

Comparative Morphology of the Expanded Epipleural and Its Associated Structures in Four Species of the Trachichthyidae

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Abstract The morphology and relation of a series of specialized structures, the expanded epipleural and associated muscle and nerves, Baudelot's ligament, and swim bladder, of *Trachichthys australis*, *Optivus elongatus*, *Paratrachichthys trailli*, and *P. prosthemi* are described. The shape and size of these structures vary according to species. Sexual dimorphism in these structures is seen in the two species of *Paratrachichthys* examined. The anatomical evidence suggests that these structures developed with a close relation of acoustic function. Based on the presence or absence of these structures, all known five genera in the family Trachichthyidae are divided into two phyletic stems, one comprising the present three genera and another comprising two genera, *Hoplostethus* and *Gephyroberyx*.

Introduction

Among the fishes of the family Trachichthyidae, *Trachichthys australis*, *Cptivus elongatus* and four species of *Paratrachichthys* have a broad, plate-like, expanded first epipleural (personal communication from Dr. C. Patterson). Woods and Sonoda (1973) described an anterior rib plate in *Paratrachichthys argyrophanus* for the first time and gave a brief comment on the relationships between *Paratrachichthys* and *Cptivus* based on the presence of this plate. However, the comparative morphology of the expanded epipleural and its associated structures, their function and relationships among the present three genera have not been examined. The author studied four western Pacific species belonging to the three genera, *Paratrachichthys trailli* (Hutton, 1876), *P. prosthemi* Jordan et Fowler, 1903, *Optivus elongatus* (Günther, 1859), and *Trachichthys australis* Shaw et Nodder, 1799. For the comparison, moreover, two species belonging to the other two genera, *Hoplostethus mediterraneus* and *Gephyroberyx japonicus*, in this family were examined.

In this paper, the comparative morphology and relation of such specialized structures as the expanded epipleural, its associated muscle, nerves, Baudelot's ligament and swim bladder, are described. A supposed acoustic

function of these specialized structures is discussed on the basis of the anatomical evidence. The relationships among five genera in this family are presented based on the presence or absence of these specialized structures.

Material and method

Data on specimens. *P. trailli*; 50 specimens from off New Zealand and Australia; FAKU (Department of Fisheries, Faculty of Agriculture, Kyoto University) 40278, 167.3 mm SL, 38°~39°S, 174°~175°E, depth 60~80 m, Sept. 1966; FAKU 43718~43719, 47737 47758, 123.9~211.8 mm SL, 43°21.9'S, 177° 13.1'E, depth 250 m, Dec. 7, 1970; HUMZ (Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University) 50292~50293, 198.1~226.2 mm SL, 35°47'S, 173°11.3'E, depth 305 m, Apr. 25, 1975; HUMZ 52076~52095, 52330~52332, 118.2~159.4 mm SL, 39°32.6'S, 143°20.6'E, depth 108 m, Dec. 18, 1975. FAKU 47747, 195.0 mm SL and FAKU 47748, 198.2 mm SL were dissected. *P. prosthemi*; 14 specimens from Japan; HUMZ 37351, 57.0 mm SL. Mimase fish market, Kochi Pref., Nov. 1956; HUMZ 40201~40211, 52.0~67.3 mm SL, Manazuru fish market, Kanagawa Pref., July 1969; HUMZ 40212, 66.9 mm SL, Sagami Bay, Odawara fish market, Kanagawa Pref., Oct. 2, 1972;

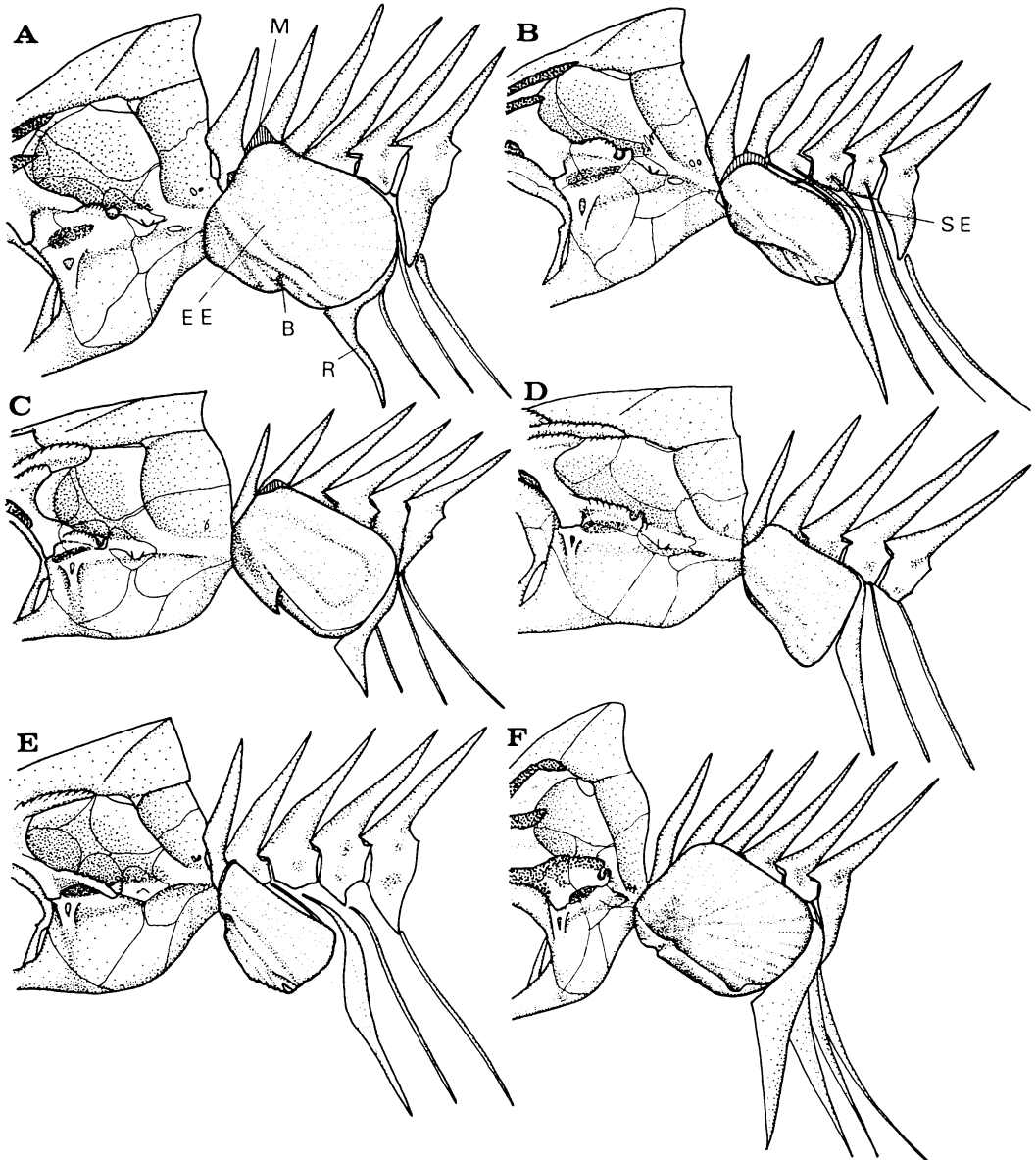


Fig. 1. Lateral view of posterior part of cranium, expanded epipleural, second epipleural, and ribs. A, *Paratrachichthys trilli*, FAKU 47747, male; B, same species, FAKU 47748, female; C, *P. prothemius*, HUMZ 40210, male; D, same species, HUMZ 40211, female; E, *Optivus elongatus*, HUMZ 40217; F, *Trachichthys australis*, HUMZ 40221. B, groove for Baudelot's ligament; EE, expanded epipleural; M, membrane between the expanded epipleural and neural spines; R, modified rib; SE, second epipleural.

HUMZ 45166, 115.3 mm SL, Suruga Bay, off Kawazu Town, Shizuoka Pref., May 1970. HUMZ 40210, 50.8 mm SL and HUMZ 40211, 61.9 mm SL were dissected. *O. elongatus*; 6 specimens from Australia; HUMZ 40213~40217, 70.1~78.2 mm SL, Port Green, Watson's

Bay, Sydney, Sep. 23, 1972; HUMZ 51112, 37.0 mm SL, Port Jackson, Cronulla, Sydney, Feb. 2, 1970. HUMZ 40213, 77.1 mm SL and HUMZ 40217, 76.1 mm SL were dissected. *T. australis*; 4 specimens from Australia; HUMZ 40220~40222, 105.5~118.7

mm SL, HUMZ 40223, 26.3 mm SL, Jervis Bay, New South Wales, Aug. 28, 1972. HUMZ 40221, 111.0 mm SL were dissected. *H. mediterraneus*; 1 specimen from Japan was dissected; HUMZ 49791, 136.4 mm SL, Mimase fish market, Oct. 12, 1972. *G. japonicus*; 2 specimens from Japan; HUMZ 47699, 49793, 148.8~160.5 mm SL, Sagami Bay, Odawara fish market, May 23, 1972. Both were dissected.

All specimens were radiographed to confirm the shape and size of the epipleurals and ribs. The bones, muscle, and nerves were dissected under a low power binocular microscope. Bones were stained by alizarine red S. Sex was determined by the observation of gonads. Measurements and counts of external characters were performed to inquire into the sexual dimorphism. In this study, epipleural is designated for the bone extending along the horizontal septum and rib is for the bone along the peritoneum. The nomenclature of muscles follows Winterbottom (1974).

Description

The epipleurals, Baudelot's ligament, ribs, muscle for the first epipleural, swim bladder, and occipito-spinal nerve in *P. trailli*, *P. prosthemi*, *O. elongatus*, and *T. australis* are specialized.

The first epipleural, expanded into a large plate, attaches to the lateral face of the

neural spine base of the first centrum by a ball-and-socket like articulation. It, also, is connected to the lateral face of the first and second neural spine bases by a stout membrane. Furthermore its posterior limb is connected to the modified first rib by a stout membrane which extends to the medial face of the upper part of the cleithrum. The shape and size of the expanded epipleural vary according to species and also to sex in the two species of *Paratrachichthys*. In male *P. trailli*, this bone is a square, thick plate with a triangular anterior flange. A ridge runs along the anteroventral edge of this bone (Fig. 1, A). In female, this bone is a rather thin, oval plate. A low ridge runs parallel to its anteroventral area (Fig. 1, B). In male *P. prosthemi*, the first epipleural is a very large, rectangular plate with a crescentic anteroventral flange. The posterodorsal, posteroventral, and anteroventral edges of this bone are lightly raised (Fig. 1, C, Fig. 2). In female, this bone is a rather trapezoid, thin plate with a low ridge along its anteroventral edge (Fig. 1, D, Fig. 2). In *O. elongatus* and *T. australis*, there is no difference of the first epipleural between the sexes. In the former, this bone is a thin, almost triangular convex plate (Fig. 1, E). In the latter, this bone is an almost square, very thick plate. Its anteroventral edge is highly raised as an acute ridge, so its cross section is L-shaped (Fig. 1, F).

Baudelot's ligament is associated with the expanded epipleural. There is a notch or groove for attachment of this ligament on the anteroventral limb of this bone. In the males of the two species of *Paratrachichthys*, this ligament adheres tightly to this bone, whereas in the females of the two species of *Paratrachichthys* and the other two species, it merely touches this bone.

The second epipleural is present only in female specimens of *P. trailli* and in *O. elongatus* (Fig. 1, B, E). In both species, this bone is a slender, string-like rod. Its proximal tip attaches to the posterolateral base of the second neural spine in the former, but is free from it in the latter. This bone is supported by the stout membrane between the expanded epipleural and first rib.

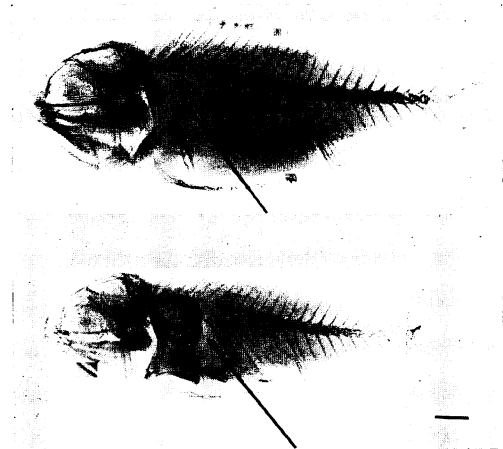


Fig. 2. Radiograph of *P. prosthemi*. Arrows indicate the expanded epipleural. Female (upper, HUMZ 40208) and male (lower, HUMZ 40209). Scale indicates 5 mm.

The first rib is modified into an approximate Z-shaped bone, extending along the posterior margin of the expanded epipleural (Fig. 1). The proximal tip of this bone tapers into a fine rod and is free from the third centrum in most cases. This bone increases its width centrally and then lessens distally. This widened first rib is intimately associated with the expanded epipleural, and connected to it by a stout membrane.

The second to fourth ribs are slightly modified. Their shapes vary according to species, and to sex in *Paratrachichthys* (Fig. 1).

The special muscle, which serves the expanded epipleural, is named here as levator epipleuralis. This muscle originates from the posterior base of the posttemporal fossa and lateral face of the posteroventral part of the occipital crest. It attaches mainly to the pterotic and exoccipital anteriorly and exclusively to the lateral face of the expanded epipleural posteriorly. But when this muscle is large, it extends far forward to the epiotic and parietal. The developmental degree of this muscle varies according to species and sex. In males of two species of *Paratrachichthys* and in *T. australis* it is large, whereas in females of two species of *Paratrachichthys* and in *O. elongatus* it is small. This muscle consists of four myomeres (Fig. 3). The first myomere occupies the posttemporal fossa. The second, just below the posttemporal,

follows the first. The third consists of two parts, the outer part follows the second and the inner part extends from the lateral face of the lower part of the occipital crest, and attaches to the anteroventral part of the expanded epipleural in most cases. But in the males of the two species of *Paratrachichthys*, it attaches to the anterior flange of this bone. The fourth myomere occupies the lateral surface of this bone.

The swim bladder is physoclistous. The tunica are thin membrane. The anterior part of the swim bladder extends laterally to attach to the medial face of the expanded epipleural. But there is no connection between the skull and swim bladder.

The occipito-spinal nerve is divided into dorsal, horizontal, and ventral branches. The three pairs of the horizontal branch innervate the levator epipleuralis. The first branch runs into the second myomere of this muscle, the second into the third one, and the third into the fourth one, respectively. The size and position of the foramina for the occipito-spinal nerve are almost constant within a species, but vary among species.

Both *H. mediterraneus* and *G. japonicus* have unspecialized above-mentioned structures. (Fig. 4). They have two slender normal epipleurals attaching to the base of the anteriormost two neural spines and extending along the horizontal septum. The first rib attaches to the third centrum.

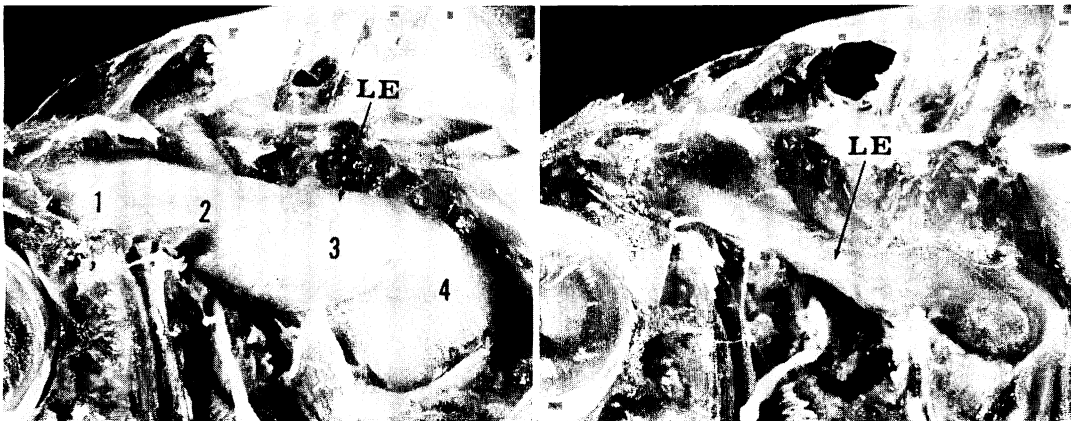


Fig. 3. Photograph of the levator epipleuralis in *P. traillii*. Male (left, FAKU 47747) and female (right, FAKU 47748). LE, levator epipleuralis; pt, posttemporal fossa; the number shows the order counted from the first myomere.

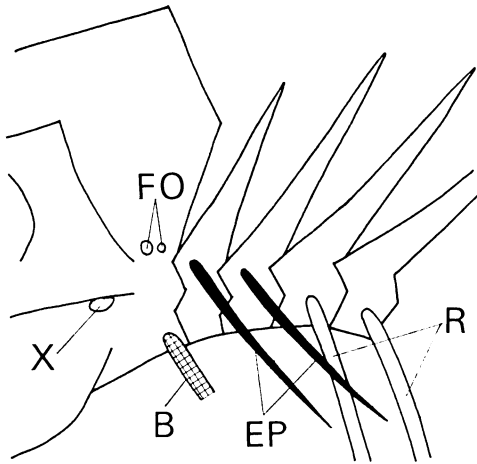


Fig. 4. Diagrammatic illustration to show the posterior part of cranium and anterior-most portion of axial skeleton found in *H. mediterraneus* and *G. japonicus*. B, Baudelot's ligament; EP, epipleurals; FO, foramina for occipito-spinal nerve; R, ribs; X, formamen for vagus nerve.

There is no special musculature serving the epipleural. The anterior end of the epaxialis inserts into the supratemporal and posttemporal fossae. There are four myomeres before the first epipleural. The anteriormost tip of the lateralis superficialis ends at the medial face of the pectoral girdle.

The occipito-spinal nerve has eight branches; three dorsal, three horizontal, and two ventral as seen in the other four species examined. The horizontal three branches extend along the horizontal septum and innervate mainly into the anteriormost part of lateralis superficialis.

The physoclistous swim bladder has no connection with the skull. The tunica are thin membrane as in the other four species examined. Baudelot's ligament attaches to the basioccipital, and has no connection with the epipleural.

Discussion

The expanded bone is called a "rib plate" by Woods and Sonoda (1973). It is difficult to decide whether this bone is derived from the epipleural or rib, since the peritoneum and horizontal septum are confluent with

each other on this bone. The first expanded bone and the second rudimental one if present in the four species attach to the first and second centra similar to the attachment of the two slender epipleurals in *H. mediterraneus* and *G. japonicus*. This similarity indicates that these bones are derived from epipleurals.

In female *P. trailli* and *O. elongatus*, the second epipleural is recognized. They also have comparatively small expanded first epipleurals. This fact shows that the loss or fusion of the second epipleural may be caused by the further expansion of the first epipleural.

The levator epipleuralis named here is a peculiar muscle associated with the expanded epipleural. Concerning the origin of this muscle, two cases, from the epaxialis and from the lateralis superficialis can be hypothesized. The former case is supported by the coincidence of the number of myomeres. This muscle consists of four myomeres, and the fifth myomere lies between the expanded epipleural and the second one. In *Scomber scomber* (Allis, 1903) and *H. mediterraneus* and *G. japonicus* observed by the author, this myomere lies also between the first and second epipleurals. This seems to suggest that the levator epipleuralis is the derivative of the anteriormost portion of the epaxialis. The latter case is supported by the innervation. The horizontal branches of the occipito-spinal nerve in *S. scomber* (Allis, 1903) and *H. mediterraneus* and *G. japonicus* extend along the horizontal septum and innervate into the lateralis superficialis, whereas these branches in the other four species innervate into the levator epipleuralis. This may suggest that this muscle is the derivative of the lateralis superficialis. But the anteriormost tip of the lateralis superficialis ends at the medial face of the pectoral girdle and does not extend further forwards. Moreover, in some fishes such as *Lampanyctus leucopsarus* some horizontal branches of the occipito-spinal nerve innervate into the epaxialis (Ray, 1950). It, therefore, is reasonable to consider that the levator epipleuralis is the derivative of the epaxialis. The innervation into this muscle may be secondarily acquired by the

derivation this muscle from the epaxialis.

The two species of *Paratrachichthys* examined show obvious sexual dimorphism in the shape and size of the expanded epipleural and levator epipleuralis (Fig. 1, A~D, Figs. 2, 3). In the other four species of this genus, *P. argyrophanus* Woods, *P. fernandizianus* Günther, *P. latus* Fowler, and *P. atlanticus* Menezes, sexual dimorphism may be present for these characters, although in the first species sexual dimorphism is not mentioned by Woods and Sonoda (1973). In *P. atlanticus* sexual dimorphism is recognized in the length of head (Menezes, 1971). But no sexual differences are found on any external characters in the two species of this genus examined here.

Two combinations are seen in the relation between Baudelot's ligament and the expanded epipleural. They are tightly adhered in the fishes with a large bone, but they merely touch in the fishes with a small bone. It is indicated that the conditions between both are closely related to the degree of the expansion of the first epipleural.

The series of specializations seen in the levator epipleuralis, expanded epipleural, swim bladder, and the innervation of occipitospinal nerve into this muscle appear to suggest an acoustic function in the four species examined. Among fishes of the order Beryciformes, the present four species are structurally similar to some fishes of the Holocentridae which are known to produce sound. They have a specialized muscle running from the skull to some modified ribs, and the anterior portion of the swim bladder attaches to these ribs. In these holocentrid fishes, such as *Myripristis berndti* (Salmon, 1965; Salmon, 1967), *Holocentrus rufus* and *H. ascensionis* (Moulton, 1958; Winn and Marshall, 1963; Gainer, Kusano, and Mathewson, 1965), the sound is produced by the contraction of the specialized muscle. But in these fishes the tunica of the swim bladder is very thick (Nelson, 1955), whereas in the present four species it is thin. The thin tunica may be ineffective for sound production. However, the Nassau grouper *Epinephelus striatus*, known as a sound producing fish, has a thin-walled air bladder in contract

with specialized muscle by the intercalation of ribs (Moulton, 1958; Hazlett and Winn, 1962). The series of specializations found in the present four species closely resembles the sound producing structures of the Nassau grouper. The "sound-producing muscle" or "sonic muscle" is under the control of the occipital nerve in *H. rufus* (Winn and Marshall; Gainer, Kusano, and Mathewson; *op. cit.*). Such nerve into sound-producing muscle is also found in *Congiopodus* (Packard, 1960) and 18 species of Atlantic sea robins (Evans, 1973). Judging from the evidence of musculature and innervation, it is strongly suggested that a series of specialized structures may be developed as a sound producing mechanism. Also, from the sexual dimorphism of these specialized structures in the two species of *Paratrachichthys*, it is probable that both sexes make different sound. The sound production of the present four species has not been known at this time. The precise function of these specialized structures would be demonstrated on the basis of further study of live fishes.

Woods and Sonoda (1973) reported that *Optivus* is closely related to *Paratrachichthys* based on the presence of the expanded epipleural. The presence of specialized structures in the three genera including the present four species reveals that *Trachichthys* is also closely related to *Optivus* and *Paratrachichthys*. Consequently, these three genera are clearly separable as a distinct phyletic stem in the Trachichthyidae from another stem comprising the two genera *Hoplostethus* and *Gephyroberyx* without such specialized structures.

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Literature cited

- Allis, E. P. 1903. The skull, and the cranial and first spinal muscle and nerves in *Scomber scomber*. J. Morph., 18: 45~328, figs. 1~68.
- Evans, R. R. 1973. The swimbladder and associated structures in western Atlantic sea robins (Triglidae). Copeia, 1973 (2): 315~321, figs. 1~3.
- Gainer, H., K. Kusano, and R. F. Mathewson. 1965. Electrophysiological and mechanical properties of squirrelfish sound-producing muscle. Comp. Biochem. Physiol., 14: 661~671, figs. 1~7.
- Hazlett, B. and H. E. Winn. 1962. Sound producing mechanism of the Nassau grouper, *Epinephalus striatus*. Copeia, 1962 (2): 447~449, fig. 1.
- Menezes, N. A. 1971. A new species of *Paratrachichthys* from the coast of Brazil (Pisces, Trachichthyidae). Pap. Avul. Zool., S. Paulo, 25(17): 143~148, figs. 1~2.
- Moulton, J. E. 1958. The acoustical behavior of some fishes in the Bimini area. Biol. Bull., 114(3): 357~374, figs. 1~16.
- Nelson, E. M. 1955. The morphology of the swim bladder and auditory bulla in the Holocentridae. Fieldiana Zool., 37: 121~137, pls. 1~3.
- Packard, A. 1960. Electrophysiological observation on a soundproducing fish. Nature, 187 (4371): 63~64, figs. 1~2.
- Ray, D. L. 1950. The peripheral nervous system of *Lampanyctus leucopsarus*. J. Morph., 87 (1): 61~178, figs. 1~40.
- Salmon, M. 1965. Acoustical behavior of the Menpachi, *Myripristis berndti*, in Hawaii. Amer. Zool., 5(4): 714. (Abstr.).
- Salmon, M. 1967. Acoustical behavior of the Menpachi, *Myripristis berndti*, in Hawaii. Pac.

- Sci., 21(3): 364~381, fig. 1.
- Winn, H. E. and J. A. Marshall. 1963. Sound-producing organs of the squirrelfish, *Holocentrus rufus*. Physiol. Zool., 36(1): 34~44, figs. 1~4.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscle of the teleostei. Proc. Acad. Nat. Sci. Philadelphia, 125(12): 225~317, figs. 1~56.
- Woods, L. P. and P. M. Sonoda. 1973. Order Berycomorphi (Beryciformes). In Fishes of the western north Atlantic. Mem. Sears Found. Mar. Res., 1(6): 263~396, figs. 1~66.

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ヒウチダイ科魚類4種での肥大した上肋骨とそれに付属する諸構造の比較形態

清水 長

キンメダイ目ヒウチダイ科魚類 *Trachichthys australis*, *Optivus elongatus*, *Paratrachichthys trailli*, *P. prothemius* (ハリダシエビス) 3属4種の脊椎骨前部側面にみられる板状に肥大した骨, およびそれに関連する特殊化した筋肉, 神経, 鰾の構造を比較, 検討した。さらにこの科の他の2属2種ヒウチダイ (*Hoplostethus mediterraneus*), ハシキンメ (*Gephyroberyx japonicus*) との比較を行った。板状の骨は付着部位からみて, 上肋骨が肥大したものと考えられる。この骨の表面には, 頭蓋骨の後面から発した特別な筋肉が付着する。この筋肉を上肋骨挙筋 (*levator epipleuralis*) と名づけた。この筋肉は4つの筋節からなり, その数から, 上部体側筋より派生したと考えられる。ハリダシエビス属 (*Paratrachichthys*) の2種には, この骨と筋肉に性的二型が認められ, 雄では雌のものより著しく大きい。鰾は壁の薄い無管鰾で, その前部は膨出して, 肥大した上肋骨の内面に付着するが, 頭蓋骨との直接の関連はない。

前記4種での特化した器官の解剖学的特徴は, この目のイトウダイ科や, 他の目の魚類での発音器官として特化したものの特徴と類似する。このことから, これらの器官は, 発音機能と関連して特化したものと考えられる。

この科の他2属ヒウチダイ属, ハシキンメ属には, これらの特化した器官は認められない。したがって, この科内で前記の3属は1つの系統幹をなし, 他の2属は独自の系統幹をなすと考えられる。

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