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The Evolution of Sea Turtles

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Chapter 1

Introduction

Sea turtles are the last of the Mesozoic marine reptiles. Today they are an instantly recognisable group from their numerous marine adaptations, such as their flippers, large body size, hydrofoil carapace, and non-retractable head. Their most prominent feature is the large fore flippers which are formed from elongated phalanges, and continuous soft tissue covering with no separation of digits (Pritchard and Trebbau 1984; Wyneken and Witherington 2001). Their hind limbs are far smaller and quite stiff, acting as rudders rather than being actively involved in propulsion (Wyneken 1996). Though these features seem ubiquitous amongst modern sea turtles these structures evolved quite gradually within sea turtles, with independent acquisitions of some features (Zangerl 1980; Evers *et al.* 2019).

There are many studies examining their biology, life history, diet, and ecology (e.g. Pritchard and Trebbau 1984; Dodd 1988; Walker and Tisdale 1990; Wyneken 1996; Wyneken and Witherington 2001; Bartol and Musick 2002; Bjorndal 2003; Bolten 2003; Houghton *et al.* 2008; Snover *et al.* 2010; Jones *et al.* 2012; Piniak *et al.* 2012; Goshe *et al.* 2016). They have a near global distribution concentrated within the tropics, but spread as far north as Alaska, and as far south as the southern tip of Argentina (Bowen and Karl 2007). Sea turtles have a relatively good fossil record, being a consistent presence in shallow marine environments for over 70 million years. Despite the charismatic nature of the group, the plentiful ecological studies, and long fossil record, much of the evolutionary story of sea turtles remains unexplored. The shape of their phylogenetic tree is constantly changing, adaptive signals and mechanisms have rarely been quantitatively examined, even the story of how or when they adapted to marine life is contentious.

Sea turtles are important tourist attractions for many cities and nations (Tisdell *et al.* 2001; Bjorndal and Jackson 2002; Wilson and Tisdell 2003), the face of many conservation

campaigns, and are keystone species in coastal environments (Jackson *et al.* 2001; Bjørndal *et al.* 2002). They are a significant part of many coastal cultures as well as being an important source of food (Campbell 2003).

With my thesis I plan to holistically examine the evolution of this charismatic group and shed light on the factors which have contributed to their current success for a focus on skull anatomy. I aim to do this by clarifying the phylogeny of the crown group by re-examining the cranial characters of the least studied species *Natator depressus*. Using these insights, I shall apply total evidence tip-dating analyses to both modern and extinct species to examine the structure of the tree and identify any significant points of extinction or radiation. I aim to examine cranial shape across modern taxa to identify the most significant determinants of shape. I also shall examine the cranial shape of extinct taxa. This will be used to examine the cranial morphospace occupied by sea turtles, with the intention to potentially identify any patterns related to changes in disparity, phylogenetic relationships, and ecomorphology.

PHYLOGENY

Modern turtles (Testudinata) are divided into two major groups, Pleurodira and Cryptodira (Krenz *et al.* 2005; Joyce 2007; Crawford *et al.* 2015; Fig 1.). The two groups have historically been distinguished by the method of neck retraction: Pleurodira retract their neck in the horizontal plane under the rim of their carapace whereas Cryptodira retract their neck in the sagittal plane within their body cavity (Joyce 2007). Morphological and molecular data both support hypotheses that this difference in neck retraction reflects phylogenetic affinity (Gaffney and Meylan 1991; Joyce 2007; Crawford *et al.* 2015). Both morphological and

genomic data place Chelonioidea within Cryptodira (Krenz *et al.* 2005; Crawford *et al.* 2015). However, the morphological signal is not as strong within the two major groups and resolving phylogenetic relationships within Cryptodira has been difficult. Both morphological data and molecular data have yielded varying results (Gaffney and Meylan 1988; Krenz *et al.* 2005; Crawford *et al.* 2015). Chelonioidea (Cheloniidae + Dermochelyidae) share a distinct morphology among turtles: enclosed box-like skull, flippers, and a streamlined shell. This specialised anatomy made placing them within the larger testudine family tree difficult. Until large scale genomic datasets were available the position of Chelonioidea in relation to other groups was uncertain (Gaffney *et al.* 1987; Gaffney and Meylan 1991; Shaffer *et al.* 1997; Krenz *et al.* 2005). However, a consensus has recently become established: Trionychia as the least nested group, with the rest of the cryptodires divided between Testudinoidea and Americhelyidia. Modern genomic analyses place Chelonioidea nested within Americhelyidia with Chelydridae (snapping turtles) and Kinosternoidea (mud and musk turtles) (Krenz *et al.* 2005; Parham *et al.* 2006; Crawford *et al.* 2015). Multiple turtle lineages have invaded the marine environment, both from within and outside of Cryptodira (summarised in Evers and Benson 2019). The notable clades include the pleurodire families Bothremyidae (Gaffney *et al.* 2006) and Stereogynia (Ferrira *et al.* 2015), and the stem turtle groups Thalassochelyidia (Gaffney 1975; Joyce *et al.* 2021) and Sandownidae (Meylan *et al.* 2000). How many times turtles have invaded the marine realm is currently up for debate. Due to the uncertain placement of several stem groups, even within Chelonioidea, the number of times marine incursion has occurred is uncertain (Hirayama 1994; Joyce 2007; Evers *et al.* 2019). In particular, the position of Protostegidae, a third entirely extinct family of sea turtles, has been contentious (Fig 2), and its position has significant implications for the number of times testudines evolved for a marine lifestyle. In

this thesis the term “sea turtle” exclusively refers to Pan-Chelonioidea (Protosetgidae + *Toxochelys* sp. + Chelonioidea) as the clade including all turtles that are more closely related to the modern marine turtles than to any other turtle clades.

Today there are seven species of sea turtles within two families, Cheloniidae and Dermochelyidae (Fig 2.). Six out of seven species belong to Cheloniidae: *Natator depressus* (flatback), *Chelonia mydas* (green), *Eretmochelys imbricata* (hawksbill), *Caretta caretta* (loggerhead), *Lepidochelys olivacea* (olive ridley), and *Lepidochelys kempii* (Kemp’s ridley). Within Cheloniidae, the genera *Caretta* and *Lepidochelys* are grouped within Carettini. Outside Cheloniidae, the monotypic Dermochelyidae includes only *Dermochelys coriacea*, the leatherback sea turtle. DNA sequence data consistently support a phylogenetic hypothesis for the group, with both mitochondrial and nuclear data recovering the same topology (Fig. 4) (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012). Morphological phylogenetic studies, by contrast, have struggled to arrive at a consensus. In particular, the positions of *N. depressus* and *Er. imbricata* have shifted throughout the tree (Hirayama 1994; Dutton *et al.* 1996; Parham and Fastovsky 1997; Lynch and Parham 2003). Using quantitative phylogenetic methods, the topology found by molecular methods has never been found using purely morphological data (Hirayama 1994; Dutton *et al.* 1996; Hirayama 1998; Lynch and Parham 2003). The seeming unreliability of morphological data, as currently represented, in reconstructing sea turtle phylogeny hinders our ability to examine the relationship of the crown group compared to the stem. A re-examination of the morphology of modern species is therefore needed. To both improve the data set available for phylogenetic reconstruction and see whether a better agreement between the molecular and morphological data can be discovered. In addition, having a more reliable

morphological data set will improve confidence in the base of comparison to extinct taxa and a more robust phylogeny for Pan-Chelonioidea.

The current phylogenetic stability based on molecular data of the crown group belies the uncertainty of the evolutionary history of the stem. The timing and origin of Chelonioidea is contentious, largely due to the unclear position of Protostegidae (Hirayama 1994; Kear and Lee 2006; Joyce 2007; Cadena and Parham 2015; Evers and Benson 2019). Their placement in relation to Chelonioidea has been highly unstable (Fig. 3). Historically, they have been united with Dermochelyidae forming a clade sister to Cheloniidae (Cadena and Parham 2015; Evers and Benson 2019). Recently it has been suggested that Protostegidae sit either as sister to a clade formed by Dermochelyidae and Cheloniidae (Evers *et al.* 2019), or as sister to Cryptodira and represent an independent incursion into the marine environment (Joyce 2007; Anquetin 2012). The latter has been suggested as protostegids retain some “primitive” morphological characters that are not found in other families (Joyce 2007). Their position outside of Cryptodira would also simplify the biogeography for marine sea turtles, removing a long ghost lineage through the early and middle Cretaceous between the node of protostegids and Chelonioidea. As stated above, the position of Protostegidae has a significant impact on the evolutionary history of marine adaptations in testudines (Evers *et al.* 2019). An independent acquisition of the distinguishing flippers and carapace shape found in modern sea turtles would suggest a strong convergent signal between the groups. A strongly convergent morphology may suggest a limited and highly channelised morphological response to the adaptive requirements of marine life.

There appears to have been an evolutionary grade of early less marine sea turtles during the Late Cretaceous, particularly in North America (Gentry 2017; Gentry *et al.* 2019). These

species were previously classified as Toxochelyidae, named after the best-known member *Toxochelys lateremis*, however Toxochelyidae is now considered a paraphyletic group representing a grade of turtles before the origin of Chelonioidea (Gentry *et al.* 2019). *Toxochelid* grade sea turtles show some adaptations for marine life such as a more hydrodynamic shell and fore flippers (Hirayama *et al.* 1994; Gentry 2017; Gentry *et al.* 2019). However, they lack several more advanced adaptations associated with marine life such as their phalanges are not as elongate or as rigid, they lack a strongly curved scapula, and their humerus is not as enlarged as is seen in either protostegids or cheloniioids (Hirayama 1994; Evers *et al.* 2019).

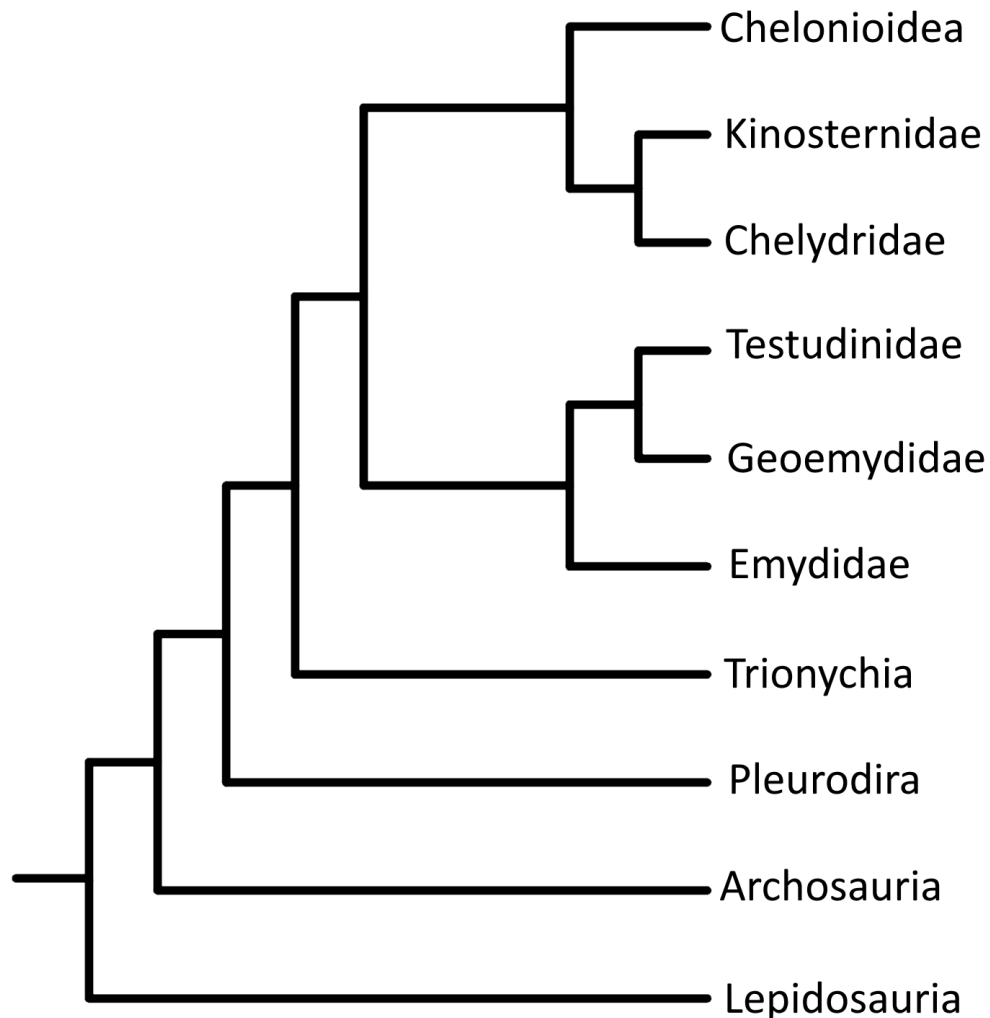


Figure 1. Phylogram displaying the current consensus tree showing the interrelationships of Testudinata as well as their position within Diapsida as sister to Archosauria. Redrawn from Crawford *et al.* (2015)

The evolutionary history of the two modern families of sea turtles is also largely unclear.

Dermochelyidae is poorly represented in the fossil record, likely due to an early adaptation to a more pelagic lifestyle (Nielson 1959; Hirayama 1997) and the comparative fragility of their skeletons (Pritchard and Trebbau 1984). They appear to have first appeared in the Late Cretaceous with such species as the Japanese *Mesodermochelys undulatus* and possibly *Allopleuron hoffmani* (Gentry *et al.* 2019), though this relationship is not widely supported.

Early members of Cheloniidae appear at the same time and have a much more extensive fossil record than Dermochelyidae.

The stem of Cheloniidae is phylogenetically unstable and has never reached anything approaching a consensus topology. This problem exists despite the existence of well-preserved specimens from much of the Late Cretaceous and Cenozoic (Moody 1974; Gaffney 1979; Weems 1980; Lynch and Parham 2003; Tong and Hirayama 2008; Matzke 2009; Parham and Pyenson 2010; Tong *et al.* 2012; Parham *et al.* 2014; Weems and Sanders 2014; Gentry 2017; Weems and Brown 2017; Myers *et al.* 2018; Gentry *et al.* 2019). The Palaeocene and Eocene have an abundance of well-preserved species, particularly from Europe, such as *Puppigerus camperi*, *Argillochelys cuniceps*, *Eochelone brabantica*, and *Erquelinnesia gosseleti* (Gaffney 1979). There are also well-preserved specimens from around the world including North America, South America, Africa, and Asia (Lynch and Parham 2003; Tong and Hirayama 2008; Parham and Pyenson 2010; Tong *et al.* 2012; Myers *et al.* 2018). The position on the cheloniid tree for these species is rarely if ever consistent between studies (Hirayama 1994; Lynch and Parham 2003; Brinkman *et al.* 2009; Parham and Pyenson 2010; de Broin *et al.* 2014; Weems and Brown 2017). This lack of clarity is likely due to widespread homoplasy between groups as well as a lack of detailed morphological description for many species, including modern species such as *N. depressus* (Kesteven 1911; Gaffney 1979; Pritchard and Trebbau 1984; Zangerl *et al.* 1988; Jones *et al.* 2012). The extinct species which do not have any well preserved cranial material are particularly vulnerable to this instability as most analyses have character matrices heavily weighted towards cranial characters (Hirayama 1994; Parham and Pyenson 2010; Caden and Parham 2015; Evers *et al.* 2019). The lack of knowledge about the evolution of Cheloniidae post K-Pg extinction greatly hinders our fundamental knowledge of this group, and how they respond

to changing environmental and climatic conditions. It prevents meaningful ancestral state estimation as well as analyses of adaptive radiation and parallel evolution (e.g. Tseng 2013).

Most morphology-based phylogenetic studies find a unified cheloniid crown with few finding any extinct species nested within (Hirayama 1998; Parham and Pyenson 2010; Weems and Brown 2017; Evers *et al.* 2019). The fossil record of the crown is sparse, with undoubted modern species recovered from only a few sites (Dodd *et al.* 1992; Zug 2001). This paucity of fossils has made dating the origin of the crown difficult. Most estimates rely on molecular clock techniques (Duchene *et al.* 2012; Crawford *et al.* 2015; Thomson *et al.* 2021) that must be calibrated based on the limited fossil record of modern taxa. Estimates for the origin of the crown range from 50 Ma estimated using mitochondrial DNA (Duchene *et al.* 2012) to roughly 20 Ma using nuclear DNA (Thomson *et al.* 2021). There is a similar disparity in dates when looking at nodes within the clade (Duchene *et al.* 2012; Thomson *et al.* 2021). Expectedly more recent divisions have smaller error bars, and hypotheses for their diversification have been proposed. For example, the recently diverged *L. kempii* is thought to have likely originated 2.5-5 Ma during the formation of the isthmus of Panama dividing the pacific and Atlantic populations of *L. olivacea* (Bowen and Karl 2007; Naro-Maciel *et al.* 2008; Duchene *et al.* 2012).

One significant problem in understanding the timing of the evolution of Cheloniidae is a lack of fossil calibration. Studies which have examined the evolutionary rates and timing in Testudinata have used node dating, with the only calibration for Chelonioidea being the split of Dermocheyidae and Cheloniidae (Thomson *et al.* 2021). The lack of stability of the cheloniid tree makes node dating difficult as no node is stable enough to act as a calibration point (Ronquist *et al.* 2012). Tip dating analyses allow for analysis of groups without stable

fossil phylogenies, by not presuming any topologies as a node dating approach does. The use of tip dating analyses with morphological datasets has shown some capacity to untangle convergent morphological signals which have muddled the phylogenetic histories of many groups (Ronquist *et al.* 2012; Babst *et al.* 2016; Lee and Yates 2018). Tip dating techniques could not only help potentially untangle cheloniid relationships but shed light on greater macroevolutionary patterns. These new techniques could help address questions such as how many times sea turtles evolved specialised marine adaptations, and when did the crown of Cheloniidae diverge and radiate?

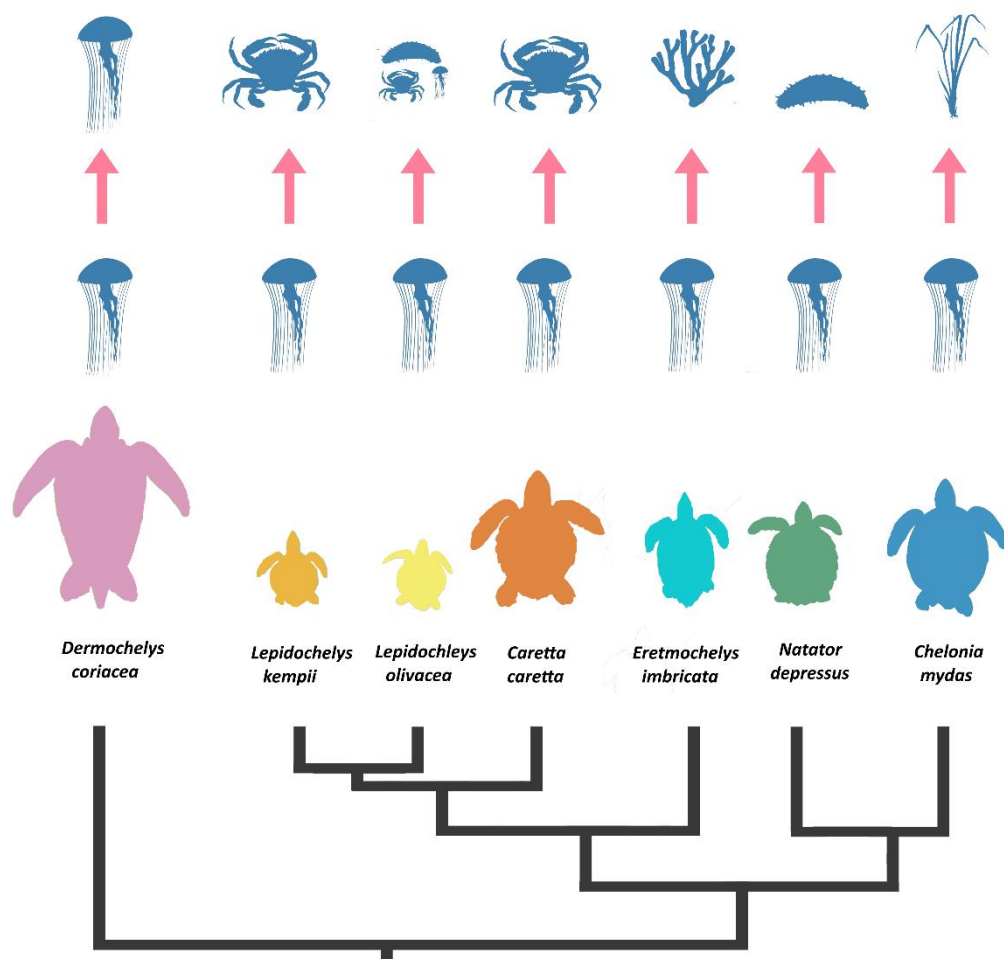


Figure 2. A cladogram of the seven extant species of sea turtles, showing their dietary transition. The jellyfish represents gelatinous pelagic invertebrates, the crab represents hard bodied invertebrates, the sponge represents a diet consisting of largely sponges, the sea cucumber represents a diet of soft bodied benthic invertebrates, the sea grass represents a diet of largely plant matter. The silhouettes of the sea turtles are scaled for size.

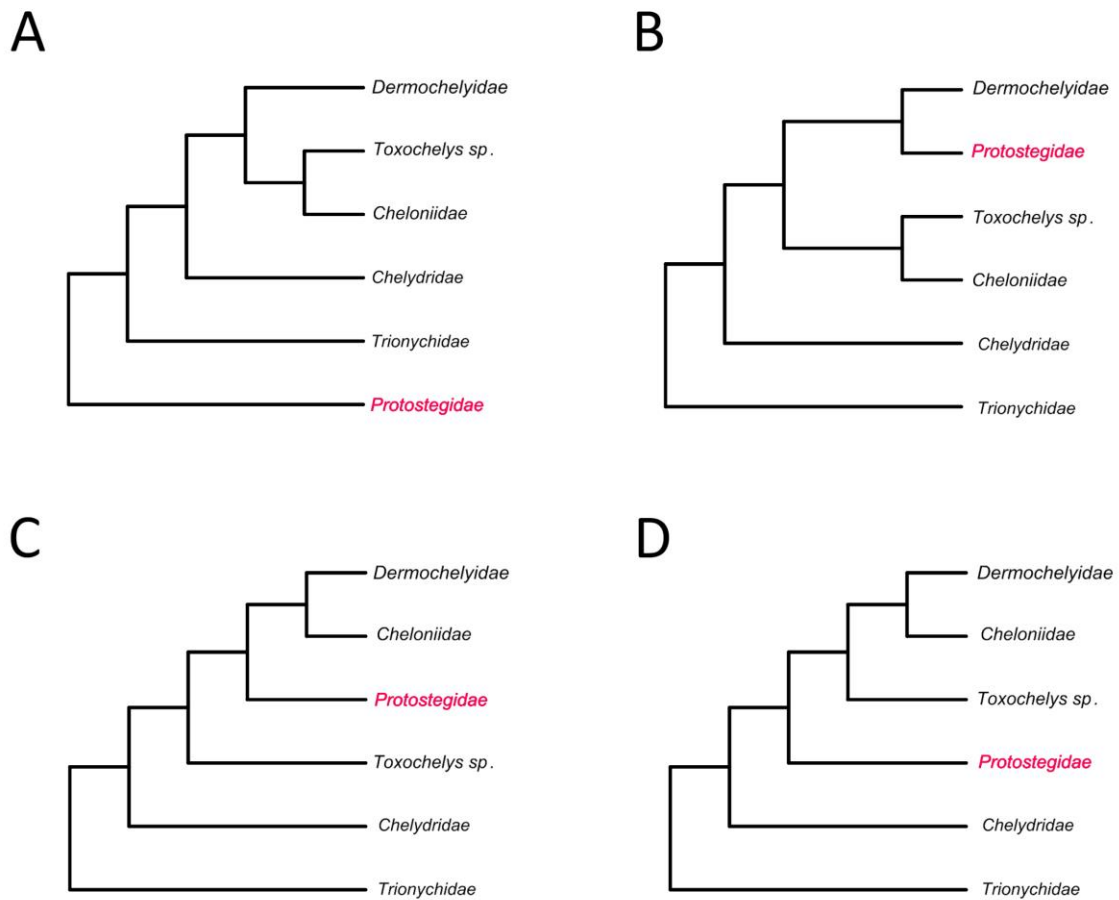


Figure 3. The differing positions of Protostegidae through the literature. A: Redrawn from Joyce (2007) showing Protostegidae outside of Cryptodira. B: Redrawn from Kear and Lee (2006), showing Protostegidae as sister to Dermochelyidae. C: Redrawn from Evers *et al.* (2019), showing Protostegidae as sister to Cheloniidae. D: Redrawn from Gentry *et al.* (2019), showing *Toxochelys* sp. as sister to Cheloniidae and Protostegidae as the least nested family of sea turtles.

SKULL MORPHOLOGY

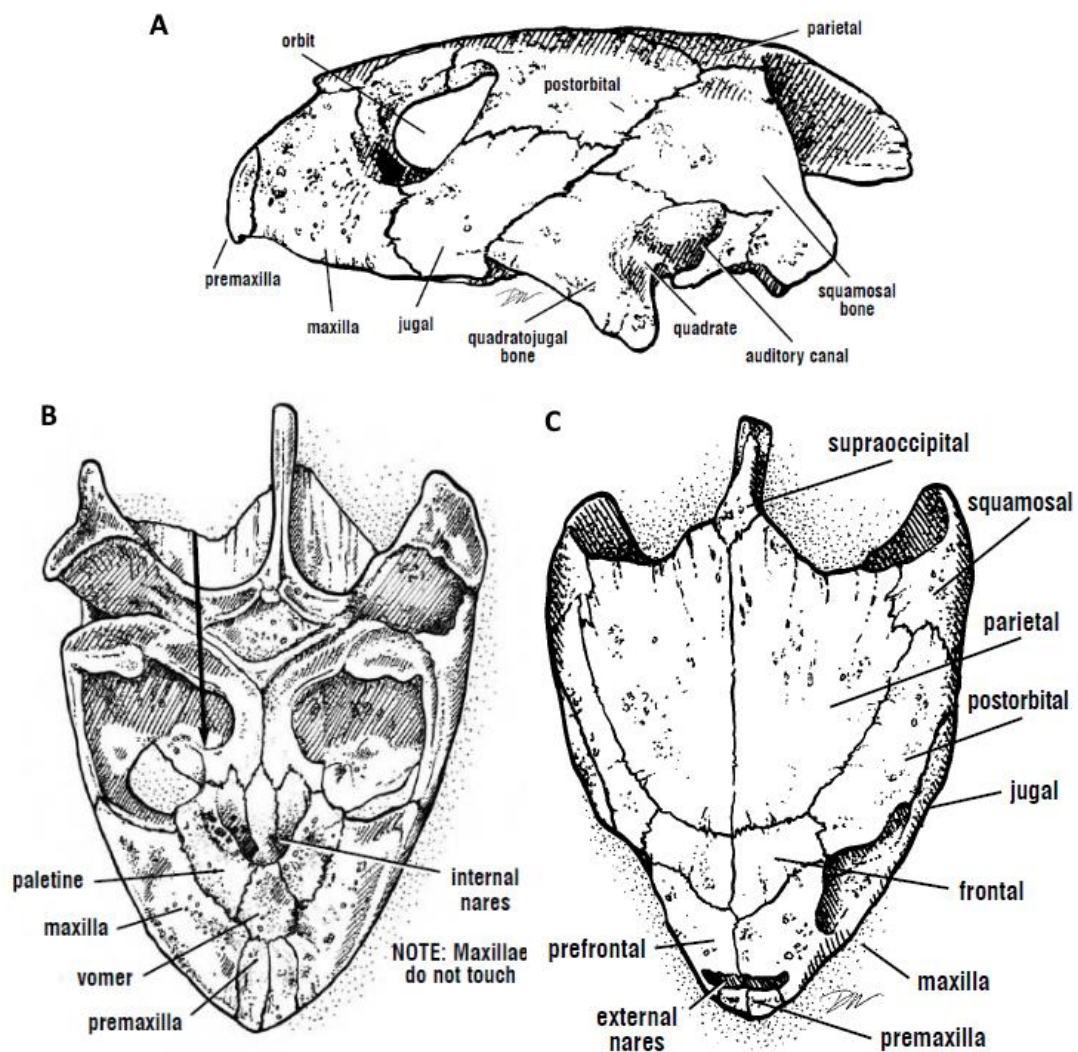


Figure 4. Diagram of the skull of *Lepidochelys kempii* in lateral (A), ventral (B), and dorsal (C) from Wyneken (2001).

The skull has the potential to reveal the most about the evolution, ecology, and lifestyle of an animal out of any single region of the body (Emmerson and Bramble 1993; Hanken and Hall 1993; Parham and Pyenson 2010; Watanabe and Slice 2014; Ferreira *et al.* 2015; Evers *et al.* 2019). The skull houses many important structures such as the brain, orbits, nasal cavity, and jaws (e.g., Paulina-Carabajal 2019; Evers *et al.* 2019). The skull is also the source

for a significant proportion of characters used in morphological phylogenetic analyses, often comprising half or more of the characters used (e.g., Hirayama 1994; Lee and Yates 2018; Evers *et al.* 2019). Due to the importance of the skull in both functional, as well as evolutionary terms more research has focused on it than virtually every other bony element combined.

The turtle skull is unusual among amniotes because it has an almost fully enclosed (anapsid) condition without obvious fenestrae (Williston 1917; Lee 1993; Werneburg 2012; Joyce 2015). The construction of the skull is dome-like without the beam –and–strut construction of lepidosaurs and many archosaurs (Romer 1956; Hanken and Hall. 1993; Emerson *et al.* 1993; Jones *et al.* 2012; Werneburg 2013). This more solid construction is now thought to be secondary, due to molecular evidence suggesting that testudines are deeply nested within Diapsida as well as recent supporting fossil evidence (Bever *et al.* 2015; Schoch *et al.* 2016). Early turtles have teeth along the maxilla, premaxilla, dentary, and palatine (Gaffney 1990; Joyce 2007). These were lost early in turtle evolution and no turtles beyond the Triassic–Jurassic boundary are known to have teeth (Gaffney *et al.* 1987; Joyce 2007; Cadena and Parham 2015). Many turtles have large emarginations of the skull, posterodorsally, and ventrolaterally (Werneburg 2012). The function of these emarginations remains largely unknown. However, skull bone grows in response to the strain environment that it is subjected to (e.g. Adams 1919; Case 1924; Olson 1961; Frazzetta 1968; Curtis *et al.* 2011). Recent studies using geometric morphometric analysis and finite element analysis suggest that the emarginations are related to neck retraction and the associated forces on the skull (Werneburg 2015; Ferreira *et al.* 2020).

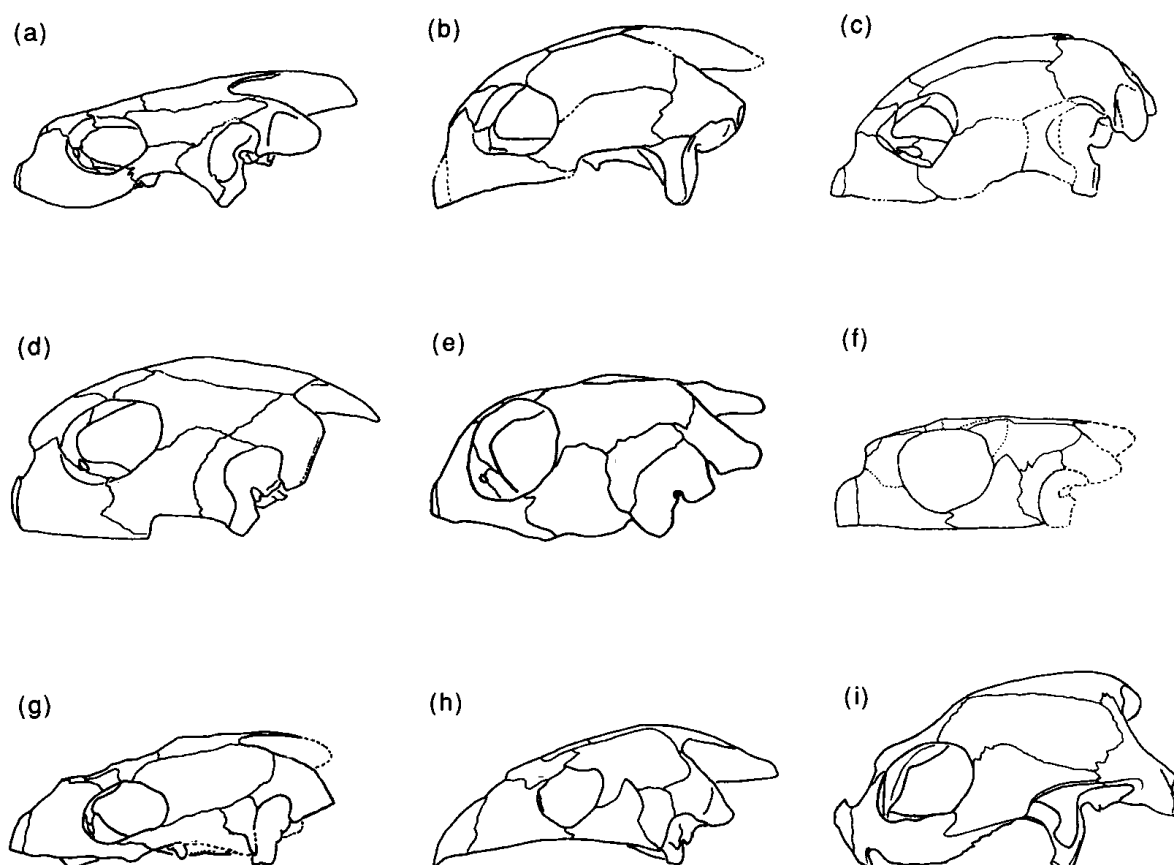


Figure 5. From Hirayama (1994). Lateral view of crania from members of Pan-Chelonioidae. A. *Toxochelys laternis* B. *Allopleuron hoffmani*. C. *Euclastes weilandi*. D. *Chelonia mydas*. E. *Santanchelys gaffneyi* F. *Rhinocelys pulchriceps*. G. *Desmatochelys lowii* H. *Protostega gigas*. I. *Dermochelys coriacea*.

There are many studies examining the morphology of the sea turtle skull (Kesteven 1911; Gaffney *et al.* 1979; Pritchard and Trebbau 1984; Kamezaki and Matsui 1995; Kamezaki *et al.* 2003; Nishizawa *et al.* 2010; Jones *et al.* 2012; Ferreria *et al.* 2015; Lunadorn *et al.* 2020). The skulls of most modern taxa are well documented, and act as the basis of comparison for the fossil species (Kesteven 1911 Gaffney 1979; Pritchard and Trebbau 1984; Dodd 1988; Jones *et al.* 2012). The exception to this resource is *Natator depressus*, which has not received a detailed description of the adult skull. Available descriptions are limited to juvenile specimens or lack details (Fry 1913; Zangerl *et al.* 1988; Limpus *et al.* 1988). The lack of thorough morphological description of *N. depressus* likely contributed to its previous phylogenetic instability.

The crania of sea turtles are distinct from other testudines, distinguished by their large, paired parietals, as well as their small to non-existent posterodorsal and ventrolateral emarginations (Gaffney *et al.* 1979; Jones *et al.* 2012; Werneburg 2013; Fig 4,5.). The highly reduced posterodorsal emarginations have been suggested to be an adaptation to the inability to retract their heads and acts as additional protection from predators (Pritchard and Trebbau 1984; Werneburg 2015). Early sea turtles such as the protostegids, *Allopleuron hoffmani*, and *Toxochelys latiremis* do have significantly larger posterodorsal emarginations, with proportionately smaller parietals (Gaffney 1979; Muller 2003; Matzke 2009). Modern cheloniid sea turtles have a significant secondary palate, as do, to varying degrees, most stem cheloniids (Gaffney 1979; Zangerl 1980; Parham and Pyenson 2010). Later Protostegids also have extensive secondary palates (Evers and Benson 2019) and this feature is likely related to durophagy (Zangerl 1980; Parham and Pyenson 2010) which would have enabled access to shelled prey items.

Though they look superficially similar in shape to other sea turtles, protostegids have multiple distinct features which separate them. The most obvious differences are the presence of nasal bones (Hirayama 1994). They are present in protostegids but absent in chelonioids as well as in toxochelyid grade sea turtles, which instead have prefrontals that meet medially at the midline. The parietals of protostegids are generally smaller than seen in chelonioid species, with the squamosal rarely making contact with them (Hirayama 1994; Evers *et al.* 2019). This results in the posterodorsal emarginations in protostegids being larger than seen in chelonioids.

DIET AND ECOLOGY OF MODERN SEA TURTLES

Modern sea turtles have a surprising dietary diversity considering the group's small taxonomic size (Bjorndal *et al.* 1997). As adults, most species have a distinct diet from other sea turtles (Fig.2). All species other than *Natator depressus* have a pelagic phase as juveniles (Carr 1987; Walker and Parmenter 1990). During this pelagic phase, these juveniles are associated with rafts of *Sargassum* (Carr 1987; Bjorndal *et al.* 1997). Their diet is largely carnivorous, consisting of soft bodied invertebrates such as small cnidarians, crustacean larvae, and other zooplankton (Dodd 1988; Bjorndal *et al.* 1997). Most sea turtles then undergo an ontogenetic diet shift as they move to the neritic environment (Bjorndal *et al.* 1997).

Dermochelys coriacea is the only species of sea turtle which remains in a pelagic environment for most of its life (Dutton *et al.* 1999). Its diet is almost completely composed of different jellyfish (Bjorndal *et al.* 1997; Desjardin 2005; Heaslip *et al.* 2012). They are also able to dive several hundred metres in search for food (Hays *et al.* 2004; Houghton *et al.* 2008).

All cheloniid sea turtles spend the majority of their adult lives in shallow water environments (Carr 1987; Bjorndal *et al.* 1997). As an adult *Chelonia mydas* is the only herbivorous sea turtle (Garnett *et al.* 1985; Seminoff *et al.* 2002; Arthur *et al.* 2008). The majority of their diet consists of sea grasses and algae. They do occasionally opportunistically predate on jellyfish and other soft bodied invertebrates, but these make up a relatively small portion of their diet (Bjorndal *et al.* 1997; Seminoff *et al.* 2002).

Eretmochelys imbricata is a carnivorous sea turtle that specialises in the consumption of sponges (Leon *et al.* 2002; Limpus and Fien 2009). In some areas, such as the Caribbean,

sponges can make up to 95% of their total diet (Meylan 1988). In other areas sponges make up a smaller percentage, but they are still normally the most significant food item (Leon *et al.* 2002; Limpus *et al.* 2009).

Caretta caretta is a carnivorous turtle. It has the widest range of food items recorded for any sea turtle (Dodd 1988). As individuals get larger their diets shift to a more durophagous diet of hard-bodied invertebrates (Dodd 1988; Bjorndal *et al.* 1997; Seney and Musick 2007). As adults the largest portion of their diet consist of crabs (Dodd 1988; Bjorndal *et al.* 1997). They also consume a wide range of other invertebrates, such as bivalves, jellyfish, salps, and sea snails (Dodd 1988). Large adults are capable of consuming large crabs, queen sea conches, as well as giant clams (Babcock 1938; Limpus 1973; Dodd 1988).

Once returning from the pelagic phase, *Lepidochelys kempii* eats almost exclusively crabs (Shaver 1991; Burke *et al.* 1994), with some other food items taken opportunistically such as salps and jellies (Shaver 1991; Bjorndal *et al.* 1997). *Lepidochelys olivacea* is arguably the least ecologically specialised of the sea turtles (Bjorndal *et al.* 1997). It consumes a wide variety of food, without any particular source being more prominent than the others (Montenegro-Silva *et al.* 1986).

There is little dietary information about *Natator depressus* in the literature. It is unique among sea turtles in lacking a pelagic phase and spending its entire life on the Australian continental shelf and near the southern islands of Indonesia and Papua (Walker and Parmenter 1990). Though lacking in a pelagic phase, the little information available suggests that juvenile *N. depressus* have a similar diet to the juveniles of other species (Limpus 2007). Feeding largely on zooplankton, in the upper part of the water column. As adults they shift

to benthic feeding, preying on slow moving soft bodied invertebrates such as soft corals, sea pens, sea cucumbers, and opportunistically jellyfish (Limpus 2007).

THE RELATIONSHIP BETWEEN DIET AND MORPHOLOGY

Adaptive signals through the evolution of sea turtles are hard to detect. There have been some clear changes, such as the orbit migrating to a more laterally facing position from a previously dorsal position (Hirayama 1994; Joyce 2007; Cadena and Parham 2015). This difference is an assumed adaptation to the marine habitat from a freshwater environment (Hirayama 1994; Joyce 2007). Other differences in skull structure have been evaluated in the context of diet and methods of oral food processing, though much of this research is a qualitative assessment rather than quantitative analysis (Gaffney 1979; Zangerl 1980; Pritchard and Trebbau 1984; Parham and Pyenson 2010; Jones *et al.* 2012; Ferreira *et al.* 2016; Ferreira *et al.* 2020; Lunadorn *et al.* 2020). Though previous authors have noted that skull shape is likely related to feeding in extant sea turtles (Pritchard and Trebbau 1984; Kear and Lee 2006; Parham and Pyenson 2010), this relationship has not been explored beyond a surface level. The lack of understanding of modern species severely inhibits our ability to understand any functional or adaptive signal in extinct species.

The relationship between diet and cranial morphology in sea turtles remains poorly known. Attempts to categorise living and fossil sea turtles into dietary niches by skull morphology must overcome a significant problem, virtually all modern sea turtles have differing dietary specialisations (Bjorndal *et al.* 1997). This range of food items consumed among the seven extant species and overlap of food items consumed make identifying morphological correlates to diet difficult. This problem is exacerbated in the absence of material properties

data for these food items. However, it is clear that among extant sea turtles, some consume soft prey (*Dermochelys coriacea* – jellyfish), others consume hard prey (e.g. *Caretta caretta* – clams), and others consume a mixture (*Eretmochelys imbricata* – sponges, echinoderms). Some adaptations, such as the length of the mandibular symphysis and size of the coronoid process are indicators of bite force capacity and in turn the ability to process with hard prey: durophagy (Parham and Pyenson 2010; Ferreira *et al.* 2015). However, for other diets there are few such obvious features. Even with this detectable signal there is the assumption that these features are solely related to durophagy. The difficulty in identifying indicators partly stems from the lack of quantitative studies.

Species can also be organised according to types of food processing rather than the food that they consume. Parham and Pyenson (2010) classified a number of extant and extinct sea turtles into three groups: non-specialised (no obvious anatomical features related to feeding), highly specialised for shearing (significant symphyseal ridges), and highly specialised for crushing (flat, wide dentaries). This system provides a framework for organising anatomical variation related to feeding but type of oral food processing does not necessarily match well to diet and food items consumed. Also, the classification of some extant turtles using this system appear in error. In Parham *et al.* (2010), *N. depressus* is categorised as neither shearing nor crushing, however by their definition of shearing in having “significant symphyseal ridges” *N. depressus* would be classified as a shearing type morphology. This miscategorisation might have been due to the lack of literature on this species. The study associates the shearing morphology to be associated with seagrass which is reasonable given that the only modern species they classified as such is an herbivore. However, *N. depressus*, which should be categorised as shearing, is a carnivore (Limpus 2007). The other species they associated with a shearing type morphology, *Allopleuron*

hoffmani, is now thought to be a carnivore (van Baal *et al.* 2013). This is not to disparage the study, this is just to demonstrate the difficulty in evaluating the link between skull morphology and diet in sea turtles.

There have been some successes relating morphology with diet in turtles using quantitative shape analyses (Claude *et al.* 2004; Ferreira *et al.* 2015). When examining the entirety of Testudinata there does not appear to be a morphological signal for either diet or habitat (Foth *et al.* 2016). However, there has been more success when narrowing the focus to the familial level. Looking at testudinoids, a significant relationship between diet and skull shape was found (Claude *et al.* 2004). Durophagous species have expanded adductor chambers and secondary palates whereas herbivorous species have a taller skull anteriorly. Examining solely the shape of the triturating surfaces, it seems possible to detect durophagy in marine turtles, however distinguishing between the range of other non durophagous diets has been met with less success (Ferreira *et al.* 2015). Morphometric studies focusing on sea turtles have tended to focus on intraspecific differences, rather than comparisons between species (Kamezaki and Matsui 1995; Kamezaki *et al.* 2003; Nishizawa *et al.* 2010; Lunadorn *et al.* 2020). These studies focus on population level differences (Kamezaki and Matsui 1995; Kamezaki *et al.* 2003) or changes across ontogeny (Nishizawa *et al.* 2010; Lunadorn *et al.* 2020), but there have been few shape comparisons across the entire group (Myers 2007). Ontogenetic changes to skull shape are associated with changes in diet (Nishizawa *et al.* 2010; Lunadorn *et al.* 2020), however, due to the broad variety of adult diets, the findings of these studies are difficult to apply to extinct species.

The effects that the ontogenetic diet shift discussed above has on skull shape has been largely unexplored. There has been relatively little study on the development of the sea

turtle skull particularly post-natal development (Miller 1982; Kaska and Downie 1999; Nishizawa *et al.* 2010; Al-Mukhaini *et al.* 2010; Sheil 2013; MacCord *et al.* 2015; Lupadorn *et al.* 2020). The studies which have studied shape change across growth have focused on sea turtles that have already returned to a neritic environment from their pelagic life stage, when their diet has already shifted from their juvenile gelatinivorous diet (Nishizawa *et al.* 2010; Lupadorn *et al.* 2020). Although these studies show significant change in skull shape, they do not capture the most significant ecological shift in each species diet, and the focus on singular species makes meaningful comparisons difficult. Given the near certainty that changes in size during growth will alter cranial shape, a more comprehensive morphometric analysis including all species and ontogenetic stages is needed to understand how diet and skull shape are related in sea turtle. This is discussed in the next section.

ALLOMETRY

Allometry (the relationship between size and shape) can be examined in a variety of different ways. Ontogenetic allometry examines the changes in morphology associated with growth (Gould 1977; Zelditch *et al.* 2004; Mitteroecker 2005; Drake 2011). Evolutionary allometry examines the allometric trend within a group and generally examines multiple species at a similar ontogenetic stage (Klingenberg 1998; Sherratt *et al.* 2014). Ontogenetic allometry is closely associated with heterochrony, which describes evolutionary changes to ontogenetic patterns (summarised in Klingenberg 1998). Heterochrony is expressed through modifications to the timing of development and growth of an animal (Gould 1977; Emerson and Bramble 1993; Mitteroecker *et al.* 2005; Weisbecker *et al.* 2008; Bhullar *et al.* 2016) and so heterochronic shifts are often accompanied by changes in life history (Denoel and

Joly 2000; Kon and Testsuo 2002; Mcnamara 2012). Studies of allometry and ontogeny among animals often focus on the effects of changes in growth and body size on ecology (Urošević *et al.* 2012; Esquerré *et al.* 2017; Morris *et al.* 2018; Gray *et al.* 2019), as well as their evolutionary and functional consequences (Mitteroecker *et al.* 2005; Wilson *et al.* 2011; Piras *et al.* 2011; Bhullar *et al.* 2016; Esquerré *et al.* 2017; Morris *et al.* 2018).

The skull in almost all vertebrates significantly changes across ontogeny (Gould 1977; Haffner 1988; Emerson *et al.* 1993; Hanken and Hall 1993; Mitteroecker *et al.* 2004; Jones 2008; Morris *et al.* 2018; Gray *et al.* 2019). Though there are broad ontogenetic shape change trends across amniotes, the shape change is often markedly different both across and within groups (Klinenberg 1998; Piras *et al.* 2011; Wilson and Sanchez-Villagra 2011; Urosevic *et al.* 2013; Koyabu *et al.* 2014; Morris *et al.* 2018). The often dramatic shifts in skull shape in ontogeny have often made identification, and taxonomy more difficult, with differing ontogenetic stages being confused for different species (Goodwin and Evans 2016; Woodward *et al.* 2020). The change in skull shape across ontogeny is also potentially affected by changes in diet across ontogeny. While some groups such as Bovidae, have little dietary shift across ontogeny, other groups have radically shifting diets as they increase in size (e.g. Tucker *et al.* 1996; Jones *et al.* 2012; Balguera-Reina *et al.* 2018). As demonstrated by the studies mentioned above, there does appear to be ontogenetic shape changes to the sea turtle skull associated with a shift in diet. So, to fully understand any correlation between function or diet with shape examination of ontogenetic allometry is essential. This greater understanding of any drivers or correlations between ecology and shape in modern species will allow us to better interpret the ecologies and evolution of extinct species of sea turtles.

Shape analysis

Geometric morphometrics is a powerful tool for understanding patterns between shape and evolution (see Adams *et al.* 2013 for summary). Over the past 20 years, geometric morphometrics has become the dominant method to quantitatively assess patterns in shape evolution (Zelditch *et al.* 1995; Rohlf 1998; Adams *et al.* 2000; Claude *et al.* 2004; Lieberman *et al.* 2007; Jones 2008; Drake 2011; Olori *et al.* 2012; Meloro and Jones, 2012; Sherratt *et al.* 2014; Bright *et al.* 2016; Gray *et al.* 2019). It has several advantages over linear morphometrics, particularly its more complete separation of size and shape (Adams *et al.* 2004), a greater potential to represent complex shapes (including landmark interrelationships, edges, and surfaces), and a greater capacity to visualise the shape differences. Geometric morphometric analyses have been improved over the last 20 years incorporating phylogenetic signal effects on the morphospace, modularity analyses, semi land landmarks, and patch landmarks (Adam *et al.* 2013; Adams 2014). One of the more significant improvements is greater ability to deal with missing data (Mitterorcker and Gunz 2009; Adams *et al.* 2013; Cardini 2016). This is particularly advantageous when dealing with fossil species. Increasing amounts of studies have been conducted on fossil groups that have allowed analysis of long-term evolutionary shape change (Figueirodo *et al.* 2008; Meloro and Slater 2012; Ferreira 2015; Foth *et al.* 2016; Foth and Joyce 2016).

AIMS

There are clear gaps in our knowledge of sea turtle evolution. The lack of morphological support for the current molecular topology is problematic. It suggests that we need a greater understanding of the morphology of the modern species. The obvious gap in our

knowledge of modern sea turtle morphology is the morphology of the least studied species *Natator depressus*.

Our incomplete understanding of the morphology of modern species not only impacts our understanding of the topology of the tree, but also our understanding of how their morphology and behaviour are related. Despite the many studies on sea turtle skull morphology, there have not been any attempts to quantitatively assess the skull shapes, and if there are any ecological correlations. Having reliable ecological proxies would enable attempts at understanding the ecology of extinct groups.

My thesis attempts to explore sea turtle evolution from two directions: phylogenetic and morphometric.

1. I aim to establish a stronger morphological basis for the sea turtle family tree. By describing the skull of the least known sea turtle *N. depressus* I attempt to discover if there is morphological support for the current molecular consensus phylogeny.

2. Using this data, along with for the first time applying total evidence tip dating techniques to sea turtle phylogenetic data, I aim to explore some of the more significant questions remaining about sea turtle evolution: the position of Protostegidae and the number of independent marine incursions within the group, and to establish patterns of evolution for Cheloniidae.

- 3 Using morphometric data, I aim to explore the relationship between skull shape, phylogeny, and ecology. I attempt to discover if there are any dietary signals in modern sea turtles or if other factors are more dominant in the shaping of their skulls. This is an attempt

to not only uncover potential selection factors which influence skull shape but also to potentially uncover the underlying mechanisms which are responsible for the modern diversity in skull shape. In particular, the role of allometry will be examined and how significant changes in diet across ontogeny influence skull shape.

4. This will establish a base to explore the shape evolution of the entire group by including some of the better-known fossil specimens with the aim to establish the cranial morphospace for the group and examine what are the most significant factors influencing sea turtle skull shape across a much larger span of time. Has skull shape been an influential factor in the success of some groups compared to others and are there instances of convergence correlated with diet as has been suggested?

My research is an attempt to better and to more fully explore the patterns and mechanisms which have shaped sea turtle evolution and further expand the story of this fascinating group of reptiles.

Statement of Authorship

Title of Paper	A redescription of the skull of the Australian flatback sea turtle, <i>Natator depressus</i> , provides new morphological evidence for the phylogenetic relationships among sea turtles (Chelonioidae)		
Publication Status	<input checked="" type="checkbox"/> Published	<input type="checkbox"/> Accepted for Publication	
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Principal Author

Name of Principal Author (Candidate)	Ray Chatterji		
Contribution to the Paper	Majority of specimens collection and processing, Specimen description, Data analysis, Writing, and Editing		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/08/2020

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- the candidate's stated contribution to the publication is accurate (as detailed above);
- permission is granted for the candidate to include the publication in the thesis; and
- the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Mark Hutchinson		
Contribution to the Paper	10%, advice and information on anatomical descriptions, editorial advice on manuscript clarity and quality of illustrations		
Signature		Date	20/08/2020

Name of Co-Author	Marc E H Jones		
Contribution to the Paper	10%: Initial conception of the chapter. Help with sourcing the flatback and comparative specimens. Provision of the software used to process the CT scans. Some guidance on organisation, literature, and formatting. Detailed feedback on the first iteration of the manuscript. Subsequent text editing of further iterations to improve clarity. Some limited [later stage] suggestions on the analyses.		
Signature		Date	21st August 2020

Please cut and paste additional co-author panels here as required.

Chapter 2

A redescription of the skull of the Australian flatback sea turtle, *Natator depressus*, provides new morphological evidence for phylogenetic relationships among sea turtles (Chelonioidea)

Ray M. Chatterji

Mark N. Hutchinson, Marc E.H. Jones

ABSTRACT

Chelonioida (sea turtles) are a group where available morphological evidence for crown group relationships are incongruent with those established using molecular data. However, morphological surveys of crown group taxa tend to focus on a recurring subset of the extant species. The Australian flatback sea turtle, *Natator depressus*, is often excluded from comparisons and it is the most poorly known of the seven extant species of Chelonioida. Previous descriptions of its skull morphology are limited and conflict. Here we describe two skulls of adult *N. depressus* and re-examine the phylogenetic relationships according to morphological character data. Using X-ray micro Computed Tomography we describe internal structures of the braincase and identify new phylogenetically informative characters not previously reported. Phylogenetic analysis using a Bayesian approach strongly supports a sister group relationship between *Chelonia mydas* and *N. depressus*, a topology which wasn't supported by previous analyses of morphological data but one that matches the topology supported by analysis of molecular data. Our results highlight the general need to sample the morphological anatomy of crown group taxa more thoroughly before concluding that morphological and molecular evidence is incongruous.

INTRODUCTION

Analysis of molecular data is the most common way to infer the phylogenetic relationships of modern groups due to numerous inherent advantages (San Mauro and Agorreta 2010; McCormack and Faircloth 2013) but morphology is still important. Firstly, understanding the morphology of modern groups is key to understanding their functional anatomy and character assembly (e.g. Jones *et al.* 2012; Cordero *et al.* 2018). Secondly, morphology still has a crucial role within phylogenetic analyses because it allows inclusion of fossil material (Donoghue *et al.* 1989; Ronquist *et al.* 2012; Schnitzler *et al.* 2017; Lee and Yates 2018). Moreover, re-examination of the morphology of extant taxa has the potential to generate new phylogenetic characters and new insights into their origins. Re-examinations of morphology in a variety of groups have identified morphological characters that support relationships previously only supported by molecular data (Shaffer *et al.* 1997; Lee 2001; Geisler and Uhen 2003; Asher and Lehmann, 2008; Asher *et al.* 2008; Legg *et al.* 2013). Modern application of morphological data can also help resolve or improve support for relationships that were otherwise contentious based on molecular data alone (Gatsey *et al.* 2003; Lee and Camens 2009; Springer *et al.* 2015).

Sea turtles (from here defined as Chelonioidea as defined by Evers *et al.* (2019a) are a well-studied group of reptiles that represent the only surviving clade of Mesozoic marine reptiles. There are seven living species, *Caretta caretta* (Linnaeus 1758), *Chelonia mydas* (Linnaeus 1758), *Eretmochelys imbricata* (Linnaeus 1766), *Lepidochelys olivacea* (Eschscholtz 1829), *Lepidochelys kempii* (Garman 1880), *Natator depressus* (Garman 1880), and *Dermochelys coriacea* (Vandelli 1761). All are large or very large in size (35 kg – 650 kg,

Pritchard and Trebbau 1984) and currently regarded as endangered or vulnerable to becoming so (Wyneken 2001; Seminoff 2004; Mortimer and Donnelly 2008; Abreu-Grobois and Plotkin 2008; Wallace *et al.* 2013; Casale and Tucker 2017; Wibbels and Tucker 2019). Members of Chelonioidea are characterised by several adaptations to a completely marine lifestyle, i.e., flippers, lack of ability to retract their heads or limbs into their shell, and salt glands (Pritchard and Trebbau 1984; Wyneken 2001, Jones *et al.* 2012). Most extant species have a near global distribution, largely centred in the tropics, although *D. coriacea* has been found as far north as the Arctic Ocean (Willgochs 1957).

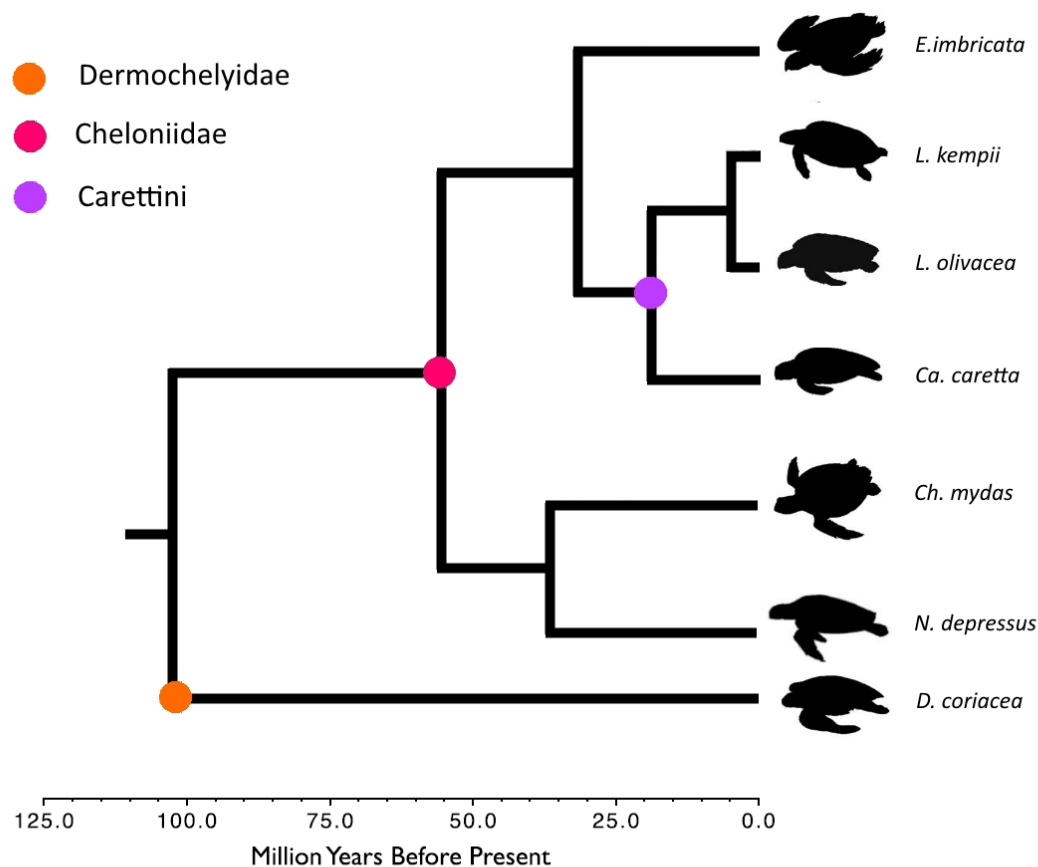


Figure 1. The current consensus for the phylogenetic relationships between extant sea turtles. The different colours represent the base of the groups in extant sea turtles. Redrawn from Duchene *et al.* (2013). Silhouettes redrawn from Jones *et al.* (2012).

The phylogenetic relationships among living sea turtles has reached a consensus based on DNA evidence (Fig. 1; Naro-Maciel *et al.* 2008; Duchene *et al.* 2012; Crawford *et al.* 2015). The deepest division is between *D. coriacea* (family Dermochelyidae) and all other sea turtles (family Cheloniidae). Within Cheloniidae there are two clades: one comprising *Natator depressus* + *Chelonia mydas* and another comprising *Eretmochelys imbricata* + Carettini (*Ca. caretta*, *L. olivacea* + *L. kempii*). Although these relationships are now considered well established the same branching topology has not been recovered using solely morphological data (Zangerl *et al.* 1988; Hirayama 1994; Parham and Fastovsky 1997; Scavezzoni and Fischer 2018). However, the lack of support from morphological characters may not be related to an inherent problem with morphological data. It may instead be a sign that our understanding of sea turtle morphology needs improvement.

Of the six species within Cheloniidae, *Natator depressus* is exceptional with respect to its ecology and life habits. *N. depressus* is the most geographically limited modern sea turtle, being confined to the northern and western Australian continental shelf (Limpus 2007). The clutch size of *N. depressus* is on average about half of that found in other species (Pritchard and Trebbau 1984; Limpus 2007), and the hatchlings are up to 20% larger (Limpus 2007). Uniquely amongst sea turtles *N. depressus* does not migrate to pelagic environments in early life, instead remaining in shallow coastal waters (Limpus *et al.* 1983; Walker and Parmenter 1990; Buskirk and Crowder 1994). Available but limited ecological data suggests it has a broad diet. Recorded stomach contents include largely soft bodied invertebrates, but also corals and molluscs (Bjorndal 1985; Bjorndal *et al.* 1997).

Morphological descriptions of *Natator depressus* that are available lack detail (Limpus *et al.* 1988; Zangerl *et al.* 1988, Hirayama 1994) or describe an immature specimen (Fry 1913) and

have been of limited use for determining relationships. Comparative studies by Gaffney (1979), Wyneken (2001) and Jones *et al.* (2012) essentially reported that the skull of *N. depressus* was superficially similar to that of *Lepidochelys olivacea* and to a lesser extent *Ch. mydas*. The paucity of data has led to a confused taxonomic and phylogenetic history for this species. For much of the Twentieth Century a close relationship between *N. depressus* and *C. mydas* had been accepted due to a few external similarities, e.g. scalation, carapace shape, and flipper length, and *N. depressus* was therefore considered to be a species of *Chelonia* (Baur 1890; Fry 1913; Williams *et al.* 1967). However, this arrangement was largely rejected after more quantitative methods failed to support it (Limpus *et al.* 1988, Hirayama 1994). Zangerl *et al.* (1988) and Limpus *et al.* (1988) re-established *N. depressus* in its own genus.

Since the late 1980's, phylogenetic studies have placed *N. depressus* within Cheloniidae in a variety of positions. These include a position as the least nested taxon (Hirayama 1994; Lynch and Parham 2003) or as more closely aligned with the Carettini (Dutton 1996), or with a sister relationship to the Mio–Pliocene sea turtle *Syllomus aegyptiacus* (Lynch and Parham 2003, Parham and Pyenson 2010). In the morphology-only study by Scavezzoni and Fischer (2018) *N. depressus* was found to be in a large polytomy with other chelonids, and not in a clade containing solely the crown. Some studies of sea turtle relationships omitted *N. depressus* altogether (e.g. Gaffney and Meylan 1988; Hirayama 1998; Kear and Lee 2006). Other studies that have included *N. depressus* were not aimed at testing relationships among the living species, and simply used it as part of a backbone constraint (see Parham and Pyenson 2010; Cadena and Parham 2015; Gentry 2017; Evers and Benson 2019a; Evers *et al.* 2019; Gentry *et al.* 2019). To date, none of the phylogenetic analyses using morphological characters has recovered *N. depressus* as the sister taxon to *C. mydas* in

agreement with DNA sequence analyses without using a constraint based on the molecular data (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012).

The lack of a sufficiently detailed adult skull description for the *N. depressus* is problematic for several reasons. Cranial osteology is an important source of characters for phylogenetics and taxonomy as well as informative for the interpretations of function and ecological habits (Emmerson and Bramble 1993; Hanken and Thorogood 1993; Cardini and Elton 2008; Parham and Pyenson 2010; Watanabe and Slice 2014; Ferreira *et al.* 2016; Evers *et al.* 2019). A full understanding of the cranial osteology of living species is valuable for phylogenetic analyses of the extensive turtle fossil record particularly given that among turtles the skull has the most phylogenetic characters of any single region (Hirayama 1998; Parham and Pyenson 2010; Candina and Parham 2015; Weems and Brown 2017; Evers and Benson 2019). The skull houses the brain, eyes, and nasal cavity, jaw muscles, as well as the mouth and pharynx (e.g. Paulina-Carabajal 2019; Evers *et al.* 2019a), therefore its morphology is intimately related to many aspects of its lifestyle.

Here we redescribe the skull of *N. depressus* in detail and identify ten new osteological characters. We test the phylogenetic utility of these characters, and their effects on the placement of *N. depressus* within the cheloniid phylogenetic tree. Using our new data and including some of the more well-preserved/characterized fossil chelonioids, we re-examine the robustness of morphological data in determining relationships among sea turtles, and the degree of concordance between the new morphological data set and existing molecular data sets.

Institutional Abbreviations

AM: Australian Museum; NHMUK: The Natural History Museum UK; SAMA: South Australian Museum; SMNS; Staatliches Museum für Naturkunde, Stuttgart; WAM; Western Australian Museum; QM: Queensland Museum.

MATERIALS AND METHODS

Three specimens of *Natator depressus* were used, two dry skulls WAM R112123 and WAM R61349, and an unregistered wet specimen (Ethanol preserved head) from Queensland Museum. It should be noted that WAM R61349 has a cranial abnormality: a broad bulge or convexity that involves the posterior portion of both parietals. The two parietals rise dramatically medially towards the supraoccipital. The deformity is larger on the left parietal but the arc across the risen area is smooth suggesting it is a singular deformity rather than a deformity arising on each parietal independently.

The skulls of four other sea turtle species were used for comparison *Chelonia mydas* (SAMA unregistered, NHMUK1967.776c), *Caretta caretta* (SAMA R33830; SAMA Unregistered), *Eretmochelys imbricata* (WAM 120113, AM J51134), and *Lepidochelys olivacea* (SAMA BM670, SMNS 11070). All specimens used were mature individuals, with skulls that are within the size range reported for adults (Gaffney 1979; Pritchard and Trebbau 1984; Dodd 1988; Zangerl *et al.* 1988; Nishizawa *et al.* 2010). The skulls were examined using classical comparative methods and measured using digital callipers and rulers. Each skull was also subject to X-ray micro computed tomography (CT). This approach enabled generation of digital three-dimensional models that facilitate further examination and description of internal structures and contacts without the need for destructive methods such as disarticulation. Six of the specimens (not SMNS 11070 and NHMUK1967.776c) were scanned

at Sound Radiology, Adelaide with a Phillips Ingenuity Core 128 scanner. The voxels were non cubic, with voxel sizes of between 170 and 210 microns in the X and Y axis and 333 microns on the Z axis (See Sup. Table 1). Specimen NHMUK1969.776c was scanned with the Nikon Metrology HMX ST 225. Segmentation and processing was executed in Avizo 8.0 Lite (FEI, Hillboro, Oregon, USA). Specimen SMNS 11070 (*Lepidochelys olivacea*) was downloaded from morphosource to provide additional CT scan data on this species. These specimen models are available for examination and download on morphosource (https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/929)

The anatomical terminology used largely follows Gaffney (1972). When referring to a structure not referred to in Gaffney (1972), terminology follows Evers *et. al* (2019a).

Phylogenetic analysis

Our phylogenetic analysis took the data of Evers and Benson (2019) as its starting point. For our initial data set (data set A) we used a modified set of 23 taxa and 358 morphological characters, focusing on Pan-Chelonioidea, adding some taxa and modifying some characters using information from personal observation, and data from the literature (Appendix 2). We then created a second data set (data set B) by augmenting this modified Evers and Benson set with 10 new characters taken from the present study (Table 1).

In both the A and B data sets, *Apalone spinifera* was used as an out group, representing the Trionychidae, which are sister to the rest of crown Cryptodira (Crawford *et al.* 2015).

Chelydra serpentina was used as a representative of Chelydridae, usually found as part of a sister clade to Pan-Chelonioidea within Americhelydia (Crawford *et al.* 2015; Cardeni and Parham 2015; Evers and Benson 2019). We assumed that the family Protostegidae was part of Cryptodira because almost all studies find them closely aligned with Chelonioidea

(Hirayama 1994; Kear and Lee 2006; Cadena and Parham 2015; Evers and Benson 2019 Raselli 2018). The protostegids included were *Rhinochelys pulchriiceps*, *Protostega gigas*, *Santanchelys gaffneyi*, and *Bouliachelys suteri*. These were chosen to represent the greatest spread of taxa, both chronologically and taxonomically. Several additional species were added that were not present in Evers and Benson 2019. Characters for these species came from their descriptive literature and Cadena and Parham (2015). These species, *Syllomus aegyptiacus* (Weems 1980; Hasegawa *et al.* 2005), *Pacifichelys hutchisoni* (Lynch and Parham 2003; Parham and Pyenson 2010), *Carolinachelys winsonii* (Weems and Sanders 2014; Weems and Brown 2017), and *Procolpochelys grandaeva* (Weems and Sanders 2014; Weems and Brown 2017) were added to better represent the Cenozoic diversity of sea turtles.

To test the validity of our taxon datasets (A and B), set we used two further datasets that included all the taxa previously used in Evers *et al.* (2019) with (D) and without the new characters (C). For D, the new characters were marked as unknown for the taxa not present in A or B. For these datasets *Proganochelys quenstedti* was used as the outgroup as the earliest occurring testudine in Evers and Benson (2019).

We employed a Bayesian analysis using Mr Bayes V 3.2.6. For rate variation, we used a Mkv model with ascertainment correction bias (Lewis 2001), as it is the most thoroughly tested model for incorporating morphological data within a Bayesian framework (Müller and Reisz 2005; Wiens 2009; Pyron 2011). The gamma parameter was chosen to allow for rate variation across characters, as a more realistic option when compared to a uniform rate variation (Nylander *et al.* 2004; Müller *et al.* 2006; Lee 2013). The Bayesian analyses ran for 30,000,000 generations, with a sample frequency of 1000. Parameters, posterior

probabilities, and branch lengths were estimated using a Markov chain Monte Carlo, with four chains used, one cold, three heated with a temperature of 0.2. The first 25% of samples were discarded as burn in.

RESULTS

The skull of *Natator depressus* is similar to that of other sea turtles in having a dome shaped cranium that tapers anteriorly and possesses relatively small posterodorsal and ventrolateral emarginations compared to many other Testudines (Fig. 2-5; Jones *et al.* 2012; Foth *et al.* 2019). The orbits are large (roughly a third the length of the cranium), and the rostrum is short and blunt. The skull in general shape has a shallow profile, a broad posterior region of the skull, and a V shaped lower jaw (Fig. 6,7). The secondary palate is well developed and has two distinct ridges that run parallel to the outer margin of the upper jaw and complement the two ridges on the lower jaw (Fig. 4). The palate is comparatively wide in comparison to other cheloniids.

Upper jaw and palate

The premaxillae are narrow and tall, contributing to the deep profile of the upper jaw. They contact the maxilla along the entirety of the lateral edge, and also posterolaterally via a shelf which also contacts the anterior end of the vomer (Fig. 4). There is a premaxillary pit as seen in other species (Pritchard and Trebbau 1984, SAMA 33830, Unregistered, BM670). The maxilla is relatively deep and fairly robust (Fig. 2.). The maxilla contacts the jugal posteriorly, the external seam for the two bones is sigmoid in lateral view and continues ventrally where it runs anteromedially on the surface of the palate (Fig. 4). In lateral view, the anterior most portion of the maxilla extends posteriorly along the ventral margin of the jugal. This

arrangement is also in contrast to the figures shown in Zangerl *et al.* (1988), where the ventral margin of the maxilla and jugal are largely continuous. The difference in the latter may be due to the angle of view, or perhaps damage to the specimen.

The palatal surface of the maxilla is marked by a prominent ridge that runs parallel to the suture of the palatine and reaches its peak height close to the contact with the vomer (Fig. 4). This ridge corresponds to a ridge on the upper beak. The maxilla contacts the vomer and palatine medially.

The vomer is divided into a ventral portion and dorsal portion separated by a relatively thin midline beam, the vomerine pillar, which also divides the two internal nares. The ventral portion of the vomer, as exposed in ventral view is roughly rectangular and forms the centre of the secondary palate, bounded by both maxillae, palatines, and the premaxillae. The dorsal portion of the vomer forms part of the margin of the *fossa nasalis* and *foramen orbito-nasale*. The premaxilla contacts the vomer dorsally and forms the anteroventral portion of the *fossa nasalis*. Posteriorly the central portion of the vomer is “I” shaped in coronal section (Fig. 8B) but anteriorly it becomes “X” shaped (Fig. 8C). The dorsal prongs of the X contact the prefrontals, whereas the ventral prongs contact the maxillae, the lateral face of the vomer forming the medial face of the *foramen orbito-nasale*. The foramen penetrates the medial and dorsomedial face of the internal nares. The vomer, the palatine, and the maxillae together form the secondary palate, and the triturating surface.

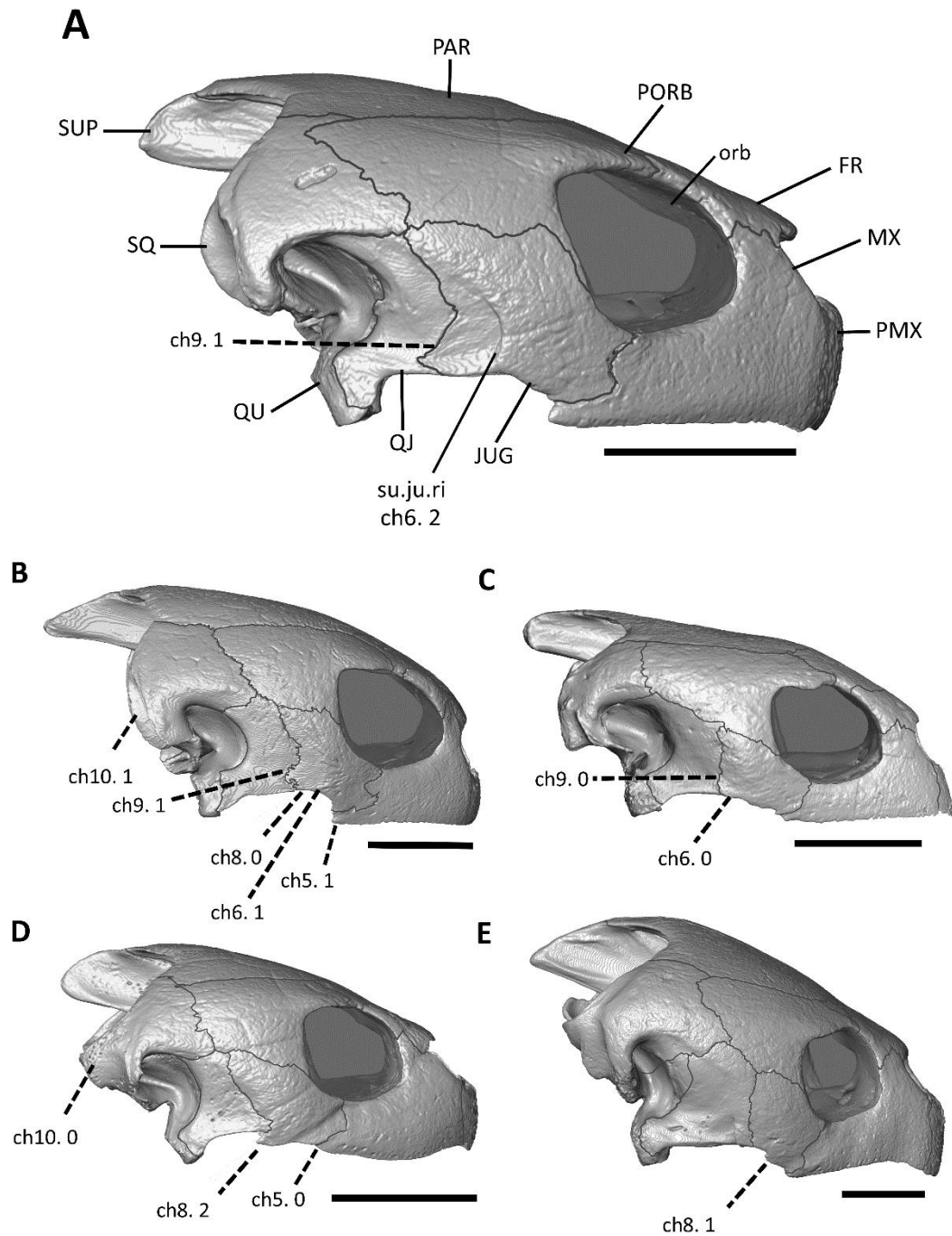


Figure 2. Lateral view of the five genera of extant cheloniid sea turtles. Images are of surface files constructed in Avizo lite 8.0 A *Natator depressus* (WAM R112123). B *Chelonia mydas* (SAMA unregistered). C *Eretmochelys imbricata* (WAM R120113). D *Lepidochelys olivacea* (SAMA BM670). E *Caretta caretta* (SAM Unregistered). Displaying the states of characters 5, 6, 8, 9, 10, based on the descriptors in Appendix 2. Abbreviations: FR, frontal; JUG, jugal; MX, maxilla; orb, orbital opening; PAR, parietal; PMX, premaxilla; PRFR, prefrontal; QJ, quadratojugal; QU, quadrate; SQ, squamosal; su.ju.ri, superficial jugal ridge; SUP, supraoccipital. Scale bars = 50mm

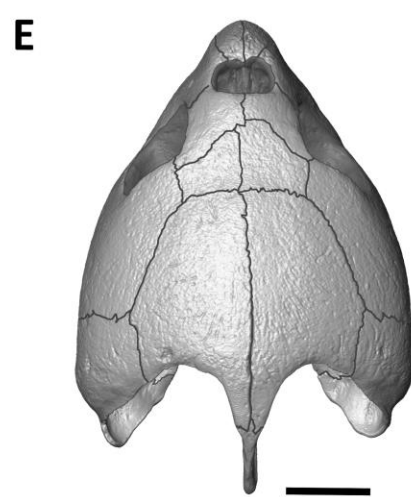
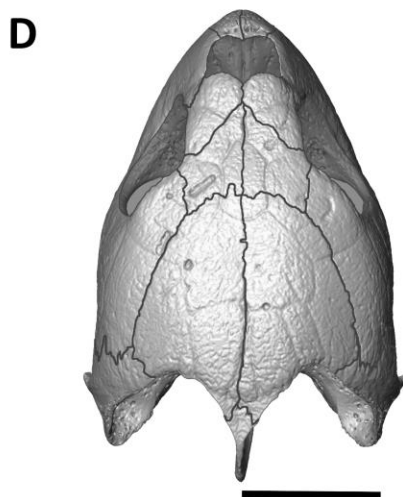
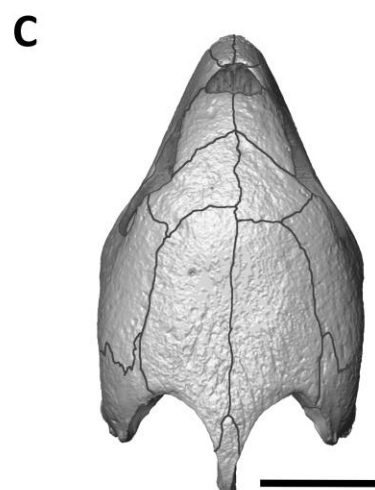
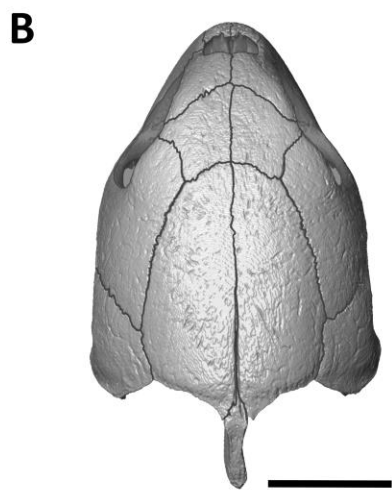
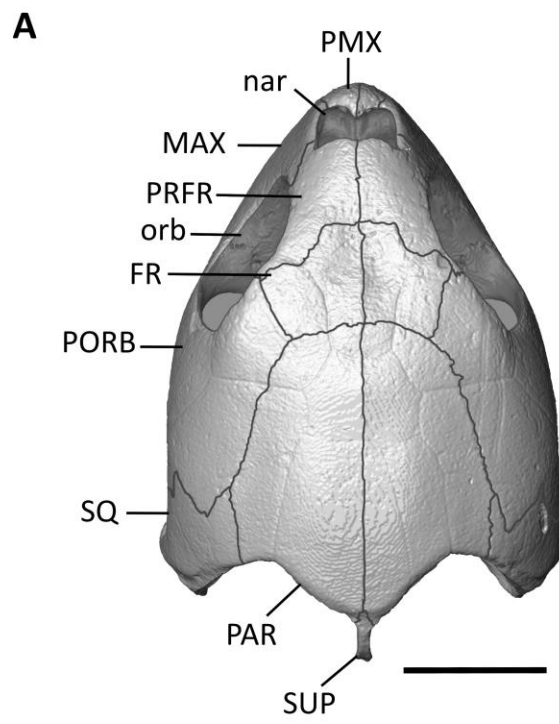


Figure 3. Dorsal view of the five genera of extant cheloniid sea turtles. Images are of surface files constructed in Avizo lite 8.0 A *Natator depressus* (WAM R112123). B *Chelonia mydas* (SAMA unregistered). C *Eretmochelys imbricata* (WAM R120113). D *Lepidochelys olivacea* (SAMA BM670). E *Caretta caretta* (SAM unregistered). Abbreviations: FR, frontal; JUG, jugal; MX, maxilla; nar, Nares; orb, orbital opening; PAR, parietal; PMX, premaxilla; PORB, postorbital; PRFR, prefrontal; SQ, squamosal; SUP, supraoccipital. Scale bar = 50mm

The palatine overlaps the dorsomedial surface of maxilla along its lateral edge, contacts the pterygoid and jugal posteriorly, and contacts the vomer medially above and below the internal naris. The pterygoid contacts the palatine anteriorly, the basisphenoid and exoccipital posteromedially, and the quadrate posteriorly. The pterygoid of *N. depressus* has prominent lateral projections. The posterior half of the pterygoid is significantly thicker than the flat anterior portion. The posterior section of the dorsal surface of the pterygoid provides most of the floor of the *fenestra postotica*. The *foramen posterius canalis cartotici interni* is prominent at the posterior margin of each pterygoid (Fig. 5). Part of the dorsal margin is formed by the exoccipital (but see Zangerl *et al.* 1988: Fig. 8). The canal runs through the posterior half of the pterygoid, ventrolateral to the braincase, though this canal bifurcates with medial branch exiting within the *sella turcica* on the dorsal surface of the *rostrum basisphenoidale*. This medial branch is not used by the internal carotid artery, but instead it is occupied by the cranial nerve (Evers *et al.* 2019B). The pterygoid has a large *crista pterygoidei* which contributes to the anterior wall of the braincase. This projection contacts and medially laps the epipterygoid. The epipterygoid is a small flat bone, contacting the parietal dorsally to form a laterally compressed vertical pillar anterior to the prootic. The contact between pterygoid and epipterygoid is barely visible in most specimens, and reportedly fuses completely on occasion (Gaffney 1979). The *foramen nervi trigemini* is bounded by the prootic posteriorly and a pillar formed by the parietal, epipterygoid, and pterygoid anteriorly. (Fig 9).

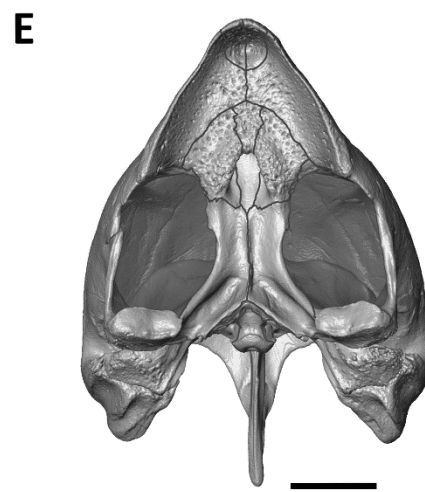
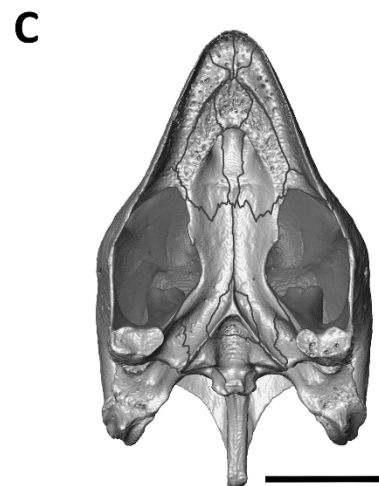
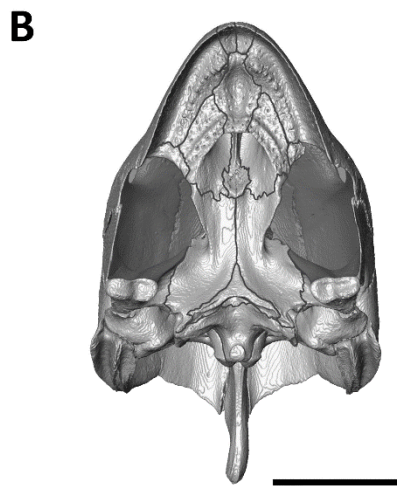
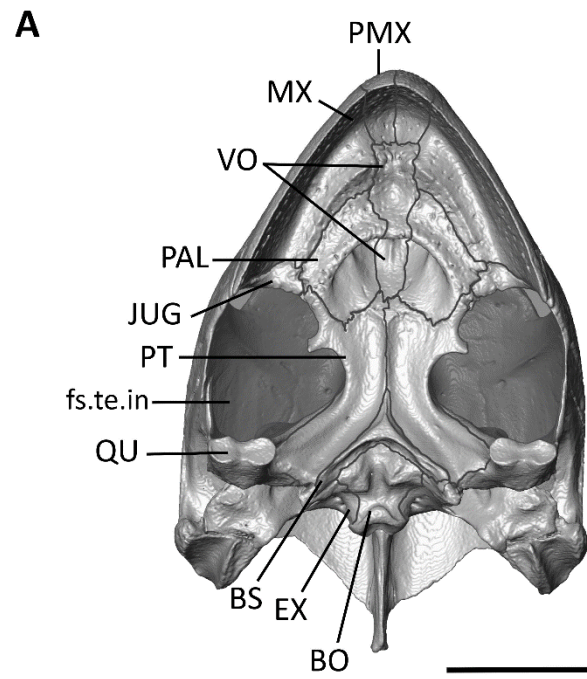


Figure 4. Ventral view of the five genera of extant cheloniid sea turtles. Images are of surface files constructed in Avizo lite 8.0 A *Natator depressus* (WAM R112123). B *Chelonia mydas* (SAMA unregistered). C *Eretmochelys imbricata* (WAM R120113). D *Lepidochelys olivacea* (SAMA BM670). E *Caretta caretta* (SAM unregistered). Abbreviations: BO, Basioccipital; BS, basisphenoid; EX, exoccipital; fo.te.in, fossa temporalis inferior; JUG, jugal; MX, maxilla; PAL, palatine; PMX, premaxilla; PT, pterygoid; QU, quadrate; VO, vomer. Scale bar = 50mm

Circumorbital series and temporal region

The orbital margin is composed of the maxilla, jugal, prefrontal, and postorbital (Fig 2). The frontal is consistently excluded from the orbit (Zangerl *et al.* 1988). Contrary to what is described in Limpus *et al.* (1988) the greatest width of the frontal occurs at the fronto-prefrontal suture, rather than the fronto-parietal suture (Fig. 3) (all three specimens). It is possible that this character varies between individuals, but a larger sample is required to estimate how variable.

The jugal of *N. depressus* is large compared to that of other extant sea turtle species, with the jugal almost equal in size to the postorbital bone or orbital opening (Fig. 2). The jugal of *N. depressus* significantly overlaps the quadratojugal: in places the contact is equal to a third of the length of the jugal; There is a prominent ridge which runs dorsoventrally through the posterior half of the jugal and on to the squamosal, quadratojugal and quadrate, Posterior to the ridge the bone is smooth and depressed compared to the rest of the external surface, while anterior to the ridge the surface is rougher and typical of the dorsal surface of the skull. (Fig. 2). The ridge and the differentiated regions do not correspond with the sutures of the head scalation (Fry 1913). The details of the associated soft anatomy were not resolvable in our scans. The anterior end of the jugal extends anteromedially alongside the palatal shelf of the maxilla and contacts the pterygoid and the palatine (Fig. 4).

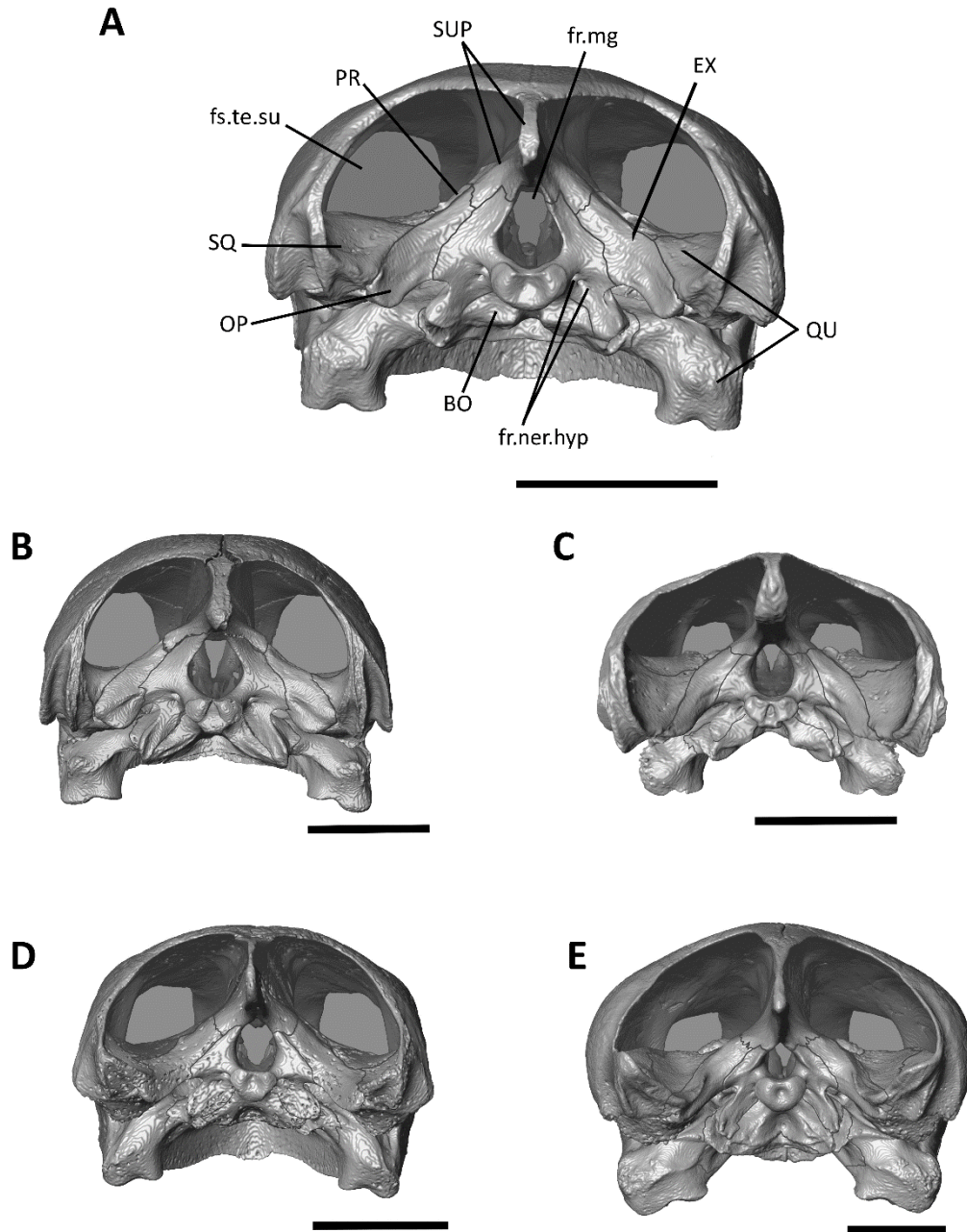


Figure 5. Posterior view of the five genera of extant cheloniid sea turtles. Images are of surface files constructed in Avizo lite 8.0 A *Natator depressus* (WAM R112123). B *Chelonia mydas* (SAMA unregistered). C *Eretmochelys imbricata* (WAM R120113). D *Lepidochelys olivacea* (SAMA BM670). E *Caretta caretta* (SAMA unregistered). Abbreviations: BO, basioccipital; EX, exoccipital; fn.po, fenestra postoticus; fr.mg, foramen magnum; fr.ner.hyp, foramen nervi hypoglossi; fs.te.su, fossa temporalis superior; OP, opisthotic; PR, prootic; PT, pterygoid; SQ, squamosal; SUP, supraoccipital. Scale bar = 50mm

In lateral view the exposed area of the quadratojugal is smaller compared to that of other sea turtles, largely due to the extensive overlap of the jugal. The external suture of the contact with the jugal is sigmoid, with a prominent anterior bow. The quadrate has a concave lateral surface which forms the medial surface of the *cavum tympani* (Fig. 2). The stapes passes through though the posteroventrally open *insisura columella auris* and the posteroventral margin of the quadrate. The ventral surface of the quadrate bears the mandibular condyle which comprises two smooth and shallow lobes. The lateral lobe projects almost directly ventrally, whereas the medial lobe faces slightly medially. The condyle is anteroposteriorly short and in ventral aspect the two lobes are clearly separated, superficially resembling a figure eight (Fig. 4). The quadrate extends medially with the dorsal surface forming the floor of the posterior end of the adductor chamber. The quadrate encapsulates the lateral part of the *fenestra postotica* (Fig. 2) (Ridgway *et al.* 1969). The channel that houses the stapes divides the bone into dorsal and ventral sections. The dorsal section of the medial surface contacts the opisthotic posteriorly and the prootic anteriorly. The ventral section contacts the pterygoid along its entire length. The anteromedial portion of the quadrate meets the lateral face of the prootic in a large and distinct boss to form the trochlear process.

Skull Roof

The skull roof is dominated by the large paired parietals, as well as including paired prefrontals, frontals, postorbitals, and squamosals (Fig. 3). The parietals are broad and relatively flat sloping away from where they meet in the midline. Each parietal contacts the postorbital and squamosal laterally, the frontal anteriorly, and the supraoccipital

posteroventrally. The parietal has a large triangular projection on the ventral surface anteriorly: the *processus inferior parietalis*. This projection contributes to the lateral wall of the braincase and contacts the prootic and epipterygoid.

The squamosal contacts the quadrate, quadratojugal, postorbital, and parietal. The squamosal forms part of the lateral wall and the posterior wall of the adductor chamber.

The extent of contact might reflect ontogeny given that the squamosal contacts the parietal late in development (Sheil 2013). The squamosal contacts the quadrate ventrally. The contact between the two is complex and extensive and migrates from the lateral wall of the skull medially across the floor of the adductor chamber. The entirety of the contact on the lateral wall occurs within the *cavum tympani*. There is an overhanging lip above this contact which forms the margin of the *cavum tympani* (Fig. 3). The posterior edge forms a significant portion of the margin of the *fossa temporalis superior*. The squamosal bears a single pronounced channel on its posterolateral corner, which serves as the site of origin for the *musculus depressor mandibulae*.

The postorbital forms most of the posterior margin of the orbit. Ventrally a thin spur-like structure extends between the orbit and the jugal, excluding the jugal from the orbit until the posteroventral corner. Anteriorly the postorbital contacts the prefrontal, excluding the frontal from the orbit. The dorsal margin is significantly longer than the ventral one.

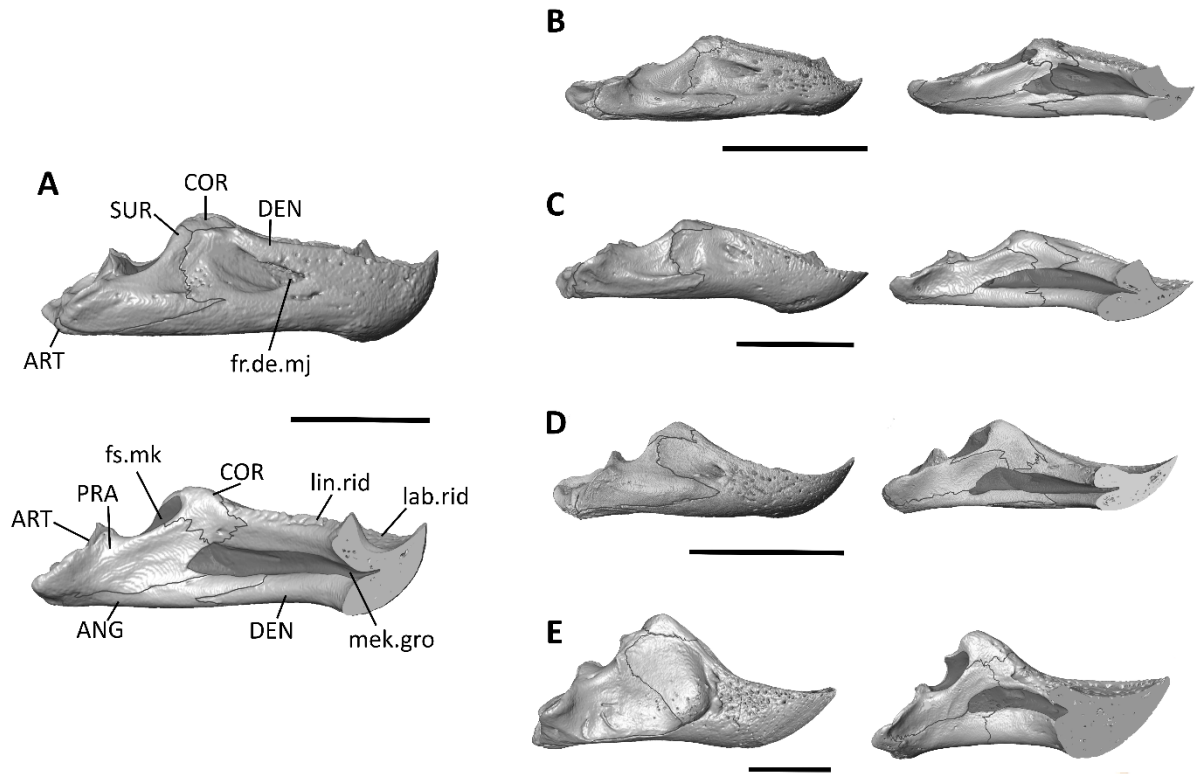


Figure 6. Lateral and medial view of the five genera of the mandibles extant cheloniid sea turtles. Images are of surface files constructed in Avizo lite 8.0 A *Natator depressus* (WAM R112123). B *Chelonia mydas* (NHMUK 1969.776) C *Eretmochelys imbricata* (WAM R120113). D *Lepidochelys olivacea* (SMNS 11070). E *Caretta caretta* (SAM unregistered). Abbreviations: ANG, angular; ART, articular; COR, coranoid; DEN, dentary; for.dent.maj, foramen dento faciale majus; fs.mk, fossa Makelii; lb.rid, labial ridge; lin.ridge; lingual ridge; mek.gro, Mekelian groove; PRA, prearticular; SUR, surangular. Scale bar = 50mm

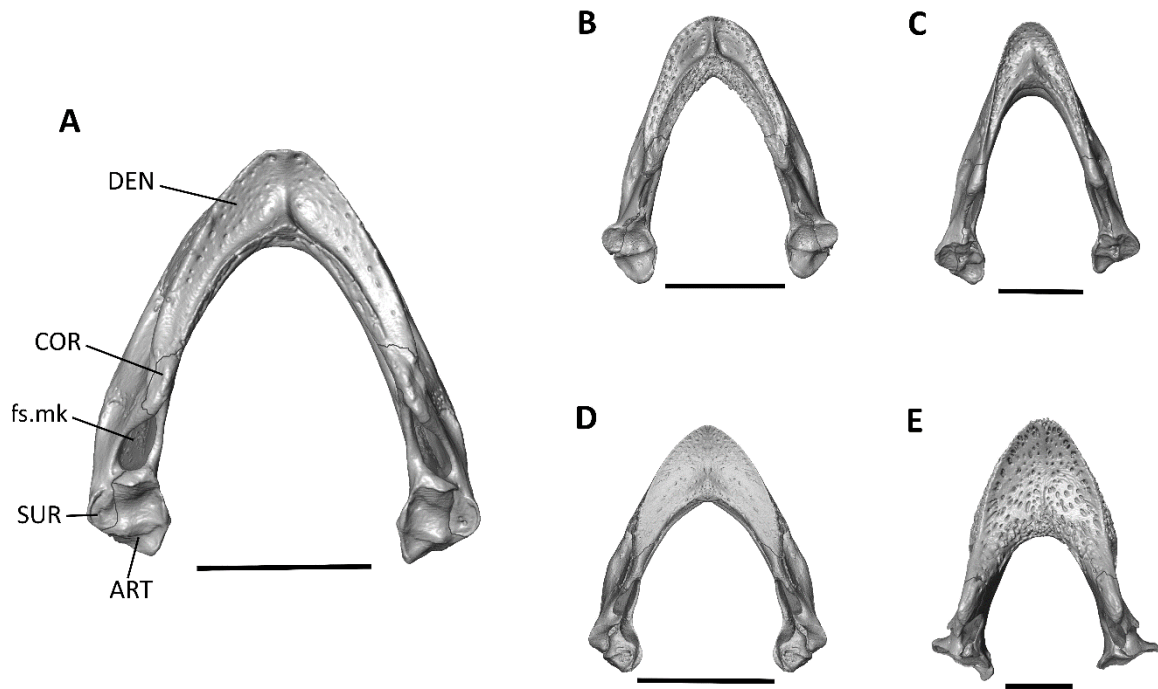


Figure 7. Dorsal view of the mandibles of the five extant cheloniid sea turtles. Images are of surface files constructed in Avizo lite 8.0 A *Natator depressus* (WAM R112123). B *Chelonia mydas* (NHMUK 1969.776) C *Eretmochelys imbricata* (WAM R120113). D *Lepidochelys olivacea* (SMNS 11070). E *Caretta caretta* (SAM unregistered). Abbreviations: ANG, angular; ART, articular; COR, coronoid; DEN, dentary; fs.mk, fossa Makelii; Scale bar = 50mm.

Braincase

The braincase is a complex structure comprising the supraoccipital, exoccipitals, parietals, basioccipital, basisphenoid, opisthotic, prootic, parietal, epipterygoid, and pterygoid. The *condylus occipitalis* is concave bounded by three lobes: one ventral and two ventrolateral, with a dimple in the centre (Fig. 5). The basioccipital contributes the ventral lobe whereas the exoccipitals contribute the two ventrolateral lobes. The posterior face of the each of the paired exoccipitals is tall and tapers dorsomedially to contact the supraoccipital (Fig. 5). Medially the exoccipitals bound the *foramen magnum* which is roughly diamond-shaped (Fig. 5). The exoccipitals continue anteriorly and provide the posterolateral walls of the brain case. They contact the opisthotic posteriorly as well as laterally. They extend ventrally below the *condylus occipitalis* continuously in contact with the basioccipital, and form part of the

dorsal margin of the opening of the *foramen posterior canalis cartotici interni*. The medial face makes up the posterolateral wall of the braincase and is perforated by two *foramina hypoglossi*. They continue to exit the exoccipital on the posterior face, on the posterolateral base of the occipital condyle. The posterior *foramen hypoglossi* is larger than the anterior one. In *N. depressus* there is a distinct *foramen jugulare posterius* consistently present in adult specimens (Fig 12). This feature is only found in *N. depressus* among Chelonioidea.

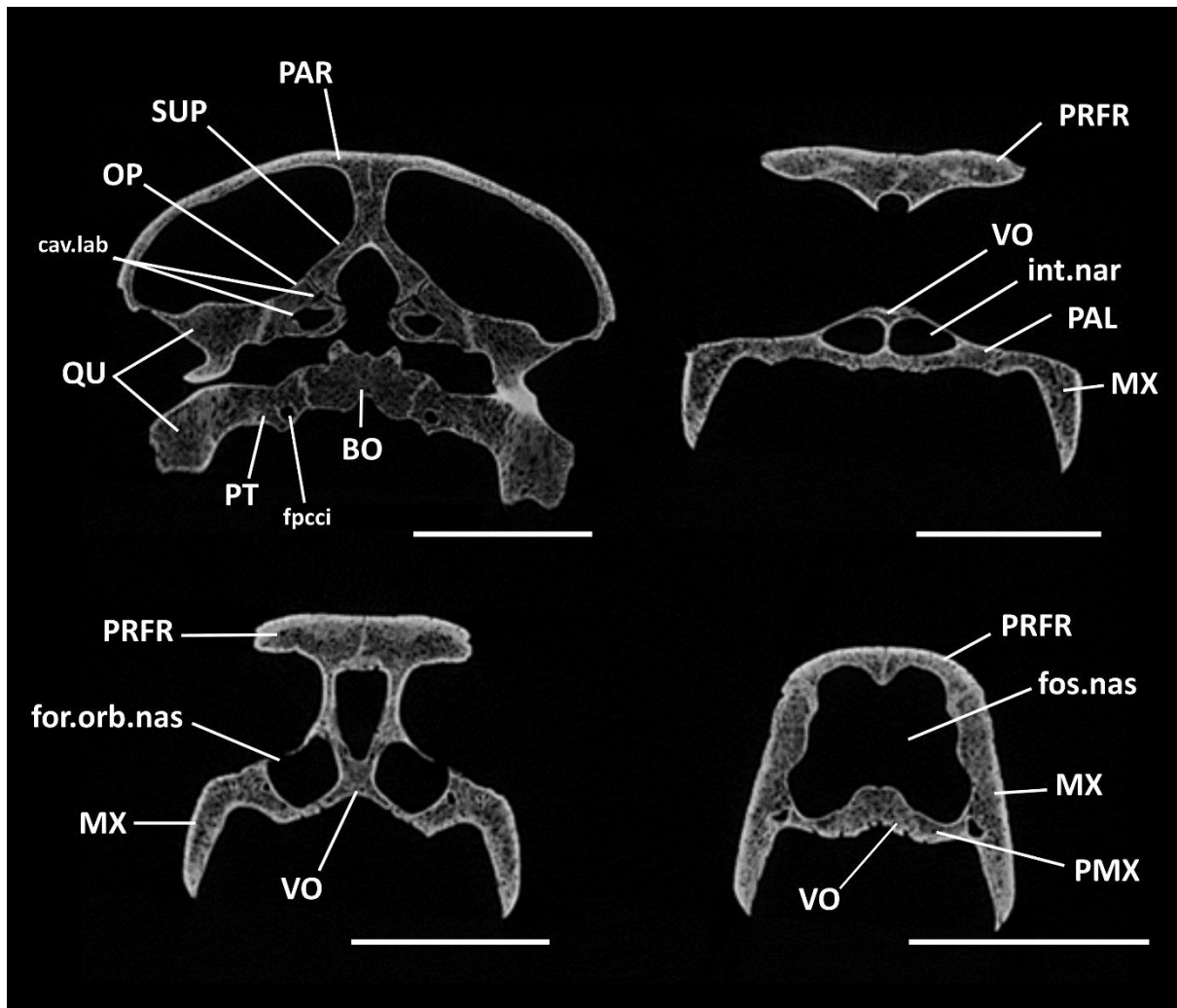


Figure 8. Transverse cross sections *Natator depressus* (WAM R120113) cranium of the posterior portion of the skull (A) and of the nasal region moving anteriorly (B-C). Abbreviations: BO, basioccipital; cav.lab, cavum labrinthicum; fpcci, foramen posterior canalis cartotici interni; fos. nar, fossa nasalis; fos.orb.nas., fossa orbito-nasalis; int.nar., internal nares; MX, maxilla; OP, opsithotic; PAL, palatine; PAR, parietal; PRFR, prefrontal; PT, pterygoid; PT, pterygoid; VO, vomer. Scale bars are 50mm.

The opisthotic forms part of the lateral wall of the braincase. It contacts the squamosal laterally, the supraoccipital dorsally, and the prootic anteriorly (Fig 9). The anterior portion of the opisthotic houses much of the semicircular canals which is otherwise housed within the supraoccipital and prootic. The lateral face of the opisthotic contributes to the medial wall of the adductor chamber as well as the posterior shelf or floor. In medial view, the contribution of the opisthotic to the braincase appears to be fairly minimal, comprising a *processus interfenestralis* located between the *foramen jugulare anterius* (posteriorly) and *hiatus acusticus* (anteriorly) (Fig. 9). The supraoccipital forms the dorsal margin of these two openings. In our specimens the *foramen jugulare anterius* is relatively large but is likely highly individually variable. In *N. depressus* there is a short triangular process of bone (from the opisthotic) protruding posteriorly along the anterior margin making the foramen more kidney-shaped than oval. In the Carettini and *E. imbricata* the foramen is narrow and crescent-like. The anterior edge of the medial face of the opisthotic forms the posterior margin of the *hiatus acusticus* (Fig. 9). The *hiatus acusticus* itself is an irregular shape, having three distinct embayments (or lobes) extending posterodorsally, anterodorsally and ventrally. This shape is seen throughout Cheloniidae except for *Ch. mydas* where the *hiatus acusticus* is relatively narrower and the two dorsal most embayments are not as prominent. In *N. depressus*, the *posterior canalis semicircularis* runs through the anterior portion of the opisthotic whereas the *anterior* and *lateral canalis semicircularis*, run through much of the posteromedial portion of the prootic. The dorsal margin bears a small notch and is mainly formed by the prootic, the anterodorsal and anterior margins are also formed by the prootic, and the ventral margin is formed by the basisphenoid (Fig. 9).

The prootic is irregularly shaped and contacts the quadrate, pterygoid, basisphenoid, supraoccipital, opisthotic, and parietal. The prootic contributes to the medial wall of the

braincase as well as the medial wall and floor of the adductor chamber (Fig. 9). The anterior margin forms most of the posterior edge of the *foramen trigemini*. Near the most dorsal point of this margin a small process extending into the foramen which is not found in the other species of sea turtle. The medial face forms a significant part of the braincase. The prootic is perforated on its medial face by the *fossa acustico-facialis*, which is roughly oval in shape. The *fossa acustico-facialis* contains three foramina, the most anterior foramen is the *foramen nervi facialis* which travels through the prootic to exit on the ventrolateral face, posterior to the *foramen trigemini*. The two posterior foramina are the *foramina nervi-acustici* (Fig. 10). The more medially located foramen perforates the posterior wall of the fossa into the inner ear. In *N. depressus* this foramen is fully enclosed, as is it is in most species.

The most conspicuous part of the supraoccipital is the *crista supraoccipitalis*. It is tongue-shaped in lateral view and mediolaterally compressed forming a vertical blade of bone projecting posteriorly from the cranium (Fig. 2, 9). The lateral face is flat with a dorsal edge that is somewhat thicker than the rest of the projection. The anterior portion of the supraoccipital broadens considerably and forms most of the roof of the braincase. The ventral surface is concave structure and the ventral margins contact the exoccipital, opisthotic, and prootic.

The floor of the braincase is formed by the basioccipital posteriorly and the basisphenoid anteriorly. The basisphenoid contacts the basioccipital posteriorly, the external seam is relatively straight and oblique to the midline of the skull (Fig. 4). At the medial most point of contact to the basisphenoid, there is a small dorsally projecting tubercle on the basioccipital, the *basis tuberculi basalis*. This prominence is where the tendon of the

Musculus retrahens Capiti Collique Pars Carapacobasioccipitalis inserts (Jones *et al.* 2012).

There is a low ridge of bone extending posteriorly from the *basis tuberculi basalis* along the midline of the basioccipital, and another running anteriorly along the midline of the basisphenoid. The basisphenoid has an anterior projection of bone the *rostrum basisphenoidale* (Fig. 11) which lies on the dorsal surface of the paired pterygoids along their midline contact. The dorsal surface of the basisphenoid is concave, and has two fairly large processes projecting anterodorsally just posterior to the *rostrum basisphenoidale*. This rostrum is relatively robust and squat in *N. depressus*, but, species in the Carettini have a thinner, longer rostrum. The basisphenoid has a ventrally projecting V- shaped crest, the tip of which merges with the central ridge along the medial contact between the two pterygoid bones. The contact is overlapping with the basisphenoid largely resting atop the pterygoids, the crest representing the posterior most contact.

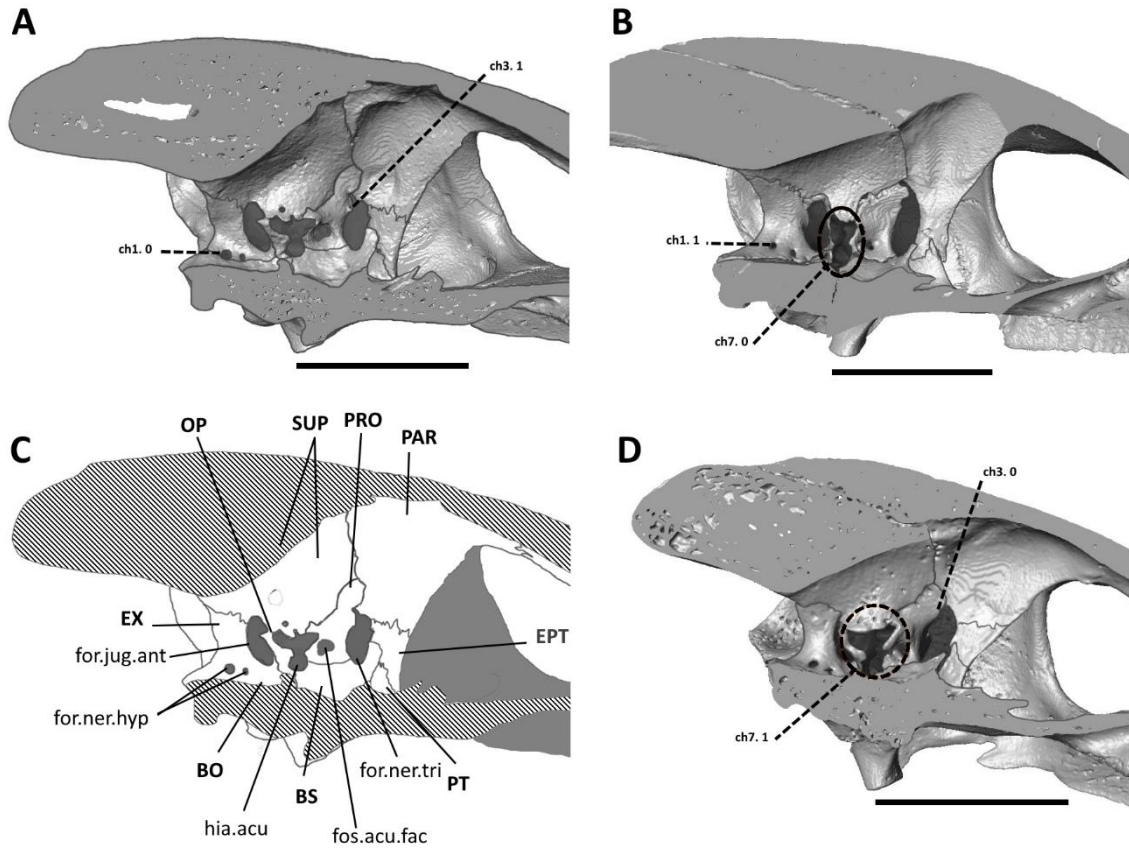


Figure 9. Parasagittal cross section of *Natator depressus* (WAM R112123) (A,D) skull, exposing the lateral wall of the braincase. B and C represent the lateral wall of the braincase of *Chelonia mydas* (SAMA Unregistered) and *Lepidochelys olivacea* (SAMA BM670) respectively. A: the original surface file, B: the surface file redrawn and labelled. Areas which are “cut through” are shaded with diagonal lines. Displaying the states of characters 1, 3, 7, based on the descriptors in Appendix 2. Abbreviations: BO, basioccipital; BS, basisphenoid; EPT, epipterygoid; EX, exoccipital; for.jug.ant., foramen jugulare anterius; hia.acu., hiatus acusticus; OP, opisthotic; PAR, parietal; PT, pterygoid; PRO, prootic; SUP, supraoccipital. Scale bars = 20mm

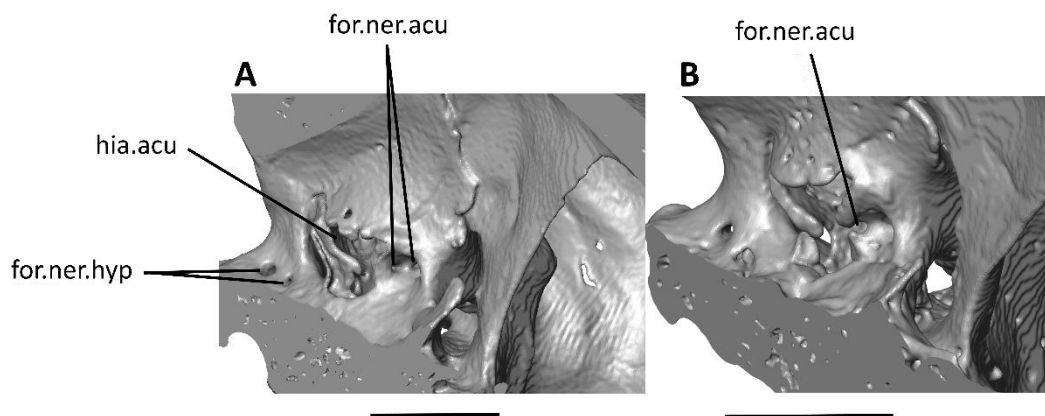


Figure 10. Antero-medial view of brain case of *N. depressus* (WAM R112123) (A) and *Lepidochelys olivacea* (SAMA BM670). (B) showing the closed (A) and open (B) states of the medial foramen nervi acustici. Abbreviations: for.ner.ac, foramen nervi acustici; for.ner.hy, foramen nervi hypoglossi; hia.acu, hiatus acusticus. Scale bars = 20mm

Lower jaw

The lower jaw is V shaped in dorsal view, and relatively heavily built (Fig. 6, 7). The two dentaries are fused with no clear suture seam visible even in cross section (Fig. 6). The tip of the dentary is located dorsal to the long-axis of the Mecklian groove (Fig. 6). The labial and lingual ridges of *N. depressus* are prominent and both form a distinct midline point; there is a distinct ridge connecting these two points. The point of the lingual margin is almost as large as the point on the labial ridge; it is visible in lateral view, there is a distinct ridge connecting the two peaks of the lingual and labial margin. There is a large triangular depression on the lateral surface of the dentary. It deepens anteriorly eventually leading to the *foramen dentofaciale majus*, this foramen travels anteriorly through the dentary meeting its counterpart at the midline of the mandibular symphysis (Fig. 6). From the *foramen dentofaciale majus* to the articular surface runs a distinct shelf along the ventral portion of the lateral surface of the lower jaw (Fig. 6). This shelf is formed at its most posterior portion by the dentary, but the majority of it is formed by the surangular. This shelf is likely related to the insertion point of the M. adductor mandibulae externus Pars superficialis (Jones *et al.* 2012). The medial face of the dentary is marked by a very obvious Meckelian groove. It runs the entire length of the dentary at mid-depth. The dentary has a large posterolateral process. The dentary contacts the surangular posterolaterally, the surangular dorsally, and the coronoid posterodorsally and medially, as well as the angular posteriorly and posteromedially (Fig. 6).

The surangular is a largely flat sheet of bone making up most of the posterior half of the lateral face of the lower jaw (Fig. 6). Anterodorsally it contacts the coronoid there is also posterior and posterodorsal contact with the articular, and ventral contact with the dentary and angular. Posteriorly it has anteromedially curved processes that contact the

prearticular. The *fossa Meckelii* is bound laterally by the surangular, anteriorly by the coronoid, medially by the prearticular, and posteriorly by the articular. The *fossa Meckelii* continues to the medial face. The articular surface at its posterior extremity on the lower jaw mirrors the surface of the condyle of the quadrate (Fig. 6, 7) (although in life both surfaces would be capped with cartilage, e.g. Jones *et al.* 2012). The lower end of the external suture seam between the dentary and surangular passes anteriorly before it passes posteroventrally (e.g. WAM R112123) in contrast to the simpler posteroventral path figured by Hirayama (1994: Fig. 5).

The biting surface is comprised of two shallow troughs either side of a subtle parasagittal ridge. The medial trough has anterior and posterior concavities and is formed by the dorsal face of the articular. The lateral trough is formed by the surangular. At the anterior most point there is a transverse ridge. A less prominent ridge also protrudes at the posterior end of the articular surface (where the articular and surangular meet posteriorly). At least in these specimens, the contact between the surangular and articular is difficult to see, unlike other species where the seam is clear. This might be due to specimen preparation or other post mortem effects. The articulating surface faces posterodorsally. The angular lies along the ventromedial edge of the lower jaw. It contributes to the most posterior section of the Meckelian groove (Fig. 6). The prearticular is a large flat bone constituting much of the posterior section of the medial face. Though largely flat it does curve medially near the articular surface. From medial view the prearticular contacts the coronoid anteriorly. The coronoid sits atop the surangular, dentary, and prearticular.

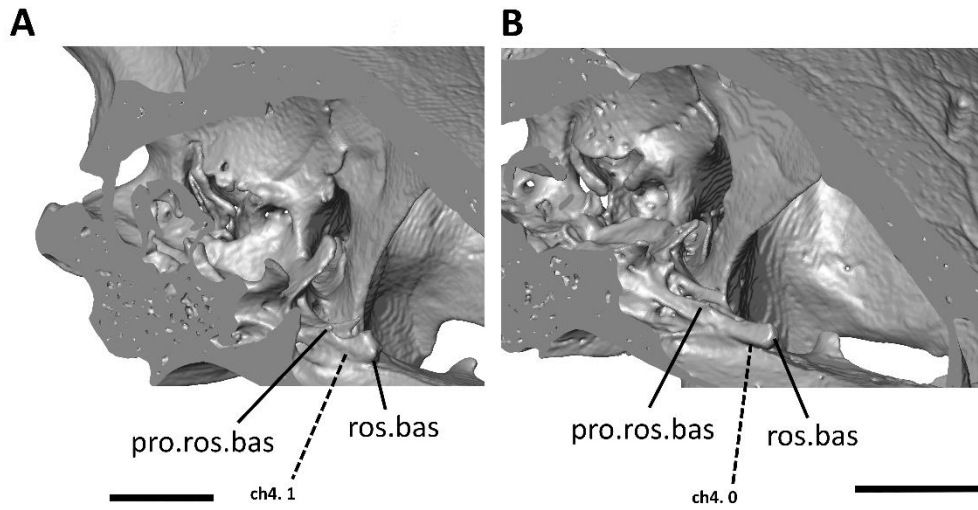


Figure 11. Antero-medial view of brain case of *N. depressus* (WAM R112123) (A) and *L. olivacea* (SAMA BM670). (B) illustrating the two states of the rostrum basisphenoidale, robust (A) and gracile (B). Displaying the states of character 4 based on the descriptor in Appendix 2. Abbreviations: pro.ros.nas processus rostrum basisphenoidale; ros.bas, rostrum basisphenoidale. Scale bars = 20mm

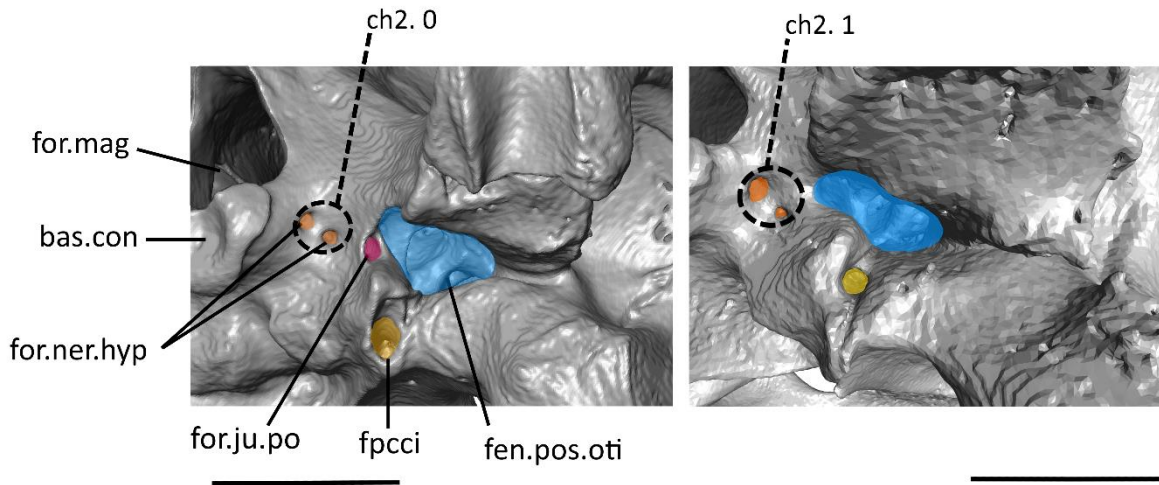


Figure 12. Ventro-posterior-lateral view of *N. depressus* (WAM R112123) (A) to highlight the *foramen jugulare posterius*, and *E. imbricata* (WAM R120113) (B) for comparison. Displaying the states of character 2 based on the descriptor in Appendix 2. Abbreviations: bas.con, basioccipital condyle; fn.po, fenestra postotica; for.ju.po, foramen jugulare posterius; for.mag, foramen magnum; for.ner.hyp, foramen nervi hypoglossi; fpcci, foramen posterior canalis cartotici. Scale bars = 20mm

Table 1. State of characters found in this study detailed further in Appendix 2

New Character	<i>N. depressus</i>	<i>Ch. mydas</i>	<i>E. imbricata</i>	<i>Ca. caretta</i>	<i>L. olivacea</i>	<i>L. kempii</i>
Anterior foramen hypoglossi alignment compared to that of the midline of the acoustic facialis	Ventral	In line	Ventral	Ventral	Ventral	Ventral
Relative size of the two posterior foramina of the nervi hypoglossi	Variable	Anterior foramen less than half of the diameter of posterior foramen	Anterior foramen less than half of the diameter of the posterior foramen	Similar in size	Similar in size	Similar in size
Anterior process intruding into the foramen trigemini	Process present	Process absent	Process absent	Process absent	Process absent	Process absent
The shape of the rostrum basisphenoidale	Robust, with large processes	Robust, with large processes	gracile with small processes	gracile with small processes	gracile with small processes	gracile with small processes
The shape of the labial margin of the maxilla	squared off	squared off	a continuous with jugal	continuous with jugal	continuous with jugal	continuous with jugal
The extent of the superficial ridge on the jugal	Distinct superficial ridge transecting jugal	Indistinct margin transecting jugal	No ridge along the jugal	No ridge along the jugal	No ridge along the jugal	No ridge along the jugal
The shape of the hiatus acousticus	two distinct sections with the dorsal portion significantly wider than the ventral portion	largely rectangular with no significant difference in width between the dorsal and ventral portions	two distinct sections with the dorsal portion significantly wider than the ventral portion	two distinct sections with the dorsal portion significantly wider than the ventral portion	two distinct sections with the dorsal portion significantly wider than the ventral portion	two distinct sections with the dorsal portion significantly wider than the ventral portion
The presence of a posteroventrally extending process from the jugal	No process	No process	Small process	Small process	Large process extending posterior to the jugal-quadratojugal margin	Large process extending posterior to the jugal-quadratojugal margin
Degree of overlap of the jugal on the quadratogual	Extensive overlap	Marginal overlap	Negligible overlap	Negligible overlap	Negligible overlap	Negligible overlap
Orientation of origin of the depressor mandibulae from the squamosal	Faces laterally or posterolaterally	Faces posteriorly	Faces laterally or posterolaterally	Faces laterally or posterolaterally	Faces laterally or posterolaterally	Faces laterally or posterolaterally

Phylogenetic relationships

All four datasets found generally the same topology, but with key differences for Chelonioidea and closely related taxa (Fig. 13 - 14).

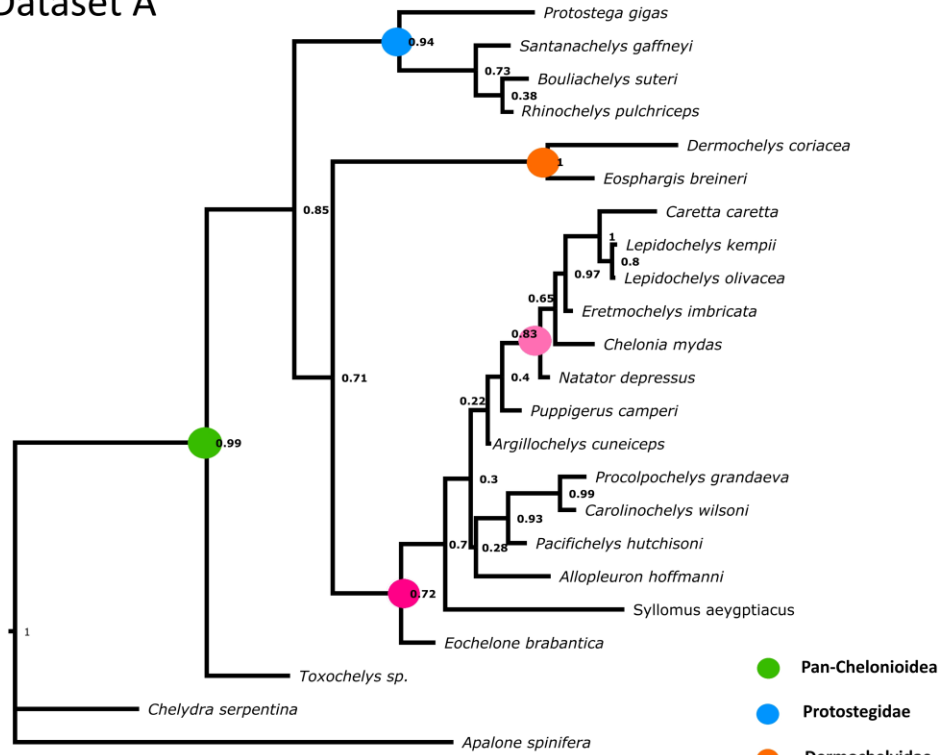
The results from all datasets place, *Toxochelys spp.* as the sister taxon to the rest of Pan-Chelonioidea and Protostegidae is a distinct sister clade to a clade including Cheloniidae and Dermochelyidae as is found in recent studies (Evers 2019; Gentry *et al.* 2019). It should be noted that the polytomy at the base of the tree is likely an artefact of character selection to optimise resolving relationships within Pan-Chelonioidea and does not reflect the relative phylogenetic position of these two genera.

Results from data set A (Includes the 23 taxa of interest and only the characters used in Evers and Benson 2019) (Fig. 13) recovers Chelonioidea ($P = 0.99$). Crown cheloniids form a monophyletic group ($P = 0.83$). Dermochelyidae (*Dermochelys coriacea* + *Eosphargis breineri*) is recovered with strong support ($P = 1$). A clade comprising three American fossil taxa (*Carolinachelys winsonii*, *Procolpochelys grandavea*, + *Pacifichelys hutchisoni*) is well supported ($P = 0.93$) and is sister to *Allopleuron hoffmani* though with weak support ($P = 0.28$). *Argillochelys cuneiceps* and *Puppigerius camperi* are along the stem of Cheloniidae, though their placement there has weak support. *Chelonia mydas* and *N. depressus* do not form a clade and instead *N. depressus* falls as sister to the rest of the crown, with *Ch. mydas* as sister to the *E. imbricata* + Carettini clade.

Results from dataset C (includes all of the taxa and only the characters used in Evers and Benson (2019)) recovered Pan-Chelonioidea ($P = 1$) (Fig 14). However, Cheloniidae was not recovered, with Dermochelyidae nested within Cheloniid turtles as a sister to *Ch. mydas* ($P =$

0.74). *Natator depressus* was recovered as sister to the rest of the crown and the *Ch. mydas* + Dermochelyidae group (P= 0.81).

Dataset A



Dataset B

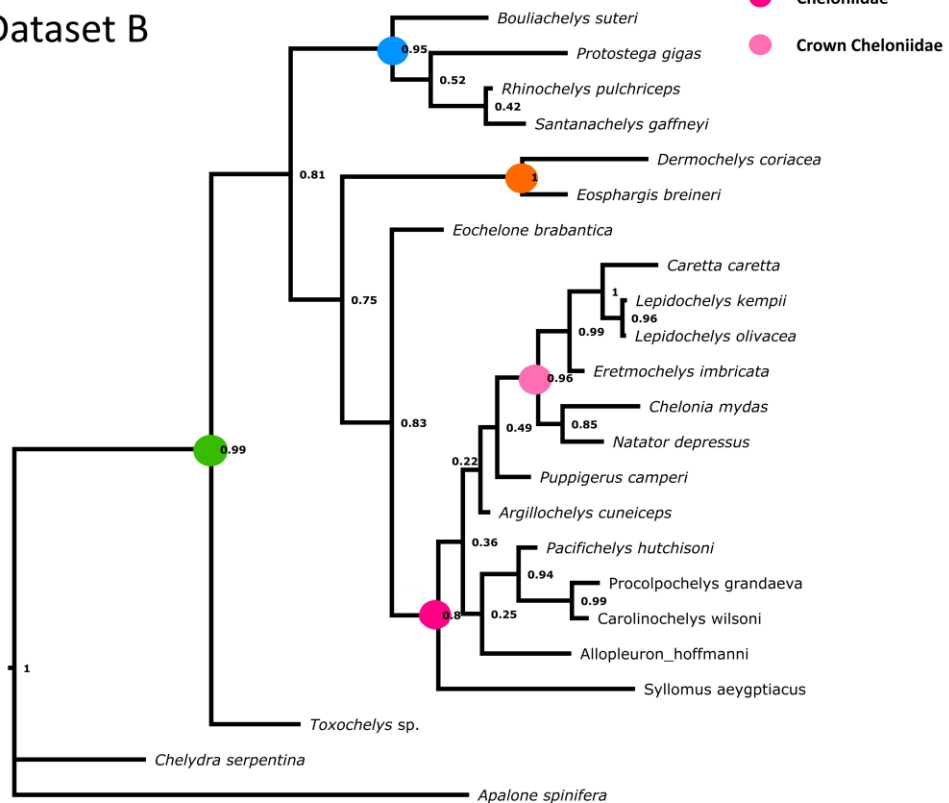
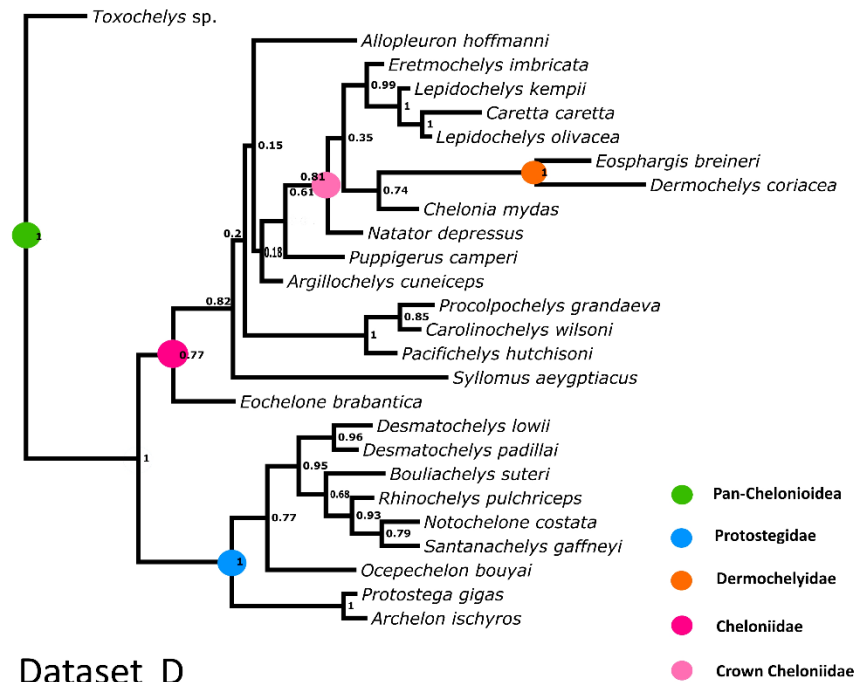


Figure 13. Maximum credibility Bayesian trees. Dataset A based on the matrix from Evers & Benson (2019). Dataset B based on matrix from Evers & Benson (2019) with added characters found in this study. Different colours at nodes represent base of clades. Numbers at the node show posterior probability value of node.

Results from data set B (includes the taxa of interest and the new characters found in this study) recovers Chelonioidea and it is well supported ($P=0.99$) (Fig. 13). Crown cheloniids form a monophyletic group with high support ($P = 0.95$), and with a branching order identical to the consensus hypothesis based on analysis of molecular data (e.g. Naro-Maciel *et al.* 2008; Duchene *et al.* 2012). That is, *N. depressus* is placed in a clade with *Ch. mydas*, and this pair is sister to the remaining cheloniids, with *E. imbricata* the sister of the Carettini. Dermochelyidae are sister to Cheloniidae. *Eochelone brabantica* is sister to the rest of Cheloniidae ($P = 0.82$). The clade of American cheloniids ($P = 0.94$) (*Carolinachelys wilsonii*, *Procolpochelys grandavea*, + *Pacifichelys hutchisoni*) is again recovered, as well as the sister relationship to *Allopleuron hoffmani* ($P = 0.26$). The topology for crown group Cheloniidae recovered matches that recovered with molecular evidence, and *N. depressus* is recovered as sister to *Ch. mydas* ($P = 0.62$).

Results from dataset D [includes the all the taxa from Evers and Benson 2019) and the new characters] are largely consistent with the trees recovered using dataset B (Fig 14). The support values are generally weaker, likely due to the necessity of marking the new characters as unknown in many taxa. The topology of the crown group recovered is consistent with the current molecular consensus (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012).

Dataset C



Dataset D

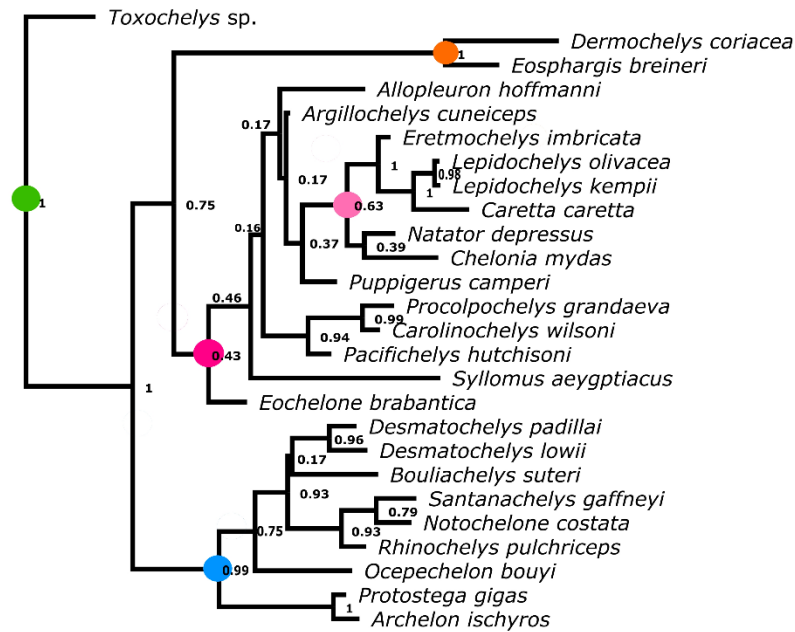


Figure 14. Pruned maximum credibility Bayesian trees. Dataset C based on the matrix from Evers & Benson (2019). Dataset D based on matrix from Evers & Benson (2019) with added characters found in this study. Colours at nodes represent base of clades. Numbers at the node show posterior probability value of node.

DISCUSSION

Natator depressus exhibits several skull features which have not been reported previously. These features include a proportionately large jugal with a high degree of overlap with the quadratojugal, the well-defined superficial jugal ridge as well as the fully enclosed *foramen jugulare posterius*. The function of these features is unclear. The extensive jugal overlap might relate to the size or shape of the *adductor mandibulae externus pars superficialis*, which has one of three origin points contacting the anterior of the quadratojugal and posterior of the jugal (Jones *et al.* 2012). The greater overlap provides greater surface area for associated connective tissues and therefore might reflect the temporal region being subjected to relatively greater strain than in other sea turtles (Jaslow 1990; Jones *et al.* 2011). The functionality of the superficial jugal ridge is unclear. Though there is evidence of this feature in all species of sea turtles it is particularly prominent in *N. depressus*. It is possible that this structure is associated with the middle ear. The prominent ridge in *N. depressus* is associated with a relatively large jugal but why the ridge is so prominent is unclear. There has been little work focusing on the external surface of the ear region of sea turtles, summarised in Bartol and Musick (2003). The prominence of the ridge may be related to the attachment of the disk of subcutaneous fat underlying the scales of the ear region (Henson 1974; Ridgway *et al.* 1969, Bartol and Musick 2003). The attachment of the cutaneous plate on the exterior of the ear of *Chelonia mydas* is reported to be loose (Ridgway *et al.* 1969); perhaps the attachment is firmer in *N. depressus*. A slightly different arrangement of this structure in *N. depressus* would be interesting given that it is a shallow water specialist, and the only modern sea turtle without a pelagic life stage (Limpus *et al.* 1983; Walker and Parmenter 1990). The auditory ability of Testudines has recently received some attention (e.g. Christensen-Dalsgaard *et al.* 2012; Piniak *et al.* 2012; Willis 2016), but

the functional anatomy of the ear is generally considered to be poorly known. A recent study by Foth *et al.* (2019) was unable to identify a relationship between middle ear shape and habitat ecology in turtles.

As stated in previous studies (Zangerl *et al.* 1988; Limpus *et al.* 1988), the general shape of the skull of *N. depressus* resembles *L. olivacea*: relatively wide skull, a broad palate, large external pterygoid processes. Several other features shared by the two species such as the shape of the *hiatus acousticus*, the orientation of the origin of the *depressor mandibulae*, and the size and location of foramina are shared by multiple species. The size of the *crista supraoccipitalis* is notably smaller than it is in other species, but it is perhaps most similar to *E. imbricata*. The shape of the *crista supraoccipitalis* is broad and rounded in contrast to *Ch. mydas* in which it is pointed and narrow. Like *Ch. mydas* but unlike other extant members of Cheloniodea, the maxilla has a significant portion lying ventral to the jugal in lateral view, a squared posterior edge, and ventral ridges.

Overall the lower jaw of *Natator depressus* resembles that of *Chelonia mydas*. It has a distinct sharp lingual and labial ridge on the dentary, with distinct anterior peaks connected by a distinct midline ridge. It lacks the large flattened area at the anterior of the dentaries found in members of Carettini. The coronoid process is significantly smaller than that of *L. olivacea* and *Ca. caretta*. Unlike both *E. imbricata* and *Ch. mydas* there is no ventral flexion at the anterior tip. There is a large variation in the direction of the mandibular articulation within crown Cheloniidae. In *N. depressus* the articulating surface faces postero-dorsally, in *Ch. mydas* the surface faces more dorsally whereas in *Ca. caretta* it faces almost entirely posteriorly. Characters previously used to unite *N. depressus* and *Lepidochelys* spp. appear to vary within the two species or appear to be plesiomorphic for the crown of Cheloniidae

(Limpus *et al.* 1988; Zangerl *et al.* 1988). Unlike what is suggested in Limpus *et al.* (1988) the contact of the prefrontal and postorbital does not occur in our sample of *L. olivacea* suggesting that it might be a variable character trait within this species (Pritchard and Trebbau 1984; Zangerl *et al.* 1988, Wyneken 2001; Jones *et al.* 2012; SAMA BM670; SMNS 11070).

In this study it was found that *Natator depressus* and *Chelonia mydas* share the following synapomorphies, a robust *rostrum basisphenoidale* and a squared off maxillary margin. Some of the other distinguishing features of *N. depressus* reported in this study, the distinct superficial jugal ridge and the extensive overlap of the quadratojugal by the jugal, are present to a lesser extent in *Ch. mydas*. The two species also completely lack a posterolateral jugal process, unlike all other species within crown Cheloniidae.

Although our study finds a number of character traits shared by *Chelonia mydas* and *Natator depressus*, the two species also show some marked differences. *Ch. mydas* has a notably blunt snout compared to other species as well as a posteriorly directed origin for the depressor mandibulae. The rectangular shape of the *hiatus acusticus* in *Ch. mydas* is markedly different from the other species (Fig. 10). Some of the difference in general skull shape could potentially be explained by the anteroposteriorly short rostrum and herbivorous diet of *Ch. mydas* (Bjorndal *et al.* 1997). The cranial similarities presented in Limpus *et al.* (1988) previously considered to indicate a close affinity between *N. depressus* and *L. olivacea*, instead highlight the strangeness of *Ch. mydas*. These data as well as our new observations suggest that *Ch. mydas* is not a particularly appropriate representative taxon for Cheloniidae.

This revision of *Natator depressus* provides another example of a study that has uncovered morphological evidence for a phylogenetic hypothesis that was previously considered supported mainly by molecular data (e.g. Asher and Geisler 2008; Lee and Camens 2009). Molecular frameworks can be valuable for analysing the datasets that include fossil taxa. However, a more comprehensive examination of modern species, particularly skeletal characters, is needed so that their morphological traits can be included within phylogenetic analyses (e.g. Nick 1912; Bell and Mead 2014, Regnault *et al.* 2017). In most cases, skeletal characters are the only means of direct comparison between fossil taxa and extant taxa. Such practice will increase our understanding of character distribution, character polarity and character evolution in the crown group. This achievement is necessary to correctly distinguishing between crown vs stem taxa in the fossil record. Coupled with tip and node dating methods (e.g. Lourenco *et al.* 2012; Lee and Yates 2018), it may be possible to resolve the total group phylogenetic relationships and address broader macroevolutionary questions.

CONCLUSION

This study recovers a sister group relationship between *Natator depressus* and *Chelonia mydas* using a quantitative analysis of only morphological evidence. This is, to the best of our knowledge, the first time the currently accepted phylogenetic tree has been found using quantitative methods without a molecular constraint. The synapomorphies uniting *N. depressus* and *Ch. mydas* found in this study: overlap of the quadratojugal by the jugal, a superficial ridge transecting the jugal, a squared off maxillary margin, and a robust *rostrum basisphenoidale*. The characters shared by *N. depressus* and *Lepidochelys* spp. are also

shared with other cheloniids. It is notable that the braincase features that appear to unite *N. depressus* and *Ch. mydas* were not examined by previous studies. This apparent omission likely relates to the previous difficulty of evaluating such characters without destructive sampling and highlights the potential unlocked by greater availability of micro Computed Tomographic imaging. The new characters identified here should be included in future studies of fossil sea turtles and CT scanning may help make this task possible.

Statement of Authorship

Title of Paper	Allometric and ontogenetic divergence in sea turtle (Chelonioidae) skull shape evolution		
Publication Status	<input type="checkbox"/> Published <input type="checkbox"/> Accepted for Publication <input type="checkbox"/> Submitted for Publication <input checked="" type="checkbox"/> Unpublished and Unsubmitted work written in manuscript style		
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Principal Author

Name of Principal Author (Candidate)	Ray Chatterji		
Contribution to the Paper	Majority of Specimen collection and Processing Majority of Data Analysis Majority of Writing and Editing of Manuscript		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/08/2020

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- the candidate's stated contribution to the publication is accurate (as detailed above);
- permission is granted for the candidate to include the publication in the thesis; and
- the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Mark Hutchinson		
Contribution to the Paper	5% Editorial advice, feedback on clarity and relevance of text		
Signature		Date	20/08/2020

Name of Co-Author	Marc E H Jones		
Contribution to the Paper	5%, contributed to the initial study design. Provision of the CT scan software. Help with sourcing some specimens and scans. Some guidance on organisation, analysis, literature, formatting, and implications. Some suggestions on the interpretations of result. Detailed feedback on the first iteration of the manuscript. Text editing of subsequent iterations.		
Signature		Date	21st of August

Please cut and paste additional co-author panels here as required.

Name of Co-Author	Christy Hipsley		
Contribution to the Paper	sample collection, data analysis, R code, interpretation of results, editing and structuring manuscript (5%)		
Signature		Date	11 August 2020

Name of Co-Author	Emma Sherratt		
Contribution to the Paper	data analysis, R code, interpretation of results, editing and structuring manuscript (5%)		
Signature		Date	13 August 2020

Please cut and paste additional co-author panels here as required.

Ontogenetic allometry underlies trophic diversity in sea turtles (Chelonioidea)

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ABSTRACT

Despite only comprising seven species, extant sea turtles (Cheloniidae and Dermochelyidae) display great ecological diversity, with most species exhibiting their own dietary niche as adults. This adult diversity is remarkable given that all species share the same dietary niche as juveniles. These ontogenetic shifts in diet, as well as a dramatic increase in body size make sea turtles an excellent group to examine how morphological diversity arises by allometric processes and life habit specialisation. Using three-dimensional geometric morphometrics, we characterise ontogenetic allometry in the skulls of all seven species and evaluate variation in the context of phylogenetic history and diet. Among the sample, the olive ridley (*Lepidochelys olivacea*) has a seemingly average skull shape and generalised diet, whereas the green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) show different extremes of snout shape associated with their modes of food gathering (grazing vs grasping, respectively). Our ontogenetic findings corroborate previous suggestions that the skull of the leatherback (*Dermochelys coriacea*) is paedomorphic. It has similar skull proportions to the hatchlings of other sea turtle species and perhaps correspondingly the leatherback retains a hatchling-like diet of relatively soft bodied organisms. The flatback sea turtle (*Natator depressus*) shows a similar but less extreme pattern. By contrast, the loggerhead sea turtle (*Caretta caretta*) shows a peramorphic signal associated with increased jaw muscle volumes that allow predation on hard shelled prey. Similarly, the Kemp's ridley (*Lepidochelys kempii*) has a peramorphic skull shape compared to its sister species the olive ridley, and a diet that includes harder prey items such as crabs. Although the small number of species limits statistical power, differences among skull shape, size, and diet are consistent with the possibility that shifts in allometric trajectory facilitated diversification in skull shape and diet as observed in an increasing number of vertebrate groups.

1. INTRODUCTION

Among vertebrates, changing shape as a consequence of changing size (allometry) has been shown to be a major mechanism for generating morphological diversity (Klingenberg 1998; Erickson *et al.* 2003; Tokita *et al.* 2017; Gray *et al.* 2019; Sherratt *et al.* 2019). Studies of allometry and ontogeny among animals often focus on the effects of changes in growth and body size on ecology (Urošević *et al.* 2012; Esquerré *et al.* 2017; Morris *et al.* 2019; Gray *et al.* 2019), as well as their evolutionary and functional consequences (Mitteroecker *et al.* 2005; Wilson *et al.* 2011; Piras *et al.* 2011; Bhullar *et al.* 2016; Esquerré *et al.* 2017; Morris *et al.* 2019). Changes in ontogenetic allometry through altered developmental timing (heterochrony) has been demonstrated to be an effective mechanism for dietary adaptations (Denoël *et al.* 2004; Esquerré *et al.* 2017; Sherratt *et al.* 2019), often resulting in differences in skull shape that permit access to new feeding niches (Denoël *et al.* 2004; Frederich *et al.* 2008; Morris *et al.* 2019).

Sea turtles represent an excellent group to study the effects of ontogenetic and evolutionary allometry on life habit. They are geographically widespread, monophyletic (Evers *et al.* 2019), exhibit a range of ecological roles and body sizes (Pritchard and Trebbau 1984; Bjorndal *et al.* 1997), and have a fossil record with the potential to trace macroecological patterns across deep time (Parham and Pyenson 2010). The seven extant species belong to two families, the monotypic Dermochelyidae and the more speciose Cheloniidae (Fig. 1) (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012). These families likely diverged during the Late Cretaceous (Duchene *et al.* 2012; Thomson *et al.* 2021), with the crown of Cheloniidae diverging during the late Oligocene or early Miocene (Thomson *et al.* 2021). There is dramatic size variation among species (average adult weights between 35 and 400kg (Pritchard and Trebbau 1984; Dodd 1988; Zug and Parham 1996) and within

species, with *Dermochelys coriacea* (leatherback) increasing in size by three orders of magnitude during growth (Pritchard and Trebbau 1984; Jones *et al.* 2011). This increase in size is one of the largest among extant amniotes, only matched by some of the largest crocodilians (Brant 1991; Leach *et al.* 2009). In contrast to terrestrial other giant testudines such as the giant tortoises of the Galapagos and Aldabra (*Chelonoidis nigra*, *Aldabrachelys gigantea*), there can be a significant change in diet across ontogeny in sea turtles (Gibson 1983; Fowler de Neira and Johnson 1985; Furrer *et al.* 2004).

Despite their low taxonomic diversity, modern sea turtles display a remarkable ecological breadth, with most species inhabiting a unique dietary niche as adults (Bjorndal *et al.* 1997) (Fig. 1). However, as juveniles all sea turtles share a similar diet of plankton and small pelagic cnidarians (Bjorndal *et al.* 1997; Bolten 2003). Given the functional roles of the vertebrate skull in food acquisition and processing (Pritchard and Trebbau 1984; Claude *et al.* 2004; Parham and Pyenson 2010; Jones *et al.* 2012), a relationship between turtle skull structure and diet has been previously investigated in sea turtles but generally with a focus on one or two species. Examinations of skull development of *Chelonia mydas* (green) and *Caretta caretta* (loggerhead) indicate that dietary shifts are associated with morphological differences between ontogenetic stages (Nishizawa *et al.* 2010; Coelho *et al.* 2018; Lunardon *et al.* 2020). However, the relationship between skull shape and size among extant turtles remains poorly known, which limits our ability to understand how to distinguish ontogenetic and phylogenetic shape differences. This problem in turn inhibits analyses of phylogeny and diversity. Within other groups of reptiles heterochrony has been suggested to be a significant factor in their evolution, contributing to recent morphological diversity (Sherratt *et al.* 2018; Morris *et al.* 2019; Gray *et al.* 2019) as well as early

divergences (Esquerré *et al.* 2017; Morris *et al.* 2019). So the understanding of differing allometric patterns can possibly give insights into the early evolution of sea turtles.

Previous morphometric analyses of sea turtle skulls have either involved linear measurements (Kamezaki and Matsui 1995, 1997; Kamezaki 2003), or landmarks (Nishizawa *et al.* 2010; Coelho *et al.* 2018), or both (Lunardon *et al.* 2020). However, most of these studies focused on variation within one species: *Ca. caretta* (Kamezaki and Matsui 1997; Lunardon *et al.* 2020) or *Ch. mydas* (Kamezaki and Matsui 1995; Nishizawa *et al.* 2010; Coelho *et al.* 2018). Moreover, although some of these studies use large sample sizes they do not include all stages of ontogeny: a study of *Ca. caretta* used 80 individuals but no individuals were younger than 10 years old (Lunardon *et al.* 2020) and a study of *Ch. mydas* used 145 individuals but all were between 3 and 5 years old (Kamezaki and Matsui 1995). Only two studies include multiple species (Kamezaki 2003; Myers 2007) and neither examined growth trajectories or ecological differences. One uses a sample of three species and focuses on the of skull characteristics of *Ca. caretta* (Kamezaki, 2003). The other includes six extant species but also found *Lepidochelys olivacea* (olive ridley) to be notably different from other Cheloniidae which appears at odds with several qualitative anatomical comparisons (Gaffney 1979, Pritchard and Trebbau 1984, Jones *et al.* 2012). Other morphometric studies of turtle skull shape have been broader in scope, examining multiple families or turtles as a whole (Claude *et al.* 2004; Foth *et al.* 2016).

Here, we use geometric morphometrics to characterise ontogenetic allometry in the skulls of modern sea turtles. We sample all seven species across a wide size range encompassing hatchlings to large adults. While characterising patterns of ontogenetic allometry in each species, we attempt to understand how the relationship between skull shape and size is

related to diet and phylogenetic history. This study represents the first systematic examination of sea turtle skull shape with three-dimensional landmarks and the most comprehensive study of allometry in the group.

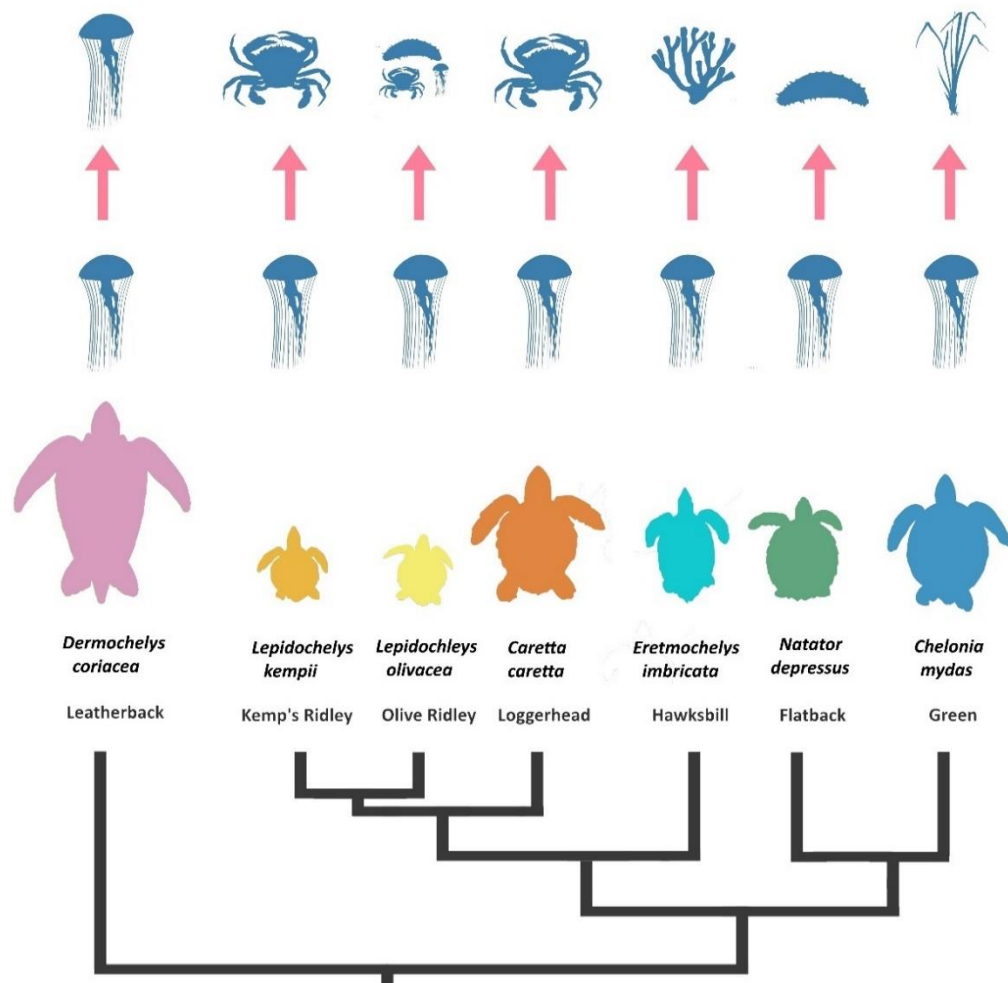


Fig. 1. Cladogram based on Naro-Maciel *et al.* 2008 and Duchene *et al.* 2012. Specimens scaled to relative size, based on available literature (Pritchard and Trebbau 1984; Dodd 1988). Top two rows of symbols represent the dietary categories of juveniles (bottom) and adult (top) members of each species: jellyfish = Pelagic, crab = Durophagous, sponge = Sponge, sea cucumber = Soft, sea grass = Herbivore, sea cucumber + crab + jellyfish = General. See table 2 for further details. Silhouettes redrawn from National Aquarium Baltimore (<https://www.aqua.org/blog/2015/April/oceans-seven>)

2. METHODS

2.1 Specimens

We sampled 63 specimens from museum collections representing all seven species of extant sea turtle, choosing as broad a size range as possible (Table 1). All hatchlings were ethanol-preserved as well as one large adult specimen of *Natator depressus* (flatback); all other specimens were dry skulls. Immature sea turtles in their pelagic stage are naturally rarer in museum collections due to their unlikelihood of being washed up on beaches. This factor limited specimen availability, although *Caretta caretta* and *Chelonia mydas* have samples representing all stages of ontogeny and total samples exceeding 10 (15 and 11 respectively). The sample of *Lepidochelys kempii* (Kemp's ridley) lacks hatchlings and large adults whereas *Dermochelys coriacea* lacks intermediate size animals. Otherwise, all species have at least one specimen for each size category (see below).

Specimens were scanned using X-ray computed tomography (CT). Some of the larger specimens were scanned in medical CT machines, whereas others were scanned using X-ray micro-CT at various facilities (Appendix 1 Table 1). The reconstructed data sets had voxel sizes between 9 and 500 μm . The resulting tiff stacks were processed in AVIZO 9.0 Lite software (Visualisation Science Group, SAS). The cranium was isolated in an associated label file using the threshold and brush tool. Surface models of the skull were exported as PLY files for measurement (details below).

Specimens were divided into three categories: hatchling, intermediate, and adult (Table 1). Hatchlings (n=14) exhibited fontanelles and lacked ossified basicranial elements, intermediates (n= 25) had closed fontanelles and ossified basicranial elements but were

smaller than the skull size reported for an adult of that species, whereas adults ($n = 24$) had a skull size within two standard deviations of the average reported adult skull size for the species (Pritchard and Trebbau 1984; Dodd 1988; Zangerl *et al.* 1988; Nishizawa *et al.* 2010; Lunardon *et al.* 2020).

This resulted in a total of four datasets used in this analysis.

1. **Cheloniioidea all age classes:** effectively a complete dataset including all seven species and all age classes ($n = 63$)
2. **Cheloniidae all age classes:** no *Dermochelys coriacea* ($n = 55$)
3. **Cheloniioidea adults only:** only adult specimens ($n = 21$)
4. **Cheloniidae adults only:** only adult specimens and no *D. coriacea* ($n = 17$)

Dataset 1 provides an holistic overview of the entire sample, dataset 3 serves to examine evolutionary allometry, whereas datasets 2 and 4 provide an understanding of the samples without potential skew from the highly specialised and taxonomically isolated *D. coriacea*. Although, *D. coriacea* is the sister taxon to Cheloniidae, their lineages diverged in the Cretaceous and they represent two distinct evolutionary lineages. These four different data sets also facilitate comparisons to previous datasets that did not include hatchlings or excluded *Dermochelys coriacea* from some analyses (e.g. Myers, 2007).

Table 1. Number of specimens for each species and age category.

<i>Species</i>	<i>Hatchlings</i>	<i>Intermediate</i>	<i>Adults</i>	<i>Total</i>
<i>Caretta caretta</i>	4	6	5	15
<i>Chelonia mydas</i>	3	4	4	11
<i>Dermochelys coriacea</i>	4	0	4	8
<i>Eretmochelys imbricata</i>	1	4	2	7
<i>Lepidochelys kempii</i>	0	8	0	8
<i>Lepidochelys olivacea</i>	3	3	3	9
<i>Natator depressus</i>	1	1	3	5
<i>Total</i>	16	26	21	63

2.2 Diet classification

Diet was classified into six categories according to food items reportedly consumed in the literature (Bjorndal 1985; Dodd 1988; Bjorndal *et al.* 1997; Bolten 2003; Limpus 2007; Limpus and Limpus 2007): pelagic (gelatinous invertebrates: jellyfish, crustacean larva, etc.), benthic soft-bodied invertebrates (soft-bodied invertebrates include neritic, benthic, largely non-gelatinous prey), plant matter (sea grass, algae), sponges (mainly sponges), durophage (hard-bodied invertebrates: clams, echinoderms, crabs), and general (mixture of jellyfish, fish, crabs, salps etc.) (Table 2; Fig. 1). The amount of data for each species is highly variable, with some species such as *Ca. caretta* having been the subjects of detailed analyses of gut contents (Nierop and Hartog 1984; Seney and Musick 2004), faecal content (Marchiori *et al.* 2018), and observational data (Babcock 1937; Limpus 1973). Other species such as *N. depressus* have received minimal dietary analysis (Limpus 2007). The diet of hatchling specimens is also comparatively understudied due to their pelagic nature, however the data

available consistently suggests a diet of soft bodied invertebrates which inhabit the upper water column (Bjorndal *et al.* 1997; Boyle and Limpus 2008)

2.3 Cranial Landmarks

The three-dimensional cranial surface models were landmarked in IDAV Landmark Editor v. 3.6 (Wiley *et al.* 2007). Forty-six landmarks were placed at equivalent locations across each specimen (Fig. 2), representing external suture junctions or distinct anatomical points, e.g., the posterior most tip of the supraoccipital. Landmarks were chosen to best characterise the entirety of cranial shape while still being applicable to every species and ontogenetic stage (Appendix 1). These criteria meant that much of the basicranium was not landmarked because in hatchlings this part of the skull is still represented largely by cartilage without distinct junctions.

The exported landmark coordinates were subjected to a generalised Procrustes superimposition in the R package *geomorph* v. 3.3.3 (Adams *et al.* 2020) standardising for variation in translation, rotation, and size using the function *gpagen*. Due to lack of body size data for all specimens, centroid size (the square root of the sum of squared distances of the landmarks to their centroid) of each cranium was used as a size proxy.

Missing landmarks were estimated using *estimate.missing* in the package *geomorph*. Only four specimens of *Lepidochelys kempii* were missing landmarks, these were from the anterior portion of the snout (landmarks 0, 1, 24, 25) and the tip of the supraoccipital (landmark 5). This function estimates missing landmarks based on the mean coordinates for each landmark across the entire dataset using the regression method of estimation.

Table 2. Diet categories and associated references.

Species	Age class	Common items	Rare items	Assigned diet category	Reference
<i>Caretta caretta</i>	Hatchling	Zooplankton, Jellyfish	Sargasm	Pelagic	Dodd 1988; Boyle and Limpus 2008
	Intermediate	Jellyfish, Snails, Crabs, Small bivalves: Sea Urchins	Algae; Coral; Salps, fish	General	Dodd 1988; Burke <i>et al.</i> 1993
	Adult	Crabs, Snails, Conches, Bivalves, Sea pens, Horseshoe crab, Sea Urchins	Jellyfish, Coral, Algae, fish	Durophage	Dodd 1988; Seney and Musick 2007
<i>Chelonia mydas</i>	Hatchling	Zooplankton, Cnidarians	Sargasm	Pelagic	Bjorndal 1985; Boyle and Limpus 2008
	Intermediate	Sea grass, Algae	Jellyfish, Coral, Salps	Herbivore	Mortimer 1982; Ross 1985; Seminoff <i>et al.</i> 2002
	Adult	Sea grass, Algae	Jellyfish, Coral, Salps	Herbivore	Mortimer 1982; Ross 1985; Seminoff <i>et al.</i> 2002
<i>Dermochelys coriacea</i>	Hatchling	Zooplankton, Cnidarians	N/A	Pelagic	Bleakney 1965
	Intermediate	Jellyfish	Salps	Pelagic	Bleakney 1965; Eckert <i>et al.</i> 1989
	Adult	Jellyfish	Salps	Pelagic	Bleakney 1965; :Frazier <i>et al.</i> 1985; Eckert <i>et al.</i> 1989
<i>Eretmochelys imbricata</i>	Hatchling	Zooplankton, Cnidarians	N/A	Pelagic	Meylan 1984
	Intermediate	Sponges, Algae	Coral, Sea Urchins, Anenomes	Sponge	Den Hartog 1979; Meylan 1985; Limpus; 1992; Andres and Uchida 1994;
	Adult	Sponges	Coral, Sea Urchins, Algae, Anenomes	Sponge	Meylan 1985; Limpus; 1992; Andres and Uchida 1994;
<i>Lepidochelys kempii</i>	Hatchling	Zooplankton, Cnidarians	Sargasm	Pelagic	Shaver 1991
	Intermediate	Crabs, Jellyfish, Sea horses	Algae, Fish	General	Shaver 1991; Burke <i>et al.</i> 1993; Seney and Musick 2005; Schmid and Tucker 2018
	Adult	Crabs, Molluscs	Algae, Fish	Durophage	Shaver 1991; Burke <i>et al.</i> 1993; Burke <i>et al.</i> 1994
<i>Lepidochelys olivacea</i>	Hatchling	Zooplankton, Cnidarians	N/A	Pelagic	Bjorndal <i>et al.</i> 1997
	Intermediate	Salps, molluscs, Crabs, Jellyfish, Snails	Fish, Fish eggs, Algae, Turnicates	General	Marquez <i>et al.</i> 1976; Montenegro <i>et al.</i> 1982; Frick <i>et al.</i> 2011; Colman <i>et al.</i> 2014
	Adult	Salps, molluscs, Crabs, Jellyfish, Snails	Fish, Fish eggs, Algae, Turnicates	General	Marquez <i>et al.</i> 1976; Montenegro <i>et al.</i> 1982
<i>Natator depressus</i>	Hatchling	Zooplankton, Cnidarians	N/A	Pelagic	Limpus 2007
	Intermediate	na	N/A	Soft	Limpus 2007
	Adult	Sea cucumbers, Jellyfish, Corals, Sea pens	N/A	Soft	Limpus 2007

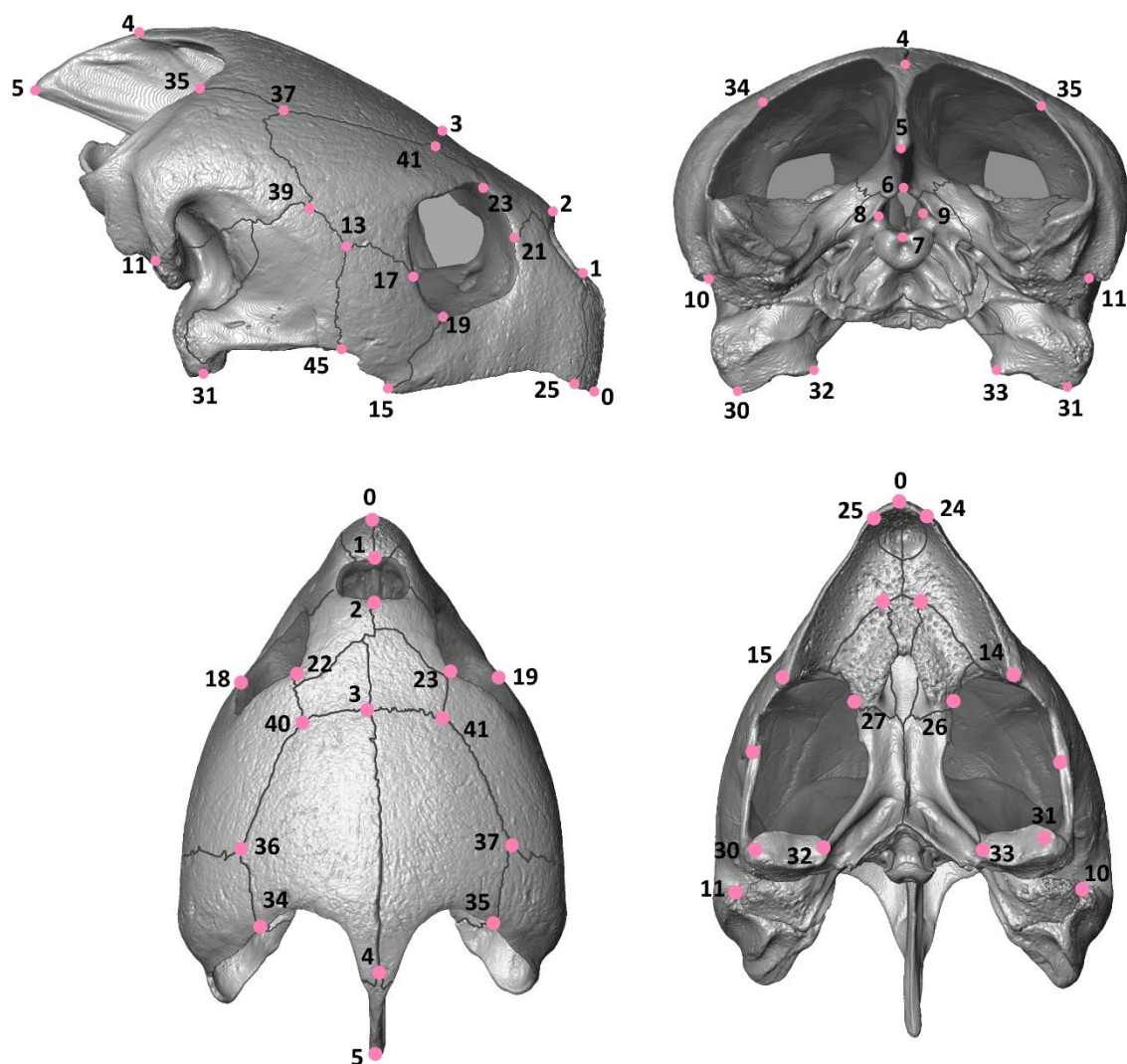


Fig. 2. A three-dimensional mesh derived from micro-CT data of *Caretta caretta* (SAMA Unregistered) used to demonstrate the placement of 46 landmarks used in this analysis (numbered 0 to 45).

2.3 Shape Analysis

Statistical analyses were performed in the R packages *geomorph* v. 3 (Adams *et al.* 2020) and *RRPP* v.0.6.2 (Collyer and Adams 2020). We performed a Principal Component Analysis (PCA) of the Procrustes aligned coordinates, using the function *gm.prcomp* to determine the components of shape variation. To interpret the variation described by the major axes we used a combination of thin-plate spline deformation grids, vector analysis, and warping a mesh of the mean shape to the extremes (minimum and maximum PC scores) of each axis. These were implemented using the *warpRefMesh* function.

To test for a relationship between size and shape we used the phylogenetic generalised least squared method (*procD.pgls*). This function performs an ANOVA within a phylogenetic framework assuming a Brownian model of evolution (Adams 2014; Adams and Collyer 2015). With this method data points are not treated as phylogenetically independent (Adams 2014). However, this technique normally relies on species being either represented by a single set of coordinates or an aggregate mean for each phylogenetic tip (Prevosti *et al.* 2012; Püschel and Sellers 2015; Wang *et al.* 2021). Since our data are multiple individuals aligned along ontogenetic trajectories of individual species, implementations currently available need a small modification to be operable. We created a tree file based on the phylogenetic tree found in Duchene *et al.* (2012) where each species was represented by a soft polytomy consisting of all their individual specimens, such that the phylogenetic relatedness can be considered while retaining the data structure (e.g., Sanger *et al.* 2013). The validity of phylogenetic comparative methods on groups with a small number of taxa, as is the case in sea turtles, is also unclear (Blomberg *et al.* 2003; Adams 2014). Therefore, we also conducted a Procrustes ANOVA which does not account for phylogeny (using *procD.lm*) for all analyses. In both cases, we evaluated whether a common ontogenetic allometry

model or a species unique allometry model better explained the data for each dataset. This was done by comparing ANOVAs of each model with the Null assumption being that they share a common allometry. The relationship between shape, size, and diet was also assessed using these methods. To assess the strength of evolutionary allometry the relationship between shape and size of the adult datasets were tested using a PGLS and the original tree (*procD.pgls*). Species pairwise comparisons were performed using the *pairwise* function from the package *RPPP*. This was done to identify differences in slope vector length and orientation where slope length is magnitude of shape change per unit size and orientation is the direction of shape change per unit size.

To assess whether any PC axes are significantly correlated with size, we calculated a Pearson's product moment correlation coefficient (*cor.test*) comparing each PC axis to centroid size, assuming a normal distribution.

We assessed the morphological disparity between ontogenetic groups using the *morphol.disaprrity* function of *geomorph*. This function estimates disparity of a group (hatchling, intermediate, and adult) as their Procrustes variance using residuals of a linear model fit, in our case using the species unique allometry model.

A residual randomisation procedure with 10,000 iterations was used to assess statistical significance for all tests.

To assess phylogenetic signal, we used the *physignal* function, which assumes a Brownian motion model of evolution, and the phylogenetic tree recovered in Naro-Maciel *et al.* (2008) and Duchene *et al.* (2012) (Fig. 1). This function estimates phylogenetic signal using a generalisation of Blomberg's K –statistic for high dimensional and multivariate data (K_{mult} ; Adams 2014). We tested phylogenetic signal for the adults and hatchlings separately, using

the mean adult shape and mean hatchling shape for each species, as demonstrated in Gray *et al.* (2019). This comparison was visualised by projecting the phylogenetic tree on to the morphospace. Phylogenetic signal was assessed to determine how important phylogenetic relatedness is in determining skull shape among living chelonioids, as well as to assess if there is a change in phylogenetic signal across ontogeny which might suggest an increased adaptive signal.

3 RESULTS

3.1 Shape differences

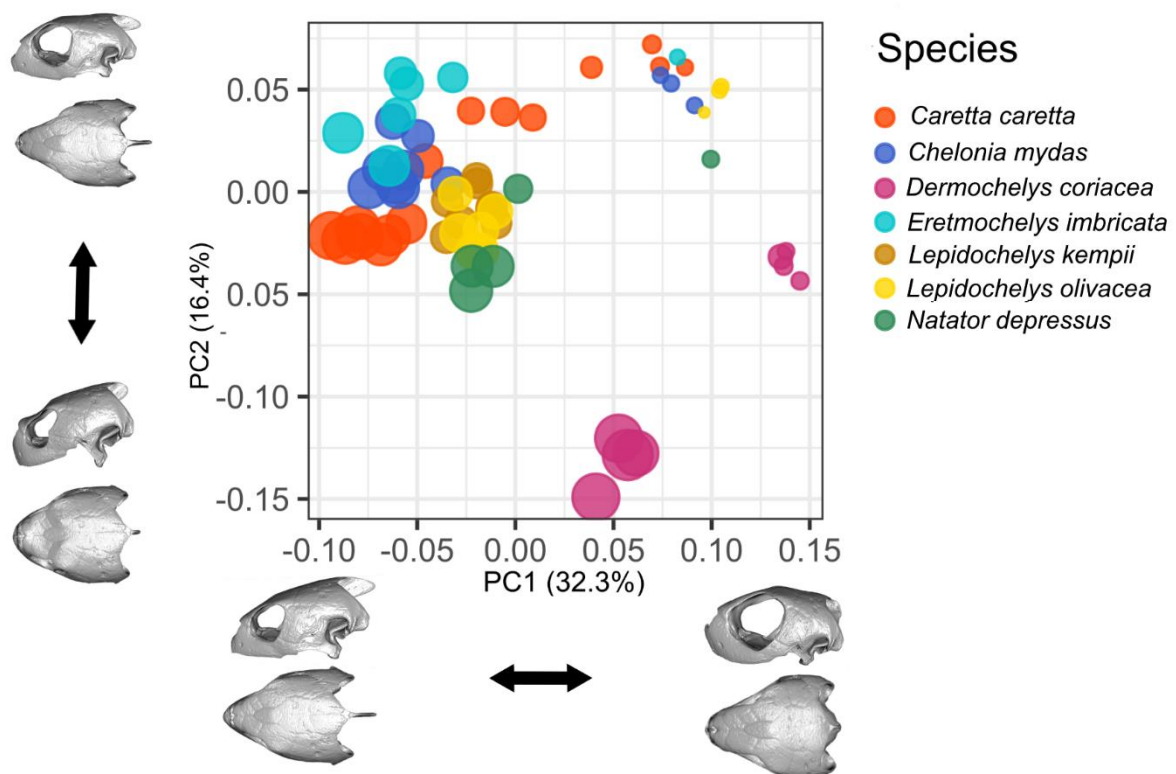


Figure 3. PC1 and PC2 of the cranial morphospace of Chelonioidea, with different colours representing different species. Skulls showing lateral and dorsal views of the mean shape

mesh warped to the coordinates of the extremes for each axis. All points scaled to centroid size.

3.1.1 Chelonioidea all age classes (total group: n =63)

The first four PC axes account for 67.9% of the total cranial shape variation and the remaining axes each account for less than 5%. PC scores vary among species (Fig. 3 ,4) reflecting differences in skull shape. Overall PC1, and to a lesser extent PC2, are broadly associated with size and ontogeny whereas the other PC axes appear to reflect species differences and individual variation.

The greatest axis of variation (PC1; 32.3%) represents differences in the relative anteroposterior length of the posterior of the skull, in particular the length of the supraoccipital crest (Landmarks 5-6), as well as the relative size of the orbit (Fig. 3). High PC1 scores represent relatively large orbits, an anteroposteriorly short posterior part of the skull, and a short supraoccipital crest whereas low PC1 scores represent relatively small orbits, an anteroposteriorly elongate posterior part of the skull, and a proportionately enlarged supraoccipital crest (Fig 3). Hatchling skulls have high PC1 scores, juveniles have moderate PC1 scores, and adults tend to have low PC1 scores. However, for *Dermochelys coriacea*, hatchlings have particularly high PC1 scores and its adults have similar PC1 scores to the hatchlings of other turtles such as *Caretta caretta*.

PC2 describes 16.4% of cranial shape variation. High PC2 scores represent a circular orbit, a small ventral projection of the mandibular condyle and a tapering pointed rostrum, whereas low PC2 scores represent an increasing ventral projection of the quadrate and jaw joint, an ovoid orbit, and laterally broader anterior rostrum (Fig. 3). The skulls of larger specimens

tend to plot with lower PC2 scores. Skulls with the lowest PC2 scores are exclusively adult *D. coriacea*.

PC3 describes 10.3% of cranial variation (Fig. 4). High PC3 scores represent skulls that have laterally narrow posterior sections of the skull and have a dorsoventrally shallow lateral profile whereas low PC3 scores represent skulls that have laterally wide posterior sections of the skull and are dorsoventrally deep (Fig 4). High PC3 scores characterise both *Chelonia mydas* and *Eretmochelys imbricata* whereas low PC3 scores characterise the wide cranium of *Ca. caretta*.

PC4 describes 8.5% of cranial variation. High PC4 scores represent skulls that have an elongated rostrum whereas low PC4 scores represent skulls with a shorter, blunt rostrum (Fig. 3B). High PC4 scores characterise the long snouted *E. imbricata* whereas low PC4 scores characterise the blunt snouted *Ch. mydas* (Fig. 4).

3.1.2 Cheloniidae all age classes (no *Dermochelys coriacea*: n =53)

When *D. coriacea* is excluded from the sample, PC1 (33.7%) is still characterised by the same variation seen in the total group dataset (Fig 5A). High PC1 scores representing relatively large orbits and small posterior part of the skulls whereas low PC1 scores are characterised by relatively small orbits and large posterior part of the skulls. The characterisation of PC2 (15.7%) is similar to that of PC3 of the total group dataset and describes the relative width of the posterior part of the skull with high PC2 scores having relatively wide skulls and low PC2 scores having relatively narrow skulls.

3.1.3 Chelonioida adults (n =21)

PC1 for the total group adult is largely similar to PC1 for the total group, with orbit size and posterior part of the skull size characterising the axis (Fig. 5B). PC2 for the adult subset is similar to PC3 for the total group, characterised by the relative width of the posterior part of the skull.

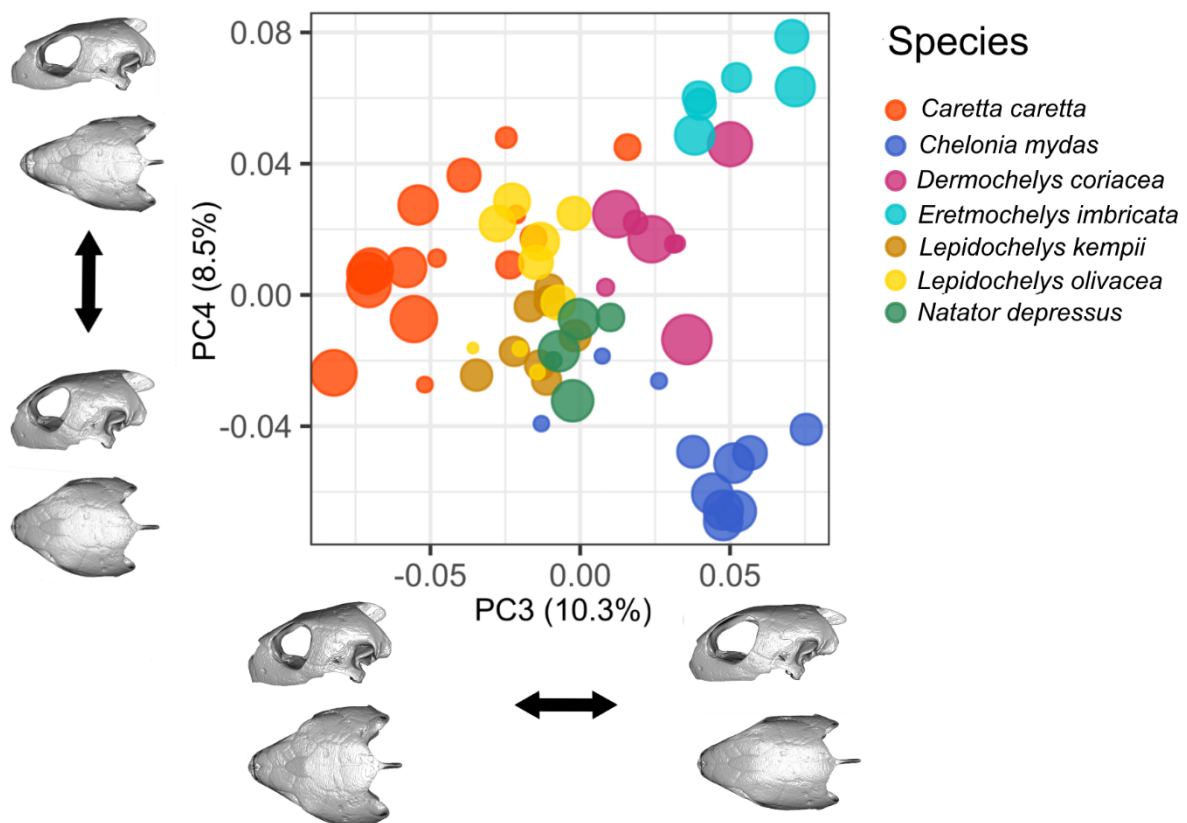


Figure 4. PC1 and PC2 of the cranial morphospace of Chelonioida, with different colours representing different species. Skulls showing lateral and dorsal views of the mean shape mesh warped to the coordinates of the extremes for each axis. All points scaled to centroid size.

3.1.4 Cheloniidae adults (no *Dermochelys coriacea*: n =17)

PC1 (30.3%) for the cheloniid adult subset is similar to PC3 for the total group, characterised by the relative width of the posterior part of the skull. PC2 (19%) is characterised by the shape of the squamosal and jugal (Fig. 5C). High PC2 scores are characterised by a more curved squamosal with the ventroposterior contact with the quadrate being more anteriorly located, and a more anteriorly located contact between the jugal and quadratojugal. Low PC2 scores are characterised by a less curved squamosal with the ventroposterior contact with the quadrate being more posteriorly located, and a more posteriorly located contact between the jugal and quadratojugal.

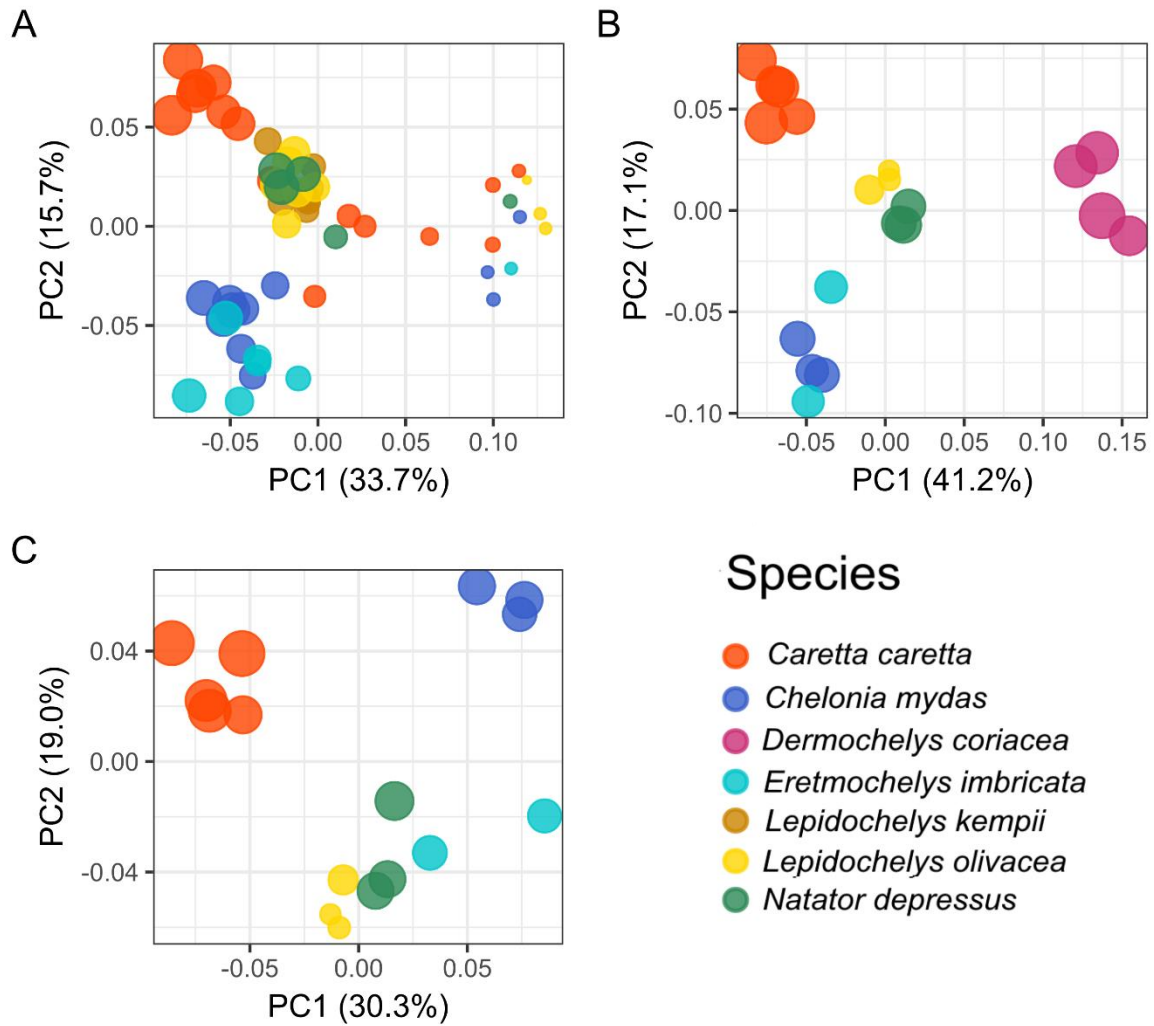


Figure 5. PC1 vs PC2 of all Cheloniidae (A), adult Chelonioidea (B), and adult Cheloniidae (C). Colours represent different species. All points are scaled by centroid size.

3.2 Ontogenetic Allometry

3.2.1 Chelonioidea all age classes (total group: n =63)

A significant relationship between shape and size is found using both phylogenetically comparative methods as well as non phylogenetically comparative methods ($p < 0.001$; Table 3; Fig. 6). Both PC1 and PC2 are significantly related to size (both $p < 0.001$), while the other PC axes are not. This suggests that relative orbit and posterior skull size are both associated with size. Species and diet were found to have a significant interaction with size,

as well as with each other. For both methods a model using unique species allometries was a significant improvement over a common allometry ($p < 0.001$) improvement over a common allometric slope. There was no significant difference in model strength between size and diet or size and species, but both are significantly better than size alone ($p < 0.001$; Table 4).

Adults occupy a significantly ($p < 0.01$) more morphologically disparate than the other two ontogenetic groups. There is not a significant difference in disparity between intermediate and hatchling specimens. Adults occupied a larger area of morphospace (Procrustes variance = 0.0131) than hatchlings (Procrustes variance = 0.008) or intermediate specimens (Procrustes variance = 0.007). This result suggests that the crania of hatchling sea turtles more closely resemble each other than do adult crania.

Most species had significantly different slope angles to each other (Table 5). However, *Natator depressus* was only significantly different to either *D. coriacea* or *L. olivacea*. *Lepidochelys kempii* is also not significantly different to any other species in slope angle but this result may be due to the small size range. *Ca. caretta* and *L. kempii* have the steepest slopes, with *L. olivacea* and *N. depressus* having the least steep slopes.

There are few differences in slope length among species (Table 6). *N. depressus* differs significantly from *Ch. mydas*, *L. olivacea*, and *E. imbricata*. Also *D. coriacea* significantly differs in slope length from *Ca. caretta*, *Ch. mydas*, and *E. imbricata* (Table 6). *L. kempii* is not significantly different to any species.

Table 3. Procrustes ANOVAs for the Chelonioida all age class dataset assessing species interaction using both phylogenetically (*procD.pgls*) comparative and non phylogenetically (*procD.lm*) comparative methods.

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	1.54	1.54	0.40	48.29	4.15	<0.001
species	6	0.09	0.01	0.02	0.45	-6.05	1
log(size):species	6	0.65	0.11	0.17	3.39	6.48	<0.001
Residuals	49	1.56	0.03	0.41			
Total	62	3.83					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.22	0.22	0.25	50.84	8.35	<0.001
species	6	0.36	0.06	0.41	13.87	12.94	<0.001
log(size):species	6	0.08	0.01	0.09	3.17	7.47	<0.001
Residuals	49	0.21	0.00	0.24			
Total	62	0.86					

Table 4. Procrustes ANOVAs for the Chelonioida all age class dataset assessing diet interaction using both phylogenetically (*procD.pgls*) comparative and non phylogenetically (*procD.lm*) comparative methods.

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	Pr(>F)
log(size)	1	1.54	1.54	0.40	50.06	4.17	<0.001
diet	5	0.60	0.12	0.16	3.89	7.31	<0.001
log(size):diet	5	0.24	0.05	0.06	1.58	2.99	0.001
log(size):diet:species	8	0.13	0.02	0.03	0.53	-5.46	1
Residuals	43	1.32	0.03	0.34			
Total	62	3.83					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.22	0.22	0.25	53.38	8.42	<0.001
diet	5	0.30	0.06	0.35	14.66	11.91	<0.001
log(size):diet	5	0.05	0.01	0.06	2.58	5.27	<0.001
log(size):diet:species	8	0.12	0.02	0.14	3.70	7.54	<0.001
Residuals	43	0.17	0.00	0.20			
Total	62	0.86					

Table 5. Pairwise table showing the pairwise relationships for vector angle for species allometric trajectories between species based on a model of unique species allometries. r = correlation coefficient. Angle is the difference in slope angle between species. UCL shows the upper confidence limits of angles from the distributions of pairwise angles.

	r	angle	UCL (95%)	Z	P value
<i>Caretta caretta</i> : <i>Chelonia mydas</i>	0.753	0.717	0.536	4.562	<0.001
<i>Caretta caretta</i> : <i>Dermochelys coriacea</i>	0.603	0.922	0.518	8.068	<0.001
<i>Caretta caretta</i> : <i>Eretmochelys imbricata</i>	0.640	0.876	0.733	3.31	0.004
<i>Caretta caretta</i> : <i>Lepidochelys kempii</i>	0.407	1.151	1.660	-1.357	0.91
<i>Caretta caretta</i> : <i>Lepidochelys olivacea</i>	0.809	0.627	0.556	2.815	0.009
<i>Caretta caretta</i> : <i>Natator depressus</i>	0.757	0.710	0.715	1.773	0.053
<i>Chelonia mydas</i> : <i>Dermochelys coriacea</i>	0.509	1.036	0.552	8.806	<0.001
<i>Chelonia mydas</i> : <i>Eretmochelys imbricata</i>	0.719	0.767	0.758	1.946	0.043
<i>Chelonia mydas</i> : <i>Lepidochelys kempii</i>	0.264	1.303	1.670	-0.475	0.674
<i>Chelonia mydas</i> : <i>Lepidochelys olivacea</i>	0.744	0.731	0.594	3.64	0.002
<i>Chelonia mydas</i> : <i>Natator depressus</i>	0.750	0.721	0.738	1.629	0.065
<i>Dermochelys coriacea</i> : <i>Eretmochelys imbricata</i>	0.466	1.084	0.744	5.338	<0.001
<i>Dermochelys coriacea</i> : <i>Lepidochelys kempii</i>	0.217	1.351	1.668	-0.183	0.559
<i>Dermochelys coriacea</i> : <i>Lepidochelys olivacea</i>	0.571	0.962	0.571	7.328	<0.001
<i>Dermochelys coriacea</i> : <i>Natator depressus</i>	0.655	0.855	0.724	3.228	0.004
<i>Eretmochelys imbricata</i> : <i>Lepidochelys kempii</i>	0.257	1.310	1.690	-0.49	0.679
<i>Eretmochelys imbricata</i> : <i>Lepidochelys olivacea</i>	0.838	0.576	0.773	-0.141	0.507
<i>Eretmochelys imbricata</i> : <i>Natator depressus</i>	0.652	0.860	0.876	1.679	0.063
<i>Lepidochelys kempii</i> : <i>Lepidochelys olivacea</i>	0.353	1.208	1.669	-1.035	0.844
<i>Lepidochelys kempii</i> : <i>Natator depressus</i>	0.332	1.231	1.689	-0.944	0.822
<i>Lepidochelys olivacea</i> : <i>Natator depressus</i>	0.688	0.811	0.751	2.449	0.018

Table 6. Pairwise table showing the pairwise relationships for vector length for species allometric trajectories based on a model of unique species allometries. d is the distance between least square means of two species. UCL is the upper confidence limit for the distance value. UCL shows the upper confidence limits of distance from the distributions of pairwise distances.

		d	UCL (95%)	Z	P value
<i>Caretta caretta</i>	: <i>Chelonia mydas</i>	9.97E-05	1.39E-04	-0.017	0.499
<i>Caretta caretta</i>	: <i>Dermochelys coriacea</i>	6.03E-05	4.10E-05	3.465	0.002
<i>Caretta caretta</i>	: <i>Eretmochelys imbricata</i>	1.58E-04	1.88E-04	0.995	0.149
<i>Caretta caretta</i>	: <i>Lepidochelys kempii</i>	1.19E-03	1.75E-03	-0.291	0.568
<i>Caretta caretta</i>	: <i>Lepidochelys olivacea</i>	2.00E-04	2.64E-04	-0.423	0.652
<i>Caretta caretta</i>	: <i>Natator depressus</i>	1.04E-05	1.24E-04	-1.961	0.986
<i>Chelonia mydas</i>	: <i>Dermochelys coriacea</i>	1.60E-04	1.50E-04	2.088	0.020
<i>Chelonia mydas</i>	: <i>Eretmochelys imbricata</i>	5.85E-05	9.22E-05	0.82	0.180
<i>Chelonia mydas</i>	: <i>Lepidochelys kempii</i>	1.09E-03	1.65E-03	-0.289	0.567
<i>Chelonia mydas</i>	: <i>Lepidochelys olivacea</i>	1.00E-04	1.70E-04	-0.364	0.635
<i>Chelonia mydas</i>	: <i>Natator depressus</i>	1.10E-04	8.54E-05	2.816	0.007
<i>Dermochelys coriacea</i>	: <i>Eretmochelys imbricata</i>	2.19E-04	1.99E-04	2.347	0.021
<i>Dermochelys coriacea</i>	: <i>Lepidochelys kempii</i>	1.25E-03	1.76E-03	-0.103	0.491
<i>Dermochelys coriacea</i>	: <i>Lepidochelys olivacea</i>	2.60E-04	2.76E-04	1.204	0.114
<i>Dermochelys coriacea</i>	: <i>Natator depressus</i>	4.99E-05	1.36E-04	-0.997	0.844
<i>Eretmochelys imbricata</i>	: <i>Lepidochelys kempii</i>	1.03E-03	1.63E-03	-0.424	0.624
<i>Eretmochelys imbricata</i>	: <i>Lepidochelys olivacea</i>	4.17E-05	1.61E-04	-1.211	0.872
<i>Eretmochelys imbricata</i>	: <i>Natator depressus</i>	1.69E-04	1.28E-04	2.962	0.009
<i>Lepidochelys kempii</i>	: <i>Lepidochelys olivacea</i>	9.85E-04	1.54E-03	-0.241	0.550
<i>Lepidochelys kempii</i>	: <i>Natator depressus</i>	1.20E-03	1.68E-03	0.014	0.446
<i>Lepidochelys olivacea</i>	: <i>Natator depressus</i>	2.10E-04	2.07E-04	1.713	0.042

3.2.2 Cheloniidae (n=55)

Both phylogenetically comparative methods ($p < 0.001$) as well as non phylogenetically comparative methods ($p < 0.001$) recovered a significant relationship between shape and size (Fig 7 A,B; Table 7). When using phylogenetically comparative methods there was a stronger correlation between size, species, and shape ($R^2 = 0.13$) than when using a non phylogenetically comparative method ($R^2 = 0.08$). There is a significant relationship (Table 8) between shape and diet using both methods ($p < 0.001$) and both found a significant ($p < 0.003$) but weak interaction between diet, shape ($R^2 = 0.07$). Both phylogenetically comparative methods and non phylogenetically comparative methods found that a species unique allometry significantly stronger than a common allometry model ($p < 0.001$), ($p < 0.001$; Table 4). Both methods found that there was no significant difference in model strength between diet and shape or species and shape as possible explanators for shape, but both are significantly better than size alone ($p < 0.001$). The Pearson correlation tests found that only PC1 was significantly related to size ($p < 0.001$).

Table 7 Procrustes ANOVAs for the Cheloniidae all age classes dataset assessing species interaction using both phylogenetically (*procD.pgls*) comparative and non phylogenetically (*procD.lm*) comparative methods.

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	1.15	1.15	0.43	44.55	3.93	<0.001
species	5	0.06	0.01	0.02	0.45	-5.55	1
log(size):species	5	0.34	0.07	0.13	2.65	5.04	<0.001
Residuals	43	1.11	0.03	0.42			
Total	54	2.66					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.20	0.20	0.32	47.84	5.58	<0.001
species	5	0.19	0.04	0.31	9.40	8.23	<0.001
log(size):species	5	0.05	0.01	0.08	2.42	4.67	<0.001
Residuals	43	0.18	0.00	0.29			
Total	54	0.62					

Table 8 Procrustes ANOVAs for the Cheloniidae all age classes dataset assessing diet interaction using both phylogenetically (*procD.pgls*) comparative and non phylogenetically (*procD.lm*) comparative methods.

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	1.15	1.15	0.43	47.30	3.99	<0.001
diet	5	0.37	0.07	0.14	3.00	6.16	<0.001
log(size):diet	5	0.19	0.04	0.07	1.55	2.76	0.0025
log(size):diet:species	7	0.08	0.01	0.03	0.48	-5.54	1
Residuals	36	0.88	0.02	0.33			
Total	54	2.66					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.20	0.20	0.32	52.32	5.66	<0.001
diet	5	0.19	0.04	0.30	9.97	8.88	<0.001
log(size):diet	5	0.04	0.01	0.07	2.20	5.07	<0.001
log(size):diet:species	7	0.06	0.01	0.09	2.12	6.14	<0.001
Residuals	36	0.14	0.00	0.22			
Total	54	0.62					

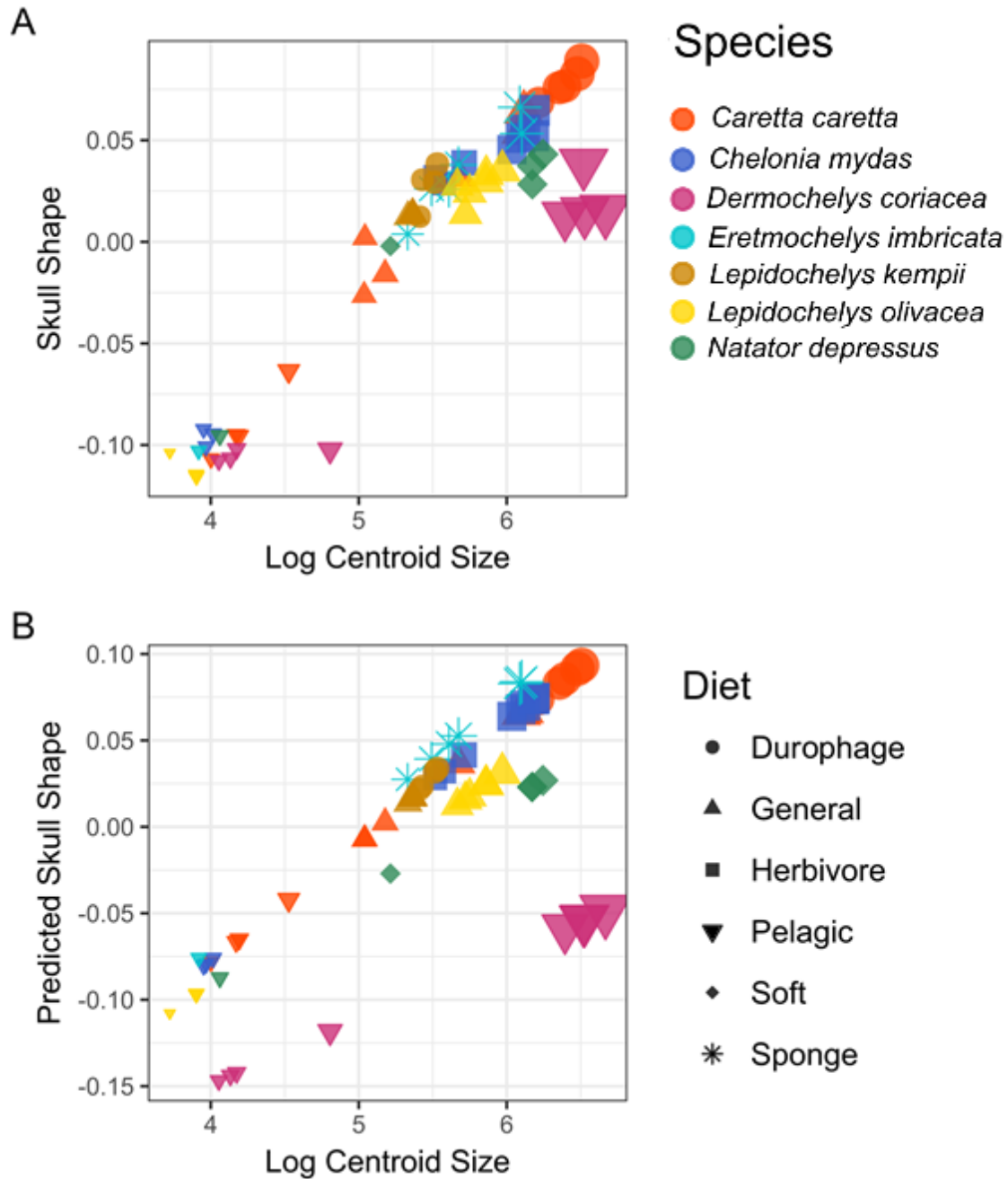


Figure 6. A. Multivariate regression of skull shape based on a common allometry against size plotted on log centroid size. B. The predicted skull shape based on the regression of skull shape on size of all species based on species allometry. Different colours represent different species, different shapes represent different diets. All points scaled by centroid size.

3.3 Evolutionary Allometry

3.3.1 Chelonioidea adults (n =21)

Both phylogenetically comparative ($p = 0.015$) and non comparative ($p < 0.001$) methods found a significant relationship between size and shape neither with particularly strong correlations ($R^2 = 0.09$ and 0.12 respectively; Table 9; Fig. 7C). However, only the phylogenetically comparative ANOVA found a significant interaction between size, shape, and species ($p = 0.005$) with a relatively strong correlation ($R^2 = 0.42$). When using phylogenetically comparative methods a species unique allometry model was significantly stronger than a common allometry model ($p = 0.005$). Using the non phylogenetically comparative methods we found that a species unique model was not significantly stronger than a common allometric model ($p = 0.167$). No individual PC axis was significantly correlated with size.

3.3.2. Cheloniidae adults only (n=17)

A significant relationship between size and cranial shape was also recovered for both models when *D. coriacea* was removed from the adult sample (Fig 7D; Table 10). Both phylogenetically comparative methods ($p = 0.016$) and non phylogenetically ($p < 0.001$) comparative methods found a significant relationship between size and shape. However, only the phylogenetically comparative ANOVA found a significant interaction between size, shape, and species ($p = 0.005$) with a relatively strong correlation ($R^2 = 0.47$), with a species unique allometry being the favoured model ($p = 0.005$). Using the non phylogenetically comparative methods we found that a species unique model was not significantly stronger than a common allometric model ($p = 0.065$). The Pearson correlation test found PC1 and

PC2 were both significantly related to size (PC1 $p = 0.049$; PC2 $p = 0.009$). No other PC axis was found to have a significant relationship with size.

Table 9 Procrustes ANOVAs for the Chelonioida adult dataset assessing species interaction using both phylogenetically (*procD.pgls*) comparative and non phylogenetically (*procD.lm*) comparative methods.

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.06	0.06	0.09	2.30	2.16	0.014
species	5	0.13	0.03	0.19	1.02	0.10	0.46
log(size):species	5	0.29	0.06	0.42	2.19	2.42	0.005
Residuals	8	0.21	0.03	0.30			
Total	19	0.69					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.03	0.03	0.12	7.98	3.26	<0.001
species	5	0.18	0.04	0.67	8.87	5.96	<0.001
log(size):species	5	0.02	0.00	0.09	1.22	0.95	0.17
Residuals	8	0.03	0.00	0.12			
Total	19	0.27					

Table 10 Procrustes ANOVAs for the Cheloniidae all age classes dataset assessing species interaction using both phylogenetically (*procD.pgls*) comparative and non phylogenetically (*procD.lm*) comparative methods.

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.04	0.04	0.10	2.52	2.16	0.016
species	4	0.08	0.02	0.19	1.23	0.60	0.27
log(size):species	4	0.20	0.05	0.47	3.00	2.51	0.005
Residuals	6	0.10	0.02	0.24			
Total	15	0.42					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.03	0.03	0.17	8.20	4.27	<0.001
species	4	0.09	0.02	0.58	6.87	4.87	<0.001
log(size):species	4	0.02	0.00	0.12	1.48	1.50	0.065 .
Residuals	6	0.02	0.00	0.13			
Total	15	0.15					

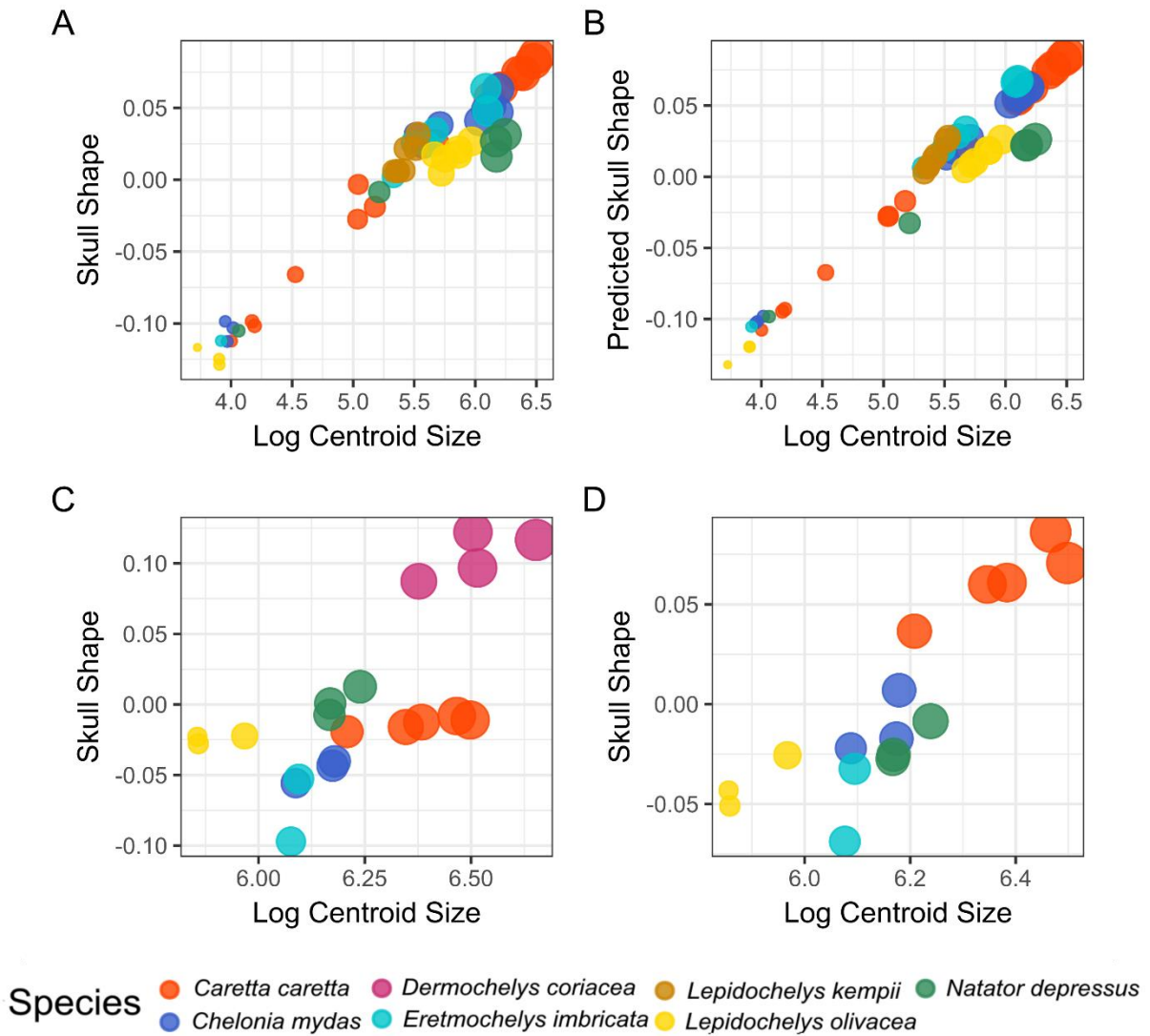


Figure 7. Allometric regressions for three of the datasets. A shows log size compared to the regression score for shape for Cheloniidae. B shows the predicted shape values compared to size based on a unique species allometry model for Cheloniidae. C shows the log size compared to the regression score for shape for the adults of Cheloniidae. D shows the log size compared to the regression score for shape for the adults of Cheloniidae all points scaled by centroid size.

Phylomorphospace

For the mean shapes of hatchlings (Fig 8A), PC1 represents 47.9% of the shape variation and PC2 represents 20.4% of the shape variation (68.3% for both combined). For the mean shapes of the adults (Fig 8B), PC1 represents 50.5% of the shape variation and PC2 represents 21.6% of the shape variation (72.1% for both combined). The phylogenetic signal for the adult specimens was not significant ($p = 0.077$; $K = 0.62$), however the signal for the hatchlings was ($p = 0.011$; $K = 0.72$). There is also a visible difference between the shape of the phylomorphospace when plotted separately for hatchlings and adults. The hatchlings plot in a manner consistent with the accepted phylogenetic hypothesis for sea turtles (Fig 1): *D. coriacea* is relatively isolated in phylomorphospace with a high PC1 score, *N. depressus* and *Ch. mydas* plot close to one another with moderate PC1 scores and low PC2 scores, whereas *E. imbricata*, and *Ca. caretta* + *L. olivacea* plot with high PC2 scores and low PC1 scores. The adults plot with less adherence to the phylogenetic tree. Species which are more distantly related (i.e., *N. depressus* and *L. olivacea*, and *Ch. mydas* and *E. imbricata*) plot with similar scores for PC1 and PC2, whereas the closely related *Ca. caretta* and *L. olivacea*, plot relatively far apart. When only the adults are plotted, PC1 represents a similar aspects of variation to PC1 for the entire dataset (Relative size of the orbits and posterior part of the skull) whereas while PC2 is similar to PC3 of the complete dataset (posterior part of the skull width and depth).

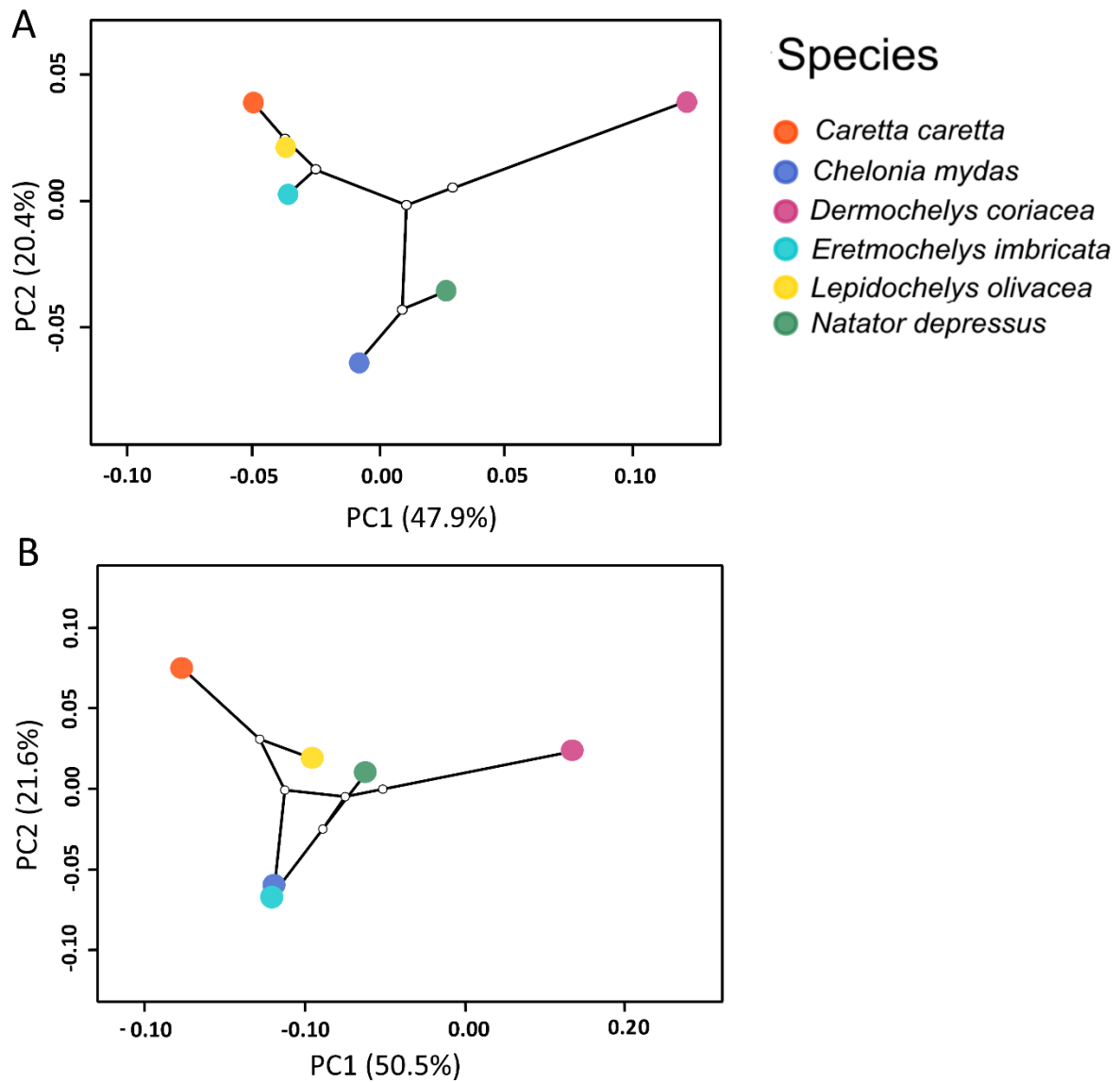


Figure 8. A. Phylomorphospace of mean shape of hatchling specimens. B. Phylomorphospace of mean shape of adult specimens. Different colours represent different species. White circles represent shape of hypothetical most recent common ancestor of the clade based on maximum likelihood estimation.

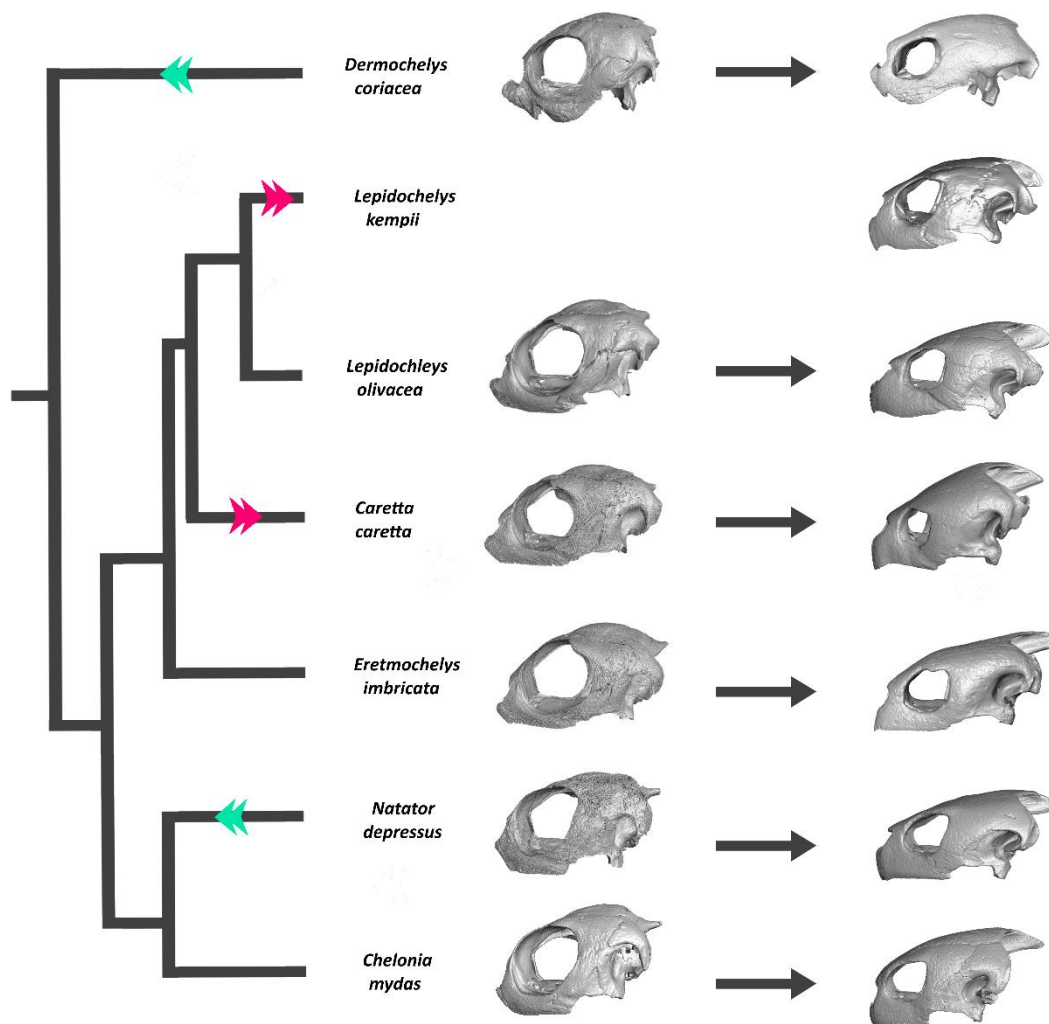


Figure 9. Cladogram of Chelonioida showing the change in skull morphology from hatchling to adults for each species, with the exception of *Lepidochelys kempii* which is represented by an intermediate individual. Blue arrows on the tree represent instances of pedomorphy, pink arrows represent instances of peramorphy. Specimens shown: *Dermochelys coriacea* (MV D6188, UMZC R3031); *Lepidochelys kempii* (WH 333); *Lepidochelys olivacea* (MV D5797, SAMA BM678); *Caretta caretta* (QM J73517, SAMA Unregistered); *Eretmochelys imbricata* (SAMA R14358, WAM 120113); *Natator depressus* (SAMA R14360, WAM R112123); *Chelonia mydas* (MV D2987, SAMA Unregistered).

DISCUSSION

Our results show that much of the diversity of the skull of modern sea turtles can be explained by variation in their size and patterns of ontogenetic allometry. We find that sea turtles at hatchling size have skull shapes that reflect the phylogenetic pattern established by molecular studies. From this starting point, differential growth appears to be an important factor in the determination of the adult skull shape, so much so that shape and phylogenetic relationships become less obviously linked and diet becomes at least as important a predictor of adult skull shape as phylogeny. We do not find that *Lepidochelys olivacea* has a highly divergent skull shape as is suggested by Myers (2007). Our results agree with other previous studies on individual sea turtle species that infer that ontogenetic changes in diet are associated with changes in skull shape (Nishizawa *et al.* 2010; Lunardon 2020). Furthermore, the differences among the species suggest multiple changes to ontogenetic patterns within the group to an extent that was not expected. Our results suggest multiple instances of paedomorphosis and peramorphosis among these seven species (Fig 9).

We find that diversity in adult skull shape corresponds to diversity in diet. The relationship appears to be stronger than found in some other groups (Maestri *et al.* 2016; Bright *et al.* 2016; Gray *et al.* 2019). The two sea turtle species with the most divergent diets *Chelonia mydas* and *Eretmochelys imbricata* show relatively clear adaptations associated with their assigned niches of herbivore and sponge respectively. The short, rounded snout of *Ch. mydas* is similar to other aquatic grazing amniotes such as sirenians (Marshall *et al.* 2007; Aragonés *et al.* 2012) and marine iguanas (Wikeleski and Trillmich 1994). The lack of other spongivorous amniotes makes comparison difficult, however the long and narrow snout of *E. imbricata* appears as a likely adaptation to reaching into the many narrow crevices in

coral reefs where sponges often grow (Hill 1998; Figgner *et al.* 2019) analogous to selective terrestrial browsers which tend to have narrow snouts (Solounias and Moelleken 1993; Dompierre and Churcher 1996). Neither of these morphotypes appear to be associated with size and instead appear to be adaptations to highly specialised diets. The other carnivorous cheloniids have skull shapes characterised by features strongly associated with ontogenetic allometry.

Shape changes associated with increased size in sea turtles are most strongly associated with a relative expansion of structures associated with the jaw muscles (Jones *et al.* 2012). We find that both of the species assigned to the durophage diet category (Bjorndal *et al.* 1997), *Caretta caretta* and *Lepidochelys kempii*, are peramorphic with respect to their sister taxa. For *Ca. caretta* the pattern of increased size and development of the skull in comparison to the similarly sized *Ch. mydas* (Pritchard and Trebbau 1984) is suggestive of “acceleration” paeramorphosis (Klingenberg 1998). Due to the small sample size the specific patterns and mechanisms of the peramorphosis seen in *L. kempii* is less clear. Both of their skulls show proportional increases in the size of the adductor chamber and supraoccipital crest (Jones *et al.* 2012). These changes are related to having larger jaw muscles that provide the greater bite forces necessary for durophagy (Claude *et al.* 2004; Huber *et al.* 2005; Jones *et al.* 2012; Marshall *et al.* 2012; Figueirido *et al.* 2013; Tseng 2013). Increasing the relative size of trophic structures through peramorphosis is seen in multiple other vertebrate groups (Denoel *et al.* 2004; Herrel and O’Reilly 2006; Chemisquy 2015; Vita *et al.* 2020). Within turtles, this phenotype (large adductor chambers, deep jaws) is consistently associated with durophagy among unrelated species such as *Malaemys subtrijuga* and *Sternotherus odoratus* (Claude *et al.* 2004; Bever 2009; Parham and Pyenson 2010; Ferreira *et al.* 2015; Lunardon *et al.* 2020). The great abundance of cheloniids that have

independently acquired durophagous traits such as those noted in this study as well as robust mandibles with an expanded triturating surface (Gaffney 1979; Parham and Pyenson 2010; Weems and Brown 2017) might be related to a clade-wide ability to pursue peramorphosis with relative ease. A broader comparative study of post-natal development among turtles is clearly required. It may also have implications for co-occurrence of phylogenetic characters related to skull shape and structure.

We find that *Dermochelys coriacea* and *Natator depressus* have a skull shape consistent with paedomorphosis, characterised by a small supraoccipital crest and relatively large orbits, which is associated with retention of a juvenile-like diet. However, unlike the other species of sea turtles there does not appear to be a strong functional link between the skull shape and dietary niche, except perhaps for the large orbits of *D. coriacea* which may help foraging in low light in deep water (Houghton *et al.* 2008; Horch *et al.* 2008; Hall 2008; Veilleux and Kirk 2014). The postcranium of *D. coriacea* also shows evidence of extensive paedomorphosis (Nick 1911; Pritchard and Trebbau 1984). Therefore, paedomorphosis of the skull may be related to the general pattern of paedomorphosis present in *D. coriacea* rather than selection directly related to diet and the skull itself. Species have developed a paedomorphic morphology for a wide variety of reasons such as retention of a juvenile life habit (Kordikova 2002), miniaturisation (Rieppel and Crumly 2009; Bright *et al.* 2019; Esquerré *et al.* 2017), diet (Denoël *et al.* 2004; Esquerré *et al.* 2017; Sherratt *et al.* 2019), or often a multitude of factors some of which are unclear (Bright *et al.* 2016; Morris *et al.* 2019; Bardua *et al.* 2021). Unfortunately, the selective pressures for *D. coriacea* to develop this phenotype has not been examined. The high degree of shell reduction as a consequence of paedomorphosis may assist in achieving very large size. This would be consistent with extensive shell reduction in other large sea turtles (Hirayama 1994; Cadena and Parham

2015). There is also perhaps a link between paedomorphy and deep diving, as other deep diving amniotes such the southern elephant seal (*Mirounga leonina*) share some paedomorphic traits such as lack of suture closure (Goswami and Weisbecker 2013) with *D. coriacea* (Pritchard and Trebbau 1984). The paedomorphic skull shape in *D. coriacea* is likely an example on multiple factors influencing skull shape including behaviour, habitat, as well as a generally paedomorphic condition rather than just selective pressure on feeding mechanics (Figgner *et al.* 2019). In *N. depressus*, paedomorphosis appears to be isolated to the skull (Zangerl *et al.* 1988) suggesting it arose independently in both sea turtles for different reasons, but this hypothesis requires further investigation.

The oldest phylogenetic divergence (*D. coriacea*-Cheloniidae) and the youngest (*L. kempii*-*L. olivacea*) effectively demonstrate how changes in ontogenetic allometry might act as a mechanism for speciation and morphological divergence. Dermochelyids likely diverged from cheloniids in the Late Cretaceous (Duchene *et al.* 2012; Thomson *et al.* 2021); unfortunately other than the Eocene *Eosphargis breineri* we have little cranial material from early dermochelyids to directly compare them to *D. coriacea* (Nielson 1959; Hirayama 1997). The high degree of similarity between the skull morphology of *Eo. breineri* (Nielsen 1959) to the modern *D. coriacea* suggests dermochelyids achieved a highly paedomorphic skull shape very early in their evolution. Thomson *et al.* (2021) suggests that crown cheloniids started diverging from each other relatively recently during the late Oligocene or Early to Mid-Miocene. Given the slow evolutionary rates of turtles (Avice *et al.* 1992; Lourenco *et al.* 2013), changes to developmental patterns may be the most effective way for cheloniids to significantly change their morphology to adapt to a wide variety of ecological niches. The two *Lepidochelys* species may be the clearest example of this evolutionary mechanism. *Lepidochelys kempii* is estimated to have diverged from *L. olivacea*

2.5-3.5 Ma during the formation of the isthmus of Panama (Bowen *et al.* 1997; Naro-Maciel *et al.* 2008; Duchene *et al.* 2012), making both sister taxa the most recently speciated sea turtles. Our finding that *L. kempii* is peramorphic compared to *L. olivacea*, and their significant dietary difference, potentially shows a rapid adaptation to exploit a different resource facilitated by changes to ontogenetic and allometric patterns.

As we suggest for sea turtles heterochrony appears to be significant mechanism for phenotypic diversification for much of Reptilia. Within closely related groups, shifts in allometric trajectory have frequently been found to be of major importance in generating adaptive diversity, whether the phenotype in question is body size (Denoel and Joly 2000; Kon and Tetsuo 2002; Sander *et al.* 2004; McNamra and Long 2012; Esquerré *et al.* 2017) or shape change (Leiberman *et al.* 2007; Adams and Nistri 2010; Piras *et al.* 2011; Morris *et al.* 2019; Gray *et al.* 2019). In other reptiles, heterochrony linked to dietary diversity is also seen in Crocodylia where shifts in allometric trajectories (deceleration, pre-displacement, acceleration etc.), are perhaps the most significant determiners of skull shape, correlating with dietary niches (Morris *et al.* 2019). Similarly, in pythons, heterochrony was found to be the main mechanism in initial divergence of phenotype, with a strong adaptive link between ontogenetic allometry and ecology (Esquerré *et al.* 2017). Though the exact genetic mechanisms for various heterochronic patterns are varied depending on taxon and body region (Brugmann *et al.* 2006; Tokita *et al.* 2013; Bhullar *et al.* 2015; Ahi 2016; Morris *et al.* 2019), and are yet to be established for sea turtles, our study has shown that changes to the timing and extent of development have played a major role in creating sea turtle diversity. Though our data is highly suggestive of allometry being an important factor in phenotypic diversification in modern sea turtles the high dietary but low taxonomic diversity as well as

small sample size makes our results less certain. The almost one to one ratio of dietary specialisation to species is one of the most interesting aspects of sea turtles. However, this makes establishing any ties between skull shape and diet with any statistical power difficult (Blomberg *et al.* 2003; Adams 2014). The difficulty in finding large sample size for some species, in particular *L. kempii* also means that our findings are preliminary and require more extensive investigation. Despite these obstacles however, we think we have shown that it is highly likely that a pattern linking ontogenetic variation, diet, and skull shape exists for sea turtles.

Conclusion

Heterochrony appears to have played a significant part in the shaping of the sea turtle skull. There are at least two instances of both paedomorphy and peramorphy among extant sea turtles. In both cases there is an association with diet: robust peramorphic skulls with large muscle chambers are associated with hard shelled prey whereas paedomorphic skulls with large orbits are associated with soft bodied prey. However, the paedomorphic skull shape of *D. coriacea* may reflect an overall paedomorphic body plan rather than selection the skull to feed on soft bodied prey. As is the case with much of Craniata, within Reptilia heterochrony appears to be one of the more important factors in driving variation in skull shape. Our study emphasises the importance of ontogenetic allometry for facilitating adaptation and morphological variation and the benefit of quantitative comparison of an entire group.

Statement of Authorship

Title of Paper	A Bayesian total evidence tip-dating analysis of the sea turtle phylogenetic tree		
Publication Status	<input type="checkbox"/> Published <input type="checkbox"/> Accepted for Publication <input type="checkbox"/> Submitted for Publication <input checked="" type="checkbox"/> Unpublished and Unsubmitted work written in manuscript style		
Publication Details			

Principal Author

Name of Principal Author (Candidate)	Ray Chatterji		
Contribution to the Paper	Data collection and analysis Majority of writing and editing of manuscript		
Overall percentage (%)	90%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/08/2020

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- the candidate's stated contribution to the publication is accurate (as detailed above);
- permission is granted for the candidate to include the publication in the thesis; and
- the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Mark Hutchinson		
Contribution to the Paper	5%, editorial advice on manuscript structure, clarity and quality of illustrations		
Signature		Date	20/08/2020

Name of Co-Author	Marc E H Jones		
Contribution to the Paper	5%, Some guidance on organisation and literature. Detailed feedback on the first iteration of the manuscript. Text editing of subsequent iterations to improve clarity.		
Signature		Date	21st August 2020

Please cut and paste additional co-author panels here as required.

**Convergent adaptation to the marine environment by
sea turtles, supported by a Bayesian total evidence
tip-dating approach.**

Ray M. Chatterji

Mark N. Hutchinson, Marc E.H. Jones

ABSTRACT

Convergent evolution can undermine parsimony as a criterion for choosing among phylogenetic hypotheses, resulting in a struggle to find consensus among conflicting trees. This struggle is exemplified in the studies of sea turtle (Pan-Chelonioidea) evolution. Despite the wide interest in this iconic clade, rigorous analyses of character acquisition are currently limited by poorly resolved, largely parsimony-based phylogenies. In particular, there is uncertainty regarding the placement of the extinct family Protostegidae which has been recovered in several different parts of the tree and even outside Pan-Chelonioidea as a separate radiation of marine turtles. The arrangement of the stem of Cheloniidae is also far from a consensus despite it having a relatively good fossil record. Here we investigate the evolution of sea turtles using a total evidence tip-dating approach, a technique not previously applied to this group. We find Protostegidae to be sister to the rest of Pan-Chelonioidea, implying convergent evolution of the sea turtle flipper and other marine adaptations. Within Cheloniidae we identify two distinct radiations: a New-World radiation and an Old-World radiation, with modern cheloniids emerging from the latter. The distinct geographic separation between groups might suggest that the early members of both groups were less capable of transoceanic dispersal compared to later species.

INTRODUCTION

Many groups of animals still lack phylogenies that robustly link living members of a radiation to their fossil relatives. This problem can be due to a lack of fossil specimens (Heath *et al.* 2008; Mayr 2017), or a lack of knowledge of modern diversity (Heath *et al.* 2008; Raj Pant *et al.* 2014). Without such information their evolutionary history remains unclear (Donoghue *et al.* 1989; Slater *et al.* 2012; Lee and Palci 2015). This issue not only hinders our understanding of an individual group's evolution but also effects our understanding of the broader evolutionary picture and the full impact of past events (Donoghue *et al.* 1989; Jones *et al.* 2013; Raj Pant *et al.* 2014; Lee and Palci 2015). It limits phylogenetic bracketing, ancestral state reconstruction, and phylogenetic comparative methods more broadly as without a solid, well support phylogeny we would be drawing conclusions based on potentially faulty assumptions (Gauthier *et al.* 1988; Finarelli and Flynn 2006; Nesbit 2011; Lee and Palci 2015; Giribet 2015).

Morphological convergence has long been recognised as a problem in evolutionary biology (e.g. Osborn 1902; Goodrich 1916; Stokely 1947; Brattstrom 1957). As molecular data began to contribute to phylogenetic analyses it was shown that many phylogenies built solely using morphological data were rife with instances of convergence (Gaubert and Veron 2003; Daniels *et al.* 2006; Pyron 2011; Tsagkogeorga *et al.* 2013; Mitchell *et al.* 2014). Molecular data has played an important role in confirming many long standing hypotheses of relationships, resolving several long standing problems (e.g. Zardoya and Meyer 2001), and identifying several unexpected relationships (e.g. Springer *et al.* 2004). However, detecting convergence among extinct taxa remains difficult due to the unavailability of DNA evidence

(Wiens *et al.* 2009; Wake *et al.* 2011; Zou and Zhang 2016). Exacerbating this issue is the heavy use of maximum parsimony as the primary basis for choosing among phylogenetic hypotheses. Parsimony is a criterion that is particularly prone to errors where morphological convergence is common (Lewis 2001; Wiens *et al.* 2003; Bendiksy *et al.* 2010) because all character state changes are considered equal and parsimony selects trees with the fewest possible character state changes so character state convergences will be recognised as synapomorphies unless outnumbered by other characters. (Wilkinson 1991; Stewart 1993; Kluge and Grant 2006; Grant and Kluge 2009). Other techniques, such as Bayesian analysis and Maximum Likelihood are potentially better suited to accounting for convergence because character state changes are weighted according to the model of evolution used. Bayesian can also test different models under differing prior assumptions to test and compare different hypotheses (Lewis 2001, Hueslenback and Ronquist 2005; Nylander *et al.* 2004; Muller *et al.* 2006; Linder *et al.* 2011; Ronquist *et al.* 2012; Lee and Palci 2015). These techniques can also incorporate other forms of data such as chronological data to further accommodate for convergence (Lewis 2001; Muller *et al.* 2006; Ronquist *et al.* 2012).

Total evidence tip-dating analyses have shown great potential to help resolve longstanding incongruences between fossil and molecular data. A tip-dating approach allows for a greater uncertainty for the phylogenetic placement of fossil taxa (Ronquist *et al.* 2012). The method has been used to investigate several different groups, including insects (Ronquist *et al.* 2012, Vea and Grimaldi 2016), fish (Arcilia *et al.* 2015), birds (Crouch *et al.* 2019), reptiles (Bapst *et al.* 2016, Lee and Yates 2018), and mammals (Lee 2016; King and Beck 2020). Tip-dated trees align better with the stratigraphic evidence for groups than under other methods (King 2020). However, chronological data will not override strong morphological evidence for a relationship. Taxa that are highly incomplete or phylogenetically unstable appear to be the

most affected by the addition of chronological data (King 2020). Sea turtles (Chelonioidea) are a potentially ideal group to apply these techniques to. They represent a well sampled group that have a well-represented but poorly understood stem lineage. The lack of consensus of internal relationships excludes the use of node dating (Ronquist 2012). However, tip-dating can provide chronological information without prior assumptions of relationships (Ronquist 2012; King 2020). Using this approach, we can apply chronological data to the sea turtle phylogeny to evaluate the clade's complex past.

There are seven extant species in Chelonioidea (Cheloniidae + Dermochelyidae), split in to two families: the monotypic Dermochelyidae, and the more speciose Cheloniidae (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012). These marine reptiles are represented in most oceans and are important members of most shallow marine ecosystems in the tropics, as well as many temperate environments (Dodd 1988; Bjorndal *et al.* 1997; Bjorndal and Jackson 2002; Limpus 2007). Sea turtles have been a consistent presence in marine ecosystems for over 100 million years, and are the only large marine tetrapod group to persist through the K–Pg extinction (Pyenson *et al.* 2014; Kelley and Pyenson 2015). This persistence in the ecosystem makes them a valuable group to understand events and cycles that might affect marine communities (e.g. Pimiento *et al.* 2017). However, the long-term evolution of this group is poorly understood restricting their use for quantitative and rigorous analyses.

A long-standing problem for the evolutionary understanding of Pan-Chelonioidea (most recent common ancestor of *Toxochelys* sp., Protostegidae, and Chelonioidea and all its descendants) is the placement of the Cretaceous species *Toxochelys* sp. and the extinct family Protostegidae (Fig. 1). These groups have been a source of instability for many years

with no clear consensus topology being found (Hirayama 1994; Kear and Lee 2006; Joyce 2007; Cadena and Parham 2015; Evers and Benson 2019; Gentry *et al.* 2019). This phylogenetic uncertainty is problematic because the precise placement of Protostegidae has major implications for the number of marine invasions by turtles, the number of times paddles and shell reduction have evolved, as well as when chelonioids first evolved (Evers and Benson 2019; Evers *et al.* 2019). Multiple recent studies (Cadena and Parham 2015; Evers and Benson 2019; Evers *et al.* 2019; Chatterji *et al.* 2020) support the unification of Protostegidae with Chelonioidea to the exclusion of more primitive species such as *Toxochelys* sp., thus suggesting a singular invasion of the marine habitat by Pan-Chelonioidea. *Toxochelys* sp. was previously placed among its own family Toxochelyidae as a sister group to Cheloniids or Chelonioidea (Zangerl 1953; Hirayama 1998). Recent studies however have found that Toxochelyidae represents an evolutionary paraphyletic grade rather than a distinct family (Gentry 2017; Gentry *et al.* 2019) and the placement of *Toxochelys* sp. has become less stable (Evers and Benson 2019; Gentry *et al.* 2019; Chatterji *et al.* 2020).

The discord among phylogenetic studies of the cheloniid stem is partly due to limited comparative research for the group (Hirayama 1994; Parham and Pyenson 2010; Weems and Brown 2017). Despite a relatively good fossil record, many species of this group have only recently been described and analysed with adequate rigour (Mulder 2003; Tong *et al.* 2012; Weems and Sanders 2014). Until very recently the American Oligo-Miocene sea turtles had received very little attention (Weems and Sanders 2014; Cadena *et al.* 2015; Weems and Brown 2017). The lack of inclusion of the American group groups in phylogenetic analyses (Cadena and Parham 2015; Gentry 2017; Evers and Benson 2019; Gentry *et al.* 2019) had left a significant temporal (and potentially morphological) gap

between early cheloniid sea turtles such as *Puppigerus* and *Argillochelys*, and the crown species (Hirayama 1994; Kear and Lee 2006; Evers and Benson 2019).

We aim to re-examine the evolution of Pan-Chelonioidea using a Bayesian approach and assess the impact of adding tip dating on the branching pattern. In particular, we aim to evaluate the position of Protostegidae within Pan-Chelonioidea, and how this phylogenetic relationship impacts the frequency of marine invasion by sea turtles. In addition, we hope to improve our understanding of the placement of stem group cheloniids and how they impacted the evolution of the modern crown.

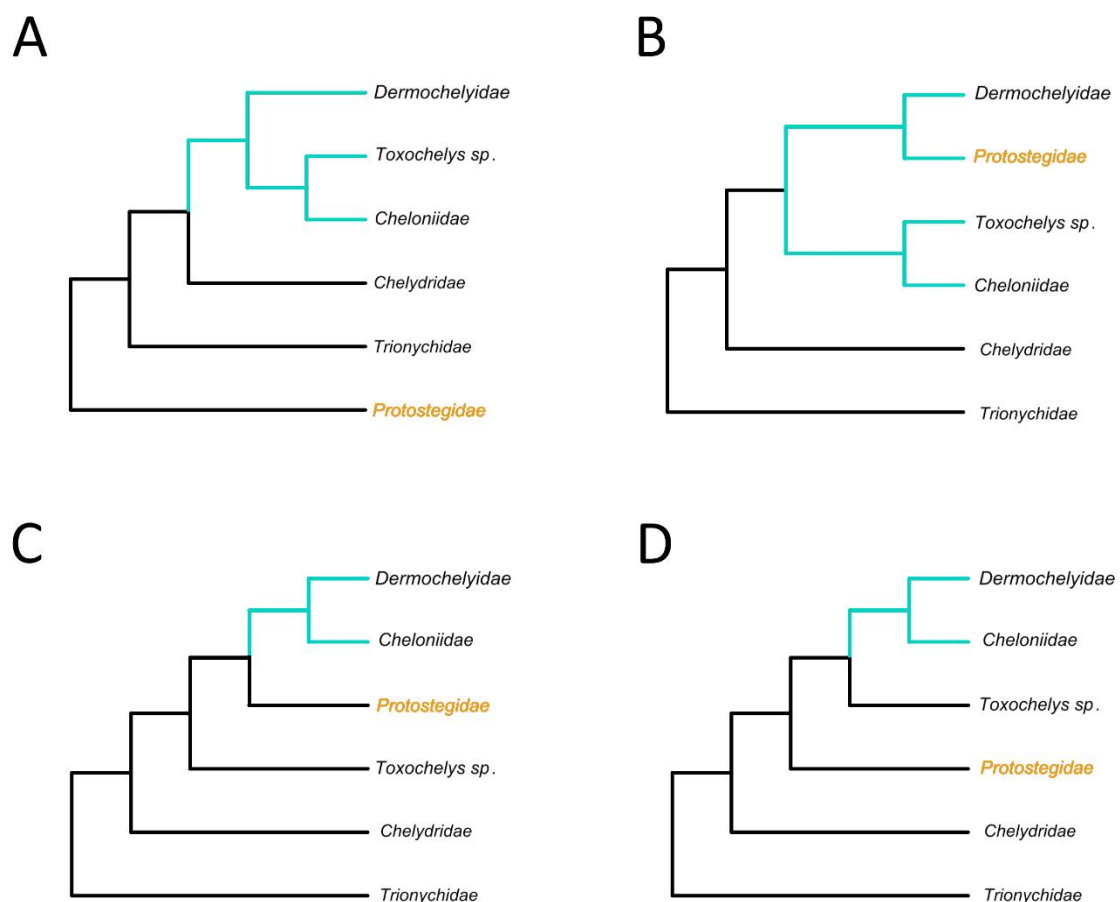


Figure 1. The differing positions of Protostegidae (Gold) and its relationship to Chelonioidea (Blue) through the literature. Figure modified from Chapter 1A: Redrawn from Joyce (2007) showing Protostegidae outside of Cryptodira. B: Redrawn from Kear and Lee (2006), showing Protostegidae as sister to Dermochelyidae. C:

Redrawn from Evers *et al.* (2019), showing Protostegidae as sister to Chelonioidea. D: Redrawn from Gentry *et al.* (2019), showing *Toxochelys* sp. as sister to Chelonioidea and Protostegidae as the least nested family of sea turtles.

METHODS

We use the character matrix from Chatterji *et al.* (2020) with new characters added from Evers *et al.* (2019) to construct a matrix with 23 taxa and 367 characters. *Apalone spinifera* was used as an outgroup, representing Trionychia, the least nested family within Cryptodira. *Chelydra serpentina* was included to represent the sister group to Pan-Chelonioidea. A further 21 species were included, to represent the Pan-Chelonioidea across their entire time span, only using species with well reported morphological data, or those to which we had access. For most OTUs direct examination of specimens as well as examination of CT data was used. The character state scoring for *Pacifichelys hutchisoni*, *Procolpochelys grandavea*, and *Carolinachelys wilsoni* were taken from Cadena and Parham (2015), the additional characters were scored using a combination of examination of 3D models available on SketchFab and evaluation of information provided in the literature (Gaffney *et al.* 1979; Lynch and Parham 2003; Weems and Sanders 2014; Weems and Brown 2017).

We use a Bayesian total evidence tip-dating method. We used a uniform clock prior as described in Ronquist *et al.* (2012). We followed this approach in an attempt to minimise assumptions of ancestry; no species were assumed ancestral to another. This method was also used because we are interested in the phylogenetic arrangement of fossil taxa more than the relatively stable crown (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012; Cadena and Parham 2015; Evers and Benson 2019). A uniform prior is used as we do not have a complete sampling of fossil taxa, and do not have data on speciation or extinction rates required for other more complex models (Ronquist *et al.* 2012; King 2020). Tip-dating also

allowed us to investigate the age of branching events without specifying components of the branching topology a priori (as required for node dating).

The tree was rooted at the base of Cryptodira, using the minimum age of the earliest known cryptodire *Yehguia tatsuensis* (Danilov and Parham 2006; Lourenço *et al.* 2012; Sterli *et al.* 2013). For each species in the study, we used the earliest and latest reasonable date (Supp table 1.). We also ran the same dataset, with the same parameters, excluding any temporal data as a control. As *Chelydra serpentina* and *Apalone spinifera* were used as representatives of the groups Chelydridae and Trionychia respectively, they were dated using the earliest members of their groups. The crown group cheloniids were not given strict dates and instead were left as unconstrained. This procedure was followed due to the lack of good fossils that can definitively be assigned to this clade and uncertainties of first occurrences in the record (Pritchard and Trebbau 1984; Dodd and Morgan 1992; Zug 2001). We performed our Bayesian analysis in Mr Bayes V 3.2.6, with a Mkv model of rate variation with ascertainment correction bias (Lewis 2001). This model is the most thoroughly tested model for incorporating morphological data within a Bayesian framework (Müller and Reisz 2005; Wiens 2009; Pyron 2011). The gamma parameter was chosen to allow for rate variation across characters, as a more realistic option when compared to a uniform rate variation (Nylander *et al.* 2004; Müller *et al.* 2006; Lee 2013). The Bayesian analyses ran for 30,000,000 generations, with a sample frequency of 1000. Parameters, posterior probabilities, and branch lengths were estimated using a Markov chain Monte Carlo, with four chains used, one cold, three heated with a temperature of 0.2. The first 25% of samples were discarded as burn in. A molecular backbone for the crown group was used based on the topology recovered in Naro-Maciel *et al.* (2008) and Duchene *et al.* (2012).

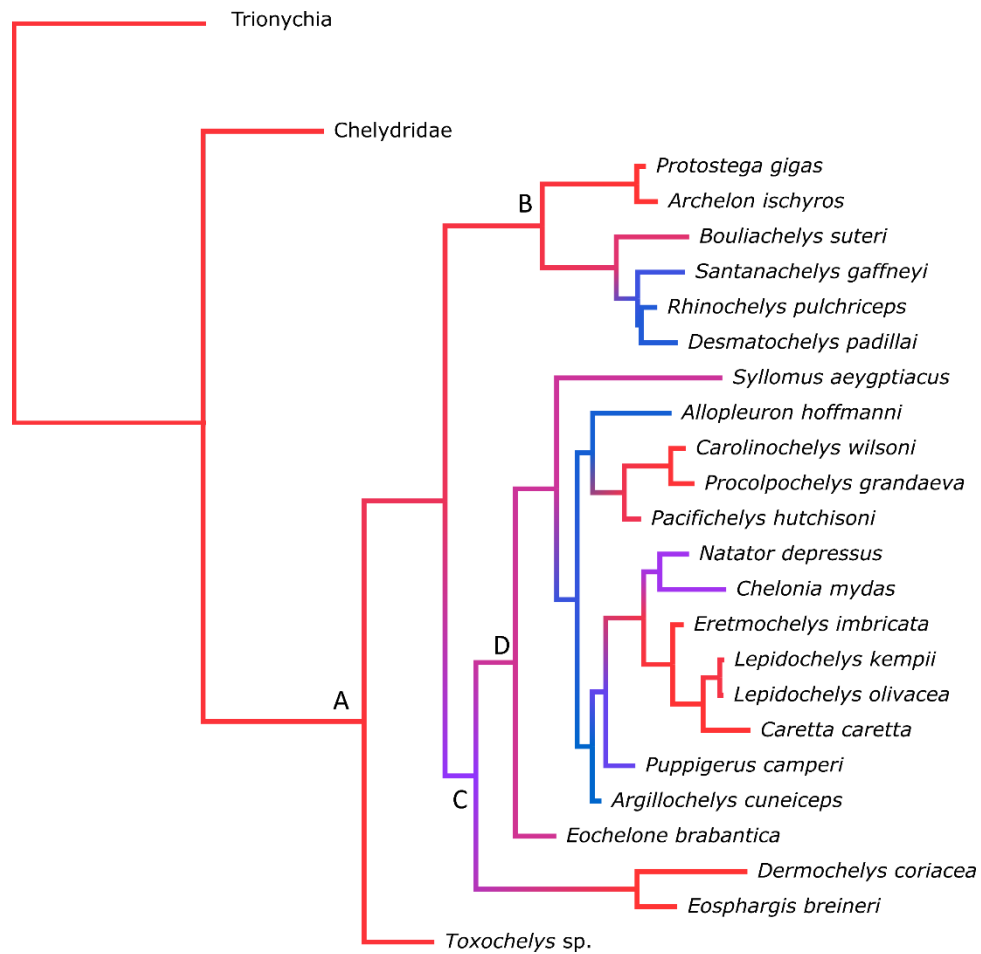


Figure 2. Control maximum clade credibility tree of Pan-Chelonioidae. Posterior probability of clade indicated by colour, blue indicating low support and red indicating high support ranging from 0.3 to 0.99. A indicates the base of Pan-Chelonioidae; B indicates the base of Protostegidae; C indicates the base of Chelonioidae; D represents the base of Cheloniidae. Posterior probability values range from 0.3 to 1.

RESULTS

Our control tree (Fig. 2) recovers *Toxochelys* sp. as sister to the rest of Pan-Chelonioidae.

There are two distinct internal clades within Protostegidae. One clade contains the later Cretaceous species *Archelon ischyros* and *Protostega gigas*. Within the other protostegid

clade *Santanachelys gaffneyi* and *Desmatochelys padilli* are recovered as the two most

nested species. Protostegidae is recovered as the sister group to Chelonioidae. Within

Cheloniidae, *Eochelone brabantica* is recovered as sister to all other cheloniids. *Allopleuron*

hoffmani is found to be sister to the clade including *Pacificchelys hutchisoni* and

Procolpochelys grandavea. *Argillochelys cuneiceps* and *Puppigerius camperi* are found to be in a clade with the crown cheloniids, the crown group is found to be monophyletic.

The topology we recover in our tip-dated tree of maximum credibility (Fig. 3) is similar to that found in the recent studies of Evers *et al.* (2019) and Gentry *et al.* (2019). Pan-Cheloniioidea (Fig. 3: clade A and 3) is recovered with good support (0.89). Protostegidae (Fig. 3: clade B and 4) is found to be monophyletic and sister the rest of Pan-Cheloniioidea. Within Protostegidae, *Arc. ischyros* and *Protostega gigas* are sister taxa to each other (clade 5) and form a clade that is sister to the rest of Protostegidae (clade 6). *Desmatochelys padillai* is sister to a clade including *Sa. gaffneyi* and *Rhinochelys pulchriceps* + *Buliachelys suteri* (clade 7). *Toxochelys* sp. is found to be sister to Cheloniioidea (Fig 3: clad C clade 9) with strong support (0.85). A monophyletic Dermochelyidae (clade 11), that includes *Dermochelys* and *Eosphargis*, is recovered with strong support (0.99).

Allopleuron hoffmani is found to be the least nested taxon within total group Cheloniidae (Fig 3: clade D and clade 12) with relatively strong support (0.92). The next node inside Cheloniidae (clade 13) involves a divergence between *Eo. brabantica* and all other Cheloniidae (clade 14). The deepest divergence within the remaining Cheloniidae (clade 14) is poorly supported (0.39) but appears to involve two large subclades: clades 15 and 18. The first of these clades, clade 15, includes *S. aegyptiacus*, *Procolpochelys grandavea* + *C. wilsoni* and *Pa. hutchisoni*. The inclusion of *S. aegyptiacus* within clade 15 is poorly supported (0.22) whereas the unification of the other taxa in clade 16 is relatively well supported (0.70). The second of these clades, clade 18, includes crown Cheloniidae, *Puppigerius camperi*, *Argillochelys cuneiceps*. This clade is poorly supported (0.32). *Argillochelys cuneiceps* is the least nested taxon whereas *Puppigerius camperi* is sister to crown Cheloniidae forming

clade 19, with poor support (0.46). Crown Cheloniidae (clade 20) is monophyletic with strong support (0.98).

Pan-Chelonioidea diverged from Chelydridae 143.32 (2) Ma (Table 1.). Protostegidae diverged from the rest of Pan-Chelonioidea 135.85 Ma. The divergence between *Toxochelys* sp. and Chelonioidea is estimated to have occurred 107.73 Ma. Dermochelyidae and Cheloniidae diverged about 99.00 Ma. *Eo. brabantica* diverged from the rest of Cheloniidae at about 64.00 Ma. The lineages of two distinct clades (15) and (18) diverged from each other 57.16 Ma. The crown of Cheloniidae emerged at 13.12 Ma (21.32 – 7.02 Ma 95%CI).

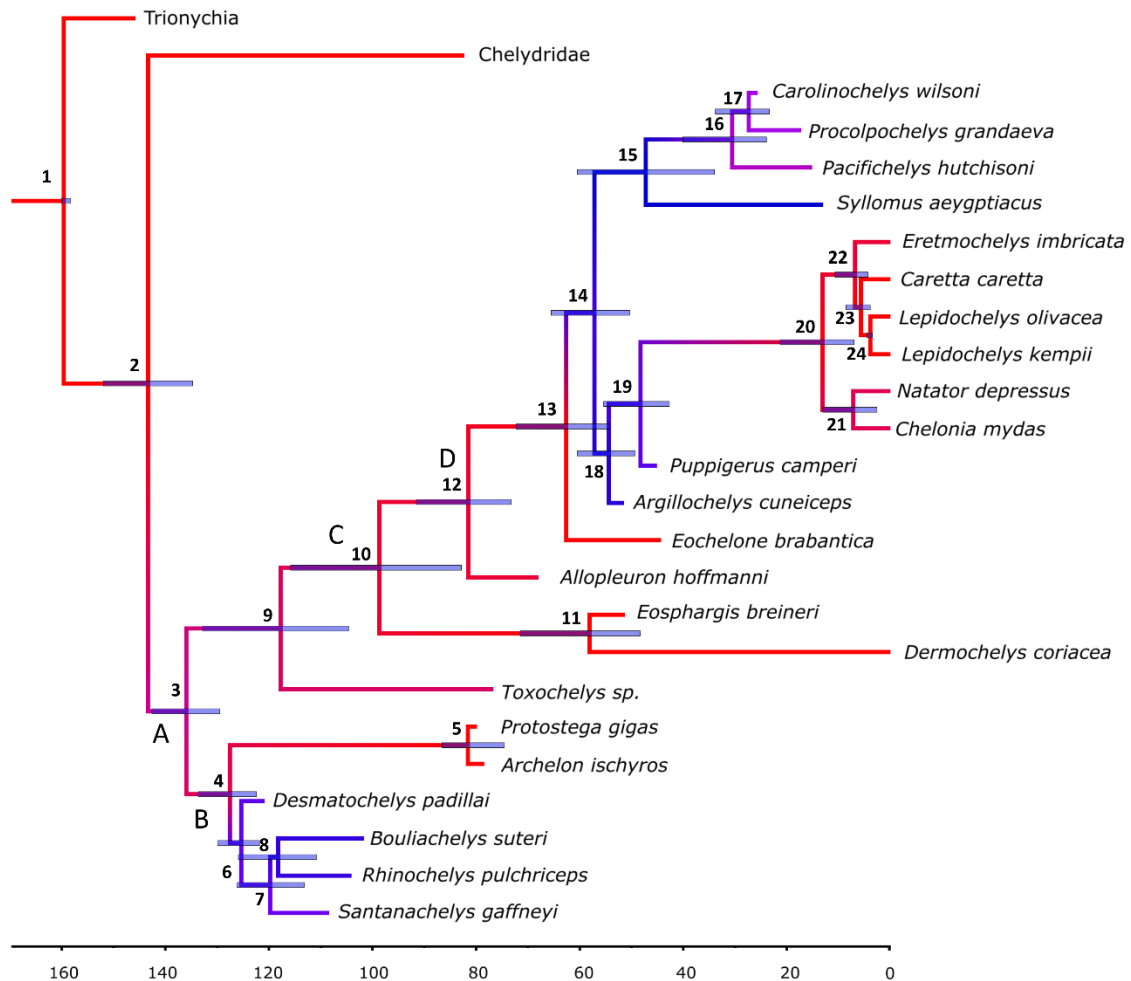


Figure 3. Tip-dated maximum clade credibility tree of Pan-Chelonoidea. Posterior probability of clade indicated by colour, blue indicating low support and red indicating high support: blue < 0.50; purple = 0.70; red > 0.90. A and 3 = Pan-Chelonoidea; B and 4 = Protostegidae; C and 10 = Chelonoidea (and divergence of Dermochelyidae and Cheloniidae); D represents the base of Cheloniidae. Scale bar in Millions of years, bars at node indicate 95% confidence interval of node age.

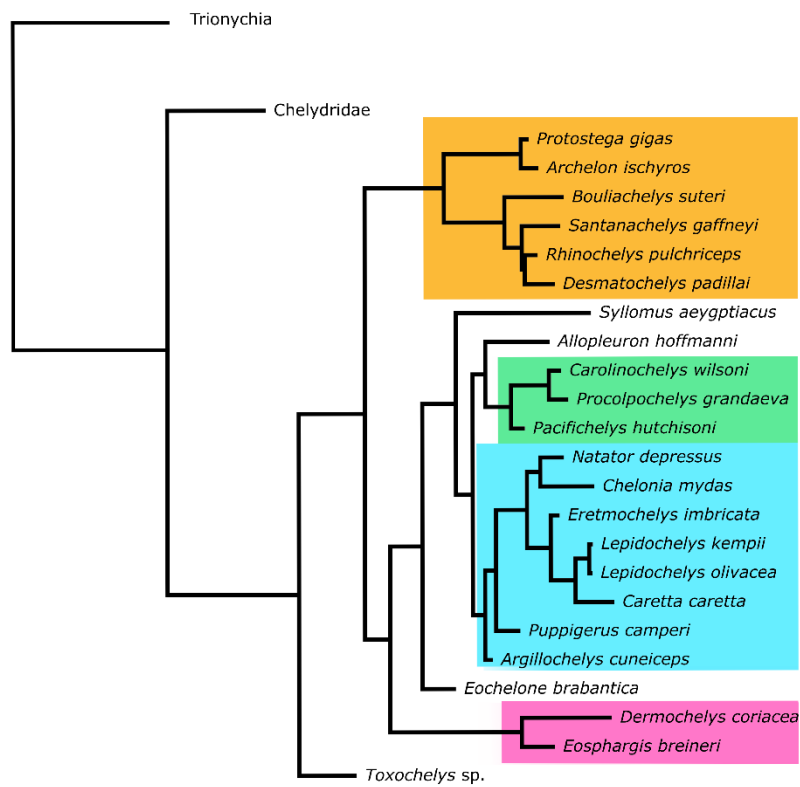
The control tree and tip-dated tree are similar but not identical (Fig. 4). Both recover clades 5, 11, 16, and 18 with identical internal topologies. The control tree and tip-dated tree also recovers the more inclusive clades 2, 3, 4, and 10 but with different internal topologies. Taxa that differ in placement with the inclusion of time include *Toxochelys* sp., *Sy. aegyptiacus*, *Al. hoffmani* and Protostegidae. Protostegidae in particular becomes the least nested group

within Pan-Chelonioidea (Clade A and 3). *Toxochelys* sp. is recovered as sister to Chelonioidea (Clade C and 10). *Allopleuron hoffmani* becomes the least nest species in Cheloniidae (Clade D and 12). *Syllomus aegyptiacus* becomes more deeply nested becoming sister to clade 16

Table 1. Posterior probability and age values for nodes labelled in Figure 3; Letters next to node numbers correspond to those in Figure 3

Node Number	Posterior Probability	Median Node age Ma	Max 95% confidence	Min 95% confidence
1	1	159.59	160.00	158.25
2	1	143.32	151.9	134.73
3 A Pan-Chelonioidea	0.78	135.95	142.59	129.46
4 B Protostegidae	0.89	127.53	133.63	122.42
5	1	81.58	86.56	74.53
6	0.46	125.34	129.91	121.79
7	0.5	119.75	126.18	113.18
8	0.36	118.21	125.90	110.83
9	0.85	117.73	132.78	104.61
10 C Chelonioidea	0.93	98.69	115.81	82.85
11	1	58.09	71.49	48.31
12 D Cheloniidae	0.92	81.51	91.45	73.25
13	0.99	62.61	72.31	54.18
14	0.39	57.16	65.48	50.38
15	0.22	47.24	60.48	33.99
16	0.70	30.57	40.01	23.93
17	0.65	27.37	33.82	23.37
18	0.32	54.38	60.49	49.29
19	0.46	48.25	55.38	42.69
20 Cheloniidae crown group	0.98	13.12	21.32	7.02
21	0.88	7.19	13.07	2.61
22	0.92	6.84	10.71	4.33
23	1	5.69	8.59	3.91
24	1	3.90	4.56	3.51

A



B

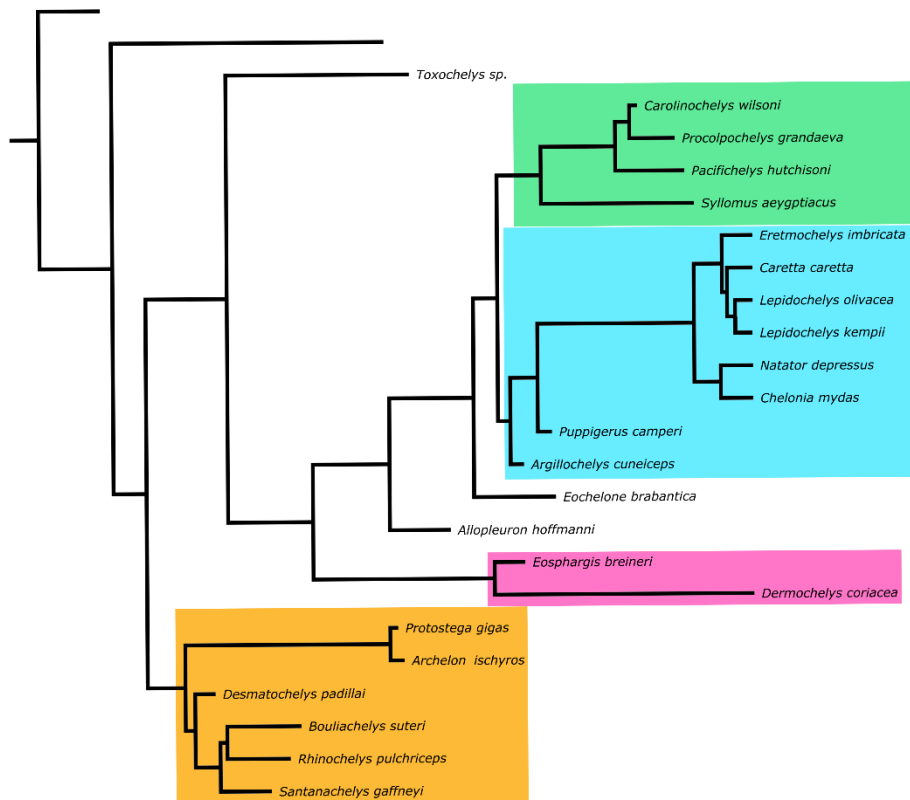


Figure 4. Comparison between our control tree (A) and our tip-dated tree (B) showing the relative position of clades. Yellow = Protostegidae; Pink = Dermochelyidae; Green = New world cheloniids; Blue = Old world cheloniids.

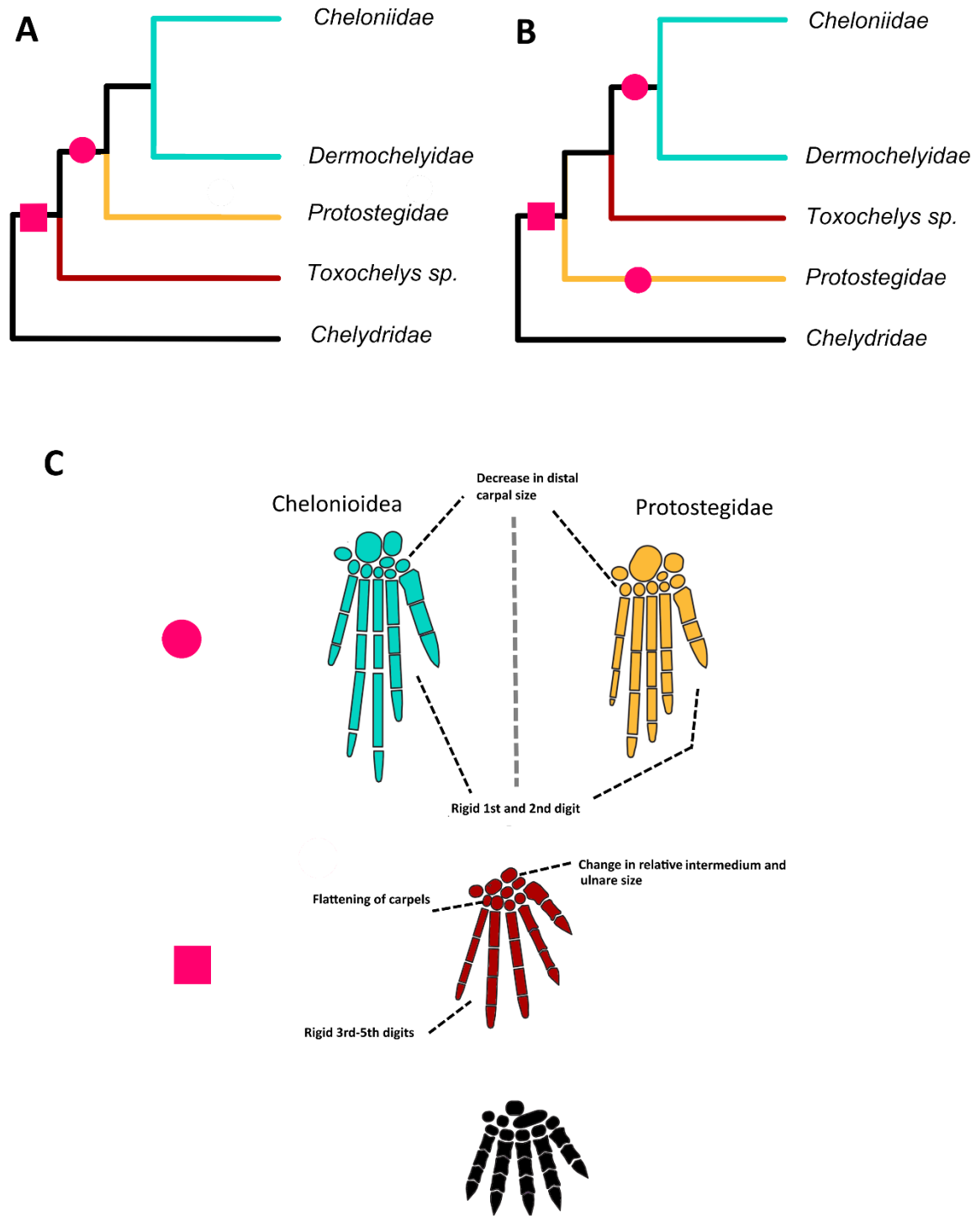


Figure 5. Differing evolutionary scenarios for the acquisition of marine traits. A shows the scenario proposed

by Evers *et al.* 2019. B shows the scenario presented by our study. Square represents the acquisition of early marine traits, circle represents the acquisition of more advanced marine traits. C shows the acquisition of flipper traits represented by the square and circle. Diagrams for the flippers modified from Evers *et al.* 2019.

DISCUSSION

Adaptation to a marine environment

Our tip-dating approach recovers Protostegidae as sister to the rest of Pan-Chelonioidea, including *Toxochelys* sp. This less nested position of Protostegidae within the tree differs from the position recovered in many recent studies where it is found to be sister to Chelonioidea (Cadena and Parham 2015, Evers and Benson 2019, Evers *et al.* 2019, and Chatterji *et al.* 2020). In our analysis the placement suggests that the divergence of Protostegidae from the rest of the phylogeny is older than that of many other recognised taxa. This result is related to the inclusion of chronological data given that it is not recovered in our undated control analysis. Therefore, although Evers and Benson (2019) showed that there was strong morphological support for the unification of Protostegidae and Chelonioidea, this support was not strong enough to overcome the chronological data (King 2020). The placement of *Toxochelys* sp. as sister Chelonioidea to the exclusion of Protostegidae has also been recovered using purely morphological data with no tip-dating (Gentry *et al.* 2019). This difference in topology to previous works (Cadena and Parham 2015; Evers and Benson 2019; Evers *et al.* 2019) largely only relates to this particular OTU, but it has significant implications for the transition to a marine lifestyle: our tree suggests that within Pan-Chelonioidea adaption to a fully marine lifestyle happened at least twice (Fig. 5).

Evers and Benson (2019) and Evers *et al.* (2019) suggested that acquisition of the specialised anatomy of the forelimbs correlated with underwater propulsion occurred early in the

history of sea turtles before the divergence of Protostegidae during the Cretaceous. However, the more crownward position of *Toxochelys* sp. recovered in this study, as well as in Gentry *et al.* (2019), suggests that the advanced marine adaptations shared by Protostegidae and Chelonioidea such as a wide internal angle of the scapula, enlargement of proximal carpals, and the stiffening of the 1st and 2nd digits, were acquired independently and represent an instance of convergent evolution. Some of these features, such as the broadening of the first digit, are known to have occurred in other unrelated marine taxa such as mesosaurs, mosasaurs and pleurosaurs (e.g. Lee *et al.* 2016). The flattening of forelimb elements and an increased relative humerus size, characters included in this and other studies (Kear and Lee 2006; Joyce 2007; Cadena and Parham 2015; Evers *et al.* 2019 Gentry *et al.* 2019), have been shown to be a consistent morphological adaptation to a marine environment (Motani and Vermji 2021). Therefore, these strongly selected functional character states might be a confounding factor in determining the phylogenies of marine lineages.

Evers and Benson (2019) did show that that morphological support for a single marine invasion persisted even when obviously marine adapted traits (e.g. forelimb and shell reduction characters) were removed from the analysis. However, it might be that the remaining morphological signal, largely due to cranial characters, is also subject to an adaptive signal. Convergence in cranial shape and design among marine tetrapods is both known and common, particularly among species with similar diets (Taylor 1987; Kelley and Motani 2015; McCurry *et al.* 2017). Given that protostegids likely filled similar dietary niches to later sea turtles (Kear and Lee 2006; Cadena and Parham 2015), and both groups belong to the same large clade Pan-Chelonioidea, there is strong chance that there was convergence in some cranial characters.

Cheloniidae

The maximum clade credibility tree, though with varying degrees of support, suggests that there were three separate lineages of cheloniid sea turtles in the Eocene, *Eochelone brambantica*, and clades 15 and 18 (Fig. 3), only one of which survived until today. This greater evolutionary diversity perhaps suggests that a wider range of sea turtle niches existed to support greater diversity. Interestingly the maximum credibility tree suggests the existence of independent Old World and New World lineages. The modern crown group of cheloniids emerged from the Old World radiation whereas most of the members of the New World radiation went extinct in the Miocene, the exception being *S. aegyptiacus*, which went extinct in the Pliocene (Supp table 1). This result is somewhat contradictory to previous phylogenetic trees, which generally have been more comb like (Brinkman *et al.* 2009; Parham and Pyenson 2010; Weems and Brown 2017) but is congruent with the tree recovered in Gentry *et al.* (2019).

The existence of two distinct clades of cheloniids could have some behavioural and ecological significance. It highlights the possibility that stem sea turtles may have had their own ecological niche that was different from that of modern sea turtles. The North American Oligo-Miocene turtles may have lacked complex life histories and transoceanic travel. Most modern species are capable of traveling long distances and across oceans, and population genomic studies show strong evidence for transoceanic dispersal, with five of seven species being found in the waters of four or more continents (Bowen 2007; Duchene *et al.* 2012; Shamblin *et al.* 2014; Vargas *et al.* 2016). Most stem cheloniids are found from singular continents, or from closely grouped continents, suggesting a lack of transoceanic

travel (Gaffney 1979; Lynch and Parham 2003; Brinkman *et al.* 2009; Pyenson and Parham 2010; Tong *et al.* 2012; Weems and Sanders 2014). Much of this transoceanic travel occurs during the pelagic juvenile stage of most sea turtles (Limpus *et al.* 1983; Walker and Parmenter 1990), which has been demonstrated to act as an important dispersal event (Putman and Mansfield 2015). The lack of transoceanic distribution amongst the stem suggests that this pelagic juvenile stage might be unique to the crown.

The dates found in our study suggest the crown group started diversifying concurrently with the extinction of the New World clade at the end of the Mid Miocene optimum. The mean divergence dates found in our study are later than those suggested in Thomson *et al.* (2021) but have broadly overlapping 95% confidence intervals. The end of the Mid Miocene optimum was characterised by rapid global cooling with the formation of icecaps at the south and north poles, and a reduction of neritic environments and possible minor extinction of marine life (Raup and Sepkoski 1984; Flower and Kennett 1994; Böhme 2003). Our results suggest that it was only after this extinction event that the crown group speciated. The ability to travel across resource sparse pelagic areas to find more suitable habitat might have been highly beneficial after the Mid Miocene optimum, where neritic areas shrank dramatically in size (Flower and Kennett 1994; Böhme 2003).

Morphological convergence is also likely to have occurred within Cheloniidae, particularly among durophagous species. In past phylogenetic analyses durophagous species have often been grouped together largely based on the traits associated with durophagy (Lynch and Parham 2003; Parham and Pyenson 2010). For example, the species *Erquelinnesia gosseleti* has been suggested to be closely related to multiple other durophagous species such as the New World *Procolpochelys grandavea* and *Pacifichelys hutchisoni* (Lynch and Parham 2003;

Parham and Pyenson 2010; Weems and Brown 2017; Evers *et al.* 2019). However, *Erq. gosselti* has only been discovered in European localities (Owen and Bell 1841; Rothausen 1986). This phylogenetic placement would either mean that pelagic capabilities evolved in the American lineage much earlier than the Old World lineage, or that there has been strong morphological convergence associated with durophagy in sea turtles (Parham and Pyenson 2010). Our study suggests convergence has occurred multiple times among sea turtles, and the strong morphological signal found in Evers and Benson (2019) suggest that these convergences occur among cranial characters as well as those related to marine life. Convergence among Cheloniidae needs further examination and testing, which is currently difficult due to the lack of post cranial remains for some of these genera (Parham and Pyenson 2010; Weems and Sanderson 2014). Further investigation into previously underreported stem species is required to fully untangle the evolution of the cheloniid tree.

Although the hypothesis of New World and Old World sea turtles is appealing there are issues that require further investigation. The placement of *Syllomus aegyptiacus* with the New World sea turtles, does not fit the pattern as well as other species because it reportedly had a global distribution (Lydecker 1889; Weems 1980; Hasegawa *et al.* 2005). It is another species with a phylogenetic position that is historically unstable (Hirayama 1994; Lynch and Parham 2003; Parham and Pyenson 2010; Myers *et al.* 2018; Scavezzoni and Fischer 2018; Chatterji *et al.* 2020). Its position in our tree has low support and should not be taken at face value; the species should be thoroughly reinvestigated. It is known from a number of specimens and may represent more than one distinct taxon. Another potential outlier is the identification of *Pacifichelys* from Australia (Fitzgerald *et al.* 2014). However, this identification is based on a single partial dentary, and as discussed above it is difficult to exclude the possibility of morphological convergence among durophagous sea turtles.

CONCLUSION

Chronological data have been shown in this study to offer important constraints for evaluating the phylogenetic relationships of modern groups. Tip dating in particular acts as an important tool for clarifying relationships of groups with unstable, parsimony-based relationships. The addition of chronological data to an established morphological dataset for sea turtles suggests new evolutionary hypotheses and has significant implications for the evolution of the marine and pelagic lifestyles. It also provides a more holistic framework with which to evaluate future fossil discoveries. Our analyses suggest that the traits which contribute to the highly specialised marine flippers evolved at least twice, and that many of the morphological similarities between Protostegidae and Chelonioidae are convergent. We also suggest that Cheloniidae have two distinct geographic radiations during the Oligocene and Miocene with possibly contrasting life histories. We also highlight the possibility that the characteristic pelagic life stage observed in modern cheloniids may be unique to the crown group.

Statement of Authorship

Title of Paper	Quantitative analysis of skull shape evolution in sea turtles
Publication Status	<input type="checkbox"/> Published <input type="checkbox"/> Accepted for Publication <input type="checkbox"/> Submitted for Publication <input checked="" type="checkbox"/> Unpublished and Unsubmitted work written in manuscript style
Publication Details	N/A

Principal Author

Name of Principal Author (Candidate)	Ray Chatterji		
Contribution to the Paper	Majority of Specimen collection and Processing Majority of Data Analysis Majority of Writing and Editing of Manuscript		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/08/2020

Co-Author Contributions

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A quantitative analysis of skull shape evolution in sea turtles.

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ABSTRACT

Understanding the breadth and origin of morphological variation is a key objective of evolutionary biology. And to fully understand the morphological evolution of a group both modern and extinct species need to be examined. Sea turtles have been a constant presence in shallow marine ecosystems for over 100 million years. Due to their solid construction, and shallow marine habitat sea turtles have a relatively good fossil record with many skulls preserved undistorted in three dimensions. Using geometric morphometric methods and 46 landmarks we characterised the skull shape of 17 species of sea turtle representing all seven extant species and ten extinct species. These species were categorised by clade (taxonomic group) and geologic age. With these data, we generated a cranial morphospace for sea turtles. We found a strong phylogenetic signal among skull shape. We also found that extant hard-shelled turtles (Cheloniidae) occupy a comparatively small amount of the morphospace such that sea turtles had greater skull shape disparity in the past. The enigmatic extinct clade Protostegidae showed the greatest skull disparity among the sampled species despite being represented by just two species. Inclusion of further species in future are likely to increase this disparity further still. Within total-group Cheloniidae, stem- and crown-cheloniids had skull shapes which were distinct from each other with the later having skulls that were generally taller and compact rather than shallow and elongate. The taller skull shape enables jaw muscle arrangements with greater mechanical efficiency and thus greater bite force capacity. This trait may have enabled the crown-group taxa to access a wider variety of food items than the stem-group taxa. Simultaneous examination of the living and extinct species revealed broad scale evolutionary differences that may not have been detectable by examination of each group individually.

INTRODUCTION

The fossil record is vital for the understanding of morphological variation because extinct members of a group often show morphological disparity that is outside the range of variation seen in the modern assemblage (Goswami *et al.* 2011; Fritz *et al.* 2013; Benton 2015; Condamine *et al.* 2016; Foth *et al.* 2016; Holt *et al.* 2020). This additional disparity is important for illustrating the morphological and adaptational potential of a group and how they can adapt to ecological conditions including those that do not currently exist (Jackson and Erwin 2006; Goswami *et al.* 2011; Mitchell 2015). Measuring morphological variation across evolutionary time can reveal macroevolutionary patterns within a group that can be undetected when observing either just the modern or extinct species separately (Finarelli and Flynn, 2006; Fritz *et al.* 2013; Benton 2015; Law 2019; Felice *et al.* 2021). Such studies can reveal both evolutionary interactions with a changing environment (Silvestro *et al.* 2018; Siqueira *et al.* 2019; Holt *et al.* 2020) and suggest significant mechanisms and processes driving morphological diversification such as ontogenetic variation (Wilson and Sánchez-Vilagra 2011; Esquerré *et al.* 2017; Jablonski 2020). Adequate sampling of extant species should improve interpretations of ecological interactions (Lee and Yates 2018; Navalon *et al.* 2019; Bright *et al.* 2019). Whereas inclusion of extinct species provides data across time that might show interaction with climatic or tectonic events (Merideth *et al.* 2011; Stubbs *et al.* 2016). Therefore, to meaningfully examine macroevolutionary patterns in morphological variation data from both extinct and extant taxa are necessary.

Geometric morphometric analysis is a powerful tool for analysing morphological variation (Claude *et al.* 2004; Jones 2008; Sherratt *et al.* 2014; Foth *et al.* 2016; Esquerré *et al.* 2017; Morris *et al.* 2018; Gray *et al.* 2019). It involves use of landmark coordinates to quantify anatomical phenotype and enables comparison among specimens of different growth stage,

ecology, or clade to identify significant differences that might reveal important macroevolutionary patterns (Claude *et al.* 2004; Adams 2014; Gray *et al.* 2019). Geometric morphometric can be applied to both extant and extinct species. However, taphonomic processes, such as breakage and distortion, can obscure the anatomy related to landmarks (Adams *et al.* 2013; Ferreira *et al.* 2015; Godoy *et al.* 2018). This problem is why there are few largescale morphometric datasets for extinct groups, particularly using 3D models. Nevertheless, there are ways to overcome it. Fossils can to some extent be digitally restored (Lautenschlager 2016; Moya-Costa *et al.* 2019). Mirroring can be used to represent missing landmarks in symmetrical specimens (Morris *et al.* 2019; Godoy *et al.* 2018; Weisbecker *et al.* 2019). Regression analyses based on a comparative dataset can also be used to infer missing landmarks by estimating the mean coordinates for those landmarks according to the rest of the sample (Arbour and Brown 2014). These techniques increase the number of fossils that can be included in an analysis and thus improve our ability to examine the evolution of shape across time (Arbour and Brown 2014, Bhullar *et al.* 2016; Foth *et al.* 2016). Even with these available techniques specimens with minimal distortion or fracturing are most preferable. In this regard sea turtles are an excellent group to use for such an analysis as they are often preserved in three dimensions with little to no distortion (Gaffney 1979; Kear and Lee 2006; Parham and Pyenson 2010; Evers *et al.* 2019).

Sea turtles have an extensive fossil record extending back to the Early Cretaceous (Gaffney 1979; Hirayama 1998; Parham and Pyenson 2010; Tong *et al.* 2012; Cadena and Parham 2015; Gentry 2017; Weems and Brown 2017). Due to their often shallow water habitat and robust construction, sea turtle fossils are abundant in many fossil deposits across the world. Sea turtle fossils are found on every continent and represent the last 113 million years, a testament to the success of the group (e.g, Gaffney 1979). They are the only marine reptiles

to have persisted from the cretaceous, surviving the KPg extinction (Pyenson *et al.* 2014). Through the Cenozoic they have survived dramatic global temperature shifts such as the Eocene thermal maximum (Turner *et al.* 2017), the Eocene-Oligocene extinction (Ivany *et al.* 2000), the global cooling after the Mid-Miocene optimum (Böhme 2003), and the cyclical ice ages of the past 3mya (Pimiento *et al.* 2017). There are two living families of sea turtles, Cheloniidae and Dermochelyidae (Duchene *et al.* 2012; Evers *et al.* 2019). Protostegidae is a third group which went extinct during the Cretaceous of uncertain affinity (Evers *et al.* 2019). However, the majority of available evidence indicates that Protostegidae are phylogenetically distinct from the other groups. They retain some morphological features the other families lost (i.e. nasals (Joyce 2007) and likely emerged and diversified earlier (Cadena and Parham 2015; Evers and Benson 2019).

Skull anatomy is perhaps the most well studied aspect of sea turtles but there has been little systematic comparison in shape or evaluation of biology and function. There appears to have been a great deal of variability in sea turtle skull morphology in the past (Fig 1) and most morphological phylogenies are dominated by cranial characters (Gaffney 1979; Hirayama 1994; Lynch and Parham 2003; Weems and Sanderson 2014; Evers *et al.* 2019; Chatterji *et al.* 2020). This focus on cranial characters for phylogenetic analysis may be problematic given potential convergence in skull shape due to diet or other aspects of ecology. Convergence or parallelism due to similarity in shared ecomorphology has led to misleading phylogenetic inferences in other aquatic reptiles such as crocodiles (Lee and Yates 2018). Convergence among sea turtles may be related to predation on hard prey items: durophagy (Parham and Pyenson 2010). However, analyses of this problem to date have either not been quantitative or not fully sampled extant taxa. Given that sea turtles vary in adult size a further problem is identifying how much shape differences are simply

related to allometry rather than ecology or phylogenetic relatedness. Allometry and heterochrony are significant mechanisms for facilitating morphological diversity in other reptile groups such as agamid lizards (Gray *et al.* 2019) and pythons (Esquerré *et al.* 2017). So, to fully understand the evolution of skull shape and morphology in sea turtles, the relationship between size and shape throughout their phylogeny must be examined.

To date, majority of studies of skull shape in sea turtles only focus on one species (Nishizawa *et al.* 2010; Lunadorn *et al.* 2020) or are part of a broad phylogenetic sample so that patterns related to sea turtles are swamped by other sources of variation (Foth *et al.* 2016). Chapter 3 demonstrates that there is a link between diet and skull shape in extant sea turtles, and that heterochrony might be a significant mechanism for diversification in cranial shape. However, it is currently unknown if this pattern also applies to fossil sea turtles.

We aim to examine five key issues. Firstly, wish to characterise extinct sea turtle skull shape in the context of extant sea turtles and identify any key differences that exist. Second, if shape differences are apparent, we will use our results to evaluate whether such differences are related to phylogenetic relatedness, size, or ecological. As the diet of extinct species is typically unknown, inferences will rely on gross similarities to extant sea turtles for which diet is well documented (chapter 3). Third, we will measure to what extent the disparity of the cranial morphospace represented by Pan-Chelonioidea is altered by the addition of extinct taxa: we will test whether it is significantly increased. Fourth, we will measure to what extent cranial disparity has changed over time. Fifth, we will also examine to what extent the skull shape differences observed may be due to differences in allometric pattern. This study will provide a preliminary framework for further analyses of Pan-Chelonioidea as more fossils become available.

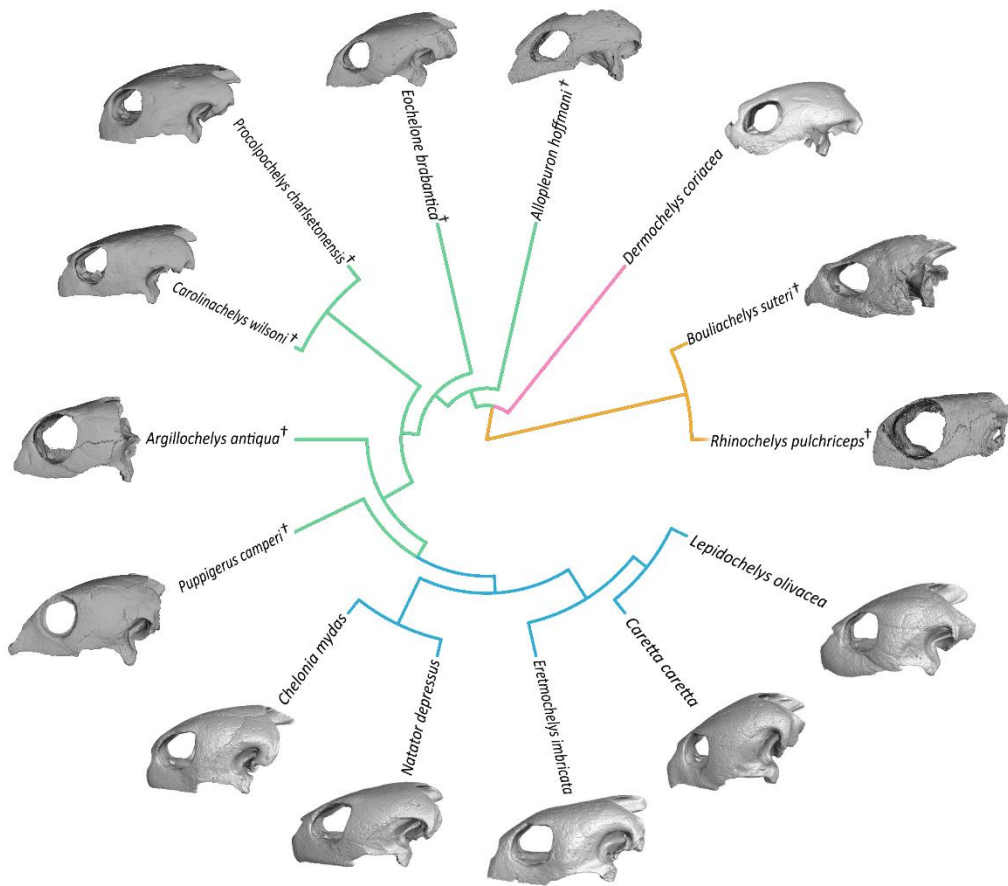


Figure 1. Unrooted phylogenetic tree of sea turtles based on Chatterji *et al.* (Chapter 40). Orange branch represent Protostegidae, Pink represents Dermochelyidae, Green represents Stem Cheloniidae, Blue represents Crown Cheloniidae. Crosses indicate extinct species

METHODS

Specimens

We sampled 79 specimens from museum collections representing all seven species of extant sea turtle, as well as eight species of extinct sea turtles. The sample of extant taxa were examined on their own in Chapter 3. Our sample of fossil specimens comprised two species of protostegid, *Rhinochelys pulchriiceps* and *Bouliachelys suteri*, and six genera of stem

cheloniid, *Allopleuron hoffmani*, *Argillochelys antiqua*, *Carolinachelys wilsoni*, *Eochelone brambantica*, *Procolpochelys charlestonensis*, and *Puppigerus camperi*. The specimens were categorised into four groups: Dermochelyidae, Protostegidae, Stem Cheloniidae, and Crown Cheloniidae. The identity of all fossil specimens has been confirmed in Evers *et al.* (2019), aside from *Carolinachelys wilsoni* and *Pr. charlestonensis* which have been confirmed in Weems and Brown (2017).

Rhinochelys pulchriceps is a small protostegid sea turtle from the cretaceous of Europe and has multiple well described cranial specimens (Evers *et al.* 2019). *Bouliachelys suteri* is medium protostegid from the cretaceous of Australia, it is known from multiple skulls (Kear and Lee 2006) though only one was complete enough to analyse in our study. *Allopleuron hoffmani* is a large sea turtle from the cretaceous of Europe (Mulder 2003). It's exact phylogenetic position is uncertain with most studies regarding it as an early cheloniid (Hirayama 1994; Evers *et al.* 2019; Chatterji *et al.* 2020) but it has been recently recovered as an early dermochelyid (Gentry *et al.* 2019). We use both placements here to examine how these alternatives affinities affect the implied evolutionary history of skull shape. *Eochelone brambantica* (Casier 1968), *A. antiqua* (König 1825), *Pu. camperi* (Moody 1974), are cheloniid sea turtles from the early to mid Cenozoic of Europe. Though each genus is known from specimens outside of Europe these are considered different species (Tong and Hirayama 2008; Grant-Mackie *et al.* 2011; Tong *et al.* 2012). *Carolinachelys wilsoni* and *Pr. charlestonensis* are large North American cheloniids from the Oligocene and Miocene. Both species have been hypothesised to be somewhat durophagous (Weems and Sanders 2014; Weems and Brown 2017).

This sample of fossil turtles was determined partly by availability but also towards establishing a representative sample for Pan-Chelonioidea. *Rhinochelys pulchriceps* and *B. suteri* represent “average” protostegids, while also being very different in size. Protostegidae have perhaps the most variable skulls shapes of any group (Hirayama 1994; Evers *et al.* 2019). These species allow us to examine the “typical” protostegid and how different they are without potentially heavily skewing the morphospace with extreme morphologies. The stem group species are sampled across the tree, with most significant clades and branches sampled. *Eochelone brabantica* is an early diverging species, likely representative of early members as well. In Chatterji *et al.* (2020) there are two distinct clades of derived cheloniid. In the clade including the crown we have sampled, *Pu. Camperi* and *Ar. antiqua* and the other major clade is represented by *Carolinachelys wilsoni* and *Pr. charelestonensis*. The latter two species are also important as representing species that are chronologically intermediate between the Eocene species (*Eo. brabantica*, *Pu. camperi*, and *Ar. antiqua*) and the inferred origin time of the crown.

To represent time differences the extinct species were categorised into three broad time bins: Cretaceous, Palaeo-Neogene, and modern. Palaeogene and Neogene specimens were grouped together due to the temporal distributions of many stem sea turtles spanning over the Oligo-Miocene boundary (Parham and Pyenson 2010; Weems and Sanders 2014; Weems and Brown 2014). We appreciate that this representation of time is limited with respect to resolution, but it remains a step forwards with respect to previous analyses.

Extant specimens included a mix of wet and dry specimens (Chapter 3). Fossil specimens were only chosen if they were minimally distorted and minimally damaged. If one side was heavily damaged the specimens were still scanned if one side was in good condition.

All specimens were scanned using X-ray computed tomography (CT)., Most specimens were scanned using a Micro CT scanner (CT, 100 – 500 micrometres, Micro CT, 9 – 50 micrometres), whereas some large extant specimens were scanned with a medical CT scanner. The reconstructed data sets had voxel size of between 9 and 330 micrometres (Sup table 1). Specimens were segmented in AVIZO 9.0 using a threshold that represented the surface appearance of the bone. Manual segmentation was sometimes required to remove matrix (fossils) or beak anatomy (extant taxa). The 3D surface models used for landmarking were created using AVIZO 9.0 Lite software with minimal smoothing. In some cases where specimens were damaged, the surface models were mirrored using the assumption of bilateral symmetry (Appendix 3 table 1) to enable subsequent landmarking.

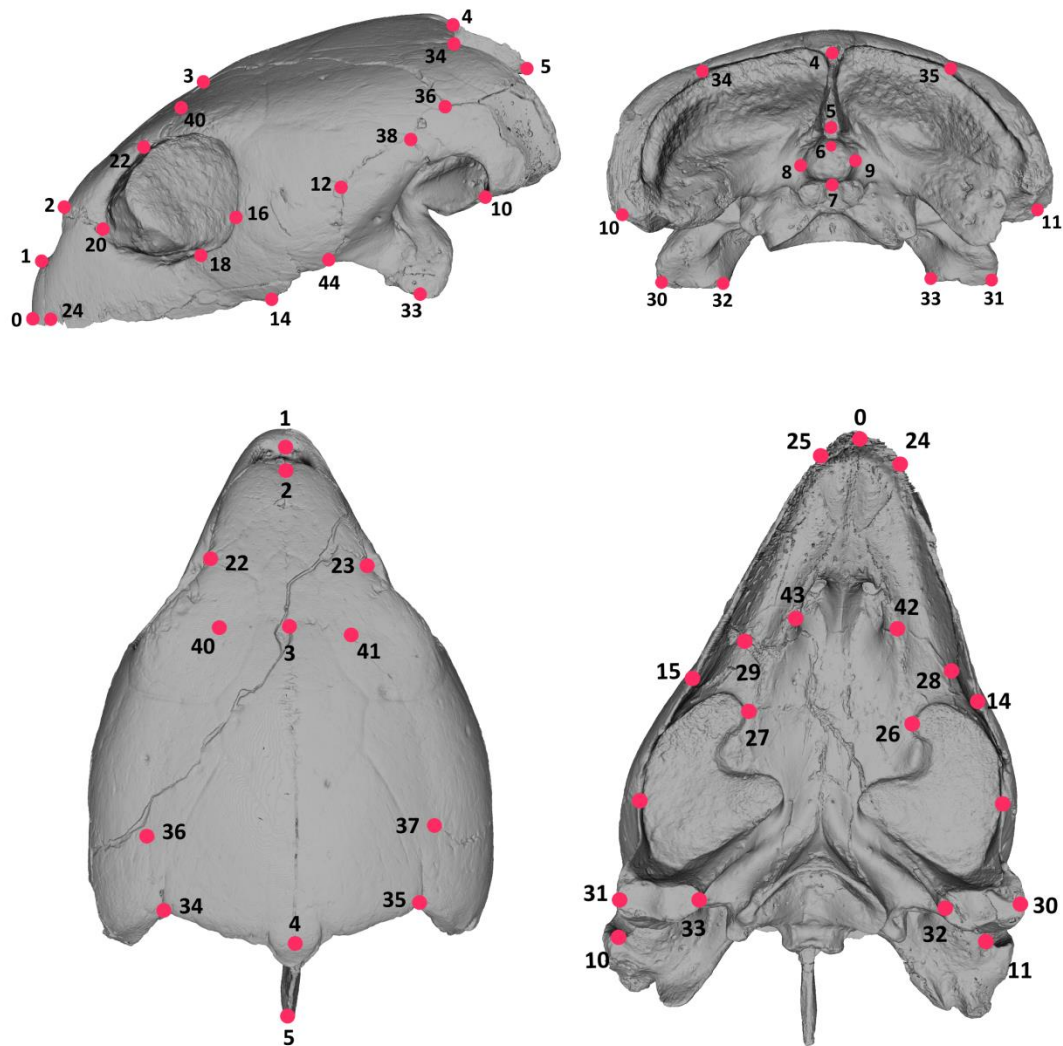


Figure 2. The 46 landmarks used in this study here placed on the skull of *Eochelone brabantica* shown in left lateral, posterior, dorsal, and ventral view.

Cranial Landmarks

The 3D cranial surface models were landmarked in IDAV Landmark v. 3.6. Forty-six landmarks (xyz coordinates) were placed at equivalent locations across each specimen (Fig 2), representing external suture junctions or distinct anatomical points, e.g., the posterior-most tip of the supraoccipital (Appendix 3). Landmarks were chosen to best characterise the entirety of cranial shape while still being applicable to every species and ontogenetic stage. These criteria meant that much of the basicranium was not landmarked because in

hatchlings this part of the skull is still represented largely by cartilage without distinct junctions. Missing landmarks were estimated using the *estimate.missing* in the package *geomorph* (Adams *et al.* 2020). This function estimates missing landmarks based on the mean coordinates for each landmark using the entire dataset, using the regression method of estimation. No more than 8 landmarks per specimen were ever inferred using this method and it wasn't necessary at all for 3 fossil specimens and 59 extant specimens.

The exported landmark coordinates were subjected to a generalised Procrustes superimposition in the R package *geomorph* function *gpagen* standardising for variation in translation, rotation, and size. Due to lack of body size data for all specimens, centroid size (the square root of the sum of squared distances of the landmarks to their centroid) of each cranium was used as a proxy for body size.

Shape Analysis

We analysed three different samplings of the dataset:

- Total dataset (n = 79)
- Adult specimens using modern species averages and extinct species largest specimen (n=14)
- Chelonioidea using modern species averages and extinct species largest specimen (n=12)

These three different samples allowed us to examine different aspects of cranial shape.

Chelonioidea were analysed separately from Protostegidae because Protostegidae are likely phylogenetically distinct and may have adapted to the marine environment independently (Gentry *et al.* 2019).

All statistical analyses were performed in the R .6.2 using packages *geomorph* and *RRPP* (Collyer and Adams 2020). Shape variation was visualised using a principal component analysis (PCA) of the Procrustes aligned coordinates, using the function *gm.prcomp*. To interpret the variation described by the major axes we used a combination of thin-plate spline deformation grids and vector analysis.

To test for a relationship between size and shape we used the phylogenetic generalised least squared method (*procD.pgls*). This function performs an ANOVA within a phylogenetic framework assuming a Brownian model of evolution (Adams 2014; Adams and Collyer 2015). With this method data points are not treated as phylogenetically independent (Adams 2014). However, this technique normally relies on species being either represented by a single set of coordinates or an aggregate mean for each phylogenetic tip (Prevosti *et al.* 2012; Püschel and Sellers 2015; Wang *et al.* 2021). Since our data are multiple individuals aligned along ontogenetic trajectories of individual species, implementations currently available need a small modification to be operable. This is further complicated by lack of a strong and robust phylogenetic tree for fossil taxa (Evers *et al.* 2019; Chatterji *et al.* 2020; Chapter 4). We created a tree file based on the phylogenetic tree found in Chapter 4 where each species was represented by a soft polytomy consisting of all their individual specimens, such that the phylogenetic relatedness can be considered while retaining the data structure (e.g., Sanger *et al.* 2013). The validity of phylogenetic comparative methods on groups with a small number of taxa, as is the case in sea turtles, is also unclear (Blomberg *et al.* 2003; Adams 2014). Therefore, we also conducted a Procrustes ANOVA which does not account for phylogeny (using *procD.lm*) for all analyses. In both cases, we evaluated whether a common ontogenetic allometry model or a species unique allometry model better explained the data for each dataset. This was done by comparing ANOVAs of each model with the

NULL assumption being that they share a common allometry. The relationship between shape and phylogenetic group was also assessed using these methods. To assess the strength of evolutionary allometry, species averages of the adult data were calculated and the relationship between shape and size was tested using a PGLS and the tree found in chapter 4 (*procD.pgls*). As the ontogenetic conditions of the extinct taxa were uncertain we used the largest specimen. For most species this was at least comparable in size to the largest reported specimens for each species. There are larger representatives for the genera *Puppigerus* (Tong *et al.* 2012) and *Argillochelys* (Tong and Hirayama 2008) found in Africa, however these have been assigned to different species.

We also ran the tests assessing allometry on a highly reduced dataset containing only *Ca. caretta*, *Ch. mydas*, *D. coriacea*, *Pu. camperi*, and *R. pulchriceps*. This subsampling reduced the stark difference in sample size between phylogenetic groups to see if the allometric patterns remain consistent. A residual randomisation procedure with 10,000 iterations was used to assess statistical significance for all tests.

We assessed the morphological disparity between phylogenetic and temporal groups using the *morphol.disapirty* function of *geomorph*. This function estimates the disparity of a group as their Procrustes variance using residuals of a linear model fit.

Phylogenetic signal was assessed to assist in determining if phylogenetically distinct species converged morphologically. To assess the phylogenetic signal, we used the *physignal* function, which assumes a Brownian motion model of evolution. This function estimates phylogenetic signal using a generalisation of Blomberg's K –statistic for high dimensional and multivariate data (K_{mult}) (Adams 2014). The phylogenetic tree used was the tree recovered in Chapter 4 (Fig 1.). We ran this test on both adult datasets. This was done

because protostegids have significantly different skull anatomy to other sea turtles that has the potential to skew the shape data and might obscure some shape data that would otherwise be significant for the other phylogenetic groups. For these two datasets we ran our analyses using two different phylogenies, one where *A. hoffmani* is treated as a stem cheloniid (as suggested in Evers *et al.* 2019; Chatterji *et al* 2020) and one where it was treated as a dermochelyid (as suggested in Gentry *et al* 2019).

RESULTS

Shape: Total group (n=79)

The first six PC axes account for a total of 66.69% of all shape variation (Fig. 3-4) with all other PC axes contributing for less than 5% each. The greatest source of variation PC1 (23.66%) is characterized by the size of the posterior skull region, in particular the size of the supraoccipital crest, as well as the size of the orbits and foramen magnum (Fig. 3, 5). High scores for PC1 are characterized by proportionately large orbits foramen magnum, and a proportionately small posterior skull region. Low PC1 scores are characterized by proportionately small orbits and a proportionately large posterior skull region. There is a general increase in specimen size from high to low PC1 scores. Notable exceptions include *Dermochelys coriacea* and *Allopleuron hoffmani* as both species are much larger than other species at similar PC1 scores.

PC2 (14.01%) is characterized by the height of the mandibular condyle and height of the premaxilla, and the shape of the orbits (Fig 3). Low PC2 scores have proportionately tall mandibular condyles, tall premaxilla and oval orbits (rather than circular). The only species with low PC2 scores is *D. coriacea*. High PC2 scores are characterized by a very short mandibular condyle, shallow rostrum, and circular orbits.

PC3 (11.1%) is characterized by the size of the ventrolateral emargination, the length of the jugal, and the relative height of the skull (Fig 4). High PC3 scores have a relatively large ventrolateral emargination and relatively long jugals which extend posteriorly pushing the squamosal quadrate contact more posteriorly, they also have relatively long low skull shape. Low PC3 scores are characterized by relatively small ventrolateral emarginations, and relatively short jugals, they are also characterised by a higher and shorter skull. For PC3, crown cheloniids have lower scores, and show little overlap with other groups.

PC4 (7.1%) is characterized by the length and shape of their facial and rostral region (Fig 4). Specimens with higher PC3 scores have a more severely anteriorly tapering skull with a longer and narrower rostral region. Specimens with lower PC3 scores are characterised by shorter and rounder skulls with short blunt snouts. These extremes are characterised by *Allopleuron hoffmani* and *Chelonia mydas* respectively.

For PC4 *Ch. mydas* has distinctly lower scores than other specimens. *Allopleuron hoffmani* has the maximum scores for both PC3 and 4.

PC5 (5.8 %) reflects the length of the pterygoids: higher PC scores represent longer pterygoids and lower scores represent shorter pterygoids (Fig 6). PC6(4.9%) represents a change in the length of the jugal and height of the premaxilla and nares; high scores having long jugals with low small premaxilla and nares, and low scores having shorter jugals with taller premaxilla and nares.

Shape: Adults all (n= 14)

PC1 (22.36%) is largely defined by the difference between Protostegidae and Cheloniodea. This is characterised by the comparatively small anterior ascension of the maxilla in

Protostegidae caused by the presence of nasals and the lateral placement of the prefrontals (Fig. 7A, 8A).

PC2 (19.48%) is similar to PC3 for the total group dataset, characterised by skull height and ventrolateral emargination size. High PC2 scores are characterised by a lower skull with large emarginations and low PC2 scores are characterised by a taller skull with smaller emarginations.

PC3 (15.46%) is characterised by the height of the premaxilla and distance of the jugal from the squamosal (Fig 9). With low scores having a shallow premaxilla and a jugal distant from the squamosal and high scores having a deeper premaxilla and a jugal closer to the squamosal.

PC4 (10.05%) is characterised by the dorsal most contact of the jugal to the orbit with specimens with low PC4 scores having a more ventrally located contact and specimens with high PC4 scores having a more dorsally located contact.

Shape: Adults Chelonioidea (n= 12)

PC1 (30 %) is similar to PC3 of the total group and PC2 of the Adults data set characterised by relative skull height and the size of the ventro lateral emargination (Fig 7B, 8B).

PC2 (20.5 %) is characterised by the jugal maxilla contact, the jugal quadrate contact, and height of the nares. Low PC2 scores have a more anteriorly positioned jugal maxilla contact, a more anteriorly located jugal quadratojugal contact, and a smaller nares. High PC2 scores have a more posteriorly positioned jugal maxilla contact, a more posteriorly located jugal quadratojugal contact, and taller nares.

PC3 (11.6%) is characterised by the length of the quadratojugal squamosal contact with high scores characterized by a shorter contact whilst lower scores have a greater length of contact (Fig 10). PC4 is characterised by the relative dorsoposterior length of the palatine bones with higher scores having longer palatines and lower scores having shorter palatine bones.

The mean skull shape of stem cheloniid adults has a lower profile and is more elongate than the mean skull shape of the crown group (Fig 11).

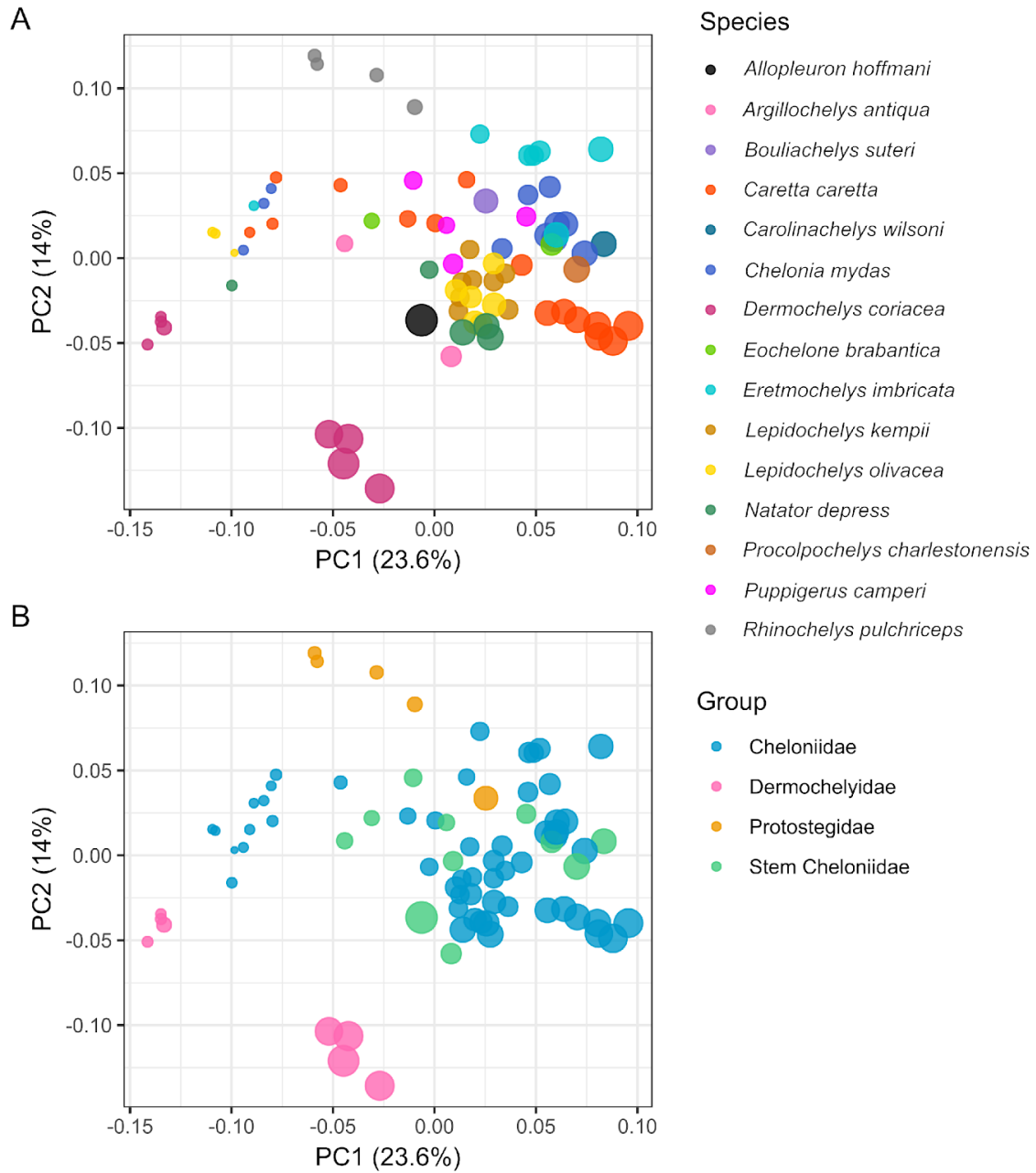


Figure 3. The PC3 and PC4 morphospace of the entire dataset. A: the different colours represent different species. B the colours represent different phylogenetic groups. The points are scaled to the centroid size of the specimen represented.

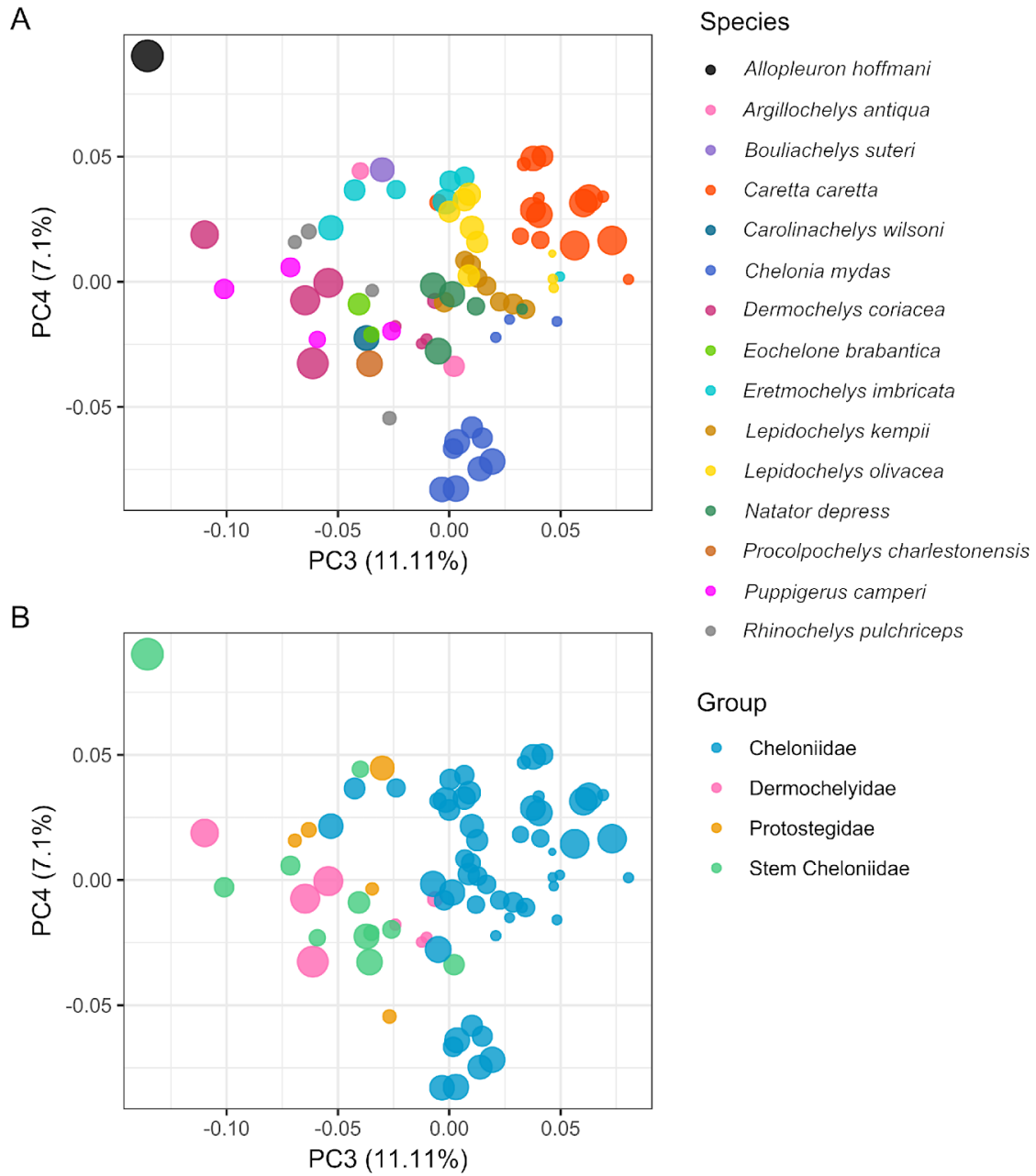


Figure 4. The PC3 and PC4 morphospace of the entire dataset. A: the different colours represent different species. B the colours represent different phylogenetic groups. The points are scaled to the centroid size of the specimen represented.

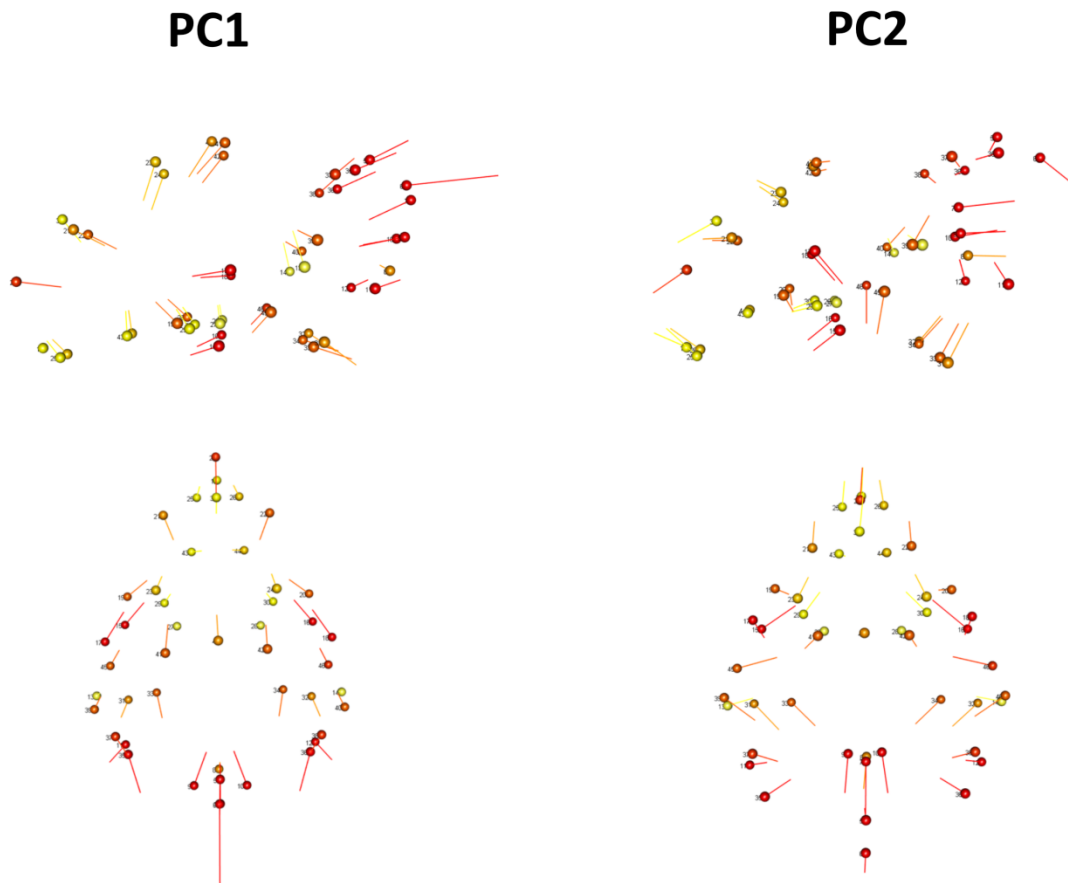


Figure 5. Heat vector map of landmark variation for PC1 and PC2. Yellow shows the landmark is a low source of total shape variation with increasing red colour represents an increasing source of total variation. The points represent the minimum value for each PC. The vector line extending from the point representing the amount, and direction of difference to the maximum for each PC

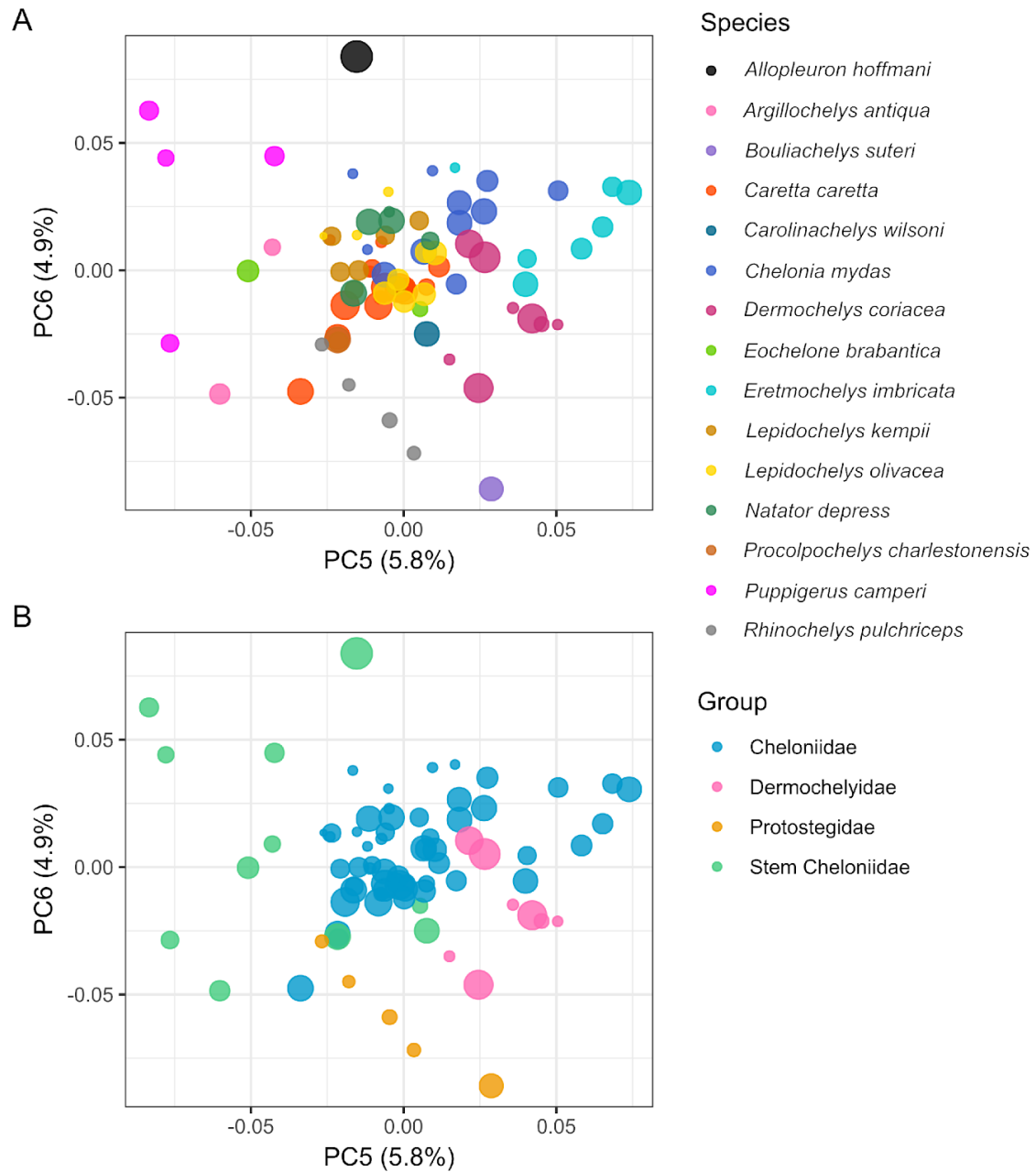


Figure 6. The PC5 and PC6 morphospace of the entire dataset. A: the different colours represent different species. B the colours represent different phylogenetic groups. The points are scaled to the centroid size of the specimen represented.

Allometry: Total group (n=79)

A significant relationship between size, shape, and species was found for both phylogenetically comparative and non phylogenetically comparative tests ($p < 0.001$) (Figs

12,13; Table 1). A unique species allometry mode (Table 2) was found to be a significant improvement over a common allometry for both phylogenetically comparative and non phylogenetically comparative tests ($p < 0.001$).

A significant relationship between size, shape, and phylogenetic group was found whether *Al. hoffmani* was considered a dermochelyid or not ($p < 0.001$) (Fig 13; Table 3). The null hypothesis of a common allometry was supported over phylogenetic group unique allometries for both phylogenetically comparative and non phylogenetically comparative tests (Table 4).

When the dataset is reduced to just *Caretta caretta*, *Chelonia mydas*, *Puppigerus camperi*, and *Rhinochelys pulchriceps* (Fig 14) there is a significant relationship with size ($p < 0.001$) and a significant interaction between shape, size, and species ($p = 0.003$).

Table 1. Procrustes ANOVA for total group allometry testing the relationship between, shape size and species using both phylogenetically comparative (*procD.pgls*) and non phylogenetically comparative methods (*procD.lm*).

<i>procD.pgls</i>	Df	SS	MS	Rsqr	F	Z	P
log(size)	1	2.50	2.50	0.24	35.53	6.84	1.00E-04
species	14	1.28	0.09	0.12	1.30	1.26	0.11
log(size):species	10	3.03	0.30	0.29	4.31	4.81	1.00E-04
Residuals	53	3.73	0.07	0.35			
Total	78	10.55					
<i>procD.lm</i>	Df	SS	MS	Rsqr	F	Z	P
log(size)	1	0.24	0.24	0.19	46.72	7.16	1.00E-04
species	14	0.64	0.05	0.50	8.78	11.44	1.00E-04
log(size):species	10	0.12	0.01	0.09	2.34	5.47	1.00E-04
Residuals	53	0.28	0.01	0.22			
Total	78	1.29					

Table 2. Model comparison between a common allometry (Null) and species unique allometries for the total group

<i>procD.pgls</i>	ResDf	Df	RSS	SS	MS	Rsq	F	Z	P Pr(>F)
shape ~ log(size) + species (Null)	63	1.00	6.76						0
shape ~ log(size) * species	53	10.00	3.73	3.03	0.30	0.29	4.31	4.8104	1.00E-04
Total	78	10.55							
<i>procD.lm</i>	ResDf	Df	RSS	SS	MS	Rsq	F	Z	P Pr(>F)
shape ~ log(size) (Null)	77	1.00	1.04	0.00					
shape ~ log(size) * species	53	24.00	0.28	0.76	0.03	0.59	6.08	14.00	1.00E-04
Total	78	1.29							

Table 3. Procrustes ANOVA for total group allometry testing the relationship between, shape size and phylogenetic group using both phylogenetically comparative (*procD.pgls*) and non phylogenetically comparative methods (*procD.lm*)

<i>procD.pgls</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	2.50	2.50	0.24	27.77	6.51	1.00E-04
group	3	0.05	0.02	0.00	0.19	-4.55	1
log(size):group	3	1.60	0.53	0.15	5.93	3.83	1.00E-04
Residuals	71	6.39	0.09	0.61			
Total	78	10.55					
<i>procD.lm</i>	Df	SS	MS	Rsq	F	Z	P
log(size)	1	0.25	0.25	0.19	26.98	6.42	1.00E-04
group	3	0.30	0.10	0.24	11.17	7.65	1.00E-04
log(size):group	3	0.09	0.03	0.07	3.32	4.59	1.00E-04
Residuals	71	0.65	0.01	0.50			
Total	78	1.29					

Table 4. Model comparison between a common allometry (Null) and phylogenetic group unique allometries for the total group

<i>procD.pgls</i>	ResDf	Df	RSS	SS	MS	Rsq	F	Z	P
shape ~ log(size) + group (Null)	74	1.00	8.00					0.00	
shape ~ log(size) * group	71	3.00	6.39	1.60	0.53	0.15	5.93	3.83	1.00E-04
Total	78	1.29							
<i>procD.lm</i>	ResDf	Df	RSS	SS	MS	Rsq	F	Z	P
shape ~ log(size) + group (Null)	74	1.00	0.74					0.00	
shape ~ log(size) * group	71	3.00	0.65	0.09	0.03	0.07	3.32	4.59	1.00E-04
Total	78	1.29							

Table 5. Procrustes ANOVA for total group allometry testing the relationship between, shape size and phylogenetic group when *Allopleuron hoffmani* is considered a Dermochelyid as is found in Gentry *et al.* (2019) using both phylogenetically comparative (*procD.pgls*) and non phylogenetically comparative methods (*procD.lm*).

<i>procD.pgls</i>	Df	SS	MS	Rsqr	F	Z	P
log(size)	1	2.50	2.50	0.24	28.02	6.53	1.00E-04
group(Gentry)	3	0.07	0.02	0.01	0.26	-3.78	1
log(size):group(Gentry)	3	1.64	0.55	0.16	6.13	3.91	1.00E-04
Residuals	71	6.33	0.09	0.60			
Total	78	10.55					
<i>procD.lm</i>	Df	SS	MS	Rsqr	F	Z	P
log(size)	1	0.03	0.03	0.12	2.51	2.33	0.01
group (Gentry)	3	0.11	0.04	0.42	3.67	3.99	1.00E-04
log(size):group(Gentry)	3	0.06	0.02	0.23	1.99	2.42	0.01
Residuals	7	0.09	0.01	0.34			
Total	13	0.25					

Table 6. Model comparison between a common allometry and a unique family allometry for when *Allopleuron hoffmani* is considered a Dermochelyid as is found in Gentry *et al.* (2019) using both phylogenetically comparative (*procD.pgls*) and non phylogenetically comparative methods (*procD.lm*).

<i>procD.pgls</i>	ResDf	Df	RSS	SS	MS	Rsqr	F	Z	P
shape ~ log(size) + group2 (Null)	9	1.00	0.51						0.00
shape ~ log(size) * group2	6	3.00	0.32	0.20	0.07	0.22	1.25	0.59	0.28
Total	13	0.92							
<i>procD.lm</i>	ResDf	Df	RSS	SS	MS	Rsqr	F	Z	P
shape ~ log(size) + group(Gentry) (Null)	9	1.00	0.11						0.00
shape ~ log(size) * group (Gentry)	6	3.00	0.06	0.06	0.02	0.23	1.99	2.42	0.01
Total	13	0.25							

Adults all

A significant relationship between size and shape was found in the adult dataset using both methods (Table 5). However, there was a significant interaction between size and phylogenetic group only for when *Allopleuron hoffmani*, was considered a dermochelyid (Table 5) for both phylogenetically comparative ($p < 0.001$) and non phylogenetically comparative tests ($p = 0.008$). For the non phylogenetically comparative ANOVA the group

allometric model was considered a significant improvement over a common allometry model ($p = 0.008$), but with a weak F statistic ($F = 1.991$) and so we can not reject the null hypothesis of a common allometric model (Table 6). Using the phylogenetically comparative ANOVA a group unique allometry model was found to be not significantly favoured over a common allometry.

Chelonioidea adults

Neither the phylogenetically comparative ($p = 0.2939$) ANOVA did not find any significant relationship with size ($p = 0.501$). The non phylogenetically comparative ANOVA found a significant interaction between size and group ($p = 0.032$) when *Al. hoffmani* was considered a dermochelyid, but the phylogenetically comparative ANOVA did not.

Phylomorphospace

Adults all

There is a significant phylogenetic signal for adult skull shape when *Al. hoffmani* is considered a stem cheloniid ($p = 0.0022$) or a dermochelyid ($p = 0.0048$). However, the K statistic is relatively weak for both phylogenetic hypotheses ($k = 0.3719$ and 0.2855 respectively).

Chelonioidea adults

There is a significant phylogenetic signal for adult skull shape when *Al. hoffmani* is considered a stem cheloniid ($p < 0.0001$) or a dermochelyid ($p = 0.0166$). The k statistic for both hypotheses is stronger than their equivalent when protostegids are included ($k = 0.5186$ and 0.3432 respectively).

Disparity

Total group

Protostegidae is found to have a significantly greater disparity in morphological shape than all other phylogenetic groups other than stem Cheloniidae (Table 7). Dermochelyids have a significantly smaller morphological disparity than the other phylogenetic groups excluding Crown Cheloniidae. Dermochelyids are found to have the smallest Procrustes variance and stem cheloniids to have the largest. When *Al. hoffmani* is considered a dermochelyid only Cheloniidae and Protostegidae have significantly different disparities from each other, retaining the smallest and largest degree of variance respectively. The Cretaceous period showed significantly more disparity than both other temporal groups (Table 8). There wasn't a significant difference between the Palaeo-Neogene and modern groups, however the Palaeo-Neogene shows a greater overall amount of Procrustes variance.

Adults all and Chelonioidea adults

No phylogenetic groups show a significant difference in morphological disparity. Within both subsets the position of *Al. hoffmani* does not change significance values. Crown Cheloniidae is consistently the phylogenetic group with the smallest degree of variance. There is no significant difference in morphological disparity between temporal groups, likely due to the small sample size. However, the pattern of descending disparity from the Cretaceous, to the Palaeo-Neogene, to the modern era is consistent.

Table 7. Disparity P values for the total group dataset based on phylogenetic grouping, with significant values in bold.

	Cheloniidae	Dermochelyidae	Protostegidae	Stem Cheloniidae
Crown Cheloniidae	1.00000000	0.76622338	0.02029797	0.01589841
Dermochelyidae	0.76622338	1.00000000	0.03379662	0.04769523
Protostegidae	0.02029797	0.03379662	1.00000000	0.58774123
Stem Cheloniidae	0.01589841	0.04769523	0.58774123	1.00000000

Table 8. Disparity P values for the total group datasets based on temporal category

	Cretaceous	Modern	Palaeo-Neogene
Cretaceous	1.0000	0.0045	0.0170
Modern	0.0045	1.0000	0.8994
Palaeo-Neogene	0.0170	0.8994	1.0000

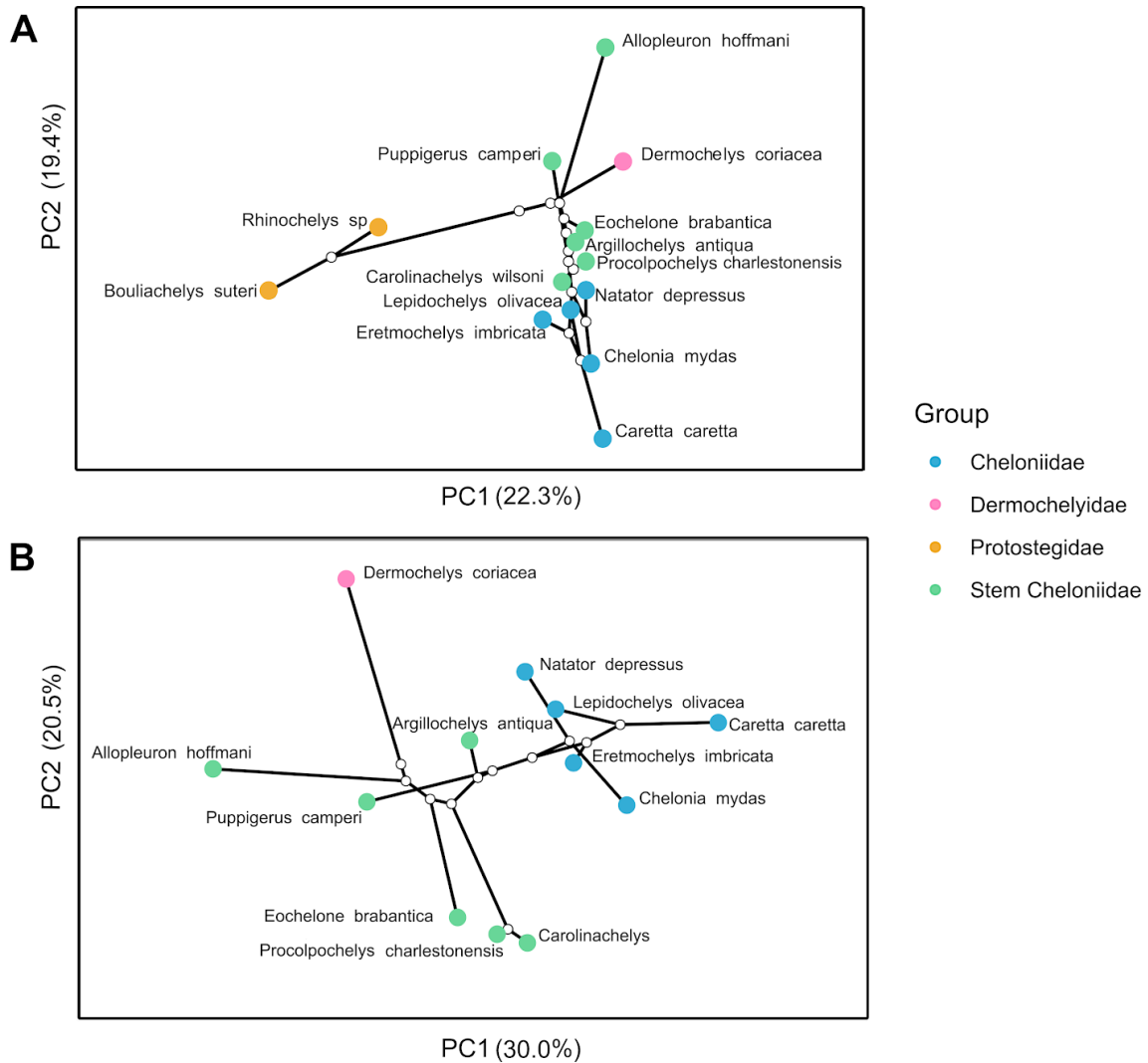


Figure 7. A phylomorphospace for the mature specimens of the dataset. B A phylomorphospace for the mature specimens of the dataset excluding Protostegidae. The different colours represent different phylogenetic groups. The white circles represent ancestral state reconstructions.

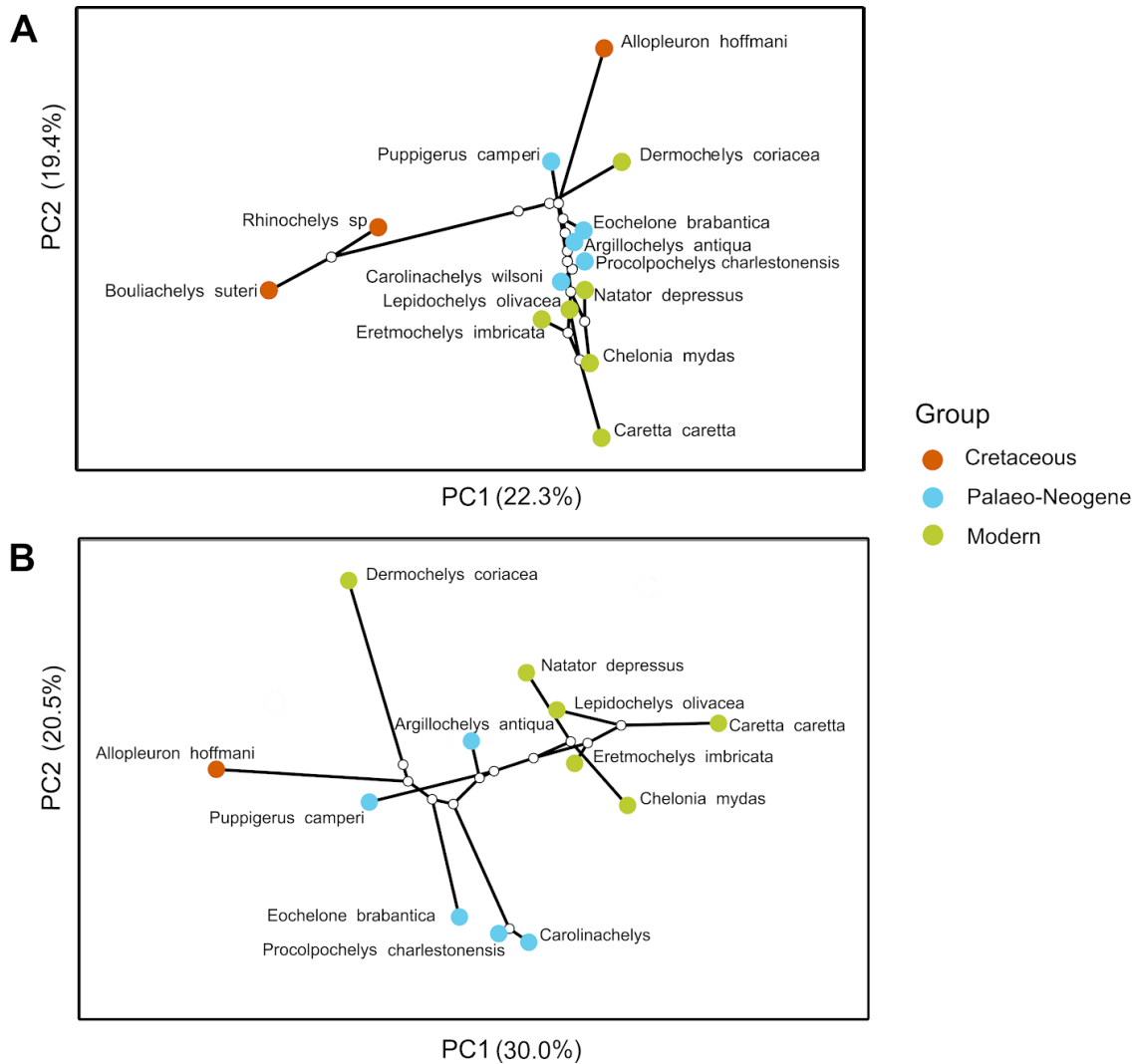


Figure 8. A phylomorphospace for the mature specimens of the dataset. B A phylomorphospace for the mature specimens of the dataset excluding Protostegidae. The different colours represent different temporal groups. The white circles represent ancestral state reconstructions.

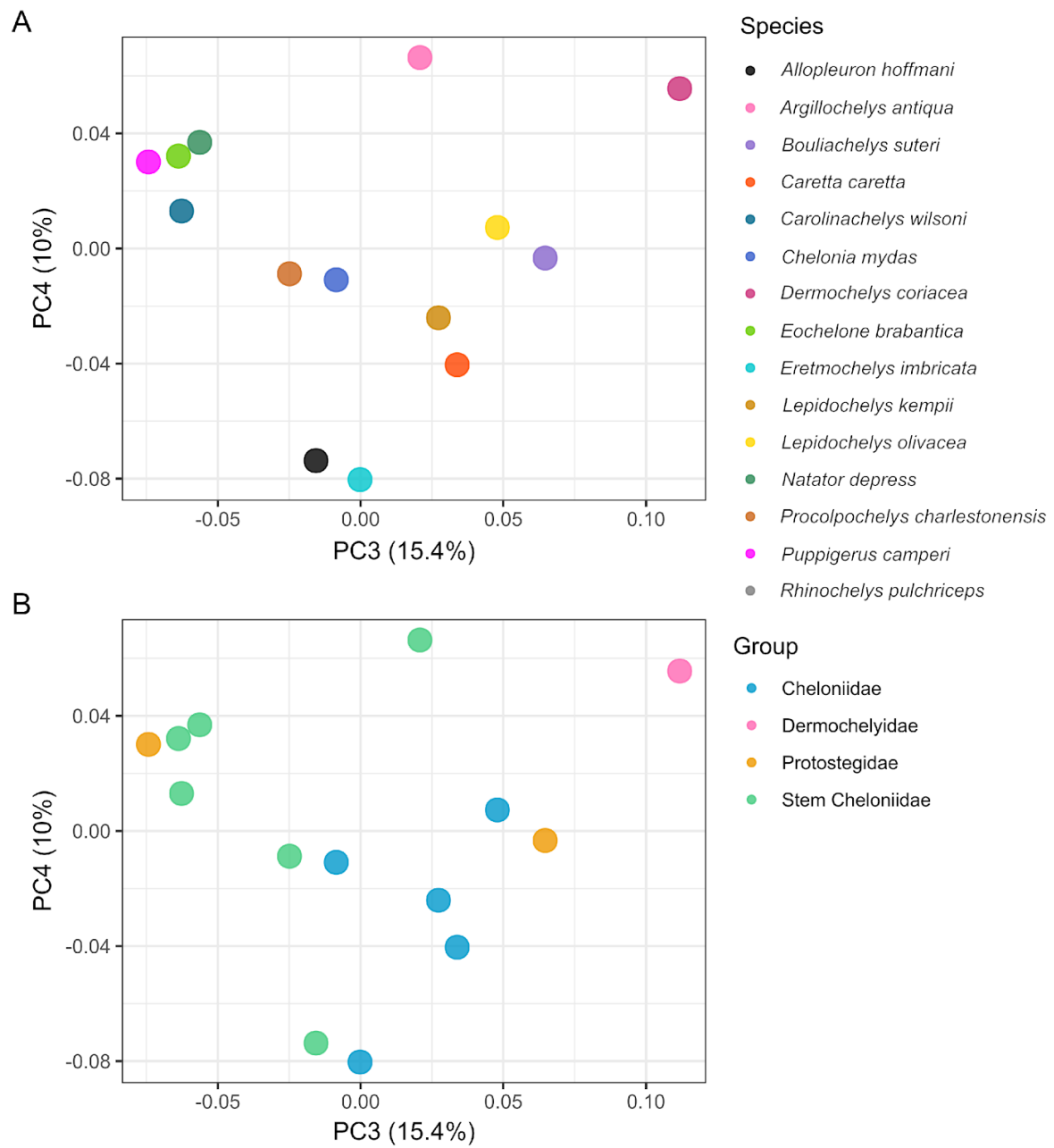


Figure 9. The PC3 and PC4 morphospace of the Total group Adults dataset. A: the different colours represent different species. B the colours represent different phylogenetic groups. The points are scaled to the centroid size of the specimen represented.

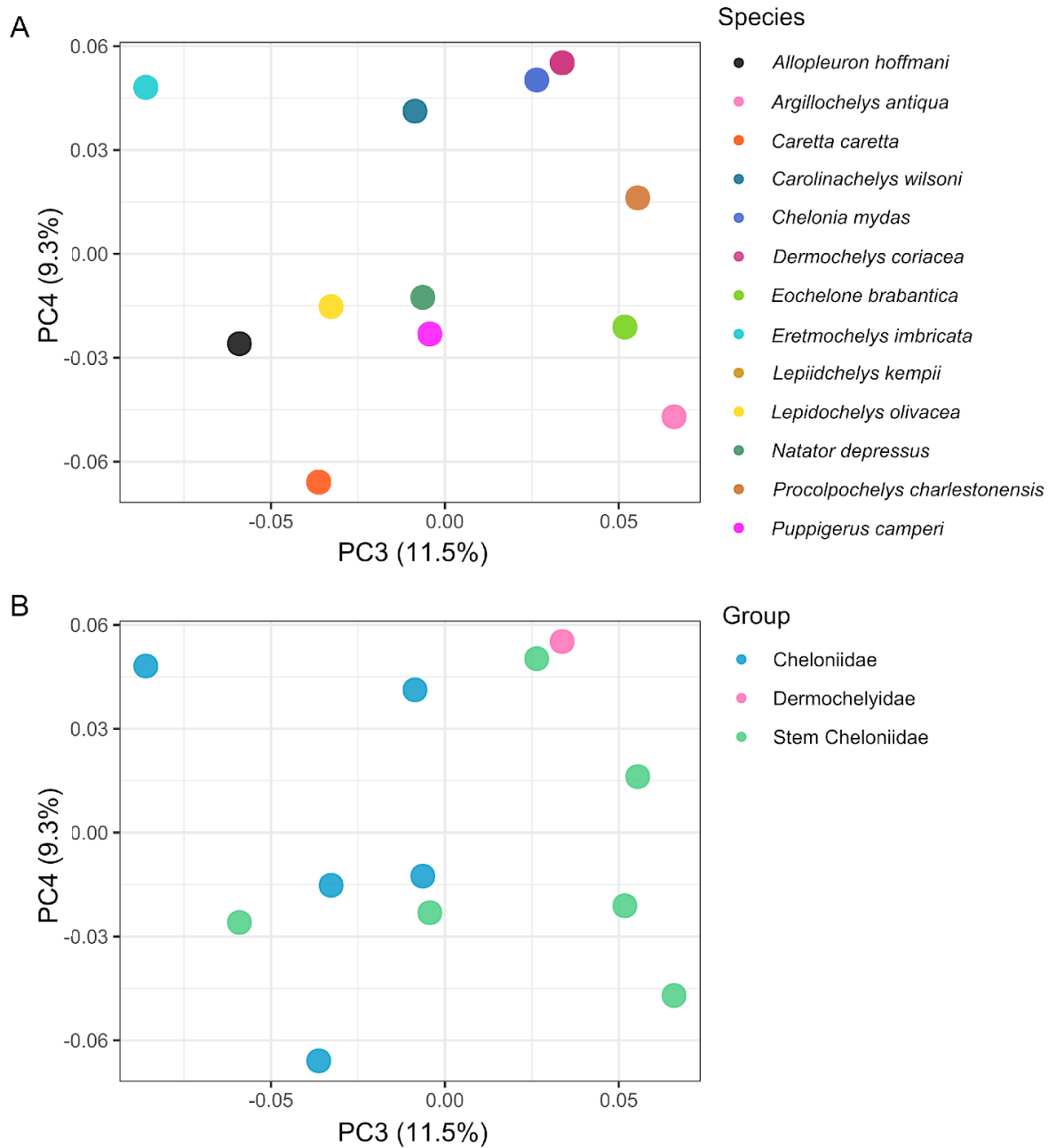


Figure 10. The PC3 and PC4 morphospace of the Chelonioida Adults dataset. A: the different colours represent different species. B the colours represent different phylogenetic groups. The points are scaled to the centroid size of the specimen represented.

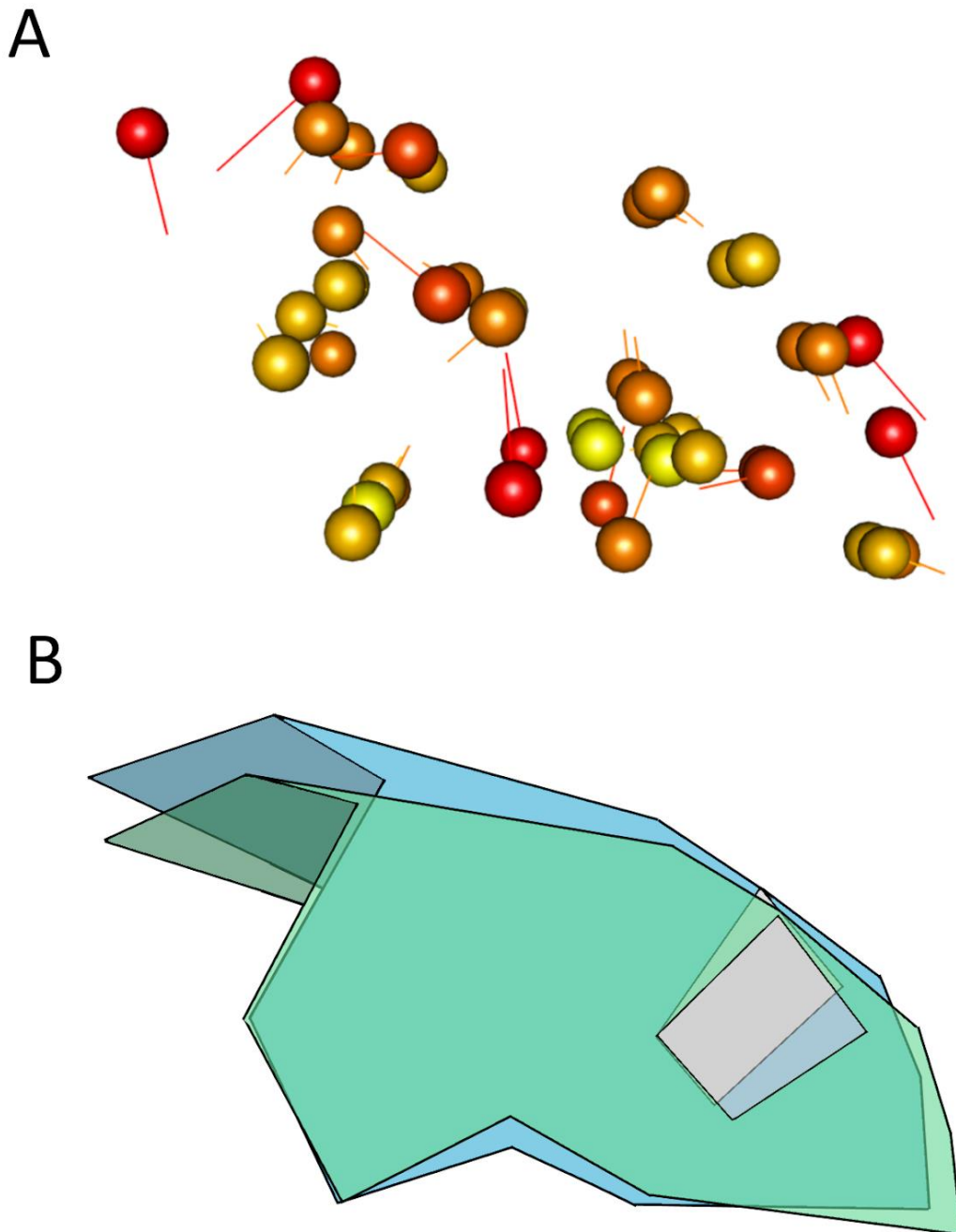


Figure 11. (A) Heat vector map of landmark variation for the mean adult crown cheloniid and the mean adult stem cheloniid. Yellow shows the landmark is a low source of total shape variation with increasing red colour represents an increasing source of total variation. The points represent the values for the mean of the crown cheloniid. The vector line extending from the point representing the amount, and direction of difference to the mean of stem cheloniids. The lines have been exaggerated by 1.5x to better highlight the most variable landmarks (B) Shows the difference in shape outline between the two means of the crown(blue) and stem (green).

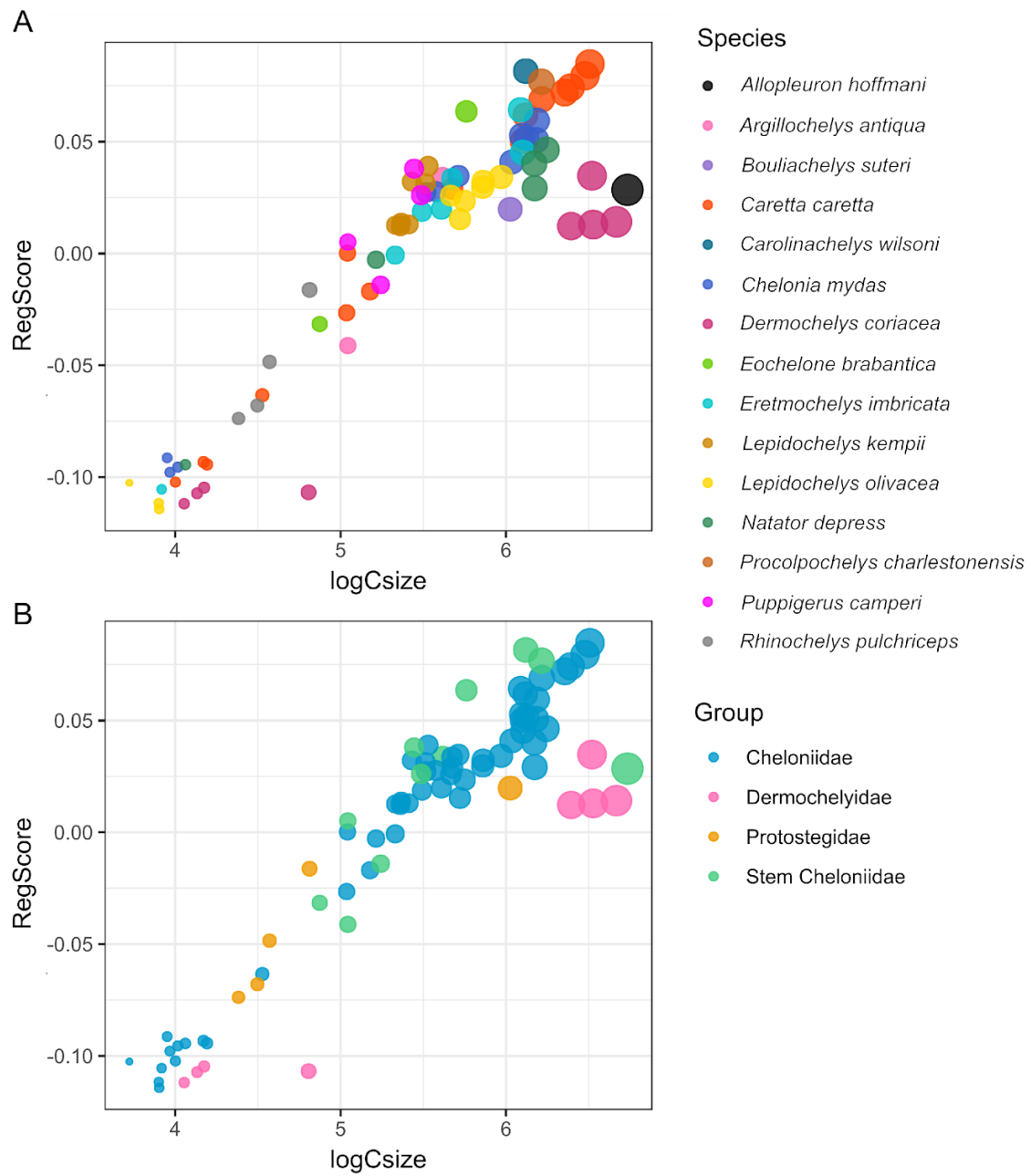


Figure 12. The multivariate regression of skull shape based on a common allometry against size plotted on log centroid size coloured based on species (A) and phylogenetic group(B).

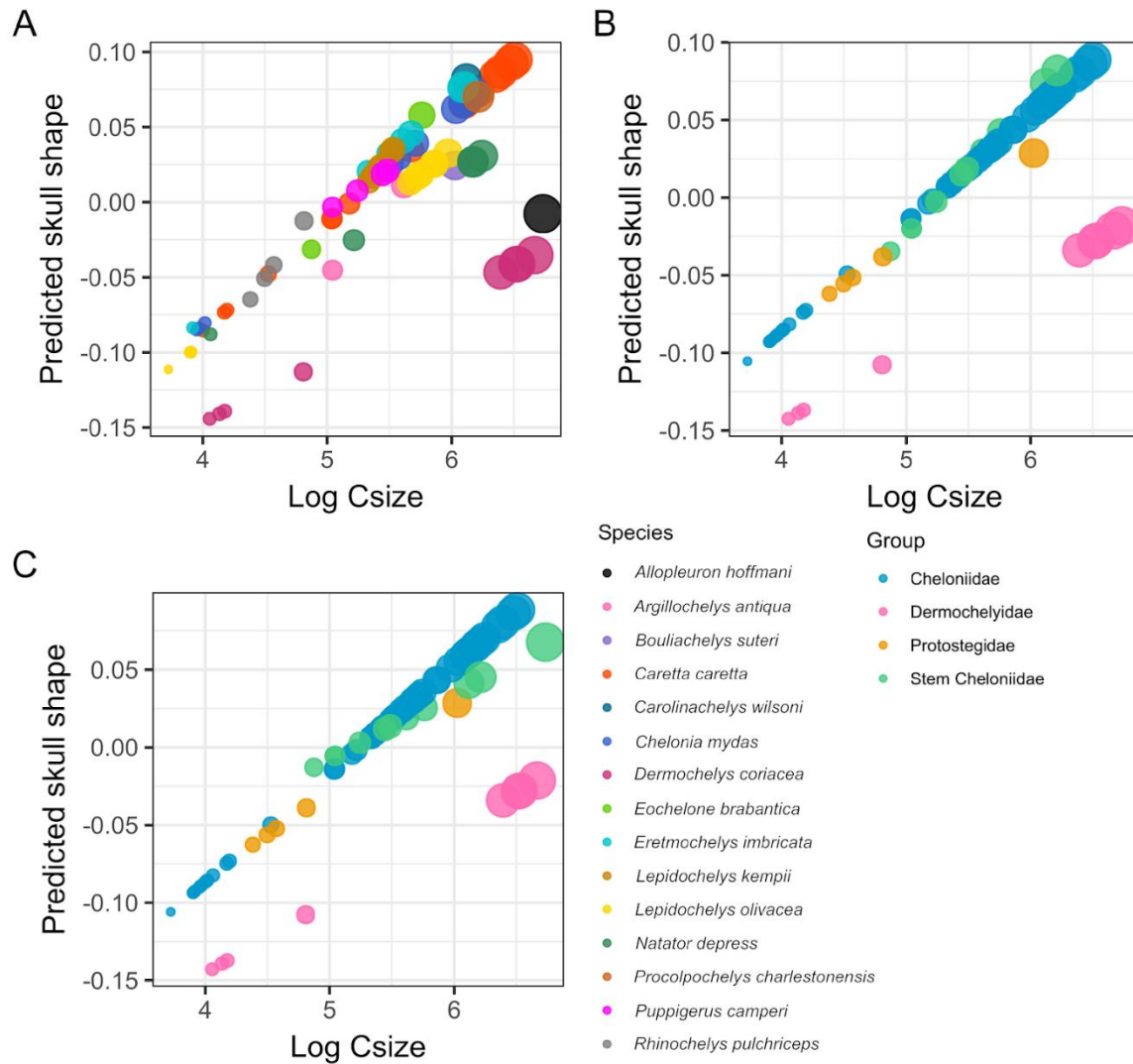


Figure 13. The predicted skull shape based on species unique allometries (A) and based on phylogenetic group allometries (B,C). B shows the phylogenetic group allometry if *Allopleuron hoffmani* is considered a stem cheloniid and C if it is considered a stem Dermochelyid.

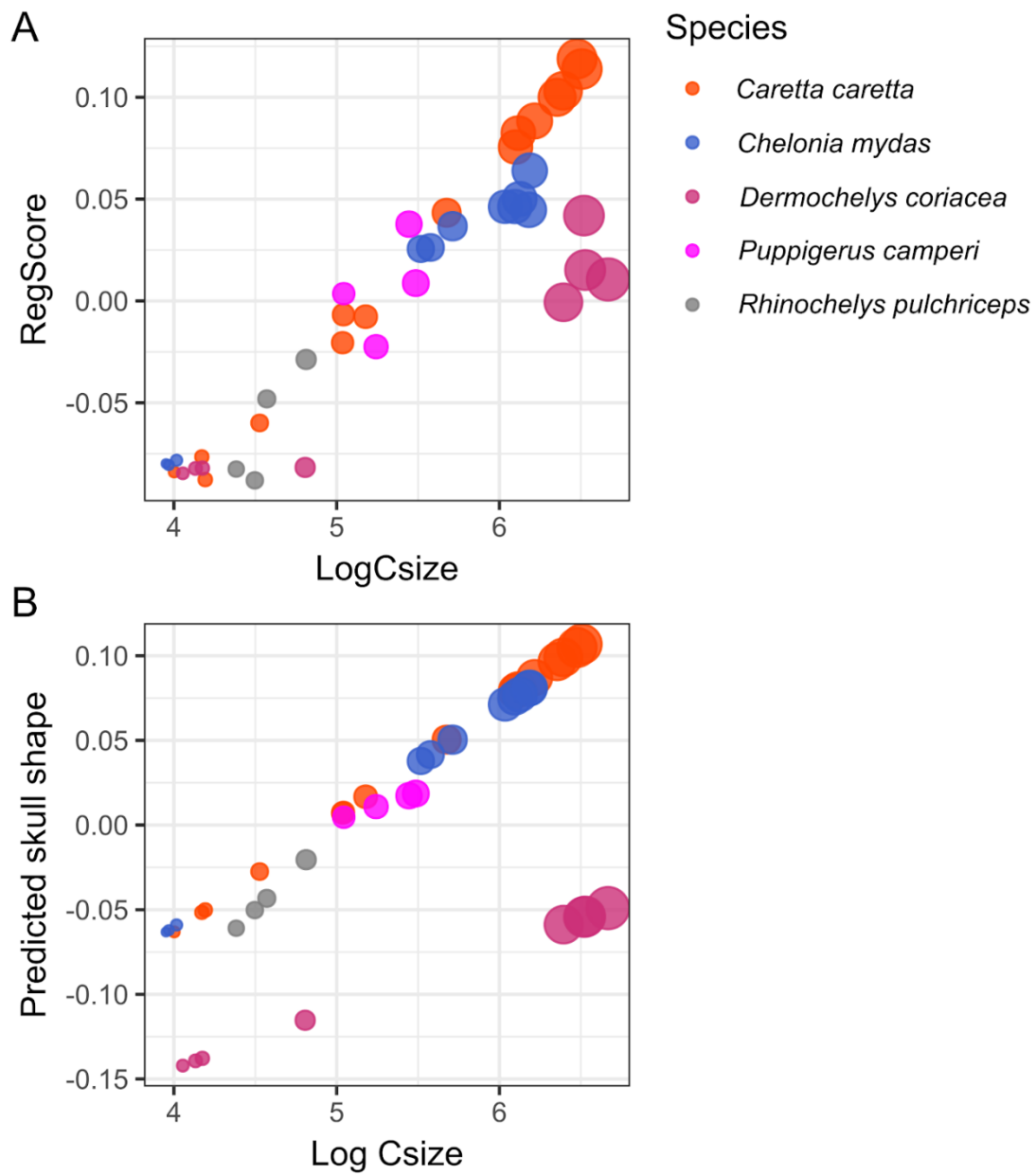


Figure 14. The multivariate regression of the reduced dataset (A) the predicted skull shape based on species unique allometries (B).

DISCUSSION

Our dataset establishes a preliminary baseline for the Pan-Chelonioidea cranial morphospace. We find that sea turtles previously had a higher degree of cranial disparity than is present today. Protostegidae have the highest degree of cranial disparity despite the small sample size, and the stem of Cheloniidae appears more disparate than the crown group. Ontogenetic patterns appear consistent across the group with the notable exception of Dermochelyidae. Skull shape variation shows clear structure related to phylogenetic relatedness, with phylogenetic groups occupying distinct areas of morphospace.

Stem cheloniids and crown cheloniids occupy distinct areas of cranial morphospace. Crown cheloniids are more uniform in their appearance having taller and more compact skulls in contrast with the more elongate crania of the stem. This might seem to be an unexpected result given previous reports of cranial convergence (Parham and Pyenson 2010; Weems and Brown 2017). Our findings fit with patterns seen for Testudinata as a whole, where convergence in skull shape is rare, and turtles with similar ecologies and diets having different skull shapes (Foth *et al.* 2016; Foth and Joyce 2016). This pattern is in contrast with other groups such as crocodyllians which repeatedly evolve similar morphotypes (slender snouted, broad snouted etc.) to exploit the same niches (Lee and Yates 2018; Morris *et al.* 2019; Felice *et al.* 2021). The morphological differences in shape between stem and crown cheloniids may reflect differences in complex interactions of habitat, behavior, and diet as is found in modern species (Figgner *et al.* 2019). Alternatively, they shared similar diets and ecologies with modern species despite differences in details of skull shape.

To find meaningful functional convergence across multiple families a different landmark scheme is likely needed. As the groups we are analysing are reasonably phylogenetically distant from one another, it is perhaps not surprising that a phylogenetic signal was stronger than a functional one. Our landmark scheme was focused on suture junctions which tend to reflect phylogenetic inheritance and can be phylogenetically important characters (Evers *et al.* 2019). A more targeted landmark scheme focused on feeding surfaces such as demonstrated in Ferreira *et al.* (2015) might be better able to recover a signal related to functional adaption. In particular, analysis of the lower jaw might yield a stronger signal reflecting functional differences (Ferreira *et al.* 2015; Weems and Brown 2017). Additionally, linear morphometric analysis of mechanically significant aspects of the jaw, such as muscle attachment points and triturating surfaces, might better distinguish feeding adaptations (Anderson 2016). Though we have demonstrated that the different phylogenetic groups did not strongly converge on total cranial shape a more targeted analysis is needed to analyse if sea turtles converged on specific feeding adaptations.

The morphological patterns among cheloniids found in this study might provide some insight into why some sea turtles survived to the present day whereas others did not. The dip in cranial disparity in the mid Miocene seen in Foth and Joyce (2016) coincided with a global extinction associated with the end of the Mid-Miocene optimum (Flower and Kennett 1994; Böhme 2003). This event involved widespread cooling and a global sea level fall. There was a decline in the area of neritic environments and therefore suitable environments for most sea turtles (Raup and Sepkoski 1984; Flower and Kennett 1994; Böhme 2003). Most stem lineages did not cross this boundary with only *Syllomus aegyptiacus* surviving before going extinct during the Pliocene. Thompson *et al.* (2021) suggests that this is around this

time, or just earlier, when the crown group started to diversify. Stem cheloniid species appear to have had a less cosmopolitan distribution than crown groups (Gaffney 1979; Lynch and Parham 2003; Bowen *et al.* 2007; Tong *et al.* 2012), which likely made them more vulnerable to extinction (Dulvy *et al.* 2003; Munday 2004; Leclerc *et al.* 2020). In addition to this, geographic isolation lends itself more readily to morphological specialization (Hoskin *et al.* 2011; Mozes *et al.* 2016). As touched on by some earlier studies (Zangerl 1980), modern cheloniids have generally more generalist skulls without some of the more extreme adaptations seen in some extinct species (i.e. *Puppigerus camperi*). This might have contributed to the survival of the crown group while other lineages went extinct, as generalists are more likely to survive times of resource scarcity (Davies *et al.* 2004; Kaiser and Boucot 2009). The taller and shorter skulls give greater mechanical advantage allowing for an increased bite force (Tseng 2013). This greater bite force possibly allowed access to a greater variety of resources, contributing to their continued survival. Here we show that shape data can be a useful tool in examining how groups respond to climatic stress and times of resource scarcity.

With few notable exceptions sea turtle species share largely similar ontogenetic trends. Given available samples, the ontogenetic trajectories of *Puppigerus camperi* and *Rhinochelys pulchriceps* are largely consistent with *Caretta caretta* and *Chelonia mydas*. The minor differences in ontogenetic trajectory between clades are not significant, however this lack of significance may be due to limited comparison. A greater number of species per clade as well as more samples for each species is likely needed to assess this sufficiently. For reasons noted above it is hard to definitively ascribe this ontogenetic pattern to Protostegidae. However, given the phylogenetic distance between *R. pulchriceps* and *Ca. caretta* (Evers *et al.* 2019; Gentry *et al.* 2019; Chatterji *et al.* 2020), it is a reasonable

assumption that this basic trend is likely ancestral to Pan-Chelonioidea. The notable exception to this ontogenetic trend is *D. coriacea*. Given the likely ancestral state this appears to be a divergence to a more paedomorphic skull shape. The other notable species is *Allopleuron hoffmani*. It clearly has a skull allometry distinct from the ancestral pattern, however the lack of samples means we do not know how this morphology was achieved, be it a divergent allometry or some other mechanism. This might be reflective of a relationship with *D. coriacea* (Gentry *et al.* 2019), but a greater sample size is needed to examine this further. When *A. hoffmani* is considered a dermochelyid the phylogenetic signal decreases. This decrease in phylogenetic signal may be supportive of *A. hoffmani* being placed within Cheloniidae as suggested by most authors (Mulder 2003; Ever *et al.* 2019; Chatterji *et al.* 2020). However, a greater similarity to more ‘standard’ sea turtle skull shape would not be unexpected in the basal dermochelyid position found in Gentry *et al.* (2019). Changes to allometry has been an important mechanism in species and morphological diversity (Esquerré *et al.* 2017; Gray *et al.* 2019; Morris *et al.* 2019), as has been demonstrated for modern sea turtles (Chapter 3), so, a greater understanding of ontogenetic allometries of extinct species is an important step in the bettering our understanding of the evolution of modern groups.

Though our sample size for Protostegidae is limited it still allows us to better understand protostegid skull shape, and how other protostegid species might fit in sea turtle morphospace. Despite having some unique aspects of morphology that separate the group from other sea turtles in most aspects of shape the two protostegid species are largely comparable to other sea turtles. The large amount of morphological disparity shown in our results suggest that the inclusion of other protostegids would have a significant effect on the morphospace. We suggest that with our knowledge of the ontogenetic shape patterns

large species such as *Archelon ischyros* and *Protostega gigas* would fit upon a largely similar allometric trajectory as Cheloniidae, not too dissimilar to what we would expect of a large individual of *R. pulchriceps*. However, the two Moroccan species *Ocephelon bouyai* (Bardet *et al.* 2013) and *Alienochelys selloumi* (de Lapparent de Broin *et al.* 2014), would likely dramatically affect the morpho space and disparity of Protostegidae. It might even change the major PC axes to represent snout length as it does in many other groups (Watanabe *et al.* 2014; Gray *et al.* 2019).

CONCLUSION

Through thorough simultaneous examination of both modern and extinct sea turtles we were able to uncover some broad scale morphological trends within the group (aim 1). We show that sea turtles' morphological disparity has generally decreased from the Cretaceous and that stem cheloniids have a greater morphological disparity compared to the crown (aim 3 and 4). The crown of Cheloniidae have less elongate and taller skull in general than their stem counterparts, likely indicating greater biting efficiency (aim 2). This skull shape along with the crown's more cosmopolitan distribution potentially aided them in persisting past the Mid Miocene optimum after which many stem lineages went extinct. We suggest that ontogenetic patterns have stayed broadly consistent within the group, with dermochelyids being the exception and shifting significantly from this early in their evolution (aim 5).

Discussion

Summary

My new investigation into the morphology of extant sea turtles (Chelonioidea) has provided a clearer view of their evolutionary history.

The re-examination of *Natator depressus* led to the identification of new characters and revision of several previous character states (Chapter 2). These data provided new morphological support for both the unification of the crown to the exclusion of all other species, and for the sister relationship between *Natator depressus* and *Chelonia mydas*. The two species are united by a shared a robust *rostrum basisphenoidale*, a squared off maxilla, secondary ridges along the maxilla and dentaries, and an enlarged jugal. Strong morphological support for these aspects of tree topology that were previously only supported by molecular data (Naro-Maciel *et al.* 2008; Duchene *et al.* 2012) is crucial for meaningful phylogenetic analysis of fossil taxa.

The addition of chronological data allowed application of techniques never before used for this group, such as Bayesian total evidence tip-dating. My analysis found strong support for a basal position for Protostegidae, corroborating the work of Gentry *et al.* (2019), and a unification of Dermochelyidae and Cheloniidae to the exclusion of all other groups (Chapter 4). This position for Protostegidae suggests an independent incursion into the marine environment, and a convergence to a marine adapted morphology with Chelonioidea. The new topology for stem cheloniid sea turtles also suggests a biogeographic split between two clades of cheloniid which emerge from the Eocene. My phylogenetic results provide a morphologically better supported foundation for the exploration of the group's evolutionary history (Parham and Pyenson 2010; Cadena and Parham 2015; Weems and Brown 2017; Evers and Benson 2019; Evers *et al.* 2019; Gentry *et al.* 2019).

The quantitative analysis of skull morphology has shed light on the possible mechanisms of morphological diversification within the crown (Chapter 3). It is the first such study to examine and compare the ontogenetic shape changes in sea turtles from hatchling to adults and shows that much of the shape variation present in the skull of extant cheloniids can be explained by shifts in allometric trajectories. In particular, the skull shape of *Dermochelys coriacea* is highly paedomorphic, and surprisingly, though to a lesser extent, so is the skull shape of *N. depressus*. By contrast, the skulls of *Caretta caretta* and *Lepidochelys kempii* are peramorphic. Much of this variation can be associated with the dietary specializations of these species.

The examination of skull shape in fossil sea turtles (Chapter 4) shows a significant phylogenetic signal in cranial shape. In particular we find that crown cheloniids have a distinct skull shape from stem species. Though superficially similar in appearance to much of the stem, the crown clustered together consistently in a morphospace characterised by a skull with a tall and expanded adductor chamber. Stem cheloniids in contrast show a greater variety in skull shape but are generally characterised by having a lower, more elongate skull than the crown. Therefore, although sea turtles today pursue a wide range of dietary niches associated with variation in their skull shape (e.g. posterior skull size, snout length), they represent only a fraction of the morphospace occupied by all previous sea turtles.

Major findings

The major findings of this research thesis include:

- Protostegidae are a distinct radiation from chelonioid sea turtles and are the least nested group of Pan-Chelonioidea. They represent an independent radiation of marine turtles.
- There is evidence for distinct and geographically separated radiations in the stem of cheloniid sea turtles which are associated with the Old and New World.
- Crown Cheloniidae seem to have emerged from the Old World branch more recently than previously thought, after the Mid-Miocene Optimum (Fig 1). The juvenile pelagic life phase may be unique to crown cheloniids and associated with their radiation.
- Heterochrony played a significant part in the shaping of the skulls of extant sea turtles. The differences in ontogenetic allometry are associated with different diets. Peramorphosis is associated with a durophagous diet (e.g. clams, crabs) while paedomorphosis is associated with consumption of soft bodied invertebrates (e.g. jellyfish).
- Crown Cheloniids and Stem Cheloniids have significantly differing skull shape, which may have contributed to the crown's current success.

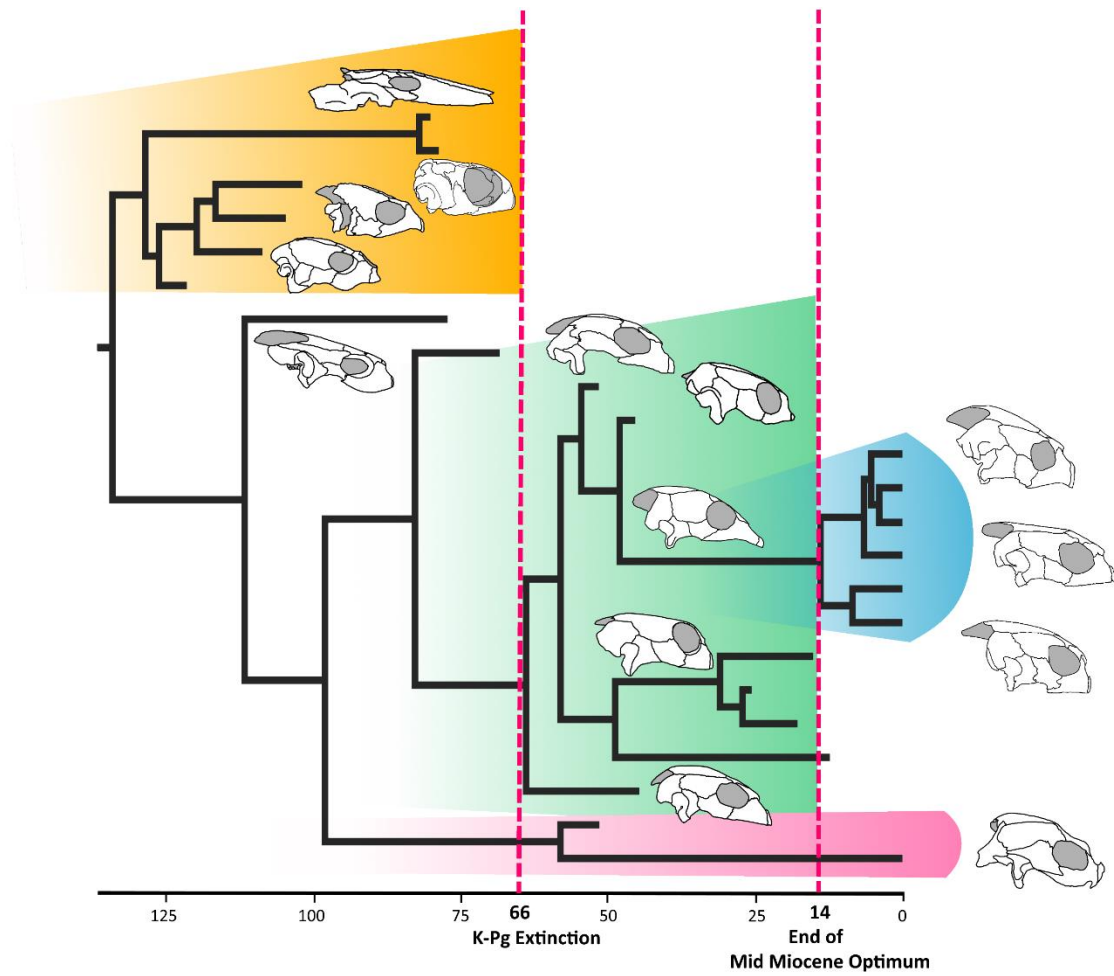


Figure 1. Chronogram of Pan-Cheloniodea displaying the skull variation across time. The different colours represent the different major groups: Orange is Protostegidae; Green is Stem Cheloniidae; Blue is Crown Cheloniidae; Pink is Dermochelyidae. The dashed pink lines represent major extinction events. Time scale in millions of years.

The modern assemblage

This study has found that modern cheloniids do not represent the remanent of an ancient lineage, but instead are a recent radiation which achieved their current success after the extinction of other cheloniid lineages. The crown cheloniids may represent an adaptive radiation of animals moving into previously occupied niches, which in this case are niches likely occupied by other lineages of sea turtle (Parham and Pyenson 2010). The pattern of groups radiating into newly empty niches is a relatively common form of adaptive radiation such as the phenotypic diversification of mammals post K–Pg extinction (Merideth *et al.* 2011) and as has been suggested for rat snake diversification into North America (Burbrink and Pyron 2010). It is also a recurring pattern among marine reptiles. Notably during the Late Cretaceous mosasaurs diversified into ecological niches previously occupied by ichthyosaurs and plesiosaurs following their extinctions and declines respectively (Stubbs and Benton 2016; Reeves *et al.* 2021). This adaptive radiation into recently vacated niches appears to have even happened previously in chelonoids as the diversification of chelonoids coincides with the extinction of protostegids (Chapter 4, Gentry *et al.* 2019). Early chelonoids' generalist and adaptively plastic skull shape likely facilitated relatively rapid radiation into more specialised dietary niches (Matzke 2009; Gentry 2017).

The subsequent modern chelonoid radiation appears to have taken advantage of the developmental efficiency afforded by heterochrony. The skull shape of crown cheloniids is differentiated from the stem by being taller and more compact. This skull shape is generally stronger and less vulnerable to torsional forces (Henderson 2003). It is also associated with a proportionally greater in-lever and thus greater mechanical advantage to biting, potentially allowing access to a greater variety of food (Jones 2008; Figueirido *et al.* 2013). From this base, remarkably simple changes to allometric patterns allowed for some

dramatic shifts in morphologies which allowed for greater dietary specialisation (Fig 2). Heterochrony is increasingly seen as one of the most significant mechanisms in phenotypic evolution (Bhullar *et al.* 2016; Esquerre *et al.* 2017; Morris *et al.* 2018; Gray *et al.* 2019). The nodes of most adaptive radiations are associated with a surprisingly small amount of genetic change (Gavrilets and Vose 2005) and heterochrony as an evolutionary mechanism allows for significant morphological change with minimal genetic change (Bhullar *et al.* 2015; Ahi 2016). Using heterochrony sea turtles were able to undergo significant phenotypic diversification despite their slow evolutionary rates (Avise *et al.* 1992; Lourenco *et al.* 2013). So, sea turtles are an excellent example of heterochrony as a mechanism for facilitating adaptive radiations.

The odd one out

A consistent theme through my research is the evolutionary distinctiveness of *Dermochelys coriacea*. Though often grouped together in studies with other sea turtles (Fujita *et al.* 2004; Foth *et al.* 2017; Thomson *et al.* 2021) this project agrees with the findings of many other studies that suggest that *D. coriacea* and Dermochelyidae by extension should be considered separately from other sea turtles (Nick 1912; Rhodin *et al.* 1981; Davenport *et al.* 2009; Jones *et al.* 2011). I suggest one marine incursion for Chelonioidea, however, post this initial point Cheloniidae and Dermochelyidae appear to have adapted to marine life in different ways. The stem of Cheloniidae consistently occupied neritic environments (Bjorndal *et al.* 1997; Parham and Pyenson 2010; Weems and Brown 2017). In contrast, dermochelyids appear to have moved to being highly pelagic early in their evolution (Nielsen 1959). This move to a pelagic environment is coupled with a series of adaptations

that are unique among sea turtles, and many of which are also unique among reptiles (e.g. brown adipose tissue (Davenport *et al.* 2009), mammalian like bone structure (Rhodin *et al.* 1981)). I show that dermochelyids have a highly divergent ontogenetic allometry, having a highly paedomorphic skull shape along with a similarly paedomorphic postcranial skeleton (Pritchard and Trebbau 1984). Other features linked with this highly pelagic lifestyle include the presence of highly vascularised epiphyses (Rhodin *et al.* 1981), an elevated body temperature (James and Mrosovsky 2004) and brown adipose tissue (Davenport *et al.* 2009), a scaleless adult condition (Pritchard and Trebbau 1984), and relatively simple cranial suturing (Goswami and Weisbecker 2013; Raselli 2018). Such simple sutures are associated with immaturity (e.g. Jones *et al.* 2011). Unfortunately, the evolutionary path from the coastal *Toxochelys spp.* to the strange pelagic giant that is *D. coriacea* is obscured by an uncertain early phylogeny and a lack of good fossil representation (Nielsen 1959; Hirayama 1997; Albright *et al.* 2003). Uncovering further details on the evolution of dermochelyids likely relies on the discovery of better fossil material of the stem, but further study can be done on the base of the chelonoid tree to attempt to determine whether any known species represent early dermochelyids. Some of this work has already been undertaken, such as the study of Gentry *et al.* (2019) which suggests that *Allopleuron hoffmani* is in fact an early dermochelyid. This line of research represents the obvious next step in sea turtle evolutionary study - trying to reveal the story of arguably the most bizarre living turtle.

The evolution of pelagic dispersal

My data suggest a dynamic evolution of dispersal ability within chelonoids. Chelonoids evolved from coastal species such as *Toxochelys spp.* and *Asmodochelys parhami* (Evers *et*

al. 2019; Gentry *et al.* 2019). These turtles had shallow skulls with large emarginations and don't show any obvious dietary adaptations. Dermochelyids likely developed a pelagic lifestyle early in their evolution as suggested by their early departure in morphology and allometry (Nielsen 1959; Chapter 5) and links between their paedomorphy and pelagic behaviors (i.e. loose suture structure Goswami and Weisbecker 2013). Unlike modern cheloniids stem cheloniids do not appear to have had cosmopolitan distributions (Bowen and Karl 2007). This trait is reflected in my phylogenetic results which suggest two geographically separate lineages of cheloniids (Chapter 3). By contrast most modern cheloniids are known to traverse large distances across open sea (Godley *et al.* 2008). Therefore, most Cheloniids appear to have converged with the entirely pelagic Dermochelyids in having a pelagic phase as hatchlings that eat a similar diet of open ocean planktonic food items: jellyfish and larvae (Bjorndal *et al.* 1997). A pelagic lifestage is a key factor in the dispersal ability of other extant sea turtles which all have a widespread distribution (Putman and Mansfield 2015). The pelagic phase in sea turtles is reminiscent of the pelagic larval phase of other marine organisms such as crabs (Jeffs *et al.* 2003; Dawson *et al.* 2011) and many coral fish (Leis and McCormick 2002), which are tied to their ability to disperse trans-oceanically (Leis McCormick 2002; Shanks 2009; Dawson *et al.* 2011; Selkoe and Toonen 2011). *Natator depressus* is an exception because it is generally coastal and lacks an ocean-going early life stage (Walker and Parmenter 1990) and has a comparatively limited geographic range (Limpus 2007). The life cycle of *N. depressus* is similar to what we might expect the cheloniid ancestral condition to be. If this hypothesis is correct we might also expect the ontogenetic slopes of stem cheloniids to more resemble that of *N. depressus* and have larger more well-developed offspring than other crown cheloniids (Chapter 3; Limpus 2007). The current state of the fossil record means that this prediction currently

cannot be rigorously tested. However, in the data shown in chapter 5, the slope for *Puppigerus camperi* is slightly less steep than that of *Chelonia mydas* or *Caretta caretta*, hinting that this species may not have had as extreme a disparity in adult and juvenile morphology as do the modern cheloniids apart from *N. depressus*.

The ability of crown cheloniids to disperse between isolated habitats and to escape increased competition from shrinking habitats during the global cooling of the mid to late Miocene (Westerhold *et al.* 2005) may have played a key role in their continued survival. The one stem cheloniid (included in the phylogenetic analysis) which survived until the Pliocene, *Syllomus aegypticaus*, is also the most widely distributed with specimens found in North America, Egypt, and Japan (Weems 1980; Hasegawa *et al.* 2005). The alpha taxonomy of this genus may require some revision, but the temporal longevity of this genus appears linked to its wide geographic distribution. Other groups such as carnivorans (Faurby *et al.* 2019) and crocodilians show a correlation between evolutionary success and dispersal ability. The success of *Crocodylus* in comparison to other genera of crocodylian has been partly attributed to their greater ability to disperse over open ocean (Nikolai and Matzke 2019). With periodic shifts in available habitat size as seen during the Mid-Miocene extinction (Flower and Kennett 1994; Böhme 2003), the ability to travel between and to other resource-rich areas would have had obvious advantages for success of living sea turtles.

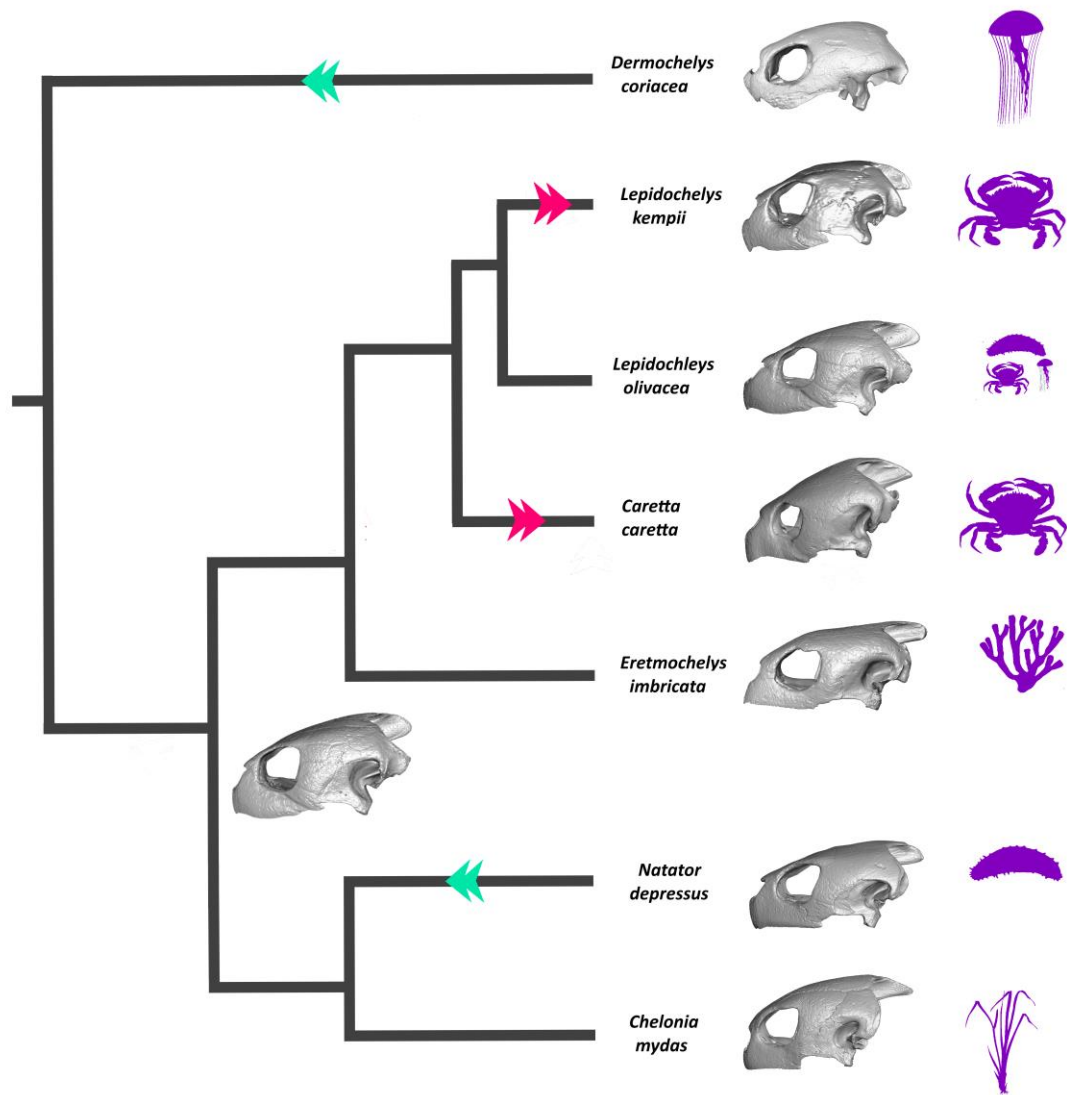


Figure 2. Cladogram of modern sea turtles. The skulls are 3D meshes of adult specimens of each species, except for *Lepidochelys kempii*, which is represented by the largest available juvenile specimen. The skull at the base of the tree is the mean skull shape of all adult cheloniids and represents a hypothetical ancestral skull shape. Arrows pointing towards the left indicate a paedomorphic ontogenetic trajectory, while arrows pointing towards the right indicate a peramorphic ontogenetic trajectory. The figures on the far right indicate adult food type, the jellyfish represents gelatinous pelagic invertebrates, the crab represents hard bodied invertebrates, the sponge represents a diet consisting of largely sponges, the sea cucumber represents a diet of soft bodied benthic invertebrates, and the sea grass represents a diet of largely plant matter. Skulls not in scale.

Marine adaptation in testudines

Testudines show multiple morphological convergences when adapting to the marine habitat. In my dataset I found support for the hypothesis that protostegids likely represent an independent incursion into the marine habitat, leading to the conclusion that the marine specialisations in protostegids and chelonoids were acquired in parallel. Protostegid forelimb adaptations are remarkably similar to chelonoids, the two clades having in common such features as a hyperextended elbow, elongate phalanges, thickened first digit, and a flattening of all forelimb elements (Evers *et al.* 2019). Other unrelated marine testudines, such as the thalassochelyidian *Thalassemys bruntrutana*, have independently achieved the same basic forelimb structure (Joyce *et al.* 2021). Though not marine, the highly aquatic *Carretochelys insculpta* has started to develop a similar “flight” adapted limb and is able to switch between lift and drag based propulsion (Rivera *et al.* 2013). As discussed in Joyce *et al.* 2021, this suggests that there is an optimum forelimb structure in testudines for a lift-based propulsion. There is a similar convergence in sea lions (Otariidae) and seals (Phocidae). Seals such as the leopard seal (*Hydrurga leptonyx*) which use forelimb-based propulsion have converged on a similar forelimb structure to the forelimb propelled sea lions (Hocking *et al.* 2021), suggesting that adaptations to a similar function from the same ancestral structure will likely converge in morphology.

Marine testudines converge with each other in multiple other aspects of morphology as well as with other marine tetrapods. Most marine testudines show morphological trends towards carapace reduction (Hirayama 1994; Cadena and Parham 2015), seen in its most extreme form in *D. coriacea* (Pritchard and Trebbau 1984), or large body size (Regis and Meik 2017; Gearty *et al.* 2018; Motani and Vermij 2021). Almost all marine tetrapods have

evolved to be significantly larger than their terrestrial relatives, a notable exception being the modern radiation of marine snakes (Motani and Vermji 2021). Interestingly, in Pan-Chelonioidea, carapace keratinous scutes have been lost at least four times, in Protostegids (Hirayama 1994; Cadena and Parham 2015), Dermochelyids (Pritchard and Trebbau 1984; Hirayama 1994), *Puppigerus camperi* (Den La Giza *et al.* 2021), and *Natator depressus* (Zangerl *et al.* 1988; Limpus 2007). A functional reason for this morphology is currently unknown, though the combination of large body size and movement being more important for protection may have reduced the need for investment in a potentially expensive structure. The development of a smooth skin is seen in multiple other groups of marine tetrapods, notably ichthyosaurs (Lindgren *et al.* 2018) and cetaceans (Reeb *et al.* 2007). This trait is likely an adaptation to increase hydrodynamic efficiency (Cozzi *et al.* 2016), as it appears unlikely that the furthest traveling and most pelagic modern species, *D. coriacea*, being scaleless is coincidental. Though other marine reptiles such as mosasaurs are not scaleless, they have small scales with structural modifications associated with hydrodynamism. (Lindgren *et al.* 2009) The numerous convergences within Testudinata associated with an invasion of the marine environment, as well as convergences with other groups of secondarily aquatic marine tetrapods, show that the dramatic shift in environment has similar selective pressure across all species leading to repeated acquisitions of similar morphotypes (Lee *et al.* 2016; Motani and Vermji 2021).

Future directions

Further morphological examination of modern taxa could be used to test my hypotheses. A greater sample size for the morphometric datasets in general would improve their statistical

power. In particular a far more complete sample of *Lepidochelys kempii* would immensely improve the study as it shares a dietary specialisation with another species, *Caretta caretta*. The findings from my shape analyses could be expanded further by increasing the breadth of ontogenetic sampling. I investigated the post-natal ontogeny of modern sea turtles but extending this analysis to include embryos may provide a strong test of my results. A geometric morphometric analysis of skull shape including embryonic individuals would allow further investigation into the origin and timing of the allometric patterns observed in my study as was done for crocodilians (Morris *et al.* 2018).

My study has shown that geometric morphometrics underwritten by a well-corroborated phylogenetic framework has been a powerful combination for revealing mechanisms of evolutionary change. The intraspecific variation between populations is another avenue to explore the evolution of skull shape and ontogeny. The morphological and ontogenetic differences between populations of sea turtles could be more thoroughly explored (Kamezaki and Matsui 1995; Kamezaki *et al.* 2003). This could potentially be used to explore potential correlations between morphology and differing local ecologies. Since heterochrony appears to have been a major evolutionary mechanism for the morphological diversification of the group, understanding shifts in ontogenetic trajectory between populations could possibly give us an idea as to how this speciation began. *Chelonia mydas agassizi* is a morphologically distinct population of *Ch. mydas* previously assigned as a distinct species (Karl and Bowen 1999). It has been proposed that this is a population in the midst of speciating (Karl and Bowen 1999; Pritchard 1999) and could be an excellent case study on the evolutionary mechanics of sea turtle morphological evolution.

Our dataset distinctly lacks a deeper evolutionary context for Dermochelyidae. Unlike the other groups this is not due to a lack of sampling but due to a lack of available data as there are virtually no known cranial remains outside of one specimen of *Eosphargis breineri* (Neilson 1959). As pointed out in chapters 3 and 5, *Eo. breineri* looks similar to *Dermochelys coriacea* despite existing 60 Ma, suggesting an early transition to this morphotype.

Unfortunately, almost nothing is known about early Dermochelyidae. Our data, as well as molecular dating data (Duchene *et al.* 2012; Thomson *et al.* 2021), suggest that Dermochelyidae and Cheloniidae last shared a common ancestor during the latter half of the Cretaceous. Therefore, the Late Cretaceous is a crucial time period to understand the evolutionary transformations which lead to the highly specialised morphology seen in *Eo. breineri* and *Dermochelys coriacea*. However, there is only one currently known Cretaceous representative of Dermochelyidae, *Mesodermochelys undulatus*, which has poor cranial remains. (Hirayama 1997). In Gentry *et al.* (2019) *Allopleuron hoffmani* was recovered as a stem dermochelyid. We found that, much like *D. coriacea*, *Al. hoffmani* showed a paedomorphic skull shape for its large size when compared to other sea turtles.

Investigation into early Dermochelyid evolution is crucial to better understand how *D. coriacea* arrived at its unique morphology. To do this we not only need to find more fossil specimens but also to thoroughly examine the evolutionary relationships of Late Cretaceous sea turtles.

As heterochrony played a significant role in the evolution of modern sea turtle skulls, a greater understanding of the allometry of the stem potentially provides invaluable information on the mechanics of morphological divergence within a slowly evolving group (Emerson and Bramble 1993; Bhullar *et al.* 2016). A greater variety of fossil sea turtles could be sampled to further explore the hypotheses presented in this thesis. Although our data

suggests that stem group cheloniids had a shallower allometric trajectories than the crown group, this result is based a limited sample and this result needs to be further explored. A greater sample of juvenile specimens would provide a greater understanding of the allometric relationships, differences between groups, and the opportunity to test some of the inferences made here (Esquerre *et al.* 2016; Morris *et al.* 2018; Gray *et al.* 2019). There are likely more samples available in some European and American institutions, however simply more juvenile specimens need to be found as well.

Including further stem taxa in our morphometric dataset, such as the heavily constructed *Erquelinnesia gosselti* (Dollo 1886) and the enigmatic *Syllomus aegyptiacus* (Weems 1980; Hasegawa *et al.* 2005), would further show the shape space explored by cheloniid sea turtles. A more complete representation of sea turtle disparity is necessary to understand changes in disparity over time and how such changes might relate to extrinsic factors such as sea level rise and global climate change. Including the earliest representatives of the modern radiation of Chelonioidea, such as *Toxochelys lateremis* or *Ctenochelys acris* (Gentry 2017), would help identify the plesiomorphic condition for the group enabling more specific hypotheses regarding their radiation.

A greater representation of stem cheloniids would also help further test my phylogenetic hypothesis of two distinct radiations within Cheloniidae., particularly species such as *Erq. gosselti* which has been previously linked with the American species but is found in European deposits. (Parham and Pyenson 2010). This greater sampling of fossils could be paired with an ancestral range reconstruction test to quantitatively assess the likelihood of this event (Wang *et al.* 2016; Gentry *et al.* 2020).

Including further fossil protostegids, such as species *Santanachelys gaffneyi*, *Archelon ischyros*, and *Ocepochelone bouyai* (Wieland 1896; Hirayama 1998; Bardet *et al.* 2013), would help identifying the range of size variation, shape disparity, and allometric trajectories exhibited by Protostegidae. This additional data would enable a more meaningful comparison to other clades of sea turtles.

Working on a morphologically conservative group such as sea turtles allows for the revelation of the large impact small and subtle changes in morphology can have. Modern techniques such as geometric morphometrics allows us to find these subtle patterns. Further work on the morphology of sea turtles may shed further light on the mechanisms and patterns of morphological evolution.

Final Conclusions

My re-examination of modern sea turtle morphology has increased our understanding of the evolution of both modern and extinct species as well as the evolutionary mechanisms that facilitated morphological diversity within the modern species. The groups' evolution is more complex than often appreciated, with multiple independent incursions into the marine environment, as well as multiple evolutions of pelagic dispersal. During the Cenozoic there were multiple lineages of sea turtle, including apparently regionally distinct evolutionary radiations. The crown of Cheloniidae is not an untouched ancient lineage but a recent adaptive radiation. The reasons for their present success are complex but appear to be tied to their ability to disperse long distances across a pelagic environment and an adaptable ancestral skull shape. They represent an excellent group to examine macroevolutionary processes and are an example of how simple changes to ontogenetic

allometry can act as effective mechanisms for adaptive radiation. There is still much about the evolution of sea turtles to explore but by re-examining what we think we know and applying new techniques we can rapidly further our knowledge of this iconic group.

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APPENDIX

The new characters found in this study for *Natator* and the other sea turtles mainly involve features of the braincase and temporal region:

1. Anterior foramen *nervi hypoglossi* posterior opening when ventral surface of braincase is horizontal: ventral to *acustico facialis* (0); in line with *acustico facialis* (1) Fig. 9.
2. Size of the two posterior foramina of the *nervi hypoglossi*: the smaller less than a half of the diameter of the larger (0); smaller half or more of the diameter of the larger (1) Fig 12.
3. Anterior process on prootic intruding into the foramen trigemini: absent (0); present (1). Fig. 9.
4. Rostrum basisphenoidale thin, long, and gracile rod: with anterior processes well away from anterior tip of rostrum (0); robust and short rod with anterior processes very close to anterior tip of rostrum (1) . (only applicable if rod shaped) Fig. 11.
5. Labial margin of maxilla: contacts jugal (0); squared off and ends ventral to jugal (1). Fig. 2.
6. Superficial jugal ridge – The superficial jugal ridge is: indistinct, no significant marginal ridge (0); no distinct ridge, but incline along margin, distinguished with texture change (1) ; distinct marginal ridge, distinct textures on either side (2). Fig. 2.
7. Shape of *hiatus accousticus*: opening roughly rectangular from medial view, the ventral portion more than three-quarters the width of the dorsal portion (0) ; differentiation between the two portions much more strongly defined, the ventral portion is half the width of the dorsal portion, the “waist” separating them pinched and narrow (1) . Fig. 9.
8. Posteroventral process of the jugal: absent (0); present, relatively small does not reach posterior to the jugal-quadratojugal margin (Fig. 2E) (1); present, large and extends beyond jugal-quadratojugal margin (2). Fig 2.
9. Extent of the overlap of quadratojugal by jugal: negligible (0); present but minor (1); present, significant overlap (2). Fig 2,
10. Orientation of the surface which provides the origin of the depressor mandibulae from the squamosal: lateral (0), posterior (1). Fig 2.

Character modifications

Referring to Evers, Serjoscha W.; Benson, Roger B. J. (2019), Data from: A new phylogenetic hypothesis of turtles with implications for the timing and number of evolutionary transitions to marine lifestyles in the group, Dryad, Dataset, <https://doi.org/10.5061/dryad.2pb356h>

Character 11: Frontal, frontal contribution to orbit: 0 = absent, contact between prefrontal and postorbital; 1 = present.

Character optimisation:

Lepidochelys olivacea changed from 0 to 1

We found that the frontal consistently contributed to the orbit in adult specimens. This is also consistent with the literature. (Gaffney 1979; Pritchard and Trebbaru 1984; Wyneken and Witherington 2001)

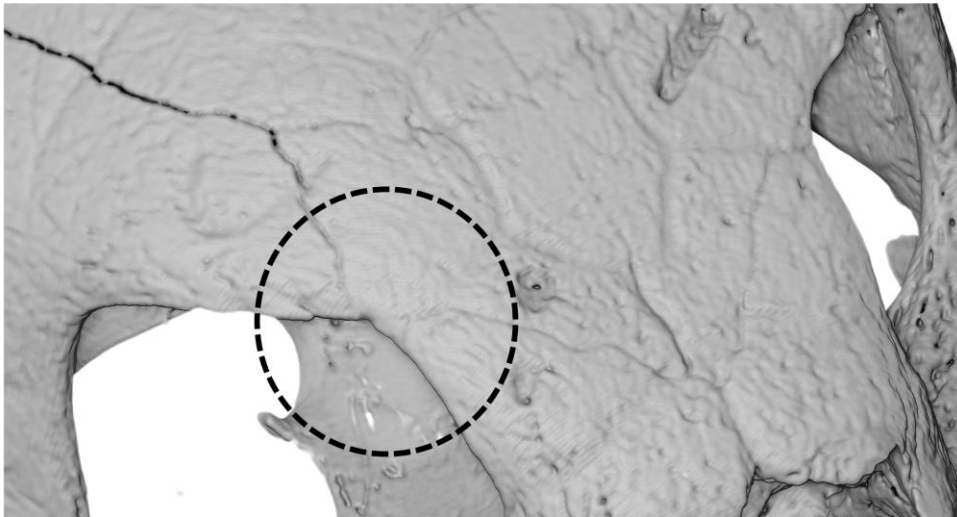


Figure 1. Character 11 coded as 1 for *Lepidochelys olivacea* NHMUK 2010.1.36

Natator depressus changed from 1 to 0

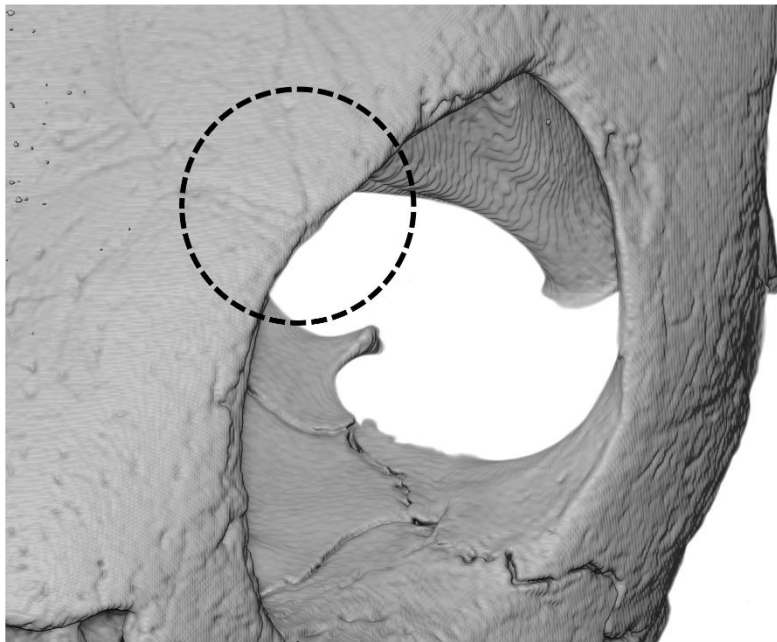


Figure 2. Character 11 coded for 0 for *Natator depressus* WAM_112123

Though the frontal approached the orbit, in all specimens examined it failed to be incorporated into the orbital margin.

This is also consistent to what it is reported in the literature (Limpus *et al.* 1988; Zangerl *et al.* 1988).

Character 75 Quadrate, anterior margin of the cavum tympanum: 0 = formed entirely by the quadrate; 1 = formed by the quadratojugal, which overlaps the lateral surface of the quadrate, reaching the anterior margin of the cavum tympanum.

Natator depressus changed from 0 to 1

We could not find a meaningful difference in the location or nature of the contact between the quadrate and quadratojugal in *N. depressus* and *L. olivacea* (Used as the example of state 1 in Appendix 1).

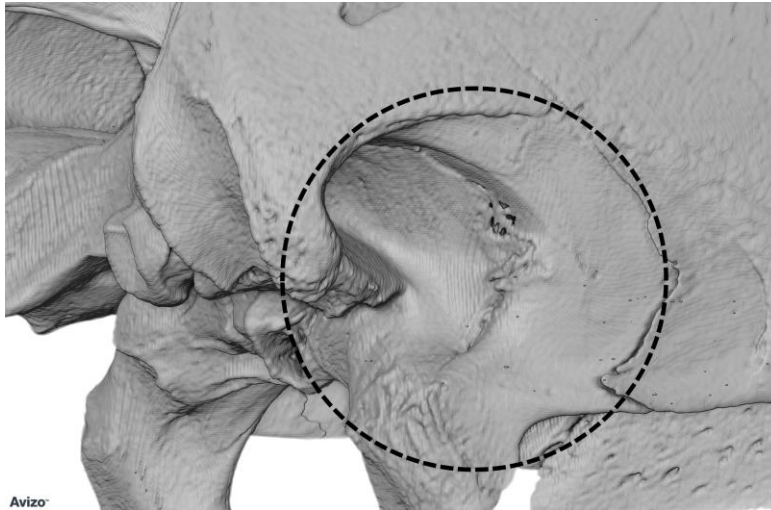


Figure 3. Character 11 coded for 0 for *Natator depressus* WAM_112123

Lepidochelys olivacea

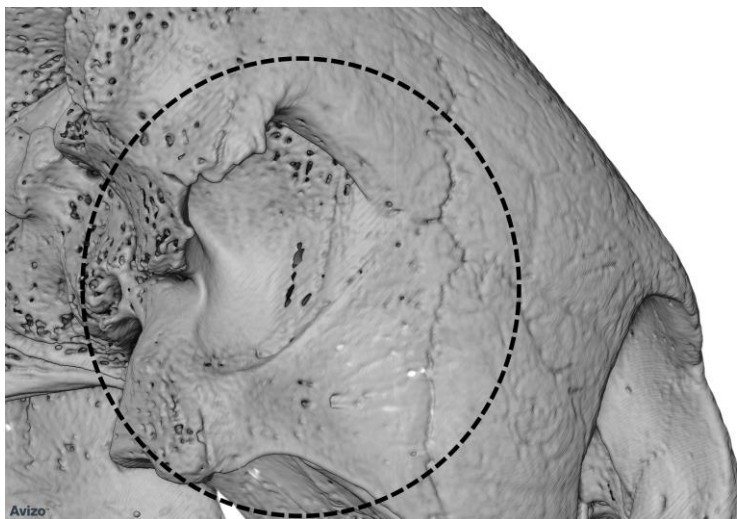


Figure 4. Character 75 coded as 1 for *Lepidochelys olivacea* NHMUK 2010.1.36

Character 100 Pterygoid, vertical flange on anterolateral margin of the pterygoid: 0 = absent; 1 = present. Zhou *et al.* (2014) & Joyce (2007: ch 67) (Pterygoid I).

Lepidochelys kempii changed from 1 to 0

Could not see meaningful difference between *L. kempii* and *L. olivacea* (used as example for state 0)

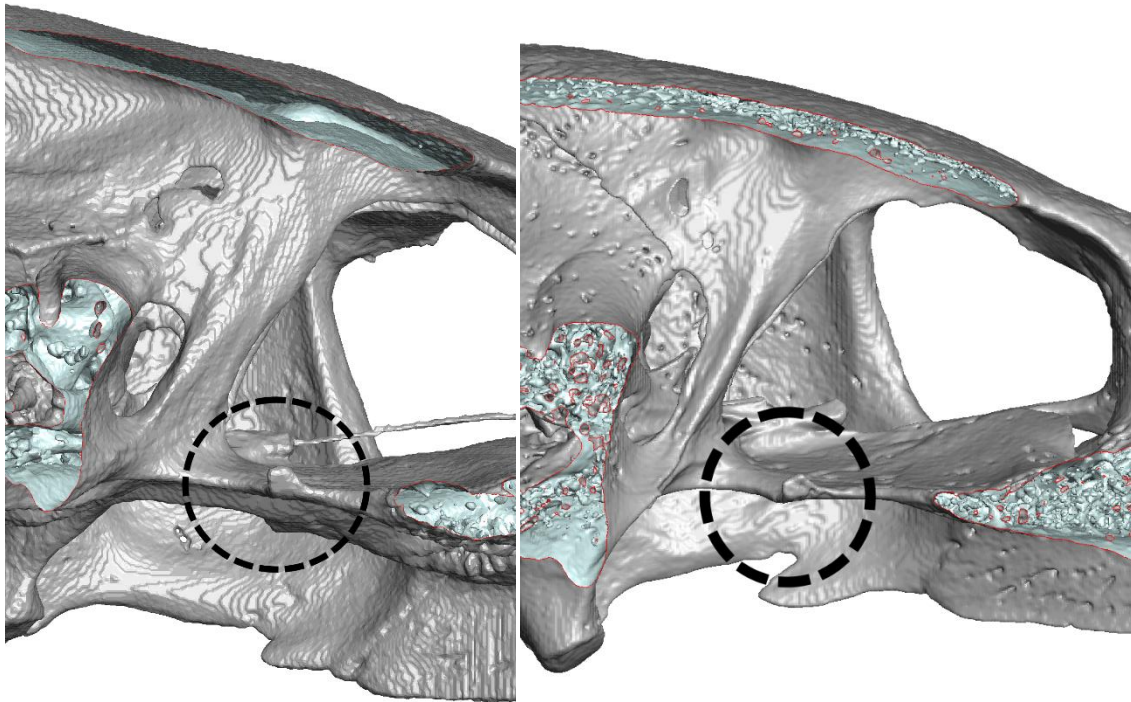


Figure 6 Character 100 coded as 0 for *L. olivacea* NHMUK 2010.1.36 and *L. kempii* M009/08

Character 102 Pterygoid, ventral median ridge: 0 = incipient to absent; 1 = present, ridge spans nearly the full length of the pterygoids, sometimes reaching the most posterior portion of the vomer. This character is scored as inapplicable for taxa in which the pterygoids lack a midline contact.

Lepidochelys olivacea changed from 0 to 1

In the specimens we examined there was a distinct ridge along the midline pterygoid contact.

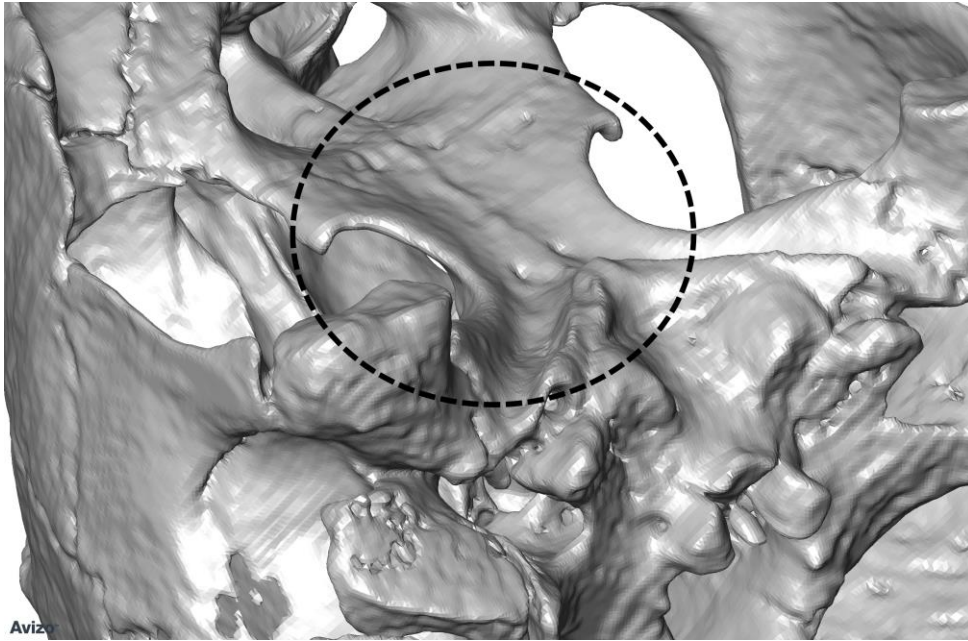


Figure 7. Character 102 coded as 1 for *Lepidochelys olivacea* NHMUK 2010.1.36

Character 173 Dentary, width triturating surface vs. jaw length: 0 = narrow triturating surface, symphysis less than 1/3 of jaw length; 1 = broad triturating surface, symphysis $\geq 1/3$ jaw length.

Caretta caretta changed from 0 to 1.

In the adult specimens we examined the dentary symphysis was well over 1/3rd of the length of the mandible.



Figure 8. Character 173 coded as 1 for *Caretta caretta* SAMA R33830

Character 184 Coronoid process: 0 = relatively low, dorsally well rounded; 1 = relatively high, process is dorsally or posterodorsally pointed.

Caretta caretta changed from 0 to 1.

In the adult specimens we examined the coronoid process was much higher than other Cheloniids and was more similar in shape to the presented example for state 1.

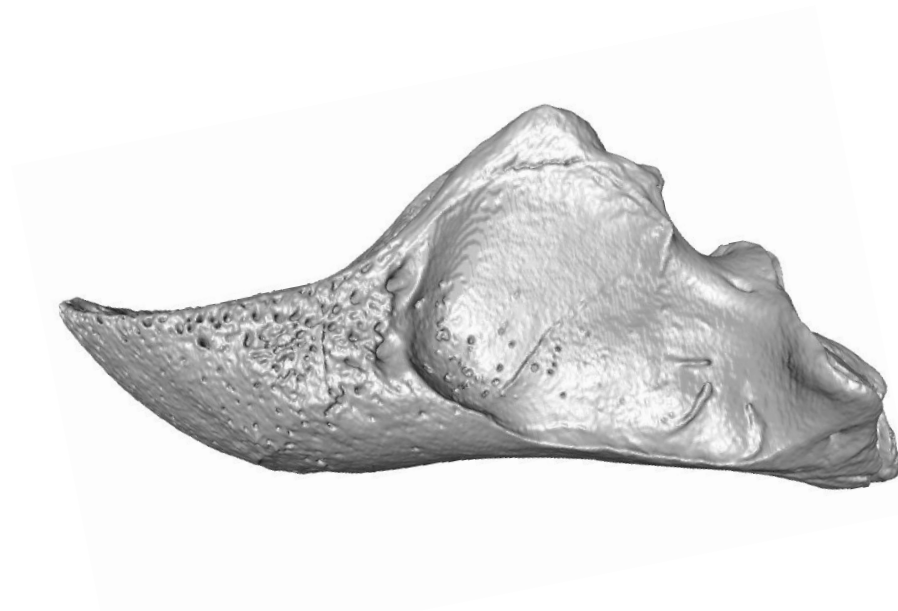


Figure 9. Character 184 coded as 1 for *Caretta caretta* SAMA R33830

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Table 1. Specimen list for Chapters 3 and 5 showing specimen label, species, condition, if the surface was modified, the missing landmarks, CT voxel information and location of scans

Specimen	Species	Condition	Modification	Missing lar	Landmarks mis	x	y	z	Scanned At	Age	
Car_car_4518203	Caretta caretta	Used	None	None		0.074265	0.074265	0.074265		Intermediate	
Car_car_D5453-1	Caretta caretta	Used	None	None		0.192381	0.192381	0.33	Sound	Intermediate	
Car_car_D60903	Caretta caretta	Used	None	None		0.051428	0.051428	0.051428	Melb UNI	Hatchling	
Car_car_D65879	Caretta caretta	Used	None	None		0.240234	0.240234	0.33	Sound	Adult	
Car_car_D74548	Caretta caretta	Used	None	None		0.244609	0.244609	0.33	Sound	Adult	
Car_car_J73517	Caretta caretta	Used	None	None		0.008702	0.008702	0.008702	Adelaide Mic	Hatchling	
Car_car_KU269218	Caretta caretta	Used	None	None		0.053277	0.053277	Melb uni		Hatchling	
Car_car_M40149	Caretta caretta	Used	None	None		0.051455	0.051455	0.051455	Melb UNI	Hatchling	
Car_car_NHMMUK1938_1_9_1	Caretta caretta	Used	None	None		0.118306	0.118306	0.118306	NHMMUK	Adult	
Car_car_NHMMUK1940_3_15_1	Caretta caretta	Used	None	None		0.041769	0.041769	0.041769	NHMMUK	Intermediate	
Car_car_R33830	Caretta caretta	Used	None	None		0.244141	0.244141	0.33	Sound	Adult	
Car_car_R38909	Caretta caretta	Used	None	None		0.175781	0.175781	0.33	Sound	Intermediate	
Car_car_SAM_Unreg	Caretta caretta	Used	None	None		0.244141	0.244141	0.33	Sound	Adult	
Car_car_T2008_14	Caretta caretta	Used	None	None		0.066979	0.066979	0.066979	Hull?	Intermediate	
Car_car_XT757_07	Caretta caretta	Used	None	None					Hull?	Intermediate	
Che_myd_aga_M40144	Chelonia mydas	Used	None	None		0.039194	0.039194	0.039194	Melb UNI	Hatchling	
Che_myd_AM_unreg	Chelonia mydas	Used	None	None		0.066422	0.066422	0.066422	Melb UNI	Intermediate	
Che_myd_AU1269	Chelonia mydas	Used	None	None		0.205078	0.205078	0.4	SAMRHI	Intermediate	
Che_myd_AU1270	Chelonia mydas	Used	None	None		0.175781	0.175781	0.33	Sound	Adult	
Che_myd_D2987	Chelonia mydas	Used	None	None		0.51428	0.51428	0.51428	Melb UNI	Hatchling	
Che_myd_D673797	Chelonia mydas	Used	None	None		0.164063	0.164063	0.33	Sound	Intermediate	
Che_myd_Hull	Chelonia mydas	Used	None	None		0.09603	0.09603	0.09603	Hull?	Adult	
Che_myd_J58978	Chelonia mydas	Used	None	None		0.0087	0.0087	0.0087	Adelaide Mic	Hatchling	
Che_myd_NHMMUK1969_776	Chelonia mydas	Used	None	None		0.116485	0.116485	0.116485	NHMMUK	Adult	
Che_myd_R185600	Chelonia mydas	Used	None	None		0.054286	0.054286	0.054286	Melb UNI	Intermediate	
Che_myd_SAM_Unreg	Chelonia mydas	Used	None	None		0.21582	0.21582	0.33	Sound	Adult	
Der_cor_06-1.3.12.2.1107.5.1.4.24358.4.2	Dermochelys coriacea	Used	None	None		0.488281	0.488281	0.5	WoodsHole	Adult	
Der_cor_D6188	Dermochelys coriacea	Used	None	None		0.51428	0.51428	0.51428	Melb UNI	Hatchling	
Der_cor_D66968	Dermochelys coriacea	Used	None	None		0.219727	0.219727	0.33	Sound	Adult	
Der_cor_JW1476	Dermochelys coriacea	Used	None	None		0.02	0.02	0.02	Ingmar	Hatchling	
Der_cor_R2100	Dermochelys coriacea	Used	None	None		0.390625	0.390625	0.33	Sound	Adult	
Der_cor_UF10362	Dermochelys coriacea	Used	None	None		0.138	0.138	0.138		Hatchling	
Der_cor_UMZC_R3031	Dermochelys coriacea	Used	None	None		0.125048	0.125048	0.125048		Adult	
Der_cor_ZMB_6438	Dermochelys coriacea	Used	None	None		0.0175	0.0175	0.0175	Ingmar	Hatchling	
Ere_imb_120113	Eretmochelys imbricata	Used	None	None		0.244141	0.244141	0.33	Sound	Adult	
Ere_imb_FMNH_22242	Eretmochelys imbricata	Used	None	None		0.064765	0.064765	0.064765	Field museur	Intermediate	
Ere_imb_J51134_2M	Eretmochelys imbricata	Used	None	None		0.3125	0.3125	0.4	SAMRHI	Adult	
Ere_imb_J59304_2M	Eretmochelys imbricata	Used	None	None		0.185547	0.185547	0.4	SAMRHI	Intermediate	
Ere_imb_M55094	Eretmochelys imbricata	Used	None	None		0.049851	0.049851	0.049851	Adelaide Mic	Intermediate	
Ere_imb_R14358	Eretmochelys imbricata	Used	None	None		0.008702	0.008702	0.008702	Adelaide Mic	Hatchling	
Ere_imb_unreg	Eretmochelys imbricata	Used	None	None		0.054286	0.054286	0.054286	Melb uni	Intermediate	
Lep_kem_M009/08	Lepidochelys kempii	Used	None	None		0.1211	0.1207	0.1208	Hull?	Intermediate	
Lep_kemp_2rdileys_Calvin_0000	Lepidochelys kempii	Used	None	Yes	0,5,24,25	0.234375	0.234375	0.5	WoodsHole	Intermediate	
Lep_kemp_329_Cmark_merge	Lepidochelys kempii	Used	None	None		0.742188	0.742188	0.5	WoodsHole	Intermediate	
Lep_kemp_331_03_merge	Lepidochelys kempii	Used	None	None		0.421875	0.421875	0.5	WoodsHole	Intermediate	
Lep_kemp_333_head_0000	Lepidochelys kempii	Used	None	Yes	5	0.421875	0.421875	0.5	WoodsHole	Intermediate	
Lep_kemp_394_buffy_0000	Lepidochelys kempii	Used	None	Yes	5	0.189453	0.189453	0.5	WoodsHole	Intermediate	
Lep_kemp_394_roadrunner_0000	Lepidochelys kempii	Used	None	Yes	5	0.185547	0.185547	0.5	WoodsHole	Intermediate	
Lep_kemp_444	Lepidochelys kempii	Used	None	None		0.205078	0.205078	0.5	WoodsHole	Intermediate	
Lep_oli_BM678	Lepidochelys olivacea	Used	None	None		0.175813	0.175813	0.33	Sound	Adult	
Lep_oli_D5797	Lepidochelys olivacea	Used	None	None		0.037297	0.037297	0.037297	Melb UNI	Hatchling	
Lep_oli_J85545_2M	Lepidochelys olivacea	Used	None	None		0.248047	0.248047	0.4	SAMRHI	Intermediate	
Lep_oli_KU319112	Lepidochelys olivacea	Used	None	None		0.040442	0.040442	0.040442	Melb UNI	Hatchling	
Lep_oli_NHMMUK_2010.1.36	Lepidochelys olivacea	Used	None	None		0.100403	0.100403	0.100403	NHMMUK	Adult	
Lep_oli_R14362	Lepidochelys olivacea	Used	None	None		0.008702	0.008702	0.008702	Adelaide Mic	Hatchling	
Lep_oli_R67237	Lepidochelys olivacea	Used	None	None		0.119141	0.119141	0.4	SAMRHI	Intermediate	
Lep_oli_R68357	Lepidochelys olivacea	Used	None	None		0.21875	0.21875	0.4	SAMRHI	Intermediate	
Lep_oli_SMNS_11070_M22068-42685_2M	Lepidochelys olivacea	Used	None	None		0.100403	0.100403	0.100403	NHMMUK	Adult	
Nat_dep_112123	Natator depressus	Used	None	None		0.208984	0.208984	0.33	Sound	Adult	
Nat_dep_J56891	Natator depressus	Used	None	None		0.041027	0.041027	0.041027	Adelaide Mic	Intermediate	
Nat_dep_R14360	Natator depressus	Used	None	None		0.008702	0.008702	0.008702	Adelaide Mic	Hatchling	
Nat_dep_R61349	Natator depressus	Used	None	None		0.175813	0.175813	0.33	Sound	Adult	
Nat_dep_Unreg_2M	Natator depressus	Used	None	None		0.30599	0.30599	0.33	Sound	Adult	
All_hof_NHMMUK_R4213.dta	Allopleuron hoffmani	Used	Mirrored	Yes	0,4,5,36,37	0.126185	0.126185	0.126185	NHMMUK	N/A	
Arg_41636	Argillochelys hoffmani	Used	Mirrored	Yes	0,1,5,24,25	0.052254	0.052254	0.052254	NHMMUK	N/A	
Arg_ant_NHMMUK-PV_OR-38955_M22202-43217.dta	Argillochelys hoffmani	Used	None	Yes	5,34,35	0.062432	0.062432	0.062432	NHMMUK	N/A	
Bou_sut_P41106.dta	Bouliachelys suteri	Used	Mirrored	None		0.148438	0.148438	0.33	Sound	N/A	
Car_wil_CCNHM_300	Corlinachelys wilsoni	Used	None	Yes	26,27	Photogran	Photogran	Photogran	CCNHM	N/A	
Eoc_bra_IRSNB_R_0061.dta	Eochelone brabantica	Used	Mirrored	None		0.064517	0.064517	0.064517	IRSNB	N/A	
Eoc_bra_R37213	Eochelone brabantica	Used	None	Yes	0,5,7,14,15,24	0.02999	0.02999	0.02999	NHMMUK	N/A	
Pro_cha_CCNHM_893	Procolopchelys charlesto	Used	None	None		Photogran	Photogran	Photogramatry		N/A	
Pup_cam_IRSNB_0074.dta	Pupigerus camperi	Used	None	Yes	5	0.05484	0.05484	0.05484	IRSNB	N/A	
Pup_cam_IRSNB_R0075.dta	Pupigerus camperi	Used	None	Yes	4,5	0.088	0.088	0.088	IRSNB	N/A	
Pup_cam_IRSNB_R0076_2M	Pupigerus camperi	Used	None	Yes	5,15,21	0.058	0.058	0.058	IRSNB	N/A	
Pup_cam_35696	Pupigerus camperi	Used	Mirrored	yes	0,5,30,31,32,3	0.047323	0.047323	0.047323	NHMMUK	N/A	
Rhi_can_CAMSM-B-55783_M22140-43004.dta	Rhinochelys pulchriceps	Used	None	Yes	5,34,35,36,37	0.0204	0.0204	0.0204	NHMMUK	N/A	
Rhi_NHMMUK-PV_OR-35197_M29984-57520.dta	Rhinochelys pulchriceps	Used	Mirrored	Yes	5	0.01709	0.01709	0.01709	NHMMUK	N/A	
Rhi_pul_CAMSM-B-55776_M29983-57498.dta	Rhinochelys pulchriceps	Used	None	Yes	5,7,8,9	0.0282	0.0282	0.0282	NHMMUK	N/A	
Rhi_ele_4637	Rhinochelys pulchriceps	Used	None	Yes	0,5,14,24,25	0.022172	0.022172	0.022172	NHMMUK	N/A	

Table 2. Dietary information for the seven extant species of sea turtles

Species		Age	Common Items	Rare Items	Category	Reference
Caretta caretta	Hatchling	Zooplankton, Jellyfish	Sargasm	Pelagic	Dodd 1988; Boyle and Limpus 2008	
	Intermediate	Jellyfish, Snails, Crabs, Small bivalves: Sea Urchins	Algae, Coral; Salps, fish	General	Dodd 1988; Burke <i>et al.</i> 1993	
	Adult	Crabs, Snails, Conches, Bivalves, Sea pens, Horseshoe crab, Sea	Jellyfish, Coral, Algae, fis	Durophage	Dodd 1988; Seney and Musick 2007	
Chelonia mydas	Hatchling	Zooplankton, Cnidarians	Sargasm	Pelagic	Bjorndal 1985; Boyle and Limpus 2008	
	Intermediate	Sea grass, Algae	Jellyfish, Coral, Salps	Herbivore	Mortimer 1982; Ross 1985; Seminoff <i>et al.</i> 2002	
	Adult	Sea grass, Algae	Jellyfish, Coral, Salps	Herbivore	Mortimer 1982; Ross 1985; Seminoff <i>et al.</i> 2002	
Dermochelys coriacea	Hatchling	Zooplankton, Cnidarians	Salps	Pelagic	Bleakney 1965	
	Intermediate	Jellyfish	Salps	Pelagic	Bleakney 1965; Eckert <i>et al.</i> 1989	
	Adult	Jellyfish	Salps	Pelagic	Bleakney 1965; Frazier <i>et al.</i> 1985; Eckert <i>et al.</i> 1989	
Eretmochelys imbricata	Hatchling	Zooplankton, Cnidarians	Coral, Sea Urchins, Anen	Sponge	Den Hartog 1980; Meylan 1985; Limpus; 1992; Andres and Uchida 1994;	
	Intermediate	Sponges, Algae	Coral, Sea Urchins, Algae	Sponge	Meylan 1985; Limpus; 1992; Diez and van Daam 1992; Andres and Uchida 1994; Cortez <i>et al.</i> 2014	
	Adult	Sponges	Sargasm	Pelagic	Shaver 1991	
Lepidochelys kempii	Hatchling	Zooplankton, Cnidarians	Algae, Fish	General	Shaver 1991; Burke <i>et al.</i> 1993; Seney and Musick 2005; Schmid and Tucker 2018	
	Intermediate	Crabs, Jellyfish, Sea horses	Algae, Fish	Durophagi	Shaver 1991; Burke <i>et al.</i> 1993; Burke <i>et al.</i> 1994	
	Adult	Crabs, Molluscs	Algae, Fish	Pelagic	Bjorndal <i>et al.</i> 1997	
Lepidochelys olivacea	Hatchling	Zooplankton, Cnidarians	Fish, Fish eggs, Algae, Tui	General	Marquez <i>et al.</i> 1976; Montenegro <i>et al.</i> 1982; Frick <i>et al.</i> 2011; Colman <i>et al.</i> 2014	
	Intermediate	Salps, molluscs, Crabs, Jellyfish, Snails	Fish, Fish eggs, Algae, Tui	General	Marquez <i>et al.</i> 1976; Montenegro <i>et al.</i> 1982	
	Adult	Salps, molluscs, Crabs, Jellyfish, Snails	Fish, Fish eggs, Algae, Tui	General	Marquez <i>et al.</i> 1976; Montenegro <i>et al.</i> 1982	
Natator depressus	Hatchling	Zooplankton, Cnidarians		Pelagic	Limpus 2007	
	Intermediate			Soft	Limpus 2007	
	Adult	Sea cucumbers, Jellyfish, Corals, Sea pens		Soft	Limpus 2007	

Landmarks

0. Anterioventral point of premaxillae connection (snout tip)
1. Anteriodorsal point of premaxillae connection
2. Anterior most point of both prefrontals
3. Posterior most point of connection of both frontals
4. Posterior most contact of both parietals
5. Posterior most point of supraoccipital
6. Ventral most point of supraoccipital that is part of the foramen magnum
7. Dorsal most point of basooccipital condyle
8. Lateral left most point of foramen magnum
9. Lateral right most point of foramen magnum
10. Lateral most connection of left quadrate to squamosal
11. Lateral most connection of right quadrate to squamosal
12. Antero-dorsal most point of left Quadratojugal
13. Antero-dorsal most point of right Quadratojugal
14. Posterior most point of left maxilla ventral margin
15. Posterior most point of right maxilla ventral margin
16. Dorsal most point of orbital contact of left jugal
17. Dorsal most point of orbital contact of right jugal
18. Anterior most point of orbital contact of left jugal
19. Anterior most point of orbital contact of right jugal
20. Dorsal most point of left maxilla
21. Dorsal most point of right maxilla
22. Posterior most point of orbital contact of left prefrontal
23. Posterior most point of orbital contact of right prefrontal
24. Ventral most contact of left maxilla to left premaxilla
25. Ventral most contact of right maxilla to right premaxilla
26. Anterior most contact of left pterygoid to inferior temporal fossa
27. Anterior most contact of right pterygoid to inferior temporal fossa
28. Posterior most contact of left palatal to maxilla
29. Posterior most contact of right palatal to maxilla
30. Lateral most point of left quadrato-condyle
31. Lateral most point of right quadrato-condyle
32. Medial most point of left quadrato-condyle
33. Medial most point of right quadrato-condyle
34. Posteromedial most point of left squamosal
35. Posteromedial most point of right squamosal
36. Dorsoposterior most contact of left post-orbital to squamosal
37. Dorsoposterior most contact of right post-orbital to squamosal
38. Ventroposterior most point of left post-orbital
39. Ventroposterior most point of right post-orbital
40. Antero-lateral corner of left parietal
41. Antero-lateral corner of right parietal
42. Anterior most contact of left palatal to maxilla
43. Anterior most contact of right palatal to maxilla
44. Posterior most point of ventral edge of left jugal
45. Posterior most point of ventral edge of right jugal

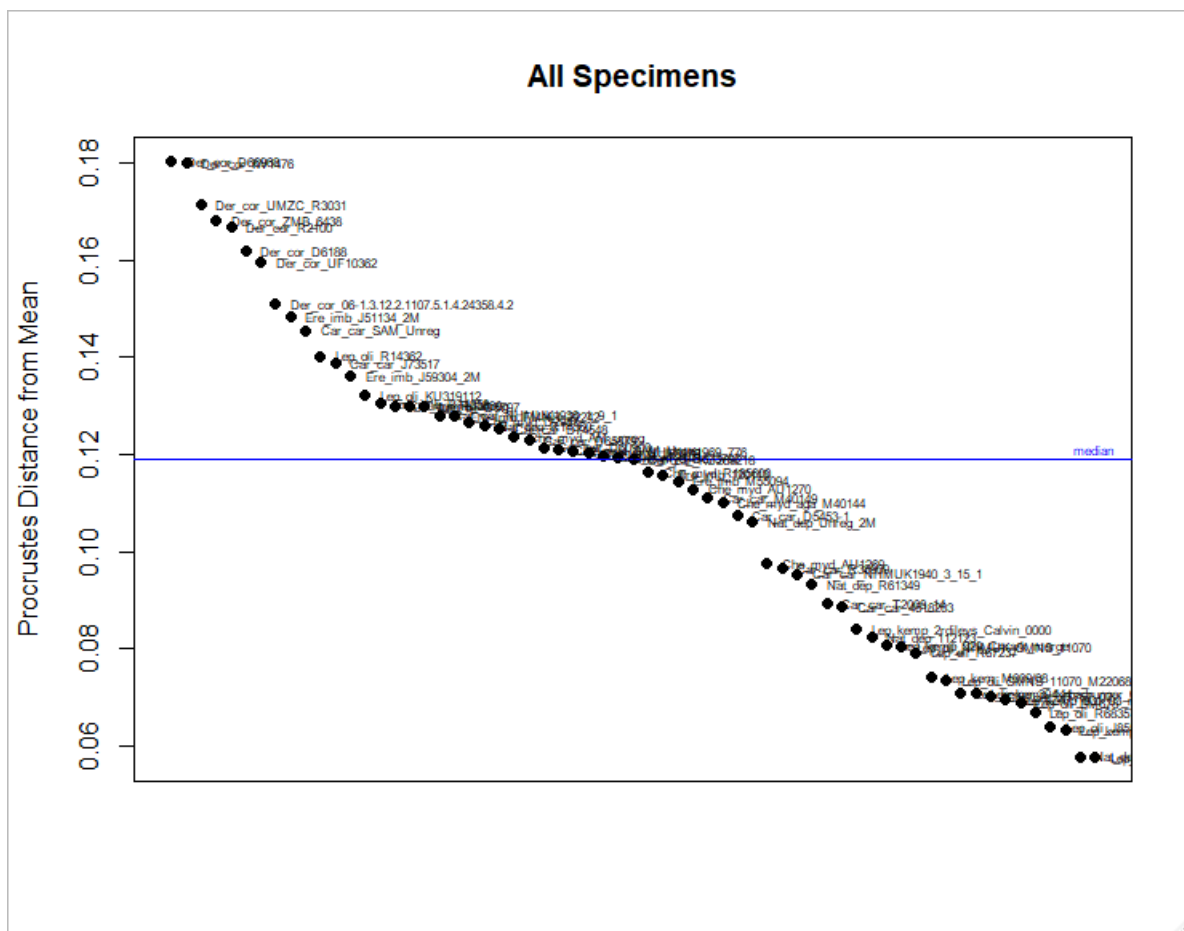


Figure 10. All specimens from Chapter 3 plotted for Procrustes distance from mean

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