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THE PRESENCE OF *MEGACHASMA* (CHONDRICHTHYES: LAMNIFORMES) IN THE NEOGENE OF BELGIUM, FIRST OCCURRENCE IN EUROPE.

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(8 figures, 2 tables and 12 plates)

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ABSTRACT: Fossil teeth of the genus *Megachasma* Taylor, Compagno & Struhsaker, 1983 are recorded for the first time in Europe. Isolated teeth have been recovered from the transgressive layer at the base of the Belgian Pliocene, extending the known paleogeographic range of this genus. These teeth are compared with fossil specimens from Greece, Chile, USA and extant specimens. The Belgian teeth seem to fit well in the gap between the early Miocene teeth from California and those of the extant taxon *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983; while the megamouth teeth found in Late Miocene to Early Pliocene sediments worldwide (Chile, North Carolina, Florida, and Greece) appear to be giant versions of modern teeth.

Juvenile teeth of modern *Megachasma pelagios* are illustrated for the first time, showing a distinct ontogenetic variation in the roots and crown surface.

KEYWORDS. Megachasmidae, Miocene, Pliocene, Kattendijk Formation, Deurganckdok, North Sea Basin.

1. Introduction

For the last 30 years, the Antwerp harbour in northwest Belgium has rapidly expanded, exposing on many occasions the basal gravel of the Kattendijk Formation (early Pliocene, Zanclean), famous for its richness in elasmobranch remains (Le Hon, 1871; Leriche, 1926; Herman *et al.*, 1974; Herman, 1979; Nolf, 1988). During the last decades, similar temporary deposits have been intensively sampled; however, megachasmid teeth were never reported. Only during excavation of the Deurganckdok in Antwerp, teeth of *Megachasma* were recognised for the first time (Fig. 5; Plates 1-7), extending the known paleogeographic range of this taxon. Another single tooth from the Miocene of Crete (Fig. 7) was incorrectly identified as a *Hexanchus* symphyseal (Keupp & Bellas, 2002). This brings the total of European records to only two localities.

From North America, *Megachasma* sp. has been described from the Neogene of the Lee Creek Mine, North Carolina (Purdy *et al.*, 2001) and very recently *Megachasma comanchensis* from the Cenomanian of Colorado (Shimada, 2007). Megachasmid teeth have also been reported from the Late Oligocene or Early Miocene of southern California and central Oregon (Phillips *et al.*, 1976). In South America, *Megachasma* teeth have been found in Chile (Walsh, 2001) and Mexico (González-Barba & Thies, 2000). Modern *Megachasma pelagios* was only discovered in 1976 and described by Taylor, Compagno & Struhsaker (1983). Additional important papers have been written about the biology of this unusual species (*e.g.* Compagno, 1990; Herman *et al.*, 1993; Yabumoto *et al.*, 1997; White *et al.*, 2004). To this date, only a very limited number of these wide-ranging sharks has been observed.

2. Locality and stratigraphy

The majority of the *Megachasma* teeth were collected between 2001 and 2005 in the Deurganckdok, Doel, Antwerp Harbour, located on the left bank of the river Scheldt (Fig. 1).

Miocene and Pliocene deposits are restricted to the northern part of the country and were deposited in a shallow marine environment along the southern margin of the North Sea Basin (Laga *et al.*, 2001; De Schepper *et al.*, 2004). Only the early Pliocene Kattendijk Formation was deposited in deeper water (Marquet, 2004). Due to this perimarine environment, the Miocene deposits in Belgium are discontinuous (*e.g.* Louwye *et al.,* 2000). In the Antwerp area, the Miocene is divided into the Berchem Formation (Edegem Sand Member, Kiel Sand Member and Antwerpen Sand Member) and Diest Formation (Deurne Sand Member) (De Meuter & Laga, 1976; Laga *et al.*, 2001). An early Burdigalian to Serravallian age is attributed to the Berchem Formation (Louwye & Laga, 2007) and a Tortonian age to the Diest Formation (Louwye, 2002). The Edegem Sand Member is unconformably overlying the early Oligocene (Rupelian) Boom Formation. The hiatus of about 10 Ma between these two units is related to the late Oligocene tectonic uplift which affected northern Belgium (Vandenberghe *et al.*, 1998; Louwye et *al.*, 2000).

Some general remarks can be made about the presence of selachian associations in the Miocene of the Antwerp area. In contrast with the Pliocene, these have never been

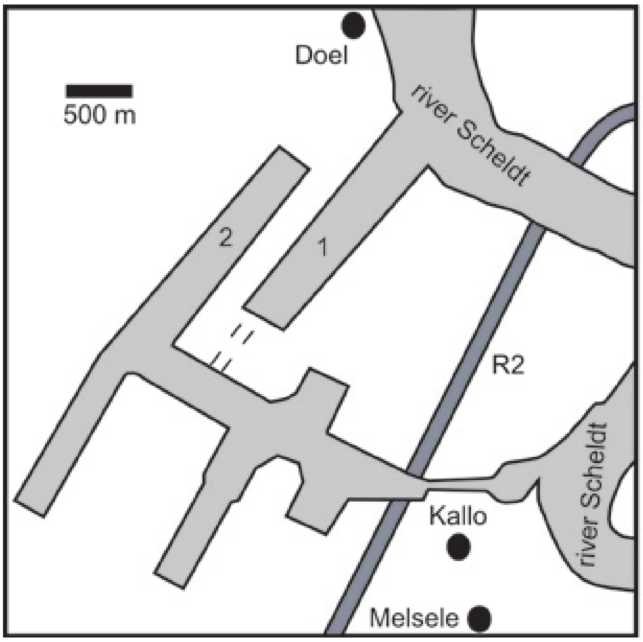

Figure 1. Map of the Antwerp harbour with the Deurganckdok (1) and Doeldok (2).(Redrawn after Herman & Marquet, 2007)

extensively sampled; especially the smaller teeth were disregarded (Leriche, 1926). Only a very limited number of shark teeth was found in the Late Miocene Deurne Sand Member (Bosselaers *et al*., 2004). Although the Middle Miocene Antwerpen Sand Member has been known for 200 years (Herman & Marquet, 2007), the genus *Megachasma* was never reported from these sands. In the area, the Early Miocene Kiel Sand Member appears to contain almost no fossils (De Meuter & Laga, 1976; Louwye *et al.*, 2000); only few selachian teeth are reported from this level (de Ceuster, 1987). The Early Miocene Edegem Sand Member contains shark teeth (De Meuter & Laga, 1976; Reinecke & Hoedemakers, 2006), present in private collections, but also this faunal assemblage has never been published.

The Kattendijk Formation was introduced by de Heinzelin (1955) as the lowermost part of the Pliocene in the Antwerp area. A type locality is only vaguely defined (surroundings of the Kattendijkdok, Amerikadok and Lefèbvredok). Type section is the outcrop of the Verbindingsdok (see De Meuter & Laga, 1976:137). Vandenberghe *et al.* (1998) and Louwye *et al.* (2004) dated it as early Zanclean. Based on dinoflagellate cysts, the age of the Kattendijk Formation is about 5.0 Ma and 4.7-4.4 Ma (Louwye *et al.*, 2004). The Kattendijk Formation consists mainly of glauconitic sands, scattered or concentrated shells, with a gravel at its base (De Meuter & Laga, 1976) (Fig. 2).

The major transgression at the beginning of the Pliocene (Van Vliet-Lanoë *et al.*, 2002) partially or even

Figure 2. Detail of the gravel at the base of the *Kattendijk Formation - in situ*. (Picture: J. Herman - 2000)

completely eroded the Miocene sediments in the Antwerp area. Marine vertebrate remains, sandstones and phosphatic concretions combined with the black-green, glauconitic sand, formed the basal gravel of the Kattendijk Formation. As the regional reduction of the Miocene sediments was not uniform, the fossil content of this gravel and its preservation may vary greatly. In the Deurganckdok, the basal gravel of the Kattendijk Formation (Fig. 2) was at a depth of -19m75 DNG/TWA (Herman & Marquet, 2007) and located on top of the Edegem Sand Member of the Berchem Formation (early Burdigalian, Early Miocene), or immediately on the abraded top of the Oligocene (without intermediate Miocene). Locally the Edegem Sand Member was covered or incised by the Burdigalian Kiel Sand Member; neither of these deposits yielded selachian remains (Herman & Marquet, 2007).

The fossil content of the Pliocene basal gravel indicates that not only Miocene material is reworked into the gravel, but also Oligocene and even Eocene. The latter fossils are usually much abraded and often unidentifiable. The taphonomic condition of the *Megachasma* teeth is mainly good to excellent; this would appear to exclude an Eocene or Oligocene origin and more strongly suggests a Miocene or early Pliocene age for these Belgian *Megachasma* specimens. Attempting to be more specific is a difficult task and highly speculative. The *in situ* specimen (LA01, Plate 7A-F) is heavily worn suggesting an age older than the other *Megachasma* specimens and/or more extensive transportation. Due to the nature of these localities with the mixing of different horizons, it is possible that more than one chronomorphology is present in this basal Pliocene gravel. An early Pliocene age for (some of) the *Megachasma* teeth might be possible as the Zanclean transgression (Van Vliet-Lanoë *et al.*, 2002) was the start of the deposition of the Kattendijk Formation in deeper water. Marquet (2004), based on bivalves, estimated the bathymetry of the Kattendijk Formation at Doel and Kallo at 45 to 70m, diminishing in the successive deposits. The genera *Somniosus*, *Oxynotus* and *Centrophorus*, all meso- and epipelagic sharks (Compagno, 1984), are reported from this formation (Herman *et al.*, 1974; pers. obs.). The presence of *Megachasma* teeth thus fits well into this pattern. However, this taxa was never reported from the early Pliocene sediments overlying the basal gravel (Zanclean, Kattendijk Formation).

3. Materials and Methods

The progressive enlargement of the most recently dug harbour dock, the Deurganckdok, provided a unique opportunity to observe and sample *in situ* the basal gravel of the Kattendijk Formation (Fig. 2). The extracted sand was first dry sieved with a 10 mm mesh to eliminate sandstone and phosphatic concretions, and the abundant cetacean remains. Next, the sediment was washed and sieved with a 5 and 1 mm mesh. The content of the 5 mm sieve was examined on-site. The finer residue (<5 mm) was processed off-site. This process yielded several thousand elasmobranch teeth. This paper includes all seven *Megachasma* specimens known to have been found on the left bank of the Scheldt River: one tooth (LA01, Plate 7A-F) *in situ* and five other teeth in the displaced sand that originated from the same large excavation (Fig. 3). The seventh specimen (IRScNB P.8263, Plate 1A-F), discovered in a private collection, was found in a similar harbour dock (Doeldok-1996) in mixed sediments containing the same Kattendijk basal gravel. Additional examples likely reside unrecognized in private collections.

IRScNB P.8263 (Plate 1A-F) represents a specimen with a damaged distal root lobe, collected *ex situ* at Doel (Doeldok) in 1996.

Deurganckdok specimens
BG01 (Plate 2A-G) - Bert Gijsen collection, *ex situ* Deurganckdok, Doel, 2005
SP01 (Plate 3A-F) - Steven Piqueur collection, *ex situ* Deurganckdok, Doel, 2005
JJ01 (Plate 4A-F) - Johan Janssen collection, *ex situ* Deurganckdok, Doel, 2005
JJ02 (Plate 5A-E) - Johan Janssen collection, *ex situ* Deurganckdok, Doel, 2005
BD01 (Plate 6A-F) - Ben D'Haese collection, *ex situ* Deurganckdok, Doel, 2005
LA01 (Plate 7A-F) - Luc Anthonis collection, *in situ* Deurganckdok, Doel, 2002

Multiple specimens representing different locations and horizons from various personal and public collections were used for comparative purposes.

DS01 (Plate 8A-F) – The author's collection, Jewett Sand, Pyramid Hill Sand Member, Temblor Formation, Kern County, California, USA; one specimen (DS02) has some wear on both heels and was not figured.
AS01 (Plate 8G-L) - Andreas Schenck collection, Jewett Sand, Pyramid Hill Sand Member, Temblor Formation, Kern County, California, USA
AS02 (Plate 9A-F) - Andreas Schenck collection, Jewett Sand, Pyramid Hill Sand Member, Temblor Formation, Kern County, California, USA
AS03 (Plate 9G-L) - Andreas Schenck collection, Jewett Sand, Pyramid Hill Sand Member, Temblor Formation, Kern County, California, USA

DS05 (Plate 10A-F) - the author's collection (commercially acquired specimen), Bahía Inglesa Formation, Middle or Late Miocene, Chile.
DS06 (Plate 10G-L) - the author's collection (commercially acquired specimen), Bahía Inglesa Formation, Middle or Late Miocene, Chile.

p.385: 20-24 (Plate 10M-Q) - Gary Grimsley collection, Yorktown Formation, Early Pliocene, Lee Creek, Beaufort County, NC, USA.

Figure 3. Locality alongside the Deurganckdok where the extracted sand could be sampled *ex situ*. **a.** The large area in the immediate region of the dock. **b.** The exit of one of the pipes used to evacuate the extracted sand. **c.** Sieving underneath the pipe's end in the heavier material: phosphatic nodules, molluscs, shark teeth, cetacean remains, etc. **d.** The sand is pushed through the pipes with a lot of water. (*Pictures*: July 2005)

p.385: 15-25 (Plate 10R-V) - Gary Grimsley collection, Yorktown Formation, Early Pliocene, Lee Creek, Beaufort County, NC, USA.

MZB12906.LLIPI.1 (Plate 11A-D) - Dirk & Maria Hovestadt collection, Megamouth #21, juvenile male, 1767mm TL, Pulau Weh, Indonesia (2004).
MZB12906.LLIPI.2 (Plate 11E-H) - Dirk & Maria Hovestadt collection, Megamouth #21, juvenile male, 1767mm TL, Pulau Weh, Indonesia (2004).
MZB12906.LLIPI.3 (Plate 11I-L) - Dirk & Maria Hovestadt collection, Megamouth #21, juvenile male, 1767mm TL, Pulau Weh, Indonesia (2004)

LACM43745-1 (Plate 11M-R) - Dirk & Maria Hovestadt collection, Megamouth #2, adult male, 4488mm TL, California, USA (1984).

TL01 (Plate 12A-E) - *Cetorhinus* cf. *parvus* (Leriche, 1908d) - Theo Lambrechts collection, *in situ* basal Kattendijk Formation, Early Pliocene, Deurganckdok, Doel

LD01 (Plate 12F-J) - *Cetorhinus* cf. *parvus* (Leriche, 1908d) - Leo Dufraing collection, *in situ* Antwerpen Sand Member, Middle Miocene, Berchem

For additional comparison with modern *Megachasma* specimens, Herman *et al.* (1993) and Yabumoto *et al.* (1997) were used.

The descriptive terminology mainly follows Herman *et al.* (1993) and Cappetta (1987). The abbreviation IRScNB stands for 'Institut royal des Sciences naturelles de Belgique' (*Royal Belgian Institute of Natural Sciences*, Brussels). Systematics follow Compagno (2001).

4. Systematic palaeontology

Class CHONDRICHTHYES Huxley, 1880
Order LAMNIFORMES Berg, 1958
Family MEGACHASMIDAE Taylor, Compagno & Struhsaker, 1983
Genus MEGACHASMA Taylor, Compagno & Struhsaker, 1983

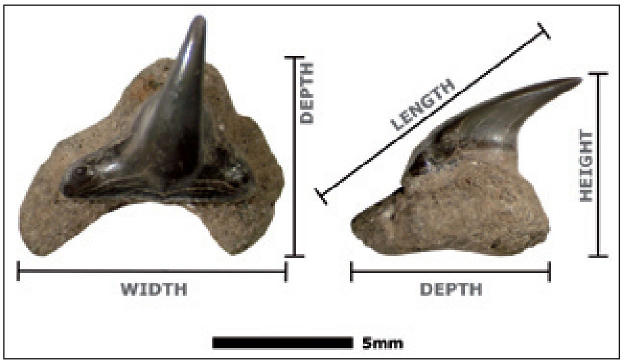

Figure 4. Measurements.

Specimen	Length	Width	Depth	Height
IRScNB P.8263	6.5	5	4	5
BD01	9	6	5.5	5.5
JJ01	10	7	6.5	8
BG01	10	10	7.5	7
JJ02	6	4.5	3	3.5
LA01	6.5	4	4.5	3
SP01	8	7.5	5	6.5
DS01	8	11	5.5	5
DS02	8	7	6	5
AS01	6	7	5	3
AS02	6	6	4	4
AS03	6	6.5	5	4

Table 1. *Megachasma* sp. - measurements (in mm)

4.1 Megachasma pelagios Taylor, Compagno & Struhsaker, 1983

The Recent *Megachasma pelagios* is a large (5 m and more), meso- to epipelagic, planktonivorous, filter-feeder shark (Compagno, 2001), first caught in November 1976 near Hawaii and described in July 1983 (Taylor, Compagno & Struhsaker, 1983). By its unusual appearance and oversized mouth, a new family, genus and species was erected. At the time of this writing, only a very limited number of these wide-ranging sharks had been observed; mainly in the Pacific, but occasionally in the Atlantic Ocean, at depths from 5 to 166m (Compagno, 2001). White *et al.* (2004) formally described the 21st *Megachasma* specimen (MZB12906.LLIPI, Plate 11A-L) and in May 2007, the 39th sighting was reported (Parco, 2007). This shark has never been spotted in the North- or Mediterranean Seas.

The modern *Megachasma* dentition may contain more than 200 weakly differentiated rows of teeth (Compagno, 1990), showing a gradient monognathic heterodonty (Herman *et al.*, 1993). In this study, a row is considered as a labio-lingual group of teeth, *sensu* Compagno, 1990; Herman *et al.*, 1993. Distally from the symphysis, the teeth in the first five or six rows increase in size, before stabilizing and becoming the largest teeth in the jaw. After 15 or 20 rows, the teeth gradually decrease in size moving distally (Yabumoto *et al.*, 1997). Lower jaw teeth are larger than their upper counterparts, having taller and more elongated crowns (Yabumoto *et al.*, 1997). In sharks, a row includes functional and replacement teeth; *Megachasma* has three to five functional teeth in each row (Yabumoto *et al.*, 1997; White *et al.*, 2004). The dentition of both jaws starts with small teeth.

Juvenile megamouth teeth appear to be similar in shape to those of adults (White *et al.*, 2004). However, the specimens MZB12906.LLIPI.1-3 (Plate 11A-L) possess a finely ornamented labial crown face (magn. 20x), a sharp cutting edge reaching from 1/3 of the crown length to almost the crown's base and a much reduced root, covered by many foramina. These juvenile specimens superficially resemble (juvenile) teeth of *Cetorhinus maximus* (Gunnerus, 1765). Additionally, the microscopic Oligocene-Miocene *Cetorhinus*-like teeth (TL01, Plate 12A-E; LD01, Plate 12F-J), traditionally attributed to *Cetorhinus parvus* (Leriche, 1908), are closer to the megamouth tooth design.

4.2 Fossil megachasmid teeth

4.2.1 Overview

The Megamouth fossil history is difficult to reconstruct since fossil finds are both rare and, with possibly one exception, represented only by isolated teeth. The published fossil record is very poor. From Cenozoic horizons, *Megachasma* sp. has been described from the Lee Creek Mine in North Carolina, USA (Purdy *et al.*, 2001:105) and very recently *Megachasma comanchensis* from the Mesozoic of Colorado, USA (Shimada, 2007).

Late Oligocene or Early Miocene megachasmid teeth (Fig. 6; pls. 8-9) are reported from Southern California (Kern County; Temblor Formation, Pyramid Hill Sand Member) and central Oregon (Nye Mudstone and the upper part of the Yaquina Formation) (Phillips *et al.*, 1976; Compagno, 1990). *Megachasma* teeth have also been reported from the Neogene of Chile (Walsh, 2001). Identical teeth to those from Chile and North Carolina have been found in the Neogene of Fernandina Beach in northeast Florida (Gordon Hubbell -- pers. comm. 2007). The megachasmid teeth from California (USA), Florida (USA) and Chile are not yet formally described. *Megachasma* sp. was reported by González-Barba & Thies (2000) from the Miocene of Baja California, Mexico, where a single specimen was found in Langhian sediments (González-Barba -- pers. comm. 2007).

4.2.2 Megachasma sp. - Belgium

Description

The largest megamouth teeth recovered from the Pliocene basal gravel measure 10 mm (Table 1), while the smallest tooth measures 6 mm in length (JJ02, Plate 5A-E). There are not enough specimens to differentiate upper and lower teeth, but the morphology of the latter compares well with an upper medio-lateral tooth (row 21) of an extant female (Megamouth #7) figured in Yabumoto *et al.* (1997:65, fig. 3e). One specimen (BG01, Plate 2A-G) measures 10 x10 mm (length x width). As the largest lower tooth found on a 4.71 m extant female adult megamouth measures 8.5 mm in length, and the largest upper 6.5 mm (Yabumoto *et al.,* 1997), these are visibly smaller than most teeth found at the basal Pliocene in Belgium. Compagno (1990: 367) notes a length of less than 6 mm in adults. The teeth of a stranded 1.77 m juvenile, male megamouth only measure around 2 mm (MZB12906.LLIPI.1-3, Plate 11A-L; White *et al.*, 2004).

All teeth have a lingually directed crown, giving them a hooked appearance. The lingual crown face is strongly convex and completely smooth. The labial crown face is convex and generally smooth, but occasionally, short, vertical basal ridges can be observed, sometimes visible with the naked eye (JJ01, Plate 4B). Herman *et al.* (1993:195) noted the presence of such labio-basal ridges (or costules) on modern lateral and posterior teeth. The tooth's crown base is encircled by a poorly visible dental band (*e.g.* SP01, Plate 3D), as observed on teeth of the extant species *Megachasma pelagios* (Taylor *et al*., 1983; Yabumoto *et al*., 1997). Most teeth bear at least a single (marginal) lateral cusplet. The root is massive and porous with a strong lingual protuberance and a large central foramen. In basal view, the attachment surface of the root is more or less triangular (Yabumoto *et al.*, 1997) or, more appropriate, D-shaped (Jim Bourdon -- pers. comm. 2007) (*e.g.* BD01, Plate 6E). Most Belgian teeth possess a small to medium nutrient groove, extending from the lingual root face to a maximum of halfway to the labial face.

Morphological comparison between the fossil specimens from Belgium, California (USA) and extant teeth

Overall the Belgian specimens fit well between the undescribed, Early Miocene specimens from California (Aquitanian, Temblor Formation, Pyramid Hill Sand Member) and those of the extant taxon *Megachasma pelagios* (Table 2).

Comparing the Californian teeth with teeth of the extant species, Compagno (1990) differentiated the Californian specimens as having a lower crown, stronger labial root lobes and tiny cusplets. Based on the observations of the Californian, Belgian and extant teeth, cusplets become less significant and there is a tendency towards shorter root lobes (Table 2). Most Californian teeth in the small sample possess a pair of tiny cusplets and two teeth are devoid of cusplets. Some Belgian specimens (IRScNB P.8263, Plate 1A-F; BG01, Plate 2A-G) have a well-marked cusplet on each side of the crown; other teeth (JJ01, Plate 4A-F; JJ02, Plate 5A-E) only possess a marginal cusplet on one side, or only a bulge (SP01, Plate 3A-F; BD01, Plate 6A-F). Modern *Megachasma* teeth very occasionally show cusplets (Herman *et al.*, 1993: Plate 45-48, fig. *p* - male lower tooth); on the contrary, the dentition of a female megamouth (Yabumoto *et al.*, 1997) doesn't seem to include any teeth with cusplets.

While the specimens BG01 (Plate 2A-G) and LA01 (Plate 7A-F) have a labially extended distal and mesial root lobe, similar to the specimens of California, most Belgian teeth have root lobes similar to those observed on extant teeth -- not or only slightly labially extended. The nutrient groove seems to be less significant on the Belgian specimens, and almost disappears in teeth of the extant taxon *Megachasma pelagios*. Usually modern *Megachasma* teeth tend to lack a distinct nutrient groove, but occasionally it can be observed (Herman *et al.,* 1993:250). In profile, the lingual face of the root is significantly higher on the Californian specimens (AS01, Plate 8 J & L) than on extant teeth and the specimens found at the base of the Belgian Pliocene, which have a more apico-basally compressed root creating a stronger protuberance (Table 2). Compared to Yabumoto *et al.* (1997: fig. 4), the small specimen LA01 (Plate 7A-F) might represent a first upper tooth.

The cutting edges on adult teeth of modern *Megachasma pelagios* are very poorly developed, reaching about 1/3 to half of the crown length (Yabumoto *et al*., 1997:69). Most specimens from Belgium share this character (*e.g.* SP01, Plate 3A-F), although specimen LA01 (Plate 7A-F) has an almost complete, distal cutting edge. The cutting edges on the Early Miocene Californian specimens are about half to 2/3 of the crown length (pers. obs.). Unlike the juvenile teeth of modern *M. pelagios*, the ornamentation on adult teeth focuses on the lower part of the labial crown face, mainly forming vertical folds. This is similar as observed on specimens from the Neogene of Belgium, but also some Californian and Chilean teeth seem to share this characteristic, generally requiring 10 x to 20 x magnification.

In modern *Megachasma*, the crowns on lower teeth are more erect and longer than those on upper teeth (Yabumoto *et al*., 1997; White *et al*., 2004). The fossil specimens from California have the shortest crowns, as noted by Compagno (1990). On the contrary, extant teeth have tall, elongated crowns, with a narrowed or sometimes stretched-out upper part (*e.g.* Yabumoto *et al*., 1997: fig. 3c, fig. 5b-d). The crowns of the Belgian specimens fit well between the short crowns of the Californian teeth and the elongated more slender crowns of the modern. In all megamouth teeth, the crown becomes wider at its base.

The specimen BG01 (Plate 2A-G) is very similar to one of the examined Californian specimens (DS01, Plate 8A-F) and its size is somewhat larger than most other Belgian specimens (Table 1). In addition, this particular tooth shares a remarkable resemblance with a modern lower tooth of an adult male figured in Herman *et al.* (1993: plate 45-48, fig. *p*). Other teeth (*e.g.* JJ01, Plate 4A-F; BD01, Plate 6A-F) are morphologically very close to the more typical teeth of the extant species *M. pelagios* as figured in Yabumoto *et al*. (1997: fig. 3 & 5).

Figure 5. Four specimens collected at the basal Pliocene of Belgium (Doel, Deurganckdok - 2005). Apical (a), labial (b), basal (c), lateral (d, f) and lingual (e) views.

Figure 6. Four specimens from the Early Miocene of California, Jewett Sand, Temblor Fm., Pyramid Hill Sand Member; apical (a), labial (b), basal (c), lateral (d, f) and lingual (e) views.

4.2.3 Megachasma cf. pelagios - North Carolina (USA) and Chile

Megachasma teeth have been found in the Bahía Inglesa Formation (Walsh, 2001: 226), outcropping on the coast of north-central Chile (Walsh & Suárez, 2005). *Megachasma* teeth have been found in two of the three members of this formation*:* the Morro Member and Bonebed Member (Mario E. Suárez -- pers. comm. 2007), which corresponds with a Middle to Late Miocene age for the Chilean *Megachasma* teeth. Walsh & Suárez (2006) suggest a possible Tortonian age for the Bonebed Mbr. of the Bahía Inglesa Formation. An associated set of 33 *Megachasma* teeth has been collected near Copiapó, Chile (JA/CH-02-33T, G. Hubbell collection); however, there is some uncertainty that all teeth originated from a single individual (G. Hubbell -- pers. comm. 2007).

The specimens from Chile (Plate 10A-L) are much larger in size (length, width and depth) than the specimens from Belgium, California and extant teeth (Table 2). The apico-basally compressed root has a strong lingual protuberance and a large attachment surface; no distinct nutrient groove is present. The root lobes are short and barely extended labially. The teeth have a tall, elongated crown with a distinct dental band; cusplets appear to be absent. These apparently uncommon Chilean teeth are well-known from the commercial market. This added *Megachasma* to the Chilean elasmobranch list (Walsh, 2001), but has also caused much damage to these localities; these sites are now protected (Rodrigo A. Otero -- pers. comm. 2007).

At the Lee Creek Mine in North Carolina, *Megachasma* teeth have been reported from the Early Pliocene Yorktown Formation and, less convincingly, from the Early Miocene Pungo River Formation (Purdy *et al*., 2001). The figured Yorktown specimens are considerably different from the Belgian examples: they are very large (up to 17 mm in length), have a more erect crown, a strongly apico-basally compressed root with a strong protuberance, and are devoid of cusplets (*p.385:20-24*, Plate 10M-Q; *p.385:15-25*, Plate 10R-V).

The limited number of reported specimens makes it difficult to draw conclusions; however there are important similarities with the Chilean teeth: similar size, short, barely extended root lobes, the same apico-basally compressed root forming a strong protuberance, and the lack of cusplets (Table 2). A prominent difference would appear to be the more erect crown of the Lee Creek specimens; however some Chilean teeth share this feature as well. Among the dozens of Chilean teeth studied in private collections, some of them also possess the more erect crown as observed on the Lee Creek specimens. No significant differences could be observed between these teeth; in fact, some Chilean teeth are virtually identical to the Yorktown specimens (Plate 10M-V; Purdy *et al.*, 2001: 106) and thus both populations seem to be closely related.

Purdy *et al.* (2001) noted that, in the Yorktown Formation teeth, the cutting edges are usually incomplete, but may extend to the base of the crown. The same observation is made on the Chilean specimens; the cutting edges seem to vary from about a half to 2/3 of the crown length, reaching the crown's base on some specimens (*e.g.* DS05, Plate 10A-F).

4.2.4 Megachasma cf. *pelagios* - Crete

Keupp & Bellas (2002: 38) figured a single tooth from the Late Miocene (late Tortonian) of Crete, Greece, incorrectly identified as a *Hexanchus* symphyseal (Fig. 7). This particular tooth undoubtedly belongs to the genus *Megachasma* and shows strong similarities in size and overall morphology with the teeth from Chile and North Carolina (Table 2). There is no other known record of *Megachasma* from the Miocene of the Mediterranean Basin (Ledoux, 1972; Ward & Bonavia, 2001; Marsili *et al.*, 2007).

Paleobiogeography

The Tethyan Seaway, connecting the Mediterranean and Indo-pacific sides of the Tethyan Ocean, closed by the end of the Burdigalian due to the collision of the African/Arabian and Iranian/Eurasian plates, although it reopened for a short time during Langhian times (Rögl, 1998; Reuter *et al.*, 2007).

The present-day gateway to the Atlantic Ocean, the Strait of Gibraltar, finds its origin in the early Pliocene (Rögl, 1998; Loget & Van Den Driessche, 2006), but in the Miocene, two connections existed between the Atlantic and Mediterranean Sea: the Betic and Rifian Corridors (Benson *et al.*, 1991; Esteban *et al.*, 1996). The former closed largely during Tortonian times (Martin *et al.*, 2001), the latter closed about 6 Ma, in the mid Messinian (Krijgsman *et al*., 1999). During the subsequent Messinian Salinity Crisis (MSC), the Mediterranean Sea evaporated into a deep and dry basin (Hsü *et al.*, 1973).

The *Megachasma* tooth from Crete indicates a possible faunal exchange between the Mediterranean Sea and the Atlantic Ocean during the Tortonian (Rögl, 1998). As teeth of this type occurred in the western Atlantic (Fig. 8), *Megachasma* probably entered the Mediterranean through its western gateways with the Atlantic Ocean, the Betic or Rifian Corridor. Perhaps this genus disappeared in the Mediterranean after the MSC (or even slightly before) as no other record of *Megachasma* was found in the available literature of the Mediterranean region: Pliocene of Spain (Mañé *et al.*, 1996), Early Pliocene of southern France (Cappetta & Nolf, 1991), Early and Middle Pliocene of Italy (Landini, 1977; Cappetta & Cavallo, 2006; Marsili & Tabanelli, 2007) and Pleistocene of Sicily, Italy (Marsili, 2007).

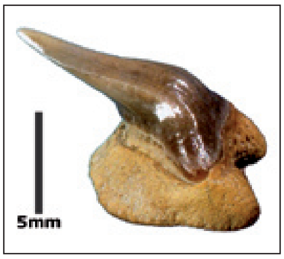

Figure 7. *Megachasma* cf. *pelagios* Taylor, Compagno & Struhsaker, 1983; Late Miocene (late Tortonian); Potamida, Crete, Greece (Keupp & Bellas, 2002) [Image courtesy of Prof. Dr. H. Keupp, Berlin University].

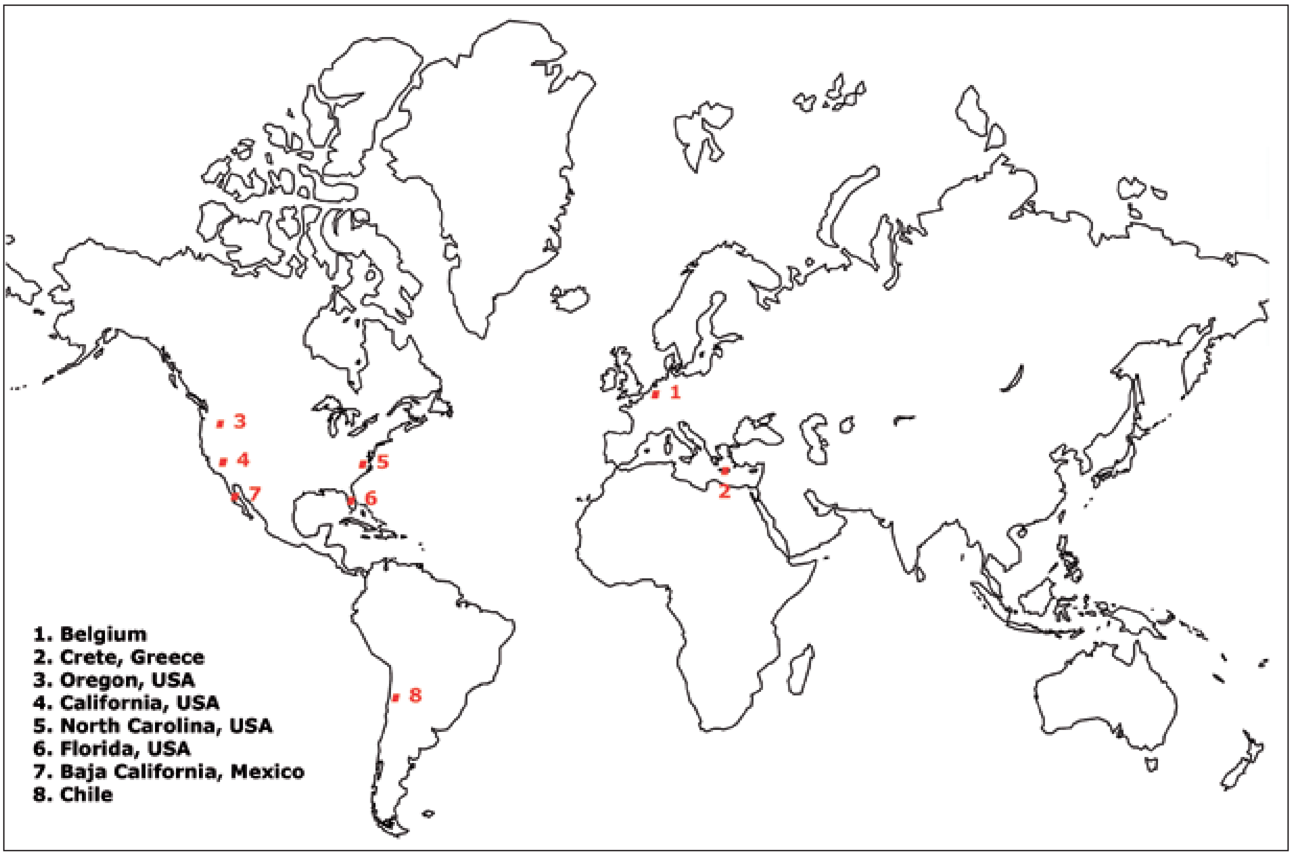

Figure 8. *Megachasma* - worldwide fossil record.

4.2.5 Possible Cretaceous origin

Based on DNA, Shirai (1996: fig. 4) and Martin *et al.* (2002) speculated about a middle Cretaceous origin for the *Megachasma* lineage. Shimada (2007) seemed to add considerable evidence to support this hypothesis by describing the oldest known megachasmid-like tooth-design to date, *Megachasma comanchensis*, found in a middle Cenomanian deposit (Lincoln Limestone Member, Greenhorn Formation) in Colorado, USA. This early Late Cretaceous species, only represented by four teeth, has a hooked crown with weak cutting edges and a massive root with a strong lingual protuberance. This tooth-design is certainly reminiscent of teeth of modern planktonivorous lamniforms such as *Megachasma pelagios* (Shimada, 2007:512). However, the absence of cusplets and extremely short root lobes are in contradiction with what is observed on the Californian teeth or the tendencies in the examined group of megachasmids (California, Belgium and extant teeth, Table 2). In addition, teeth of *M. comanchensis* share a remarkable resemblance with those of the Cretaceous odontaspidid *Johnlongia* Siverson, 1996, to which they were previously attributed (Shimada *et al.*, 2006). These observations and the time gap of 70 million years between these Cenomanian teeth and the Miocene specimens from California makes this taxonomic assignment somewhat suspect.

5. Conclusions

When comparing the teeth found at the base of the Belgian Pliocene to the Early Miocene specimens from California and extant specimens, some trends were recognised: the crowns are getting taller and more elongated. The cusplets, root lobes and nutrient groove become reduced and almost disappear. The root becomes more apico-basally compressed, producing a larger protuberance and a flat attachment surface (Table 2).

The tooth-design of the Lee Creek specimens appears considerably different than that of the Belgian *Megachasma* teeth, but shows strong similarities with the teeth from Chile and Florida. The single tooth from Greece, the only other European occurrence of this genus, seems more closely related to the latter group. These megamouth teeth found in Late Miocene to Early Pliocene sediments worldwide (Chile, North Carolina, Florida, and Greece) appear to be giant versions of modern teeth; apart from their size, these teeth are almost identical (Table 2). Many shark species attained a larger size during the Late Miocene - Early Pliocene interval (*e.g.* Purdy *et al.*, 2001; Adnet & Martin, 2007; Chandler *et al.*, 2006). The Early Miocene teeth from California are clearly different from the above group (Table 2).

By the limited number of Belgian specimens, mostly found *ex situ*, and the limited knowledge of fossil megamouth teeth worldwide, the former are left in open nomenclature.

California (USA) **(Early Miocene)** ***Megachasma* sp.**	**BELGIUM** **(?E. Mio. - ?E. Plio)** ***Megachasma* sp.**	**CHILE, NC & FL (USA)** **(L. Mio./E. Plio.)** ***Megachasma* cf. *pelagios***	**GREECE (Crete)** **(Late Miocene)** ***Megachasma* cf. *pelagios***	**EXTANT** ***Megachasma pelagios***
Short crown	Tall crown	Tall and elongated crown	Tall and elongated crown	Tall and elongated crown
Extended root lobes	Not or slightly extended root lobes	Short, barely extended root lobes	Short, barely extended root lobes	Not or slightly extended root lobes
Cusplets common and well-developed	Cusplets common, less developed	Cusplets absent	Cusplets absent	Cusplets rare
Strong nutrient groove	Nutrient groove less important	Distinct nutrient groove absent	? (*)	Distinct nutrient groove rare
High root, weak protuberance	Protuberance getting stronger	Root apico-basally compressed; (very) strong protuberance	Root apico-basally compressed; strong protuberance	Root apico-basally compressed; strong protuberance
Cutting edges 1/2 -> 2/3 of crown length	Cutting edges 1/3 -> ½ of crown length	Cutting edges half to entire crown length	Cutting edges half to entire crown length	Cutting edges 1/3 -> ½ of crown length
Crown slightly lingually inclined	Crown strongly lingually inclined	Crown slightly to strongly lingually inclined	Crown lingually inclined	Crown strongly lingually inclined
Small teeth (generally less than 10mm)	Small teeth (generally less than 10mm)	Large teeth (up to 20mm)	Large tooth (15mm)	Small teeth (generally less than 10mm)

Table 2. *Megachasma* - overview.
(*) No other views of this single Greek tooth, located in the collections of the Berlin University, could be obtained, despite various efforts.

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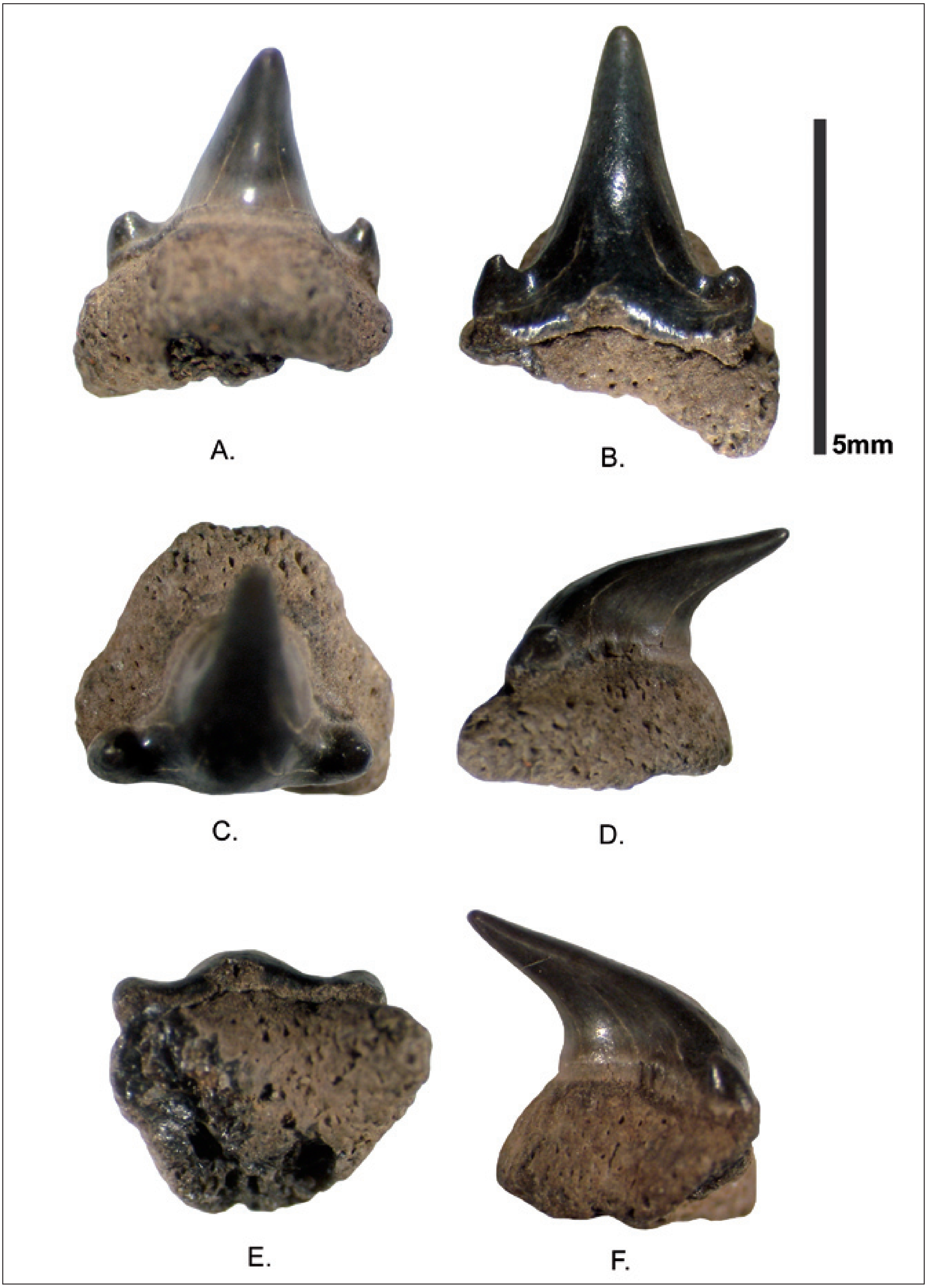

Plate 1. (A-F) - IRScNB P.8263 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium. Lingual (A), labial (B), apical (C), lateral (D, F) and basal (E) views.

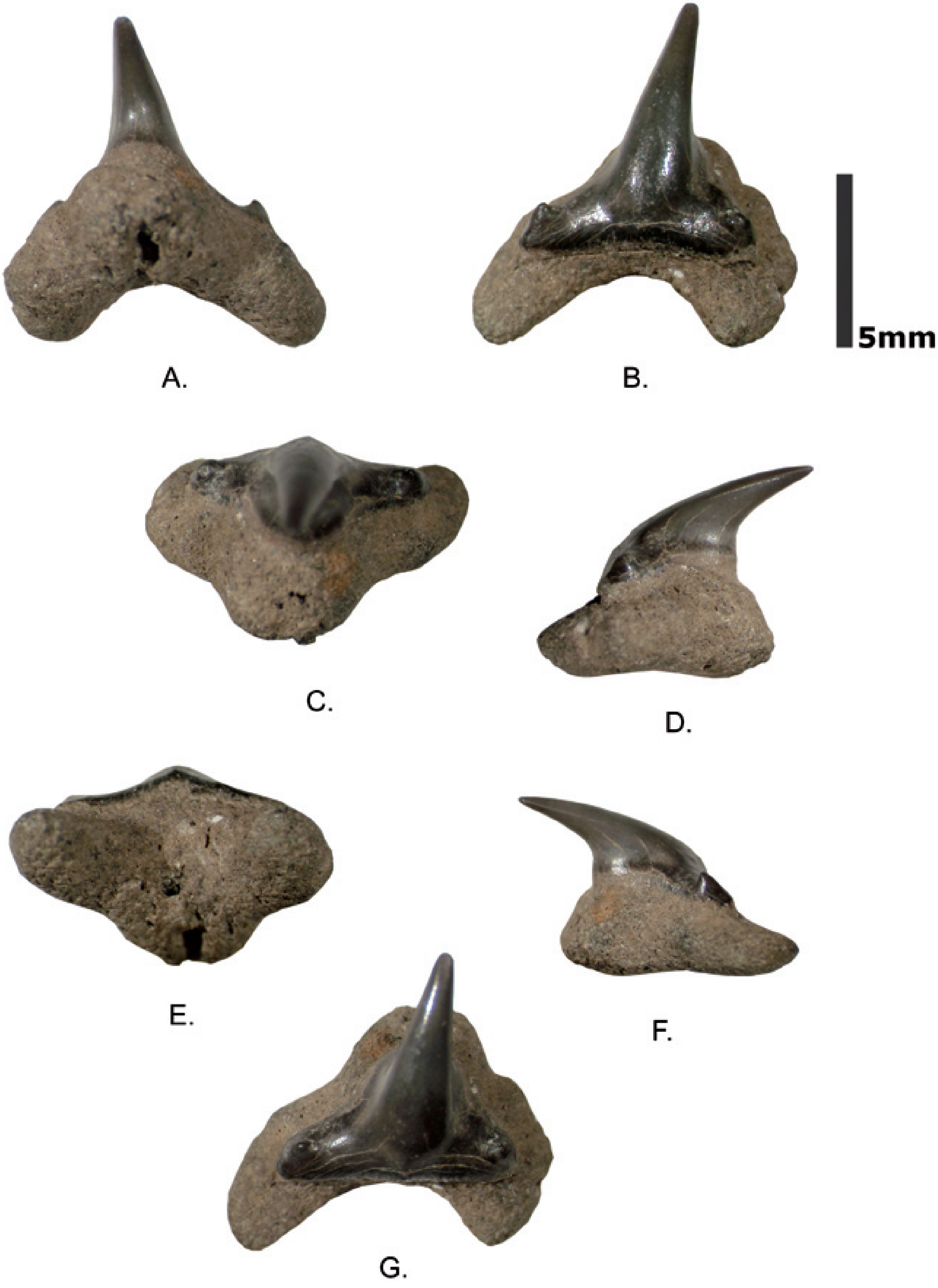

Plate 2. (A-G) - BG01 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium.
Lingual (A), labial (B), apical (C), lateral (D, F), basal (E) and apico-labial (G) views.

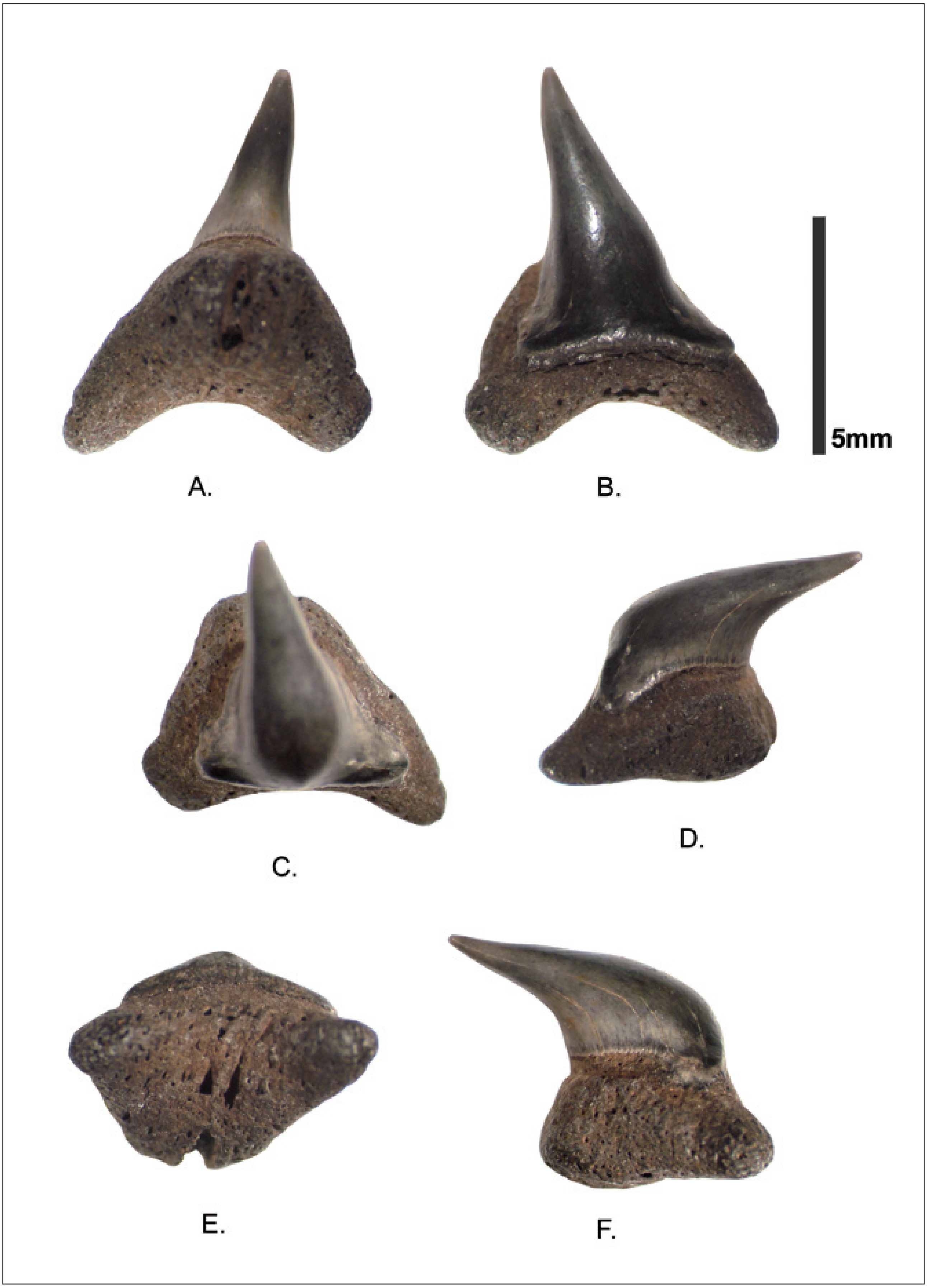

Plate 3. (A-F) - SP01 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium. Lingual (A), labial (B), apical (C), lateral (D, F) and basal (E) views.

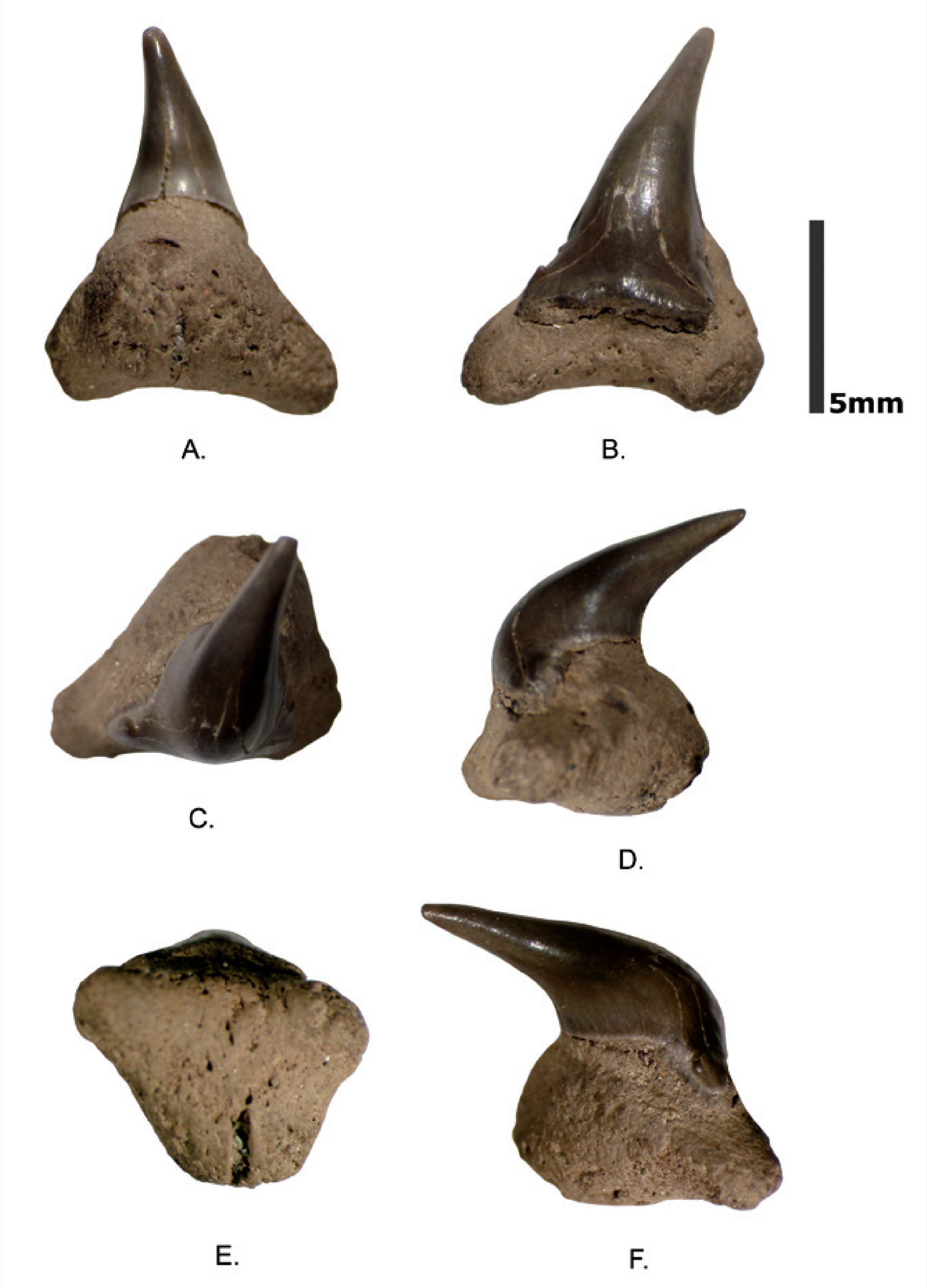

Plate 4. (A-F) - JJ01 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium. Lingual (A), labial (B), apical (C), lateral (D, F) and basal (E) views.

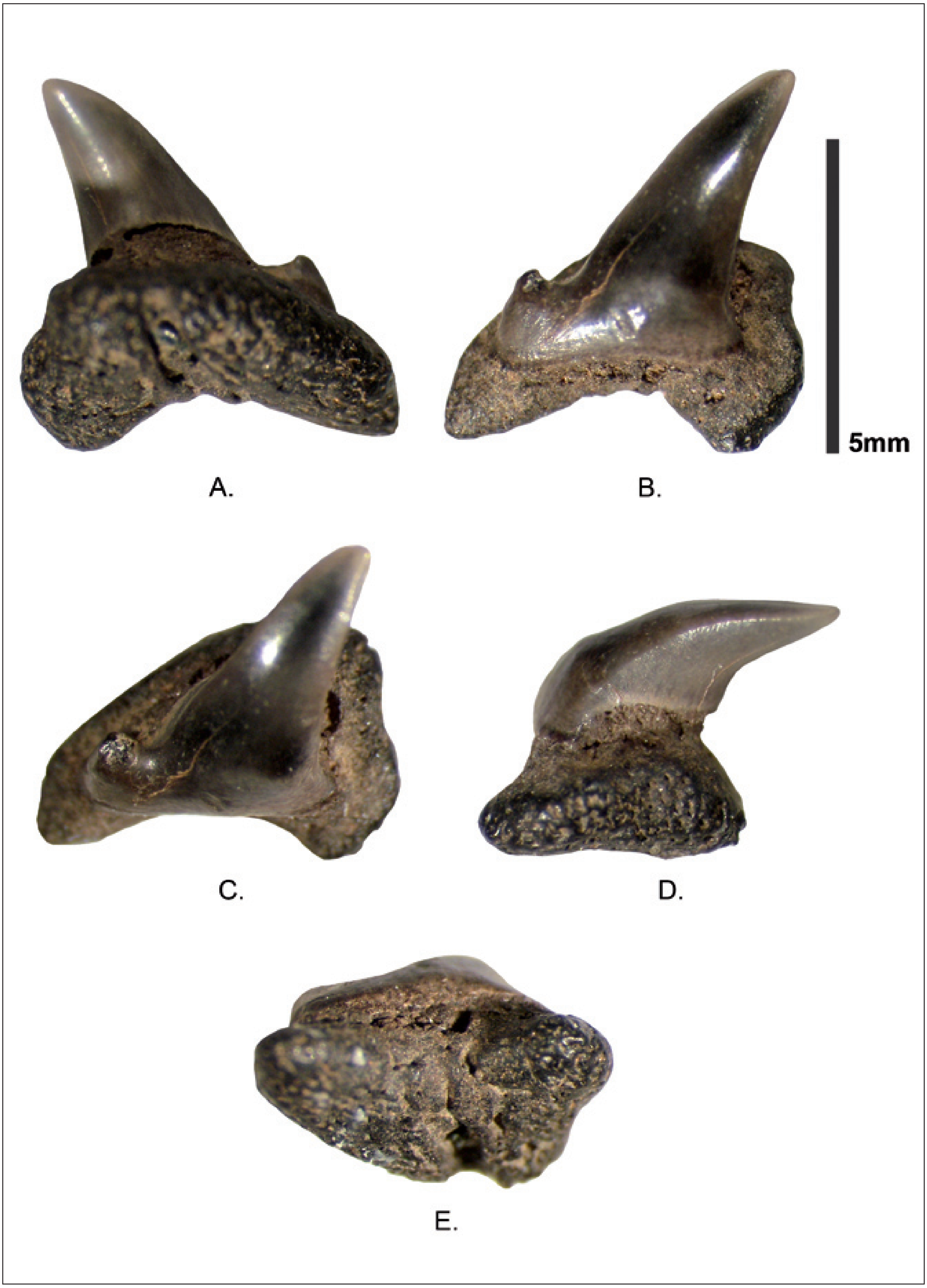

Plate 5. (A-E) - JJ02 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium. Lingual (A), labial (B), apical (C), lateral (D) and basal (E) views.

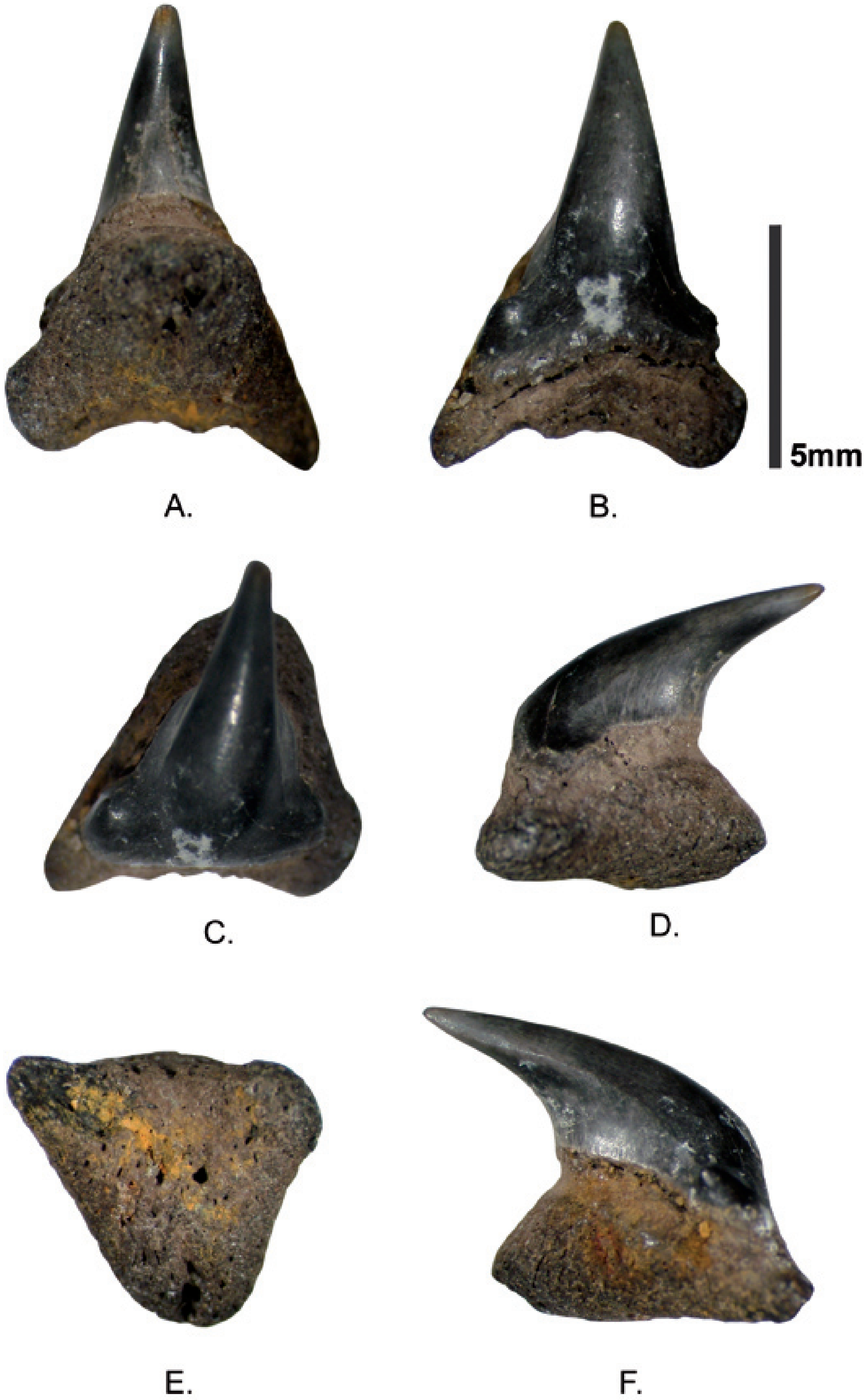

Plate 6. (A-F) - BD01 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium. Lingual (A), labial (B), apical (C), lateral (D, F) and basal (E) views.

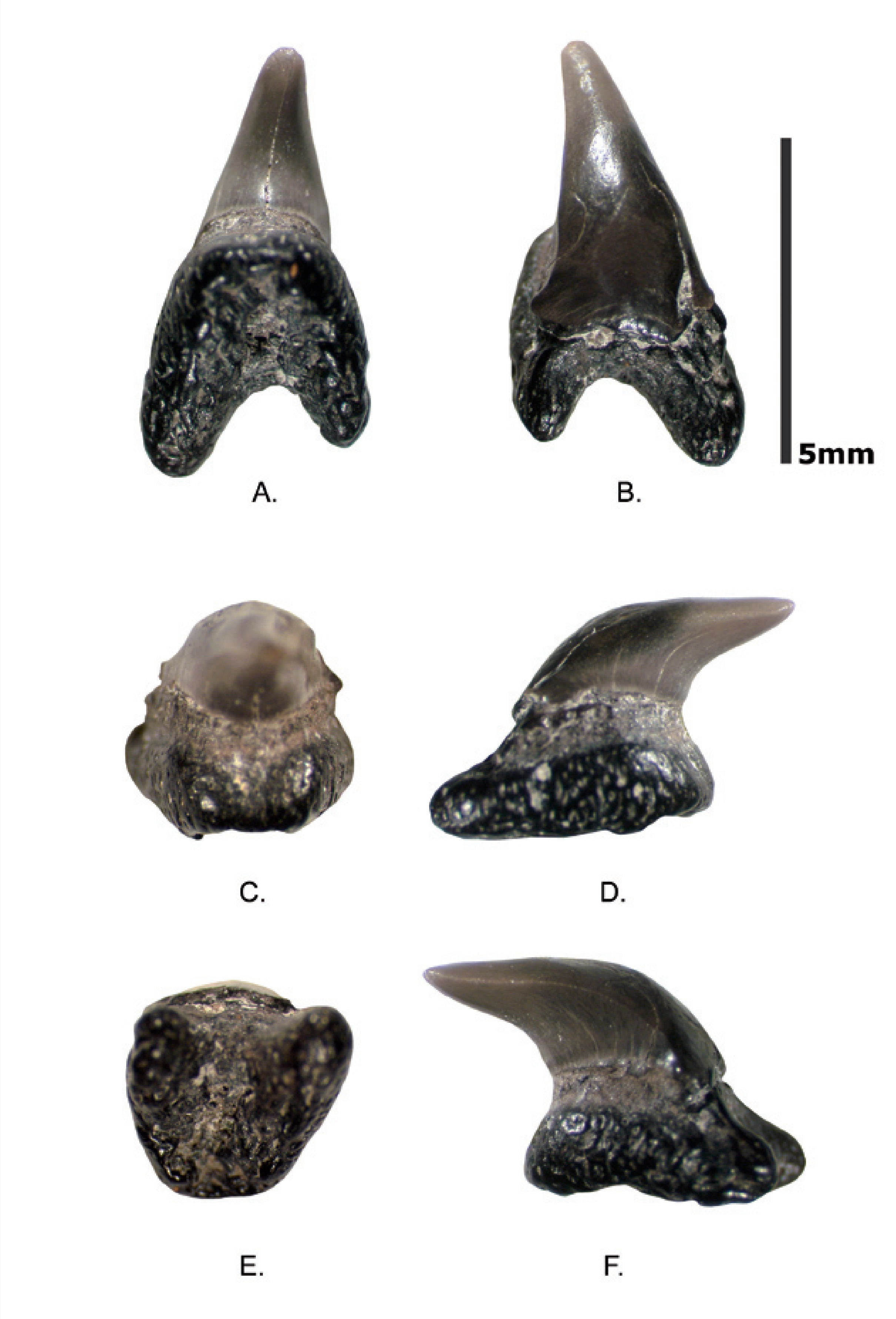

Plate 7. (A-F) - LA01 - *Megachasma* sp.; basal Kattendijk Formation (Early Pliocene), Belgium.
Lingual (A), labial (B), apical (C), lateral (D, F) and basal (E) views.

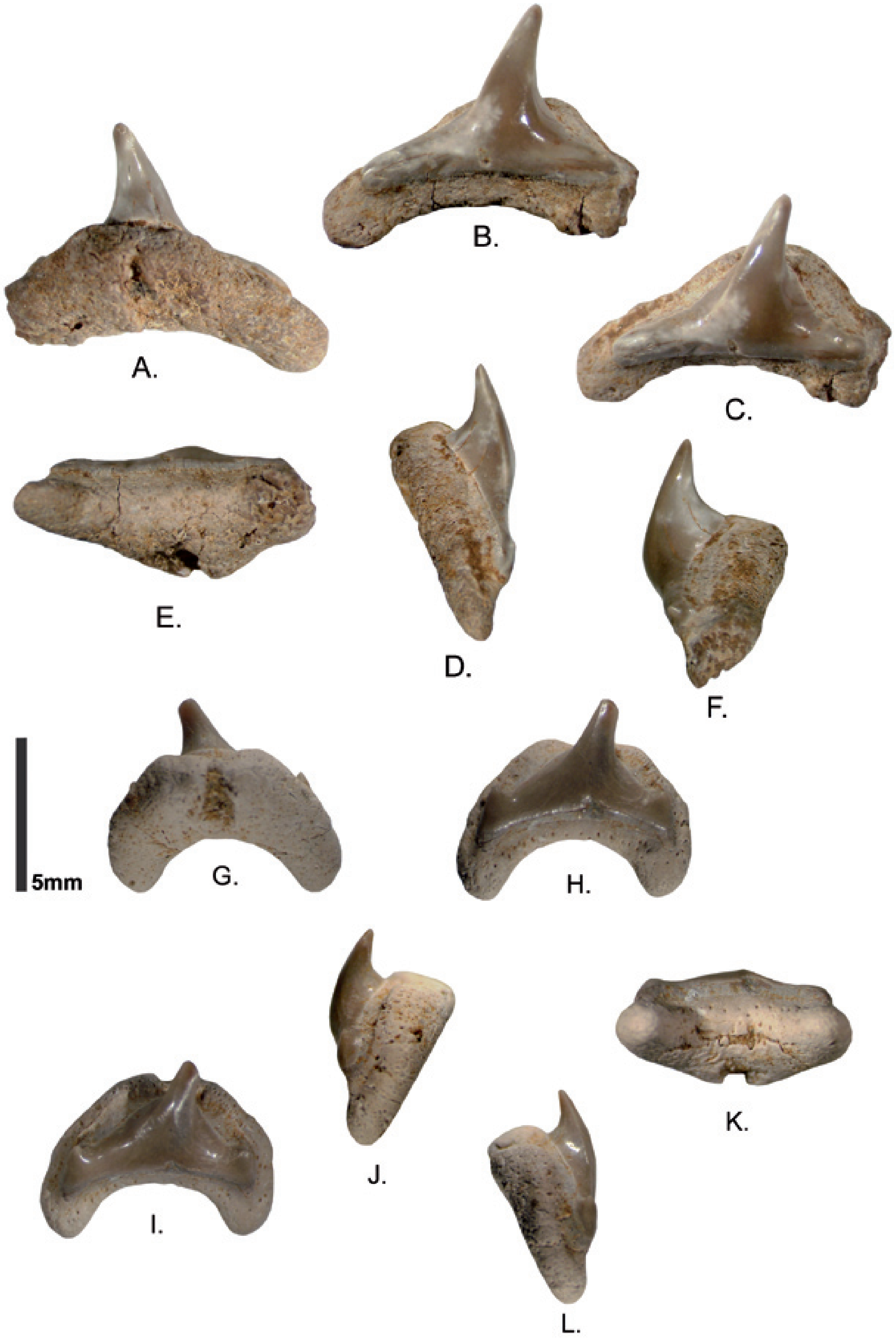

Plate 8. (A-F) DS01 & (G-L) AS01 - *Megachasma* sp.; Temblor Formation (Early Miocene), Kern Co.,California, USA. Lingual (A), labial (B), apical (C), lateral (D, F), basal (E), lingual (G), labial (H), apical (I), lateral (J, L) and basal (K) views.

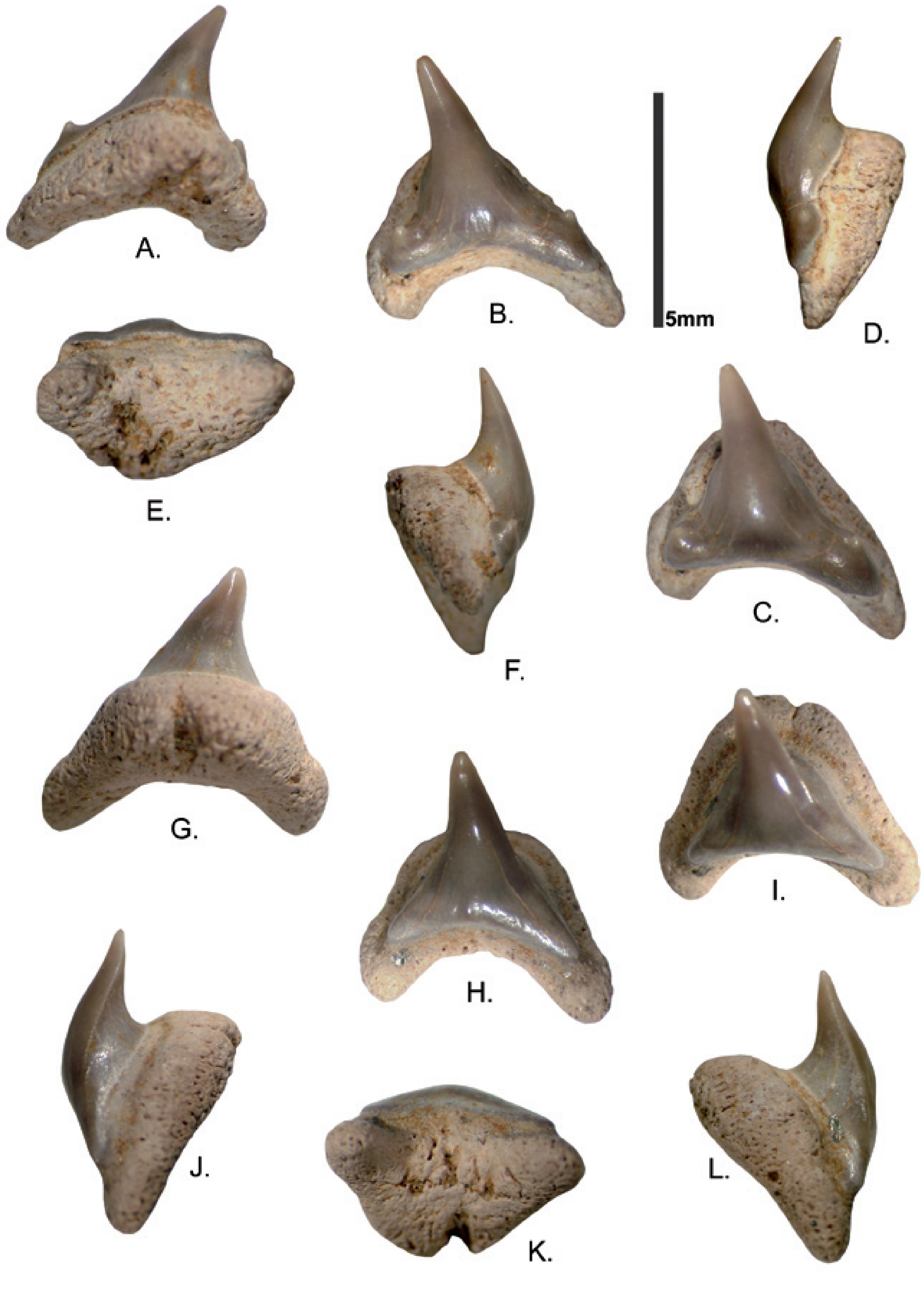

Plate 9. (A-F) AS02 & (G-L) AS03 - *Megachasma* sp.; Temblor Formation (Early Miocene), Kern Co., California, USA
Lingual (A), labial (B), apical (C), lateral (D, F), basal (E), Lingual (G), labial (H), apical (I), lateral (J, L) and basal (K) views.

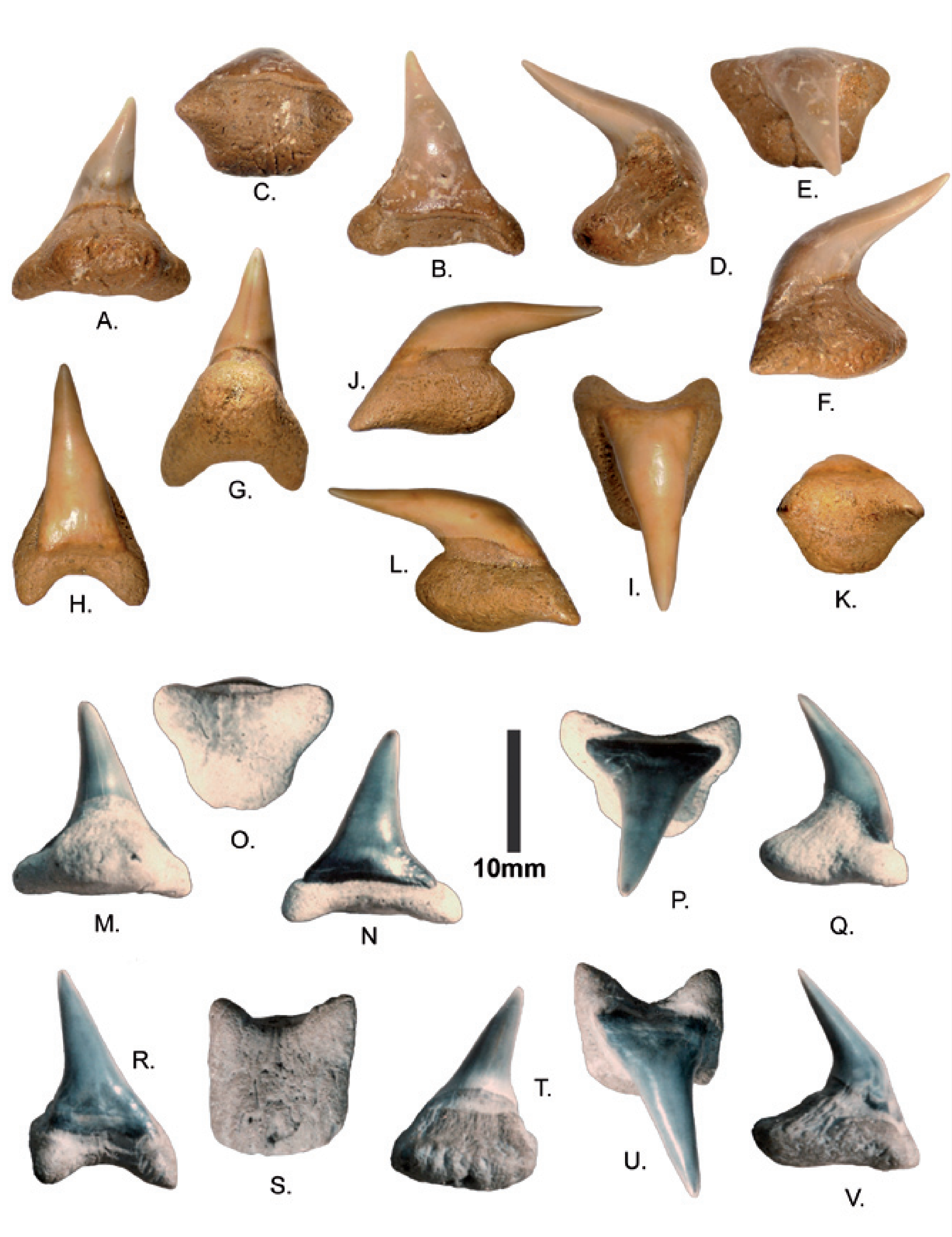

Plate 10. (A-F) DS05 & (G-L) DS06 - *Megachasma* cf. *pelagios* Taylor, Compagno & Struhsaker, 1983; Bahía Inglesa Formation (Middle or Late Miocene), Chile.
Lingual (A), labial (B), basal (C), lateral (D, F), apical (E), lingual (G), labial (H), apical (I), lateral (J, L) and basal (K) views.
Plate 10. (M-Q) p.385:20-24 & (R-V) p.385:15-25 - *Megachasma* cf. *pelagios* Taylor, Compagno & Struhsaker, 1983; Yorktown Formation (Early Pliocene), Lee Creek, Beaufort Co., NC, USA; Gary Grimsley collection (image courtesy of Jim Bourdon).
Lingual (M), labial (N), basal (O), apical (P), lateral (Q), labial (R), basal (S), lingual (T), apical (U) and lateral (V) views.

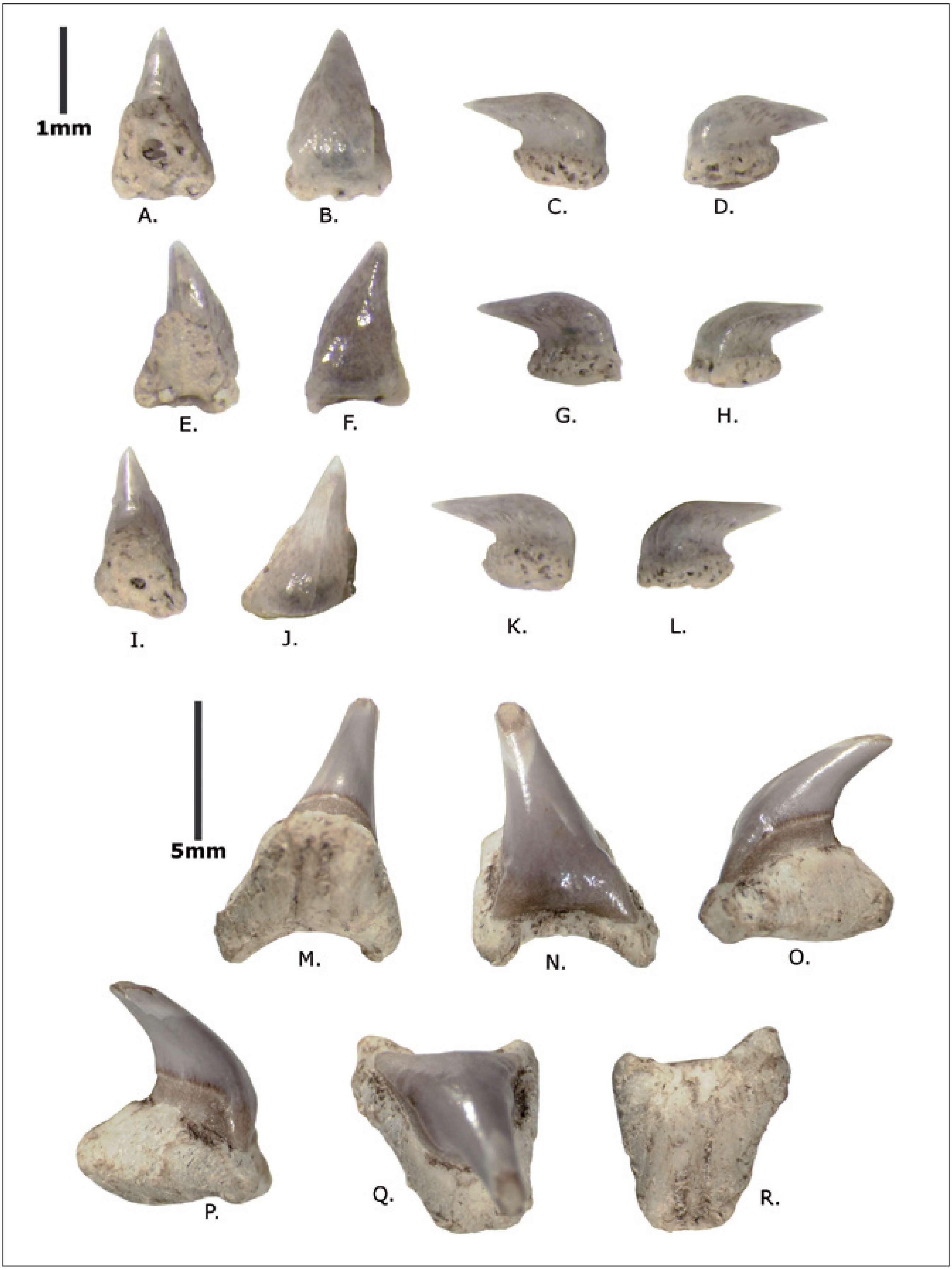

Plate 11. (A-D; E-H; I-L) - MZB12906.LLIPI.1-2-3 - *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983; Megamouth #21 - Pulau Weh, Indonesia
Lingual (A), labial (B), lateral (C, D), lingual (E), labial (F), lateral (G, H), lingual (I), labial (J) and lateral (K, L) views.
Plate 11. (M-R) - LACM43745-1 - *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983; Megamouth #2 - California, USA
Lingual (M), labial (N), lateral (O, P), apical (Q) and basal (R) views.

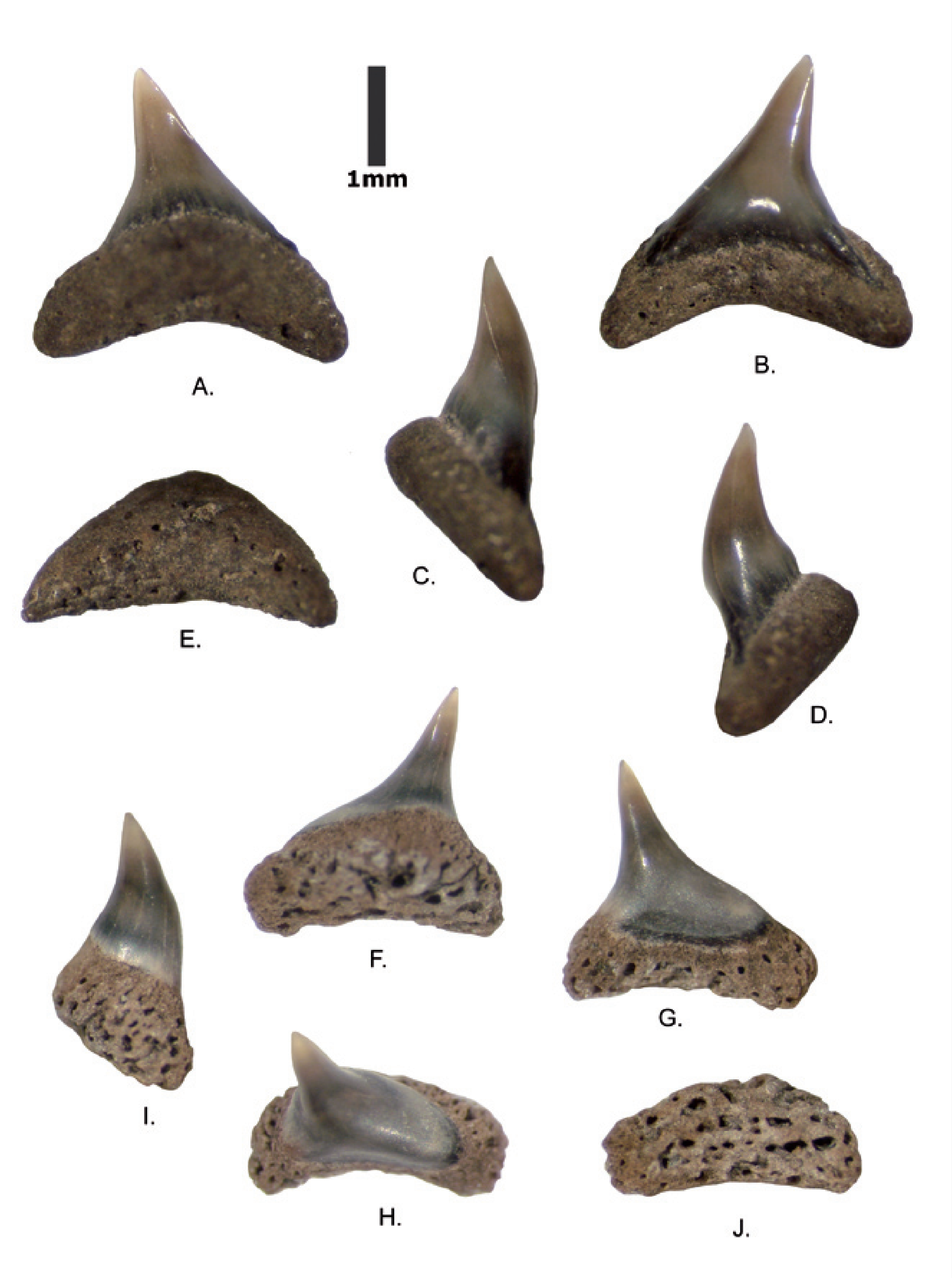

Plate 12. (A-E) - TL01 - *Cetorhinus* cf. *parvus* (Leriche, 1908d); basal Kattendijk Formation (Early Pliocene), Belgium; Theo Lambrechts collection.
Lingual (A), labial (B), lateral (C, D) and basal (E) views.
Plate 12. (F-J) - LD01 - *Cetorhinus* cf. *parvus* (Leriche, 1908d); Antwerp Sand Mbr. (Middle Miocene), Belgium; Leo Dufraing collection.
Lingual (F), labial (G), apical (H), lateral (I) and basal (J) views.