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Instytut Paleobiologii PAN
ul. Twarda 51/55
PL-00-818 Warszawa, Poland

e-mail: app@twarda.pan.pl; tel.: (+48 22) 697 88 79; fax: (+48 22) 620 62 25

Late Cretaceous (Cenomanian-Campanian) mid-palaeolatitude sharks of *Cretalamna appendiculata* type

MIKAEL SIVERSON, JOHAN LINDGREN, MICHAEL G. NEWBREY,
PETER CEDERSTRÖM, and TODD D. COOK

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The type species of the extinct lamniform genus *Cretalamna*, *C. appendiculata*, has been assigned a 50 Ma range (Albian to the Ypresian) by a majority of previous authors. Analysis of a partly articulated dentition of a *Cretalamna* from the Smoky Hill Chalk, Kansas, USA (LACM 128126) and isolated teeth of the genus from Cenomanian to Campanian strata of Western Australia, France, Sweden and the Western Interior of North America, indicates that the name of the type species, as applied to fossil material over the last 50 years, represents a large species complex. The middle Cenomanian part of the Gearle Siltstone, Western Australia, yielded *C. catoxodon* sp. nov. and '*Cretalamna*' *gunsoni*. The latter, reassigned to the new genus *Kenolamna*, shares several dental features with the Paleocene *Palaeocarcharodon*. Early Turonian strata in France produced the type species *C. appendiculata*, *C. deschutteri* sp. nov. and *C. gertericorum* sp. nov. *Cretalamna* teeth from the late Coniacian part of the Smoky Hill Chalk in Kansas are assigned to *C. ewelli* sp. nov., whereas LACM 128126, of earliest Campanian age, is designated as holotype of *C. hattini* sp. nov. Early Campanian deposits in Sweden yielded *C. borealis* and *C. sarcoportheta* sp. nov. A previous reconstruction of the dentition of LACM 128126 includes a posteriorly situated upper lateroposterior tooth, with a distally curved cusp, demonstrably misplaced as a reduced upper 'intermediate' tooth. As originally reconstructed, the dentition resembled that of cretoxyrhinids (*sensu stricto*) and lamnids. Tooth morphology, however, indicates an otodontid affinity for *Cretalamna*. The root is typically the most diagnostic feature on an isolated *Cretalamna* tooth. This porous structure is commonly abraded and/or corroded and, consequently, many collected *Cretalamna* teeth are indeterminable at species level.

Key words: Otodontidae, *Cretalamna*, *Kenolamna*, lamniform, Gearle, Kansas, Sweden, France.

Mikael Siverson [mikael.siversson@museum.wa.gov.au], Department of Earth and Planetary Sciences, Western Australian Museum, 49 Kew Street, Welshpool, WA 6106, Australia;
Johan Lindgren [johan.lindgren@geol.lu.se], Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden;
Michael G. Newbrey [mike.newbrey@gov.ab.ca], Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta, T0J 0Y0, Canada; and Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada;
Peter Cederström [peter.cederstrom@eslov.se], Axelvoldsvägen 27, SE-241 35 Eslöv, Sweden;
Todd D. Cook [tdcook@ualberta.ca], Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

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Introduction

One of the most frequently reported nominal species of sharks from Upper Cretaceous rocks is the lamniform taxon *Cretalamna appendiculata* (Agassiz 1843). It has been regarded as an extremely long ranging species, reportedly spanning the latest Albian (Early Cretaceous) to Ypresian (Early Eocene) interval (Cappetta 1987; Shimada et al. 2006; Ward 2009), amounting to approximately 50 Ma. Cappetta (1987, 2012), building on the observations of Casier (1960), indicated that different lineages of *Cretalamna* gave rise to *Cretoxyrhina* Glikman, 1958, *Palaeocarcharodon* Casier, 1960, the Otodontidae Glikman, 1964, and the Lamnidae Müller and Henle, 1838. Applegate and Espinosa-Arrubarrena (1996) envisioned *C. appendiculata* as the direct ancestor of *'Carcharodon' orientalis* Sinzow, 1899 (a senior synonym of the type species of *Palaeocarcharodon*, *Carcharodon landanensis* Leriche, 1920), which in turn, they speculated, ultimately gave rise to both the white shark *C. carcharias* (Linnaeus, 1758) and the 'mega-tooth' shark '*Carcharodon*' *megalodon* (Agassiz, 1843). Purdy (1996)

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shared the view of Applegate and Espinosa-Arrubarrena, although the link between *Cretalamna* and ‘*Carcharodon*’ *orientalis* was supported with some reservation. Siverson (1992*a*), Zhelezko (2000) and Ward (2009) linked *Cretalamna* to the otodontids by suggesting a direct evolutionary transition from *Cretalamna* to *Otodus* Agassiz, 1843 in the Paleocene.

The nominal *C. appendiculata* is viewed as the most likely Cretaceous ancestor of the iconic white shark (by e.g. Applegate and Espinosa-Arrubarrena 1996; Purdy 1996) and/or the ancestor of the *Otodus* group, which culminated in *Otodus* (*Megaselachus*) *megalodon*, (e.g. Cappetta 1987, 2012; Siverson 1992*a*; Zhelezko 2000; Zhelezko and Kozlov 1999; Ward 2009). The debate about phylogenetic relationships and the taxonomy of *Cretalamna* is therefore of interest to a broader audience. Our study is based on one associated dentition (including *in situ* replacement teeth on the right palatoquadrate) from the Smoky Hill Chalk in Kansas, USA (LACM 128126) and several hundred isolated teeth of Cenomanian-Campanian age from Australia, France, Sweden, and the USA.

Up until 2007, reconstructions of the dentition in populations of *C. appendiculata* type were based exclusively on collections of shed, isolated teeth (Welton and Farish 1993; Applegate and Espinosa-Arrubarrena 1996). However, that year Shimada described a partial skeleton (LACM 128126) from the Smoky Hill Chalk, Niobrara Formation, western Kansas. His description included a reconstruction of the dentition based on a few replacement teeth in a natural *in situ* position on the right palatoquadrate and about 110 additional, disarticulated teeth from the same individual. An initial assessment of isolated teeth of *C. appendiculata* type from the early Campanian of Sweden raised concerns regarding Shimada’s (2007) reconstruction of the dentition in LACM 128126. Shimada (2007: fig. 8; Fig. 16A) referred a tooth with a moderately tall and strongly distally curved cusp to the upper ‘intermediate’ file [= third upper anterior (A3) *sensu* Siverson, 1999]. Campanian *Cretalamna* teeth from the Kristianstad Basin, Sweden, with a crown morphology comparable to that of Shimada’s ‘intermediate’ in LACM 128126 (e.g. Fig. 6C) show none of the diagnostic features on the root that characterise ‘intermediate’ teeth in modern lamnids and in e.g. *Cretoxyrhina mantelli* (Agassiz, 1843), which all have A3s (= third upper anterior teeth) with an overall root morphology in basal view strikingly different from that of posteriorly situated upper jaw teeth. In e.g. extant *Isurus* Rafinesque, 1810, the distal lobe of the root is labiolingually compressed relative to the mesial lobe and is commonly lingually curved. As Shimada (2007) did not illustrate any of the teeth of LACM 128126 in basal view, we examined LACM 128126 first hand to determine whether the basal view of the ‘intermediate’ tooth deviated from that of posteriorly situated upper jaw teeth (which would then have supported Shimada’s reconstruction). Our review of LACM 128126 is based on a re-examination of the right palatoquadrate with its *in situ* teeth, the partial vertebral column and the isolated teeth pertaining to this individual.

Reconstruction of dentitions and assignment of isolated teeth to specific tooth files

Although reference is given in the descriptions to specific tooth positions, we recognise the uncertainty involved doing this with isolated teeth. All assigned tooth positions in the descriptions and, where more abundant material is available, reconstructed dentitions of the various species (except for some of the *in situ* teeth of LACM 128126) are ‘presumed’ and thus open to alternative interpretations. In order to avoid excessive repetition of the term ‘presumed’, it is not explicitly stated in the descriptions of the various species that assigned tooth positions might be incorrect. The separation of isolated teeth into anteriors and lateroposteriors is based on comparisons with modern macrophagous lamniform sharks. The basic principles for reconstructing fossil dentitions of lamniform sharks were outlined by e.g. Siverson (1999), Cunningham (2000), Purdy et al. (2001), and Bourdon and Everhart (2011) and we refer to their work for a more in-depth discussion of e.g. recognition of anterior teeth and diagnostic features in upper versus lower anterior teeth. Examination of LACM128126 greatly facilitated the work and the original description of this specimen by Shimada (2007) was indeed the catalyst for the initiation of our revision of the genus. Although we disagree with some of the conclusions by Shimada (2007) we recognise the significance of his work as it paved the way for major progress in our understanding of early otodontid sharks.

The reconstructed dentitions in Figure 19 are based on both inferred left and right (mirror images) teeth, although all teeth in the dentition of *C. hattini* sp. nov. are from the same side of the jaw (right, mirror image teeth). The variable magnifications of individual teeth in Figure 19B-D (see Appendix 1) were largely based on the largest size of a particular tooth type, whereas the selection of individual teeth for photography was based on their superior state of preservation. There are some notable exceptions to the former guideline where, as a result of the small sample size, the largest teeth available for a presumed tooth file were deemed to be either exceptionally large (illustrated a3 of *K. gunsoni* gen. nov.; Fig. 23F) or uncharacteristically small (illustrated A2 of *C. catoxodon* sp. nov.; Fig. 20C) and magnifications were adjusted accordingly. In some cases the best preserved tooth is considerably smaller (e.g. inferred A3 in *K. gunsoni* gen. nov.; Fig. 23C) or larger (e.g. inferred A1 in *C. sarcoportheta* sp. nov.; Fig. 4A) than the average-sized tooth for that tooth position. In all species examined, isolated upper jaw teeth are more common than lower jaw teeth.

Diagnostic features of *Cretalamna* teeth

Features most commonly utilised herein in identification of the various species include: (1) the curvature of the cusp in labial/lingual views, e.g. posteriorly situated teeth are more strongly distally curved in *C. borealis*-group species (Fig. 11E$_1$) than they are in *C. appendiculata*-group species (Fig. 2F$_4$); (2) degree of labiolingual compression of the cusp, e.g. upper lateroposteriors have a thick cusp in *C. hattini* sp. nov. (Fig. 15H$_3$) and *C. appendiculata* (Fig. 2E$_2$) but a thin cusp in *C. deschutteri* sp. nov. (Fig. 18B$_2$); (3) cusplet shape, e.g. cusplets are rounded in most upper lateroposteriors of *C. catoxodon* sp. nov. (Fig. 21) but have a well-defined apex in the other species; (4) basal view of the root, e.g. the distal lobe is often labiolingually compressed relative to the mesial lobe in anteriorly situated upper lateroposterior teeth of *C. appendiculata*-group species (Fig. 2C$_1$, D$_3$, E$_3$); (5) relative size and morphology of the median indentation of the basal edge of the root in lateroposterior teeth, e.g. small and often U-shaped in *C. gertericorum* sp. nov. (Fig. 11G$_2$); (6) shape of the lingual protuberance in profile view, e.g. low and dome-shaped in *C. hattini*-group species (Figs. 17B$_3$, 18G$_2$) but more protruding in *C. appendiculata*- and *C. borealis*-group species (Figs. 3A$_2$, 7A$_2$, 11F$_2$); (7) the relative width of commissural teeth; moderately wide in *C. borealis*-group species (Fig. 11E) but very wide in *C. hattini*-group (Figs. 17L, 18E) and *C. appendiculata*-group species (Fig. 6E). Because of the highly diagnostic root in *Cretalamna*, isolated teeth of this genus with a moderately to severely abraded root are often indeterminable at species level.

Material and methods

The material included in this study is derived from a number of sources. The Western Australian material from the Gearle Siltstone was surface collected (primarily by MS) and is clearly biased towards larger teeth. Commissural teeth are rare in the collection from the CY Creek site and this is reflected in major gaps in the posterior part of the reconstructed dentitions of *Kenolamna gunsoni* gen. nov. and *Cretalamna catoxodon* sp. nov. (Fig. 19B, D).

The *Cretalamna* teeth from the SECAB quarry, Bettrechies, France, are derived from bulk sampling although a few teeth were extracted *in situ*. This locality was not visited or sampled by any of the authors, and the material at hand is instead the result of collecting efforts by Gert De Bier, Eric Collier, Pieter De Schutter, Bert Gijsen, and David J. Ward. A large portion of the *Cretalamna* teeth examined from the *Mytiloides labiatus* Zone are indeterminable at species level because of poor root preservation. Only the best preserved teeth were registered and included in the study. Because of the low number of well-preserved teeth at hand, no attempts were made to reconstruct the dentition of any of the three species of *Cretalamna* from the *M. labiatus* Zone.

The specimens (isolated teeth and a partial skeleton) from the Smoky Hill Chalk of the Niobrara Formation, western Kansas, USA, are derived from three stratigraphical levels. The partial skeleton of *C. hattini* sp. nov. (LACM 128126), previously described by Shimada (2007), but not collected by him, includes about 120 teeth. The numerical dominance of more-or-less fully mineralised teeth indicates a certain degree of selective collecting of elements pertaining to this individual. The isolated teeth, assigned to *C. ewelli* sp. nov., from the two lower stratigraphical levels in the Smoky Hill Chalk were surface collected (in situ or as float) by Keith Ewell and MS (one tooth). Like the *Cretalamna* collection from the Gearle Siltstone, the material is biased towards larger teeth from the anterior half of the dentition. Selachian teeth from the Smoky Hill Chalk in western Kansas are exceptionally well preserved but weather quickly after exposure. They are also easily damaged by acetic acid at pH levels that would cause no visible damage to teeth from other deposits. As we were aware of this issue, the acetic acid solution used to remove adhering carbonates was weak (pH around 5.0) and heavily buffered with calcium acetate.

Almost all of the teeth from the early Campanian of the Kristianstad Basin, Sweden, included in this study are derived from wet-sieving the unconsolidated calcareous sand at the Åsen locality (work carried out by MS, JL and PC). Unlike the surface collected material from the Gearle Siltstone and the Smoky Hill Chalk, there is no bias towards larger teeth in the collection from Åsen. Selachian teeth from this locality have a rather poorly mineralised root and require the application of a stabiliser (polyvinyl butural used in this case) for long term preservation.

The various localities are described in the Appendix 2.

Terminology.—Tooth terminology is after Cappetta (1987). Row group terminology follows Siverson (1999); see also Siverson and Lindgren (2005: 303) for additional comments. Description of vertebral centra primarily follows Kozuch and Fitzgerald (1989) except where cranio-caudal length is referred to as length and medio-lateral breadth is referred to as width.

Institutional abbreviations.—AMNH FF, American Museum of Natural History, Fossil Fish, New York; FHSM, Sternberg Memorial Museum, Fort Hays State University; LACM, Los Angeles County Natural History Museum; LO, (Lund Original), Department of Geology, Lund University; NHMUK P, Natural History Museum, London; RM PZ, Swedish Museum of Natural History, Department of Palaeozoology, Stockholm; UM, Université de Montpellier II; WAM, Department of Earth and Planetary Sciences, Western Australian Museum.

Systematic palaeontology

Lamniformes Berg, 1958

Otodontidae Glikman, 1964

Remarks.—Several associated dentitions of *Otodus obliquus* (the species upon which the Otodontidae is ultimately based) have been recovered from early Paleogene phosphates of Morocco. In the absence of formal accounts of one or more of these specimens, the Otodontidae is defined by the shape of individual isolated teeth (Zhelezko and Kozlov 1999). Our assignment of *Cretalamna* to the Otodontidae is based on striking similarities in tooth morphology between *Otodus* of the *O. obliquus* group and Late Cretaceous *Cretalamna*, particularly in the more anteriorly situated lower jaw tooth files (see Dartevelle and Casier 1943: pl. 6: 1, 9 and Fig. 17A, F).

Cretalamna Glikman, 1958

Type species.—By original designation, *Otodus appendiculatus* Agassiz, 1843, within the early Cenomanian to early Coniacian interval, Lewes, England.

Emended diagnosis.—Quadrate process more than twice as high as dorsoventrally narrowest part of palatoquadrate, anterior to quadrate process but posterior to section harbouring anterior tooth files. Most distal upper anterior tooth and most mesial upper lateroposterior tooth not markedly reduced in size relative to adjacent teeth. Intermediate teeth absent. Root typically without median groove. Median indentation of basal edge of root shallow in labial/lingual views in lateroposterior teeth. Lobes of root more-or-less quadrangular in lateroposterior tooth files. Radial lamellae of vertebral centra moderately robust with spacing equivalent to thickness. Neural arch foramina subovate, extending full length of centrum between corpus calcarea.

Remarks.—There is no visible evidence of an orbital process (*sensu* Compagno 2001) on the palatoquadrates of LACM 128126 (Fig. 13A, B). However, the dorsal edge of the more complete, right palatoquadrate is not well enough preserved to reveal if a cartilaginous orbital process was originally present.

Agassiz's former syntypes of *Otodus appendiculatus* (Agassiz 1843: pl. 32: 1-25) are a heterogeneous mix, comprising several genera (*Cretodus*? [Sokolov, 1965] in fig. 9, *Cretalamna* in e.g. fig. 10, *Dwardius* Siverson, 1999 in fig. 15, and *Cretoxyrhina* in fig. 25) and probably about half a dozen species if not more. Siverson (1999) designated the upper? lateroposterior tooth in Agassiz's figure 10 as lectotype for *C. appendiculata* (Fig. 1). This species concept conformed to that of most current authors of that time (e.g. Müller and Diedrich 1991; Manning and Dockery 1992; Welton and Farish 1993; Williamson et al. 1993). However, the evolution of *C. appendiculata sensu lato* turns out to be more complex than perhaps anyone could have imagined. The lectotype of *C. appendiculata* was collected from 'White Chalk' near Lewes, East Sussex, southern England (Agassiz 1843: 270). About a dozen more-or-less overgrown quarries are spread around Lewes and expose or exposed strata of early Cenomanian to mid-Santonian age (Dineley and Metcalf 1999). The Turonian stage is particularly well represented with current or former exposures in a majority of the local quarries (Dineley and Metcalf 1999: fig. 13.18). Mining activity in the mid 1800's exposed strata of Cenomanian to early Coniacian age (A. Gale, pers. comm. 2010), effectively bracketing the possible age range of the lectotype.

The lectotype of *C. appendiculata* is from the Gideon A. Mantell collection but may not have been transferred to the Natural History Museum in London as it was not listed as a British Museum (NHMUK) specimen by Woodward (1889). Several of the paralectotypes of '*Otodus*' *appendiculatus*, derived from Mantell's collection, did however end up in the NHMUK collections (Agassiz 1843: pl. 32: 1, 5, 6, 11, and 14). One could argue that *C. appendiculata* is a *nomen dubium* because the whereabouts of the lectotype are currently unknown, the type stratum is likewise unknown and possible source rocks around Lewes exposed in the mid 1800s span approximately 10 Ma (early Cenomanian to early Coniacian). However, as *C. appendiculata* is the type species of a nominal genus that has become well known to many palaeontologists outside the arena of fossil shark studies, there is arguably a strong case for preserving taxonomic stability. Doing so would also be in the spirit of the latest edition of the International Code of Zoological Nomenclature (Ride et al. 2000). Complete teeth of *Cretalamna* with an uncorroded root are seemingly extremely rare in the Cenomanian-early Coniacian of the Lewes area, as we are only aware of one well preserved specimen (although the tip of the mesial lobe is missing), a lower lateroposterior of *C.* aff. *C. gertericorum* sp. nov. from the middle Cenomanian *Acanthoceras rhotomagense* Zone, Southerham Grey Pit (David Ward collection). Lateroposterior teeth in species of the *C. borealis* group (like *C. gertericorum* sp. nov.) are readily separable from the lectotype of *C. appendiculata* by their strongly distally curved cusp in teeth with a comparable profile view (compare Fig. 1B with Fig. 11D$_2$).

The *Mytiloides labiatus* Zone (early Turonian) in the SECAB quarry, Bettrechies, northern France, is right in the middle of the possible age range of the lectotype (Cenomanian-early Coniacian) and produces abundant teeth of

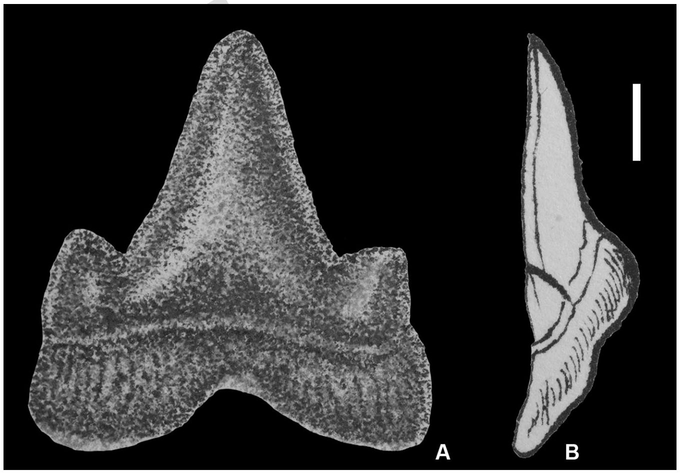


Fig. 1. *Cretalamna appendiculata* (Agassiz, 1843), reproduced from Agassiz, 1843: pl. 32, fig. 10; scale bar represents 3 mm. **A-B**, Lectotype. **A**, labial and **B**, tilted profile view.

Cretalamna. Examination of several collections of *Cretalamna* teeth from the *M. labiatus* Zone of the SECAB quarry, derived from bulk sampling, resulted in the recognition of three species of *Cretalamna*, one of which includes teeth with a morphology very close to that of the lectotype of *C. appendiculata* (straight thick cusp, rounded root-lobes and a profile view indicating an upper jaw position; Fig. 2E). The latter was illustrated by Agassiz (1843: pl. 32: 10) in profile and labial views. The profile view (Fig. 1B) is however of somewhat limited use in this case (other than for indicating an upper jaw position) as the tooth does not appear to have been illustrated at right angles to the vertical height axis, hence the position of the apex of the cusplet in the same horizontal plane as the summit of the lingual protuberance of the root. A good match was achieved by tilting the cusp of the tooth in Figure 2E$_2$ about 45° towards the viewer. The relatively low protuberance of the lectotype is probably a result of abrasion. Several of the *Cretalamna* teeth from Bettrechies are very well preserved except for a 'polished-looking' lingual protuberance (see high magnification view of e.g. Fig. 2B$_3$, the area between the main lingual foramen and the root/neck boundary). The ten teeth from the *M. labiatus* Zone in the SECAB quarry, assigned to *C. appendiculata* (Figs. 2, 3), enabled the formulation of a meaningful diagnosis for the species and a much improved understanding of its relationship to other Cretaceous *Cretalamna*.

The spelling of the name of the genus is controversial. While strictly adhering to the Code of Zoological Nomenclature in force at the time (Ride et al. 1985), Siverson (1999) reinstated the original spelling *Cretalamna*, replacing the unjustified but universally adopted subsequent spelling *Cretolamna*. Within a few years, usage of the original spelling was embraced by a growing number of workers (e.g. Cook et al. 2008; Everhart 2005; Kriwet and Benton 2004; Kriwet et al. 2008; Shimada 2007; Shimada et al. 2006). Over the last few years a majority of researchers discussing or mentioning the genus in publications have used the original spelling *Cretalamna* (e.g. Adolfssen and Ward in press; Andreev and Motchurova-Dekova 2010; Becker et al. 2010; Bogan and Gallina 2011; Bourdon et al. 2011; Bourdon and Everhart 2011; Cook et al. 2011, in press; Cumbaa et al. 2010; Cuny et al. 2012; Einarsson et al. 2010; Eriksson et al. 2011; Hamm and Cicimurri 2011; Retzler et al. in press; Sato et al. 2012; Shimada et al. 2010; Siverson et al. 2013; Underwood and Cumbaa 2010; Underwood et al. 2011; Ward 2009). The replacement of *Cretolamna* with *Cretalamna* was strongly opposed by Cappetta (2000, 2012). He presented his case to a representative for the International Commission for Zoological Nomenclature (Cappetta 2000) who (in litt.), while citing Article 33.3.1 of the 2000 Edition of the Code, supported the retention of the spelling *Cretolamna*. However, it is our view that the 2000 edition cannot be used retrospectively, without a formal ruling by the Commission, to alter justified nomenclatural acts carried out before the 2000 edition came into effect. Moreover, article 33.3.1 states that 'when an unjustified emendation is in prevailing usage and is attributed to the original author and date it is deemed to be a justified emendation'. Given that a majority of current students have adopted the original spelling *Cretalamna*, Article 33.3.1 can no longer be invoked in support of the spelling *Cretolamna*. Cappetta (2012) indicated that the spelling *Cretolamna* is used by an overwhelming number of workers and cited a number of publications, all of which were published before Siverson's 1999 work. Cappetta would have had a stronger case if the original spelling had been reinstated in 2000 or later as this would have represented a violation of Article 33.3.1. As it stands, however, the reinstatement of the original spelling strictly adhered to the Code in force at the time and *Cretalamna* is in prevailing usage and, if anything, is supported rather than threatened by Article 33.3.1 of the 2000 edition.

Cretalamna appendiculata (Agassiz, 1843)

Figs. 2, 3

Otodus appendiculatus [partim]; Agassiz 1843: 270, pl. 32: 10.

Lectotype: Lateroposterior tooth (presumably from the upper jaw) from the Lewes area (within the Cenomanian-early Coniacian interval), East Sussex, southern England.

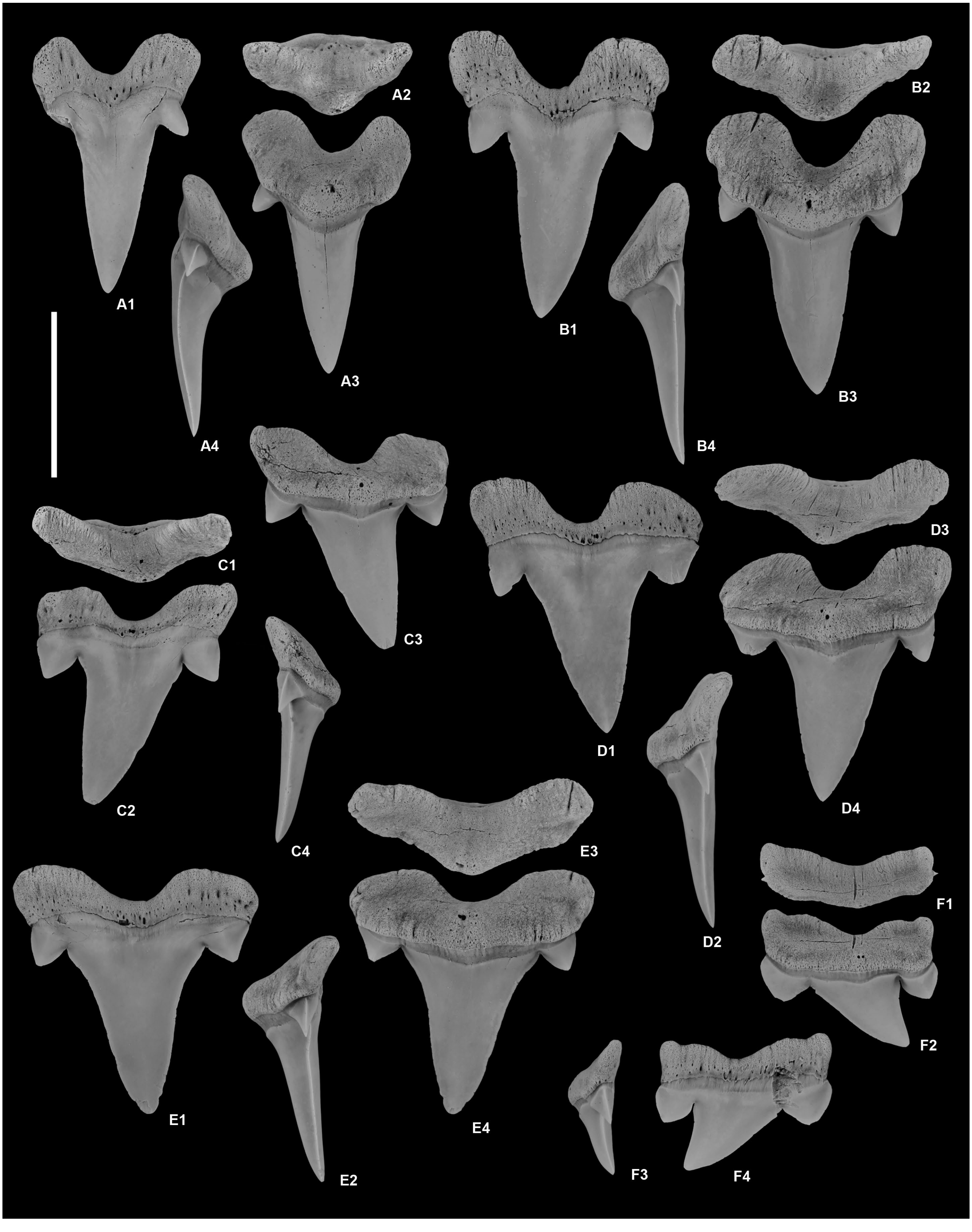
Material: Ten teeth from the *M. labiatus* Zone (early Turonian), SECAB quarry, Bettrechies, France.

Emended diagnosis.—Cusplets relatively small in upper lateroposterior teeth and moderately divergent. Cusp labially curved in profile view in upper lateroposterior teeth. Lower anterior teeth with high root but moderately tall, triangular cusp in lingual view. Root massive in lower anteriors of large individuals, displaying protruding lingual protuberance in profile view and triangular outline in basal view. Upper anterior and anteriorly situated upper lateroposterior teeth with deeply U-shaped median indentation of basal edge of root and rounded lobes. Distal lobe of root labiolingually compressed relative to mesial lobe in anteriorly situated upper lateroposterior teeth. Lingual protuberance of root high but apico-basally narrow in profile view in upper and lower lateroposterior teeth.

Description

First upper anterior tooth.—A 15.5 mm high tooth is referred to the first upper right file (Fig. 2A). One cusplet is missing, presumably the distal one. The cusp is straight in labial/lingual views and lingually curved in profile view. The preserved cusplet is symmetrical and set at a 45° angle to the cusp. The lingual protuberance of the root is well demarcated in basal view. The root is almost symmetrical in labial/lingual views although the mesial? lobe is somewhat wider and labiolingually less compressed.

Second upper anterior tooth file.—A well-preserved, 17 mm high tooth is assigned to the right A2 position (Fig. 2B). The robust cusp is moderately tall and very slightly curved in labial/lingual views, presumably towards the commissure. In profile view, the cusp is slightly labially curved. The cus-


A1
A2
A3
A4
B1
B2
B3
B4
C1
C2
C3
C4
D1
D2
D3
D4
E1
E2
E3
E4
F1
F2
F3
F4

plets are sub-triangular and moderately divergent. The root is relatively gracile and slightly asymmetrical in labial view, with the mesial lobe somewhat shorter and broader than is the distal lobe. In basal view, the root is asymmetrical with the distal lobe more compressed than the mesial lobe.

Upper lateroposterior tooth files.— Of the four well-preserved upper lateroposterior teeth at hand range, three of them (Fig. 2C-E), 14-15 mm high, are from anteriorly situated tooth files (probably within the LP1-LP4 range), whereas one (Fig. 2F), 9 mm high, is a posteriorly situated tooth (estimated position LP7 or LP8). All teeth have cutting edges somewhat labially curved in profile view. The cusp is slightly- to moderately distally inclined in the anteriorly situated teeth but strongly distally curved in the posteriorly situated tooth. The root is markedly asymmetrical in the two most anteriorly situated teeth (Fig. 2C-D) which both also have a deep, U-shaped median indentation of the basal edge of the root. The lateral cusplets are sub-triangular, moderately large and relatively upright on all four teeth. In basal view, the root is symmetrical in the posteriorly situated tooth (Fig. 2F$_1$) but asymmetrical in the anteriorly situated teeth with the distal lobe labiolingually compressed relative to the mesial lobe (Fig. 2C$_1$, D$_3$, E$_3$).

Second lower anterior tooth file.—A complete, 21.5 mm high tooth from a large individual is referred to the second lower anterior file (Fig. 3A). The triangular cusp is very slightly distally inclined in labial/lingual views and moderately thick. The cutting edges of the cusp are straight in profile view. The root is massive and asymmetrical in labial view, as the mesial lobe is longer and narrower than the distal lobe. A triangular outline characterises the basal view. In profile view, the neck and lingual protuberance rise sharply from the lingual demarcation of the cusp.

Lower lateroposterior tooth file.—Three teeth are referred to the lower lateroposterior files. The largest of the three (probably an lp1), measuring 18 mm in height, is well preserved with the exception of a small missing portion of the mesial lobe of the root (Fig. 3B). The cusp is slightly distally inclined in labial/lingual views and very slightly lingually curved in profile view. The root is markedly asymmetrical with its angular and broad distal lobe and more acute and narrower mesial lobe. The lingual protuberance is relatively narrow and well demarcated in basal view (Fig. 3B$_4$). The median indentation of the basal edge of the root is deeply U-shaped. The medium-sized tooth is missing the tip of the cusp (Fig. 3C$_3$). As preserved it measures 10 mm in height and would have been located in the middle part of the inferred lower lateroposterior hollow. The cusp moderately distally curved in labial/lingual views and slightly lingually curved in profile view. The mesial cusplet is noticeably larger than the distal cusplet. The median indentation of the basal edge of the root forms a wide-angled V. The smallest of the well-preserved lower lateroposterior teeth is 6.5 mm high (Fig. 3D). The apex of the distally inclined cusp is missing. The rounded median indentation of the basal edge of the root is both wide and deep. Both lobes of the root are sub-rectangular in basal view. A narrow median groove divides the lingual protuberance of the root.

Comparison.—Teeth of *C. appendiculata* most closely resemble the teeth of the early Campanian *C. sarcoportheta* sp. nov., and both species are included in the *C. appendiculata* group. Presumed derived characters uniting them include a marked asymmetry of the root in basal view in anteriorly (but noticeably not in posteriorly) situated upper lateroposterior teeth, with the distal lobe being labiolingually compressed relative to the mesial lobe (Figs. 2C$_1$, D$_3$, E$_3$, 5B$_2$, E$_1$, F$_1$), a strongly compressed distal lobe in presumed second upper anterior teeth (Figs. 2B$_2$, 4D$_3$, E$_3$, F$_1$; note that the cusp appears to be somewhat distally curved in *C. appendiculata* but very slightly recurved in *C. sarcoportheta* sp. nov.) and a very prominent lingual protuberance of the root in lower anterior teeth (Figs. 3A$_2$, 7A$_2$, B$_2$, C$_2$). Apart from the morphology of the putative A2, comparable teeth of the Campanian species differ from those of *C. appendiculata* by their more protruding lingual protuberance of the root (see e.g. Figs. 2C$_4$, 5F$_4$), less concave labial face in profile view in upper lateroposterior teeth from comparable files (compare Figs. 2D$_2$ and E$_2$ with 5F$_4$ and H$_2$), somewhat broader cusp (on average), more divergent cusplets, and less tightly curved median indentation of the root in anteriorly situated lateroposterior teeth.

Anterior teeth of the co-existing *C. gertericorum* sp. nov. are much taller relative to their width than are those of *C. appendiculata*. The cusp is straight in profile view in the lower anterior tooth at hand of *C. appendiculata* (Fig. 3A$_2$), but lingually curved in the probable a1 of *C. gertericorum* sp. nov., as it is in other species of the *C. borealis* group (Figs. 10A$_2$, 11F$_2$). Upper lateroposterior teeth of *C. gertericorum* sp. nov. have generally a more strongly distally curved cusp than have teeth of *C. appendiculata*. The median indentation of the basal edge of the root is smaller and more tightly curved in lateroposterior teeth of *C. gertericorum* sp. nov. than it is in comparable teeth of *C. appendiculata* (compare Figs. 2F$_4$, 3D$_2$ with Fig. 11E$_1$, G$_1$). The lingual protuberance of the root is very small but well demarcated in basal view of most lateroposterior teeth of *C. gertericorum* sp. nov. (Fig. 11E$_3$, G$_3$) but much wider and less well demarcated in *C. appendiculata* (Figs, 2F$_1$, 3D$_4$).

Lower anterior teeth of *C. deschutteri* sp. nov. have a lingually curved cusp in profile view (straight in the probable

← Fig. 2. *Cretalamna appendiculata* (Agassiz, 1843), upper jaw teeth, *Mytiloides labiatus* Zone (early Turonian), SECAB quarry, Bettrechies, northern France; scale bar represents 10 mm. **A**. WAM 13.5.2, right A1?; labial (A$_1$), basal (A$_2$), lingual (A$_3$), and profile (A4) views. **B**. UM-BET 1, right A2?; labial (B$_1$), basal (B$_2$), lingual (B$_3$), and profile (B4) views. **C**. UM-BET 2, right LP1?; basal (C$_1$), labial (C$_2$), lingual (C$_3$), and profile (C$_4$) views. **D**. UM-BET 3, left LP2?; labial (D$_1$), profile (D$_2$), basal (D$_3$), and lingual (D$_4$) views. **E**. WAM 13.5.7, left LP3?; labial (E$_1$), profile (E$_2$), basal (E$_3$), and lingual (E4) views. **F**. WAM 13.5.3, right LP8?; basal (F$_1$), lingual (F$_2$), profile (F$_3$), and labial (F$_4$) views.

a2 of *C. appendiculata*), a lingual protuberance of the root well defined in basal view (poorly defined in *C. appendiculata*) but poorly demarcated from the main body of the root in profile view (protruding in *C. appendiculata*). Upper lateroposterior teeth of *C. deschutteri* sp. nov. have a symmetrical root in basal view (as in *C. hattini* sp. nov., whereas it is strongly asymmetrical in at least more anteriorly situated teeth of *C. appendiculata*) and a labiolingually compressed

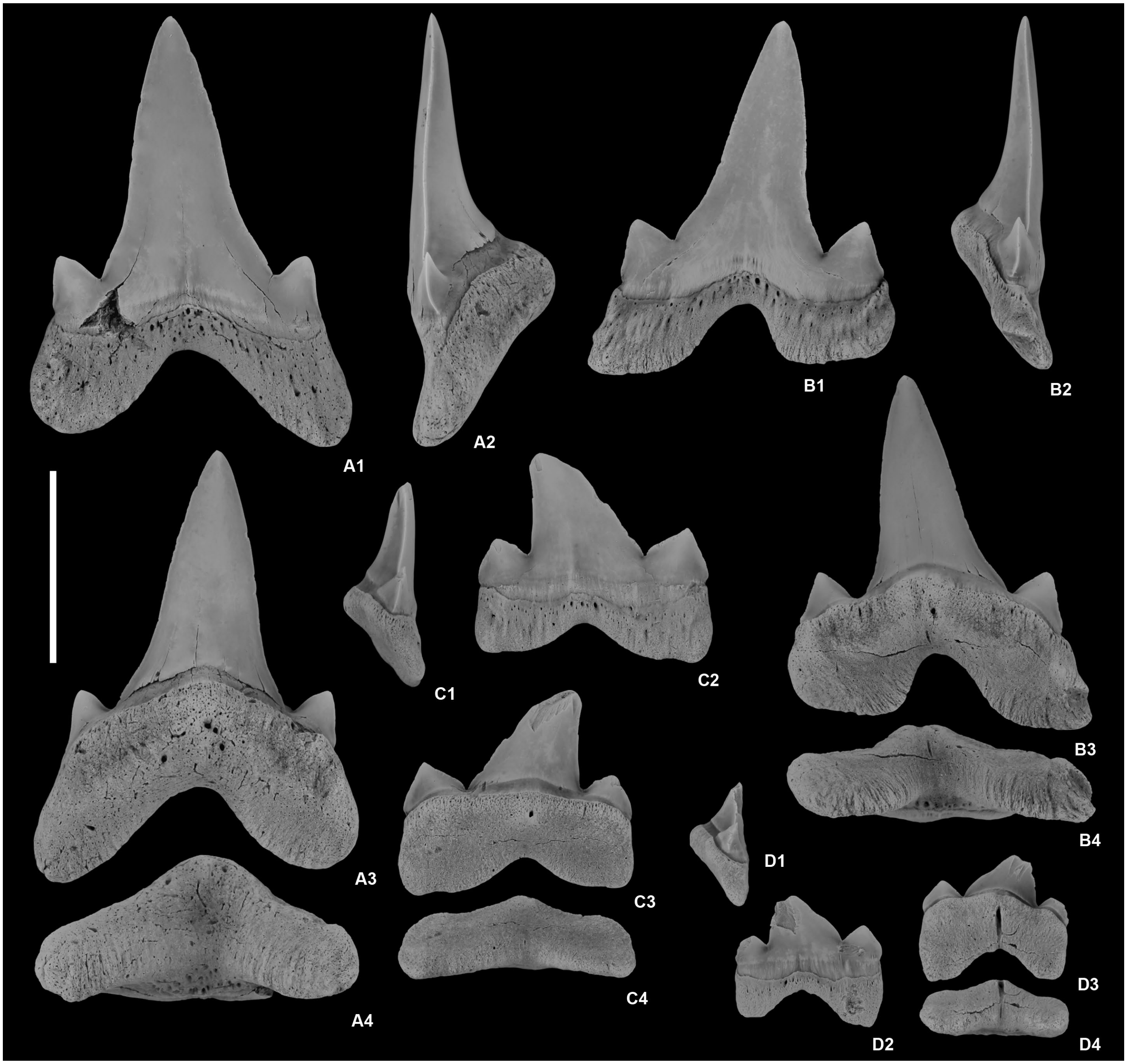


Fig. 3. *Cretalamna appendiculata* (Agassiz, 1843), lower jaw teeth, *Mytiloides labiatus* Zone (early Turonian), SECAB quarry, Bettrechies, northern France; scale bar represents 10 mm. **A**. WAM 13.5.6, right a2? from a large individual; labial (A_1), profile (A_2), lingual (A_3), and basal (A4) views. **B**. WAM 13.5.5, left lp1?; labial (B_1), profile (B_2), lingual (B_3), and basal (B4) views. **C**. WAM 13.5.4, right lp6?; profile (C_1), labial (C_2), lingual (C_3), and basal (C_4) views. **D**. WAM 13.5.1, right lp8?; profile (D_1), labial (D_2), lingual (D_3), and basal (D_4) views.

Fig. 4. *Cretalamna sarcoportheta* sp. nov., upper anterior teeth, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen locality, Kristianstad Basin, southern Sweden. All specimens prefixed by LO; scale bar represents 10 mm. **A**. 10889 t, paratype, left A1?; labial (A_1), profile (A_2), basal (A_3), and lingual (A4) views. **B**. 10890 t, paratype, right A1?; profile (B_1), basal (B_2), lingual (B_3), and labial (B4) views. **C**. 10891 t, paratype, right A1?; basal (C_1), lingual (C_2), labial (C_3), and profile (C_4) views. **D**. 10888 T, holotype, left A2?; profile (D_1), labial (D_2), basal (D_3), and lingual (D_4) views. **E**. 10892 t, paratype, left A2?; labial (E_1), profile (E_2), basal (E_3), and lingual (E4) views. **F**. 10893 t, paratype, right A2?; basal (F_1), lingual (F_2), profile (F_3), and labial (F_4) views.

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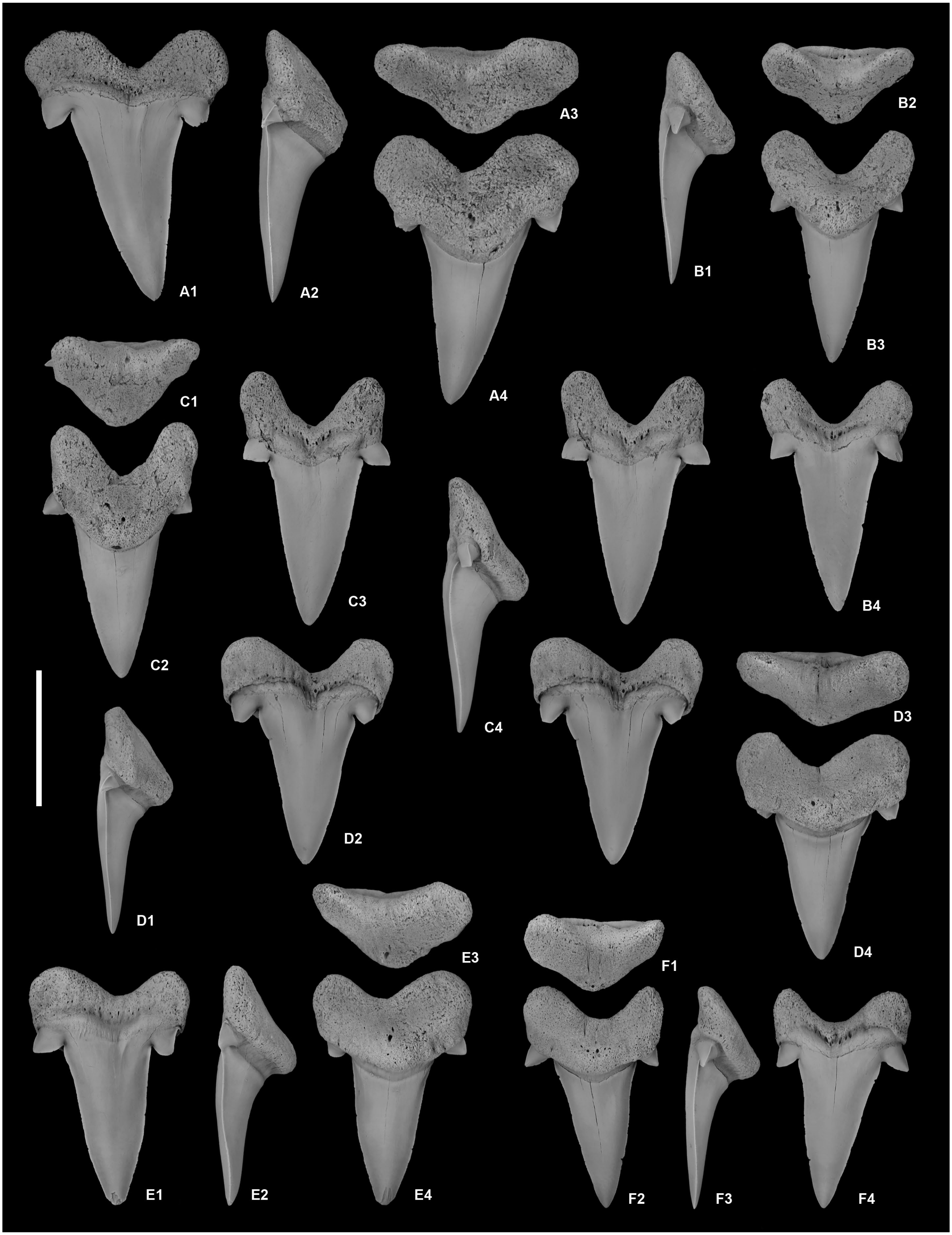
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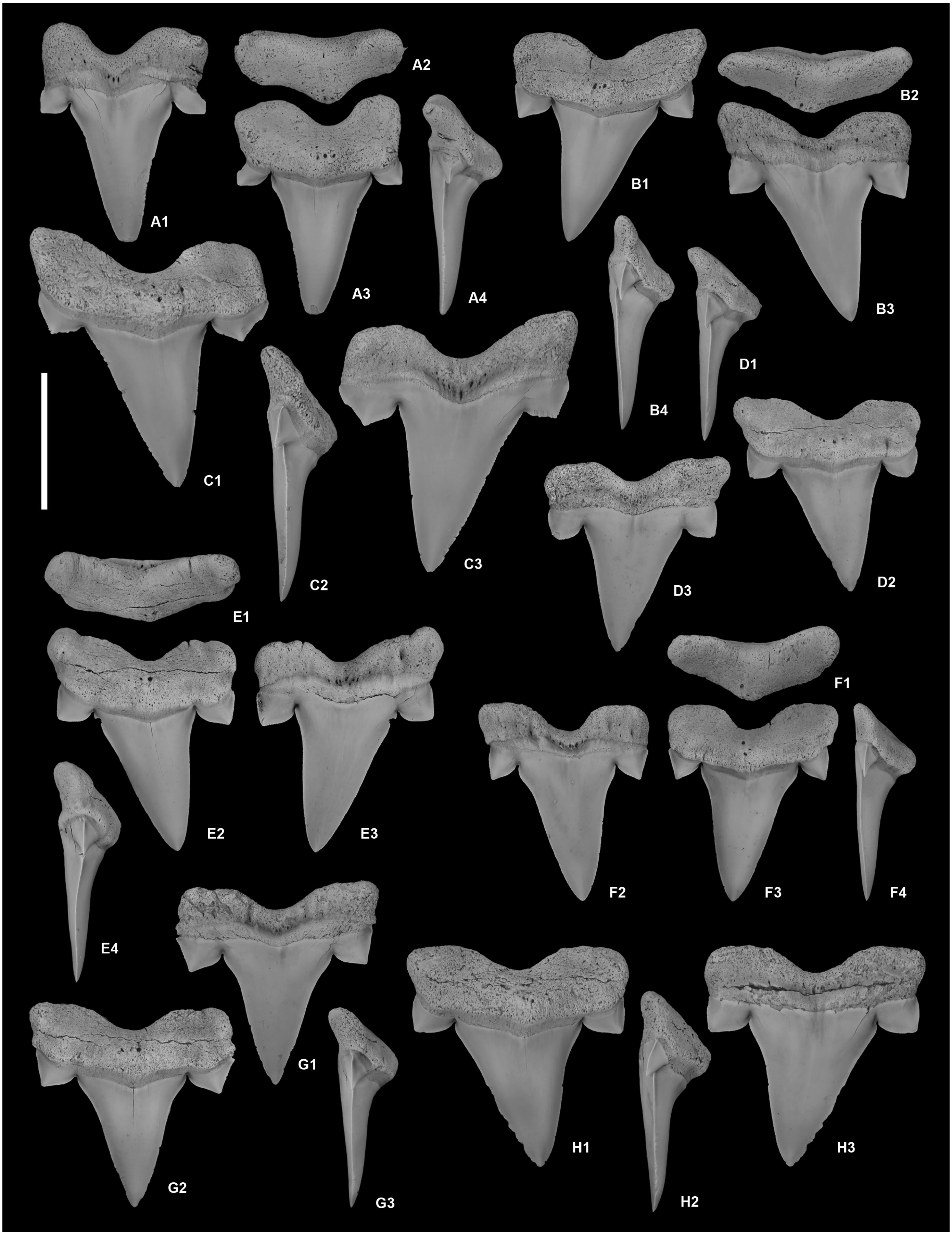
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cusp. In contrast, the cusp is thick and robust in comparable upper lateroposteriors of *C. appendiculata* (compare Fig. 2F$_3$ with Fig. 18D$_2$).

Remarks.—Herman (1977: pl. 9: 2) illustrated 12 teeth [five from the late Cenomanian *P. plenus* Zone and seven from the middle Turonian *Terebratulina rigida* Zone (= *T. lata* Zone, see Appendix)] from the SECAB quarry, Bettrechies, as *Cretolamna appendiculata* var. *appendiculata*. One of the teeth from the *T. lata* Zone (Herman, 1977: pl. 9: 2c) is an upper anterior (probably A2) of a *C. borealis*-group species (possibly *C. gertericorum* sp. nov.). We are uncertain about the identity of the other 11 teeth as we have not had the opportunity to examine them first hand. Even moderate abrasion of the root may render a *Cretalamna* tooth indeterminable at species level.

Cretalamna sarcoportheta sp. nov.

Figs. 4-8, 19C

Cretolamna appendiculata var. *pachyrhiza* [partim]; Herman 1977: 210-216, pl. 9: 3e [*non* figs. 3a-d (*C. borealis*), 3g-f (undescribed *Cretalamna* and/or *Otodus* ex gr. *obliquus*)].

Cretolamna appendiculata [partim]; Siverson 1992a: 528, pl. 1: 1-4, 9-13, 16-17 [*non* figs. 5-8, 14-15 (*Cretalamna borealis*)].

Etymology: Destroyer of flesh; combination of *sarkos* (Greek), flesh, and *porthetor* (Greek), destroyer.

Type material: Holotype: Second upper left anterior tooth, LO 10888 T; Fig. 4D. Paratypes: LO 6347t, LO 6348 t, LO 6351 t, LO 10889 t-10920 t; Figs. 4A-C, E, F, 5A-H, 6A-E, 7A-C, 8A-J, 19C (lp7); Siverson 1992*a*: pl. 1: 1-4, 11.

Type horizon: Unknown horizon within an up to 2 m thick sequence of poorly consolidated calcareous sand of latest early Campanian age (informal *Belemnellocamax mammillatus* belemnite zone),

Type locality: Åsen, Kristianstad Basin, southern Sweden.

Material.—216 teeth from the informal *Belemnellocamax mammillatus* zone, Åsen locality, Kristianstad Basin (LO 6352 t, LO 6354 t, and LO 10921 t-11134 t).

Diagnosis.—Robust anterior teeth with thick, moderately tall, triangular cusp; either straight, somewhat distally inclined or very slightly curved/recurved. Root asymmetrically subtriangular in basal view in anterior teeth with one lobe considerably broader than other lobe. Cusp very broad and triangular in anteriorly situated lateroposterior teeth with flat labial face of cusp in profile view. Cusp narrower, generally more upright in lateroposterior teeth with slightly lingually curved cusp in profile view. Root markedly asymmetrical in basal view in anteriorly situated upper lateroposterior teeth with distal lobe narrower than mesial lobe in all but one tooth type. Latter, distinct tooth type with apically curved cusp and sub-rectangular root in basal view, with root-lobe on same side of vertical mid-line of tooth as apex of cusp more compressed than other lobe.

Description.

Parasymphyseal teeth.—There are no complete parasymphyseal teeth from the Åsen and Ignaberga localities as the root is corroded to a variable degree in all specimens. The cusp is thick, triangular and set at an angle (Siverson 1992*a*: pl. 1: 16). Some teeth have at least one small, triangular cusplet (Siverson 1992*a*: pl. 1: 13; Fig. 19C). The root is asymmetrical in basal view with one side being thinner than the other. The thinner root-lobe is on the same vertical side of the tooth in lingual/labial views as the apex of the inclined cusp (Siverson 1992*a*: fig. 12).

First upper anterior tooth file.—Three complete teeth are referred to this tooth file (additional to several incomplete specimens). They measure 17.5, 18.5 and 19 mm in height. The cusp is labiolingually very thick, even more so than in the first lower anterior tooth. The cusp is straight (Fig. 4B$_4$) to moderately distally curved (Fig. 4A$_1$). The cusplets are small on all first upper anterior teeth and divergent to sub-parallel to the vertical axis of the cusp. The neck is rather narrow and of even apico-basal width along the entire root-crown boundary. The root is symmetrical in labial/lingual views but variable in both total width and the width of the lobes. The distal lobe of the root is labiolingually compressed relative to the inferred mesial lobe (Fig. 4A$_3$, B$_2$, C$_1$).

Second upper anterior tooth file.—Three complete teeth are referred to this tooth file (additional to several incomplete specimens), measuring 16.5-17 mm in height. The cusp is triangular, labiolingually moderately compressed and straight (Fig. 4D$_2$) to somewhat distally inclined (Fig. 4F$_4$) with a very slightly recurved apex. The cusplets are small and more-or-less divergent. The root is markedly asymmetrical with a broad mesial lobe and narrower, shorter and less divergent distal lobe. In labial and lingual views, the basal edge of the mesial lobe is straight to slightly convex whereas the basal edge of the distal lobe is straight to slightly concave. The 'maximum root width/tooth height ratio' is larger in the second upper anterior teeth than it is in the first upper anterior teeth, as the former are slightly shorter on average but at the same time somewhat wider.

Upper lateroposterior tooth files.—The first upper lateroposterior tooth has a distinctive morphology in this species. The cusp is vertical in its basal half but has a slightly to moderately distally curved apex (Fig. 5A$_1$). The root is asymmetrical, displaying a sub-vertical, rounded mesial lobe

← Fig. 5. *Cretalamna sarcoportheta* sp. nov., anteriorly situated upper lateroposterior teeth, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen locality, Kristianstad Basin, southern Sweden. All specimens paratypes and prefixed by LO; scale bar represents 10 mm. **A**. 10894 t, left LP1?; labial (A$_1$), basal (A$_2$), lingual (A$_3$), and profile (A$_4$) views. **B**. 10895 t, left LP2?; lingual (B$_1$), basal (B$_2$), labial (B$_3$), and profile (B$_4$) views. **C**. 10896 t, right LP2?; lingual (C$_1$), profile (C$_2$), and labial (C$_3$) views. **D**. 10897 t, right LP3?; profile (D$_1$), lingual (D$_2$), and labial (D$_3$) views. **E**. 10898 t, right LP3?; basal (E$_1$), lingual (E$_2$), labial (E$_3$), and profile (E$_4$) views. **F**. 10899 t, left LP3?; basal (F$_1$), labial (F$_2$), lingual (F$_3$), and profile (F$_4$) views. **G**. 10900 t, right LP4?; lingual (G$_1$), labial (G$_2$), and profile (G$_3$) views. **H**. 10901 t, right LP4?; lingual (H$_1$), profile (H$_2$), and labial (H$_3$) views.

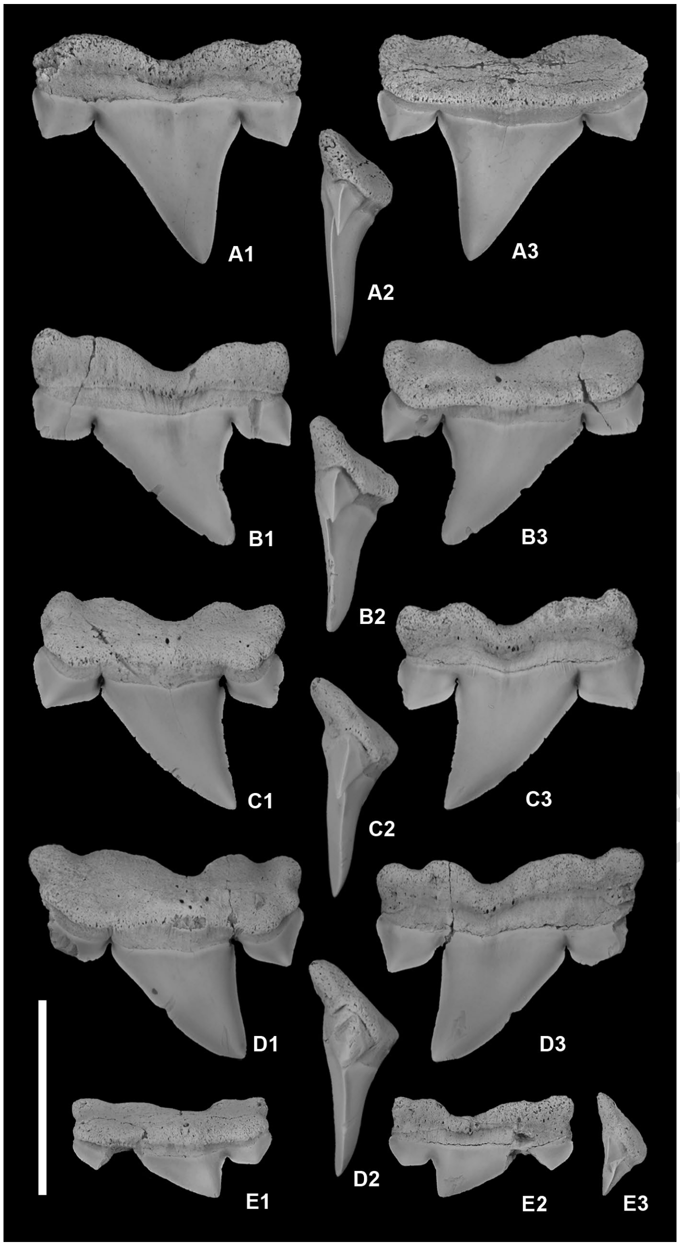


Fig. 6. *Cretalamna sarcoportheta* sp. nov., posteriorly situated upper lateroposterior teeth, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen locality, Kristianstad Basin, southern Sweden. All specimens paratypes and prefixed by LO; scale bar represents 10 mm. **A**. 10902 t, left LP5?; labial (A$_1$), profile (A$_2$), and lingual (A$_3$) views. **B**. 10903 t, left LP6?; labial (B$_1$), profile (B$_2$), and lingual (B$_3$) views. **C**. 10904 t, right LP7?; lingual (C$_1$), profile (C$_2$), and labial (C$_3$) views. **D**. 10905 t, right LP7?; lingual (D$_1$), profile (D$_2$), and labial (D$_3$) views. **E**. 10906 t, right LP9?; lingual (E$_1$), labial (E$_2$), and profile (E$_3$) views.

and a broader, more angular distal lobe. The mesial lobe is markedly compressed labiolingually (Fig. 5A$_2$), presumably a result of a position adjacent to an intermediate bar. The root is likewise asymmetrical in the second upper lateroposterior tooth, featuring a sub-quadrangular distal lobe and a more acute mesial lobe. Putative second upper lateroposterior teeth have a straight to slightly concave profile view (Fig. 5B$_4$, C$_2$). As reconstructed (Fig. 19C), the root becomes increasingly more symmetrical moving posteriorly through the upper jaw files and reaches near-perfect symmetry in the middle part of the lateroposterior row (Fig. 5G$_2$). Posteriorly, beyond this point, the root becomes increasingly more asymmetrical again exhibiting an enlarged mesial lobe (Fig. 6D$_1$). The cusp is slightly distally inclined in the mesial half of the files and distally curved rather than inclined in most teeth in the posterior half of the lateroposterior files. In basal view, the distal lobe of the root is typically compressed, relative to the mesial lobe, in anteriorly situated upper lateroposterior teeth (Fig. 5B$_2$, E$_1$, F$_1$).

First lower anterior tooth file.—A near perfectly preserved tooth along with an incomplete specimen, in addition to several less well preserved teeth, are referred to the first lower anterior tooth file (Fig. 7A, B). The well preserved tooth is a nearly 19 mm high, symmetrical tooth. The tightly curved basal edge of the root and the symmetry of the specimen indicate that it originates from the first anterior file. One of its lateral cusplets is rudimentary whereas the other one is small but well formed. The tooth is assigned to the first lower rather than the first upper anterior file on the basis of its massive root with a large lingual protuberance and a somewhat lingually curved cusp, although the difference in curvature of the cusp in profile view between inferred upper and lower anterior teeth is relatively minor in this species. As far as can be determined from its incomplete preservation, the other tooth referred to this position is very similar to the complete tooth.

Second lower anterior tooth file.—A large, incomplete tooth (additional to several other, even more incomplete teeth) is referred to this file (Fig. 7C). As preserved, the tooth measures just over 21 mm in height and would have been about 22 mm high originally. The distal portion of the mesial lobe of the root is incomplete but the tooth is otherwise well preserved. The cusplets are divergent and larger than those of the other anterior teeth. The massive cusp is distally bent and the preserved distal lobe of the root is rectangular. The neck is relatively narrow as in other anterior teeth of this species. The basal edge of the root is v-shaped. The lingual protuberance of the root is prominent.

Lower lateroposterior tooth files.—The most mesially located lower lateroposterior teeth feature a distally directed cusp (e.g. Fig. 8C$_1$). Moving posteriorly through the lower jaw teeth the cusp becomes progressively lower and more symmetrical. The root is markedly asymmetrical in the first two or three lateroposterior files, with a short, rounded to quadrangular distal lobe and an elongated tapering mesial lobe, but becomes increasingly more symmetrical in more posteriorly situated teeth. The lower lateroposterior teeth differ from upper lateroposterior teeth by their straight to lingually curved labial face of the cusp in profile view (as opposed to a straight to labially curved labial face) and generally more upright cusp.

Comparison.—See the description of *C. appendiculata* above for a comparison with the closely related *C. sarco-*

portheta sp. nov.

The teeth of *C. sarcoportheta* sp. nov. differ in several aspects from those of the coexisting *C. borealis*. The teeth of the latter species reach a much larger size, with anterior teeth measuring up to an estimated 38-40 mm in height in the Kristianstad Basin population (Fig. 9A) compared to about 23 mm (first upper anterior tooth) for a much larger sample of *C. sarcoportheta* sp. nov. teeth. The anterior teeth of *C. sarcoportheta* sp. nov. have a comparatively short, robust cusp (Fig. 19C) and a massive root (e.g. Fig. 7A$_3$), whereas the cusp is very tall and relatively slender in small to medium-sized (relatively speaking) anterior teeth of *C. borealis* (Fig. 9B, C). Scaled down in size to the same height as the anterior teeth of *C. sarcoportheta* sp. nov., anterior teeth of *C. borealis* up to about 32-33 mm in height are gracile by comparison. Above that size the cusp becomes broader in *C. borealis* and the root increases exponentially in thickness approaching maximum tooth height/width in both anterior and lateroposterior teeth. The cusp on teeth of *C. borealis* has typically a more convex labial face than in teeth of *C. sarcoportheta* sp. nov. This is taken to the extreme in earliest early Campanian *C. borealis* (*Gonioteuthis granulataquadrata* Zone, conglomerate C, Ullstorp 1 quarry; see Lindgren et al. 2007: 930) in which the labial face is occasionally more convex than the lingual face in some of the lager lateroposterior teeth. The lateral cusplets are often more divergent in *C. borealis* and the inner edge is commonly strongly convex (Fig. 9D$_2$, E$_4$). In basal view the root is rectangular in upper lateroposterior teeth of *C. borealis* (Fig. 9D$_1$) but asymmetrical with a compressed distal lobe (compressed mesial lobe in inferred LP1) in the majority of anteriorly situated upper lateroposterior teeth of *C. sarcoportheta* (Fig. 5B$_2$, E$_1$, F$_1$).

Agassiz's (1843) '*Otodus*' *latus* (*sensu* Herman 1977) is clearly a distinct, Maastrichtian species. However, it needs to be defined on the basis of homogeneous material, collected from a narrow stratigraphical interval, from northwest Europe. Its teeth are larger in absolute terms and wider in relative terms than are those of latest early Campanian *C. sarcoportheta* sp. nov. The cusplets are lower and, on average, smaller in the Maastrichtian species and they may lack a well-defined apex (Herman, 1977: pl. 9: 4c). The mesial and distal lobes of the root in lateroposterior teeth are sepa-

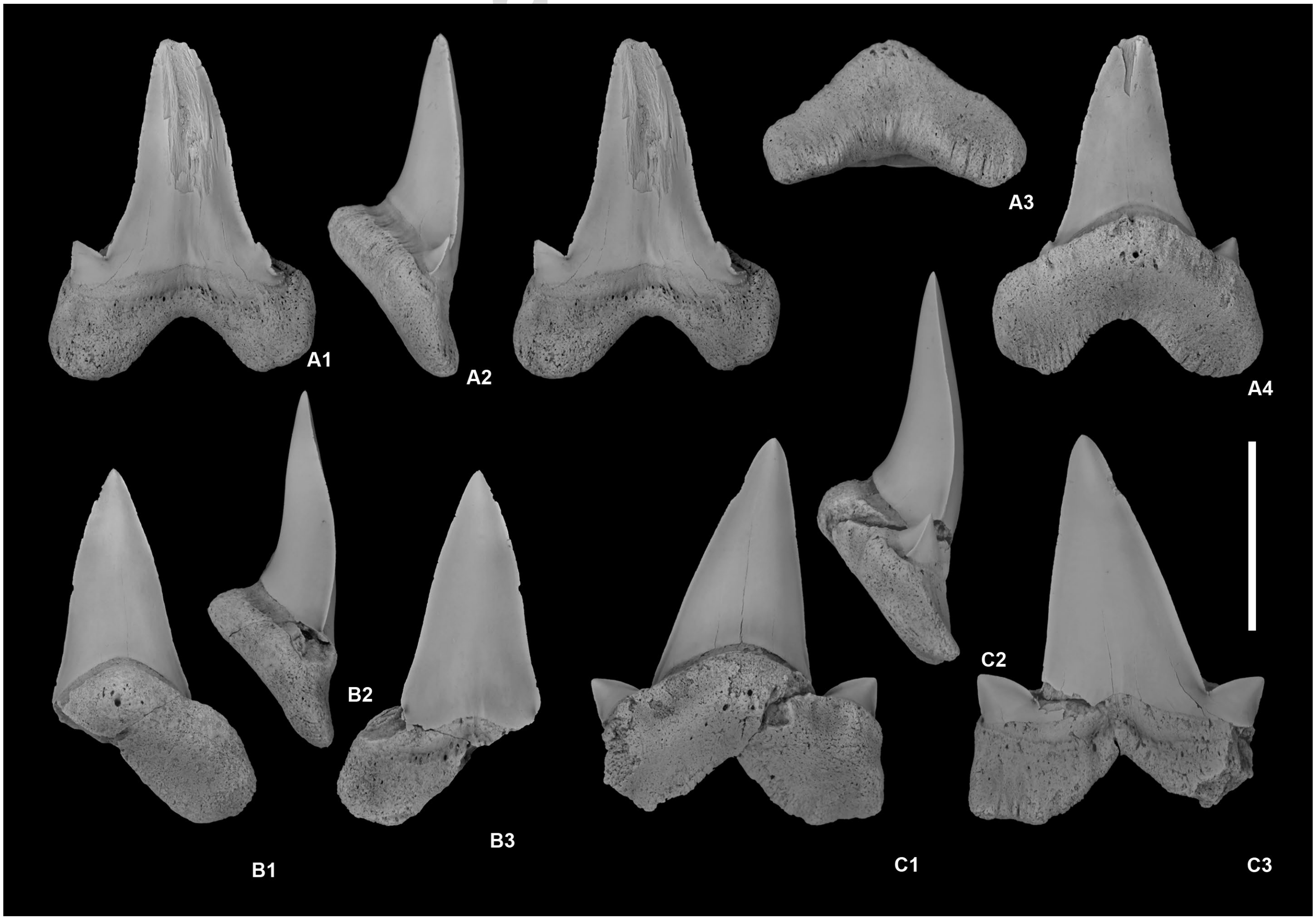
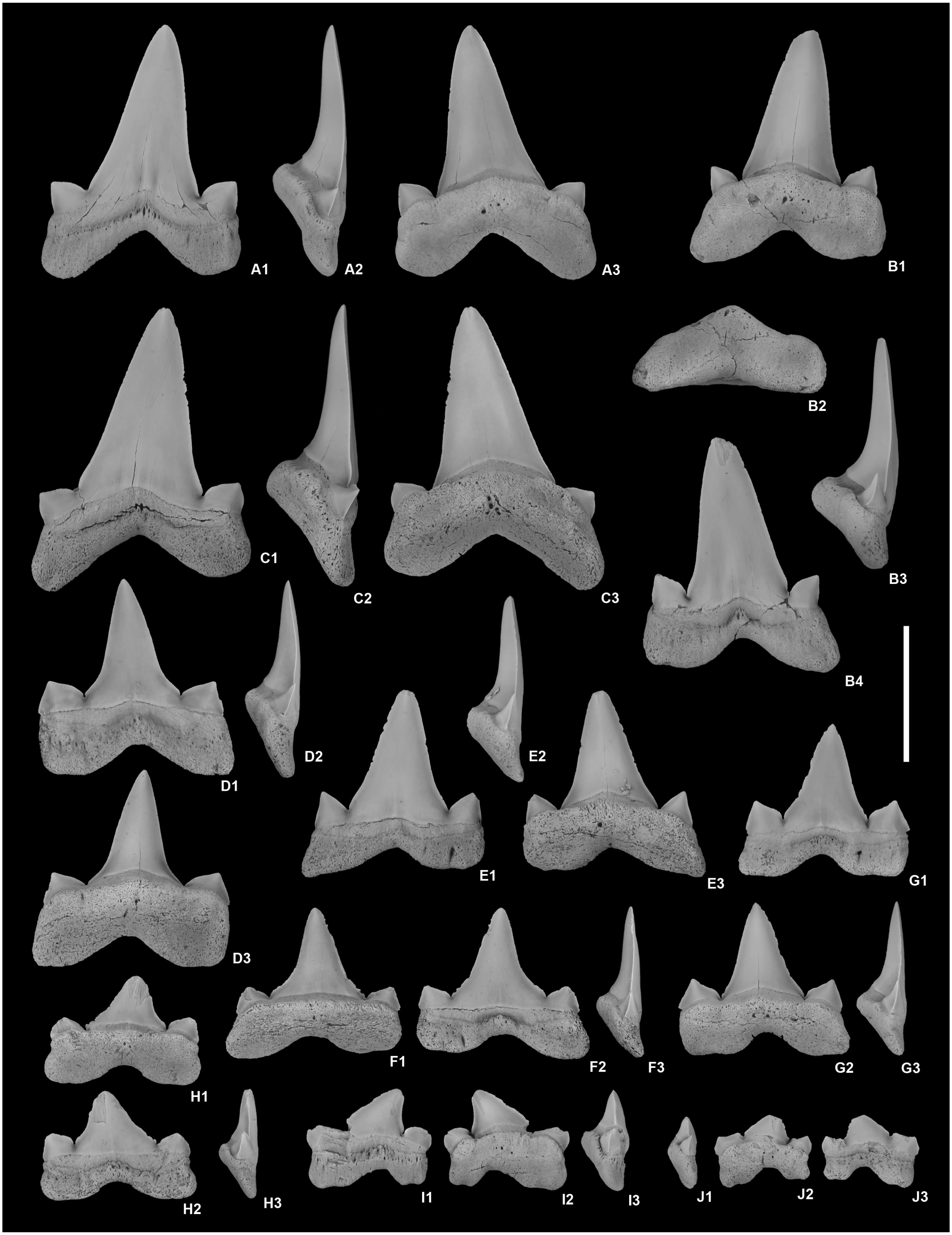


Fig. 7. *Cretalamna sarcoportheta* sp. nov., lower anterior teeth, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen locality, Kristianstad Basin, southern Sweden. All specimens paratypes and prefixed by LO; scale bar represents 10 mm. **A**. 10907 t, left a1?; labial (A$_1$), profile (A$_2$), basal (A$_3$), and lingual (A$_4$) views. **B**. 10908 t, right a1?; lingual (B$_1$), profile (B$_2$), and labial (B$_3$) views. **C**. 10909 t, right a2?; lingual (C$_1$), profile (C$_2$), and labial (C$_3$) views.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rated by a rather conspicuous median indentation in *C. sarcoportheta* sp. nov., whereas the median indentation is rather shallow in *C. lata*. Although it is probable that *C. lata* belongs to the *C. appendiculata* group it is in need of revision.

Cretalamna sarcoportheta sp. nov. differs from *C. arambourgi* Cappetta and Case (1975) from the Danian? of Youssoufia, Morocco, by having upper anterior teeth with a broader cusp relative to the width of the root and a more protruding lingual protuberance in profile view (compare Fig. 2 and Arambourg, 1952: pl. 14: 1, 14), lower anterior teeth with a wider cusp and more robust root (compare Fig. 5 and Arambourg, 1952: pl. 14: 12, 13), and a shallower median indentation of the basal edge of the root in both anterior and lateroposterior teeth. Several of the lateroposterior teeth illustrated by Arambourg (1952) have a second, minute pair of lateral cusplets whereas almost all lateroposterior teeth of *C. sarcoportheta* sp. nov. have only a single pair of cusplets.

Remarks.—The reconstruction of the lateroposterior part of the dentition in *C. sarcoportheta* sp. nov. with ten upper jaw tooth files (LP10 not shown in Fig. 19C as all presumed LP10s available to us are poorly preserved) is based on anterior/lateroposterior tooth ratios for the collected material from the Åsen locality and should be regarded as nothing more than a rough approximation.

The synonymy list is restricted to records near the early/late Campanian boundary of northwest Europe. All previous reports of isolated teeth of *C. appendiculata* type need re-evaluation. Siverson (1992*a*) noted the presence of low-cusped, small *Cretalamna* teeth (i.e. *C. sarcoportheta* sp. nov.) co-occurring with large, tall-cusped *Cretalamna* teeth (i.e. *C. borealis*) in the *B. mammillatus* zone of the Kristianstad Basin. In order to accommodate both morphologies within the accepted species concept of *C. appendiculata* of that time, Siverson (1992*a*) envisioned a somewhat unlikely ontogenetic development whereby the cusp grew relatively slimmer with increasing age of the shark.

The late Campanian/early Maastrichtian teeth from New Jersey, USA, illustrated as *C. appendiculata lata* by Cappetta and Case (1975: pl. 3: 10-27) are close in morphology and tooth-type range to *C. sarcoportheta* sp. nov. In the absence of a thorough revision of the dentally similar *C. lata* and precise stratigraphical data for the New Jersey material, it is probably unproductive to elaborate any further on the identification. The same applies to the vast majority of previous records of *Cretalamna* of *C. appendiculata* type, as these accounts invariably lack teeth with pristine root preservation illustrated in basal and profile views (the most diagnostic views in this group of sharks as long as the root is perfectly preserved).

Cretalamna borealis (Priem, 1897)

Figs. 9-10

Lamna appendiculata [*partim*]; Priem 1897: 40, pl. 1: 4.

Lamna borealis; Priem 1897: 41, pl. 1: 9.

Cretolamna appendiculata var. *pachyrhiza* [*partim*]; Herman 1977: 210, pl. 9: 3a-d [*non* fig. 3e (*C. sarcoportheta* sp. nov.), 3g-f (undescribed *Cretalamna* and/or *Otodus* ex gr. *obliquus*)].

Cretolamna borealis; Glikman 1980: pl. 10: 12 and pl. 21: 1-5.

Cretolamna appendiculata pachyrhiza; Lauginiger and Hartstein 1983: 31, pl. 2:11-14.

Cretolamna appendiculata [*partim*]; Siverson 1992*a*: 528, pl. 1: 5-8 [*non* figs. 1-4 and 9-11 (*Cretalamna sarcoportheta* sp. nov.)].

Cretolamna sp.; Vullo 2005: 620, fig. 4S, T.

Lectotype: An upper lateroposterior tooth, illustrated by Priem 1897: pl. 1: 9.

Type horizon: Unknown horizon within the latest early to middle late Campanian (see Christensen 1986)

Type locality: Köpinge Sandstone, Scania, Sweden.

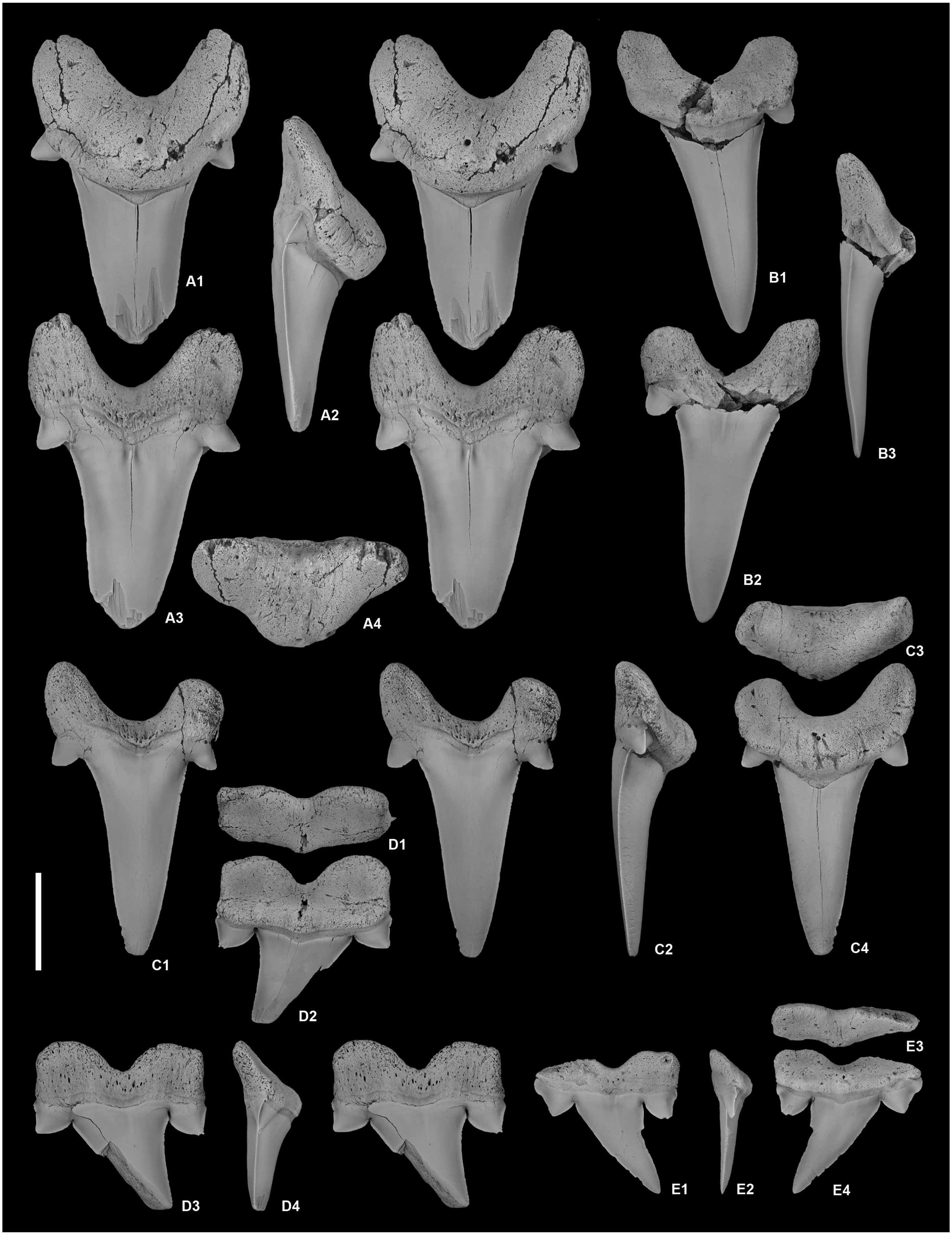
Material: Eleven teeth from Åsen (LO 6349 *t*, LO 11135 *t* – 11142 t, LO 11350 *t*, WAM 13.5.22), two teeth from Ugnsmunnarna (WAM 13.5.20-21), and one tooth from Ignaberga (LO 6350 *t*), Kristianstad Basin, southern Sweden (latest early Campanian). An upper lateroposterior tooth of *C. borealis* (LO 11351 *t*) from the older, earliest early Campanian *Gonioteuthis granulataquadrata* Zone (conglomerate C, Ullstorp 1 quarry; Lindgren et al. 2007, p. 930) is also included for comparative purpose as it represents a small, juvenile tooth, demonstrating the difference in cusp width between teeth of comparable size of *C. borealis* and the dentally similar *C. gertericorum* sp. nov.

Emended diagnosis.—Anterior teeth elongated and flanked by pair of relatively small, commonly rounded and strongly divergent cusplets. Labial face of cusp almost as convex as lingual face in most lateroposterior teeth. Large, vertical folds commonly present in the basal part of the labial face of the cusp in lateroposterior teeth. Cusplets large on lateroposterior teeth and typically with convex inner edge and concave outer edge. Root rectangular and symmetrical with a small but relatively well demarcated protuberance in basal view in most lateroposterior teeth.

Description

First upper anterior tooth file.—One tooth is referred to the

← Fig. 8. *Cretalamna sarcoportheta* sp. nov., lower lateroposterior teeth, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen locality, Kristianstad Basin, southern Sweden. All specimens paratypes and prefixed by LO; scale bar represents 10 mm. **A**. 10910 t, left lp1?; labial (A$_1$), profile (A$_2$), and lingual (A$_3$) views. **B**. 10911 t, right lp1?; lingual (B$_1$), basal (B$_2$), profile (B$_3$), and labial (B$_4$) views. **C**. 10912 t, left lp1?; labial (C$_1$), profile (C$_2$), and lingual (C$_3$) views. **D**. 10913 t, right lp4?; labial (D$_1$), profile (D$_2$), and lingual (D$_3$) views. **E**. 10914 t, left lp2?; labial (E$_1$), profile (E$_2$), and lingual (E$_3$) views. **F**. 10915 t, right lp5?; lingual (F$_1$), labial (F$_2$), and profile (F$_3$) views. **G**. 10916 t, left lp4?; labial (G$_1$), lingual (G$_2$), and profile (G$_3$) views. **H**. 10917 t, right lp5?; lingual (H$_1$), labial (H$_2$), and profile (H$_3$) views. **I**. 10918 t, left lp7?; labial (I$_1$), lingual (I$_2$), and profile (I$_3$) views. **J**. 10919 t, right lp8?; profile (J$_1$), lingual (J$_2$), and labial (J$_3$) views.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E4

first upper right anterior file (Fig. 9A). As preserved it measures 32 mm in height. Both tips of the root lobes are damaged, resulting in a reduction of the tooth height by an estimated 1-2 mm. The cusp is, as is typical for teeth of this species found in near-shore strata of the Fennoscandian Shield, heavily worn from prey manipulation, resulting in a further reduction of the original height by an estimated 5-6 mm. The original height is thus an estimated 38-40 mm. The tall cusp is slightly distally curved. Its labial base is flush with the labial face of the root (Fig. 9A_3). Both cusplets have a rounded, poorly defined apex and are divergent, especially the mesial one. The basal edge of the massive root is tightly curved. Both elongated lobes are labiolingually compressed. The root is rather symmetrical in labial/lingual views but asymmetrical in basal view, with a more compressed distal lobe.

Second upper anterior tooth file.—Three teeth are referred to this file. The better preserved ones are illustrated and described. The larger right tooth (Fig. 9B) measures 32.5 mm in height, whereas the slightly smaller, left tooth (Fig. 9C) measures 30 mm in height. The latter has a somewhat worn apex and would have been about 1 mm taller originally. The left tooth is virtually complete whereas the larger right tooth is missing the mesial cusplet and part of the lingual protuberance of the root. In profile view, both teeth exhibit a slightly lingually curved cusp (Fig. 9B_3, C_2). The cusplets are divergent on both teeth and the cusp is somewhat distally inclined with a very slightly recurved apex. The root is asymmetrical with a longer mesial lobe. The well demarcated lingual protuberance of the root occupies a rather small area at the centre of the root's lingual face.

Third upper anterior tooth file.—There is no A3 available with the root preserved intact amongst the teeth from the *B. mammillatus* zone of the Kristianstad Basin. However, a poorly preserved tooth from the Ugnsmunnarna site (WAM 13.5.20, estimated original height 30 mm) features a relatively broad cusp, recurved in labial/lingual views and labially curved in profile view (similar to the cusp of the A3 in *C. ewelli* sp. nov.; Fig. 12E). The tooth is not illustrated herein because of the very poor root preservation. Several additional teeth of *C. borealis* from Ugnsmunnarna (Peter Cederström collection) are likewise poorly preserved, an inconvenient fact given that the species appears to be relatively common at this site. We have seen photographs of a well-preserved A3 tooth (private collection) of *C. borealis* from the *O. pilula* Zone, Beauval quarry, northern France, displaying a cusp comparable to that of the tooth from Ugnsmunnarna and an asymmetrical root with the mesial lobe longer and narrower than the distal lobe (very similar to that of the A3 in *K. gunsoni*; Fig. 23C).

Upper lateroposterior tooth files.—Anteriorly situated upper lateroposterior teeth have a triangular cusp, slightly distally inclined in labial/lingual views and straight in profile view. The root is markedly asymmetrical with a short, angular and broad distal lobe and a more elongated and acute mesial lobe (WAM 13.5.22). The median indentation of the basal edge of the root is V-shaped. More posteriorly situated teeth have a distally curved cusp (Fig. 9D, E). The lateral margins of the lobes of the root are typically vertical (Fig. 9D_3). The lateral

Fig. 10. *Cretalamna borealis* (Priem, 1897), lower jaw teeth, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen (11137 t) and Ignaberga quarry (6350 t), Kristianstad Basin, southern Sweden. Both specimens prefixed by LO; scale bar represents 10 mm. **A**. LO6350 t, right a1?; lingual (A_1), profile (A_2), labial (A_3), and basal (A_4) views. **B**. 11137 t, left lateroposterior tooth; labial (B_1), profile (B_2), and lingual (B_3) views.

←

Fig. 9. *Cretalamna borealis* (Priem, 1897), upper jaw teeth. **A-D**, *Belemnellocamax mammillatus* zone (latest early Campanian), Åsen locality. **E**, *Gonioteuthis granulataquadrata* Zone (earliest early Campanian), conglomerate C, Ullstorp 1 quarry. Both localities within the Kristianstad Basin, southern Sweden. All specimens prefixed by LO; scale bar represents 10 mm. **A**. 11350 t, right A1? from a very large individual; lingual (A_1), profile (A_2), labial (A_3), and basal (A_4) views. **B**. 6349 t, right A2?; lingual (B_1), labial (B_2), and profile (B_3) views. **C**. 11135 t, left A2?; labial (C_1), profile (C_2), basal (C_3), and lingual (C_4) views. **D**. 11136 t, left lateroposterior tooth; basal (D_1), lingual (D_2), labial (D_3), and profile (D_4) views. **E**. 11351 t, left lateroposterior tooth from a juvenile individual; labial (E_1), profile (E_2), basal (E_3), and lingual (E_4) views.

cusplets are large and most have a convex inner cutting edge and a concave outer edge (Fig. 9D$_2$). The labial face of the cusp may have strong vertical folds (LO 11139 *t*). Commissural teeth are moderately elongated in a mesiodistal direction and have a strongly distally curved cusp (LO 11140 *t*).

First lower anterior tooth file.—A well preserved, 32.5 mm high tooth has features typical for the first lower anterior file in modern macrophagous lamniform sharks and is therefore assigned to this tooth-position (Fig. 10A). The cusp is almost perfectly straight in labial/lingual views and rather thick compared to the cusp on the two illustrated second upper anterior teeth. In profile view the cusp is moderately lingually curved. The cusplets are sub-triangular, divergent and have a blunt apex. The root is robust and nearly symmetrical with rather acute lobes. The lingual protuberance of the root is broad in basal view.

Lower lateroposterior tooth files.—Teeth assigned to the inferred lower lateroposterior hollow differ from upper lateroposterior teeth in having a cusp that is more upright and more-or-less lingually curved in profile view. Like in the upper jaw, some lower lateroposterior teeth have coarse, vertical folds in the lower part of the labial face of the cusp (WAM 13.5.21).

Comparison.—Teeth of *C. borealis* most closely resemble those of the other two species referred herein to the *C. borealis* group; *C. gertericorum* sp. nov. and *C. ewelli* sp. nov. This species group is characterised by the elongated anterior teeth, an A3 type with a cusp that is recurved in labial/lingual views (Fig. 12E$_1$) and labially curved in profile view (Fig. 12E$_2$), strongly lingually curved lower anterior teeth in profile view (Figs. 10A$_2$, 11F$_2$), often rectangular root in basal view in lateroposterior teeth (Figs. 9D$_1$, 11G$_3$) with a small but well demarcated protuberance (Figs. 9D$_1$, E$_3$, 11G$_3$, 12F$_4$), and moderately laterally expanded commissural teeth (Fig. 11E). Posteriorly situated upper lateroposterior teeth are greatly elongated in a mesiodistal direction in species of the *C. appendiculata*- and *C. hattini* groups (Figs. 6E, 16E-H, 17L, M, 18E).

Although the second upper anterior tooth of *C. gertericorum* sp. nov. (Fig. 11A) is inseparable from the A2s of *C. borealis*, the first lower anterior tooth at hand of the former is more slender (Fig. 11F) than is the corresponding tooth of *C. borealis* (Fig. 10A). The latter is admittedly a larger tooth (13 per cent wider root), but the difference in size may not be enough to explain the marked difference in slenderness as part of the ontogenetic change in *C. borealis*-group species. The upper lateroposterior teeth of *C. gertericorum* sp. nov. differ from those of *C. borealis* by e.g. their more labially curved cusp in profile view (Figs. 9D$_4$, E$_2$, 11B$_2$, D$_2$, E$_2$) and differently shaped cusplets. In *C. borealis* the inner edge is typically convex whereas the outer edge is concave (Fig. 9D$_3$, E$_1$; Priem 1897: pl. 1: 4, 9; Lauginiger and Hartstein 1983: pl. 2: 14). In contrast, the average *C. gertericorum* sp. nov. tooth shows little difference in curvature between the inner and outer edges of the cusplets (Fig. 11B, C). In lateroposterior teeth of the same size (presumably adult *C. gertericorum* sp. nov. and juvenile *C. borealis*) the cusp is considerably broader in *C. gertericorum* sp. nov. (Fig. 11C$_2$) than it is in *C. borealis* (Fig. 9E$_1$). The widening of the cusp is thus related to the ontogenetic stage in these two species rather than to absolute tooth size.

First and second upper anterior teeth of *C. ewelli* sp. nov. differ from those of *C. borealis* by their smaller, less divergent cusplets (the relative size of the cusplets does, however, overlap between the two species) and awl-shaped cusp (Fig. 12B$_1$). In *C. borealis*, the cusp is labiolingually compressed in first and second upper anterior teeth to a much larger degree than it is in *C. ewelli* sp. nov. The awl-shaped cusp in first and second upper anterior teeth does not appear to simply be a juvenile feature in *C. ewelli* sp. nov. as this cusp shape is most pronounced in the largest anterior tooth at hand (Fig. 12B).

See the comparison section for *C. sarcoportheta* sp. nov. regarding dental differences between this species and *C. borealis*.

Remarks.—Priem (1897) described ‘*Lamna*’ *borealis* on the basis of a large, upper lateroposterior tooth from the ‘chalk’ yielding *Belemnitella mucronata* at Köping (= Stora Köpinge), Skåne, southern Sweden and on another, even larger upper lateroposterior tooth from the Faxe quarry (NP3 Zone, Danian), Demark, illustrated as *Otodus appendiculatus* by Davis (1890: pl. 41: 4). The tooth from Köpinge is here designated as lectotype. The designation is warranted because we have seen no evidence indicating that any species of *Cretalamna* of Campanian age ranges into the Danian stage. Unpublished otodontid material from the Danian (NP3 Zone) of the Limhamn quarry, Scania, southern Sweden, includes a large-toothed *Cretalamna* species (same taxon as the Faxe tooth above) probably closely related to *C. borealis* but nonetheless readily separable from the latter (e.g. lateral cusplets are much larger in anterior teeth of the Danian species and the median indentation of the basal edge of the root is considerably wider and deeper in lateroposterior teeth with a well-preserved root of this taxon). The selection of the Campanian tooth as lectotype rather than the Danian specimen from the Faxe quarry is based on the fact that the description by Priem (1897) is based primarily on the Campanian specimen.

The ‘chalk’ in the Köpinge area is in fact a highly calcareous sandstone (‘Köpinge sandstone’) and ranges in age (on the basis of abundant belemnites and ammonites) from the latest early Campanian to the middle late Campanian (Christensen 1986: 9).

The basal third of the labial face of the cusp in the lectotype is heavily wrinkled. This feature is present in two of the registered specimens from the *B. mammillatus* zone of the Kristianstad Basin; one upper lateroposterior tooth from Åsen (LO 11139 t) and one lower lateroposterior tooth from Ugnsmunnarna (WAM 13.5.21). These teeth are not illustrated herein because of their poor state of preservation (severely abraded root). The mesial, well-preserved lateral margin of the root in the lectotype is vertical and the cusp is tall (for a lateroposterior position) and strongly distally curved. The inner edge of the cusplets is convex whereas the outer edge is straight or slightly concave. The tooth is inseparable at species level from upper lateroposterior teeth of a similar jaw position (middle part of the inferred upper lateroposterior hollow) referrable to a second species (besides *C. sarcoportheta* sp. nov.) of *Cretalamna* in the early Campanian of southern Sweden. The Kristianstad Basin specimens share two or more of the following characters that can be observed in the lectotype: (1) vertical lateral margin of one or both lobes of the root (Fig. 9D$_3$, E$_4$); (2) convex inner edge and straight or concave outer edge on one or both lateral cusplets (Fig. 9D$_3$, E$_1$); (3) tall, distally curved rather than distally inclined cusp (Fig. 9E$_1$); (4) coarsely folded basal third of the labial face of the cusp (see above).

Lateroposterior teeth of *C. borealis* type occur together with tall anterior teeth, of a type referred to as *C. appendiculata* var. *pachyrhiza* by Herman (1977), in the *B. mammillatus* zone of the Kristianstad Basin (Fig. 9B, C). The co-occurrence of upper lateroposterior teeth of *C. borealis* type with anterior teeth of *C. appendiculata* var. *pachyrhiza* type indicates that the nominal *C. appendiculata* var. *pachyrhiza* is a junior synonym of *C. borealis*. Herman and Van Waes (2012) 'elevated' the variety *pachyrhiza* (which, as such, is not regulated by the Code as it was published as a 'variété' after 1960; ICZN 15.2) to species level although they used a slightly different spelling (*Cretalamna pachyrhyza*) and inadvertently referred to Herman's (1977) illustrations of *C. lata* (Agassiz, 1843) rather than to his *C. appendiculata* var. *pachyrhiza*. As the nominal *C. pachyrhyza* lacks a defined holotype or syntypes it will not be considered further here.

Cretalamna borealis has consistently been regarded as a valid species over the last 30 years by Russian students. Glikman (1980) correctly grouped large, upper lateroposterior teeth (Glikman 1980: pl. 21: 2, 3) of *C. borealis* type from Campanian deposits in the Kyzyl Kum desert with a tall upper anterior tooth (Glikman 1980: pl. 21: 4) of *C.* '*appendiculata* var. *pachyrhiza*' type from the same deposit. Averianov and Popov (1995) listed *C. borealis* from a phosphatic conglomerate near the village of Shyrokyi Karamysh, approximately 50 km west of Saratov, Russia. On the basis of a molluscan assemblage, they assigned a late early Campanian age to this unit. One of us (MS) collected *C. borealis* from this horizon in 1997. In a study of Campanian elasmobranchs from Delaware, USA, Lauginiger and Hartstein (1983) correctly distinguished teeth of *C. borealis* (described by them as *C. appendiculata pachyrhiza*) from the basal Mount Laurel Sand (early late Campanian in the three-fold North American division of the stage) from teeth of *C. appendiculata* group type (described as *C. appendiculata lata*) from the late middle Campanian Marshalltown Formation.

Shimada et al. (2010) described isolated, shed teeth of *Cretalamna* (referred to as *C. appendiculata*) found in direct association with a plesiosaur skeleton (holotype of *Futabasaurus suzukii*) in the early Santonian Tamayama Formation, central Japan. The illustrations of 82 shed teeth indicate the presence of more than one species of *Cretalamna*. One incomplete (apex of cusp appears to be missing) anterior tooth with blunt cusplets (Shimada et al. 2010: fig. 2.41) is similar to the A1 of *C. borealis* (Fig. 9A). Teeth from the middle part of the inferred lateroposterior hollow, typical for species of the *C. borealis* group (strongly distally curved cusp, divergent cusplets and relatively deeply excavated mesial concavity of the basal edge of the root), are represented by at least three specimens illustrated by Shimada et al. (2010: figs. 2.35, 47, 48; compare the latter tooth with the lectotype of *C. borealis*). Two large and broad-bladed lateroposterior teeth (Shimada et al. 2010: figs. 2.43, 2.69) correspond well with teeth from a similar position in *C. hattini* sp. nov. (Fig. 15).

Cretalamna gertericorum sp. nov.

Fig. 11

? *Cretolamna appendiculata* var. *appendiculata* [*partim*]; Herman 1977: 210-216, pl. 9: 2c.

Etymology: Named after Gert De Bie and Eric Collier, who collected most of the *Cretalamna* teeth from the SECAB Quarry, Bettrechies, examined herein.

Type material: Holotype: Lower right, posteriorly situated lateroposterior tooth, UM-BET 5; Fig. 11G. Paratypes: WAM 13.5.8-12, UM-BET 4; Fig. 11A-F.

Type horizon: Conglomeratic pocket (with black pebbles and fish coprolites) in the basal part of the grey-coloured *Mytiloides labiatus* Zone.

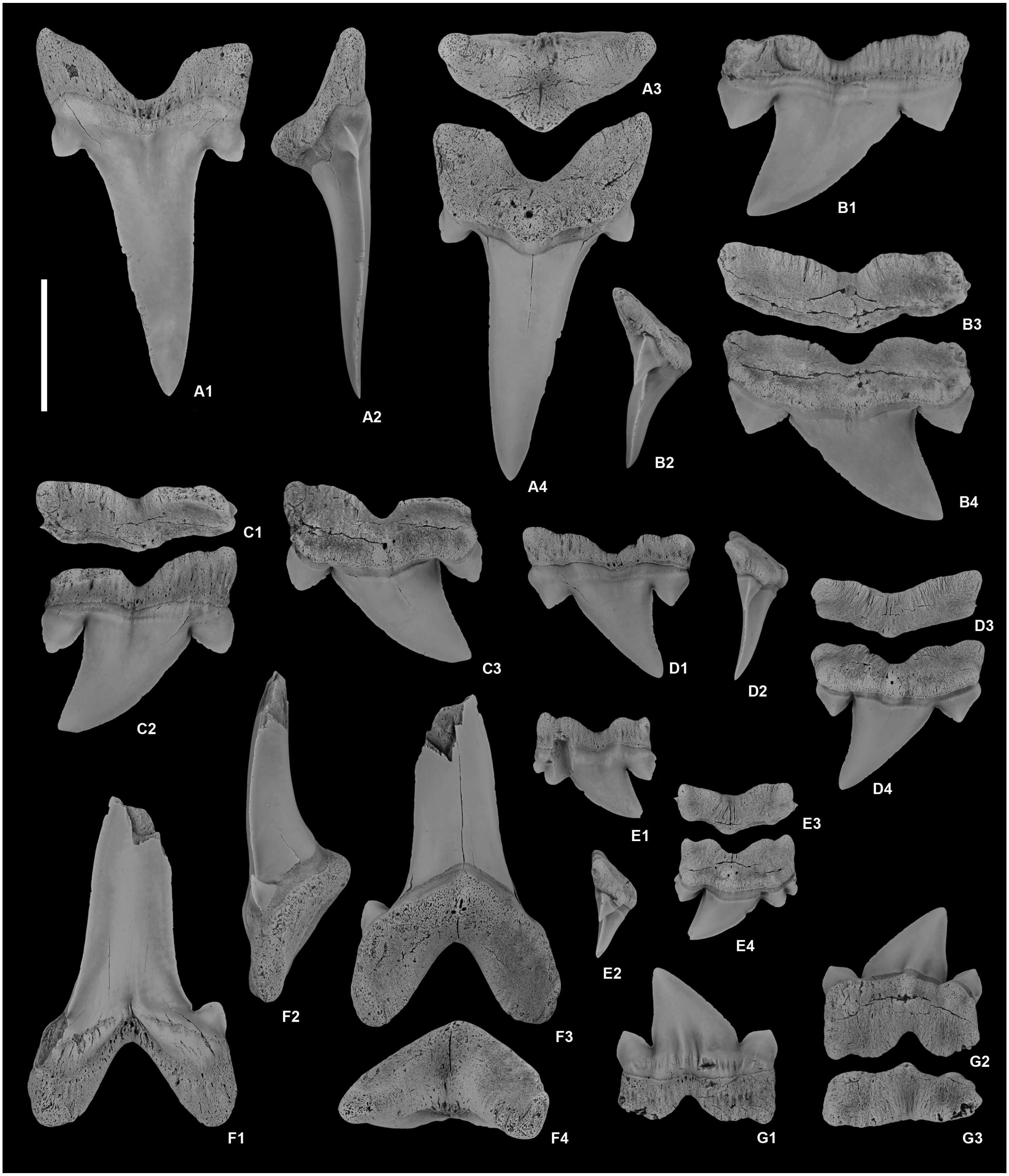
Type locality: SECAB quarry, Bettrechies, northern France.

Diagnosis.—Anterior teeth with slender, elongated cusps. Basal view of root triangular in upper and lower anterior teeth. Upper lateroposterior teeth from posterior half of inferred lateroposterior hollow with concave labial profile and broad, strongly distally curved cusp in labial/lingual views. Cusplets relatively upright in lateroposterior teeth but divergent in anterior teeth. Median indentation of basal edge of root small and tightly curved in lateroposterior teeth.

Description

Second upper anterior tooth file.—A complete tooth, 27 mm high, is referred to the A2 position (Fig. 11A). The cusp is elongated and distally inclined in labial/lingual views. The cutting edges are slightly sigmoidal in profile view. A small, sub-triangular and divergent cusplet is present on either side of the cusp. The root is asymmetrical in labial/lingual views, with the mesial lobe being longer and more slender than the distal lobe. The extremities of both lobes form an acute angle. A rather symmetrical basal view characterises the root, with a triangular lingual protuberance, well demarcated from the rest of the root. The basal face of the root is concave in profile view.

Upper lateroposterior tooth files.—Four teeth included in the study are regarded as upper lateroposterior teeth (Fig. 11B-E). They are most likely derived from the mid- to posterior part of the inferred upper lateroposterior hollow. They range in height from 8-14 mm. The cusp is more-or-less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strongly distally curved and broader in the larger teeth than it is in the smaller ones. The labial side of the tooth is concave in profile in all teeth. The cusplets are relatively large and upright or slightly divergent. The root is asymmetrical in all teeth with the mesial lobe larger than the distal lobe. The median indentation of the basal edge of the root is rather small and tightly curved in the two largest teeth. The lingual protuberance is very small in basal view but well demarcated except in the largest tooth, in which this part of the root is somewhat abraded (Fig. 11B$_3$).

First lower anterior tooth file.—An incomplete tooth is assigned to the a1 position (Fig. 11F). One cusplet and the tip of the cusp are broken off. The breakage surfaces are both fresh looking, without any signs of feeding related, subsequent abrasion. This indicates that the tooth was damaged during extraction from the stratum. As preserved, it measures 24.5 mm in height. The original height is estimated to have been 27-29 mm. The narrow cusp is very slightly inclined in labial/lingual views and labially curved in profile view. The base of the crown forms a rather acute angle medially on the labial side. The remaining cusplet is almost identical in morphology to those of the A2 tooth, displaying a sub-triangular shape with slightly convex cutting edges. The root is nearly perfectly symmetrical, both in labial/lingual and basal views. As in the a1 of *C. borealis* (Fig. 10A), and unlike upper anterior teeth, the lingual protuberance is not well demarcated in basal view (Fig. 11F$_4$). The basal edge of the root is V-shaped.

Lower lateroposterior tooth file.—A single, 11 mm high tooth is referred to the inferred lower lateroposterior hollow (Fig. 11G; holotype). The cusp is triangular and moderately distally inclined. The labial face of the cusp is folded medially in the basal part (a common feature in species of the *C. borealis* group). A sub-triangular, divergent cusplet with convex edges is situated on either side of the cusp. The labial side of the tooth is very slightly concave in profile view. The root is deep and strongly asymmetrical in lingual/labial views with the mesial lobe being much larger than is the distal lobe. The outer edges of the root are straight and vertical and the median indentation of the basal edge is small and U-shaped.

Comparison.—Teeth of *C. gertericorum* sp. nov. most closely resemble those of *C. borealis* and *C. ewelli* sp. nov. The differences between the former two species are outlined above in the description of *C. borealis*. The assigned A2 of *C. gertericorum* sp. nov. (Fig. 11A) differs from the corresponding teeth in *C. ewelli* sp. nov. (Fig. 12B, C) by its considerably more labiolingually compressed cusp. Upper lateroposterior teeth of the former differ from similarly sized ones of *C. ewelli* sp. nov. by their broader cusp (Figs. 11C$_3$, 12D$_3$), more concave labial profile and narrower, more tightly curved median indentation of the basal edge of the root.

Remarks.—Although the anterior teeth are markedly different in *C. gertericorum* sp. nov. and the co-existing *C. appendiculata* and *C. deschutteri* sp. nov. in the *M. labiatus* Zone of the SECAB quarry, lateroposterior teeth may have an overlapping crown morphology in the three species. Many of the examined laterposterior teeth are difficult to identify at species level, as the highly diagnostic root is rarely preserved intact. The lateroposterior teeth of the three species described and illustrated herein do not represent the average state of preservation in the *M. labiatus* Zone but comprise handpicked, unusually well-preserved examples.

Cretalamna ewelli sp. nov.

Fig. 12

Etymology: Named after Keith Ewell, who collected the material in 2004.

Type material: Holotype: First upper left anterior tooth, FHSM VP-18510; Fig. 12A. Paratypes: FHSM VP-18511-18516; Fig. 12C-H.

Type horizon: Between 1-2 m below Hattin's (1982) Marker Unit 2 (late Coniacian).

Type material: Trego County, Kansas, USA (see Appendix 1).

Material: One A2 tooth from the 'Quinter South' site (FHSM VP-18517), collected 0.3 m below the base of MU4; Fig. 12B.

Diagnosis.—Upper anterior teeth with awl-shaped, slightly distally inclined cusp or with broader, recurved cusp. Cusplets minute to moderately large and erect to divergent on upper anterior teeth. Lateroposterior teeth with slender cusp and deep, moderately tightly curved median indentation of basal edge of root. Inner cutting edge of cusplets in lateroposterior teeth typically more convex than outer edge.

Description

First upper anterior tooth file.—A 17.5 mm high tooth is referred to the A1 position (Fig. 12A). The tooth is complete apart from a worn apex and slight weathering damage on one side of the cusp. The cusp is very slender and slightly inclined in labial/lingual views, presumably in a distal direction. It is lingually curved in profile view. The cusplets are very small, divergent and relatively blunt. The root is symmetrical in labial/lingual views but asymmetrical in basal view, with one lobe, presumably the distal one, being more compressed than the other lobe (Fig. 12A$_3$). Although the

← Fig. 11. *Cretalamna gertericorum* sp. nov., *Mytiloides labiatus* Zone (early Turonian), SECAB quarry, Bettrechies, northern France; scale bar represents 10 mm. **A**. WAM 13.5.12, paratype, left A2?; labial (A$_1$), profile (A$_2$), basal (A$_3$), and lingual (A$_4$) views. **B**. UM-BET 4, paratype, right upper lateroposterior tooth; labial (B$_1$), profile (B$_2$), basal (B$_3$), and lingual (B$_4$) views. **C**. WAM 13.5.9, paratype, right upper lateroposterior tooth; basal (C$_1$), labial (C$_2$), and lingual (C$_3$) views. Distal half of distal lobe of root broken off. **D**. WAM 13.5.8, paratype, left upper lateroposterior tooth; labial (D$_1$), profile (D$_2$), basal (D$_3$), and lingual (D$_4$) views. **E**. WAM 13.5.11, paratype, left upper lateroposterior tooth; labial (E$_1$), profile (E$_2$), basal (E$_3$), and lingual (E$_4$) views. **F**. WAM 13.5.10, paratype, a1?; labial (F$_1$), profile (F$_2$), lingual (F$_3$), and basal (F$_4$) views. **G**. UM-BET 5, holotype, right lower lateroposterior tooth; labial (G$_1$), lingual (G$_2$), and basal (G$_3$) views.


A1
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A3
A4
B1
B2
B3
B4
C1
C2
C3
C4
D1
D2
D3
E1
E2
E3
E4
F1
F2
F3
F4
G1
G2
G3
G4
H1
H2
H3
H4

strongly lingually curved cusp in profile view is a characteristic feature in lower anterior teeth of the *C. borealis* group, the well demarcated lingual protuberance in basal view and the relatively straight labial root/crown boundary indicate that the tooth is derived from an upper anterior file.

Second upper anterior tooth file.—Two teeth are referred to the A2 position. One is complete and measures 20.5 mm in height (Fig. 12C). The second tooth is considerably larger than the other specimen, measuring 25 mm in height, and is missing the mesial cusplet (Fig. 12B). It is also somewhat younger as it was collected from a stratum just below MU4 (the other tooth was collected below MU2). The cusp is awl-shaped, especially in the larger tooth, and moderately distally inclined. The tip of the cusp is very slightly recurved. The cusplets are erect (in the largest tooth) or divergent and minute (the largest tooth) to moderately large. The cusp is somewhat sigmoidally curved in profile view (Fig. 12B$_2$, C$_3$). The root is gracile (the smaller tooth) to robust (the larger tooth) and moderately asymmetrical in labial/lingual views with the mesial lobe being more elongated and longer than the distal lobe.

Third upper anterior tooth file.—One complete tooth, 18 mm high, is assigned to the A3 file (Fig. 12E). The cusp is relatively broad, labiolingually compressed (compared with that of the A1 and A2 teeth) and distally inclined but with a markedly recurved apex. It is strongly labially curved in profile view (Fig. 12E$_2$). The relatively small cusplets are sub-triangular and divergent. The root is asymmetrical in labial/lingual views with a longer but narrower mesial lobe. The lingual protuberance is well demarcated in basal view. The distal lobe is more labiolingually compressed than is the mesial lobe.

Upper lateroposterior tooth files.—An incomplete tooth (mesial lobe of the root broken off), 12.5 mm high, is referred to the middle part of the inferred upper lateroposterior hollow (Fig. 12D). The cusp is strongly distally curved and slender. The median indentation of the basal edge of the root is relatively deep and U-shaped. A more-or-less rectangular outline characterises the root in basal view (Fig. 12D$_2$). The lingual protuberance is small but relatively well-defined in basal view. The lobes of the root are strongly labiolingually compressed.

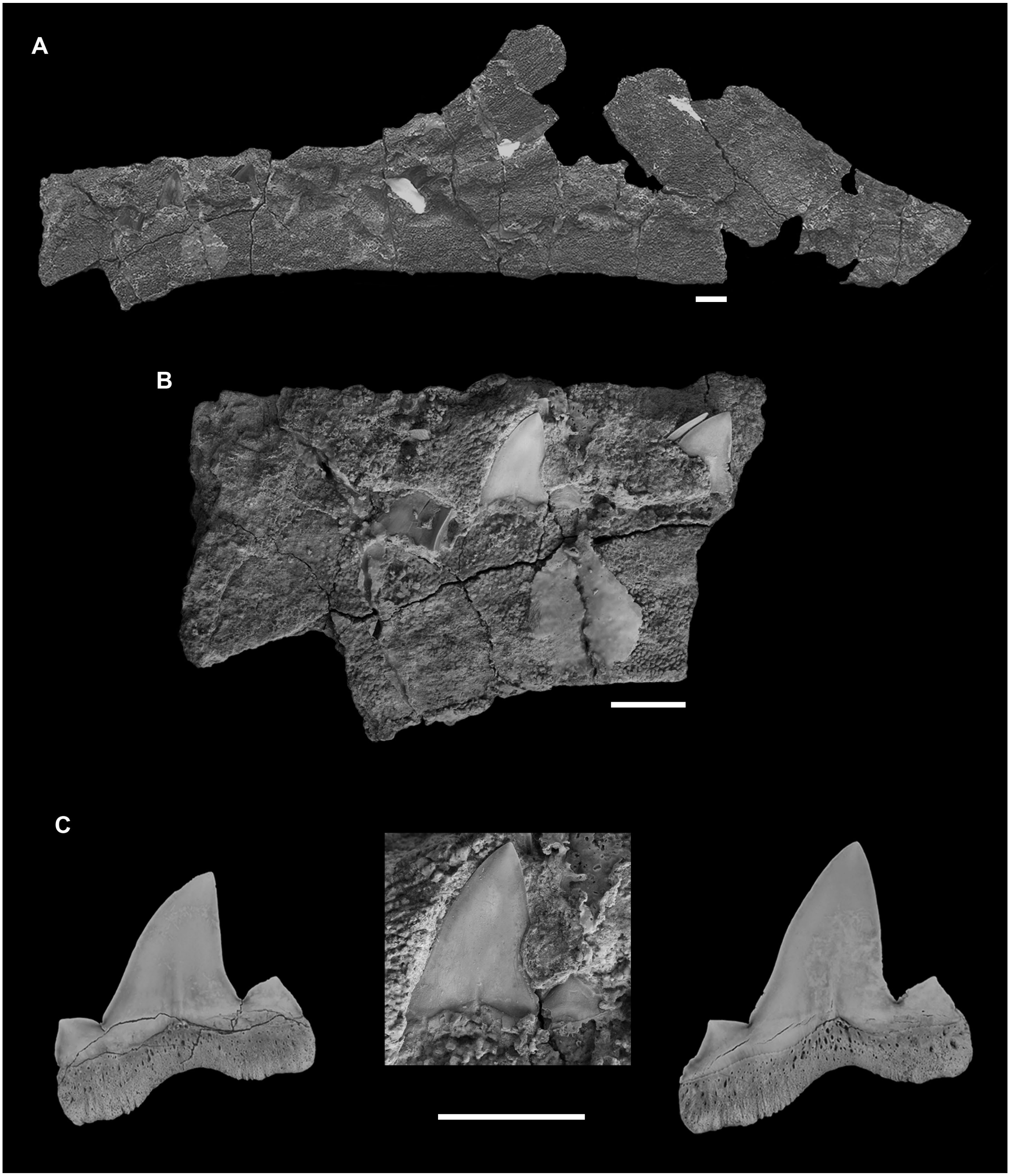
Lower lateroposterior tooth files.—Three teeth are referred to the lower lateroposterior hollow. One of them, 19 mm high, has a labiolingually compressed but strongly asymmetrical root, indicating the lp1 position (Fig. 12F). The cusp is slender, distally inclined and the cusplets divergent. In profile view, the cusp is somewhat lingually curved. The inner cutting edges of the cusplets are convex whereas the outer edges are concave. The lingual protuberance is very well demarcated in basal view (Fig. 12F$_4$) and the median indentation of the basal edge is deep and U-shaped (Fig. 12F$_3$). Another tooth is most likely from a significantly larger individual. It measures 18 mm in height and 17.5 mm in width (Fig. 12G). One of its lobes of the root is broken off. The tooth is symmetrical with an erect cusp, slightly lingually curved in profile view. The moderately divergent cusplets are very sharp. A low and relatively poorly demarcated lingual protuberance is seen in basal view (Fig. 12G$_4$). A well-preserved tooth, measuring 10 mm in height, is referred to the posterior half of the inferred lower lateroposterior hollow (Fig. 12H). Apart from its much smaller size, it differs from the previously described, incomplete lateroposterior tooth by its distally inclined cusp, and shallower and less tightly curved median indentation of the basal edge of the root.

Comparison.—See the descriptions above for a comparison of the teeth of *C. ewelli* sp. nov. with those of the dentally similar *C. borealis* and *C. gertericorum* sp. nov. The upper anterior teeth of the narrow-cusped *C. catoxodon* sp. nov. differ from those of *C. ewelli* sp. nov. by their poorly demarcated lingual protuberance in basal view (compare Figs. 12A$_3$ with 20A$_4$). In profile view, the protuberance is more prominent in upper anteriors of *C. catoxodon* sp. nov. (Fig. 20A$_2$) than it is in those of *C. ewelli* sp. nov. (Fig. 12B$_2$). The likely A3 tooth (Fig. 12E) in *C. borealis*-group group species, like *C. ewelli*, does not have an equivalent amongst the teeth from CY Creek. One of the upper jaw teeth (Fig. 21A) is vaguely similar in crown morphology to that of the assigned A3 in *C. ewelli* sp. nov. but does not show any features on the root in basal view indicating that it is an A3 tooth rather than an LP1 masquerading as an upper anterior tooth (i.e. median indentation of the basal edge is shallow and the basal view shows a more-or-less rectangular outline without any labiolingual compression of the distal lobe). The upper lateroposterior teeth of *C. ewelli* sp. nov. differ from those of *C. catoxodon* sp. nov. by their generally sharp cusplets.

Remarks.—The moderate size of the teeth at hand (largest tooth, a probable A2, is 25 mm high; Fig. 12B), compared to the teeth of early Campanian *C. borealis* from the Kristianstad Basin, may reflect a smaller adult size in the Smoky Hill Chalk species. It is noteworthy, however, that the maximum size (height) of the teeth of *C. borealis* from the early Campanian of the nearshore, archipelago deposits in southern Sweden (~40 mm) is much greater than it

← Fig. 12. *Cretalamna ewelli* sp. nov., late Coniacian, Smoky Hill Chalk [all specimen originating from strata above Hattin's (1982) Marker Unit 1 but below Marker Unit 4], Niobrara Formation, Kansas, USA; scale bar represents 10 mm. **A**. FHSM VP-18510, holotype, left A1?; labial (A$_1$), profile (A$_2$), basal (A$_3$), and lingual (A$_4$) views. **B**. FHSM VP-18517, paratype, right A2? from a large individual; labial (B$_1$), profile (B$_2$), basal (B$_3$), and lingual (B$_4$) views. **C**. FHSM VP-18511, paratype, left A2?; basal (C$_1$), labial (C$_2$), profile (C$_3$), and lingual (C$_4$) views. **D**. FHSM VP-18512, paratype, right upper lateroposterior tooth; labial (D$_1$), basal (D$_2$), and lingual (D$_3$) views. **E**. FHSM VP-18513, paratype, left A3?; labial (E$_1$), profile (E$_2$), basal (E$_3$), and lingual (E$_4$) views. **F**. FHSM VP-18514, paratype, left lp1?; labial (F$_1$), profile (F$_2$), lingual (F$_3$), and basal (F$_4$) views. **G**. FHSM VP-18515, paratype, lower lateroposterior tooth; labial (G$_1$), profile (G$_2$), lingual (G$_3$), and basal (G$_4$) views. **H**. FHSM VP- 18516, paratype, lower lateroposterior tooth; labial (G$_1$), profile (G$_2$), lingual (G$_3$), and basal (G$_4$) views.

is in early Campanian (*Offaster pilula* Zone) examples of the same species from more offshore, phosphatic chalks in northern France (~30 mm in the Beauval quarry; Pieter De Schutter pers. com. 2013 and examination of photographs of teeth of his collection of *C. borealis* from the Beauval quarry). It is therefore possible that the Smoky Hill Chalk material represents sizes of larger juveniles and/or smaller adults. The fact that the geologically older *C. gertericorum* sp. nov. is dentally closer to *C. borealis* than is *C. ewelli* sp. nov. (probable A2s are virtually identical in *C. gertericorum*



sp. nov. and *C. borealis*), indicates that the latter did not give rise to *C. borealis* and might represents a short-lived lineage of the *C. borealis* group, adapted to the atypical environmental conditions of the restricted Western Interior Seaway.

The documentation of *C. ewelli* sp. nov. and *C. hattini* sp. nov. from the Smoky Hill Chalk should by no means be viewed as a complete account of *Cretalamna* from this lithostratigraphical unit. Future work, especially from the middle part of the unit, might well reveal additional species of the genus, previously described or new to science.

Cretalamna hattini sp. nov.

Figs. 13-17, 19A

Cretolamna appendiculata (Agassiz); Shimada 2007.

Cretalamna appendiculata [*partim*]; Shimada et al. 2010:

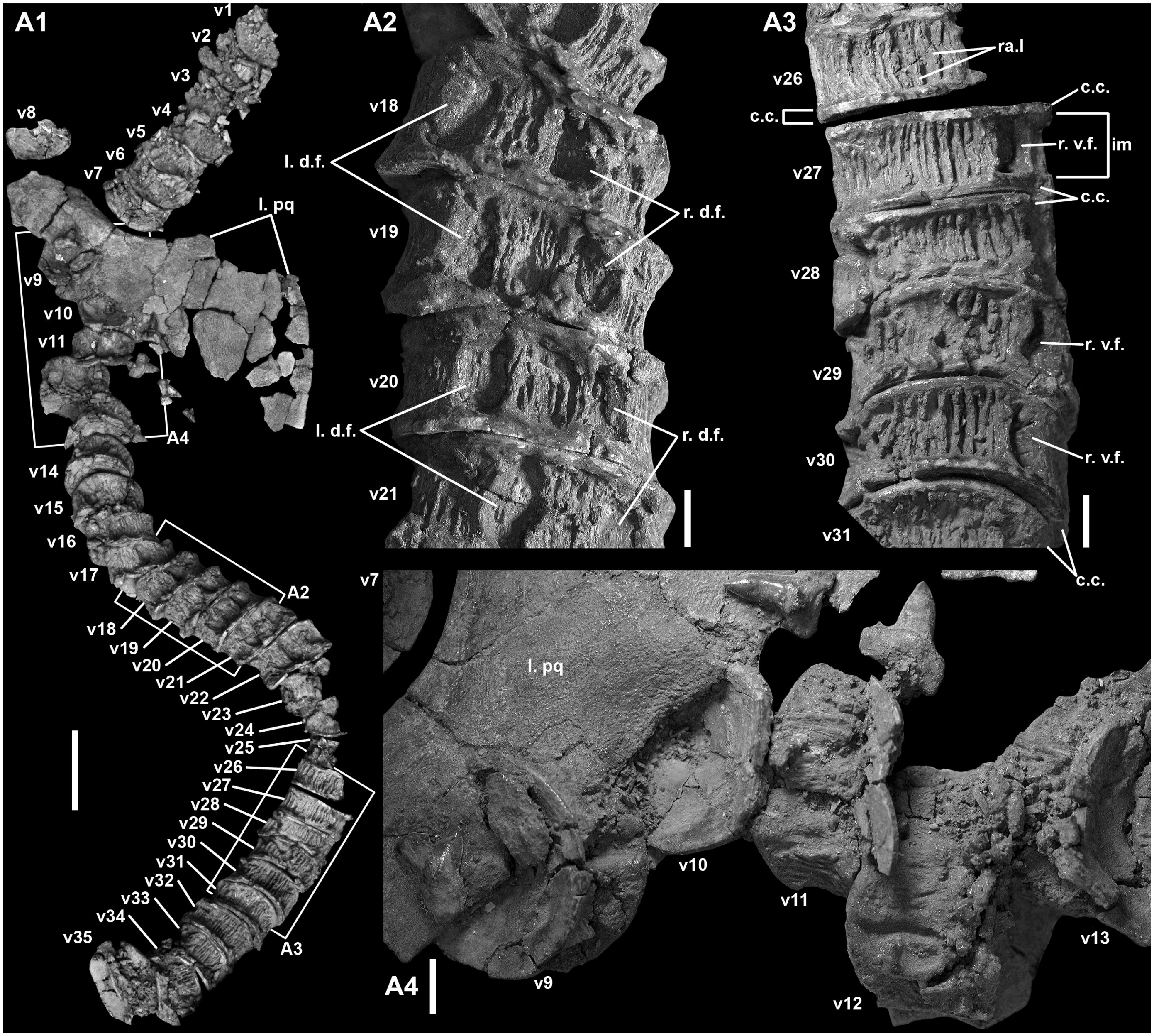


Fig. 14. *Cretalamna hattini* sp. nov., LACM 128126; anteriormost preserved centrum equals one (designations follow Shimada 2007), A_1 scale bar represents 50 mm; A_2–A_4 scales bars represent 10 mm. **A**. partial vertebral column and left palatoquadrate (A_1), centra 17–21 in dorsal view (A_2), centra 25–31 in lateral view (A_3), and centra 9–13 viewed in various angles (A_4). Abbreviations: **c.c.**, corpus calcareum; **d.f.**, dorsal foramen; **im**, intermedialia; **l.**, left; **pq**, palatoquadrate; **r.**, right; **v**, vertebral centrum; **v.f.**, ventral foramen.

← Fig. 13. *Cretalamna hattini* sp. nov., LACM 128126, earliest Campanian, upper Smoky Hill Chalk, Niobrara Formation, Kansas, USA; all scale bars 10 mm. **A**, right palatoquadrate in lingual view, **B**, anterior section of right palatoquadrate showing embedded replacement teeth, re-interpreted as (from left to right) A2, LP1 and LP2 (two cusps), **C**, *in situ* tooth compared with disarticulated teeth from the same individual assigned to the same file by Shimada (2007: left tooth) and in this work (right tooth).

figs. 2.43 and 2.69.

Etymology: Named in honour of Donald E. Hattin, for his work on the stratigraphy of the Niobrara Formation, western Kansas.

Holotype: LACM 128126, partial skeleton comprising the palatoquadrates, Meckel's cartilages, 35 vertebrae and about 120, mostly disarticulated, teeth.

Type horizon and locality: Close to MU 16, Logan County, Kansas (precise locality data on file at LACM; see Shimada 2007: 584).

Diagnosis.—Quadrate process more than twice as high as dorsoventrally narrowest part of palatoquadrate, anterior to quadrate process but posterior to section harbouring anterior tooth files. No tooth-size reduction across the anterior/lateroposterior boundary in upper jaw. Gradational change in root morphology in basal view from second upper anterior to lateroposterior teeth. All aspects of tooth morphology in second upper jaw tooth closer to those of adjacent upper lateroposterior teeth than to first upper anterior tooth. No teeth in dentition with recurved cusp. Apical two thirds of mesial cutting edge of cusp markedly convex in all teeth. Vertebral centra with moderately robust, densely packed radial lamellae, sometimes bifurcating distally, next to corpus calcarea. Circular lamellae absent. Neural arch foramina moderately narrow, subovate, extending full length of centrum. Thickness of corpus calcareum 1/7th of length of centrum.

Description

See Shimada (2007) for a description of palatoquadrates, Meckel's cartilage and teeth. His description of the disarticulated teeth pertaining to LACM 128126 was based largely on suboptimally prepared material. Subsequent preparation revealed important additional information regarding the morphology of the root in basal view. However, rather than repeating much of Shimada's (2007) description we have restricted our revision of LACM 128126 to the inclusion of a diagnosis for *C. hattini* sp. nov., a revised reconstruction of the dentition, a somewhat more in-depth description of the vertebral morphology, and photographs (including basal views of the root) of fully prepared teeth.

Vertebral column.—The preserved part of the vertebral column comprises 35 midtrunk centra (denominated 'v1' through 'v35' by Shimada 2007) ranging in size from 38-48 mm diameter. The centra are approximately 2.5 times wider than they are long (v30 *sensu* Shimada 2007, fig: 1D, is 45 mm wide and 19 mm long). As indicated by Shimada (2007), many of the centra are severely deformed, preventing many meaningful measurements. The dorsal foramina are subovate with very rounded corners and abut the anterior and posterior corpus calcareum (Fig. 14A_2). The neural arch interforaminal width is 10-13 mm, whereas the intraforaminal width is 7-8 mm. Ventral foramina extend the full length of the centrum, abutting each corpus calcareum (Fig. 14A_2), and are narrow (4.25 mm; v11 and v32 in Shimada 2007) relative to their length (14 mm; v10); although, most are greatly distorted. The region around the ventral foramina is greatly reinforced with calcified cartilage giving it a smooth and even raised appearance (Fig. 14A_3).

The centra are round and have straight, moderately robust radial lamellae, which may bifurcate next to the corpus calcareum. The radial lamellae are 0.9-1.2 mm thick and are generally equidistantly spaced being 1.2-1.7 mm apart. There are no concentric lamellae. The rim of the corpus calcareum is narrow (Fig. 14A_3). In hemisected view, it is straight to slightly rounded on the lateral side. The corpus calcareum is consistently thin (v8 in Shimada 2007: fig. 1) and does not greatly thicken toward the margin. At the lateral margin, the corpus calcareum thickness is approximately 1/14th of centrum diameter. The thickness of the corpus calcareum is approximately 1/7th of the length of the centrum. No pores or radial canals are present next to the corpus calcareum.

Comparison.—The teeth of *C. hattini* sp. nov. most closely resemble those of *C. deschutteri* sp. nov., and both taxa are here referred to as *C. hattini*-group species. This species group is characterised (dentally) by the great width of the root in basal view relative to its height in lower anterior teeth (compare Figs. 17A_2, 18F_4 with 7A_3, 10A_4, 11F_4; all probable a1), relatively well demarcated lingual protuberance of the root in basal view of both upper and lower anterior teeth, wide but often poorly demarcated protuberance in basal view in upper lateroposterior teeth, and broad and dome-shaped protuberance of the root in anterior teeth in profile view. In other species of the genus, the protuberance is narrower (apicobasally) and more protruding (see e.g. Figs. 4C_4, 7A_2, 9C_2, 11A_2, 12A_2, 20A_2). Note that the protuberance is corroded in Figure 4A_2, hence the low profile.

The anterior teeth of *C. deschutteri* sp. nov. are markedly enlarged whereas the anteriorly situated upper lateroposterior teeth of *C. hattini* sp. nov. are almost as large as are the upper anterior teeth (Fig. 19A). This is well exemplified by a simple tooth-size comparison between the two species. The largest anterior teeth of *C. deschutteri* sp. nov. from the *M. labiatus* Zone are slightly larger than are the equivalent anteriors of LACM 128126. In contrast, the lateroposterior teeth at hand of *C. deschutteri* sp. nov. are significantly smaller than are the corresponding teeth of LACM 128126. Although the lingual and basal views of the root are similar in lateroposterior teeth of the two species, the cusp is narrower in *C. deschutteri* sp. nov. and much thinner labiolingually than it is in *C. hattini* sp. nov.

Remarks.—Shimada (2007: fig. 6C) illustrated the right

Fig. 15. *Cretalamna hattini* sp. nov., upper jaw teeth of LACM 128126 (A1?-LP4?); scale bar represents 10 mm. **A**. right A1?; basal (A_1), lingual (A_2), profile (A_3), and labial (A_4) views. **B**. symphyseal tooth; profile (B_1), lingual (B_2), basal (B_3), and labial (B_4) views. **C**. right A2?; basal (C_1), lingual (C_2), labial (C_3), and profile (C_4) views. **D**. right LP1?; basal (D_1), lingual (D_2), and labial (D_3) views. **E**. left LP2?; basal (E_1) and lingual (E_2) views. **F**. right LP3?; labial (F_1) and lingual (F_2) views. **G**. right LP2?; labial (G_1), basal (G_2), and lingual (G_3) views. **H**. right LP4?; basal (H_1), lingual (H_2), profile (H_3), and labial (H_4) views.

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palatoquadrate of LACM 128126 accompanied by what Shimada regarded to represent the first seven teeth in the upper jaw (using disarticulated teeth of LACM 128126 and excluding parasymphyseals) and assigned by him to the first and second anterior files (A1-A2), an intermediate file (I1=most distal upper anterior file *sensu* Siverson 1999) and the first four teeth in the upper lateroposterior hollows (denominated L1-4 by Shimada 2007). All disarticulated teeth in Shimada's figure 6C, except for the tooth assigned to the A1 position, were each linked to partially exposed *in situ* cusps of replacement teeth on the palatoquadrate. The disarticulated tooth regarded by Shimada (2007) as the upper intermediate tooth (I1) is reduced in size compared to the adjacent teeth in Shimada's (2007: fig. 7B) reconstruction and has a strongly distally curved cusp. We initially attempted to examine *in situ* teeth using a Siemens Somatom Sensation 64 slice computed tomography (CT) scanner. The CT scan revealed no additional teeth in the right palatoquadrate apart from those figured in Shimada (2007) and no hidden teeth in the left Meckel's cartilage. In addition, the CT scan indicated that no roots were attached to the cusps protruding through the medial wall of the flattened lateroposterior hollow of the right palatoquadrate. Therefore, our verification of the presence of a reduced third upper tooth with a strongly, distally curved cusp is based on characteristics of the *in situ* cusp.

As shown in Figure 13C, there is little resemblance in cusp shape between the *in situ* tooth indicated as the upper 'intermediate' by Shimada (2007: fig. 6C) and the disar-

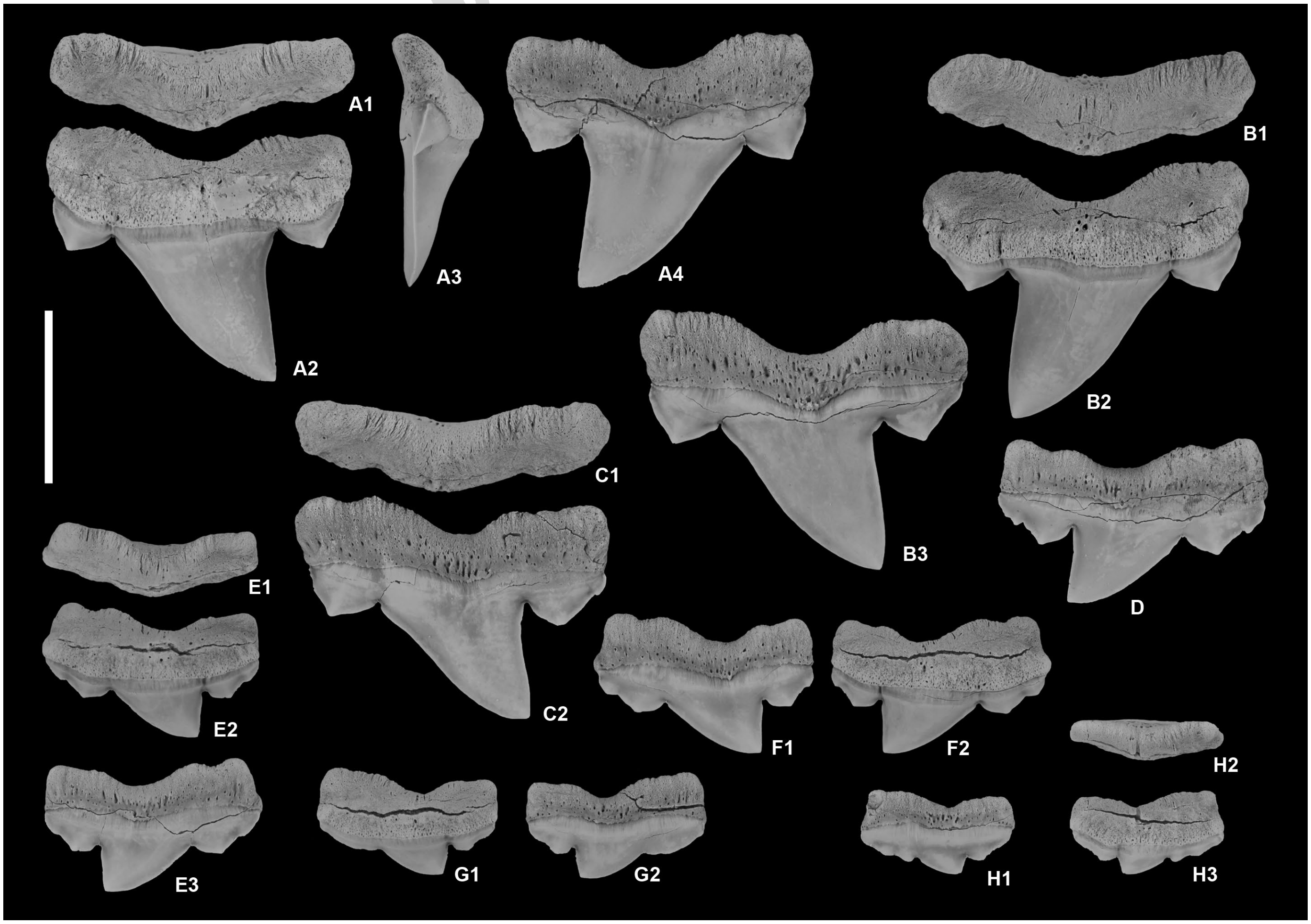

Fig. 16. *Cretalamna hattini* sp. nov., upper jaw teeth of LACM 128126 (LP5?-LP10?); scale bar represents 10 mm. **A**. right LP5?; basal (A$_1$), lingual (A$_2$), profile (A$_3$), and labial (A$_4$) views. **B**. left LP5?; basal (B$_1$), lingual (B$_2$), and labial (B$_3$) views. **C**. left LP6?; basal (C$_1$) and labial (C$_2$) views. **D**. right LP7?, labial view. **E**. right LP8?; basal (E$_1$), lingual (E$_2$), and labial (E$_3$) views. **F**. left LP8?; labial (F$_1$) and lingual (F$_2$) views. **G**. right LP9?; lingual (G$_1$) and labial (G$_2$) views. **H**. left LP10?; labial (H$_1$), basal (H$_2$), and lingual (H$_3$) views.

Fig. 17. *Cretalamna hattini* sp. nov., lower jaw teeth of LACM 128126; scale bar represents 10 mm. **A**. right a1?; labial (A$_1$) and basal (A$_2$) views. **B**. left a2?; labial (B$_1$), basal (B$_2$), and profile (B$_3$) views. **C**. right a2?; lingual (C$_1$), basal (C$_2$), and labial (C$_3$) views. **D**. right lp2?; labial (D$_1$) and basal (D$_2$) views. **E**. left lp1?; labial (E$_1$), profile (E$_2$), lingual (E$_3$), and basal (E$_4$) views. **F**. right lp1?, labial view. **G**. right lp3?; profile (G$_1$), labial (G$_2$), lingual (G$_3$), and basal (G$_4$) views. **H**. right lp4?, labial view. **I**. right lp5?; lingual (I$_1$) and labial (I$_2$) views. **J**. right lp6?; lingual (J$_1$) and labial (J$_2$) views. **K**. left lp6?; labial (K$_1$) and lingual (K$_2$) views. **L**. right lp7?; profile (L$_1$), labial (L$_2$), and basal (L3) views. **M**. left lp8?, lingual view.

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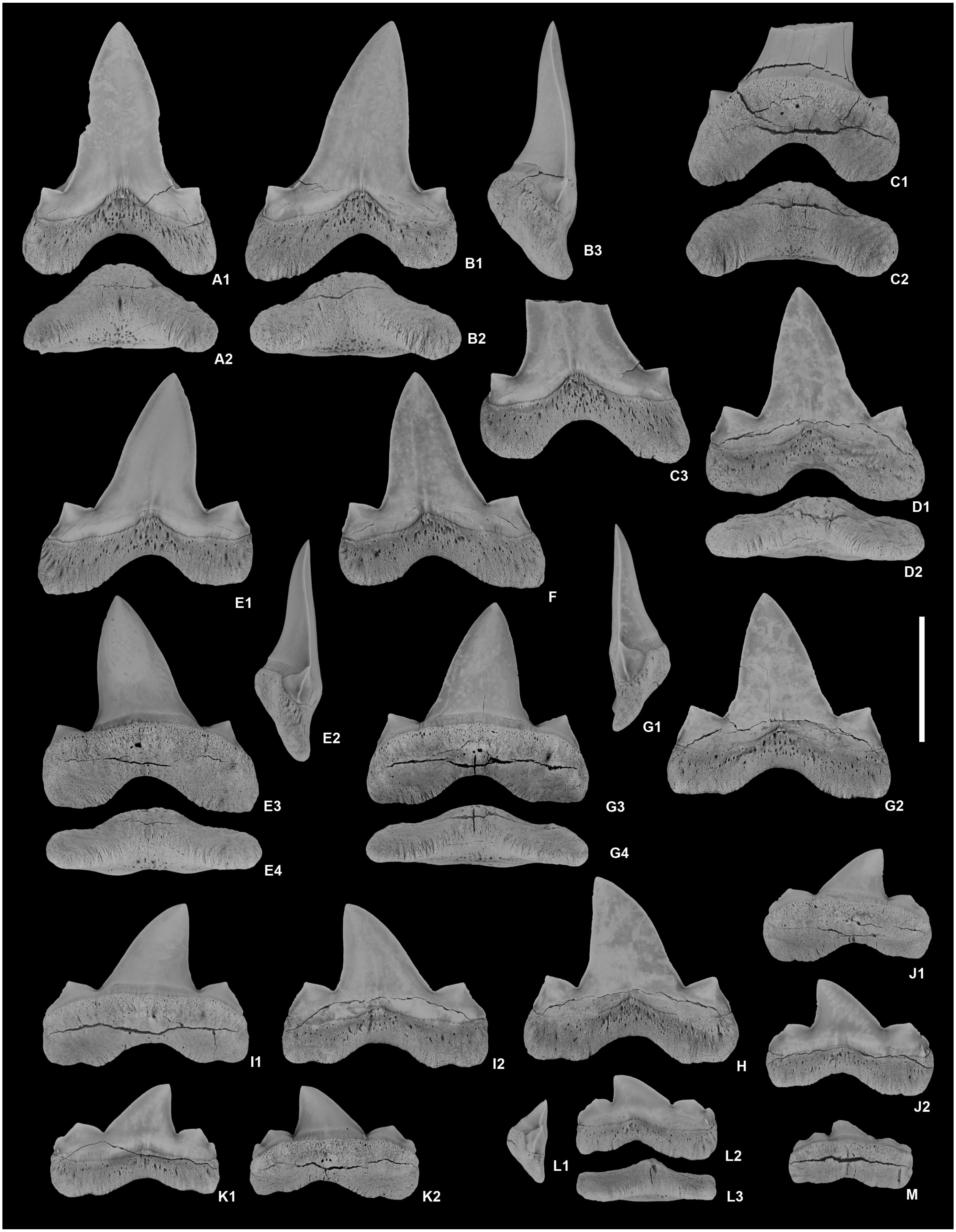
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ticulated tooth assigned by him to the same tooth file (Fig. 13C, left tooth). The *in situ* cusp is larger and has a distally inclined as opposed to distally curved cusp. The cusp of Shimada's (2007: figs. 7B, 8) L1, on the other hand, makes a good match after adjusting for the obvious displacement of the cusplet (Fig. 13C, right tooth). There is thus no evidence of a reduced 'intermediate' tooth in LACM 128126. The disarticulated teeth assigned to the upper 'intermediate' tooth file by Shimada (2007) do not show any of the specialised features of the root that characterises upper 'intermediates' of modern lamnids. Instead, the basal face of the root features an unremarkable outline (Fig. 16A$_1$, B$_1$), very similar to that of other upper jaw teeth from the mid-portion of the inferred lateroposterior hollow (Figs. 15H$_1$, 16C$_1$). In lamnids (Lamnidae) the distal lobe of the root, facing the intermediate bar, is typically labiolingually compressed and may be lingually curved in basal view.

Shimada (2007: 586) indicated the presence of up to 15 indentations on the medial surface of the right palatoquadrate, each potentially corresponding to a separate tooth file (although he assigned 13 upper jaw tooth files, excluding parasymphyseals, to LACM 128126 in fig. 5C). We have not been able to verify the presence of 15 distinct indentations and question that number. In our reconstruction of the dentition of LACM 128126, we assigned 12 tooth files to the upper jaw (in addition to at least one file of parasymphyseals) and 10 tooth files to the lower jaw (LP10 and lp8 not shown in Fig. 19A but in Fig. 16H and 17M). Several of the teeth assigned to the upper jaw by Shimada (2007) are probably lower jaw teeth as indicated by their narrower, more upright cusps and straight to convex profile view of the labial side of the crown (i.e. Shimada 2007: fig. 8, L4 [lp4], L5 [lp5], L7 [lp6], L10 [lp8]). We agree with the relative position of all but two of the lower jaw teeth in Shimada's (2007) figure 9. In our reconstruction, the two teeth illustrated as l1 and l2 by Shimada (2007) have swapped places and we have added two additional commissural teeth. Contrary to Shimada (2007), we believe that the second and third tooth files (A2 and LP1) in the upper left jaw are missing. The tooth assigned to the left A2 position by Shimada (2007) is reassigned to the LP2 position as the basal view of its root (Fig. 15E$_1$) is very similar to that of the right LP2 (Fig. 15G$_2$). Overall the collection of disarticulated teeth pertaining to LACM 128126 indicates a fairly strong collecting bias towards fully mineralised teeth. The percentage of incompletely mineralised teeth in, e.g. the holotype dentition of the Cenomanian *Cardabiodon ricki* Siverson, 1999 (WAM 96.4.45; collected by MS and field assistants) is considerably higher than it is in LACM 128126. As in WAM 96.4.45, right and left teeth from the same relative position are not always mirror images of each other [see e.g. the right and left LP5s (Fig. 16A$_4$, B$_3$)]. Because of this we chose to illustrate teeth from the same side of the jaw in Fig. 19A even though this meant that a few positions are not represented in the reconstructed dentition.

Shimada (2007) described the centra of LACM 128126 as anteriormost. We suggest that at least the first 10-20 vertebral centra are missing from LACM 128126 because the preserved centra are relatively consistently sized with no marked increase in diameter from v1 as seen in *Cretoxyrhina*, *Archaeolamna*, or *Squalicorax* (see Cook et al. 2011: fig. 6A).

Cretalamna deschutteri sp. nov.

Fig. 18

Etymology: Named after Pieter De Schutter, in recognition of his work on Cenozoic elasmobranchs from Belgium and assistance in making teeth from the SECAB quarry available to us.

Type material: Holotype: Lower anterior tooth, WAM 13.5.17; Fig. 18G. Paratypes: WAM 13.5.13-16, 18-19 and UM-BET 6; Fig. 18A-F, H.

Type horizon: Conglomeratic pocket (with black pebbles and fish coprolites) in the basal part of the grey-coloured *Mytiloides labiatus* Zone.

Type locality: SECAB quarry, Bettrechies, northern France.

Diagnosis.—Upper and lower anterior teeth markedly enlarged. Most upper and lower lateroposterior teeth with markedly compressed cusp in labiolingual direction. Lingual protuberance of root relatively well demarcated in basal view in both upper and lower anterior teeth but wide and with poorly defined base in lateroposterior teeth. Median indentation of basal edge of root deep and U-shaped in anterior teeth but forming wide and shallow V with rounded apex in lateroposterior teeth. Lingual protuberance of root in anterior teeth broad and dome-shaped in profile view.

Description

First upper anterior tooth file.—An incomplete, 23.5 mm high tooth is assigned to the A1 position (Fig. 18A). The mesial cusplet is missing and the distal end of both lobes of the root is damaged. The cusp is very slightly inclined, presumably in distal direction. The labial face of the tooth is moderately convex in profile. The distal cusplet is triangular, divergent and, curiously, with an apex considerably more worn from prey manipulation than is the apex of the cusp. The base of the crown forms a prominent shelf at the crown/root boundary. The root is markedly asymmetrical in basal view with the mesial lobe significantly more compressed

Fig. 18. *Cretalamna deschutteri* sp. nov., *Mytiloides labiatus* Zone (early Turonian), SECAB quarry, Bettrechies, northern France; scale bar represents 10 mm. **A**. WAM 13.5.18, paratype, left A1?; labial (A$_1$), basal (A$_2$), lingual (A$_3$), and profile (A$_4$) views. **B**. WAM 13.5.14, paratype, left upper lateroposterior tooth; labial (B$_1$), profile (B$_2$), basal (B$_3$), and lingual (B$_4$) views. **C**. WAM 13.5.15, paratype, left upper lateroposterior tooth; labial (C$_1$), profile (C$_2$), basal (C$_3$), and lingual (C$_4$) views. **D**. WAM 13.5.13, paratype, right upper lateroposterior tooth; labial (D$_1$), profile (D$_2$), basal (D$_3$), and lingual (D$_4$) views. **E**. UM-BET 6, paratype, right upper lateroposterior tooth; labial (E$_1$), profile (E$_2$), basal (E$_3$), and lingual (E$_4$) views. **F**. WAM 13.5.19, paratype, a1?; labial (F$_1$), profile (F$_2$), lingual (F$_3$), and basal (F$_4$) views. **G**. WAM 13.5.17, holotype, left a2?; labial (G$_1$), profile (G$_2$), lingual (G$_3$), and basal (G$_4$) views. **H**. WAM 13.5.16, paratype, right lower lateroposterior tooth; labial (H$_1$), profile (H$_2$), lingual (H$_3$), and basal (H$_4$) views.

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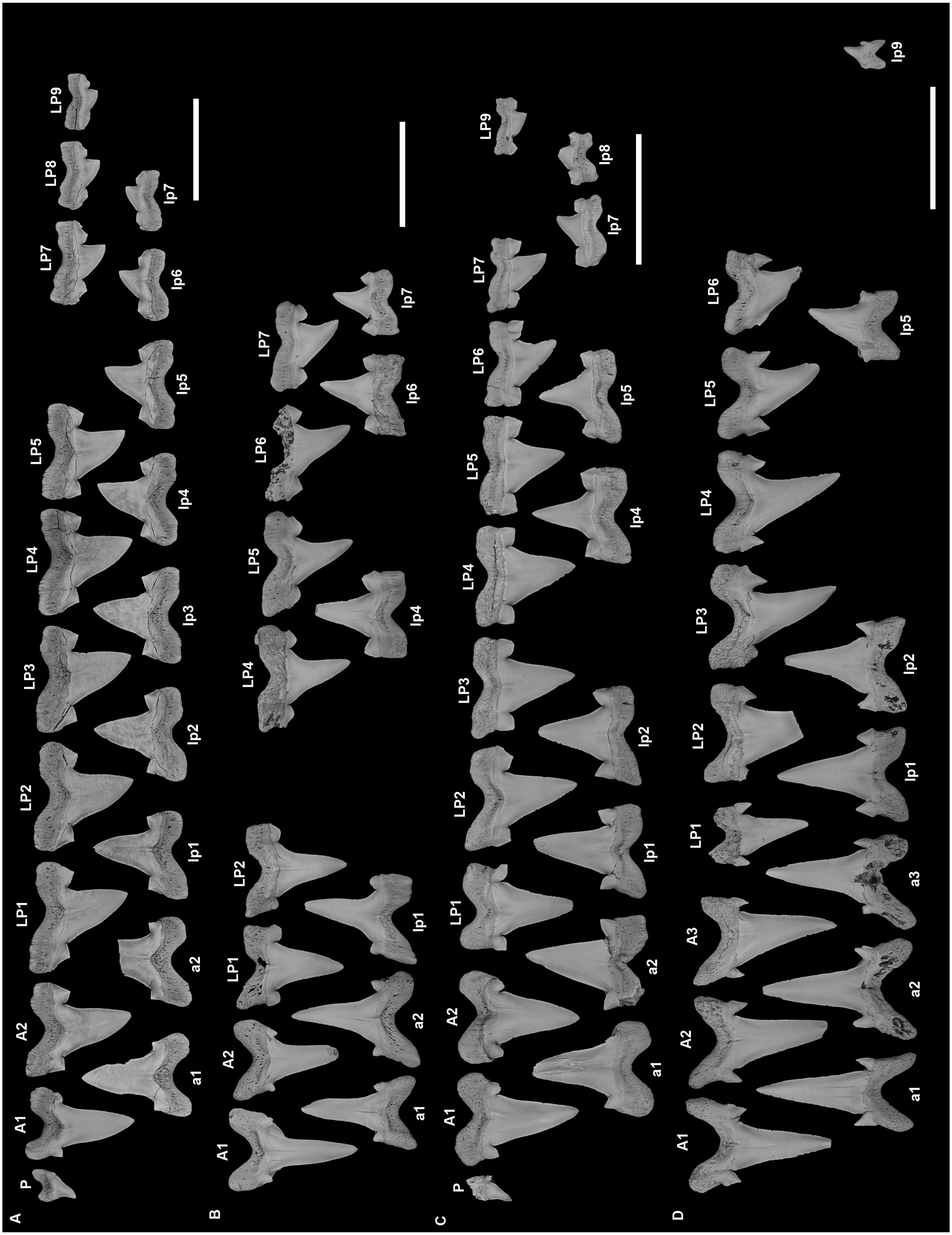
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lp6
lp7
C
P
A1
A2
LP1
LP2
LP3
LP4
LP5
LP6
LP7
LP9
a1
a2
lp1
lp2
lp4
lp5
lp7
lp8
D
A1
A2
A3
LP1
LP2
LP3
LP4
LP5
LP6
a1
a2
a3
lp1
lp2
lp5
lp9

than the distal lobe. The base of the lingual protuberance is well defined in basal view. The basal third of the cusp, neck and lingual protuberance of the root form a gently curved arch in profile view. The basal edge of the root is U-shaped and the mesial lobe is narrower than is the distal lobe.

Upper lateroposterior tooth files.—Four teeth are referred to the inferred upper lateroposterior hollow; two from the left side of the jaw (Fig. 18B, C) and two from the right side (Fig. 18D, E). The upper left teeth are both most likely from the anterior half of the inferred upper lateroposterior hollow, whereas the two right teeth are from the posterior part of the hollow. The cusp is moderately (more anteriorly situated teeth) to strongly (posteriorly situated teeth) distally curved in labial/lingual views. It is markedly labiolingually compressed and straight (posteriorly situated teeth) to labially curved in profile view. The cusplets are large and well defined in the anteriorly situated teeth but the mesial cusplet is largely merged with the mesial cutting edge of the cusp in the two posteriorly situated teeth (Fig. 18D_1, E_1). The lingual view of the root is progressively more asymmetrical in more posteriorly situated teeth with an enlarged mesial side. The median indentation of the basal edge is wide and shallow. The basal view is very similar in all four teeth and shows a wide, very poorly demarcated protuberance and a lingual outline and V-shaped rather than parallel lingual and labial edges.

First lower anterior tooth file.—One complete tooth, 19 mm high, is referred to the a1 file (Fig. 18F). The cusp is triangular, relatively short and erect. It is strongly lingually curved in profile view. A relatively small, triangular cusplet is situated on either side of the cusp. The root is nearly perfectly symmetrical in labial/lingual views and has rounded lobe-extremities. A low, nearly symmetrical basal view features a relatively well demarcated, broad protuberance (Fig. 18F_4).

Second lower anterior tooth file.—A 22 mm high tooth (holotype) is assigned to the right a2 position (Fig. 18G). The tooth is missing a small section of the lingual face of the root but has otherwise the best root surface preservation of all examined teeth from the SECAB quarry. The cusp is slightly distally inclined in labial/lingual views and tapers off rather abruptly in the distal third of its length. The cutting edges of the cusp are lingually curved in profile and slightly sigmoidal. A pair of divergent, triangular cusplets is present at the base of the cusp. The labial base of the crown is developed into a shelf-like structure. A markedly asymmetrical root features a short, broad and angular distal lobe, in contrast to a more elongated, narrower and rounded mesial lobe. The base of the lingual protuberance is well-defined in basal view. In profile view, the lingual protuberance is low.

Lower lateroposterior tooth files.—One tooth, 10.5 mm high, is referred to the lower right lateroposterior hollow (Fig. 18H). The tip of the cusp is broken off and the mesial lobe of the root has sustained some damage, primarily affecting the tip of the lobe, which is more rounded that it would have been originally. A small piece of the root is also missing at the mesial base of the lingual protuberance (clearly visible in basal view). The triangular cusp is labiolingually compressed (compared to equivalent teeth in other species of the genus) and distally inclined. It is lingually curved in profile view (Fig. 18H_2). The cusplets are large, relatively upright and feature a convex inner edge, shorter than the straighter outer edge. The median indentation of the basal edge is very similar to that in upper lateroposterior teeth, being wide and V-shaped with a rounded apex.

Comparison.—See the description above of *C. hattini* sp. nov. for a comparison of the two species. The root is taller in lingual view (relative to its width) in lower anteriors of the two coexisting species *C. appendiculata* (Fig. 3A_3) and *C. gertericorum* sp. nov. (Fig. 11F_3) than it is in *C. deschutteri* sp. nov. (Fig. 18F_3, G_3). Most lateroposterior teeth of *C. gertericorum* sp. nov. have a small and shallow but tightly curved median indentation of the basal edge of the root (e.g. Fig. 11C_3) whereas the equivalent indentation is wide and V-shaped in *C. deschutteri* sp. nov. (Fig. 18B_4). In *C. appendiculata* it is deep and U-shaped in anteriorly situated upper lateroposterior teeth (Fig. 2D_4). The lingual protuberance is very small and well demarcated in basal view in most lateroposterior teeth of *C. gertericorum* sp. nov. (Fig. 11G_3) but larger and poorly demarcated from the sloping legs of the lingual edge of the root in *C. deschutteri* sp. nov. (Fig. 18H_4). The often rectangular basal view of the root in *C. gertericorum* sp. nov. (Fig. 11C_1) has not been observed in *C. deschutteri* sp. nov. In mid- to anteriorly situated upper lateroposterior teeth of *C. appendiculata*, the distal lobe is labiolingually compressed compared with the mesial lobe (Fig. 2C_1, D_3). Teeth from middle part of the inferred upper lateroposterior hollow in *C. deschutteri* sp. nov. (Fig. 18B_3) have a rather symmetrical basal view of the root, like in *C. hattini* sp. nov. (Fig. 15H_1). This difference between the two taxa seems to be reversed in upper commissural teeth as the distal lobe is more compressed than is the mesial lobe in *C. deschutteri* sp. nov. (Fig. 18E_3) and *C. hattini* sp. nov. (Fig. 16H_2) whereas posteriorly situated upper lateroposterior teeth of *C. appendiculata* have a rather symmetrical root in basal view (Fig. 2F_1).

← Fig. 19. Reconstructed dentitions. **A**. *Cretalamna hattini* sp. nov. (LACM 128126), **B**. *Cretalamna catoxodon* sp. nov., **C**. *Cretalamna sarcoportheta* sp. nov., **D**. *Kenolamna gunsoni* gen. nov. The almost complete lack of posteriorly situated lateroposterior teeth in *C. catoxodon* sp. nov. and *K. gunsoni* gen. nov. is a result of the collecting method used at CY Creek (surface picking). Only teeth from one side of the jaws were used for the reconstruction of the dentition of *C. hattini* sp. nov. (right side – mirror image) whereas teeth from both the right (mirror image) and left side were used for the other dentitions. The missing tooth files (LP6, LP10 and lp8) on the right side of the jaws in *C. hattini* sp. nov. appear to be present on the opposing side of the jaw (and are illustrated in figures 16 and 17). All tooth file designations are inferred. Scale bars represent 20 mm and apply to the average magnification of the teeth in dentitions B-D. See the Appendix for re-scaling of the individual teeth.


A1
A2
A3
A4
B1
B2
B3
B4
C1
C2
C3
C4
D1
D2
E1
E2
E3
E4
F1
F2
F3

Remarks.—The late middle to early late Turonian teeth from the Arcadia Park Formation, illustrated and described as *Cretolamna woodwardi* by Welton and Farish (1993) probably belong to the *C. hattini*-species group. The two anterior teeth illustrated (Welton and Farish 1993: 105, figs. 1, 2) might both be first upper anteriors as the difference in cusp inclination is well within the range seen in other *Cretalamna* (e.g. *C. sarcoportheta* sp. nov.). The two teeth are superficially similar to the A1s of *C. catoxodon* sp. nov. but the profile view of the lingual protuberance is much closer to that of *C. deschutteri* sp. nov. (Fig. 18A$_4$) than it is to that of *C. catoxodon* sp. nov. (Fig. 20A$_2$). The upper lateroposterior tooth illustrated along with the two upper anterior teeth as *C. woodwardi* by Welton and Farish (1993: 105, figs. 1, 2) clearly differ from the corresponding teeth of *C. deschutteri* sp. nov. by its labiolingually thick cusp (see Fig. 18B$_2$). Teeth of the *C. hattini* group, very similar to those misidentified by Welton and Farish (1993) as *C. woodwardi*, occur in the basal part of the Fairport Member of the Carlile Shale at Mosby, Montana (MS, pers. observ.), indicating the presence of two coexisting species of the *C. hattini* group. The North American species lacks the marked labiolingual compression of the cusp in lateroposterior files that characterises *C. deschutteri* sp. nov. and is in this regard closer to *C. hattini* sp. nov.

Cretalamna catoxodon sp. nov.

Figs. 19B, 20-22

Cretolamna appendiculata [*partim*]; Siverson 1996: 826, pl. 3: 5, 6.

Cretalamna appendiculata; Siverson 1999: fig. 6.1A, B.

Etymology: Combination of *catoxys* (Greek), very sharp, and *odus* (Greek), tooth. The name refers to the unusually sharp cutting edges on the cusp in the first and second lower anterior teeth.

Type material: Holotype: First upper right anterior tooth, WAM 09.6.2; Fig. 20A, 'Main Site'. Paratypes: WAM 98.11.7 (Siverson 1999: fig. 6.1), 09.6.1, 4-7, 9, 15-21, 11.12.2-3, 'Main Site'; WAM 09.6.8, 'New Site'; WAM 09.6.12, 'Camp Site'.

Type horizon: Surface collected from the uppermost 2-3 m of the Gearle Siltstone (middle Cenomanian).

Type locality: CY Creek, Giralia Anticline, Western Australia.

Material.—44 teeth, including WAM 09.6.3, 10-11, 13, 10.9.7-39, 'Main Site'; WAM 10.9.1, 'New Site; WAM 09.6.14, 10.9.2-6, 'Camp Site'.

Diagnosis.—Anterior teeth equipped with slender cusp; straight, very slightly curved or moderately distally inclined. Outer margin of cusplets more-or-less vertical on upper anterior teeth. Root symmetrical in labial/lingual views on first upper and lower anterior teeth but asymmetrical in basal view with one lobe more compressed than the other. Lingual protuberance of root poorly demarcated in basal view in upper anterior teeth but highly protruding in profile view, overhanging the neck. Most upper lateroposterior teeth equipped with rounded cusplets, lacking distinct apex.

Description

First upper anterior tooth file.—Four teeth are referred to the first upper anterior file. They are all similar in size and overall morphology and can be characterised by their symmetrical or near-symmetrical root and very slightly distally curved or inclined cusp. One of the teeth is nearly perfectly preserved and designated as holotype for this species (Fig. 20A). It is slightly larger than the other three teeth and, at 24 mm in height, is the largest tooth of this species in our collection. The lobes of the root are more acute in the other three teeth (Fig. 20B$_3$), but this is probably largely a result of their slightly corroded preservation. The lateral cusplets are small with a rather blunt apex on all four teeth. The root is massive in the well-preserved holotype with a prominent lingual protuberance overhanging the neck (Fig. 20A$_2$).

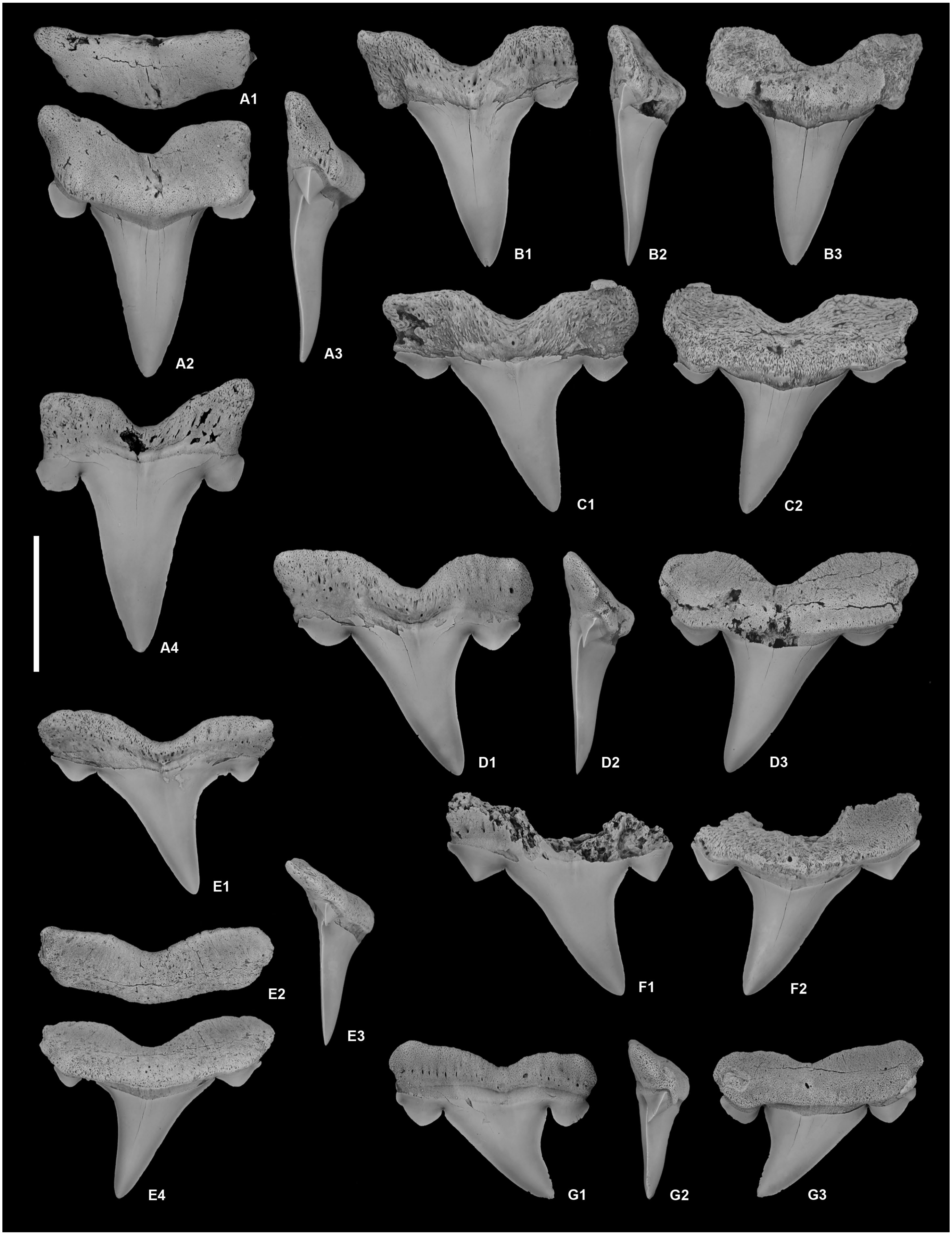
Second upper anterior tooth file.—A single tooth is assigned to this file (Fig. 20C). The apex is worn down, almost certainly from prey manipulation, and as preserved, the tooth measures 17 mm in height. The cusp is markedly distally bent. As in the teeth assigned to the first upper anterior file, the cusplets are very small. The root is nearly symmetrical in labial/lingual views with a slightly less tightly curved basal edge of the root in labial/lingual views, compared to the teeth referred to the first upper anterior file.

Upper lateroposterior teeth.—Teeth, from this part of the jaw, have a slender but labiolingually thick, slightly recurved (Fig. 21A$_2$) to strongly distally curved cusps (more posteriorly situated teeth; Fig. 21G$_3$). The lateral cusplets are low with an unusually blunt and poorly defined apex in most teeth (e.g. Fig. 21D$_1$). The cutting edges are sigmoidal (most anteriorly situated teeth; Fig. 21A$_3$) to straight in profile view (Fig. 21E$_3$). The median indentation of the basal edge of the root is of *C. deschutteri* type, forming a wide V with a rounded apex. In basal view, the lingual protuberance is wide but poorly demarcated from the rest of the root's lingual edge (Fig. 21E$_2$).

First lower anterior tooth file.—A single, 18 mm high tooth is referred to this file. The tooth has a bleached enameloid and has sustained some corrosion of the root along the lingual root-neck boundary and on the inside of one of the lobes (the latter damage is minor). Apart from these slight imperfections the tooth is well preserved. The cusp is symmetrical and narrow. Its middle third is mesio-distally concave (Fig. 20E$_1$). There is one pair of small cusplets. The root is massive, nearly perfectly symmetrical and with a large lingual

←

Fig. 20. *Cretalamna catoxodon* sp. nov., upper and lower anterior teeth, uppermost Gearle Siltstone (middle Cenomanian; Zone CC10a), CY Creek, Giralia Range, Western Australia. All specimens prefixed by WAM; scale bar represents 10 mm. **A**. 09.6.2, holotype, right A1?; lingual (A$_1$), profile (A$_2$), labial (A$_3$), and basal (A$_4$) views. **B**. 09.6.1, paratype, right A1?; lingual (B$_1$), basal (B$_2$), labial (B$_3$), and profile (B$_4$) views. **C**. 09.6.5, paratype, left A2?; basal (C$_1$), labial (C$_2$), lingual (C$_3$), and profile (C$_4$) views. **D**. 09.6.6, paratype, left a2?; labial (D$_1$) and lingual (D$_2$) views. **E**. 09.6.4, paratype, left a1?; labial (E$_1$), lingual (E$_2$), basal (E$_3$), and profile (E$_4$) views. **F**. 09.6.8, paratype, left a2?; labial (F$_1$), profile (F$_2$), and lingual (F$_3$) views.


A1
A2
A3
A4
B1
B2
B3
C1
C2
D1
D2
D3
E1
E2
E3
E4
F1
F2
G1
G2
G3

protuberance. The extremities of the lobes are rather acute.

Second lower anterior tooth file.—Two teeth are referred to the a2 file. One, 22 mm high, is somewhat corroded (Fig. 20F), whereas the other, larger tooth is severely corroded (Fig. 20D). The latter measures nearly 23 mm in height but

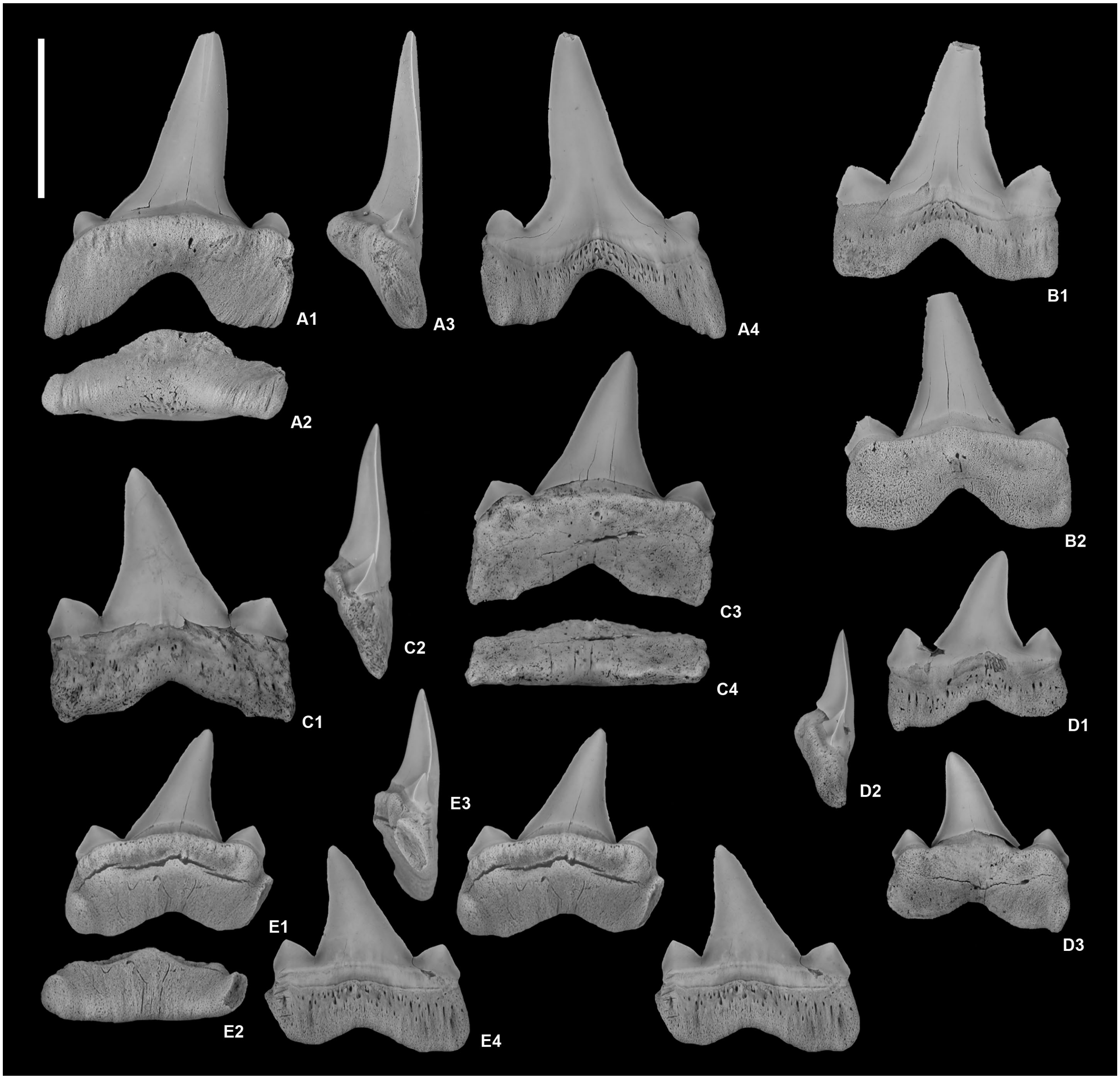


Fig. 22. *Cretalamna catoxodon* sp. nov., lower lateroposterior teeth, uppermost Gearle Siltstone (middle Cenomanian; Zone CC10a), CY Creek, Giralia Range, Western Australia. All specimens paratypes and prefixed by WAM; scale bar represents 10 mm. **A**. 11.12.2, right lp1?; lingual (A_1), basal (A_2), profile (A_3), and labial (A_4) views. **B**. 11.12.3, left lp4?; labial (B_1) and lingual (B_2) views. **C**. 09.6.17, right lp6?; labial (C_1), profile (C_2), lingual (C_3), and basal (C_4) views. **D**. 09.6.20, left lp7?; labial (D_1), profile (D_2), and lingual (D_3) views. **E**. 09.6.19, right lp7?; lingual (E_1), basal (E_2), profile (E_3), and labial (E_4) views.

← Fig. 21. *Cretalamna catoxodon* sp. nov., upper lateroposterior teeth, uppermost Gearle Siltstone (middle Cenomanian; Zone CC10a), CY Creek, Giralia Range, Western Australia. All specimens paratypes and prefixed by WAM; scale bar represents 10 mm. **A**. 09.6.7, right LP1?; basal (A_1), lingual (A_2), profile (A_3), and labial (A_4) views. **B**. 09.6.9, left LP2?; labial (B_1), profile (B_2), and lingual (B_3) views. **C**. 09.6.12, left LP4?; labial (C_1) and lingual (C_2) views. **D**. 09.6.15, left LP5?; labial (D_1), profile (D_2), and lingual (D_3) views. **E**. 09.6.16, left LP6?; labial (E_1), basal (E_2), profile (E_3), and lingual (E_4) views. **F**. 09.6.18, left LP6?; labial (F_1) and lingual (F_2) views. **G**. 09.6.21, left LP7?; labial (G_1), profile (G_2), and lingual (G_3) views.

would have been 24-25 mm high originally. The two teeth differ from the assigned a1 tooth by their asymmetrical root and wide-based cusp.

Lower lateroposterior tooth files.—The cusp is relatively upright in lower lateroposterior teeth and the cusplets have typically a well-defined apex. The root is deeper in lower

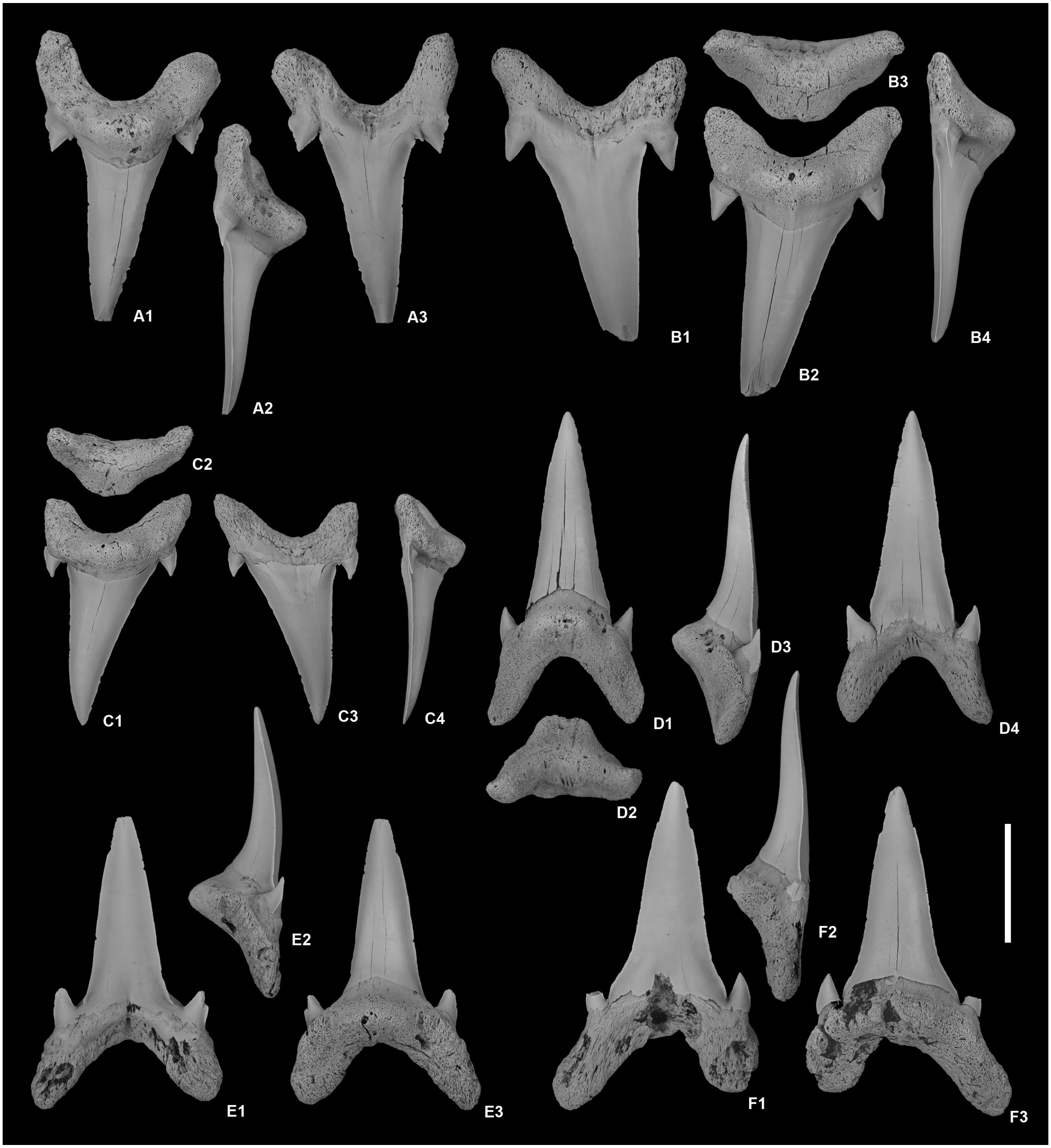


Fig. 23. *Kenolamna gunsoni* gen. nov., upper and lower anterior teeth, uppermost Gearle Siltstone (middle Cenomanian; Zone CC10a), CY Creek, Giralia Range, Western Australia. All specimens prefixed by WAM; scale bar represents 10 mm. **A**. 09.6.22, left A1?; lingual (A_1), profile (A_2), and labial (A_3) views. **B**. 09.6.24, left A2?; labial (B_1), lingual (B_2), basal (B_3), and profile (B_4) views. **C**. 09.6.26, left A3?; lingual (C_1), basal (C_2), labial (C_3), and profile (C_4) views. **D**. 09.6.23, left a1?; lingual (D_1), basal (D_2), profile (D_3), and labial (D_4) views. **E**. 09.6.25, left a2?; labial (E_1), profile (E_2), and lingual (E_3) views. **F**. 09.6.27, left a3?; labial (F_1), profile (F_2), and lingual (F_3) views.

jaw teeth than it is in the corresponding upper jaw teeth (Figs. 21G$_3$, 22E$_1$) and does not expand laterally beyond the lateral demarcation of the crown to the same extent as it does in upper lateroposterior teeth (Figs. 21D$_1$, 22B$_1$).

Comparison.—*Cretalamna catoxodon* sp. nov. cannot readily be placed in any of the three species groups recognised in the Turonian-Campanian of the Northern Hemisphere. Its teeth resemble those of the slender-toothed *C. ewelli* sp. nov. from the Smoky Hill Chalk in some aspects but differs, e.g. in lacking a typical A3 tooth with a labially curved cusp in profile view and a labiolingually compressed distal lobe of the root. Lateroposterior teeth of *C. catoxodon* sp. nov., particularly in the upper jaw, differ from those of *C. ewelli* sp. nov. by having blunt cusplets in a much larger percentage of the teeth. The putative third upper jaw tooth in *C. catoxodon* sp. nov. has a sigmoidally curved cusp in profile view and possess a distal lobe much thicker than that in *C. ewelli* sp. nov. and *C. gertericorum* sp. nov.

Remarks.—Underwood et al. (2011: fig. 4) illustrated six teeth from the early Cenomanian part of the Karai Formation of the Cauvery Basin, Tamil Nadu, India, as *Cretalamna appendiculata*. We disagree with the assigned position of at least one of the teeth (Underwood et al. 2011: fig. 4C, D), which they cautiously referred to the third lower anterior file. The shape of the root and the slightly recurved cusp indicates that it is the third upper jaw tooth. Third lower jaw teeth in *Cretalamna* would typically have a more robust root with a rather tightly curved basal edge in labial/lingual views. One of the teeth referred to the first lower lateral file (Underwood et al. 2011: fig. 4E, F) might be a LP1 or LP2 but the lack of profile and basal images makes it difficult to fully evaluate the positional assignment of the tooth. Teeth of *C. catoxodon* sp. nov. with a near-identical labial/lingual outline have a profile view typical of upper jaw teeth (Fig. 21B$_2$); although, probable first lower lateroposterior teeth have a similar labial/lingual outline. The latter differ in profile view from the corresponding upper jaw teeth by their slightly lingually curved cutting edges and more protruding protuberance (Fig. 22A). The median indentation of the basal edge of the root is deeper in probable lp1s than it is in the corresponding upper jaw teeth. The Indian taxon appears to represent an undescribed species of *Cretalamna*.

Genus *Kenolamna* nov.

Type species: By original designation, *Cretalamna gunsoni* Siverson, 1996.

Etymology: Combination of Ken (after the former Curator of Palaeontology at the Western Australian Museum, Kenneth McNamara, in recognition of his work on various groups of fossils from Western Australia) and *Lamna*, the genus name for Porbeagle sharks.

Diagnosis.—Upper anterior teeth with cusp labially curved in profile view and straight, distally inclined or recurved in labial/lingual views. Lower anterior teeth with cusp lingually curved in profile view and straight in labial/lingual views. Root gracile in all anterior teeth. Cusplets, present on all teeth, often taller than wide and with elongated, concave outer cutting edge. Posteriorly situated lower lateroposterior teeth taller than wide. Posteriorly situated upper lateroposterior teeth with basal face of root set almost at right angle to labial face of crown in profile view.

Kenolamna gunsoni (Siverson, 1996)

Figs. 19D, 23-25

Cretolamna gunsoni; Siverson 1996: 829, pl. 3: 9-13.
Cretalamna gunsoni; Siverson 1999: 52, fig. 4.

Holotype: WAM 95.7.49, an A1 (originally described as an A2). Holotype illustrated by Siverson (1996: text-fig. 3, pl. 3: 9-11). The precise age of the type stratum is yet to be determined. The overlying basal part of the Haycock Marl yields *Cretoxyrhina* teeth comparable in morphology to those from the Greenhorn Limestone in the Western Interior Seaway of North America.

Type horizon:'Upper Gearle Siltstone' (previously referred to as the uppermost Alinga Formation at Thirindine Point), 0.5 m below the base of the Haycock Marl (= Beedagong Claystone of Siverson, 1996),

Type locality: Thirindine Point East, Pillawarra Plateau, Southern Carnarvon Basin, Western Australia.

Material: 73 teeth, including WAM 09.6.22, '*Cardabiodon* Site', tooth found *in situ*, 5 cm below the top of the Gearle Siltstone; WAM 98.11.1, 5, 09.6.23-39, 10.9.53-91, 11.12.4, 'Main Site; WAM 10.9.40-41, 'New Site'; WAM 10.9.42-52, 'Camp Site'.

Emended diagnosis.—As for genus until additional species of the genus are described.

Description

First upper anterior tooth file.—The best preserved tooth assigned to the A1 file is described and illustrated (Fig. 23A). As preserved, the specimen is 24 mm high but would originally have been slightly taller. The cusp is somewhat distally directed. In profile view, the labial face of the tooth is slightly concave (Fig. 23A$_2$). The basal view of the root is of limited use for comparison as portions of the tall lingual protuberance and the lingual side of the distal lobe are missing. As a result of the corrosion of the root's basal side, the U-shape of the basal edge of the root in labial/lingual views appears slightly more pronounced than it would have originally.

Second upper anterior tooth file.—Several teeth are referred to this file. Collectively, they differ from the teeth assigned to the first upper anterior file by having a slightly less tightly curved basal edge of the (near perfectly symmetrical) root and a distinctly distally inclined and more labiolingually compressed cusp. The best preserved example measures 24 mm in height (Fig. 23B). The apex of the cusp is worn as a result of prey manipulation, which has reduced the original height by 1-2 mm. The root is almost perfectly symmetrical in this specimen, displaying relatively acute lobes.

Third upper anterior tooth file.—Teeth referred to this file have a cusp that is recurved in labial/lingual views (Fig. 23C$_1$, C$_3$) and labially curved in profile view (Fig. 23C$_4$). They are similar in height to the inferred A1 and A2 but have a somewhat broader cusp. The root is markedly asymmetri-


A1
A2
B1
B2
B3
C1
C2
D1
D2
D3
D4
E1
E2
E3
F1
F2
F3
G1
G2
G3
H1
H2
H3
H4

cal in most A3's, with an elongated mesial lobe. The illustrated example (Fig. 23C) is considerably smaller than some of the other teeth referrable to the A3 position but happened to be the best preserved A3.

Upper lateroposterior tooth files.—The teeth (measuring up to an estimated 26 mm in height) from the upper lateroposterior hollow have a tall, slightly recurved (LP1; Fig. $24A_1$) to strongly distally curved cusp. The LP1 is significantly smaller than the adjacent A3 and LP2 and has a tightly curved basal edge of the root. The recurved cusp of the LP1 is similar to that of the A3 (in labial/lingual views) but it is more labio-lingually compressed, relatively shorter and has

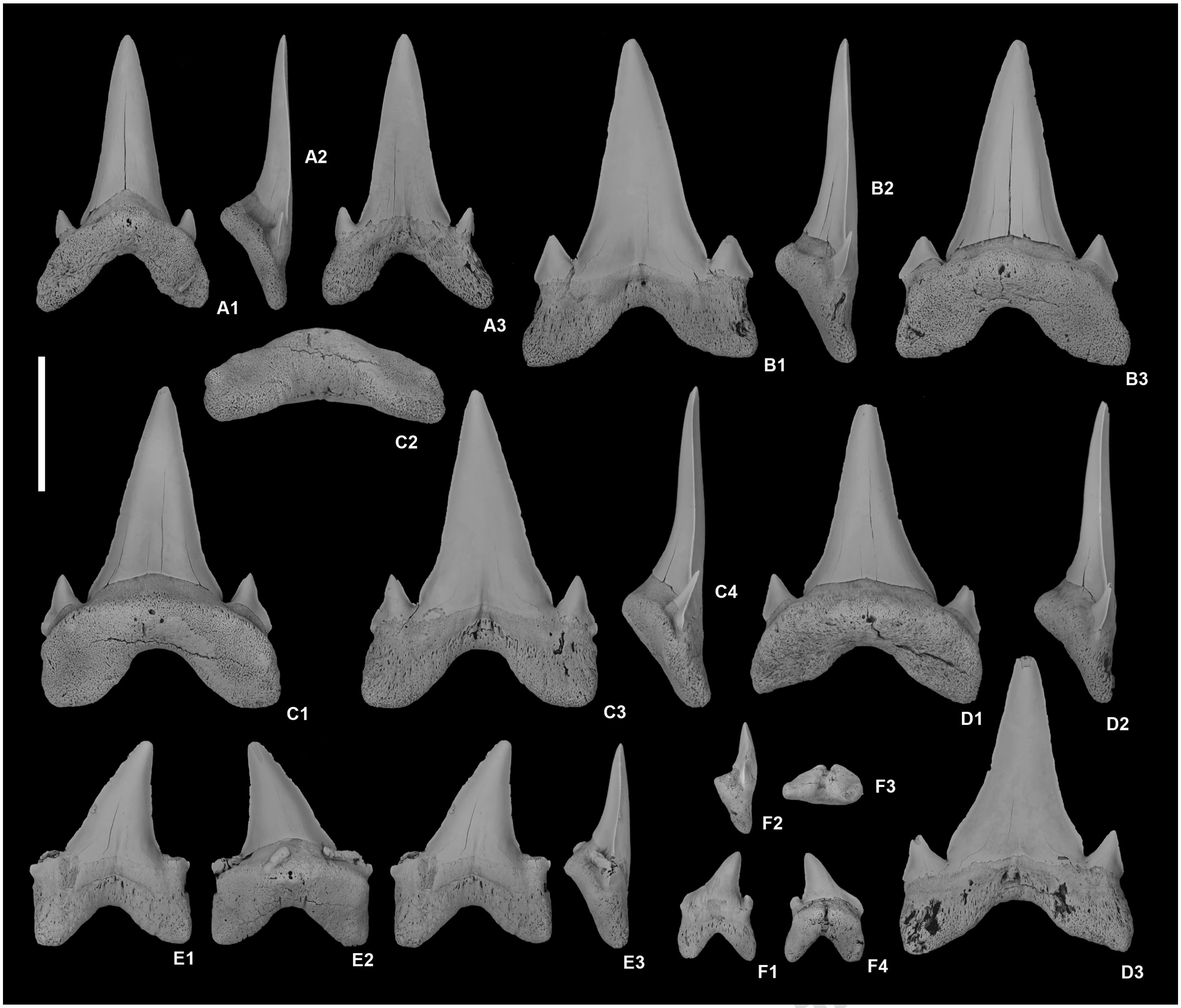


Fig. 25. *Kenolamna gunsoni* gen. nov., lower lateroposterior teeth, uppermost Gearle Siltstone (middle Cenomanian; Zone CC10a), CY Creek, Giralia Range, Western Australia. All specimens prefixed by WAM; scale bar represents 10 mm. **A**. 09.6.29, right lp1? from a juvenile individual; lingual (A_1), profile (A_2), and labial (A_3) views. **B**. 09.6.32, left lp1?; labial (B_1), profile (B_2), and lingual (B_3) views. **C**. 09.6.31, left lp1?; lingual (C_1), basal (C_2), labial (C_3), and profile (C_4) views. **D**. 09.6.35, left lp2?; lingual (D_1), profile (D_2), and labial (D_3) views. **E**. 09.6.38, left lp5?; labial (E_1), lingual (E_2), and profile (E_3) views. **F**. 11.12.4, left lp9?; labial (F_1), profile (F_2), basal (F_3), and lingual (F_4) views.

← Fig. 24. *Kenolamna gunsoni* sp. nov., upper lateroposterior teeth, uppermost Gearle Siltstone (middle Cenomanian; Zone CC10a), CY Creek, Giralia Range, Western Australia. All specimens prefixed by WAM; scale bar represents 10 mm. **A**. 10.9.40, left LP1?; labial (A_1) and profile (A_2) views. **B**. 09.6.28, left LP2?; labial (B_1), basal (B_2), and lingual (B_3) views. **C**. 09.6.33, right LP3?; labial (C_1) and profile (C_2) views. **D**. 09.6.30, right LP3?; basal (D_1), lingual (D_2), profile (D_3), and labial (D_4) views. **E**. 09.6.34, left LP4?; labial (E_1), profile (E_2), and lingual (E_3) views. **F**. 09.6.36, right LP5?; labial (F_1), profile (F_2), and lingual (F_3) views. **G**. 09.6.39, right LP6?; labial (G_1), profile (G_2), and lingual (G_3) views. **H**. 09.6.37, right LP5?; lingual (H_1), basal (H_2), labial (H_3), and profile (H_4) views.

a straight labial face in profile view (labially curved in the A3). In profile view, the labial face of the teeth is progressively more concave, moving posteriorly through the upper lateroposterior files. A concave profile view characterises upper lateroposterior teeth of most modern macrophagous lamniform sharks but it is particularly pronounced in this Cretaceous species (Fig. 24H_4). A pair of relatively large and sharp cusplets accompanies the labiolingually compressed cusp. The inner cutting edge of the cusplets is shorter than the outer edge. The root exhibits a deeply notched basal edge and sub-rectangular lobes.

First lower anterior tooth file.—Two relatively well-preserved teeth can be referred to the a1 position with some confidence, one 26mm high (Fig. 23D) and the other 28 mm high. The basal edge of the root is tightly curved in both specimens. The cusp is tall and perfectly symmetrical in one of the two teeth (Fig. 23D) but slightly recurved in the other tooth. In profile view, the labial side of the cusp is moderately or strongly lingually curved. The cusplets are erect or slightly divergent.

Second lower anterior tooth file.—Teeth assigned to the a2 position differ from first lower anterior teeth by having a very slightly distally bent cusp (as opposed to a perfectly straight or slightly recurved cusp) and a wider, asymmetrical root with a mesial lobe longer than the distal lobe. Like all teeth assigned to the lower anterior files, the cusp is lingually curved, giving the labial face of the tooth a convex profile (Fig. 23E_2).

Third lower anterior tooth file.—A 27 mm high tooth from a large individual is referred to the a3 position (additional to a few poorly preserved but probable third lower anteriors). The outline of the root is reasonably complete, but large sections of the root are missing on both the labial and lingual side (Fig. 23F_1, F_3). The cusp is barely inclined in labial/lingual views and increases rapidly in width in its basal part. In profile view, the labial side of the tooth is moderately lingually curved. The mesial lobe is slender and elongated whereas the distal lobe is broader and shorter.

Lower lateroposterior tooth files.—The teeth from the lower lateroposterior hollows are up to 24 mm high. The cusp is straight (in anteriorly situated teeth) to moderately distally curved or inclined (in posteriorly situated teeth). The cusp is labiolingually compressed but not to the same degree as in upper lateroposterior teeth. In profile view, the labial side of the cusp is typically straight in anteriorly situated teeth (e.g. Fig. 25C_4) and lingually curved in more posteriorly situated teeth (Fig. 25E_3, F_2). The root and cusplets are similar to those in upper lateroposterior teeth.

Comparison.—The range of tooth-morphologies in *Kenolamna* gen. nov. most closely resembles that of *Cretalamna* and *Palaeocarcharodon*.

The dentition differs from that of *Cretalamna* in the following aspects: (1) the LP1 is not significantly smaller than the other anteriorly situated upper lateroposterior teeth in LACM 128126, the only *Cretalamna* specimen with a preserved palatoquadrate showing *in situ* teeth across the anterior/lateroposterior hollows boundary (Fig. 13B). In contrast, evidence at hand [presence of small, labiolingually compressed teeth with a recurved cusp, large cusplets and a flat labial face in profile view (latter two characters separating the teeth from the otherwise similar A3)] indicate that the LP1 is reduced in size compared to the adjacent teeth in *Kenolamna* gen. nov.; (2) posteriorly situated lateroposterior teeth in *Cretalamna* are wider than tall and have quadrangular root-lobes. Posteriorly situated teeth of *Kenolamna* gen. nov. have rounded to acute root-lobes and are taller than wide; (3) cusplets are taller than wide in *Kenolamna* gen. nov. but typically wider than tall in *Cretalamna*.

Differences between *Kenolamna* gen. nov. and *Palaeocarcharodon* include: (1) cutting edges are smooth in *Kenolamna* gen. nov. compared with smooth to strongly serrated in *Palaeocarcharodon* (Cappetta 2012: fig: 238A-E); (2) anterior teeth of *Palaeocarcharodon* have a broad, labiolingually compressed cusp, whereas the corresponding teeth in *Kenolamna* gen. nov. are equipped with a slender, slightly to moderately compressed cusp; (3) the basal edge of the root is more deeply excavated medially in *Kenolamna* gen. nov. than it is in *Palaeocarcharodon*.

Remarks.—There are a number of similarities in tooth morphology (and total range of tooth-types) between *Kenolamna gunsoni* gen. nov. and the Paleocene taxon *Palaeocarcharodon orientalis*. In both species the cusp is strongly labiolingually compressed in lateroposterior files (although primarily in the upper jaw in the former), the inner edge of the cusplets is shorter than the outer edge, and the labial face of the tooth is strongly concave in profile view in posteriorly situated upper lateroposterior teeth (Dartevelle and Casier 1943: pl. 11: 1b, Fig. 24H_4). An origin of *Palaeocarcharodon* from a species of *Kenolamna* in the Southern Hemisphere could explain the current lack of a plausible ancestor of the former in the comparatively well researched Late Cretaceous of the Northern Hemisphere.

The assignment of *Kenolamna* gen. nov., and by inference, *Palaeocarcharodon*, to the Otodontidae is based on the curvature of the cusps on the upper anterior teeth [slightly curved or inclined (A1), moderately distally inclined (A2) and recurved (A3)] and their similar size. The morphology and relative size of the upper anterior teeth strongly resembles those of *Cretalamna* of the *C. borealis* group (Fig. 12A, C, E), but this morphology is in stark contrast to those of other Cretaceous lamniforms known from associated/articulated dentitions (*Cretoxyrhina*, *Archaeolamna* Siverson, 1992*a*, *Cardabiodon* Siverson, 1999, *Dwardius* Siverson, 1999, and *Paraisurus* Glikman, 1957). The commissural teeth of *Kenolamna* gen. nov. are, however, quite different from the laterally expanded ones in *Cretalamna*; *Kenolamna* may have had a more typical ‘lamnoid tooth-pattern’ (see Siverson et al. 2013 for a discussion of the term) than did *Cretalamna*, with a disjunct transition in tooth size between the upper anterior and lateroposterior teeth (Fig. 19D). Because of the latter two differences between *Cretalamna* and *Kenolamna* gen. nov. (the latter admittedly largely inferred as it depends on the accuracy of the tooth file assignment of a single tooth-type), we regard our referral of *Kenolamna* gen. nov. (and *Palaeocarcharodon*) to the Otodontidae as tentative.

Palaeoecology

Tooth wear indicates markedly different feeding habits and/or tooth-replacement rates in *C. borealis* compared with the sympatric *C. sarcoportheta* sp. nov. Teeth of the former, particularly large specimens, show very heavy wear, either in the form of a rounded apex of the main cusp (Figs. $9B_1$, C_4, $10A_1$) or by a broken and subsequently abraded cusp (Figs. $9A_1$, D_3, $10B_1$). In *C. sarcoportheta* sp. nov., on the other hand, the tip of the cusp shows little wear on most teeth (compare, e.g. the upper anteriors in Fig. 4 with those in Fig. 9A-C). Two out of four illustrated teeth of *C. borealis* from the Mount Laurel Formation, Delaware, USA, described by Lauginiger and Hartstein (1983: pl. 2: 11-14) as *C. appendiculata pachyrhiza*, show similar heavy wear of the cusp. Most teeth of the other two *C. borealis*-group species recognised herein, *C. gertericorum* sp. nov. and *C. ewelli* sp. nov. show little wear of the cusp. As the teeth of both species are considerably smaller than are those of *C. borealis* it is possible that a shift in diet causing the extreme wear seen in many of the larger teeth of *C. borealis*, took place at a given absolute body size in the *C. borealis* group. There is little if any difference in apical wear of the cusp between *C. catoxodon* sp. nov. and *Kenolamna gunsoni* gen. nov. and between the three *Cretalamna* species in the *M. labiatus* Zone of the SECAB quarry. The identification of *C. borealis* as a predator or scavenger of an elasmosaur, excavated from the early Santonian Tamayama Formation, central Japan (see discussion of *C. borealis*) is noteworthy given the severe damage to the cusp that characterises large *C. borealis* teeth from the early Campanian of the Kristianstad Basin. Marine reptiles (turtles, mosasaurs and juvenile plesiosaurs) were abundant in the area (Persson 1959; Lindgren and Siverson 2002, 2004, 2005) and it is possible that adult *C. borealis* preyed on some of these tetrapods to a significant degree, perhaps explaining the extreme wear of their teeth.

Isolated teeth of *Cretalamna* from the various localities show modest variation in size for comparable tooth files. The size ratio between the largest and smallest comparable teeth (measured by tooth-width) is smaller than 2:1 in the material examined (e.g. the largest anteriorly situated upper lateroposteriors are less than twice as wide as are the smallest anteriorly situated upper lateroposteriors in *C. sarcoportheta* sp. nov.). Although this can be interpreted in a number of ways (e.g. by size segregation, niche partitioning and/or collecting bias toward larger teeth), the perhaps most plausible explanation, given that the ratio is low in all eight species examined regardless of collecting technique deployed, is that females of *Cretalamna* gave birth to pups of large relative size, as is the case with e.g. the extant lamniform shark *Carcharias taurus* Rafinesque, 1810 (see Compagno 2001). We note, however, that the relative size-range ratio for a given tooth file is similar in *C. sarcoportheta* sp. nov. and *C. ewelli* sp. nov. The former is based on a large number of teeth extracted from nearshore strata (sieving of bulk samples and thus no collecting bias towards larger teeth), whereas the latter is based on a much smaller number of surface collected teeth (clear bias towards larger, more anteriorly situated teeth) from offshore sediments laid down in a much deeper-water palaeoenvironment. Further collecting in the Smoky Hill Chalk Member might increase the size ratio well beyond 2:1 (for the more diagnostic anterior teeth such as the A2) which would then indicate that *Cretalamna* pups spent their first few years in deeper, offshore environments. In *Cretoxyrhina*, a large size range, exceeding a 2:1 ratio, is the rule rather than the exception when abundant material is at hand (Siverson and Lindgren 2005: fig. 2C, D; Siverson et al. 2013: fig. 5J, Q) and it is likely that *Cardabiodon*, another early Late Cretaceous lamniform shark, likewise gave birth to small pups (Siverson and Lindgren 2005: fig. 3).

Conclusions

The traditional view of *Cretalamna appendiculata* as a single, incredibly slowly evolving species, lasting 50 Ma (latest Albian to the Ypresian), is demonstrably incorrect. The current study has not revealed a single case where a species of *C. appendiculata* type has been shown to range across more than two stages. With a minimum range of 10-11 Myr. from early Santonian (Tamayama Formation, central Japan) to early late Campanian, in the three-fold division of the stage as used in North America (basal Mount Laurel Sand, Delaware, USA), *C. borealis* has currently the longest temporal range recorded of all *Cretalamna* of *C. appendiculata* type.

We have described eight species of *C. appendiculata* type in the Late Cretaceous alone and have indicated the presence of additional, undescribed or poorly diagnosed species. Some deposits contain as many as three coexisting species of *Cretalamna*. The seven species recorded from the Turonian-early Campanian of the Northern Hemisphere are referred to three distinct species groups, including the *C. appendiculata* group, the *C. borealis* group and the *C. hattini* group. Species of the *C. appendiculata* group are diagnosed by their labiolingually thick cusp in all tooth files, strong root asymmetry in basal view (distal lobe compressed relative to the mesial lobe) in anteriorly situated upper lateroposterior teeth, massive root in lower anterior teeth, triangular basal view with a poorly demarcated protuberance in lower anterior teeth, and laterally protruding lingual protuberance in profile view in lateroposterior teeth (especially in *C. sarcoportheta* sp. nov.). Species of the *C. borealis* group are diagnosed by the slenderness of the cusp in anterior teeth, the presence of a highly diagnostic tooth type (regarded herein as the A3) with a recurved cusp (markedly labially curved in profile view) and a labiolingually compressed distal lobe of the root, a strongly lingually curved cusp (profile view) in lower anterior teeth, a rectangular basal view of the root in most upper lateroposterior files, a very small but well defined protuberance in basal view of lateroposterior teeth, and laterally moderately expanded commissural teeth. Species of the *C. hattini* group are diagnosed by the well demarcated lingual protuberance of the root in basal view in upper and lower anterior teeth, sloping rather than horizontal legs of the lingual edge of the root in basal view in lateroposterior teeth, low and thin root in lateroposterior teeth, moderately protruding lingual protuberance of the root in profile view in all tooth files, and very wide median indentation of the basal edge of the root in lateroposterior teeth, which forms a wide V with a rounded apex. The middle Cenomanian *C. catoxodon* sp. nov. from Western Australia cannot be placed in any of the three groups with confidence at this stage.

Heavy wear on a majority of the teeth from large individuals of the large-toothed *C. borealis* found in deposits yielding abundant and diverse marine tetrapod remains (and numerous teeth of *C. sarcoportheta* sp. nov. showing very little wear on the vast majority of teeth) in combination with the direct association of shed teeth of this species with a shark-bitten elasmosaur skeleton provide some circumstantial evidence of tetrapod predation in this species.

Positive identification of teeth of *C. appendiculata* type at species level typically requires specimens with an uncorroded root. Even moderate abrasion/corrosion will result in reshaping of the edges of the root and a rounding of the lingual protuberance in basal and profile views. These changes will in many cases render the tooth indeterminable below genus level.

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References

Adolfssen, J.S. and Ward, D.J. In press. Neoselachians from the Danian (Early Paleocene) of Denmark. *Acta Palaeontologica Polonica*.

Agassiz, J.L.R. 1833–1844. *Recherches sur les poissons fossils*, 3. 390 pp. Imprimerie de Petitpierre, Neuchâtel.

Andreev, P. and Motchurova-Dekova, N. 2010. Checklist of the fossil shark and bony fish teeth (Elasmobranchii and Actinopterygii) housed at the National Museum of Natural History, Sofia. *Bulletin of the Natural History Museum* 3: 115-129.

Applegate, S.P. and Espinosa-Arrubarrena, L. 1996. The fossil history of *Carcharodon* and its possible ancestor, *Cretolamna*: A study in tooth identification. *In*: A.P. Klimley and D.G. Ainley (eds), *Great white sharks, the biology of* Carcharodon carcharias, 19–36. Academic Press, San Diego.

Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc, Algérie, Tunisie). *Service Géologie Maroc*, *Notes et Mémoires* 92: 1–372.

Averianov, A. and Popov, E. 1995. A new species of chimaeroid fish from the Upper Cretaceous of the Saratov region, Russia. *Palaeontology* 38: 659–664.

Becker, M.A., Wellner, R.W., Mallery, C.S., and Chamberlain, J.A. 2010. Chondrichthyans from the Lower Ferron Sandstone Member of the Mancos Shale (Upper Cretaceous: middle Turonian) of Emery and Carbon counties, Utah, USA. *Journal of Paleontology* 84: 248-266.

Berg, L.S. 1958. *System der rezenten und fossilen Fischartigen und Fische*. 310 pp. Deutscher Verlag Wissenschaft, Berlin.

Blair, S.A. and Watkins, D.K. 2009. High-resolution calcareous nannofossil biostratigraphy for the Coniacian/Santonian stage boundary, Western Interior Seaway. *Cretaceous Research* 30: 367-384.

Bogan, S. and Gallina, P.A. 2011. Consideraciones sobres el registro de *Hypolophodon* (Chondrichthyes, Myliobatiformes) en el techo de la Formacion Jagüel (Maastrichtiense), provincia de Río Negro, Argentina. *Studia Geologica Salmanticensia* 47: 57-67.

Bourdon, J. and Everhart, M.J. 2011. Analysis of an associated *Cretoxyrhina mantelli* dentition from the Late Cretaceous (Smoky Hill Chalk, Late Coniacian) of western Kansas. *Transactions of the Kansas Academy of Science* 114: 15-32.

Bourdon, J., Wright, K., Lucas, S.G., Spielmann, J.A., and Pence, R. 2011. Selachians from the Upper Cretaceous (Santonian) Hosta Tongue of the Point Lookout Sandstone, central New Mexico. *New Mexico Museum of Natural History and Science, Bulletin* 52: 1-54.

Brotzen, F. 1960. The Mesozoic of Scania, southern Sweden. *International Geological Congress*, *XXI Session*, *Norden 1960*. *Guide to excursions nos A 21 and C 16*, 15 pp.

Bruun-Petersen, J. 1975. Upper Cretaceous shelf limestone from Ignaberga, Scania (Sweden) and its diagenesis. *Congrès International de Sédimentologie* 9: 33–38.

Cappetta, H. 1977. Sélaciens nouveaux de l'Albien supérieur de Wissant (Pas-de-Calais). *Geobios* 10 : 967-973.

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

Cappetta, H. 2000. *Cretolamna* Glikman, 1958 (Chondrichthyes, Lamniformes): proposed confirmation as the correct original spelling (Case 3161). *Bulletin of zoological nomenclature* 57: 137.

Cappetta, H. 2012. Mesozoic and Cenozoic Elasmobranchii: teeth. Chondrichthyes. *In*: H.P. Schultze (ed.). *Handbook of palaeoichthyology*, 3E.

512 pp. Verlag Dr. Friedrich Pfeil, München.

Cappetta, H. and Case, G.R. 1975. Contribution à l'étude des sélaciens du groupe Monmouth (Campanien-Maestrichtien) du New Jersey. *Palaeontographica*, *Abteilung A* 151: 1–46.

Casier, E. 1960. Note sur la collection des poissons Paléocènes et Eocènes de l'Enclave de Cabinda (Congo). *Annales du Musée Royal du Congo Belge* 1: 1–48.

Christensen, W.K. 1975. Upper Cretaceous belemnites from the Kristianstad area in Scania. *Fossils and Strata* 7: 1–69.

Christensen, W.K. 1986. Upper Cretaceous belemnites from the Vomb trough in Scania, Sweden. *Sveriges Geologiska Undersökning* Ca57: 1–57.

Compagno, L.J.V. 2001. *FAO (Food and Agriculture Organization of the United Nations) Species Catalogue for Fishery Purposes, 1: Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date, Vol. 2: Bullhead, Mackerel and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. 269 pp. FAO, Rome.

Cook, T.D., Wilson, M.V.H., and Murray, A.M. 2008. A middle Cenomanian euselachian assemblage from the Dunvegan Formation of northwestern Alberta. *Canadian Journal of Earth Sciences* 45: 1185-1197.

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.

Cook, T.D., Wilson, M.V.H., Murray, A.M., Plint, G., Newbrey, M.G., and Everhart, M.J. In press. A high latitude euselachian assemblage from the early Turonian of Alberta, Canada. *Journal of Systematic Palaeontology*.

Cumbaa, S., Shimada, K., and Cook, T.D. 2010. Mid-Cretaceous vertebrate faunas of the Western Interior Seaway of North America and their evolutionary, paleobiogeographical, and paleoecological implications. *Paleogeography, Paleoclimatology, Paleoecology* 295: 199-214.

Cunningham, S.B. 2000. A comparison of isolated teeth of early Eocene *Striatolamia macrota* (Chondrichthyes, Lamniformes), with those of a Recent sand shark, *Carcharias taurus*. *Tertiary Research* 20: 17-31.

Cuny, G., Martin, J.E., and Sarr, R. 2012. A neoselachian shark fauna from the Late Cretaceous of Senegal. *Cretaceous Research* 34: 107-115.

Dartevelle, E. and Casier, E. 1943. Les poissons fossiles du Bas-Congo et des regions voisines (premiere partie). *Annales du Museé du Congo Belge, A. Ser. 3* 2: 1–200.

Davis, J.W. 1890. On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society* 4: 363–434.

Dineley, D.L. and Metcalf, S.J. 1999. *Fossil fishes of Great Britain*. 675 pp. Joint Nature Conservation Committee, Peterborough.

Einarsson, E., Lindgren, J., Kear, B.P., and Siverson, M. 2010. Mosasaur bite marks on a plesiosaur propodial from the Campanian (Late Cretaceous) of southern Sweden. *GFF* 132: 123-128.

Eriksson, M., Lindgren, J., Chin, K., and Mansby, U. 2011. Coprolite morphotype from the Upper Cretaceous of Sweden: novel views on an ancient ecosystem and implications for coprolite taphonomy. *Lethaia* 44: 455-468.

Erlström, M. and Gabrielson, J. 1992. Petrology, fossil composition and depositional history of the Ignaberga limestone, Kristianstad Basin, Scania. *Sveriges Geologiska Undersökning* Ca80: 1–30.

Everhart, M.J. 2005. Earliest record of the genus *Tylosaurus* (Squamata; Mosasauridae) from the Fort Hays Limestone (Lower Coniacian) of western Kansas. *Transactions of the Kansas Academy of Science* 2005: 149-155.

Glikman, L.S. 1957. Genetic relations of the Lamnidae and Odontaspidae and new genera of lamnids from the Upper Cretaceous [in Russian]. *Trudy Geologicheskogo Muzeia Akademiia Nauk SSSR* 1: 110-117.

Glikman, L.S. 1958. Rates of evolution in lamnoid sharks [in Russian]. *Doklady Akademii Nauk SSSR* 123: 568–571.

Glikman, L.S. 1964. *Sharks of the Paleogene and their stratigraphic significance* [in Russian]. 229 pp. Nauka Press, Moscow-Leningrad.

Glikman, L.S. 1980. *Evolution of Cretaceous and Cenozoic lamnoid sharks* [in Russian]. 247 pp. Akademii Nauk SSSR, Moscow.

Hamm, S.A. and Shimada, K. 2007. The Late Cretaceous anacoracid shark, *Pseudocorax laevis* (Leriche), from the Niobrara Chalk of western Kansas. *Transactions of the Kansas Academy of Science* 110: 44-52.

Hamm, S.A. and Cicimurri, D.J. 2011. Early Coniacian (Late Cretaceous) selachian fauna from the basal Atco Formation, lower Austin Group, north central Texas. *Paludicola* 8: 107-127.

Hattin, D. E., Siemers, C. T., and Stewart, G. F. 1978. Upper Cretaceous stratigraphy and depositional environments of western Kansas. *Kansas Geological Survey, Guidebook Series* 3: 1-102.

Hattin, D. E. 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. *Kansas Geological Survey, Bulletin* 225: 1-108.

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

Herman, J. and Van Waes, H. 2012. Observations concernant l'evolution et la systématique de quelques Euselachii, Neoselachii et Batoidei (Pisces - Elasmobranchii), actuels et fossiles. *Geominpal Belgica* 2: 1-89.

Howe, R.W., Haig, D.W., and Apthorpe, M.C. 2000. Cenomanian-Coniacian transition from siliciclastic to carbonate marine deposition, Giralia Anticline, Southern Carnarvon Platform, Western Australia. *Cretaceous Research* 21: 517–551.

Jefferies, R.P.S. 1963. The stratigraphy of the *Actinocamax plenus* Subzone (Turonian) in the Anglo-Paris Basin. *Proceedings of the Geologists' Association* 74: 1-33.

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

Kriwet, J. and Benton, M.J. 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214: 181-194.

Kriwet, J., Klug, S., Canudo, J.I., and Cuenca-Bescos, G. 2008. A new Early Cretaceous lamniform shark (Chondrichthyes, Neoselachii). *Zoological Journal of the Linnean Society* 154: 278-290.

Lauginiger, E.M. and Hartstein, E.F. 1983. A guide to fossil sharks, skates, and rays from the Chesapeake and Delaware Canal area, Delaware. *Delaware Geological Survey Open File Report* 21:1-64.

Leriche, M. 1920. Sur des poissons fossiles de la région côtière du Congo et sur la présence de l'Eocènes dans cette région. *Comptes Rendus de l'Academie des Sciences Paris* 169: 479–481 [date of imprint 1919].

Lindgren, J. and Siverson, M. 2002. *Tylosaurus ivoensis*: a giant mosasaur from the Early Campanian of Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 93: 73–93.

Lindgren, J. and Siverson, M. 2004. The first record of the mosasaur *Clidastes* from Europe and its palaeogeographical implications. *Acta Palaeontologica Polonica* 49: 219-234.

Lindgren, J. and Siverson, M. 2005. *Halisaurus sternbergi*, a small mosasaur with an intercontinental distribution. *Journal of Paleontology* 79: 763-773.

Lindgren, J., Currie, P.J., Siverson, M., Rees, J., Cederström, P., and Lindgren, F. 2007. The first neoceratopsian dinosaur remains from Europe. *Palaeontology* 50: 929–937.

Linnaeus, C. 1758. *Systema naturae*, *10th ed.*, *vol. 1*. 824 pp. Salvi, Stockholm.

Lundegren, A. 1934. Kristianstadsområdets kritbildningar. *GFF* 56:125-313.

Manning, E.M. and Dockery, D.T. III. 1992. A guide to the Frankstown vertebrate fossil locality (Upper Cretaceous), Prentiss County, Mississippi. *Mississippi Department of Environmental Quality, geology circular* 4: 1–43.

Müller, A. and Diedrich, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoburger Wald (Nordrhein-Westfalen), NW- Deutschland). *Geologie und Paläontologie in Westfalen* 20: 1–105.

Müller, J. and Henle, J. 1838-41. *Systematische Beschreibung der Plagiostomen*. i-xxii + 200 pp, 60pls. Berlin.

Persson, P.O. 1959. Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). *Arkiv för Mineralogi och Geologi* 2: 431-478.

Persson, P.O. 1960. En intressant kritlokal på Ivö. *Skånes Natur* 47: 433-442.

Priem, F. 1897. Sur des dents d'élasmobranches de divers gisements Sénoniens (Villedieu, Meudon, Folx-les-Caves). *Bulletin de la Société Géologique de la France* 25: 40–56.

Purdy, R.W. 1996. Paleoecology of fossil white sharks. *In*: A.P. Klimley and D.G. Ainley (eds). *Great white sharks, the biology of Carcharodon carcharias*, 55–66. Academic Press, San Diego.

Purdy, R.W., Schneider, V.P., Applegate, S.P., McLellan, J.H., Meyer, R.L., and Slaughter, B.H. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. *In*: C.E. Ray and D.J. Bohaska (eds.), Geology and paleontology of the Lee Creek Mine, North Carolina, III. *Smithsonian Contributions to Paleobiology* 90: 71-202.

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

Retzler, A., Wilson, M.A., and Avni, Y. In press. Chondrichthyans from the Menuha Formation (Late Cretaceous: Santonian-early Campanian) of the Makhtesh Ramon region, sothern Israel. *Cretaceous Research*. In press.

Ride, W.D.L., Sabrosky, C.W., Bernardi, G., and Melville, R.V. (eds). 1985. *International code of zoological nomenclature*. 3rd edition. 338 pp. London, Berkely and Los Angeles.

Ride, W.D.L., Cogger, H.G., Dupuis, C., Kraus, O., Minelli, A., Thompson, F.C., and Tubbs, P.K. (eds). 2000. *International code of zoological nomenclature*. 4th edition. The International Trust for Zoological Nomenclature 1999. 306 pp. London.

Sato, T., Konishi, T., Hirayama, R., and Caldwell, M.W. 2012. A review of the Upper Cretaceous marine reptiles from Japan. *Cretaceous Research* 37: 319-340.

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

Shimada, K., Schumacher, B.A., Parkin, J.A., and Palermo, J.M. 2006. Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado. *Journal of Paleontology*, *supplement to no 2* 80: 1–45.

Shimada, K., Tsuihiji, T., Sato, T., and Hasegawa, Y. 2010. A remarkable case of a shark- bitten elasmosaurid plesiosaur. *Journal of Vertebrate Paleontology* 30: 592–597.

Sinzow, I.F. 1899. Notizen über die Jura-, Kreide- und Neogen-Ablagerungen der Gouvernements Saratow, Simbirsk, Samara und Orenburg. *Odessa Univirsitet, Zapiski*, 77: 1–106.

Siverson, M. 1992*a*. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. *Palaeontology* 35: 519–554.

Siverson, M. 1992*b*. Late Cretaceous *Paraorthacodus* (Palaeospinacidae, Neoselachii) from Sweden. *Journal of Paleontology* 66: 994–1001.

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

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 90: 49–66.

Siverson, M. and Lindgren, J. 2005. Late Cretaceous sharks *Cretoxyrhina* and *Cardabiodon* from Montana, USA. *Acta Palaeontologica Polonica* 50: 301–314.

Siverson, M., Lindgren, J., and Kelley, L.S. 2007. Anacoracid sharks from the Albian (Lower Cretaceous) Pawpaw Shale of Texas. *Palaeontology* 50: 939-950.

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

Sokolov, M. 1965. *Teeth evolution of some genera of Cretaceous sharks and reconstruction of their dentition* [in Russian]. 61 pp. Izdatel'stvo, Niedra.

Surlyk, F. 1973. Autecology and taxonomy of two Upper Cretaceous craniacean brachiopods. *Bulletin of the Geological Society of Denmark* 22: 219–243.

Surlyk, F. 1980. Upper Cretaceous and Danian outcrops in Scania and east Denmark. *The Upper Cretaceous and Danian of NW Europe. 26th International Geological Congress*. *Guide-book, excursion 069 A, Paris*, 31–74.

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

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

Vullo, R. 2005. Selachians from the type Campanian area (Late Cretaceous), Charentes, western France. *Cretaceous Research* 26: 609-632.

Ward, D.J. 2009. Sharks and rays. *In*: J.R. Young, A.S. Gale, R.I. Knight, and A.B. Smith (eds). *Fossils of the Gault Clay*, 275–299. The Palaeontological Association, London.

Welton, B.J. and Farish, R.F. 1993. *The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas*. 204 pp. Before Time, Dallas.

Williamson, T.E., Kirkland, J.I., and Lucas, S.G. 1993. Selachians from the Greenhorn cyclotheme ("Middle" Cretaceous: Cenomanian-Turonian), Black Mesa, Arizona, and the paleogeographic distribution of Late Cretaceous selachians. *Journal of Paleontology* 67: 447–474.

Woodward, A.S. 1889. *Catalogue of the fossil fishes in the British Museum* (*Natural History*). *1. Elasmobranchii*. xliv + 474 pp. British Museum (Natural History), London.

Zhelezko, V.I. 2000. The evolution teeth system of sharks of *Pseudoisurus* Gluckman, 1957 genus—the biggest pelagic sharks of Eurasia [in Russian]. *In*: B.I. Čuvasov (ed.). *Materialy po stratigrafii i paleontologii Urala 4*, 136–141 + 4 pls. Izdatel'stvo Uralskogo Otdeleniâ Rossijskoj Akademii Nauk, Ekanterinburg.

Zhelezko, V.I. and Kozlov, V.A. 1999. Elasmobranchii and Palaeogene biostratigraphy of Trans Urals and Central Asia [in Russian]. *In*: E.O. Amon (ed.). *Materialy po stratigrafii i paleontologii Urala 3*. 1–321. Izdatel'stvo Uralskogo Otdeleniâ Rossijskoj Akademii Nauk, Ekanterinburg

Appendix 1

Table. Individual magnifications of the teeth in Figure 19 (∑ set at 1.00 for each species).

Assigned position	*C. hattini*	*C. catoxodon*	*C. sarcoportheta*	*K. gunsoni*
A1	1.00	0.95	0.98	1.02
A2	1.00	1.10	1.10	0.94
A3				1.20
LP1	1.00	0.93	1.08	1.08
LP2	1.00	1.01	0.91	0.87
LP3	1.00		1.09	1.01
LP4	1.00	0.98	0.94	0.99
LP5	1.00	0.96	1.11	1.21
LP6		1.00	1.09	1.05
LP7	1.00	1.04	0.82	
LP8	1.00			
LP9	1.00		0.93	
LP10				
a1	1.00	1.13	1.01	1.01
a2	1.00	1.03	0.89	1.06
a3				0.90
lp1	1.00	0.98	1.02	0.90
lp2	1.00		1.15	0.92
lp3	1.00			
lp4	1.00	1.04	0.96	
lp5	1.00		1.02	0.98
lp6	1.00	0.90		
lp7	1.00	0.99	0.83	
lp8			1.05	
lp9				0.87

Appendix 2

LOCALITIES

CY Creek, Giralia Anticline, Southern Carnarvon Basin, Western Australia

WGS84 coordinates. 'Main Site', S22°53´23.8´´, E114°08´39.6´´; 'Camp Site', S22°53´27.5´´, E114°08´35.8´´; 'New Site', S22°53´29.2´´, E114°08´36.7´´, '*Cardabiodon* Site', S22°53´15.3´´, E114°08´38.6´´.

Stratigraphical logs. Siverson 1999: fig. 2; Howe et al., 2000: fig. 4.

Age. Middle Cenomanian nannofossil Zone CC10a (Howe et al. 2000).

Remarks. The uppermost part of the Gearle Siltstone is exposed in gullies and gently inclined slopes in the CY Creek area. The selachian material from the CY Creek localities was surface collected from the uppermost 2-3 m of the Gearle Siltstone during field expeditions organised by the Western Australian Museum and/or the School of Earth and Geographical Sciences, The University of Western Australia. The state of preservation of the selachian material is highly variable and ranges from recently exposed and therefore perfectly preserved teeth, to extremely bleached specimens. In most places where the uppermost Gearle Siltstone crops out, weathering of the outcrops has resulted in extensive mixing of selachian remains from this part of the sequence with younger fossil material from a nodule bed at the top of the Gearle Siltstone, the overlying thin (up to 0.5 m) late early Turonian Haycock Marl, and the nodule bed separating the latter from the Toolonga Calcilutite. Mixed assemblages are, wherever present, indicated by e.g. an abundance of

Cretoxyrhina mantelli (Agassiz, 1843) and the presence of species of *Ptychodus* Agassiz, 1839 other than *P. decurrens* Agassiz, 1843. Uppermost Gearle Siltstone, uncontaminated by the overlying units, yields a (surface collected) selachian macrofauna completely dominated by *Cretalamna catoxodon* sp. nov. and *Kenolamna gunsoni* gen. nov. Preliminary bulk sampling indicates a diverse, cool water selachian fauna dominated by *Protosqualus* Cappetta, 1977. The teeth of *C. catoxodon* sp. nov. and *K. gunsoni* gen. nov. included in this study are derived from three sites where a clean, uncontaminated surface of the uppermost Gearle Siltstone was present at the time of collecting. The location of the excavation pit for the holotype of *Cardabiodon ricki* Siverson, 1999 is 250 m north of the 'Main Site', at WGS84 coordinates S22°53´15.3´´, E114°08´38.6´´ (please note that the coordinates given for the holotype in Siverson 1999 are not in the global WGS84 datum standard).

Smoky Hill Chalk, Niobrara Formation, western Kansas, USA

Locality. Unnamed outcrop, Trego County.

WGS84 coordinates. N38°49´57´´, W100°03´49´´.

Stratigraphical log. The material was collected from a flat area (exposing approximately one metre of the Smoky Hill Chalk), situated stratigraphically 1-2 m below Hattin's (1982) Marker Unit 2. We refer to his log for Locality 1 (Hattin 1982) as it is situated close enough to the collecting site to be relevant.

Age. Late Coniacian.

Remarks. All teeth from the Trego County site included in this study were collected by Keith Ewell in 2004. Hamm and Shimada (2007) described a tooth of *Pseudocorax* Priem, 1897 from this locality.

Locality. Quinter South, Gove County.

WGS84 coordinates. N38°43´53.1´´, W100°13´39.7´´. A large number of isolated teeth (mainly *Squalicorax* spp.) were collected *in situ* at Quinter South by MS in 1998 and 1999 but GPS coordinates were not recorded for each individual tooth (although the stratigraphical position was noted). The *Cretalamna* tooth from Quinter South was found within a 100 m radius of the given coordinates.

Stratigraphical log. The single tooth of *C. ewelli* sp. nov. from this site was collected 0.3 m below the base of Hattin's (1982) Marker Unit 4. Hattin's (1982) log for his Locality 12 (situated less than 1 km north of the collecting site) is also applicable to the area where the tooth was found.

Age. Late Coniacian.

Remarks. The index fossil for the base of the Santonian, *Cladoceramus undulatoplicatus*, appears near the top of an approximately 15 metre thick interval, bounded by Marker Units 5 and 6 in the area (at Hattin's locality 13, see Blair and Watkins 2009).

Locality. Central Logan County, LACM Locality 6068 (more precise locality data on file at the LACM).

Stratigraphical log. Hattin et al. 1978: fig. 24.

Age. Earliest Campanian (Shimada 2007).

Remarks. LACM 128126 was collected from the upper part of the Smoky Hill Chalk. Shimada (2007) noted that the Smoky Hill Chalk at the collecting site ranges up to Hattin's Marker Unit 16 and assigned an earliest Campanian age to the specimen (a Campanian age is suggested by the label accompanying the specimen).

SECAB quarry, Bettrechies, northwestern France

WGS84 coordinates. N50°19´35.4´´, E3°45´18.4´´

Stratigraphical log. Jefferies (1963).

Age. *Mytiloides labiatus* Zone, early Turonian (Herman 1977).

Remarks. Mid-Cenomanian to mid-Turonian strata disconformably overlies Givetian (Middle Devonian) limestones in the SECAB quarry. Fissures in the Givetian limestone are filled with continental Wealden-age deposits. Jefferies (1963) included a log and a description of the basal metre of the Cretaceous part of the section. He assigned a middle Cenomanian age to the approximately 0.5 m thick limestone bench that forms the base of the Cretaceous sequence in the quarry ('Sarrasin de Bellignies'). The overlying half metre of marls, exposed at that time, was assigned to the late Cenomanian *Praeactinocamax plenus* Zone. Since Jefferies' description quarrying activities has resulted in the exposure of approximately 10 metres of Cenomanian to Turonian strata. The late Cenomanian *P. plenus* Zone occurs as green, discontinuous lenses between the 'Sarrasin de Bellignies' and the lower, grey half of the Turonian marls (Pieter De Schutter and Eric Collier pers. com. 2013). The base of the Turonian in the SECAB quarry is defined by the appearance of *Mytiloides labiatus*. Yellowish, mid-Turonian marls with *Terebratulina lata* (=*T. rigida* of Herman 1977; Andy Gale pers. com. to MS via David Ward 2013) cap the Cretaceous sequence. The material at hand is almost entirely derived from bulk sampling of small, conglomeratic pockets (with black pebbles and coprolites; Pieter De Schutter pers. com. 2013) in the basal part of the *M. labiatus* Zone.

Kristianstad Basin, Scania, Sweden

Locality. Åsen.

WGS84 coordinates. N56°08´56.1´´, E14°29´56.0´´

Stratigraphical log. Eriksson et al. (2011: fig. 2).

Age. Informal *Belemnellocamax mammillatus* zone, a lateral equivalent to the German *Belemnitella mucronata senior*/*Gonioteuthis quadrata gracilis* Zone, latest early Campanian (Christensen 1975).

Additional references. Siverson 1992a; Lindgren and Siverson 2002; Lindgren et al. 2007.

Remarks. Up to 3.5 m of marine, poorly consolidated, more-or-less calcareous sands and storm-generated shell beds overlie late Santonian/early Campanian fluviatile clays, sands and gravel at the Åsen locality (under a cover of Quaternary deposits). The lower, up to 2 m thick part of the marine sequence (1.2 m thick in Eriksson et al., 2011, fig. 2) can be referred to the informal *Belemnellocamax mammillatus* zone. The upper 1.5 m of the marine strata yields *Belemnellocamax balsvikensis* (Brotzen, 1960) with a rather shallow pseudoalveolus, indicating the very earliest part of the late Campanian (W. K. Christensen pers. comm. 2001). Field parties from the Department of Geology, Lund University, excavated the marine Campanian deposits at the Åsen locality between 1991 and 2003. Large scale operations utilising a front loader truck were carried out over three field seasons in 1999-2001. All material of *Cretalamna sarcoportheta* sp. nov. and *C. borealis*, described in this work, is derived from the latest early Campanian part of the sequence. Extraction of the vertebrate remains was carried out by means of wet sieving. The vast majority of the teeth of *C. sarcoportheta* sp. nov. are derived from an oyster bed constituting the uppermost bed in the *B. mammillatus* zone at Åsen (Eriksson et al. 2011: fig. 2; the bed is about 0.2 m thick in their section but it ranges up to 0.5 m in thickness in parts of the section unaffected by glacial tectonics). The selachian-yielding strata are only exposed during major excavations, sanctioned by the Bromölla Municipality (there is therefore no visible outcrop in e.g. Google Earth view).

Locality. Ugnmunnarna.

WGS84 coordinates. N56°07´09´´, E14°23´10´´

Stratigraphical logs. Persson (1960: fig. 1); Christensen (1975: fig. 13).

Age. Informal *Belemnellocamax mammillatus* zone, latest early Campanian (Christensen 1975).

Additional references. Lundegren 1934; Persson 1959; Siverson 1992*a*.

The Ugnsmunnarna site comprises a 130 m long natural cliff-section exposing 2-5 m of predominantly medium- to coarse-grained calcarenite with a high content (up to 50 per cent) of quartz sand. Belemnites are extremely common and concentrated in five conglomeratic beds. A moderate number of *Cretalamna* teeth have been collected from the Ugnsmunnarna site by MS and PC, almost all from conglomerate 5 *sensu* Persson 1960: fig. 1. This level was referred to as 'bed IV' by Christensen (1975: fig. 13). All collected *Cretalamna* teeth from this locality have an abraded root. Two specimens of *C. borealis* were registered (but not illustrated because of poor root preservation) as they represent morphologies relevant to the species concept (an A3 and a lower lateroposterior tooth with coarse basal wrinkles on the labial side of the cusp, similar to those of the lectotype).

Locality. Ignaberga quarry.

WGS84 coordinates. N56°06´39´´, E13°51´34´´

Stratigraphical logs. Christensen (1975: fig. 7); Erlström and Gabrielson (1992).

Age. Informal *Belemnellocamax mammillatus* zone, latest early Campanian (Christensen 1975).

Additional references. Bruun-Petersen 1975; Lindgren and Siverson 2002; Lundegren 1934; Persson 1959; Siverson 1992*a*, *b*; Surlyk 1973, 1980.

Remarks. The single tooth of *Cretalamna borealis* from Ignaberga quarry included in this study (the only well preserved *Cretalamna* tooth with pristine root surface preservation from this locality out of a total of 71 *Cretalamna* teeth; see Siverson 1992*a*, table 1) was collected from the latest early Campanian *Belemnellocamax mammillatus* zone in the 1960's by Per-Ove Persson.