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Morphology of Throat Barbels of *Cirrhoscyllium japonicum* (Elasmobranchii, Parascylliidae), with Comments on Function and Homology

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Abstract The morphology of the throat barbels of *Cirrhoscyllium japonicum* is described in detail. Each barbel is supported by a basal cartilage and a cartilaginous core, and innervated by ramus mandibularis externus from truncus hyomandibularis VII. Neither muscles nor taste buds or other sensory receptors are associated with the barbels, which are thought to function as sensory organs, responding to physical or mechanical stimulation. Comparison of the throat barbels with head appendages found in related shark groups suggests that the former are not homologous with any of the latter, but are better interpreted as an autapomorphic character of the genus *Cirrhoscyllium*.

The order Orectolobiformes, comprising eight families and 14 genera, includes many benthic sharks living in tropical to temperate waters (Compagno, 1984). One of the morphological characteristics of the order is the presence of various appendages on the head, including barbels on the throat, anterior nasal flap or rostrum, and dermal lobes on the side of the head. Although such appendages seem to be associated with the benthic habit of these sharks, their manner of functioning is still uncertain.

The genus *Cirrhoscyllium* includes three species, i.e., *C. expolitum* Smith and Radcliffe, 1913, *C. japonicum* Kamohara, 1943, and *C. formosanum* Teng, 1959, each having a pair of barbels on the ventral surface of the throat (termed throat barbels by Compagno [1988]). The throat barbels are regarded as one of the diagnostic features of the genus, no other taxa having corresponding appendages (Smith, 1913; Kamohara, 1943; Teng, 1959; Applegate, 1972; Compagno, 1984; Dingerkus, 1986). However, the internal morphology, functions and phylogenetic implications of the throat barbels are still unknown.

This paper presents a detailed description of the throat barbels (referred to in the singular hereafter) of *Cirrhoscyllium japonicum*, both externally and internally, and discusses the barbel function, and possible homology with structures in other shark groups.

Materials and Methods

All materials used in this study were deposited at the Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University (HUMZ). Four specimens of *Cirrhoscyllium japonicum* (HUMZ 40017, female, 385 mm TL; HUMZ 40057, female, 431 mm TL; HUMZ 80495, female, 455 mm TL; HUMZ 118481, male, 370 mm TL) were studied, and one each of *Orectolobus japonicus* Regan, 1906 (HUMZ 114394, female, 221 mm TL) and *Pristiophorus japonicus* Günther, 1870 (HUMZ 125940, male, 1145 mm TL) for comparison. The specimens were preserved in 50% isopropyl alcohol after fixation in 10% formalin.

External and internal morphology were examined as follows: by dissection after staining with Alcian Blue 8G (Dingerkus and Uhler, 1977) and Sudan Black B (Rasmussen, 1961), illustrations being made using a camera lucida (HUMZ 40057, 80495 and 118481), and by microscopic investigation of 10 μm transverse sections, (embedded in paraffin wax), stained with hematoxylin and eosin (HUMZ 40017). The comparative material (HUMZ 114394; HUMZ 125940) was examined using both methods.

Terminology follows Norris and Hughes (1920), Daniel (1934), Edgeworth (1935) and Compagno (1984, 1988).

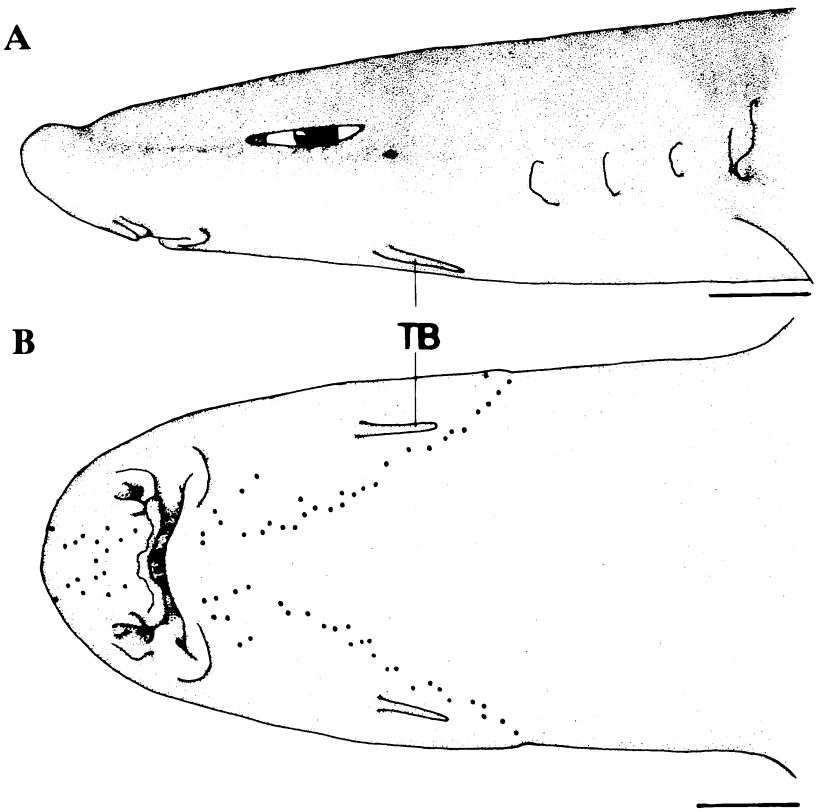

Fig. 1. A) Lateral and B) ventral views of head of *Cirrhoscyllium japonicum*, HUMZ 80495, 455 mm TL. Scale bars indicate 10 mm. *TB*—throat barbel.

Results

External morphology (Figs. 1, 2)

The cylindrical throat barbel is directed posteriorly from the lateral edge of the ventral surface of the head posteroventrally to the eye (Fig. 1), being a slender, feeble appendage. Barbel length is 1.3–1.6 times eye horizontal diameter and 4.7–7.5 times barbel diameter. (Barbel length and width [%TL] of HUMZ 40017, 40057, 80495 and 118481 are 1.6 and 0.3, 1.5 and 0.2, 1.6 and 0.3, and 1.4 and 0.3, respectively.) Each barbel is densely covered with distally-directed dermal denticles, which are continuous with the denticles on the ventral surface of the head (Fig. 2A). Each barbel denticle is clearly smaller than the latter, consisting of a relatively stout peduncle and somewhat flattened, leaf-like crown with a pair of inconspicuous ridges on the lateral edges and a weak protuberance between the ridges (Fig. 2B, C). Although the ridges vary to some degree between barbel denticles, all tend to be more strongly developed than those on the ventral head denticles.

Internal morphology (Figs. 3, 4)

The throat barbel stands loosely on reticulated connective tissue covering the intermandibularis and constrictor branchiales superficiales muscles, being supported by a basal cartilage and a cartilaginous core (Fig. 3). The basal cartilage, an extremely small, globular cartilage buried in connective tissue, provides a relatively unstable base for the barbel. The cartilaginous core, entirely enveloped by fibrous connective tissue, is an elongated, cylindrical rod which passes through the center of the barbel from the base to the distal end. The two cartilages loosely articulate with one another by means of a massive ligament. The barbel lacks muscles and is not associated with any muscles of the head (Fig. 3). The integument consists of dermis and epidermis (Fig.

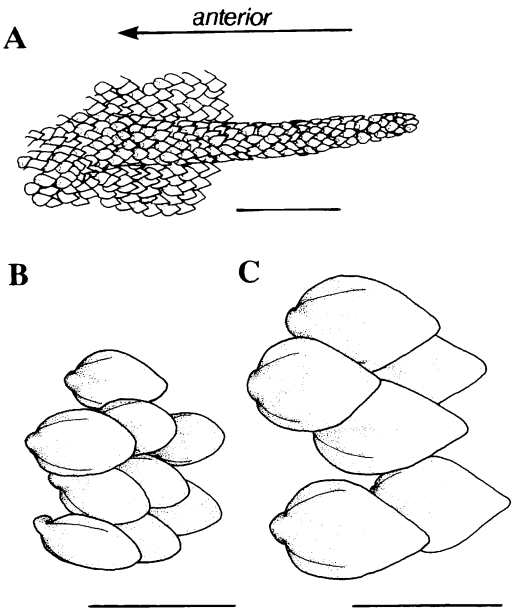

Fig. 2. Throat barbel and dermal denticles of *Cirrhoscyllium japonicum*, HUMZ 118481, 370 mm TL. A) Ventral view of left throat barbel; B) dermal denticles on ventral surface of throat barbel; C) dermal denticles on head anterior to throat barbel. Scale bars indicate 0.5 mm.

4). The former comprises massive fibrous tissue penetrated by nerve fibers (Fig. 4), and is innervated being by sub-branches from the posterior component of ramus mandibularis externus from truncus hyomandibularis VII (Fig. 3B). The latter is a relatively thick, but fragile layer consisting of cube-shaped epidermal cells. The sub-branches within the barbel consist of fibers lying around the cartilaginous core, running along it towards the barbel tip (Fig. 4). Taste buds and other sensory receptors are absent.

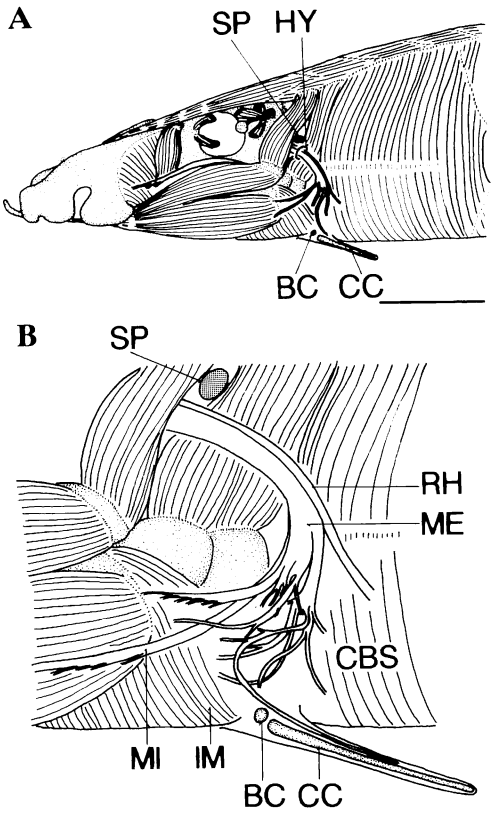

Fig. 3. Muscles and nerves of *Cirrhoscyllium japonicum*, HUMZ 40057, 431 mm TL. A) Lateral view of head after removal of skin; B) internal morphology of throat barbel and distribution of truncus hyomandibularis VII. Scale bars indicate 10 mm. *BC*—basal cartilage; *CBS*—constrictor branchiales superficiales; *CC*—cartilaginous core; *HY*—truncus hyomandibularis VII; *IM*—intermandibularis; *ME*—ramus mandibularis externus; *MI*—ramus mandibularis internus; *RH*—ramus hyoideus; *SP*—spiracle.

Discussion

The throat barbel of *Cirrhoscyllium japonicum* is thought to be a sensory organ because of its innervation by sub-branches of ramus mandibularis externus from truncus hyomandibularis VII. According to Norris and Hughes (1920), Dijkgraaf (1963) and McCready and Boord (1976), truncus hyomandibularis VII can be primarily divided into lateral-line, visceral sensory and visceral motor components. The lateral-line component, which includes ramus mandibularis externus, innervates the ordinary lateral line, Lorenzini ampullae and pit organs, together with ramus maxillaris V and ramus buccalis VII. The visceral sensory component, which includes ramus mandibularis internus, innervates the lower jaw and ventrolateral floor of the mouth. The visceral motor component, which includes ramus hyoideus, innervates constrictor muscles associated with the visceral arches. The nerve branch for the throat barbel, i.e., ramus mandibularis externus, is an element of the lateral-line component, the throat barbel being regarded as a sensory organ. However, taste buds and other sensory receptors are apparently

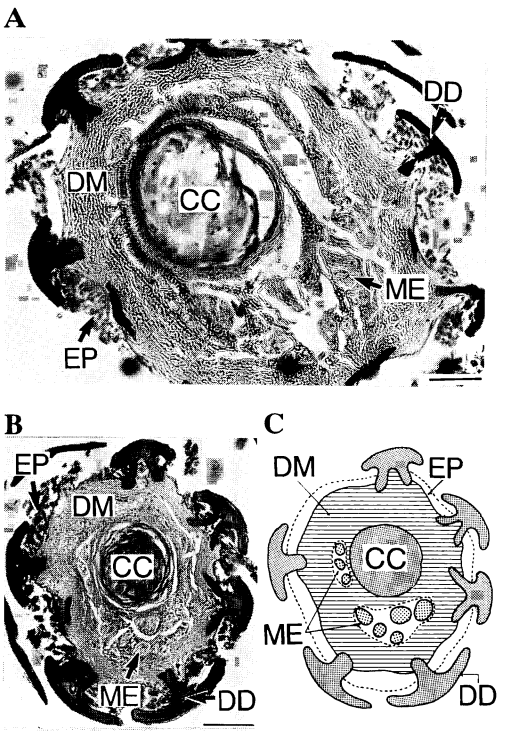

Fig. 4. Transverse sections of throat barbel of *Cirrhoscyllium japonicum*, HUMZ 40017, 385 mm TL. A) Proximal; B) distal regions; C) schematic diagram. Scale bars indicate 0.1 mm. *CC*—cartilaginous core; *DD*—dermal denticle; *DM*—dermis; *EP*—epidermis; *ME*—ramus mandibularis externus.

absent from the barbel of *C. japonicum*. On the other hand, the throat barbel is thought to be immovable by itself because of the lack of associated muscles, although movement may occur to some degree, corresponding to movement of the head, since the barbel stands directly on connective tissue covering the intermandibularis and constrictor branchiales superficiales muscles, which are associated with throat movements. Consequently, the barbel seems to be a tactile organ responding to physical or mechanical stimulation. Possible functions include the detection of other substances (e.g., prey or substrata) or changes in water flow, and maintenance of body balance, such functions being likely related to the benthic habit of the species. However, the lack of living specimens for observation during the study, precluded any firm conclusions. Furthermore, the biology of *Cirrhoscyllium* is unknown.

A throat barbel is present only in the genus *Cirrhoscyllium* (Smith, 1913; Kamohara, 1943; Teng, 1959; Applegate, 1972; Compagno, 1984; Dingerkus, 1986), although various other appendages occur on the head in other shark groups (i.e., nasal barbel, dermal lobe and rostral barbel).

A nasal barbel is found in all orectoloboids, some carcharhinoids (e.g., *Poroderma*, *Schroederichthys* and *Furgaleus*) and the squalid *Cirrhigaleus* (Compagno, 1984; Shirai, 1992; Bell, 1993). It is a cylindrical rod situated on the outer edge of the anterior nasal flap, being composed of a fibrous, noncartilaginous core enveloped by an integument cov-

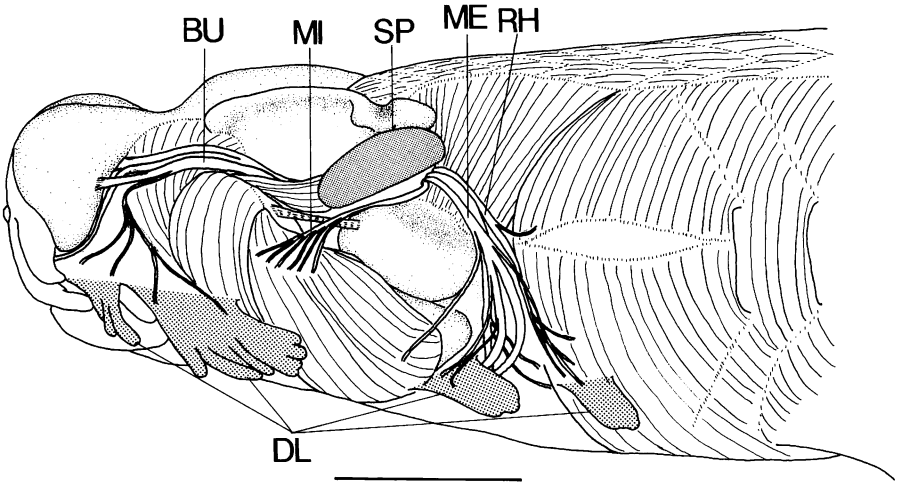

Fig. 5. Muscles and nerves of *Orectolobus japonicus*, HUMZ 114394, 221 mm TL. Scale bar indicates 10 mm. *BU*—ramus buccalis VII; *DL*—dermal lobe; *ME*—ramus mandibularis externus; *MI*—ramus mandibularis internus; *RH*—ramus hyoideus; *SP*—spiracle.

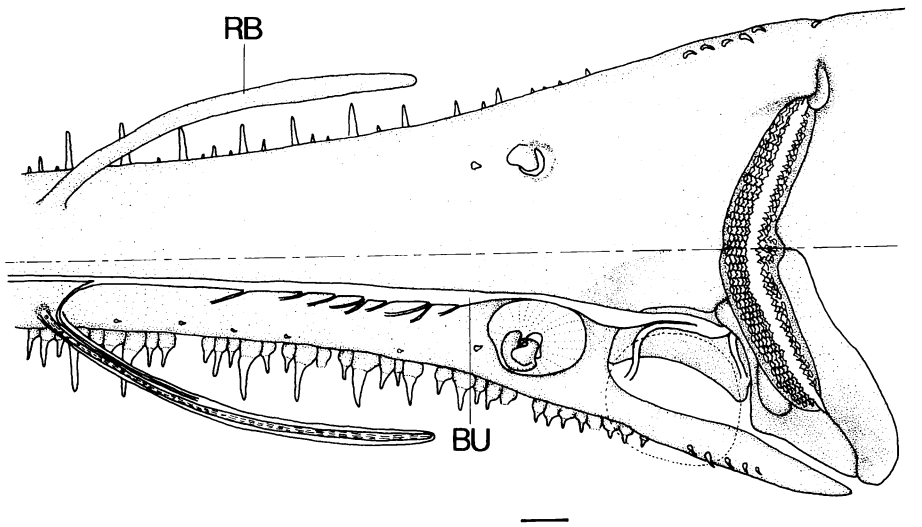

Fig. 6. Ventral view of rostrum of *Pristiophorus japonicus*, HUMZ 125940, 1145 mm TL, showing innervation of rostral barbel (lower half). Scale bar indicates 10 mm. *BU*—ramus buccalis VII; *RB*—rostral barbel.

ered with dermal denticles and lacking any association with muscles (Shirai, 1992). Such barbels include at least two types in regard to nerve innervation, in orectoloboids being by ramus ophthalmicus superficialis VII, and in *Cirrhigaleus* by ramus buccalis VII (Holmgren, 1941; Shirai, 1992). The innervation in carcharhinoids is unknown. It is similarly unknown whether or not the nasal barbels of the above groups possess taste buds. The nasal barbel apparently differs from the throat barbel in respect of both location, structure and nerve innervation.

Dermal lobes are found in all orectolobid wobbegongs, being arrayed on the side of the head from the nasal region to the front of the first gill slit (Fig. 5; Compagno, 1984). One of the lobes, situated below the spiracle, is somewhat similar in position to the throat barbel of *Cirrhoscyllium*. Externally, the lobes are flattened and furcated, differing greatly in shape from the throat barbel of *Cirrhoscyllium*. Structurally, they comprise an integument with dermal denticles, but have neither a base nor a core composed of cartilages. There are no associated muscles. The lobes are innervated by two components of the lateral-line nerves. The anterior lobes in front of the eye are innervated by sub-branches of ramus buccalis VII, and the posterior ones behind the eye are innervated by sub-branches of ramus mandibularis externus of truncus hyomandibularis VII. However, the nerve branches in the lobes are so thin that whether or not they extend to the distal region can not be confirmed. Taste buds or other sensory receptors have never been reported in the dermal lobes of orectolobids. It is clear, however, that the dermal lobes, including that below the spiracle, differ from the throat barbel of *Cirrhoscyllium* in both the absence of cartilaginous base and core, and external morphology.

The rostral barbel found in all pristiophorid sawsharks is situated on the ventral surface of the saw-like blade (Fig. 6; Compagno, 1977, 1984). It is extremely elongated and flattened, consisting of a fibrous, non-cartilaginous core and integument. There are no associated muscles. The barbel is innervated by a relatively stout bundle of ramus buccalis VII. Although Compagno (1984) suggested the presence of taste buds, such could not be found in this study. Clearly, the rostral barbel differs from the throat barbel of *Cirrhoscyllium* in respect of its location, core structure and nerve innervation, on the other hand, being rather similar to the nasal barbel of *Cirrhigaleus*, both being supported by a non-cartilaginous core and innervated by ramus buccalis VII.

As discussed above, the throat barbel is characterized by its position on the throat, innervation by ramus mandibularis externus of truncus hyomandibularis VII, and support by the basal cartilage and the cartilaginous core. In particular, cartilaginous support is seen only in *Cirrhoscyllium*, barbels and lobes in other sharks being supported by non-

cartilaginous tissues. In conclusion therefore, it is considered that the throat barbel in *Cirrhoscyllium* is not homologous with any other appendages in related shark groups, and should be considered an autapomorphic character of *Cirrhoscyllium*.

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クラカケザメの喉部のひげの形態と，その機能および相同性

後藤友明・仲谷一宏・尼岡邦夫

クラカケザメの喉部のひげを詳細に記載した．その結果，このひげが基底軟骨および軟骨性の中軸により支持されること，顔面神経の舌顎枝の1分枝である ramus mandibularis externus が分布すること，筋肉がないこと，そして味蕾や他の感覚受容体を持たないことが明らかになった．これらは，このひげが物理的刺激に対する感覚器官の一種であることを示唆している．また，このひげの相同性を推定するため，他の板鰓類にみられるいくつかの類似した器官と比較したところ，クラカケザメの喉部のひげはこれらのいずれとも相同ではない固有なものであることが明らかになった．

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