

Interrelationships of the Etmopterinae (Chondrichthyes, Squaliformes)

SHIGERU SHIRAI and KAZUHIRO NAKAYA

Laboratory of Marine Zoology
Faculty of Fisheries
Hokkaido University, Japan

ABSTRACT

A cladistic analysis of the etmopterine sharks was conducted based on skeletal, muscular, and external characters using the outgroup rule. Within the Squaliformes, the subfamily Etmopterinae should be recognized as a monophyletic group by having the following autapomorphies: keel-process of basal cranium present, and labial cartilages composed of two separate parts. The present study indicates that *Etmopterus* + *Centroscyllium sheikoi*, and the rest of *Centroscyllium* + *Aculeola* are sister groups. These findings necessitate that *C. sheikoi* must be raised to the generic rank (*Miroscyllium*). Diagnostic characters are given for these natural taxa.

Introduction

The Squaliformes, equivalent to the Squaloidea of Bigelow and Schroeder (1957), traditionally has been divided into subgroups based on the presence or absence of dorsal fin spines. This subdivision led to the definition of two higher taxa, the Squalidae and Dalatiidae (sometimes regarded as subfamilies of the Squalidae); the Echinorhinidae was sometimes recognized separately as well. Hubbs and McHugh (1951) inferred that the loss of fin spines had occurred in more than one phyletic line and suggested that these subgroups were artificial and unnatural. Bigelow and Schroeder (1957), however, retained the traditional classification, because there seemed to be no securely objective basis for the subdivision of this group, and because they emphasized convenience in classification over phylogenetic implications. Their review is still the most comprehensive account of this group, and most subsequent workers have continued to use their scheme of squaliform classification.

Recently, Compagno (1973, 1977) introduced an "eclectic and provisional" taxonomic system based on the phylogenetic scheme and all-around comparisons of character conditions among living elasmobranchs. He recognized two higher taxa, Echinorhinidae, for the genus *Echinorhinus*, and Squalidae for the rest of the order, and he erected six subfamilies in the latter (later amended to four or five in Compagno 1984).

We have collected much information in an effort to elucidate squaliform phylogeny and suggest that a small group equivalent to the Etmopterinae of Compagno (1973,

1984) and Cadenat and Blache (1981) should be recognized. This higher taxon is composed of three known genera, *Etmopterus*, *Centroscyllium*, and *Aculeola*, and is not equal to the Etmopterinae of Fowler (1934), which included a large part of the squalids sharing grooved fin spines and a distinct subterminal notch of the caudal fin. We made this study in order to a) investigate monophyly of Etmopterinae, b) analyze the interrelationships of this group, and c) elucidate taxonomic changes and give diagnostic characters for each taxa.

Materials and Methods

Two major principles were applied to examine phylogenetic relationships: Hennig's principle of synapomorphy (1966) and Nelson's principle of parsimony (1970). The polarity of each morphocline of characters was determined by the outgroup rule (Wiley 1981). The phylogenetic relationships which are the basis of the present character analysis were taken from the superorder Squalomorpha of Compagno (1973, 1977). Some authors have questioned his synapomorphies (e.g., Maisey 1980); however, we consider only Compagno's scheme to be useful in the context of this study because no other study has paid attention to squaliform monophyly. We investigated the character distributions of the squalomorph species as much as possible in order to ascertain polarity. Since Compagno (1973, 1977) did not refer to the relationships of the six squalid subfamilies, we estimated the conditions of the common ancestor of the

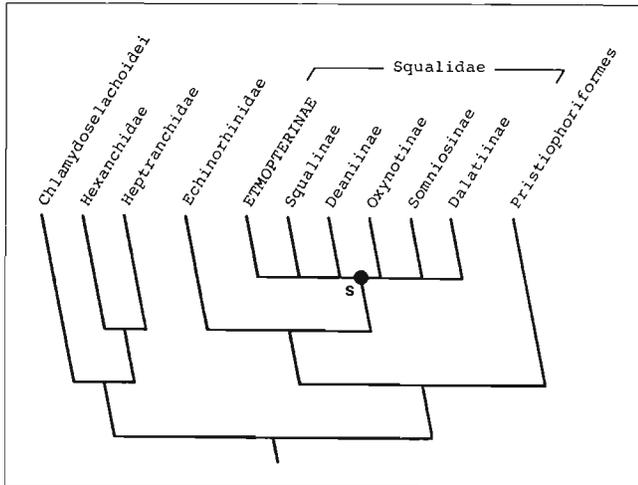


Figure 1.

The phylogenetic relationships used in the present character analysis (based on Compagno 1973, 1977). Node S shows the common ancestor of his Squalidae, which was estimated to examine both monophyly of Etmopterinae and its interrelationships.

Etmopterinae from those of the Squalidae to examine both monophyly of Etmopterinae and its interrelationships (Fig. 1).

External structures, skeletal, and muscular systems of whole sharks were examined. Illustrations were drawn using a camera lucida from cleared and stained specimens prepared by the method of Dingerkus and Uhler (1977). Terminology of skeletal and muscular systems mainly follow that of Edgeworth (1935) and Holmgren (1940, 1941). The terminology of Allis (1923), Daniel (1934), and Compagno (1973) are used as supplements. The study materials examined belong to the following collections of museums and institutions: FRSKU (Fisheries Research Station, Kyoto University, Maizuru); FSFL (Far Seas Fisheries Research Laboratory, Shimizu); HUMZ (Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate); NMNZ (National Museum of New Zealand, Wellington); NSMT (Department of Zoology, National Science Museum, Tokyo); RUSI (J.L.B. Smith Institute of Ichthyology, Grahamstown); SU (Natural History Museum, Stanford University [now housed in the California Academy of Sciences, San Francisco]); and USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.).

Etmopterinae

- Aculeola nigra*—HUMZ 90412, 439 mm TL, male, off Chile; USNM 220266, 385 mm TL, male, off Peru.
Centroscyllium fabricii—FSFL 0863d, 500 mm TL, male, western North Atlantic; HUMZ 112559, 382 mm TL, male, west of Greenland (Davis Strait).

- C. kamoharai*—HUMZ 95207, 367 mm TL, male, East China Sea.
C. nigrum—HUMZ 110329, 380 mm TL, male, off California.
C. Ritteri—HUMZ 72523, 485 mm TL, female, off Fukushima, Japan; HUMZ 93929, 412 mm TL, male, off Iwate, Japan (both western North Pacific).
C. sheikoi (= *Miroscyllium sheikoi*)—HUMZ 74977, 293 mm TL, male; HUMZ 74982, 399 mm TL, male; HUMZ 74984, 213 mm TL, male; all from Kyushu-Palau Ridge (western North Pacific).
Etmopterus baxteri—HUMZ 91313, 428 mm TL, female; HUMZ 91316, 457 mm TL, male; both south of New Zealand.
E. brachyurus—HUMZ 74601, 295 mm TL, male, western South Indian Ocean.
E. lucifer—HUMZ 34580, 355 mm TL, female, off Kochi, Japan (western North Pacific); HUMZ 74985, 355 mm TL, male, Kyushu-Palau Ridge; HUMZ 90230, 337 mm TL, male, off Fukushima, Japan.
E. pusillus—HUMZ 74595, 395 mm TL, male, western South Indian Ocean.
E. schultzi—NSMT-P 10944, 240 mm TL, male, off Patagonia.
E. spinax—FSFL-S 348, 292 mm TL, male, eastern Atlantic; SU 20617, 252 mm TL, male, off Italy Mediterranean.
E. unicolor—HUMZ 95257, 412 mm TL, female, East China Sea.
E. virens—SU 66821, 223 mm TL, male, the Gulf of Mexico.

Squalidae

- Centrophorus acus*—HUMZ 101726, 515 mm TL, male, off Okinawa Is., Japan.
C. granulatus—USNM 220221, 385 mm TL, male, Caribbean Sea.
C. uyato—HUMZ 90414, 659 mm TL, male, off western North Africa.
C. squamosus—HUMZ 87099, 453 mm TL, male, off western North Africa.
Centroscymnus crepidater—HUMZ 73509, 685 mm TL, male, off South Africa; FRSKU-S 1661, 554 mm TL, female, off Chile.
C. owstoni—NMNZ 2359, 582 mm TL, female, off New Zealand; HUMZ 101723, 652 mm TL, male, off Okinawa Is., Japan.
Cirrhigaleus barbifer—HUMZ 95177, 584 mm TL, female, East China Sea.
Dalatia licha—HUMZ 74603, 390 mm TL, male, off South Africa; HUMZ 95229, 621 mm TL, male, East China Sea.
Deania calcea—FRSKU-S 1662, 589 mm TL, female, off Chile.

- Euprotomicrus bispinatus*—HUMZ 90413, 197 mm TL, male, off Hawaii Is.
- Isistius brasiliensis*—HUMZ 86585, 480 mm TL, female; HUMZ 89900 516 mm TL, female; both from western North Pacific.
- Oxynotus brunienensis*—HUMZ 91383, 545 mm TL, male, off New Zealand.
- O. centrina*—FSFL-M 232, 350 mm TL, male, the Gulf of Guinea.
- Somniosus pacificus*—HUMZ 88828, 1,010 mm TL, male, south of Bering Sea.
- Squaliolus laticaudus*—HUMZ 74972, 250 mm TL, female; HUMZ 74974, 245 mm TL, female; both from Kyushu-Palau Ridge.
- Squalus acanthias*—HUMZ 87733, 495 mm TL, male, off Hokkaido, Japan (western North Pacific); HUMZ 91553, 525 mm TL, male, south of New Zealand.
- S. asper*—RUSI 6039, 225 mm TL, female, off South Africa.
- S. blainvillei*—HUMZ 95192, 825 mm TL, male, East China Sea.
- S. japonicus*—HUMZ 95213, 502 mm TL, male, East China Sea.
- S. megalops*—HUMZ 37664, 445 mm TL, female, off Borneo Is.
- S. mitsukurii*—HUMZ 68767, 620 mm TL, male, Emperor Seamount Chain.
- Zameus squamulosus*—HUMZ 75872, 526 mm TL, male, off New Zealand; HUMZ 95248, 435 mm TL, female, East China Sea.

Echinorhinidae

- Echinorhinus cookei*—USNM 179085, 178 mm TL, male, off California.

Pristiophoriformes

- Pristiophorus japonicus*—HUMZ 49349, 387 mm TL, male, off Kochi Pref., Japan.
- P. nudipinnis*—FSFL-EA 735, 687 mm TL, male, off south Australia.

Hexanchiformes

- Chlamydoselachus anguineus*—FSFL-D 2802, 652 mm TL, off South Africa.
- Heptanchias perlo*—HUMZ 101712, 542 mm TL, male, off Okinawa Is.
- Hexanchus griseus*—HUMZ 95104, 698 mm TL, male, East China Sea.
- Notorynchus cepedianus*—HUMZ 6749, 740 mm TL, female, Shimomoseki Fish Market, Japan.

Results and Discussion

Monophyly of Etmopterinae

The subfamily Etmopterinae, which includes three known genera: *Etmopterus*, *Centroscyllium*, and *Aculeola*, is characterized by two autapomorphies (the following numerical values noted in the parentheses identify each apomorphic character used in our reconstruction of etmopterine phylogeny, discussed later). The first is (1) anterior part of palatobasal process with a rod-like projection (keel-process of basis cranii: kp) extending anteroventrally related to articulation with palatoquadrate (Fig. 2). The keel part of ventral surface of ethmoid to orbital region is more or less developed in squalids (absent in echinorhinids, pristio-phoriforms, and hexanchiforms), and in *Zameus*, *Squaliolus*, and *Euprotomicrus* this part expands subtriangularly and is probably involved in the ethmoid-orbital articulation. However, the condition of this part in etmopterines is unique among squaliforms because of its simple rod-like shape. The second autapomorphy is (2) labial cartilages (lc) composed of two separate parts, a prominent paddle-like lower cartilage and a short and slender upper one (Fig. 3). Other squalids and chlamydoselachoids have three developed labial cartilages, two of which are on the upper jaw and one on the lower, and the posterior upper and the lower cartilages are articulated in almost of all the species. In Pristiophoriformes and hexanchoids, one or two reduced pieces of cartilages are present on the upper jaw or may be absent in some cases.

This monophyletic group is equal to the Etmopterinae of Compagno (1973, 1984); however, he has not revealed the monophyly and character conditions of this group. Although we do not refer to the systematic position of the Etmopterinae within the family here (partly because the character distributions in the Squalidae are most complex), the two autapomorphic states noted above strongly support the monophyly of the Etmopterinae. Our phylogenetic study also shows two synapomorphies within the Etmopterinae which, although not autapomorphic, further strengthen the certainty of etmopterine monophyly [conditions of other squalomorphs in brackets]: (3) absence of a supraotic shelf (sos) for the origins of levator dorsalis and the most anterior part of the constrictor hyoideus dorsalis [other squalomorphs except for the genus *Isistius* have a developed supraotic shelf along the upper margin of otic region] (Fig. 2), and (4) second dorsal fin with more or less developed cartilaginous plates or pieces anterior to the fin spine (prespinal radials) [also observed only in the genus *Squalus*].

As Burgess and Springer (1986) pointed out, it appears that the distribution of black pigment spots (probably photophores) shows the close relationships between these genera. This character may prove very useful when more ultrastructural information becomes available for other squalomorphs.

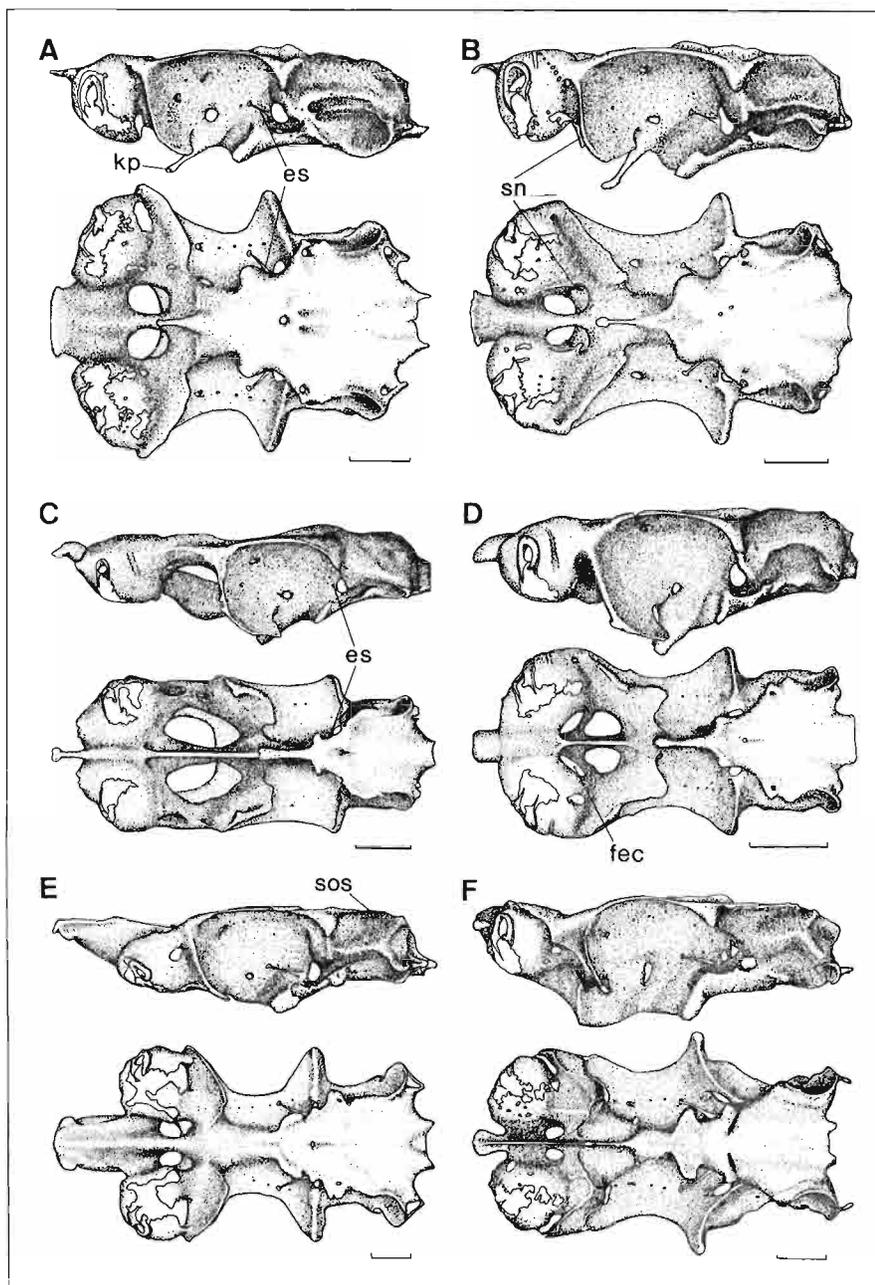


Figure 2.

Lateral (above) and ventral (below) aspects of neurocrania. A, *Aculeola nigra*; B, *Centroscyllium ritteri*; C, *Miroscyllium sheikoi*; D, *Etmopterus lucifer*; E, *Squalus mitsukurii*; F, *Zameus squamulosus*. es = eye stalk; fec = fenestra at anterior wall of ectethmoid chamber; kp = keel-process of basis cranii; sn = subnasal stay; sos = supraotic shelf. Scale bars indicate 10 mm.

Interrelationships of Etmopterinae

Eleven morphological differences for character analysis are recognized within the subfamily Etmopterinae, and are briefly described below. In each, the derived state is mentioned first and the plesiomorphy is shown in brackets. The conditions of other squalomorphs are also described.

Neurocranium (Fig. 2)—(5) In *Etmopterus*, the nasal capsule uniquely has a relatively large fenestra (fec) piercing the ectethmoid chamber [absent in other etmopterine genera and other squalomorphs]. (6) All *Centroscyllium* (except *C. sheikoi*) possess a simple rod-like process (sn)

extending ventrally at outer margin of subnasal fenestra, which is called a "subnasal stay" in this study [absent in all other squalomorphs]. (7) *C. sheikoi* has a wide interspace between nasal capsule and the antorbital wall [very narrowly spaced in all other etmopterines]. In most squalomorphs, the nasal capsule is close to or almost unified with the antorbital wall. The elongation between them is notably developed in *Deania* and is also observed in *Centroscyllium crepidater*. (8) The eye stalk (es) is a short rod-like process, not chondrified distally, in *Etmopterus*, *C. nigrum*, and *C. sheikoi* [it is a long and slender process with a disc at its extreme point in other etmopterine species]. The former

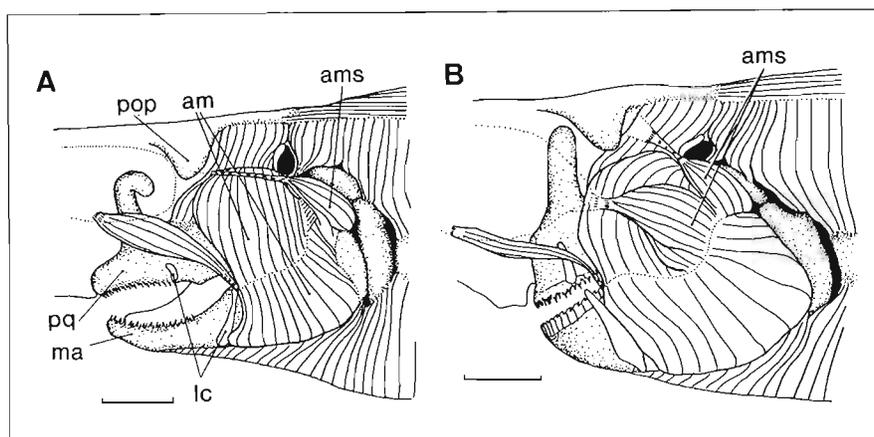


Figure 3.

Lateral aspect of head muscles. A, *Aculeola nigra*; B, *Etmopterus spinax*. am = adductor mandibulae; ams = adductor mandibulae superficialis; lc = labial cartilages; ma = mandibula; pop = postorbital process; pq = palatoquadrate. Scale bars indicate 10 mm.

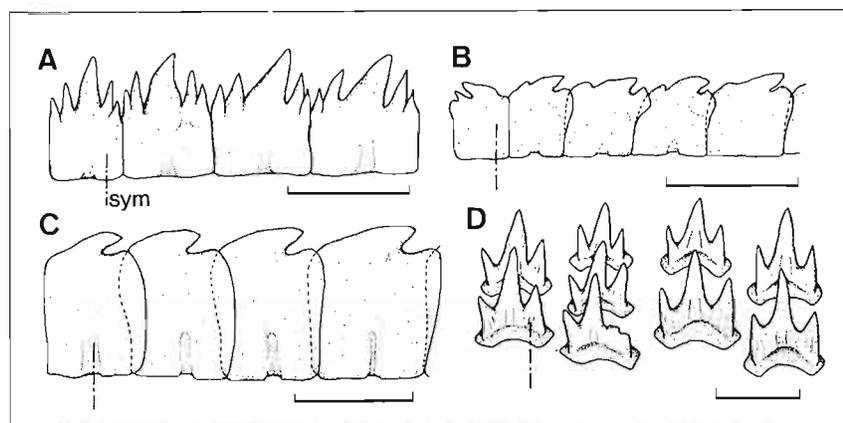


Figure 4.

Frontal aspect of anterior lower jaw teeth. A, *Miroscyllium sheikoi* (adult male: HUMZ 74982); B, *M. sheikoi* (young male: HUMZ 74984); C, *Etmopterus spinax* (SU 20617); D, *Centroscyllium ritteri* (HUMZ 93929). sym = jaw symphysis. Scale bars indicate 1 mm.

condition for the eye stalk is also observed in the genera *Deania* and *Oxynotus*, and the latter is found in all other squalomorphs except for *Isistius*, which does not have any process to support the eye and rectus muscles.

Visceral Arches and Related Parts—(9) Lower jaw teeth interlock their neighbors to form a continuous serrated edge in *Etmopterus* and *Centroscyllium sheikoi*: the overlapping condition of *C. sheikoi* occurs only in younger stages, and are normally lost with growth [teeth neither interlock nor touch their neighbors in all the other etmopterines] (Fig. 4). The interlocking of lower jaw teeth is observed in all of the other squalids. In hexanchoids and echinorhinids, they are arranged along the jaw but separated from the neighbors, and in pristiphoriforms, teeth are arranged quincuncially as are those of *Centroscyllium* and *Aculeola*. *Chlamydoselachus* has a unique dentition among living species. Its lower jaw teeth form many transverse rows widely separated from their neighbors. (10) In *E. baxteri*, *E. schultzi*, *E. spinax*, *E. unicolor*, and *E. virens*, the adductor mandibulae superficialis (ams) is divided into anteroventral and posterodorsal portions [only the latter is present in other squalomorphs] (Fig. 3). (11) The geniocoracoideus (gco) has its origin on the ventral surface of the symphysis of the coracoid

cartilages (co) in *Centroscyllium* and *Aculeola* [from the septum that is formed by the rectus cervicis (rc) and the pericardial membrane in *Etmopterus*]. The former condition for this muscle also occurs in *Dalatias* and *Zameus*, and the latter condition is seen in all other squalid genera except *Isistius*, in which the geniocoracoideus originates from the surface of the continuous muscle mass from the voluminous rectus cervicis and ventral longitudinal bundle. In echinorhinids, pristiphoriforms, and hexanchiforms, the geniocoracoideus originates on the aponeurotic septum which is formed by anterior and posterior portions of rectus cervicis (Fig. 5). (12) In *Aculeola*, the basihyal cartilage (bh) has a double-pointed expansion (dp) at its rear margin [absent in other squalomorphs] (Fig. 6A).

Other Parts—(13) *Aculeola* also possesses a double-pointed expansion (dp) at the anterior edge of the puboischiadic bar (pb) [absent in other squalomorphs] (Fig. 6B). (14) In *Etmopterus* and *Centroscyllium sheikoi*, the transformation from monospondylous to diplospondylous vertebral centra occurs well behind the haemal canal origin, and the most anterior five to nine precaudal tail centra are monospondylous [generally, such extensive monospondyly is not observed in the precaudal tail centra of other squalomorphs]

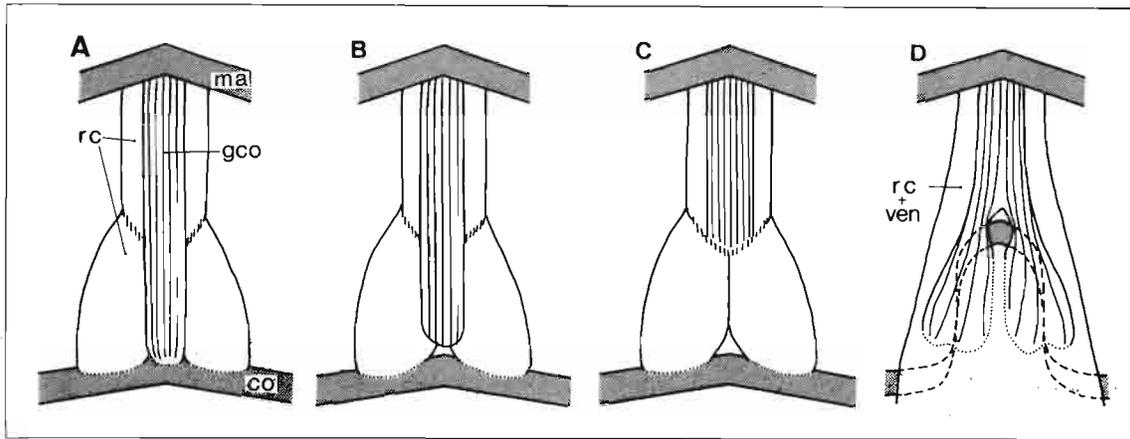


Figure 5.

Diagrams of ventral surface of head muscles, showing the four patterns of origin of genioacoracoideus. Genioacoracoideus originates from: A, ventral surface of coracoid; B, septum of rectus cervicis and pericardial membrane; C, aponeurotic septum of anterior and posterior portions of rectus cervicis; D, ventral surface of a continuous muscle mass from rectus cervicis and ventral longitudinal bundle. co = coracoid; gco = genioacoracoideus; ma = mandibula; rc = rectus cervicis; ven = ventral longitudinal bundle.

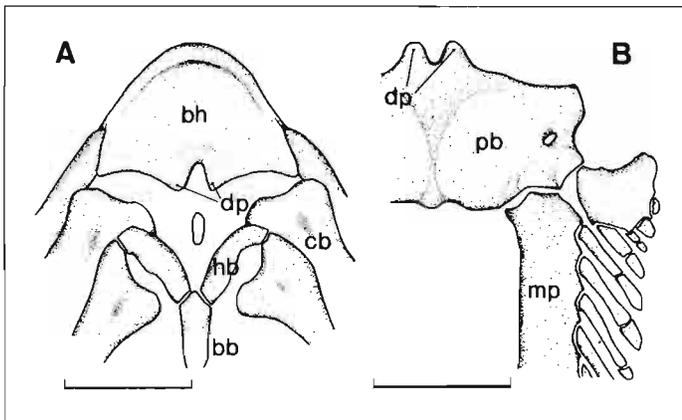


Figure 6.

Unique double-pointed expansions of *Aculeola nigra*. A, dorsal aspect of basal component of hyoid and branchial arches (anterior part); B, ventral aspect of pelvic girdle. bb = basibranchial; bh = basihyal; cb = ceratobranchial; dp = double-pointed expansion; hb = hypobranchial; mp = metapterygium; pb = puboischiadic bar. Scale bars indicate 10 mm.

(Fig. 7). (15) The dermal denticles are almost absent on the body surface in *C. kamoharai* [the distribution of denticles is more or less described on the bodies of other squalomorphs].

The most parsimonious hypothesis of etmopterine relationships is shown in Fig. 8. The Etmopterinae is inferred to be composed of two major phyletic lines. The first line is monophyletic by virtue of synapomorphy (11) and has two branches corresponding to genera *Aculeola* and *Centroscyllum* (except *C. sheikoi*). These results support the view of Burgess and Springer (1986), who recognized the close relationship between the two genera based on oral structures and dermal denticles. The genus *Aculeola* is monotypic (*A. nigra*) and is defined by two apomorphies, (12) and (13). As suggested by Compagno (1973), Maisey (1980) and Burgess and Springer (1986), it is concluded that *Aculeola* is the least specialized genus within the Squalidae because it shares some symplesiomorphies with

echinorhinids or hexanchiforms, i.e., a long palatoquadrate without developed otic process, "amphystylic" jaw protrusion as hexanchoids (but, no postorbital articulation), coracoid cartilages extending extremely forward, comparatively broad pelvic girdle and no calcified vertebral centra. The *Centroscyllum* branch is considered monophyletic by virtue of synapomorphy (6). The interspecific relationships of the genus *Centroscyllum* remains obscure in this study, because we find only two autapomorphies exhibited by both *C. kamoharai* and *C. nigrum* and no shared derived condition (synapomorphy) in the group. We also cannot address the validity of *Paracentroscyllum* Alcock (1889), proposed for *C. ornatum* and revived by Fowler (1941) as a subgenus of *Centroscyllum*, because we have not examined the appropriate specimens. External and internal morphology of *Centroscyllum* species are so conservative that this genus (except *C. sheikoi*) is considered to form a well defined unit.

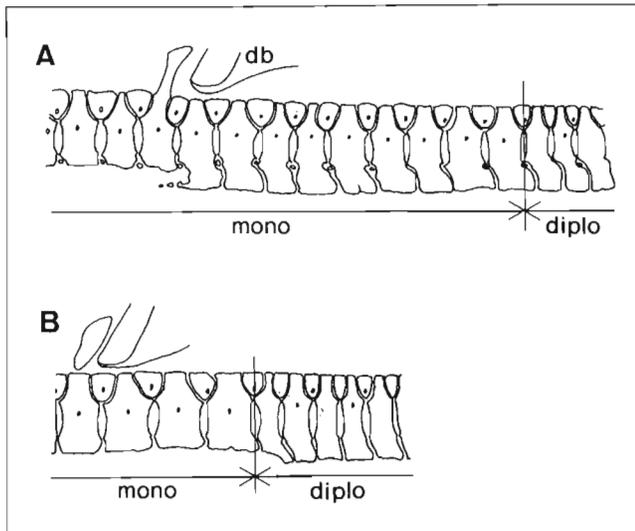


Figure 7.

Diagrams showing the transformation from monospondyly to diplospondyly under 2nd dorsal fin. A, *Miroscyllium sheikoi*; B, *Centroscyllium ritteri*. db = basal cartilage of 2nd dorsal fin; diplo = diplospondylous centra; mono = monospondylous centra.

The second phyletic line also consists of a pair of sister groups which correspond to the genus *Etmopterus* and *Centroscyllium sheikoi*. The close relations between these two groups are supported by the synapomorphies (8), (9), and (14). *Etmopterus* forms a monophyletic group by virtue of (5), and is the most varied genus (over 20 nominal species) in the Etmopterinae. In this genus, *E. baxteri*, schultzi, spinax, virens, and unicolor are united by an autapomorphic character (10). These five species also characterized by having spine-like dermal denticles spaced randomly in adult forms. The remaining members of the *Etmopterus* do not share any derived character states. This hypothesis of *Etmopterus* interrelationships eliminates Fowler's (1941) subgenera, *Etmopterus* and *Acanthidium*, which are proposed on the relative positions of pectoral, pelvic, and two dorsal fins. The last group contains *Centroscyllium sheikoi* (= *Miroscyllium sheikoi*), which is defined by the synapomorphies (7) and (11). This species was originally described as a species of *Centroscyllium* based on a mature male specimen from Kyushu-Palau Ridge (Dolganov 1986). It corresponds to species tentatively reported by Nakaya (1982) as *Centroscyllium* sp. (adult males) and *Etmopterus* sp. (young males). Its lower jaw tooth is blade-like and touches its neighbors in adult males, whereas in young

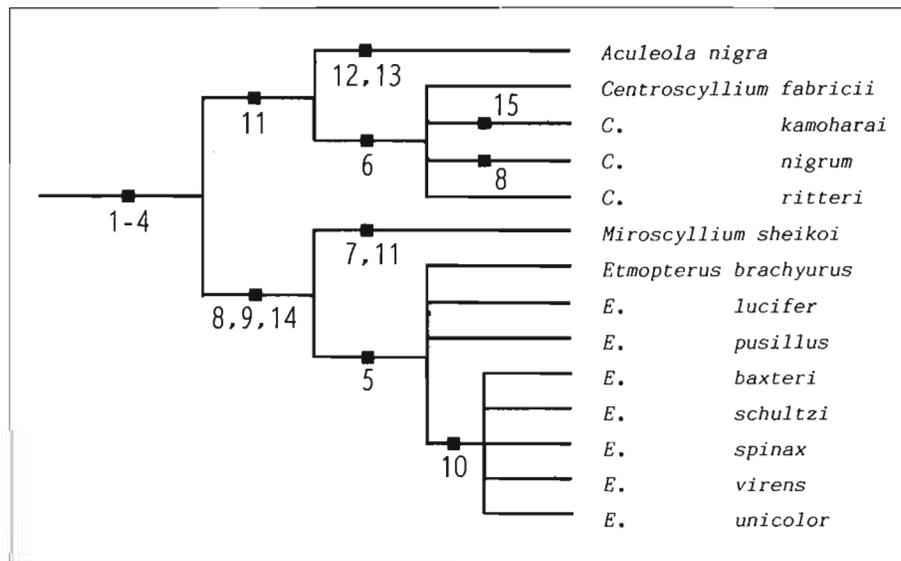


Figure 8.

Proposed interrelationships of the subfamily Etmopterinae. Numbers in the figure showing following apomorphies: 1, keel-process of basal cranium present; 2, labial cartilages composed of two separated parts; 3, supraotic shelf absent; 4, prespinal radial present; 5, fenestra at anterior wall of ectethmoid chamber present; 6, subnasal stay present; 7, wide interspace between nasal capsule and antorbital wall; 8, eye stalk not chondrified distally; 9, lower jaw teeth interlocking; 10, adductor mandibulae superficialis divided into two parts; 11, genioacoracoides immediately originating from ventral surface of coracoid; 12, double-pointed expansion at rear margin of basihyal present; 13, double-pointed expansion at anterior margin of puboischiadic bar; 14, most anterior five to nine precaudal tail centra monospondylous; 15, dermal denticles almost absent on body.

males it is monocuspid (one or two minute lateral cusps in some teeth) and interlocking like that of *Etmopterus*. This morphological change is considered to occur with growth, and we are very interested in observing the female dentition of *Etmopterus*.

Taxonomic Conclusions

The present phylogenetic study expressed the monophyly of the Etmopterinae and the presence of four equally ranked taxa in the group. Of these supraspecific taxa, all the *Etmopterus species* + *Centroscyllium sheikoi*, and the rest of the *Centroscyllium* + *Aculeola* are the sister groups. These findings necessitate that *C. sheikoi* be excluded from the genus *Centroscyllium*, and that it be raised to the generic rank. We propose the new genus name, *Miroscyllium*, for the taxon.

Diagnostic characters of each taxa are described below.

Subfamily Etmopterinae

Diagnosis—Both dorsal fins with a grooved spine, the second relatively larger; caudal fin with a long upper margin and a subterminal notch; neither abdominal ridge, precaudal ridge nor precaudal pits present; mouth with thin lips and labial furrows, lips not fringed; upper jaw teeth with a conical and slender central cusp rising from bilobed and semi-hexagonal bases, arranged quincuncially; minute to prominent lateral cusps present in almost all of the species (recognized even in the genus *Aculeola*: Burgess and Springer, 1986: our USNM specimen of this study); keel-process of basis cranii present; two labial cartilages on the mouth corner developed; supraotic shelf absent; prespinal radials of second dorsal fin more or less developed.

Other Features—Precerebral fontanelle large and oval; ectethmoid chamber developed, and subnasal fenestra present; antorbital wall large, with a membranous part below the eye; foramen prooticum for trigeminal and facial nerve (except hyomandibular branch) single; posterior part of palatobasal process moderately expanded laterally; short subotic shelf in front of articular fossa for hyomandibula. Palatoquadrate large, consisting of only a single thick plate, with a long orbital process and no symphyseal plate; suborbitalis inserted on inner side of labials (and its adjacent tissues) and on the anteroventral part of adductor mandibulae by a short tendon, not directly inserted on mandibula; second and third hypobranchials of both sides not fused; subspinalis muscle present. Pectoral fin skeletons including three basal cartilages and radials; iliac process of pelvic girdle weakly developed. Each dorsal fin with a triangular basal cartilage but lacks three jointed rays; postspinal rays are moderately elongated.

Genus *Etmopterus* Rafinesque

Diagnosis—Upper jaw teeth with one to five pairs of lateral cusps; lower jaw teeth, dissimilar to the uppers in shape, with blade-like and single oblique cusp, arranged

linearly along the jaw and overlapping the neighboring teeth; fenestra at anterior wall of ectethmoid chamber piercing the nasal capsule; eye stalk short, not chondrified distally, without a disk at the extreme point; anterior several vertebral centra of the precaudal tail monospondylous.

Other Features—Snout moderately rounded, not elongated, with a more or less wedge-shaped tip; oral cleft relatively short and transverse; dermal denticles with a slender, acute and erect to weakly inclined thorn-like, bristle-like, or flat truncated cusp, spaced relatively close together, forming longitudinal rows in some species; flank marks at caudal region conspicuous or almost absent. Rostral process short, simple and club-like, separable from precerebral fontanelle; keel-process rather thick. Mandibular arch rather short; palatoquadrate with laterally expanded otic process for adductor mandibulae; adductor mandibulae superficialis divided into two portions in some species; geniocoracoideus having its origin from an aponeurotic septum that is formed by the rectus cervicis and pericardial membrane.

Genus *Centroscyllium* Müller and Henle

Diagnosis—Upper and lower jaw teeth similar in shape and quincunx arrangement, with one to two pairs of minute but prominent lateral cusps; subnasal stay at outer margin of subnasal fenestra; geniocoracoideus having its origin from the ventral surface of the midline of the coracoid.

Other Features—Snout moderately rounded to slightly pointed; oral cleft relatively long and arcuate; dermal denticles with a short, slender, acute or blunt, erect to weakly inclined cusp, spaced very sparsely and randomly, or almost naked; flank marks at the caudal region conspicuous or absent. Rostral process thin, plate-like, forming the anterior edge of precerebral fontanelle, not supported ventrally; keel-process comparatively slender. Mandibular arch rather long; palatoquadrate with otic process; adductor mandibulae superficialis consisting of only posterodorsal portion; trunk centra monospondylous, and precaudal tail centra diplospondylous in many specimens.

Genus *Aculeola* de Buen

Diagnosis—Upper jaw teeth similar to the lower in shape and arrangement, without lateral cusps or with very minute ones in some specimens; dorsal fin spines relatively slender, not curved strongly, not reaching halfway to the fin apex; geniocoracoideus having its origin from the ventral surface of the midline of the coracoid bar; double-pointed expansions at the posterior edge of the basihyal and at the frontal edge of the puboischiadic bar.

Other Features—Snout short; oral cleft relatively long and arcuate; dermal denticles with a short, nearly erect and conical cusp, spaced sparsely and randomly; no flank marks at the caudal region. Rostral process thin, plate-like, forming the anterior edge of precerebral fontanelle; keel-

process comparatively slender. Mandibular arch rather long; palatoquadrate without otic process for adductor mandibulae; palatoquadrate almost in contact with the rear margin of the postorbital process (Maisey 1980); adductor mandibulae superficialis consisting of only posterodorsal portion. Coracoid cartilage relatively thick, extending forward at ventral surface of body, forming wedge-shaped bar; vertebral centra poorly developed, uncalcified; trunk centra monospondylous and precaudal tail centra diplospondylous.

Miroscyllium gen. nov.

Type species. *Centrosyllium sheikoi* Dolganov, 1986.

Synonymy. *Centrosyllium* (in part) Nakaya, 1982.

Etmopterus (in part) Nakaya, 1982.

Diagnosis—A slender-bodied etmopterine shark with a long snout and relatively short trunk; lower jaw teeth blade-like with one central and several short lateral cusps (in the adult male; the latter are sometimes absent in younger males), touching (in adult male) or overlapping (in young male) neighboring teeth. One or more functional tooth series in both jaws: eye stalk short, not chondrified distally, without a cartilaginous disk supporting the eye ball; recti anterior, superior, and inferior, having origins at the proximal part of eye stalk; genicoracoides originating directly from the ventral surface of the symphysis of coracoid cartilages; transformation from monospondylous to diplospondylous centra well behind the haemal canal origin; there are about nine monospondylous centra in the precaudal tail.

External—Snout relatively elongated and flattened, with a wedge-shaped tip; oral cleft relatively short and transverse; upper jaw teeth with a central cusp and two to four pairs of lateral cusps (sometimes two prominent cusps can be observed), arranged quincuncially; lower jaw teeth in adult males small and blade-like with a multicuspid crown, arranged linearly along the jaw, not overlapping but touching their neighbors to form a serrated edge; in young males, lower teeth with an inclined main cusp, with or without 1 or 2 minute lateral cusps, and interlocking as seen in *Etmopterus* species (Fig. 4A, B). Dorsal fin spines strong, relatively curved posteriorly, the second strikingly larger than the first, extending nearly to the apex of the fin; upper and lower caudal lobes are poorly developed. Dermal denticles are very flat, truncated at the top, spaced relatively close together and in random order; flank marks at the caudal region conspicuous.

Internal—Rostral process rather long, simple, and club-like, separable from precerebral fontanelle; subethmoid ridge comparatively well developed; interspace between nasal capsule and antorbital wall moderately elongated; keel-process comparatively thick. Mandibular arch rather short; palatoquadrate with otic process and long orbital process; palatoquadrate not in contact with rear margin of postorbital process; the anteroventral portion of the

adductor mandibulae superficialis absent. Coracoid cartilage rather slender, not extending forward at ventral surface of body, forming a moderately curved bar; pelvic girdle relatively narrow, moderately curved. Vertebral central with a calcified double cone.

Etymology—From the Latin *mir* (strange) in reference to the unique tooth series on the lower jaw.

Remarks—Only a few adult and young male specimens of *Miroscyllium sheikoi* have been captured from Kyushu-Palau Ridges, western North Pacific.

Acknowledgments

We wish to express our gratitude to Kunio Amaoka of HUMZ for his guidance and valuable advice in the course of this study. We are also very grateful to Keiichi Matsuura (NSMT) for his useful advice and support of this study.

We are deeply indebted to the following people for advice and information, especially their kind assistance in providing materials as a gift or loan: S. J. Jewett, J. A. F. Garrick, Graham S. Hardy, Hiroshi Hatanaka, P. C. Heemstra, Tomio Iwamoto, Izumi Nakamura, R. Rosenblatt, J. A. Seigel, Matthias Stehmann, and Toru Taniuchi. We thank Katsuhiko Tokusa and the crew of the *Shinkai-Maru* (the 6th cruise of *Showa 55 nendo*).

Finally, the first author's special thanks go to Takehiko Koga and many of the graduate students of HUMZ, who spent countless hours discussing the ideas of this study and helped with the loan of materials, and to Mitsuaki Sato and Atsushi Fukui of Japan NUS Co. Ltd., for their help in this study.

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