

A PARTIAL ROSTRUM OF THE PORBEAGLE SHARK *LAMNA NASUS* (LAMNIFORMES, LAMNIDAE) FROM THE MIOCENE OF THE NORTH SEA BASIN AND THE TAXONOMIC IMPORTANCE OF ROSTRAL MORPHOLOGY IN EXTINCT SHARKS

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(4 figures, 3 plates)

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ABSTRACT. A fragmentary rostrum of a lamnid shark is recorded from the upper Miocene Breda Formation at Liessel (Noord-Brabant, The Netherlands); it constitutes the first elasmobranch rostral process to be described from Neogene strata in the North Sea Basin. Based on key features of extant lamniform rostra and CT scans of chondrocrania of modern Lamnidae, the Liessel specimen is assigned to the porbeagle shark, *Lamna nasus* (Bonnaterre, 1788). In addition, the taxonomic significance of rostral morphology in extinct sharks is discussed and a preliminary list of elasmobranch taxa from Liessel is presented.

KEYWORDS. Lamniformes, Lamnidae, *Lamna*, rostrum, shark, rostral node, rostral cartilages, CT scans.

1. Introduction

In general, chondrichthyan fish fossilise only under exceptional conditions and (partial) skeletons of especially large species are extremely rare (Cappetta, 1987). Therefore, the fossil record of Lamniformes primarily comprises only teeth (see e.g. Agassiz, 1833-1844; Leriche, 1902, 1905, 1910, 1926), which occasionally are available as artificial, associated or natural tooth sets (*sensu* Welton & Farish, 1993). In view of the general absence or scarcity of skeletal material available, especially in strata of Cenozoic age, palaeontologists often have to rely on dental morphology only. Although tooth morphology is considered to be a valuable feature in elasmobranch taxonomy (see Herman, 1987), other skeletal characteristics such as used in cladistic analyses of extant Lamniformes (see Compagno, 1990; Shirai, 1996; de Carvalho, 1996; Shimada, 2005), remain unknown for most fossil taxa, thus leaving many questions unanswered. This also explains why relationships amongst extinct lamniforms are hotly debated to date (see e.g. Cappetta & Nolf, 2005; Purdy & Francis, 2007; Ehret *et al.*, 2009). Large-sized and abundant Neogene species such as *Megaselachus megalodon* (Agassiz, 1835) and *Cosmopolitodus hastalis* (Agassiz, 1838) are no exception; their phylogeny will undoubtedly remain difficult to unravel if no additional skeleton material is forthcoming. In the past, cranial and rostral characteristics in particular have proved to be highly useful in investigating interrelationships amongst lamniform sharks (see Compagno, 1990), but are rarely described in palaeontological studies. Although Purdy *et al.* (2001) recorded post- and preorbital processes and no fewer than a hundred tripodal rostra, amongst them several of different types, from the Yorktown Formation (Zanclean,

Pliocene) of North Carolina (USA), detailed descriptions and discussions were not presented, unfortunately. Only recently has Jerve (2006) reported on an ongoing study of two Miocene otic capsules from the Calvert Formation (lower-middle Miocene) of Maryland (USA); this will yield additional data to the often ambiguous dental studies. These well-preserved cranial structures were stated to be homologous to those seen in extant lamnids and thus useful for future phylogenetic studies of this group. It is for this reason that more detailed studies of available chondrocranial material should be encouraged in the near future. The present paper aims to illustrate, describe and assign a partial shark rostrum from upper Miocene strata at Liessel (province of Noord-Brabant, The Netherlands). A preliminary key to modern post-natal lamniforms, based on rostral characters, is provided as is a list of all elasmobranch taxa known to date from the Breda Formation at that locality.

2. Locality and stratigraphy

The Hoogdonk brickyard at the hamlet of Liessel (municipality of Deurne, province of Noord-Brabant, The Netherlands) is situated about 25 km east of Eindhoven (National Rectangular Co-ordinate System, x = 185.500, y = 382.500, Dutch Land Registry Office, 2004, topographic map of The Netherlands, sheet 52C, Deurne). Here, for more than three decades, sand and clay deposits have been exploited at a large scale and down to a maximum depth of about 40 m. The exploitation yielded diverse fossil faunas, both freshwater/terrestrial and marine (Fraaye & Fraaye, 1995; Peters *et al.*, 2004), including rich elasmobranch faunas that have not yet been published in detail. Due to the underwater excavation technique used at this locality (see Peters *et al.*, 1991;

Peters, 1994), data on stratigraphic provenance of the material remained limited for many years (Collins & Fraaye, 1991), but on the basis of a borehole core, Peters *et al.* (2004) have recently presented valuable data on the geology of the site, inclusive of a detailed lithological log down to a depth of 45 m. Dinoflagellate cyst assemblages collected from the borehole cores have allowed Munsterman (2007) to present a stratigraphic interpretation: the section exploited includes strata of both Miocene and Gelasian (disputed Pliocene/Pleistocene; see Clague, 2006) age. Although all elasmobranch material from the Hoogdonk brickyard was collected *ex situ*, the geological context of these specimens, including the partial rostrum described below, is clear. According to depth distribution data of faunal assemblages (see Peters *et al.*, 2004, fig. 6), the occurrence of elasmobranch remains is limited to the interval between -15 m to -43.5 m, confirming the provisional biostratigraphy presented earlier by Collins & Fraaye (1991). This entire section is represented by a complex of greenish sand layers rich in glauconite, all assigned by Munsterman (2007) to the Breda Formation (upper Miocene, Tortonian-Messinian).

3. Material and methods

3.1. Fossil material

The single fragmentary rostrum from the Hoogdonk brickyard described here was kindly brought to my attention by Harold van der Steen (Oss); it is now deposited in the collections of the Nationaal Beiaard- en Natuurmuseum Asten (registration number Li6116). The preservation of the rostral process is very good and comparable to all associated selachian faunas (a preliminary list of all taxa known to date from the Breda Formation at Liessel is presented in Appendix 1). In addition to the Liessel specimen, at least two other analogous rostral nodes are known (*ex situ*) from Neogene strata at Langenboom (Noord-Brabant, The Netherlands) (van der Vliet & Reijs collections, pers. obs.), but these are more fragmentary and well less preserved and are not included in the present study.

3.2. Comparative extant material

Fresh specimens, representing all genera of modern Lamnidae (*i.e.*, *Carcharodon* Smith, in Müller & Henle, 1838; *Isurus* Rafinesque Schmaltz, 1810; *Lamna* Cuvier, 1816), were collected at several fish markets all over southwestern Europe or were obtained from scientific institutions worldwide. Prior to conventional dissection - which often leads to broken structures in the rostral cartilages (Compagno, 1988) - computed tomography (CT) was used to describe and illustrate rostral morphology. Detailed methodology, CT parameter settings and conclusions will be the subject of a separate paper, but preliminary results of two scans of *Lamna nasus* are presented here. To this end, two deep-frozen porbeagle heads were simultaneously scanned (courtesy of Frank Hilde and Johan Bauwens; medical imaging department of

Middelheim (ZNA hospitals), Antwerp), using a Philips *Brilliance 40*-slice CT scanner with parameter settings as follows: 120.0 kV, 499.0 mA, 1.0 mm slice thickness and 0.5/1 interleaving of successive scans. Viewing and volume rendering was made possible through *Philips Extended Brilliance Workspace V 3.5.0.225* and *eFILM Lite™* software. This resulted in clear three-dimensional images and a series of coronal slices (*i.e.* transverse sections) through the chondrocranium and in particular the rostrum without leading to destruction of the specimens. Subsequently, the heads were dissected and chondrocrania were prepared using hot water maceration following methods described by Stohler (1945) and Compagno (1988). To prevent loss of teeth, jaws were separately cleaned using only cold water. In addition, microstructures of the rostra were studied, because this was not possible on the basis of CT scans. The entire chondrocrania and jaws were then dried and deposited in the collections of Elasmobranch Research, Belgium (ERB). In addition to the fresh material scanned and prepared by myself, dry chondrocrania of an additional ten specimens were examined. All of these are housed in the collections of the Royal Belgian Institute of Natural Sciences (IRScNB) and Natal Sharks Board (NSB). A complete list of comparative Recent material examined for the present study, including references to published illustrations of chondrocrania of Recent Lamnidae, is provided in Appendix 2.

4. Neogene shark rostra

Systematics of fossil and Recent taxa follows Cappetta (2006) and Compagno (2001, 2005), respectively, while descriptive terminology is adapted mainly from Compagno (1988, 1990, 2001). For publication dates of taxa described by Agassiz (1833-1844), I follow Woodward & Sherborn (1890) and Cahuzac *et al.* (2007).

4.1. The Liessel specimen

Description. The Liessel specimen is a highly robust, partial rostrum of simple tripodal form that has completely broken off from the chondrocranium (Fig. 1A-F). None of the observed fractures are recent, which is why they likely occurred early during the fossilisation process. The rostral node is preserved in its entirety; a significant portion of both lateral rostral cartilages also remains. The rostral node is not elongated and at its most anterior part is equally rounded in dorsal, ventral and lateral views. Rostral appendices are absent. The medial rostral cartilage is missing, having completely broken off at the base of the rostral node, leaving a circular pattern on the ventral side of the node. The position of this pattern suggests that the medial rostral cartilage did not join the lateral rostral cartilages prior to entering the node. The remains of the lateral rostral cartilages are rectilinear, almost equal in size and are still connected to the rostral node. They are very swollen, but remain individualised and therefore do not form a massive knob. In dorsal view, the outer sides of the rostrum are not rectilinear but a weak angle is present

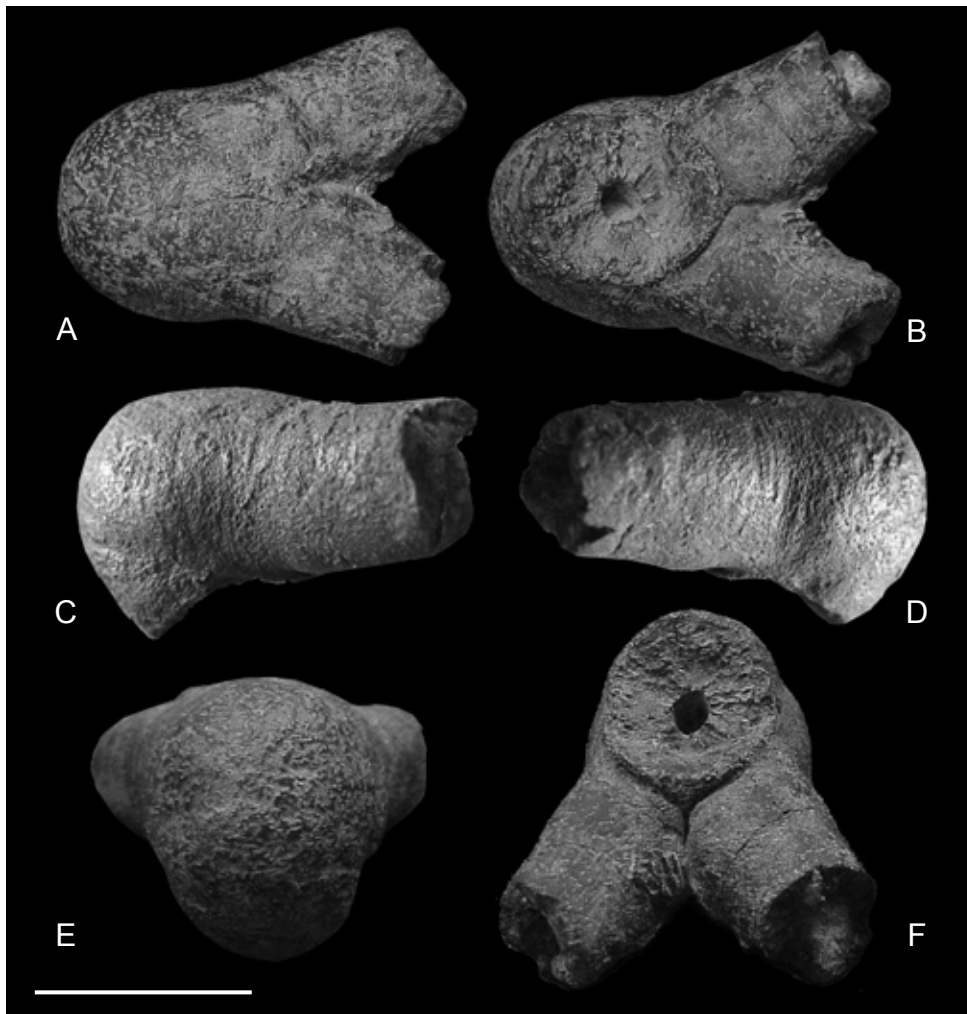


Figure 1. *Lamna nasus* (Bonnaterre, 1788), partial rostrum (NBNA Li6116; ex van der Steen Collection), Breda Formation (upper Miocene), Liessel (municipality of Deurne, province of Noord-Brabant, The Netherlands), in dorsal (A), ventral (B), lateral (C-D), anterior (E) and postero-ventral (F) views. Scale bar equals 30 mm.

near the junction of the rostral node and the lateral rostral cartilages. In contrast to the medial cartilage, both lateral rostral cartilages already meet under an angle of ca. 58 degrees, before joining the rostral node together. At the tangent of both lateral rostral cartilages a groove is present on the dorsal and ventral sides. Both lateral rostral cartilages are broad at the base of the rostral node and decrease only slightly in size towards their ends. In cross

section, both lateral rostral cartilages are circular and show a hollow central core. The central core of the left rostral cartilages is completely filled with indurated, cemented matrix, while that of the right rostral cartilage shows a similar filling at its deepest part, but is empty at the end. The cracked surface at the ventral side of the rostral nodes also indicates that the central core of the medial rostral cartilage was hollow, penetrating the rostral

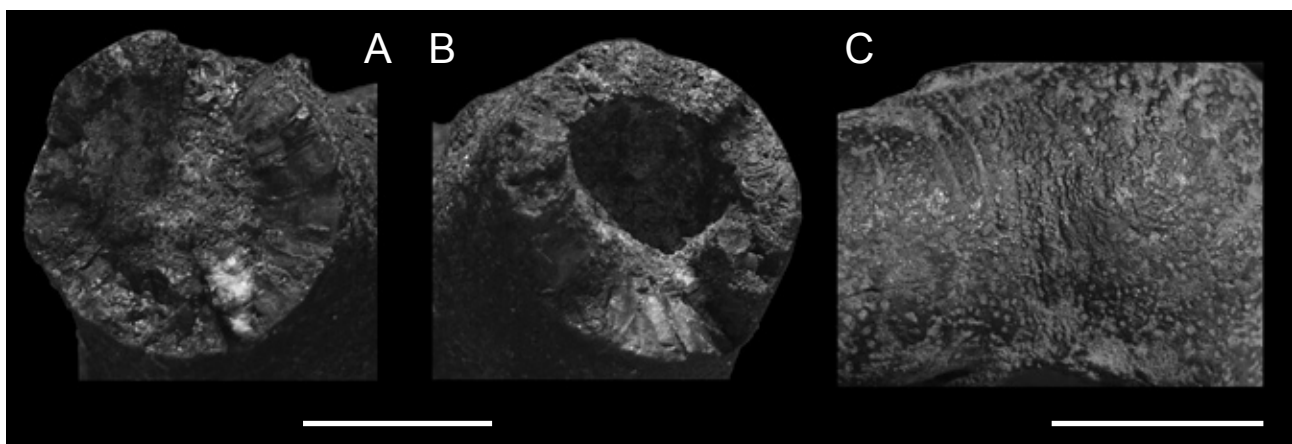


Figure 2. *Lamna nasus* (Bonnaterre, 1788), details of partial rostrum (NBNA Li6116; ex van der Steen Collection), Breda Formation (upper Miocene), Liessel (municipality of Deurne, province of Noord-Brabant, The Netherlands), showing ends of left (A) and right (B) lateral rostral cartilages, and rostral surface (C). Scale bars equal 10 mm.

node deeply. Although the rostral cartilages are incomplete, no structures are present that would indicate the former presence of vertical and/or horizontal rostral fenestra. The surface of the rostral node is not smooth, but shows a pattern of equally, albeit randomly, spaced rostral pits. Near the rostral node junction, several vertical ridges are seen on the lateral rostral cartilages (see Fig. 2C). The cracked surfaces of the lateral rostral cartilages are not smooth either, but are composed of prismatic structures (see Fig. 2A-B).

Dimensions. Standard measurements for elasmobranch rostra have been presented for both sharks (Compagno, 1988, fig. 6.13) and rajids (Ishiyama, 1952, p. 5, fig. 1; Hubbs & Ishiyama, 1968, p. 487, fig. 1). However, such cannot be employed in the case of incomplete rostra, such as the Liessel specimen. Therefore, *ad hoc* measurements, relevant to the present specimen, are listed in Fig. 3A-B.

Discussion. Regan (1906) was the first to introduce rostral morphology as an important character in shark taxonomy. Only subsequent to the publication of White's papers (1936, 1937) did the use of rostral cartilages become more widely adopted in classificatory and phylogenetic schemes of elasmobranchs. Although the phylogenetic significance of the rostral cartilages in the distinction of higher

taxonomic groups remained more or less controversial in the following decades (see El-Toubi, 1949; Hamdy, 1972; Maisey, 1984; Miyake *et al.*, 1992), their use in cladistic analyses is still widely accepted to date, both in sharks (see *e.g.* Compagno, 1990; Shirai, 1992, 1996; de Carvalho, 1996) and batoids (see *e.g.* McEachran & Miyake, 1990; McEachran & Dunn, 1998; McEachran & Aschliman, 2004).

According to Compagno (1973, 1977, 1988), tripodal rostra occur exclusively in Lamniformes and Carcharhiniformes. However, while referring to Cappetta's (1980a) description of the Cretaceous orectoloboid *Acanthoscyllium sahelalmae* (Pictet & Humbert, 1866), Maisey (1984, p. 41) observed a "prominent rostrum consisting of three slender cartilages" suggesting that a tripodal rostrum might have been more widely distributed than previously thought. Subsequently, Compagno (2001, p. 26) adopted this view in his latest edition of the FAO species catalogue, stating that a tripodal rostrum may be present in some fossil orectoloboids. After having examined the illustrations by Pictet & Humbert (1866, pl. 18, figs 2-4) and Cappetta (1980a, p. 115, fig. 22; pl. 14, figs 3-5; pl. 15, fig. 1), however, I subscribe to Cappetta's observation that the rostrum of *A. sahelalmae* is bifid, not trifid. Because no other piece of evidence was given in support of a potential presence of a tripodal rostrum in fossil Orectolobiformes, I here assume, at least for the time being, that this character is restricted to Lamniformes and Carcharhiniformes.

Compagno (1988) rejected Glikman's (1967) statement that Lamniformes differed from Carcharhiniformes in showing their rostral lateral cartilages to originate from the preorbital wall and supraorbital crest, leaving no unique character to distinguish rostra of both orders. But, based on illustrations of a wide array of carcharhinid and lamnid taxa by Compagno (1988, 1990, respectively), very large and robust rostra such as the Liessel specimen are restricted to Lamniformes. In contrast to the few large Carcharhiniformes that have so far been recorded from Liessel, lamniforms are presented by numerous genera, including both extinct and modern taxa (see Appendix 1).

In 1990, Compagno presented a detailed cladistic analysis of extant Lamniformes. With the exception of *Odontaspis noronhai* (Maul, 1955), cranial characters were presented for all lamnid species. Rostrum-related synapomorphies and autapomorphies listed in that analysis, supplemented by data presented by Compagno (2001), Mollet *et al.* (2002) and personal observations, have been used to present a preliminary key to species of post-natal Recent Lamniformes based on rostral characters (see Appendix 3). In addition, data on cranial morphology of *O. noronhai* were supplied by M.R. de Carvalho (pers. comm.); these confirm the presence of a lateral vertical fenestra in all odontaspidid rostra. However, additional data presented by de Carvalho (1996), including evidence of a node *Alopias* + ((*Mitsukurina* + *Pseudocarcharias*) + (*Carcharias* + *Odontaspis*)) which was supported by, amongst other characters, the presence of lateral rostral

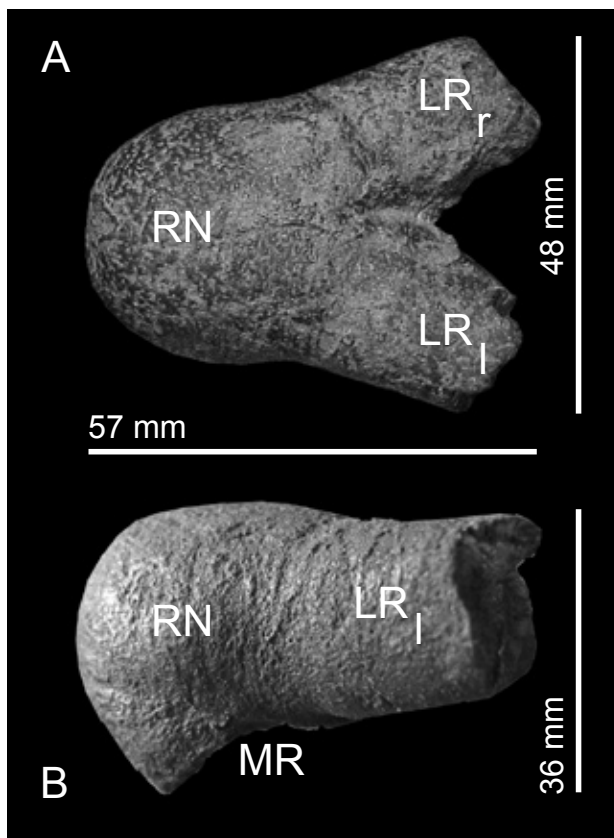


Figure 3. *Lamna nasus* (Bonnaterre, 1788), *ad hoc* measurements of partial rostrum (NBNA Li6116; *ex van der Steen* Collection), Breda Formation (upper Miocene), Liessel (municipality of Deurne, province of Noord-Brabant, The Netherlands), in dorsal (A) and lateral (B) views. Terminology: RN - rostral node, MR - medial rostral cartilage, LR - lateral rostral cartilages, l - left, r - right.

fenestrae and a 'rostral apex', were not included in the key presented here. Although this could separate the genus *Alopias* more easily from Cetorhinidae, Megachasmidae and especially Lamnidae, more detailed studies are needed to confirm this hypothesis. Although a small lateral vertical fenestra might be present in rostra of *Alopias vulpinus* (Bonnaterre, 1788) (see Parker, 1887, p. 33; Compagno, 1990, figs 3E, 7G), this has not yet been observed in *A. superciliosus* (Lowe, 1841), nor in *A. pelagicus* Nakamura, 1935, but this character could have been secondarily lost (see Compagno, 1990, p. 371). If de Carvalho's (1996) hypothesis is accepted as valid, it should be noted that these characters are synapomorphies only for the taxa mentioned and not for all Lamniformes, as stated by Shimada (2007).

The Liessel specimen is very robust, not elongated, of simple tripod form and the lateral rostral cartilages meet under an angle which is much less than 100°, eliminating the possibility that it could be assigned to the Alopiidae, Mitsukurinidae, Cetorhinidae or Megachasmidae (see key, Appendix 3). In addition, there is no evidence of a lateral vertical fenestra, which thus excludes Odontaspidae and Pseudocarchariidae. With only the Lamnidae left, the lateral rostral cartilages of the Liessel specimen are very swollen and this points to the genus *Lamna*.

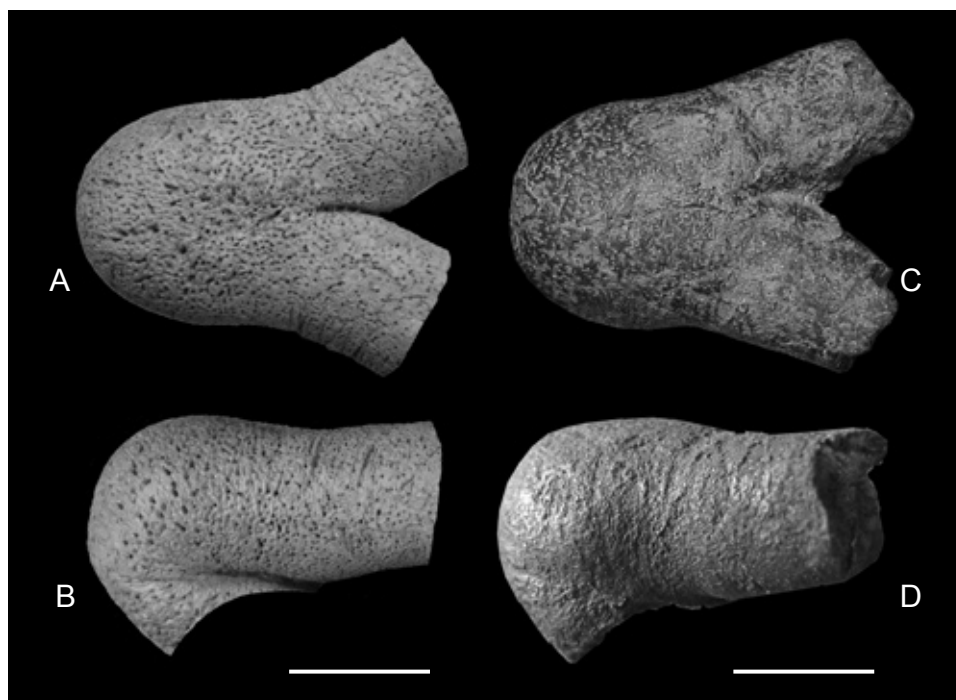
This genus is represented by two extant species, *L. nasus* (Bonnaterre, 1788) and *L. ditropis* Hubbs & Follett, 1947. Both attain total lengths in excess of 3.0 m, occur in coastal and oceanic waters, but have different geographic distributions. *Lamna nasus* inhabits the North Atlantic and in a circumglobal belt of temperate water in the southern hemisphere, whereas *L. ditropis* is restricted to the North Pacific (Compagno, 2001). The original description of *Lamna ditropis* is a very brief note which lacks a detailed comparison with *L. nasus*; its sole purpose

was to make the species name available in compliance to the International Code of Zoological Nomenclature (ICZN). Although announced by the authors at the time, they never complemented the original description. Only two decades later, Nakaya (1971) presented a comparative study of both *Lamna* species, but unfortunately he did not include skeletal data either. Despite the fact that illustrations of *L. ditropis* chondrocrania had been provided by Matsubara (1955) and Compagno (1977, 1988), albeit with almost no comments, this long-term lapse was eventually corrected by Compagno (1990, 2001), who compared the chondrocrania of both species and presented more detailed data on rostral morphology.

The rostra of both species of *Lamna* can be differentiated quite easily. In contrast to the rostrum of *L. nasus*, the rostral node is thicker and more massive in *L. ditropis*. In the latter, the individualised rostral cartilages are much shorter and, in adults, comprised in a real knob. In addition, the distance between the preorbital processes and rostral node base is very short in *L. ditropis*, while it is large in *L. nasus*. As a result, the rostral space is much larger in the latter species.

In spite of the limited number of specimens available for the present study, ontogenetic changes do appear to occur at least in rostra of *L. nasus*. Lateral rostral cartilages are almost rectilinear in juveniles and thus of a pyramidal form, but become more or less sigmoidal in adults, resulting in variations of rostral space shape, especially in dorsal view. Therefore, in dorsal view, the outer side of the rostrum is rectilinear in juveniles, whereas in adults a weak angle is present at the point where the lateral rostral cartilages and the rostral node meet. According to Compagno (1988, p. 62), such ontogenetic changes only exceptionally occur in chondrocrania of elasmobranchs as a result of hypercalcification.

Figure 4. *Lamna nasus* (Bonnaterre, 1788), comparison of Recent and fossil specimens; A-B. Recent (IRScNB 1353), adult specimen, sex, length and provenance unknown. C-D. Fossil, partial rostrum (NBNA Li6116; ex van der Steen Collection), Breda Formation (upper Miocene), Liessel (municipality of Deurne, province of Noord-Brabant, The Netherlands), in dorsal (C) and lateral (D) views. Scale bar equals 20 mm.



In the Liessel specimen, the rostral cartilages are not comprised in a genuine knob, but are identical to those seen in Recent adult *L. nasus* (see Fig. 4; Pls 1-3). In both the Liessel specimen and rostra of adult *L. nasus*, a weak angle is present near the rostral node/lateral rostral cartilages junctions and the latter already meet prior to entering the rostral node, resulting in a groove at their tangent (see Figs 4A, C). In Recent *L. nasus* the central cores of all three rostral cartilages are much less calcified (see Pl. 3) and most likely for that reason are not preserved in the Liessel specimen, which could explain the hollow central cores. In addition to general morphology, the specific crack-surface of both lateral rostral cartilages and the small pits on the rostral node of the Liessel specimen are homologous to the calcified prismatic tesserae structure and the ostrich eggshell-like surface of fresh *L. nasus* rostra. Therefore, I assign the fossil rostrum to an adult specimen of the porbeagle shark *Lamna nasus*, an extant species which is well known from isolated teeth in strata assigned to the Breda Formation (upper Miocene) at Liessel.

The localisation of all three fractures seen in the Liessel rostrum are not coincidental. In extant *Lamna nasus*, the medial and lateral rostral cartilages are weakest near the rostral node base and halfway the rostral process, respectively (see Pl. 2, Figs A-D).

4.2. Rostra of extinct lamnids

Even though rostral morphology remains unknown for most extinct lamniform sharks recorded to date from Liessel (see Appendix 1), I exclude other species from consideration for the following reasons. First, rostra of all extant lamniform species are unique and diagnostic, allowing specific identification, even in genera that contain more than one species (e.g., *Odontaspis*, *Alopias*, *Isurus* and *Lamna*). It is therefore very unlikely that the rostra of these extinct taxa would be identical to those of Recent *Lamna nasus*. In addition, none of the extinct lamniform taxa occurring in the Neogene of the North Sea Basin, and in particular known from Liessel, are closely related to the genus *Lamna*.

According to Casier (1960), the very large-sized and abundant *Cosmopolitodus hastalis* (Agassiz, 1838) and possibly '*Carcharodon*' *escheri* (Agassiz, 1844), might be closely related to the white shark *Carcharodon carcharias* (Linnaeus, 1758), which has a rostrum that is much less developed than in *Lamna* (see key, Appendix 3). In *Cosmopolitodus* Glikman, 1964, one could therefore suspect a rostrum which is shorter than in *Lamna* and which has a much thinner rostral node and rostral cartilages that are neither swollen nor hypercalcified. Mewis & Klug (2006) recorded an articulated skeleton of '*C.*' *escheri* from the Miocene of northern Germany, but unfortunately the rostrum, which could have confirmed or rejected the above hypothesis, was missing in this specimen (S. Klug, pers. comm.).

However, the taxonomic position of both *Cosmopolitodus hastalis* and '*Carcharodon*' *escheri* is controversial (see e.g. Purdy *et al.*, 2001); some authors

referred these species to the genus *Isurus*. Should these turn out to be isurids after all, their rostra would not be shorter than in *Lamna*, but would still be less calcified and have less well-developed rostral cartilages. The same applies for *Anotodus retroflexus* (Agassiz, 1838) and *Parotodus benedenii* (Le Hon, 1871). However, Cappetta (2006) assigned the former to the Alopiidae; all modern representatives have very thin and delicate rostral cartilages in comparison to *Lamna*. *Parotodus benedenii*, on the other hand, was assigned by Cappetta (1980b) to the Otodontidae, an extinct family of lamniforms which also includes *Megaelachus megalodon* (Agassiz, 1835) (see Cappetta, 1987, 2006), making direct comparisons with living taxa difficult. Nevertheless, Gottfried *et al.* (1996) reconstructed the chondrocranium of *M. megalodon*, based on extrapolations of *C. carcharias* (Lamnidae). This resulted in a shorter and but slightly more robust rostrum than in *C. carcharias*. With regard to Cappetta's view, I wish to point out that this reconstruction should be assessed with caution. Although Neogene lamniform phylogeny is beyond the scope of the present paper, it is clear that whatever hypothesis prevails, it is highly unlikely that the rostra of these extinct Lamniformes would be identical to those of *Lamna*, and of *L. nasus* in particular.

5. Conclusions

In spite of some controversy in the past, rostral morphology is an important character in cladistic analyses of Recent Elasmobranchii. In addition to its taxonomic value to separate higher groups (orders, families and genera), rostra of all extant lamniforms recorded to date are unique and diagnostic, permitting specific distinction. A preliminary key to species of Recent Lamniformes based on rostral characters is presented below; this allows the partial rostrum from the Breda Formation (upper Miocene) at Liessel to be assigned to the porbeagle shark *Lamna nasus*. In view of the fact that rostral morphology has proved to be useful in unraveling interrelationships amongst modern lamniforms, it could turn out helpful in future phylogenetic studies of extinct (Neogene) Lamniformes which are surrounded by numerous taxonomic questions to this day. In this light, more detailed studies of the limited fossil chondrocranial material available are encouraged, especially when found in association with teeth.

6. Acknowledgements

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7. Appendices

Appendix 1. Preliminary list of elasmobranch species from the Breda Formation (upper Miocene) at Liessel (municipality of Deurne, province of Noord-Brabant, The Netherlands).

List based on de Jong (1999), Peters (2009), Wijnstekers (pers. comm.), Herman and Wille collections (pers. obs.). Systematics and dates of publication follow Cappetta (2006), Woodward & Sherborn (1890) and Cahuzac *et al.* (2007).

- Hexanchiformes
 - Hexanchidae
 - Hexanchus griseus* (Bonnaterre, 1788)
 - Notorynchus primigenius* (Agassiz, 1835)
- Squaliformes
 - Squalidae
 - Squalus acanthias* Linnaeus, 1758
- Pristiophoriformes
 - Pristiophoridae
 - Pristiophorus* sp.
- Squatiniiformes
 - Squatiniidae
 - Squatina* sp.
- Lamniformes
 - Alopiidae
 - Anotodus retroflexus* (Agassiz, 1838)
 - Cetorhinidae
 - Cetorhinus maximus* (Gunnerus, 1765)
 - Lamnidae
 - '*Carcharodon*' *escheri* (Agassiz, 1844)
 - Cosmopolitodus hastalis* (Agassiz, 1838)
 - Isurus oxyrinchus* Rafinesque Schmaltz, 1810
 - Lamna nasus* (Bonnaterre, 1788)
 - Odontaspidae
 - Carcharias* sp.
 - Otodontidae
 - Megaselachus megalodon* (Agassiz, 1835)
- Carcharhiniiformes
 - Carcharhinidae

- Carcharhinus acanthodon* (Le Hon, 1871)
- Galeocерdo aduncus* (Agassiz, 1835)
- Scyliorhinidae
 - Scyliorhinus* sp.
- Triakidae
 - Galeorhinus* sp.
 - Mustelus* sp.
- Rajiformes
 - Rajidae
 - '*Raja*' sp.
- Torpediniiformes
 - Torpedinidae
 - Torpedo* sp.
- Myliobatiformes
 - Dasyatidae
 - '*Dasyatis*' sp.
 - Mobulidae
 - '*Myliobatis*' sp.
 - Myliobatidae
 - Aetobatus arcuatus* (Agassiz, 1843)

Appendix 2. Comparative material of Recent Lamnidae. Institutional abbreviations: Royal Belgian Institute of Natural Sciences (IRScNB), Elasmobranch Research, Belgium (ERB), Frederik H. Mollen field number (FHM) and Natal Sharks Board (NSB).

Genus *Carcharodon* Smith, in Müller & Henle, 1838. *Carcharodon carcharias* (Linnaeus, 1758). Fresh material – 1 specimen. NSB-UMT-07015 (= ERB-FHM-(2007-11-26)-1), female, 2120 mm TL, 26th November 2007, protective gill nets off Umtentweni, South Africa, SW Indian Ocean. Additional material – 2 dried chondrocrania. IRScNB 1385γ (I.G. 6728, 1900-05-01, by R. Storms), sex and length unknown, Mediterranean; NSB-unlabelled, female, 3740 mm TL (based on skeleton), date unknown, protective gill nets off KwaZulu-Natal, South Africa, SW Indian Ocean. Additional illustrations – Haswell (1884, pl. 1, figs 1-2); Parker (1887, Pl. 4, figs 1, 3; Pl. 5, fig. indet. (upper part of plate only), not Pl. 8, figs 24-25, misidentified by the author, see Francis (1996) and Mollet *et al.* (2002); Compagno (1990, figs 3G, 5J, 6/J, 7/J); Gottfried *et al.* (1996, fig. 5B); Wroe *et al.* (2008, fig. 1A-B).

Genus *Isurus* Rafinesque Schmaltz, 1810. *Isurus oxyrinchus* Rafinesque Schmaltz, 1810. Fresh material – 1 specimen. ERB-FHM-(2009-02-20)-1, female, 1940 mm TL, 20th February 2009, Algeciras fish market, Spain, 29°10'N, 15°20'W, NE Atlantic Ocean. Additional material – 3 dried chondrocrania, all in IRScNB collections. IRScNB 1384γ (I.G. 6862, 1902-04-03, by V. Frič), juvenile specimen, sex and length unknown, Mediterranean; IRScNB 2190 (I.G. 6888, 1894, by R. Storms), juvenile specimen, sex and length unknown, Nice, France, Mediterranean; IRScNB 2190β (I.G. 6888, 1892-03-31, by R. Storms), juvenile specimen, sex and length unknown, Nice, France, Mediterranean. Additional

illustrations – Matsubara (1955, fig. 15D-F); Glikman (1967, figs 8-9, 38); Compagno (1990, Figs 5K, 6K, 7K); Compagno (2001, fig. 12A-C); Wilga (2005, Fig. 3D; rostrum much smaller in proportion to the entire chondrocranium compared to all other illustrations and material available, specimen probably seen under an oblique angle). *Isurus paucus* Guitart Manday, 1966. Fresh material – 1 specimen. ERB-FHM-(2008-07-23)-1, female, 2540 mm TL, 23rd July 2008, 40°24'N, 67°23'W, NW Atlantic Ocean. Additional material – none. Additional illustrations – Compagno (1990, figs 5L, 6L, 7L).

Genus *Lamna* Cuvier, 1816. *Lamna ditropis* Hubbs & Follett, 1947. Fresh material – none. Additional material – none. Additional illustrations – Matsubara (1955, fig. 15A-C); Compagno (1977, fig. 7Q); Compagno (1988, fig. 7.1.A); Compagno (1990, figs 5M, 6N, 7M (not fig. 6M, mislabelled); Purdy *et al.* (2001, fig. 32A). *Lamna nasus* (Bonnaterre, 1788). Fresh material – 3 specimens, all in ERB collections. ERB-FHM-(2007-09-21)-1, male, 1620 mm TL, 21st September 2007, La Rochelle fish market, France, NE Atlantic Ocean; ERB-FHM-(2007-09-21)-2, male, 1740 mm TL, 21st September 2007, La Rochelle fish market, France, NE Atlantic Ocean; ERB-FHM-(2007-09-21)-3, male, 1660 mm TL, 21st September 2007, La Rochelle fish market, France, NE Atlantic Ocean. Additional material – 5 dried chondrocrania, all in IRScNB collections. IRScNB 476 (I.G. 9054), juvenile specimen, sex, length and provenance unknown; IRScNB 1352β (I.G. 5567, Berhheim), subadult specimen, male, length unknown, Belgium, North Sea; IRScNB 1353, adult specimen, sex, length and provenance unknown; IRScNB 2189 (I.G. 6888, year 1892, by R. Storms), juvenile specimen, sex and length unknown, Nice, France, Mediterranean; IRScNB 2189β (I.G. 6888, May 1902, by R. Storms), juvenile specimen, sex, length and provenance unknown. Additional illustrations – Parker (1887, Pl. 4, figs 2, 4; Pl. 5, fig. indet. (lower part of plate only); Garman (1913, Pl. 62, figs 1-3); Chevrier (1986, p. 6, figs indet.); Compagno (1990, figs 5N, 6M, 7N) (not fig. 6N, mislabelled); Goto (1996, fig. 5D); Wilga (2005, fig. 3C; rostrum different in shape and proportions from all other illustrations and material available, specimen probably distorted and shown under an oblique angle).

Appendix 3. Preliminary key to species of Recent post-natal lamniform sharks, based on rostral morphology, based on Compagno (1990, 2001), Mollet *et al.* (2002) and Mollen (unpubl. data; present study). Unpublished data on *O. noronhai* not included.

- 1a. Rostrum simple tripodal, formed by a medial rostral cartilage which is single bar shaped and two lateral rostral cartilages that do not form a separate false rostral node before meeting the real rostral node 2
- 1b. Rostrum tripodal, but complex, medial rostral cartilage extremely broad and relatively flat, formed by two separate

- bars that fuse near the rostral node base; lateral rostral cartilages very thin and joining into a separate false tripodal rostral node that gives rise to a separate rostral cartilage bar before meeting the real rostral node *Cetorhinus maximus*
- 2a. Rostrum and rostral node elongated, rostral length > 100% of nasobasal length *Mitsukurina owstoni*
- 2b. Rostrum or rostral node elongated, rostral length < 100% of nasobasal length 3
- 3a. Large vertical rostral fenestra present 4
- 3b. Large vertical rostral fenestra absent or insignificant and entirely embedded in the medial rostral cartilage 6
- 4a. Lateral rostral cartilages with long and slender rostral appendices that are positioned in anterior direction *Pseudocarcharias kamoharai*
- 4b. Rostral appendices absent 5
- 5a. Rostral cartilages rather short, rostral length < 40% of nasobasal length, vertical rostral fenestra smaller than rostral open space in lateral view..... *Carcharias taurus*
- 5b. Rostral cartilages rather long, rostral length > 40% of nasobasal length, vertical rostral fenestra at least as large as the rostral open space in lateral view..... *Odontaspis ferox*
- 6a. Distance between bases of both lateral rostral cartilages > 30% of total chondrocranium length, bases of the lateral rostral cartilages extremely broad, both lateral rostral cartilages meet under an angle in excess of 100° *Megachasma pelagios*
- 6b. Distance between bases of lateral rostral cartilages < 30% of total chondrocranium length, bases of the lateral rostral cartilages rather narrow or but moderately broad, both lateral cartilages meet under an angle smaller than 100° 7
- 7a. Lateral rostral cartilages very thin and delicate, medial rostral cartilage narrow and not significantly broader at its base 8
- 7b. Lateral rostral cartilages well developed, base of the medial rostral cartilage thick in ventral view and, together with the anteroventral edges of the nasal capsules forming a short, yet broad horizontal internasal septum that is concave at its posterior edge 10
- 8a. Lateral rostral cartilages not laterally expanded and as thin as the medial one, rostral open space more or less triangular shaped in lateral view, a small vertical rostral fenestra might be present at the end of the medial rostral cartilage *Alopias vulpinus*

- 8b. Lateral rostral cartilages laterally expanded and broader than medial one, rostral open space more or less oval shaped in lateral view, rostral fenestra absent **9**
- 9a. Rostral lateral cartilages extended, forming vertical rostral plates, rostral appendices present on lateral cartilages *Alopias superciliosus*
- 9b. Rostral lateral cartilages not extended, horizontal rostral plates and rostral appendices absent
..... *Alopias pelagicus*
- 10a. Bases of the lateral rostral cartilages positioned on the preorbital processes, rostral cartilages more or less swollen and hypercalcified **11**
- 10b. Bases of the lateral rostral cartilages positioned on the nasal capsules, rostral cartilages not swollen, nor hypercalcified **12**
- 11a. Rostral node very thick and massive, individualised rostral cartilages short, comprised in a real knob (in adults), base of the rostral node close to the preorbital walls, rostral space rather small *Lamna ditropis*
- 11b. Rostral node thick, individualised rostral cartilages long, not forming a massive knob, base of the rostral node distant from the preorbital walls, rostral space large
..... *Lamna nasus*
- 12a. Rostral node length smaller than the individualised maximal lateral rostral cartilages width, rostral cartilages rather short, rostral length < 30% of nasobasal length, rostral open space height > 50% of rostral open space length in lateral view *Carcharodon carcharias*
- 12b. Rostral node length larger than the individualised maximal lateral rostral cartilage width, rostral cartilages rather long, rostral length > 30% of nasobasal length, rostral open space height < 50% of rostral open space length in lateral view **13**
- 13a. Rostrum narrow in dorsal view, rostral open space width < 35% of rostral open space length in dorsal view, width of rostral node base relatively small
..... *Isurus oxyrinchus*
- 13b. Rostrum broad in dorsal view, rostral open space width > 35% of rostral open space length in dorsal view, width of rostral node base relatively large
..... *Isurus paucus*

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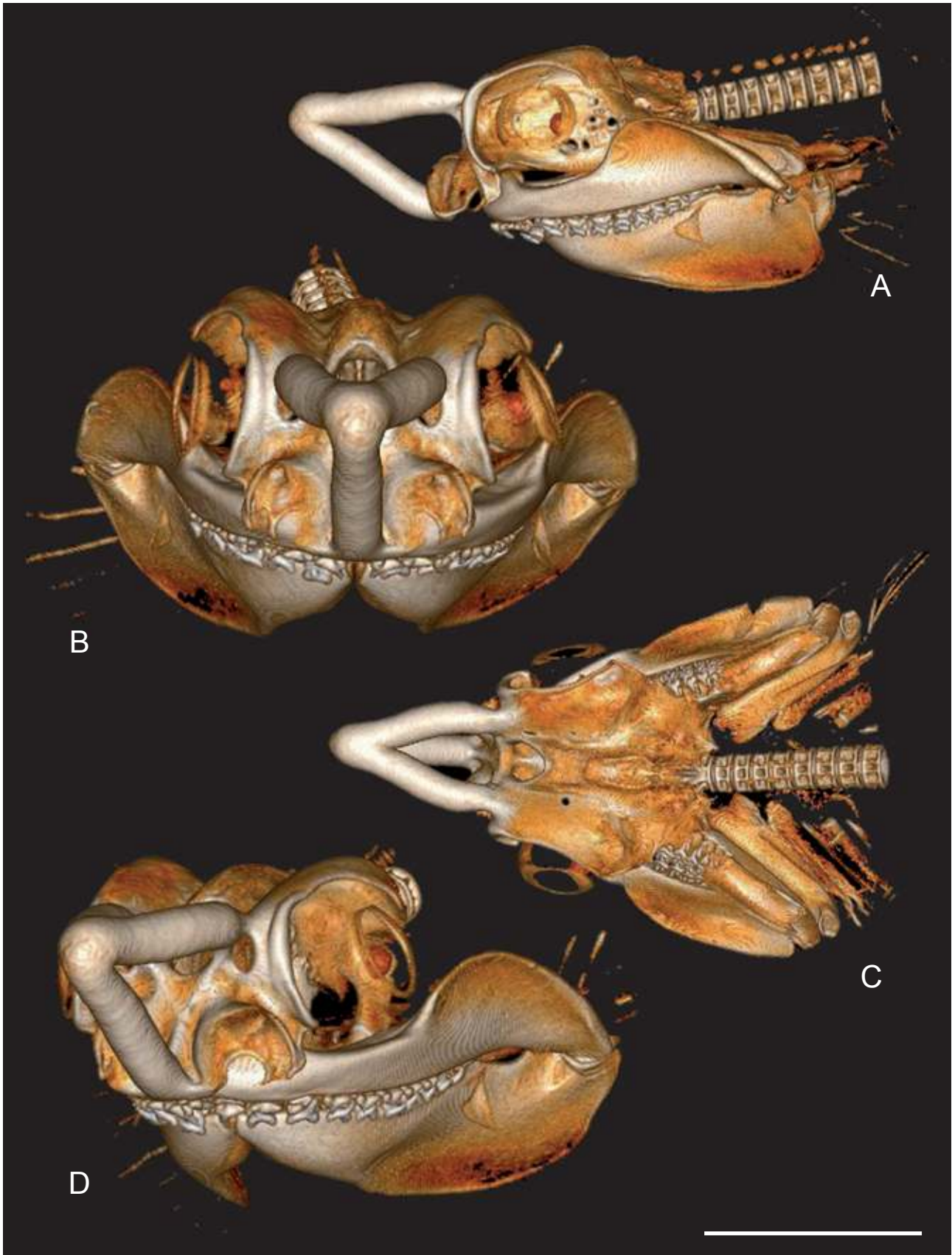


Plate 1. *Lamna nasus* (Bonnaterre, 1788), Recent (ERB-FHM-(2007-09-21)-2), juvenile male, 1740 mm TL, 21st September 2007, La Rochelle fish market, France, NE Atlantic Ocean, in lateral (A), anterior (B), dorsal (C) and antero-lateral (D) views of three-dimensional volume rendered images based on CT scan of the entire head, showing all cartilage structures. Scale bar equals 100 mm.

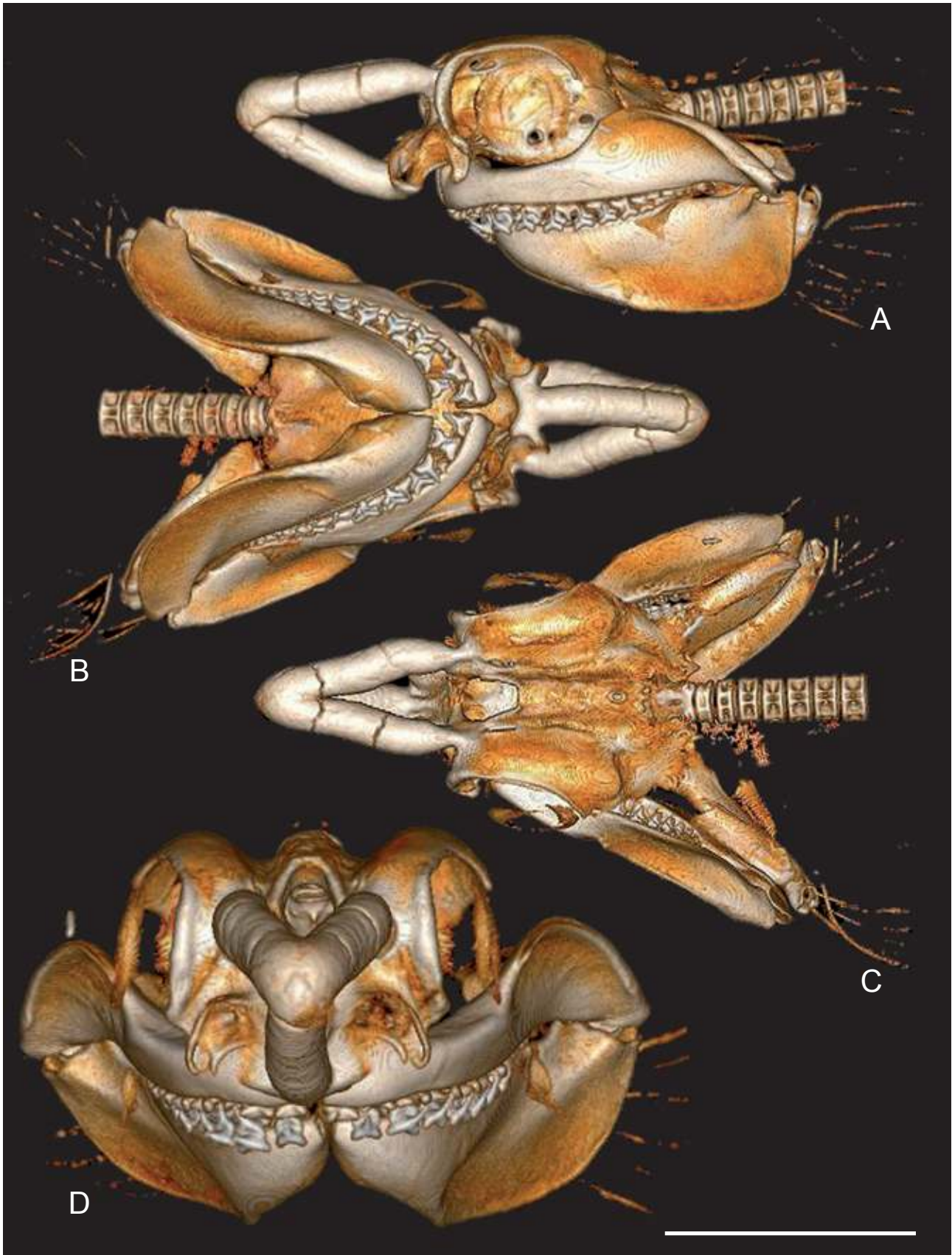


Plate 2. *Lamna nasus* (Bonnatere, 1788), Recent (ERB-FHM-(2007-09-21)-3), juvenile male, 1660 mm TL, 21st September 2007, La Rochelle fish market, France, NE Atlantic Ocean, in lateral (A), ventral (B), dorsal (C) and anterior (D) views of three-dimensional volume rendered images based on CT scan of the entire head, showing all cartilage structures (rostrum shows multiple *post mortem* fractures, but all parts preserved *in situ*). Scale bar equals 100 mm.

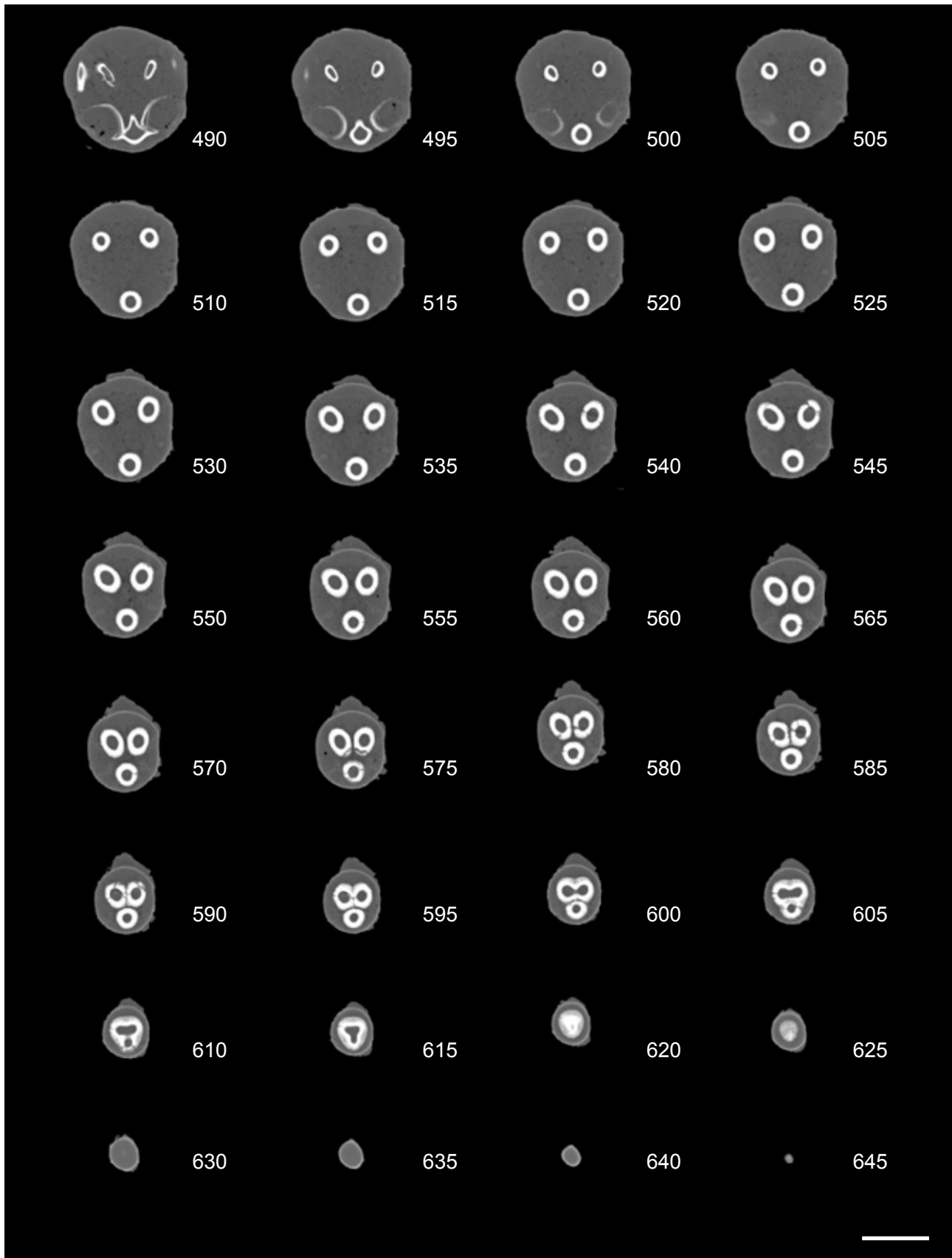


Plate 3. *Lamna nasus* (Bonnatere, 1788), Recent (ERB-FHM-(2007-09-21)-3), juvenile male, 1660 mm TL, 21st September 2007, La Rochelle fish market, France, NE Atlantic Ocean, selected images (*i.e.* one out of every five successive transverse slices) of a complete set of coronal views through the entire rostrum based on CT scans, dorsum up. Rostral base (490), rostral end (625) and snout tip (645). Scale bar equals 50 mm.