University of Alberta

Late Cretaceous Euselachians from the Northern Region of the Western Interior Seaway

by

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ABSTRACT

Canadian deposits yielding marine euselachian (shark and ray) remains from the Western Interior Seaway, an epicontinental sea that extended north–south through the middle of North America during the last half of the Cretaceous, have received less attention than those from the United States. Numerous isolated teeth were recovered from several localities situated in northwestern Alberta, Canada. These high-paleolatitude assemblages include 20 species belonging to at least three orders, at least 12 families, and 17 genera. Reported here are the first Canadian occurrences of cf. *Polyacrodus illingsworthi*, *Scapanorhynchus*, *Carcharias* aff. *C. striatula*, *Johnlongia parvidens*, *Protolamna carteri*, and *Pseudohypolophus mcnultyi*. It is also the first North American report of *Dwardius woodwardi* and the first report of *Cardabiodon ricki* from the Northern Hemisphere. The recovered material extends the northern geographical range of these taxa and demonstrates that there was strong taxonomic homogeneity of pelagic sharks within the seaway when compared with temporally equivalent southern assemblages. However, the lamniform species *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon ricki*, *Johnlongia parvidens*, and *Dwardius woodwardi* have not been found from well sampled deposits of the southernmost region of the seaway and may have been restricted to cooler waters. To test this purported antitropical distribution, the latitudinal and thermal ranges of these species are compared to those of the extant antitropical shark, *Lamna nasus* (porbeagle).

The recovery of a partial skeleton of *Archaeolamna kopingensis* provides the first ever detailed description of this lamniform species. The specimen preserves the first unequivocal occurrence of a fossilized dental bulla, an expanded region of the mesial jaw that houses the anterior teeth and is a synapomorphy of the Order Lamniformes. The articulated tooth set demonstrates that the tooth morphology and dental arrangement is distinct from that of all other extinct and extant lamniforms, validating its placement into the previously proposed Archaeolamnidae. An amended set of diagnostic criteria to define the family Archaeolamnidae is provided. In addition, an analysis of the jaw circumference of this specimen suggests that this species grew to a size much larger than had previously been thought, exceeding that of a 3.2 m *Isurus oxyrinchus* (shortfin mako) and a 3.8 m *I. paucus* (longfin mako).

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LIST OF ABBREVATIONS

Institutional Abbreviations

CMN	Canadian Museum of Nature, Ottawa, Ontario, Canada;
FHSM VP	Sternberg Museum of Natural History, Vertebrate Paleontology, Hays, Kansas, USA;
KUVP	University of Kansas Museum of Natural History, Vertebrate Paleontology, Lawrence, Kansas, USA;
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA;
SDSM	South Dakota School of Mines and Technology, Vertebrate Paleontology, Rapid City, South Dakota, USA;
UALVP	University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada;
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA;
USNM	National Museum of Natural History, Smithsonian Institution, Paleontology, Washington, D.C., USA;
UWGM	University of Wisconsin, Geology Museum (New Series), Madison, Wisconsin, USA;
WAM	Western Australian Museum, Perth, Western Australia, Australia.

ANATOMICAL ABBREVIATIONS

For anatomical abbreviations, please refer to the respective figure caption.

CHAPTER 1

Introduction and Background

Chondrichthyan Dentitions and Terminology

The Class Chondrichthyes (sharks, rays, and chimaeras) is a monophyletic group based on synapomorphies, of which prismatic perichondral tissue is “most convincing” (Maisey, 1984b: p. 359). The chondrichthyan cartilaginous endoskeleton does not readily fossilize (Cappetta, 1987; Welton and Farish; 1993; Kent, 1994). Consequently, the fossil record largely consists of isolated teeth owing to the durable histological nature of these elements (Fig. 1.1). Dermal denticles, vertebral centra, and fin spines are also quite resilient to erosive forces and may contribute to the study of extinct forms.

The abundance of elasmobranch teeth in the fossil record is in part due to the condition of polyphyodontism where teeth are continuously produced and replaced throughout the life of an individual. The teeth are not ankylosed to the jaw cartilage but are instead embedded in the oral mucosa called the dental lamina (Reif, 1980; Kemp, 1999). Developing teeth migrate labially along the inner aspect of the jaw within this tissue. The developing tooth bud passes through stages of mineralization until a fully functional tooth is produced and found on the outer margin of the jaw. This tooth is eventually shed and replaced by the succeeding tooth (Kemp, 1999) (Fig. 1.2). The labiolingual sequence of functional and replacement teeth constitute a tooth file (Fig. 1.3). A tooth row is the mesiodistal sequence of teeth along the jaw. The rate of tooth replacement (expressed as time per file) varies among species (see Luer et al., 1990) and can range from 8-10 days/file in *Negaprion brevirostris* (lemon shark) (Moss, 1967) to as much as 5 weeks/file for *Scyliorhinus canicula* (small-spotted catshark)

(Luer et al., 1990). The replacement rate increases with a higher metabolic rate (Luer et al, 1990) and during the period of rapid growth (Moss, 1967). Despite the inadequate preservation of the cartilaginous endoskeleton, the durability and continual lifetime production of elasmobranch teeth provides one of the most complete fossil records of any vertebrate group (Moss, 1967; Maisey, 1984; Kent, 1994).

The elasmobranch tooth consists of two distinct parts, the crown and the root. The crown is the portion of the tooth that is exposed and utilized during feeding. The morphology of the crown is species specific and is described using a particular set of terms (Fig. 1.4). Typically, sharks have a crown that consists of a large median cusp, which may be flanked by a single or multiple pairs of lateral cusplets. The labial and lingual faces of the crown may be smooth or ornamented with enameloid folding. Depending on the species, the crown may possess a distinct cutting edge of variable length, which can be smooth or serrated. The teeth of some species have an enameloid-free region at the base of the lingual crown face called the lingual neck. Often, the base of the labial crown face may overhang the labial face of the root forming a basal ledge.

Concerning batoid dentitions, the crown varies considerably. For example, in the crushing-type dentition of *Rhinobatos* (guitarfish), the globular crown often contains a distinct transverse crest that separates the labial face from the lingual face. The labial edge of the crown is called the labial visor and the lingual edge of the crown is termed the lingual visor. The latter may be indented to form distinct uvulae in some species (Cappetta, 1987). Batoids with a grinding-type dentition have crowns with distinct margins and often have a rhombic or hexagonal occlusal face. The labial and lingual faces are separated by a pair of labial marginal faces and a pair of lingual marginal faces. Depending on the species, the crown faces may bear enameloid folding (Cappetta, 1987).

Histologically, the elasmobranch crown is typically covered with a thin layer of enameloid, which is ectodermal and mesodermal in origin (Reif, 1982). Neoselachian enameloid consists of three distinct layers (Rief, 1973): (1) an outer shiny layered enameloid made of individual hydroxyfluorapatite crystallites, (2) a middle parallel-fibered enameloid, and (3) an inner tangle-fibered enameloid. The presence of the middle layer is considered a synapomorphy of the neoselachians (Reif, 1977; Thies, 1982; Maisey, 1984a, b, 1985; Thies and Reif, 1985; Gaudin, 1991; Cuny et al., 2001; Gillis and Donoghue, 2006) (Fig. 1.5). The parallel-fibred enameloid has been lost in some neoselachians with a crushing-type dentition such as *Heterodontus* (Maisey, 1985; Thies, 1982). Underlying the enameloid layer is a region of dense pallial dentine containing numerous fibrous tubules. This layer rests directly upon a dense region of apatitic orthodentine tissue. Deep to this layer is either a region filled with spongy osteodentine or there is a pulp cavity. Two histologically distinct tooth types are based on the presence or absence of this cavity. Teeth with orthodont tooth histology contain the enlarged pulp cavity which is devoid of hard tissue, whereas teeth with osteodont tooth histology have a center that is filled with spongy osteodentine tissue (Welton and Farish, 1993; Kent, 1994) (Fig. 1.6A, B). In general, lamniforms (mackerel sharks) have osteodont teeth, whereas carcharhiniforms (ground sharks) have orthodont teeth (Kent, 1994). However, using the presence or absence of the pulp cavity as an exact means to differentiate taxa is questionable as there are many exceptions. For example, the extant *Hemipristis elongatus* (snaggletooth shark) has osteodont teeth; whereas the Oligocene species *H. serra* has orthodont teeth (Compagno, 1988; Kent, 1994). The anterior teeth of the extant *Heterodontus francisci* (California horn shark) are orthodont; whereas the posterior teeth are osteodont (Compagno, 1970; Kent, 1994).

The root serves as an anchor within the dental lamina and is the entry point for tooth vascularisation. While the root receives its blood supply directly via vascular canals, the rest of the tooth is supplied by vasculature entering the nutrient canal of the root. Histologically, the root consists entirely of osteodentine and lacks an enameloid covering (Cappetta, 1987). There are four variations in the root morphology in elasmobranch teeth (Casier, 1947; Cappetta, 1987; Welton and Farish, 1993). The anaulacorhizous root, observed in hybodonts and hexanchids (cow sharks), has a highly porous root with a flat basal face (Fig. 1.7A). *Squatina* (angel shark), heterodontids (bullhead sharks) and some orectolobiforms (carpet sharks) have a hemiaulacorhizous root (Fig. 1.7B). This root has a large central foramen contained within a central hollow, which is connected to the medio-internal foramen (located on the lingual protuberance) via the medio-internal canal and medio-external foramen. The holaulacorhizous root, found in lamniforms, carcharhiniforms, rajiforms, and dasyatids, has a well developed nutrient groove that divides the basal face (Fig. 1.7C). Myliobatids (eagle rays) possess a polyaulacorhizous root that has multiple root lobes that are separated by labiolingually directed nutrient grooves that contain numerous foramina (Fig. 1.7D).

Information pertinent to taxonomic relationships may be revealed from tooth morphology. Unfortunately, selachian taxonomy based on isolated tooth elements is potentially problematic due to the condition of heterodonty. Variation in tooth morphology along the jaw of an individual may be mistakenly recognized and described as multiple taxa when the teeth are recovered as isolated elements. Heterodonty may simply be a gradual mesiodistal increase in tooth size and cusp inclination or it can be an abrupt and distinct change in tooth shape and size along the jaw margin (Welton and Farish, 1993). Compagno (1970) recognized four categories of heterodonty: (1) monognathic heterodonty, where there is variation in tooth morphology along the dental series in either the upper or lower jaw as observed in the dentition of *Galeocerdo cuvier* (tiger shark) (Fig. 1.8A); (2) dignathic heterodonty, where variation in tooth morphology exists between opposing teeth as demonstrated in the dentition of *Hexanchus nakamurai* (six-gill shark) (Fig. 1.8B); (3) ontogenetic heterodonty, where there is variation in tooth morphology as the individual ages, as seen in the dentition of *Heterodontus francisci* (California horn shark) (Fig. 1.8C); and (4) sexual dimorphic heterodonty where tooth morphology of similarly positioned teeth varies between males and females of similar age, as observed in species of *Dasyatis* (whiptail stingray) (Fig. 1.8D) (Compagno, 1970; Welton and Farish, 1993). Another potential source of confusion is the occurrence of pathological teeth. These teeth are abnormal due to developmental abnormalities or direct trauma. The abnormal tooth morphology may appear completely different from the typical form and could potentially be recognized and described as a new taxon (see Becker et. al, 2000). Fortunately, the fossil record of many taxa, including the lamniforms (mackerel sharks), extends back to the Cretaceous; thus, modern relatives can be utilized to determine whether isolated teeth of varying morphology belong to multiple species or a single species with dentition that displays strong heterodonty.

Identifying an accurate dental arrangement of a species is essential for establishing phylogenetic relationships (Siverson, 1999; Shimada, 2002). Most often, an artificial tooth set of an extinct euselachian species is reconstructed using isolated teeth from different individuals of one species (Welton and Farish, 1993). If closely related extant taxa exist, the reconstruction of the dentition can be based on the modern example. For instance, both extant and extinct lamniforms (see Shimada, 1997) most often contain a unique dental pattern where the teeth are “weakly or strongly differentiated along the jaws, with or without (*Megachasma*) enlarged anterior teeth but without enlarged molariform posterior teeth; usually with a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw” (Compagno, 2001: p. 51). An associated tooth set is reconstructed using the disarticulated dental set from one individual. In very rare instances, a natural tooth set is recovered that can verify various tooth positions and exact file arrangements.

Elasmobranch dentition varies considerably, reflecting the trophic preference of a species. Cappetta (1987) categorized elasmobranch dentitions into six “types” based on functional morphology. Type: (1) taxa with a clutching-type dentition, as seen in benthic scyliorhinids (catsharks) and orectolobiforms (carpet sharks), have multiple functional rows of small teeth with weak heterodonty (Fig. 1.9A). The teeth usually have reduced ornamented median cusps and lateral cusplets that are sharp which aids in grasping prey. The teeth of males of many rajid (skates) and dasyatid (whiptail stingrays) species, which bear a tall narrow cusp, also have this type of dentition, which may decrease intraspecific competition and/or aid in mating. (2) Taxa with tearing-type dentitions, as observed in odontaspidids (sand tiger sharks), have teeth with tall and narrow median cusps containing a distinct cutting edge and small lateral cusplets. There are usually multiple functional rows. This dentition is effective for grasping active prey that is swallowed whole (Kent, 1994) (Fig. 1.9B). (3) Taxa with cutting-type dentitions, such as *Galeocerdo cuvier* (tiger shark), have very weak monognathic and diagnathic heterodonty along a single functional row. The tooth crown is typically mesiodistally wide and labiolingually compressed and often bears a serrated cutting edge. This dentition is effective at tearing apart large prey (Fig. 1.9C). Some species possess a cutting-clutching subtype dentition where there is a strong diagnathic heterodonty. The upper anterior teeth of hexanchids (cow sharks) are tall and narrow making them effective for grasping prey, while the wide and compressed lower teeth cut into it (Fig. 1.9D). (4) Taxa possessing a crushing-type dentition, such as female *Rhinobatos* (guitarfish) and rajids, possess teeth of similar morphology with bulging crowns. The dentition consists of numerous tooth files and functional rows, which together form an embossed occlusal surface, effective for crushing shelled invertebrates (Fig. 1.9E). (5) Taxa with grinding-type dentitions, including myliobatids (eagle rays), have high crowns that are rhombic or hexagonal in occlusal view and interlock to form a dental plate. The grinding-type dentition of *Aetobatus* (spotted eagle ray) is reduced to a single file. The flat and smooth occlusal surface is effective for grinding thick-shelled prey (Fig. 1.9F). (6) A clutching-grinding-type dentition is observed in adult heterodontids (bullhead sharks) where the clutching teeth in anterior files are cuspidate and possess lateral cusplets, whereas the grinding teeth of lateral files are robust with a flat occlusal surface (Fig. 1.9G).

Systematics

The vast majority of the teeth discussed in this study belong to species of the order Lamniformes (mackerel sharks). There are 15 extant lamniform species with an external morphology that includes two spineless dorsal fins, five broad gill slits, a mouth that extends behind laterally placed eyes that lack a nictitating membrane, small spiracles, and no barbels (Compagno, 2001; Nelson, 2006). The majority of the species are macrophagous; however, *Megachasma pelagios* (megamouth shark) and *Cetorhinus maximus* (basking shark) have secondarily evolved a filter feeding lifestyle with reduced dentition. As mentioned above, the dentition of the macrophagous species is described as having a “lamnoid tooth pattern” (Compagno, 1984, 2001) consisting of enlarged anterior teeth that are separated from lateral teeth by a file of reduced teeth.

There have been numerous morphological (Maisey, 1985; Compagno, 1990; Long and Waggoner, 1996) and molecular (Boyes and Stepien; 1995; Martin, 1995, 1996; Martin and Naylor, 1997; Morrissey, et al., 1997; Maisey et al., 2004) studies describing the phylogenetic relationships of the extant species in the order Lamniformes. Shirai (1996), using morphological data, recognized *Mitsukurina* as the sister taxon to all other lamniformes. Shirai (1996) also suggested a close relationship between Lamnidae and Cetorhinidae, with the two being sister to Alopiidae, which in turn all together form the sister with Megachasmidae. It was also recognized that *Carcharias* and *Odontaspis* are closely related (Fig. 1.10A). Based on molecular data, Naylor et al. (1997, NADH-2 and cytochrome b mitochondrial genes) suggested *Alopias* belonged to a clade with *Odontaspis*, *Pseudocarcharias*, and *Megachasma* and that Odontaspididae are polyphyletic (Fig. 1.10B). Maisey et al. (2004, based on RAG-1 nuclear gene) suggested a close relationship between *Cetorhinus* and lamnids, with the two being sister to *Carcharias*. It was also shown that *Megachasma* and *Pseudocarcharias* are sister taxa, which in turn are sister with *Alopias* (Fig. 1.10C). Long and Waggoner (1996), using dental morphology, suggested monophyly for Odontaspididae. Herein, the views of Compagno (1984, 2001) and Long and Waggoner (1996) are followed and Odontaspididae is recognized as retaining both *Odontaspis* and *Carcharias.*

Thesis Organization

Canadian deposits yielding selachian remains from the Western Interior Seaway, an epicontinental sea that extended north–south through the middle of

North America during the last half of the Cretaceous, have received considerably less attention than those from the United States. This thesis will focus on two euselachian assemblages that were collected from northwestern Alberta. These assemblages are the most northern known within the seaway and therefore can provide important insights into the euselachian faunal diversity of this little-known region of the seaway. Faunal comparisons with temporally equivalent assemblages from high-paleolatitudinal localities situated in the Southern Hemisphere, specifically Australia, and assemblages from the southern region of the Western Interior Seaway will be made to reveal general patterns of paleobiogeography. A significant number of sharks, particularly species from the order Lamniformes, had wide geographic distributions and evolved rapidly; thus their teeth could be utilized as an effective biostratigraphical tool to temporally correlate separate geographical regions. As such, a detailed taxonomic study of these assemblages will facilitate the construction of the intercontinental zonation system based on shark teeth.

Introduction to Chapter 2—This chapter describes a euselachian assemblage that was recovered from the middle Cenomanian Dunvegan Formation situated in northwestern Alberta. This assemblage is one of the most northern known within the Western Interior Seaway and provides an important insight into the euselachian faunal diversity of this little-known region of the seaway. Despite its high paleolatitude, the assemblage contains a number of elasmobranch taxa, including *Meristodonoides*, *Squalicorax*, *Archaeolamna,* and *Cretoxyrhina*. The Dunvegan assemblage also contains the first known reports from Canada of the sharks *Johnlongia parvidens*, *Protolamna carteri*, *Cretodus semiplicatus*, and the ray *Pseudohypolophus mcnultyi*. This assemblage extends the northern geographical range of all these taxa. Preliminary comparisons with other middle Cenomanian Western Interior Seaway assemblages show that the core composition of the Dunvegan assemblage is remarkably similar to that of other time-equivalent assemblages; however, conspicuously absent are species that are exceedingly common in other localities situated farther south. The absence of these taxa from the Dunvegan localities may be caused by a temperature intolerance associated with latitude and sea-water circulation patterns, or by an inability to inhabit environments that exhibit salinity variation.

Introduction to Chapter 3—This chapter describes numerous isolated euselachian teeth that were recovered from the early Turonian Kaskapau Formation situated in northwestern Alberta, Canada. This high-paleolatitude assemblage was collected from a sandstone lens along the bank of the Smoky River and includes 18 species belonging to at least three orders, at least 11 families, and 15 genera. Herein, I describe the new species *Odontaspis watinensis* and report the first Canadian occurrence of cf. *Polyacrodus illingsworthi*, *Scapanorhynchus* sp., and *Carcharias* aff. *C. striatula*, and the first North American occurrence of *Dwardius woodwardi.* The scarcity of benthic taxa in this assemblage supports the previous notion that bottom waters in this region of the Western Interior Seaway experienced enduring anoxic episodes. By comparing the taxa comprising this assemblage with middle Cenomanian Canadian assemblages, I show that seven species have a biostratigraphic range that extended across the Cenomanian-Turonian boundary in the northern region of the seaway. Of the taxa reported herein, 12 species have also been reported in assemblages from Texas. Conversely, *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon ricki*, *Carcharias* aff. *C. striatula*, *Odontaspis watinensis* n. sp., *Johnlongia parvidens*, and *Dwardius woodwardi* have not been found from deposits of the southernmost region of the seaway and may have been restricted to cooler waters.

Introduction to Chapter 4—This chapter discusses the paleobiogeography of the lamniforms *Archaeolamna*, *Cardabiodon*, *Johnlongia*, and *Dwardius.* These taxa have been hypothesized in the published literature as having an antitropical distribution. Herein, a novel methodology to test the purported hypothesis of an antitropical distribution for these taxa is implemented by examining two paleoecological aspects. The paleolatitudinal and paleothermal (sea surface temperatures) ranges of the localities, from which involved taxa were recovered, are compared to those of the extant antitropical shark, *Lamna nasus*. It is predicted that an extinct antitropical species should exhibit similar latitudinal and thermal ranges to those of *L. nasus*. Furthermore, the paleodistribution of localities should shift with climate change. Of the taxa tested, only *Johnlongia* satisfies the two conditions that support the hypothesis of an antitropical distribution by (1) having a paleolatitudinal range less than the modern range for *L. nasus* and (2) a paleothermal range similar to that recorded for *L. nasus.* The paleolatitudes of the localities are also positively correlated with global temperature to indicate that, during warm periods, *Johnlongia* was found at higher paleolatitudes in both hemispheres, but was found at warmer, lower latitudes during cooler periods.

Introduction to Chapter 5—This chapter describes the rare recovery of a partial shark skeleton from the middle Campanian Sharon Springs of western Kansas. The remarkable specimen is identified as *Archaeolamna kopingensis* and includes a portion of the neurocranium, multiple vertebral centra, and portions of the upper and lower jaws with preserved articulated tooth files. The preservation of the dental arrangement provides the first ever detailed description of this lamniform species, as the true dental arrangement is essential in determining its systematic position. The specimen also preserves the first unequivocal occurrence of a fossilized dental bulla, an expanded region of the mesial jaw that houses the anterior teeth and is a synapomorphy of the Order Lamniformes. It is demonstrated that the tooth morphology and dental arrangement of *A. kopingensis* was distinct from that of all other extinct and extant lamniforms, validating its placement into the previously proposed Archaeolamnidae. An amended set of diagnostic criteria to define the family Archaeolamnidae is provided. A method to estimate the length of this individual in the absence of a complete set of vertebral centra is also devised. Values obtained by measuring the partially complete upper jaw are compared to jaw circumference values for modern lamniform sharks. It is determined that this specimen had a jaw circumference larger than that of a 3.2 m *Isurus oxyrinchus* (shortfin mako) and a 3.8 m *I. paucus* (longfin mako). The size of this individual demonstrates that this species grew to a size much larger than had previously been thought.

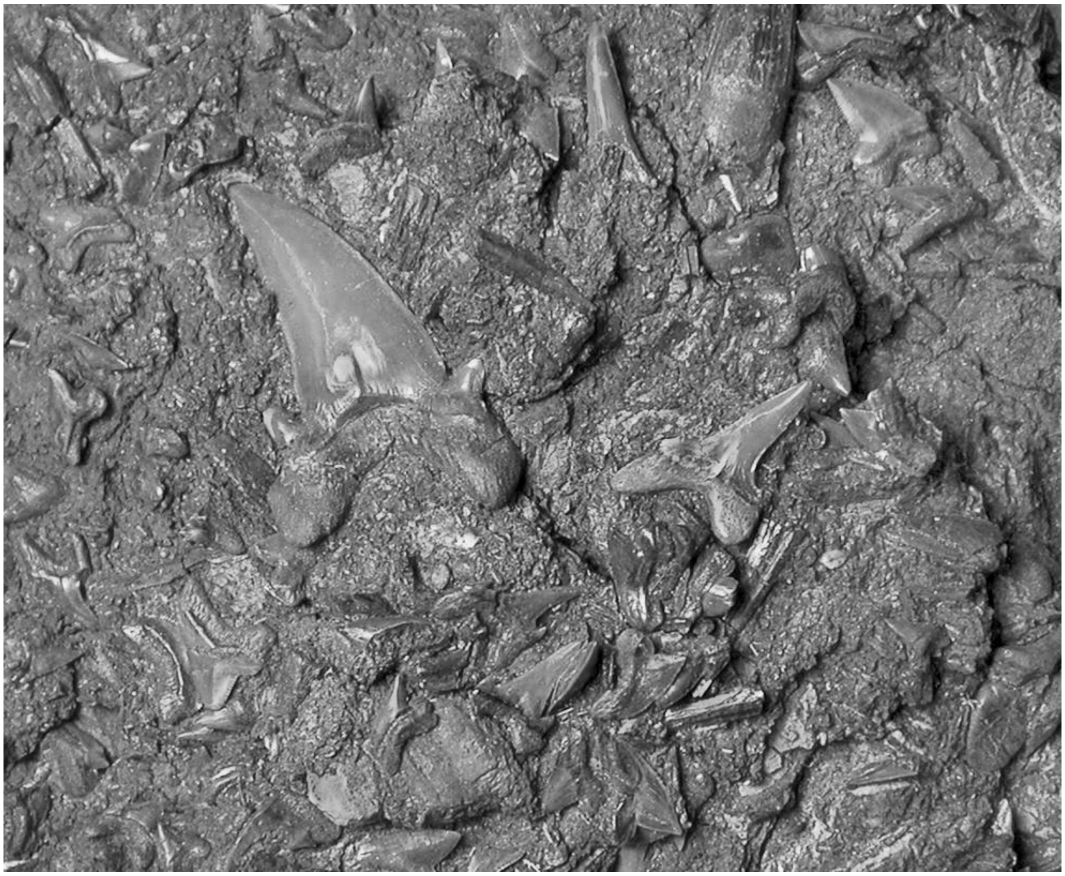

Figure 1.1. Isolated teeth (UALVP 17339) collected near Watino, Alberta, Canada.

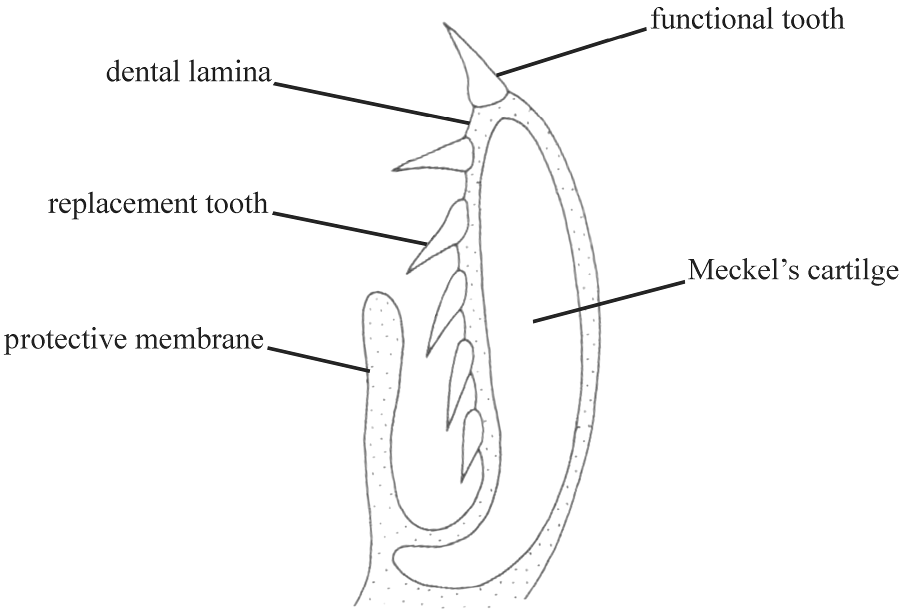

Figure 1.2. Cross section of Meckel's cartilage demonstrating tooth replacement (modified from Cappetta, 1987).

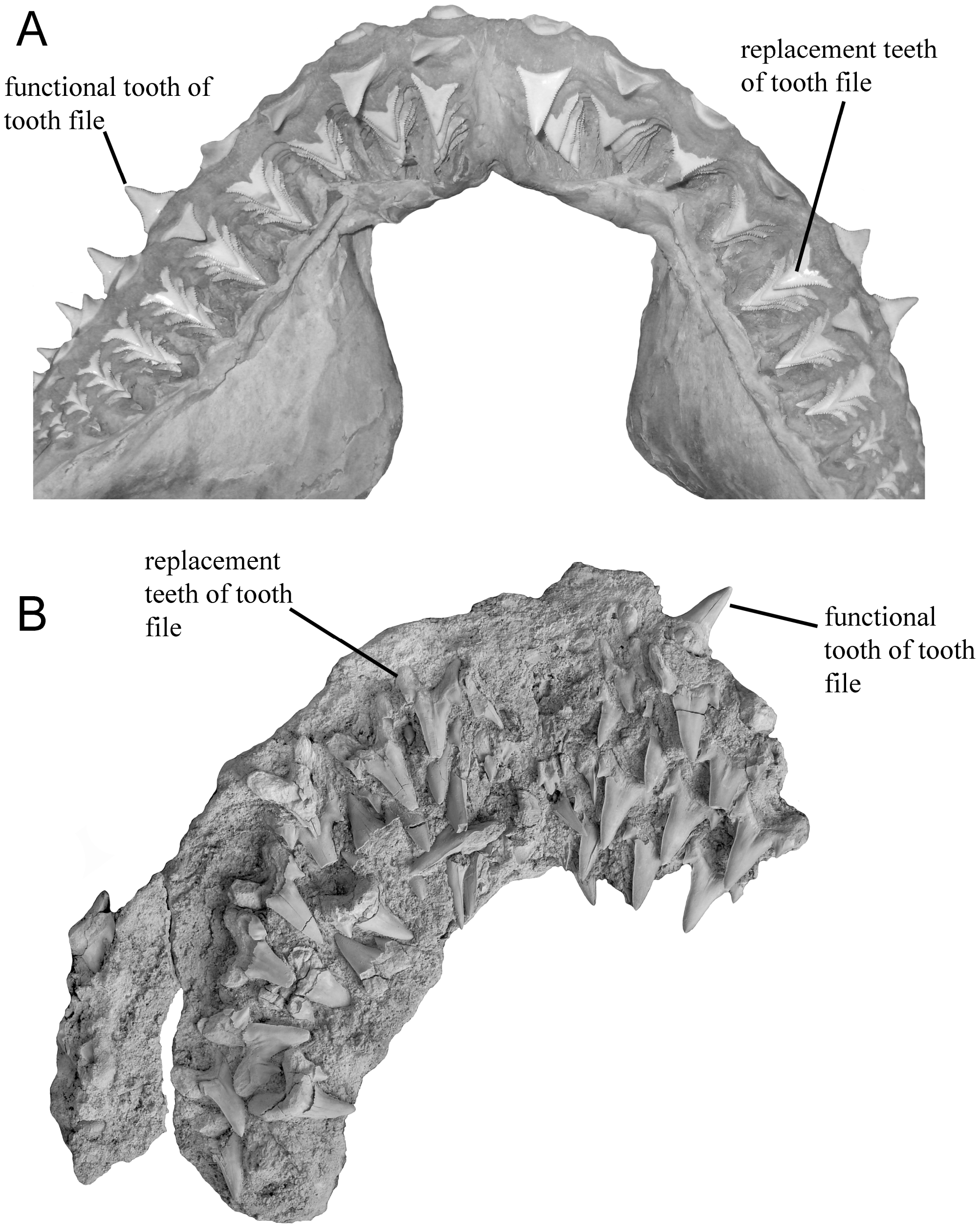

Figure 1.3. Meckel's cartilage of (A) *Carcharodon carcharias* (LACM 38194-1) and (B) *Archaeolamna kopingensis* (LACM 128125) showing a functional tooth and replacement teeth of a tooth file.

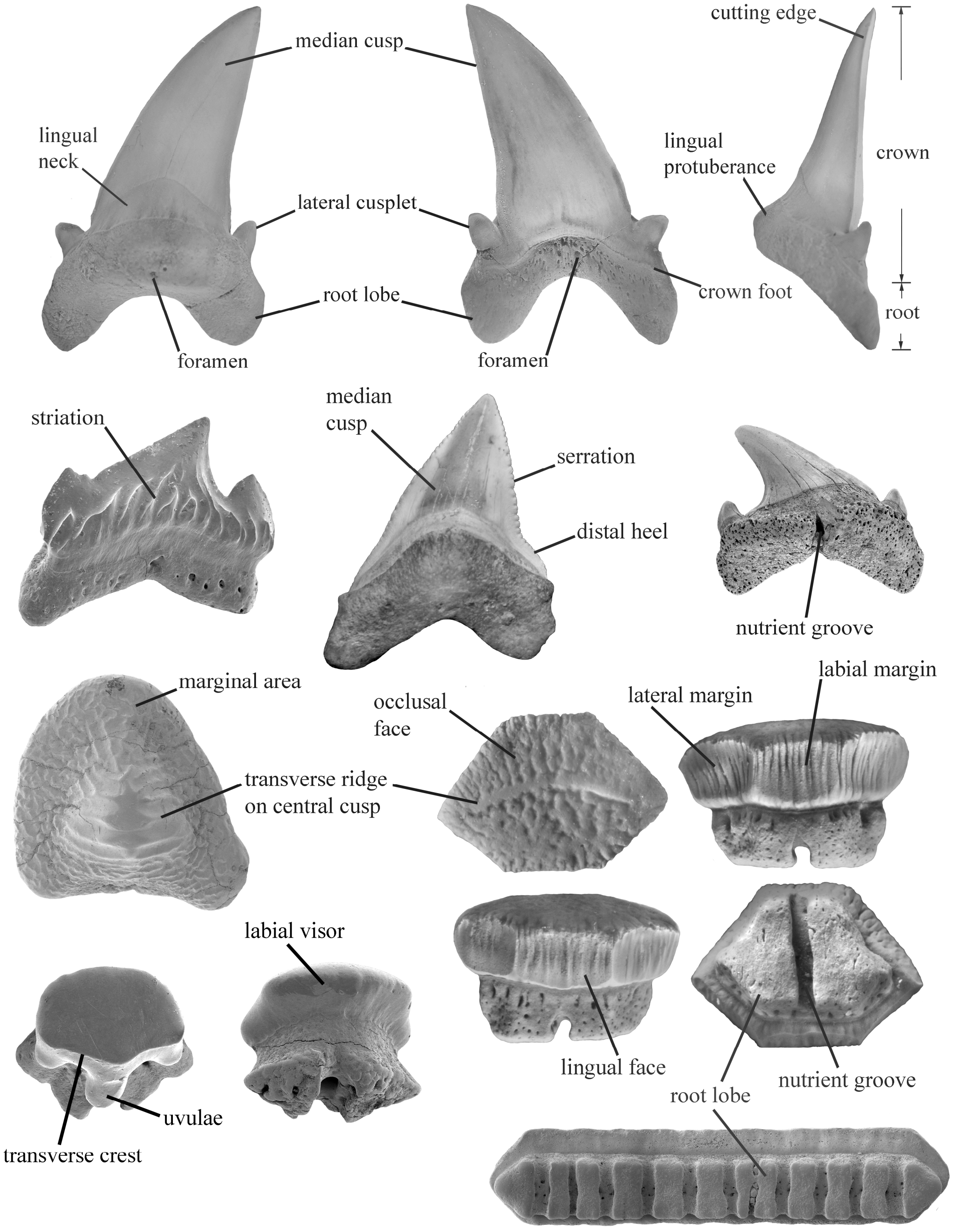

Figure 1.4. Tooth terminology associated with euselachians.

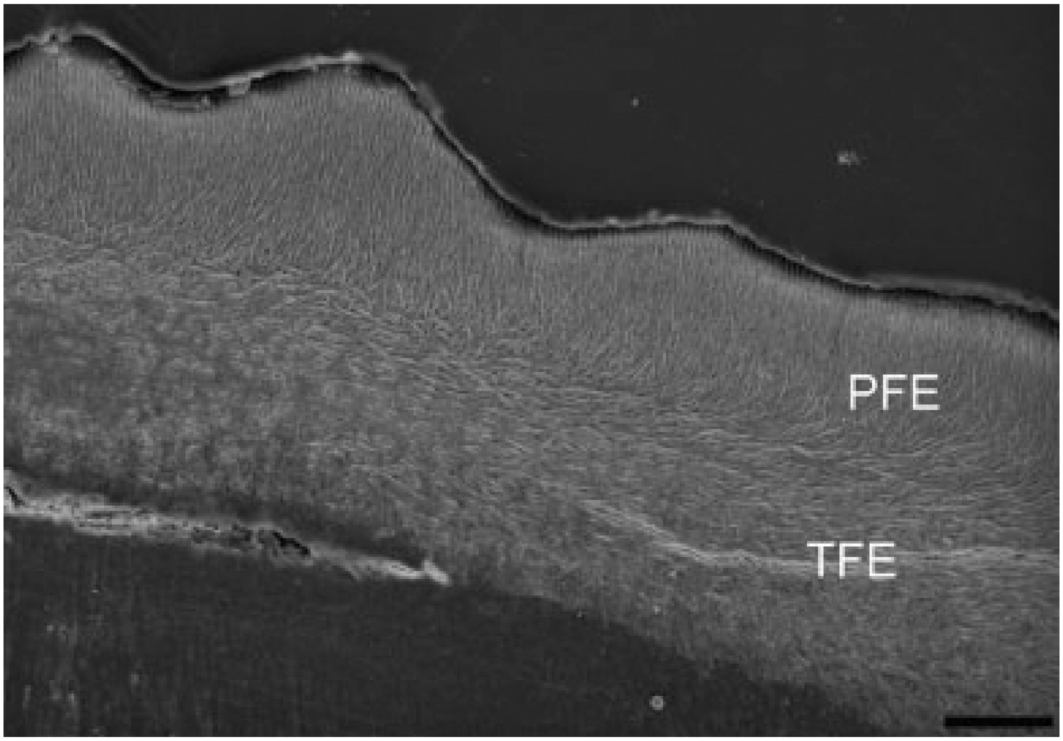

Figure 1.5. SEM image of the enameloid layer of a *Carcharhinus plumbeus* tooth showing the parallel fibered enameloid (PFE) and deeper tangled fiber bundles (TFE). Shiny layer enameloid missing due to etching (image from Gillis and Donoghue, 2006). Scale bar = 100 um.

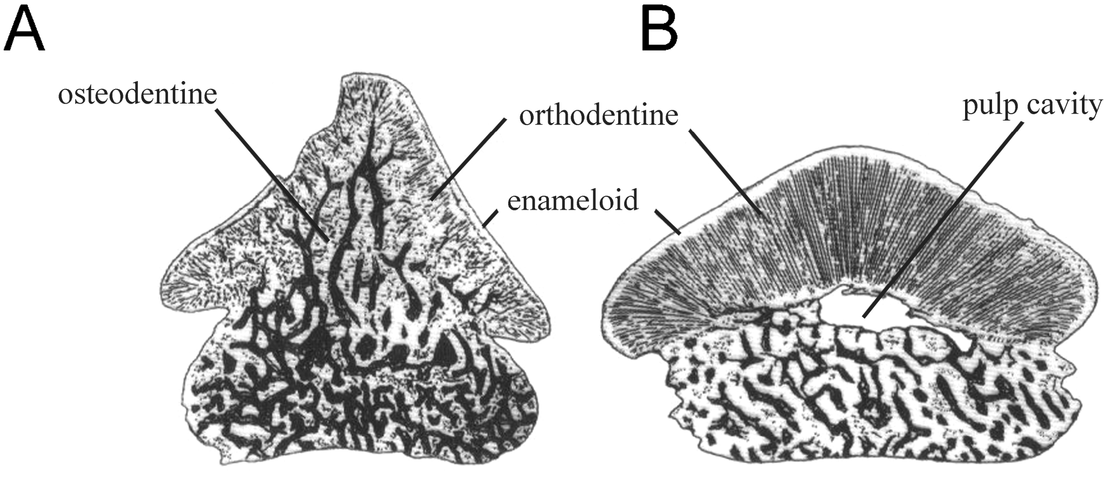

Figure 1.6. Cross section of (A) osteodont and (B) orthodont tooth types (image from Rees, 2001).

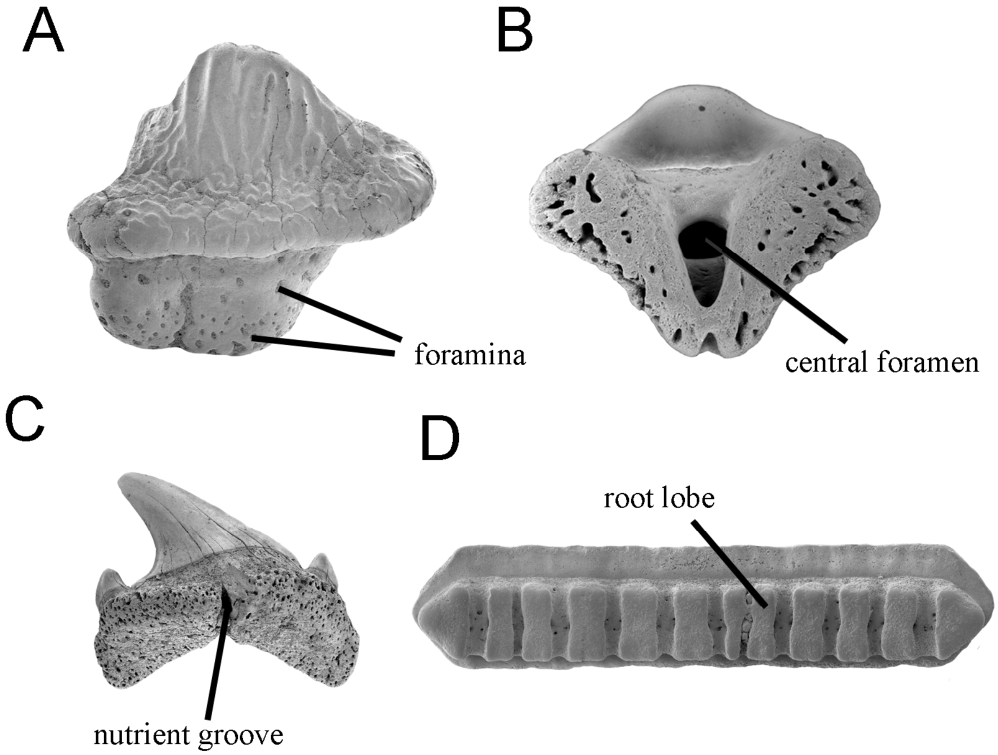

Figure 1.7. Root types: (A) anaulacorhizous, (B) hemiaulacorhizous, (C) holaulacorhizous, and (D) polyaulacorhizous.

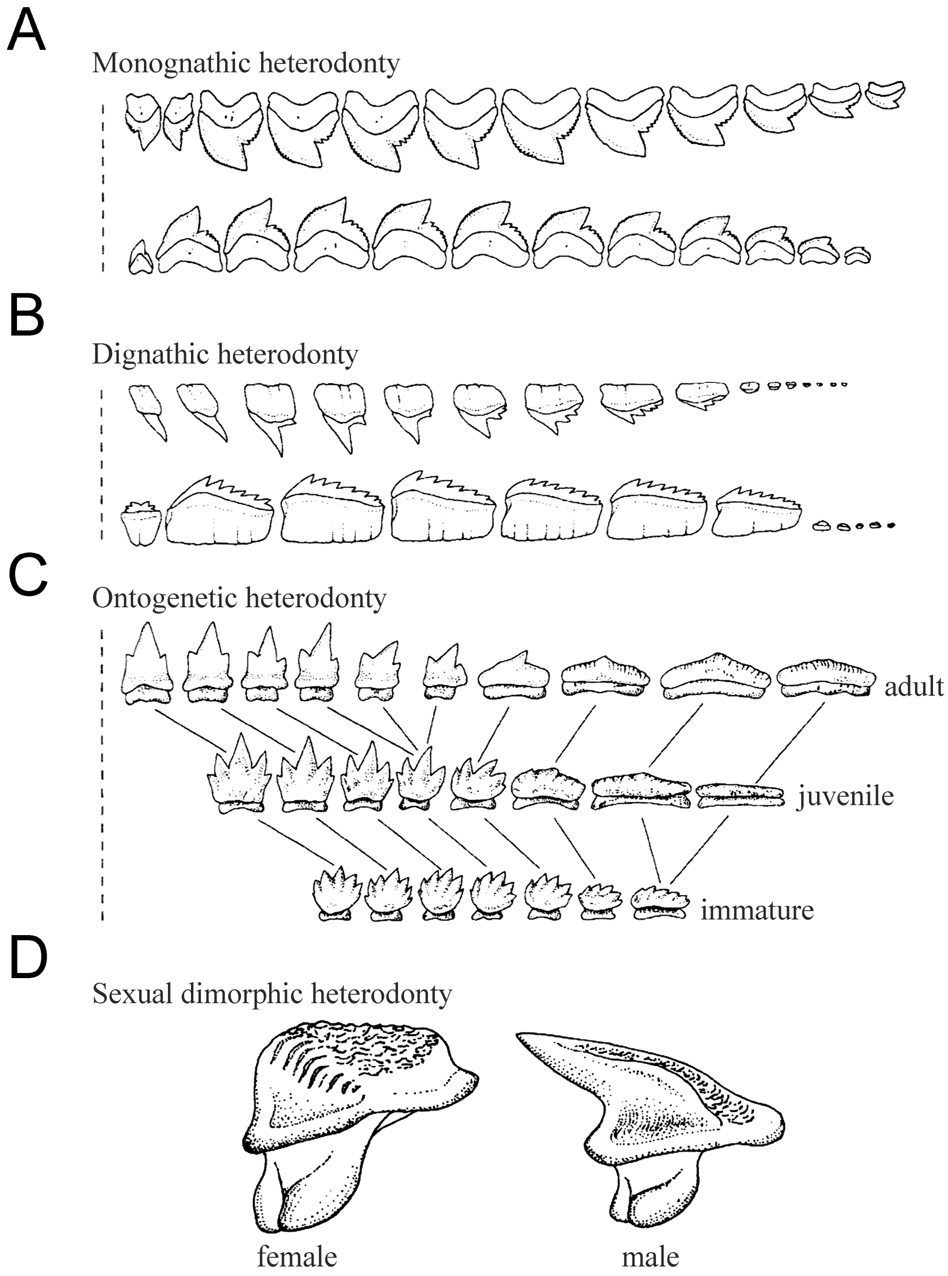

Figure 1.8. Types of heterodonty: (A) monognathic, (B) dignathic, (C) ontogenetic, and (D) sexual dimorphism (modified from Welton and Farish, 1993).

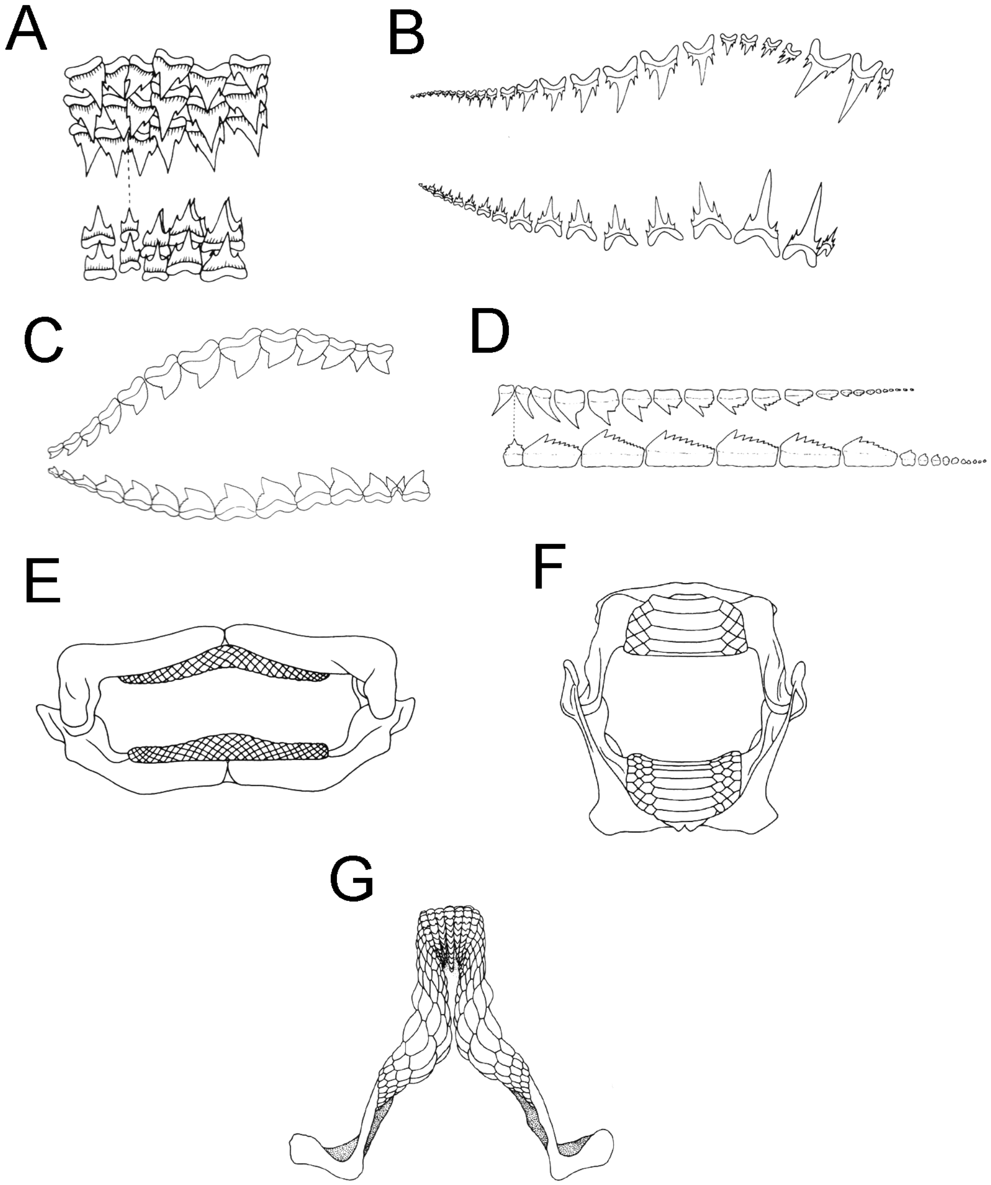

Figure 1.9. Dentition types based on trophic adaptation: (A) clutching-type, (B) tearing-type, (C) cutting-type, (D) cutting clutching-type, (E) crushing-type, (F) grinding-type, and (G) clutching grinding-type (modified from Cappetta, 1987).

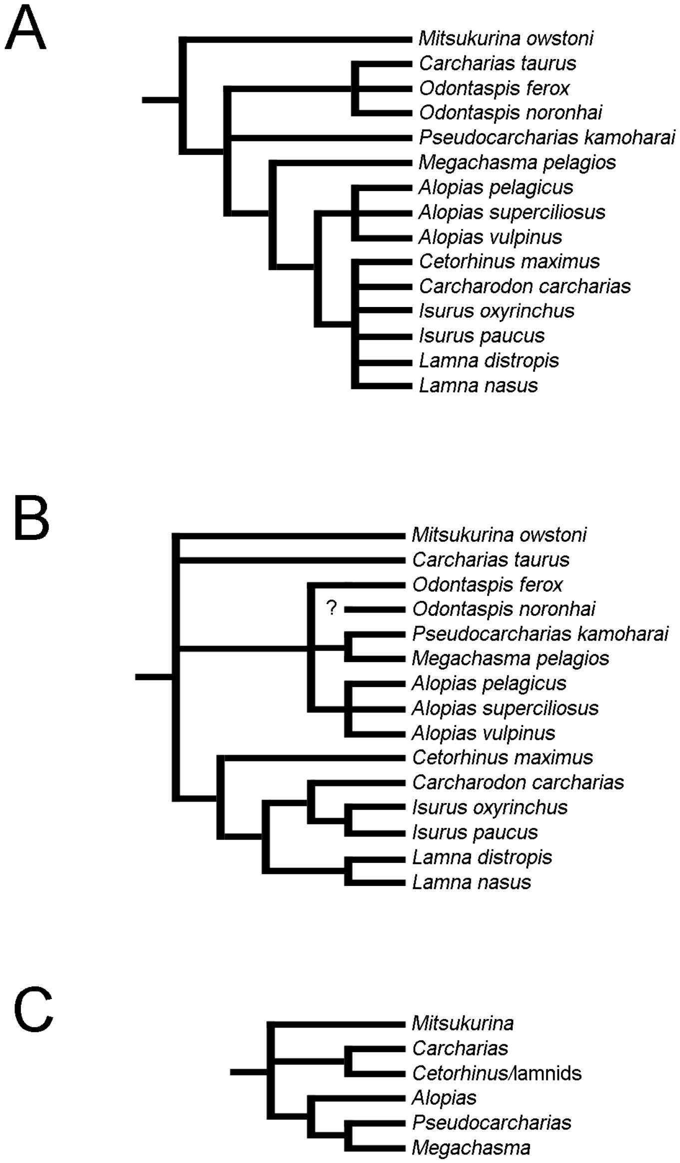

Figure 1.10. Phylogenetic relationships of extant lamniform species based on morphological data by (A) Shirai (1996) and molecular data by (B) Naylor et al. (1997, based on NADH-2 and cytochrome b mitochondrial genes) and (C) Maisey et al. (2004, based on RAG-1 nuclear gene).

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CHAPTER 2

A middle Cenomanian euselachian assemblage from the Dunvegan Formation of northwestern Alberta, Canada

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INTRODUCTION

An assemblage of euselachian remains of Cenomanian (early Late Cretaceous) age was recovered from the Dunvegan Formation of northwestern Alberta (Fig. 2.1). The assemblage not only provides records of taxa that extend their geographical ranges, but also sheds light on euselachian diversity in this under-sampled region of the Western Interior Seaway (WIS). In contrast to the well-prospected southern localities, the northern portion of this epicontinental seaway has received less attention (Fielitz, 1996). Examination of northern localities is essential to understanding the paleoenvironments and faunal composition of Cenomanian vertebrate faunas within the seaway as a whole. The purpose of this study is, therefore, to complement the large body of euselachian studies that detail southern seaway assemblages by providing a comparison with a northern assemblage. With the present treatment, the Dunvegan assemblage becomes the highest-paleolatitude euselachian assemblage yet described from the WIS.

GEOLOGICAL SETTING

The euselachian assemblage reported here was recovered near Dunvegan, Alberta and comes from the middle Cenomanian Dunvegan Formation. The specimens were collected from a cluster of localities located along the northern bank of the Peace River and designated DWK1–6 and DBS1–2. The Dunvegan localities are situated at 55°55′ N, 118° 35′ W (Fig. 2.2).

The Dunvegan Formation (Fig. 2.3) is believed to be a deltaic complex that advanced into the seaway from the western side in a southeasterly direction (Stott, 1982; Bhattacharya and Walker, 1991; Plint, 2000; Hay et al., 2007). It overlies the Shaftesbury Formation and is overlain by the Kaskapau Formation (Bhattacharya and Walker, 1991; Plint, 2000). Lithologically, it consists of interbedded mudstone, sandstone, and conglomerate, with a thickness reaching 350 m (Bhattacharya and Walker, 1991). It grades eastward into the marine shale of the Bell Fourche Formation (Bloch et al., 1993; Plint, 2000; Hay et al., 2007). It correlates with the Bell Fourche Shale in the Black Hills (Cumbaa et al., 2006) of South Dakota, USA which is assigned to the *Verneuilinoides perplexus* foraminiferal zone (Caldwell et al., 1978; Stott, 1982; Singh, 1983; Bhattacharya and Walker, 1991) and the *Acanthoceras athabascense* ammonite zone (Jeletzky, 1968; Bhattacharya and Walker, 1991).

The Dunvegan deposits formed in relatively cool and low-salinity waters of Arctic origin (Hay et al., 1993; Hay et al., 2007). Kauffman (1984) proposed a paleobiogeographic division of the Seaway based on invertebrate faunas. Alberta would have been situated in the cool temperate climatic zone during the Cenomanian (Kauffman 1984). This region extended from the Circum-Boreal Sea to the southern borders of Montana, Idaho, and North Dakota. Planktic foraminiferal porosity analyses also places the province within the coolest water masses during this stage (Fisher, 2003).

METHODS

The specimens reported here were surface collected in the early 1970s and early 1980s by teams from the University of Alberta. Teeth were mechanically prepared using pneumatic drills and were subsequently immersed in an acetic acid solution to dissolve cement holding any remnants of sandstone matrix. Any fractures were repaired using an adhesive. The resulting teeth were imaged using a Jeol Field Emission Scanning Electron Microscope (JSM-6301 FXV). The material is catalogued in the collections of the University of Alberta Laboratory for Vertebrate Paleontology (UALVP).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Zangerl, 1981

Family Hybodontidae Owen, 1845

Genus *Meristodonoides* Underwood and Cumbaa, 2010

Type species—*Hybodus rajkovichi* Case, 2001 from the Cenomanian of Minnesota, USA.

Meristodonoides cf. *rajkovichi* (Case, 2001)

(Fig. 2.4A)

1993 *Hybodus* sp.; Williamson et al., p. 448, fig. 3.1.

1999 *Hybodus* sp. 1; Cappetta and Case, p. 8, pl. 1, figs 1, 2.

1999 *Hybodus* sp.; Cumbaa and Tokaryk, p. 61, fig. 5 (left 2 columns).

2001 *Hybodus rajkovichi* Case; p. 105, pl. 1, fig. 5, pl. 2, figs. 1, 2.

2001b *Hybodus* sp.; Cicimurri, p. 182, fig. 5a.

2006 *Hybodus* sp.; Cumbaa et al., p. 142, fig. 4.1.

2010 *Meristodonoides rajkovichi* (Case, 2001); Underwood and Cumbaa, p. 908, pl. 1, figs. 3–18.

Referred material—UALVP 49406, fractured tooth, locality DWK 1; UALVP 49407, 4 fractured teeth, locality DWK 1; UALVP 49413, fractured tooth, locality DWK 3; UALVP 49427, fractured tooth, locality DBS 2.

Description—UALVP 49406 preserves a tall, broad median cusp that is slightly labiolingually compressed. There is minimal damage to the apical region. The lingual and labial faces of the median cusp bear numerous, weak, widely spaced, enameloid folds. The labial folds are restricted to the lower ¼ of the cusp, whereas the lingual folds extend approximately ¾ the height of the median cusp. A cutting edge is present along the entire cusp and is directed lingually as it approaches the apex. The remainder of the crown is missing and the root has been fractured and lost. The teeth assigned to UALVP 49407, 49413, and 49427 conform to this general description.

Remarks—Underwood and Cumbaa (2010) recently reassigned a number of *Hybodus* species to their newly erected genus *Meristodonoides.* The involved North America taxa include *Meristodonoides rajkovichi*, *M. butleri*, *M. montanensis,* and *M. novojerseyensis.* The tooth morphology of these species differ from *Hybodus reticulatus* and "similar forms" by having "a single well-developed cusp, very low root and, for some species, lack of a labial boss" (Underwood and Cumbaa, 2010: p. 906). The tooth morphology of *Meristodonoides* can also be distinguished from *Planohybodus*, the latter being significantly more labiolingually compressed, having a more developed cutting edge, and a root with a more strongly excavated labial face (Underwood and Cumbaa, 2010).

Despite the incomplete nature of the *Meristodonoides* teeth recovered from the Dunvegan localities, the cusp morphology is most similar to the *M. rajkovichi* type material recovered from the late Cenomanian Coleraine Formation of Minnesota, USA (Case, 2001). Teeth from both assemblages have a slightly labiolingually compressed median cusp that is somewhat lingually directed, possess a complete cutting edge, and have weak labial enameloid folds that are restricted to the lower ¼ of the cusp. Unlike the *M. rajkovichi* type material, the Dunvegan specimens have lingual enameloid folds that are slightly more elongated. Numerous *M. rajkovichi* teeth reported by Underwood and Cumbaa (2010) from the Bainbridge bonebed of the Belle Fourche Member of the Ashville Formation in east-central Saskatchewan also bear lingual folds of various length, many of which are equally elongated. Consequently, the difference in the lingually ornamentation is likely attributed to intraspecific variation (Underwood and Cumbaa, 2010).

The teeth of *Meristodonoides butleri*, originally reported from the Aptian-Albian of Texas by Thurmond (1971), differ from *M. rajkovichi* by possessing a shorter medial cusp with stronger crown ornamentation (Underwood and Cumbaa, 2010). *Meristodonoides montanensis*, originally reported from the Campanian Judith River Formation of Montana by Case (1978), has also been reported from the upper Campanian of Dinosaur Provincial Park in Alberta (Beavan and Russell, 1999, as *H. montanensis*). The teeth of this species differs from *M. rajkovichi* in being significantly larger and bearing enameloid folds that extend only ¼ the height of the medial cusp on both the labial and lingual face (Case, 1978). The teeth of *M. novojerseyensis*, originally described from the early Maastrichtian of New Jersey by Case and Cappetta (2004), have weaker crown enameloid folding which is missing altogether in the medial region on the labial face of the median cusp.

Until additional and better preserved teeth are recovered from the Dunvegan localities, we cautiously assign these teeth to *Meristodonoides* cf. *rajkovichi*. It is certain, however, that the teeth of *Meristodonoides* are a rare element in the Dunvegan assemblage. This is in stark contrast to the thousands of *Meristodonoides* teeth reported from the contemporaneous northern Bainbridge assemblage (Cumbaa et al., 2006; Underwood and Cumbaa, 2010).

Order Lamniformes Berg, 1958

Family Anacoracidae Casier, 1947

Genus *Squalicorax* Whitley, 1939

Type species—*Corax pristodontus* Agassiz, 1843 from the Maastrichtian of the Netherlands.

Squalicorax sp. A

(Fig. 2.4B)

1900 *Corax curvatus* Williston, p. 253, pl. 30, figs. 7, 8.

1974 *Squalicorax curvatus* (Williston, 1900); Meyer, p. 298, fig. 89.

1974 *Squalicorax baharijensis* Agassiz, 1843); Slaughter and Thurmond, p. 32, fig. 2a, b.

1990 *Squalicorax falcatus* (Agassiz, 1843); Case et al., p. 1088, fig. 10a–p, p. 1092, fig. 11a, b.

1993 *Squalicorax curvatus* (Williston, 1900); Welton and Farish, p. 116, figs. 3, 4.

1993 *Squalicorax falcatus* (Agassiz, 1843); Williamson et al., p. 457, fig. 7.4, 7.5.

1999 *Squalicorax curvatus* (Williston, 1900); Cappetta and Case, p. 13, pl. 7, figs. 6–8.

1999 *Squalicorax falcatus* (Agassiz, 1843); Cappetta and Case, p. 13, pl. 5, figs. 10–12, pl. 6, figs. 1–3.

1999 *Squalicorax* sp. (group *falcatus*); Cappetta and Case, p. 14, pl. 6, figs. 4–9.

1999 *Squalicorax* sp.; Cumbaa and Tokaryk, p. 61, fig. 5 (right 2 columns).

2001a *Squalicorax curvatus* (Williston, 1900); Cicimurri, p. 32, fig. 7a.

2001a *Squalicorax falcatus* (Agassiz, 1843); Cicimurri, p. 32, fig. 7b.

2001b *Squalicorax* sp. cf. *S. curvatus* (Williston, 1900); Cicimurri, p. 186, fig. 5g.

2002 *Squalicorax* sp. 2; Antunes and Cappetta, p. 120, pl. 7, figs. 13, 14.

2004 *Squalicorax falcatus* (Agassiz, 1843); Cicimurri, p. 9, fig. 5c.

2006 *Squalicorax curvatus* (Williston, 1900); Cumbaa et al., p. 143, fig. 4.8.

2006 *Squalicorax falcatus* (Agassiz, 1843); Cumbaa et al., p. 143, fig. 4.9.

2006 *Squalicorax curvatus* (Williston, 1900); Shimada et al., p. 8, fig. 8.2–8.4.

2006 *Squalicorax falcatus* (Agassiz, 1843); Shimada et al., p. 10, fig. 8.5–8.9.

2006 *Squalicorax* sp.; Shimada et al., p. 11, fig. 8.10–8.14.

2008 *Squalicorax curvatus* (Williston, 1900); Shimada and Martin, p. 91, fig. 5a.

2008 *Squalicorax falcatus* (Agassiz, 1843); Shimada and Martin, p. 91, fig. 5b.

2008 *Squalicorax* sp.; Shimada and Martin, p. 91, fig. 5c, d.

2010 *Squalicorax* sp.; Becker et al. p. 260, fig. 6.5–6.7.

2010 *Squalicorax curvatus* (Williston, 1900); Underwood and Cumbaa, p. 928, pl. 7, figs. 1–23, pl. 8, fig. 2.

Referred material—UALVP 49408, tooth, locality DWK 1.

Description—This specimen has a crown that is high and distally inclined. The lingual crown face is strongly convex, whereas the labial face is only slightly convex. The slightly convex mesial cutting edge is damaged. The undamaged area of this cutting edge is finely serrated and forms a sharply angled apex with the distal cutting edge. The distal cutting edge is also convex and finely serrated but is shorter than the mesial cutting edge. A finely serrated, low, distal heel intersects the distal cutting edge forming a distinct notch. The lingual neck is wide. A distinct basal edge is present at the labial crown foot. The root contains a very weak lingual protuberance and lacks a nutrient groove. The distal root lobe is slightly more robust than the mesial root lobe. The basal concavity is shallow.

Remarks—The reported temporal range of *Squalicorax* extends from the late Albian to the late Maastrichtian and the genus has been found in localities in Europe, Russia, North and South America, Africa, India, Japan and Australia (Cappetta, 1987). In Canada, *Squalicorax falcatus* has been described by Case et al. (1990) from the Coniacian of east-central Saskatchewan. The age of the selachian assemblage from which the specimens were recovered has been revised and is now believed to be early Turonian in age (Cumbaa and Tokaryk, 1999; Cumbaa et al., 2006; Cumbaa et al., 2010). In addition to *S. falcatus*, Cumbaa et al. (2006) reported *S. curvatus* and *S. volgensis* from the middle Cenomanian Bainbridge and Carrot River bonebeds of Saskatchewan. Underwood and Cumbaa (2010) also reported numerous *Squalicorax curvatus* teeth from the Bainbridge locality.

The overall tooth morphology of the specimen herein bears similarities to many of the teeth described as *Squalicorax falcatus* by Case et al. (1990: fig. 10a, b, and g) from Saskatchewan. Both the Dunvegan and Saskatchewan teeth have a moderately erect crown with finely serrated cutting edges, a low distal heel that forms a distinct notch with the distal cutting edge, a broad lingual neck, and a relatively deep basal concavity between the root lobes. Unfortunately, only the lingual surface was figured by Case et al. (1990) and the similarities in labial features cannot be assessed at this time. According to Siverson et al. (2007), *S. falcatus* is among the most commonly cited anacoracids from North American deposits. However, the tooth description of this species by many North American authors does not agree with the lectotype from the Turonian chalks of England. Siverson et al. (2007: text–fig. 5) recently illustrated the lectotype of *S. falcatus*. Unlike UALVP 49048, the lectotype of *S. falcatus* does not bear a distinct notch or a deep basal concavity between the root lobes. The labial crown face of the lectotype also differs from the Dunvegan specimen by having a flat labial crown face and lacks a distinct basal ledge.

UALVP 49048 most closely resembles *Squalicorax curvatus* teeth described by Williston (1900, as *Corax curvatus*). Williston (1900: p. 253) noted in his original description that the teeth of this species "while not differing much in outline from certain ones referred to *C. falcatus* [*S. falcatus*], show a marked variance in structure." Williston's original illustration (1900: pl. 30, figs. 7, 8) shows that the teeth bear a distinct notch, a well-developed basal ledge, a relatively deep basal concavity between the root lobes and a root that is as high as the crown in lingual view. UALVP 49048 exhibits all of the aforementioned characters. He also noted that the labial crown face is more convex than that of *S. falcatus*, a feature also shared by the Dunvegan specimen. According to Williston (1900: p. 253), the tooth morphology of *S. curvatus* can be differentiated from other anacoracids by the oblique angle formed by the labial crown and root "so that when resting upon a plane the tooth forms a high arch, touching only by the extreme tips of the roots and crown." When viewed in profile, the labial surface of UALVP 49048 does exhibit a slight concavity. Siverson et al. (2007) noted, however, that this condition is not restricted to this species and can be found in other time-equivalent anacoracids and in the upper lateroposterior teeth of extant macrophagous lamniforms. Given that the species description was based on only two syntypes, Siverson et al. (2007) questioned the validity of *S. curvatus* and regarded it as *nomen dubium* until a reassessment involving the re-examination of the type material and the recovery of additional topotypic teeth can be made. It has also been reported that previous descriptions of *S. curvatus* may actually represent *S. baharijensis* (Cappetta and Case, 1999; Siverson et al., 2007). As a result of this taxonomic uncertainty, UALPV 49048 is conservatively placed in open nomenclature; however, it is noted that this specimen has a morphology very similar to the tooth described as *Squalicorax curvatus* by Underwood and Cumbaa (2010: pl. 7, figs. 5, 6) from the Bainbridge bonebed of Saskatchewan.

Family Archaeolamnidae Underwood and Cumbaa, 2010

Genus *Archaeolamna* Siverson, 1992

Type species—*Odontaspis kopingensis* Davis, 1890 from the Campanian of Sweden.

Archaeolamna ex. gr. *kopingensis* (Davis, 1890)

(Fig. 2.4C)

1890 *Odontaspis kopingensis* Davis, p. 390–391, pl. 38, figs. 27, 28.

1894 *Lamna arcuata* Woodward, p. 198, pl. 6, figs. 11, 12.

1912 *Lamna arcuata* Woodward, 1894; Woodward, p. 208, pl. 44, figs. 8, 9.

1975a *Plicatolamna arcuata* (Woodward, 1894); Cappetta and Case, p. 23, pl. 4, figs. 1–18.

1977 *Plicatolamna arcuata* (Woodward, 1894); Herman, p. 203–205, pl. 8, fig. 4a–j.

1978 *Plicatolamna arcuata* (Woodward, 1894); Case, p. 191, pl. 4, figs. 5a, b, 6a, b.

1985 *Plicatolamna arcuata* (Woodward, 1894); Wolberg, p. 4, fig. 3h, i.

1986 *Plicatolamna arcuata* (Woodward, 1894); Lauginiger, pl. 1, figs. 15, 17.

1987 *Plicatolamna arcuata* (Woodward, 1894); Case, p. 10, pl. 3, figs. 6–13.

1990 *Cretodus* sp.; Case et al., p. 1087, fig. 7a, b.

1991 *Cretolamna* ? *arcuata* Woodward, 1894; Müller and Diedrich, p. 32, pl. 7, fig. 6, pl. 8, figs. 1–3.

1992 *Archaeolamna kopingensis* (Davis, 1890); Siverson, p. 531–534, pl. 2, figs. 1–20.

1993 *Archaeolamna kopingensis* (Davis, 1890); Biddle, p. 206, pl. 4, figs. 1–4.

1996 *Archaeolamna* aff. *kopingensis* (Davis, 1890); Siverson, p. 825, pl. 2, figs. 1–6.

1997 *Archaeolamna* sp.; Siverson p. 462, fig. 4a–h.

2000 *Archaeolamna kopingensis* (Davis, 1890); Becker et al., fig. 6d.

2001 *Cenocarcharias tenuiplicatus* (Cappetta and Case, 1999); Case, pl. 2, figs. 4, 6.

2006 *Archaeolamna* sp.; Cumbaa et al., p. 143, fig. 4.10.

2006 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Cumbaa et al., p. 146, fig. 4.11.

2006 *Archaeolamna cf. A. kopingensis* (Davis, 1890); Shimada et al. p. 15, fig. 10.1.

2007 *Archaeolamna* sp.; Vullo et al., p. 104, fig. 2c.

2008 *Archaeolamna* cf. *A. kopingensis* (Davis, 1890); Shimada and Martin, p. 94, fig. 6h.

Referred material—UALVP 49412, tooth, locality DWK 2.

Description—UALVP 49412 bears a tall, broad-based triangular cusp. Both the mesial and distal cutting edges are complete. The crown is thick, with a smooth, strongly convex lingual face. The smooth labial face is slightly convex. A pair of lateral cusplets has been fractured and is missing. The root contains a well-developed lingual protuberance that lacks a nutrient groove. The robust root lobes are separated by a U-shaped basal concavity.

Remarks—Teeth allocated to *Archaeolamna kopingensis* from various Albian-Maastrichtian deposits are of variable morphology, thus this taxon most likely represents a group of closely related taxa rather than a single species. Teeth from Albian-Turonian deposits are smaller in all dimensions compared to those from younger deposits and often have a well-developed nutrient groove. Siverson (1992) proposed that the type species *A. kopingensis* consisted of two geographically separated subspecies: *A. kopingensis kopingensis* from the Campanian-Maastrichtian of the Anglo-Franco-Belgian Basin and Sweden; and *A. kopingensis judithensis* from the Campanian of Alberta, Montana, and Wyoming (Case, 1978, 1987; Siverson, 1992, 1996; Beavan and Russell, 1999). Siverson (1992: p. 534) reported the latter subspecies as "having broader, less elongated and more labio-lingually compressed cusps." He also noted that the "root is slightly more massive with shorter branches and a lower lingual protuberance" in *A. kopingensis judithensis.*

The teeth of *Archaeolamna* have been recovered from a number of WIS localities. Shimada et al. (2006) reported numerous specimens of *Archaeolamna* cf. *A*. *kopingensis* from the middle Cenomanian of Colorado. Case et al. (1990) described teeth of *Cretodus* sp. from Saskatchewan, which Siverson (1992: p. 530) reported to be "quite similar to those of *A*. *kopingensis*" despite slight differences in tooth morphology. Siverson (1992) noted that the Saskatchewan material had a higher root, a rectilinear mesial cutting edge, and lateral tooth cusplet with outer edges that converge apically. The posterior teeth of the Saskatchewan species also differ from those of *A. kopingensis* by lacking strong vertical enameloid folds. Cumbaa et al. (2006: p. 143) reportedteeth from the middle Cenomanian of Saskatchewan that "appear almost indistinguishable" from the teeth reported by Case et al. (1990). UALVP 49412 shares a similar general morphology to lower lateral teeth figured by Underwood and Cumbaa (2010: text-fig. 4, fig. j, k). The Dunvegan specimen also shows a striking resemblance to *Archaeolamna* aff. *kopingensis* figured by Siverson (1996: pl. 2, figs. 1, 2) from the Thirindine Point ridge of Western Australia. However, UALVP 49412 is conservatively placed in open nomenclature until better preserved teeth are recovered from the Dunvegan localities.

Family Cretoxyrhinidae

Genus *Cretoxyrhina* Glickman, 1958

Type species—*Oxyrhina mantelli* Agassiz, 1843 from the Late Cretaceous of England.

Cretoxyrhina sp.

(Fig. 2.4D)

Referred material—UALVP 49429, tooth, locality DWK 4.

Description—UALVP 49429 has been extensively damaged and consists only of a mesiodistally wide and distally inclined median cusp. Both faces are smooth. A distinct cutting edge runs the entire length of the cusp.

Remarks—The overall cusp morphology resembles a lateral tooth of *Cretoxyrhina*. However, it is recognized that UALVP 49429 is severely damage, making a specific diagnosis difficult. We therefore keep this tooth in open nomenclature.

According to Welton and Farish (1993), the lateral teeth of *Cretoxyrhina* have a crown that contains a large, broad-based median cusp that is distally inclined. The anterior teeth lack lateral cusplets, whereas lateral cusplets may be present on the lateral teeth. The labial and lingual faces are always smooth and contain a cutting edge that is continuous from the apex to the crown foot. A well-developed lingual neck is always present. The bilobate root contains a well-developed lingual protuberance and a central lingual foramen but lacks a nutrient groove. The teeth of *Cretoxyrhina* can be large, up to about 63 mm in crown height (Welton and Farish, 1993). Based on the small cusp dimensions, UALVP 49429 may represent a juvenile or sub-adult form. However, it should be noted that *Cretoxyrhina* teeth recovered from Cenomanian-Turonian deposits are significantly smaller than the teeth recovered from Coniacian-Santonian deposits (Shimada, 1997, Siverson and Lindgren, 2005).

Cretoxyrhina was wide ranging and has been found in various localities throughout Europe (Cappetta, 1987; Siverson, 1996), Madagascar (Cappetta, 1987), and Australia (Siverson, 1996). The teeth of *Cretoxyrhina* have been reported from the North American deposits including the Cenomanian through Coniacian of Texas (Welton and Farish, 1993), the late Cenomanian of Arizona (Williamson et al., 1993), the middle Cenomanian of Colorado (Shimada et al., 2006), the late Cenomanian of Kansas (Shimada and Martin, 2008), and the middle Cenomanian-middle Turonian of South Dakota and Wyoming (Cicimurri, 2001a, 2001b, 2004). In Canada, the teeth of *Cretoxyrhina mantelli* were reported from the early Turonian of Saskatchewan (Case, 1990); whereas *C. denticulata* was recovered from middle Cenomanian deposits of that province (Cumbaa et al., 2006, as *C. mantelli*; Underwood and Cumbaa, 2010).

Family Eoptolamnidae Kriwet, Klug, Canudo, and Cuenca-Bescos, 2008

Genus *Protolamna* Cappetta, 1980b

Type specimen—*Protolamna sokolovi* Cappetta, 1980b from the upper Aptian of France.

Protolamna carteri Cappetta and Case, 1999

(Fig. 2.5A)

1999 *Protolamna carteri*, p. 25, pl. 12, figs. 3–5.

Referred material—UALVP 49419, tooth, locality DWK 5.

Description—UALVP 49419 contains a short, tapering median cusp that is slightly distally inclined and lingually directed. The slightly convex labial face is smooth, whereas the strongly convex lingual face has striations that extend to the apex of the cusp. A complete cutting edge runs the entire length of the median cusp. The root contains a massive lingual protuberance with a well-developed nutrient groove placed high on the root. The lateral cusplets and the root lobes have been fractured and are missing.

Remarks—In the original description of *Protolamna carteri*, Cappetta and Case (1999) reported the presence of a pair of divergent needle-like lateral cusplets and a robust root that contained lobes that were long and parallel. In addition, there are several irregular foramina that are located in the medial labial region of the root just below crown-root border. Unfortunately, extensive damage to UALVP 49419 prevents observation and confirmation of these characters.

The massive lingual protuberance of *Protolamna carteri* is reminiscent of that of *Johnlongia parvidens*; however, the median cusp of *P. carteri* is shorter and significantly more robust, bears distinct lingual enameloid folds, and contains cutting edges that extend the entire length.

This species differs from other species of *Protolamna* through variation in cusp and root morphology. The teeth of *P. carteri* can be distinguished from the closely related species *P. roanokeensis* by its smaller size and having a larger lingual protuberance with a distinct groove. The nutrient groove is also absent in the latter (Cappetta and Case, 1999). As well, *P. carteri* has a lingual crown surface with lingual folds that are more numerous but protrude less. The anterior teeth are also much more narrowed mesiodistally than those of *P. roanokeensis*. The tooth morphology of *P. carteri* is also similar to the teeth described by Müller and Diedrich (1991) as *P. acuta* from the Cenomanian of Germany. According to Cappetta and Case (1999) the teeth of the latter possess lateral cusplets that are thinner and relatively higher than those of *P. carteri*. The median cusp of *P. acuta* is also narrower and lacks the lingual striations characteristic of *P. carteri*.

The geographic distribution of *P. carteri* is poorly known. Cappetta and Case (1999) reported the only other occurrence of this species from the late Cenomanian Woodbine Formation of Texas. The age of the locality from which this species was recovered has been recently revised and is now believed to be middle Cenomanian in age (Hancock, 2004; Siverson et al., 2007).

Family Odontaspididae Müller and Henle, 1839

Genus *Johnlongia* Siverson, 1996

Type species—*Johnlongia allocotodon* Siverson, 1996 from the Cenomanian of Western Australia (revised stratigraphy indicates Cenomanian-Turonian boundary in Siverson, 2007).

Johnlongia parvidens (Cappetta, 1973)

(Fig. 2.5B)

1973 *Odontaspis parvidens* Cappetta p. 507, p1. 3, figs. 1–7.

2001a *Johnlongia parvidens* (Cappetta, 1973); Cicimurri, p. 32, fig. 7u–w.

2004 *Johnlongia parvidens* (Cappetta, 1973); Cicimurri, p. 10, fig. 5i.

2004 *Johnlongia parvidens* (Cappetta, 1973); Shimada et al., p. 131, fig. 1.

2006 *Johnlongia* cf. *J. parvidens* (Cappetta, 1973); Shimada et al., p. 13, fig. 9.7.

Referred material—UALVP 49421, tooth, locality DWK 7.

Description—UALVP 49421 has a tall and slender median cusp that is slightly distally inclined, sigmoid in profile, and lingually directed. Both mesial and distal cutting edges are restricted to the apical third of the cusp. The labial face is convex and smooth. The lingual face is strongly convex and is also smooth. Flanking the median cusp is a needle-like mesial lateral cusplet. The distal lateral cusplet has been fractured and is missing. A lingual neck separates the cusp from the root. The root is asymmetrical and has an elongated mesial root lobe that is missing a portion of the distal part. The distal lobe is complete and is significantly shorter. The root has a massive lingual protuberance bisected by a deep nutrient groove. Numerous foramina are distributed throughout the lingual protuberance. A V-shaped basal concavity is apparent.

Remarks—*Odontaspis parvidens* was first described by Cappetta (1973). Later, Siverson (1996) erected *Johnlongia* and considered it to accommodate the teeth of this species. This was based on the frequent absence of the distal lateral cusplet and apical restriction of the cutting edges in adult anterior teeth of this species, compared to other species of *Odontaspis* which normally have the distal lateral cusplet and continuous cutting edges. The massive lingual protuberance is also unique to this genus, separating it from other odontaspids (Siverson, 1996). UALVP 49421 is identified as a lateral tooth based on the slightly distally inclined narrow cusp and asymmetrical root lobes.

Johnlongia has been described from localities in both hemispheres. Within North America, this taxon has been reported from the middle Cenomanian of Colorado (Shimada et al., 2006), and the Turonian in South Dakota (Cappetta, 1973; Cicimurri, 2001a, 2004). Shimada et al. (2004) described the youngest occurrence of *Johnlongia* from the upper Coniacian of the Niobrara Chalk in western Kansas.

Siverson (1996) reported *Johnlongia allocotodon* from the early and/or middle Cenomanian of Western Australia. According to Siverson et al. (2007), the age of the selachian assemblage from which this species was recovered has been revised and is now believed to be closer in age to the Cenomanian-Turonian boundary. This species was established on three characters distinguishing it from Cappetta's (1973) original description of *J. parvidens.* The first, according to

Siverson (1996), is that all anterior teeth of *J. allocotodon* have a distal cutting edge that is restricted to the apical third of the median cusp. This is in contrast to the anterior teeth of *J. parvidens,* which have a distal cutting edge that is “missing or localized in [the] region of [the] tooth tip” (Cappetta, 1973: p. 507). Cicimurri (2001a) also reported the presence of a distal cutting edge on the anterior teeth of *J. parvidens.* However, the length of the cutting edge was not specified. Although the observed variation in distal cutting edge length may exemplify a transitional state from its unvarying presence in *J. allocotodon* to a reduced or complete absence in *J. parvidens*, the significance of such a character in erecting a new species is questionable. The tooth recovered from Dunvegan locality DBS2 has the distal cutting edge restricted to the upper third of the median cusp.

The second character is the presence of labial enameloid folding at the crown base of the lateral teeth of *J. allocotodon* (Siverson, 1996). According to Cappetta (1973: p. 507) “there may be some short spaced striae at [the] base on inner face of [the] crown” on the lateral teeth of *J. parvidens*. However, there is no mention of enameloid folding on the labial (outer) face in his original description. Cicimurri (2001a), in a description of the labial face of *J. parvidens* from the Turonian of South Dakota, reported the presence of “longitudinal ridges that are restricted to the lower half of the cusp.” Thus, this character is not exclusive to *J. allocotodon* and its diagnostic value should be questioned.

According to Siverson (1996) the final character that differentiates these species is a difference in tooth height. Cappetta (1973) reported that the teeth of *J. parvidens* do not exceed 6 mm in height. Siverson (1996) stated that the largest tooth of *J. allocotodon* recovered was 2.5 mm taller than the largest tooth of *J. parvidens* described by Cappetta (1973). Again, the merit of this character is debatable. The tooth of *J. parvidens* recovered from Dunvegan locality DBS2 is 8 mm in height. Based strictly on the considerable geographical distances among the localities from which these teeth have been recovered, the possibility of two species within the genus *Johnlongia* is not unreasonable. However, a careful morphological re-examination of Cappetta's (1973) type series may reveal that *J. allocotodon* and *J. parvidens* are indeed synonymous. Until this issue is resolved, the Dunvegan tooth is identified provisionally as *J. parvidens*, in agreement with other North American specimens with similar morphology.

UALVP 49421 represents the first occurrence of the genus *Johnlongia* in Canada.

Family Incertae sedis

Genus *Cretodus* Sokolov, 1965

Type species—*Otodus sulcatus* Geinitz, 1843 from the Coniacian of the Czech Republic.

Cretodus semiplicatus (Münster in Agassiz, 1843)

(Fig. 2.5C)

1843 *Otodus semiplicatus* Münster in Agassiz, p. 272, pl. 36, fig. 32.

1843 *Otodus sulcatus* Geinitz, p. 5, pl. 4, fig. 2.

1845 *Otodus semiplicatus* Münster in Agassiz, 1843; Reuss, p. 5, pl. 3, figs. 20, 21.

1846 *Otodus sulcatus* Geinitz, 1843; Reuss, p. 100, pl. 21, fig. 41.

1856 *Otodus sulcatus* Geinitz, 1843; Fischer, p. 141, pl. 2, fig. 41.

1872 *Otodus semiplicatus* Münster in Agassiz, 1843; Sauvage, p. 26, pl. 16, figs. 25, 26.

1872 *Otodus sulcatus* Geinitz, 1843; Sauvage, p. 29, pl. 17, figs. 60–69.

1873 *Otodus divaricatus* Leidy, p. 305, pl. 18, figs. 26–28.

1875 *Otodus semiplicatus* Münster in Agassiz, 1843; Geinitz, p. 109, pl. 38, figs. 55–60.

1875 *Otodus sulcatus* Geinitz, 1843; Geinitz, p. 294, pl. 65, figs. 4, 5.

1878 *Otodus semiplicatus* Münster in Agassiz, 1843; Fritsch, p. 7, fig. 10.

1888 *Otodus crassus* Woodward, p. 292.

1888 *Otodus semiplicatus* Münster in Agassiz, 1843; Woodward, p. 292.

1889 *Lamna semiplicata* (Münster in Agassiz, 1843). Woodward, 1889, p. 397.

1889 *Lamna sulcata* (Geinitz, 1843); Woodward, p. 398.

1894 *Lamna semiplicata* (Münster in Agassiz, 1843); Woodward, p. 197, pl. 9, figs. 3, 4.

1894 *Lamna sulcata* (Geinitz, 1843); Woodward, p. 197.

1900 *Scylliorhinus rugosus* Williston, p. 244, pl. 24, fig. 5.

1902 *Otodus semiplicatus* Münster in Agassiz, 1843; Leriche, p. 114, pl. 3, fig. 48.

1902 *Otodus sulcatus* Geinitz, 1843; Leriche, p. 115, pl. 3, fig. 47

1903 *Otodus sulcatus* Geinitz, 1843; Hay, p. 397, pl. 26, figs. 3, 4.

1906 *Otodus semiplicatus* Münster in Agassiz, 1843; Leriche, p. 62.

1911 *Lamna semiplicata* (Münster in Agassiz, 1843); Woodward, p. 208, pl. 44, figs. 10, 11.

1911 *Lamna sulcata* (Geinitz, 1843); Woodward, p. 209, pl. 44, figs. 12, 13.

1929 *Lamna semiplicata* (Münster in Agassiz, 1843); Leriche, p. 248.

1936 *Lamna semiplicata* (Münster in Agassiz, 1843); Leriche, p. 380, pl. 26, figs. 1–4.

1974 *Lamna sulcata* (Geinitz, 1843); Slaughter and Thurmond, p. 31, fig. 2h, i.

1977 *Plicatolamna semiplicata* (Münster in Agassiz, 1843); Herman, p. 197, pl. 8, fig. 1.

1980a *Plicatolamna semiplicata* (Münster in Agassiz, 1843); Cappetta, p. 97, pl. 7, fig. 3.

1985 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Wolberg, p. 4, fig. 3, f, g, i.

1987 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Cappetta, p. 98, fig. 86.

1989 *Cretodus longiplicatus* Werner, p. 33, fig. 12; p. 33, fig. 13.

1991 *Cretodus* aff. *semiplicatus* (Münster in Agassiz, 1843); Müller and Diedrich, p. 33, text-fig. 5.1, 5.2.

1993 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Welton and Farish, p. 100, figs. 1–5.

1993 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Williamson et al., p. 453, fig. 5.6–5.11.

1999 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Cappetta and Case, p. 21, text-fig. 3a–c; p. 22, text-fig. 4a–d, pl. 14, figs. 1–4.

2001 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Case, 2001, p. 108, pl. 2, fig. 8.

2001a *Cretodus semiplicatus* (Münster in Agassiz, 1843); Cicimurri, p. 34, fig. 7f, g.

2001b *Cretodus semiplicatus* (Münster in Agassiz, 1843); Cicimurri, p. 187, fig. 5i.

2002 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Antunes and Cappetta, p. 125, pl. 10, figs. 4–6.

2006 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Shimada et al., p. 14, figs. 10.3–10.4.

2008 *Cretodus semiplicatus* (Münster in Agassiz, 1843); Shimada and Martin, p. 94, fig. 6i.

2011 *Cretodus longiplicatus* Werner, 1989; Underwood et al., p. 548, fig. 8a–f.

Referred material—UALVP 49415, tooth, locality DWK 4; UALVP 49416, tooth, locality DWK 4; UALVP 49425, 2 teeth, locality DBS 2.

Description—UALVP 49415 contains a tall, triangular median cusp with convex labial and lingual faces. There are two mesial, triangular lateral cusplets that are divergent and contain a cutting edge that is continuous with the median cusp. The distal cusplets have been fractured and are missing. Strong vertical enameloid folds are present on the basal half of both faces of the median cusp and extend to the apex on the mesial lateral cusplets. The root is heavily damaged and the lingual protuberance appears to lack a nutrient groove. The other teeth listed also conform to this description, but are less well preserved.

Remarks—According to Cappetta and Case (1999) teeth from juvenile *Cretodus semiplicatus* are of small size, with a relatively short, triangular median cusp. Anterior and lateral teeth may possess lateral cusplets that are distinctly split, forming two cusplets per side. Juveniles also have more prominent lingual folds that extend higher up the cusp. The specimen herein is likely an anterior juvenile tooth because it possesses these characters. Welton and Farish (1993) report the maximum tooth size of *C. semiplicatus* as 41 mm. UALVP 49415 is significantly smaller, further support the notion that this tooth was from an immature individual.

Cappetta (1987) reported this species from Europe, the Middle East and North America. Reports from the WIS include the Albian and Cenomanian of Texas (Welton and Farish, 1993; Cappetta and Case, 1999), the middle Turonian of New Mexico (Wolberg, 1985), the late Cenomanian-middle Turonian of Arizona (Williamson et al., 1993), the middle Cenomanian of Colorado (Shimada et al., 2006), the Cenomanian of South Dakota (Cicimurri, 2001a, 2001b), and the Cenomanian of Minnesota (Case, 2001). Cumbaa et al. (2006: fig. 4.11) reported posterior teeth of this species from the Bainbridge bone bed of Saskatchewan; however, Underwood and Cumbaa (2010) suggested that those teeth belong to

Archaeolamna ex. gr. *kopingensis*, an observation shared herein. Consequently, the Dunvegan specimens are the first accepted report of *Cretodus semiplicatus* from Canada and extend the northern geographical range of this species within the WIS.

Genus *Dallasiella* Cappetta and Case, 1999

Type specimen—*Dallasiella willistoni* Cappetta and Case, 1999 from the Turonian-Coniacian boundary of Texas, USA.

Dallasiella willistoni Cappetta and Case, 1999

(Fig. 2.5D)

1974 ?*Odontaspis subulata* Agassiz, 1843; Meyer, p. 213, p. 214, fig. 68.

1990 *Cretodus sp.*; Case et al., p. 1087, fig. 7e, f.

1999 *Dallasiella willistoni* Cappetta and Case, p. 27, pl. 13, figs. 1–9.

Referred material—UALVP 49424, tooth, locality DBS 2.

Description—UALVP 49424 has a tall median cusp that is slightly distally inclined. The crown has a smooth, slightly convex labial face and a smooth, strongly convex lingual face. The cutting edges are slightly sigmoidal in profile view and are continuous with the large, triangular lateral cusplets that flank the cusp. The root contains labiolingually compressed mesial and distal lobes with the latter being slightly more expanded. The lingual protuberance has a short, basally placed nutrient groove that houses a large foramen. The basal edge forms a large U-shaped concavity.

Remarks—Cappetta and Case (1999) observed that the general tooth morphology of *Dallasiella willistoni* is very similar to that of *Cretalamna*; however, the two taxa are differentiated by the absence of a nutrient groove in the latter.

Reports of *Dallasiella willistoni* from North American localities have been limited. The species was originally described from material collected from the Turonian-Coniacian of Texas (Cappetta and Case, 1999). Siverson and Lindgren (2005) noted the recovery of teeth of *Dallasiella willistoni* from the middle Turonian of Montana. Teeth described by Cumbaa et al. (2006) as *D. willistoni* from the middle Cenomanian of Saskatchewan have a morphology more similar to *Roulletia canadensis* (Underwood and Cumbaa, 2010).

Order Rajiformes Berg, 1940

Family Rhinobatoidei incertae sedis

Genus *Pseudohypolophus* Cappetta and Case, 1975b

Type species—*Hypolophus mcnultyi* Thurmond, 1971 from Aptian-Albian boundary of Texas, USA.

Pseudohypolophus mcnultyi (Thurmond, 1971)

(Fig. 2.5E)

1964 Hypolophid teeth, Thurmond, p. 537, pl. 1, fig. 1a–f.

1971 *Hypolophus mcnultyi* Thurmond, p. 220, p. 221, fig. 12.

1974 *Parahypolophus mcnultyi* (Thurmond, 1971); Meyer, p. 156, fig. 48.

1975b *Pseudohypolophus mcnultyi* (Thurmond, 1971); Cappetta and Case,

p. 306.

1985 Batoids indet.; Wolberg, p. 6, fig .5k–o.

1987 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Cappetta, p. 141, fig. 119i–o.

1988 *Pseudohypolophus* sp.; Case and Schwimmer, p. 297, fig. 6.1– 6.5.

1991 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Landemaine, p. 30, pl. 15, figs. 1–7.

1993 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Williamson et al., p. 458, p. 459, fig. 9.1–9.10.

1993 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Welton and Farish, p. 134, figs. 1–4.

1999 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Cappetta and Case, p. 42, pl. 28, figs. 1–9, pl. 29, figs. 1–4.

2002 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Johnson and Lucas, p. 88, figs. 1, 2.

2004 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Becker et al., p. 786, fig. 4w–z.

2010 *Pseudohypolophus mcnultyi* (Thurmond, 1971); Becker et al., p. 259, fig. 6.8–6.11.

Referred material—UALVP 49428, tooth, locality DWK 3; UALVP 49410, 13 teeth, locality DWK 1; UALVP 49411, 12 teeth, locality DWK 2; UALVP 49414, 7 teeth, locality DWK 3; UALVP 49417, 12 teeth, locality DWK 4; UALVP 49418, 2 teeth, locality DWK 5; UALVP 49420, 7 teeth, locality

DWK 5; UALVP 49422, 2 teeth, locality DBS 1; UALVP 49423, 8 teeth, locality DBS 2; UALVP 49426, 17 teeth, locality DBS 2.

Description—UALVP 49428 has a low rhomboidal crown that possesses a smooth and slightly convex occlusal surface. The crown overhangs the low root in all directions. When viewed basally, the root consists of two triangular lobes. Each lobe contains multiple foramina just below the crown-root boundary, with a large pair of foramina located lingually. Dividing the two lobes is a deep nutritive groove that possesses a central basal foramen. The multiple specimens recovered from the Dunvegan localities all are less than 5 mm in size and show little variation in morphology.

Remarks—*Pseudohypolophus mcnultyi* has been described from various North American localities including the Aptian-Cenomanian of Texas (Thurmond, 1971 as *Hypolophus mcnultyi*; Cappetta and Case, 1975b; Welton and Farish, 1993; Cappetta and Case, 1999), the Turonian-Santonian of New Mexico (Wolberg, 1985 as Batoids indet.; Johnson and Lucas, 2002), and the upper Cenomanian of Arizona (Williamson et al., 1993). Case and Schwimmer (1988) reported this species from the Campanian of Georgia, while Meyer (1974, as *Parahypolophus mcnultyi*) reported an Albian-Campanian range from the Gulf Coast. Williamson et al. (1993) noted that *P. mcnultyi* is usually recovered from nearshore deposits.

UALVP 49428 represents the first Canadian account of this species, greatly extending the northern boundary of its distribution within the WIS.

DISCUSSION

The Dunvegan assemblage includes nine euselachian species from nine genera. With the exception of *Meristodonoides* and *Archaeolamna*, which were reported by Beavan and Russell (1999, as *Hybodus montanensis* and *Archaeolamna kopingensis judithensis*) from the late Campanian Dinosaur Park Formation, this is the first description of these euselachian taxa from the province of Alberta. It is also the first known report of the odontaspid shark *Johnlongia parvidens*, the eoptolamnid shark *Protolamna carteri,* and the batoid *Pseudohypolophus mcnultyi* from Canada. Cumbaa et al. (2006) reported *Cretodus semiplicatus* from the Bainbridge bonebed of Saskatchewan; however, the teeth were reassigned to *Archaeolamna* ex. gr. *kopingensis* by Underwood and Cumbaa (2010). As such, the *Cretodus semiplicatus* teeth described herein are now the only accepted report of the species from Canada. The Dunvegan assemblage not only extends the northern geographical range of the aforementioned taxa but also offers valuable insight into the paleoenvironment of this particular region of the seaway. Although the Dunvegan assemblage shares some taxa with other time-equivalent assemblages, conspicuously absent are species that are exceedingly common in other localities situated farther south (Table 1).

On the basis of the Dunvegan euselachian fauna, the paleoenvironment of the deposits may be inferred. The particular mix of taxa indicates deposition in a shallow, nearshore environment. A nearshore assemblage from the Greenhorn marine cycle of Black Mesa, Arizona, has a similar faunal association to that of the Dunvegan assemblage. Williamson et al. (1993) reported that the shallow water assemblage "is distinguished by the association of *Hybodus* sp. [= *Meristodonoides* sp.], *Cretodus semiplicatus, Ptychotrygon* sp., and *Pseudohypolophus mcnultyi* or *Protoplatyrhina hopii*, and the absence or rarity of *Ptychodus* sp. and *Cretoxyrhina mantelli.*" Meyer (1974) reported a euselachian association from the Texas Gulf Coast, which included an abundance of *Hybodus* (= *Meristodonoides*) and *Parahypolophus* (= *Pseudohypolophus*) and the absence or rarity of *Cretoxyrhina* and *Ptychodus*. These findings are consistent with the taxa recovered from the Dunvegan localities. The absence of *Ptychodus*, along with the presence of *Meristodonoides* sp., *Cretodus semiplicatus* and *Pseudohypolophus mcnultyi,* suggest that the Dunvegan localities were likely situated in a nearshore, shallow-water environment. It should be noted however, that *Cretodus semiplicatus* can also be found in deep water assemblages (see Shimada et al., 2006).

The Dunvegan euselachian assemblage shares taxa with other middle Cenomanian assemblages (Fig. 1). Shimada et al. (2006) described a middle Cenomanian offshore assemblage from southeastern Colorado. The calcarenite beds of the Tobe locality are situated at the lowest portion of the Greenhorn Limestone. Recovered from this diverse vertebrate assemblage were 22 euselachian species. In common with the Dunvegan assemblage is *Cretodus semiplicatus.* Shimada et al. (2006) also reported *Squalicorax curvatus* and *Cretoxyrhina mantelli* from the Colorado assemblage. Subsequently, Underwood and Cumbaa (2010) reassigned the latter to *C. denticulata*, a view shared herein. Both species may indeed be present in the Dunvegan assemblage, but a revision of *S. curvatus* is needed before this taxon can be confidently said to be present there. Regarding *Cretoxyrhina*, until better teeth are recovered, the presence of this species at the Dunvegan localities will remain suspect. Two other elasmobranch taxa, *Archaeolamna* ex. gr. *kopingensis* and *Johnlongia parvidens*, are also potentially shared. Numerous teeth tentatively identified as *Archaeolamna* cf. *A. kopingensis* were recovered from the Tobe locality. Shimada et al. (2006) reported that the root morphology differs slightly from that of *A. kopingensis,* hence its cautious placement. The root lobes of the Tobe locality specimens appear to be shorter than the lobes found on the Dunvegan tooth identified as *Archaeolamna* ex. gr. *kopingensis*. It is therefore possible, that these teeth represent different species. Two teeth of the genus *Johnlongia* were also reported by Shimada et al. (2006). Shimada (2007) later reassigned the tooth described as cf. *Johnlongia* to *Megachasma comanchensis*. The second highly fractured tooth was given the conservative identification of *Johnlongia* cf. *J. parvidens* (Shimada et al., 2006).

Cicimurri (2001b) described a middle Cenomanian nearshore euselachian assemblage consisting of 11 species from the Bell Fourche Shale of South Dakota and Wyoming. The majority of the species were collected from two calcarenite beds that were believed to be deposited in warm, shallow, marine water. Of the species described, *Meristodonoides rajkovichi* and *Cretodus semiplicatus* are found within both the Bell Fourche Shale and the Dunvegan Formation assemblages. The former, described by Cicimurri (2001b) as *Hybodus* sp., was later reassigned to *M. rajkovichi* by Underwood and Cumbaa (2010). The tooth described as *Squalicorax* sp. A herein and *Squalicorax* sp. cf *S. curvatus* from the Bell Fourche assemblage are most likely conspecific. Cicimurri (2001b) also reported *Cretoxyrhina mantelli* from the Bell Fourche assemblage, which was also reassigned to *C. denticulata* by Underwood and Cumbaa (2010). Again, the presence of this species in the Dunvegan assemblage remains suspect until additional and better preserved teeth are recovered.

Of particular interest is the comparison of the Dunvegan assemblage with the taxa recovered from the middle Cenomanian Bainbridge bonebed in the Pasquia Hills of east-central Saskatchewan (Cumbaa et al., 2006). A re-evaluation of this latter assemblage was later preformed by Underwood and Cumbaa (2010). Geographically, the Bainbridge locality would have been situated along the eastern margin of the WIS at a paleolatitude only 6º south (PLATES project, 2010) of the Dunvegan localities. Consequently, a comparison between the two assemblages would be expected to show a relatively similar faunal composition. The Bainbridge euselachian assemblage yielded 15 species (Underwood and Cumbaa, 2010). When compared with the Dunvegan assemblage, only three taxa are present at both locations: *Meristodonoides rajkovichi* (as *Meristodonoides* cf. *rajkovichi* herein), *Squalicorax* sp. A (as *Squalicorax curvatus* in Underwood and Cumbaa, 2010), and *Archaeolamna* ex. gr. *kopingensis*. *Cretoxyrhina* may also be shared. Cumbaa et al. (2006) also reported the teeth of *Cretodus semiplicatus* and *Dallasiella willistoni* from the Bainbridge locality; however, Underwood and

Cumbaa (2010) re-assigned these specimens to *Archaeolamna* ex. gr. *kopingensis* and *Roulletia canadensis*, respectively.

Conspicuously absent from the Alberta assemblage are taxa common to the aforementioned WIS localities. Well represented from the other assemblages are the durophagous species of *Ptychodus.* Williamson et al. (1993) indicated that *Ptychodus* species were likely limited to deep-water deposits at Black Mesa, Arizona. The presence of *P. anonymus*, *P. decurrens*, and *P. occidentalis* from the offshore Tobe locality is consistent with this claim. *Ptychodus occidentalis* teeth were also recovered from the gray, non-calcareous Belle Fourche Shale, which is believed to be a deep-water deposit (Cicimurri, 2001b). However, the recovery of numerous *Ptychodus rhombodus* and a few teeth described as *Ptychodus* ex. gr. *decurrens* and *Ptychodus* sp. from the nearshore Bainbridge locality (Underwood and Cumbaa, 2010) questions the previous notion that this taxon was restricted to a deep-water habitat within the WIS. Until more is known about the physical and biotic factors influencing the habitat selection of *Ptychodus*, the absence of this taxon from the nearshore Dunvegan localities is interpreted as consistent with an off-shore environmental preference for some, but not all, members of this genus.

The odontaspidid species *Carcharias paucicorrugata* and *Roulletia canadensis* have been recovered from the Bainbridge (Cumbaa et al., 2006; Underwood and Cumbaa, 2010) and Bell Fourche (Cicimurri, 2001b) localities. The absence of these species from the Dunvegan localities is puzzling, as all three localities are believed to near-shore deposits. Welton and Farish (1993) stated that

Carcharias amonensis is particularly common in shallow water, nearshore deposits; however, this species is only reported from the off-shore Tobe locality.

The rarity of anacoracid teeth in the Alberta assemblage is also perplexing. Only a single tooth of *Squalicorax* sp. A was recovered from the Dunvegan assemblage. This is in stark contrast to the 800 teeth reported from the Bainbridge locality (Underwood and Cumbaa, 2010, as *S. curvatus*) and the 1,017 teeth reported from the Tobe locality (Shimada et al., 2006, as *S. curvatus*). Numerous teeth described as *Squalicorax volgensis* were reported from the South Dakota and Saskatchewan assemblages (Cicimurri, 2001b; Cumbaa et al., 2006). Underwood and Cumbaa (2010) also reported the teeth of *Palaeoanacorax* aff. *P. pawpawensis* from the Bainbridge locality.

Physical factors such as temperature and salinity are known to shape the habitat structure in extant elasmobranchs (Simpfendorfer and Heupel, 2004). Accordingly, we suggest that absence of these taxa from the Dunvegan localities may be caused by a temperature intolerance associated with latitude and sea-water circulation patterns, or by an inability to inhabit environments that exhibit salinity variation.

Slingerland et al. (1996) generated a model that determined the pattern of large-scale movement of water within the WIS. The simulation produced a strong counterclockwise gyre that occupied the entire basin. According to Slingerland et al. (1996), the mechanism driving the circulation included factors such as fresh-water runoff, temperature and salinity gradients and mean annual winds. With respect to the upper 10 m of the water column, western drainage run-off produced a southerly directed jet that drew cooler Boreal water from the north into the Seaway and that carried it down the western margin. The eastern drainage produced a coastal jet that was directed northward and drew in warmer Tethyan water that was carried along the eastern shoreline. This counter clockwise gyre resulted in distorted isotherms that would extend cooler regions farther south along the western margin and warmer regions farther north along the eastern margin. The effect produced a significant variation of upper column water temperature between eastern and western localities along similar paleolatitudes.

With respect to the early Turonian model developed by Slingerland et al. (1996: see p. 946, fig. 6), the Dunvegan localities would have been situated within an isotherm that was cooler than the isotherms housing the Bainbridge, Bell Fourche, and Tobe localities. Consequently, the absence of the aforementioned taxa from the Dunvegan assemblage may be owing to an intolerance of these species to the cooler waters.

Salinity fluctuation might also explain a specific faunal curiosity. Undoubtedly the most abundant teeth recovered from the Dunvegan localities was the grinding teeth of the batoid *Pseudohypolophus mcnultyi*. Its tooth morphology suggests a benthic durophagous habitat. Previous to this study, the only reported middle Cenomanian finds of this species were from the Woodbine Formation of Texas (Welton and Farish, 1993). The presence of *Pseudohypolophus mcnultyi* in the Dunvegan Formation greatly extends the geographical range of the species. Consequently, evidence of this batoid should be expected in the shallow marine localities of the WIS that lie between these two outlying locations. Welton and

Farish (1993) reported that teeth of *P. mcnultyi* were frequently collected from brackish deposits throughout the Cenomanian of Texas. The abundance of this species in the Dunvegan Formation may indicate an environment of varying salinity; such an environment may also exclude taxa that are sensitive to such variation. In support of this hypothesis, there is evidence for salinity variation during the deposition of the Dunvegan Formation. Hay et al. (2007) described the remarkable preservation of the paraclupeid fish *Tycheroichthys dunveganensis*. The articulated specimen was believed to have died during a major river flood that covered this fish with a volume of suspended mud. That study indicates that large volumes of fresh water may well have entered the seaway in this region. The rare occurrence of lamniform sharks suggest normal marine conditions also existed, at least intermittently.

Of course, we cannot rule out a collecting bias, which almost certainly exists due to the small size of these teeth. The Dunvegan material was only surface collected; this may have led to smaller specimens being overlooked. For example, the microscopic teeth of the batoids *Rhinobatos* and *Cretomanta* were reported in the other aforementioned assemblages, yet are absent from the Dunvegan assemblage. Additional collecting and screening at the Dunvegan locations in the future may produce these smaller taxa. Nevertheless, based on the material collected, we believe it likely that the Dunvegan Formation localities represent shallow-water habitat characterized by cool water that underwent periodic fluctuations in salinity with the influx of fresh water.

TABLE 2.1. Vertebrate taxa reported from four middle Cenomanian localities in North America: Alberta [**AB**], Canada (Dunvegan assemblage: Cook et al., 2008, this Chapter); Saskatchewan [**SK**], Canada (Bainbridge assemblage: Cumbaa et al., 2006; Underwood and Cumbaa, 2010); South Dakota [**SD**], USA (Bell Fourche assemblage: Cicimurri, 2001b); and Colorado [**CO**], USA (Tobe assemblage: Shimada et al., 2006).

	AB	**SK**	**SD**	**CO**
Meristodonoides rajkovichi[1]	X	X	X	-
Ptychodus anonymus[2]	-	X	-	X
Ptychodus decurrens[3]	-	X	-	X
Ptychodus occidentalis[4]	-	-	X	X
Ptychodus rhombodus[5]	-	X	-	-
cf. *Pararhincodon* sp.[6]	-	-	-	X
Cretorectolobus robustus	-	X	-	-
Orectoloboides angulatus	-	X	-	-
Microcorax crassus	-	-	-	X
Squalicorax sp. A[7]	X	X	X	X
Squalicorax sp. B[8]	-	X	X	-
Paleoanacorax aff. *P. pawpawensis*	-	X	-	-
Archaeolamna ex. gr. *kopingensis*[9]	X	X	-	X
Cretoxyrhina denticulata[10]	-	X	X	X
Cretoxyrhina sp.	X	-	-	-
Protolamna carteri	X	-	-	-
Megachasma comanchensis[11]	-	-	-	X
Carcharias amonensis[12]	-	-	-	X
Carcharias paucicorrugata[13]	-	X	X	-
Carcharias saskatchewanensis	-	-	X	X
Carcharias tenuiplicatus	-	-	-	X
Johnlongia parvidens[14]	X	-	-	X
Roulletia canadensis[15]	-	X	X	X
Cretalamna ex. gr. *appendiculata*[16]	-	X	-	X
Cretodus semiplicatus	X	-	X	X
Carcharhiniformes indet.	-	-	-	X
Squatina sp.	-	-	X	-
Pseudohypolophus mcnultyi	X	-	-	-
Rhinobatos cf. *R. incertus*[17]	-	X	-	X
Rajidae *incertae sedis*	-	-	-	-
Ptychotrygon sp.	-	-	-	X
Onchopristis dunklei	-	-	-	-
Sclerorhynchidae indet.	-	X	-	X
Cretomanta canadensis	-	X	X	X

[1] Cicimurri (2001b: fig. 5a) and Cumbaa et al (2006: fig. 4.1) and reported material as *Hybodus* sp.

[2] Shimada et al. (2006: Fig. 6.1, 6.2) reported material as *Ptychodus* cf. *P. anonymus*; Underwood and Cumbaa (2010: pl. 2, figs. 18–21) reported material as *Ptychodus* sp.

[3] Underwood and Cumbaa (2010: pl. 3, figs. 1–6) reported material as *Ptychodus* ex. gr. *decurrens.*

[4] Cicimurri (2001b: fig. 5c,d) reported material as *Ptychodus* cf. *P. occidentalis*.

[5] Cumbaa et al. (2006: fig. 4.2) reported material as *P. occidentalis.*

[6] Taxon that may consist of multiple species.

[7] Cumbaa et al. (2006: fig 4.8), Shimada et al. (2006: fig. 8.2–8.4), and Underwood and Cumbaa (2010: pl. 7, figs. 1–23, pl. 8, fig. 2) reported material as *Squalicorax curvatus*; Cicimurri (2001b: fig. 5g) reported material as *Squalicorax* sp. cf. *S. curvatus*; Shimada et al. (2006: fig. 8.10–8.14) reported material as *Squalicorax* sp.; Cumbaa et al. (2006: fig. 4.9) and Shimada et al. (2006: fig. 8.5–8.9) reported material as *Squalicorax falcatus*.

[8] Cicimurri (2001b: fig. 5h) and Cumbaa et al. (2006: fig 4.7) reported material as *Squalicorax volgensis*. See Chapter 3, for details regarding *Squalicorax* sp. B.

[9] Cumbaa et al. (2006: fig. 4.10) reported material as *Archaeolamna* sp.; Cumbaa et al. (2006: fig. 4.11) reported material as *Cretodus semiplicatus*; Shimada et al. (2006: fig. 10.1) reported material as *Archaeolamna* cf. *A. kopingensis*.

[10] Cicimurri (2001b: fig. 5j), Cumbaa et al. (2006: fig. 4.13), and Shimada et al. (2006: fig. 10.9–10.10) reported material as *Cretoxyrhina mantelli.*

[11] Shimada et al. (2006: fig. 9.8) reported material as cf. *Johnlongia* sp. (see Shimada, 2007).

[12] Shimada et al. (2006: fig. 9.3) reported material as *Carcharias saskatchewanensis*.

[13] Cicimurri (2001b: 5r) reported material as *Carcharias tenuiplicatus*; Cumbaa et al. (2006: fig. 5.2) reported material as *Cenocarcharias tenuiplicatus*; Underwood and Cumbaa (2010: pl. 4, figs. 3–23) reported material as *Eostriatolamia paucicorrugata.* See Chapter 3 regarding for details regarding *Eostriatolamia*.

[14] Shimada et al. (2006: fig. 9.7) reported material as *Johnlongia* cf. *J. parvidens.*

[15] Cicimurri (2001b: fig. 5q), Cumbaa et al. (2006: fig. 5.1), and Shimada et al. (2006: fig. 9.1–9.2) reported material as *Carcharias amonensis*; Cumbaa et al. (2006: fig. 5.3) reported material as *Dallasiella willistoni.*

[16] Cumbaa et al. (2006: fig. 4.12**)** and Shimada et al. (2006: fig. 10.5–10.8) reported material as *Cretalamna appendiculata*; Underwood and Cumbaa (2010: pl. 4, figs. 1–2) reported material as *Cretalamna* sp.

[17] Shimada et al. (2006: fig. 11.3–11.4) reported material as *Rhinobatos* sp.; Underwood and Cumbaa (2010: text-fig. 6a–h) reported material as *Rhinobatos* cf. *incertus*

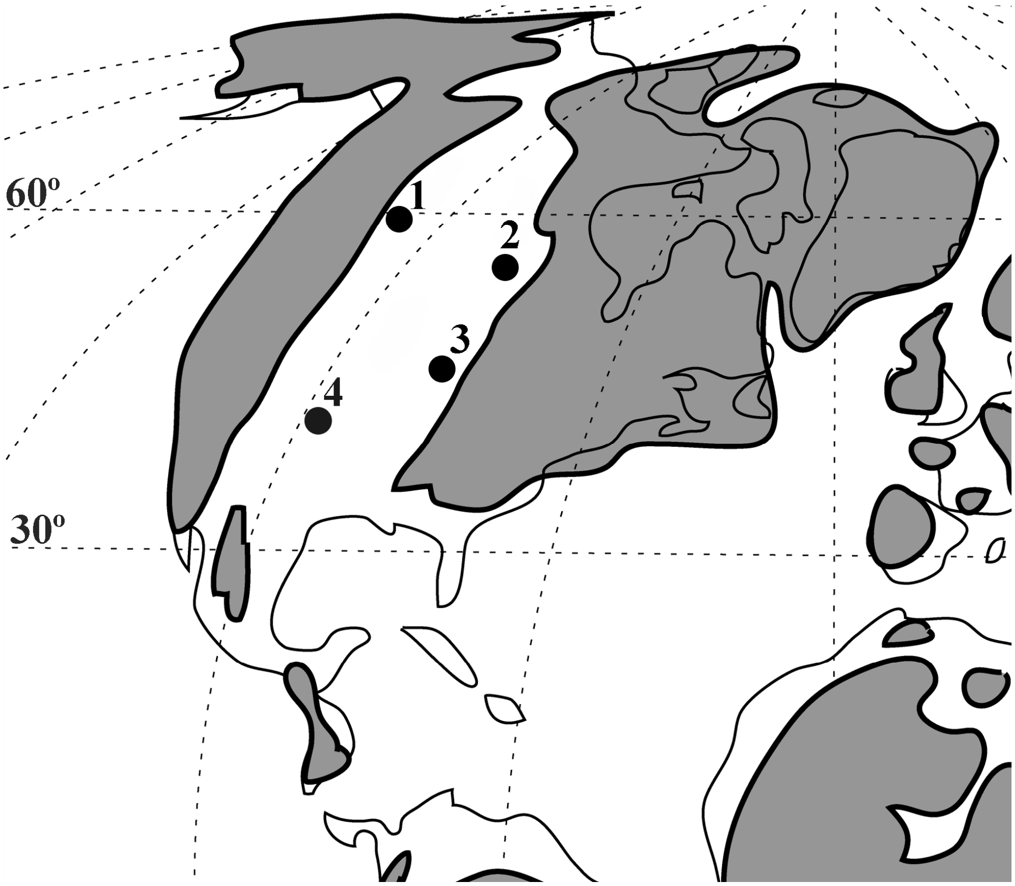


Figure 2.1. Location of middle Cenomanian euselachian assemblages throughout the WIS (based on Smith et al., 1994). (1) Alberta; (2) Saskatchewan (Cumbaa et al., 2006); (3) South Dakota and Wyoming (Cicimurri, 2001); (4) Colorado (Shimada et al., 2006).

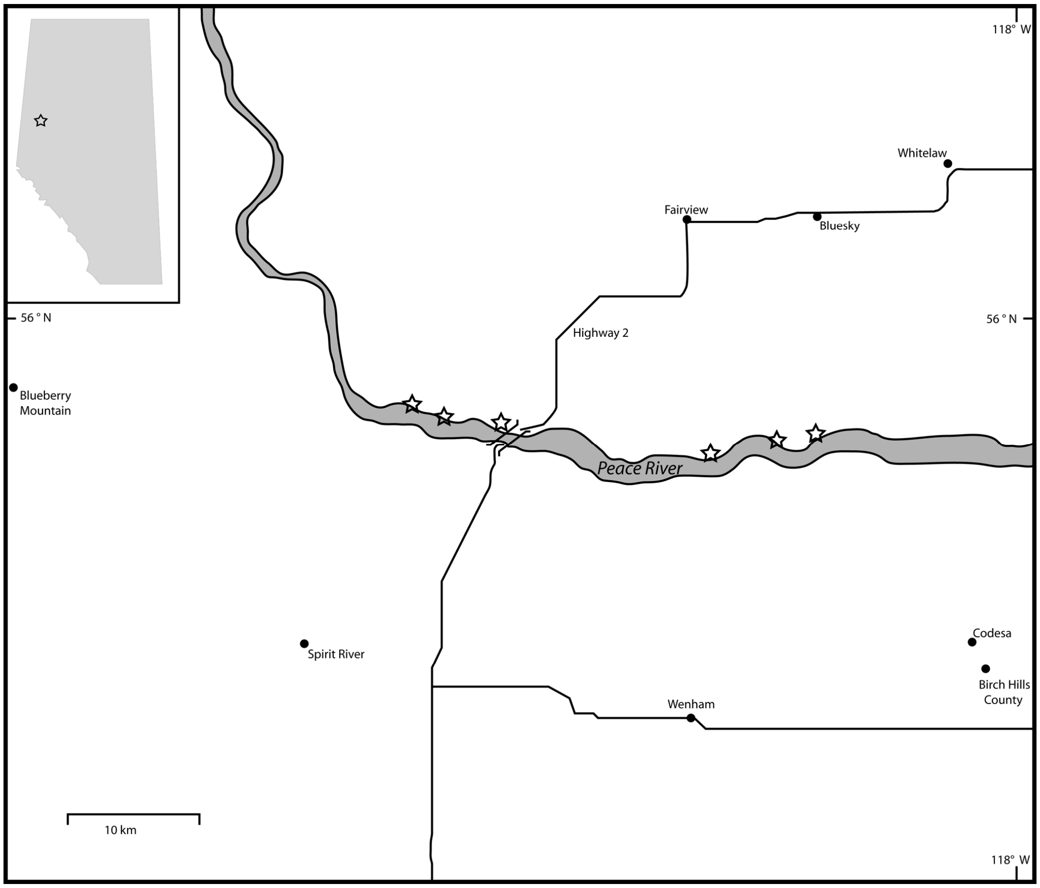


Figure 2.2. Map of northwestern Alberta showing the Dunvegan fossil localities, indicated by stars, on the north bank of the Peace River.

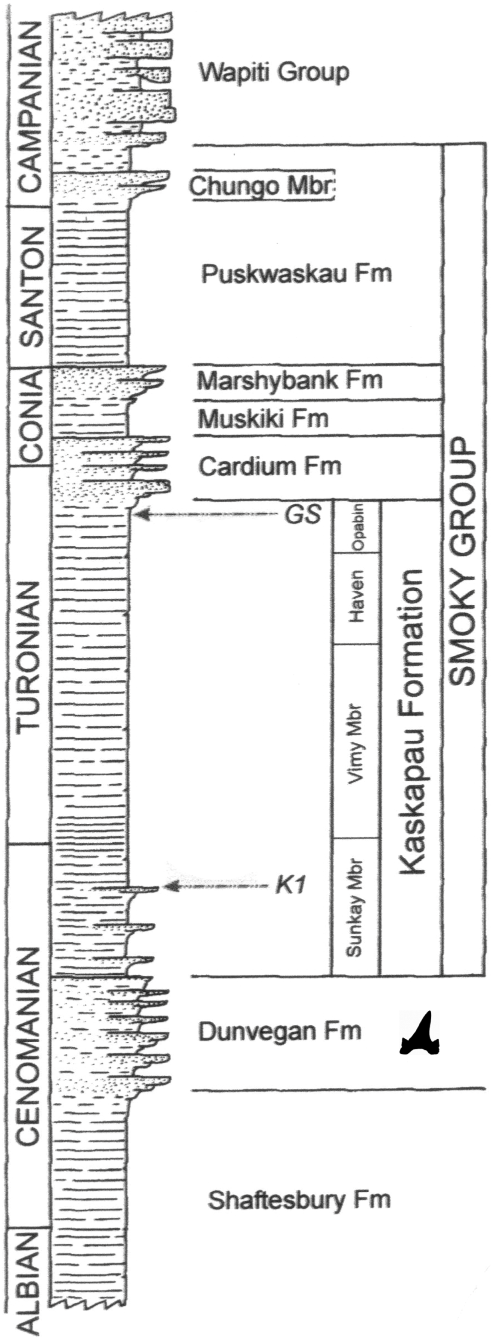


Figure 2.3. Stratigraphical position of the Dunvegan Formation (modified from Varban and Plint, 2005).

Figure 2.4. *Meristodonoides*, *Squalicorax*, *Archaeolamna*, and *Cretoxyrhina* teeth recovered from the Dunvegan Formation. (A) *Meristodonoides* cf. *rajkovichi* (Case, 2001), fractured lateral tooth, UALVP 49406; (B) *Squalicorax* sp. A, fractured lateral tooth, UALVP 49415; (C) *Archaeolamna* ex. gr. *kopingensis* (Davis, 1890), fractured lateral tooth, UALVP 49412; (D) cf. *Cretoxyrhina*, fractured lateral tooth, UALVP 49429. Views: labial (left), profile (center), and lingual (right). All scales = 1 mm.

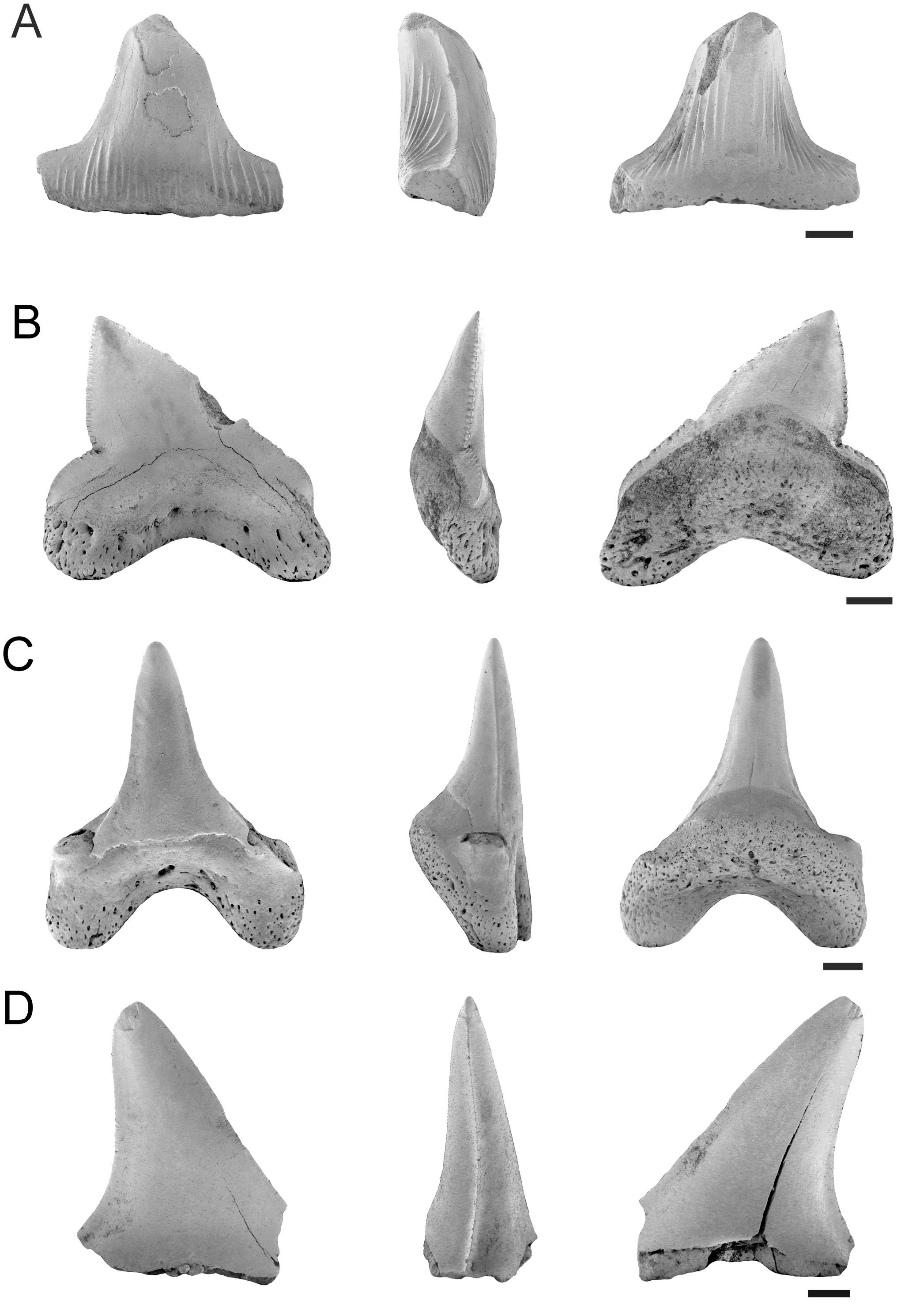
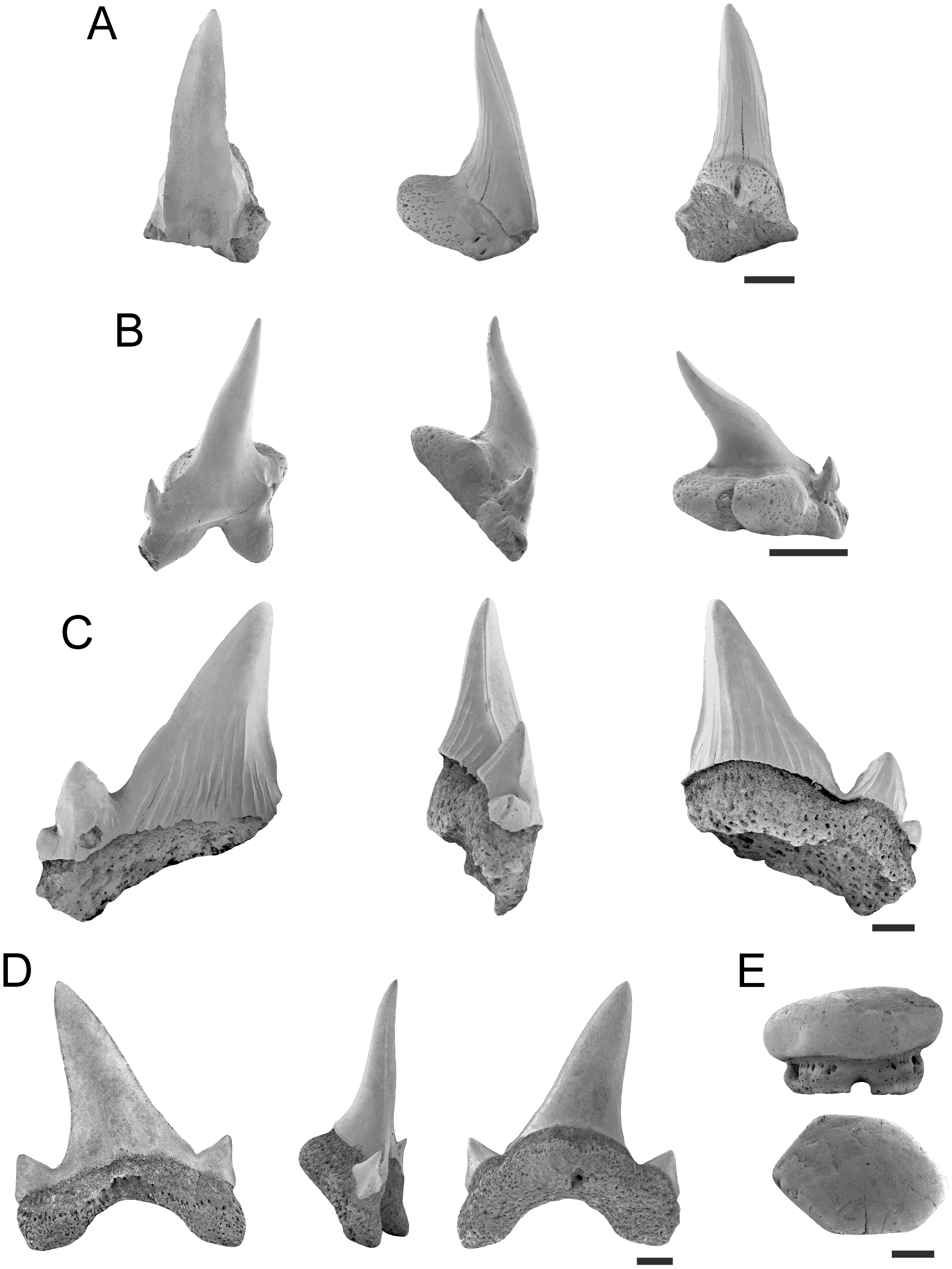

A
B
C
D

Figure 2.5. *Protolamna*, *Johnlongia*, *Cretodus*, *Dallasiella*, and *Pseudohypolophus* teeth recovered from the Dunvegan Formation. (A) *Protolamna carteri* Cappetta and Case, 1999, fractured anterior tooth, UALVP 49419; (B) *Johnlongia parvidens* (Cappetta, 1973), fractured lateral tooth, UALVP 49421; (C) *Cretodus semiplicatus* (Münster *in* Agassiz, 1843), fractured lateral tooth, UALVP 49415; (D) *Dallasiella willistoni* Cappetta and Case, 1999, lateral tooth, UALVP 49424; (E) *Pseudohypolophus mcnultyi* (Thurmond, 1971), tooth, UALVP 49428. Views: labial (left), profile (center), and lingual (right) for A–D; lingual (top) and occlusal (bottom) for E. All scales = 1 mm.


A
B
C
D
E

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CHAPTER 3

A high latitude euselachian assemblage from the early Turonian of Alberta, Canada

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The various authors contributed to this work by performing a sedimentology analysis and preparing information regarding the geology of the Kaskapau Formation information (AGP), providing supervisory, editorial and financial support (MVHW and AMM), by helpful discussion (MN), or by providing access to specimens in their care (MJE).

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INTRODUCTION

Only recently has there been a concerted effort to examine the diversity of Late Cretaceous euselachian assemblages from the northern region of the Western Interior Seaway (WIS) (see Case et al., 1990; Cumbaa and Tokaryk, 1999; Cumbaa et al., 2006; Cumbaa et al., 2010; Underwood and Cumbaa, 2010). Cook et al. (2008, Chapter 2) described a middle Cenomanian euselachian assemblage from the Dunvegan Formation of northwestern Alberta which included eight species from three orders. The study contained the first Canadian report of *Cretodus semiplicatus, Johnlongia parvidens*, *Protolamna carteri* and the ray *Pseudohypolophus mcnultyi*. Prior to the publication of that assemblage, the recovery of fossil euselachians from Alberta focused on more southern and younger deposits (Beavan and Russell, 1999; Brinkman et al., 2004).

The Watino fossil localities, discussed herein, are significantly more productive than the aforementioned Dunvegan fossil localities in regards to the number of teeth recovered and overall euselachian diversity. The existence of this assemblage has been previously documented. Fox (1984) described a left humerus of *Ichthyornis* from Watino, but also compiled a preliminary faunal list that included cf. *Hybodus* sp., cf. *Ptychodus* sp., cf. *Squalicorax* sp., cf. *Cretolamna* sp., cf. *Odontaspis* sp., and Pristidae, gen. and sp. indeterminate. Later, Wilson and Chalifa (1989) described an assemblage of disarticulated and fragmentary bones and scales of actinopterygians from Watino that included *Belonostomus, Ichthyodectes, Apateodus, Cimolichthys,* Dercetidae and *Enchodus.* Also reported at that time were the remains of Hybodontidae, Ptychodontidae, Rajiformes and

Lamniformes. Recently, a single tooth belonging to the lamniform *Cardabiodon ricki* was reported from Watino (Cook et al., 2010). This tooth documented the first North American occurrence of this large shark.

Other important northern WIS euselachian assemblages have been reported from east-central Saskatchewan. Case et al. (1990) described eight species from the lower Turonian Keld Member of the Favel Formation (see Cumbaa and Tokaryk, 1999; Cumbaa et al., 2006; Cumbaa et al., 2010 regarding the revised stratigraphy and age of this assemblage). Cumbaa et al. (2006) reported 19 species from the Carrot River and Bainbridge bone beds of the Belle Fourche Member of the Ashville Formation. Recently, Underwood and Cumbaa (2010) reexamined the latter bone bed and reported one species of hybodont shark, three species of *Ptychodus*, 10 species of neoselachian sharks and two species of batoid.

Although these localities have provided us with some knowledge of the diversity of euselachian taxa that were present in the northern parts of the WIS during the Late Cretaceous, there is still considerable work to be done. Herein, we provide a detailed examination of an early Turonian euselachian assemblage from the Canadian region of the seaway (paleolatitude = 59ºN; PLATES Program, 2010) and compare the composition with northern middle Cenomanian assemblages and other Turonian assemblages from more southerly WIS environments. This study also provides insights into euselachian paleoecology and paleobiogeography within this region of the WIS.

GEOLOGICAL SETTING

Late Cretaceous rocks near Watino Alberta, located at 55° 42′ 50.3” N, 117° 36′ 16.4” W (Fig. 3.1), provided fossils that were collected from a sandstone lens along the bank of the Smoky River that is identified as University of Alberta Laboratory for Vertebrate Paleontology (UALVP) locality 76. This locality is located at the margin of a large slump on the right bank of the Smoky River situated on a sharp bend, approximately 1 km below the highway bridge. We are lacking detailed information on a second locality, UALVP 848, from which an earlier collection of euselachian teeth came. Although collection details are limited, information associated with the specimens stated, “Teeth-Lower Smokey River-on Smokey River above Watino, T77 R24 W5, at river level, I.D. Crawford” (Wilson and Chalifa, 1989). All euselachian taxa associated with this locality are also present at locality 76.

Regional Stratigraphic Setting—Because of extensive slumping, Cretaceous strata tend to be poorly exposed in the Smoky River valley. At Watino, Cretaceous sandstone is exposed at river level, and the bone bed material is known only from loose blocks in heavily slumped debris. The nearest well-exposed section is at Hunting Creek, located 8 km NNE of Watino. At Hunting Creek, the upper part of the Dunvegan Formation and lower part of the overlying Kaskapau Formation are exposed (Fig. 3.2). Using sea level as a datum, the top of the Dunvegan Formation can be traced southward from Erin Lodge on the Peace River, to Hunting Creek near the Smoky River, and then projected south to Watino where the Dunvegan-Kaskapau contact is predicted to lie about 70 m above the level of the Smoky River. Therefore, rocks exposed near water level in the vicinity of Watino are probably part of the Dunvegan Formation.

The Dunvegan Formation has been mapped extensively in outcrop in the Rocky Mountain Foothills and in the Peace River Plains (e.g. Stott, 1982). Although long-recognized as of deltaic origin, the internal stratal organization of the Dunvegan Formation was not revealed until the seminal study of Bhattacharya and Walker (1991), who used log and core data to develop an allostratigraphic division based on regionally-mappable marine flooding surfaces. This framework, initially restricted to subsurface, was extended to outcrops in the Rocky Mountain Foothills in the west, and along the Peace and Smoky river valleys in the north and east (Plint, 1996, 2000; Hay and Plint, 2009).

A similar allostratigraphic approach was used to analyse the stratal architecture and facies distribution in the Kaskapau Formation (Plint, 2000; Varban and Plint, 2005, 2008a; Kreitner and Plint, 2006). The Kaskapau Formation represents a broad shallow marine shelf that gradually became less restricted as a result of progressive marine transgression in the latest Cenomanian and early Turonian. The Kaskapau Formation has been divided into two major parts, separated by a basin-wide disconformity termed the K1 surface. Below K1, the Kaskapau Formation was divided into three informal allostratigraphic ‘units’ (A-X, Doe Creek and Pouce Coupe in ascending order), bounded by regionally mappable marine flooding surfaces (Plint, 2000; Kreitner and Plint, 2006). The top of the Pouce Coupe Unit is defined by the K1 disconformity. The upper part of the Kaskapau Formation, above the K1 surface was divided into five informal units (I-V), each characterized by a broadly transgressive-regressive facies distribution with progradational shoreface sandstones at the top of each unit (Varban and Plint, 2005). The five units were divided into 28 component allomembers, each bounded by a marine flooding surface.

Eastward, the Kaskapau strata thin dramatically, from about 900 m in the Chetwynd area of British Columbia to <100 m in the Hunting Creek-Watino area of Alberta (Varban and Plint, 2005). In the west, between Chetwynd and Tumbler Ridge, Kaskapau strata are dominated by near-shore sandstones, whereas ~200 km to the east at Erin Lodge and Hunting Creek, silty claystones and organic-rich calcareous claystones dominate (Varban and Plint, 2008a). The eastward thinning of the Kaskapau strata is a consequence of deposition in an actively-subsiding foreland basin in which stratal packages thin and even lap out eastwards against the flank of the forebulge (Varban and Plint, 2008b). Storm-driven geostrophic flows were responsible for sediment transport across the Kaskapau shelf, which is interpreted to have been of extremely low relief, always above storm wave base, and probably no more than ~40 m deep at a distance of ~200 km offshore (Varban and Plint, 2008a, 2008b). Sand and then silt were progressively extracted along the transport pathway until only very fine-grained silt and clay were available at distances of > 200 km from shore.

Hunting Creek Section—Note that the initial interpretation of the Hunting Creek section (Plint, 2000), has been revised in light of subsequent work by Varban (2004), resulting in the position of the top Dunvegan surface being raised by 6 m, and the X and K1 surfaces both being raised by one sequence: the revised stratigraphic interpretation is shown in Figures 3.2, 3.3. The lower part of the Hunting Creek section exposes about 75 m of the Dunvegan Formation from the upper part of allomember G to the top of the formation. In the adjacent subsurface, allomembers A and B appear to lap out towards the northeast and hence allomember C forms the top of the formation at this locality (Fig. 3.3; Plint, 2000). At Hunting Creek, allomember C consists largely of a valley-filling sandstone that cuts deeply into underlying transgressive marine mudstone. The upper 8 m of the valley-fill comprises inclined heterolithic strata interpreted as the upper part of a point-bar which is capped by a rooted zone sharply overlain by marine mudstone; this contact marks the local top of the Dunvegan Formation (Fig. 3.3). As a whole, allomember C represents a southeast-prograding deltaic complex, the maximum regressive shoreface of which prograded to about 150 km southeast of Hunting Creek (e.g. Hay and Plint, 2009: fig. 15).

The Kaskapau Formation exposed at Hunting Creek is interpreted with reference to well logs to the south and west, to sections through equivalent strata at Erin Lodge and Howard Creek (on the Peace River), and to core at 15-34-77-1W6 (Plint, 2000; Varban and Plint, 2005). It is important to recognize that the Kaskapau strata at Hunting Creek are highly attenuated due to deposition on the flank of the forebulge where subsidence rate was low, and in consequence, rock units tend to be thin and bounded by unconformities. Because of limited subsidence, the area was strongly affected by relative sea-level oscillations that generated a succession of erosion surfaces and lag deposits.

The lower part of the Kaskapau above the Dunvegan Formation and below the K1 surface consists of shallow marine sandstones and mudstones of the A-X and Doe Creek units (e.g. Fig. 3.3; Plint, 2000: fig. 13). The X surface is a sharp transgressive surface mantled with wood fragments with *Teredolites*, overlain by marine mudstone. The overlying, intensely bioturbated very fine-grained silty sandstone (between 49 and 51.5 m in Fig. 3.3) is interpreted to be a very attenuated equivalent of the Doe Creek sandstone. The top of this sandstone contains phosphatic ooids (Varban, 2004) which also mantle the K1 surface throughout the Peace River region and support the interpretation of this surface as K1 (Plint, 2000; Varban and Plint, 2005). Above the K1 surface, a 60 cm bed of silty clay and 30 cm of fine sandstone is interpreted to be the remnant of Kaskapau unit I. The 30 cm thick sandstone may be a remnant of the Erin Lodge sandstone that is interpreted to be of eastern (forebulge) provenance (Varban and Plint, 2008a).

The Erin Lodge sandstone is sharply overlain (at 52.5 m, Fig. 3.3) by laminated, slightly silty organic-rich claystone that contains numerous bands and nodules of fibrous (cone-in-cone) gypsum. This facies is typical of the 'Hard Platy Shale' that crops out extensively along the Peace River valley (Stelck and Wall, 1954; Wallace-Dudley and Leckie, 1995) and which is equivalent to the lower part of the 'Second White Speckled Shale' of subsurface terminology. On the basis of comparison with Howard Creek and Erin Lodge sections, for which biostratigraphic control is available (Varban and Plint, 2005), the Cenomanian-Turonian boundary is placed at the base of the organic-rich claystone at 52.2 m (Fig. 3.3). The claystone is punctuated at 54.3 m by a 5 cm thick, quartz-rich phosphatic sandstone with sharp lower and upper contacts (Fig. 3.3). The detrital grains comprising this bed consist of about 78% well-sorted, angular to sub-angular, upper very fine-grained monocrystalline quartz sand, about 2% glaucony grains and a trace amount of chert and feldspar. Phosphatic debris forms about

20% of grains and includes bones, scales and teeth. The framework grains are separated by a highly displacive cement that forms about 60% of the rock volume (Fig. 3.4A). Cements include calcite, gypsum and phosphate (Fig. 3.5A, B).

A compositionally and texturally similar quartz-rich phosphatic sandstone, 0-30 cm thick, erosively overlies pyritic, organic-rich claystone of the Hard Platy Shale at Howard Creek, 85 km to the west. At this locality, the phosphatic sandstone, which is highly lenticular, forms wave ripples, hummocky cross-stratification and gutter casts, suggestive of at least intermittent storm wave action. This bed can also be traced to the 15-34-77-1W6 core where it is only 3 cm thick. Although phosphatic lags occur at other horizons in the claystone facies of the Kaskapau, none contain more than a trace of quartz sand and therefore the quartzose bone bed noted at Hunting Creek, Howard Creek and in the 15-34 core are interpreted to be the same bed.

A micrograph of the phosphatic sandstone from Watino is shown in Figure 3.4B. The detrital grains consist of about 82% well-sorted, angular to sub-angular, upper very fine-grained monocrystalline quartz sand, about 3% chert; glaucony and feldspar are present in trace amounts. Phosphatic material forms about 15% of the framework grains. The cement, which forms about 60% of the rock volume, is highly displacive and consists mainly of calcite with minor gypsum (Fig. 3.5C, D).

The detrital grains forming the phosphatic sandstones shown in Figs. 3.4, 3.5 bear a very close similarity in terms of grain size, sorting, angularity and composition, and in the similarity of the phosphatic debris. On this basis, it is concluded that the Hunting Creek phosphatic sandstone and the bone-bearing sandstone recovered from slumped debris at Watino are the same bed. Correlation of the phosphatic sandstone bed from Howard Creek to wells to the south and west suggest that the bed marks the top of Kaskapau unit II (Varban and Plint, 2005). This bone bed is interpreted as a winnowed lag deposit and suggests a period of increased wave energy at the sea floor. This interpretation is supported by the presence of forced-regressive shoreface sandstones at the top of unit II in the British Columbia Foothills (Varban and Plint, 2005). Thus Kaskapau unit II can be interpreted to have terminated with a period of relative sea-level fall that led to forced regression on the western margin of the basin, and also resulted in shallowing and erosion of offshore claystones in the distal, forebulge region. The abundance of quartz sand in the bone bed is in marked contrast to the claystones above and below which lack sand-sized quartz: this relationship is interpreted as evidence for re-exposure and erosion of sandy sediments on the forebulge during sea-level lowstand at the termination of unit II. The concentration of phosphatic material presumably reflects protracted shallow-water winnowing and by-pass of muddy sediment during the period of sea-level lowstand. Relative sea-level rise initiated deposition of Kaskapau unit III which comprises claystones and silty claystones from which the absence of quartz sand suggests that the forebulge was again submerged and yielded no coarse sediment.

METHODS

Most specimens were surface collected, although others were obtained from acid-dissolved matrix. Larger teeth embedded in the sandstone matrix were mechanically removed using a pneumatic hand drill and a dental pick. Teeth deeply embedded within the matrix were placed in a buffered 10% acetic acid solution to dissolve the surrounding sandstone. Following the acid bath the specimens were washed with water to remove any acid residue. Specimens were separated from the dissolved matrix using 0.5 mm sieve, followed by manual picking of teeth from the residues. A binocular microscope was used to examine and identify the isolated euselachian teeth. Any fractured teeth were hand picked and repaired using an adhesive. For detailed imaging of small teeth, a Jeol Field Emission Scanning Electron Microscope (JSM-6301 FXV) was used. Larger teeth were coated with ammonium chloride and imaged using a Nikon DXM 1200c digital camera mounted on a Zeiss Discovery V8 stereo microscope. The Watino teeth are catalogued in the collections of the University of Alberta Laboratory of Vertebrate Paleontology (UALVP). Tooth morphological terminology largely follows Cappetta (1987), whereas tooth type terminology follows Shimada (2002).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Order Hybodontiformes Maisey, 1989

Superfamily Hybodontoidea Zangerl, 1981

Family Hybodontidae Owen, 1845

Genus *Meristodonoides* Underwood and Cumbaa, 2010

Type species—*Hybodus rajkovichi* Case, 2001 from the Cenomanian of Minnesota, USA.

Meristodonoides cf. *rajkovichi* (Case, 2001)

(Fig. 3.6A, B)

Synonomy list—Refer to Chapter 2, p. 33.

Referred Material—UALVP 53121, fractured tooth, locality 76; UALVP 53122, fractured tooth, locality 76; UALVP 53123, fractured tooth, locality 848.

Description—These specimens are median cusps of highly fractured teeth. The apex of each cusp is missing. The strongly convex lingual and labial faces contain numerous large, widely spaced, longitudinal ridges. The labial ridges are restricted to the lower ¼ of the cusp, whereas the lingual ridges extend ¾ up the cusp. A distinct cutting edge extends the full length of the medial cusp. The cusp has a lingual curvature in profile. The teeth are missing the root.

Remarks— Species of *Meristodonoides* recovered from northern localities situated in Canada include *M. rajkovichi*, *M. butleri*, and *M. montanensis*. Numerous *M. rajkovichi* teeth have been reported by Cumbaa et al. (2006, as *Hybodus* sp.) and Underwood and Cumbaa (2010) from the Bainbridge bone bed in east central Saskatchewan. A small number of the teeth were assigned to *M. butleri* by Cumbaa et al. (2006, as *H. butleri*). Underwood and Cumbaa (2010) suggested that the tooth figured by Cook et al. (2008: fig. 4A) as *Hybodus* sp. from the middle Cenomanian Dunvegan Formation of Alberta, should be assigned to *M. rajkovichi*. Given its fragmented condition, Cook et al. (2008) conservatively left the reported specimen in open nomenclature; however, the crown contour and ornamentation of the specimen does resemble teeth figured as *M. rajkovichi* (see Case, 2001: pl. 1, fig. 5, pl. 2, figs. 1, 2; Underwood and Cumbaa, 2010: pl. 1, figs. 3–17), as adopted in Chapter 2.

Due to the incomplete nature of specimens, species determination is problematic. However, based strictly on cusp morphology, the specimens most closely resemble *M. rajkovichi*. Despite this conservative identification, it should be noted that the occurrence of *Meristodonoides* at the Watino localities is rare with the recovery of only three specimens. This is in stark contrast to abundant *Meristodonoides* teeth reported in the middle Cenomanian Saskatchewan assemblage (Cumbaa et al., 2006; Underwood and Cumbaa, 2010).

Family Polyacrodontidae Glickman, 1964

Genus *Polyacrodus* Jaekel, 1889

Type species—*Hybodus polycyphus* Agassiz, 1837 from the Middle Triassic of Lunéville, France.

cf. *Polyacrodus illingsworthi* (Dixon, 1850)

(Fig. 3.6C)

1850 *Acrodus illingsworthi*; Dixon, p. 364, pl. 30, figs. 11, 12, pl. 32 , fig. 9.

1912 *Synechodus illingsworthi* (Dixon, 1850); Woodward, pl. 46, figs. 5–7.

1973 *Synechodus* sp.; Cappetta, p. 504, pl. 1, fig. 28.

1979 *Synechodus illingsworthi* (Dixon, 1850); Evetts, p. 61, pl. 1, fig. 1.

1993 *Polyacrodus illingsworthi* (Dixon, 1850); Welton and Farish, p. 51, figs. 1, 2.

2004 *Polyacrodus illingsworthi* (Dixon, 1850); Cicimurri, p. 5.

Referred material—UALVP 53124, fractured tooth, locality 76.

Description—This specimen consists of a highly fractured crown that contains a blunt median cusp that is very slightly distally inclined. Distal to the cusp are two lateral cusplets; the more distal cusplet is significantly reduced. The portion of the tooth mesial to the median cusp is fractured. The lingual and labial crown faces are strongly convex and contain multiple well developed enameloid folds that extend from the crown foot to the apex of the medial cusp and lateral cusplets. A weak labial protuberance is present. The root is missing.

Remarks—Isolated teeth belonging to this genus have been reported from the Lower Triassic to the Upper Cretaceous of Europe and Greenland (Cappetta, 1987). Given the poor preservation of UALVP 53124, we cautiously assign this tooth to *Polyacrodus illingsworthi.* This assignment is based strictly on the low median cusp and lateral cusplets, weak labial protuberance, and strong enameloid folding that extends to the crown apex.

Teeth of *Polyacrodus illingsworthi* have been recovered from other WIS localities including the middle Turonian of Texas (Welton and Farish, 1993) and late Turonian of South Dakota, and Wyoming, USA (Cappetta, 1973, as *Synechodus* sp.; Evetts, 1979, as *S. illingsworthi*; Cicimurri, 2004). UALVP 53124 is the first documented occurrence of *P. illingsworthi* in Canada and expands its known northern geographical range within the WIS. It is also the oldest reported North American occurrence of this species. Recently, Rees and Underwood (2008) questioned the validity of this genus as the tooth morphology closely resembles that of certain *Hybodus* species. Unfortunately, the incomplete nature of UALVP 53124 does not allow us to contribute any additional insights into this matter.

Order Incertae sedis

Family Ptychodontidae Jaekel, 1898

Genus *Ptychodus* Agassiz, 1835

Type species—*Ptychodus mammillaris* Agassiz, 1839 from the Late Cretaceous of Europe.

Ptychodus anonymus Williston, 1900

(Fig. 3.6D–H)

1900 *Ptychodus anonymus* Williston, p. 241, figs. 5–8, 16–24.

1985 *Ptychodus anonymus* Williston, 1900; Wolberg, p. 2, fig. 3c, d.

1990 *Ptychodus* cf. *P. rugosus* Dixon, 1850; Case et al., p. 1084, figs. 2, 3.

1993 *Ptychodus anonymus* Williston, 1900; Welton and Farish, p. 57, figs. 1–7.

2001a *Ptychodus anonymus* Williston, 1900; Cicimurri, p. 4. fig. 6a, b.

2004 *Ptychodus anonymus* Williston, 1900; Cicimurri, p. 5.

2006 *Ptychodus* cf. *P. anonymus* Williston, 1900; p.6, figs. 6.1, 6.2.

2008 *Ptychodus* cf. *P. anonymus* Williston, 1900; p. 91, fig. 4a.

Referred material—UALVP 53125, medial tooth, locality 76; UALVP 53126, medial tooth, locality 848; UALVP 53127, lateral tooth, locality 76; UALVP 53128, lateral tooth, locality 848; UALVP 53129, lateral tooth, locality 848; UALVP 53130, nine teeth, locality 848.

Description—Teeth positioned medially in the jaw possess a crown with a high and rounded cusp. Restricted to this cusp are multiple fine transverse ridges that do not extend into the surrounding granular marginal region. The crown overhangs the root in all directions and has a distinct concave notch along its lingual margin. The root is positioned somewhat lingually under the crown and contains multiple foramina of various sizes with larger foramina situated under the crown-root border. The labial root face is flat and is at an oblique angle to the base of the crown. The lingual root face may be slightly convex or concave. The basal root face is more or less flat.

Laterally positioned teeth contain a low asymmetrical crown that overhangs the root in all directions. There is a small rounded cusp placed lingually on the crown. Distinct transverse ridges extend across the cusp, with many of them bifurcating upon reaching the reduced granular margin. The roots of these teeth are low and bear multiple foramina. Larger foramina are located near the crown-root boundary.

Remarks—The teeth of *Ptychodus* are arranged in a row-locking configuration which forms a crushing pavement dentition in both jaws (see Shimada et al., 2009). The symmetrical nature of UALVP 53125 and 53126 suggests that these teeth are from a medial position, whereas the more asymmetrical UALVP 53127, 53128, and 53129 are from a more lateral position.

The latter teeth bear some resemblance to the teeth of *Ptychodus rhombodus,* reported from the Bainbridge bone bed of Saskatchewan by Underwood and Cumbaa (2010). According to those authors, the small teeth of *P. rhombodus* are unique among other described species of *Ptychodus* by possessing a low and flat crown that bears a small but distinct cusp and lacks a defined marginal region. The teeth of *P. rhombodus* can be distinguished from *P. anonymus* by the presence of a more developed cusp and distinct granular margin in the latter (Underwood and Cumbaa, 2010); these features are observed in the specimens herein.

Many *Ptychodus anonymus* teeth, recovered from various assemblages throughout the WIS, recently have been re-diagnosed as *P. rugosus*. According to Hamm (2010a), distinct crown morphologies separate these two species. In addition, "*Ptychodus anonymus* is found in [m]iddle Cenomanian through [m]iddle Turonian deposits, whereas *P. rugosus* is known only from [l]ate Coniacian through [l]ate Santonian deposits" (Hamm, 2010a: p. 45). In accordance with this re-assessment, *P. anonymus* has been recovered from the late Cenomanian and Turonian of Texas (Welton and Farish, 1993), the middle Turonian of New Mexico (Wolberg, 1985), the middle Cenomanian of Colorado (Shimada et al., 2006, as *Ptychodus* cf. *P. anonymus*), the late Cenomanian of Kansas (Shimada and Martin, 2008, as *Ptychodus* cf. *P. anonymus*), the late Cenomanian and middle Turonian of South Dakota and Wyoming, USA (Cicimurri, 2001a, 2004), and the lower Turonian of Saskatchewan (Case et al., 1990, as *Ptychodus* cf. *P. rugosus*). A medial tooth of *P. anonymus* was reported from the Saskatchewan Bainbridge bone bed by Cumbaa et al. (2006); however

Underwood and Cumbaa (2010) subsequently re-assigned this tooth to their newly erected species *P. rhombodus*. Also recovered from the Saskatchewan bone bed were two teeth indentified as *Ptychodus* sp. that resembled *P. anonymus* but lacked the granular marginal area (Underwood and Cumbaa, 2010). The tooth morphology of *P. anonymus* also closely resembles *P. mammillaris*; however, the latter has fewer and coarser transverse ridges and a concentric granular pattern on the marginal region. The specimens described herein represent the first description of *P. anonymus* from Alberta and extends the northern geographical range of this species.

Order Lamniformes Berg, 1958

Family Anacoracidae Casier, 1947

Genus *Squalicorax* Whitley, 1939

Type species—*Corax pristodontus* Agassiz, 1843 from the Maastrichtian of the Netherlands.

Squalicorax sp. A

(Fig. 3.7A–M)

Synonomy list—Refer to Chapter 2, p. 36.

Referred material—UALVP 53131, anterior tooth, locality 76; UALVP 53141, anterior tooth, locality 848; UALVP 53142, symphyseal tooth, locality 76; UALVP 53143, lateral tooth, locality 848; UALVP 53144, lateral tooth, locality 848; UALVP 53145, lateral tooth, locality 76; UALVP 53146, lateral tooth, locality 76; UALVP 53147, lateral tooth, locality 76; UALVP 53148, lateral tooth, locality 848; UALVP 53149, lateral tooth, locality 76; UALVP 53150, lateral tooth, locality 848; UALVP 53151, lateral tooth, locality 76; UALVP 53152, fractured lateral tooth, locality 76; UALVP 53153, 19 complete and fractured teeth, locality 76; UALVP 53154, 95 complete and fractured teeth, locality 848.

Description—The upper anterior teeth are taller than wide and have a cusp that is slightly distally inclined. The labial crown face is slightly convex, whereas the lingual crown face is strongly convex. Both faces are smooth. The mesial cutting edge is slightly sigmoidal and contains coarse serrations that become reduced in size towards the apex. This cutting edge forms a sharp apex with the distal cutting edge which is shorter and also contains serrations that become more robust towards the base. The distal heel is short, low and finely serrated. There is a distinct lingual neck that is slightly wider in the medial region of the crown. The sigmoidal labial basal edge of the crown overhangs the labial root face which is particularly prominent in the medial region. The bilobate root contains a weak lingual root protuberance and lacks a nutrient groove. The distal root lobe is slightly more robust than the mesial root lobe. These rounded root lobes are separated by a distinct basal concavity. Multiple small foramina are present throughout the labial, lingual and basal root faces with larger foramina located at the apex of the lingual protuberance and below the labial crown-root border. Lower anterior teeth have a more erect and narrow cusp (Underwood and Cumbaa, 2010).

Symphyseal teeth are considerably smaller and mesodistally compressed. The labial crown face is flat, whereas the lingual crown face is convex. The mesial cutting edge is irregular and sigmoidal, whereas the distal cutting edge is slightly convex and smooth. A distinct distal heel also lacks serrations. The distal lobe of the root is more robust than the mesial lobe and the basal concavity is shallow.

Teeth from a more lateral position are wider than tall and possess a cusp that is strongly distally inclined. Typically, the basal one-third of the mesial cutting edge is straight, whereas the remainder of the cutting edge is slightly convex. The distal cutting edge is shorter and is either straight or slightly convex. Both cutting edges have well developed serrations that become smaller towards the apex. The heel is straight to convex and bears fine serrations. The height of the lingual neck is relatively constant across the tooth. The sigmoidal labial basal ledge of the crown is well developed and overhangs the labial root face. The distal root lobe is slightly more robust than the mesial root lobe and the basal concavity may be quite shallow in the most distally positioned teeth.

Remarks—Teeth from many North American assemblages that were initially reported as *Squalicorax falcatus* (e.g., Case et al., 1990; Williamson et al., 1993; Cumbaa et al., 2006; Shimada et al., 2006) have been re-assigned to *S. curvatus* by Underwood and Cumbaa (2010). This corroborates the notion presented by Siverson et al. (2007) that teeth identified as *S. falcatus* by some North American authors do not agree with the lectotype from the Turonian chalks of England and that the presence of *S. falcatus* within North American deposits is suspect.

The teeth described herein conform to the general morphology of *Squalicorax curvatus*, originally described and illustrated by Williston (1900: pl. 30, fig. 8, as *Corax curvatus*) from the Benton Formation of Kansas, U.S.A.

Siverson et al. (2007) questioned the validity of this species as the description was based on only two poorly preserved syntypes. We agree with the concerns of Siverson et al. (2007) about the validity of *S. curvatus* and also regard it as *nomen dubium* until re-examination of the type material and the recovery of additional topotypic teeth can be made. Despite this issue, the teeth listed herein have a similar overall morphology to teeth described as *Squalicorax* sp. from the Dunvegan Formation of Alberta (Cook et al., 2008) and *S. curvatus* from the Bainbridge bone bed and Favel Formation of Saskatchewan (Case et al., 1990; Underwood and Cumbaa, 2010), Canada.

Squalicorax sp. B

(Fig. 3.8A–M)

1996 *Squalicorax volgensis* (Glickman in Glickman and Shvazhaite, 1971); Siverson, p. 845, pl. 6, figs. 1–12.

1999 *Squalicorax volgensis* (Glickman in Glickman and Shvazhaite, 1971); Cappetta and Case, p. 14, pl. 5, fig. 1.

2006 *Squalicorax volgensis* (Glickman in Glickman and Shvazhaite, 1971); Cumbaa et al., p. 143, fig. 4.7.

2008 *Squalicorax volgensis* (Glickman in Glickman and Shvazhaite, 1971); Shimada and Martin, p. 92, fig. 5c.

Referred material—UALVP 53155, symphyseal tooth, locality 76; UALVP 53156, anterior tooth, locality 76; UALVP 53157, anterior tooth, locality 76; UALVP 53158, fractured anterior tooth, locality 848; UALVP 53159, lateral tooth, locality 848; UALVP 53160, lateral tooth, locality 848; UALVP 53161, lateral tooth, locality 76; UALVP 53162, lateral tooth, locality 848; UALVP 53163, lateral tooth, locality 76; UALVP 53164, lateral tooth, locality 848; UALVP 53165, lateral tooth, locality 848; UALVP 53166, lateral tooth, locality 76; UALVP 53167, lateral tooth, locality 76; UALVP 53168, 17 complete and fractured teeth, locality 76; UALVP 53169, 158 complete and fractured teeth, locality 848; UALVP 53170, 206 complete and fractured teeth, locality 848.

Description—The anterior teeth are taller than wide. The crown contains a median cusp that is slightly distally inclined. The upper two-thirds of the labial crown face is slightly convex, whereas the basal one-third is flat. The lingual crown face is strongly convex. Both faces are smooth. The mesial cutting edge is gently sigmoidal and is devoid of distinct serrations. The apex forms an acute angle. The distal cutting edge is straight and shorter than the mesial cutting edge and also lacks serrations. It intersects the smooth distal heel at an obtuse angle. The lingual neck is broad, particularly in the medial region. The labial basal edge is sigmoidal and overhangs the labial root face to a greater extent medially. The bilobate root contains a weak lingual root protuberance and lacks a nutrient groove. The distal root lobe is typically more robust than the mesial root lobe. These rounded root lobes are separated by a deep basal concavity. The root is porous with small foramina present throughout the labial, lingual and basal root faces. Larger foramina are typically located under the labial crown-root boundary.

Symphyseal teeth are significantly smaller and mesodistally compressed. The labial crown face is flat, whereas the lingual crown face is convex. The cutting edges are smooth and there is a distinct distal heel. The root has a lingual protuberance and is porous, containing multiple foramina. A very shallow basal concavity separates the mesial root lobe from the smaller distal root lobe.

Lateral teeth are wider than tall and possess a narrow median cusp that is strongly distally inclined. Both the mesial and distal cutting edges are straight to slightly convex. Both edges lack distinct serrations but weak crenulations may be present. A distinct notch may be present where the distal cutting edge and the distal heel meet. The distal heel lacks serrations. A lingual neck is broad and may bear short ridges. The labial basal crown edge is sigmoidal and overhangs the labial root face. In the distal-most files, this edge is more or less straight. The root is porous. The distal root lobe is more robust than the mesial root lobe. The deep basal concavity becomes shallow in only the most distally positioned teeth.

Remarks—The teeth of *Squalicorax* sp. B can be distinguished from *Squalicorax* sp. A by possessing: (1) a median cusp that is narrower; (2) a straighter mesial cutting edge; (3) smooth cutting edges; (4) a higher distal heel; (5) a more developed distal notch; (6) a distal root lobe more robust than the mesial root lobe; (7) a more porous root; and (8) a deeper basal concavity on all but the most distally positioned teeth. Although *Squalicorax* sp. A teeth are abundant at Watino, the teeth of *Squalicorax* sp. B are three-times more common.

The tooth morphology of *Squalicorax* sp. B is indistinguishable from the teeth of a species recovered from the Haycock Marl of Western Australia (Siverson, 1996: pl. 6, figs. 1–12; Siverson et al., 2007) and we consider them conspecific. A re-description of the Haycock Marl specimens is currently being undertaken (M. Siverson, personal communication, 2010). The Australian teeth (originally described as *S. volgensis* from the Beedagong Claystone in Siverson,

1996) and the Watino teeth are similar in overall size and have narrow cusps that lack distinct serrations. Other comparable features include similar lingual neck and labial basal crown edge morphology, a high distal heel, and a distal root lobe that is considerably more robust than the mesial lobe and is separated by a very deep basal concavity.

Squalicorax sp. B can be distinguished from teeth identified as *S. pawpawensis* from the late Albian of Texas; the latter possess more developed serrations along the cutting edges, a more or less straight labial basal crown edge, and a shallower basal concavity separating the root lobes. Teeth recovered from the Bainbridge of Saskatchewan, and identified as *Paleoanacorax* aff. *pawpawensis* by Underwood and Cumbaa (2010: p. 935) are smaller and contain "faint crenulations or incipient serrations" on the mesial cutting edge of most teeth. In addition, the root is more robust and the basal concavity is shallower. The overall morphology of the Saskatchewan teeth is different from the Texas *Squalicorax pawpawensis* and likely represents yet another new species. *Squalicorax* sp. B is also distinct from the teeth identified as *S. volgensis* from the early Cenomanian of Russia (Glickman and Shvazhaite, 1971) by the more prominent overhang of the labial basal crown edge and possessing cutting edges that are very weakly serrated (see Siverson et al., 2007: text-fig. 4c–f). Teeth identified as *S. volgensis* from the middle Cenomanian of Saskatchewan (Cumbaa et al., 2006: fig. 4.7) and South Dakota (Cicimurri, 2001b: fig. 5h), the late Cenomanian of Kansas (Shimada and Martin, 2008: fig. 5c), and the Turonian-Coniacian boundary of Texas (Cappetta and Case, 1999: pl. 5 fig. 1) conform to the tooth morphology of *Squalicorax* sp. B herein, and to the Haycock Marl specimens.

Family Archaeolamnidae Underwood and Cumbaa, 2010

Genus *Archaeolamna* Siverson, 1992

Type species—*Odontaspis kopingensis* Davis, 1890 from the Campanian of Sweden.

Archaeolamna ex. gr. *kopingensis* (Davis, 1890)

(Fig. 3.9A–H)

Synonomy list—Refer to Chapter 2, p. 41.

Referred material—UALVP 53171, lateral tooth, locality 76; UALVP 53172, anterior tooth, locality 76; UALVP 53173, fractured anterior tooth, locality 848; UALVP 53174, fractured lateral tooth, locality 76; UALVP 53175, fractured lateral tooth, locality 848; UALVP 53176, lateral tooth, locality 76; UALVP 53177, lateral tooth, locality 848; UALVP 53178, lateral tooth, locality 76; UALVP 53179, 32 complete teeth, locality 76; UALVP 53180, 45 complete and fractured teeth, locality 848.

Description—Anterior teeth contain a tall, broad-based triangular median cusp that is erect; however, the third upper anterior teeth (= intrabullar intermediate teeth of Shimada, 2002) have a median cusp in which the apical half is strongly distally curved (see Cook et al., 2011). The labial face of the crown is slightly convex, whereas the smooth lingual face is strongly convex. Both crown faces are smooth. A pair of triangular lateral cusplets flanks the median cusp. A sharp cutting edge runs continuously across the median cusp and the lateral cusplets. The height of the narrow lingual neck is relatively constant between the lateral cusplet and the median cusp regions. The root is robust and has a well-developed lingual protuberance with one or more nutrient foramina. A large portion of the root lobes are missing in the figured specimens.

Lateral teeth have a median cusp that is strongly distally inclined. The smooth labial crown face is slightly convex, whereas the smooth lingual crown face is strongly convex. The cutting edge runs continuously between the median cusp and a pair of triangular lateral cusplets. A narrow lingual neck is present. The root contains a well developed lingual protuberance with a large foramen that may or may not be situated in a shallow nutrient groove. The root lobes are more or less symmetrical and separated by a deep basal concavity that becomes shallow in the distal-most lateral teeth.

Remarks—The teeth of *Archaeolamna* have been recovered from numerous Albian to Maastrichtian deposits throughout the WIS, Europe, and Australia, as summarized by Cook et al. (2011). Subtle differences in tooth morphology from different stratigraphic horizons suggest that *Archaeolamna* likely includes multiple species (Cumbaa et al., 2006; Cook et al., 2008; Underwood and Cumbaa, 2010) although only two species have been named to date. The teeth herein share a similar morphology to middle Cenomanian teeth recovered from the Bainbridge bone bed assemblage of Saskatchewan and described as *Archaeolamna* ex. gr. *kopingensis* (Underwood and Cumbaa, 2010). Accordingly, we follow this taxonomic assignment. Similar teeth were also recovered from the middle Cenomanian Dunvegan assemblage of Alberta (Cook et al., 2008) and the lower Turonian of Saskatchewan (Case et al., 1990: fig. 7a, b, as *Cretodus* sp.).

Family Cardabiodontidae Siverson, 1999

Genus *Cardabiodon* Siverson, 1999

Type species—*Cardabiodon ricki* Siverson, 1999 from the middle Cenomanian of Western Australia.

Cardabiodon ricki Siverson, 1999

(Fig. 3.9I–K)

1957 ?*Pseudoisurus tomosus* Glickman 1957, p. 116, pl. 1, fig. 20.

1996 *Pseudoisurus*? sp.; Siverson, p.534, pl. 4, figs. 5–10.

1993 *Cretolamna woodwardi* Herman, 1975; Williamson et al., p. 456, fig. 6.7–6.9.

1999 *Cardabiodon ricki*; Siverson, p. 63, figs. 5, 7–11.

Referred material—UALVP 49430, lateral tooth, locality 848; UALVP 53181, neonate anterior tooth, locality 848; UALVP 53182, fractured tooth, locality 76.

Description—The lateral tooth contains a large median cusp that is distally inclined. The labial face is convex. The labial basal edge of the crown overhangs the labial root face. The lingual face is strongly convex and contains a distinct lingual neck that is thicker medially. A distinct cutting edge runs continuously between the median cusp and a pair of blunt lateral cusplets. A pair of weakly developed heels occur lateral to the cusplets. The large bilobate root has a large lingual protuberance with no nutrient groove. The root lobes are asymmetrical, with the mesial lobe being slightly longer and narrower than the more robust distal lobe. Numerous foramina are distributed throughout the labial face of the root, with a noticeable concentration situated at the crown-root border. The U-shaped basal concavity is deep.

The anterior neonate tooth has a crown with a triangular robust median cusp that is slightly distally inclined and lingually directed. The slightly convex labial face and strongly convex lingual face are smooth. The distal cusplet is missing, whereas the short triangular medial cusplet is directed distally. The cutting edge is continuous between the median cusp and the cusplet. A distinct broad lingual neck is present. The labial basal edge of the crown overhangs the labial root face. The bilobate root is missing the medial root lobe. The lingual protuberance is high, massive, and contains a large nutrient foramen. Numerous smaller foramina are distributed throughout the root faces but are particularly concentrated below the labial crown root border.

Remarks— *Cardabiodon ricki* was initially described from an associated tooth set recovered from the uppermost Gearle Siltstone in the Giralia Anticline located on the southern Carnarvon Platform of Western Australia (Siverson, 1999). Siverson (1999: p. 52) also reported another Cenomanian occurrence of *C. ricki* from Peter's Pit in the Lower Chalk, Burham, Kent, UK. The sister taxon *Cardabiodon venator* has been recovered from two North American localities. Siverson and Lindgren (2005) described numerous teeth of *C. venator* from the middle Turonian Fairport Member of the Carlile Shale in east-central Montana, USA. Teeth identified by Williamson et al. (1993) as *Cretalamna* (*Cretolamna*) *woodwardi* Herman, 1977, were collected from deep-water, lower Turonian deposits of the Mancos Shale of Black Mesa, Arizona, USA. Siverson (1996) subsequently re-identified *C. woodwardi* as *Pseudoisurus*? sp. Glickman, 1957, which was later re-described as *Cardabiodon* (Siverson and Lindgren, 2005).

Three localities in Kansas, USA, have also produced specimens identified as *Cardabiodon* species. First, Shimada and Martin (2008: fig. 6) reported some teeth of *Cardabiodon* sp. from the late Cenomanian of central Kansas. They are from the base of the Lincoln Limestone Member, Greenhorn Limestone, in Russell County. Second, a *Cardabiodon* tooth was found in Russell County at about 1 m below the Fencepost Limestone layer of the Pfeifer Shale Member of the Greenhorn Limestone Formation (Everhart, personal communication). The Fencepost Limestone layer is situated on top of the Greenhorn Formation and contacts the base of the Carlile Shale (Fairport Chalk Member). The Pfeifer Shale Member of the Greenhorn Limestone is early middle Turonian. Third, a *Cardabiodon* tooth was recovered from Lincoln County of the late Cenomanian near the base of the Lincoln Limestone Member, Greenhorn Limestone.

Cook et al. (2010) reported the first North American occurrence of this species based on an upper lateral tooth (UALVP 49430) recovered from the UALVP locality 848. In that document, the Watino locality was described as being late Cenomanian in age; however, subsequent work (see above) now indicates an early Turonian age for the Watino localities.

The size and general cusp morphology of UALVP 53182 is comparable to UALVP 49430. However, it is recognized that this specimen is severely damaged, making a specific diagnosis difficult. UALVP 53181 is the first description of a neonate *C. ricki* tooth. Juvenile teeth of the congeneric, but younger, species *C.*

venator have a similar overall morphology but have a less developed labial basal edge overhang than that of *C. ricki* (M. Siverson, personal communication, 2010). The various deposits from which the remains of *C. ricki* have been recovered are summarized in Cook et al. (2010). As discussed in that document, UAVLP 49430 has the tall cusp and enlarged lateral cusplets of *C. ricki* from the middle Cenomanian but has a foraminal pattern resembling *C. venator* from the middle Turonian. Consequently, the early Turonian teeth described herein may represent a transitional form. A tooth described as *Cretolamna woodwardi* by Williamson et al. (1993) from the basal Turonian of Arizona (J.I. Kirkland, personal communication, 2011) was reassigned to *Cardabiodon* by Siverson and Lindgren (2005).

Family Cretoxyrhinidae Glickman, 1958

Genus *Cretoxyrhina* Glickman, 1958

Type species—*Oxyrhina mantelli* Agassiz, 1843 from the Late Cretaceous of England.

Cretoxyrhina mantelli (Agassiz, 1843)

(Fig. 3.10A–H)

1843 *Oxyrhina mantelli* Agassiz, 1843, p. 280, pl. 33, figs. 1–5, 7–9.

1845 *Oxyrhina mantelli* Agassiz, 1843; Reuss, p. 5, pl. 3, figs. 1, 3, 5, 6.

1850 *Oxyrhina mantelli* Agassiz, 1843; Dixon, pl. 30, fig. 24.

1852 *Oxyrhina mantelli* Agassiz, 1843; Gervais, pl. 76, figs. 3, 20.

1856 *Oxyrhina mantelli* Agassiz, 1843; Fischer, p. 141, pl. 2, fig. 43.

1867 *Oxyrhina mantelli* Agassiz, 1843; Sauvage, p. 71, pl. 3, fig. 16.

1870 *Oxyrhina mantelli* Agassiz, 1843; Roemer, 1870, p. 323, pl. 36, figs. 3–5.

1872 *Oxyrhina mantelli* Agassiz, 1843; Sauvage, 1872, p. 21, figs. 33–35.

1873 *Oxyrhina extenta* Leidy, p. 302, pl. 18, figs. 21–25.

1875 *Oxyrhina mantelli* Agassiz, 1843; Geinitz, p. 207, pl. 38, figs. 1–21.

1878 *Oxyrhina mantelli* Agassiz, 1843; Fritsch, p. 7, fig. 12.

1888 *Oxyrhina mantelli* Agassiz, 1843; Woodward, p. 291.

1889 *Oxyrhina mantelli* Agassiz, 1843; Woodward, p. 376, pl. 17, figs. 9–21.

1895 *Oxyrhina mantelli* Agassiz, 1843; Eastman, p. 154, pls. 16–18.

1900a *Oxyrhina mantelli* Agassiz, 1843; Williston, p. 36, pl. 8, fig. 5; pl. 13, figs. 41–46, 50–52; pl. 14, figs. 2, 2a–m, 6, 7.

1900b *Oxyrhina mantelli* Agassiz, 1843; Williston, p. 246, pl. 26, fig. 5; pl. 31, figs. 41–46, 50–52; pl. 32, figs. 2, 2a–m, 6, 7.

1902 *Oxyrhina mantelli* Agassiz, 1843; Leriche, p. 116, pl. 3, figs. 49–53.

1906 *Oxyrhina mantelli* Agassiz, 1843; Leriche, p. 51.

1908 *Oxyrhina mantelli* Agassiz, 1843; Priem, p. 47, pl. 2, fig. 3.

1911 *Oxyrhina mantelli* Agassiz, 1843; Woodward, p. 202, figs. 60, 61; pl. 43, figs. 10, 15.

1929 *Oxyrhina mantelli* Agassiz, 1843; Leriche, 1929, p. 251.

1936 *Oxyrhina mantelli* Agassiz, 1843; Leriche, p. 381, pl. 25, figs. 12, 13.

1943 *Oxyrhina mantelli* Agassiz, 1843; Dartevelle and Casier, p. 138, pl. 5, fig. 32.

1970 *Isurus mantelli* (Agassiz, 1843); Applegate, p. 397, fig. 178i–k.

1975a *Cretoxyrhina mantelli* (Agassiz, 1843); Cappetta and Case, p. 20, pl. 5, fig. 27.

1977 *Cretoxyrhina mantelli* (Agassiz, 1843); Herman, p. 219, pl. 9, fig. 6a–e.

1980 *Cretoxyrhina mantelli* (Agassiz, 1843); Glickman, 1980, pl. 27, figs. 13, 14; pl. 29, figs. 19–21.

1981 *Isurus mantelli* (Agassiz, 1843); Thurmond and Jones, p. 54, fig. 20.

1987 *Cretoxyrhina mantelli* (Agassiz, 1843); Cappetta, 1987, p. 99, fig. 87e–i.

1987 *Cretoxyrhina mantelli* (Agassiz, 1843); Longbottom and Patterson, p. 250, text-fig. 11.2r, pl. 54, fig. 5.

1990 *Cretoxyrhina mantelli* (Agassiz, 1843); Case et al., 1990, p. 1087, fig. 9a–9f.

1991 *Cretoxyrhina mantelli* (Agassiz, 1843); Müller and Diedrich, p. 31.

1992 *Cretoxyrhina mantelli* (Agassiz, 1843); Siverson, p. 526, pl. 1, figs. 18, 19.

1993 *Cretoxyrhina mantelli* (Agassiz, 1843); Biddle, p. 40.

1993 *Cretoxyrhina mantelli* (Agassiz, 1843); Stewart and Martin, 1993, p. 244.

1993 *Cretoxyrhina mantelli* (Agassiz, 1843); Welton and Farish, 1993, p. 101, figs. 1–12, p. 102.

1993 *Cretoxyrhina mantelli* (Agassiz, 1843); Williamson et al., p. 456, fig. 6.10–6.15.

1995 *Cretoxyrhina mantelli* (Agassiz, 1843); Uyeno and Suzuki, 1995, p. 62, fig. 1g, 1h.

1996 *Cretoxyrhina mantelli* (Agassiz, 1843); Shimada, p. 8, fig. 5f–5h.

1996 *Cretoxyrhina mantelli* (Agassiz, 1843); Siverson, p. 819, pl. 1, figs. 1–18, text-fig. 4.

1997a *Cretoxyrhina mantelli* (Agassiz, 1843); Shimada, p. 270, figs. 1–10.

1997b *Cretoxyrhina mantelli* (Agassiz, 1843); Shimada, figs. 1–4, 5, 6 (in part).

1997c *Cretoxyrhina mantelli* (Agassiz, 1843); Shimada, fig. 1 (inset), appendix 1.

1997d *Cretoxyrhina mantelli* (Agassiz, 1843); Shimada, p. 642, figs. 1–6, ?7, 8–11.

1999 *Cretoxyrhina mantelli* (Agassiz, 1843); Cappetta and Case, p. 22.

1999 *Cretoxyrhina* sp.; Tanimoto and Kadota, p. 140, fig. 1.

1999 *Cretoxyrhina mantelli* (Agassiz, 1843); Trbušek, 1999, p. 55, pl. 2, figs. 7, 8, 10.

1999 *Cretoxyrhina mantelli* (Agassiz, 1843); Underwood and Mitchell, p. 39, text-fig. 6j.

2000 *Cretoxyrhina mantelli* (Agassiz, 1843); Mustafa, p. 605, fig. 4.9–4.19.

2001a *Cretoxyrhina mantelli* (Agassiz, 1843); Cicimurri, p. 34, fig. 7i, 7k.

2001b *Cretoxyrhina mantelli* (Agassiz, 1843); Cicimurri, p. 187, fig. 5j.

2002 *Cretoxyrhina mantelli* (Agassiz, 1843); Mustafa et al., p. 428, fig. 5.3, 5.4.

2002 *Cretoxyrhina mantelli* (Agassiz, 1843); Antunes and Cappetta, p. 127, pl. 11, figs. 1–7.

2004 *Cretoxyrhina mantelli* (Agassiz, 1843); Cicimurri, p. 10.

2004 *Cretoxyrhina mantelli* (Agassiz, 1843); Shimada and Hooks, p. 205, figs. 1.2, 3.1.

Referred material—UALVP 53183, fractured anterior tooth, locality 76; UALVP 53184, fractured anterior tooth, locality 76; UALVP 53185, fractured anterior tooth, locality 76; UALVP 53186, anterior tooth, locality 76; UALVP 53187, lateral tooth, locality 76; UALVP 53188, lateral tooth, locality 848; UALVP 53189, lateral tooth, locality 76; UALVP 53190, lateral tooth, locality 848; UALVP 53191, 11 fractured teeth, locality 76; UALVP 53192, 14 fractured teeth, locality 848.

Description—The anterior teeth are relatively large and contain a narrow median cusp that is erect or slightly distally inclined depending upon position in the jaw. The flat labial and strongly convex lingual faces are both smooth and contain a cutting edge that is continuous to the crown foot and is sigmoidal in profile view. Lateral cusplets are absent but a distinct heel may be present. The lingual neck is broad medially. The mesial root lobe is slightly more elongated and is separated from the distal root lobe by a deep basal concavity. A well developed lingual protuberance is present and contains a large nutrient foramen but lacks a nutrient groove. Additional foramina are present throughout the labial root face.

Lateral teeth possess a broad and distally inclined median cusp that is flanked by a pair of short and broad lateral cusplets on most teeth. A cutting edge runs across these cusps. The lingual neck is narrow. The root lobes are more or less symmetrical and become more divergent, thus forming a shallow basal concavity in the most distal lateral teeth. The lingual protuberance is well developed and contains a large nutrient foramen. Additional foramina are present throughout the labial root face.

Remarks—By comparing the maximum tooth size of the Watino specimens with *Cretoxyrhina* teeth recovered from other Cenomanian and Turonian WIS assemblages (Welton and Farish, 1993; Williamson et al., 1993; Siverson and Lindgren, 2005; Shimada et al., 2006; Shimada and Martin, 2008; Underwood and Cumbaa, 2010), it is evident that the teeth described herein are from juvenile and sub-adult forms. *Cretoxyrhina* tooth size within the Watino assemblage varies to a great extent and represents various stages of ontogeny.

Teeth of similar size recovered from the middle Cenomanian Bainbridge bone bed of Saskatchewan, were assigned to *Cretoxyrhina denticulata* by Underwood and Cumbaa (2010). They stated that the teeth of this species can be readily distinguished from the younger congeneric *C. mantelli* by its smaller maximum size, narrower cusps, and more developed cusplets throughout ontogeny. They noted that “teeth from almost all jaw positions of juveniles of *C. denticulata* had lateral cusplets” which are retained in adult lateral teeth but lost in adult anterior teeth (Underwood and Cumbaa, 2010: p. 914). Siverson and Lindgren (2005) noted that *Cretoxyrhina* was in the process of cusplet reduction during the late Albian to middle Turonian. Lateral cusplets in teeth identified as *C. mantelli* by Siverson and Lindgren (2005), from the lower middle Turonian of

Montana, are restricted to only the distally situated lateral teeth in both juvenile and sub-adult/adult forms.

The Watino specimens likely represent a transitional form of *Cretoxyrhina* in which the lateral cusplets of anterior teeth are lost in both juvenile and sub-adult stages (and presumably adult forms) but are retained in most juvenile and sub-adult lateral teeth although reduced. Juvenile anterior teeth from the late Cenomanian of Kansas (Shimada and Martin, 2008: fig. 6f) and Colorado, USA (Shimada et al., 2006: fig. 10.11) also lack lateral cusplets and share a similar general tooth morphology. The overall morphology of the teeth described herein, closely resembles both *C. denticulata* and *C. mantelli*, but has a closer affinity to the latter based on the lack of lateral cusplets in juvenile anterior teeth. Whether or not the Watino teeth represent a distinct species is debatable. A lateral tooth referred to *Cretodus* sp. by Case et al. (1990: fig. 7c, d) from the Favel Formation of Saskatchewan likely belongs to a *Cretoxyrhina* neonate.

Cook et al. (2008) conservatively identified a severely fragmented cusp, recovered from the Dunvegan Formation of Alberta, as *Cretoxyrhina* cf. *C. mantelli*. Given that we now have evidence that *C. denticulata* inhabited this region of the WIS during the middle Cenomanian, it is likely that the Alberta Dunvegan tooth belongs to this species (see Underwood and Cumbaa, 2010).

Family Mitsukurinidae Jordan, 1898

Genus *Scapanorhynchus* Woodward, 1889

Type species—*Rhinognathus lewisii* Davis, 1887 from the late Santonian of Sahel Alma, Lebanon.

Scapanorhynchus sp.

(Fig. 3.11A)

Referred material—UALVP 53193, fractured lateral tooth, locality 76.

Description—The large incomplete lateral tooth contains a tall broad-based median cusp that is labiolingually compressed and distally inclined. The smooth labial crown face is flat, whereas the basal one-third of the weakly convex lingual crown face bears strong parallel striations. A distinct cutting edge runs the entire length of the cusp and is sigmoidal in profile view. A narrow lingual neck is present. The preserved portion of the root is very low and contains a strong lingual protuberance that bears a deep nutrient groove. The root lobes are missing but are typically sub-rectangular in specimens recovered from other deposits (see Siverson, 1992: pl. 4, figs. 8–11; Welton and Farish, 1993: p. 94, figs. 1, 4; Cappetta and Case, 1999: pl. 11, figs. 8–11).

Remarks—The labiolingually compressed and sigmoidal median cusp, the low medial region of the root, and the parallel basal striations of UALVP 53193 are characters observed in the lateral teeth of *Scapanorhynchus*. The latter feature distinguishes the teeth of this taxon from the irregular and flexuous striations of odontaspidid teeth (Siverson, 1992).

Scapanorhynchus raphiodon has been recovered from Cenomanian-Coniacian deposits throughout the WIS (e.g. Wolberg, 1985; Welton and Farish, 1993; Williamson et al., 1993; Cicimurri, 2001a, 2004; Hamm and Shimada, 2002; Becker et al. 2010). Siverson (1992) questioned the validity of this species. Unfortunately, the incomplete nature of this specimen precludes determination to species level and further taxonomic discussion.

Family Odontaspididae Müller and Henle, 1839

Carcharias Rafinesque, 1810

Type species—*Carcharias taurus* Rafinesque, 1810; extant.

Carcharias aff. *C. striatula* (Dalinkevicius, 1935)

(Fig. 3.11B–E)

Referred material—UALVP 53194, fractured anterior tooth, locality 76; UALVP 53195, lateral tooth, locality 848; UALVP 53196, lateral tooth, locality 76; UALVP 53197, lateral tooth, locality 848.

Description—The anterior teeth possess an erect broad-based median cusp that tapers to a sharp apex and is slightly sigmoidal in profile view. The labial crown face is weakly convex and strongly overhangs the labial root face. This basal ledge may be smooth or bear weak striations that are restricted to the ledge. The lingual crown face is strongly convex and bears weak flexuous striations that are restricted to the basal half of the median cusp. The cutting edges of the median cusp do not extend to the pair of short needle-like lateral cusplets. A narrow lingual neck separates the median cusp and lateral cusplets from the lingual root face. The end of the distal root lobe and the entire mesial root lobe are missing. The lingual protuberance is well developed and contains a deep nutrient groove. Multiple small foramina are situated throughout the preserved portion of the root.

The lateral teeth possess a median cusp that is distally inclined. The labial crown face is flat and does not overhang the labial root face. Short and strong enameloid folding is present along the base of the labial crown. The lingual crown face is convex and contains very weak striations that are restricted to the lower half of the cusp. Flanking the median cusp is a pair of short triangular lateral cusplets. A distinct cutting edge runs continuously between the median cusp and lateral cusplets. A narrow lingual neck is present. The root is relatively robust and more or less symmetrical. The basal concavity is V-shaped and is relatively shallow in distally positioned lateral teeth. The lingual protuberance contains a well developed nutrient groove. Numerous large foramina are present in the medial region of the labial root face. Additional small foramina are situated throughout the root.

Remarks—Glickman (1980) erected *Eostriatolamia* to accommodate odontaspidid-like teeth originally described as *Lamna venusta* by Leriche (1906) from the Santonian of Lonzée, Belgium. Tooth morphology included the presence of short striations along the base of the labial crown face and weak striations on the lower half of the lingual crown face. Glickman and Averianov (1998) noted the importance of the lingual striations as a principal character distinguishing this taxon from other odontaspidids and assigned additional species (including *Carcharias striatula*) to *Eostriatolamia* based on this character. However, the taxonomic significance of this feature is questionable as lingual striations also occur in *Carcharias* (Purdy, 1998). Glickman and Averianov (1998) also stated that despite having a similar tooth morphology to the extant species *Carcharias taurus*, the dentition of *Eostriatolamia* is more primitive as it lacks distally positioned files of reduced crushing teeth. This assertion was based on the failure to recover the isolated teeth of this morphology during sampling. It is possible however, that “physical parameters acting on the sediment” may separate small distal teeth from larger more medially positioned teeth (Siverson, 1992: p. 916). Underwood and Cumbaa (2010) also supported the creation of *Eostriatolamia* by reassigning *Carcharias tenuiplicatus* and *Carcharias striatula* to this genus. In addition, they erected a new species, *E. paucicorrugata*. Given that validity of *Eostriatolamia* is based on the absence of reduced crushing teeth, the assignment of this new species to *Eostriatolamia* is questionable as it was noted that there was a "lack of sufficient material to reconstruct the dentition" and that the dental arrangement would be similar to *Odontaspis ferox*. We caution that in the absence of an articulated dentition confirming this primitive condition (i.e., the lack of files of reduced posterior teeth) we consider *Eostriatolamia* to be highly provisional. Consequently, we conservatively assign odontaspid-like dentition herein to either *Carcharias* or *Odontaspis*. According to Compagno and Follett (1986: p. 89, 90), the anterior teeth of the former have median cusps that are "stout and broad-tipped" and cusplets that are "short and strongly hooked", whereas teeth from equivalent files in the latter have median cusps that are "slender and narrow-tipped" and cusplets that are "long and straight or weakly curved". The lateral teeth of *Carcharias* are also more "compressed and blade-like, with flattened cusplets".

Carcharias striatula (Dalinkevicius, 1935) was originally described as *Odontaspis* (*Synodontaspis*) *striatula* from the late Albian Jiesia Formation of Lithuania; it has also been recovered from the late Aptian of southern France (Cappetta, 1975b, as *Odontaspis striatula*), the middle Albian of northeastern France (Landemaine, 1991, as *Scapanorhynchus striatula*; Biddle et al., 1993), and the middle to late Albian of Western Australia (Siverson, 1997). The teeth of this species were reported to be morphologically similar to those of *C. tenuiplicatus* (Welton and Farish, 1993); however, Cappetta and Case (1999) noted that the teeth of *C. striatula* are thicker and larger in overall size, have a straighter median cusp, and less developed striations of the lingual crown face.

The Watino specimens differ only slightly from the chronostratigraphically older *Carcharias striatula* type material by having anterior teeth with a more robust and shorter median cusp with less developed labial striations, and lateral teeth with a higher lingual root face. However, the overall morphology most likely suggests that the Watino specimens are either conspecific or very closely related. This material can also be distinguished from *C. tenuiplicatus* by having a larger overall size, erect median cusps on anterior teeth, weak labial and lingual crown striations, and shallower labial basal ledge. Consequently, we consider the Watino teeth to be congeneric but not conspecific with *C. tenuiplicatus*. Teeth identified as *Carcharias* sp. A from the basal Haycock Marl of Western Australia (Siverson, 1996) are also somewhat similar to the Watino specimens but bear stronger lingual striations and have a more gracile morphology.

Genus *Odontaspis* Agassiz, 1838

Type species—*Squalus ferox* Risso, 1810; extant.

Odontaspis saskatchewanensis Case, Tokaryk, and Baird, 1990

(Fig. 3.11F)

1990 *Odontaspis saskatchewanensis* Case et al., p. 1085, figs. 4a–j, 5a–b.

1993 *Carcharias* sp. A; Welton and Farish, p. 91, figs. 1–6.

2001a *Carcharias saskatchewanensis* (Case, Tokaryk, and Baird, 1990);
Cicimurri, p. 36, fig. 7n.

2001b *Carcharias saskatchewanensis* (Case, Tokaryk, and Baird, 1990);
Cicimurri, p. 188, fig. 5q.

2008 *Carcharias saskatchewanensis* (Case, Tokaryk, and Baird, 1990);
Shimada and Martin, p. 92, fig. 5h.

Referred material—UALVP 53198, lateral tooth, locality 76.

Description—This lateral tooth is very small. The broad based median cusp narrows to a sharp apex and is slightly distally inclined. The smooth convex labial crown face is slightly convex, whereas the lingual face is strongly convex and also lacks ornamentation. A distinct cutting edge runs continuously between the median cusp and a pair of needle-like lateral cusplets. The slightly eroded root appears symmetrical; however, the terminal portion of the distal root lobe is missing. The lingual protuberance bears a nutrient groove.

Remarks—The general morphology of this specimen closely resembles lateral teeth originally described as *Odontaspis saskatchewanensis* by Case et al. (1990: fig. 4e–g) from the early Turonian of Saskatchewan. This species was also reported from the middle Cenomanian of the province (Cumbaa et al., 2006, as *Carcharias saskatchewanensis*), the middle and late Cenomanian of South Dakota (Cicimurri, 2001a, 2001b, as *C. saskatchewanensis*), the middle Cenomanian of Colorado (Shimada et al., 2006, as *C. saskatchewanensis*), the late Cenomanian of Kansas (Shimada and Martin, 2008, as *C. saskatchewanensis*), and the Cenomanian of Texas (Welton and Farish, 1993, as *Carcharias* sp. A). Although these later authors assigned this species to *Carcharias*, we follow the original description in attributing it to the genus *Odontaspis* based on the delicate median cusp and lateral cusplet morphology. Until more and better preserved teeth are collected from the Watino localities, we tentatively assign this single specimen to this species.

Odontaspis watinensis sp. nov. Cook

(Fig. 3.11G–J)

Holotype—UALVP 53199, anterior tooth, locality 76.

Paratypes—UALVP 53200, fractured anterior tooth, locality 76; UALVP 53201, fractured lateral tooth, locality 76; UALVP 53202, fractured lateral tooth, locality 76.

Etymology—Named after the town of Watino, Alberta, Canada, near the type locality.

Diagnosis—The teeth of *Odontaspis watinensis* can be distinguished from the teeth of other odontaspidids by possessing a single pair of needle-like lateral cusplets that extend nearly half the height of the median cusp. The median cusp contains no ornamentation. A well developed and slightly recessed lingual neck is present on all cusps. The bilobate root with a well developed lingual protuberance possesses a shallow nutrient groove.

Description—Anterior teeth possess an erect median cusp that tapers to a sharp apex. The labial face is flat whereas the lingual face is strongly convex. Both faces are smooth. The cutting edge is continuous with a pair of extremely tall needle-like lateral cusplets that extend to half the height of the median cusp. A well developed and slightly recessed lingual neck clearly separates the median cusp and lateral cusplets from the root lingually. The basal ledge of the labial crown face is concave and slightly overhangs the labial root face. The slightly more elongated mesial root lobe is separated from the distal root lobe by a deep U-shaped basal concavity. A very shallow nutrient groove is situated on the basal region of the lingual protuberance. Numerous large foramina are concentrated throughout the labial root face.

The lateral teeth have a median cusp that is more robust than anteriorly positioned teeth and is distally curved. The labial crown face is flat whereas the lingual face is convex. No ornamentation is present. A well developed and slightly recessed lingual neck is present on all cusps. The basal ledge is arched and slightly overhangs the labial root face. The bilobate root forms a deep basal concavity even in the more distally positioned lateral teeth.

Remarks—The overall morphology of *O. watinensis* is somewhat reminiscent of three odontaspidids occurring in Cenomanian and Turonian deposits of the WIS: *O. saskatchewanensis, Carcharias tenuiplicatus*, and *C. paucicorrugata*.

The tooth morphology of *Odontaspis watinensis* differs from *O. saskatchewanensis* by: (1) possessing a narrower median cusp; (2) having significantly taller lateral cusplets; and (3) having an overall larger size. Case et al. (1990) described an average tooth height of 3.5 mm for the latter species. Welton and Farish (1993, as *Carcharias* sp. A) reported *O. saskatchewanensis* as having a maximum tooth size of 4.7 mm, while Cicimurri (2001a, 2001b) described numerous teeth all measuring less than 5 mm in total height. Shimada et al. (2006) examined more than 300 specimens of *O. saskatchewanensis* with no teeth exceeding 5 mm in total height. The height of *O. watinensis* teeth reported herein exceeds by more than double any previously reported *O. saskatchewanensis* teeth.

The tooth morphology of *Odontaspis watinensis* differs from *Carcharias tenuiplicatus* by possessing: (1) significantly taller lateral cusplets; (2) completely smooth labial and lingual crown faces; (3) a labial crown basal ledge that does not overhang the labial root face to the same degree; and (4) a larger overall size.

The teeth of *Odontaspis watinensis* differs from *Carcharias paucicorrugata* by having: (1) anterior teeth with a narrower median cusp; (2) lateral cusplets that are significantly taller and less divergent; (3) a labial crown face that is completely smooth; (4) a more developed labial basal ledge; (5) a single pair of lateral cusplets; and (6) a shallower nutrient groove.

Odontaspis watinensis tooth morphology bears some resemblance to *O. subulata* (Agassiz, 1843: pl. 37a, figs. 5, 6, as *Lamna subulata*) originally described from the Cenomanian of Germany. Both species have teeth with smooth crowns and needle-like cusps; however, the latter has a straight labial crown base, shorter cusplets, and more elongated root lobes.

Teeth with similar morphology have not been reported from any other known deposit.

Genus *Johnlongia* Siverson, 1996

Type species—*Johnlongia allocotodon* Siverson, 1996 from the Cenomanian of Western Australia (revised stratigraphy indicates Cenomanian-Turonian boundary in Siverson, 2007).

Johnlongia parvidens (Cappetta, 1973)

(Fig. 3.11K–N)

Synonymy list—Refer to Chapter 2, p. 49.

Referred material—UALVP 53203, fractured anterior tooth, locality 76; UALVP 53204, fractured lateral tooth, locality 76; UALVP 53205, anterior tooth, locality 76; UALVP 53206, lateral tooth, locality 76; UALVP 53207, 10 fractured teeth, locality 848.

Description—The anterior teeth have a tall and slender median cusp that is slightly distally inclined and strongly lingually directed. The convex labial face and strongly convex lingual face are smooth. The cutting edge is restricted to the apical third of the cusp. The lateral cusplets are missing but are needle-like in specimens recovered from other deposits. The lingual neck is narrow. The root contains a massive lingual protuberance that is bisected by a deep nutrient groove and has numerous foramina. The mesial lobe is typically more elongated than the distal lobe.

Lateral teeth have a broad-based median cusp that tapers to a sharp apex and is distally inclined. The slightly convex labial crown face has numerous strong enameloid folds that are restricted to the crown base. The lingual face is strongly convex and generally smooth. The mesial lateral cusplet is tall and needle-like, whereas the distal lateral cusplet is missing in the figured specimen (3.11L). The root is asymmetrical and is missing the distal root lobe and the terminal portion of the mesial root lobe. The lingual protuberance has a well developed nutrient groove and is significantly more labiolingually compressed compared to anteriorly positioned teeth. The median cusp and lateral cusplets are expanded mesodistally in distally positioned lateral teeth.

Remarks—The Watino specimens are the second documented report of *Johnlongia parvidens* from Canada. The first account was a single anterior tooth recovered from the Dunvegan Formation of Alberta (Cook et al., 2008). The anterior teeth described herein have a morphology similar to that anterior tooth.

Siverson (1996) erected *J. allocotodon* based on teeth collected from late Cenomanian deposits of Western Australia. According to Siverson (1996), the teeth of this species were readily distinguishable from the late Turonian *J. parvidens* type material (Cappetta, 1973) by the anterior teeth having a longer distal cutting edge, lateral teeth bearing ornamentation on the labial crown face, and the teeth having an overall larger size. A comparison of the distally positioned lateral teeth of these species could not be made because teeth from the posterior half of the jaw of *J. parvidens* were not included in the description of the type material (Siverson, 1996). The significance of these characters and the validity of *J. allocotodon* were discussed in Cook et al. (2008).

The lateral teeth recovered from the Watino localities have strong labial crown face ornamentation and a relatively labiolingually compressed root similar to the lateral teeth of *Johnlongia allocotodon.* As well, the anterior teeth described herein also have a distal cutting edge of similar length and are comparable in overall size to the Australian material (see Siverson, 1996: pl. 5). Although it is possible that both the Dunvegan and the Watino teeth belong to *J. allocotodon*, until re-examination of the type material and the recovery of additional topotypic teeth can be made, we conservatively assign these teeth to *J. parvidens*.

Family Otodontidae Glickman, 1964

Genus *Cretalamna* Glickman, 1958

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

Cretalamna ex. gr. *appendiculata* (Agassiz, 1843)

(Fig. 3.11O)

1843 *Otodus appendiculatus* Agassiz, p. 270, pl. 32, figs. 1–25.

1843 *Otodus latus* Agassiz, 1843; Agassiz, p. 271, pl. 32, fig. 26.

1845 *Otodus appendiculatus* Agassiz, 1843; Reuss, p. 5, pl. 3, figs. 23, 24.

1850 *Otodus appendiculatus* Agassiz, 1843; Dixon, 1850, pl. 30, fig. 25, pl. 31, fig. 17.

1852 *Otodus latus*? Agassiz, 1843; Gervais, pl. 76, fig. 23.

1856 *Otodus appendiculatus* Agassiz, 1843; Fischer, p. 141, pl. 2, fig. 38.

1870 *Otodus appendiculatus* Agassiz, 1843; Roemer, p. 323, pl. 36, fig. 6.

1872 *Otodus appendiculatus* Agassiz, 1843; Sauvage, p. 26, pl. 2, figs. 57–59.

1875 *Otodus appendiculatus* Agassiz, 1843; Geinitz, p. 294, pl. 65, figs. 6, 7.

1888 *Otodus appendiculatus* Agassiz, 1843; Fritsch, p. 5, fig. 5

1889 *Lamna appendiculata* (Agassiz, 1843); Woodward, p. 393.

1890 *Otodus appendiculatus* Agassiz, 1843; Davis, p. 402, pl. 41, figs. 1–11.

1897 *Lamna appendiculata* (Agassiz, 1843); Priem, p. 40, pl. 1, figs. 1–8

1900a *Lamna appendiculata* (Agassiz, 1843); Williston, p. 37, pl. 13, figs. 47, 48; pl. 14, fig. 3–3b.

1900b *Lamna appendiculata* (Agassiz, 1843); Williston, p. 247, pl. 31, figs. 47, 48; pl. 32, fig. 3–3b.

1900a *Lamna* sp.; Williston, pl. 12, fig. 12.

1900b *Lamna* sp.; Williston, pl. 30, fig. 12.

1902a *Lamna appendiculata* (Agassiz, 1843); Leriche, p. 111, pl. 3, figs. 28–38

1902b *Lamna appendiculata* (Agassiz, 1843); Leriche, p. 11.

1906 *Lamna appendiculata* (Agassiz, 1843); Leriche, p. 60 (in part), 70, 83, 84, 109.

1908 *Lamna appendiculata* (Agassiz, 1843); Priem, p. 464, fig. 5.

1911 *Lamna appendiculata* (Agassiz, 1843); Woodward, p. 206, pl. 44, figs. 3–5.

1913 *Lamna appendiculata* (Agassiz, 1843); Leriche, p. 78, pl. 10, figs. 3–5.

1929 *Lamna appendiculata* (Agassiz, 1843); Leriche, p. 242.

1935 *Odontaspis gigas* (Woodward, 1889); Dalinkevicius, p. 270 (in part), pl. 4, fig. 103.

1935 *Lamna appendiculata* (Agassiz, 1843); Dalinkevicius, p. 271.

1936 *Lamna appendiculata* (Agassiz, 1843); Leriche, p. 379, pl. 25, figs. 9, 10.

1943 *Lamna appendiculata* (Agassiz, 1843); Dartevelle and Casier, p. 128, pl. 6, figs. 1–12.

1952 *Lamna appendiculata* (Agassiz, 1843); Arambourg, p. 91, pl. 14.

1958 *Cretalamna appendiculata* (Agassiz, 1843); Glickman, p. 570.

1959 *Lamna appendiculata* (Agassiz, 1843); Dartevelle and Casier, p. 294, pl. 25, fig. 25, pl. 26, figs. 1–6, 8–10; pl. 27, fig. 5.

1960 *Lamna appendiculata* (Agassiz, 1843); Casier, p. 12, pl. 1, fig. 16.

1964 *Cretolamna appendiculata* (Agassiz, 1943); Glickman, p. 47, 104, pl. 3, figs. 4–6.

1967 *Cretolamna appendiculata* (Agassiz, 1843); Glickman, p. 340, pl. 5, figs. 15, 24.

1970 *Lamna appendiculata* (Agassiz, 1843); Applegate, p. 396, figs. 178f–h, 179c.

1975 *Cretolamna appendiculata lata* (Agassiz, 1843); Cappetta and Case, p. 21, pl. 3, figs. 10–28.

1977 *Cretolamna appendiculata* (Agassiz, 1843); Herman, p. 210, pl. 9, figs. 2–4.

1979 *Lamna appendiculata* (Agassiz, 1843); Evetts, p. 63, pl. 1, figs. 45–47.

1979 *Cretolamna appendiculata lata* (Agassiz, 1843); Case, p. 83, figs. 15–18.

1980 *Cretolamna borealis* (Priem, 1897); Glickman, pl. 10, fig. 12; pl. 21, figs. 1–5.

1981 *Cretolamna appendiculata* (Agassiz, 1843); Thurmond and Jones, p. 53, fig. 18.

1984 *Cretolamna appendiculata* (Agassiz, 1843); Lauginiger, pl. 1, fig.

15.

1985a *Cretolamna appendiculata* (Agassiz, 1843); Wolberg, p. 2, 4, fig. 3r–t.

1987 *Cretolamna appendiculata* (Agassiz, 1843); Cappetta, p. 99.

1987 *Cretolamna appendiculata* (Agassiz, 1843); Longbottom and Patterson, p. 249, text-fig. 11.2z, pl. 54, fig. 4.

1988 *Cretolamna appendiculata* (Agassiz, 1843); Case and Schwimmer, p. 295, fig. 5.9–5.12.

1989 *Cretolamna appendiculata* (Agassiz, 1843); Case, p. 67, fig. 2a.

1991 *Cretolamna appendiculata* (Agassiz, 1843); Kemp, pl. 4, fig. d.

1991 *Cretoxyrhina* cf. *mantelli* (Agassiz, 1843); Kemp, pl. 4, fig. h.

1991 *Cretolamna appendiculata* (Agassiz, 1843); Landermaine, p. 13, fig. 4a.

1991 *Cretolamna appendiculata* (Agassiz, 1843); Müller and Diedrich, p. 31, pl. 21, figs. 7, 8.

1992 *Cretolamna appendiculata* (Agassiz, 1843), Siverson, p. 528, pl. 1, figs. 1–17.

1993 *Cretolamna appendiculata* (Agassiz, 1843); Welton and Farish, p. 103, figs. 1–5; p. 104.

1993 *Cretolamna woodwardi* (Herman, 1977); Welton and Farish, p. 105, figs. 1–3.

1993 *Cretolamna appendiculata* (Agassiz, 1843); Williamson et al., p. 454, fig. 6.1–6.6.

1995 *Cretolamna appendiculata* (Agassiz, 1843); Uyeno and Suzuki, p 62, fig. 2a–d.

1996 *Cretolamna appendiculata* (Agassiz, 1843); Shimada, p. 8, fig. 5d, e.

1996 *Cretolamna appendiculata* (Agassiz, 1843); Siverson, p. 828, pl. 3, figs. 1–8.

1999 *Cretolamna appendiculata* (Agassiz, 1843); Trbusek, p. 56, pl. 3, figs. 2, 5.

1999 *Cretolamna* sp.; Trbusek, p. 56, pl. 3, fig. 1.

1999 *Cretolamna appendiculata* (Agassiz, 1843); Cappetta and Case, p. 22, text-figs. 5a–5h, 6, p. 62, pl. 6, fig. 10.

1999 *Cretolamna appendiculata* (Agassiz, 1843); Cappetta and Corral, p. 346, text-fig. 3a–c.

2000 *Cretolamna appendiculata* (Agassiz, 1843); Mustafa, p. 604, fig. 4.1–4.8.

2001 *Cretolamna appendiculata* (Agassiz, 1843); Case, p. 108, pl. 2, fig. 9.

2001a *Cretolamna appendiculata* (Agassiz, 1843); Case et al., p. 91, pl. 3, figs. 49–58.

2001b *Cretolamna appendiculata* (Agassiz, 1843); Case et al., p. 118, pl. 2, figs. 19, 20.

2001a *Cretolamna appendiculata* (Agassiz, 1843); Cicimurri, p. 34, fig. 7h.

2001 *Cretolamna appendiculata* (Agassiz, 1843); Gottfried et al., p. 495, fig. 2j.

2002 *Cretolamna appendiculata* (Agassiz, 1843); Mustafa et al., p. 428, fig. 5.1, 5.2.

2002 *Cretolamna appendiculata* (Agassiz, 1843); Antunes and Cappetta, p. 126, pl. 10, figs. 8–13.

2004 *Cretolamna appendiculata* (Agassiz, 1843); Cicimurri, p. 10, fig. 5f.

2006 *Cretalamna appendiculata* (Agassiz, 1843); Shimada et al., p. 15, fig. 10.5–10.8.

2008 *Cretalamna appendiculata* (Agassiz, 1843); Shimada and Martin, p. 94, fig. 6g.

2010 cf. *Cretalamna appendiculata* (Agassiz, 1843); Becker et al., p. 257, fig. 6.2–6.4.

2010 *Cretalamna* sp.; Underwood and Cumbaa, p. 914, pl. 4, fig. 1–2.

Referred material—UALVP 53208, fractured lateral tooth, locality 76.

Description—Lateral tooth containing a broad triangular median cusp that is labiolingually compressed and distally inclined. The labial crown face is slightly convex, whereas the lingual crown face is more strongly convex. Both faces are smooth. A distinct cutting edge runs continuously across the median cusp and a pair of triangular lateral cusplets. The preserved portion of the distal root lobe appears to be more robust than the rectangular-shaped mesial root lobe. A shallow U-shaped basal concavity separates the lobes. There is a very weak lingual protuberance that lacks a nutrient groove.

Remarks—The teeth of *Cretalamna appendiculata* species group have been reported from various North American deposits including: the Albian through Maastrichtian of Texas (Welton and Farish, 1993), the Turonian of New Mexico (Wolberg, 1985), the late Cenomanian and Turonian of Arizona

(Williamson et al., 1993), the middle Cenomanian of Colorado (Shimada et al., 2006), the late Cenomanian of Kansas (Shimada and Martin, 2008), and the late Cenomanian and middle Turonian of South Dakota and Wyoming (Cappetta, 1973; Cicimurri, 2001a, 2004). Cumbaa et al. (2006) reported the teeth of this species from the Carrot River bone bed of Saskatchewan. Underwood and Cumbaa (2010: p. 916) noted that these teeth, along with a single tooth recovered from the Bainbridge bone bed, differ from *C. appendiculata* by "possessing a more robust root with a far more rounded profile." As such, these teeth were left in open nomenclature. They also suggest that teeth allocated to *C. appendiculata* from different localities are of variable morphology and most likely represent multiple species, a view shared herein. Compared to the Saskatchewan material, UALVP 53208 has an angular root morphology that is more reminiscent of *C. appendiculata.* However, more and better preserved material will need to be recovered from the Watino localities before we can conclusively report the presence of *C. appendiculata*. Despite this taxonomic uncertainty, *Cretalamna* material from the Cenomanian of Canada appears to be rare (Cumbaa et al., 2006; Underwood and Cumbaa, 2010).

Family Incertae sedis

Genus *Cretodus* Sokolov, 1965

Type species—*Otodus sulcatus* Geinitz, 1843 from the Coniacian of the Czech Republic.

Cretodus semiplicatus (Münster *in* Agassiz, 1843)

(Fig. 3.12A)

Synonomy list—Refer to Chapter 2, p. 52.

Referred material—UALVP 53209, fractured lateral tooth, locality 76; UALVP 53210, fractured lateral tooth, locality 76.

Description—This lateral tooth contains a tall, triangular median cusp that is slightly distally inclined. The labial crown face is slightly convex, whereas the lingual crown face is strongly convex. A pair of divergent triangular lateral cusplets flanks the median cusp. A distinct cutting edge runs continuously between the cusps. Strong vertical enameloid folding is restricted to the basal half of the median cusp and lateral cusplets labially. The lingual face of the median cusp and lateral cusplets contains folds that approach the apex. The distinct lingual neck is narrow. The root is damaged and is missing a large portion of the distal lobe and the terminal region of the mesial lobe. The root lobes are separated by a deep basal concavity. The well developed lingual protuberance lacks a nutrient groove but contains a cluster of large foramina.

Remarks—Cook et al. (2008) reported the recovery of juvenile teeth of *Cretodus semiplicatus* from the middle Cenomanian Dunvegan Formation of Alberta. The recovery of *C. semiplicatus* teeth from various middle Cenomanian-middle Turonian deposits throughout the WIS was summarized in that paper. Cumbaa et al. (2006: fig. 4.11) figured posterior teeth of this species from the Bainbridge bone bed of Saskatchewan. Subsequently, Underwood and Cumbaa (2010) suggested that these posterior teeth in fact belong to *Archaeolamna kopingensis*, an observation shared herein.

Teeth from the congeneric taxon *Cretodus longiplicatus* were first described by Werner (1989) from the late Cenomanian of Bahariya, Egypt. Later, Cappetta and Case (1999) synonymised this taxon with *C. semiplicatus*. Based on teeth recovered from the early Cenomanian of India, Underwood et al. (2011: p. 548) reinstated *C. longiplicatus* as a valid species based on the "long and very robust longitudinal ridges on both labial and lingual faces of the crown" present throughout the ontogeny of the species. They proposed that this crown ornamentation was less developed and the maximum tooth size was larger in the chronostratigraphically younger *Cretodus semiplicatus.* Underwood et al. (2011: p. 549) also stated that *C. longiplicatus* was "absent north of Tethys in either Eurasia or the Western Interior Seaway." The partially complete *C. longiplicatus* anterior tooth figured by Underwood et al. (2011: fig. 8e, f) is approximately the same size as the *C. semiplicatus* specimen described herein. Both the Watino and Indian teeth have a similar overall morphology and pattern of enameloid folding. A juvenile tooth from the middle Cenomanian of Alberta also has prominent enameloid folds that extend most of the length of the crown. Consequently, the re-validation of *C. longiplicatus* based on the length of crown folding and stratigraphy is contraindicated by the Alberta specimens and this taxon is considered invalid herein. Differences in the length of enameloid folding between early-middle Turonian occurrences of *C. semiplicatus* is likely attributed to intraspecific variation.

Genus *Dallasiella* Cappetta and Case, 1999

Type species—*Dallasiella willistoni* Cappetta and Case, 1999 from the Turonian-Coniacian boundary of Texas, USA.

Dallasiella willistoni Cappetta and Case, 1999

(Fig. 3.12B–H)

Synonomy list—Refer to Chapter 2, p. 57.

Referred material—UALVP 53211, lateral tooth, locality 76; UALVP 53212, fractured lateral tooth, locality 848; UALVP 53213, fractured anterior tooth, locality 848; UALVP 53214, fractured lateral tooth, locality 848; UALVP 53215, fractured lateral tooth, locality 76; UALVP 53216, lateral tooth, locality 848; UALVP 53217, fractured lateral tooth, locality 76; UALVP 53218, 10 fractured teeth, locality 848.

Description—Anterior teeth have a tall narrow median cusp that is more or less erect and is slightly lingually directed. The cusp has a more or less flat labial face and a strongly convex lingual face. Both faces are smooth. The cutting edge runs continuously between the median cusp and a pair of tall triangular lateral cusplets. The height of the narrow lingual neck is constant between the median cusp and lateral cusplets. The sigmoidal basal ledge of the labial crown face overhangs the labial root face. The root is more or less symmetrical and contains root lobes that are distinctly labiolingually compressed. The lingual protuberance is very well developed and bears a large nutrient foramen that is situated in a small nutrient groove. Additional foramina are present throughout the labial root face, particularly concentrated in the medial region below the crown root border. The basal concavity is deep and U-shaped.

Lateral teeth have a narrow median cusp that is distally inclined. The labial crown face is more or less flat, whereas the lingual crown face is strongly convex. Both faces are smooth. A distinct cutting edge runs continuously across the median cusp and a pair of broad triangular lateral cusplets. A second mesial cusplet may be present in distally positioned lateral teeth. The lingual neck is narrow. The basal ledge only slightly overhangs the labial root face and is sigmoidal. The mesial and distal root lobes are more or less symmetrical, divergent and labiolingually compressed. The lingual protuberance is well developed and contains a deep nutrient groove that houses a large nutrient foramen. Numerous smaller foramina are concentrated below the crown root border on the labial root face. The basal concavity is shallow in the most distally positioned lateral teeth.

Remarks—Cook et al. (2008, Chapter 2) described *Dallasiella willistoni* from the middle Cenomanian of Alberta. This species has been reported from the Turonian-Coniacian of Texas (Cappetta and Case, 1999) and the middle Turonian of Montana (Siverson and Lindgren, 2005). The general tooth morphology of *Dallasiella* is similar to that of *Cretalamna*; however, the latter lacks a deep nutrient groove (Cappetta and Case, 1999). The strong labiolingual compressed root lobes also differentiate this species from juvenile *Archaeolamna* teeth which may also possess a nutrient groove, although less developed (Underwood and Cumbaa, 2010). A tooth described as *Cretodus* sp. by Case et al. (1990: fig. 7e, f) from the lower Turonian Favel Formation of Saskatchewan strongly resembles the Watino specimens and is considered conspecific herein.

Genus *Dwardius* Siverson, 1999

Type species—*Cretolamna woodwardi* Herman, 1977 from the Cenomanian of England.

Dwardius woodwardi (Herman, 1977)

(Fig. 3.12I)

1911 *Lamna appendiculata* Agassiz, 1835; Woodward, p. 206, figs. 63–64.

1977 *Cretolamna woodwardi* Herman, p. 207, pl. 9, fig. 1.

1996 *Pseudoisurus tomosus* Glickman, 1957; Siverson, p. 831, pl. 3, figs. 14–16, pl. 4, figs. 1–4.

Referred material—UALVP 53219, lateral tooth, locality 76.

Description—This is a large lateral tooth that possesses a tall, broad-based triangular median cusp. The labial face of the crown is slightly convex, whereas the lingual face is strongly convex. Both faces are smooth. A well developed cutting edge runs continuously across the median cusp and a robust pair of triangular lateral cusplets. A well developed and medially thick lingual neck is present. The distal root lobe is slightly more robust than the mesial root lobe. The root lobes are separated by a deep U-shaped basal concavity. A well-developed lingual protuberance contains a large nutrient foramen. Numerous additional foramina are distributed throughout the labial face of the root, with a noticeable concentration situated at the crown-root boundary.

Remarks—Glickman (1958) erected the genus *Cretalamna* and designated *C. appendiculata* as the type species. Later, Herman (1977) erected the species *Cretalamna woodwardi* based on teeth collected from the middle or late Cenomanian deposits of southern England. Siverson (1999) recognized that the root morphology of *C. woodwardi* was distinct from that of the *C. appendiculata* and erected the genus *Dwardius* to accommodate the species.

The tooth morphology of *Dwardius* and *Cardabiodon* is difficult to distinguish. The primary means of separating these two taxa is based on differences in the relative size and median cusp inclination of anterior teeth compared to lateral teeth within the jaw of each species (Siverson, 1999). However, the teeth of *Dwardius* have a flatter labial crown face (Siverson, 1996), more robust lateral cusplets, lack a pair of weakly developed heels situated outside the cusplets, and have a higher positioned lingual protuberance (see Siverson, 1999: fig. 10.4–10.6).

The teeth of *Dwardius woodwardi* also share a similar morphology to the teeth of *Archaeolamna kopingensis judithensis* which has been recovered from Campanian deposits of Alberta, Montana, and Wyoming (Case, 1978, 1987; Siverson, 1992, 1996; Beavan and Russell, 1999). Siverson (1999) noted that the narrow lingual neck of the teeth of *Archaeolamna* varies very little in height between the lateral cusplet and the median cusp regions, whereas the lingual neck of teeth of *Dwardius* is narrow towards the lateral cusplets and much higher in the region of the median cusp. As well, the upper two-thirds of the median cusp is generally narrower in large *Archaeolamna* teeth than it is in *Dwardius.* Juvenile anterior teeth of the latter are also more robust and all *Dwardius* teeth show little ontogenetic change in lateral cusplet morphology (Siverson, 1999; M. Siverson, personal communication, 2010). UALVP 53219 is consistent with the tooth morphology of *D. woodwardi*.

This is the first known report of *Dwardius woodwardi* from North America. Teeth identified by Williamson et al. (1993) as "*Cretolamna*" *woodwardi* from the lower Turonian of Arizona, USA have been reassigned to

Cardabiodon venator (Siverson and Lindgren, 2005). As well, teeth identified as *Cretalamna woodwardi* from the Turonian of Texas by Welton and Farish (1993) have an overall morphology more similar to *Cretalamna* than to *Dwardius,* and should therefore be retained in the genus *Cretalamna*.

Order Rajiformes Berg, 1940

Family Rhinobatidae Müller and Henle, 1838

Genus *Rhinobatos* Linck, 1790

Type species—*Rhinobatos rhinobatos* Linnaeus, 1758; extant.

Rhinobatos incertus Cappetta, 1973

(Fig. 3.12J–K)

1973 *Rhinobatos incertus* Cappetta, p. 508, figs. 26–33.

1973 *Rhinobatos* sp.; Cappetta, p. 508, figs. 18–25.

1990 *?Rhinobatos* sp.; Case et al., p. 1093, figs. 12, 13.

1993 *Rhinobatos* sp.; Williamson et al., p. 458, fig. 8.

1993 *Rhinobatos incertus* Cappetta, 1973; Welton and Farish, p. 132, figs 1, 2.

2001a *Rhinobatos incertus* Cappetta, 1973; Cicimurri, p. 185, fig. 7x.

2004 ?*Rhinobatos incertus* Cappetta, 1973; Cicimurri, p. 9, fig. 5j.

2006 *Rhinobatos* sp.; Shimada et al., p. 19, fig. 11.3–11.4.

2007 *Rhinobatos incertus* Cappetta, 1973; Everhart, p. 230, fig 6a–d.

Referred material—UALVP 53220, female tooth, locality 76; UALVP 53221, male tooth, locality 76; UALVP 53222, 79 teeth, locality 76; UALVP 53223, 109 teeth, locality 848.

Description—Teeth are extremely small. The crown is mesodistally elongated and lacks ornamentation. The labial face is slightly convex and contains a rounded crown foot. A distinct lingually directed narrow cusp may be present (UALVP 53221; Fig. 3.12K) or may be reduced or absent (UALVP 53220; Fig. 3.12J). In the non-cuspate condition, there is a cutting edge separating the labial and lingual crown faces. In the cuspate condition, this cutting edge is not defined. The lingual crown face bears a narrow and elongated central uvula which is separated by less developed lateral uvulae by deep grooves. The root is displaced slightly lingually below the crown and is divided into two lobes by a deep nutritive groove which contains a large foramen. Additional foramina are located on the basal surface of each root lobe and on the root face on either side of the central uvula.

Remarks—The teeth of *Rhinobatos* are sexually dimorphic. Males in the breeding phase possess a crown with a distinct sharp and elongated cusp, whereas females and non-breeding males lack this structure (Kajiura and Tricas, 1996; Everhart, 2007). Cappetta and Case (1999) noted that *Rhinobatos incertus* can be differentiated from other species of *Rhinobatos* by its distinct cusp, lack of sharp cutting edges, and lateral uvulae that are weakly developed. These characteristics are observed in the male specimens recovered from Watino.

Rhinobatos incertus has been described from North American localities including the lower Turonian and Coniacian of Texas (Welton and Farish, 1993), the lower Turonian of Arizona (Williamson et al., 1993, as *Rhinobatos* sp.), the middle Cenomanian of Colorado (Shimada et al., 2006, as *Rhinobatos* sp.), late Albian to early Campanian of Kansas (Shimada and Martin, 2008; Everhart, 2007), the late Cenomanian and middle and late Turonian of South Dakota (Cappetta, 1973; Cicimurri, 2001a, 2004), and the middle Cenomanian (Underwood and Cumbaa, 2010, as *Rhinobatos* cf. *incertus*) and the lower Turonian (Case et al., 1990, as *Rhinobatos* sp.) of Saskatchewan.

DISCUSSION

The assemblage described herein includes 18 species belonging to at least 3 orders, at least 11 families, and 15 genera, with the most abundant remains belonging to two different species of *Squalicorax*. It is the first description of the new species *Odontaspis watinensis*. It is also the first known occurrence of cf. *Polyacrodus illingsworthi*, *Scapanorhynchus* sp., and *Carcharias* aff. *C. striatula* from Canada and extends the northern geographical range of these taxa within the WIS. It is also the first North American report of *Dwardius woodwardi.*

The Watino euselachian assemblage has many species in common with an early Turonian assemblage recovered from the Keld Member of the Favel Formation in east-central Saskatchewan (Case et al., 1990) (Table 1). The latter assemblage was situated at a relatively similar paleolatitude and deposited in an offshore environment (Cumbaa and Tokaryk, 1999; Cumbaa et al., 2006; Wu et al., 2001). Both the Watino and Favel assemblages share at least five taxa (*Ptychodus anonymus*, *Squalicorax* sp. A, *Archaeolamna* ex. gr. *kopingensis*, *Odontaspis saskatchewanensis*, and *Rhinobatos incertus*). As mentioned above, a tooth identified as *Cretodus* sp. by Case et al. (1990: fig. 7e, f) from the Favel assemblage strongly resembles *Dallasiella willistoni.* A second *Cretodus* sp. tooth

(Case et al., 1990: fig. 7c, d) may belong to a *Cretoxyrhina* neonate. The Saskatchewan assemblage has two species (*Carcharias lilliae* and *Cretomanta canadensis*) that have not been recovered from Watino. Conversely, 11 species (*Meristodonoides rajkovichi,* cf. *Polyacrodus illingsworthi*, *Squalicorax* sp. B, *Cardabiodon ricki*, *Scapanorhynchus* sp., *Carcharias* aff. *C. striatula*, *Odontaspis watinensis*, *Johnlongia parvidens*, *Cretalamna* ex. gr. *appendiculata*, *Cretodus semiplicatus*, and *Dwardius woodwardi*) are present in the Watino assemblage but absent in the Favel assemblage.

Temperature and salinity are the principal physical factors influencing extant selachian distribution (Simpfendorfer and Heupel, 2004). Accordingly, habitat selection may have contributed to the difference in the faunal composition between the Watino and Favel assemblages. Despite only a 6º separation in paleolatitude (PLATES project, 2010), sea surface temperature along each coast of the WIS was likely disparate. Using model simulations, Slingerland et al. (1996) proposed a counterclockwise estuarine circulation for the WIS. The outflow of freshwater drainage drew cooler Boreal water down the western margin and carried warmer Tethyan water up the eastern shoreline resulting in distorted isotherms. It is possible that there may have been a 6ºC difference in water temperature between the Watino and Favel localities during the early Turonian (see Slingerland et al., 1996: fig. 6). The northward movement of warm Tethyan warm along the eastern side of the WIS is supported by foraminiferal distribution studies (Eicher and Diner, 1985; Fisher et al., 1994; Schröder-Adams et al., 1996, 2001). Temperature intolerance to warmer water may account for the absence of *Carcharias* aff. *C. striatula*, *Odontaspis watinensis*, and *Dwardius* *woodwardi* from the Favel assemblage, as these species have not been recovered from additional WIS assemblages situated in presumed warmer WIS isotherms. Conversely, the absence of *Carcharias lilliae* and *Cretomanta canadensis* from Watino may suggest that these species avoided cooler waters. It should be noted that *Odontaspis watinensis* and *Carcharias lilliae* have not been reported outside of the Watino and Favel assemblages, respectively, and may indicate that these species were endemic to these particular regions. Temperature intolerance, however, cannot explain the absence of *Meristodonoides rajkovichi,* cf. *Polyacrodus illingsworthi*, *Squalicorax* sp. B, *Cardabiodon ricki*, *Scapanorhynchus* sp., *Johnlongia parvidens*, *Cretalamna* ex. gr. *appendiculata*, and *Cretodus semiplicatus* from the Favel assemblage, as these species have been recovered from contemporaneous assemblages in similar or warmer isotherms of the WIS. Salinity, an additional factor shaping elasmobranch distribution, does not appear to be markedly different according to the model at both localities (see Slingerland et al., 1996: fig. 8) and likely did not contribute to the variation in diversity.

Biotic factors, such as the availability of prey, also influence elasmobranch distribution (Simpfendorfer and Heupel, 2004; Heithaus et al., 2002). Associated with the Favel euselachian assemblage, Cumbaa and Tokaryk (1999) reported the teleost remains of *Xiphactinus audax*, *Ichthyodectes*, *Gillicus*, *Apsopelix anglicus*, *Pachyrhizodus minimus*, *Enchodus*, and *Protosphyraena.* From the Watino sandstone, Wilson and Chalifa (1989) reported *Belonostomus* cf. *B. longirostris*, *Ichthyodectes ctenodon*, *Apateodus* sp., *Cimolichthys* cf. *C. levesiensis*, cf. *Dercetoides* sp., and *Enchodus* cf. *E. shumardi.* Additional early

Turonian taxa were recovered from Watino concretions and included cf. *Gillicus* sp., cf. *Xiphactinus* sp., *Osmeroides* cf. *O. delicates*, and *Leucichthyops* sp. material (Wilson and Chalifa, 1989). Both the Watino and Favel localities have numerous teleosts, as juvenile and/or adult forms, that could serve as potential prey items. Therefore, a disparate food source fails to adequately explain the variation in euselachian diversity between the Watino and Favel assemblages.

With the exception of *Squalicorax* sp. B., the aforementioned taxa absent from the Favel assemblage are only represented by rare elements in the Watino euselachian assemblage. Hence, the difference in faunal composition may be the result of collecting bias. The absence of *Squalicorax* sp. B teeth in the Favel assemblage is puzzling, as it is among the most abundant euselachian material recovered from Watino and has been reported from the middle Cenomanian of Saskatchewan (Cumbaa et al., 2006, as *S. volgensis*).

Comparing the early Turonian Watino assemblage with the middle Cenomanian assemblages recovered from the Bainbridge bone bed of east-central Saskatchewan (Cumbaa et al., 2006; Underwood and Cumbaa, 2010) and the Dunvegan Formation of northwestern Alberta (Cook et al., 2008), we are able to document changes in faunal composition from middle Cenomanian to early Turonian in the northern region of the seaway (Table 1). The Bainbridge assemblage, recovered from the Bell Fourche Member of the Ashville Formation, contains five species (*Meristodonoides rajkovichi*, *Squalicorax* sp. A, *Archaeolamna* ex. gr. *kopingensis*, *Cretalamna* ex. gr. *appendiculata*, and *Rhinobatos incertus*) in common with the Watino assemblage. Nine species (*Ptychodus* ex. gr. *decurrens*, *Ptychodus rhombodus*, *Palaeoanacorax* aff.

pawpawensis, *Cretoxyrhina denticulata*, *Carcharias paucicorrugata*, *Roulletia canadensis*, *Orectoloboides angulatus*, *Cretorectolobus robustus*, and *Cretomanta canadensis*) are present in the Bainbridge assemblage but absent in the Watino assemblage. Conversely, 11 species (cf. *Polyacrodus illingsworthi*, *Squalicorax* sp. B, *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *Scapanorhynchus* sp., *Carcharias* aff. *C. striatula*, *Odontaspis saskatchewanensis*, *Odontaspis watinensis*, *Cretodus semiplicatus*, *Dallasiella willistoni*, and *Dwardius woodwardi*) are present in the Watino assemblage but absent in the Bainbridge assemblage.

The Dunvegan assemblage is believed to represent a marginal marine fauna that likely endured periodic fluctuations in salinity due to the influx of fresh water (Cook et al., 2008). Although less productive than the Watino assemblage, five species (*Meristodonoides rajkovichi*, *Squalicorax* sp. A, *Archaeolamna* ex. gr. *kopingensis*, *Cretodus semiplicatus*, and *Johnlongia parvidens*) are common to both assemblages. Two species *(Protolamna carteri* and *Pseudohypolophus mcnultyi*) are present in the Dunvegan assemblage but absent in the Watino assemblage, whereas 13 species (cf. *Polyacrodus illingsworthi*, *Ptychodus anonymus*, *Squalicorax* sp. B, *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *Scapanorhynchus* sp., *Carcharias* aff. *C. striatula*, *Odontaspis saskatchewanensis*, *Odontaspis watinensis*, *Cretalamna* sp., *Dallasiella willistoni*, *Dwardius woodwardi*, and *Rhinobatos incertus*) are exclusive to the latter.

Of the 10 species (*Ptychodus* ex. gr. *decurrens*, *Ptychodus rhombodus*, *Palaeoanacorax* aff. *pawpawensis*, *Protolamna carteri, Carcharias paucicorrugata*, *Roulletia canadensis*, *Orectoloboides angulatus*, *Cretorectolobus* *robustus*, *Pseudohypolophus mcnultyi*, and *Cretomanta canadensis*) present in the middle Cenomanian Dunvegan and Bainbridge assemblages but absent in the early Turonian Watino assemblage, five species (*Ptychodus rhombodus*, *Palaeoanacorax* aff. *pawpawensis*, *Protolamna carteri*, *Orectoloboides angulatus,* and *Cretorectolobus robustus*) have not been recovered from WIS deposits younger than the middle Cenomanian. Teeth recovered from early late Cenomanian deposits of South Dakota (Cicimurri, 2001a: fig. 7m) and Kansas (Shimada and Martin, 2008: fig. 5g) and identified as *Carcharias* aff. *amonensis* and *Carcharias amonensis*, respectively, have a morphology more similar to that of *Roulletia canadensis.* This latter species was reported to be "extremely common" in the Bainbridge assemblage (Underwood and Cumbaa, 2010: p. 9210) but is absent at Watino. As such, this species may have been restricted to middle to early late Cenomanian deposits. *Cretoxyrhina denticulata* also appears to be restricted to the Cenomanian.

Of the 10 species (cf. *Polyacrodus illingsworthi*, *Squalicorax* sp. B, *Cardabiodon ricki*, *Scapanorhynchus* sp., *Carcharias* aff. *C. striatula*, *Odontaspis saskatchewanensis*, *Odontaspis watinensis*, *Dallasiella willistoni*, and *Dwardius woodwardi*) recovered from the early Turonian Watino assemblage but absent from the middle Cenomanian Dunvegan and Bainbridge assemblages, only two species (*Odontaspis watinensis* and *Dallasiella willistoni*) have not been reported from other deposits older than the Cenomanian-Turonian boundary.

In summary, euselachians that occurred before the Cenomanian-Turonian boundary in the Canadian region of the WIS include: *Ptychodus* ex. gr. *decurrens*, *Ptychodus rhombodus*, *Palaeoanacorax* aff. *pawpawensis*, *Cretoxyrhina* *denticulata*, *Carcharias paucicorrugata*, *Roulletia canadensis*, *Protolamna carteri*, *Orectoloboides angulatus*, *Cretorectolobus robustus*, and *Pseudohypolophus mcnultyi*. Euselachians present after the Cenomanian-Turonian boundary in this region include: cf. *Polyacrodus illingsworthi*, *Ptychodus anonymus*, *Squalicorax* sp. B, *Cardabiodon ricki*, *Cretoxyrhina mantelli*, *Scapanorhynchus* sp., *Carcharias* aff. *C. striatula*, *Odontaspis saskatchewanensis*, *Odontaspis watinensis*, *Dallasiella willistoni*, and *Dwardius woodwardi.* Species with a biostratigraphical range extending across the Cenomanian-Turonian boundary in the northern region include: *Meristodonoides rajkovichi*, *Squalicorax* sp. A, *Archaeolamna* ex. gr. *kopingensis*, *Cretalamna* ex. gr. *appendiculata*, *Johnlongia parvidens*, and *Rhinobatos incertus*. Including the species recovered from the aforementioned early Turonian Favel assemblage (Case et al., 1990), *Cretomanta canadensis* spans the Cenomanian-Turonian boundary, whereas *Carcharias lilliae* is reported only from the early Turonian.

Benthic and/or nectobenthic euselachians are a rare faunal component in the Watino assemblage. Only two taxa, *Ptychodus* and *Rhinobatos*, reported from this assemblage likely had a benthic and/or nectobenthic habitat preference. The former has a grinding-type tooth morphology indicative of a durophagous lifestyle (Cappetta, 1987); this lifestyle is also supported by the observation of Shimada et al. (2009: p. 334), who noted that the scale morphology of *Ptychodus occidentalis* suggested this species was a “sluggish swimmer that likely cruised near or at the ocean floor at low speeds.” The crushing-type dentition of the batoid *Rhinobatos* also indicates a benthic habit (Cappetta, 1987). Modern representatives of this taxon occur in the tropical to temperate waters of continental shelves (Nelson, 2006).

The scarcity of benthic euselachians at Watino, and in other northern assemblages, may be due to the persistent anoxic bottom waters of a stratified water column (Cumbaa et al., 2010). This stratification may have been the result of a freshwater layer sitting on top of the marine waters, or the production of a denser intermediate body of water through the mixing of boreal and Tethyan water masses. The migration of a planktonic Tethyan fauna into the northern region of the seaway during the time of peak transgression resulted in an accumulation of organic-carbon in the bottom waters, which in turn lead to an anoxic environment (Hay et al., 1993; Schröder-Adams et al., 1996, 2001). Schröder-Adams et al. (1996) noted that during the Cenomanian-Turonian sea-level high stand, the diversity of calcareous and agglutinated benthic foraminifera and nannofossils in the northern region of the WIS was significantly reduced compared to the southern region of the WIS, probably because of strong circulation between the seaway and the Tethys. The rarity of benthic and/or nectobenthic euselachian taxa at Watino is consistent with the presence of an anoxic bottom environment. However, the occurrence of *Ptychodus* and *Rhinobatos* indicates at least some periodic mixing of deeper anoxic waters with oxygenated surface layers in this region, possibly as major storms tracked across the seaway allowing benthic organisms to survive in the area at least occasionally.

Underwood and Cumbaa (2010: p. 940) also noted that the Bainbridge assemblage was “dominated by pelagic predators” with few benthic or nectobenthic species recovered. In addition to *Ptychodus* and *Rhinobatos*, they reported the orectolobiforms *Orectoloboides angulatus* and *Cretorectolobus robustus*. The clutching-type tooth morphology of these species is also consistent with a benthic or nectobenthic paleoenvironmental preference (Case, 1978; Cappetta, 1987; Bourdon & Everhart, 2010). With the notable exception of the tropical and warm temperate pelagic species *Rhincodon typus*, extant orectolobiforms are typically tropical, coastal, and benthic (Musick et al., 2004). The rare recovery of the teeth of benthic species in the Bainbridge fauna was attributed to infrequent transient individuals to the region (Underwood and Cumbaa, 2010).

Watino shares many species with two lower middle Turonian assemblages recovered from the Fairport Chalk Member of the Carlile Formation in western Russell and southern Ellis counties of north central Kansas (Figs. 3.13, 3.14; Table 3.2). Approximately 3 m of basal Fairport Chalk and the entire underlying Pfeifer Member of the Greenhorn Limestone is exposed at the western Russell County site. The teeth from this locality were surface collected from the lowermost 2 m of the Fairport Chalk in 2007 and 2008 (by MJE). Along with the euselachian teeth were the remains of *Inoceramus culveri* and *Pseudoperna bentonensis*, and small molds of *Collignoniceras woollgari* (MJE, personal observation). The stratigraphy of the southern Ellis County site was previously described by Everhart and Darnell (2004) during the description of a *Ptychodus mammillaris* tooth recovered from this locality. Fragmentary valves of *Inoceramus culveri* and *Pseudoperna congesta* were also observed in this exposure. The Kansas localities are believed to represent an offshore environment of normal salinity at a probable depth of less than 100 m (Hattin, 1962).

The Kansas teeth figured herein (Figs. 3.13, 3.14) are catalogued in the collections at the Fort Hays State University Sternberg Museum of Natural History (FHSM). Of the seven species (*Ptychodus mammillaris*, *Squalicorax* sp. A, *Squalicorax* sp. B, *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon* sp., *Cretoxyrhina mantelli*, and *Dallasiella willistoni*) recovered from these Kansas localities, only one species (*Ptychodus mammillaris*) has not been recovered at Watino. In addition, a single *Johnlongia parvidens* (FHSM VP-15721) tooth was also recovered from the southern Ellis County locality (MJE, personal observation).

Williamson et al. (1993) reported numerous euselachian taxa from late Cenomanian-middle Turonian deposits at Black Mesa, Arizona (Table 3.2). The early Turonian lower shale member of the Mancos shale was deposited in water exceeding storm wave-base (Kirkland, 1991). Six species (*Squalicorax* sp. A, *Cardabiodon* sp. (as *Cretodus woodwardi*, see Siverson and Lindgren, 2005), *Cretoxyrhina mantelli*, *Scapanorhynchus* sp., *Cretalamna* ex. gr. *appendiculata*, and *Rhinobatos incertus*) reported from the lower Turonian Mancos Shale are also present in the Watino assemblage. Five species (*Ptychodus decurrens*, *P. marginalis* (as *P*. cf. *P. mammillaris*, see Hamm, 2010b), *P. whipplei*, *Chiloscyllium greeni*, and *Texatrygon rubyae* (as *Ptychotrygon rubyae*, see Cappetta, 2006)) are reported from the Arizona assemblage but are absent at Watino. Conversely, ten species (*Meristodonoides rajkovichi*, cf. *Polyacrodus illingsworthi*, *Ptychodus anonymus*, *Squalicorax* sp. B, *Archaeolamna* ex. gr. *kopingensis*, *Carcharias* aff. *C. striatula*, *Odontaspis watinensis*, *Johnlongia parvidens*, *Dallasiella willistoni*, and *Dwardius woodwardi*) are present in the

Watino assemblage but absent in the lower Turonian of Arizona. Williamson et al. (1993) reported *Meristodonoides rajkovichi* (as *Hybodus* sp., see Underwood and Cumbaa, 2010) from late Cenomanian and middle Turonian deposits of this southern region. As discussed above, the three *Ptychodus* species recovered from Arizona likely had a benthic and/or nectobenthic habitat. The clutching-type dentition of the orectolobiform *Chiloscyllium greeni* and the grinding-type dentition of the batoid *Texatrygon rubyae* also suggest a preference for a benthic habitat (Cappetta, 1987). The greater number of benthic species in this assemblage suggests the bottom waters of this region were likely more productive, quiet, and better oxygenated compared to waters further north.

In summary, seven species (*Squalicorax* sp. A, *Cretoxyrhina mantelli*, *Scapanorhynchus* sp., *Cretalamna* ex. gr. *appendiculata*, *Cretodus semiplicatus*, *Rhinobatos incertus*, and *Cretomanta canadensis*) have a distribution within the WIS that spans approximately 20º of paleolatitude (PLATES project, 2010) from Arizona to northwest Alberta during the early Turonian. All seven species have also been recovered from Cenomanian and/or Turonian deposits of Texas (Welton and Farish, 1993; Cappetta and Case, 1999). Of the additional species recovered species recovered from the Canadian region of the WIS, *Meristodonoides rajkovichi*, cf. *Polyacrodus illingsworthi*, *Ptychodus anonymus*, *Squalicorax* sp. B, and *Odontaspis saskatchewanensis* have also been reported from Cenomanian and/or Turonian deposits of Texas (Welton and Farish, 1993; Cappetta and Case, 1999). *Dallasiella* material has also been reported from the Turonian-Coniacian of Texas (Cappetta and Case, 1999). Conversely, *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon ricki*, *Carcharias* aff. *C. striatula*, *Odontaspis watinensis*, *Johnlongia parvidens*, and *Dwardius woodwardi* have not been recovered from the rich deposits of Texas and may have been restricted to cooler waters.

Table 3.1. List of euselachian taxa in the early Turonian Watino assemblage and comparison with the early Turonian Favel assemblage (Case et al., 1990) and middle Cenomanian Bainbridge bonebed assemblage of Saskatchewan (Underwood and Cumbaa, 2010), and middle Cenomanian Dunvegan Formation assemblage of Alberta, Canada (Cook et al., 2008, Chapter 2).

	early Turonian		**middle Cenomanian**	
	Alberta (Watino)	**Saskatchewan (Favel)**	**Alberta (Dunvegan)**	**Saskatchewan (Bainbridge)**
Meristodonoides rajkovichi[1]	X	-	X	X
Polyacrodus illingsworthi[2]	X	-	-	-
Ptychodus anonymus[3]	X	X	-	-
Ptychodus ex. gr. *decurrens*	-	-	-	X
Ptychodus rhombodus	-	-	-	X
Ptychodus sp.	-	-	-	X
Squalicorax sp. A[4]	X	X	X	X
Squalicorax sp. B	X	-	-	-
Palaeoanacorax aff. *pawpawensis*	-	-	-	X
Archaeolamna ex. gr. *kopingensis*[5]	X	X	X	X
Cardabiodon ricki	X	-	-	-
Cretoxyrhina denticulata[6]	-	-	X	X
Cretoxyrhina mantelli	X	X	-	-
Protolamna carteri	-	-	X	-
Scapanorhynchus sp.	X	-	-	-
Carcharias lilliae	-	X	-	-
Carcharias paucicorrugata[7]	-	-	-	X
Carcharias aff. *C. striatula*	X	-	-	-
Odontaspis saskatchewanensis	X	X	-	-
Odontaspis watinensis nov. sp.	X	-	-	-
Johnlongia parvidens	X	-	X	-
Roulletia canadensis	-	-	-	X
Cretalamna ex. gr. *appendiculata*[8]	X	-	-	X
Cretodus semiplicatus	X	-	X	-
Dallasiella willistoni[9]	X	X	X	-
Dwardius woodwardi	X	-	-	-
Orectoloboides angulatus	-	-	-	X
Cretorectolobus robustus	-	-	-	X
Pseudohypolophus mcnultyi	-	-	X	-
Rhinobatos incertus[10]	X	X	-	X
Cretomantis canadensis	-	X	-	X

[1] Cook et al. (2008) reported it as *Hybodus* sp.; incomplete teeth reported herein as *Meristodonoides* cf. *rajkovichi*.

[2] Incomplete teeth reported herein as cf. *Polyacrodus illingworthi.*

[3] Case et al. (1990) reported it as *Ptychodus* cf. *P. rugosus.*

[4] Case et al. (1990) reported it as *Squalicorax falcatus*; Underwood & Cumbaa (2010) reported it as *S. curvatus*; Cook et al. (2008) reported it as *Squalicorax* sp.

[5] Reported as *Cretodus* sp. by Case et al. (1990, fig. 7a, b); robust root morphology suggests tooth reported as *Dallasiella willistoni* by Cook et al. (2008) is more likely *Archaeolamna* ex. gr. *kopingensis.*

[6] Tooth reported as *Cretodus* sp. by Case et al. (1990, fig. 7c, d) may belong to a *Cretoxyrhina* neonate; Cook et al. (2008) reported it as *Cretoxyrhina* cf. *C. mantelli*.

[7] Underwood and Cumbaa (2010) reported it as *Eostriatolamia paucicorrugata*

[8] Underwood and Cumbaa (2010) reported it as *Cretalamna* sp.

[9] Tooth reported as *Cretodus* sp. by Case et al. (1990, fig. 7e, f) has a similar morphology.

[10] Reported as *Rhinobatos* sp. by Case et al. (1990); reported as '*Rhinobatos'* cf. *incertus* by Underwood and Cumbaa (2010).

Table 3.2. A comparison of the euselachians recovered from the early Turonian Canada (Case et al., 2001; this Chapter), the lower middle Turonian of Kansas (this Chapter), and the early Turonian of Arizona (Williamson et al., 1993).

	Canada (Watino and Favel)	**Kansas (Fairport Chalk)**	**Arizona (Mancos Shale)**
Meristodonoides rajkovichi[1]	X	-	-
Polyacrodus illingsworthi[2]	X	-	-
Ptychodus anonymus	X	-	-
Ptychodus decurrens	-	-	X
Ptychodus mammillaris	-	X	-
Ptychodus marginalis[3]	-	-	X
Ptychodus whipplei	-	-	X
Squalicorax sp. A[4]	X	X	X
Squalicorax sp. B	X	X	-
Archaeolamna ex. gr. *kopingensis*	X	-	-
Cardabiodon ricki	X	-	-
Cardabiodon venator[5]	-	X	X
Cretoxyrhina mantelli	X	X	X
Scapanorhynchus sp.[6]	X	-	X
Carcharias lilliae	X	-	-
Carcharias aff. *C. Striatula*	X	-	-
Odontaspis saskatchewanensis	X	-	-
Odontaspis watinensis	X	-	-
Johnlongia parvidens	X	X	-
Cretalamna ex. gr. *appendiculata*[7]	X	X	X
Cretodus semiplicatus	X	-	-
Dallasiella willistoni	X	X	-
Dwardius woodwardi	X	-	-
Chiloscyllium greeni	-	-	X
Rhinobatos incertus[8]	X	-	X
Texatrygon rubyae[9]	-		X
Cretomanta canadensis	X	-	-

[1] Incomplete teeth reported herein as *Meristodonoides* cf. *rajkovichi*.
[2] Incomplete teeth reported herein as cf. *Polyacrodus illingworthi.*
[3] Reported as *Ptychodus cf. P. mammillaris* by Williamson et al. (1993).
[4] Reported as *Squalicorax falcatus* by Case et al. (1990) and Williamson et al. (1993).
[5] Reported as *Cretolamna woodwardi* by Williamson et al. (1993).
[6] Reported as *Scapanorhynchus raphiodon* by Williamson et al. (1993).
[7] Reported as *Cretolamna appendiculata* by Williamson et al. (1993).
[8] Reported as *Rhinobatos* sp. by Williamson et al. (1993).
[9] Reported as *Ptychotrygon rubyae* by Williamson et al. (1993).

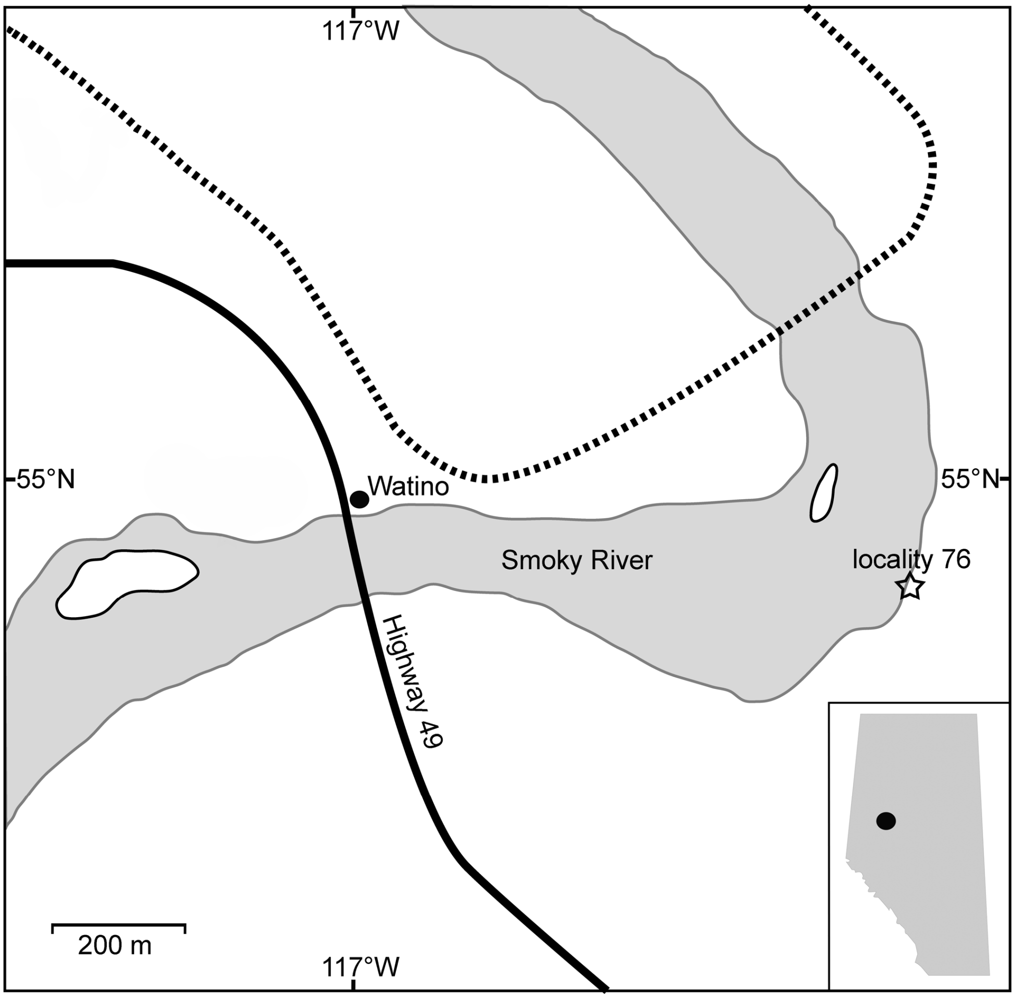

Figure 3.1. Map of northwestern Alberta showing the location of the mainWatino fossil locality. Dotted line indicates railway track.

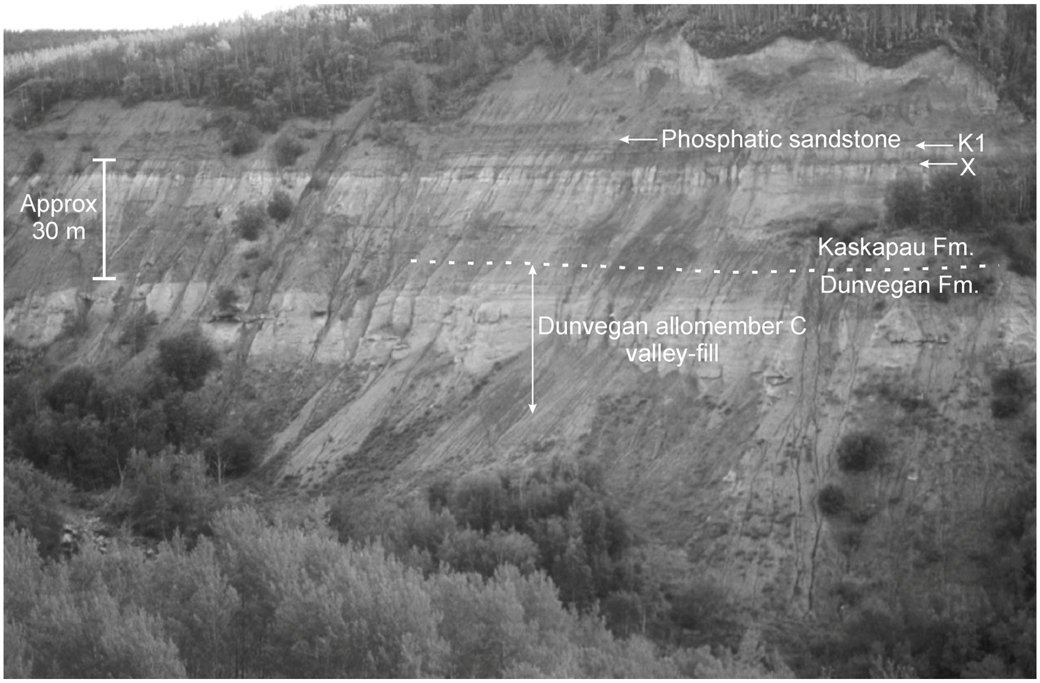

Figure 3.2. Overview photograph of the Hunting Creek section (NTS Grid Reference 83N/13 672852) showing the position of the Dunvegan-Kaskapau boundary, the regional flooding surfaces X and K1, and the phosphatic sandstone.

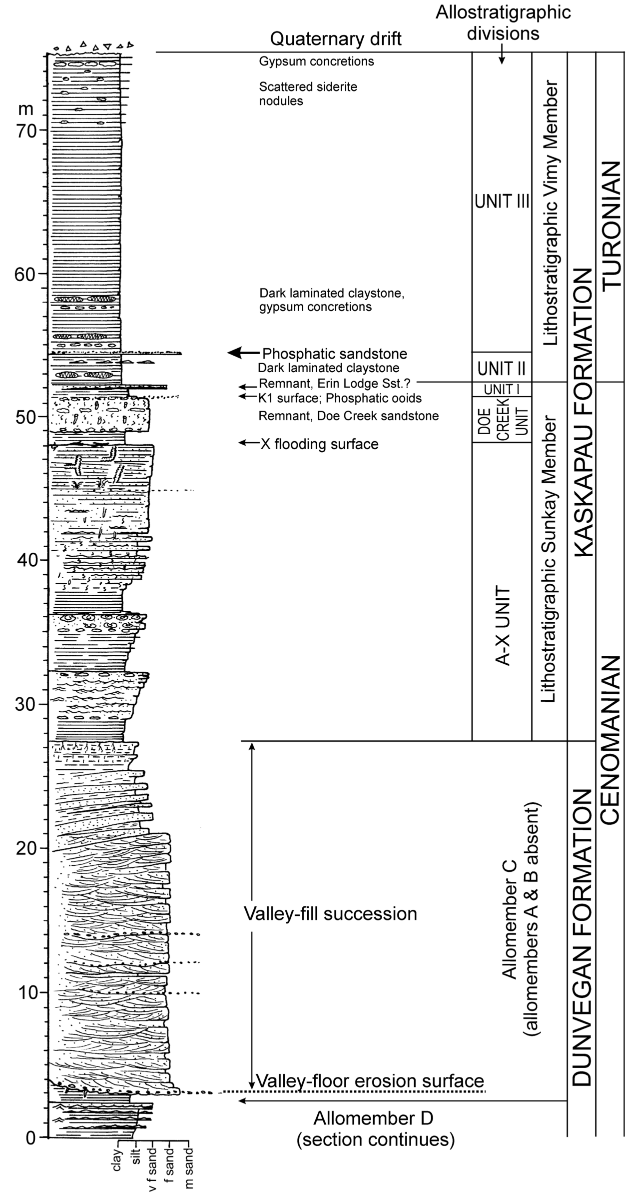

Figure 3.3. Stratigraphic log for the upper part of the section exposed in Hunting Creek (lower 48 m of Dunvegan Formation is not shown). Both lithostratigraphic and allostratigraphic divisions are shown; allostratigraphic interpretations are based on regional subsurface analyses in Plint (2000) and Varban and Plint (2005).

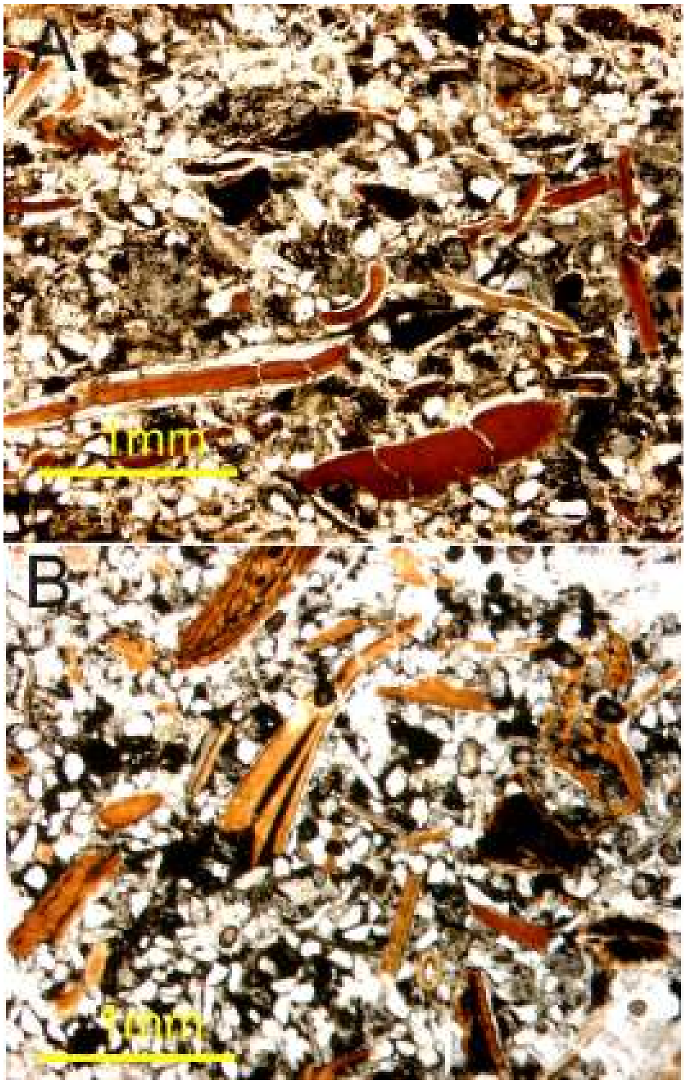

Figure 3.4. (A) Micrograph of phosphatic sandstone from Hunting Creek, showing angular quartz grains and fragmented phosphatic material in a displacive cement of calcite and minor gypsum. Plane polarized light. (B) Micrograph of phosphatic sandstone from Watino, showing angular quartz grains and fragmented phosphatic material in a displacive cement of calcite and gypsum. Plane polarized light.

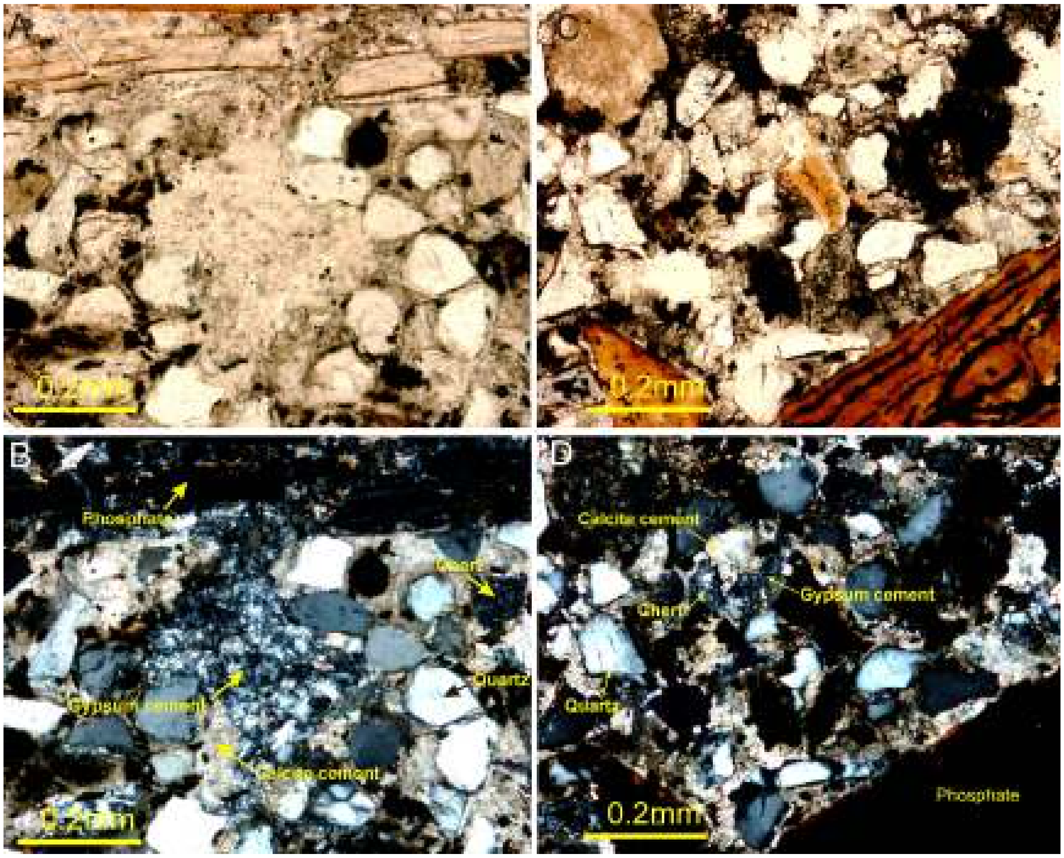

Figure 3.5. (A) Micrograph of phosphatic sandstone from Hunting Creek showing detrital grains and displacive cement. Plane polarized light. (B) As in A with crossed nichols showing detrital quartz, chert and phosphatic grains, and calcite and gypsum cement. (C) Micrograph of phosphatic sandstone from Watino showing detrital grains and displacive cement. Plane polarized light. (D) As in C with crossed nichols, showing detrital quartz, chert and phosphate grains, and calcite and gypsum cement.

Figure 3.6. *Meristodonoides*, *Polyacrodus*, and *Ptychodus* teeth recovered from the Watino localities. (A) *Meristodonoides* cf. *rajkovichi* (Case, 2001), fractured tooth, UALVP 53121; (B) *M.* cf. *rajkovichi* (Case, 2001), fractured tooth, UALVP 53122; (C) cf. *Polyacrodus illingsworthi* (Dixon, 1850), fractured tooth, UALVP 53123; (D) *Ptychodus anonymus* Williston, 1900, medial tooth, UALVP 53125; (E) *P. anonymus* Williston, 1900, medial tooth, UALVP 53126; (F) *P. anonymus* Williston, 1900, lateral tooth, UALVP 53127; (G) *P. anonymus* Williston, 1900, lateral tooth, UALVP 53128; (H) *P. anonymus* Williston, 1900, lateral tooth, UALVP 53129. Views: labial (left), profile (center), and lingual (right) for A; labial (left) and lingual (right) for B; occlusal (left) and profile (right) for C and D; occlusal for F–H. A, C, D, F, and G are SEM images. All scales = 1 mm.

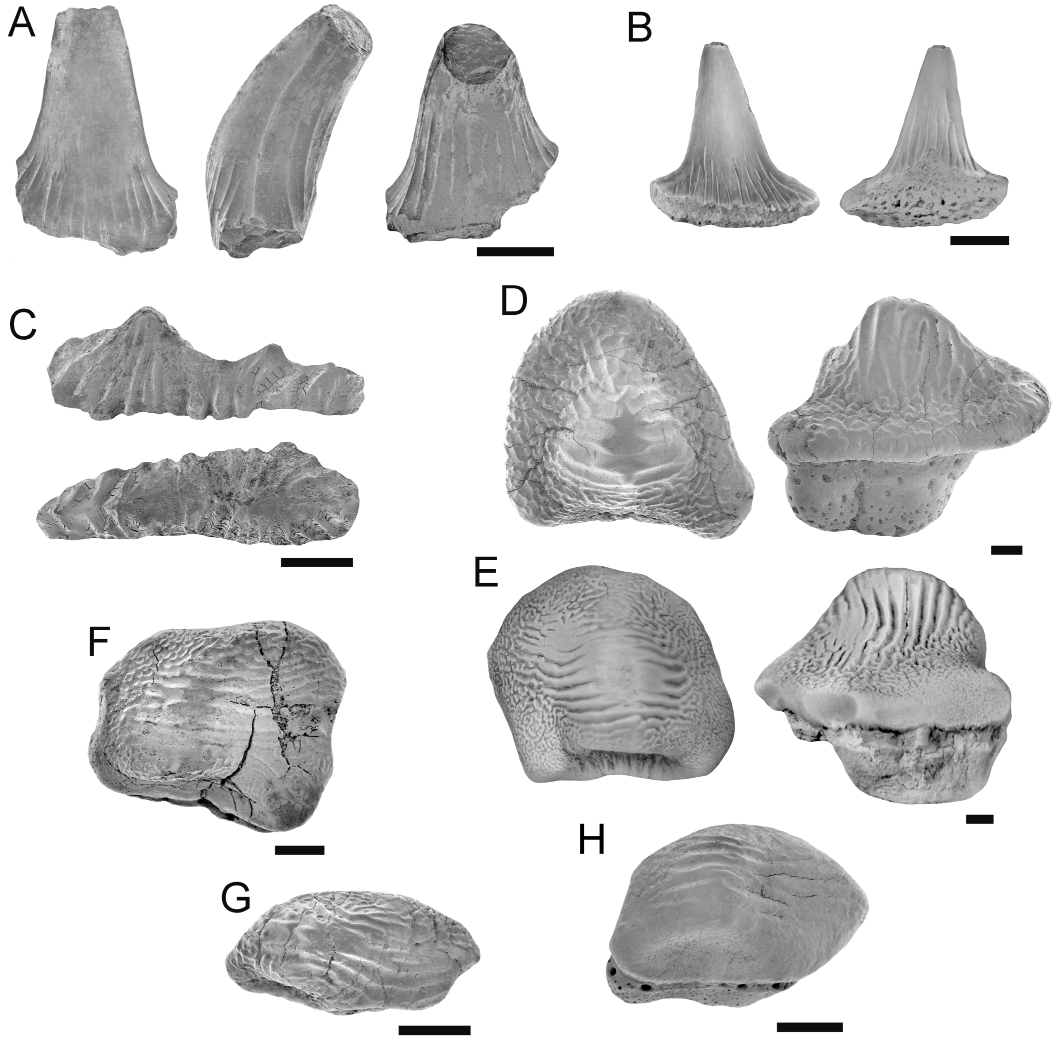
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Figure 3.7. *Squalicorax* sp. A teeth recovered from the Watino localities. (A) anterior tooth, UALVP 53131; (B) lower anterior tooth, UALVP 53141; (C) symphyseal tooth, UALVP 53142; (D) lateral tooth, UALVP 53143; (E) lateral tooth, UALVP 53144; (F) lateral tooth, UALVP 53145; (G) lateral tooth, UALVP 53146; (H) lateral tooth, UALVP 53147; (I) lateral tooth, UALVP 53148; (J) lateral tooth, UALVP 53149; (K) lateral tooth, UALVP 53150; (L) lateral tooth, UALVP 53151; (M) fractured lateral tooth, UALVP 53152. Views: labial (left), profile (center), and lingual (right) for A; labial (top) and lingual (bottom) for C; labial (left) and lingual (right) for B and D–M. D is a SEM image. All scales = 1 mm.

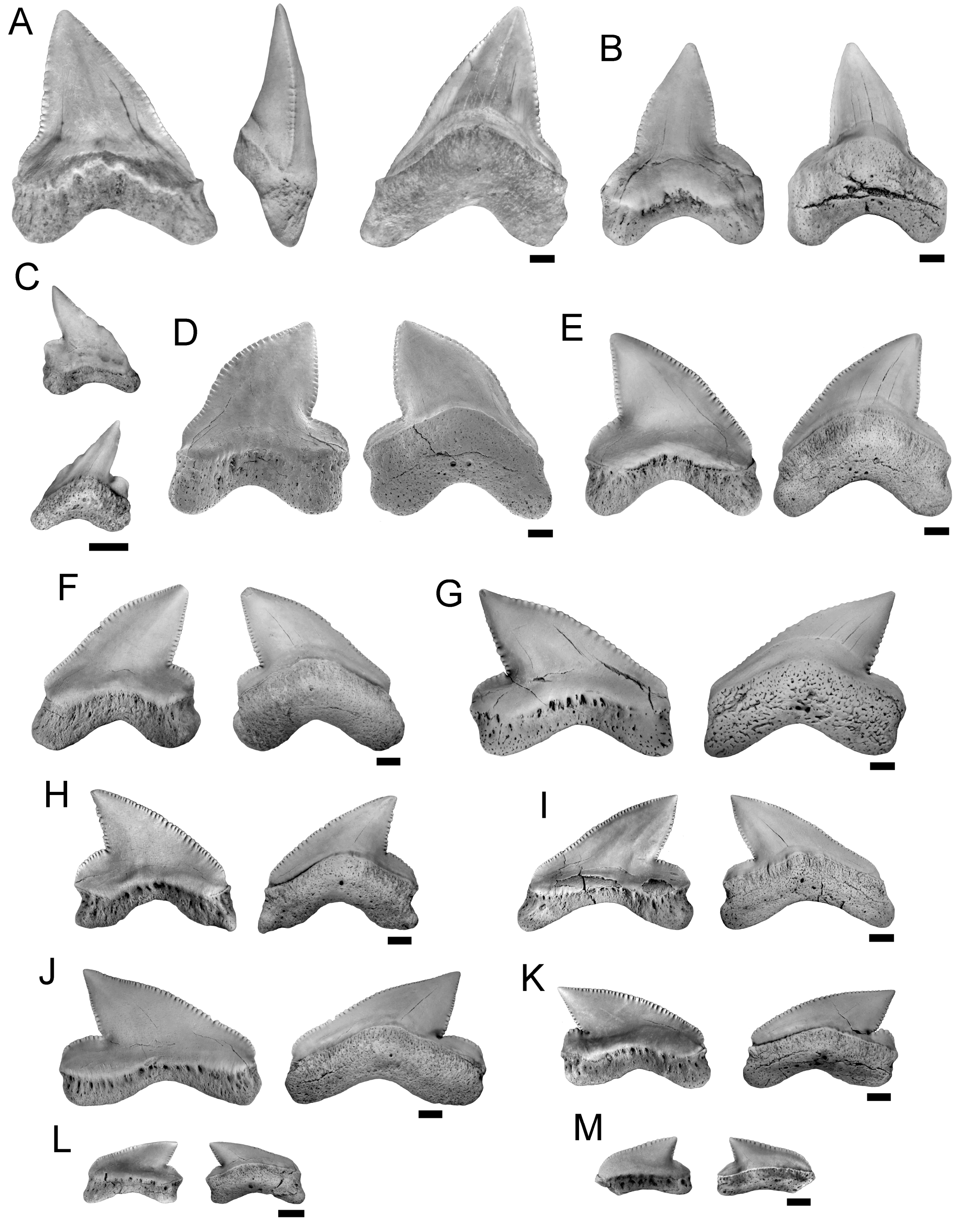
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Figure 3.8. *Squalicorax* sp. B teeth recovered from the Watino localities. (A) symphyseal tooth, UALVP 53155; (B) anterior tooth, UALVP 53156; (C) lateral tooth, UALVP 53157; (D) fractured lateral tooth, UALVP 53158; (E) lateral tooth, UALVP 53159; (F) lateral tooth, UALVP 53160; (G) lateral tooth, UALVP 53161; (H) lateral tooth, UALVP 53162; (I) lateral tooth, UALVP 53163; (J) lateral tooth, UALVP 53164; (K) lateral tooth, UALVP 53165; (L) lateral tooth, UALVP 53166; (M) lateral tooth, UALVP 53167. Views: labial (top) and lingual (bottom) for A; labial (left), profile (center), and lingual (right) for B; labial (left) and lingual (right) for C–M. G is a SEM image. All scales = 1 mm.

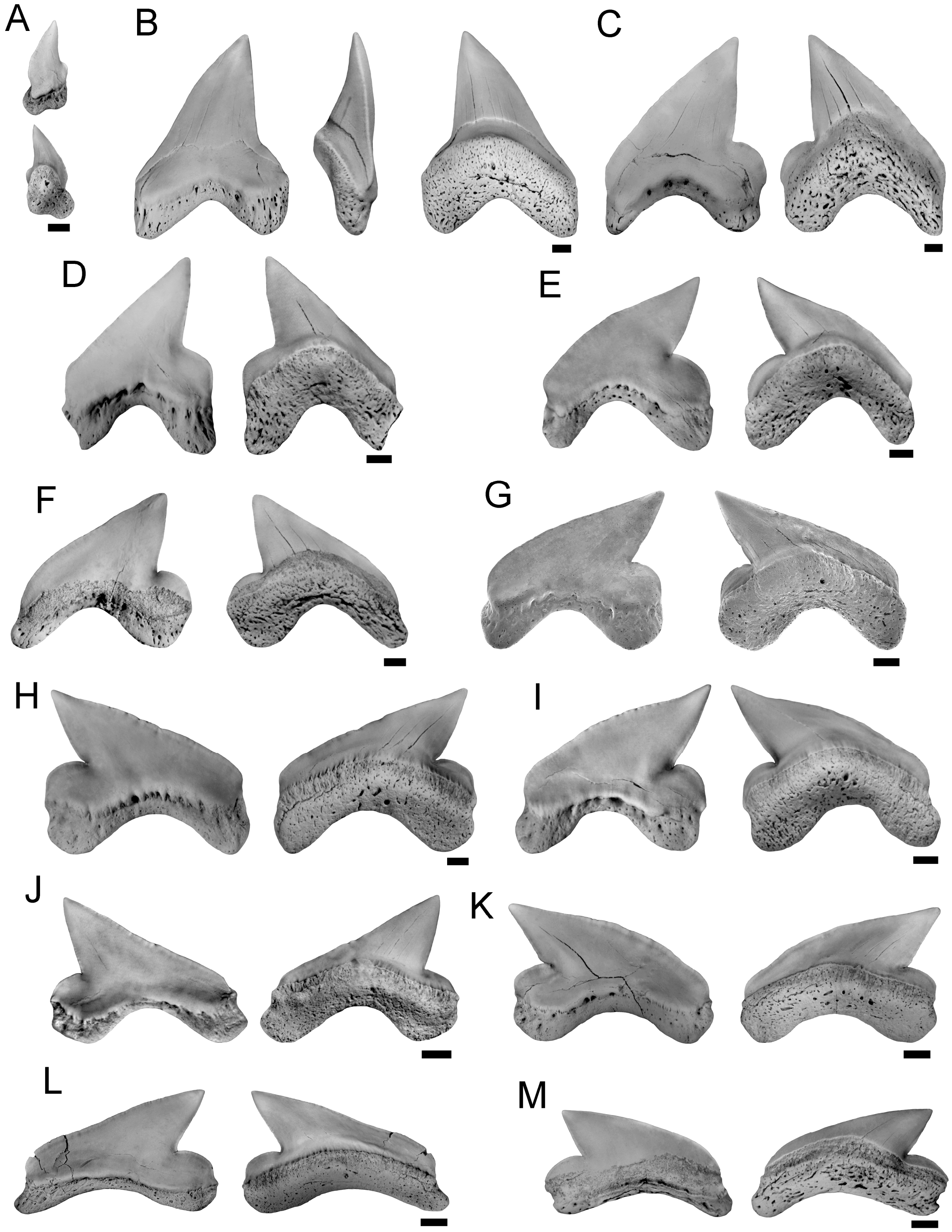
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Figure 3.9. *Archaeolamna and Cardabiodon* teeth recovered from the Watino localities. (A) *Archaeolamna* ex. gr. *kopingensis* (Davis, 1890), lateral tooth, UALVP 53171; (B) *A.* ex. gr. *kopingensis*, anterior tooth, UALVP 53172; (C) *A.* ex. gr. *kopingensis*, fractured anterior tooth, UALVP 53173; (D) *A.* ex. gr. *kopingensis*, fractured anterior tooth, UALVP 53174; (E) *A.* ex. gr. *kopingensis*, fractured lateral tooth, UALVP 53175; (F) *A.* ex. gr. *kopingensis*, lateral tooth, UALVP 53176; (G) *A.* ex. gr. *kopingensis*, lateral tooth, UALVP 53177; (H) *A.* ex. gr. *kopingensis*, lateral tooth, UALVP 53178; (I) *Cardabiodon ricki* (Siverson, 1999), lateral tooth, UALVP 49430; (J) *C. ricki*, juvenile lateral tooth, UALVP 53181; (K) ?*C. ricki*, fractured lateral tooth, UALVP 53182. Views: labial (left), profile (center), and lingual (right) for A and I; labial (top), profile (center), and lingual (bottom) for J; labial (top) and lingual (bottom) for H; labial (left) and lingual (right) for B–G; labial for K. B and J are SEM images. Scales for A–H and J = 1 mm; scales for I and K = 1 cm.

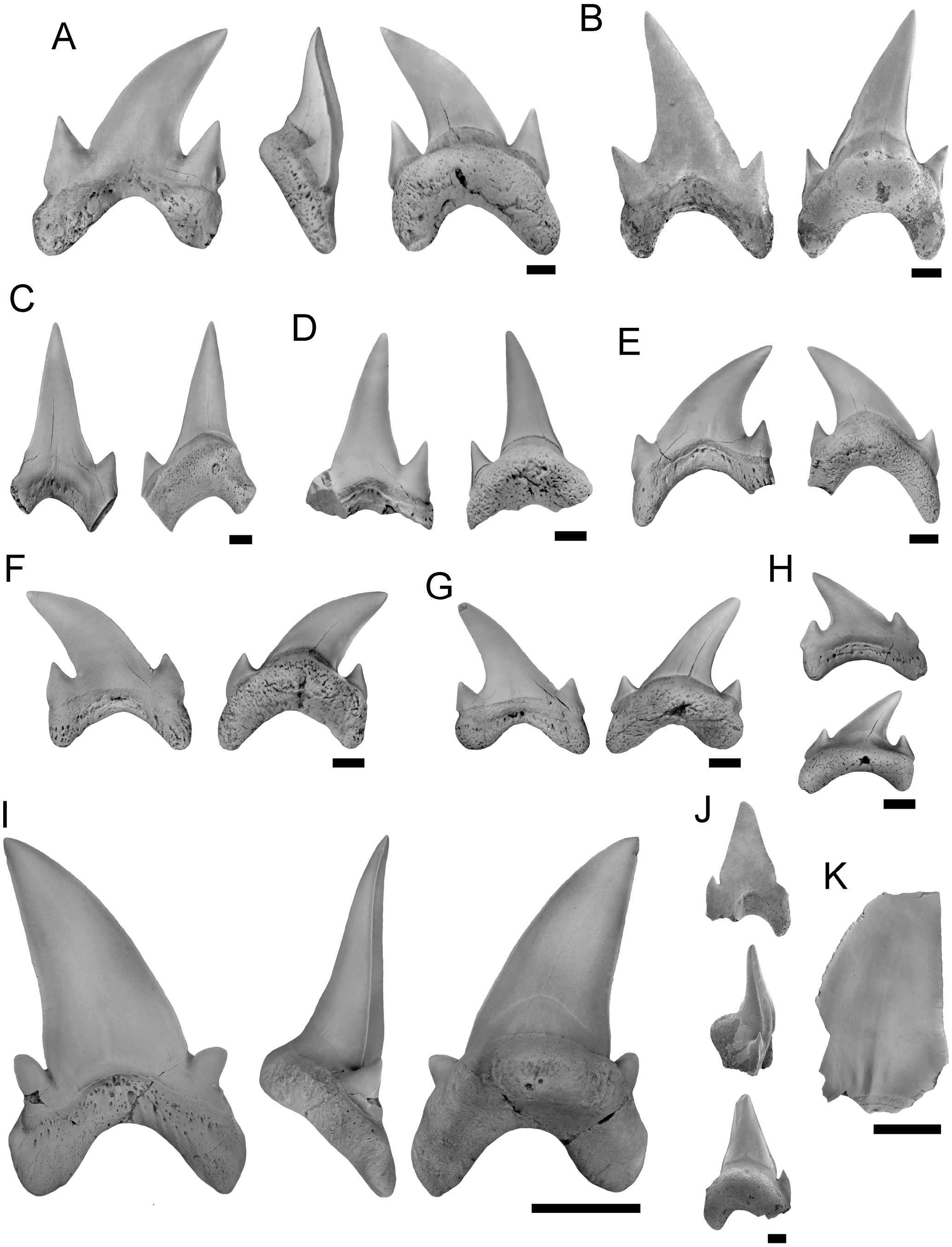
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Figure 3.10. *Cretoxyrhina mantelli* (Agassiz, 1843) teeth recovered from the Watino localities. (A) fractured anterior tooth, UALVP 53183; (B) fractured anterior tooth, UALVP 53184; (C) fractured lateral tooth, UALVP 53185; (D) lateral tooth, UALVP 53186; (E) lateral tooth, UALVP 53187; (F) lateral tooth, UALVP 53188; (G) lateral tooth, UALVP 53189; (H) lateral tooth, UALVP 53190. Views: labial (left), profile (center), and lingual (right) for A; labial (left) and lingual (right) for B–H. All scales = 5 mm.

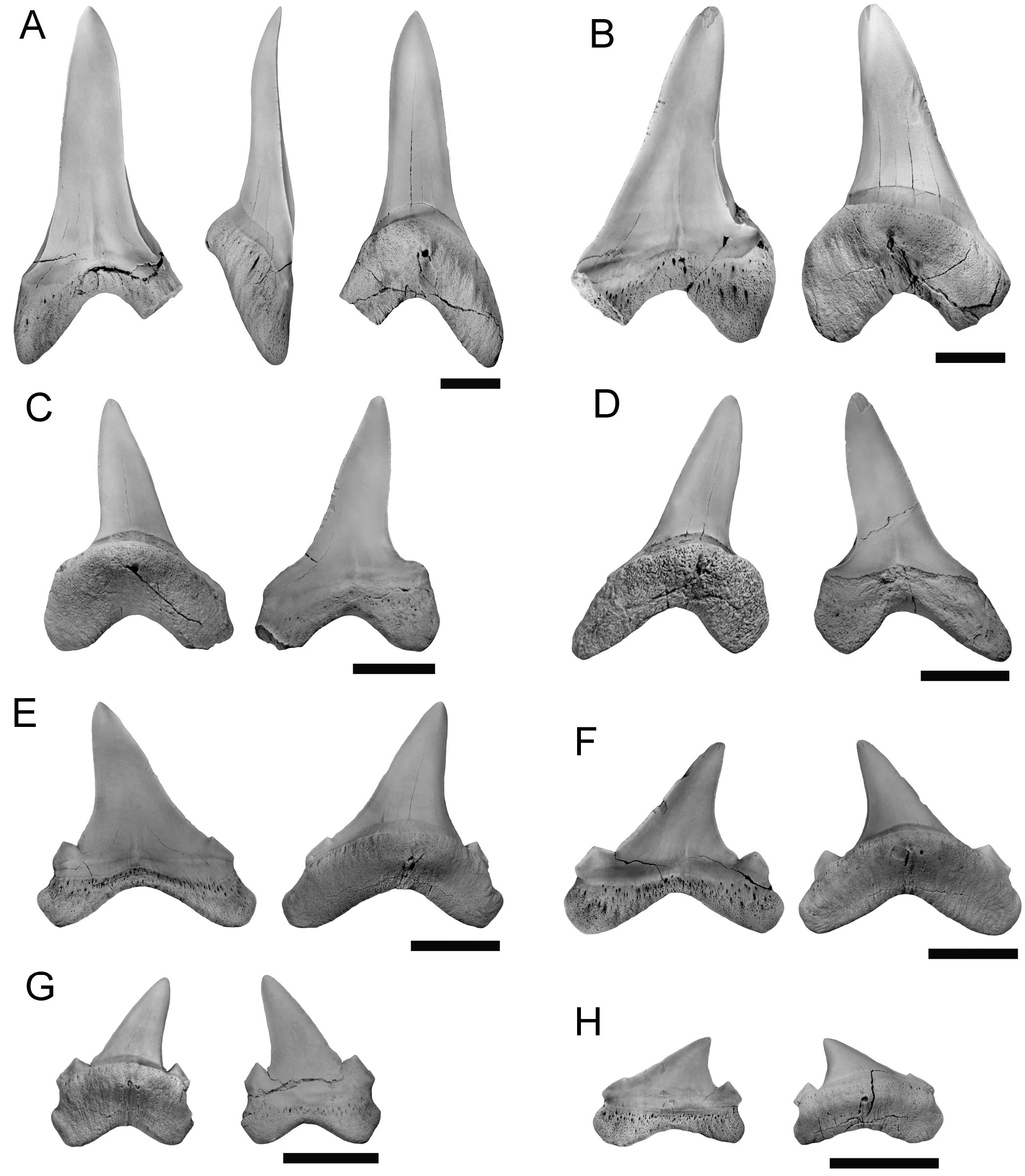
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Figure 3.11. *Scapanorhynchus,* odontaspidid, and *Cretalamna* teeth recovered from the Watino localities. (A) *Scapanorhynchus* sp., fractured lateral tooth, UALVP 53193; (B) *Carcharias* aff. *C. striatula* (Dalinkevicius, 1935), fractured anterior tooth, UALVP 53194; (C) *C.* aff. *C. striatula*, lateral tooth, UALVP 53195; (D) *C.* aff. *C. striatula*, lateral tooth, UALVP 53196; (E) *C.* aff. *C. striatula*, lateral tooth, UALVP 53197; (F) *Odontaspis saskatchewanensis* Case, Tokaryk, and Baird, 1990, lateral tooth, UALVP 53198; (G) *Odontaspis watinensis* sp. nov., anterior tooth, UALVP 53199 (Holotype); (H) *O. watinensis* sp. nov., fractured anterior tooth, UALVP 53200; (I) *O. watinensis* sp. nov., fractured lateral tooth, UALVP 53201; (J) *O. watinensis* sp. nov., fractured lateral tooth, UALVP 53202; (K) *Johnlongia parvidens* (Cappetta, 1973), fractured anterior tooth, UALVP 53203; (L) *J. parvidens*, fractured lateral tooth, UALVP 53204; (M) *J. parvidens*, fractured anterior tooth, UALVP 53205; (N) *J. parvidens*, lateral tooth, UALVP 53206; (O) *Cretalamna* ex. gr. *appendiculata*, fractured lateral tooth, UALVP 53208. Views: labial (left), profile (center), and lingual (right) for A, B, G, and O; labial (top) and lingual (bottom) for F, L, and N; labial (left), profile (center), and occlusal (right) for K; labial (left) and lingual (right) for C–E, H–J, and M. E, G, I–L, and N are SEM images. All scales = 1 mm.

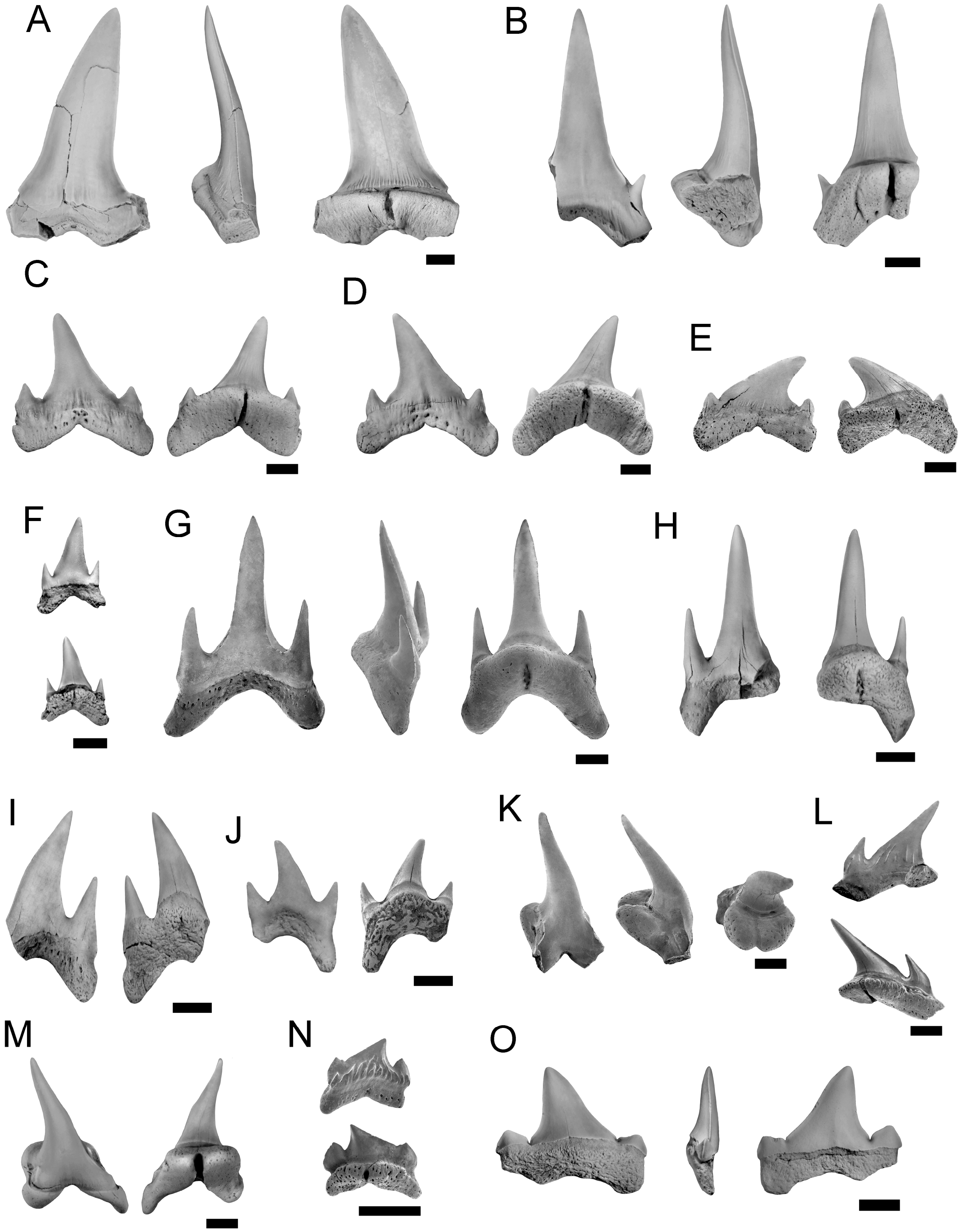
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Figure 3.12. *Cretodus*, *Dallasiella*, *Dwardius*, and *Rhinobatos* teeth recovered from the Watino localities. (A) *Cretodus semiplicatus* (Münster *in* Agassiz, 1843), fractured lateral tooth, UALVP 53209; (B) *Dallasiella willistoni* Cappetta & Case, 1999, lateral tooth, UALVP 53211; (C) *D. willistoni*, fractured lateral tooth, UALVP 53212; (D) *D. willistoni*, fractured anterior tooth, UALVP 53213; (E) *D. willistoni*, fractured lateral tooth, UALVP 53214; (F) *D. willistoni*, fractured lateral tooth, UALVP 53215; (G) *D. willistoni*, lateral tooth, UALVP 53216; (H) *D. willistoni*, fractured lateral tooth, UALVP 53217; (I) *Dwardius woodwardi* (Herman, 1977), lateral tooth, UALVP 53219; (J) *Rhinobatos incertus* Cappetta, 1973, tooth from female, UALVP 53220. (K) *R. incertus*, tooth from male, UALVP 53221. Views: labial (left), profile (center), and lingual (right) for A, C, and I; labial (top) and lingual (bottom) for G and H; occlusal (left) and labial (right) for J; occlusal (left), and profile (right) for K; labial (left) and lingual (right) for B, and D–F. B, J, and K are SEM images. Scales for A–I = 1 mm; scales for J and K = 100 um.

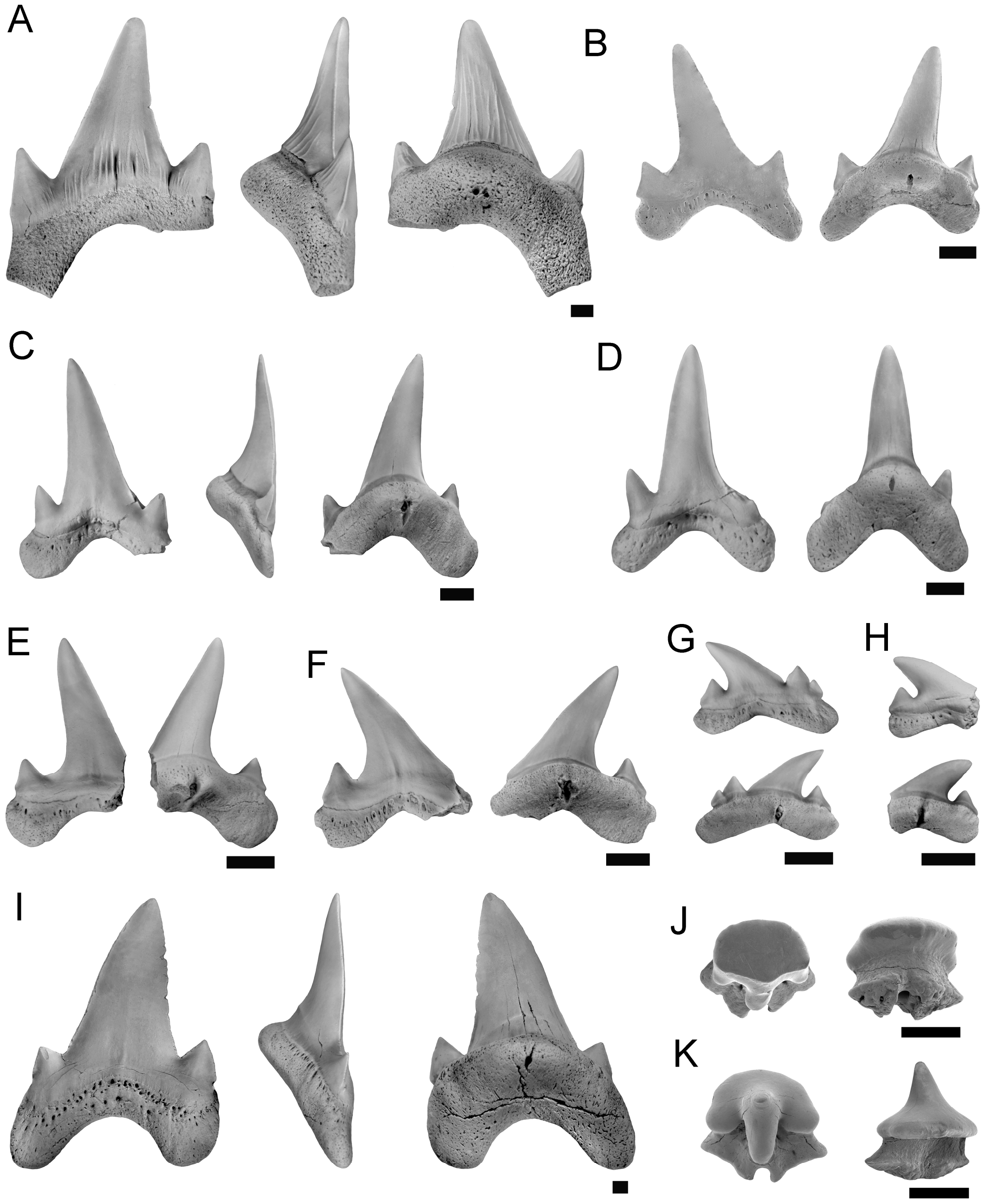
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Figure 3.13. *Ptychodus* and *Squalicorax* teeth recovered from the lower middle Turonian of Kansas. (A) *Ptychodus mammillaris* Agassiz, 1835, medial tooth, FHSM VP-17682; (B) *P. mammillaris*, lateral tooth, FHSM VP-17683; (C) *Squalicorax* sp. A, anterior tooth, FHSM VP-17684; (D) *Squalicorax* sp. A, anterior tooth, FHSM VP-17685; (E) *Squalicorax* sp. A, anterior tooth, FHSM VP-17686; (F) *Squalicorax* sp. A, lateral tooth, FHSM VP-17687; (G) *Squalicorax* sp. A, lateral tooth, FHSM VP-17688; (H) *Squalicorax* sp. B, lateral tooth, FHSM VP-17689; (I) *Squalicorax* sp. B, lateral tooth, FHSM VP-17696; (J) *Squalicorax* sp. B, lateral tooth, FHSM VP-17690; (K) *Squalicorax* sp. B, lateral tooth, FHSM VP-17697. Views: occlusal (left) and profile (right) for A and B; labial (top) and lingual (bottom) from C; labial (left) and lingual (right) for D–K. All scales = 1 mm.

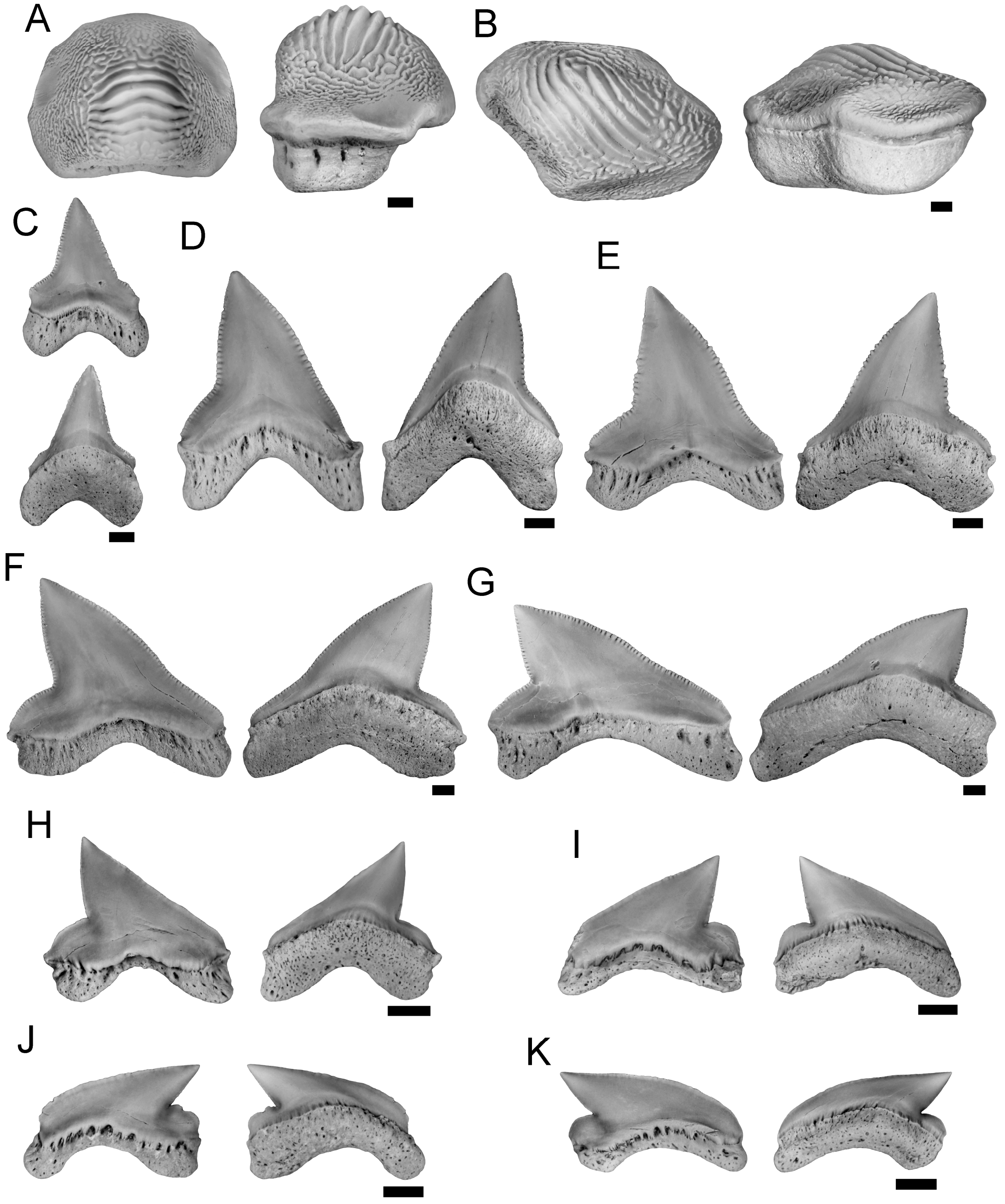
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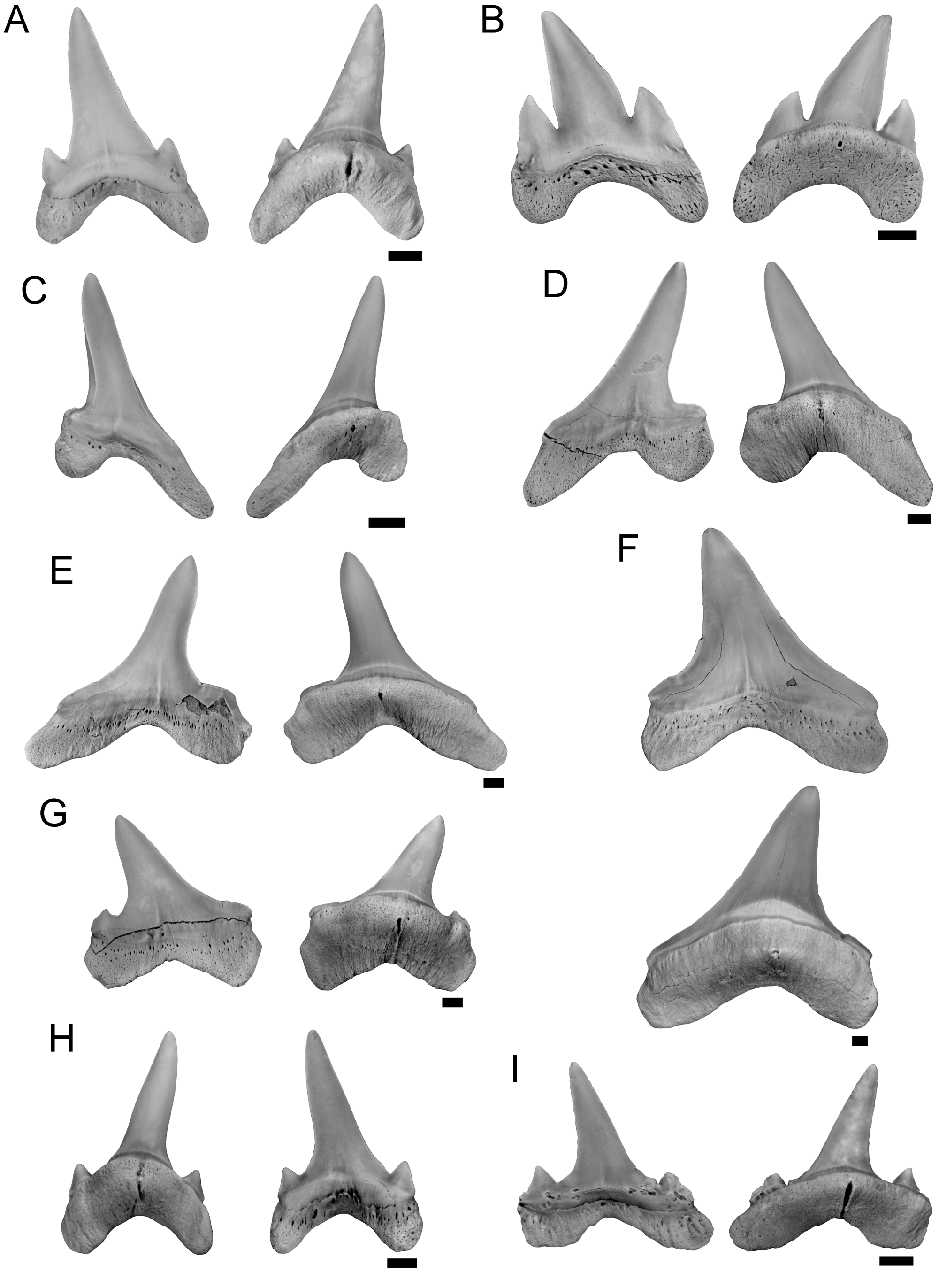
Figure 3.14. *Archaeolamna*, *Cardabiodon*, *Cretoxyrhina*, and *Dallasiella* teeth recovered from the lower middle Turonian of Kansas. (A) *Archaeolamna* ex. gr. *kopingensis* (Davis, 1890), lateral tooth, FHSM VP-17691; (B) *Cardabiodon venator* Siverson & Lindgren, 2005, juvenile lateral tooth, FHSM VP-17692; (C) *Cretoxyrhina mantelli* (Agassiz, 1843), lateral tooth, FHSM VP-17693; (D) *C. mantelli*, lateral tooth, FHSM VP-17698; (E) *C. mantelli*, lateral tooth FHSM VP-17699; (F) *C. mantelli*, lateral tooth, FHSM VP-17700; (G) *C. mantelli*, lateral tooth, FHSM VP-17694; (H) *Dallasiella willistoni* Cappetta and Case, 1999, anterior tooth, FHSM VP-17701; (I) *D. willistoni*, lateral tooth, FHSM VP-17695. Views: labial (left) and lingual (right) for A–E and G–I; labial (top) and lingual (bottom) from F; labial. All scales = 1 mm.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CHAPTER 4

Antitropical sharks of the Late Cretaceous

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INTRODUCTION

Selachians are found throughout the world's oceans and have adapted to a wide variety of environments. Many species have a biogeographic distribution that is constrained to the cooler waters found at higher latitudes. For example, the apex predator porbeagle shark, *Lamna nasus* (Lamnidae), frequents temperate waters and has an antitropical distribution that includes a latitudinal region of the North Atlantic of 30–70°N and a southern circumglobal region of 30–60°S (Compagno, 2001; Campana et al., 2002; Campana and Joyce, 2004; Francis et al., 2008). *Lamna nasus*, like all lamnids, can maintain a body temperature that is 7–10°C higher than ambient water temperature and is most often observed in waters with a sea surface temperature (SST) 5–10°C, with little variation among seasons (Carey and Teal, 1969; Campana and Joyce, 2004). Its sister taxon, the salmon shark, *L. ditropis* (Lamnidae), occurs in the North Pacific at a latitudinal region of 35–65°N and is most frequently found in waters with a SST between 9–16°C (Goldman and Musick, 2008). The white shark, *Carcharodon carcharias* (Lamnidae), also frequents mostly cold and warm temperate to subtropical waters, although reports have also placed this species in tropical waters (Compagno, 2001; Musick et al., 2004). The endothermic condition displayed by these sharks is achieved through the retia mirabilia and allows these lamnids to exploit cold-water prey in the absence of non-thermoregulating competitors (Campana and Joyce, 2004). The retia mirabilia consist of a venous blood supply that transfers metabolic heat generated by the body tissue to a closely associated arterial blood supply which in turn carries the heat back to the tissue via counter current flow

(Campana and Joyce, 2004). These vascular networks are situated in the cranium and locomotor musculature as the orbital and lateral cutaneous retia, respectively. The viscera include the suprahepatic and renal retia (Carlson et al., 2004).

Other extant sharks are known to have an antitropical distribution without endothermic properties provided by the retia mirabilia. The large lamniform planktivorous basking shark, *Cetorhinus maximus* (Cetorhinidae), is primarily observed in the boreal to warm temperate waters of both hemispheres (Compagno, 2001; Musick et al., 2004). An antitropical distribution is also reported for non-lamniform sharks such as the tope shark, *Galeorhinus galeus* (Triakidae), the brown smooth-hound shark, *Mustelus henlei* (Triakidae), the black dogfish shark, *Centroscyllium fabricii* (Etmopteridae), the frog shark, *Somniosus longus* (Somniosidae), and the spiny dogfish shark, *Squalus acanthias* (Squalidae) (Compagno, 2001; Musick et al., 2004).

Not all lamniforms favour cool higher latitudinal waters. For example, the bigeye thresher shark, *Alopias superciliosus* (Alopiidae), is “virtually circumglobal in tropical and temperate seas” (Compagno, 2001: p. 84). Despite having endothermic properties, the shortfin mako shark, *Isurus oxyrinchus* (Lamnidae), is found in tropical and warm-temperate waters above 16ºC (Compagno, 2001).

Many Late Cretaceous selachians have been previously reported as having a paleobiogeographic distribution that was restricted to the cooler temperate waters of high-paleolatitude regions. In the description of the large lamniform *Cardabiodon venator* from the middle Turonian of Montana, Siverson and Lindgren (2005) suggested that *Cardabiodon* had an antitropical (versus cosmopolitan) distribution because the taxon has not been reported from tropical regions. Underwood et al. (2011), in describing a high paleolatitude euselachian assemblage from India, proposed that the hexanchids *Gladioserratus* and *Notidanodon*, the squalid *Protosqualus*, and the lamniform *Dwardius* had a similar biogeographic distribution. Underwood and Cumbaa (2010) also reported the lamniform *Archaeolamna* ex gr. *kopingensis* to have an antitropical distribution. According to Underwood and Cumbaa (2010: p. 194) the distribution is “strongly indicative of it as a cool water taxon, being also present in northern Europe (e.g. Biddle 1993; Vullo et al. 2007) and Australia (Siverson 1996; 1997) but absent in Texas”. Cook et al. (2011: p. 19) also proposed that “*Archaeolamna* likely had an antitropical distribution reminiscent of that of the extant porbeagle shark”.

A diverse euselachian assemblage was recovered from the lower Turonian Kaskapau Formation near Watino in northwestern Alberta, Canada (Chapter 3). At a paleolatitude of 59ºN (PLATES Program 2010), this assemblage is one of the most northern described within the Western Interior Seaway (WIS) and provided an important insight into the euselachian faunal diversity of this little-known region of the seaway. Despite its high-paleolatitude, the assemblage contained 18 species. Many of the recovered species had broad distributions within the WIS during the Late Cretaceous that extended to the warm Tethyan waters of Texas, USA; however, the taxa *Archaeolamna*, *Cardabiodon*, *Johnlongia*, and *Dwardius* appeared to have been restricted to higher paleolatitude waters of the WIS, as there is no record of these species from the highly sampled Texas deposits of the southern region of the seaway (see Cappetta and Case, 1975; Russell, 1988; Welton and Farish, 1993; Cappetta and Case, 1999).

The lamniforms associated with the Watino assemblage most closely resemble another high-paleolatitudinal assemblage that was recovered from the basal part of the Haycock Marl of Western Australia at a paleolatitude of 53ºS (PLATES Program 2010). In the description of the Australian material, Siverson (1996) reported that the lamniform teeth were recovered from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone, with the latter placed near the early-middle Cenomanian boundary. The age of the basal part of the Beedagong Claystone, now referred to as Haycock Marl, has been revised and is now believed to be closer to the Cenomanian-Turonian boundary (Siverson et al., 2007; Siverson, personal communication, 2010). Based on the overall similarity of the faunal composition between the two assemblages, the age of the Australian assemblage is likely also early Turonian. The Australian assemblage contains several lamniform taxa, including *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon*, *Johnlongia*, and *Dwardius woodwardi*, in common with the Watino assemblage. The anacoracid sharks *Squalicorax* sp. A and *Squalicorax* sp. B and the cretoxyrhinid shark *Cretoxyrhina mantelli* have also been reported from both assemblages; however, these species are also known from the warm Tethyan waters of Texas. The absence of *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon*, *Johnlongia*, and *Dwardius woodwardi* from the well sampled Texas deposits, together with their occurrence in the high paleolatitude Watino and Haycock Marl assemblages, supports the notion that these lamniforms may have been restricted to temperate waters.

The Canadian and Australian assemblages also share taxa that are considered to have a cosmopolitan distribution, with fossil remains being recovered from both temperate and warm water sites. For example, *Cretalamna appendiculata* has also been reported from various Late Cretaceous marine deposits from the southern regions of the WIS of North America and North Africa (Cappetta, 1987; Antunes and Cappetta, 2002). *Cretodus*, although not reported from the Haycock Marl assemblage, also appears to have a cosmopolitan distribution, as it has been reported from early Cenomanian–early Campanian marine deposits of Texas, Europe, North Africa, and Lebanon (Cappetta, 1987; Werner, 1989; Antunes and Cappetta, 2002).

Other Late Cretaceous lamniforms appear to have been absent from higher paleolatitudinal waters and may have had a circumtropical distribution. For example, the odontaspidid *Carcharias amonensis* is a common faunal component in many Cenomanian Texas deposits, as well as mid-latitude WIS deposits, yet has not been reported from Canadian deposits.

The current reports of *Archaeolamna*, *Cardabiodon*, *Johnlongia*, and *Dwardius* from only high-latitude deposits may suggest an antitropical distribution; however, sampling for Late Cretaceous selachian material in the tropics is considerably less than sampling in North America and Europe. Plate tectonics can also skew our perceptions of the distribution of a species as the fossil remains have moved from the original resting place. As well, there was substantial fluctuation in marine temperature throughout the Late

Cretaceous. The occurrence of a species at a high-paleolatitude does not necessarily suggest that the species avoided warmer water, as there were times when higher latitudinal waters were significantly warmer. Herein, aspects of both paleolatitudinal and paleothermal distribution are used as evidence to infer an antitropical distribution for a taxon.

The assumption presented by Musick et al. (2004), that extinct selachians had thermal and habitat preferences akin to those of closely related extant taxa, is followed herein. As such, the extant lamniforms *Lamna ditropis* and *L. nasus* can be used as modern analogs to gain insights into the biology of taxa with an antitropical distribution. We predict that, if an extinct taxon had an antitropical distribution, its remains should be found in fossil localities that fall within a narrow paleolatitudinal range and a narrow relatively cooler paleothermal range, similar to the restricted latitudinal and thermal range of the *Lamna nasus*. Taxa with a cosmopolitan distribution would be predicted to have a much wider paleolatitudinal and paleothermal range.

METHODS

Antitropical Hypothesis Test—We evaluated two criteria to explore the plausibility of the antitropical distribution for *Archaeolamna*, *Cardabiodon*, *Johnlongia*, and *Dwardius*: (1) a limited paleolatitudinal range, and (2) a narrow cooler paleothermal range. We would expect the paleolatitudinal range, either northern or southern hemispheres, of the aforementioned taxa to be above about 30° as is the case for *Lamna nasus* and *L. ditropis* (which is restricted to the northern hemisphere). Regarding paleothermal range, we would expect the median SST range of the localities from which suspected antitropical taxa were recovered to be within a narrow thermal range of 5°C as is the case for *L. nasus*. The thermal range of *L. nasus* was used instead of *L. ditropis* because the former has a more restricted range (Goldman and Musick, 2008). Values for the fossil species greatly exceeding these two ranges exhibited by the extant species will be taken as indicative of a broader, possibly cosmopolitan distribution, as predicted for *Cretalamna* ex. gr. *appendiculata*, *Cretodus*, and *Carcharias amonensis.*

The geographic and stratigraphic data of each locality utilized in this analysis was gathered from the published literature (Table 4.1). A total of 41 assemblages are reported herein (Fig. 4.1). It should be noted that there are additional occurrences of the aforementioned taxa in the literature; however, due to the lack of precise geographic and/or chronostratigraphic data these reports could not be included in this study. The paleolatitudes of the fossil localities were determined using the 2010 plate model of the PLATES Project (University of Texas Institute for Geophysics) (Table 4.1; Appendix 4.1). This model uses an Atlantic-Indian Ocean hotspot framework to link its relative hierarchical plate motions to the globe. In the absence of radiometric dates, marine biostratigraphic indicators were used to derive an age estimate. The ages of those various localities used herein were standarized using information from the USGS Zonal Table of Cobban et al. (2006). The median values of the absolute ages associated with each substage used in this analysis are as follows (in Ma): 97.5 (early Cenomanian), 95.35 (middle Cenomanian), 94.6 (late Cenomanian), 93.35 (early Turonian), 91.25 (middle Turonian), 89.76 (late Turonian), 86.47 (late Coniacian), 83.5

(Santonian-Campanian boundary), 75.1 (late Campanian), and 70.1 (early Maastrichtian) (Table 4.1).

Paleothermal estimates of the localities from which the material was recovered were obtained using a "grossplot of Cretaceous marine paleotemperatures" produced by Frakes (1999: table 1) (Table 4.1; Fig. 4.2). The temperature data used in the construction of the grossplot were derived from oxygen isotope data from numerous sources within the published literature (Frakes, 1999). For the purposes of corroboration, the paleothermal variation of the grossplot at a paleolatitude of 40º (Frakes, 1999) was compared to values for a global proxy for paleotemperature estimated from δ^{18}O in bulk chalk from southern England at a depositional paleolatitude of ~40º N (Jenkyns et al., 2004; Table 4.2). With the exception of the difference of 5.5ºC obtained for the late Turonian at ~40º paleolatitude, the difference in the paleotemperature values between these two studies was less than 5 ºC for all other time periods. Both studies indicate that there was a significant interval of warming at ~40º during the early Turonian.

Any taxon found to satisfy the two criteria supporting the hypothesis of an antitropical distribution were further evaluated to determine if paleobiogeographic distribution was correlated with paleotemperature. During warm periods, it is predicted that an antitropical taxon would be found in higher paleolatitudes and conversely that it would be found at lower paleolatitudes during cooler periods. To ascertain whether a taxon shifts its latitudinal range in response to paleotemperature, the paleolatitudes of the fossil localities were regressed against values for a global proxy for paleotemperature produced by Jenkyns et al. (2004)

as described above. Least squares regression was used to examine for a relationship between global temperature (independent variable) and paleolatitude (dependent variable) of the fossil localities in the statistical program SYSTAT (2004). Alpha was set at 0.05.

RESULTS

To reiterate, two conditions must be satisfied to support the hypothesis of an antitropical distribution (as defined by the modern analog *Lamna nasus*): (1) paleolatitudinal distribution must be within a narrow range of 30°; and (2) SSTs must be within a narrow cooler range of approximately 5°C.

Archaeolamna—The examined localities (n = 23) are temporally distributed before, during, and after the Cenomanian/Turonian Thermal Optimum, ranging in age from 95.35 to 70.1 Ma. The paleolatitudinal distribution of the examined *Archaeolamna* localities falls between 58.42° and 33.8° paleolatitude (Fig. 4.3A). The difference in range of paleolatitudes for *Archaeolamna* (24.62°) was 5.38° latitude less than that for *Lamna nasus*, which ranges from 60° to 30° latitude. The median SST range of the examined *Archaeolamna* localities was 12.5° to 22.5°C, a difference of 10°C (Fig. 4.3B). The range for *Archaeolamna* was greater (by 5°C SST) than that recorded for *Lamna nasus* (range of 5°C SST), which ranges from 5° to 10°C SST. *Archaeolamna* thus meets the paleolatitudinal condition, but not the paleothermal condition.

Cardabiodon—The examined localities (n = 7) are temporally distributed before, during, and after the Cenomanian-Turonian Thermal Optimum, ranging in age from 95.35 to 91.25 Ma. The paleolatitudinal distribution of the examined *Cardabiodon* localities falls between 58.42° and 38.79° paleolatitude (Fig. 4.4A). The difference in paleolatitude range for *Cardabiodon* (19.63°) was 10.37° latitude less than that for *Lamna nasus*. The median SST range of the examined *Cardabiodon* localities was 12.5° to 28°C, a range of 15.5°C (Fig. 4.4B). The range for *Cardabiodon* was considerably greater (10.5°C more) than that recorded for *Lamna nasus* (5°C SST). *Cardabiodon* thus meets the paleolatitude condition, but not the SST condition.

Johnlongia—The examined localities (n = 8) are temporally distributed before, during, and after the Cenomanian-Turonian Thermal Optimum, ranging in age from 94.84 to 86.47 Ma. The paleolatitudinal distribution of all presently reported *Johnlongia* localities falls between 58.94° and 37.13° paleolatitude (Fig. 4.5A). The range in paleolatitudes for *Johnlongia* (21.81°) was 8.19° latitude less than that for *Lamna nasus*. The median SST range of all reported *Johnlongia* localities was 15° to 20°C, a difference of 5°C (Fig. 4.5B). The paleothermal range for *Johnlongia* was similar to that recorded for *L. nasus* (5°C SST). *Johnlongia* passes both paleolatitude and SST conditions.

Dwardius—The examined localities (n = 4) are temporally distributed before, during, and after the Cenomanian-Turonian Thermal Optimum, ranging in age from 97.67 to 93.35 Ma. The paleolatitudinal distribution of the reported *Dwardius* localities falls between 58.94 and 39.80° paleolatitude (Fig. 4.6A). The difference in range of paleolatitudes for *Dwardius* (19.14°) was 10.86° latitude less than the range for *Lamna nasus*. The SST range of the reported *Dwardius* localities was 12.5° to 22.5°C, a difference of 10°C (Fig. 4.6B). The range for

Dwardius was greater (5°C SST) than that recorded for *L. nasus* (5°C SST). *Dwardius* passes the paleolatitude condition, but not the paleotemperature condition.

Cretodus—The examined localities (n = 34) are temporally distributed before, during, and after the Cenomanian-Turonian Thermal Optimum, ranging in age from 97.53 to 83.08 Ma. The paleolatitudinal distribution of the reported *Cretodus* localities falls between 58.94° and 7.03° paleolatitude (Fig. 4.7A). The difference in paleolatitude for *Cretodus* (51.91°) was 21.91° latitude more than that for *Lamna nasus*. The SST range of the reported *Cretodus* localities was 12.5° to 28°C, a difference of 15.5°C (Fig. 4.7B). The range for *Cretodus* was greater (by 10.5°C SST) than that recorded for *L. nasus* (5°C SST). *Cretodus* fails both the paleolatitudinal and SST conditions.

Cretalamna* ex. gr. *appendiculata—The examined localities (n = 32) are temporally distributed before, during, and after the Cenomanian-Turonian Thermal Optimum, ranging in age from 97.67 to 70.1 Ma. The paleolatitudinal distribution of the reported *Cretalamna* ex. gr. *appendiculata* localities falls between 58.94° and 12.5° paleolatitude (Fig. 4.8A). The range of paleolatitudes for *Cretalamna* ex. gr. *appendiculata* (46.44°) was 16.44° latitude more than that for *Lamna nasus*. The SST range of the reported *Cretolamna* ex. gr. *appendiculata* localities was 12.5° to 28°C, a difference of 15.5°C (Fig. 4.8B). The range for *Cretolamna* ex. gr. *appendiculata* was greater (10.5°C SST) than that recorded for *L. nasus* (5°C SST). *Cretalamna* ex. gr. *appendiculata*, like *Cretodus*, fails both conditions.

Carcharias amonensis—The examined localities (n = 16) are temporally distributed before the Cenomanian-Turonian Thermal Optimum, ranging in age from 97.53 to 94.6 Ma. The paleolatitudinal distribution of the reported *Carcharias amonensis* localities falls between 37.13° and 7.03° paleolatitude (Fig. 4.9A). The range of paleolatitudes for *Carcharias amonensis* (30.1°) is the same as that for *Lamna nasus*; however, this range is at a lower paleolatitude. The median SST range of the reported *Carcharias amonensis* localities was 17.5° to 22.5°C, a difference of 5°C (Fig. 4.9B). The paleothermal range for *Carcharias amonensis* was similar to that recorded for *L. nasus* (5°C SST); however, this range was at a higher temperature.

Tracking climate—The paleolatitudes of *Johnlongia* localities were plotted against global paleotemperature to examine if the latitudinal distribution is significantly and positively correlated with global climate change. The paleolatitudes of the localities are positively correlated with global temperature (least squares regression: $y = 2.6797x - 15.453$; $n = 9$; $R^2 = 0.603$; $P = 0.012$) (Fig. 4.10). The significant relationship indicates that, during warm periods, fossils of *Johnlongia* were found at higher latitudes in both hemispheres, but during cooler periods the remains were found at lower latitudes.

DISCUSSION

Paleodistributions—The limited paleodistribution and paleoecological conditions supporting an antitropical distribution hypothesis (as defined by the modern analog *Lamna nasus*) is only strictly observed with *Johnlongia*. First, all reported *Johnlongia* localities occurred within a paleolatitude range of 21.81º of latitude, well within the extant latitudinal range of both *Lamna nasus* and *L. ditropis*. Second, all reports of *Johnlongia* are within a 5°C estimated SST range, which is the same as that of the extant *L. nasus*. This limited paleothermal and paleolatitudinal distribution of *Johnlongia* is similar to that exhibited by the modern analog and supports the hypothesis of an antitropical distribution for this species. The latitudinal distribution of the taxon changes significantly with climate change; however, it should be noted that the sample is small (n = 9) and additional material is needed.

The paleodistribution of *Archaeolamna* and *Dwardius* falls within the extant latitudinal range of *Lamna nasus* but the SST range of both taxa somewhat exceeds (is greater than 5°C) that of the thermal range of *Lamna nasus*. Not withstanding the potential error associated with the grossplot of Cretaceous marine paleotemperatures or the reconstruction of the Cretaceous paleomaps, the SST range of 5–10°C is the most frequently observed thermal range of *Lamna nasus*. There have been rare reports of the species in waters as cold as -1°C and as warm as 15°C (Goldman and Musick, 2008). Consequently, a reported thermal range for *Archaeolamna* and *Dwardius* that exceeds that of *Lamna nasus* by 5°C is likely inconsequential. Therefore, these two taxa may well have had an antitropical distribution despite narrowly failing our initial criterion for SST. It should be noted that there are only four reports of *Dwardius* in the literature, thus the small sample size is certainly at issue. Conversely, *Archaeolamna* has been reported from numerous localities throughout North America, Europe, and Australia. Repeatedly, this taxon is found along with *Cretodus* and/or *Cretalamna* (i.e., in Alberta (Cook et al., 2008, Chapter 2, 3) and Saskatchewan (Underwood and Cumbaa, 2010), Canada; Minnesota (Case, 2001), Colorado (Shimada et al., 2006), New Jersey, (Cappetta and Case, 1975), Alabama (Schwimmer et al., 2002); USA; Sweden (Siverson, 1992), Germany (Müller and Diedrich, 1991), France (Vullo et al., 2007); and Western Australia (Siverson, 1996)). Unlike *Cretodus* and *Cretalamna*, *Archaeolamna* has not been reported from subtropical and tropical localities (i.e.,Texas (Cappetta and Case 1975; the Middle East (Cappetta, 1980; Mustafa et al., 2002); and Africa (Kassab and Mohamed, 1996; Werner, 1989; Antunes and Cappetta, 2002). Therefore, the absence of *Archaeolamna* from the tropics seems to be a real absence.

The paleodistribution of *Cardabiodon* falls within the restricted latitudinal range of *Lamna ditropis* and *L. nasus*, however, the thermal range for this taxon greatly exceeds that recorded for *Lamna nasus*. During the early Turonian, warm waters from the Tethys extended into the Canadian region of the Western Interior Seaway (WIS) and correlated with this was a northward migration of subtropical planktonic foraminifera and macroscopic invertebrates (Kauffman, 1984; Schröder-Adams et al. 1996, 2001). The SST at Black Mesa, Arizona would have been exceptionally warm (28°C) during this time. The presence of *Cardabiodon* from this warm region of the WIS questions the previous notion that *Cardabiodon* had an antitropical distribution (see Cook et al., 2010). However, the Mancos Shale represents a deep-water deposit, so one may speculate that the occurrence of *Cardabiodon* at this location may have been attributed to the sharks descending to cooler deeper waters and so the SST would not be an appropriate indication of its temperature tolerance. The apparent absence of *Cardabiodon* material from

Middle Eastern and North African deposits suggests that this taxon may have had a geographical distribution reminiscent that of *Carcharodon carcharias* which occurs mostly in temperate and subtropical waters.

As predicted, *Cretodus* and *Cretalamna* ex .gr. *appendiculata* have latitudinal and thermal ranges that greatly exceed those of *Lamna ditropis* and *L. nasus*. The paleodistributions of *Cretalamna* ex. gr. *appendiculata* and *Cretodus* span the warm tropical waters of North Africa to cooler temperate waters of Canada, Australia, India, and northern Europe during the Late Cretaceous. This broad distribution is reminiscent that of the shortfin mako shark, *Isurus oxyrinchus* (Lamnidae), which is found in tropical and temperate waters throughout the world's oceans from 50°N to 50°S with SST greater than 13°C (Stevens, 2008).

The distribution of *Carcharias amonensis* appears to be restricted to warmer water at lower paleolatitudes. Underwood and Cumbaa (2010) noted that the lateral teeth of *C. amonensis* and *Roulletia canadensis* have a similar morphology. Teeth recovered from late Cenomanian deposits of South Dakota (Cicimurri 2001a, fig. 7m) and Kansas (Shimada and Martin 2008,fig. 5g) and identified as *Carcharias* aff. *amonensis* and *Carcharias amonensis*, respectively, have a morphology more similar to that of *Roulletia canadensis* (Cook et al., *in review*, Chapter 3). As such, there are currently no reports of *Carcharias amonensis* at a paleolatitude higher than 37.13 º or SST less than 17.5°C. This distribution is consistent with that of the extant *Carcharias taurus*, which occurs in warm-temperate and tropical coastal waters of the Mediterranean Sea, Atlantic and Indo-Pacific Oceans (Compagno, 2001).

Interhemispheric Dispersal—To explain the geographic occurrence of *Johnlongia*, *Archaeolamna*, *Dwardius*, and *Cardabiodon* at higher paleolatitudes in both northern and southern hemispheres, a possible dispersal scenario is suggested. Individual sharks could have dispersed from one hemisphere to the other following isotherms at variable depths in the ocean, utilizing deeper habitats in more tropical or subtropical seas and shallower depths in more polar latitudes. Although direct evidence that these sharks were able to use deeper habitats is lacking, indirect evidence might be that the teeth of these taxa have been found in the deep-water deposits of Arizona and Colorado (Williamson et al., 1993; Shimada et al., 2006; Chapter 3). Modern lamniform analogs demonstrate how an antitropical distribution can be formed through dispersals from one hemisphere to the other. As mentioned above, the basking shark *Cetorhinus maximus*, primarily inhabits cold temperate waters in both hemispheres (Compagno, 2001; Musick et al., 2004). The rare report of this species from warmer, lower latitude, waters was believed to be the result of individual sharks following cooler isotherms into deep tropical waters (Springer and Gilbert, 1976). Using satellite archival tags, Skomal et al. (2009) were able to demonstrate that individuals of *C. maximus* seasonally migrate from temperate feeding areas off the coast of New England, USA, to southern hemisphere waters by descending to cooler mesopelagic depths.

Musick et al. (2004) postulated that the modern distribution of *Lamna nasus* may have been attained during the Pleistocene glaciations when the tropical zone was constricted by the cooler waters. By entering deeper water the species could have dispersed from the Northern to the Southern Hemisphere while the tropical zone was reduced. Although there was no glaciation during the Late

Cretaceous Thermal Optimum (Jenkyns et al., 2004), *Cardabiodon* may have similarly dispersed across the equatorial zone via cooler isotherms during cooler times.

The physiological attribute of counter-current heat exchange to maintain a high body temperature in modern antitropical sharks may not have been necessary for antitropical species during the early Late Cretaceous. Based on marine macrofauna, the Watino localities are believed to have been situated in a relatively cool temperate climatic zone during the late Cenomanian (Kauffman, 1984). Planktonic foraminiferal porosity analyses also place Alberta (and with it, Watino) within the coolest water masses of the Western Interior Seaway during this stage (Fisher, 2003). However, the paleogradient in temperature was not as great as that seen in the present-day oceans and the temperature at the North Pole at the Cenomanian-Turonian boundary was considerably warmer than today (Frakes, 1999; Jenkyns et al., 2004). Therefore, the Cretaceous antitropical sharks were not subjected to temperatures as cold as those now encountered by extant species in high-latitude areas.

Collecting Bias—Shimada et al. (2006) noted that there is a bias towards the collection of large, well-preserved specimens in the Cretaceous vertebrate fossil record of North America, leaving smaller taxa potentially underrepresented in collections. Fortunately, the taxa discussed herein have teeth that are easily collected without use of bulk-sampling techniques. The majority of the *Archaeolamna* teeth recovered from the Watino assemblage approach or exceed 1 cm in height. This size is consistent with the thousands of teeth reported from the middle Cenomanian Bainbridge assemblage of Saskatchewan by Underwood and

Cumbaa (2010). To date, the largest reported *Archaeolamna* tooth measures 3.2 cm in height (Siverson, 1999), recovered from the Campanian Kristianstad Basin of Sweden (Siverson, 1999). The teeth of *Cardabiodon* and *Dwardius* were the largest teeth recovered from the Watino assemblage, measuring 3.4 cm and 2.0 cm in height, respectively. To date, the largest reported *Cardabiodon* tooth measures 3.6 cm in height and was collected from the Gearle Siltstone on the southern Carnarvon Platform of Western Australia (Siverson, 1999). Underwood et al. (2011) reported *Dwardius* teeth reaching 2.8 cm in height from the early Cenomanian of India. The teeth of *Johnlongia* are smaller, with a maximum height approaching 1.0 cm; however, the teeth are easily identifiable because of the unique massive lingual protuberance. A *Cretodus semiplicatus* tooth recovered from the middle Cenomanian of Alberta, Canada measured 3.1 cm in height. Based on teeth collected from Texas deposits, Welton and Farish (1993) reported a height of 4.1 cm and 6.6 cm for *Cretodus semiplicatus* and *C. crassidens*, respectively. Welton and Farish (1993) also reported a tooth height of 2.6 cm for *Cretalamna* ex gr. *appendiculata* and 1.1 cm for *Carcharias amonensis*. The large size of the teeth of these taxa indicates that a bias in collecting against smaller taxa would not have significantly altered the data used here. Therefore, the absence of the taxa described herein at specific localities is unlikely due to a collecting bias.

Preservational Bias—Selachian teeth are extremely durable due to the presence of a thick layer of enameloid. The histological nature of these elements allows for “survival in environments not conducive to the preservation of most invertebrate hard parts” (Williamson et al., 1993: p. 447). Nicholls and Russell

(1990: p. 161) noted that “[w]here present, shark teeth preserve well, even in gypsiferous shales.” The condition of polyphyodontism, where teeth are continuously produced and replaced throughout the individual’s life, also increases the probability of preservation by increasing the number of teeth per individual that is available for potential fossilization. Underwood et al. (1999) noted that the post-mortem damage of vertebrate remains by microborings may produce a taphonomic bias. However, the durability of the enameloid in shark teeth makes complete destruction of these elements through bioerosion unlikely, and again indicates that the absence of shark teeth from a locality is a real absence of the taxa.

Paleoenvironment—Despite the durability of shark teeth, and the size of the taxa studied here, there are other factors that may affect the presence or absence of a specific taxon in a particular deposit. In a comparison of mid-Cenomanian vertebrate faunas of the WIS, Cumbaa et al (2010) noted that variation in composition of the fauna might be related to environmental preference of the taxa, including factors such as water depth, temperature and salinity, as well as distance offshore or even type of substrate. They also noted that trophic structure can play a role in presence or absence of specific taxa. Although the presence and/or absence of the taxa at specific localities described herein is identified as being the result of a thermal preference (i.e., antitropical versus cosmopolitan distribution), these additional factors that could effect the absence of taxa from specific areas must be addressed.

Seasonal changes: Many modern lamniform species respond to seasonal temperature changes, moving to higher latitudes in the summer months (see

Compagno, 2001). It is assumed that extinct lamniforms also displayed this behaviour. However, the lack of a fossil record for an extinct lamniform species from a specific locality may not be completely explained by seasonal migration of that species out of the area during deposition of the sediments. To some extent, time averaging plays a role in every geological record (Kidwell and Behrensmeyer, 1993), such that each deposit may contain elements that accrued over a significant period of time, covering many years, decades or millennia. In their description of a vertebrate assemblage recovered from Comanche National Grassland in southeastern Colorado, Shimada et al. (2006) noted that time averaging records long-term paleocommunity structure. Short-lived changes in a paleocommunity, such as those caused by seasonal variation within a single year, would fail to be recorded and therefore cannot completely explain the absence of a species at a particular locality.

Habitat Variability: Extant lamniforms are most often found in epipelagic waters and are able to exploit a variety of marine habitats and food sources. For example, *Lamna ditropis* is found in coastal-littoral and offshore waters from the surface to a depth below 152 m (Compagno, 2001). As an opportunistic feeder, this species preys on a variety of pelagic and demersal bony fishes, squid, crab, shrimp, and the spiny dogfish shark, *Squalus acanthias* (Compagno, 2001; Goldman and Musick, 2008). *Lamna nasus* is also most often found in coastal waters and deeper water over continental shelves (Compagno, 2001; Francis et al., 2008). This active predator can be found from the surface to a depth of 700 m, where it feeds on small to medium sized schooling fishes, demersal fishes, squid, *Squalus acanthias*, and the tope shark, *Galeorhinus galeus*

(Compagno, 2001). *Carcharodon carcharias* can be found in offshore waters of continental shelves, but most often frequents coastal waters where it feeds on pinnipeds (Compagno, 2001; Bruce, 2008). Other prey includes large and small pelagic and demersal bony fishes, a variety of shark and ray species, and marine birds. This species can be found from the surface to a depth of 1280 m (Compagno, 2001). The odontaspidid, *Carcharias taurus*, can be found in mostly warm-temperate and coastal waters throughout the world. This species is most often found inshore from the surface to least 191 m. It migrates to higher latitudes during the summer but is rarely found in waters exceeding 40° latitude (Compagno, 2001). It preys on small bony fishes, small sharks and rays, crustaceans, and cephalopods (Compagno, 2001). These modern analogues are found in a variety of different marine environments, and therefore type of depositional environment for the extinct lamniforms may not be a factor.

Similar to these modern species, the extinct lamniforms likely occupied a variety of different habitats. For example, the middle Cenomanian Dunvegan assemblage, which includes *Archaeolamna* ex. gr. *kopingensis*, *Johnlongia parvidens*, and *Cretodus semiplicatus*, is believed to represent a marginal marine fauna that likely endured periodic fluctuations in salinity due to the influx of fresh water (Cook et al., 2008, Chapter 2). The early Turonian Watino assemblage (discussed above), which includes all the taxa described herein except *Carcharias amonensis*, is believed to have accumulated as a winnowed lag deposit in water no more than ~40 m deep (Varban and Plint 2008a, b; Chapter 3). *Archaeolamna* ex. gr. *kopingensis*, *Carcharias amonensis*, and *Cretodus semiplicatus* have been reported from the late Cenomanian of Charentes, France (units C4-D) which "corresponds to a transgressive episode, with a transitional paleoenvironment interpreted as a very shallow lagoon progressively open to outer shelf influences" (Vullo et al., 2009: p. 124). The two latter species are also reported from the tidal influenced estuarine environment of the Gebel Dist Member of southern Egypt (Werner, 1989). All of the taxa analysed in this paper have also been recovered from offshore localities such as the middle Cenomanian Greenhorn Limestone of southeastern Colorado (Shimada et al., 2006) and the late Cenomanian Greenhorn Limestone of Kansas (Shimada and Martin, 2008). *Dwardius*, *Cretodus,* and *Cretalamna* have also been reported from the early Cenomanian Karai Formation of India, which is interpreted as an offshore high-stand environment (Underwood et al., 2011). It is clear that while the type of depositional environment might affect the presence or absence of particular taxa from a fossil locality, the species used in our analysis (above) are generalists that were found in many different environments, and thus their absence from particular deposits is less likely to reflect differences in depositional environment such as water depth, salinity, distance from shore, type of substrate or tropic level, and instead is more consistent with an absence based on temperatures. We therefore consider that the distributions of *Johnlongia* in particular, but also likely *Archaeolamna*, *Cardabiodon*, and *Dwardius* are best interpreted as reflecting a true antitropical distribution, based on our current knowledge.

Table 4.1. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Archaeolamna* material used in this analysis.

	Location	**Geology**	**Substage**	**Median Age (Ma)**	**Modern Lat/Long (DD)**	**Paleo Lat/Long (DD)**	**Local SST (ºC)**	**Reference**
North America:								
A. ex. gr. *kopingensis*	Dunvegan, Alberta	Dunvegan Formation	middle Cenomanian	95.35 (Cobban et al. 2006; Cumbaa et al., 2010)	55.92, -118.6	58.42, -70.21	15	Cook et al. (2008, Chapter 2)
A. ex. gr. *kopingensis*	Bainbridge River, Saskatchewan	Ashville Formation (Belle Fourche Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	53.47, -101.87	52.06, -56.73	17.5	Underwood and Cumbaa (2010)
A. ex. gr. *kopingensis*	Comanche National Grassland, Colorado	Greenhorn Limestone (Lincoln Limestone Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	37.22, -102.9	37.13, -65.91	17.5	Shimada et al. (2006)
A. ex. gr. *kopingensis*	Itasca County County, Minnesota	Coleraine Formation	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008	47.4, 93.1	47.7, -57.22	22.5	Case (2001), as *Cenocarcharias tenuiplicatus*

A. ex. gr. *kopingensis*	Russell County, Kansas	Greenhorn Limestone (Lincoln Limestone Member)	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008)	38.75, -99.5	38.31, -62.39	22.5	Shimada and Martin (2008), as *A.* cf. *A. kopingensis*
A. ex. gr. *kopingensis*	Watino, Alberta	Kaskapau Formation (unit II)	early Turonian	93.35 (Cobban et al., 2006)	55.72, -117.62	58.94, -69.93	15	Cook et al. (*in review*, Chapter 3)
A. ex. gr. *kopingensis*	Carrot River, Saskatchewan	Favel Formation (Keld Member)	early Turonian	93.35 (Cobban et al., 2006)	53.28, -103.58	53.21, -58.64	20	Case et al. (1990), as *Cretodus* sp.
A. ex. gr. *kopingensis*	Schoenchen, Kansas	Carlile Shale (Fairport Chalk Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	38.73, -99.33	39.47, -62.78	17.5	Cook et al. (*in review*, Chapter 3)
A. kopingensis	Trussels Creek, Alabama	Eutaw (Tombigbee Sand Member)	Santonian-Campanian boundary	83.5 (Cobban et al., 2006)	32.9, -87.98	33.8, -56.78	17.5	Becker et al. (2000)
A. kopingensis	Dinosaur Provincial Park, Alberta	Dinosaur Park Formation (Lethbridge Coal Zone)	late Campanian	75.1 (Eberth, 2005; Cobban et al., 2006)	50.83, -111.32	58.58, -77.19	12.5	Beavan and Russell (1999), as *A. kopingensis judithensis*
A. kopingensis	Washakie County, Wyoming, USA	Mesaverde (Teapot Sandstone Member)	late Campanian	75.1 (Cobban et al., 2006)	44.13, -107.7	51.54, -78.28	15	Case (1987), as *Plicatolamna arcuata*

A. kopingensis	Chesapeake and Delaware Canal, Delaware	Marshalltown Formation	late Campanian	75.1 (Cobban et al., 2006)	39.6, -75.7	39.12, -45.57	17.5	Lauginiger (1984), as *Plicatolamna arcuata*
A. kopingensis	Florence County, South Carolina	Donoho Creek Formation (calcareous nannofossil zone CC 22c)	late Campanian	75.1 (Cobban et al., 2006)	34.1, -79.5	34.7, -51.4	17.5	Cicimurri (2007)
A. kopingensis	Monmouth, New Jersey	Navesink Formation	early Maastrichtian	70.1 (Cobban et al., 2006)	40.29, -74.15	40.49, -48.26	15	Cappetta and Case (1975), as *Plicatolamna arcuata*
A. kopingensis	Monmouth County, New Jersey	Mount Laurel Formation (upper member)	early Maastrichtian	70.1 (Cobban et al., 2006)	40.3, -74.3	40.5, -48.36	15	Krause and Baird (1979), as *Plicatolamna arcuata*
Europe:								
A. ex. gr. *kopingensis*	Traslemaine at Champniers, Charente, France	subunit B2, lithological levels B2ms–B2gl	early Cenomanian	97.53 (Cobban et al., 2006)	45.72, 0.28	34.1, 2.39	17.5	Vullo et al. (2007), *Archaeolamna* sp.
A. ex. gr. *kopingensis*	Vauban cliff, Fouras and Traslemaine, Champniers, France	subunit B2, lithological level B2ms	early Cenomanian	97.53 (Cobban et al., 2006)	45.98, -1.08	34.26, 1.21	17.5	Vullo et al. (2007), *Archaeolamna* sp.

A. ex. gr. *kopingensis*	Les Renardières, Tonnay−Charente, France	subunit B1, lithological level B1s	early Cenomanian	97.53 (Cobban et al., 2006)	45.93, -0.9	34.22, 1.37	17.5	Vullo et al. (2007), *Archaeolamna* sp.
A. ex. gr. *kopingensis*	Ascheloh, Teutoburger Wald, Germany	"German Cenomanian Chalks" (Underwood and Mitchell, 1991)	middle Cenomanian	95.35 (Cobban et al., 2006)	52.08, 8.3	41.04, 8.10	17.5	Müller and Diedrich (1991), as *Cretolamna* ? *arcuata*
A. ex. gr. *kopingensis*	Le Puits des Insurgés at Madame Island, Charente−Maritime, France	subunits C4–D, lithological levels C4ms–Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2009), as *Archaeolamna* sp.
A. ex. gr. *kopingensis*	l'Amas, Roullet–Saint-Estèphe, Charente, France	subunit D, lithological level Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2007), *Archaeolamna* sp.
A. kopingensis	Kristianstad Basin, Sweden	*Belemnellocamax mammillatus* Zone	early Campanian	81.22 (Cobban et al., 2006)	56.13, 14.48	46.75, 14.72	15	Siverson (1992)
A. kopingensis	Norwich, England	*Belemnitella mucronata* Zone	early Campanian	81.22 (Cobban et al., 2006)	52.62, 1.28	43.12, 3.95	15	Woodward (1912), as *Lamna arcuata*

Australia:

A. ex. gr. *kopingensis*	Thirindine Ridge Point, Western Australia	Haycock Marl Formation	early Turonian	93.35 (Cobban et al., 2006)	-27.6, 114.22	-52.74, 93.56	20	Siverson (1996), as *A*. aff. *kopingensis*

Table 4.2. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Cardabiodon* material used in this analysis.

	Location	**Geology**	**Substage**	**Median Age (Ma)**	**Modern Lat/Long (DD)**	**Paleo Lat/Long (DD)**	**Local SST (ºC)**	**Reference**
North America:								
Cardabiodon sp.	Russell County, Kansas	Greenhorn Limestone (Lincoln Limestone Member)	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008)	38.75, -99.5	38.31, -62.39	22.5	Shimada and Martin (2008)
C. ricki	Watino, Alberta	Kaskapau Formation (unit II)	early Turonian	93.35 (Cobban et al., 2006)	55.72, -117.62	58.94, -69.93	15	Cook et al. (*in review*, Chapter 3)
C. ricki	Black Mesa, Arizona	Mancos Shale (Lower Shale Member)	early Turonian	93.4 (Eaton et al., 1987; Cobban et al., 2006)	36.22, -109.53	38.79, -73.26	28	Williamson et al. (1993)
C. venator	Mosby, Montana	Carlile Shale (Fairport Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	46.98, -107.87	49.38, -66.92	12.5	Siverson and Lindgren (2005)

C. venator	Schoenchen, Kansas	Greenhorn Limestone (Pfeifer Shale Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	38.73, -99.33	39.47, -62.78	17.5	Cook et al. (*in review*, Chapter 3)
Europe:								
C. ricki	Peter's Pit, Wouldham, Kent, England	*Holaster subglobosus* Zone	middle Cenomanian	95.35 (Cobban et al., 2006)	51.33, 0.37	39.77, 1.83	17.5	Siverson (1999); Cook et al. (2010)
Australia:								
C. ricki	Southern Carnarvon Plateau, Western Australia	Gearle Siltsone in the Giralia Anticline	middle Cenomanian	95.35 (Cobban et al., 2006)	-22.88, 114.13	-47.66, 93.96	17.5	Siverson (1999)

Table 4.3. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Johnlongia* material used in this analysis.

	Location	**Geology**	**Substage**	**Median Age (Ma)**	**Modern Lat/Long (DD)**	**Paleo Lat/Long (DD)**	**Local SST (ºC)**	**Reference**
North America:								
J. parvidens	Dunvegan, Alberta	Dunvegan Formation	middle Cenomanian	94.84 (Cobban et al., 2006)	55.92, -118.6	58.42, -70.21	15	Cook et al. (2008, Chapter 2)
J. parvidens	Comanche National Grassland, Colorado	Greenhorn Limestone (Lincoln Limestone Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	37.22, -102.9	37.13, -65.91	17.5	Shimada et al. (2006)
J. parvidens	Watino, Alberta	Kaskapau Formation (unit II)	early Turonian	93.35 (Cobban et al., 2006)	55.72, -117.62	58.94, -69.93	15	Cook et al. (*in review*, Chapter 3)
J. parvidens	Belle Fourche Reservoir	Greenhorn Formation (uppermost)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	44.67, -103.85	46.20, -64.31	15	Cicimurri (2001b)

J. parvidens	Fall River County, South Dakota	Carlile Shale (Pool Creek Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	43.3, -103.83	44.91, -64.99	15	Cicimurri (2004)
J. parvidens	Schoenchen, Kansas	Carlile (Fairport Chalk Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	38.73, -99.33	39.47, -62.78	17.5	Cook et al. (*in review*, Chapter 3)
J. parvidens	Hot Springs, South Dakota	Carlile Shale (Turner Sandy Member)	late Turonian	89.76 (Cobban et al., 2006)	43.43, -103.48	45.58, -64.98	15	Cappetta (1973), as *Odontaspis parvidens*
J. parvidens	Trego County, Kansas	Niobrara Chalk (Smoky Hill Chalk Member)	late Coniacian	86.47 (Cobban et al., 2006)	38.73, -100.08	41.39, -65.09	17.5	Shimada, Ewell and Everhart (2004)
Australia:								
J. allocotodon	Thirindine Ridge Point, Western Australia	Haycock Marl	early Turonian	93.35 (Cobban et al., 2006)	-27.6, 114.22	-52.74, 93.56	20	Siverson (1996)

Table 4.4. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Dwardius* material used in this analysis.

	Location	Geology	Substage	Median Age (Ma)	Modern Lat/Long (DD)	Paleo Lat/Long (DD)	Local SST (ºC)	Reference
North America:								
D. woodwardi	Watino, Alberta	Kaskapau Formation (unit II)	early Turonian	93.35 (Cobban et al., 2006)	55.72, -117.62	58.94, -69.93	15	Cook et al. (*in review*, Chapter 3)
Europe:								
D. woodwardi	Maidstone, England	*Holaster subglobosus* Zone, English Chalk	late Cenomanian	94.62 (Cobban et al., 2006)	51.27, 0.22	39.80, 1.82	22.5	Herman (1977), as *Cretolamna woodwardi*
India:								
D. sudindicus	Garudamangalam, Tamil Nadu, India	Karai Formation (Odiyam Member)	early Cenomanian	97.67 (Cobban et al., 2006)	11.07, 78.92	-49.32, 41.53	12.5	Underwood et al. (2011)
Australia:								
D. woodwardi	Thirindine Ridge Point, Western Australia	Haycock Marl Formation	early Turonian	93.35 (Cobban et al., 2006)	-27.6, 114.22	-52.74, 93.56	20	Siverson (1996)

Table 4.5. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Cretodus* material used in this analysis.

	Location	**Geology**	**Substage**	**Median Age (Ma)**	**Modern Lat/Long (DD)**	**Paleo Lat/Long (DD)**	**Local SST (ºC)**	**Reference**
North America:								
C. semiplicatus	Dunvegan, Alberta	Dunvegan Formation	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	55.92, -118.6	58.42, -70.21	15	Cook et al. (2008, Chapter 2)
C. semiplicatus	Pennington County, South Dakota	Bell Fourche Shale	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	43.97, -103.18	43.57, -63.25	17.5	Cicimurri (2001a)
C. semiplicatus	Comanche National Grassland, Colorado	Greenhorn Limestone (Lincoln Limestone Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	37.22, -102.9	37.13, -65.91	17.5	Shimada et al. (2006)
C. semiplicatus	Dallas County, Texas	Woodbine (Arlington Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	32.77, -96.78	31.37, -61.76	17.5	Welton and Farish (1993)

C. semiplicatus	Itasca County County, Minnesota	Coleraine Formation	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008	47.4, 93.1	47.7, -57.22	22.5	Case (2001)
C. semiplicatus	Belle Fourche Reservoir	Greenhorn Formation (Orman Lake Member)	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008	44.67, -103.85	44.97, -63.83	22.5	Cicimurri (2001b)
C. semiplicatus	Russell County, Kansas	Greenhorn Limestone (Lincoln Limestone Member)	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008	38.75, -99.5	38.31, -62.39	22.5	Shimada and Martin (2008)
C. semiplicatus	Black Mesa, Arizona	Dakota Formation and basal Mancos Shale	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008	36.22, -109.53	38.42, -73.04	22.5	Williamson et al. (1993)
C. semiplicatus	Watino, Alberta	Kaskapau Formation (unit II)	early Turonian	93.35 (Cobban et al., 2006)	55.72, -117.62	58.94, -69.93	15	Cook et al. (*in review*, Chapter 3)

C. semiplicatus	Black Mesa, Arizona	Mancos Shale (Lower Shale Member)	early Turonian	93.35 (Eaton et al., 1987; Cobban et al., 2006)	36.22, -109.53	38.79, -73.26	28	Williamson et al. (1993)
C. semiplicatus	Black Mesa, Arizona	Toreva Formation (Lower Sandstone Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	36.22, -109.53	39.70, -73.77	17.5	Williamson et al. (1993)
C. crassidens	Belle Fourche Reservoir	Greenhorn Formation (uppermost)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	44.67, -103.85	46.20, -64.31	15	Cicimurri (2001b)
C. crassidens	Fall River County, South Dakota	Carlile Shale (Pool Creek Member)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	43.3, -103.83	44.92, -64.99	15	Cicimurri (2004)
C. crassidens	Weston County, Wyoming	Carlile Shale (Turner Sandy Member)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	44.1, -104.7	45.89, -65.42	15	Cicimurri (2004)
C. crassidens	Carbon County, Utah	Mancos Shale (Ferron Sandstone Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	39.45, -110.63	42.71, -74.66	17.5	Becker et al. (2010)

C. semiplicatus	La Joya, New Mexico	Tres Hermanos (Atarque Member)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	32.98, -105.95	35.71, -71.5	17.5	Wolberg (1985)
C. crassidens	Hot Springs, South Dakota	Carlile Shale (Turner Sandy Member)	late Turonian	89.76 (Cobban et al., 2006)	43.43, -103.48	45.58, -64.89	15	Cappetta (1973), as *Lamna semiplicatus*
C. crassidens	Chattahoochee County (Fort Benning), Georgia	Eutaw Formation	late Santonian - early Campanian	83.08 (Cobban et al., 2006)	32.35, -84.83	32.47, -53.96	17.5	Schwimmer et al. (2002), as *C. semiplicatus*
C. crassidens	Catoma Creek, Montgomery County, Alabama	Eutaw Formation (Tombigbee Sand Member)	late Santonian - early Campanian	83.08 (Cobban et al., 2006)	32.28, -86.27	32.77, -55.36	17.5	Schwimmer et al. (2002), as *C. semiplicatus*
Europe:								
C. semiplicatus	Font−de−Benon quarry at Archingeay, Les Nouillers, Charente−Maritime, France	subunit B1, lithological level B1cs	early Cenomanian	97.53 (Cobban et al., 2006)	45.88, -0.68	34.19, 1.56	17.5	Vullo et al. (2007)
C. semiplicatus	Les Renardières, Tonnay−Charente, France	subunit B1, lithological level B1s	early Cenomanian	97.53 (Cobban et al., 2006)	45.93, -0.9	34.22, 1.37	17.5	Vullo et al. (2007)

C. semiplicatus	Vauban cliff, Fouras and Traslemaine, Champniers, France	Subunit B2, lithological level B2ms	early Cenomanian	97.53 (Cobban et al., 2006)	45.98, -1.08	34.26, 1.21	17.5	Vullo et al. (2007)
C. semiplicatus	Traslemaine at Champniers, Charente, France	subunit B2, lithological levels B2ms–B2gl	early Cenomanian	97.53 (Cobban et al., 2006)	45.72, 0.28	34.10, 2.39	17.5	Vullo et al. (2007)
C. semiplicatus	Montagan at Mainxe, Charente, France	subunit B2, lithological levels B2ms–B2gl	early Cenomanian	97.53 (Cobban et al., 2006)	45.67, -0.17	34.02, 2.01	17.5	Vullo et al. (2007)
C. semiplicatus	Merstham, Surrey, England	*Holaster subglobosus* Zone, English Chalk	late Cenomanian	94.6 (Cobban et al., 2006)	51.27, -0.13	42.01, -0.4	22.5	Woodward (1912), as *Lamna semiplicatus*
C. semiplicatus	Ascheloh, Teutoburger Wald, Germany	“German Cenomanian Chalks” (Underwood and Mitchell, 1999)	middle Cenomanian	95.35 (Cobban et al., 2006)	52.08, 8.3	41.04, 8.10	17.5	Müller and Diedrich (1991), as *Cretodus* aff. *semiplicatus*
C. semiplicatus	Asturias, Spain	La Cabaña Formation	late Cenomanian	94.6 (Cobban et al., 2006)	43.3, -5.8	34.12, -5.7	22.5	Vullo et al. (2009)

C. semplicatus	Le Puits des Insurgés at Madame Island, Charente−Maritime, France	subunits C4–D, lithological levels C4ms–Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2009)
C. semiplicatus	l’Amas, Roullet–Saint-Estèphe, Charente, France	subunit D, lithological level Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2007)
C. semiplicatus	Le Mas quarry at La Couronne, Charente, France	subunit D, lithological level Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.63, 0.1	34.26, 2.32	22.5	Vullo et al. (2007)
C. semiplicatus	Moravská Tøebová in Eastern Bohemia, Czech Republic	Peruc.Korycany Formation (Peruc Member)	late Cenomanian	94.6 (Cobban et al., 2006)	49.55, 16.63	39.05, 16.23	22.5	Trbušek (1999)
C. semiplicatus	Moravská Tøebová in Eastern Bohemia, Czech Republic	Bílá Hora Formation (Korycany Member)	early Turonian	93.35 (Cobban et al., 2006)	49.55, 16.63	39.05, 16.23	28	Trbušek (1999)
Asia:								
C. semiplicatus	Hadjula, Lebanon	N/A	middle Cenomanian	95.35 (Cobban et al., 2006)	34.1, 35.9	10.03, 29.65	20	Cappetta (1980)

Africa:								
C. semiplicatus	Bahariya, Egypt	Bahariya Formation (Gebel Dist Member)	late Cenomanian	94.6 (Cobban et al., 2006)	28.43, 28.88	7.03, 23.34	22.5	Werner (1989), as *Cretodus longiplicatus*
C. crassidens	Tadi in the Kwanza Basin, Angola	Itombe Formation (Tadi Beds)	late Turonian	89.76 (Cobban et al., 2006)	-8.28, 13.35	-24.98, 1.18	17.5	Antunes and Cappetta (2002); Jacobs et al. (2006)
India:								
C. semiplicatus	Garudamangalam, Tamil Nadu, India	Karai Formation (Odiyam Member)	early Cenomanian	97.67 (Cobban et al., 2006)	11.07, 78.92	-49.32, 41.53	12.5	Underwood et al. (2011), as *Cretodus longiplicatus*

Table 4.6. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Cretalamna* material used in this analysis.

	Location	**Geology**	**Substage**	**Median Age (Ma)**	**Modern Lat/Long (DD)**	**Paleo Lat/Long (DD)**	**Local SST (ºC)**	**Reference**
North America:								
C. ex. gr. *appendiculata*	Bainbridge River, Saskatchewan	Ashville Formation (Belle Fourche Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	53.47, -101.87	52.06, -56.73	17.5	Underwood and Cumbaa (2010)
C. ex gr. *appendiculata*	Comanche National Grassland, Colorado	Greenhorn Limestone (Lincoln Limestone Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	37.22, -102.9	37.13, -65.91	17.5	Shimada et al. (2006), as *Cretalamna appendiculata*
C. ex gr. *appendiculata*	Tarrant County, Texas	Woodbine (Arlington Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	32.77, -96.78	31.37, -61.76	17.5	Welton and Farish (1993), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Itasca County County, Minnesota	Coleraine Formation	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008)	47.4, 93.1	47.7, -57.22	22.5	Case (2001), as *Cretolamna appendiculata*

C. ex gr. *appendiculata*	Belle Fourche Reservoir	Greenhorn Formation (Orman Lake Member)	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008)	44.67, -103.85	44.97, -63.83	22.5	Cicimurri (2001b), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Russell County, Kansas	Greenhorn Limestone (Lincoln Limestone Member)	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008)	38.75, -99.5	38.31, -62.39	22.5	Shimada and Martin (2008), as *Cretalamna appendiculata*
C. ex gr. *appendiculata*	Black Mesa, Arizona	Dakota Formation and basal Mancos Shale	late Cenomanian	94.6 (Cobban et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008)	36.22, -109.53	38.42, -73.04	22.5	Williamson et al. (1993), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Watino, Alberta	Kaskapau Formation (unit II)	early Turonian	93.35 (Cobban et al., 2006)	55.72, -117.62	58.94, -69.93	15	Cook et al. (*in review*, Chapter 3)
C. ex gr. *appendiculata*	Black Mesa, Arizona	Mancos Shale (Lower Shale Member)	early Turonian	93.35 (Eaton et al., 1987; Cobban et al., 2006)	36.22, -109.53	38.79, -73.26	28	Williamson et al. (1993), as *Cretolamna appendiculata*

C. ex gr. *appendiculata*	Belle Fourche Reservoir, South Dakota	Greenhorn Formation (uppermost)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	44.67, -103.85	46.20, -64.31	15	Cicimurri (2001b), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Fall River County, South Dakota	Carlile Shale (Pool Creek Member)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	43.3, -103.83	44.92, -64.99	15	Cicimurri (2004), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Weston County, Wyoming	Carlile Shale (Turner Sandy Member)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	44.1, -104.7	45.89, -65.42	15	Cicimurri (2004), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Carbon County, Utah	Mancos Shale (Ferron Sandstone Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	39.45, -110.63	42.71, -74.66	17.5	Becker et al. (2010); as cf. *Cretalamna appendiculata*
C. ex gr. *appendiculata*	Black Mesa, Arizona	Toreva Formation (Lower Sandstone Member)	middle Turonian	91.25 (Polcyn and Bell, 2005; Cobban et al., 2006)	36.22, -109.53	39.70, -73.77	17.5	Williamson et al. (1993), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	La Joya, New Mexico	Tres Hermanos (Atarque Member)	middle Turonian	91.25 (Polcyn and Bell 2005; Cobban et al. 2006)	32.98, -105.95	35.71, -71.5	17.5	Wolberg (1985), as *Cretolamna appendiculata*

C. ex gr. *appendiculata*	Chesapeake and Delaware Canal, Delaware	Marshalltown Formation	late Campanian	75.1 (Cobban et al., 2006)	39.6, -75.7	39.12, -45.57	17.5	Lauginiger (1984), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Monmouth County, New Jersey	Mount Laurel Formation (upper member)	early Maastrichtian	70.1 (Cobban et al., 2006)	40.3, -74.3	40.5, -48.36	15	Krause and Baird (1979)
Europe:								
C. ex gr. *appendiculata*	Ascheloh, Teutoburger Wald, Germany	“German Cenomanian Chalks” (Underwood and Mitchell, 1999)	middle Cenomanian	95.35 (Cobban et al., 2006)	52.08, 8.3	41.04, 8.10	17.5	Müller and Diedrich (1991), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Asturias, Spain	La Cabaña Formation	late Cenomanian	94.6(Cobban et al., 2006)	43.3, -5.8	34.12, -5.7	22.5	Vullo et al. (2009), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Le Puits des Insurgés at Madame Island, Charente−Maritime, France	subunits C4–D, lithological levels C4ms–Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2009), as *Cretolamna appendiculata*

C. ex gr. *appendiculata*	l'Amas, Roullet–Saint-Estèphe, Charente, France	subunit D, lithological level Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2007), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	LeMas quarry at La Couronne, Charente, France	subunit D, lithological level Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.63, 0.1	34.26, 2.32	22.5	Vullo et al. (2007), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Moravská Tøebová in Eastern Bohemia, Czech Republic	Peruc.Korycany Formation (Peruc Member)	late Cenomanian	94.6 (Cobban et al., 2006)	49.55, 16.63	39.05, 16.23	22.5	Trbušek (1999), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Moravská Tøebová in Eastern Bohemia, Czech Republic	Bílá Hora Formation (Korycany Member)	early Turonian	93.35 (Cobban et al., 2006)	49.55, 16.63	39.05, 16.23	28	Trbušek (1999), as *Cretolamna* sp.
C. ex gr. *appendiculata*	Port−des−Barques, Charente−Maritime, France	subunit T1, lithological level T1m	early Turonian	93.35 (Cobban et al., 2006)	45.93, -1.07	39.35, -1.04	28	Vullo et al. (2007), as *Cretolamna appendiculata*
C. ex gr. *appendiculata*	Kristianstad Basin, Sweden	*Belemnellocamax mammillatus* Zone	early Campanian	81.22 (Cobban et al., 2006)	56.13, 14.48	46.75, 14.72	15	Siverson (1992), as *Cretolamna appendiculata*

C. ex gr. *appendiculata*	Castilla y Leon, Spain	Vitoria Formation (L1B)	late Campanian	75.1 (Cobban et al., 2006)	42.7, -2.6	33.65, -2.56	20	Astibia et al. (1990), as *Cretolamna* sp.
Asia:								
C. ex gr. *appendiculata*	Central Jordan	Wadi Umm Ghudran Formation	latest Santonian	83.5 (Cobban et al., 2006)	31.2, 35.7	12.5, 30.6	25	Mustafa et al. (2002)
Africa:								
C. ex gr. *appendiculata*	Tadi in the Kwanza Basin, Angola	Itombe Formation (Tadi Beds)	late Turonian	89.76 (Cobban et al., 2006)	-8.28, 13.35	-24.98, 1.18	17.5	Antunes and Cappetta (2002), as *Cretolamna* sp
C. ex gr. *appendiculata*	Nile Valley, southern Egypt	Duwi Formation	late Campanian	75.1 (Cobban et al., 2006)	30.1, 31.3	13.5, 27.3	28	Kassab and Mohamed (1996), as *Cretolamna* sp.
India:								
C. ex gr. *appendiculata*	Garudamangalam, Tamil Nadu, India	Karai Formation (Odiyam Member)	early Cenomanian	97.67 (Cobban et al., 2006)	11.07, 78.92	-49.32, 41.53	12.5	Underwood et al. (2011), as *Cretalamna appendiculata*

Australia:

C. ex gr. *appendiculata*	Southern Carnarvon Plateau, Western Australia	Gearle Siltsone in the Giralia Anticline	middle Cenomanian	95.35 (Cobban et al., 2006)	-22.88, 114.13	-47.66, 93.96	17.5	Siverson (1999), as *Cretalamna appendiculata*
C. ex gr. *appendiculata*	Thirindine Ridge Point, Western Australia	Haycock Marl Formation	early Turonian	93.35 (Cobban et al., 2006)	-27.6, 114.22	-52.74, 93.56	20	Siverson (1996), as *Cretalamna appendiculata*

Table 4.7. Geographical, stratigraphical, age, and thermal information on the various assemblages containing *Carcharias amonensis* material used in this analysis.

	Location	Geology	Substage	Median Age (Ma)	Modern Lat/Long (DD)	Paleo Lat/Long (DD)	Local SST (ºC)	Reference
North America:								
C. amonensis	Comanche National Grassland, Colorado	Greenhorn Limestone (Lincoln Limestone Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	37.22, -102.9	37.13, -65.91	17.5	Shimada et al. (2006)
C. amonensis	Dallas County, Texas	Woodbine (Arlington Member)	middle Cenomanian	95.35 (Cobban et al., 2006; Cumbaa et al., 2006)	32.77, -96.78	31.37, -61.76	17.5	Welton and Farish (1993); Cappetta and Case (1975), (1999)
Europe:								
C. amonensis	Font−de−Benon quarry at Archingeay, Les Nouillers, Charente−Maritime, France	subunit B1, lithological level B1cs	early Cenomanian	97.53 (Cobban et al., 2006)	45.88, -0.68	34.19, 1.56	17.5	Vullo et al. (2007)

C. amonensis	Les Renardières, Tonnay−Charente, France	subunit B1, lithological level B1s	Early Cenomanian	97.53 (Cobban et al., 2006)	45.93, -0.9	34.22, 1.37	17.5	Vullo et al. (2007)
C. amonensis	Vauban cliff, Fouras and Traslemaine, Champniers, France	Subunit B2, lithological level B2ms	Early Cenomanian	97.53 (Cobban et al., 2006)	45.98, -1.08	34.26, 1.21	17.5	Vullo et al. (2007)
C. amonensis	Traslemaine at Champniers, Charente, France	subunit B2, lithological levels B2ms–B2gl	Early Cenomanian	97.53 (Cobban et al., 2006)	45.72, 0.28	34.10, 2.39	17.5	Vullo et al. (2007)
C. amonensis	Montagan at Mainxe, Charente, France	subunit B2, lithological levels B2ms–B2gl	Early Cenomanian	97.53 (Cobban et al., 2006)	45.67, -0.17	34.02, 2.01	17.5	Vullo et al. (2007)
C. amonensis	Le Puits des Insurgés at Madame Island, Charente−Maritime, France	subunits C4–D, lithological levels C4ms–Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2009)
C. amonensis	l'Amas, Roullet–Saint-Estèphe, Charente, France	subunit D, lithological level Dm	late Cenomanian	94.6 (Cobban et al., 2006)	45.62, 0.08	34.24, 2.30	22.5	Vullo et al. (2007)

C. amonensis	Asturias, Spain	La Cabaña Formation	late Cenomanian	94.6(Cobban et al., 2006)	43.3, -5.8	34.12, -5.7	22.5	Vullo et al. (2009)
Africa:								
C. amonensis	Bahariya, Egypt	Bahariya Formation (Gebel Dist Member)	late Cenomanian	94.6 (Cobban et al., 2006)	28.43, 28.88	7.03, 23.34	22.5	Werner (1989), as *Carcharoides planidens*

Table 4.8. A comparison of the paleothermal variation of the grossplot at a paleolatitude of 40º (Frakes, 1999) with values for a global proxy for paleotemperature estimated from δ^{18}O in bulk chalk from southern England at a depositional paleolatitude of ~40º N (Jenkyns et al., 2004).

Age (Ma)	97.5	95.35	94.6	93.35	91.25	89.76	86.47	83.5	82.11	75.1	70.1
Grossplot thermal values (ºC) at 40º by Frakes (1999)	17.5	20	22.5	>25	17.5	17.5	17.5	15	17.5	17.5	12.5
Values (ºC) from δ^{18}O in bulk chalk at ~40º by Jenkyns et al. (2004)	21	24	25	27	22	23	22	19	18	17	17
Difference (ºC)	3.5	4	2.5	<2	4.5	5.5	4.5	4	1.5	-0.5	4.5

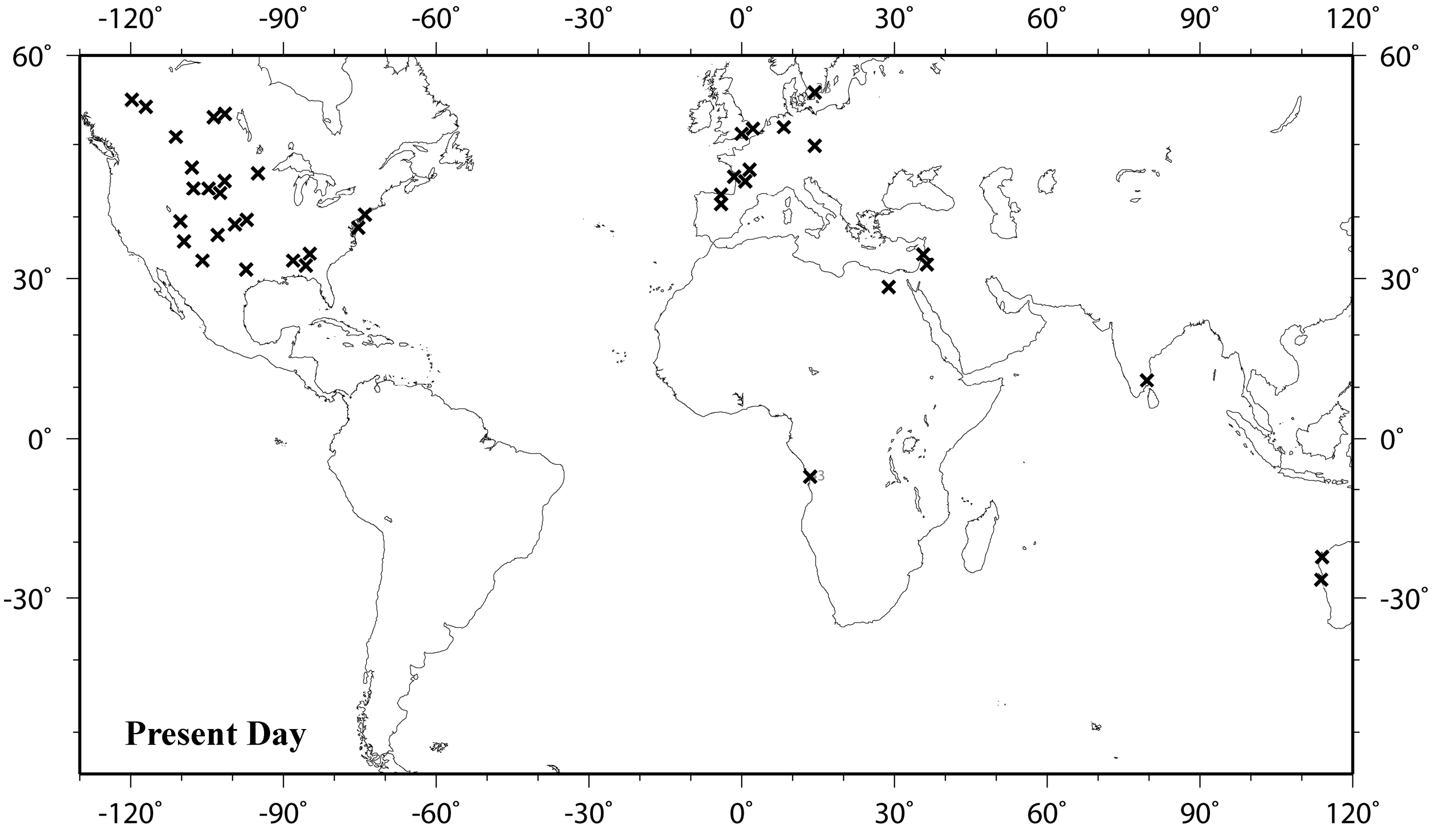

Figure 4.1. Geographical distribution of the selachian assemblages used in this study (PLATES project, 2010).

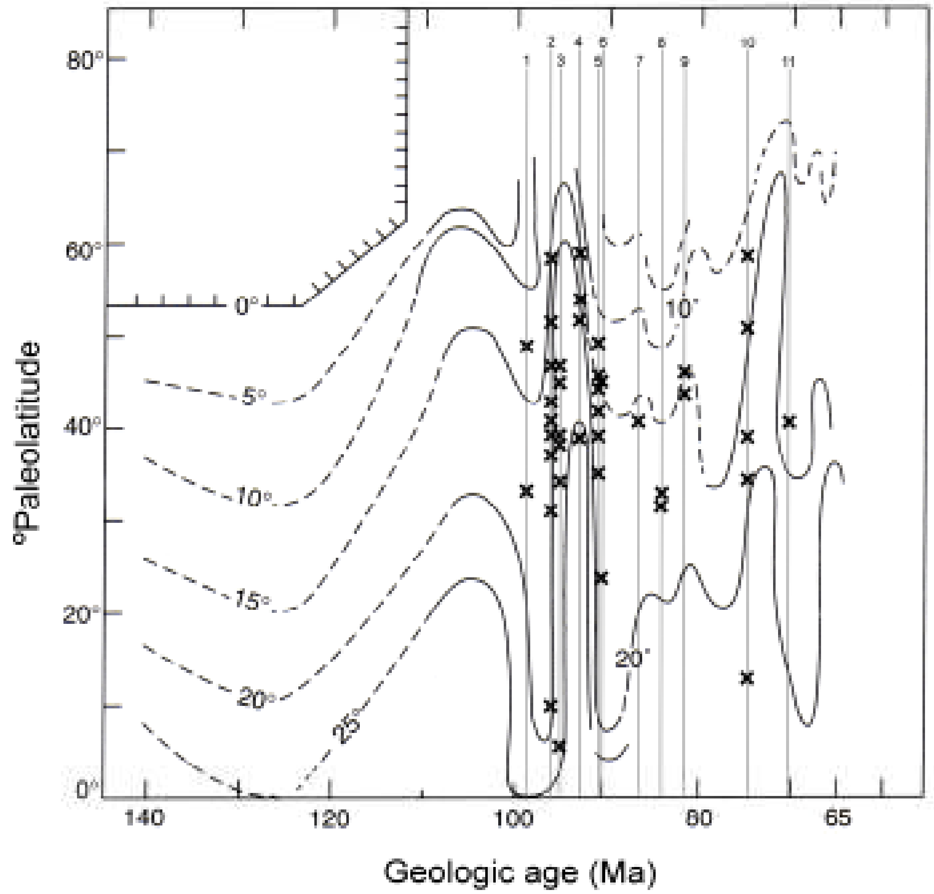

Figure 4.2. Grossplot of Late Cretaceous marine paleotemperature with plotted assemblages (**X**) at: (1) early Cenomanian (97.5 Ma,), (2) middle Cenomanian (95.35), (3) late Cenomanian (94.6), (4) early Turonian (93.35), (5) middle Turonian (91.25 Ma), (6) late Turonian (89.76), (7) late Coniacian (86.47), (8) Santonian-Campanian boundary (83.5), (9) early Campanian (81.22), (10) late Campanian (75.1), and (11) early Maastrichtian (70.1) (modified from Frakes, 1999).

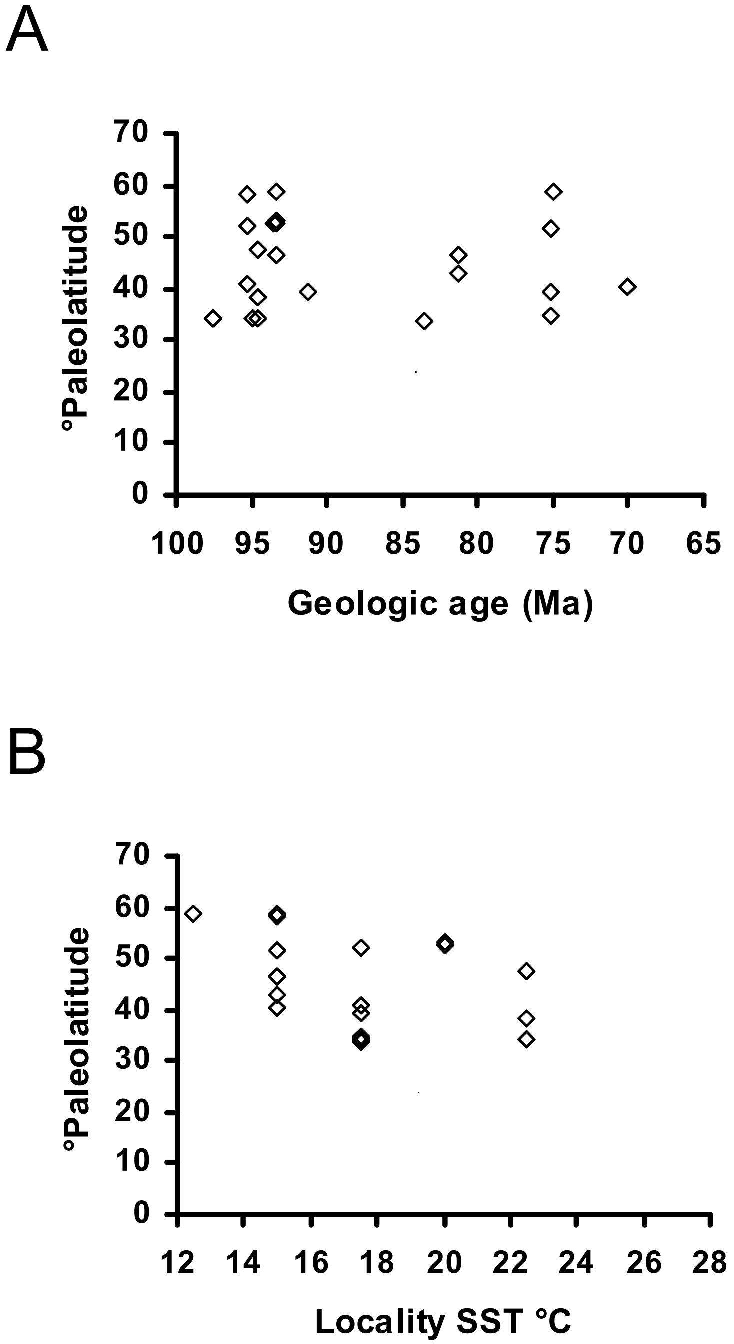

Figure 4.3. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Archaeolamna* localities.

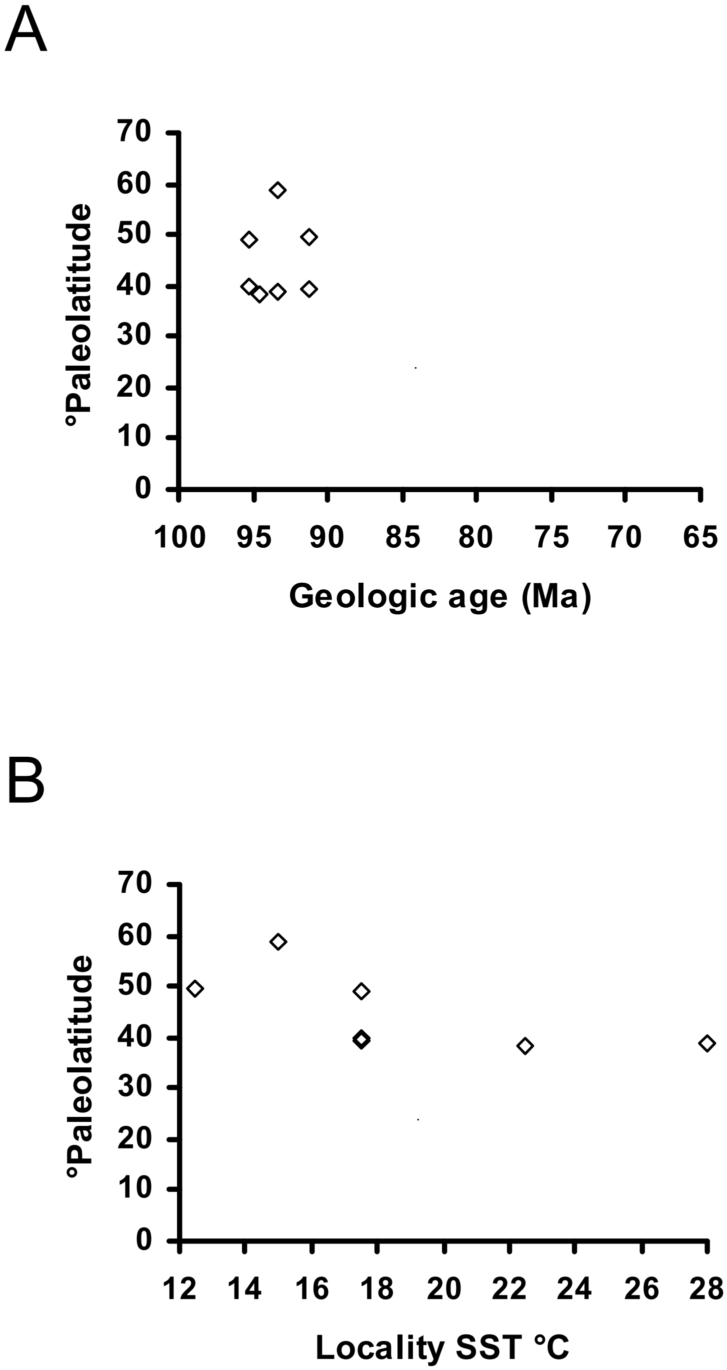

Figure 4.4. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Cardabiodon* localities.

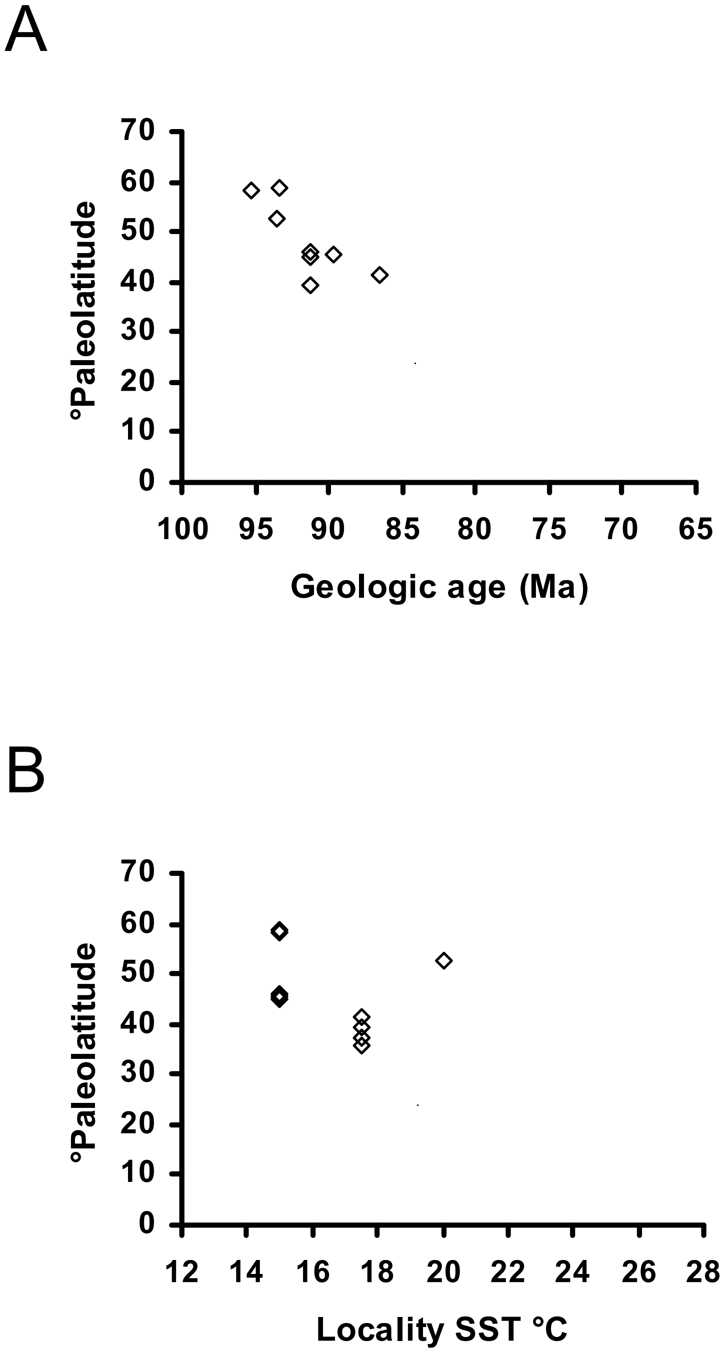

Figure 4.5. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Johnlongia* localities.

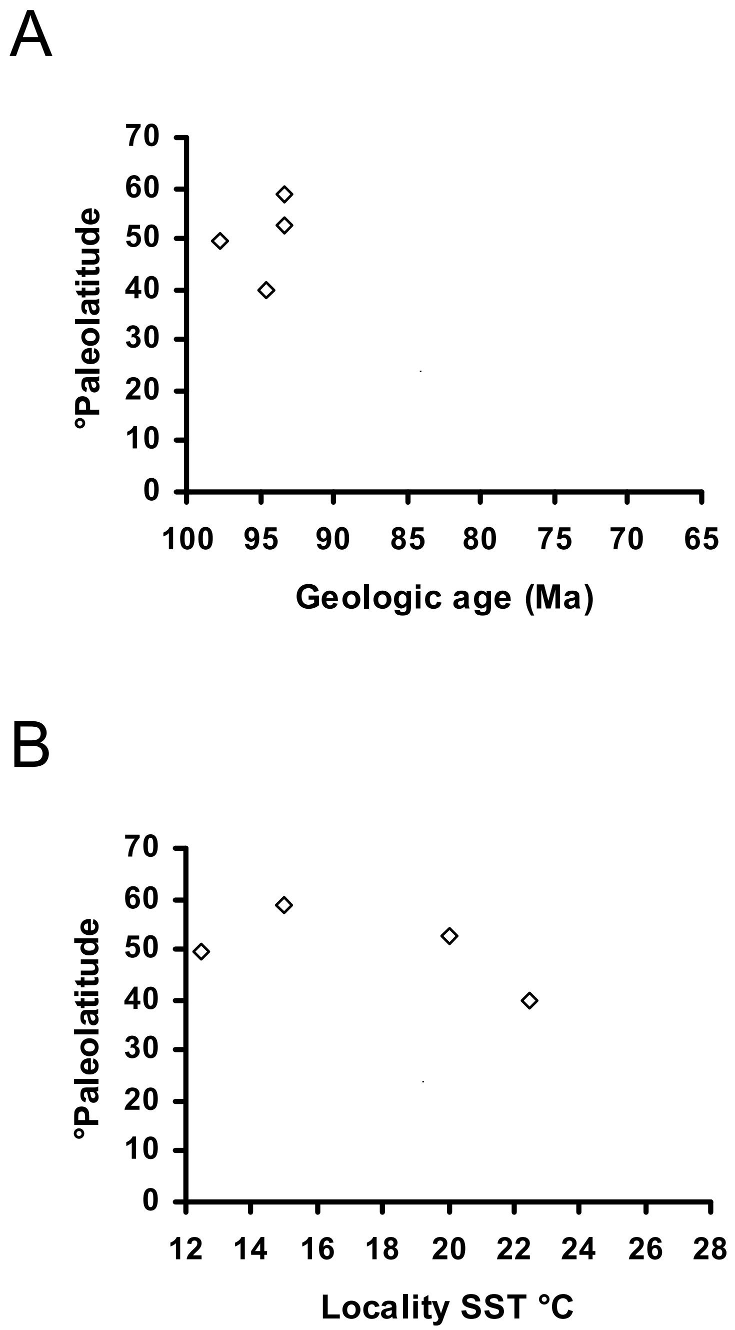

Figure 4.6. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Dwardius* localities.

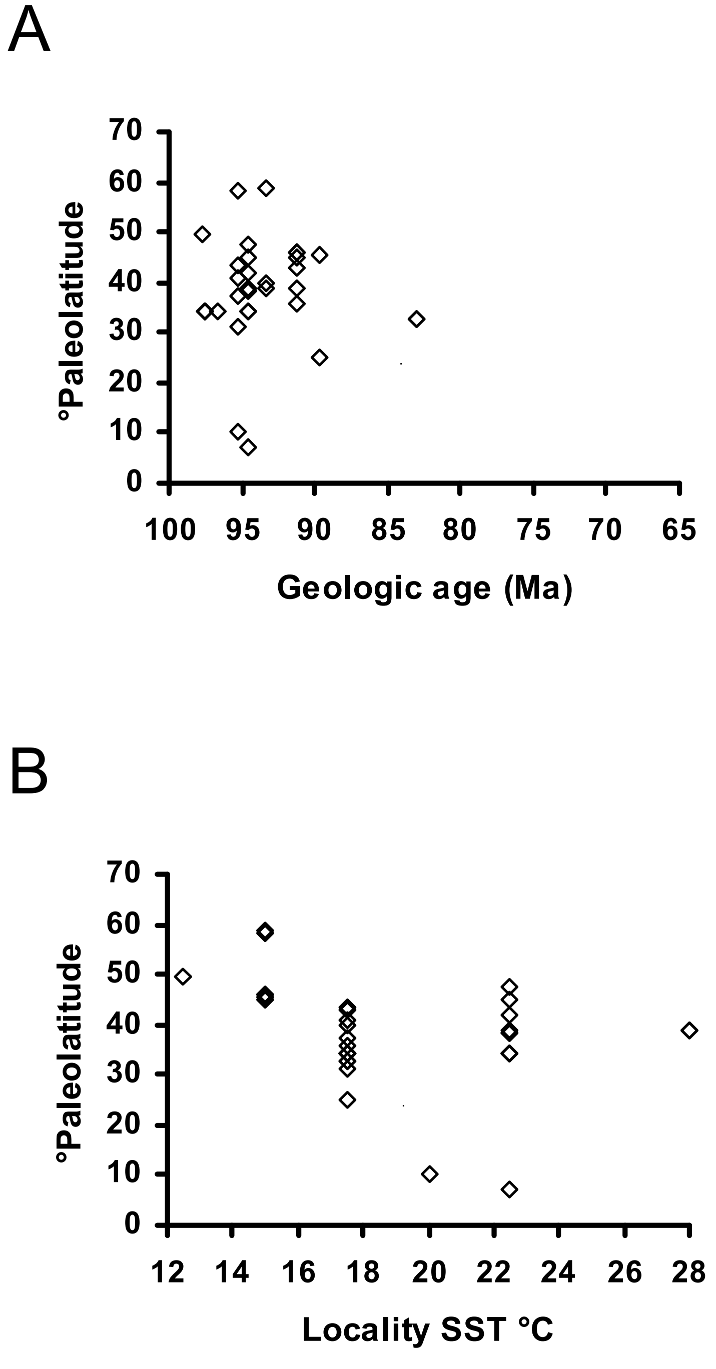

Figure 4.7. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Cretodus* localities.

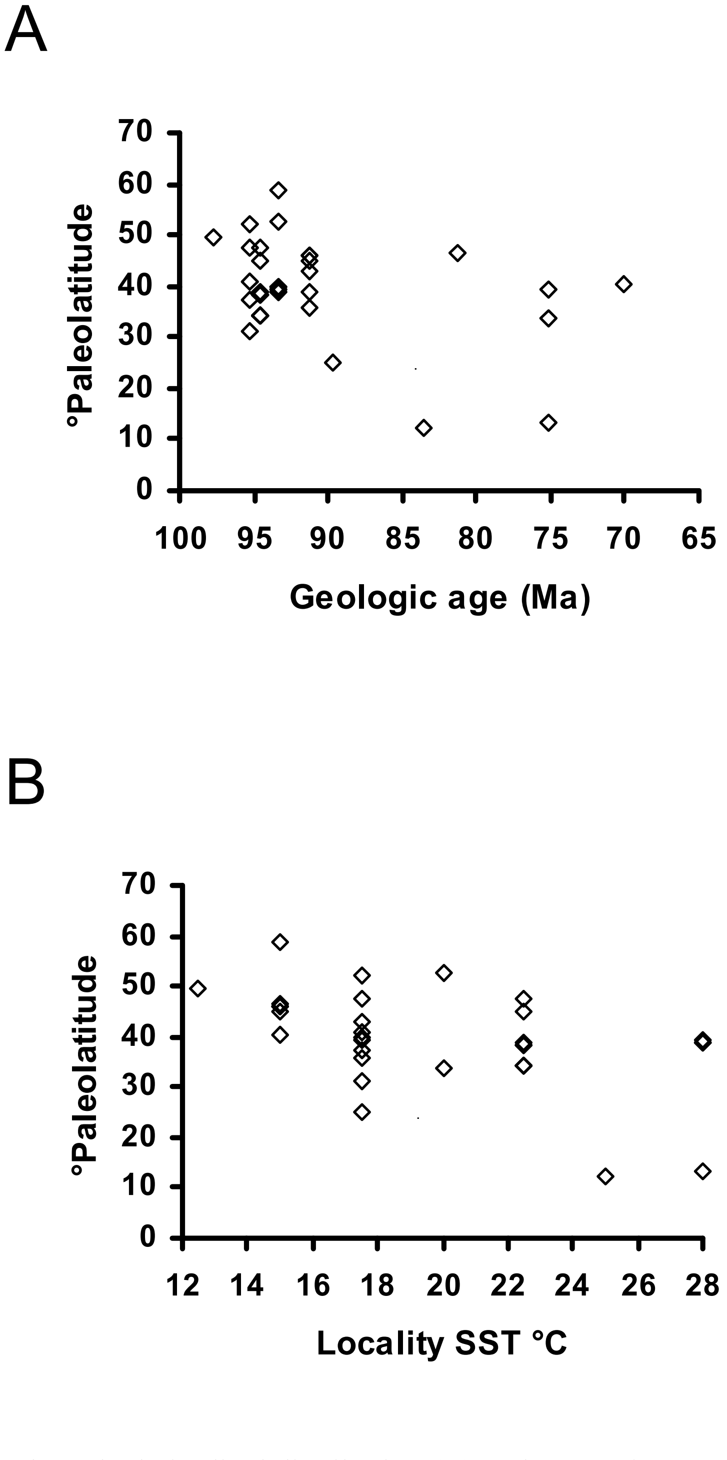

Figure 4.8. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Cretalamna* ex. gr. *appendiculata* localities.

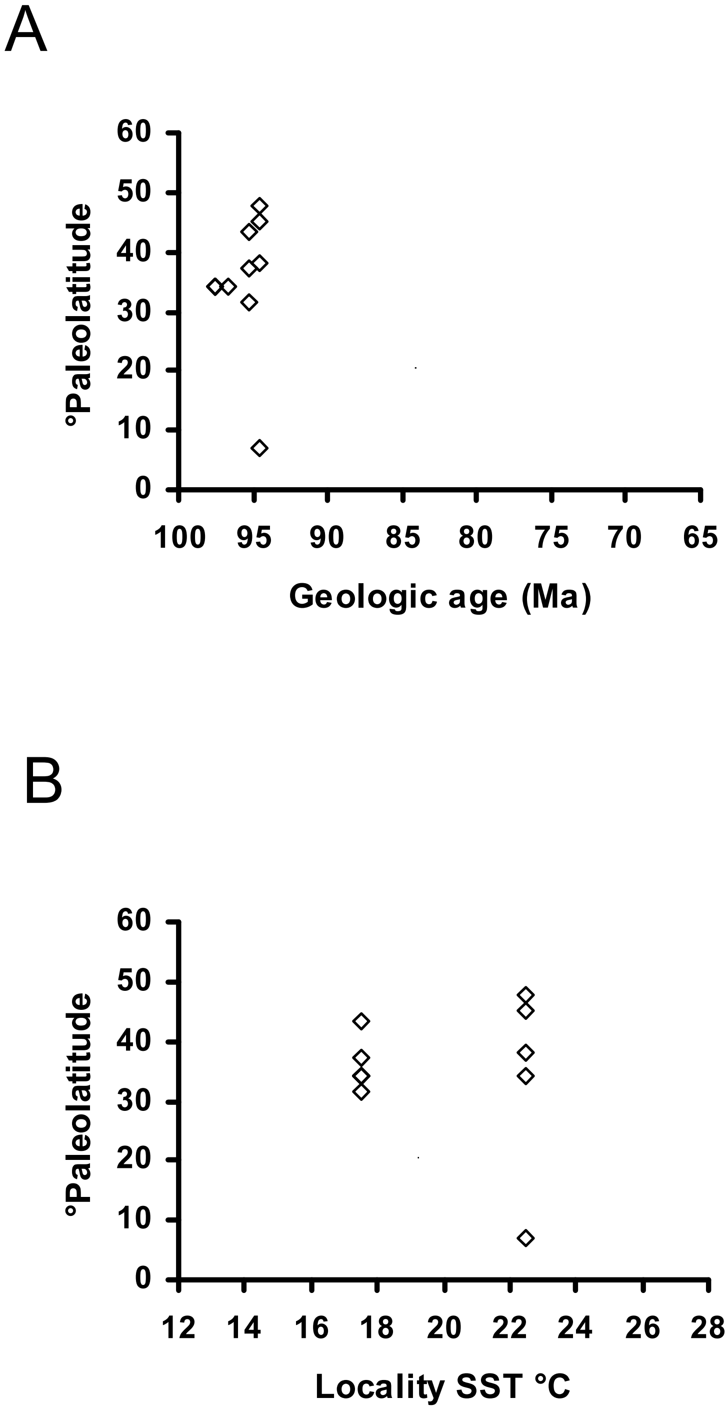

Figure 4.9. The paleolatitudinal distribution (A) and sea surface temperature (SST) range (B) of the examined *Carcharias amonensis* localities.

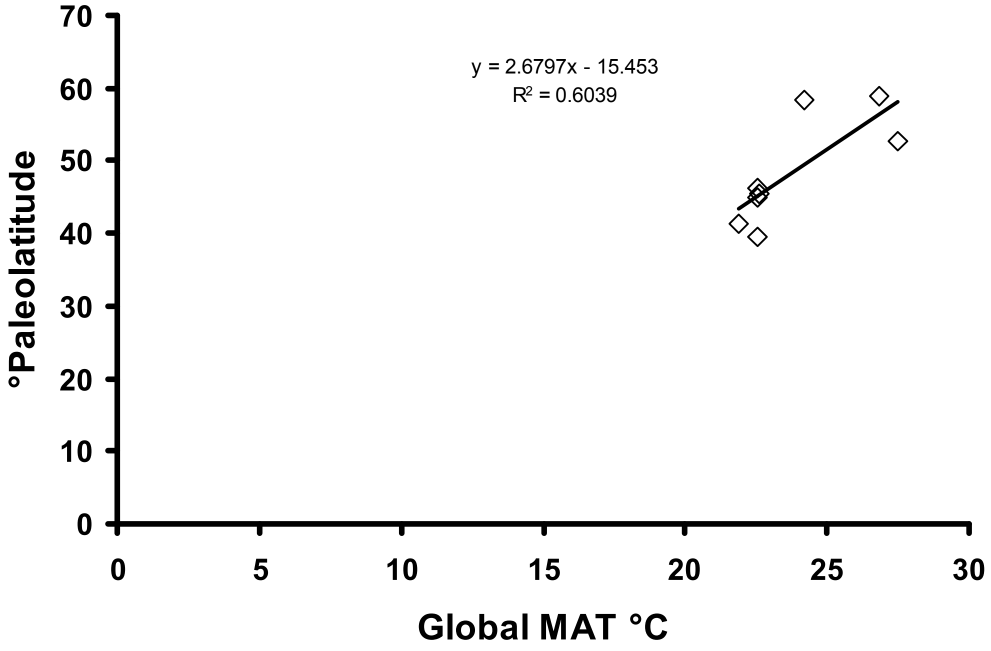

Figure 4.10. Relationship between paleolatitudes of *Johnlongia* fossil localities from both hemispheres and global climate change (paleolatitude data from PLATES project, 2010; paleothermal data from Jenkyns et al., 2004).

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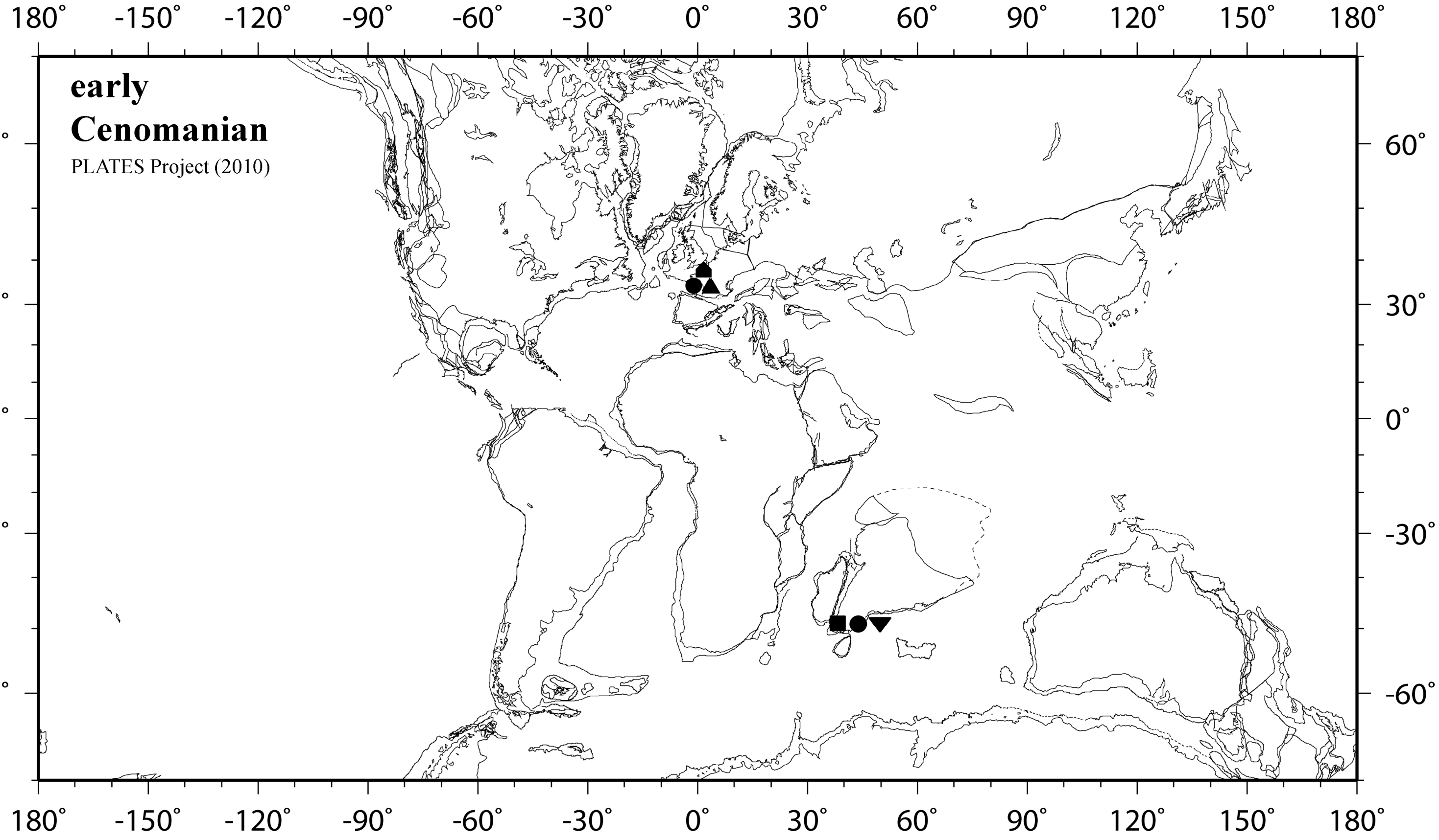
Appendix 4.1. Paleomaps generated by PLATES project (2010) used in this analysis. Taxa are indicated as the following symbols: triangle (*Archaeolamna*), star (*Cardabiodon*), diamond (*Johnlongia*), circle (*Cretodus*), square (*Dwardius*), inverted triangle (*Cretalamna* ex. gr. *appendiculata*) with associated selachian assemblage.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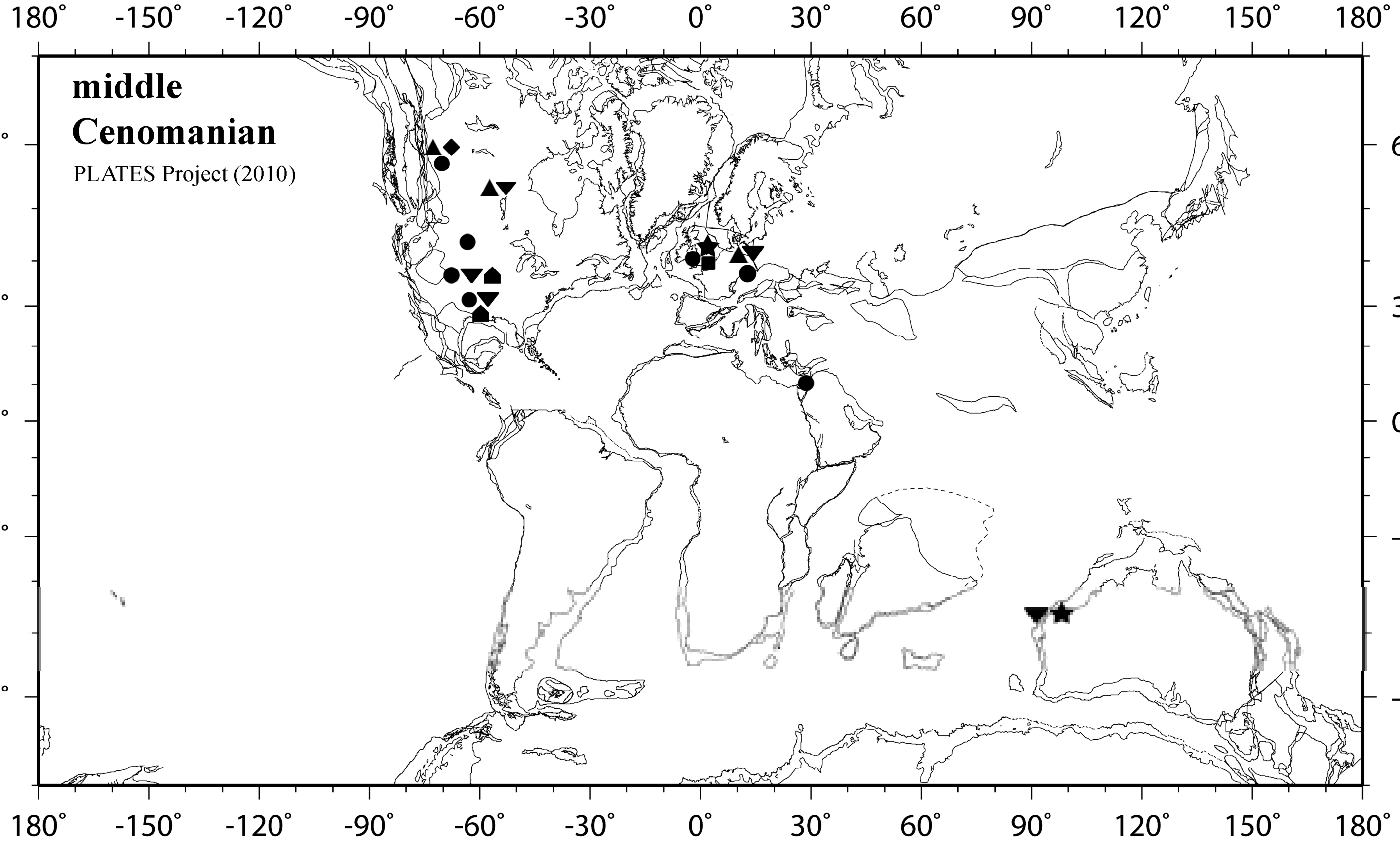
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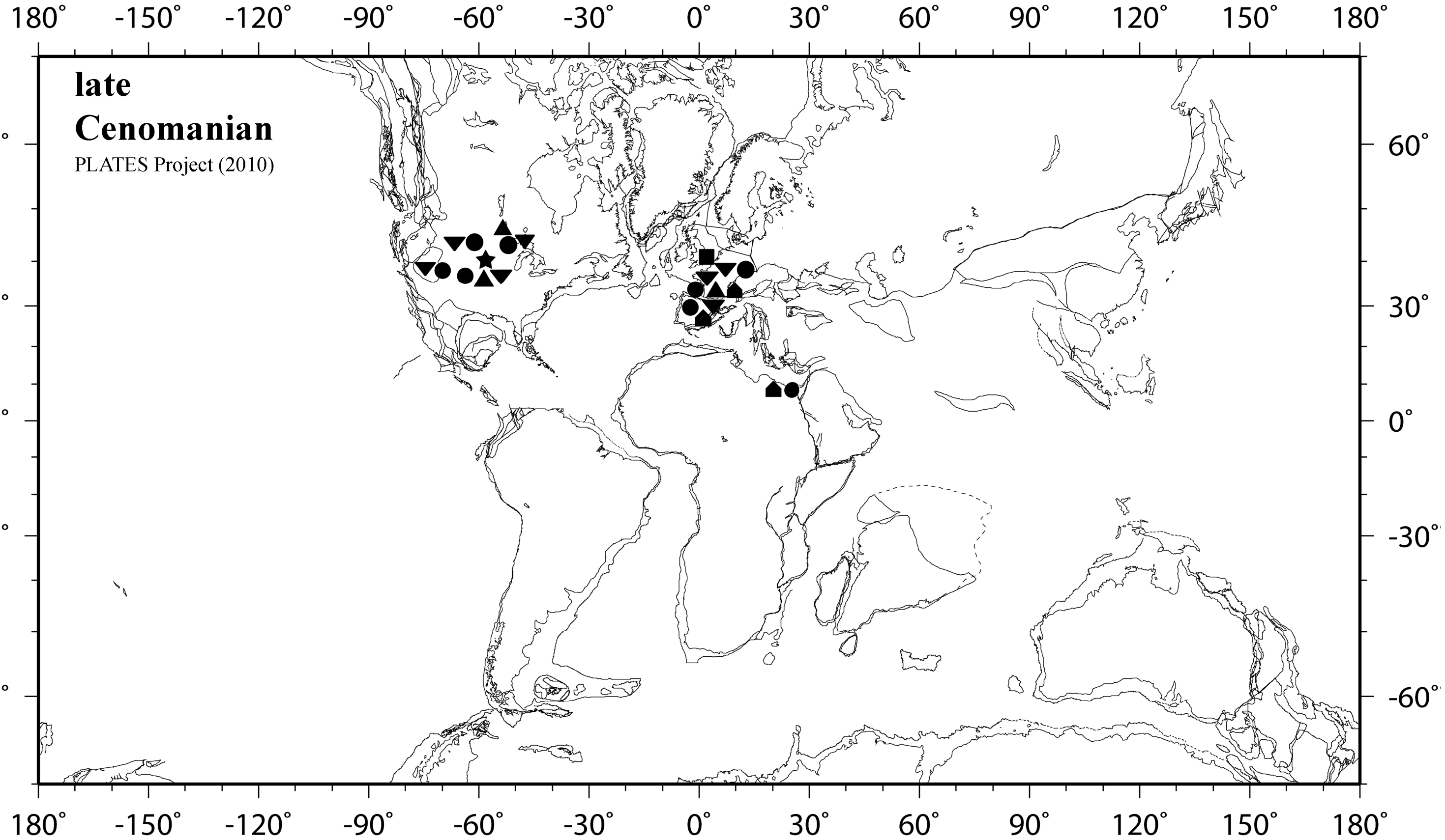
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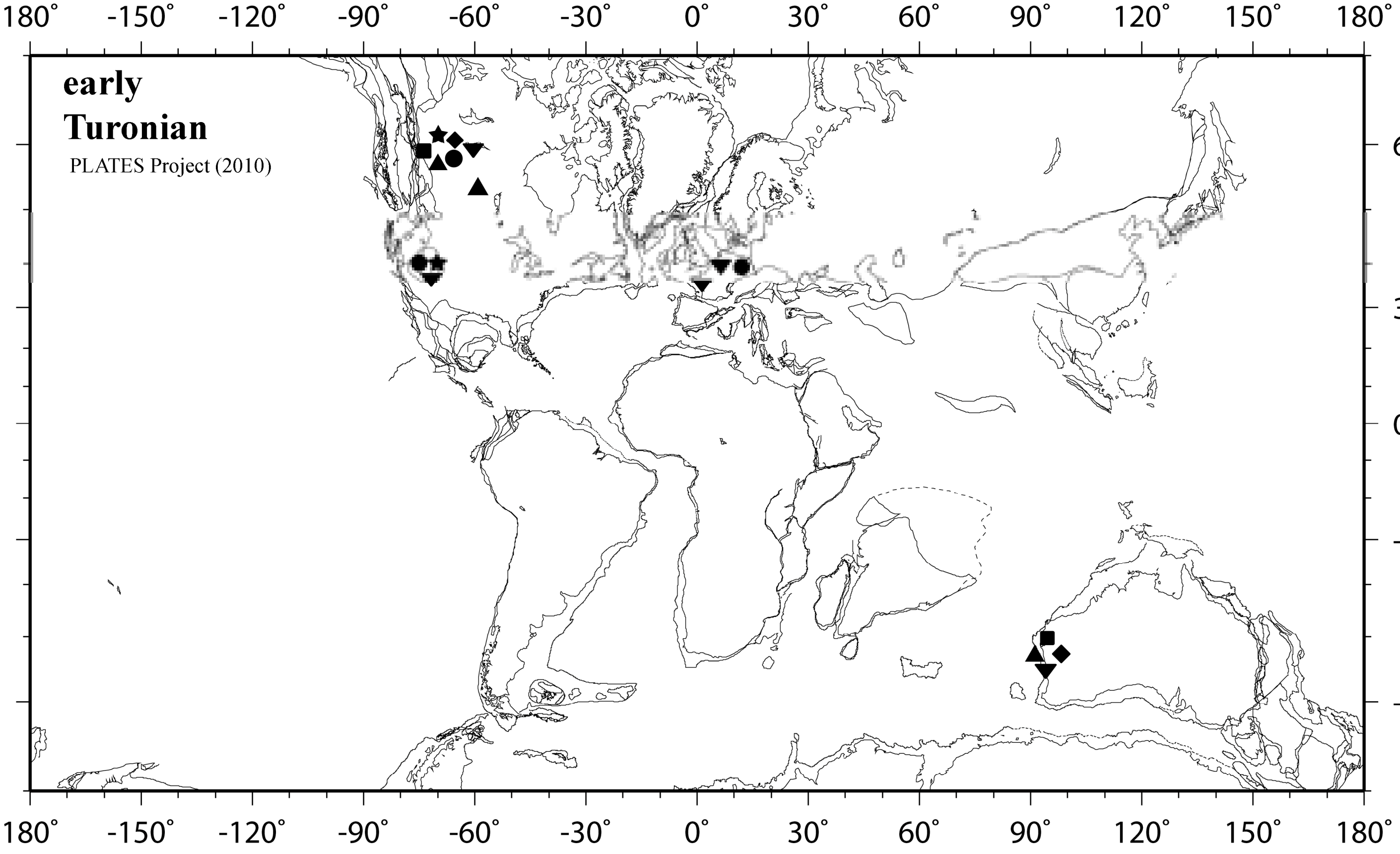
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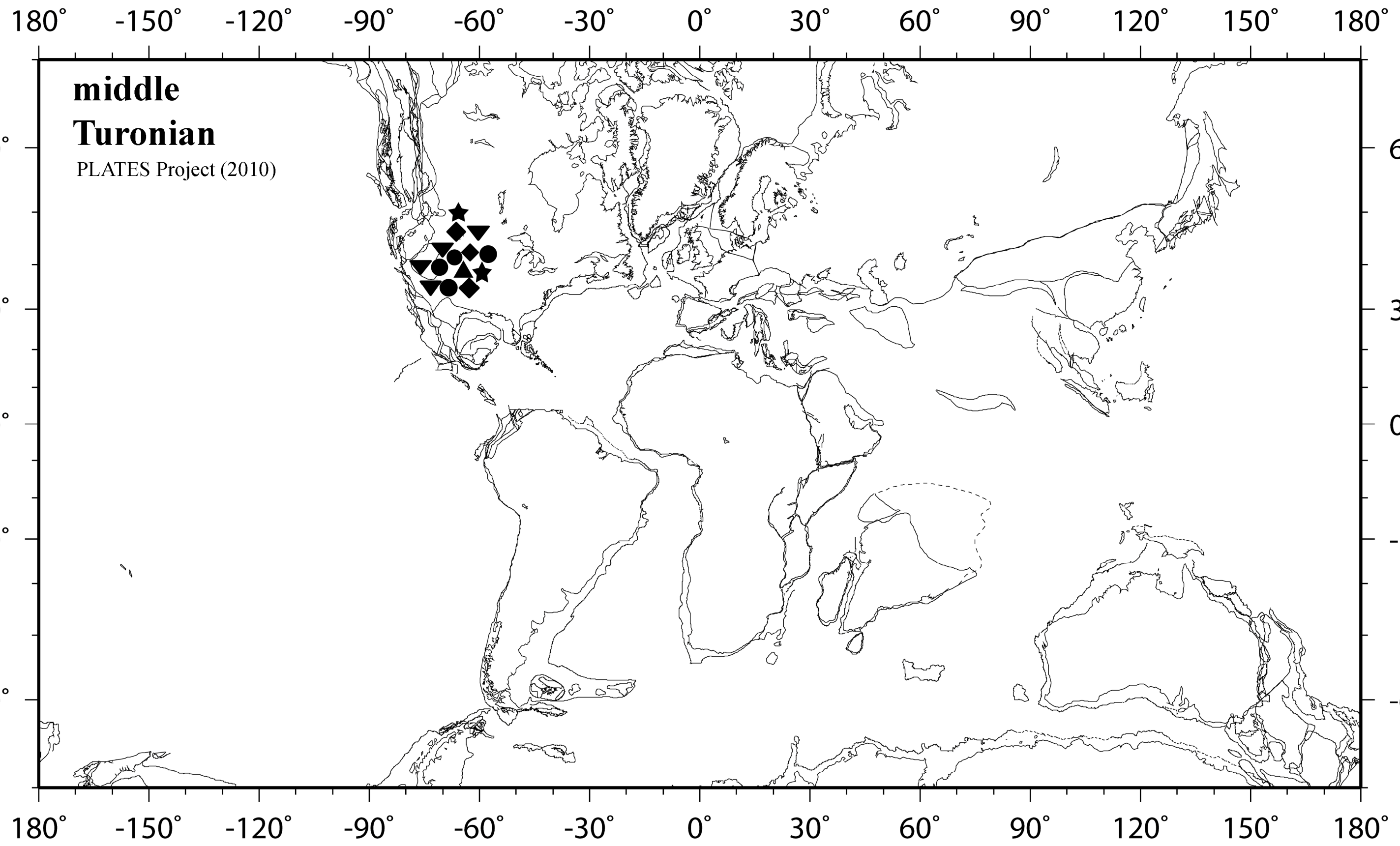
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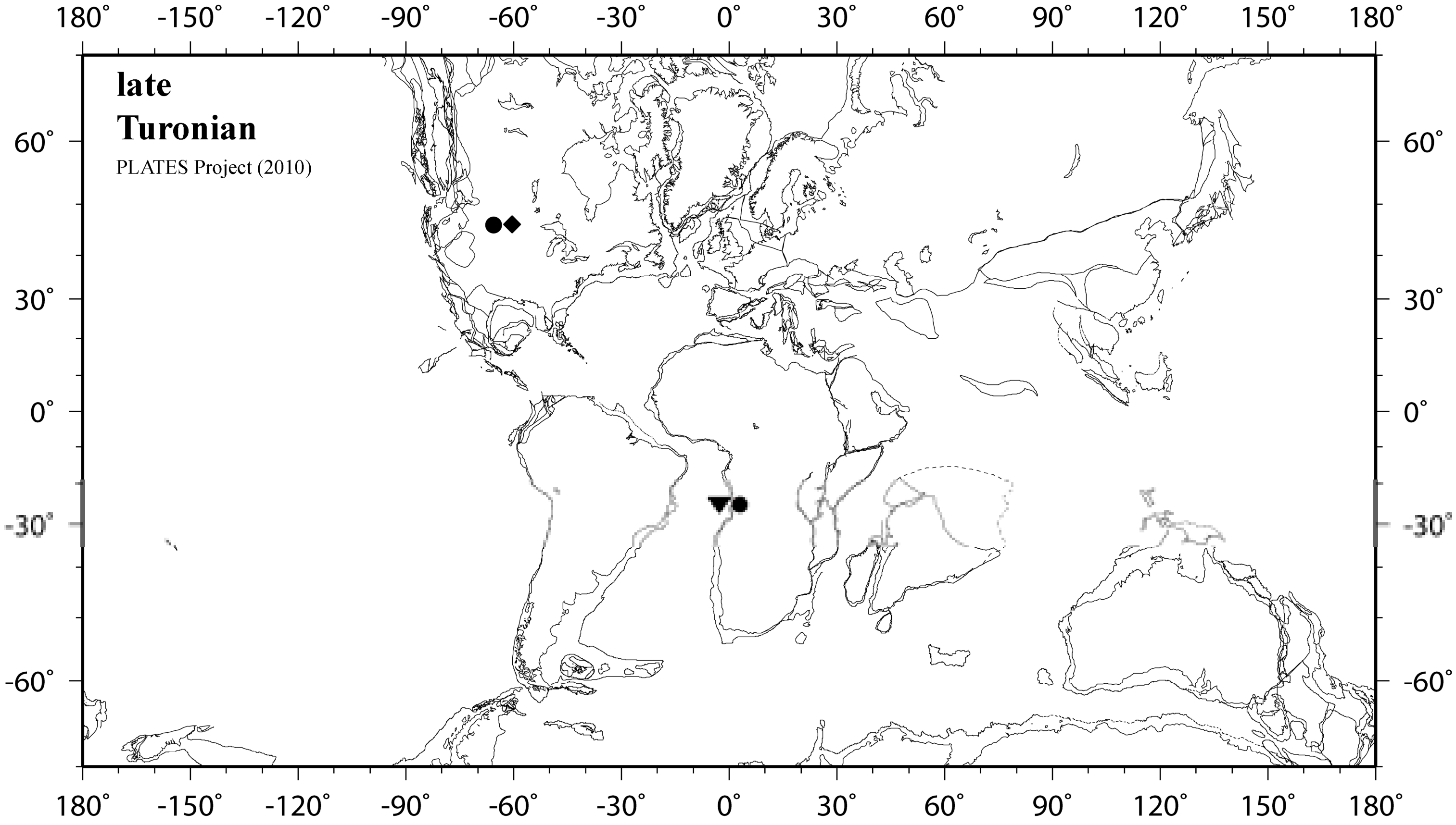
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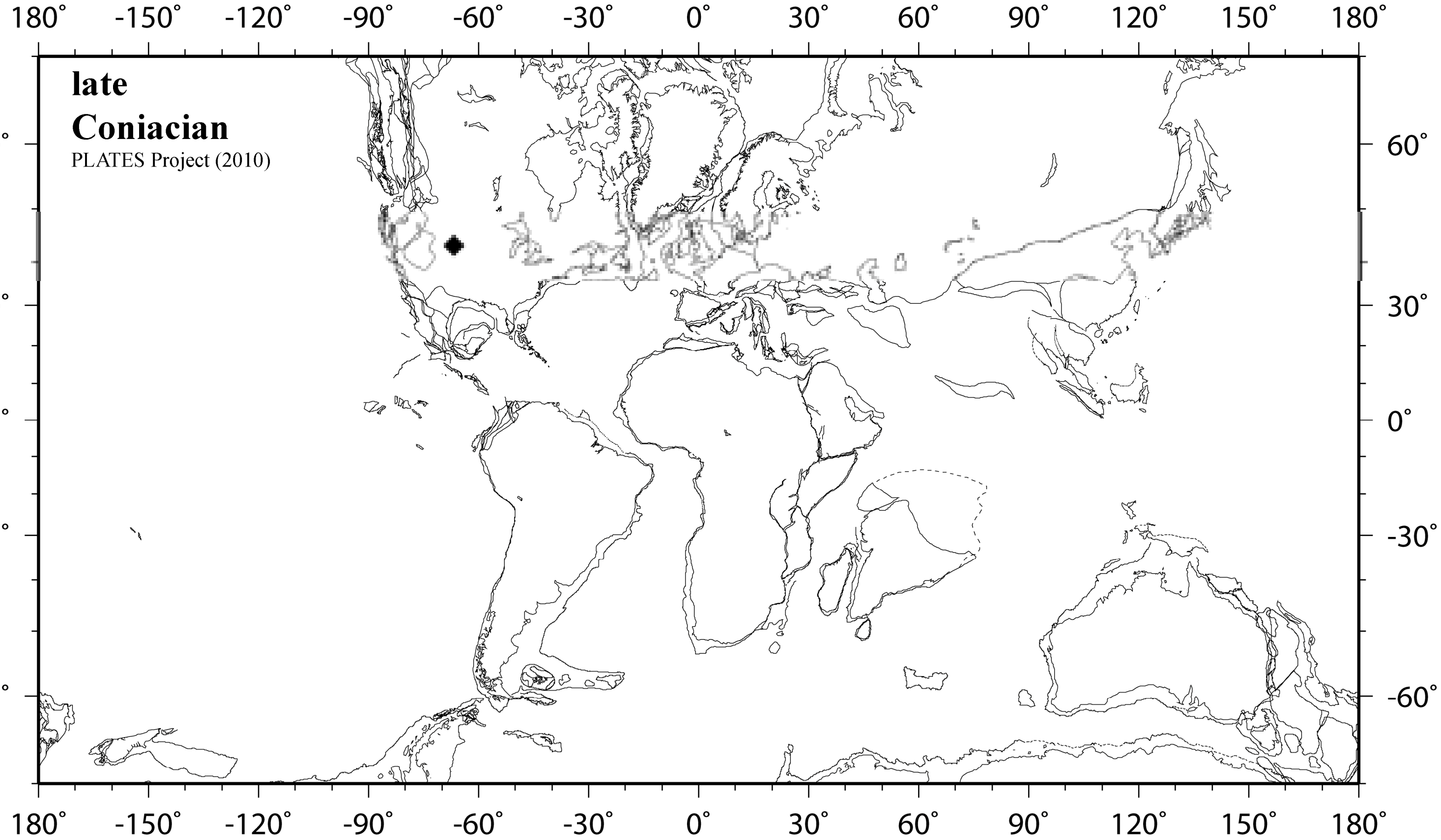
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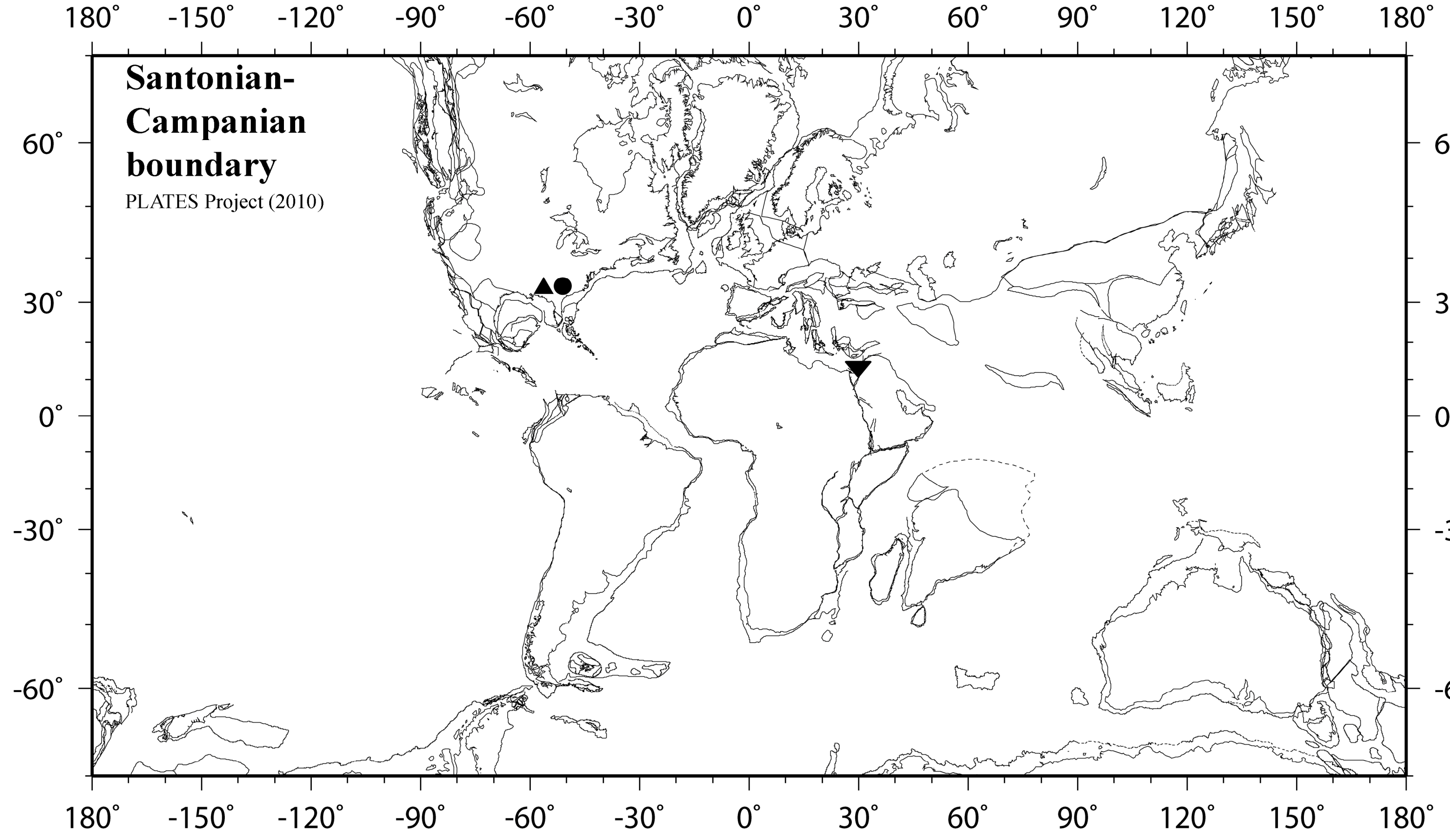

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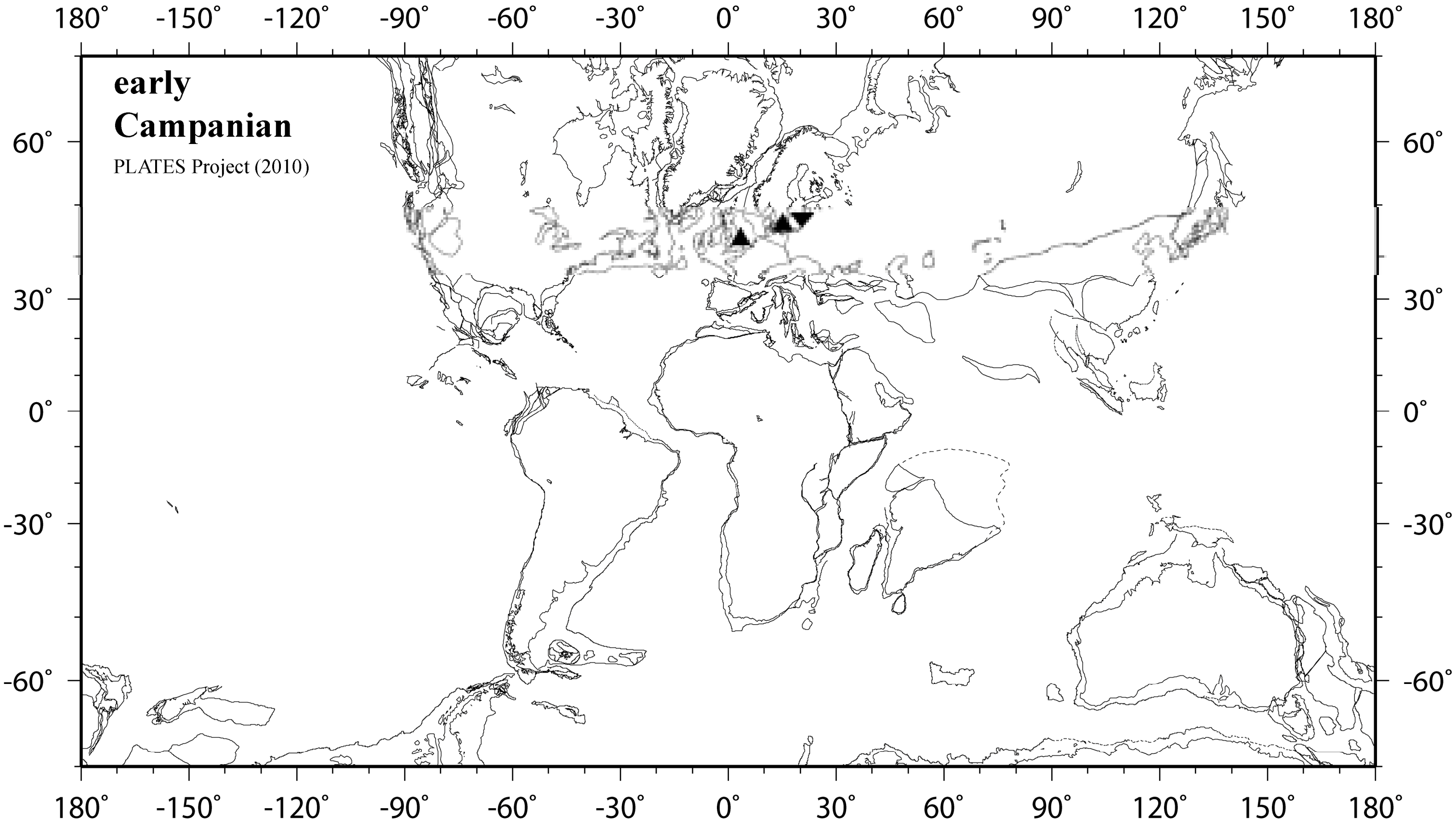

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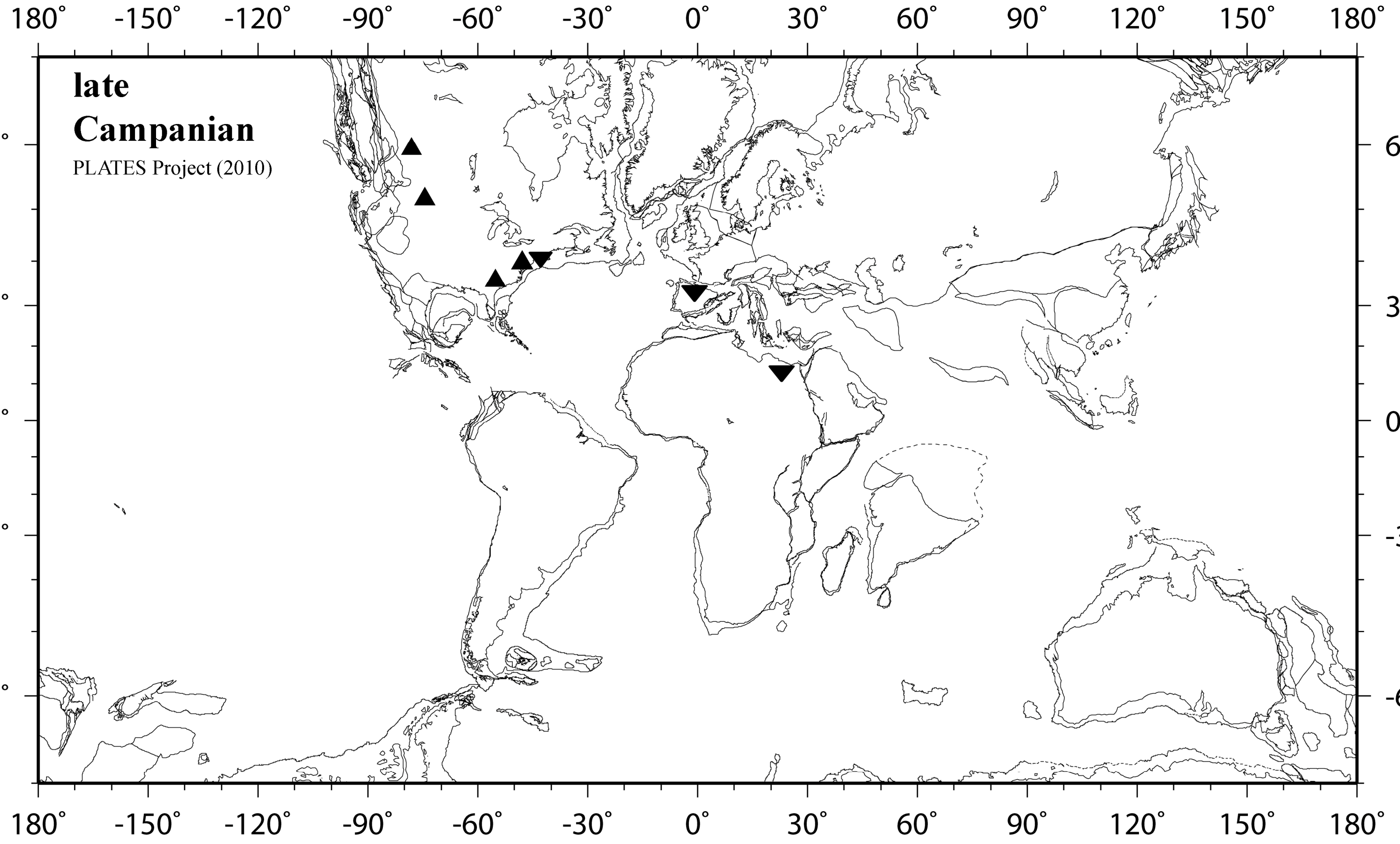
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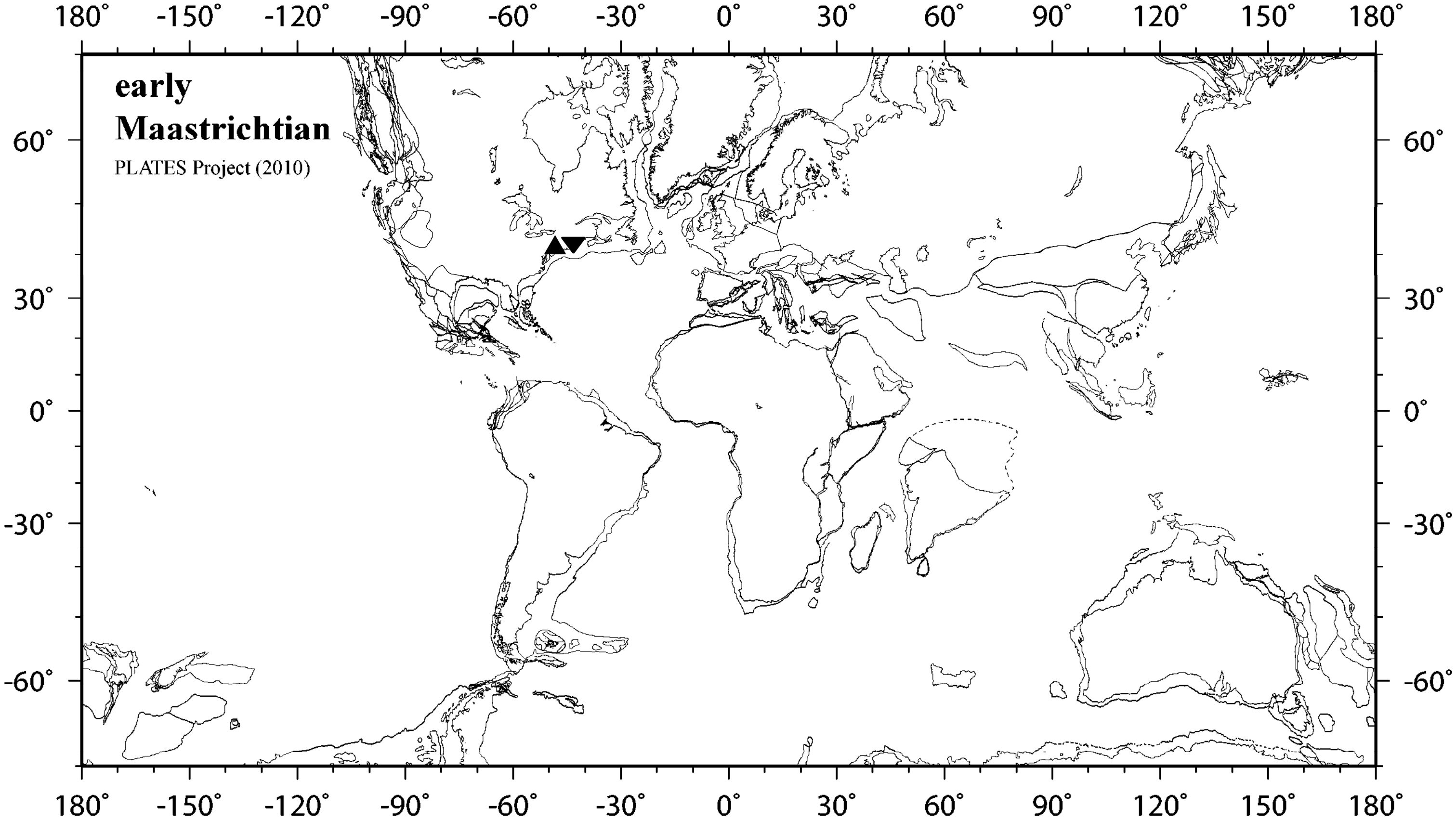
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CHAPTER 5

A partial skeleton of the Late Cretaceous lamniform shark, *Archaeolamna kopingensis*, from the Pierre Shale of western Kansas

A nearly identical version of this chapter was published as:

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.

The various authors contributed to this work by providing information on age and growth of the specimen (MGN), providing editorial comments (MVHW, AMM, KS, NGM), supervisory and financial support (MVHW and AMM), by helpful discussion (KS), or by providing access to specimens in their care (GT, JDS).

INTRODUCTION

The euselachian fossil record largely consists of isolated teeth because of the poor preservation of the cartilaginous endoskeleton. A taxonomy based strictly on isolated teeth is potentially problematic because of the condition of heterodonty. Variation in tooth morphology along the jaw of an individual may be mistakenly recognized and described as multiple taxa when teeth are recovered as isolated elements. In rare instances, natural tooth sets (see Welton and Farish, 1993) are found, allowing us to establish exact dental arrangements at least for some individual specimens (e.g., Maisey, 1983; Maisey and Carvalho, 1997; Shimada, 1997; Kriwet and Klug, 2004; Shimada and Cicimurri, 2005; Ehert et al., 2009). Identifying an accurate dental arrangement of a species is essential for determining its systematic position (Applegate, 1965; Siverson, 1999; Shimada, 2002).

In this chapter, we describe a partial skeleton of the large shark *Archaeolamna kopingensis* (Davis, 1890) housed in the Natural History Museum of Los Angles County. *Archaeolamna kopingensis* is a Late Cretaceous lamniform that was previously referred to *Lamna arcuata* (e.g., Woodward, 1894) and *Plicatolamna arcuata* (e.g., Herman, 1977). The genus *Archaeolamna* chronostratigraphically ranges from the Albian to the Maastrichtian (Siverson, 1996). *Archaeolamna kopingensis* and closely allied but unnamed taxa of *Archaeolamna* (e.g., *A.* cf. *A. kopingensis*, *A.* ex. gr. *A. kopingensis*, and *A.* aff. *A. kopingensis*) are reported from the Campanian of Sweden (Davis, 1890; Siverson, 1992), the Albian–Cenomanian of France (Biddle, 1993; Vullo et al., 2007), the

Campanian–Maastrichtian of Belgium (Herman, 1977), and the Albian–Cenomanian of Western Australia (Siverson, 1996; 1997) as well as from various Cenomanian–Maastrichtian marine deposits of North America (e.g., Cappetta and Case, 1975; Case, 1978, 1987; "*Cretodus* sp." of Case et al., 1990: fig. 7a, b, but not c–f; Kent, 1994; Beaven and Russell, 1999; Becker et al., 2000; Cumbaa et al., 2006; Cook et al., 2008; Shimada and Martin, 2008; Underwood and Cumbaa, 2010). However, these earlier reports were based on isolated teeth. The specimen described here includes fragments of the neurocranium, vertebral centra, and portions of the upper and lower jaws with preserved tooth files. Because many of the teeth show their natural arrangement, the specimen allows us to provide a detailed description of this taxon for the first time, as well as an opportunity to evaluate previous conclusions regarding the dental arrangement of this species. This specimen also offers insight into the systematic position of *A. kopingensis* within the Lamniformes and provides information regarding its paleoecological role.

METHODS

Terminology—Shimada (2002) recognized four tooth types within each jaw quadrant. Moving distally along the jaw from the symphysis are symphysial, anterior, intermediate, and lateral teeth. The inflated region housing the anterior teeth is called a dental bulla on both the palatoquadrate and Meckel's cartilage (Compagno, 1990; Shimada, 2002). Siverson (1999) referred to the concave inner surface of this structure as the anterior hollow. The teeth situated in the distal-most file (= labiolingual tooth arrangement) of the bulla are referred to by Shimada (2002) as intrabullar intermediate teeth. Alternatively, Siverson (1999) recognized intermediate teeth as those reduced teeth that form on the intermediate bar, teeth referred to by Shimada (2002) as extrabullar intermediate teeth. The intermediate bar is a thickened area of cartilage separating the teeth of the dental bulla from the more distally positioned teeth that are situated in a shallower dental trough (Shimada, 2002) or lateroposterior hollow (Siverson, 1999). The teeth situated in the distal-most file of the bulla are referred to by Siverson (1999) as anterior teeth. Cigala-Fulgosi (1992) and Shimada (2002) noted that the division between lateral and posterior teeth in lamniforms is subjective. Shimada (2002) proposed that the latter term be removed from the description of lamniform dentitions.

Tooth Measurements—Nine measurements (Appendix 5.1) were taken from a tooth in each tooth file, where all teeth belong to the same row (= mesiodistal tooth arrangement). The measurement procedures predominantly followed the criteria used by Shimada (2007: fig. 4) and include: (1) tooth height; (2) crown height; (3) median cusp height; (4) mesial cutting edge length; (5) distal cutting edge length; (6) median cusp width; (7) mesial cusplet height; and (8) tooth width. The ninth variable, the distal inclination of the median cusp, was calculated by dividing the distal cutting length by the mesial cutting length.

Age Protocols—To quantify age of the shark individual, the protocol and criteria established by Goldman and Musick (2006) and Shimada (2008) was utilized. Three centra of LACM 128125 were sectioned to expose a sagittal view of the corpus calcareum. Annular measurements were made from the focus to the outer margin of each band to determine growth in radial distance. Centra were sectioned using a lapidary trim saw (Lortone Inc. Model # FS6) with a 15 cm diameter, and a 1 mm-thick diamond-impregnated blade. The sectioned faces were polished on a glass plate using slurry of silicon carbide powder (1000 grit: E.T. Enterprises) and water (ca. 1.5 parts powder to 1 part water).

Institutional Abbreviations—CMN, Canadian Museum of Nature, Ottawa, Canada; **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**, Natural History Museum of Los Angeles County, California, USA; **SDSM**, South Dakota School of Mines and Technology, Vertebrate Paleontology, Rapid City, USA; **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.

Comparative Specimens—*Cretoxyrhina mantelli*: FHSM VP-323, FHSM VP-2187, KUVP 55060. *Cretalamna appendiculata*: LACM 128126. *Squalicorax* spp.: FHSM VP-2213, KUVP 69712, LACM 135929, SDSM 34975, USNM 425665, UWGM NS.1509.34. *Alopias abdutus*: LACM 39330-1. *Alopias superciliosus*: LACM 39321-1. *Alopias vulpinus*: LACM 36864-1, LACM 39324-1, LACM 39325-1. *Carcharodon carcharias*: LACM 38194-1, LACM 42728-1.

Lamna ditropis: LACM 56781-1. *Lamna nasus*: LACM 38174-1, UMMZ 60591. *Odontaspis ferox*: LACM 39445-1. *Carcharias taurus*: LACM 39336-5, UMMZ 147001.

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobrachii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Superorder Galeomorphii Compagno, 1973

Order Lamniformes Berg, 1958

Family Archaeolamnidae Underwood and Cumbaa, 2010

Type Genus—*Archaeolamna* Siverson, 1992.

Included Genera—Monotypic.

Diagnosis—As for the only known genus.

Genus *Archaeolamna* Siverson, 1992

Type species—*Odontaspis kopingensis* Davis, 1890.

Included species—*Archaeolamna kopingensis* (Davis, 1890) and *A. haigi* Siverson, 1996.

Emended Diagnosis—Lamniform shark with teeth that bear a tall, triangular median cusp. A distinct cutting edge runs continuously across the median cusp and a pair of triangular lateral cusplets that flank the median cusp. The height of the distinct lingual neck is relatively constant along the crown-root boundary. The robust bilobate root has rounded lobes, a high basal concavity, and a well-developed lingual protuberance with one or more nutrient foramina. *Archaeolamna* differs from all other lamniforms in having a dental arrangement that consists of at least one file of upper and two files of lower symphysial teeth; three files of anterior teeth within the dental bulla; large first and second upper anterior teeth that are equal in height; large third anterior (= intrabullar intermediate) teeth with a median cusp that is strongly distally curved; reduced first lower anterior teeth; and absence of reduced extrabullar intermediate teeth and intermediate bar.

Archaeolamna kopingensis (Davis, 1890)

(Figs. 5.1–5.5)

Synonomy list—Refer to Chapter 2, p. 41.

Diagnosis—*Archaeolamna kopingensis* differs from *A. haigi* by the teeth of the latter having enameloid folding on the lingual crown face and a more gracile root. As well, the anterior teeth of *A. haigi* typically have a concave labial crown face and the lower lateral teeth are symmetrical (Siverson, 1996).

Referred Material—LACM 128125, a partial skeleton that consists of fragments of the neurocranium including the occipital centrum, seven vertebral centra, an incomplete left and right upper (palatoquadrate) and lower (Meckel's cartilage) jaws. With the exception of the right palatoquadrate, associated with the jaw elements are multiple files of articulated and disarticulated teeth.

Horizon and Locality—The specimen was collected in 1966 from the Sharon Springs Formation of the Pierre Shale Group (Martin et al. 2007: formerly

Sharon Springs Shale Member, Pierre Shale Formation) of Logan County, Kansas, U.S.A. (its exact locality data are available at LACM). In the region, the Sharon Springs Formation has two members and an informal unit: in ascending order, (1) Nicholas Creek Member; (2) Boyer Bay Member; and (3) 'organic rich shale' (Bertog et al. 2007); however, the exact horizon of LACM 128125 within the Sharon Springs Formation is uncertain. The age of the formation is considered to be early middle Campanian (Gill et al., 1972; Parrish and Gautier, 1993; Cobban, 1993).

Description

Mandibular Arch—The left and the presumed right palatoquadrates (Figs. 5.1A, B and 5.2) are well preserved in three dimensions but are missing the most distal regions. Both palatoquadrates meet in a symphysis. This region preserved a single symphysial tooth. The incomplete left palatoquadrate has an arched contour and has a mesiodistal length of 23.5 cm, and a maximum preserved depth of 6.1 cm. The lingual side has nine files of well preserved in-situ replacement teeth that are arranged in a juxtaposed series (see Welton and Farish, 1993). Four additional files have teeth that are severely eroded or missing. The distal-most lateral tooth files of the left palatoquadrate are missing. A well-developed dental ridge is present and spans the length of the palatoquadrate. No significant morphological details are apparent on the labial side of this structure (Fig. 5.1B). The presumed right palatoquadrate is less complete than the left palatoquadrate and is preserved in two pieces (Fig. 5.1A, B). The preserved portion is 19.2 cm in mesiodistal length and has a maximum preserved depth of 3.9 cm. Unlike the left palatoquadrate, the presumed right palatoquadrate does not preserve any in-situ teeth. Nonetheless, it is identified as the right palatoquadrate because (1) the overall curvature of this structure closely matches the left palatoquadrate, (2) it is too robust to be a hyomandibula, ceratohyal, or any other branchial element, and (3) two right anterior teeth are preserved adjacent to it. The labial surface exhibits no significant morphological details (Fig. 5.1B).

Most of the replacement teeth are lost from the left palatoquadrate; however, two replacement teeth in the first tooth file and three replacement teeth in the second and third files are preserved deep into the cartilage in a region we infer to be a dental bulla. Only a single replacement tooth from each lateral tooth file remains along the rest of the palatoquadrate. This condition suggests that the lateral teeth were housed in a shallow dental trough of the palatoquadrate, a region that was not as conducive to the preservation of multiple replacement teeth. There is no apparent diastema or any indication of an intermediate bar between the teeth of the third and fourth tooth files. The right palatoquadrate does not preserve replacement teeth (Fig. 5.1A).

The Meckel's cartilage (Figs. 5.1A, B and 5.3) is deeper than the palatoquadrate, with a maximum preserved depth of 7.3 cm. There are at least two files of symphysial teeth present in the symphysial region. The lingual side of the left Meckel's cartilage preserved at least seven tooth files of replacement teeth in situ. As in the palatoquadrate, these teeth are arranged in a juxtaposed series. The distal region of this structure is missing, resulting in the loss of the distal-most lateral tooth files. The right Meckel’s cartilage has four preserved tooth files of replacement teeth in situ. The left Meckel’s cartilage is arched and has a mesiodistal length of 20.5 cm. Like the palatoquadrate, the preservation of multiple replacement teeth in the first three tooth files on the Meckel’s cartilage may suggest the presence of a dental bulla. The first tooth file on the left Meckel’s cartilage preserved only two replacement teeth, whereas the second file preserved five and the third file preserved four. Tooth files distal to the third file tend to have fewer preserved replacement teeth. Many of the teeth are also displaced, suggesting the possible presence of a shallower dental trough that provided less refuge for the preservation of the teeth in these files. The first file on the right Meckel’s cartilage preserved four replacement teeth, whereas the second tooth file preserved five and the third file preserved three replacement teeth. In addition to the replacement teeth, the first and second files have in-situ functional teeth. Other than the presence of a single symphysial tooth, the labial surface of both portions of the Meckel’s cartilage contain no significant morphological detail.

General Tooth Morphology—In general, teeth of LACM 128125 bear a tall, broad-based, triangular median cusp. The apical two-thirds of the median cusp is narrower than the basal one-third. Depending on the tooth position within the jaw, this cusp has varying degrees of distal inclination. The labial face of the crown is slightly convex, whereas the lingual face is strongly convex. Both faces are smooth. The median cusp is flanked by a pair of well-developed, triangular lateral cusplets. Sharp mesial and distal cutting edges run continuously along the median cusp and the lateral cusplets. The height of the distinct lingual neck is relatively constant along the crown-root boundary. The bilobate root is robust and has a well-developed lingual protuberance with one or more nutrient foramina. The rounded root lobes may or may not be symmetrical depending on tooth position and may form a very deep basal concavity.

Upper Dental Series—There is a single fractured symphysial tooth (S1) located in the symphysial region of the palatoquadrate. It preserves a portion of the median cusp and the distal lateral cusplet, but no root. The median cusp is approximately one-third the height of the median cusp of the adjacent anterior tooth (Figs. 5.2B and 5.4). The first and second upper anterior teeth (A1 and A2) have a similar morphology and are mesiodistally narrower than the laterally positioned teeth (Figs. 5.2C and 5.4). The A1 and A2 possess a narrow and nearly erect median cusp. The lateral cusplets on these teeth are non-divergent, forming a low angle between the median cusp and the inside edge of the lateral cusplets. The distal root lobe is slightly more robust than the mesial root lobe on both teeth. These rounded root lobes are separated by a deep basal concavity. The third upper anterior tooth (A3; = upper intrabullar intermediate tooth (I1) of Shimada, 2002) has a median cusp with the apical half forming a strong and distinctive distal curvature (Figs. 5.2C and 5.4). This tooth is shorter than the A1 and A2 in total tooth height, but it is approximately equal in stature when considering the cusp slant height. The mesial cusplet is slightly more divergent than the mesial cusplet of the preceding anterior teeth. The basal concavity between the robust root lobes is also slightly wider than that in the A1 and A2. Two additional replacement teeth situated in the A3 (I1) file have a portion of their cusps visible. These cusps share the distinct median distal curvature of the cusp. The consistent occurrence of this unique feature within the file suggests that it is not an isolated tooth pathology, but rather a distinct character for this particular file. Distal to the A3 (I1) are the lateral teeth (Figs. 5.2D and 5.4). The first upper lateral tooth (L1) is damaged and the apex of the median cusp has been fractured; however, its general morphology can still be determined. This tooth is mesiodistally wider than the upper anterior teeth and the subsequent second and third upper lateral teeth (L2 and L3). The median cusp is broad and distally inclined. The angle between the median cusp and the inside edge of the mesial lateral cusplets is slightly larger than the angle produced by the anterior teeth. The distal root lobe is slightly more robust than the mesial lobe. The total tooth height of L2 and L3 is essentially equal. The fourth upper lateral tooth (L4) is slightly mesiodistally wider and shorter than the preceding tooth and the fifth upper lateral tooth (L5) is severely eroded. Teeth belonging to the next two files are severely eroded with only small portions of the root lobes preserved. The teeth of the adjacent distal file are completely missing. A severely eroded tooth is present in the ninth upper lateral tooth (L9) file. The tenth upper lateral tooth (L10) (Figs. 5.2E and 5.4) is significantly smaller in all dimensions compared with the preserved preceding lateral teeth. The median cusp has a strong distal inclination and the root lobes are less elongated than the lobes of the medially positioned teeth, forming a shallow basal concavity. Although the L10 is the last observed tooth on the palatoquadrate, it does not represent the distal-most tooth in the upper jaw because the distal region of the left palatoquadrate is not preserved.

Lower Dental Series— One symphysial tooth is preserved on the labial surface and two symphysial teeth are preserved on the lingual surface of the lower jaw symphysial region (Figs. 5.3C, D and 5.4). The more mesially positioned symphysial tooth (s1) situated on the lingual surface is symmetrical. It has a median cusp that is short, broad, and has a rounded apex that would have been most likely sharp in an undamaged state. A single pair of lateral cusplets is divergent and offset from the median cusp. The root is bilobate with lobes that are long and parallel. The observed portion of the symphysial tooth located on the labial surface appears to have a similar morphology and is likely located in the same tooth file. On the lingual surface, a second symphysial tooth (s2) is situated adjacent to the first lower anterior tooth (a1) on the right Meckel's cartilage. This tooth is incomplete, preserving only a portion of the median cusp that appears to be slightly narrower than the median cusp of the medially positioned symphysial tooth (s1). Adjacent to the symphysial region are the anterior teeth (Figs. 5.3B, E and 5.4). The a1 on the right Meckel's cartilage is approximately two-thirds the height of the adjacent second lower anterior tooth (a2). The median cusp is erect and is flanked by a pair of slightly diverging lateral cusplets. The root lobes of the a1 appear symmetrical and parallel, forming a deep basal concavity. Teeth of the a1 file on the left Meckel's cartilage are severely damaged and provide little information. On both Meckel's cartilages, the a2 has a large median cusp that is slightly distally inclined, although the apex is missing on the left a2. The mesial cusplet is more divergent than the distal cusplet. The distal root lobe of the a2 is slightly more robust than the mesial lobe. The teeth of the third lower anterior (a3;

= lower intrabullar intermediate (i1) of Shimada, 2002) file, the first lower lateral tooth (l1) file on both Meckel's cartilage, and the second lower lateral (l2) tooth file on the left Meckel's cartilage are similar in tooth height, crown morphology, and cusp inclination (Figs. 5.3B, E, F and 5.4). The l1 is slightly mesiodistally wider when compared to the anterior teeth. The third lower lateral tooth (l3) on the left Meckel's cartilage is damaged and is missing portions of the median cusp, lateral cusplets, and root lobes. The fourth lower lateral tooth (l4) on the left Meckel's cartilage differs from the anterior teeth and from l1 and l2 in having a median cusp that is shorter, broader, and markedly distally inclined. The root lobes are also more robust and more divergent.

Neurocranium—The neurocranium is severely fragmented. The largest piece, identified as the basal plate, measures 7.1 cm in maximum length and 5.8 cm in maximum width (Fig. 5.5A), but significant morphological detail of this structure is not apparent. Associated with the basal plate is the occipital centrum, which has a single row of irregularly sized circular fossae anterior to the amphicoelous corpus calcareum. The diameter of the occipital centrum measures 37 mm. This is only 20% smaller than the occipital centrum diameter of 46 mm seen in a 5 m-long specimen of *Cretoxyrhina mantelli* (FHSM VP-2187), but 1.9 times larger than the occipital centrum diameter of 19 mm seen in a 2 m long *Squalicorax* sp. (USNM 425665; MGN personal observation).

Vertebral Centra—In LACM 128125, the corpus calcareum is thick and readily shows growth increments in cross-section (Fig. 5.5C). Eighteen growth increments (presumed annuli) are visible as black bands (MGN, personal observation, Fig. 5.5D). The growth profile shows a considerable inflection in growth with 70% of adult size attained by the fifth band (i.e., putative sexual maturity). Little growth (i.e., 15%) occurred after band 10 indicating an adult in age and size (Fig. 5.6).

DISCUSSION

Generic and Species Determination

The general tooth morphology of *Archaeolamna* superficially resembles that of *Dwardius* Siverson, 1999, but can be readily distinguished. Siverson (1999) noted that the height of the lingual neck of teeth of *Archaeolamna* is relatively constant between the lateral cusplet and the median cusp regions, whereas the lingual neck of teeth of *Dwardius* is much higher in the region of the median cusp and narrows toward the lateral cusplets. As well, juvenile *Dwardius* have anterior teeth that are greatly enlarged relative to the lateral teeth, whereas those of *Archaeolamna* are not (see Woodward, 1894: pl. 6, fig. 2). The upper two-thirds of the median cusp is also generally narrower in *Archaeolamna* than it is in *Dwardius* and the latter has an elongated mesial lobe on the most mesially situated upper lateral teeth (M. Siverson, personal communication, April, 2010). The taxonomic assignment of LACM 128125 is based on the fact that its tooth morphology is consistent with that of *Archaeolamna*. Siverson (1999) also noted that the teeth near the commissure in *Archaeolamna* are small and bear enameloid folding on the labial crown surface, whereas the equivalent teeth in *Dwardius* have a smooth labial crown face and are more robust. However, this observation cannot be made for LACM 128125 because the distal region of the jaws is not preserved.

The anterior teeth of LACM 128125 are morphologically similar to those identified as *Archaeolamna kopingensis kopingensis* from the early Campanian of Sweden (Siverson, 1992), whereas the median cusp of the lateral teeth appears to be slightly more robust (see Siverson, 1992: pl. 2, figs. 12–13). According to Siverson (1992), the teeth of this subspecies can be readily distinguished from those of *A. kopingensis judithensis* by their narrower, labiolingually thicker and more elongated median cusps. Furthermore, the roots of the teeth of *A. kopingensis kopingensis* are more gracile and bear long root lobes. The robust teeth of *A. kopingensis judithensis* have been recovered from the upper Campanian deposits of Alberta, Canada (Beavan and Russell, 1999), Montana (Case, 1978; Siverson, 1992) and Wyoming, USA (Case, 1987). The teeth of LACM 128125 appear to have a morphology reminiscent of the narrow-cusped form of northern Europe but perhaps slightly intermediate between it and the broad-cusped form of the Western Interior Seaway (Siverson, personal communication, April, 2010).

Comparisons

Siverson (1992: p. 530) noted that the dental sequence of *Archaeolamna kopingensis*, with its pronounced disjunct monognathic heterodonty, is somewhat reminiscent of the “odontaspidid condition”; however, it was suggested that the lack of a well-developed nutrient groove on the root indicated a relationship with lamnids. Siverson (1992) described the dentition of this species as having: (1) small symphysial teeth without lateral cusplets; (2) reduced and mesiodistally compressed lower parasymphysial teeth (re-classified as the first lower anterior teeth in Siverson, 1999) which are approximately one-third the height of the adjacent anterior teeth; (3) larger upper parasymphysial teeth (re-classified as first upper anterior teeth in Siverson, 1999) which are approximately half the height of the anterior teeth; (4) one file of mesiodistally compressed intermediate teeth that bear a distally bent cusp and are significantly smaller than the adjacent anterior teeth; and (5) small posterior teeth that have strong enameloid folding on the labial crown face and lateral cusplets that are reduced or absent.

The recovery of a natural tooth set can provide concrete evidence of the exact tooth arrangement for a species (Welton and Farish, 1993). Thus, LACM 128125 provides us with the rare opportunity to assess previous hypotheses about the dental arrangement of this species, although the single specimen does not offer information about possible intraspecific variation in tooth morphology and dental arrangement. For example, LACM 128125 supports Siverson’s (1992) contention that *Archaeolamna kopingensis* has reduced symphysial teeth. The fully preserved symphysial teeth in LACM 128125 bear well developed lateral cusplets. This is different from the teeth described by Siverson (1992) that lacked lateral cusplets, thus confirming that the symphysial teeth exhibit a considerable amount of morphological variation. Siverson’s (1992) assumption that this species has reduced first lower anterior teeth (originally referred to as lower parasymphysials), is also confirmed by LACM 128125. In addition, the first upper anterior teeth (originally referred to as upper parasymphysials), are larger than the first lower anterior teeth. However, the height of the A1, as observed in LACM 128125, is not as reduced as previously thought (Siverson, 1992), as it is approximately equal to that of the A2. Siverson (1992) also proposed the presence of a single file of mesodistally compressed and reduced intermediate teeth (= intrabullar intermediate teeth sensu Shimada, 2002). LACM 128125 confirms that *A. kopingensis* had a large A3 (I1) which possessed a median cusp with a strong distal curvature and that reduced extrabullar intermediate teeth were absent. The distal-most lateral teeth preserved in this specimen do not show strong enameloid folding or reduced lateral cusplets, but the most distal tooth files are missing in LACM 128125 because of incomplete preservation; these files most likely included teeth similar to those described by Siverson (1992).

Underwood and Cumbaa (2010) constructed an artificial tooth set of *Archaeolamna* ex. gr. *kopingensis* based on numerous disassociated teeth from the Cenomanian Bainbridge River bonebed of Saskatchewan, Canada. Their reconstructed dental series included three files of upper and lower anterior teeth, a single file of reduced upper and lower parasymphyseal (= symphysial teeth, herein) and intermediate teeth (= extrabullar intermediate, herein), and nine files of lateral teeth that grade into posterior teeth (= distal-most laterals, herein). Again, LACM 128125 refutes the hypothesis that *A. kopingensis* possessed reduced extrabullar intermediate teeth and suggests that the intermediate tooth in their reconstruction is likely a symphysial tooth or a tooth from a young individual. In addition, given the close approximation between the A3 (I1) and L1 in LACM 128125, there is no indication that this species had an intermediate bar that would accommodate these teeth. Based on the distal curvature of the median cusp, the A2 in Underwood and Cumbaa's (2010) reconstruction is likely the A3 (I1). Also, the reduced a1 in their tooth set is confirmed by LACM 128125, but their reduced A1 is refuted. As well, *A. kopingensis* would have had more than nine files of lateral teeth, given that the most distal tooth (L10) preserved in LACM 128125 is of a different general morphology than teeth identified as 'posterior teeth' recovered as isolated elements in other studies (see Siverson, 1992).

Cretoxyrhina mantelli—Shimada (1997) examined an articulated tooth set of *Cretoxyrhina mantelli* (FHSM VP-2187) from the Niobrara Chalk in Kansas, U.S.A. That specimen represents one of the most complete fossil lamniform specimens known to date and provides the opportunity for a comparison with LACM 128125. According to Shimada (1997; 2002), the upper jaw of *C. mantelli* contains four small symphysial teeth that are followed by two erect or slightly distally inclined anterior teeth designated the A1 and A2. Distal to the A2 are four smaller teeth assigned as intermediate teeth. The first of these smaller teeth has a distally curved median cusp and is assumed to be the most distal tooth within the upper dental bulla, whereas the remaining smaller teeth have cusps that are distally inclined, similar to more laterally positioned teeth (Shimada, 1997; 2002). Shimada's (1997; 2002) assignment of intermediate teeth was based on the notion that the tallest upper tooth distal to the anterior teeth is the L2, the condition seen in extant macrophagous lamniforms (Shimada, 2002). Distal to the intermediate teeth are at least 11 distally inclined lateral teeth with the L2 being the tallest lateral tooth. Siverson (1999) suggested that the teeth of *C. mantelli* described as upper intermediates most likely represent the A3 and successive lateral (lateroposterior of Siverson, 1999) teeth. The lower jaw includes at least one small symphysial tooth that is medial to two tall and erect teeth identified as the a1 and the a2 (Shimada, 1997; 2002). Following the anterior teeth is the a3 (i1), which is presumed to be the most distal tooth situated within the lower dental bulla (Shimada, 2002). It is slightly smaller than the a2 and is strongly inclined distally. Distal to this tooth are at least 15 lower lateral teeth, with the l1 and l2 being the tallest (Shimada, 1997; 2002).

The dental morphology and arrangement of *Archaeolamna kopingensis* (LACM 128125) are different from those of *Cretoxyrhina mantelli* (FHSM VP-2187). The differences include: (1) the anterior teeth lacking lateral cusplets in *C. mantelli* (Shimada, 1997), with lateral cusplets being well developed on the anterior teeth of *A. kopingensis*; (2) *C. mantelli* having four upper symphysial teeth, but *A. kopingensis* having only a single symphysial tooth (although the absence of additional symphysial teeth may be an issue of incomplete preservation); (3) compared to the A1 and A2, the A3 (I1) in *A. kopingensis* being relatively larger than the A3 (I1) in *C. mantelli* and having a median cusp that is more strongly distally curved; (4) the teeth of the three files distal to A3 (I1) being reduced in size in *C. mantelli*, with the anatomically equivalent teeth in *A. kopingensis* being unreduced; and (5) the a1 of *A. kopingensis* being reduced in size compared to the a2, but the a1 being equal in size to the a2 in *C. mantelli*.

Cardabiodon ricki—Siverson (1999) reconstructed the dental sequence of *Cardabiodon ricki* (WAM 96.4.45), a large lamniform shark, using an associated, but disarticulated, tooth set from the middle Cenomanian of Western Australia. This species has at least one file of symphysial teeth (Siverson, 1999). There are four files of upper anterior teeth. The A1 has an erect median cusp and is significantly reduced in size compared to the A2. The A2, A3, and A4 have a distally curved median cusp. Siverson (1999) noted that there are approximately 14 files of lateroposterior teeth (lateral teeth herein). These teeth have a distally inclined median cusp and a root that becomes increasingly symmetrical moving distally along the jaw. There is an increase in tooth size from the L1 to the L6, followed by a decrease in size of the subsequent lateral (L7-14) teeth. In the lower jaw, Siverson (1999) also recognized four files of anterior teeth. The a1 is reduced in size compared to the tall a2 and the a3. These teeth have an erect median cusp, whereas the a4 has a median cusp that is distally inclined. This tooth has an asymmetrical root and is slightly shorter than the a2 and the a3. Following the anterior teeth are approximately 14 files of lateral teeth. The l1 and the l2 are the largest teeth in the jaws of *C. ricki*. There is a gradual decrease in size from the l1 to the l7, followed by a sharp decrease in tooth size toward the commissure. The lateral teeth distal to the l7 have median cusps that are strongly distally inclined.

The dental differences between *Archaeolamna kopingensis* (LACM 128125) and *Cardabiodon ricki* (WAM 96.4.45) include: (1) the lateral cusplets of anterior teeth are well developed in *A. kopingensis*, whereas the lateral cusplets may be reduced or absent in *C. ricki* (Siverson, 1999); (2) *C. ricki* has four files of upper and four lower anterior teeth, whereas *A. kopingensis* has two files of upper and two lower anterior teeth followed by a file of upper and lower intrabullar intermediate teeth; (3) the A1 in *C. ricki* is markedly reduced in size compared to the A2, whereas the A1 and the A2 are of similar size in *A. kopingensis*; (4) there is an increase in size from the L1 to the L6 in *C. ricki*, whereas *A. kopingensis* has a gradual decrease in total tooth height from the L1 to the distal lateral teeth; and (5) the l1 and the l2 are the largest teeth in *C. ricki*, whereas in *A. kopingensis*, the a3 (i1) and the l1 and l2 are similar in tooth height, crown morphology, and cusp inclination.

Cretalamna appendiculata—Shimada (2007) reconstructed the dentition of *Cretalamna appendiculata* (LACM 128126) based on an associated tooth set that consists of some articulated teeth and many disarticulated teeth recovered from the Niobrara Chalk of Kansas, U.S.A. According to Shimada (2007), the upper jaw contains at least two files of symphysial teeth. These teeth are followed distally by the erect A1 and the slightly distally inclined A2. The A3 (I1) follows the A2 and is reduced in size when compared with both the preceding A2 and the succeeding L1. This tooth has a median cusp that is distally curved. The lateral teeth are shorter than the anterior teeth and have a median cusp that is distally inclined. The L1 is the largest lateral tooth and the subsequent teeth gradually decrease in size moving toward the commissure. Shimada (2007) figured 10 upper lateral (L1-10) teeth. The lower jaw did not include symphysial teeth, but this absence may be the result of lack of preservation, not an anatomical absence (Shimada, 2007). There are two erect lower anterior teeth with the a2 being the tallest tooth among the teeth of the upper and lower jaws. Distal to a2 is a3 (i1). This tooth is smaller than the a2, but taller than the adjacent l1. There are at least five distally inclined lateral teeth that become progressively smaller toward the commissure (Shimada, 2007).

Differences in dental anatomy are present between *Archaeolamna kopingensis* (LACM 128125) and *Cretalamna appendiculata* (LACM 128126). They include: (1) the teeth of *A. kopingensis* have a root with more rounded lobes and a basal concavity that is higher than those of *C. appendiculata*; (2) the a1 of *C. appendiculata* is only slightly shorter than the a2, whereas the a1 of *A. kopingensis* is more significantly reduced in size compared to the a2; and (3) the a3 (i1) is shorter than the preceding a2 in *C. appendiculata*, whereas the a3 (i1) in *A. kopingensis* is larger than the a2.

Familial Placement

Cappetta (1987) placed eight genera within the family Cretoxyrhinidae: *Cretodus*, *Cretalamna* (= *Cretolamna*), *Cretoxyrhina*, *Leptostyrax*, *Palaeocarcharodon*, *Paraisurus*, *Protolamna*, and *Pseudoisurus*. Siverson (1992) added *Archaeolamna* to Cretoxyrhinidae but later (Siverson, 1999) suggested that the family is a ‘waste basket taxon’ and put forth the notion that the family should be restricted to the type genus *Cretoxyrhina mantelli*. We agree with this proposal as the dental series of *C. mantelli* is unique among the lamniforms.

Underwood and Cumbaa (2010) erected the family Archaeolamnidae to accommodate a number of fossil taxa including *Archaeolamna*, *Cretodus*, *Dallasiella*, and *Telodontaspis*. Their familial diagnosis included the following criteria pertaining to the dental arrangement: (1) well-developed 'lamniform' heterodonty; (2) three upper and lower anterior teeth; (3) reduced upper and lower parasymphyseal teeth (= symphysial teeth, herein); (4) reduced intermediate teeth (= extrabullar intermediate teeth, herein); and (5) lateral teeth that grade into posterior teeth (= distal-most lateral teeth, herein). We agree that *A. kopingensis* merits its own family because the teeth and dental series differ from those of all other known lamniforms. However, the articulated dentition of LACM 128125 indicates the need to emend the initial diagnosis for Archaeolamnidae. We propose that the family Archaeolamnidae should be diagnosed by the following characters: (1) presence of a reduced a1; (2) presence of two files of anterior and one file of intrabullar intermediate (third anterior) teeth within the dental bullae; (3) A1 equal to the A2 in height; (4) presence of a large A3 (I1) with a distinctive distal curvature of the median cusp; and (5) absence of reduced extrabullar intermediate teeth and an intermediate bar. The relatively large A3 (I1) and the lack of extrabullar intermediate teeth observed in LACM 128125 reveal that *A. kopingensis* exhibits monognathic heterodonty that is not as strong as Underwood and Cumbaa (2010) described. Furthermore, we here restrict the family Archaeolamnidae to *Archaeolamna.* Although *Archaeolamna* shares a similar tooth morphology with *Cretodus*, *Dallasiella*, and *Telodontaspis*, the latter taxa are known only from isolated teeth with the true dental arrangement being uncertain.

Total Length

The partially complete palatoquadrate with associated teeth of LACM 128125 allows us to infer the approximate jaw size of the individual shark. The incomplete left palatoquadrate of LACM 128125 has a mesiodistal length of 23.5 cm. If we do not account for the missing posterior region of the palatoquadrate, the jaw circumference is estimated to have been at least 47 cm (circumference is defined as "the distance along the tooth bases from the last tooth on one side to the last tooth on the other side in the upper or lower jaw of a jaw set" by Lowry et al., 2009: p. 2485). If we assume that the recovered portion represents two-thirds of the left palatoquadrate and we add an additional one-third to compensate for the missing posterior region, we estimate the total jaw circumference to be 70.5 cm. Using jaw circumference values for modern sharks (Lowry et al., 2009), LACM 128125 would have a jaw circumference larger than that of a 3.2 m-long *Isurus oxyrinchus* (shortfin mako, upper jaw circumference of 58 cm) and a 3.8 m *I. paucus* (longfin mako, upper jaw circumference of 64.5 cm).

An accurate estimate of total length is not possible because the total number of vertebrae of LACM 128125 is unknown. One approach to estimate total length might be to compare the occipital centrum diameter from LACM 128125 to that of a shark of known length. However, length is not only correlated with occipital centrum size but also with the total number of centra in the vertebral column. The number of centra and length in the Cretaceous lamniforms *Cretoxyrhina mantelli* and *Squalicorax* is considerably different. *Squalicorax* sp. (USNM 425665) has 135 centra (MGN, personal observation) and is approximately 2 m in length (Shimada and Cicimurri, 2005), whereas *C. mantelli* (FHSM VP-2187) attains 5 m (Shimada, 1997) in length and has 225 centra (MGN, personal observation). We suggest that the length of *Archaeolamna kopingensis* (LACM 128125) was much greater than 2 m but less than 5 m. This estimate based on centra is vague for two reasons. First, *A. kopingensis* (LACM 128125) has an occipital centrum size that is intermediate between those of two known complete specimens of *Squalicorax* and *C. mantelli*. Second, the vertebral count of *A. kopingensis* is unknown and the vertebral counts in *Squalicorax* and *Cretoxyrhina* are highly variable. The estimated range in length of *A. kopingensis* does not disagree with that provided by the jaw circumference data of the extant *Isurus oxyrinchus* and *I. paucus.* Thus, taking into account the jaw circumference information and occipital centrum size, and assuming that vertebral counts were similar to those of *C. mantelli*, we suggest LACM 128125 would have been 3 to 4 m in total length.

To date, the largest anterior tooth recovered from this species was documented by Siverson (1999). The tooth, recovered from the Campanian Kristianstad Basin of Sweden, measures 32 mm in height (Siverson, 1999) and is from the second upper anterior tooth file (Siverson, personal communication, April, 2010). The A2 of LACM 128125 is 26.3 mm in height, approximately 82% the height of the Swedish tooth. Recognizing that LACM 128125 is an adult shark, as discussed above, we can speculate that the differences in adult tooth size may be the result of size variation within the species or sexual dimorphism in this species. Generally, male lamnids mature at a smaller size than females and reach a smaller maximum size (see Compagno, 2001).

Paleoecology

Siverson (1992) reported evidence of scavenging or predation of a plesiosaur by a large individual of *Archaeolamna kopingensis judithensis* from the uppermost Judith River Formation (early late Campanian) of north-central Montana. The broad median cusps in this subspecies of *Archaeolamna* would be conducive for tearing off large pieces of flesh of a prey item according to Siverson (1992). Conversely, the narrower median cusps of LACM 128125 are more suitable for grasping and holding active, medium to large-sized prey. As well, the large spaces between adjacent median cusps produced by broad roots and lateral cusplets in LACM 128125 provide for efficient means of penetrating this prey (Shimada, 2007). The Sharon Springs Formation of the Pierre Shale Group, from which LACM 128125 was recovered, was deposited during a time of high biological productivity caused by significant upwelling (Parrish and Gautier, 1993). This upwelling would have resulted in nutrient-rich water that could have attracted a large number of potential prey items for *A. kopingensis*. Carpenter (2006) reported the remains of 17 osteichthyan fish taxa and 11 marine reptiles from the Sharon Springs Formation. *Archaeolamna kopingensis* likely hunted fish or marine reptiles that attained relatively large sizes.

Paleobiogeography

Herman (1977) reported that *Archaeolamna kopingensis* (as *Plicatolamna arcuata*) had a northern distribution. Kent (1994) also suggested that this species was restricted to the northern regions of the Atlantic. Later Siverson (1996; 1997) described teeth belonging to this genus from the high paleolatitude Albian and Cenomanian of Western Australia. Underwood and Cumbaa (2010) also noted that *A. kopingensis* inhabited the temperate waters of both Northern and Southern Hemispheres. We suggest that *Archaeolamna* likely had an antitropical distribution reminiscent of that of the extant porbeagle shark, *Lamna nasus* (Bonnaterre, 1788) (Lamnidae).

Figure 5.1. Composite of upper and lower jaws of *Archaeolamna kopingensis* (LACM 128125) from Sharon Springs Formation of Pierre Shale Group of Kansas. (A) ventral view; (B) dorsal view. Scale bar equals 1 cm. Abbreviations: Mc, Meckel's cartilage; Pq, palatoquadrate; Sym, symphysis.

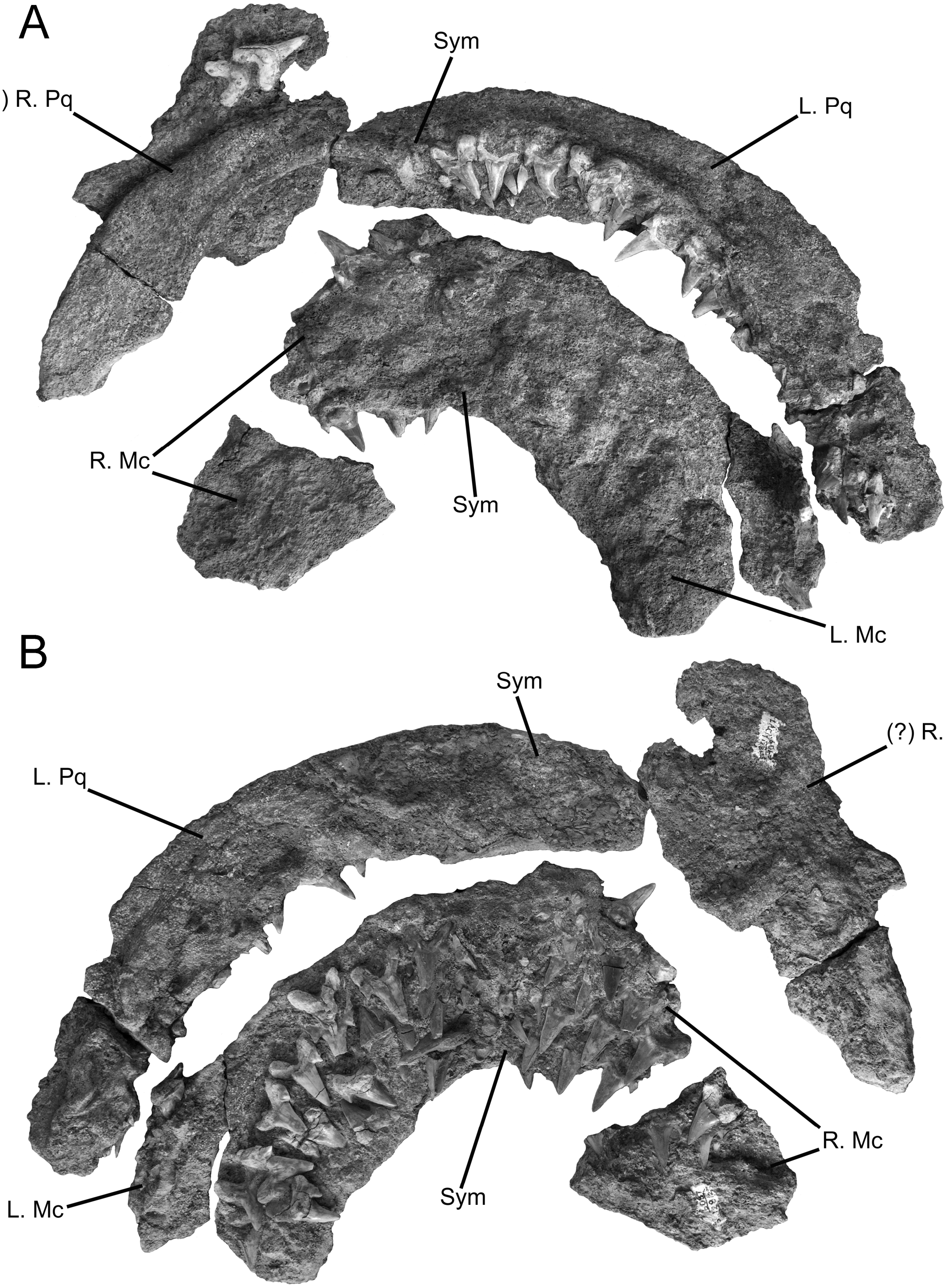

A
Sym
(?) R. Pq
L. Pq
R. Mc
Sym
L. Mc
B
Sym
(?) R. Pq
L. Pq
R. Mc
L. Mc
Sym

Figure 5.2. Left palatoquadrate of *Archaeolamna kopingensis* (LACM 128125; coated with ammonium chloride for close-up images). (A) entire preserved portion in lingual view; (B) close-up view of symphysial tooth; (C) close-up view of anterior and intermediate teeth; (D) close-up view of lateral teeth; (E) close-up view of tenth lateral tooth. Scale bars equal 1 cm. Abbreviations: (A1) first upper anterior tooth; (A2) second upper anterior tooth; (A3) third upper anterior tooth (sensu Siverson, 1999); (I1) upper intrabullar intermediate tooth; (L1) first upper lateral tooth; (L2) second upper lateral tooth; (L3) third upper lateral tooth; (L4) fourth upper lateral tooth; (L5) fifth upper lateral tooth; (L10) tenth upper lateral tooth; S1, upper symphysial tooth.

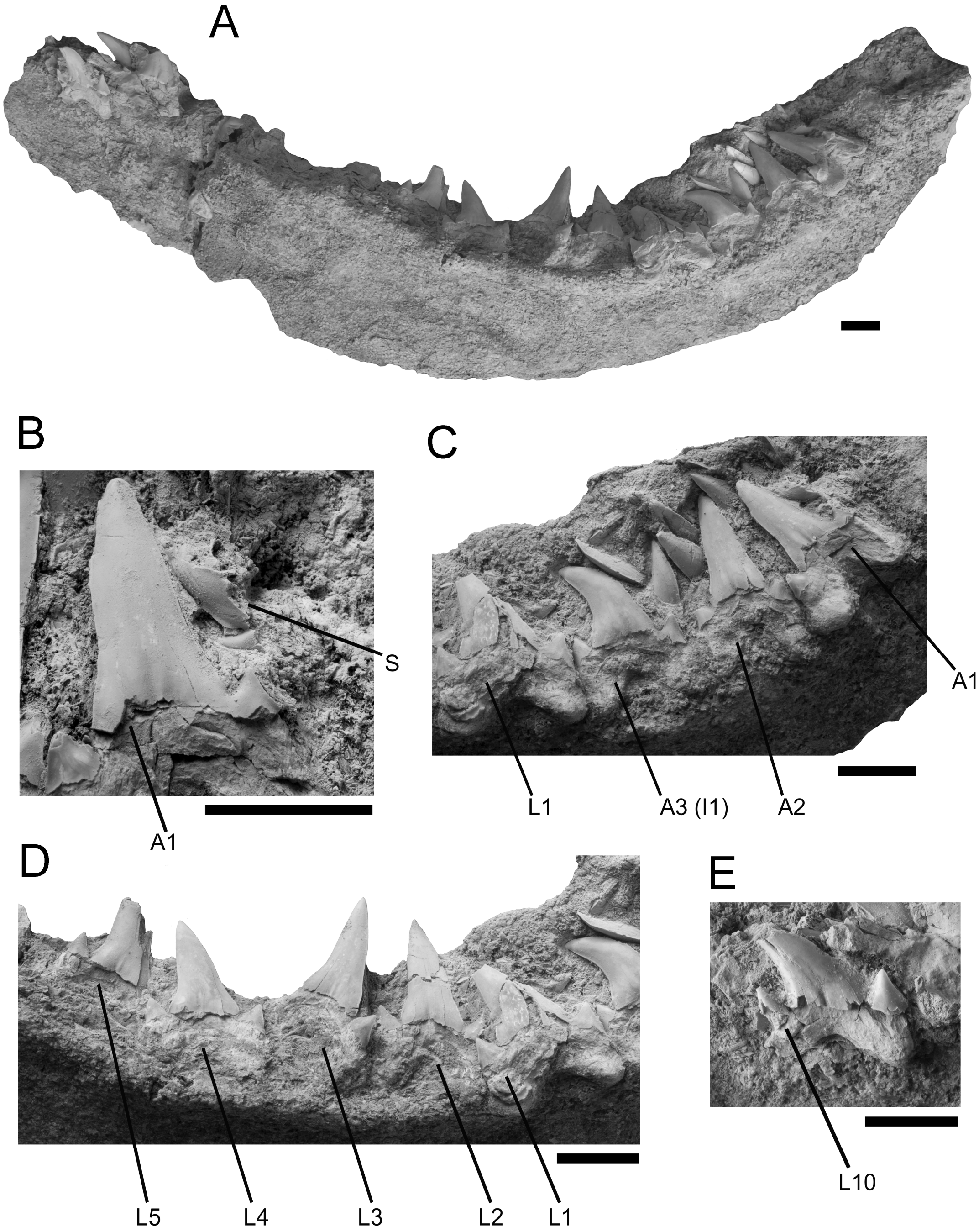

A
B
S
A1
C
A1
L1
A3 (I1)
A2
D
L5
L4
L3
L2
L1
E
L10

Figure 5.3. Meckel's cartilages of *Archaeolamna kopingensis* (LACM 128125); coated with ammonium chloride for close-up images). (A) left Meckel's cartilage and a smaller portion of right Meckel's cartilage in lingual view; (B) close-up view of the anterior teeth through first lateral teeth of right Meckel's cartilage; (C) close-up view of functional teeth and symphysial tooth on labial surface; (D) close-up view of symphysial teeth; (E) close-up view of anterior teeth through second lateral tooth of left Meckel's cartilage; (F) close-up view of lateral teeth on left Meckel's cartilage. Scale bars equal 1 cm. Abbreviations: (a1) first lower anterior tooth; (a2) second lower anterior tooth; (a3) third lower anterior tooth (sensu Siverson, 1999); (i1) lower intrabullar intermediate tooth; (l1) first lower lateral tooth; (l2) second lower lateral tooth; (l3) third lower lateral tooth; (l4) fourth lower lateral tooth; (l5) fifth lower lateral tooth; s1, first lower symphysial tooth; (s2) second lower symphysial tooth.

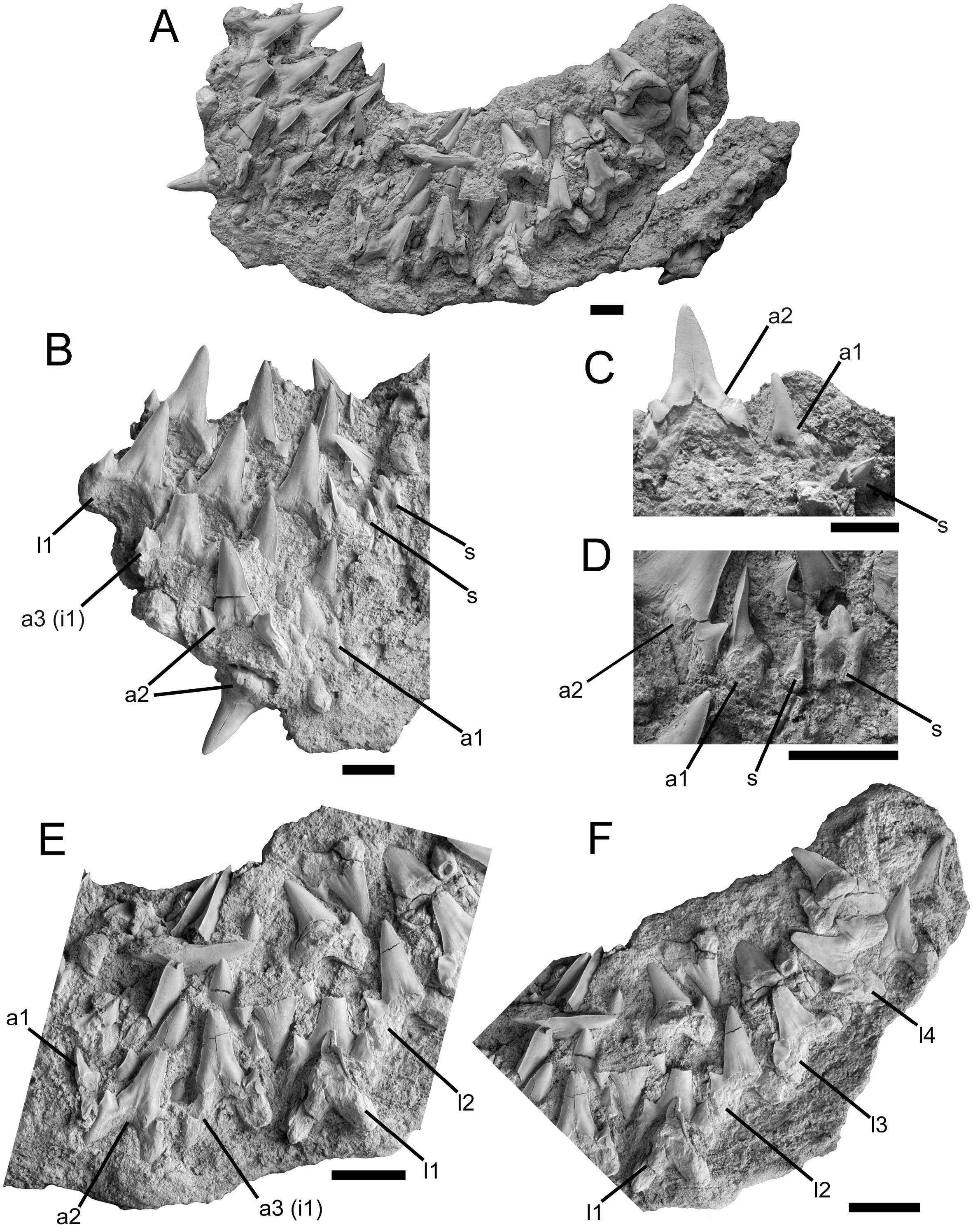

A
B
l1
a3 (i1)
a2
s
s
a1
C
a2
a1
s
D
a2
a1
s
s
E
a1
l2
l1
a2
a3 (i1)
F
l4
l3
l2
l1

Figure 5.4. Illustrated dentition of *Archaeolamna kopingensis* based on the observed teeth from LACM 128125. Spaces between teeth are artifacts of the reconstruction; \\ indicates a large space between L5 and L10; dashed lines indicate missing structures; the illustrated a2 and a3 (i1) were reconstructed using morphological features from the corresponding teeth on both Meckel's cartilage; the illustrated a1 and l1 are mirror images of better preserved corresponding teeth from the right Meckel's cartilage. Scale bar equals 1 cm. Abbreviations: as for Figs. 5.2 and 5.3.

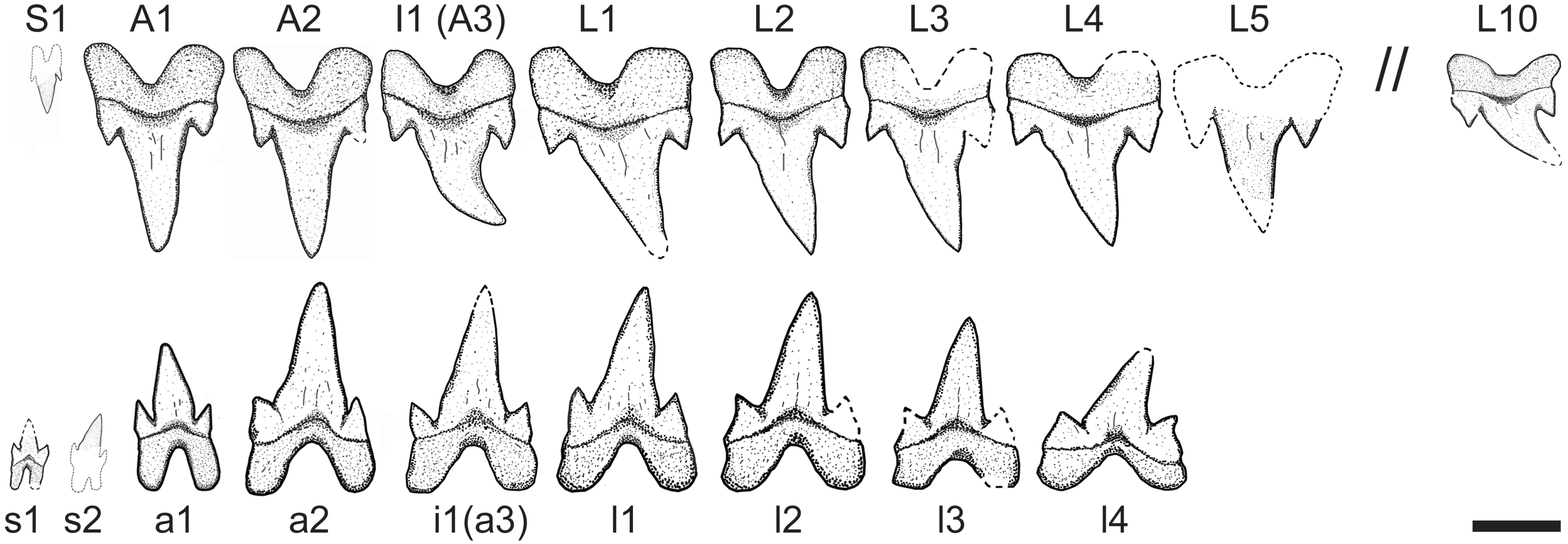
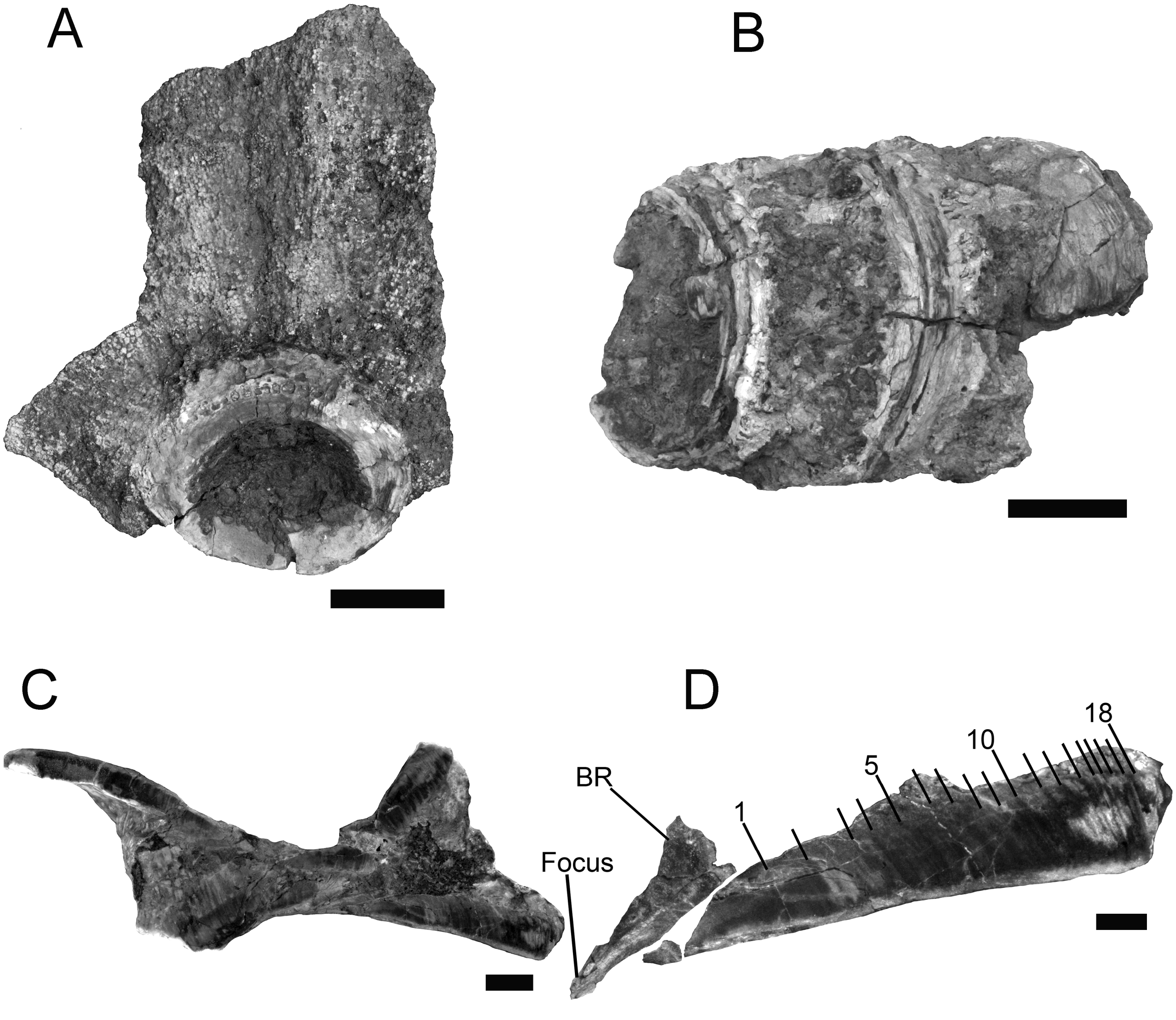

S1
A1
A2
I1 (A3)
L1
L2
L3
L4
L5
//
L10
s1
s2
a1
a2
i1(a3)
l1
l2
l3
l4

Figure 5.5. Cranial and vertebral elements of *Archaeolamna kopingensis* (LACM 128125). (A) portion of neurocranium with occipital centrum (OC); (B) three anterior vertebral centra; (C) sagittal section through centrum showing bands on corpus calcareum and intermedialia; (D) enlargement of right side of centra showing focus, birth ring (BR) and 18 presumed annular bands as indicated by arrows and numbers.; Scale bars equal 1 cm in A and B, 5 mm in C, and 2 mm in D.


A
B
C
D
18
10
5
1
BR
Focus

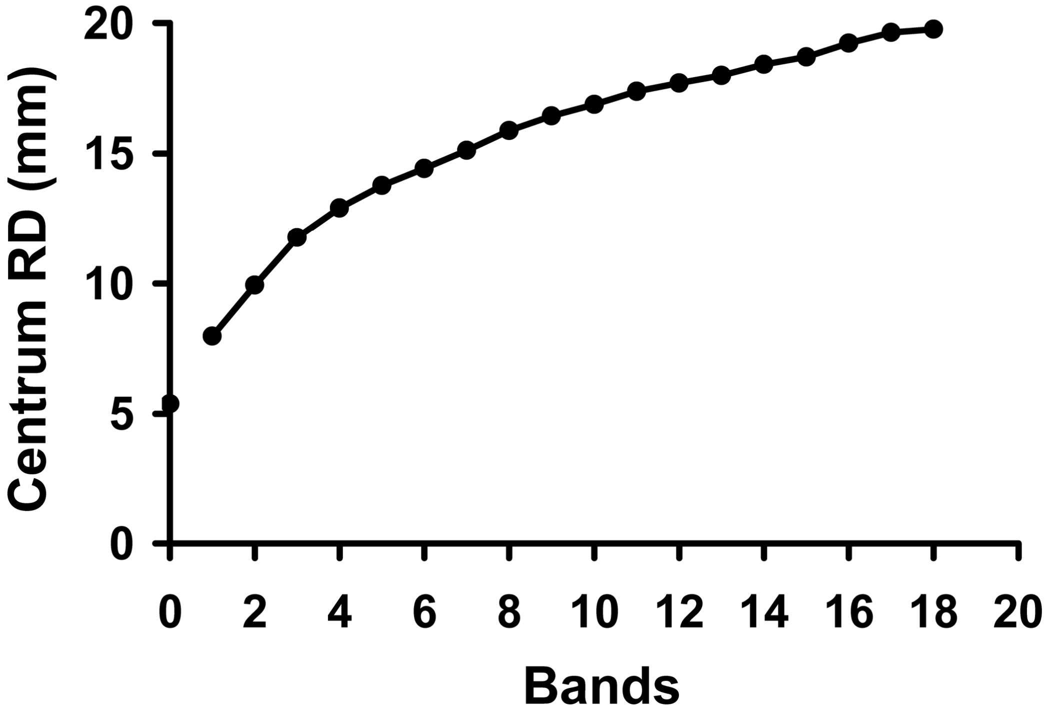


Figure 5.6. Growth profile from *Archaeolamna kopingensis* (LACM 128125)

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APPENDIX 5.1. Tooth Measurments for LACM 128125

	TH	CH	MCH	MCL	DCL	MCW	LCH	TW	DI
Left palatoquadrate									
S1	–	5.1	4.9	–	5.0	–	1.6	–	–
A1	25.1	17.7	14.7	14.8	14.6	8.4	4.1	16.5	0.99
A2	26.3	18.5	15.4	15.7	15.6	8.3	4.1	16.2	0.99
A3	22.9	15.4	12.6	16.9	10.3	9.3	4.2	17.1	0.62
L1	26.4+	20.1+	13.3+	16.3+	13.3+	10.5	5.4	19.1	0.81
L2	26.5	21.2	16.6	17.9	15.6	9.1	5.4	16.8	0.87
L3	26.4	21.2	16.4	16.4	–	9.8	5.1	–	–
L4	24.8	16.8	13.5	15.9	13.6	10.1	5.3	18.9	0.85
L5	–	–	–	–	–	10.4	–	–	–
L6	–	–	–	–	–	–	–	–	–
L7	–	–	–	–	–	–	–	–	–
L8	–	–	–	–	–	–	–	–	–
L9	–	–	–	–	–	–	–	–	–
L10	15.1	10.6	9.5	11.9	7.7	8.4	4.5	15.6	0.65
Left Meckel’s Cartilage									
s1	8.3+	4.4+	3.4+	3.5+	3.5+	2.8	2.1	4.8	1
s2	–	–	4.3	4.4	4.4	–	–	–	1
a1	14.6+	–	–	–	–	–	–	–	–
a2	25.8+	19.9+	17+	14.8+	14.5+	9.5	6.9	16.9	0.98
a3	26.7+	18.8+	19.4+	–	15.2+	9.8	–	20	–
l1	23.7+	14.4+	11.9+	–	–	9.8	7.0	20.1+	–
l2	26.2	17.9	16.3	16.4	15.7	9.3	6.3	18.9	0.96
l3	23.1+	18.1+	12.4+	–	–	9.9	–	19.9	–
l4	22.5	17.4	16.3	14.1	11.9	10.1	8.7	22.2	0.84
Right Meckel’s Cartilage									
a1	19.6	13.8	10.7	10.2	10.4	5.9	5.6	11.2	1.1
a2	27.2	20.5	20	15.8	15.6	9.9	7.4	19.8	0.98
a3	23.5+	17.4+	13.6+	–	–	10	8.2	18.4+	–
l1	26.9	22.5	16.7	17.5	16.1	10.3	7.9	21.1	0.92

All tooth measurements in millimetres. Abbreviations: TH, tooth height; CH, crown height; MCH, median cusp height; MCL, mesial cutting edge length; DCL, distal cutting edge length; MCW, median cusp width; LCH, lateral cusplet (mesial) height; TW, tooth width; DI, distal inclination. See text for tooth type abbreviations.

CHAPTER 6

General Conclusions

The middle Cenomanian Dunvegan assemblage (Chapter 2) is significant as it is the most northern shark assemblage within the Western Interior Seaway. Euselachian research in this region of the seaway had been largely understudied; thus, this study provided important insight into selachian diversity of this little-known region of the seaway. Despite its high-paleolatitude, the assemblage surprisingly contained nine species from seven families, and greatly extended the northern geographical range of these taxa. It was also demonstrated, through faunal comparisons with temporally equivalent southern middle Cenomanian assemblages, that the northern region of the seaway had many lamniform species in common with the southern assemblages, but unlike them had low batoid diversity. The recovered selachian remains were used to infer the paleoenvironment during the deposition of the Dunvegan Formation, assuming that Late Cretaceous shark and ray taxa occupied ecological niches similar to those of their extant counterparts. As such, the particular mix of taxa indicated deposition in a shallow, nearshore environment. Using a previously developed model of large-scale water circulation within the Western Interior Seaway, it was proposed that absence of certain taxa from the Dunvegan assemblage, common in more southern assemblages, may have been caused by a temperature intolerance associated with latitude and sea-water circulation patterns, or by an inability to inhabit environments that exhibit salinity variation.

The early Turonian Watino assemblage (Chapter 3) was significantly more productive than the Dunvegan assemblage and included 18 species belonging to at least three orders, at least 11 families, and 15 genera; many of these were previously unknown from Canadian deposits. The scarcity of benthic taxa in this assemblage supports the previous notion that bottom waters in this region of the Western Interior Seaway experienced enduring anoxic episodes. By comparing the faunal composition of this assemblage with middle Cenomanian Canadian assemblages, it was shown that seven species had a biostratigraphic range that extended across the Cenomanian-Turonian boundary in this northern region of the seaway. Of the taxa recovered from this assemblage, 12 species have also been reported from the well-sampled deposits of Texas, USA. Conversely, *Archaeolamna* ex. gr. *kopingensis*, *Cardabiodon ricki*, *Carcharias* aff. *C. striatula*, *Odontaspis watinensis*, *Johnlongia parvidens*, and *Dwardius woodwardi* have not been found from deposits of the southernmost region of the seaway and may have been restricted to cooler waters.

The selachian diversity reported from Watino most closely resembles another high-paleolatitudinal assemblage recovered from Western Australia. Both assemblages share the lamniforms *Archaeolamna*, *Cardabiodon*, *Johnlongia*, and *Dwardius.* These taxa have been reported in the published literature as having an antitropical distribution. In Chapter 4, a novel methodology to test the purported hypothesis of an antitropical distribution for these taxa was implemented by comparing the paleolatitudinal and paleothermal (sea surface temperature) ranges of the localities from which involved taxa were recovered, to the latitudinal and thermal ranges of the extant antitropical shark, *Lamna nasus*. Of the taxa tested, only *Johnlongia* satisfied the two conditions that support the hypothesis of an antitropical distribution. The paleolatitudinal range of *Johnlongia* was less than that of the modern range for *L. nasus* and the thermal ranges were similar. The paleolatitudes of localities from which *Johnlongia* has been recovered were shown to be positively correlated with global temperature. During warm periods, *Johnlongia* was found at higher paleolatitudes in both hemispheres, but was found at warmer, lower latitudes during globally cooler periods. Consequently, this study demonstrates the ability of an ancient shark to respond to changes in global climate.

The paleodistribution of *Archaeolamna* and *Dwardius* fell within the extant latitudinal range of *Lamna nasus* but the SST range of both taxa somewhat exceeded that of the thermal range of *Lamna nasus*. Due to potential error, it is likely that these taxa had an antitropical distribution, as their remains have not been recovered from the warmer, well-sampled deposits of Texas or from localities of North Africa. The paleodistribution of *Cardabiodon* fell within the restricted latitudinal range of *Lamna nasus*; however, the thermal range greatly exceeded that recorded for *L. nasus*. It was speculated that the occurrence of this taxon at lower latitudes during an exceptionally warm episode was due to the ability to descend to cooler deeper waters. As predicted, *Cretodus* and *Cretalamna* were shown to have wide paleolatitudinal and paleothermal ranges, consistent with a cosmopolitan distribution. *Carcharias amonensis* demonstrated a paleolatitudinal range that was limited to the subtropical and tropical zones and a paleothermal range that was higher than that of *Lamna nasus*.

Among the most common selachian fossils recovered from the Alberta localities were the teeth of *Archaeolamna* ex. gr. *kopingensis*. Previous reconstructions of the dentition of *Archaeolamna* were based strictly on isolated teeth and assembled in a primitive odontaspidid-like condition. LACM 128125 (Chapter 5) demonstrated that the dentition of *A. kopingensis* was considerably more derived, revealing the potential hazard associated with an artificial tooth set. The dental sequence and tooth morphology of *A. kopingensis* was unique among both extinct (in which the dentition has been determined) and extant lamniforms validating its placement within the family Archaeolamnidae.

A sagittal section through a centrum of LACM 128125 showed that this shark deposited 18 annual marker bands after its birth and adult size was attained by the 10th band. A method was devised to estimate the length of this individual in the absence of a complete set of vertebral centra. Values obtained by measuring the partially complete upper jaw were compared to jaw circumference values for modern lamniform sharks. It was determined that this specimen had a jaw circumference larger than that of a 3.2 m *Isurus oxyrinchus* (shortfin mako) and a 3.8 m *I. paucus* (longfin mako). The size of this individual demonstrated that this species grew to a size much larger than had previously been thought.

The condition of polyphyodontism and the durable histological nature of shark and ray teeth provide for an extensive fossil record. A significant number of sharks, particularly species from the order Lamniformes, had wide geographic distributions and evolved rapidly. Accordingly, their teeth could be utilized as a biostratigraphical tool to temporally correlate separate geographical regions. The value of a practical intercontinental zonation system based on shark teeth has been previously suggested in the literature. Its construction would assist in dating marine deposits that lack diagnostic microfossils and invertebrate macrofossils. Thus, the detailed examination (accompanied with high resolution imaging) of the teeth discussed herein will assist in establishing suitable markers. The early Turonian Watino assemblage is particularly important in that the specimens were recovered from a specific stratigraphic horizon with little time averaging.

Continued research involving high-paleolatitudinal assemblages from both hemispheres is essential for understanding the overall picture of euselachian biogeography during the Late Cretaceous. Similarities in faunal composition will provide additional information that may be utilized in testing the response of an extinct antitropical species to changes in marine paleotemperature. Such findings may allow for predictions regarding the distribution of extant taxa in relation to future climate change.