The Australian Cretaceous ichthyosaur *Platypterygius australis*: understanding its taxonomy, morphology, and palaeobiology

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TABLE OF CONTENTS

ABSTRACT

The Cretaceous ichthyosaur *Platypterygius* was one of the last representatives of the Ichthyosauria, an extinct, secondarily aquatic group of reptiles. Remains of this genus occur worldwide, but the Australian material is among the best preserved and most complete. As a result, the Australian ichthyosaur fossil finds were used to investigate the taxonomy, anatomy, and possible locomotory methods and behaviours of this extinct taxon.

Understanding the importance of the Australian *Platypterygius* species has been complicated by the use of two specific names, *P. australis* and *P. longmani*, and confused further by the loss of holotype material. Examination of Australian material has demonstrated that both species belong to the same taxon. *P. australis* was shown as the valid taxon name, relegating *P. longmani* to a junior synonym, and thus resolving the taxonomic uncertainty of the only Australasian ichthyosaur that can be identified to species-level.

Examination of *P. australis* postcranial anatomy revealed four postcranial characters that, used in conjunction with previously identified cranial and postcranial diagnostic features, distinguish the Australian taxon from other species of *Platypterygius*. The morphology of the postcranial elements (including bones that had not previously been described for the genus) was then used to hypothesise the locomotory mode in this ichthyosaur based on osteological comparisons with extant marine mammals. Results indicated that a decoupled locomotor system was most plausible for *P. australis*, where the caudal fin was used for long distance swimming and the broad forelimbs for manoeuvring. In addition, the broad forelimbs, for which the genus is named, are thought to increase acceleration when either stationary or whilst moving.

In addition to the functional studies, palaeobehaviour in this ichthyosaur could also be inferred from bite traces. Palaeopathologies in the form of bite marks on a partial ichthyosaur skull were examined. The bite marks were attributed to another ichthyosaur (most likely of

the same species), thus indicating that *P. australis* individuals engaged in aggressive behaviour.

This thesis examined the known Australian ichthyosaur material to address taxonomic, anatomical, and behavioural aspects of *Platypterygius*, and demonstrated the utility of the Australian Cretaceous record for this purpose. Collection of additional specimens, particularly from localities in Western Australia and South Australia where diagnostic remains are yet to be found, would significantly add to our knowledge of this extinct taxon.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university of other tertiary institution to Maria Zammit and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text.

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Maria Zammit

10 January 2011

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I am extremely grateful to the following institutions and their curators and collection managers for granting access to specimens, or facilitating loans: **AM**, Australian Museum, Sydney, New South Wales: Robert Jones; **AU**, University of Auckland, Auckland, New Zealand: Neville Hudson; **KKM**, Kronosaurus Korner Museum, Richmond, Queensland: Paul Stumkat; **MV**, Museum Victoria, Melbourne, Victoria: David Pickering; **NMMUK**, Natural History Museum United Kingdom, London, UK: Sandra Chapman; **QM**, Queensland Museum, Brisbane, Queensland: Scott Hocknull, Kristen Spring, Heather Janetzki, and Patrick Couper; **SAM**, South Australian Museum, Adelaide, South Australia: Ben McHenry, Mary-Anne Binnie, Natalie Schroeder, David Stemmer, Catherine Kemper, Philippa Horton, and Carolyn Kovach. Travel to these institutions was supported by the University of Adelaide and funding from the Sir Mark Mitchell Foundation.

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CHAPTER 1

INTRODUCTION

Ichthyosaurs are a group of extinct, fish-shaped marine reptiles that were first described from Jurassic deposits of Europe in the early 19th century (Home 1814, 1816). Their remains are now known from the Lower Triassic (Olenekian: Callaway and Massare 1989) through to the Upper Cretaceous (Cenomanian: Bardet 1992), and can be found all over the world. The origins of the ichthyosaurs have proved problematic, and almost all major vertebrate groups have been hypothesised as the possible sister group – such groups include fish, crocodiles, turtles, squamates, and monotremes (McGowan and Motani 2003). Studies on more basal Triassic forms suggested that the Ichthyosauria are diapsid reptiles (Massare and Callaway 1990; Motani *et al.* 1998), though some ichthyosaur researchers consider the evidence for this hypothesis to be inconclusive (Maisch and Hungerbühler 2001). Post-Triassic ichthyosaurs are still considered the 'typical' ichthyosaurian form, and the majority of previous studies have focused on these genera, particularly the Jurassic representatives. For example, phylogenetic, ontogenetic, functional, and palaeobiological studies have been undertaken mainly on Jurassic ichthyosaurs (Johnson 1977; Buchholtz 2001), but have rarely been extended to their Cretaceous counterparts.

1.1 The genus *Platypterygius*

The Cretaceous genus *Platypterygius* is one of the last representatives of the Ichthyosauria (Neocomian–Cenomanian: McGowan and Motani 2003), and is found on almost every continent (Maisch and Matzke 2000). Until recently, most Cretaceous ichthyosaurs were referred to this genus (McGowan 1991), resulting in *Platypterygius* becoming almost the default taxon for any Cretaceous ichthyosaur material. However, several Jurassic genera are now known to extend into the Cretaceous (*Brachypterygius*, McGowan and Motani 2003; *Aegirosaurus*, Fischer 2009; Fischer *et al.* in press; and *Ophthalmosaurus*, McGowan and Motani 2003; Fischer 2009), and two new genera have been erected for Cretaceous material (*Maiaspondylus*, Maxwell and Caldwell 2006a; and *Athabascasaurus*, Druckenmiller and Maxwell 2010). Thus, a reassessment of the genus *Platypterygius* is required to aid in the taxonomic identification of new Cretaceous specimens.

The most extensive recent review of ichthyosaurs to date (McGowan and Motani 2003) recognised five valid species of *Platypterygius*: *P. americanus* (Nace 1939, 1941) from the Albian–Cenomanian of North America (Maxwell and Kear 2010); *P. australis* (McCoy 1867a) from the Albian of Australia (Kear 2003); *P. campylodon* (Carter 1846; Kiprijanoff 1881) from the Albian–Cenomanian of England, France, and Russia (McGowan and Motani 2003); *P. hauthali* (von Huene 1927) from the Barremian of Argentina (Fernández and Aguirre-Urreta 2005); and *P. platydactylus* (Broili 1907) from the Aptian of Germany (McGowan and Motani 2003). McGowan and Motani (2003) consider their review to be taxonomically inflated, and suggested that fewer species would probably be maintained if more data were available for adequate comparisons. However, recently the resurrection of *P. hercynicus* (from *P. platydactylus*) from the Aptian of Germany has been proposed (Kolb and Sander 2009), and two additional species, *P. sachicarum* (Páramo 1997) and *P. ochevi* (Arkhangelsky *et al.* 2008) have been established, from the Barremian–Aptian of Colombia and the Albian–Cenomanian of Russia, respectively. Despite this, species diversity within *Platypterygius* remains unclear (Maxwell and Kear 2010), with McGowan (1991) raising the possibility that the genus may comprise only a single species if more individuals were known. Recent studies have reviewed the cranial (Kear 2005a) and postcranial (Fernández and Aguirre-Urreta 2005; Kolb and Sander 2009; Maxwell and Kear 2010) anatomy of well-known species of *Platypterygius* to provide greater discrimination between species, a necessary step in establishing species diversity within the genus. The reviews of postcranial material also showed its usefulness for taxonomic identification. Postcranial remains of *P. australis* and *P. platydactylus* are yet to be discriminated from other *Platypterygius* species –

this is difficult as the holotypes of these two species have been lost (Wade 1990) or destroyed (McGowan and Motani 2003), respectively. Additionally, the collection of further material is required to distinguish the two South American species, *P. hauthali* and *P. sachicarum*, as there are no comparable elements between the type specimens.

Most research undertaken on *Platypterygius* has focussed on the description of specimens and taxonomy of the genus. However, some studies have inferred feeding habits and method of locomotion. Stomach contents (Kear *et al.* 2003) and dentition (Kear 2002; Lingham-Soliar 2003) of *P. australis* indicated a diet predominantly of fish and belemnites with opportunistic predation upon larger vertebrates. Shake feeding was also hypothesised in this ichthyosaur species based on the presence of dental caries in a juvenile specimen (Kear 2002b). The osteological morphology of *Platypterygius* has been used to infer two different locomotory methods. Wade (1984, 1990) proposed that *P. australis* was capable of using both caudal and forelimb propulsion at different speeds, while von Huene (1923), McGowan (1972a), and Riess (1982) suggested that *Platypterygius* used forelimb propulsion only. Both of these hypotheses are contrary to the caudal propulsion inferred for other post-Triassic ichthyosaurs (Lingham-Soliar 2003). Of the studies mentioned, only the research of Riess (1982) used functional morphology to support the hypothesis – Wade (1984, 1990) did not present evidence, and the functional significance of von Huene's (1927) and McGowan's (1972) observations were not tested. While Riess (1982) utilised functional morphology, the swimming style inferred for one of the extant taxa examined casts doubt on the swimming style proposed for post-Triassic ichthyosaurs. Therefore, the propulsive method of *Platypterygius* is unclear despite the importance of swimming style in diet, habitat preferences, and geographical distribution.

1.2 Australian material

Platypterygius material from the Australian Cretaceous is among the most complete and best preserved (Maxwell and Kear 2010). All specimens are currently referred to a single species (Kear 2006), although there is some debate regarding the correct specific name for this taxon. Both *P. australis* (McCoy 1867a) and *P. longmani* (Wade 1990) persist as species names for this material in the literature, and a reassessment of the original *P. australis* remains is required to resolve the taxonomic status of the Australian species (Kear 2005a).

Most skeletal elements are represented (not, however, in a single specimen), providing the material necessary for a description of elements previously unknown for the genus and a functional interpretation of the postcranial remains. Foetal material has also been preserved within the body cavity of an adult skeleton (Kear *et al.* 2003), providing the only example currently known of viviparity in the genus *Platypterygius*. Further, pathological specimens are preserved in the Australian fossil record, as highlighted by Kear (2002), and include a partial jaw exhibiting tooth marks, which has been figured (Kear 2006) but not described. Bite marks are rarely recorded on ichthyosaurian elements, but have been well documented among other Mesozoic vertebrates (e.g. Clarke and Etches 1991; Everhart 2004; Shimada and Hooks 2004). Thus, a detailed examination of ichthyosaur specimens from the Australian fossil record has the potential to greatly enhance what is currently known regarding Cretaceous ichthyosaurs.

1.3 Aims and structure of the thesis

The overall aim of this thesis is to understand the taxonomy, morphology, and palaeobiology of the ichthyosaur *Platypterygius* through examining material referred to the Australian exemplar of this genus. The research is divided into four complementary aims: (1) to resolve the taxonomy of the Australian Cretaceous ichthyosaur material; (2) to describe the postcranial anatomy of the endemic Australian species of *Platypterygius*; (3) to develop an hypothesis of swimming style in this extinct animal based on osteological comparisons to extant marine taxa; and (4) to infer behaviour in this ichthyosaur based on available palaeopathological evidence.

This thesis consists of six chapters (including this introductory chapter) prepared in manuscript format to allow submission for publication with minimal alteration. The preparation of each chapter in manuscript format results in some repetition, particularly in the introduction of each chapter, and in indirect cross-referencing of chapters.

A single appendix is included within this thesis. It is a paper that has been accepted for publication in *Alcheringa*, and describes the only Jurassic ichthyosaur fossil known from the Australasian region. While the remains discussed are indeterminate, they show that ichthyosaurs were present in New Zealand during the Early Jurassic.

CHAPTER 2

A review of Australasian ichthyosaurs

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STATEMENT OF AUTHORSHIP
A review of Australasian ichthyosaurs
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Maria Zammit (Candidate)
Designed research, examined all fossils, wrote the manuscript, produced all figures, was responsible for its submission, and acted as corresponding author.

I hereby certify that the statement of contribution is accurate.

Signed…………………………………………………………………….Date……………

Zammit, M. (2010) A review of Australasian ichthyosaurs.
Alcheringa, v. 34 (3), pp. 281-292, September 2010

CHAPTER 3

The Australian Cretaceous ichthyosaur *Platypterygius australis*: a description and review of postcranial remains

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Rachel M. Norris (Co-supervisor)
Aided in research design, and contributed to organisation of the paper and improvements to the text.

I hereby certify that the statement of contribution is accurate, and permission is given for the inclusion of the paper in the thesis.

Signed…… ……………………………………….Date. 7/1/11

Benjamin P. Kear (External supervisor)
Instrumental in research design and arranging transport of specimens to the South Australian Museum, and contributed to organisation of the paper and extensive edits to the text.

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CHAPTER 4

An assessment of locomotory capabilities in the Australian Early Cretaceous ichthyosaur *Platypterygius australis* based on functional comparisons with extant marine mammal analogues

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An assessment of locomotory capabilities in the Australian Early Cretaceous ichthyosaur *Platypterygius australis* based on functional comparisons with extant marine mammal analogues

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ABSTRACT

Swimming style in modern marine tetrapods has critical implications for diet, habitat preferences, and geographical distribution, and is therefore also important for inferring the palaeobiology of comparable extinct lineages. Ichthyosaurs are one group that has long been the subject of investigation in this regard, because, alongside cetaceans, they can be characterised by a highly specialised 'fish-like' body plan. The dominant locomotory mode for the majority of derived, post-Triassic ichthyosaurs is thought to have been caudal fin-driven propulsion. However, forelimb-based swimming has been suggested for the widespread Cretaceous genus *Platypterygius* because of its robust humeral morphology. This uncertainty has led us to assess the locomotory capabilities of *Platypterygius* through functional comparisons with extant marine tetrapods because different forms of propulsion are reflected in different skeletal frameworks. Detailed anatomical examination of the postcranial skeleton of one of the best known species, *Platypterygius australis* from the Early Cretaceous of Australia, showed that its pelvic girdle and limbs most closely resembled those of cetaceans in the following features: shape of the propodials, hyperphalangy, absence of functional elbow/knee joints, tightly interlocking carpals, and extreme reduction of the pelvic girdle. Since cetaceans swim via caudal fin propulsion with the forelimbs aiding in stabilisation and steering, it is reasonable to extrapolate a similar locomotory mode for *P. australis*. The relatively wide forelimb and apparently complex musculature also suggest a role in manoeuvrability and increased acceleration performance.

INTRODUCTION

Ichthyosaurs were a group of extinct marine amniotes whose fossil record extends from the Lower Triassic (Olenekian) through to the Upper Cretaceous (Cenomanian: McGowan and Motani 2003). Their characteristic fish-like body shape, convergent on that of dolphins and sharks (e.g. Hildebrand 1974; Webb 1984), implies efficient cruising and sprinting (i.e. long distance swimming) over acceleration and manoeuvring (Webb 1984), giving evidence for a pursuit predator lifestyle (e.g. Massare 1988; Buchholtz 2001a). The hypotheses of swimming styles for ichthyosaurs have traditionally been based on body outline (Alexander 1975), but more recently hydrodynamic (McGowan 1992; Massare 1994) and mathematical models (Motani 2002) have been employed. Comparative vertebral morphology has also identified cetaceans as the most viable functional analogues for post-Triassic ichthyosaur taxa (Buchholtz 2001a; Massare and Sharkey 2003) in contrast to sharks (Massare and Faulkner 1997). However, to date no study has compared ichthyosaur postcranial anatomy to a wide range of marine swimming analogues to eliminate other forms of propulsion as implausible.

In an alternative thesis, Riess (1986) proposed that the broader osteology of the postcranium, particularly the limb girdles and limbs, could be used to classify ichthyosaurs into several locomotory ‘types’, with post-Triassic ichthyosaurs conforming to an *Inia*-type (Amazon River dolphin) forelimb-driven method of propulsion. However, this finding contradicts those of Klima *et al.* (1980) who previously showed that swimming in the Amazon River dolphin relied predominantly on the caudal fin, with the limbs being used to manoeuvre around its complex habitat.

Swimming style in the latest surviving, and arguably the most derived of the post-Triassic ichthyosaurs, *Platypterygius* (Motani 1999a; Maisch and Matzke 2000), is still very unclear. Forelimb propulsion has been suggested by von Huene (1923) and McGowan (1972) based on humeral morphology and the presumed size of the caudal fin, but the functional significance of these observations has yet to be investigated. In contrast, Wade (1984) proposed that the most completely known species, *Platypterygius australis* from the Lower Cretaceous (Albian) of Australia (see Zammit 2010 for taxonomic review), used both the caudal fin and forelimbs for propulsion but at different speeds (i.e. caudal fin for fast and forelimb for slower propulsion); this is termed ‘decoupled locomotion’ (Blake 2004), and has been reported in the Amazon River dolphin (Klima *et al.* 1980) and various species of fish

(Webb and Keyes 1981). As with the observations of von Huene (1923) and McGowan (1972), Wade's (1984) proposal was not supported by comparisons with extant swimming tetrapods. It is important to note that decoupled locomotion is not a defined swimming style – rather, it involves the use of varying locomotory behaviours.

In this paper, we aim to assess the locomotory capabilities of *P. australis* through detailed osteological comparisons with a number of marine tetrapod analogues: (1) the bottlenose dolphin (*Tursiops aduncus*), a fast caudal propulsor; (2) the dugong (*Dugong dugon*), a slow caudal propulsor; (3) the Australia sea lion (*Neophoca cinerea*), a forelimb propulsor; and (4) two genera of phocid seal (*Lobodon carcinophagus* and *Hydrurga leptonyx*), hind limb propulsors.

Institutional abbreviations: **AM**, Australian Museum, Sydney; **KKM**, Kronosaurus Korner Museum, Richmond; **QM**, Queensland Museum, Brisbane; **SAM**, South Australian Museum, Adelaide.

METHODS

Thirty-nine bottlenose dolphins, *Tursiops aduncus* (SAM), six dugongs, *Dugong dugon* (SAM, QM), 23 Australian sea lions, *Neophoca cinerea* (SAM), and three phocids, one *Lobodon carcinophagus* and two *Hydrurga leptonyx* (SAM), were examined. Dolphins were used for the cetacean model of propulsion rather than their larger cetacean counterparts because: (a) swimming in cetaceans does not appear to vary across different groups (Buchholtz 2001b); (b) their swimming style has been widely investigated (e.g. Buchholtz and Schur 2004; Buchholtz *et al.* 2005); and (c) dolphin specimens were more widely available for study. Other non-mammalian marine analogues, such as penguins and marine turtles were eliminated from this study because of their highly modified osteological anatomy due to specialised adaptations towards flight and the formation of a carapace, respectively. The ichthyosaur specimens used in this study were: QM F2453, 83 vertebral centra (cranial-most

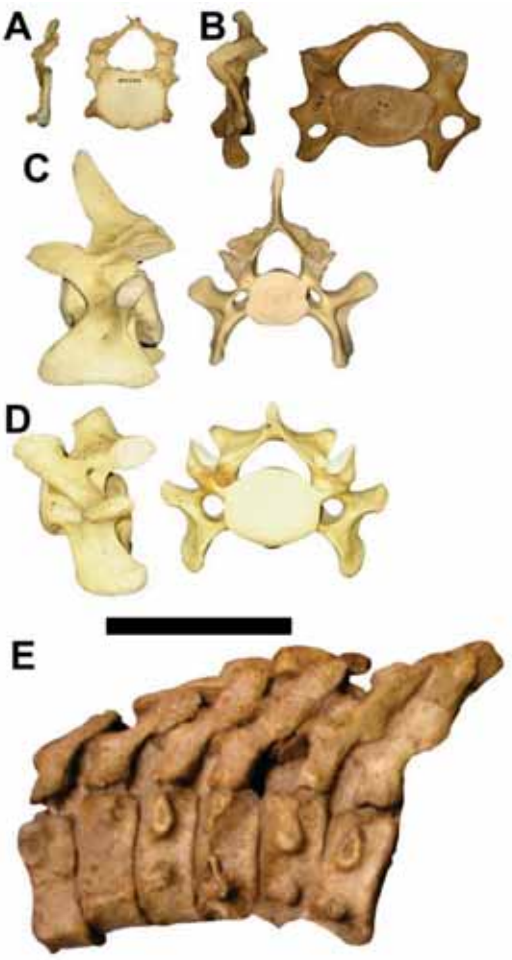

Figure 1: Cervical vertebrae of (A) bottlenose dolphin SAM M21243, (B) dugong SAM M847, (C) Australia fur seal SAM M15964, (D) leopard seal SAM M16638, and (E) *Platypterygius australis* QM F2453. Mammalian taxa are shown in lateral (left) and anterior (right) views. *P. australis* is shown in lateral view only. The fifth vertebra (C5) is shown for the extant mammalian taxa, while vertebrae 3–8 are shown for *P. australis*. The traditional vertebral regions (e.g. cervical thoracic) are difficult to define in the *P. australis* vertebral column, and are conventionally numbered according to their position in the vertebral column rather than their position in a given vertebral region. However, the vertebrae of extant mammalian taxa are conventionally numbered according to their position in a vertebral region. Thus, for the mammalian specimens used in this study, vertebral number in this and all proceeding figures is given as both the position within the vertebral column (to compare with *P. australis*) and in the more conventional method of position within a region of the vertebral column. Scale bar = 10 cm.

20 associated with partial neural arches), coracoids, scapulae, humeri, and partial forelimbs; QM F2473, a humerus and partial forelimb; QM F3389, a scapula, humerus, and partial forelimb; QM F10686, two incomplete forelimbs, numerous vertebral centra, and pectoral girdle material; QM F18906, partial hind limbs; QM F40821, fused ischiopubis and unidentifiable elements; QM F40822, complete right and incomplete left coracoid; and SAM P44323, unprepared specimen including vertebrae, pectoral girdle elements, and forelimb elements. Features that have previously been correlated with swimming style (e.g. height of the vertebral neural spines: Buchholtz and Schur 2004; areas for forelimb muscle attachment on the humerus: Klima *et al.* 1980) were identified in the ichthyosaur specimens.

SWIMMING IN EXTANT MAMMALIAN ANALOGUES

Caudal propulsors

Caudal propulsion is used by many

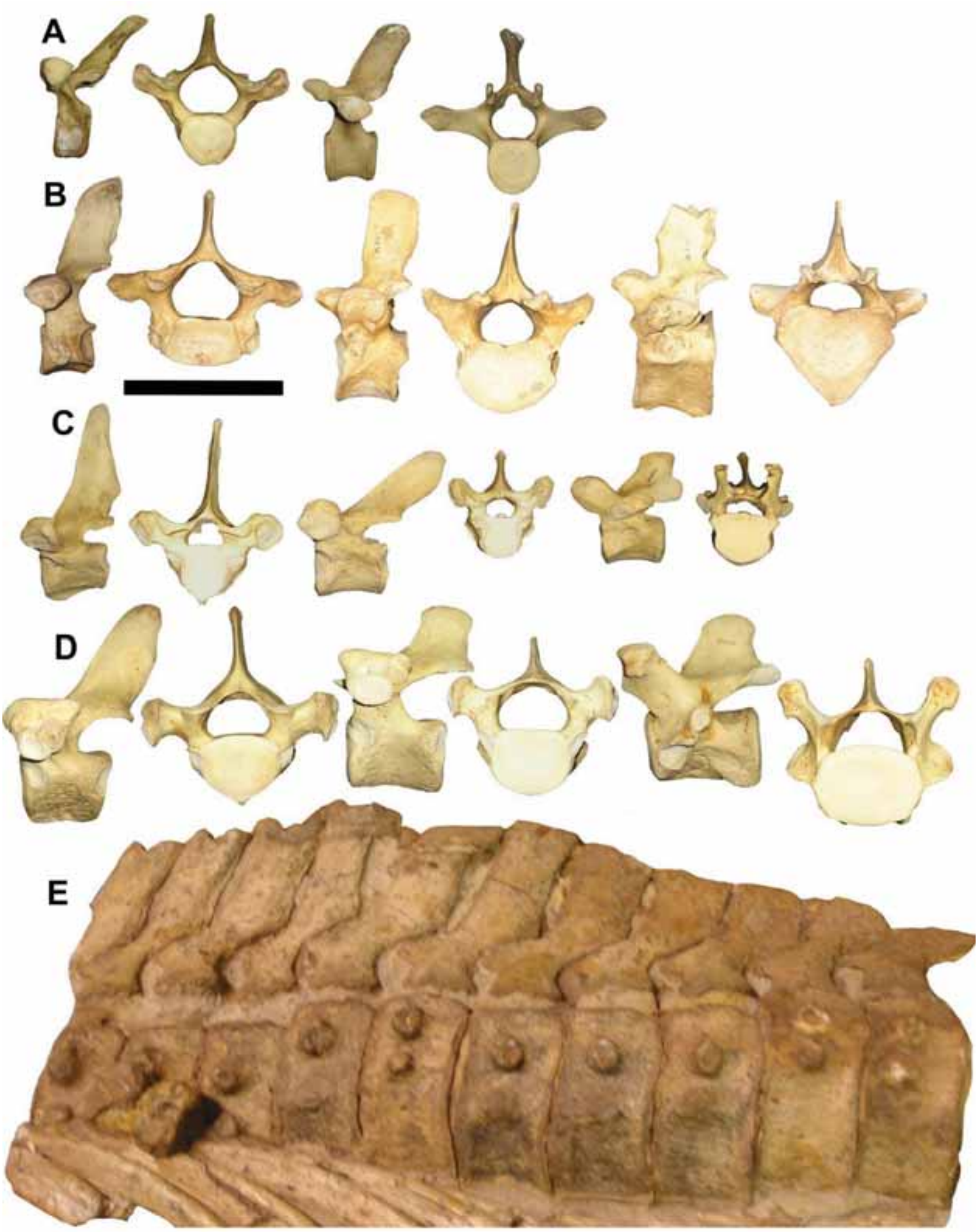

Figure 2: Thoracic vertebrate of (A) bottlenose dolphin SAM M21243, (B) dugong SAM M847, (C) Australian fur seal SAM M15964, (D) leopard seal SAM M16638, and (E) *Platypterygius australis* QM F2453. Mammalian taxa are shown in lateral (left) and anterior (right) views. *P. australis* is shown in lateral view only. The vertebrae shown are as follows (left to right): tenth (T3) and 15th (T8) for the dolphin; tenth (T3), 15th (T8), 20th (T13), and 25th (T18) for the dugong; tenth (T3), 15th (T8), and 20th (T13) for the otariid and phocid seal; and vertebrate 14–23 for *P. australis*. Scale bar = 10 cm.

marine taxa, including the secondarily aquatic cetaceans, dugongs, and manatees. Of these three mammalian taxa, cetaceans are fast swimmers, while dugongs generally swim at slower speeds.

Axial skeleton. Short cervical centra are common to all caudal propulsors (manatees, Buchholtz *et al*. 2007; dolphins, Figure 1A and Buchholtz and Schur 2004; dugongs, Figure 1B), but is only obvious when compared to the height of the centrum (i.e. cervical centra are disc-like in shape for caudal propulsors, but cylindrical in pectoral propulsors). This is considered an adaptation to streamline the anterior torso (Hildebrand 1974) and reduce drag (Alexander 1975). In addition, fusion of the atlas and axis, or the entire cervical region can occur, limiting movement at the atlanto-axial joint (Osburn 1903). However, in extant taxa

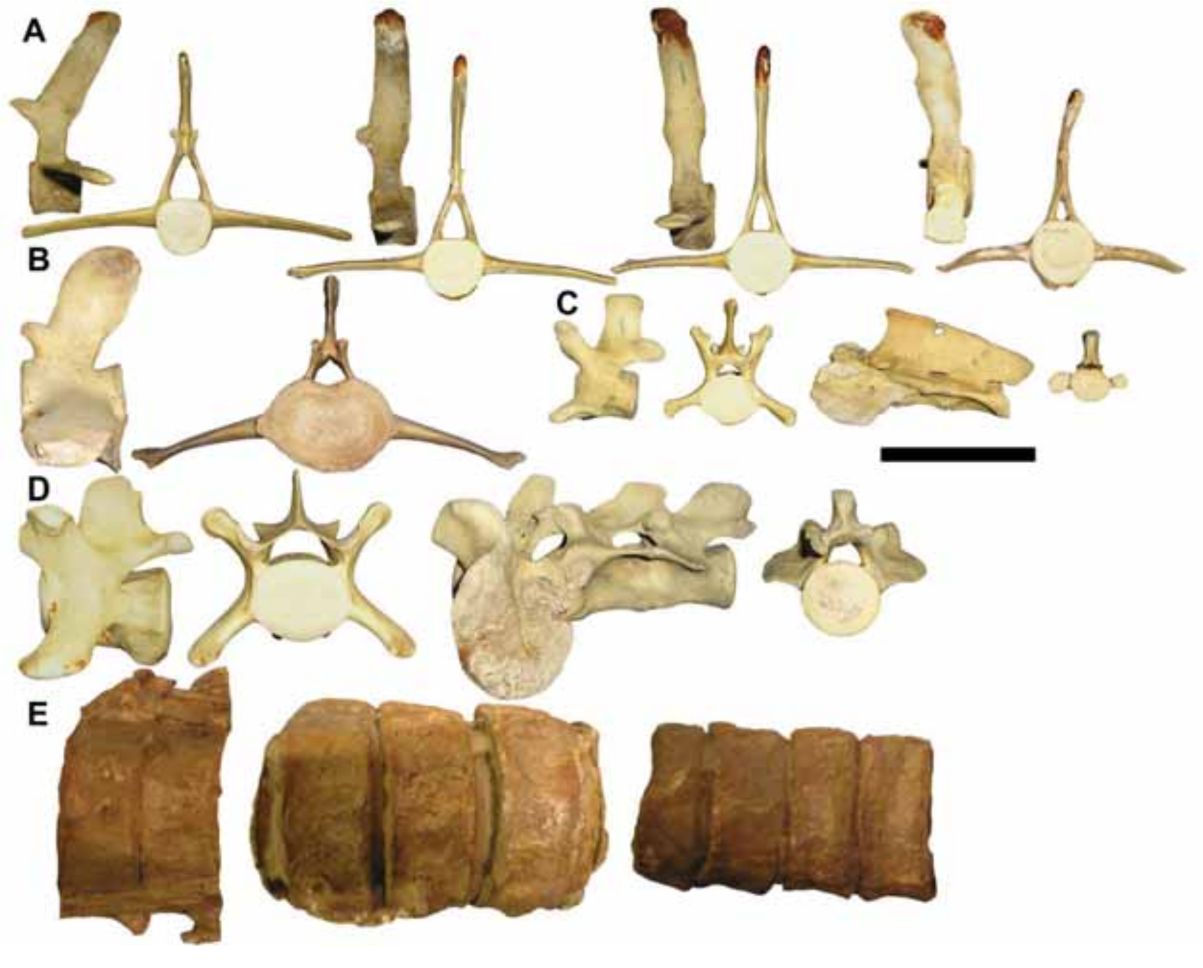

Figure 3: Lumbar and sacral vertebrae of (A) bottlenose dolphin SAM M21243, (B) dugong SAM M847, (C) Australian fur seal SAM M15964, (D) leopard seal SAM M16638, and (E) lumbosacral vertebrae of *Platypterygius australis* QM F2453. Mammalian taxa are shown in lateral (left) and anterior (right) views. *P. australis* is shown in lateral view only. The vertebrae shown are as follows (left to right): 20th (L1), 25th (L6), 30th (L11), and 35th (S5) for the dolphin; 30th (L5) for the dugong; 25th (L3) and 28–30th (S1–3) for the otariid and phocid seal; and vertebrae 36–37, 45–47, and 48–51 for *P. australis*. Scale bar = 10 cm.

this is restricted to fast caudal propulsors, as the manatee (Buchholtz *et al*. 2007) and dugong do not have fused cervicals.

The thoracic vertebrae in caudally propulsive tetrapods also have restricted movement. This is evidenced by the increasing height of the neural spine and the presence of rib facets (Figure 2A-B), both correlated with decreasing flexibility through limiting rotation between adjacent vertebrae (Buchholtz and Schur 2004). Mobility within the vertebral column is generally greater posteriorly, and is often associated with dorsoventrally short, caudally-inclined neural spines (Buchholtz and Schur 2004) (Figure 3A-B). The precise point at which

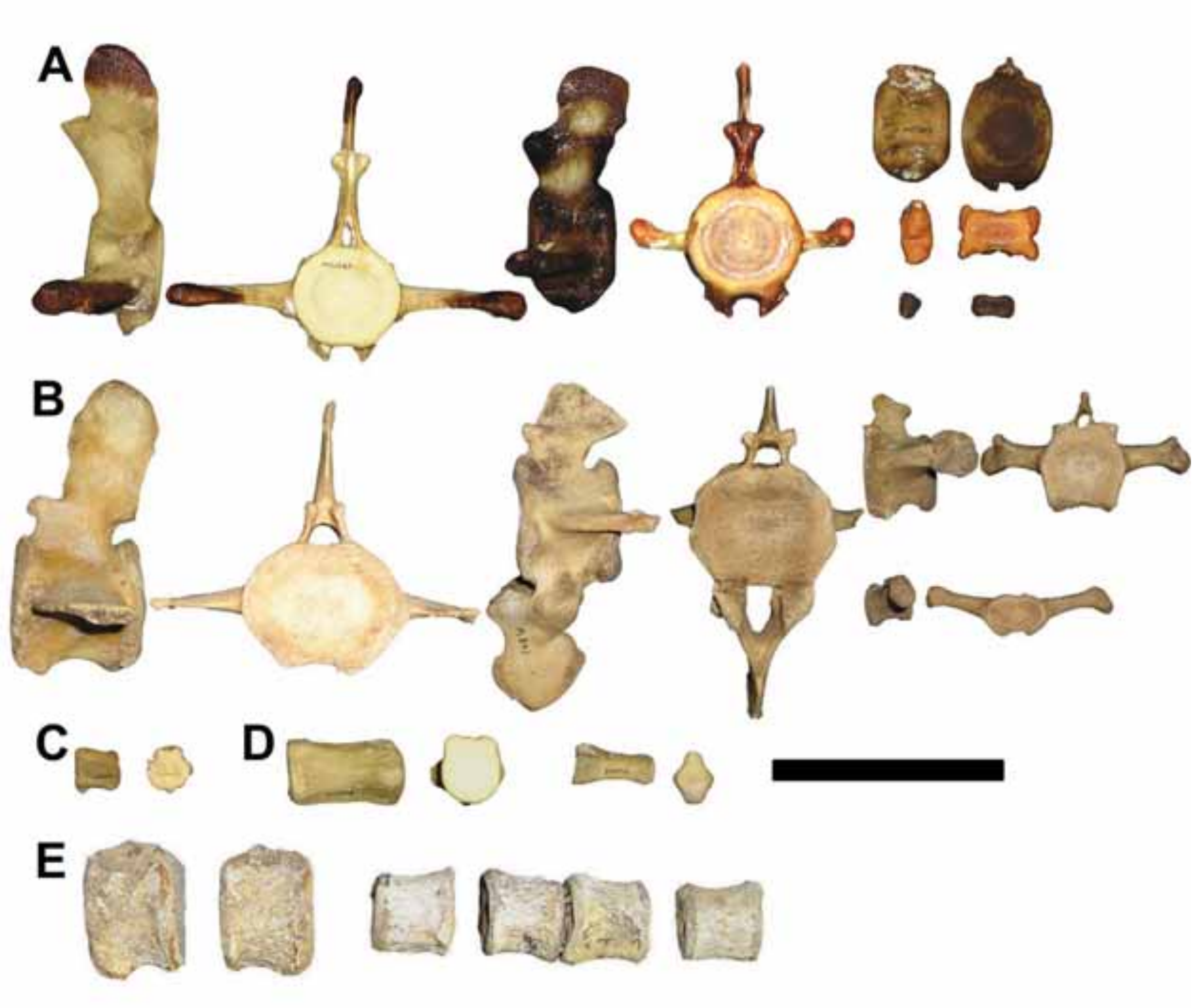

Figure 4: Caudal vertebrae of (A) bottlenose dolphin SAM M21243, (B) dugong SAM M847, (C) Australian fur seal SAM M15964, (D) leopard seal SAM M16638, and (E) lumbosacral vertebrae of *Platypterygius australis* KKM R519. Mammalian taxa are shown in lateral (left) and anterior (right) views. *P. australis* is shown in lateral view only. The vertebrae shown are as follows (left to right): 40th (Ca4), 45th (Ca9), 50th (Ca14), 55th (Ca19), and 60th (Ca24) for the dolphin; 35th (Ca3), 40th (Ca8), 45th (Ca13), and 50th (Ca18) for the dugong; and 35th (Ca5) and 40th (Ca10) for the otariid and phocid seal. The position of the vertebrae for *P. australis* is unknown as the anterior section of the skeleton is unpreserved. Scale bar = 10 cm.

flexibility increases is species-specific in the Cetacea and depends upon the length of vertebral column used in propulsion – in *Tursiops*, this occurs at the beginning of the caudal region (approximately at vertebra 40 in SAM M21243). The lack of discrete morphological boundaries between the classically defined lumbar, sacral, and caudal vertebrae are also typical in caudal propulsors. The centra in the caudal region correspond to the most mobile part of the spinal column, with the neural spines either greatly reduced or absent, and the centra dorsoventrally compressed (Figure 4A-B) – the latter feature allows for increased dorsoventral versus lateral mobility (Hildebrand 1974), and is related to the dorsoventral axial movement of the mammalian vertebral column.

Pectoral girdle and forelimb. Both caudal propulsors had 'symmetrical' scapulae – except for this feature, scapular shape and morphology differed between the two caudal propulsors examined (Figure 5). In the fast caudal propulsor (i.e. the dolphin, *Tursiops aduncus*), the scapula was generally broader than long (Table 1) with concave and convex surfaces, but did not bear a spinous process on its external surface. The scapula of the slow caudal propulsor (i.e. the dugong, *Dugong dugon*), however, was longer than broad (Table 1) with a spinous process on its external surface. A more complex surface texture (i.e. not completely smooth) has been correlated with greater differentiation of musculature in the Amazon River dolphin, *Inia geoffrensis*, and associated with the greater manoeuvrability achieved by the extensive movements of the forelimb (Klima *et al.* 1980). The forelimbs of

Table 1: Length:width ratio of appendicular elements for each taxon.

	Length/width ratio of appendicular elements for each taxon				
Element	*Platypterygius*	Fast caudal propulsor	Slow caudal propulsor	Pectoral propulsor	Pelvic propulsor
Scapula	Unknown	0.6-1.1	1.3-1.6	0.7-1.0	0.7-0.8
Humerus	1.3	1.7-2.1	1.9-2.8	2.6-2.9	1.8
Radius	0.7-1.2	2.5-3.5	5.9-6.9	4.9-5.8	4.8
Ulna	0.7-1.5	1.9-2.7	3.6-4.8	2.3-3.3	2.6-2.9
Metacarpals	1.1	1.2-1.8	3.5-4.2	2.7-3.2	3.7-4.0
Forelimb phalanges	0.6-0.9	0.5-1.7	1.7-2.4	3.2-3.8	3.7-4.7
Femur	1.9	Absent	Absent	2.1-2.3	1.9
Tibia	1.0	Absent	Absent	4.8-6.0	4.2
Fibula	1.3	Absent	Absent	8.3-14.6	10.6
Metatarsals	0.8	Absent	Absent	2.9-3.3	3.3-3.4
Hind limb phalanges	0.8	Absent	Absent	3.9-4.7	4.0-4.5

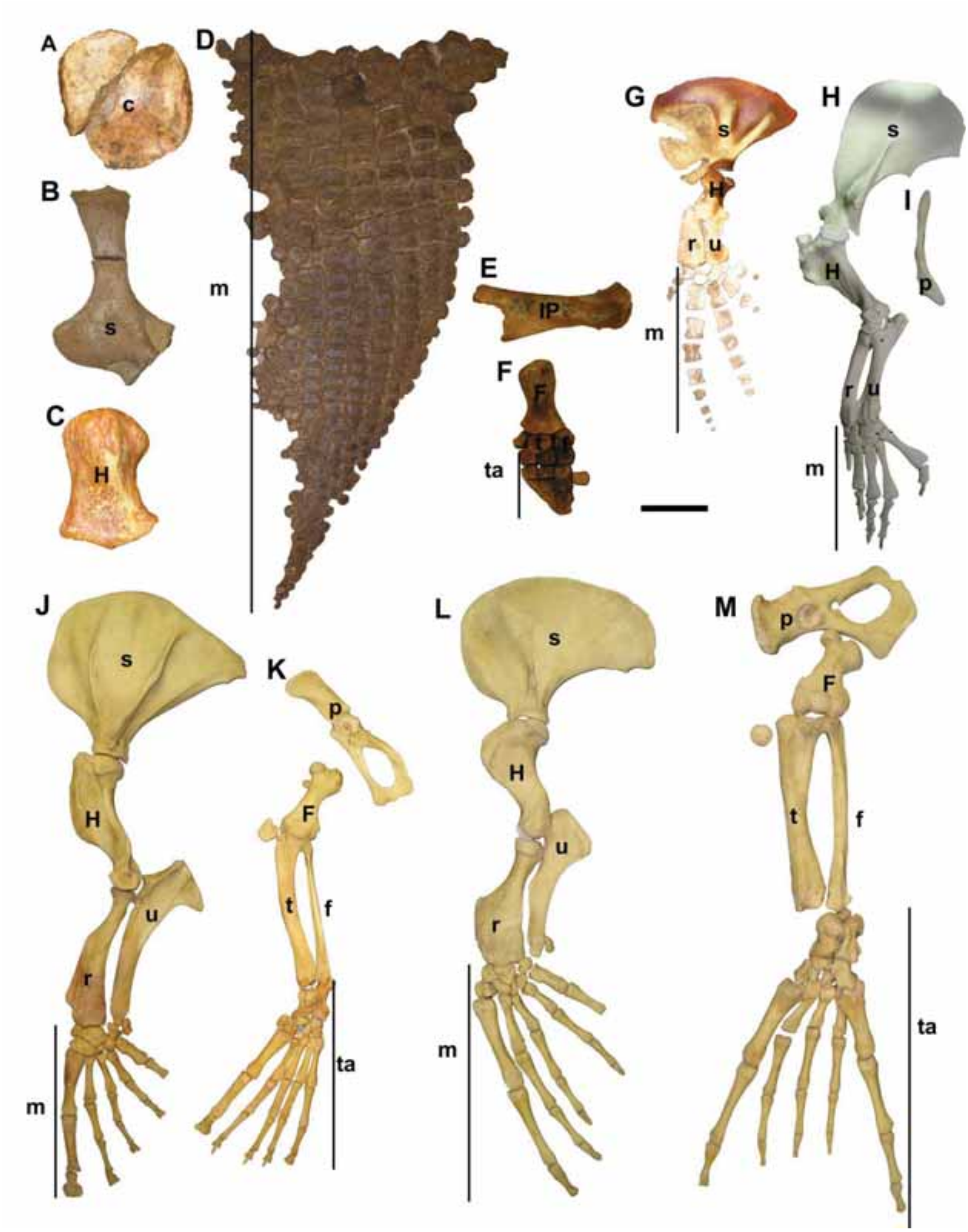

Figure 5: Forelimb and hind limb material of *Platypterygius australis* including (A) right coracoid QM F40822 in dorsal view; (B) left scapula SAM P44323 in external view; (C) right humerus QM F2573 in dorsal view; (D) manus of QM F10686 in dorsal/ventral view; (E) ischiopubis QM F40821 in internal view; and (F) left hind limb of QM F18906 in dorsal view. Left forelimbs (G, H, J, L) and left hind limbs (I, J, M) of the bottlenose dolphin (G), dugong (H–I), Australian fur seal (J–K), and leopard seal (L–M) shown in dorsal view. Abbreviations: c, coracoid; F, femur; f, fibula; H, humerus; IP, ischiopubis; m, manus; p, pelvis; r, radius; s, scapula; t, tibia; ta, tarsus; u, ulna. Scale bar = 10 cm.

the slow caudal propulsor may be capable of a wider range of motion than the fast caudal propulsor, and this is supported by the range of functions served by the limbs in the dugong (Brown 1878; Harrison and King 1975; Berta and Sumich 1999). Further, the scapula appeared to have a smaller surface area in the slow caudal propulsor, despite the size ranges of the two species only differing by approximately 20 cm (sensu van Dyck and Strahan 2008), indicating that the fast caudal propulsor had a greater scapular area for muscle attachment.

The humerus also differed considerably between the two caudal propulsors (Figure 5). Humeral morphology in the fast caudal propulsor reflected the flipper formed by the distal section of the forelimb (Figure 5G). The proximal head of the dolphin humerus had a single tubercle for muscle attachment and formed a ball-and-socket articulation with the scapula, while the distal end was antero-posteriorly expanded into the plane of the flipper. Between the two ends, the humeral shaft narrowed to exhibit a ‘waisted’ appearance. In contrast, the humerus of the slow caudal propulsor was expanded proximally and tapered towards its distal end (in lateral view, Figure 5H). Additional tuberosities were present on the proximal end of the dugong humerus, a feature that has been correlated with increased muscle attachment to improve slow manoeuvring in the Amazon River dolphin (Klima *et al.* 1980). Further, the humerus of the slow caudal propulsor was longer (both in absolute length and relative to body size) than the fast caudal propulsor, and more elongate. Shortening of the humerus has been correlated with increased streamlining of the body (Hildebrand 1974), indicating that the fast caudal propulsor was the more streamlined of the two taxa considered here.

The most obvious difference in the distal portion of the forelimb for these two taxa is the presence of an elbow joint in the slow caudal propulsor (Hill 1945) while the joints distal to the shoulder exhibit little or no movement in the fast caudal propulsor (Cooper *et al.* 2007b). This limb stiffness may be related to the use of the flipper as a hydrofoil in the dolphin (Cooper and Dawson 2009), while the use of the forelimb in the dugong is more varied, and includes feeding (Harrison and King 1975) and manoeuvring (Berta and Sumich 1999). However, movement of the radius and ulna is somewhat restricted in the dugong by the fusion of the two elements at both the proximal and distal ends. The carpals are also fused in the slow caudal propulsor, limiting movement in the wrist. In contrast, fusion in the distal forelimb of the fast caudal propulsor is more varied (i.e. sometimes radius and ulna are fused, sometimes the two elements fused with the humerus, and sometimes carpal elements fuse). For both taxa, the radius and ulna are longer than broad, and carpal elements are broader than long.

In the manus, digit morphology varies between the two taxa examined. All phalanges are longer than broad, although the distal phalanges of the fast caudal propulsor are almost circular. The fourth digit is the longest in the slow caudal propulsor, while the second is the longest in the fast caudal propulsor – this might be associated with the formation of the flipper in the latter taxon. Individual phalanges are longer in the slow caudal propulsor; however, the fast caudal propulsor exhibits hyperphalangy (i.e. where the number of phalanges exceeds the ancestral condition), and has the longer manus of the two taxa. Hyperphalangy has been correlated with a steering and stabilising function in fast-swimming caudally propulsive marine tetrapods (Cooper *et al.* 2007a; Cooper and Dawson 2009). Cetaceans have also been known to exhibit hyperdactyly in rare cases as a digital anomaly (Cooper and Dawson 2009), and a single modern cetacean, *Phocoena sinus*, is known to show non-anomalous hyperdactyly within its populations (Ortega-Ortiz *et al.* 2000). However, the significance of hyperdactyly for function is currently unclear.

Pelvic girdle and hind limb. Loss or reduction of the hind limb and corresponding girdle in cetaceans is thought to have occurred after the evolution of caudal propulsion (Thewissen *et al*. 2006). All extant mammalian caudal propulsors have no external hind limbs and a greatly reduced pelvis. Indeed, one species of manatee, *Trichechus inunguis*, has lost all elements of the pelvic girdle (Husar 1977). The ilia also lack any connection to the vertebral column, which is reflected in the loss of an identifiable sacrum in these animals (Fig. 3A–B).

Summary. In summary, the important skeletal features correlated with caudal propulsion include: (1) shortened cervical region; (2) dorsoventral compression for increased dorsoventral flexibility in the most mobile vertebrae; (3) difference in neural spine height and inclination posteriorly, associated with increased flexibility; (4) lack of discrete morphological boundaries between regions of the vertebral column; (5) absence of a fused sacrum; (6) reduction or loss of the pelvic girdle; and (7) loss of the hind limb. Several skeletal features also appear to distinguish fast and slow caudal propulsors. Fast caudal propulsors have a fused cervical region, which would limit movement at the atlanto-axial joint. The propodials were also shorter in the fast caudal propulsor, perhaps to increase streamlining, while the shape of the humerus was associated with the formation of the flipper. In addition, the forelimb of the fast caudal propulsor had very little movement distal to the shoulder joint – this is perhaps related to the flipper functioning as a single unit, and its use a hydrofoil. In contrast, the slow caudal propulsor had an unfused cervical region and more elongate propodials, possibly as a result of streamlining being less important at lower speeds. The greater mobility in the forelimbs of the slow caudal propulsor reflects its multiple functions.

Pectoral propulsors

Pectoral propulsion, where the forelimbs are used as the main swimming apparatus, is present in a wide range of secondarily aquatic tetrapods. The most highly adapted extant mammalian forms include otariid seals (fur seals and sea lions).

Axial skeleton. Cervical centra (Figure 1C) in the pectoral propulsor are cylindrical (i.e. long relative to their height and width), and the vertebrae in this region are unfused. Both of these characteristics indicate a flexible cervical region (Buchholtz and Schur 2004), and likely relate to the use of the neck during terrestrial locomotion (English 1976b in Berta and Sumich 1999) and in changing direction during swimming (Ray 1963). The neural spines increase in height posteriorly through the cervical vertebrae (in contrast to the pelvic propulsor), providing a greater area for attachment of the neck musculature (Berta and Sumich 1999), and, again, likely relates to its use in terrestrial locomotion.

High neural spines are also present in the thoracic region – as the main muscular power is concentrated at the anterior end (Harrison and King 1965) – specifically for attachment of the multifidus lumborum and longissimus thoracics (Berta and Sumich 1999). The length of the neural spines also increases posteriorly (Howell 1929), possibly decreasing the flexibility present between adjacent vertebrae. Howell (1929) also noted that the flexibility in the posterior region of the thorax in one pectoral propulsor was reduced by tight interlocking of the zygapophyses. Further, the presence of ribs decreases movement between adjacent vertebrae as Buchholtz and Schur (2004) found in caudal propulsors. Thus, the thoracic region of the spinal column is less flexible that the cervical vertebrae.

Unlike in the caudal propulsors, the lumbar, sacral, and caudal regions are readily distinguishable in the pectoral propulsor examined. The lumbar vertebrae share a similar morphology to the posterior-most thoracic vertebrae, except for the presence of looser articulations (Howell 1929), and the absence of rib facets. The centra in the lumbar region have a cylindrical shape (length > width > height), a feature also present in both the sacral and caudal regions. A fused sacrum consisting of three vertebrae is present (though the first caudal was fused to the sacrum in one specimen examined), and the three centra show a regular decrease in width (Howell 1929). The neural spine decreases in height throughout the caudal region, and is virtually absent in the posterior-most caudal vertebrae. This morphology indicates that the immobile, fused sacrum separates two relatively flexible regions – the lumbar region anteriorly, and the caudal region posteriorly.

Pectoral girdle and forelimb. The scapula in the pectoral propulsor examined was broader than long (Table 1), and was longer than the equivalent element in the caudal propulsors (Figure 5). This provides a much greater surface area for muscle attachment (Howell 1929) compared with non-pectoral propulsive tetrapods. In addition, the fan-shape of the scapula (Figure 5J) is also associated with muscle attachments (English 1977). The scapula also bears two prominent ridges which, in addition to the enlargement of the supraspinous fossa, are correlated to the strong development of the supraspinatus muscle

(Berta and Sumich 1999). Further support for the strong development of the supraspinatus includes the greater area for the attachment of this muscle, giving the scapula an asymmetric appearance. This is perhaps unsurprising, as the supraspinatus assists in movement of the humerus (Howell 1929).

In comparison to the caudal propulsors, the humerus of the pectoral propulsor is both longer and more elongate (Figure 5, Table 1) – however, the element is described as short and massive (Howell 1929; English 1977), thus exhibiting characteristics Hildebrand (1974) associated with increased streamlining. Additionally, the otariid humerus is more robust with more surfaces for muscle attachment than the fast caudal propulsor. This is demonstrated by the two enlarged tubercles present adjacent to the proximal head, while the well-developed deltoid crest on the humeral shaft also provides a greater surface area for muscle attachment. The former feature is also associated with increasing the moment arm of the rotator cuff musculature (Berta and Sumich 1999), thus increasing the power and manoeuvrability in the otariid seal. Howell (1929) also interpreted the extension of the humerus as being more powerful in pectoral propulsors relative to pelvic propulsors among the Pinnipedia. The proximal articular surface of the humerus forms a ball-and-socket articulation at the shoulder joint, and this articular surface is quite extensive, providing a large surface area for increased ranges of movement (English 1977).

Like the humerus, the radius and ulna of the pectoral propulsor have been shortened, and thus exhibit adaptations to streamlining (English 1977) – however, both elements are also longer and more elongate than the comparable bones in the fast caudal propulsor (Figure 5, Table 1). The epipodial elements do not exhibit any fusion, in contrast to the caudal propulsors, perhaps reflecting the employment of a rowing swim stroke (Feldkamp 1987) or the use of the forelimb in both aquatic propulsion and terrestrial locomotion (English 1976b). English (1977) described the elbow joint as functioning as a modified hinge joint – this is in stark contrast to the absence of a functional elbow joint in the fast caudal propulsor. However, most movement seems to occur at the glenohumeral joint with the elbow possibly being used for control (English 1977). The radius and ulna, along with the more distal forelimb elements, exhibit flattening associated with the formation of the flipper (English 1977); in fact, Howell (1929) considered the broadness of the bones distally and proximally, respectively, to be unique to the Pinnipedia.

The remainder of the pectoral propulsor forelimb has more in common with the pelvic propulsor than the caudal propulsors (Figure 5). None of the wrist bones exhibit fusion (in contrast to the caudal propulsors), and the differences in morphology between the carpal elements of the two types of limb propulsors has been attributed to the position of the pectoral propulsor's forelimb during terrestrial locomotion (Howell 1929). Like many of the mammalian taxa examined in this study, the otariid seal exhibits flattening and elongation of the digits (Figures 5J–K, Table 1), perhaps related to the formation of the flipper and/or to increase the surface area of the distal forelimb – however, in the pectoral propulsor, the first digit is the longest, with the digits progressively decreasing in size anterior to posterior.

Pelvic girdle and hind limb. In contrast to caudal propulsors, pectoral propulsors do not show any reduction in the pelvic girdle, perhaps resulting from the use of the hind limbs in terrestrial locomotion. All modern pectoral propulsors return to land, and therefore none are purely aquatic. An obligate aquatic animal that uses only its forelimbs for propulsion and does not require its hind limbs for terrestrial locomotion might exhibit reduction of the pelvis – however, this hypothesis cannot be examined using modern taxa as no obligate aquatic, pectoral propulsor is currently known. The pectoral propulsor exhibits a lengthening of the ischium and pubis, and migration of muscle attachments distally to increase leverage – the importance of the former feature is unclear (Howell 1929).

The femur in the pectoral propulsor is a flattened bone with expanded proximal and distal ends (Figure 5K). As with the cetacean humerus, the femoral shaft has a 'waisted' appearance. Two trochanters are present (the greater adjacent to the ball-and-socket articulation to the pelvic girdle, and the lesser on the lateral surface on the femoral shaft), allowing muscles to insert separately on the femur (Howell 1929). Separate insertions may allow for more manoeuvrability in the hind limb of the pectoral propulsor, as reported in the forelimb for the Amazon River dolphin (Klima *et al.* 1980).

Both the tibia and fibula are elongate elements in the pectoral propulsor (Figure 5K, Table 1). Fusion of these two bones occurs at the proximal end of these elements, and the fused head of these elements is sharply angled to allow greater flexibility of the knee (Howell 1929). This may reflect a steering or manoeuvring function for the hind limb in aquatic locomotion, and/or its use in terrestrial movement. The morphology of the astragalus, however, indicates restricted movement relative to the surrounding elements when compared to that of the pelvic propulsor (Howell 1929) – the reason for this remains unclear. Like the forelimb, the metatarsals and phalanges are elongate and flattened, and probably for similar reasons – the formation of the flipper and to increase the surface area of the hind limb. However, while the first digit is clearly the most robust and well-developed, and the first metatarsal is the longest of the five, none of the digits appear to be longer than the others.

Summary. Several important features appear to correlate with pectoral propulsion. These include: (1) a longer cervical region than found in caudal propulsors; (2) large surface areas for muscle attachment on the pectoral girdle and forelimb elements; (3) elongate epipodial elements; and (4) flattened and elongate digits. Further, the rowing style employed by the pectoral propulsor examined may require flexibility at the elbow joints and in the wrist – however, the forelimb is also used extensively in terrestrial locomotion, and the flexibility observed in these joints may also reflect this function of the limb.

Pelvic propulsors

Only a single group of extant, secondarily aquatic tetrapods rely upon their pelvic limbs for propulsion – phocid seals (true seals). Usually, pelvic propulsors generate thrust through alternating strokes of the left and right hind limbs (Alexander 1975) assisted by lateral movements of the lumbar and caudal vertebrae (King 1989). Additionally, the hind limbs can be moved as a single unit (Ray 1963) via lateral sweeps of the vertebral column

(Alexander 1975). In contrast to the pectoral propulsors, the forelimbs have a reduced role in both aquatic and terrestrial locomotion – in aquatic locomotion the pectoral limbs are generally folded against the body, but may be used for an initial acceleration (Ray 1963) or for stabilisation and manoeuvring (Feldkamp 1987).

Axial skeleton. The cervical vertebrae in the pelvic propulsor exhibit an anatomy intermediate between the pectoral and caudal propulsors. Like the pectoral propulsors, the vertebrae of this region are unfused and cylindrical in shape, suggesting that this region was capable of greater flexibility than in the caudal propulsors. This is perhaps to be expected as the neck is used to change direction, and assumes an S-shape to achieve a more streamlined body (Ray 1963). However, the cervical centra are shorter in the pelvic propulsor compared to the pectoral propulsor (Howell 1929), and are wider than they are long or high – in the caudal propulsors, shorter centra are associated with a more streamlined, torpedo-shaped body, and this may be the reason for shortened centra in the pelvic propulsor. Additionally, there is virtually no neural spine present in the vertebrae in the cervical region (Howell 1929) – in contrast to the otariids, but similar to the caudal propulsors (Figure 1) – this is likely a result of the neck not being used in terrestrial locomotion as in the otariid seals. Thus, the cervical region of the pelvic propulsor exhibits several features associated with a flexible neck, while others are correlated with the requirement to improve streamlining, as observed in the pectoral and caudal propulsors respectively.

Like the majority of the cervical centra, the thoracic centra (all but the most posterior) are wider than they are long or high, indicating a decreased flexibility compared with the lumbar region. In addition, the presence of ribs (as with caudal propulsors: Buchholtz and Schur 2004) decrease the mobility in this region relative to the cervical vertebrae. The reduced neural spines (Figure 2D) have been noted by several authors (e.g. Howell 1929) – this likely results from the reduced musculature, relative to the pectoral propulsor, required anteriorly (Harrison and King 1965). Conversely, the elongate transverse processes of the lumbar region are for the attachment of the vertebral muscle blocks involved in the lateral movements of the hind body, reflecting the importance the location of the main muscular power in the posterior part of the body and thus the mode of swimming (Harrison and King 1965; King 1989; Berta and Sumich 1999). In addition, the lumbar vertebrae are also characterised by the loose articulations that allow great flexibility (Harrison and King 1965), and the zygapophyseal shape in the last lumbar and first sacral that allow the sacrum to be raised above the vertebral axis (Howell 1929) – the latter feature was not observed by Howell (1929) in the pectoral propulsor. Otherwise, the morphology of the lumbar region are similar to that of the posterior thoracic vertebrae (Howell 1929), including a centrum length that is greater than both width and height (as observed in the last thoracic centra).

As in the pectoral propulsor, but unlike the caudal propulsors, a fused sacrum and clearly defined vertebral regions are present in the pelvic propulsor (Figure 3). However, unlike the pectoral propulsor, the width of the first sacral is considerably greater than the remaining two centra (Howell 1929), demonstrated by the width being the greatest dimension in the first sacral centrum (unlike in the pectoral propulsor) while length was the largest measurement in the remaining centra (as observed in the pectoral propulsor). Similarly, the caudal vertebrae are cylindrical with low neural spines, indicating a greater flexibility than the preceding sacral region, though the centra appear to be more elongate than the corresponding centra in the pectoral propulsor (Figure 4).

Pectoral girdle and forelimb. The scapula in the pelvic propulsor examined was almost oval in shape (Figure 5L), in contrast to the fan- or sickle-shape Howell (1929) observed in an otariid and phocid, respectively. As with the pectoral propulsor, but unlike the caudal propulsors, the scapula is asymmetric in appearance – however, in the phocid propulsor, this results from a greater area for muscle attachment caudad to the spinous process, and thus a less developed supraspinatus musculature. Only a single spine can be observed on the external surface (like the slow caudal propulsor), compared with two in the pectoral propulsor and none in the fast caudal propulsor, and the scapula is otherwise relatively smooth. This indicates a smaller area for muscle attachment compared to the former

(King 1989), but a greater area of muscle attachment relative to the latter. There is also a tendency for this spine to be reduced in the phocids relative to their otariid counterparts (Harrison and King 1965). As with the pectoral and fast caudal propulsors, but unlike the slow caudal propulsor, the scapula is broader than it is long (Table 1) – however, the scapula is reduced relative to the total size of the animal compared to the pectoral propulsors.

As suggested by Harrison and King (1965), the general humeral morphology (as well as the rest of the forelimb) of the pelvic propulsor is similar to that of the pectoral propulsor. The humerus has a deltoid crest (though this is less robust than in the otariid seal) and two tubercles, which, as discussed for the pectoral propulsor, are associated with greater areas for muscle attachment and increased power and manoeuvrability (Berta and Sumich 1999). A ball-and-socket articulation is present at the glenohumeral joint, indicating a similar flexibility was present at the shoulder as in the pectoral propulsor. This element is also longer than it is wide and described as short (Howell 1929; King 1989) with the latter feature associated with increased streamlining – however, the humerus is not as elongate as that of the pectoral propulsor, exhibiting a length:width ratio more comparable with the caudal propulsors (Table 1). An additional difference to the otariid seal includes the position of the greater tuberosity no higher than the humeral head, related to the different movement requirements of the forelimb compared to pectoral propulsors (Howell 1929). Thus, the musculature of the forelimb does not appear to be as developed as in the pectoral propulsor, but the amount of flexibility is similar – perhaps the flexibility is required to fold the forelimbs alongside the body during aquatic locomotion, while the musculature is less important as the primary propulsive power is at the posterior part of the body.

The radius and ulna (Figure 5L) of the pelvic propulsor are also similar in overall morphology to the pectoral propulsor (Harrison and King 1965). Both elements are shortened, flattened distally (radius) or proximally (ulna), and longer than broad (Osburn 1903; Howell 1929; Harrison and King 1965; King 1989) (Table 1). A functional elbow joint is present, and fusion is absent between these elements – the forelimb of the pelvic propulsor has not been as extensively studied as the pectoral propulsor, but it may also have functioned as a modified hinge joint as the morphology does not differ considerably between the two propulsors. However, the radial styloid process of English (1977) appears to extend further proximally and the proximal end of the ulna does not appear to be as broad in the pelvic propulsor. The reasons for this are unclear, but the latter perhaps relates to the greater muscle attachments required in the pectoral propulsor.

As outlined above, the pelvic and pectoral propulsors showed the greatest similarity in the morphology of the manus. These similarities included the absence of fusion in the carpal elements, lengthening (Table 1) and flattening of the digits, and the first digit being the longest with the remaining digits decreasing in size anterior to posterior. The decrease in size of the digits, however, appears to be more pronounced in the pectoral propulsor (Howell 1929). One difference in manus morphology includes the crowding of the carpal elements on the ulnar side of the limb (Harrison and King 1965), attributed to the position in which the phocid seal holds its forelimb (Harrison and King 1965).

Pelvic girdle and hind limb. Unsurprisingly, the pelvic propulsors show no reduction of the pelvic girdle – instead, the innominate bone in this type of propulsor shows several adaptations that highlight the importance of the pelvic girdle in locomotion. The ilium shows the lateral eversion characteristic of the phocines (Harrison and King 1965; King 1983 in Berta and Sumich 1999). This morphology provides a much greater attachment area for the iliocostalis lumboram muscle, which flexes the lateral part of the body during swimming, and to increase the area for the attachment of muscles that insert on the femur (m. gluteus medius, minimis, and pyriformis), which serve as the lateral abductors of the hip (Berta and Sumich 1999). The iliac wing of the innominate bone is deflected outwards, providing attachment points for the iliocostalis muscles (Smith and Savage 1956). Both the ischium and pubis are long relative to the ischium to increase the lever arm of the muscles used in the adductional movements while swimming (Howell 1929). As a result of the morphology of the last lumbar and first sacral vertebrae, the ischium can be elevated to the level of the backbone (Howell 1929), lengthening the ischiopubic muscles (Smith and Savage 1956).

Overall, the femur of the pelvic propulsor is very similar to that of the pectoral propulsor – it is a shortened, flat element (Harrison and King 1965) with a ‘waisted’ shaft, and bears a greater trochanter lateral to the femoral head. Howell (1929) described this trochanter to be wedge-shaped, with a deep fossa resulting from complete fusion of the tendons inserting at this point. In addition, the lesser trochanter is absent in the pelvic propulsor, correlated with a decrease in the attachment area of muscles that rotate the femur posteriorly (e.g. mm. iliacus and psoas major) – instead, these muscle insert either onto the iliac wing or distal to the medial femur, increasing the flexibility of the leg and lateral undulation of the lumbosacral region of the vertebral column (Berta and Sumich 1999). Further, the femur of the pelvic propulsor is ‘stockier’ and less elongate than that of the pectoral propulsor (Table 1), particularly at this distal end. This could be related to the greater development of the gluteus maximus, gastrocneumius medialis, and plantaris Howell (1929) noted for the phocid seals.

The remaining elements of the pelvic limb show many similarities to the pectoral propulsor. Both the tibia and fibula of the pelvic propulsors are elongate elements (Table 1), and are fused into a single head at the proximal end. However, the fused head of the two elements is approximately level, compared with the sharp angle observed in the pectoral propulsor, indicating that less flexibility was present in the knee joint compared to the otariid seal (Howell 1929). As stated previously, the morphology of the astragalus indicates that a greater range of movement relative to the surrounding elements was present in the pelvic propulsor (Howell 1929). The metatarsals and phalanges are elongate and flattened (Table 1), associated with the formation of the flipper and to increase the surface area of the hind limb (Hildebrand 1974) – however, while the first metatarsal is the more robust, the first and fifth digits are both longer than the middle three. Howell (1929) described the metatarsals of the phocid seal he examined as being crowded and thus having restricted movement – this may also be true of the pelvic propulsors examined in this study.

Summary. Pelvic propulsion appears to correlate with several morphological features. This includes: (1) a cervical region intermediate in length between caudal and pectoral propulsors; (2) large surface areas for muscle attachment on the pelvic girdle; and (3) flattened and elongate digits. In addition, the lumbar region of the pelvic propulsor appears to be quite flexible, but this may result from the lumbar part of the body assisting with propulsion rather than pelvic propulsion *per se*.

DISCUSSION

Comparisons with *Platypterygius australis*

The vertebral centra of *Platypterygius australis* are deeply amphicoelous, a feature typical of caudally propulsive ichthyosaurs (Buchholtz 2001a). Fusion of the atlas and axis occurs in both *P. australis* and caudally propulsive ichthyosaurs (McGowan and Motani 2003?), and was only observed in the fast caudal propulsor examined in this study. Disc-like centra are present throughout the vertebral column of this ichthyosaur, and are more similar in appearance to the shortened cervical centra of the caudal propulsors rather than the cylindrical centra of the pectoral and pelvic propulsors. The latter two features have been correlated with shortening of the cervical region, which, in turn, is an adaptation to increase streamlining (Hildebrand 1974). There is a pronounced lack of sharply defined regions along the vertebral column (a feature shared with both the fast and slow caudal propulsors but not the pectoral or pelvic propulsor, pers. obs.) – this may be due to the absence of a fused sacrum and corresponding disconnection of the pelvis from the vertebral column. The occurrence of definitive tail fluke centra demonstrates the presence of a caudal fin, and the lateral compression of these elements facilitates lateral movement of the vertebral column (similar to caudal propulsors). However, the length of the tail region cannot be estimated as only a few centra are preserved (contrary to McGowan' s1972 interpretation of a small caudal fin). The neural arches are also incompletely preserved (associated only with the anterior-most centra), preventing examination of changes in neural spine morphology throughout the vertebral column. Dorsal facets for articulation with an unpreserved neural arch were observed for all centra examined in the vertebral column.

Scapular morphology varied widely among the different extant taxa (Figure 5), and more investigations of the functional significance is required before conclusions can be drawn on how these differences relate to propulsive method. However, what can be observed is that animals using their forelimbs as a hydrofoil have a less complex (i.e., smoother) surface texture (as well as fewer areas for insertion on their humerus). Further, relative areas for muscle attachment appear to vary between the caudal, pectoral, and pelvic propulsors, but mycological studies are required for *Tursiops* and *Dugong* to confirm these observations. How these observations relate to ichthyosaurs is also unclear, for several reasons: (1) the ichthyosaur shoulder girdle is composed of four bones rather than the single element observed in all extant mammalian taxa examined; (2) a complex terminology for reptilian limb musculature exists, with several names being used for the same muscle (Romer 1956); and (3) the difficulties in inferring muscle origins and insertions (and thus function) in extinct species. Thus, the functional significance of the shoulder girdle morphology in *P. australis* remains unresolved.

Reduction of the pelvis in the caudal propulsors is considered an adaptation to increase streamlining (Hildebrand 1974). Only the ischium and pubis are fused in *P. australis*, and reflect a decreasing role of the hind limb in locomotion (vis-à-vis caudal propulsors). The absence of the obturator foramen implies that the obturator nerve (Romer 1956) and blood vessels passed around rather than through the pubis. Further, the muscles typically associated with this foramen, such as the puboischiofemoralis (Romer 1956) and rotators of the hind limb, must have been similarly reduced or absent.

The humerus and femur of *P. australis* have a very similar morphology (Zammit *et al.* 2010), and will therefore be discussed together – this is in contrast to the pectoral and pelvic propulsors, where the humeral and femoral morphology differ, and the caudal propulsors, where the femur and hind limb are absent. Both propodials are short and broad, showing a general morphology more similar to the stout cetacean humerus than the elongate morphology of the dugong, otariid, and phocid humeri. The proximal head of the humerus and femur is characterised by prominent dorsal and ventral trochanters (termed dorsal trochanter and deltopectoral crest respectively in the humerus, Motani 1999b). This is indicative of strong attachments for muscles originating on the limb girdles (e.g. m. latissimus dorsi, subscapulocoracoideus, scapulohumeralis anterior, deltoid, pectoralis and supacoracoideus; and m. pubioischiofemoralis externus and adductor femoris respectively), and were probably used to achieve joint stability as well as movement for the limb (Romer 1956). McGowan (1972) correlated this with some degree of forelimb propulsion, perhaps as a compensator for the hypothesised low aspect ratio small caudal fin (McGowan 1972). However, increased attachment surfaces for musculature do not necessarily impart better propulsive ability, and indeed robust humeral morphology might have aided in manoeuvring, especially at low speeds (see Klima *et al.* 1980 for observations of the Amazon River dolphin). It can also be linked to increased stability (Moore *et al.* 2010).

Both propodials of *P. australis* have a ‘waisted’ shaft that expands into distal ends that follow the same plane as the remainder of the limb (Figure 5C and F). Narrowing of the shaft distal to the proximal head (in dorso-ventral view) is not observed in the humeri of the slow caudal, pectoral, and pelvic propulsors – this is perhaps related to the formation of the deltaic crest in these extant taxa, a feature which has no equivalent in *P. australis* or the fast caudal propulsor. The humerus of the fast caudal propulsor (Figure 5G), and the femora of the pectoral and pelvic propulsors (Figure 5K and M, respectively) all exhibit a ‘waisted’ shaft. However, the femora of the pectoral and pelvic propulsors exhibit a slightly different morphology to that of *P. australis* – the femur of the former has trochanter on its femoral shaft to increase the area for muscle attachment, while the femur of both taxa do not show the same gradual distal expansion observed in both *P. australis* and the fast caudal propulsor. The distal expansion of the propodial occurs in all taxa examined (but perhaps to a lesser extent in the slow caudal, pectoral, and pelvic propulsors), and is associated with the formation of the paddle. Of all extant taxa examined, the cetacean humerus shows the greatest similarity to the morphology observed in *P. australis*.

The fore- and hind limb of *P. australis* exhibit the following features: tightly interlocking elements that do not have functional elbow or knee joints; pronounced hyperphalangy; and hyperdactyly that is amongst the most extreme of all ichthyosaurs. Comparable immobile joints distal to the humerus have been noted in cetaceans (Cooper *et al.* 2007b), where they serve to stiffen the limb as it moves as a unit (Hildebrand 1974), but the remaining extant taxa examined in this study did not exhibit this morphology. However, some pectoral propulsors (e.g. penguins) also exhibit relatively stiff forelimbs, indicating that immobile limbs are not correlated with a particular method of propulsion. Instead, it may affect the potential of the limb to function as a lift-generating structure (Fish 2004; Cooper *et al.* 2007b).

Hyperphalangy has been linked with increasing the rigidity in the distal parts of the limbs (Hildebrand 1975). Cetaceans are the only modern mammals to exhibit hyperphalangy, where it has been related to steering and balance (Richardson and Chipman 2003). The fast caudal propulsor was the only extant taxa examined in this study to show hyperphalangy – the slow caudal, pectoral, and pelvic propulsors did not have additional phalanges beyond the ancestral number. The presence of hyperphalangy in plesiosaurs, a group of extinct marine reptiles inferred to use pectoral and/or pelvic propulsion, suggests that this morphology may not correlate directly with method of propulsion, and supports the proposal of Cooper *et al.* (2007b) that it may instead be indicative of the use of the limb as a hydrofoil to generate lift.

The hyperdactyly observed in *Platypterygius* is the most extreme of all ichthyosaurs, having at least seven digits (McGowan and Motani 2003). Hyperdactyly was not observed in any of the extant taxa examined in this study – however, individuals of some cetacean species have been reported as exhibiting this feature (Watson *et al.* 2008; Cooper and Dawson 2009), and hyperdactyly is consistently expressed in a single porpoise species (e.g. *Phocoena sinus*: Ortega-Ortiz *et al.* 2000). Thus, hyperdactyly cannot be considered evidence of a particular method of locomotion. Instead, it may be correlated with increasing the size, particularly the width of the limb (Hildebrand 1974), and as such, it could have improved acceleration performance (Webb 1977) and/or function as a hydroplane.

The postcranial anatomy of *P. australis* shows several features that can be used to elucidate their propulsive method. Three morphological characteristics were common to *P. australis* and both caudal propulsors – shortened neck, compression of the caudal centra, and complete fusion of the ischiopubis. An additional feature, fusion of the atlas-axis complex, was observed only in *P. australis* and the fast caudal propulsor. Further, the limbs exhibited features correlated with a lift-generating function – propodial morphology, hyperphalangy, hyperdactyly, and tightly interlocking phalanges. In contrast, very few features were shared between *P. australis* and the pectoral or pelvic propulsors, and some characters, such as the short, broad phalanges, were in direct contrast to the morphology observed in these extant taxa.

CONCLUSIONS

P. australis has many postcranial features in common with caudal propulsors. Further, some of these features, such as the shortened neck, are in direct contrast to the morphology observed in pectoral or pelvic propulsors. Thus, *P. australis* is inferred to use caudal propulsion as the predominant method of locomotion. The convergence in limb anatomy between *P. australis* and the cetaceans was particularly striking, specifically in the stiffness of the limbs and hyperphalangy, and indicates a similar function – that of a hydrofoil used for steering and balance. However, the additional areas for muscle attachment, which are also observed in *Inia* in comparison to marine dolphins (Klima *et al.* 1980), indicate that use of the fore (and perhaps hind) limbs for low speed propulsion and manoeuvring is feasible (Wade 1984). *P. australis* might have had a decoupled locomotor system – where the caudal fin was used for long-distance cruising and the limbs for acceleration and movement – as some fish (Webb and Keyes 1981; Blake 2004) and aquatic mammals (e.g. *Inia*, Klima *et al.* 1980) do today. The increased surface area of the limbs, particularly the distal forelimb, would have improved acceleration (sensu Hildebrand 1974).

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CHAPTER 5

Healed bite marks on a Cretaceous ichthyosaur

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Maria Zammit (Candidate)
Was instrumental in research design, undertook the research, interpreted the data, wrote the manuscript, prepared original figures, and acted as corresponding author.

I hereby certify that the statement of contribution is accurate.

Signed..... ....Date.....9/1/11

Benjamin P. Kear
Identified specimen as relevant for research, aided in data interpretation, contributed to manuscript structure, provided extensive edits of the manuscript, and revised figures for the manuscript.

I hereby certify that the statement of contribution is accurate, and permission is given for the inclusion of the paper in the thesis.

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CHAPTER 6

CONCLUDING DISCUSSION

Platypterygius was a geographically widespread ichthyosaur genus (Maisch and Matzke 2000), and one of the last representatives of the Ichthyosauria (McGowan and Motani 2003). The genus itself requires extensive revision, having become a ‘waste-basket’ taxon for Cretaceous ichthyosaur material, and very few ontogenetic, functional, or palaeobiological studies have been undertaken (both for *Platypterygius* and Cretaceous ichthyosaurs in general) despite the availability of material. Thus, Australian occurrences of *Platypterygius* were used to address some of these gaps in knowledge by meeting the following objectives: (1) resolving the taxonomy of the Australian Cretaceous ichthyosaur material; (2) describing the postcranial anatomy of the endemic Australia species of *Platypterygius*; (3) developing an hypothesis of swimming style in this extinct animal; and (4) inferring behaviour in this ichthyosaur based on palaeopathological evidence.

Examination of the neotype of *P. australis* (designated by Zammit 2010) and holotype of *P. longmani* confirmed the supposition of Kear (2003) that both species belong to the same taxon – thus, *P. australis* is considered as the valid taxon and *P. longmani* its junior synonym. The taxonomic stabilisation of the Australian ichthyosaur material resolves the two-decade debate surrounding the nomenclature of *P. australis*, allowing future work to concentrate on species diversity of *Platypterygius*. In Australia, such research should concentrate on collecting additional fossil material from South Australian and Western Australian deposits that are stratigraphically older and younger, respectively, than Queensland occurrences. Determining the ichthyosaur species present in these regions will demonstrate if *P. australis* remains span this entire range in Australia (Berriasian–Cenomanian: Kear 2003), or if other forms of the genus were present as suggested by Choo (1999). In addition, further collecting in Western Australia (which includes the youngest deposits containing ichthyosaurs in the country) may indicate that ichthyosaurs persisted in Australia until their extinction in the Cenomanian.

The redescription of *P. australis* postcranial material identified diagnostic characters that, when combined with previously identified cranial and postcranial features, distinguish it from other species of *Platypterygius*. This study provides a valuable resource for other researchers as the description and illustrations can be compared with other ichthyosaurs. Further, re-examination of *P. australis* remains decreases the number of *Platypterygius* species requiring redescription and comparison to other members of the genus. Future work could follow several directions. Firstly, this study can be used in conjunction with other papers (e.g. Kolb and Sander 2009; Maxwell and Kear 2010) to identify phylogenetically significant, postcranial characters within *Platypterygius*. These characters can then be included in previously developed character matrices (e.g. Motani 1999b; Maisch and Matzke 2000) to investigate phylogenetic relationships within the genus. Secondly, foetal material can be examined to determine which diagnostic characters alter between life stages. In Australia, foetal remains are associated with gravid females (Kear *et al.* 2003), and can therefore be confidently assigned to species. This would allow morphological comparisons between the two life stages (e.g. foetal versus adult) that can shed light on how diagnostic characters vary during ontogeny.

Osteological comparisons between *P. australis* and extant mammalian analogues suggested that the most plausible swimming style in this extinct ichthyosaur was a decoupled system using the caudal fin and forelimbs for different types of propulsion. In this marine reptile, it is hypothesised that the caudal fin was used for long distance cruising, and the forelimbs for manoeuvring and possibly improving fast start acceleration (i.e. the type of acceleration employed to escape predators). Applying a similar methodology to other Australian Cretaceous marine reptiles could allow their dispersal abilities and hunting styles to be explored, and may result in understanding the niche specialisation of the extinct marine reptile fauna present during this period.

Bite marks on a partial ichthyosaur snout were hypothesised to result from aggressive interactions with another ichthyosaur. This is the first record of such behaviour in ichthyosaurs, despite being recorded in many extinct reptilian taxa (e.g. mosasaurs: Everhart 2008; crocodiles: Avilla *et al.* 2004; Mackness and Sutton 2000; dinosaurs, Tanke and Currie 1998). However, injuries have been figured (Martill 1996) or noted (Lingham-Soliar 2003) on ichthyosaur remains, but are yet to be described – further studies could examine such pathologies in detail, leading to a greater understanding of the interactions between Mesozoic vertebrates.

The research presented in this thesis adds to our understanding of the Australian Cretaceous ichthyosaur *Platypterygius australis*. It has resolved the taxonomy of this taxon, examined the postcranial remains of this ichthyosaur and developed functional hypotheses for several characteristic features of the genus, and inferred palaeobehaviours from pathological remains. However, the Australian Cretaceous record has much more to contribute regarding the species diversity and ontogeny of this ichthyosaur, and the collection of additional fossils will allow many more discoveries in the future.

CHAPTER 7

BIBLIOGRAPHY

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APPENDIX I

Zammit, M. 2010

Australasia's first Jurassic ichthyosaur fossil: an isolated vertebra from the lower Liassic Arataura Formation of the North Island, New Zealand.

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