

# The genetics-morphology-behaviour trifecta: unravelling the single greatest limitation affecting our understanding of chondrichthyan evolution

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## Abstract

Sharks, rays and chimaera form the clade Chondrichthyes, an ancient group of morphologically and ecologically diverse vertebrates that has played an important role in our understanding of gnathostome evolution. Increasingly studies have been seeking to investigate evolutionary processes operating within the chondrichthyan crown group, with the broad aim of understanding the driving forces behind the vast phenotypic diversity observed amongst its constituent taxa. Genetic, morphological and behavioural studies have all contributed to our understanding of phenotypic evolution yet are typically considered in isolation in the context of Chondrichthyes. I argue that integrating these core fields of organismal biology is vital if we are to understand the evolutionary processes operating in contemporary chondrichthyan taxa, and how such processes have contributed to past phenotypic evolution. In light of the global extinction crisis facing this clade, this understanding is crucial if we are to successfully conserve rapidly declining chondrichthyan populations.

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## Statements and declarations

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JHG conceptualised the study and prepared the entirety of the manuscript.

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No experimental work was carried out at any point during this study, either involving animals or otherwise.

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There is no data to be archived associated with this study

## Abstract:

Sharks, rays and chimaera form the clade Chondrichthyes, an ancient group of morphologically and ecologically diverse vertebrates that has played an important role in our understanding of gnathostome evolution. Increasingly studies have been seeking to investigate evolutionary processes operating within the chondrichthyan crown group, with the broad aim of understanding the driving forces behind the vast phenotypic diversity observed amongst its constituent taxa. Genetic, morphological and behavioural studies have all contributed to our understanding of phenotypic evolution yet are typically considered in isolation in the context of Chondrichthyes. I argue that integrating these core fields of organismal biology is vital if we are to understand the evolutionary processes operating in contemporary chondrichthyan taxa, and how such processes have contributed to past phenotypic evolution. In light of the global extinction crisis facing this clade, this understanding is crucial if we are to successfully conserve rapidly declining chondrichthyan populations.

**Key words:** natural selection – Elasmobranchii – shark – ecomorphology – quantitative genetics

## Overview

Sharks, rays, and chimaera form the clade Chondrichthyes, a group of cartilaginous fishes that first arose during the Palaeozoic and has subsequently survived at least five mass extinction events (Stiassny et al., 2004; Soldo, 2013). Over the course of its long history the clade has undergone major transitions in diversity (Grogan et al., 2012; Kriwet and Benton, 2004; Kriwet and Klug, 2008), however remains a morphologically and ecologically diverse component of modern ecosystems (Cailliet et al., 2005; Compagno, 2008; Kolmann et al., 2022; Stein et al., 2018), performing various important ecological functions (Flowers et al., 2021; Heupel et al., 2014; Navia et al., 2010). Chondrichthyan taxa have long been influential in studies of vertebrate, and particularly gnathostome evolution (Gillis et al., 2009; Smith, 2003). As the basal-most extant crown gnathostomes chondrichthyans are frequently used to represent the ancestral gnathostome condition when considering evolutionary transitions in specific morphological/developmental characters (Gillis et al., 2013; Mallatt, 1996). Chondrichthyan taxa have also been used as case studies for phenomena such as genetic conflict (Crespi and Semeniuk, 2004; DiBattista et al., 2008). Unfortunately, chondrichthyans are currently facing a global extinction crisis (Stein et al., 2018), with over 300 species vulnerable to extinction (Dulvy et al., 2021). For this reason, it has never been more important to improve our understanding of chondrichthyan evolution – particularly in the context of contemporary populations.

The fields of genetics, morphology and behaviour have each played important roles in our understanding of evolution. Phylogenetics has revolutionised our understanding of phenotypic evolution and interrelationships (Lee and Palci, 2015; Naylor et al., 2005), whereas morphological and behavioural studies have both provided insight into how organisms interact with other components of the ecosystem (Wainwright, 1994; Wainwright, 1996) and the evolutionary processes operating within natural populations (Davies et al., 2012; Le Roy et al., 2019; Owens, 2006). Whilst important in isolation, it is the interplay between genetics, morphology and behaviour that is most significant for understanding evolutionary processes, their phenotypic consequences, and how such phenotypes engage with the wider ecological community (Lewontin and Krimpas, 2000; Owens, 2006; Wainwright, 1994). Regrettably studies of chondrichthyan evolution rarely unify these concepts, fundamentally limiting our ability to identify and understand the nature of evolutionary processes operating in this clade.

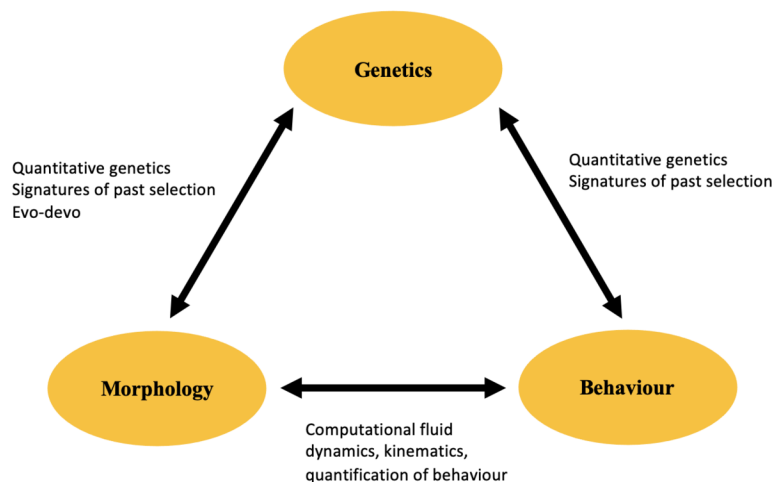
Here I explain how this failure to integrate between core fields of organismal biology has significantly hampered our understanding of chondrichthyan evolution, both past and present. I provide reasons for such failures as well as potential solutions and examples of their application in other taxa. I suggest that integration of genetics, morphology and behavioural studies is crucial to our understanding of phenotypic evolution in both past and present chondrichthyan populations.

## Linking morphology to genetics

Comparative morphological studies of vertebrate anatomy and morphogenesis have contributed significantly to our understanding of evolutionary history and taxonomic interrelationships (Lee and Palci, 2015), and this is no different in Chondrichthyes (Naylor et al., 2005; Shirai, 1996). Despite this, the interrelationships of various chondrichthyan subclades have long been debated (Klug, 2010; Naylor et al., 2005; Qiao et al., 2016), and it is only relatively recently, upon the development of molecular phylogenies with high taxonomic coverage (Naylor et al., 2005; Stein et al., 2018) that these controversies have been resolved. Phylogenetics is likely the most universally applicable integration of genetics and morphology, however increasingly evolutionary-developmental (evo-devo) studies and evolutionary genetics are being used to uncover the genetic basis of morphological traits (Abzhanov et al., 2002; Mallarino and Abzhanov, 2012) and the selective regimes under which they have evolved (Ho et al., 2017; Rolland et al., 2018). Evo-devo studies targeting chondrichthyan taxa are present in the literature, yet these target the expression of a small number of morphological characters in a minute proportion of extant species (Gillis et al., 2009; Gillis et al., 2013). Besides this, we have extremely minimal knowledge of the genetic and developmental underpinnings of morphological variation in Chondrichthyes.

This of course represents a knowledge gap in itself, but also fundamentally constrains our ability to understand morphological evolution within Chondrichthyes. Most such studies rely on an ecomorphological approach (Gayford et al., 2023) under the assumption that ecological selection is dominant and has shaped the evolution of morphological structures (Andrew-Barr, 2018). Crucially, these studies typically negate the potential role of constraint in morphological evolution (Gayford et al., 2023). The importance of these constraints to morphological evolution in other taxa is well known (Beldade et al., 2002; Wagner, 1996), however such an understanding relies upon knowledge of the genetic architectures or gene regulatory networks underlying morphology (Davidson and Erwin, 2006; Hegmann and Possidente, 1981). Evolutionary constraints such as genetic correlations can substantially alter the pace of evolution by modulating the response to selection (Crespi, 2000; Greenbury et al., 2016), whilst others such as lack of additive variance can make ‘optimal’ genotypes effectively unattainable (Hansen et al., 2003) or result in maladaptive evolution (Crespi, 2000). There is debate surrounding the extent to which short-term genetic constraints influence long-term evolution (Dooren, 2020; Hadfield et al., 2007), however even if we ignore mounting evidence regarding the importance of such constraint to past evolution (Futuyma, 2010), the relevance of these concepts to the immediate future of chondrichthyans and their contemporary evolution is unquestionable: in light of their dire conservation status (Dulvy et al., 2021; Stein et al., 2018), low fecundity, and long generation times (Cailliet et al., 2005), an understanding of the extent to which constraint may influence future morphological adaptation to environmental change should be one of the key priorities of contemporary chondrichthyan evolutionary research.

There are several explanations for the lack of previous integration between morphological and genetic studies of chondrichthyan evolution. In the case of evo-devo studies, research effort appears to be the primary limitations, with only a relatively low number of morphological structures considered from a handful of species (Gillis et al., 2009). Conducting such studies in a greater range of taxa would increase our understanding of the genetic basis of morphological variation within Chondrichthyes and the extent to which evolutionary constraints relating to gene regulatory networks appear to be present (Figure 1). Quantitative genetic studies of chondrichthyan populations have previously been limited by the costs of genome sequencing however technological advances are rapidly increasing the accessibility of sequencing technologies (Mardis, 2017). The requirement of pedigree information for quantitative trait loci (QTL) and genome wide association studies (GWAS) also provides a limitation to their usage in wild populations (Day-Williams et al., 2011). Recent advances have softened this requirement, with several routes available for quantitative genetic analyses in wild populations where pedigree information is absent (Johnston et al., 2022). Finally, where the genetic basis of morphological traits is known, signatures of past selection can be detected through phylogenetic analysis (Vitti et al., 2013). These methodologies are not mutually exclusive, and should all contribute to future research, through which we can improve our understanding of past morphological evolution and future ‘evolvability’ of morphological traits in chondrichthyan taxa.



**Figure 1: Methodologies that can be utilised to increase integration between genetic, behavioural, and morphological studies of chondrichthyan evolution**

### Linking behaviour to genetics

Whilst there is no consensus definition of behaviour in the literature (Levitis et al., 2009), behavioural traits do not differ fundamentally from any other class of traits, and many have been shown to have some degree of genetic underpinning (Bleakley et al., 2010; Fitzpatrick et al., 2005). Studying behaviour in extinct species is challenging (Hsieh and Plotnick, 2020), and understanding the relevance of behavioural studies to past evolutionary events can be difficult. Nevertheless, integrative studies combining genetics and behavioural ecology are essential to our understanding of the adaptive value (or lack thereof) of behaviours (Penke et al., 2007). This is of paramount importance to our understanding of evolution both past and present given that behaviour is the suite of traits by which ecological interactions (both inter and intraspecific) are directly mediated. Unfortunately, our understanding of chondrichthyan behaviour (Bres, 1993; Guttridge et al., 2009), let alone the genetic basis of behaviour is severely limited. This hampers our understanding of chondrichthyan evolution in much the same way as a lack of integration between morphology and genetics: without an understanding of the genetic architectures and adaptive landscapes underlying behavioural traits we are fundamentally constrained in our ability to understand behavioural evolution, how it has contributed to the evolution of phenotypic diversity observed in extant taxa, and how it may influence organismal evolution in the face of rapid environmental change. Of particular importance to contemporary populations, it is not possible to evaluate the posited ‘special’ role of behaviour in evolution without an understanding of the genetic basis of behavioural traits (Levis and Pfennig, 2016; McGlothlin and Brodie III, 2009).

The importance of behaviour to evolution has long been understood (Corning, 2014), however recent integrative studies combining genetics and behavioural ecology point towards two phenomena of particular importance to our understanding of contemporary chondrichthyan evolution. Indirect genetic effects (IGEs) occur the genotype of one individual alter the phenotype of another (Wolf et al., 1998). These effects – which are often cryptic and difficult to detect – are important in an evolutionary context as they can modulate the response to selection (McGlothlin and Brodie III, 2009), thus acting as ‘pacemakers’ of adaptive evolution (Bailey et al., 2018). The other phenomenon of particular importance is plasticity first evolution – the proposition that phenotypic plasticity (including behaviour, which is intrinsically plastic) may precede and facilitate adaptive evolution by providing the ‘raw material’ upon which selection can act in the absence of

de novo, mutation-based adaptations (Levis and Pfennig, 2016; Perry et al., 2018). This, like IGEs, could increase the rate at which adaptive evolution occurs, although debate exists regarding the validity of such hypotheses (Levis and Pfennig, 2016). As many chondrichthyan populations have low effective population sizes (Pazmiño et al., 2017) and long generation times (Cailliet et al., 2005), both IGEs and plasticity first adaptations could play a major role in determining the vulnerability of contemporary populations to rapid environmental change, yet until now both of these phenomena have been ignored in the context of chondrichthyan evolution.

This lack of integration is driven by many of the same limitations affecting integration between genetics and morphology, and as such can be overcome using broadly similar methodological approaches (Figure 1). Studies of past selection may provide valuable insights into the evolution of behavioural traits (Eusebi et al., 2018; Grams et al., 2015), and quantitative genetic studies are valuable not only for uncovering the genetic basis of these traits (Bubac et al., 2020) but for providing direct evidence of IGEs and plasticity first evolution. The major difference is that whilst morphology is easily quantified, relatively little is known about chondrichthyan behavioural ecology (Bres, 1993; Guttridge et al., 2009), and most existing studies are descriptive or qualitative in nature. This will have to be overcome before quantitative genetic methodologies can be applied, and thus I suggest that future studies of chondrichthyan behaviour must focus on quantifying behavioural variation within and between populations.

### Linking morphology to behaviour

Uncovering the genetic basis of behavioural and morphological traits and the factors influencing their evolution is undoubtedly of great significance, yet this only provides one half of the story; it is one thing to establish the mechanisms of evolution and their phenotypic consequences, but another entirely to elucidate the functional link between them. The associations between morphology and behaviour are perhaps the best-studied of the three integrative pathways discussed here as in a broad sense uncovering these associations is the express goal of functional morphology (Wainwright, 1994). Several experimental studies have addressed the functional significance of chondrichthyan morphology (Wilga and Lauder, 2004a). As a result, the contribution of structures such as the dorsal, caudal, and pectoral fins to locomotor performance in elasmobranchs is relatively well understood (Maia and Wilga, 2013; Wilga and Lauder, 2001; Wilga and Lauder, 2004b). There are however several major limitations of this approach that constrain integration between morphological and behavioural studies. This experimental approach rarely captures ecologically relevant complex behaviours, and where it does, influence of the laboratory setting on expressed behaviour cannot be ruled out (Moore and Biewener, 2015). Moreover, population and species-specific morphologies (Grover, 1972; Keeney and Heist, 2006; Sternes and Shimada, 2020) mean that there is little reason to suggest that existing kinematic studies should be representative of all – or even a substantial proportion of extant chondrichthyan diversity. The lack of studies linking morphology to complex behaviours in wild populations fundamentally constrains our understanding of evolution as without such studies the true adaptive value of morphology. This in turn constrains our understanding of ecological interactions, the evolution of complex behaviours such as foraging strategies, and how future environmental change may influence them. Novel technological advancements are increasingly enabling quantitative study of chondrichthyan behaviour in wild populations (Butcher et al., 2021; Renshaw et al., 2023) and thus with sufficient research effort this knowledge gap is likely to decrease, however significant further study combining experimental and observational approaches will be required in order to achieve this goal.

### Conclusions:

Much progress has been made in recent years towards understanding chondrichthyan evolution and ecology. However, it is undeniable that many major knowledge gaps remain, and in particular our understanding of trait evolution in this clade is less robust than in many other vertebrate radiations. I argue that the key driver of this uncertainty is a lack of integration between genetic, morphological, and behavioural studies. Failure to integrate these key areas of organismal biology fundamentally constrains our understanding of phenotypic evolution, both past and present. Most significantly, this impedes study of the genetic architectures underlying phenotype and how selection acts upon them. Despite this, the necessary tools to overcome this major

limitation already exist and have been applied to other taxa (Figure 1). Future studies should focus on increasing the taxonomic breadth of existing studies of chondrichthyan genetics, morphology, and behaviour, as well as the implementation of more quantitative genetic approaches. Only though this will we truly be able to understand trait evolution in Chondrichthyes to a comparable extent to other major vertebrate radiations, and its implications for past evolution and vulnerability in the face of climate change.

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