

Description and Identification of Turtle Fossils from the
Canterbury Museum

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Frontispiece



"You cannot fight against the future. Time is on our side."

William Ewart Gladstone (1866)

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Abstract

The fossil remains of three turtles and one penguin which was previously believed to be a turtle are described and compared to the New Zealand and global palaeobiota. The fossil remains are stored at the Canterbury Museum. The turtles are Cretaceous, Palaeocene, and Eocene aged while the Penguin is from the Miocene. X-ray computed tomography (CT scanning), comparative research using published descriptions, and measurements of skeletons were used to generate descriptions and determine systematics of each specimen. Raw CT data was refined using the Materialise Software Suite to create 3D models of each specimen component. The Cretaceous specimen, discovered within the body cavity of *Mosasaurus mokoia* is the first Cretaceous New Zealand specimen assigned to the Panchelonidae and exhibits trace evidence of Mosasaur predation in the form of acid etching and teeth marks, the first from the Southern Hemisphere. The Palaeocene specimen is assigned to the macrobaenid family, previously only known from the high latitude regions of Asia, Canada, and North America. Comparison with marine turtle species found that the most comparable marine turtle was *Osteopygis* the postcrania of which belong to the Macrobaenidae. Comparison with macrobaenids show marked similarities in plastron morphology. While macrobaenids are exclusively freshwater species the specimen in this study is considered to have been washed out into the marine environment. The Eocene specimen is assigned to the species *Eochelone monstigris* previously known from the Northland region of New Zealand. Assignment of this species is primarily based upon similarities in size, humeral morphology, and geographic proximity. The Miocene penguin is assigned to the species *Pygoscelis tyreei* previously known from Motunau Beach New Zealand, confirming the presence of this species in the Middle Miocene. Assignment of this species has been made on the basis of comparative measurements of the holotype specimen stored at the Canterbury Museum.

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1 Chapter 1

Introduction

1.1 Thesis Goals

The primary goal of this thesis is to scientifically describe the fossilized remains of turtles currently stored at the Museum of Canterbury. This goal will be achieved by implementing CT scanning technology and 3-dimensional (3D) model generation in conjunction with comparisons with published turtle morphologies. Secondly this thesis will look at the taxonomic placement of New Zealand turtle fossils in an attempt to better understand their implications for New Zealand's turtle palaeofauna.

1.2 Turtle Palaeontology, Current Model Review

Most modern turtle clade origins can be traced back to the Middle Jurassic. Despite this, the interrelationships of these clades are not fully understood (Sterli, 2010; Crawford et al., 2014). The currently most widely accepted model of turtle evolution claims that there are four turtle clades that can be traced back to four specific biogeographic evolutionary centres: Paracryptodira traces back to North America and Europe, Pan-Cryptodira from Asia, Pan-Pelomedusoides originates from landmasses in northern Gondwanan, and Pan-Chelidae evolved in landmasses in southern Gondwana (Joyce & Rabi 2015). Turtles proceeded to diversify from these locations to become the global taxa seen today. This biogeographic model is also partially applicable to three, primarily terrestrial, basal turtle clades: Solemydidae from North American and Europe, Sichuanchelyidae from Asia, and Meiolaniformes from southern Gondwanan landmasses.

1.3 *Global Cryptodire Palaeontology*

In this section turtle palaeontology will be briefly summarised. This section is not designed to be a complete overview of turtle palaeontology and will instead focus upon turtles that follow the evolutionary lineage of New Zealand turtles, namely the ‘hidden-necked’ turtles *Cryptodira*. This has been done in order for readers to better understand how New Zealand turtles relate to worldwide turtle diversification.

1.3.1 *Cryptodire Turtle Phylogeny Overview*

The evolutionary origins of turtles are heavily debated, not just in terms of position in the amniote phylogeny, but in how each turtle clade is related to each other (Krenz et al., 2005; Sterli, 2010; Lourenço et al., 2012; Crawford et al., 2014). Modern molecular techniques are being combined with more traditional morphological methods for extant turtles in order to better understand turtle evolutionary history. Amongst extinct turtles, molecular hypotheses are unavailable and so the morphology of the specimens must be relied on to determine phylogeny.

The turtle phylogeny begins with the diversification of the Testudines from other reptiles. Exactly how the Testudines relate to other amniotes is debated but currently it is believed to be a sister taxon to sphenodonts and archaosaurs with alligators or chickens being used as outgroups for phylogenetic analysis (Krenz et al., 2005). It is considered that Pleurodira and Cryptodira evolved in the Jurassic (Joyce, 2007).

Cryptodires or “hidden-necked” turtles differ substantially from the Pleurodira, most notably in how their heads are retracted into their shells. Pleurodira move their necks to the side in order to retract their heads, thus their name which translates to “side-neck”. Cryptodires retract their heads directly which results in a number of internal differences in morphology to accommodate this movement (Werneburg et al., 2014a; Werneburg et al., 2014b).

Cryptodires further diversified so that by the Late Cretaceous the first Trionychia and Durocryptodira fossils are found. The Durocryptodira are made up of the Testudinoidea and Americhelydia. Americhelydia includes superfamilies Chelydroidea and the marine turtles, Chelonioidea. Chelonioidea includes large marine turtle species such as the leatherback and green turtles (Crawford et al., 2014).

1.3.2 *Jurassic*

During the Jurassic, turtles diversified from the basal Testudines into Pleurodira and Cryptodira. This section shall examine the cryptodires as this is the group to which New Zealand turtles belong.

The turtle fossil record of China is very important for the Jurassic, despite the majority of Jurassic Chinese turtles not being comprehensively studied. Part of what makes the Chinese fossil record interesting is it is currently the only geographic locality that contains multiple genera of similar ages in the Middle Jurassic (Danilov and Parham, 2008). The Xiashaximiao Formation at the Dashanpu locality in Zigong Prefecture, Sichuan Province, China has yielded fossils from both the *Chengyuchelys* and *Xinjiangchelys* genera comprised of at least four species. *Chengyuchelys* is currently one of the oldest known stem cryptodires indicating the basal group Testudines began to diversify into the cryptodires in the Early to Middle Jurassic. Due to the temporal and geographical proximity to *Chengyuchelys* as well as a number of similar traits *Xinjiangchelys*, while a separate genera, is quite likely to be closely related (Danilov and Parham, 2008).

Jurassic turtles are known from a variety of other locations worldwide. By the end of the Jurassic period there is evidence of turtle habitation in South Africa (Gaffney and Kitching, 1994) America (Sterli and Joyce, 2007; Gaffney and Jenkins, 2010), India (Datta et al., 2000),

and Central Europe (Gaffney, 1975; Anquetin et al., 2014a; Anquetin et al., 2014b). There are no records of turtles from the high latitudes of the southern hemisphere at this time.

1.3.3 *Cretaceous*

The late Hauterivian–early Barremian localities of the Spanish Iberian Range have provided information on the Early Cretaceous stem cryptodires of Europe. *Larachelus morla* is a pancryptodire that marks the node between the previously mentioned more basal Jurassic species such as *Xinjiangchelys* and the more derived Cretaceous cryptodires. Lower Cretaceous stem cryptodires are poorly resolved in Europe however the presence of the Iberian Range specimens indicates their presence in Europe in the earliest Cretaceous (Pérez-García and Murelaga, 2012; Pérez-García et al., 2013).

Turtle remains from the Quiriquina Formation in Chile have been assigned to the genus *Euclastes* (Parham et al., 2014). *Euclastes* are known from a number of Maastrichtian localities around the world including Angola, northern Africa, eastern United States, and California. The Chilean specimens are of particular interest as they represent specimens from the same palaeolatitude of Maastrichtian New Zealand. *Euclastes* is a durophagous chelonioid, meaning it subsisted on a diet of hard shelled organisms as opposed to the more common soft bodied organisms like squid. *Euclastes*' wide distribution is also important in highlighting the rapid dispersal of the Cheloniidae following their appearance in the Late Cretaceous Western Interior Seaway of North America (Parham et al., 2014).

The Upper Cretaceous Santa Marta Formation from the James Ross Basin provides the oldest known Antarctic turtle specimen. The partially preserved carapace found in the Santa Marta formation was determined to be between late Coniacian and latest Campanian in age, significantly older than any other Antarctic turtle remains (De La Fuente et al., 2010). Due to

the limited remains found, a species was unable to be determined however the carapace was assigned to the Chelonioidea superfamily. These remains indicate marine turtles were present in Antarctic waters by at least 72 Ma.

Allopleuron hofmanni is known from a variety of locations in Central Europe, especially the Netherlands. Teyler's Museum holds a vast number of Maastrichtian specimens of this species of protostegid (Van Baal and Janssen, 2009). Of particular interest are the specimens which contain evidence of predation on this very large marine turtle, presumably by Mosasaurs.

1.3.4 *Palaeocene*

Macrobaenids are a poorly differentiated family of large freshwater turtles that arose in the Early Cretaceous of Asia and had expanded to high latitude North America and Canada by the Palaeocene (Hutchison and Holroyd, 2003; Parham and Hutchison, 2003; Vandermark et al., 2009). As no truly robust systematic description of the family exists members of this species are readily confused with the Jurassic Xinjiangchelyids such as *Xinjiangchelys*, and the Cretaceous Sinemydidae however a phylogenetic description has been formalised in order to address the confusion surrounding these families (Rabi et al., 2014). The Macrobaenidae is now defined as the most inclusive clade containing *Macrobaena mongolica* but not *Xinjiangchelys junggarensis*, *Sinemys lens*, or any Recent turtle species. (Rabi et al., 2014)

The Denver Basin in Colorado contains turtle remains ranging in age from the Late Cretaceous to the Early Palaeocene. The Palaeocene assemblage is of particular interest in turtle palaeontology for its uniquely diverse combination of taxa, most specifically the presence of the Macrobaenidae (Hutchison and Holroyd, 2003). The presence of macrobaenids in this assemblage is believed to be due to the development of the Cannonball Sea as macrobaenids in

North America tend to be more common in coastal plain areas (Hutchison and Holroyd, 2003).

This assemblage does not feature any members of Cheloniidae however it does indicate a turnover of fauna across the K/T boundary.

Euclastes is also known from Palaeocene littoral sediments in Morocco (Jalil et al., 2009). The Oulad Abdoun Basin contains abundant phosphates including a phosphate horizon of Danian-Thanetian age well known for its marine vertebrate fossil assemblage. The turtle remains found within the basin were assigned to the genus *Euclastes* based on a number of diagnostic features of the skull. *Euclastes* is therefore present across the K/T boundary and is therefore important for understanding how cheloniid turtles responded to the faunal turnover and dispersal which resulted from the K/T extinction event.

1.3.5 Eocene

Fragmentary remains of cheloniids are known from the Lugansk Region of Ukraine. The fragments have been assigned to six taxa including cheloniids *Argillochelys*, *Eochelone*, *Glossochelys*, and *Puppigerus* (Zvonok et al., 2013). The fragments were found in the Ikovo locality and are Middle Eocene in age. The turtle palaeofauna of the Ikovo locality has been with other turtle assemblages in England, Belgium, and the Ukraine. The assemblages are similar in composition indicating successful dispersion of these cheloniid turtles over a wide geographic area in Eurasia.

The La Meseta Formation on Seymour Island yielded the first fossil turtle to be found in Antarctica. Remains, largely epithelial plates, were found at three different localities within the formation and were all attributed to the Dermochelyidae family, a cheloniid family that contains the modern leatherback turtle (De La Fuente et al., 1995). The taxonomic position of the Antarctic specimens is difficult to determine due to its fragmentary nature, despite clearly

belonging to Dermochelyidae. It is possible that it could belong to the genus *Psephophorus* which is known from New Zealand from similarly fragmentary remains. The dermochelyidae family is known from a number of locations around the world however, only the New Zealand, Antarctic, and Egyptian *Psephophorus* specimens, *Cosmochelys* from Nigeria, and the *Eosphargis* specimens from England and Belgium are of Eocene age. The Antarctic fossils combined with other worldwide specimens indicate a truly global distribution of Dermochelyids by the Eocene.

The genus *Eochelone* was initially discovered and described by Dollo in 1903. *Eochelone brabantica* was found in late Eocene sediments in Belgium which led to the formation of the *Eochelone* genus, a member of which is known from New Zealand (Grant-Mackie et al., 2011).

1.4 Miocene Penguin Diversity

During the Miocene Penguins began to transition from the more ancestral forms to the extant ones (Jadwiszczak et al., 2012). This is therefore a crucial time in the evolutionary history of the species. While New Zealand penguin diversity is largely diverse, containing species ranging from the Palaeocene to a number of extant species (Ksepka et al., 2006; Slack et al., 2006), Miocene penguin fossils are relatively limited. Other localities especially Patagonia (Haidr and Acosta Hospitaleche, 2014) and Chile (Paulina-Carabajal et al., 2015) Antarctica (Jadwiszczak et al., 2012) and Australia (Park, 2014) contain a much wider range of specimens.

1.5 New Zealand Turtle Palaeontology

Fossilised remains of turtles known from New Zealand deposits are limited to specimens from the Late Cretaceous, the Palaeocene, the Eocene, and the Early Miocene. The

Late Cretaceous is known from specimens described by Wiffen in 1981 and McKee and Wiffen in 1989. The Palaeocene turtle is known from a collection of plastral, rib, and carapace fragments (Buchanan et al., 2007) and a partial humerus (Fordyce, 1979). The Eocene turtle fauna is slightly more diverse, including at least three different species (Kohler, 1995a; Karl and Tichy, 2007; Grant-Mackie et al., 2011). Most of these turtle fossils come from marine sea turtle families. No terrestrial or freshwater turtles younger than the Cretaceous were known in New Zealand until a study by Worthy et al. (2011). Worthy described the fragmental remains of a large turtle which most closely resembled the terrestrial *Meiolania platyceps*. The study by Worthy was unable to determine a genus for the fossils however it does demonstrate convincingly that the New Zealand Early Miocene fauna did include a freshwater and possibly terrestrial turtle.

1.5.1 *The Mangahouanga Stream Specimens*

These New Zealand turtles described in (Wiffen, 1981) and (McKee and Wiffen, 1989) include one specimen attributed to the Protostegidae family, one specimen attributed to the genus *Glyptos*, and a specimen assigned to *Desmatochelys iowi*. These specimens are of Late Cretaceous age. *Desmatochelys iowi* is known from a single femur, as is the specimen assigned to *Glyptos*. The specimen assigned to the family Protostegidae is known from eight plastral and carapace fragments.

1.5.2 *The Ward Specimen*

Discovered in the Teurian aged limestone above Ward Beach in Marlborough in the South Island, this specimen consists of a single bone. Provisionally identified as a humerus lacking condyles or a humerus head, it does appear to have the proximal end of the epicondylar

groove. Due to the incomplete nature of the specimen no attempt has been made to determine more than the ordinal level of the systematics of the specimen.

1.5.3 *The Wangaloa Specimen*

A Teurian stage (Palaeocene) unit from south eastern Otago, The Wangaloa Formation is a highly fossiliferous, well-cemented, concretionary, quartz sandstone and conglomerate. The turtle specimen from this unit consists of carapace and plastral fragments as well as a fragment of a rib and some indeterminate fragments. Due to the fragmentary nature of the specimen it is only described as a member of the superfamily Chelonioidea.

1.5.4 *The Northland Specimens*

Two specimens are known from Northland, one from a roadside exposure north of Whangarei, and one from Pahi on the Kaipara Harbour coast, both of which are described by Grant-Mackie et al. (2011) and are considered to be Eocene in age. The specimen from the roadside exposure has been described as *Eochelone monstigris*, and is the holotype for this species. The holotype includes the partial right humerus, the right radius, an articulated portion of right manus with additional complete and fragmentary phalanges, two thoracic and three posterior cervical vertebrae in articulated association, fragments of two scapulae, anterior portion of the carapace (nuchal and parts of adjoining marginal plates), fragments of ribs, carapace fragments, and some unidentified fragments. The specimen from Pahi is assigned to the family Toxochelyidae. The collection representing this specimen consists of five small blocks of rock with multiple bone fragments and four isolated fragments, all incomplete. The fragments from these rocks include a right humerus, a fragmentary cervical vertebra, a posterior thoracic vertebra with fused neural plate, three rib fragments and parts of hyo- or hypoplastral elements.

1.5.5 *The Oamaru Specimens*

Multiple specimens are known from the Oamaru area and have been donated to the Otago University. The majority of specimens have been assigned to the species *Psephophorus terrypratchetti* following work by Köhler (Kohler, 1995a; Kohler, 1995b). A total of 5 specimens from the Waihao River have been assigned to this species. Specimen OU 22176 consists of 45 single platelets and 2 platelet fields as well as a poorly preserved cervical vertebra. The holotype for *Psephophorus terrypratchetti*, specimen OU 22177, consists of a large platelet-field, two anterior ribs, four anterior thoracic vertebrae, the proximal half of a first rib and fragments of ribs, vertebrae and many isolated platelets. Specimen OU 22215 consists of a single platelet field. Specimen OU 22219 contains a platelet field of over 115 platelets, a fragmentary nuchal bone, a partial neural arch of a cervical vertebra, scapular bone elements, and a hyoid fragment. Specimen OU 22258 is made up of three platelets still connected via sutures.

The New Zealand Eocene turtle fauna was revised in 2007 in order to determine the exact phylogenetic location of the turtle fossils. The specimen designated OU 22021, a turtle humerus of Bartonian age from Boulder Hill near Dunedin, is at the centre of the revision. Specimen OU 22021 was originally described by Kohler (Kohler, 1995a; Kohler, 1995b) along with other fossil elements belonging to *Psephophorus terrypratchetti*. Kohler concluded OU 22021 was a member of the genus *Psephophorus*; however the material was insufficient to determine a species. The material has subsequently been revised Karl and Tichy (2007) who determined that the humerus should be assigned to a new genus and species, *Maorichelys wiffenae* (formerly *Maorichelys Wiffeni*, renamed using correct feminine ending in Grant-Mackie et al., 2011). Karl and Tichy found that OU 22021 was not similar enough to the *Psephophorus* holotype to be considered as the same genus. *Psephophorus* is known only from the United States, Egypt and Europe, this combined with the differences between the two fossil humeri

presented sufficient evidence for OU 22021 to be assigned to a new genus. Phylogenetically *Maoricheyls wiffenae* was found to be closer to *Eosphargis* than *Psephophorus*.

1.6 Canterbury Museum Specimens

The Canterbury Museum contains a number of previously undescribed fossil elements which were believed to belong to turtles. This project describes several including two large sections of the lower shell or plastron, as well as a collection of fragmental limb bones and vertebrae. The fossils come from three different turtles and as it turned out, a penguin. One was found in Eocene sediments (Ototara Limestone), another from the Cretaceous (Conway Formation), one from the Palaeocene of the Waipara River (Waipara Greensand), and the penguin from a concretion near the Glenafric beach (Mt Brown Formation). None of these fossils had been fully scientifically described; this is necessary in order to expand upon the currently sparse New Zealand turtle palaeofauna. It is possible that the fossils could be crucial in the description of completely new species of turtles should more related material be discovered. Alternatively these fossils will expand the distribution range of the known Cretaceous Paleocene, Eocene turtle species, while the penguin expands the diverse penguin palaeofauna of New Zealand.

One specimen in Canterbury Museum, the fragmentary remains of a Cretaceous turtle are of particular interest. The only other turtles of similar age that have been described in New Zealand is a few fragments of femura and some plastron described in 1981 (Wiffen, 1981) and in 1989 (McKee and Wiffen, 1989). McKee and Wiffen determined these belonged to two marine turtles, a Protostegidae and a species apparently similar to *Desmatochelys iowli*, They also described a potentially terrestrial turtle from the Cretaceous of what would become the North Island of New Zealand. Those specimens were found in Mangahouanga Stream and were

determined to be Late Cretaceous: Piripauan – Haumaurian in age. As all previous Cretaceous turtle specimens were found in the North Island, the Canterbury material represents the first specimen to be found in the South Island of Cretaceous age.

1.7 Geological Setting

1.7.1 New Zealand

New Zealand formed by accretion along the Pacific facing Gondwana continental margin. This process began to change during the Mid-Cretaceous when the accreted arc system began to rift away from the Gondwanan continent (Laird and Bradshaw, 2004). The process of rifting and then drifting continued throughout the rest of the Cretaceous and into the Cenozoic. The modern plate boundary was developed and the regime of tectonic uplift began subsequent to the drifting period. The turtle fossils that are the key focus of this study originated during the prolonged period where New Zealand was rifting and drifting away from the Gondwanan landmass.

1.7.2 Canterbury

The Canterbury regional geology from the Late Cretaceous consists of a transgressive-regressive mega-sequence unconformably overlying the Torlesse basement rocks. The mega-sequence is interspersed with volcanic inputs and unconformities related to a variety of events such as sediment starvation and ocean current changes. The marine transgression began in the Haumarian (80 Ma) and reached its maximum extent with the near total inundation of the New Zealand landmass in the Oligocene (Forsyth et al., 2008). A period of cooling in northern Canterbury occurs during this transgression coinciding with the K/T Boundary.

Cooling is evidenced by a decrease in carbonate concentration and an increase in biosiliceous sediments in the middle Waipara River K/T exposure (Hollis and Strong, 2003). Tectonically the offshore segment of the Canterbury Basin has been relatively stable with subsidence of the centre of the basin being the main control on accumulation space since the end Cretaceous (Lu et al., 2003).

1.7.3 *Conway Formation*

The Conway Formation was deposited from the middle Late Cretaceous (Maastrichtian) through to the earliest Palaeocene (Hiller et al., 2014). The deposit is massive, soft, grey to dark grey, silty sandstone to siltstone. There is prominent bioturbation which likely has resulted in the lack of other sedimentary structures. Large calcareous concretions are a conspicuous feature of this unit (Browne and Field, 1985). The concretions have been shown to contain a number of fossils, especially marine reptiles. The Conway Formation was deposited in a fully marine setting with restricted bottom circulation (Buckeridge, 2011; O’Gorman et al., 2014)

1.7.4 *Waipara Greensand*

The Waipara Greensand outcrops predominantly at the Waipara River in North Canterbury although outcrops are known from other locations throughout the region (Mannering and Hiller, 2008). The Waipara Greensand is glauconitic sparsely fossiliferous, fine- to medium-grained, richly glauconitic quartzose sandstone, 88m thick, thinning towards the North and South (Browne and Field, 1985; Andrews et al., 1987). The microfossil assemblage within the greensand indicates deposition of the unit occurred during the Teurian (Palaeocene) (Mannering and Hiller, 2008; Mayr and Scofield, 2014). The greensand is commonly believed to have been

deposited in a shallow marine, possibly mid-shelf marine environment (Browne and Field, 1985; Mayr and Scofield, 2014). Some of the known fossils from this unit include a sea bird (Mayr and Scofield, 2014), sixteen genera of Neoselachian sharks, a species of barnacle (Mannering and Hiller, 2008) and two separate penguin specimens (Slack et al., 2006). The Waipara Greensand conformably overlies the Loburn Formation of Teurian age (Browne and Field, 1985; Andrews et al., 1987). The Ashley Mudstone overlies the Waipara Greensand and is considered sub-tropical with an approximate average temperature of between 28 and 30°C (Hollis et al., 2012; Mayr and Scofield, 2014). The upper boundary of the Waipara Greensand unit is also the boundary between the Palaeocene and Eocene (Mannering and Hiller, 2008; Raine et al., 2015).

1.7.5 *Ototara Limestone*

The Ototara Limestone was deposited through the late Eocene and early Oligocene (Kaiatan to mid-Whaingaroan). Strontium dating of the limestone has determined an age range of 35.18 and 34.13 Ma (Nelson et al., 2004). It is a bryozoan packstone with a median calcite (CaCO₃) purity of 93.4%, making it one of the most pure limestones in New Zealand (Hayton et al., 1995; Mortimer and Strong, 2014). This limestone was deposited at inner to mid-shelf depths around localised offshore topographic volcanic highs resulting in very limited terrestrial input and therefore the exceptionally high calcite purity. The Ototara Limestone contains predominantly bryozoan fossil material but other fossils that have been found within it include silicious sponges which have been diagenetically replaced by calcite (Kelly et al., 2003), shark teeth, whale bones, penguin bones (Fordyce, 1979), bivalves (Robinson and Lee, 2011), and the Eocene turtle fragments from this study. The Ototara Limestone is interbedded by the Waireka-Deborah Volcanics (Forsyth, 2001; Corcoran and Moore, 2008; White and Hicks, 2009; Thompson et al., 2014). These volcanics originate from a number of centres, one of which is visible on the south side of the Kakanui river mouth, where the remnants of the main conduit are

exposed. The volcanic cluster that produced these flows was also the cause of the offshore topographic high point where the thickest sections of the Ototara was deposited. The deposition of the Ototara was helped by the presence of offshore currents moving around the topographic high, depositing bryozoan fragments that were swept along in the current (Thompson et al., 2014). The limestone varies by locality between soft and cemented (Lee, 2009; Thompson, 2013). While generally massive or with indistinct bedding, at some locations cross-beds are clearly visible (Thompson, 2013). The limestone also grades into a muddier wackestone to the west as it the depocentre moves closer to the Eocene coast line (Thompson et al., 2014). The upper boundary of the Ototara limestone is the Marshall Paraconformity, representing a massive shift in New Zealand's sea level (Fulthorpe et al., 1996; Thompson et al., 2014). First the sea level dropped, exposing and karsting the upper surface of the limestone. Sea level rapidly rose, initially depositing the Kokoamu Greensand before once again reaching levels that facilitated limestone production and beginning the deposition of the Otakaike Limestone.

1.7.6 *Mt Brown Formation*

Glenafric Beach is known by both amateur and professional fossil hunters for its crustacean fossils. Fossils are found in concretions that have eroded out of the sandstone-siltstone lithofacies at the top of the Mt Brown Formation and accumulate upon the beach. The concretions are dense and are cemented by carbonate or ferruginous minerals (Feldmann et al., 2006). The majority of concretions contain *Tumidocarcinus giganteus*, *Metacarcinus novaezealandiae*, or *Actinotocarcinus chidgeyorum*, all of which are decapod crustaceans (Glaessner, 1960; Feldmann et al., 2006). As the majority of concretions are derived from erosion and deposition upon the beach the exact age of the concretions is difficult to determine. The difficulty derives from the instability of the beach cliff face, making it difficult to work directly upon it, as well as the lack of available index fossils. The sandstone-siltstone lithofacies at the top of the Mt Brown Formation, where the concretions are limited to are generally

considered to be Middle Miocene (Lillburnian to Waiauian) (Browne and Field, 1985; Andrews et al., 1987). The Mt Brown Formation fossil bearing rocks were deposited in an outer shelf environment, resulting in the excellent preservation of the decapod fauna (Browne and Field, 1985; Feldmann et al., 2006).

1.8 Thesis Aims

This thesis aims to further expand the understanding of both the New Zealand and global turtle palaeofauna. By scientifically describing the turtle fossils currently stored at the Canterbury Museum a more complete understanding of the turtles that were present in New Zealand in the Cretaceous and Eocene will be available. A more complete understanding of New Zealand turtles will be beneficial for understanding turtle radiation and potentially turtle phylogeny and evolution.

2 Chapter 2

Methods

2.1 *Photostacking*

Photostacking or image focus stacking is a technique using multiple photographs of the same object with differing focal points. Combining the photographs and averaging the focal points creates an image where the entire object is in focus. By generating an image in which everything is in focus it is easier to zoom in on key potentially diagnostic features. The photostacking was done over two separate days due to data limitations. Both sessions were carried out at the Canterbury Museum using their pre-established photography station (Figure 2.1).

The first session was done on Tuesday the 17th of March, 2015. The photographs were taken using a Canon EOS 5D Mark II camera with a 50mm macro lens and 16GB memory card owned by the Museum of Canterbury. The focal image stacking set up consisted of mounting the camera on vertically mounted StackShot™ Focus Stacking Rail System designed by Cognisys, Inc., also the property of the Museum of Canterbury. Photographs were made using the Auto Step setting of the Focus Stacking Rail System. The Auto Step setting works by choosing a start and end focus point for the camera as well as a set number of images to take or steps. Distance between steps is calculated by the Focus Stacking Rail System to ensure an equal distance between each of the steps. Fossils were placed upon a white cushion beneath the photography apparatus for contrast and two objects were placed beside the fossils for scale; a 30cm metal ruler and a KODAK Colour Control Patch card. Large floor lamps were used to control the lighting.

The remainder of the photostacking was done on Tuesday the 28th of July, 2015. For this day the set up was slightly altered. Instead of the previously used 50mm macro lens a 100mm lens was used. Further the fossils were placed upon a black cushion for contrast instead of the previously used white one; the items used as scales were also different, in this case a white plastic 30cm ruler. All other aspects of the photography apparatus were consistent with the day one set up. None of the changes in day two significantly alter the photostacking process and so are only minor.



Figure 2.1: Photography station Photostacking layout for day 1

2.2 *3D Models*

2.2.1 *X-ray Computed Tomography*

X-ray computed tomography or CT scanning uses x-rays to generate images of individual layers of the fossil known as tomographs or slices. Scanning with CT provides mapped x-ray attenuation through the scanned material. X-rays attenuate due to object density and as density usually changes between materials such as the fossil and the matrix (Ketcham and Carlson, 2001) this technology allows researchers to generate 3 dimensional digital versions of the specimen as well as reconstruct the internal fossil surfaces (Iurino et al., 2013). This also allows the researcher to study fossils which are entrapped in hard substrates where traditional methods would likely result in damage to the fossil and may destroy potential trace evidence (Iurino and Sardella, 2014). The ability to generate high quality models of irreplaceable, unprepared or internal structures of fossils has made this a very important tool for palaeontology. CT scanning has now been used for a variety of studies allowing researchers to study the structure of endocasts of extinct species (Rogers, 1999; Witmer and Ridgely, 2009; Lautenschlager et al., 2012), respiratory system evolution (Claessens et al., 2009), to virtually prepare specimens and extract key parts of the fossil (Schwarzhan et al., 2012), and to enlarge key aspects of the fossils for closer study (Garwood and Sutton, 2010). Overall this technology allows multimedia 3 dimensional images to be created which allow researchers to obtain the maximum amount of information from specimens.

CT scans for this study were done at the St Georges Hospital Radiology department using a Siemens SOMATOM definition CT scanner. 512 16 bit slices at 200 microns were taken with a slice thickness of 400 microns. The radiation setting for the scans was 140 KVP.

2.2.2 *Materialise Software Suite*

Slices generated from the CT scanning procedure as DICOM files were compiled using Mimics version 17 software, part of the Materialise Software Suite. The use of DICOM files allowed for a more streamlined upload of the slices as the key parameters required by mimics such as orientation and distance between slices were already incorporated into the files. Mimics allows the user to generate 'masks' over the slices by selecting desired parts of the slice. The desired parts of each slice are then combined to generate a 3D image. This is an extremely powerful tool as it allows the user to virtually remove matrix that is still present on a prepared fossil or even excavate a completely unprepared fossil with no risk of damage to the fossil itself. This technique is limited by the resolution and number of the slices taken.

In order to ease the creation of masks mimics uses a tool named thresholding. Thresholding allows the user to select pigments only of a specific brightness or a range of brightness. As brightness is primarily controlled by the density of the material fossils are generally brighter than surrounding matrix in slices; by only selecting bright pixels a mask of the fossil can be easily made. Conversely should reflective minerals that disperse the X-rays used during CT scanning be present within the matrix, such as pyrite, the distinctive flares they produce can be reduced by removing the most bright pixels from the threshold however this can make preparation of the material extremely difficult.

Thresholded masks may sometimes include undesired pixels to deal with this mimics has three ways of removing undesired pixels. Firstly the edit mask tool allows you to remove, add or threshold pixels on a single slice. Secondly the multiple slice mask edit tool allows you to edit on two or more slices and then average it across the intermediary slices. Finally the edit in 3D tool allows you to directly remove pixels from the 3D image generated by the mask. These techniques allow for much finer control and differentiation between matrix and fossil material, especially in cases where the brightness difference is minor.

In this study each element was made into different masks allowing each individual bone to be examined. Large pyrite flares were present in the Palaeocene turtle plastron plate scans and as a result the masks generated are more likely to contain minor errors however these are unlikely to significantly detract from the overall morphological comparisons.

Masks created in the Mimics software can be exported as .stl files. .stl files can be used by the 3Matic software also included in the Materialise Software Suite. 3Matic software is used for visualisation of the fossils and contains a number of useful features, especially measurement and alignment tools. All fossil elements were measured using this software as some are unable to be measured using more conventional means due to a lack of preparation. This software was also used to reconstruct the three Cretaceous coracoid fragments into a single bone fragment. 3Matic software also allows the 3D images to be exported as a number of different file types. This study chose to use 3DPDF format as these are able to be viewed using standard PDF reading software packages which are commonly available rather than more specialised formats which require specific programs to be viewed

2.3 Comparative Palaeontological Work

The comparative work done as a part of this study was done in two main ways: comparison with physical specimens from the Museum of New Zealand Te Papa Tongarewa collection in Wellington, New Zealand; and by comparison with published descriptions in scientific literature.

2.3.1 Te Papa National Museum Comparative Work

This work took place occurred on the 2.11.2015 at the museum collection building at 169 Tory Street, Wellington 6011. This work was done under the supervision of Thomas

Schultz, the collections manager for science at the Te Papa Museum. While the collection contained a large number of turtle skeletal remains, these were mostly limited to the modern turtle fauna. The measurements made using this collection served as baseline for comparisons between the fossil remains of this study with the modern turtle fauna. Specimens examined as part of this work include: RE 7395, a complete specimen of *Lepidochelys olivacea*; RE 007365, Tokelau Island humerus of an unknown modern cheloniid; DM 880 a complete specimen of *Dermochelys coriacea*; RE 5307, a complete specimen of *Eretmochelys imbricata*; DM 891, a partial skeleton of *Chelonia mydas*; RE 2492, a specimen with the label “Chelonia”, possibly a hawksbill turtle; and RE 007443, a complete specimen of *Trachemys scripta elegans*. Due to time constraints with the specimens not all were able to be fully measured however photographs of all specimens were taken for visual comparisons. Measurements that were able to be taken were done using protractors, rulers and a pair of digital calipers.

2.3.2 Literature Comparisons

Comparisons were made with numerous works within the scientific literature in order to further the understanding of the Canterbury Museum specimens. The majority of these articles and books were found using a number of scientific search engines, the University of Canterbury Library and collections, and the Canterbury Museum collection. Other articles were kindly supplied by Herman Voogd, collection manager for science, Teylers Museum, Haarlem in the Netherlands. While most papers were either originally written in English or were available as a translated copy, a select number by Dollo required translation from French. Translation from French was mainly done using online translators such as Google Translate and Babelfish.

3 Chapter 3

The Cretaceous Specimen: ZFR16

3.1 *Locality and Horizon*

The specimen was discovered during the preparation of the mosasaur *Mosasaurus mokoroa* in the late 1960's by S. P. Welles and D. R. Gregg (Welles and Gregg, 1971). The specimen consists of four bone fragments; three of which form the proximal end of the coracoid, and the final fragment is from a peripheral all of which were found within the body cavity of the mosasaur, presumably as the result of predation. The mosasaur and turtle remains are believed to have been found in a concretion at the Jed River, Cheviot district, North Canterbury between 1874 and 1895 (Welles and Gregg, 1971) however this is the limit of the collection notes. The concretion is from the Conway Formation which was deposited from the middle Late Cretaceous (Maastrichtian) through to the earliest Palaeocene (Hiller et al., 2014). The mosasaur has been determined be Haumurian (Maastrichtian) in age. As the Conway Formation is massive and lacks prominent sedimentary differentiation, the exact horizon is unknown.

3.2 *Material*

CMC ZFR16 contains the proximal end of a coracoid which is fractured into three pieces, and a highly degraded peripheral fragment. The identity of the coracoid was determined based upon the articulation surface morphology and the medial curvature of the bone. Visual comparison with mosasaurs, plesiosaurs, ichthyosaurs, pterosaurs, tyrannosaurs, ankylosaurs, ceratopsians, sauropods, crocodiles, sphenodon, teleost fish and a selection of mammals show significantly less morphological similarity to the

coracoid than marine turtles. As the material was part of the concretion containing *Mosasaurus mokoroa* the fossils were prepared using a combination of manual techniques and weak acetic acid by Welles and Gregg. The prepared fossils were CT scanned for this study and were digitally prepared to further remove the remaining matrix present within grooves in the fossil.

3.3 Systematics

Testudines (Batsch, 1788)

Chelonioidea (Baur, 1893)

Pancheloniidae (Joyce et al., 2004)

Pancheloniidae is described as a clade of sea turtles belonging to the superfamily Chelonioidea that are more closely related to the cheloniids than the dermochelyids. Pancheloniidae includes a variety of taxon including the less specialized members of Chelonioidea and the more derived cheloniids



Figure 3.1: focus stacked photograph of coracoid fragment A. This fragment contains the articulation surface.



Figure 3.2: Focus stacked photograph of coracoid fragment B. This fragment is central in the reconstruction



Figure 3.3: Focus stacked photograph of coracoid fragment C. This is the most posterior end of the coracoid that is preserved in this assemblage.

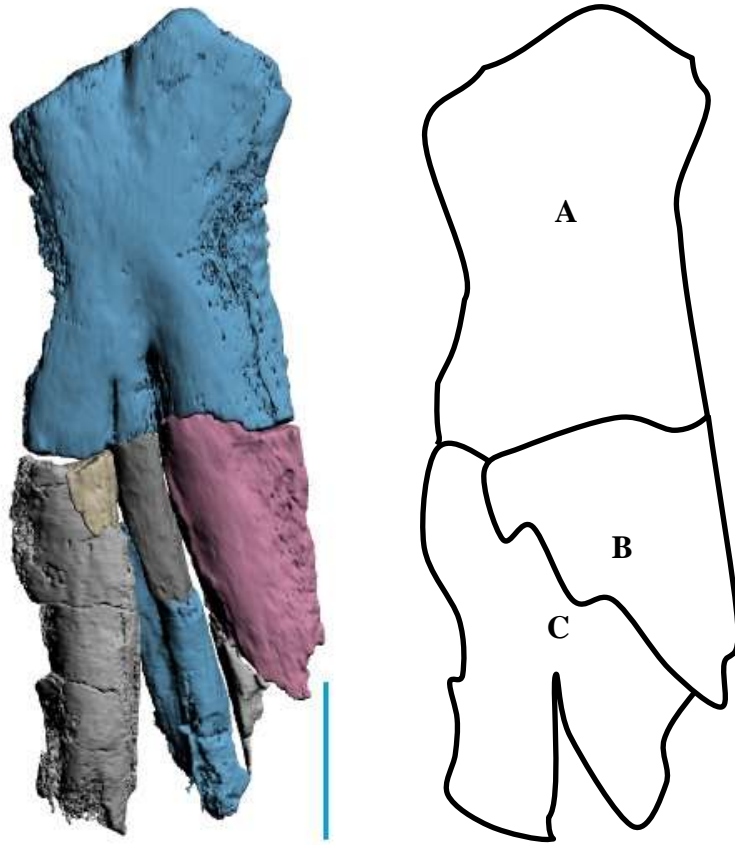


Figure 3.4: Coracoid reconstruction. Blue line = 50mm

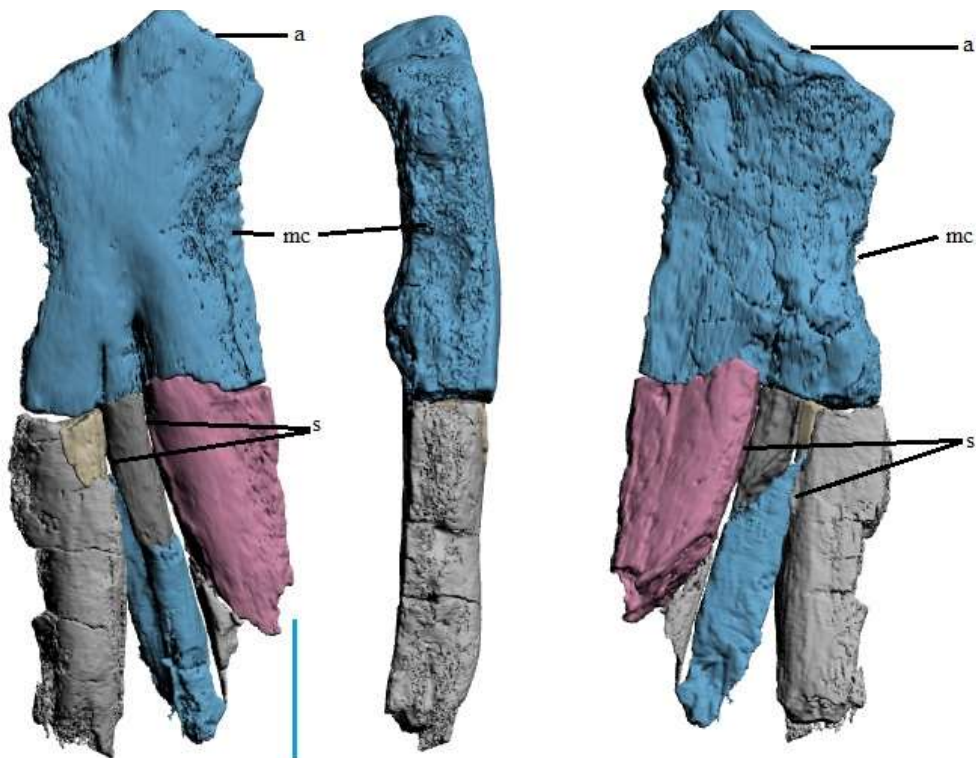


Figure 3.5: Key features of the ZFR16 coracoid. Abbreviations used: a, articulation surface; mc, medial constriction; s, striations

3.3.1 *Right Coracoid fragment*

The right coracoid fragment is broken into three separate fragments (Figure 3.1, Figure 3.2, and Figure 3.3) which have been reassembled for this study (Figure 3.4). Orientation is able to be confidently determined due to the preservation of the articulation surface with the humerus and scapula.

The striations along the surface of the coracoid are extremely pronounced (Figure 3.5). Considering the fragmentation of the specimen, the degraded nature of the peripheral compared to the associated mosasaur, and the association with the mosasaur itself it seems more likely that the striations became pronounced due to etching caused by the mosasaur's stomach acid during partial digestion than as a diagnostic feature or as an artifact of the preparation process.

The fragments when combined into a single bone fragment have a greatest length of 248mm however when one compares this with other taxa of cheloniid the fragment should be considered to represent almost half of the length of the complete bone. Using the Cretaceous Chelonioida *Toxochelys latiremus* as a reference the full length of the coracoid could be estimated to be approximately 550mm. From the approximate length of the coracoid an approximate carapace length can be determined following the ratio (using maximum proposed length) of Parham and Stidham (1999). Calculations using this ratio indicate that in ZFR16 the carapace length may be a minimum of 256.2cm or 2.562m

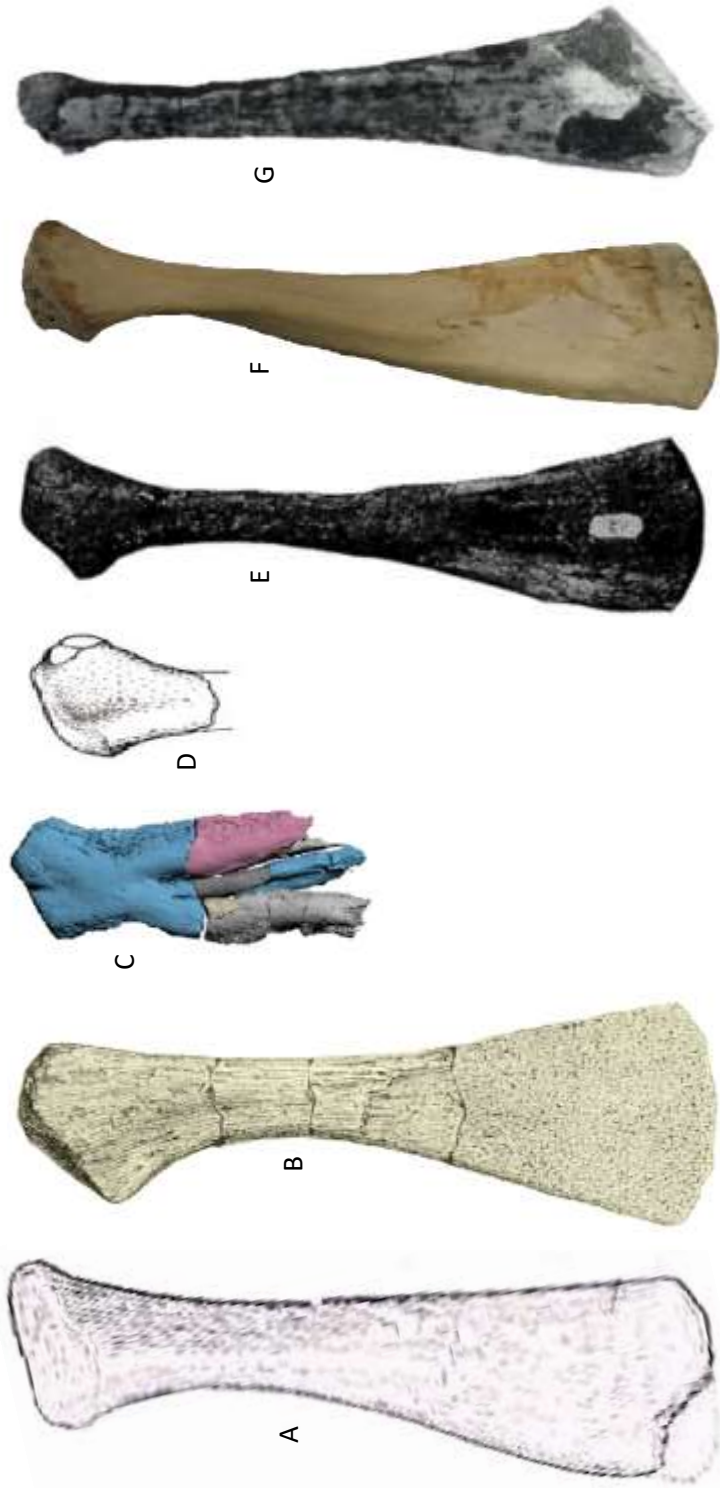


Figure 3.6: Coracoids of turtles compared to ZFR16. Scaled to in order for the coracoids to be of equal length, ZFR16 scaled to be equivalent to *Toxochelys*. A) *Protostega gigas* modified from Hay, 1908; Santonian of North America. B) *Toxochelys latiremis* modified from Cope, 1875; Late Cretaceous (Coniacian to Earliest Maastrichtian) of North America. C) ZFR16 reassembled using 3matic and Mimics software. D) *Terlinguachelys fischbecki* modified from Lehman and Tomlinson, 2004; Campanian of North America. E) *Mesodermochelys undulatus* modified from Hirayama and Chitoku, 1996; Santonian to Early Maastrichtian of Japan. F) *Chelonia mydas* Te Papa National Museum Collection Specimen DM 891; photograph taken 02.Nov.2015; Late Miocene to Recent, tropical and subtropical Oceans. G) Unnamed dermochelyid modified from Parham and Stidham, 1999; Campanian of North America

Discussion – Comparison with extinct marine turtles *Toxochelys latiremus* (Cope, 1875), *Mesodermochelys undulates* (Hirayama and Chitoku, 1996), *Terlinguachelys fischbecki* (Lehman and Tomlinson, 2004), *Protostega gigas* (Hay 1908), the Mesozoic dermocheylid described by (Parham and Stidham, 1999), and the modern marine turtle *Chelonia mydas* (DM 891 Te Papa National Museum Collection) have shown ZFR16 to have a unique coracoid morphology (Figure 3.6). ZFR16 is dorso-laterally flattened and proximally compressed compared to other turtle coracoids. While superficially the coracoid articulation surface angles appears similar to that of *Terlinguachelys fischbecki*, ZFR16 is twice the size, has less significantly less medial constriction, and is constricted medially at an even more proximal location on the shaft. The medial constriction is morphologically more similar to *Toxochelys latiremus* however the constriction is significantly closer to the anterior in ZFR16. Further the coracoid is much too wide to be included in the rod-like morphology of the dermocheylids and their close relatives.



Figure 3.7: Focus stacked photograph of the ZFR16 acid etched peripheral fragment

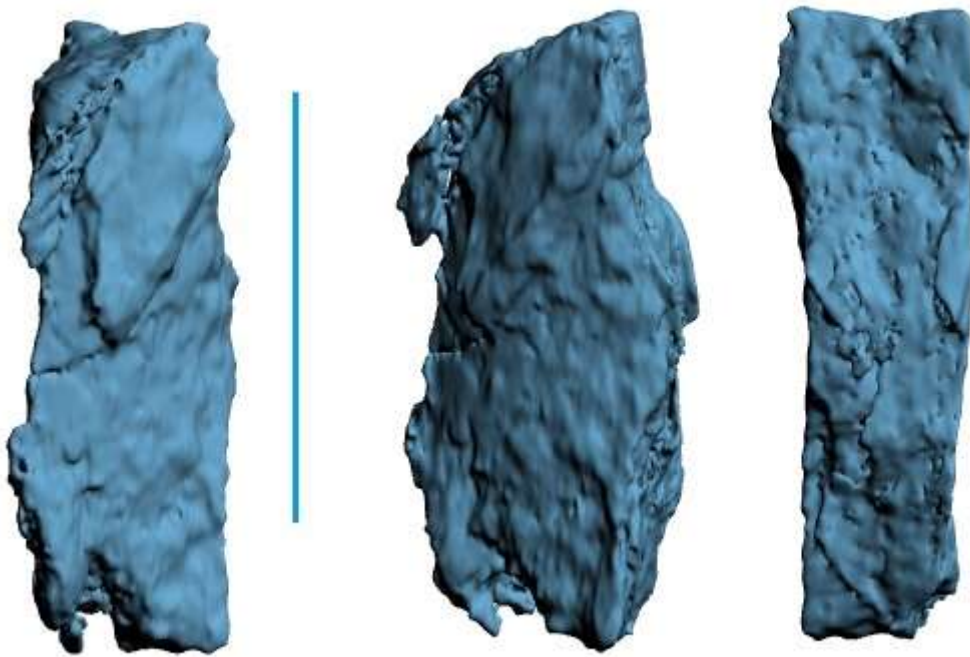


Figure 3.8: 3D model of the peripheral fragment created using the Mimics software. Blue line = 50mm

3.3.2 *Peripheral Fragment*

The ZFR16 peripheral fragment (Figure 3.7, Figure 3.8) is extremely degraded. The fragment is assigned as a peripheral due to its triangular cross section however identification beyond this point is effectively impossible. As the peripheral number is unknown it is not viable to estimate shell curvature based on the technique of Lehman and Tomlinson (2004).

Discussion – The peripheral appears to have been eaten away by acid. It is unlikely that this would be the result of the weak acetic acid used to prepare the specimen, especially as the *Mosasaurus mokoroa* specimen does not share the same appearance (Welles and Gregg, 1971). The coracoid fragments of ZFR16 show the same effect but to a lesser extent indicating that the effect is specific to the turtle remains, likely as a result of predation.

3.4 Summary

The Coracoid fragment is dorso-ventrally flattened as well as considerably wider than that of dermochelyids with medial curvature more in line with the Pancheloniid *Toxochelys* and can therefore be assigned to the family Cheloniidae. The peripheral fragment is too degraded to determine its carapace position whoever this degradation appears to be the result of predation and partial digestion by *Mosasaurus mokoroa*.

4 Chapter 4

The Palaeocene Turtle Plastron 2010.108.6

4.1 Locality and Horizon

Two elements of a turtle plastron were collected in September 2012 by Mr Leigh Love and Al Mannering from the Waipara River, North Canterbury. The specimen was accessioned into the collections of Canterbury Museum as 2010.108.6. The specimen consists of two plastral elements. The specimen is Teurian in age based upon the microfossil evidence cited by Mannering and Hiller (2008). The Waipara Greensand is generally considered shallow marine, possibly mid-shelf deposited (Browne and Field, 1985; Mayr and Scofield, 2014) and is sparsely fossiliferous but sea birds (Mayr and Scofield, 2014), neoselachian sharks of sixteen different genera (Mannering and Hiller, 2008), and two penguins (Slack et al., 2006) are known from the deposit.

4.2 Materials

Specimen 2010.108.6 comprises two plastral plate elements from a Cryptodiran turtle. Based upon the morphology of the elements these represent a hyoplastral fragment and a large fragment of the hypoplastron. Both fragments were prepared by Mr Alan Mannering before being deposited in the Canterbury Museum. The dorsal sides of the plates are covered in unprepared greensand matrix in order for the fossil to be more durable. Although this is important for the continued survival of the fossil, it required further virtual preparation using CT scanning and virtual dissection using the Materialise software suite in order to be readily described.

A combination of the surface fracturing on the ventral side of the plates and the distortion created by the pyritic inclusions in the greensand matrix supporting the plastron have limited the effectiveness of the virtual preparation process. Pyritic inclusions result in light radiation in the MRI slices which obscures the affected area making virtual preparation extremely difficult. It is entirely possible that the use of more advanced scanning such as those preformed using a synchrotron could avoid these complications but that is beyond the scope of this study.

4.3 Systematics

Testudines (Batsch, 1788)

Cryptodira (Cope, 1868)

Paracryptodira (Gaffney, 1975)

Panacryptodira (Joyce et al., 2004)

Macrobaenidae (Sukhanov, 1964)

While an explicit diagnosis of the Macrobaenidae does not exist (Parham and Hutchison, 2003), Macrobaenidae has been phylogenetically defined to refer to the most inclusive clade containing *Macrobaena mongolica* but not *Xinjiangchelys junggarensis*, *Sinemys lens*, or any species of Recent turtle (Rabi et al., 2014).

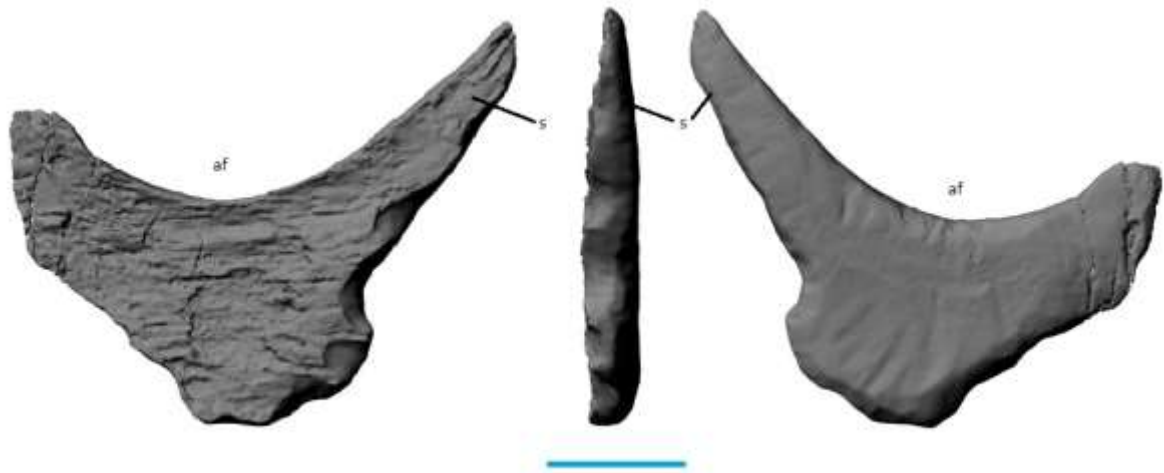


Figure 4.1: Hyoplastron from the Palaeocene specimen. Blue line = 50mm. Abbreviations: af, anterior fontanelle; s, sunburst splay projections

4.3.1 *Hyoplastron fragment*

The fragment has been assigned as a hyoplastron on the basis of the curvature of the anterior surface and the preservation of a large anterior projection and smaller more posterior splays (Figure 4.1 and Figure 4.2). The projections are morphologically equivalent to the splays of the irregularly edged ‘sunburst’ pattern seen in aquatic turtle plastrons and most similar to the splays of a hyoplastron.



Figure 4.2: focus stacked photograph of the hyoplastron

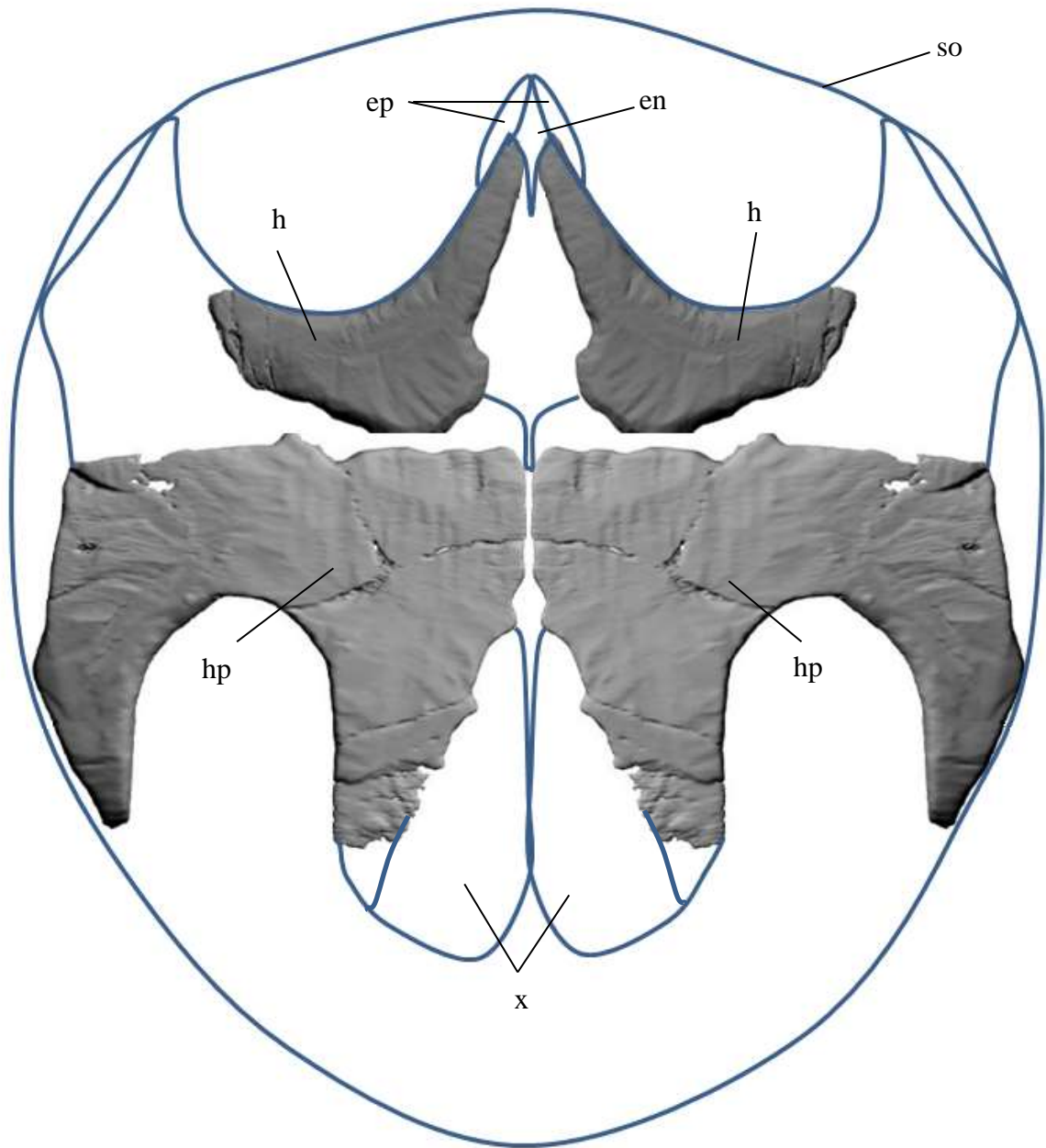


Figure 4.3: hypothetical plastron of the Palaeocene specimen. Abbreviations used: ep, epiplastron plate; en, entoplastron plate; h, hyoplastron plate; hp, hypoplastron plate; x, xiphiplastron plate; so, shell outline

The hyoplastron fragment consists of the most proximal and a subsequent splay of the limited ‘sunburst’ pattern. This pattern is used to describe the partial reduction of the plastral plate into a series of spikes, usually on the medial surface, in members of the cheloniidae (Pritchard, 2008).

The medial side of the plastral fragment retains evidence of the edging of the plate in the form of the limited ‘sunburst pattern’ splays, indicating that the medial side is morphologically more definitive. The missing posterior and lateral ends make it difficult to ascertain the exact morphology of the entire hyoplastron. The curvature at the anterior end formed by the preserved splay allows some morphological comparisons to be made and an approximate inferred shape can be determined (Figure 4.3) however without further comparative contemporaneous material the true morphology of the hyoplastron of this undescribed species will remain unknown.

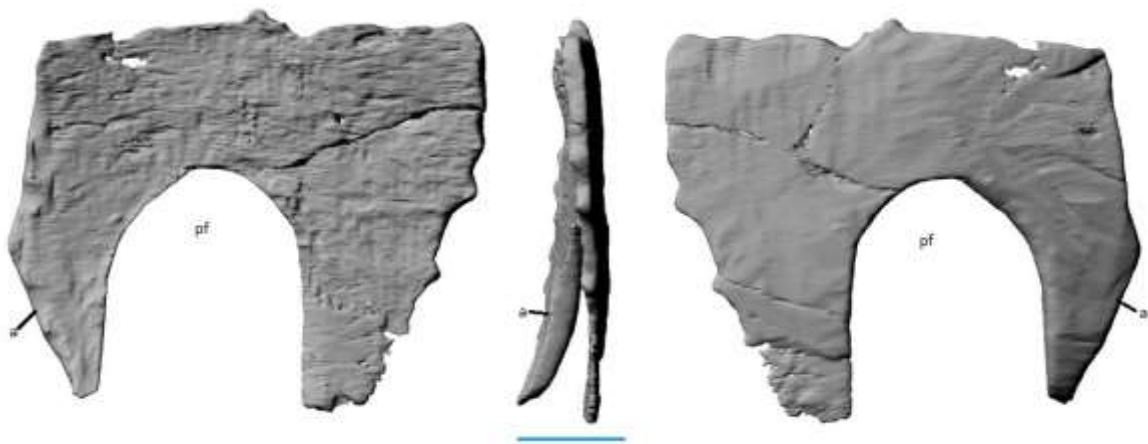


Figure 4.4: Hypoplastron from the Palaeocene specimen. Blue bar = 50mm. Abbreviations used: pf, posterior fontanelle; a, peripheral articulation surface



Figure 4.5: focus stacked photograph of the hypoplastron of the Palaeocene specimen

4.3.2 *Hypoplastron fragment*

This fragment has been determined to be a left hypoplastron fragment (Figure 4.4 and Figure 4.5). The assignment has been made due to a collection of features: 1) The posterior fontanelle curvature is extensive and significantly narrower than those seen at the anterior end of hypoplastrons. 2) The curvature and articulation of the distal margin in the anterior section indicates an intimate articulation between the plate and the peripherals of the carapace, however this articulation is not consistent with any marine hypoplastron. 3) The medial posterior edge appears to show evidence of articulation with another plastral plate but based upon its curvature this could not articulate with another mirrored hypoplastron indicating it cannot be a hypoplastral element as hypoplastrons do not articulate with other plastral plates medially to this extent. The plate is determined to be the left plate due to the curvature of the posterior distal projection, as if this plate was the right side the projection would be medial and the curvature would decrease available space in the body cavity.

The pronounced extension of the posterior could potentially be consistent with the combination of a hypoplastron and a xiphiplastron, despite no clear articulated surface being preserved. The size of the plate and the shape of the posterior fontanelle might imply such a relationship in a marine turtle however the shape of the medial edge and lack of articulation surface within the fossil and the potential articulation surface indicated by the edge of the medial side are not consistent with this theory.

The hypoplastron appears to be for the greater part intact despite apparent surface fracturing. However fragmentation has occurred at the most posterior section of the medial process and in places along the articulation surface where the hypoplastron and hyoplastron interact. Limited evidence of a sunburst growth pattern is visible in photographs of the plate (Figure 4.5) as the plate appears to have grown in irregular splays from the center of the plate.

Discussion - Comparisons with a variety of extant and extinct marine turtles (Figure 4.6) has made it apparent that the hypoplastron morphology of 2010.108.6 is significantly different from most marine turtle morphologies (Williston, 1925; Hirayama, 1994a; Wyneken, 2001; Lehman and Tomlinson, 2004; Parham, 2005). The hypoplastron for this specimen appears to have intimate articulation with peripherals much further posteriorly than normal and a less open posterior fontanelle. There are limited similarities with *Puppigerus*, *Lepidochelys*, and *Glyptochelone* however the morphological differences clearly exclude the specimen from being assigned to any of these genera.

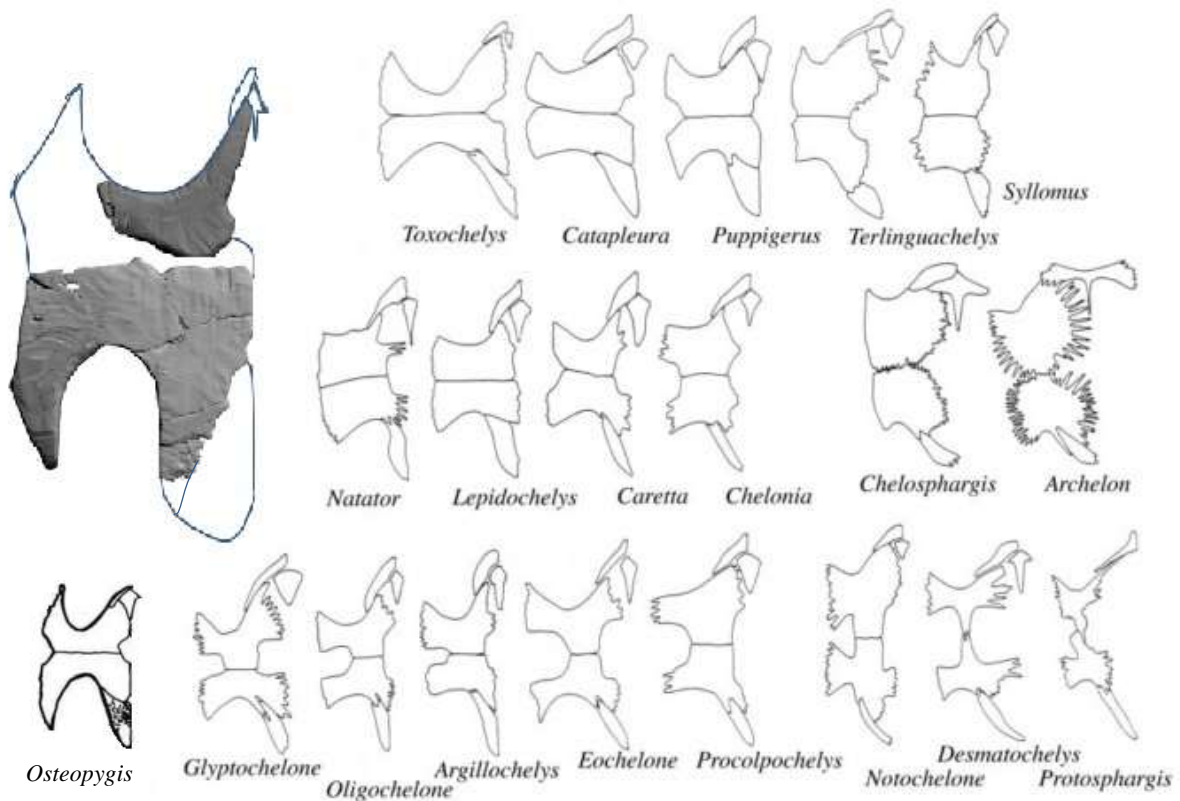


Figure 4.6: comparison of the left side of the proposed plastral morphology (Figure 4.3) of the Palaeocene specimen and the macrobaenid postcrania of *Osteopygis* [modified from Hirayama (1994)] with a variety of marine turtle plastron left sides modified from Lehman and Tomlinson (2004)

Morphologically the intimate articulation between the hypoplastron and the peripherals is intriguing for a marine turtle. The only other genera known to have this was *Osteopygis* however the validity of this taxon has been disputed by Parham (2005). Parham has determined that the postcranial anatomy of *Osteopygis* is more consistent with basal cryptodires, specifically the macrobaenids. Macrobaenids are large freshwater turtles known from North America and Asia. This specimen is from a mid to shallow marine environment which is not consistent with the habitat of macrobaenids however the articulation of the hypoplastron with the peripherals is consistent. Sadly lacking the skull of the specimen means further comparison with *Osteopygis* is impossible. It is possible that this specimen is of a freshwater individual that has

been transported by rivers into a marine environment however it is also possible that this is a unique New Zealand marine fauna that retained or redeveloped ancestral traits. As macrobaenids are only known from the northern hemisphere in Asia, Canada, Morocco, and North America (Hutchison and Holroyd, 2003; Lynch and Parham, 2003; Parham, 2005; Jalil et al., 2009; Vandermark et al., 2009) the Palaeocene specimen would likely still represent a new species.

4.4 Summary

Specimen 2010.108.6 contains a hyoplastral fragment and a mostly intact hypoplastral plate. Amongst described taxa the plastron is morphologically most consistent with the post-crania of *Osteopygis* due to the morphology of the posterior fontanelle, and intimate articulation between the plastron and the peripherals. Due to *Osteopygis* being a chimerical species the post-crania has been reassigned to the freshwater Macrobaenidae by Parham (2005) and as such the Palaeocene specimen must also be assigned to the Macrobaenidae. Specimen 2010.108.6 is therefore considered that to be a freshwater turtle that was transported and deposited into the marine environment.

5 Chapter 5

The Eocene Collection: ZFR105

5.1 Locality and Horizon

ZFR105 was probably found in the Parkside Quarry (Fordyce, 1979) sometime between 1906 (when the quarry opened) and 1949 (when it was first mentioned in the literature) (New Zealand Fossil Record Number J41/f0047; Marples 1949). The attribution to this quarry is based on the similarity between the matrix still attached to some specimens and specimen from the quarry. Parkside Quarry contains well sorted Ototara Limestone bryozoan grainstone with little or no volcanic ash and a creamy colour and uniform texture. This formation is of Late Eocene age (dated using strontium isotopes at 35.18-34.13Ma; Nelson et al., 2004). The Ototara Limestone is considered to have been deposited on a palaeohigh removed from terrestrial input (Thompson, 2013) and is an exceptionally pure with a 93.4% median purity (Mortimer and Strong, 2014).

5.1 Material

Canterbury Museum collection ZFR105 consists of: a proximal left humerus of a cheloniid turtle broken into three pieces and reconstructed (Figure 5.1 and Figure 5.2); the broken posterior portion of right mandible comprising most of the prearticular and a small part of the angular though missing the anterior-most (broken behind the Inferior alveolar foramen) and posterior-most parts (missing the articular) of the angular (Figure 5.4 and Figure 5.6); the majority of the right plastron comprising the inner portion of the right hyoplastron and hypoplastron (Figure 5.7); a partial suprapygial plate (Figure 5.6 and Figure 5.9); two peripherals, an articulated pair broken into three pieces and reconstructed (Figure 5.10 and Figure 5.12) and an isolated one (Figure 5.11 and Figure 5.12), a medial section of a coastal carapace fragment

(Figure 5.13 and Figure 5.14), and some unidentifiable small fragments. Fordyce (1979) considered this specimen to include two broken plastron or carapace plates still embedded in matrix, fragments of ribs, possible fragments of skull, the head of a humerus, and indeterminate pieces of bone. Since 1979 when Fordyce catalogued it this specimen has undergone acid and manual preparation that has enabled more rigorous identification of the various elements

5.2 Systematics

Testudines (Batsch, 1788)

Chelonioidea (Baur, 1893)

Cheloniidae (Oppel, 1811)

Following Grant-Mackie et al. (2011)

Eochelone (Dollo, 1903)

Eochelone is diagnosed as having an obvious anterior indentation of the nuchal plate when viewed dorsally and obvious rounded projections at the junctions of the nuchal with the adjacent marginals. Further the humerus is described to be thalassic but less so than modern turtles while the ectepicondylar canal of the humerus is higher and more laterally placed than in modern marine turtles. The plastron has relatively large fontanelles while the carapace is cordiform, thin; low arched, both longitudinally and transversely (Grant-Mackie et al., 2011).

Eochelone monstigris (Grant-Mackie et al., 2011)

This species is significantly larger than other member of the genus, *Eoachelone brabantica* with a ventrally curved humerus at the distal end. The nuchal is less inflated and the projections at the nuchal marginal junctions are less pronounced while the phalanx of digit I is more robust.

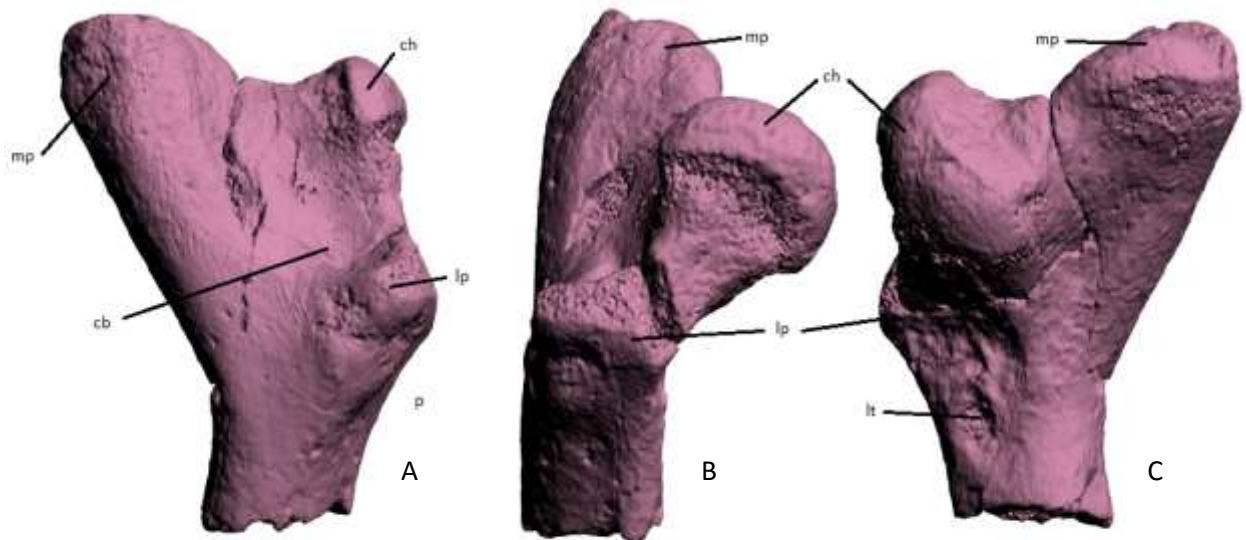


Figure 5.1: Humerus fragment of ZFR105 in ventral (A), anterior (B), and dorsal (C) views. Blue line is equivalent to 50 mm. Abbreviations used: cb, coracobrachialis brevis muscle insertion scar; ch, caput humeri; lp, lateral process; lt, latissimus dorsi muscle and teres major muscle insertion scar; mp, medial process



Figure 5.2: focus stacked photograph of the humerus fragment

5.2.1 *Left Humerus*

The proximal end or head of this bone is all that is contained within the specimen (Figure 5.1 and Figure 5.2). The humerus has been reconstructed following breakages during preparation. Turtle humeri are diverse between species however this element is most similar to the superfamily Chelonioidea due to the nearly straight shaft and the lateral process being distal to the medial process (Hirayama, 1994b). Comparison with a selection of Chelonioidea members shows overall morphological similarities, firmly confirming ZFR105 as a member of this superfamily (Figure 5.3).

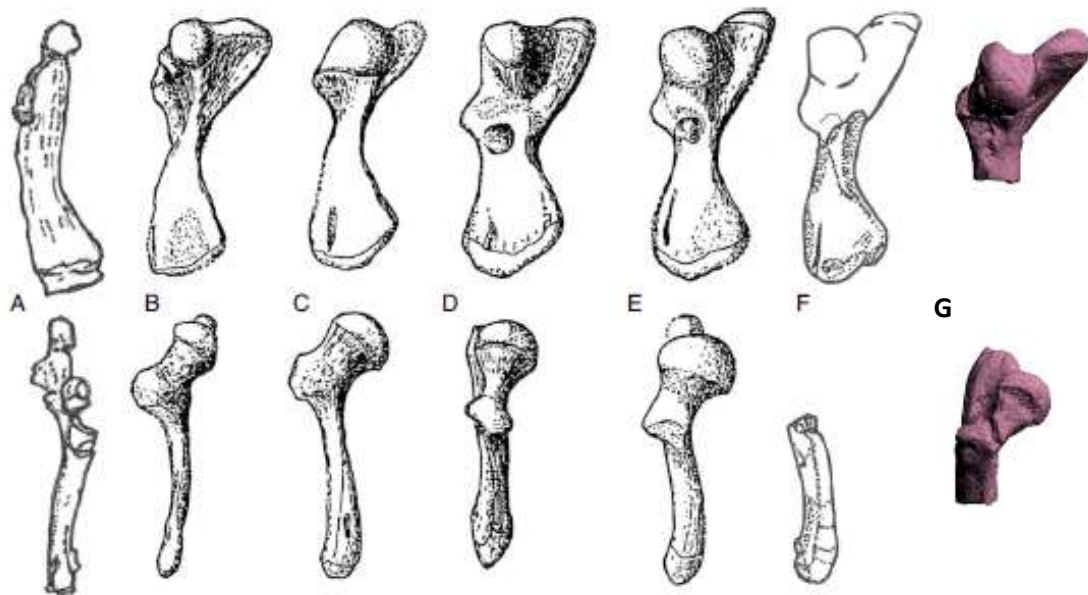


Figure 5.32: Comparison of ZFR105 humerus with line drawings of various chelonian left humeri. All humeri have been reduced to the same length as in Hirayama 1992. Each pair shows dorsal (upper) and anterior (lower) views. (A) Pahi turtle (?Toxochelyidae indet.); (B) *Toxochelys moorevillensis* Zangerl, 1953 (Toxochelyidae), Campanian; (C) *Lophochelys stenoporus* (Hay 1905) (Cheloniidae), Campanian; (D) *Allopleuron hoffmanni* (Gray 1831) (Allopleuronidae), Maastrichtian; (E) *Eochelone brabantica* Dollo, 1903 (Cheloniidae), Lutetian; (F) *Eochelone monstigris* n. sp., Priabonian (Runangan), with dorsal view reconstructed and lower view untouched; (G) ZFR105 (Late Runangan to earliest Whaingaroan) Modified from Grant-Mackie et al. (2011).

The ZFR105 humerus exhibits a number of key features which can be used to narrow down the Chelonioidea superfamily members namely: (1) a flattened thalassic shaft (0.79) though less flattened than modern chelonids (0.6 for *Lepidochelys*); (2) lateral process reduced and flattened on the ventral plane; (3) the medial process projects proximally beyond the extent of the caput humeri; caput humeri is large and has a significant narrowing distally; (4) in anterior view the caput humeri is deflected from the shaft at an angle of c. 120 degrees; (5) m. coracobrachialis brevis insertion scar is pronounced but shallow; in ventral view the angle between the lateral process and the distal shaft is obtuse. These key features are most consistent with the Eocene turtle *Eochelone* as it is described by Hirayama (1994), Grant-Mackie et al. (2011), and in Dollo (1903; translated).

The Humerus is incomplete with a length of 93.39mm; comparison with other turtle material indicates this length is likely only half of the full length of the full humerus making the approximate length of 186.74mm. *Eochelone barbantica*, the type specimen for *Eochelone* from Belgium, has a humerus of up to 141mm making this specimen significantly larger. The ZFR105 humerus is closer to the estimated proportions of *Eochelone monstigris*, described by Grant-Mackie et al. (2011) from Northland, New Zealand.

The Northland humerus lacks the proximal end making comparisons of the ZFR105 key features impossible however based upon the similarity between the proximal head of *Eochelone barbantica* combined with the similarities in dimensions with the *Eochelone monstigris* humerus, ZFR105 can be tentatively be assigned to the species *Eochelone monstigris*. The humerus for ZFR105 is approximately 1.29x (table 5.1) the size of *Lepidochelys*. *Lepidochelys* has a carapace length of 700mm indicating ZFR105 would have had a carapace length of 900mm, the same carapace length as that of Grant-Mackie et al. (2011).

	Measurements (mm)	
Humerus Head	ZFR105	RE. 7395 (complete)
Anterolateral plane	76.53 x 93.39	67 x 145
Ventrodorsal height	65.15	55
Medial process deflection	143.17°	158.5°
Shaft height/width	21.22/27.02	15/25
Shaft to Caput Humeri angle	120.83°	121°
Caput humeri projection	39.28	28
Caput Humeri to medial process	137.11°	132°
Lateral Process width	6.43	12
Lateral process deflection from shaft	156.03°	120°
Caput humeri to Lateral process	155.45°	127°
Lateral process to medial process	119.68°	112°

Table 5.1: Measurements of the humerus fragments of ZFR105 against *Lepidochelys* RE 7395 currently in storage at Te Papa Museum, Wellington

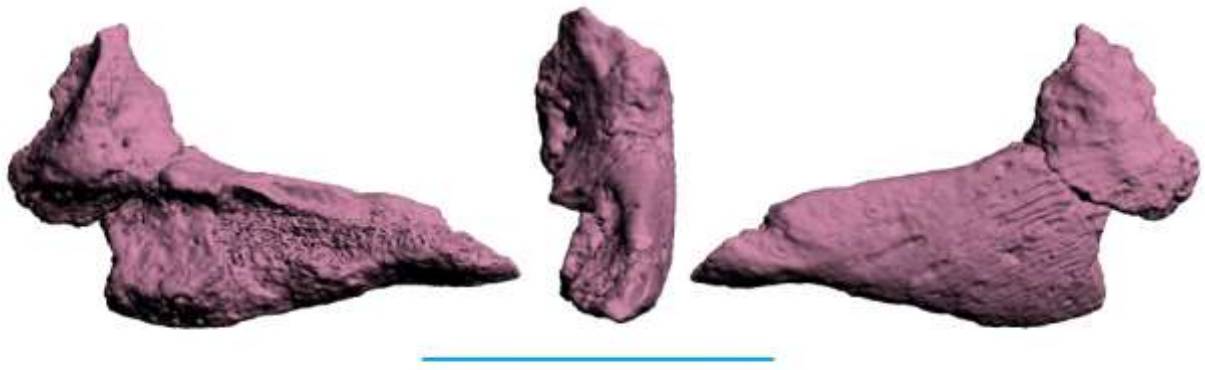


Figure 5.4: ZFR105 Mandible fragment. From left to right: medial view; anterior view; distal view. Blue line = 50mm

5.2.2 Mandible Fragment

The mandible present in the ZFR105 specimen is only a small fragment of a complete right cheloniid mandible (Figure 5.4, Figure 5.6) however it is still clearly discernable as part of the mandible when viewed medially (Figure 5.5). The key measurements of this fragment are: (1) the posterior entrance of the Meckelian fossa slopes ventrally steep angle (c 60 degrees) from the coronoid process; (2) anteriorly the coronoid process projects at 130 degrees from the angular. These angles are significantly smaller that of *Lepidochelys* (Table 5.2)

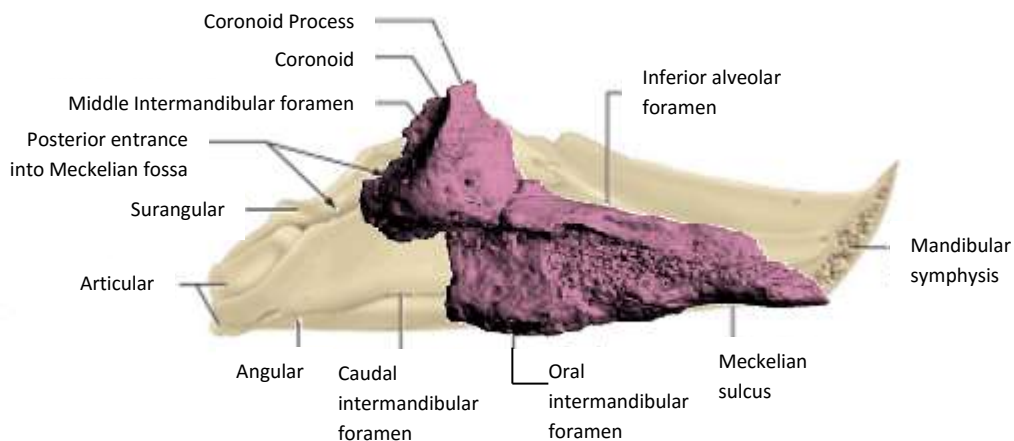


Figure 5.5: ZFR105 Mandible fragment overlaid on the medial view of a snapping turtle mandible. Modified from Iuliis and Pulera (2006)



Figure 5.63: focus stacked photograph of the mandible and suprapygal fragments of ZFR105

	Measurements (mm)	
Mandible Fragment	ZFR105	RE. 7395 (complete)
Anterolateral plane	73.31 x 19.51	102.98 x 98
Ventrodorsal height	39.65	30
Meckelian fossa to coronoid process angle	60.56°	101°
Coronoid process to Inferior Aveolar Foramen	128.04°	154°

Table 5.2: Measurements of the mandible fragments of ZFR105 against *Lepidochelys* RE 7395 currently in storage at Te Papa Museum, Wellington

5.2.3 Plastron Fragments

ZFR105 contains two articulated plastral plates, namely the right hyoplastron and hypoplastron (figure 5.7). Due to overpreparation or acid damage the plates have been mounted to prevent breakage due to their fragility. The mounting prevents CT scanning techniques from being used on the plastron as well as obscuring the dorsal side. The articulated plastron is 378.67mm long with the hyoplastron and hypoplastron making up 186.67mm and 192mm respectively. The features of note include: (1) The medial margins of the hyoplastron and hypoplastron form a distinct concavity on the ventral surface. (2) The lateral projections are not present however the curvature of the anterior of the hyoplastron is preserved. (3) A ‘sunburst’ growth pattern (Pritchard, 2008) is visible on the hyoplastron but not the hypoplastron. The morphologically closest Chelonioidea family members to ZFR105 are *Eoachelone* and *Oligoachelone* when compared to the line drawings presented by Lehman and Tomlinson (2004).

The plastron of ZFR105 noticeably differs from that of *Eoachelone barbantica* as illustrated in Hirayama (1994) and Lehman and Tomlinson (2004). The angle of the anterior fontanelle of the hyoplastron closely resembles *Eoachelone barbantica*. The lateral fontanelle is

morphologically similar however it is less extensive even than *Oligochelone*. Equally while the hyoplastron is morphologically similar the hypoplastron is significantly larger. ZFR105 appears to be transitional between *Eochelone* and *Oligochelone* when only considering the hyoplastron however the hypoplastron does not readily match either species profile as it is too large compared to the hyoplastron. As no plastral elements of *Eochelone monstigris* have been discovered it is possible that this species had a larger hypoplastron due to its comparatively larger size. A proposed transitional plastron for ZFR105 can be seen in figure 5.8

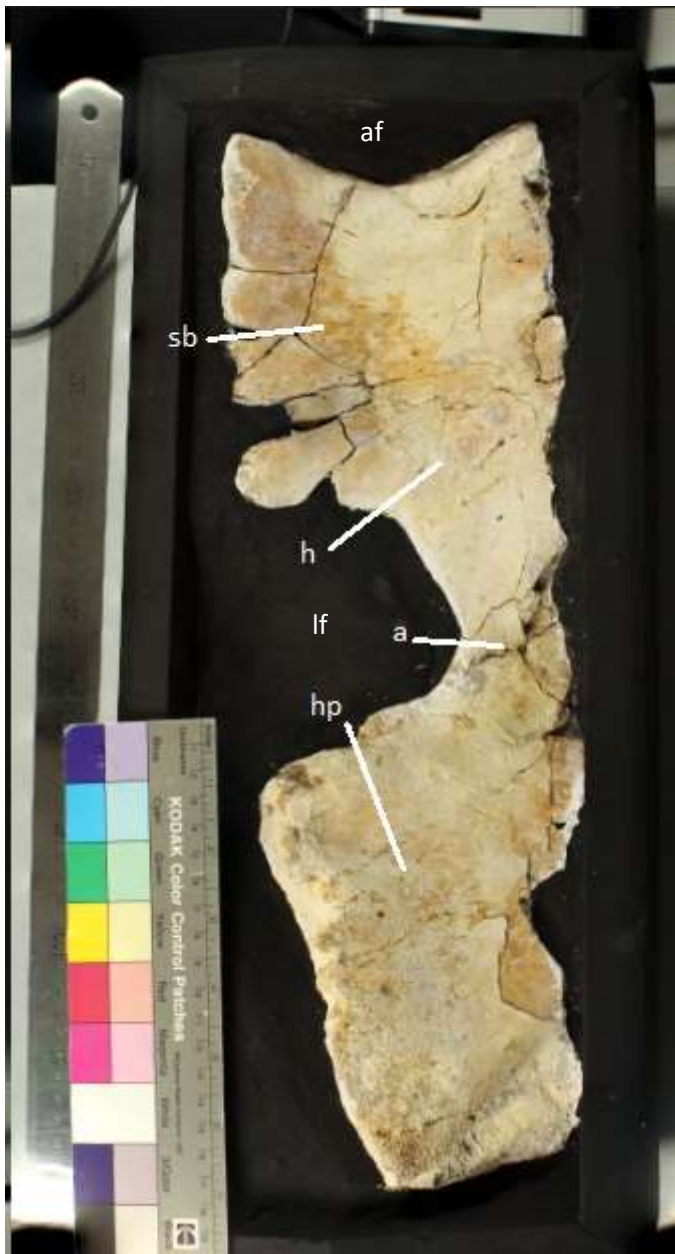


Figure 5.7: Photograph of the articulated hyoplastron and hypoplastron plates from ZFR105.

Abbreviations: h, hyoplastral plate; hp, hypoplastral plate; a, articulation zone; sb, sunburst growth pattern; af, anterior fontanelle; lf, lateral fontanelle

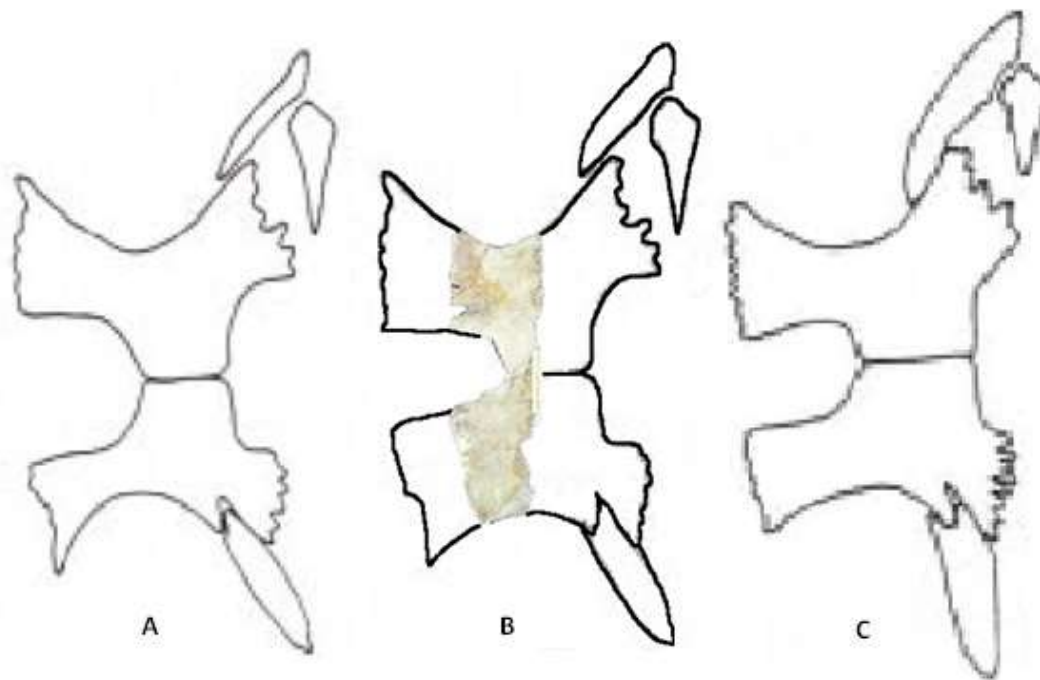


Figure 5.8: Comparison of right plastrons, scaled to have hyoplastrons of the same size. A) *Eoachelone*; B) ZFR105; C) *Oligoachelone*; A and C are modified from Lehman and Tomlinson (2004) B is a proposed transitional complete reconstruction for *Eoachelone monstigris* based upon the plastron of ZFR105

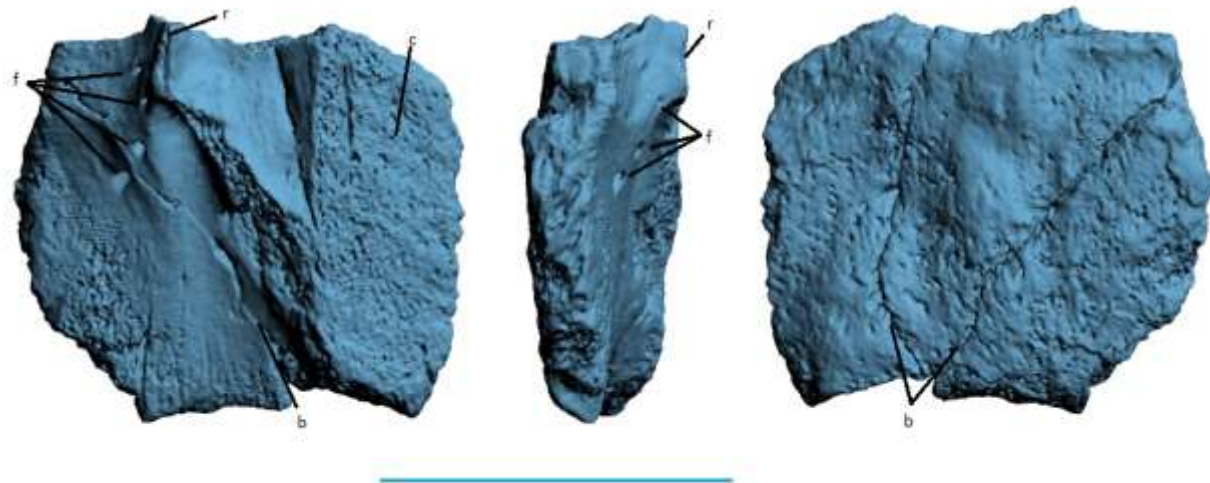


Figure 5.9: The suprapygal plate viewed in dorsally, medially, and ventrally. Blue line = 50mm. Abbreviations: b, breaks in the fossil during preparation; c, surface cut during extraction; f, foramen; r, ridge left by broken articulation surface

5.2.4 *Suprapygal Plate*

A small carapace segment from the ZFR105 specimen is considered to be a suprapygal plate (Figure 5.6, Figure 5.9). A section of the plate has been sawn off probably during the excavation of the fossil from Parkside Quarry. The presence of prominent ridges and foramen makes this plate more likely to be medial however the lack of a nuchal crest or vertebral attachment zones means it is unlikely to be part of the nuchal or coastals (Williston, 1925). The suprapygal is still medial but lacks vertebral attachments and so this is considered to be more likely.

As this is only a partial plate it is difficult to determine which side of the central plate this is. Due to the presence of both right plastral plates and a right humerus fragment, this fragment is likely also from the right side. This is also reinforced by the thickening of the left side of the plate.

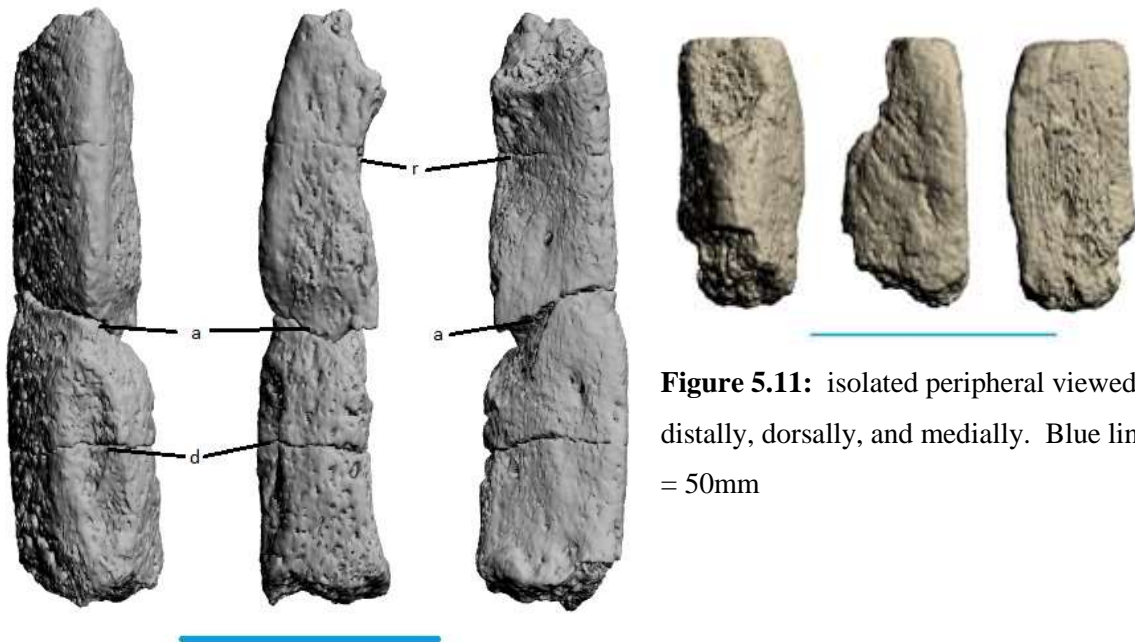


Figure 5.11: isolated peripheral viewed distally, dorsally, and medially. Blue line = 50mm

Figure 5.10: articulated peripherals viewed distally, dorsally, and medially. Blue line = 50mm. Abbreviations: a, articulation zone; d, shallow depression; r, possible area of rib articulation



Figure 5.12: focus stacked image of the two peripheral fragments.

5.2.5 *Peripherals*

ZFR105 contains three peripherals, an articulated pair (Figure 5.10, Figure 5.12) and one isolated peripheral (Figure 5.11, Figure 5.12). None of the peripherals contain deep sockets for rib articulation however the curvature of the articulated specimen could potentially have a shallow rib connection. During preparation the articulated pair was broken into three pieces and was reconstructed. Due to the size of the isolated peripheral it is not possible to determine whether it retains any natural curvature. The articulated peripherals have a slight degree of curvature and widens posteriorly. The articulated peripheral does contain a broad shallow depression.

The cross sectional profile of the peripherals indicates that these peripheral fragments are from the third, fourth, or fifth peripheral. The angle of divergence between the dorsal and ventral faces is 49.38° for the articulated peripherals indicating an arched shell form (Lehman and Tomlinson, 2004).

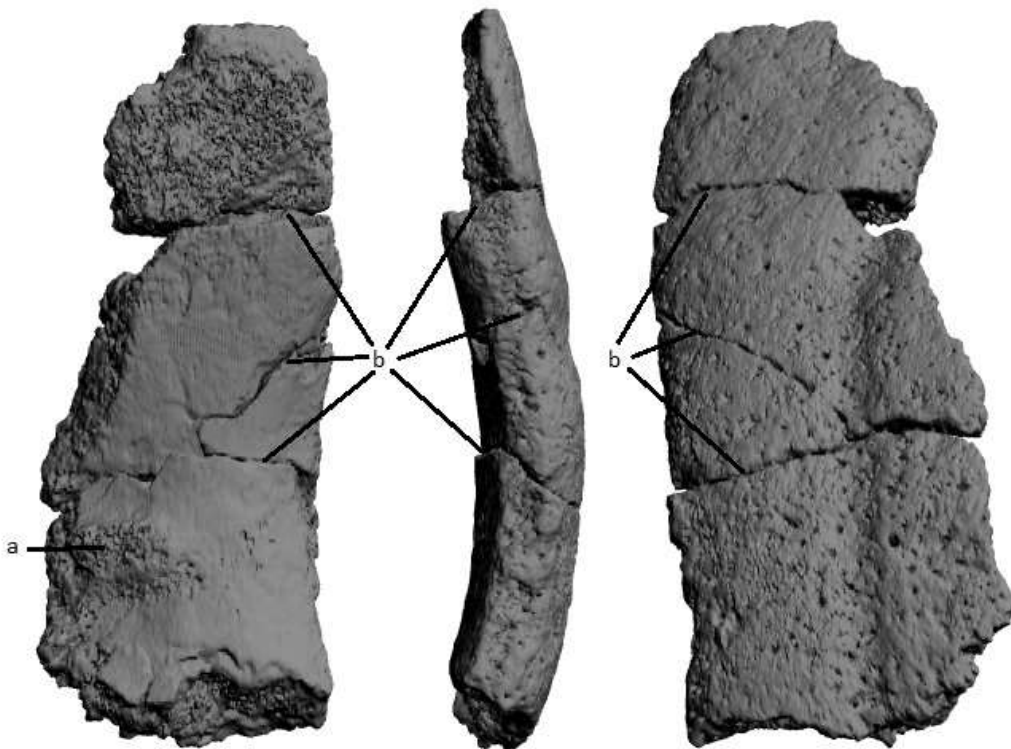


Figure 5.13: coastal viewed ventrally, anteriorly, and dorsally. Blue line = 50mm. Abbreviations: a, articulation surface remnant; b, breaks in the fossil repaired during preparation



Figure 5.14: focus stacked photograph of the coastal element

5.2.6 *Coastal Carapace fragment*

One fragment of carapace is preserved as part of the ZFR105 specimen (Figure 5.13, Figure 5.14). This fragment maintains a measure of its natural curvature with the ventral face being clearly concave. The fragment has been reassembled following breakages during preparation. There is the presence of an articulation surface on the medial edge of the ventral side, presumably where the vertebrae connected to the carapace (Pritchard, 2008). This connection indicates that the most medial edge of the coastal likely connected to the neural. The position of the coastal is unclear due to the lack of a discernable rib or well preserved articulation surface. The lack of pronounced thickening on the anterior edge indicates this was not part of the nuchal however the curvature of the coastal indicates it is likely from the anterior portion of the carapace.

5.2.7 *Unidentified fragments*

There are a number of small fragments of bone associated with ZFR105. Due to the lack of diagnostic value, detailed descriptions are not included however 3D PDF format files of the fragments are available.

5.3 *Summary*

Based on humeral and plastral evidence ZFR105 can be confidently assigned to the genus *Eochelone* (sensu Grant Markie et al. 2011.) As the type material of the sole Southern Hemisphere species of this genus -*Eochelone monstigris* (from Northland, New Zealand) it is not possible to assign ZFR105 to this taxon with certainty however this does seem probable. The estimated size and humeral morphology of ZFR105 and the type specimen of *Eochelone monstigris* are extremely similar as are the ages and they are relatively geographically close (See

Figure 5.15). This study recommends assigning ZFR105 to *Eochelone monstigris*. By assigning ZFR105 to *Eochelone monstigris* the range of the species must be expanded to include the East Coast South Island of New Zealand as far south as Oamaru (Figure 5.15).

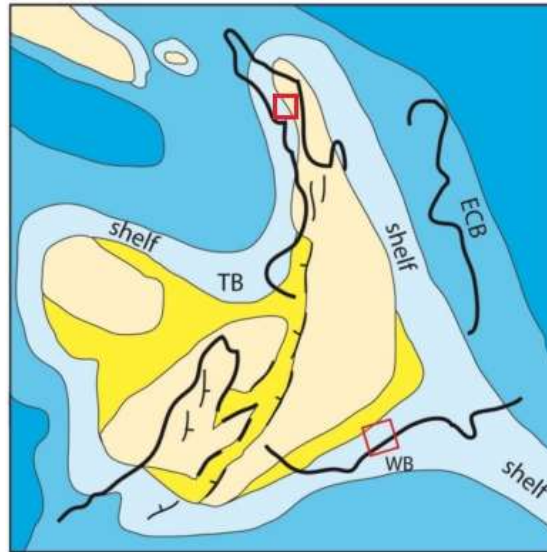


Figure 5.15: map of the New Zealand during the Eocene (modified from Thompson, 2013). Red squares indicate the areas where *Eochelone monstigris* specimens have been found. The thick red square is the holotype specimen and previous range while the thin square is this study.

Abbreviations: TB, Taranaki Basin; ECB, East Coast Basin; WB, Waitaki Basin

Using the aforementioned assignments, the bones have been plotted on a generic illustration of a cheloniid turtle (figure 5.16.). The majority of the fragments that comprise ZFR105 are from the right side of the skeleton. For this reason fragments without a clear orientation have been indicated as belonging to the right side.



Figure 5.16: *Eochelone* skeleton viewed ventrally modified from Hirayama (1994). Red areas indicate sections of the skeleton present in ZFR105; unidentifiable small fragments have been omitted.

6 Chapter 6

The Miocene Penguin: ZFp1134

6.1 Overview

This fossil (ZFp1134) held in the collections of the Canterbury Museum was originally considered to be the remains of an Osteichthyes (fish); following preparation it was considered to probably belong to the Testudines. Further study as part of this thesis has determined that this is also incorrect and ZFp1134 should be considered as avian, specifically a penguin (Aves: Sphenisciformes).

6.2 Locality and Horizon

The penguin remains were found in a concretion near the Glenafric farm station, North Canterbury. Concretions from this area are sourced from the sandstone-siltstone lithofacies of the Mt Brown Formation. The exact age of the concretions themselves within the formation is unknown as they lack index fossils (Feldmann et al., 2006) however the concretionary beds are limited to the upper part. The Mt. Brown Formation is considered Early to Middle Miocene (late Otaian to Waiauan) in age however concretions are limited to the sandstone-siltstone lithofacies which is present at the top of the formation (Lillburnian to Waiauan) (Browne and Field, 1985; Andrews et al., 1987). The concretions weather out of the cliff face above Glenafric beach and are commonly collected by fossil hunters. This formation is known usually for decapod crustaceans, a number of holotypes of which have been discovered there (Glaessner, 1960; Feldmann et al., 2006).

6.3 Material

The concretion containing the material has been partially prepared by the Canterbury Museum to expose a number of bones (Figure 6.1). Preparation was taken further using the Mimics Software Suite in order for the assemblage to be properly described. All the material was described according to Baumel and Witmer (1993).



Figure 6.14: High resolution photograph of ZFp1134. Abbreviations used: s, Synsacrum; df, Distal femur fragment; rf, Radius fragment; tv, Thoracic vertebra. Photograph taken by Paul Scofield

6.4 Systematics

Aves (Linnaeus, 1758)

Sphenisciformes (Sharpe, 1891)

Spheniscidae (Bonaparte, 1831)

Pygoscelis (Wagler, 1832)

c.f. *Pygoscelis tyreei* (Simpson, 1972)

The holotype for this species is currently stored at the Canterbury Museum as CM AV 22631.

This species stood between seventy and eighty centimetres. Comparisons between the holotype and ZFp1134 show similarities in the size and morphology of the femur and radius.

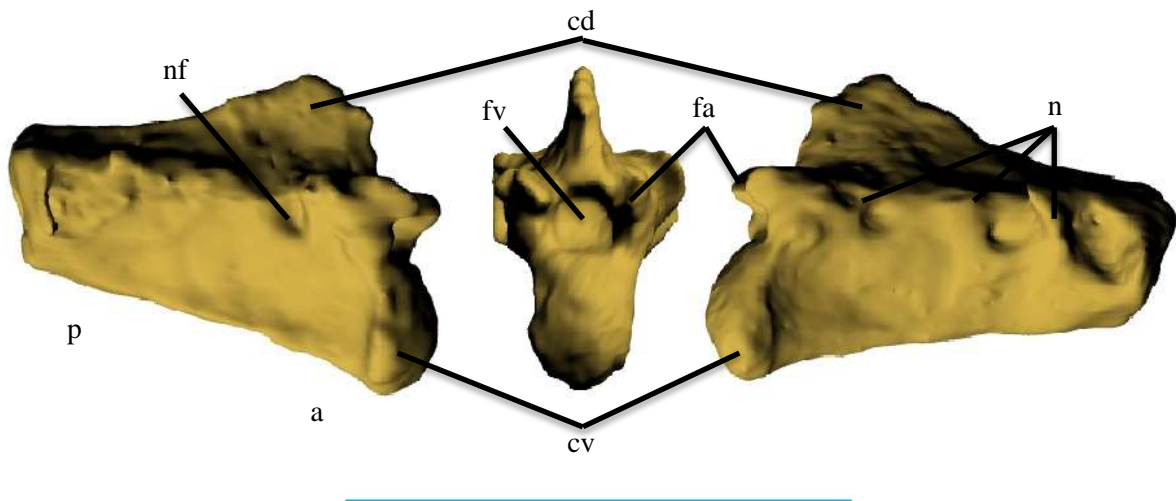


Figure 6.2: 3D model of the synsacrum created using the Materialise Software Suite. Blue line = 50mm. Abbreviations: a, Anterior; p, Posterior; nf, Nutrient foramen; fv, Foramen vertebrate (sediment infill still present); cd, Cresta dosalis; cv, Cresta ventralis; fa, Facies articulares; n, Notaria.

6.4.1 Synsacrum

A cursory examination of this element identified this bone as a cervical vertebra and led to ZFp1134 being considered a member of the Testudines. Upon segmentation and further virtual preparation this was clearly revealed to be an avian synsacrum fragment

(Figure 6.2) consisting of the three ankylosed anterior vertebrae. The element has been highly weathered both externally and within the matrix, especially on the posterior face, resulting in the appearance of a single elongate vertebra. Closer inspection reveals three notaria and the worn remains of the processus costalis. As the detail illustrated and described is still mostly encased in matrix it is easy to see how this was misinterpreted. The foramen vertebrate does not appear to continue through the bone in Figure 6.2 because sediment is still included within the foramen vertebrate due to difficulties in differentiation between the matrix and fossil in the Mimics Software.

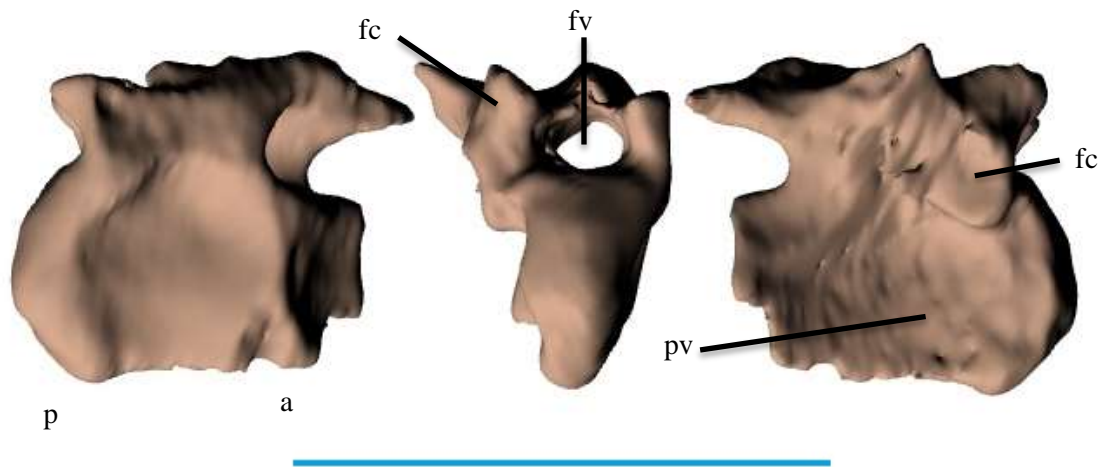


Figure 6.3: 3D model of the deformed thoracic vertebra. Blue line = 50mm. Abbreviations used: a, Anterior; p, Posterior; fc, foveae costalis; fv, Foramen vertebrate; pv, Processus ventralis.

6.4.2 *Eroded Thoracic Vertebra*

A vertebra closely associated with the synsacrum fragment is present in the concretion (Figure 6.3). Due to the erosion of the vertebrae it is difficult to ascertain the exact vertebral number but it is considered closely related to the known synsacrum fragment due to its morphology and length. It appears to have lost the processus spinosus and the zygapophyses are also eroded. The fovea costalis is well developed indicating a rib attachment. The morphology differs from the synsacrum vertebrae and does not match the morphologies of a pygostyle or cervical vertebrae.

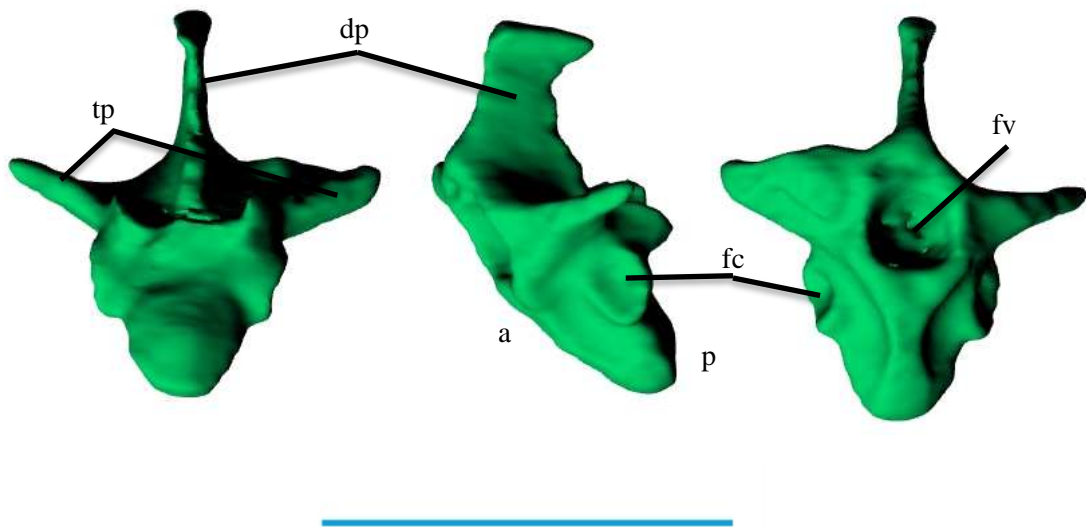


Figure 6.4: 3D model of thoracic vertebra exhibiting fovea costalis. Blue line = 50mm.

Abbreviations used: a, Anterior; p, Posterior; fv, Foramen vertebrae; fc, Fovea costalis; tp, Transverse process; dp, Dorsal process.

6.4.3 *Thoracic Vertebra*

The second thoracic vertebra shows the presence of the rib attachment fovea, the fovea costalis (Figure 6.4). When combined with the morphological differences compared to other vertebrae this excludes any interpretation other than a thoracic vertebra. Due to the pronounced processes and relatively shortened anterior-posterior length this is likely a higher numbered thoracic vertebra and subsequently closer to the synsacrum. As was previously stated for the synsacral vertebrae, the foramen vertebrae could not be fully cleared of sediment due to difficulties in differentiation between the sediment and bone.

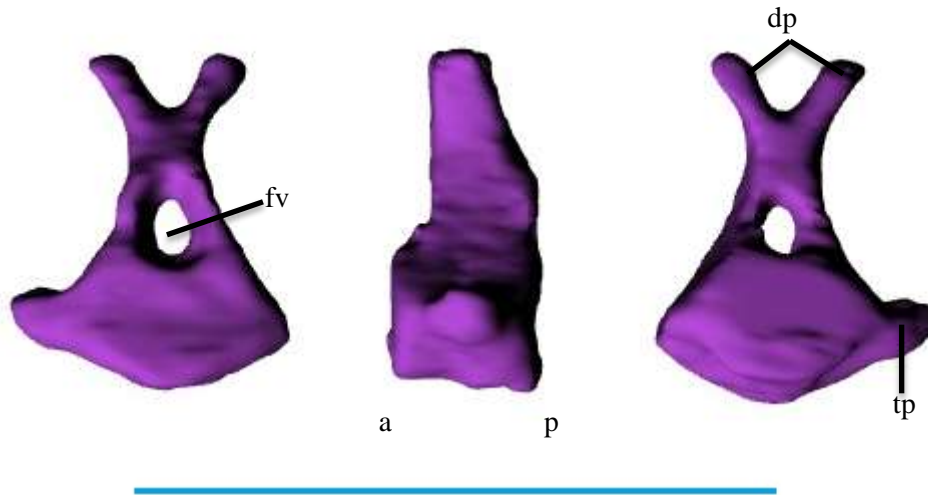


Figure 6.5: 3D model of the caudal vertebra. Blue line = 50mm. Abbreviations used: a, Anterior; p, Posterior; fv, Foramen vertebrae; dp, Distal process; tp, Transverse process.

6.4.4 *Caudal Vertebrae*

This vertebra (Figure 6.5) exhibits the twin distal process typical of avian caudal vertebrae. Its small size and lack of fovea costalis exclude any possibility of it being thoracic, and its relative size means it is not part of the pelvic girdle, it is very different morphologically from the cervicals, and is not a fused part of the pygostyle. The bone is therefore from the lower numbered caudal vertebrae before they fuse into a pygostyle

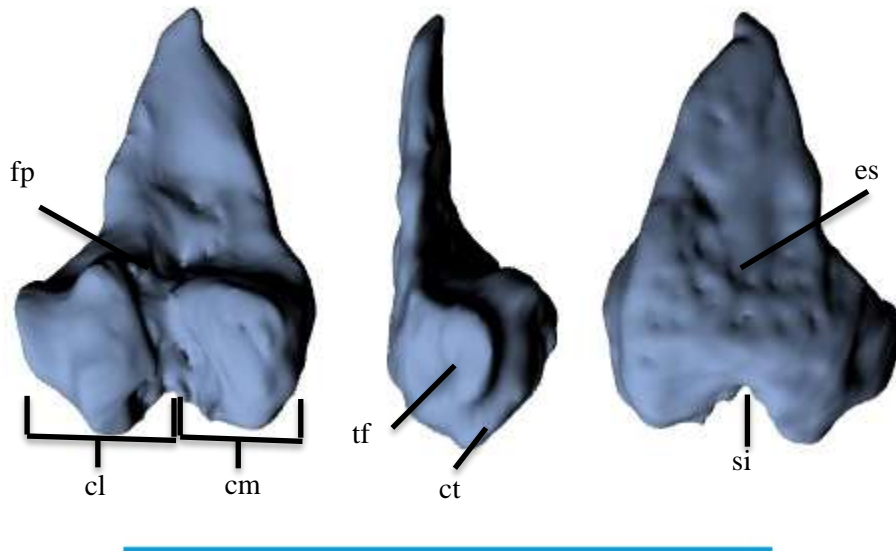


Figure 6.6: 3D model of the distal femur fragment. Blue line = 50mm.
 Abbreviations used: es, Heavily eroded surface; si, Sulcus intercondylarus; tf, Trochlea fibularis; ct, Crista tibiofibularis; fp, Fossa poplitea; cm, Condylus medialis; cl, Condylus lateralis.

6.4.5 *Distal left femur fragment*

This bone is heavily eroded especially on the cranial surface however the distal part of the caudal surface still retain much of its original morphology (Figure 6.6). The presence of obvious femoral epicondyles and the presence of a deep sulcus intercondylarus between them indicates that the bone fragment is a distal the femur.

Penguin femora normally exhibit a strong crista tibiofibularis, a shallow fossa poplitea, a robust distal end, approximately equal sized condyles medialis and condylus lateralis, equally distad condyles medialis and condylus lateralis projection, and a moderately deep sulcus intercondylarus. This distal femur fragment is consistent with all of these features and so can be concluded to be the remains of a penguin.

Comparisons of measurements with other penguin species indicates that ZFp1134 is of a similar size to the extinct penguin *Pygoscelis tyreei* (Table 6.1)

	sulcus width	sulcus depth	Condylus medialis width	Crista tibiofibularis width	Trochlea fibularis width	Condylus lateralis height
ZFp1134	7.64	3.96	7.64	5.61	3.23	11.82
<i>Eudyptula minor albosignata</i>	4.14	2.74	4.14	2.58	1.65	6.71
<i>Aptenodytes forsteri</i>	14.17	7.73	14.17	7.57	4.93	17.35
<i>Pygoscelis adeliae</i>	5.29	5.15	5.29	3.79	2.83	10.9
<i>Eudyptes robustus</i>	5.78	5.25	5.78	4.45	2.85	10.44
† <i>Pygoscelis tyreei</i>	*	*	*	5.50	3.57	12.24

Table 6.1: Table of distal femur measurements taken comparing ZFp1134 to extant and extinct penguin species. All measurements are recorded in mm, * indicates that the measurement was not able to be taken due to the state of the specimen. † indicates an extinct species

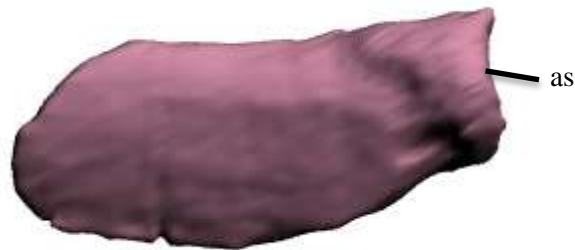


Figure 6.7: Fragment of radius. Blue line = 50mm.
Abbreviation used: as, Articulation surface.

6.4.6 Radius Fragment

This element is considered to be a penguin radius (Figure 6.7). It has been eroded, removing the majority of its length however the remaining bone includes a concave ovoid articulation surface and a constriction immediately distad of the articulation. When the size of the bone fragment is considered, this morphology is most consistent with a penguin radius. The dimensions of the articulation surface are consistent with a penguin of similar size to *Pygoscelis tyreei* (Table 6.2).

	Articulation Surface Height	Articulation Surface Width
ZFp1134	7.77	7.66
<i>Eudyptula minor albosignata</i>	4.96	3.88
<i>Pygoscelis adeliae</i>	4.8	3.24
<i>Eudyptes robustus</i>	5.24	3.52
† <i>Pygoscelis tyreei</i>	8.17	7.52

Table 6.2: Table comparing the radius articulation surface measurements of ZFp1134 with those of extant and extinct penguins. All measurements are recorded in mm. † indicates an extinct species.

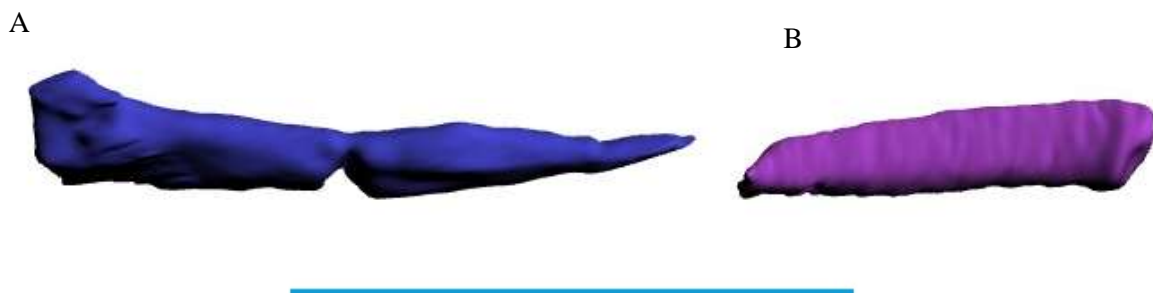


Figure 6.8: 3D models of the manus phalanges A and B. Blue line = 50mm.

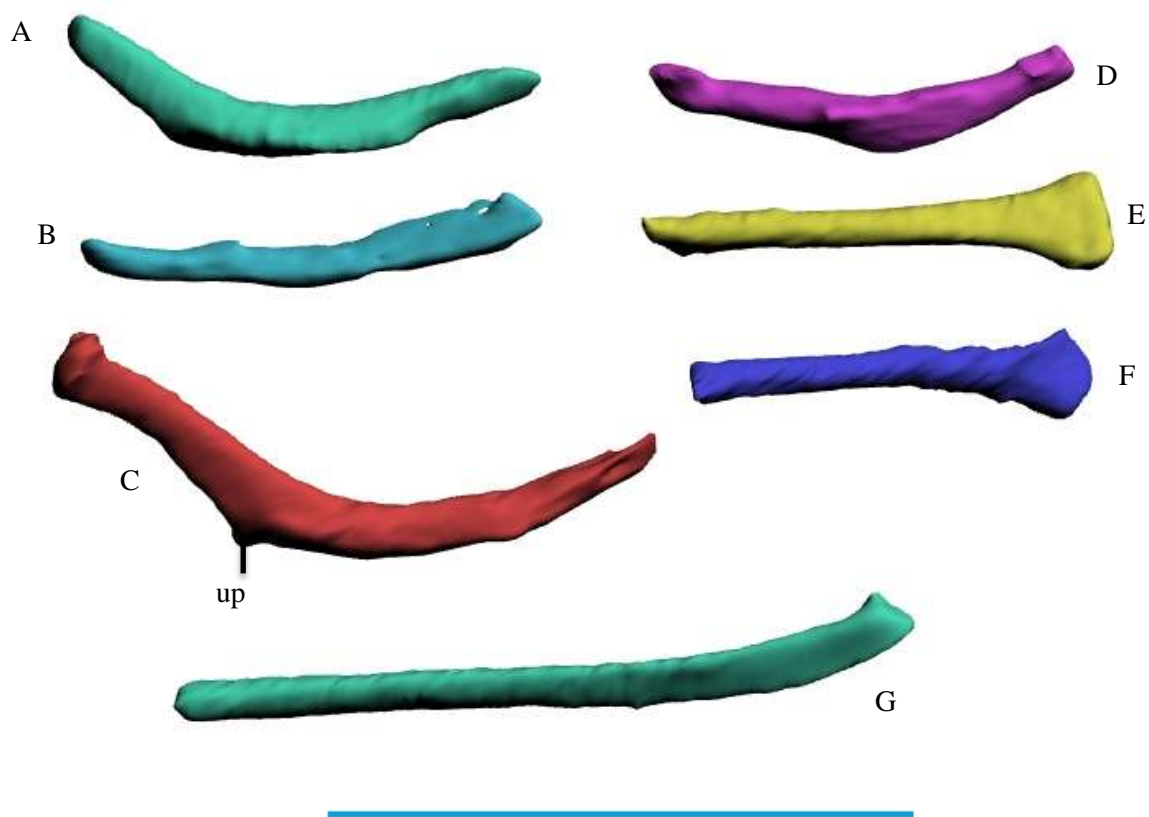


Figure 6.9: 3D models of the ribs included within the Miocene collection. Blue line = 50mm. Abbreviation used: up, Uncinate process.

6.4.7 *Manus Phalanges*

The manus phalanges A and B (Figure 6.8) are too worn to accurately determine the exact positions of each bone however based on the preserved morphology they are most consistent with phalanges digit minoris. While manus phalange B is an isolated bone Manus phalange A maybe two articulated phalanges.

6.4.8 *Ribs*

Two different types of ribs are present within the collection (Figure 6.9) however ribs are not often recorded in descriptions, presumably due to their lack of diagnostic

potential making more than generalized comments difficult. In Figure 6.9 Ribs A, B, C, and D appear to be most similar to thoracic ribs while ribs E, F, and G appear most similar to sternal ribs. Figure 6.9 (C) contains a medial process which appears to be the remnant of an uncinata process.



Figure 6.10: 3D model of the trochlea metatarsus, a fragment of the tarsometatarsus. Blue line = 50mm.

6.4.9 *Tarsometatarsus fragment*

The bone fragment (Figure 6.10) is a trochlea metatarsal three, a component of the distal end of a tarsometatarsus. The deep groove separating the condyle into two halves is typical of most avian groups.



Figure 6.11: 3D model of the apex pubis fragment. Blue line = 50mm. Abbreviation used: d, Depression.

6.4.10 *Apex pubis fragment*

This elongated fragment (Figure 6.11) contains a prominent depression which is consistent with the apex pubis of the pelvic girdle of a penguin.

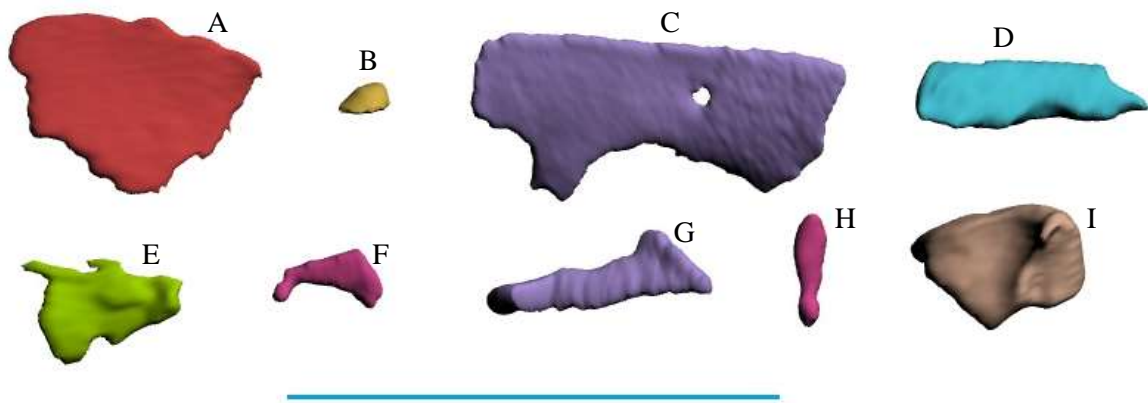


Figure 6.12: Assorted fragments from the Miocene collection.

6.4.11 *Assorted other fragments*

ZFp1134 contains a number of small fragments which are difficult to assign to a specific element. In Figure 6.12, fragments A, C, D, and E are considered to be thin bone plates which may be parts of the ichium of the pelvis. Fragments F, G, H, and I do not appear to contain any identifiable characteristics making it impossible to assign them to a specific bone. Fragment B appears most similar to the upper valve of a brachiopod however due to its size and the lack of reserved detail exact determination is not feasible.

6.5 *Summary*

ZFp1134 is undoubtedly the fossilized remains of a Middle Miocene penguin. The morphology of the fused vertebrae of the synsacrum precludes any non-avian species while the characteristics of the distal femur fragment and the radius confirm that the remains

are those of a penguin. While there has been no described penguin fossils from the Mt Brown Formation, the nearby Motunau Beach concretions are the type locality of three species. Concretions from Motunau Beach are considered to be Miocene to Pliocene (Lewis, 1976; Browne and Field, 1985). Comparison of the features of this fossil with those of Recent and fossil Penguins indicate that this bird was larger than the Extant Little Blue Penguin (*Eudyptula minor*) and similar in size to those of extant *Pygoscelis* species. ZFp1134 is considered to be of similar size and morphology to the type material of *Pygoscelis tyreei* Simpson, 1972 (CM AV 22631). The exact age of the type of *Pygoscelis tyreei* is debated with Simpson (1972) suggesting it may be Miocene to Pliocene (22-3 million-years-old), but that it was probably Late Pliocene (c.3 million-years-old). The apparent existence of this species or a near relative in the Middle Miocene (late Lillburnian to Waiuan) (Browne and Field, 1985; Andrews et al., 1987) is of considerable interest in our understanding of crown group penguin evolution.

7 Chapter 7

Discussion

7.1 *Summary of Fossils*

I have identified in the collections of Canterbury Museum three unique turtle fossils and a fossil penguin specimen. The turtle fossils cover a period of time encompassing the Late Cretaceous, Palaeocene, and the latest Eocene while the penguin specimen is of Miocene age. A number of turtles of similar ages are known from other New Zealand locations, notably Oamaru, Northland and Mangahouanga Stream in the North Island. The Cretaceous specimen, Specimen ZFR16, includes a fragmental coracoid and a peripheral. The Palaeocene specimen, Specimen 2010.108.6, is comprised of a hyoplatron and a hypoplastron. The Eocene specimen, Specimen ZFR105, includes a partial humerus and mandible, an articulated hyoplastron and hypoplastron, a coastal carapace fragment, an articulated pair of peripherals and an isolated peripheral, and a partial suprapygial plate. The Miocene specimen, Specimen ZFp1134, contains a selection of post-cranial elements including two thoracic vertebrae, a section of the synsacrum, a caudal vertebra, a highly weathered distal femur fragment, an articulated pair of manus phalanges and an isolated manus phalange, a section of the apex pubis, and a trochlea metatarsus fragment.

7.2 *New Zealand Turtle Diversity*

7.2.1 *Cretaceous*

Prior to this study the entire known New Zealand Cretaceous turtle biota was limited to one terrestrial and two marine species. All Cretaceous species were limited to the

Manganui River system, the field area of the late Joan Wiffen. The sole Cretaceous terrestrial New Zealand turtle is thought to be a member of the genus *Glyptos* (McKee and Wiffen, 1989). The marine realm was populated by the cryptodires: *Desmatochelys iowi* (McKee and Wiffen, 1989) and another member of the Protostegidae family, associated with the *Chelospharginae* subfamily (Wiffen, 1981). This study adds a further specimen to the known Cretaceous cryptodires, Specimen ZFR16. Specimen ZFR16 is the first Chelonioidea member to be known from the Cretaceous of New Zealand which does not clearly belong to the Protostegidae family. Consisting of a fragmental coracoid and an extremely acid etched peripheral; Specimen ZFR16 exhibits none of the synapomorphic traits in the coracoid articulation zone that are diagnostic of Protostegidae and the Dermochelyidae, leaving only the Pancheloniid family within Chelonioidea to which the specimen can belong. Protostegids and dermochelyids are described as having an elongate rod shaped coracoid (Parham and Stidham, 1999) however, Specimen ZFR16 appears to be distally shortened, resulting in a more anterior constriction of the shaft than any of the coracoids that it has been compared to. The prominent degradation of the peripheral means it has not yielded any meaningful comparisons.

7.2.2 *Palaeocene*

Palaeocene turtles fossil remains in New Zealand are rare. Two other Palaeocene aged turtle fossils have been reported; the Ward specimen; a partial humerus from Marlborough (Fordyce, 1979) and the Wangaloa collection; an unknown Chelonioidea superfamily member from Otago (Buchanan et al., 2007). The Ward specimen was collected in January 1977 from a limestone cobble “above Ward Beach” by Mr B. Priddle and has since been donated to the N.Z. Geological Survey under the identification GS12538. The lack of condyles or head of the Ward specimen has prevented any attempt to assign the taxon

beyond the ordinal level (Fordyce, 1979). The Wangaloa collection contains a number of post-cranial fragments. These remains are very fragmental making identification beyond the superfamily level difficult however; they are believed to be from a single individual. The Wangaloa collection specimens are stored at GNS Sciences, New Zealand as Specimens CD631 – CD636 (Buchanan et al., 2007). The Canterbury Museum Specimen 2010.108.6 comprises two plastron fragments determined to be a hyoplastron and a hypoplastron. While the Wangaloa collection also contains plastral fragments, the fragments are described as thinner than those of the Canterbury Museum specimen. The small size of the fragment believed to be either a hyo- or hypoplastron from the Wangaloa collection means the shape of the plastral elements cannot be compared; as such the possibility of the two specimens belonging to the same or closely related species cannot be entirely dismissed due to the difficulties encountered in the virtual preparation of the Canterbury Museum specimen potentially affecting thickness.

Specimen 2010.108.6 exhibits intimate articulation of the hypoplastron with the peripherals, a trait known to be present in macrobaenids and *Osteopygis* (Hirayama, 1994a; Parham, 2005). Due to Specimen 2010.108.6 being sourced from the Waipara Greensand, a mid to inner shelf deposited sandstone, it seems intuitive to dismiss the freshwater macrobaenids and assign the remains to the genus *Osteopygis*. The work of Parham (2005) discovered that *Osteopygis* was in fact a chimerical species with the skull of the durophagous *Euclastes* and the post-crania of a macrobaenid-grade freshwater turtle (Parham, 2005; Parham et al., 2014). The discovery of the chimerical nature of *Osteopygis* complicates the assignment of the Canterbury Museum specimen as the only non-chimera species that has this intimate peripheral articulation are exclusively freshwater species. This makes the assessment of the Canterbury Museum Specimen 2010.108.6 problematic; it appears to have the plastral elements of an exclusively freshwater group of cheloniids yet was discovered in

marine sediment considered to be of mid to inner shelf depth (Browne and Field, 1985). In my opinion the work of Parham is logical, well researched, and until proven otherwise should be considered definitive. In light of this I propose the Canterbury Museum specimen 2010.108.6 should be assigned to the Macrobaenidae, the first turtle specimen in the southern hemisphere to be assigned to this family. The deposition in marine sediment is believed to be the result of postmortem transport of the specimen until further fossil evidence to the contrary is discovered. This also suggests the Canterbury Specimen 2010.108.6 is the first Palaeocene aged freshwater turtle in New Zealand.

7.2.3 Eocene

New Zealand's most diverse turtle palaeofauna is found in the Eocene. Recorded species include *Psephophorus terrypratchetti*, *Maorichelys wiffeni*, *Eochelone monstigris*, and a member of the family Toxochelyidae. Both *Psephophorus terrypratchetti* (Kohler, 1995a; Kohler, 1995b; Karl and Tichy, 2007) and *Maorichelys wiffenae* (Karl and Tichy, 2007; Grant-Mackie et al., 2011) are known from the limestone deposits of Oamaru in the South Island while *Eochelone monstigris* and the Toxochelyidae member are known only from Northland deposits in the North Island (Grant-Mackie et al., 2011). The Canterbury specimen, Specimen ZFR105, was discovered at Parkside Quarry (formerly known as Gay's Quarry) and donated to the museum at some time prior to 1949. The assemblage that makes up Specimen ZFR105 most closely resembles the genus *Eochelone*, initially described by Dollo (1903, translated). The Northland specimen of *Eochelone* is most likely the same species as Specimen ZFR105. Despite the lack of truly comparable elements, both specimens share elements that are extremely close in size and morphology. Specimen ZFR105 is therefore assigned as a specimen of *Eochelone monstigris* (Grant-Mackie et al., 2011). The presence of Specimen ZFR105 is therefore the first example of *Eochelone monstigris* in the

South Island of New Zealand. The confirmed range of *Eochelone monstigris* is therefore duly expanded to encompass the entire eastern coast of New Zealand from Northland to Oamaru.

The material included in Specimen ZFR105 does not greatly add to the diagnosis of *Eochelone monstigris* as published by Grant-Mackie et al. (2011) however, as the specimen is comprised primarily of different elements to the Northland holotype it greatly expands the diagnosis of the taxon as a whole. The lack of a skull in both specimens means it isn't possible to determine what *Eochelone* ate with any certainty; despite the presence of a mandible in Specimen ZFR105. The lack of any complete limbs or the shoulder girdle makes determining locomotion difficult however; the more complete view of the humeral morphology allowed by the combination of these two specimens will be instrumental in this endeavor. Overall, Specimen ZFR105 gives insight into the shape of a completed humerus, and the first look at the plastron and mandible of *Eochelone monstigris*.

7.2.4 Miocene

The Miocene turtle palaeofauna is limited to the marine turtle *Lepidochelys waikatoica* and a meiolaniid terrestrial turtle from the St. Bathans fauna. As the Miocene collection has been determined to be a penguin it does not further the understanding of the turtle palaeofauna of New Zealand. The penguin palaeofauna is well established in New Zealand and the Canterbury Museum specimen (Specimen ZFp1134) instead adds to this significantly more diverse group.

Penguins are known from New Zealand from the Palaeocene (Slack et al., 2006) and have persisted in the New Zealand fauna to the modern day. *Pygoscelis tyreei* was previously only known from the holotype stored at the Canterbury Museum as CM AV 22631

(Simpson, 1972). This specimen is of unknown age ranging from the Early Miocene to the Pliocene (Simpson, 1972; McKee, 1987). The *Pygoscelis tyreei* specimen, Specimen ZFp1134, is crucial in confirming a Middle Miocene (late Altonian to Lillburnian) age for this species. A Middle Miocene age for this species is significant in light of the relatively reduced number of New Zealand penguin specimens during this period (Davis and Darby, 2012). The Miocene marks the transition between stem penguins and the more modern crown fauna. There is potential for the more complete holotype, in conjunction with Specimen ZFp1134, to assist in bridging this gap in the penguin record in New Zealand. This is promising area for future research now that this study has determined that Specimen ZFp1134 is a penguin fossil.

7.3 *Relation of Canterbury Specimens to the Global Turtle Palaeofauna*

7.3.1 *Cretaceous*

Specimen ZFR16 is assigned to the Pancheloniidae making it the first to be described of Cretaceous age in New Zealand. Consequently the global distribution of this family can be expanded to include New Zealand as early as the Late Cretaceous. Specimen ZFR16 is only the fourth documented pancheloniid from the Southern Hemisphere, the others being the collection of *Euclastes* species from South America (Lynch and Parham, 2003), a South African species, and an Antarctic species (De La Fuente et al., 2010). The distribution of the pancheloniids therefore encompasses most of the southern ocean, the only notable exemption being Australia.

The unique coracoid morphology of Specimen ZFR16, while probably most closely related to the North American toxochelyids due to the medial constriction angles, is markedly different from the majority of Cretaceous turtle family morphologies. The coracoid

morphology of Specimen ZFR16 may potentially be unique due to an adaption to an environmental constraint however; this cannot be fully explored until more fossil remains are discovered.

7.3.2 *Palaeocene*

All previously known macrobaenid turtles are from the high latitudes of the Northern Hemisphere. The Palaeocene specimen, Specimen 2010.108.6, therefore expands the distribution of macrobaenids to the Southern Hemisphere. Given their rise in northern Central Asia during the Early Cretaceous and subsequent expansion eastward (Vandermark et al., 2009) there is presumably sufficient time for the macrobaenids to also move further south by the Late Cretaceous. The distinct lack of macrobaenid fossils recorded from the intervening areas, between northern Central Asia and New Zealand, may be due to lack of discovery or lack of preservation. It is possible that this turtle is a unique Southern Hemisphere equivalent with similar environmental constraints causing homologous characteristics to develop but this cannot be explored thoroughly due to the lack of preserved materials.

7.3.3 *Eocene*

Eochelone specimens are previously known from Denmark (Dollo, 1903) and Northland, New Zealand (Grant-Mackie et al., 2011). The Canterbury Museum specimen, Specimen ZFR105, has limited influence globally beyond what has previously been established in Grant-Mackie et al. (2011). Specimen ZFR105 does expand the range of *E. monstigris* from the North Island to both the North and South Islands of New Zealand.

7.4 *Mosasaur Predation on Turtles*

The renowned Belgian naturalist and turtle expert Louis Dollo stated "However, *Hainosaurus* undoubtedly fed upon marine tortoises, because their remains have been found in its carcass." (Dollo, 1887) and this has consequently been considered fact. At the time of this study the location of specimen upon which Dollo made this claim remains unknown. The only other clear record of Mosasaur depredation upon large marine turtles are two specimens currently displayed at Teylers Museum in Haarlem, the Netherlands. The Teylers Museum Specimens are both partial carapaces of *Allopleuron hoffmanni*; one of which has a very large compression fracture caused by a Mosasaur, while the other shows large surface striations inferred to be teeth marks from a mosasaur (Van Baal and Janssen, 2009).

The Canterbury Museum specimen, Specimen ZFR16, was discovered within the remains of *Mosasaurus mokoroa*. There are clear signs of acid etching upon the peripheral and indication of further etching on the coracoid fragment that comprise the specimen. The indicators of predation on Specimen ZFR16 are clear; making this only the third recorded specimen exhibiting definitive Mosasaur predation on large marine turtles, and the first from the Southern Hemisphere.

The prominent striations along the coracoid fragment are parallel and not consistent with any known turtle coracoid. The coracoid is undoubtedly that of a turtle and so the striations are of interest. This study suggests that the striations are the result of the feeding technique of *Mosasaurus mokoroa*. The distance between the parallel striations are equivalent to the distance between the proximal teeth of *Mosasaurus mokoroa* with which the turtle was discovered (Welles and Gregg, 1971). The striations are therefore proposed to be the result of an initial strike by the *Mosasaurus mokoroa* which grabbed the turtle medially without completely crushing the turtle. The turtle was then shaken by the mosasaur to kill it, forming the initial striations seen on the coracoid. The turtle, now dead, was then eaten by

the mosasaur where the acid in the mosasaur's stomach began to etch the bone, expanding the striations. Shaking of the turtle is inferred based upon the formation of striations. As striations are not present on the Teylers Museum specimen, which purely exhibits compression, an additional action would be required to initiate these markings.

7.5 Conclusions

The Canterbury Museum contains a total of three turtle fossil collections and one penguin that have been described as part of this study. The turtle and penguin specimens were partially prepared prior to this study and underwent virtual preparation using the Materialise Software Suite. The turtle specimens are from the Cretaceous sediment of the Conway Formation, the Palaeocene specimen is from the Waipara Greensand, and the Eocene specimen is from the Ototara Limestone while the penguin remains are from the Miocene Mt Brown Formation.

The Cretaceous turtle can only be assigned to the family Chelonioidea until such time as further fossil evidence is discovered and genus assignment is appropriate. The Palaeocene specimen is the first example of the Macrobaenidae family to be described in the Southern Hemisphere. The Eocene specimen represents the second individual of the species *Eochelone monstigris* originally described from the Ruatangata Sandstone of Northland, New Zealand, expanding the distribution of this species to include the South Island of New Zealand. The penguin specimen has been determined to be a specimen of *Pygoscelis tyreei*.

The Cretaceous specimen expands the global distribution of the pancheloniids, leaving only Australia as a large Southern Ocean landmass without any clear remains assigned to this family. The Palaeocene specimen expands the Macrobaenidae to the Southern Hemisphere despite the previously known global distribution which was limited to

high latitude Northern Hemisphere localities. The Eocene specimen has limited global impact.

The Cretaceous specimen in this study was found within the remains of *Mosasaurus mokoroa*. The discovery of the turtle within a mosasaur and the presence of acid etching on the fossilized bones are considered to be indicative of consumption of the turtle by the associated *Mosasaurus mokoroa*. Parallel striations upon the coracoid are suggested to be the result of the feeding strategy of *Mosasaurus mokoroa*.

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Appendix

Measurements of Canterbury Museum Specimen

All measurements are shown in mm excluding angles which are measured in degrees, indicated by the presence of the symbol: °. Anterolateral plane encompasses the maximum width x maximum length when viewed dorsally this definition applies to all measurements save the Miocene penguin manus phalanges, ribs, and apex pubis which are viewed medially instead of dorsally. The manus phalanges, ribs, and apex pubis of the Miocene penguin are viewed medially as this view is more inclusive of the key features of each of these elements than a dorsal view. Miocene Penguin ribs follow labelling set forth in Figure 6.9

Cretaceous Turtle			
Coracoid		Peripheral	
Anterolateral plane	87.19 x 270.81	Anterolateral plane	21.87 x 77.91
Ventrodorsal height	39.46	Ventrodorsal height	34.15
Width between striations	18.24		
Medial constriction left side angle	135.58°		
Medial constriction right side angle	157.31°		
Angle between articulation zones	112.31°		

Palaeocene Turtle			
Hyoplastron		Hypoplastron	
Anterolateral plane	189.65 x 125.06	Anterolateral plane	244.42 x 191.35
Ventrodorsal height	14.07	Ventrodorsal height	10.79
Anterior fontanelle width	162.75	Posterior fontanelle width	108.05
Anterior fontanelle length	38.43	Posterior fontanelle length	121.46

Eocene Turtle Part 1					
Humerus		Mandible		Plastron	
Anterolateral plane	76.53 x 93.39	Anterolateral plane	73.31 x 19.51	Anterolateral plane	122.00 x 378.67
Ventrodorsal height	65.15	Ventrodorsal height	39.65	Hyoplastron length	186.67
Medial process deflection	143.17°	Meckelian fossa to coronoid process angle	60.56°	Hyoplastron width	122
Shaft height/width	21.22/27.02	Coronoid process to Inferior Aveolar Foramen	128.04°	Hypoplastron length	192
Shaft to Caput Humeri angle	120.83°			Hypoplastron width	122
Caput humeri projection	39.28				
Caput Humeri to medial process	137.11°				
Lateral Process width	6.43				
Lateral process deflection from shaft	156.03°				
Caput humeri to Lateral process	155.45°				
Lateral process to medial process	119.68°				

Eocene Turtle Part 2							
Suprapygial		Articulated periheral		isolated peripheral		coastal carapace fragment	
Anterolateral plane	62.95 x 52.41	Anterolateral plane	26.88 x 111.50	Anterolateral plane	22.06 x 51.12	Anterolateral plane	131.82 x 50.03
Ventrodorsal height	19.58	Ventrodorsal height	24.9	Ventrodorsal height	22.87	Ventrodorsal height	17.71
Ridge height	6.75					Articulation Zone	9.44 x 14.08

Miocene Penguin Part 1					
Synsacrum		Eroded Thoracic vertebra		Thoracic vertebra	
Anterolateral plane	19.71 x 30.92	Anterolateral plane	14.7 x 20.11	Anterolateral plane	29.87 x 30.68
Ventrodorsal height	37.41	Ventrodorsal height	23.25	Ventrodorsal height	14.39
Articulation width	11.72	Articulation width	7.76	Articulation width	11.89
vertebrate foramen to third notaria	24.49				

Miocene Penguin Part 2					
Caudal vertebra		femur		Radius	
Anterolateral plane	18.28 x 14.45	Anterolateral plane	19.26 x 26.94	Anterolateral plane	35.72 x 14.9
Ventrodorsal height	7.6	Ventrodorsal height	9.47	Ventrodorsal height	9.65
		sulcus width	7.64	Articulation surface height	7.77
		sulcus depth	3.96	Articulation surface width	7.66
		Condylus medialis width	7.64		
		Crista tibiofibularis width	5.61		
		Trochlea fibularis width	3.23		
		Condylus lateralis height	11.82		

Miocene Penguin Part 3					
Manus Phalanges (Articulated)		Manus Phalanges		Rib A	
Anterolateral plane	47.28 x 8.07	Anterolateral plane	29.93 x 6.57	Anterolateral plane	36.93 x 3.61
Anterior -posterior height	6.49	Anterior -posterior height	2.65	Anterior -posterior height	5.37

Miocene Penguin Part 4					
Rib B		Rib C		Rib D	
Anterolateral plane	36.09 x 4.08	Anterolateral plane	48.37 x 7.38	Anterolateral plane	32.96 x 4.65
Anterior -posterior height	2.15	Anterior -posterior height	4.88	Anterior -posterior height	4.01

Rib E		Rib F		Rib G	
Anterolateral plane	37.05 x 7.77	Anterolateral plane	34.00 x 6.74	Anterolateral plane	58.29 x 6.01
Anterior -posterior height	3.27	Anterior -posterior height	3.96	Anterior -posterior height	2.55

Miocene Penguin Part 6			
Tarsometatarsus fragment		Apex pubis fragment	
Anterolateral plane	5.06 x 10.73	Anterolateral plane	64.93 x 10.71
Ventrodorsal height	5.69	Anterior -posterior height	5.95