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［Original report］

Cranial musculature in extant crocodile shark, *Pseudocarcharias kamoharai* (Lamniformes : Pseudocarchariidae) and its evolutionary implications

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Abstract

The crocodile shark, *Pseudocarcharias kamoharai*, is a small lamniform shark that lives in tropical oceans nearly worldwide. Here, its cranial musculature and ligaments associated with jaw suspension are described in detail for the first time. The anatomical data are then mapped onto previously proposed phylogenetic trees to examine the evolutionary pattern of jaw morphology through lamniform phylogeny. Our results show that the evolution of characters associated with jaw suspension is more parsimonious in the morphology-based phylogenetic tree than the molecular-based trees. Additionally, the evolutionary scenario of lamniform jaws is found to be more complex than previously thought regardless of the tree used.

Key words : anatomy, Elasmobranchii, lamniform shark, muscle

Introduction

Sharks (Chondrichthyes : Elasmobranchii) are evolutionarily successful aquatic predators as they employ a variety of feeding strategies, including ram, suction, bite, and filter to capture prey (Motta, 2004). The morphology of cranial musculature and the mode of 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 (Motta, 2004 ; Wilga, 2008). Yet, the evolutionary patterns of the anatomy and feeding types are still not well understood (Motta, 2004 ; Motta and Huber, 2012).

Lamniformes is a monophyletic group of sharks represented by 15 modern species, such as the goblin (*Mitsukurina*), sandtiger (*Carcharias/Odontaspis*), megamouth (*Megachasma*), thresher (*Alopias*), basking (*Cetorhinus*), porbeagle/salmon (*Lamna*), mako (*Isurus*), and white (*Carcharodon*) sharks (Compagno, 2001). The crocodile shark, *Pseudocarcharias kamoharai* (Matsubara), is the smallest (up to about 1 m TL [total length]) lamniform species that lives in epipelagic zones of tropical oceans nearly worldwide (Compagno, 2001 ; Fig. 1a). The fossil record of the genus *Pseudocarcharias* extends as far back as the early Miocene (Cappetta, 2012), and the family Pseudocarchariidae may have already been in existence by the Cretaceous on the basis of molecular studies (Martin *et al*., 2002 ; Heinicke *et al*., 2009). Despite its relatively wide

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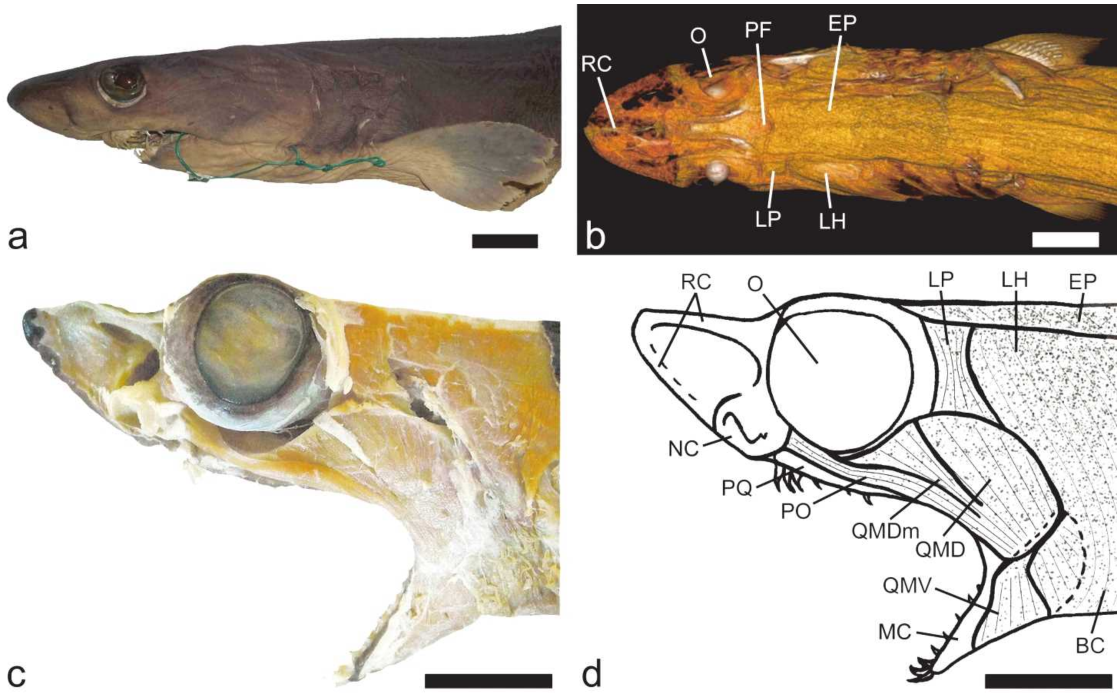


Fig. 1. Head region of crocodile shark, *Pseudocarcharias kamoharai* (anterior to left).
a, External morphology (BPBM 37113 in lateral view). **b**, Computed tomography image showing anterior extent of epaxial muscles and adjacent muscles (BPBM 37113 in dorsal view). **c**, Dissected superficial cranial 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 palatoquadrati; 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.

geographic distribution and long geologic history, the biology of *Pseudocarcharias*, including its basic anatomy, remains poorly understood. In this paper, we describe the cranial musculature of *P. kamoharai* in detail for the first time and discuss its evolutionary implications.

Materials and Methods

Three preserved specimens of *Pseudocarcharias kamoharai* were examined: (1) FMNH 117474, a 1,011-mm-TL male from Hawaiian waters, housed in the Field Museum of Natural History in Chicago, Illinois, U.S.A., (2) BPBM 37113, a 1,080-mm-TL female from Hawaiian waters, housed in the Bernice P. Bishop Museum in Honolulu, Hawaii, U.S.A., and (3) LACM 45857, a 922-mm-TL female from the Pacific coast of Mexico, housed in the Natural History Museum of Los Angeles, California, U.S.A. We used a Siemens Medical Systems' SOMATOM Sensation® 64-slice computed tomography (CT) scanner at the Children's Memorial Hospital in Chicago, Illinois, to image their muscles (scanning settings: 120 kVp, effective mAs 200 with automatic exposure control activated, rotation time 0.33 sec, 0.75 pitch, 32 detectors using z-flying focal spot technique, 0.625mm slice thickness and 0.4 mm overlapping slice reconstruction; used Siemens' InSpace software for imaging). However, CT images did not sufficiently differentiate small or thin muscles, and thus we also conducted a dissection on the right side of the head of FMNH 117474 and BPBM 37113. Muscles on the dorsal and ventral sides were dissected just enough to confirm their conditions (e.g., fiber orientation, origin, and insertion), but they were not fully exposed as a consequence to minimize damage to the specimens and to retain their structural integrity. Whereas this method allowed us to observe and document most of the

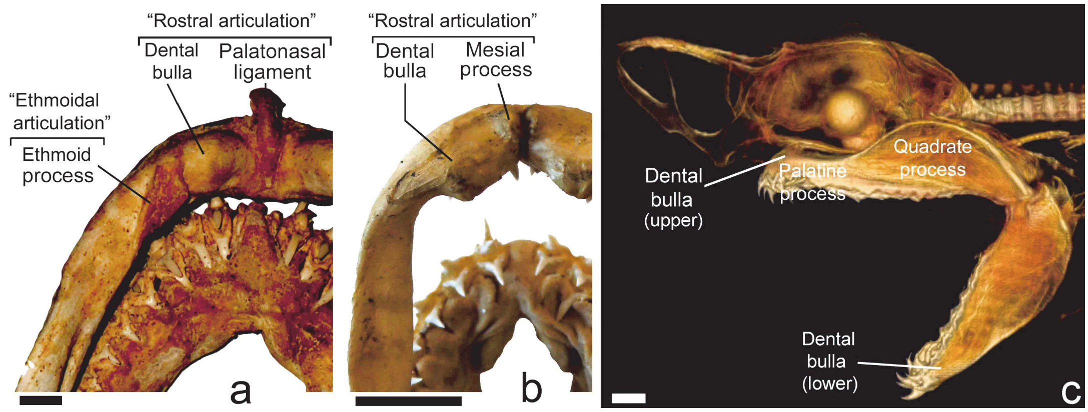


Fig. 2. Examples of lamniform jaws showing types of dorsally-directed projections on anterior portion (palatine process) of palatoquadrate (upper jaw) and types of articulation they make to neurocranium (based on Maisey, 1980 ; Shimada, 2002 ; Wilga, 2005). **a**, Jaw specimen of sandtiger shark, *Carcharias taurus*, in dorsal view showing dental bulla and ethmoid process on left palatoquadrate (notes : this species lacks mesial process beneath palatonasal ligament ; AMNH 79962 SD 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.

cranial muscles sufficiently, the coracohyoideus and coracoarcualis muscles, which were not sufficiently exposed, are not included in our description.

We follow Wilga (2005) for muscle and ligament terminology. However, for skeletal terminology of jaw structures, we use a set of terms (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 upper dental bulla, a jaw structure that is independent of the ethmoid process. To make the matter more confusing, Shimada (2002) referred to the ethmoid process as the orbital process following the classical usage of Compagno (1988) (cf. Maisey, 1980, who appropriately differentiated the ethmoid process from the orbital process). In addition, Wilga (2005) referred the orbital process as 'OP' in Figure 1, but confusingly used the same abbreviation 'OP' to denote the ethmoid process in Figure 3. 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). Maisey (1980, p. 4) referred to this process as the 'palatine process' (see also "pp" in Maisey's Figure 6 in which the meaning of the abbreviation was not given but it presumably represents this process). However, here we follow Compagno (1988) and Shimada (2002) by using the palatine process to describe the mesial portion of each palatoquadrate and to differentiate it from the distal portion of the palatoquadrate, the quadrate process (Fig. 2c).

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. The mesial process and dental bulla together form the rostral articulation (Fig. 2b; cf. Maisey, 1980), but the rostral articulation may also occur without the mesial process (Fig. 2a). The ethmoidal articulation (Fig. 2b; cf. Maisey, 1980) only occurs when the ethmoid process is present. It should be noted that Maisey (1980, fig. 6c) showed the ethmoidal articulation in *Isurus*, but it is here considered to be a form of rostral articulation because the ethmoid process is absent in the taxon. Rather, it is the dental bulla that makes the rostral articulation in the taxon.

Results

Ethmopalatine Ligament—The ethmopalatine ligaments are paired, rope-like ligaments, and each of them originate from the base of the neurocranium immediately below the orbit and extends to the ethmoid process of the palatoquadrate (Wilga, 2005; Fig. 2a). The ligament is present in *Mitsukurina owstoni*, *Carcharias taurus*, *Alopias vulpinus*, and *Megachasma pelagios*, and it is absent in *Lamna nasus*, *Isurus oxyrinchus*, and *Carcharodon carcharias* (Wilga, 2005; Nakaya *et al*., 2008). On the other hand, the ligament is absent along with the ethmoid process of the palatoquadrate in *Pseudocarcharias kamoharai*.

Palatonasal Ligament—The palatonasal ligament is an unpaired ligament that originates ventrally between the two nasal capsules of the neurocranium and inserts to the dorsal side of the upper jaw symphysis (Wilga, 2005; Fig. 2a). In *Lamna, Isurus*, and *Carcharodon*, the ligament attaches to the mesial process of the palatoquadrate (Wilga, 2005; Fig. 2b). The palatonasal ligament is thin and strap-like in *Mitsukurina owstoni*, whereas it is prominent and rope-like in *Carcharias taurus, Alopias vulpinus, L. nasus, I. oxyrinchus*, and *Carcharodon carcharias* (Wilga, 2005). In addition, a cartilaginous rod embedded inside supports the palatonasal ligament in *A. vulpinus*, *L. nasus*, *I. oxyrinchus*, and *C. carcharias* (Wilga, 2005). The ligament is absent in *Megachasma pelagios* (Nakaya *et al*., 2008). In *Pseudocarcharias kamoharai*, the palatonasal ligament (not figured) is prominent and rope-like but does not contain a cartilaginous rod, and the mesial process on the palatoquadrate is absent.

Epaxialis—The epaxialis (EP) is an axial muscle that originates around the parietal fossa located between the two otic capsules of the neurocranium and extends posteriorly (Wilga, 2005). The origin of the epaxialis differs among species. It is located just anterior to the postorbital process in *Mitsukurina owstoni*, *Carcharias taurus*, and *Isurus oxyrinchus*, at the level of the preorbital processes of the neurocranium in *Alopias vulpinus*, and at the mid-orbital region in *Lamna nasus* and *Carcharodon carcharias* (Wilga, 2005). In *Pseudocarcharias kamoharai*, it originates from the dorsal surface of the neurocranium immediately posterior to the postorbital process (Fig. 1b-d).

Levator Palatoquadrati—The levator palatoquadrati (LP) is a vertically oriented, sheet-like muscle situated immediately anterior to the levator hyomandibularis (Wilga, 2005). In *Mitsukurina owstoni, Alopias vulpinus*, and *Megachasma pelagios*, the muscle originates from the lateral surface of the otic capsule (Wilga, 2005; Nakaya *et al*., 2008). In *Carcharias taurus, Carcharodon carcharias, Isurus oxyrinchus*, and *Pseudocarcharias kamoharai*, the muscle originates from the dorsolateral edges of the anterior portion of the epaxialis (Wilga, 2005; this study). *Lamna nasus* exhibits either of these connectivities in addition to another one on the posterior surface of the postorbital process, and this additional point of origin is also found in *A. vulpinus* and *C. carcharias* (Wilga, 2005). The exact insertion point of the muscle varies among lamniforms, but in most species including *P. kamoharai*, it extends ventrally to the ascending (quadrate) process of the palatoquadrate (Wilga, 2005; this study; Fig. 1b-d).

Preorbitalis—The preorbitalis (PO) is a strap-like muscle generally originating from the mid-lateral raphe of the quadratomandibularis muscles (Wilga, 2005). In *Mitsukurina owstoni*, *Carcharias taurus*, *Megachasma pelagios*, *Carcharodon carcharias*, and *Pseudocarcharias kamoharai*, the preorbitalis is a single muscle mass, whereas it is represented by dorsal and ventral divisions in *Alopias vulpinus, Lamna nasus*, and *Isurus oxyrinchus* (Wilga, 2005; Nakaya *et al*., 2008). In *Carcharias taurus*, *L. nasus*, *Carcharodon carcharias*, and *I. oxyrinchus*, the preorbitalis extends anterodorsally inserting along the anterior portion of the palatoquadrate (Wilga, 2005). The insertion of the preorbitalis is situated on, or close to, the posteroventral surface of each nasal capsule in *Mitsukurina owstoni*, *A. vulpinus*, *Megachasma pelagios*, and *Pseudocarcharias kamoharai* (Wilga, 2005;

Nakaya *et al*., 2008 ; this study ; Fig. 1c, d).

Mid-Lateral Raphe of Quadratomandibularis—The mid-lateral raphe appears as a white fibrous connective tissue situated immediately dorsal to the jaw articulation, and serves as a ligamentous attachment point for multiple divisions of the quadratomandibularis muscle (Wilga, 2005). In *Mitsukurina owstoni* and *Carcharias taurus*, raphe tissue extends in all direction separating divisions of the quadratomandibularis muscle, whereas *Carcharodon carcharias* and *Isurus oxyrinchus* exhibit conditions in which the raphe extends from immediately above the jaw articulation to the palatoquadrate (Wilga, 2005). In *Pseudocarcharias kamoharai*, the raphe extends from the meeting point of the various divisions of the quadratomandibularis muscles to the posterior end of the Meckel's cartilage (i.e., junction between QMD and QMV in Fig. 1d).

Dorsal Quadratomandibularis Superficial Division—Whereas there are two major types of quadratomandibularis, the dorsal quadratomandibularis and the ventral quadratomandibularis, as many as three divisions are recognized in the dorsal quadratomandibularis in lamniforms : (1) the superficial division, (2) medial division, and (3) deep division (Wilga, 2005). The dorsal quadratomandibularis superficial division (QMD) originates from the dorsal aggregation of muscle tissue at the mid-lateral raphe and extends anterodorsally to insert along the lateral edge of the palatoquadrate (Wilga, 2005). This condition is present in all the lamniform taxa so far examined, including *Mitsukurina owstoni*, *Carcharias taurus*, *Alopias vulpinus*, *Megachasma pelagios*, *Lamna nasus*, *Isurus oxyrinchus*, *Carcharodon carcharias*, and *Pseudocarcharias kamoharai* (Wilga, 2005 ; Nakaya *et al*., 2008 ; this study). In *P. kamoharai*, the muscle is broad and occupies two-thirds of the quadrate process of the palatoquadrate (Fig. 1c, d).

Dorsal Quadratomandibularis Medial Division—The dorsal quadratomandibularis medial division (QMDm) originates from the mid-lateral raphe and fans out (i.e., sheet-like and triangular) anterodorsally to insert along the anterior margin of the quadrate process of the palatoquadrate (Wilga, 2005). The muscle is found in *Mitsukurina owstoni*, *Carcharias taurus*, *Alopias vulpinus*, *Lamna nasus*, *Isurus oxyrinchus*, *Carcharodon carcharias*, and *Pseudocarcharias kamoharai* (Wilga, 2005 ; this study; Fig. 1c, d), but not in *Megachasma pelagios* (Nakaya *et al*., 2008).

Dorsal Quadratomandibularis Deep Division—The dorsal quadratomandibularis deep division originates from the dorsal surface of the Meckel's cartilage and extends to the dorsoposterior rim of the quadrate process of the palatoquadrate (Wilga, 2005). The division is situated beneath the ventral rim of the dorsal quadratomandibularis superficial division and is thus not exposed externally. The dorsal quadratomandibularis deep division is present in *Mitsukurina owstoni*, *Carcharias taurus*, *Alopias vulpinus*, *Lamna nasus*, *Isurus oxyrinchus* (Wilga, 2005), and *Pseudocarcharias kamoharai* (this study; the division not figured), but not in *Megachasma pelagios* (Nakaya *et al*., 2008).

Ventral Quadratomandibularis—The ventral quadratomandibularis (QMV) is a broad sheet-like muscle generally originating from the mid-lateral raphe and fanning out ventrally to insert along the ventral surface of the Meckel's cartilage. This muscle is present in all the lamniforms examined, including *Mitsukurina owstoni*, *Carcharias taurus*, *Alopias vulpinus*, *Lamna nasus*, *Isurus oxyrinchus*, and *Pseudocarcharias kamoharai* (Wilga, 2005, Nakaya *et al*., 2008 ; this study ; Fig. 1c, d). In *Megachasma pelagios*, the muscle originates from the dorsal surface of the palatoquadrate and extends to the posterior half of the Meckel's cartilage (Nakaya *et al*., 2008).

Intermandibularis—The intermandibularis is a sheet-like muscle that bridges between the right and left Meckel's cartilages (Wilga, 2005). It is paired in *Mitsukurina owstoni*, *Alopias vulpinus*, *Isurus oxyrinchus*, *Megachasma pelagios*, and *Pseudocarcharias kamoharai* in which the right and left sides meet medially as a white longitudinal connective tissue referred to as the mid-ventral raphe (Wilga, 2005; Nakaya *et al*., 2008 ; this study). The intermandibularis is considered to be unpaired in *Carcharias taurus* and *Lamna nasus* because the mid-ventral raphe is not evident (Wilga, 2005). In *Pseudocarcharias kamoharai*, the muscle extends laterally to the base of the ventral quadratomandibularis. Posteriorly, it grades into the branchial constrictor muscles (Fig. 1d, intermandibularis not figured).

Intermandibular Plates—The intermandibular plates are heterotopic cartilaginous elements attached to the mid-ventral raphe (Wilga, 2005).

Their morphological condition varies among lamniform species. In *M. owstoni*, the intermandibular plate is unpaired and triangular, whereas small, paired plates are present in *Carcharias taurus*, *Alopias vulpinus*, *Lamna nasus*, and *Carcharodon carcharias* (Wilga, 2005). *Pseudocarcharias kamoharai* has paired intermandibular plates (not figured) that are located along the ventral margin of each Meckel's cartilage at the level of the first and second lower lateral teeth (tooth types, sensu Shimada, 2002). Each of them is teardrop-shaped in which its anterior end is pointed and connects to the posterior margin of the lower dental bulla (sensu Shimada, 2002; Fig. 2c).

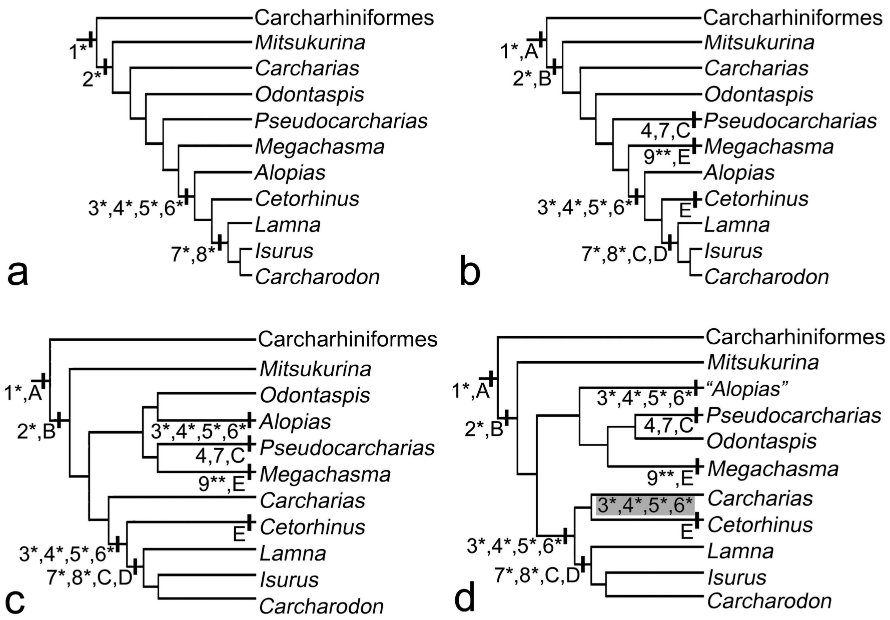
Levator Hyomandibularis—The origin of the levator hyomandibularis (LH) muscles is generally located at the dorsolateral edge of the anterior end of the epaxialis muscle or the otic crest of the neurocranium in lamniforms (Wilga, 2005; Nakaya *et al*., 2008). Its insertion point, however, varies among species. In *Mitsukurina owstoni*, it is located on the dorsal edge of the hyomandibula, whereas it inserts along the entire dorsal surface of the hyomandibula in *Carcharias taurus* and *Megachasma pelagios* (Wilga, 2005; Nakaya *et al*., 2008). In *Alopias vulpinus*, *Carcharodon carcharias*, and *Isurus oxyrinchus*, the bulk of the muscle inserts along the proximal end of the hyomandibula, whereas it inserts distally in *Lamna nasus* (Wilga, 2005). In *Pseudocarcharias kamoharai*, the levator hyomandibularis originates from the anterior portion of the epaxialis and inserts to the mid-lateral raphe and much of the posterodorsal portion of the hyomandibula (Fig. 1b-d).

Interhyoideus—The interhyoideus is a sheet-like muscle situated immediately beneath the intermandibularis muscle (Wilga, 2005). In *Pseudocarcharias kamoharai*, the interhyoideus originates from the posterior end of the ceratohyal and inserts onto the Meckel's cartilage immediately posterior to the intermandibularis plate where both skeletal elements meet (not figured). The condition of the interhyoideus has not been examined in other lamniforms (e.g., Wilga, 2005; Nakaya *et al*., 2008).

Coracomandibularis—The coracomandibularis is a long, mid-ventral muscle situated immediately beneath the interhyoideus and intermandibularis (Wilga, 2005). In *Alopias vulpinus*, it originates from the coracoid bar, whereas it originates from the anteroventral end of the coracoarcualis at the coracoid bar in *Isurus oxyrinchus* and *Megachasma pelagios* (Wilga, 2005; Nakaya *et al*., 2008). Its origin is unknown in other species. In *A. vulpinus*, *Carcharias taurus*, *Lamna nasus*, *Carcharodon carcharias*, and *I. oxyrinchus*, the coracomandibularis extends anteriorly and splits immediately before reaching their insertion point on the posterior end of the Meckel's cartilage (Wilga, 2005). In *M. pelagios*, it does not reach the Meckel's cartilage but rather extends to the posterior end of the basihyal (Nakaya *et al*., 2008). In *Pseudocarcharias kamoharai*, the coracomandibularis (not figured) is massive and unpaired, originates presumably at the coracoid bar (that was not fully exposed in this study), and inserts between the right and left lower dental bulla (sensu Shimada, 2002; Fig. 2c).

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



Muscle/ligament character evolution:
1. Presence of ethmopalatine ligament
2. Presence of palatonasal ligament
3. Presence of subdivided preorbitalis
4. Presence of new insertion of levator hyomandibularis to palatoquadrate
5. Presence of new insertion of levator hyomandibularis to mandible
6. Presence of cartilaginous rod within palatonasal ligament
7. Loss of ethmopalatine ligament
8. Presence of new insertion of preorbitalis to connective tissue
9. Loss of palatonasal ligament

Upper jaw character evolution:
A. Presence of ethmoid process on palatoquadrate
B. Presence of dental bulla in palatoquadrate
C. Loss of ethmoid process on palatoquadrate
D. Presence of mesial process on palatoquadrate
E. Loss of dental bulla on palatoquadrate

Fig. 3. 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].

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 (for character mapping technique, see Harvey and Pagel, 1991 ; also note that our mapped characters are independent from the original construction of these trees). 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. 3 d), unlike Martin *et al.*'s molecular-based tree (Fig. 3 c). 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. 3 b) 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). For example, Wilga's (2005) study that did not include *Pseudocarcharias* or *Megachasma* does not show the loss of the ethmopalatine ligament (Character 7 in Fig. 3) in *Pseudocarcharias* or the loss of the palatonasal ligament in *Megachasma* (Character 9 in Fig. 3).

Our 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, whereas the palatonasal ligament is present broadly in Lamniformes, the evolution of the cartilaginous rod within the palatonasal ligament and that of the mesial process of the palatoquadrate took place separately. 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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References

Cappetta, H. (2012) Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze, H.-P. (ed) *Handbook of Paleoichthyology, Volume 3E*, pp. 1-512, Verlag Dr. Friedrich Pfeil, Munich.

Compagno, L. J. V. (1988) *Sharks of the Order Carcharhiniformes*. Princeton University Press, Princeton, New Jersey, 486 pp.

Compagno, L. J. V. (1990) Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. *NOAA Tech. Rep., NMFS* **90**, 357-379.

Compagno, L. J. V. (2001) Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Volume 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). *FAO Sp. Cat. Fish. Purp.* **1**(2), 1-269.

Harvey, P. H. and Pagel, M. D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford Univ. Press, Oxford, U.K.

Heinicke, M. P., Naylor, G. J. P. and Hedges, S. B. (2009) Cartilaginous fishes (Chondrichthyes). In: Bedges, S. B. and Kumar, S. (eds) *The Timetree of Life*, pp. 320-327. Oxford University Press, Oxford.

Maisey, J. G. (1980) An evaluation of jaw suspension in sharks. *American Museum Novitates* **2706**, 1-17.

Martin, A. P., Pardini, A. T., Noble, L. R. and Jones, C. S. (2002) Conservation of a dinucleotide simple sequence repeat locus in sharks. *Mol. Phyl. Evol.*

23, 205-213.

Motta, P. J. (2004) Prey capture behavior and feeding mechanics of elasmobranchs. In: Carrier, J., Musick, J. and Heithaus, M. (eds) *Biology of Sharks and Their Relatives*, pp. 165-202. CRC Press, Boca Raton, Florida.

Motta, P. J. and Huber, D. R. (2012) Prey capture behavior and feeding mechanics of elasmobranchs. In : Carrier, J. C., Musick, J. A. and Heihaus, M. R. (eds) *Biology of Sharks and Their Relatives, Second Edition*, pp. 153-209. CRC Press, Boca Raton, Florida.

Nakaya, K., Matsumoto, R. and Suda, K. (2008) Feeding strategy of the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae). *Jour. Fish. Biol.* **73**, 17-34.

Naylor, G. J. P., Martin, A. P., Mattison, E. G. and Brown, W. M. (1997) Interrelationships of lamniform sharks: testing phylogenetic hypotheses with sequence data. In : Kocher T. D. and Stepien, C. A. (eds) *Molecular Systematics of Fishes*, pp. 199-218. Academic Press, San Diego, California.

Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., Straube, N. and Lakner, C. (2012) Elasmobranch phylogeny : a mitochondrial estimate based on 595 species. In : Carrier, J. C., Musick, J. A., Heihaus, M. R. (eds) *Biology of Sharks and Their Relatives, Second Edition*, pp. 31-57. CRC Press, Boca Raton, Florida.

Shimada, K. (2002) Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). *Jour. Morphol*. **251**, 38-72.

Shimada, K. (2005) Phylogeny of lamniform sharks (Chondrichthyes : Elasmobranchii) and the contribution of dental characters to lamniform systematics. *Paleont. Res.* **9**, 55-72.

Shirai, S. (1996) Phylogenetic interrelationships of neoselachians (Chondrichthyes : Euselachii). In : Stiassny, M. L. J., Parenti, L. R. and Johnson G. D. (eds) *Interrelationships of Fishes*, pp. 9-34. Academic Press, San Diego, California.

Wilga, C. D. (2005) Morphology and evolution of the jaw suspension in lamniform sharks. *Jour. Morphol.* **265**, 102-119.

Wilga, C. D. (2008) Evolutionary divergence in the feeding mechanism of fishes. *Acta Geol. Polonica* **58**, 113-120.