The biomechanical consequences of longirostry in crocodilians and odontocetes

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ABSTRACT

Unrelated clades of aquatic tetrapod have evolved a similar range of skull shapes, varying from longirostrine (elongate and narrow rostrum) to brevirostrine (short rostrum). However, it is unclear which aspects of organismal performance are associated with this convergence in the range of skull shapes. Furthermore, it is not known how fundamental anatomical differences between groups influence these relationships. Here we address this by examining the load bearing capabilities of the skulls of two of the most diverse groups of living aquatic tetrapod: crocodilians and odontocetes. We use finite element analysis to examine the abilities of different cranial morphologies to resist a range of biologically relevant feeding loads including biting, shaking and twisting. The results allow for form/function relationships to be compared and contrasted between the two groups. We find that cranial shape has similar influences on performance during biting, shaking or twisting load cases at the anterior tooth positions, e.g. brevirostrine species experienced less strain than longirostrine species. The pattern of this form/function relationship is similar for both crocodilians and odontocetes, despite their fundamentally different anatomies. However, when loading teeth at the posterior end or middle of the tooth row the results do not follow the same pattern. Behavioural differences in bite location plays a key role in determining functional abilities in aquatic tetrapod taxa.

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1. Introduction

Living crocodilians and odontocetes (toothed whales) have evolved a similar range of variation in rostral shape, varying from longirostrine with an elongate and narrow rostrum, to brevirostrine with a short and broad rostrum (Brochu, 2001; McHenry et al., 2006; Walmsley et al., 2013b). Elongation of the rostrum is also associated with a relatively longer mandibular symphysis in the most longirostrine taxa (e.g. river dolphins or gharials) (Walmsley et al., 2013b). Within crocodilians longirostry is also associated with a loss of pseudoheterodonty (differences in tooth size) and a loss of undulation in the jaw margins (Cleuren and De Vree, 2000). Busbey (1995) classified longirostrine crocodilians as those with rostral

length/condylobasal length values over 0.7, mesorostrine crocodilians as those with values between 0.55 and 0.7, and brevirostrine crocodilians as any with values under 0.55. The morphology of the skull within this spectrum (brevirostrine-longirostrine) has been hypothesised to relate to the functional and ecological limitations of the species (McHenry, 2009; McHenry et al., 2006; Walmsley et al., 2013b). Specifically, it has been suggested that brevirostrine morphotypes are able to handle higher loads during feeding, an adaptation that would allow them to feed on larger or harder prey (Busbey, 1995; McHenry et al., 2006; Walmsley et al., 2013b). Extensive analyses have been undertaken on the load bearing and force producing capabilities of crocodilian cranial systems (Busbey, 1989, 1995; Cleuren and De Vree, 2000; Erickson et al., 2003, 2012; McHenry et al., 2006; Pierce et al., 2008; Porro et al., 2011; Rayfield et al., 2007; Reed et al., 2011; van Drongelen and Dullemeijer, 1982; Walmsley et al., 2013b) but no studies have directly compared their functional abilities to odontocetes to under-

stand exactly why these different groups have evolved such a similar range of morphologies.

Crocodilians and odontocetes are often used as extant morphological and ecological analogues for extinct marine tetrapods such as archaeocetes, ichthyosaurs, thallatosuchians and pliosaurs because of their similarities in body form, limb shape and rostral proportions (Massare, 1987, 1988; Walmsley et al., 2013b; Young et al., 2012). While crocodilians, odontocetes and these extinct marine reptile groups qualitatively appear to have a similar range of cranial variation, varying in rostral dimensions from short and broad through to elongate and slender (Walmsley et al., 2013b), we still do not know whether these similarities in morphology translate to performance characteristics. Identifying similar form/-function relationships between aquatic reptiles and mammals is a necessary step before using living odontocetes or crocodilians to predict the biomechanical and ecological characteristics of extinct taxa.

Furthermore, while odontocetes and crocodilians occupy similar aquatic environments and feed using similar "raptorial feeding" tactics, they vary considerably in other aspects of sensory biology and feeding behaviour. These differences in sensory biology and feeding behaviour are reflected in the anatomy of the skull (Fig. 1). Odontocetes have the ability to produce suction to aid in feeding, although the use of this tactic varies considerably between species, with some species only using suction for intra-oral transport (Bloodworth and Marshall, 2005; Werth, 2000, 2006a; Werth, 2006b). Within the skull this influences the shape of the mandible as well as the palate morphology, with suction feeding specialists having blunter mandibles and more highly vaulted palates (Werth, 2006a). Crocodilians also engage in some prey processing behaviours not undertaken by odontocetes, including twisting off pieces of prey using a "death roll" (Fish et al., 2007). In terms of sensory ability, odontocetes have the ability to echolocate prey using specialised sound production and reception organs such as the melon and phonic lips (Nachtigall, 1980). The odontocete mandible also plays a role in echolocation by allowing sound to

be received by the ear through an extremely thin section of bone in the posterior of the mandible called the pan bone (Norris, 1968) (Fig. 1). In crocodilians this posterior region of the mandible acts to withstand biting forces generated by the jaw muscles (Walmsley et al., 2013b). Crocodilians also possess pterygoid flanges (Fig. 1) that act to prevent medial bending of the mandible during loading (Porro et al., 2011). It is unclear to what extent these morphological differences might alter the fundamental form/function relationships that could be expected in a range of brevirostrine-longirostrine morphologies.

Predictions of the mechanical response of brevirostrine - longirostrine forms can be generated using principles such as beam theory (Bauchau and Craig, 2009; Metzger et al., 2005; Walmsley et al., 2013b), but applying beam theory to capture the morphological differences between phylogenetically disparate taxa is very difficult. Testing how well form/function relationships match basic predictions requires an approach that can account for complex differences in morphology. Finite element analysis is a modelling technique that can predict the response of complex structures to applied load using numerical methods. Previous studies using this technique have shown that the cranial morphology of a species often relates to its preferences in feeding (Dumont et al., 2005; McCurry et al., 2015b; McHenry et al., 2007; Moreno et al., 2008; Soons et al., 2010). Here we aim to use finite element analysis to:

(1) Determine whether longirostry has similar effects on structural performance during biting, shaking and twisting in crocodilians and odontocetes.
(2) Examine the effects of differences in anatomy between crocodilians and odontocetes on the location and magnitude of strain.

We hypothesise that more longirostrine morphotypes will exhibit higher levels of strain than more brevirostrine morphotypes during all loading scenarios (biting, shaking and twisting at any tooth position). This is expected to occur in a relative sense (e.g. patterns within each group) rather than in an absolute sense.
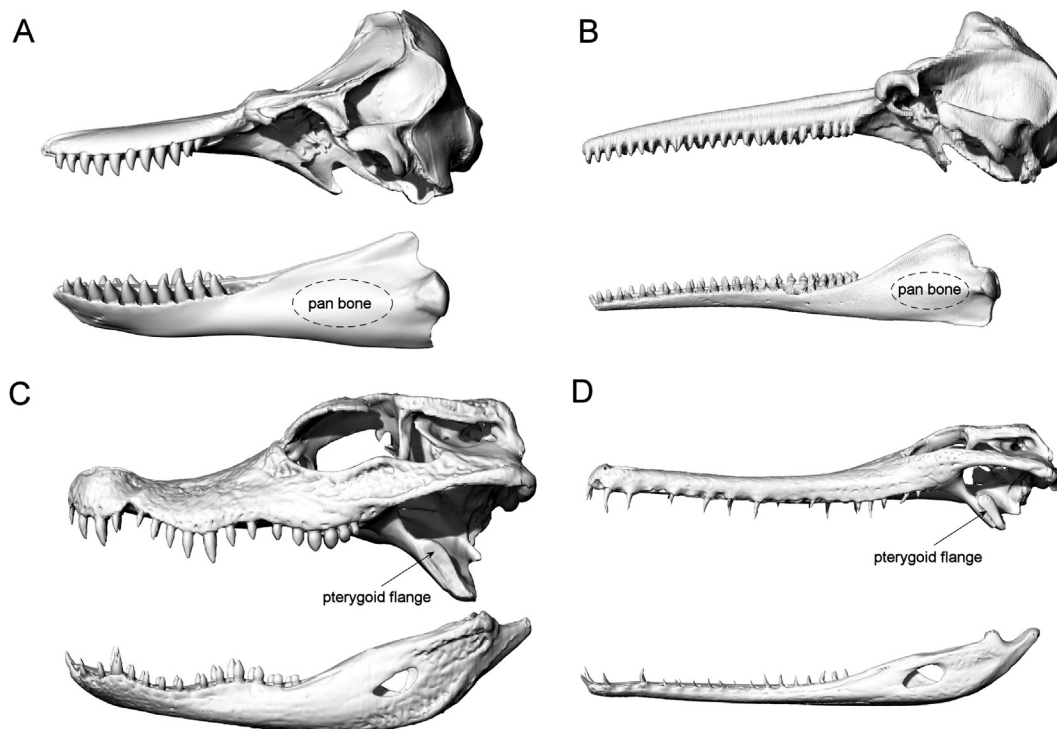

Fig. 1. Comparison of the skulls of longirostrine and brevirostrine crocodilians and odontocetes with the pan bone and pterygoid flanges identified. (A) The killer whale (*Orcinus orca*), (B) the Amazon River dolphin (*Inia geoffrensis*), (C) the dwarf crocodile (*Osteolaemus tetraspis*) and (D) the false gharial (*Tomistoma schlegelii*).