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Cranial Musculature in Extant Crocodile Shark, Pseudocarcharias kamoharai (Lamniformes: Pseudocarchariidae) and its Evolutionary Implications

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Cranial Musculature in Extant Crocodile Shark, Pseudocarcharias kamoharai (Lamniformes: Pseudocarchariidae) and its Evolutionary Implications
INTRODUCTION

Sharks (Chondrichthyes: Elasmobranchii) are efficient aquatic predators with a variety of feeding strategies, including ram, suction, bite, and filter to capture prey (Motta, 2004). The morphology of jaw musculature and jaw suspension play an important role in determining the extent to which a shark can effectively execute a particular feeding behavior, such as gouging, crushing, and head shaking. Whereas bite feeding is interpreted to be the ancestral mechanism chondrichthyans use to catch prey, a number of evolutionary modifications to the feeding apparatus have taken place through shark phylogeny (e.g., Wilga, 2005). Yet, the evolution of shark feeding behaviors influenced by the anatomy of their jaw suspension is still not entirely understood (Motta, 2004).

Lamniformes is a monophyletic group of sharks represented by 15 modern species, such as the goblin, sandtiger, thresher, basking, mako, and white sharks (Compagno, 2002). The crocodile shark, *Pseudocarcharias kamoharai* (Matsubara) (Fig. 1a) is the smallest (up to ca. 1 m TL [total length]) of all lamniform species and is found in epipelagic zones of tropical oceans worldwide (Compagno, 2002). Despite its relatively wide geographic distribution, its biology remains poorly understood. This paper describes the cranial musculature of *P. kamoharai* in detail and discusses its evolutionary and ecological implications.

MATERIALS AND METHODS

Three preserved specimens of *P. kamoharai* were examined: 1) FMNH 117474, 1,011-mm-TL male from the Hawaiian water, housed in the Field Museum of Natural History in Chicago, Illinois, 2) BPBM 37113, 1,080-mm-TL female from the Hawaiian water, housed in the Bernice P. Bishop Museum in Honolulu, Hawaii, and 3) LACM 45857, 922-mm-TL female from the Pacific coast of Mexico, housed in the Natural History Museum of Los Angeles.
California. A Siemens Medical Systems’ SOMATOM Sensation® 64-slice computed tomography (CT) scanner at the Children’s Memorial Hospital in Chicago, Illinois was used to image jaw muscles. However, CT images could not separate small muscles apart, and thus a ‘peel dissection’ was performed on the right side of the head of FMNH 117474 and BPBM 37113 where the skin was transected and reflected to expose cranial musculature.

The study follows Wilga (2005) for muscle and ligament terminology. However, for skeletal terminology of jaw structures, a set of terms is used (Fig. 2) emended from the usage by Maisey (1980), Shimada (2002), and Wilga (2005). For example, Wilga (2005, fig. 3C, D) identified the ethmoid process on the palatoquadrate in *Isurus* (mako shark) and *Carcharodon* (white shark), but the projection is actually the dorsally inflated upper dental bulla. The dental bulla that houses enlarged mesially-located teeth is common to all macrophagous lamniforms (Shimada, 2002), but the ethmoid process is absent in *Isurus* and *Carcharodon* (this study). Wilga (2005) notes the presence of ‘a small process’ on the dorsal surface of each palatoquadrate immediately lateral to the symphysis in *Lamna nasus* (porbeagle shark). This process is called the mesial process and is unique to Lamnidae (*Lamna, Isurus, and Carcharodon; Compagno, 1990, Shimada, 2002, 2005*). In summary, there are three types of dorsally-projected processes recognized on the palatoquadrate of lamniforms: 1) the mesial process that connects to the palatonasal ligament, 2) the upper dental bulla that makes no connection to any ligament or muscle, and 3) the ethmoid process that attaches to the ethmopalatine ligament. Whereas the orbital process is completely absent in all lamniforms as ‘non-orbitostylic sharks’ (Maisey, 1980; Wilga, 2005), no lamniform species possesses all three processes on one jaw.

**RESULTS**

The following list describes the morphology of ligamentous and musculoskeletal elements that are involved in jaw suspension in *Pseudocarcharias kamoharai* (Fig. 1b–d): The ethmopalatine ligament and orbital process of the palatoquadrate are absent. The palatonasal ligament is prominent and rope-like but is not accompanied by a cartilaginous rod. The epaxialis muscle extends posteriorly from the dorsoposterior surface of the neurocranium in which it loops around the parietal fossa. The mid-lateral raphe extends from the posterior end of Meckel’s cartilage to the midpoint of the quadratomandibularis muscles. The preorbitalis inserts to the posteroventral region of the nasal capsule. The quadratomandibularis superficial division is broad and occupies two-thirds of the quadrate process of the palatoquadrate. The quadratomandibularis medial division is a triangular and sheet-like muscle. The quadratomandibularis deep division originates from between sheaths of cartilage on the mandible, and extends to the posterodorsal rim of the quadrate process of the palatoquadrate. The quadratomandibularis ventral division originates from the ventral margin of the mid-lateral raphe and inserts along the ventral posterior margin of Meckel’s cartilage. The intermandibularis originates from the mid-ventral raphe to insert onto the quadratomandibularis ventral division. The cartilaginous intermandibular plates are teardrop-shaped, attach to the mid-ventral raphe, and are located immediately below the first and second lower lateral teeth. Muscles of the hyoid muscle plate insert at the posterior end of the lower dental bulla; the origin of these muscles however remains unclear. The levator hyomandibularis connects to the anterior margin of the quadrate process of the palatoquadrate and inserts into much of the hyomandibula. The interhyoideus muscles originate from the posterior end of the ceratohyal and the posterior edge of Meckel’s cartilage. The interhyoideus muscles insert onto the posterior end of the ceratohyal and Meckel’s cartilage immediately posterior to the intermandibularis plate. The coracomandibularis is a massive muscle that originates at the coracoid bar and inserts between the lower dental bulla. The coracoarcualis extends from the mid-ventral coracoid bar to meet with the hypaxialis and pectoral fin muscles.
DISCUSSION

Wilga (2005) (Fig. 3a) proposed an evolutionary scenario of lamniform jaws using a phylogenetic tree that largely agreed with the first hypothesis of phylogenetic interrelationships of all extant lamniform species proposed by Compagno (1990) (Fig. 3a). Although the lamniform monophyly is strongly supported, the phylogenetic trees based on morphological data (Fig. 3b: Compagno, 1990; Shirai, 1996; Shimada, 2005) are found to differ significantly from those based on molecular data (Fig. 3c, d: Naylor et al., 1997, 2012; Martin et al., 2002). In particular, the morphology-based trees show Alopias to represent a sister taxon to a clade uniting Cetorhinus and Lamnidae, and indicated that Mitsukurina, Carcharias, Odontaspis, Pseudocarcharias, and Megachasma represent less derived taxa in the trees compared to the clade uniting Alopias, Cetorhinus, and Lamnidae (Fig. 3b). This tree topology contrasts with practically all molecular-based trees that include all lamniform genera. Alopias was consistently separated from the clade comprising Cetorhinus and Lamnidae and instead clustered with a clade uniting Odontaspis, Pseudocarcharias, and Megachasma (e.g., Naylor et al., 1997, 2012; Martin et al., 2002; Fig. 3c, d). The systematic position of Carcharias remains uncertain, but Martin et al. (2002) and Naylor et al. (2012) showed that the genus is closely allied to Cetorhinus and Lamnidae (Fig. 3c, d).

The topological differences between morphology-based and molecular-based trees provide contrasting evolutionary scenarios. Figure 3 shows a morphology-based tree (Fig. 3b) and two molecular-based trees (Fig. 3c, d) with anatomical structures involved in jaw suspension mapped on them based on skeletal data presented by Shimada (2002) and ligamentous and myological data presented by Wilga (2005), Nakaya et al. (2008), and this present study. Notably, the systematic disassociation of Alopias from a clade uniting Cetorhinus and Lamnidae in the molecular-based trees (Fig. 3c, d) results in additional steps to character evolution compared to the morphology-based scenario (Fig. 3b). Furthermore, besides the very unlikely ‘Alopias non-monophyly’ in their study, Naylor et al.’s (2012, fig. 2.2) molecular-based phylogenetic tree shows a sister relationship between Cetorhinus and Carcharias (Fig. 3d), unlike Martin et al.’s molecular-based tree (Fig. 3c). The mapping of the ligamentous, myological, and skeletal data on to Naylor et al.’s (2012) tree yields a set of evolutionary reversals in the Carcharias clade, and thus is least parsimonious. In short, character evolution based on the morphology-based tree (Fig. 3b) is the most parsimonious tree among the three trees (cf. Figs. 3c, d), followed by Martin et al.’s (Fig. 3c) and then by Naylor et al.’s molecular-based tree (Fig. 3d). Regardless, every presented scenario indicates that the evolution of jaw ligaments and muscles in lamniforms is more complex than initially proposed by Wilga (2005). In particular, Wilga’s (2005) study did not include Pseudocarcharias and Megachasma to show the independent acquisition of an insertion of the levator hyomandibularis to the palatoquadrate (Character 4 in Fig. 3) and the loss of the ethmopalatine ligament (Character 7 in Fig. 3) in Pseudocarcharias as well as the loss of the palatonasal ligament in Megachasma (Character 9 in Fig. 3).

Character mapping (Fig. 3a and 3b) offers some additional evolutionary insights. For example, the evolution and loss of the ethmopalatine ligaments and ethmoid processes of the palatoquadrate are tightly associated. In contrast, features related to the palatonasal ligament, such as the cartilaginous rod within the palatonasal ligament and the mesial process of the palatoquadrate, evolved independent of the ligament and one another. However, it is important to note that ligamentous and musculoskeletal elements have not been investigated for Odontaspis ferox, O. noronhai, and Cetorhinus maximus as well as a few other lamniform species, such as Alopias pelagicus (pelagic thresher shark), A. superciliosus (bigeye thresher shark), and Lamna ditropis (salmon shark). Therefore, it is possible that the evolution of these anatomical elements may be even more complex than shown in Figure 3a and 3b.

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FIGURE 1

Head region of crocodile shark, Pseudocarcharias kamoharai (anterior to left). a, External morphology (BPBM 37113 in lateral view). b, Computed tomography image showing anterior extent of epaxial muscles and adjacent muscles (BPBM 37113 in dorsal view). c, Dissected superficial cranial musculature (FMNH 117474 in lateral view; cf. Fig. 2c). d, Line drawing showing identified superficial cranial musculature (FMNH 117474 in lateral view; cf. Figs. 1c, 2c). Abbreviations: BC, branchial constrictors; EP, epaxialis; LH, levator hyomandibularis; LP, levator palatoquadral; MC, Meckel’s cartilage; NC, nasal capsule; O, orbit; PF, parietal fossa; PO, preorbitalis; PQ, palatoquadrate; QMD, dorsal quadratomandibularis superficial division; QMDm, dorsal quadratomandibularis medial division; QMV, ventral quadratomandibularis, RC, rostral cartilage. Bar scale = 5 cm.
Examples of lamniform jaws showing types of dorsally-directed projections on anterior portion (palatine process) of palatoquadrate (upper jaw) and types of articulation they make to neurocranium (based on Maisey, 1980; Shimada, 2002; Wilga, 2005). a, Jaw specimen of sandtiger shark, *Carcharias taurus*, in dorsal view showing dental bulla and ethmoid process on left palatoquadrate (notes: this species lacks mesial process beneath palatonasal ligament; AMNH 79962SD housed in American Museum of Natural History, New York, New York). b, Jaw specimen of porbeagle shark, *Lamna nasus*, in dorsal view showing mesial process and dental bulla on left palatoquadrate (notes: palatonasal ligament that connected to mesial process is removed in this specimen; this species lacks ethmoid process; MCZ 36258 housed in Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts). c, Computed tomography image of cranial skeleton of crocodile shark, *Pseudocarcharias kamoharai*, in left lateral view showing position of palatine and quadrate processes of palatoquadrate with dental bulla as well as Meckel's cartilage (lower jaw) with dental bulla (FMNH 117474; cf. Fig. 1c, d). Bar scale = 2 cm.
Alternative phylogenetic hypotheses of extant lamniform sharks with mapping of ligamentous and muscular characters (1–9) as well as skeletal characters (A–E) participating in jaw suspension (* = data based on Wilga, 2005; ** = data based on Nakaya et al., 2008; no asterisk = ligament and muscle data based on this present study and skeletal data based on Shimada 2005). a, Wilga’s (2005) hypothesis about character evolution mapped onto morphology-based phylogenetic tree (Compagno 1990). b, hypothesis about character evolution mapped onto morphology-based phylogenetic tree (Compagno 1990) by combining data from Wilga (2005), Nakaya et al. (2008), and this study. c, hypothesis about character evolution mapped onto Martin et al.’s (2002) molecular-based phylogenetic tree by combining data from Wilga (2005), Nakaya et al. (2008), and this study. d, hypothesis about character evolution mapped onto Naylor et al.’s (2012, fig. 2.2) molecular-based phylogenetic tree by combining data from Wilga (2005), Nakaya et al. (2008), and this study [notes: Alopias in Naylor et al.’s (2012) study was depicted as non-monophyletic where A. superciliosus (not depicted here) was clustered with a clade uniting Pseudocarcharias, Odontaspis, and Megachasma; numbers in gray box indicate characters with polarity reversal, where those features are suggested to be secondarily lost in the Carcharias clade].

**FIGURE 3**

Cranial musculature in extant crocodile shark.
LITERATURE CITED


