Late Cretaceous sharks *Cretoxyrhina* and *Cardabiodon* from Montana, USA

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The middle part of the Cretaceous represents a time of high diversity and rapid rates of dental evolution in lamniform sharks. Several species had a very wide spatial distribution with recorded occurrences in both hemispheres. We have examined isolated teeth of *Cretoxyrhina* and *Cardabiodon* from eastern Russia, Mangyshlak in Kazakhstan, and the Western Interior of the USA. The material indicates that samples of isolated teeth of the two genera have high potential in intercontinental correlation of the upper Albian to mid-Turonian interval in mid-palaeolatitude deposits, poor in other age-diagnostic fossil groups. The utilization of these lamniforms in mid-Cretaceous biostratigraphy is currently hampered by the nearly total absence in the literature of well illustrated, well dated and sufficiently large samples of isolated teeth of the two genera. As a first step towards the establishment of an intercontinental elasmobranch zonation for mid-Cretaceous strata in temperate palaeo-regions, we describe and illustrate samples of teeth of *Cardabiodon venator* sp. nov. and *Cretoxyrhina mantelli* from the lower middle Turonian *Collignoniceras woollgari regulare* Zone in the Fairport Member of the Carlile Shale in east-central Montana, USA. These samples could serve as reference points for future biostratigraphic studies of *Cretoxyrhina* and *Cardabiodon*. The extinction of *Cretoxyrhina* may be diachronous, as regional last appearance data range from the upper Santonian (*Marsupites testudinarius* Zone) in Western Australia to the uppermost lower Campanian (informal *Belemnellocamax mammillatus* zone; a lateral equivalent to the German *Gonioteuthis quadrata gracilis*/*Belemnitella mucronata* Zone) in southern Sweden.

Key words: *Cardabiodon*, *Cretoxyrhina*, Lamniformes, sharks, biostratigraphy, Cretaceous.

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Introduction

Most living species of the order Lamniformes have a very wide spatial distribution (see Compagno 2001) and most, if not all (we have not had the opportunity to examine *Lamna ditropis* Hubbs and Follett, 1947 with the dentally similar *Lamna nasus* Bonnaterre, 1788 but see Compagno 2001: figs. 78 and 79) of them can be identified by their teeth. Shed fossil teeth from lamniform sharks are commonly found in shelf sediments of Albian to Maastrichtian (and younger) age. In spite of the significant potential in intercontinental biostratigraphy of these vertebrate fossils, there has been no serious effort to establish a workable intercontinental shark zonation scheme for any part of the Cretaceous.

Several regional biozonations based largely or solely on anacoracids (presumably a lamniform group; see Compagno 1988) have been published for parts of the Albian to Maastrichtian interval on the Russian Platform and adjacent areas (Glikman and Shvazhaite 1971; Zhelezko and Glikman 1971; Zhelezko 1990). These biozonations all suffer from insufficiently illustrated index taxa and in some cases extremely poorly preserved type material of key species (e.g., the nominal *Palaeoanacorax pamiricus* Glikman in Glikman and Shvazhaite 1971). We do, however, agree with Glikman, Shvazhaite and Zhelezko's view on anacoracids as potentially useful biostratigraphic markers. Nevertheless, much taxonomic work remains to be done before these sharks can be fully utilized in intercontinental correlation of Cretaceous marine strata.

The main aim of this communication is to lay the foundation for future biostratigraphic investigations of mid-Cretaceous cosmopolitan lamniforms of temperate climatic zones. As a starting point, we describe and illustrate teeth of *Cretoxyrhina* Glikman, 1958 and *Cardabiodon* Siverson, 1999 from the lower middle Turonian *Collignoniceras woollgari regulare* Zone of the Fairport Member, Carlile Shale in east-central Montana, USA (Fig. 1). The two genera evolved rapidly in the late Albian to middle Turonian interval and are amongst the most wide-spread lamniforms in the mid-Cretaceous, although the spatial distribution of *Cardabiodon* is somewhat patchy.

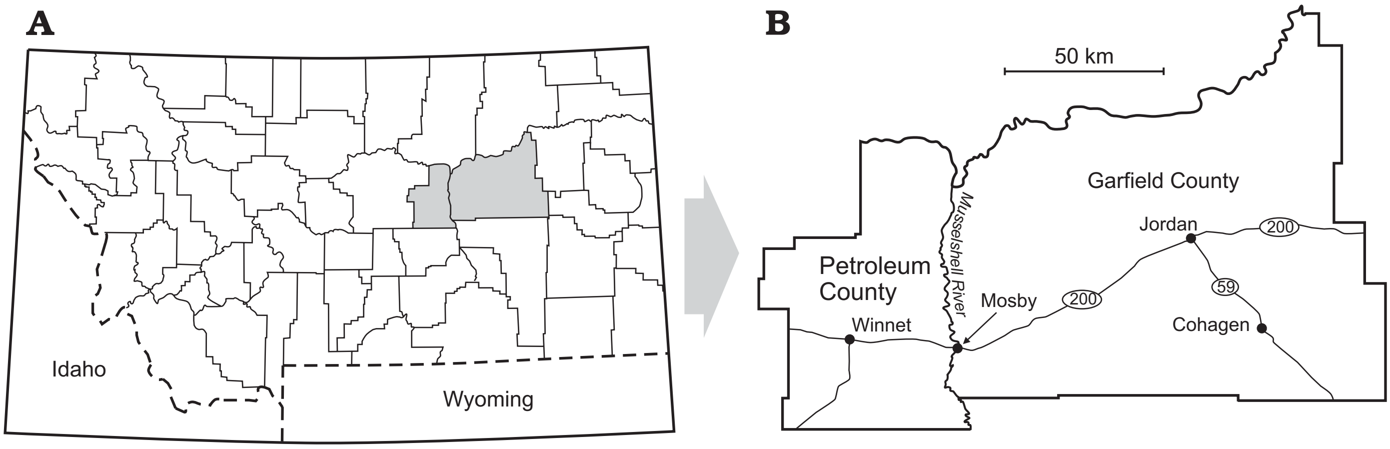

Fig. 1. Map showing the location of studied area in Montana (**A**) and location of Mosby (**B**). All selachian remains were collected on private land. Precise locality data is on file at the Department of Earth and Planetary Sciences, Western Australian Museum, Perth.

Geology

The Carlile Shale is well exposed in badlands on the Mosby Dome of the Cat Creek Anticline, particularly along the eastern side of the Musselshell Valley, north of the old Mosby Post Office. In this area the formation attains a thickness of about 94 m (310 feet in Cobban 1951). The lowermost unit comprises the Fairport Member, which measures about 3.7 m in thickness and consists of calcareous and non-calcareous shales (Porter 1990), several bentonite layers and thin limestone lenses (Cobban 1953). The member weathers orange brown and is readily recognisable in the field, although it is commonly covered by grass and shrubbery. It is overlain by dark bluish grey shales with an almost metallic sheen that makes up the lower part of the Blue Hill Member. The Fairport overlays calcareous shales of the Greenhorn Formation (Porter 1990), which weathers to form a cream coloured surface of low relief.

Macrofossils in the Fairport Member include selachian teeth, oysters, inoceramids, and ammonites (Cobban 1951). The presence of the zonal index taxon *Collignoniceras woollgari regulare* (see Cobban and Hook 1980) in the upper half of the member places the fauna in the lower, but not lowermost, part of the middle Turonian.

Previous work

The only previous report of selachians from the Fairport Member in the Mosby area, is that of Cobban (1951), in which he listed *Isurus* cf. *I. appendiculatus* (Agassiz, 1843), *Isurus* cf. *I. semiplicata* (Agassiz, 1843), *Squalicorax falcatus* (Agassiz, 1843), and *Ptychodus whipplei* (Marcou, 1858) from the upper half of the member. The material was identified by D.H. Dunkle. Both *Cretalamna appendiculata* (referred to *Isurus* Rafinesque, 1810 by Cobban) and *Ptychodus whipplei* are very rare in the Fairport Member (except in lag deposits at its base; see below) at Mosby (two teeth of each species collected out of a total of 1130 specimens). The record of the former taxon might have been based on teeth of *Cretoxyrhina mantelli* (Agassiz, 1843) with lateral cusplets, while it is likely that the report of *Ptychodus whipplei* was based on another tall-crowned species which is very common in the Fairport Member at Mosby (referred to as *Ptychodus* sp. nov. in this work). Both *C. appendiculata* and *P. whipplei* are far more common in limestone lenses at the base of the member, but, as indicated below, this material is significantly older, from a biostratigraphic point of view, than the vertebrates from the main portion of the Fairport Member. We have seen no examples of *Cretodus* Sokolov, 1965 from the Mosby area. The reported occurrence of *Isurus* cf. *I. semiplicatus* (= *Cretodus semiplicatus*) in Cobban (1951) may instead have been based on teeth of *Cardabiodon venator* sp. nov.

Material

Three field trips to the Mosby area in 1996, 1998, and 1999 resulted in a fairly large collection of selachian teeth (n = 1130) from the Fairport Member. The species identified include: *Cretoxyrhina mantelli*, *Cardabiodon venator* sp. nov., *Cretalamna appendiculata*, *Dallasiella willistoni* Cappetta and Case, 1999, *Johnlongia parvidens* (Cappetta, 1973), *Carcharias* sp., *Squalicorax* "*falcatus*" (Agassiz, 1843), *Squalicorax* sp. nov. (*S. volgensis* group), *Squalicorax* sp., Anacoracidae sp. 1, Anacoracidae sp. 2, *Cretamanta canadensis* Case, Tokaryk, and Baird, 1990, *Ptychodus whipplei*, *Ptychodus* sp. nov., and *Ptychodus* spp.

The larger teeth were all surface collected, but great care was taken to avoid mixing with selachian material that is present locally in limestone lenses at the base of the Fairport Member (basal 0.4 m of Cobban 1953). Teeth from the basal

0.4 m of the Fairport differ from those higher up in the member (i.e., 1.8–3.5 m above the base of the member; see Cobban 1953) in coloration (crown dark greenish rather than, with a few notable exceptions, lighter brownish) and faunal composition. The 30 teeth collected from the basal lag include five *Ptychodus* Agassiz, 1838, none of which belong to *Ptychodus* sp. nov. In complete contrast, the latter is far more common than all other *Ptychodus* species combined higher up in the Fairport Member. Four of the 30 teeth from the base of the Fairport Member belong to *Cretalamna appendiculata*, whereas only two out of 1130 can be assigned to this species higher up in the member. The cusp on the teeth of *Squalicorax* "*falcatus*" from the base of the Fairport member is less inflated than it is on teeth from higher up in the member. The precise age of the basal 0.4 m (1.3 feet) of the member is not known. No ammonites were reported from this part of the section by Cobban (1951). The Fairport Member rests upon the Greenhorn Formation, which is about 9 m thick in the area (Porter 1990). No selachian remains have been positively identified from the Greenhorn Formation in the Mosby area. The nature of the outcrops and the abundance of selachian teeth in the overlying Fairport Member make it difficult to establish the origin of those few teeth that were found lying on the low relief surfaces exposing the light coloured sediments of weathered upper Greenhorn Formation.

The great majority of the smaller teeth in the collection that form the basis for this work were collected from a few ant hills located on surfaces exposing the upper half of the Fairport Member. A few of the teeth from the ant hills resemble the teeth from the base of the member in colouration and state of preservation and are therefore not included in this study.

The risk of contamination by material from the overlying Blue Hill Member is minimal. More than 10 hours of intensive search for selachian teeth in the Blue Hill Member, which is about 21 m thick in the Mosby area (Porter 1990), resulted only in a single, badly corroded tooth from *Squalicorax* Whitley, 1939.

Institutional abbreviations.—DJW, David J. Ward private collection (Orpington, England); FHSM, Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas, USA; UWA, School of Earth and Geographical Sciences, University of Western Australia, Perth, Australia; WAM, Western Australian Museum, Perth, Australia.

Systematic palaeontology

Tooth terminology is after Cappetta (1987). Row group terminology follows that of Siverson (1999). Based on the occlusional relationship of the teeth in preserved jaws of modern macrophagous lamniforms, Shimada (2002) identified what he believed to be dental homologies and also presented a revised row group terminology. His dental homology hypothesis relies heavily (Shimada 2002: 45) on the assumption that the fixed occlusional relationship between the teeth of skeletonized jaws in alcohol and unprepared "fresh" jaws can be applied to live individuals of all living macrophagous lamniform species. Observations by one of us (MS) of sand tiger sharks, *Carcharias taurus* Rafinesque, 1810, kept in captivity (the Aquarium of Western Australia, Hillarys, WA) indicated that this assumption is in error. In the relaxed mode, the tip of the first upper anterior teeth ("symphysial" of Shimada 2002) points medially and often lies across the apical part of the cusp of the opposing first upper anterior tooth on the other side of the symphysis. The second lower anterior tooth (first lower anterior of Shimada) occludes between the second and third upper anterior teeth (first and second upper anterior teeth *sensu* Shimada 2002). This is also the occlusional relationship described by Shimada (2002: 50) for this species. Nevertheless, as the shark engages in biting a food item or simply projects the jaws without manipulation of prey, the occlusional relationship changes up to one full step in the anterior tooth-files (viewing the labial side of the teeth at a right angle). The third lower anterior tooth (second lower *sensu* Shimada 2002) for example, may occlude between the second and third upper anterior teeth (*sensu* Siverson 1999) rather than between the most distal anterior tooth and the most mesial lateroposterior tooth (see Shimada 2002: fig. 6). The variable occlusional relationships in *C. taurus* undermines much of the foundation for Shimada's dental homology hypothesis.

Lamniformes Berg, 1958

Cretoxyrhinidae Glikman, 1958 *sensu* Siverson (1999)

Cretoxyrhina Glikman, 1958

Type species: By original designation, *Oxyrhina mantelli* Agassiz, 1843. All but one of the nine syntypes (including a *Cretodus*-tooth in Agassiz 1843: pl. 33: 5) are from Late Cretaceous Chalk deposits near Lewis, England. Precise age of various syntypes unknown.

Cretoxyrhina mantelli (Agassiz, 1843)

Fig. 2.

For synonyms.—See Siverson (1992).

Material.—61 teeth (WAM 04.10.3–04.10.63).

Description.—For a general description of *Cretoxyrhina mantelli* teeth, see Eastman (1895), Welton and Farish (1993), and Shimada (1997a). Below we describe more specific characters possibly unique to Fairport-age populations.

The collection includes 18 small to moderate-sized anterior teeth (three complete), of which 13 are from larger juveniles (and a few possibly from small adults) and five from very young sharks, possibly yearlings (original height of the smaller anterior teeth ranging from 5–7 mm). The gap in tooth size between the two groups of juvenile teeth is large. This may be a result of different collecting techniques (surface collecting *versus* ant hill exploration).

Five different types of anterior teeth are present, presumably corresponding to the first, second and third lower anterior files and the first and second upper anterior files. Two imperfectly preserved teeth may belong to the third upper anterior files (the teeth from the third upper anterior files are reduced in size in *Cretoxyrhina mantelli*; Siverson 1999). The root is relatively symmetric (as far as can be determined) and the cusp is slightly distally bent in two of the five identified anterior tooth-types. One of these two tooth-types is characterized by having a flat basal portion of the labial side of the cusp and cutting edges reaching the base of the cusp. In the other type, the base of the labial face of the cusp is convex and the cutting edges terminate about two millimetres above the base of the cusp (Fig. 2E). Comparison with the dentally similar modern short fin mako (*Isurus oxyrinchus* Rafinesque, 1810) and crocodile shark—*Pseudocarcharias kamoharai* (Matsubara, 1936) indicates that the first type represents the first upper anterior file while the second type represents the first lower anterior file.

Of the remaining three anterior tooth-types, one has a relatively tightly curved root with a markedly longer mesial lobe (Figs. 2F, G). The cutting edges reach the base of the cusp. We refer this type to the second lower anterior file. Another morphology is represented by a complete tooth showing features typical for the third, most distal lower anterior file in makos (Fig. 2H). The cusp is distally bent and slightly lingually curved. The cutting edges reach the base of the cusp. The root is asymmetric, with a short but broad and angular distal lobe in contrast to a narrow but much longer and acute mesial lobe. The fifth type has a cusp curved in the same manner as the second upper anterior tooth in juvenile short fin makos (Fig. 2D). The basal two thirds are distally bent whereas the apical third is mesially curved. Both the mesial and the distal cutting edges terminate some distance above the base of the cusp. Unlike the teeth assigned to the lower anterior files, the cusp has no lingual curvature in profile view. The root is markedly asymmetric with a longer mesial lobe.

None of the anterior teeth at hand have any traces of lateral cusplets. Our material of anterior teeth does not include large specimens. These are more generalised in morphology (i.e., not as differentiated as in juveniles) and sturdier (see Williamson et al. 1993: figs. 6.10, 6.11; Antunes and Cappetta 2002: pl. 11: 2).

We have not been able to separate upper lateroposterior teeth from lower lateroposterior teeth with much confidence, as they are much alike. In all lateroposterior teeth, the crown and the root are flushed in the same plane labially and the whole labial surface of the tooth is very flat (see Fig. 2O$_1$). The angle between the labial faces of the root-lobes and the cusp is close to 180° in both upper and lower lateroposterior teeth. In living macrophagous lamniforms this angle is usually markedly less than 180° in upper lateroposterior teeth. The cusp is thick and terminates relatively abruptly at its apex. The heels are fairly short and oblique. Lateral cusplets are present on posteriorly situated lateroposterior teeth. There is no clear correlation between the presence of lateral cusplets and the ontogenetic stage of the tooth. The only ontogenetic difference, other than size, includes a broader more triangular cusp on larger teeth from a similar position.

Comparisons.—We have adopted a conservative taxonomic approach by referring the Fairport sample of *Cretoxyrhina* to the type species *C. mantelli*, but recognise that this sample differs significantly from late Coniacian to middle Santonian samples of *Cretoxyrhina* teeth from the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas (the Niobrara specimens correspond closely to the syntypes of *C. mantelli*). Besides a marked difference in maximum size (early middle Turonian teeth reach a considerably smaller maximum size than do late Coniacian to middle Santonian ones; Shimada 1997d and personal observations), the cusp is, on average, narrower at its base on lateroposterior teeth from late Coniacian to middle Santonian strata than it is on the corresponding teeth from middle Turonian deposits. This results in relatively longer and more horizontal heels on a typical tooth from the Smoky Hill Chalk. There is considerable overlap between middle Turonian and late Coniacian to middle Santonian samples in these characters but the number of lateroposterior teeth needed to demonstrate the difference is still rather small, probably in the order of a dozen lateroposterior teeth. Shimada (1997d) noted a significant increase in tooth size, coupled with a decrease in the crown-height/

Fig. 2. *Cretoxyrhina mantelli* (Agassiz, 1843), *Collignoniceras woollgari regulare* Zone, Fairport Member of the Carlile Shale, Petroleum and Garfield Counties, Mosby, Montana. **A**. WAM 04.10.3, perfectly preserved symphysial tooth; lingual (A$_1$) and labial (A$_2$) views. **B**. WAM 04.10.4, incomplete first upper left anterior tooth from a sub-adult individual; lingual (B$_1$) and labial (B$_2$) views. **C**. WAM 04.10.5, incomplete second upper left anterior tooth from a very young individual (probably a yearling); lingual (C$_1$) and labial (C$_2$) views. **D**. WAM 04.10.6, second upper right anterior tooth from a larger juvenile individual; labial (D$_1$) and lingual (D$_2$) views. **E**. WAM 04.10.7, incomplete first lower right anterior tooth from a sub-adult individual; lingual (E$_1$) and labial (E$_2$) views. **F**. WAM 04.10.8, perfectly preserved, second lower right anterior tooth from a juvenile; lingual (F$_1$), profile (F$_2$), and labial (F$_3$) views. **G**. WAM 04.10.9, perfectly preserved, second lower left anterior tooth from a juvenile; labial (G$_1$, stereo pair) and lingual (G$_2$, stereo pair) views. **H**. WAM 04.10.10, perfectly preserved, third lower right anterior tooth from a larger juvenile; lingual (H$_1$) and labial (H$_2$) views. **I**. WAM 04.10.11, incomplete anteriorly situated lateroposterior tooth from a juvenile; labial (I$_1$) and lingual (I$_2$) views. **J**. WAM 04.10.12, incomplete lateroposterior tooth from a juvenile; labial (J$_1$) and lingual (J$_2$) views. **K**. WAM 04.10.13, well preserved lateroposterior tooth from a sub-adult or small adult individual; labial (K$_1$) and lingual (K$_2$) views. **L**. WAM 04.10.14, incomplete lateroposterior tooth from a larger, possibly adult? individual; labial (L$_1$) and lingual (L$_2$) views. **M**. WAM 04.10.15, perfectly preserved lateroposterior tooth from a larger juvenile; labial (M$_1$), profile (M$_2$), and lingual (M$_3$) views. **N**. WAM 04.10.16, incomplete lateroposterior tooth from an adult? individual; lingual (N$_1$) and labial (N$_2$) views. **O**. WAM 04.10.17, perfectly preserved lateroposterior tooth from a juvenile, note well developed lateral cusplets; labial (O$_1$, stereo pair) and lingual (O$_2$, stereo pair) views. **P**. WAM 04.10.18, incomplete lateroposterior tooth from a juvenile individual; labial (P$_1$) and lingual (P$_2$) views. All in the same scale.

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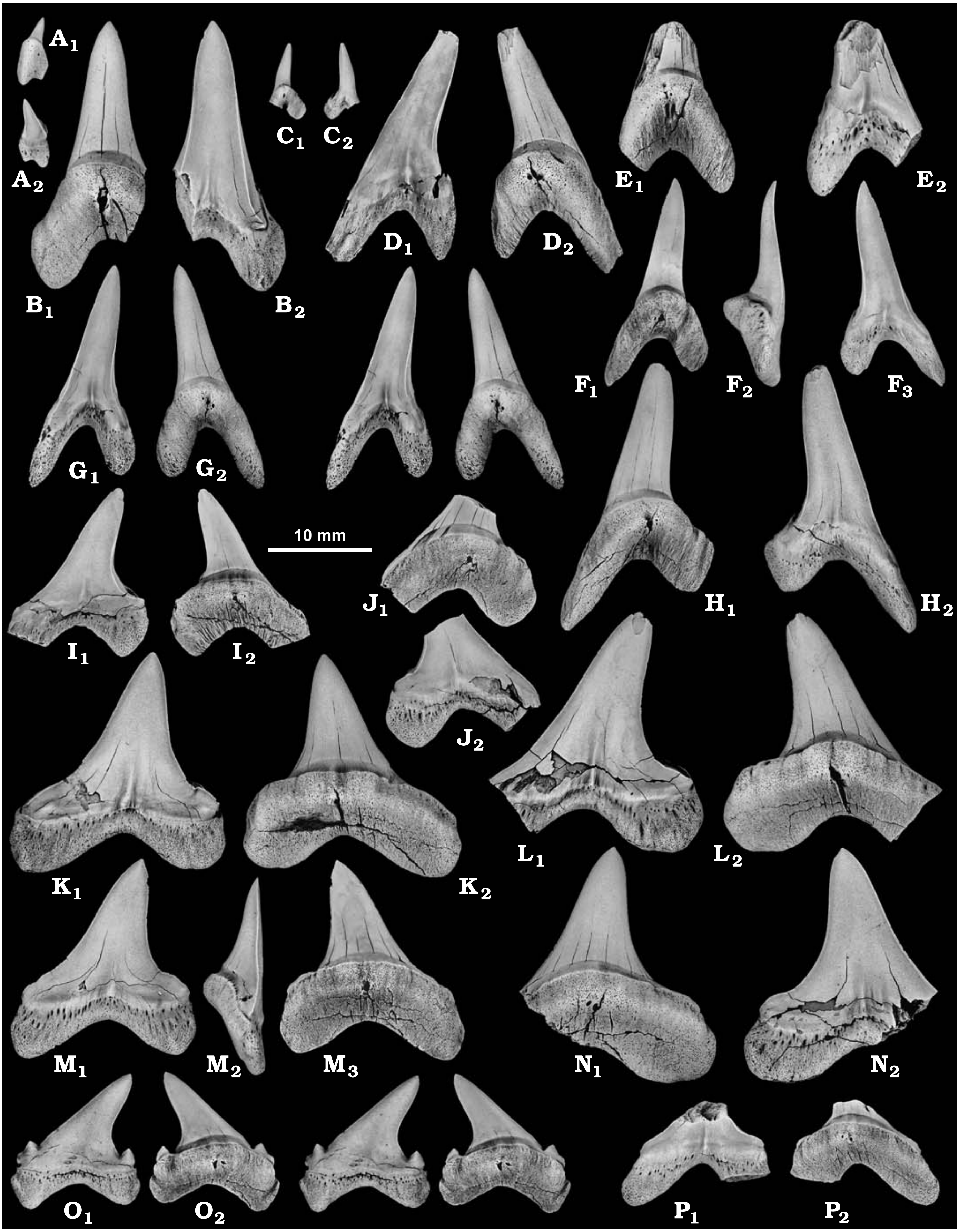
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I1
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L1
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M1
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O2
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crown-width ratio for anterior files in Niobrara *C. mantelli* compared to Cenomanian–Turonian populations.

In two different types of small, presumably juvenile anterior teeth of *Cretoxyrhina* from the Fairport Member, here interpreted as the first lower (Fig. $2E_2$) and the second upper teeth (Fig. $2C_2$ and D_1), the distal cutting edge terminates well above the base of the cusp. The character is present on first lower anterior teeth up to a maximum slant height of at least 25 mm and on second upper anterior teeth up to a maximum slant height of at least 28 mm. This feature may have had a relatively short temporal distribution in *Cretoxyrhina*. The distal cutting edge is complete in latest Albian *Cretoxyrhina* from Mangyshlak, Kazakhstan (DJW collection) and in early–middle Santonian *C. mantelli* from Kansas, USA (collected by us). The temporal distribution of an incomplete distal cutting edge on small, presumably juvenile anterior teeth is thus within the early Cenomanian to late Coniacian interval. This amounts to a maximum of 10.6 Ma using the data in Kauffman et al. (1994).

Another feature in Fairport-age *Cretoxyrhina* that we believe to be of importance from a biostratigraphic point of view is the very flat labial side of both upper and lower lateroposterior teeth. In latest Albian *Cretoxyrhina*, the angle (in profile view) between the labial side of the root-lobes and the labial side of the cusp, is typically 150–170° in upper lateroposterior teeth. This is in contrast to the corresponding teeth in Fairport-age *Cretoxyrhina* which have a labial angle very close to 180° (Fig. $2M_2$).

Antunes and Cappetta (2002) illustrated seven teeth of *C. mantelli* from the upper Turonian of Angola. None of these teeth represents anterior tooth-files from smaller juveniles, preventing a comparison with the juvenile anterior teeth from the Fairport Member at Mosby.

Discussion.—*Cretoxyrhina* extends back in time to the late Albian, where it is present in Texas (Pawpaw Formation, MS unpublished data), Mangyshlak (Zhelezko 2000; described as *Pseudoisurus*; a *nomen dubium*; see Siverson 1999) and Stary Oskol in eastern Russia (personal observations of material in DJW's collection). The three teeth illustrated by Zhelezko (2000: pl. 1: 3–5) as *Pseudoisurus vraconensis*, is a mixture of *Cretoxyrhina vraconensis* (Zhelezko, 2000) and *Cretalamna appendiculata* (see Zhelezko 2000: pl. 1: 5). The Stary Oskol selachian fauna includes three large selachian apex predators, including *Cretoxyrhina vraconensis*, *Cardabiodon* sp., and *Dwardius siversoni* (Zhelezko, 2000). In contrast, the late Albian selachian faunas from Mangyshlak (DJW collection) and Texas (Scott Kelley private collection, Dallas, Texas, USA, in addition to unregistered specimens collected by MS) lacked both *Cardabiodon* and *Dwardius* Siverson, 1999.

There is currently nothing to suggest that there was ever more than one species of *Cretoxyrhina* present at any given time during the late Albian to early Campanian interval. Any sub-division of the *Cretoxyrhina*-lineage should be based on well preserved and well illustrated material collected from a narrow stratigraphic interval. Zhelezko (2000) described a new species of *Cretoxyrhina* from the Turonian of Mangyshlak, Kazakhstan, and named it *Pseudoisurus sulukapensis* (= *Cretoxyrhina sulukapensis*). He relied on a total of 13 teeth (of which he illustrated two) lacking published information on their stratigraphic provenance within the Turonian stage. The presumed rarity of the nominal species at Sulukapy in Mangyshlak, Kazakhstan, from where the holotype was collected (not all of the 13 teeth are from this locality) indicates that it would be difficult to collect additional material of this nominal species from the (unpublished) type stratum. The holotype is probably early or late Turonian in age, as the middle Turonian is missing at Sulukapy (see Marcinowski et al. 1995).

Available data indicate that the extinction datum of *Cretoxyrhina mantelli*, the last representative of the genus, is diachronous. In Western Australia, the youngest occurrence is an undescribed tooth from the late Santonian *Marsupites testudinarius* Zone in the Gingin Chalk, Molecap Hill Quarry, Perth Basin (see also Siverson 1996: 822).

In the Western Interior of the USA, *Cretoxyrhina mantelli* persisted well into the early Campanian. On a field trip in 1999, Jerome (Pete) Bussen, Wallace (Kansas), collected a *C. mantelli* tooth (WAM 04.10.101) from within the uppermost metre of the Smoky Hill Chalk Member of the Niobrara Chalk in Logan County, western Kansas (locality data on file at the WAM). This level is 30–45 m above the Santonian–Campanian boundary, as defined by nannofossils, which lies somewhere within a 15 m thick interval bounded biostratigraphically by the First Appearance Datum of regular *Calculites obscurus* (Deflandre) and the FAD of *Broinsonia parca parca* (Stradner), as determined by Watkins et al. (1994).

In northwestern Europe, the last known occurrence of *Cretoxyrhina mantelli* is about two million years younger than that in the Western Interior of the USA. Siverson (1992) recorded the species from the local *Belemnellocamax mammillatus* zone in the Kristianstad Basin in southern Sweden. This informal biozone correlates with the uppermost lower Campanian in the German zonation; the *Gonioteuthis quadrata gracilis*/*Belemnitella mucronata senior* Zone of Schultz et al. (1984). The species was recorded from three localities within the Kristianstad Basin (i.e., Ullstorp 1 *sensu* Erlström and Gabrielson 1986, Ignaberga and Ivö Klack localities). The *C. mantelli*-yielding horizon in the Ullstorp 1 quarry (Bed C; see Erlström and Gabrielson 1986: fig. 3) was originally thought to be latest early Campanian in age (*Belemnellocamax mammillatus* zone) but Siverson (1993) indicated that it was older. This suspicion was later confirmed by the finding of a diverse belemnite assemblage placing the bed in the oldest biozone of the lower Campanian (*Gonioteuthis granulataquadrata* Zone; Siverson and Lindgren, unpublished data). Likewise, the geology at Ignaberga allows for the possibility that the *C. mantelli* teeth from this locality are reworked from an upper middle Santonian sandstone (see Erlström and Gabrielson

1992). At Ivö Klack, however, there is no evidence of marine strata or fossils of pre-*B. mammillatus*-age and the eight teeth of *C. mantelli* listed in Siverson (1992) show no obvious sign of being reworked (unlike the teeth from Ignaberga) and have the same state of preservation as selachian teeth of other species from Ivö Klack typical for the *B. mammillatus* zone.

Cretoxyrhina mantelli was also reported from the lowermost upper Campanian by Siverson (1992: 526) but this record rests on a single, much worn tooth (in the private collection of Peter Cederström, Eslöv, Sweden) from the *B. balsvikensis*-conglomerate at the Balsvik quarry (see Christensen 1998: fig. 2). Its state of preservation indicates extensive reworking.

During the latest Albian to middle Turonian interval, *Cretoxyrhina* and *Cardabiodon* were in the process of loosing the lateral cusplets on their teeth. In both genera this process commenced in the anterior files. The loss of cusplets on anterior teeth was well under way by the latest Albian in *Cretoxyrhina* (see Zhelezko 2000: pl. 1: 3) and by the middle Cenomanian in *Cardabiodon* (see Siverson 1999: fig. 9.1a). As is evident from the illustrations in this paper, Fairport-age *Cretoxyrhina* had reached a more advanced stage of cusplet-reduction than had the sympatric *Cardabiodon.*

Cardabiodontidae Siverson, 1999

Discussion.—This family comprises an extinct group of large-sized lamniform sharks sharing a unique combination of dental characters (see Siverson 1999: 59). The enlargement of the anteriorly situated lower lateroposterior teeth (relative to the upper and lower anterior teeth) is probably a unique derived feature in cardabiodontids.

Siverson (1999) included *Parotodus* Cappetta, 1980 in the Cardabiodontidae, and noted the presence of cardabiodontids in the Eocene of Morocco and middle–upper Eocene of Mangyshlak (based on photographs of material in DJW's collection). The Eocene records seemingly reduced the large gap in the fossil record of cardabiodontids between the middle Cenomanian *Cardabiodon ricki* Siverson, 1999 from the uppermost Gearle Siltstone in Western Australia and the oldest *Parotodus* from the lower Oligocene Boom Clay in Belgium, described and illustrated by Leriche (1910). However, in December 1999, one of us (MS) and David J. Ward had the opportunity to directly compare the teeth of the Cenomanian and Turonian *Cardabiodon* with those of the alleged cardabiodontids from the Eocene of Morocco and Kazakhstan.

The alleged (in Siverson 1999) cardabiodontid from the middle/upper Eocene Schorym Formation in Mangyshlak, was described formally by Kozlov in Zhelezko and Kozlov (1999) as *Parotodus mangyshlakensis*. It differs though from both the type species of *Parotodus*, *P. benedeni* (LeHon, 1871) and *Cardabiodon* in several aspects. In "*Parotodus*" *mangyshlakensis*, the lingual neck is broad in anterior teeth but much narrower in lateroposterior files, whereas there is no marked difference in the relative apicobasal width of the neck in neither *Cardabiodon* nor in *Parotodus benedeni*. Compare for example the narrow neck on an upper lateroposterior tooth of "*P*". *mangyshlakensis* (Zhelezko and Kozlov 1999: pl. 26: 2a) with the very broad neck in a upper lateroposterior tooth of *C. ricki* (Siverson 1999: fig. 8.4A) and *P.* aff. *P. benedeni* (Kemp 1991: pl. 32: M). In profile view, the lower anterior teeth of "*P*". *mangyshlakensis* have an extremely prominent lingual protuberance of the root, a feature absent in *Cardabiodon* and *Parotodus benedeni*. The sample of teeth from the Rupelian Boom Clay, illustrated by Leriche (1910) as *Oxyrhina benedeni*, may be a heterogeneous mix of true *Parotodus* and "*Parotodus*" *mangyshlakensis*. One of the lower anterior teeth has an extremely large lingual protuberance of the root (Leriche 1910: pl. 16: 10a) that is in stark contrast to the much lower protuberance in the other lower anterior teeth (e.g., Leriche 1910: pl. 16: 13a). We have not seen this feature on any Miocene–Pliocene *P. benedeni*, but it characterizes the lower anterior teeth of "*P*". *mangyshlakensis*. Two of the lateroposterior teeth illustrated by Leriche (1910: pl. 16: 5, 6) as *P. benedeni* differ from the other illustrated lateroposteriors in being larger, having more angular lobes of the root, and in having lateral cusplets. They conform extremely well to two of the lateroposteriors of "*P*". *mangyshlakensis* illustrated by Zhelezko and Kozlov (1999: pl. 26: 2, 3). Purdy et al. (2001) pointed out that the former two teeth (i.e., those illustrated by Leriche 1910: pl. 16: 5, 6) are not *Parotodus*, but erroneously referred them to "*Lamna*" *rupeliensis* Le Hon, 1871 (see Ward and Bonavia 2001).

The undescribed Eocene Morrocan teeth referred to the Cardabiodontidae by Siverson (1999) differ from those of *Cardabiodon* and *Parotodus* in having a considerably narrower lingual neck, rendering their assignment to the Cardabiodontidae questionable. Moreover, these specimens (DJW collection) were purchased from commercial dealers and do not have absolutely reliable collecting data. As it is, the gap in the fossil record between *Cardabiodon venator* sp. nov. from the Fairport Member of the Carlile Shale and the earliest known unquestionable *Parotodus* from the upper Rupelian Boom Clay amounts to no less than approximately 60 Ma.

The absence of cardabiodontids in the upper Turonian–lower Rupelian strata may be artificial, as few selachian faunas have been recorded from this time interval at higher palaeolatitudes. The appearance of *Parotodus* in the fossil record (Boom Clay in Belgium) followed the onset of Antarctic glaciation (see e.g., Zachos et al. 2001). If *Parotodus* was primarily a cool-water shark during the Paleogene, its appearance in the lower Oligocene of western Europe could be interpreted as a temperature induced migration from high palaeolatitudes (which are poorly sampled for selachians) to mid-palaeolatitudes.

The current lack of confirmed occurrences of cardabiodontids in upper Turonian–lower Rupelian strata, does however weaken the rationale for Siverson's (1999) assignment of *Parotodus* to the Cardabiodontidae.

Cardabiodon Siverson, 1999

Type species: *Cardabiodon ricki* Siverson, 1999, uppermost Gearle Siltstone (middle Cenomanian; see Siverson 1999 and Howe et al. 2000), CY Creek, Giralia Anticline, Southern Carnarvon Platform, Western Australia.

Cardabiodon venator sp. nov.

Figs. 3, 4.

Pseudoisurus tomosus; Siverson 1992: 530.

Cretolamna woodwardi; Williamson et al. 1993: 457, figs. 4, 5.

Pseudoisurus? sp. [partim]; Siverson 1996: 834, pl. 4: 8–10 [not figs. 5–7, which depict a tooth very similar to the third lower anterior tooth in the reconstructed dentition of *Cardabiodon ricki* (see Siverson 1999)].

Etymology: *Venator* (Latin for hunter), referring to its presumed position near or at the very top of the food chain.

Holotype: WAM 04.10.64, interpreted as a left second lower anterior tooth.

Paratypes: WAM 04.10.65–04.10.71.

Additional material: 29 teeth (total number, including types, is 37), WAM 04.10.72–04.10.100.

Type horizon: A 1.7 m (5.6 feet) thick interval of the Fairport Member with dark-grey shale and thin limestone lenses, weathering to orange brown. The beds are 1.83–3.54 m (6.0–11.6 feet) above the base of the Carlile Shale (see Johnson and Smith 1964: 33).

Type locality: Badlands near Mosby, in Petroleum and Garfield Counties, Montana. Precise locality data is on file at the Department of Earth and Planetary Sciences, Western Australian Museum.

Diagnosis.—Dignathic heterodonty relatively weaker in lateroposterior files than in *C. ricki*, with both upper and lower teeth exhibiting a distally curved cusp. Cusplets usually present on lateroposterior teeth of large size but often poorly developed, especially on the mesial side of the cusp. In contrast, both mesial and distal cusplets are large in *C. ricki*. Lateroposterior teeth of small juveniles frequently lack a mesial cusplet, and some also lack a distal cusplet. Root and crown flushed in the same plane labially in most large lateroposterior teeth, whereas the base of the crown overhangs the root in most teeth from small juvenile individuals, both in anterior and lateroposterior files. The root is thick and bulky, and differs significantly in this regard from the more slender root of *C. ricki*. Its lingual protuberance lacks a median groove, except in some teeth from very young individuals, which exhibit a very shallow groove. Most teeth display a string of densely spaced, circular foramina along the labial crown-root boundary, whereas labial foramina on the root are fewer and more randomly distributed in *C. ricki*.

Description.—All type specimens are described below. WAM 04.10.64 (holotype; Fig. $3A_1$–A_3); a perfectly preserved, second, left lower anterior tooth (position based on the type specimen of *Cardabiodon ricki*, WAM 94.4.45). It is 31.6 mm high (32.6 mm in maximum slant height). The robust cusp is erect and has a conspicuous constriction near its base. The cutting edges have a sigmoid profile view. Labially, the cusp is markedly convex in its apical third, but rather flat in the middle part. The lingual side of the cusp is strongly convex. The mesial and distal cusplets are both rudimentary and barely noticeable. The lingual neck, separating the crown from the root is very broad. It measures 3.6 mm in height medially, which corresponds to 11 per cent of the height of the tooth. The basal edge of the root is tightly curved. A string of small, labial foramina is present on the root, just below the strongly curved basal edge of the crown.

WAM 04.10.65 (paratype; Fig. $3B_1$, B_2); a lower? right lateroposterior tooth, probably from the middle part of the lateroposterior hollow (possibly lp7–lp9; see Siverson 1999: fig. 5), measuring 22 mm in height (26.1 mm in maximum slant height). The cusp is curved towards the commisure. Labially, the cusp is markedly convex. The distal cusplet is blunt, lacking a well defined apex. The outer edges of the mesial cusplet are much longer than the inner edge. A small indentation separates both the mesial and the distal cusplets from the cusp. The neck is 2.5 mm high medially. The crown and the root are flushed in the same plane labially. The mesial lobe of the root is missing.

WAM 04.10.66 (paratype; Fig. $3C_1$, C_2); a well preserved, 20.5 mm high (26.9 mm in maximum slant height) upper right lateroposterior tooth. The neck is 2.1 mm high medially. In combination, the relatively large size of the tooth, the strong distal curvature of the cusp and the symmetrical root indicate that the tooth belonged to a file from the middle part of the lateroposterior hollow (see Siverson 1999: fig. 5). Although the labial angle between the root-lobes and the cusp (almost 180°) is more in line with that of lower lateroposterior teeth, this tooth is assigned to the upper jaw on the basis of the strong distal curvature and flat labial face of the cusp, which is rather broad in its apical half (again indicating an upper jaw position). Like in WAM 04.10.65, there is no labial overhang of the root by the crown. The string of labial foramina on the root, just below the base of the crown, that characterizes this species, is particularly well developed on this tooth.

WAM 04.10.67 (paratype; Fig. $3D_1$–D_3); an incomplete (distal root-lobe and cusplet broken off), 23.5 mm high (28.3 mm in maximum slant height) upper left lateroposterior tooth. The neck is 2.6 mm high medially. The angle between the labial face of the only preserved root-lobe and the labial face of

Fig. 3. *Cardabiodon venator* sp. nov., *Collignoniceras woollgari regulare* Zone, Fairport Member of the Carlile Shale, Petroleum and Garfield Counties, Mosby, Montana. **A**. WAM 04.10.64, holotype, second left lower anterior tooth; labial (A_1, stereo pair), profile (A_2), and lingual (A_3, stereo pair) views. **B**. WAM 04.10.65, paratype, incomplete lower right lateroposterior tooth; lingual (B_1, stereo pair) and labial (B_2, stereo pair) views. **C**. WAM 04.10.66, paratype, upper right lateroposterior tooth; labial (C_1, stereo pair) and lingual (C_2, stereo pair) views. **D**. WAM 04.10.67, paratype, incomplete upper left lateroposterior tooth; lingual (D_1), labial (D_2), and profile (D_3) views. **E**. WAM 04.10.68, paratype, incomplete lower left lateroposterior tooth; labial (E_1, stereo pair) and lingual (E_2) views. **F**. WAM 04.10.69, paratype, lower left lateroposterior tooth from a yearling?; labial (F_1) and lingual (F_2) views. **G**. WAM 04.10.70, paratype, upper? left lateroposterior tooth from a small juvenile; lingual (G_1) and labial (G_2) views. **H**. WAM 04.10.71, paratype, incomplete upper left lateroposterior tooth from a very young individual; labial (H_1) and lingual (H_2) views. All in the same scale.

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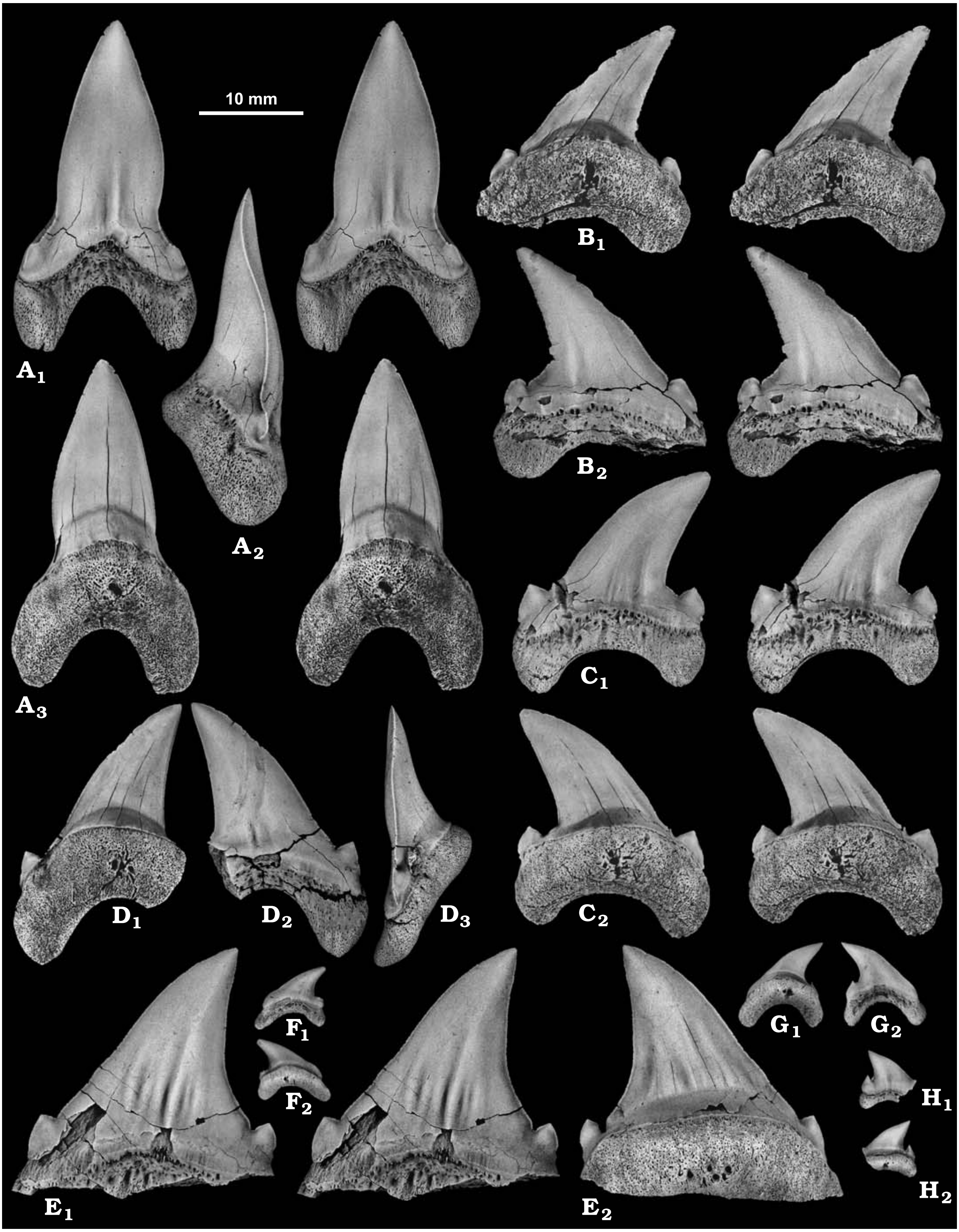
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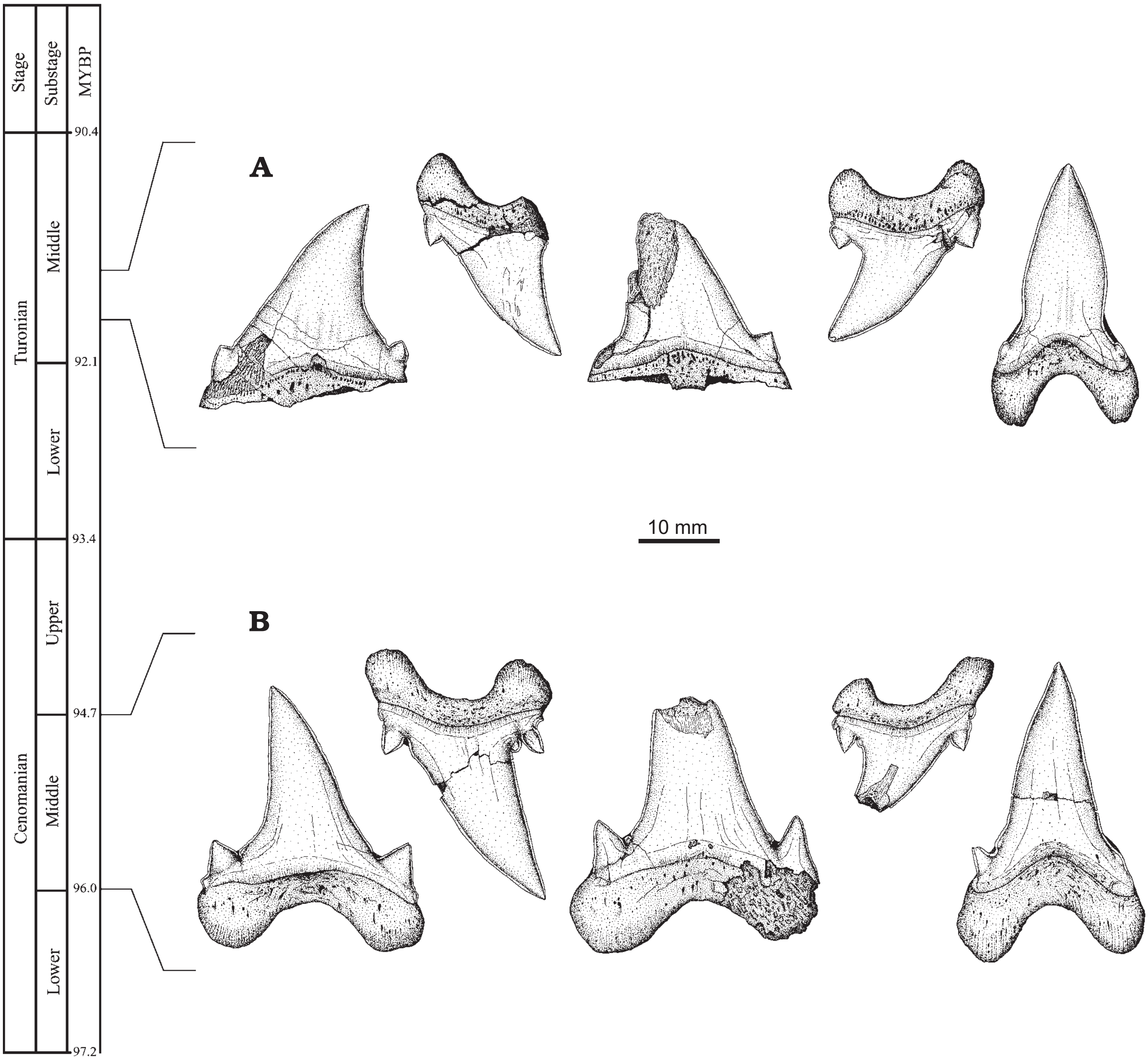

Fig. 4. Comparison of *Cardabiodon venator* sp. nov. from the Fairport Member, Carlile Shale, Mosby, Montana, USA (**A**) and *Cardabiodon ricki* Siverson, 1999 from the uppermost Gearle Siltstone, Giralia Anticline, Western Australia (**B**).

the cusp is considerably less than 180°, strongly indicating that this is an upper jaw tooth. An upper jaw position is also indicated by the comparatively flat labial face of the cusp.

WAM 04.10.68 (paratype; Fig. 3E$_1$, E$_2$); an incomplete (lacking both lobes of the root) lower left lateroposterior tooth from a large individual, measuring, as preserved, 24 mm in height (31.5 mm in maximum slant height). The tooth is referred to the lower lateroposterior hollow (as opposed to the upper lateroposterior hollow) on the basis of its broad-based cusp (see Siverson 1999: fig. 5), marked convexity of the labial side of the cusp, and the moderate distal curvature of the cusp. The relatively short cusp in combination with the large size of the tooth indicates that it originated from the middle part of the lateroposterior hollow. The mesial cusplet is much reduced in size and exhibits an outer edge much longer than the inner one. There is no indentation at the junction between the inner cutting edge of the mesial cusplet and the mesial cutting edge of the cusp. The cutting edges of the distal cusplet are more equal in length and there is an indentation present at the junction between the inner cutting edge of the distal cusplet and the distal cutting edge of the cusp. The lingual neck, separating the crown from the root, is 3.0 mm high medially. There is a conspicuous string of densely spaced, labial foramina on the root, just below the base of the crown. Several foramina open medially on the basal face of the root, near the summit of the lingual protuberance.

WAM 04.10.69 (paratype; Fig. $3F_1$, F_2); a well preserved, 5.8 mm high (8.8 mm in maximum slant height) lower? left lateroposterior tooth from a very small juvenile. The cusp is strongly distally curved and worn at its apex. A single, damaged cusplet is present on the distal blade of the crown. The tooth is tentatively assigned to the lower jaw on the basis of its moderately developed lingual protuberance of the root.

WAM 04.10.70 (paratype; Fig. $3G_1$, G_2); a perfectly preserved 8.1 mm high (10.9 mm in maximum slant height) upper? left lateroposterior tooth from a small juvenile. The cusp is strongly distally curved. Like in most juvenile lateroposterior teeth of this species, there is no mesial cusplet. The inner edge of the distal cusplet is far shorter than the outer edge. The root is bulky, measuring 3.7 mm in labiolingual thickness, and symmetrical.

WAM 04.10.71 (paratype; Fig. $3H_1$, H_2); a damaged (mesial root-lobe broken off), 5.7 mm high (5.9 mm in maximum slant height) upper left lateroposterior tooth from a juvenile. The low cusp and the short preserved distal lobe of the root indicate that it belonged to one of the more posteriorly situated lateroposterior files. The distal cusplet is relatively large and the breakage surface at the mesial border of the tooth indicates that a mesial cusplet was originally present on this tooth.

Comparisons.—The Fairport *Cardabiodon* differs from the middle Cenomanian type species *C. ricki* by the following features: (1) in *C. ricki*, there is a marked dignathic heterodonty in the anterior half of the lateroposterior files. The lower teeth have a wide and slightly distally bent cusp, whereas the cusp on the corresponding upper teeth is narrower and markedly distally curved. The difference in distal curvature of the cusp appears to be less prominent in *C. venator* sp. nov., making it more difficult to separate isolated upper and lower ones in this species; (2) the cusp is considerably taller in *C. ricki* than it is on teeth of the same width and approximately the same position of *C. venator* sp. nov.; (3) the cusp on the second lower anterior tooth of *C. venator* sp. nov. have a distinct constriction near its base, a feature absent in the type specimen of *C. ricki*; (4) lateral cusplets are reduced to a larger extent in *C. venator* sp. nov. than they are in *C. ricki*; (5) the root is significantly thicker labiolingually in *C. venator* sp. nov. than it is in *C. ricki*; (6) most teeth of *C. venator* sp. nov. have a conspicuous string of densely spaced, circular foramina just below the base of the crown, whereas the labial foramina are more scattered in *C. ricki*.

There may be differences in the ontogeny but juvenile teeth of *Cardabiodon* are only known from the early middle Turonian (this study).

Dental differences between *Cardabiodon* and the dentally similar genera *Archaeolamna* Siverson, 1992 and *Dwardius* Siverson, 1999, were outlined by Siverson (1999: 61). In addition to these differences, the *Parotodus*-like morphology of juvenile *C. venator* teeth (which have much reduced cusplets) sets them apart from juvenile teeth of *Archaeolamna*. In the latter genus, juvenile teeth have relatively larger lateral cusplets than have teeth from large, presumably adult individuals (see Siverson 1997: fig. 4A, H).

Discussion.—The presence of *Cardabiodon venator* sp. nov. in the Fairport Member of the Carlile Shale, extends the published stratigraphic range of *Cardabiodon* to span the middle Cenomanian–lower middle Turonian, an interval spanning approximately four million years. Siverson (1996: 834, pl. 4: 5–10) described two teeth as *Pseudoisurus*? sp. from the mid-Cretaceous deposits at Thirindine Point in the lower Murchison River area, Western Australia. They were both surface collected, and their origin was thought to be either the uppermost metre of the Alinga Formation or the basal 0.1 m of an overlying pinkish claystone referred to the Beedagong Claystone by Siverson (1996). The colour and state of preservation of one of the teeth (Siverson 1996: pl. 4: 8–10) indicate, however, that it is derived from the nodule bed at the base of the Toolonga Calcilutite (see Siverson 1996: text-fig. 3). The upper part of the pinkish claystone at Thirindine Point has yielded Turonian planktic foraminifera (David Haig, UWA, personal communication 1995), whereas the base of the overlying Toolonga Calcilutite is of Santonian (Belford 1958) or possibly late Coniacian age (Shafik 1990). The tooth from the claystone-Toolonga contact is very similar to those of the Mosby *Cardabiodon* and indicates an intercontinental distribution of *C. venator* sp. nov.

The second tooth referred to *Pseudoisurus*? sp. by Siverson (1996) is possibly a *Cardabiodon ricki* (third lower anterior tooth) and was probably derived from the uppermost part of the Alinga Formation (which is somewhere within the late Albian to mid-Cenomanian in age; see Siverson 1999: 50–52).

It is our hope that this investigation will stimulate further research on this genus, as it is quite common in upper Cenomanian–middle Turonian offshore facies of the Western Interior Seaway and northeastern Texas. Teeth of *Cardabiodon* are consistently mislabelled, either as *Cretoxyrhina*, *Cretodus* or "*Cretolamna*" *woodwardi* (= *Dwardius woodwardi*; see Siverson 1999), in US collections that we have examined but this work is hopefully highlighting the rather marked dental differences between *Cardabiodon* and *Cretoxyrhina*.

Palaeoecology

The spatial distribution of *Cretoxyrhina mantelli* in the Western Interior Seaway and its southern continuation into Texas indicates that this species tolerated a wide range of water temperatures, contributing to its potential in biostratigraphy. It is common in northeast Texas in the early middle Turonian (i.e., Kamp Range Limestone, Dallas County; see Welton and Farish 1993: fig. 40), a time during which this area lay within the subtropical climatic zone (Kauffman 1984). At the same time the species occurred (at most ontogenetic stages, with the notable exception of large individuals) in east-central Montana, which, according to Kauffman (1984), lay within the cool temperate climatic zone. In Kauffman's model, northeastern Texas lay just within the northern boundary of the subtropical zone in the early middle Turonian. By migrating northwards in the summer and southwards in the winter, individuals of *C. mantelli* could theoretically have stayed within a narrow temperature interval. There is, however, little to suggest that central Montana represented the northernmost boundary of *C. mantelli*'s distribution in then Western Interior Seaway during the middle Turonian, populated only during the summer months. Limited data on living macrophagous lamniforms indicate, if anything, that larger (older) individuals tend to range more widely than smaller (younger) ones and are more likely to be found in cooler waters at higher latitudes. Compagno (2001: 87) noted that modern thresher sharks, *Alopias vulpinus* (Bonnaterre, 1788), off the west coast of North America are migratory and exhibit seasonal segregation by sex. The adult males penetrate further north than do females, reaching the cooler coastal waters of British Columbia. Juveniles appear to remain in the warmer coastal waters of southern California. Another living lamniform, *Lamna ditropis*, shows a segregation by size, with larger individuals ranging more northerly than young ones (Compagno 2001).

Instead of finding a relative abundance of teeth, almost exclusively from juvenile and (presumably also) sub-adult sharks (as was the case at Mosby), one would expect the northern boundary of *C. mantelli*'s distribution in the Western Interior Seaway to be marked in the fossil record by the rare occurrence of large teeth, representing adult individuals.

Our limited data indicate that *Cardabiodon* had its main distribution in temperate, off-shore neritic environments. We have not seen any examples of the genus in the literature from areas that were situated within the tropical zone. East-central Montana was perhaps a nursery ground for *C. venator* sp. nov., as teeth from comparable positions on the jaws fall largely into two size categories; large ones (presumably from adult individuals) and very small to small ones (presumably from yearlings to somewhat older juveniles).

If present in a selachian fauna, *Cretoxyrhina mantelli* was usually the largest macrophagous shark and probably occupied the top position in the food chain (see Shimada 1997c). The Fairport Member in the Mosby area is, however, one of few instances where evidence indicate that even the largest, albeit possibly sub-adult, individuals of the local population of *C. mantelli* were dwarfed by sharks of a different species. The largest teeth of *C. mantelli* from Mosby reach about 60 percent of the size of comparable teeth in a nearly complete skeleton (FHSM VP-2187) of an approximately 5.0 m total length (TL) *C. mantelli* from the Smoky Hill Chalk Member, Niobrara Formation of western Kansas (see Shimada 1997a, b). This indicates that the largest *C. mantelli* in the Mosby area reached about 3 m in TL. The diameter of the largest undistorted vertebra in the type specimen of *Cardabiodon ricki* (WAM 96.4.45) correspond to that of a 5.4 m white shark (see Siverson 1999), and is slightly larger than that of the largest vertebra in FHSM VP-2187 (89.5 mm *versus* 87 mm). The largest lateroposterior teeth of *C. venator* sp. nov. from the Fairport Member are only slightly narrower (compare crown-width in Fig. 4) than the largest corresponding lateroposterior teeth in WAM 96.4.45, indicating a TL of roughly 5 m for large individuals of *C. venator*.

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