ANNUAL REVIEWS

Annual Review of Earth and Planetary Sciences

Diving Deeper: Leveraging the Chondrichthyan Fossil Record to Investigate Environmental, Ecological, and Biological Change

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Annu. Rev. Earth Planet. Sci. 2025. 53:8.1–8.28

The *Annual Review of Earth and Planetary Sciences* is online at earth.annualreviews.org

https://doi.org/10.1146/annurev-earth-040523-010455

Keywords

extinction, shark, morphology, isotope, diversity, paleobiology

Abstract

The extensive chondrichthyan fossil record spans 400+ million years and has a global distribution. Paleontological studies provide a foundation of description and taxonomy to support deeper forays into ecology and evolution considering geographic, morphologic, and functional changes through time with nonanalog species and climate states. Although chondrichthyan teeth are most studied, analyses of dermal denticle metrics and soft tissue imprints are increasing. Recent methodological advances in morphology and geochemistry are elucidating fine-scale details, whereas large datasets and ecological modeling are broadening taxonomic, temporal, and geographic perspectives. The combination of ecological metrics and modeling with environmental reconstruction and climate simulations is opening new horizons to explore form and function, demographic dynamics, and food web structure in ancient marine ecosystems. Ultimately, the traits and taxa that endured or perished during the many catastrophic upheaval events in Earth's history contribute to conservation paleobiology, which is a much-needed perspective for extant chondrichthyans.

- The longevity and abundance of the chondrichthyan fossil record elucidates facets of ecological, evolutionary, and environmental histories.
- Though lacking postcranial, mineralized skeletons, dental enameloid and dermal denticles exquisitely preserve morphology and geochemistry.
- Technical advances in imaging, geochemistry, and modeling clarify the linkages between form and function with respect to physiology, diet, and environment.
- Conservation efforts can benefit from the temporal and spatial perspective of chondrichthyan persistence through past global change events.

1. INTRODUCTION

Chondrichthyes (sharks, skates, rays, and chimeras) originated and persisted since the Paleozoic (Gardiner & Schaeffer 1989, Gardiner et al. 2005, Turner 2004) despite global climate change and mass extinction events, indicating that their carnivorous and aquatic traits are a successful evolutionary strategy. The earliest remains are fragments from stem group Chondrichthyes that are found in the Early Silurian [443.8–433.4 million years ago (Ma)] with potential evidence extending to the Middle Ordovician (470.0–467.3 Ma) (Schnetz et al. 2024). Because chondrichthyans have cartilaginous skeletons with high organic content and poor preservation, there are challenges to studying this group compared to other vertebrates. The primary body fossils preserved are teeth and dermal denticles (**Figure 1*b*,*f***), which provide abundant and diverse records similar to invertebrates made of carbonate, phosphate, or silicate. In contrast to invertebrates, chondrichthyans shed mineralized elements continuously throughout their lives, which persist due to their chemical composition in the fossil record and are therefore abundant, although shedding rates vary between tooth (e.g., teeth versus plates) or denticle type (e.g., small and thin versus large and robust) as well as among species (Botella et al. 2009, Dillon et al. 2022, Maisey 2012). Most chondrichthyan fossil studies rely on preserved teeth for taxonomical and descriptive analyses, but recent studies are analyzing denticles from deep-sea and coral reef sediments to elucidate community structure and abundance (Dillon et al. 2021, Sibert & Rubin 2021, Sibert et al. 2016). While much rarer, there are even early fossils of soft tissues, such as the 394 Ma braincase of a chondrichthyan revealed via computerized tomography (CT), a methodology with minimal destruction (Maisey & Anderson 2001) (**Figure 1*c***). The chondrichthyan fossil record is patchy, so paleoecologists employ methods from ecology to understand uncertainties in their estimates of abundance and discovery of diversity. The rich paleontological literature and fossil archives of Chondrichthyes provide a foundation for advancing paleoecology using morphology (e.g., Bazzi et al. 2021a,b; Dillon et al. 2021; Sibert & Rubin 2021), geochemistry (e.g., Li et al. 2024, McCormack et al. 2022, Tütken et al. 2020), ecological metrics (Whitenack et al. 2022), and computational models (e.g., Kim et al. 2020, 2022) to elucidate linkages between diet and habitat across temporal and spatial scales (**Figure 1**).

The fossil record offers glimpses of how communities and taxa responded to past periods of climate change (e.g., Finnegan et al. 2024, Harnik et al. 2012). Although taphonomy usually results in coarse temporal resolution, the temporal scope accommodates evolutionary processes without human influences whose signal is now pervasive throughout all ecosystems. The primary threat to extant sharks today is human fishing, followed by other human-induced changes such

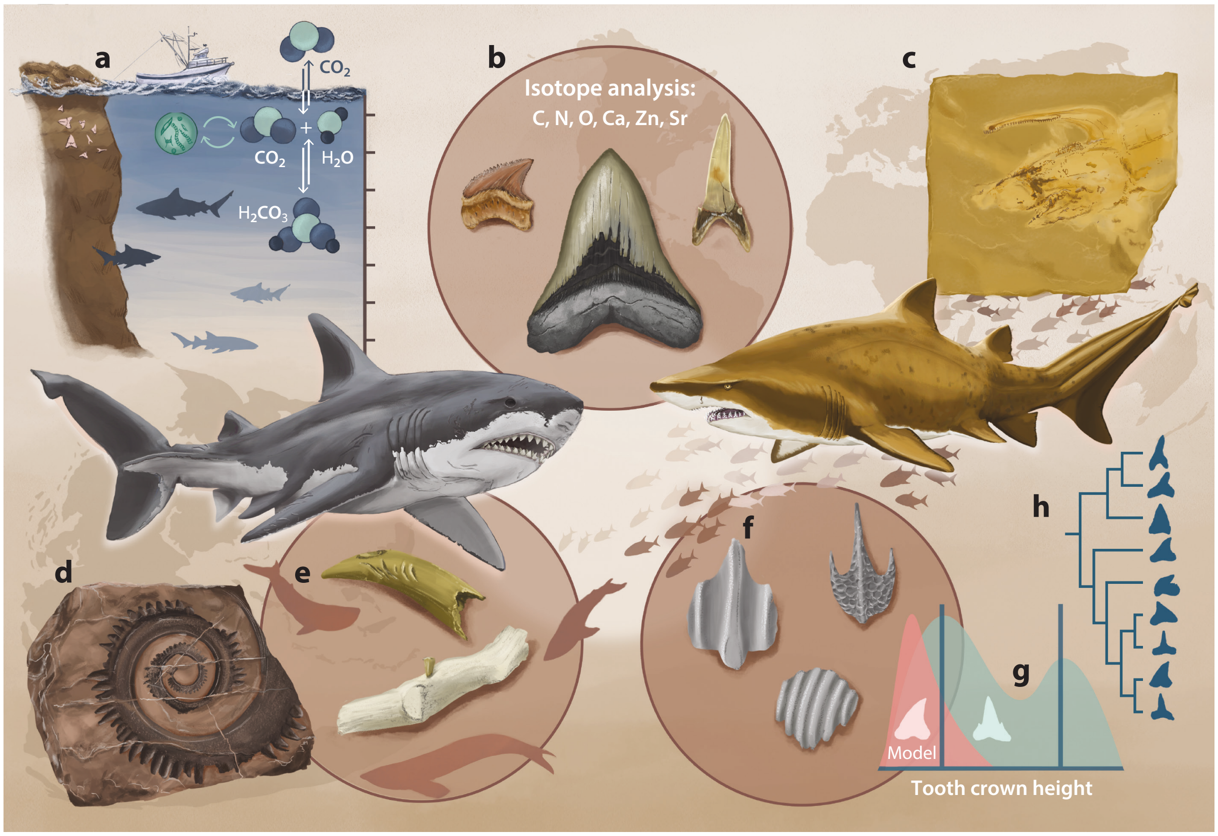

Figure 1

The chondrichthyan fossil record includes soft and hard tissues that preserve ecological and evolutionary details in their morphology, chemistry, abundance, and diversity. This conceptual diagram includes (*a*) a schematic of modern ocean systems and notes major drivers of change, including commercial fishing and ocean acidification, which are affecting chondrichthyan ecology. Some approaches to studying chondrichthyan paleoecology include (*b*) isotopic analyses of fossil teeth to reconstruct environmental conditions and trophic position (as listed in **Table 2**); morphology from body fossils, such as (*c*) *Damocles* body fossil from the Bear Gulch lagerstätte or (*d*) iconic *Helicoprion* tooth whorls from the Paleozoic; trace fossils, such as (*e*) bite marks from preserved bones and teeth of marine megafauna (USNM 391894; USNM 391896); and emerging patterns from (*f*) dermal denticles that vary in shape, diversity, and distribution. The empirical results generated from fossil chondrichthyan material can also be compared to model outputs, simulating environmental conditions or (*g*) demographic dynamics. Ecological inferences within a (*h*) phylogenetic context (depicted here with representative tooth silhouettes after Whitenack et al. 2011) can provide insights to important constraints and pressures during chondrichthyan evolution, an important facet of conservation paleobiology as chondrichthyan populations continue to dramatically decline.

as habitat loss, pollution, and climate change (Dulvy et al. 2014, Pacoureau et al. 2021, Sherman et al. 2023) (**Figure 1*a***). These modern ecological studies take place over years or decades where human fishing may be the dominant force, but the impacts of climate change may be apparent over millennia. Further, the evolutionary history of chondrichthyans indicates ecological plasticity and resilience evidenced by survival through four or five mass extinction events [depending on their origin during the Ordovician or Silurian (Schnetz et al. 2024)]. However, most paleobiological studies on chondrichthyans are temporally, spatially, and/or taxonomically limited and do not leverage this long-lived, ecologically resilient group to explore questions that are macroecological and macroevolutionary in scope. These initial studies are critical case studies to establish new approaches that offer proof of concept with geochemistry, morphology, ecological metrics, and/or modeling methods. We anticipate future studies to integrate environmental (i.e., temperature, salinity, oceanography) and biological (i.e., diet, movement, distribution, diversity) factors as well as collaborations to combine methodologies and explore greater spatial, temporal, and taxonomical scope (**Figure 2**).

The abundance and distribution of fossil chondrichthyan teeth have enormous potential for paleobiological studies. While chondrichthyans have cartilaginous skeletons with low preservation potential, there is a rich dental record due to the abundance of teeth produced and their mineral-heavy composition. Chondrichthyan enameloid is largely fluorapatite [$Ca_5(PO_4,CO_3)_3(OH,F,CO_3)$; often referred to as bioapatite or hydroxyapatite] and less than 5% organic material, while dentine is approximately 20% organic material (Chen et al. 2014). Both teeth and denticles have a very similar layered structure, with a hard enameloid on the outside surrounding a layer of dentine around a central pulp cavity (Cooper et al. 2023, Whitenack et al. 2022). In addition, taphonomic processes often concentrate marine fossil material, integrating across individuals and time within sediments. Although stratigraphic sequences and absolute ages are often difficult to decipher for fossiliferous sediments, there is opportunity to make temporal, spatial, and taxonomical comparisons in relation to global climate change. A higher-resolution approach with finer detail but less temporal range is to examine lagerstätte that preserve entire marine communities, including chondrichthyans (see Section 3). The richness and diversity of the chondrichthyan fossil record are unique among vertebrates, and many of the approaches to study molluscs, mammals, and microfossils can be adapted to inspire future paleobiological studies (**Figure 1**). Following a brief introduction to chondrichthyan evolution, we explore approaches to leverage the fossil record and highlight advances to learn more about past environmental, ecological, and biological change. We then address human-induced concerns, ecological responses, and paleobiological results to highlight how the chondrichthyan fossil record can be leveraged for conservation outcomes (**Figure 3**).

2. A BRIEF HISTORY OF CHONDRICHTHYAN EVOLUTION

Traditional paleontological studies of Chondrichthyes consider only the taxonomic occurrences of particular species in space and time. This approach created a robust qualitative, albeit temporally and spatially patchy, record of chondrichthyan evolution stretching back well over 400 Ma (Cappetta 2012, Ginter et al. 2010). However, chondrichthyans do not exist in taxonomic isolation and are intimately connected to the structure and function of the ecosystem that supports them. In addition, chondrichthyans are higher-order consumers with some highly mobile taxa. They occupy meso- to apex predator roles within their ecosystems, which also changes with ontogeny and seasonality. Therefore, small changes in environmental condition or ecosystem structure may reverberate through the food web with disproportionate impacts, driving evolutionary processes that can be observed in the fossil record. Thus, the evolutionary history of chondrichthyans, in addition to providing insights into the tempo and mode of evolutionary processes of this clade, can be an indicator of underlying changes in environment and ecosystem dynamics through time. Further, changes in the relative and absolute abundance of different chondrichthyan fossils, even without major changes in taxonomic diversity, can be an indicator of underlying bottom-up paleoecological and paleoenvironmental processes. Finally, the fossil record allows a unique window into not only the timing of evolutionary events but also the long-term variability of shark abundance and diversity, providing a baseline for understanding the impact of anthropogenic environmental and ecological changes on shark populations and biodiversity today.

The Chondrichthyes clade is generally considered to be monophyletic, based on both morphological and molecular analyses (Coates et al. 2018, Grogan et al. 2012, Heinicke et al. 2009,

(*Caption appears on following page*)

Figure 2 *(Figure appears on preceding page)*

Teeth and distribution maps for (*top*, *clockwise*) *Rhinoptera bonasus* (cownose ray) (IUCN SSC Shark Spec. Group 2018), *Carcharhinus leucas* (bull shark) (IUCN SSC Shark Spec. Group 2020a), *Squalus acanthias* (dogfish shark) (IUCN 2019), *Ginglymostoma cirratum* (nurse shark) (IUCN SSC Shark Spec. Group 2020b), and *Heterodontus francisci* (horn shark) (IUCN 2009). All species are categorized vulnerable by the Internation Union for Conservation of Nature (IUCN) except *H. francisci*, which is categorized as data deficient (IUCN 2014). The scale bar is reference for chondrichthyan body sizes.

Naylor et al. 2012, Sorenson et al. 2014, Stein et al. 2018). Stem groups arose in the early Paleozoic (at least 443 Ma), and descendants of these early chondrichthyans split between (stem) Holocephali (Petalodontiformes, Iniopterygiformes, Eugeneodontia) and Elasmobranchii. Extant chondrichthyans currently are the Holocephali (Euchondrocephali) and the Elasmobranchii, which consists of the superorders Selachii, commonly referred to as sharks (and including the extinct form Synechodontiformes), and Batoidea, composed of skates, rays, and sawfish

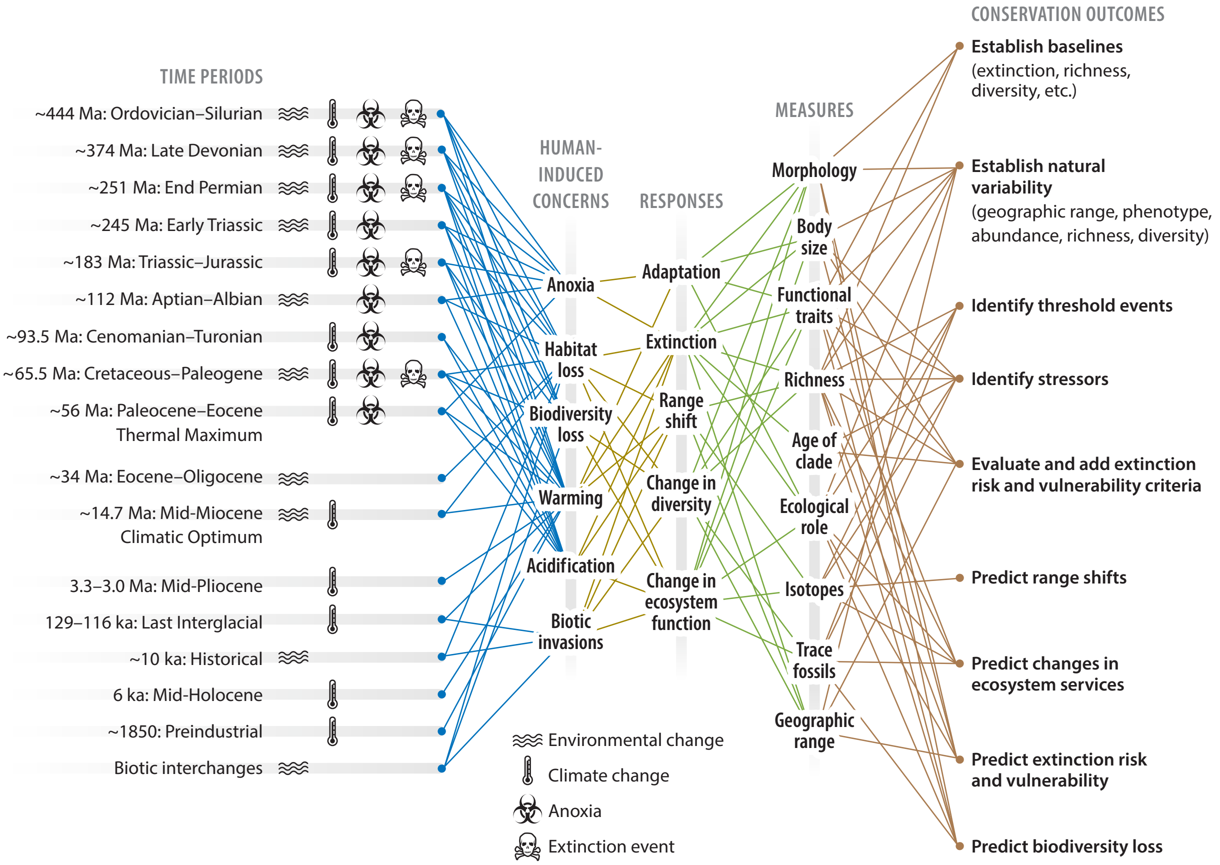

Figure 3

Linking paleobiological studies on sharks to conservation initiatives. The time periods and conservation concerns are an amalgamation of previous studies, including Finnegan et al. (2024), Harnik et al. (2012), Burke et al. (2018), Dillon & Pimiento (2024), Kiessling et al. (2019, 2023), Pimiento & Antonelli (2022), and Dietl et al. (2015), with examples of measures from this review. The recovery from the Ordovician–Silurian mass extinction was just before stem chondrichthyans originated. Examples of marine biotic exchanges include transatlantic interchanges during the Pliocene (Lindberg 1991), the opening of the Bering Strait and subsequent circulation changes (known as the Great Trans-Arctic Interchange), the opening of the Drake Passage, and the start of the Antarctic Circumpolar Current (Vermeij 1991).

Table 1 Potential number of localities for chondrichthyan fossils (potential number of lagerstätte sites indicated in parentheses)

Taxonomic level	Paleozoic	Mesozoic	Cenozoic
Stem Chondrichthyan	247 (14)	20 (0)	0 (0)
Stem Holocephalii	167 (5)	5 (0)	0 (0)
Holocephalii	762 (9)	107 (6)	42 (2)
Hybodontiformes	51 (0)	479 (43)	4 (0)
Batoidea	0 (0)	307 (41)	371 (5)
Selachii	6 (0)	500 (25)	759 (5)

Occurrence data are from the Paleobiology Database (PaleoBioDB; **https://paleobiodb.org/#/**). Localities are defined as a formation, site, or collection, where the broadest unit is used. The number of lagerstätte are the number of localities explicitly reported and defined as such (i.e., conservation or concentration) in PaleoBioDB. Lagerstätte mentioned in this review were checked and added if not already reported (e.g., Bear Gulch and Cleveland Shale). Taxonomic groupings are discussed in Section 2. Both finer-scale taxonomy and geologic scale are available, suggesting these numbers are a gross underestimation of possible assemblages ripe for research. Data, scripts, and methods for coding of taxonomy, localities, geologic eras, and lagerstätte are available at **https://doi.org/10.5061/dryad.qnk98sfsh**.

(Nelson et al. 2016). The sharks, skates, and rays of the Elasmobranchii dominate both the biodiversity and ecological diversity of modern Chondrichthyes, with over 1,400 species across 70 families inhabiting nearly all marine environments (Nelson et al. 2016). Today, the Holocephali have only 59 species across 3 families (Fricke et al. 2024) and are primarily restricted to the deep sea (Didier 2004). The number of fossil localities containing chondrichthyans varies, especially when considering time and lagerstätte distribution (**Table 1**).

Both extant chondrichthyan groups (Holocephali and Elasmobranchii) have fossil records spanning 400+ Ma into the Devonian Period; however, they represent only a small fraction of the chondrichthyan diversity that has existed on the planet. Paleozoic chondrichthyans displayed a much larger range of habitats and body plans than extant chondrichthyans and were taxonomically more significant and diverse with an additional six superorders thriving in Paleozoic ecosystems (Cappetta 2012, Ginter et al. 2010, Grogan et al. 2012, Nelson et al. 2016). For example, Paleozoic sharks inhabited freshwater lake and river habitats, as well as brackish and saltwater systems. Further, they filled a wide array of ecological niches, from small primary consumers to large predators. While most Paleozoic chondrichthyans did not persist through the Mesozoic Era and were outcompeted by the rapidly diversifying ray-finned fishes, the Hybodontiformes survived through the Cretaceous and became restricted to freshwater environments, while the Holocephali and Elasmobranchii dominated saltwater assemblages. Although the diversity of chondrichthyan body plan and ecological niche in the Cenozoic is considerably diminished from their height in the Paleozoic, chondrichthyans play an ecologically significant role as predators in marine ecosystems today (Ferretti et al. 2010), and their declines in recent years due to overfishing have disrupted marine food webs across a wide range of habitats (Dulvy et al. 2021, Robbins et al. 2006). These major shifts in shark diversity have been driven both by mass extinctions (e.g., Guinot & Condamine 2023, Guinot et al. 2013, Kriwet & Benton 2004) and by smaller but no less influential shifts in habitat availability, prey type, and marine ecosystem composition changes throughout Earth's history (Carrillo-Briceño et al. 2018, Heinicke et al. 2009, Pimiento et al. 2017, Underwood 2006).

Indeed, while chondrichthyans do have significant turnovers at mass extinction events, they also have significant background evolutionary turnover throughout the Phanerozoic that could be driven by a wide array of factors including environmental variability or habitat loss that can shift ecological niches and disproportionately impact consumers and predators (e.g., Benson et al. 2021, Monarrez et al. 2021, Pimiento & Balk 2015; reviewed in Whitenack et al. 2022).

3. MORPHOLOGY: LEVERAGING FORM AND FUNCTION

For those lucky enough to study extinct organisms that have extant relatives, we can leverage studies on extant organisms to make inferences about the form and function of extinct taxa. One of the central paradigms of anatomy is the intricate linkage between form (morphology, or the shape of the anatomical feature) and function (how it works) (e.g., Arnold 1983, Wainwright 1996). Thick shells in molluscs are helpful for protecting against predators (e.g., Vermeij 2015), the shape of a fish's body can tell us something about how it swims (e.g., Lauder 2015), and we can predict what mammals eat based on the shape of their teeth (e.g., Evans & Pineda-Munoz 2018). The existence of form-function relationships is a boon for paleobiologists, who can use morphology to glean information about how organisms lived their lives in the absence of being able to directly observe the organism.

As with many organisms, chondrichthyan soft parts, such as organs, tissues, and lightly mineralized cartilage, tend not to be preserved in the fossil record. Exceptions most often occur in lagerstätte such as the Cleveland Shale (Late Devonian, USA), Bear Gulch Limestone (Late Mississippian, USA), Solenhofen Limestone (Late Jurassic, Germany), Agua Nueva Formation (Late Cretaceous, Mexico), Bolca Konservat-Lagerstätte (Eocene, Italy), and Pisco Formation (Miocene–Pliocene, Peru) (temporal distribution noted in **Table 1**) (e.g., Ehret et al. 2009, Grogan et al. 2012, Marramà et al. 2018, Vullo et al. 2024, Williams 2001). These fossils have yielded information about potential feeding mechanisms (e.g., Lund et al. 2015, Maisey 1989, Vullo et al. 2024, Williams 2001), blood circulation (Williams 1998), diet (Williams 1990), swimming mechanics (Lund et al. 2015, Vullo et al. 2024), and more. These lagerstätte also preserve more complete information about the environment these chondrichthyans lived in, including potential soft-bodied prey items that would not otherwise be preserved.

Three-dimensional morphology reconstruction enables the study of fine details, and the widespread availability in the twenty-first century with various types of CT scanning has revolutionized paleobiology. For example, several recent studies focused on the feeding mechanics in Paleozoic chondrichthyans that may not have been possible without the use of this technology (Coates et al. 2019, Dearden et al. 2023, Frey et al. 2020). Each study leveraged CT scans of well-preserved early chondrichthyans to understand how mandibular and hyoid arch cartilages articulated and moved, which suggested likely feeding mechanisms. Understanding whether chondrichthyans are ram feeding, as proposed for the Late Devonian *Ferromirum* (Frey et al. 2020), or suction feeding, as proposed for the Middle Mississippian *Tristychius* (Coates et al. 2019) and Pennsylvanian *Inioptera* (Dearden et al. 2023), also allows paleobiologists to hypothesize potential prey items and the chondrichthyans' place in their food webs. The ram and biting feeding modes are considered more ancestral than suction feeding within chondrichthyans based on jaw shape, jaw articulation, and tooth shape (Motta & Huber 2012). A comparative approach coupled with technological advances could ultimately impact our understanding of chondrichthyan feeding behavior, evolutionary patterns, and phylogenetic relationships.

Most studies that focus on the form and function of extinct chondrichthyans are focused on teeth and feeding (e.g., Abler 1992, Ramsay et al. 2015, Whitenack & Motta 2010). Because chondrichthyans are also extant, it is common to predict the function via analogy from extant chondrichthyans (e.g., Cappetta 1987, Cooper et al. 2023, Wroe et al. 2008) (**Figure 2**). For example, modeling of extant great white shark, *Carcharodon carcharias*, jaws has been used to predict bite force in the extinct *Otodous megalodon*, a species that is known only from its teeth and occasional vertebrae (Wroe et al. 2008). Individual teeth have also been subject to analogy. Modern shark teeth tend to be placed into functional morphotypes (**Figure 1*b***)—categories that consider both morphology and putative function—and then those morphotypes are applied to extinct elasmobranch species (e.g., Cappetta 1987, 2012; Frazzetta 1988; Stahl & Parris 2004). For example, wide serrated teeth are thought to be excellent at cutting large prey items, whereas narrow long teeth are thought to be well suited for puncture (Cappetta 1987).

However, there is a wide diversity of tooth morphologies across the 400+ Ma of chondrichthyan evolution with no extant analog (e.g., cladodont-type teeth) or that do not neatly fall into these morphotypes (e.g., holocephalans). In addition, morphotypes are largely based on single teeth when in reality Chondrichthyes can be heterodont. Teeth within a jaw and between jaws work together, complicating the morphological-functional relationships based only on tooth morphology (Cohen et al. 2020). Further, biomechanical testing and modeling on extinct and extant shark teeth indicate that functional morphotypes often do not hold (Ballell & Ferrón 2021, Corn et al. 2016, Whitenack & Motta 2010) as tooth morphologies often perform multiple functions equally well. It is worth noting that only a handful of extant and extinct chondrichthyan species have been examined in this fashion, and similarly, only a few prey items (mostly teleosts) were tested in these studies. The relationship between prey and tooth morphology is also complicated. Most extant chondrichthyans are not limited to just one prey type (e.g., fish) (e.g., Cortes 1999, Martin & Mallefet 2023), and particular species within a prey type can have different biomechanical properties (Bergman et al. 2017, Whitenack & Motta 2010). There have been recent studies that seek to correlate prey items and tooth morphology using a variety of techniques (e.g., Bazzi et al. 2021b, Cooper et al. 2023), and they represent a good starting point for this line of research. Necessarily, these first forays are limited in terms of taxonomic and temporal breadth and make broad assumptions.

Further quantitative testing of tooth performance and prey mechanical and functional properties is needed, and we need to expand our work to encompass a broader scope of taxa and time. We know from studies focused on extant sharks that this is a complex and nuanced system, and we need to incorporate that complexity and nuance into our research to better understand the link between tooth morphology, function, and prey. In this context, chondrichthyan teeth—both extant and extinct—are understudied at best, and much remains to be done to truly understand these links.

4. GEOCHEMISTRY: RECONSTRUCTING ENVIRONMENT AND DIET

The chemical composition of chondrichthyan teeth preserves environmental and biological signals with paleoclimate, paleoceanography, and paleoecology significance (**Table 2**). The most common geochemical measurements on teeth are isotope composition of oxygen and strontium for water temperature and stratigraphic age, respectively. There are other isotopic systems, such as with neodymium, calcium, and uranium, to reconstruct seawater chemistry and elucidate changes in ocean circulation, carbonate deposition, and redox history, respectively. These environmental factors indirectly influenced the evolutionary history of chondrichthyans by impacting prey distribution and trophic dynamics. However, studying biological traits in extinct chondrichthyans remained elusive given the limited longevity of protein, the substrate most often used in extant diet studies. Recently, calcium, mineral-bound nitrogen, and zinc emerged as trophic level indicators preserved in enameloid (Akhtar et al. 2020, Kast et al. 2022, McCormack et al. 2022). Chondrichthyan teeth provide an opportunity to explore environmental and biological traits from

Table 2 Summary of isotope systems and indicators used in shark paleoecology to date

Isotope system	Indicator(s)	Material(s) and/or substrate(s)	Consideration(s)	Key reference(s) or review(s)
Carbon ($^{13}C/^{12}C$)	Diet + environment	Carbonate	Carbonate $\delta^{13}C$ values do not track collagen $\delta^{13}C$ values from dentine, which reflect diet, and are exceptionally ^{13}C enriched	Karnes et al. 2024
Nitrogen ($^{15}N/^{14}N$)	Diet, trophic level	Remnant organic from enameloid mineralization	Measurements from extant specimens indicate ^{15}N enrichment in enameloid-bound $\delta^{15}N$ values	Kast et al. 2022
Oxygen ($^{18}O/^{16}O$)	Ambient water temperature and $\delta^{18}O$ values (also associated with salinity)	Phosphate	Phosphate $\delta^{13}C$ is robust to alteration in the fossil record	Larocca Conte et al. 2024a, Vennemann et al. 2001
		Carbonate	Carbonate $\delta^{13}C$ in modern and fossil bioapatite may be subject to exchange	Karnes et al. 2024
Clumped (D_{47})	Temperature	Carbonate	Tracks body temperature, which often corresponds to environmental water but can be elevated for endotherms	Griffiths et al. 2023
Calcium ($^{44}Ca/^{42}Ca$ or $^{44}Ca/^{40}Ca$)	Diet + global carbonate weathering cycle	Bioapatite	Extant shark teeth have higher $\delta^{44}Ca$ values than Miocene fossil teeth; fossil shark teeth track secular trends observed in other materials over the past 100 Ma	Akhtar et al. 2020
Zinc ($^{66}Zn/^{64}Zn$)	Diet, trophic level	Bioapatite	$\delta^{66}Zn$ decreases with trophic level; fossil enameloid is ^{66}Zn depleted relative to dentine; [Zn] is highest at the fossil tooth tip	McCormack et al. 2022, 2024
Neodymium ($^{143}Nd/^{144}Nd$)	Water mass	Nd substitutes for Ca in bioapatite	Nd is incorporated from seawater and early diagenetic fluids	Tütken et al. 2011
Strontium ($^{87}Sr/^{86}Sr$)	Chemostratigraphy, fresh/brackish water habitat	Sr substitutes for Ca in bioapatite	Diagenetic Sr must be removed	Tütken et al. 2020
Uranium ($^{238}U/^{235}U$)	Marine anoxia	Dentine uptakes U and then diffuses to enameloid	Fossil enameloid is not in [U] equilibrium, and burial conditions likely affect $d^{238}U$	Li et al. 2024

a single sample. In many cases, the geochemical markers are independent indicators of complementary traits, but interpretation requires understanding some of the underlying environmental and biological processes.

4.1. Paleoceanography

Ocean temperature is often sought in climate studies given its importance to global system processes. One of the primary indicators of water temperature is stable isotope analysis of oxygen in biological minerals, such as calcium carbonate or bioapatite. Biological mineral $\delta^{18}O$ values reflect isotope composition and mineralization temperature of environmental water (Grossman & Joachimski 2020). In aquatic ectotherms, body water and temperature are considered to be in steady state with the environment (Koch 2008), but some invertebrates have vital effects where mineralization occurs in disequilibrium with ambient water (Grossman & Joachimski 2020). Most paleoceanography and paleoclimate studies focused on global dynamics rely on compiled records of foraminifera, whereas nearshore or regional studies use single localities or other invertebrate records (e.g., molluscs, brachiopods, conodonts, etc.) (Grossman & Joachimski 2020). Chondrichthyans also record marine environmental conditions in the isotope composition of enameloid, which has similar mineralogical properties to enamel.

Enameloid carbonate is analogous to calcium carbonate from invertebrates but used less frequently in paleoceanography and paleoclimate studies. Although bulk carbonates are straightforward to prepare and analyze, derived paleotemperature estimates are not reliable because fractionation processes associated with chondrichthyan enameloid remain enigmatic (Karnes et al. 2024) (see Section 4.2). An alternative carbonate paleothermometer is clumped isotopes (Δ_{47}), where the proportion of heavy isotopes (e.g., ^{18}O and ^{13}C) bound in CO_{3-} is purely temperature dependent (Eiler 2011). Clumped isotope compositions therefore reflect the formation temperature of enameloid and should be in equilibrium with local water temperature for most chondrichthyans. The exceptions are species that are partially endothermic, such as some extant Lamniformes, such as the great white shark, *C. carcharias*. Clumped isotope analysis has also revealed elevated body temperatures for fossil *O. megalodon*, the megatooth shark, similar to *C. carcharias* and Mysticetes (Griffiths et al. 2023). While clumped isotopes are a reliable paleothermometer and can detect endothermy, the low carbonate content (~1–2%) of chondrichthyan enameloid requires large sample quantities that require collating multiple small teeth for a single analysis.

In addition to carbonate, chondrichthyan bioapatite contains oxygen within phosphate that is more robust against diagenetic alteration (Kohn & Cerling 2002), but accurate and precise measurements remain a challenge, but a recent methodological study may improve future analyses. The $\delta^{18}O$ value of enameloid phosphate is often analyzed as silver phosphate, which precipitates best from pure bioapatite. However, many chondrichthyan teeth are very small, and enameloid cannot be reliably separated from dentine (see examples in **Figure 2**); therefore, until recently, stable isotope analysis has been limited to larger teeth. Larocca Conte et al. (2024b) adapted the methods to use an anion exchange resin to isolate phosphate in solution and prevent contamination from organic matter (i.e., altered dentine), facilitating analysis of small fossil teeth and denticles. Further, this study highlighted the effects of silver carbonate on analytical uncertainty (Larocca Conte et al. 2024b), which will enable analysis of more taxa with smaller teeth [i.e., chondrichthyans inhabiting benthic habitats (Larocca Conte et al. 2024a)]. Characterizing the temperature range for specific chondrichthyan species at a locality can indicate thermal gradients (Zacke et al. 2009), while comparisons through time can elucidate habitat preference and indicate fundamental versus realized niche (reviewed in Whitenack et al. 2022). While carbonate and phosphate analyses of chondrichthyan enameloid are long-standing, how these results are considered within paleoceanographic and paleoecological contexts is being refined with Bayesian modeling

(Kim et al. 2014), climate simulations (Kim et al. 2020), and extant shark teeth as interpretative frameworks (**Figure 2**).

The chemistry of fossil chondrichthyan teeth records paleoceanographic conditions in heavy isotope systems, such as calcium, neodymium, strontium, and uranium. Calcium isotopes reveal the chemical weathering fluxes between carbonate and silicate rocks on a global scale. Although often measured from calcium carbonates, there are concerns with diagenetic alteration or exchange and biological effects. Chondrichthyans incorporate calcium during the mineralization process, and there is limited exchange postmortem. However, there is also isotopic fractionation with biological processes that associate calcium isotope composition with trophic level (Akhtar et al. 2020). In contrast, neodymium, strontium, and uranium isotopes are incorporated postmortem as calcium exchanges with sediment porewater, and there is some replacement within the bioapatite (reviewed in Li et al. 2024, Whitenack et al. 2022). Isotope systems record different paleoceanographic facets depending on their input sources and fluxes to oceans as well as processes dictating isotopic fractionation. For example, neodymium isotopes track ocean currents and circulation, whereas strontium isotopes discern freshwater inputs or chemostratigraphic dating (reviewed in Whitenack et al. 2022). In contrast, uranium isotopes (δ^{238}U) indicate marine anoxia, as the efficiency of U removal is dependent on oxygen availability and ^{235}U is preferentially buried in sediments (reviewed in Li et al. 2024). Recently, chondrichthyan enameloid was explored as a substrate for U isotopes, and variation among localities suggests congruency between δ^{238}U values in porewater and enameloid (Li et al. 2024). The exquisite preservation of chondrichthyan teeth in the fossil record combined with the relatively large sample size—in terms of specimen size and sample abundance—make them excellent targets for developing geochemical indicators for environmental signals. However, there are some unique biological considerations dictating the biochemical processes and isotopic fractionation of chondrichthyan tissues, which are important for paleoecological interpretations.

4.2. Biological Considerations

Paleoecological application of stable isotopes flourished with mammals where oxygen tracks the hydrological system and carbon serves as a dietary indicator; however, carbonate isotopes from chondrichthyan enameloid indicate different processes and mechanisms that impede ecological interpretation. For example, carbonate and phosphate oxygen are thought to reflect body water with temperature-dependent isotopic fractionation, which would result in a constant offset between δ^{18}O values of carbonate and phosphate. This isotopic spacing (~8‰) is fairly well constrained for mammalian bioapatite, and deviations are considered an indicator of diagenetic alteration (Koch 2008, Kohn & Cerling 2002). In contrast, shark teeth have larger and more variable differences in carbonate and phosphate δ^{18}O values (9–11‰) (Kocsis et al. 2007, Vennemann et al. 2001). A comparison across 5 extant families, including 18 species and 8 localities (including captive individuals), revealed low correlation in carbonate versus phosphate δ^{18}O values, suggesting chondrichthyan enameloid mineralization differs from mammalian enamel (Karnes et al. 2024).

Carbon isotope values of carbonate reinforce the uniqueness of chondrichthyan enameloid mineralization. Carbon in dental collagen and carbonate of mammals are sourced from diet, and the protein and mineral carbon isotope offset varies with diet classification and digestive physiology (Codron et al. 2018). The dental collagen from extant chondrichthyans has a similar distribution to other soft tissues (e.g., blood, muscle, etc.), which reflects diet (Karnes et al. 2024, Kim et al. 2012, Zeichner et al. 2017), but enameloid carbonate is substantially ^{13}C enriched (Karnes et al. 2024, Vennemann et al. 2001) compared to all biological sources that range from −60 to 4‰ in methanogenic pathways (Conrad 2005) to coral structures (Meibom et al. 2006), respectively. Aquatic ectotherms are known to incorporate both respired CO_2 from diet and dissolved inorganic carbon from ambient water into calcium carbonate (Chung et al. 2019) but not bioapatite. Karnes et al. (2024) noted the carbonate and collagen $\delta^{13}C$ offset varies with carbonate, but not phosphate, $\delta^{18}O$ values. This incongruity in comparing phosphate and carbonate $\delta^{18}O$ values suggests kinetic rather than thermal equilibrium processes and different mineralization mechanisms or processes from mammals (Karnes et al. 2024). Finally, the correlation between carbonate-collagen $\delta^{13}C$ offset to carbonate $\delta^{18}O$ values is preliminary but significant; understanding this relationship could provide insight to facets of past marine ecosystems, such as $p\text{CO}_2$ and alkalinity (**Figure 1**).

Many extant chondrichthyans are known to migrate, which would affect the biological and environmental conditions recorded in their teeth in vivo. There are diurnal (e.g., cookiecutter shark, *Isistius brasiliensis*), seasonal (e.g., great white shark, *C. carcharias* , and sand tiger, *Carcharias taurus*), and ontogenetic (salmon shark, *Lamna ditropis*, and great white shark, *C. carcharias*) movement patterns that affect diet and $\delta^{18}O$ values of teeth (e.g., Kim et al. 2014, McCormack et al. 2023). Because chondrichthyan teeth are formed and mineralized before eruption, there is a time lag as a tooth transitions to the functional position (Zeichner et al. 2017). For migratory taxon, this time lag results in a mismatch between the signal recorded in enameloid and fossil locality. Past studies attributed $\delta^{18}O$ values and variation to the possibility of migration, including brackish and freshwater systems (e.g., Fischer et al. 2011, Kim et al. 2014, Kocsis et al. 2009, Vennemann & Hegner 1998), but interpretation or hypotheses were limited. One possibility is to track the variation in $\delta^{18}O$ values and discern residents versus migratory taxa, similar to approaches using stable isotope analysis to track diet. Another approach uses isotope-enabled climate simulations [e.g., isotope-enabled version of the Community Earth System Model (iCESM) (Zhu et al. 2020)] to predict bioapatite $\delta^{18}O$ values (Kim et al. 2020) or assemble an isoscape. Comparisons among taxa, including invertebrate and vertebrate taxa in different habitats within a region, could reveal seasonal or spatial heterogeneity within a geographical range (Larocca Conte et al. 2024a). Although spatial resolution is limited in global climate models, an analysis across the community could provide insight to how chondrichthyans coped with past environmental and biological change, especially with respect to ecological plasticity and trait conservation over timescales relevant for evolution.

4.3. Emerging Trophic Indicators

Diet is a central but elusive ecological trait often sought in paleobiology. Carbon isotope composition varies by productivity regime in marine ecosystems with subtle differences (1–3‰) with coastal proximity, depth, upwelling, and latitude. Modern ecological studies often report $\delta^{13}C$ values from organic substrates, but the largest differences in marine ecosystems are from terrestrial inputs (Kohn & Cerling 2002). Modern ecological studies focus on $\delta^{15}N$ values as a trophic level indicator, which has implications for food web dynamics. Chondrichthyans vary in trophic positioning from meso- to apex predator; insight into diet variation and trophic positioning through Earth's history would provide context for conservation and management. Today, all ecosystems are impacted by human activity, and the realized niche may be an artifact of human activity. Further, trophic level is an important trait to capture for species and compare within a community, among populations/localities, and through time. There are promising trophic indicators, such as calcium, mineral-bound nitrogen, and zinc isotopes, with recent applications on chondrichthyan enameloid.

Modern systems study trophic level using nitrogen isotopes from protein, but this organic substrate degrades quickly during fossilization and rarely preserves in specimens over 1 million years old (Clementz 2012). Biominerals, such as carbonate and apatite, contain and preserve trace organics (reviewed in Whitenack et al. 2022). The first study to analyze enameloid-bound (EB) $\delta^{15}N$ values explored the interplay between diet and gigantism within the *Otodus* lineage that includes the charismatic *O. megalodon* (Kast et al. 2022). Although a plethora of ecological studies with chondrichthyan soft tissue provides an interpretive framework for $\delta^{15}N_{EB}$ values, the results from *O. megalodon* were exceptionally high compared to extant fish, sharks, and marine mammals (Kast et al. 2022). Potential explanations include a 1.5‰ offset between EB and dental collagen $\delta^{15}N$ values, elevated baseline $\delta^{15}N$ values, or additional trophic levels in ancient ecosystems (Kast et al. 2022). Given this uncertainty with interpretative implications, studies to date featuring EB $\delta^{15}N$ values took a comparative approach. For example, baseline differences between localities and time were accommodated by comparing $\delta^{15}N_{EB}$ values of *Otodus* and co-occurring piscivorous sharks to discern trophic level (Kast et al. 2022). Another study established trophic segregation between lamniforms and hybodontiforms at a Late Cretaceous locality (Comans et al. 2024), which contrasts with the generalist classification and niche redundancy often assumed for chondrichthyan communities (e.g., Cortes 1999). Additional $\delta^{15}N_{EB}$ measurements from extant chondrichthyans spanning trophic levels, habitats, and locality would allow for a more robust interpretative framework, but the analytical complexity is a constraint. We encourage future interdisciplinary collaborations that include geochemists, paleobiologists, and modern ecologists.

Other potential diet indicators are calcium and zinc isotopes, but these are not regularly used in modern ecology, so the frames of reference for mechanisms and interpretation are in progress. Calcium and zinc are essential minerals for key biological functions, especially related to bioapatite mineralization; however, the metabolic processes dictating isotopic fractionation in chondrichthyans are not fully characterized. In both isotope systems, the lighter isotope is preferentially incorporated into mineralized tissues resulting in lower calcium and zinc isotope values with trophic level (reviewed in Martin et al. 2015, McCormack et al. 2022). The resistance of chondrichthyan enameloid to diagenesis preserves calcium, and zinc isotope signals make them promising trophic indicators across other taxonomic systems.

The recognition of calcium isotopes as a trophic indicator resulted from exploratory sampling from modern and ancient marine ecosystems (Clementz et al. 2003, Skulan et al. 1997). There is limited variation in calcium isotope composition of modern seawater that serves as the source of Ca to all bioapatite in marine organisms (Martin et al. 2015). Calcium intake primarily occurs through diet rather than seawater absorption given the association with trophic level, but there are baseline or source effects as evidenced by the systematic shift observed in extant bull sharks, *Carcharhinus leucas* (Akhtar et al. 2020). Extant chondrichthyan enameloid demonstrates a systematic and biologically mediated ^{44}Ca depletion attributed to diet [0.14‰ $\delta^{44/42}Ca$ trophic offset (Martin et al. 2015); 0.3‰ $\delta^{44/40}Ca$ trophic offset (Akhtar et al. 2020)]. There are substantial variation and overlap among species likely related to dietary breadth, seasonal prey, and/or ontogenetic shifts (Akhtar et al. 2020, Assemat et al. 2022), but to date, there is no investigation of consumers across trophic levels or multiple specimens within an ecosystem. Calcium isotopes from geologic and biologic minerals demonstrate a secular trend over Earth's history due to changes in global silicate and carbonate weathering (reviewed in Akhtar et al. 2020). Fossil chondrichthyan enameloid also follows this secular trend, including a $\delta^{44/40}Ca$ increase over the past 100 Ma, which coincides with planktonic calcifier origination and affected carbonate balance in neritic versus pelagic habitats (Akhtar et al. 2020). We note the similar calcium isotope variation for extant and fossil chondrichthyan enameloid that suggests similarities in trophic levels present within food webs (Akhtar et al. 2020), which is in contrast to the high $\delta^{15}N_{EB}$ values from *O. megalodon*.

Zinc isotopes ($\delta^{66}Zn$) are also an emerging trophic indicator with minimal postmortem exchange and alteration during fossilization. Initial food web studies focused on mammalian diet and recognized paleoecological applications (Bourgon et al. 2020; Jaouen et al. 2013, 2016; McCormack et al. 2022). Zinc is a trace metal and, for humans, plays an important role in protein synthesis, enzyme reactions, and metabolic pathways (reviewed in Junqueira et al. 2024). There are diet-tissue δ^{66}Zn differences observed for mammals and fish spanning terrestrial and marine environments, but biochemical processes associated with trophic fractionation are not well characterized and trophic fractionation may differ for herbivores versus carnivores, including some dependence on biomineral consumption (Bourgon et al. 2020; Jaouen et al. 2013, 2016; McCormack et al. 2022, 2023). Initial studies suggested minimal baseline differences as species had similar δ^{66}Zn values despite different localities spanning time and basins (McCormack et al. 2022). However, an investigation of extant sand tiger, *C. taurus*, in the western Atlantic found substantial variation in enameloid δ^{66}Zn values that track known differences with ontogeny and sex, which also corresponded to dental collagen δ^{13}C values (McCormack et al. 2023). A comparison of Miocene–Pliocene and extant sharks (*Galeocerdo*, *Carcharhinus*, and *Carcharias*) suggests trophic level is a conserved ecological trait (McCormack et al. 2022). Further, *O. megalodon* exhibited high δ^{66}Zn variation, suggesting a wide dietary breadth and the highest trophic level in the sampled fossil localities (except North Carolina, USA, where *C. carcharodon* has similar δ^{66}Zn values) (McCormack et al. 2022). Future paleoecological studies featuring chondrichthyans can compare trophic level and variation to discern the dietary plasticity among taxa. Coupling trophic indicators with body size could also elucidate ontogenetic shifts among ancient chondrichthyans (**Figure 1**).

5. EVOLUTIONARY PROCESSES: WHAT CAN TEMPORAL PATTERNS IN CHONDRICHTHYAN FOSSILS REVEAL ABOUT ECOLOGY?

Ecological and environmental context from geochemical indicators combined with diversity dynamics offers insight into drivers of evolutionary processes. In addition to being taxonomically informative and giving insights into the drivers of chondrichthyan evolutionary processes, chondrichthyan fossil assemblages have the potential to provide information about their ecological and environmental context. As discussed above, teeth are the primary way chondrichthyans interact with their prey; therefore, shifts in tooth morphology through time may indicate changing prey type and availability (e.g., Bazzi et al. 2021b, Cooper et al. 2023). Documenting changes in tooth morphology also allows for the exploration of nontaxonomic evolutionary processes across major extinction events. For example, while there was a significant extinction of sharks at the Cretaceous–Paleogene mass extinction event (Guinot & Condamine 2023), the overall tooth assemblage morphological variation stayed relatively stable from the Cretaceous through the early Paleogene, indicating that sharks were able to maintain their ecological niche space across the extinction event (Bazzi et al. 2018). This result also suggests the prey type that sharks were consuming in greatest abundance—most likely ray-finned fishes—were able to maintain their ecological roles across the extinction event, which was independently confirmed via both fossil and genetic evidence (Alfaro et al. 2018, Sibert & Norris 2015). Sibert & Norris (2015) focused on data from all available fossils collected and explored ecological diversity with consideration of relative abundance and richness metrics. In contrast to this approach, Bazzi et al. (2018) was taxonomically restricted and focused on a subset of pelagic sharks through the end-Cretaceous mass extinction. These divergent applications of morphometrics demonstrate the potential of exploring ecological metrics of shark tooth assemblages. Future studies that consider all observed fossil teeth from a particular locality will continue to improve our understanding of the ecological roles sharks play in their ecosystems during critical intervals in Earth's history.

Dermal denticles can also provide insights into environmental or ecological shifts. Denticles—the small tooth-like scales that cover a chondrichthyan's body (**Figure 1**)—are hypothesized to perform a variety of functions, from reducing drag (e.g., Lauder 2015) to protection from abrasion (Dillon et al. 2017, Reif 1978) to improved scattering of bioluminescence (e.g., Ferrón 2023, Lourtie et al. 2022). These different morphologies indicate the potential habitat use of chondrichthyans within an environment, and therefore shifts in relative abundance of dermal denticle types can indicate shifts in behavior and habitat use through time. Further, as denticles are present in abundances that far exceed teeth, albeit at significantly smaller size fractions (Dillon et al. 2017, Sibert & Norris 2015), the absolute abundance of denticles can elucidate changes in overall chondrichthyan abundance through time, independent of taxonomic or functional diversity metrics. For example, Dillon et al. (2021) found that while overall denticle abundance declined on coral reefs over the past 7,000 years, there was a greater reduction of denticles commonly associated with drag reduction compared to other types. Chondrichthyans that engage in migratory and active swimming-based predation typically have drag-reduction-type denticles, and a selective reduction in this trait could indicate a change in prey availability. In this case, as humans entered the region, fishing pressure reduced the number of larger fish in the region, which reverberated up the food web and resulted in reduced predators of large fish (Dillon et al. 2021). Denticles can also be indicative of habitat occupation. For example, Sibert & Rubin (2021) found a major change in dermal denticle morphotype diversity in the Early Miocene, with a selective extinction of geometric-type denticles commonly associated with deep-sea taxa today. Although the cause of this extinction event is currently unknown—the time interval is relatively undersampled—the selective survival of Chondrichthyes with linear, drag-reduction denticles compared to geometric, deep-sea denticles indicates a potential shift in habitat use of oceanic Chondrichthyes away from deep-sea residency toward a more migratory lifestyle (Sibert & Rubin 2021), perhaps due to an environmental or ecological change that made deep-sea habitats less favorable. In this case, Chondrichthyes, as top predators, may serve as a proverbial canary in the coal mine that passed some kind of biological threshold driving major extinction in the group during this interval.

Tooth and denticle assemblages are powerful tools for exploring the interactions between chondrichthyan evolution and their ecological and environmental context, but we have only scratched the surface of integrating ecological and evolutionary records with paleoenvironmental processes. Future work will continue to fill these gaps and help elucidate marine predator interactions, especially within the context of changing environmental conditions (**Figure 1**). For example, a recent study explored the relationship between distributions of tooth size and nursery habitats, using a demography model that tracked migration and body size via anterior tooth height to give insights into the geographic and ontogenetic distribution of the species (Kim et al. 2022). Future ecological models could include bottom-up processes, where underlying environmental or ecological variation is implicated in the analysis of tooth and denticle assemblages. Another consideration is the top-down influence of Chondrichthyes on ecosystems as meso- and apex predators (e.g., Estes et al. 2011, Kast et al. 2022, Pimiento et al. 2017), which in turn can be used to explore questions about ecosystem resilience and function, changes in nutrient cycling, trophic level/links through time, thresholds for biodiversity shifts, and abundance shifts by predation release. Finally, global patterns in chondrichthyan abundance, distribution, and evolutionary hotspots can shed light on ecosystem dynamics in both time and space (**Figure 2**). The chondrichthyan fossil record is one of the most numerically abundant vertebrate fossil records on the planet; however, historical work has focused only on enumerating taxonomic richness from individual localities, rather than cataloging full assemblages and relative abundance data, limiting the scope of ecological questions that can be explored. With the increase in open access datasets and databases, along with efforts to improve digitization, more datasets are becoming available for paleobiological investigation, which will only deepen our understanding of chondrichthyan evolution and ecology, and interaction with the environments where these ancient predators thrived.

6. CONSERVATION: HOW DO WE PUT THE PALEO-RECORD OF SHARKS INTO ACTION FOR CONSERVATION EFFORTS?

The fossil record is full of natural experiments. A paleontological perspective on conservation contextualizes rates of change, vulnerabilities, and resilience of populations, species, communities, and ecosystems (Dietl et al. 2015, McClenachan et al. 2012). In a recent review of conservation paleobiology (CPB), only 4.3% of studies were on marine vertebrates, with a little over half on Chondrichthyes (Dillon et al. 2022). This gap is important to fill, as the majority of threatened chondrichthyan species are from coastal areas (75%) (Dulvy et al. 2021) where we have the greatest recovered fossil record. The Anthropocene is characterized by rapid and severe habitat degradation, especially in coastal ecosystems (Waters et al. 2016, Wernberg et al. 2016). Given this changing world, the past provides past natural experiments regarding which species survived mass extinctions and climate change as well as baselines before human disturbance (**Figure 3**).

Extinction baselines provide context for today's anthropogenic stressors (Finnegan et al. 2015, 2024). However, extinction and diversification baseline analyses are limited among Chondrichthyes. Carcharhiniformes, the most speciose order of sharks (284, representing about half of extant shark species) and that span a range of habitats and body sizes, have higher extinction (and speciation) rates during warmer periods and lower extinction rates associated with reef expansion (Brée et al. 2022). Likewise, Lamniformes diversity decreased during cooling periods and during period of higher competition (Condamine et al. 2019). A CPB approach using the chondrichthyan fossil record should incorporate more taxa and time to quantify the rates of past extinction and speciation, and then compare these to future climatic scenarios. One imminent scenario is the degradation of habitats, such as reefs, either through direct removal or via human-induced climate change, on chondrichthyan extinction rates (e.g., Pinsky et al. 2013, VanderWright et al. 2021).

6.1. Assessing Extinction Risk

Predictors of extinction risk in sharks and rays are shallow habitat and body size (Dulvy et al. 2014). Fishing—a uniquely human phenomenon—often targets larger-bodied species or individuals, tends to be focused in shallower areas (<1,000 m depth), and is currently considered the biggest threat to chondrichthyans (Dulvy et al. 2021) (**Figure 1*a***). In recent decades, fisheries have shifted into deeper waters (Morato et al. 2006, Simpfendorfer & Kyne 2009), which has devastating impacts on marine organisms (Danovaro et al. 2014). The deep sea was a refugium for many marine taxa, including cladodontomorph sharks, a stem Chondrichthyes group that was initially thought to go extinct at the end-Permian mass extinction (Guinot et al. 2013). Given the lower productivity of the deep sea and slower growth rate of Chondrichthyes inhabiting this biome, population recovery is projected to take decades or centuries (Simpfendorfer & Kyne 2009). More work is needed to understand the role of the deep sea in past extinction events, and if extinction rates and recovery times in the modern world are exacerbated by human activity as they are in mammals (Davidson et al. 2017, Dirzo et al. 2014, Smith et al. 2018).

Most work on extinction and climate events emphasizes what was lost or on post-extinction recovery communities (Bazzi et al. 2018, Belben et al. 2017, Rodríguez-Tovar et al. 2020, Smith et al. 2022, Stiles et al. 2020, Zhao et al. 2020; but see Bazzi et al. 2021a, Jablonski 2001, Vellekoop et al. 2020). Loss can be categorized as either loss of groups or loss of functional diversity, such as the differential extinction of pelagic sharks in the Miocene (Sibert & Rubin 2021) or two-thirds of the macropredator genera in the Pliocene (*Carcharocles* and *Parotodus*) (Pimiento et al. 2017). Understanding ecological traits, evolutionary histories, and responses of the so-called winners—those with higher survival rates—is important for setting conservation priorities, especially as many of the Chondrichthyes threatened today are evolutionary winners who persisted the longest in the fossil record and demonstrated resilience to past change (Paillard et al. 2021). For example, after the Cretaceous–Paleogene event, Chondrichthyes that fed on benthic molluscan prey tended to go extinct (Guinot & Condamine 2023), whereas the winners were pelagic species. However, these trends are not consistent across time and may be group specific. Today, we may not have many winners; only 37.4% of chondrichthyan species are considered safe from extinction based on population-level analyses or by proxies (Dulvy et al. 2014). Therefore, expansion of this CPB approach to more taxa, environmental conditions (i.e., anoxia, temperature, acidification), and extinction events is necessary to understand trends and patterns of triggers and responses (**Figure 3**).

Assessments of extinction risk in the modern world often investigate trends at the population level (e.g., Dulvy et al. 2014, 2021; Field et al. 2009; Pacoureau et al. 2021; Sherman et al. 2023). Understanding population size and demography in the fossil record can be a challenge but not impossible (Kidwell & Flessa 1995). For example, the comparison of historical fossil dermal denticles to modern denticle counts suggests chondrichthyan abundance was three times greater prior to human exploitation (Dillon et al. 2020, O'Dea et al. 2020). Likewise, fossil dermal denticles from deeper time (<85 Ma) demonstrate the stability of the fish to chondrichthyan ratio in oceanic ecosystems over tens of millions of years, highlighting robustness to major global climate change events during the Cenozoic (Sibert & Rubin 2021, Sibert et al. 2016). In fact, fish and chondrichthyan community structure was reset twice during the last 85 Ma—once at the Cretaceous–Paleogene extinction event and again approximately 19 Ma (Sibert & Rubin 2021)—indicating that while the community dynamics are characterized by resilience to change, they can be disrupted and reset by extinction events. Additional periods of massive Chondrichthyes diversity loss further back in time remain unknown, but we suggest further investigations to periods when there are perturbations to the top or bottom of the food chain. Identifying the drivers behind such tipping points in community structure is essential to identifying conservation priorities moving forward.

6.2. Contribution to Demography

Quantifying morphological diversity within assemblage-level records also provides insight into key conservation-based metrics. Different morphologies are typically used to assess species richness of a sample; within-species differences can be used to assess demographic changes within or among sites. For example, the fossil tooth record of Eocene sand tiger sharks, *Striatolamia macrota*, from four localities was leveraged to reconstruct size structure, and a mechanistic model of demography dynamics determined the timing of juveniles from a nursery and migration timing of adults (Kim et al. 2022). This approach was ground-truthed with modern sand tiger sharks, *C. taurus*, and correctly predicted dispersal and migration timing to and from Delaware Bay (Kim et al. 2022). The location of past nurseries, ontogenetic movement patterns, and reasons for nursery disuse (e.g., Pimiento et al. 2010) during periods of past climate change can help inform decisions related to marine protected areas (Davidson & Dulvy 2017, Di Lorenzo et al. 2022, Dwyer et al. 2020, MacKeracher et al. 2019, van Zinnicq Bergmann et al. 2022).

Many Chondrichthyes have slow life histories, with low fecundity-low mortality. A low fecundity-low mortality life history means that they are not resilient to density-dependent changes—even without additional hunting/fishing pressure (Stevens 2000, Zuo et al. 2013). Fishing that frequently targets larger individuals, which have reached sexual maturity and have the most reproductive opportunities, compounds this issue (Stevens 2000). Although life history strategies are assumed for extinct chondrichthyans, using a theoretical modeling approach to reconstruct demography of past populations (e.g., Kim et al. 2022) or a phylogenetic approach to reconstruct patterns (e.g., Kriwet et al. 2009) could be adapted to assess timing for recovery given an amount of reproductive output. Applying these methods to the fossil record can reveal patterns of recovery after periods of major environmental change. Future studies can utilize the global chondrichthyan fossil tooth record to determine relative abundances, population structure, and demographic dynamics, especially with respect to changing biological and environmental conditions (**Figure 3**).

6.3. Ecological Function

The loss of taxa within a community, especially key and nonredundant taxa, results in a loss of ecological function and biodiversity (Estes et al. 2011). Much work, however, is focused on large, apex predators (Estes et al. 2011, Pauly et al. 1998), although some work explores the functional diversity of all sharks (Ferretti et al. 2010, Pimiento et al. 2023). In general, larger species (and their resulting fossil specimens) are more likely to be recovered and studied (Kidwell & Flessa 1995), which is also true for large sharks (Estes et al. 2016, Pimiento et al. 2023, Smith et al. 2016). There is much to learn from these larger species; for example, during the Pliocene marine megafaunal extinction, coastal habitat loss and oceanographic changes caused a 17% loss in functional richness from species extinction (Pimiento et al. 2017). There is a need to expand research to include smaller-bodied groups to fully understand how the loss or addition of species occupying different trophic positions may impact ecosystem function.

The chondrichthyan fossil record is ripe to inform conservation for the present (Dietl & Flessa 2009, 2011) (**Table 1**). The paleo-community has identified important time periods of climate change or mass extinction as analogs for our changing planet (Finnegan et al. 2024) (**Figure 3**). These selected time periods emphasize using the historical record to understand the effect of habitat loss and restoration, dietary shifts, and ecological implications (Newsome et al. 2007). In addition to historical archives, the fossil record can help establish biotic baselines (i.e., biotic interactions, community structure, assessment of invasives) and discern biotic responses to environmental changes, such as global warming, ocean acidification, hypoxic events, and/or sea level change (**Figure 3**). Recently, Dillon & Pimiento (2024) demonstrated how the Elasmobranchii fossil record can be used to answer pressing conservation priorities. The need for chondrichthyan conservation is critical as current shark populations have shifted dramatically from historical baselines (Dillon et al. 2017). The rate of change and ecological scope are similar between past mass extinctions and today's decline in elasmobranchs, indicating that we may be at the precipice of a new mass extinction. Importantly, aligning Chondrichthyes paleobiology and ecology—such as recovery rates, extinction risk, and distribution changes—with known conservation priorities can start to close the gap between research and action (Groff et al. 2023). In addition, there is recent recognition and interest in Indigenous interactions and knowledge of sharks to elucidate historic baselines (Gilson & Lessa 2021, Gilson et al. 2021, Johannes et al. 2000, Lowery et al. 2011). Chondrichthyans have an excellent fossil record, although it is dispersed and heterogeneous (**Table 1**). Mobilizing and coalescing this knowledge is no easy task but is integral for reducing extinction risk and biodiversity loss for chondrichthyans with implications across all marine ecosystems.

7. CONCLUSION

The chondrichthyan fossil record is robust with respect to temporal longevity, spatial distribution, and absolute abundance. Past paleontological studies established taxonomical presence/absence, alpha diversity, and relative ages. These results are foundational to deeper dives into paleoecology with explorations into how chondrichthyans interact with other taxa and their marine ecosystem, especially in response to environmental, biological, and climatic change. There are recent advances in morphological and geochemical techniques as well as computational approaches associated with ecological metrics, climate simulations, and theoretical models, which are leveraging larger and more detailed datasets (**Figure 1**). Higher-resolution CT imaging from lagerstätte provide finer detail of soft tissues, revealing nonanalog functional morphology from the past. These studies build into larger datasets that can be used for temporally and taxonomically broadened studies to reveal patterns and processes linking form to function. A limited temporal, geographic, or taxonomic scope is necessary for proof of concept/approach, but chondrichthyan paleoecology is at a cusp. For example, *O. megalodon*, the largest and popular extinct chondrichthyan, is at the center of many isotope studies as its large teeth provide ample material for analysis; these geochemical approaches can now be applied more widely to discern food web dynamics, body temperature, and movement patterns of other, smaller chondrichthyans.

In this new era of chondrichthyan paleoecology, we promote bridging concepts and theories from modern ecology, such as species interaction, niche conservation, and food web dynamics, to examine evolutionary processes. Recent studies are also taking a nontaxonomical approach and instead using function to discern community turnover and ecosystem shifts, especially during periods of environmental and climate change. Finally, we can build upon classic paleo-questions about extinction rates, biodiversity change, functional turnover, morphological disparity, etc. using new techniques and methodologies, and we can contribute to CPB by selecting specific time periods to serve as analogs to today's changing world (**Figure 3**). The results of CPB are especially useful for chondrichthyans because the best-preserved fossils and taxa are the apex predators from shallow, nearshore habitats—the areas determined to be of highest conservation concern today.

SUMMARY POINTS

- Past paleontological studies focused on description and taxonomy form the basis of paleoecological studies using morphology, geochemistry, ecological metrics, and models spanning climate simulations to demography dynamics.
- Studies featuring chondrichthyan paleoecology often have limited temporal, spatial, and/or taxonomic scope to develop emerging concepts and approaches.
- The complicated relationship between form and function requires studies to look beyond modern analog, especially because these do not exist for many extinct taxa. Recent advances in chondrichthyan morphology have benefited from higher-resolution datasets, such as larger sample sizes for morphometrics or three-dimensional computerized tomography.
- The excellent preservation of chondrichthyan enameloid makes it an ideal substrate for isotopic analyses that serve as environmental and biological indicators, such as water/body temperature, trophic level, water mass, and anoxia extent.
- An emphasis on function, rather than taxonomy, leverages the diverse and abundant chondrichthyan fossil record.
- In addition to teeth, dermal denticles are also abundant fossils that record key ecological details in their form, presence, and distribution, which includes deep-sea sediments.
- Conservation paleobiology applies the lessons learned from past environmental, biological, and climate events—which Chondrichthyes persisted through—to assess extinction risk, population demographics, and ecological function in light of modern threats.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Support for S.L.K. came from the National Science Foundation (NSF) Division of Earth Sciences (award 2239981). E.C.S. was supported by the NSF Integrative Research in Biology (award 2403839). We thank Christina Spence Morgan for producing illustrations for **Figures 1** and **2** as well as R. Trayler and G. Larocca Conte for their comments on an earlier draft of this manuscript. This is Paleobiology Database Publication no. 509; all data and code for analysis related to **Table 1** are available on DRYAD, **https://doi.org/10.5061/dryad.qnk98sfsh**.

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