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Dentition of the modern basking shark, *Cetorhinus maximus* (Lamniformes: Cetorhinidae), and its paleontological and evolutionary implications

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Abstract

The dentition of the modern basking shark, *Cetorhinus maximus* (Lamniformes: Cetorhinidae) consists of numerous rows of small teeth. It shows a remarkable intraindividual variation of teeth, particularly at the anterior portion of the upper jaw. The wide variation even in a small portion of an individual suggests that tooth morphology may not necessarily be a reliable character for the taxonomy of extinct sharks, that are represented mostly by isolated teeth. The occurrence of polarity switch and tooth splitting in its dentition suggests that repeated tooth splitting events through evolution could be responsible for the large number of tooth rows in this species.

Introduction

The basking shark, *Cetorhinus maximus* (Lamniformes: Cetorhinidae; Fig.1), is the second largest extant fish (next to the whale shark, *Rhincodon typus*: Orectolobiformes), that may reach 15 m or more in total length (TL) (e.g., Bigelow and Schroeder, 1953; Stead, 1963). It is a migratory, coastal-pelagic shark living in temperate to boreal waters nearly worldwide. It is a filter feeder, opening its mouth widely with a low cruising speed and straining small food particles with gill rakers (Matthews and Parker, 1951; Fig. 1C). In this paper, its dental morphology is reviewed, and some new data concerning the intraindividual variation of its tooth morphology are introduced. The dental information offers some perspectives in paleontological practices as well as in the evolution of its dentition.

Materials examined

Shark specimens in the following collections in the U.S.A. are discussed in this paper: American Museum of Natural History (AMNH), New York; California Academy of Sciences (CAS), San Francisco; Natural History Museum of Los Angeles County (LACM), California;

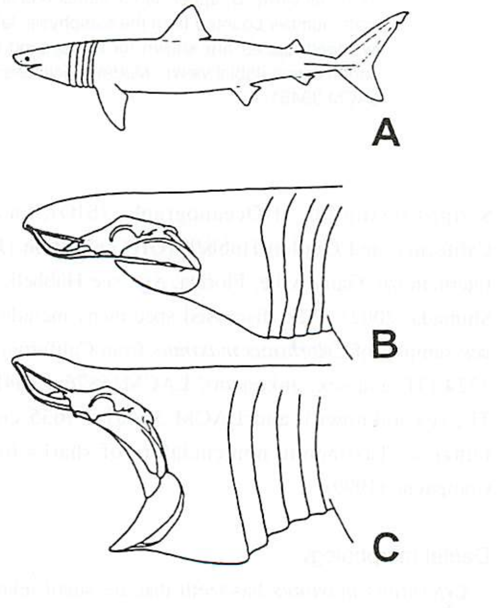

Fig.1. Modern basking shark, *Cetorhinus maximus* (A) and close-up view of its head region showing positions of cephalic skeletal elements at rest (B) and during feeding (C). A, after Compagno (1984); B, composite sources: Pavesi (1874, table 2, fig. 5), Hallacher (1977, fig. 1), Compagno (1981: 14), and Stevens (1987: 60). For size of the animal, see text.

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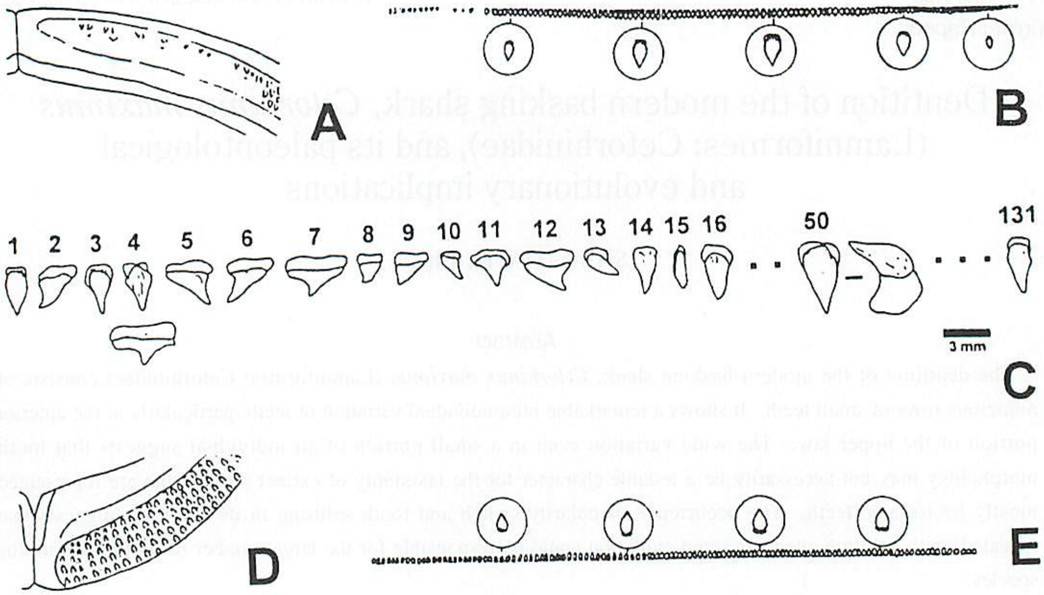

Fig.2. Dentition of modern basking shark, *Cetorhinus maximus* (all mesial to the left). A, mesial part of left upper jaw (occlusal view); B, upper dental series (labial view); C, close up view of selected upper teeth (number indicates the tooth number counted from the symphysis; labial view, except for the fiftieth tooth row which also shows distal view; two tooth series are shown for the second tooth row); D, mesial part of left lower jaw (occlusal view); E, lower dental series (labial view). Model specimens: A-B and D-E, composite data from CAS 2224 and LACM 39461-1; C, LACM 39461-1.

Scripps Institution of Oceanography (SIO), La Jolla, California; and Gordon Hubbell (GH) collection (JAWS International, Gainesville, Florida; e.g., see Hubbell, 1996; Shimada, 2002). The discussed specimens include three jaw samples of *Cetorhinus maximus* from California: CAS 2224 (TL and sex, unknown), LACM35876-1 (641? cm TL, sex unknown), and LACM 39461-1 (635 cm TL; female). Taxonomic nomenclature of sharks follows Compagno (1999).

Dental morphology

Cetorhinus maximus has teeth that are small relative to the body size (Fig. 2). The crown is usually hooked-shaped (Compagno, 1984; Springer and Gilbert, 1976). The crown points lingually with smooth mesial and distal cutting edges (Sadowsky, 1973; Walford, 1935). The crown surface lack striations (Compagno, 1982), except near the base (Bigelow and Schroeder,1948), which may appear "tuberculated" (Scott and Scott, 1988). The root has "moderately long labial root lobes, small lingual protuberances, and strong basal grooves" (Compagno, 1990: 367).

Intraindividual variation in tooth morphology occurs in *Cetorhinus maximus* (Herman *et al.*, 1993). An edentulous space is present at and around the upper and lower symphyses (Pavesi, 1874; Compagno, 1990; Fig. 2A). In the upper jaw, this space is followed by a small group of tooth rows that is followed by another edentulous space before reaching the rest of the dental series (Siccardi, 1960; Fig. 2B). The crown of teeth in the small group of tooth rows may be compressed labiolingually and triangular (Blainville, 1811; Barnard, 1937; Gomon *et al.*, 1994) with variable inclinations mesiodistally (Fig. 2C). Compagno (1984) called these teeth "anterior teeth," which appears to be his basis of stating that the teeth of *Cetorhinus maximus* are "weakly differentiated into row groups" (Compagno, 1990: 367). Teeth distal to the small group of tooth rows become successively more conical (Barnard, 1937). The lower teeth are usually larger and less conical than the upper teeth (Kay, 1842). Lower teeth are morphologically less variable than upper teeth (Fig. 2).

Kunzlik (1988) noted that each tooth series in *Cetorhinus maximus* may contain more than 100 tooth rows (cf. Siccardi, 1960). The total row count ranges 100?-

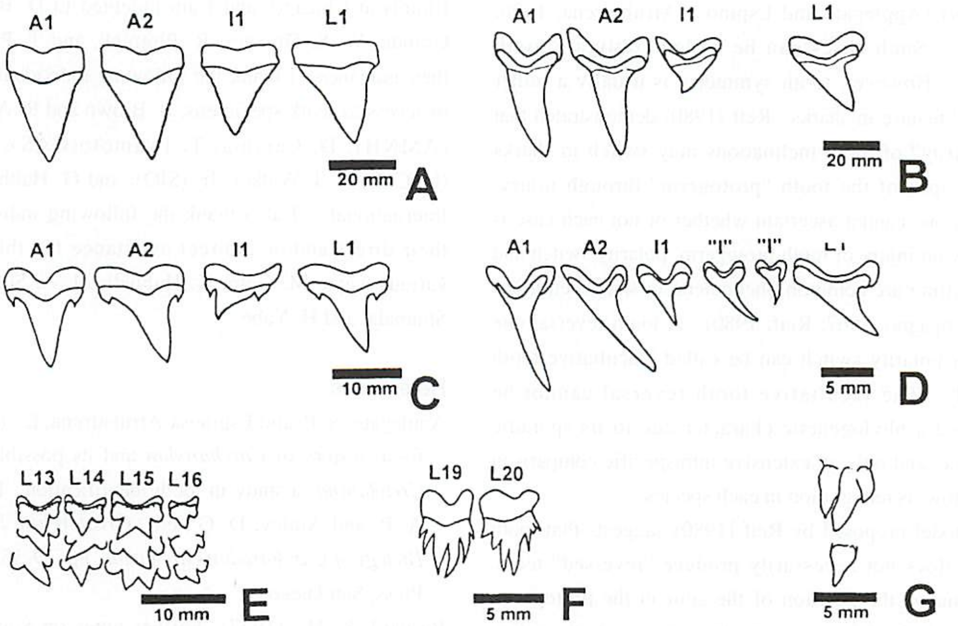

Fig.3. Examples of reversed teeth and crown splitting in various lamniform sharks (mesial to the left; labial view). A, left upper teeth of *Carcharodon carcharias* (drawing based on Uyeno and Matsushima [1979, fig.2]); B, left upper teeth of *Isurus paucus* (GH-Isur2-09); C, right upper teeth of *Lamna nasus* (GH-Lamn1-09; image reversed); D, right upper teeth of *Pseudocarcharias kamoharai* (GH-Pseud1-01; image reversed); E, left upper teeth of *Carcharias taurus* (AMNH 79962SD); F, left upper teeth of *Odontaspis ferox* (SIO 80-255); G, two tooth series in the thirty-seventh upper tooth row of *Cetorhinus maximus* (LACM 35876-1). Tooth type abbreviations: A, upper anterior tooth; I, upper intermediate tooth; L, upper lateral tooth (tooth type identification based on Shimada, 2002).

131 for the upper dentition and 100?-139 for the lower dentition (Shimada, 2002). These row counts are much greater than all other modern lamniform sharks (Shimada, 2002). Due to the lack of dental bullae and accurate occlusional information (e.g., Fig. 2), tooth homologies between *Cetorhinus maximus* and other modern lamniform sharks are uncertain (Shimada, 2002).

Discussion

Paleontological perspective

The fossil record of sharks is excellent, but most of them are represented by isolated teeth. The skeleton of sharks consists almost entirely of cartilage, so an entire shark is rarely preserved as a fossil. Thus, paleontologists must usually rely on the tooth morphology of modern sharks for the determination of the taxonomic identity of fossil taxa. Yet, it is not uncommon for paleontologists to suffer from the lack of reasonable comparative data on the dentitions of modern sharks, such as the data on various intraspecific tooth variation (e.g., Gruber and Compagno, 1981; Raschi *et al.*, 1982) as well as on the range and types of sporadically occurring dental abnormalities (e.g., Gudger, 1937; Compagno, 1967; Becker *et al.*, 2000). Therefore, descriptions of dental variation in modern sharks are essential for building a foundation for paleontological practices.

LACM 39461-1 shows a remarkable morphological variation of teeth, particularly at the anterior portion of the upper jaw (Fig. 2C). Broad-based triangular teeth in the specimen (e.g., teeth 5-7 and 11-12 in Fig. 2C) are similar to teeth of some macrophagous lamniforms, such as *Alopias, Isurus,* and *Pseudocarcharias*. Fossil cetorhinids are known from post-Paleocene marine deposits worldwide (for review, see Cappetta, 1987). However, the presence of teeth that resemble macrophagous lamniforms in LACM39461-1 warns paleontologists that overall tooth morphology may not necessarily be a reliable character in determining the taxonomic identity of extinct sharks.

Evolutionary perspective

Certain teeth in certain taxa always show mesial inclinations (i.e.,"tooth reversal" *sensu* Compagno, 1967), such as the upper intermediate tooth (I1) in *Carcharodon* *carcharias* (Applegate and Espinosa-Arrubarrena, 1996; Fig. 3A). Such cases can be called "obligate tooth reversal". However, tooth symmetry is usually a rather "flexible" feature in sharks. Reif (1980) demonstrated that the "polarity" of tooth inclinations may switch in sharks due to a split of the tooth "protogerm" through injury. Although one cannot ascertain whether or not each case is caused by an injury of tooth protogerm, polarity switch and tooth splitting are common phenomena in shark dentitions (e.g., Compagno, 1967; Reif, 1980). A tooth reversal due to such a polarity switch can be called "facultative tooth reversal". The facultative tooth reversal cannot be considered a phylogenetic character due to its sporadic occurrence, and only an extensive intraspecific comparison would allow its recognition in each species.

The model proposed by Reif (1980) suggests that tooth splitting does not necessarily produce "reversed" teeth. Depending on the position of the split in the protogerm, two teeth derived from one protogerm may both incline distally. In lamniforms, facultative tooth reversals as well as apparent and presumed tooth split often occur between anterior and lateral tooth rows, and at the distal portion of lateral tooth series (Fig. 3B-G). The tooth split may be incomplete resulting in a "split crown" (Fig. 3E-F), and the number of splits on a crown may be greater than two (e.g., "trifid" tooth in Fig. 3G). Such irregularities may occur within a tooth row (Fig. 3E, G). Teeth with incomplete crown splitting are known in the fossil record (e.g., Welton and Farish, 1993, fig. 17JK).

The total tooth row count of *Cetorhinus maximus* is much higher than that of other modern lamniform sharks (Shimada, 2002). *Cetorhinus maximus* underwent a significant modification of jaw cartilage by losing their dental bullae (Shimada, 2002); however, the loss of dental bullae does not explain its increase in the tooth row counts. Based on the present data, the mechanism that may explain its increase in the tooth row count is repeated tooth splitting events through evolution. For instance, the observation of many "reversed" teeth in the mesial portion of the dental series in *Cetorhinus maximus* (Fig. 2C) may represent the result of tooth splitting. This implies theoretically that homologous teeth must exist between *Cetorhinus maximus* and other lamniforms, although their recognition is impossible at the present time.

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