A new lamniform shark: *Eoptolamna eccentrolopha* gen. et sp. nov. (Chondrichthyes: Lamniformes) from the Lower Cretaceous of Iberia

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New Early Cretaceous shark

Eoptolamna eccentrolopha **gen. et sp. nov.** (Chondrichthyes, Lamniformes) from the near coastal upper Barremian Artoles Formation (Early Cretaceous) of Castellote (northwestern Spain) is described on the basis of about 50 isolated teeth. This taxon represents one of the earliest lamniform sharks known to date. We hypothesize that most pre-Aptian lamniforms belong to a plesiomorphic group characterised, amongst others, by a very weak gradient monognathic heterodont dental pattern, and tearing-type dentition. There is a nutritive groove in the lingual root protuberance in juveniles of *Eoptolamna* which persists in adults. A single pair of symphysial and a pair of upper intermediate teeth might have been present. Consequently, a new family, Omoiodontidae, is introduced to include the new form as well as *Protolamna* and probably *Leptostyrax*. The Omoiodontidae represent a basal family within Lamniformes. The origin of lamniform sharks remains, however, ambiguous despite recent advances in identifying plesiomorphic characters of lamniform dental patterns. The new Spanish taxon is wide-spread in the Barremian of north-eastern Spain and occurs in a wide range of facies from near-coastal to lake deposits. This lamniform also occurs in the Lower Cretaceous of northern Africa.

ADDITIONAL KEYWORDS: morphology – *Protolamna* – *Leptostyrax* – plesiomorphic condition

INTRODUCTION

Neoselachian sharks are a highly diversified group of marine vertebrates occupying top levels in food webs with almost all major clades being seemingly present in the Late Jurassic with the exception of Squaliformes and Lamniformes (e.g. Thiollière, 1854; Saint-Seine, 1949; Beaumont, 1960; Schweizer, 1964; Cappetta, 1987; Thies, 1992; Duffin & Ward, 1993, Cavin, Cappetta & Seret, 1995; Brito & Seret, 1996; Leidner & Thies, 1999; Kriwet & Klug, 2004; Underwood, 2006). During the latest Jurassic and beginning of the Cretaceous, neoselachians seem to have diversified rapidly and in the late Early Cretaceous, shark faunas of 'truly' modern character appeared (Kriwet & Klug, in press). However, the fossil record of neoselachians from the uppermost Jurassic and Early Cretaceous continues to be incomplete and interpreting Early Cretaceous lamniform diversity is still ambiguous (e.g. Rees, 2005; Kriwet & Klug, in press).

Early Cretaceous neoselachian sharks have been less intensively studied compared to those from the Late Cretaceous (e.g. Cappetta, 1975; Batchelor & Ward, 1990; Biddle & Landemaine, 1988; Biddle, 1993; Underwood, 2004; Underwood & Mitchell, 1999; Underwood, Mitchell & Veltkamp, 1999; Rees, 2005). This is especially evident for those from the Iberian Peninsular. Here, the knowledge of Early Cretaceous Iberian neoselachians, although it has improved in recent years, is mainly based on small assemblages comprising only few taxa from near-coastal to brackish and even freshwater deposits in the province of Teruel (Estes & Sanchiz, 1982; Kriwet & Kussius, 1996; Canudo, Cuenca-Bescós & Ruiz-Omenaca, 1995; Kriwet, 1999).

This paper provides the description of one of the oldest fossil lamniform species. The new species from the upper Barremian of Castellote (northeastern

Spain) is assigned to a new genus based on its tooth morphology. The suprageneric placement within lamniforms and the generalized and plesiomorphic dental condition within Lamniformes are discussed.

MATERIAL AND GEOLOGICAL SETTING

This paper focuses on about 50 teeth recovered from the fossil site of Vallipón in the northwestern part of the Maestrat sub-basin near the city of Castellote, ca. 150 km southeast of Zaragoza (Fig. 1). Most teeth are damaged lacking parts of the root and/or crown. Sediment samples of ca. 500 kg containing vertebrate bones and teeth were collected from the basal part of the Artoles Formation in this sub-basin and dissolved in buffered acetic acid for a maximum of 24 hours. The residues were screen-washed with a 500 µm sieve and the vertebrate remains were sorted under a stereoscopic microscope.

The Maestrat sub-basin is one of four Early Cretaceous sub-basins (Maestrat, Cameros, Columbres, South Iberian) in the Iberian Basin and forms the easternmost Iberian Range. The Iberian Basin is a wide intracratonic Mesozoic basin located in the northeast of Iberia (Aurell, Bosence & Waltham, 1995; Salas & Guimer, 1996; Canudo *et al.*, 1996; Martín-Chivelet *et al.*, 2002). Its devolopment is related to an anticlock-wise rotation of the Iberian plate and crustal thinning during the Mesozoic (Martín-Chivelet *et al.*, 2002). This thinning was inverted in the Palaeogene producing the present-day Iberian and Catalonian Coastal Ranges and parts of the surroundings of the Ebro, Duero and Tajo basins. Generally, two rifting phases are identified spanning the Late Permian to Triassic and the late Oxfordian to Early Cretaceous (Martín-Chivelet *et al.*, 2002).

The development of the Maestrat, Cameros, Columbres and South Iberian sub-basins is related to a prolonged phase of intracontinental rifting and coincided with the gradual opening of the North Atlantic (e.g. Ziegler, 1988; Vergés & Garcia-Senz, 2001). They contain a sedimentary and structural record of three main phases of tectonic subsidence (Salas *et al.*, 2001) and 13 depositional sequences, which are characterized by massive successions of continental to shallow-marine carbonates and clastics.

The Maestrat sub-basin is filled with Upper Jurassic to Lower Cretaceous palustrine and marine sediments. The Valanginian-Barremian sequence (K1.1-K1.7) is up to 1500 m thick and characterized by estuarine shallow-water carbonate platforms along the basin margins with important freshwater discharges. Molluscs and calcareous algae dominated the carbonate production. Three Early Cretaceous formations are recognized in the Vallipón section (from bottom to top): Miramble, Artoles and Utrillas formations. The Artoles Formation, which is 8 m thick yielded abundant isolated vertebrate remains (bones, teeth) in a reddish to yellowish sandstone and conglomeratic bed (30 to 50 cm thick) at its base (e.g. Canudo *et al.*, 1996; Cuenca-Bescós & Canudo, 2003). The vertebrate remains are firmly cemented by iron carbonates and many isolated remains are damaged or broken. The top of the Artoles Formation is dated on the basis of the macroforaminifer *Paleorbitolina lenticularis lenticularis* confirming a late Barremian age for the fossiliferous layers (Canudo *et al.*, 1995). Up to now, 43 vertebrate taxa representing a mixture of marine and continental forms have been identified (Ruiz-Omeñca & Canudo, 2001). Canudo *et al.* (1996) proposed a coastal setting for the fossiliferous layer with a hard substrate. The isolated bones and teeth of vertebrates were accumulated by predators, shallow streams and tidal action.

SYSTEMATIC PALAEONTOLOGY

The terminology and homologies applied here follow those of Cappetta (1987), Siverson (1996) and Shimada (2002).

Class CHONDRICHTHYES HUXLEY, 1880

Subclass ELASMOBRACHII BONAPARTE, 1838

Infraclass NEOSELACHII COMPAGNO, 1977

Superorder GALEMORPHII COMPAGNO, 1973

Order LAMNIFORMES BERG, 1958

Family Omoiodontidae nov.

Derivatio of name. From the Greek words “omoiommorfos”: “uniform” and “donti”: “tooth”, in allusion to the rather uniform dental pattern of these lamniform sharks.

Diagnosis. Lamniform sharks characterized by very weak heterodonties, mesio-distally compressed teeth and characteristic root morphologies.

Genera included: *Eoptolamna* gen. nov., *Leptostyrax*, *Protolamna*.

Genus *EOPTOLAMNA* gen. nov.

Derivatio of name. From the Greek words “eos”: “dawn, early” and “adruptos”: “tearing”; and “*Lamna*”: “modern lamniform shark”, in allusion to the early occurrence and tearing-type dentition of this lamniform.

Type species. *Eoptolamna eccentrolopha* gen. et sp. nov.

Diagnosis. Lamniform shark characterized by small teeth. Tearing-type dentition with very weak gradient monognathic heterodonty. A single pair of symphysials(?) present. Anterior and lateral teeth mesio-distally compressed. Crown high and narrow. Cusps in anterior teeth very slender and erect, in all other tooth positions sub-triangular to leaf-shaped and distally inclined. Labial and lingual crown faces with distinct vertical median crest extending almost from cusp-root junction to apex. Few additional ridges present labially. All folds flexuous and not extending to the apex. Lateral cusplets broad, massive and accentuated, broadly united with main cusp and stronger inclined lingually than main cusp. Cusplets very close to the base of the cusp. In profile view, lateral cusplets in front of the labial cusp plane. Labial face flat, lingual face very convex. Cutting edge very sharp and continuous, running through apices of main cusp and lateral cusplets. Labial basal sledge smooth and delineates a short and narrow concavity reaching up between the base of the cusplets. Enameloid extends onto the upper parts of the root lobes. Root high and coalescing in the upper parts, free in the lower part. Lingual protuberance well-developed but low. Root lobes divergent and more or less in the same plane as basal face of lingual protuberance. Root lobes narrow with rounded extremities. Lingual protuberance divided by a narrow nutritive groove in juveniles and adults.

EOPTOLAMNA ECCENTROLOPHA GEN. ET SP. NOV.

1995 *Protolamna* cf. *sokolovi* Cappetta, 1980; Canudo *et al*.: 51, fig. 8

1999 *Protolamna* cf. *P. sokolovi* Cappetta, 1980; Kriwet: 120, text-fig. 2, pl. 2, fig. 4 (non fig. 5)

2003 *Protolamna* cf. *sokolovi* Cappetta, 1980; Mendiola & Martinez: 36.

2004 *Protolamna* cf. *sokolovi* Cappetta, 1980; Cuny *et al.:* 132, pl. 1, fig. 17-19, pl. 2, fig. 1-3.

Derivatio of name. From the Latin word “eccentricus”: “eccentric”; and the Greek word “lophos”: “crest”, in allusion to the distinctive labial crests.

Type specimen. Antero-latera tooth, MPZ 2005-4 (Fig. 2A-D), housed in the Museo Paleontológico, Universidad de Zaragoza, Spain.

Type locality and age. Vallipón, west of Castellote, ca. 150 km southeast of Zaragoza. Artoles Formation, upper Barremian.

Stratum typicum. Basal conglomeratic bed.

Referred material. About 30 teeth from the Albian of Castellote, Province of Teruel (Figs. 2E-Z, 3).

Diagnosis. As for genus (by monotomy).

ANATOMICAL DESCRIPTION

HOLOTYPE

The holotype, an anterior tooth (Fig. 2A-D), displays a mesio-distally compressed and erect main cusp that is slender and acute. In profile view, the crown is bent lingually and in its upper part very slightly sigmoidal. The labial crown face is very flat and bears a vertical median crest, which is broad and superficially flattened. This crest is accompanied by a pair of short flexuous folds. All folds originate well above the crown-root junction at the level of the notch separating the lateral cusplets from the main cusp and do not reach the apex. The base of the labial face is constricted giving the crown a lanceolate appearance. The cutting edges are well-developed and continuous with the cutting edges of the lateral cusplets. Basally, the cutting edges are very close together so that the margino-lingual portions of the strongly cambered lingual crown face are visible in labial view.

The base of the crown is quite high and devoid of any ornamentation. The enameloid extends tongue-like onto the upper portions of the root lobes. There is a single pair of lateral cusplets without any ornamentation, the distal one being slightly abraded. They are massive, broad and acute with a rounded base in cross-section. Both are divergent from the main cusp rising from bases below that of the cusp but being broadly united with the base of the cusp. The lateral cusplets are separated from the main cusp by narrow notches. In lateral view, the lateral cusplets are inclined lingually and well in front of the labial cusp plane. The basal portion of the cusp is bulbous and overhangs the root to some extend.

The lingual crown face is very convex from side to side and bears some closely arranged and flexuous folds that originate at the base of the crown and reach up to the middle of the crown. The lingual neck, which separates the crown from the root is broad and completely smooth.

The root of the holotype is badly damaged with no root lobes being preserved. The preserved upper portions of the root lobes are coalescing in their upper parts.

The lingual protuberance is well-developed and quite massive. A narrow and shallow nutritive groove with a small central foramen divides the protuberance.

VARIATION AND HETERODONTY

The dentition of *Eoptolamna eccentrolopha* gen. et sp. nov. is characterized by a very weak gradient monognathic heterodonty, almost homodont dentition, as exemplified by the preserved tooth morphologies. It is not discernible confidently whether any real dignathic heterodonty pattern was developed. It is also impossible to establish the number of anterior, intermediate, lateral and posterior tooth rows because of the taphonomic processes that operated at the time of deposition of the shark remains resulting in the accumulation of isolated teeth from probably different individuals in a bone bed. Consequently, all teeth were obtained by processing large sediment quantities and distinguishing numbers of tooth rows or upper from lower teeth is very tentative.

All teeth are morphologically very similar and bear a more or less well-developed vertical median crest from which the species name is derived. In lateral positions the median crest may bifurcate basally. We hypothesize that upper teeth have slightly stronger distally inclined cusp than lower ones.

The labial face of the tooth crowns is barely convex but without a medial flattening as in several odontaspidids. The basal portion of the labial crown face slightly bulges out over the root in anterior teeth, less so in lateral ones. The enameloid boundary labially delineates a long and narrow concavity reaching up between the bases of the lateral cusplets in all teeth.

There are few small and mesio-distally compressed teeth (Fig. 3F-G) that display with their very narrow and lanceolate cusps, low number of labial folds, closely arranged lateral cusplets and irregular length of the root lobes the general morphology of symphyseal teeth. Symphyseal teeth are those located near the jaw symphysis, but not directly on it and are generally small by convention (Shimada, 2002).

The root lobes of all teeth are coalescing in their upper but are free in their lower parts. The lobe extremities, as far as being preserved, are sub-tabular but not spatulate.

The number of anterior and lateral tooth rows remains indeterminate, because these teeth are formed in the anterior and posterior dental bullae respectively, which generally are not preserved in fossil forms. Anterior and antero-lateral of the new taxon (Fig. 2A-J, Fig. 3A-C) are characterized by high and slender main cusps and display only few labial folds. The root is very narrow with root lobes forming an acute angle in labial view. The angle between basal face of the root and long-axis of the crown is 30 to 40º in profile view. Unfortunately, all anterior to antero-lateral teeth are damaged so that the exact morphology of the root lobes of most tooth positions is not detectable. However, several specimens (Fig. 2E-G) display mesial or distal, or both, root lobes, which are elongated, quite delicate and narrow with rounded, not-spatulate extremities. In lateral view, the attachment surface of the root is almost horizontal with slightly basally curved root lobes in lateral positions. The angle between the basal root face and the axis of the crown generally is 30º. In few teeth, the root lobes are slightly curved or bent basally.

Identification of intermediate teeth is very difficult. Intermediate teeth are considered to be small teeth formed more or less directly on the intermediate bar separating the anterior from posterior dental bullae in the upper jaw (Siverson, 1999). Several small specimens (Fig. 3G) display morphological features that may correspond to that of upper intermediate teeth. However, because of the size of these teeth they also may come from juvenile individuals.

In lateral teeth, the number of labial folds increases (Fig. 2K-P). The median labial fold is longer and reaches the apex in most teeth from these positions. In addition, the lateral cusplets also bear vertical and flexuous labial and lingual folds reaching the apex. The root lobes are more distinctly separated forming a more obtuse angle in more lateral tooth positions (Fig. 3D). The lingual root protuberance is also less well-developed in antero-lateral to lateral teeth (Fig. 2F, M, U). The vertical nutritive groove separating the lingual protuberance is narrow but deeper than in anterior teeth.

The tooth crowns become lower towards the commissure and the number of labial folds increases progressively (Fig. 2W-Z). The lateral cusplets are less well-separated from the main cusp.

The material contains abundant small teeth with total heights less than 1 mm. These teeth most probably belong to juveniles. Hypothetical juvenile teeth mainly differ in their overall size and a deeper vertical nutritive groove in the lingual root protuberance. This lingual nutritive groove is still present in adult individuals although it is less well-marked.

SYSTEMATIC AFFINITIES AND DISCUSSION

Lamniform sharks constitute a well-defined monophyletic group (e.g. Shirai, 1996; Carvalho, 1996; Martin & Naylor, 1997; Naylor *et al.*, 1997) with a fossil record that mainly consists of isolated teeth or artificial tooth sets. The order comprises 15 living species in mid to low latitude oceans worldwide, ranging from intertidal zones to deep seas (Compagno, 1999). Most lamniforms possess a unique heterodont dentition called the ‘lamnoid tooth pattern’ indicating that lamniform sharks possess teeth, which are well-differentiated in the jaws depending on their formation in the anterior and posterior dental bullae respectively. These generally include enlarged anterior teeth, a gap or small intermediate teeth separating the anterior teeth from the lateral teeth in the upper jaw, lateral teeth and smaller posterior ones (Compagno, 1984; Shimada, 2001). Symphysial teeth are present in some modern lamniforms such as *Mitsukurina*, *Carcharias* and *Odontaspis* (Shimada, 2002). According to Compagno (1990), lamniform sharks share three synapomorphies: (1) lamnoid dental pattern (symphysial, anterior, intermediate, lateral tooth rows), (2) reduction of labial cartilages, (3) elongate ring-type intestinal valve with more than 15 turns. In addition, Shimada (2002) considers the presence of upper and lower dental bullae supporting the symphysial and anterior teeth a synapomorphy of Lamniformes. The absence of these bullae in the microphageous lamniforms, *Megachasma* and *Cetorhinus*, are supposed to be secondarily losses. The presence of such bullae in *Hemipristis*, conversely, is regarded as convergent development. However, identification of isolated teeth and their assignment to distinct tooth rows in fossil lamniforms is generally hampered by the fact that the teeth are generally not found associated or articulated. Complete lamniform skeletons are, for instance, only known from the Upper Cretaceous limestones of Lebanon (e.g. Cappetta, 1980).

The origin of Lamniform sharks and first appearance in the fossil record has been argued continuously. For instance, Maisey, Naylor & Ward (2004) placed the Jurassic neoselachian *Sphenodus* within lamniforms based on selected dental characters. However, the skeletal and dental morphology (Böttcher & Duffin, 2000; Duffin & Ward, 1993; Kriwet & Klug, 2004) of this shark is more similar to *Synechodus*, an extinct and basal Mesozoic galeomorph, suggesting closer relationships between both. Another Jurassic shark, *Palaeocarcharias* from the Tithonian of southern Germany, which is known by several well-preserved skeletons, was considered to be a basal lamniform by Beaumont (1960). Duffin (1988), however, concluded that this shark shows many orectolobiform characters but has teeth more similar to lamniforms and thus represents a stem group representative of Lamniformes. In the following, Cappetta (1987) placed this selachian in the vicinity of lamniforms and Applegate (2001) suggested to place *Palaeocarcharias* within its own family because of the intermediate morphology. We do not confer with Underwood's (2006) statement that the intermediate morphology of *Palaeocarcharias* would suggest an origin of lamniforms (and probably carcharhiniforms) within a paraphyletic clade Orectolobiformes. According to molecular data, Orectolobiformes is monophyletic and sister to Lamniformes (e.g. Winchell, Martin & Mallatt, 2004, Goto, 2001).

A major reason for disputing the origin of lamniforms (as well as other neoselachians) is that Early Cretaceous marine sediments are quite rare and, additionally, the lowermost Early Cretaceous is still not well-studied. The Albian is the earliest Cretaceous period that was extensively studied for neoselachian remains from a wide array of facies and that yielded abundant lamniform remains (e.g. Biddle, 1993; Siverson, 1997; Underwood & Mitchell, 1999; Welton & Farish, 1993; Underwood & Rees, 2002; Cuny *et al.*, 2004; Kriwet, 2006). Conversely, Berriasian to Barremian sediments were only rarely targeted for neoselachians (e.g. Biddle, 1988; Canudo *et al.*, 1995; Kriwet, 1999; Rees, 2005; Sweetman & Underwood, 2006).

The systematic arrangement of Cretaceous lamniforms is very controversially discussed. So far, the following lamniform taxa have been indicated in Early Cretaceous strata (Cappetta, 1987; Siverson, 1997; Kriwet, 2006; JK pers. obser.): Anacoracidae: *Eoanacorax*, *Microcorax*, *Palaeoanacorax* and *Squalicorax*;

Cretoxyrhinidae sensu Cappetta (1987): *Archaeolamna*, *Cretalamna*, *Cretodus*, *Cretoxyrhina*, *Leptostyrax*, *Paraisurus* and *Protolamna*; Mitsukurinidae: *Anomotodon*, *Paranomotodon* and *Scapanorhynchus*; Odontaspididae: *Eostriatolamia*, *Hispidaspis* and *Johnlongia*; Cardabiodontidae: *Cardabiodon*; Family incertae sedis: *Dwardius, Priscusurus*. The arrangement of these taxa into families, however, differs more or less among researchers and depends on the interpretation of dental formulas derived from arranging isolated teeth into artificial tooth sets. For instance, Siverson (1999) considers Cretoxyrhinidae to be monotypic and taxa, which have been assigned to Cretoxyrhinidae so far (e.g. Cappetta, 1987) should be placed into other suprageneric taxa. Others (e.g. Underwood, 2006) follow a more traditional approach. Here, we follow the arguments of Siverson (1999) and Siverson & Lindgren (2005) and consider Cretoxyrhinidae to represent a opportune genus within to which to place different Cretaceous lamniforms with similar tooth morphologies. Nevertheless, grouping of fossil lamniforms according to their dental pattern (e.g. number of tooth rows) interpreted from artificial tooth sets (e.g. Siverson, 1996, 1999) is quite precarious. Consequently, we don't use the number of individual tooth rows (e.g. number of anterior tooth rows and presence/absence of intermediate upper tooth rows) in fossil taxa only known from isolated teeth for arranging fossil lamniforms into systematic categories but use general morphological traits.

Most Early Cretaceous lamniforms are not known from sediments older than the Aptian. So far, teeth of *Eostriatolamia*, *Cretalamna* and *Protolamna* have been recovered from Valanginian to Barremian strata. Kriwet (1999) described and figured fragmentary teeth from the Barremian of Galve (northeastern Spain) as *Carcharias* sp., which most probably belong to *Eostriatolamia*. The only record of a single pre-Aptian tooth of *Cretalamna* also comes from the same locality (Kriwet, 1999). All other pre-Aptian lamniform records were assigned to *Protolamna*, which also include the oldest known lamniform remains from the Valanginian to date (Rees, 2005). Additional lamniform teeth from the Barremian of Spain and France were also placed into *Protolamna* (Biddle, 1988; Canudo *et al.*, 1995; Kriwet, 1999; Canudo *et al*., 1995).

Of these genera, the teeth of *Protolamna* and *Leptostyrax* resemble those of *Eoptolamna* gen. nov. However, as demonstrated below, *Eoptolamna* gen. nov. is easily separable from these two genera.

Dental differences between *Eoptolamna* gen. nov. and *Protolamna* include: (1) teeth of adult individuals of *Eoptolamna* gen. nov. comparably smaller; (2) lateral teeth more mesio-distally compressed in *Eoptolamna* gen. nov.; (3) lateral cusplets separated by a comparably broad notch from main cusp in lateral teeth of *Protolamna*; (4) teeth of *Protolamna* have only the basal part of the crown covered by folds; (5) no distinct vertical median fold in *Protolamna* present; (6) lateral cusplets more or less in the same plane as the labial crown face, in *Eoptolamna* gen. nov. significantly in front of labial face plane; (7) lateral cusplets without ornamentation in anterior teeth of *Eoptolamna* gen. nov.; (8) root lobes generally long and parallel in *Protolamna* giving the root a rectangular appearance in labial and lingual view, more divergent in *Eoptolamna* gen. nov.; (9) lingual root protuberance of the root very pronounced and high in *Protolamna*, whereas the protuberance is less well-developed and lower in *Eoptolamna* gen. nov.; (10) lingual protuberance of anterior teeth sometimes divided by median grove in *Protolamna*, whereas teeth of all positions and all sizes (ontogenetic stages?) of *Eoptolamna* gen. nov. display a more or less well-developed median nutritive groove; (11) basal face of root protuberance and root lobes in the same plane in *Eoptolamna* gen. nov., whereas the root lobes are bent basally compared to the basal face of the protuberance in *Protolamna*.

The genus *Protolamna* originally was described for teeth from the Aptian of France by Cappetta (1980). Teeth of this taxon are characterized by a very massive root with a protruding lingual protuberance, which is at least half as high as the total tooth. Other characteristics include strongly lingually inclined lateral cusplets and that the lateral margins of the crown are visible in labial view, a character also present in *Leptostyrax* and *Eoptolamna* gen. nov. So far, five species have been assigned to *Protolamna*: *P. carteri* Cappetta & Case, 1999 from the Cenomanian of Texas; *P. compressidens* (Herman, 1977) from the Coniacian of Belgium, Turonian of France and Turonian-Coniacian of Texas (Cappetta & Case, 1999); *P. gigantea* from the Cenomanian of Minnesota (Case, 2001); *P. roanokeensis* Cappetta & Case, 1999 from the Albian of Texas; *P. sokolovi* Cappetta, 1980 from the Aptian of France and Albian of Russia (Sokolov, 1978). Biddle (1988), Kriwet (1999) and Rees (2005) described small samples of lamniform teeth from the Barremian and Valanginian respectively that superficially resemble those of *Protolamna*. All teeth are comparably small not reaching 10 mm in total height and characterized by a well discernable nutritive foramen in the lingual protuberance. Although similar, the assignment of the Barremian teeth to *Protolamna* already was questioned by Kriwet (1999), who, however, maintained a conservative interpretation. All lowermost Iberian Cretaceous teeth assigned to *Protolamna* share a more or less well-pronounced nutritive groove in the lingual root protuberance of supposed juvenile and adult teeth and are morphologically more or less identical with the teeth from Castellote.

Dental differences between *Eoptolamna* gen. nov. and *Leptostyrax* include: (1) teeth of adult individuals of *Eoptolamna* gen. nov. distinctly smaller; (2) labial ornamentation of *Eoptolamna* gen. nov. characterized by a distinct median vertical crest, whereas the labial ornamentation of *Leptostyrax* consists of short, flexuous and densely arranged folds, which are restricted to the basal portion of the crown; (3)

lateral cusplets more needle-like and well-separated from the main cusp by a deep notch in *Leptostyrax*, whereas the lateral cusplets are more massive and smaller in *Eoptolamna* gen. nov.; (4) cutting edges continuous between main cusp and lateral cusplets not so in *Leptostyrax*; (5) two pairs of lateral cusplets may be present in lateral teeth of *Leptostyrax*; (6) lingual ornamentation by long, flexuous ridges with the middle one extending up to the tip of the cusp; (7) lingual protuberance of the root more pronounced and high in *Leptostyrax*; (8) lingual protuberance of the root always devoid of a median nutritive groove in *Leptostyrax*; (9) root lobes more strongly curved basally in profile view in *Leptostyrax*.

Leptostyrax is a lamniform shark that is generally assigned to the Cretoxyrhinidae although its tooth morphologies strongly differ from those of *Cretoxyrhina*. This genus is best known from the Albian – Cenomanian of the U.S.A. (Welton & Fraish, 1993; Cappetta & Case, 1999) but also occurs in the ?lower Campanian of Germany (Albers & Weiler, 1964), ?Santonian of Sweden (Siverson, 1992), Albian-Cenomanian of England (Underwood & Mitchell, 1999), Albian of Australia (Siverson, 1997) and Albian of Angola (Antunes & Cappetta, 2002).

So far, no associated dentition of this shark has been recovered. However, Welton & Farish (1993) presented a tentative dental reconstruction of *Leptostyrax macrorhiza*, a species seemingly restricted to the Albian of the U.S.A. (Cappetta & Case, 1999) that shows a pair of symphysials and an intermediate upper tooth. In the reconstruction of Welton & Farish (1993), all teeth bear a single pair of lateral cusplets. However, Cappetta & Case (1999) and others indicate that lateral teeth of *L. macrorhiza* often bear two pairs of lateral cusplets indicating some degree of gradient monognathic heterodonty.

Teeth of *Leptostyrax* differ in many aspects from teeth of *Protolamna* (see also Cuny *et al.* (2004) for a listing of dental differences between both). A very remarkable difference is the lingual crown ornamentation, which is very faint and restricted to the crown base in *Leptostyrax*, whereas it comprises long folds reaching up to the cusp tip in *Protolamna*. However, Cappetta & Case (1999) figured a tooth of *Protolamna compressidens* from the Turonian/Coniacian of Texas, which displays a completely smooth lingual crown face. Teeth of *Protolamna compressidens*, however, are easily separated from those of *Eoptolamna* gen. nov. by having more delicate and higher lateral cusplets, which are more acute and distinctly curved inwards towards the main cusp. More over, the root is almost as high as the crown.

The Spanish teeth are remarkably small and display different degrees of labial ornamentation. In anterior teeth, there are only few labial folds, whereas the number of folds increases towards the commissure of the jaws. This pattern indicates some sort of heterodonty, although teeth of anterior and lateral positions are rather similar in morphology. The teeth described as *Protolamna* sp. cf. *P. sokolovi* by Kriwet (1999) from the Barremian of Galve and Alcaine and as cf. *Protolamna* by Cuny *et al.* (2004) from the Albian of Tunisia also display this variation in fold numbers and are referred to the new genus, *Eoptolamna* gen. nov. Lamniform teeth described from the Valanginian of Poland (Rees, 2005) and Barremian of France (Biddle, 1988), conversely, display the characteristic morphology and ornamentation of teeth of *Protolamna*.

Eoptolamna gen. nov. forms together with *Leptostyrax* and *Protolamna* a distinct species-group that is characterized by a very weak gradient monognathic heterodonty with a ?single pair of symphysial teeth and anterior and lateral teeth characterized by a distinct root morphology (high and robust) with a more or less well-developed vertical nutritive groove dividing the lingual root protuberance. Assignment to any known family of Cretaceous lamniform family is difficult. Similarities exist to members of the Cretoxyrhinidae, Odontaspididae and

Miitsukurinidae. Cretoxyrhinidae sensu Siverson (1999) only contain *Cretoxyrhina* (conversely to Cappetta, 1987; Underwood, 2006). Teeth of *Cretoxyrhina* are characterized by a very well-developed lingual root protuberance with a vertical nutritive groove in juveniles, which is absent in adult individuals. In addition, the overall-morphology of the crown and root differs from that of *Eoptolamna* gen. nov. and similar forms. Teeth of members of Mitsukurinidae differ most significantly in the lingual crown ornamentation consisting of folds, which are basally always parallel. More similar are teeth of odontaspidids. These generally are characterized *inter alia* by very irregular and flexuous lingual folds, a well-developed lingual root protuberance with a well-marked nutritive groove in all ontogenetic stages. The teeth of *Eoptolamna* gen. nov., however, differ in the presence of a faint, almost completely closed nutritive groove in adult teeth, although it is more marked in juveniles. Additionally, the crown morphology of *Eoptolamna* gen. nov., remarkably differ from odontaspidid teeth. We therefore assign the new Spanish species and similar forms to a new family of Early Cretaceous lamniform sharks, Omoiodontidae. The presence of a quite homodont dentition with a single pair of symphysials is considered to represent the plesiomorphic dental pattern in lamniform sharks.

CONCLUSIONS

The taxon recorded in this study represents one of the earliest lamniform sharks known to date. Previously, most lamniform teeth from the Early Cretaceous have been assigned to the genus *Protolamna* displaying quite generalized tooth and dental morphologies. This taxon generally has been, along with others, arranged into the Cretoxyrhinidae, which is, however, considered to be monotypic (sensu Siverson, 1999). Here, we hypothesize that most pre-Aptian lamniforms belong to a plesiomorphic group that is *inter alia* characterised by a very weak homodont dental pattern and robust root.

Consequently, we introduce a new family, Omoiodontidae, for these taxa. Unfortunately, it is not possible to reconstruct the number of rows because the material of all these taxa comprises isolated findings that cannot be arranged unambiguously into tooth sets. The Omoiodontidae represent a basal family within the Lamniformes. Other pre-Aptian lamniform records include few teeth of *Cretalamna* (Otodontidae) and *Eostriatolamia*? (Odontaspididae). The origin of lamniform sharks remains, however, ambiguous. The dental pattern of *Palaeocarcharias* from the Upper Jurassic of southern Germany differs significantly from the earliest Cretaceous lamniform teeth especially in the morphology of the root.

Isolated lamniform shark teeth are quite common in marine to lagoonal and even brackish deposits of the Early Cretaceous throughout Europe. The oldest lamniform remains are from the Valanginian of Poland (Rees, 2005). In the Barremian, lamniform remains were reported from the Paris Basin, France (Biddle, 1988) and northeastern Spain (Canudo *et al.,* 1995; Kriwet, 1999). The Poland and France specimens display the characteristics of *Protolamna*, whereas the Spanish material has very distinctive dental features and represents a new genus of plesiomorphic lamniforms. This taxon is very common in the Lower Cretaceous ofOliete, Aguilón and Aliaga in north-eastern Spain where it occurs in near-coastal to even lake depositional settings (JK and SK, pers. obser.).

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FIGURE CAPTIONS

Figure 1. Gegraphical and geological situation of the Vallipón site, upper Barremian, near Teruel in northeastern Spain.

Figure 2. ***Eoptolamna eccentrolopha* gen. et sp. nov.** from the upper Barremian of Vallipón. **A-D,** antero-lateral tooth, MPZ 2005-4, holotype. A, labial view. B, profile view. C, lingual view. D, occlusal view. **E-G,** symphyseal? tooth, MPZ 2005-5, paratype. E, labial view. F, profile view. G, lingual view. **H-J,** anterior tooth, MPZ 2005-6, paratype. H, labial view. I, profile view. J, lingual view. **K-N,** lateral tooth, MPZ 2005-7, paratype. K, labial view. L, labio-occlusal view. M, profile view. N, lingual view. **O-R,** lateral tooth, MPZ 2005-8, paratype. O, labial view. P, labio-occlusal view. Q, profile view. R, linguo-occlusal view. **S-V,** lateral tooth, MPZ 2005-9, paratype. S, labial view. T, labio-occlusal view. U, profile view. V, lingual view. **W-Z,** posterior tooth, MPZ 2005-10, paratype. W, labial view. X, profile view. Y, lingual view. Z, occlusal view. Scale bar equals 0.5 cm.

Figure 3. ***Eoptolamna eccentrolopha* gen. et sp. nov.** from the upper Barremian of Vallipón. **A,** antero-lateral tooth, MPZ 2005-11, paratype, labial view. **B,** lateral tooth, MPZ 2005-12, paratype, labial view. **C,** lateral tooth, MPZ 2005-13, paratype, lingual view. **D,** lateral tooth, MPZ 2005-14, paratype, lingual view. **E-F,** antero-lateral tooth, MPZ 2005-15, paratype. E, lingual view. F, labial view. **G,** intermediate? tooth, MPZ 2005-16, paratype, labial view. Scale bars equal 0.25 cm.

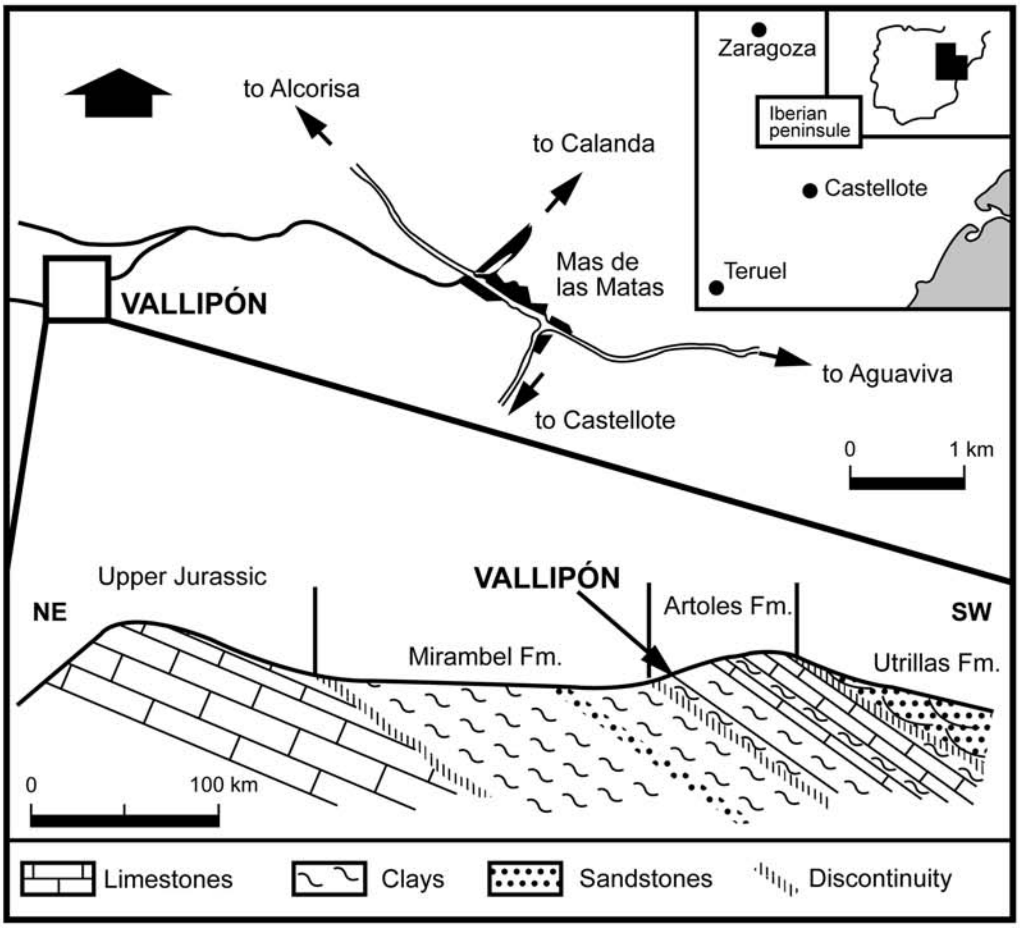

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Figure 1

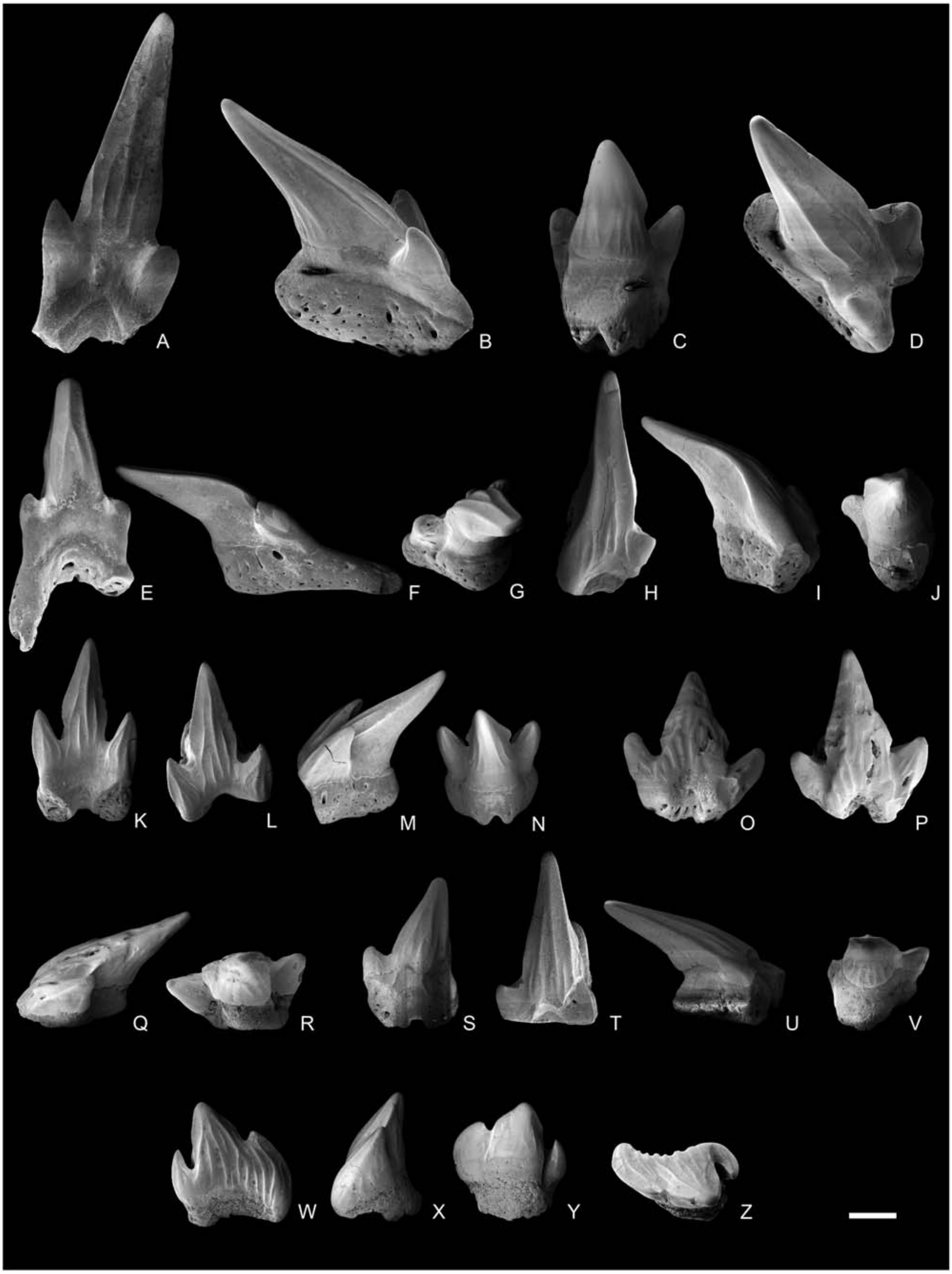

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Figure 2

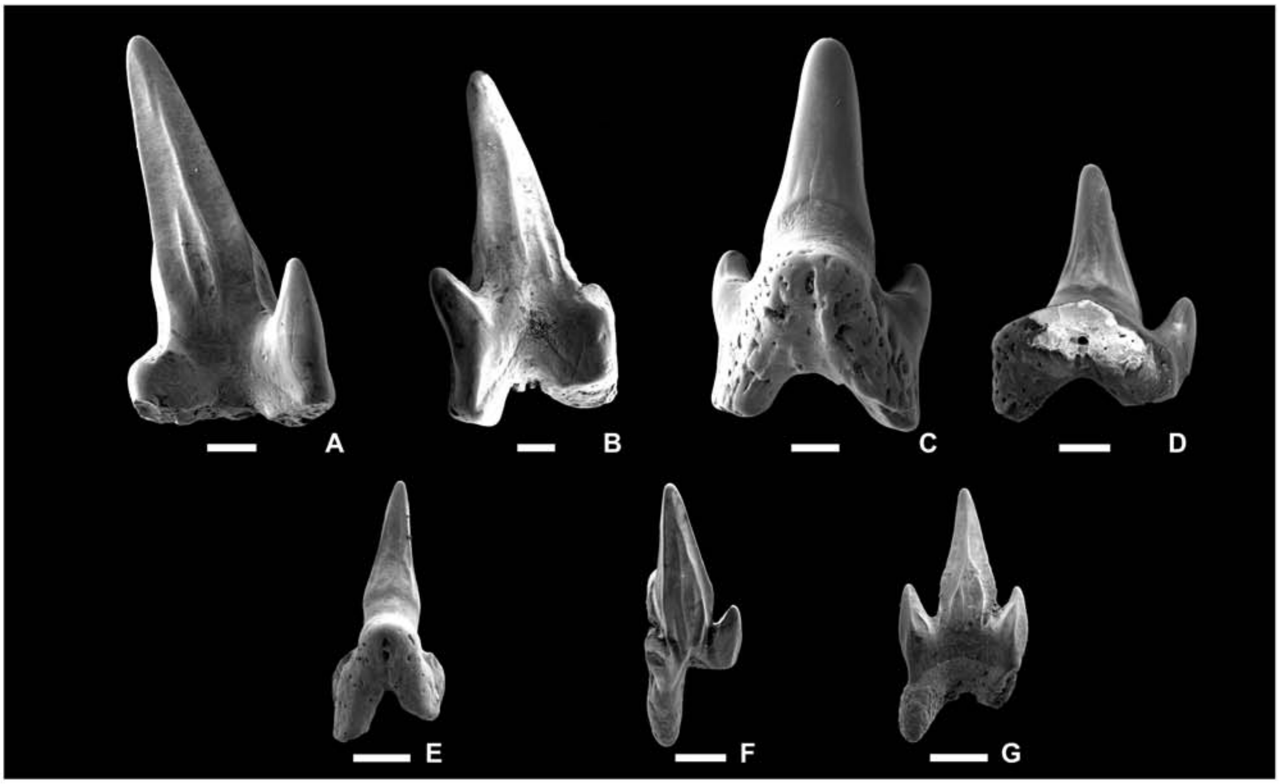

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Figure 3