Teeth of embryos in lamniform sharks (Chondrichthyes: Elasmobranchii)

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Synopsis

The dentitions of lamniform sharks possess a unique heterodonty, the lamnoid tooth pattern. However, in embryos, there are 'embryonic' and 'adult' dentitions. The teeth in the embryonic dentition are peg-like and appear to be attached to the jaw in an acrodont fashion. The adult dentition is characterized by the presence of replacement tooth series with the lamnoid tooth pattern. The embryonic–adult transition in dentitions appears at around 30–60 cm TL. Tooth replacement generally begins before birth in embryos with adult dentitions. The adult dentition becomes functional just before or after parturition. An embryo of one species (*Lamna nasus*) shows a tooth directly on the symphysis of the upper jaws, marking the first record of a medial tooth for the order Lamniformes.

Introduction

Intraspecific variation in tooth row count and dental morphology occurs in various elasmobranchs. Variation can result from sexual differences (Kajiura & Tricas 1996, Springer 1966) and ontogeny (Reif 1976, 1984). However, data on such dental variations are still limited for most elasmobranchs.

The order Lamniformes (mackerel sharks) consists of 15 living species in mid to low latitude oceans worldwide, ranging from intertidal zones to deep seas (Compagno 1999; exclude a dubious *Carcharias tricuspidatus* and an undescribed *Alopias* sp.; Figure 1). Most lamniforms possess a unique heterodont dentition called the 'lamnoid tooth pattern'. The pattern is characterized as 'teeth usually well differentiated along jaws, with enlarged anterior teeth, a gap or small intermediate teeth separating the anterior teeth from the lateral teeth in the upper jaw, but with posterior teeth not enlarged' (Compagno 1984,

p. 212; see also Shimada 2001). However, in some lamniform species, the dental morphology of embryos differs greatly from that of adults (e.g., Gilmore 1993).

Specimens of lamniform embryos are limited due to three reasons. First, reproduction of lamniforms is obligate lecithotrophic (Wourms et al. 1988), and catches of pregnant females are uncommon (e.g., Francis 1996, Stevens 1987). Second, in captivity, care is difficult and costs are high (Gruber & Keyes 1981, Murru 1990, Smith 1992, Stevens 1995). Third, embryos of presumably all lamniforms show intra-uterine cannibalism (mostly oophagy), reducing the number of individuals that survive (e.g., Castro et al. 1997, Gilmore 1993, Villavicencio-Garayzar 1996).

Scarcity of embryos has hampered studies concerning various aspects of early development of lamniforms. The aim of this paper is to investigate early ontogenetic development of lamniform teeth. This study integrates my observation of embryonic specimens with published data.
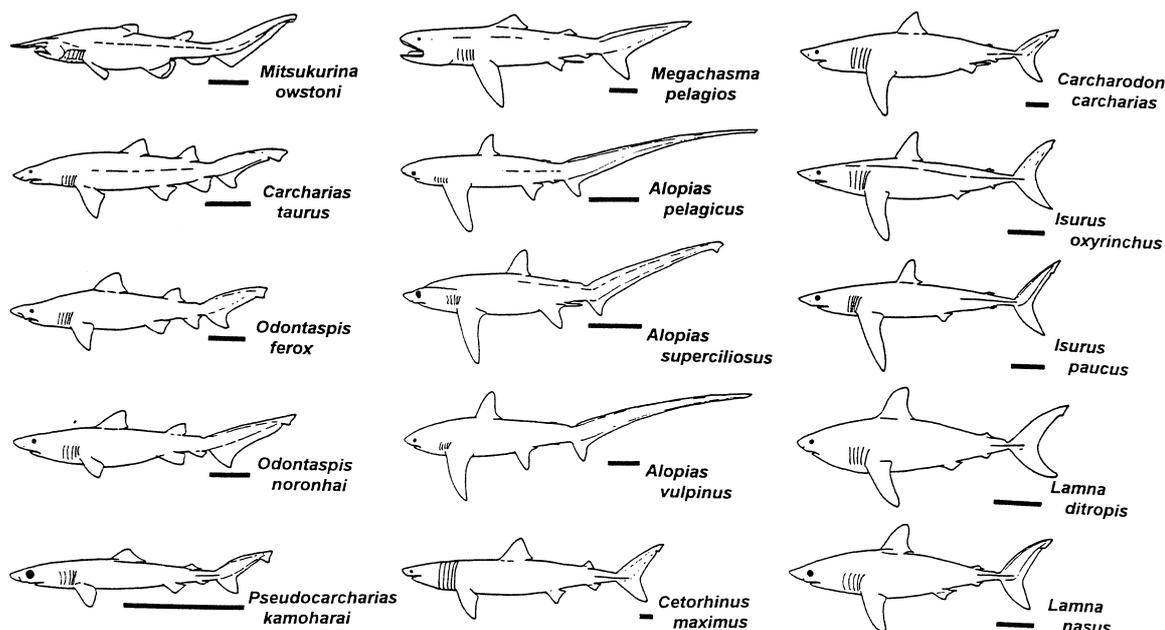
Figure 1. Modern lamniform species (all illustrations depict adults; bar scale = 50 cm; after Compagno 1984, Shimada 2001).

Materials, methods, and terminology

One or more embryos of *Alopias pelagicus*, *Alopias superciliosus*, *Alopias vulpinus*, *Isurus oxyrinchus*, and *Lamna nasus* in the following collections were examined (Appendix 1): Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; Field Museum of Natural History (FMNH), Chicago, Illinois; National Museum of Natural History (NMNH), Washington, D.C.; and Natural History Museum of Los Angeles County (LACM), California. Most specimens were whole and preserved in alcohol or in glycerin (for cleared and stained specimens), but a few were represented by jaw specimens. Teeth were examined visually, sometimes with the aid of a dissecting microscope.

In sharks, tooth replacement occurs continuously throughout life (Reif et al. 1978). New teeth develop at the lingual side of each jaw cartilage, move labially, and successively replace the old ones. Each linguo-labial succession of teeth makes up a 'tooth row', and a mesiodistal alignment of teeth or tooth rows along the jaw cartilage, a 'tooth series' (Compagno 1988, Welton & Farish 1993). In lamniforms, tooth replacement in each tooth row occurs independently of the other rows.

Tooth morphology of embryos

Dental morphology in embryos is reviewed here for each lamniform species, except for the following six taxa which have no known embryonic tooth data: *Mitsukurina owstoni*, *Odontaspis ferox*, *Odontaspis noronhai*, *Megachasma pelagios*, *Cetorhinus maximus*, and *Isurus paucus*. New dental data are added for species I examined. In addition, Table 1 shows a list of the largest embryo on record, typical size at birth, and smallest free-swimming individual on record for each lamniform species based on the literature (Appendix 2).

Carcharias taurus – Teeth in embryos of *Carcharias taurus* have been described occasionally. On each jaw, a 5 cm TL embryo already possesses multiple (at least seven), stiff, sharp, broad triangular teeth, which are erect and apparently functional (Gilmore et al. 1983, figure 11). Embryos of about 10 cm TL use their multiple (at least nine) erect teeth to attack egg capsules and other embryos in the same uterus (Gilmore et al. 1983). Teeth are undoubtedly functional in embryos measuring 26–27 cm TL, as Springer (1948) was bitten by an active embryo when he inserted his hand through a slit in the oviduct of a pregnant female. Springer noted that there was no sheath covering the teeth, as in embryos ranging 83–97 cm TL. In embryos ranging

Table 1. Recorded largest embryo (LE), typical size at birth (SAB), and recorded smallest free-swimming individual (SFI) for each lamniform species (asterisk = approximate value; for list of literature, see Appendix 1).

Species (family)	LE	SAB	SFI
Mitsukurina owstoni (Mitsukurinidae)	?	?	107
Carcharias taurus (Odontaspididae)	106	91–105	79?
Odontaspis ferox (Odontaspididae)	?	?	105*
Odontaspis noronhai (Odontaspididae)	?	?	171
Pseudocarcharias kamoharai (Pseudocarchariidae)	43	40–43	59
Megachasma pelagios (Megachasmidae)	?	?	180
Alopias pelagicus (Alopiidae)	158	96–190	96
Alopias superciliosus (Alopiidae)	106	60?–140	60?
Alopias vulpinus (Alopiidae)	161	91–150	91
Cetorhinus maximus (Cetorhinidae)	170	150–200	165
Carcharodon carcharias (Lamnidae)	151	120–151	122
Isurus oxyrinchus (Lamnidae)	70?	60–70	68*
Isurus paucus (Lamnidae)	97	100*	106
Lamna ditropis (Lamnidae)	74	65–80?	40?
Lamna nasus (Lamnidae)	79	60?–80	70

50–80 cm TL (n = 24), teeth generally slant into the oral cavity (Sadowsky 1970). These embryos possess 19–22 teeth on each side of the upper jaws and 17–20 teeth on each side of the lower jaws.

A typical dental feature of *Carcharias taurus* embryos is the lack of lateral cusplets (Cadenat 1956, Sadowsky 1970, Cadenat & Blache 1981, Gilmore et al. 1983). Gomes & Reis (1990) examined teeth in four embryos of 54–56 cm TL. Their dental series showed the 'lamnoid tooth pattern' with 17–22 teeth on each upper jaw and each lower jaw. Teeth were functional (perhaps for oophagy), but their tips were blunt, possibly to prevent injury to the mother. The tips of replacement teeth were more acute than those in the functional series (sensu Shimada 2001). Gomes & Reis (1990) found dental abnormalities in the embryos, that also occur in adults ('reversed teeth': Lucifora et al. 2001).

Pseudocarcharias kamoharai – Teeth are absent in embryos of *Pseudocarcharias kamoharai* measuring 4 cm TL (Fujita 1981). Embryos ranging from 40–43 cm TL possess teeth that are as well-developed as those in mature individuals with 13–15 teeth on each upper jaw and 11–13 teeth on the lower jaw (Fujita 1981, see also Cigala-Fulgosi 1992). However, Cigala-Fulgosi (1992, p. 54) noted that, in the 'second lower anterior tooth' row of a large embryo (40 cm TL), the crown in the first tooth series was considerably shorter than that in the next replacement series, indicating 'rapid tooth growth [through replacement] at early embryonic stages'.

Alopias pelagicus – Gruber & Compagno (1981, p. 634) noted that *Alopias pelagicus* 'does not acquire functional teeth until it reaches considerably larger size' (cf. their two 21 cm TL embryos of *Alopias superciliosus*). Otake & Mizue (1981) found 'sheathed teeth' in four embryos, ranging from 42 to 52 cm TL. Liu et al. (1999, p. 71) found that 'teeth appear in 13 cm TL embryos and disappear at about 60 cm TL'. Although Nakamura (1935) found no functional teeth in 97 cm TL embryos, erect teeth were usually present in embryos >80 cm TL (Liu et al. 1999).

The teeth of *Alopias pelagicus* embryos I examined (60–80 cm TL) are not functional because they are not erect. However, the lamnoid tooth pattern is present even in the smallest embryo examined (Figure 2b). In specimens that allow for accurate tooth row counts (FMNH 52100, 74150, and 76800), 21–22 and 20–24 tooth rows are present for each side of the upper and lower jaws, respectively. Distinct lateral cusplets or heels are present on the crowns of many teeth, and the mesialmost teeth (i.e., probable symphysial teeth) are like placoid scales (for scales of alopiids, see Welton & Farish 1993, figure 20).

Alopias superciliosus – Moreno & Moron (1992) observed 'reflexed teeth' in embryos of *Alopias superciliosus* that ranged from 32 to 94 cm TL, where the first (= labialmost) tooth series in an average-sized embryo (ca. 52 cm TL) was erect and possibly functional. Gruber & Compagno (1981) found 'fully functional teeth' in two small embryos (ca. 21 cm TL) and suggested that early tooth formation may assist oophagy. However, teeth apparently do not need to be erect for oophagy, because large complete egg capsules can be found in fetal stomachs (Moreno & Moron 1992). Chen et al. (1997) found that teeth emerge in 11 cm TL embryos and shed at about 60 cm TL. 'Adult teeth' were present in embryos greater than 60 cm TL, and became erect when nearing parturition
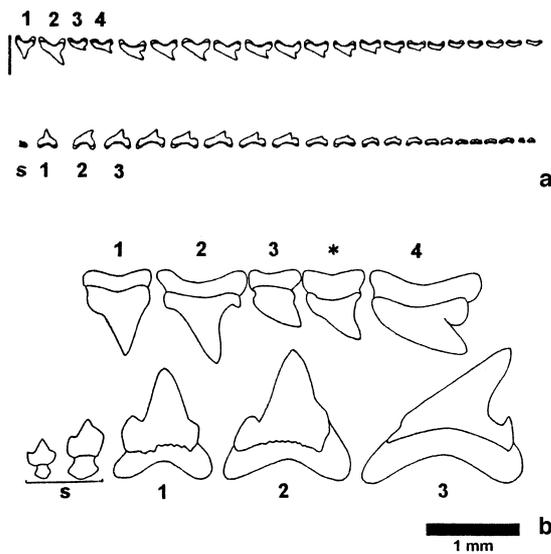
Figure 2. Teeth of *Alopias pelagicus* (mesial to the left; labial view). a – Upper and lower dental series of adult (after Bass et al. 1975; vertical line = symphysis; length of upper dental series = e.g., 8.5 cm in individual measuring 241 cm TL; mesialmost teeth are labeled to show corresponding teeth in the embryo illustrated in b; cf. Shimada 2001). b – Mesial portion of left upper and lower dental series in embryo (FMNH 52100, 60 cm TL; asterisk = additional tooth).
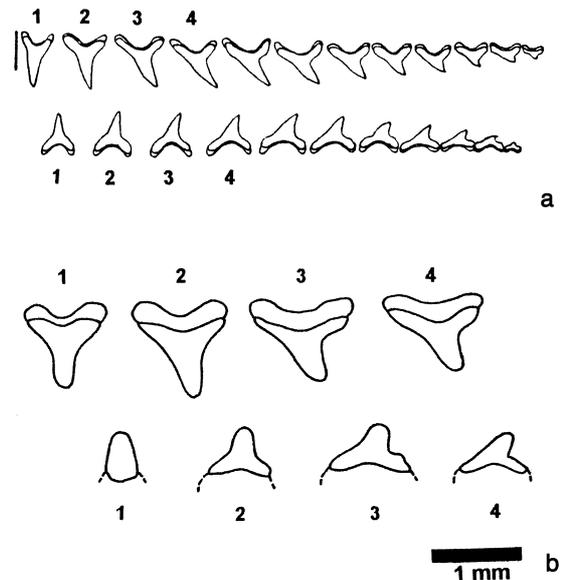

Figure 3. Teeth of *Alopias superciliosus* (mesial to the left; labial view). a – Upper and lower dental series of adult (after Bass et al. 1975; vertical line = symphysis; length of upper dental series = e.g., 14.5 cm in individual measuring 404 cm TL; mesialmost teeth are labeled to show corresponding teeth in embryo illustrated in b; cf. Shimada 2001). b – Mesial portion of left upper and lower dental series in embryo (MCZ 36154, 63 cm TL).

(Chen et al. 1997, Moreno & Moron 1992). Well-developed, nonerect teeth were present in a 60 cm TL embryo, and, unlike in larger embryos (105–106 cm TL), teeth were not sheathed below a membrane (Gilmore 1983). In an 85 cm TL embryo, both upper and lower teeth were 'undeveloped' (Nakaya 1982; also in 72 cm TL embryos reported by Nakamura 1935). Teeth in the first series were much smaller than those in the second series in large embryos (>60 cm TL), and the tooth morphology of *Alopias superciliosus* embryos resembled that of *Alopias vulpinus* (Moreno & Moron 1992).

A 63 cm TL embryo of *Alopias superciliosus* I examined (MCZ 36154) possesses at least nine tooth rows on the left upper jaw and 12 tooth rows on the left lower jaw. Although its teeth are similar to those of adults, they are not erect, and their apex is rounded (Figure 3). Tooth replacement had apparently occurred in this embryo, because there is a series of depressions on the soft oral tissue left by the teeth of the first tooth series that had already been shed (Shimada 2001). In the specimen, there are at least six tooth series (including the shed tooth) in some rows, where the crown of the tooth on the third series is at least twice as tall as the one on the first series. This suggests the notable ontogenetic size increase of teeth through replacement in the early life intervals of this shark.

Alopias vulpinus – Teeth in 114–159 cm TL embryos of *Alopias vulpinus* are similar to those in adults, but teeth of the first series are smaller than those of the successive replacement series (Moreno et al. 1989). The upper teeth are depressed and covered by an extension of the anterior face of the gum, which Moreno et al. (op. cit.) called a 'crenullated formation'. Posterior to this formation, another covering forms a thin 'false half palate', which is granular on the outside and smooth on the inside. Teeth are also hidden by soft tissue in the lower jaw, and they presumably remain depressed and hidden until shortly before birth.

LACM 36227-1 consists of two embryos of *Alopias vulpinus*, that measure 35 and 48 cm TL. All of their teeth are covered by a sheath of soft tissues and are not functional. Most teeth of the embryos' first tooth series are peg-like, typically with blunt crown apices (Figure 4b), and a pair of lateral cusplets in some cases (Figure 4c). Teeth become progressively more similar to adult teeth by the fourth tooth series, by which time
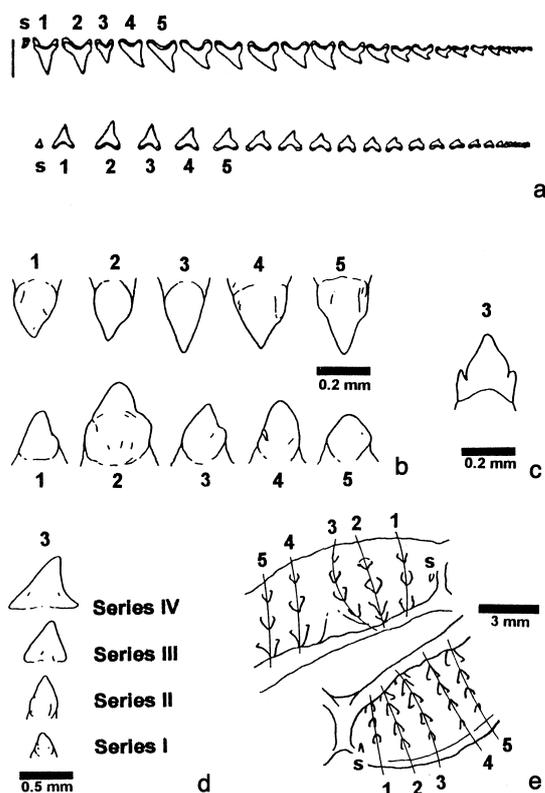
Figure 4. Teeth of *Alopias vulpinus*. a – Upper and lower dental series of adult (after Bass et al. 1975; mesial to the left; labial view; vertical line = symphysis; length of upper dental series = e.g., 13.9 cm in individual measuring 397 cm TL; mesialmost teeth are labeled to show corresponding teeth in embryo illustrated in b–e; cf. Shimada 2001). b – Mesial portion of left upper and lower dental series in embryo (LACM 36227-1, one of two specimens, 35 cm TL; mesial to the left; labial view). c – Right lower tooth in the same specimen as b (mesial to the right; labial view). d – Four tooth series in left lower tooth row in the same specimen as b (mesial to the left; labial view). e – Teeth in situ on mesial portion of upper right (top; mesial to the right) and lower left (bottom; mesial to the left) jaws (LACM 36227-1, 48 cm TL; each curved lines represents the 'axis' of each tooth row).

a clear lamnoid tooth pattern is present (Figure 4d). A bulbous inflation on the mesial part of each jaw cartilage, the dental bulla (sensu Compagno 1990, Shimada 2001), appears to be present based on the directions of the 'axis' of each tooth row (Figure 4e). The total tooth row count cannot be determined in the two specimens of LACM 36227-1, but a 58 cm TL embryo (LACM 37713-1) with a lamnoid tooth pattern appears to possess 22 and 21 rows on either side of the upper and lower jaws, respectively.

Carcharodon carcharias – Teeth of *Carcharodon carcharias* usually exhibit serrations on their cutting edges but lack lateral cusplets (Irvine 1947). However, in smaller individuals (<214 cm TL free-swimming individuals and >143 cm TL embryos), one or two pairs of lateral cusplets tend to occur with a lanceolate central cusp that may lack serrations partly or entirely on its edges (composite data: Ray 1928, Smith 1951, Follett 1966, Francis 1996, Kato et al. 1967, Bass et al. 1975, Uyeno & Matsushima 1979, Eschmeyer & Herald 1983, Compagno 1984, Bass 1986a, Last & Stevens 1994). The lamnoid tooth pattern was already present in a 140 cm TL embryo (Uchida et al. 1996, figure 6). Uchida et al. (1996) found varying sizes of teeth in the intestine of embryos ranging 125–151 cm TL, suggesting that tooth replacement occurs during embryonic development (see also Francis 1996, Gottfried & Francis 1996). In embryos measuring 143–145 cm TL, the lamnoid tooth pattern was present; however, the upper teeth were not generally erect, whereas lower teeth located mesially were erect. Francis (1996) found 14 and 12 tooth rows on either side of upper and lower jaws, respectively, in a 143 cm TL embryo, whereas a 145 cm TL embryo had 12 rows in each side of the upper and lower jaws.

Isurus oxyrinchus – Gilmore (1993, figure 8) showed scanning electron micrographs of a jaw of a 48 cm TL embryo of *Isurus oxyrinchus*. Gilmore's specimen showed the lamnoid tooth pattern; however, teeth were all peg-like and not erect. Mollet et al. (2000) reported 'emerging adultlike teeth' in both upper and lower jaws of nine 60 cm TL embryos from a pregnant female. A 61 cm TL embryo of *Isurus oxyrinchus* I examined (MCZ 37994; see also Garrick 1967) has 13 tooth rows on the left upper jaw and 12 rows on the left lower jaw. Its dentition is adultlike, showing the lamnoid tooth pattern (Figure 5). However, teeth are not erect, and the crowns of many lack obvious cutting edges and have small distal cusps or distal heels. Successive replacement teeth progressively increase in size and sometimes change morphology. For example, the first tooth series of the first (= mesialmost) tooth row is small and conical, and teeth in this row become larger and more elongate in each successive tooth series (Figure 5b).

Lamna ditropis – Kakizawa (1984) reported a tooth row count of 12 for one side of the upper jaw and lower jaw in two embryos of *Lamna ditropis* (50 and 60 cm TL). However, morphology of embryonic teeth has not been documented.

Lamna nasus – Embryos of *Lamna nasus* develop large, erect, recurved 'fangs' early in development
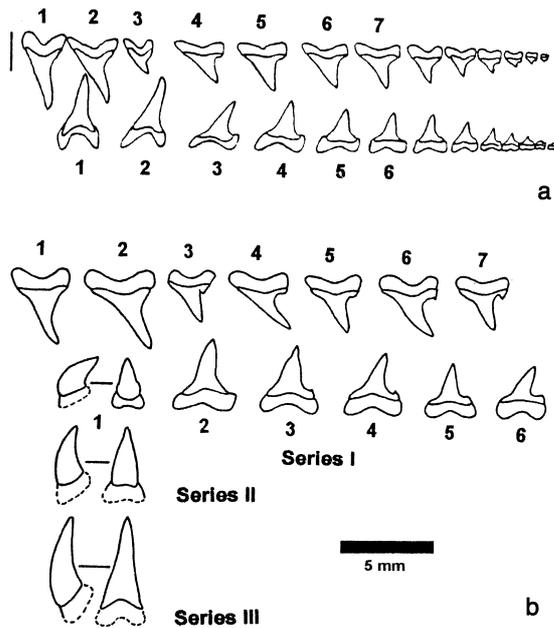
Figure 5. Teeth of *Isurus oxyrinchus*. a – Upper and lower dental series of adult (after Compagno 1984; mesial to the left; labial view; vertical line = symphysis; length of upper dental series = e.g., 26.8 cm in individual measuring 304 cm TL; mesialmost teeth are labeled to show corresponding teeth in embryo illustrated in b; cf. Shimada 2001). b – Mesial portion of left upper and lower dental series in embryo (MCZ 37994, 61 cm TL; mesial to the left; labial view but distal view is also shown for three tooth series in tooth row 1).

(Duhamel & Ozouf-Costaz 1982, Francis & Stevens 2000). Embryos measuring 12–13 cm TL possessed one such fang on each jaw, whereas those measuring 24–45 cm TL had at least three and one on each upper jaw and lower jaw, respectively (Francis & Stevens 2000). Prominent fangs were also present in embryos ranging from 32 to 45 cm TL examined by Shann (1923), Swenander (1907) and Templeman (1963). In 24–45 cm TL embryos, Francis & Stevens (2000) noted the presence of 'replacement fangs' behind the functional series, but between the functional teeth at irregular intervals. Francis & Stevens (op. cit.) stated that embryos appear to shed their fangs between 41 and 45 cm TL, although Lohberger (1910) showed several distally curved fangs without lateral cusplets in embryos up to 55 cm TL. Those teeth appear to be situated on the jaws in acrodont fashion (sensu Hildebrand 1988) without an apparent tooth root and replacement series. Although the exact sizes of embryos were not specified, Francis & Stevens (2000) noted that

near-term litters had adultlike teeth that are generally nonerect and nonfunctional.

I examined four embryonic specimens of *Lamna nasus*. The largest specimen (65 cm TL; NMNH 47528) shows the lamnoid tooth pattern with 14 and 11 tooth rows on either side of the upper and lower jaws, respectively; however, the teeth are not erect and thus not functional. All other embryonic specimens (17–34 cm TL) possess several functional teeth without the lamnoid tooth pattern. Embryonic teeth are peg-like and lack lateral cusplets, and they are directed distally or posteriorly (except for the 'medial tooth' described below; Figure 6). Jaw cartilages are covered by a layer of oral tissues continuous with the roof and floor of the mouth. There is no gap or break between the jaw cartilage and roof/floor, and all teeth are situated in an acrodont fashion without replacement tooth series. In addition, the jaws apparently lack dental bullae (see above), and the number of teeth appears to increase through embryonic ontogeny (17, 29, and 34 cm TL: 3, 6, and 8 teeth on each side of the upper jaw, respectively; 4, 5, and 5 teeth on each side of the lower jaw, respectively).

The term 'medial tooth' is here restricted to a tooth located at the jaw symphysis (cf. Applegate 1965). The smallest embryo of *Lamna nasus* I examined (17 cm TL, MCZ 35901; perhaps the same specimen described by Bigelow & Schroeder 1948, figure 17) deserves special attention for the presence of an upper medial tooth (Figure 6b,c). This marks the first record of a medial tooth in the order Lamniformes. This medial tooth is conical and pointed anteroventrally, has its basal half covered by a layer of soft tissues (Figure 6b), and is not followed by replacement series (Figure 6c).

Discussion

Gilmore (1993, p. 104) examined various species of lamniform embryos and noticed that there seemed to be 'two distinct types of dentition, an embryonic set and a set similar to the adult form'. Following Gilmore (1993), I refer to them as 'embryonic dentition' and 'adult dentition', respectively. My study supports Gilmore's hypothesis that lamniforms undergo a major tooth replacement event during embryonic development.

Embryonic tooth morphology is often peg-like and thus quite different from adult morphology. Based on the embryos of *Lamna nasus* I examined (and also some small *Carcharias taurus* embryos described
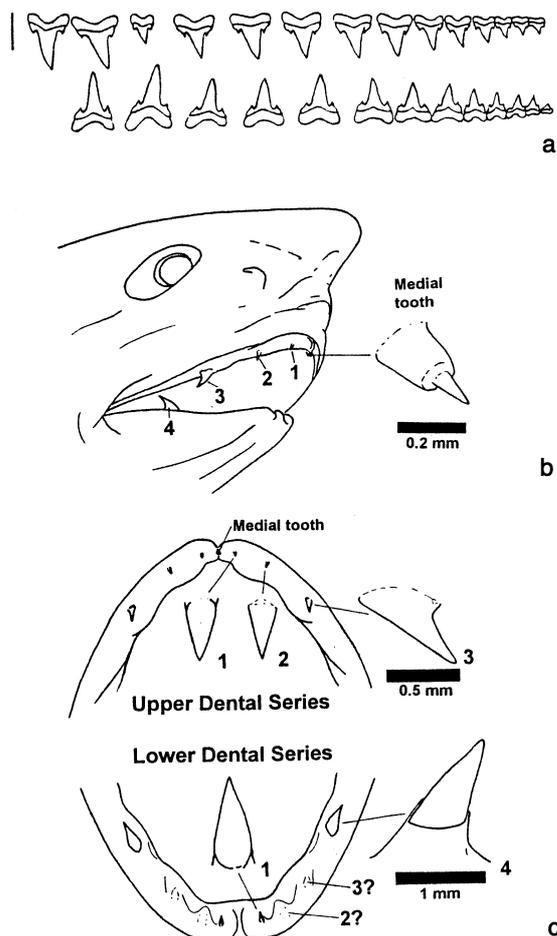
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Figure 6. Teeth of *Lamna nasus*. a – Upper and lower dental series of adult (after Compagno 1984; mesial to the left; labial view; vertical line = symphysis; length of upper dental series = e.g., 18.0 cm in individual measuring 234 cm TL). b – Head region of embryo with a close-up view of anteroventrally pointed medial tooth (MCZ 35901, 17 cm TL; each number indicates tooth number counted from symphysis). c – Upper and lower dental series (occlusal view) of embryo (same specimen as b) with close-up view of teeth.

by Gilmore et al. 1983), it appears that teeth of the embryonic dentition are attached on the jaws in an acrodont fashion (i.e., each tooth probably without a tooth root). On the other hand, the adult dentition is characterized by rooted teeth with replacement series and the lamnoid tooth pattern (Shimada 2001). However, unlike in free-swimming individuals, the teeth are almost always not erect and usually covered by soft tissues. Francis & Stevens (2000) described 'replacement fangs' in *Lamna nasus* embryos with the embryonic dentition. However, whether or not those fangs actually

replace preexisting functional teeth as in the adult dentition is uncertain, because each 'replacement fang' is not located immediately behind a functional tooth like in adults (see Shimada 2001). In addition, due to the lack of distinct anatomical markers in embryonic jaws (e.g., 'dental bullae' in free-swimming individuals), the correspondence of teeth or tooth positions cannot be made between embryos with the embryonic dentition and individuals with the adult dentition.

The embryonic dentition develops between 4 and 6 cm TL in *Carcharias taurus*. Gilmore (1993, p. 103) stated that it 'apparently aids the embryo to escape from the egg capsule'. Gilmore (op. cit.) also stated that the embryonic dentition is used also to puncture other capsules after hatching aiding their oophagous behavior. A similar interpretation was made for *Lamna nasus* (Francis & Stevens 2000).

Chen et al. (1997) examined embryos of *Alopias superciliosus* and stated that a set of 'embryonic teeth' is shed at about 60 cm TL, and another set of teeth emerges when the shark becomes greater than 60 cm TL. Similarly, Liu et al. (1999) found that teeth in embryos of *Alopias pelagicus* are shed at about 60 cm TL. The 60 cm TL embryo of *Alopias pelagicus* and 63 cm TL embryo of *Alopias superciliosus* I examined have adult dentitions (Figures 2b, 3b). The TL of about 60 cm may be the timing of the replacement of the embryonic dentition by the adult dentition in these *Alopias* species. *Lamna nasus* appears to shed its embryonic dentition between 41 and 45 cm TL (Francis & Stevens 2000), but the exact timing for such a transition is uncertain for other lamniform species at the present time. The smallest embryo with adult dentition recorded is 54 cm TL for *Carcharias taurus* (Gomes & Reis 1990), 40 cm TL for *Pseudocarcharias kamoharai* (Fujita 1981), 35 cm TL for *Alopias vulpinus* (this study, Figure 4; cf. embryonic dentition in 62 cm TL embryos: Gilmore 1993), 48 cm TL for *Isurus oxyrinchus* (Gilmore 1993), and 65 cm TL for *Lamna nasus* (this study, 45+ cm TL in Francis & Stevens 2000). The timing of the embryonic–adult transition in dentitions may differ from species to species, but it may occur on the order of 30–60 cm TL at least for macrophagous lamniforms in general.

Tooth replacement usually occurs in embryos with adult dentitions even before their birth. Evidence depending on the species includes (1) scars of shed teeth left on the soft oral tissues (depressions indicating previous root attachments: Shimada 2001), (2) great morphological differences between teeth in near-term/newborn individuals and those in the

smallest embryos with adult dentitions (composite data: e.g., Moreno & Moron 1992, Gilmore 1993, this study), and (3) shed teeth found as stomach contents of embryos (which may indicate the ingestion of its own shed teeth) and as uterine contents (e.g., Uchida et al. 1996, Francis 1996).

Teeth of the adult dentition are large but generally do not become erect until just before or after parturition (e.g., Moreno & Moron 1992, Chen et al 1997, Francis & Stevens 2000). Teeth of the early stage of the adult dentition often possess bluntly pointed crowns without distinct cutting edges, serration, and/or lateral cusplets (e.g., Smith 1951, Gilmore et al. 1983, Gomes & Reis 1990, this study). A possible explanation for these observations is that nonerect teeth without sharp points or edges in developing embryos would avoid internal injury to the mother. Teeth of the embryonic dentition are usually erect. However, because those teeth are much smaller than teeth of adult dentition (e.g., Figure 6), they presumably do little harm to the mother's uterus.

Acknowledgements

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Appendix 1. Embryonic specimens examined (catalogue number, total length, sex, locality).

Alopias pelagicus: FMNH 52100, 60 cm TL, female, Japan; FMNH 74150, 71 cm TL, male, Japan; FMNH 76800, 71 cm TL, female, Japan; NMNH 202675, 75 cm TL, female, Mombasa, Kenya; NMNH 202675, 80 cm TL, male, Mombasa, Kenya.

Alopias superciliosus: MCZ 36154, 63 cm TL, male, Cuba.

Alopias vulpinus: LACM 36227-1, 35 cm TL, sex unknown, California, USA; LACM 36227-1, 48 cm TL, sex unknown, California, USA; LACM 37713-1, 58 cm TL, sex unknown, California, U.S.A.

Isurus oxyrinchus: MCZ 37994, 61 cm TL, male, Bahamas.

Lamna nasus: MCZ 35901, 17 cm TL, male, Massachusetts, U.S.A.; NMNH 47528, 65 cm TL, female, north Atlantic; NMNH 72473, 34 cm TL, sex unknown, north Atlantic; NMNH 89929, 29 cm TL, sex unknown, Massachusetts, U.S.A.

Appendix 2. List of literature used for the compilation of data in Table 1.

Mitsukurina owstoni: Jordan 1898, Stead 1963.

Carcharias taurus: Gilmore et al. 1983, Scott & Scott 1988.

Odontaspis ferox: Bass et al. 1975.

Odontaspis noronhai: Maul 1955.

Pseudocarcharias kamoharai: Abe et al. 1969, Fujita 1981, Compagno 1984.

Megachasma pelagios: Seret 1995.

Alopias pelagicus: Compagno 1984, Liu et al. 1999.

Alopias superciliosus: Bigelow & Schroeder 1948, Osipov in Gubanov 1978, Gilmore 1983, Compagno 1984, Bass 1986b, Moreno & Moron 1992, Last & Stevens 1994, Chen et al. 1997.

Alopias vulpinus: Wheeler 1969, Cailliet et al. 1983, Compagno 1984, Springer 1990.

Cetorhinus maximus: Pennant's observation in Fries et al. 1895, Pavesi in Bigelow & Schroeder 1948, Wheeler 1969, Compagno 1984, Last & Stevens 1994.

Carcharodon carcharias: Bigelow & Schroeder 1958 (cf. Bigelow & Schroeder 1953), Scattergood 1962, Klimley 1985, Ellis & McCosker 1991, Francis 1996, Uchida et al. 1996.

Isurus oxyrinchus: Garrick 1967, Bass et al. 1975, Guitart-Manday 1975, Cailliet et al. 1983, Castro 1983, Stevens 1983, Bass 1986a, Allen & Robertson 1994.

Isurus paucus: Castro 1983, Gilmore 1983, Mochizuki & Noze 1986.

Lamna ditropis: Kato et al. 1967, Castro 1983, Gilmore 1993, Blagoderov 1994.

Lamna nasus: Shann 1923, Fowler 1936, Bigelow & Schroeder 1948, McKenzie & Tibbo 1964, Wheeler, 1969, Burgess 1970, Castro 1983, Gauld 1989, Last & Stevens 1994, Lucifora & Menni 1998, Francis & Stevens 2000.