Journal of Fish Biology (2008) **73,** 17–34
doi:10.1111/j.1095-8649.2008.01880.x, available online at http://www.blackwell-synergy.com

Feeding strategy of the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae)

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(Received 14 August 2007, Accepted 27 February 2008)

The feeding biology of the planktivorous megamouth shark *Megachasma pelagios* was investigated. Morphological examination disclosed that the megamouth has a suite of unique characteristics among sharks, such as large mouth, large bucco-pharyngeal cavity, elongate jaw cartilages, long palatoquadrate levator and preorbital muscles, long ethmopalatine ligament and elastic skin around the pharynx. The combination of these characters suggests that the megamouth shark performs engulfment feeding that is typically seen in the rorqual and humpback whales. Engulfment is a new feeding method for sharks, and the detailed mechanism of the engulfment feeding is discussed.

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Key words: balaenopterid; *Cetorhinus*; engulfment; ram 'suction'; *Rhincodon* 'suction'.

INTRODUCTION

The first specimen of the megamouth shark *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983, was accidentally collected in 1976 in Hawaii. In the new species description of the megamouth shark, Taylor *et al.* (1983) disclosed that the megamouth shark is the third species of plankton-feeding shark, along with the basking shark *Cetorhinus maximus* (Gunnerus, 1765) and the whale shark *Rhincodon typus* Smith, 1828. The feeding method of the megamouth shark was further inferred from its morphology that the fish feeds on plankton by slowly swimming through schools of prey with its jaws opened wide. Later, Compagno (1990) concluded that the megamouth shark feeds on plankton by 'suction' created by the sudden protrusion of the jaws and the lowering of the tongue and pharynx. Motta & Wilga (2001) also suggested that the megamouth shark employs intermittent suction filter feeding.

'Suction' feeding is accomplished by the sudden and strong intake of water, typically generated by rapid bucco-pharyngeal expansion, a small gape and hypertrophied abductor muscles (Motta & Wilga, 2001; Motta *et al.*, 2002).

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Wainwright *et al.* (2007) compared the suction feeding mechanics in small-mouthed and large-mouthed teleosts, and showed that the large-mouthed fishes performs suction feeding successfully accompanied by ram swimming towards the prey. Wilga *et al.* (2007) also recognized two modes of suction feeding in fishes, *i.e.* high-velocity, low-volume suction in the small-mouthed fishes, and low-velocity, high-volume suction in the large-mouthed fishes.

The megamouth shark is characterized by the large terminal mouth, no labial cartilage, small gill openings and long bucco-pharyngeal cavity, and these features indicate that the fish employs a kind of low-velocity, high-volume suction feeding. Some unique features, such as elastic skin, wavy naked lines and loose connective tissue around the pharyngeal region, however, are considered to indicate a different method of feeding other than suction.

The purpose of the present paper is to describe the morphological characteristics associated with the feeding, and to discuss the feeding strategy of the megamouth shark.

MATERIALS AND METHODS

Material examined: HUMZ 197412 (Fish Collection of the Hokkaido University Museum, deposited at Fisheries Science Center in Hakodate Campus), female, 5440 mm in total length (L_T), 1040 kg, caught off Owase, Mie Prefecture by surrounding net on 30 April 1997.

The specimen was frozen at −30° C immediately after landing in very fresh condition. When the specimen was examined in June 1997 at Toba Aquarium in Mie Prefecture, it was thawed gradually in the refrigerator, and the body temperature was kept between −3 and −5° C (Yano *et al.*, 1999). After examination, the head, all fins and vertebral centra were deeply frozen again, and transported to Hokkaido University at Hakodate, where the samples were immediately thawed and fixed in 10% formalin. The specimen has been preserved in the formaldehyde solution since 1997.

The terminology used to describe the muscles and tendons mainly follows Wilga (2005), and that of the skeleton follows Compagno (1990). Measurements of the basking shark and the whale shark were taken from Bigelow & Schroeder (1948), Teng (1962), Bass *et al.* (1975), Springer & Gilbert (1976) and Nishida (2001).

RESULTS

Measurements of skeleton, muscles and ligaments are given in Table I.

SKELETAL SYSTEM

Chondrocranium (Fig. 1)

The chondrocranium is wide and flat, with a wide and rounded rostrum, which is composed of a pair of wide lateral rostral cartilages and a slender medial rostral cartilage. The rostrum overhangs antero-ventrally, forming a wide and deep rostral groove, which embraces palatoquadrate cartilage when retracted. The hyomandibular facet is situated at the ventrolateral otic region, large and triangular in shape, with a shallow rounded concavity at the antero-dorsal part of the facet, and with a rounded knob above the posterior portion of the facet (Fig. 1).

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TABLE I. Measurements of skeleton, muscles and ligaments, associated with jaw movements

	mm (%)
Skeleton	
Chondrocranium	
Length from anterior tip to	
Posterior end	551 (100·0)
Origin of epaxial musculature	486 (88·2)
Height at middle between postorbital processes	220 (39·9)
Width between tips of right and left	
Lateral rostral cartilages	473 (85·8)
Supraorbital crests	350 (63·5)
Antorbital processes	455 (82·5)
Postorbital processes	496 (90·0)
Hyomandibular facets	329 (59·7)
Rostral groove	
Width	405 73·5
Depth	103 (18·6)
Palatoquadrate cartilage	
Length from anterior tip to	
Posterior end	765 (138·8)
Orbital process	247 (44·8)
Length of tooth band	655 (118·8)
Minimum depth before orbital process	76 (13·7)
Maximum depth of quadrate process	178 (32·3)
Meckel's cartilage	
Length	918 (166·6)
Length of tooth band	700 (127·0)
Maximum depth	228 (41·3)
Hyomandibular cartilage	
Length	419 (76·0)
Width at	
Proximal end	173 (31·3)
Distal end	110 (19·9)
Ceratohyal cartilage	
Length	546 (99·0)
Width at	
Proximal end	61 (11·0)
Distal end	178 (32·3)
Basihyal cartilage	
Length from anterior tip to	
Posterior concavity	197 (35·7)
Left tip	329 (59·7)
Maximum width	287 (52·0)
Maximum depth	72 (13·0)
Muscles	
Preorbitalis	
Length	572 (103·8)
Width at	
Origin	53 (9·6)
Insertion	170 (30·8)

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TABLE I. Continued

	mm (%)
Levator palatoquadrati	
Length along	
Anterior margin	519 (94·1)
Posterior margin	591 (107·2)
Width at	
Origin	99 (17·9)
Insertion	97 (17·6)
Levator hyomandibularis	
Length along	
Anterior margin	434 (78·7)
Posterior margin	541 (98·1)
Width at	
Origin	135 (24·5)
Insertion	257 (46·6)
Coracomandibularis	
Length	296 (53·7)
Maximum width	24 (4·3)
Coracoarcualis	
Length	490 (88·9)
Coracohyoideus	
Length	520 (94·3)
Maximum width	104 (18·8)
Ligaments	
Palatorostoral ligament	
Length	194 (35·2)
Width	120 (21·7)
Ethmopalatine ligament	
Length	315 (57·1)

Palatoquadrate cartilage (Fig. 2)

The palatoquadrate cartilage is a long and slender cartilage with an orbital process at about the anterior one third, and a moderate elevation of the quadrate process. The palatoquadrate cartilage is suspended by a wide palatorostral ligament anteriorly, by an ethmopalatine ligament at the orbital process and by ligamentous connections to the hyomandibula posteriorly.

Meckel's cartilage (Fig. 2)

Meckel's cartilage is a long and wide cartilage, with a slight elevation at the articulation with the palatoquadrate cartilage. Meckel's cartilage articulates with the palatoquadrate cartilage posteriorly, and it is suspended by the hyomandibular cartilage through ligaments. Labial cartilages are absent.

Hyomandibular cartilage (Fig. 2)

The hyomandibular cartilage is a robust log-like cartilage, with a wide proximal end and a slender distal end. The proximal end of the hyomandibular cartilage articulates with the cranium at the hyomandibular facet, suspended

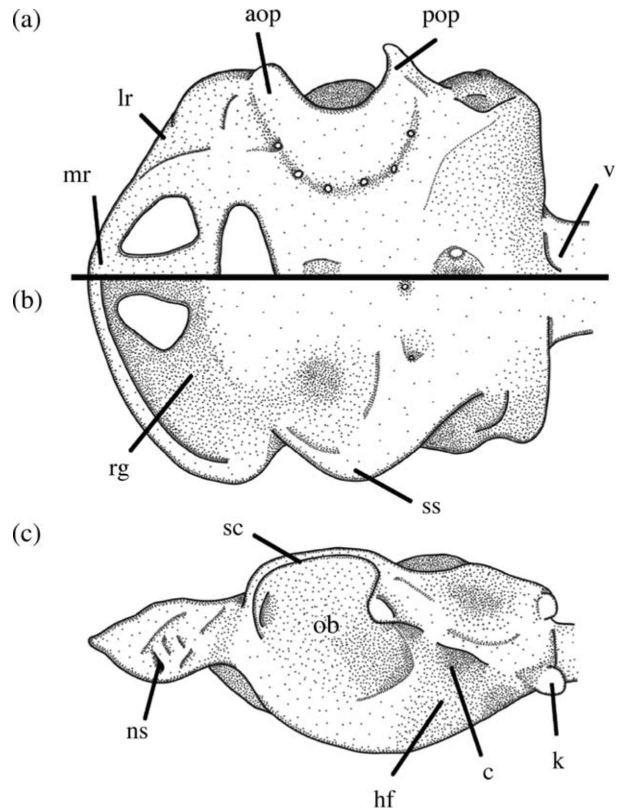

FIG. 1. (a) Dorsal, (b) ventral and (c) lateral views of the chondrocranium. aop, antorbital process; c, concavity; hf, hyomandibular facet; k, knob; lr, lateral rostral cartilage; mr, medial rostral cartilage; ns, nostril; ob, orbit; pop, postorbital process; rg, rostral groove; sc, supraorbital crest; ss, suborbital shelf; v, vertebrae.

anteriorly by a ligament. The anterior part of the proximal end is rounded and is embraced in a shallow concavity [Fig. 1(c) c] located at antero-dorsal part of the hyomandubular facet. The posterior half of proximal end is free, not articulating with the hyomandibular facet, when the hyomandubular cartilage is swung out. The distal end articulates with the ceratohyal cartilage, and suspends both jaws through ligaments.

Ceratohyal cartilage (Fig. 2)

The ceratohyal cartilage is a long, thick and slightly arched cartilage, with a slender articulation head at the proximal end and a triangular head at the distal end. The ceratohyal cartilage articulates with the hyomandibular cartilage at the upper end, and with the basihyal cartilage by the triangular distal end.

Basihyal cartilage (Fig. 2)

The basihyal cartilage is a single cartilage in the shape of a wide arrowhead. It is very thick anteriorly, and acutely thin posteriorly, with a flat surface on the

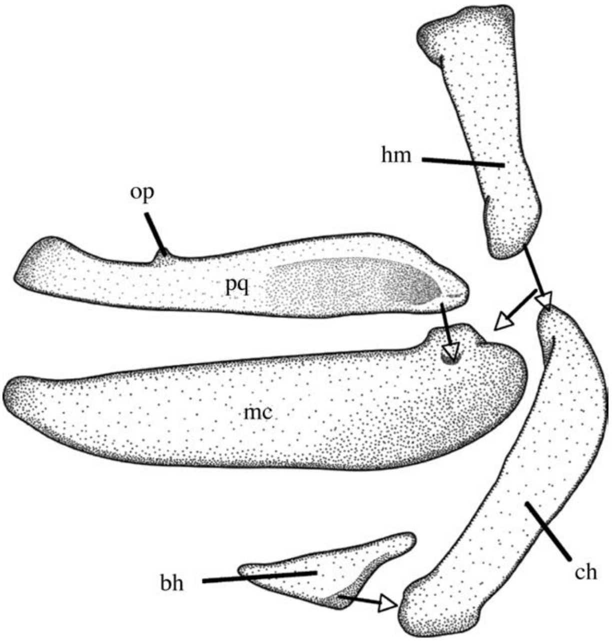

Fig. 2. Lateral view of left mandibular and hyoid arches. bh, basihyal cartilage; ch, ceratohyal cartilage; hm, hyomandibular cartilage; mc, Meckel's cartilage; op, orbital process; pq, palatoquadrate cartilage. Arrows indicate articulation.

oral side. The basihyal cartilage is very loosely articulated with the ceratohyal cartilage at the postero-vental side of the basihyal cartilage (Fig. 2).

MUSCULAR SYSTEM

Preorbitalis (Fig. 3)

The preorbitalis is a long, ribbon-like muscle. It originates from the ventral portion of preorbital process, extends postero-ventrally over the levator palatoquadrati, and inserts into the posterior part of the quadratomandibularis.

Levator palatoquadrati (Fig. 3)

The levator palatoquadrati is a long and ribbon-like muscle, running almost dorso-ventrally. It originates from the otic region behind the postorbital process, extends ventrally between the preorbital muscle and palatoquadrate cartilage, and then over the anterior portion of the quadratomandibularis. It then inserts onto the outer surface of the palatoquadrate cartilage behind the orbital process.

Quadratomandibularis (Fig. 3)

The quadratomandibularis is relatively small and thin, especially when compared with the enormous sizes of the palatoquadrate and Meckel's cartilages. The dorsal division of the quadratomandibularis fans out antero-dorsally from

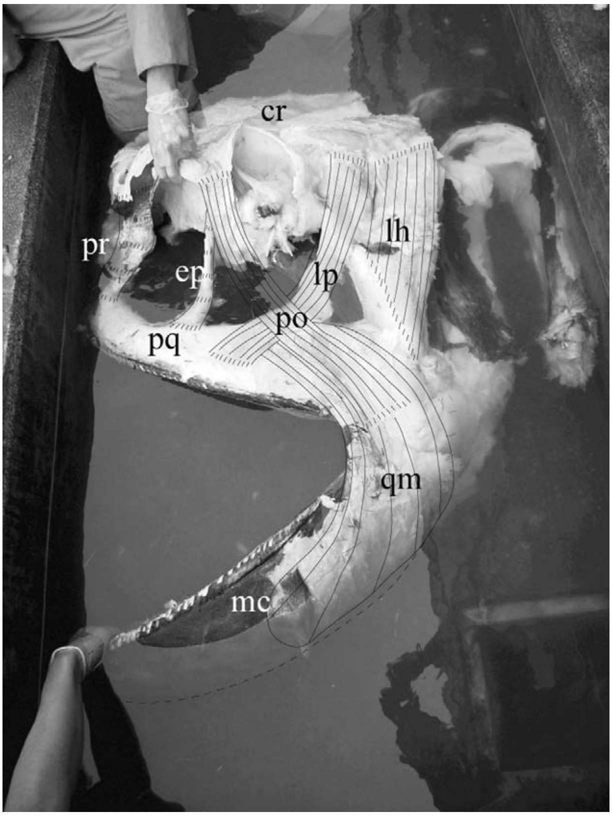

FIG. 3. Lateral view of head with both jaws maximally protruded. cr, chondrocranium; ep, ethmopalatine ligament; lh, levator hyomandibularis; lp, levator palatoquadrati; mc, Meckel's cartilage; pq, palatoquadrate cartilage; po, preorbitalis; pr, palatorostral ligament; qm, quadratomandibularis.

the corner of the mouth to the outer dorsal surface of the palatoquadrate cartilage, and extends anteriorly to insert onto the palatoquadrate cartilage below the levator palatoquadrati. The ventral division of the quadratomandibularis fans out ventrally from the corner of the mouth to the outer surface of posterior half of the Meckel's cartilage.

Levator hyomandibularis (Fig. 3)

The levator hyomandibularis is a thick and wide muscle, originating from the dorso-lateral edge of anterior epaxialis just behind the levator palatoquadrati and inserts widely into the posterodorsal surface of the hyomandibular cartilage.

Coracomandibularis

The coracomandibularis is a thin and short muscle situated on the ventral side of the coracohyoideus, a little <60% of the coracohyoideus in length, and does not reach Meckel's cartilage. The muscle originates from a point 90 mm

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before the anterior end of coracoarcualis and extends to a point 176 mm behind the posterior end of the basihyal cartilage.

Coracohyoideus

The coracohyoideus is a paired, large and robust muscle, originating from the ventral surface of the anterior end of the coracoarcualis muscle and inserting into the ventral surface of the basihyal cartilage.

Coracoarcualis

The coracoarcualis is a large, paired muscle, originating from the ventral surface of the anterior end of the pectoral girdle and inserting into the posterior end of the coracohyoideus.

Intermandibularis and superficial constrictor muscles

These muscles are thin, thread-like (*c.* 8 mm in thickness) in shape, sparse in distribution and extend transversely just below the skin of the pharyngeal region.

LIGAMENTS

Palatorostral ligament (Fig. 3)

The palatorostral ligament is a single wide (*c.* 120 mm) and thick (*c.* 30 mm) tissue that emanates from the mid-ventral part of the anterior margin of the rostral cartilage and extends to the symphysis of the palatoquadrate cartilages. This ligament is newly termed here as palatorostral ligament from its distribution. A palatonasal ligament is absent.

Ethmopalatine ligament

The ethmopalatine ligament is paired and is very long and rope-like in shape and is connected to the ventral side of the preorbital wall and orbital process of the palatoquadrate cartilage (Fig. 3).

SKIN AND DERMAL DENTICLES

Dermal denticles are regularly and densely distributed on the dorsal and dorso-lateral sides of the head. The chin, pharyngeal region, corners of the mouth and the skin along the upper jaws and ventro-lateral side of the head to the level of the gill openings are densely covered by numerous irregular naked lines. Dermal denticles on these regions are distributed in groups separated by the naked lines [Fig. 4(a)]. The naked lines between the denticle groups form continuous wavy lines and an irregular network running in one direction. These lines on the chin run posteriorly and then curve laterally along Meckel's cartilage. Those on the corner of the mouth and along the upper jaw run posteriorly or postero-ventally in rather parallel rows. The lines and network run transversely on middle of the pharyngeal region, and continue postero-dorsally onto the ventro-lateral side of the head.

The skin on the lateral and ventral sides of head is thick (*c.* 3 mm), tough and still very elastic [Fig. 4(b), (c)] even after preservation in formalin for >10 years. The skin, intermandibularis and superficial constrictor muscles are thickly underlain by two layers of very loose and elastic white connective tissue, which is especially thickened in the pharyngeal region around the basihyal cartilage and ventral portion of the ceratohyal cartilage.

The oral valve, which is *c.* 30 mm in width, lines on the inner side along the palatoquadrate and Meckel's cartilage.

DISCUSSION

MORPHOLOGICAL BACKGROUND

The skeleton, muscles and ligaments that mainly regulate the mouth movements are summarized in Fig. 5. When the jaws are retracted and closed [Fig. 6(a)1, (b)1, (c)1], the palatoquadrate and Meckel's cartilages rest just beneath the chondrocranium, with the anterior one third of the palatoquadrate

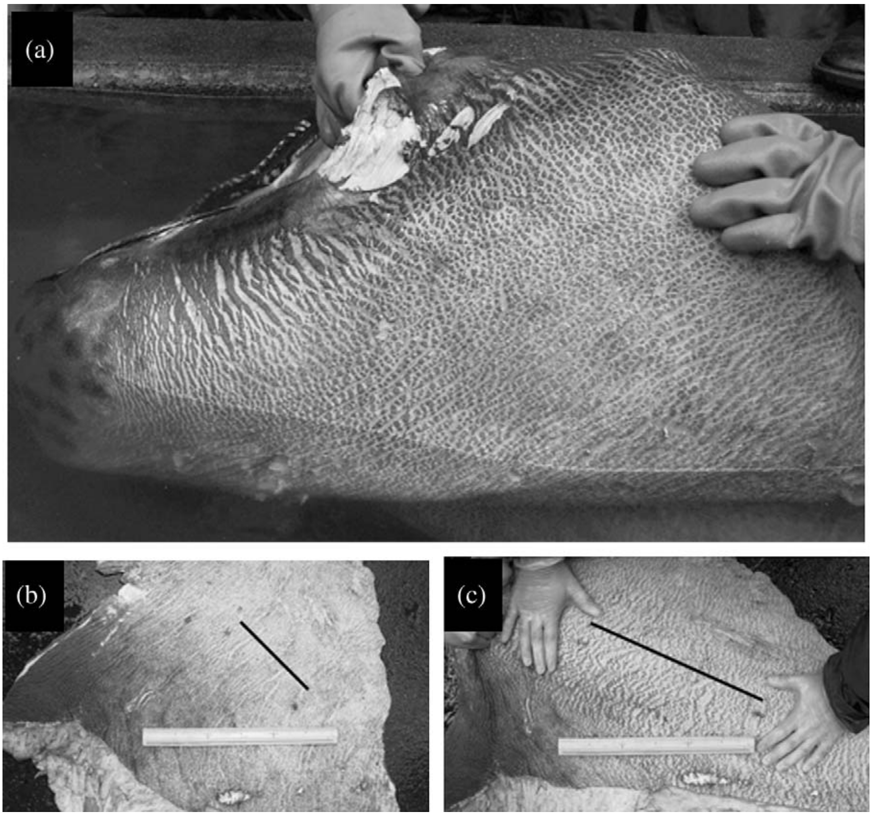

FIG. 4. Skin of pharyngeal region, showing naked lines and network. (a) Ventro-lateral side of head, with the lower jaw to the left and skin in (b) natural and (c) stretched conditions. A black bar in (b) stretches to the length of the bar in (c).

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cartilage embraced within a wide and deep rostral groove formed by overhanging rostral cartilages. The anterior two thirds of the palatoquadrate cartilage and the anterior three fifths of the Meckel's cartilages lie under the chondrocranium, but the posterior one third and two fifths of the respective jaw cartilages project posteriorly beyond the chondrocranium.

The lengths of the palatoquadrate and Meckel's cartilages in the present specimen are 1·4 and 1·7 times longer than the length of the chondrocranium, respectively, while the jaws of the other extant sharks are equal to, or much shorter than the length of the chondrocranium (Compagno, 1990; Wilga, 2005), indicating the jaws of the megamouth shark are unusually long.

The megamouth shark has therefore quite a large gape, but the mouth widths of the megamouth are variously reported in the literature, ranging maximally from 18·5% of L_T in the Hawaiian megamouth (male, 4460 mm L_T; Taylor *et al.*, 1983) to 9·6% L_T in the Fukuoka megamouth minimally (female, 4710 mm L_T; Nakaya *et al.*, 1997). These specimens are almost same in size, but their actual mouth widths are reported as 827 mm in the smaller Hawaiian megamouth, while only 450 mm in the larger Fukuoka megamouth. In a recent re-examination of the Fukuoka specimen that is well preserved,

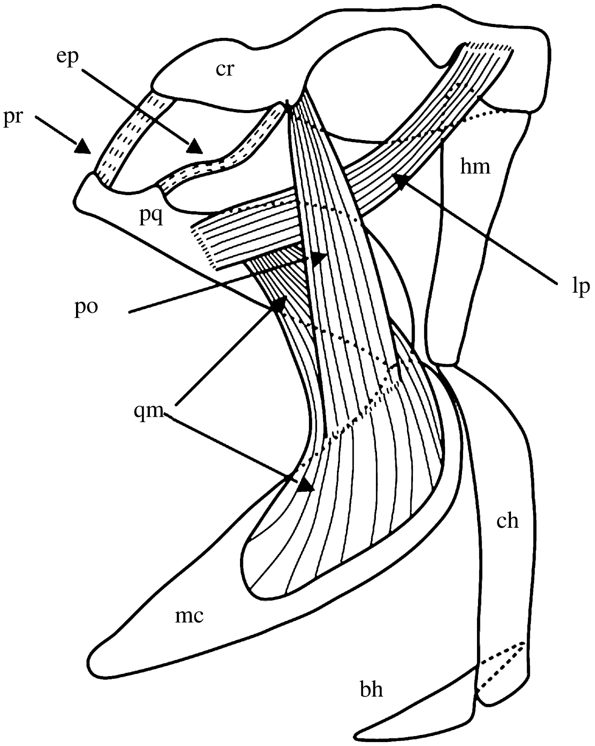

FIG. 5. Diagrammatic figure showing skeleton, muscles and ligaments associated with jaw movements. bh, basihyal cartilage; ch, ceratohyal cartilage; cr, chondrocranium; ep, ethmopalatine ligament; hm, hyomandibular cartilage; lp, levator palatoquadrati; mc. Meckel's cartilage; po, preorbitalis; pq, palatoquadrate cartilage; pr, palatorostral ligament; qm, quadratomandibularis.

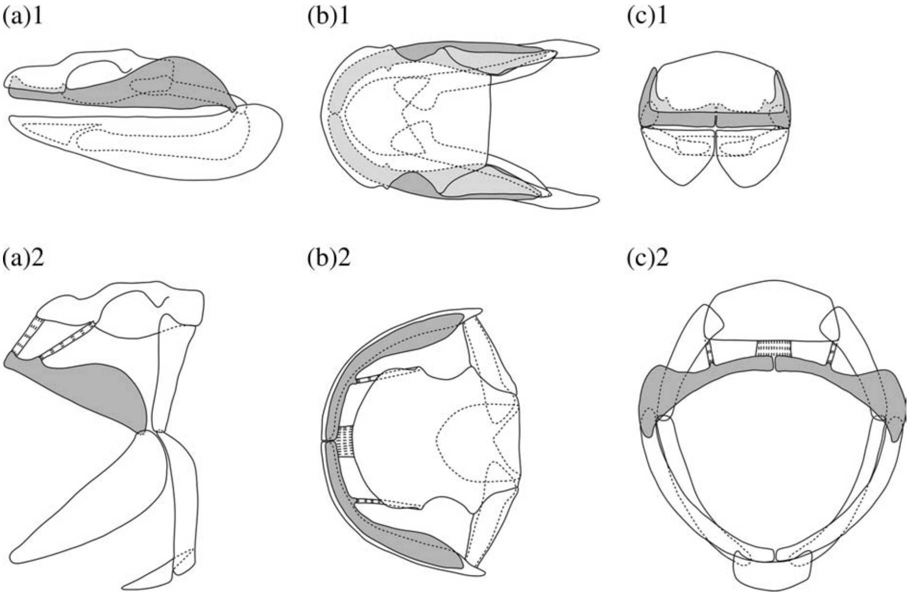

FIG. 6. Jaw movements: (a) lateral, (b) dorsal and (c) frontal views; 1, retracted and closed conditions and 2, protruded, expanded and depressed conditions. Palatoquadrate cartilage is coloured grey.

with the jaws completely retracted, the mouth width was 470 mm, almost same as before. Therefore, the approximate mouth width in retracted condition is considered to be a little $<10\%$ L_T for the megamouth shark. Judging from this, the mouth width of the present specimen can be estimated to be *c.* 520 mm in the retracted condition.

The jaws were manually opened in order to determine the gape size. The jaws were quite movable, and could be dislocated anteriorly, laterally and ventrally to a considerable degree. The maximum height of the gape obtained was 700 mm, and the width was estimated to be *c.* 1000 mm in a distended condition. If the proportional measurement given by Taylor *et al.* (1983; 18·5% L_T) is taken as a maximum width of the gape, the mouth width is calculated to be 1006 mm for the present specimen, which agrees well with the estimate.

Protrusion, lateral expansion and depression of the jaws are regulated by the lengths of ligaments, jaw muscles and the associated cartilages. In comparison with other sharks (Compagno, 1990; Wilga, 2005), the megamouth shark has long palatorostral and ethmopalatine ligaments, long preorbitalis and levator palatoquadrate muscles, and long hyomandibular and ceratohyal cartilages. These unique features in the megamouth shark may imply a kinetic jaw mechanism that is capable of extreme jaw protrusion, lateral expansion and depression [Fig. 6(a)2, (b)2, (c)2] that is not seen in other sharks. The outstanding abilities of the megamouth shark in anterior protrusion and lateral expansion of jaws could be also demonstrated by a Taiwanese megamouth shark (Fig. 7).

The large gape is advantageous for intake of a large amount of water, which is easily achieved by ram swimming with the mouth open. In case of the basking shark, which has a large gape, water flows into the bucco-pharyngeal cavity

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and exits from the large external gill openings. Despite its large gape, however, the megamouth shark's gill openings are much smaller than those of the basking shark. The length of the third external gill opening, for example, ranges only 4·4–5·9% L_T for the megamouth shark (Taylor *et al.*, 1983; Berra & Hutchins, 1990; Nakaya *et al.*, 1997; Yano *et al.*, 1999), while it is 15·6–20·0% L_T for the basking shark (Bigelow & Schroeder, 1948; Bass *et al.*, 1975), indicating that the gill openings in the megamouth shark are only one fourth or one third of those in the basking shark. Therefore, if the water is taken in by the large gape in continuous ram swimming, the amount of water appears to be disproportionately large for such small gill openings of the megamouth shark.

The lengths of the bucco-pharyngeal cavities are also different among the three plankton feeders. The mouth is located on ventral side of the head in the basking shark, while it is on the anterior end of the head in the whale shark and the megamouth shark. The lengths of the bucco-pharyngeal cavity, measured from the anterior end of mouth to the fifth gill opening, are 16·6–17·7% L_T in the basking shark (Bigelow & Schroeder, 1948; Bass *et al.*, 1975; Springer & Gilbert, 1976) and 18·0–24·9% L_T in the whale shark (Teng, 1962; Nishida, 2001), while it is 24·9–28·7% L_T in the megamouth shark (Taylor *et al.*, 1983; Berra & Hutchins, 1990; Nakaya *et al.*, 1997; Yano *et al.*, 1999). These facts indicate that the megamouth shark has the longest bucco-pharyngeal cavity among the three plankton-feeding sharks.

A specimen completely loses its elasticity when preserved in formaldehyde solution. Surprisingly, however, the skin on the ventral and lateral sides of head in the megamouth shark is still quite elastic and stretchable like a rubber sheet even after 10 years preservation. In observations of skin elasticity, the skin taken from the ventral side of the head [Fig. 4(b)] could manually be stretched to at least two times the original length [Fig. 4(c)], and it returned to the original state when released. A network of naked wavy lines runs in one direction on this elastic skin between the dermal denticles, and the presence of these naked lines may also indicate that the skin has been frequently stretched. If the skin is stretched two times the original length, a doubling of

FIG. 7. A megamouth shark collected in Taiwan, showing fully protruded and distended jaws.

the length and width will result in a four-fold increase in area. This means that the skin on the ventral and lateral sides of the head is considerably stretchable. In addition, the skin is underlain by thick, loose and elastic white connective tissue. Although histological observations were not made, the very loose and elastic nature of the tissue could suggest that it might function to co-ordinate the different movements of the skin and of the cartilages and muscles.

Assuming that the bucco-pharyngeal cavity is a simple cylinder of 1470 mm long (27% L_T) and 700 mm in diameter, the water volume taken in could be calculated to be 565 l in the present 5440 mm L_T specimen. In addition, the jaws of the megamouth shark are protrusible, further lengthening its bucco-pharyngeal cavity, and the bucco-pharyngeal cavity is distensible, enlarging the volume. Therefore, the bucco-pharyngeal cavity of the megamouth shark is enormous among the plankton-feeding sharks.

FEEDING METHODS OF PLANKTON-FEEDING SHARKS

The whale, basking and megamouth sharks feed on zooplankton. The basking shark continuously swims forward in the aggregation of plankton with the mouth open, which is called ram filter feeding (Fairfax, 1998; Sims, 2000; Motta & Wilga, 2001). The jaws of the basking shark are slightly protrusible, but swing ventrally and spread laterally to form a circular mouth (Compagno, 1990). As the basking shark swims forward with its mouth open, the water is scooped into the buccal cavity from the large subterminal mouth and flows out from the large gill openings, which open from the ventral to the dorsal side of the head.

The whale shark can also use continuous ram filter feeding, as the basking shark does, but can also use pulsatile suction filter feeding (Clark & Nelson, 1997; Motta & Wilga, 2001). Compagno (2001) also considered that the whale shark is a versatile suction filter-feeder, and that the whale shark does not depend on ram swimming to take water in the mouth, but can probably achieve relative high intake velocities of water into its mouth by suction. Actually, the whale shark can be seen to achieve strong suction without ram swimming during feeding in aquaria (pers. obs.).

Taylor *et al.* (1983) suggested that the megamouth shark feeds on planktonic animals by slowly swimming through the school with its jaws opened wide, which is ram filter feeding similar to the basking shark. Later, Compagno (1990) gave a revised situation for the feeding of the megamouth shark, opining that the fish swims through or floats in the aggregations of planktonic prey animals with its jaws retracted and mouth open, then suddenly protrudes its jaws, drops its tongue and pharynx, greatly increasing the volume of its pharynx, and 'sucks' the prey inside. He also observed that the heavy, long jaws of the megamouth shark are not widely distensible laterally, but are highly protrusible anteriorly, like a bellows. Hence, he concluded that the megamouth shark conducts suction filter feeding.

Wainwright *et al.* (2007) discussed the suction feeding mechanics of the bluegill *Lepomis macrochirus* Rafinesque, 1819 and the large-mouth bass *Micropterus salmoides* (Lacepède, 1802), which represent opposite ends of the spectrum of performance in suction feeding. The small-mouthed bluegill generated higher

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in-flow velocities and acceleration in the water suction than the large-mouth bass. The large-mouth bass, however, combined ram swimming towards the prey, and the time taken to bring the prey to the margin of the mouth was actually slightly shorter than the bluegill. These facts mean that the large-mouthed predator is able to accomplish successful suction feeding with ram swimming towards the prey. Wilga *et al.* (2007) called the feeding of the bluegill as high-velocity, low-volume suction, and as low-velocity, high-volume suction for that of the large-mouth bass.

According to Wilga *et al.* (2007), the suction specialists of the elasmobranchs have terminal or subterminal mouths that are laterally occluded by large labial cartilages to form a rounded gape ringed by relatively small teeth and hypertrophied abductor muscles that generate great expansive forces. The nurse shark *Ginglymostoma cirratum* (Bonnatere, 1788) performs effective 'suction' feeding, with a small terminal mouth (Motta *et al.*, 2002), and this species may be refereed to a high-velocity, low-volume suction feeder.

The megamouth shark is characterized by the terminal mouth, large gape, no labial cartilage, small gill openings and long bucco-pharyngeal cavity, and these features indicate that the megamouth shark is not a high-velocity, low-volume suction feeder, but the fish employs a kind of low-velocity, high-volume suction feeding. The presence of unique characteristics such as the elastic skin, wavy naked lines and loose connective tissue around pharyngeal region, however, may further indicate a different method of feeding other than suction feeding.

FEEDING PROCESS OF MEGAMOUTH SHARK

The feeding process in the megamouth shark is shown in Fig. 8. The *x*-axis indicates time, and the *y*-axis shows volume of the bucco-pharyngeal cavity. The straight lines OP and PZ indicate volume change of the water and prey in the bucco-pharyngeal cavity. The feeding process of the megamouth shark is divided into following five phases. (1) Phase 1 (time T_o). This is the beginning of the feeding behaviour, and the bucco-pharyngeal cavity is emptied (Volume, Vo). (2) Phase 2 (time $T_o \rightarrow T_k$). The mouth is slightly opened, the mouth floor is lowered, and the water and prey are taken into the bucco-pharyngeal cavity by suction (volume $V_o \rightarrow V_k$), following the line OK (suction phase). (3) Phase 3 (time $T_k \rightarrow T_m$). The mouth is widely opened, and the water and prey are gulped in until the bucco-pharyngeal cavity is fully filled by ram suction (volume $V_k \rightarrow V_m$), following the line KM (ram-suction phase). (4) Phase 4 (time $T_m \rightarrow T_p$). The water and prey are engulfed by ram swimming with distention of the bucco-pharyngeal cavity, which is termed here as engulfment-feeding (volume $V_m \rightarrow V_p$), following the line MP. The engulfment feeding ceases when the bucco-pharyngeal cavity is fully distended with the pharyngeal skin maximally stretched by water (time T_p) (engulfment phase). (5) Phase 5 (time $T_m \rightarrow T_z$). The prey in the mouth is sieved by the gill rakers and the water is pushed out through the gill openings (volume $V_p \rightarrow V_z$), following the line PZ.

The suction feeding is caused by rapid expansion of bucco-pharyngeal cavity, and this results in a sharp drop of bucco-pharyngeal pressure, causing water to move into bucco-pharyngeal cavity from the regions of higher pressure in front

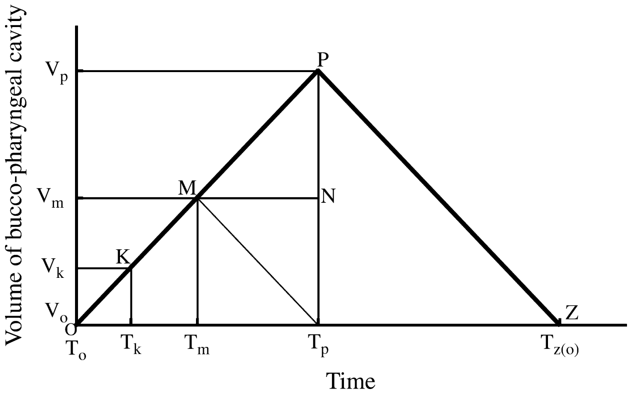

FIG. 8. Feeding process of megamouth shark. k, end of suction phase; m, bucco-pharyngeal cavity full without distention; o, beginning of feeding behaviour; p, bucco-pharyngeal cavity maximally distended with fully stretched skin; z, end of feeding behaviour.

of the open mouth (Wainwright *et al.*, 2007). The engulfment feeding clearly contrasts with the suction feeding in the pressure of the bucco-pharyngeal cavity. During engulfment feeding (phase 4), water flows into bucco-pharyngeal cavity solely by ram swimming, and this results in a rise of bucco-pharyngeal pressure, causing distention of the bucco-pharyngeal cavity. During phase 5 after engulfment, the bucco-pharyngeal pressure will rise more through pumping action by the constrictor and other muscles.

As shown above, the feeding process of the megamouth shark may be divided into the five phases from the feeding events that take place, with three kinds of feeding methods, *i.e.* suction, ram suction and engulfment. The triangle MPN in Fig. 8 indicates the amount obtained by the engulfment feeding.

The engulfment feeding is typically seen in the balaenopterid whales, such as rorquals and humpback whales (Bouetel, 2005). According to Bouetel (2005), when whales feed, the lower jaw is opened at a 90° angle, forced by the amount of water engulfed, and the ventral pleats expand in order to support the engulfment of water and prey. The engulfment feeding of the megamouth shark is similar to that of the balaenopterids in that they take large amount of water in the bucco-pharyngeal cavity by ram swimming with mouth open, and that the elastic skin on ventral and lateral sides of the head is expanded to support larger amount of water and prey, just like ventral pleats in whales. The engulfment feeding in the megamouth shark is a unique feeding method that is not seen in other elasmobranch fishes.

FEEDING SEQUENCE

Based on the morphological characteristics, simulation and photographic evidence, the sequence of the megamouth shark feeding is inferred as follows (Fig. 9). Finding the aggregation of the zooplankton, the megamouth shark slowly approaches it [Fig. 9(a)]. The mouth is almost closed, with the mouth floor elevated near the mouth roof, to minimize the mouth cavity (phase 1).

Raising the head, the basihyal, basibranchial and hypobranchial cartilages are pulled posteriorly and ventrally by the coracomandibularis, coracohyoideus and coracobranchialis muscles. Meckel's cartilage is also pulled posteriorly and ventrally by the movement of the basihyal cartilage, resulting in opening of the mouth. The water flows into the mouth by 'suction' (phase 2).

The anterior ends of the right and left ceratohyal cartilages are pushed posteriorly by the backward relocation of the basihyal cartilage, and the posterior portions of the ceratohyal cartilages are swung out laterally. The posterior ends of the Meckel's and palatoquadrate cartilages are pushed out laterally by the swinging action of the ceratohyal and hyomandibular cartilages, which widens the gape. At the same time, the fish swims forward to gulp water, and the jaws are further opened by the water and by the backward movement of the basihyal cartilage [Fig. 9(b)]. The tongue and mouth floor are pulled backwards and depressed by the movements of the basihyal, basibranchial and hypobranchial cartilages, and by the water pressure created by ram swimming. The bucco-pharyngeal cavity is filled with water and prey, and the water forces the jaws fully open (phase 3).

With the palatoquadrate and Meckel's cartilages fully extended, the fish keeps swimming forward to engulf water, and the bucco-pharyngeal cavity is expanded maximally, with the skin around the pharyngeal regions fully

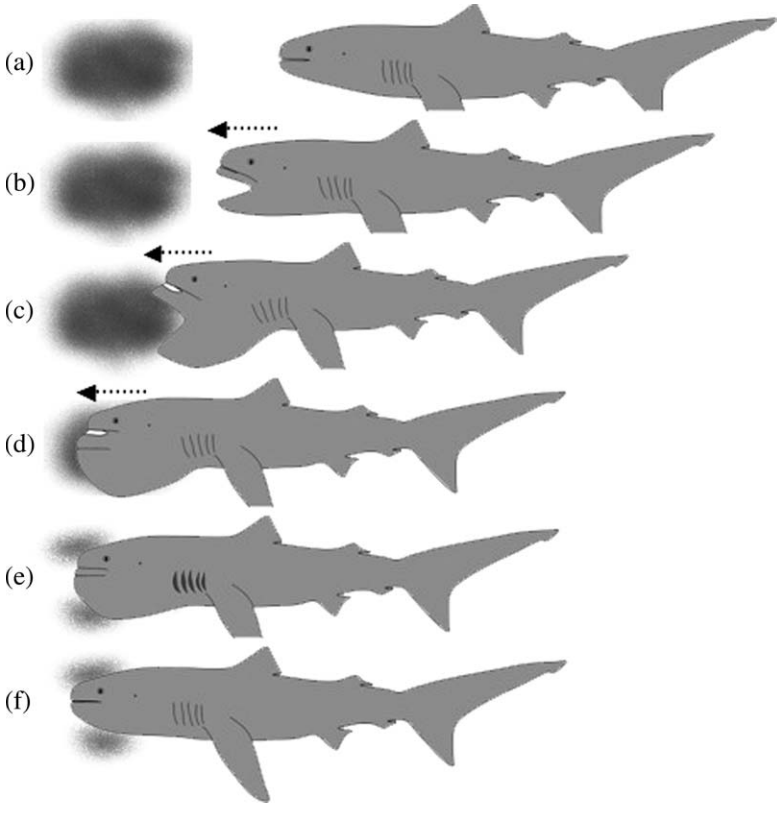

FIG. 9. Sequence of feeding behaviour of the megamouth shark: (a) phase 1 and 2, (b) phase 3, (c), (d) phase 4, and (e), (f) phase 5.

stretched by the water [Fig. 9(c)]. The palatoquadrate cartilage is pulled forward by the preorbitalis muscle and is protruded to the maximal length of the ethmopalatine ligament to surround the water before the mouth. Lowering the head, the jaws are closed by the quadratomandibularis muscle to enclose the water and keep the prey inside [Fig. 9(d)]. The oral valves that line along margins of both jaws trap the water inside the mouth. The engulfed water bulges the ventral and lateral walls of the head, like a large ball (phase 4).

The palatoquadrate and hyomandibular cartilages are pulled back by the levator palatoquadrati and levator hyomandibularis muscles, respectively, and the jaws are retracted to the resting position. As a result of the water pressure created by mouth closure, the oral valves seal the mouth cleft to prevent the water from leaking. The bucco-pharyngeal cavity is squeezed by the intermandibularis and constrictor superficialis muscles, and the water inside is expelled from the gill openings through gill rakers [Fig. 9(e)]. Planktonic prey are sieved out and swallowed [Fig. 9(f)] (phase 5).

We are obliged to the following persons: M. Furuta for supplying us with the invaluable specimen, P.F. Lee for the photograph of Taiwan megamouth shark, T. Mori for measurements of the Fukuoka megamouth shark and M. Wald for the English review. Three anonymous reviewers supplied constructive criticism and informative suggestions that greatly improved this paper.

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