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Vertebral morphology, dentition, age, growth, and ecology of the large lamniform shark *Cardabiodon ricki*

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Cardabiodon ricki and *Cardabiodon venator* were large lamniform sharks with a patchy but global distribution in the Cenomanian and Turonian. Their teeth are generally rare and skeletal elements are less common. The centra of *Cardabiodon ricki* can be distinguished from those of other lamniforms by their unique combination of characteristics: medium length, round articulating outline with a very thick corpus calcareum, a corpus calcareum with a laterally flat rim, robust radial lamellae, thick radial lamellae that occur in low density, concentric lamellae absent, small circular or subovate pores concentrated next to each corpus calcareum, and papillose circular ridges on the surface of the corpus calcareum. The large diameter and robustness of the centra of two examined specimens suggest that *Cardabiodon* was large, had a rigid vertebral column, and was a fast swimmer. The sectioned corpora calcarea show both individuals deposited 13 bands (assumed to represent annual increments) after the birth ring. The identification of the birth ring is supported in the holotype of *Cardabiodon ricki* as the back-calculated tooth size at age 0 is nearly equal to the size of the smallest known isolated tooth of this species. The birth ring size (5–6.6 mm radial distance [RD]) overlaps with that of *Archaeolamna kopingensis* (5.4 mm RD) and the range of variation of *Cretoxyrhina mantelli* (6–11.6 mm RD) from the Smoky Hill Chalk, Niobrara Formation. The revised, reconstructed lower jaw dentition of the holotype of *Cardabiodon ricki* contains four anterior and 12 lateroposterior files. Total body length is estimated at 5.5 m based on 746 mm lower jaw bite circumference reconstructed from associated teeth of the holotype.

Key words: Chondrichthyes, Lamniformes, *Archaeolamna*, *Squalicorax*, vertebral centra, Cretaceous, Cenomanian, Turonian, Australia.

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Introduction

Cardabiodon Siversson, 1999 is a lamniform shark with a dentition comprising a unique set of tooth types and a global, high latitude distribution in the middle Cenomanian to middle Turonian (Siversson and Lindgren 2005; Cook et al. 2010, 2013). Fossil teeth from these sharks are typically rare and vertebral centra are even less common (Siversson 1999; Cook et al. 2010).

Siversson (1999) described *Cardabiodon ricki* from associated teeth and vertebral centra recovered from the uppermost, middle Cenomanian, part of the Gearle Siltstone at CY Creek, Giralia Anticline, Western Australia (Fig. 1). Siversson and Lindgren (2005) described a second species, *Cardabiodon venator*, from teeth in the Fairport Member of the Carlile Shale (early middle Turonian), Montana, USA. To date, *Cardabiodon* teeth have been identified from nine localities in North America, Europe, and Australia (Siversson

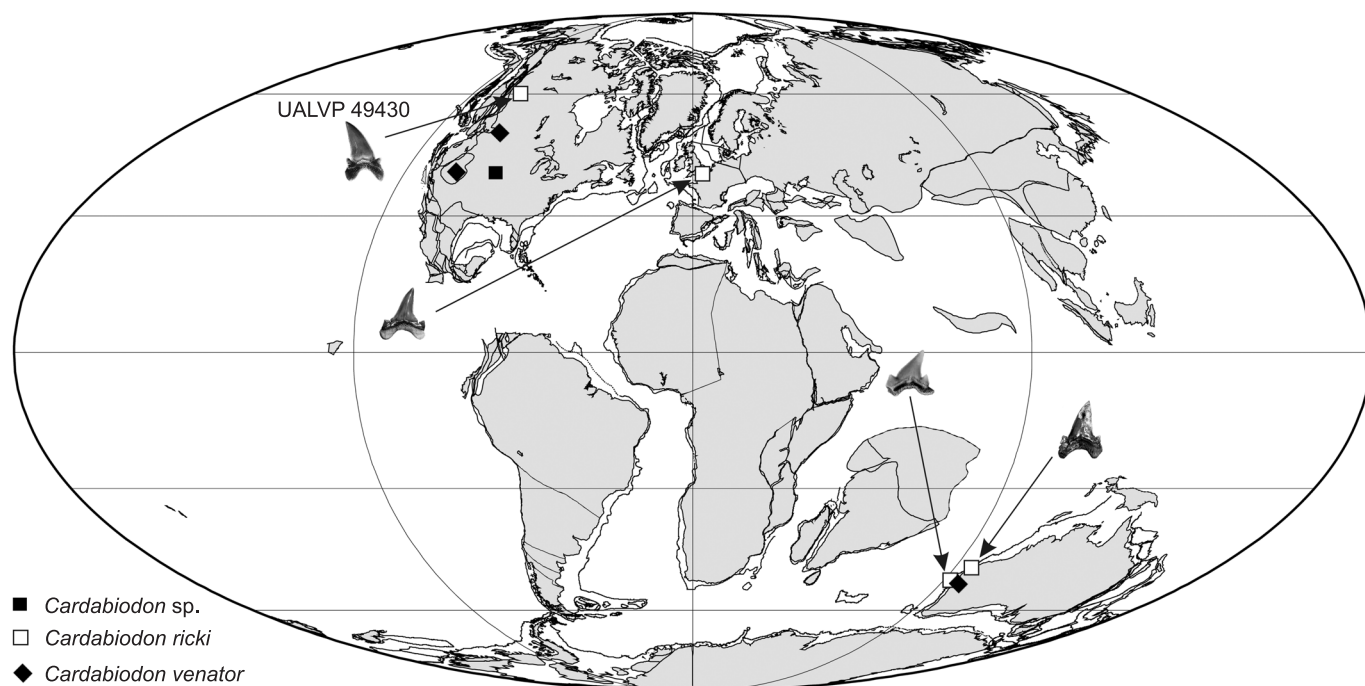


Fig. 1. Early Late Cretaceous map (90 Ma; PLATES Program 2009) showing locations of fossil localities (late Cenomanian to middle Turonian) yielding *Cardabiodon* spp. (see Cook et al. 2010). UALVP 49430 from Canada is likely a transitional morphotype between *Cardabiodon ricki* and *Cardabiodon venator*.

1999; Siverson and Lindgren 2005; Dickerson et al. 2013 [excluding amendment; see Siverson et al. 2013 regarding the validity of *Pseudosurus* Glikman, 1957a]; see Cook et al. 2010 for a review of localities) (Fig. 1). *Cardabiodon* is classified as a lamniform based on the presence of radial lamellae in vertebral centra and morphological tooth variation consistent with a lamnoid type dentition (Siverson 1999).

Little is known about the ecology of *Cardabiodon*. Yet it has been recognized that *Cardabiodon* had a global, antitropical distribution mimicking the distribution of the extant lamnid *Lamna nasus* Bonnaterre, 1788 (the porbeagle shark) (Siverson and Lindgren 2005). Cook et al. (2010) tested the antitropical hypothesis and concluded that the genus had an antitropical distribution based on three characteristics. First, the palaeodistribution of the two known species was concentrated in middle to higher northern and southern latitudes. Second, the range of estimated sea surface temperatures was within 1.7°C of the actual temperature range of extant *L. nasus*. Third, the palaeodistribution of *Cardabiodon* was positively correlated with Cenomanian–Turonian temperature change.

There is a dearth of information about the age and growth of fossil sharks. Shimada (2008) examined the age and growth of two specimens of the lamniform *Cretoxyrhina mantelli* and reported ages of up to 21 bands (presumably years). Ehret et al. (2009) reported 20 bands for a specimen of *Carcharodon* Smith in Müller and Henle, 1838, from the Pisco Formation (late Miocene, 6–8 Ma; Ehret et al. 2012) of Peru. Relatively little is also known about the age and growth of extant sharks (Cailliet and Goldman 2004). The longevity of many extant sharks is estimated to be much older than what is actually observed. For example, Shimada (2008), in

a review of 25 lamniforms, reported the oldest observed age of *Carcharodon carcharias* (Linnaeus, 1758) as 22 years (Francis 1996), whereas the lifespan was estimated to be 48 years (Cailliet et al. 1985). We now know the longevity of *Carcharodon carcharias* to be 70 years old (Hamady et al. 2014). These discrepancies may stem from sampling that fails to include the oldest members of the population or there is a lack of data to make accurate estimates.

Our objectives are to augment the description of the dentition, describe the age and growth of *Cardabiodon ricki* from vertebral centra, and discuss the relative size and palaeoecology of this shark compared primarily to another large Cretaceous lamniform, *Cretoxyrhina mantelli* (Agassiz 1843: 280). The latter species is known from, e.g., a nearly complete specimen (FHSM VP-2187) that was recovered from the Niobrara Chalk of Kansas, USA (Shimada 1997a, c). The age and growth of *Cardabiodon ricki* are determined on the basis of growth bands visible on the corpus calcareum of the centra. Lastly, growth, vertebral morphology, and biogeographical distribution are discussed.

Institutional abbreviations.—AMNH FF, American Museum of Natural History, Fossil Fish, New York, USA; FFHM, Fick Fossil and History Museum, Oakley, USA; FHSM VP, Sternberg Museum of Natural History, Vertebrate Paleontology, Hays, USA; KUVF, University of Kansas Museum of Natural History, Vertebrate Paleontology, Lawrence, USA; LACM (I-, Ichthyology; P-, Paleontology, our designation to distinguish the two collections), Natural History Museum of Los Angeles County, Los Angeles, California, USA; SDSM, South Dakota School of Mines and Technology, Vertebrate

Paleontology, Rapid City, USA; SMNH P, Royal Saskatchewan Museum of Natural History (Palaeontology), Regina, Saskatchewan, Canada; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor, USA; USNM, National Museum of Natural History, Smithsonian Institution, Paleontology, Washington D.C., USA; UWGM, University of Wisconsin, Geology Museum (New Series), Madison, USA; WAM, Western Australian Museum, Perth, Australia.

Other abbreviations.—A, upper anterior; a, lower anterior; CRD, centrum radial distance; LP, upper lateroposterior; lp, lower lateroposterior; RD, radial distance; TL, total length; TW, tooth width.

Material and methods

Material examined.—*Cardabiodon ricki* Siverson, 1999, Cenomanian–Turonian: WAM 96.3.175 (centra) and WAM 96.4.45 (holotype, teeth and centra), both from the uppermost Gearle Siltstone, CY Creek, Giralia Range, Western Australia; WAM 13.6.1 (tooth), basal 0.1 m of the Haycock Marl, Thirindine Point, lower Murchison River area, Western Australia; UALVP 49430 (tooth), Watino locality, Alberta, Canada. *Cardabiodon venator* Siverson and Lindgren, 2005, Turonian: WAM 95.7.28, uppermost Haycock Marl, Thirindine Point, Pillawarra Plateau, Western Australia; WAM 04.10.62–100 (teeth), Mosby, Montana, USA. *Cretoxyrhina mantelli* (Agassiz, 1843), late Coniacian to early Campanian (see Siverson et al. 2013 for more information): AMNH FF 7210 (teeth, partial head, centra), FHSM VP-323 (teeth, partial head, centra), FHSM VP-2184 (teeth, centra), FHSM VP-2187 (teeth, partial head, centra), KUVF 55060 (teeth, centra), all from late Coniacian to middle Santonian, Smoky Hill Chalk, Niobrara Chalk, Kansas, USA. *Cretoxyrhina agassizensis* (Underwood and Cumbaa, 2010), late Cenomanian or earliest Turonian: WAM 13.6.2 (tooth), basal 0.1 m of the Haycock Marl, Pillawarra Plateau, Western Australia; DMNH 746C (centrum), basal Eagle Ford Group, Tarrant County, Texas, USA. *Cretoxyrhina* sp. of Glickman (1958), Cenomanian: NHMUK OR.25939 and OR.49015, both from White Chalk Formation (?), near Sussex, UK. *Cretalamna hattini* Siverson, Lindgren, Newbrey, Cederström, and Cook, 2015, latest Santonian or earliest Campanian: LACM P-128126 (teeth, partial head, centra), Smoky Hill Chalk, Niobrara Chalk, Logan County, Kansas, USA. *Dwardius woodwardi* Herman 1977, Cenomanian: NHMUK P.45 (paratype dentition), Dover, UK. *Squalicorax* spp. of Whitley (1939), late Coniacian–Campanian: FHSM VP-2213 (teeth, jaws), Niobrara Chalk, Rooks County, Kansas, USA; KUVF 69712 (teeth, partial head, centra), Pierre Shale, Wyoming, USA; LACM P-135929 (teeth, partial head, centra), Smoky Hill Chalk Member, Niobrara Chalk, Logan County, Kansas, USA; SDSM 34975 (teeth, partial head,

centra), Sharon Springs Member, Pierre Shale, southwestern Fall River County (“Wallace Ranch”), South Dakota, USA; USNM 425665 (teeth, head, centra), Smoky Hill Chalk Member(?), Niobrara Chalk, Logan County, Kansas, USA; UWGM NS.1509.07 (teeth, centra), Smoky Hill Chalk Member, Niobrara Chalk, Logan County, Kansas, USA; UWGM NS.1509.34 (teeth, centra), Smoky Hill Chalk Member, Niobrara Chalk, Logan County, Kansas, USA. *Archaeolamna kopingensis* (Davis, 1890), Campanian: LACM P-128125 (teeth, jaws, centra), Sharon Springs Member, Pierre Shale, Logan County, Kansas, USA. *Hypotodus verticalis* (Agassiz, 1843), Eocene: NHMUK OR.12377 (teeth, cartilage, centrum), NHMUK OR.28763 (teeth, cartilage, centrum), and NHMUK OR.38867 (teeth, cartilage, centra), all from London Clay, Sheppey, Kent, UK.

The specimens listed below represent extant species. *Carcharias taurus* Rafinesque, 1810: LACM I-39336-5, UMMZ 147001. *Odontaspis ferox* (Risso, 1810): LACM I-39445-1. *Alopias superciliosus* Lowe, 1840: LACM I-39321-1. *Alopias vulpinus* (Bonnaterre, 1788): LACM I-36864-1, I-38158-1, I-39324-1, I-39325-1, I-39330-1. *Isurus paucus* Guitart, 1966: LACM I-57284-1, I-57285-1. *Isurus oxyrinchus* Rafinesque, 1810: LACM I-39470-2. *Carcharodon carcharias* (Linnaeus, 1758): LACM I-35875-1, I-38194-1, I-42728-1, I-57280-1, I-57281-1, I-57282-1, I-57283-1, I-42094-1, I-42094-2, I-42100-2. *Lamna ditropis* Hubbs and Follett, 1947: LACM I-56781-1. *Lamna nasus* Bonnaterre, 1788: LACM I-38174-1, UMMZ 60591. *Cetorhinus maximus* (Gunnerus, 1765): LACM I-35593-1.

Terminology.—Tooth terminology is after Cappetta (1987, 2012) and row group terminology follows Siverson (1999). Description of vertebral centra primarily follows Kozuch and Fitzgerald (1989) except where cranio-caudal length is referred to as length, medio-lateral breadth is referred to as width, and dorso-ventral height is referred to as height. We also employ the terminology of Cailliet et al. (1983b, 2006), Cailliet and Goldman (2004), and Ridewood (1921) for morphological description and identification of age and growth marks and characteristics.

Age and growth.—Shark centra grow to form a double-cone calcification (Ridewood 1921) meaning that the anterior and posterior conical ends, collectively referred to as corpora calcarea, are hardened by a dense calcification. The calcification pattern shows seasonal deposition that can be quantified. Between the corpora calcarea is the intermedialia, which is softer than the corpus calcareum but also records seasonal deposition. In lamniforms, the intermedialia is pierced by radial and/or concentric lamellae, which add to the structural integrity of the centrum. Vertebral centra exhibit three types of calcification patterns: areolar, prismatic, and globular calcification (Dean and Summers 2006). However, double-cone calcification only proceeds from areolar calcification (Dean and Summers 2006), which is characterized as a web-like infiltration of mineral in a hyaline cartilage matrix and varies in morphology by species (Porter et al. 2007). The mineral

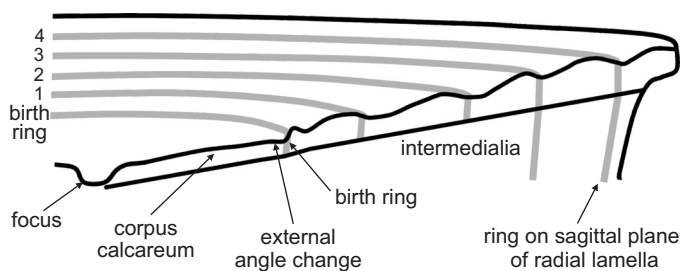


Fig. 2. Schematic drawing of a hypothetical shark centrum in hemisected view showing potential criteria used for age determination.

pattern has not yet been examined in *Cardabiodon ricki*. Cartilage is laid down along the distal margin of the corpus calcareum and intermedialia and then calcifies. Regarding extant age and growth, two types of deposition are generally present and used to identify annual banding patterns. Opaque deposition is denser than translucent deposition and can be used to quantify age. Opaque deposition is preceded by translucent deposition in a band.

We followed the protocol and criteria established by Cailliet et al. (1983b), MacNeil and Campana (2002), Cailliet and Goldman (2004), Goldman and Musik (2006), and Shimada (1997b, 2008) to quantify age and growth (see Fig. 2 for a schematic of characteristics used to identify growth characteristics). Only the largest precaudal centra were selected for taxonomic comparison. Growth of two precaudal centra of *Cardabiodon ricki* was compared to four vertebral centrum specimens of *Cretoxyrhina mantelli* and one of *Archaeolamna kopingensis* (LACM P-128125; Cook et al. 2011). One specimen of *Cardabiodon ricki* (the holotype) had associated teeth and vertebrae but these were disarticulated (WAM 96.4.45). Four specimens of *Cretoxyrhina mantelli* have teeth and vertebrae associated with each other (FHSM VP-2184, VP-2187, VP-14010 [Shimada 2008], KUV 55060). A single centrum of *Cretoxyrhina* from the lower Eagle Ford Group (late Cenomanian) was not found with teeth (DMNH 746C). Two centra of *Cretoxyrhina* sp., from the English Chalk, were not preserved with teeth (NHMUK OR.25939, OR.49015).

Centra were hemi-sectioned for a view of the corpus calcareum: three specimens of *Cardabiodon ricki* centra (WAM 96.4.45.128 [precaudal], 96.4.45.129 [caudal], 96.3.175.1 [precaudal]), three specimens of *Cretoxyrhina mantelli* (FHSM VP-2187, VP-14010 [sectioned by Shimada 2008]) including one naturally sectioned (KUV 55060), and three centra of *Ar. kopingensis* (LACM P-128125, sectioned by Cook et al. 2011). Centra of *Cardabiodon ricki* were aged after an initial examination of *Cretoxyrhina mantelli* centra, in hemisected views, to identify bands (pairs of light + dark rings = one band). The surface on the corpus calcareum also has characteristics that are useful for aging (MacNeil and Campana 2002), but in some instances can be misleading (see MacFadden et al. 2004). To obtain additional annual criteria, light was angled at 45° across the conical surface to highlight the annual features present, such as ridges (Newbrey et al. 2008). Measurements were made along a transverse plane situated on the anterior or posterior ends of the

centrum. The distance from the focus to the outer margin of each dark ring, which is part of a circular crest (followed by a circular groove), was quantified to determine growth in radial distance (RD). The growth profile of each centrum was plotted for comparison within taxa and among taxa (Newbrey et al. 2008). Plotting the growth profiles for comparison assists in detecting aging error, near the margin, where bands crowd together. Sharp or anomalous increases in growth are indicative of aging error especially near the distal part of the arm of the corpus calcareum.

Sectioning centra.—We followed the general sectioning protocol in Cook et al. (2011), but modified the method due to the fragile condition of the *Cretoxyrhina* centra used in this study. Delicate fossil centra were first fixed in 20% Acryloid (Rohm and Haas, Paraloid B72 and acetone), an ethyl methacrylate copolymer, to augment centrum structural integrity while sectioning, as small pieces would otherwise be lost during the cutting process. Centra were placed in a small, single layer, thin cardboard specimen box (for example, 5.5 × 3.5 × 1.75 inches, 0.040 inches thickness, white lined, plain white litho, manufactured by Four Four Four Limited, Mississauga, Ontario, Canada). Acryloid was added until the centrum was completely submerged. Each application was permitted to dry 24 h resulting in ~5–8 mm thick layers of soft, pliable, semi-dry, Acryloid. This process was repeated until the entire centrum was embedded in Acryloid. The semi-dry state of the Acryloid permitted manipulation for cutting and final cleaning.

Once the Acryloid was semi-dry, the sides of the box were separated from each other at the corners and laid flat. One side of the box was removed to eliminate excess cardboard for ease of sectioning and manipulation. The remaining sides of the box were used as handles to hold and guide the centrum during sectioning. A scalpel was used to remove the semi-dry Acryloid and cardboard from the path of the saw blade in order to prevent clogging. Centra were sectioned using a lapidary trim saw (Lortone Inc. Model # FS6) with a 15 cm diameter, 1 mm thick, diamond impregnated blade. Centra were sectioned about 1–1.5 mm from the focus of the centrum. After sectioning, a scalpel was used to remove the excess Acryloid, leaving embedded Acryloid in the centrum to enhance its structural integrity.

The sectioned faces were polished on a glass plate using a slurry of silicon carbide powder (E.T. Enterprises) with a particle size of 1000 grit and water: about 1.5 parts powder to 1 part water. The centrum was polished with a circular motion until the cut face intersected the centrum focus. The remainder of the Acryloid was then removed with a scalpel. The centrum was further cleaned by submersion in a bath of pure acetone for about a minute, but only if the specimen was preserved whole. In fragmented specimens, the surface was cleaned by brushing acetone with a soft toothbrush or stiff paint brush to thin or remove Acryloid residue.

Calibration of birth ring.—Inspection of the surface of the corpus calcareum in aged samples of *Cardabiodon ricki* indicates relatively poor surface preservation. Back-calculation of

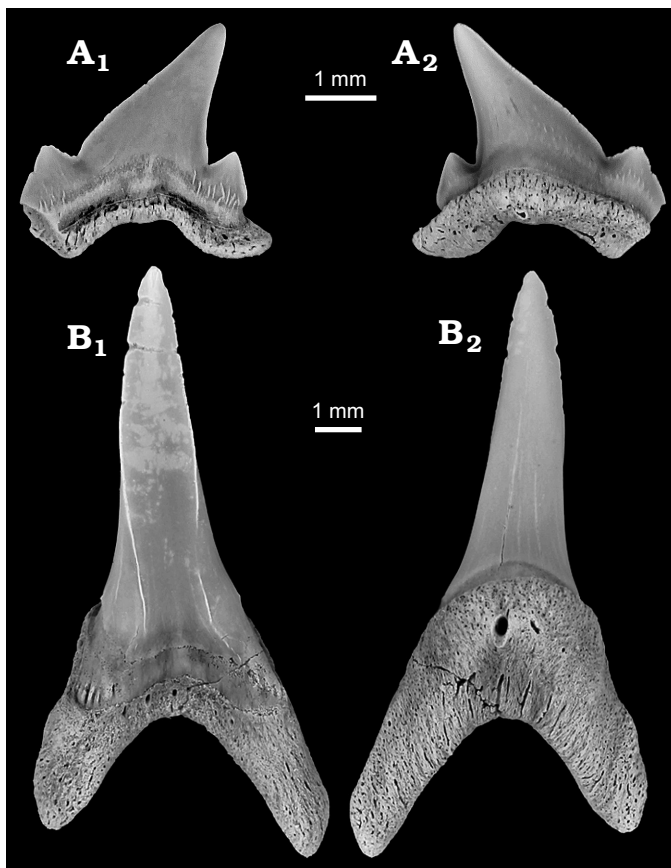


Fig. 3. Isolated, small juvenile teeth of *Cardabiodon ricki* Siverson, 1999 (WAM 13.6.1: lp7–9?) (A) and *Cretoxyrhina agassizensis* (Underwood and Cumbaa, 2010) (WAM 13.6.2: a2?) (B) from the basal (0.1 m) of the Haycock Marl, Pillawarra Plateau, Western Australia, late Cenomanian or early Turonian. In labial (A₁, A₂) and lingual (B₁, B₂) views.

tooth width to age 0 is used to compare estimated tooth width at age 0 to the size of the smallest isolated, juvenile tooth of *Cardabiodon ricki* (Fig. 3A) from comparable jaw positions.

Tooth width (TW) is the maximum horizontal distance between the outer margins of the mesial and distal root lobes when the tooth is positioned with the distal and mesial root/crown boundaries lined up along the same plane on the labial side of the tooth. Tooth width was selected because there is less variability in width than crown height (Bass et al. 1975). Once age was ascertained from centra, the proportion in RD size from age 0 to the RD at the oldest ring was used to back-calculate tooth size to age following this modification of the Dahl-Lea method (Carlander 1969):

$$TW_{\text{Age } x} = \frac{TW_{\text{Maximum}}}{\text{CRD}_{\text{Age } x} / \text{CRD}_{\text{t max}}}$$

where TW is tooth width, CRD is centrum radial distance, and t max is the oldest age (t). Total length (TL) can be substituted for TW for back-calculated estimations of length. Back-calculation of TW permits comparison but with a degree of error as the precise relationship between TW, TL, and CRD is unknown (Shimada 2008).

The basal part of the Haycock Marl in the lower Murchison River area has also yielded a dozen teeth of *Cretoxyrhina*. These teeth can be used to develop a ratio between largest and smallest tooth sizes that can be compared to the ratio between the RD of the birth ring and maximum RD of *Cretoxyrhina*. The largest tooth was illustrated by Siverson (1996: pl. 1: 17, 18). The incomplete tooth's original width is estimated at 22 mm and its morphology corresponds with the A2 position in *Cretoxyrhina* (see Bourdon and Everhart 2011: fig. 6). Second lower anterior teeth are approximately 15% wider than are second upper anterior teeth of *Cretoxyrhina* from the Smoky Hill Chalk of western Kansas (Bourdon and Everhart 2011: fig. 5). A 22 mm wide A2 would thus correspond to a 25 mm wide a2. However, it is possible that actual a2 are somewhat smaller in *Cretoxyrhina* of late Cenomanian–earliest Turonian age as second lower anterior teeth appear to be relatively smaller in *Cretoxyrhina* of latest Albian–earliest Cenomanian age than they are in specimens from the late Coniacian–earliest Campanian Smoky Hill Chalk of Kansas (Siverson et al. 2013). A well-preserved *Cretoxyrhina* tooth from the basal Haycock Marl measures 6.2 mm in width and is assigned to the a2 position (WAM 13.6.2; Fig. 3B₁). The two *Cretoxyrhina* teeth discussed above indicate a tooth size ratio of 4:1 (or very roughly 3:1 if *Cretoxyrhina vracensis* (Zhelezko, 2000), is used as template) for the same tooth file (Siverson et al. 2013). Given that this large size range is based on no more than a dozen teeth, it indicates that vertebrae of large individuals of Smoky Hill Chalk *Cretoxyrhina* should preserve a birth ring RD below 29% of the actual RD of the vertebra (assuming the A2/a2 ratio of the Haycock Marl population is halfway between the ratio in Smoky Hill Chalk individuals and the estimated one in *Cretoxyrhina vracensis*).

Comparison of neonate birth ring size.—Birth ring radial distance was plotted for comparison among the fossil lamniforms; *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *Cretoxyrhina* sp., and *Archaeolamna kopingensis*. Birth ring RD was also taken from specimens at the LACM: *Alopias vulpinus* (I-38158-1), *Isurus paucus* (I-57284-1, I-57285-1), *I. oxyrinchus* (I-39470-2), *Carcharodon carcharias* (I-35875, I-57280-1, I-57281-1, I-57282-1, I-57283-1, I-42094-1, I-42094-2, I-42100-2). Birth ring RD was also taken from the literature: *Al. vulpinus* (Cailliet et al. 1983a: fig. 5A, B), *I. oxyrinchus* (Cailliet et al. 1983a: fig. 9A, B; Ardizzone et al. 2006: fig. 1; Natanson et al. 2006: fig. 2; Ribot-Carballal et al. 2005: figs. 3, 4A–C), *Carcharodon carcharias* (Cailliet et al. 1985: table 1; Wintner and Cliff 1999: fig. 1A, B), and *Lamna nasus* (Campana et al. 2002: fig. 1; Natanson et al. 2002: fig. 1).

Systematic palaeontology

The Haycock Marl has produced several teeth of juveniles; one tooth, of a small individual of *Cretoxyrhina*, is particularly well preserved (WAM 13.6.2; Fig. 3B), and used to develop

a ratio in tooth sizes that aid in bracketing the size of the birth ring on centra of *Cretoxyrhina*.

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Order Lamniformes Berg, 1958

Family Cretoxyrhinidae Glickman, 1958

Genus *Cretoxyrhina* Glickman, 1958

Type species: *Oxyrhina mantelli* Agassiz, 1843. Eight of nine syntypes listed in Agassiz (1843: pl. 33, excluding a different taxon represented by fig. 5) are from the Chalk of the Lewes area, East Sussex, UK. The precise stratigraphical origin of the syntypes is unknown. In the mid-1800's there were several pits around Lewes with chalks of Cenomanian to early Coniacian age (see Siverson et al. 2013: 89).

Cretoxyrhina agassizensis (Underwood and Cumbaa, 2010) comb. nov.

Holotype: SMNH P2989.144, tooth from Bainbridge River Bonebed, Royal Saskatchewan Museum locality number 63E09-0003, Belle Fourche Member, Ashville Formation ("middle" to late Cenomanian benthic foraminiferal *Verneuilinoides perplexus* Zone), Pasquia Hills region, Saskatchewan, Canada.

Referred material.—WAM 13.6.2 (Fig. 3B), WAM 95.7.29–32, 34, 36, 37 (Siverson 1996: pl. 1: 1–6, 9, 10, 13–18; the colour of the teeth in figs. 7, 8, 11, 12 indicates that they may not originate from the basal Haycock Marl); late Cenomanian or early Turonian, Western Australia.

Emended diagnosis.—*Cretoxyrhina agassizensis* (Underwood and Cumbaa, 2010) can be diagnosed as a species with a very slender cusp in anterior teeth in the juvenile to sub-adult stage (broader at the same height in the older *Cretoxyrhina denticulata* (Glickman, 1957) and the younger *Cretoxyrhina mantelli*), presence of cusplets with a sharp apex on many of the lateroposterior teeth (not rounded as is commonly the case in topotypic *Cretoxyrhina denticulata*) and the lack of complete cutting edges on small juvenile anterior teeth. The labial face of the cusp is increasingly more constricted basally in anterior teeth with decreasing age of the individual.

Remarks.—The tooth WAM 13.6.2 from the basal Haycock Marl, lower Murchison River area, Western Australia (Fig. 3B) is inseparable from anterior teeth of *Telodontaspis agassizensis* Underwood and Cumbaa, 2010. The narrow median furrows along the lower part of the basal face of the root (Fig. 3B₂) is a common feature in early *Cretoxyrhina* (Siverson and Lindgren 2005: fig. 2I₂, P₂; Siverson et al. 2013: fig. 5Z, D', 7R, B'; Underwood and Cumbaa 2010: pl. 5: 5, misidentified as a *Roulletia* tooth). Similar furrows are present on the holotype of *T. agassizensis* (Underwood and Cumbaa 2010) described from the Belle Fourche Member (probably the late middle Cenomanian *Acanthoceras amphibolum* Zone) of the Ashville Formation, Saskatchewan, Canada. The nominal *Telodontaspis* co-occurs with larger, typical *Cretoxyrhina* at its type locality and in the basal Haycock Marl

(compare Siverson 1996: pl. 1: 5, 6 with Underwood and Cumbaa 2010: pl. 6: 16, 17 and Fig. 3B₁ with Underwood and Cumbaa 2010: pl. 6: 27). The gradual transition in basal constriction of the labial face of the cusp in anterior teeth from a "*Telodontaspis*" morphology (Fig. 3B₁); Underwood and Cumbaa (2010: pl. 6: 27) via a "juvenile" *Cretoxyrhina*-stage (Siverson 1996: pl. 1: 9) to the sub-adult or adult stage (Siverson 1996: pl. 1: 15) and the identical furrows on the basal face of the root in the two nominal taxa, indicate that the generic names denominate different ontogenetic stages in a single species. Synonymy is likewise indicated by the fact that *Telodontaspis* has not been shown to occur in deposits lacking typical, larger *Cretoxyrhina* teeth. As indicated by Siverson et al. (2013), the ontogenetic heterodonty is very marked in *Cretoxyrhina* and it appears that Underwood and Cumbaa (2010) underestimated the degree of ontogenetic heterodonty during the first few years in individuals of this genus. The earliest occurrence of this species is in the Belle Fourche Member of the Ashville Formation (described as *Cretoxyrhina denticulata*, *Telodontaspis agassizensis*, and *Roulletia canadensis* [the "A3" in the reconstructed dentition of the latter species] by Underwood and Cumbaa 2010) whereas the youngest occurrence is in the early middle Turonian of the Fairport Member of the Carlile Shale (described as *Cretoxyrhina mantelli* by Siverson and Lindgren 2005). A sample of middle Cenomanian *Cretoxyrhina* from the uppermost Gearle Siltstone at CY Creek, Giralia Anticline (type stratum for *Cardabiodon ricki*) includes anterior teeth of *Cretoxyrhina agassizensis*-type and lateroposterior teeth of *Cretoxyrhina denticulata*-type (cusplets present on all lateroposterior teeth and commonly rounded) and it is possible if not likely that the two species are chrono-segments of a single lineage (i.e., the early to early middle Cenomanian *Cretoxyrhina denticulata* followed by the late middle Cenomanian to early middle Turonian *Cretoxyrhina agassizensis*).

Stratigraphic and geographic range.—The late middle Cenomanian to early middle Turonian, United States, Canada, and Australia.

Family Cardabiodontidae Siverson, 1999

Genus *Cardabiodon* Siverson, 1999

Type species: *Cardabiodon ricki* Siverson, 1999, middle Cenomanian, CY Creek, Giralia Range, Western Australia.

Cardabiodon ricki Siverson, 1999

Holotype: WAM 96.4.45, vertebrae and 104 teeth from uppermost 10 cm of the Gearle Siltstone (middle Cenomanian), CY Creek, Giralia Range, Western Australia.

Material.—WAM 96.4.45 and WAM 96.3.175.

Emended diagnosis.—Anterior teeth not enlarged relative to largest lateroposterior teeth. Multiple files of full-sized teeth equipped with massive root, somewhat mesiodistally compressed lobes, and distally curved apical half of cusp. Two types of reduced teeth with erect symmetrical cusp in dentition, including larger type (2/3 height of tallest ante-

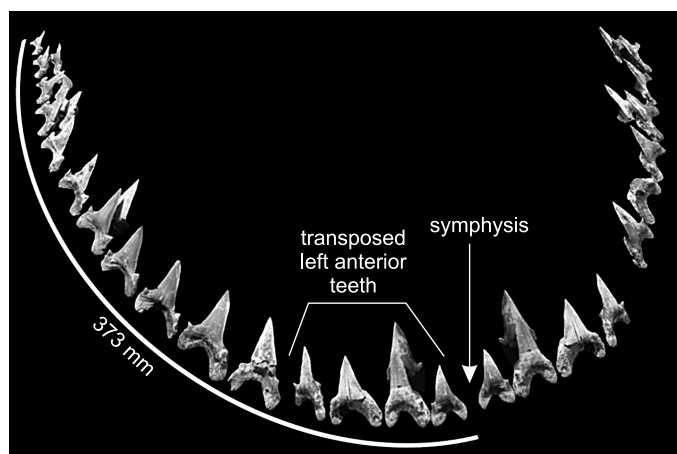


Fig. 4. Reconstructed lower dentition of *Cardabiodon ricki* Siverson, 1999 (WAM 96.4.45) from uppermost 10 cm of the Gearle Siltstone (middle Cenomanian), CY Creek, Giralia Range, Western Australia, depicting mirror images of left anterior teeth on the right side.

rior teeth) with labiolingually compressed root and smaller type (1/2 height of tallest anterior teeth) with mesiodistally compressed root. Minute, rounded cusplet commonly present between cusp and main cusplets. Cusplets reduced on full-sized anterior teeth with upright cusp. Lingual neck very wide medially. Diameter of largest vertebral centrum approximately 2.5 times height of tallest tooth in dentition. Centra of medium length and round. Corpus calcareum thick with laterally flat rims. Radial lamellae robust, widely spaced. Concentric lamellae absent. Small circular or subovate pores concentrated next to each corpus calcareum in the vicinity of the dorsal and ventral articular foramina. Papillose circular ridges on the surface of the corpus calcareum.

Dental morphology.—Siverson (1999) reconstructed the dentition of *Cardabiodon ricki* from CY Creek (middle Cenomanian) based on 100 teeth from a single individual (WAM 96.4.45). Four additional teeth pertaining to the holotype have since been collected (WAM 96.4.45.124–127). In his reconstruction, Siverson (1999: fig. 5) indicated that two tooth positions in the lower jaw were missing; lp10 and lp13. In modern lamnids, the ecological equivalents to *Cardabiodon ricki* (i.e., selachian apex predators), the most posteriorly situated teeth diminish in size more rapidly than shown in the reconstructed dentition of the holotype of *Cardabiodon ricki* (e.g., Bass et al. 1975: pls. 8 and 9; Compagno 2001: figs. 78, 79). We suspect that the two “missing” tooth files were never present (teeth from these “missing” tooth files have not been recovered despite collection of additional teeth belonging to the holotype individual following the publication of Siverson’s [1999] paper). This would reduce the number of putative lower lateroposterior teeth from 14 to 12 in WAM 96.4.45 (Fig. 4).

The teeth assigned to the anterior tooth files in WAM 96.4.45 differ from those assigned to the lateroposterior files by having a massive root with lobes exhibiting a circular cross-section (lobes are labiolingually compressed in the assigned lateroposterior teeth). The lateroposterior teeth in

WAM 96.4.45 can be separated into two groups based on their profile view. One group comprises teeth with a slightly to strongly labially curved cusp in profile view (e.g., Siverson 1999: fig. 7.6B) and the other group comprises teeth with a slightly to strongly lingually curved cusp in profile view (e.g., Siverson 1999: fig. 10.6B). Teeth of the latter group are wider and have a more erect cusp. By comparison with extant macrophagous lamnid sharks (*Isurus* spp., *Carcharodon carcharias*, *Lamna* spp.), the latter group of teeth exhibit one character typical for teeth of the upper jaw (great width) and two characters indicating a lower jaw position (more upright cusp in labial/lingual views and a lingually curved cusp in profile view). On the basis of these characteristics, and the degree of root symmetry versus absolute tooth size, the latter group was assigned to the lower jaw and the former group (narrow teeth with a cusp that is distally curved in lingual/labial views and labially curved in profile view) to the upper jaw by Siverson (1999), a designation followed here.

The diagnosis of *Cardabiodon* (Siverson 1999) relies in part on hypothesized dentition morphology. It therefore seems prudent to present a revised, somewhat more objective diagnosis. Nevertheless, regardless of how the teeth of WAM 96.4.45 are arranged, it is clear that the dentition design is not comparable to that of any other extinct or extant lamniform genus. The reduced anterior teeth are a particularly conspicuous feature in *Cardabiodon* that sets it apart from living macrophagous lamniforms. As reconstructed by Siverson (1999), there is a unique, abrupt increase in tooth size at the anterior/lateroposterior transition in the lower jaw. The designated a4 has a cusp and root comparable to those of the most distal lower anterior tooth of *Isurus oxyrinchus*. Apart from having a strongly lingually curved cusp in profile view (a typical feature in anteriorly situated lower anterior teeth of modern macrophagous lamniforms) its labial/lingual profile view is similar to that of the reduced first upper lateroposterior tooth in *I. oxyrinchus*. In the latter species, the LP1 has a labially curved cusp in profile view as opposed to the strongly lingually curved cusp on the designated a4 of WAM 96.4.45. A perfect match for a LP1 (reduced size, strongly asymmetrical root and a labially curved cusp in profile view) is indeed present among the teeth of WAM 96.4.45.30 (Siverson 1999: fig. 8.7), indicating that the assigned a4 is not a misplaced anteriorly situated upper lateroposterior tooth. The direction of the lateral cusplets in the assigned a4 is very similar to that in the putative lp1 and lp2 (Siverson 1999: fig. 5).

The juvenile *Cardabiodon ricki* tooth (WAM 13.6.1) is derived from the basal 0.1 m of the Haycock Marl (= Beedagong Claystone of Siverson 1996) in the lower Murchison River area, Western Australia. Recent work on selachians from the basal part of the Haycock Marl indicates a late Cenomanian or early Turonian age (*Cretoxyrhina* teeth corresponding in morphology with those from the Greenhorn Limestone in Kansas [Mike Everhart collection], below the *Collignonicerias woollgari* Zone). This age determination is supported by nannofossil data (Watkins in Gunson 1995) and the laminated appearance of the mid- to outer shelf sediment,

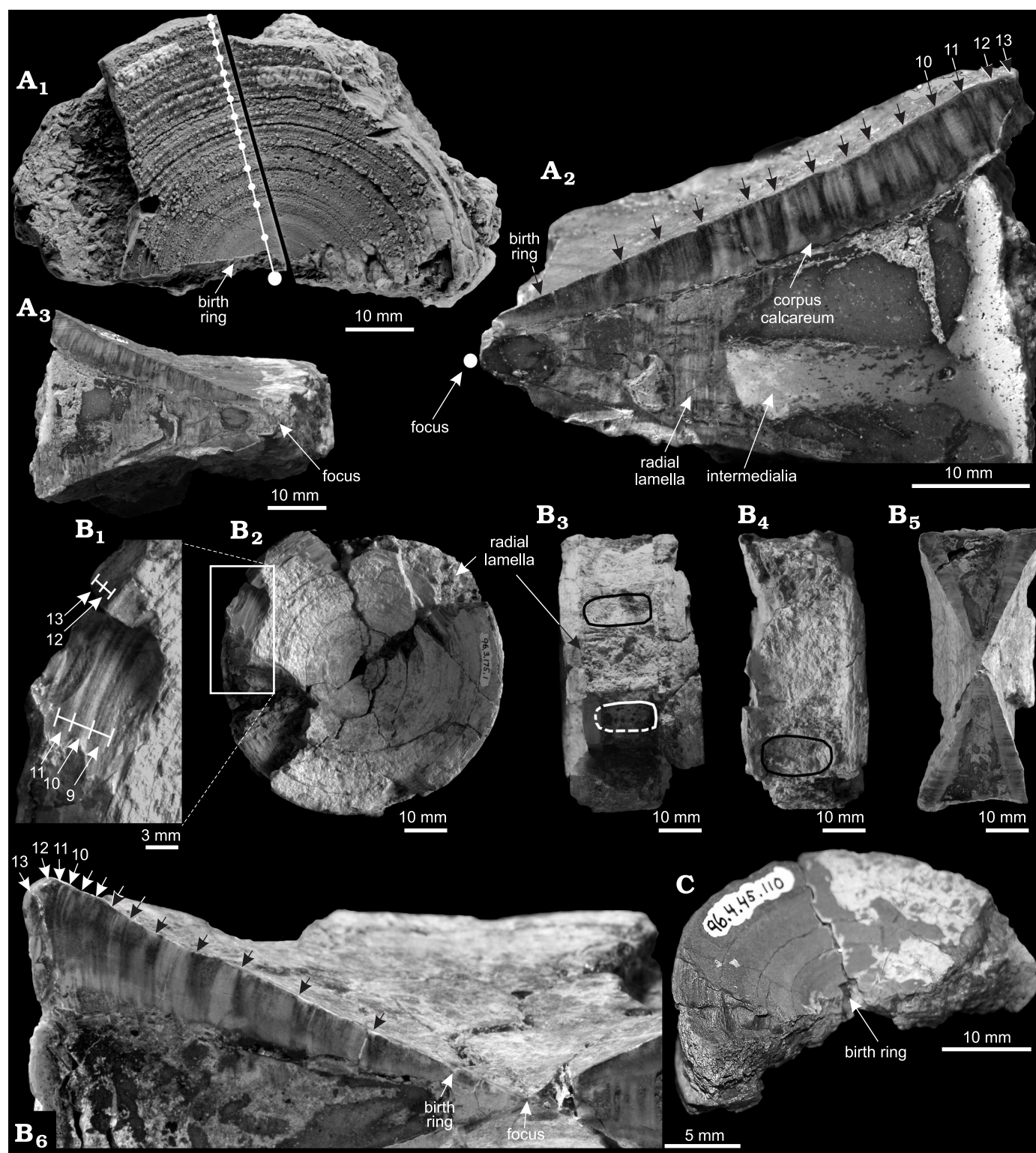


Fig. 5. Centra of *Cardabiodon ricki* Siverson, 1999 from uppermost 10 cm of the Gearle Siltstone (middle Cenomanian), CY Creek, Giralia Range, Western Australia. **A.** Precaudal centrum, WAM 96.4.45.128. Face of the corpus calcareum (A_1) showing line of section (black line) and transect with points of measurement (white line and circles), large filled circle represents focus, left half of the section centrum corresponds to A_2 , right half of the centrum corresponds to A_3 . "Hemisected" view of centrum (A_2) showing the number of bands, angle of the section does not intersect the focus as it was missing from the originally incomplete centrum, the point of the focus occurs in -z space (behind the plain of the page). Opposing view showing focus (A_3). **B.** Precaudal centrum, WAM 96.3.175.1. Anterior view of corpus calcareum with surface removed to show bands (B_1); centrum (B_2); dorsal view of centrum (B_3), ovals show outline and position of articular foramina for the neural arch (anterior to left); lateral view of centrum (B_4) oval outlines rib articular foramen (anterior to left); hemisected section of centrum (B_5) (anterior to left); enlarged, hemisected view (B_6) showing bands. **C.** Caudal centrum, WAM 96.4.45.110 (oblique angle), anterior view showing birth ring.

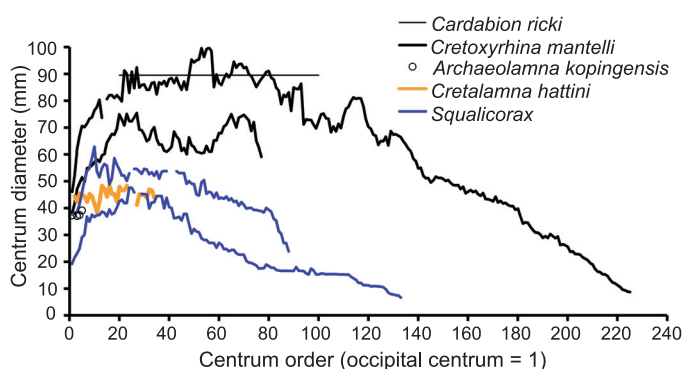


Fig. 6. Centrum size profiles of *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *Cretalamna hattini*, *Archaeolamna kopingensis*, and *Squalicorax* sp. Centrum diameter of *Cardabiodon ricki* (WAM 96.4.45.108) compared to those of other lamniforms: *Ar. kopingensis* (LACM P-128125), *Cretoxyrhina mantelli* (FHSM VP-323, VP-2187), *Cretalamna hattini* (LACM P-128126), and *Squalicorax* (LACM P-120090; USNM 425665). Centrum sizes for *Ar. kopingensis*, *Cretoxyrhina mantelli*, and *Squalicorax* spp. are taken from Cook et al. (2011).

indicating that it was formed during the Cretaceous Oceanic Anoxic Event II.

The very small, juvenile tooth is assigned to *Cardabiodon ricki* on the basis of its extremely wide neck and greatly elongated outer cutting edge of the mesial cusplet (see Siverson 1999: fig. 10.4B). The compressed, flared out root indicates that it belonged to a very young individual as this feature is only present in the very smallest teeth of *Cardabiodon venator* (e.g., WAM 04.10.91). A similar root, distinctly different from that in larger juveniles and adults, characterised the smallest juvenile tooth of another extinct lamniform shark, *Carcharocles megalodon* (Agassiz, 1843), described and illustrated by Pimiento et al. (2010: fig. 2, specimen UF 237959). Labial and lingual folds are absent on all juvenile teeth examined of early middle Turonian *Cardabiodon venator* (see Siverson and Lindgren 2005). Their presence on the Haycock Marl tooth is likely a result of its older geological age (the occurrence of folds on the crown increases with increasing geological age in Cretaceous lamniform genera; MS personal observations) and very early ontogenetic stage (e.g., the smallest teeth of *Dwardius woodwardi* [Herman, 1977] from the basal Haycock Marl do likewise have folds on the crown). The labial base of the crown forms a shelf relative to the labial face of the root. This feature, absent in large teeth of *Cardabiodon*, likewise characterises juvenile teeth of *Cardabiodon venator* (Siverson and Lindgren 2005). Although WAM 13.6.1 represents the only known occurrence of *Cardabiodon ricki* in the basal Haycock Marl, the species is present (large lower anterior tooth) in the uppermost bed of the underlying “Upper” Gearle Siltstone (WAM 13.8.1) and *Cardabiodon venator* occurs in the overlying nodule bed at the Haycock Marl/Toolonga Calcilutite contact (see Siverson 1996: pl. 4: 8–10). The presence of a very young *Cardabiodon* in the basal Haycock Marl follows the pattern seen in *D. woodwardi*, *Cretoxyrhina agassizensis*, *Johnlongia allocotodon* Siverson, 1996, *Squalicorax* sp. (described as *S. vol-*

gensis by Siverson 1996) and *Echinorhinus* sp., all of which are represented largely or almost exclusively by teeth from small juveniles in this part of the section.

Vertebral centra.—An examination of the *Cardabiodon ricki* centra from the two individuals from the CY Creek localities indicates that centrum morphology is very similar. Although WAM 96.3.175, comprising four associated centra, was found without teeth, it is also assumed to belong to *Cardabiodon ricki* based on similar proportions and shared characteristics including robust radial lamellae, very thick corpus calcareum, no concentric lamellae, and other characteristics as described and diagnosed below.

Examined precaudal centra of *Cardabiodon ricki* are large midtrunk centra (i.e., relative to the posterior precaudal centra) comparable in diameter to those of *Cretoxyrhina mantelli* (WAM 96.4.45.128, 96.3.175.1) (Figs. 5A, B, 6). The midtrunk centra are 2.3–3 times wider than they are long and have a double-cone (biconcave) calcification with slightly convex lateral sides. The centrum from the holotype (WAM 96.4.45.128) is incomplete but has a radius of 42 mm, suggesting a diameter of 84 mm (Fig. 5A), and a length of 30 mm. The ventral, articular interforamen width is 36 mm and the interforamen angle is 65°. The second centrum (WAM 96.3.175.1) measures 72 mm in diameter and 32 mm in length (Fig. 5B). The neural arch interforamen width is 12 mm and the interforamen angle is 45°. The neural arch interforamen and intraforamen widths are the same. The ventral interforamen width is 25 mm with an interforamen angle of 64°. The midtrunk dorsal foramina for articulation with the neural arch are large rectangles with rounded corners and abut the anterior corpus calcareum (WAM 96.3.175.1). The neural arch foramina extend 90% of the distance to the posterior corpus calcareum (Fig. 5B₃). Ventral foramina are situated posteriorly on the centrum and extend 90% of the distance between each corpus calcareum.

The centra of *Cardabiodon ricki* are classified as round with height equal to width (WAM 96.3.175.1; Siverson 1999: fig. 11.3A). Centra of *Cardabiodon ricki* are short (among all neoselachians) ranging from 0.3 to 0.51 (ratio of length/width), but medium in length for lamniforms. Centrum length is comparable to *Carcharodon carcharias* (0.51), but shorter than in *Carcharias taurus* (0.55), *Ce. maximus* (0.61), and *I. oxyrhincus* (0.65) (Kozuch and Fitzgerald 1989). The centrum length/width ratio of *Cretoxyrhina mantelli* ranges from 0.28 (posterior precaudal, FHSM VP-2184) to 0.31 (mid-precaudal, FHSM VP-2187), and up to 0.44 (anterior precaudal, FHSM VP-233) (Figs. 7, 8). The centra of *Cretalamna hattini* are shorter than those of *Cardabiodon ricki* and short for lamniforms ranging from 0.40 to 0.42 (LACM P-128126).

Centra are septate with straight, complete septae as in *Carcharodon carcharias* (Fig. 9A; Kozuch and Fitzgerald 1989: fig. 7; LACM I-35875-1 [5 m TL, 83 mm centrum diameter]). The radial lamellae originate from the focus and are more robust (1.3–1.6 mm thick, WAM 96.4.45.128) than those (1.0–1.2 mm thickness) from centra of *Ce. maximus*,

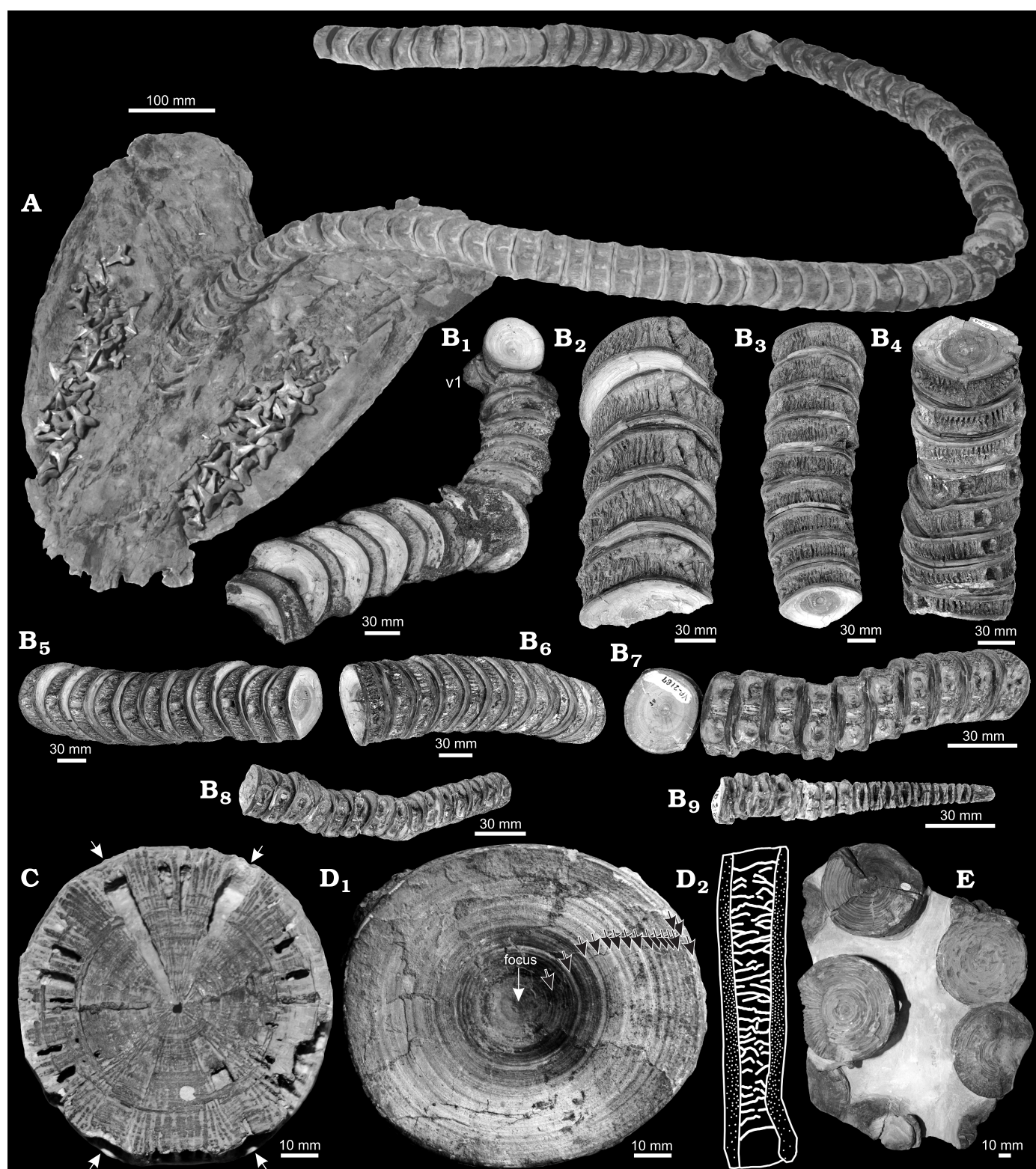


Fig. 7. Centra of *Cretoxyrhina* spp. **A, B.** *Cretoxyrhina mantelli* (Agassiz, 1843), late Coniacian–middle Santonian, Smoky Hill Chalk, Niobrara Chalk, Gove County, Kansas, USA. **A.** FHSM VP-323. **B.** FHSM VP-2187, articulated centra from various positions in the vertebral column; v1–14 (**B**₁), v1 = occipital centrum, order corresponds to Fig. 6; v62–66 (**B**₂); v67–75 (**B**₃); v86–93 (**B**₄); v94–104 (**B**₅); v129–139 (**B**₆); v183–193 (**B**₇); v194–208 (**B**₈); v209–227 (**B**₉). **C.** Centrum in transverse section through about inner margin of the corpus calcareum of *Cretoxyrhina mantelli*, NHMUK OR.25939, White Chalk Formation (?), near Sussex, UK; arrows indicate articular foramina for neural and ribs or haemal arches (see also Woodward 1912: pl. 43: 14). **D.** Centrum of *Cretoxyrhina* sp. (probably *Cretoxyrhina agassizensis*), DMNH 746C, Eagle Ford Group, Cenomanian, Tarrant County, Texas, USA; view of face (**D**₁) showing focus and 15 bands (black arrows) after the birth ring; tracing of left lateral view of centrum (**D**₂). **E.** Centra of *Cretoxyrhina* sp. (probably *Cretoxyrhina agassizensis*), NHMUK OR.49015, Cenomanian–Turonian, near Kent (?), UK.

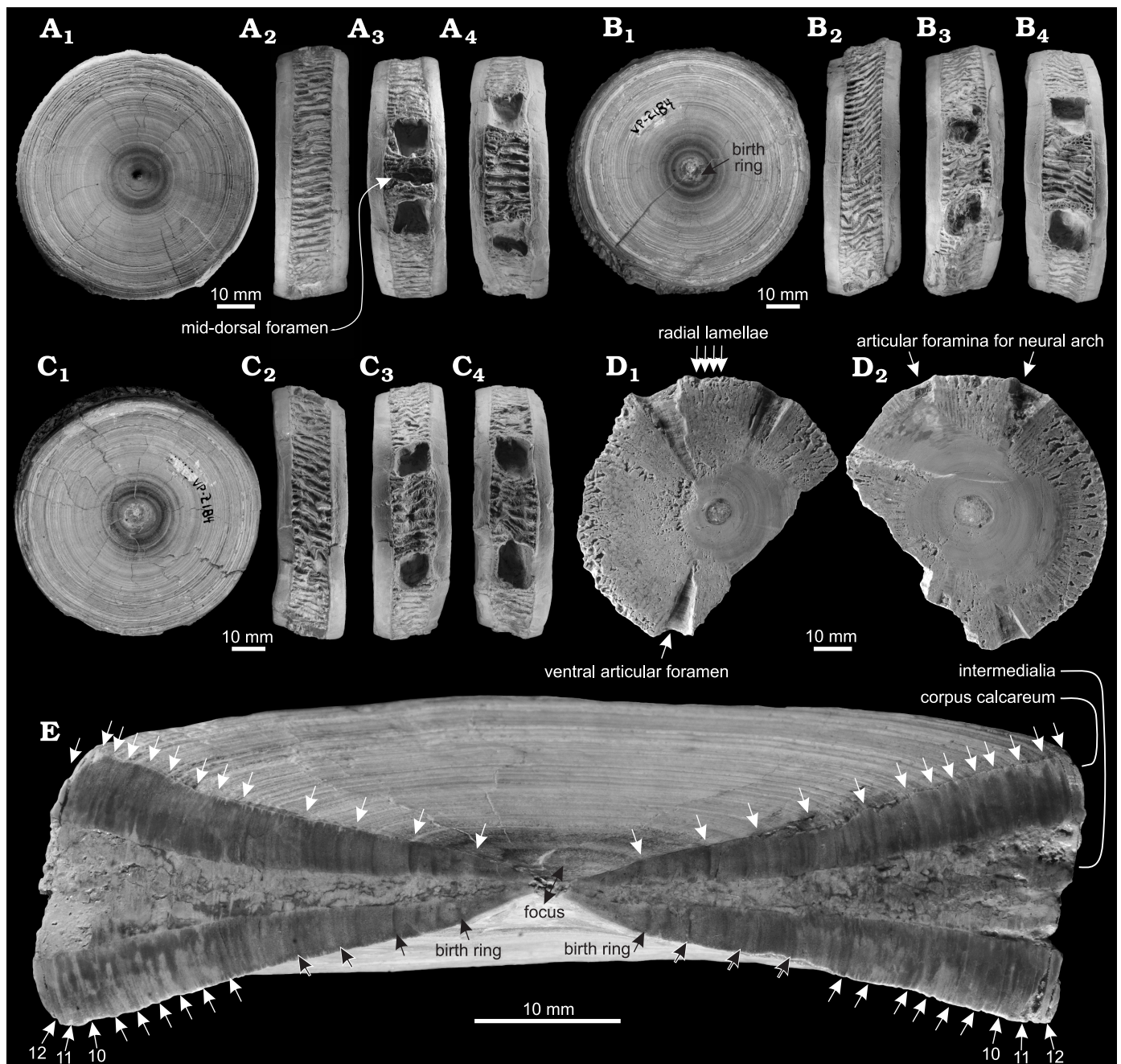


Fig. 8. Five posterior precaudal(?) centra of *Cretoxyrhina mantelli* Agassiz, 1843, late Coniacian–early Santonian, Smoky Hill Chalk of the Niobrara Chalk, Kansas, USA. A–C. Centra, FHSM VP-2184a (A), FHSM VP-2184b (B), and FHSM VP-2184c (C), in anterior or posterior (A₁–C₁), left lateral (A₂–C₂), dorsal (A₃–C₃), and ventral (A₄–C₄) views. D. Centrum, FHSM VP-2184d, in transverse section showing radial lamellae and dorsal and ventral articular foramina; in anterior and posterior (D₁, D₂) views. E. Centrum, FHSM VP-2184e, in hemisected view showing 12 bands (arrows).

10 m TL, 98 mm centrum diameter (Fig. 9B, C; LACM I-35593-1). Radial lamellae can bifurcate anteriorly and posteriorly at the corpus calcareum. In lateral view, density of radial lamellae is low with interseptal spaces being 2.9–3.8 times the thickness of the lamellae as in *Carcharias taurus* Rafinesque, 1810 (see centrum in Kozuch and Fitzgerald 1989: fig. 5) and *Hypotodus verticalis* (NHMUK OR.12377, OR.38867). *Carcharodon carcharias* has moderate density for a 5 m long individual with gracile lamellae being 1 mm thick and having interseptal spaces ranging 1.7–1.9 times

the thickness of the lamellae (Fig. 9A; LACM I-3578-1). In contrast, radial lamellae are gracile and very densely packed in *Ar. kopingensis* (Cook et al. 2011; LACM I-128125) and *Cretalamna hattini* (LACM P-128126; also figured in Shimada 2007: fig. 3D and Siversson et al. 2015: fig. 14). The radial lamellae in *Cretoxyrhina mantelli* (Figs. 7, 8; FHSM VP-323, VP-2184, VP-2187; KUV P 55060; DMNH 746C) are gracile and densely packed with interseptal spaces being 1–1.5 times the thickness of the lamellae (1 mm thick; FHSM VP-2184) (Fig. 8). No radial lamellae are present in

Ce. maximus; septae are incomplete and do not extend to the focus (Fig. 9B₁; LACM I-35593-1). No radial lamellae were present in any of the centra of *Squalicorax* spp. examined (KUVP 55190; SDSM 34975, 82067; UWGM NS.1509.07, 1509.34), and all *Squalicorax* centra, included in this study, were associated with teeth.

The intermedialia, the region between the corpora calcarea, is open (not solid). There are no concentric lamellae in the intermedialia of centra of *Cardabiodon ricki* (WAM 96.3.175.1, 96.4.45.128), unlike those thin concentric lamellae present in *Cretoxyrhina mantelli*, figured by Shimada (2008: fig. 7B). The expanded bases of the concentric lamellae can be seen in hemisected view of fig. 7b of Shimada (2008). The radial lamellae of *Cretoxyrhina mantelli* have densely-spaced, low, longitudinal ridges (?bases of concentric lamellae) on both sides of the lamella (FHSM VP-2184); the radial lamellae of *Cardabiodon ricki* are smooth. Concentric lamellae are also absent in *Ar. kopingensis* (LACM P-128125), *Cretalamna hattini* (LACM P-128126; Siversson et al. 2015), *Isurus paucus* (LACM I-57284-1, I-57285-1), and *I. oxyrinchus* (LACM I-39470-2). Concentric lamellae are not visible in *Carcharodon carcharias* (LACM I-35875-1, I-42094-1, I-57280-1, I-57281-1, I-57282-1, I-57283-1). Concentric lamellae are present in *Ce. maximus* (LACM I-35593-1).

No diagonal septa are present around the dorsal and ventral foramina in *Cardabiodon ricki*, *Cretoxyrhina mantelli* (Figs. 5, 7, 8), or *Cretalamna hattini* (LACM P-128126; Siversson et al. 2015). The diagonal septa create an appearance of a network of irregularly situated septa, which can be seen in centra of *Ce. maximus* (Fig. 9C₁; LACM I-35593-1).

The biconcave surface of the corpus calcareum shows numerous concentric ridges with papillose texture and grooves (Fig. 5A₁, A₂). The rim of the corpus calcareum is wide in lateral view. In hemisected view, the rim of the corpus calcareum is overall flat on the lateral side and not greatly curved as seen in *Cretalamna hattini* (LACM P-128126), *Cretoxyrhina mantelli* (FHSM VP-2187), *Carcharodon carcharias* (LACM I-35875-1), but unlike the rounded rim of *Ce. maximus* (LACM I-35593-1) (Figs. 7–9). In *Ce. maximus* (LACM I-35593-1) the rim curvature is antero- or postero-medial (Fig. 9B₄, C₃). The corpus calcareum is thick and greatly thickens laterally towards the margin (Fig. 5B₆). In contrast, *Ce. maximus* has a very thin corpus calcareum at small centrum diameters, but the distal end of the arm of the corpus calcareum thickens in larger sizes (Fig. 9C₃; LACM I-35593-1; Natanson et al. 2008). At the margin of centra of *Cardabiodon ricki* the corpus calcareum is 8–11% the thickness of the centrum diameter as is that of *Ce. maximus* (9%; LACM I-35593-1). In contrast, the corpus calcareum has a relatively uniform thickness in centra of *Cretoxyrhina mantelli* at ~7–8% (Figs. 7, 8A–C, E; FHSM VP-2184, VP-2187; Shimada 2008: fig. 7A), *Ar. kopingensis* (8%; Cook et al. 2011: fig. 5D), *Cretalamna hattini* (7%; LACM P-128126; Siversson et al. 2015), *Squalicorax* spp. (3–5%; KUVP 55190; SDSM 34975, 82067; UWGM NS.1509.07,

1509.34), and *Carcharodon carcharias* (4–7%; LACM I-35875-1; Kozuch and Fitzgerald 1989: fig. 7).

The thickness of the corpus calcareum in *Cardabiodon ricki* is especially evident with regard to the length of the centrum. *Cardabiodon ricki* has a corpus calcareum thickness that is 28% the length of the mid-trunk centrum (WAM 96.3.175.1, 96.4.45.128). When compared to *Cardabiodon ricki*, the corpus calcareum is much thinner in anterior and mid-trunk precaudal centra of *Cretoxyrhina mantelli* (10–16%; anterior precaudal centra AMNH FF 7210; FHSM VP-233, VP-2187; but 23% in posterior precaudal centra FHSM VP-2184), *Ar. kopingensis* (14%; LACM P-128125), *Cretalamna hattini* (14%; LACM P-128126; Siversson et al. 2015), *Carcharodon carcharias* (9–14%; LACM I-35875-1; Kozuch and Fitzgerald 1989: fig. 7), and *Lamna nasus* (22%, n = 1; Natanson et al. 2002: fig. 3, n = 3) (Figs. 5, 7, 8).

Pores (1–2 mm oval foramina) are found on the sides of the centra adjacent to the anterior and posterior corpus calcareum near the dorsal and ventral articular foramina of *Cardabiodon ricki* (WAM 96.3.175.1, 96.4.45.128; Siversson 1999: fig. 11.2B). *Archaeolamna kopingensis* (LACM P-128125; Cook et al. 2011: fig. 5B) has round to elongate, subovate pores adjacent to the anterior and posterior corpus calcarea in a continuous pattern. Pores are present on *Cretoxyrhina mantelli* adjacent to the corpus calcareum but only situated next to the dorsal and ventral articular foramina (Fig. 8A–C; FHSM VP-2184). No pores were visible on *Cretalamna hattini* (LACM P-128126; Siversson et al. 2015), *Hypotodus verticalis* (NHMUK OR.12377, 38867), or *Squalicorax* spp. (KUVP 55190; SDSM 34975, 82067; UWGM NS.1509.07, 1509.34; USNM 425665). Very small pores are scattered across the lateral faces of *Carcharodon carcharias* (LACM I-35875-1) and *Ce. maximus* (LACM I-35593-1) (Fig. 9). No fine radial canals are visible on the inner surface of the corpus calcareum of centra of *Cardabiodon ricki*.

The centra of *Cardabiodon ricki* can be distinguished from those of other lamniforms by a combination of the following characteristics; medium length, round centrum with a very thick corpus calcareum, a corpus calcareum with a flat rim, very robust radial lamellae, radial lamellae that occur in low density, concentric lamellae absent, and small circular or subovate pores concentrated next to each corpus calcareum.

Bands and growth characteristics.—The birth ring may be associated with an angle change on the interior surface of the corpus calcareum of *Cardabiodon ricki* (Fig. 5A₂, B₆). There is a crack running through this region but a change in thickness also occurs across the crack to suggest an angle change might be present, but further observations are needed. Cracks often follow the angle change as there is a change in thickness (MGN personal observation). Post birth, the surface of the corpus calcareum has more numerous fine concentric ridges but only robust, papillose ridges are associated with annual rings. In hemisected view, the birth ring consists of a broad darker ring that extends into the intermedialia (Fig. 5A₂).

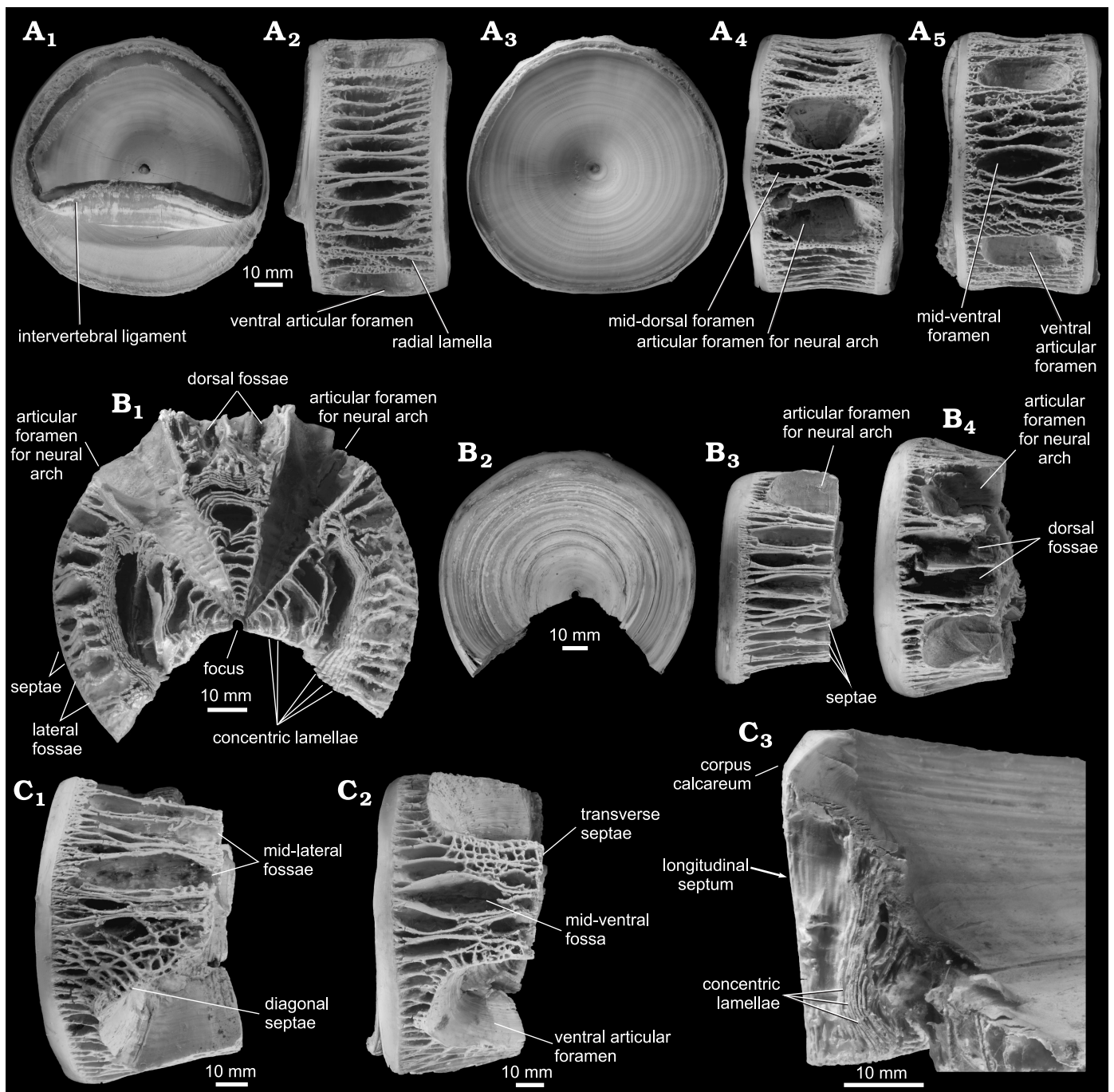


Fig. 9. Centra from extant *Carcharodon carcharias* Linnaeus, 1758 (A) and *Cetorhinus maximus* Gunnerus, 1765 (B, C). A. Centrum, LACM I-35875-1, in anterior (A₁), left lateral (A₂), posterior (A₃), dorsal (A₄), and ventral (A₅) views. B. Partial centrum (LACM I-35593-1a) in transverse section (B₁) posterior (B₂), left lateral (B₃), and dorsal (B₄) views. C. Partial centrum (LACM I-35593-1b) in left lateral (C₁), ventral (C₂), and one-half hemi-section (C₃) views.

The birth ring of *Cretoxyrhina mantelli* is associated with an angle change on the inner surface of the corpus calcareum, but the outer surface of the corpora calcarea show little difference in surface relief on some centra (FHSM VP-2187; Shimada 2008). In *Ar. kopingensis* the birth ring is not associated with an angle change in the corpus calcareum and no surface features on the corpus calcareum can be seen due to poor preservation (LACM P-128125).

After birth, the banding pattern in *Cardabiodon ricki*

(WAM 96.4.45.128) usually consists of a light, wide ring, and four dark rings separated by light rings in each band cycle. Three of the dark rings are very thin and occur following a broad light ring. The fourth dark ring is also broad and extends into the region of the intermedialia on the radial plates. The ring starts in a concentric groove, but ends concurrently with a papillose ridge and on the surface of the corpus calcareum (Fig. 5A₂, B₂). The fourth ring is assumed to be an annual mark. Occasionally a second, low papillose

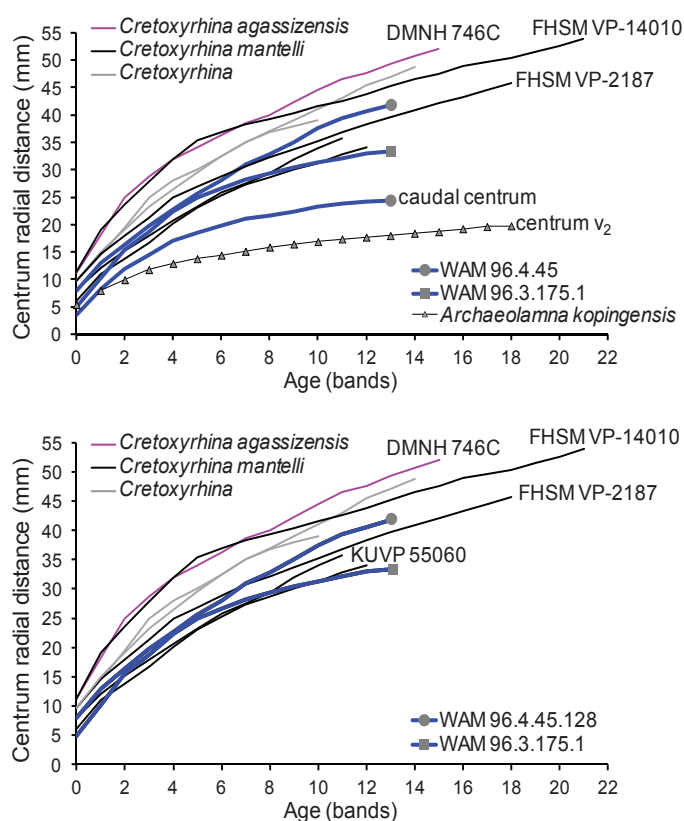


Fig. 10. Centrum growth profiles and size profiles of *Cardabiodon ricki* (blue lines), *Cretoxyrhina mantelli*, *Cretoxyrhina agassizensis*, and *Archaeolamna kopingensis*. Centrum radial distance is distance from focus toward the margin along a transverse plane at the anterior or posterior ends of the centrum (note: no line is figured between birth ring and band 1 in *A. kopingensis* because of damage in corpus calcareum where distance between them was extrapolated from size of retained fragments of corpus calcareum [see Cook et al. 2011]; filled symbols represent presumed annual rings); specimens depicted as “*Cretoxyrhina* spp.” are those centra not preserved with teeth but have a matching morphology to those found with teeth; the growth profile of WAM 96.4.45.128 was measured from the face of the corpus calcareum (Fig. 5A₁) and does not reflect the exact proportions of growth recorded in the “hemisected” view of the centrum in Fig. 5A₂ as the angle of the section does not intersect the focus.

ridge falls on the white rings between the dark rings. The banding pattern can be seen on both arms of the corpora calcarea. Bands crowd toward the distal part of the arm of the corpus calcareum.

Following birth in *Cretoxyrhina mantelli*, the banding pattern is relatively simple with broad, dark rings interspersed with lighter coloured rings (FHSM VP-2187, VP-2184; Shimada 2008). Sometimes lighter rings in the banding cycle contain thin or incomplete darker rings but these are considered artefact of some banding cycles (Shimada 2008). In *Ar. kopingensis* the banding cycle contains broad dark rings that extend onto the radial plate and are assumed to be annual marks (LACM P-128125; Cook et al. 2011). These dark, annual rings are interspersed with lighter, broad rings to form the complete band.

Age and growth.—The birth rings of *Cardabiodon ricki* occur at sizes of 5 and 6.6 mm RD, which overlap in RD with

those of *Cretoxyrhina mantelli* (6–11.6 mm RD) (Figs. 7, 8, 10, 11). The birth ring of *Carcharodon carcharias* is 9.5 mm RD (LACM I-35875-1). The birth ring RD for *Ar. kopingensis* (LACM P-128125) is 5.4 mm and is comparable in size to those of *Cardabiodon ricki* (Fig. 10).

Both specimens of *Cardabiodon ricki* (WAM 96.4.45.128, 96.3.175.1) have 13 bands, which are assumed to represent years (Fig. 10); other studies have reported bands to represent years (Natanson et al. 2002, 2006). In contrast, *Cretoxyrhina mantelli* lived to at least 21 years (bands; FHSM VP-14010). To determine if there was consistency in age

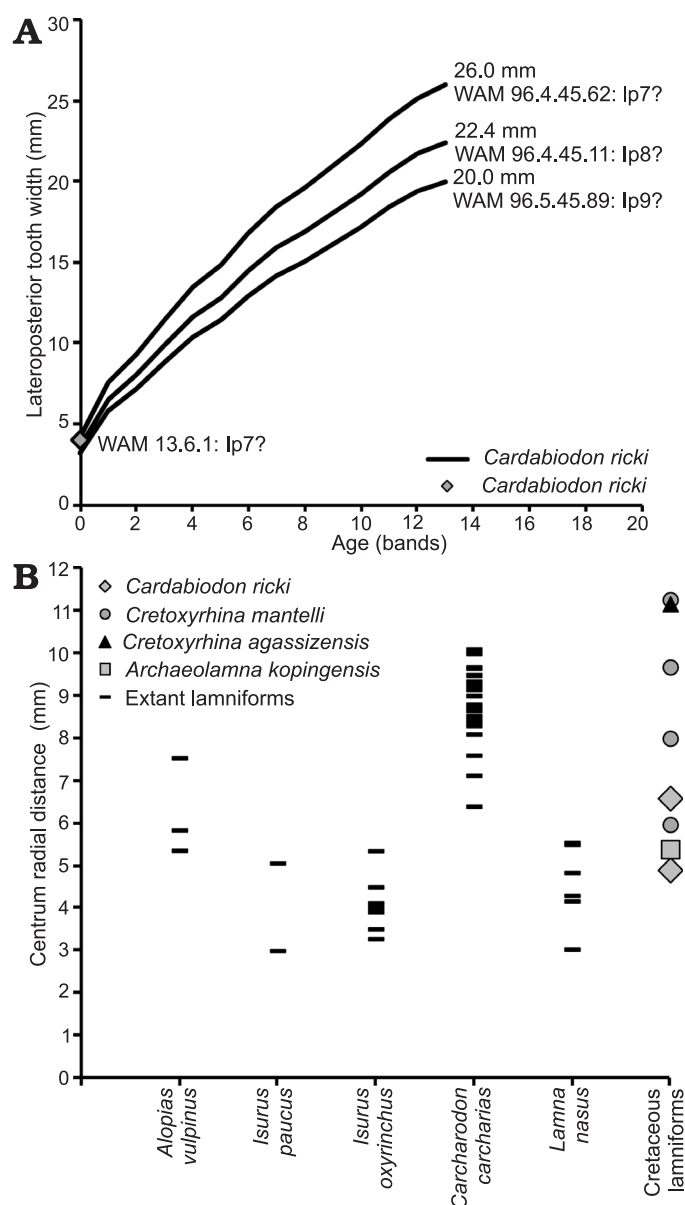


Fig. 11. Comparisons of teeth and centra at approximate neonate ages. **A.** Dahl-Lea back-calculated growth profiles of tooth width (maximum mesiodistal distance of the root) for lower lateroposterior (Ip) teeth (7–9?) of *Cardabiodon ricki*. **B.** Birth ring radial distance (measured along a transverse plane at the anterior or posterior ends of the centrum) for neonates of six extant species (Cailliet et al. 1985; Compagno 2001) and Cretaceous lamniforms including *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *Cretoxyrhina agassizensis*, and *Archaeolamna kopingensis* (large symbols).

along the vertebral column, two centra were aged from the holotype of *Cardabiodon ricki* and both produced the same age estimates; a precaudal centrum (WAM 96.4.45.128) and a relatively small caudal centrum (WAM 96.4.45.129; Fig. 5C). The maximum RD of both *Cardabiodon ricki* precaudal centra ranges from 33–42 mm RD and up to 45 mm RD (Siverson 1999), which fall within the range of those radial distances of *Cretoxyrhina mantelli* at the same age (32–47 mm RD) (Fig. 10). Growth tapers off after age 5 in WAM 96.3.175.1 with 86% of its total size attained by age 5. In the holotype (WAM 96.4.45.128), an inflection in growth is not apparent. In both precaudal specimens of *Cardabiodon ricki*, the growth profile is somewhat to strongly curvilinear (Fig. 10). The inflections in growth of *Cretoxyrhina mantelli* start to occur at age 4 (58% of total RD) but range up to age 9 (83% of total RD) (Fig. 10). The inflection in growth for *Ar. kopingensis* (LACM P-128125) occurs at age 5 (69% of total RD).

Confirmation of birth ring size.—An isolated tooth (WAM 13.6.1) from a very young, possibly neonate was used to determine whether the proper ring was identified as the birth ring in *Cardabiodon ricki*. Lower lateroposterior teeth from three consecutive positions, estimated to include the tooth position of WAM 13.6.1, were plotted with back-calculated sizes from *Cardabiodon ricki* (WAM 96.4.45.62: lp7?, WAM 96.4.45.88: lp8?, WAM 94.4.45.89: lp9?) (Fig. 11A). The back-calculated tooth TW for lower lateroposteriors assigned to lp7–9 range from 3.8–4.9 mm TW (Fig. 11A). This corresponds closely with the estimated 4 mm original TW (3.6 mm as preserved) of WAM 13.6.1.

In comparison, the birth rings of two specimens of *Cretoxyrhina mantelli* are 4.8:1 (i.e., 21%; FHSM VP-14010) and 4.7:1 (i.e., 21%; FHSM VP-2187) of maximum size at oldest age (Fig. 10). A specimen likely belonging to *Cretoxyrhina agassizensis* (because of its late Cenomanian age) is 4.4:1 (i.e., 22%; DMNH 746C). The juvenile a2 tooth of *Cretoxyrhina agassizensis* (WAM 13.6.2) from the basal Haycock Marl is 6.2 mm TW and the largest anterior tooth of this taxon from the same stratum is an incomplete A2 with an estimated TW of 22 mm. This produces a 4:1 ratio for comparable teeth if we use data from Smoky Hill Chalk *Cretoxyrhina mantelli* (a2's approximately 15% wider than A2's) and a 3:1 ratio if we use *Cr. vraconensis* as template (the A2's appears to be wider than the a2's in this taxon; Siverson et al. 2013). Given that the 3–4:1 ratio for isolated teeth is based on no more than a dozen teeth, the ratio between vertebral diameter and the birth ring in large centra should exceed at least 3:1 by some margin, assuming an isometric relationship between anterior tooth width and centrum growth as measured by the diameter.

The sizes of birth rings of *Cardabiodon ricki*, *Cretoxyrhina mantelli*, and *Ar. kopingensis* overlap in diameter with birth rings of six extant lamniforms (Fig. 11B). In general, birth rings can vary in size by 36% (6.4–10.0 mm RD) in *Carcharodon carcharias* and up to 45% (3.0–5.5 mm RD) in *L. nasus* (Fig. 11B).

Discussion

Dental morphology of *Cardabiodon ricki*.—Adhering to the view of Underwood et al. (2011), Dickerson et al. (2013) implied that Siverson's (1999: fig. 5) reconstruction of the lower jaw dentition of WAM 96.4.45 is "likely quite artificial" (e.g., duplication amongst the first five lower lateroposterior teeth). Lower right lateroposterior teeth assigned to the lp2–5 files were illustrated by Siverson (1999: fig. 10). The four teeth are clearly different from each other and additional replacement teeth not illustrated by Siverson (1999) fall nicely into these four tooth-type categories. In Siverson's (1999: fig. 5) reconstruction of the dentition of *Cardabiodon ricki*, a tooth from the left side of the jaw was used for the lp1 position (Siverson 1999: fig. 9.3). Since the publication of his work an isolated root was found that belongs to a previously collected cusp pertaining to the holotype. The reassembled tooth (WAM 96.4.45.79) is very similar to the assigned left lp1 but has a more complete root and indicates the existence a fifth, more anteriorly situated lower right lateroposterior tooth.

The lack of specificity (other than implying that the assigned a4 is a LP1, addressed above in the "dental morphology" section) in Dickerson et al. (2013) makes it difficult to address their concerns. It is noteworthy that Dickerson et al. (2013) did not examine WAM 96.4.45 first hand. They cited Underwood et al. (2011) in support of their view, but these authors likewise did not examine the holotype.

Morphology of centra.—For close to 200 years isolated or associated fossil shark teeth have been used in classification and to assess diversity. Isolated teeth lack characteristics that more complete skeletal material can offer to refine classification (Shimada 1997c; Shimada and Cicimurri 2005; Cook et al. 2011). We describe the morphology of centra of *Cardabiodon ricki* and compare it to other lamniforms with the intention of refining the system for classification of lamniforms.

Historically, Ridewood (1921) outlined the morphology of shark centra, but the publication contains poorly defined terms and schematic line drawings. Compagno (1977, 2001) and Kozuch and Fitzgerald (1989) introduced other characteristics and terminology to describe centra. In our study, *Cardabiodon ricki* can be distinguished from *Cretoxyrhina* by having longer centra, robust radial lamellae occurring at a low density, a much thicker corpus calcareum, no concentric lamellae, and papillose circular ridges on the surface of the corpus calcareum.

Size of birth ring.—We used the smallest (relative to its estimated position) isolated tooth, presumably from a neonate, of *Cardabiodon ricki* to confirm the size of birth rings on centra (Figs. 3A, 10, 11A). The growth profile of a centrum from the holotype of *Cardabiodon ricki* was used to back-calculate the size of teeth from a comparable, assigned position (lp7–9) to age 0. The back-calculated TW was then

compared to the TW of WAM 13.6.1 and the two TWs were very similar (Fig. 11A). Initially, there was some discussion about the selection of the birth ring.

An earlier erroneous interpretation identified the second ring (now identified as age 1) as the birth ring. Using the second, erroneous ring provided a larger birth ring size and an erroneous larger back-calculated tooth size that was nearly 1.4–3.4 mm larger than the observed neonate tooth width (WAM 13.6.1). Using the erroneous growth profile from the centrum, a ratio (3.5:1) was developed between the RD at the last ring and the second ring. The actual ratio of $lp7-9?$ (WAM 96.4.45.11) to the isolated neonate tooth is 5.0–6.5:1, indicating the neonate birth ring should be much smaller in size. Consequently, the first ring was reinterpreted as the birth ring, which provided a ratio of 6.2:1 (Fig. 10, Appendix 1).

No neonate teeth of *Cretoxyrhina mantelli* or *Archaeolamna kopingensis* were available for study to corroborate birth ring size. However, we examined a tooth identified as a juvenile *Cretoxyrhina agassizensis* (probable a2; WAM 13.6.2; Fig. 3B). The range in ratios from centrum radial distance of *Cretoxyrhina mantelli* is 4.5–5.7:1 (Appendix 1; FHSM VP-2184, VP-2187, VP-14010; KUVVP 55060), which is a larger ratio than predicted (3–4:1) from tooth sizes using a small sample of teeth of *Cretoxyrhina agassizensis*. The ratio between birth ring size and maximum recorded radial distance of centra suggests smaller teeth for *Cretoxyrhina agassizensis* should exist. We assume the ratio of smallest to largest known teeth is the same between taxa of *Cretoxyrhina*, but we also do not know if the centra included in the study represent the largest known for the taxon. The more ideal way to corroborate birth ring size is to use associated specimens that include centra and teeth that are from the same horizon or biozone as the isolated neonate teeth.

Ideally, tooth-size ratios derived from samples from the Smoky Hill Chalk should be used to evaluate growth data deduced from centra collected from the same deposit. We are, however, not aware of any samples of *Cretoxyrhina* teeth from a narrow stratigraphical interval in the Smoky Hill Chalk producing a range in tooth-size for a given file close to that of the basal Haycock Marl sample. Shimada (2008: fig.6) illustrated the largest and smallest anterior teeth known from the Smoky Hill Chalk of western Kansas. The smaller tooth (FHSM VP-16522) is probably an A1 and the large tooth is likely an A1 or a1 (FFHM 1972.196). The tooth-width ratio between the two teeth is approximately 4.8:1. This corresponds to a ratio of 4.1–4.2:1 for comparable positions if the larger tooth is an a2 (as a2's are approximately 15% wider than A2's in Smoky Hill Chalk *Cretoxyrhina*; see Bourdon and Everhart 2011). This ratio is larger than that recorded for the basal Haycock Marl sample but the precise stratigraphical origin of the two teeth is unknown (or at least not stated by Shimada 2008) and the Smoky Hill Chalk spans no less than 5 Ma. It seems highly likely that both the maximum size of the largest individuals in a population and the relative size of pups varied across a 5 Ma interval. It therefore seems prudent to deduce tooth width ratios from material collected from a narrower stratigraphical

Table 1. Total length (TL) at birth, age at maturity, and TL at maturity for five families of lamniforms. Unless otherwise noted information is from Compagno (2001), ^ALiu et al. (1998), ^BCampana et al. (2002), ^CHamady et al. (2014).

Taxon	Sex	TL at birth (cm)	Age at maturity (years)	TL at maturity (cm)
Carchariidae				
<i>Carcharias taurus</i>	both	95–105	10	–
	female	–	–	220
	male	–	–	190–195
Odontaspidae				
<i>Odontaspis ferox</i>	both	105	–	–
	female	–	–	364
	male	–	–	275
Mitsukurinidae				
<i>Mitsukurina owstoni</i>	both	–	–	–
	female	–	–	335
	male	–	–	264–384
Alopiidae				
<i>Alopias pelagicus</i>	both	130–160	–	–
	female	–	8–9	282–292
	male	–	6–9	267–276
<i>Alopias superciliosus</i>	both	100–140	–	–
	female	–	12–13	294–355 ^A
	male	–	9–10	279–300 ^A
<i>Alopias vulpinus</i>	both	114–160	3–8	–
	female	–	–	315–400
	male	–	–	288
Lamnidae				
<i>Carcharodon carcharias</i>	both	100–160	–	–
	female	–	–	–
	male	–	<44 ^C	<442 ^C
<i>Isurus oxyrinchus</i>	both	60–70	7–8	–
	female	–	7	275–293
	male	–	4.5	203–215
<i>Isurus paucus</i>	both	97–120	–	–
	female	–	–	245–417
	male	–	–	245
<i>Lamna ditropis</i>	both	40–85	–	–
	female	–	8–10	221
	male	–	5	182
<i>Lamna nasus</i>	both	60–80	–	–
	female	–	14 ^B	212 ^B
	male	–	7 ^B	175 ^B
	female	–	–	185–250
	male	–	–	150–200

interval. Future discoveries of small *Cretoxyrhina* teeth will help to test whether the birth ring sizes of *Cretoxyrhina* are realistic (Appendix 1). Birth ring sizes in extant taxa vary 36–45% (Fig. 11B).

Age at maturity.—There is an inflection in growth in *Cardabiodon ricki* from 5–7 bands suggesting sexual maturity, when energy from somatic growth is diverted to gonadal growth (Carlander 1969). This inflection in growth can be seen in the growth profile of *Carcharodon carcharias* at 8–10

years old (Cailliet et al. 1985: 57, fig. 2; known to be 9–10 years old). In four extant lamniform families (i.e., Carchariidae, Mitsukurinidae, Alopiidae, and Lamnidae), age at maturity ranges up to 14 years old, with females maturing at a later age and at a larger size than males (Table 1). Females mature at 7–14 years old in *Carcharias*, *Alopias*, *Isurus*, and *Lamna*. Among the same genera, males mature from 4.5–10 years old and 3.4 years earlier (on the average) than females. Females mature at 185–400 cm TL in *Carcharias*, *Odontaspis*, *Mitsukurina*, *Alopias*, *Isurus*, and *Lamna*. However, the extant lamniform males mature from 150–350 cm TL, which is 82 cm TL on the average less than females for all previously listed genera.

Estimated length.—The estimated lower jaw circumference in *Cardabiodon ricki* is 746 mm (an estimate from summed tooth widths with 1 mm spacing between teeth and excludes the diastema at the corner of the mouth) based on the revised reconstruction of its dentition (the upper row is most likely still incomplete and can thus not be used to estimate jaw circumference in a meaningful way). The estimated total length of the holotype of *Cardabiodon ricki* is 5.5 m based on the relationship between bite circumference and TL for *Carcharodon carcharias* (Lowry et al. 2009). Shimada (1997c) estimated one individual of *Cretoxyrhina mantelli* (FHSM VP-2187) at 5 m. However, we offer a refined estimate of 5.3 m for FHSM VP-2187 by taking into account 20% for anteroposterior shrinkage or crushing of centra (Fig. 7) by measuring the straight line distance of radial lamellae that were preserved in a sinuous line; sum of the length of all centra is 350 cm (Shimada 1997c: 650), add 20% for compression, 10% for the intervertebral discs, plus 10 cm for the missing tail section, and 60 cm for the skull, equals 532 cm ($= 350 \times 1.2 \times 1.1 + 10 + 60$ cm).

Longevity.—The growth rates are slower than those of *Cretoxyrhina mantelli*, which also suggests a greater longevity than 13 years. Furthermore, growth starts to taper off after age 7 in WAM 96.4.45.128 suggesting a much later maturity and longer lifespan. Longevity of extant lamniforms (both sexes combined) ranges from 10–70 years old (see citations listed in Shimada 2008: table 2 and Hamady et al. 2014). *Carcharias taurus* lives from 10–20 years old depending on the study population (Govender et al. 1991; Branstetter and Musick 1994; Goldman et al. 2006). *Isurus oxyrinchus* has been reported to live from 17–32 years old depending on the study population (Cailliet et al. 1983a; Campana et al. 2005; Ribot-Carballal et al. 2005; Ardizzone et al. 2006; Bishop et al. 2006; Natanson et al. 2006). Future studies of age and growth of additional *Cardabiodon ricki* specimens will shed light on the hypothesis that longevity exceeded 13 years.

Our quantitative age and growth data shows that *Cretoxyrhina* could live to 21 years. Shimada (2008: 24) estimated L_{∞} (theoretical maximum TL; Bertalanffy 1938) from FHSM VP-2187 as 6.91 m TL and then used that value to estimate longevity of 38 years. Based on our data, Shimada's (2008) estimate is probably too young given our revised length es-

timate, but we caution the reader to consider longevity estimates from one individual as only a point estimate (not a mean); understandably, palaeontology collections yield very small sample sizes for such studies. With regard to the estimate of L_{∞} of *Cretoxyrhina mantelli*, a point estimate likely does not reflect the maximum possible TL and should be viewed as a minimum estimate of L_{∞} . L_{∞} is more reliably estimated from a population with a sample size commensurate with relatively stable error (i.e., $n > 30$ individuals, preferably $n > 100$). We do not have any data on L_{∞} from described individuals but we do agree that L_{∞} for *Cretoxyrhina mantelli* is larger than 6 m TL. The larger sizes of isolated teeth support this suggestion (see Agassiz 1843). One of the syntype teeth of *Cretoxyrhina mantelli* would have been close to 80 mm high (Agassiz 1843: pl. 33: 9), which is about 50% taller (main cusp) than the tallest tooth in FHSM VP-2187 suggesting a L_{∞} of about 8 m TL.

Girth.—Growth in girth is correlated with the exponential increase in weight; i.e., a length/weight relationship (Carlander 1969; Natanson et al. 2008). We predict that *Cardabiodon ricki* had a large girth. The corpus calcareum and radial lamellae are thicker (relatively speaking) than are those of *Carcharodon carcharias*. The centra of *Cretoxyrhina mantelli* have much thinner corpora calcarea and radial lamellae than do *Cardabiodon ricki*. Often the corpora calcarea of *Cretoxyrhina mantelli* are fractured and the two corpora calcarea are collapsed on each other thereby folding the thin radial lamellae (Figs. 7, 8). We have not observed antero-posteriorly crushed centra for *Cardabiodon ricki*. The observation of non-collapsed centra is not due to differences in sediment thickness and pressure as other centra from CY Creek are collapsed, for example, centra of an anacoracid (WAM 12.4.4–9).

The number of bands is consistent in both the precaudal and caudal centra of *Cardabiodon ricki*, which suggests the number of bands is not related to girth. In *Ce. maximus* the band pair deposition along vertebral column is not consistent and is positively correlated with girth in the trunk region suggesting more “bands” provide extra structural support (Natanson et al. 2008).

Swimming ecology.—The morphology of centra of *Cardabiodon ricki* suggest a rigid vertebral column and a fast swimmer. *Cardabiodon ricki* has very robust centra that are moderately long compared to those of *Cretoxyrhina mantelli* and Santonian *Squalicorax*. The vertebral centra of *Cretoxyrhina mantelli* are relatively short. Buchholtz (2001) found that an increased vertebral count of the torso is strongly correlated with a decrease in relative centrum length but an increase in vertebral column flexibility in cetaceans. However, longer centra permit less absolute displacement, which is the distance between the posterior and anterior faces of the centrum and functions to reduce vertebral column flexure (Buchholtz and Schur 2004). The anterior and posterior faces of centra of *Cardabiodon ricki* lack rounded margins, thereby reducing rotation from one centrum to the next. Rotation is the angle through which a centrum can “pivot” (not spin)

from the adjacent centrum. Among cetaceans, the presence of longer centra suggests a rigid body and fast swimming speeds (Buchholz and Schur 2004).

Ridewood (1921: 324–325) notes that centra and arches are fairly rigid in elasmobranchs, but it is the fibrous notochordal sheath (= Ridewood's "intervertebral ligaments") that provides the majority of intervertebral flexure. Porter et al. (2007) showed that *Mustelus californicus* Gill, 1864 vertebrae did not have a substantial viscoelastic response at biologically relevant strain rates, suggesting that for their function they are sufficiently rigid to eliminate flexure within the centrum.

A vertebral column with longer centra and low flexure is a characteristic of fast cruising lamnid sharks with a thunniform swimming mode. Lamnids have a low-drag fusiform body shape and they undulate a narrow caudal peduncle with a high aspect ratio tail to generate speed (Sfakiotakis et al. 1999). Thunniform swimmers show high thrust and acceleration but tend to lack in maneuverability (Sfakiotakis et al. 1999). *Cretoxyrhina mantelli* exhibits the vertebral morphology of a carangiform swimmer: high vertebral count, and great vertebral column elasticity. Carangiform swimming is characteristic of moderately fast swimmers with higher maneuverability than thunniform swimmers (Sfakiotakis et al. 1999).

Our suggestion that *Cardabiodon ricki* is a fast swimmer is corroborated by the morphology of the placoid scales in another associated specimen. Dickerson et al. (2013: fig. 3) concluded the keeled placoid scales for *Cardabiodon* indicate a morphology characteristic for drag reduction associated with fast swimming sharks. Keeled placoid scales are also found on *Cretoxyrhina mantelli* (Shimada 1997c).

Distribution and reproduction.—The Western Interior Seaway (WIS) was probably an important area for reproduction for *Cardabiodon* spp. (see Siverson and Lindgren 2005). Most records of *Cardabiodon* are from offshore but moderately deep, inner to mid-neritic deposits (e.g., Gearle Siltstone, Southern Carnarvon Basin, Western Australia; Greenhorn Limestone, Kansas, USA; Fairport Member of the Carlile Shale, Montana, USA; Lower Chalk, southern England). Recently, Cook et al. (2013) reported the teeth of very small juveniles from the early Turonian of Alberta, Canada and the middle Turonian of Kansas, USA, corroborating the notion proposed by Siverson and Lindgren (2005) that the restricted WIS may have served as a nursery area.

The small juvenile *Cardabiodon ricki* tooth from the basal, laminated Haycock Marl is the only Australian example of a very early ontogenetic stage in this genus from an open marine environment. All other records, published or unpublished, of the genus from the Cenomanian–Turonian of Western Australia are based on remains from large individuals.

Conclusions

Cardabiodon ricki can now be viewed as being distinct in morphology, biology, and ecology from *Cretoxyrhina man-*

telli, *Archaeolamna kopingensis*, and *Squalicorax*. Centra of *Cardabiodon ricki* indicate slower growing individuals compared to *Cretoxyrhina mantelli*, and living to at least 13 years old. The lower jaw bite circumference of *Cardabiodon ricki* is estimated at 746 mm at age of 13. Age and growth information suggest a later age at maturity for *Cardabiodon ricki* (5–7 years or older) than *Cretoxyrhina mantelli* (5 years). The birth ring sizes of the fossil taxa included in this study are comparable to sizes of extant lamniforms, and an isolated "neonate" tooth of *Cardabiodon ricki* has a size predicted by back-calculated lateroposterior tooth sizes based on growth profiles from centra. *Cardabiodon* has medium-length, robust centra, for a lamniform, indicating a large shark with significant girth and a rigid vertebral column adapted for fast swimming and acceleration but low manoeuvrability.

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Appendix 1

Lamniform ages (in presumed years) and radial distances (in mm) for each point of measurement in the growth series from birth ring to band 21.

Catalogue number	Age	Birth ring	Band																					
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
<i>Cardabiodon ricki</i>																								
WAM 96.3.175.1	13	4.9	10.2	15.4	18.7	22.4	24.9	26.6	28.2	29.4	30.4	31.4	32.1	33.0	33.4									
WAM 96.4.45.128	13	6.6	11.8	14.6	18.0	21.1	23.3	26.3	28.9	30.7	32.9	35.0	37.5	39.5	40.8									
WAM 96.4.45.129	13	3.5	8.3	11.8	14.4	17.0	18.5	19.8	21.1	21.7	22.4	23.3	23.8	24.2	24.3									
<i>Cretoxyrhina mantelli</i>																								
FHSM VP-2184	12	6.0	11.1	13.8	16.7	20.1	23.1	25.2	27.3	28.6	30.0	31.2	32.8	34.1										
FHSM VP-2187	18	9.7	14.6	18.0	21.3	25.0	26.9	28.8	30.7	32.2	33.7	35.3	36.8	38.3	39.7	40.9	42.1	43.3	44.5	45.8				
FHSM VP-14010	21	11.3	19.1	23.6	27.9	31.9	35.3	36.9	38.3	39.3	40.3	41.6	42.6	43.7	45.2	46.5	47.5	48.9	49.6	50.4	51.5	52.6	53.9	
KUVP 55060	11	8.0	12.0	15.2	17.9	20.7	23.2	25.8	27.6	29.3	31.9	34.0	35.8											
<i>Cretoxyrhina agassizensis</i>																								
DMNH 746C	15	11.2	18.2	24.9	28.7	32.0	34.1	36.3	38.6	40.0	42.3	44.6	46.5	47.6	49.3	50.7	52.0							
<i>Cretoxyrhina</i> sp.																								
NHMUK OR.25939	10	9.7	15.0	19.0	23.2	26.4	29.5	32.4	35.0	36.8	38.0	39.0												
NHMUK OR.49015	14	9.7	14.5	19.5	25.0	28.0	30.0	32.5	35.0	37.0	39.0	41.0	43.0	45.5	47.0	48.7								
<i>Archaeolamna kopingensis</i>																								
LACM P-128125	18	5.4	8.0	9.9	11.8	12.9	13.8	14.4	15.1	15.9	16.4	16.9	17.4	17.7	18.0	18.4	18.7	19.2	19.6	19.8				