

The fossil record of extant elasmobranchs

Adele Paillard¹ | Kenshu Shimada^{2,3} | Catalina Pimiento^{1,4,5} 

¹Department of Biosciences, Swansea University, Swansea, UK

²Department of Environmental Science and Studies and Department of Biological Sciences, DePaul University, Chicago, Illinois

³Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas

⁴Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland

⁵Smithsonian Tropical Research Institute, Balboa, Panama

Correspondence

Catalina Pimiento, Paleontological Institute and Museum, University of Zurich, Zurich CH-8006, Switzerland.
Email: catalina.pimientoherandez@pim.uzh.ch

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Abstract

Sharks and their relatives (Elasmobranchii) are highly threatened with extinction due to various anthropogenic pressures. The abundant fossil record of fossil taxa has allowed the tracing of the evolutionary history of modern elasmobranchs to at least 250 MYA; nonetheless, exactly how far back the fossil record of living taxa goes has never been collectively surveyed. In this study, the authors assess the representation and extent of the fossil record of elasmobranchs currently living in our oceans by collecting their oldest records and quantifying first appearance dates at different taxonomic levels (*i.e.*, orders, families, genera and species), ecological traits (*e.g.*, body size, habitat and feeding mechanism) and extinction risks (*i.e.*, threatened, not threatened and data deficient). The results of this study confirm the robust representation of higher taxonomic ranks, with all orders, most of the families and over half of the extant genera having a fossil record. Further, they reveal that 10% of the current global species diversity is represented in the geological past. Sharks are better represented and extend deeper in time than rays and skates. While the fossil record of extant genera (*e.g.*, the six gill sharks, *Hexanchus*) goes as far back as *c.* 190 MYA, the fossil record of extant species (*e.g.*, the sand shark, *Carcharias taurus* Rafinesque 1810) extends *c.* 66 MYA. Although no significant differences were found in the extent of the fossil record between ecological traits, it was found that the currently threatened species have a significantly older fossil record than the not threatened species. This study demonstrate that the fossil record of extant elasmobranchs extends deep into the geologic time, especially in the case of threatened sharks. As such, the elasmobranch geological history has great potential to advance the understanding of how species currently facing extinction have responded to different stressors in the past, thereby providing a deep-time perspective to conservation.

KEYWORDS

extinction, fossil record, geological time, rays, sharks, traits

1 | INTRODUCTION

Sharks and their relatives (Elasmobranchii) are a diverse lineage with over 1000 living species (Naylor *et al.*, 2012; Stein *et al.*, 2018; Weigmann, 2016). They have a wide geographical range, occupying nearly every marine habitat as well as some freshwater systems (Martin, 2005; White & Sommerville, 2012). Elasmobranchs have also been found to inhabit a range of vertical positions, from the highly

diverse epipelagic zone above the depth of 200 m to the abyssopelagic zone below the depth of 1000 (Froese & Pauly, 2017; Kyne & Simpfendorfer, 2012). Because of anthropogenic pressures, elasmobranchs have suffered severe depletions around the world (Baum & Myers, 2004; Ferretti *et al.*, 2010; Ward-Paige *et al.*, 2012). Of the 1077 species assessed, *c.* 30% of elasmobranchs are threatened with extinction (IUCN, 2016). Accordingly, elasmobranchs are among the organisms with the highest extinction risk in the marine

realm (Dulvy *et al.*, 2014; Stein *et al.*, 2018). A reduced number of apex predatory sharks has already caused breakdowns in some ecosystems as their ecological niches become vacant (Myers *et al.*, 2007). The threat faced by elasmobranchs and their importance in their environment qualify the group for immediate conservation attention (Dulvy *et al.*, 2014; Pimiento *et al.*, 2020).

Crown group elasmobranchs have an evolutionary history of at least 250 MYA (Cappetta, 2012; Maisey *et al.*, 2004). This history has been traced back using their fossil record, which is abundant relative to most marine vertebrate groups and consists primarily of well-preserved teeth (Hubbell, 1996; Maisey, 2012; Pimiento & Benton, 2020). The elasmobranch fossil record has revealed that they have withstood major environmental changes and extinctions (e.g., Pimiento *et al.*, 2017). It also includes many living taxa (Cappetta, 2012), which facilitates biological and ecological interpretations of their geological past, particularly during the Cretaceous Era or last 66 MYA (e.g., Aguilera & De Aguilera, 2001; Carrillo-Briceno *et al.*, 2018; Kocsis, 2007; Landini *et al.*, 2017; Marsili, 2007; Martinez-Perez *et al.*, 2018; Pimiento *et al.*, 2013,b; Pollerspöck & Straube, 2017; Szabo & Kocsis, 2016; Villafana & Rivadeneira, 2018). Although it is widely recognised that many fossil elasmobranchs have living representatives, which (and how many) extant taxa have a fossil record and how far does their record go in geologic time have not been directly surveyed.

In this study, the authors provide a first comprehensive assessment on the fossil record of extant elasmobranchs by evaluating their representation (*i.e.*, whether there is a fossil record) and extent [*i.e.*, the oldest fossil record or first appearance date (FAD)]. They further describe the fossil record of extant elasmobranchs in relation to species' ecological traits and current extinction risk, as a means to gauge possible biological patterns, and the potential for the geological history of elasmobranchs to inform conservation. The results of this study set the basis for the use of the fossil record to provide deep-time perspective on a group that is highly threatened today.

2 | MATERIALS AND METHODS

2.1 | Data collection and analyses

A database of all known extant elasmobranch species (subclass: Elasmobranchii) was downloaded from FishBase (<http://www.fishbase.org>, last accessed January 2019) (Froese & Pauly, 2017) using the R package "rfishbase" (Boettiger *et al.*, 2012). Species names were contrasted against Weigmann (2016) to follow a consistent and up-to-date nomenclature. By doing so, the authors assessed and fixed synonyms. They also assigned each species (and genus) to a family, order and superorder based on Naylor *et al.* (2012). The data set of this study consisted of 1115 species, 193 genera, 58 families and 12 orders. The authors then searched for the oldest fossil record of each extant genus and species using relevant literature. For genera, the authors used Cappetta (2012) and for species Cappetta (2006). Additional records were searched using the Paleobiology Database

(<http://paleobiodb.org/>; last accessed December 2019) and Shark-References (<http://shark-references.com>; last accessed January 2020). The authors checked the references associated with each new record and only considered those from which they could evaluate the taxonomic identifications (e.g., published illustrations: see Supporting Information). In total, they gathered the oldest fossil record of 110 extant species (*i.e.*, taxa identified to the species level) and of 108 extant genera (*i.e.*, taxa identified to the genus level). All records consisted of teeth (see Supporting Information). In no instance was the fossil record of a genus represented only by a taxon identified to the species level.

The age of each fossil record was recorded at the Stage level following Gradstein *et al.* (2012). Whenever the Stage was not provided, a conservative approach was used and the record was assigned to the Epoch's youngest Stage, unless further information was provided suggesting otherwise. To each of the 110 species (*i.e.*, taxa identified to the species level) with a fossil record, the authors assigned level of endangerment and the following broad ecological traits: maximum body size, habitat, vertical position, maximum depth and feeding mechanism. Trait scores (Table 1) were assigned based on the species information provided by FishBase, IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>, last accessed January 2019) and primary literature.

TABLE 1 Traits assigned to elasmobranchs with a fossil record

Trait	Possible scores
Threat ^a	<ol style="list-style-type: none"> 1. Data deficient: IUCN status data deficient (DD) 2. Not endangered: IUCN status least concern (LC) or near threatened (NT) 3. Endangered: IUCN status vulnerable (VU), endangered (EN) or critically endangered (CR)
Body size	<ol style="list-style-type: none"> 1. Small: <1.5 m of total length (TL) 2. Medium: >1.5 m to <3 m of TL 3. Large: >3 m of TL
Habitat	<ol style="list-style-type: none"> 1. Coastal: lives in the neritic zone (above 200 m depth in the continental shelf) 2. Oceanic: lives in the oceanic zone (below 200 m depth offshore) 3. Both: lives in coastal and oceanic zones
Vertical position	<ol style="list-style-type: none"> 1. Benthic: feeds in the bottom of the ocean 2. Pelagic: feeds in the water column 3. Benthopelagic: feeds in both the benthic and pelagic zones
Maximum depth	<ol style="list-style-type: none"> 1. Epipelagic: up to 200 m of maximum depth 2. Mesopelagic: from 200 m to 1000 m of maximum depth 3. Bathyal: more than 1000 m of maximum depth
Feeding mechanism	<ol style="list-style-type: none"> 1. Active predator 2. Filter-feeder

^aNo extant elasmobranch species with a fossil record was found to be Not Evaluated by IUCN.

Based on the data collected, the authors assessed (a) the representation of extant elasmobranchs in the fossil record, specifically whether an extant taxon (species, genus, family and order) has a fossil record; and (b) the oldest extent of the fossil record of extant elasmobranchs, particularly the FADs of elasmobranch taxa at the genus and species levels. The age of FADs in millions of years was regarded as the lower end of the fossil record's temporal range (e.g., for a fossil record in the Danian 66 MYA was used; Gradstein *et al.*, 2012). The authors also described the fossil representation and FADs of species' traits with two goals: (a) to identify life-history traits potentially associated with the representation of extant species in the fossil record; and (b) to make a first assessment of the potential for the fossil record of elasmobranchs to inform conservation. The authors statistically tested for differences between the FADs of superorders, among orders, and among trait scores using Wilcoxon–Mann–Whitney, Kruskal–Wallis and Dunn's tests. These nonparametric tests assess if different samples (or groups) come from the same or different

populations. All pair-wise comparisons were made using samples with similar distributions, and therefore, the tests can be interpreted in terms of medians (Dinno, 2017; Hart, 2001). It must be noted here that FADs do not necessarily represent the time of origination of a taxon, as the true origination times can occur beyond fossil occurrence (Marshall, 1997; Paul, 2005; Silvestro *et al.*, 2014). Therefore, the authors' findings in terms of FADs are interpreted as the extent of fossil record only, and not as proxies of speciation times. All the analyses were performed in the R environment (R Core Team, 2017).

2.2 | Ethical statement

This research was based on an analysis of the fossil record, and it did not use experimental animals. Accordingly, animal welfare laws, guidelines and policies are not applicable.

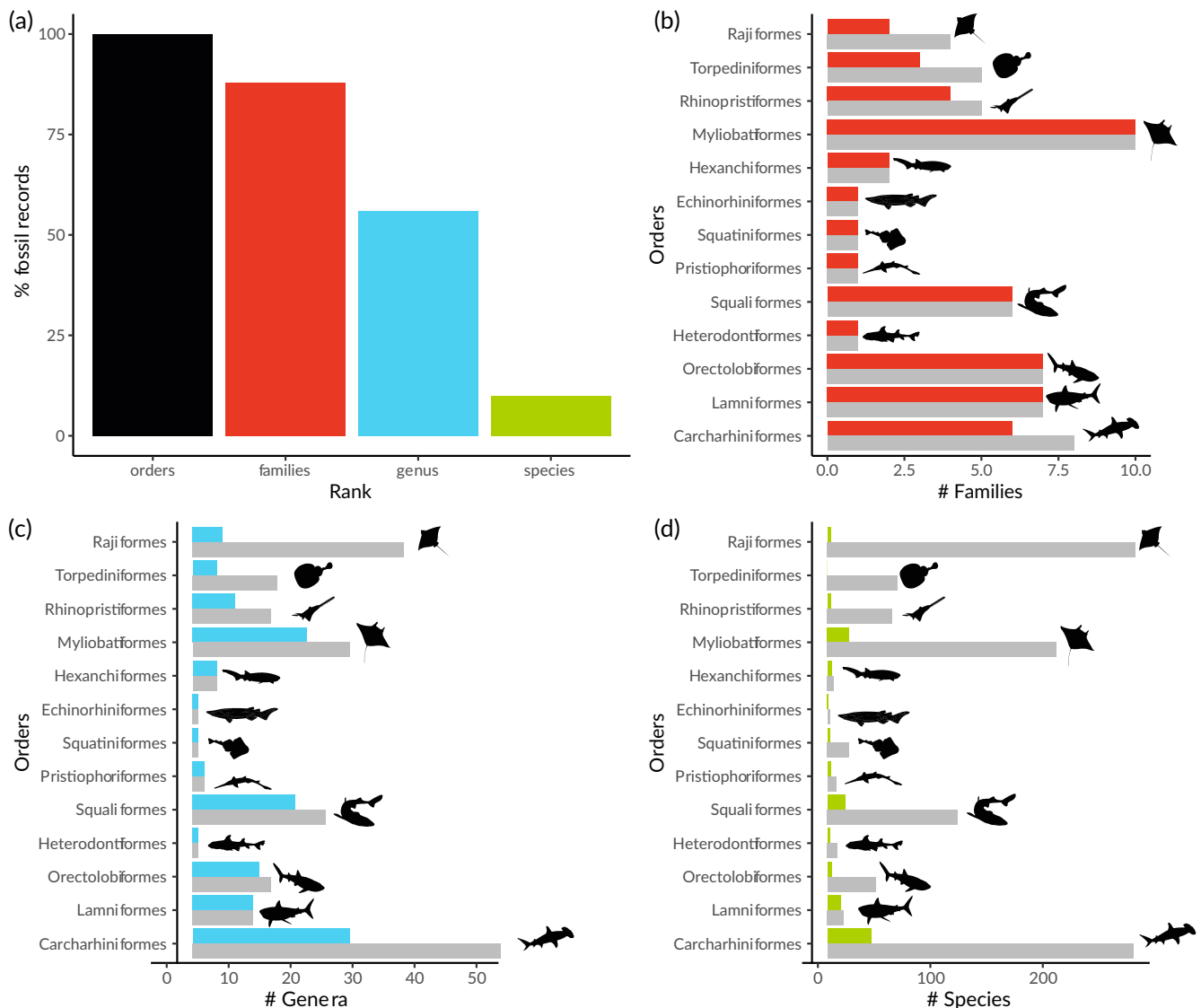


FIGURE 1 Representation of extant elasmobranchs in the fossil record. (a) Percentage of extant orders, families, genera and species with a fossil record. (b–d) Representation of each taxonomic order by: (b) family; (c) genera; and (d) species. (■) all, (■) fossil

3 | RESULTS

3.1 | Representation of extant elasmobranchs in the fossil record

At the order level, there is a 100% representation of extant elasmobranchs in the fossil record (Figure 1a). At the family level, there is 88% representation, with the following seven families not having any fossil record: Proscylliidae, Pseudotriakidae, Anacanthobatidae, Gurgesiellidae, Zanobatidae, Narkidae and Hypnidae. Carchariniformes is the only shark order not having all of its extant families represented in the fossil record (75% representation: Supporting Information Table S1; Figure 1b), whereas Myliobatiformes is the only batoid order with a full representation of its extant families (Figure 1b). At the genus and species levels, there is a 56% and 10% representation, respectively (Figure 1a). Six orders have total representation of their extant genera, all of them being sharks (Hexanchiformes, Echinorhiniformes, Squatiniformes, Pristiophoriformes, Heterodontiformes and Lamniformes: Figure 1c; Supporting Information Table S1). Extant hexanchiforms and lamniforms have the highest representation in the fossil record at the species level, whereas Torpediniformes (batoid) is the only order not having any species represented in the fossil record (Figure 1d; Supporting Information Table S1). Notably, Lamniformes has the most complete representation across all taxonomic ranks, with 100% of its extant family and genera having a fossil record, as well as 80% of its extant species (Figure 1b–d; Supporting Information Table S1).

3.2 | Extent of the fossil record of extant elasmobranchs

The fossil record of extant elasmobranch genera (blue colour in Figure 2) extends to the lower Jurassic with the oldest record being

that of the six gill sharks *Hexanchus* in the Pliensbachian (maximum age 190 MYA; Supporting Information; Cappetta, 2012). Nevertheless, the distribution of FADs at the genus level is skewed towards the Cainozoic with the highest frequency of FADs taking place in the early Eocene between 56 and 48 MYA (Ypresian: Figure 2a). The youngest FADs at the genus level are those of *Nasolamia*, *Prionace* and *Zameus* in the early Pliocene (maximum age 5.3 MYA; Supporting Information).

The fossil record of extant species (green colour in Figure 2) extends to the Palaeocene (maximum age 66 MYA), with the oldest record being that of the sand tiger shark *Carcharias taurus* (Supporting Information; Cvanara & Hoganson, 1993). FADs of extant elasmobranch species are skewed towards the Neogene, with most of them occurring primarily in the early Pliocene around 5 MYA (Zanclean; Figure 2d). Only the following four extant species have a FAD in the quaternary: the broad nose sevengill shark *Notorynchus cepedianus* Perón 1807, the longnose velvet dogfish *Centroscymnus crepidater* Barbosa du Bocage & de Brito Capello 1864, the Pacific angel shark *Squatina californica* Ayres 1859 and the Atlantic sharpnose shark *Rhizoprionodon terraenovae* Richardson 1836 (Supporting Information).

When the genus- and species-level records of extant elasmobranchs are divided by superorders, despite the fact that shark (Selachii) FADs at the genus level extend deeper in geologic time than batoids (Batoidea: Figure 2b), there are no significant differences between the two superorders (genus-level Mann–Whitney *U*-test: $W = 1499.5$, $P = 0.14$; species-level Mann–Whitney *U*-test: $W = 1125.5$, $P = 0.81$; Figure 2b,e). When the different orders are examined, extant shark genera (light blue in Figure 2c) have FADs that extend deeper in time than batoids (dark blue in Figure 2c). As such, extant hexanchiform, echinorhiniform, squatiniform and heterodontiform genera display the oldest FADs (Figure 2c). These orders have significantly older genus-level fossil records than squaliform, lamniform, carcharhiniform, rajiform and myliobatiform genera

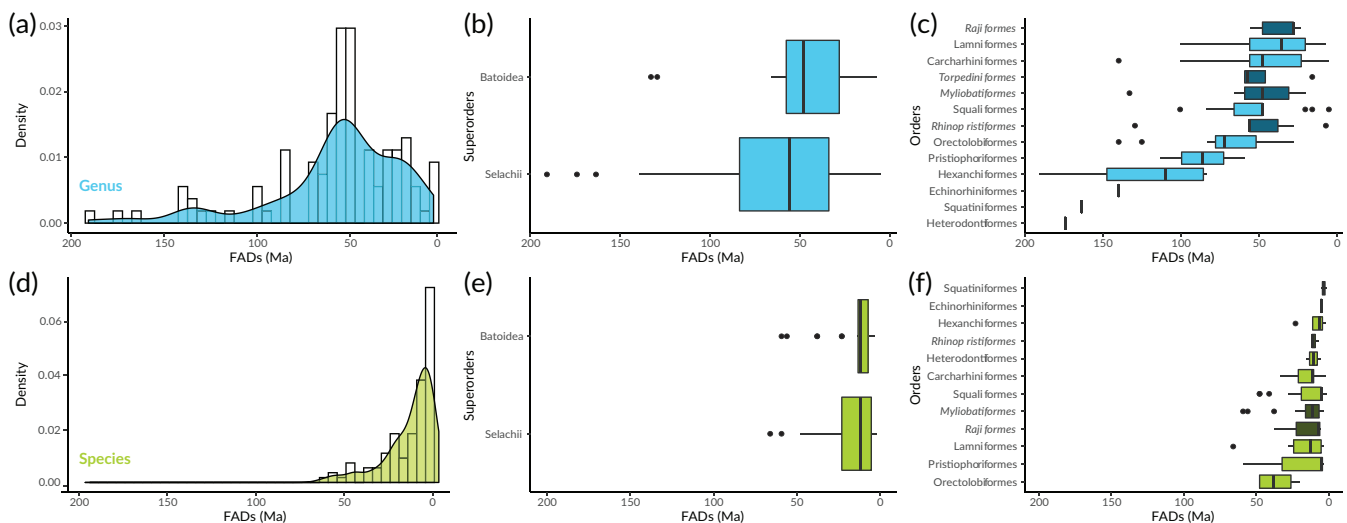


FIGURE 2 First appearance dates (FADs) of extant elasmobranchs. (a–c) FADs at the genus level (in blue). (d–f) FADs at the species level (in green). (a, d) Frequency of FADs. (b, e) Extent of FADs across superorders. (c, f) Extent of FADs across orders organised from oldest (bottom) to youngest (top) with darker colours denoting batoids (also in *italics* along the y-axis) and lighter colours denoting selachians

(Dunn's test, $P < 0.05$: Supporting Information Table S2). Notably, Hexanchiformes is the only order where the FADs of its extant genera are statistically different from those of the order Torpediniformes (Dunn's test, $P = 0.02$: Supporting Information Table S2). Batoids display younger FAD ranges, with Rajiform genera having the most recent FAD median, which is significantly younger than not only the four aforementioned orders, but also from pristiophoriforms and orectolobiforms (Dunn's test, $P < 0.05$: Supporting Information Table S2; Figure 2c).

At the species level, extant rajiforms, Lamniformes, pristiophoriforms and orectolobiforms display the oldest FADs (Figure 2f) with lamniforms showing the oldest range. Although extant orectolobiforms have FAD medians significantly older than all other orders (Dunn's test, $P < 0.05$: Supporting Information Table S3), the FADs of extant pristiophoriform and rajiform species are not significantly different from any other order except for orectolobiforms. Extant lamniforms display FADs significantly older than those of squatiniforms (Dunn's test, $P = 0.02$: Supporting Information Table S3) in addition to orectolobiforms (Dunn's test, P -value = 0.02: Supporting Information Table S3). Squatiniforms display the youngest FADs, which are significantly different from orectolobiforms, lamniforms, carchariniforms and myliobatiforms (Dunn's test, $P < 0.05$: Supporting Information Table S3).

3.3 | Species' traits in the fossil record

Species currently considered as threatened with extinction by IUCN display significantly older FADs than not threatened or data-deficient species (Dunn's test, $P < 0.05$: Supporting Information Table S4; Figure 3a). Notably, all but three of these species are sharks (Supporting Information Table S9). Critically endangered species include the common sawfish *Pristis pristis* L. 1758 (FAD = 11.6 MYA) and the angel shark *Squatina squatina* L. 1758 (FAD = 5.3 MYA). Endangered species include the zebra shark *Stegostoma fasciatum* Hermann 1783 (FAD = 47.8), the whale shark *Rhincodon typus* Smith 1828 (FAD = 28.1 MYA), the scalloped hammerhead *Sphyrna lewini* Griffith & Smith 1834 (FAD = 15.9 MYA), the great hammerhead *Sphyrna mokarran* Rüppell 1837 (FAD = 11.6 MYA) and the African wedgefish *Rhynchobatus luebberti* Ehrenbaum 1915 (FAD = 11.6 MYA). Vulnerable species include that with the oldest fossil record, *C. taurus* (FAD = 66 MYA), as well as 23 other species (Supporting Information Table S9). It is important to note here that IUCN statuses are dynamic and change with time. As such, some of the species mentioned here have progressed to higher-risk categories since the time we accessed the IUCN data (Table S9). Data-deficient species display the youngest range of FADs (from 48 to 2 MYA: Figure 3a). Notably, this category has the lowest number of fossil records [data deficient = 24% ($n = 26$);

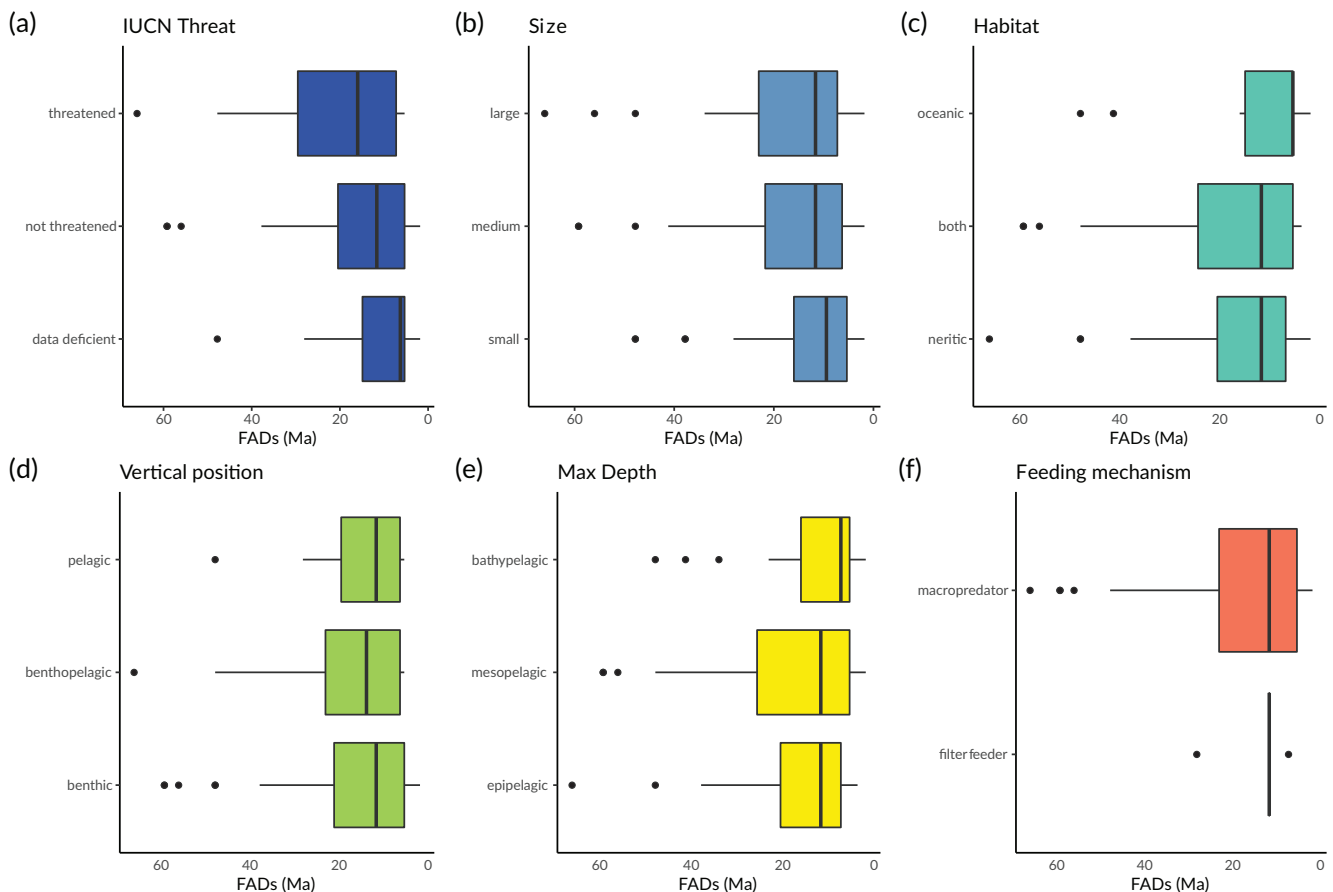


FIGURE 3 Extent of the fossil record of species' IUCN category and ecological traits. See Table 1 for details on trait scores

threatened = 29% ($n = 32$); not threatened = 44% ($n = 52$): Supporting Information Figure S1a]. This differs from extant species without a fossil record, where the data-deficient category has the highest species richness [data deficient = 47% ($n = 476$); not threatened = 36% ($n = 368$); threatened = 16% ($n = 161$): Supporting Information Figure S1].

In terms of the extent of extant species' ecological traits in the fossil record, large- (>3 m in maximum total length (TL): Table 1) and medium-sized species (1.5–3 m in maximum TL: Table 1) have a wider range of FADs than small species (<1.5 m in maximum TL: Table 1; Supporting Information Figure S1b). Nevertheless, there are no statistically significant differences among size groups (Dunn's test, $P > 0.05$: Supporting Information Table S5). Although there are no distinguishable differences in the number of fossil records across size types (Supporting Information Figure S1), small species are far more common than medium- or large-sized species within the much larger sample of species without a fossil record (Supporting Information - Figure S1). The FADs of extant species are not significantly different (Dunn's tests, $P > 0.05$: Tables S6–S8) among habitat types (Figure 3c), vertical positions (Figure 3d) and maximum depths (Figure 3e; Table 1). Nonetheless, the range of FADs of extant neritic (also epipelagic above 200 m depth) and benthopelagic (feeding both at the bottom of the ocean and in the water column) species extends deeper in geologic time than their counterparts (Figure 3c–e). There are also notable differences in the number of species across trait scores (Supporting Information Figure S1c–e), with fewer species exclusively inhabiting the oceanic zone (below 200 m depth: Table 1), being strictly pelagic (feeding in the water column: Table 1) and reaching bathyal depths (>1000 m: Table 1) than their counterparts. This is the case for species both with and without a fossil record (Supporting Information Figure S1c–e; Table 1). Finally, although the range of FADs of extant macropredatory species extends longer than filter-feeders (Figure 3f; Table 1), there are no statistically significant differences between feeding mechanisms (Kruskal–Wallis test, $\chi^2 = 0.09$, $df = 1$, $P = 0.76$). As expected from their low diversity (only 13 living species), the filter-feeder category presents a much smaller number of species than macropredators when looking at species both with and without a FAD (Supporting Information - Figure S1f; Table 1).

4 | DISCUSSION

It has been established that many fossil elasmobranchs have living representatives, and that the fossil record of modern taxa extends deep in geological time (Cappetta, 2012). Nonetheless, the questions of which (and how many) extant taxa have a fossil record and exactly how far back in time can these records go remained open until now. Given that the geological record can be used as a natural laboratory from which the most common responses of species to environmental change can be predicted (Dietl & Flessa, 2011), answering these questions can set the basis for the potential use of the fossil record to provide a deep-time perspective on a group that is highly threatened

today. Indeed, a link between the geologic past and conservation can be more tangible if made using the fossil record of living species facing extinction.

4.1 | The fossil record of extant elasmobranchs is dominated by sharks

The representation of extant elasmobranchs decreases with taxonomic rank (Pimiento & Benton, 2020). This study shows that all extant orders, most extant families and more than half of the extant genera are known in the fossil record, whereas only 10% of the extant species have a fossil representation (Figure 1a). The lower representation of extant species relative to genera has been attributed to a recent appearance of living forms given that the fossil record of elasmobranchs is worse towards the present day (Pimiento & Benton, 2020). Nevertheless, this can also be the result of problems associated with the identification of fossils. Heterodonty (*i.e.*, intra-specific variation of tooth morphology) obscures taxonomic identifications of fossils to the species level (Cappetta, 2012; Guinot *et al.*, 2018). Such intraspecific variations can occur across a jaw quadrant and between upper and lower jaws (Applegate, 1965; Compagno, 1970, 1988; Moyer & Bemis, 2016; Shimada, 2002a) as well as at different ontogenetic stages (Bemis *et al.*, 2015; Reif, 1976; Shimada, 2002b), between sexes and even between different mating seasons (Gruber & Compagno, 1981; Kajiura & Tricas, 1996; McCourt & Kerstitch, 1980; Nordell, 1994) or among different geographic regions (Lucifora *et al.*, 2003). Intraspecific dental variations can also occur in the form of different numbers of tooth files (Compagno, 1988; Hovestadt & Hovestadt-Euler, 2013), in a number of teeth's lateral cusplets (Gudger, 1937; Sadowsky, 1969; Taniuchi, 1970) and in abnormally developed forms (Gudger, 1937; Kaneko & Goto, 2001; Raschi *et al.*, 1982). The problem of fossil identification at the species level is exacerbated by its reliance on isolated teeth (Maisey, 2012), where identifications of extinct elasmobranchs are highly dependent on the knowledge about the dental variation in extant taxa (Guinot *et al.*, 2018). On the contrary, the morphological characteristics of elasmobranch teeth at the genus level are much easier to identify (Forey *et al.*, 2004), likely explaining, at least to a certain extent, why the representation of extant genera in the fossil record is much greater than that of extant species.

In general, batoids (orders: Rhinopristiformes, Torpediniformes and Rajiformes) are underrepresented in the fossil record compared to sharks (Pimiento & Benton, 2020), with the exception of Myliobatiformes which has full representation at the family level (Figure 1b–d; Supporting Information Table S1). Fossil and extant dental plates of this order have been widely studied in the literature (*e.g.*, Adnet *et al.*, 2012; Claeson *et al.*, 2010; Reinecke *et al.*, 2011). Myliobatiformes is also one of the most diverse elasmobranch orders in today's oceans (Dulvy *et al.*, 2014) with the highest number of families per order (Figure 1b) and with the third highest diversity at the genus and species levels (Figure 1c,d). Extant families and genera of shark orders are, on the other hand, highly represented in the fossil

record. Contrary to the batoid case where the most diverse order today is also the best represented in the fossil record, the most diverse order of sharks, Carcharhiniformes, is the least represented (Figure 1). This could be due to the fact that the dental morphology among congeneric extant carcharhiniform species is generally subtle (e.g., Naylor & Marcus, 1994; Voigt & Weber, 2011). Lamniformes, which is far less speciose than Carcharhiniformes (Figure 1d), has the most complete fossil record of extant taxa across taxonomic levels (also see Pimiento & Benton, 2020). Although it is tempting to attribute the lower representation of batoids and the exceptional representation of Lamniformes to tooth size, it has been shown that size does not explain the quality of the fossil record of extant elasmobranchs (Pimiento & Benton, 2020). In the particular case of extant batoids' preservation potential, outcrop availability, sampling intensity and identification constraints could be important factors driving their underrepresentation in the fossil record. For instance, batoids have a thinner layer of enameloid (hard mineralised outer layer of elasmobranch teeth) than sharks (Cappetta, 2012), potentially influencing preservation. Similarly, assemblages with higher diversity of batoids relative to sharks usually derive from outcrops with exceptionally well-preserved conditions (e.g., Marramà *et al.*, 2018). Furthermore, although batoid elements are mostly sampled using screen washing techniques, surface collecting is the most common sampling method in elasmobranch studies, which usually results in higher abundance of shark teeth (Cappetta, 2012). In addition, batoid taxa are generally difficult to identify given the lack of diagnostic characters to define species (Schultz *et al.*, 2010). As for the overrepresentation of extant Lamniformes, this could be explained by their low extant diversity (15 species) and the readily identifiable dental morphology of its species (e.g., Shimada, 2002a, Figure 6). Regardless of the mechanisms driving the representation of the different clades, the results of this study suggest that sharks dominate the fossil record of extant elasmobranchs.

4.2 | Extant elasmobranch species have a fossil record that goes back 66 MYA

The oldest fossil record of extant elasmobranchs is that of the genus *Hexanchus*, with a FAD of 190 MYA (Supporting Information). Indeed, Hexanchiformes has been proposed to be the basal group and first order to diverge from the rest of the Squalomorphii (Barnett *et al.*, 2012; Musick *et al.*, 2004). The genus *Hexanchus* includes three extant species of deep water sharks (Compagno *et al.*, 2005), none of which are currently considered to be threatened by extinction (IUCN, 2016). In contrast, the fossil record of extant elasmobranchs at the species level extends 66 MYA, with *C. taurus* having the oldest record. This is a circumtropical, migratory, relatively large species (maximum TL = 3 m) living mostly in coral reefs and shallow waters where it feeds on smaller fishes and invertebrates (Compagno *et al.*, 2005). It is currently threatened by extinction (IUCN status = Vulnerable) as a result, mostly, of direct pressure from fisheries as its meat is used for human consumption (IUCN, 2016).

The early Eocene (c. 48 MYA) presents a peak in the number of genus-level FADs (Figure 2a). This time frame has been previously proposed as being important for the diversity of sharks, as its increased global temperatures (Zachos *et al.*, 2001) could have led to high degrees of niche partitioning, and in turn, elasmobranch diversification (Underwood *et al.*, 2016). Furthermore, the increased ocean productivity of this time has been proposed to have enabled the evolution of elasmobranch filter-feeding (Pimiento *et al.*, 2019). Conversely, much of species-level FADs occurred in the past 11 MYA, but mostly in the early Pliocene, c. 5 MYA (Figure 2d). This time frame was relatively cool compared to the rest of the Cainozoic (Zachos *et al.*, 2001) and also highly productive (Pyenson & Vermeij, 2016). Increased nearshore primary productivity during this time, specifically from the late Miocene onwards, has been linked to the evolution of giantism in cetaceans (Slater *et al.*, 2017) and could have potentially influenced the evolution of today's elasmobranch species as well. Nevertheless, it has also been proposed that significant sea level oscillations and habitat loss occurred in the late Pliocene and throughout the Pleistocene, likely resulting in the extinction of c. 10% of shark genera (Pimiento *et al.*, 2017). Regardless of the environmental factors potentially driving FAD peaks, the present data suggest that most of the extant genera represented in the fossil record have an oldest geologic occurrence around the Eocene, and most extant species around the Pliocene. Although it is tempting to use this information to make inferences about the origination times, it is widely recognised that the first appearance of an organism is rarely recorded as a fossil (Marshall, 1997; Paul, 2005; Silvestro *et al.*, 2014). As such, further analyses of *all* fossil occurrences that account for sampling and preservation biases are needed to more accurately elucidate the true origination times of extant genera and species.

The authors found no statistically significant differences between shark and batoid FAD medians (Figure 2b,e), especially at the species level (Figure 2e,f). Nonetheless, at the genus level, the range of the fossil record of extant sharks extends deeper in geologic time than that of batoids. For instance, the fossil record of extant shark genera goes c. 50 MYA further in geologic time than batoids (Figure 2b). In addition, the genera of four shark orders (Hexanchiformes, Echinorhiniformes, Squatiniformes and Heterodontiformes) are significantly older than most other orders, and the genera of one batoid order, Rajiformes, display significantly younger FADs than the six orders of sharks (Echinorhiniformes, Heterodontiformes, Hexanchiformes, Orectolobiformes, Pristiophoriformes and Squatiniformes: Figure 2c; Supporting Information Table S2). At the species level, despite the fact that the range of FADs is very similar between sharks and batoids (Figure 2e), orectolobiform shark species have significantly older FADs than all other elasmobranch orders (Supporting Information Table S3). Although rajiform species have the fourth oldest range of FADs, these are not significantly older than any other elasmobranch order.

While these results indeed point to a deeper fossil record for extant sharks, they can also be a product of the better quality of their records (*i.e.*, less affected by the Pull of the Recent; Pimiento & Benton, 2020) and their overrepresentation relative to batoids in the

fossil record (see above; Figure 1). Nevertheless, the authors' comprehensive survey of the fossil record of extant elasmobranchs provides the basis for future studies by identifying the genus and species that have the most extensive geological histories, and by showing that species currently living in oceans can be traced back as far as 66 MYA.

4.3 | Endangered shark species have the oldest fossil record

Although the analyses of this study based on the 110 extant species with a fossil record showed no significant differences in FADs among trait categories (Figure 3), they revealed that threatened species have a deeper fossil record than their not threatened or data-deficient counterparts (Figure 3a,b; Table 1). Given that species' IUCN statuses are constantly updated, often progressing to a higher-risk category (Table S9), this result is rather conservative. The authors found important differences in the distribution of species with and without a fossil record across not only threat categories but also body size types (Supporting Information Figure S1a,b; Table 1). While the majority of extant species without a fossil record are categorised as data deficient, the opposite is true when extant species with a fossil record are examined, where data-deficient species are the least represented (Supporting Information Figure S1a). Similarly, although most extant species without a fossil record are small, there are limited differences across the body size types among those that do have a fossil record (Supporting Information Figure S1b; Table 1). All other traits (*i.e.*, habitat, vertical position, maximum depth and feeding mechanism: Table 1) present no noticeable differences between the number of species with or without a fossil record across trait scores (Supporting Information Figure S1c–f). These results suggest that, despite the fact that fossil sampling tends to favour neritic sediments in warm, coastal waters (Underwood, 2006), the fossil record of extant elasmobranchs has a relatively fair representation of their current habitats, vertical positions, depth preferences and feeding mechanisms. Nevertheless, given that the analyses of this study are based on the oldest records (FADs) and not all fossil occurrences, the authors cannot rule out sampling intensity influencing the representation of ecological traits in the fossil record.

It has been shown that elasmobranchs are the most evolutionary distinct vertebrate group; that is, they have the longest branches on their path to the root of their tree of life (Stein *et al.*, 2018). This means that the extinction of elasmobranch species could result in the loss of millions of years of evolutionary history. Yet, elasmobranchs are also one of the marine groups facing the highest extinction risk today, with *c.* 30% of their species being threatened (Dulvy *et al.*, 2014). Notably, threatened elasmobranch species are, on average, more evolutionarily distinct than not threatened species (Stein *et al.*, 2018). Furthermore, among the global marine megafauna (>45 kg of body mass), elasmobranchs are predicted to face the largest taxonomic and functional losses in the next century (at least *c.* 20% and 45%, respectively; Pimiento *et al.*, 2020). Elasmobranchs are therefore a group in urgent need for conservation. Although the

portion of extant species with a fossil record is by no means a representative sample of the global elasmobranch diversity (10%: Figure 1), it is interesting to note that 50% of threatened species with a fossil record (16 of 32) are among the most evolutionary distinct chondrichthyans (Stein *et al.*, 2018; Supporting Information Table S9). With a fossil record of at least *c.* 12 MYA, *P. pristis* is one of the most evolutionary distinct elasmobranch (Stein *et al.*, 2018). This is also a critically endangered species mainly because of by-catch in the fishing industry, habitat modification and pollution (IUCN, 2016). *C. taurus*, the species with oldest fossil record (*c.* 66 MYA), is the nineteenth most evolutionary distinct species (Stein *et al.*, 2018) and is currently vulnerable to extinction because of overfishing (IUCN, 2016).

It has been previously proposed that large sharks are not only the most evolutionary distinct, but also at greater risk of extinction (Dulvy *et al.*, 2014; Stein *et al.*, 2018). Interestingly, five of the species with a fossil record which are considered threatened by IUCN are also giants (>6 m of TL: Pimiento *et al.*, 2019): the largetooth sawfish *P. pristis*, the whale shark *R. typus*, the basking shark *Cetorhinus maximus* Gunnerus 1765, the great white shark *Carcharodon carcharias* L. 1758 and the great hammerhead *S. mokarran* (Supporting Information - Table S9). All these species are among the most functionally unique and specialised elasmobranchs within the global marine megafauna (Pimiento *et al.*, 2020; Supporting Information Table S9). The other four extant giants also have a fossil record but are not threatened (*i.e.*, the Greenland shark *Somniosus microcephalus* Bloch & Schneider 1801, the megamouth shark *Megachasma pelagios* Taylor, Compagno & Struhsaker 1983 the goblin shark *Mitsukurina owstoni* Jordan 1898 and the tiger shark *Galeocerdo cuvier* Péron & Lesueur 1822) or data deficient (*i.e.*, the bignose Shark *Carcharhinus altimus* Springer 1950; IUCN, 2016; Pimiento *et al.*, 2019).

Different conservation metrics have been proposed to preserve the most evolutionary distinct and endangered elasmobranchs (EDGE; Stein *et al.*, 2018) and the most functionally unique, specialised and endangered ones (FUSE; Pimiento *et al.*, 2020). These and future conservation efforts could be aided by the rich fossil record of the long-lived elasmobranch group. For instance, the deep fossil record of threatened species (or genera, or family) could be used to trace their responses to environmental change in the past (*e.g.*, shifts in distribution, use of refugia and recovery times). Such information could be incorporated in current conservation metrics (*e.g.*, as an additional variable) to add a deep-time dimension to prioritisation. Nonetheless, to be able to do so, first it is necessary to know what species do have a fossil record and how far does it go. This level of understanding could reveal, at least preliminary, which elasmobranch species could be the candidates to link the geological record with conservation. This study shows that the fossil record of extant elasmobranch species is scarce relative to higher taxonomic ranks. As such, its potential to provide a deep-time perspective to conservation is limited to 10% of the elasmobranch diversity. Nevertheless, the authors' analyses show that extant species, and particularly those currently threatened, span deep into geological time. For instance, the extinction of threatened sand tiger shark (*C. taurus*) which has a fossil record that extends to *c.* 66 MYA, spanning the entire Cenozoic Era, would result in a loss of

the entire genus *Carcharias* and family Carchariidae (Stone & Shimada, 2019), and therefore, million years of evolutionary history. As such, the fossil record of this particular species represents an ideal case study to explore the potential links between the fossil records and conservation.

In sum, despite the fact that many fossil elasmobranchs have living representatives and that the fossil record of modern clades extends deep in geologic time (Cappetta, 2012), this study represents the first comprehensive survey specifically analysing the representation and extent of extant elasmobranchs in the geologic record. When taken together, the results of this study reveal that the fossil record of living elasmobranchs is dominated by sharks and extends as far as 190 MYA at the genus level (*Hexanchus*) and 66 MYA at the species level (*C. taurus*). Importantly, among all elasmobranchs assessed by IUCN, species facing the highest extinction risk today have the oldest fossil record, and as such, their geological history holds great potential to provide a deep-time perspective to conservation.

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AUTHOR CONTRIBUTIONS

Catalina Pimiento and Kenshu Shimada conceived the idea; Adele Paillard and Kenshu Shimada compiled the data; Kenshu Shimada evaluated the data; Catalina Pimiento and Adele Paillard analysed the data and Catalina Pimiento and Adele Paillard led the writing with input from Kenshu Shimada.

ORCID

Catalina Pimiento  <https://orcid.org/0000-0002-5320-7246>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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