THE IMPACT OF THE PULL OF THE RECENT IN EXTANT ELASMOBRANCHS

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Abstract: Modern elasmobranchs have a long evolutionary history and an abundant fossil record that consists mainly of teeth. Many fossil taxa have living representatives. However, the representation of extant taxa in the fossil record is unknown. To begin to understand the geological history of extant elasmobranchs, here we assess the quality of their fossil record. We do so by assessing the Pull of the Recent (herein, POR). The POR can bias the fossil record because the rather complete record of living taxa allows palaeontologists to identify fossil members of the modern clades and to bridge time bins where fossils are absent. We assessed the impact of the POR by quantifying the proportion of extant elasmobranchs that have a fossil record, but do not occur in the last 5 million years (Pliocene and Pleistocene). We found that the POR does not affect orders and families, but it does affect 24% of elasmobranch genera. Within the different elasmobranch orders, the Lamniformes display the most complete generic fossil record, with no impact of the POR. Although modest, the impact of the POR in extant elasmobranch genera is higher than that found in other taxa. Overall, the geological history of elasmobranchs contradicts the usual assumption that the fossil record becomes worse backwards in time. This is the case across geographical regions and tooth size, further suggesting that sampling intensity and outcrop availability might explain the POR effect on sharks and rays.

Keywords: Fossil teeth, Neogene, Plio-Pleistocene, rays, sharks.

THE Pull of the Recent (POR) is an apparent bias of the fossil record, in which the modern biota is assumed to be better sampled and preserved than the extinct one (Jablonski *et al.* 2003; Sahney and Benton 2017). Hence, under the effect of the POR, the stratigraphic range and diversity of extant taxa is artificially extended across preceding time spans where there is no fossil record (Jablonski, *et al.* 2003). This problem has been invoked when interpreting the exponential increase in biodiversity from the Cenozoic to present time (Raup 1972; Alroy *et al.* 2001). However, to our knowledge, only two works have quantified the effect of the POR on biodiversity: one for marine bivalves (Jablonski, *et al.* 2003) and one for terrestrial tetrapods (Sahney and Benton 2017). In both cases it was found that the POR does not distort the pattern of diversification, suggesting rapid diversity increase towards Recent time could be a genuine biological pattern.

Sharks and their relatives (Elasmobranchi) offer an interesting case to assess the POR because relative to most groups of marine vertebrates, they have an abundant fossil record (Hubbell 1996; Cappetta 2012). The fossil record of elasmobranchs consists mainly of teeth, which are composed of enameloid, whereas the cartilaginous skeleton is only rarely preserved (Labs-Hochstein and MacFadden 2006; Wang and Cerling 1994). Further, because sharks shed their teeth continuously throughout their lifetimes, they do not need to die in order to leave a record of their teeth (Hubbell 1996; Cappetta 2012). Importantly, it has been widely stated in the literature that modern elasmobranchs have a fossil record that extends deep into geological time (Maisey 2012), and are hence thought to have survived major environmental changes (Martin *et al.* 1992) and extinctions (Pimiento *et al.* 2017).

Here we assess the quality of the fossil record of extant elasmobranchs by assessing how it is affected by the POR. Because we are particularly interested in extant species, we ignored the record of extinct taxa. Nevertheless, our counting protocols match the two previous studies. Today, sharks are the most threatened marine vertebrate group in the world (Dulvy *et* *al.* 2014). The fossil record of modern sharks and their relatives has the potential to provide valuable information to directly asses how they have responded to climate change and extinctions in the past. Assessing the completeness of the fossil record of modern elasmobranchs is a first step towards this goal.

MATERIALS AND METHODS

We gathered a list of all extant elasmobranchs (class: Elasmobranchii) from FishBase (http://www.fishbase.org) using the R package "rfishbase" (Boettiger *et al.* 2012) and cross-referenced it with Weigmann (Weigmann 2016). In total, we gathered a list of 1,163 species, 193 genera, 58 families and 12 orders. Then, we downloaded all available fossil occurrences of these taxa from the Paleobiology Database (http://paleobiodb.org/) using the package "paleobioDB" (Varela *et al.* 2015). Because our objective was to assess the completeness of the fossil record of living taxa in the last 5 million years, we limited our search to the Neogene and the Quaternary. Additional records were found in Shark-References (http://shark-references.com). In total, we studied 310 publications not previously entered in the Paleobiology Database, adding new fossil occurrences for 58 genera and 59 species. We searched for records using valid names and their synonyms.

We assessed the number of *extant* taxa (at the order, family, genera and species level) that have a fossil record in the in the Neogene and Quaternary (the last 23 myr), recording fossil occurrences in seven geological time bins as follows: early Miocene (Aquitanian and Burdigalian), middle Miocene (Langhian and Serravallian), late Miocene (Tortonian and Messinian), early Pliocene (Zanclean), late Pliocene (Piacenzian), early Pleistocene (Gelasian and Calabrian), and late Pleistocene (Middle and Upper). Whenever an age covered multiple time bins (e.g. Pliocene), we counted it in all bins covered (e.g. both the early and late Pliocene). Based on this number, we calculated the proportion of taxa that do, and do not have a record in the Pliocene or Pleistocene (Sahney and Benton 2017; Jablonski, *et al.* 2003). We also recorded the geographical distribution of the fossil occurrences [based mainly on the Paleobiology Database and Cappetta (2012)], categorized tooth size [macro-teeth: >1cm of crown height; micro-teeth: <1cm; based on Cappetta (2012)], and assessed the effect or POR across regions and tooth size. All analyses were done in the R environment (R Development Core Team 2017).

RESULTS AND DISCUSSION

We found that 100% of the 12 extant elasmobranch orders have a fossil record in the last 23 myr, with no effect of the POR. From the 58 extant families, 44 (76%) have a fossil record, none of which are affected by the POR. From the 193 extant genera of elasmobranchs, 89 (46%) have a record in the last 23 myr, 24% of which are affected by the POR (Fig. 1A). The fossil record of extant species is poor, with only 89 (8%) of the 1,163 species having a fossil occurrence during the last 23 myr, 27% of which are affected by the POR (Table 1). As found in the two previous studies on the POR, extant orders and families are robustly represented in the Neogene and Quaternary fossil record and are unaffected by POR (Table 1). The generic and specific level have a substantially different representation in the fossil record, but in both cases, roughly one quarter of the taxa are affected by POR (Table 1). This is substantially higher than what was found in molluscs (Jablonski, *et al.* 2003) and terrestrial tetrapods (Sahney and Benton 2017).

Even though the value of the fossil record of modern elasmobranchs in informing current extinctions would be higher at the species level, the generic level is more complete and reliable (Table 1). Indeed, heterodonty obscures the identification of elasmobranch teeth to the species level (Cappetta 2012). Reports of fossil occurrences for elasmobranch genera through the past 23 myr show sporadic occurrences, with 22 genera recorded in all seven time bins (Fig. 1A). Others, though, show gaps in one, or more time bins: seven genera have fossil records in six time bins, 19 genera in five time bins, nine in four time bins, 10 in three time bins and 13 genera have a record only in one time bin. Three genera, the ray *Pteroplatytrygon* and the sharks *Chiloscyllium* and *Oxynotus* have a record in the early Miocene, and then the present day, leaving a gap of six time bins, and providing extreme examples of the POR (Fig. 1A).

There are differences in representation between major clades. For example, the family Lamnidae has the most complete generic fossil record, and no POR effect (Fig. 1A). This family includes the largest teeth of all elasmobranchs, measuring from 2 to 7 cm of crown height (Cappetta 2012; Purdy 1996; Gottfried *et al.* 1996). Across diverse taxonomic orders (> 5 extant genera), Lamniformes display the most complete generic fossil record and no POR effect. Rhinopristiformes has a fairly complete record, and no POR effect. Rajiformes has a proportionally high influence of POR, and generally, a poor fossil record compared with other orders (Fig. 1B). Overall, genera of extant sharks are better represented in the fossil record than rays and skates (57% *vs.* 33%) with a moderate POR effect (17% *vs*. 38%; Fig. 1C).

Throughout the last 23 myr, the fossil record of modern genera is richer in the early Miocene (87% of the occurrences), followed by the middle and late Miocene (83% of the fossil occurrences). The Pleistocene is the poorest represented period in the fossil record of modern elasmobranchs, with 40% of the fossil occurrences in the early Pleistocene and 48% in the late Pleistocene. The fact that the fossil record becomes *less* complete towards the present day [also see Maisey (2012)] is opposite to the usual assumption that the record becomes worse backwards in time (Raup 1972).

The general decrease of fossil records through geological time is also evidenced across the different geographical regions and tooth sizes (Fig. 2). Europe has the richest elasmobranch fossil record, but the number of genera decreases from the late Pliocene onwards. The Americas, Asia and Africa have a comparable fossil record, also following the general pattern of a richest record in the early Miocene and a poorest in the early Pleistocene. Australia and New Zealand, and the Antarctica present the poorest fossil record. Interestingly, such a record is rather uniform throughout the Neogene (from the early Miocene to the late Pliocene, Fig. 2A). Although Lamnidae, the family with the largest fossil teeth, has the most complete generic record (Fig. 1), size does not seem to determine the richness of the fossil record of elasmobranch fossils. In general, microscopic teeth are better represented than macroscopic teeth (Fig. 2B). Indeed, 65% of the fossil examples of extant genera are known in the fossil record by their small teeth, which can often be recovered only using screenwashing techniques. The record of micro-teeth is fairly uniform up to the early Pliocene and decreases thereafter. The record of macro-teeth is uniform throughout the Neogene and poor in the Pleistocene. In sum, the fossil record of extant elasmobranch genera becomes *less* complete towards the present day across regions and tooth-size, suggesting that outcrop availability and sampling intensity, and not tooth-size, determine the effect of the POR.

CONCLUSIONS

Our study shows that the fossil record of extant elasmobranchs is complete at the order and family levels during the last 23 myr. However, it is more affected by the POR than other groups previously studied at the generic and specific level (Sahney and Benton 2017; Jablonski, *et al.* 2003), with 24% and 27% POR effect, respectively. Even so, the generic level is more complete and reliable than the specific level. At the generic level, the family Lamnidae is the most complete, with records of all extant genera across all time periods studied. Overall, and different to the assumption that the fossil record improves through time (Raup 1972), the fossil record of extant elasmobranchs is worse towards the present day. This is true across geographical regions and tooth size, suggesting that sampling intensity and outcrop availability may be a mechanism driving the POR effect.

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DATA ARCHIVING STATEMENT

Datasets of species and genus of extant sharks, their fossil presence or absence across time bins and geographic regions and tooth type are available in the Dryad Digital Repository https://datadryad.org/stash/share/5eU1s7QX5fxxhbGDD_4HA1OnPhwEjV3PFP60hAbNJ70.

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FIGURE CAPTIONS

FIG. 1 The fossil record of extant elasmobranch genera. A, Stratigraphic ranges of extant genera (left) and families (right). Colour represents taxonomic orders (see B). B, Number of fossil genera by order. C, Proportions for the two major clades, Selachii (sharks) and Batoidea (skates and rays). In B, C, darker colour denotes the fossil genera not affected by POR; lighter colour the fossil record affected by POR; grey colour the extant genera without a fossil record.

FIG. 2. Elasmobranch fossil record per region and tooth size across the different geological time bins studied. A, Number of fossil genera in the main geographic regions as provided, mainly by Cappetta (2012). B, Number of fossil genera with micro-teeth (< 1 cm) and macro teeth (>1 cm). Circles denote the number of genera present in each time bin.

TABLE 1. Pull of the Recent (POR) bias the fossil record of extant of sharks and rays. Number of extant taxa represented in the fossil record and affected by POR.

	Extant taxa	Extant taxa w/fossil record	Extant taxa in Plio-Pleistocene	POR taxa	% POR taxa
Order	12	12	12	0	0
Family	58	44	39	0	0
Genus	193	89	68	21	23.59
Species	1,163	89	65	24	26.97