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**Osteological Review of the Family Icelidae Berg, 1940, (Pisces;
Scorpaeniformes), with Comment on the Validity of this Family**

MAMORU YABE*

Abstract

The osteology of the family Icelidae Berg, 1940, composed of *Ereunias*, *Marukawichthys* and *Icelus*, was reviewed. It is concluded that Berg's Icelidae is unwarranted, because the osteological features regarded as the diagnostic for this family are not observed in these three genera. Moreover, the osteological features of these three genera are compared with those of the primitive cottid genus *Hemilepidotus*. It is concluded that the genus *Icelus* is a member of the family Cottidae, while *Ereunias* and *Marukawichthys* compose the family Ereuniidae.

Introduction

Ereunias grillator and *Marukawichthys ambulator* are unique sculpins known only from the deep sea around Japan. They are characterized by having four free pectoral fin rays similar to those of triglid fishes. The systematic position of these two species has not been satisfactorily shown. *Ereunias grillator* was described as a new species in a new genus, and placed in the new subfamily Ereuniinae of Cottidae by Jordan and Snyder¹). Later Jordan²) ranked this subfamily with the family Ereuniidae. *Marukawichthys ambulator* was described as a new species and genus, and placed in the new family Marukawichthyidae by Sakamoto³). Mukerji⁴) placed these two species in the subfamily Ereuniinae of Cottidae. Later, Matsubara⁵) examined the osteology of these two species, and retained them in the subfamily Ereuniinae which he treated as very closely allied to the subfamily Icelinae of the family Cottidae. Berg⁶) established the family Icelidae for *Ereunias*, *Marukawichthys* and *Icelus*, based on the osteological characters described by Matsubara⁵). On the other hand, Taranetz⁷) placed *Ereunias* in the family Ereuniidae, *Marukawichthys* in Marukawichthyidae, and *Icelus* in the subfamily Icelinae of Cottidae. Rass and Lindberg⁸) modified the ranking of Taranetz⁷), and placed *Ereunias* and *Marukawichthys* in the family Ereuniidae and *Icelus* in Cottidae without giving any evidence for the change. Despite confusion in the systematic position of these genera, Berg's Icelidae has been used by many investigators⁹)¹⁰)¹¹). Recently, the author observed osteological features of the three genera of Berg's Icelidae, and found that these genera do not possess the conditions of osteological characters which were regarded as the diagnostic of the family Icelidae as defined by Berg⁶). The conditions of these characters in the three genera are the same as those in the family Cottidae. It is considered that

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these facts contradict the foundation of the Berg's Icelidae.

In the present study, the osteological features of *Ereunias*, *Marukawichthys*, and *Icelus* are redescribed and compared with those of the typical cottid genus *Hemilepidotus*, and their systematic positions are reviewed using a cladistic analysis based on the osteological features.

Materials and Methods

The anatomical evidence presented is based on the following specimens which are deposited in the Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University. These specimens were dissected after being stained with alizarin red-S, and observed with a binocular microscope. The drawing of bones and muscle were made with a Wild M-8 drawing tube. The relationships among these genera are inferred following the principles advocated in Camin and Sokal¹²⁾, Hennig¹³⁾, Kluge and Farris¹⁴⁾, and Nelson¹⁵⁾. The character state of each anatomical feature is evaluated through the general evolutionary trends of the Scorpaeniformes and other teleosts. The nomenclature used here follows Uyeno¹⁶⁾ for the osteology, and Winterbottom¹⁷⁾ for the myology.

Ereunias grallator Jordan and Snyder, 5 specimens (81.0–262.5 mm SL): HUMZ 5672–5675, off Misaki, Kanagawa Pref., Japan, on Apr., 1971; HUMZ 49488, off Kôchi, Kôchi Pref., Japan, on May, 1972.

Marukawichthys ambulator Sakamoto, 3 specimens (90.7–128.0 mm SL): HUMZ 59313 and 59315, off Onahama, Fukushima Pref., Japan, on Sept. 19, 1976; HUMZ 77522, off Shiriya-saki, Aomori Pref., Japan, on Sept. 26, 1978.

Icelus spiniger Gilbert, 4 specimens (132.9~194.2 mm SL): HUMZ 56086, 56091 and 56092, 44°27'N, 140°19'E, 330 m in depth (the Japan Sea), on June 21, 1976; HUMZ 56906, off the Cape Erimo, Hokkaido, Japan, on Sept. 7, 1976.

Icelus canaliculatus Gilbert, 1 specimen (120.7 mm SL): HUMZ 82954, 54°20.9'N, 167°28.2'W, 805 m in depth (eastern Bering Sea), on June 14, 1979.

Icelus euryopus Gilbert, 1 specimen (96.3 mm SL): HUMZ 84833, 58°51.2'N, 177°57.8'W, 350 m in depth (eastern Bering Sea), on June 25, 1979.

Icelus uncinalis Gilbert, 2 specimens (75.4~119.3 mm SL): HUMZ 76835 and 76838, 56°33.5'N, 163°47.0'W, 78 m in depth (eastern Bering Sea), on May 21, 1978.

Hemilepidotus gilberti Jordan and Starks, 2 specimens (213.5~249.0 mm SL): HUMZ 56847 and 56866, off the Cape Erimo, Hokkaido, Japan, on Sept. 7, 1976.

Hemilepidotus papilio (Bean), 2 specimens (230.0~258.4 mm SL): HUMZ 56337, 57°59'N, 150.00'E, 166 m in depth (northern Okhotsk Sea), on June 10, 1976; HUMZ 76941, 58°39.5'N, 172°47.5'W, 110 m in depth (eastern Bering Sea), on June 15, 1978.

Description

Cranium (Figs. 1, 2, and 3)

The cranium is composed of five unpaired elements (prevomer, ethmoid, parasphenoid, supraoccipital, and basioccipital), and eleven paired elements

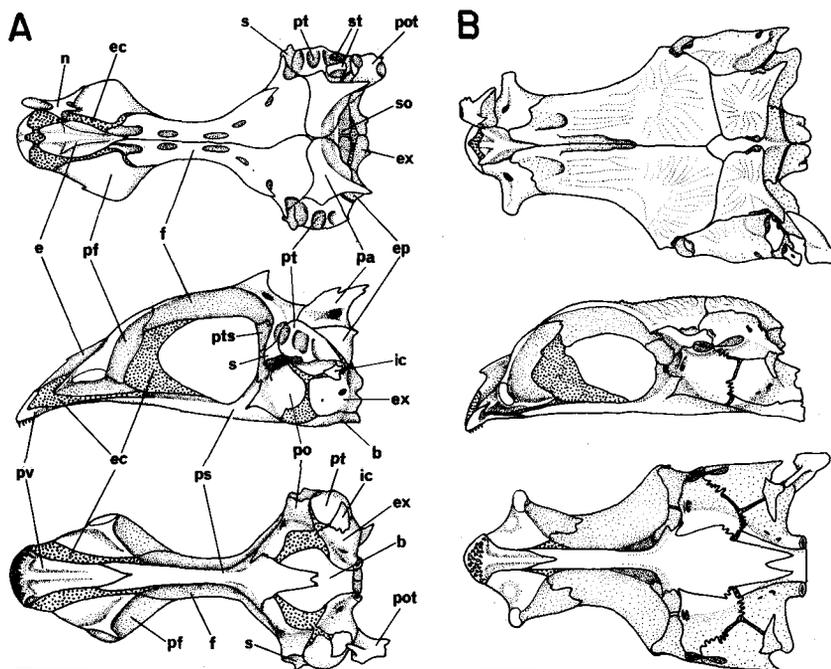


Fig. 1. Dorsal (above), lateral (middle) and ventral (below) aspects of the cranium. A, *Marukawichthys ambulator*; B, *Hemilepidotus gilberti*. b, basioccipital; e, ethmoid; ec, ethmoid cartilage; ep, epiotic; ex, exoccipital; f, frontal; ic, intercalar; n, nasal; pa, parietal; pf, prefrontal; po, prootic; pot, posttemporal; ps, parasphenoid; pt, pterotic; pts, pterosphenoid; pv, prevomer; s, sphenotic; so, supraoccipital; st, supratemporal. Scale bars indicate 5 mm.

(prefrontal, frontal, pterosphenoid, sphenotic, prootic, parietal, pterotic, epiotic, intercalar, exoccipital, and nasal). The basisphenoid is absent.

The prevomer (pv) lies on the anterolateral and ventral sides of the ethmoid cartilage (ec), and is joined with the parasphenoid posteriorly. In *Ereunias*, *Marukawichthys*, and *Icelus*, this bone is separated from the prefrontal by the ethmoid cartilage, while it is usually connected with the prefrontal in *Hemilepidotus*.

The ethmoid (e) lies on the anterodorsal side of the ethmoid cartilage, and is united to the frontal posteriorly. In *Hemilepidotus*, this bone is connected with the prefrontal posterolaterally.

The prefrontal (pf) is lateral to the ethmoid cartilage and articulates with the frontal posterodorsally. In *Ereunias*, *Marukawichthys*, and *Icelus*, this bone is separated from the ethmoid and prevomer by the cartilage, while it is connected with the ethmoid anterodorsally, and with the prevomer ventrally in *Hemilepidotus*. This bone possesses a lateral wing which forms the anterior border of the orbit and articulates with the lachrymal ventrally (Fig. 3).

The frontal (f) forms dorsal margin of the orbit, and is bordered by the ethmoid, prefrontal, parietal, pterotic, supraoccipital, pterosphenoid, and sphenotic. Anteroventrally, this bone is attached to the ethmoid cartilage which forms a

median septum in the anterior part of the orbit. On the dorsal surface, it has a tubular structure for the cephalic sensory canal.

The sphenotic (s) forms the posterodorsal wall of the orbit, and is bordered by the frontal, pterosphenoid, prootic, parietal and pterotic. Posterolaterally, this bone is connected with the prootic, and makes a circular socket which receives the articular head of the hyomandibular (Fig. 2). It supports the fifth infraorbital dorsally (Fig. 3).

The pterosphenoid (pts) forms the dorsal corner of posteromedial wall of the orbit. It is joined with the frontal dorsally, and with the sphenotic and prootic posteriorly. In *Icelus* and *Hemilepidotus*, but not in *Ereunias* and *Marukawichthys*, this bone meets the lateral wing of the parasphenoid (Fig. 2).

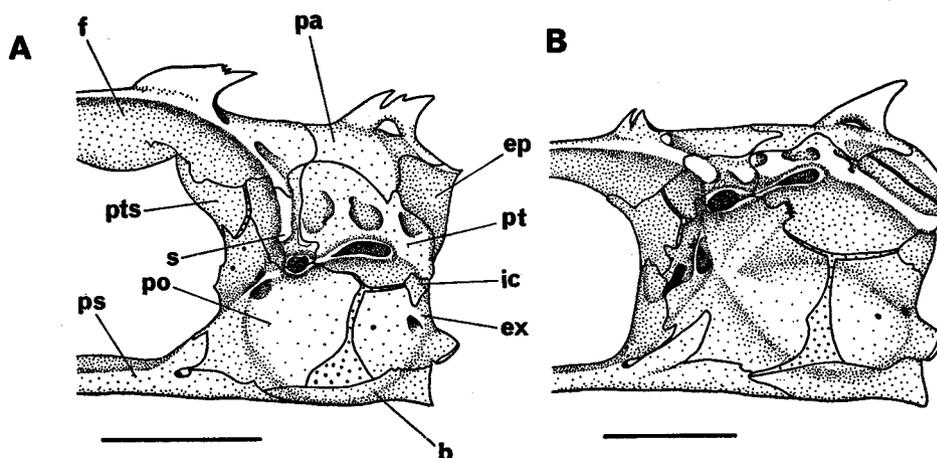


Fig. 2. Lateral aspects of the occipital region of; A. *Ereunias grallator*; B. *Icelus spiniger*. b, basioccipital; ep, epiotic; ex, exoccipital; f, frontal; ic, intercalar; pa, parietal; po, prootic; ps, parasphenoid; pt, pterotic; pts, pterosphenoid; s, sphenotic. Scale bars indicate 10 mm.

The prootic (po) forms ventrolateral side of the otic region, and attaches to the pterosphenoid, parasphenoid, sphenotic, pterotic, and basioccipital. In *Ereunias*, *Marukawichthys*, and *Icelus*, this bone is separated from exoccipital by cartilage, while it is connected to the exoccipital by a jagged suture in *Hemilepidotus*. This bone possesses a thin vertical bridge crossing over the trigemino-facialis chamber. In *Ereunias* and *Marukawichthys* this bone is interposed between the pterosphenoid and parasphenoid and helps to form the posteromedial margin of the orbit (Fig. 2, A). In *Icelus* and *Hemilepidotus* the prootic does not form the posterior margin of orbit, because the pterosphenoid and the parasphenoid attach to each other in front of the anterior margin of the prootic (Fig. 2, B).

The parasphenoid (ps) forms the greater part of the cranial base, and is joined with the prevomer, prootic, and basioccipital. It is connected with the ethmoid cartilage anterodorsally. It possesses a lateral wing which forms the posteroventral wall of the orbit. This wing meets the pterosphenoid in *Icelus* and

Hemilepidotus, but not in *Ereunias* and *Marukawichthys*.

The parietal (pa) forms the posterodorsal roof of the cranium, and is bordered by the frontal, pterotic, epiotic, and supraoccipital. It possesses a tubular structure for the supratemporal sensory canal.

The pterotic (pt) forms posterolateral face of the cranium, and is joined to the sphenotic, frontal, parietal, prootic, exoccipital, intercalar, and epiotic. It makes a circular socket which receives the posterior articular head of hyomandibular (Fig. 2). This bone possesses tubular structure for the cephalic sensory canal. This bone supports the supratemporals posterodorsally.

The intercalar (ic) is a small bone which is situated between the pterotic and exoccipital; it does not attach to the prootic. This bone is ligamentously connected with the anteroventral process of the posttemporal.

The exoccipital (ex) forms the posterolateral face of the otolith chamber, and is joined with the basioccipital ventrally, and with pterotic, intercalar, and epiotic anterodorsally. It is separated from the prootic by the cartilage in *Ereunias*, *Marukawichthys*, and *Icelus*, while it is connected with the prootic in *Hemilepidotus*. This bone meets with its opposite member posteromedianly, and forms the dorsolateral wall of the foramen magnum. Posteroventrally, this bone possesses the condyle which receives the lateral articular head of the first vertebra. The vagus foramen opens on this bone.

The supraoccipital (so) forms the posteromedian portion of the cranial roof and is bordered by the frontal, parietal, epiotic, and exoccipital. The supraoccipital crest is present but not well developed. This bone does not form the posterior margin of the foramen magnum.

The epiotic (ep) forms the posterolateral corner of the cranium, and is bordered by the parietal, pterotic, intercalar, exoccipital, and supraoccipital. On the posterolateral face, this bone articulates the anterodorsal process of the posttemporal.

The basioccipital (b) forms the posteroventral part of the cranial base, and is joined with parasphenoid and prootic anteriorly, and with the exoccipital dorsally. This bone forms the occipital condyle which articulates with the first vertebra. The

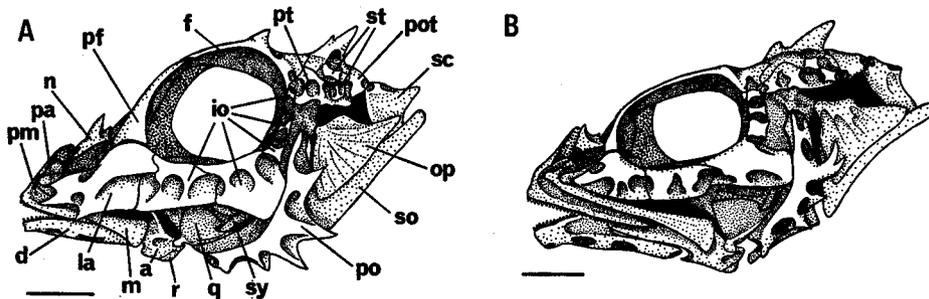


Fig. 3. Cranium and face bones of: A, *Marukawichthys ambulator*; B, *Icelus uncinalis*. a, angular; d, dentary; f, frontal; io, infraorbital; la, lachrymal; m, maxillary; n, nasal; op, opercle; pa, palatine; pf, prefrontal; pm, premaxillary; po, preopercle; pot, posttemporal; pt, pterotic; q, quadrate; r, retroarticular; se, supraclathrum; so, subopercle; st, supratemporal; sy, symplectic. Scale bars indicate 5 mm.

anterodorsal wings of this bone form the wall of the posterior part of the otolith chamber. Baudelot's ligament attaches to the posteroventral end of this bone.

Circumorbital bones (Fig. 3)

The circumorbitals are composed of the lachrymal and five infraorbitals and form a serial tubular structure penetrated by the infraorbital sensory canal. The lachrymal (la) is a large plate-like bone forming the anterolateral side of snout. This bone articulates with the palatine anterodorsally, and with the prefrontal posterodorsally and joins the first infraorbital posteriorly. In *Ereunias* and *Marukawichthys* this bone possesses two spines anteroventrally.

The first and second infraorbital (io) are large plate-like bones forming the ventral margin of the orbit. The second infraorbital extends posteriorly and attaches to the upper ridge of the preopercle. The three posterior infraorbitals are small and tubular bone and lie on the muscle of the postorbital region.

Suspensory apparatus (Figs. 3 and 4)

The suspensory apparatus is composed of seven bones, the hyomandibular, symplectic, quadrate, metapterygoid, endopterygoid, ectopterygoid, and palatine. Cartilage fills up the interspace among the suspensory elements. There is a gap between the hyomandibular and metapterygoid and between the symplectic and the preopercle.

The hyomandibular (hm) is connected with the metapterygoid anteriorly and with the preopercle posteriorly. It possesses two articular heads dorsally which are lodged in round sockets of the lateral side of the cranium. Posteriorly, this bone has a rounded knob which articulates with the opercle.

The symplectic (sy) is a slightly curved bone, and inserts on the dorsal fossa of the quadrate anteriorly. It lies among the metapterygoid, hyomandibular, and preopercle.

The quadrate (q) is a triangular bone bearing a transverse condyle for the mandibular. It is joined to the ectopterygoid anteriorly, to the preopercle posteroventrally, and to the endopterygoid, through the cartilage, dorsally. Dorsally, this bone bears a distinct fossa to house the symplectic.

The metapterygoid (me) is joined to the endopterygoid anteriorly and to the hyomandibular posteriorly; it approaches the quadrate and symplectic ventrally.

The endopterygoid (en) is an elongate bone extending from the palatine to the metapterygoid. This bone attaches to the ectopterygoid ventrally.

The ectopterygoid (ec) extends from the palatine to the quadrate and attaches to the endopterygoid dorsally.

The palatine (pa) articulates with the maxillary and lachrymal anteriorly, and is connected to the prefrontal and the ascending process of the premaxillary by strong ligaments. The oral surface of the palatine bears villiform teeth.

Opercular apparatus (Figs. 3 and 4)

The opercular apparatus is composed of four bones; preopercle, opercle, subopercle, and interopercle.

The opercle (op) is a triangular bone, which possesses the anterodorsal

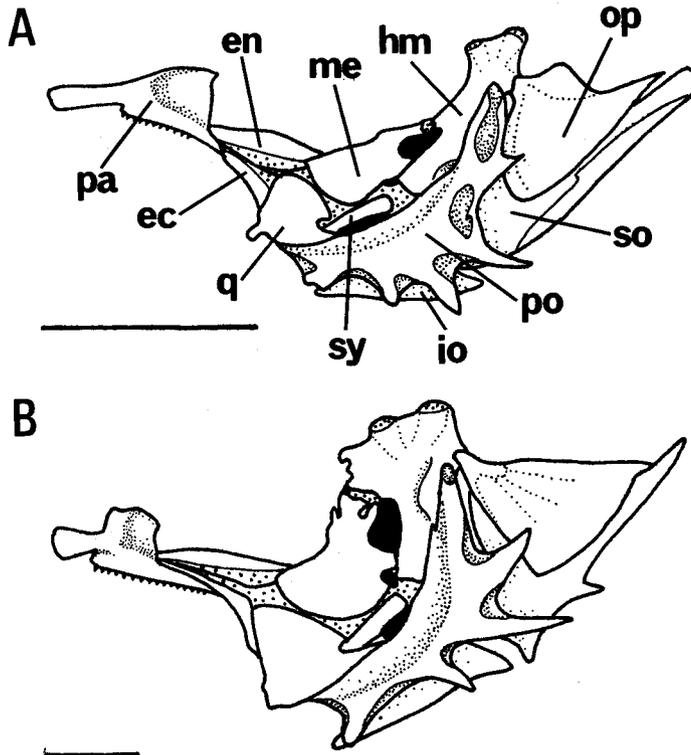


Fig. 4. The lateral view of suspensorium and opercular apparatus of: A, *Marukawichthys ambulador*; B, *Hemilepidotus gilberti*. ec, ectopterygoid; en, endopterygoid; hm, hyomandibular; io, interopercle; me, metapterygoid; op, opercle; pa, palatine; po, preopercle; q, quadrate; so, subopercle; sy, symplectic. Scale bars indicate 5 mm.

condyle which is connected with the posterior process of the hyomandibular. The subopercle (so) is ligamentously connected to the opercle.

The interopercle (io) is a slender triangular bone connected to the retroarticular anteriorly and to the subopercle posteriorly by strong ligaments. This bone is ligamentously connected to the epihyal medially.

The preopercle (po) is ligamentously connected to the hyomandibular and quadrate. The posterior margin of this bone bears strong spines. The uppermost spine is bifid in *Icelus*, while simple in the other three genera. The sensory canal penetrates the posterior margin of this bone.

Jaws (Figs. 3 and 5)

The upper jaw is composed of the premaxillary and maxillary. The premaxillary (pm) possesses four processes; the alveolar process (alp) bearing villiform teeth, the ascending process (acp) attached to the rostral cartilage, the articular process (arp) connected to the maxillary head, and the postmaxillary process (pmp).

The maxillary (mx) is an elongate and slightly curved bone. The maxillary

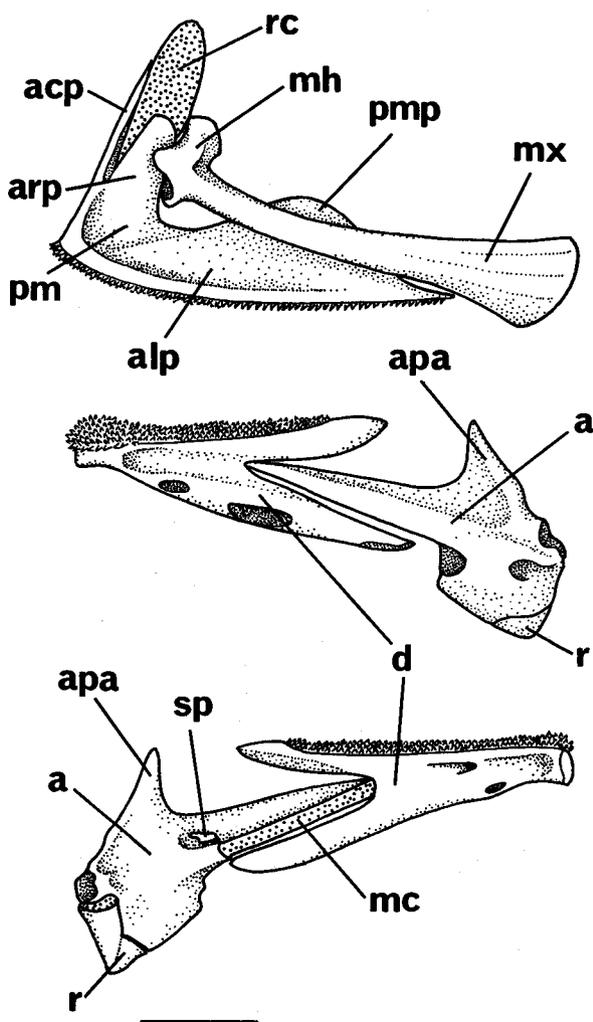


Fig. 5. Jaws in *Ereunias grillator*; above, lateral aspect of upper jaw; middle, lateral aspect of lower jaw; below, medial aspect of lower jaw. a, angular; acp, ascending process of premaxillary; alp, alveolar process of premaxillary; apa, ascending process of angular; arp, articular process of premaxillary; d, dentary; mc, meckelian cartilage; mh, maxillary head; mx, maxillary; pm, premaxillary; pmp, postmaxillary process of premaxillary; r, retroarticular; rc, rostral cartilage; sp, splenial. Scale bar indicates 10 mm.

head (mh) articulates with the articular process of the premaxillary and with the anterolateral face of the cranium through meniscuses. The anterodorsal face of this bone is attached to the anterior end of the palatine.

The lower jaw is composed of the dentary, angular, retroarticular, splenial, and meckelian cartilage. The dentary (d) forms the anterior part of lower jaw, and

possesses villiform teeth on the dorsal face. Posteriorly, this bone possesses a deep notch where the angular and the meckelian cartilage insert.

The angular (a) forms the posterior half of the lower jaw. This bone is joined with the dentary anteriorly, and with the retroarticular posteroventrally. Posterodorsally, this bone has the ascending process (apa), and has a fossa to receive the condyle of quadrate. The anterior part of the operculomandibular sensory canal penetrates the ventral parts of the dentary and angular.

The retroarticular (r) forms the posteroventral corner of the lower jaw. This bone attaches to the angular anterodorsally, and is connected to the interopercle by a strong ligament posteriorly.

The splenial (sp) is a small bone which lies on the medial face of the angular. The meckelian cartilage (mc) is a rod-like shape lying on the medial face of the angular, and joins the dentary with the angular.

Hyoid apparatus (Fig. 6)

The hyoid apparatus is composed of dorsal and ventral hypohyals, ceratohyal, epihyal, interhyal, urohyal, and six branchiostegals. The basihyal is absent.

The hypohyals (hh) form the anterior corner of the hyoid region. The

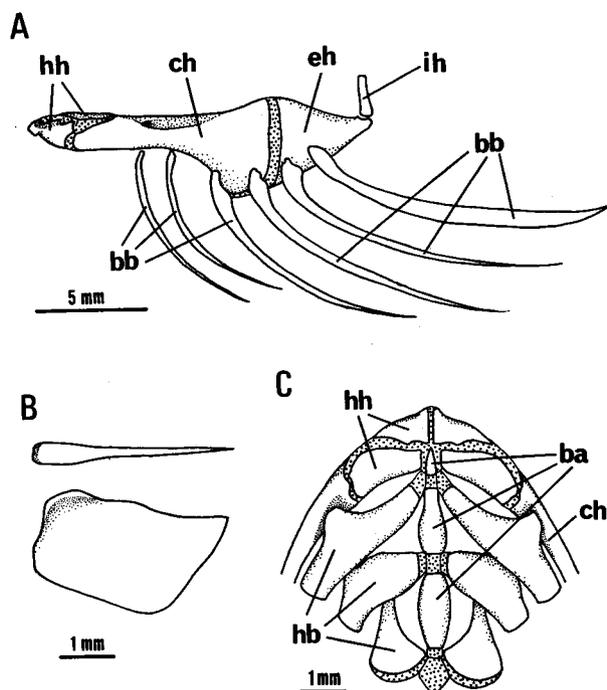


Fig. 6. Hyoid apparatus in *Marukawichthys ambulator*. A; lateral aspect of hyoid arch; B, dorsal (above) and lateral (below) aspects of urohyal; C, dorsal aspect of anterior part of the oral base (ceratobranchials are removed). ba, basibranchial; bb, branchiostegal; ch, ceratohyal; eh, epihyal; hb, hypobranchial; hh, hypohyal; ih, interhyal.

ventral hypohyal is united to its opposite member in the median line through the cartilage. The dorsal hypohyal is connected with the first basibranchial medially through the cartilage (Fig. 6, C).

The ceratohyal (ch) is the largest bone in the hyoid elements. It is joined to the hypohyals anteriorly and to the epihyal posteriorly through intervening cartilages and supports the anterior four branchiostegals. Dorsolaterally, this bone possesses a small slit penetrated by the hyoid artery.

The epihyal (eh) articulates anteroventrally with the ceratohyal and postero-dorsally with the interhyal. Anteroventrally, it supports the posterior two branchiostegals. This bone is ligamentously connected with median face of interopercle.

The interhyal (ih) is short and rod-shaped. It articulates ventrally with the epihyal and dorsally with the median surface of the preopercle.

The urohyal is a plate-like bone situated under the hypohyals and ligamentously connected with the ventral hypohyal.

Branchial apparatus (Figs. 6 and 7)

The branchial apparatus is composed of the basibranchial, hypobranchial, ceratobranchial, epibranchial, and pharyngobranchial. The basibranchials (bb)

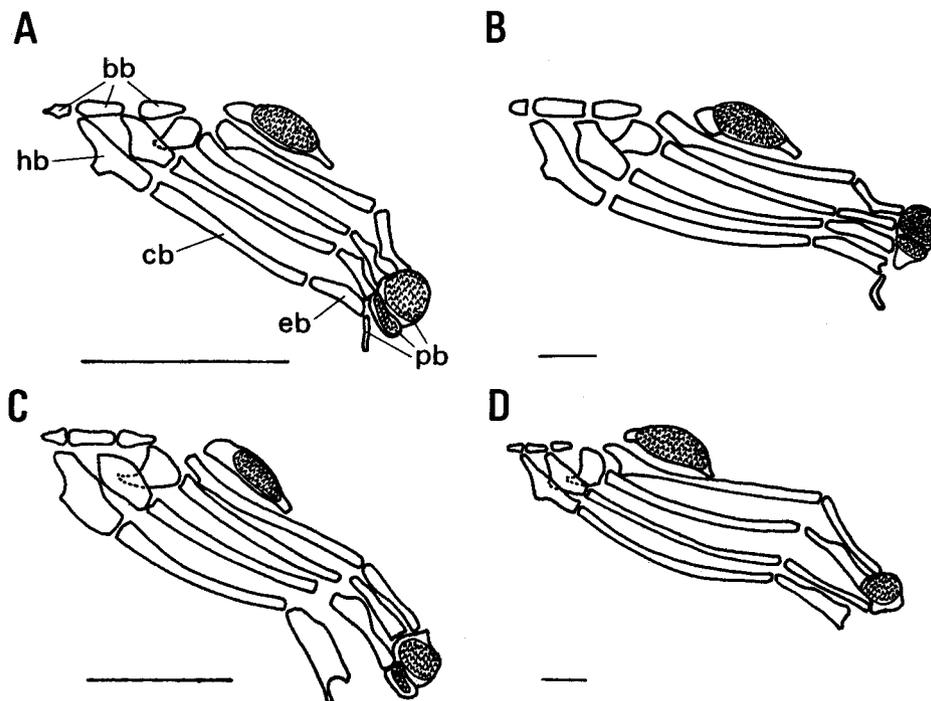


Fig. 7. Dorsal aspect of branchial apparatus in; A, *Marukawichthys ambulator*; B, *Ereunias grillator*; C, *Hemilepidotus gilberti*; D, *Icelus spiniger*. bb, basibranchial; cb, ceratobranchial; eb, epibranchial; hb, hypobranchial; pb, pharyngobranchial. Scale bars indicate 5 mm.

are three bones lying in the median line of the oral base, and are connected with each other through intervening cartilage. The anteriormost basibranchial is sandwiched between the dorsal hypohyals (Fig. 6, C).

The hypobranchials (hb) are three paired bones and are placed between the basibranchial series and the ceratobranchials. The first hypobranchial possesses the lateral process attaching to the anterodorsal face of the ceratohyal. The third hypobranchial possesses the descending process in *Icelus* and *Hemilepidotus*, but not in *Ereunias* and *Marukawichthys*.

The ceratobranchials (cb) are five paired bones. The anterior four bones are elongated and slightly curved, while the posteriormost one is a stout and triangular bone bearing villiform teeth dorsally. The first to third bones are connected with the hypobranchials proximally and with the epibranchials distally. The fourth bone is proximally connected with the cartilage which lies behind the third basibranchial, and with the fourth epibranchial distally. The fifth ceratobranchial articulates with the posterior cartilage of the basibranchial series anteriorly and with the center of the fourth ceratobranchial posteriorly.

The epibranchials (eb) are rod-like bones placed between ceratobranchials and pharyngobranchials. In *Ereunias* and *Marukawichthys* the first epibranchial attaches to the first pharyngobranchial distally (Fig. 7, A and B). In *Icelus* and *Hemilepidotus*, it possesses a distal process which connects with the parasphenoid through a thin ligament (Fig. 7, C and D).

The pharyngobranchials (pb) are the uppermost elements of the branchial apparatus and connect with their opposite members on the dorsal wall of the oral cavity. The first one is rod-like and is present in *Ereunias* and *Marukawichthys*, but absent in *Icelus* and *Hemilepidotus*. When present, this bone articulates to the parasphenoid through a thin ligament distally. The second pharyngobranchial, which is present in *Ereunias*, *Marukawichthys*, and *Hemilepidotus* but absent in *Icelus*, is a plate-like bone and lies on the ventral surface of the third pharyngobranchial. This bone is connected with the second epibranchial proximally and bears a villiform tooth plate on the ventral face. The third pharyngobranchial is a plate-like bone and bears numerous villiform teeth ventrally. This bone articulates to the third and fourth epibranchials in *Ereunias*, *Marukawichthys*, and *Hemilepidotus*, but to the second to fourth epibranchials in *Icelus*.

Pectoral girdle and fin rays (Figs. 1, 3, 8, and 9)

The pectoral girdle is composed of two supratemporals, posttemporal, supracleithrum, cleithrum, scapula, coracoid, four actinosts, and two postcleithra.

The supratemporals (st) are small and tubular bones situated on the dorsal surface of the pterotic and parietal (Fig. 3). The sensory canal penetrates these bones.

The posttemporal (pot) possesses two process: the anterodorsal process articulates with the dorsal surface of the epiotic, while the anteroventral process is ligamentously connected with the intercalar (Fig. 1). This bone articulates with the supracleithrum posteromedially. The sensory canal penetrates this bone.

The supracleithrum (c) is somewhat triangular in shape and articulates with the posttemporal anterodorsally and with the cleithrum posteromedially. This

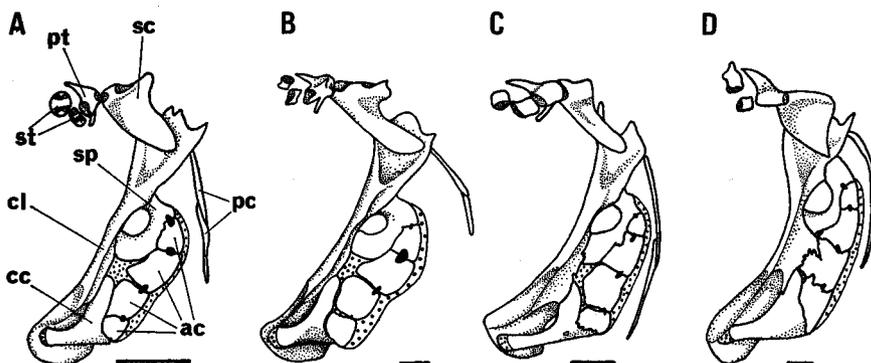


Fig. 8. Lateral aspect of pectoral girdle in; A, *Marukawichthys ambulator*; B, *Ereunias grillator*; C, *Icelus spiniger*; D, *Hemilepidotus gilberti*. ac, actinost; cc, coracoid; cl, cleithrum; pc, postcleithrum; pt, posttemporal; sc, supracleithrum; sp, scapula; st, supratemporal. Scale bars indicate 5 mm.

bone possesses a tubular structure on the dorsal margin penetrated by the sensory canal. Baudelot's ligament comes from the basioccipital and attaches to the posteromedial surface of this bone.

The cleithrum (cl) is the largest element in the pectoral girdle. Dorsally, this bone is fixed to the supracleithrum by ligamentous tissue. It joins with the scapula and coracoid posteriorly and with the opposite member ventromedially.

The scapula (sp) is connected to the cleithrum by two arms. The scapula

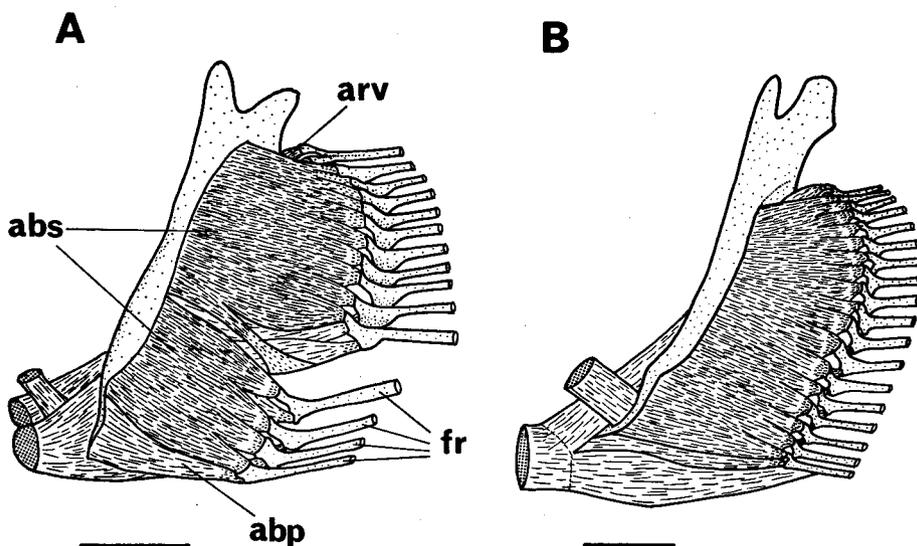


Fig. 9. Lateral aspect of musculature of the left pectoral girdle in; A, *Ereunias grillator*; B, *Icelus spiniger*. abp, abductor profundus; abs, abductor superficialis; arv, arrector ventralis; fr, free rays. Scale bars indicate 10 mm.

foramen is surrounded by the scapula and cleithrum. Posteroventrally, this bone is joined to the two upper actinosts.

The coracoid (cc) is connected to the cleithrum by two arms. Anterodorsally, it fixes to the posterior ridge of the cleithrum. Anteroventrally, it is connected with the ventrolateral face of the cleithrum through the cartilage. This bone is joined to the two lower actinosts.

The actinosts (ac) are plate-like bones which lie between the scapula and coracoid. Small pores intervene between these bones. In *Marukawichthys* and *Ereunias* the lower four fin rays are free (they attach to the lower two actinosts), and the abductor superficialis (abs) is separated into two parts (Fig. 9, A). There are no free fin rays and no separated abductor superficialis in *Icelus* and *Hemilepidotus* (Fig. 9, B). Two slender postcleithra (pc) are present. The upper postcleithrum attaches to the cleithrum dorsally.

Pelvic girdle and fin rays (Fig. 10)

The pelvic girdle is composed of a pair of pelvis uniting with one another medianly. The anterolateral face of this bone articulates with the ventromedial face of the cleithrum.

The number of the pelvic fin rays is variable among these four genera. There is one spine and four soft rays in *Marukawichthys* and *Hemilepidotus*, one spine and three soft rays in *Icelus*, and only one spine and no soft rays in *Ereunias*. The spine of *Ereunias* is vestigial and buried under the skin (Fig. 10, s). In five specimens of *Ereunias*, two have the spine on each pelvis while the other three have the spine on only one side.

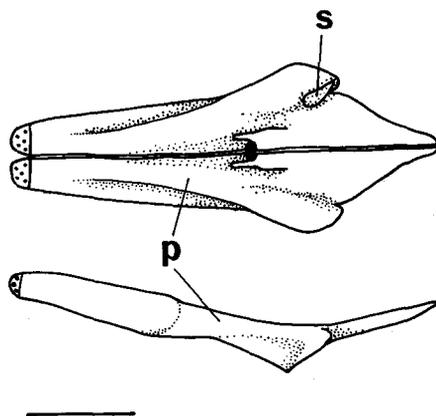


Fig. 10. Ventral (above) and lateral (below) aspects of the pelvic girdle in *Ereunias grillator*. p, pelvis; s, rudimental spine. Scale bar indicates 5 mm.

Postcranial axial skeleton (Figs. 11 and 12)

The vertebrae are divided into two types, the abdominal vertebrae (av) and the caudal vertebrae (cv). The first caudal vertebra is the anteriormost vertebra

Table 1. Number of vertebrae in eight examined species

Species	Abdominal + Caudal vertebrae (Specimens)	Total vertebrae
<i>Ereunias grillator</i>	13+25 (3) 13+26 (2)	38~39
<i>Marukawichthys ambulator</i>	13+23 (2) 13+24 (1)	36~37
<i>Icelus spiniger</i>	11+29 (2) 11+30 (2)	40~41
<i>Icelus uncinialis</i>	12+28 (2)	40
<i>Icelus canaliculatus</i>	11+31 (1)	42
<i>Icelus euryopus</i>	12+29 (1)	41
<i>Hemilepidotus gilberti</i>	13+24 (1) 13+25 (1)	37~38
<i>Hemilepidotus papilio</i>	13+26 (1) 13+27 (1)	39~40

possessing a complete haemal spine (hs). The number of vertebrae in each examined species is shown in Table 1. All vertebrae except the first one possess neural arches which are fused dorsally, and elongate neural spines (ns). The first abdominal vertebra has a neural arch not fused to the opposite member dorsally and lacks the neural spine. Each abdominal vertebra has a parapophysis which supports the ribs and epipleurals directly. In the posterior abdominal vertebrae, the parapophysis fused to the opposite member to form the haemal arch. In *Ereunias*, *Marukawichthys*, and *Icelus*, the posterior several caudal vertebrae possess developed lateral processes (Fig. 12, 1p), which are not in *Hemilepidotus*.

In *Ereunias* and *Marukawichthys*, the epipleurals (ep) are present on the abdominal vertebrae and never on any caudal vertebrae, while they are present on the abdominal and some anterior caudal vertebrae in *Icelus* and *Hemilepidotus*. Ribs (r) are present on some posterior abdominal vertebrae. They are usually attached to the parapophysis but a few anterior rudimentary ones are free and lie solely in the muscle.

Median fin supports (Figs. 11 and 12)

The median fins are supported by three elements, the proximal and distal pterygiophores and stay. The median pterygiophore was not observed as an independent bone.

The proximal pterygiophores (por) are slenderly triangular bones located between the neural spines on the dorsal series and between the haemal spines on the anal series. In *Marukawichthys*, *Icelus*, and *Hemilepidotus* the dorsal fin is continuous and each proximal pterygiophore supports one or two fin rays, while in *Ereunias* the fin is discontinuous but two proximal pterygiophores exist in the gap (Fig. 11). The first proximal pterygiophore locates in front of the first vertebra in *Ereunias* and *Marukawichthys*, while it locates between the first and second vertebrae in *Icelus* and *Hemilepidotus*.

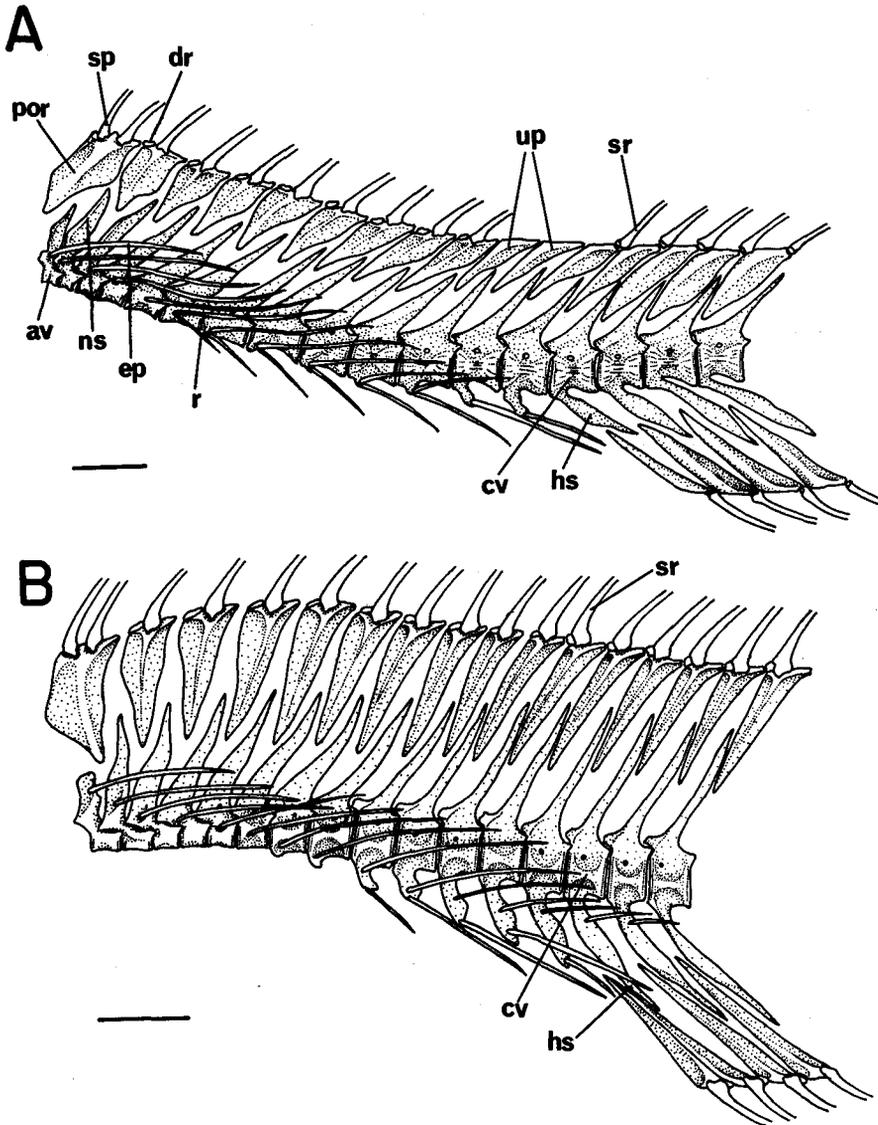


Fig. 11. Lateral view of anterior vertebrae and associated bones in; A, *Ereunias grillator*; B, *Hemilepidotus gilberti*. av, first abdominal vertebra; cv, first caudal vertebra; dr, distal pterygiophore; ep, epipleural; hs, first haemal spine; ns, first neural spine; por, first proximal pterygiophore; r, rib; sp, first spiny ray of dorsal fin; sr, first soft ray of dorsal fin; up, pterygiophore not supporting fin ray. Scale bars indicate 10 mm.

The distal pterygiophore (dr) is a small bone placed between each proximal pterygiophore and fin rays. The distal pterygiophore supporting the spiny ray is an unpaired bone, while that supporting the soft ray is a paired. The first distal pterygiophore is usually fused to the dorsal face of the proximal pterygiophore and

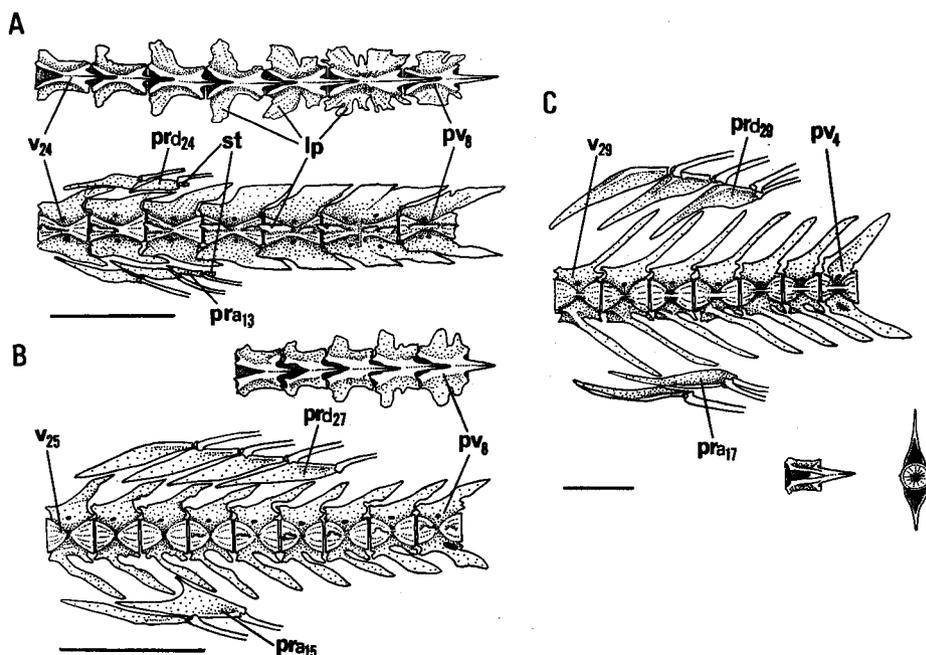


Fig. 12. Dorsal (above) and lateral (below) aspects of caudal vertebrae and associated bones in: A, *Marukawichthys ambulator*; B, *Icelus uncinalis*; C, *Hemilepidotus gilberti* (above, lateral aspect; below, anterior (right) and dorsal (left) aspects of 5th preuralcentrum). lp, lateral process of caudal vertebra; pra₁₃, 13th proximal pterygiophore of anal series; prd₂₄, 24th proximal pterygiophore of dorsal series; pv₈, 8th preuralcentrum; st, stay; v₂₄, 24th vertebra. Scale bars indicate 5 mm.

forms a small pore on the dorsolateral face of the proximal. In one specimen of *Icelus spiniger*, the first distal pterygiophore is present as an independent bone. The last distal pterygiophore of the dorsal and anal series are absent in *Ereunias*, *Marukawichthys*, and *Icelus*, while it is present in *Hemilepidotus*.

The stay (st) is observed as a small one behind the last proximal pterygiophore in *Ereunias* and *Marukawichthys*, while it is absent in *Icelus* and *Hemilepidotus*.

Caudal skeleton (Fig. 13)

The caudal skeleton is composed of three epurals, a stegural, and the hypural-parhypural complex bone.

The hypural-parhypural complex bone (hc) is fan-like and supports the principal caudal fin rays posteriorly. In *Hemilepidotus* this complex bone is separated into upper and lower lobes, while it is a single plate-like bone in the other three genera. The epurals (eu) are slightly curved bones and support dorsal procurrent rays. The stegural (st) is a slender bone placed between the epurals and the hypural-parhypural complex. This bone is absent in *Icelus*.

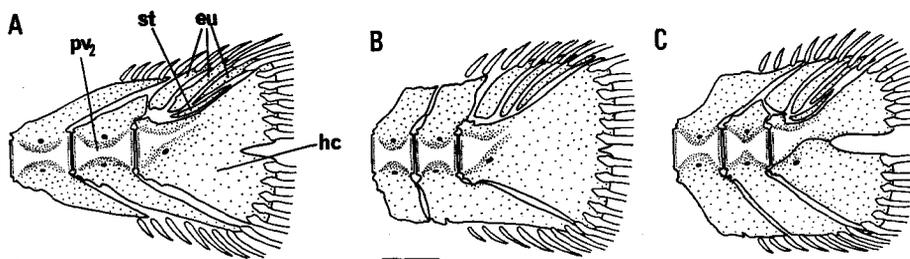


Fig. 13. Lateral aspect of caudal skeleton and fin rays in: A, *Marukawichthys ambulator*; B, *Icelus spiniger*; C, *Hemilepidotus gilberti*. eu, epural; hc, hypural and parhypural complex bone; pv₂, second preuralcentrum; st, stegural. Scale bars indicate 2.5 mm.

Discussion

Berg⁶⁾ established the family Icelidae for *Ereunias*, *Marukawichthys*, and *Icelus*, based on the osteological features described by Matsubara⁵⁾. The diagnostic features of Berg's Icelidae are: 1) unossified prevomer (vomer) and ethmoid (mesethmoid), 2) large intercalar (opisthotic) forming the upper margin of the foramen magnum, and 3) the vagus foramen situated in the intercalar. The present study establishes that these three genera do not possess the above osteological conditions. They are characterized by having 1) small intercalar situated between the pterotic and exoccipital, 2) the posterior margin of the foramen magnum formed by the exoccipital and basioccipital, 3) the vagus foramen opened on the exoccipital, and 4) ossified prevomer and ethmoid (Figs. 1 and 2). Judging from these facts it is concluded that Matsubara⁵⁾ misidentified the exoccipital for the large intercalar and the well developed ethmoid cartilage for the unossified prevomer and ethmoid.

Some other inaccuracies occur in Matsubara's⁵⁾ description of the osteological feature of *Ereunias* and *Marukawichthys*. He stated that 1) the branchial arches are cartilaginous, 2) the hyoid apparatus is typical as in percoid fishes and in other mail-cheeked fishes, and 3) the third and fourth or fifth infraorbitals (suborbitals) are entirely absent. However, in these three genera all branchial elements are completely ossified (Fig. 7), the hyoid apparatus of these genera differs from that of many percoid and scorpaeniform fishes by the absence of the basihyal (Fig. 6), and there are the third to fifth infraorbitals (Fig. 3). The conditions in *Ereunias* and *Marukawichthys* are the same as found in *Icelus* and in *Hemilepidotus* in the osteological features mentioned above. It, therefore, is concluded that the Berg's Icelidae is unwarranted.

In order to elucidate the reasonable systematic positions of members of Berg's Icelidae, the osteological conditions of *Ereunias*, *Marukawichthys*, and *Icelus* are compared with those of the primitive cottid representative *Hemilepidotus*. The relationships among these four genera are inferred by a cladistic analysis, on the basis of seven osteological characters.

1. *The relation between the parasphenoid and pterosphenoid*: Two conditions are observed in this character. In *Ereunias* and *Marukawichthys* the pterosphenoid does not meet the parasphenoid because of the interposition of the prootic (Fig. 2,

A). The prootic forms part of the posterior margin of the orbit in these two genera. In *Hemilepidotus* and *Icelus* the pterosphenoid meets the parasphenoid and the prootic does not form part of the posterior margin of the orbit (Fig. 2, B). According to Quast⁹⁾ who discussed this character in the Scorpaeniformes, it may be considered that the former condition found in serranid and scorpaenid fishes is more generalized condition, and that the latter condition found in Hexagrammidae, Zaniolepididae, Cottidae, Agonidae, and Cyclopteridae is the more derived condition. Moreover, many ichthyologists believe that the cottid fishes are derived from the primitive scorpaenid-like ancestor⁷⁾¹⁸⁾¹⁹⁾²⁰⁾²¹⁾. Therefore, it is considered that the pterosphenoid was separated from parasphenoid in the cottoid ancestor, and that both bones became connected to each other during cottoid evolution. It is regarded that the condition in *Ereunias* and *Marukawichthys* is more primitive than that in *Hemilepidotus* and *Icelus*.

2. *The number of pharyngobranchials*: There are three conditions for this character. *Ereunias* and *Marukawichthys* possess three pharyngobranchials (Fig. 7, A and B). The first one is small and rod-like and the second and third ones are plate-like bones bearing villiform teeth. *Hemilepidotus* possesses two pharyngobranchials which are plate-like bones bearing villiform teeth (Fig. 7, C). *Icelus* possesses only one large pharyngobranchial bearing villiform teeth (Fig. 7, D). Nelson²²⁾ discussed the phyletic trends of gill arches in fishes, and inferred that the number of pharyngobranchials and their tooth plates has been independently reduced in many teleostean groups. It may be concluded that this reduction occurred in the cottoid evolution. Judging from his hypothesis, the condition observed in *Ereunias* and *Marukawichthys* is regarded as the most primitive, that in *Icelus* is the most derived, and that in *Hemilepidotus* as intermediate.

3. *The structure of the pectoral fin rays*: In *Ereunias* and *Marukawichthys* the lower four fin rays are free from the upper lobe and are supported by the lower two actinosts. The abductor superficialis muscle is separated into two parts (Fig. 9, A). In *Icelus* and *Hemilepidotus* all fin rays are connected with each other by the fin membrane and the separation of the abductor superficialis is absent (Fig. 9, B). In the cottoid fishes, only two genera, *Ereunias* and *Marukawichthys*, possess the free pectoral fin rays. Furthermore they have reduced pelvic fin rays; *Ereunias* has only one vestigial spine and no soft ray, and *Marukawichthys* has one spine and four rays which are reduced in length. Therefore, it is considered that the free pectoral fin rays of these two genera have the function which is support of the body on the bottom, in compensation for the function of the pelvic fin rays in other cottoid fishes. The muscular pattern of the pectoral fin in *Ereunias* and *Marukawichthys* is clearly distinguished from that in *Hemilepidotus* and *Icelus* which is same as that in many teleostean groups¹⁷⁾²³⁾²⁴⁾²⁵⁾²⁶⁾. This unique muscular pattern suggests that the free pectoral fin rays are closely related to the particular function which may be supporting of the body or ambulation on bottom. Judging from these facts, it is reasonable to consider that the free pectoral fin rays and its muscular pattern in *Ereunias* and *Marukawichthys* were derived from the conditions in *Hemilepidotus* and *Icelus*.

4. *The number of pelvic fin rays*: Three conditions are observed in this character. The pelvic fin is composed of one spine and four soft rays in

TABLE 2. Hypothetical evolutionary trends of seven characters in four cottoid genera

	Primitive condition	Derived condition
1. Relation between parasphenoid and pterosphenoid	separated	→ touched
2. Number of pharyngobranchials	3	→ 2 → 1
3. Free rays of pectoral fin	absent	→ present
4. Number of pelvic fin rays	I,4	→ I,3 → I,0
5. Position of anterior dorsal pterygiophore	between first and second vertebrae	→ before first vertebra
6. Number of hypural-parhypural complex bones	2	→ 1
7. Stegural	present	→ absent

Marukawichthys and *Hemilepidotus*, and one spine and three soft rays in *Icelus*. *Ereunias* has been regarded as the unique cottoid fishes possessing no fin ray elements of the pelvic^{1,4,5,20,27,28}). But in this examination, it was clarified that *Ereunias* is possessed with a vestigial spine buried under the skin. It is generally said that the rather primitive members of this order (Scorpaenidae, Hexagrammidae, etc.) have five soft rays in the pelvic fin, while relative derived members have two (Agonidae and Aploactinidae), or none (some of Pataecidae and Comephoridae). Bolin¹⁸) postulated that the primitive cottoid was a fish somewhat similar to the primitive scorpaenids, and possessing five soft rays of pelvic fin. Judging from these evidences, it is reasonable to consider that the progressive reduction of number of pelvic fin rays has occurred in each sublineage of this order. It, therefore, is considered that the condition in *Marukawichthys* and *Hemilepidotus* is the most primitive among these four genera, and that in *Ereunias* is the most derived.

5. *Position of the anterior dorsal pterygiophores*: In this character, two conditions are observed. The anteriormost pterygiophore is located in front of the first vertebra in *Ereunias* and *Marukawichthys*, while it is located between the first and second vertebrae in *Hemilepidotus* and *Icelus* (Fig. 11). Matsubara¹⁹) suggested the anterior extension of dorsal pterygiophores in scorpaenoid fishes. According to his hypothesis, the condition of the supraoccipital separated from the anteriormost pterygiophore as seen in *Sebastes*, *Scorpaena*, etc. is the generalized type, while the condition of the anterior pterygiophores firmly rooted on the anterior half of the supraoccipital as in *Hypodytes* and *Erisphex* is the most specialized type. On the other hand, the evolutionary trends of dorsal pterygiophores in percoid fishes are shown by Smith and Bailey²⁹). One of those trends is the anterior extension of dorsal fin with the reduction of predorsal bones. Judging from this tendency, it is considered that the anterior extension of dorsal pterygiophores progressed in the process of cottoid evolution. It, therefore, is regarded that the condition in *Ereunias* and *Marukawichthys* is more derivative than that in *Icelus* and *Hemilepidotus*.

6. *The number of the hypural-parhypural complex*: Two conditions are observed in this character. In *Hemilepidotus*, the complex bone is separated into two lobes (Fig. 13, C). The lower lobe is a single bone fused with the parhypural, hypural I, and hypural II, and the upper lobe is a bone fused with the preural centrum I, hypural III and hypural IV³⁰). On the other hand, these two lobes are

fused to make a plate-like bone in *Ereunias*, *Marukawichthys*, and *Icelus* (Fig. 13, A and B). Gosline³¹), who discussed the caudal skeleton of the lower teleosts, inferred that there had been the sequence in the fusion of parts of caudal skeleton, and a progressive reduction in number of parts. Rosen and Patterson³²) discussed the progressive fusion of caudal elements in evolutionary change of caudal skeleton in teleostean fishes. In the Scorpaeniformes, Quast⁹) also noted this tendency of the caudal elements. It was considered that the caudal elements were progressively fused from five elements (three hypurals, parhypural and urostyle) of typical scorpaenid to three elements of hexagrammids, and finally to only one element in zaniolepid and cottid representatives. Judging from their view points, it may be reasonable to consider that the condition of the complex bone in *Hemilepidotus* is more primitive than that in the other three genera.

7. *The stegural*: This small caudal element is present in *Ereunias*, *Marukawichthys* and *Hemilepidotus*, while it is absent in *Icelus* (Fig. 13). According to Rosen and Patterson³²), the uroneural (stegural of Monod³⁰) is absent in the derived types of various teleostean groups. Additionally, there are many studies indicating progressive fusion or loss of the stegural in various teleostean groups³⁰)³³)³⁴)³⁵). Judging from this tendency, it is considered that the condition in *Icelus* is more derived than in the other three genera.

Other clear differences observed among these four genera are as follows; 1) dorsal pterygiophores not supporting fin rays are present in *Ereunias*, while they

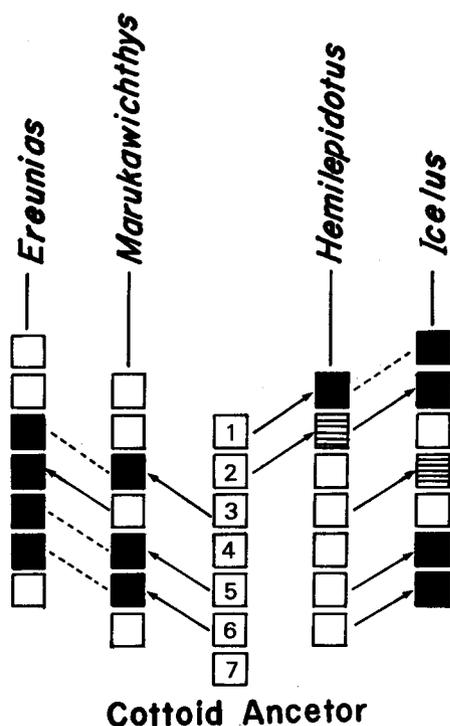


Fig. 14. Correlation of transformation series of seven characters among four cottoid genera and hypothetical cottoid ancestor. Character 1, relation between pterosphenoïd and parasphenoïd; 2, number of pharyngobranchials; 3, structure of pectoral fin; 4, number of pelvic fin rays; 5, position of anterior dorsal pterygiophore; 6, number of hypural and parhypural complex bones; 7, stegural. Black square indicates a derived condition; white square indicates a primitive condition; striped square indicates an intermediate condition. Arrow indicates the evolutionary trend of each character. Dotted line indicates sharing derived condition of each character.

are absent in the other three genera; 2) the stay of the last pterygiophore is present in *Ereunias* and *Marukawichthys*, while it is absent in *Icelus* and *Hemilepidotus*; 3) the lateral processes of the caudal vertebrae are present in *Ereunias*, *Marukawichthys* and *Icelus*, while it is absent in *Hemilepidotus*. But the evolutionary trends of these three characters can not be inferred, because there is little information available about these characters in scorpaeniform and other teleostean fishes. Therefore, these characters are not analyzed.

The result of the cladistic analysis of relationships among these four genera is presented in Fig. 14. As far as inferred from these seven characters, this is the cladogram which is satisfied with the minimum number of parallel evolution events (two parallelism; character numbers 4 and 6 in Fig. 14) and no reversal of evolutionary trends. This cladogram indicates that these four genera are divided into two monophyletic groups; *Hemilepidotus-Icelus* group, and *Ereunias-Marukawichthys* group. The former group is characterized by sharing the derived conditions of two characters (character numbers 1 and 2 in Fig. 14). In this group, the pterosphenoid and parasphenoid are directly connected, and the number of pharyngobranchials is two or less. On the other hand, the latter group is characterized by sharing the derived conditions of two characters; the unique structure of pectoral fin, and anterior dorsal pterygiophore inserting in front of the first vertebra (character numbers 3 and 5 in Fig. 14).

To decide the hierarchical rank of these two monophyletic groups will be impossible unless these group are compared with other cottoid genera, because the definition of the family Cottidae has not been satisfactorily shown. But in this study, the hierarchical rank of these two groups is expediently decided through the comparison with the family Cottidae which was defined by Taranetz⁷⁾, since he showed the osteological diagnoses of his family Cottidae based on the comparison of almost all cottid and other related fishes. The osteological features of the *Hemilepidotus-Icelus* group agree well with the diagnosis of the family Cottidae, especially the condition between the pterosphenoid and parasphenoid, one of the shared derived conditions in *Hemilepidotus-Icelus* group. Therefore, this group is included in Taranetz's Cottidae. On the other hand, the *Ereunias-Marukawichthys* group is different from the family Cottidae in not sharing the derived condition of the pterosphenoid-parasphenoid connection. In this character, this group shows a more primitive condition than that of the family Cottidae. But this group is characterized by the derived conditions of two characters (pectoral fin structure, position of the anterior dorsal pterygiophore) which are not shared in another group. It is a sister group of the family Cottidae. Therefore, it may be reasonable to recognize the family Ereuniidae which was established by Jordan²⁾ for the *Ereunias - Marukawichthys* group.

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YABE: Osteological review of the family Icelidae

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