



Comparative morphology of rostral cartilages in extant mackerel sharks (Chondrichthyes, Lamniformes, Lamnidae) using CT scanning

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Abstract

A comparative study of rostral morphology of extant mackerel sharks (Lamniformes, Lamnidae) is presented. Based on computed tomography (CT) scans of fresh specimens, 3D reconstructions, dried museum chondrocrania and the available literature, detailed morphological descriptions of the rostral cartilages are provided for the type species of all three extant lamnid genera, namely *Carcharodon carcharias* (Linnaeus, 1758), *Isurus oxyrinchus* Rafinesque, 1810 and *Lamna nasus* (Bonnaterre, 1788), and compared with those of *I. paucus* Guitart Manday, 1966 and *L. ditropis* Hubbs & Follett, 1947. Despite intraspecific variation, the rostral cartilages of all extant lamnids present significant differences that allow genus- and species-level identification, which is especially of use to identify fossil rostral nodes of these particular taxa. The main differences were found to be in overall calcification of the rostrum (*Lamna* > *Isurus* > *Carcharodon*), general configuration of the rostral open space, position of the base of the lateral rostral cartilages, (non-)abutting lateral cartilages, (absent) rostral keels and shape of the rostral node. In cross section, the base of the rostral node is rounded in *Lamna*, Y-shaped in *Isurus* and uncalcified in juvenile and subadult *Carcharodon* (tesserae absent).

Key words: *Carcharodon*, *Isurus*, *Lamna*, taxonomy, rostrum, computed tomography.

Introduction

Rostral morphology is an important character in cladistic analyses of elasmobranchs (see *e.g.*, Regan 1906; White 1936, 1937; Carvalho 1996; Shirai 1996). Moreover, the rostra of all extant lamnoids are diagnostic, permitting species identification (see Compagno 1990; Mollen 2010), with the possible exception of *Odontaspis noronhai* (Maul, 1955) for which no data are available. Based on dental records, many of these extant lamnoids are also known from Miocene and Pliocene deposits worldwide (see, *e.g.*, Cappetta 1987, 2006; Purdy *et al.* 2001). Their rostra can thus be determined also, even when found unassociated with other skeletal remains such as teeth, and can therefore be used in compiling extinct faunal lists (see Purdy *et al.* 2001; Mollen 2010; Mollen & Jagt 2012).

Although chondrichthyan fish fossilise well only in exceptional conditions, making skeletal material rare (see Zangerl 1981; Cappetta 1987), Purdy *et al.* (2001) recorded more than a hundred shark rostral nodes of different types, all from the Yorktown Formation, of Pliocene (Zanclean, 5.33–3.60 Ma) age, in North Carolina (USA). However, those authors were able to assign them only to the orders Lamniformes and Carcharhiniformes, with the exception of the genus *Lamna*. Their attempt to assign the material to lower-ranking taxa was hampered by the fact that data on rostral morphology are very limited, even for lamnids (see Compagno 1990; Mollen 2010); all original species description, as well as many subsequent papers on their comparative morphology (*e.g.* Garrick 1967; Moreno & Morón 1992; Nakaya 1971), lack detailed skeletal information.

Based on CT scanning of fresh specimens, dried museum specimens and illustrations available in literature, the present study aims to illustrate and describe the rostral cartilages of the type species of all extant lamnid genera (*Carcharodon carcharias*, *Isurus oxyrinchus* and *Lamna nasus*), and to compare them with those of *Isurus paucus* and *Lamna ditropis*.

Material and methods

Fresh specimens were either acquired at fish markets throughout southwest Europe or obtained from scientific institutions (for details see below). All specimens were sexed, measured and photographed prior to dissection. Heads were cut off near the first gill slit and kept deep frozen in secured plastic bags to prevent dehydration during storage. Prior to conventional dissection (which often leads to broken structures in the rostrum; Compagno 1988), computed tomography (CT) was applied to illustrate and describe rostral morphology. This medical visualisation technique allows series of transverse sections through the chondrocranium to be obtained, in particular through the rostrum, leaving the specimen undamaged (Rowe *et al.* 1997).

Terms used in the literature to describe cranial and, in particular, rostral morphology in chondrichthyans varies markedly (see *e.g.*, Gegenbaur 1872; Garman 1913; de Beer 1937; Holmgren 1940; Gilbert 1967). For descriptive terminology, we follow mainly Compagno (1988, 1990, 2001) and Mollen (2010).

Two specimens (heads only) of *L. nasus* (Elasmobranch Research, Belgium; ERB 0929; ERB 0930) were scanned using a Philips Brilliance 40-slice helical-spiral CT scanner at the ZNA hospitals Antwerp (courtesy of F. Hilde and J. Bauwens, medical imaging department), in anatomical position, *i.e.* horizontally, dorsum up and snout first. During scanning, all specimens were still frozen and secured in plastic bags for hygienic purposes, without influencing results. Viewing and volume rendering was made possible through an eFILM Lite™ and Philips Extended Brilliance Workspace V 3.5.0.2254, respectively. Subsequently, the heads of *C. carcharias* (ERB 0932), *I. oxyrinchus* (ERB 0933; ERB 0934), *I. paucus* (ERB 0935) and *L. ditropis* (ERB 0854; ERB 0937) were scanned using the same method, but with new software (iQ-VIEW, version 2.6.0, 2009) to allow viewing of transverse slices. For specific CT parameter settings, reference is made to Mollen (2010). In addition, an alcohol-preserved specimen of *C. carcharias* (Field Museum of Natural History, Chicago; FMNH 38335) was CT scanned (protocol unknown) at Children's Memorial Hospital, Chicago for which a set of transverse views through the rostrum was made available (courtesy of K. Shimada).

Based on CT software, measurements were taken of all specimens, except for specimen FMNH 38335 (see Table 1). Morphometrics follow Compagno (1988) for 'rostral length' (RL) and 'width across bases of lateral rostral cartilages' (WLR_b), and Mollen (2010) for '(open) rostral space length' (ROSL), '(open) rostral space height' (ROSH), and '(open) rostral space width' (ROSW). Rostral space length corresponds to the maximum longitudinal distance of the rostral space. It can be measured dorsally (ROSL_d) or laterally (ROSL_l), yielding different results. When measured dorsally, rostral space length is related to the lateral rostral cartilages (LR) only. Therefore, this dimension might be greater in the same individual than rostral length as defined by Compagno (1988), which is related to the medial rostral cartilage (MR). In lateral view, rostral space length is measured perpendicularly, not obliquely. Rostral space height is the maximum height, viewed laterally, and is measured perpendicular to the rostral space length. Finally, rostral space width is measured dorsally, between perpendiculars, as the maximum distance between the two lateral rostral cartilages. For comparison, all rostral measurements were expressed as percentages of cranial length (CL). In addition, total length (TL) and nasobasal length (NBL) are supplied for each specimen as a general reference point.

As soon as series of transverse slices, 3D images, and measurements were obtained, the heads were dissected and chondrocrania prepared using hot-water maceration following the method outlined by Stohler (1945) and Compagno (1988). To prevent loss of teeth, jaws were cleaned separately using cold water only.

In addition to the fresh material, dried chondrocrania of ten additional specimens of the type species of all three lamnid genera were examined. All of these are housed in the collections of the Royal Belgian Institute of Natural Sciences (IRScNB) and KwaZulu-Natal Sharks Board (KZNSB), and are listed below. Nearly all of these specimens were collected more than a century ago and lack basic data such as sex and total length, but they were still useful in determining individual variations and possible ontogenetic changes.

TABLE 1. Morphometry of lamnid rostra. Abbreviations: _b, base; _d, dorsal; F, female; M, male; _l, lateral; n.a., not available; **TL**, total length; **CL**, cranial length; **NBL**, nasobasal length; **RL**, rostral length; **WLR_b**, width across bases of lateral rostral cartilages; **ROSL**, rostral (open) space length; **ROSW**, rostral (open) space width; **ROSH**, rostral (open) space height.

	Sex	TL	CL	NBL	RL	WLR _b	ROSL _d	ROSW	ROSL _l	ROSH
	(F/M)	(mm)	(mm)	(% CL)	(% CL)	(% CL)	(% CL)	(% CL)	(% CL)	(% CL)
<i>C. carcharias</i>										
ERB 0932	F	2120	203	79.5	33.6	10.2	26.2	18.0	20.5	9.8
<i>I. oxyrinchus</i>										
ERB 0933	F	1940	234	70.7	37.6	5.3	33.1	12.0	21.8	6.8
ERB 0934	n.a.	2300 ±100	311	71.2	35.9	6.8	34.8	12.9	22.4	7.6
<i>I. paucus</i>										
ERB 0935	F	2540	272	68.8	40.1	8.6	32.0	16.4	23.1	11.3
<i>L. nasus</i>										
ERB 0929	M	1740	189	69.1	48.3	13.4	26.0	13.4	29.1	16.6
ERB 0930	M	1660	167	63.7	44.7	16.0	31.2	16.0	34.9	13.6
<i>L. ditropis</i>										
ERB 0854	F	2340	189	80.8	40.4	14.4	13.9	14.4	17.3	8.7
ERB 0937	F	900	108	75.4	35.6	20.3	18.6	20.3	23.3	12.7

Even though dried museum specimens are often distorted or incomplete, opportunities to collect fresh material have drastically decreased during the past decade, even for species that are not protected and even commercially exploited. Therefore, all published illustrations of lamnid chondrocrania are relevant for this study and added to the list of material examined:

Carcharodon carcharias

Fresh material: 1 specimen, ERB 0932 (= KZNSB–UMT 07015), female, 2120 mm TL, 26 November 2007, protective gill nets off Umtentweni, South Africa, southwest Indian Ocean.

Additional material: one set of transverse views through rostrum based on CT scans (unpublished data, courtesy of K. Shimada) of a female, FMNH 38335, c. 2714 mm TL (based on crown height of first anterior teeth, following the method described by Shimada 2003), off southern Florida, USA, Atlantic Ocean, and 2 dried chondrocrania, IRScNB 1385γ, no data, Mediterranean; KZNSB unlabelled, female, c. 3740 mm TL (based on skeleton), date unknown, protective gill nets off KwaZulu-Natal, South Africa, southwest Indian Ocean.

Additional illustrations: Haswell (1884, pl. 1, figs. 1–2), Parker [1887, pl. 4, figs. 1, 3; pl. 5, unnumbered fig. (upper part of plate only)]; *non* pl. 8, figs. 24–25, misidentified by the author, see Francis (1996) and Mollet *et al.* (2002)], Compagno (1990, figs. 3G, 5J, 6J, 7J), Gottfried *et al.* (1996, fig. 5B), Wroe *et al.* (2008, fig. 1A–B), and Shimada *et al.* (2009, fig. 2D).

Isurus oxyrinchus

Fresh material: 2 specimens, ERB 0933, female, 1940 mm TL, 20 February 2009, Algeciras fish market, Spain, 29°10'N, 15°20'W, northeast Atlantic Ocean; ERB 0934, sex unknown (said to be male but unverified), 2300 (+/- 100) mm TL, 26 February 2009, Concarneau fish market, France, northeast Atlantic Ocean.

Additional material: 3 dried chondrocrania, IRScNB 1384γ, IRScNB 2190 and IRScNB 2190β, juvenile specimens, no data, Nice, France, Mediterranean.

Additional illustrations: Matsubara (1955, fig. 15D–F), Glikman (1967, figs. 8–9, 38; 1980, pls 1–4, fig. 2), Compagno (1990, figs. 5K, 6K, 7K), Muñoz-Chápuli & De Andrés (1995, fig. 1C), Compagno (2001, fig. 12A–C), Wilga (2005, fig. 3D), and Shimada *et al.* (2009, fig. 2C).

Isurus paucus

Fresh material: 1 specimen, ERB 0935, female, 2540 mm TL, 23 July 2008, 40°24'N, 67°23'W, northwest Atlantic Ocean.

Additional illustrations: Compagno (1990, figs. 5L, 6L, 7L).

Lamna ditropis

Fresh material: 2 specimens, ERB 0937, female, 900 mm TL, August 2009, beached south of Monterey Bay near San Luis Obispo and Cambria, northeast Pacific Ocean; ERB 0854 (= NMFS–AFSC–09SS004), female, 2340 mm TL, 2 October 2009, northeast side of Kodiak Island, northeast Pacific Ocean.

Additional illustrations: Matsubara (1955, fig. 15A–C), Compagno (1977, fig. 7Q; 1988, fig. 7.1.A; 1990, figs 5M, 6N, 7M (*non* fig. 6M, mislabelled), Glikman (1980, fig 1.1–2), and Purdy *et al.* (2001, fig. 32A).

Lamna nasus

Fresh material: 3 specimens, ERB 0928, male, 1620 mm TL, 21 September 2007, La Rochelle fish market, France, northeast Atlantic Ocean; ERB 0929, male, 1740 mm TL, same date and provenance; ERB 0930, male, 1660 mm TL, same date and provenance.

Additional material: 5 dried chondrocrania, IRScNB 476 and IRScNB 2189 β , juvenile specimens, sex, no data; IRScNB 1352 β , subadult specimen, male, length unknown, Belgium, North Sea; IRScNB 1353, adult specimen, no data; IRScNB 2189, juvenile specimen, no data, Nice, France, Mediterranean.

Additional illustrations: Parker (1887, pl. 4, figs. 2, 4; pl. 5, unnumbered fig. (lower part of plate only), Garman (1913, pl. 62, figs. 1–3); Block & Carey (1985, fig. 4A–B), Chevrier (1986, p. 6, unnumbered figs.), Compagno (1990, figs. 5N, 6M, 7N; *non* fig. 6N, mislabelled), Goto (1996, fig. 5D), Wilga (2005, fig. 3C), and Mollen (2010, fig. 4A–B; pls 1–3).

Results

Overview of rostral structure

In elasmobranchs, the rostrum is the anteriormost cartilaginous structure of the chondrocranium, positioned in front of the nasal capsules (NC), anterior fontanelle (AF) and underlying precerebral fossa, and supporting the prenasal snout (Compagno 1988, 2001) (see Figs 1–6). Together with the nasal capsules, it forms the ethmoidal region of the chondrocranium (see Gegenbaur 1872). The rostrum in elasmobranchs is formed by the outgrowths of the trabecula and/or lamina orbitonasalis (Miyake *et al.* 1992; Carvalho 1996), but embryological growth patterns differ significantly between galeomorph and squaloid sharks (Holmgren 1940). From a histological point of view, the rostrum consists of hyaline cartilage. In species with calcified rostra, however, the hyaline cartilage is restricted to the core of the rostrum and covered by mineralised, calcified blocks, referred to as tesserae (or prismatic cartilage). Tesserae are occasionally present in several layers (Dingerkus *et al.* 1991; Compagno 2001) and extreme calcification has been observed at times in the external surface of rostra in a number of elasmobranchs and is known as hypercalcification (Compagno 1988).

Lamnoids, as well as carcharhinoids, have tripodal rostra (Compagno 1973, 1977, 1988), which consist of a medial (MR) and two lateral rostral cartilages (LR), all three merging into a 'rostral node' (RN) (Gilbert 1967) (see Figs 1–6). In morphological studies, and with reference to the terminology and subsequent definitions used by Compagno (1988, 1990, 2001), the nasal structures and rostrum are generally treated as separate structures. In extant lamnids, however, the nasal capsules are well separated, but their anteriormost and medial edges give rise to an internasal plate (IP). In ventral view, the anteriormost edge of this internasal plate projects ventrally and completely merges with the base of the medial rostral cartilage, forming a single structure.

In addition to the above terminology (see Material and methods), two additional terms are of specific interest to describe rostral morphology in sharks. In lateral and dorsal views, Mollen (2010) introduced the 'rostral open space' as a specific term to describe the general appearance of the tripodal rostra in lamnoids, abbreviated below to '(inter)rostral space' (ROS). Contrary to the rostral cartilages themselves, the description of the 'space' between them is often much simpler and more accurate. It should be noted, however, that the rostral space and the anterior

fontanelle (AF), with its underlying precerebral cavity (= precerebral fossa), are two distinct structures, but are, in dorsal view, often inaccurately or erroneously illustrated as one (see discussion). The rostral space is also different from the ‘rostral fenestra’, a term introduced to indicate an aperture in the rostral node (RN) (Gilbert 1967) or a partition of the rostral space by the rostral transverse bars (Compagno 1988, 1990), such as present in Odontaspidae and Pseudocarchariidae.

Despite the available terminology, there is currently no standard format to describe elasmobranch rostra. In order to study intraspecific variations and interspecific differences, rostral descriptions are standardised in the present study using the following sequence: general appearance of the entire rostrum, inclusive of rostral space (ROS), lateral rostral cartilage (LR), medial rostral cartilage (MR), including the anteriormost edge of the internasal plate (IP), and rostral node (RN). All structures are described individually on the basis of external observations, as well as from successive cross sections, always beginning at the base moving towards the rostral end. When describing cross sections, the histology of the different rostral elements is discussed as well.

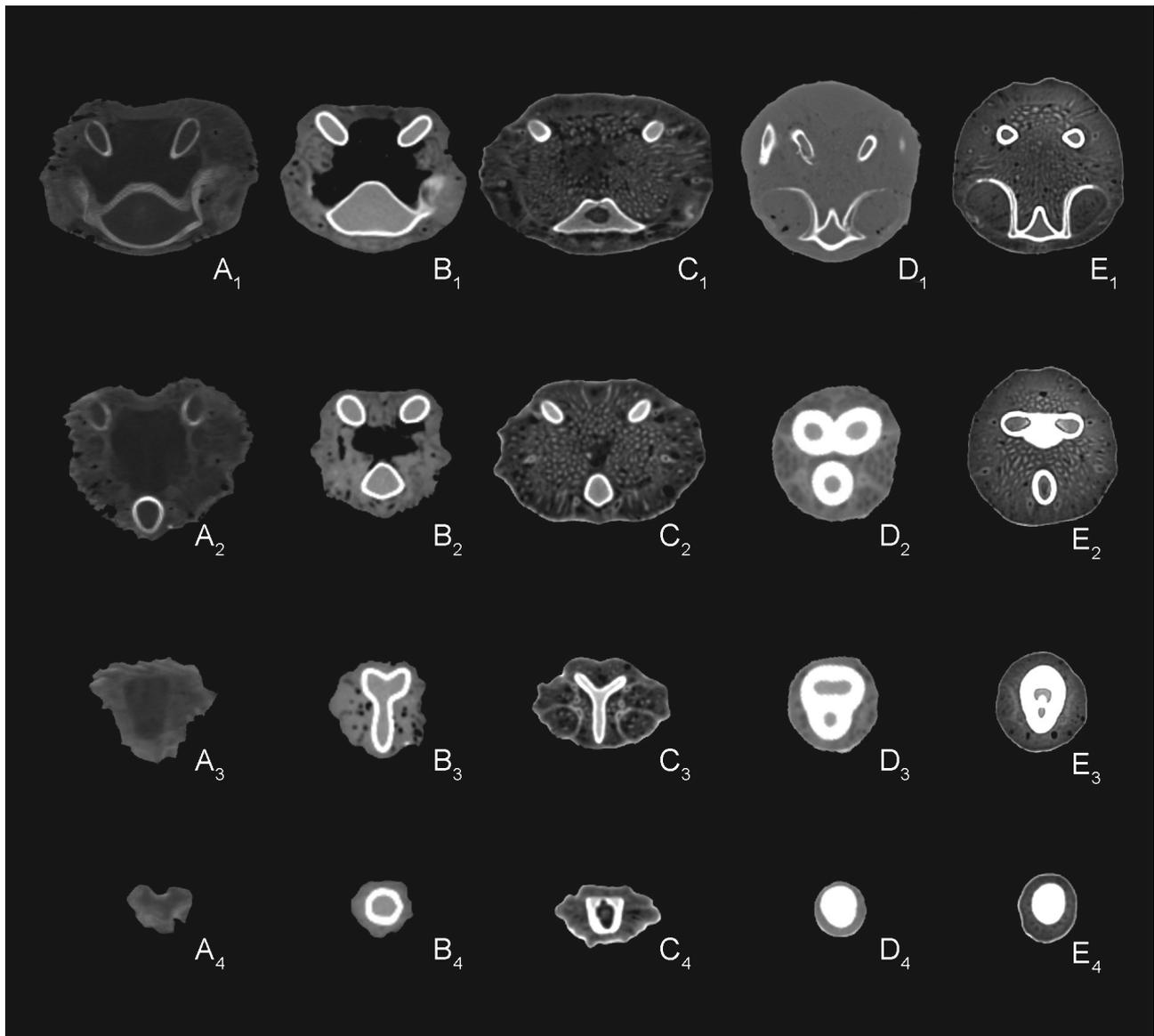


FIGURE 1. Transverse slices through the rostrum (not to scale): rostral base (₁); in between mid-portion of rostrum and rostral node base (₂); rostral node base (₃) and rostral node (₄). **A.** *Carcharodon carcharias* (FMNH 38335); **B.** *Isurus oxyrinchus* (ERB 0933); **C.** *I. paucus* (ERB 0935); **D.** *Lamna nasus* (D₁, ERB 0930; D₂–D₄, ERB 0929) and **E.** *L. ditropis* (ERB 0854).

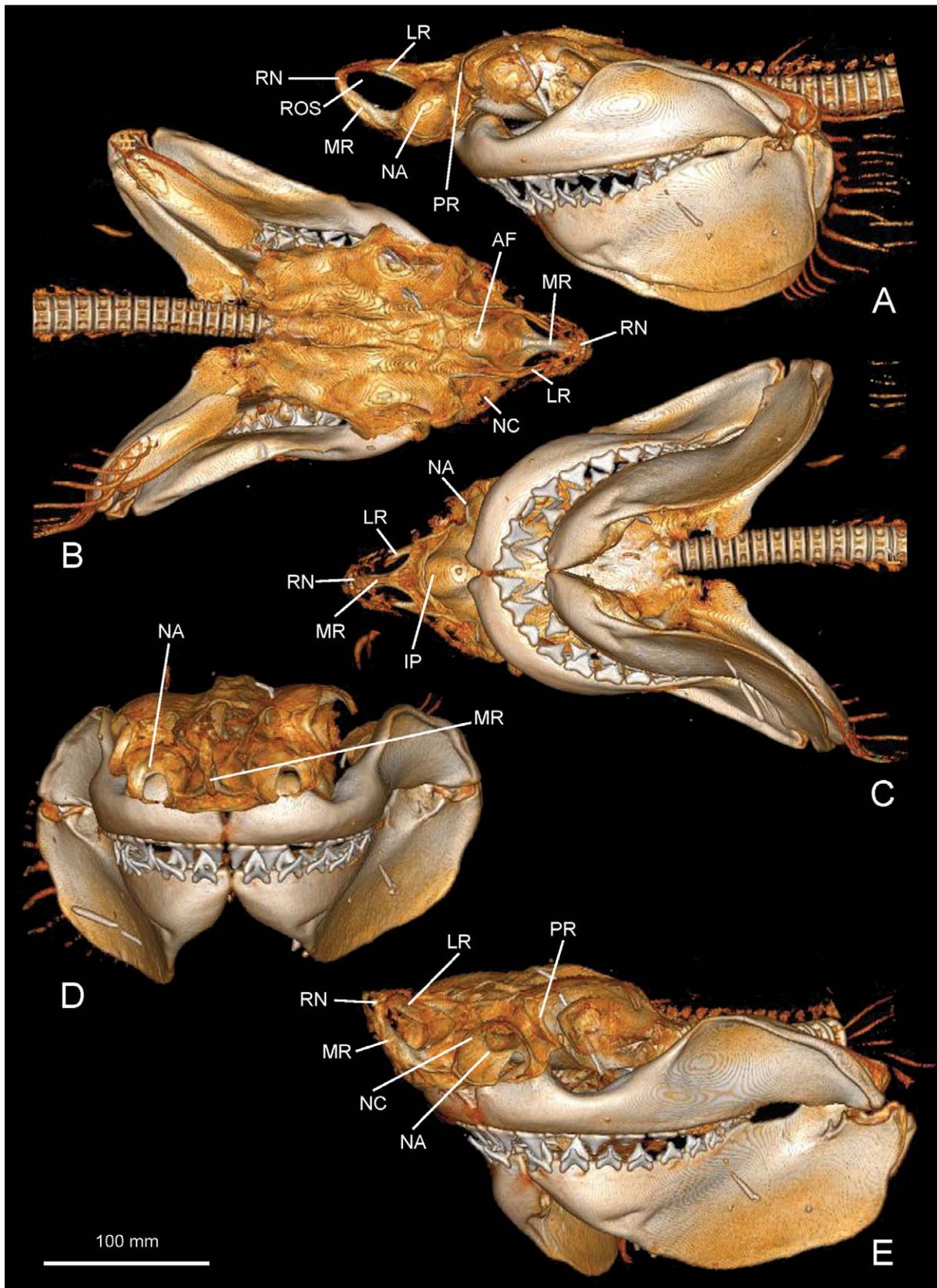


FIGURE 2. *Carcharodon carcharias* (Linnaeus, 1758), female, 2120 mm TL, southwest Indian Ocean (ERB 0932), 3D reconstructions based on CT scans of the entire head, showing all cartilaginous structures: lateral (A), dorsal (B), ventral (C), anterior (D) and anterolateral (E) views. Abbreviations: **AF**, anterior fontanelle; **IP**, internasal plate; **LR**, lateral rostral cartilages; **MR**, medial rostral cartilage; **NA**, nasal aperture; **NC**, nasal capsule; **PR**, preorbital process; **RN**, rostral node; **ROS**, rostral space.

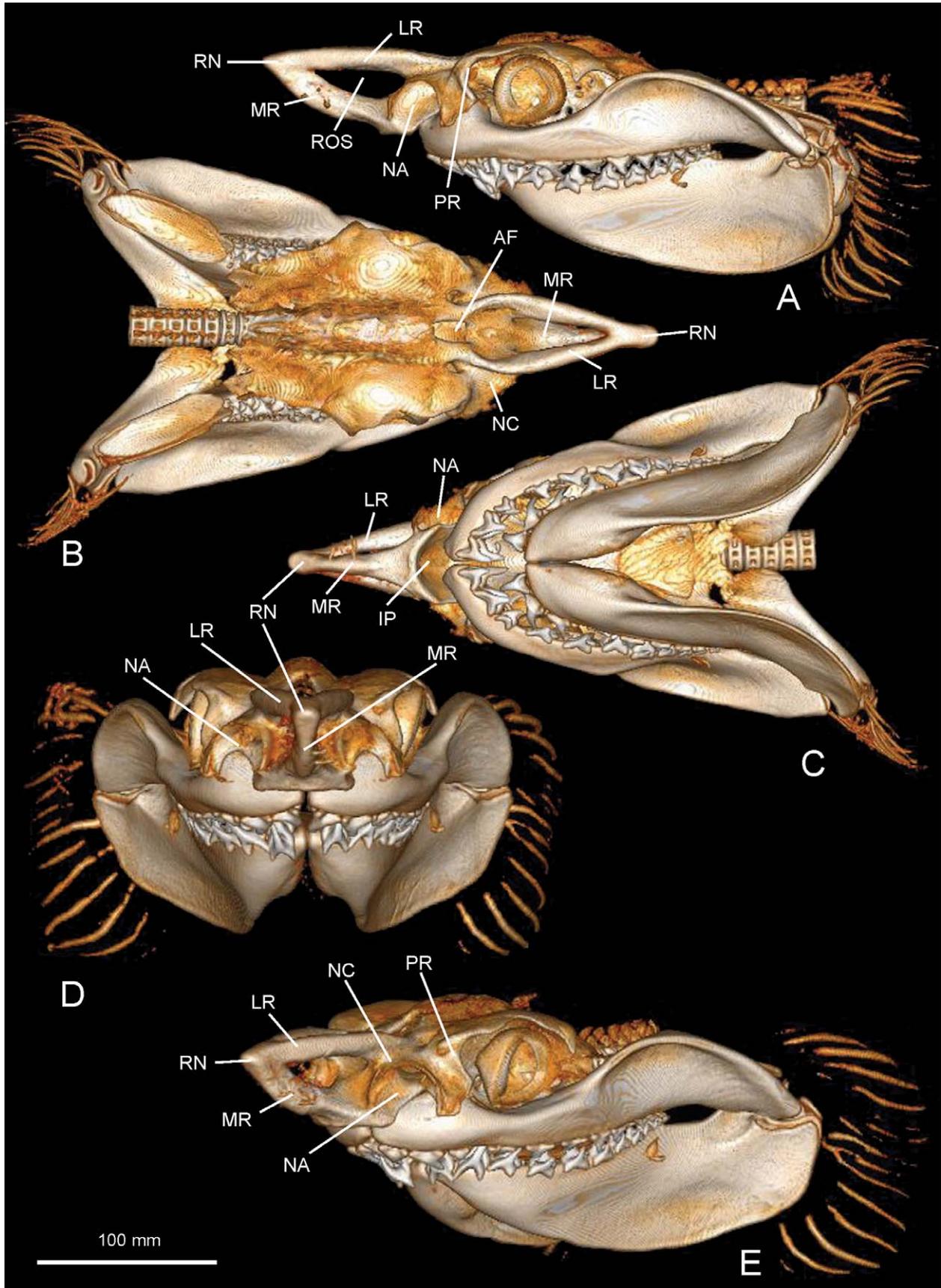


FIGURE 3. *Isurus oxyrinchus* Rafinesque, 1810, female, 1940 mm TL, northeast Atlantic Ocean (ERB 0933), 3D reconstructions based on CT scans of the entire head, showing all cartilaginous structures: lateral (A), dorsal (B), ventral (C), anterior (D) and anterolateral (E) views. Abbreviations: see Fig. 2.

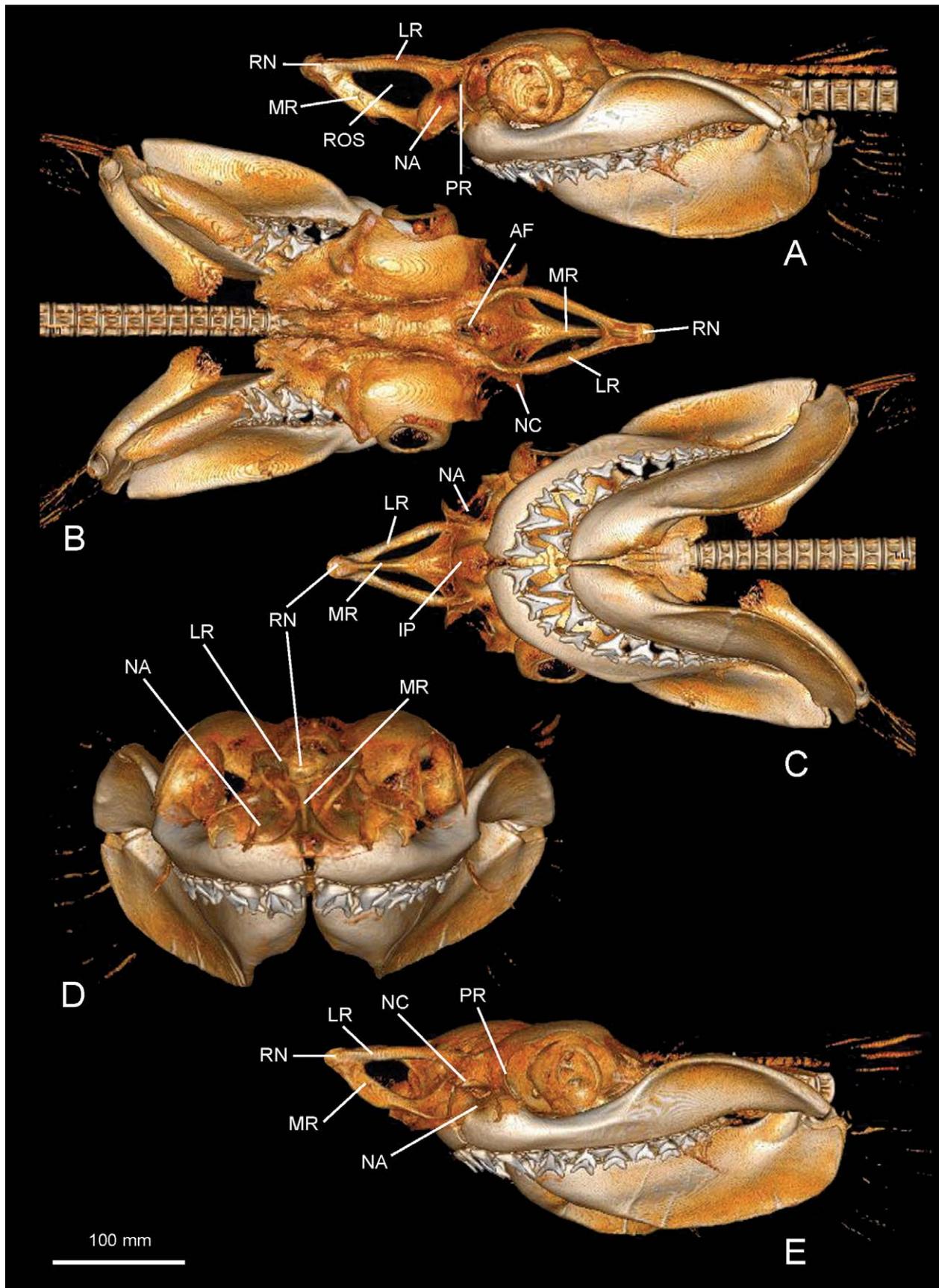


FIGURE 4. *Isurus paucus* Guitart Manday, 1966, female, 2540 mm TL, northwest Atlantic Ocean (ERB 0935), 3D reconstructions based on CT scans of the entire head, showing all cartilaginous structures: lateral (A), dorsal (B), ventral (C), anterior (D) and anterolateral (E) views. Abbreviations: see Fig. 2.

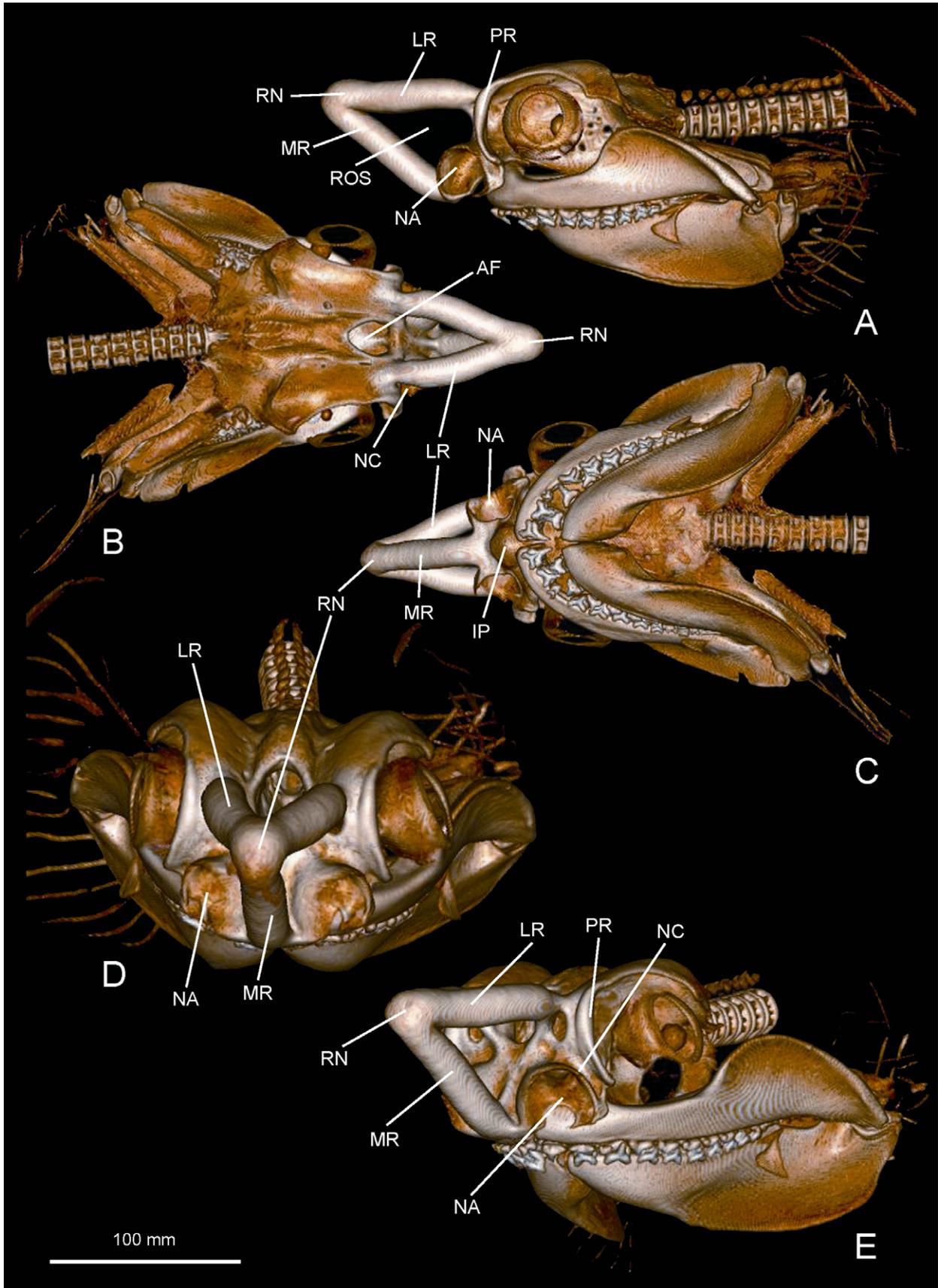


FIGURE 5. *Lamna nasus* (Bonnaterre, 1788), male, 1740 mm TL, northeast Atlantic Ocean (ERB 0929), 3D reconstructions based on CT scans of the entire head, showing all cartilaginous structures: lateral (A), dorsal (B), ventral (C), anterior (D) and anterolateral (E) views. Abbreviations: see Fig. 2.

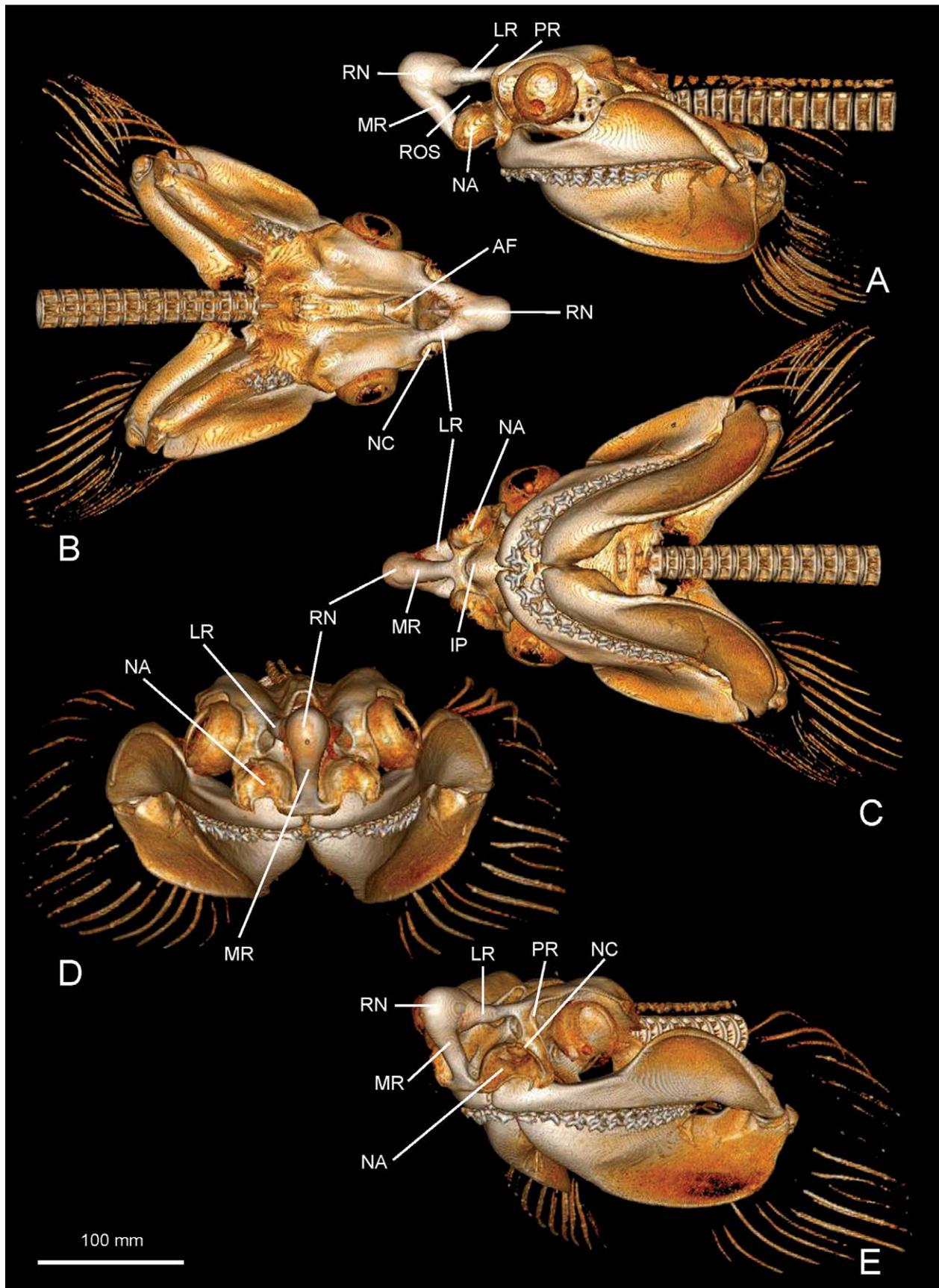


FIGURE 6. *Lamna ditropis* Hubbs & Follett, 1947, female, 2340 mm, TL, northeast Pacific Ocean (ERB 0854), 3D reconstructions based on CT scans of the entire head, showing all cartilaginous structures: lateral (A) (image reversed), dorsal (B), ventral (C), anterior (D) and anterolateral (E) views. Abbreviations: see Fig. 2.

Descriptions and comparisons

***Carcharodon carcharias* (Figs. 1A, 2).** The rostrum is slightly calcified, relatively short. The rostral space (ROS) varies from oval, especially in lateral view, to pentagonal dorsally. Rostral fenestra and rostral appendices are absent. The rostral cartilages (LR, MR) are not stout, but rather reduced. The lateral rostral cartilages (LR) are aligned with the lateral margins of the anterior fontanelle (AF). Their bases are merged with the nasal capsules (NC) and the preorbital processes (PR). They narrow towards the rostral end and meet only at the base of the rostral node (RN). The outer sides of the lateral rostral cartilages are convex, both in lateral and dorsal views. In cross section, the lateral rostral cartilages are flattened laterally and more or less elliptical in shape (see Fig. 1A₁). The medial rostral cartilage (MR) arises from the nasal capsules and from the internasal plate (IP). In ventral view, the medial rostral cartilage is straight, very broad based, but narrows quickly towards the rostral node (see Fig. 2C). Its ventral base, which is merged with the internasal plate, is very broad and concave at its posterior edge. In lateral view, the medial rostral cartilage is convex, meeting the lateral rostral cartilages at the rostral node base at an obtuse angle (see Fig. 2A). In cross section, the medial rostral cartilage is trapezoidal in shape at its base, becoming triangular or elliptical anteriorly (see Fig. 1A₁₋₂). Near the mid-portion of the medial rostral cartilage, its cross section becomes elliptical. The rostral node is small and does not encapsulate the rostral cartilages, not even in adults. At its anterior edge, the rostral node is slightly rounded. A rostral node appendix and rostral node fenestra are absent. The overall calcification of the rostrum is very weak, even in adults. The rostral node and the extremities of the rostral cartilages, and in particular the lateral ones, remain almost uncalcified (tesserae absent, at least in juveniles and subadults).

***Isurus oxyrinchus* (Figs. 1B, 3).** The rostrum is well calcified, relatively long, yet neither elongated, nor robust. Both in lateral and dorsal view, the rostral space (ROS) is oblong and lanceolate in shape. A rostral fenestra and rostral appendices are absent. The rostral cartilages (LR, MR) are neither stout, nor reduced. The bases of the lateral rostral cartilages (LR) are merged with the nasal capsules (NC) and the preorbital processes (PR), and aligned with the lateral margins of the anterior fontanelle (AF), which are almost parallel to each other, making the width across their bases very small (see Fig. 3B). The lateral rostral cartilages do not significantly narrow towards the rostral end, merging only at the rostral node base. Dorsal to the nasal capsules, in lateral view, a weak bend is present in the rostral lateral cartilages (see Fig. 3A). In cross section, the lateral rostral cartilages are flattened laterally at their base, but they become increasingly more circular towards the rostral node (RN) (see Fig. 1B). The medial rostral cartilage (MR) arises from the nasal capsules (NC) and the internasal plate (IP). In ventral view, the medial rostral cartilage is straight, very broad based and narrows almost gradually towards the rostral node base (see Fig. 3C). Therefore, in ventral view, the medial rostral cartilage is more or less triangular over its entire length. Its ventral base, which is in part merged with the internasal plate, is very broad and concave at its posterior margin, which is marked with a weak cartilaginous ridge. The medial edges of the nasal capsules are relatively well calcified near their junction with the medial rostral cartilage ventrally, and, resemble short, anteriorly directed extensions of the medial rostral cartilage base (see Fig. 3C). In lateral view, the outer side of the medial rostral cartilage is slightly convex. It meets the lateral rostral cartilages at the rostral node base at an acute angle (see Fig. 3A). In cross section, the shape of the medial rostral cartilage varies drastically along the rostrum. At its base it is trapezoidal to triangular in shape (see Fig. 1C₁). The ventral angles of the basal trapezoidal and triangular shapes result in well-marked lateral keels that gradually terminate near the mid-portion of the medial rostral cartilage (see Fig. 3A, 3E). At this point, in cross section, the medial rostral cartilage becomes elliptical and flattened laterally towards the rostral node, forming a ventral keel on the anterior half of the rod (see Fig. 3C). The rostral node is of medium size, elongated, but not stout. It does not encapsulate the rostral cartilages. At its anterior edge, the rostral node end is rounded in dorsal and ventral views, but more or less pointed in lateral view. The rostral node appendix and rostral node fenestra are absent. In cross section, the base of the rostral node is Y-shaped and becomes circular only towards the rostral end (see Fig. 1B₃₋₄). The overall calcification of the rostrum is moderate. The outer surface consists of a very thin layer of calcified, prismatic cartilage, except for the lateral keel of the medial rostral cartilage that remains mostly uncalcified (tesserae absent).

***Isurus paucus* (Figs. 1C, 4).** The rostrum is very similar to *I. oxyrinchus*, but is different in having divergent lateral margins of the anterior fontanelle (*vs* near-parallel in *I. oxyrinchus*), more slender rostral cartilages, especially the posterior half of the medial rostral cartilage, a dorsal longitudinal groove in the rostral node (see Fig. 1C₄), and larger width of the rostral space dorsally. As a result of the latter feature, the lateral rostral cartilages meet under a more obtuse angle in *I. paucus* than they do in *I. oxyrinchus*.

***Lamna nasus* (Figs. 1D, 5).** The rostrum is hypercalcified, moderately long, but not elongated, very robust and of tripodal shape. The rostral space (ROS) is large and triangularly shaped, both in dorsal and lateral views. A rostral fenestra and rostral appendices are absent. All rostral cartilages (LR, MR) are very stout and do not narrow towards the rostral node base. The lateral rostral cartilages (LR) are not aligned with the lateral margins of the anterior fontanelle (AF), but are exclusively attached to the preorbital processes (PR) (see Fig. 5A, 5E). Both lateral rostral cartilages join before they meet the medial rostral cartilage (MR), forming a deep rostral groove on both dorsal and ventral sides (see Fig. 1D₂). In juveniles, the lateral rostral cartilages are straight in lateral and dorsal views, but they become more or less sigmoidal in adults. Therefore, in dorsal view, the anteriormost angle of the rostral space is markedly acute in juveniles, but becomes less so in adults. In cross section, the lateral rostral cartilages are flattened laterally at their base, but are more or less circular for the entire remaining part (see Fig. 1D₁₋₂). The medial rostral cartilage arises from the nasal capsules (NC) and the internasal plate (IP). In juveniles, it is rectilinear both in lateral and ventral views. In adults, however, the outer side of the medial rostral cartilage also becomes sigmoidal in shape. Ventrally, the medial rostral cartilage base is merged with the internasal plate which is concave at its posterior edge. The medial edges of the nasal capsules are well calcified near their junction with the medial rostral cartilage ventrally, and, resemble anteriorly directed extensions of the medial rostral cartilage base (see Fig. 5C). In cross section, the medial rostral cartilage is more or less circular over the entire length, except for its base that is significantly broader at the ventral side and protuberant dorsally, forming a short, but well-marked longitudinal keel (see Figs 1D₁; 5B). The rostral node (RN) is robust, but does not encapsulate the rostral cartilages. At its anterior edge, it is equally rounded. In all successive transverse sections, the rostral node is more or less circular in shape (see Fig. 1D₄). The rostral node appendix and rostral node fenestra are absent. The overall calcification of the rostrum is very strong. The outer surface of the entire rostrum consists of prismatic cartilage, sometimes present in several layers, and the hyaline cartilage is restricted to the central core of both the rostral cartilages and the posterior part of the rostral node. The anteriormost part of the rostral node is completely calcified.

***Lamna ditropis* (Figs 1E, 6).** The rostrum of *L. ditropis* differs from *L. nasus* in having rostral cartilages (LR, MR) that are much shorter, less stout and, almost fully encapsulated in a knob. As a result, the distance between the preorbital processes (PR) and rostral node base is very short in *L. ditropis* (vs. large in *L. nasus*). Therefore, *L. ditropis* has a much smaller rostral space (ROS). In both *L. ditropis* and *L. nasus*, the lateral rostral cartilages join before they meet the medial rostral cartilage (Fig. 1D₂-E₂), but only forming longitudinal grooves in *L. nasus* (see Fig. 1D₂).

Discussion

Intraspecific variation of rostral cartilages

Although allometric changes and individual variations are minimal in many galeomorph sharks (Compagno 1988), intraspecific variations are observed in *I. oxyrinchus*, *L. nasus* and *L. ditropis*.

***Isurus oxyrinchus*.** The rostral morphology in the present study differs slightly from several chondrocrania illustrated in the literature. Here we show the medial rostral cartilage (MR) to be relatively robust and the anterior edge of the rostral node rounded, whereas in a rendition of the dorsal side by Glikman (1967, p. 341, fig. 38), these are very thin and transversally flattened, respectively. The medial rostral cartilage as illustrated by Glikman resembles that seen in *I. paucus*. However, Glikman's species identification is correct, as can be seen from the cranial characteristics such as rostral space width, width across postorbital processes, and size of supraorbital crests that are significantly smaller than in *I. paucus*. In the present study the shape of the rostral space is lanceolate in dorsal view, whereas in illustrations by Compagno (1990, p. 363, fig. K, female, 1360 mm (? TL); 2001, p. 9, fig. 12, no data), it is more or less rhomboidal. This difference results from the longitudinal position of the lateral margins of the anterior fontanelle that are shown to be almost parallel here, whereas they are quite divergent in Compagno's illustrations. In addition, the anterior fontanelle (plus underlying precerebral fossa), and rostral space clearly represent two different structures as seen in the 3D reconstructions based on CT scans, but look like a single structure in Compagno's two-dimensional drawings.

In a drawing of the lateral side by Wilga (2005, p. 107, fig. 3D), the rostrum is much smaller in proportion to the entire chondrocranium compared to all other illustrations and material available. The specimen was probably drawn from an oblique angle, because no evidence of deformation can be observed (Mollen 2010). For the above

reasons, the differences in rostral morphology in the literature are not considered to express intraspecific variations but are probably the result of inaccuracies in those illustrations.

An exception is the divergent position of the lateral margins of the anterior fontanelle in illustrations by Compagno (1990, 2001); these are in need of additional studies on larger samples. Based on the material available, it seems already unlikely that this is a result of sexual dimorphism because this specific difference was observed in specimens of the same sex (*i.e.*, all specimens for which data were presented were females).

Lamna nasus. Despite the limited material available, chondrocrania of *L. nasus* are undoubtedly the best studied amongst lamnids (see material above). Based on the results of the present study (see also Mollen 2010), *L. nasus* exhibits ontogenetic changes. Rostral cartilages are almost straight in juveniles and thus of triangular form, but become more or less sigmoidal in adults, resulting in variations in the shape of the rostral space, especially in dorsal view. Such ontogenetic changes are rare in elasmobranch chondrocrania (Compagno 1988), but occur in *Lamna* as a result of the hypercalcification.

In spite of these ontogenetic changes, the rostrum of *L. nasus* depicted by Wilga (2005, fig. 3C, in lateral view) differs in shape and proportions from all other illustrations and available material, in having shorter rostral cartilages and an irregular rostral space. The specimen was probably illustrated from an oblique angle, which may also be the case of the lateral drawing of *I. oxyrinchus* by the same author (see above). The irregular shape of the rostral space, however, cannot be explained in this way. In Wilga's drawing, the lateral rostral cartilage has two kinks, whereas they are straight or slightly sigmoidal in all other specimens studied. It is not clear whether this is a pathological specimen, or if it is due to storage conditions that might have led to distortion of the specimen (*e.g.*, wet storage in a jar, rostrum down). In the present study, these rostral differences are not considered to be of intraspecific significance.

Lamna ditropis. Compagno (1977, 1988, 1990) provided illustrations of the neurocranium of two specimens for which data were available, an immature male of 1830 mm (? TL) and an adult male of 2280 mm (? TL) (see Compagno 1988, fig 7.1.A; 1990, figs. 5M, 6N, 7M [*non* fig. 6M, mislabelled], respectively). In contrast to our material, Compagno's specimens differ markedly in rostral morphology by having a larger, bullet-shaped knob that encapsulates most of the rostral cartilages except for the bases, resulting in a smaller rostral space. This intraspecific variation seems to be the result of a variable degree of hypercalcification in rostra of *L. ditropis*, which is, at least according to our studies, significantly greater in males than in females, irrespective of their ontogenetic stage.

Intergeneric differences of rostral cartilages

The rostra of *Lamna* are easily distinguished from those of *Carcharodon* and *Isurus* (see Parker 1887; Compagno 1990, 2001; Mollen 2010; present study). *Lamna* significantly differs from *Carcharodon* by its stout rostral cartilages (*vs.* reduced cartilages), robust, hypercalcified rostrum, triangular rostral space (especially in non-adults, dorsally and laterally), dorsal keel at the base of the medial rostral cartilage, lateral rostral cartilages that are not aligned with the lateral margins of the anterior fontanelle, and that are exclusively attached to the preorbital processes. Additionally, the ventral side of the medial rostral cartilage is straight or slightly sigmoidal in juveniles and adults of *Lamna*, respectively, but convex in *C. carcharias*, meeting the lateral rostral cartilages at the rostral node base under a much more obtuse angle. Finally, the width of the rostral space (ROSW) exceeds the width across the bases of the lateral rostral cartilages (WLR_b) in *Carcharodon* (and *Isurus*), but is (near-) equal in *Lamna* (see Table 1). *Lamna* differs notably from *Isurus* also by its stout rostral cartilages, shorter (*vs.* elongated) hypercalcified rostrum, triangular (*vs.* lanceolate) rostral space (*i.e.*, dorsally), circular rostral node base (*vs.* Y-shaped), and lateral cartilages that are not aligned with the lateral margins of the anterior fontanelle, and exclusively attached to the preorbital processes. In addition, the bend and keels (ventral and lateral ones) present on the lateral and medial rostral cartilages of *Isurus* are absent in *Lamna*. In contrast, a longitudinal dorsal keel is present in the base of the medial rostral cartilage of *Lamna*, but this is absent in *Isurus*.

The rostra of *Isurus* differ markedly from those of *Carcharodon* by having longer, less reduced and better-calcified rostral cartilages, lateral rostral cartilage bend dorsally to the nasal capsules, lateral and ventral rostral keels on the medial rostral cartilage, Y-shaped rostral node base, and an elongated rostral node. In addition, the angle between the lateral and medial rostral cartilages is acute or moderately so in *Isurus*, but obtuse in *Carcharodon*. Therefore, the rostral space is oblong and lanceolate (*i.e.* dorsally) in *Isurus*, whereas it is oval, especially in lateral view, to more or less pentagonal dorsally in *Carcharodon*.

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