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[Original report]

# Types of tooth sets in the fossil record of sharks, and comments on reconstructing dentitions of extinct sharks

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## Abstract

Reconstructing shark dentitions, using one or more sets of fossil teeth, has become a recent trend in shark paleontology. If a tooth set is defined as more than one tooth belonging to a single taxon, three major preservation types of tooth sets are recognized in the fossil record of sharks: isolated, associated, and semiassociated tooth sets. An isolated tooth set consists of isolated teeth and may represent more than one individual shark. An associated tooth set is a tooth set referable to one individual shark, and it can be either an articulated tooth set or disarticulated tooth set. A semiassociated tooth set consists of one or more disarticulated tooth sets and/or an isolated tooth set, and it includes two subtypes, feed-shed tooth set and coprolitic tooth set. A feed-shed tooth set consists of an assemblage of fallen teeth formed presumably during feeding, and a coprolitic tooth set represents teeth enclosed in a coprolitic matter. Complex taphonomic processes, including both before and after the recovery of teeth, may make an associated tooth set or semiassociated tooth set to become an isolated tooth set by means of disassociated teeth. For effective communication among shark paleontologists, it is important to accurately identify and record the preservation type of each tooth set used to reconstruct dentitions of fossil sharks.

Key words: dentition, fossil record, shark, taphonomy, teeth

## Introduction

Complete sharks are rare in the fossil record because their cartilaginous skeleton is usually not well mineralized. Thus, one main obstacle in paleontological studies of sharks is the fact that most extinct sharks are represented only by isolated teeth. However, the practice of basing a study solely on isolated teeth (isolated-, or single-tooth taxonomy) has been criticized recently (e.g., Maisey, 1983; Compagno, 1988; Applegate, 1991; Applegate and Espinosa-Arrubarrena, 1996; Gottfried *et al.*, 1996; Gottfried and Francis, 1996; Hubbell, 1996; Gottfried and Fordyce, 2001). This is because, in sharks, heterodonty is usually present (e.g., "lamnoid tooth pattern" in Lamniformes: Shimada, 2002a), and various dental variations occur. Examples of dental variations (other than pathologic or abnormal teeth: e.g., Gudger, 1937) include individual (e.g., Sadowsky, 1970; Taniuchi, 1970), sexual (e.g., Springer, 1966; Kajiura and Tricas, 1996), ontogenetic (e.g., Reif, 1976; Shimada, 2002b), and geographic differences (e.g., Lucifora *et al.*, 2003).

The capacity of each paleontological study depends on the "quality" of fossil preservation shaped through various taphonomic processes. Applegate (1965) introduced several terms describing the "quality" of shark fossils in terms of the concept of "tooth sets." However, I have found most of Applegate's definitions ambiguous or inconvenient. For example, Applegate's "tooth set" is concerned with teeth arranged as a reconstructed dentition, whereas his "associated

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tooth set" describes its preservation mode. His "natural tooth set" as defined, on the other hand, can be taken either way. In addition, some additional expressions, such as "natural set," "associated set" (e.g., Applegate, 1965, p.14 ; Applegate and Espinosa-Arrubarrena, 1996, p.30), and "associated dentition" (e.g., Gottfried, 1993, p.59 ; Welton and Farish, 1993, p.102) have been used in the literature.

The "accuracy" of reconstructed dentitions of extinct sharks (i.e., "how close it is to the original dentition?") is strongly influenced by the types of "tooth sets" used for the reconstruction. Therefore, a clearly defined terminology for describing tooth sets is necessary to avoid misunderstanding and loss of information through description. Here, solely from a taphonomic standpoint, I first redefine Applegate's tooth type terminology with some new terms added (Fig. 1). Then, I extend Applegate's (1965) discussion on the issues associated with reconstructing the dentition of extinct sharks.

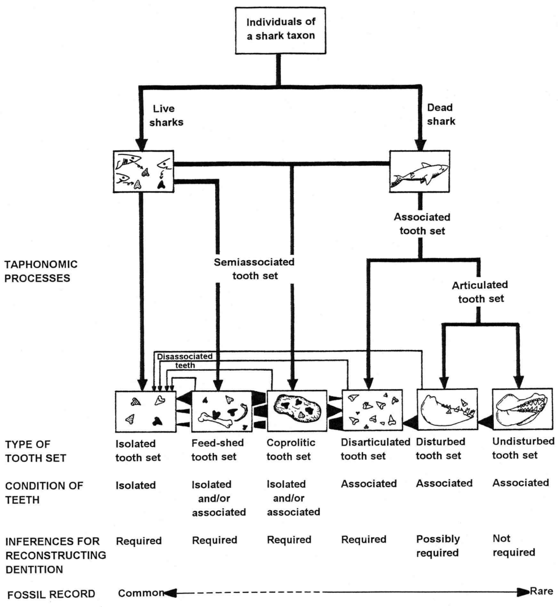


Fig.1 Taphonomy of shark teeth showing the formation of six tooth set types in the fossil record. Note : "Individuals of a taxon" do not necessarily share the same temporal and spatial ranges ; "Associated tooth set" is not necessarily limited to teeth from a dead shark (cf. semiassociated tooth set) ; arrows between illustrations of tooth set types indicate the general directions of reworking and/or curatorial processes, whereas other arrows above the illustrations denote initial preburial processes.

### Taphonomy-based tooth sets

A *tooth set* is defined here simply as more than one tooth belonging to a single taxon. Thus, all terms which contain the expression "tooth set" refer to teeth of one taxon. There are three major types of tooth sets : isolated, associated, and semiassociated tooth sets (Fig. 1).

An *isolated tooth set* is a tooth set consisting of isolated teeth. It is the most common tooth set type in the fossil record. One example is a set of tiger shark teeth described by Applegate (1978). An isolated tooth set may include disassociated teeth from one or more semiassociated, disarticulated, and/or disturbed tooth sets (see below), but the identification of disassociated teeth within an isolated tooth set is virtually impossible.

An *associated tooth set* is a tooth set referable to one individual shark. Teeth of an associated tooth set can be either disarticulated or articulated. A *disarticulated tooth set* is an associated tooth set that does not show the original tooth arrangement. Examples include specimens described by Eastman (1895), Goto (1977), Goto *et al*. (1978, 1983), Uyeno *et al*. (1989, 1990), Kent and Powell (1998), Siverson (1999), Gottfried and Fordyce (2001), and Hamm and Shimada (2002). An *articulated tooth set* is an associated tooth set that shows the original tooth arrangement. It consists of two subtypes, undisturbed and disturbed tooth sets. An *undisturbed tooth set* is an articulated tooth set without postmortem disturbance (biotic and/or abiotic factors). It is the rarest type of tooth set in the fossil record. One example is a hybodont specimen described by Maisey (1983). A *disturbed tooth set* is an articulated tooth set with postmortem disturbance. Such sets are represented in a wide range of preservation, from a set of a few teeth to a complete tooth series. Examples include specimens described by Cappetta (1980), Duffin (1988), Gottfried (1993), MacLeod (1982), and Shimada (1997a).

A *semiassociated tooth set* is a tooth set presumably formed through feeding activities or ingestion of teeth, requiring taphonomic and paleoecologic considerations. It can be divided into two subtypes, feed-shed and coprolitic tooth sets, both consisting of one or more associated tooth sets and/or an isolated tooth set. A *feed-shed tooth set* is a tooth set consisting of an assemblage of fallen teeth formed presumably during feeding. Examples include shark teeth reported by Repenning and Packard (1990), Bigelow (1994), Schwimmer *et al*. (1997, in parts), and Shimada (1997c, in parts). It should also be noted that a feed-shed tooth set may also occur as embedded teeth in a skeletal remain of another animal (e.g., Shimada, 1997c, in parts; Shimada and Hooks, 2004). A *coprolitic tooth set* is a tooth set enclosed in coprolitic matter (ejecta, gastric residue, cololite, or coprolite: McAllister, 1988). Excellent examples are the hybodontid teeth reported by McAllister (1988). Self-ingested shark teeth (e.g., Stransburg, 1963; Uchida *et al.*, 1996) may become a coprolitic tooth set (e.g., see discussion in Shimada, 1997b), but such an example is not known in the present fossil record.

Taphonomic processes affecting fossil shark teeth are complex (Fig. 1). For example, postmortem disturbance by various scavengers as well as sorting, reworking, and erosion processes may make teeth of an associated tooth set or semiassociated tooth set to become mere isolated teeth (for an experiment of the disintegration of a shark body, see Schafer, 1972). Loss of taphonomic information through collecting and curatorial processes is also a bitter reality in paleontological collections (Shimada, personal observation). These endless possibilities suggest that the six tooth set types described here are a continuum in reality.

## Reconstructing dentitions of extinct sharks

Whereas articulated tooth sets are rare in the fossil record, reconstructing dentitions of extinct sharks based on one or more isolated or disarticulated tooth sets has become a common practice in shark paleontology (e.g., Applegate, 1978; Eisvogel, 1979; Uyeno *et al.*, 1989, 1990; Welton and Farish, 1993; Kent and Powell, 1998; Siverson, 1999; Gottfried and Fordyce, 2001; Purdy *et al.*, 2001; but also see, e.g., Eastman, 1895). By assembling isolated and disarticulated teeth, such reconstructed dentitions are "*artificial*" (sensu Applegate, 1965; include "composite dentition" in Purdy *et al.*, 2001; note that the word "composite" should be reserved for a reconstructed dentition based on more than one tooth set). Applegate and Espinosa-Arrubarrena (1996) went one step further and assessed the phylogeny of white sharks based on their "artificial" dentitions (for critiques, see Castro, 1998; Springer, 1997).

The reconstruction of "artificial" dentitions, particularly those based solely on isolated tooth sets should not be regarded as a scientific result or conclusion. This is because such reconstructions are often not repeatable by others, where "repeatability" is a fundamental requirement in science. Instead, each artificial dentition should be regarded as no more than a hypothesis that can be tested by the future discovery of one or more articulated tooth sets.

I endorse Welton and Farish's (1993, p.17) view, which states: "One should never hesitate to construct a [dentition] of any kind as long as it is based on an adequate sample size and a reasonable modern analog. Once developed, the merits of the [reconstructed dentition] can be debated; otherwise, there is nothing to discuss!" However, one must be careful not to infer the phylogenetic relationships of extinct sharks based on artificial dentitions, because considering the phylogenetic position of fossil taxa from artificial dentitions based on modern sharks suffers severe circularity. The only truly phylogenetically informative tooth sets are articulated tooth sets, although disarticulated tooth sets may provide some phylogenetic signal if each of them preserves a large number of teeth from the original dentition.

## Concluding remarks

Various factors, including the "quality" of tooth sets examined, influence the accuracy of a reconstructed dentition. To make a reconstructed dentition scientifically meaningful and informative, it is always important to describe: 1) specimens examined, 2) types of tooth sets, 3) number of teeth contained in each tooth set, 4) number of tooth types represented in each tooth set, 5) comparative materials, and 6) rationalized reconstruction procedures. I hope the tooth set terminology proposed here facilitates effective communication among shark paleontologists.

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