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# 100 million years of shark macroevolution

*A morphometric dive into tooth shape diversity*

MOHAMAD BAZZI



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### **Abstract**

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Few vertebrate clades exhibit the evolutionary longevity and versatility of sharks, which constitute nearly half of all current chondrichthyan biodiversity and represent an ecological diversity of mid-to-apex trophic-level predators in both marine and freshwater environments. The rich fossil record of shark teeth from Mesozoic and Cenozoic rocks also makes the group amenable to large-scale quantitative analyses. This thesis reconstructs the morphological tooth disparity of dominant lamniform (Mackerel sharks) and carcharhiniform (Ground sharks) clades over the last 100 million years. The relative diversity of these major lineages is strongly skewed, with lamniforms, including the famous White shark, making up less than 3% of the total species richness, whereas carcharhiniforms, such as Tiger sharks, comprise over 290 described species. Paradoxically, this long-recognized disproportionate representation was reversed in the distant geological past. Indeed, the fossil record shows that lamniforms accounted for nearly all of the documented shark diversity during the final stages of the Late Cretaceous — the terminal time interval of the ‘Age of Dinosaurs’, which ended 66 million years ago. The causes of this radical diversity turnover are debated, with recent research suggesting that competition and/or climate change drove major shifts in shark evolution. Perhaps more surprisingly, most analyses of diversity dynamics of sharks centre largely on taxonomic data, thus omitting more direct proxies of ecology, such as morphological diversity, or disparity. To mitigate this shortfall, I adopt a Procrustes framework combined with phylogenetic comparative and multivariate statistics to shed light on the deep-time morphological evolution of sharks. My work indicates that the end-Cretaceous mass extinction initiated a sustained evolutionary turnover in ecological dominance between lamniforms and carcharhiniforms. More specifically, the morphospace of these clades, indicate a selective extinction at the K/Pg Boundary affecting ‘large-bodied’ anacoracid lamniform sharks, whereas triakid carcharhiniforms proliferated in the extinction aftermath, perhaps as a response to new prey sources. Overall, my thesis suggests that the modern shark assemblages are the synergistic result of feeding ecology (including dietary niche breadth) and environmental shifts in global sea levels and temperature acting over the last 100 million years.

**Keywords:** Sharks, Macroevolution, Extinction recovery dynamics, Geometric Morphometrics, Morphospace-Disparity Framework, Teeth

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*To my family*



# List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Bazzi, M., Kear, B. P., Blom, H., Ahlberg, P. E. & Campione, N. E. (2018). Static dental disparity and morphological turnover in sharks across the end-Cretaceous mass extinction. *Current Biology*, 28(16), 2607-2615.
- II Bazzi, M., Campione, N. E., Kear, B. P., Blom, H. & Ahlberg, P. E. The extinction and survival of sharks across the end-Cretaceous mass extinction.
- III Bazzi, M., Campione, N. E., Kear, B. P. & Ahlberg, P. E. Feeding ecology has shaped the evolution of sharks.
- IV Bazzi, M., Kear, B. & Siversson, M. Southern higher-latitude lamniform sharks track mid-Cretaceous environmental change.

Additionally, the following papers were prepared during the course of the PhD, but are not included in this thesis.

- I Conte, G. L., Fanti, F., Trevisani, E., Guaschi, P., Barbieri, R. & Bazzi, M. (2019). Reassessment of a large lamniform shark from the Upper Cretaceous (Santonian) of Italy. *Cretaceous Research*, 99, 156-168.
- II Zhu, Y., Giles, S., Young, G., Hu, Y., Zhu, M., Bazzi, M., Ahlberg, P. E. & Lu, J. (2021). Endocast and bony labyrinth of a Devonian 'placoderm' challenges stem gnathostome phylogeny *Current Biology*.
- III Kear, B. P., Bazzi, M., Campione, N. E., Madzia, D., Lindgren, J., Sachs, S. & Lee, M. Polar plesiosaurs elucidate environmental interplay in marine reptile evolution.

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# Abbreviations

k	number of dimensions of the object or of the configuration
p	number of landmarks
n	number of objects or observations
PCA	principal component analysis
dP	partial Procrustes distance
Be	bending energy matrix
GPA	generalised Procrustes analysis
TPS	Thin-Plate Splines



# Introduction

**Biodiversity** is unevenly partitioned across the Tree of Life (Raup *et al.*, 1973; Slowinski and Guyer, 1993; Mooers and Heard, 1997). For example, in the marine realm, actinopterygian fishes reign supreme, with > 33.000 extant species, outnumbering the combined diversity of cartilaginous fishes, jawless fishes, lobe-finned fishes, and marine tetrapods (Nelson, Grande and Wilson, 2016). This imbalance in richness distribution also persists at lower taxonomic levels (e.g., acanthomorphs comprise at least half of actinopterygian fish diversity) (Near *et al.*, 2013). We observe a similar trend of richness asymmetries between clades in the fossil record, and it is, therefore, one of the most pervasive patterns in organismal biology (Benton, 2015; Scholl and Wiens, 2016; Wiens, 2017). Prevailing evolutionary hypotheses suggests that clades will achieve higher richness either because 1) they have had more time to evolve (i.e., they are older) or 2) as an outcome related to faster rates of net diversification (i.e., speciation minus extinction over time) (reviewed in Wiens, 2017) (but also see: McPeck and Brown, 2007; Ricklefs, 2007). Yet, on a larger phylogenetic-scale — the analytical support for variation in diversification rates, generally surpass that of clade ages, as an explanation, for the dramatic difference in species richness between clades (Scholl and Wiens, 2016; Wiens, 2017). Underlying factors, such as trait variability (e.g., morphology, ecology) and species interactions (e.g., competition), are consecutively invoked to explain rate difference among clades (Wiens, 2017). Pertinently, such factors are considered key components of the ecological theory of **adaptive radiation**<sup>1</sup> — a concept introduced by Simpson (1953a) — and that attributes accelerated diversification with reduced competition in response to ecological opportunity (Schluter, 2000; Gavrillets and Losos, 2009). The acquisition of new traits is also hypothesised to reduce competition by allowing the exploitation of new resources and thereby increase diversification rates (Schluter, 2000).

Clades with living representatives and a rich fossil record are particularly suitable models for testing hypotheses about the drivers of diversification and the role that intrinsic and extrinsic mechanisms have had in shaping evolutionary trajectories (Alroy, 2000; Benton and Pearson, 2001; Benton, 2015).

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<sup>1</sup> Evolutionary radiations involving the rapid diversification of new lineages into a variety of ecological niches (instigated by ecological opportunity) are referred to as adaptive radiations (Gavrillets and Losos, 2009).

Comparisons between sister-taxa with opposite diversity profiles (e.g., sturgeons and paddle fish versus derived bony fishes) form a powerful approach by which to assess the historical basis for modern richness imbalances (Gavrillets and Losos, 2009; Benton, 2015).

Historically, **taxonomic richness**<sup>2</sup> has occupied centre stage in macroevolutionary studies, as a viable proxy for reconstructing diversity through time. Importantly, however, organisms don't only evolve in numbers, but also in form and function. These represent different aspects of the organismal complex and have been widely investigated across the animal kingdom (Foote, 1991; Alroy *et al.*, 2008; Brusatte *et al.*, 2008; Friedman, 2010; Anderson *et al.*, 2011; Huang, Roy and Jablonski, 2015; Guinot and Cavin, 2016; Oyston *et al.*, 2016). In particular, studies predicated on examining morphological diversity (i.e., disparity) have gained momentum in palaeontology. Unlike taxonomic measures, disparity is often a better reflection of ecological diversity and offers a more direct exploration of adaptive evolutionary change than counting species through time (Foote, 1997). However, interpreting ecology in the deep past is not without complication, with many examples of decoupling between morphology, ecology, and function (e.g., Foote, 1997; Alfaro, Bolnick and Wainwright, 2005; Wainwright, 2007). Past ecological interpretations are further complicated by the rarity with which direct evidence of trophic interactions (i.e., gut-content) are preserved. While the problems appear to be many, the study of ecomorphology (i.e., the covariation between morphology and ecology) in living species may serve to ground-truth ecological interpretations of the past (Foote, 1997). For example, the jaws and teeth of many mammalian and reptilian species, but also the beak of birds, are widely treated as proxies of dietary adaptations (Grossnickle and Newham, 2016; Melstrom, 2017; Olsen, 2017; Benevento, Benson and Friedman, 2019; Grossnickle, Smith and Wilson, 2019).

It may come as a surprise to many, but much of the fossil record of vertebrate groups including mammals, sharks, many teleosts, and reptiles is comprised of isolated teeth (Cappetta, 2012; Evans, 2013; Sibert, Hull and Norris, 2014; Larson, Brown and Evans, 2016; Wills, Underwood and Barrett, 2020). The study of vertebrate teeth has a long history in both palaeontology and neontology. However, most studies of vertebrate teeth have been focused on mammals (e.g., Evans, 2013; Hulsey *et al.*, 2020). In contrast, sharks, prominent members of the cartilaginous fishes (Chondrichthyes), have received comparably less analytical attention, despite their extensive evolutionary history [~450 million years] and omnipresence in marine deposits world-wide (Miller, Cloutier and Turner, 2003; Cappetta, 2012) (**Figure 1**). To paraphrase Stephen Jay Gould's joke on mammals:

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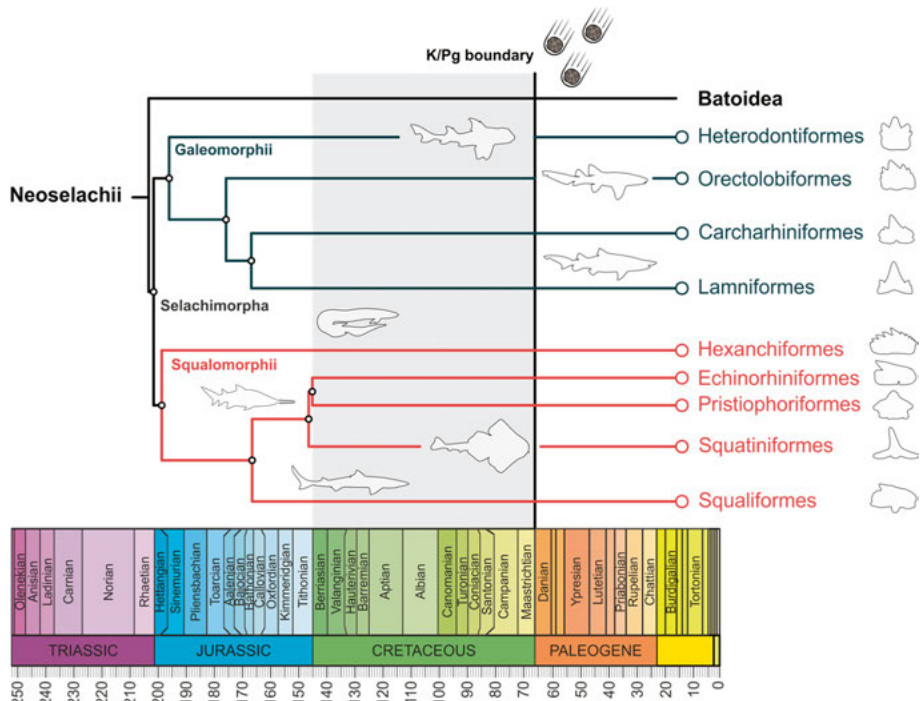
<sup>2</sup> Taxonomic richness—measures related to the number (alpha diversity) or heterogeneity (beta diversity) of species in a particular region or temporal interval.

“[Shark] evolution is a tale told by teeth mating to produce slightly altered descendant teeth.” (Gould, 1989).

Their isolated teeth have formed the primary source for nearly 200 years of fossil shark research (L. Agassiz, 1843), although such efforts have been almost entirely focused on their alpha-level taxonomy (Cappetta, 2012; Guinot *et al.*, 2018). Naturally, a tooth-biased fossil record imposes many restrictions on the realistic aspect of what can be learned from long-extinct sharks. However, their sheer abundance in marine deposits makes them unique among marine vertebrates and enable us to explore taxonomy, origination, extinction, and potentially feeding ecology. I say ‘potentially’, because, unlike mammals, the relationship between feeding ecology and tooth morphology has traditionally relied on qualitatively defined functional categories (Cappetta, 2012), whereas the quantitative relationship is yet to be established in sharks. This lack of analytical exploration has led to much speculation about the role of biotic mechanisms (e.g., dietary ecology) in their evolution. Up until now, most work on shark palaeobiodiversity has focused on estimating taxa and phylogenetic richness (Kriwet and Benton, 2004; Underwood, 2006; Guinot, Adnet and Cappetta, 2012; Guinot and Cavin, 2016; Condamine, Romieu and Guinot, 2019). Comparatively less is known about the morphological variability of their teeth, not just as a general characteristic, but also as a causative agent in shark macroevolution (but see Belben *et al.*, 2017; Bazzi *et al.*, 2018). To this end, my thesis is the first to reconstruct the morphological succession of dental morphology in two shark sister-clades: Lamniformes (Mackerel sharks) and Carcharhiniformes (Ground sharks).

The work that I have conducted for this thesis brings together the better of two worlds, the deep-time empirical data afforded by the fossil record and the analytical rigour of morphometric techniques. My goal is to interpret the mechanisms responsible for diversification and extinction of sharks in the geological past (**Paper I–IV**). More specifically, my work fills a notable gap in our understanding about the role of shark ecology in the evolution of sharks, by studying tooth shape variability over time.

In closure, the results presented in this thesis should be read and understood within the broader context of the fossil record. The purpose behind the ‘macroevolutionary approach’ adopted in this thesis is to identify and provide an explanation (albeit neither exact nor complete) for modern shark biodiversity using available data sources (extant and fossil). I demonstrate how external physical mechanisms (e.g., sea-level and temperature) and feeding ecology have influenced the establishment of shark communities over time.



*Figure 1.* Phylogenetic relationships of living neoselachian clades combined with chronostratigraphic information. The Neoselachii form a monophyletic group that includes sharks (Selachimorpha), skates and rays (Batoidea). Within sharks, two large clades are identified: Squalomorphii (includes five orders) and Galeomorphii (includes four orders).

## Survey of the field

Studies on species diversity through time are traditionally based on taxic and/or phylogenetic methodologies (Raup, 1972; Sepkoski *et al.*, 1981; Raup and Sepkoski, 1982; Benton, 2009). The taxic approach (as the name implies) treats taxonomic ranks as independent entities and count their occurrences against time (Purvis, 2008). Phylogenetic methods incorporate the hypothesised evolutionary history of clades, which are derived from molecular or morphological data, and then either counts all lineages present through time (i.e., lineage accumulation) or calculates the patristic distance of said lineages (Ricklefs, 2007; Morlon, 2014). Both approaches form standard tools in macroevolutionary studies and have contributed immensely to our understanding of evolving biodiversity (e.g., Raup *et al.*, 1973; Foote *et al.*, 2007; Rabosky, 2009; Wiens, 2011; Alfaro *et al.*, 2018). At the same time, there is a real concern that the curves generated from taxonomic datasets reflect sampling biases more than a genuine biological reality (e.g., Alroy *et al.*, 2001; Smith, 2001). The problems of the taxic approach are well articulated in the primary literature (Smith, 2001; Smith, Gale and Monks, 2001; Peters and Foote, 2002) but can be summarised as:

1. The applicability of the biological species concept (*sensu* Mayr, 1963) to the fossil record.
2. The smearing effects caused by taphonomic artefacts, geological incompleteness, and differential sampling strategies (e.g., Benton *et al.*, 2011).

The first point touches on the never-ending discussion of how to define species (Wheeler and Meier, 2000). While it is generally agreed amongst most neontologists that ‘species’ (i.e., naturally occurring, discontinuous clusters of phenotypes and genotypes) exist independently of human perception (Allmon, 2013), this concept has proven much more difficult to extend to the realm of palaeontology (Miller, 2016). Unlike, living organisms, fossils preserve no genetic-information, which means that any notion of species in palaeontology is necessarily grounded on the morphology. Groups such as sharks are particularly challenging because as stated earlier most of our understanding of their diversity and evolution is based on isolated teeth (Cappetta, 2012). The question that follows is: how reliable are taxonomic treatments of extinct organisms whose main identification rest on teeth? The question may seem unfair because teeth are sometimes all that we have to ground our research upon and creates a false dilemma between choosing to accept or deny shark alpha-taxonomy as a valid practice. Shark workers do however generally agree that teeth are sufficiently diagnostic in living species (Guinot *et al.*, 2018), which form the working assumption for palaeontologist (Siverson, 1999; Cappetta, 2012; Berkovitz and Shellis, 2016; Guinot *et al.*, 2018). Nonetheless, I consider there are some key issues worth highlighting. Since species form the

basis of biodiversity, it is paramount that taxic designations of fossils to be well founded. The excessive and poorly justified creation of new species can artificially skew (i.e., overestimate) biodiversity dynamics and subsequently lead to wrong conclusions about past speciation and extinction events. Unlike living sharks, we only have a rudimentary understanding of most fossil sharks, with most specimens represented by isolated teeth, making it difficult to fully comprehend the full range of variation that typify any one given species (Siverson, 1996, 1999; Siverson, Lindgren and Kelley, 2007). The identification of teeth is also made difficult by factors such as:

1. **Monognathic heterodonty**: shape and size differences in teeth along the tooth row.
2. **Dignathic heterodonty**: shape and size difference in teeth between upper and lower jaws (e.g., hook-like upper anterior versus comb-like anterolateral lower teeth in hexanchids).
3. **Gynandric heterodonty**: mature female nursehound sharks (*Scyliorhinus stellaris*) have tooth morphologies closer in shape to neonates than mature males (Berio *et al.*, 2020).
4. **Ontogenetic dietary shifts**: tooth shape (e.g., loss or gain of serrations) and size alteration during growth and in response to dietary shifts (French *et al.*, 2017).

## A ‘taxon-free’ approach

The low preservation potential of cartilaginous elements and the continuous tooth replacement of sharks has resulted in a tooth-dominated fossil record (Whitenack, Simkins and Motta, 2011; Cappetta, 2012). Investigations of extinct sharks have resulted in the documentation of their highly diverse tooth structures over geologic time (e.g., Cappetta, 2012). The images of isolated shark teeth provide an important source of phenotypic information and the opportunity to evaluate alternative measures of diversity that are independent of taxonomic assignments. This measuring rod is called disparity (see forthcoming sections) and is a powerful means to characterise the range of morphological variability (Foote, 1993a; Roy and Foote, 1997). Disparity enables us to relax the philosophical discussion between taxonomic splitters and lumpers and more directly focus on phenotypic diversity. The shape of shark teeth is not trivial but offers vital clues about the evolution of sharks and can be used to track clade-level phenomena.

Using a ‘taxon-free’ approach (i.e., without references to lower hierarchical units), my objective is to characterise the parallel evolution of the shark sister-clades Lamniformes and Carcharhiniformes (**Figure 2** and **3**). The justification of tracking shape changes through time with minor reference to taxic units are two-fold: 1) the classification of many fossil sharks is still unclear and

debated for several species and genera; and 2) tooth morphology should provide a more direct proxy for the interaction between sharks and their environment, especially when compared to traditional taxonomic measures. That being said, patterns of shark tooth disparity are complicated to interpret, as variability may be associated with a suite of factors that are neither taxonomic nor ecological (**Paper I–IV**). My assessment of tooth disparity is therefore tied to the assumption that changes in disparity represent a biological signal associated with ecological adaptations.

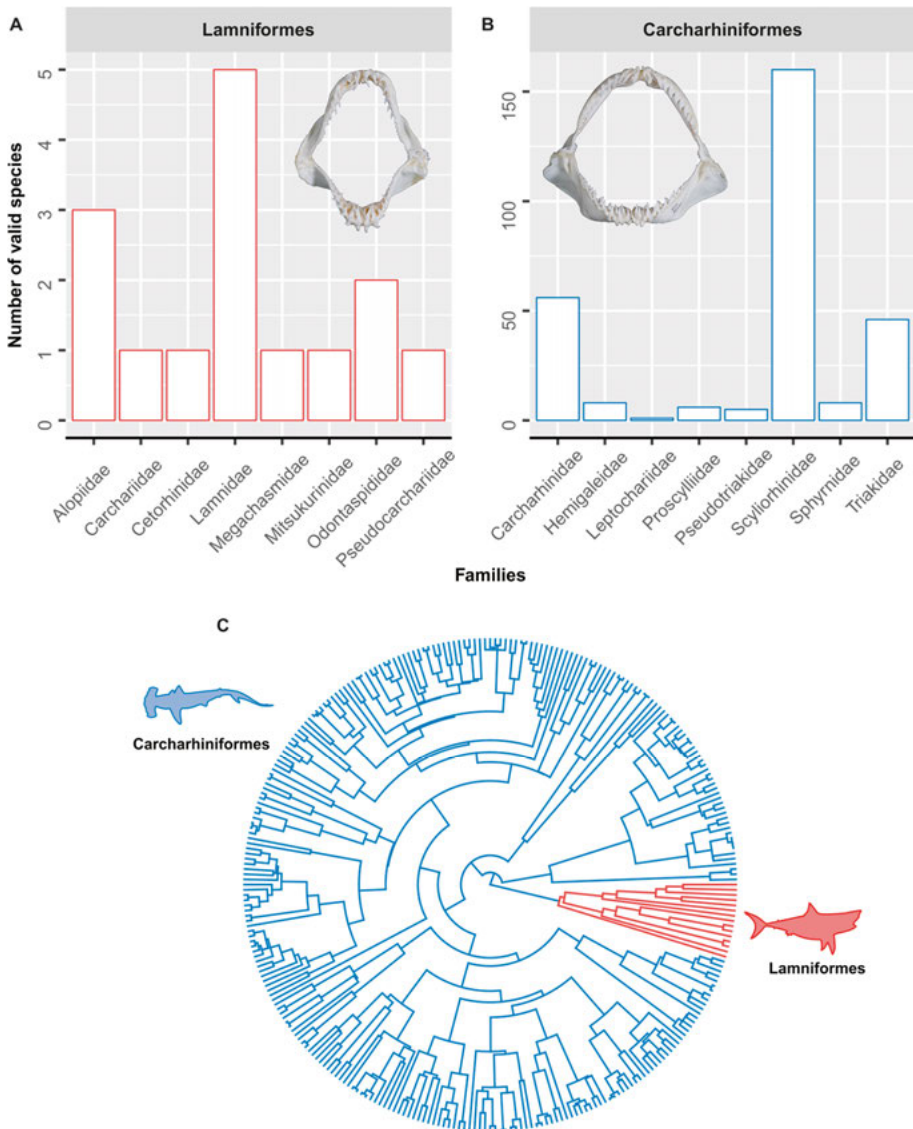
The reliance upon dental data is further justified by the demonstrated ecologically, functionally, and taxonomically informative nature of fossil shark teeth (Cappetta, 2012; Wilga and Ferry, 2015; Huber *et al.*, 2019). However, none of these parameters are designated *a priori*, and thus, ‘specimens’ rather than ‘species’ were chosen as the fundamental sampling unit with which to quantify morphological variability (**Paper I–IV**).

## Comparing sister taxa

Sharks exhibit a bewildering diversity of shapes and sizes (Ebert, Fowler and Compagno, 2013) and are important in maintaining the health of marine food webs (e.g., via top-down regulation) (Heithaus *et al.*, 2009; Hussey *et al.*, 2014; Dulvy *et al.*, 2017). The richness distribution pattern of modern sharks is notably skewed towards two groups: the galeomorph Carcharhiniformes (>290 species) and the squalan Squaliformes (~119) (Compagno, 1990; Ebert, Fowler and Compagno, 2013; Weigmann, 2016). Conversely, carpet sharks (Orectolobiformes), mackerel sharks (Lamniformes), the frilled and cow sharks (Hexanchiformes), saw sharks (Pristiophoriformes), angel sharks (Squatiniiformes) and bullhead sharks (Heterodontiformes), are comparably less diverse in terms of species numbers (Ebert, Fowler and Compagno, 2013).

Extant carcharhiniform sharks largely inhabit shelf and slope habitats (Compagno, 2009), and their exceptionally high diversity is mostly attributed to the families Carcharhinidae (requiem sharks), Scyliorhinidae (catsharks), and Triakidae (houndsharks) (**Figure 2** and **3**). A literal reading of the fossil record suggests that carcharhiniforms did not always dominate marine ecosystems in terms of species richness (Adnet *et al.*, 2007; Underwood *et al.*, 2011). Rather, during the late Mesozoic, their sister-group, Lamniformes, were considerably more speciose and dominant in terms of richness (Compagno, 2009) (**Figure 4**). In contrast, modern lamniform sharks include 15 species, 11 of which inhabit open pelagic environments (Compagno, 2009) (**Figure 2** and **3**). Despite their low numbers, the group nonetheless exhibits high diversity in cranial morphology (e.g., blade-like snout of *Mitsukurina owstoni*), body size (e.g., ranging from 1 meter in *Pseudocarcharias kamoharai* to ~8 meters in the *Cetorhinus maximus*), physiological adaptations (ectothermic and endothermic), behaviours (e.g., immobilization of prey using the tail in alopiid

sharks), and feeding strategies (e.g., planktivorous to macrophagous feeding modes) (Compagno, 1990; Ebert, Fowler and Compagno, 2013).

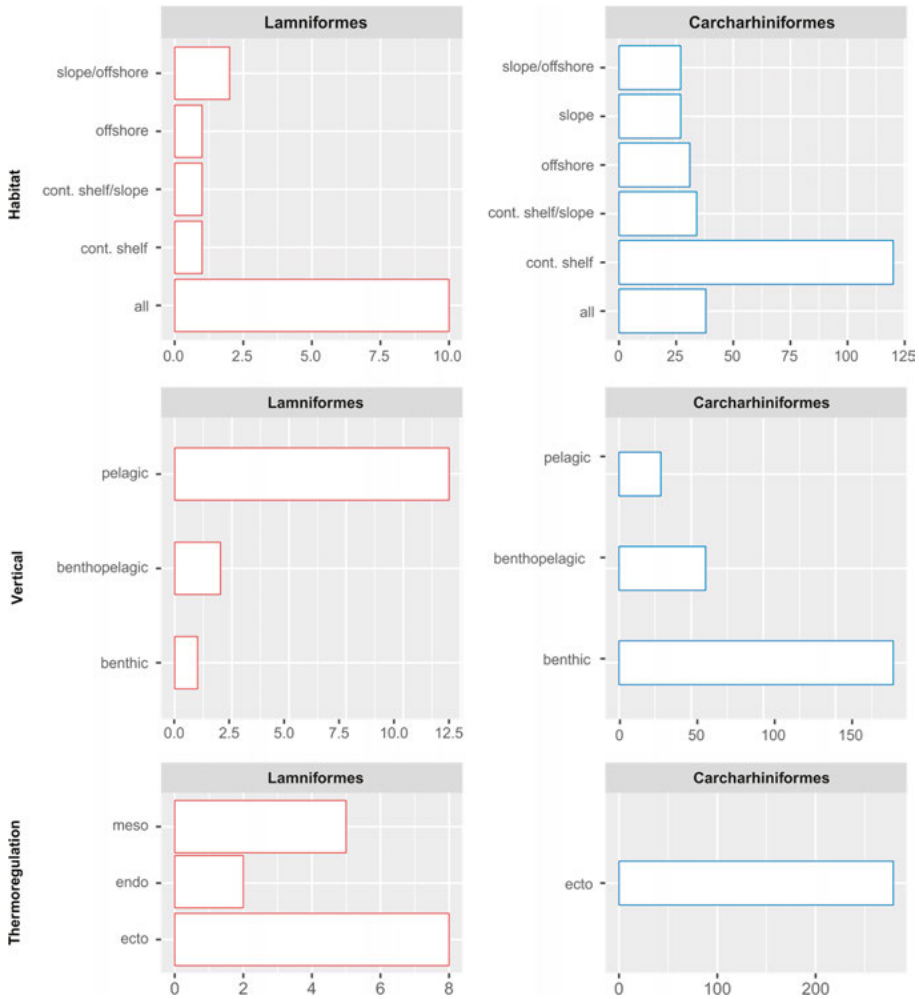


*Figure 2.* Species richness in the major clades of extant Lamniformes and Carcharhiniformes. (A–B) Bar plots show species numbers within families with images of exemplary lamniform (Snaggletooth shark) and carcharhiniform (Crocodile shark) jaws. (C) Total-clade lamniform and carcharhiniform phylogeny depicting diversity asymmetry in the number of species (Stein *et al.*, 2018).

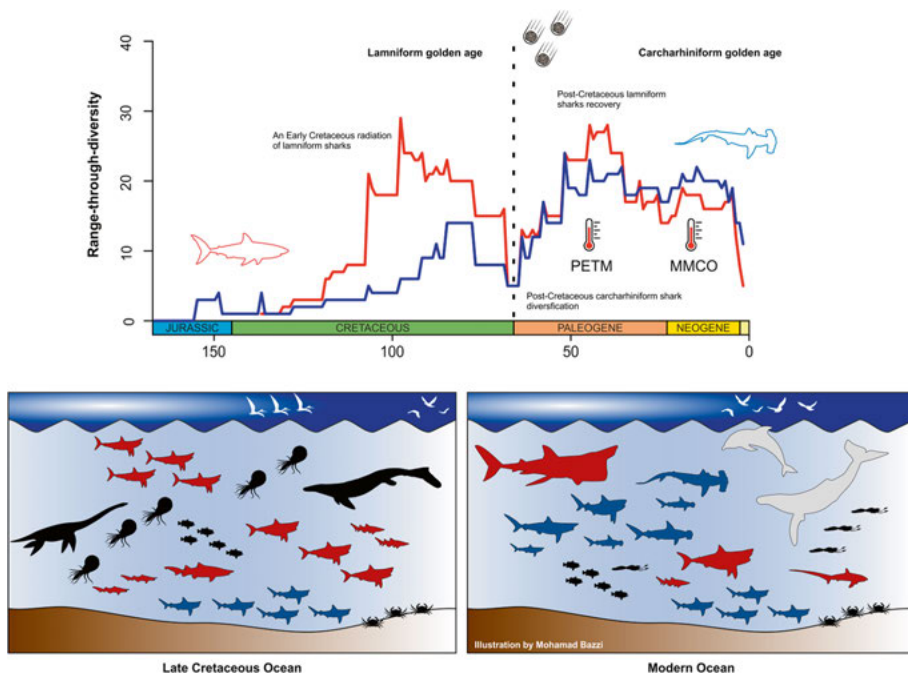
The seemingly opposed richness distributions between lamniform and carcharhiniform sharks stand out in diversity assessments of cartilaginous fishes



(Condamine, Romieu and Guinot, 2019) and raise two major questions. What are the drivers of long-term species decline in groups that were more speciose in the distant past? Are these species richness patterns coupled with morphological variation (i.e., phenotypic diversity) over time?



*Figure 3.* Habitats, oceanic zone, and thermophysiologic status of extant lamniform and carcharhiniform sharks. Abbreviations: meso = mesothermic, endo = endothermic, ecto = ectothermic. Data courtesy of Catalina Pimiento.



**Figure 4.** Lamniform and carcharhiniform diversity profiles shown over the last 170 million years. A literal reading of the fossil record suggests that lamniform shark were more diverse and abundant in marine settings during the late Mesozoic. One may refer to it as a ‘golden age’ of lamniform sharks. Carcharhiniform sharks show a different diversification pattern and appear to have started a journey towards ‘ecological’ dominance in the aftermath of the end-Cretaceous mass extinction (**Paper I** and **III**). From the perspective of carcharhiniform sharks the Recent represent a golden age for this group. Data used to generate range-through-diversity were taken from (Condamine, Romieu and Guinot, 2019).

## Tooth morphology and diet

Shark evolution has produced an extensive range of tooth morphologies, from the classic combination of cutting and tearing type, to durophagous dentition for feeding on hard-shelled prey (Cappetta, 2012). Most sharks possess a **polyphodont** dentition – the ability to replace teeth throughout their lives continuously. In the case of sharks, polyphyodonty is achieved by generating new rows along the medial surface of the jaws (Wilga and Ferry, 2015; Huber *et al.*, 2019). This near-infinite supply of developing teeth (Martin *et al.*, 2016; Rasch *et al.*, 2016) is important to maintain a healthy and functioning dentition. Aside from their primary use in feeding, sharks also use their teeth for various non-trophic tasks (e.g., mating) (Springer, 1967; Kajiura and Tricas, 1996; Pratt and Carrier, 2001). The incredible diversity of shark tooth morphology is a product of multiple factors acting at different levels of biological organisation — ranging from the genomics of tooth formation to the physical

interaction with prey (Rasch *et al.*, 2016; Fraser *et al.*, 2020; Hulsey *et al.*, 2020).

That the shapes of shark teeth bear the stamp of their primary function — to capture and process prey — is hardly a controversial statement (Whitenack and Motta, 2010; Herbert and Motta, 2018). But the relationship between tooth shape and function is far more complex and rarely produce a one-to-one match; a testament of the functional versatility of shark dentitions (Whitenack and Motta, 2010). The vast majority of sharks feed extensively on teleost fishes but will nonetheless utilise different resources (Wetherbee and Cortés, 2004) (**Paper III**). A standing question in shark ecology is whether the diet of a shark species can be predicted from the shape of its teeth. For the most part, this ecomorphological relationship have been assumed, through the generation of functional categories, without any quantitative support (e.g., Cappetta, 2012). But this association has more recently been questioned and described as merely putative (Whitenack and Motta, 2010; Moyer and Bemis, 2017; Huber *et al.*, 2019).

Indeed, macrophagous shark species exhibit high dietary plasticity, which is thought to weaken the relationship between tooth shape and feeding ecology (Munroe, Simpfendorfer and Heupel, 2014). For example, the raptorial dentition of the White shark (*Carcharodon carcharias*) can be used to retain an assortment of prey items, such as marine tetrapods, teleost fish, other elasmobranchs, and even cephalopods (Cortés, 1999; Hussey and Dudley, 2012). *C. carcharias* also exhibit ontogenetic dietary shifts, with smaller individuals consuming a different diet from that of adults (French *et al.*, 2017) (**Paper III**). In addition to ontogeny related differences, the prey consumption of shark species can vary depending on sexual affinity, seasonality, and geographic population (Cortés, 1999; Bizzarro *et al.*, 2017; Dicken *et al.*, 2017). Collectively, these observations attest to the inherent versatility of shark feeding ecology.

Despite the vast interest on the topic of shark ecomorphology, there has been no published account that quantitatively demonstrated the presence or lack of a relationship. To this end, I have ventured deeper into the domain of the living to resolve the matter of how tooth shape and diet covary in lamni-form and carcharhiniform sharks (**Paper III**). If tooth morphology drives feeding ecology in living sharks than such a relationship provides a basis upon which to infer feeding ecology among fossil taxa.

## The Procrustes paradigm

To probe into the evolutionary history of sharks, I use geometric morphometrics (GM) (**Box**). The modern application of GM uses **Procrustes methods**, which are based on the least-squares estimation of translation, rotation, and scale, to align a set of landmark coordinates taken from a set of given specimens (Gower, 1975; Rohlf and Slice, 1990; Dryden and Mardia, 2016). The underlying theory, mathematical and algorithmic details of the Procrustes framework are well documented in the primary literature (Bookstein, 1989, 1991; Rohlf and Slice, 1990; Adams, Rohlf and Slice, 2013). The defining feature of GM is its reliance on landmarks and/or sliding semi-landmarks both of which are commonly used to characterise the shape of an object. In GM, the placement of **landmarks**<sup>3</sup> on a structure is not arbitrary but instead must accord with a criterion of repeatability and operational homology (i.e., correspondence in the position of structures) (**Box**). Using landmarks as the basis for shape analyses allows the geometry of a structure to be retained but does not eliminate the effect of non-shape attributes (i.e., location, orientation, and size) from the raw landmark data. While several solutions exist (e.g., two-point registration, generalised resistant-fit) to address this problem, the most robust for most situations, and the main tool of morphometrics is Procrustes superimposition (also called Generalised Procrustes Analysis) (Dryden and Mardia, 2016) (**Box**). This procedure is the most important step in any GM study as it both provides 1) a formal mathematical definition of shape where the geometric properties of an object are invariant to non-shape components; and 2) the required shape variables for downstream multivariate analyses (Slice, 2007; Dryden and Mardia, 2016; Klingenberg, 2020). More specifically, the shape of aligned landmark configurations, can be represented as points in a shape tangent space. The magnitude of (dis)-similarity between points in a shape space is determined by the distance between the corresponding points (a measure called Procrustes distance: the square root of the sum of squared distances between landmarks) (Dryden and Mardia, 2016; Klingenberg, 2020). The shape space produced by aligning landmark configuration through the Procrustes fitting procedure, is a curved multidimensional space (Dryden and Mardia, 2016). In the context of shape analysis, the non-linear properties of such shape spaces are commonly deemed prohibitive towards the standard use of multivariate statistics. For the purpose of statistical analysis, the shape space of landmark configurations, is commonly projected orthogonally to tangent space (tangent to the consensus). This provides a local linear approximation of the shape space (Rohlf, 1999; Slice, 2001) whereby the distances between specimens will approximate the Procrustes distances between the corresponding landmark configurations (Slice, 2001).

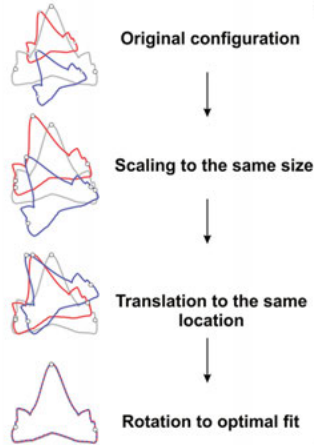
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<sup>3</sup> Landmarks are coordinate points used to represent a shape. More specifically, a landmark is a point of correspondence on each specimen whose position can be recognized in all specimens in a sample (Dryden and Mardia, 2016).

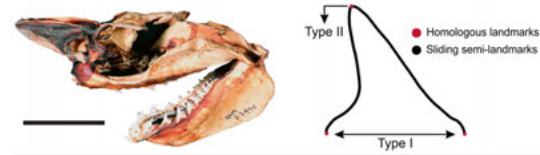
## Box | Extracting shape information: the core of geometric morphometrics

### Generalized Procrustes Superimposition

Euclidean similarity transformations



**What is shape?** In geometric morphometrics the shape of an object is defined as the properties that remain after size, position, and orientation been removed (Dryden & Mardia 2016). The procedure by which these attributes are removed is called the **generalized Procrustes superimposition (GPA)** – a method for fitting empirical data to Kendall's shape space. For 2D data, the shape space of aligned configurations of landmarks has  $2p-4$  dimensions (degrees of freedom).



The above image shows the dentition of *Isurus oxyrinchus*, and the geometric parameterization of a tooth. The red points represent fixed locations (i.e., the root-crown junction and apex), whereas the black points are semi-landmarks used to define curvature (**Paper I–IV**). 'Type I' and 'Type II' designations refer to the terminology of Bookstein (1991).

**Box.** The ability to mathematically factor out nuisance parameters and the graphic depiction of shape changes as deformation grids (Adams, Rohlf and Slice, 2013) makes geometric morphometrics an ideal technique by which to investigate shark tooth morphology.

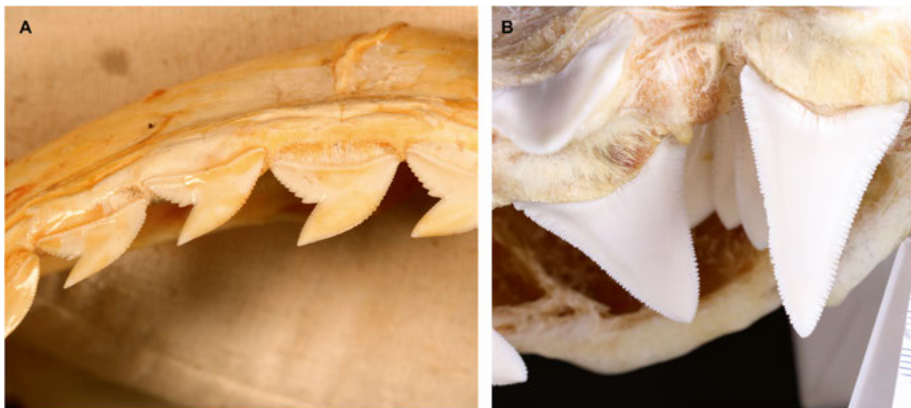
## Data acquisition

The core methodology for coordinate-based shape analysis, while well established, require initial case-by-case considerations with respect to data acquisition. More specifically, the variation in shape for the majority of lamniform and carcharhiniform shark teeth is sufficiently encoded in a 2D view of the teeth and represented equivalently in either labial or lingual perspectives (**Paper II and III**). However, the image data that I have collected relied mainly on the labial side. This is because the lingual side of some teeth may introduce relief-induced distortion. Furthermore, shark teeth do vary in complexity, sometimes reflecting their primary functions (e.g., the low-crowned pavement-like crushing dentition of the Port Jackson shark, *Heterodontus portusjacksoni*). Such morphotypes are likely better characterised by 3D GM but are still amenable to a 2D approach (**Paper II**).

For shark teeth, the choice of landmarks and sliding semi-landmarks were determined mainly on positional similarities of structures identified in all studied specimens. The digitisation was done by tracing the outer perimeters of the crown, starting at the root-crown junction and stopping at the apex along the mesial and distal margins of the tooth (**Paper I–IV**). This scheme resulted in two open curves for a total of 160 uniformly spaced points, three of which are fixed (i.e., homologous) (**Box**). Worthy of note, for semi-landmarks, which

were used to define curvature, the statement of homology is applied to the curves, and not for individual points. To compare shape similarities in tooth morphology, the scheme described above does provide a reliable starting point. However, not all information is captured by this landmarking scheme, such as serrations, striations, and the root architecture. The latter, in particular, forms a substantial portion of the tooth. But, unlike the crown, the root is more frequently damaged and is problematic from the point of view of obtaining a ‘sufficient’ sample size of teeth. The emphasis placed on the crown morphology can, however, be further justified by its direct role in prey procurement, which makes the crown more ecologically informative and presumably the subject of selection pressures. Serrations, on the other hand, could not reliably nor consistently be digitised for all specimens as a consequence of image resolution. These are often very delicate small structures appearing in some but not all macrophagous sharks (e.g., the Tiger shark, *Galeocerdo cuvier*, and White shark, *Carcharodon carcharias*) (**Figure 5**).

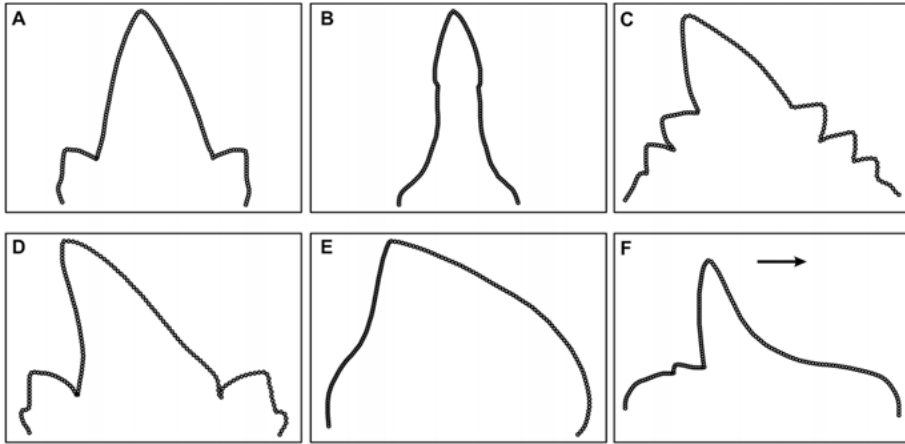
An additional limitation may be identified with the above-described digitisation scheme. For some teeth, such as the lower symphyseal teeth of hexanchids (e.g., *Hexanchus nakamurai*) that lack a median cusp, there is no possibility to identify the apex. Such special teeth were, therefore, not considered as part of the data collected to evaluate morphological patterns in most shark groups (**Paper II**).



*Figure 5. Examples of serrated teeth in modern taxa. (A) Tiger shark, *Galeocerdo cuvier* (B) White shark, *Carcharodon carcharias* [P.342806.001].*

But special teeth are not only limited to species outside of the lamniform and carcharhiniform divisions. The apex for some teeth (e.g., in *Xiphodolamia ensis* and *Rhizoprionodon acutus*) can have a natural mesial slant (**Figure 6F**). Indeed, asymmetries in crown shape are widespread among modern and extinct shark species. Finally, given the complexity of tooth shapes (e.g., multi-cusped versus bicuspid: **Figure 6**), the numbers of points needed to suffi-

ciently summarise the shape of the crown had to be determined. Such determination was done qualitatively by comparing resampled and aligned landmark configurations with different point numbers (**Paper I and II**).



*Figure 6.* Morphological diversity in shark teeth. Both extinct and extant shark teeth encompass a wide variety of shapes, including teeth with triangular serrated cusps, oblique serrated and non-serrated cusps, notched serrated cusps, non-serrated re-curved cusps, multi-cusped teeth, and flattened pavement teeth. Arrow in panel F represent the natural mesial slant of teeth found in some shark species.

## Definitions of morphological disparity

**Disparity** is a measure that describes the degree of variability in phenotypic traits exhibited by organisms (Foote, 1997; Wills, 2001; Erwin, 2007; Wagner, 2010; Hopkins and Gerber, 2017). Disparity is, in essence, a relative term (Foote, 1997), which means that any discussion on disparity includes a sample comprised of more than one single observation (Wills, 2001). Disparity is also both conceptually and empirically distinct from taxonomic diversity (Foote, 1993a, 1997; Wills and Fortey, 1994; Ciampaglio, Kemp and McShea, 2001) (**Paper I–IV**). In the palaeontological literature, two main approaches to the quantification of morphological disparity are used (Wills, 2001). The approaches include **taxic-based definitions**, which relies on phylogenetic discrete characters as the fundamental sampling units, and **shape-based definitions**, that use continuous variables, such those obtained from geometric morphometric analyses of morphological variability (Erwin, 2007). Regardless of whether discrete or morphometric data are used to measure morphological diversity, the term ‘disparity’ nearly always refers to the dispersion of variables (i.e., specimens or taxa) in a multidimensional space (Wills and Fortey, 1994; Wills, 2001; Brusatte *et al.*, 2008; Lloyd, 2016; Hopkins and Gerber, 2017; Guillaume, 2018; Guillaume *et al.*, 2020).

Worthy of mention is that most palaeontological studies on vertebrate animals estimate disparity using discrete character descriptors (Brusatte *et al.*, 2008; Prentice, Ruta and Benton, 2011; Thorne, Ruta and Benton, 2011; Butler *et al.*, 2012; Ruta *et al.*, 2013; Hetherington *et al.*, 2015). The discrete-character framework has however recently been criticised on methodological grounds, raising important concerns about the conceptual and operational value of phylogenetic data matrices for estimating disparity (Hopkins and Gerber, 2017; Gerber, 2019; Brougham and Campione, 2020). Among the issues identified are: (i) the subjective nature of character constructions; (ii) the proportions of missing data; (iii) the removal of autapomorphic characters in cladistic matrices; and (iv) the influence of body size on many discrete character–taxon matrices (Gerber, 2019; Brougham and Campione, 2020). In contrast, continuously valued variables, such as morphometric data (e.g., Procrustes shapes), are not burdened by the similar drawbacks of discrete variables (see above) when estimating disparity (Zelditch, Sheets and Fink, 2003; Zelditch, Swiderski and Sheets, 2012; Gerber, 2019). The use of morphometric data is however far from being perfect. An obvious disadvantage of using landmark-based data to estimate disparity is that this approach only allows the analytical treatment of one anatomical structure at the time (but see Collyer, Davis and Adams, 2020). A clear advantage, however, with using continuous variables is that the observed disparity of a sample is biologically intuitive as it reflects variance of a chosen anatomical feature (Zelditch *et al.* 2003). However, the suitability of data selection is ultimately determined by the working hypothesis and reflects the desired properties of resultant disparity. If the research question is more encompassing and seeks to generalise differences between taxic-units, then the amalgamation of markedly distinct morphologies (including novel evolutionary traits) through discrete character coding could present a more powerful approach (Wills, 2001; Gerber, 2019).

## Disparity metrics

Disparity can be calculated in many ways (reviewed by Foote, 1997; Ciampaglio, Kemp and McShea, 2001; Erwin, 2007). Each metric has its characteristics, limitations, and peculiar sensitivity to various parameters (Guillerme *et al.*, 2020). For example, the measures of range could be used to explore the farthest regions of morphospace explored by taxa (Ciampaglio, Kemp and McShea, 2001). For geometric landmark datasets, an intuitive and natural metric of disparity is the Procrustes variance (PV) (Zelditch, Sheets and Fink, 2003), because the units (i.e., landmarks) under consideration are Euclidean similarity transformed variables (**Box**). The use of PV for landmark data is appealing because it adheres to a statistical theory for how shape is defined (Zelditch, Sheets and Fink, 2003). Formally, PV is based on summarising the squared Procrustes distances (= Euclidean distances) between group means and group subjects (**Paper I** and **II**).



$$PV = \frac{\sum \sum d_{wi}^2}{n}$$

Computationally, the distances ( $d_i^2$ ) are found from residuals of a linear model that predicts group means (Adams *et al.*, 2020). Since the properties of this metric are Euclidean, PV is equivalent to the trace (sum of the diagonal elements) of the variance-covariance (VCV) matrix [S] (Zelditch, Sheets and Fink, 2003).

$$PV = Trace[S]$$

Unlike most disparity metrics applied to discrete characters, the distances (i.e., difference) between Procrustes shape variables, can be traced directly in locations of landmarks (Zelditch, Sheets and Fink, 2003). Another strength of PV is that it is additive; the disparity of sub-groups can be combined to represent the disparity of the whole group (Foote, 1993a; Zelditch, Swiderski and Sheets, 2012) (**Paper II–IV**).

$$Partial\ PV = \frac{\sum d_{wi}^2}{n_i}$$

## Temporal strategies

A narrative understanding of the evolution of disparity requires a time-series approach (Wills, 2001). Procedurally, this means that the data under consideration is time-binned, either according to stratigraphy or an arbitrary scale (e.g., time-bins of approximately equal duration) (Guillerme and Cooper, 2018). Binning by chronostratigraphic units could bias disparity toward longer stages. The effect of unequal duration can be examined through a correlation test (e.g., spearman’s test) to assess the strength of correlation between paired data, but also via rarefaction (**Paper I–IV**). Using rarefaction with or without replacement (bootstrapping or jack-knifing) can help interpret the effect of differential sample-size between time-bins on disparity, and yield a measure of statistical uncertainty. Unintentionally, the binning approach gives precedence to a punctuated equilibria model of evolution (Eldredge and Gould, 1972; Guillerme and Cooper, 2018). In other words, ‘gradual’ evolutionary modifications that may occur within a stage (often represented by millions of years) are guaranteed to be veiled by the temporal coarseness of the analysis. A binning strategy is, therefore, a sub-optimal solution to explore patterns in the fossil record (**Paper I–IV**) (also see the limitation section for more details).

## Assumptions

The premise of my research draws on similar assumptions made for teleost fishes (Sibert, Hull and Norris, 2014; Sibert and Norris, 2015; Sibert *et al.*, 2016, 2018); that the shape and size of shark teeth are functions of phylogeny and feeding habits, so that changes in the environment including prey-availability, will be reflected in shark tooth shape diversity (**Paper I–II** and **IV**). The hypothesised ecological link afforded by various measures of disparity is, however, not fully understood in sharks. Contra to many studies, including those on teleost fish, I take the next necessary step by validating the assumption of ecomorphology using well established multivariate protocols to explore the relationship between tooth shape and diet (**Paper III**).

# Research Aims

The overarching aim of my PhD project is to reconstruct the morphological tooth evolution of lamniform and carcharhiniform sharks across the last 83 million years. I focus on disparity – a largely ignored aspect of shark evolution – and investigated patterns within the context of mass extinction, ecology, and climatic/environmental turnovers. I adopt a combined macroevolutionary and ecological framework to investigate both pattern and process-based features of phenotypic trajectories of sharks. The specific aims were to:

- I      Test for extinction selectivity in sharks during the K/Pg mass extinction, compare global to regional patterns on tooth disparity and compare morphological patterns with taxic richness (**Paper I and II**).
- II     Establish an ecomorphological framework by which to assess the adaptive importance of modern shark tooth shape diversity (**Paper III**).
- III    Test the hypothesis that the K/Pg event initiated a reversal in ecological dominance observed between lamniform and carcharhiniform sharks (**Paper III**).
- IV    Reconstruct lamniform shark tooth morphology and size based on a high-resolution fossil record in Australia across the Early–Late Cretaceous boundary and Cenomanian–Turonian boundary (that brackets the OAE2) (**Paper IV**).

# Summary of results

## Mass extinction and its impact on sharks (Papers I and II)

The end-Cretaceous mass extinction event is by far the most studied among the big five extinctions of the Phanerozoic (Raup and Sepkoski, 1982; Jablonski, 2005; Schulte *et al.*, 2010). Many animal groups did not survive this event (e.g., the non-avian dinosaurs, marine and flying reptiles, ammonites, and rudist bivalves) (Fastovsky and Sheehan, 2005). Even surviving clades experienced substantial species-level losses along with a restructuring of community structures (Nichols and Johnson, 2008; Longrich, Bhullar and Gauthier, 2012; Sibert *et al.*, 2018). From an evolutionary perspective, the aftermath of the K/Pg event brought an immense opportunity for many organisms (e.g., mammals) by clearing the eco-space occupied by former incumbents (Alroy, 1999; Jablonski, 2001; Meredith *et al.*, 2011; Wilson *et al.*, 2012; Slater, 2013).

The fossil record is unambiguous in showing that the K/Pg event altered both terrestrial and marine ecosystems. Historically, however, less emphasis has been placed on marine vertebrate animals, but with some notable exceptions (e.g., mosasaurs and plesiosaurs) (Bardet, 1994; Martin *et al.*, 2017). Notably understudied is sharks, often informally considered to have ‘sailed through’ the extinction. However, richness patterns for sharks across the K/Pg boundary have revealed a 17% and 56% extinction loss for family and genus levels, respectively (Kriwet and Benton, 2004). Intriguingly, it was proposed that extinction dynamics were selective (i.e., non-random process) towards apex predators and durophagous rays, with significant phylogenetic clustering across the extinction event (Kriwet and Benton, 2004; Friedman and Sallan, 2012). A contrasting view asserted that the extinction of sharks was general and did not selectively target certain guilds (Guinot and Cavin, 2016), as observed in actinopterygian fishes (Friedman, 2009, 2010). A key issue, however, is that previous studies were not ideally suited to test selectivity, as their focus was taxonomic and not ecomorphological.

**Paper I** investigates the dental disparity of lamniform and carcharhiniform sharks across the K/Pg boundary. The results revealed compelling evidence that the tooth disparity of both clades was largely unaffected by the extinction event and evinced a decoupled relationship between disparity and previously reported declines in taxic richness. Nevertheless, specific patterns of morphol-

ogy (i.e., tooth shapes) indicated that an asymmetric extinction affected members of lamniform sharks possessing low crowned/triangular teeth, whereas, narrow and tall-crowned tooth morphotypes were comparatively unaffected (also see **Paper II**). The most severely affected lamniform dental morphotypes belonged to the ubiquitous Cretaceous anacoracids (e.g., *Squalicorax pristodontus*). These were the large ‘meat cutters’ of the Maastrichtian and are typically diagnosed by large body sizes comparable to modern White and Tiger sharks (Shimada and Cicimurri, 2005; Belben *et al.*, 2017). Idealised and simulation-based extinction models suggest that the disparity of a group should decline in response to a selective extinction (Foote, 1993b; Korn, Hopkins and Walton, 2013; Puttick, Guillaume and Wills, 2020). Yet, the tooth disparity for lamniform sharks was virtually unaffected (or at least statistically non-differentiable) across the boundary at a global and regional scale. At face value, this static signal conforms with the expectations of a random extinction and not a selective extinction. However, many factors are likely to influence the outcome for disparity, including the relative strength of selection on any given trait (Puttick, Guillaume and Wills, 2020). The failure to detect a drop in tooth disparity for lamniform sharks may otherwise also be related with the Paleocene survival of other lamniforms bearing low-crowned, triangular teeth. Alternatively, the selective removal of anacoracid tooth morphologies was simply not sufficient to cause a clade-level decline (i.e., Lamniformes) as a result of their minor contribution to the overall global disparity signal. Importantly, however, this does not detract from the reality that some groups of lamniform sharks were morphologically affected by the extinction event.

An additional key finding of **Paper I** relates to the proliferation of carcharhiniform tooth morphologies during the early Paleocene in areas of morphospace that were underutilised during the Maastrichtian and that were dominated by lamniform extinction victims (i.e., the anacoracids). A detailed examination of the morphospace patterns reveal that the post-extinction increase of carcharhiniforms with ‘cutting teeth’ were driven by triakids (Hound sharks) — a modern group comprised of small-bodied taxa with feeding preferences on small teleost fish (Compagno, 1984). Incidentally, they also represent the fourth largest radiation among extant members of Carcharhiniformes (Ebert, Fowler and Compagno, 2013) (**Figure 2B**).

At face value, the combined patterns recovered for lamniform and carcharhiniform sharks, suggest a classic extinction-replacement scenario whereby the ‘success’ of post-extinction lineages is causally linked with the demise of ecologically equivalent taxa. There is little, however, to suggest that early Paleocene small-bodied triakid sharks were ecologically similar to the large anacoracid sharks of the Late Cretaceous. The overlap in morphospace occupation along PC1 between triakids and anacoracids is not evidence for trophic substitution following the extinction event.

What prompted the extinction of anacoracid lamniform sharks at the K/Pg event, remains unknown, but is consistent with the loss of other contemporaneous large-bodied marine animals, including bony-fishes and predatory marine reptiles (Friedman, 2009; Martin *et al.*, 2017). It is possible that some late Maastrichtian anacoracids were specialized towards feeding on larger prey-items, including bony fishes, cephalopods, and even mosasaurs within a similar size-cohort. To reiterate, all of these groups were severely affected by extinction at the K/Pg boundary, suggesting that the decline in resource availability (i.e., prey) may have caused the final demise of anacoracid sharks.

Conversely, the rapid diversification of small-to-intermediate-sized teleost fishes (Sibert and Norris, 2015) in the extinction aftermath might have triggered a correlated shift at higher trophic levels filled by triakids. Such a shift assumes that biotic controls, specifically prey availability, was the main driver behind the radiation of triakid carcharhiniforms during the early Paleocene. As with lamniform sharks, it is possible that the carcharhiniform diversification was influenced by several factors (e.g., sea-level, temperature) and not necessarily limited to prey. In conclusion, the results presented in **Paper I** fundamentally implicates the K/Pg boundary in staging the subsequent rise to ecological dominance by carcharhiniform sharks and provide quantitative evidence for a selective extinction of lamniform sharks.

**Paper II** extends from the first by exploring the wider effect of the K/Pg extinction on nearly all shark groups (galean and squalan) (**Figure 1**) at a global and regional scale. In brief, the regional subsample of analysed shark teeth was obtained from the UNESCO World Heritage site at Stevns Klint in Denmark. This site preserve a near-continuous marine deposit from the latest Maastrichtian across to the middle Danian and was historically critical for identifying the end of the Mesozoic, including the occurrence of the globally-represented Iridium anomaly (Alvarez *et al.*, 1980). More important, the Stevns Klint locality represent one of few regions preserving shark fossil material spanning the boundary event (Adolfssen and Ward, 2014, 2015).

The results from the disparity analyses reveal that sharks maintained virtually static levels of disparity across the K/Pg extinction event. This result is consistently recovered at multiple levels of analysis and was insensitive to taxic, intra-individual (i.e., heterodonty), and geographic variation, and is consistent with clade-specific results reported in **Paper I** and the elasmobranch fossil record in general (Sibert and Norris, 2015). The fact that there were no major shifts in dental disparity in most groups of sharks across the K/Pg mass extinction is probably the most intriguing pattern. The implications of this result are, however, a bit harder to understand but suggest that ‘most’ ecological roles may have survived into the Paleocene despite the evident selective extinction of some taxa (**Paper I** and **II**). Perhaps, more importantly, is that heterodonty, from which at least as can be assumed from the fossil record, does not greatly affect the variation across the boundary (i.e., changes in disparity correspond with real evolutionary successions).

The case for phylogenetic selectivity of sharks is further corroborated here with patterns of morphospace occupation revealing a compositional shift in the predominance of certain tooth morphotypes across the K/Pg boundary. Morphologically, members of the galean order Lamniformes were particular hard-hit (see **Paper I**), whereas other clades, including carcharhiniforms, hexanchiforms, and squaliforms, may have ‘radiated’ in the extinct aftermath. Patterns of morphospace and partial disparity do, however, support additional intricacy of lamniform shark diversity dynamics across the extinction event. Tall cuspidate teeth, epitomised by odontaspidids (grey nurse sharks) are relatively more abundant in the Paleocene than in during the Cretaceous. This morphological radiation of odontaspidids may reflect an increase in prey availability (e.g., teleost fishes) such as was hypothesised for triakid carcharhiniforms (**Paper I**). From a modern perspective, such tooth morphologies are particularly useful for capturing and holding ‘slippery’ prey, such as bony fishes (Huber *et al.*, 2019). Results across both papers suggest that the adaptive radiation of teleost fishes (Friedman, 2010; Sibert and Norris, 2015; Alfaro *et al.*, 2018) may have had a profound and independent effect on multiple groups of sharks.

The results conveyed so far are based on a global assessment of shark tooth disparity and morphology. As discussed more in **Paper IV**, the global approach may potentially be problematic from the point of view that the fossil record of sharks varies geographically and over time (**Figure 7**). However, in both **Papers I** and **II**, patterns based on tooth specimens retrieved via bulk-sampling from the Stevens Klint locality revealed comparable results. Such results suggest some concordance between global and regional patterns, although I cannot unambiguously reject the possibility of geographic heterogeneity in post-disaster ecosystems for sharks, as it was shown for teleost fishes (Sibert, Hull and Norris, 2014) (**Paper II**).

### A swim through the Cenozoic (Paper III)

A major theme across **Papers I** and **II** is that the end-Cretaceous mass extinction event may have laid the foundation for the present-day asymmetry in richness distribution among lamniform and carcharhiniform sharks. The objective of **Paper III** was, therefore, to test this hypothesis by reconstructing the morphological succession of these sister-taxa across the extinction event through to the present (66–0 million years). The assumption here, as before, is that changes in tooth morphology over time can track clade-level phenomena, including the apparent pattern of shifting ecological dominance between the aforementioned clades.

The main results revealed that lamniform and carcharhiniform sharks attained peak dental disparity before the K/Pg event and, unexpectedly, that the disparity for both groups seemingly rebounded to pre-Cenozoic levels during the Recent (i.e., Holocene). This result, while evocative, is nonetheless at odds

with the fossil record at the species level (Condamine, Romieu and Guinot, 2019), as there is no fossil evidence of any extinction or speciation at least for lamniform sharks throughout the Pleistocene–Holocene interval. While, it is true that disparity and taxic richness are not bound to correlate with each other, in this specific case the resurgence in tooth disparity is more likely to reflect a deeper problem with combining extant and fossil data into a single framework (also see the **Limitation section**). Accordingly, factors including shape heterodonty, geographic, and taxonomic sampling, may better explain the ‘Holocene rebound’ observed for both lamniform and carcharhiniform sharks (i.e., it’s not real).

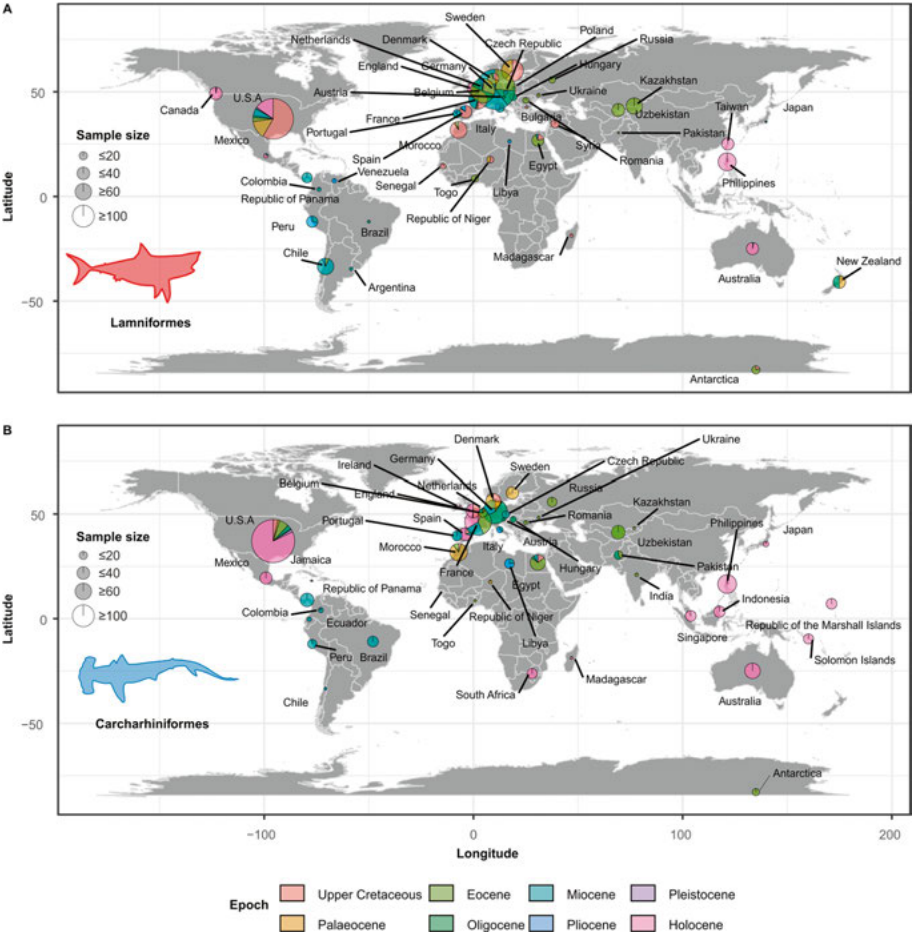


Figure 7. Spatiotemporal visualisation of the shark tooth dataset assembled for **Paper III**. Scatter pie plots depict the total sample size and relative proportions of geologically time-constrained lamniform (A) and carcharhiniform (B) tooth specimens.



Despite the problems of heterogeneous sampling, tooth heterodonty, and collection biases, the disparity of lamniform sharks appears to have crashed several times during the last 66 million years. Most apparent is the decline during the mid-Miocene to early Pliocene. A careful evaluation of this signal revealed that it was driven by now-extinct ecologically specialised apex predatorial otodontid shark, mostly famously *Otodus megalodon*. The comparably less heterodont dentition of such taxa may be responsible for the low disparity during this time-frame. While, the ecological implication of possessing a heterodont versus homodont dentition among sharks remain poorly understood; the size and shape of *O. megalodon* teeth all point towards dietary specialisation of large-prey (e.g., baleen whales).

Aside from the Miocene-Pliocene interval, the tooth disparity of lamniform sharks declined throughout most of the Cenozoic. Results obtained from fitting generalised least-squares models to assess potential abiotic drivers of lamniform disparity found a weak, but significant, association with sea-level. A possibly climate-driven evolution of sharks is further supported by contractions in lamniform taxic richness, and is associated with the disappearance of many epicontinental seas (= their living space: Compagno, 2009). The neritic zone covered vast areas during much of the Cretaceous and early Eocene, which is the source of much of the fossil material. Small to mid-sized lamniforms, which dominated Cretaceous neritic facies, evolved in a world where the shelf extended onto the continental crust, penetrating deep into the interior of the continents and fertilised by run-off in a way that was unique to these more-or-less restricted water bodies (e.g., Siversson *et al.*, 2019). The loss of such unique habitats undoubtedly affected their associated faunas.

A morphological overview of temporal patterns in both lamniform and carcharhiniform sharks also implicates diet as a key or complimentary driver of their evolution. Contrary to previous claims (e.g., Huber *et al.*, 2019), tooth morphology broadly predicts diet among living lamniform and carcharhiniform species. For example, piscivory is consistently associated with mesiodistally compressed, pointed teeth. Such tooth shapes became increasingly prevalent in the aftermath of the K/Pg event, suggesting an extinction-mediated shift towards more teleost fish-based diets in both groups (e.g., triakid carcharhiniforms and odontaspimid lamniforms). The extent to which different shark groups used specific resources in the past cannot easily be reconstructed. However, using dietary information obtained from modern species suggests that lamniform sharks are, on average, more specialised (i.e., low dietary niche breadth) in their diets than carcharhiniforms, many species of which occupy more intermediate levels along a specialist-generalist continuum (**Paper III**). All macrophagous sharks, including the most specialised forms (e.g., white sharks on mammals), still opportunistically feed on a wide range of prey-items (e.g., Hussey and Dudley, 2012). It remains, therefore, unclear to what extent niche strategies involving feeding may have played in sustaining the diversity of lamniform and carcharhiniform sharks over time. A generalist

feeding ability would hypothetically favour species during times of environmental stress (Munroe, Simpfendorfer and Heupel, 2014). My results provide a potential lead for how niche strategies, as measured for modern species, may have acted to produce the exceptional diversity of carcharhiniforms (see **Conclusions and future prospects**). Examples from the fossil record, including anacoracids across the K/Pg event (**Paper I and II**) and the later demise of otodontids in the late Neogene (while likely insufficient), provide nonetheless a clue about how feeding specialisation may have disadvantaged some lamniforms, but alone does not explain the decline of lamniforms over time. Ultimately, the interplay between habitat, diet, and reproductive strategies may afford a more accurate explanation.

## The Mackerel Shark Rises (Paper IV)

The mid-Cretaceous (Albian–Turonian) experienced several episodes of enhanced burial of organic carbon into oceanic systems (Jenkyns, 1980). These events, are known as oceanic anoxic events and are usually recognised by the local development of anoxia (Kuypers *et al.*, 2002). Perhaps most famously is the global latest Cenomanian–earliest Turonian Oceanic Anoxic Event 2 (OAE2), which is hypothesised to have triggered marine extinctions and turnovers, in particular among benthic communities. From the perspective of sharks, and more specifically lamniforms, it is unclear what effect, if any, this event had on their taxic and morphological diversity.

Notably, lamniform sharks are considered to have adaptively radiated during the Cenomanian, only a few million years prior to OAE2, reaching an all-time-peak in richness distribution (Guinot, Adnet and Cappetta, 2012). Furthermore, the diversification of lamniforms temporally coincided with increased global sea-levels and the decline of some marine reptiles (e.g., ichthyosaurs) and the radiation of euteleost fishes. However, the radiation dynamics of lamniform sharks across both the Albian/Cenomanian and Cenomanian/Turonian boundaries is currently solely recognised on taxonomic grounds and occurrences are heavily skewed to those from the Northern Hemisphere (e.g., Guinot, 2013).

The main objective of **Paper IV** was to explore these patterns in other parts of the world, namely from the Southern Hemisphere. Here, both the dental disparity and taxic richness of lamniform sharks was reconstructed based on specimens collected from the Southern Carnarvon (late Albian–early Turonian) and Eromanga basins (late Albian) in Australia.

My regional assessment based on Australian mid-Cretaceous localities revealed that lamniform species-level richness did not markedly change across the Early/Late Cretaceous Boundary. By contrast, the only observable increase in lamniform richness takes place during the early Turonian (increasing from 8 to 13 species). The tooth disparity of lamniform sharks increased from the late Albian to the late Cenomanian, although this signal appears to be

strongly influenced by compositional features of the assemblages in question (i.e., neonate versus osteologically mature individuals) and possibly by differences in depositional environment (partly enclosed interior sea versus outer shelf) across basins. To clarify, the late Albian Eromanga Basin represent a high productivity environment with a high density of large-bodied apex predators including cardabiodontid sharks, ophthalmosaurid ichthyosaurs, and brauchaenine pliosaurs. A reverse situation is observed in the late Cenomanian Southern Carnarvon Basin (Siversson *et al.*, 2019). Here, despite a similar dissolved oxygen profile, coupled with a highly productive upper water column (as indicated by the enormous number of marine vertebrate remains in the sampled stratum), larger bodied lamniform sharks are notably much rarer. Here, the lamniform assemblage is compositionally skewed towards small-bodied species and small juveniles of large-bodied species (Siversson *et al.*, 2019; Berrell *et al.*, 2020).

Interestingly, the removal of putative juvenile specimens from the overall dataset did not produce a conflicting signal (i.e., disparity remained high during the late Cenomanian). Notwithstanding, a more detailed evaluation revealed how monognathic heterodonty among neonate anacoracids inflates the disparity during the late Cenomanian.

Patterns across the late Cenomanian/early Turonian Boundary in the Southern Carnarvon basin recovered overall stability in tooth disparity, despite the increase in richness during the early Turonian. These results show that the OAE2 did not affect the richness of lamniform sharks on a local level in the Southern Hemisphere, as it did in the north. Interestingly, however, sub-clade specific patterns (i.e., families) revealed a notable rearrangement in disparity contribution across the boundary event. In particular, the tooth disparity of carchariid sharks increase substantially during the early Turonian. Modern analogues (e.g., the Sand tiger shark) flourish near or on well-oxygenated bottom waters and it is possible that their near absence in the early Turonian reflects a behavioural response to the prevailing anoxic conditions on the outer-shelf during the late Cenomanian. Accordingly, I hypothesise that environmental recovery (i.e., oxygenation of bottom waters) in the early Turonian may have facilitated small-sized carchariids to re-colonise outer-neritic habitats.

In conclusion, the near stable pattern in richness in Australia suggests that 1) the putative Cenomanian diversification (Guinot, Adnet and Cappetta, 2012; Condamine, Romieu and Guinot, 2019) was either limited to northern deposits, or perhaps even artefactual; and 2) the OAE2 can be considered a minor event for lamniform sharks inhabiting the Gondwana shelves.

## Limitations

When I started my PhD in 2016 the idea was to supplant what I previously believed to be ‘useless’ taxonomic datasets with actual shape variables obtained in a quantitative fashion. The premise (mind you a rather naïve one) was that disparity was a better metric of diversity than taxic richness. As I have discovered, however, disparity and taxic diversity simply provide different information to one another, and more importantly are biased in different ways. For sharks, a main difficulty has been to interpret the biological signal of episodic low and high tooth disparity. Among the main issues identified for disparity, morphospace occupation, and feeding ecology are:

1. Heterodonty
2. Tooth size
3. Collection biases
4. Geographic coverage
5. Time-binning

How to account for the effect of heterodonty in the fossil record of sharks is perhaps the main problem I have had to deal with. This is because, the disparity and morphospace occupation of shark clades, are influenced by varied tooth positions (e.g., anterior versus lateroposterior teeth may produce different signals) (**Paper I–IV**). The issue is somewhat further exacerbated by the fact that row-group terminology (i.e., the categorization of teeth based on their position in the upper and/or lower jaw) are usually applied differently among shark workers for different species and clades (e.g., Siverson, 1999; Shimada, 2002; Capetta, 2012).

Related to heterodonty is the fact that the shape of shark teeth may also vary with size (**Paper IV**). However, the effect of size on tooth shape for most sharks was not investigated in any detail as part of this thesis. Having blithely ignored ‘size’ as part of my broader assessment of changing patterns over time (but see **Paper IV**) is undoubtedly a weakness of the study design presented here. That being said, a preliminary analysis, revealed that the shape difference in tooth morphology due to variation in size, only account for a minimal proportion (<4%) of the overall shape difference. Similarly, the effect of tooth size (measured as the logarithm of centroid size) on mid-Cretaceous lamniform tooth disparity, was demonstrably small (see supplementary information in **Paper IV**).

The issue as related to difference in field sampling strategies (bulk versus surface collection) represent a crucial source of variation, and in a direct way is also linked to the issues identified above. For example, some morphotypes and size dimensions are either underrepresented or completely missing for some time bins, simply as a consequence of how the samples were obtained. This is particularly true for groups such as Carchariids and Odontaspids that

are almost invariably represented by teeth from anterior and lateral tooth positions, when in fact most of them have numerous, extremely low crushing teeth at the commissural end of the tooth row (M.S., personal communication) (**Paper II**).

A notable proportion of the image data of shark teeth collected and analysed as part of this thesis derive originally from marine deposits in North America and Europe. The extent to which this geographic bias influences current disparity estimates in sharks remain however unknown. Nonetheless, it does reveal a reality often overlooked in studies on palaeobiodiversity, which is, that the fossil record not only varies over time, but also across geographic area (e.g., Africa, Asia, and South America are particular under-sampled: **Figure 7**).

The use of coarser time-binning schemes have its own sets of limitations (e.g., skewed sampling and variable temporal duration) (**Paper I–IV**). Time averaging (i.e., temporally pooled assemblages) have the undesired effect of masking the true diversification patterns of clades (Hunt, 2004). A case in point, is the mid-Miocene decline in lamniform tooth disparity, which under an epoch-level time-binning scheme, was no longer returned as a phase of low disparity (**Paper III**). This shows how a higher degree of time-averaging can inflate variance and provide unreliable patterns.

Finally, my analysis of shark tooth shape and diet, establishes a relationship between feeding ecology and morphology in living lamniform and carcharhiniform sharks. However, the results also revealed that a lot of variation in tooth morphology remains unexplained (~50% in the full dataset: **Paper III**), suggesting that feeding selection pressures are insufficient to produce a one-to-one match between tooth shape and feeding ecology. This result is however expected in that sharks generally exhibit highly complex foraging behaviours which may override the tooth–diet signal (e.g., *G. cuvier* possess highly autapomorphic dentitions yet are generalized in their feeding ecology, an example of Liem’s Paradox). As it stands, there is a fair bit of ambiguity in what the morphological signal actually means. Factors, including body size, and other dental attributes (e.g., the number of teeth in the jaw and their sizes) should be incorporated as part of future research on shark ecomorphology.

## Conclusions and future prospects

My work clearly demonstrates the many strengths of exploring phenotypic variation of shark tooth morphology. More specifically, the ecomorphological relationship found in both lamniform and carcharhiniform sharks provide some support to the idea that we can interpret certain aspects of shark feeding ecology in the fossil record (e.g., across major radiation and extinction events) (**Paper I–IV**) through the use of teeth. Morphological patterns reconstructed over the last 83 million years suggest that lamniform and carcharhiniform sharks largely evolved into predominantly distinct areas of morphospace, which are likely related to the contrasting richness profiles observed between these sister-taxa in today's oceans. Based on the observations that diet and niche breadth only account for a moderate portion of shape, it is possible that other factors such as reproductive strategies and habitat specialisation (i.e., pelagic vs. slope/shelf environments) played key roles in facilitating, in part, the rise to ecological dominance of carcharhiniform sharks and the concomitant decline of lamniform sharks. These factors were however not tested for as part of the current study design, but should be explored in more detail in future research. Ultimately, both trait differentiation and adaptive capacity may explain the ability of some sharks to resist extinction more adamantly than others.

The story of lamniform and carcharhiniform sharks is not complete yet, as there is much more to be said about these majestic creatures. Lamniform shark diversity peaked during the Cretaceous — the terminal time period of the 'Age of Dinosaurs' — when lamniform sharks radiated as dominant marine predators alongside many marine reptiles. Conversely, the post-Mesozoic Era seemed to have slowly favoured the rise of carcharhiniform sharks — representing the most taxonomic shark clade in modern oceans. Understanding these complex patterns will require further investigation into how biotic and abiotic mechanisms have shaped their evolutionary trajectories.

On a methodological note, it is possible that the 2D geometric morphometric approach I've adopted here is too simplistic to characterise tooth morphology. Conversely, 3D approaches, such as orientation patch counting for measuring dental complexity or 3D shape analyses would be better. The OPC utilises GIS mapping techniques to map dental topography and tally the number of patches (surfaces) with a different orientation. This approach has been used to investigate mammalian ecomorphological patterns across the K/Pg boundary (Wilson *et al.*, 2012) and should more accurately represent complex dental

morphotypes (such as in Heterodontiformes which have clutching type teeth anteriorly and molariform teeth posteriorly: **Paper II**) and provide a better representation of serrations and striations that are difficult to investigate through morphometric techniques.

Finally, tracking clade-level shifts in oceanic systems would also benefit from continued exploration of regional patterns as oppose to the standard ‘global’ approach, which inevitably suffers from differential geographic sampling over time. This is because patterns of richness as described for many animal groups have been shown to correlate with the geographic size of the fossil record (Close *et al.*, 2017, 2020). The impact of differential geographic sampling on measures of disparity, however, remains underexplored. Significantly, the results of **papers II** and **IV** are among the first to demonstrate that regional and global disparity patterns do not always match. Such comparisons provide a more nuanced account of shark evolution and how they coped and responded to major Earth System events within the distant past, providing a much-needed context for equivalent dynamics in today’s oceans.

# Svensk sammanfattning

Hajar är en oerhört framgångsrik grupp av broskfiskar som uppstod redan under slutskedet av Ordovicium (ungefär 444 miljoner år sedan). Levande former uppvisar en fantastisk morfologisk diversitet och artrikedom. Det fossila registret av hajar är väldigt rikt men till skillnad från andra grupper av ryggradsdjur bevaras sällan mer än tänder. Detta reflekterar en kontrast mellan hajarnas mjuka och broskartade skelett, som lätt bryts ner och därför sällan fossiliserar, och deras motståndskraftiga, mineraliserade tänder som regelbundet tappas och ersätts under hela livet. Dessa tänder ger information om flertalet aspekter om hajarnas biologi, särskilt taxonomisk och morfologisk mångfald, uppkomst av nya grupper, utdöenden, evolution och födorelaterad ekologi. Bland levande hajar utmärker sig två grupper utöver det vanliga, nämligen ordningarna Lamniformes (håbrandsartade hajar) och Carcharhiniformes (gråhajartade hajar). I nutida marina miljöer är de gråhajartade hajarna ( $N > 290$  arter) den mest artrika gruppen bland samtliga hajar, medan de håbrandsartade hajarna är en relativt artfattig grupp med enbart 15 medlemmar (däribland Vithajen). Däremot tyder studier av fossil på att fördelningen av artrikedom var omvänd under slutfasen av den Mesozoiska eran, den period vi kallar för Krita: det fanns då betydligt fler håbrandsartade hajar än gråhajartade hajar.

Min avhandling fokuserar på dessa två grupper av hajar med det specifika ändamålet att rekonstruera deras evolutionshistoria genom storskaliga massutdöden och miljöförändringar över geologisk tid.

I det första kapitlet i min avhandling visar jag hur massutdöendet vid Krita/Paleogen-gränsen (K/Pg), för 66 miljoner år sedan, också satte sin prägel på hajarnas evolution. Mina resultat tyder på att K/Pg utdöendet ledde till en selektiv förlust av somliga tandformer associerade med stora rovdjur, samtidigt som andra grupper visar ett tydligt mönster av morfologisk diversifiering i efterdyningarna av massutdöendet (t.ex. hundhajar, medlemmar av den artrika ordningen gråhajartade hajar).

I mitt andra kapitel expanderar jag de tidsmässiga och taxonomiska ramarna för att utforska mönster (både utdöende och återhämtning) genom K/Pg-gränsen bland samtliga hajgrupper. Som en del av denna studie jämför jag dessutom globala och regionala signaler i syfte att utvärdera potentiella geografiska skillnader i hur hajar påverkats av massutdöendet. Mina resultat visar på att medlemmar av de håbrandsartade (Anacoracidae) drabbades hårdast bland hajar överlag. Däremot lyckades andra håbrandsartade hajar såsom



odontaspidida hajar inte bara överleva utan även diversifiera efter utdöende-perioden. På en global skala förblev hajarnas morfologiska disparitet oberörd, men i likhet med benfiskarna, ändrades sammansättningen av tandmorfologier efter massutdöendet.

I det tredje kapitlet undersöker jag förhållandet (dvs kovarians) mellan tandmorfologi och diet hos nulevande hajar och rekonstruerar den morfologiska evolutionen av de håbrandsartade och gråhajartade hajarna över en gemensam tidsperiod på 83 miljoner år. Mina resultat visar att K/Pg-utdöendet inledde en permanent separation av de två gruppernas morfologiska utveckling i ett så kallat 'morphospace' – ett matematiskt plan, vanligtvis multidimensionellt, med axlar som representerar omfånget av möjliga värden på fenotyper. Resultaten av denna studie visar dessutom att tidsperioden Miocen (~ 23–5.3 miljoner år sedan) representerar en ekologisk vändpunkt för de håbrandsartade hajarna, med rekordlåg disparitet, på en nivå som överensstämmer med hypotesen om ett skifte till en mer specialiserad diet bland topprovdjur såsom *Otodus megalodon*.

Dessutom visar jag för första gången ett entydigt samband mellan tandform och diet hos levande hajarter och hur de flesta levande håbrandsartade hajar i genomsnitt är dietspecialister medan de flesta gråhajartade arter upptar mellanpositioner inom ett specialist-generalist-spektrum. Utifrån dessa resultat lägger jag fram hypotesen att den moderna ojämna fördelningen av artrikedom mellan de håbrandsartade och gråhajartade hajar delvis har uppstått som ett resultat av tidigare trofiska anpassningar, särskilt tillgången på resurser.

Det fjärde kapitlet behandlar den tidiga evolutionen av de håbrandsartade hajarna långt innan K/Pg-massutdöendet. Mer specifikt undersöker jag två aspekter av deras utveckling under den mellersta fasen av Kritperioden baserat på ett geografiskt lokaliserat prov som erhållits från australiensiska lokalteter. Mina resultat tyder på att de håbrandsartade hajarna inte ökade i antal genom Alb-Cenomangränsen (~100 miljoner år sedan) vilket står i strid med både globala mönster och hypotesen att gruppen genomgick en adaptiv diversifiering under denna tid. I rådande stund är det också oklart om gruppen ökade i disparitet genom detta tidsintervall. Övergången mellan Cenoman och Turon (93.9 miljoner år sedan) visar likaså ingen större skillnad i dispariteten bland de håbrandsartade hajarna. Mer detaljerade mönster tyder däremot på att somliga grupper såsom sandtiger-hajar återhämtade sig under den tidiga Turon. Denna fas utmärker sig främst av ett globalt utbrett syrefattigt tillstånd (betecknat som OAE2) i haven som kan ha orsakat omfattande utdöende bland diverse djupshavsgrupper. Mina resultat visar att inverkan av OAE2 troligvis varierat geografiskt och haft ett flertal effekter på sammansättningen och mångfalden av håbrandsartade hajar.

## ملخص باللغة العربية

البحوث العلمية التي أجريتها في إطار هذه الأطروحة تجمع أروع ما في عالمي البيانات التحليلية المعقدة التي يوفرها السجل الأحفوري والدقة التحليلية لتقنيات قياس التشكل. هدفي هو تفسير الآليات المسؤولة عن تنوع وانقراض أسماك القرش في العصور الجيولوجية القديمة (المنشورات 1-4). وبشكل أدق، تملاً بحوثي فجوة ملحوظة في فهمنا لتطور أسماك القرش من خلال النظر إلى كيفية تغير شكل الأسنان عبر العصور.

في الفصل الأول من هذه الرسالة (المنشور 1)، أوضحت كيف أن الانقراض الجماعي في نهاية العصر الطباشيري (قبل 66 مليون سنة)، ترك بصماته أيضاً على تطور أسماك القرش. وتشير نتائج بحوثي إلى أن فترة الانتقال بين العصرين الطباشيري والباليجيني (حدث K/Pg أدت إلى: 1) الانقراض الانتقائي للأنماط المورفولوجية للحيوانات المقترسة الضخمة في أعلى السلاسل الغذائية (2) كما كان بمثابة محفز للتنوع المورفولوجي لبعض الأصناف مباشرة عقب الانقراض (مثلاً، triakid carcharhiniform أسماك القرش من نوع triakid carcharhiniform).

في الفصل الثاني (المنشور 2)، قمت بتوسيع النطاق الزمني والتصنيفي لإعادة تصور ديناميكا الانقراض خلال فترة الانتقال K/Pg. ليشمل جل المجموعات الرئيسية لأسماك القرش. في هذا الصدد، أجريت مقارنة شاملة للدلالات العالمية والإقليمية، ولتباين التركيبات الزمكانية الخاصة بأسنان أسماك القرش خلال الحدث K/Pg. ما أستنتجه هو أن القروش الصفيحية من نوع (Anacoracidae) تمثل الفئة الأكثر تضرراً خلال فترة الانقراض. على الرغم من ذلك، يبدو أن أسماك القرش الصفيحية قد استجابت بطرق مختلفة وهو ما يتضح من خلال إشعاع عناصر نوع odontaspids بعد الانقراض. علاوة على ذلك، يظهر أن التباين الكلي بين أسماك القرش خلال حدث الانقراض كان مستقرًا على مستوى العالم، بينما شهدت بعض مجموعاتها تحولات تركيبية في مورفولوجيا الأسنان في أعقاب هذا الحدث.

في الفصل الثالث (المنشور 3)، بحثت في العلاقة (والمقصود هنا التغيرات) بين مورفولوجيا الأسنان وايكولوجيا التغذية لدى أسماك القرش الحية وأعدت بناء التطور المورفولوجي لشكلي Lamniformes و Carcharhiniformes لفترة زمنية تمتد على مدى 83 مليون سنة. تظهر نتائجي أن الفصل المورفولوجي هو الذي يميز تطور شكلي Lamniformes و Carcharhiniformes وليس التداخل التنافسي. علاوة على ذلك، أثبت لأول مرة وجود علاقة واضحة بين شكل الأسنان والنظام الغذائي لدى أنواع أسماك القرش الحية وأثبت أن معظم الأشكال الحية من نوع Lamniformes متخصصة، في المتوسط، في التغذية، بينما تصنف معظم أنواع carcharhiniform في مواقع وسيطة من الطيف كمتخصصة-عامة. بناءً على هذه النتائج، أقترح فرضيتين متناقضتين لتطور شكلي Lamniformes و Carcharhiniformes (1: التخصص الايكولوجي المقترن بتقلص موطن العيش أدى إلى تدمير مجموعة Lamniformes و (2) تعميم الظروف الايكولوجية أدى إلى توسع هيمنة نوع Carcharhiniformes).

الفصل الرابع (المنشور 4)، يهتم بالإشعاع المبكر لأشكال lamniforms، قصد استكشاف الأنماط قبل حدث K/Pg. وبأكبر دقة، استكشف خاصيتين من إشعاعات أسماك قرش lamniforms من حقبة منتصف العصر الطباشيري من خلال عينة معروفة المصدر من الأحواض الأسترالية.

تتضمن النتائج الرئيسية التي توصلت إليها ما يلي: (1) زيادة ملحوظة في تباين أسماك قرش lamniforms خلال فترة الانتقال بين العصرين الطباشيريين المبكر والمتأخر (100.5 مليون سنة) والتي نعزوها إلى الظروف البيئية المختلفة التي تؤثر على مواطن القروش في الأنظمة البحرية القارية و المقابلة للجرف القاري، والانحراف الجيني الناتج عن ارتفاع عدد العينات الفتية في بعض التجمعات المحلية. (2) التباين الثابت لدى أسماك قرش lamniforms خلال حدود C/T مع إعادة تنظيم إيكومورفولوجي داخل المجموعة يؤثر بشكل أساسي على قروش carchariids صغيرة الجسم (قرش النمر الرملي). نفس هذا على أنه استجابة محتملة لإعادة تشبع المياه العميقة بالأكسجين بعد OAE2. وبالتالي، تدعم نتائجنا تأثير OAE2 المتنوع عالميًا على مجموعات أسماك قرش lamniform، مع وجود أنظمة إيكولوجية إقليمية مختلفة تثبت درجات مختلفة من تداول المجموعات وركودها و/أو تعديلها التكيفي.

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يا أمي بدونك أنا لا شيء

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