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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 *C. 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 *C. mantelli* (6–11.6 mm RD) from the Smoky Hill Chalk, Niobrara Formation. The revised, reconstructed lower jaw dentition of the holotype of *C. 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: Lamniformes, *Cardabiodon ricki*, *Cardabiodon venator*, *Cretoxyrhina mantelli*, *Archaeolamna*, *Squalicorax*, vertebral centra, Cenomanian, Turonian, Cretaceous.

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Introduction

Cardabiodon (Siverson 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 (Siverson and Lindgren 2005; Cook et al. 2010; Cook et al. 2013). Fossil teeth from these sharks are typically rare and vertebral centra are even less common (Siverson 1999; Cook et al. 2010).

Siverson (1999) described *Cardabiodon ricki* from associated teeth and vertebral centra recovered from the uppermost, middle Cenomanian, part of the Gearle Siltstone, Western Australia (Fig. 1). Siverson 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 (Siverson 1999; Siverson and Lindgren 2005; Dickerson et al. 2013 [excluding amendment; see Siverson et al. 2013 regarding the validity of *Pseudoisurus* Glikman, 1957b]; 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).

[Insert Figure 1 here at page width]

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). This discrepancy 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 a nearly complete specimen (FHSM VP-2187) that was recovered from the Niobrara Chalk of Kansas, USA (Shimada 1997a, b). The age and growth of *C. 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, New York, USA; FFHM, Fick Fossil and History Museum, Oakley, Kansas,

USA; FHSM VP, Sternberg Museum of Natural History, Vertebrate Paleontology, Hays, Kansas, USA; KUVP, 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, California, USA; SDSM, South Dakota School of Mines and Technology, Vertebrate Paleontology, Rapid City, USA; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, 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; TL, total length; TW, tooth width.

Materials and methods

Material Examined.—Cardabiodon ricki, Cenomanian–Turonian: WAM 96.3.175 (centra), WAM 96.4.45 (holotype, teeth and centra), WAM 13.6.1 (tooth); UALVP 49430 (tooth). *Cardabiodon venator*, Turonian: WAM 04.10.64─100 (teeth), WAM 95.7.28 (tooth). *Cretoxyrhina mantelli*: AMNH FF 7210 (teeth, partial head, centra), FHSM VP-323 (teeth, partial head, centra), FHSM VP-2184 (teeth, centra, upper Coniacian, Smoky Hill Chalk, Niobrara Chalk, Kansas, Mike Everhart pers. comm.), FHSM VP-2187 (teeth, partial head, centra, upper Coniacian, Smoky Hill Chalk of the Niobrara Chalk, Kansas), KUVP 55060 (teeth, centra). *Cretoxyrhina agassizensis*: WAM 13.6.2 (late Cenomanian or earliest

Turonian, tooth), DMNH 746C (late Cenomanian, centrum). *Cretoxyrhina* sp. NHMUK OR.25939, NHMUK OR.49015. *Cretalamna hattini*, Siverson et al., in press, Campanian: LACM P-128126 (teeth, partial head, centra). *Dwardius woodwardi* (Herman 1977), Cenomanian: NHMUK P.45 (paratype dentition). *Squalicorax* spp. (Whitley 1939); late Coniacian–Campanian: FHSM VP-2213 (teeth, jaws), KUVP 69712 (teeth, partial head, centra), LACM P-135929 (teeth, partial head, centra), SDSM 34975 (teeth, partial head, centra), USNM 425665 (teeth, head, centra), UWGM NS.1509.07 (teeth, centra), UWGM NS.1509.34 (teeth, centra). *Archaeolamna kopingensis* (Davis, 1890), Campanian: LACM P-128125 (teeth, jaws, centra). *Hypotodus verticalis* (Agassiz 1843), Eocene: NHMUK OR.12377 (teeth, cartilage, centrum), OR.28763 (teeth, cartilage, centrum), OR.38867 (teeth, cartilage, centra).

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: p. 9): LACM I-36864-1, LACM I-38158-1, LACM I-39324-1, LACM I-39325-1, LACM I-39330-1. *Isurus paucus* Guitart, 1966 : LACM I-57284-1, LACM I-57285-1. *Isurus oxyrinchus* Rafinesque, 1810: LACM I-39470-2. *Carcharodon carcharias*: LACM I-35875-1, LACM I-38194-1, LACM I-42728-1, LACM I-57280-1, LACM I-57281-1, LACM I-57282-1, LACM I-57283-1, LACM I-42094-1, LACM I-42094-2, LACM I-42100-2. *Lamna ditropis* Hubbs and Follett 1947: LACM I-56781-1. *Lamna nasus*: 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), Calliet 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 circular 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 pattern has not yet been examined in *C. 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 (1997c, 2008) to quantify age and growth (see Figure 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 *C. ricki* was compared to four vertebral centrum specimens of *C. mantelli* and one of *A. kopingensis* (LACM P-128125, Cook et al. 2011). One specimen of *C. ricki* (the holotype) had associated teeth and vertebrae but these were disarticulated (WAM 96.4.45). Four specimens of *C. mantelli* have teeth and vertebrae associated with each other (FHSM VP-2184, VP-2187, VP-14010 [Shimada 2008], KUVP 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).

[Insert Figure 2 here at column width]

Centra were hemi-sectioned for a view of the corpus calcareum: three specimens of *C. ricki* centra (WAM 96.4.45.128 [precaudal], 96.4.45.129 [caudal], 96.3.175.1 [precaudal]), three specimens of *C. mantelli* (FHSM VP-2187, VP-14010 [sectioned by Shimada 2008]) including one naturally sectioned (KUVP 55060), and three centra of *A. kopingensis* (LACM P-128125, sectioned by Cook et al. 2011). This centrum was aged after an initial examination of *C. mantelli* centra in hemisected views to identify bands (pairs of light + dark rings = one band) as 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 annular criteria, light was angled at 45° across the conical surface to highlight the annular features present, such as ridges (Newbrey et al. 2008). Annular measurements were made from the focus to the outer margin of each dark ring, which is part of a circular ridge (followed by a circular groove), 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 determining aging error near the margin when 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 x 3.5 x 1.75 inches, 0.040" 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 *C. ricki* indicates relatively poor surface preservation. Back-calculation of 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 *C. ricki* (Fig. 3A) from comparable jaw positions.

[Insert Figure 3 here at column width]

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):

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

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, figs 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. $3B_1$). The two *Cretoxyrhina* teeth discussed above indicate a tooth size ratio of 4:1 (or very roughly 3:1 if *C. vraconensis* Siverson et al., 2013, is used as template) for the same tooth file. 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 *C. vraconensis*).

Comparison of neonate birth ring size.—Birth ring radial distance was plotted for comparison among the fossil lamniforms; *C. ricki*, *C. mantelli*, *Cretoxyrhina* sp., and *A. kopingensis*. Birth ring RD was also taken from specimens at the LACM: *Alopias vulpinus*, I-38158-1; *A. pelagicus*; *Isurus paucus*, I-57284-1, I-57285-1; *I. oxyrinchus*, I-39470-2; *C. 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: *A. 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. (2006: figs. 3, 4A–C); *C. carcharias*, Cailliet et al. (1985: table 1), Wintner and Cliff (1999: fig. 1A, B); *L. nasus*, Campana et al. (2002: fig. 1), Natanson et al. (2002: fig. 1).

Results

This study incorporates *Cretoxyrhina* centra and teeth from late Cenomanian and/or earliest Turonian deposits in North America (Eagle Ford Formation) and Australia (basal Haycock Marl). The Haycock Marl has produced a tooth of *Cretoxyrhina* from a small individual (WAM 13.6.2; Fig. 3B), which is used to develop a ratio in tooth sizes that would 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

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

Type species: *Oxyrhina mantelli* Agassiz 1843

Holotype: P2989.144 (Royal Saskatchewan Museum).

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

Diagnosis.—Cretoxyrhina agassizensis (Underwood and Cumbaa 2010) can be diagnosed as a species with very slender anterior teeth in the juvenile to sub-adult stage (broader at the same height in the older *C. denticulata* and the younger *C. mantelli*), presence of cusplets with a sharp apex on many of the lateroposterior teeth (not rounded as is commonly the case in topotypic *C. 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.

Comments.—The tooth (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. $3B_2$) is a common feature in early *Cretoxyrhina* (Siverson and Lindgren 2005: fig. $2I_2$, P_2 ; Siverson et al. 2013: fig. 5Z, D', 7R, B'; Underwood and Cumbaa, 2010: pl. 5, fig. 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, figs. 5, 6 with Underwood and Cumbaa 2010: pl. 6, figs. 16, 17 and Fig.

$3B_1$ with Underwood and Cumbaa 2010: pl. 6, fig. 27). The gradual transition in basal constriction of the labial face of the cusp in anterior teeth from a '*Telodontaspis*' morphology (Fig. $3B_1$); Underwood and Cumbaa (2010: pl. 6, fig. 27) via a 'juvenile' *Cretoxyrhina*-stage (Siverson 1996: pl. 1, fig. 9) to the sub-adult or adult stage (Siverson 1996: pl. 1, fig. 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 *C. denticulata*, *T. 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 *C. 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 *C. ricki*) includes anterior teeth of *C. agassizensis*-type and lateroposterior teeth of *C. 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 *C. denticulata* followed by the late middle Cenomanian to early middle Turonian *C. agassizensis*).

Family Cardabiodontidae Siverson, 1999

Genus *Cardabiodon* Siverson, 1999

Cardabiodon ricki Siverson, 1999

Holotype: WAM 96.4.45

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 anterior 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 design.—Siverson (1999) reconstructed the dentition of *C. 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 *C. 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 *C. 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).

[Insert Figure 4 here at column width]

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 vs. 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 design. 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 *I. 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 *C. 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 *Collignoniceras 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, indicating that it was formed during the Cretaceous Oceanic Anoxic Event II.

The very small, juvenile tooth is assigned to *C. 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 *C. 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, *Otodus* (*Megaselachus*) *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 *C. 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 pers. observ.) 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 *C. venator* (Siverson and Lindgren, 2005). Although WAM 13.6.1 represents the only known occurrence of *C. 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 *C. venator* occurs in the overlying nodule bed at the Haycock Marl/Toolonga Calcilutite contact (see Siverson, 1996: pl. 4, figs 8-10). The presence of a very young *Cardabiodon* in the basal Haycock Marl follows the pattern seen in *Dwardius woodwardi*, *Cretoxyrhina agassizensis*, *Johnlongia allocotodon* Siverson, 1996, *Squalicorax* sp. (described as *S. volgensis* 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 *C. 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 *C. 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 *C. ricki* are large midtrunk centra (i.e. relative to the posterior precaudal centra) comparable in diameter to those of *C. mantelli* (WAM 96.4.45.128, 96.3.175.1) (Figs. $5A_{1-3}$, B_{1-6}, 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. $5A_{2-3}$), 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. $5B_{2-3}$). 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. $5B_3$). Ventral foramina are situated posteriorly on the centrum and extend 90% of the distance between each corpus calcareum.

[Insert Figure 5 here at page width]

[Insert Figure 6 here at page width]

The centra of *C. ricki* are classified as round with height equal to width (WAM 96.3.175.1; Siverson 1999: fig. 11.3A). Centra of *C. 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 *C. carcharias* (0.51), but shorter than in *Carcharias taurus*

(0.55), *C. maximus* (0.61), and *I. oxyrhincus* (0.65) (Kozuch and Fitzgerald 1989). The centrum length/width ratio of *C. 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. 7–9). The centra of *Cretalamna hattini* are shorter than those of *C. ricki* and short for lamniforms ranging from 0.40 to 0.42 (LACM 128126).

[Insert Figure 7 here at page width]

[Insert Figure 8 here at page width]

Centra are septate with straight, complete septae as in *C. 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 *C. maximus*, 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 *A. kopingensis* (Cook et al. 2011; LACM I-128125) and *C. hattini* (LACM P-128126: also figured in Shimada 2007: fig. 3D and Siverson et al. in press:fig. 14). The radial lamellae in *C. mantelli* (Figs. 7, 8; FHSM VP-323, VP-2184, VP-2187; KUVP 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 *C. maximus*; septae are incomplete and do not extend to the focus (Fig. $9B_4$, 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, NS.1509.34), and all *Squalicorax* centra, included in this study, were associated with teeth.

[Insert Figure 9 here at page width]

The intermedialia, the region between the corpora calcarea, is open (not solid). There are no concentric lamellae in the intermedialia of centra of *C. ricki* (WAM 96.3.175.1, 96.4.45.128), unlike those thin concentric lamellae present in *C. 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 *C. mantelli* have densely-spaced, low, longitudinal ridges (? bases of concentric lamellae) on both sides of the lamella (FHSM VP-2184); the radial lamellae of *C. ricki* are smooth. Concentric lamellae are also absent in *A. kopingensis* (LACM P-128125), *C. hattini* (Siverson et al. in press, LACM P-128126), *I. paucus* (LACM I-57284-1, I-57285-1), and *I. oxyrinchus* (LACM I-39470-2). Concentric lamellae are not visible in *C. carcharias* (LACM I-35875-1, I-42094-1, I-57280-1, I-57281-1, I-57282-1, I-57283-1), but one specimen of *C. carcharias* (LACM I-42094-2) has some concentric lamellae. It is not clear if this character changes with position in the vertebral column or if concentric lamellae are sometimes present; regardless, concentric lamellae should be considered present for the taxon. Concentric lamellae are present in *A. vulpinus* (LACM I-38158-1), and *C. maximus* (LACM I-35593-1).

No diagonal septa are present around the dorsal and ventral foramina in *C. ricki*, *C. mantelli* (Figs. 5, 7, 8), or *C. hattini* (Siverson et al. in press, LACM P-128126). The diagonal septa create an appearance of a network of irregularly situated septa, which can be seen in centra of *C. maximus* (Fig. $9C_1$; LACM I-35593-1).

The biconcave surface of the corpus calcareum shows numerous concentric ridges with papillose texture and grooves (Fig. $5A_{1-2}$, C). The rim of the corpus calcareum is wide

and 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* sp. (LACM P-128126), *C. mantelli* (FHSM VP-2187), *C. carcharias* (LACM I-35875-1), but unlike the rounded rim of *C. maximus* (LACM I-35593-1) (Figs. $5B_6$, 7–9). In *C. maximus* (LACM I-35593-1) the rim curvature is antero- or posteromedial (Fig. $9B_3$, C_3). The corpus calcareum is thick and greatly thickens laterally towards the margin (Fig. $5B_6$). In contrast, *C. maximus* has a very thin corpus calcareum at small centrum diameters, but the distal end of the arm of the corpus calcareum greatly thickens in larger sizes (Fig. $9C_3$; LACM I-35593-1 and Natanson et al. 2008). At the margin of centra of *C. ricki* the corpus calcareum is 8–11% the thickness of the centrum diameter as is that of *C. maximus* (9%, LACM I-35593-1). In contrast, the corpus calcareum has a relatively uniform thickness in centra of *C. mantelli* at ~7–8% (Figs. 7, 8A-C, E; FSHM VP-2184, VP-2187; Shimada 2008: fig. 7A), *A. kopingensis* (8%, Cook et al. 2011: fig. 5D), *Cretalamna* sp. (7%, LACM P-128126, Siverson et al. in press), *Squalicorax* spp. (3–5%, KUVP 55190; SDSM 34975, 82067; UWGM NS.1509.07, NS.1509.34), and *C. carcharias* (4–7%, LACM I-35875-1; Kozuch and Fitzgerald 1989: fig. 7).

The thickness of the corpus calcareum in *C. 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 *C. ricki*, the corpus calcareum is much thinner in anterior and mid-trunk precaudal centra of *C. mantelli* (10–16%, anterior precaudal centra, AMNH FF 7210; FHSM VP-233, VP-2187; but 23% in posterior precaudal centra, FHSM VP-2184), *A. kopingensis* (14%, LACM P-128125), *C. hattini* (14%, LACM P-128126, Siverson et al. in press), *C. carcharias* (9–14%, LACM I-35875-1, Kozuch and Fitzgerald, 1989: fig. 7), and *L. nasus* ($\overline{x}$ = 22%, Natanson et al. 2002: figure 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 *C. ricki* (WAM 96.3.175.1, 96.4.45.128; Siverson 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 *C. 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 *C. hattini* (LACM P-128126, Siverson et al. in press), *H. verticalis* (NHMUK OR.12377, OR.38867), or *Squalicorax* spp. (KUVP 55190; SDSM 34975, 82067; UWGM NS.1509.07, NS.1509.34; USNM 425665). Very small pores are scattered across the lateral faces of *C. carcharias* (LACM I-35875-1) and *C. maximus* (LACM I-35593-1) (Fig. 9). No fine radial canals are visible on the inner surface of the corpus calcareum of centra of *C. ricki*.

The centra of *C. 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 *C. ricki* (Fig. $5A_2$, D). 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 (M.G.N. pers. obs.). Post birth, the surface of the corpus calcareum has more numerous fine concentric ridges but only robust, papillose

ridges are associated with annular rings. In hemisected view, the birth ring consists of a broad darker ring that extends into the intermedialia (Fig. $5A_2$).

The birth ring of *C. 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 *A. 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 *C. 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 valley, but ends concurrently with a papillose ridge, both on the surface of the corpus calcareum (Fig. $5A_2$, B_1). The fourth ring is assumed to be an annular mark. Occasionally a second, low papillose ridge falls in 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 *C. 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 *A. kopingensis* the banding cycle contains broad dark rings that extend onto the radial plate and are assumed to be annular marks (LACM P-128125, Cook et al. 2011). These dark, annular rings are interspersed with lighter, broad rings to form the complete band.

Age and growth.— The birth rings of *C. ricki* occur at sizes of 5 and 8 mm RD, which overlap in RD with those of *C. mantelli* (6–11.6 mm RD) (Figs. 7, 8, 10, 11). The birth ring of *C. carcharias* is 9.5 mm RD (LACM I-35875-1). The birth ring RD for *A. kopingensis* (LACM P-128125) is 5.4 mm and is comparable in size to those of *C. ricki* (Fig. 10).

[Insert Figure 10 here at page width]

Both specimens of *C. 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, *C. mantelli* lived to at least 21 years (bands, FHSM VP-14010). To determine if there was consistency in age along the vertebral column, two centra were aged from the holotype of *C. ricki* and both produced the same age estimates; a precaudal centrum (WAM 96.4.45.128) and a small caudal centrum (WAM 96.4.45.129). The maximum RD of both *C. 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 *C. 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 *C. 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 *A. kopingensis* (LACM P-128125) occurs at age 5 (69% of total RD). One centrum from extant *C. carcharias* (LACM I-35875-1) shows a slight inflection after age 4 (Fig. 10).

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

[Insert Figure 11 here at column width]

In comparison, the birth rings of two specimens of *C. 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 *C. agassizensis* (because of its late Cenomanian age) is 4.4:1 (i.e. 22%, DMNH 746C). The juvenile a2 tooth of *C. 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 *C. mantelli* (a2's approximately 15% wider than A2's) and a 3:1 ratio if we use *C. 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 *C. ricki*, *C. mantelli*, and *A. 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 *C. carcharias* and up to 45% (3.0–5.5 mm RD) in *L. nasus* (Fig. 11B).

Discussion

Dental design 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 *C. 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 design' section) in Dickerson et al. (2013) makes it somewhat 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 1997b; Shimada and Cicimurri 2005; Cook et al. 2011). We describe the morphology of centra of *C. 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, *C. ricki* can be distinguished from *Cretoxyrhina* by having longer centra, robust radial lamellae occurring at a low density, a thick 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 *C. ricki* to confirm the size of birth rings on centra (Figs. 3A, 10, 11A). The growth profile of a centrum from the holotype of *C. 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 *C. agassizensis* (probable a2, WAM 13.6.2, Fig. 3B). The range in ratios from centrum radial distance of *C. mantelli* is 4.5–5.7:1 (Appendix 1; FHSM VP-2184, VP2187,

VP-14010, KUVP 55060), which is a larger ratio than predicted (3–4:1) from tooth sizes using a small sample of teeth of *C. agassizensis*. The ratio between birth ring size and maximum recorded radial distance of centra suggests smaller teeth for *C. 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 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 *C. 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 *C. 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*, *Carcharodon*, *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* Jordan 1898, *Alopias*, *Carcharodon*, *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 *C. ricki* is 746 mm (an estimate from summed tooth widths with 1 mm spacing between teeth) 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 *C. ricki* is 5.5 m based on the relationship between bite circumference and TL for *C. carcharias* (Lowry et al. 2009). Shimada (1997b) estimated *C. 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 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 1997b: p. 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 532cm (= 350 x 1.2 x 1.1 + 10 + 60 cm).

Longevity.—The growth rates are slower than are those of *C. 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 10–32 years old (see citations listed in Shimada 2008: table 2). *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 *C. 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 estimate, 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 *C. 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 *C. 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 *C. mantelli* would have been close to 80 mm high (Agassiz 1843: pl. 33, fig. 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 *C. ricki* had a large girth. The corpus calcareum and radial lamellae are thicker (relatively speaking) than are those of *C. carcharias*. The centra of *C. mantelli* have much thinner corpora calcarea and radial lamellae than do *C. ricki* or *C. maximus*. Often the corpora calcarea of *C. 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 *C. 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 *C. ricki*, which suggests the number of bands is not related to girth. In *C. 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 *C. ricki* suggest a rigid vertebral column and a relatively fast swimmer. *Cardabiodon ricki* has very robust centra that are moderately long compared to those of *C. mantelli* and Santonian *Squalicorax*. The vertebral centra of *C. 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 *C. 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 relatively fast swimming speeds (Buchholtz 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 *C. ricki* is a fast swimmer is corroborated by the morphology of the placoid scales in another associated specimen. Dickerson et al. (2012: 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 *C. mantelli* (Shimada 1997b).

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 *C. 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 *C. mantelli*, *A. kopingensis*, and *Squalicorax*. Centra of *C. ricki* indicate slower growing individuals compared to *C. mantelli*, and living to at least 13 years old. The lower jaw bite circumference of *C. ricki* is estimated at 746 mm at age 13. Age and growth information

suggest a later age at maturity for *C. ricki* (5–7 years or older) than *C. 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 *C. 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 relatively fast swimming and acceleration but low manoeuvrability.

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References

Agassiz, L. 1833–1843. Recherches sur les Poissons Fossiles, 5 volumes and 3 volumes atlas, Petitpierre, Neuchâtel. Dates for publication of individual parts are given by W. Quenstedt (1963) (ref. cited below).

Ardizzone, D., Cailliet, G.M., Natanson, L.J., Andrws, A.H. Kerr, L.A., and Brown, T.A. 2006. Application of bomb radiocarbon chronologies to shortfin mako (Isurus oxyrinchus) age validation. Environmental Biology of Fishes 77: 355–366. http://dx.doi.org/10.1007/s10641-006-9106-4

Bass, A.J., D'Aubrey, J.D.D., and Kistnasamy, N. 1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. South African Association for Marine Biological Research, Oceanographic Research Institute Investigational Report 39: 1–102.

Bishop, S.D., Francis, M.P., Duffy, C., and Montgomery, J.C. 2006. Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (Isurus oxyrinchus) in New Zealand waters. Marine and Freshwater Research 57: 143–154. http://dx.doi.org/10.1071/MF05077

Berg, L.S. 1958. System der rezenten und fossilen Fischartigen und Fische. Hochschulbücher für Biologie, Berlin, 310 pp.

Bertalanffy, von, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Human Biology 10: 181–213.

Bonaparte, C.L. 1838. Selachorum tabula analytica. Nuovi Annali della Scienze Naturali, Bologna 1: 195–214.

Bonnaterre, J.P. 1788. Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature. Ichthyologie, 215pp., Chez Panckoucke, Paris. http://dx.doi.org/10.5962/bhl.title.11660

Bourdon, J. and Everhart, M.J. 2011. Analysis of an associated Cretoxyrhina mantelli dentition from the Late Cretaceous (Smoky Hill Chalk, Late Coniacian) of western Kansas. Transactions of the Kansas Academy of Science 114: 15–32. http://dx.doi.org/10.1660/062.114.0102

Branstetter, S. and Musick, J.A. 1994. Age and growth estimate for the sand tiger in the northwestern Atlantic Ocean. Transactions of the American Fisheries Society 123: 242–254. http://dx.doi.org/10.1577/1548-8659(1994)123<0242:AAGEFT>2.3.CO;2

Buchholtz, E.A. 2001. Vertebral osteology and swimming style in living and fossil whales (Order: Cetacea). Journal of Zoology, London 253: 175–190. http://dx.doi.org/10.1017/S0952836901000164

Buchholtz, E.A. and Schur, S.A. 2004. Vertebral osteology in Delphinidae (Cetacea). Zoological Journal of the Linnean Society 140: 383–401. http://dx.doi.org/10.1111/j.1096-3642.2003.00105.x

Cailliet, G.M. and Goldman, K.J. 2004. Age determination and validation in chondrichthyan fishes. In: J. Carrier, J.A. Musick and M. Heithaus (eds.), The Biology of sharks and their relatives, p. 399−447. CRC Press, Boca Raton, Florida, USA.

Cailliet G.M., Natanson L.J., Weldon B.A., and Ebert, D.A. 1985. Preliminary studies on the age and growth of the white shark Carcharodon carcharias, using vertebral bands. Memoirs Southern California Academy of Sciences 9: 49–60.

Cailliet, G.M., Smith, W.D., Mollet, H.F., and Goldman, K.J. 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environmental Biology of Fishes 77: 211–228. http://dx.doi.org/10.1007/s10641-006-9105-5

Cailliet, G.M., Martin, L.K., Harvey, J.T., Kusher, D., and Welden, B.A. 1983a. Preliminary studies on the age and growth of blue, Prionace glauca, common thresher, Alopias vulpinus, and shortfin mako, Isurus oxyrinchus, sharks from California waters. In: E.D. Prince and L.M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 8: 179−188.

Cailliet, G.M., Martin, L.K., Kusher, D., Wolf, P., and Welden, B.A. 1983b. Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 8: 157–165.

Campana, S.E., Marks, L., and Joyce, W. 2005. The biology and fishery of shortfin mako sharks (Isurus oxyrinchus) in Atlantic Canadian waters. Fisheries Research 73: 341–352. http://dx.doi.org/10.1016/j.fishres.2005.01.009

Campana, S.E., Natanson, L.J., and Myklevoll, S. 2002. Bomb dating and age determination of a large pelagic shark. Canadian Journal of Fisheries and Aquatic Sciences 59: 450–455. http://dx.doi.org/10.1139/f02-027

Cappetta, H. 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. In: H.-P. Schultze (ed.), Handbook of Palaeoichthyology 3B. 193 pp. Gustav Fisher Verlag, Stuttgart.

Cappetta, H. 2012. Mesozoic and Cenozoic elasmobranchii: teeth. Chondrichthyes. In: H.P. Schultze (ed.). Handbook of Palaeoichthyology, 3E. 512 pp. Verlag Dr. Friedrich Pfeil, München.

Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vol. I. 752 pp. Iowa State University Press, Ames.

Compagno, L.J.V. 1977. Phyletic relationships of living sharks and rays. American Zoologist 17: 303–322.

Compagno, L.J.V. 2001. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes no. 1, 2: 1–269. FAO, Rome.

Cook, T.D., Wilson, M.V.H., and Newbrey, M.G. 2010. The first record of the large Cretaceous lamniform shark, Cardabiodon ricki, from North America and a new empirical test for its presumed antitropical distribution. Journal of Vertebrate Paleontology 30: 643–649.
http://dx.doi.org/10.1080/02724631003758052

Cook, T.D., Newbrey, M.G., Murray, A.M., Wilson, M.V.H., Shimada, K., Takeuchi, G.T., and Stewart, J.D. 2011. A partial skeleton of the Late Cretaceous lamniform shark, Archaeolamna kopingensis, from the Pierre Shale of western Kansas. Journal of Vertebrate Paleontology 31: 8–21.
http://dx.doi.org/10.1080/02724634.2011.539968

Cook, T.D., Wilson, M.V.H., Murray, A.M., Plint, A.P., Newbrey, M.G., and Everhart, M.J. 2013. A high latitude euselachian assemblage from the early Turonian of Alberta, Canada. Journal of Systematic Palaeontology 11: 555–587.

Davis, J.W. 1890. On the fossil fish of the Cretaceous formations of Scandinavia. Scientific transactions of the Royal Dublin Society (2), 4: 363–434.

Dean, M.N., and Summers, A.P. 2006. Mineralized cartilage in the skeleton of chondrichthyan fishes. Zoology 109: 164–168.
http://dx.doi.org/10.1016/j.zool.2006.03.002
PMid:16584875

Dickerson, A.A. Shimada, K., Reilly, B., and Rigsby, C.K. 2013. New data on the Late Cretaceous cardabiodontid lamniform shark based on an associated specimen from Kansas. Transactions of the Kansas Academy of Science 115: 125-133.

Ehret, D.J., Hubbell, G., and MacFadden, B.J. 2009. Exceptional preservation of the white shark Carcharodon (Lamniformes, Lamnidae) from the early Pliocene of Peru. Journal of Vertebrate Paleontology 29: 1–13.
http://dx.doi.org/10.1671/039.029.0113

Ehret, D.J., MacFadden, B.J., Jones, D.S., Devries, T.J., Foster, D.A., and Sslas-Gismondi, R. 2012. Origin of the white shark Carcharodon (Lamniformes: Lamnidae) based on recalibration of the Upper Neogene Pisco Formation of Peru. Palaeontology 55: 1139–1153.

Francis, M.P. 1996. Observations on a pregnant white shark with a review of reproductive biology. In: A. Kimley and D. Ainley (eds.), Great White Sharks: the Biology of Carcharodon carcharias. pp. 157–172. Academic Press, San Diego, California.
http://dx.doi.org/10.1016/B978-012415031-7/50016-1

Gill, T. 1864. Second contribution to the selachology of California. Proceedings of the Academy of Natural Sciences of Philadelphia 16: 147–51.

Glikman, L.S. 1957a. O sistematicheskom znachenii dobavochnykh zubtsov na zubakh akul semeistv Lamnidae i Scapanorhynchidae [On the systematic significance of accessory denticles in the teeth of sharks of the families Lamnidae and Scapanorhynchidae]. Trudy Geologicheskogo Muzeia Akademiia Nauk SSSR 1:103–109. [Russian]

Glikman, L.S. 1957b. O geneticheskoi sriazi semeistv Lamnidae i Odontaspidae i novykh rodakh verkhnemelovykh lamnid [Genetic relations of the Lamnidae and Odontaspidae and new genera of lamnids from the Upper Cretaceous.] Trudy Geologicheskogo Muzeia Akademiia Nauk SSSR 1: 110–117. [In Russian].

Goldman, K.J. and Musick, J.A. 2006. Growth and maturity of salmon sharks (Lamna ditropis) in the eastern and western North Pacific, and comments on back-calculation methods. Fishery Bulletin - National Oceanic and Atmospheric Administration 104: 278–292.

Goldman, K.J., Branstetter, S., and Musick, J.A. 2006. A re-examination of the age and growth of sand tiger sharks, Carcharias taurus, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques. Environmental Biology of Fishes 77: 241–252.
http://dx.doi.org/10.1007/s10641-006-9128-y

Govender, N., Kistnasamy, N., and Van der Elst, R.P. 1991. Growth of spotted ragged-tooth sharks Carcharias taurus (Rafinesque) in captivity. South African Journal of Marine Science 11: 15–19.
http://dx.doi.org/10.2989/025776191784287718

Gunnerus, J.E. 1765. Brugden (Squalus maximus). Skrifter - Det Kongelige Norske Videnskabers Selskabs 3: 33–49, pl. 2.

Gunson, M.J. 1995. Ichnofacies, biostratigraphy, and sequence stratigraphy of mid

Cretaceous strata in the lower Murchison area of the Southern Carnarvon Basin. Unpublished Honours Thesis, 87 pp.

Guitart-Manday, D.J. 1966. Nuevo nombre para una especie de Tiburón del género Isurus (Elasmobranchii: Isuridae) de Aguas Cubanas. Poeyana, ser. A, 15: 1–9.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata in North America. United States Geological Survey Bulletin 179: 1–868.

Herman, J. 1977. Les Sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphique intercontinentale. Mémoires pour servir à l'explication des Cartes Géologique et Minières de la Belgique. Service Géologique de Belgique 15: 1–401. [Date of imprint 1975].

Hubbs, C.L. and Follett, W.I. 1947. Lamna ditropis, new species, the salmon shark of the North Pacific. Copeia 1947: 194.
http://dx.doi.org/10.2307/1438851

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880: 649–662.

Jordan, D.S. 1898. Description of a species of fish (Mitsukurina owstoni) from Japan, the type of a distinct family of lamnoid sharks. Proceedings of the California Academy of Sciences (Series 3, Zoology) 1: 199–202, pl. 11–12.

Kozuch, L. and Fitzgerald, C. 1989. A guide to identifying shark centra from southeastern archaeological sites. Southeastern Archaeology 8: 146–157.

Leidy, J. 1857. Remarks on Saurocephalus and its allies. Transactions of the American Philosophical Society 11: 91–95, with pl. vi.
http://dx.doi.org/10.2307/3231930

Linnaeus, C. 1758. Systema Naturae. 10th ed. – 824 pp. Laurentii Salvii, Stockholm.

Liu, K.-M., Chiang, P.-J., and Chen, C.-T. 1998. Age and growth estimates of the bigeye thresher shark, Alopias superciliosus, in northeastern Taiwan waters. Fishery Bulletin 96: 482–491.

Lowe, R.T. 1840. [A paper from the Rev. R.T. Lowe, M.A., describing certain new species of Madeiran fishes, and containing additional information relating to those already described]. Proceedings of the Zoological Society of London 1840: 36–39.

Lowry, D., de Castro, A.L.F., Mara, K., Whitenack, L.B., Delius, B., Burgess, G.H., and Motta, P. 2009. Determining shark size from forensic analysis of bite damage. Marine Biology 156: 2483–2492.

http://dx.doi.org/10.1007/s00227-009-1273-3

MacFadden, B.J, Labs, J., Quitmyer, I., and Jones, D.S. 2004. Incremental growth and diagenesis of skeletal parts of the lamnoid shark Otodus obliquus from the early Eocene (Ypresian) of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 206: 179–192. http://dx.doi.org/10.1016/j.palaeo.2004.01.002

MacNeil, M.A. and Campana, S.E. 2002. Comparison of whole and sectioned vertebrae for determining the age of young blue shark (Prionace glauca). Journal of Northwest Atlantic Fishery Science 30: 77–82.
http://dx.doi.org/10.2960/J.v30.a5

Müller J. and Henle, J. 1839 (1838–1841). Systematische Beschreibung der Plagiostomen. Veit, Berlin.

Natanson, L.J., Mello, J.J., and Campana, S.E. 2002. Validated age and growth of the porbeagle shark, Lamna nasus, in the western North Atlantic. Fishery Bulletin 100: 266–278.

Natanson, L.J., Kohler, N.E., Ardizzone, D., Cailliet, G.M., Wintner, S.P., and Mollet, H.F. 2006. Validated age and growth estimates for the shortfin mako, Isurus oxyrinchus, in the North Atlantic Ocean. Environmental Biology of Fishes 77: 367–383.
http://dx.doi.org/10.1007/s10641-006-9127-z

Natanson, L.J., Wintner, S.P., Johansson, F., Piercy, A., Campbell, P., de Maddalena, A., Gulak, S.J.B., Human, B., Fulgosi, F.C., Ebert, D.A., Hemida, F., Mollen, F.H., Vanni, S., Burgess, G.H., Compagno, L.J.V., and Wedderburn-Maxwell, A. 2008. Ontogenetic vertebral growth patterns in the basking shark Cetorhinus maximus. Marine Ecology Progress Series 361: 267–278.
http://dx.doi.org/10.3354/meps07399

Newbrey, M.G., Wilson, M.V.H., and Ashworth, A.C. 2008. Climate Change and Evolution of growth in Late Cretaceous to Recent North American Esociformes. In: G. Arratia, H.P. Schultze, and M.V.H. Wilson (eds.), Mesozoic Fishes 4 - Homology, and Phylogeny. pp. 311–350. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Pimiento, C., Ehret, D.J., MacFadden, B.J., and Hubbell, G. 2010. Ancient nursery area for the extinct giant shark megalodon from the Miocene of Panama. PLoS ONE 5:e10552.
PLATES program. 2009. The PLATES Project; L. Lawver and I. Dalziel (principal investigators), L. Gahagan (database and software manager). University of Texas Institute for Geophysics, Austin.

Porter, M.E., Koob, T.J., and Summers, A.P. 2007. The contribution of mineral to the material properties of vertebral cartilage from the smooth-hound shark Mustelus californicus. The Journal of Experimental Biology 210: 3319–3327.
http://dx.doi.org/10.1242/jeb.006189
PMid:17872985

Quenstedt, W. 1963. Louis Agassiz: Recherches sur les poissons fossiles (1833-1843 "Tableau général": 1844). Fossilium Catalogus I: Animalia. F. Westphal (ed.). Pars 102, pages 77–85. W. Junk, The Hague, Netherlands.

Rafinesque, C.S. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia con varie osservazioni sopra i medesimi. 105 pp., San Filippo, Palermo.

Ribot-Carballal, M.C, Galvan-Magana, F., and Quinonez-Velaszquez, C. 2005. Age and growth of the shortfin mako, Isurus oxyrinchus, from the western coast of Baja California Sur, Mexico. Fisheries Research 76: 14–21.
http://dx.doi.org/10.1016/j.fishres.2005.05.004

Ridewood, W.G. 1921. On the calcification of the vertebral centra in sharks and rays. Philosophical Transactions of the Royal Society of London. Series B 210: 311–407.
http://dx.doi.org/10.1098/rstb.1921.0008

Risso, A. 1810. Ichthyologie de Nice, ou histoire naturelle des poissons du Département des Alpes Maritimes. F. Schaellk, Paris.

Sfakiotakis, M, Lane, D.M., and J. Davies, J.B.C. 1999. Review of fish swimming modes for aquatic locomotion. Institute of Electrical and Electronics Engineers Journal of Oceanic Engineering 24: 237–252.

Shimada, K. 1997a. Dentition of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli, from the Niobrara Chalk of Kansas. Journal of Vertebrate Paleontology 17: 269–279.

Shimada, K. 1997b. Skeletal anatomy of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli, from the Niobrara Chalk in Kansas. Journal of Vertebrate Paleontology 17: 642–652.

Shimada, K. 1997c. Periodic marker bands in vertebral centra of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli. Copeia 1997: 233–235.

Shimada, K. 2007. Skeletal and dental anatomy of lamniform shark, Cretalamna appendiculata, from Upper Cretaceous Niobrara chalk of Kansas. Journal of Vertebrate Paleontology 27: 584–602.

Shimada, K. 2008. Ontogenetic parameters and life history strategies of the Late Cretaceous lamniform shark, Cretoxyrhina mantelli, based on vertebral grown increments. Journal of Vertebrate Paleontology 28: 21–33.

Shimada, K. and Cicimurri, D.J. 2005. Skeletal anatomy of the Late Cretaceous shark,

Squalicorax (Neoselachii: Anacoracidae). Paläontologische Zeitschrift 79: 241–261.

Siverson, M. 1996. Lamniform sharks of the mid−Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. Palaeontology 39: 813–849.

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltstone

(Cenomanian, Late Cretaceous) of Western Australia. Transactions of the Royal Society of Edinburgh: Earth Sciences 90: 49–65.

Siverson M. and Lindgren, J. 2005. Late Cretaceous sharks Cretoxyrhina and Cardabiodon from Montana, USA. Acta Palaeontologica Polonica 50: 301–334.

Siverson, M., Ward, D.J., Lindgren, J., and Kelley, L.S. 2013. Mid-Cretaceous Cretoxyrhina (Elasmobranchii) from Mangyshlak, Kazakhstan and Texas, USA. Alcheringa 37: 87–104.

Siverson, M., Lindgren, J., Newbrey, M.G., Cederström, P., and Cook, T.D. In press. Late Cretaceous sharks of Cretalamna appendiculata type. Acta Palaeontologica Polonica, available online 6 August 2013, doi: http://dx.doi.org/10.4202/app.2012.0137. http://dx.doi.org/10.4202/app.2012.0137

Underwood, C.J. and Cumbaa. S.L. 2010. Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. Palaeontology 53: 903–944.

Underwood, C.J., Goswami, A., Prasad, G.V.R., Verma O., and Flynn, J.J. 2011. Marine vertebrates from the 'middle' Cretaceous (early Cenomanian) of South India. Journal of Vertebrate Paleontology 31: 539–552.

Whitley, G.P. 1939. Taxonomic notes on sharks and rays. Australian Journal of Zoology 9: 227–262.

Wintner, S.P. and Cliff, G. 1999. Age and growth determination of the white shark, Carcharodon carcharias, from the east coast of South Africa. United States Fishery Bulletin 97: 153–169.

Woodward, A.S. 1911. The fossil fishes of the English Chalk. Part 6. Palaeontographical Society, London 1910: 185–224, pls. 39–46.

Tables

Table 1. Total length (TL) at birth, age at maturity, and TL at maturity for five families of lamniforms.

Taxon / Sex	TL at birth (cm)	Age at maturity	TL at maturity (cm)
Carchariidae			
Carcharias taurus			
B	95-105	10	-–
F	-–	-–	220
M	-–	-–	190-195
Odontaspididae			
Odontaspis ferox			
B	105	-–	-–
F	-–	-–	364
M	-–	-–	275
Mitsukurinidae			
Mitsukurina owstoni			
B	-–	-–	-–
F	-–	-–	335
M	-–	-–	264-384
Alopiidae			
Alopias pelagicus			
B	130-160	-–	-–
F	-–	8-9	282-292
M	-–	6-9	267-276
Alopias superciliosus			
B	100-140	-–	-–
F	-–	12-13	294-355[A]
M	-–	9-10	279-300[A]
Alopias vulpinus			
B	114-160	3-8	-–
F	-–	-–	315-400
M	-–	-–	288
Lamnidae			
Carcharodon carcharias			
B	100-160	-–	-–
F	-–	12-14	400-500
M	-–	9-10	350-410
Isurus oxyrinchus			
B	60-70	7-8	-–
F	-–	7	275-293
M	-–	4.5	203-215
Isurus paucus			
B	97-120	-–	-–
F	-–	-–	245-417
M	-–	-–	245
Lamna ditropis			
B	40-85	-–	-–
F	-–	8-10	221
M	-–	5	182
Lamna nasus			
B	60-80	-–	-–
F	-–	14[B]	212[B]
M	-–	7[B]	175[B]
F	-–	-–	185-250
M	-–	-–	150-200

Unless otherwise noted information is from Compagno (2001)

[A]Liu et al. (1998)

[B]Campana et al. (2002)

Abbreviations: B, both; F, female; M, male

Figure Captions

Figure 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). Localities of *C. ricki* are indicated by squares with arrows and teeth; (UALVP 49430 from Canada is likely a transitional species between *C. ricki* and *C. venator*. *Cardabiodon venator* (diamonds) and *Cardabiodon* sp. are indicated only by squares.

Figure 2. Schematic drawing of a hypothetical shark centrum in hemisected view showing potential criteria used for age determination. Abbreviations: br, birth ring.

Figure 3. Isolated, small juvenile teeth of *Cardabiodon ricki* (WAM 13.6.1: lp7-9?) and *Cretoxyrhina agassizensis* (WAM 13.6.2: a2?) from the basal (0.1 m) of the Haycock Marl, Pillawarra Plateau, Western Australia. Scale bars equal 1 mm.

Figure 4. Reconstructed lower dentition of *Cardabiodon ricki* (WAM 96.4.45) depicting mirror images of left anterior teeth on the right side. Scale bar equals 373 mm. Abbreviations: **t.l.a.**, transposed left anterior teeth.

Figure 5. Centra of *Cardabiodon ricki*. **A**. Precaudal centrum, WAM 96.4.45.128; (A1) face of the copus calcareum showing line of section (black line) and transect with points of measurement (white line and small filled circles), large filled circle represents focus, left half of the section centrum correseponds to A_2, right half of the centrum corresponds to A_3; (A2) "hemisected" view of centrum 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 from the plain of the page; (A3) opposing view of WAM 96.4.45.128 showing focus. **B**. Precaudal centrum, WAM 96.3.175.1; (B1) anterior view of corpus calcareum with surface removed to show bands; (B2) anterior view of centrum; (B3) dorsal view of centrum showing articular foramina for the neural arch (anterior to left); (B4) lateral view of centrum showing rib articular foramen (anterior to left); (B5) hemisected section of centrum (anterior to left); (B6) enlarged, hemisected view showing bands. **C**. Anterior view of caudal centrum (oblique angle) showing birth ring, WAM 96.4.45.110. Scale bars: A_{1-3}, B_{2-5}, C = 10 mm, B_1 = 3 mm, B_6 = 5 mm. Abbreviations: **br**, birth ring; **rl**, radial lamella.

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

Figure 7. Centra of *Cretoxyrhina* spp. **A**. *C. mantelli*, FHSM VP-323, Niobrara Chalk. **B**. Articulated centra from various positions in the vertebral column of *C. mantelli*, FHSM VP-2187, upper Coniacian, Smoky Hill Chalk of the Niobrara Chalk in Ellis County, Kansas; (B1) v1–14 (1= occipital centrum, order corresponds to Fig. 6); (B2) v62–66; (B3) v67–75; (B4) v86–93; (B5) v94–104; (B6) v129–139; (B7) v183–193; (B8) v194–208; (B9) v209–227. **C**. Centrum in transverse section through about inner margin of the corpus calcareum of *C. mantelli*; arrows indicate articular foramina for neural and ribs or haemal arches, NHMUK OR.25939, White Chalk Formation (?), near Sussex (see also Woodward 1910: plate XLIII, fig. 14). **D**. Centrum of *Cretoxyrhina* sp. (probably *C. agassizensis*), DMNH 746C, Eagle

Ford Group, Cenomanian; (D1) view of face showing focus and 15 bands (short arrows) after the birth ring; (D2) tracing of left lateral view of centrum. **E**. Centra of *Cretoxyrhina* sp. (probably *C. agassizensis*), NHMUK OR.49015, Cenomanian-Turonian. Scale bars: A = 10 cm, $B_{1\text{-}9}$ = 3 cm, C–E = 1 cm.

Figure 8. Five posterior precaudal(?) centra of *Cretoxyrhina mantelli* (FHSM VP-2184), upper Coniacian, Smoky Hill Chalk of the Niobrara Chalk. **A–C**. Centra are depicted in four views: anterior or posterior, left lateral, dorsal, ventral; in the latter three views anterior is to the left. **D**. Centrum in transverse section showing radial lamellae and dorsal and ventral articular foramina. **E**. Centrum in hemisected view showing 12 bands. Scale bars equal 1 cm.

Figure 9. Centra from extant *Carcharodon carcharias* and *Cetorhinus maximus*. **A**. Centrum of *C. carcharias* (LACM I-35875-1) in five views: anterior, left lateral, posterior, dorsal, and ventral. **B**. Partial centrum of *C. maximus* (LACM I-35593-1a) in four views: anterior, left lateral, dorsal, and posterior in transverse section. **C**. Partial centrum of *C. maximus* (LACM I-35593-1b) in three views: left lateral, ventral, and one-half hemi-section. Scale bars equal 1 cm.

Figure 10. Centrum growth profiles and size profiles of *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *C. agassizensis*, and *Archaeolamna kopingensis*. Centrum radial distance (RD) is distance from focus toward the margin in hemisected view (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*" 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. $5A_1$) and does not reflect the exact proportions of growth recorded in the "hemisected" view of the centrum in Fig. $5A_2$ as the angle of the section does not intersect the focus.

Figure 11. Comparisons of teeth and centra at approximate neonate ages. **A**. Dahl-Lea back-calculated growth profiles of tooth width (TW, maximum mesiodistal distance of the root) for lower lateroposterior (lp) teeth (7–9?) of *Cardabiodon ricki*. **B**. Birth ring radial distance (RD mm) for neonates of six extant (Cailliet et al. 1985, Compagno 2001) and some Cretaceous lamniforms (large symbols).

Appendix 1. Lamniform ages and radial distances (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
Cardabiodon ricki																							
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								
Cretoxyrhina mantelli																							
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										
Cretoxyrhina agassizensis																							
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						
***Cretoxyrhina* 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							
Archaeolamna kopingensis																							
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			
Carcharodon carcharias																							
LACM I-35875-1	10	9.5	14.9	20.1	24.4	27.7	29.8	32.4	34.8	36.7	39.1	40.9											

Figure 1.

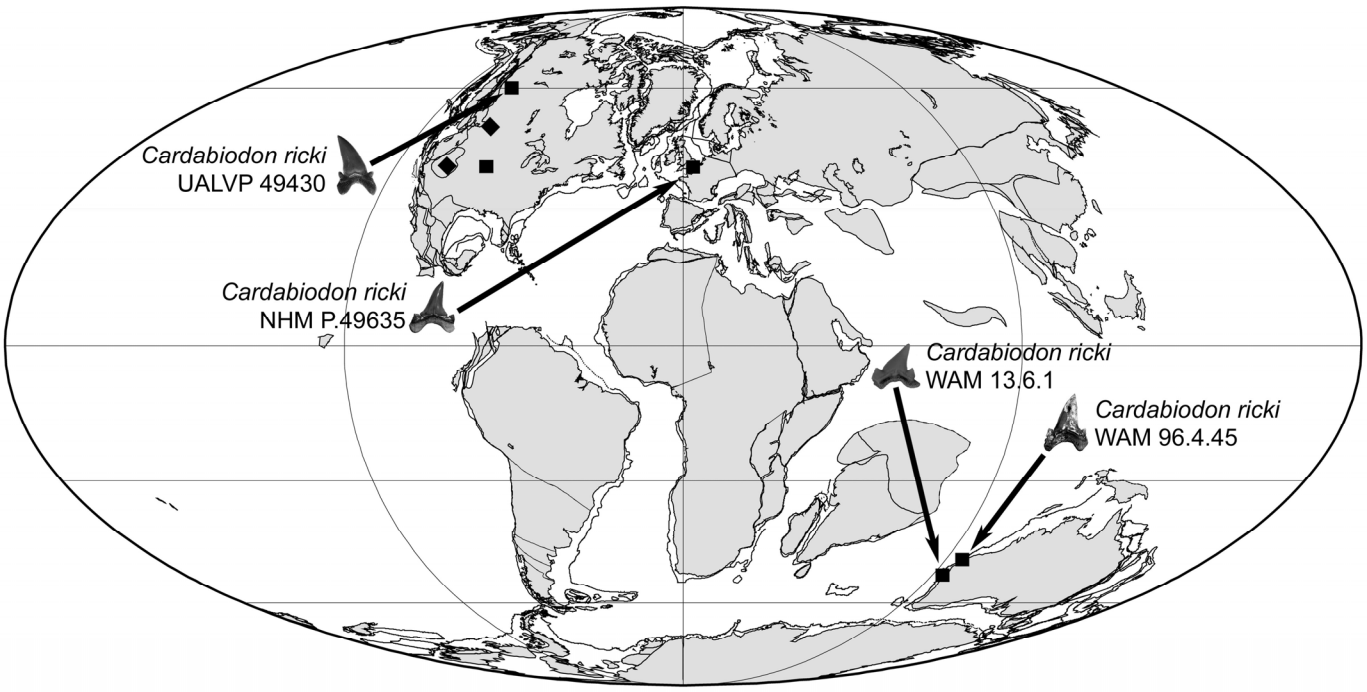

Cardabiodon ricki
UALVP 49430
Cardabiodon ricki
NHM P.49635
Cardabiodon ricki
WAM 13.6.1
Cardabiodon ricki
WAM 96.4.45

Figure 2.

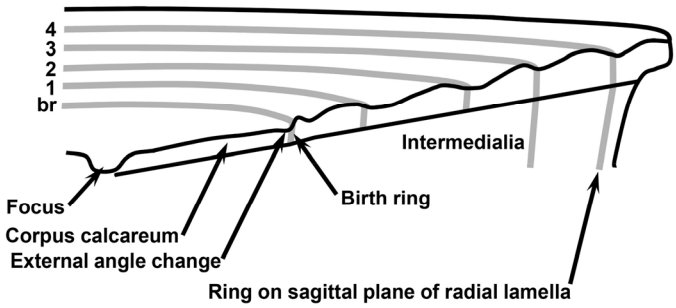

4
3
2
1
br
Intermedialia
Focus
Corpus calcareum
External angle change
Birth ring
Ring on sagittal plane of radial lamella

Figure 3.

Figure 4.

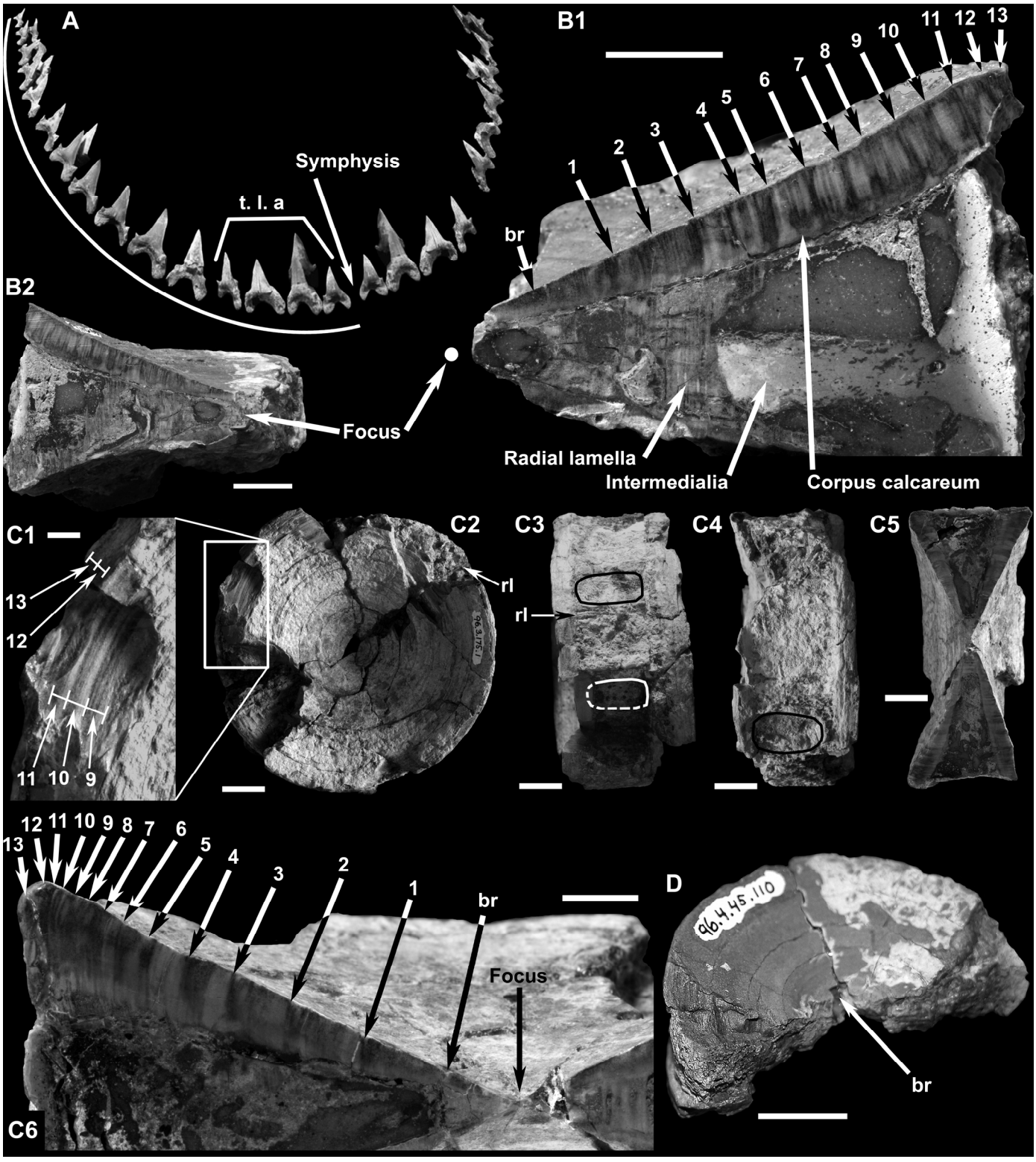

A
Symphysis
t. l. a
B1
1
2
3
4
5
6
7
8
9
10
11
12
13
br
B2
Focus
Radial lamella
Intermedialia
Corpus calcareum
C1
13
12
11
10
9
C2
rl
96.3.75.1
C3
rl
C4
C5
C6
13
12
11
10
9
8
7
6
5
4
3
2
1
br
Focus
D
96.4.45.110
br

Figure 5.

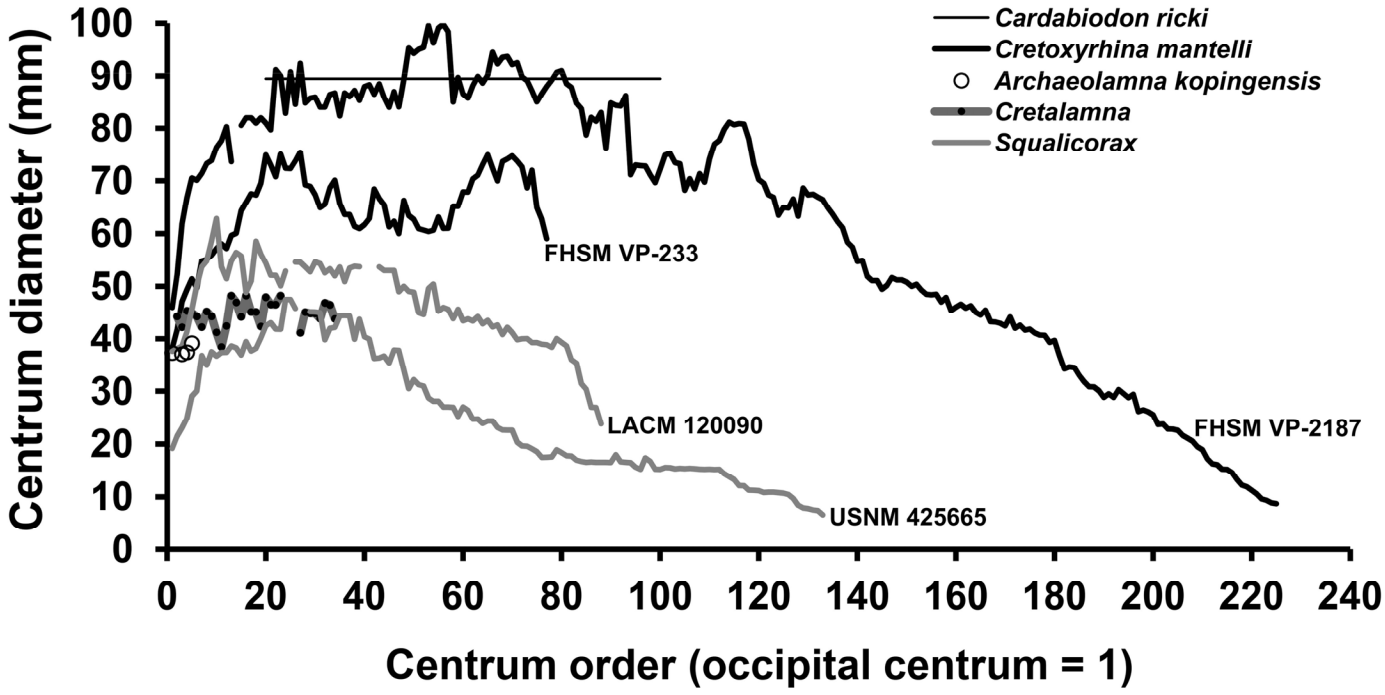

Cardabiodon ricki
Cretoxyrhina mantelli
Archaeolamna kopingensis
Cretalamna
Squalicorax
FHSM VP-233
LACM 120090
USNM 425665
FHSM VP-2187
Centrum diameter (mm)
Centrum order (occipital centrum = 1)
0
10
20
30
40
50
60
70
80
90
100
0
20
40
60
80
100
120
140
160
180
200
220
240

Figure 6.

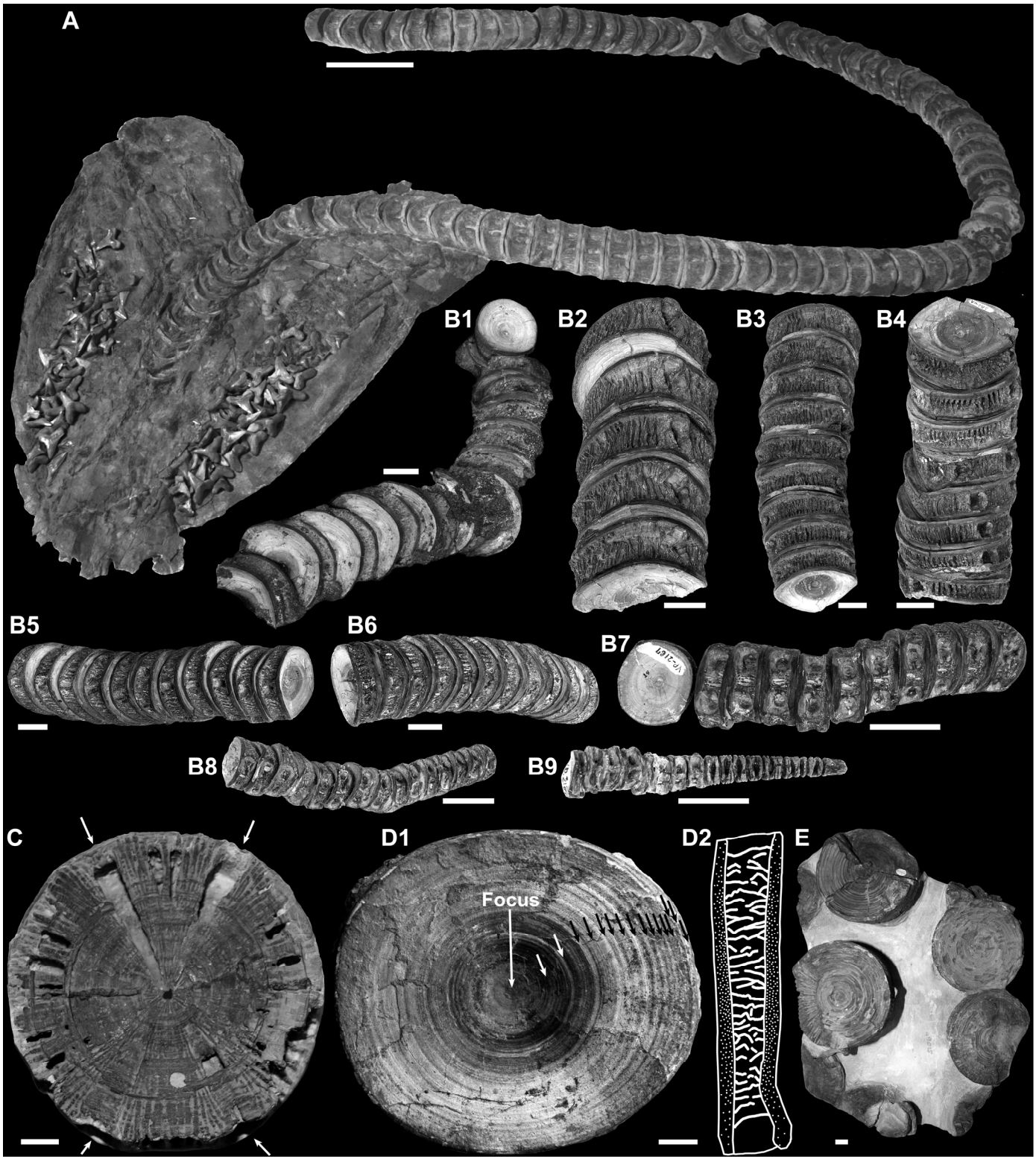


Figure 7.

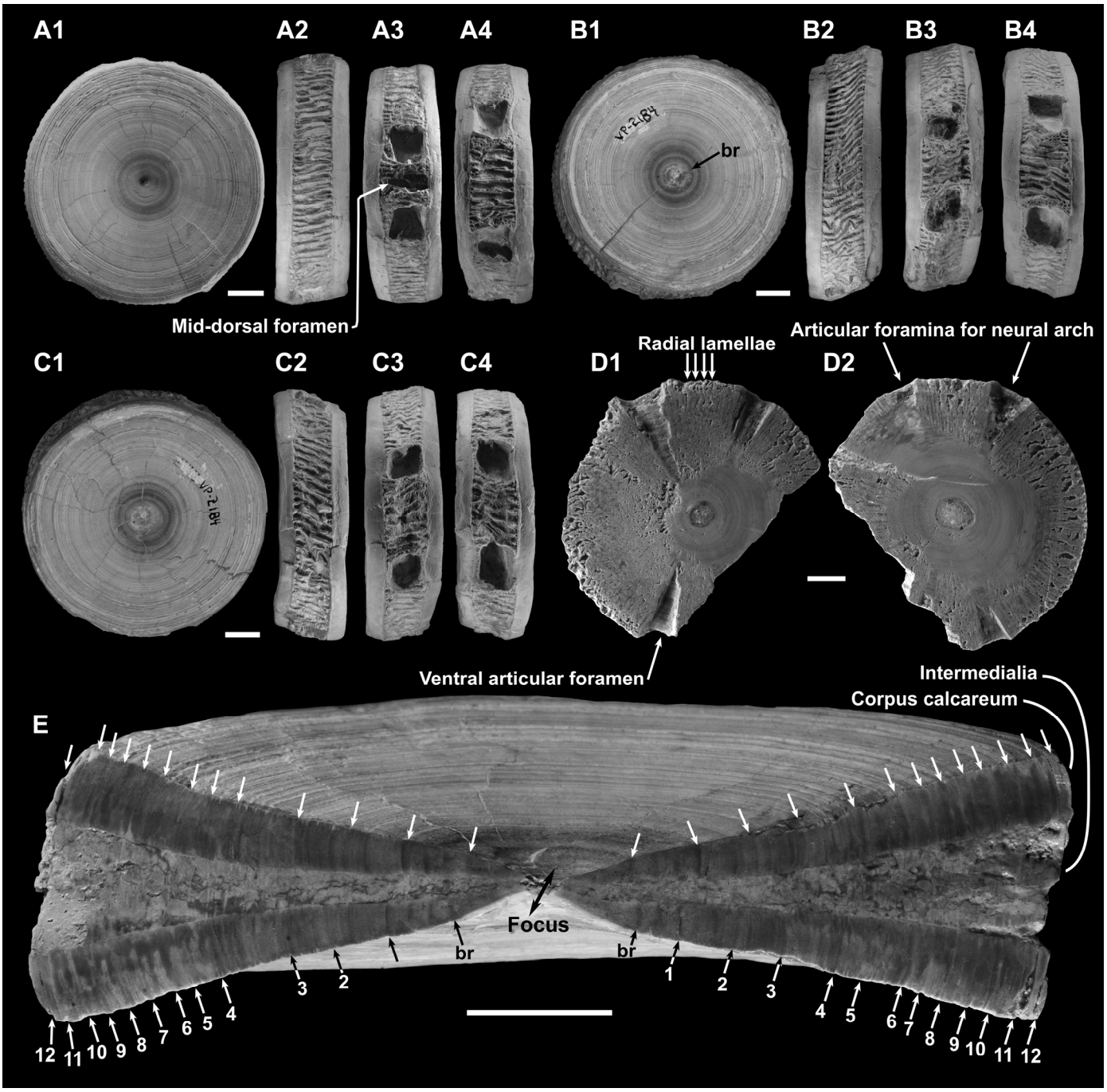

A1
A2
A3
A4
B1
B2
B3
B4
br
Mid-dorsal foramen
C1
C2
C3
C4
D1
Radial lamellae
D2
Articular foramina for neural arch
Ventral articular foramen
Intermedialia
Corpus calcareum
E
Focus
br
br
12 11 10 9 8 7 6 5 4
3 2
1 2 3 4 5 6 7 8 9 10 11 12

Figure 8.

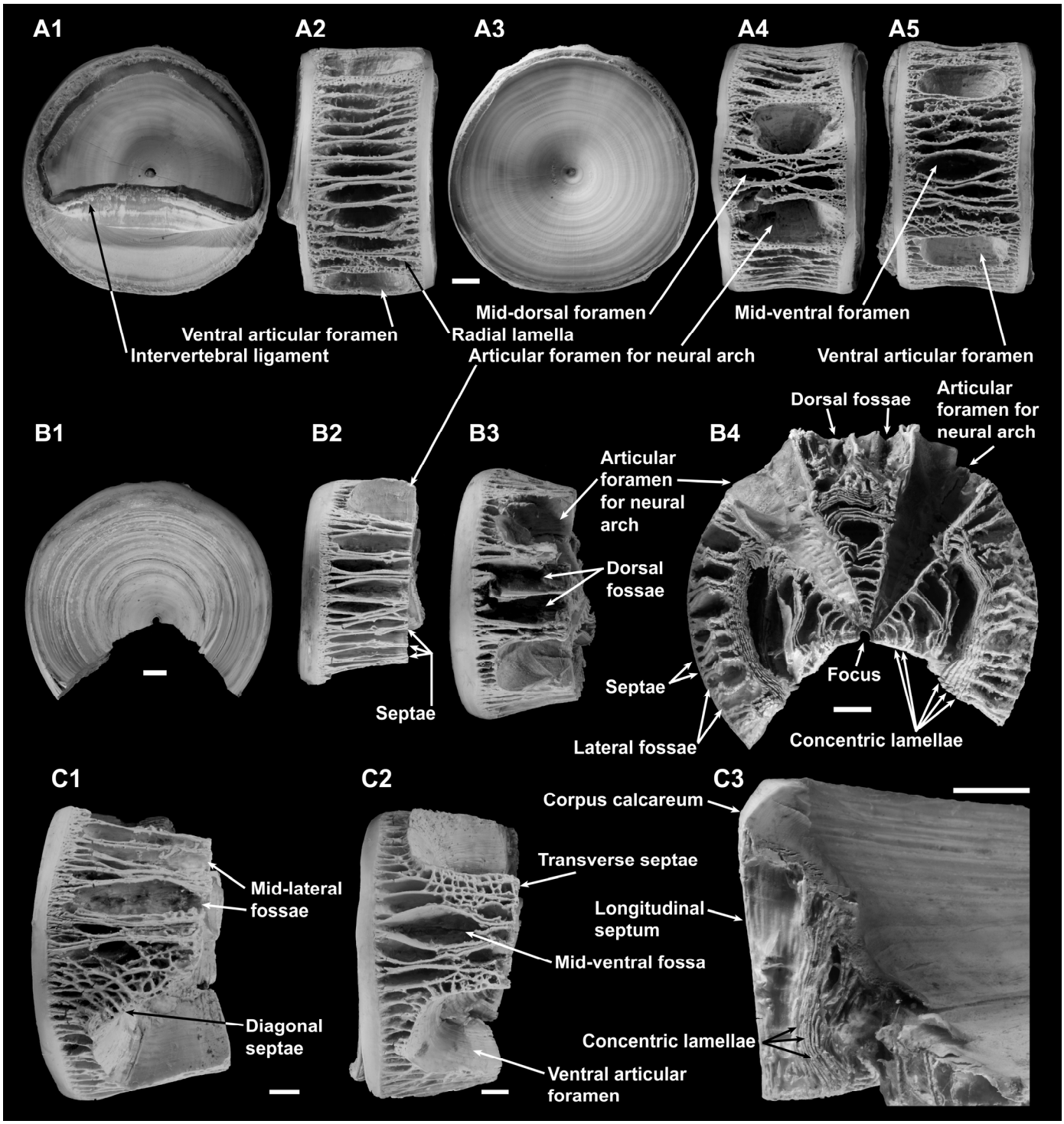

A1
A2
A3
A4
A5
Ventral articular foramen
Intervertebral ligament
Radial lamella
Mid-dorsal foramen
Articular foramen for neural arch
Mid-ventral foramen
Ventral articular foramen
B1
B2
B3
B4
Septae
Articular foramen for neural arch
Dorsal fossae
Dorsal fossae
Articular foramen for neural arch
Septae
Lateral fossae
Focus
Concentric lamellae
C1
C2
C3
Mid-lateral fossae
Diagonal septae
Corpus calcareum
Transverse septae
Longitudinal septum
Mid-ventral fossa
Concentric lamellae
Ventral articular foramen

Figure 9.

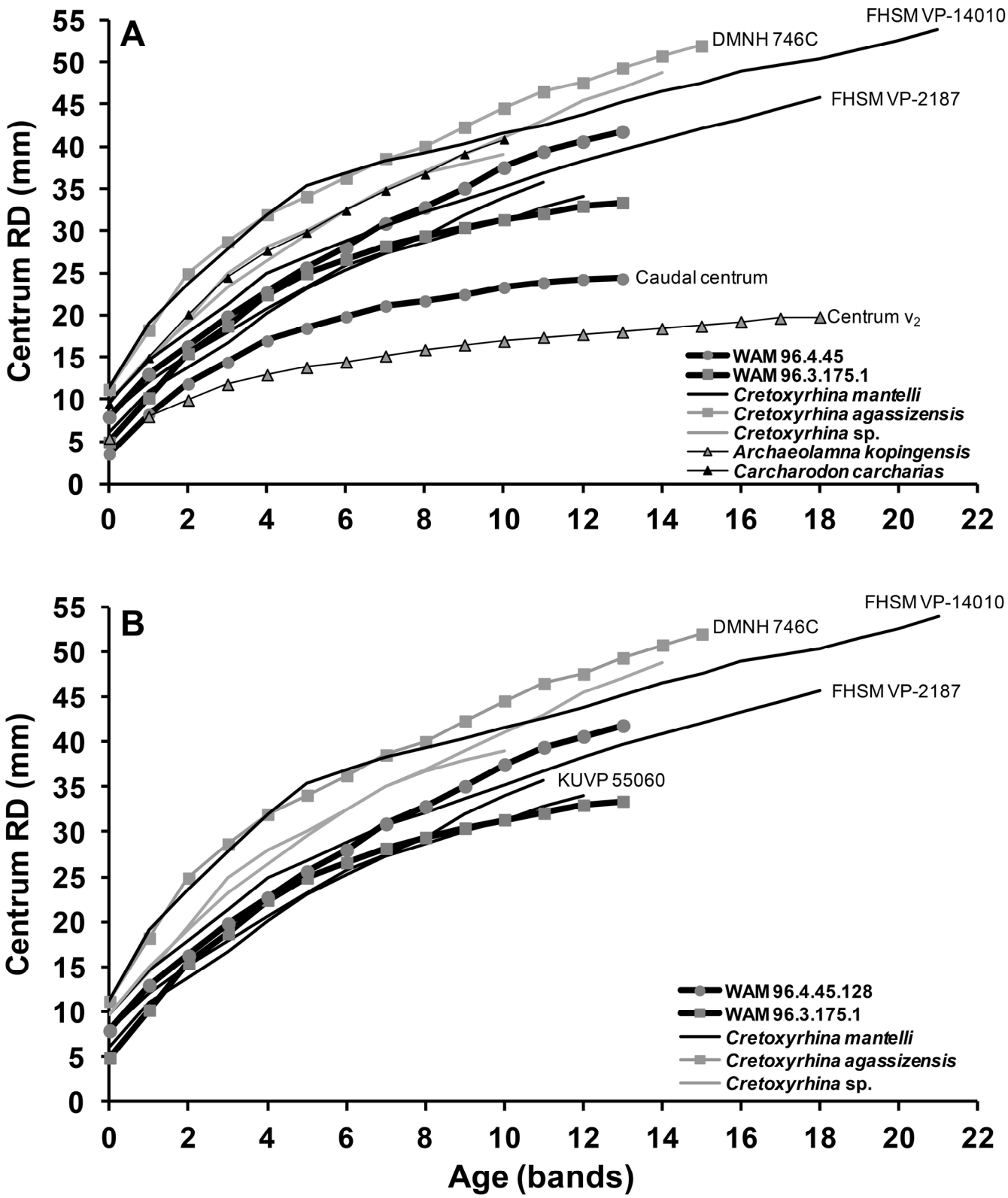
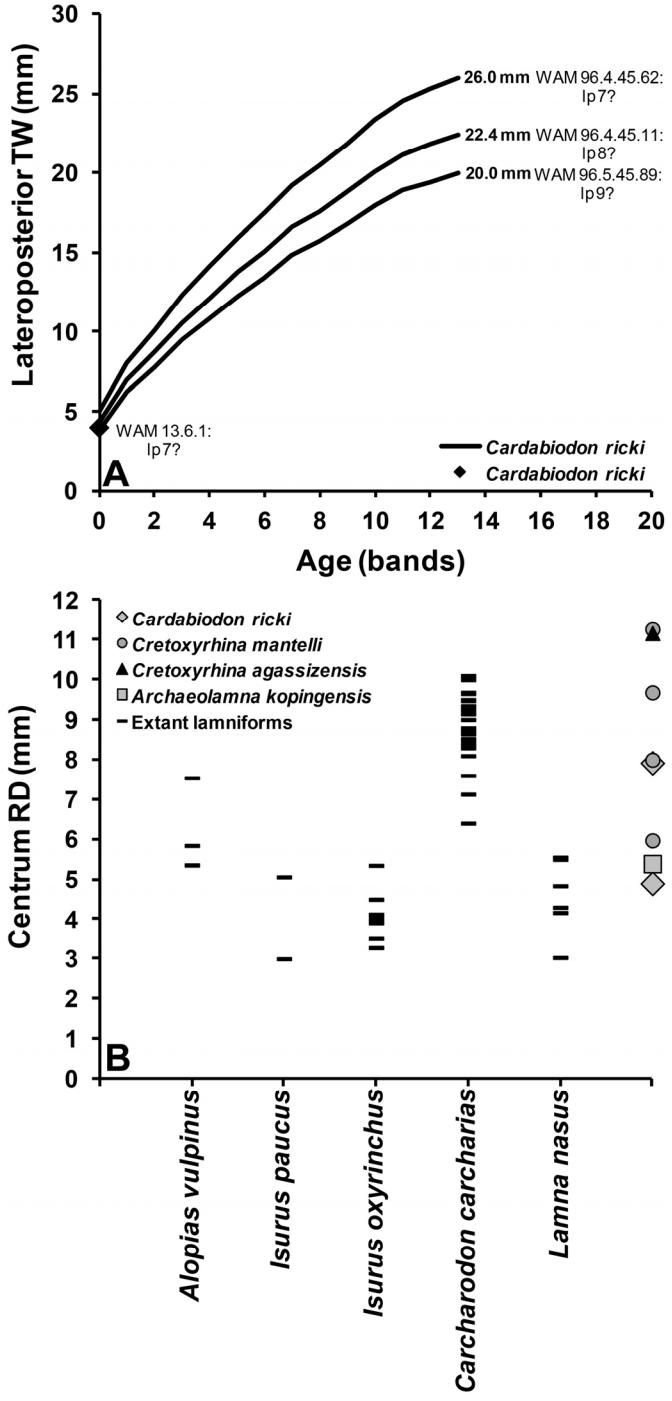

A
Centrum RD (mm)
FHSM VP-14010
DMNH 746C
FHSM VP-2187
Caudal centrum
Centrum v2
WAM 96.4.45
WAM 96.3.175.1
Cretoxyrhina mantelli
Cretoxyrhina agassizensis
Cretoxyrhina sp.
Archaeolamna kopingensis
Carcharodon carcharias
B
Centrum RD (mm)
FHSM VP-14010
DMNH 746C
FHSM VP-2187
KUVP 55060
WAM 96.4.45.128
WAM 96.3.175.1
Cretoxyrhina mantelli
Cretoxyrhina agassizensis
Cretoxyrhina sp.
Age (bands)

Figure 10.


Lateroposterior TW (mm)
Age (bands)
26.0 mm WAM 96.4.45.62: lp7?
22.4 mm WAM 96.4.45.11: lp8?
20.0 mm WAM 96.5.45.89: lp9?
WAM 13.6.1: lp7?
Cardabiodon ricki
Cardabiodon ricki
A
Centrum RD (mm)
Cardabiodon ricki
Cretoxyrhina mantelli
Cretoxyrhina agassizensis
Archaeolamna kopingensis
Extant lamniforms
B
Alopias vulpinus
Isurus paucus
Isurus oxyrinchus
Carcharodon carcharias
Lamna nasus