.

GEOLOGY

In the onshore part of the Southern Carnarvon Basin (basin nomenclature of Hocking *et al.* 1994), south of Shark Bay, the Alinga Formation (named by Clarke and Teichert 1948; amended by Johnstone *et al.* 1958) forms the uppermost unit of the siliciclastic Winning Group ('Winning Series' of Raggatt 1936; amended by Fairbridge 1953 and Johnstone *et al.* 1958). The formation comprises a 3–22 m thick marine sequence of dark green greensand, clayey siltstone and silty claystone (Hocking *et al.* 1987). It crops out mainly in the lower Murchison River area, at the southern end of the Southern Carnarvon Basin, where it rests conformably on the late Aptian to early Albian Windalia Radiolarite (see Ellis 1993) and, at most localities, is succeeded

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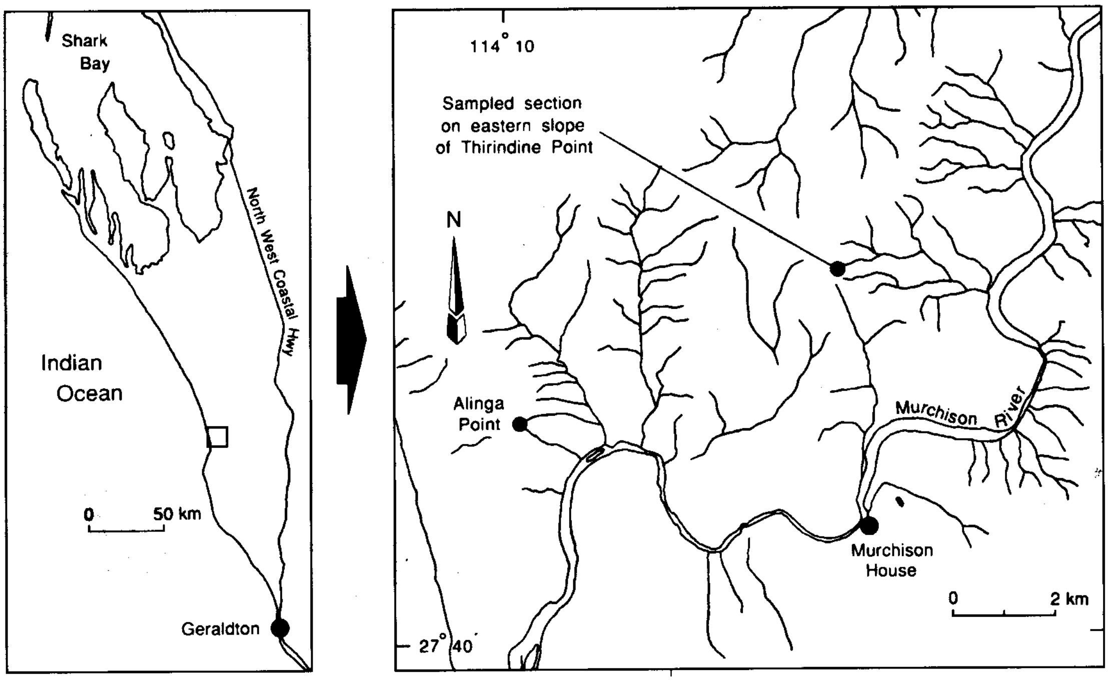


TEXT-FIG. 1. Map of the lower Murchison River area, Western Australia, showing the location of the sampled section on the eastern slope of Thirindine Point.

disconformably by the Toolonga Calcilutite of Santonian to early Campanian age (Belford 1958). However, in places, a thin sequence of the Beedagong Claystone is present between the Alinga Formation and the Toolonga Calcilutite. This lithostratigraphical unit was introduced formally by Shafik (1990) for a calcareous claystone between the Gearle Siltstone, which is a thicker lateral equivalent of the Alinga Formation (Condon 1968), and the Toolonga Calcilutite farther north in the Exmouth Sub-basin of the Northern Carnarvon Basin. Shafik (1990) assigned a late Turonian to late Coniacian age to the 83 m thick type section of the Beedagong Claystone in the Rough Range South #1 well, near Exmouth. This contrasts somewhat with Belford and Scheibnerova's (1971) study of planktic Foraminifera. They gave an early Turonian age for a sample from about 10 m above the base of the type Beedagong (core log 68). Until now, the Beedagong Claystone was not known to crop out in the lower Murchison River area.

PREVIOUS WORK ON THE ALINGA FORMATION

Due to the assumed absence of age-diagnostic fossils, Clarke and Teichert (1948) did not specifically discuss the age of their new lithostratigraphical unit, the Alinga Beds (= Alinga Formation of Johnstone *et al.* 1958), but it is quite clear from their discussion that they believed it to be of Late Cretaceous age. Moreover, their finds of *Marsupites* Miller, 1821 and *Uintacrinus* Grinnel, 1876 in the overlying Toolonga Chalk (= lower half of the Toolonga Calcilutite of Johnstone *et al.* 1958) further constrained the presumed age of the Alinga Beds to within the Cenomanian to Santonian interval. The only fossils from the Alinga Formation reported by Clarke and Teichert were belemnite guards.

Johnstone *et al.* (1958) gave a brief description of the type section at Alinga Point (Text-fig. 1). They correlated the formation with the Gearle Siltstone (*sensu* Condon *et al.* 1956) and concluded that it was Albian to Cenomanian in age based on an unspecified microfauna. McWhae *et al.* (1958) favoured a correlation with part of the Gearle Siltstone but admitted that the Albian to early Turonian age assigned by them to the Alinga Formation had not yet been verified by fossils. As well as belemnites, they also reported radiolarians and fish remains. A probable Cenomanian to early Turonian age was advocated by Belford (1958), yet again an estimate unsupported by age-diagnostic fossils.

Edgell's (1964) description of his Lancelin Beds in the Perth Basin also included a table showing, but not explaining, his view on the correlation of the Cretaceous formations of the Carnarvon and Perth basins. Instead of correlating the Alinga Formation with the Gearle Siltstone, he considered the former to be considerably younger, approximately spanning the late Coniacian to mid Santonian.

Playford *et al.* (1975) did not add any new information but were of the opinion that the Alinga Formation may be Albian to Turonian in age. Likewise, Hocking *et al.* (1987) concluded that the stratigraphical position of the unit suggests that it is Albian to Turonian in age. They also stated that the formation yields radiolarians, foraminifers, belemnites, and microscopic fish teeth but that none of these groups is abundant nor has any been studied. However, at least some work has been undertaken on the belemnites, with Stevens (1965) recording *Dimitobelus diptychus* from the Alinga Point section.

In a work devoted to the Upper Cretaceous nannofossils of the Australian western margin, Shafik (1990) recorded some poorly preserved coccoliths from two beds in the upper half of the formation at Toolonga Point. On the basis of these he referred this part of the unit to the early Turonian.

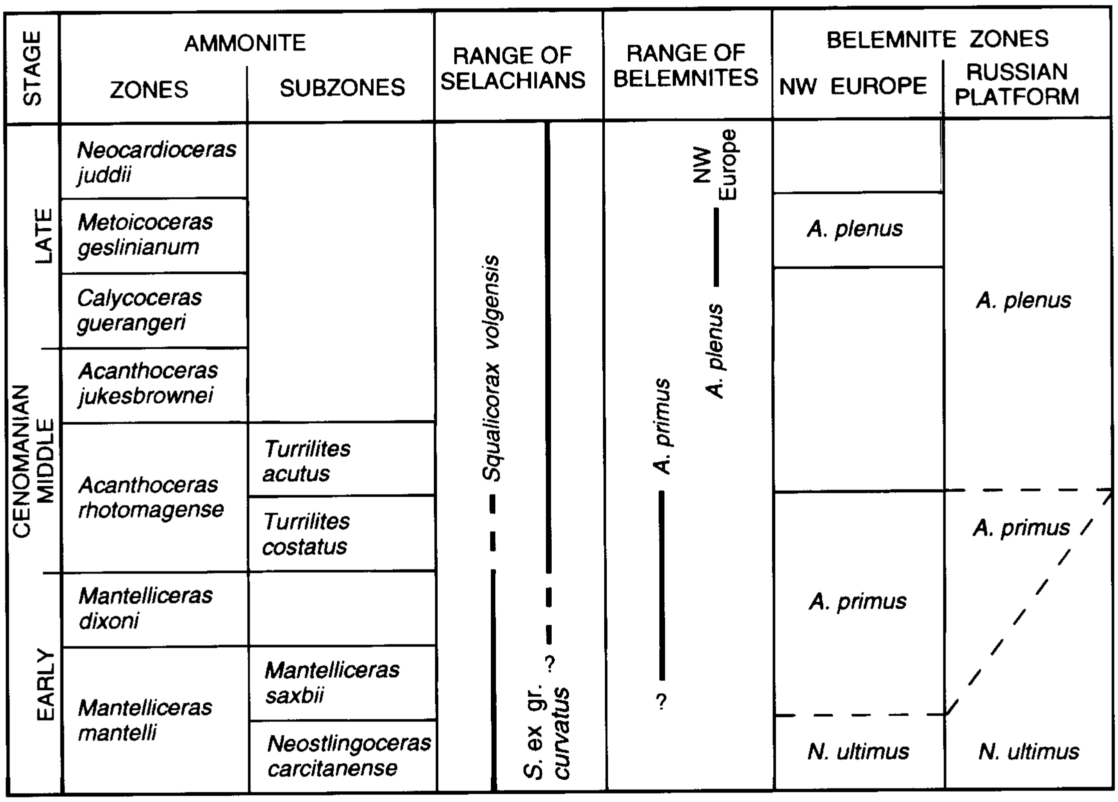
MATERIALS AND METHODS

Surface-collecting confined to the uppermost metre of the Alinga Formation and the basal part of the Beedagong Claystone along the Thirindine Point ridge yielded 122 determinable teeth from lamniform sharks. In addition, two horizons of the Beedagong Claystone on the eastern slope of the Thirindine Point ridge were targeted for bulk sampling. A total of 158 kg (dry weight) was processed. The sediments were dried, then soaked in water for an hour before being gently sieved through a 330 μm mesh. When necessary, the residue was further soaked in water to which had been added automatic-washing-machine powder. Subsequent wet-sieving completely disaggregated the remaining matrix, leaving a clean residue comprising selachian teeth and dermal denticles, various skeletal remains of bony fishes, coprolites, rare phosphatic brachiopods, and glauconite. The two samples, picked down to 500 μm, yielded 324 teeth of lamniform sharks, as well as several thousand teeth of other selachians that will be described elsewhere.

AGE OF THE ALINGA–BEEDAGONG TRANSITIONAL BEDS

Thirindine Point section

At the Thirindine Point ridge (Text-fig. 1), the Beedagong Claystone is separated from the overlying Toolonga Calcilutite by a bed of elongated and irregularly shaped phosphatic nodules. On the eastern slope of the ridge, the Beedagong Claystone does not exceed about 0·5 m in thickness. *Chondrites*-bioturbated laminae, littered with glauconite grains and fish debris, occur abundantly in the lower part and are especially densely packed in the basal 20 mm which separates it from the underlying greenish clayey siltstones of the Alinga Formation. On the western slope of the ridge the Beedagong is thicker, reaching approximately one metre. Preliminary bulk sampling of the uppermost metre of the Alinga Formation, which is about 6 m thick at Thirindine Point, has revealed selachian faunas completely different in composition from that of the basal Beedagong Claystone, demonstrating a profound shift in palaeoenvironment.



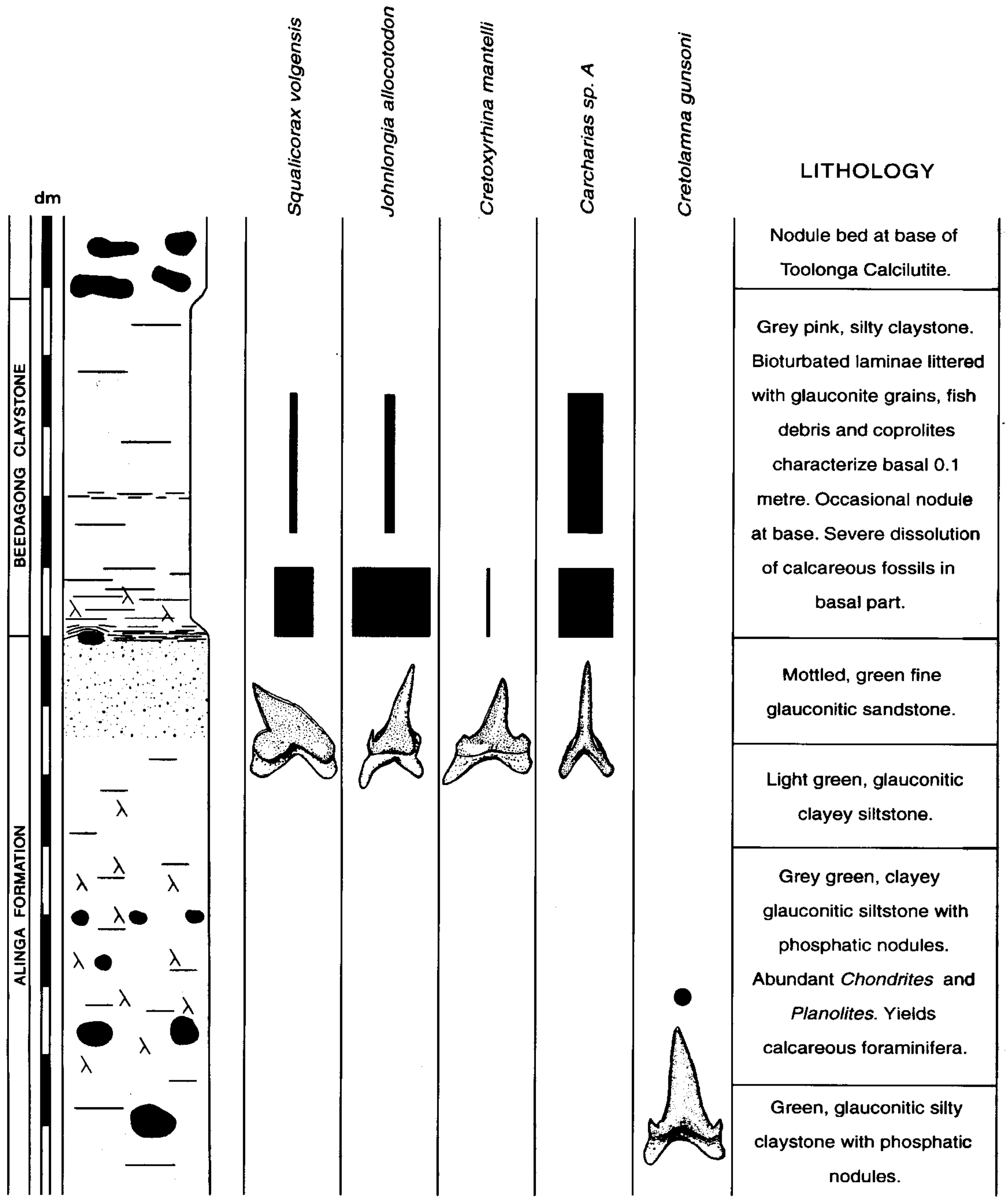
TEXT-FIG. 2. Stratigraphical diagram of the Cenomanian in northern Europe, including ammonite zones and subzones, belemnite zones, and the ranges of squalicoracid sharks and belemnites. *A.* = *Actinocamax*; *N.* = *Neohibolites*. Modified from Christensen (1993).

Beedagong Claystone. Bulk sampling (78 kg dry) of the basal 0·1 m of the Beedagong yielded teeth of four lamniform species: *Carcharias* sp. A, *Johnlongia allocotodon* gen. et sp. nov., *Squalicorax volgensis* Glikman *in* Glikman and Shvazhaite, 1971, and *Cretoxyrhina mantelli* (Agassiz, 1843).

Carcharias sp. A occurs elsewhere in the *Mantelliceras dixoni* and/or *Turrilites costatus* Zone/Subzone of Germany (described as *Eostriatolamia*? *subulata* by Müller and Diedrich 1991).

Another species of *Johnlongia* gen. nov., closely related to *J. allocotodon* gen. et sp. nov., occurs in the Turonian Carlile Shale of South Dakota and was described as *Odontaspis parvidens* by Cappetta (1973). The genus is also present in the Albian of Queensland (Noel Kemp and David Ward, pers. comm.).

Squalicorax volgensis was originally described from the *Actinocamax primus* Zone (Text-fig. 2) of the Saratov Province, Russia (Glikman and Shvazhaite 1971). It was later recorded by Müller and Diedrich (1991), as *Pseudocorax primulus*, from the *Mantelliceras dixoni* and/or the *Turrilites costatus* Zone/Subzone of Ascheloh at the Teutoburger Wald, north-west Germany. It ranges down into the late Albian; Welton and Farish (1993) described it from the Weno Formation in Tarrant County, Texas as *Squalicorax* sp. Moreover, Naidin (1981) reported it from the south-western part of the Crimean Range, Ukraine, in beds yielding *Turrilites costatus*. However, no teeth were illustrated, so this record cannot as yet be confirmed. The species has not been recorded from the younger half of the Cenomanian although descendants of it, having evolved teeth with a shorter and broader cusp, occur in the middle Turonian of the Western Interior of the United States (pers. obs.).



TEXT-FIG. 3. Section of the Beedagong Claystone and the uppermost 0·8 m of the underlying Alinga Formation at the eastern slope of the Thirindine Point ridge, showing known vertical distribution of lamniform sharks' teeth, identified at species level. Width of the bars correlates directly with the abundance of teeth in the sediment.

There is a minor difference between the late Albian *S. volgensis* teeth from Texas and the Cenomanian ones from Germany in that the basal edge of the root is more deeply notched in the latter ones. The Beedagong teeth conform perfectly in this regard with those from Germany, indicating an age closer to the late early/early mid Cenomanian than to the late Albian.

Cretoxyrhina mantelli is represented by five teeth, one from an adolescent or adult individual (Pl. 1, figs 13–14), the other four from very young ones. Lateral cusplets are developed in two of the four juvenile teeth (see e.g. Pl. 1, figs 5–6). The most conspicuous evolutionary trend in *Cretoxyrhina* Glikman, 1958 is the progressive loss of lateral cusplets, starting with the teeth of the anterior files. Biddle (1993) illustrated teeth from the middle Albian of the Saint-Dizier region, north-east France that appear to belong to the earliest known *Cretoxyrhina*. In this species, referred to *Cretoxyrhina woodwardi* (Herman, 1977) by Biddle, lateral cusplets are still present on all teeth.

Unfortunately, there is a total lack of well-dated and well-illustrated teeth of *Cretoxyrhina* from the late Albian to mid Cenomanian interval. Although Welton and Farish (1993) provided excellent documentation of an associated set of teeth from one individual from the Cenomanian part of the Britton Formation, Eagle Ford Group, in Dallas County, Texas, this reveals nothing about the intraspecific dental variation in the Britton population of *C. mantelli*. The precise stratigraphical position of the specimen within the formation was not mentioned. In the Dallas area the basal 1·5 m of the Britton Formation is of mid Cenomanian *Acanthoceras amphibolum* Zone age (Kennedy and Cobban 1990). No diagnostic macrofossils were recorded by Kennedy (1988) from the succeeding 35 m of bentonitic Britton shales, after which the mid late Cenomanian *Sciponoceras gracile* Zone fauna appears and continues to near the top of the formation (Kennedy 1988). The uppermost 2·5 m are of early Turonian age. In the Britton *C. mantelli*, minute cusplets are present on the second upper lateral tooth and on teeth of the posterior half of both the upper and lower jaw dental series.

Typical *C. mantelli* are also present in the late Cenomanian *Actinocamax plenus* Zone of Bettrechies, northern France (Herman 1977, pl. 9, fig. 6*a*–*b*) and Chercq, Belgium (Leriche 1902, pl. 3, fig. 49). The French specimens are both anterior teeth lacking cusplets, whereas the tooth figured by Leriche is a lateral one, likewise without cusplets. The species persisted into the Campanian with a youngest reliably dated occurrence (Siverson 1992) in strata in southern Sweden correlating with the latest early Campanian *Gonioteuthis quadrata gracilis/Belemnitella mucronata senior* Zone of Schulz *et al.* (1984).

As it is, the presence of *C. mantelli* in the basal part of the Beedagong Claystone does not allow a more precise dating than can be deduced from the presence of *S. volgensis*, *Carcharias* sp. A, and *Johnlongia allocotodon* gen. et sp. nov.

A sample (80 kg dry) from the middle third of the Beedagong on the eastern slope of the Thirindine Point ridge, 0·15–0·35 m above its base, yielded the lamnoids *Carcharias* sp. A, *Johnlongia allocotodon* gen. et sp. nov. and *Squalicorax volgensis* (Text-fig. 3).

Alinga Formation. Preliminary bulk sampling from a level 0·70–0·95 m below the top of the formation has yielded fragments of squalicoracid teeth, showing well-developed serrations on the cutting edges. Comparison with complete teeth of *Squalicorax volgensis* from the basal Beedagong Claystone revealed that the Alinga fragments cannot be assigned to that species. The material is, however, taxonomically indistinguishable from some of the surface collected teeth referred herein to *Squalicorax* ex gr. *curvatus* (Williston, 1900). The earliest well-dated squalicoracids of the *S. curvatus* group with regular serrations on the cutting edges are from near the lower/middle Cenomanian boundary. Müller and Diedrich (1991) figured two serrated cusps of a large squalicoracid, possibly *S. curvatus* itself, as *S. falcatus* (Agassiz, 1843) from their *Mantelliceras dixoni* Zone/Subzone or *Turrilites costatus* Zone/Subzone fauna of the Teutoburger Wald.

Conclusions. The basal part of the Beedagong Claystone at Thirindine Point is probably of early and/or mid Cenomanian age. The presence of *Squalicorax* ex gr. *curvatus* close to a metre below the base of the Beedagong, suggests that the uppermost beds of the Alinga Formation are of post-Albian age. This part of the section is provisionally assigned to the early Cenomanian.

Alinga Point section

Preliminary bulk sampling of the upper 5 m of the Alinga Formation at Alinga Point, where the 15 m thick type section is located, showed that the Beedagong Claystone is missing here. So far, only a small number of selachian teeth has been recovered from the Alinga Point samples, none of which belongs to lamniform sharks. The faunal composition from the various sampled levels is much the same as from the uppermost metre of the Alinga Formation at Thirindine Point. This indicates that the top of the Alinga Formation at Alinga Point is not younger than early Cenomanian or possibly mid Cenomanian.

Institutional abbreviations. FHSM: Sternberg Memorial Museum, Fort Hays State University, Fort Hays, Kansas; WAM: Western Australian Museum, Perth.

SYSTEMATIC PALAEONTOLOGY

Tooth terminology. In accordance with the recommendation by Ward (1987), the terminology used herein is after Cappetta (1987).

Order LAMNIFORMES Berg, 1958
Family CRETOXYRHINIDAE Glikman, 1958 *sensu* Cappetta, 1987
Genus CRETOXYRHINA Glikman, 1958

Type species. By original designation, *Oxyrhina mantelli* Agassiz, 1843.

Remarks. In spite of having designated *Oxyrhina mantelli* as the type species of *Cretoxyrhina* in the original description of that genus, published in 1958, Glikman (1964*a*) gave *Isurus denticulatus* Glikman, 1957 as the type species of *Cretoxyrhina*. An English translation of Glikman's 1964*a* paper was published in Jerusalem in 1967. Unfortunately, western workers relied on the misleading information in the translated, 1964 paper (e.g. Cappetta 1987; Siverson 1992).

In Glikman's figured sample of teeth from *C. denticulata* (pl. 1, figs 1–17), described from Cenomanian strata near Saratov, Russia, lateral cusplets are present in lateroposterior teeth but absent in anterior ones. In *C. mantelli*, absence or presence of cusplets on lateral and posterior teeth is largely related to the age of the material. In earlier populations, such as that from the basal Beedagong Claystone, cusplets are commonly present, whereas in later populations (Santonian–early Campanian) cusplets are usually absent, at least in lateral files.

Besides the two nominal species discussed above, Herman (1977) also referred *Lamna acuminata* Agassiz, 1838 to *Cretoxyrhina*. I strongly suspect that similarities in tooth morphology between '*L.*' *acuminata* and *Cretoxyrhina denticulata/mantelli* are due to convergent evolution. Zhelezko (1990) made '*L.*' *acuminata* the type of his new genus *Acrolamna*.

Teeth of a new, as yet unnamed *Cretoxyrhina* occur in the middle Albian of north-eastern France and were described as *Cretoxyrhina woodwardi* by Biddle (1993). This taxon is also present in the Albian of Western Australia (pers. obs).

Cretoxyrhina mantelli (Agassiz, 1843)

Plate 1, figures 1–18

*1843	*Oxyrhina mantelli* Agassiz, p. 280, pl. 33, figs 1–5, 7–9, *non* fig. 6.
.1975	*Cretoxyrhina mantelli* (Agassiz); Cappetta and Case, p. 20, pl. 5, fig. 27.
.1977	*Cretoxyrhina mantelli* (Agassiz); Herman, p. 219, pl. 9, fig. 6*a–e* [contains synonyms prior to 1973].
v.1978	*Oxyrhina mantelli*; Bergström and Sundquist, p. 11, fig. 2*g*.
.1980	*Cretoxyrhina mantelli* (Agassiz); Glikman, pl. 27, figs 13–14; pl. 29, figs 19–21.
1981	*Isurus mantelli*; Witzke, p. 108, pl. 1, figs 22–28.
v.1983	*Oxyrhina mantelli*; Bergström, p. 101, fig. 30*g*.
.1987	*Cretoxyrhina mantelli* (Agassiz); Longbottom and Patterson, p. 250, text-fig. 11.2r, pl. 54, fig. 5.

. 1987 *Cretoxyrhina mantelli* (Agassiz); Cappetta, p. 99, fig. 87*e–i*.
. 1990 *Cretoxyrhina mantelli* (Agassiz); Case *et al.*, p. 1087, fig. 9*a–f*.
v. 1992 *Cretoxyrhina mantelli* (Agassiz); Siverson, p. 526, pl. 1, figs 18–19.
. 1993 *Cretoxyrhina mantelli* (Agassiz); Welton and Farish, p. 101, unnumbered plate; p. 102, unnumbered plate.
. 1993 *Cretoxyrhina mantelli* (Agassiz); Williamson *et al.*, p. 456, fig. 6.10–6.15.

Material. Twenty teeth from the Thirindine Point ridge; five of these are from the basal 0·1 m of the Beedagong Claystone (WAM 95.7.32, 95.7.36, 96.3.10–96.3.12) and 15 teeth (WAM 95.7.29–95.7.31, 95.7.33–95.7.35, 95.7.37, 96.3.1–96.3.8) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. Cosmopolitan, for details see Cappetta (1987, p. 99) and also Siverson (1992) for post-Santonian occurrences.

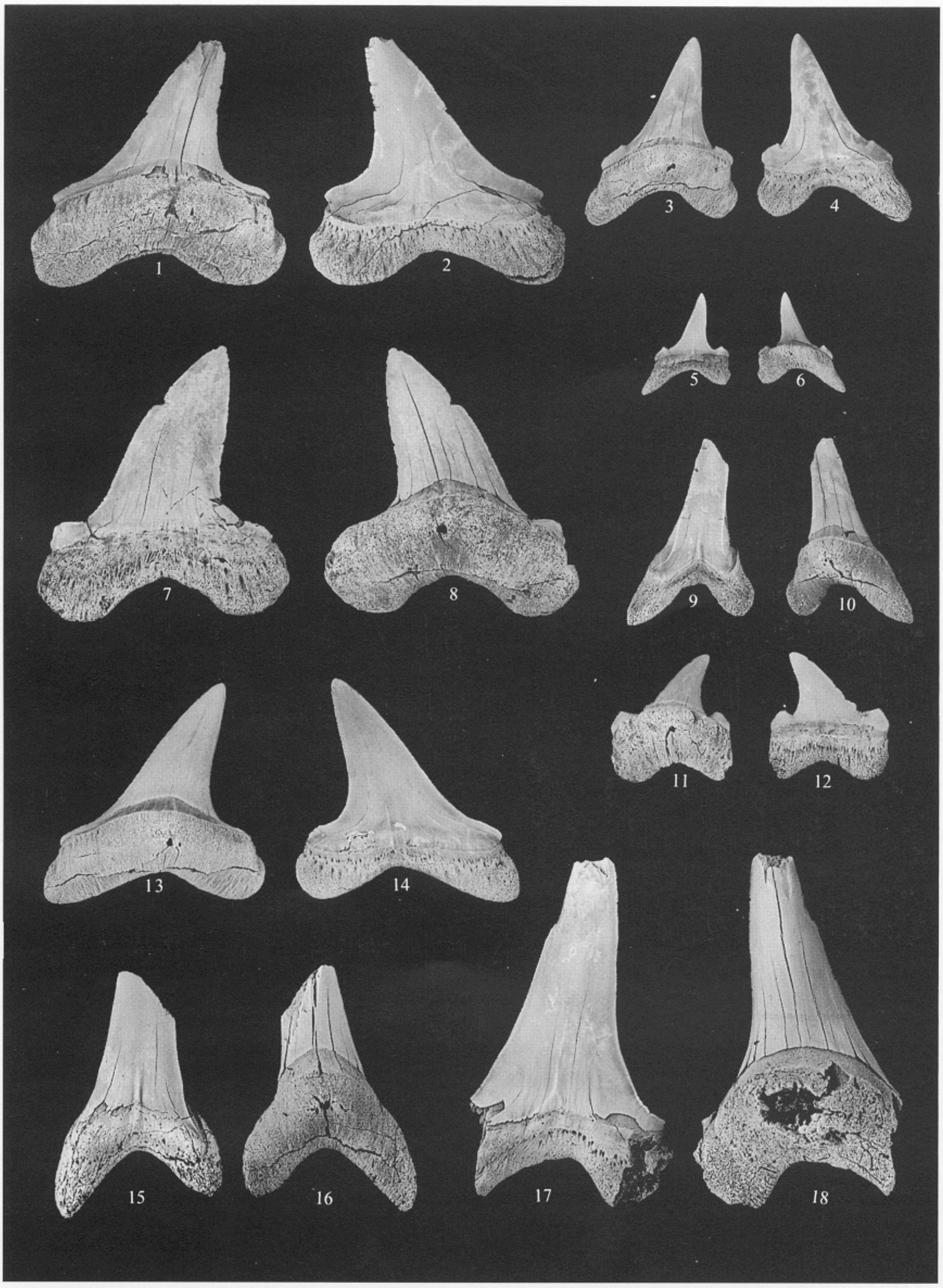
Description. In addition to the direct evidence of the arrangement of the upper jaw dental series presented here (Text-fig. 4), see also Eastman (1895) and Welton and Farish (1993) for different reconstructions of the dentition of this species based on associated but displaced teeth belonging to single individuals.

Remarks. The Western Interior Cretaceous Seaway of North America has yielded excellent material of *Cretoxyrhina mantelli*. As well as isolated teeth, the fossil remains include associated sets of teeth from single individuals (Eastman 1895; Welton and Farish 1993) together with articulated skeletons showing parts of the dentition still in place (Text-fig. 4; Siverson 1992; Shimada 1993). An associated set of displaced teeth from one individual of *C. mantelli*, collected from the mid to late Cenomanian (Kennedy 1988) part of the Britton Formation of Texas, provided Welton and Farish (1993, p. 102) with an opportunity to reconstruct the dentition. Their interpretation is in part at variance with what can be observed in the partly articulated upper dental series of a *C. mantelli* from the Smoky Hill Chalk Member of the Niobrara Formation of Kansas (FHSM VP-2187). The Niobraran specimen features two files of large, upper anterior teeth (Text-fig. 4), contrasting with the single one in Welton and Farish's reconstruction. In VP-2187 there is one file of intermediate teeth, identified as such by their distally curved cusps and almost symmetrical roots with a deeply notched basal edge. The intermediate tooth is larger than that of the first lateral file. Not appreciating this unusual condition, Siverson (1992, p. 528) considered the smallish teeth of the first lateral file to belong to a second intermediate file. The upper intermediate tooth in VP-2187 looks much like the tooth illustrated in a parasymphysial position by Welton and Farish. To the intermediate file, Welton and Farish referred a minute tooth with a morphology very similar to that of some of the upper symphysial teeth in VP-2187. The lateral teeth in VP-2187 show an initial increase in size towards the commissure followed by a decrease. This pattern is also present in some living lamnoids, such as *Isurus oxyrinchus* Rafinesque, 1810 (see Bass *et al.* 1975, pl. 9).

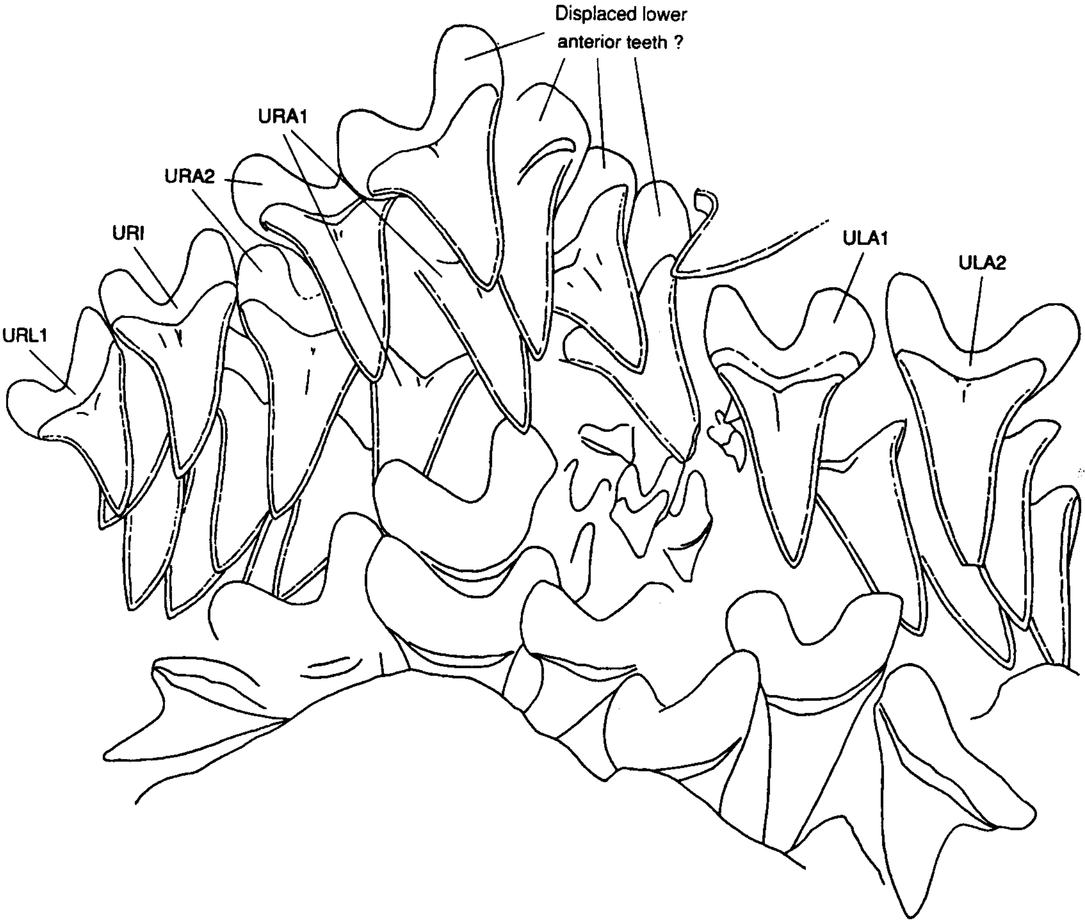
EXPLANATION OF PLATE 1

Figs 1–18. *Cretoxyrhina mantelli* (Agassiz, 1843). 1–2, WAM 95.7.30; 21·5 mm high lateral tooth, lingual and labial view; Thirindine Point west. 3–4, WAM 95.7.31; 16·5 mm high upper lateral tooth (UL2?) from a juvenile individual, lingual and labial view; Thirindine Point east. 5–6, WAM 95.7.32; 8·5 mm high upper lateral tooth (UL2?) from a very young individual, labial and lingual view; Thirindine Point east, 78 kg sample from the basal 0·1 m of the Beedagong Claystone. 7–8, WAM 95.7.33; 23·5 mm high lateral tooth, labial and lingual view; Thirindine Point west. 9–10, WAM 95.7.34; 16 mm high ?upper anterior tooth from a juvenile individual, apex of cusp broken off, labial and lingual view; Thirindine Point west. 11–12, WAM 95.7.35; 11 mm high posterior tooth, lingual and labial view; Thirindine Point east. 13–14, WAM 95.7.36; 19·5 mm high lateral tooth, lingual and labial view; Thirindine Point east, 78 kg sample from the basal 0·1 m of the Beedagong Claystone. 15–16, WAM 95.7.37; 22 mm high anterior tooth, labial and lingual view; Thirindine Point west. 17–18, WAM 95.7.29; 31 mm high anterior tooth from a large individual, apex of the cusp and both extremities of the root are broken off, labial and lingual view; Thirindine Point east. All × 1·8.

PLATE 1



SIVERSON, *Cretoxyrhina mantelli*



TEXT-FIG. 4. Symphysial area of the dentition of a *Cretoxyrhina mantelli* from the Niobrara Formation of Kansas (FHSM VP-2187). Note the presence of two files of anterior teeth in the upper jaw and the large size of the upper intermediate tooth. ULA1 = upper left 1st anterior; ULA2 = upper left 2nd anterior; URA1 = upper right 1st anterior; URA2 = upper right 2nd anterior; URI = upper right intermediate; URL1 = upper right 1st lateral. *Camera lucida* drawing from a photograph.

In his work on Cretaceous and Tertiary chondrichthyans of Australia, Kemp (1991) referred three of the teeth illustrated to *Cretoxyrhina*. One of them (WAM 60.90.1; Kemp 1991, pl. 4, fig. g), supposedly from the late Maastrichtian Miria Marl, Southern Carnarvon Basin, Western Australia, was figured as *Cretoxyrhina mantelli*. Examination of the imperfectly preserved tooth has revealed that it is not from a *Cretoxyrhina* but probably belonged to *Otodus obliquus* (Agassiz, 1843). The latter species is quite common in the Boongerooda Greensand of Thanetian (late Palaeocene) age which overlies the Miria Marl unconformably in the Giralia Anticline of the Southern Carnarvon Basin. The tooth is thus both misidentified and misplaced stratigraphically. The youngest reliable records of *C. mantelli* appear to be from the Kristianstad Basin, southern Sweden (Siverson 1992). There, it occurs sparsely in strata that correlate with the latest early Campanian *Gonioteuthis quadrata gracilis*/*Belemnitella mucronata senior* Zone (*sensu* Schulz *et al.* 1984). The second tooth (WAM 62.8.29), from the late Santonian *Uintacrinus*/*Marsupites* zones of the Gingin Chalk, Molecap Hill Quarry, Perth Basin, was illustrated by Kemp (1991, pl. 4, fig. h) under the name *Cretoxyrhina* cf. *mantelli*. This identification is also in error. The tooth-crown probably belongs to *Cretolamna appendiculata*. The third specimen, from the Aptian or Albian of Aramac, central Queensland, is poorly preserved and generically indeterminable. Kemp figured it as *Cretoxyrhina*? (pl. 4, fig. i).

Genus ARCHAEOLAMNA Siverson, 1992

Type species. Odontaspis kopingensis Davis, 1890, 'Köpinge sandstone' (latest early Campanian to mid late Campanian [*sensu* germanico]), Skåne, Sweden.

Remarks. Until now *Archaeolamna* was monospecific, comprising the type species *A. kopingensis* with its two geographically separated subspecies *A. k. kopingensis*, from the Campanian–Maastrichtian of the Anglo–Franco–Belgian Basin and southern Sweden, and *A. k. judithensis*, from the Campanian of the Western Interior Seaway of North America. The type species was recently also recorded under various names from the Santonian–Campanian of the Russian Platform (Zhelezko, 1990, pl. 9, figs 1–14 and pl. 10, figs 1–25). An *Archaeolamna* from the middle Albian of north-eastern France was described by Biddle (1993) as *A. kopingensis*. However, in *A. kopingensis* the lingual protuberance of the root displays a small median foramen, whereas in the Albian teeth from France the protuberance is divided by a distinct median groove. In an Albian population of *Archaeolamna* from the Gearle Siltstone in the Giralia Anticline of the Southern Carnarvon Basin, Western Australia, a median groove is present in juveniles but closed in adults (pers. obs.). Teeth of juvenile Campanian *A. kopingensis* conform with those of coeval adults in lacking a median groove. Loss of a median groove on the root protuberance took place independently in several of the Cretaceous cretoxyrhinids.

Archaeolamna aff. *kopingensis*

Plate 2, figures 1–6

Material. Four teeth from the Thirindine Point ridge; all of them (WAM 95.7.38–95.7.40, 96.3.9) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. In size and morphology these teeth are very close to those of mid Campanian *A. kopingensis* from southern Sweden (see Siverson 1992 for a detailed description). One of the upper lateral teeth from the Alinga Formation/Beedagong Claystone has short but strong labial folds along the base of the crown below the cusplets (WAM 95.7.40; Pl. 2, fig. 6). In *A. kopingensis*, such folds are present only in teeth from approximately the posterior quarter of the tooth row (see Siverson 1992, pl. 2, figs 8–9).

Remarks. One of the upper lateral teeth (WAM 95.7.40) of *A.* aff. *kopingensis* resembles one of the type specimens of *Pseudoisurus tomosus*, the latter figured in lingual view by Glikman (1957, pl. 1, fig. 20). However, the Russian specimen has a relatively broader neck and is much larger (about 30 mm high) than any upper lateral teeth of *Archaeolamna* that I have examined, including WAM 95.7.40, which is 18 mm high.

Archaeolamna haigi sp. nov.

Plate 2, figures 7–13

Derivation of name. After Dr David Haig, Department of Geology, University of Western Australia, in recognition of stimulating discussions on the Cretaceous geology of Western Australia.

Holotype. WAM 95.7.41; Plate 2, figures 7–9, upper anterior tooth; Thirindine Point Ridge (eastern slope); uppermost metre of Alinga Formation or basal part of Beedagong Claystone.

Paratypes. WAM 95.7.42 and WAM 95.7.43; Plate 2, figures 10–13.

Additional material. Nine teeth from the Thirindine Point ridge; all of them (WAM 96.3.13–96.3.21) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Diagnosis. Lingual face of crown with flexuous folds. Labial face of cusp often concave in anterior teeth. Lower laterals erect and symmetrical. Root slender and, in lateral files, labiolingually compressed.

Description. Anterior teeth are up to 20·5 mm high. There is one pair of triangular cusplets. The labial face of the cusp is slightly convex to concave and smooth; the lingual face is much more cambered and, together with the cusplets, with weak to moderately well-marked flexuous folds. The lingual face of the cusp is medially flattened in some anterior teeth, giving the cusp a sub-rectangular cross section. Lower lateral teeth are erect, have one pair of triangular cusplets and feature prominent lingual folds. The lingual protuberance of the gracile root features an apicobasally elongated median foramen.

Comparison. The teeth of *A. haigi* sp. nov. are easily separated from those of the only other valid named species of the genus, *A. kopingensis*, by their lingual folds on the crown and significantly more slender root. Moreover, lower lateral teeth are always asymmetrical in *A. kopingensis* with a cusp slightly bent towards the commissure, whereas in *A. haigi* sp. nov. the lower lateral teeth are symmetrical. In most of the anterior teeth of *A. haigi* sp. nov., the labial face of the cusp is concave. In *A. kopingensis* the labial face is slightly convex, never concave.

Remarks. With dental features like flexuous lingual folds, bilateral symmetry and a labiolingually compressed root in lower lateral files, and slender anterior teeth, *A. haigi* had convergently acquired a tooth morphology approaching that of some odontaspidids like *Carcharias*.

Genus LEPTOSTYRAX Williston, 1900

Type species. Leptostyrax bicuspidatus Williston, 1900, from the Albian Mentor Beds of Kansas, USA.

Remarks. Cappetta (1987) and Siverson (1992) referred *Leptostyrax* to the family Cretoxyrhinidae. This view was apparently not shared by Biddle (1993), who argued that there are important differences in the dental series between *Leptostyrax* and true cretoxyrhinids. According to Biddle, cretoxyrhinids possess no parasymphysial teeth and only a single upper intermediate file, whereas in *Leptostyrax* there is a parasymphysial file as well as multiple files of intermediate teeth. A *Cretoxyrhina mantelli* specimen (FHSM VP-2187) from the Niobrara Formation of Kansas includes parts of the upper jaw dentition still in place, showing the presence of dwarfed parasymphysial teeth (Text-fig. 4). Thus, application of Biddle's definition of Cretoxyrhinidae would exclude *Cretoxyrhina*

EXPLANATION OF PLATE 2

Figs 1–6. *Archaeolamna* aff. *kopingensis* (Davis, 1890). 1–2, WAM 95.7.38; 16·5 mm high lower lateral tooth, root incomplete, labial and lingual view; Thirindine Point west. 3–4, WAM 95.7.39; 15 mm high upper lateral tooth, tip of cusp missing, lingual and labial view; Thirindine Point east. 5–6, WAM 95.7.40; 18 mm high upper lateral tooth, lingual (stereo pair) and labial view; Thirindine Point east. All × 2·4.

Figs 7–13. *Archaeolamna haigi* sp. nov. 7–9, WAM 95.7.41, holotype; 18·5 mm high upper anterior tooth, labial (stereo pair), lingual (stereo pair) and profile view; Thirindine Point east. 10–11, WAM 95.7.42, paratype, 12·5 mm high upper ?anterior tooth, labial and lingual view; Thirindine Point east. 12–13, WAM 95.7.43, paratype; 9·5 mm high lower lateral tooth, root incomplete, labial and lingual view; Thirindine Point east. All × 2·4.

Fig. 14. *Leptostyrax* sp.; WAM 95.7.44; 9 mm high anterior tooth, root poorly preserved, labial view; Thirindine Point east; × 3.

SIVERSON, *Archaeolamna*, *Leptostyrax*

mantelli from the family. Biddle's interpretation of the dentition in the designated (Cappetta 1980) type species of *Leptostyrax* was at least in part influenced by Sokolov's (1978) reconstruction of the dental series of a species from the Vraconian of the Mangyshlak Province, Kazakhstan, referred by him to *Megarhizodon macrorhiza* (Cope, 1875). Cappetta (1987) showed that *Megarhizodon* Sokolov, 1978 is a junior synonym of *Leptostyrax*. According to Cappetta (1987) the sample figured by Sokolov is not from a *Leptostyrax* but belongs to a species of *Protolamna* Cappetta, 1980. Biddle (1993) was of the opinion that the latter nominal genus is synonymous with the older *Leptostyrax*. While applying Cappetta's definition of *Protolamna* and *Leptostyrax*, Welton and Farish (1993) had no difficulty separating the two genera in a late Albian fauna from the Weno Formation of Texas.

Leptostyrax sp.

Plate 2, figure 14

Material. One tooth (WAM 95.7.44) from the Thirindine Point ridge, surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. An 8·9 mm high imperfectly preserved tooth. The labial face of the cusp is almost flat with the cutting edges so close together that the marginal parts of the strongly cambered lingual side can be seen in labial view. The lateral cusplets, parallel to the cusp, rise from bases below that of the cusp and are separated from it by narrow grooves. In profile view, their labial faces are in front of that of the cusp. Flexuous folds, present on both sides of the cusp and cusplets, are a little stronger and extend higher up on the labial face. The neck, separating the lingual face of the crown from the root, is about 0·6 mm wide.

The root is poorly preserved, having sustained corrosion. The lingual protuberance is mesiodistally narrow, very high and lacks a median groove.

Remarks. The small size of the tooth, compared with that of other illustrated examples of the genus, indicates that it may be from a juvenile individual. The tooth differs from those of the designated type species, *L. macrorhiza* (Cope, 1875) from the Albian of Kansas and Texas, by its mesiodistally narrower lingual protuberance of the root and relatively longer folds. The latter difference could, however, be largely or wholly due to the small size of the tooth. In *Leptostyrax* the folds are relatively shorter in larger teeth.

Genus CRETOLAMNA Glikman, 1958

Type species. Otodus appendiculatus Agassiz, 1843, from the Turonian of Lewes, England.

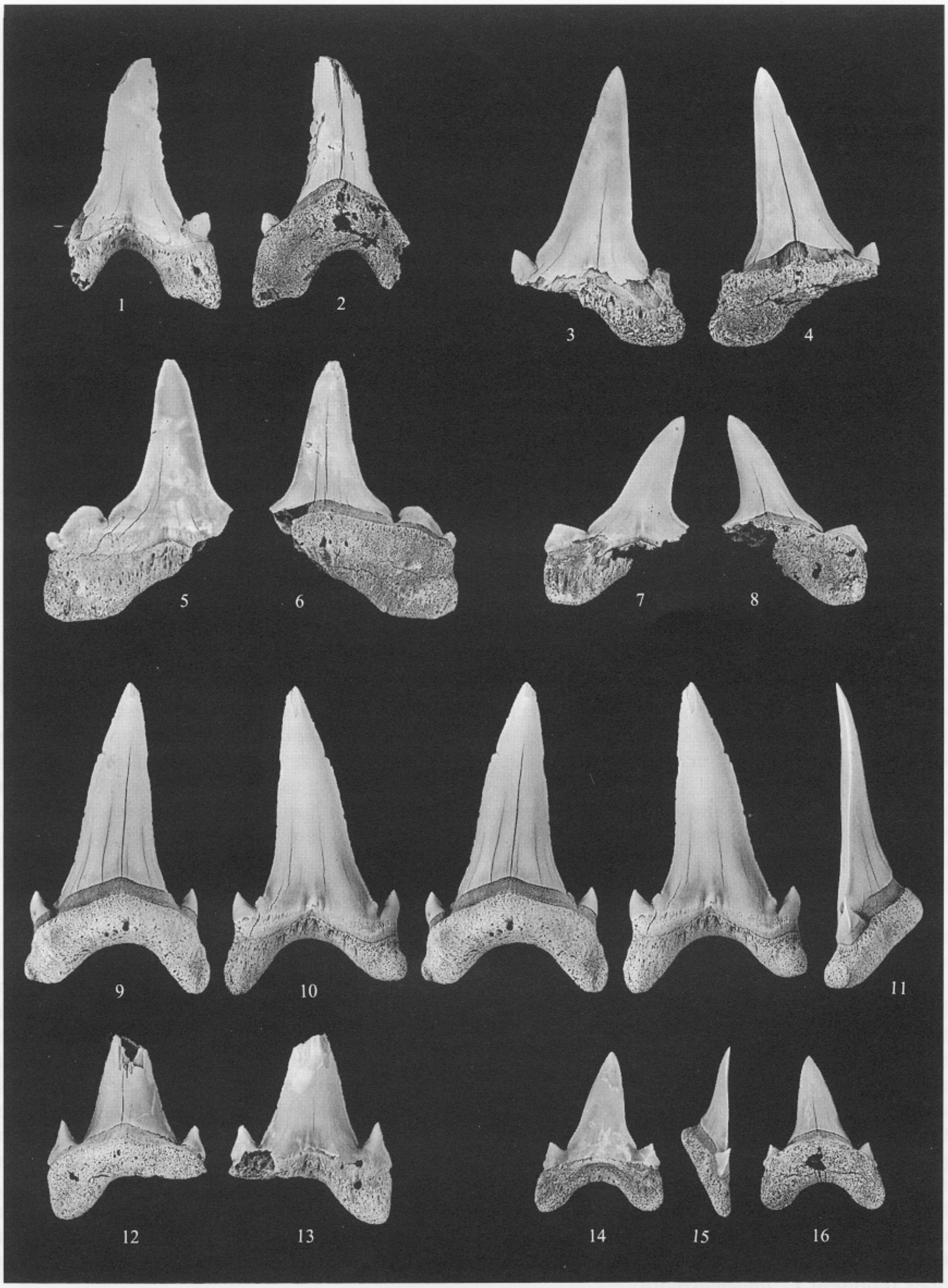
EXPLANATION OF PLATE 3

Figs 1–8. *Cretolamna appendiculata* (Agassiz, 1843). 1–2, WAM 95.7.45; 16 mm high lower anterior tooth, tip of cusp and mesial extremity of root broken off, labial and lingual view; Thirindine Point east. 3–4, WAM 95.7.46; 18 mm high upper anterior tooth (UA2), distal cusplet and mesial portion of the root missing, labial and lingual view; Thirindine Point east. 5–6, WAM 95.7.47; 16·5 mm high lower lateral tooth, cusplet and root lobe broken off on one side, labial and lingual view; Thirindine Point east. 7–8, WAM 95.7.48; 12·5 mm high upper lateral tooth, distal lobe of root and distal cusplet missing, labial and lingual view; Thirindine Point east. All ×2·4.

Figs 9–13. *Cretolamna gunsoni* sp. nov. 9–11, WAM 95.7.49; holotype; 24 mm high upper left anterior tooth (UA2), lingual (stereo pair), labial (stereo pair) and profile view; Thirindine Point east, *in situ* 0·52 m below the base of the Beedagong Claystone. 12–13, WAM 95.7.50; paratype; 14 mm high lower lateral tooth, apex of cusp and one root lobe broken off, lingual and labial view; Thirindine Point south. Both ×2.

Figs 14–16. *Pseudoisurus tomosus* Glikman, 1957, WAM 95.7.51; 13·5 mm high lower lateral tooth, labial, profile and lingual view; Thirindine Point east; ×1·8.

PLATE 3



SIVERSON, *Cretolamna*, *Pseudoisurus*

Cretolamna appendiculata (Agassiz, 1843)

Plate 3, figures 1–8

*1843 *Otodus appendiculatus* Agassiz, p. 270, pl. 32, figs 2–8, 10–14, 16, 19, 22, 24–25, ?figs 20, 23, *non* figs 1, 9, 15, 17–18, 21.
.1977 *Cretolamna appendiculata* (Agassiz); Herman, p. 210, pl. 9, figs 2–4 [contains synonyms prior to 1973].
.1987 *Cretolamna appendiculata* (Agassiz); Longbottom and Patterson, p. 249, text-fig. 11.2z, pl. 54, fig. 4.
v.1991 *Cretolamna appendiculata* (Agassiz); Kemp, pl. 4, fig. d.
v.1991 *Cretoxyrhina* cf *mantelli* (Agassiz); Kemp, pl. 4, fig. h.
.1991 *Cretolamna appendiculata* (Agassiz); Müller and Diedrich, p. 31, pl. 21, figs 7–8.
.1991 *Cretolamna appendiculata*; Landemaine, p. 13, fig. 4*a*.
v.1992 *Cretolamna appendiculata* (Agassiz); Siverson, p. 528, pl. 1, figs 1–17 [contains synonyms from 1975 to 1989].
.1992 *Otodus appendiculatus* Agassiz; Manning and Dockery III, p. 26, pl. 4, figs 5–6.
.1993 *Cretolamna appendiculata* (Agassiz); Welton and Farish, p. 103, unnumbered plate, figs 1–5; p. 104, unnumbered plate, figs 1–2.
.1993 *Cretolamna woodwardi* (Herman); Welton and Farish, p. 105, unnumbered plate, figs 1–3.
.1993 *Cretolamna appendiculata* (Agassiz); Williamson *et al.*, p. 454, fig. 6.1–6.6.

Material. Five teeth from the Thirindine Point ridge; all of them (WAM 95.7.45–95.7.48, 96.3.22) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. Cosmopolitan; for details see Herman (1977, p. 215).

Description. See Welton and Farish (1993) for illustration of a reconstructed tooth set of the species.

Remarks. Welton and Farish (1993, p. 104) constructed a composite tooth set of *C. appendiculata*, based on well-preserved teeth from the late Albian Weno Formation of Texas. In their reconstruction, there are two files of upper anterior teeth. As in *C. gunsoni* sp. nov., described below, I believe that there were in fact three upper anterior files in *C. appendiculata*. The two upper anterior teeth in Welton and Farish's tooth set are probably from the first and third anterior files respectively. Welton and Farish referred a dwarfed tooth to the upper jaw intermediate file. Similar teeth from the lower Campanian of the Kristianstad Basin, southern Sweden, were interpreted by Siverson (1992, pl. 1, figs 12–17) as parasymphysial teeth of the same species. Although this interpretation may be incorrect, similar teeth are indeed located at the symphysis in another cretoxyrhinid, *Cretoxyrhina mantelli* (Text-fig. 4; Siverson, 1992, p. 528).

Kemp (1991, pl. 4, figs a–e) figured five teeth from the Australian Cretaceous as *C. appendiculata*, one from the early Late Cretaceous Molecap Greensand of the Perth Basin, Western Australia (fig. d; WAM 63.9.25) and four from the Albian of the Eromanga Basin, Queensland. The Western Australian tooth is unquestionably from *C. appendiculata*. The tooth in Kemp's figure e can also be assigned with confidence to *Cretolamna* but probably not *C. appendiculata*. Very similar teeth have recently been collected from Albian strata of the Gearle Siltstone in the Giralia Anticline of the Southern Carnarvon Basin, Western Australia. They may represent a new species of *Cretolamna* and are the oldest examples of the genus. Of the remaining three teeth figured by Kemp, two (figs a–b) are definitely not *C. appendiculata*. In size and general morphology, they most closely resemble the teeth of *Pseudoisurus* Glikman, 1957 and primitive *Cretoxyrhina*. The last tooth (fig. c) is too poorly preserved to comment upon. In addition to these five specimens assigned by Kemp to *C. appendiculata*, he also illustrated a tooth under the name *Cretolamna* cf. *appendiculata* (pl. 4, fig. f). The age of this Queensland specimen is not known and it does not look like the teeth of *C. appendiculata*. Finally, as suggested above, the late Santonian tooth-crown from the Gingin Chalk of the Perth Basin, referred by Kemp to *Cretoxyrhina* cf *mantelli* (pl. 4, fig. h) probably does represent *C. appendiculata*.

Cretolamna gunsoni sp. nov.

Plate 3, figures 9–13

Derivation of name. After Mark Gunson, Department of Geology, University of Western Australia, in recognition of field assistance.

Holotype. WAM 95.7.49; Plate 3, figures 9–11, second upper left anterior tooth; eastern slope of the Thirindine Point ridge; middle of a 0·35 m thick bed characterized by conspicuous *Chondrites* and *Planolites*, 0·52 m below the base of the Beedagong Claystone (see Text-fig. 3).

Paratype. WAM 95.7.50; Plate 3, figures 12–13, lower lateral tooth.

Additional material. Five teeth from the Thirindine Point ridge; all of them (WAM 96.3.23–96.3.27) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Diagnosis. Upper anterior teeth with gracile root, moderately labiolingually compressed. Tip of cusp curved outwards. Cusplets, narrow in juveniles, with straight to convex outer margin. Base of crown may overhang root labially.

Upper laterals with cambered labial face of distally directed cusp almost as convex as lingual face. In anteriorly situated lateral teeth, cusplets erect, higher than broad and with straight to convex outer margins. In middle part of tooth-row, cusplets usually asymmetrical with outer margin much longer than inner one. Root labiolingually compressed with angular extremities.

Lower laterals erect with cusplets higher than broad. Labial face of cusp less convex than in upper lateral teeth. Root labiolingually compressed and relatively slender.

Description. Upper anterior teeth, of which there are probably three on each side of the symphysis, reach at least 24 mm high in the Alinga Formation population. There is one pair of comparatively small cusplets which are higher than wide. The tip of the cusp is curved outwards on all upper anterior teeth. In teeth of the first upper anterior file the cusp is symmetrical. In the second upper anterior file (Pl. 3, figs 9–11), the cusp is slightly curved towards the commissure. The third upper anterior tooth features a cusp with its basal half bent somewhat distally whereas the apical half is slightly mesially curved, much as in the third upper anterior tooth of the extant *Carcharias taurus* Rafinesque, 1810. Labially, the base of the crown may overhang the root, which is rather gracile and moderately labiolingually compressed. A single circular foramen opens on a relatively high lingual protuberance.

Mesially situated upper lateral teeth have a high, distinctly distally bent cusp. The labial face of the cusp is cambered and the cusplets are erect, higher than broad and with straight inner and convex outer edges. The root is gracile and labiolingually compressed. In more posteriorly situated lateral teeth, the cusp is lower and the cusplets are distinctly asymmetrical with the outer margin significantly longer than the inner one.

Lower lateral teeth possess a more-or-less erect cusp with a relatively flat labial face. The root is labiolingually compressed and slender.

Comparisons. The teeth of *Cretolamna gunsoni* are readily separable from those of coeval *C. appendiculata* by the following features: (1) the root is markedly labiolingually compressed in the upper anterior teeth of *C. appendiculata*, less so in those of *C. gunsoni*; (2) cusplets are usually broader than high in *C. appendiculata* whereas the reverse condition prevails in *C. gunsoni*, at least in the anterior half of the dentition; (3) in upper anterior files of *C. gunsoni* the cusplets have a straight to convex outer cutting edge and are often curved toward the cusp, whereas in the corresponding teeth of *C. appendiculata* the outer edge of the cusplets is straight to concave and the cusplets are curved away from the cusp; (4) the labial face of the cusp is flat in upper lateral teeth of *C. appendiculata*, markedly convex in *C. gunsoni*; (5) in upper lateral files near the centre of the tooth row of *C. gunsoni* the outer margins of the cusplets are significantly longer than the inner ones, whereas in *C. appendiculata* they are roughly the same length; (6) in young *C. gunsoni* the cusplets are narrow and elongated in anterior files, in contrast to juvenile *C. appendiculata* which display cusplets with a wide base on their anterior teeth.

Remarks. Teeth of *Cretolamna gunsoni* sp. nov. are common in the transitional beds between the Gearle Siltstone and the overlying Beedagong Claystone at C-Y Creek in the Giralia Anticline of the Southern Carnarvon Basin (pers. obs.).

This is the second known mid Cretaceous species of *Cretolamna*. As shown below, Herman's (1977) nominal *Cretolamna woodwardi* has a tooth morphology quite different from that of true *Cretolamna* and is here regarded as a junior synonym of *Pseudoisurus tomosus*.

Genus PSEUDOISURUS Glikman, 1957

Type species. Pseudoisurus tomosus Glikman, 1957, from the upper Cenomanian (in the Russian two-fold division of the stage) of the Volga area, Russia.

Remarks. Siverson (1992) shared the views of Herman (1977) and Cappetta (1987) that *Pseudoisurus* is a poorly defined genus and indicated that it might prove to be synonymous with *Archaeolamna* Siverson, 1992. New material from the Albian and Cenomanian of Western Australia indicates that both nominal genera are valid. Glikman's (1957) original description of *Pseudoisurus tomosus* is accompanied by illustrations of four teeth (pl. 1, figs 17–20). One of them is rather poorly preserved (fig. 18) and another is figured in profile view only (fig. 19), limiting their usefulness for comparisons. The remaining two teeth (figs 17, 20) are both from upper lateral tooth-files. They are almost perfectly matched by two corresponding teeth from the Thirindine Point ridge (Pl. 4, figs 3–4, 8–10). However, the latter two teeth are probably specifically, if not generically, distinct from each other. Both are imperfectly preserved, lacking their distal cusplet and parts of the distal lobe of the root. The larger tooth (WAM 95.7.28; Pl. 4, figs 8–10), very similar to the tooth in Glikman's figure 20, is markedly curved toward the rear. The labial face of the cusp is distinctly convex and the mesial and distal cutting edges of the mesial cusplet are equal in length. Moreover, in occlusal view the apical half of the cusp is slightly rotated anti-clockwise. The smaller tooth (WAM 95.7.53; Pl. 4, figs 3–4), closely resembling the tooth in Glikman's figure 17, features a cusp moderately bent toward the commissure. The labial face of the cusp is flat and the mesial cutting edge of the mesial cusplet is almost twice as long as the distal edge. Six additional teeth in the collection from the transitional beds between the Alinga Formation and the Beedagong Claystone conform closely to WAM 95.7.53 with regard to the very flat labial face of the cusp and shape of the lateral cusplets. These seven latter teeth grouped together appear specifically inseparable from two sets of associated teeth from the middle or upper Cenomanian of southern England, figured as *Lamna appendiculata* (Agassiz, 1843) by Woodward (1894). The latter taxon is the type species of *Cretolamna* Glikman, 1958. Herman (1977) rightly considered the English teeth to be distinct from those of *C. appendiculata* and proposed the new nominal species *Cretolamna woodwardi* to accommodate them.

As can be gathered from the discussion above, the Western Australian material indicates that the Cenomanian nominal species *Cretolamna woodwardi* and *Pseudoisurus tomosus* are at least in part synonomous and that the latter may be based on a mixture of two different taxa. For the time being I treat Glikman's figured sample of *P. tomosus* as homogeneous and wholly conspecific with Herman's *C. woodwardi*. The former nominal species takes priority by 20 years. I do not agree with Herman's generic assignment of the species, in particular the morphology of the root in upper lateral teeth is very different in true *Cretolamna* and *P. tomosus* (= *C. woodwardi*).

Dental differences between *Pseudoisurus*, as defined herein, and *Archaeolamna* include: (1) in upper lateral files the cusp usually expands more or less abruptly in width within the basal third of its height in *Archaeolamna* (see e.g. Woodward 1894, pl. 6, fig. 10; Herman 1977, pl. 8, fig. 4*i*; Siverson 1992, pl. 2, fig. 12; Pl. 2, fig. 6), whereas in adult *Pseudoisurus* the cusp increases more linearly in width toward its base (Woodward 1894, pl. 5, fig. 25; pl. 6, fig. 2); (2) the lingual neck is medially very wide in anterior teeth of *Pseudoisurus* (Woodward 1894, pl. 6, fig. 2f); less so in

Archaeolamna (Herman 1977, pl. 8, fig. 4*d*, *g*; Case 1987, pl. 3, fig. 8); (3) the inner and outer cutting edges of the cusplets are of equal length in *Archaeolamna* whereas in *Pseudoisurus* the outer one is often significantly longer than the inner one, especially on the mesial cusplet (Pl. 4, fig. 1); (4) the dental ontogeny in the two genera differs in that the shape of the lateral cusplets does not change markedly during ontogeny in *P. tomosus*, whereas in *Archaeolamna* the cusplets are high and slender in juveniles but relatively lower and with a broader base in adults.

It should also be pointed out that the teeth of *P. tomosus* reach a considerably larger maximum size (about 40 mm in height) than those of coeval *Archaeolamna* (about 25 mm in height).

Pseudoisurus tomosus Glikman, 1957

Plate 3, figures 14–16; Plate 4, figures 1–4

1894	*Lamna appendiculata* (Agassiz); Woodward, p. 197, pl. 5, fig. 25, pl. 6, fig. 2.
1912	*Lamna appendiculata* (Agassiz); Woodward, p. 206, text-figs 63–64; pl. 44, figs 6, ?7.
* 1957	*Pseudoisurus tomosus* Glikman, p. 116, pl. 1, figs 17–20.
1964*a*	*Pseudoisurus tomosus* Glikman; Glikman, p. 230, pl. 4, fig. 6.
?1977	*Cretolamna woodwardi* Herman, p. 207, pl. 9, fig. 1*a*–*b*.
1980	*Pseudoisurus tomosus* Glikman; Glikman, pl. 17, fig. 14.

Material. Seven teeth from the Thirindine Point ridge; all of them (WAM 95.7.51–95.7.53, 96.3.28–96.3.31) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. Upper Cenomanian (in the Russian two-fold division of the stage) of the Saratov region, Russian Platform; middle or upper Cenomanian of Maidstone and Dover, southern England; and possibly the upper Cenomanian (*Actinocamax plenus* Zone) of Bettrechies, northern France and the Turonian (*Terebratulina rigida* Zone) of Chercq, Belgium.

Emended diagnosis. Anterior teeth erect with tall, narrow to moderately broad cusp. Lower laterals almost symmetrical; upper ones with distally directed cusp. Crown smooth, at least in anterior and lateral teeth. Labial face of cusp very flat. Cutting edges continuous, without serrations. One pair of broad-based lateral cusplets. Mesial cusplet with outer margin about one-and-a-half times to twice as long as the inner one. Root thick and of similar appearance in all files with basal edge forming open, evenly curved arch. Lingual protuberance without median grooves. Lobes well separated and diverging with rounded extremities. Lingual neck wide at centre of cusp in anterior teeth but diminishes rapidly in width toward lateral margins of crown. Relative size and shape of lateral cusplets remain constant throughout ontogeny.

Description. The three selected teeth described below are the best preserved from the Thirindine Point ridge.

WAM 95.7.51 (Pl. 3, figs 14–16); a 13·5 mm high well preserved lower lateral tooth from a juvenile individual. Outer margins of the cusplets are almost twice as long as the inner ones. The basal edge of the root forms a broadly rounded open arch. Maximum labiolingual thickness of the root is about 4·1 mm.

WAM 95.7.52 (Pl. 4, figs 1–2); a 21 mm high tooth, probably from the third anterior file in the lower jaw. The specimen compares well in size and proportions with a tooth from the type series of *C. woodwardi* (see Woodward, 1894, pl. 5, fig. 25*n*).

WAM 95.7.53 (Pl. 4, figs 3–4); a 16 mm high upper lateral tooth from a young individual. The distal cusplet and the tip of the distal lobe of the root are missing. The mesial cusplet shows typical features of the species with an outer margin much longer than the inner one. This tooth is close in morphology to one of the type specimens of *P. tomosus* (see Glikman, 1957, pl. 1, fig. 17).

Remarks. The type material of the nominal *Cretolamna woodwardi* is Cenomanian in age. Herman (1977), Williamson *et al.* (1993) and Welton and Farish (1993) also reported it from the Turonian.

Herman's example is a well-preserved anterior tooth from Belgium. It does indeed display features typical for anterior teeth in *C. woodwardi*, including a medially well-developed neck and a markedly concave base of the labial enameloid. However, at present, I cannot assign it to the nominal *C. woodwardi* with confidence, as it may belong to the poorly known *Pseudoisurus*? sp., described below.

The early Turonian tooth from Arizona, figured as *C. woodwardi* by Williamson *et al.* (1993, fig. 6.7–6.8) belonged to a lateral file, probably in the upper jaw. This specimen exhibits some typical traits of *C. woodwardi*, such as a well-developed neck and root lobes wide apart with the basal edge of the root forming a broad, evenly curved open arch. Nevertheless, it differs from lateral teeth of Cenomanian *C. woodwardi* by its distinctly convex rather than flat labial face of the cusp and thicker cusp in profile view. It is closer in morphology to *Pseudoisurus*? sp., described below.

Welton and Farish (1993, p. 105) figured as *C. woodwardi* three teeth from the late mid to early late Turonian (Kennedy, 1988) Arcadia Park Formation of Texas. Two of them are from anterior files whereas the third is an upper lateral tooth. The two authors were of the opinion that their material is very close in morphology to Herman's (1977) figured examples of *C. woodwardi*. It is not absolutely clear whether Welton and Farish's reference to Herman's figured material meant the English type specimens of *C. woodwardi* or the two isolated teeth from, respectively, Belgium and northern France, also referred to the species by Herman. Welton and Farish also suggested that *C. woodwardi* may be a junior synonym of *Cretolamna appendiculata*, being based on teeth from old individuals of the latter. In this view, the type specimens of *C. woodwardi* are from an old individual and the three smaller teeth from Texas figured by them as *C. woodwardi* are likewise from old sharks of the same nominal species which actually may be denominating old individuals of *C. appendiculata*. As shown herein, the uppermost beds of the Alinga Formation and/or the basal Beedagong Claystone have yielded teeth taxonomically inseparable from the type specimens of *C. woodwardi*. The collection includes teeth from juveniles as well as older individuals. The juvenile specimens are as distinct from the teeth of *C. appendiculata* as are those from old individuals. Consequently, Welton and Farish's hypothesis that *C. woodwardi* possibly denominates teeth from old individuals of *C. appendiculata* is rejected. In the description of their material referred to *C. woodwardi*, Welton and Farish pointed out that the lateral teeth are very close in morphology to those of *C. appendiculata*. It seems likely that the upper lateral tooth figured by them as *C. woodwardi* resembles the corresponding ones of *C. appendiculata* simply because it is indeed a tooth from the latter species. From Woodward's illustrations of the two English sets of associated teeth, one of which comprises the type series of *C. woodwardi*, it is obvious that the root in upper lateral teeth of that species is different from the characteristic, angular one in *C. appendiculata*. The two anterior teeth figured by Welton and Farish are superficially similar to the Turonian tooth from Belgium figured by Herman as *C. woodwardi*, which, as indicated above, may not be from a *C. woodwardi*. Nevertheless, a closer examination reveals important differences. In the Belgian specimen, the neck is medially very well developed and in labial view the enameloid reaches

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EXPLANATION OF PLATE 4

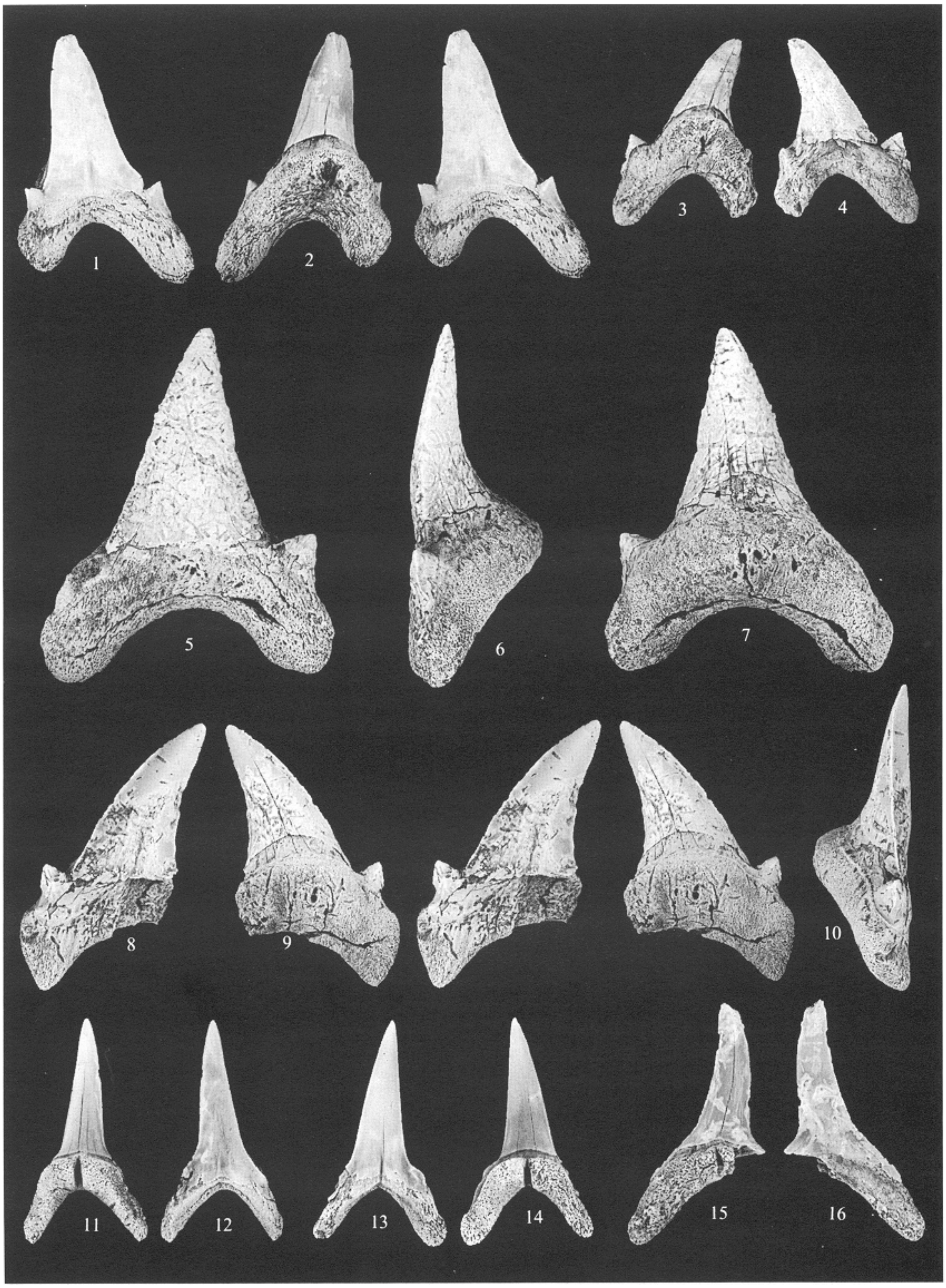
Figs 1–4. *Pseudoisurus tomosus* Glikman, 1957. 1–2, WAM 95.7.52; 21 mm high lower anterior tooth (LA3), labial (stereo pair) and lingual view; Thirindine Point east. 3–4, WAM 95.7.53; 16 mm high upper lateral tooth (UL1 or UL2), specimen corroded and lacks distal cusplet, lingual and labial view; Thirindine Point east. Both × 1·8.

Figs 5–10. *Pseudoisurus*? sp. 5–7 WAM 95.7.27; 29·5 mm high lower lateral tooth, one cusplet missing, labial, profile and lingual view; Thirindine Point west. 8–10, WAM 95.7.28; 21·5 mm high upper lateral tooth, distal root lobe and cusplet broken off, labial (stereo pair), lingual (stereo pair) and profile view; Thirindine Point west. Both × 1·8.

Figs 11–14. *Paranomotodon* sp. 11–12, WAM 95.7.54; 14 mm high anterior tooth, lingual and labial view; Thirindine Point east. 13–14, WAM 95.7.55; 14 mm high anterior tooth, labial and lingual view; Thirindine Point east. Both × 2·4.

Figs 15–16. '*Anomotodon*' sp.; WAM 95.7.56; 16 mm high upper left anterior tooth (UA3), distal half of the root missing, lingual and labial view; Thirindine Point east; × 2·4.

PLATE 4



SIVERSON, *Pseudoisurus*, *Paranomotodon*, '*Anomotodon*' downward beyond the base of the cusplets, giving the base of the crown a markedly acute, concave outline. In contrast, the neck is only moderately developed in the two Texan teeth which are considerably smaller (assuming the scale bar is accurately drawn), and the enameloid does not extend much beyond the base of the cusplets. All three Texan teeth fall well within the range of late Cenomanian/Turonian *C. appendiculata* (see Herman, 1977, pl. 9, fig. 2). Finally, as demonstrated above, the nominal *Cretolamna woodwardi* is probably in part or wholly synonymous with the nominal *Pseudoisurus tomosus.*

Pseudoisurus? sp.

Plate 4, figures 5–10

?1977 *Cretolamna woodwardi* Herman, p. 207, pl. 9, fig. 1*a*–*b*.
?1992 *Pseudoisurus tomosus* (Glikman); Siverson, p. 530.
?1993 *Cretolamna woodwardi* Herman; Williamson *et al.*, p. 456, fig. 6.7–6.9.

Material. Two teeth from the Thirindine Point ridge; both (WAM 95.7.27–95.7.28) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. The same or a closely related species occurs in the Turonian of the Western Interior (Montana, Arizona) of the USA, and possibly in the Turonian of Belgium.

Description. WAM 95.7.27 (Pl. 4, figs 5–7); a 29·5 mm high lower lateral tooth, lacking its mesial cusplet. The cusp is moderately high with straight margins and separated lingually from the root by a broad neck. The root is massive, about 12 mm in maximum labiolingual thickness. Its lingual protuberance is not well demarcated. The basal edge of the root is smoothly concave, forming a broad open arch.

WAM 95.7.28 (Pl. 4, figs 8–10); an incomplete 21·5 mm high upper lateral tooth. It lacks a distal cusplet and the distal lobe of the root is broken off. The cusp is curved toward the commissure and its labial face is markedly convex. In occlusal view, the apical half of the cusp is slightly rotated anti-clockwise. The mesial cusplet is rather small, broad-based and with its inner margin at right angles to the base of the mesial edge of the cusp. The neck is broad and well set off from the root by a distinct ridge. As in WAM 95.7.27, the root is bulky.

Comparison. The lower jaw tooth resembles similar-sized lower lateral teeth of *P. tomosus*, but differs, in profile view, by its significantly more slender and slightly lingually curved cusp. Moreover, in *P. tomosus* the labial face of the cusp is perfectly flat whereas in WAM 95.7.27 it is slightly convex.

Remarks. The two teeth are referred tentatively to *Pseudoisurus* but may represent a new genus. Very similar teeth have recently been described from the Turonian of the Western Interior of the USA. Siverson (1992, p. 530) mentioned specimens from Montana (Carlile Shale) and referred them to *Pseudoisurus tomosus.* Williamson *et al.* (1993, p. 456, fig. 6.6–6.9) illustrated another example from the Mancos Shale of Arizona as *Cretolamna woodwardi.* Minor differences between the Australian teeth and the Turonian ones from the USA include a labiolingually thicker cusp and less well developed cusplets in the American teeth.

Family Incertae sedis

Genus PARANOMOTODON Herman *in* Cappetta and Case, 1975

Type species. Oxyrhina angustidens Reuss, 1845, from the Turonian of Bohemia.

Remarks. Cappetta and Case (1975) referred *Paranomotodon* to the Alopiidae, which comprises the thresher sharks. There is, however, a major gap in the fossil record between the youngest

Paranomotodon and the oldest *Alopias* Rafinesque, 1810. *Paranomotodon* sp. from the uppermost Campanian (*Nostoceras* (*N.*) *hyatti* Zone) of New Jersey, USA is the youngest record of the genus, whereas *Alopias denticulatus* Cappetta, 1981 from the lower Ypresian of Morocco is the oldest thresher shark.

The genus, *sensu* Herman (1977) and Cappetta (1987), *non* Landemaine (1991), is at present monotypic, comprising only the type species. This is largely due to the poor quality of the type material of that species. Because *P. angustidens* cannot be properly diagnosed using the type material, it is difficult to present formal descriptions of new species diagnosing them critically from the type.

Paranomotodon sp.

Plate 4, figures 11–14

Material. Two teeth from the Thirindine Point ridge; both (WAM 95.7.54–95.7.55) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. WAM 95.7.55 (Pl. 4, figs 13–14); a 14 mm high anterior tooth. The cusp is narrow with smooth surfaces. Its labial face is slightly convex with a gentle medio-basal hollow; the lingual face is strongly cambered. The neck is well developed and of equal width (0·7 mm) along the lingual base of the crown. A well-developed lingual protuberance of the root bears a median groove. The tip of the mesial lobe is mesiodistally compressed whereas the extremity of the distal one is flattened labiolingually.

WAM 95.7.54 (Pl. 4, figs 11–12); the second tooth is almost identical to WAM 95.7.55 and possibly from the same file on the opposite side of the symphysis. It differs only in having a mesiodistally compressed extremity of the distal root lobe and in its slightly more robust root.

Remarks. The narrow cusp and almost flat labial face of the crown are features typical for Cenomanian–Turonian examples of the genus. In Campanian *Paranomotodon*, the cusp is broader in anterior teeth and the labial face of the crown is almost as convex as the lingual face.

Genus ANOMOTODON Arambourg, 1952 *sensu lato*

Type species. Anomotodon plicatus Arambourg, 1952, from the Maastrichtian of Morocco.

Remarks. Some anterior teeth from very young individuals of *Carcharias* sp. A described below, have short and abrupt, oblique heels instead of cusplets. Moreover, in upper lateral files of juveniles of the same species, cusplets are either very small, barely separated from the heel or absent altogether. The branches of the root are short, not extending laterally beyond the crown. The lateral margins are subvertical with a small central concavity. These juvenile specimens of *Carcharias* sp. A are very similar to the teeth of the late Santonian–Maastrichtian *Anomotodon plicatus.* The latter taxon is the type species of *Anomotodon.* Cappetta (1975) referred *Anomotodon* to the family Mitsukurinidae Jordan, 1898 which comprises the goblin sharks, including the extant genus *Mitsukurina* Jordan, 1898 and the fossil genus *Scapanorhynchus* Woodward, 1889. Cappetta's assignment of *Anomotodon* to the mitsukurinids has found support among other authors, e.g. Case (1980, 1994), Wolberg (1985), Kemp (1991), Landemaine (1991), Long (1992*a*, 1992*b*), Siverson (1992), and Biddle (1993). Siverson (1995) tentatively also included *Striatolamia* Glikman, 1964*b* in the Mitsukurinidae. In my view, the latter genus is probably derived from one of the larger Cretaceous species assigned to *Anomotodon*, e.g. *A. hermani* Siverson, 1992. I have (Siverson 1995), however, questioned the supposed mitsukurinid affinity of *Anomotodon* and, in consequence, *Striatolamia.* While still considering *Anomotodon* to be a true mitsukurinid, Cappetta (1987) suggested that the genus might be polyphyletic by including species from different lineages. Nevertheless, he believed that *Anomotodon* was probably derived, by loss of the lateral cusplets, from a form dentally similar to the species of *Scapanorhynchus*.

As shown below, juvenile teeth of *Carcharias* sp. A are often close in morphology to the teeth of *A. plicatus*. It is quite possible that the latter evolved through paedomorphic processes operating on the former. Contrary to the opinion of previous authors, I suspect that *A. plicatus* may not be a mitsukurinid and, if that is the case, has to be reassigned to the family Odontaspididae.

As well as the type species, at least seven additional nominal species have been assigned to *Anomotodon* (Long 1992*a*, Siverson 1992). It is beyond the scope of this paper to review them all but provided my hypothesis on the origin of *A. plicatus* reflects reality, at least the Cretaceous taxa, i.e. *A. principialis*, *A. senessei* (Leriche, 1936) and *A. hermani*, must be assigned to another genus.

'*Anomotodon*' sp.

Plate 4, figures 15–16

Material. Six teeth from the Thirindine Point ridge; all of them (WAM 95.7.56, 96.3.32–96.3.36) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. Because of the poor state of preservation of the Australian teeth, a detailed description of the dentition of this species is not possible. The teeth do, however, exhibit features typical for Cretaceous species referred to the genus, such as absence of cusplets, a smooth labial face and a folded lingual face of the crown and presence of a median groove on the lingual protuberance of the root.

Remarks. WAM 95.7.56 (Pl. 4, figs 15–16) is a left upper jaw anterior tooth, probably from the third file. It measures 16·0 mm high. The tip of the cusp is missing and the distal part of the only preserved root lobe is somewhat corroded. Originally the tooth was probably about 18 mm high. Considering the size and probable position in the jaw of this specimen and the very small sample of teeth available, it seems certain that the larger teeth from the first or second anterior files of this species reached more than 20 mm in height in old females. The rather large size of the teeth, in combination with heels tapering gradually away from the cusp, indicate a close relationship with the early Campanian '*A*'. *hermani* from Belgium and southern Sweden.

Family ODONTASPIDIDAE Müller and Henle, 1839

Genus JOHNLONGIA gen. nov.

Type species. Johnlongia allocotodon gen. et sp. nov.

Derivation of name. After Dr John Long, Western Australian Museum, in recognition of his work on Palaeozoic fishes from Gondwana.

Diagnosis. Anterior teeth with conical cusp, slightly bent towards commissure. Sharp lateral cusplet usually present on mesial or both sides of cusp. Cutting edges continuous and prominent in juveniles; incomplete in adults, often limited to apical third of cusp. Lingual face of crown smooth; labial face basally folded in juveniles but smooth in adults. Root bulky with extremely large and protruding lingual protuberance in adults, divided by deep median groove. Lobes mesiodistally compressed and short, but well separated; mesial one most developed. Two to four well marked lingual marginal foramina open on each side of root.

Lateroposterior teeth labiolingually compressed. Cusp strongly bent toward commissure in upper laterals but more or less erect in lower jaw. Crown may have strong vertical folds on one or both sides, depending on species, ontogenetic stage and tooth position. Enameloid folds progressively more prominent posteriorly, especially on labial face of crown, and more developed in juveniles than in adults. Crown markedly lingually directed in posterior teeth; its labial face parallel to basal face of root in rearmost teeth. Root distinctly asymmetrical in lateral and posterior teeth of adult individuals with mesial lobe more developed than distal one. Basal face concave, divided by deep and rather broad median groove.

Referred species. Odontaspis parvidens Cappetta, 1973, from the Turonian Carlile Shale of South Dakota, USA.

Comparison. The combination of large cusplets in lateral and posterior teeth, a very well marked, deep, median groove on the lingual protuberance of the root in all but some of the extreme posterior files, and strong labial folds, at least in the posterior half of the dentition, sets *Johnlongia* gen. nov. apart from all other lamniform genera except for those of the family Odontaspididae. The common absence of a distal cusplet on anterior teeth from adult individuals, cutting edges confined to the tip of the cusp and a root with an enormous lingual protuberance and short mesiodistally compressed branches are features each of which separates *Johnlongia* gen. nov. from all other genera of Odontaspididae.

Remarks. The genus is also present in the Albian of Queensland (Noel Kemp and David Ward. pers. comm.) and possibly in the Turonian of New Mexico (see Wolberg 1985).

Johnlongia allocotodon gen. et sp. nov.

Plate 5, figures 1–15; Text-figure 5A–F

Derivation of the name. Combination of the Greek *allocotus* (of unusual form) and *odus* (tooth).

Holotype. Lower lateral tooth, WAM 95.9.1; Plate 5, figures 8–9; Thirindine Point ridge (eastern slope); basal 0·1 m of Beedagong Claystone.

Paratypes. WAM 95.9.2–WAM 95.9.10; Plate 5, figures 1–7, 10–15, Text-figure 5A–F.

Additional material. 120 teeth from the Thirindine Point ridge; 100 of these are from the basal 0·1 m of the Beedagong Claystone (WAM 96.3.43 [40 teeth] and 96.3.44–96.3.48, 96.3.49–96.3.53 [three teeth each], 96.3.54–96.3.55 [five teeth each] and 96.3.56–96.3.58 [ten teeth each]), 14 teeth are from 0·15–0·35 m above the base of the Beedagong Claystone (WAM 96.3.59–96.3.61 [12 teeth]) and six teeth were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone (WAM96.3.37–96.3.42).

Diagnosis. Anterior teeth with smooth enameloid in adults; basal half of labial face of crown with strong vertical folds in juveniles. Cutting edges incomplete in teeth of adults, usually limited to apical third or so of cusp. Distal edge in distolingual position on anteriormost teeth. In juveniles, cutting edges strong and continuous, reaching base of cusp. Lingual protuberance of root progressively more protruding with age.

Lateral teeth labiolingually compressed. Cusp strongly bent towards commissure in upper jaw teeth; more or less erect in lower jaw. Lingual face of crown usually smooth in adults but folded in juveniles. Labial face with strong vertical folds, often relatively short and widely spaced in adults.

Posterior teeth less differentiated between upper and lower jaw than laterals. Lingual face of crown with well-marked folds. Labial folds progressively stronger posteriorly through files. Rearmost teeth display simple root, sometimes lacking median groove.

Description. Anterior teeth reach at least 8·5 mm high. In adult individuals, the enameloid of the crown is smooth. The cusp is conical, sigmoidal in profile and slightly bent toward the rear. Narrow, pointed lateral cusplets are present on the mesial or both sides of the cusp but occasionally anterior teeth of adults are devoid of cusplets. The cutting edges, more developed on the mesial side, are usually incomplete in teeth from adult individuals, often limited to the apical third of the cusp. The distal cutting edge is in a distolingual position on anteriormost teeth. The root is very large relative to the crown and features an extremely bulky and protruding lingual protuberance (Pl. 5, fig. 2) divided by a deep median groove. The lobes are short, mesiodistally compressed, but well separated.

Upper lateral teeth have a distinctly commissurally bent cusp (Pl. 5, fig. 11). The crown is relatively wider than in anterior teeth and bears one or two cusplets on each side of the cusp. Lingually, the crown is cambered, smooth or with folded enameloid. When present, lingual folds are usually well-marked. The labial face of the cusp is convex but less so than the lingual side. There are strong but sometimes sparsely spaced labial folds, relatively shorter in adults. The root is very asymmetrical in adults, with a much longer mesial extremity, and labiolingually compressed with a slightly concave basal face divided by a prominent deep median groove.

Lower lateral teeth (Pl. 5, figs 8–9) feature an erect cusp and almost symmetrical crown, but are otherwise as upper laterals.

Posterior teeth are of similar morphology in both jaws. The cusp is lower and more lingually directed than in laterals. There is one pair of lateral cusplets. Labial folds are very coarse (Pl. 5, fig. 12); lingual ones are finer (Pl. 5, fig. 13). The lobes are progressively less well differentiated from the rest of the root posteriorly through the files. The rearmost teeth may lack a median groove on the lingual protuberance of the root.

There is a very marked ontogenetic heterodonty in anterior files of this species, with teeth from juveniles displaying prominent and continuous cutting edges and strong labial folds on the basal half of the crown, as opposed to the incomplete cutting edges and smooth enameloid in adults. Moreover, the lingual protuberance of the root is less protruding in juveniles (Pl. 5, figs 4–7). In lateral files, teeth of juveniles are more robust (Text-fig. 5A–F), with a more symmetrical root and much stronger folds on the crown than those of adults (Pl. 5, figs 8–11).

Comparison. According to Cappetta (1973, p. 507), the distal cutting edge on anterior teeth of *J. parvidens* is either restricted to near the tip of the cusp or missing altogether. All examined anterior teeth of *J. allocotodon* do possess a distal edge although it is limited to approximately the apical third of the cusp. In juveniles of the latter, the cutting edges are strong and continuous on anterior teeth. The labial face of the crown is smooth in lateral teeth of *J. parvidens* whereas in *J. allocotodon* there are strong, but sometimes sparsely spaced, labial folds along the base of the crown. Unfortunately, the description and illustrations of the dentition of *J. parvidens* do not include teeth from the posterior half of the tooth row. Cappetta (1973) noted a maximum tooth height of 6 mm in his sample of *J. parvidens*, whereas the largest examined tooth of *J. allocotodon* is considerably larger at 8·5 mm.

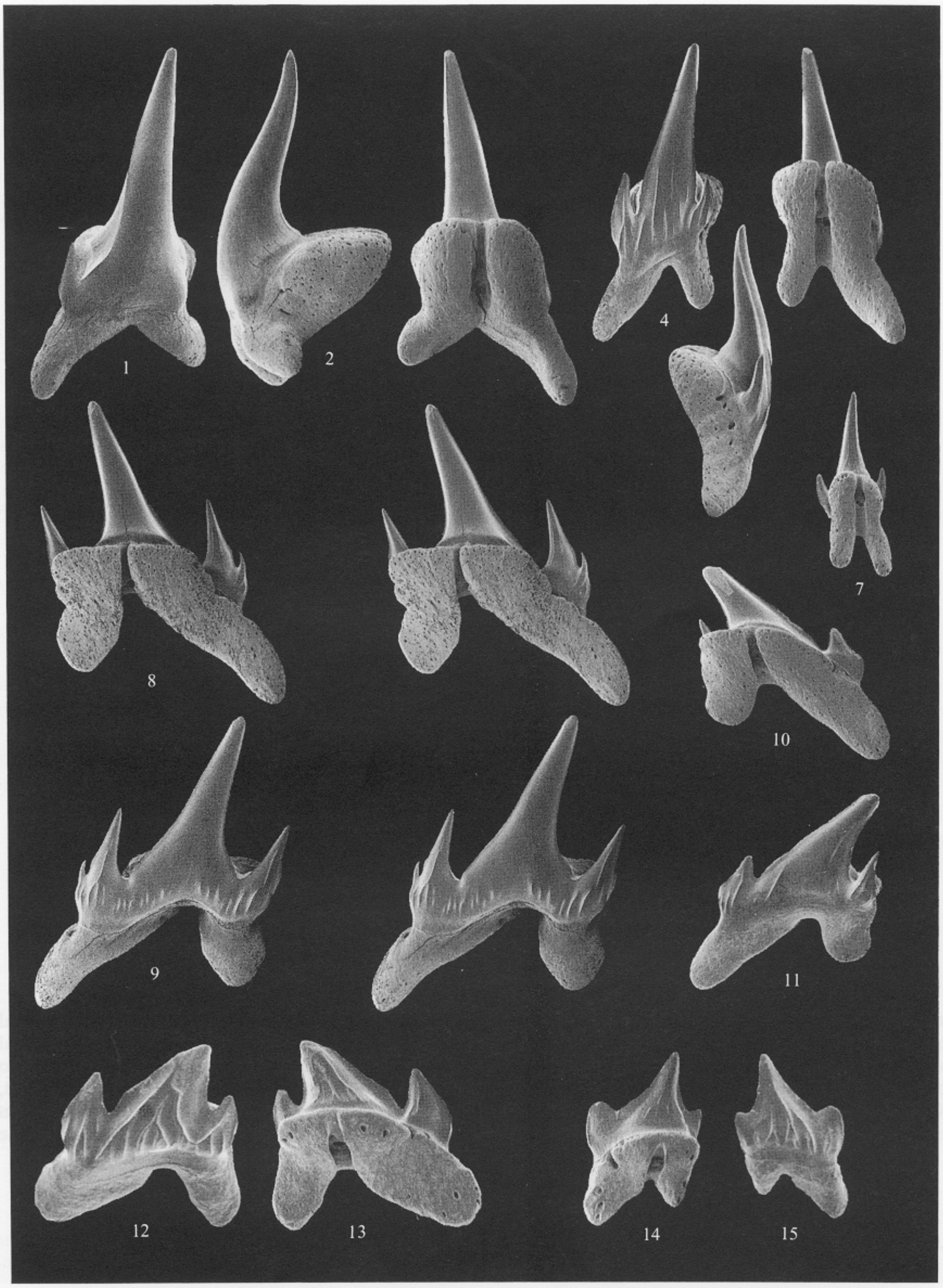
Genus CARCHARIAS Rafinesque, 1810

Type species. Carcharias taurus Rafinesque, 1810, extant, on the shelves in temperate and tropical seas; usually in shallow, inshore waters.

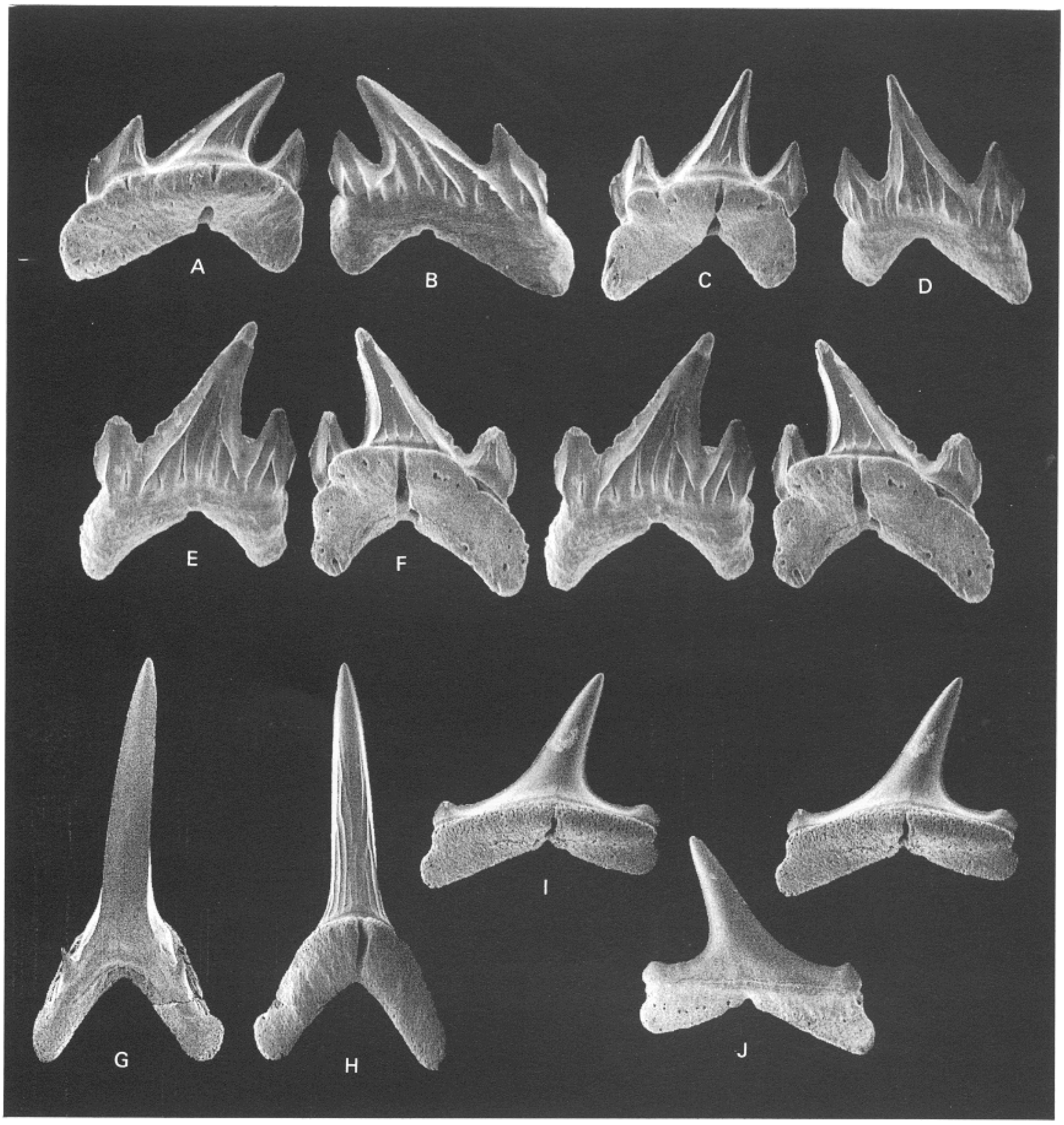
EXPLANATION OF PLATE 5

Figs 1–15. *Johnlongia allocotodon* gen. et sp. nov. 1–3, WAM 95.9.2, paratype; 7·4 mm high anterior tooth from an adult individual, labial, profile and lingual view; ×7·7. 4–6, WAM 95.9.3, paratype; 4·9 mm high anterior tooth from a juvenile individual, labial, profile and lingual view; ×9·5. 7, WAM 95.9.94, paratype; 3·0 mm high anterior tooth from a very young individual, lingual view; ×9·7. 8–9, WAM 95.9.1, holotype; 6·1 mm high lower lateral tooth from an adult individual, lingual (stereo pair) and labial (stereo pair) view; ×8·3. 10–11, WAM 95.9.5, paratype; 3·4 mm high upper lateral tooth from an adult individual, lingual and labial view; ×9·6. 12–13, WAM 95.9.6, paratype; 1·3 mm high posterior tooth from an adult individual, labial and lingual view; ×22. 14–15, WAM 95.5.7, paratype; 1·2 mm high commissural tooth, lingual and labial view; ×22. All teeth from the basal 0·1 m of the Beedagong Claystone (78 kg sample), Thirindine Point east.

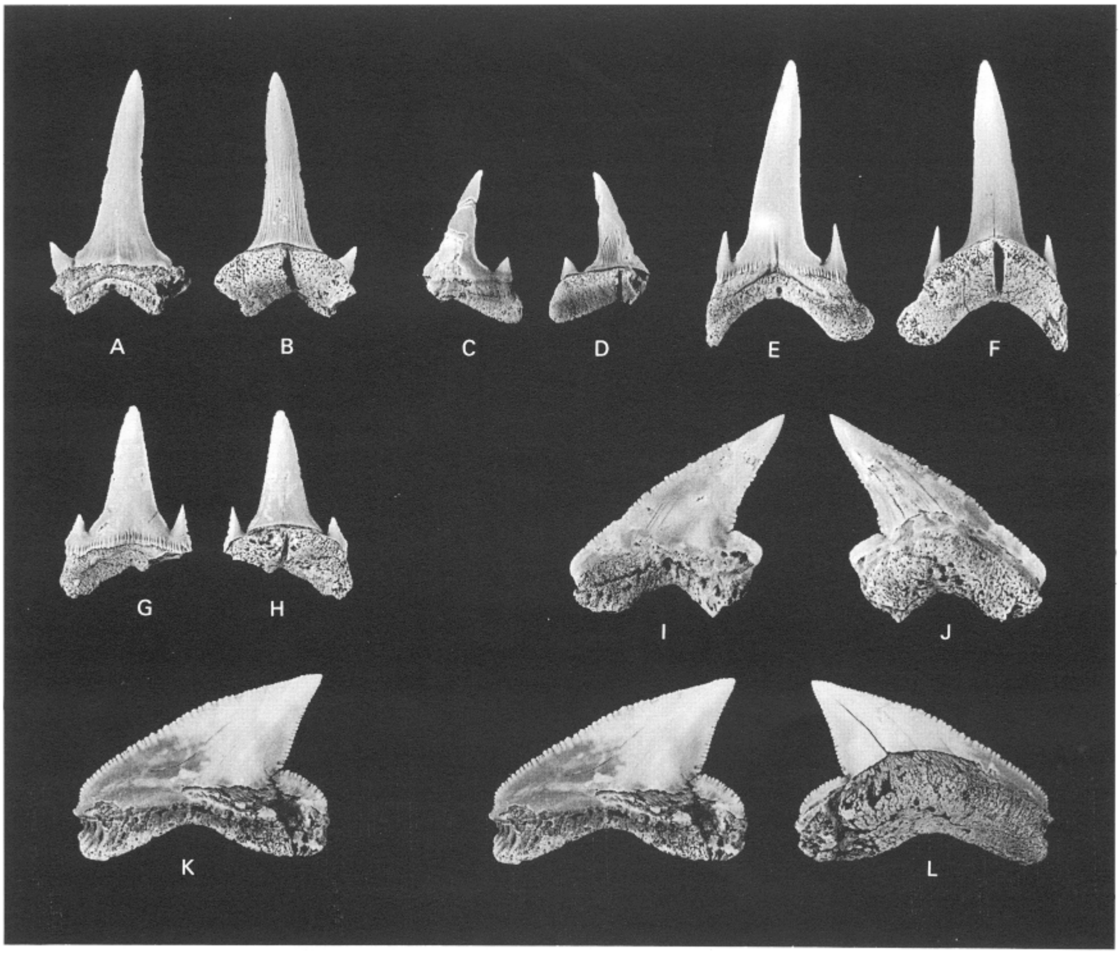
PLATE 5



SIVERSON, *Johnlongia allocotodon*



TEXT-FIG. 5. A–F, *Johnlongia allocotodon* gen. et sp. nov. A–B, WAM 95.9.8; paratype; 1·4 mm high upper lateral tooth, lingual and labial view. C–D, WAM 95.9.9; paratype; 1·4 mm high lower lateral tooth, lingual and labial view. E–F, WAM 95.9.10; paratype; 1·7 mm high ?lower lateral tooth, labial (stereo pair) and lingual (stereo pair) view. G–J, *Carcharias* sp. A. G–H, WAM 95.9.11; 6·6 mm high anterior tooth, labial and lingual view. I–J, WAM 95.9.12; 3·6 mm high upper lateral tooth, lingual (stereo pair) and labial view. A–F from the basal 0·1 m of the Beedagong Claystone (78 kg sample); all × 22; G–J from the middle third of the Beedagong Claystone (80 kg sample); both × 8·7. All teeth in the text-figure are from juvenile individuals.



TEXT-FIG. 6. A–D, *Carcharias* sp. A. A–B, WAM 95.7.57; 11 mm high lower ?anterior tooth (LA3?), both lobes of the root and one cusplet broken off, labial and lingual view; Thirindine Point east. C–D, WAM 95.7.58; 6·5 mm high upper right lateral tooth, mesial root-lobe and cusplet broken off, labial and lingual view; Thirindine Point east. E–H, *Carcharias* sp. B. E–F, WAM 95.7.59; 13 mm high upper right anterior tooth (UA2), mesial lobe of root poorly preserved, labial and lingual view; Thirindine Point east. G–H, WAM 95.7.60; 8 mm high lower lateral tooth, root poorly preserved, labial and lingual view; Thirindine Point east. I–L, *Squalicorax* ex gr. *curvatus* (Williston, 1900). I–J, WAM 95.7.61; 9·5 mm wide anterolateral tooth, labial and lingual view; Thirindine Point west. K–L, WAM 95.7.62; 11·3 mm wide lateral tooth, labial (stereo pair) and lingual view; Thirindine Point east. All × 3.

Carcharias sp. A

Text-figures 5G–J, 6A–D

Material. 137 teeth from the Thirindine Point ridge; 76 of these are from the basal 0·1 m of the Beedagong Claystone (WAM 96.3.62–96.3.63 [two teeth each], 96.3.64 [12 teeth], 96.3.65–96.3.68 [15 teeth each]), 50 teeth are from 0·15–0·35 m above the base of the Beedagong Claystone (WAM 95.9.11–95.9.12, 96.3.69, 96.3.70, 96.3.71–96.3.72 [15 teeth each] and 96.3.73 [16 teeth]) and 11 teeth were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone (WAM95.7.57–95.7.58, 96.3.74–96.3.82).

Additional occurrences. The *Mantelliceras dixoni* and/or *Turrilites costatus* Zone/Subzone of Germany (described as *Eostriatolamia*? *subulata* by Müller and Diedrich 1991).

Description. Anterior teeth, reaching at least 14·5 mm high (incomplete tooth), with one pair of small, sharp lateral cusplets. Some of the juvenile teeth have short oblique heels instead of well-defined cusplets. Upper lateral teeth are bent toward the commissure, whereas lower laterals are almost symmetrical with an erect cusp. There is one pair of triangular cusplets in lateral teeth from adults. In juveniles, cusplets are often poorly developed (Text-fig. 5I–J) or absent. In the latter case the teeth have low, abruptly terminating heels. Posterior teeth are strongly distally directed and usually lack cusplets. The labial face of the cusp is flat to slightly convex in anterior teeth; it becomes progressively more convex posteriorly so that in posterior teeth the lingual and labial faces are equally convex. All anterior teeth have strong flexuous lingual folds. In lateral and posterior teeth the folds are often less conspicuous or may even be missing altogether. Lingual folds are roughly equally dense in all teeth so that the number of folds increases with tooth size. In anterior and most lateral teeth the labial face is completely smooth. In posterior and some lateral teeth there are short basal folds. The labial face of the crown does not overhang the root in lateral teeth and the basal face of the root is flat to slightly concave. Root branches are very short in juveniles, not extending much beyond the crown. Also, in young individuals the marginal edges of the root are subvertical with a small central concavity. In adults the extremities of the root are longer, extending well beyond the crown.

Remarks. See the discussion on *Anomotodon.*

Carcharias sp. B

Text-figure 6E–H

Material. Two teeth from the Thirindine Point ridge; both (WAM 95.7.59–95.7.60) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

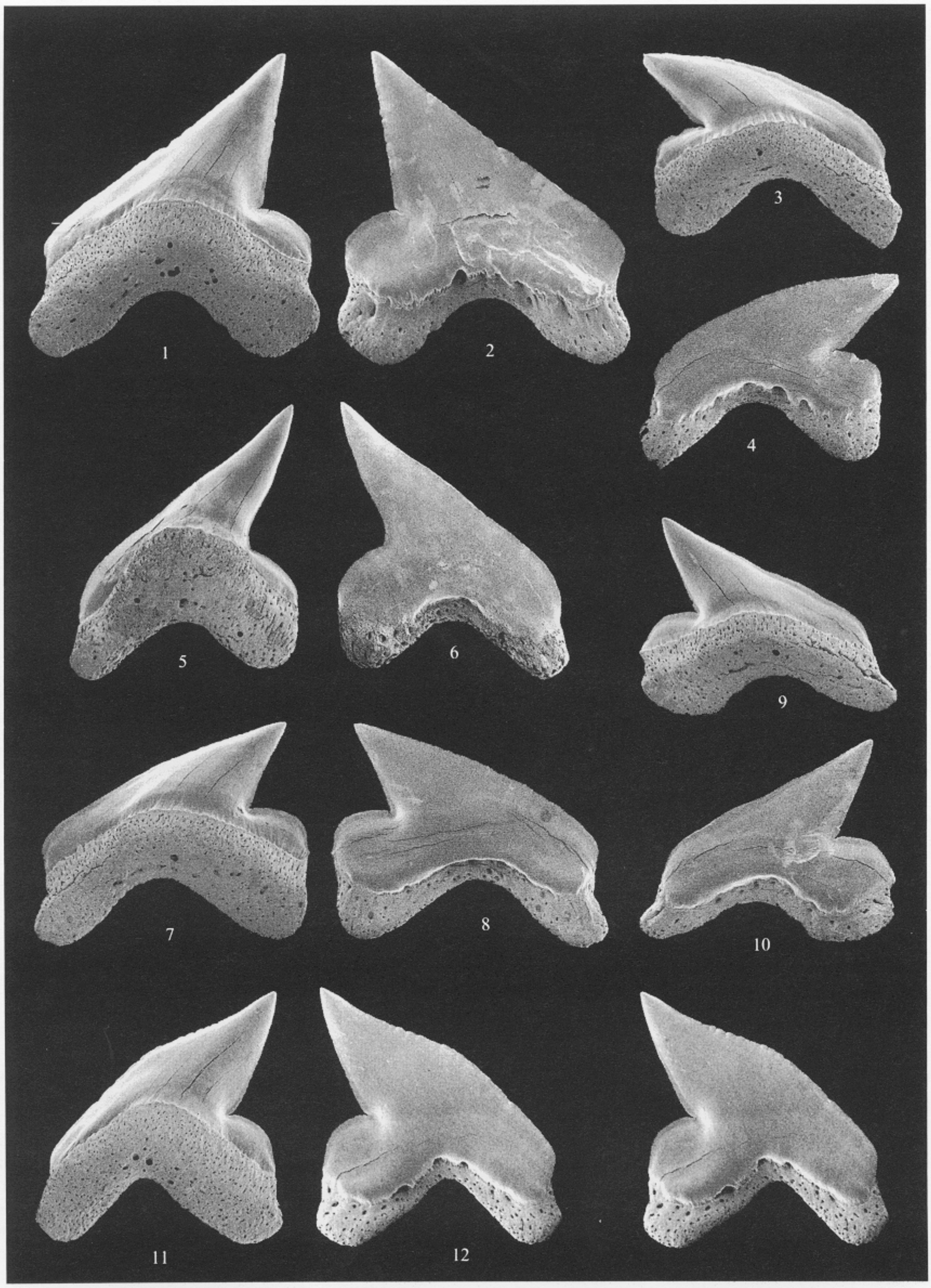
Description. WAM 95.7.59 (Text-fig. 6E–F); a 13 mm high, second upper right anterior tooth. The cusp is high, slender, sigmoid in profile and possesses continuous cutting edges. There is one pair of high cusplets, parallel to the cusp. The lingual face of the cusp bears a few, weak folds. The labial face of the crown has short, but strong vertical folds along its base. The lingual protuberance of the root is divided by a distinct median groove. The distal extremity of the root is labiolingually compressed, whereas the mesial lobe, which lacks its tip, is more slender and much less flattened.

WAM 95.7.60 (Text-fig. 6G–H); an 8 mm high, imperfectly preserved lower lateral tooth. The cusp is erect with a completely smooth lingual face. Short, prominent labial folds are present along the base of the crown. There is one pair of rather high and slender cusplets.

Comparison. The short but strong labial folds along the base of the crown, relatively high cusplets and more or less smooth lingual face of the crown are features each of which separates this species from *Carcharias* sp. A.

EXPLANATION OF PLATE 6

Figs 1–12. *Squalicorax volgensis* (Glikman *in* Glikman and Shvazhaite, 1971). 1–2, WAM 95.9.13; 7·2 mm wide anterolateral tooth, lingual and labial view; surface-collected but probably from the lower part of the Beedagong Claystone. 3–4, WAM 95.9.14; 6·4 mm wide lateral tooth, lingual and labial view; basal 0·1 m of the Beedagong Claystone (78 kg sample). 5–6, WAM 95.9.15; 5·8 mm wide anterolateral tooth, lingual and labial view; surface-collected from the uppermost metre of the Alinga Formation or the basal Beedagong. 7–8, WAM 95.9.16; 7·0 mm wide lateral tooth, lingual and labial view; basal 0·1 m of the Beedagong Claystone (78 kg sample). 9–10, WAM 95.9.17; 6·4 mm wide anterolateral tooth, lingual and labial view; basal 0·1 m of the Beedagong Claystone (78 kg sample). 11–12, WAM 95.9.18; 6·1 mm wide anterolateral tooth, lingual and labial (stereo pair) view; surface-collected but probably from the lower part of the Beedagong Claystone. All from Thirindine Point east; × 6·3.



SIVERSON, *Squalicorax volgensis*

Family ANACORACIDAE Casier, 1947

Remarks. Prior to this publication, Australian records of squalicoracids were confined to a single tooth from the Albian of north-central Queensland, possibly the Toolebuc Formation, figured as *Pseudocorax australis* by Kemp (1991, pl. 4, fig. M). He also illustrated (pl. 4, figs N–W), under the same name, ten teeth of a typical echinorhinid, possibly *Echinorhinus* de Blaineville, 1816. The species *australis* was originally described by Chapman (1909) from the Toolebuc Formation (see Pledge 1992, p. 17) of the Eromanga Basin, Queensland, and referred by him to *Corax* (= *Squalicorax*). Pledge (1992) correctly pointed out that *Corax australis* is not a squalicoracid and should be reassigned to the echinorhinids.

Genus SQUALICORAX Whitley, 1939

Type species. Corax pristodontus Agassiz, 1843, from the Maastrichtian of Maastricht, Holland.

Squalicorax ex gr. *curvatus* (Williston, 1900)

Text-figure 6I–L

Material. Nine teeth from the Thirindine Point ridge; all of them (WAM 95.7.61–95.7.62, 96.3.83–96.3.89) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. The two selected teeth described below are the best preserved ones from Thirindine Point.

WAM 95.7.62 (Text-fig. 6K–L); an 11·3 mm wide ?upper lateral tooth. The cusp is triangular and distally directed. All cutting edges have strong serrations. The mesial cutting edge is gently convex, whereas the distal edge is slightly concave. The distal heel is gently convex and well detached from the distal edge of the cusp. Labially, the crown overhangs the root medially by a distinct bulge. Several foramina open along the labial face of the root, just below the crown. The labial face of the cusp is gently convex but the labial face of the tooth as a whole is concave.

WAM 95.7.61 (Text-fig. 6I–J); a 9·5 mm wide anterolateral tooth. The distally directed cusp is elongated and narrow with a slightly convex mesial edge and a gently concave distal edge. Serrations are somewhat poorly preserved due to corrosion. The labial face of the crown overhangs the root medially, but not as markedly as in WAM 95.7.62. Both extremities of the root are incomplete.

Remarks. WAM 95.7.62 is close in morphology to one of the two teeth comprising the type series of *Corax curvatus* (Williston, 1900, pl. 30, fig. 8). Cenomanian squalicoracids have otherwise commonly been assigned to Agassiz's *Corax falcatus*, e.g. Woodward (1912), Herman (1977), Sokolov (1978), Cappetta (1987) and Müller and Diedrich (1991). It is obvious that '*C.*' *falcatus* is based on more than one species. The teeth in Agassiz's plate 26a, respectively figures 5 and 8–11, are examples of two different squalicoracids both included in this nominal species. One (fig. 5) is typical of the *S. kaupi* group with its large serrations and characteristic labial ridge, stretching from the tip of the cusp down medially toward the base of the crown. The others (figs 8–11) are of the same type as the Texan material figured as *S. falcatus* by Welton and Farish (1993). Typical dental features include a strikingly flat labial face of the crown in adults, an often convex distal edge of the cusp, and a straight to gently convex mesial edge of the cusp. Furthermore, the serrations are usually finer and the cusp is more erect than in coeval species of the *S. kaupi* group.

Glikman (1980, p. 107) chose the tooth in Agassiz's plate 26a, figure 1 as the lectotype for *Corax falcatus*. This specimen, now being the fixed standard of *S. falcatus* (see the ICZN article 74*a* in Ride *et al.* 1985, p. 153), differs significantly from the Western Australian teeth in two important aspects. First, the labial face of the root is medially much higher in *S. falcatus*. Secondly, in the Alinga Formation/Beedagong Claystone teeth the base of the labial face of the crown overhangs the root medially by a distinct bulge, whereas in the lectotype of *S. falcatus* the root and the crown appear to be flush in the same plane labially.

Squalicorax volgensis (Glikman *in* Glikman and Shvazhaite, 1971)

Plate 6, figures 1–12

*1971 *Palaeoanacorax volgensis* Glikman *in* Glikman and Shvazhaite, p. 187, pl. 1, figs 5–6, (?*non* fig. 7).
?1980 *Palaeoanacorax volgensis* (Glikman); Glikman, p. 97, pl. 13, fig. 18.
.1991 *Pseudocorax primulus* Müller and Diedrich, p. 40, pl. 22, figs 1–5.
.1993 *Squalicorax* sp.; Welton and Farish, p. 120, figs 1–2.

Material. One hundred teeth from the Thirindine Point ridge; 56 of these are from the basal 0·1 m of the Beedagong Claystone (WAM 95.9.14, 95.9.16–95.9.17, 96.3.90–96.3.100, 96.3.101 [two teeth] and 96.3.102–96.3.105 [ten teeth each]), ten teeth are from 0·15–0·35 m above the base of the Beedagong Claystone (WAM 96.3.106, 96.3.107 and 96.3.108 [eight teeth]) and 34 teeth were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone (WAM 95.9.13, 95.9.15, 95.9.18, 96.3.109–96.3.113 [five teeth each] and 96.3.114 [six teeth]).

Additional occurrences. Actinocamax primus Zone of the Saratov Province, Russian Platform; within the *Mantelliceras dixoni* to *Turrilites costatus* Zone/Subzone interval of Ascheloh, Teutoburger Wald, north-west Germany; Weno Formation (late Albian), Tarrant County, Texas, USA; and possibly in beds yielding *Turrilites costatus* of the Bakhchisaraj region of the Crimean Range, Ukraine (Naidin 1981, species list only).

Description. The teeth are of moderate size, not exceeding about 9 mm wide in the Western Australian population. The cusp is sub-erect to erect in anterior files. It is progressively more distally bent posteriorly. The mesial edge of the crown is straight, slightly convex or sigmoid. Cutting edges are usually more or less smooth, but teeth with irregularly developed serrations are not uncommon. The labial face of the cusp is usually very flat in adults (Pl. 6, figs 11–12, stereo pair). In some teeth the lingual neck, separating the crown from the root, displays short vertical hollows separated by ridges (Pl. 6, fig. 3; compare Welton and Farish 1993, p. 120, fig. 2*a*). The crown overhangs the root labially by a distinct median bulge. Lobes of the root are well separated due to a deeply notched basal edge.

Remarks. For a given category of teeth, there is a considerable degree of heterodonty in this species. Whether this heterodonty is mainly of a dignathic or gynandric nature remains to be determined. Unlike several other species of shark, there does not appear to be any clear-cut correlation between the ontogenetic stage of the tooth and the onset of development of serrations in *S. volgensis*.

When Glikman (*in* Glikman and Shvazhaite 1971) first described the species *volgensis*, he made it the type of the new nominal genus *Palaeoanacorax*. Cappetta (1987, p. 109) synonymized *Palaeoanacorax* with *Squalicorax*. This conservative taxonomic approach is applied here. However, it is quite possible that future work will demonstrate that *S. volgensis* is indeed generically distinct from coeval members of *S.* ex gr. *curvatus*.

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