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# PHYLOGENY OF THE SUPERFAMILY BALISTOIDEA (PISCES : TETRAODONTIFORMES)

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## Contents

## I. Introduction

The Balistoidea is one of seven superfamilies of the order Tetraodontiformes, and includes about 40 genera and 70 species which are divided into two families, the Balistidae and Monacanthidae. They show great variation in their general appearance and are able to adapt themselves to various habitats, such as coral reefs, sandy bottoms, and oceans.

The phylogenetic interrelationships of the balistoids have been studied by many authors, for instance Cuvier (1817), Hollard (1853, 1860), Regan (1903), Rosen (1916), Gregory (1933), Fraser-Brunner (1935, 1941), Smith (1935), Breder and Clark (1947), Matsubara (1955), Tyler (1962a, 1962b, 1970), and Winterbottom (1974). From their studies it has been accepted that the balistoids consist of a natural group, because they share many specialized characters, such as a reduced pelvic complex and a peculiar trigger mechanism in the first dorsal fin. However, these authors, except for Fraser-Brunner (1935, 1941), mainly confined their research to the interrelationships among the balistoid families based on only a few characters which are insufficient for phylogenetic studies. Fraser-Brunner (1935, 1941) was a pioneer to work on the generic interrelationships of the balistoids, but he just briefly mentioned the phylogeny of the genera on the basis of a few characters which gave a key to the families and genera of the balistoids. Unfortunately some important mistakes were made in the study. Thus, all of the previous studies were short to discuss the phylogeny of the balistoids, because they treated only the familial interrelationships or relied on only few characters for the phylogenetic interrelationships among the genera. It is necessary, therefore, to clarify the whole phylogenetic interrelationships of the balistoids based on many anatomical characters.

The purpose of the present study is to reveal the phylogenetic interrelationships of the balistoids, at both the familial and generic levels, by the application of Hennig's (1966) method using many anatomical characters. This method has increasingly been accepted during the last decade by many biologists including the ichthyologists (Brundin, 1968; Nelson, 1969, 1970, 1971, 1972a, 1972b, 1973, 1974; Rosen, 1973; Johnson, 1974; Winterbottom, 1974; Wiley, 1975, 1976, 1977). Of these authors, Rosen (1973), Johnson (1974), Winterbottom (1974), and Wiley (1976, 1977) applied this method to clarify the phylogenetic interrelationships of a particular group of fishes. This method is considered to be most reasonable for studying the phylogeny, because it is logically consistent. There are two alternative methods, the conventional method and the numerical taxonomy. The former is not used here, since it arbitrarily selects the characters for phylogenetic analyses. The latter is not adequate to the research of phylogenetic relationships, because it is concerned with phenetic relationships, and not phylogenetic relationships.

## II. Material and methods

The specimens used for the present study are deposited at the following institutions: Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University (HUMZ); Marine Science Museum, Tokai University (MSM); Department of Zoology, National Science Museum (NSMT-P); Yokosuka City Museum (YCM).

The data of the specimens examined for the anatomical study are shown as follows:

**Balistidae.** *Abalistes stellatus*, three specimens, 200.0~230.2 mm in standard length. HUMZ 13482, 13982, 04°00′N, 105°49′E; HUMZ 45175, South China Sea.

*Balistapus undulatus*, 11 specimens, 41.8~226.0 mm in standard length. HUMZ 40541~40543, 40626, 40632, 40640, 41334, 45169, 46100, 46103, Ishigaki Isl. (24°25′N, 124°10′E), Ryukyu Isls.; HUMZ 46123, Pila Pila Beach, Rabaul.

*Balistes vetula*, one specimen, 83.3 mm in standard length. HUMZ 31234, 07°04.7′N, 53°38.2′W.

*Balistoides conspicillum*, one specimen, 235.0 mm in standard length. HUMZ 45173, Yonagusuku, Okinawa Isl., Ryukyu Isls.

*Canthidermis maculatus*, two specimens, 218.4～251.5 mm in standard length. HUMZ 40572, 40573, Okinawa Isl., Ryukyu Isls.

*Melichthys vidua*, two specimens, 173.2～179.4 mm in standard length. HUMZ 40589, Kita-Daito Isl., Ryukyu Isls.; HUMZ 45174, Ishigaki Isl., Ryukyu Isls.

*Odonus niger*, four specimens, 163.3～191.6 mm in standard length. HUMZ 40574, 40575, 45177, Okinawa Isl., Ryukyu Isls.; HUMZ 46137, Ishigaki Isl., Ryukyu Isls.

*Pseudobalistes flavimarginatus*, two specimens, 171.6～180.8 mm in standard length. HUMZ 41325, 45170, Ishigaki Isl., Ryukyu Isls.

*P. fuscus*, one specimen, 179.0 mm in standard length. HUMZ 46129, Ishigaki Isl., Ryukyu Isls.

*Rhinecanthus aculeatus*, six specimens, 46.0～187.5 mm in standard length. HUMZ 40568, 41317, 45171, Itoman, Okinawa Isl., Ryukyu Isls.; HUMZ 41386, 41446, Ishigaki Isl., Ryukyu Isls.; MSM 70–308, Okinawa Isl., Ryukyu Isls.

*R. echarpe*, one specimen, 165.0 mm in standard length. HUMZ 41310, Itoman, Okinawa Isl., Ryukyu Isls.

*Sufflamen bursa*, one specimen, 201.0 mm in standard length. HUMZ 49779, Chichi-jima, Ogasawara Isls.

*S. chrysopterus*, two specimens, 112.9～137.0 mm in standard length. HUMZ 45172, Chinen, Okinawa Isl., Ryukyu Isls.; HUMZ 46133, Ishigaki Isl., Ryukyu Isls.

*S. fraenatus*, three specimens, 182.1～188.1 mm in standard length. HUMZ 38729, Ishigaki Isl., Ryukyu Isls.; HUMZ 40548, Itoman, Okinawa Isl.; HUMZ 45176, Yonagusuku, Okinawa Isl., Ryukyu Isls.

*Xanthichthys mento*, two specimens, 204.8～207.2 mm in standard length. HUMZ 42303, Tori-shima, Izu Isls.; HUMZ 48933, Sagami Bay.

**Monacanthidae**. *Acreichthys hajam*, one specimen, 66.8 mm in standard length. HUMZ 35533, Minamihara, Katsuren Peninsula, Okinawa Isl., Ryukyu Isls.

*Alutera monoceros*, five specimens, 107.3～155.2 mm in standard length. HUMZ 37833, 38353, 03°06.6′N, 109°43.8′E; HUMZ 37885, off western North Borneo; HUMZ 38062, 02°36′N, 109°53′E; HUMZ 50039, 03°35′N, 190°03′E.

*A. schoepfii*, two specimens, 118.3～226.2 mm in standard length. HUMZ 31021, 07°10.0′N, 56°36.3′W; HUMZ 69408, 32°06.5′N, 79°17.8′W.

*A. scripta*, four specimens, 59.0～295.8 mm in standard length. HUMZ 41327, Ishigaki Isl., Ryukyu Isls.; HUMZ 48988, 49037, Sagami Bay; MSM 73–554, Shizuoka Prefecture.

*A. heudelotii*, one specimen, 83.4 mm in standard length. HUMZ 69409, 33° 20.0′N, 79°10.0′W.

*Amanses scopas*, one specimen, 149.3 mm in standard length. HUMZ 40792, Goto Isls., Nagasaki Prefecture.

*Anacanthus barbatus*, two specimens, 157.1～206.4 mm in standard length. HUMZ 50356, 02°21.4′N, 110°09′E; HUMZ 50357, 03°06.8′N, 109°51.7′E.

*Arotrolepis filicaudus*, two specimens, 77.7～81.6 mm in standard length. HUMZ 51355, Queensland, Australia; HUMZ 51356, 12°37′S, 140°57′E.

*Brachaluteres ulvarum*, two specimens, 38.7～40.4 mm in standard length. YCM 2258, 3273, Tenjin-jima, Miura Peninsula, Kanagawa Prefecture.

*Cantherhines dumerili*, one specimen, 175.5 mm in standard length. HUMZ 50363, Ishigaki Isl., Ryukyu Isls.

*Chaetoderma penicilligera*, two specimens, 131.6～168.1 mm in standard length. HUMZ 50362, Singapore; HUMZ 50375, off western North Borneo.

*Eubalichthys mosaicus*, two specimens, 71.1～228.2 mm in standard length. HUMZ 21089, 34°00′S, 125°00′E; HUMZ 51249, Albany, Western Australia.

*Meuschenia freycineti*, one specimen, 58.2 mm in standard length. HUMZ 51247, Garden Isl., off Perth, Western Australia.

*M. hippocrepis*, one specimen, 69.9 mm in standard length. HUMZ 51250, Rotlnest Isl., off Perth, Western Australia.

*M. trachylepis*, one specimen, 114.0 mm in standard length. HUMZ 51357, Minnie Waters, New South Wales, Australia.

*Monacanthus chinensis*, one specimen, 64.8 mm in standard length. HUMZ 52841, Singapore.

*Navodon modestus*, five specimens, 57.0～220.2 mm in standard length. HUMZ 48444, Miho, Shizuoka Prefecture; HUMZ 49445, 64844, Kochi Prefecture; HUMZ 52577, Sado Isl., Niigata Prefecture; HUMZ 53991, off Usujiri, Hokkaido.

*N. tessellatus*, one specimen, 171.3 mm in standard length. HUMZ 50377, Kochi Prefecture.

*Nelusetta ayraudi*, one specimen, 362.1 mm in standard length. HUMZ 21072, 34°20′S, 120°19′E.

*Oxymonacanthus longirostris*, two specimens, 64.7～65.0 mm in standard length. HUMZ 41481, Itoman, Okinawa Isl., Ryukyu Isls.; HUMZ 50365, Ishigaki Isl., Ryukyu Isls.

*Paraluteres prionurus*, two specimens, 56.2～74.9 mm in standard length. HUMZ 41471, Kuro-shima, Ryukyu Isls.; NSMT-P 17686, Kabira, Ishigaki Isl., Ryukyu Isls.

*Paramonacanthus japonicus*, seven specimens, 68.4～98.7 mm in standard length. HUMZ 40667, 50379, Kochi Prefecture; HUMZ 45143, Oita Prefecture; HUMZ 51251, 51252, Exmouth Gulf, Western Australia; HUMZ 52410, 52842, no data available.

*Pervagor melanocephalus*, two specimens, 69.6～79.0 mm in standard length. HUMZ 51246, North West Cape, Western Australia; MSM 72–902, Itoman, Okinawa Isl., Ryukyu Isls.

*Pseudalutarius nasicornis*, four specimens, 124.3～150.2 mm in standard length. HUMZ 38066, off western North Borneo; HUMZ 38074, 03°06.6′N, 109° 43.8′E; HUMZ 40667, Kochi Prefecture; HUMZ 64846, 03°07.8′N, 110°45.4′E.

*Pseudomonacanthus peroni*, two specimens, 83.7～150.7 mm in standard length. HUMZ 6535, Indian Ocean; HUMZ 51248, Gulf of Carpentalia, Northern Australia.

*Rudarius ercodes*, 11 specimens, 34.0～59.2 mm in standard length. HUMZ 35899, 50583, 50584, Kochi Prefecture; HUMZ 45130, 45131, 45135, 45137, 45138, 45141, Oita Prefecture; HUMZ 48452, 48613, Miho Shizuoka Prefecture.

*Scobinichthys granulatus*, one specimen, 207.8 mm in standard length. HUMZ 21148, 32°30′S, 126°30′E.

*Stephanolepis cirrhifer*, 14 specimens, 34.7～177.5 mm in standard length. HUMZ 3580, 3581, Hagi, Yamaguchi Prefecture; HUMZ 35433, no data available; HUMZ 41205, 41207, 41208, 41211, 41214, Kanagawa Prefecture; HUMZ 49030, Sagami Bay; HUMZ 50385, 73040, Kochi Prefecture; HUMZ 51950, 52627, Sado Isl., Niigata Prefecture; HUMZ 53341, Tokyo Bay.

The primary method of anatomical study used here is clearing and alizarin Red-S staining. After the bones had been stained the flesh was removed from the specimens. Then, the bones were divided into their parts so as to easily observe them. The drawings of the relatively large bones were prepared by photograph. The negatives were projected in order to make the outline drawings. Details of the bones were examined through a binocular microscope to correct the drawings. The drawings of the small bones were made with a Wild M-8. The osteological nomenclature used here follows Tyler (1962a, 1970).

The phylogenetic consideration in the present study is based on the following method. (1) The character state of each anatomical feature is evaluated by the general evolutional trends of the tetraodontiforms and teleosts. (2) The shared advanced character conditions (synapomorphy) are used to analyze the phylogenetic interrelationships of the balistoids. (3) When the phylogenetic interrelationships of some balistoids can not be clarified by just the shared advanced character conditions, the law of parsimony is applied to them. The law of parsimony used here is derived from the papers of Nelson (1970) and Sneath and Sokal (1973), and is defined as follows: (i) minimum parallel evolution; (ii) minimum reversal of evolutional trends; and (iii) minimum evolutional steps.

## III. Acknowledgments

I express my sincere thanks to Dr. Takao Igarashi, Professor of Hokkaido University, for his guidance in the course of the present study and critical readings of the manuscript. My special thanks go to Dr. Kunio Amaoka, Associate Professor of the same university, who gave me valuable advice and spent many hours in discussing the problems of fish phylogeny and for a critical reading of the manuscript. My thanks also go to Dr. Keikichi Hamada, Professor of the same university, who crtically read the manuscript. I wish to express my thanks to Dr. Kazuhiro Nakaya and the graduate students of our laboratory for discussing fish phylogeny and giving valuable advice.

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Laboratory; Dr. Tamotsu Iwai and Messrs. Izumi Nakamura and Shuichi Tani of Kyoto University; Mr. Tsutomu Kobata of Sagami Branch Station, Kanagawa Prefectural Fisheries Experiment Station; Dr. Osamu Okamura of Kochi University; Dr. John R. Paxton of Australian Museum; Dr. Tetsuo Sato and Mr. Hiroshi Hatanaka of Far Seas Fisheries Research Laboratory; Mr. Takeshi Shimizu of Hokkaido University; Messrs. Katsumi Suzuki and Hirokazu Kishimoto of Marine Science Museum, Tokai University; Dr. Yoshiaki Tominaga of the Department of Zoology, University Museum, University of Tokyo; Dr. Teruya Uyeno and Mr. Eiichi Fujii of Nippon Luther Shingaku Daigaku; Mr. Takeshi Yamakawa of Kochi Senior High School; Dr. Fujio Yasuda and Mr. Akira Zama of Tokyo University of Fisheries; and Mr. Tetsuo Yoshino of Ryukyu University.

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## IV. Comparative anatomy

### 1. Pelvic complex

**Description.** The pelvic complex is composed of three major units, the pelvis, the incasing scales, and the rudimentary fin ray element, in many species of the superfamily Balistoidea.

The pelvis is a single shaft-like bone which articulates anteriorly by connective tissue between the cleithra of the pectoral girdles (Fig. 1). There is a concavity for muscle attachment on the antero-lateral surface of the pelvis.

The most generalized structure of the posterior part of the pelvic complex in the balistoids is shown in the diagrammatic illustration (Fig. 2). The dorsal lobe is present on the postero-dorsal portion of the pelvis to which the skin of the distensible abdomen attaches by connective tissue. Just behind the dorsal lobe the posterior end of the pelvis forms a slightly tapering projection which is enclosed by the thickened incasing scales.

The incasing scales are composed of modified and thickened scales, varying in number among the families and genera, and held to one another by connective tissue. They also enclose the rudimentary fin ray element, the cartilage plug, and the dorsal and ventral tendons.

The rudimentary fin ray element is a partially ossified rod which attaches through the cartilage plug to the posterior end of the pelvis by the dorsal and ventral tendons. It is movable in the dorso-ventral plane by the function of both tendons.

The dorsal tendon runs forward in the longitudinal tube passing through the dorsal lobe and opening anteriorly into the dorsal concavity on the pelvis, and attaches to the elevator muscles of the pelvis. The ventral tendon runs also

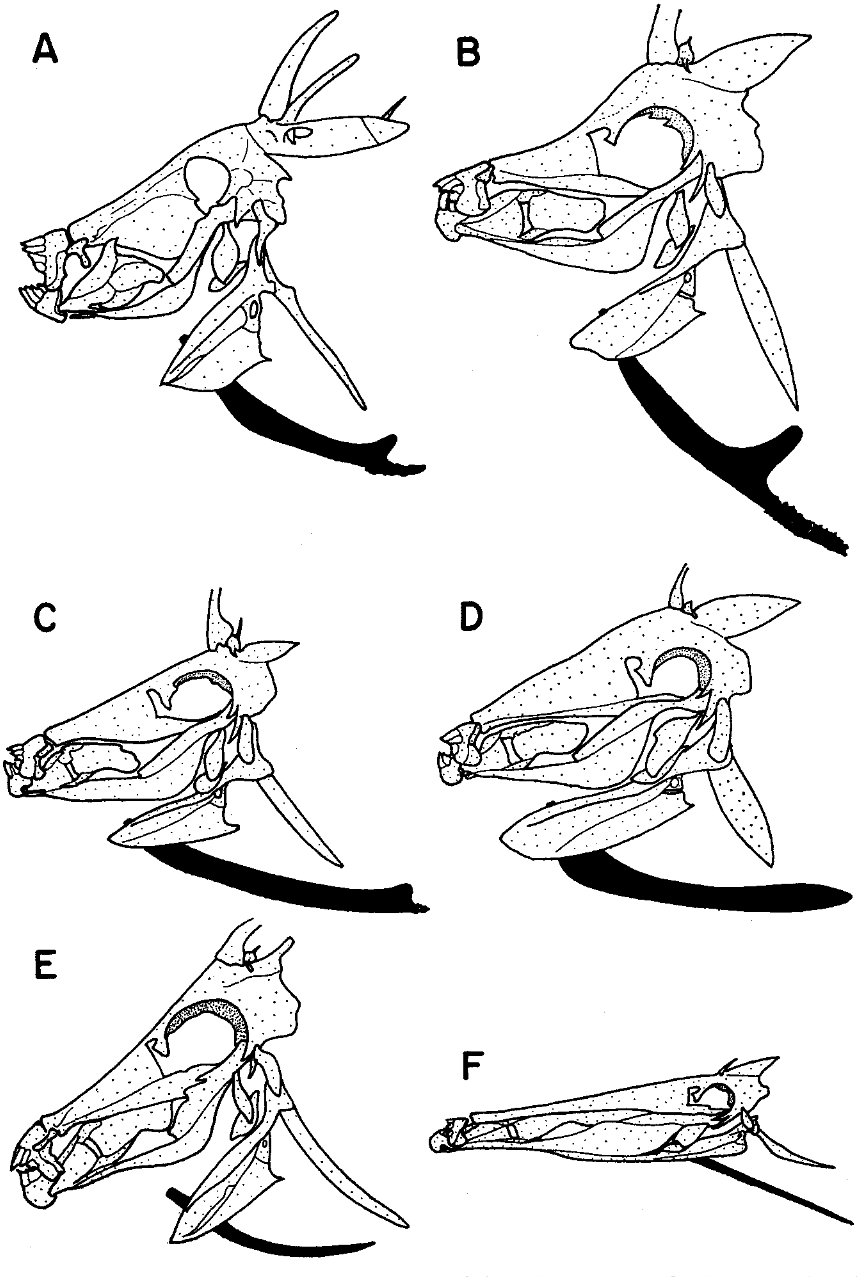

Fig. 1. Diagram showing the position of the pelvis and incasing scales in six species of the Balistoidea. A, *Balistapus undulatus*; B, *Monacanthus chinensis*; C, *Navodon modestus*; D, *Alutera monoceros*; E, *Paraluteres prionurus*; F, *Anacanthus barbatus*.

forward through the ventral depression of the pelvis which contains the depressor muscles of the rudimentary fin ray element.

The cartilage plug is rounded in shape and is embraced posteriorly by the rudimentary fin ray element. Its anterior surface attaches to the posterior end of the pelvis.

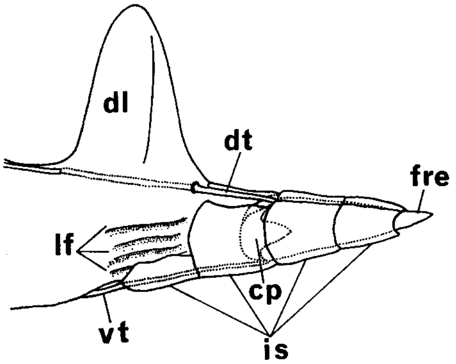

Fig. 2. Diagrammatic illustration showing the posterior portion of the pelvic complex in a member of the primitive balistoids. cp, cartilage plug; dl, dorsal lobe; dt, dorsal tendon; fre, rudimentary fin ray element; is, incasing scales; lf, lateral flanges; vt, ventral tendon.

In the pelvic complex the fishes of the family Balistidae are almost identical, but the members of the Monacanthidae show much variation and an apparent reduction in series. Therefore, the members of the two families are described independently in the following section.

Balistidae. The pelvic complex of the Balistidae consists of the three major units mentioned above accompanying the cartilage plug, the dorsal and ventral tendons, and the lateral flanges (Figs. 3, 5, and 6). Since no significant difference is found in the pelvic complex among the members of the Balistidae, they are included in a single group, Group A.

The pelvis is like a stout shaft in shape and articulates anteriorly between the cleithra by connective tissue. The bone is used for the strut which enlarges the distensible abdominal flap. The posterior part of the pelvis has a dorsal lobe which serves as the place for the strong attachment of the abdominal skin. The lateral flanges to which the first two segments of the incasing scales articulate are present on the postero-lateral part of the pelvis below the dorsal lobe.

The incasing scales are composed of four segments (Figs. 3 and 4). Segment I has a single pair of scales (I left and I Right) relatively immovably articulated to the lateral flanges by connective tissue. Segment II consists of three scales. II Left and II Right enclose the posterior end of the pelvis and the anterior part of the rudimentary fin ray element dorso-laterally and ventro-laterally. The third scale, II Medial, is rather elongated in shape and encloses the mid ventral portion of the segment. Segment III has two pairs of scales. The smaller pair (III Left Ventral and III Right Ventral) is present on the ventral surface of the segment. It is slightly larger than II Medial. The larger pair (III Left Dorsal and III Right Dorsal) encloses the rudimentary fin ray element dorso-laterally. These scales of Segment III are articulated with one another in the mid line of dorsal and ventral surfaces

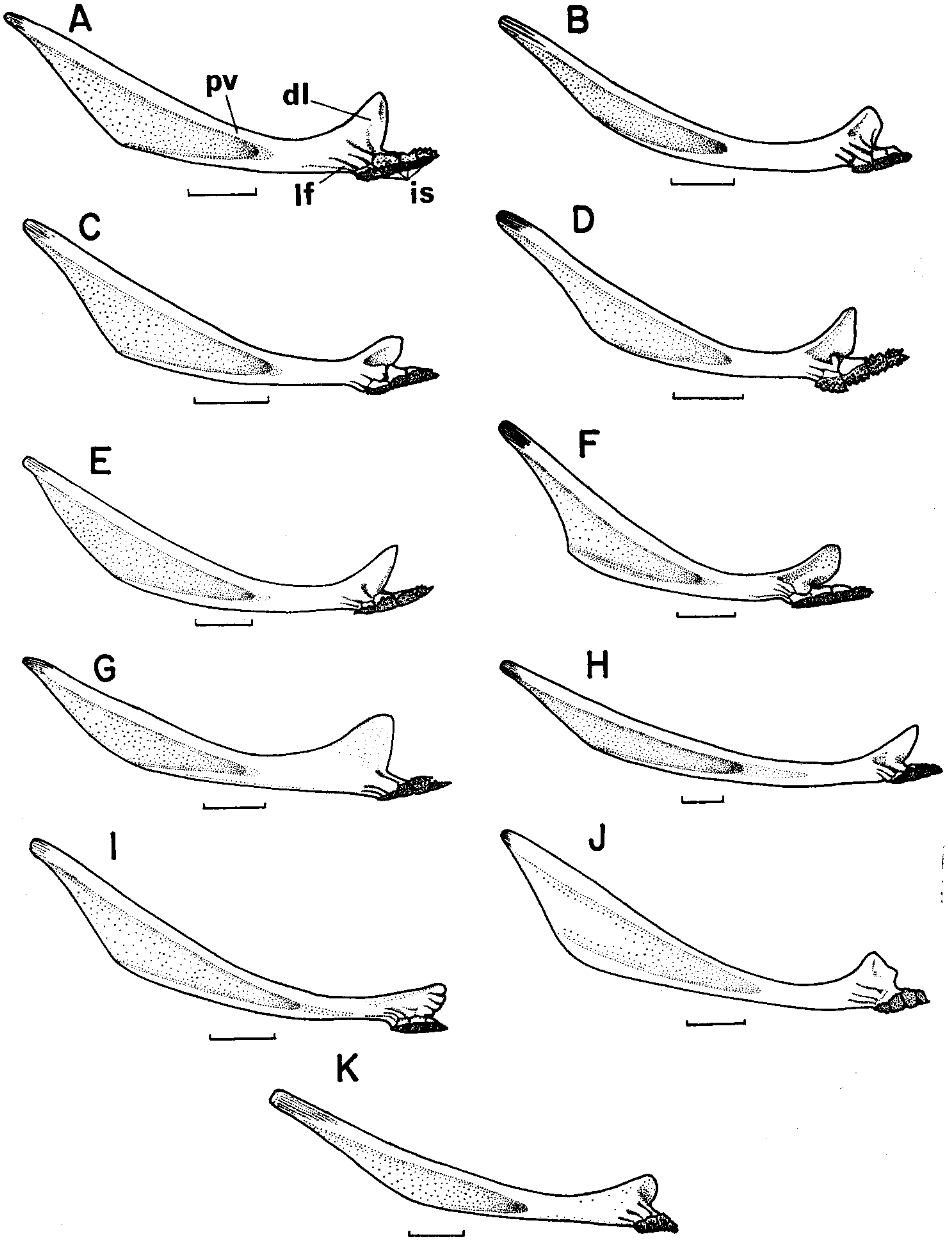

Fig. 3. Diagram showing the pelvis and incasing scales in 11 balistid species. A, *Pseudobalistes flavimarginatus* ; B, *Balistapus undulatus*; C, *Sufflamen fraenatus*; D, *Rhinecantus aculeatus*; E, *Balistes vetula*; F, *Odonus niger*; G, *Abalistes stellatus*; H, *Balistoides conspicillum*; I, *Melichthys vidua*; J, *Xanthichthys mento*; K, *Canthidermis maculatus*. dl, dorsal lobe; is, incasing scales; lf, lateral flanges; pv, pelvis. Scale bars indicate 10 mm.

to make the sheath for the rudimentary fin ray element. Segment IV is composed of a single pair of scales (IV Left and IV Right) which meet in the mid line on the segment both dorsally and ventrally. However, the mid dorsal portion of these scales does not meet at the posterior end of the segment so as to make the space from which the rudimentary fin ray element projects posteriorly.

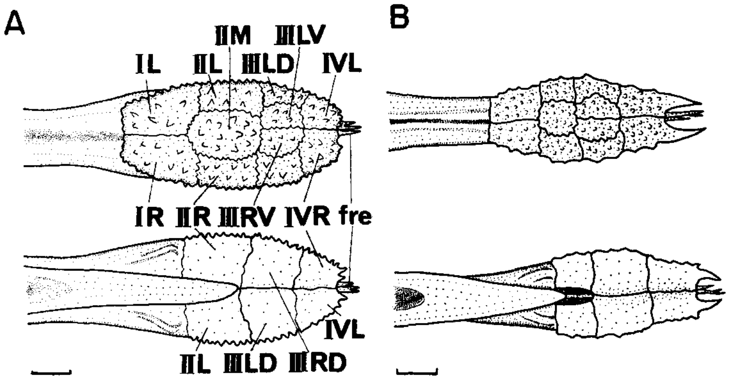

Fig. 4. Diagram showing the posterior end of the pevlis and incasing scales of: A, *Balistapus undulatus*; B, *Abalistes stellatus*. IL, I Left; IR, I Right; IIL, II Left; IIM, II Medial; IIR, II Right; IIILD, III Left Dorsal; IIILV, III Left Ventral; IIIRD, III Right Dorsal; IIIRV, III Right Ventral; IVL, IV Left; IVR, IV Right; fre, rudimentary fin ray element. Top, ventral view; bottom, dorsal view. Scale bars indicate 2 mm.

All the scales making the bony sheath for the rudimentary fin ray element have the spinulose surface ventrally and the smooth one dorsally. The flexibility is mainly present between Segments I and II. Thus, the posterior part of the bony sheath, including Segments II, III, and IV, is movable in the dorso-ventral plane.

All the members of the balistids have the same number and arrangement in the incasing scales, although they show a slight difference in shape among the different genera (Fig. 4).

The rudimentary fin ray element forms the elongated and partially ossified rod. The rod is rather long in the fishes belonging to seven genera, *Pseudobalistes*, *Balistapus*, *Sufflamen*, *Rhinecanthus*, *Balistes*, *Odonus*, and *Abalistes* (Fig. 5), while it is short in the members of four genera, *Balistoides*, *Melichthys*, *Xanthichthys*, and *Canthidermis* (Fig. 6). The dorso-ventral bifurcation of the rudimentary fin ray element has its origin at the anterior portion of the element and extends backward in seven genera, *Balistapus*, *Sufflamen*, *Rhinecanthus*, *Balistes*, *Odonus*, *Melichthys*, and *Canthidermis*, but the element does not bifurcate in the fishes belonging to four genera, *Pseudobalistes*, *Abalistes*, *Balistoides*, and *Xanthichthys*. On the other hand, the shallow medial grooves run on both the dorsal and ventral surfaces of the rudimentary fin ray element. They superificially divide the element into the left and right halves. At the posterior end of the element, it is divided into two or three branches.

There are dorsal and ventral tendons at the anterior portion of the rudimentary fin ray element. Both the tendons attach the element to the posterior end of the pelvis.

The rounded cartilage plug is found between the element and the end of the pelvis, and is embraced posteriorly by the element.

Monacanthidae. An apparent reduction series in the pelvic complex is found in the members of the Monacanthidae which are divided into the following groups and subgroups based on the degree of reduction.

Group B. This group is composed of nine genera, *Acreichthys*, *Amanses*, *Arotrolepis*, *Cantherhines*, *Chaetoderma*, *Monacanthus*, *Paramonacanthus*, *Pervagor*, and *Stephanolepis*. They are mainly characterized by having three segments of the incasing scales.

The pelvis of this group is essentially similar to that of the Balistidae, though the dorsal lobe is longer and thinner (Fig. 7). The lateral flanges are placed below the dorsal lobe.

Segment I of the incasing scales has a single pair of scales (I Left and I Right) immovably articulated to the lateral flanges. These scales meet one another on the mid line in the segment both dorsally and ventrally.

The number of scales in Segment II varies from two to three among the members of this group. In the members belonging to the genera, *Stephanolepis*, *Arotrolepis*, and *Paramonacanthus*, Segment II has two or three scales (Fig. 8, A, B, and C). The larger scales (II Left and II Right) enclose the greater part of the segment. In *Arotrolepis filicaudus* one specimen has a small medial scale (II Medial) but another specimen shows no trace of the scale in Segment II. In four specimens of *Paramonacanthus japonicus* examined here, there are three scales in the segment. II Medial is also found in two of six specimens of *Stephanolepis cirrhifer*, though in the other four specimens there is no vestige of the scale. In the remaining members of the group comprising five genera, *Acreichthys*, *Amanses*, *Cantherhines*, *Chaetoderma*, and *Pervagor*, Segment II has a single pair of scales (II Left and II Right).

Segment III has a single pair of scales (III Left and III Right) in all members of the group. The scales, however, tend to be fused to one another in the members, *Paramonacanthus japonicus*, *Monacanthus chinensis*, and *Pervagor melanocephalus* (Fig. 8, C, D, and E). The articulation between III Left and III Right are recognizable on the dorsal surface but obscure on the ventral one in *Paramonacanthus japonicus* and *Monacanthus chinensis* (Fig. 8, C and D). The scales show a slight trace of the articulation both on the dorsal and ventral surfaces in *Pervagor melanocephalus* (Fig. 8, E). Thus, it appears that the scales tend to become fused to one another to make the bony sheath in the species.

Surfaces of all the scales of the three segments are spinulose ventrally and smooth dorsally. The dorso-ventral movement is possible between Segments II and III in the members of the group excluding the genera, *Amanses* and *Cantherhines*, in which the whole series of the incasing scales is relatively inflexible.

The rudimentary fin ray element is divided into the dorsal and ventral small ossified nubbins in seven genera, *Acreichthys*, *Arotrolepis*, *Chaetoderma*, *Monacanthus*, *Paramonacanthus*, *Pervagor*, and *Stephanolepis* (Fig. 9), however, there is no trace

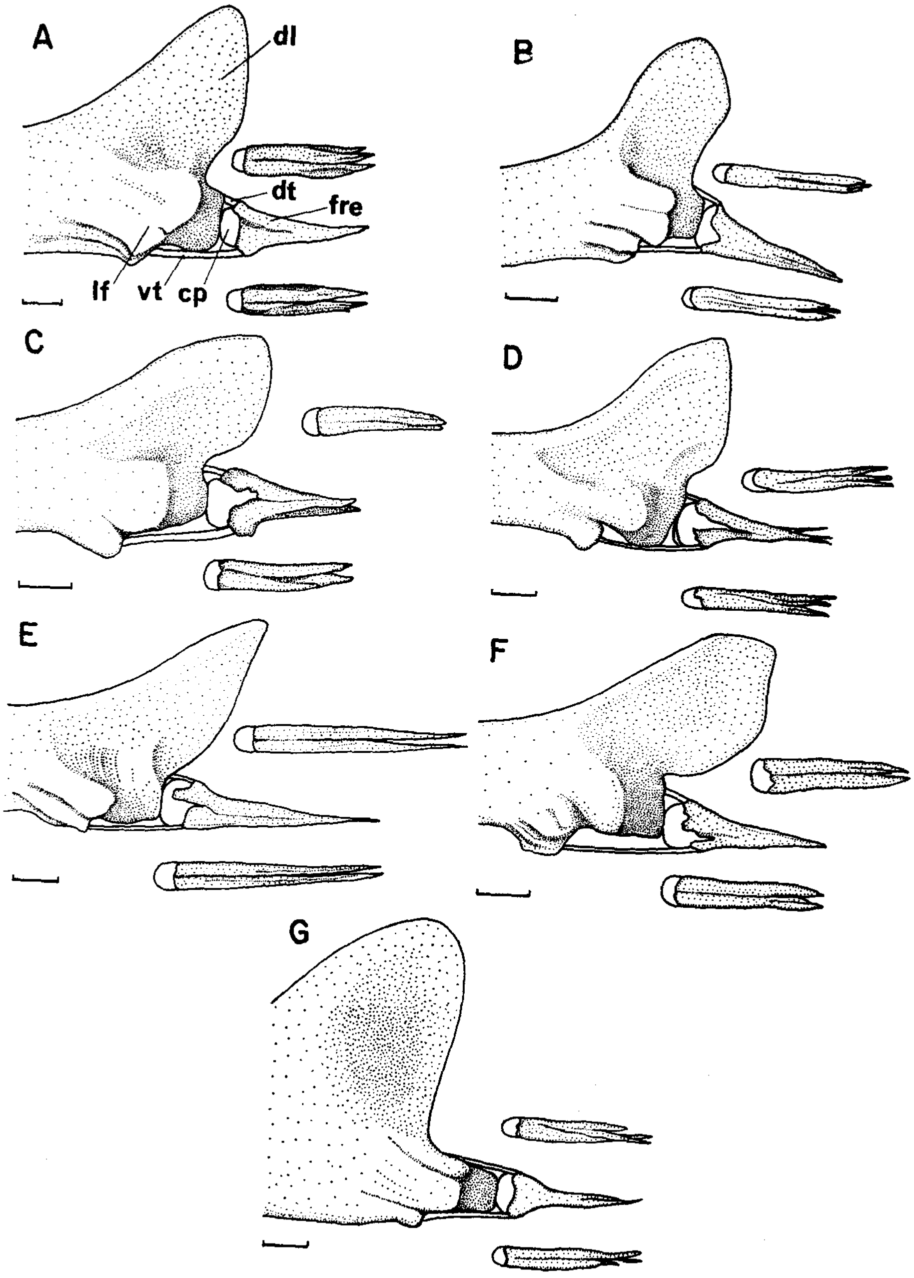

Fig. 5.

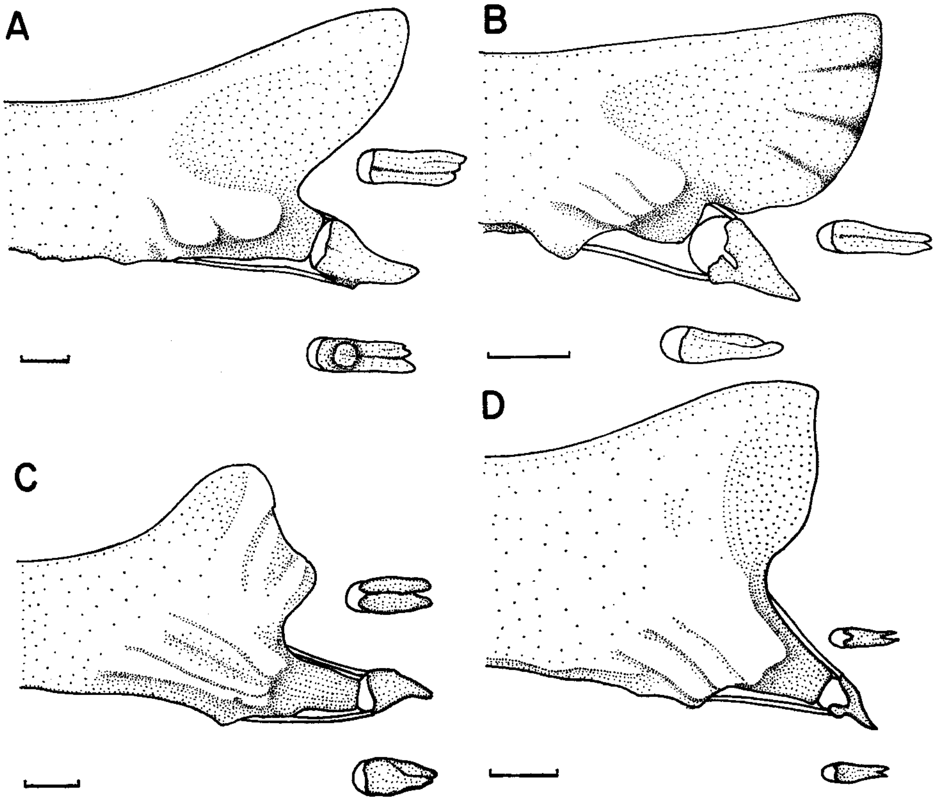

Fig. 6. Diagram showing the posterior end of the pelvis in four balistid species, with incasing scales removed to expose the rudimentary fin ray element and associated structures. A, *Balistoides conspicillum*; B, *Melichthys vidua*; C, *Xanthichthys mento*; D, *Canthidermis maculatus*. Top, dorsal view; middle, lateral view; bottom, ventral view. Scale bars indicate 2 mm.

of the ossified nubbins in the genera, *Cantherhines* and *Amanses* (Fig. 12, A and B). The structure of the element in the two genera are essentially similar to that found in the fishes belonging to Group C.

The nubbins are held to long cartilage plug by connective tissue and attached to the pelvis by the dorsal and ventral tendons. The dorsal tendon passes through the tube in the dorsal lobe and runs forward on the depression of the dorsal surface

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Fig. 5. Diagram showing the posterior end of the pelvis in seven balistid species, with incasing scales removed to expose the rudimentary fin ray element and associated structures. A, *Pseudobalistes flavimarginatus*; B, *Balistapus undulatus*; C, *Sufflamen fraenatus*; D, *Rhinecanthus aculeatus*; E, *Balistes vetula*; F, *Odonus niger*; G, *Abalistes stellatus*. cp, cartilage plug; dl, dorsal lobe; dt, dorsal tendon; fre, rudimentary fin ray element; lf, lateral flanges; vt, ventral tendon. Top, dorsal view; middle, lateral view; bottom, ventral view. Scale bars indicate 2 mm.

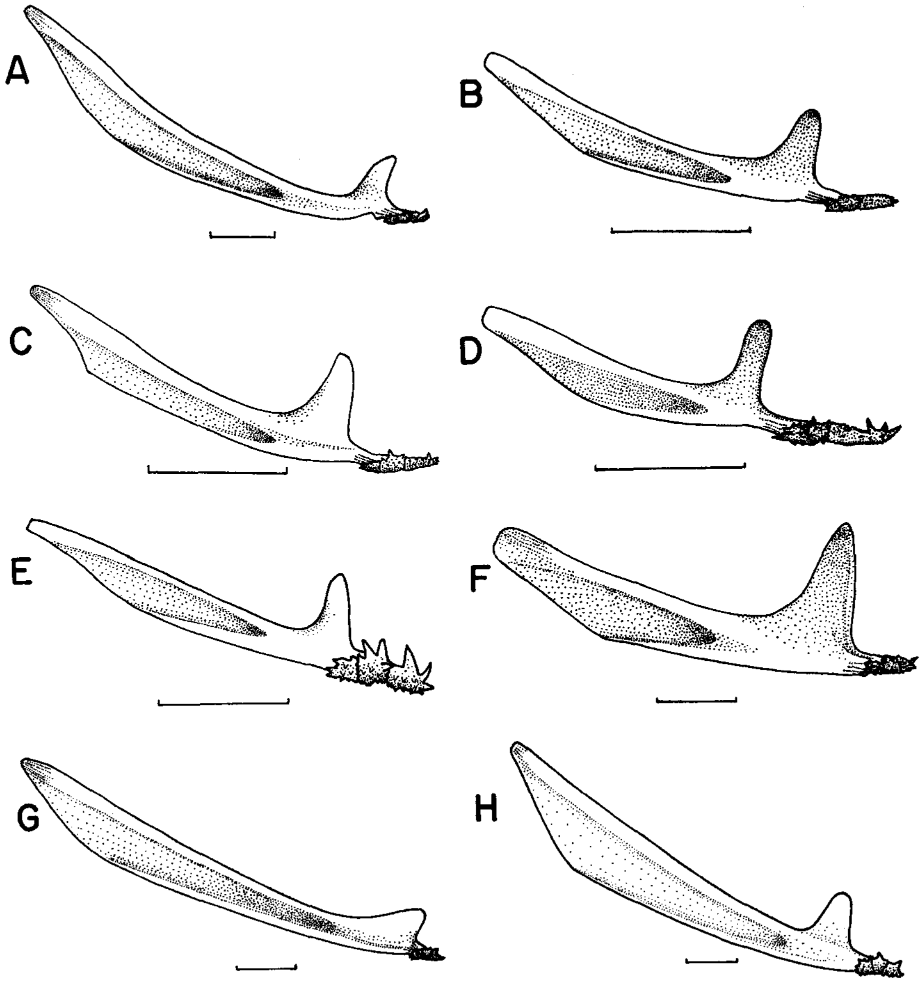

Fig. 7. Diagram showing the pelvis and incasing scales in eight monacanthid species. *A, Stephanolepis cirrhifer*; B, *Arotrolepis filicaudus*; C, *Paramonacanthus japonicus*; D, *Monacanthus chinensis*; E, *Pervagor melanocephalus*; F, *Chaetoderma penicilligera*; G, *Cantherhines dumerili*; H, *Amanses scopas*. Scale bars indicate 10 mm.

of the pevlis. The ventral tendon extends forward on the trough of the ventral surface of the pelvis. Both tendons are attached to their muscles anteriorly. Thus, the rudimentary fin ray element is movable in the dorso-ventral plane. The long cartilage plug is present in all the members of the group. It is attached to the posterior end of the pelvis.

Group B can be subdivided into two subgroups based on the structure of the rudimentary fin ray element as mentioned above. The first subgroup comprises

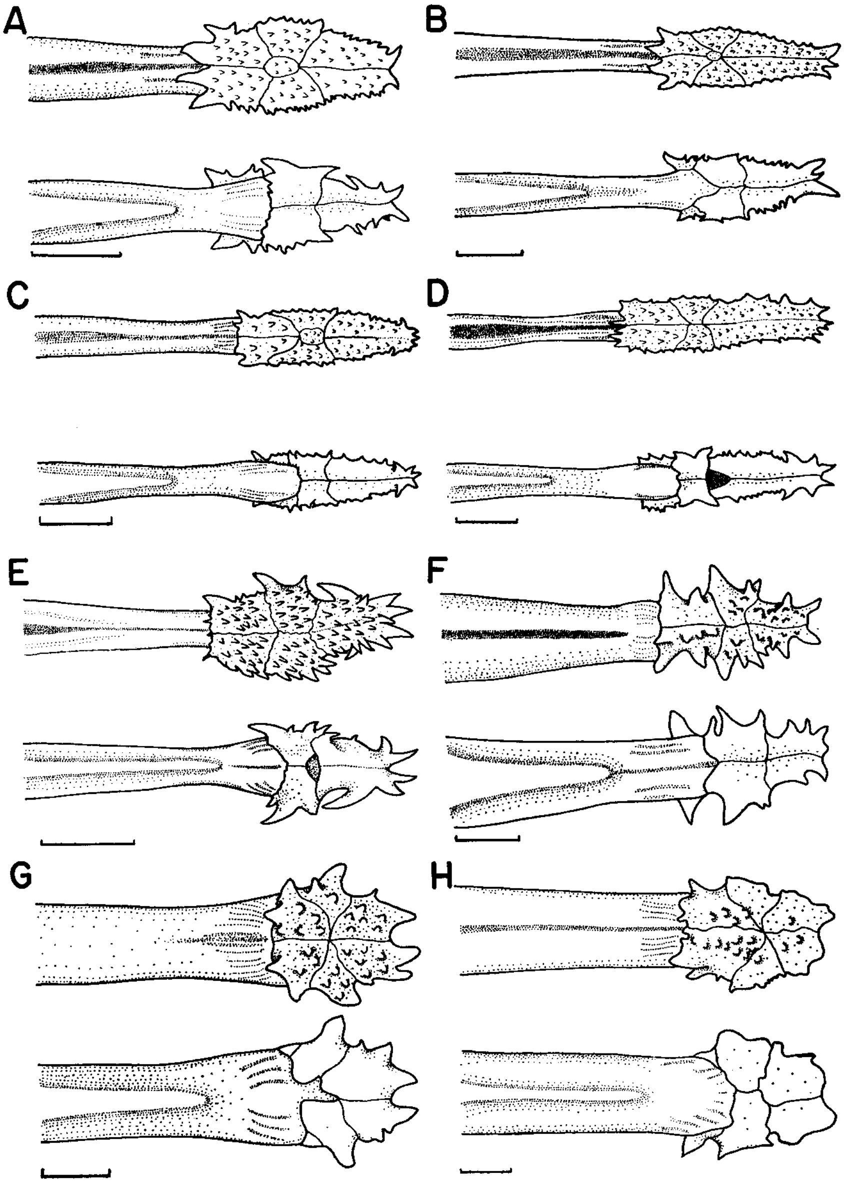

Fig. 8. Diagram showing the posterior end of the pelvis and incasing scales in eight monacanthid species. A, *Stephanolepis cirrhifer*; B, *Arotrolepis filicaudus*; C, *Paramonacanthus japonicus*; D, *Monacanthus chinensis*; E, *Pervagor melanocephalus*; F, *Chaetoderma pencilligera*; G, *Cantherhines dumerili*; H, *Amanses scopas*. Top, ventral view; bottom, dorsal view. Scale bars indicate 2 mm.

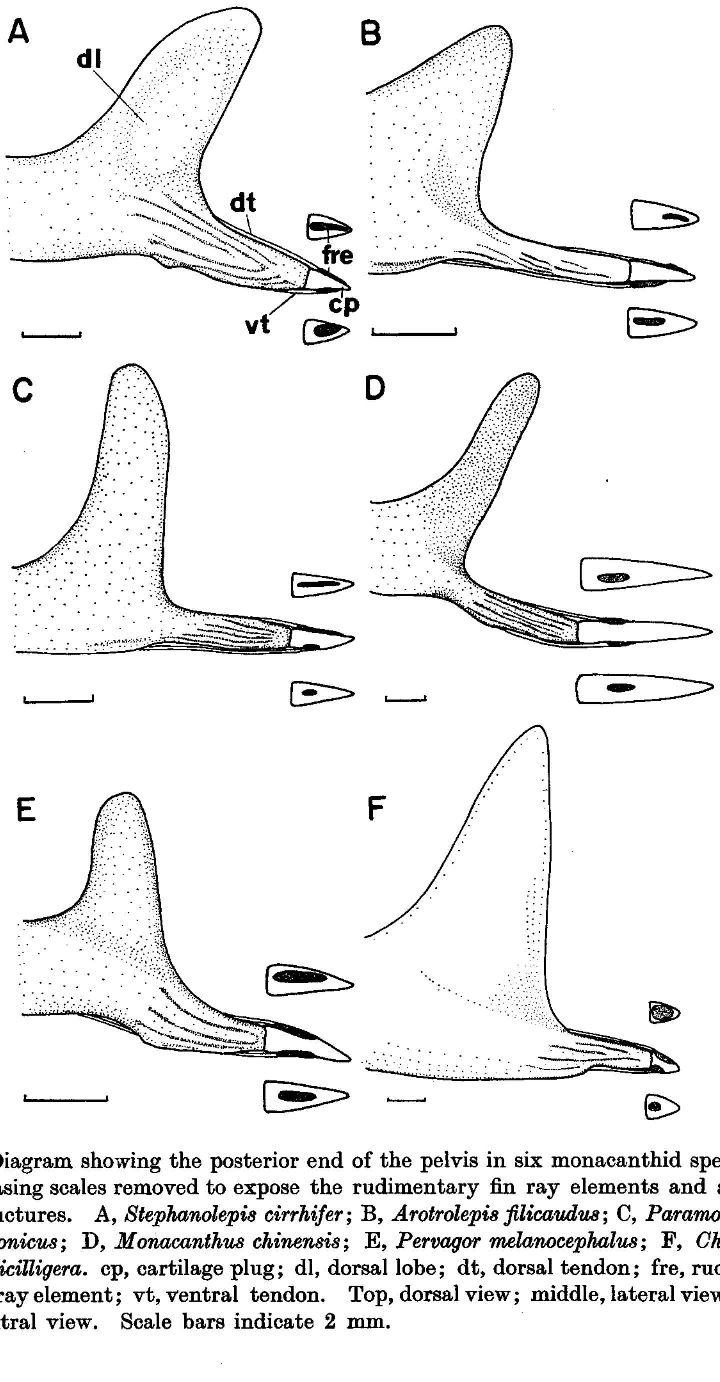

Fig. 9. Diagram showing the posterior end of the pelvis in six monacanthid species, with incasing scales removed to expose the rudimentary fin ray elements and associated structures. A, *Stephanolepis cirrhifer*; B, *Arotrolepis filicaudus*; C, *Paramonacanthus japonicus*; D, *Monacanthus chinensis*; E, *Pervagor melanocephalus*; F, *Chaetoderma penicilligera*. cp, cartilage plug; dl, dorsal lobe; dt, dorsal tendon; fre, rudimentary fin ray element; vt, ventral tendon. Top, dorsal view; middle, lateral view; bottom ventral view. Scale bars indicate 2 mm.

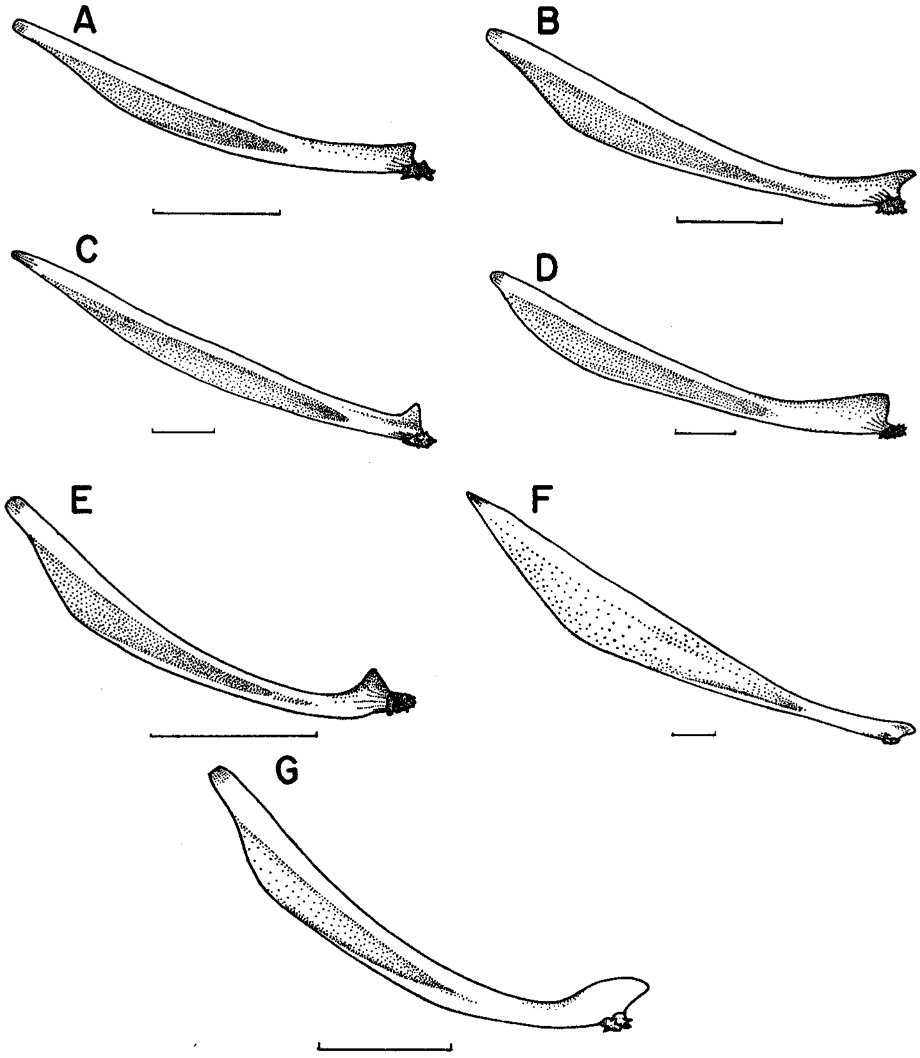

Fig. 10. Diagram showing the pelvis and incasing scales in seven monacanthid species. A, *Pseudomonacanthus peroni*; B, *Meuschenia trachylepis*; C, *Scobinichthys granulatus*; D, *Navodon modestus*; E, *Rudarius ercodes*; F, *Nelusetta ayraudi*; G, *Eubalichthys mosaicus*. Scale bars indicate 10 mm.

seven genera, *Acreichthys*, *Arotrolepis*, *Chaetoderma*, *Monacanthus*, *Paramonacanthus*, *Pervagor*, and *Stephanolepis*. The second subgroup is made of two genera, *Amanses* and *Cantherhines*.

Group C. This group is composed of seven genera, *Eubalichthys*, *Meuschenia*, *Navodon*, *Nelusetta*, *Pseudomonacanthus*, *Rudarius*, and *Scobinichthys*. Their primary common features are found in the number of segments of the incasing scales, namely they have two segments each (Figs. 10 and 11).

The structure of the pelvis shows a slight modification from that found in Group B. The dorsal lobe of this group is shorter than that of Group B.

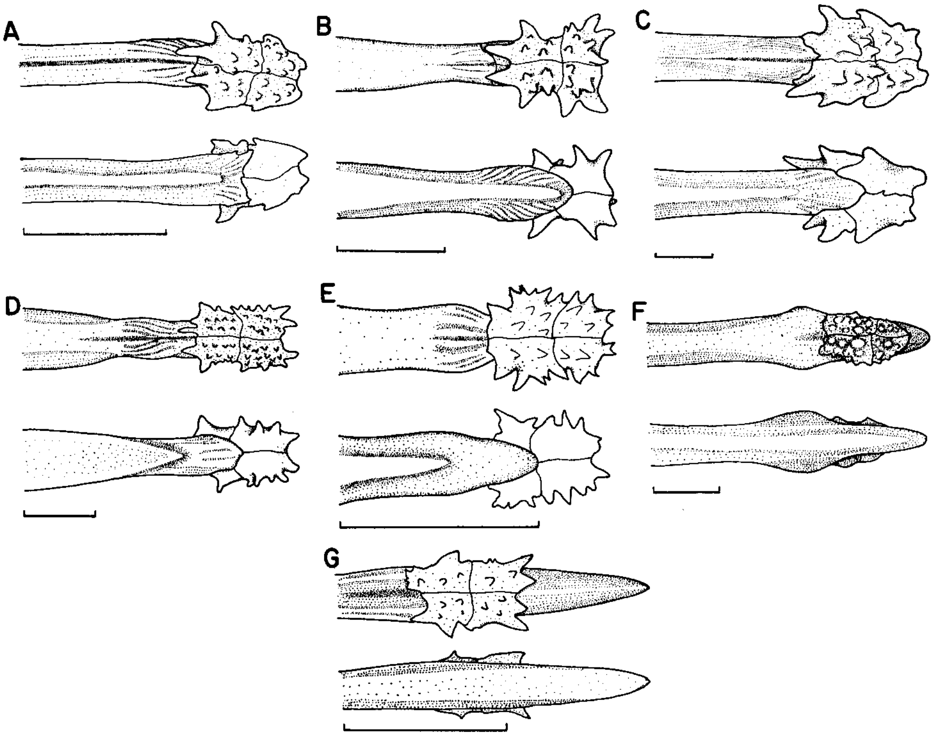

Fig. 11. Diagram showing the posterior end of the pelvis and incasing scales in seven monacanthid species. A, *Pseudomonacanthus peroni*; B. *Meuschenia trachylepis*; C, *Scobinichchys granulatus*; D, *Navodon modestus*; E, *Rudarius ercodes*; F, *Nelusetta ayraudi*; G, *Eubalichthys mosaicus*. Top, ventral view; bottom, dorsal view. Scale bars indicate 2 mm.

Segment I of the incasing scales has a single pair of scales (I Left and I Right). Segment II also has a single pair of scales (II Left and II Right). The incasing scales of both segments are spinulose ventrally and smooth dorsally. The whole series of incasing scales is firmly held together by connective tissue and is almost inflexible.

The rudimentary fin ray element is not found in all the members of the group except for *Pseudomonacanthus peroni* (Fig. 12). One specimen of *Pseudomonacanthus peroni* has a vestigial ossified nubbin on the ventral portion of the short cartilage plug (Fig. 12, C), while another specimen shows no trace of the nubbin on either the dorsal or ventral surface of the cartilage plug. The dorsal ligament* attaches to the posterior porition of the dorsal lobe, and the ventral one ends under the dorsal lobe in the members of Group C. The same condition is also found in the two genera, *Amanses* and *Cantherhines*, of Group B. The most reduced condition of the ligament is found in *Eubalichthys mosaicus* which has feeble ligaments both dorsally and ventrally (Fig. 12, I).

Group D. This group consists of only one genus *Alutera*. The pelvic complex of this group shows a more reduced condition than that found in the previous

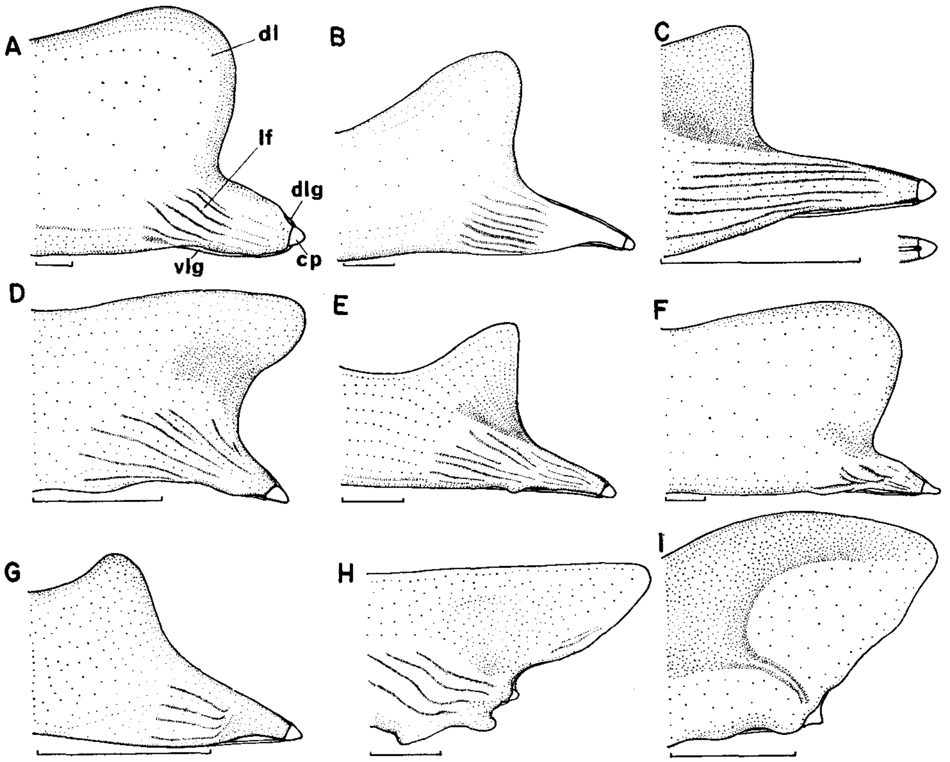

Fig. 12. Diagram showing the posterior end of the pelvis in nine monacanthid species, with incasing scales removed to expose the cartilage plug and associated structures. A, *Cantherhines dumerili*; B, *Amanses scopas*; C, *Pseudomonacanthus peroni*; D, *Meuschenia trachylepis*; E, *Scobinichthys granulatus*; F, *Navodon modestus*; G, *Rudarius ercodes*; H, *Nelusetta ayraudi*; I, *Eubalichthys mosaicus*. cp, cartilage plug; dl, dorsal lobe; dlg, dorsal ligament; lf, lateral flanges; vlg, ventral ligament. Scale bars indicate 2 mm.

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* Since both tendons do not connect with the muscles and must be non-functional, Tyler (1962 b) applied the term "ligament" to such structure. In the present study, the term "ligament" is also adopted to illustrate the structure of the fishes belonging to Group C and the two genera of Group B, *Amanses* and *Cantherhines*.

members (Groups B and C) of the Monacanthidae. The members of this group have no prominent dorsal lobe, nor lateral flanges at the posterior end of the pelvis. Further, there is no trace of the rudimentary fin ray element, nor of the cartilage plug or the ligaments (Fig. 13, A and C). A vestigial incasing scale, however, is found in the postero-ventral surface of the pelvis (Fig. 13, B and D). The scale is immovably attached to the pelvis by connective tissue. In the young it is larger than the other body scales and easily recognizable. Since it is reduced to the small plate-like scale in the adult, it is almost impossible to distinguish the scale from the other body scales surrounding it.

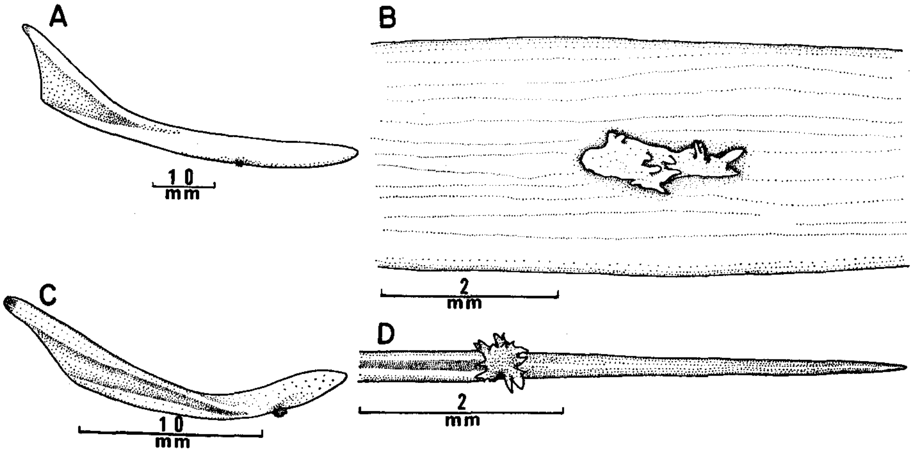


Fig. 13. Diagram showing the pelvis and an incasing scale of the young specimen in *Alutera monoceros* (A, B) and *A. scripta* (C, D). Lateral view, A and C; ventral view, B and D.

Group E. This group includes three genera, *Brachaluteres*, *Oxymonacanthus*, and *Pseudalutarius*. The members of this group are characterized by having a cartilage plug but no trace of the incasing scales on the pelvis (Fig. 14). At the posterior portion of the pelvis there are rudimentary lateral flanges in the two genera, *Oxymonacanthus* and *Pseudalutarius* (Fig. 15, A and B). However, the genus *Brachaluteres* has no trace of lateral flanges at the posterior portion of the pelvis (Fig. 15, C). The dorsal lobe is present in only the genus *Oxymonacanthus*. The cartilage plug is found in three genera, though it shows a vestigial condition in the genus *Brachaluteres*. The dorsal and ventral ligaments are relatively developed in the genera, *Oxymonacanthus* and *Pseudalutarius*, however, in the genus *Brachaluteres* they are reduced to the rudimentary feeble tissue.

Group F. The genera, *Anacanthus* and *Paraluteres*, are included in this group. They show the most extreme reduction of the pelvic complex in the superfamily Balistoidea. There is a simplified feeble pelvis which is slightly bent in the genus *Paraluteres* and almost straight in the genus *Anacanthus* (Fig. 14, D and E).

The two genera show no evidence of any kind for the incasing scales, the rudimentary fin ray element, the cartilage plug, or the ligaments.

**Discussion.** *Terminology*: The pelvic complex is one of the most interesting characters of the superfamily Balistoidea. It has been described by many authors (Cuvier, 1817; Hollard, 1853; Günther, 1870; Jordan and Fowler, 1902; Regan, 1903; Rosen, 1913, 1916; Fraser-Brunner, 1935, 1940, 1941), but a detailed description of the structure of the pelvic complex has not been given by them. Hollard (1853) is the pioneer to describe more or less precisely the pelvic complex. He described the posterior projection of the pelvis, "pointe pelvienne", as being enclosed by scales having thickened and spinulose surfaces. Günther (1870: p. 212) stated that the ventral fins are reduced to a simple osseous appendage. Jordan and Fowler (1902: p. 254) reported that the balistids have no ventral fins but a thick spine at the end of the very long, usually movable pubic bone. Regan (1903: pp. 288~289) also wrote ventrals, if present, are represented by a single

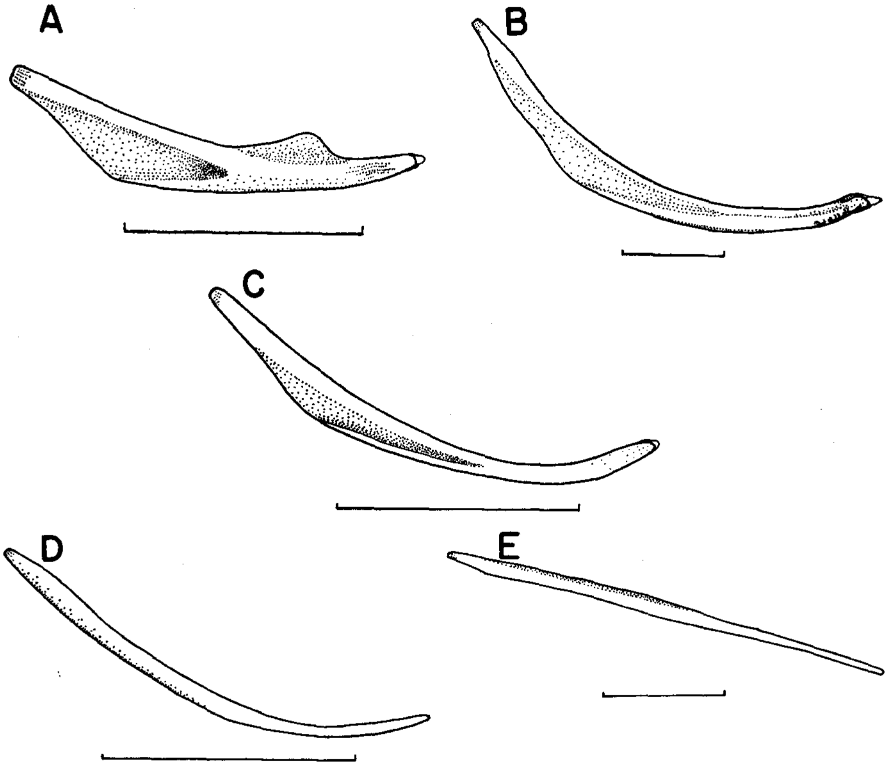


Fig. 14. Diagram showing the pelvis in five monacanthid species. A, *Oxymonacanthus longirostris*; B, *Pseudalutarius nasicornis*; C, *Brachaluteres ulvarum*; D, *Paraluteres prionurus*; E, *Anacanthus barbatus*. Scale bars indicate 10 mm.

short rough spine at the end of the pelvis. Though Rosen (1913) studied the muscles and tendons of the pelvis, he called the incasing scales "the spine". In subsequent work he still applied the term "short single spine" to the incasing scales (Rosen, 1916: p. 22). Fraser-Brunner (1935, 1940, 1941) reviewed the many balistoid fishes, and he also belonged to the conservatives in the use of terminology for the incasing scales. He stated that the pelvic fins are greatly modified to make a single stout spine (Fraser-Brunner, 1935: p. 658). Later (1941: p. 183) he distinguished the pelvic shield from the pelvic spine and defined the shield as the spinate plate of dermal origin which embraces the end of the pelvis just in front of the pelvic spine. Since the authors mentioned above applied the term "pelvic spine" to the incasing scales, it became accepted by subsequent ichthyologists (Breder and Clark, 1947; Clark, 1950; Clark and Gohar, 1953; Matsubara, 1955; Berry and Vogele, 1961). Monod's (1959) pioneer work appeared to clarify the true nature of the pelvic complex. He described the rudimentary fin ray element at the posterior end of the pelvis in *Balistes forcipatus*, a member of the balistids. Tyler (1962b) found that a prominent reductive tendency appears in the pelvic complex of the fishes belonging to the order Tetraodontiformes. He used the term "incasing scales" to describe the structure which had been termed "pelvic spine" by many previous authors. Randall (1964) substituted the term "pelvic terminus" for the pelvic spine based on Tyler's (1962b) work. However, the term "pelvic terminus" is not appropriate in describing the structure, because in the genus *Alutera* a single incasing scale does not lie on the terminal portion of the pelvis but on the ventral and more or less anterior portion of the pelvis. Therefore, I agree with Tyler (1962b) on the terminology for the structure. With respect to the other elements of the pelvic complex, for example, the rudimentary fin ray element and the cartilage plug, I would also agree with him, because his description is based on excellent anatomical studies.

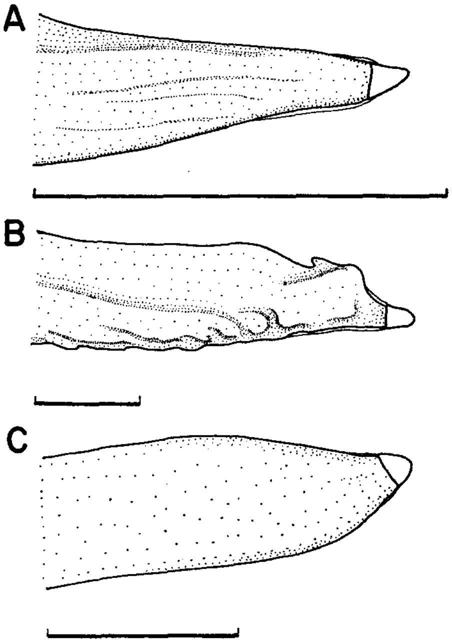


Fig. 15. Diagram showing the posterior end of the pelvis and cartilage plug with the ligaments in three monacanthid species. A, *Oxymonacanthus longirostris*; B, *Pseudalutarius nasicornis*; C, *Brachaluteres ulvarum*. Scale bars indicate 2 mm.

*Interrelationships*: In the present study the interrelationships of the balistoids are made out to be based on the apparent series of reduction in the various parts of the pelvic complex. It seems probable, however, that the reversed series, developing tendency, might occur in the structure of the balistoid pelvic complex. In that case we must speculate the following process, because the triacanthids, which possess the generalized paired pevlic girdles and spines, have been considered to be the ancestor of the balistoids (Breder and Clark, 1947; Fraser-Brunner, 1950; Matsubara, 1955, 1963; Tyler, 1962a, 1962b, 1968, 1970). The triacanthid pelvic girdles are immediately reduced to a simple pelvis found in the monacanthid genera, *Anacanthus* and *Paraluteres*, which have no trace of the pelvic spines, nor the incasing scales or the cartilage plug. Thus, a simple pelvis returned to a generalized (developed) pelvic complex. It is, however, very difficult to accept the above speculation as reasonable.

In the balistoid members, the fishes of Group A, the balistids, show the most generalized condition in respect to all the elements of the pelvic complex (Table 1). One needs to evaluate the phylogenetic significance of each element in order to clarify the systematic position of the balistids. Among those elements the incasing scales show a paired structure, in other words they have the medial articulation both dorsally and ventrally. On the other hand, there are medial grooves on the rudimentary fin ray element both dorsally and ventrally which divide the element into the left and right halves, at least superficially. The medial grooves suggest that the rudimentary fin ray element is probably derived from the paired structures. Unfortunately there are no ontogenetical studies to prove the certainty of the original paired structure of the element in the balistids. Thus, at the present time we must accept the description given with respect to the ontogenetical development of the monacanthid pelvic fin (Hildebrand and Cable, 1930). Hildebrand and Cable (1930: p. 483) described the larval and post-larval stages of *Monacanthus hispidus*, a member of the Monacanthidae. At the stage of 1.7 mm long the species has two ventral fins. Then at the stage of 2 mm long these two ventral fins are replaced by a single flexible membraneous fin on the median line of the abdomen. It is not evident from these specimens whether the pair of ventral fins at the very young stage are lost, or become united to form a single membraneous fin on the ventro-medial line of body. Tyler (1962b: p. 241) responded to the question by his excellent studies of the pelvic complex. He described the medial longitudinal grooves that occur both dorsally and ventrally on the rudimentary fin ray element of such a balistid species as *Verrunculus polylepis* (=*Balistes polylepis*) as representing the area of fusion between the originally separate right and left fin rays. The balistid species examined here also possess the longitudinal median grooves on the rudimentary fin ray element. Thus, I would certainly agree with Tyler's (1962b) opinion on the original structure of the rudimentary fin ray element. Since the triacanthids have the paired pelvic girdles and spines, the relationship between the balistids and triacanthids is confirmed by the fact that in the balistids the rudimentary fin ray element shows the paired structure. Therefore, the balistids are consequently placed at the nearest systematic position to the triacanthids, in other words they are assigned to the most

Table 1. *Differentiation of the pelvic complex in the balistoids. Roman and arabic numerals indicate respectively the numbers of the segments and scales in the incasing scales.*

| Group | | Genus | Incasing scales | Fin ray element | Tendons or ligaments | Cartilage plug | Dorsal lobe | Lateral flanges | Antero-lateral concavity of pevlis |
|---|---|---|---|---|---|---|---|---|---|
| A | | all genera of balsitids | IV–11 | a rod with medial grooves both dorsally and ventrally | tendons | present | present | present | present |
| B | a | *Acreichthys*<br>*Arotrolepis*<br>*Chaetoderma*<br>*Monacanthus*<br>*Paramonacanthus*<br>*Pervagor*<br>*Stephanolepis* | III–6～7 | divided into dorsal and ventral elements | | | | | |
| | b | *Amanses*<br>*Cantherhines* | III–6 | absent | ligaments | | | | |
| C | | *Pseudomonacanthus*<br>*Meuschenia*<br>*Navodon*<br>*Rudarius*<br>*Scobinichythys*<br>*Eubalicthys*<br>*Nelusetta* | II–4 | | | | | | |
| D | | *Alutera* | I–1 | | absent | absent | absent | absent | |
| E | | *Oxymonacanthus*<br>*Pseudalutarius*<br>*Brachaluteres* | 0–0 | | ligaments | present | present | present | |
| F | | *Paraluteres*<br>*Anacanthus* | | | absent | absent | absent | absent | absent |

primitive systematic position in the superfamily Balistoidea. This conclusion is reinforced by the fact that the other elements of the pelvic complex also shows the most primitive condition to be in the balistoids (Table 1).

On the other hand, the interrelationships in the balistid members can not be clarified by the comparative anatomy of the pelvic complex, because they all show essentially the same condition. However, Tyler (1962b) described the differences between *Balistapus undulatus* and the other two species, *Balistes vetula* and *Verrunculus polylepis*, with respect to the incasing scales. As I described in the previous section, the formula for the incasing scales of the Balistidae is shown as follows: I Left and I Right; II Left, II Right, and II Medial; III Left Dorsal, III Left Ventral, III Right Dorsal, and III Right Ventral; IV Left and IV Right. Tyler (1962b: p. 228) defined a different formula for the incasing scales of *Balistapus undulatus* as follows: I Right and I Left; II Right, II Left, and II Medial; III Right and III Left; IV Right and IV Left. With the comparison of 11 specimens examined here, I found the same formula in Segments I, II, and IV, but a different formula in Segment III which does not have a single pair of scales as described by Tyler (1962b), but two pairs of scales. The articulations between these four scales of the segment are easily recognizable in the young, but they become inconspicuous or tightly held to one another in the adult. It may be that Tyler (1962b) overlooked the articulation or that his adult specimen had only a single pair of scales in the segment. If specimens of the species have a single pair of scales in the segment, I believe that to be a very rare and exceptional case. Therefore, it is to be concluded that the balistid members can not be separated into different groups but must be included in a single group based on the structure of the pelvic complex.

The monacanthids have a more reduced pelvic complex than that found in the balistids. The members of the monacanthids are divided into five groups and two subgroups (Table 1). The fishes belonging to Group B show a more reduced condition in the incasing scales and the rudimentary fin ray element than that found in the balistids. Moreover, they share such structures as the tendons (except for *Amanses* and *Cantherhines*), the cartilage plug, the dorsal lobe, the lateral flanges, and the antero-lateral concavity of pelvis, with the balistids (Table 1). Thus, they are considered to be the most primitive representative of the monacanthids. All the members of the group have three segments of the incasing scales, however, the scales of Segment II are different in number among the members. In *Paramonacanthus japonicus* Segment II has three scales, though in *Arotrolepis filicaudus* and *Stephanolepis cirrhifer* some specimens have three scales and the other specimens possess only two scales in the segment. Tyler (1962b) described *Monacanthus ciliatus* as possessing two pairs of scales in the segment. He stated that Segment II has two pairs of scales, one pair of which (II Right Ventral and II Left Ventral) is very small, nonspinulose, and placed ventrally between the postero-medial edges of the other pair (Tyler, 1962b: p. 231). However, in the present study the other species of the same genus, *Monacanthus chinensis*, shows only a single pair of scales in Segment II. Judging from these facts, the number of scales in Segment II is not considered to be constant in the genus or even in the species. Thus, I believe that it is premature to take the number of scales in the segment into account for our phylogenetic studies. All the members of Group B, except for two genera *Amanses* and *Cantherhines,* have the rudimentary fin ray element which is reduced to two bony nubbins. In the two genera, however, there is no trace of the rudimentary fin ray element. Thus, the two genera are the most advanced members of Group B and are sort of transitional forms between Groups B and C.

The fishes of Group C are characterized by having in common two segments of the incasing scales and having no trace of the rudimentary fin ray element. They show more advanced states of formation of these two characters than that of Group B, but they have the ligaments which are present in the Subgroup b of Group B as mentioned above (Table 1). Based on these facts they are considered to be more advanced members in the structure of the pelvic complex than the fishes of Group B. With regard to the interrelationships among the members of Group C, the rudimentary fin ray element provides us with a little information. *Pseudomonacanthus peroni* is the most interesting member in which a single vestigial fin ray element is present or absent on the ventral surface of the cartilage plug. In any other member of the group there is no trace of a rudimentary fin ray element. Thus, *Pseudomonacanthus peroni* is considered to be the most primitive member in Group C. The incasing scales of *Eubalichthys* and *Nelusetta* seem to be smaller than that of the other genera of the group. However, it is unnecessary to separate them from the group. It, therefore, is concluded that the fishes of Group C make a single group in relation to the structure of the pelvic complex.

Group D includes one genus *Alutera* which has a simple pelvis and single incasing scale on the ventral surface of the pelvis. An incasing scale of *Alutera* is peculiar in position. In the other monacanthid members mentioned above the incasing scales are attached to the posterior end of the pelvis, while in *Alutera* an incasing scale is placed on the more anterior portion of the ventral surface of the pelvis than that found in the other monacanthid members. An incasing scale of *Alutera* has been described by several authors (Longley, 1935; Smith, 1935; Longley and Hildebrand, 1940; Berry and Vogele, 1961; Tyler, 1962b). Smith (1935: p. 362) pointed out the change of a scale with age in the species, *A. monoceros.* He stated that in the very young the ventral spine (=an incasing scale) is fairly prominent. With growth, the apical projections diminish, until in adults the whole is reduced to a minute more or less translucent knob, which can nearly always be located by loosening the skin in the last third of the pelvis and viewing it against a light. In the present specimens of the genus, a prominent difference is also found between the young and adult in size and shape of the incasing scale. In the young an incasing scale is fairly prominent, while in the adult it is modified to a very small plate-like scale. On the other hand, in the genus, Group D, there is no trace of any other element of the pelvic complex except for the antero-lateral concavity of the pelvis (Table 1). Curiously, the four elements found in Subgroup b of Group B, that is, the ligaments, the cartilage plug, the dorsal lobe, and the lateral flanges, are not present in Group D, but in some members of the next group, Group E (Table 1). These facts and the peculiar position of an incasing scale may indicate that the fishes of Group D have progressed to a different evolutional lineage which deviated from the course of the other monacanthid members mentioned above.

In the fishes of Group E including three genera, *Brachaluteres*, *Oxymonacanthus*, and *Pseudalutarius*, there is no trace of the incasing scales, nor of the rudimentary fin ray element. The extreme reduced condition in these parts shows that the fishes of Group E occupy a more advanced state than that found in any other of the foregoing members of the monacanthids. On the other hand, the remaining five elements of the pelvic complex are retained in the group, at least in the genus *Oxymonacanthus* (Table 1). These facts suggest that the group is closely related to the fishes of Group C rather than to those of Group D. With regard to the intergeneric relationships, the pelvic complex provides us with the best information. *Oxymonacanthus* has the small dorsal lobe, the rudimentary lateral flanges, the cartilage plug, and the dorsal and ventral ligaments, while in the other two genera, *Pseudalutarius* and *Brachaluteres*, the dorsal lobe is absent. Therefore, *Oxymonacanthus* is placed in the most primitive position among the three genera of this group. In *Oxymonacanthus* the many enlarged spinulose scales are present on the postero-ventral surface of the pelvis, and they seem at first glance to be the incasing scales. However, the enlarged scales are gradually reduced in size antero-dorsally and are indistinguishable from the other body scales. Thus, they are considered to be the body scales. Since *Brachaluteres* has the most reduced cartilage plug with ligaments, and no dorsal lobe and lateral flanges, the genus is placed at the most advanced position in the group. At the posterior end of the pelvis, *Pseudalutarius* possesses the cartilage plug, the ligaments, and the rudimentary lateral flanges, but it has no dorsal lobe. Thus, the genus should be placed between *Oxymonacanthus* and *Brachaluteres*.

An extreme reduction in the pelvic complex is found in the fishes of the genera, *Anacanthus* and *Paraluteres*, which are included in Group F. These two genera have only a single feeble pelvis and no trace of any other element of the pelvic complex. Thus, they are placed at the most advanced position in the monacanthids.

The interrelationships of the balistoids based on the structure of the pelvic complex are summarized in the three-dimensional diagram (Fig. 16) and Table 1.

*Function*: The many species of the balistids are found in the coastal waters of warm and tropical regions, but a few species, for example *Canthidermis maculatus* and *Xanthichthys mento*, occur offshore. When the coastal species encounter their enemies, they dash into a hole or crevice of some rocky or coral formation. Then they erect the first dorsal spine which is locked by the second one, and extend the pelvis downward. These actions serve to securely wedge the balistids in a hole or crevice, and make them very difficult to dislodge. These peculiar actions have been described by the previous authors (Clark and Gohar, 1953; Tyler, 1962b; Munro, 1967; Böhlke and Chaplin, 1968; Randall, 1968). Tyler (1962b: p. 240) described the presence of the spinulose incasing scales at the end of the balistid pelvis as increasing the ability of the fish to fix itself in holes. In the species that live in coral or rocky waters, the mechanism of the incasing scales provides them with an advantage in the battle for existence.

The offshore species, such as *Canthidermis maculatus* and *Xanthichthys mento*, have a more reduced rudimentary fin ray element than that found in the coastal species. In the offshore waters they can not find a hideaway to wedge themselves into, thus they are not able to use the incasing scales which can be moved in the dorso-ventral plane by the actions of the rudimentary fin ray element and its associated structures. In other words, the significance of the rudimentary fin ray element for existence is possibly less than that found in the coastal species. Therefore, the reduction of the element in these offshore species may be brought about in relation to their habitats. However, *Abalistes stellatus*, another offshore species, possesses a rather developed element which is in conflict with the speculation mentioned above. Further ecological and ontogenetical studies of the balistids are needed in order to clarify why the element is reduced in size.

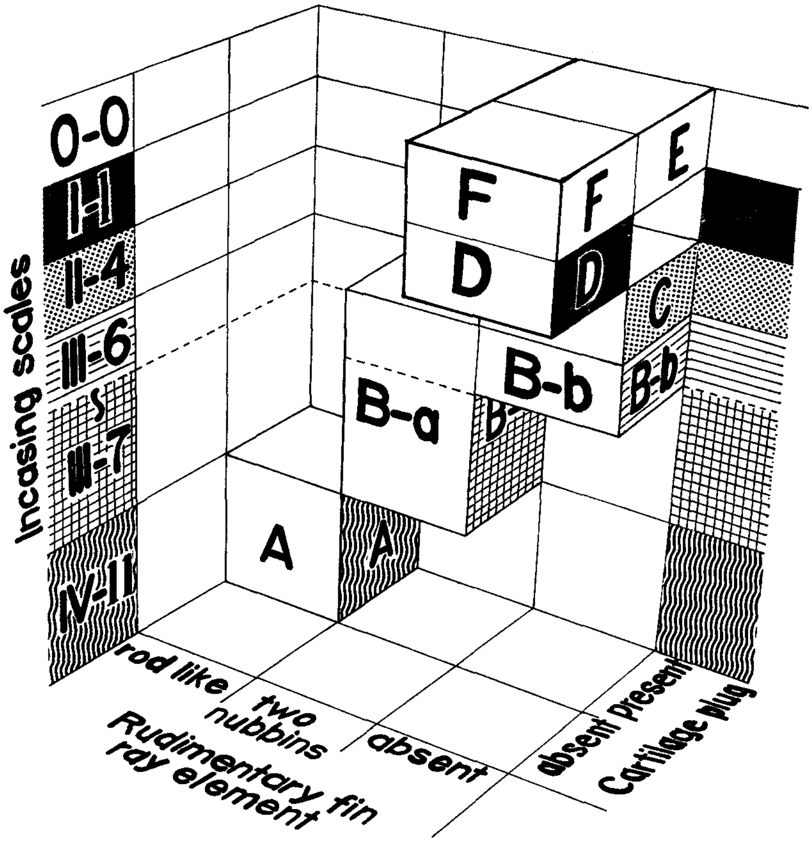


Fig. 16. Three-dimensional diagram showing the interrelationships of the balistoids based on the structure of the pelvis and associated elements. Roman and arabic numerals indicate respectively the number of the segments and scales in the incasing scales.

On the other hand, most of the monacanthid members tend to bear some relation with the sandy bottoms and the seagrasses where they can not find a crevice or hold to hide themselves. However, they have acquired an other defensive mechanism, namely the distensibility of the abdomen.

With regard to the function of the distensibility, Breder and Clark (1947: p. 303) described in the tetraodontoids that the inflation is employed as a defensive mechanism, and fishes in a swollen state are both difficult to seize and to swallow. In the monacanthids the tremendous inflation of the body is not found, as seen in the tetraodontoids, although considerable distensibility of the abdomen is present.

The primitive monacanthids, for example *Monacanthus chinensis* and *Stephanolepis cirrhifer*, can greatly extend the pelvis downward to dilate the outline of the abdomen. When these fishes extend the pelvis to its maximum possible extent, they can acquire a deeper body in combination with erected dorsal spine than that found in the normal condition. Whether one fish will fit into another fish's mouth depends upon its maximum diameter, and fin spines which add to its diameter make difference between fitting and not fitting (Gosline, 1971: p. 44). Therefore, I believe that in the primitive monacanthids the extended pelvis and the incasing scales are possibly effective enough to protect them from their predators.

In contrast with the primitive monacanthids, the advanced monacanthids such as the fishes of the genus *Brachaluteres* can only slightly extend downward the reduced pelvis without the incasing scales, however, they have the other mechanism to inflate their abdomen. In the present study *Brachaluteres ulvarum* possesses an enlarged stomach which is much greater than that found in the primitive monacanthids. It seems possible that the species can distend its abdomen by inflating of the stomach. Indeed, Clark and Gohar (1953: pp. 46~47) reported that the other member of the genus, *B. baueri fahaqa*, has an inflatable stomach.

Judging from these facts the reductive tendency of the pelvic complex in the monacanthids is possibly related to the modification of the inflating mechanism which is found through the evolutional lines from the balistids to the tetraodontoids. The tetraodontoids have been considered to be the derivatives of the balistoids (Breder and Clark, 1947; Matsubara, 1955; Tyler, 1962a, 1968; Winterbottom, 1974). They can inflate the body by means of the distensible stomach for defense, though they show no trace of any element of the pelvic complex (except for the rare species, *Triodon macropterus*). In other words the tetraodontoids have replaced the pelvic complex by the distensible stomach as the defensive mechanism. It seems that along the evolutional processes from the balistoids to the tetraodontoids the pelvic complex has been gradually reduced and the stomach has been gradually increased in size. This speculation is supported by the following facts.

First, the balistids and the primitive monacanthids possess the pelvic complex which can be extend downward to dilate the abdomen. The advanced monacanthids, such as the fishes of the genus *Brachaluteres*, have the reduced pelvic complex and the inflatable stomach. The inflating mechanism of the genus shows a basic similarity to the more developed mechanism in the tetraodontoids (Clark and Gohar, 1953: p. 47).

Second, the most primitive member of the tetraodontoids, *Triodon macropterus*, shows a reduced pelvic complex which is not found in any other member of the tetraodontoids. In the species there is a long strut-like pelvis which lies in the ventral part of the abdomen. In contrast with the balistoids, the pelvis of the species is composed of the left and right halves which are tightly articulated with one another by interdigitation on the mid line. At the posterior end of the pelvis I found a very small cartilage plug which is quite similar to the structure found in the advanced monacanthids (Fig. 17), though Tyler (1962b: p. 243) reported no evidence of the presence of the cartilage plug. I believe that he overlooked the cartilage plug in the species, because it is very difficult to locate since the plug is tightly enclosed by tough connective tissue at the end of the posterior part of the pelvis.

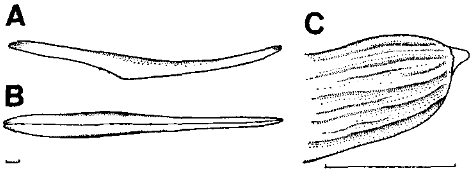


Fig. 17. Diagram showing the pelvic complex of *Triodon macropterus*. A, lateral view; B, dorsal view; C, posterior end of the pelvis. Scale bars indicate 5 mm.

## 2. Pectoral girdle

**Description.** The balistoid pectoral girdle is composed of seven or eight bones, the posttemporal, the supracleithrum, the postcleithrum or two postcleithra, the scapula, the coracoid, and the four actinosts. The position of the girdle is shown in Figure 18. The posttemporal is rigidly wedged into the cranium, thus the bone has close relation to the cranium rather than to the pectoral girdle. Therefore, it will be described in the section of the cranium. Since the balistids are readily distinguished from the monacanthids, they are independently described in the following section.

Balistidae. The pectoral girdle shows little variation among the balistid members. The illustrations of two species (Fig. 19) cover the variation found in the balistid members.

The supracleithrum is placed vertically at the uppermost part of the pectoral girdle. The bone articulates ventrally with the cleithrum and dorsally with the posttemporal by fibrous connective tissue.

The cleithrum, the largest element in the girdle, articulates posteriorly with the coracoid and scapula, and postero-dorsally with the supracleithrum and dorsal postcleithrum. Between the bone and the coracoid some members have the interosseous space which is covered by a sheet of connective tissue (Fig. 19, A).

The two postcleithra are tightly held to one another to form a long strut which extends postero-ventrally along the abdominal wall. The dorsal postcleithrum articulates dorsally with the cleithrum and ventrally with the ventral postcleithrum which is free ventrally on the abdominal wall.

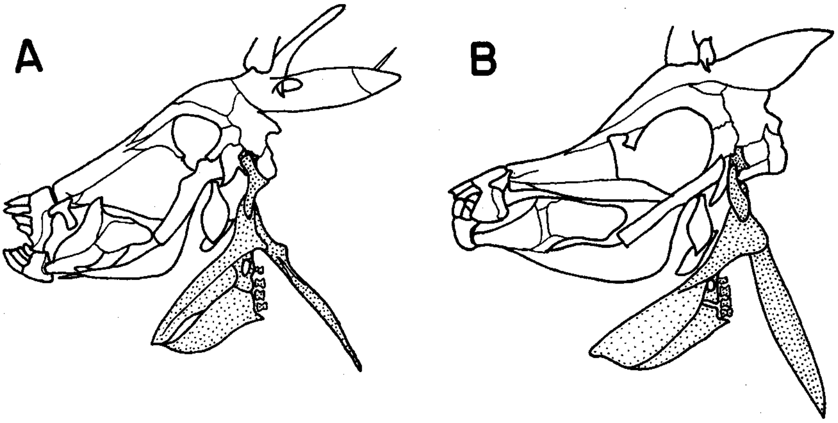


Fig. 18. Diagram showing the position of the pectoral girdle represented by dotted area. A, *Balistapus undulatus*; B, *Monacanthus chinensis*.

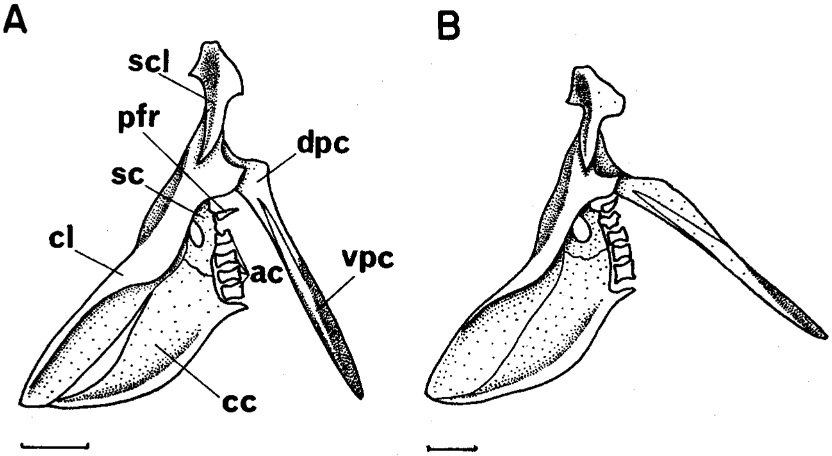


Fig. 19. Diagram showing the pectoral girdle in two balistid species. A, *Pseudobalistes flavimarginatus*; B, *Balistoides conspicillum*. ac, actinosts; dpc, dorsal postcleithrum; pfr, rudimetnary pectoral fin ray; sc, scapula; scl, supracleithrum; vpc, ventral postcleithrum. Scale bars indicate 10 mm.

The scapula articulates anteriorly with the cleithrum and ventrally with the coracoid. The scapula foramen is completely enclosed by the bone. The uppermost rudimentary pectoral fin ray articulates with the posterior edge of the scapula by fibrous connective tissue. Along its posterior edge the scapula supports the first, the second, and the upper half of the third actinosts.

The coracoid is expanded dorsally and tapered to a blunt point ventrally. The bone articulates anteriorly with the cleithrum and dorsally with the scapula.

There is a short posteriorly directed projection at the postero-dorsal corner of the bone. The bone articulates posteriorly with the lower half of the third actinost and the fourth.

There are four actinosts which increase in size from the first to the fourth in the series. The first actinost is small and articulates closely with the small stubby projection on the scapula. The second to the fourth actinosts are constricted in the middle part to form an hourglass shape, and articulate with the scapula and coracoid by fibrous connective tissue.

Monacanthidae. The monacanthids are essentially similar to the balistids in the structure of the pectoral girdle, though reduction is found in the postcleithrum. In contrast with the balistids the postcleithrum is composed of a single bone in the monacanthids. The monacanthid pectoral girdle shows more variation among the genera than that found in the balistid members. The variation found in the monacanthids is represented by the illustrations for 10 species (Fig. 20).

The supracleithrum is more or less vertically placed at the uppermost part of the pectoral girdle. The ventral part of the bone is relatively rounded, although in the genus *Brachaluteres* the lower one-third of the bone is triangular in shape (Fig. 20, H). The bone articulates dorsally with the posttemporal and ventrally with the cleithrum.

In many monacanthid members the cleithrum shows a similar condition to that seen in the balistids. The genus *Anacanthus*, however, possesses a greatly enlarged cleithrum which is overlain by the ventral edge of the long preopercular (Fig. 20, J).

The scapula articulates dorsally with the cleithrum and ventrally with the coracoid. The inner surface of the scapula foramen completely enclosed by the scapula in all the monacanthid members, though the anterior edge of the outer surface of the scapula foramen is surrounded by the cleithrum in these members: *Stephanolepis*, *Rudarius*, *Alutera*, *Oxymonacanthus*, *Pseudalutarius*, and *Anacanthus*. The scapula articulates posteriorly with the rudimentary fin ray and the first, the second, and the upper half of the third actinosts.

The coracoid is an elongated triangular bone tapering to a blunt point ventrally. The bone articulates anteriorly with the cleithrum and dorsally with the scapula. The postero-dorsal projection varying in shape among the genera is found at the upper part of the bone. The lower half of the third actinost and the fourth actinost articulate with the bone by fibrous connective tissue. The extremely elongated coracoid is found in the genus *Anacanthus* (Fig. 20, J).

There are four actinosts which are constricted in the middle part. They increase slightly in size from the first to the fourth in the series.

**Discussion.** Many authors described the balistoid pectoral girdle, but they overlooked the fact that the balistids and monacanthids are clearly distinguished by the number of postcleithrum (Gill, 1885; Regan, 1903; Rosen, 1916; Starks, 1930; Gregory, 1933). In the balistids it is composed of two elements, dorsal and ventral postcleithra, however, in the monacanthids there is no trace of the articulation between the two elements. It seems that they are fused to one another

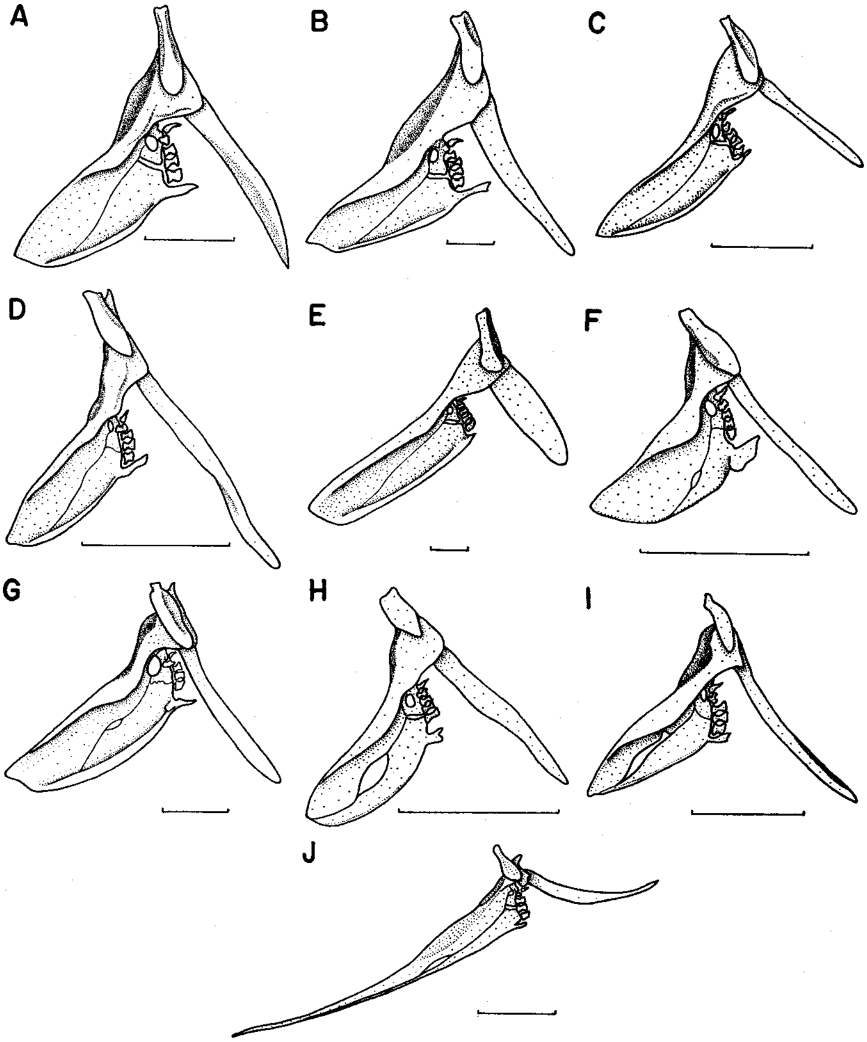


Fig. 20. Diagram showing the pectoral girdle in 10 monacanthid species. A, *Stephanolepis cirrhifer*; B, *Cantherhines dumerili*; C, *Pseudomonacanthus peroni*; D, *Rudarius ercodes*; E, *Alutera monoceros*; F, *Oxymonacanthus longirostris*; G, *Pseudalutarius nasicornis*; H, *Brachaluteres ulvarum*; I, *Paraluteres prionurus*; J, *Anacanthus barbatus*. Scale bars indicate 10 mm.

to make a single rod-like bone in the monacanthids, since the rod in the monacanthid members is similar in size to the two postcleithra of the balistid members. Consequently, with regard to the structure of the pectoral girdle the balistids are more primitive than the monacanthids, since the triacanthids which have been considered to be the ancestor of the balistoids possess the dorsal and ventral postcleithra.

## 3. Jaws

**Description.** In the balistoids the upper jaw consits of two elements, the premaxillary and the maxillary. The lower jaw is composed of four elements, the dentary, the articular, the sesamoid articular, and the angular. The balistids and monacanthids are clearly separated by the number of teeth as described below.

Balistidae. The balistid jaws show slight variation in structure which is essentially covered by the illustration of three species (Fig. 21). Since, the variation is too small to divide the balistid members into an independent group, they are naturally included in a single group, Group A.

The premaxillary is a large bone which is curved and expanded dorsally. The dorsal surface of the bone is covered and filled with cartilage to articulate with the anterior parts of the ethmoid and vomer by fibrous connective tissue. The bone also articulates postero-dorsally with the antero-medial surface of the palatine. Along the posterior edge of the premaxillary it articulates immovably with the maxillary by fibrous connective tissue and interdigitation. Dorso-medially the bone is closely held to its opposite fellow by fibrous connective tissue.

Each premaxillary possesses seven teeth on its dorsal edge, four in an outer row and three in an inner row. These outer teeth are notched at their edges in all the balistid members except for the fishes of the genus *Melichthys* (Fig. 21, B) in which the anterior two teeth have more or less truncate edges. These teeth decrease in size posteriorly in most balistid members, though in the genus *Odonus* the second tooth is greatly projected to form the canine tooth (Fig. 21, C). The three inner teeth are present to reinforce the outer teeth (Fig. 21).

The dentary is larger and expanded posteriorly. Its posterior edge is concave in order to articulate with the articular and angular. On its dorsal edge the dentary possesses four teeth in a single row which decrease in size posteriorly.

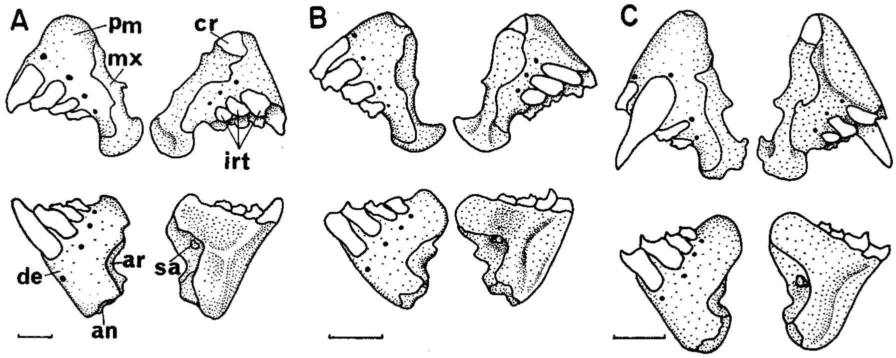


Fig. 21. Diagram showing the jaws in three balistid species. A, *Pseudobalistes flavimarginatus*; B, *Melichthys vidua*; C, *Odonus niger*. an, angular; ar, articular; cr, cartilage; de, dentary; irt, inner row of teeth; mx, maxillary; pm, premaxillary; sa, sesamoid articular. Left, lateral view; right, medial view; top, upper jaw; bottom, lower jaw. Scale bars indicate 5 mm.

These teeth are notched at their edges, and correspond with the teeth in the upper jaw.

The articular encloses the posterior margin of the dentary. The bone has a concave facet to articulate with the anterior knob of the quadrate by fibrous connective tissue.

The sesamoid articular is a very small and thicknened bone which is held to the inner surface of the articular (Fig. 21).

The angular is a small bone placed at the lowermost part of the lower jaw. The bone articulates dorsally with the articular, and anteriorly with the dentary. The bone also connects posteriorly with the long interopercular by a ligament.

Monacanthidae. The monacanthid jaws show greater variation than that found in the balistids, and indicate an apparent reduction in the number of the teeth. The monacanthid members are divided into the following two groups based on the degree of the reduction.

Group B. This group is composed of 18 genera, *Acreichthys*, *Alutera*, *Amanses*, *Arotrolepis*, *Brachaluteres*, *Cantherhines*, *Chaetoderma*, *Eubalichthys*, *Meuschenia*, *Monacanthus*, *Navodon*, *Nelusetta*, *Paramonacanthus*, *Pervagor*, *Pseudalutarius*, *Pseudomonacanthus*, *Scobinichthys*, and *Stephanolepis*. The variation of the jaws found in this group is covered by the illustration of six species (Fig. 22).

The jaws of this group are essentially similar to that of the balistids except for the number of the teeth. In the upper jaw there are five teeth, three in an outer row and two in an inner row. These outer teeth are notched at their edges reinforced by the inner teeth. On the other hand, three teeth are found in a single row on the lower jaw. They decrease gradually in size posteriorly in most members of the group, though in some members such as the fishes of the genera *Pseudomonacanthus* and *Brachaluteres* (Fig. 22, C and F) the posterior-most tooth is extremely reduced in size.

Group C. This group is composed of four genera, *Rudarius*, *Oxymonacanthus*, *Paraluteres*, and *Anacanthus*. They show a more reduced condition in the number of the teeth on the lower jaw than that found in the fishes of the preceding groups. The members of this group have only two teeth on the dentary, although they possess the same condition in the other features of the jaws as seen in the fishes of Group B (Fig. 23).

**Discussion**. The balistoid jaws have been described in many articles because they show differences in the number of the teeth so as to distinguish the balistids and monacanthids (Günther, 1870; Smith, 1935; Fraser-Brunner, 1941; Matsubara, 1955). However, these authors did not study in detail the jaws of many balistoid members, and thus they overlooked the fact that the reductive tendency of the teeth is present within the monacanthids as well as between the balistids and monacanthids. The aspects of differentiation in the balistoid jaws examined here are only recognizable by the number of the teeth (Table 2).

Prior to discussion of the interrelationships, there is a need to answer the question whether the reductive tendency in the teeth corresponds to the trend of the evolution. Generally speaking, the number of teeth has not been considered to

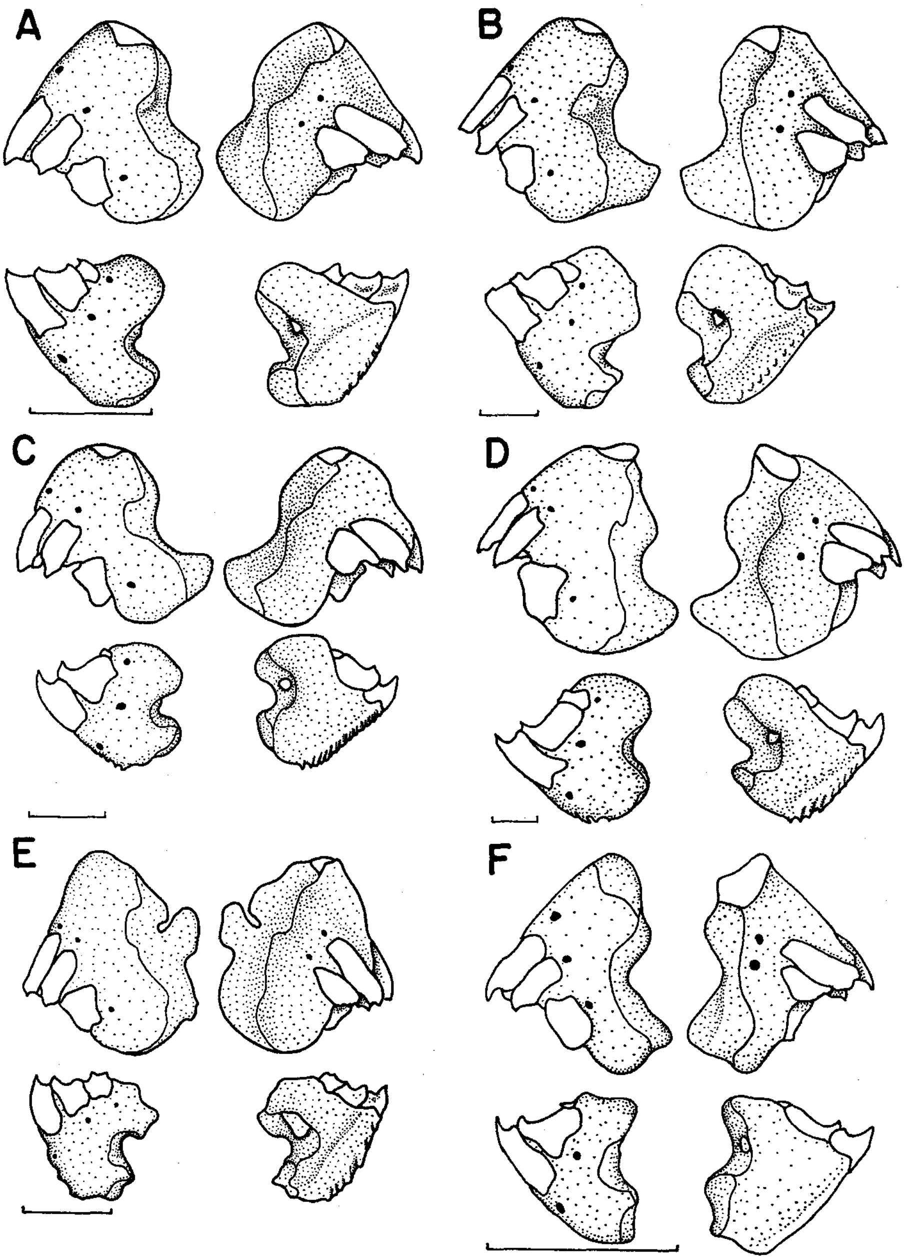


Fig. 22. Diagram showing the jaws in six monacanthid species. A, *Monacanthus chinensis*; B, *Navodon modestus*; C, *Pseudomonacanthus peroni*; D, *Alutera monoceros*; E, *Pseudalutarius nasicornis*; F, *Brachaluteres ulvarum*. Left, lateral view; right, medial view; top, upper jaw; bottom, lower jaw. Scale bars indicate 3 mm.

be an important character for the phylogenetic interpretation of fishes. However, it has been significant to study the phylogenetic relationships within the order Tetraodontiformes, which shows the reductive tendency throughout the evolutional lineages within the order (Breder and Clark, 1947; Tyler, 1962a). The triacanthids which have been considered to be the ancestor of the balistoids possess five teeth in an outer row and two in an inner row on each premaxillary. On the dentary they have 10 teeth in an outer row and only one in an inner row (Tyler, 1968). On the other hand, the primitive tetraodontoid *Triodon macropterus*, which is considered to be a connection between the Balistoidei and Tetraodontoidei (Tyler, 1962a,

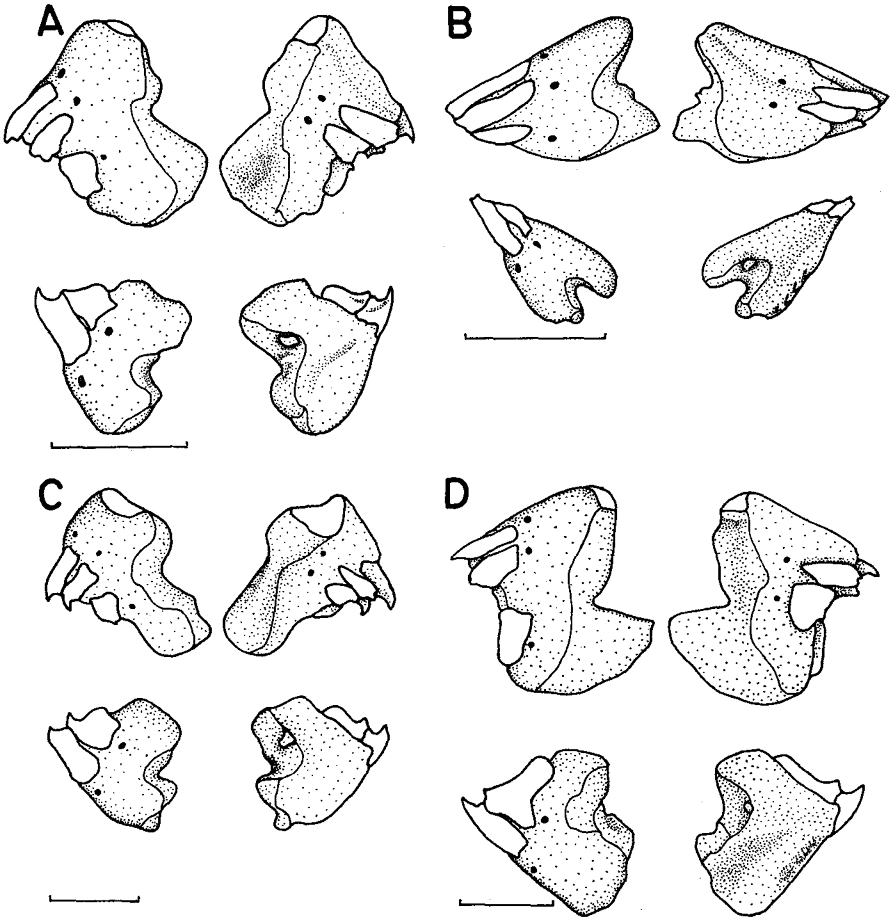


Fig. 23. Diagram showing the jaws in four monacanthid species. A, *Rudarius ercodes*; B, *Oxymonacanthus longirostris*; C, *Paraluteres prionurus*; D, *Anacanthus barbatus*. Left, lateral view; right, medial view; top, upper jaw; bottom, lower jaw. Scale bars indicate 3 mm.

Table 2. *Differentiation of the number of the teeth in the balistoids.*

| Group | Genus | Number of outer teeth on each premaxillary | Number of inner teeth on each premaxillary | Number of teeth on each dentary |
|---|---|---|---|---|
| A | all genera of balistids | 4 | 3 | 4 |
| B | *Acreichthys*<br>*Alutera*<br>*Amanases*<br>*Arotrolpeis*<br>*Cantherhines*<br>*Chaetoderma*<br>*Meuschenia*<br>*Monacanthus*<br>*Navodon*<br>*Nelusetta*<br>*Paramonacanthus*<br>*Pervagor*<br>*Pseudalutarius*<br>*Stephanolepis*<br>*Scobinichthys*<br>*Eubalichthys*<br>*Pseudomonacanthus*<br>*Brachaluteres* | 3 | 2 | 3 |
| C | *Rudarius*<br>*Oxymonacanthus*<br>*Paraluteres*<br>*Anacanthus* | | | 2 |

1962c), has two large teeth on the upper jaw and a single beak-like tooth on the lower jaw. These facts suggest strongly that the reductive tendency in the number of the teeth does correspond with the trend in the evolution of the order Tetraodontiformes. Thus, it is clear that a large number of teeth indicates a primitive condition. Judging from this criterion, the balistids (Group A) having the greatest number of teeth in the balistoids are considered to be placed at the most primitive systematic position. The monacanthid members of Group C characterized by the smallest number of teeth are assigned to the most advanced systematic position, and another monacanthid group, Group B, occupies the intermediate position between Groups A and C.

## 4. Suspensorium and opercular apparatus

**Description**. The balistoid suspensorium is composed of seven bones, the palatine, the ectopterygoid, the mesopterygoid, the metapterygoid, the quadrate, the symplectic, and the hyomandibular. They are suspended from the cranium by two props formed by the anterior part of the palatine and the posterior edge of the hyomandibular. The opercular apparatus is made up of four bones, the opercular, the subopercular, the preopercular, and the interopercular. The balistids are clearly distinguished from the monacanthids by the shape of the palatine, thus they are independently described in the following section.

Balistidae. The balistid members show little variation in the suspensorium and opercular apparatus, thus they are included in a single group, Group A. The illustrations of two species cover the variation found in the balistid members (Fig. 24).

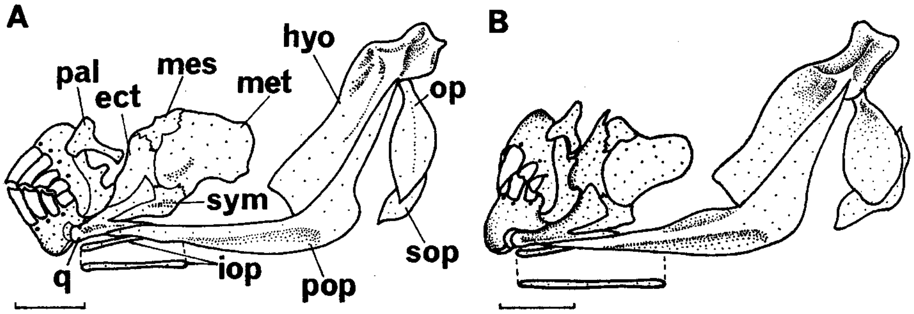


Fig. 24. Diagram showing the lateral view of the suspensorium and opercular apparatus, and the relation between the jaws and them in two balistid species. A, *Rhinecanthus aculeatus*; B, *Odonus niger*. Interopercular displaced. ect, ectopterygoid; hyo, hyomandibular; iop, interopercular; mes, mesopterygoid; met, metapterygoid; op, opercular; pal, palatine; pop, preopercular; q, quadrate; sop, subopercular; sym, symplectic. Scale bars indicate 10 mm.

The palatine is T-shaped bone which articulates ventrally with the ectopterygoid, antero-dorsally with the maxillary and premaxillary, and posteriorly with the anterior parts of the ethmoid and vomer by fibrous connective tissue.

The ectopterygoid articulates antero-ventrally with the quadrate, ventrally with the symplectic, and posteriorly with the mesopterygoid and metapterygoid by interdigitation.

The mesopterygoid is a small bone placed at the upper part of the suspensorium. It articulates anteriorly with the ectopterygoid and ventrally with the metapterygoid.

The metapterygoid is a large rounded bone which articulates antero-dorsally with the mesopterygoid, anteriorly with the ectopterygoid, and antero-ventrally with the symplectic. The bone connects posteriorly with the hyomandibular by a sheet of connective tissue which is present among the metapterygoid, the hyomandibular, the symplectic, and the preopercular. At its postero-ventral edge the metapterygoid articulates with the dorsal edge of the interhyal by fibrous connective tissue.

The quadrate is triangular in shape, and possesses a deep cleft on its posterior part. The bone is anteriorly tapered to a knob shape to which the articular of the lower jaw is attached. It articulates posteriorly with the ectopterygoid and symplectic, and ventrally with the preopercular.

The symplectic is placed at the postero-ventral portion of the suspensorium. It articulates anteriorly with the posterior cleft on the quadrate, dorsally with the ectopterygoid, and postero-dorsally with the metapterygoid.

The hyomandibular is elongated and more or less expanded dorsally. The bone articulates dorsally with the prootic and pterotic. Along the lower two thirds of its posterior edge the hyomandibular articulates with the preopercular. Just behind the dorsal end of the preopercular the bone thickens to articulate with the dorsal concavity of the opercular.

The opercular is a small flattened bone, and articulates dorsally with the hyomandibular, and partly overlies the upper part of the subopercular.

The subopercular is a thin, leaf-like bone, and articulates dorsally with the opercular by connective tissue.

The opercular is elongated and slightly bent in the middle part. The bone articulates postero-dorsally with the hyomandibular and antero-dorsally with the quadrate. It is connected with the symplectic and metapterygoid by a sheet of connective tissue.

The interopercular is rod shaped and placed at the ventro-medial parts of the quadrate and preopercular. The bone articulates anteriorly with the angular by a ligament. Posteriorly it also has two ligaments; one is short and connected with the dorsal end of the epihyal, and the other is long and extends posteriorly to the antero-medial surface of the opercular.

Monacanthidae. The monacanthid suspensorium and opercular apparatus are essentially similar to those of the balistids, but show more variation than that found in the latter. The monacanthid members are divided into the following two groups based on the feature of the palatine.

Group B. This group includes all the monacanthid members other than the fishes of the genus *Anacanthus*, and is characterized by a short, rod-like palatine. The illustrations of seven species cover the variation found in this group (Fig. 25, A to G).

The T-shaped palatine as seen in Group A is not found in this group. The bone is more reduced and simple than that found in Group A. It articulates antero-dorsally with the maxillary and premaxillary, and postero-dorsally with the anterior parts of the ethmoid and vomer. It also connects with the ectopterygoid by tough connective tissue, although there is some distance between them. In most members of the group, except for the genera *Oxymonacanthus* and *Pseudalutarius*, the elements of the suspensorium and opercular apparatus besides the palatine are very similar to those of Group A. In the genus *Oxymonacanthus* the metapterygoid is elongated rather than rounded, and tapered to a blunt posterior projection. The hyomandibular of the genus *Pseudalutarius* is peculiar in that it articulates antero-dorsally with the ventral projection of the frontal.

Group C. This group is composed of a single genus *Anacanthus* and is characterized by having a direct articulation between the palatine and ectopterygoid. The palatine is small and triangular in shape, and is expanded ventrally. Along its ventral edge the palatine articulates directly with the antero-dorsal edge of the ectopterygoid. It also articulates dorsally with the maxillary and

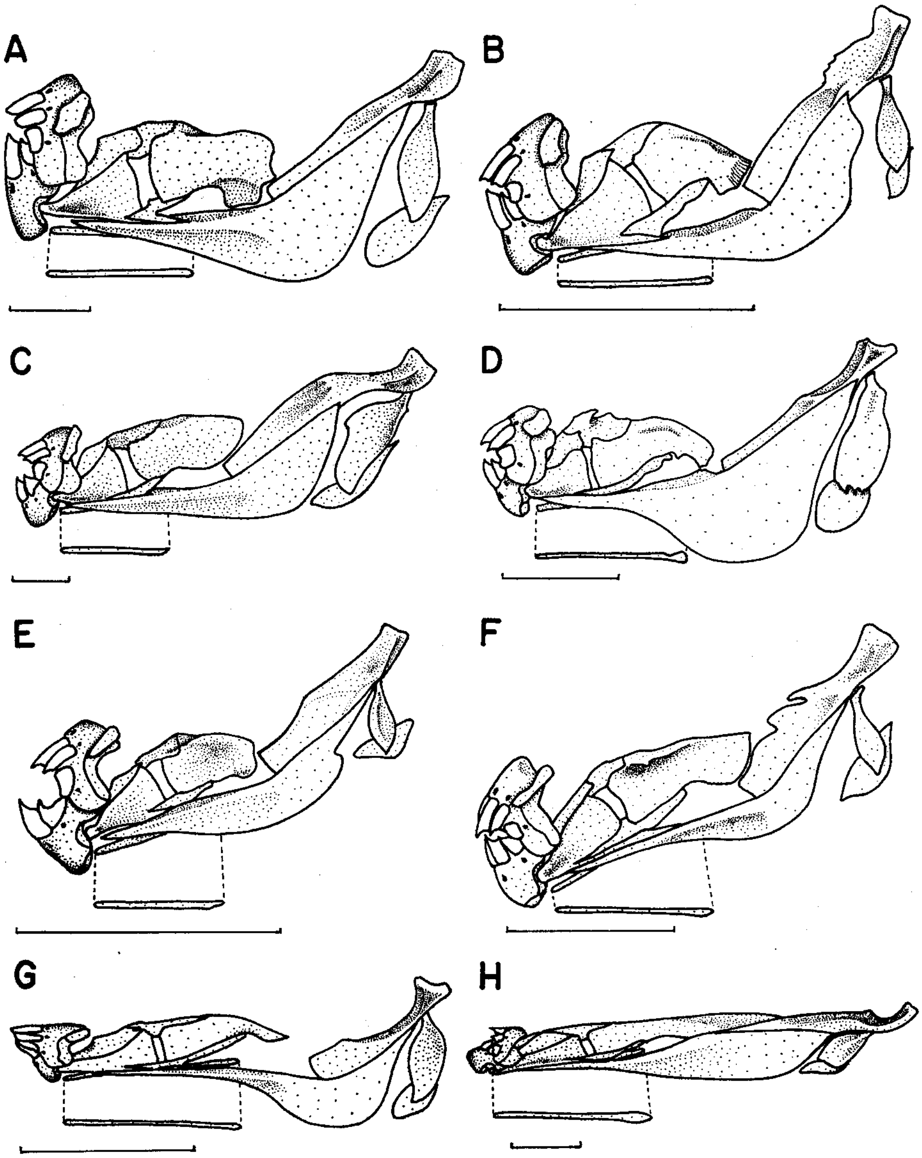


Fig. 25. Diagram showing the lateral view of the suspensorium and opercular apparatus, and the relation between the jaws and them in eight monacanthid species. A, *Stephanolepis cirrhifer*; B, *Rudarius ercodes*; C, *Alutera monoceros*; D, *Pseudalutarius nasicornis*; E, *Brachaluteres ulvarum*; F, *Paraluteres prionurus*; G, *Oxymonacanthus longirostris*; H, *Anacanthus barbatus*. Interopercular displaced. Scale bars indicate 10 mm.

premaxillary, and postero-dorsally with the anterior parts of the ethmoid and vomer by fibrous connective tissue. The elements of the suspensorium and opercular apparatus except for the palatine are essentially the same as those of Groups A and B, though they are extremely elongated and inclined forward to form an almost horizontal edge dorsally (Fig. 25, H).

**Discussion.** Several authors described the balistoid suspensorium and opercular apparatus (Regan, 1903; Gregory, 1933; Fraser-Brunner, 1941) and found that the balistids and monacanthids are clearly separated by the shape of the palatine. Fraser-Brunner (1941) used the feature of the palatine for a diagnostic character in order to define the families Balistidae and Monacanthidae (his Aluteridae), although he made no reference to the phylogenetic significance of the bone. Until the present time studies on the suspensorium and opercular apparatus have been insufficient to clarify the interrelationships among the balistoids, and the peculiar palatine of the genus *Anacanthus* has not been reported by any author.

Judging from the description in the preceding section, significant information for phylogenetic consideration is to be acquired from the palatine. The bone shows tendencies of reduction in size and simplification in shape from Group A to Group C. These tendencies probably correspond to the evolutional trends, because the triacanthids have a larger and more complex palatine than that found in the balistoids. Therefore, Group A is considered to be the most primitive member in the balistoids. On the other hand, in the monacanthids Group B is reasonably considered to be more primitive than Group C based on both tendencies mentioned above. Within Group B, the genera *Oxymonacanthus* and *Pseudalutarius* are possibly considered to be more advanced than the other members of the group because of the peculiar structure in the suspensorium. Group C is assigned to the most advanced systematic position in the balistoids on the basis of the reductive tendencies found in the palatine. This conclusion is reinforced by the fact that in this group the palatine articulates directly with the ectopterygoid. This condition is considered to be a derived character, since it is not seen in any other balistoid member and triacanthids.

From the functional view point, it is noteworthy that the significant difference between the balistoids and perciform fishes in the suspensorium and opercular apparatus centers in the feature of the palatine. This difference of the palatine between both groups may be related to the feeding mechanism.

In the perciform fishes the palatine articulates with the medial surface of the maxillary, thus the forward push on the palatine is transmitted to the maxillary and premaxillary for the protrusion of the upper jaw by which they grasp the prey. Then, they can engulf it in part by extending the jaws and in part by creating a negative pressure in the oral cavity that draws the prey and surrounding water toward the mouth (Gosline, 1971: p. 58).

On the other hand, the balistoids feed on corals, echinoderms, crustaceans, and algae (Hiatt and Strasburg, 1960: pp. 108～110) by nibbling action of the mouth which is carried out by the rotation of the jaws. With regard to the upper jaw, ventrally the palatine is tightly held by tough connective tissue, or directly attached to the dorsal edge of the ectopterygoid, and postero-dorsally it is immovably attached to the anterior parts of the ethmoid and vomer. At the antero-dorsal end it is immovably articulated with the lateral surface of the maxillary and premaxillary, thus the upper jaw can rotate around this articular point. Therefore, the palatine plays an important role in rotation of the upper jaw. The interopercular and quadrate are related to the rotation of the lower jaw.

Consequently, it may be considered that the specialized palatine as seen in the balistoids is derived from the generalized perciform palatine in response to the change of the feeding mechanism.

Regarding the balistoids, Group A (balistids) has the strongest palatine, and can mostly feed on hard-bodied organisms such as echinoderms which are avoided by most predaceous animals (Hiatt and Strasburg, 1960: p. 109). Group B (monacanthids) possesses a more reduced palatine than that found in Group A, however, the fishes of this group do not eat the hard-bodied animals but select other food items, such as the organisms which can not be eaten by Group A, using skilfull nibbling action of the jaws. Group C (monacanthids), a bottom-dweller on the sand, shows an extreme reduced palatine, and the specimens examined fed on very small crustaceans. Thus, it is concluded that the reductive tendency of the palatine may be related to the feeding habits of each group.

### 5. Hyoid apparatus

**Description.** The balistoid hyoid apparatus is composed of six elements, the ceratohyal, the epihyal, the interhyal, the dorsal and ventral hypophyals, the urohyal, and the branchiostegal rays. The basihyal is absent. This apparatus is attached by connective tissue to the first basibranchial antero-dorsally and to the symplectic postero-dorsally. Since the features of the elements except for the urohyal and branchiostegal rays do not show great variation among the families and genera, it is appropriate to describe the general features of the elements.

The ceratohyal is short and expanded posteriorly. The bone articulates through cartilage anteriorly with the ventral hypohyal and antero-dorsally with the dorsal hypophyal. It articulates posteriorly through cartilage and interdigitation with the epihyal.

The epihyal is found between the ceratohyal and interhyal. The bone articulates antero-ventrally with the ceratohyal and dorsally with the interhyal and interopercular by fibrous connective tissue.

The interhyal is short rod shaped. The bone articulates by fibrous connective tissue ventrally with the epihyal and dorsally with the symplectic.

The dorsal and ventral hypohyals are well developed and placed at the most anterior part of the hyoid arch. Both hypohyals are articulated with one another by cartilage. The dorsal hypohyal is attached to the first basibranchial dorsally by fibrous connective tissue.

The urohyal is a single flattened bone situated under the anterior part of the branchial arches. The bone is articulated by fibrous connective tissue antero-ventrally with the medial surface of the hypohyal and dorsally with the ventral surface of the first and second basibranchials.

The branchiostegal rays are sword-like in shape, and vary in number from four to six among the families and genera. They increase in length posteriorly in the series in which the first ray is the widest and most flattened element. They are attached to the ceratohyal and epihyal by fibrous connective tissue.

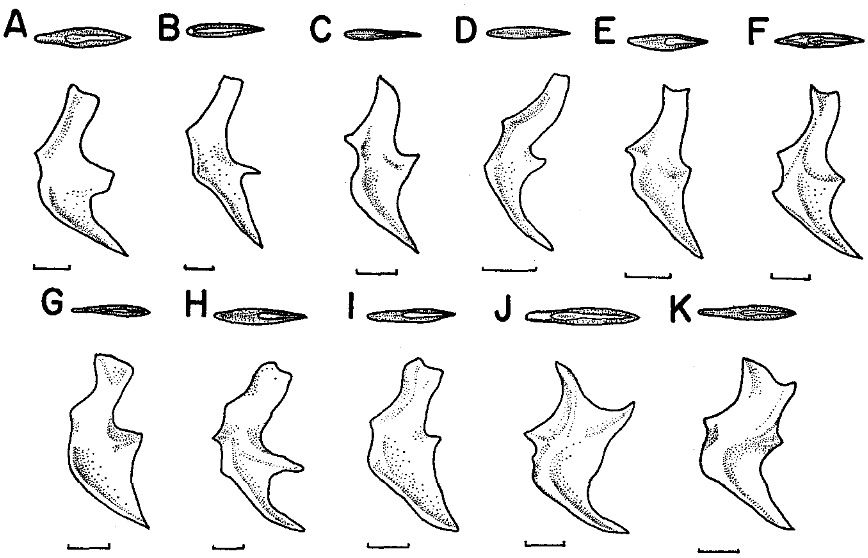


Fig. 26. Diagram showing the urohyal in 11 balistid species. A, *Balistapus undulatus*; B, *Balistodies conspicillum*; C, *Balistes vetula*; D, *Melichthys vidua*; E, *Pseudobalistes flavimarginatus*; F, *Abalistes stellatus*; G, *Odonus niger*; H, *Canthidermis maculatus*; I, *Xanthichthys mento*; J, *Rhinecanthus aculeatus*; K, *Sufflamen fraenatus*. Top, dorsal view; bottom, lateral view. Scale bars indicate 5 mm.

Since the balistids and monacanthids are primarily separated by the shape of the urohyal (Figs. 26 and 28), they are described independently in the following section.

Balistidae. There is little difference among the balistid members in the hyoid apparatus, thus they are grouped into a single group, Group A (Figs. 26 and 27). In this group the urohyal is an irregular plate with several projections at its edge. The genera *Rhinecanthus* and *Sufflamen* are different from the other genera in the feature of the interhyal (Fig. 27, J and K). In these two genera the interhyal is expanded and has a rather rough rectangular shape, while in the other genera the bone is like a short rod in shape. The branchiostegal rays are six in number and attached to the ceratohyal and epihyal. The first two rays articulate by fibrous connective tissue with the shallow depression on the ventral edge of the ceratohyal. The other four rays are attached to the lateral surface of the ceratohyal and epihyal.

Monacanthidae. The monacanthid members are clearly separated from the balistids by the shape of the urohyal which is like a flattened boomerang in shape except for *Pseudalutarius nasicornis* (Fig. 28, Q) which has a small knob on each ventral side of the urohyal. The monacanthid members are divided into the following three groups based on the number of the branchiostegal rays.

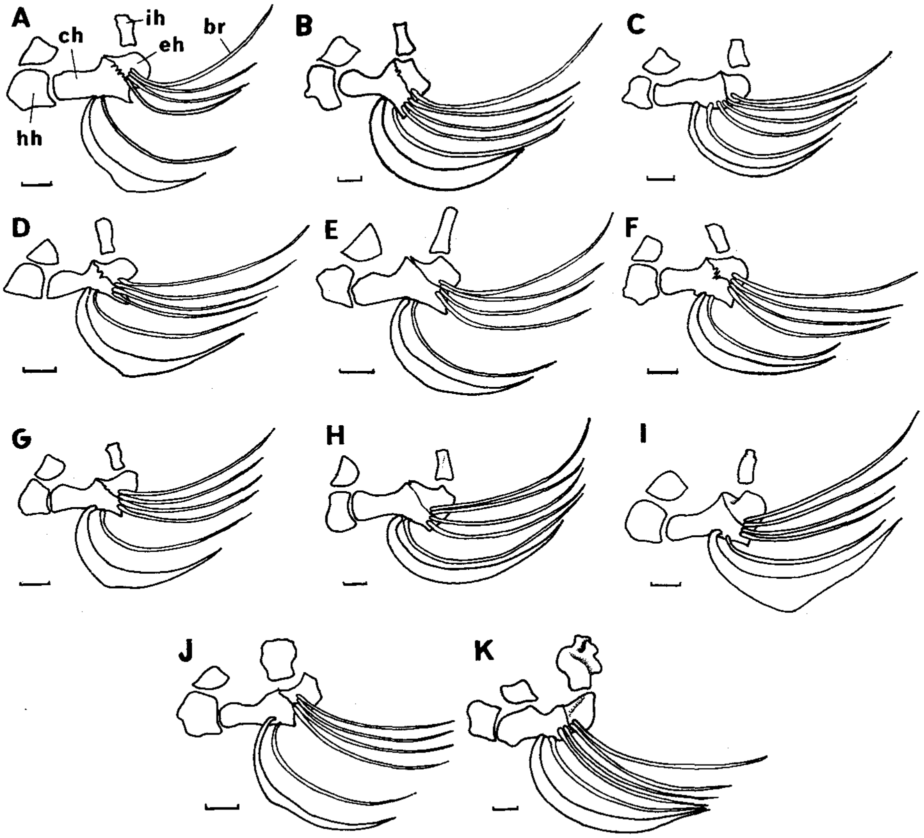
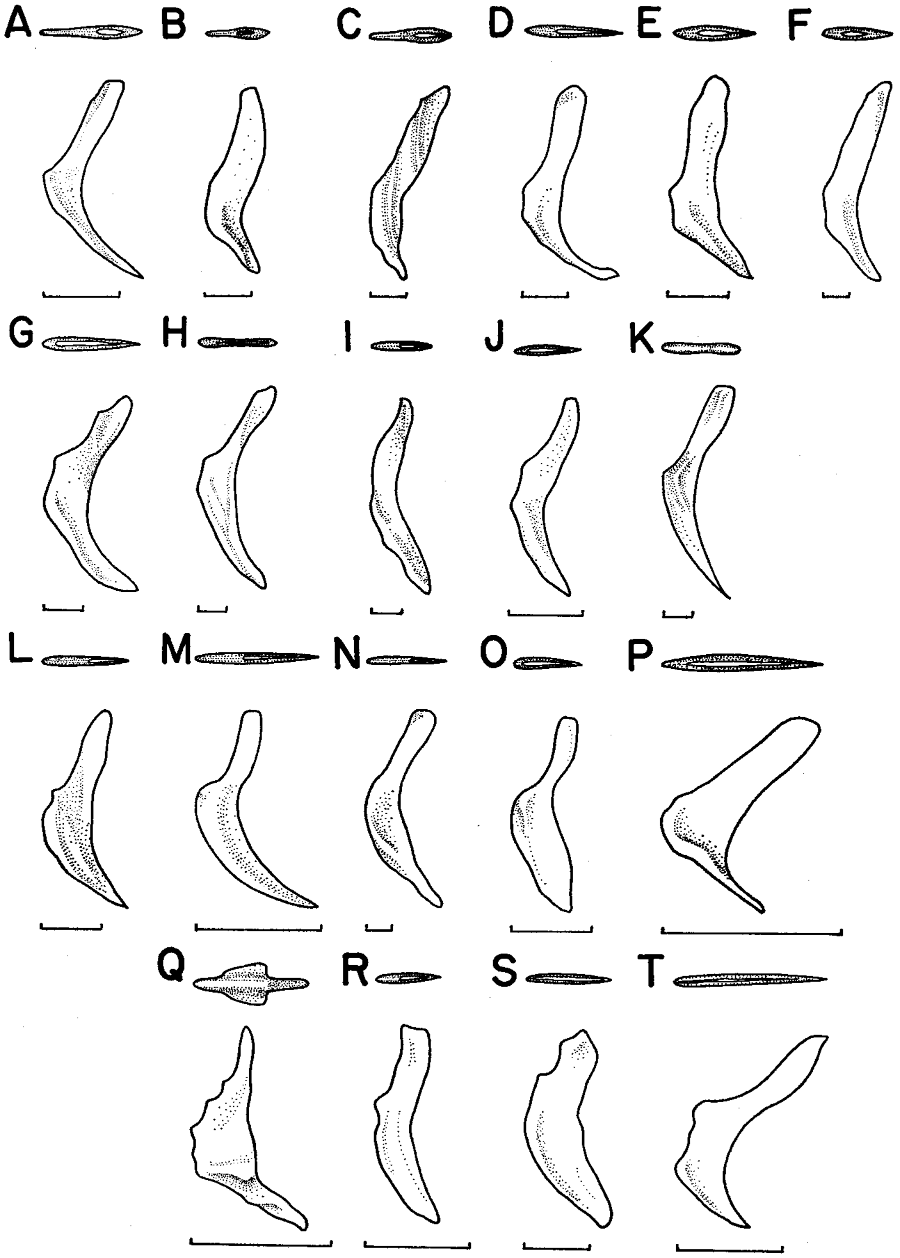


Fig. 27. Diagram showing the hyoid arch and branchiostegal rays in 11 balistid species from lateral view. A, *Balistapus undulatus*; B, *Balistoides conspicillum*; C, *Balistes vetula*; D, *Melichthys vidua*; E, *Pseudobalistes flavimarginatus*; F, *Abalistes stellatus*; G, *Odonus niger*; H, *Canthidermis maculatus*; I, *Xanthichthys mento*; J, *Rhinecanthus aculeatus*; K, *Sufflamen fraenatus*. br, branchiostegal rays; ch, ceratohyal; eh, epihyal; hh, hypohyal; ih, interhyal. Scale bars indicate 5 mm.

Group B. This group is composed of nine genera, *Alutera*, *Amanses*, *Cantherhines*, *Eubalichthys*, *Meuschenia*, *Navodon*, *Nelusetta*, *Pseudomonacanthus*, and *Stephanolepis* (Fig. 29). They are characterized by having six branchiostegal rays just like the balistids. The branchiostegal rays are attached to the ceratobranchial and epihyal in the same fashion as seen in the balistids. However, the genus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*Nelusetta* is distinguished from the other genera by having a thickened and greatly expanded first branchiostegal ray (Fig. 29, G).

Group C. This group includes 12 genera, *Acreichthys, Arotrolepis, Brachaluteres, Chaetoderma, Monacanthus, Oxymonacanthus, Paraluteres, Paramonacanthus, Pervagor, Pseudalutarius, Rudarius,* and *Stephanolepis.* The illustrations of 11 species cover the variation found in this group (Fig. 30). In this group the branchiostegal rays are five in number. The first branchiostegal ray is attached to the groove on the ventral edge of the ceratohyal, while the other four rays are attached to the lateral surface of the ceratohyal and epihyal by fibrous connective tissue. In the genera *Oxymonacanthus* and *Pseudalutarius*, the longest branchiostegal ray is more than two times as long as the hyoid arch (Fig. 30, H and I), while in the other genera the longest ray is less than two times as long as the arch. With regard to the other elements of the hyoid apparatus, the members of this group show only slight differences from that found in the fishes of Group B, although the genera *Pervagor* and *Paraluteres* are peculiar in the shape of the ventral hypohyal which projects antero-ventrally (Fig. 30, C and K).

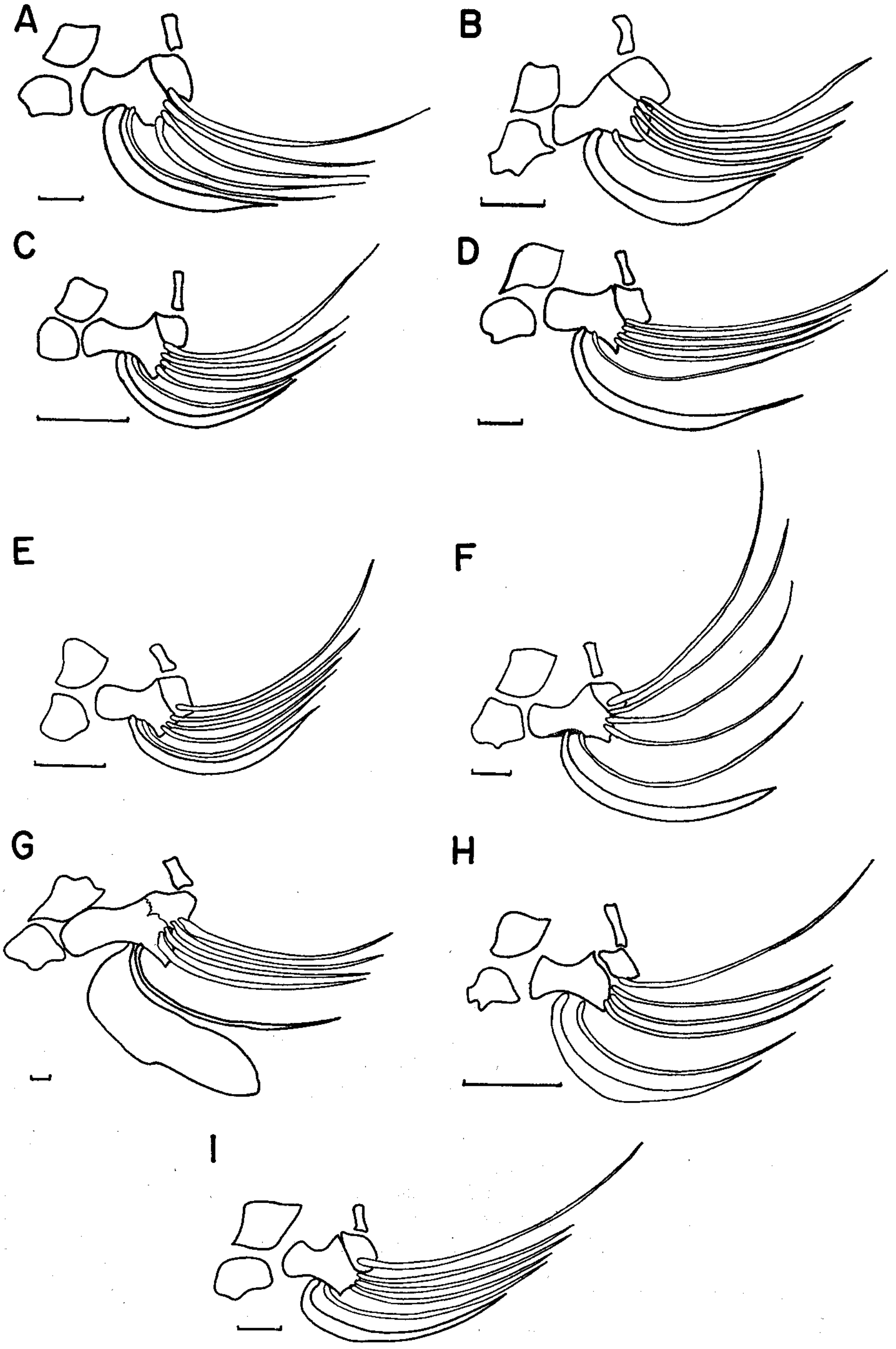
Group D. This group consists of a single genus *Anacanthus* which has four branchiostegal rays (Fig. 31). The first branchiostegal ray is attached to the depression on the ventral edge of the ceratohyal, however, the other three rays are attached to the lateral surface of the ceratohyal and epihyal. The other elements of the hyoid apparatus show no essential difference from those of the other monacanthid members.

**Discussion**. The balistoid hyoid apparatus is unusual in having the enlarged hypohyals and in lacking the basihyal among the teleostean fishes. It has been studied by several authors (Thilo, 1899, 1914; Tyler, 1962a; McAllister, 1968). Of these authors, McAllister (1968: pp. 153∼155) described accurately the hyoid apparatus of many balistoid members, however, it was insufficient for making out the whole aspect of the interrelationships in the balistoid members.

In the elements of the hyoid apparatus, the urohyal and branchiostegal rays provide us with important information from the phylogenetic view point. With regard to the urohyal, the balistids (Group A) are considered to be more primitive than the monacanthids (Groups B, C, and D), because the triacanthids, which are considered to be the ancestor of the balistoids, are closely similar to the balistids in the configuration of the urohyal (Fig. 32, A).

On the other hand, McAllister (1968: p. 177) studied the evolution of the branchiostegal rays of the teleostome fishes, and wrote that the forms with a high

Fig. 28. Diagram showing the urohyal in 20 monacanthid species. A, *Cantherhines dumerili*; B, *Amanses scopas*; C, *Pseudomonacanthus peroni*; D, *Navodon modestus*; E, *Meuschenia trachylepis*; F, *Scobinichthys granulatus*; G, *Nelusetta ayraudi*; H, *Eubalichthys mosaicus*; I, *Alutera monoceros*; J, *Monacanthus chinensis*; K, *Stephanolepis cirrhifer*; L, *Arotrolepis filicaudus*; M, *Paramonacanthus japonicus*; N, *Chaetoderma penicilligera*; O, *Rudarius ercodes*; P, *Oxymonacanthus longirostris*; Q, *Pseudalutarius nasicornis*; R, *Brachaluteres ulvarum*; S, *Paraluteres prionurus*; T, *Anacanthus barbatus*. Top, dorsal view; bottom, lateral view. Scale bars indicate 3 mm.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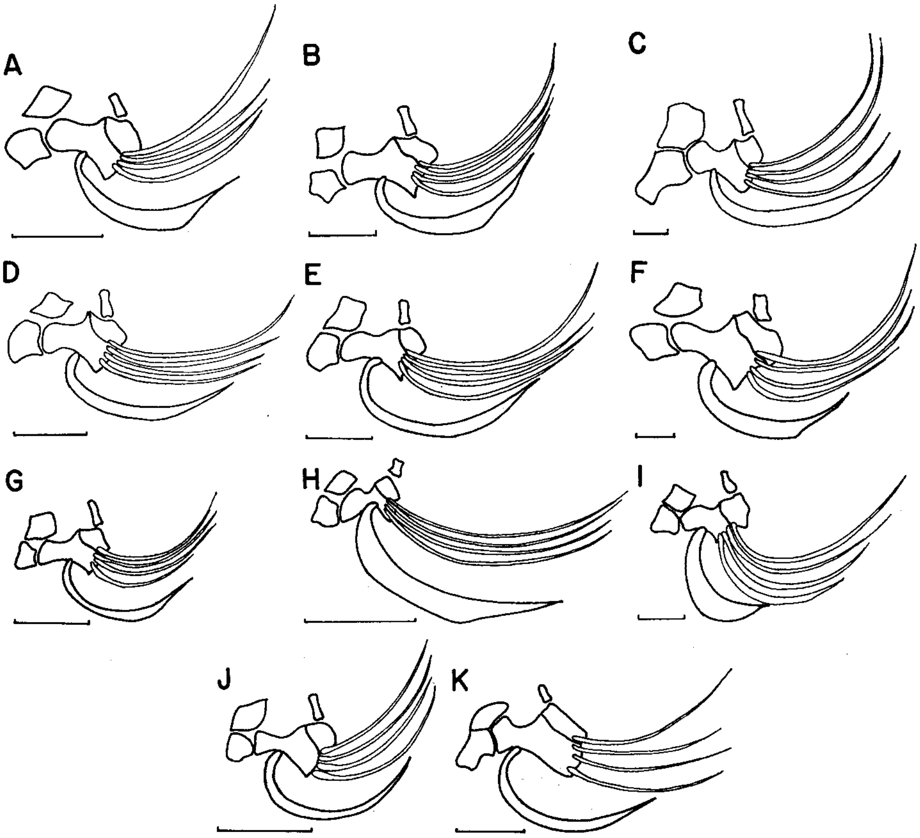

Fig. 30. Diagram showing the hyoid arch and branchiostegal rays in 11 monacanthid species from lateral view. A, *Monacanthus chinensis*; B, *Stephanolepis cirrhifer*; C, *Pervagor melanocephalus*; D, *Arotrolepis filicaudus*; E, *Paramonacanthus japonicus*; F, *Chaetoderma penicilligera*; G, *Rudarius ercodes*; H, *Oxymonacanthus longirostris*; I, *Pseudalutarius nasicornis*; J, *Brachaluteres ulvarum*; K, *Paraluteres prionurus*. Scale bars indicate 5 mm.

number of branchiostegal rays were generally found to be more primitive. Judging from this, the fishes of Groups A and B having the greatest number of branchiostegal rays in the balistoids would be more primitive than the other members. This speculation is reinforced by the fact that these two groups share six branchiostegal rays with the triacanthids (Fig. 32, B). With the combination of the features in the urohyal and branchiostegal rays, the fishes of Group A are consequently placed

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Fig. 29. Diagram showing the hyoid arch and branchiostegal rays in nine monacanthid species from lateral view. A, *Cantherhines dumerili*; B, *Amanses scopas*; C, *Pseudomonacanthus peroni*; D, *Navodon modestus*; E, *Meuschenia trachylepis*; F, *Scobinichthys granulatus*; G, *Nelusetta ayraudi*; H, *Eubalichthys mosaicus*; I, *Alutera monoceros*. Scale bars indicate 5 mm

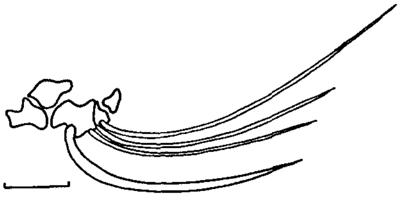


Fig. 31. Diagram showing the hyoid arch and branchiostegal rays in *Anacanthus barbatus* from lateral view. Scale bar indicates 5 mm.

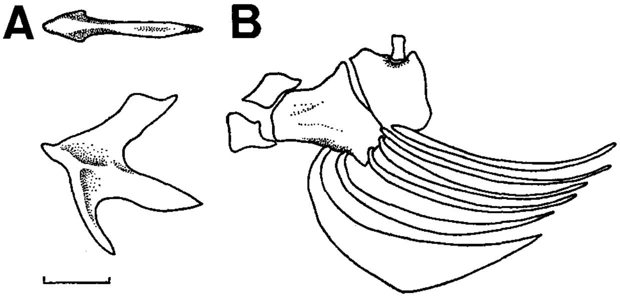


Fig. 32. Diagram showing the hyoid apparatus of a triacanthid species, *Trixiphichthys weberi*. A, the urohyal; B, the hyoid arch and branchiostegal rays. Scale bar indicates 5 mm.

at the most primitive systematic position among the balistoids. In the members of Group A, the genera *Rhinecanthus* and *Sufflamen* show a close similarity in their interhyals which are peculiarly like a rectangular in shape. This condition is not found in any other balistoid member, therefore these two genera are considered to be more advanced than the other members of Group A. In the monacanthids the fishes of Group B are assigned to the most primitive systematic stage, because they have the greatest number of the branchiostegal rays. The fishes of Group C having five branchiostegal rays are considered to be more advanced than the members of Group B. Finally, Group D, the genus *Anacanthus*, is considered to be the most advanced representative in the balistoids based on the fact that it has only four branchiostegal rays. Since McAllister (1968: p. 154) reported that in the genus *Anacanthus* (his *Psilocephalus*) the branchiostegal rays were three in number, the fishes of the genus show possibly an individual variation in the number of the branchiostegal rays. Though the discrepancy is recognizable between the results of the present study and McAllister (1968), it is not important for the phylogenetic consideration of the genus. The interrelationships of the balistoids based on the hyoid apparatus are summarized in Table 3.

It is noteworthy from the functional view point that the balistids have a larger urohyal than that of the monacanthids. Hiatt and Strasburg (1960: pp. 108 ~110) reported that the balistids fed on hard-bodied organisms with their massive, stout jaws but the monacanthids took the various items with their more or less feeble jaws. Since the urohyal is closely related to the opening mechanisms of the jaws through the sternohyoideus (Gosline, 1971: pp. 67 ~68), a larger urohyal may be able to acquire stronger power in opening the jaws because of the wider attachment of the sternohyoideus. Thus, it is considered that the balistids have more power to open their jaws than that of the monacanthids in relation to their food-habits.

Table 3. *Differentiation of the hyoid apparatus in the balistoids.*

| Group | Genus | Urohyal | Number of banchistegal rays |
|---|---|---|---|
| A | all genera of balistids | plate-like with several projections | 6 |
| B | *Alutera*<br>*Amanses*<br>*Cantherhines*<br>*Eubalichthys*<br>*Meuschenia*<br>*Navodon*<br>*Nelusetta*<br>*Pseudomonacanthus*<br>*Scobinichthys* | flattened boomerang-like | |
| C | *Acreichthys*<br>*Arotrolepis*<br>*Brachaluteres*<br>*Chaetoderma*<br>*Monacanthus*<br>*Oxymonacanthus*<br>*Paraluteres*<br>*Paramonacanthus*<br>*Pervagor*<br>*Pseudalutarius*<br>*Rudarius*<br>*Stephanolepis* | | 5 |
| D | *Anacanthus* | | 4 |

As previously described, the first branchiostegal ray is greatly expanded in the balistoids. Several authors reported that in the tetraodontiforms the branchiostegal rays might almost completely replace the opercular apparatus as a suction pump for the gill cavities (Gabriel, 1940; Williem, 1947; Gosline, 1971). Of these authors, Gosline (1971: p. 74) stated that in the tetraodontiform fishes, the opercles and branchiostegal rays seemed to form two wholly separate systems with different functions: the opercles via the long interopercles were used for lowering the mandible, while the branchiostegal rays formed a respiratory pump. On the other hand, McAllister (1968: p. 153) wrote that the expansion of the first branchiostegal ray was probably related to the small gill opening and to the stiffening of the wall of the branchial chamber by thick skin or bony plates. Therefore, it is concluded that the expanded first branchiostegal ray is related with the following two factors: to reinforce the respiratory pump and to stiffen the gill chamber.

## 6. Branchial arches

**Description.** The branchial arches support the gills and gill rakers, and are composed of three (usually) unpaired basibranchials, three pairs of the hypobranchials, five pairs of the ceratobranchials, four (usually) pairs of the epibranchials, and two or three pairs of the pharyngobranchials. These bones are filled with cartilage at their edges. In the branchial arches the fishes of the Balistidae are almost the same, though the members of the Monacanthidae show great variation and apparent reductive tendency. Therefore, the members of the two families are described independently in the following section.

Balistidae. The balistid members do not show great variation in their branchial arches, thus they are included in a single group, Group A. The balistid branchial arches always composed of five elements, three unpaired basibranchials, three pairs of the hypobranchials, five pairs of the ceratobranchials (the fifth element toothed), four pairs of the epibranchials, and three pairs of the pharyngobranchials. The illustrations of two species (Fig. 33) cover the variation in the balistid members.

The three basibranchials articulate with one another by fibrous connective tissue. The first basibranchial is like a short rod in shape. The second basibranchial is longer than the first, and is constricted in the middle portion. The bone articulates with the first hypobranchial by fibrous connective tissue. The third basibranchial is shorter than the second but longer than the first. The bone articulates antero-laterally with the second hypobranchial and postero-laterally with the third hypobranchial by fibrous connective tissue.

The hypobranchials are composed of three paired elements which decrease in size posteriorly in the series. They are placed between the basibranchials and ceratobranchials. The largest in the hypobranchial elements is the first hypobranchial which articulates laterally with the first ceratobranchial and posteriorly with the second hypobranchial by fibrous connective tissue. The second hypobranchial articulates laterally with the second ceratobranchial and posteriorly with the third hypobranchial which articulates postero-laterally with the third ceratobranchial.

The ceratobranchials consist of five slender paired bones which lie between the hypobranchials and epibranchials. The anterior four elements of the series are similar to one another in shape, and support the gill rakers. These four bones are connected postero-dorsally with the epibranchial by fibrous connective tissue. The fifth ceratobranchial is expanded proximally and tapered to a point distally. In contrast with the other ceratobranchial elements, the bone possesses two rows of teeth on its dorsal surface in which the posterior row is larger than the anterior one.

There are four pairs of the epibranchials in the upper limbs of the branchial arches. The first epibranchial is the largest element in the series and rounded at the ventral edge, although its dorsal portion forms two stubby projections. The anterior and posterior projections articulate respectively with the first and second pharyngobranchials. The second epibranchial is like a short rod in shape, and articulates drosally with the second pharyngobranchial by fibrous connective tissue. The third epibranchial is similar to the second in shape, and possesses the rounded ventral edge. The bone articulates dorsally with the third pharyngobranchial and posteriorly with the fourth slender epibranchial by fibrous connective tissue. The fourth epibranchial is longer than the second and third epibranchials, and articulate anteriorly with the third epibranchial and dorsally with the ventral portion of the third pharyngobranchial by fibrous connective tissue.

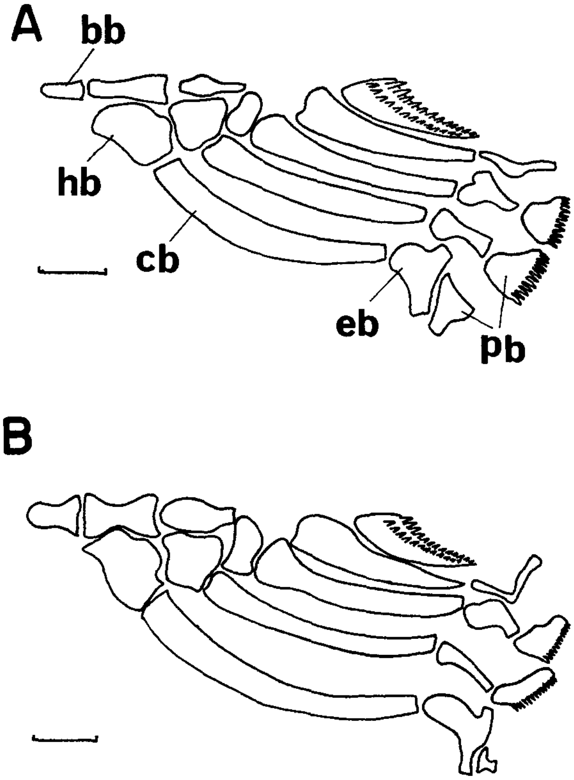


Fig. 33. Diagram showing the branchial arches in two balistid species from dorsal view. A, *Pseudobalistes flavimarginatus*; *B*, *Rhinecanthus aculeatus*. bb, basibranchial; cb, ceratobranchial; eb, epibranchial; hb, hypobranchial; pb, pharyngobranchial. Scale bars indicate 5 mm.

The pharyngobranchials are composed of three pairs of bones which are located at the uppermost part of the branchial arches. The first pharyngobranchial is a small bone expanded ventrally. The bone articulates ventrally with the first epibranchial and dorsally with the ventral portion of the parasphenoid at the level of the center of the orbit. The second pharyngobranchial is expanded dorsally and possesses a row of elongated teeth on its dorsal edge. The bone articulates ventrally with the second epibranchial. The third pharyngobranchial is similar to the second in shape, although it is somewhat smaller than the latter. These two pharyngobranchials are held together by fibrous connective tissue.

Monacanthidae. The monacanthid branchial arches show a great variation among the genera. There are two to four unpaired basibranchials, three paris of the hypobranchials, five pairs of the ceratobranchials (the fifth element toothless), three or four pairs of the epibranchials, and two or three pharyngobranchials. The monacanthid members are divided into the following groups based on the diffrentiation of the branchial arches.

Group B. This group is represented by a single genus *Oxymonacanthus*. The fishes of this group are clearly different from the balistids in having no teeth on the fifth ceratobranchial, though they are essentially similar to the members of the latter in other branchial arch elements (Fig. 34, A).

There are three unpaired basibranchials on the mid-line of the branchial arches. The interspaces between the three elements filled with cartilage are wider than that found in the balistids. The first basibranchial is the shortest element in the series. The third basibranchial shows an intermediate length between the first and second basibranchials.

There are three pairs of the hypobranchials which are short rod and more feeble than that found in the fishes of Group A.

Five pairs of the ceratobranchials are found in the fishes of Group B. The anterior three ceratobranchials are slender rod in shape, though the fourth

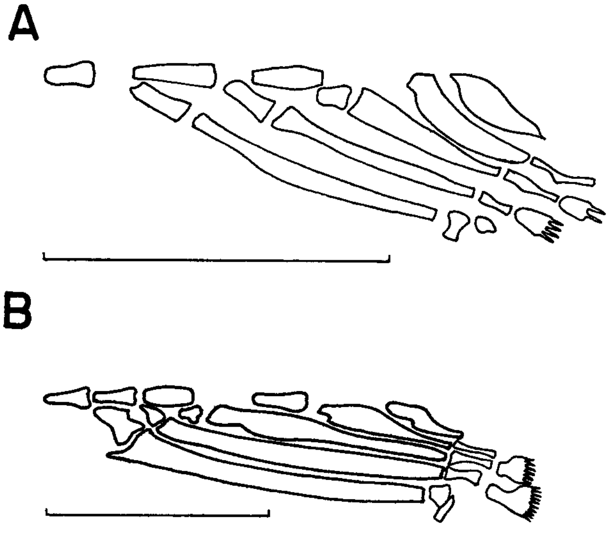


Fig. 34. Diagram showing the branchial arches in two monacanthid species from dorsal view. A, *Oxymonacanthus longirostris*; B, *Paraluteres prionurus*. Scale bars indicate 5 mm.

element is relatively wide. The fifth ceratobranchial, without teeth, is expanded proximally and tapered to a point distally.

There are four pairs of the epibranchials in the upper limbs of the branchial arches. The first element is constricted at the middle portion. The posterior elements are like a short rod in shape, and increase in size posteriorly in the series.

Three pairs of the pharyngobranchials are present at the uppermost portion of the branchial arches. The first element is rounded at the ventral edge and articulated with the first epibranchial by fibrous connective tissue. The bone also articulates dorsally with the ventral portion of the parasphenoid to make the suspension for the branchial arches. The second element is larger than the first, and bears four small elongated teeth on the dorsal edge. The third element is slightly smaller than the second, and also possesses the small elongated teeth at the dorsal edge, though the number of teeth is reduced to only two. The second and third elements are articulated with one another by fibrous connective tissue.

Group C. This group includes only one genus *Paraluteres*. The fishes of the group are clearly distinguished from the members of Groups A and B in having four unpaired basibranchials (Fig. 34, B). The anterior three basibranchials are normal in position, though the fourth basibranchial is present posteriorly some distance from the third element. The fourth element articulates anteriorly with the third element, laterally with the third ceratobranchial, and posteriorly with the fourth ceratobranchial by fibrous connective tissue.

Three pairs of the pharyngobranchials are present at the same position as seen in Groups A and B. They decrease in size posteriorly in the series. There are five pairs of the ceratobranchials in this group. The first three elements are slender rod and similar to one another in shape. The fourth element is distinguished from the former by its smaller size and shape. The bone is expanded proximally and tapered to a blunt point postero-dorsally. The fifth element is shorter than the fourth, and shows no trace of teeth on its dorsal surface.

Four pairs of the epibranchials are found in the upper limbs of the branchial arches. The first element is expanded dorsally and connected with the first ceratobranchial. The posterior three epibranchials are different from the first in shape. They are short rod in shape and increase in size posteriorly in the series.

There are three pairs of the pharyngobranchials. The first element is a small bone which is tightly held ventrally to the first epibranchial and dorsally to the ventral portion of the parasphenoid at the level of the center of the orbit. The second element bearing six small elongated teeth on the dorsal edge is the largest in the series. The third element is smaller than the second in size, and possesses 10 small elongated teeth on the dorsal edge. These two toothed elements are held together by fibrous connective tissue.

Group D. This group is composed of 19 genera, *Acreichthys*, *Alutera*, *Amanses*, *Arotrolepis*, *Brachaluteres*, *Cantherhines*, *Chaetoderma*, *Eubalichthys*, *Meuschenia*, *Monacanthus*, *Navodon*, *Nelusetta*, *Paramonacanthus*, *Pervagor*, *Pseudalutarius*, *Pseudomonacanthus*, *Rudarius*, *Scobinichthys*, and *Stephanolepis*. The illustrations of 16 species (Figs. 35 and 36) cover the variation found in the members of this group. They are primarily characterized by having no trace of the first pharyngobranchial which is present in the foregoing groups.

There are three unpaired basibranchials in the fishes of this group. The first element is triangular in shape. The second and third elements are short rod in shape, though in *Pseudalutarius nasicornis* the second element is well expanded posteriorly (Fig. 36, I).

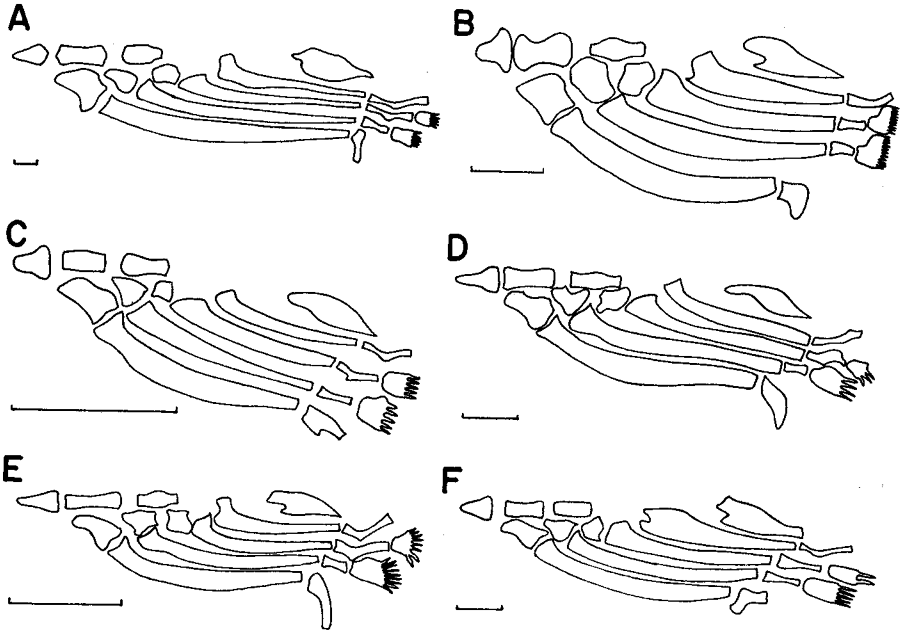


Fig. 35. Diagram showing the branchial arches in six monacanthid species from dorsal view. A, *Arotrolepis filicaudus*; B, *Chaetoderma penicilligera*; C, *Monacanthus chinensis*; D, *Paramonacanthus japonicus*; E, *Stephanolepis cirrhifer*; F, *Cantherhines dumerili*. Scale bars indicate 5 mm.

Three pairs of the hypobranchials are found between the basibranchials and ceratobranchials in the lower limbs of the branchial arches. The hypobranchials decrease in size posteriorly in the series.

There are five pairs of the ceratobranchials. The anterior four ceratobranchials are similar to one another in shape, and decrease in size posteriorly in the series. The fifth element is expanded proximally and tapered to a point dorsally. There is no trace of any teeth on its dorsal surface.

Four pairs of the epibranchials are found in the upper limbs of the branchial arches. The first element varies in shape among genera, though it is always larger than the second element. In contrast with the other groups the first element articulates dorsally with the ventral portion of the parasphenoid at the level of the center of the orbit. In other words, its function is to suspend the branchial arches

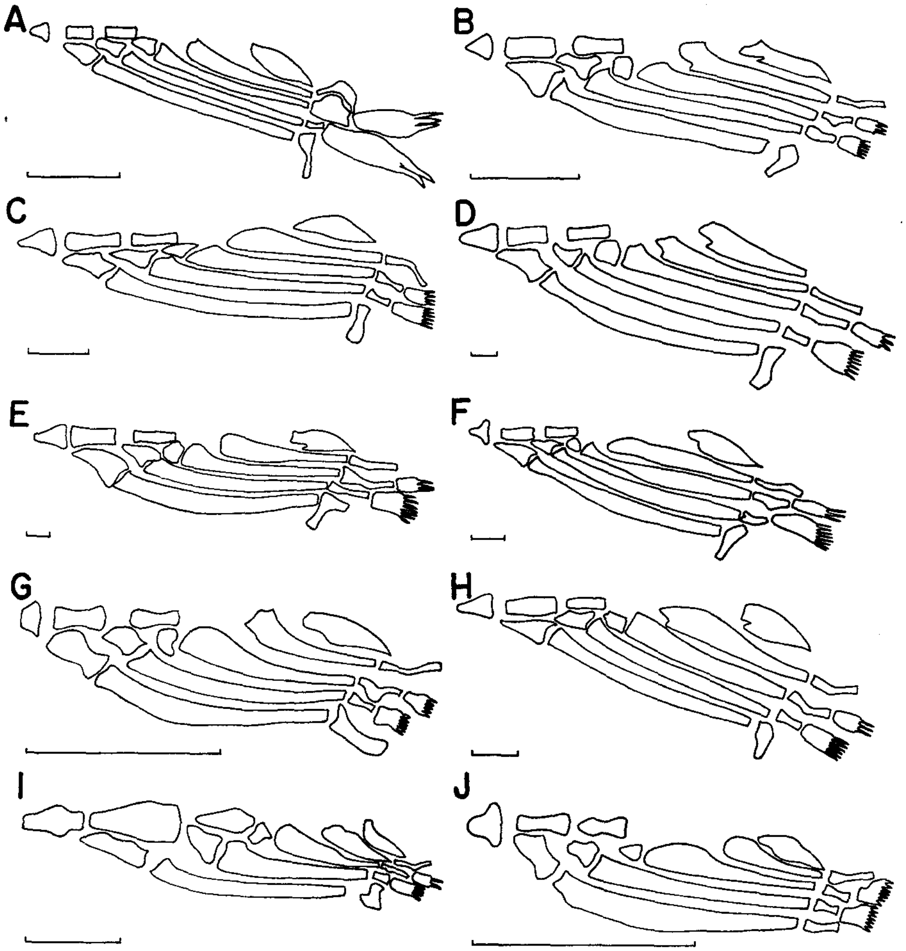


Fig. 36. Diagram showing the branchial arches in 10 monacanthid species from dorsal view. A, *Pseudomonacanthus peroni*; B, *Meuschenia trachylepis*; C, *Navodon modestus*; D, *Nelusetta ayraudi*; E, *Scobinichthys granulatus*; F, *Eubalichthys mosaicus*; G, *Rudarius ercodes*; H, *Alutera monoceros*; I, *Pseudalutarius nasicornis*; J, *Brachaluteres ulvarum*. Scale bars indicate 5 mm.

from the parasphenoid in this group. The second to fourth elements are short rod in shape in many members of this group, in *Pseudomonacanthus peroni* the third element is greatly expanded at the middle portion and projected posteriorly to articulate with the concave anterior edge of the fourth element (Fig. 36, A). Except for the species the epibranchials increase in size posteriorly from the second to fourth elements in the members of this group.

Two pairs of the pharyngobranchials are found at the uppermost part of the branchial arches. There is no trace of the first pharyngobranchial. The second element is rounded at the ventral edge, and slightly expanded dorsally. The element has many small elongated teeth on the dorsal side which vary in number from two to 11 among genera. The third element is slightly smaller than the second in size. *Pseudomonacanthus peroni* is peculiar in having a greatly enlarged second element bearing two teeth which seem to be a paired claw. It also has three claw-like teeth prominent on the dorsal edge of the enlarged third element.

Group E. This group consists of a single genus *Anacanthus* which is characterized by an apparent reduction in the basibranchials, epibranchials, and pharyngobranchials (Fig. 37).

Fig. 37. Diagram showing the branchial arches in *Anacanthus barbatus* from dorsal view. Scale bar indicates 5 mm.

There are only two unpaired basibranchials which are elongated rod in shape. The place for the third basibranchial as seen in the other groups is occupied by cartilage only.

Three pairs of the hypobranchials are present in this group. Five pairs of the ceratobranchials are found in a normal position. The first ceratobranchial is greatly elongated and slightly expanded proximally. The second element is shorter than the first, though its proximal portion is wider than that of the first. The third to fifth elements decrease in size posteriorly in the series. The fifth element has no trace of teeth on its dorsal surface.

There are three pairs of the epibranchials in the upper limbs of the branchial arches. In contrast with the other members of the balistoids, the first element is absent in the group. The epibranchials increase in size posteriorly in the series.

Very small two pairs of the pharyngobranchials are found at the uppermost part of the branchial arches. There is no trace of the first pharyngobranchial just as in the fishes of Group D. The second and third elements possess two small elongated teeth on each dorsal edge. The second element articulates dorsally with the ventral portion of the parasphenoid at the level of the center of the orbit to suspend the branchial arches. These toothed elements articulate with one another by fibrous connective tissue.

**Discussion**. Hitherto, with respect to the balistoid branchial arches, adequate anatomical studies have not been carried out by any author other than Tyler (1962a) who described the branchial arches of a balistid species *Balistapus undulatus*. Therefore, we must define the criterion in order to evaluate the phylogenetic significance of the balistoid branchial arch elements.

As seen in the preceding description, an apparent reductive tendency is found in the balistoid branchial arches, and seems to be a criterion for this phylogenetic consideration. Thus, it is appropriate to answer whether or not the reductive tendency corresponds with the evolutional trends in the balistoids. The triacanthids considered to be the ancestor of the balistoids have three unpaired basibranchials, three pairs of the hypobranchials, five pairs of the ceratobranchials (the fifth element toothed), four pairs of the epibranchials, and four pairs of the pharyngobranchials (the second to fourth elements toothed) (Tyler, 1968: p. 53). This triacanthid condition, except for the pharyngobranchials, is very similar to that found in the fishes of Group A which have the most developed branchial arches in the balistoids. Thus, it is recognizable that the more developed branchial arches indicate a more primitive condition. In other words, the more reduced branchial arches suggest a more advanced state. Therefore, we can reasonably come to the conclusion that the reductive tendency in the branchial arches corresponds with the evolutional trends in the balistoids.

Judging from this criterion, the fishes of Group A are considered to be placed at the most primitive systematic position in the balistoids, because they have the most developed branchial arches. The fishes of the monacanthids (Groups B to E) seem to be more advanced than the members of the balistids (Group A) on the basis of the fact that the teeth on the fifth ceratobranchial is absent in Groups B to E but present in Group A as well as in the triacanthids.

With respect to the interrelationships of the groups in the monacanthids, the branchial arches provide us with significant information. The fishes belonging to Group B are essentially similar to the members of Group A in the branchial arches other than the toothless fifth ceratobranchial, thus they are considered to be situated at the most primitive systematic position in the monacanthids.

Group C, the genus *Paraluteres*, resembles the fishes of Group B but distinct from the latter in the number of the basibranchials. In this group the fourth basibranchial is added to the normal three basibranchials. Nelson (1969: p. 511) stated the ossified fourth and fifth basibranchials were known in some teleosts (Ostariophysi), in which both possibly arose secondarily. Moreover, he wrote that there was no evidence that the separately ossified fourth and fifth basibranchials were very primitive structures among vertebrates, therefore they might be regarded as of secondary origin also in lower actinopterygians. Thus, the fourth basibranchial found in this group is considered to be the secondary structure. Judging from this criterion the group is therefore placed at a more advanced state than that of Group B.

The fishes of Group D possess more reduced branchial arches than that found in the preceding groups. The members of the group do not possess any trace of the first pharyngobranchial, though in the other branchial arch elements they show a similar condition to that seen in the foregoing groups. Thus, the first epibranchial serves to suspend the branchial arches from the parasphenoid in the members of this group. In other words, it replaced functionally the first pharyngobranchial as a suspending apparatus. These facts lead us to conclude that the group is more advanced than Groups A, B, and C. The shape and number of teeth on the second and third pharyngobranchials show the great variation among genera, however, it is premature to take these characters into consideration of the phylogeny, because the feeding habits may have an effect on the teeth of these bones.

An extreme reduction of the branchial arches is found in the fishes of Group E including a single genus *Anacanthus*. There are only two basibranchials and three pairs of the epibranchials in this group, though the other elements are present in the same position as seen in the fishes of Group D. Since the first pharyngobranchial or the first epibranchial, which is used for the suspending apparatus in the preceding groups, is absent in this group, the second pharyngobranchial is employed as the new suspending apparatus. Thus, it is concluded that Group E is considered to be the most advanced representative among the balistoids. The differentiation of the branchial arches in the balistoids is summarized in Table 4.

Table 4. *Differentiation of the branchial arches in the balistoids.*

| Group | Genus | Number of basibranchials | Teeth on fifth ceratobranchials | Number of epibranchials | Number of pharyngobranchials |
|---|---|---|---|---|---|
| A | all genera of balsitids | 3 | present | 4 | 3 |
| B | *Oxymonacanthus* | | absent | | |
| C | *Paraluteres* | 4 | | | 2 |
| D | *Acreichthys*<br>*Alutera*<br>*Amanses*<br>*Arotrolepis*<br>*Brachaluteres*<br>*Cantherhines*<br>*Chaetoderma*<br>*Eubalichthys*<br>*Meuschenia*<br>*Monacanthus*<br>*Navodon*<br>*Nelusetta*<br>*Paramonacanthus*<br>*Pervagor*<br>*Pseudalutarius*<br>*Pseudomonacanthus*<br>*Rudarius*<br>*Scobinicthys*<br>*Stephanolepis* | 3 | | | |
| E | *Anacanthus* | 2 | | 3 | |

## 7. Cranium

**Description.** The balistoid cranium is nearly always composed of 13 bones, the ethmoid, the vomer, the frontal, the prefrontal, the parasphenoid, the pterosphenoid, the sphenotic, the prootic, the pterotic, the epiotic, the supraoccipital, the exoccipital, and the basiocciptial. In addition to these bones a scale bone is found in only the balistid genus *Canthidermis*. Since the posttemporal, although essentially an element of the pectoral girdle, is rigidly wedged into the cranium, it is described here. The balistids and monacanthids are clearly separated by the relation between the cranium and the first dorsal fin, and the features of the ethmoid, the parasphenoid, and the posttemporal. Thus, they are described independently in the following section.

Balistidae. The balistid members are mainly characterized by the following features: the supraoccipital and epiotic form postero-dorsally the concavity into which the ventral shaft of the first dorsal fin is wedged; the dorsal keel of the parasphenoid is developed for muscle attachment; the posttemporal articulates with the epiotic. They are divided into the following three groups based on the absence or presence of the scale bone, and the feature of the frontal.

Group A. This group includes only one genus *Canthidermis* which is unique in having the scale bone among the balistid members (Fig. 38, A).

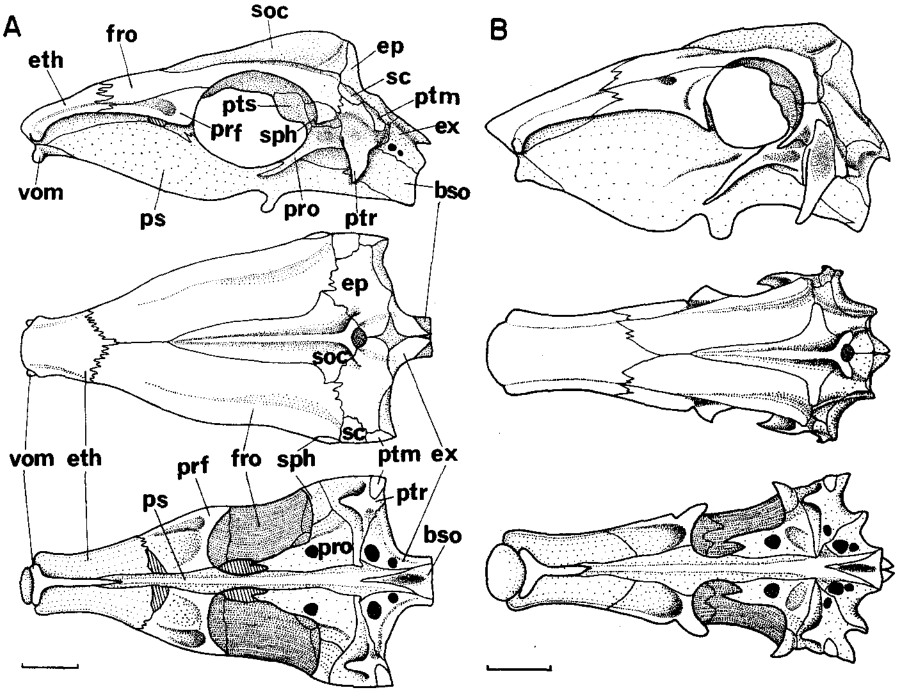


Fig. 38. Diagram showing the cranium in two balistid species. A, *Canthidermis maculatus*; B, *Pseudobalistes flavimarginatus*. bso, basioccipital; eth, ethmoid; ep, epiotic; ex, exoccipital; fro, frontal; prf, prefrontal; pro, prootic; ps, parasphenoid; ptm, posttemporal; ptr, pterotic; pts, pterosphenoid; sc, scale bone; sph, sphenotic; soc, supraoccipital; vom, vomer. Cartilaginous mass is indicated by the regions with oblique lines. Top, lateral view; middle, dorsal view; bottom ventral view. Scale bars indicate 10 mm.

The ethmoid is expanded laterally and posteriorly, and is placed at the most anterior region of the cranium. The bone has a keel ventrally to which the parasphenoid and vomer articulates by slight interdigitation. It articulates postero-laterally with the prefrontal and postero-dorsally with the frontal by interdigitation. At its anterior portion the ethmoid articulates with the upper jaw and the inner surface of the palatine by fibrous connective tissue.

The vomer is a small T-shaped bone and situated just below the ethmoid. The bone articulates posteriorly with the concavity on the parasphenoid, and dorsally with the ethmoid. It also connects antero-laterally with the medial surface of the palatine by fibrous connective tissue.

The frontal is a large bone which forms the dorsal edge of the orbit. Along its dorso-medial edge the frontal articulates with the opposite fellow. It articulates anteriorly with the ethmoid, antero-laterally with the prefrontal, postero-laterally with the sphenotic, posteriorly with the epiotic and scale bone, and ventrally with the pterosphenoid by interdigitation. At the antero-ventral portion of the frontal there is a cartilaginous mass which connects with the ethmoid, the parasphenoid, and the prefrontal.

The prefrontal is laterally expanded and along its medial edge articulates with the frontal. The bone articulates anteriorly with the ethmoid and ventrally with the parasphenoid.

The parasphenoid is the largest bone which occupies almost the entire length of the ventral surface of the cranium. It forms the ventral edge of the orbit, and is expanded antero-dorsally to form a large portion of the keel. It articulates antero-ventrally with the vomer, antero-dorsally with the ethmoid and prefrontal, and postero-dorsally with the prootic by interdigitation. At its posterior edge the parasphenoid is divided to make forked projection which lies on the anterior half of the basioccipital.

The pterosphenoid is located on the inner surface of the posterior half of the orbit. The bone articulates dorsally with the frontal, laterally with the sphenotic, and ventrally with the prootic by interdigitation. Dorso-medially it also articulates with its opposite fellow.

The sphenotic is situated at the postero-lateral corner of the orbit, and has an antero-ventrally directed projection. The bone articulates dorsally with the frontal, anteriorly with the pterosphenoid, ventrally with the prootic, and postero-ventrally with the pterotic.

The posttemporal is rigidly wedged into the cranium and embraced by the epiotic, the scale bone, and the pterotic. At its ventral surface the posttemporal articulates with the dorsal end of the supracleithrum by fibrous connective tissue.

The prootic lies on the postero-ventral portion of the orbit, and at its posterior part the bone has a concavity to which the anterodorsal edge of the hyomandibular attaches by fibrous connective tissue. The bone possesses an anteriorly directed projection which forms the shelf for the eye ball. It articulates antero-medially with the pterosphenoid, medially and ventrally with the parasphenoid, dorsally with the sphenotic, and posteriorly with the pterotic.

The pterotic is a triangular shaped bone tapering to a point ventrally. Postero-dorsally the bone is projected to make a flange, and just anterior to the flange it has a concavity to which the postero-dorsal end of the hyomandibular attaches by fibrous connective tissue. The pterotic articulates anteriorly with the sphenotic and prootic, antero-dorsally with the frontal, dorsally with the scale bone and posttemporal, postero-dorsally with the exoccipital, and ventro-medially with the basioccipital.

The epiotic lies on the postero-dorsal portion of the cranium. At the dorso-medial edge of the bone there is a deep concavity into which the ventral shaft of the basal pterygiophore of the first dorsal fin inserts. The bone articulates anteriorly with the supraoccipital and frontal, laterally with the scale bone and posttemporal, ventro-laterally with the pterotic, posteriorly with the exoccipital, and medially with its opposite fellow.

The supraoccipital forms the roof of the cranium and is tapered to a point anteriorly. The low crest runs along the mid line of the dorsal surface of the bone. At its posterior end the crest is thickened to make an articular facet to which the ventral shaft of the basal pterygiophore of the first dorsal fin is wedged. The bone articulates antero-laterally with the frontal and postero-laterally with the epiotic.

The exoccipital is situated at the postero-dorsal portion of the cranium, and projected posteriorly to form the wall of the foramen magnum. It articulates anteriorly with the epiotic and pterotic, and ventrally with the basioccipital by interdigitation. Posteriorly, it also articulates with the bifid neural spines of the first vertebra by fibrous connective tissue and slight interdigitation.

The basioccipital forms the postero-ventral part of the cranium and is like a short column in shape. The ventro-medial surface of the bone has a longitudinal depression running through almost its entire length. The bone articulates anteriorly with the prootic, antero-laterally with the pterotic, antero-ventrally with the forked posterior end of the parasphenoid, and dorsally with the exoccipital.

The scale bone, a distinct character of this group, lies on the postero-lateral surface of the cranium, and is almost rounded in shape. The bone articulates anteriorly with the frontal, dorsally with the epiotic, posteriorly with the posttemporal, and ventrally with the pterotic.

Group B. This group is composed of nine genera, *Balistes, Balistapus, Melichthys, Sufflamen, Odonus, Pseudobalistes, Balistoides, Rhinecanthus,* and *Xanthichthys.* It is clearly distinguished from Group A by the absence of the scale bone and the relation of the frontal, the epiotic, and the pterotic, although it essentially resembles the latter in the other cranial bones. The illustrations of four species essentially cover the variation found in this group (Figs. 38, B; 39 and 40, A).

The members of this group have no trace of the scale bone. The place occupied by the bone in Group A is covered by the epiotic and sphenotic in this group. The frontal does not articulate postero-ventrally with the pterotic by the intervention of the sphenotic in this group, though in Group A it articulates directly with the pterotic.

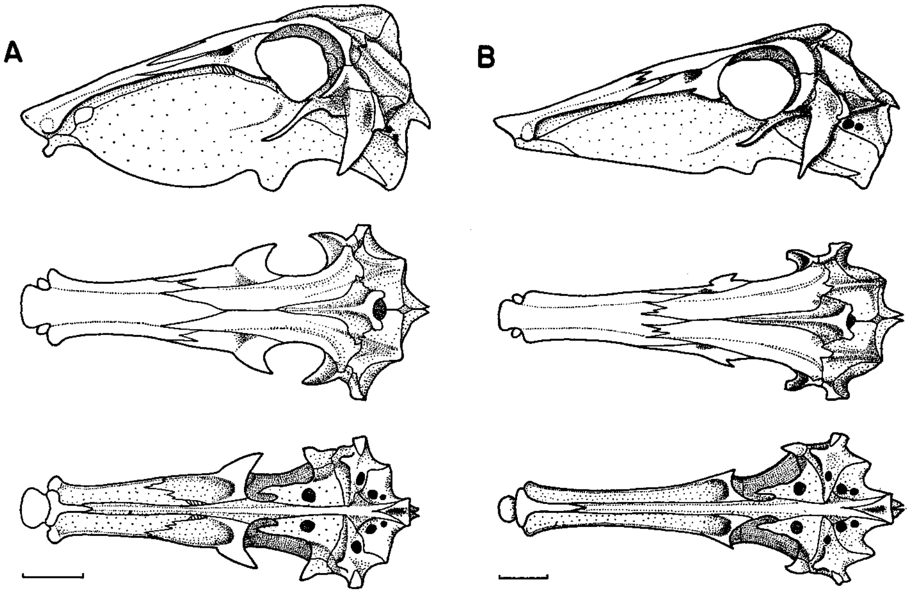


Fig. 39. Diagram showing the cranium in two balistid species. A, *Balistapus undulatus*; B, *Sufflamen fraenatus*. Top, lateral view; middle dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

Group C. This group comprises only one genus *Abalistes* and is characterized by having the frontal expanded greatly (Fig. 40, B). The frontal is expanded posteriorly beyond the level of the posterior edge of the posttemporal, and forms the rounded postero-dorsal surface of the cranium. In the other cranial bones this group has close resemblance to the fishes of Group B.

Monacanthidae. The monacanthids are distinguished from the balistids in the following characters: the supraoccipital and epiotic do not form postero-dorsally the concavity for support of the first dorsal fin, but the large part of the dorsal surface of the cranium is overlain by the basal pterygiophore of the first dorsal fin; the longitudinal dorsal keel of the parasphenoid as seen in the balistids is almost completely replaced by the ventral keel of the ethmoid; the posttemporal does not articulate with the epiotic. The monacanthid members are divided into the following groups and subgroups based on the relations between the cranial bones and the basal pterygiophore of the first dorsal fin, and the features of the frontal and posttemporal. The following description is limited to the significant differences from the balistids to avoid repeating the account described in the preceding section. In the illustrations for the monacanthid members the dorsal fin and the first vertebra are shown with the cranium, because these elements have a closer relation with the cranium than that found in the balistids.

Group D. This group is primarily distinguished from the balistids in having the articulation between the dorsal surface of the cranium and the basal pterygio-

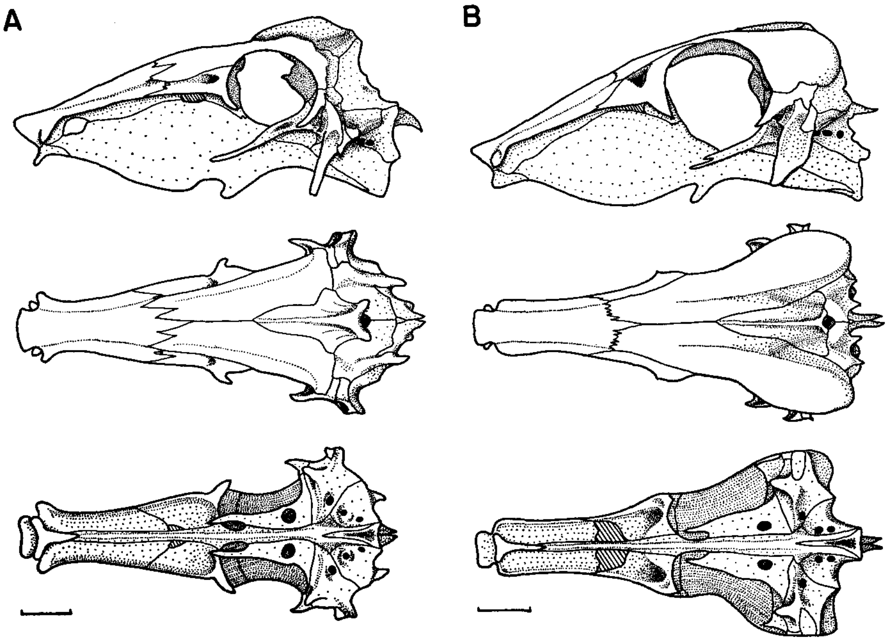


Fig. 40. Diagram showing the cranium in two balistid species. A, *Balistoides conspicillum*; B, *Abalistes stellatus*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

phore of the first dorsal fin. Furthermore, the members of the group are subdivided into three subgroups on the basis of the relation between the cranial bones and the basal pterygiophore of the first dorsal fin. In other words, it is based on the tendency of the forward migration of the basal pterygiophore of the first dorsal fin on the dorsal surface of the cranium.

The first subgroup, Subgroup a, comprises 10 genera, *Acreichthys*, *Alutera*, *Arotrolepis*, *Chaetoderma*, *Eubalichthys*, *Monacanthus*, *Nelusetta*, *Paramonacanthus*, *Scobinichthys*, and *Stephanolepis*. The illustrations of six species cover the variation found in this subgroup (Figs. 41 to 43). This subgroup is characterized by the fact that the anterior tip of the basal pterygiophore of the first dorsal fin does not articulate with the ethmoid but with the supraoccipital.

The ethmoid is greatly expanded ventrally to make a large keel for muscle attachment. With regard to the vomer there is little to say here, since it is closely similar to that of the balistids. The frontal is concave dorsally and articulates postero-medially with the basal pterygiophore of the first dorsal fin. The prefrontal is more reduced in size than that found in the balistids. The parasphenoid is slightly reduced in size, and most of the dorsal expansion of the bone as seen in the balistids is replaced by the ventral keel of the ethmoid. The pterosphenoid and sphenotic do not indicate any significant difference from those of the balistids. In contrast with the balistids the posttemporal does not show any

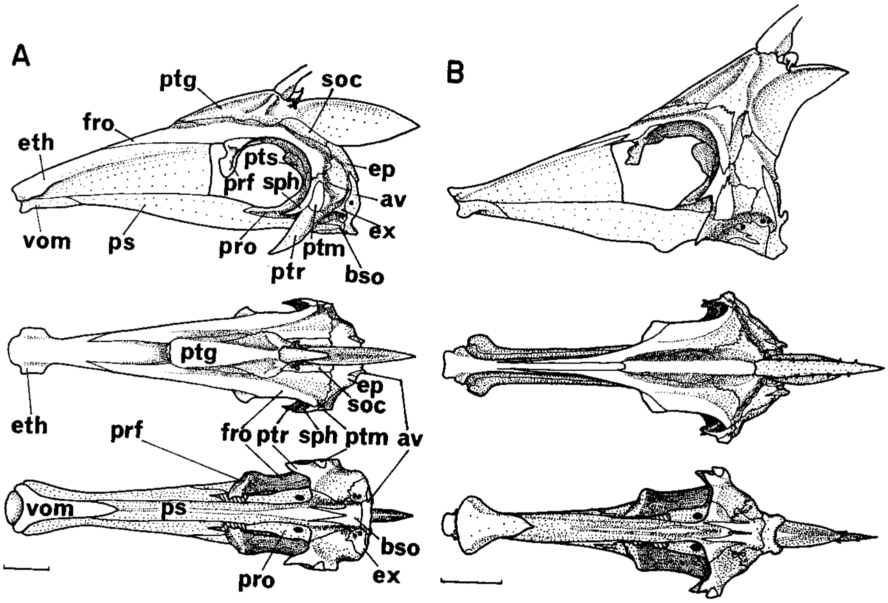


Fig. 41. Diagram showing the cranium, the first drosal fin, and the first abdominal vertebra in two monacanthid species. A, *Alutera monoceros*; B, *Chaetoderma penicilligera*. ab, the first abdominal vertebra; ptg, pterygiophore of the first dorsal fin. Other abrreviations as in Fig. 38. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

trace of the articulation with the epiotic, though the bone articulates with the sphenotic and pterotic. The prootic is very similar to that of the balistids, however, the anterior projection of the bone is much shorter than that of the latter. The pterotic is very similar to that of the balistids. The epiotic has no concavity on its postero-dorsal surface as seen in the balistids, but articulates dorsally with the postero-ventral surface of the basal pterygiophore of the first dorsal fin. The supraoccipital is almost covered by the basal pterygiophore of the first dorsal fin, though the anterior and postero-lateral portions of the bone are excluded from the edge of the basal pterygiophore. The exoccipital and basioccipital are quite similar to those of the balistids.

The second subgroup, Subgroup b, is composed of two genera, *Brachaluteres* and *Paraluteres* (Fig. 44). The members of this subgroup are different from the fishes of Subgroup a in having a direct articulation between the anterior tip of the basal pterygiophore of the first dorsal fin and the frontal, though they are similar to the latter in the other cranial elements.

The third subgroup, Subgroup c, includes seven genera, *Amanses*, *Cantherhines*, *Meuschenia*, *Navodon*, *Pervagor*, *Pseudomonacanthus*, and *Rudarius*. The illustrations of four species cover the variation found in this subgroup (Figs. 45 and 46). They are distinguished from the members of Subgroups a and b in having the

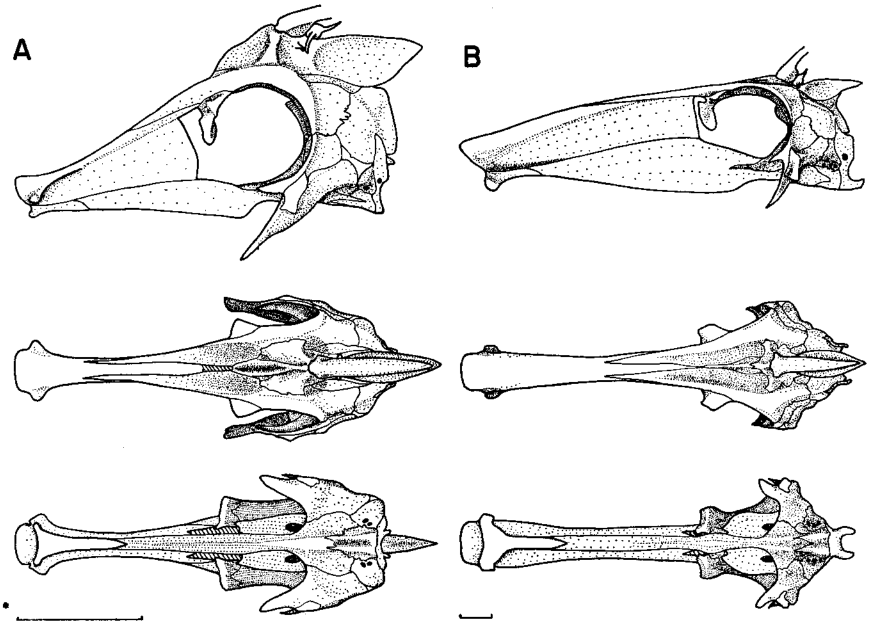


Fig. 42. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in two monacanthid species. A, *Eubalichthys mosaicus*; B, *Nelusetta ayraudi*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

direct articulation between the basal pterygiophore of the first dorsal fin and the ethmoid, but are similar to the foregoing members in the other cranial bones.

Group E. This group is composed of two genera, *Oxymonacanthus* and *Pseudalutarius*, and is characterized by the postero-ventral projection of the frontal (Fig. 47). In the genus *Oxymonacanthus* the ethmoid shows a similar condition to that seen in the fishes of Group D. But in the other genus, *Pseudalutarius*, it is peculiar in having the dorsal keel which articulates posteriorly by interdigitation with the anterior edge of the basal pterygiophore of the first dorsal fin. The vomer of this group is essentially the same as found in the members of Group D, although it is expanded to the level of the posterior edge of the ethmoid in the genus *Oxymonacanthus*. The frontal is tapered postero-ventrally to a point at which the antero-dorsal edge of the hyomandibular attaches by fibrous connective tissue in the genus *Pseudalutarius*. However, the genus *Oxymonacanthus* shows the normal articulation between the antero-dorsal edge of the hyomandibular and the concavity of the prootic. The prefrontal is normal in the genus *Pseudalutarius*, but it articulates ventrally with the dorsal edge of the parasphenoid in the genus *Oxymonacanthus*. In contrast with the preceding groups the sphenotic is reduced in size and does not form a postero-ventral edge of the orbit. The posttemporal is located near the frontal in the genus *Pseudalutarius*, and in the other genus

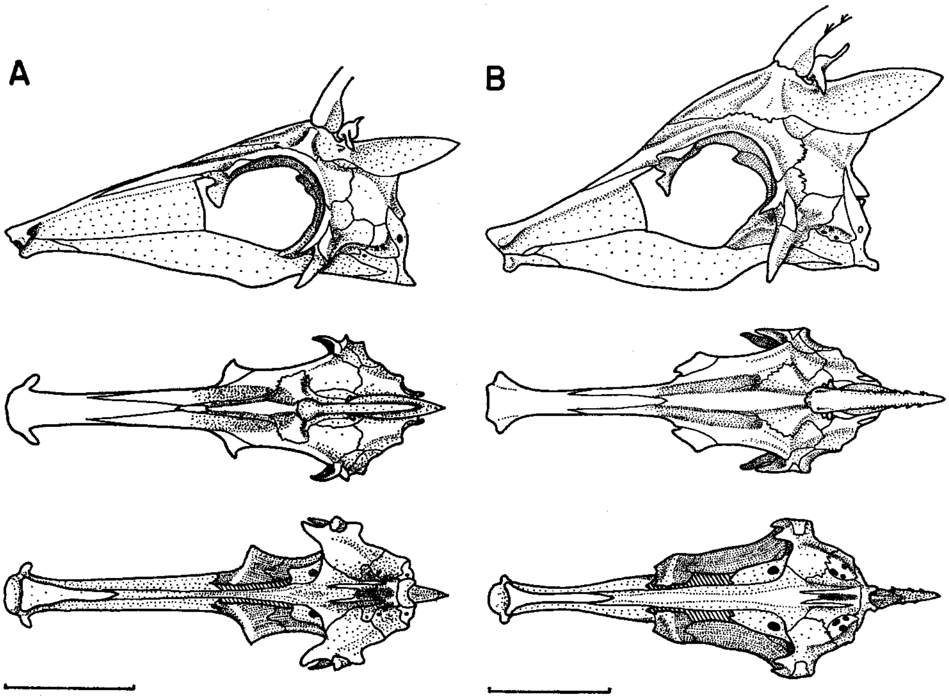


Fig. 43. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in two monacanthid species. A, *Paramonacanthus japonicus*; B, *Stephanolepis cirrhifer*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

*Oxymonacanthus* it is directly attached at its antero-dorsal tip to the frontal. In the other cranial elements the fishes of this group are essentially similar to those of Group D.

Group F. This group is composed of only one genus *Anacanthus*, and is characterized by a greatly elongated cranium and the fusion of the posttemporal and pterotic (Fig. 48). The ethmoid, the vomer, and the frontal are so elongated that their length occupies three-fourths of the entire length of the cranium. The posttemporal is like a small stub in shape and fused to the pterotic. The other cranial bones are similar to those of Group D.

**Discussion.** The balistoid cranium has been studied by many authors (Siebenrock, 1901; Regan, 1903; Supino, 1905; Kaschkaroff, 1914; Rosen, 1916; Starks, 1926; Gregory, 1933; Garnaud, 1956; Tyler, 1962a), however, misinterpretations are unfortunately found in several articles. Though, Siebenrock (1901) and Kaschkaroff (1914) mentioned that the parietal was present in the genus *Balistes*, the bone was actually a part of the epiotic. Supino (1905) and Rosen (1916) reported erroneously the parietal was fused to the frontal. Regan (1903) applied

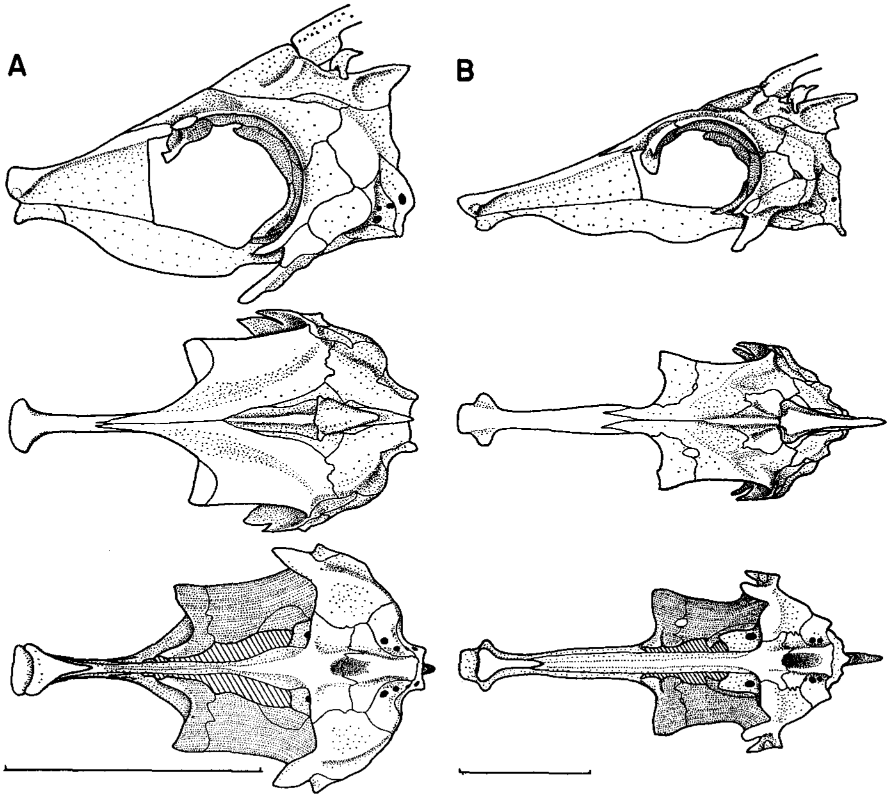


Fig. 44. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in two monacanthid species. A, *Brachaluteres ulvarum*; B, *Paraluteres prionurus*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

the term "parietal" to a cranial element which should have been described as the epiotic. Other erroneous descriptions are related to the "opisthotic" which is actually not found in any member of the order Tetraodontiformes. Kaschkaroff (1914) and Garnaud (1956) said that the "optisthotic" was present in the balistoid fishes, however, what they recognized as the "opisthotic" was a part of the pterotic. The absence of both the parietal and opisthotic is a remarkable character of the balistoids, because these bones are usually found in the teleostean fishes. In contrast with the works mentioned above, the anatomical studies on a few balistoid members carried out by Starks (1926) and Gregory (1933) were accurate and useful but insufficient to clarify the interrelationships of the balistoids.

The balistids (Groups A, B, and C) are primarily separated from the monacanthids (Groups D, E, and F) on the basis of the relation between the cranium and the basal pterygiophore of the first dorsal fin. In the balistids the ventral shaft of the basal pterygiophore of the first dorsal fin is wedged into the concavity which is

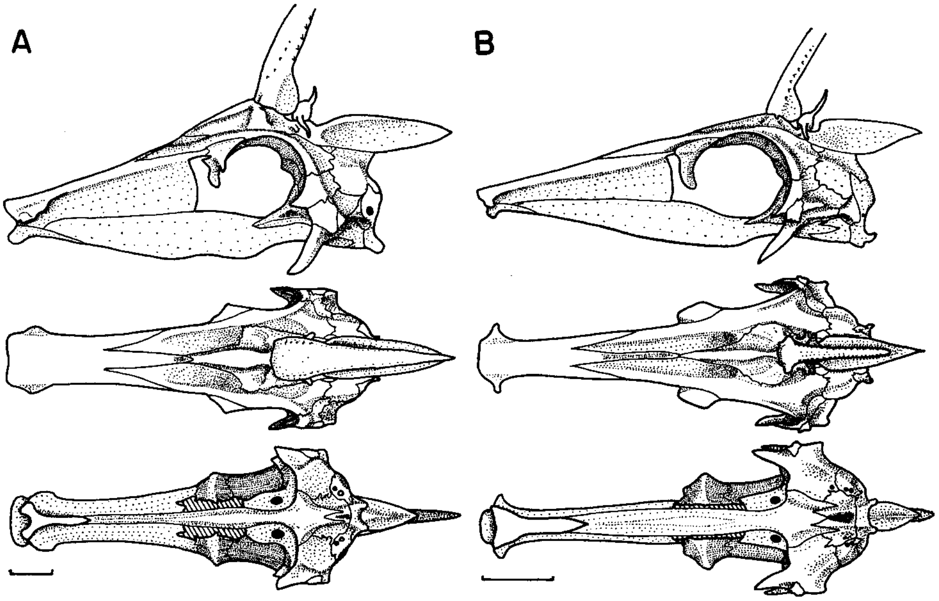
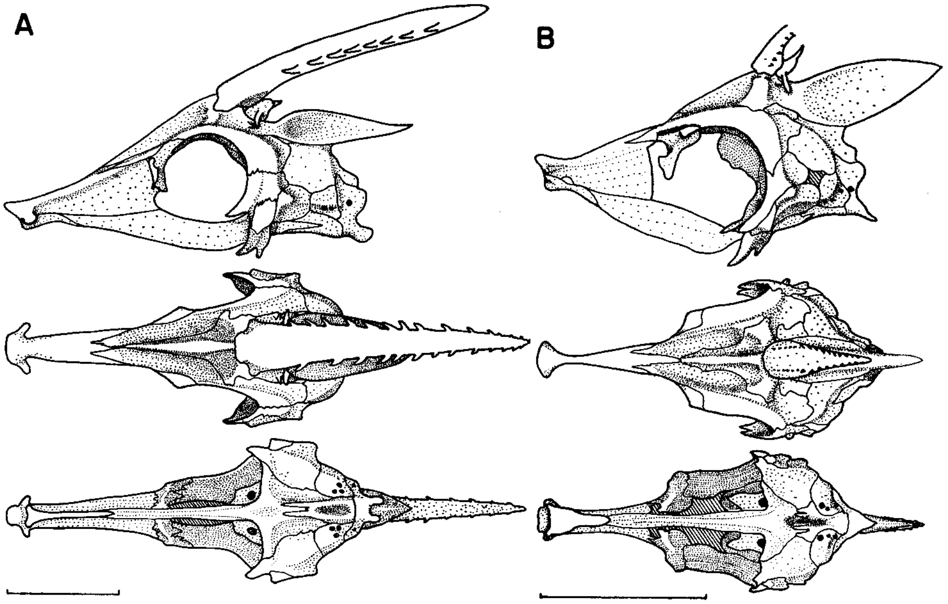


Fig. 45. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in two monacanthid species. A, *Cantherhines dumerili*; B, *Navodon modestus*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.



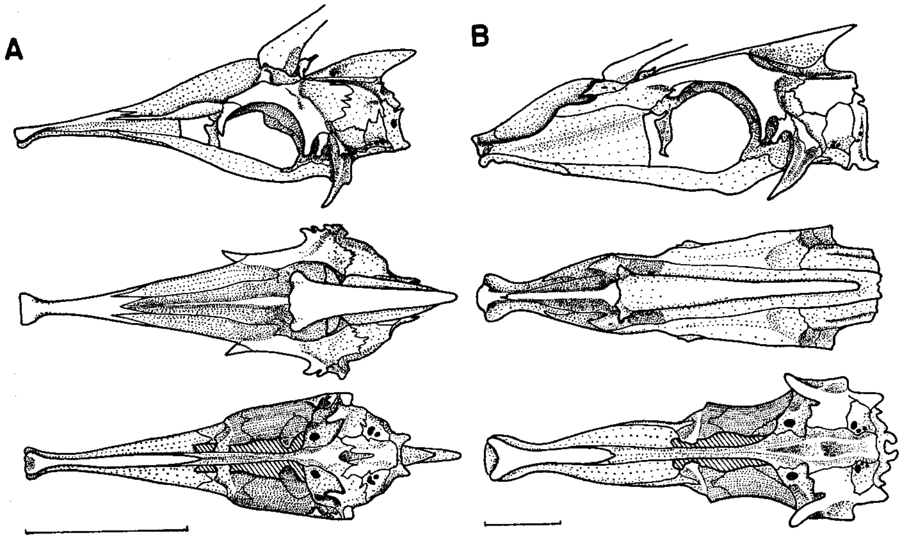


Fig. 47. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in two monacanthid species. A, *Oxymonacanthus longirostris*; B, *Pseudalutarius nasicornis*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

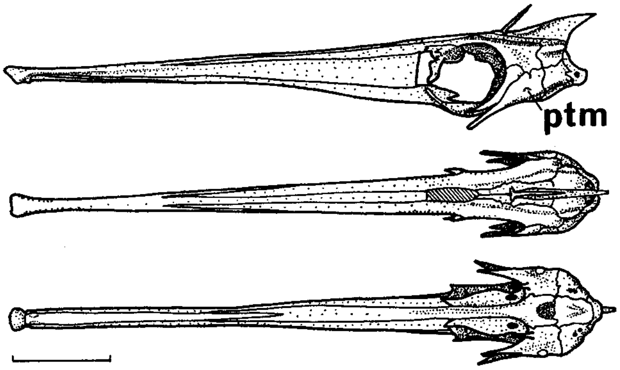


Fig. 48. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in a monacanthid species, *Anacanthus barbatus*. ptm, posttemporal. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bar indicates 10 mm.

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Fig. 46. Diagram showing the cranium, the first dorsal fin, and the first abdominal vertebra in two monacanthid species. A, *Pervagor melanocephalus*; B, *Rudarius ercodes*. Top, lateral view; middle, dorsal view; bottom, ventral view. Scale bars indicate 10 mm.

composed of the supraoccipital and exoccipital, but in the monacanthids the first dorsal fin lies on the dorsal surface of the cranium. In the triacanthids which have been considered to be the ancestor of the balistoids, the ventral shaft of the basal pterygiophore of the first dorsal fin fits into the postero-dorsal surface of the cranium formed by the epiotic, exoccipital, and the first vertebra (Tyler, 1968: p. 37). This triacanthid condition is similar to that of the balistids rather than the monacanthids, thus the balistids are considered to be more primitive than the monacanthids. This speculation is confirmed by the fact that the articulation between the epiotic and posttemporal is not found in the monacanthids but in both the balistids and triacanthids. The balistids are also distinguished from the monacanthids by the size of the ethmoid and parasphenoid, however, this character can not be used for the phylogenetic consideration.

With respect to the interrelationships in the balistids, the scale bone provides us with the most important information. The bone is found in only Group A. This is something of an enigma, since the bone is absent not only in any other balistoid member but also in the triacanthids. On the other hand, the bone is usually present in the perciform fishes including the acanthurids which have been considered to be the ancestor of the triacanthoids (Breder and Clark, 1947; Matsubara, 1955; Tyler, 1968). Thus, the presence of the bone shows a primitive condition. Based on this criterion, Group A is placed at the most primitive systematic position in the balistoids. The other balistid groups, Groups B and C, have no trace of the scale bone, thus they are considered to be more advanced than Group A. In these groups, Group C is peculiar in having the greatly expanded frontal. This condition is not found in any other balistoid member. Therefore, it is reasonable to assume the feature shows the derived condition rather than the primitive one. Thus, we come to the speculation that Group C is possibly the most advanced member in the balistids. However, I conceive that based on only the cranial characters it is impossible to answer the question whether Group C is directly derived from an ancestor similar to Group A or originating from it through the evolutional steps of the fishes in Group B (Fig. 49).

With regard to the monacanthids we can take the following characters into the phylogenetic consideration: (1) the relation between the cranial bones and the basal pterygiophore of the first dorsal fin; (2) the feature of the frontal; (3) the feature of the sphenotic; (4) the feature of the posttemporal.

As previously stated, in both the triacanthids and balistids, the first dorsal fin is situated at a more posterior portion of the cranium than that found in the monacanthids. In other words, the tendency of forward migration of the first dorsal fin corresponds with the evolutional trends in the balistoids.

Judging from this criterion Subgroup a of Group D is considered to be the most primitive representative of the monacanthids. Group F also shows the same condition of this character as seen in Subgroup a, however, the feature of the posttemporal separates the former from the latter and from the other balistoid members. In Group F the posttemporal is reduced in size and fused to the pterotic. This is considered to be the derived condition, since the bone is not fused to the pterotic in any other balistoid members or triacanthid members.

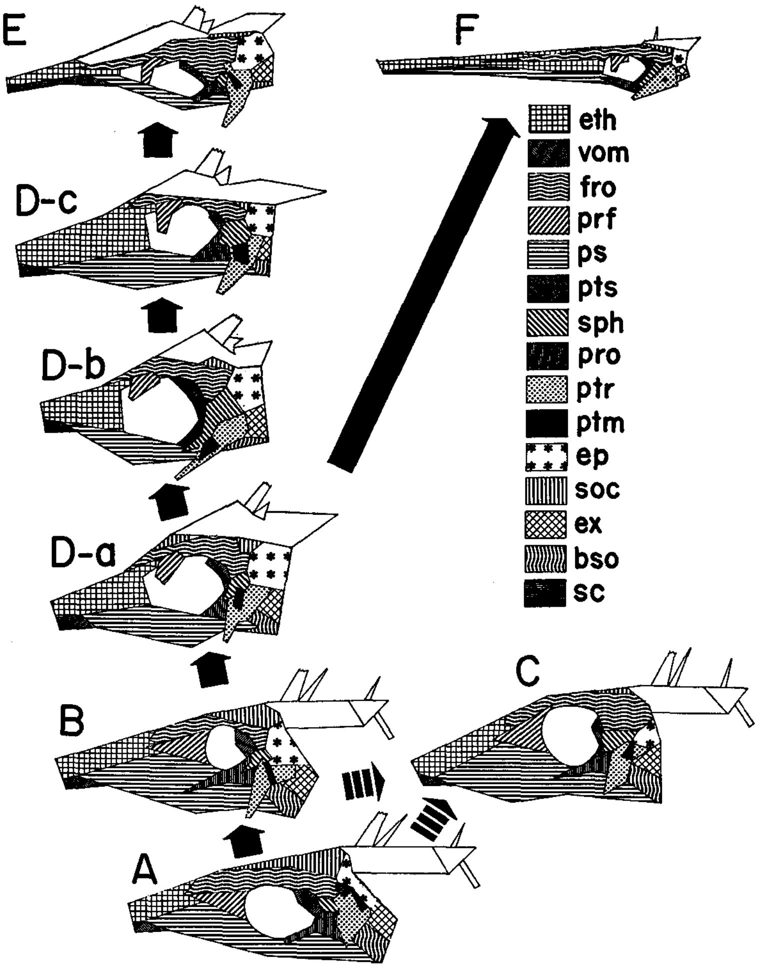


Fig. 49. Schematic diagram showing the interrelationships of the groups and subgroups based on the cranial characters. Abbreviations as in Fig. 38. Solid and broken arrows indicate respectively certain and uncertain relationships.

The combination of these two characters leads us to conclude that Group F is probably derived from an ancestor similar to the fishes of Subgroup a (Fig. 49).

With respect to the remaining monacanthid members, the relation between the cranial elements and the basal pterygiophore of the first dorsal fin can be used as an important yardstick for any phylogenetic comparison. In Subgroup b the basal pterygiophore of the first dorsal fin articulates with the frontal. On the other hand, in Subgroup c it articulates with the frontal and attaches anteriorly to the posterior part of the ethmoid. Therefore, Subgroup b is assigned to the more primitive systematic position than that of Subgroup c (Fig. 49).

Table 5. *Differentiation of the cranial bones in*

| Group | | Genus | SC | ETH |
|---|---|---|---|---|
| A | | *Canthidermis* | present | not articulated with PTG; dorsal keel absent |
| B | | *Balistapus*<br>*Balistes*<br>*Balistoides*<br>*Melichthys*<br>*Odonus*<br>*Pseudobalistes*<br>*Rhinecanthus*<br>*Suffamen*<br>*Xanthicthys* | absent | |
| C | | *Abalistes* | | |
| D | a | *Alutera*<br>*Arotrolpeis*<br>*Chaetoderma*<br>*Eubalicthys*<br>*Monacanthus*<br>*Nelusetta*<br>*Paramonacanthus*<br>*Scobinichthys*<br>*Stephanolepis* | | |
| | b | *Brachaluteres*<br>*Paraluters* | | |
| | c | *Acreichtys*<br>*Amanses*<br>*Cantherhines*<br>*Meuschenia*<br>*Navodon*<br>*Pervagor*<br>*Pseudomonacanthus*<br>*Rudarius* | | articulated with PTG; dorsal keel absent |
| E | | *Oxymonacanthus*<br>*Pseudalutarius* | | articulated with PTG; dorsal keel present |
| F | | *Anacanthus* | | not articulated with PTG; dorsal keel absent |

Based on the same criterion, Group E is considered to be more advanced than any member of Group D, since the basal pterygiophore of the first dorsal fin lies anteriorly on the ethmoid. This speculation is reinforced by the fact that in Group E the frontal is ventrally projected to form the postero-ventral edge of the

*the balistoids. Abbreviations as in Figs. 38 and 41.*

| FRO | SOC | EP | PTM | SPH |
|---|---|---|---|---|
| not articulated with PTG; postero-ventral projection absent; articulated with PTR | postero-dorsal concavity present | articulated with PTM; postero-dorsal concavity present | not fused to PTR | included in orbital region |
| not articulated with PTG; postero-ventral projection absent; not articulated with PTR | | | | |
| not articulated with PTG; postero-ventral projection absent; not articulated with PTR; greatly expanded postero-dorsally | | | | |
| not articulated with anterior tip of PTG; postero-ventral projection absent | postero-dorsal concavity absent | not articulated with PTM; postero-dorsal concavity absent | | |
| articulated with anterior tip of PTG; postero-ventral projection absent | | | | |
| articulated with anterior tip of PTG; postero-ventral projection present | | | | not included in orbital region |
| not articulated with anterior tip of PTG; postero-ventral projection absent | | | fused to PTR | included in orbital region |

orbit which is made by the sphenotic in the other balistoid members and triacanthids. Within Group E the genus *Pseudalutarius* is possibly more advanced than the other genus *Oxymonacanthus*, because the former possesses the derived characters such as the dorsal keel of the ethmoid and the articulation between the hyomandibular and the postero-ventral projection of the frontal. On the other hand, in these two genera the posttemporal is not fused but tightly held to the pterotic. This posttemporal condition is conceived to be more primitive than that of Group F. However, the relation between the cranial elements and the basal pterygiophore of the first dorsal fin indicates that Group E is more advanced than Group F. Thus, we come to a difficult question; which case is true ? I believe that it is impossible to answer this question based on only the cranial characters. It will be discussed on the basis of all the osteological characters in the chapter on general consideration. Thus, it is reasonable here to recognize two major evolutional pathways in the monacanthids which came to Groups E and F (Fig. 49). The interrelationships based on the cranial elements in the balistoids are summarized in Figure 49 and Table 5.

### 8. First dorsal fin

**Description.** The first dorsal fin consists of two or three elements, the dorsal spines, one or two basal pterygiophores, and the supraneural (found in the balistids only). The balistids and monacanthids are readily distinguished by the number of the dorsal spines and basal pterygiophores, and the presence or absence of the supraneural, thus they are described independently in the following section.

Balistidae. The first dorsal fin is placed just behind the cranium (Fig. 50, A). and is composed of three elements, the dorsal spines, the basal pterygiophores, and the supranerual. The balistid members show little variation in the structure of the first dorsal fin, hence they are included in a single group, Group A. The illustrations of six species cover the variation found in the balistid members (Fig. 51).

Three dorsal spines are located on the two basal pterygiophores and decrease in size posteriorly in the series. The first dorsal spine is long and stout, and is locked on the medial edge of the greatly enlarged first basal pterygiophore when it is erected. The posterior surface of the spine possesses a deep groove which runs along the entire length of the spine. The second dorsal spine is slightly shorter and narrower than the first, and is situated on the ridge of the first basal pterygiophore. The basal portion of the second dorsal spine is expanded anteriorly, and has the

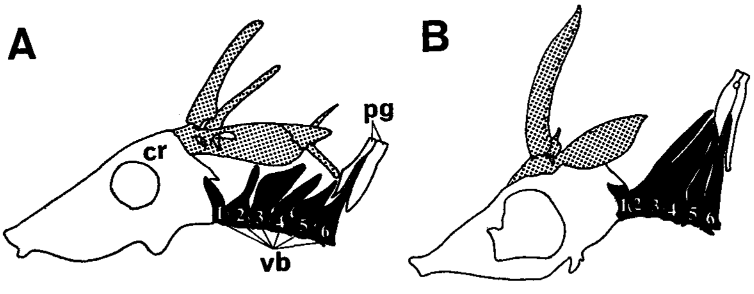


Fig. 50. Diagrammatic illustration of the first dorsal fin and its associated structures in the balistoids. A, *Balistapus undulatus*; B, *Rudarius ercodes*. cr, cranium; pg, pterygiophores of the second dorsal fin; vb, abdominal vertebrae.

bifid lateral projections which are produced from the fenestra of the first basal pterygiophore. These two dorsal spines are able to rotate over the dorsal edge of the first basal pterygiophore, and comprise the trigger mechanism. When the first dorsal spine is erected, the second dorsal spine is simultaneously raised up.

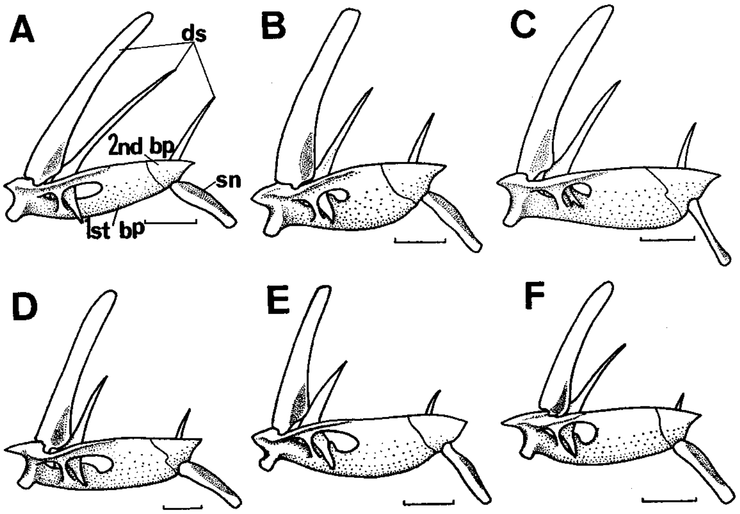


Fig. 51. Diagram showing the first drosal fin in six balistid species. A, *Abalistes stellatus*; B, *Pseudobalistes flavimarginatus*; C, *Balistapus undulatus*; D, *Balistoides conspicillum*; E, *Sufflamen fraenatus*; F, *Melichthys vidua*. 1st bp, 1st basal pterygiophore; 2nd bp, 2nd basal pterygiophore; ds, dorsal spines; sn, supraneural. Scale bars indicate 10 mm.

The convex antero-basal portion of the second drosal spine fits into the groove on the posterior surface of the first dorsal spine, then these two dorsal spines are effectively locked together. This locking condition can only be released by the downward action of the second dorsal spine. The third dorsal spine is short and feeble, and is placed on the second basal pterygiophore.

The basal pterygiophores are two in number, and boat-like in shape. The first basal pterygiophore is like an enlarged trough in shape. The antero-ventral shaft of the bone is wedged into the concavity of the postero-dorsal portion of the cranium which is formed by the supraoccipital and epiotic. The first basal pterygiophore articulates posteriorly with the second basal pterygiophore by interdigitation, and is placed above the first, second, and third abdominal vertebrae. The second basal pterygiophore is much smaller than the first, and articulates postero-ventrally with the supraneural. The bone is situated above the third, fourth, and fifth abdominal vertebrae.

The supraneural is shaped like a short shaft, and is slightly expanded dorsally. The bone articulates dorsally with the second basal pterygiophore, ventrally with the neural spine of the fifth abdominal vertebra, and posteriorly with the anterior edge of the first pterygiophore of the second dorsal fin by fibrous connective tissue (Fig. 50, A).

Monacanthidae. In contrast with the balistids, the first dorsal fin is not wedged anteriorly into the cranium but lies on the dorsal surface of the cranium (Fig. 50, B). The monacanthids show a more reduced condition in the structure of the first dorsal fin than that found in the balistids. In the monacanthids the dorsal spines are reduced to one or two in number, the basal pterygiophore is composed of only one bone, and the supraneural is absent. The monacanthid members are divided into two groups on the basis of the number of the dorsal spines.

Group B. This group comprises all of the monacanthid members except for the genus *Anacanthus*, and is characterized by having two dorsal spines. The illustrations of 14 species cover the variation found in this group (Figs. 41 to 47).

The dorsal spines are two in number, and possess the same locking mechanism as seen in the balistids. The first dorsal spine is very long and is covered by many spinules and/or tubercles. At its posterior edge there is a deep groove into which the greatly reduced second dorsal spine fits. The second dorsal spine is expanded basally and has small ventro-lateral projections. It is so reduced in size that in several species it is invisible unless the skin is removed.

The basal pterygiophore is composed of a single enlarged element. It has two very small lateral protuberances around which the second dorsal spine rotates in order to lock the first dorsal spine. The basal pterygiophore lies anteriorly on the dorsal surface of the cranium. It extends posteriorly beyond the posterior end of the cranium, and is located above the first and second abdominal vertebrae.

Group C. This group is composed of a single genus *Anacanthus*. The genus is clearly distinguished from the other balistoid members in having only one dorsal spine (Fig. 48). In this group the dorsal spine is short and very feeble. The other features of the first dorsal fin are essentially similar to those of the preceding groups.

**Discussion**. Many authors have called attention to the balistoid first dorsal fin because of its peculiar trigger-like structure (Hollard, 1853; Sørensen, 1884, 1897; Gregory, 1933; Fraser-Brunner, 1935, 1941; Clothier, 1939; Monod, 1950, 1960; Matsubara, 1955; Tyler, 1962a, 1968). Of these authors, Fraser-Brunner (1935), Matsubara (1955), and Tyler (1962a) pointed out that a reductive tendency in the first dorsal fin is present in the balistoids and throughout the whole members of the order Tetraodontiformes, in other words, the forms with the more reduced first dorsal fin are considered to be placed at the more advanced systematic position. I agree with their consideration. Judging from this criterion and the description of the present study, the number of dorsal spines and basal pterygiophores, and the presence or absence of the supraneural are important in discussing the phylogenetic interrelationships of the balistoids. In addition to these characteristics the cephalization (forward migration) of the first dorsal fin also is useful (described previously in the section of the cranium).

The balistids (Group A) are placed at the most primitive systematic position in the balistoids, since they have the most developed first dorsal fin; the three dorsal spines, two basal pterygiophores, and a supraneural. Within the balistid members a reductive tendency seems to be present in the size of the third dorsal spine. When we compare the two extreme conditions of the spine in the genera *Abalistes* and *Melichthys* (Fig. 51, A and F), we can see the difference between them. However, the intermediate condition found in the genera *Pseudobalistes*, *Balistapus*, *Balistoides*, and *Sufflamen*, appears to prevent us from coming to a clear decision. Actually, it is very difficult to distinguish the size of the third dorsal spine from among these four members (Fig. 51, B to E). Therefore, I conclude that it is premature to divide the balistid members into groups based on the feature of the third dorsal spine. In the present study it is found that all the balistid members possess the three dorsal spines. On the other hand, Jordan and Gilbert (1882: p. 228) reported that the third dorsal spine is absent in *Xanthichthys mento* (their *Balistes mento*). Unfortunately, this is erroneous description, since the spine is actually present in the species.

The monacanthids (Groups B and C) should be considered to be more advanced than the balistids, since the former possess the more reduced first dorsal fin: that is, a decrease in the number of the basal pterygiophores and dorsal spines, and loss of the supraneural. It seems that a single basal pterygiophore of the monacanthids is formed by fusion of the two elements, since it is similar in relative size to the two basal pterygiophores of the balistids. With regard to the interrelationships among

Table 6. *Differentiation of the first dorsal fin in the balistoids.*

| Group | Genus | Number of dorsal spines | Number of basal pterygiophores | Supraneural |
|---|---|---|---|---|
| A | all genera of balistids | 3 | 2 | present |
| B | *Acreichtys*<br>*Alutera*<br>*Amanses*<br>*Arotrolepis*<br>*Brachaluteres*<br>*Cantherhines*<br>*Chaetoderma*<br>*Eubalichthys*<br>*Meuschenia*<br>*Monacanthus*<br>*Navodon*<br>*Nelusetta*<br>*Oxymonacanthus*<br>*Paraluteres*<br>*Paramonacanthus*<br>*Pervagor*<br>*Pseudalutarius*<br>*Pseudomonacanthus*<br>*Rudarius*<br>*Scobinichthys*<br>*Stephanolepis* | 2 | 1 | absent |
| C | *Anacanthus* | 1 | | |

the monacanthid members, the number of the dorsal spines is very important. Group C is consequently considered to be more advanced than Group B on the basis of an apparent reductive tendency in the number of the dorsal spines (Table 6). Some authors described several monacanthid members as having only one dorsal spine (Kamohara, 1940; Fraser-Brunner, 1941; Abe, 1963), but the monacanthid members, except for *Anacanthus barbatus*, always possess two dorsal spines. These erroneous descriptions might be due to the very small size of the second dorsal spine.

It seems that the balistoid first dorsal fin has two major functions. The first function is related to the maneuverability of the fish. Gosline (1971: p. 32) stated that in higher teleosts the first dorsal fin frequently extends further forward over the anterior part of the body. He also pointed out that with such anterior extension the dorsal fin comes to serve as a rudder. Since the balistoid first dorsal fin is located on the anterior part of the body or head, it has an effective function as a rudder.

On the other hand, the balistoid first dorsal fin has another important function, namely a defensive mechanism. The erected dorsal spines play an important role for defense in combination with pelvic complex (see also the section of the pelvic complex). When the coastal species of the balistids encounter their enemies, they dash into a hole or crevice of rocky or coral formation. Then they erect the first dorsal spine which is locked by the second one, and extend the pelvis downward. The enlarged pterygiophores reinforced with the supraneural effectively support the locked dorsal spines. These actions provide them with an ability to fix themselves in a hole or crevice, and thus they gain an advantage in the struggle for existence. With regard to the offshore balistids and primitive monacanthids, the first dorsal fin is also used as another defensive mechanism. When they erect the first dorsal spine and simultaneously extend the pelvis downward, they acquire a deeper body in order to protect themselves from their enemies. In contrast with the primitive monacanthids, the advanced monacanthids such as the genus *Brachaluteres* have a weak and small first dorsal spine (pelvic complex is also reduced), however, they do possess the other defensive mechanism, namely the distensible abdomen. Judging from these facts, the reduction of the elements in the first dorsal fin is possibly related to a reductive tendency in the pelvic complex. The differentiation of the first dorsal fin is summarized in Table 6.

## 9. Vertebrae

**Description.** The vertebrae are divided into two regions, abdominal and caudal vertebrae. The abdominal vertebrae are defined as the elements anterior to the vertebra to which the first enlarged pterygiophore of the anal fin is attached by fibrous connective tissue. Thus, the remaining posterior elements are described under the name of the caudal vertebrae. The balistoid members are divided into the following groups on the basis of the number of vertebrae, the features of the neural spines anterior to the second dorsal fin, and the presence or absence of the pleural ribs.

Group A. This group comprises all genera of the balistids. They are clearly distinguished from the other balistoid members by having seven abdominal vertebrae and 11 caudal vertebrae, though in aberrant specimens six abdominal and 10 caudal vertebrae are recognizable respectively (Table 7). The illustration of one species cover essentially the vertebral features of the balistid members (Fig. 52).

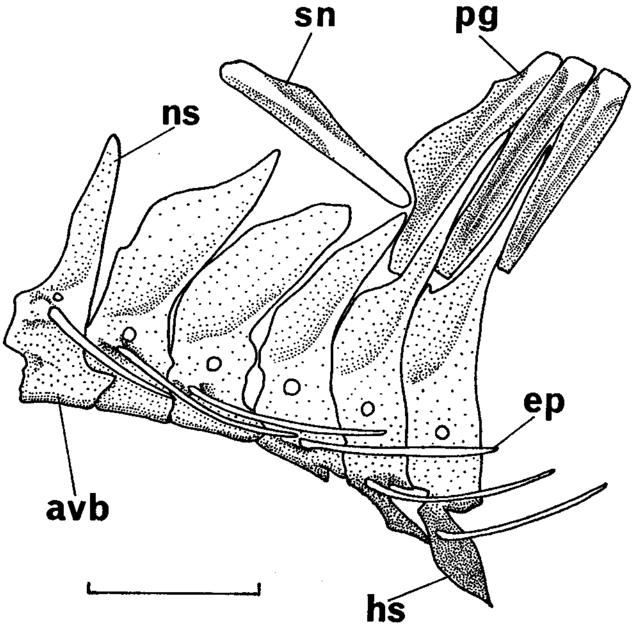


Fig. 52. Diagram showing the abdominal vertebrae (second to seventh) and associated bones in a blistid species *Abalistes stellatus*. avb, abdominal vertebra; ep, epipleural rib; hs, haemal spine; ns, neural spine; pg, pterygiophore of the second dorsal fin; sn, supraneural. Scale bar indicates 10 mm.

The first abdominal vertebra is different from the other vertebrae in having bifid neural spines (Fig. 53) which are attached firmly to the posterior surface of the exoccipital by fibrous connective tissue. Each neural spine has a neural foramen on each side. The centrum of the first vertebra articulates anteriorly with the concavity on the posterior surface of the basioccipital, and posteriorly with the second abdominal vertebra by fibrous connective tissue. The first centrum possesses backward directed projections which are employed to make close cantact with the ventro-lateral part of the centrum of the second abdominal vertebra.

In contrast with the first abdominal vertebra, the second to seventh abdominal vertebrae possess complete neural arches and single normal neural spines, and support the epipleural ribs. The neural spines of the third and fourth abdominal vertebrae are greatly expanded forward and backward. The neural spine of the fifth abdominal vertebra is connected dorsally with the supraneural and postero-dorsally with the first pterygiophore of the second dorsal fin by fibrous connective tissue. The sixth and seventh neural spines are extended and wedged into the pterygiophores of the second dorsal fin. The neural spines of the abdominal vertebrae are articulated with one another by fibrous connective tissue. Each neural arch possesses a neural foramen on its side.

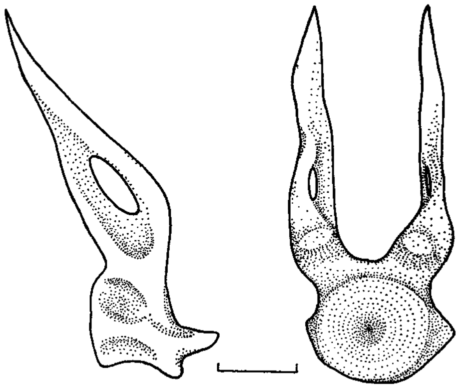


Fig. 53. Diagram showing the first abdominal vertebra of a balistid species *Abalistes stellatus*. Left, laterll view; right, anterior view. Scale bar indicates 3 mm.

The second to seventh abdominal vertebrae have the transverse processes which support the epipleural ribs. These transverse processes become progressively larger and stouter posteriorly in the series. The processes of the sixth and seventh abdominal vertebrae are different from those of the preceding abdominal vertebrae

Table 7. *Frequency distributions in counts of the abdominal and caudal vertebrae in the balistids.*

| Species | Abdominal vertebrae | | Caudal vertebrae | |
|---|---|---|---|---|
| | 6 | 7 | 10 | 11 |
| *Abalistes stellatus* | | 20 | | 20 |
| *Balistapus undulatus* | | 76 | 1 | 75 |
| *Balistes vetula* | | 10 | | 10 |
| *Balistoides conspicillum* | | 7 | | 7 |
| *B. viridescens* | | 9 | | 9 |
| *Canthidermis maculatus* | | 9 | | 9 |
| *Melicthys niger* | | 4 | | 4 |
| *M. vidua* | | 7 | | 7 |
| *Odonus niger* | | 16 | | 16 |
| *Pseudobalistes flavimarginatus* | | 4 | | 4 |
| *P. fuscus* | | 10 | | 10 |
| *Rhinecanthus aculeatus* | 1 | 49 | | 50 |
| *R. echarpe* | | 4 | | 4 |
| *R. verrucosus* | | 2 | | 2 |
| *Sufflamen bursa* | | 3 | | 3 |
| *S. chrysopterus* | | 16 | | 16 |
| *S. fraenatus* | | 28 | | 28 |
| *Xanthichthys auromarginatus* | | 1 | | 1 |
| *X. caeruleolineatus* | | 9 | | 9 |
| *X. lineopunctatus* | | 2 | | 2 |
| *X. mento* | | 14 | | 14 |

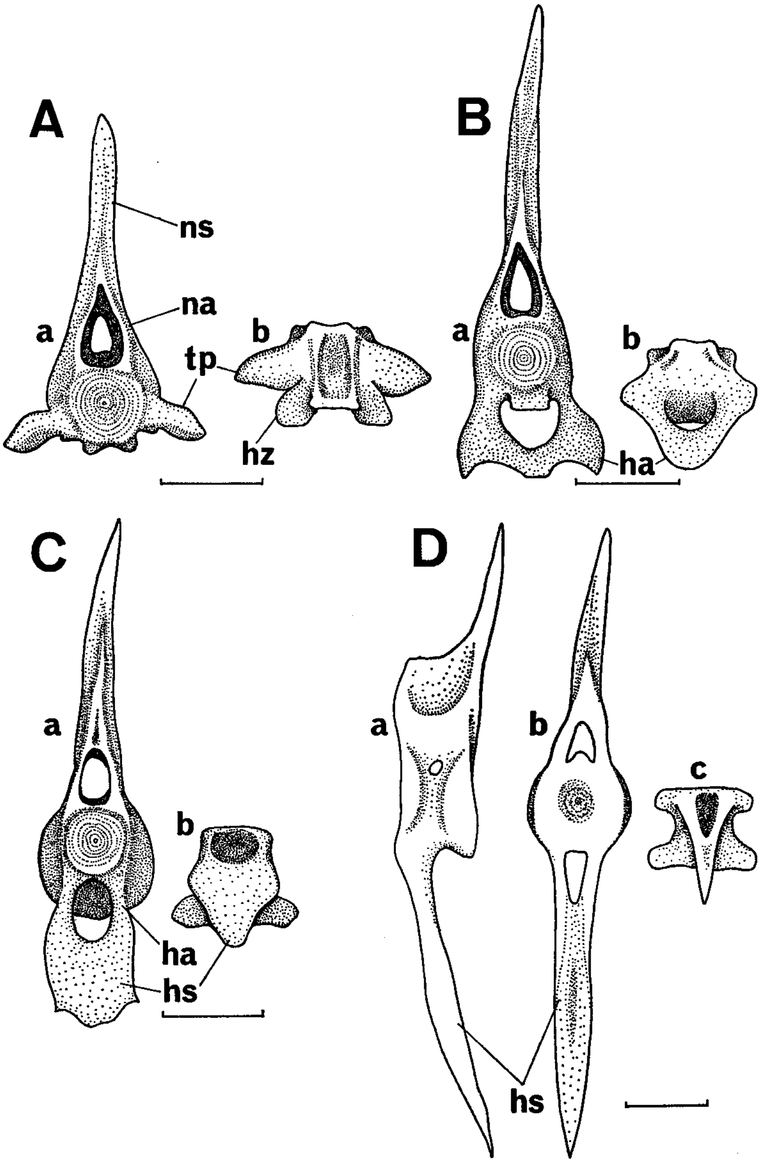


Fig. 54. Diagram showing the vertebrae of a balistid species *Abalistes stellatus*. A, fifth abdominal vertebra; B, sixth abdominal vertebra; C, seventh abdominal vertebra (a, anterior view; b, ventral view); D, second caudal vertebra (a, lateral view; b, anterior view; c, ventral view). ha, haemal arch; hs, haemal spine; hz, haemal postzygapophysis; na, neural arch; ns, neural spine. Scale bars indicate 5 mm.

(Fig. 54). In the sixth abdominal vertebra the process is expanded ventrally and fused to the opposite member to make the haemal arch (Fig. 54, B), while that of the seventh abdominal vertebra is more expanded ventrally than that found in the sixth, thus it forms the haemal arch and spine (Fig. 54, C).

In the abdominal vertebrae there are short haemal postzygapophyses which overlie the ventro-lateral portion of the succeeding centra.

The caudal vertebrae are 11 in number except for rare aberrant specimens. Since the last caudal vertebra is specialized in structure in order to support the caudal fin, it will be described in the caudal fin section. The neural arches and spines of the first to ninth caudal vertebrae are morphologically similar to those of the sixth and seventh abdominal vertebrae (Fig. 54, D). These neural spines decrease in size posteriorly in the series. The neural spine of the 10th caudal (penultimate) vertebra is longer than that just anterior to it.

The haemal arches and spines of the caudal vertebrae are well developed in

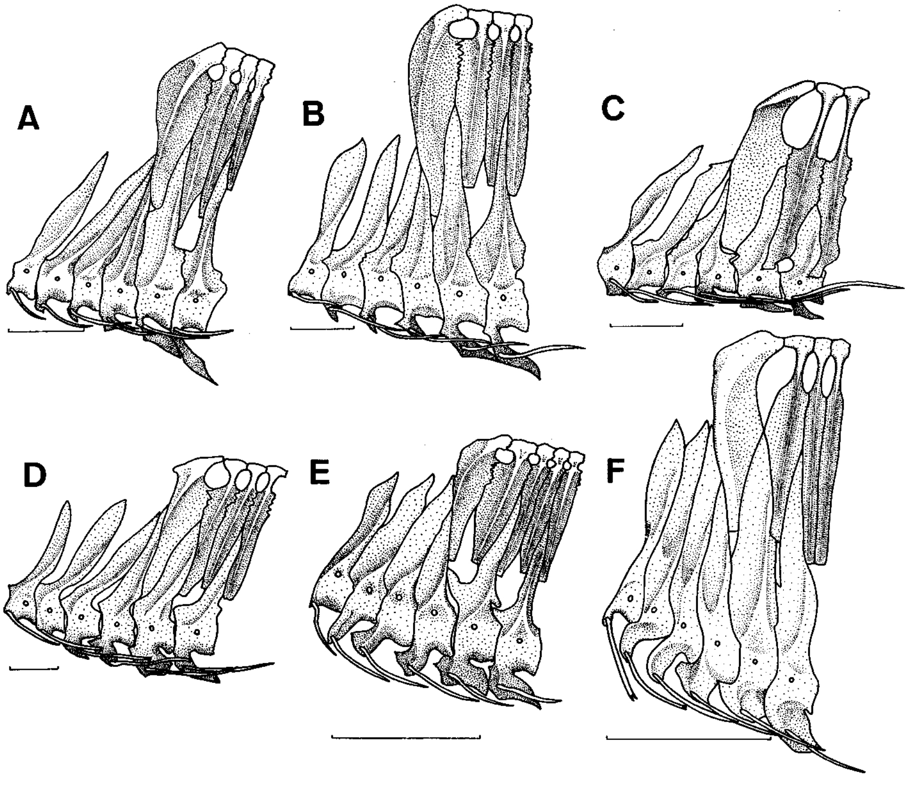


Fig. 55. Diagram showing the abdominal vertebrae (second to seventh) and associated bones in six monacanthid species. A, *Monacanthus chinensis*; B, *Stephanolepis cirrhifer*; C, *Paramonacanthus japonicus*; D, *Navodon modestus*; E, *Pseudomonacanthus peroni*; F, *Eubalichthys mosaicus*. Scale bars indicate 5 mm.

contrast with those of the abdominal vertebrae. The haemal spine of the first caudal vertebra is firmly attached to the antero-dorsal surface of the first pterygiophore of the anal fin by fibrous connective tissue. The second caudal vertebra has the largest haemal spine in the caudal vertebrae. The haemal spines of the third to ninth caudal vertebrae become progressively shorter and smaller posteriorly in the series. The haemal spine of the 10th caudal (penultimate) vertebra is longer than that just anterior to it, and is not fused but interdigitated with the centrum. The transverse process is not found in the caudal vertebrae. The small haemal postzygapophyses are only present on a few anterior caudal centra. The epipleural ribs always start on the second abdominal vertebra and end on the first caudal vertebra.

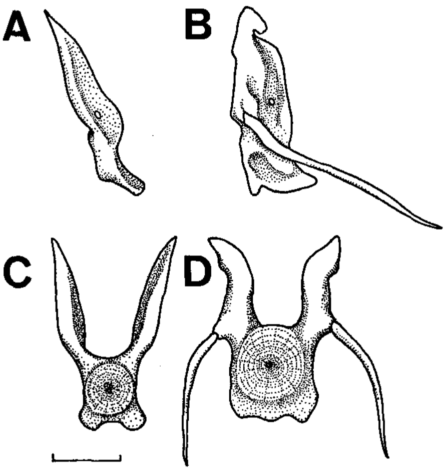


Fig. 56. Diagram showing the first abdominal vertebra and epipleural ribs in two monacanthid species, *Stephanolepis cirrhifer* (A and C) and *Pseudalutarius nasicornis* (B and D). Top, lateral view; bottom, anterior view. Scale bars indicate 3 mm.

Group B. This group is composed of 10 monacanthid genera, *Amanses, Arotrolepis, Cantherhines, Eubalichthys, Monacanthus, Navodon, Paramonacanthus, Pervagor, Pseudomonacanthus*, and *Stephanolepis*. The illustrations of six species cover the variation found in this group (Fig. 55). They are different from the member of Group A in having 12 caudal vertebrae (Tables 7 to 9).

The abdominal vertebrae are seven in number. The first abdominal vertebra possesses bifid neural spines (Fig. 56, A and C) which are attached to the postero-lateral surface of the epiotic and exoccipital by fibrous connective tissue and slight interdigitation. In most of the other features of those vertebrae, many of this group closely resemble the members of Group A. However, the genera, *Arotrolepis, Monacanthus*, and *Paramonacanthus*, are distinguished from the other genera of this group and the members of Group A in bearing the haemal arch on the fifth abdominal vertebra. The epipleural ribs start on the second abdominal vertebra in all the members of this group, and end on different caudal vertebrae, namely the second, third or fourth caudal vertebra. In other words, the end point of the epipleural ribs shows the interspecific or individual variation.

Group C. This group includes nine monacanthid genera, *Acreichthys, Alutera, Brachaluteres, Chaetoderma, Meuschenia, Nelusetta, Paraluteres, Rudarius*, and *Scobinichthys*. The illustrations of seven species cover the variation found in this group (Figs. 57 and 58). They are distinct from the members of the foregoing groups in having 13 (usually), 14 or 16 caudal vertebrae (Tables 8 and 9). The number of caudal vertebrae is 13 in all the members of this group except for three species of the genus *Alutera*. The genus shows interspecific variation in the caudal vertebral number as follows; the number is 13 in *A. heudelotii*, 14 in *A. scripta*, and 16 in *A. monoceros* and *A. schoepfii*.

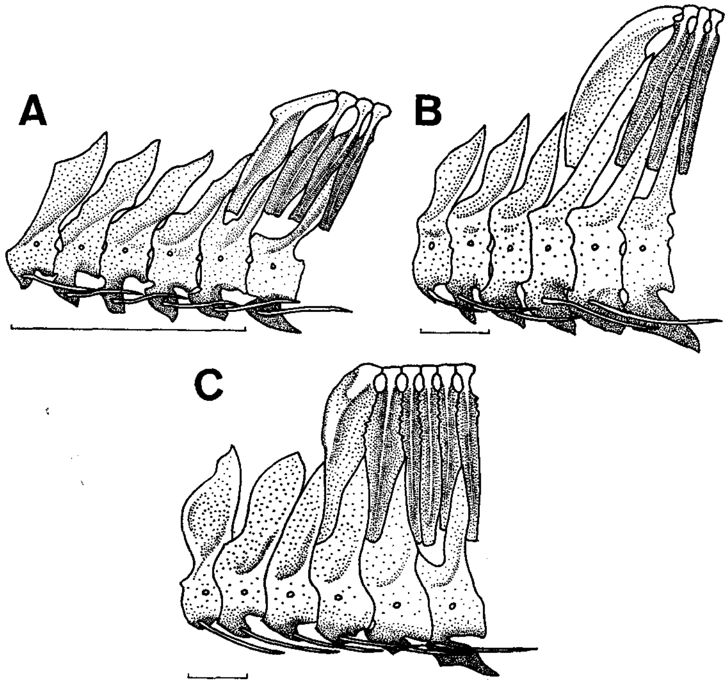


Fig. 57. Diagram showing the abdominal vertebrae (second to seventh) and associated bones in three monacanthid species. A, *Alutera scripta*; B, *Alutera monoceros*; C, *Meuschenia trachylepis*. Scale bars indicate 5 mm.

The position of the first haemal arch shows significant variation among the genera of this group. In the genera, *Brachaluteres*, *Paraluteres*, and *Rudarius*, the haemal arch begins with the fifth abdominal vertebra. In the genus *Nelusetta* the haemal arch starts from the seventh abdominal vertebra. On the other hand, the remaining genera possess the first haemal arch on the sixth abdominal vertebra as seen in Group A and many other genera of Group B.

With regard to the neural spines of the abdominal vertebra, the genus *Meuschenia* and *Alutera monoceros* are different from the other members of this group. These members possess three single neural spines anterior to the second dorsal fin (Fig. 57, B and C), while the remaining members have four single neural spines on the same portion.

The epipleural ribs are normal in most members, but in the genus *Brachaluteres* they are very peculiar. In this genus the second to sixth epipleural ribs are fan-

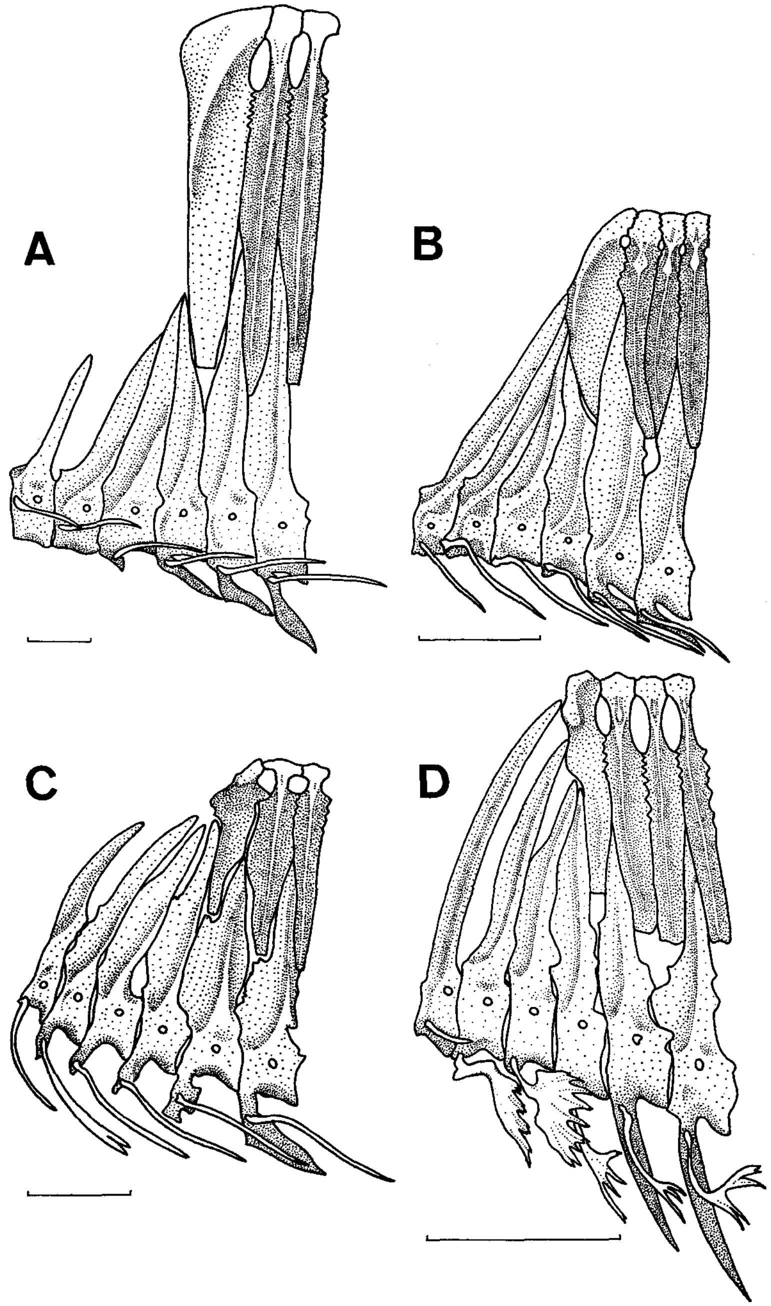
Table 8. *Frequency distributions in counts of the abdominal and caudal vertebrae in the monacanthids.*

| Species | Abdominal vertebrae | | Caudal vertebrae | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7 | 8 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
| *Acreichthys hajam* | 3 | | | | | 3 | | | | | | | | | | | |
| *Alutera heudelotii* | 1 | | | | | 1 | | | | | | | | | | | |
| *A. monoceros* | 20 | | | | | | | | 20 | | | | | | | | |
| *A. schoepfii* | 1 | | | | | | | | 1 | | | | | | | | |
| *A. scripta* | 16 | | | | | | 16 | | | | | | | | | | |
| *Amanses scopas* | 2 | | | | 2 | | | | | | | | | | | | |
| *Anacanthus barbatus* | 4 | | | | | | | | | | | | | | | 1 | 3 |
| *Arotrolepis filicaudus* | 2 | | | | 2 | | | | | | | | | | | | |
| *A. sulcatus* | 3 | | | | 3 | | | | | | | | | | | | |
| *Cantherhines dumerili* | 8 | | | | 8 | | | | | | | | | | | | |
| *C. fronticinctus* | 1 | | | | 1 | | | | | | | | | | | | |
| *C. multilineatus* | 2 | | | | 2 | | | | | | | | | | | | |
| *C. pardalis* | 7 | | | | 7 | | | | | | | | | | | | |
| *Chaetoderma penicilligera* | 7 | | | | | 7 | | | | | | | | | | | |
| *Eubalichthys mosaicus* | 2 | | | | 2 | | | | | | | | | | | | |
| *Meuschenia freycineti* | 1 | | | | | 1 | | | | | | | | | | | |
| *M. hyppocrepis* | 1 | | | | | 1 | | | | | | | | | | | |
| *M. trachylepis* | 1 | | | | | 1 | | | | | | | | | | | |
| *Monacanthus chinensis* | 5 | | | | 5 | | | | | | | | | | | | |
| *Navodon modestus* | 24 | | | | 23 | 1 | | | | | | | | | | | |
| *N. tessellatus* | 4 | | | | 4 | | | | | | | | | | | | |
| *Nelusetta aryraudi* | 3 | | | | | 3 | | | | | | | | | | | |
| *Oxymonacanthus longirostris* | | 8 | | | | | | | | 1 | 7 | | | | | | |
| *Paraluteres prionurus* | 4 | | | | | 4 | | | | | | | | | | | |
| *Paramonacanthus japonicus* | 21 | | | | 20 | 1 | | | | | | | | | | | |
| *P. nipponensis* | 2 | | | | 2 | | | | | | | | | | | | |
| *Pervagor melanocephalus* | 10 | | | 1 | 9 | | | | | | | | | | | | |
| *Pseudalutarius nasicornis* | | 20 | | | | | | | | | 1 | 17 | 2 | | | | |
| *Pseudomonacanthus peroni* | 2 | | | | 2 | | | | | | | | | | | | |
| *Rudarius ercodes* | 22 | | | | 1 | 21 | | | | | | | | | | | |
| *Scobinichthys granulatus* | 3 | | | | | 3 | | | | | | | | | | | |
| *Stephanolepis cirrhifer* | 36 | | 1 | | 35 | | | | | | | | | | | | |

like and branched distally, though the first epipleural ribs are still normal (Fig. 58, D).

Group D. A single genus *Oxymonacanthus* is included in this group, and characterized by having eight abdominal and 18 (usually) caudal vertebrae, and rough rectangular neural spines of the second to fifth abdominal vertebrae (Fig. 59, A). The other vertebral characters are not essentially different from those of the foregoing groups.

Group E. This group comprises only one genus *Pseudalutarius*, and is distinguished from all other balistoid members by having pleural ribs (Fig. 59, B). In addition to this unique character, the group is distinct from the preceding groups in bearing eight abdominal and 19 (usually) caudal vertebrae (Tables 8 and 9), and rough rectangular neural spines on the second to sixth abdominal vertebrae. Furthermore, the group is peculiar with respect to the epipleural ribs. In all other


A
B
C
D

balistoid members the epipleural ribs begin with the second abdominal vertebra, while in this group the first epipleural ribs are found on the first abdominal vertebra (Fig. 56, B and D).

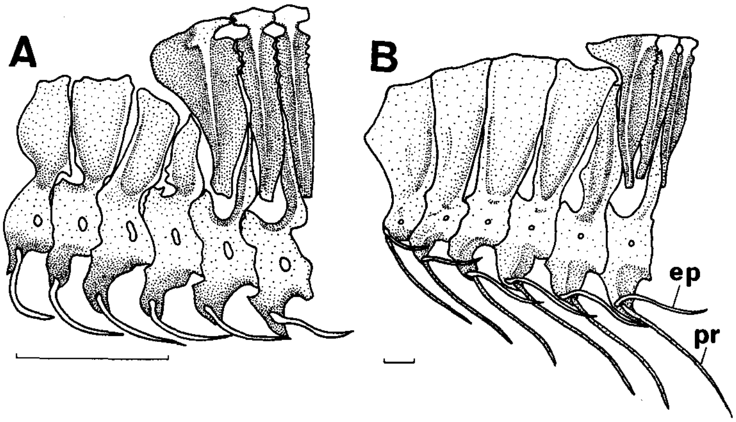


Fig. 59. Diagram showing the abdominal vertebrae (second to seventh) and associated bones in two monacanthid species. A, *Oxymonacanthus longirostris*; B, *Pseudalutarius nasicornis*. ep, epipleural rib; pr, pleural rib. Scale bars indicate 5 mm.

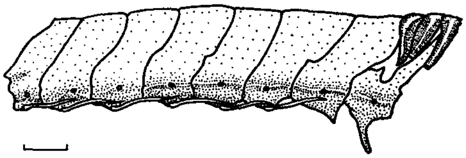


Fig. 60. Diagram showing the vertebrae (second to ninth) and associated bones of a monacanthid species *Anacanthus barbatus*. Scale bar indicates 5 mm.

Group F. This group is composed of a single genus *Anacanthus* which is clearly different from all other balistoid members in having 23 or 24 caudal vertebrae (Tables 8 and 9). The fishes of this group have rectangular neural spines from the second abdominal vertebra to the first caudal vertebra (Fig. 60). These neural spines are firmly articulated with one another by fibrous connective tissue.

**Discussion**. The balistoid vertebrae have been studied by many authors (Hollard, 1853; Regan, 1903; Rosen, 1916; Fraser-Brunner, 1935, 1941; Ford, 1937; Hotta, 1961; Takahashi, 1962; Tyler, 1962a, 1968). Most of their descriptions were confined to several balistoid members, thus they could not clarify the whole

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Fig. 58. Diagram showing the abdominal vertebrae (second to seventh) and assoicated bones in four monacanthid species. A, *Chaetoderma penicilligera*; B, *Rudarius ercodes*; C, *Paraluteres prionurus*; D, *Brachaluteres ulvarum*. Scale bars indicate 5 mm.

aspect of the vertebrae of the balistoids. On the other hand, Fraser-Brunner (1935, 1941) worked with many balistoid members and established a key to the genera by using the number of vertebrae as an important feature. Unfortunately, there were many errors in his later paper (1941). He included the genera, *Amanses*, *Eubalichthys*, *Oxymonacanthus*, and *Navodon* in the group having 20 vertebrae. However, *Oxymonacanthus* possesses actually 26 (usually) vertebrae and the remaining four genera have 19 vertebrae. Therefore, the previous researches were insufficient in determining the complete interrelationships of the balistoids on the basis of vertebral features.

Judging from the present examination, it seems that the following characters provide us with important information from the phylogenetic view point: (1) the number of vertebrae; (2) the features of epipleural ribs; (3) the presence or absence of pleural ribs; (3) the features of neural spines anterior to the second dorsal fin.

Since the triacanthids, considered to be the ancestor of the balistoids, have eight abdominal and 12 caudal vertebrae, two hypotheses can be made with regard to the differentiation of the vertebral number through the phylogenetic lineages of the balistoid members.

The first hypothesis is composed of the following evolutional speculation. The triacanthid vertebral number, $8+12=20$, is reduced to $7+11=18$ in Group A (balistids), then the number is secondarily increased to $7+24=31$ in Group F along the monacanthid evolutional pathways.

The second hypothesis is given as follows. The differentiation of the vertebral number originates in the members of Group C which show the same condition in the total vertebral number as seen in the triacanthids. Then, its basic number $7+13=20$ is increased on one lineage to $7+24=31$ of Group F through $8+18=26$ of Group D and $8+19=27$ of Group E, and at the same time the number is reduced on another lineage to $7+11=18$ of Group A through $7+12=19$ of Group B. Therefore, it is necessary from a phylogenetic view point to answer the question of which hypothesis is the most reasonable.

If the second hypothesis is true, the balistids must be assigned to the more advanced systematic position than the monacanthid members of Groups B and C. However, all other anatomical features examined in the present study are opposed to this speculation. On the other hand, in the first hypothesis there is little conflict with the other anatomical characters. Therefore, I favor the possiblity of the first over the second.

Judging from this point of view, the members of Group A (balistids) are then considered to be placed at the most primitive systematic position in the balistoids. The members of Groups B to F are systematically arranged in the order of their vertebral number, thus the most advanced systematic position is occupied by the members of Group F.

On the other hand, in most members of the balistoids the abdominal vertebrae are seven in number except for the members of Groups D and E which have eight abdominal vertebrae. Therefore, it may be considered that Groups D and E have

Table 9. *Differentiation of the vertebrae in the balistoids.*

| Group | Genus | Neural spines anterior to the second dorsal fin | Number of abdominal vertebrae | Number of caudal vertebrae | Pleural ribs | Epipleural ribs | |
|---|---|---|---|---|---|---|---|
| A | all genera of balsitids | triangular | 7 | 11 | absent | rod-like | starting from the second abdominal vertebra |
| B | *Amanses*<br>*Arotrolepis*<br>*Cantherhines*<br>*Eubalicthys*<br>*Monacanthus*<br>*Navodon*<br>*Paramonacanthus*<br>*Pervagor*<br>*Pseudomonacanthus*<br>*Stephanolepis* | | | 12 | | | |
| C | *Acreichthys*<br>*Chaetoderma*<br>*Meuschenia*<br>*Meuschenia*<br>*Nelusetta*<br>*Paraluteres*<br>*Rudarius*<br>*Scobinichthys* | | | 13 | | | |
| | *Brachaluteres*<br>*Alutera* | | | 13, 14, or 16 | | branched distally | |
| D | *Oxymonacanthus* | rectangular | 8 | 18 (usually) | | rod-like | |
| E | *Pseudalutarius* | | | 19 (usually) | present | | starting from the first abdominal vertebra |
| F | *Anacanthus* | | 7 | 23 or 24 | absent | | starting from the second abdominal vertebra |

possibly progressed in a different evolutional pathways from the other monacanthid groups.

The epipleural ribs are normal in most balistoid members but peculiar in the genera *Brachaluteres* and *Pseudalutarius*. The former possesses greatly modified epipleural ribs on the third to seventh abdominal vertebrae. Thus, it is conceived that the genus is more advanced than the other members of Group C. The latter is distinct from all other balistoid members in having the first epipleural ribs on the first abdominal vertebra. This is considered to be a primitive feature, since the same condition is found in the perciform fishes (Katayama, 1959; Akazaki, 1962). In addition to this fact, the genus *Pseudalutarius* is unique among the balistoids in having pleural ribs. This is not found in the tetraodontiform fishes (except for *Triodon macropterus*) (Tyler, 1962a, 1962c, 1973), but in the perciform fishes. Therefore, this condition implies that the genus may be situated at a rather primitive systematic position.

With respect to the neural spines anterior to the second dorsal fin, Groups D, E, and F are peculiar. Their rectangular neural spines are significantly different from the normal triangular neural spines found in the other balistoid members. Since the triacanthids have the triangular neural spines anterior to the second dorsal fin, these three groups are considered to be more advanced than the other balistoid members. This finding goes very well with the speculation that is based on the number of vertebrae.

The interrelationships in the balistoids based on the vertebral characters are summarized in Table 9, however, the systematic position of Group E is rather provisional. Indeed, it is very difficult to decide the systematic position of the group only by the vertebral characters. This enigmatic problem will be discussed in detail in the general consideration chapter.

### 10. Caudal skeleton and fin

**Description.** The balistoid caudal skeleton consists of four elements, a single epural, nearly always an upper free hypural, a centrum-hypural plate, and a free parhypural. These elements support the caudal fin. The penultimate vertebra assists these elements in supporting the caudal fin. The haemal spine of the penultimate vertebra is autogenous but its neural spine is fused to the centrum. The caudal fin, which is composed of only 12 principal rays, varies in shape among the balistoid members, especially in the monacanthids members. The balistids and monacanthids are clearly distinguishable by the feature of the crest on the centrum-hypural plate, thus they are described independently in the following section.

Balistidae. The members of the Balistidae are characterized by having the vertical crest on the anterior part of the centrum-hypural plate. The illustrations of 11 species cover the variation found in the balistid caudal fin structure (Figs. 61 and 62).

The epural is a single peg-like shape, and is narrow dorsally and expanded ventrally. The bone articulates by fibrous connective tissue anteriorly with the neural spine of the penultimate vertebra, ventrally with the neural arch element of the last centrum, and posteriorly with the upper free hypural.

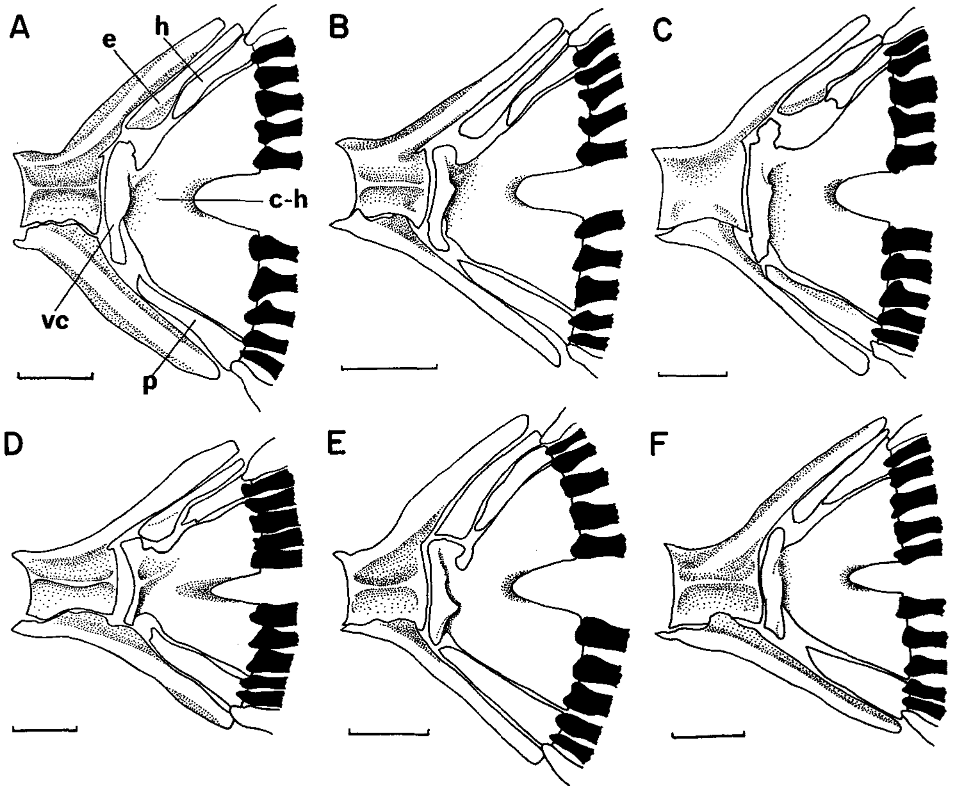

Fig. 61. Diagram showing the caudal skeleton and fin rays in six balistid species. A, *Balistapus undulatus*; B, *Rhinecanthus aculeatus*;, C, *Balistoides conspicillum*; D, *Balistes vetula*; E, *Melichthys vidua*; F, *Sufflamen fraenatus*. c-h, centrum-hypural plate; e, epural; h, free hypural; p, parhypural; vc, vertical crest. Solid regions show branched rays; open regions indicate unbranched rays. Scale bars indicate 5 mm.

The upper free hypural is wedged between the epural and the centrum-hypural plate. The bone is like a narrow shaft in shape and expanded dorsally. It articulates by fibrous connective tissue anteriorly with the epural and posteriorly with the centrum-hypural plate. It supports the uppermost two caudal fin rays.

The other hypurals are fused with one another and with the last centrum to make the centrum-hypural plate. The plate is triangular in shape and divided into dorsal and ventral parts by a deep cleft extending forward in the posterior half of the plate. The plate is attached by cartilage anteriorly to the posterior surface of the penultimate vertebra. The vertical crest for muscle attachment is present at the anterior part of the plate. The plate possesses anteriorly dorsal and ventral projections, namely the neural and haemal arch elements. The dorsal half of the plate supports three or four fin rays, and the ventral part also supports three or four fin rays.

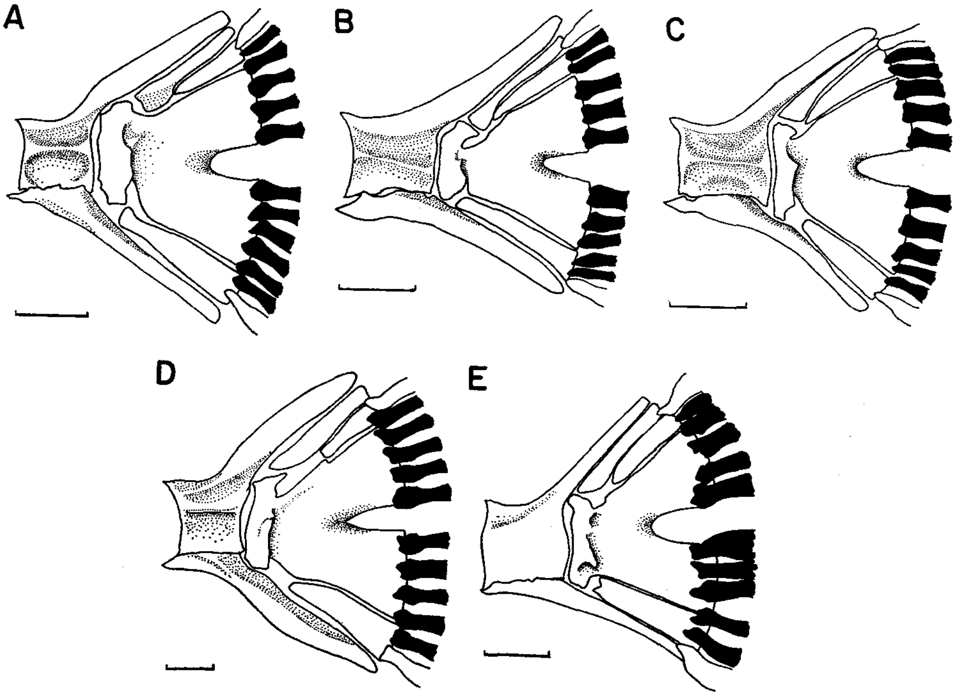

Fig. 62. Diagram showing the caudal skeleton and fin rays in five balistid species. A, *Pseudobalistes flavimarginatus*; B, *Abalistes stellatus*; C. *Odonus niger*; D, *Canthidermis maculatus*; E, *Xanthichthys mento*. Scale bars indicate 5 mm.

The free parhypural is an elongated triangular shape. The bone articulates by fibrous connective tissue with the centrum-hypural plate dorsally and with the haemal spine of the penultimate vertebra ventrally. The bone supports the lowermost two or three caudal fin rays.

There are 12 principal caudal fin rays. The uppermost and lowermost rays are unbranched and the remaining 10 rays are branched.

The balistid members show their variation by the shape of the caudal fin. In the coastal species such as *Balistoides conspicillum* and *Rhinecanthus aculeatus* the caudal fin is rounded or truncated in shape, however, in the oceanic species belonging to the genera *Canthidermis* and *Xanthichthys* the caudal fin is subemarginate or lunate. In another oceanic species, *Abalistes stellatus*, the uppermost and lowermost caudal fin rays are greatly extended posteriorly in the large specimens. The caudal peduncle is compressed in the balistid members except for *Abalistes stellatus* which has a greatly depressed caudal peduncle.

Monacanthidae. The monacanthids are clearly distinguished from the balistids in having the horizontal crest on the anterior part of the centrum-hypural plate. The illustrations of 22 species cover the variation found in the monacanthids (Figs. 63 to 66).

The monacanthid caudal skeleton is essentially similar to that of the balistids, though it shows more variation in shape than that found in the latter. Thus, the following description is limited to the significant features in order to avoid repeating the account of the preceding section.

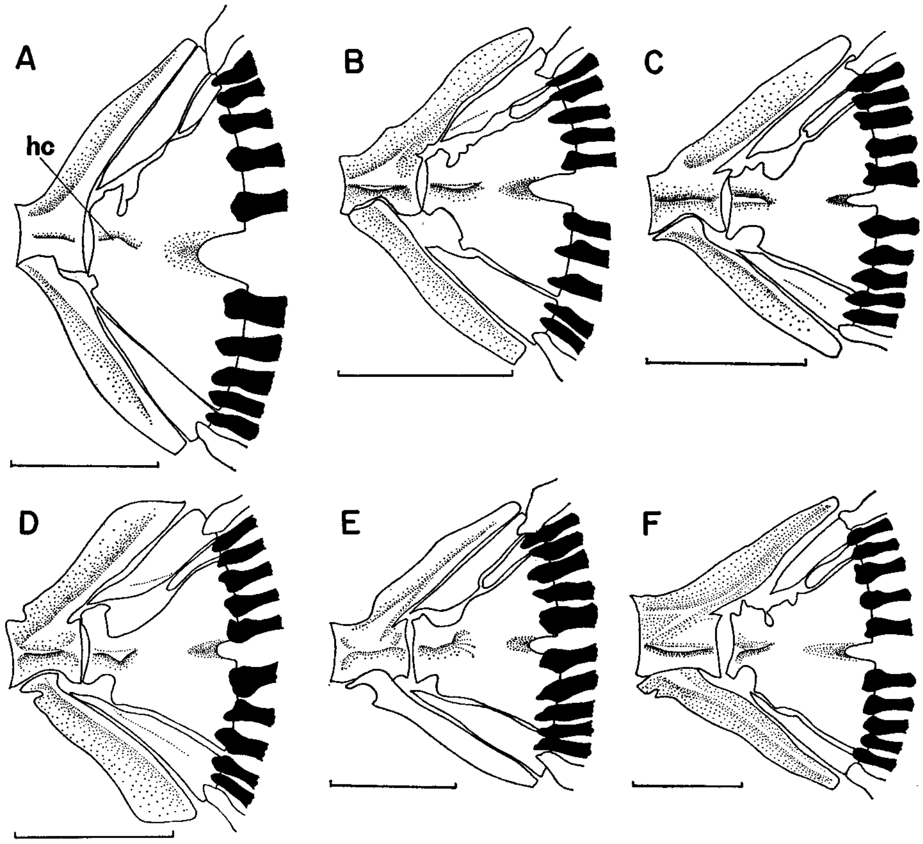

Fig. 63. Diagram showing the caudal skeleton and fin rays in six monacanthid species. A, *Pervagor melanocephalus*; B, *Monacanthus chinensis*; C, *Arotrolepis filicaudus*; D, *Paramonacanthus japonicus*; E, *Stephanolepis cirrhifer*; F, *Chaetoderma penicilligera*. hc, horizontal crest. Scale bars indicate 5 mm.

The epural is peg-like in shape and tapered to a point ventrally. The upper free hypural is placed between the epural and the centrum-hypural plate. The bone is absent in some members such as *Brachaluteres ulvarum* and *Rudarius ercodes* (Fig. 66, C and D). In *Alutera scripta* the bone is present in two specimens at the juvenile and young stages, while in an adult specimen it is absent (Fig. 66, A and B).

The centrum-hypural plate is triangular in shape and divided into dorsal and ventral parts by a posterior cleft which is less developed than that found in the balistid members. In *Anacanthus barbatus* the cleft is reduced to a very small concavity. The crest for muscle attachment is present at the anterior part of the plate, although it is horizontal rather than vertical. The neural and haemal arch elements are found at the anterior part of the centrum-hypural plate, however, they are smaller than that of the balistids.

The parhypural of many monacanthid members is similar to that of the balistids. However, in *Anacanthus barbatus* the bone is rather short and rectangular in shape.

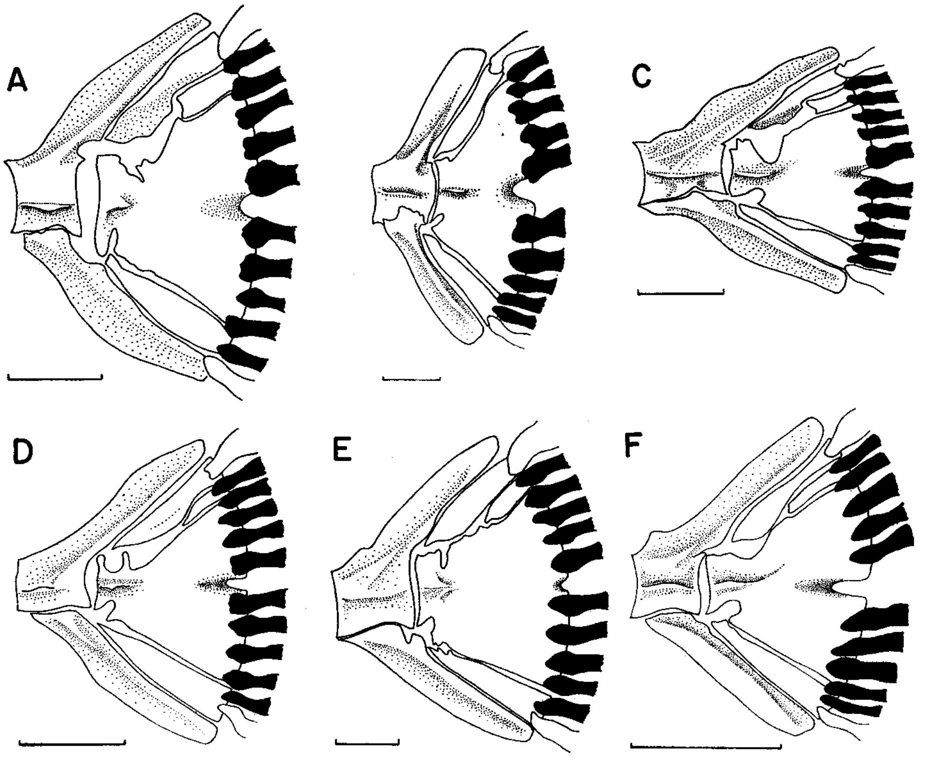

Fig. 64. Diagram showing the caudal skeleton and fin rays in six monacanthid species. A, *Cantherhines dumerili*; B, *Amanses scopas*; C, *Navodon modestus*; D, *Meuschenia trachylepis*; E, *Scobinichthys granulatus*; F, *Pseudomonacanthus peroni*. Scale bars indicate 5 mm.

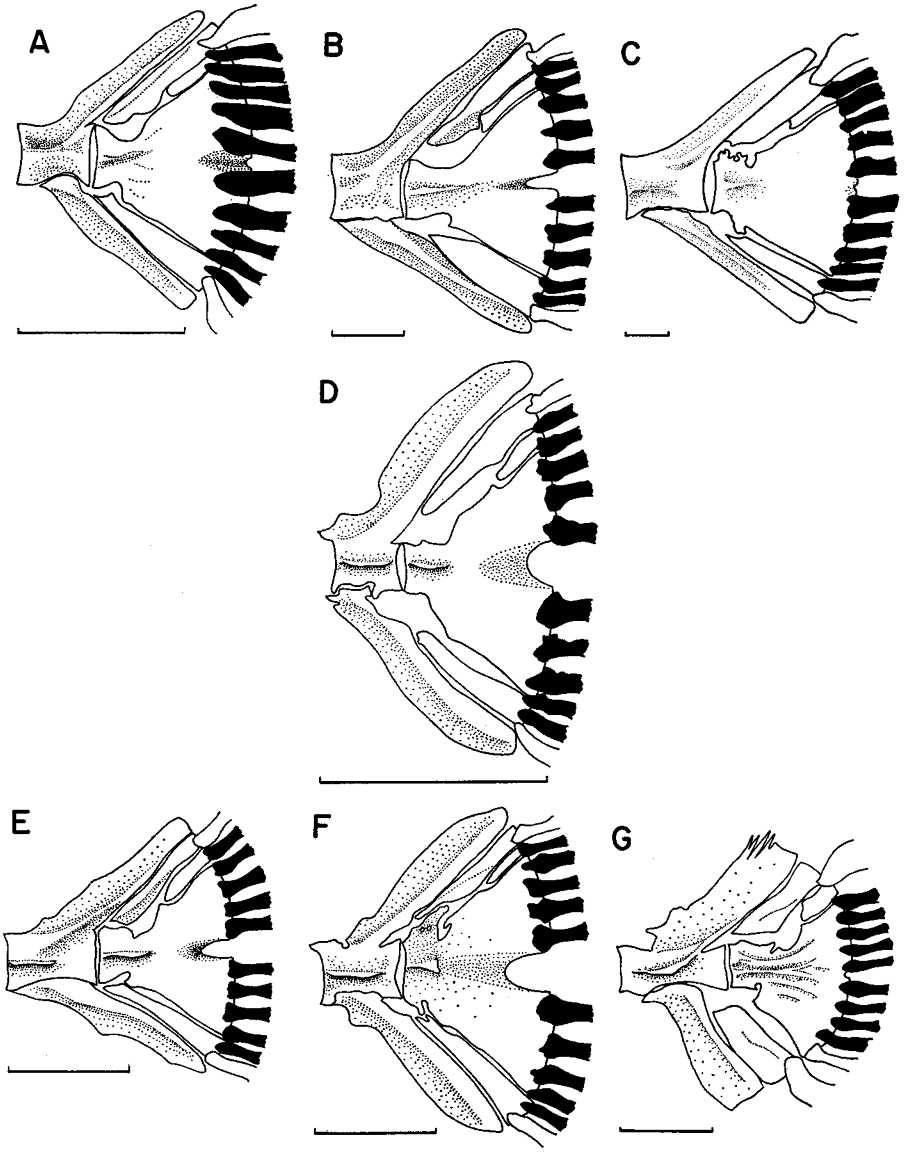

Fig. 65. Diagram showing the caudal skeleton and fin rays in seven monacanthid species. A, *Eubalichthys mosaicus*; B, *Alutera monoceros*; C, *Nelusetta ayraudi*; D, *Oxymonacanthus longirostris*; *E*, *Pseudalutarius nasicornis*; F, *Paraluteres prionurus*; G, *Anacanthus barbatus*. Scale bars indicate 5 mm.

There are 12 principal caudal fin rays in all members of the monacanthids. The uppermost and lowermost rays are unbranched and the remaining 10 rays are branched in the monacanthids except for *Anacanthus barbatus* in which the uppermost and the two lowermost rays are unbranched (Fig. 65, G).

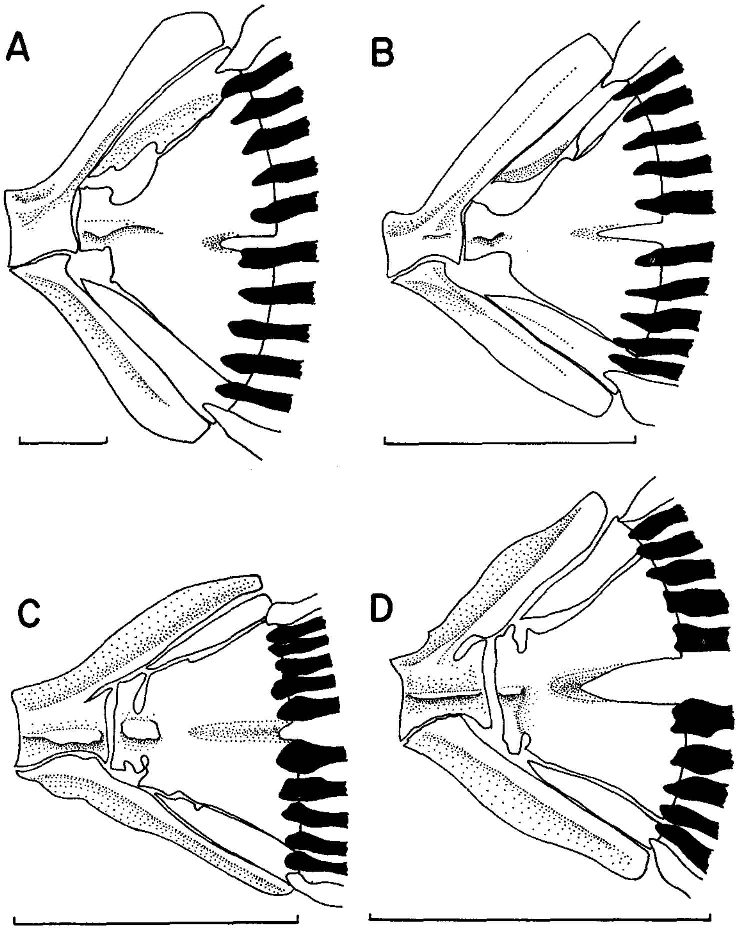

Fig. 66. Diagram showing the caudal skeleton and fin rays in three monacanthid species. A, *Alutera scripta* (adult); B, *Alutera scripta* (juvenile); C, *Rudarius ercodes*; D, *Brachaulteres ulvarum*. Scale bars indicate 5 mm.

The caudal fin shows greater variation in shape than that found in the balistids. In many monacanthid members the caudal fin is rounded or truncated in shape. However, in *Monacanthus chinensis* the uppermost ray is greatly extended posteriorly. In *Paramonacanthus japonicus* both the uppermost and lowermost rays are projected posteriorly into the filaments. *Alutera scripta* and *Anacanthus barbatus* possess a greatly elongated caudal fin. The caudal peduncle is compressed in all of the monacanthid members.

**Discussion.** The balistoid caudal skeleton has been studied by several authors (Whitehouse, 1910; Monod, 1968; Tyler, 1962a, 1970). Of these works, Tyler's (1970) paper is excellent and useful for phylogenetic consideration. Since he described accurately many of the balistoid caudal skeletons, the descriptions in the present paper are essentially the same as his work with a few additions.

As described in the preceding section, there is very little essential variation in the balistoid caudal skeleton. This fact seems to confirm the commonly accepted concept that the superfamily Balistoidea forms a natural group.

On the other hand, slight but significant differences are found between the balistids and monacanthids in the features of the cleft and crest on the centrum-hypural plate. The cleft dividing the plate into the dorsal and ventral parts is more developed in the balistids than that found in the monacanthids. The cleft is considered to be a remnant of the fusion between the hypurals, since the most primitive tetraodontiform fishes, the triacanthodids, have five separate hypurals (Tyler, 1970). Gosline (1961: p. 265) stated that in general the evolution of the caudal skeleton in percoid fishes and derivative groups is primarily one of the fusion of parts. Actually, Tyler (1970) found that the progressive reduction and simplification of the caudal skeleton by the fusion of the elements is present in the tetraodontiform fishes along their evolutional lineages. Therefore, it is concluded that the larger cleft suggests a more primitive condition. Thus, the balistids are considered to be more primitive than the monacanthids.

With regard to the crest on the anterior part of the centrum-hypural plate, the balistids and monacanthids are clearly distinguishable. In the former the vertical crest is found, but in the latter a horizontal one is present on the plate. These crests are similar in shape to the part of the ridge on the penultimate vertebra. The vertical crest of the balistids resembles the anterior part of the ridge, and the horizontal crest of the monacanthids looks like the middle part of the ridge. Thus, it seems that in the balistids the anterior part of the ridge on the last centrum is retained and developed up to the large vertical crest, but the middle and posterior parts of it are reduced and absent. On the other hand, in the monacanthids the anterior and posterior parts of the ridge are seemingly reduced and absent, but the middle part of it is enlarged. However, at the present time there is not enough information to answer as to which condition is the more primitive. Thus, it is premature to take this feature into a phylogenetic view point.

In the balistid members, *Abalistes stellatus* is slightly advanced than the other members, since it has a peculiarly depressed caudal peduncle.

On the other hand, the upper free hypural is an important element to considering the interrelationships among the monacanthid members. The bone is present in most balistoid members, but it is absent in several monacanthid members such as *Alutera scripta*, *Rudarius ercodes*, and *Brachaluteres ulvarum* (Fig. 66). In the adult specimens of the first species the bone is not found in the caudal skeleton, but in the juvenile it is present in the normal position. This fact suggests that the bone is fused to the centrum-hypural plate during the growth of the fish. While in the 10 specimens of *Rudarius ercodes* and two of *Brachaluteres ulvarum* there are no trace of the bone. These facts indicate that the three species are slightly more advanced than the other balistoid members.

In the present study I can not find any trace of the uroneurals in any of the balistoid members. However, Tyler (1970) described the uroneurals of a balistid species *Balistapus undulatus*. He stated (p. 14) that three out of the five specimens showed no evidence of separate uroneural elements, but the other two did. Since there was no trace of the uroneurals in the 10 specimens (87.8~195.0 mm in standard length) of the same species examined here, I could not confirm Tyler's finding. I believe that it requires an ontogenetic study in order to decide whether the true uroneurals are present or absent in the species. Therefore, at the present time it seems safe to exclude the uroneural elements from the phylogenetic consideration with respect to the balistoid members.

## V. General consideration

### 1. Osteological definition of the superfamily Balistoidea

The fishes of the Balistoidea belong to the suborder Balistoidei of the order Tetraodontiformes. Though the members of the Balistoidea are greatly different in their general appearance, they have been considered as a single natural group by many ichthyologists (Regan, 1903; Fraser-Brunner, 1935, 1941; Breder and Clark, 1947; Matsubara, 1955; Tyler, 1968; Winterbottom, 1974). I agree with them on this point, since the Balistoidea are distinguishable from the other tetraodontiform fishes by having the following characters: the pelvic complex is composed of a single pelvis with or without the following elements, the incasing scales, the rudimentary fin ray elements, a cartilage plug, and/or the tendons or ligaments; posttemporal is present and rigidly wedged into the cranial bones; each premaxillary possesses five or seven teeth; each dentary has two to four teeth; the palatine is specialized into a T-shaped or simple rod-like bone; the basihyal is absent; the first dorsal fin is directly attached to the cranium and forms the specialized locking mechanism; and the hypurals and the last centrum are fused to make the centrum-hypural plate in the caudal skeleton.

### 2. Osteological definition of the families Balistidae and Monacanthidae

The fishes, here divided into two families, Balistidae and Monacanthidae are grouped into one family Balistidae by some authors (Böhlke and Chaplin, 1968; Kuronuma and Abe, 1972; Winterbottom, 1974). However, as described in the previous chapters these two families are clearly distinguished from one another by many anatomical features. Thus, I conclude that the recognition of these two families is quite reasonable.

**Balistidae**: The pelvic complex is composed of a single pelvis with the incasing scales in four segments, a rudimentary fin ray element, a cartilage plug, and the dorsal and ventral tendons. The postcleithrum consists of dorsal and ventral elements which are tightly held to one another by fibrous connective tissue. The posttemporal articulates with the epiotic. Seven teeth are present on each premaxillary, four in an outer row and three in an inner row. Each dentary possesses four teeth in a single row. The palatine is modified into a T-shaped bone articulating ventrally with the ectopterygoid, antero-dorsally with the maxillary and premaxillary, and posteriorly with the anterior parts of the ethmoid and vomer by fibrous connective tissue. The branchiostegal rays are always six in number. The basihyal is absent. The supraoccipital and epiotic form postero-dorsally the concavity into which the ventral shaft of the first dorsal fin is wedged. The dorsal keel of the parasphenoid is developed for muscle attachment. Three dorsal spines are located on the two basal pterygiophores. The supraneural is present. The number of vertebrae is $7+11=18$. The epipleural ribs start on the second abdominal vertebra and end on the first caudal vertebra. The pleural ribs are absent. The caudal skeleton consists of a single epural, an upper free hypural, a centrum-hypural plate having a vertical crest at its anterior part, and a free parhypural.

**Monacanthidae**: There is a single pelvis in the pelvic complex. The incasing scales are composed of one to six scales in one to three segments, although they are absent in some members. A cartilage plug, two nubbins of the rudimentary fin ray elements, and/or the dorsal and ventral tendons or ligaments are present or absent. The postcleithrum consists of a single element. The posttemporal does not articulate with the epiotic. Five teeth, three in an outer row and two in an inner row, are present on each premaxillary. Each dentary possesses two or three teeth in a single row. The palatine is modified into a simple rod-like bone articulating antero-dorsally with the anterior parts of the ethmoid and vomer. It also connects with the ectopterygoid by tough connective tissue, though there is some distance between them. The branchiostegal rays vary in number from four to six. The basihyal is absent. The supraoccipital and epiotic do not form a concavity postero-dorsally, but a large part of the dorsal surface of the cranium is overlain by the basal pterygiophore of the first dorsal fin. The longitudinal keel of the parasphenoid as seen in the balistids is almost completely replaced by the ventral keel of the ethmoid. Two dorsal spines (one only in the genus *Anacanthus*) are placed on a single basal pterygiophore. Any trace of the supraneural is absent. The number of vertebrae vary among the genera, $7\sim8+12\sim24=19\sim31$. The epipleural ribs start on the second abdominal vertebra (on the first abdominal vertebra in the genus *Pseudalutarius*). The pleural ribs are absent (present only in the genus *Pseudalutarius*). The caudal skeleton is composed of a single epural, an upper free hypural (absent in a few members), a centrum-hypural plate having a horizontal crest on its anterior part, and a free parhypural.

## 3. Ancestor of the Balistoidea

With regard to the ancestor of the balistoids, there are two main assertions. The first is that the triacanthids are considered to be the ancestor of the balistoids. This opinion has been supported by many ichthyologists. The second has been recently proposed by Winterbottom (1974) on the basis of the comparative myology. He considered that the triacanthoids and balistoids were derived from different ancestors. These two views are shown in Figures 67 and 68.

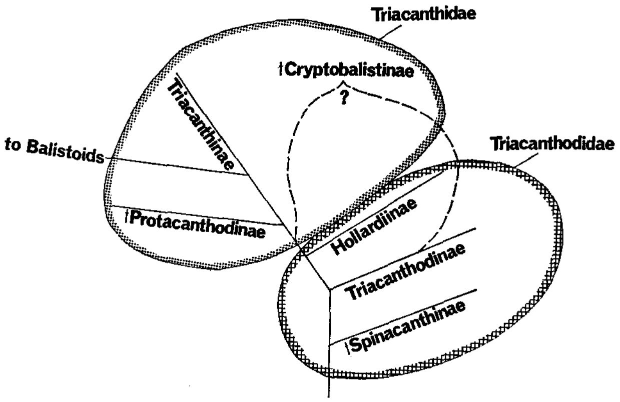

Fig. 67. Diagram showing the phylogenetic relationships of the primitive tetraodontiforms. Daggers indicate fossil groups. (Drawn from Tyler, 1968, Fig. 6).

The first view is expressed in Tyler's (1968) monograph. He pointed out (pp. 34 ~35) that many characters are shared by the triacanthids and balistoids. These characters are as follows: the teeth are heavy incisors in an outer series but more molariform in the inner series; the hyomandibular has a well developed crest variously placed obliquely across its outer surface; the pterotic has a large ventral extension over the lateral surface of the postero-dorsal region of the hyomandibular; the opercle is elongated and expanded in the middle about equally anteriorly and posteriorly; the basihyal is absent; the pterosphenoids meet and suture to one another in the mid-line of the posterior wall of the orbit; the spiny dorsal fin has a much shorter base than that of the soft dorsal fin; the epipleural ribs tend to be thicker; the basal pterygiophores of the soft dorsal and anal fins have lateral flanges along their lengths to increase the surface available for muscle attachment and the pterygiophores are sutured to one another distally; the number of separate hypural elements is reduced to two or three; the number of principal caudal rays is 12; and the pelvic complex is present. From the Hennigian view point, Winterbottom (1974) attacked Tyler's list of characters. He said (pp. 94 ~ 95) "Nearly all these character conditions may also be found in acanthurids (including the flanges of the pterotic overlying the posterodorsal region of the hyomandibular, and the meeting and suturing of the pterosphenoids in the midline). This brings the state of these characters into question—if the acanthurids form the sister (or close) group to the tetraodontiforms, then it is reasonable to assume the triacanthid-balistoid condition is one of symplesiomorphy (in which case the triacanthoid subfamilies are synapomorph, and the characters cannot be used to link the triacanthids and balistoids phylogenetically)." Indeed, many characters described by Tyler (1968) are found in the acanthurids. Neverthelass, I can show that a few, but important, characters in Tyler's list are shared by the triacanthids and balistoids, but are not present in the acanthurids. These characters are as follows: (1) the teeth are heavy incisors in an outer series but more molariform in

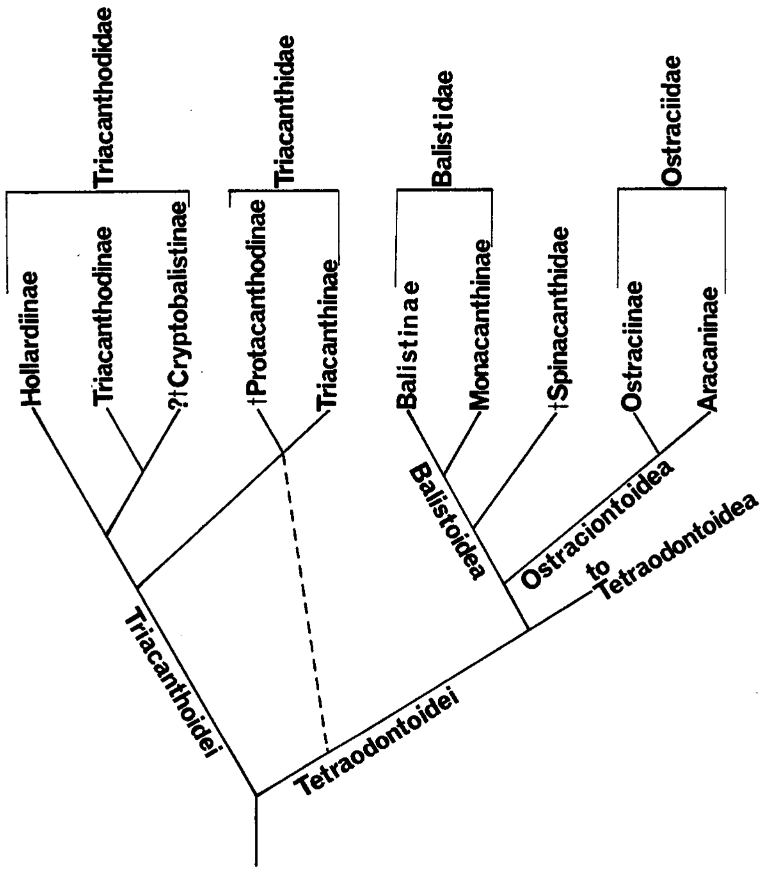

Fig. 68. Diagram showing the phylogenetic relationships of the balistoids and their relatives. Daggers indicate fossil groups. (Drawn from Winterbottom, 1974, Fig. 47).

the inner series; (2) the spiny dorsal fin has a much shorter base than that of the soft dorsal fin; (3) the number of separate hypural elements is reduced to two or three; (4) the number of principal caudal rays is 12. Moreover, the triacanthids and balistoids share advanced character conditions which are not found in the acanthurids: (1) the basisphenoid is absent; (2) the parietals are not present; and (3) the pleural ribs are lacking (except for the genus *Pseudalutarius*). Judging from these facts, it is considered that the triacanthids have a closer relationship to the balistoids than to the acanthurids.

On the other hand, the triacanthids are clearly more primitive than the balistoids in many characters, such as, the normal paired pelvic girdles, slightly protractile upper jaw, six dorsal spines, four pharyngobranchials, etc. Therefore, it is quite reasonable to assume that the triacanthids are to be considered as the ancestor of the balistoids. This speculation is reinforced by the fossil evidence. The Oligocene triacanthid member, *Cryptobalistes brevis* (Rath) known from a single specimen, provides us with important information concerning the relationship between the triacanthids and balistoids. According to Tyler (1968: p. 244), "*Cryptobalistes* is in most ways an excellent anatomical intermediary between the triacanthids and balistoids, except for one very important characteristic: the form of pelvis." Then, he placed *Cryptobalistes brevis* in the triacanthids as the subfamily Cryptobalistinae.

All of the evidence mentioned above proves, in contrast with Winterbottom's (1974) opinion, that the triacanthids should be linked phylogenetically to the balistoids and be considered as the ancestor of the latter.

## 4. Phylogenetic interrelationships of the balistoids

The phylogenetic relationships between the balistids and monacanthids have been studied by many authors (Fraser-Brunner, 1935, 1941; Breder and Clark, 1947; Matsubara, 1955, 1963; Tyler, 1962a, 1962b, 1970; Winterbottom, 1974). They accepted that these two groups form a single natural group, and pointed out that the monacanthids are more specialized than the balistids. Then, it was generally accepted without any doubt that the monacanthids were derived from the balistids or, at least the balistid-like ancestor. On the other hand, the phylogenetic interrelationships of the balistoid genera are not well known because of a lack of detailed anatomical studies. With regard to the generic interrelationships, we can find only Fraser-Brunner's (1935, 1941) papers, in which he described briefly the phylogenetic interrelationships of the balistid and monacanthid genera, and illustrated the dendrogram for the latter. Since his interpretation was dependent upon only a few characters, it was insufficient to clarify the whole phylogenetic aspect of the balistoid genera. Therefore, it is necessary to interpret the phylogenetic interrelationships of the balistoid genera on the basis of the many anatomical characters. The purpose of this section is to answer this question by a synthesis of the analyses in the previous chapters.

*The method used for the phylogenetic inferences.* Prior to discussion it is best that this section shows the method which is used to infer the phylogenetic interrelationships of the balistoid genera. This method is based on two criteria and several principles described below.

I. The shared advanced character condition.

1. The taxa sharing the advanced character conditions are placed into an identical group or lineage.

2. If the phylogenetic relationships can not be made from 1, then the number of advanced character conditions can be used for the phylogenetic inferences.

3. If the dichotomous relationships can not be reasonably found in the taxa because of the mosaic conditions of the advanced characters, then trichotomous relationships are given for the taxa.

II. The law of parsimony.

1. The minimum parallel evolution.

2. The minimum reversal of evolutional trends.
3. The minimum evolutional steps.

In order to show the practical use of this method, simplified examples are given below. In Figure 69 the interrelationships of 10 taxa *a* to *j* are infered by the analyses of 10 anatomical characters A to J.

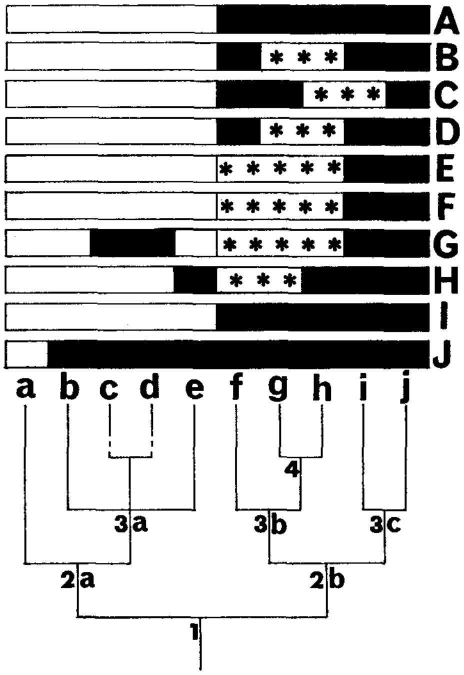

Fig. 69. Diagram showing the phylogenetic interrelationships among 10 taxa *a* to *j* based on the analyses of 10 characters A to J. Black rectangles indicate an advanced condition; white rectangles, a primitive condition; marked rectangles refer to an intermediate condition.

Branch point 1 is derived from the seven characters A to F and I, because in all of these characters the five taxa *f* to *j* show more advanced conditions than those of the other taxa. This inference is an example of the application of the principle I–1. On the other hand, it seems best to separate the taxon *a* from the other nine taxa *b* to *j* on the basis of the character J. However, it is not reasonable to accept this speculation in order to form branch point 1, since the characters A to F and I indicate the opposite evidence. This judgment is based on the principle I–2. This shows that a speculation derived from many characters is more reasonable than that based on a very few characters.

Branch point 2a separates the taxon *a* from the other taxa *b* to *e*. This hypothesis is proposed from the analysis of the character J. On the other hand, it seems feasible to accept the other hypothesis which separates the taxon *e* from the other taxa *a* to *d* based on the character H (Fig. 70). However, in this case we must accept an additional branch point, marked with 4a, for the taxa *b*, *c*, and *d*, in other words this hypothesis needs more evolutional steps than that found in the first hypothesis. By the principle II–3, the second hypothesis (Fig. 70) is to be rejected from the phylogenetic inference. Thus, at the branch point 2a the taxon *a* is reasonably separated from the other taxa.

At the branch point 3a we find the trichotomy among the taxa *b* to *e* (Fig. 69). However, it seems possible to speculate the other two branching patterns at this branch point. The first is that the taxa *c* and *d* are separated from the taxa *b* and *e* by the analysis of the character G (Fig. 71, A). The second is that the taxon *e*, having the advanced character H, is separable from the taxa *b*, *c*, and *d* (Fig. 71, B). Of course, it is impossible to answer the question of which hypothesis is the most reasonable. On the basis of the analyses of the characters presented in Figure 69, we can only say that the taxa, *b*, *c-d*, and *e* are distinguishable from one another, and that the taxa *c* and *d* and the taxon *e* are more advanced than the taxon *b*. Therefore, it is reasonable, here, to accept the trichotomy at the branch point 3a for these four taxa. This is an example of the application of the principle I–3.

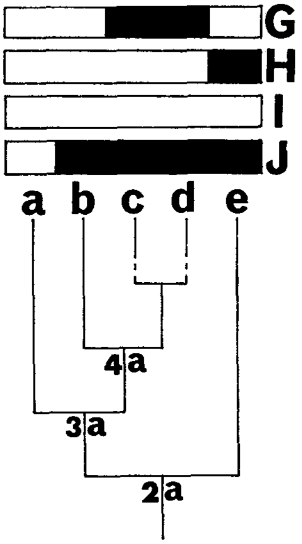

Fig. 70. Diagram showing branching sequences primarily based on character H.

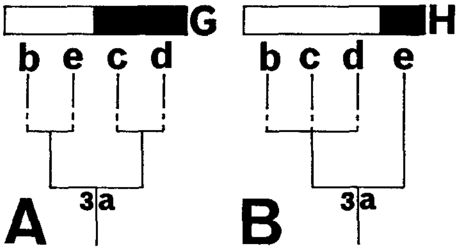

Fig. 71. Diagram showing two branching patterns at branch point 3a. A, based on character G; B, based on character H.

It is impossible to establish the branch point for the taxa *c* and *d* by the present anatomical data, though these two taxa are clearly distinct from one another in the external characters which can not be phylogenetically evaluated. Thus, no branch point is proposed for them.

Branch point 2b is derived from the analyses of the three characters E, F, and G. In this hypothesis the parallelism is found in character C only. On the other hand, it seems possible to establish another branching pattern which separates the taxa *f* and *g* from the taxa *h*, *i*, and *j* at the branch point 2b (Fig. 72). This speculation is based on the analyses of the character H. In this case there are two parallelisms found in the characters B and D. Thus, the first hypothesis is more reasonable than the second one by the principle II–1.

*Practical inference of the phylogenetic interrelationships of the balistoids.* The anatomical characters have been studied in the foregoing chapters to clarify the phylogenetic trends through the balistoid members. Based on these analyses the character conditions are summarized in Figure 73 which also indicates the cladogram for the balistoids.

Branch point 1 is easily derived from the following characters; the incasing scales, the fin ray elements, the pectoral girdles, the upper jaw, the lower jaw, the suspensorium, the ceratobranchials, the urohyal, the posttemporal, the relation between the cranium and the first dorsal fin, the dorsal spines, the basal pterygiophores of the first dorsal fin, the suspensorium, and the number of vertebrae. In all these characters, the monacanthids show a more advanced condition than that of the balistids. Thus, it is reasonaly considered that these character conditions are quite strong for establishing this dichotomy in the balistoids.

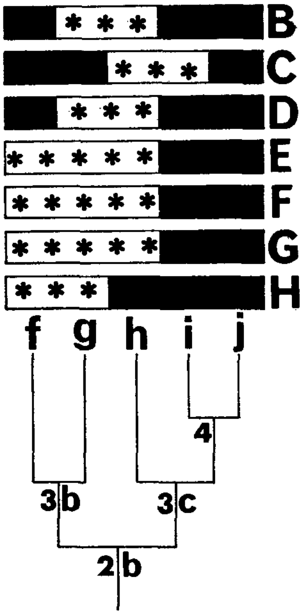

Fig. 72. Diagram showing a different branching pattern from that of Fig. 69. Branch point 2b is made from character H.

Branch point 2a separates the genus *Canthidermis* from the other balistid genera. This hypothesis is proposed from the analysis of the scale bone. All the balistid genera, except for this genus, have no trace of the bone, in other words they show an advanced condition in common with respect to this character. Therefore, it is reasonable to accept this branch point in the balistid genera based on the principle I–1. On the other hand, it seems possible to establish the other two branching patterns also. The first one separates the genus *Abalistes* from the other 10 balistid genera based on the character conditions of the frontal and caudal fin (Fig. 74, A). However, in this case we must accept an additional branch point, marked with 4a. Thus, by the principle II–3 this hypothesis is rejected from the phylogenetic inference. The second separates the genera *Rhinecanthus* and *Sufflamen* from the other 10 balistid genera by the character condition of the interhyal (Fig. 74, B). This hypothesis is also eliminated by the principle II–3.

At the branch point 3a we find the trichotomy in 10 balistid genera. However, at first glance, it appears that the dichotomy is present between the genus *Abalistes*, showing the advanced character conditions in the frontal and caudal

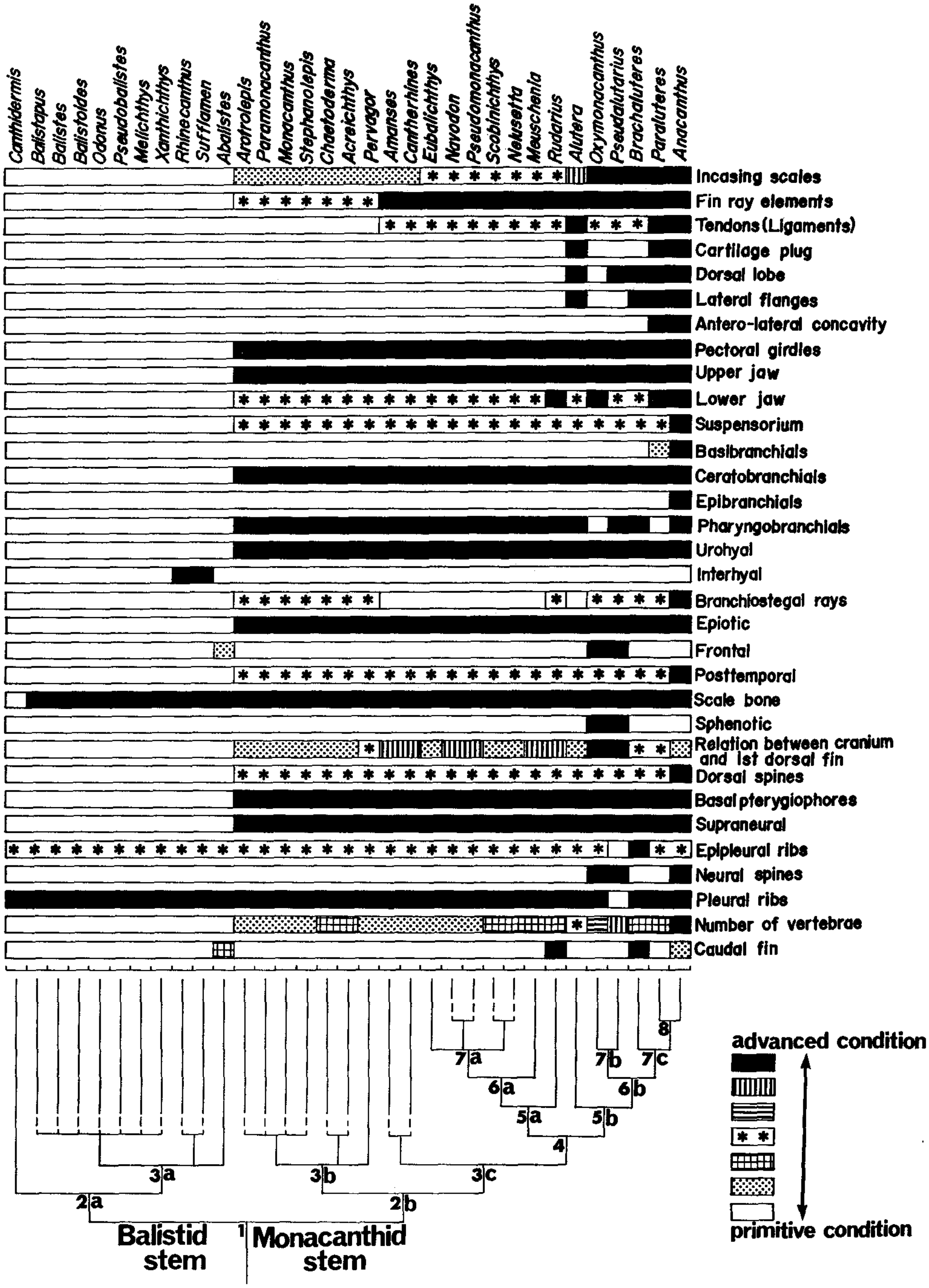

Fig. 73. Diagram showing the phylogenetic interrelationships of the balistoids based on the analyses of anatomical characters.

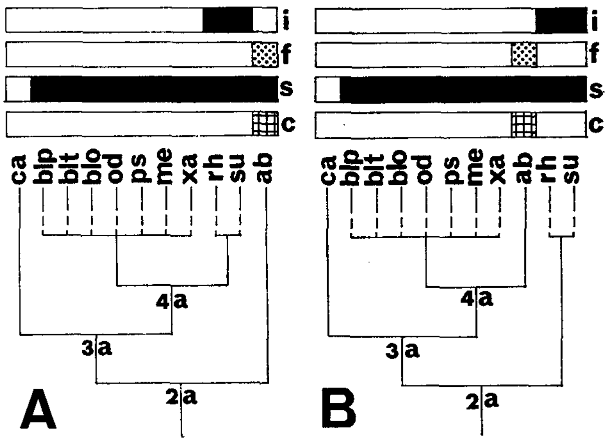

Fig. 74. Diagram showing the different branching patterns from that of Fig. 73. A, branch point 2a is derived from the character conditions of the frontal and caudal fin; B, branch point 2a is derived from the character condition of the interhyal. ab, *Abalistes*; blo, *Balistodies*; blp, *Balistapus*; blt, *Balistes*; c, caudal fin; ca, *Canthidermis*; f, frontal; i, interhyal; me, *Melichthys*; od, *Odonus*; ps, *Pseudobalistes*; rh, *Rhinecanthus*; s, scale bone; su, *Sufflamen*; xa, *Xanthichthys*.

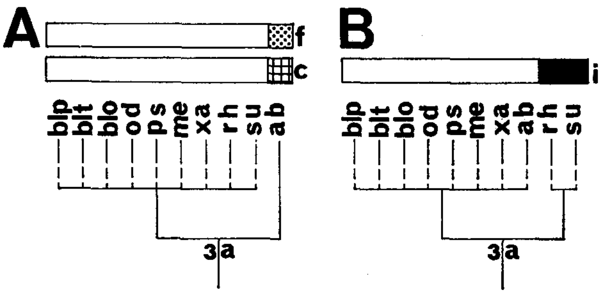

Fig. 75. Diagram showing two branching patterns of 10 balistid genera. A, based on two characters, the frontal and the caudal fin; B, based on one charactes, the interhyal. ab, *Abalistes*; blo, *Balistoides*; blp, *Balistapus*; blt, *Balistes*; c, caudal fin; f, frontal; i, interhyal; me, *Melichthys*; od, *Odonus*; ps, *Pseudobalistes*; rh, *Rhinecanthus*; su, *Sufflamen*; xa, *Xanthichthys*.

fin, and the other nine balistid genera (Fig. 75, A). On the other hand, it seems possible to separate the genera *Rhinecanthus* and *Sufflamen*, both having an advanced character condition of the interhyal, from the other eight genera including the genus *Abalistes* (Fig. 75, B). Of course, it is impossible to answer the question of which hypothesis is the most reasonable. Thus, based on the present data it is reasonable to accept the trichotomy in the balistid genera at the branch point 3a by the principle I–3.. With respect to the interrelationships of these 10 balistid genera, it is possible to say here that three groups, the genus *Abalistes*, the genera *Rhine-*

*canthus* and *Sufflamen*, and the other seven genera, are distinguished from one another, and that the former two groups are more advanced than the last group. Though the genera *Balistapus*, *Balistes*, *Balistoides*, *Odonus*, *Pseudobalistes*, *Melichthys*, and *Xanthichthys* are distinct from one another in the external characters which can not be evaluated phylogenetically, it is impossible to make a branch point for them by the present data of the internal characters. The same case is found in the genera *Rhinecanthus* and *Sufflamen*.

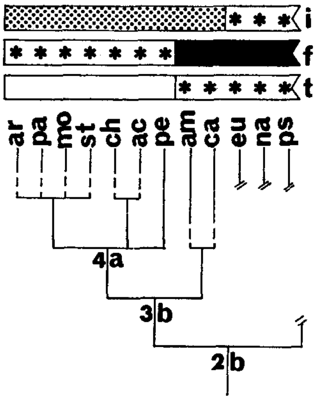

Fig. 76. Diagram showing a different branching pattern from that of Fig. 73. Branch point 2b is derived from the character condition of the incasing scales. ac, *Acreichthys*; am, *Amanses*; ar, *Arotrolepis*; ca, *Cantherhines*; ch, *Chaetoderma*; eu, *Eubalichthys*; f, frontal; i, interhyal; mo, *Monacanthus*; na, *Navodon*; pa, *Paramonacanthus*; pe, *Pervagor*; ps, *Pseudomonacanthus*; st, *Stephanolepis*; t, tendons (ligaments).

With respect to the monacanthid genera, the first dichotomy is found at the branch point 2b. The conditions of the fin ray elements and tendons are available to form this dichotomy, though the other anatomical features show the mosaic condition in the monacanthid genera. Thus, the monacanthids are divided into two main groups: the first is composed of seven genera, *Arotrolepis*, *Paramonacanthus*, *Monacanthus*, *Stephanolepis*, *Chaetoderma*, *Acreichthys*, and *Pervagor*; the second includes the other 15 genera.

On the other hand, if we put the emphasis on the incasing scales, we come to the other phylogenetic inference (Fig. 76). However, this hypothesis is incompatible with the condition of the fin ray elements and tendons. Thus, it is clearly concluded by the principle I–2 that this hypothesis is not reasonable for establishing branch point 2b.

The three lineages of the monacanthids, leading to the seven genera, are derived from the branch point 3b. However, if we adopt only the feature of the relation between the cranium and the first dorsal fin for the phylogenetic consideration, it seems that the genus *Pervagor* is separated from the other six genera. On the other hand, if we put the emphasis upon the condition of the number of vertebrae we come to a different speculation, that is, the genera *Chaetoderma* and *Acreichthys* are distinct from the other five genera including the genus *Pervagor*. Since it is impossible to answer the question of which speculation is the most reasonable, it is adequate to assume the presence of the three lineages at branch point 3b. Based on the present data it is concluded that the four genera, *Arotrolepis*, *Paramonacanthus*, *Monacanthus*, and *Stephanolepis*, are more primitive than the other three genera.

However, it is very difficult to say here whether the genus *Pervagor* is more primitive than the genera *Chaetoderma* and *Acreichthys* or vice versa.

The four genera, *Arotrolepis*, *Paramonacanthus*, *Monacanthus*, and *Stephanolepis* are distinct from one another in the external characters which can not be analyzed phylogenetically. Thus, it is impossible to form the branch point for these genera by the present data. Based on the same reason no branch point can be established for the genera *Chaetoderma* and *Acreichthys*.

Branch point 3c suggests that the genera *Amanses* and *Cantherhines* form the sister group of the other 13 genera, *Eubalichthys*, *Navodon*, *Pseudomonacanthus*, *Scobinichthys*, *Nelusetta*, *Meuschenia*, *Rudarius*, *Alutera*, *Oxymonacanthus*, *Pseudalutarius*, *Brachaluteres*, *Paraluteres*, and *Anacanthus*. The evidence for this hypothesis is derived from the analysis of the incasing scales, though the other anatomical characters are not available because of their mosaic condition. These 13 genera show clearly a more advanced condition of the incasing scales than that found in the genera *Amanses* and *Cantherhines*. Therefore, it is quite reasonable to accept this dichotomy.

The genera *Amanses* and *Cantherhines* are clearly separable from one another by the presence or absence of the long spines or setae on either side of body. This character is unique in the monacanthids, but it can not be analyzed from the phylogenetic view point. Thus, no branch point proposed for these two genera in the present study.

Branch point 4 suggests that the six genera, *Alutera*, *Oxymonacanthus*, *Pseudalutarius*, *Brachaluteres*, *Paraluters*, and *Anacanthus*, form the sister group of the remaining seven genera, *Eubalichthys*, *Navodon*, *Pseudomonacanthus*, *Scobinichthys*, *Nelusetta*, *Meuschenia*, and *Rudarius*. The evidence for the hypothesis is derived from the condition of the incasing scales. The former six genera are clearly more advanced in this character than the latter seven genera. Therefore, it is assumed that this dichotomy is reasonable.

Branch point 5a shows that the genus *Rudarius* forms the sister group of the other six genera, *Eubalichthys*, *Navodon*, *Pseudomonacanthus*, *Scobinichthys*, *Nelusetta*, and *Meuschenia*. The evidence is provided by the condition in the following characters; the lower jaw, the branchiostegal rays, and the caudal fin. The genus *Rudarius* shows a more advanced condition in all of these characters than that found in the other six genera. This fact is sufficient to separate the genus from the other genera at branch point 5a.

Branch point 6a suggests that the genus *Meuschenia* forms the sister group of the other five genera, *Eubalichthys*, *Navodon*, *Pseudomonacanthus*, *Scobinichthys*, and *Nelusetta*. The evidence is furnished by a combination of the two characters; the relation between the cranium and the first dorsal fin, and the number of vertebrae. In contrast with these five genera, the genus *Meuschenia* shows a more advanced condition in both characters, thus it is reasonable to accept their forming branch point 6a.

At the branch point 7a we find the trichotomy among the five genera mentioned at the branch point 6a. This trichotomy is derived from the analyses of the two characters; the relation between the cranium and the first dorsal fin, and the number of vertebrae. Since the genera *Navodon* and *Pseudomonacanthus* show the same advanced condition of the former character, they thus form a single group. The genera *Scobinichthys* and *Nelusetta* form the other group on the basis of the advanced condition of the latter character. The remaining genus *Eubalichthys*, showing relatively primitive conditions in both characters, is distinguishable from these two groups. It is clear that three groups are distinct from one another, but no dichotomy can be made from the present data for these groups. Thus, it is reasonable to accept the trichotomy at the branch point 7a by the principle I–3.

On the other hand, the genera *Navodon* and *Pseudomonacanthus* are separable from one another in the external characters which can not be evaluated phylogenetically. Thus, no dichotomy is established for them by the present data. The genera *Scobinichthys* and *Nelusetta* are, here, treated in the same way.

Branch point 5b suggests that the genus *Alutera* forms the sister group of the five genera, *Oxymonacanthus*, *Pseudalutarius*, *Brachaluteres*, *Paraluteres*, and *Anacanthus*. The evidence for this hypothesis is acquired from the analyses of the two characters; the incasing scales and the branchiostegal rays. In both the characters the latter five genera show more advanced conditions than that found in the genus *Alutera*. Therefore, it is reasonable to assume the dichotomy in these monacanthid genera.

Branch point 6b indicates that the genera *Oxymonacanthus* and *Pseudalutarius* form a sister group of the genera, *Brachaluteres*, *Paraluteres*, and *Anacanthus*. This dichotomy is supported by the analyses of the following four characters; the lateral flanges, the frontal, the sphenotic, and the relation between the cranium and the first dorsal fin. However, it seems possible that another branching pattern can be proposed for these five genera (Fig. 77). In this hypothesis the genera *Oxymonacanthus*, *Pseudalutarius*, and *Brachaluteres* are separable from the other two genera, *Paraluteres* and *Anacanthus*, based on the following four characters; the tendons (ligaments), the cartilage plug, the antero-lateral concavity, and the basibranchials. Since these two hypotheses are derived from four different characters, we must use the principle II–1 to judge which hypothesis is the most reasonable. In the first hypothesis (Fig. 73) the parallelisms are found in the two characters, the lower jaw and pharyngobranchials, while in the second hypothesis (Fig. 77) the parallelisms are present in the four characters, that is, the pharyngobranchials, the neural spines, the number of vertebrae, and the caudal fin. This fact shows that the first hypothesis is more reasonable than the second one.

Branch point 7b is derived from the analyses of the following characters; the dorsal lobe, the lower jaw, the pharyngobranchials, the epipleural ribs, the pleural ribs, and the number of vertebrae. Of these characters, the pharyngobranchials, the epipleural ribs, and the pleural ribs need more discussion, since these characters show the same condition as that seen in the balistid genera or a more primitive condition. With respect to the pharyngobranchials the primitive condition as seen in the balistid genera is found in the genus *Oxymonacanthus*. If one makes a great account of this character condition, he must come to either of the following two speculations. The first is that the genus is included in the Balistidae on the basis of the same primitive condition of the pharyngobranchials.

However, it is very difficult to accept this speculation, since in many character conditions clear differences are found between the genus and the balistid genera. The second is composed of the following assumption. An unknown ancestor of the genus, belonging to the primitive monacanthids, might form the sister group of the balistid genera (Fig. 78), and give rise to two main lineages: the first reached the genus *Oxymonacanthus*; and the second led to the many other monacanthid genera. If this assumption is true, we must accept the presence of many parallelisms between these two lineages, since the advanced condition of many of the characters, such as the incasing scales, the fin ray elements, the lower jaw, and so on, are found in the genus and in the other monacanthid genera which are speculated to be the offshoot from the second lineage, for example the genera *Brachaluteres* and *Anacanthus*. However, there are too many parallelisms in order to interpret reasonably the phylogeny of the genus *Oxymonacanthus*. Thus, this should be rejected from the phylogenetic consideration as well as the first speculation.

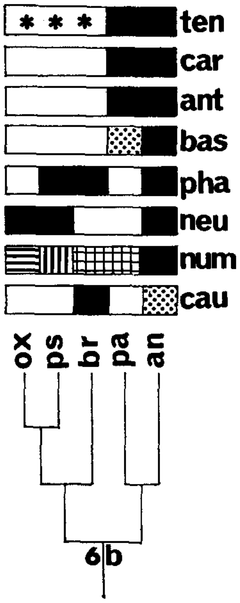

Fig. 77. Diagram showing a branching pattern for five monacanthid genera based on four characters, they are: the tendons (ligaments), the cartilage plug, the antero-lateral concavity of pelivs; and the basibranchials. an, *Anacanthus*; ant, antero-lateral concavity of pevlis; bas, basibranchials; br, *Branchaluteres*; car, cartilage plug; cau, caudal fin; neu; neural spines; num, number of vertebrae; ox, *Oxymonacanthus*; pa, *Paraluteres*, pha, pharyngobranchials; ps, *Pseudalutarius*; ten, tendons (ligaments).

Consequently, it may be feasible to explain the primitive condition of the pharyngobranchials in the genus as a holdover from an unknown ancestor at the same level, at least in this character, of organization as seen in the balistid genera.

The condition of the epipleural ribs in the genus *Pseudalutarius* is distinct from that of the other monacanthids and even balistids. In the genus the first epipleural ribs are found on the first abdominal vertebra, but in the other balistoids they start on the second abdominal vertebra. Besides the genus, the only recent tetraodontiform fishes having the first epipleural ribs on the first abdominal vertebra are found in the triacanthodids (Tyler, 1968: p. 59). Thus, if the feature of the epipleural ribs is of great importance for the phylogenetic consideration, the triacanthodids are assumed to be the direct ancestor of the genus. However, this is an untenable speculation, since the many characters of the genus show a more advanced condition than that of the balistids which are considered to be the offshoot from the triacanthids. Thus, the feature of the first epipleural ribs of the genus is probably considered as a remnant taken over from the primitive tetraodontiform fishes which might have belonged to the triacanthodids.

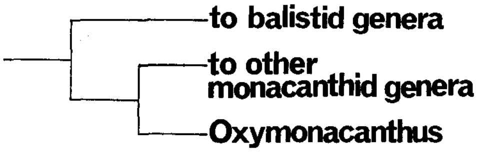

Fig. 78. Diagram showing the phylogenetic relationships between the genus *Oxymonacanthus* and the other balistoid members when the primitive condition of pharyngobranchials is recognized as an important element for phylogenetic consideration.

The presence of the pleural ribs in the genus *Pseudalutarius* is an enigmatic problem. The pleural ribs are absent not only in all of the other balistoid members but also in any other living tetraodontiform members except for *Triodon macropterus* (Tyler, 1962a, 1962c, 1973). The pleural ribs are usually found in the fishes belonging to the order Perciformes including the acanthurids, which are considered to be the ancestor of the order Tetraodontiformes (Breder and Clark, 1947; Tyler, 1968). Therefore, if the bones are to be recognized as an important character for phylogenetic consideration, then we must affiliate the genus with the perciform fishes or elevate the genus to an order rank which is distinct from the order Tetraodontiformes. However, these two hypotheses can not be accepted as a reasonable interpretation, since the genus shows advanced conditions in many characters which are not found in the perciform fishes or even in the balistids but are found in the monacanthids. Tyler (1973: p. 142) said "None of the other monacanthids or their ancestral balistids, nor the triacanthoid ancestors of the latter, have ribs (=pleural ribs), and this implies either that the ribs in *Pseudaluteres* (=*Pseudalutarius*) have arisen de novo or that the genetic coding for the production of ribs has been retained but not used throughout the various familial groupings leading to the monacanthids and one of its most specialized species." At the present time we can not find any datum supporting the first half of Tyler's statement. Moreover, the pleural ribs of the genus seem to have no particular functional role. Therefore, I tentatively agree with the second half of Tyler's statement that the genus takes over the pleural ribs from an unknown ancestor, although this seems, at least superficially, to be incompatible with the principle II-2.

Branch point 7b is supported by the conditions of the following characters; the dorsal lobe, the lower jaw, the pharyngobranchials, the epipleural ribs, the pleural ribs, and the number of vertebrae. These characters are quite strong for separating the genus *Oxymonacanthus* from the genus *Pseudalutarius* at this branch point.

Branch point 7c suggests that the genus *Brachaluteres* forms the sister group of the genera *Paralusteres* and *Anacanthus*. This hypothesis is supported by the conditions of the following characters; the tendons (ligaments), the cartilage plug, the antero-lateral concavity of pevlis, the lower jaw, the basibranchials, and the epipleural ribs. These characters are sufficient for establishing a dichotomy.

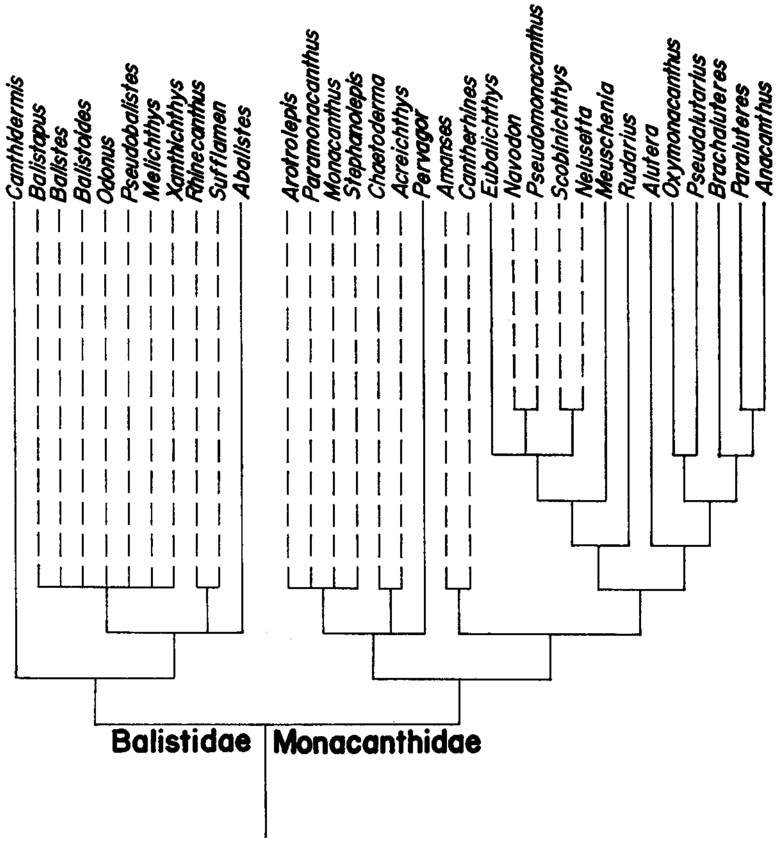

Fig. 79. Diagram showing the phylogenetic interrelationships among the balistoid families and genera.

Branch point 8 shows that the genus *Paraluteres* forms the sister group of the genus *Anacanthus*. This dichotomy is derived from the following characters; the suspensorium, the basibranchials, the epibranchials, the pharyngobranchials, the branchiostegal rays, the posttemporal, the relation between the cranium and the first dorsal fin, the dorsal spines, the neural spines, the number of vertebrae, and the caudal fin. Thus, it is reasonable to accept this dichotomy.

My view of the phylogenetic interrelationships of the balistoids is consequently presented as Figure 79.

## VI. Summary

The present study was made to establish the phylogenetic interrelationships of the families and genera of the superfamily Balistoidea. The specimens of 33 genera and 43 species collected from nearly all waters of the world were used for the study of comparative anatomy. The following parts of the specimens were dissected: the pelvic complex, the pectoral girdle, the jaws, the suspensorium and opercular apparatus, the hyoid apparatus, the branchial arches, the cranium, the first dorsal fin, the vertebrae, and the caudal skeleton with fin rays. The 32 characters obtained from these parts were evaluated by the general evolutional trends of the tetraodontiforms and teleosts. The character states were analyzed to clarify the phylogeny of the superfamily Balistoidea based on Hennig's (1966) method with a slight modification. The final conclusion concerning the phylogenetic interrelationships was as follows:

(1) Remarkable reductive tendencies in the evolution of the balistoids were found in nearly all anatomical features: the pelvic complex, the pectoral girdle, the jaws, the hyoid apparatus, the branchial arches, the cranial elements, the first dorsal fin, the caudal skeleton, and so on. An opposite tendency was present in the vertebral elements.

(2) Anatomical features showed that the superfamily Balistoidea was considered to be a monophyletic group, and to be composed of two families, the Balistidae and Monacanthidae. The family Balistidae was found to be more primitive in many characters than the family Monacanthidae.

(3) In the family Balistidae the genus *Canthidermis* was assumed to be more primitive than all other balistid genera by having a scale bone which is not found in any other tetraodontiform fishes. In the other balistid genera, the genera *Abalistes*, *Rhinecanthus*, and *Sufflamen* are more advanced than the other seven balistid genera in the feature of the frontal, the caudal fin, or the interhyal.

(4) The family Monacanthidae is separated into two main evolutional lineages: the first one consists of seven genera, *Arotrolepis*, *Paramonacanthus*, *Monacanthus*, *Stephanolepis*, *Chaetoderma*, *Acreichthys*, and *Pervagor*; the second one covers the other 15 genera. The first seven genera were considered to be more primitive than the latter 15 genera because of the conditions of the rudimentary fin ray elements and the tendons (ligaments).

(5) From the first lineage the following three groups are derived: (i) *Arotrolepis*, *Paramonacanthus*, *Monacanthus*, and *Stephanolepis*; (ii) *Chaetoderma* and *Acreichthys*; and (iii) *Pervagor*. The latter two groups, (ii) and (iii), were found to be more advanced than the first one, because they showed more derived condition in the relation between the cranium and the first dorsal fin, or in the number of vertebrae than that found in the first group

(6) In the 15 genera derived from the second lineage two groups were recognizable by the difference in the number of incasing scales. The first

group is represented by the two genera *Amanses* and *Cantherhines* in which the incasing scales are composed of six scales forming three segments. The second group, made up of the remaining 13 genera, has less than three segments in its incasing scales. Thus, the second group was assigned to a more advanced systematic position than that of the first one.

(7) In these 13 genera two subgroups were distinguishable by the number of incasing scales: the first subgroup covers the seven genera, *Eubalichthys*, *Navodon*, *Pseudomonacanthus*, *Scobinichthys*, *Nelusetta*, *Meuschenia*, and *Rudarius* which were characterized by having two segments in their incasing scales; the second subgroup is composed of the six genera, *Alutera*, *Oxymonacanthus*, *Pseudalutarius*, *Brachaluteres*, *Paraluteres*, and *Anacanthus* which have only one incasing scale or no trace of it at all. The first subgroup was, therefore, assumed to be more primitive than the second one.

(8) In the first subgroup, the genus *Rudarius* is placed in the most advanced systematic position because of specialized conditions in the lower jaw, the branchiostegal rays, and the caudal skeleton. The next systematic position is occupied by the genus *Meuschenia*. The most primitive systematic position was assigned to the other five genera, *Eubalichthys*, *Navodon*, *Pseudomonacanthus*, *Scobinichthys*, and *Nelusetta*. In these five genera the genus *Eubalichthys* was considered to be more primitive than the other genera because of having relatively primitive conditions in the relation between the cranium and the first dorsal fin, and the number of vertebrae.

(9) In the second subgroup composed of six genera, *Alutera*, *Oxymonacanthus*, *Pseudalutarius*, *Brachaluteres*, *Paraluteres*, and *Anacanthus*, the genus *Alutera* is more primitive than the other five genera in having an incasing scale. The remaining five genera were distinguishable from all other balistoid genera in not having incasing scale. The two genera *Oxymonacanthus* and *Pseudalutarius* were considered to be clearly different in their evolutional processes from that of the three genera, *Brachaluteres*, *Paraluteres*, and *Anacanthus*, because they have a peculiar and derived condition in the frontal and sphenotic which are not present in the latter three genera. The genus *Pseudalutarius* is unique among the balistoids in having pleural ribs. In the genera *Brachaluteres*, *Paraluteres*, and *Anacanthus*, the latter two genera were considered to be more advanced than the genus *Brachaluteres*, since they have more specialized conditions in many characters than the genus *Brachaluteres*. The genus *Anacanthus* was assumed to be more advanced than the genus *Paraluteres* in having specialized conditions in the suspensorium, the branchial arches, the branchiostegal rays, the dorsal spines, etc. Therefore, the most advanced systematic position in the balistoids was assigned to the genus *Anacanthus*.

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