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Phylogeny of the Suborder Scorpaenoidei (Pisces: Scorpaeniformes)

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Fifty-five genera of the suborder Scorpaenoidei were examined in order to reconstruct their phylogenetic relationships. Ninety-five characters were selected following both myological and osteological examinations of the whole body as follows: muscles of the cheek, ventral surface of the head, serving the branchial arches, between the pectoral girdle, neurocranium, hyoid arch, and branchial arches, serving the pectoral fin, pelvic fin, dorsal and anal fins, and caudal fin, carinal muscles, body muscles, and swimbladder and associated muscles; neurocranium, nasal and circumorbital bones, jaws, suspensorium, hyoid arch, branchial arches, vertebrae and associated bones, caudal skeleton, pectoral girdle, pelvic girdle, and dorsal and anal fin supports.

Character polarities were primarily determined by comparisons with generalized percoids as an out-group, secondarily as unquestionably specialized conditions, or by comparisons with sebastids and scorpaenids as a functional out-group. Cladistic analyses based on the minimum number of evolutionary steps, without character reversals were performed.

The Scorpaenoidei was considered a natural group, because the other members of the Scorpaeniformes, including Hexagrammidae, Anoplopomatidae, Platycephaloidei, Triglidae, Peristediidae, and Cottoidei, have been shown to be derived from non-scorpaenoid ancestors. The relationships between the genera included in Scorpaenoidei were shown, the 11 major stems corresponding to familial categories. The relationships of the families were expressed as follows, using a sequencing convention: the Sebastidae, the Setarchidae plus Neosebastidae, the Scorpaenidae, the Apistidae plus Tetrarogidae, the Synanceiidae plus Congiopodidae, the Gnathanacanthidae, the Aploactinidae, and the Pataecidae. The following classification for Scorpaenoidei is proposed (only genera examined during this study are included): Sebastidae, including *Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes, Sebastolobus, Trachyscorpia,* and *Plectrogenium;* Setarchidae, including *Setarches, Lioscorpius,* and *Ectreposebastes*; Neosebastidae, including *Neosebastes* and *Maxillicosta*; Scorpaenidae, including *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias,* and *Taenianotus; Apistidae,* including *Apistus;* Tetrarogidae, including *Gymnapistes, Centropogon, Notesthes, Neocentropogon, Ocosia, Paracentropogon, Hypodytes, Liocranium, Ablabys,* and *Richardsonichthys*; Synanceiidae, including *Inimicus, Synanceia, Erosa, Choridactylus,* and *Minous*; Congiopodidae, including *Congiopodus, Alertichthys,* and *Zanclorhynchus*; Gnathanacanthidae, including *Gnathanacanthus*; Aploactinidae, including *Aploactis, Erisphex,* and *Sthenopus*; Pataecidae, including *Aetapcus, Pataecus,* and *Neopataecus.*

Key words: scorpaenoid fishes, myology, osteology, phylogeny, new classification

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Contents

The suborder Scorpaenoidei is a large and diverse group of about 100 genera and 500 species distributed in tropical and temperate seas world wide. Studies on scorpaeniforms made by GILL (1888), EIGENMANN and BEESON (1893, 1894), CRAMER (1895), ALLIS (1909), REGAN (1913), GUTBERLET (1915), GREGORY (1933), MATSUBARA (1934, 1936, 1940), DE BEER (1937), and BERG (1940) mainly described osteology, without considering phylogenetic relationships. MATSUBARA (1943) published the first comprehensive systematic work, in which he discussed the phylogenetic position and origin of the Scorpaenoidei within the Scorpaeniformes and the intergeneric relationships among the Scorpaenoidei, based on analyses of the infraorbitals, suspensorium, hyoid arch, neurocranium, pectoral girdle, and swimbladder of predominantly Japanese specimens. Many workers have subsequently investigated relationships of and within the Scorpaenoidei (MATSUBARA 1955, MATSUBARA and OCHIAI 1955, ESCHMEYER 1965ab, 1969, 1972, 1983, MORELAND 1960, BARSUKOV 1964, 1968, 1970, 1972ab, 1973ab, 1981, QUAST 1965, ESCHMEYER and COLLETTE 1966, ESCHMEYER and HUREAU 1971, CHEN 1971, 1981, ESCHMEYER *et al.* 1973, ESCHMEYER, ABE, and NAKANO 1979, ESCHMEYER, HALLACHER, and RAMA-RAO 1979, ESCHMEYER, RAMA-RAO, and HALLACHER 1979, ESCHMEYER and RAMA-RAO 1973, 1977, POSS and ESCHMEYER 1975, 1978, 1979, 1980, ESCHMEYER and POSS 1976, KANAYAMA and AMAOKA 1981, POSS 1982, POSS and SPRINGER 1983, ISHIDA and AMAOKA 1986, 1989, 1992). In addition to osteological characters, myological characters have also been considered important in the construction of teleostean phylogenies (GREENWOOD *et al.* 1966, LIEM 1970, 1978, 1981, GREENWOOD 1971, GREENWOOD and LAUDER 1981, WINTERBOTTOM 1974ab, HOWES 1976, 1980, LIEM and GREENWOOD 1981, KAUFMAN and LIEM 1982, LAUDER and LIEM 1983). Myological studies of Scorpaeniformes were carried out by HALLACHER (1974) and YABE (1985), the former examining the extrinsic muscles of *Sebastes* and the other scorpaeniforms, and the latter, musculature of several scorpaenoids in a detailed study on cottoid phylogeny.

Many authors have suggested, rather than a monophyletic origin, a polyphyletic derivation of Scorpaeniformes from several perciforms or lower groups (MATSUBARA 1943, QUAST 1965, GREENWOOD *et al.* 1966, NELSON 1976, 1984, WASHINGTON *et al.* 1984). However, for half a century, a comprehensive analysis of the phylogeny of scorpaenoids has not been made, most authors essentially following a higher classification along the lines proposed by MATSUBARA (1943).

This study attempts to reconstruct the phylogenetic relationships of the Scorpaenoidei by the examination and analyses of overall skeletal and muscular systems of scorpaenoid fishes worldwide, and thereby propose a new and "up-to-date" classification of the Scorpaenoidei.

I. Materials and Methods

Specimens were stained with alizarin red and variously counterstained for cartilage with alcian blue. After dissection, they were drawn using a stereoscopic dissecting microscope with a drawing tube. Institutional abbreviations follow LEVITON *et al.* (1985). Specimen sizes indicate standard length.

Specimens Examined:

Sebastidae

Sebastes vulpes, HUMZ 63771, 162.8 mm

Sebastiscus marmoratus, HUMZ 33139, 180.2 mm

Hozukius emblemarius, HUMZ 35282, 168.4 mm

Helicolenus hilgendorfi, HUMZ 49329, 129.8 mm

Adelosebastes latens, HUMZ 71927, 250.0 mm

Sebastolobus macrochir, HUMZ 92139, 161.9 mm

Trachyscorpia capensis, FSFL-EB 611, 217.6 mm

Plectrogenium nanum, HUMZ 74811, 60.8 mm

Setarchidae

Setarches longimanus, HUMZ 51734, 141.1 mm

Lioscorpius longiceps, CAS 34866, 76.9 mm

Ectreposebastes imus, HUMZ 75110, 145.8 mm

Neosebastidae

Neosebastes pandus, HUMZ 33214, 192.3 mm

Maxillicosta raoulensis, HUMZ 110724, 67.2 mm

Scorpaenidae

Pontinus macrocephalus, HUMZ 63115, 180.3 mm

Neomerinthe rufescens, BPBM 23893, 80.6 mm

Phenacoscorpius megalops, CAS 47299, 77.2 mm

Parascorpaena aurita, CAS 54038, 77.4 mm

Scorpaena neglecta, HUMZ 65961, 146.6 mm

Iracundus signifer, BPBM 13767, 92.9 mm

Scorpaenopsis cirrhosa, HUMZ 48346, 175.1 mm

Scorpaenodes kelloggi, HUMZ 48608, 69.7 mm

Hoplosebastes armatus, HUMZ 37449, 92.6 mm

Pterois lunulata, HUMZ uncatalogued, 141.0 mm

Ebosia bleekeri, HUMZ 37431, 111.7 mm

Brachypterois serrulatus, HUMZ 35083, 81.0 mm

Dendrochirus zebra, HUMZ 96496, 134.2 mm

Parapterois heterurus, HUMZ 35091, 103.8 mm

Rhinopias frondosa, KUSHIMOTO 7-058, 127.4 mm

Taenianotus triacanthus, BPBM 13800, 57.1 mm

Apistidae

Apistus carinatus, HUMZ 71706, 114.0 mm, HUMZ 110443, 102.7 mm

Tetrarogidae

Gymnapistes marmoratus, LACM-V 67-141-1, 89.5 mm

Centropogon australis, LACM 30823-8, 51.7 mm

Notesthes robusta, LACM 42623-6, 74.4 mm

Neocentropogon aeglefinus japonicus, HUMZ 74745, 89.7 mm

Ocosia fasciata, BSKU 4960, 86.3 mm

Paracentropogon longispinis, LACM 35978-5, 65.1mm

Hypodytes rubripinnis, HUMZ 36445, 71.0 mm, HUMZ 109270, 69.5mm

Liocranium pleurostigma, HUMZ 64246, 82.1mm

Ablabys taenianotus, FSFL uncatalogued, 94.2 mm

Richardsonichthys leucogaster, NSMT-P uncatalogued, 61.3 mm

Synanceiidae

Inimicus japonicus, HUMZ 49017, 188.6 mm

Synanceia verrucosa, HUMZ 105128, 223.5 mm

Erosa erosa, HUMZ 97727, 94.6 mm
Choridactylus multibarbus, CAS 33951, 69.5 mm
Minous monodactylus, HUMZ 39758, 84.2 mm, HUMZ 101862, 93.7 mm
Congiopodidae,
Congiopodus coriaceus, HUMZ 91198, 155.6 mm
Alertichthys blacki, HUMZ 66620, 173.6 mm
Zanclorhynchus spinifer, HUMZ 73652, 168.0 mm
Gnathanacanthidae
Gnathanacanthus goetzeei, AMS-IB 668, 158.1 mm
Aploactinidae
Aploactis aspera, HUMZ 74746, 51.9 mm
Erisphex potti, HUMZ 65922, 88.6 mm
Sthenopus mollis, NSMT-P uncatalogued, 54.2 mm
Pataecidae
Aetapcus vincenti, SAMA-F 652, 126.5 mm
Pataecus fronts, SAMA-F 1541, 60.9 mm
Neopataecus waterhousii, SAMA-F 2369, 70.2 mm

Scorpaenoids were grouped for respective characters. The groups are numbered in the same order as the character descriptions, as: 'consecutive number' - 'grade of derivation beginning from 0'. Following the subsequent determination of character polarity reversal of a character is expressed as 'R' for its grade of derivation. The character number corresponds to the group number, although the first as grade of derivation is omitted unless at least two grades were recognized. The name given for each taxon throughout this work is in accordance with the classification proposed here. Terminology follows WITERBOTTOM (1974a) for myology and recent ichthyological works (WEITZMAN 1962, NELSON 1973, PATTERSON 1975, etc.) for osteology unless denoted. Scale bars in figures indicate 10 mm unless otherwise indicated.

Abbreviations used in the figures:

Muscles of the cheek

a1, a1 section of adductor mandibulae; a23, a23 section of adductor mandibulae; aw, aw section of adductor mandibulae; lap, levator arcus palatini; aap, adductor arcus palatini; do, dilatator operculi; lo, levator operculi.

Muscles of the ventral surface of the head

im, intermandibularis; prhy, protractor hyoidei; hin, hyohyoides inferioris; haba, hyohyoides abductores anterior; habp, hyohyoides abductores posterior; had, hyohyoides adductores,

Muscles serving the branchial arches

lext, levator externus; lint, levator internus; lpost, levator posterior; obld, obliquus dorsalis; oblp, obliquus posterior; ad, adductor; trda, transversus dorsalis anterior; trdp, transversus dorsalis posterior; rdors, retractor dorsalis; spho, sphincter oesophagi; oblv, obliquus ventralis; trva, transversus ventralis anterior; trvp, transversus ventralis posterior; rctv, rectus ventralis; rcomm, rectus communis.

Muscles between the pectoral girdle, neurocranium, hyoid, and branchial arches

sth, sternohyoideus; phce, pharyngocleithralis externus; phci, pharyngocleithralis internus; prp, protractor pectoralis; lpect, levator pectoralis.

Muscles serving the pectoral fin

abs, abductor superficialis; abp, abductor profundus; arrv, arrector ventralis; ads, adductor superficialis; adp, adductor profundus; arrd, arrector dorsalis; adr, adductor radialis; cr, coracoradialis.

Muscles serving the pelvic fin

absp, abductor superficialis pelvicus; abpp, abductor profundus pelvicus; arrvp, arrector ventralis pelvicus; adsp, adductor superficialis pelvicus; adpp, adductor profundus pelvicus;arrdp, arrector dorsalis pelvicus; extp, extensor proprius.

Muscles of the dorsal and anal fins

erecd, erector dorsalis; deprd, depressor dorsalis; incld, inclinator dorsalis; ereca, erector analis; depra, depressor analis; incla, inclinator analis.

Carinal muscles

scara, supracarinalis anterior; scarm, supracarinalis medius; scarp, supracarinalis posterior; icara, infracarinalis anterior; icarm, infracarinalis medius; icarp, infracarinalis posterior.

Muscles serving the caudal fin

int, interradialis; hl, hypochordal longitudinalis; fd, flexor dorsalis; fds, flexor dorsalis superior; fv, flexor ventralis; fvi, flexor ventralis inferior; fve, flexor ventralis externus; add, adductor dorsalis.

Body muscles

epax, epaxialis; hyp, hypaxialis; obls, obliquus superioris; obli, obliquus inferioris.

Swimbladder and associated muscles

extr, extrinsic; intr, intrinsic; Bl, Baudelot's ligament.

Neurocranium

EC, ethmoid cartilage; E, ethmoid; LE, lateral ethmoid; PV, prevomer; PTS, pterosphenoid;

BS, basisphenoid; F, frontal; SP, sphenotic; PTO, pterotic; PO, prootic; EO, epiotic; EOC, exoccipital; SOC, supraoccipital; P, parietal; IC, intercalar; ST, supratemporal; BOC, basioccipital; PS, parasphenoid.

Nasal and circumorbital bones

N, nasal; L, lachrymal; IO, infraorbital; DS, dermosphenotic.

Jaws

PM, premaxillary; M, maxillary; D, dentary; AN, angular; RA, retroarticular.

Suspensorium

PL, palatine; Q, quadrate; MTP, metapterygoid; ECP, ectopterygoid; ENP, entopterygoid; HM, hyomandibular; SY, symplectic; POP, preopercle; OP, opercle; SOP, subopercle; IOP, interopercle.

Hyoid arch

IH, interhyal; EH, epihyal; CH, ceratohyal; HH, hypohyal; BH, basihyal; UH, urohyal; BR, branchiostegal ray.

Branchial arches

PB, pharyngobranchial; UP, upper pharyngeal; INARC, interarcual cartilage; EB, epibranchial; CB, ceratobranchial; HB, hypobranchial; BB, basibranchial; LP, lower pharyngeal.

Vertebrae

AV, abdominal vertebra; CV, caudal vertebra; NS, neural spine; HS, hemal spine; INS, interneural space; PR, pleural rib; EP, epipleural.

Caudal skeleton

CF, caudal fin; PV1, preural vertebra 1; US, urostyle; UN, uroneural; EU, epural; PHU, parhypural; HUA, hypurapophysis; HU, hypural.

Pectoral girdle

PT, posttemporal; SCL, supracleithrum; CL, cleithrum; PCL, postcleithrum; S, scapula; CO, coracoid; R, radial; P1F, pectoral fin.

Pelvic girdle

P2S, pelvis; P2F, pelvic fin.

Pterygiophore

SN, supraneural; DP, distal pterygiophore; MP, median pterygiophore; PP, proximal pterygiophore; STY, stay; DF, dorsal fin; AF, anal fin.

Alphabetically, abbreviations are:

Myology

a1, a1 section of adductor mandibulae; a23, a23 section of adductor mandibulae; aap, adductor arcus palatini; abp, abductor profundus; abpp, abductor profundus pelvicus; abs, abductor superficialis; absp, abductor superficialis pelvicus; ad, adductor; add, adductor dorsalis; adp, adductor profundus; adpp, adductor profundus pelvicus; adr, adductor radialis; ads, adductor superficialis; adsp, adductor superficialis pelvicus; arrd, arrector dorsalis; arrdp, arrector dorsalis pelvicus; arrv, arrector ventralis; arrvp, arrector ventralis pelvicus; aw, aw section of adductor mandibulae; Bl, Baudelot's ligament; cr, coracoradialis; depra, depressor analis; deprd, depressor dorsalis; do, dilatator operculi; epax, epaxialis; ereca, erector analis; erecd, erector dorsalis; extp, extensor proprius; extr, extrinsic; fd, flexor dorsalis; fds, flexor dorsalis superior; fv, flexor ventralis; fve, flexor ventralis externus; fvi, flexor ventralis inferior; haba, hyohyoides abductores anterior; habp, hyohyoides abductores posterior; had, hyohyoides adductores; hin, hyohyoides inferioris; hl, hypochordal longitudinalis; hyp, hypaxialis; icara, infracarinalis anterior; icarm, infracarinalis medius; icarp, infracarinalis posterior; im, intermandibularis; incla, inclinator analis; incld, inclinator dorsalis; int, interradialis; intr, intrinsic; lap, levator arcus palatini; lext, levator externus; lint, levator internus; lo, levator operculi; lpect, levator pectoralis; lpost, levator posterior; obld, obliquus dorsalis; obli, obliquus inferioris; oblp, obliquus posterior; obls, obliquus superioris; oblv, obliquus ventralis; phce, pharyngocleithralis externus; phci, pharyngocleithralis internus; prhy, protractor hyoidei; prp, protractor pectoralis; rcomm, rectus communis; rctv, rectus ventralis; rdors, retractor dorsalis; scara, supracarinalis anterior; scarm, supracarinalis medius; scarp, supracarinalis posterior; spho, sphincter oesophagi; sth, sternohyoideus; trda, transversus dorsalis anterior; trdp, transversus dorsalis posterior; trva, transversus ventralis anterior; trvp, transversus ventralis posterior.

Osteology

AF, anal fin; AN, angular; AV, abdominal vertebra; BB, basibranchial; BH, basihyal; BOC, basioccipital; BR, branchiostegal ray; BS, basisphenoid; CB, ceratobranchial; CF, caudal fin; CH, ceratohyal; CL, cleithrum; CO, coracoid; CV, caudal vertebra; D, dentary; DF, dorsal fin; DP, distal pterygiophore; DS, dermosphenotic; E, ethmoid; EB, epibranchial; EC, ethmoid cartilage; ECP, ectopterygoid; EH, epihyal; ENP, entopterygoid; EO, epiotic; EOC, exoccipital; EP, epipleural; EU, epural; F, frontal; HB, hypobranchial; HH, hypohyal; HM, hyomandibular; HS, hemal spine; HU, hypural; HUA, hypurapophysis; IC, intercalar; IH, interhyal; INARC, interarcual cartilage; INS, interneural space; IO, infraorbital; IOP, interopercle; L, lachrymal; LE, lateral ethmoid; LP, lower pharyngeal; M, maxillary; MP, median pterygiophore; MTP, metapterygoid; N, nasal; NS, neural spine; OP, opercle; P, parietal; P1F, pectoral fin; P2F, pelvic fin; P2S. pelvis; PB, pharyngobranchial; PCL, postcleithrum; PHU, parhypural; PL, palatine; PM, premaxillary; PO, protic; POP, preopercle; PP, proximal pterygiophore; PR, pleural rib; PS, parasphenoid; PT, posttemporal; RTO, pterotic; PTS, pterosphenoid; PV, prevomer; PV1, preural vertebra 1; Q, quadrate; R, radial; RA, retroarticular; S, scapula; SCL, supracleithrum; SN, supraneural; SOC, supraoccipital; SOP, subopercle; SP, sphenotic; ST, supratemporal; STY, stay; SY, symplectic; UH, urohyal; UN, uroneural; UP, upper pharyngeal; US, urostyle.

II. Myology

1. MUSCLES OF THE CHEEK (Figs. 1-5; Table 1)

The following five muscles serve the cheek: the adductor mandibulae, levator arcus palatini, addutor arcus palatini, dilatator operculi, and levator operculi.

Adductor mandibulae: The adductor mandibulae is composed of three sections: a1, a23, and aw.

Section a1: A1 is separated from a23 by the path of ramus mandibularis 5. A1 overlaps a23 posteriorly. A1 and a23 are joined to aw by an aponeurosis. A1 is connected with a primordial ligament anteroventrally, forming the maxillary tendon that is inserted high on the posterodorsal face of the maxillary head. In most scorpaenoids (group 1-0), a1 does not taper posteriorly, having its origin from the anterior face of the upper portion of the

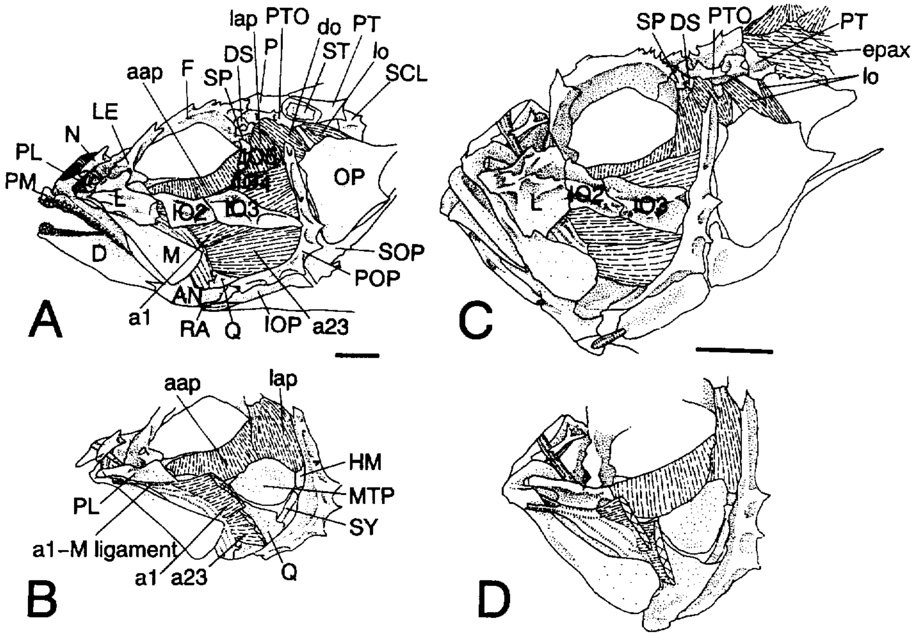

Fig. 1. Lateral view of head: A and B, *Adelosebastes latens*; C and D, *Dendrochirus zebra*. A and C, superficial muscles and bones; B and D,after removal of a1 and a23.

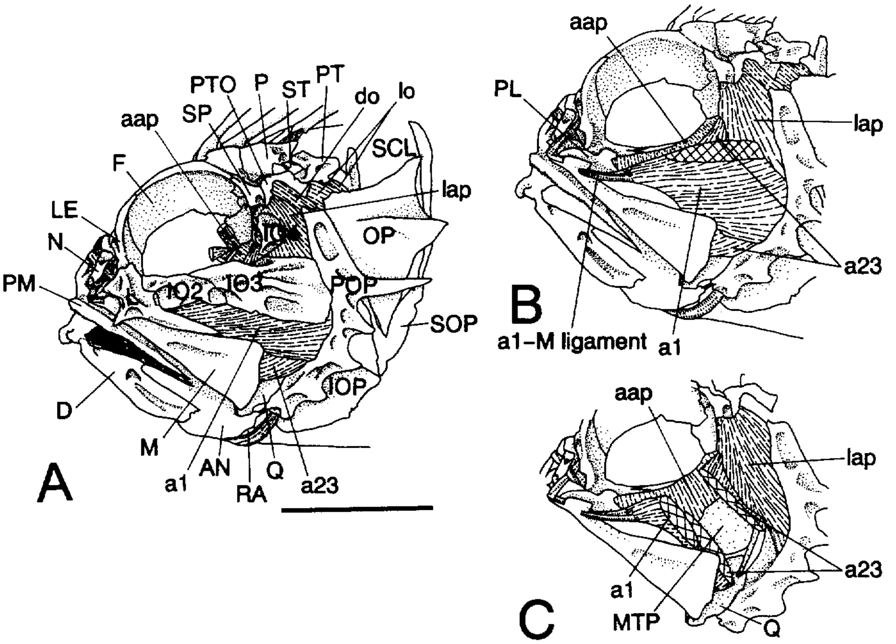

Fig. 2. Lateral view of head of *Richardsonichthys leucogaster*. A, superficial muscles and bones; B, after removal of infraorbitals; C, after removal of al and a23.

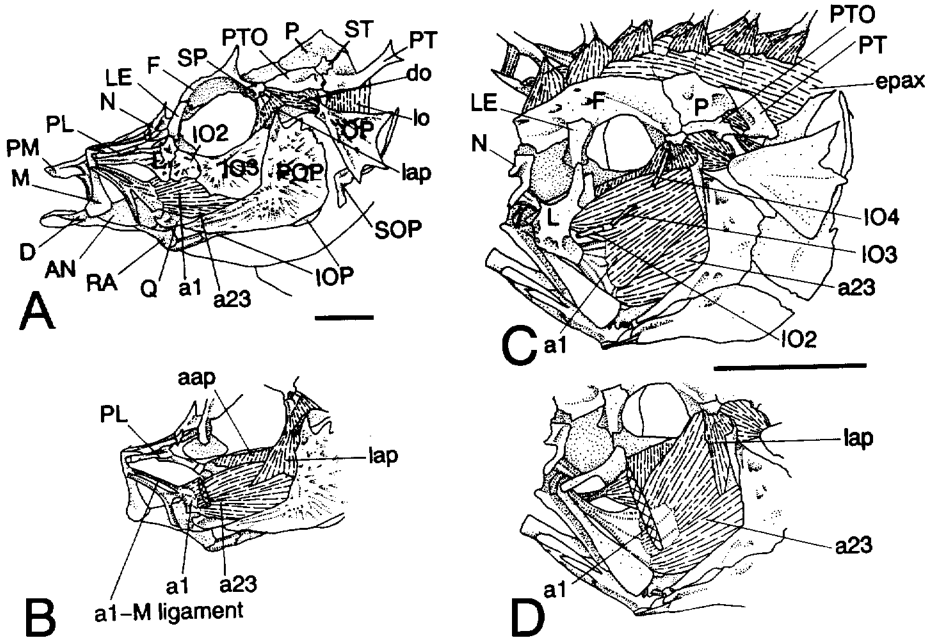

Fig. 3. Lateral view of head: A and B, *Zanclorhynchus spinifer*; C and D, *Neopatacus waterhousii*. A and C, superficial muscles and bones; B and D, after removal of al and a23.

preopercle and the face of the lateral process of the hyomandibular by an aponeurosis (Figs. 1A, C, 2A, 3A); in pataecids (group 1-1), a1 is narrow posteriorly, the origin including only the anterior face of the lateral process of the hyomandibular (Fig. 3C). In sebastids, setarchids, neosebastids, scorpaenids, synanceiids, congiopodids, the gnathanacanthid, the aploactinids *Erisphex* and *Sthenopus*, and pataecids (group 2-0), the a1 fibers have no association with the infraorbitals, in the apistid, tetrarogids, and the aploactinid *Aploactis* (group 2-1), the dorsolateral portion of the a1 origin is on the medial face of infraorbital 3 (Fig. 2B). In most scorpaenoids (group 3-0), the a1 fibers extend well forward along the primordial ligament between the lower jaw and the maxilla, the maxillary tendon of a1 consequently being short (Figs. 1D, 2B, 3D); in sebastids and congiopodids (group 3-1), the a1 fibers do not extend so far forward anteriorly, the maxillary tendon therefore being long (Figs. 1B, 3A, B). In most scorpaenoids (group 4-0), the maxillary tendon branches into two anteriorly, one branch leading to a small process on the anteromedial face of the maxillary head and the other, to a small process on the anterolateral surface of the maxillary (Figs. 1B, 1D, 2B, 3B); in pataecids (group 4-1), the maxillary tendon branches into three anteriorly, two branches resembling those of group 4-0 and the third leading to the anteromedial face of the maxillary just posterior to the anteromedial process (Fig. 3D).

Section a23: A23 lies ventrally to a1, its components, a2 and a3 being united into a single muscle mass in all scorpaenoids. In sebastids, setarchids, neosebastids, and scorpaenids (group 5-0), the origin, which includes the lateral faces of the metapterygoid and symplectic, dorsolateral face of the quadrate and anterolateral face of the preopercle, lies ventrally to the levator arcus palatini and is not overlain by the ventral part of the levator arcus palatini (Fig. 1B, D); in the apistid, synanceiids, congiopodids, the gnathanacanthid, and the aploactinids *Erisphex* and *Sthenopus* (group 5-1), the posterior part of a23 branches into two muscle masses, sandwiching the ventral part of the levator arcus palatini (Fig. 3B); in tetrarogids and the aploactinid *Aploactis* (group 5-2), the posterior part of a23 lies medially to the well developed levator arcus palatini, the muscle originating not only from the lateral face of the hyomandibular but also from the posterodorsal face of the metapterygoid and dorsolateral face of the symplectic (Fig. 2B, C); in pataecids (group 5-3), the origin includes the neurocranium, that is, the dorsolateral face of the pterosphenoid and anteroventral face of the sphenotic in *Pataecus* and *Aetapcus*, but the dorsolateral face of the pterosphenoid only in *Neopataecus* (Fig. 3D).

Section aw: The origin of aw is tendinous from the medial face of the preopercle. Its insertion is on the medial face of the dentary. The fibers fill the Meckelian fossa (Fig. 5A-E).

Levator arcus palatini (lap): The levator arcus palatini is a bulging muscle, narrowed at each end, with vertically running fibers. Its origin is from the ventrolateral face of the

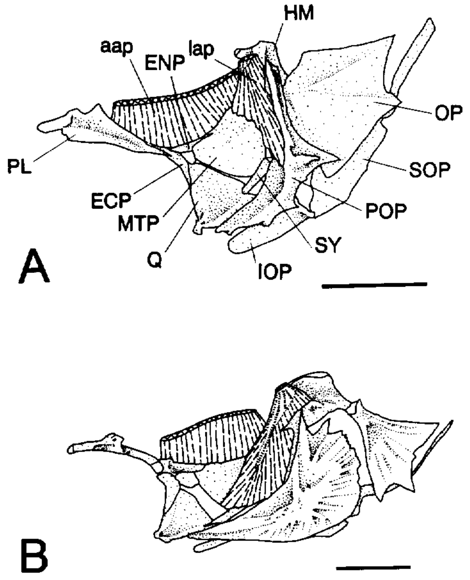

Fig. 4. Lateral view of suspensorium and associated muscles: A, *Neomerinthe rufescens*; B, *Zanclorhynchus spinifer*.

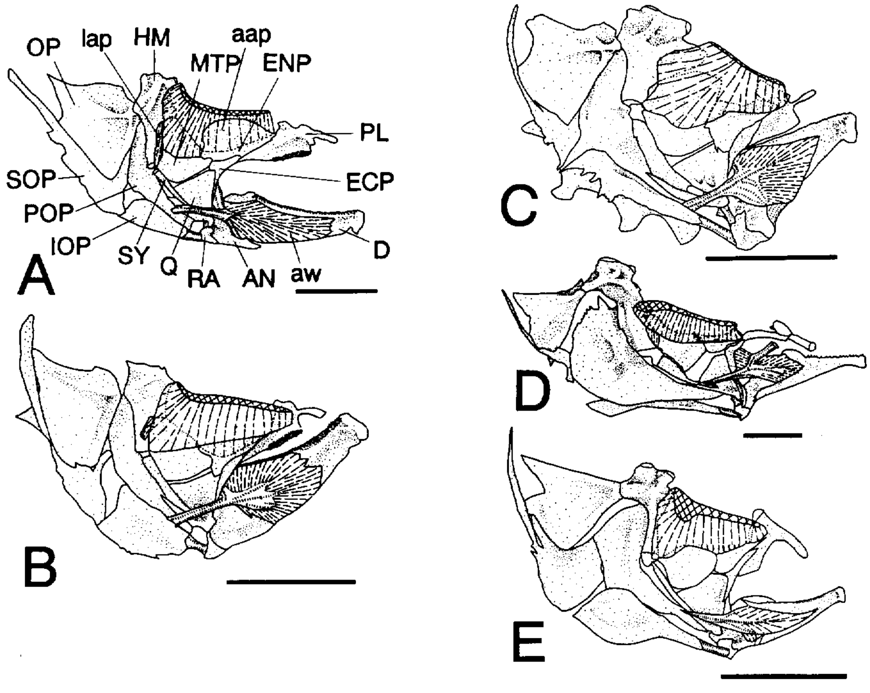

Fig. 5. Medial view of suspensorium and associated muscles: A, *Neomerinthe rufescens*; B, *Richardsonichthys leucogaster*; C, *Erosa erosa*; D, *Zanclorhynchus spinifer*; E, *Neopataecus waterhousii*.

sphenotic. In most scorpaenoids (group 6-0), the insertion is on the lateral face of the hyomandibular and dorsolateral margin of the metapterygoid (Figs. 1B, D, 2C, 4A); in the congiopodids *Congiopodus* and *Zanclorhynchus* (group 6-1), the fibers extend to the posteroventral face of the metapterygoid and the dorsal face of the symplectic (Fig. 4B).

Adductor arcus palatini (aap): The adductor arcus palatini is a plate-shaped muscle between the neurocranium and palatal arch, forming the floor of the orbit. It originates from the ventrolateral face of the parasphenoid and the anterolateral face of the prootic, and is inserted on the posterodorsal face of the palatine and entopterygoid. In sebastids, setarchids, neosebastids, and scorpaenids (group 7-0), the muscle insertion covers most of the dorsolateral face of the broad entopterygoid (Fig. 5A); in the apistid, tetrarogids, the synanceiids *Inimicus* and *Choridactylus*, and the aploactinid *Sthenopus* (group 7-1), the insertion covers less than half of the dorsolateral face of the crescent-shaped entopterygoid (Fig. 5B); in the synanceiid *Minous*, the congiopodids *Congiopodus* and *Alertichthys*, the gnathanacanthid, the aploactinids *Aploactis* and *Erisphex*, and pataecids (group 7-2), insertion is on the dorsal margin or dorsomedial face of the crescent-shaped entopterygoid (Fig. 5E); and in the synanceiids *Synanceia* and *Erosa*, and the congiopodid *Zanclorhynchus* (group 7-3), on a longitudinal ridge on the medial face of the entopterygoid (Fig. 5C, D).

Dilatator operculi (do): The dilatator operculi, a thin, plate-shaped muscle between theopercle and the neurocranium, originates from the longitudinal groove of the sphenotic and pterotic, and is inserted on the anterodorsal margin of the opercle.

Levator operculi (lo): The levator operculi is a plate-shaped muscle posterior to the dilatator operculi. Its origin varies in scorpaenoids. In sebastids, setarchids, neosebastids, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Scorpaenodes, Hoplosebastes, Rhinopias*, and *Taenianotus*, the gnathanacanthid, and pataecids (group 8-0), the origin is from the ventrolateral face of the pterotic (Figs. 1A, 3C); in the scorpaenids *Pterois, Ebosia, Brachypterois, Dendrochirus*, and *Parapterois*, the apistid, tetrarogids, synanceiids, the congiopodid *Alertichthys*, and aploactinids (group 8-1), the muscle originates from two branches, one from the ventrolateral face of the pterotic and the other from the ventral face of the posttemporal (Figs. 1C, 2A); in the congiopodids *Congiopodus* and *Zanclorhynchus* (group 8-2), it originates from the ventral face of the posttemporal and is inserted on the dorsomedial face of the opercle (Fig. 3A).

Table 1. Comparison of cheek muscle characters in scorpaenoids. Nemerals in parentheses correspond to group numbers.

Taxon	A1 origin	A1 and infraorbital 3	A1-maxillary tendon	A1-maxillary tendon	A23 origin	Lavator arcus palatini insertion	Adductor arcus palatimi insertion	Levator operculi origin
Sebastidae	broad (1-0)	not associated (2-1)	long (3-1)	bifid (4-0)	lateral to levator arcus palatini (lap) (5-0)	not including symplectic (6-0)	overlaps most of entopterygoid dorsolaterally (7-0)	pterotic (8-0)
Setarchidae Neosebastidae Scorpaenidae *Pontinus* *Neomerinthe* *Phenacoscorpius* *Parascorpaena* *Scorpaena* *Iracundus* *Scorpaenopsis* *Scorpaenodes* *Hoplosebastes* *Rhinopias* *Taenianotus*			short (3-0)					
Scorpaenidae *Pterois* *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois*								pterotic and posttempoal (8-1)
Apistidae		associated (2-1)			sandwiching lap (5-1)		overlaps less than half of entopterygoid dorsolaterally (7-1)	
Tetrarogidae					medial to lap (5-2)			
Synanceiidae *Inimicus* *Choridactylus* Aploactinidae *Sthenopus*		not associated (2-0)			sandwiching lap (5-1)			
Synanceiidae *Synanceia* *Erosa*							medial ridge of entopterygoid (7-3)	
Synanceiidae *Minous* Aploactinidae *Erisphex*							dorsal margin of dorsomedial face of entopterygoid (7-2)	
Congiopodidae *Congiopodus*			long (3-1)			including symplectic (6-1)		posttemporal (8-2)
Congiopodidae *Alertichthys*						not including symplectic (6-0)		pterotic and posttemporal (8-1)
Congiopodidae *Zanclorhynchus*						including symplectic (6-1)	medial ridge of entopterygoid (7-3)	posttemporal (8-2)
Gnathanacanthidae			short (3-0)			not including symplectic (6-0)	dorsal margin or dorsomedial face of entopterygoid (7-2)	pterotic (8-0)
Aploactinidae *Aploactis*		associated (2-1)			medial to lap (5-2)			
Pataecidae	narrow (1-1)	not associated (2-0)		trifid (4-1)	neurocranium (5-3)			

2. MUSCLES OF THE VENTRAL SURFACE OF THE HEAD (Figs. 6-8; Table 2)

The following five muscles serve the ventral surface of the head: the intermandibularis, protractor hyoidei, hyohyoides inferioris, hyohyoidei abductores, and hyohyoidei adductores.

Intermandibularis (imd): The intermandibularis is an unpaired muscle between the anteromedial faces of the dentaries, just behind the symphysis. In scorpaenoids, this muscle is sandwiched between the dorsal and ventral branches of the tendinous insertion of the protractor hyoidei.

Protractor hyoidei (prhy): The protractor hyoidei, a large muscle below the mandible bones, is subdivided by two myosepta. The anterior attachment behind the symphysis is divided into dorsal and ventral branches, which sandwich the intermandibularis. The posterior attachment is on the ventral face of the ceratohyal. In sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, and synanceiids (group 9-0), the posterior attachment is anterior to the base of the fourth branchiostegal ray (Fig. 6); in the congiopodids *Alertichthys* and *Zanclorhynchus*, the gnathanacanthid, aploactinids, and pataecids (group 9-1); in the congiopodid *Congiopodus* (group 9-2), it is anterior to the bases of the third and second branchiostegal rays respectively.

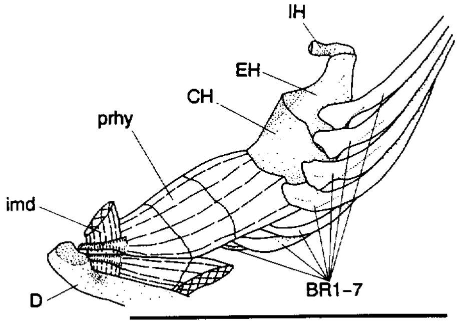

Fig. 6. Ventral view of ventral muscles of hyoid arch of *Centropogon ausralis*.

Hyohyoides inferioris (hin): The hyohyoides inferioris lies anteriorly to the hyohyoidei abductores, the fibers of the two muscles running in parallel. The hyohyoides inferioris lies dorsally to the bases of the anterior three branchiostegal rays, with its insertion on the medial face of the ceratohyal near the base of the fourth branchiostegal ray. In sebastids, scorpaenids, tetrarogids except *Ablabys* and *Richardsonichthys*, and the gnathanacanthid (group 10-0), the left and right fiber bundles cross over each other, with the element from the right ventral hypohyal being ventral to the other (Fig. 7A); in the tetrarogids *Ablabys* and *Richardsonichthys*, synanceiids, aploactinids, and pataecids (group 10-1), the left and

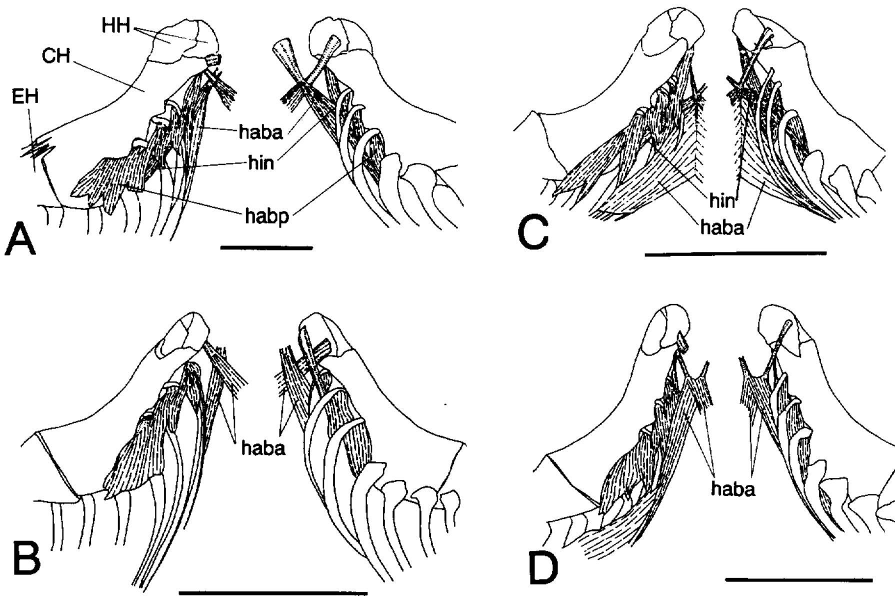

Fig. 7. Muscles of hyoid arch: A, *Rhinopias frondosa*; B, *Maxillicosta raoulensis*; C, *Richardsonichthys leucogaster*; D, *Apistus carinatus*. A and B, dorsal view; C and D, ventral view.

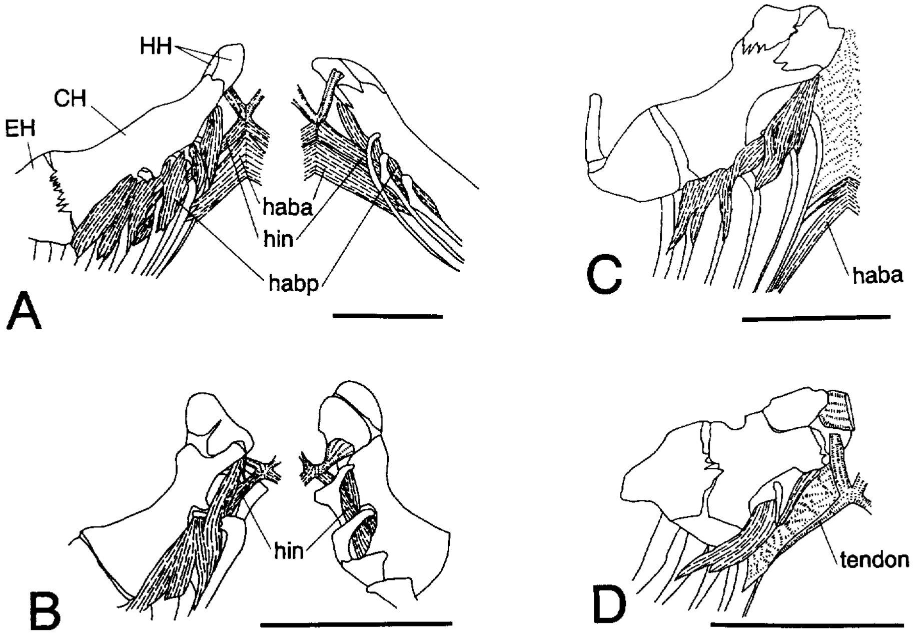

Fig. 8. Muscle of the hyoid arch: A, *Erosa erosa*; B, *Erisphex potti*; C, *Zanclorhynchus spinifer*; D, *Congiopodus coriaceus*. Left figures of A and B, C, and D, dorsal view; right of A and B, ventral view.

right origins are tendinous and meet in the midline, from which point the fiber bundles arise (Figs. 7C, 8A, B); in setarchids, neosebastids, the apistid, and congiopodids (group 10-2), the hyohyoides inferioris is absent (Figs. 7B, D, 8C, D).

Hyohyoidei abductores: The hyohyoidei abductores lie between the hypohyal and branchiostegal rays, and between the proximal portions of the branchiostegal rays, there being two sections, anterior and posterior.

The hyohyoidei abductores anterior (**haba**) originates from the ventral face of the ventral hypohyal, and is inserted on the branchiostegal rays of the opposite side. The fibers of this muscle run parallel to those of the hyohyoides inferioris, if present. In sebastids, setarchids, neosebastids, scorpaenids except *Taenianotus*, tetrarogids except *Ablabys* and *Richardsonichthys*, and the gnathanacanthid (group 11-0), the left and right fiber bundles cross over between the first branchiostegal rays, the element from the right ventral hypohyal to the left branchiostegal rays being ventral to the other (Fig. 7A, B); in the apistid (group 11-1), the left and right elements meet in the midline giving rise posteriorly to muscle bundles, the fibers from the right side to the left branchiostegal rays being ventral to those from the left side (Fig. 7D); in the scorpaenid *Taenianotus*, the tetrarogids *Ablabys* and *Richardsonichthys*, synanceiids, the congiopodids *Alertichthys* and *Zanclorhynchus*, and pataecids (group 11-2), the left and right elements meet in the midline, the fibers from each side being in broad contact (Figs. 7C, 8A, C); in the congiopodid *Congiopodus* (group 11-3), muscle fibers are absent, with only a pair of tendons extending from the ventral midline to the medial surfaces of the first branchiostegal rays (Fig. 8D); in aploactinids (group 11-4), the hyohyoidei abductores anterior are entirely absent (Fig. 8B).

The origin of the hyohyoidei abductores posterior (**habp**) is from the ventrolateral face of the ceratohyal, being dorsal to the insertion of the hyohyoides inferioris, and its insertion, on the branchiostegal rays of the same side.

Hyohyoidei adductores (had): The hyohyoidei adductores are thin muscles with sparse fibers, lying between the distal portions of the branchiostegal rays, and between the posteriormost branchiostegal ray and the medial face of the subopercle and opercle.

3. MUSCLES SERVING THE BRANCHIAL ARCHES (Figs. 9-12; Table 3)

The following eight muscles serve the dorsal parts of the branchial arches: the levator externus, levator internus, levator posterior, obliquus dorsalis, obliquus posterior, adductores, transversus dorsalis, and retractor dorsalis.

Levator externus (lext): The levatores externi comprise three or four muscles, connecting the epibranchials with the neurocranium. Their origins are from the

Table. 2. Comparison of characters of muscles serving the ventral head surface in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Posterior margin of protractor hyoidei	Hyohyoides inferioris	Anterior section of hyohyoidei abductores
Sebastidae Scorpaenidae except *Taenianotus* Tetraogidae except *Ablabys* and *Richardsonichthys*	base of 4th branchiostegal ray (9-0)	fiber bundles of left and right pairs cross over each other (10-0)	fiber bundles of left and right pair cross over each other (11-0)
Gnathanacanthidae	base of 3rd branchiostegal ray (9-1)		
Scorpaenidae *Taenianotus*	base of 4th branchiostegal ray (9-0)		tendinous origins meet in the midline at which point fibers form a raphé (11-2)
Tetrarogidae *Ablabys* *Richardsonichthys* Synanceiidae		left and right pairs of tendinous origins meet in the midline at which point fiber bundles arise (10-1)	
Pataecidae	base of 3rd branchiostegal ray (9-1)		
Aploactinidae			entirely absent (11-4)
Setarchidae Neosebastidae	base of 4th branchiostegal ray (9-0)	absent (10-2)	fiber bundles of left and right pairs cross over each other (11-0)
Apistidae			tendinous origins meet in the midline at which point fiber bundles arise (11-1)
Congiopodidae *Alertichthys* *Zanclorhynchus*	base of 3rd branchiostegal ray (9-1)		tendinous origins meet in the midline at which point fibers form a raphé (11-2)
Congiopodidae *Congiopodus*	base of 2nd branchiostegal ray (9-2)		fibers are absent, a pair of tendons remain (11-3)

dorsolateral face of the prootic or the ventrolateral face of the pterotic, with insertions on the dorsolateral faces of the epibranchials of the same arch near their articulation with the ceratobranchials. Levator externus 3, if present, is the least developed among these muscles, levator externus 4 usually being the most developed. Sebastids, setarchids, the neosebastid *Maxillicosta*, scorpaenids, the apistid, tetrarogids except *Liocranium* and *Richardsonichthys*, the synanceiids *Choridactylus* and *Minous*, congiopodids, and the gnathanacanthid (group 12-0) have levatores externi 1 to 4 (Figs. 9A, B, 10A-C, F), but the neosebastid *Neosebastes*, the tetrarogids *Liocranium* and *Richardsonichthys*, the

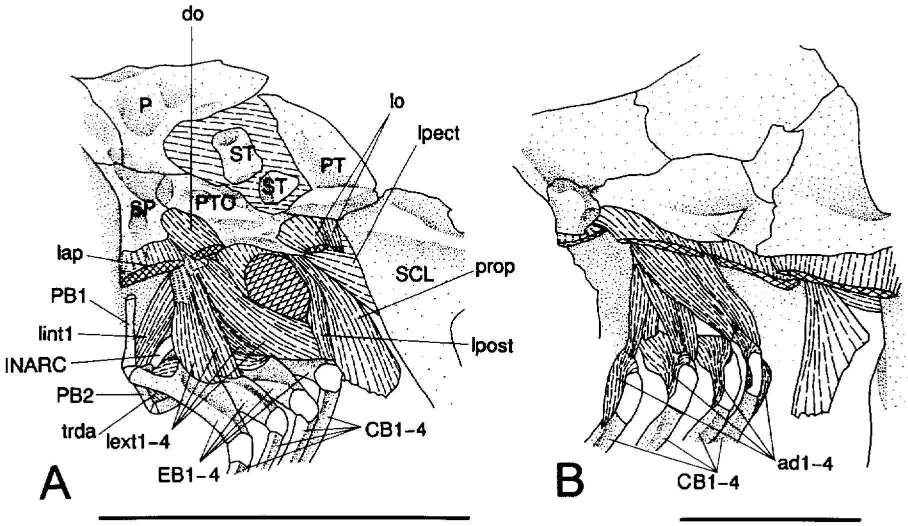

Fig.9. Left lateral view of dorsal branchial arch muscles: A, *Ocosia fasciata*; B, *Zanclorhynchus spinifer*.

synanceiids *Inimicus*, *Synanceia*, and *Erosa*, aploactinids, and pataecids (group 12-1) lack levator externus 3 (Fig. 10D, E).

Levator internus (lint): The levatores interni comprise two muscles, levatores interni 2 and 3, originating from the prootic, just medially to levatores externi, and connecting the neurocranium with the pharyngobranchials. The insertion of levator internus 2 is on the dorsal face of pharyngobranchial 2 or the complex of pharyngobranchials 2 and 3, and the upper pharyngeal, and that of levator internus 3, on the dorsal face of pharyngobranchial 3 or the complex of pharyngobranchials 2 and 3, and the upper pharyngeal.

Levator posterior (lpost): The levator posterior is a small, slender muscle, originating from the dorsolateral face of the prootic or the ventrolateral face of the pterotic, and having its insertion on the dorsal face of the upper pharyngeal just posteriorly to that of levator externus 4. Although most scorpaenoids (group 13-0) have this muscle (Fig. 10A-E), it is absent in congiopodids (group 13-1)(Figs. 9B, 10F).

Obliquus dorsalis (obld): The obliqui dorsales connect the epibranchials with the pharyngobranchials of the same arch. Most scorpaenoids (group 14-0) have only obliquus dorsalis 3, connecting the dorsal faces of pharyngobranchial 3 and the articulation of epibranchials 3 and 4 (Fig. 10B-E), but setarchids and the congiopodid *Zanclorhynchus* (group 14-1) also have obliqui dorsales 2 and 3, which connect the dorsal faces of pharyngobranchial 2 and epibranchial 2 (Fig. 10A, F). In most scorpaenoids (group 15-0), obliquus dorsalis 3 lies posteriorly to levator internus 3 (Fig. 10A-D, F); in the apistid, aploactinids, and pataecids (group 15-1), obliquus dorsalis 3 sandwiches levator internus 3

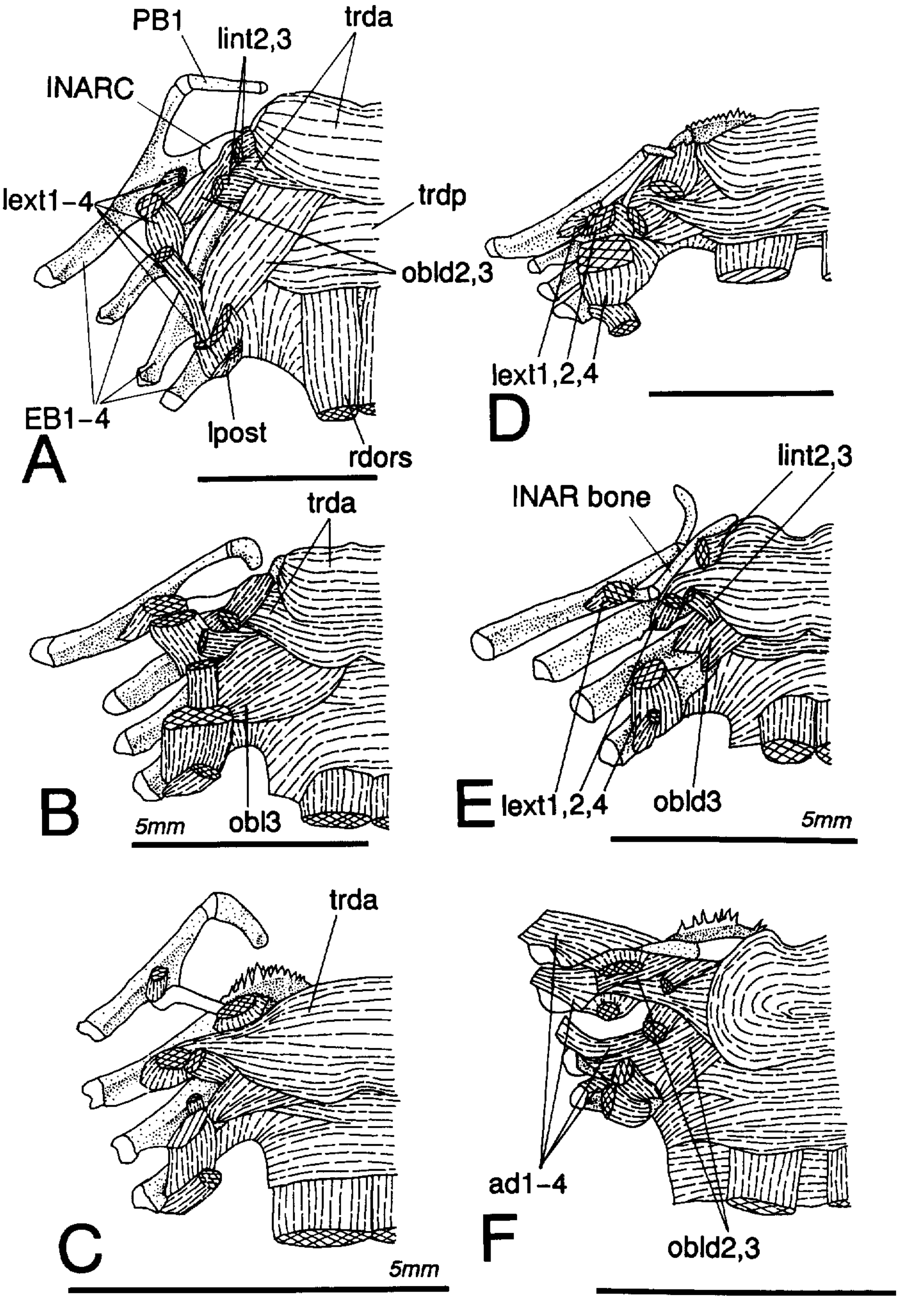

Fig. 10. Dorsal view of left side of dorsal branchial arch muscles: A, *Ectreposebastes imus*; B, *Ocosia fasciata*; C, *Centropogon australis*; D, *Erosa erosa*; E, *Erisphex potti*; F, *Zanclorhynchus spinifer*.

(Fig. 10E).

Obliquus posterior (oblp): The obliquus posterior is a small muscle, connecting the posterodorsal tip of the lower pharyngeal to the posteromedial face of epibranchial 4. This muscle lies medially to adductores 4 and 5, its fibers running parallel to those of the

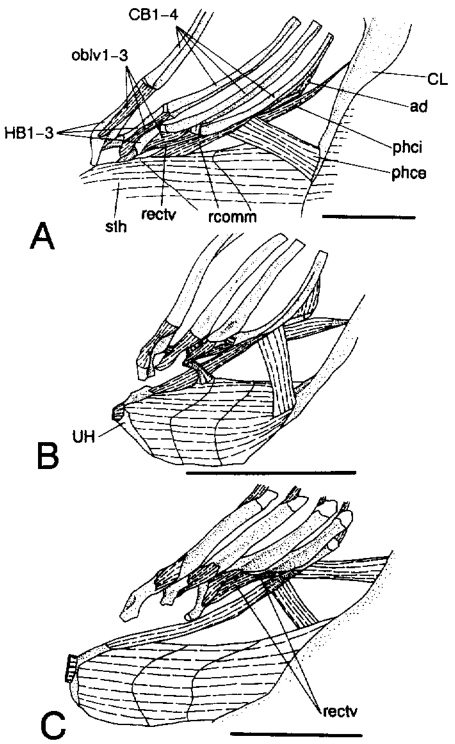

Fig. 11. Left lateral view of ventral branchial arch muscles: A, *Scorpaenodes kelloggi*; B, *Choridactylus multibarbus*; C, *Alertichthys blacki*.

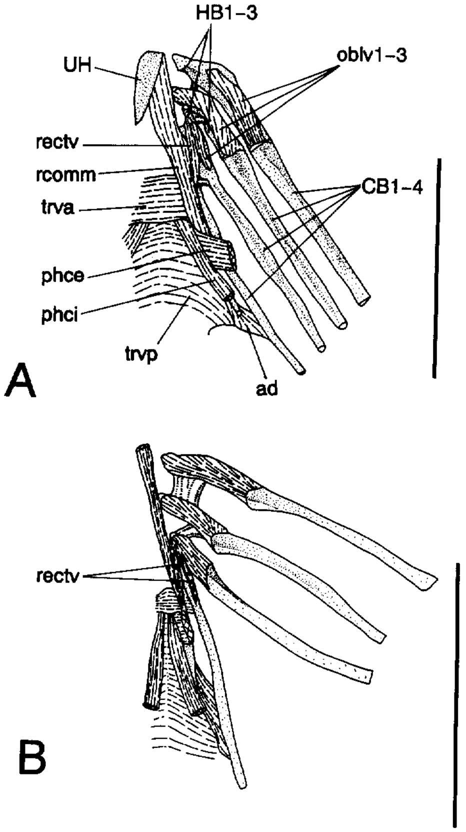

Fig. 12. Dorsal view of left side of ventral branchial arch muscles: A, *Scorpaenodes kelloggi*; B, *Taenianotus triacanthus*.

sphincter oesophagi.

Adductor (ad): The adductores interconnect the epibranchial and ceratobranchial or the ceratobranchial and lower pharyngeal. In most scorpaenoids (group 16-0), the adductores are composed of two muscles, adductor 4, interconnecting the medial face of epibranchial 4 and the posterodorsal tip of ceratobranchial 4 medially to the connection of the obliquus posterior, and adductor 5, interconnecting the posterolateral face of ceratobranchial 4 and the posterodorsal tip of the lower pharyngeal (Figs. 11A-C, 12A, B); in congiopodids (group 16-1), adductores 1 to 5 are present, 4 and 5 being the same as in group 16-0, and 1, 2, and 3 running from the posterolateral margins of the corresponding epibranchials to those of the articulated ceratobranchials (Figs. 9B, 10F).

Transversus dorsalis: The transversi dorsales are composed of two large muscles, the transversus dorsalis anterior and posterior. The fibers run transversely.

The origin of the transversus dorsalis anterior (**trda**) is a mid-dorsal raphé below the posteroventral face of the parasphenoid. In sebastids except *Plectrogenium*, setarchids, neosebastids, scorpaenids, the tetrarogids *Neocentropogon, Ocosia, Hypodytes, Liocranium, Ablabys,* and *Richardsonichthys*, the synanceiids *Inimicus, Synanceia,* and *Erosa,* aploactinids, and pataecids (group 17-0), the insertion of the muscle is divided into two, one part usually being the anterodorsal tip of pharyngobranchial 2 or its complex with pharyngobranchial 3 and the upper pharyngeal, and the other being on the anterodorsal face of epibranchial 2 and sandwiched by levatores interni 2 and 3 (Fig. 10A, B, D, E); in the sebastid *Plectrogenium*, the apistid, the tetrarogids *Gymnapistes, Centropogon, Notesthes,* and *Paracentropogon*, the synanceiids *Choridactylus* and *Minous*, congiopodids, and the gnathanacanthid (group 17-1), the insertion is not branched, the latter part only being present (Fig. 10C, F).

The transversus dorsalis posterior (**trdp**) lies ventrally to the anterior part of obliquus dorsalis 3 and dorsally to the retractor dorsalis.

Retractor dorsalis (rdors): The retractor dorsalis connects the dorsal parts of the branchial arches to the vertebrae, the muscles of both sides lying closely parallel to each other. The muscle originates from the ventral face of the vertebrae, usually abdominal vertebrae 2 to 5, and is inserted on the dorsal faces of pharyngobranchial 3 and the upper pharyngeal or their complex.

The following five muscles serve the ventral parts of the branchial arches: the sphincter oesophagi, obliquus ventralis, transversus ventralis, rectus ventralis, and rectus communis.

Sphincter oesophagi (spho): The fibers of the sphincter oesophagi run around the oesophagus. The anterodorsal distinction of this muscle from the transversus dorsalis posterior was not clear.

Obliquus ventralis (oblv): The obliqui ventrales are composed of three muscles: obliqui ventrales 1, 2, and 3, originating from the anteroventral faces of hypobranchials 1-3, and being inserted on the anteroventral margins of the corresponding ceratobranchials.

Transversus ventralis: The transversi ventrales are composed of two muscles, the transversus ventralis anterior and posterior.

The transversus ventralis anterior (**trva**) spans the ventromedial face of ceratobranchial 4. This unpaired muscle lies dorsally to the rectus communis and ventrally to the origin of the pharyngocleithralis internus.

The transversus ventralis posterior (**trvp**) originates from the ventromedial face of the lower pharyngeal, the muscle lying dorsally to the pharyngocleithralis internus. The fibers run transversely, meeting on the midline raphé above the heart.

Rectus ventralis (rectv): The rectus ventralis lying between obliquus ventralis 3 and the rectus communis, originates from the anteroventral tip of hypobranchial 3, posterior to the origin of obliquus ventralis 3. In most scorpaenoids (group 18-0), the insertion of the rectus ventralis is on the anteroventral face of ceratobranchial 4 (Figs. 11A, B, 12A); in the scorpaenids *Brachypterois* and *Taenianotus*, the synanceiid *Inimicus*, and congiopodids (group 18-1), the insertion of the muscle is branched being on the anteroventral faces of

Table 3. Comparison of branchial arch muscles characters in scorpaenoids. Numerals in paraentheses correspond to group numbers.

Taxon	Levator externus 3	Levator posterior	Obliquus dorsalis 2	Obliquus dorsalis 3 and levator internus 3	Adductores 1 to 3	Transversus dorsalis insertion	Rectus ventralis insertion
Sebastidae except *Plectrogenium* Neosebastidae *Maxillicosta* Scorpaenidae except *Brachyterois* and *Taenianotus* Tetrarogidae *Neocentropogen* *Ocosia* *Hypodytes* *Ablabys*	present (12-0)	present (13-0)	absent (14-0)	obliquus dorsalis 3 lying posteriorly to levator internus 3 (15-0)	absent (16-0)	branched into two (17-0)	unbranched (18-0)
Setarchidae			present (14-1)				
Scorpaenidae *Brachypterois* *Taenianotus*			absent (14-0)				branched into two (18-1)
Apistidae				obliquus dorsalis 3 sandwiching levator internus 3 (15-1)		unbranched (17-1)	unbranched (18-0)
Sebastidae *Plectrogenium* Tetrarogidae *Gymnapistes* *Centropogon* *Notesthes* *Paracentropogon* Synanceiidae *Choridactylus* *Minous* Gnathanacanthidae				obliquus dorsalis 3 lying posteriorly to levator internus 3 (15-0)			
Neosebastidae *Neosebastes* Tetrarogidae *Liocranium* *Richardsonichthys* Synanceiidae *Synanceia* *Erosa*	absent (12-1)					branched into two (17-0)	
Synanceiidae *Inimicus*							branched into two (18-1)
Aploactinidae Pataecidae				obliquus dorsalis 3 sandwiching levator internus 3 (15-1)			unbranched (18-0)
Congiopodidae *Congiopodus* *Alertichthys*	present (12-0)	absent (13-1)		obliquus dorsalis 3 lying posteriorly to levator internus 3 (15-0)	present (16-1)	unbranched (17-1)	branched into two (18-1)
Congiopodidae *Zanclorhynchus*			present (14-1)				

ceratobranchial 4 and the lower pharyngeal (Figs. 11C, 12B).

Rectus communis (rcomm): The origin of the rectus communis is from the posterodorsolateral face of the urohyal. The tendinous insertion is on the posteroventral face of the lower pharyngeal.

4. MUSCLES BETWEEN THE PECTORAL GIRDLE, NEUROCRANIUM, HYOID ARCH, AND BRANCHIAL ARCHES (Figs. 9, 11, 13, 14; Table 4)

There are six muscles between the pectoral girdle, neurocranium, hyoid, and branchial arches: the sternohyoideus, pharyngocleithralis externus, pharyngocleithralis internus, protractor pectoralis, levator pectoralis, and sternobranchialis.

Sternohyoideus (sth): The sternohyoideus is a large muscle, connecting the hyoid arch, branchial arch, and pectoral girdle. In most scorpaenoids, it originates from the anteroventral face of the cleithrum and anterior face of the obliquus inferioris, forming a myocomma. In congiopodids, the origin of the sternohyoideus is restricted to the anteroventral face of the cleithrum. The relationship between the sternohyoideus and pharyngocleithralis externus is mentioned in the description of the latter muscle (groups 19-0, 1, and 2). The sternohyoideus is inserted on the posteroventral face of the urohyal. The muscle comprises three myomeres. A tendon connects the dorsal face of the first myocomma and the anteroventral tip of hypobranchial 3.

Pharyngocleithralis externus (phce): Although WINTERBOTTOM (1974a) used the name pharyngoclavicularis, the muscle connecting the cleithrum with the lower pharyngeal is better termed pharyngocleithralis, following the current name of the bony element from which it originates.

The plate-shaped pharyngocleithralis externus, originating from the anteroventral face of the cleithrum, connects the branchial arch with the pectoral girdle as does the pharyngocleithralis internus. In sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, and the gnathanacanthid (group 19-0), the origin is lateral to the origin of the sternohyoideus (Figs. 11A, 13A - E); in synanceiids, the congiopodid *Congiopodus*, aploactinids, and pataecids (group 19-1), the origin is sandwiched by the origin of the sternohyoideus (Figs. 11B, 14B); in the congiopodids *Alertichthys* and *Zanclorhynchus* (group 19-2), the origin is dorsomedial to that of the sternohyoideus. The insertion of the pharyngocleithralis externus is on the anteroventral face of the lower pharyngeal, dorsal to that of the pharyngocleithralis internus (Fig. 11C).

Pharyngocleithralis internus (phci): Like the pharyngocleithralis externus, the pharyngocleithralis internus connects the branchial arch with the pectoral girdle. Its origin is usually tendinous from the anterior face of the cleithrum, being dorsal to that of the pharyngocleithralis externus. In most scorpaenoids (group 20-0), the origin is simple (Figs. 11, 13, 14); in the setarchid *Ectreposebastes* (group 20-1), the origin is bifid, having dorsal and ventral elements. The insertion is on the anteroventral face of the lower pharyngeal, medial to that of the pharyngocleithralis externus, and is sandwiched by the transversi ventrales anterior and posterior.

Protractor pectoralis (prp): The fan-shaped protractor pectoralis, lying ventromedially to the levator pectoralis, connects the neurocranium with the pectoral girdle. Its origin is just posterior to that of the levator posterior, if the latter is present. The anterior fibers of the protractor pectoralis grade into the membranous tissue of the posterior wall of the branchial chamber medial to the cleithrum. The posterior fibers are attached to the anterior face of the dorsal part of the cleithrum.

Levator pectoralis (lpect): The levator pectoralis, lying dorsally to the protractor pectoralis, like the latter connects the neurocranium with the pectoral girdle. The insertion of the levator pectoralis is on the anterior face of the anterodorsal process of the cleithrum.

Table 4. Comparison of characters of muscles between the pectoral girdle, neurocranium, hyoid arch, and branchial arches in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Pharyngocleithralis externus origin	Pharyngocleithralis internus origin
Sebastidae Setarchidae *Setarches* *Lioscorpius* Neosebastidae Scorpaenidae Apistidae Tetraogidae Gnathanacanthidae	lateral to origin of sternohyoideus (19-0)	simple (20-0)
Setarchidae *Ectreposebastes*		bifid (20-1)
Synanceiidae Congiopodidae *Congiopodus* Aploactinidae Pataecidae	sandwiched by origin of sternohyoideus (19-1)	simple (20-0)
Congiopodidae *Alertichthys* *Zanclorhynchus*	dorsal to origin of sternohyoideus (19-2)	

5. MUSCLES SERVING THE PECTORAL FIN (Figs. 13, 14; Table 5)

The following eight muscles serve the pectoral fin: the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, arrector dorsalis, arrector radialis, and coracoradialis.

Abductor superficialis (abs): The abductor superficialis forms the superficial division of

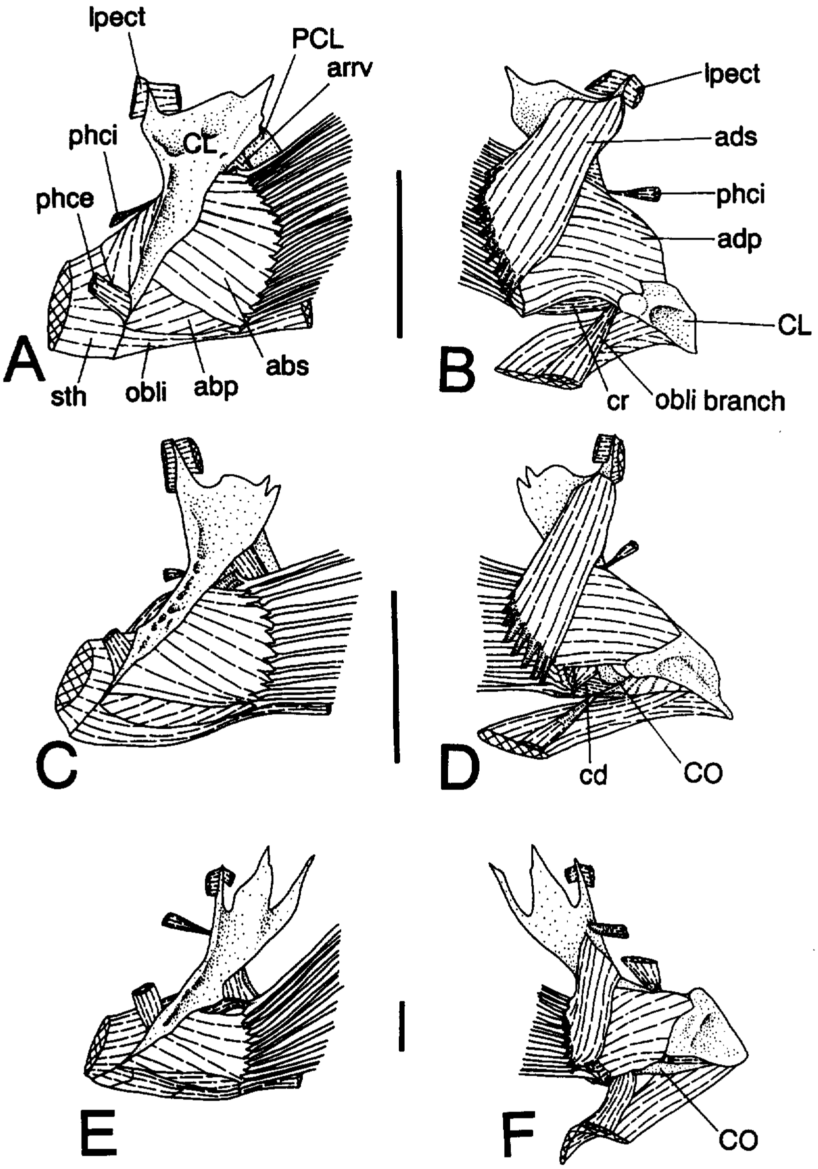

Fig. 13. Muscles of left pectoral girdle: A and B, *Scorpaenodes kelloggi*; C and D, *Hypodytes rubripinnis*; E and F, *Gnathanacanthus goetzeei*. A, C, and E, lateral view; B, D, and F, medial view.

the lateral muscle mass of the pectoral fin. The origin is from the posterolateral face of the cleithrum, and the tendinous insertions, on the dorsolateral base of the fin rays, except the uppermost.

Abductor profundus (abp): The abductor profundus forms the medial division of the lateral muscle mass of the pectoral fin. The origin is from the posterior face of the lateral flange of the cleithrum, and the lateral faces of the scapula, coracoid and, sometimes, radials. The muscle insertions are tendinous, being on the anterior bases of the fin rays, except the uppermost.

Arrector ventralis (arrv): The arrector ventralis, forming the anterodorsomedial division of the lateral muscle mass of the pectoral fin, lies medially to the abductor superficialis and anterodorsally to the abductor profundus. The origin of the arrector ventralis is from the posteroventral face of the posterior flange of the cleithrum, and its tendinous insertion on the anteromedial base of the medial half of the uppermost fin ray.

Adductor superficialis (ads): The adductor superficialis forms the dorsal and superficial divisions of the medial muscle mass of the pectoral fin. Its origin is from the dorsomedial face of the cleithrum and dorsolateral tip of the upper postcleithrum, and its tendinous insertions, on the anterodorsomedial face of the fin rays, some distance from their bases.

Adductor profundus (adp): The adductor profundus forms the medial division of the medial muscle mass of the pectoral fin, superficial to the adductor radialis, if the latter is present. The origin of the adductor profundus is from the ventromedial faces of the cleithrum and scapula, and the medial face of the coracoid. Its tendinous insertions are on the posteroventral flanges at the base of the fin rays except the uppermost.

Arrector dorsalis (arrd): Lying medially to the adductor superficialis and anterodorsally to the adductor profundus, the arrector dorsalis forms the anterodorsomedial division of the medial muscle mass of the pectoral fin. It originates from the anteromedial and often anterior face of the cleithrum, sometimes anteromedial face of the coracoid and scapula, and has tendinous insertion on the base of the medial half of the uppermost fin ray.

Adductor radialis (adr): The adductor radialis lies on the medial side of the pectoral girdle, medially to the adductor profundus. It originates from the medial faces of the lower three radials, and is inserted on the posteroventral flanges on the bases of the lower several fin rays, just medial to the insertions of the adductor profundus.

Coracoradialis (cr): The coracoradialis lies between the posteroventral margin of the coracoid and the proximal margin of the lowermost radial. Most scorpaenoids (group 21-0) have the coracoradialis (Figs. 13B, D, 14B, D); in the apistid and gnathanacanthid (group 21-1), a space is absent between the coracoid and lowermost radial, the coracoradialis

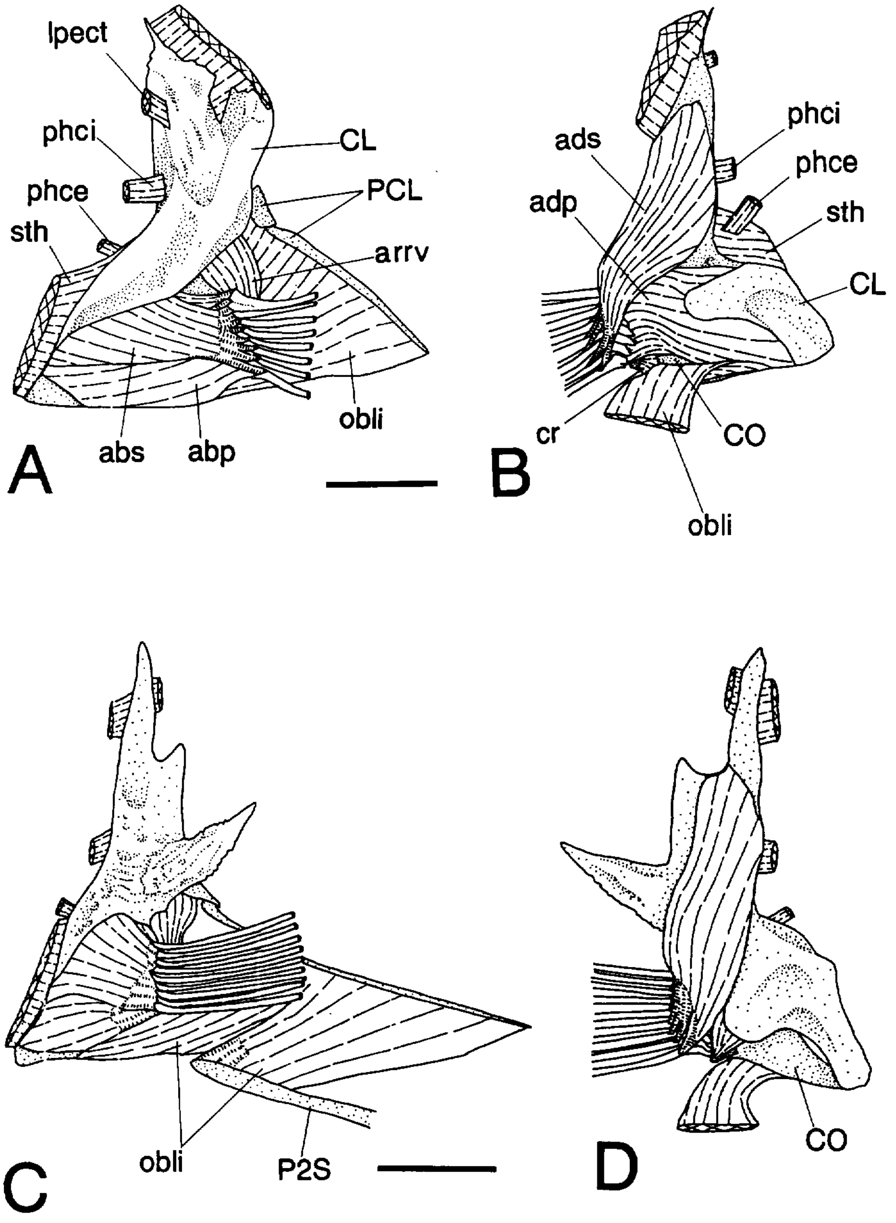

Fig. 14. Muscles of left pectoral girdle muscles: A and B, *Congiopodus coriaceus*; C and D, *Alertichthys blacki*. A and C, lateral view; B and D, medial view.

accordingly not developing (Fig. 13F). In sebastids, setarchids, neosebastids, and scorpaenids (group 22-0), the coracoradialis originates from the posteromedial face of the posterior process of the coracoid and is inserted on the ventromedial face of the lowermost radial (Fig. 13B). In tetrarogids, synanceiids, aploactinids, and pataecids (group

22-1), the origin includes the posteromedial face of the posterior process of the coracoid as in group 22-0, but the posterolateral face of the posteroventral process of the cleithrum is connected with the posteroventral process of the coracoid by a membrane, on which rather sparse fibers run from the cleithrum to the coracoradialis (Fig. 13D). The insertion is as in group 22-0. (Although group 21-1 lacks the coracoradialis, the above membrane is present (Fig. 13F)). In the congiopodids *Alertichthys* and *Zanclorhynchus* (group 22-2), the coracoradialis is short and remarkably developed between the lowermost radial and the posterolateral face of the cleithrum posteroventral process, and the posteroventral process of the coracoid (Fig. 14B). In the congiopodid *Congiopodus* (group 22-3), only a short coracoradialis is present (Fig. 14D).

Table 5. Comparison of pectoral fin muscle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Coracoradialis	Coracoradialis origin
Sebastidae Setarchidae Neosebastidae Scorpaenidae Congiopodidae *Congiopodus*	present (21-0)	posteromedial face of posterior process of coracoid (22-0)
Tetrarogidae Synanceiidae Aploactinidae Pataecidae		including cleithrum, sparse fibers present on membrane between cleithrum and coracoid (22-1)
Congiopodidae *Alertichthys* *Zanclorhynchus*		including cleithrum, developed fibers present between cleithrum and coracoid (22-2)
Apistidae Gnathanacanthidae	absent (21-1)	

6. MUSCLES SERVING THE PELVIC FIN (Fig. 15; Table 6)

The following seven muscles serve the pelvic fin: the abductor superficialis pelvicus, abductor profundus pelvicus, arrector ventralis pelvicus, adductor superficialis pelvicus, adductor profundus pelvicus, arrector dorsalis pelvicus, and extensor proprius. Pataecids do not have pelvic fin muscle elements.

Abductor superficialis pelvicus (absp): The abductor superficialis pelvicus lies ventrally to the abductor profundus pelvicus and arrector ventralis pelvicus, having originated from the ventromedial face of the pelvis. It is inserted tendinously on the bases of the pelvic fin spine and rays. Most scorpaenoids (group 23-0) have the abductor superficialis pelvicus (Fig. 15A, C, E, G);

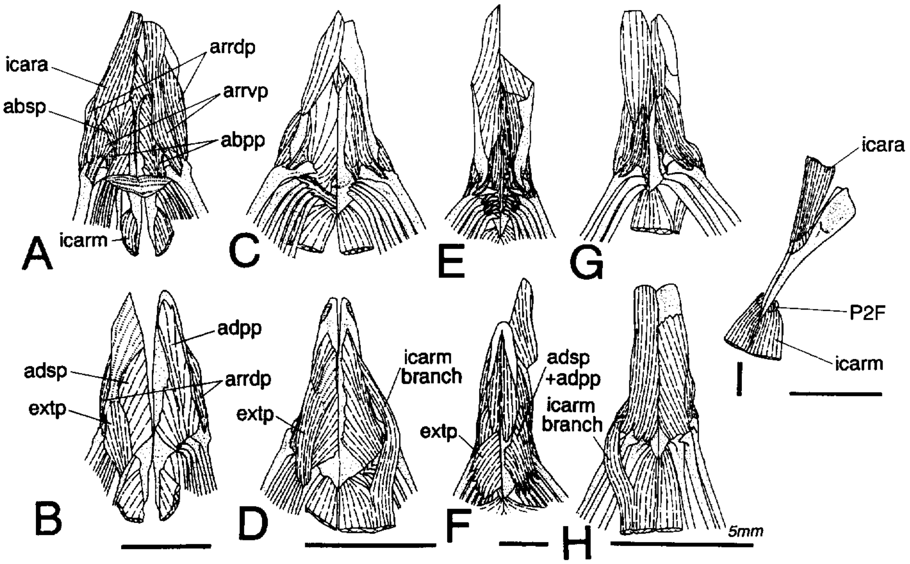

Fig. 15. Pelvic girdle muscles: A and B, *Setarches longimanus*; C and D, *Ocosia fasciata*; E and F, *Zanclorhynchus spinifer*; G and H, *Sthenopus mollis*; I, *Aetapcus vincenti*. A, C, E, and G, ventral view; B, D, F, and H, dorsal view; I, left posterolateral view.

pataecids (group 23-1) do not (Fig. 15I).

Abductor profundus pelvicus (abpp): The abductor profundus pelvicus lies medially to the abductor superficialis pelvicus, having originated from the ventral face of the pelvis. It is inserted tendinously on the bases of the pelvic fin rays. Most scorpaenoids (group 24-0) have the abductor profundus pelvicus (Fig. 15A, C, E, G); pataecids (group 24-1) do not (Fig. 15I).

Arrector ventralis pelvicus (arrvp): This muscle originates from the ventrolateral face of the pelvis and is inserted tendinously on the ventrolateral face of the base of the pelvic fin spine. Most scorpaenoids (group 25-0) have the arrector ventralis pelvicus (Fig. 15A, C, E, G); pataecids (group 25-1) do not (Fig. 15I).

Adductor superficialis pelvicus (adsp): This muscle originates from the dorsomedial face of the pelvis and is inserted on the bases of the pelvic fin spine and rays. Most scorpaenoids (group 26-0) have the adductor superficialis pelvicus (Fig. 15B, D, F, H); pataecids (group 26-1) do not (Fig. 15I). In most members of group 26-0 (group 27-0), the adductor superficialis pelvicus is separate from the adductor profundus pelvicus (Fig. 15B, D, H); in the congiopodids *Alertichthys* and *Zanclorhynchus* (group 27-1), the fibers of these muscle are united (Fig. 15F).

Adductor profundus pelvicus (adpp): The adductor profundus pelvicus, which lies ventrally to the adductor superficialis pelvicus, originates from the dorsal face of the pelvis and is inserted on the bases of the pelvic fin rays. Most scorpaenoids (group 28-0) have the adductor profundus pelvicus (Fig. 15B, D, F, H); pataecids (group 28-1) do not (Fig. 15I).

Arrector dorsalis pelvicus (arrdp): This muscle originates from the dorsolateral face of the pelvis and is inserted tendinously on the dorsolateral face of the base of the pelvic fin spine. Most scorpaenoids (group 29-0) have the arrector dorsalis pelvicus (Fig. 15B, D, F, H); pataecids (group 29-1) do not.

Extensor proprius (extp): The extensor proprius is the dorsalmost of the muscles serving the dorsal part of the pelvic fin. The muscle originates membranously from the pelvis, dorsally to the origin of the adductor superficialis pelvicus and is inserted on the base of the inner four rays of the pelvic fin and the pelvic fin spine. Most scorpaenoids (group 30-0) have the extensor proprius (Fig. 15B, D, F); aploactinids and pataecids (group 30-1) do not (Fig. 15H, 1).

Table 6. Comparison of pelvic fin muscle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Abductor superficialis pelvicus	Abductor profundus pelvicus	Arrector ventralis pelvicus	Adductor super-ficiails pelvicus	Adductor superficialis pelvicus and adductor profundus pelvicus	Adductor profundus pelvicus	Arrector dorsalis pelvicus	Extensor proprius
Sebastidae Setarchidae Neosebastidae Scorpaenidae Apistidae Tetrarodidae Synanceiidae Congiopodidae *Congiopodus* Gnathanacanthidae	present (23-0)	present (24-0)	present (25-0)	present (26-0)	separate (27-0)	present (28-0)	present (29-0)	present (30-0)
Congiopodidae *Alertichthys* *Zanclorhynchus*					united (27-1)			
Aploactinidae					separate (27-0)			absent (30-1)
Pataecidae	absent (23-1)	absent (24-1)	absent (25-1)	absent (26-1)	(both absent)	absent (28-1)	absent (29-1)	

7. MUSCLES OF THE DORSAL AND ANAL FINS (Figs. 16-18; Table 7)

The muscles of the dorsal fin are composed of three elements: the erector dorsalis, depressor dorsalis, and inclinator dorsalis. These paired muscles, which lie along the dorsal midline, support the dorsal fin rays.

Erector dorsalis (erecd): In tetrarogids, congiopodids, the gnathanacanthid, aploactinids, and pataecids, the dorsal fin is connected to the posterodorsal face of the neurocranium, the origin of the anterior erectores dorsales being from a more posterior position than that of the supported fin spines.

Depressor dorsalis (deprd): The origin is from the posterolateral face of the pterygiophore and the insertion, on the posterolateral base of the ray.

Inclinator dorsalis (incld): In sebastids, setarchids, the neosebastid *Neosebastes*,

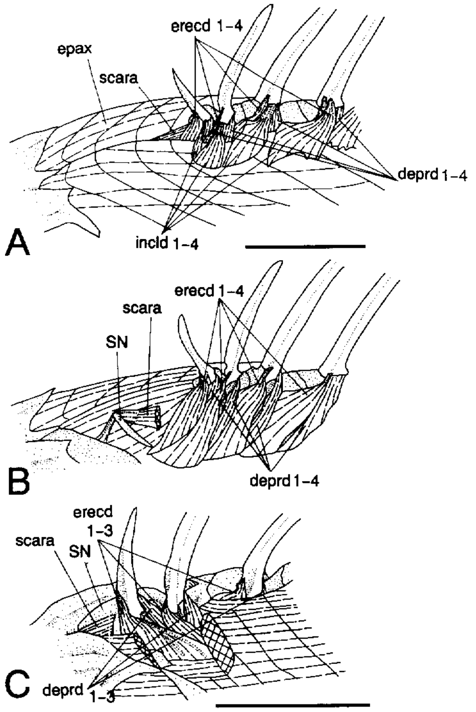

Fig. 16. Left dorsolateral view of anterior dorsal fin muscles: A and B, *Setarches longimanus*; C, *Gymnapistes marmoratus*. A, superficial muscles; B and C, deeper muscles.

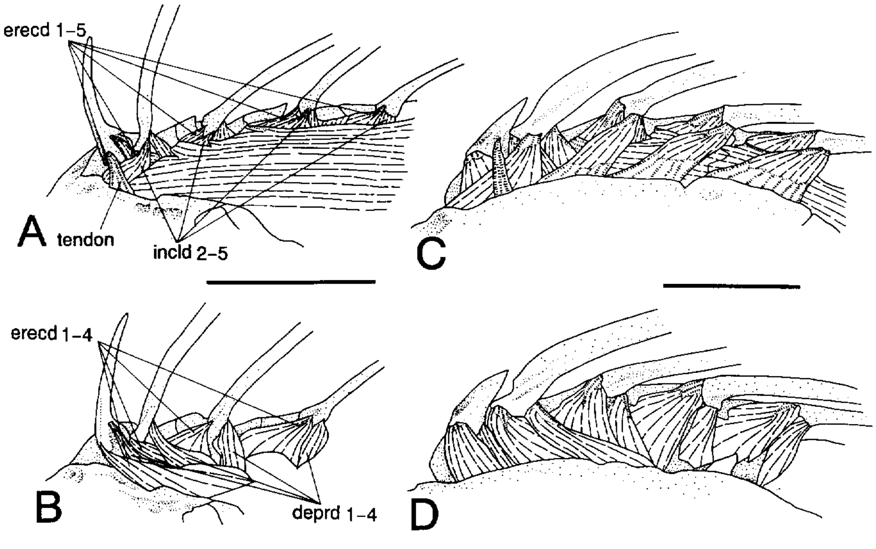

Fig. 17. Left lateral view of anterior dorsal fin muscles: A and B, *Hypodytes rubripinnis*; C and D, *Aetapcus vincenti*. A and C, superficial muscles; B and D, deeper muscles.

scorpaenids, the synanceiid *Minous*, the congiopodids *Congiopodus* and *Alertichthys*, and the gnathanacanthid (group 31-0), inclinator dorsalis 1 supporting dorsal spine 1 is present (Fig. 16A); in the neosebastid *Maxillicosta*, the apistid, tetrarogids, synanceiids except *Minous*, the congiopodid *Zanclorhynchus*, aploactinids, and pataecids (group 31-1), inclinator dorsalis 1 fibers are absent, with only a tendon remaining (Figs. 17A, C, 18A).

The muscles of the anal fin are composed of three elements: the erector analis, depressor

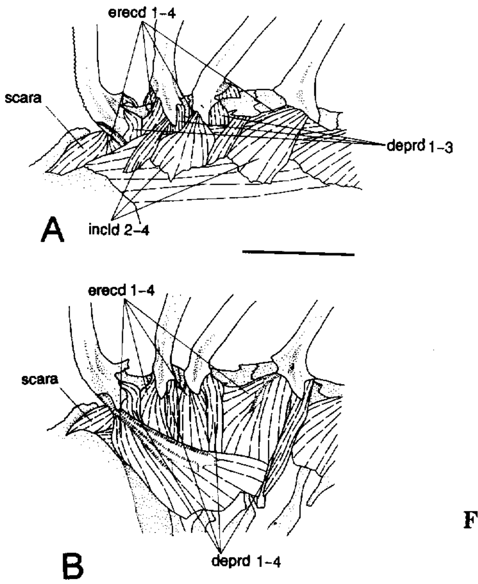

Fig. 18. Left lateral view of *Zanclorhynchus spinifer*. A, superficial muscles; B, deeper muscles.

Table 7. Comparison of dorsal fin muscle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Inclinator dorsalis 1 fibers
Sebastidae Setarchidae Neosebastidae *Neosebastes* Scorpaenidae Synanceiidae *Minous* Congiopodidae Gnathanacanthidae	normally developed (31-0)
Neosebastidae *Maxillicosta* Apistidae Tetraogidae Synanceiidae except *Minous* Aploactinidae Pataecidae	reduced (31-1)

analis, and inclinator analis. These paired muscles, which lie along the ventral midline, support the anal fin rays in much the same manner as the dorsal fin.

8. CARINAL MUSCLES (Figs. 15-18; Table 8)

The carinal muscles comprise five paired elements: the supracarinalis anterior, supracarinalis posterior, infracarinalis anterior, infracarinalis medius, and infracarinalis

Table 8. Comparison of carinal muscle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Supracarinalis anterior	Anterior limit of infracarinalis medius
Sebastidae Setarchidae Neosebastidae *Neosebastes* Scorpaenidae except *Ebosia*, *Brachypterois*, *Dendrochirus*, and *Parapterois* Apistidae Congiopodidae Gnathanacanthidae	present (32-0)	simple, on posterior process of pelvic girdle (33-0)
Neosebastidae *Maxillicosta* Scorpaenidae *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois* Tetrarogidae *Gymnapistes* *Centropogon* *Notesthes* *Neocentropogon* *Ocosia* Synanceiidae		branched, medial branch on posterior process of pelvic girdle, lateral branch on ventral face of base of pelvic girdle (33-1)
Tetrarogidae *Paracentropogon* *Hypodytes* *Liocranium* *Ablabys* *Richardsonichthys* Aploactinidae	absent (32-1)	
Pataecidae		simple, on posterior process of pelvic girdle (33-0)

posterior. The right and left elements of each muscle lie along the dorsal and ventral midlines, the fibers running parallel to each other.

Supracarinalis anterior (scara): This muscle connects the supraoccipital with the first proximal pterygiophore of the dorsal fin and sandwiches the supraneural, if present. Sebastids, setarchids, neosebastids, scorpaenids, the apistid, the tetrarogids *Gymnapistes, Centropogon, Notesthes, Neocentropogon,* and *Ocosia,* synanceiids, congiopodids, and the gnathanacanthid (group 32 - 0) have the supracarinalis anterior, (Figs. 16, 18); the tetrarogids *Paracentropogon, Hypodytes, Liocranium,* and *Ablabys,* aploactinids, and pataecids (group 32-1) do not have this muscle, owing to the direct articulation of the supraoccipital with the anterior proximal pterygiophores of the dorsal fin (Fig. 17).

Supracarinalis posterior (scarp): This muscle connects the dorsal stay with the distal tip of the last neural spine.

Infracarinalis anterior (icara): This muscle connects the posteroventral tip of the cleithrum with the anteroventral face of the pelvic girdle.

Infracarinalis medius (icarm): This muscle connects the pelvic girdle with the first proximal pterygiophore of the anal fin. In sebastids, setarchids, the neosebastid *Neosebastes,* scorpaenids except *Ebosia, Brachypterois, Dendrochirus,* and *Parapterois,* the apistid, congiopodids, the gnathanacanthid, and pataecids (group 33-0), the anterior limit of the muscle extends to the posterior process of the pelvic girdle (Fig. 15B, F); in the neosebastid *Maxillicosta,* the scorpaenids *Ebosia, Brachypterois, Dendrochirus,* and *Parapterois,* tetrarogids, synanceiids, and aploactinids (group 33-1), the anterior part of the muscle is divided, the medial branch extending to the pelvic girdle in group 33-0 and the lateral branch being attached to the ventral face of the base of the pelvic girdle or pelvic spine (Fig. 15D, H).

Infracarinalis posterior (icarp): This muscle connects the anal stay with the distal tip of the last hemal spine.

9. MUSCLES SERVING THE CAUDAL FIN (Figs. 19, 20; Table 9)

The following eight muscles serve the caudal fin: the interradialis, hypochordal longitudinalis, flexor dorsalis, flexor dorsalis superior, flexor ventralis, flexor ventralis inferior, flexor ventralis externus, and adductor dorsalis.

Interradialis (int): The interradialis is the posteriormost muscle, being composed of several muscle bundles interconnecting the principal caudal rays. The muscle bundle between the base of the uppermost ray of the lower lobe and the rays of the upper lobe lies superficially to the muscle bundle between the base of the lowermost ray of the upper lobe and the rays of the lower lobe.

Hypochordal longitudinalis (hl): The triangular hypochordal longitudinalis, which overlaps the posterior limit of the epaxialis, originates from the dorsolateral face of the lower hypural or its complex and is inserted tendinously on the dorsal bases of the upper three to five principal rays of the upper lobe.

Flexor dorsalis (fd): The flexor dorsalis, which is covered by the posterior part of the epaxialis, originates from the dorsolateral face of the centra of a few preural vertebrae, the urostyle, and upper hypurals or their complex, and is inserted on the bases of the principal rays of the upper lobe.

Flexor dorsalis superior (fds): The flexor dorsalis superior, which lies dorsally to the flexor dorsalis, originates from the neural spines of a few preural vertebrae and epurals, and is inserted on the bases of a few upper procurrent and principal rays of the upper lobe.

Flexor ventralis (fv): The flexor ventralis, which is covered by the posterior part of the hypaxialis, originates from the ventrolateral face of the centra of a few preural vertebrae, the urostyle, parhypural, and lower hypurals or their complex, and is inserted on the bases of the principal rays of the lower lobe.

Flexor ventralis inferior (fvi): The flexor ventralis inferior, which lies ventrally to the flexor ventralis, originates from the hemal spines of a few preural vertebrae and is inserted on the bases of a few lower procurrent and principal rays of the lower lobe.

Flexor ventralis externus (fve): In most scorpaenoids (group 34-0), the flexor ventralis

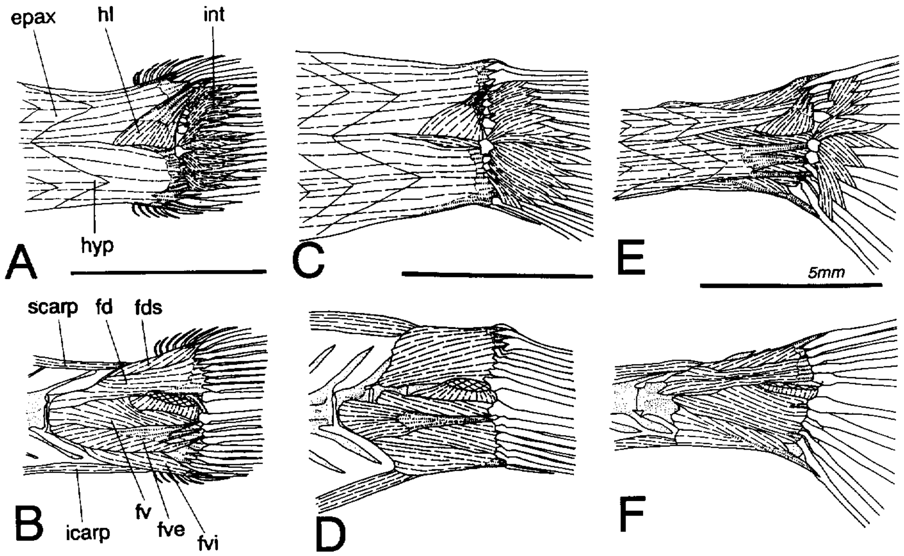

Fig. 19. Caudal muscles: A and B, *Lioscorpius longiceps*; C and D, *Choridactylus multibarbus*; E and F, *Pataecus fronts*. A, C, and E, superficial muscles; B, D, and F, deeper muscles.

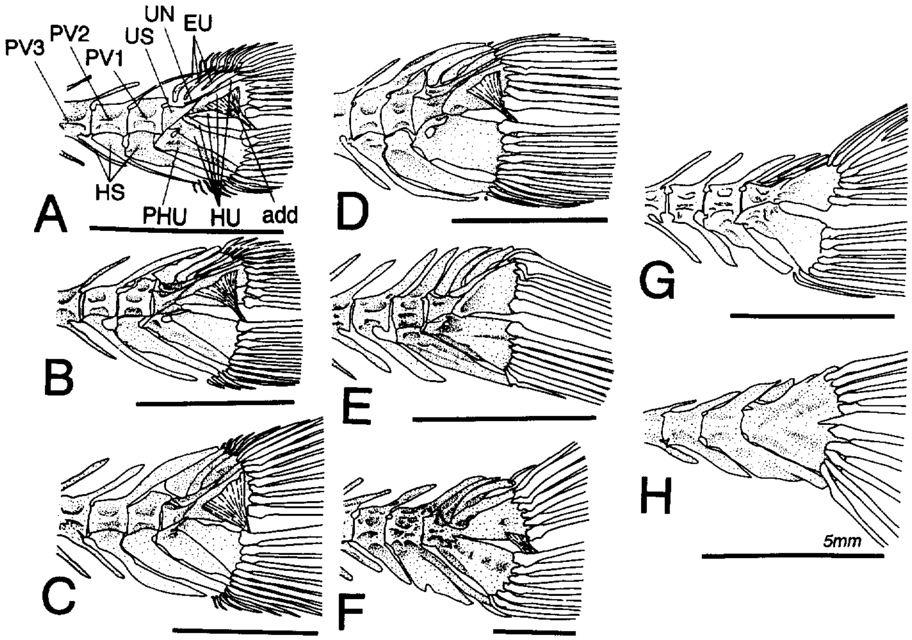

Fig. 20. Caudal skeletons and adductor dorsalis: A, *Lioscorpius longiceps*; B, *Hoplosebastes armatus*; C, *Iracundus signifer*; D, *Centropogon australis*; E, *Choridactylus multibarbus*; F, *Gnathanacanthus goetzeei*; G, *Erisphex potti*; H, *Pataecus fronts.*

Table 9. Comparison of caudal fin muscle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Flexor ventralis externus	Adductor dorsalis
Sebastidae Setarchidae Neosebastidae Scorpaenidae Apistidae Tetrarogidae Gnathanacanthidae	present (34-0)	present (35-0)
Synanceiidae *Inimicus* *Choridactylus* *Minous* Aploactinidae		absent (35-1)
Synanceiidae *Synanceia* *Erosa* Congiopodidae Pataecidae	absent (34-1)	

externus is present (Fig. 19B, D), overlying the flexor ventralis. The origin of the former is usually from the ventrolateral face of the centrum and hemal spine of preural vertebra 2, sometimes including the base of the hemal spine of preural vertebra 3. The insertions are tendinous on the bases of a few upper principal rays of the lower lobe. In the synanceiids *Synanceia* and *Erosa*, congiopodids, and pataecids (group 34-1), this muscle is absent (Fig. 19F).

Adductor dorsalis (add): In sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, and the gnathanacanthid (group 35-0), the adductor dorsalis is present (Fig. 20A-D). This triangular muscle, which lies medially to the flexor dorsalis, originates from the dorsolateral face of the upper hypurals or their complex and is inserted on the dorsal base of the uppermost principal ray of the lower lobe. In synanceiids, congiopodids, aploactinids, and pataecids (group 35-1), this muscle is absent (Fig. 20E-H).

10. BODY MUSCLES (Figs. 13, 14, 16-19, 21-24; Tables 10, 11)

The body muscles comprise two elements: the epaxialis and hypaxialis. The latter is subdivided into two entities: the obliquus superioris and obliquus inferioris. The lateralis superficialis is absent in scorpaenoids.

Epaxialis (epax): The epaxialis is the dorsal component of the body muscle above the horizontal septum.

Hypaxialis (hypax): The hypaxialis is the ventral component of the body muscle below the horizontal septum.

Obliquus superioris (obls): The obliquus superioris is that part of the hypaxialis with fibers running in an anterodorsal-posteroventral direction. The anterior part of the

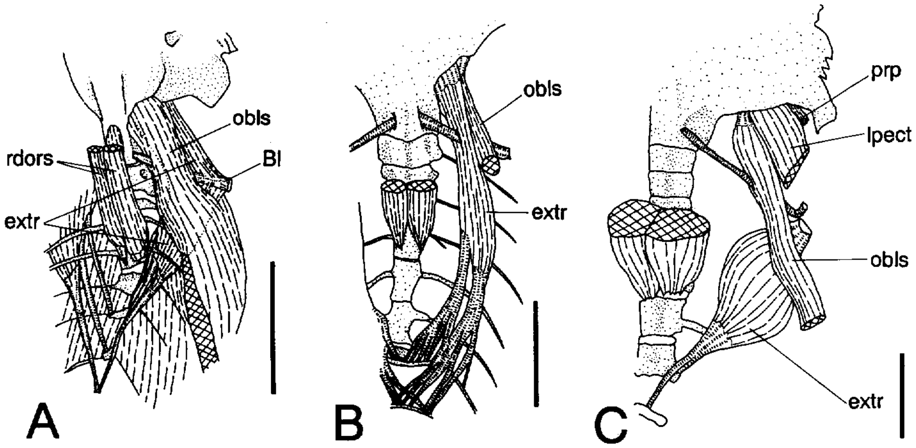

Fig. 21. Ventral view of roof of abdominal cavity: A, *Iracundus signifer*; B, *Ectreposebastes imus*; C, *Neosebastes pandus* (swimbladder removed).

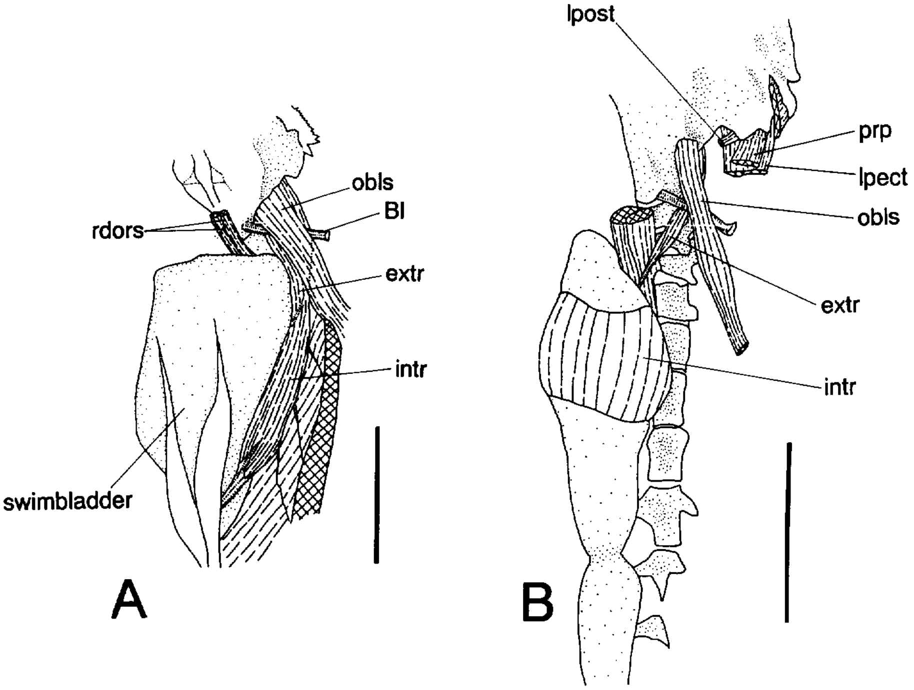

Fig. 22. Ventral view of swimbladder and associated muscles: A, *Brachypterois serrulatus*; B, *Apistus carinatus*.

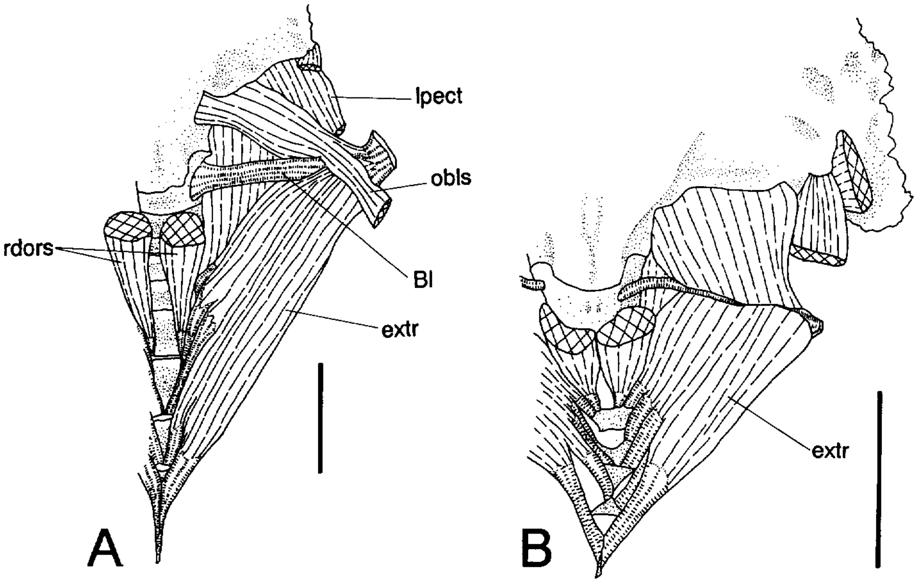

Fig. 23. Ventral view of roof of abdominal cavity: A, *Inimicus japonicus*; B, *Erosa erosa*.

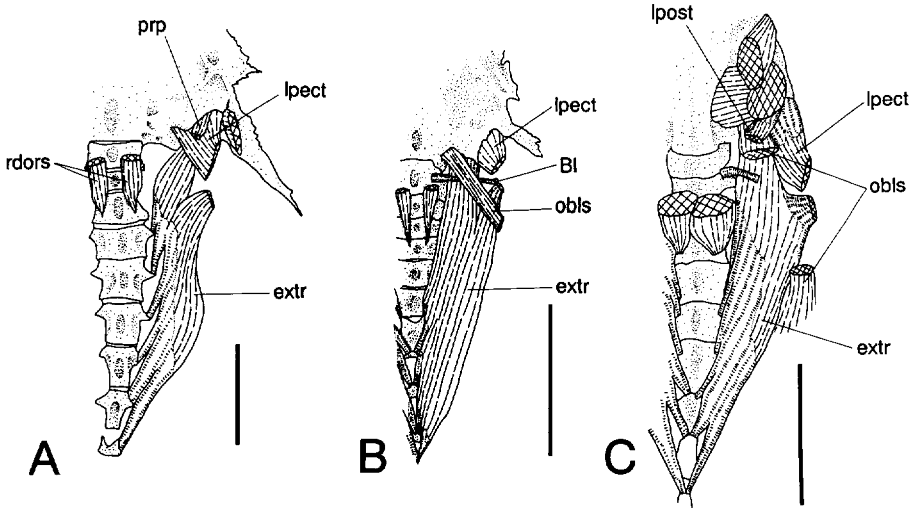

Fig. 24. Ventral view of roof of abdominal cavity: A, *Zanclorhynchus spinifer*; B, *Erisphex potti* (swimbladder removed); C, *Aetapcus vincenti* (swimbladder removed).

obliquus superioris forms the roof of the abdominal cavity. In sebastids, the setarchid *Setarches*, neosebastids, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus*, and *Scorpaenopsis*, and the tetrarogids *Centropogon, Notesthes*, and *Paracentropogon* (group 36-0), the obliquus superioris from the posterior face of the neurocranium is penetrated by Baudelot's ligament (Fig. 21A, C); in the setarchids *Lioscorpius* and *Ectreposebastes*, the scorpaenids *Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, the apistid, the tetrarogids *Gymnapistes, Neocentropogon, Ocosia, Hypodytes, Liocranium, Ablabys*, and *Richardsonichthys*, synanceiids, the gnathanacanthid, aploactinids, and pataecids (group 36-1), the obliquus superioris from the posterior face of the neurocranium lies ventrally to Baudelot's ligament (Figs. 21B, 22, 23, 24B, C). In most scorpaenoids (group 37-0), the obliquus superioris from the posterior face of the neurocranium is not connected with the supracleithrum (Figs. 21, 22, 24); in synanceiids except *Erosa* (group 37-1), fibers from the lateral part of the obliquus superioris from the posterior face of the neurocranium are connected with the medial face of the supracleithrum, together with Baudelot's ligament and the lateral branch of the extrinsic (Fig. 23A); in the synanceiid *Erosa* (group 37-2), all fibers of the obliquus superioris from the posterior face of the neurocranium are connected with the supracleithrum (Fig. 23B).

Obliquus inferioris (obli): The obliquus inferioris is that part of the hypaxialis with fibers running in an anteroventral-posterodorsal direction. Variations in the relationship between the obliquus inferioris and the pectoral girdle were observed in scorpaenoids. In

Table 10. Comparison of characters of obliquus superioris and muscles associated with swimbladder in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Obliquus superioris from posterior face of neurocranium and Baudelot's ligament		Swimbladder	Extrinsic and pleural rib	Each insertion of extrinsic	Extrinsic origin	Extrinsic and supracleithrum		Intrinsic	Intrinsic and extrinsic	Baudelot's ligament
Sebastidae *Sebastes* *Sebastiscus* *Hozukius* Setarchidae *Setarches* Scorpaenidae *Pontinus* *Phenacoscorpius*	penetrated by Baudelot's ligament (36-0)	not connected with supracleithrum (37-0)	present (41-0)	lying dorsally to several anterior pleural ribs (42-0)	simple (43-0)	includes neurocranium (44-0)	connected (45-0)	connected through Baudelot's ligament (46-0)	absent (47-0)		present (49-0)
Sebastidae *Helicolenus* *Adelosebastes* *Sebastolobus* *Trachyscorpia* *Plectrogenium* Neosebastidae *Maxillicosta* Scorpaenidae *Neomerinthe* *Parascorpaena* *Scorpaena* *Iracundus*			absent (41-1)								
Tetrarogidae *Paracentropogon*			present (41-0)	lying ventrally to several anterior pleural ribs (42-1)							
Neosebastidae *Neosebastes*						excludes neurocranium (44-1)					
Scorpaenidae *Scorpaenopsis* Tetrarogidae *Centropogon* *Notesthes*			absent (41-1)			includes neurocranium (44-0)					
Tetrarogidae *Gymnapistes* *Neocentropogon* *Hypodytes* *Ablabys* Gnathanacanthidae Pataecidae	bypassing and lying ventrally to Baudelot's ligament (36-1)		present (41-0)								
Scorpaenidae *Rhinopias* Tetrarogidae *Ocosia* *Richardsonichthys*			absent (41-1)								
Setarchidae *Ectreposebastes*					branched (43-1)						
Scorpaenidae *Taenianotus*					simple (43-0)	excludes neurocranium (44-1)					
Setarchidae *Lioscorpius*						includes neurocranium (44-0)	not connected (45-1)				
Scorpaenidae *Scorpaenodes* *Hoplosebastes* *Pterois* Tetrarogidae *Liocranium*			present (41-0)						present (47-1)	connected (48-0)	
Scorpaenidae *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois*			absent (41-1)								
Apistidae			present (41-0)							separate(48-1)	
Aploactinidae *Erisphex*							connected (45-0)	directly connected (46-1)	absent (47-0)		
Aploactinidae *Aploactis* *Sthenopus*			absent (41-1)								
Synanceiidae *Synanceia* *Choridactylus* *Minous*		fibers of lateral part connected with supracleithrum (37-1)	present (41-0)					connected through Baudelot's ligament (46-0)			
Synanceiidae *Inimicus*			absent (41-1)								
Synanceiidae *Erosa*		entirely connected with supracleithrum (37-2)									
Congiopodidae *Congiopodus* *Alertichthys*	(Baudelot's ligament absent)	not connected with supracleithrum (37-0)	present (41-0)					directly conncceted (46-1)			absent (49-1)
Congiopodidae *Zanclorhynclus*			absent (41-1)								

most scorpaenoids (group 38-0), a plate-shaped fiber bundle lying laterally to the main muscle fibers originates from the anterior margin of the ventral postcleithrum and is inserted on the posterolateral process of the coracoid just ventral to the coracoradialis (Fig. 13B, D, F). In pataecids, which lack postcleithra, such a plate-shaped fiber bundle of the obliquus inferioris is present, but in congiopodids (group 38-1), it is absent (Fig. 14B, D). Among group 38-0, insertion of the bundle is by broad muscle fibers in sebastids, setarchids, the neosebastid *Neosebastes*, scorpaenids except *Rhinopias* and *Taenianotus*, and the gnathanacanthid (group 39-0) (Fig. 13B, F); it is tendinous in the neosebastid *Maxillicosta*, the scorpaenids *Rhinopias* and *Taenianotus*, the apistid, tetrarogids, synanceiids, aploactinids, and pataecids (group 39-1) (Fig. 13D). In most scorpaenoids (group 40-0), the anteroventral limit of the main part of the obliquus inferioris is on the posteroventral face of the cleithrum, ventral to the abductor profundus (Fig. 13B, D, F); in the congiopodid *Congiopodus* (group 40-1), the anteroventral limit of the muscle is on the

Table 11. Comparison of obliquus inferioris muscle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxion	Plate-shaped element of obliquus inferious between ventral postcleithrum and coracoid		Anteroventral limit of obliquus inferioris
Sebastidae Setrachidae Neosebastidae *Neosebastes* Scorpaenidae except *Rhinopias* and *Taenianotus* Gnathanacanthidae	present (38-0)	insertion by rather broad muscle fibers (39-0)	posteroventral face of cleithrum ventral to abductor profundus (40-0)
Neosebastidae *Maxillicosta* Scorpaenidae *Rhinopias* *Taenianotus* Apisitidae Tetrarogidae Synanceiidae Aploactinidae Pataecidae		insertion tendinous (39-1)	
Congiopodidae *Congiopodus*	absent (38-1)		ventrolateral face of anteroventral arm of coracoid (40-1)
Congiopodidae *Alertichthys* *Zanclorhynchus*			branched, one branch connected to coracoid and adductor profundus, the other to pelvis (40-2)

ventrolateral face of the anteroventral arm of the coracoid (Fig. 14B); in the congiopodids *Alertichthys* and *Zanclorhynchus* (group 40-2), the anteroventral part of the muscle is divided, one branch being connected with the ventrolateral margin of the anteroventral arm of the coracoid and the ventral face of the adductor profundus, and the other with the pelvis (Fig. 14C).

11. SWIMBLADDER AND ASSOCIATED MUSCLES (Figs. 21-23; Table 10)

Swimbladder: Although not a muscular organ itself, the swimbladder is closely associated with the extrinsic and intrinsic, which show structural variations among scorpaenoids. Accordingly, the presence or absence of the swimbladder is noted here. In the sebastids *Sebastes, Sebastiscus*, and *Hozukius*, the setarchid *Setarches*, the neosebastid *Neosebastes*, the scorpaenids *Pontinus, Phenacoscorpius, Scorpaenodes, Hoplosebastes*, and *Pterois*, the apistid, the tetrarogids *Gymnapistes, Neocentropogon, Paracentropogon, Hypodytes, Liocranium*, and *Ablabys*, the synanceiids *Synanceia, Choridactylus*, and *Minous*, the congiopodids *Congiopodus* and *Alertichthys*, the gnathanacanthid, the aploactinid *Erisphex*, and pataecids (group 41 - 0), the swimbladder is present; in the sebastids *Helicolenus, Adelosebastes, Sebastolobus, Trachyscorpia*, and *Plectrogenium*, the setarchids *Lioscorpius* and *Ectreposebastes*, the neosebastid *Maxillicosta*, the scorpaenids *Neomerinthe, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, the tetrarogids *Centropogon, Notesthes, Ocosia*, and *Richardsonichthys*, the synanceiids *Inimicus* and *Erosa*, the congiopodid *Zanclorhynchus*, and the aploactinids *Aploactis* and *Sthenopus* (group 41 - 1), the swimbladder is absent.

Extrinsic (extr): In sebastids, the setarchid Setarches, the neosebastid *Maxillicosta*, and the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena*, and *Iracundus* (group 42-0), the muscle fibers of the extrinsic lie dorsally to several anterior pleural ribs (Fig. 21A); in the setarchids *Lioscorpius* and *Ectreposebastes*, the neosebastid *Neosebastes*, the scorpaenids *Scorpaenopsis, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, the apistid, tetrarogids, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 42-1), the muscle fibers of the extrinsic lie ventrally to the pleural ribs (Figs. 21B, C, 22 - 24). In most scorpaenoids (group 43 - 0), the insertion of the muscle on the swimbladder or on the vertebral parapophyses is simple (Figs. 21A, C, 22 - 24); in the setarchid *Ectreposebastes* (group 43 - 1), the insertion on the vertebral parapophyses is branched (Fig. 21B). This variation parallels the origin of the pharyngocleithralis internus (groups 20-0 and 20-1). In most scorpaenoids (group 44-0), the origin of the extrinsic is from the occipital face of the neurocranium and, often, the supracleithrum (Figs. 21A, B, 22-24); in the neosebastid *Neosebastes* and the scorpaenid *Taenianotus* (group 44-1), the origin is only from the medial face of the supracleithrum (Fig. 21C). In sebastids, the setarchids *Setarches* and *Ectreposebastes*, neosebastids, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Scorpaenopsis, Iracundus, Rhinopias*, and *Taenianotus*, tetrarogids except *Liocranium*, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 45-0), the extrinsic is connected with the supracleithrum (Figs. 21, 23, 24); in the setarchid *Lioscorpius*, the scorpaenids *Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus*, and *Parapterois*, the apistid, and the tetrarogid *Liocranium* (group 45-1), the simple extrinsic is not connected with the supracleithrum (Fig. 22). Among group 45-0, the extrinsic is connected with the supracleithrum through Baudelot's ligament in sebastids, the setarchids *Setarches* and *Ectreposebastes*, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Scorpaenopsis, Iracundus, Rhinopias*, and *Taenianotus*, tetrarogids except *Liocranium*, synanceiids, the gnathanacanthid, and pataecids (group 46-0) (Figs. 21A, B, 23, 24C); the extrinsic is directly connected with the supracleithrum in neosebastids, congiopodids, and aploactinids (group 46-1) (Figs. 21C, 24A, B).

Intrinsic (intr): The origin and insertion of the intrinsic are on the swimbladder. In sebastids, setarchids, neosebastids, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Scorpaenopsis, Iracundus, Rhinopias*, and *Taenianotus*, tetrarogids except *Liocranium*, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 47-0), the intrinsic is absent (Figs. 21, 23, 24); in the scorpaenids *Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus*, and *Parapterois*, the apistid, and the tetrarogid *Liocranium* (group 47-1), the intrinsic is present (Fig. 22); in most of group 47-1 (group 48-0), the intrinsic is connected with the extrinsic (Fig. 22A); in the apistid (group 48-1), the intrinsic and extrinsic are not connected (Fig. 22B).

Baudelot's ligament: Baudelot's ligament connects the posterolateral face of the basioccipital or lateral face of the first or second vertebral centrum with the medial face of the supracleithrum. Most scorpaenoids (group 49-0) have Baudelot's ligament (Figs. 21-23, 24B, C); congiopodids (group 49-1) do not (Figs. 24A).

III. OSTEOLOGY

1. NEUROCRANIUM (Figs. 25-28; Table 12)

The neurocranium of scorpaenoids is generally robust, often bearing ridges, spines, and grooves on the dorsal surface. It comprises the following 17 bony elements: the ethmoid, lateral ethmoid, prevomer, pterosphenoid, basisphenoid, frontal, sphenotic, pterotic, epiotic, prootic, exoccipital, supraoccipital, parietal, intercalar, supratemporal, basisphenoid, and parasphenoid.

Ethmoid (E): The ethmoid is an unpaired bone in the anterodorsal part of the neurocranium, overlying the ethmoid cartilage and articulating with the lateral ethmoid laterally and the frontal posteriorly. The relationships between the ethmoid, parasphenoid, lateral ethmoid, and prevomer are noted in the description of the lateral ethmoid.

Lateral ethmoid (LE): The lateral ethmoid, a paired bone lying on the posterolateral side of the ethmoid and pierced by an olfactory nerve, form the anterodorsal margin of the orbit. The dorsolateral margin often bears a preorbital spine. This bone articulates with the ethmoid anteromedially and the frontal posterodorsally. In sebastids, setarchids, neosebastids, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Scorpaenodes*, and *Hoplosebastes*, the apistid, tetrarogids, synanceiids, the gnathanacanthid, and the aploactinids *Aploactis* and *Erisphex* (group 50-0), the lateral ethmoid articulates directly with the prevomer anteroventrally, thus separating the ethmoid and parasphenoid (Fig. 25), although in the sebastids *Sebastolobus* and *Trachyscorpia*, cartilage fills the narrow space between the lateral ethmoid and prevomer; in the scorpaenids *Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, congiopodids, the aploactinid *Sthenopus*, and pataecids (group 50-1), the lateral ethmoid is separated from the prevomer by the articulation of the ethmoid and parasphenoid, or a large mass of cartilage (Fig. 26-28).

Prevomer (PV): The prevomer, an unpaired bone lying in the anteriormost region of the neurocranium, forms the anterior end of the roof of the oral cavity, being adjacent to the premaxilla anteriorly. In sebastids, setarchids, neosebastids, scorpaenids except *Taenianotus*, the apistid, tetrarogids, the synanceiids *Inimicus, Erosa*, and *Minous*, the congiopodid *Zanclorhynchus*, aploactinids, and the pataecids *Pataecus* and *Neopataecus* (group 51-0), a villiform tooth band is present on the prevomer (Figs. 25, 27); in the scorpaenid *Taenianotus*, the synanceiids *Synanceia* and *Choridactylus*, the congiopodids *Congiopodus* and *Alertichthys*, the gnathanacanthid, and the pataecid *Aetapcus* (group 51-1), prevomerine teeth are absent (Figs. 26, 28). The prevomer articulates with the ethmoid

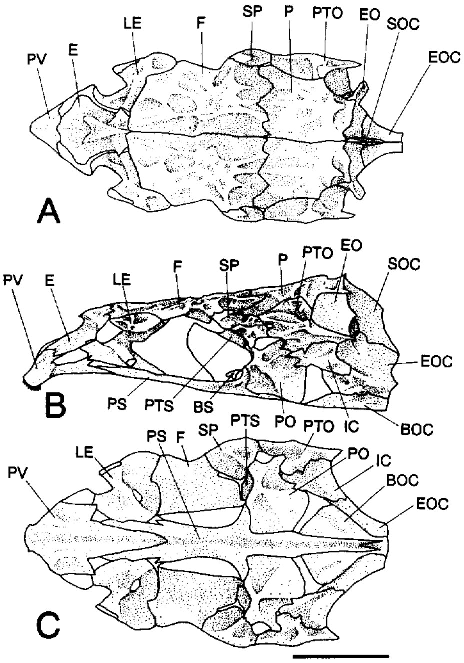

Fig. 25. Neurocranium of *Ectreposebastes imus*. A, dorsal view; B, left lateral view; C, ventral view.

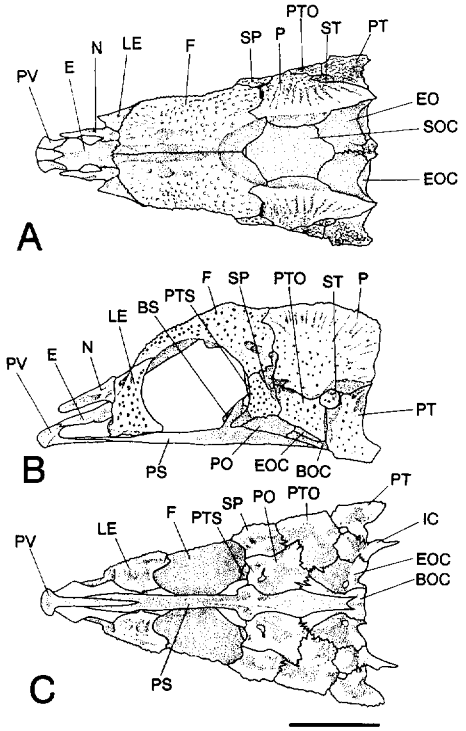

Fig. 26. Neurocranium of *Congiopodus coriaceus*. A, dorsal view; B, left lateral view; C, ventral view.

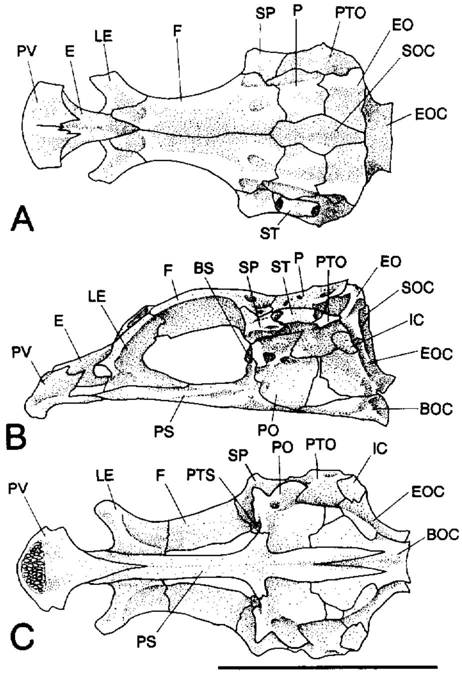

Fig. 27. Neurocranium of *Sthenopus mollis*. A, dorsal view; B, left lateral view; C, ventral view.

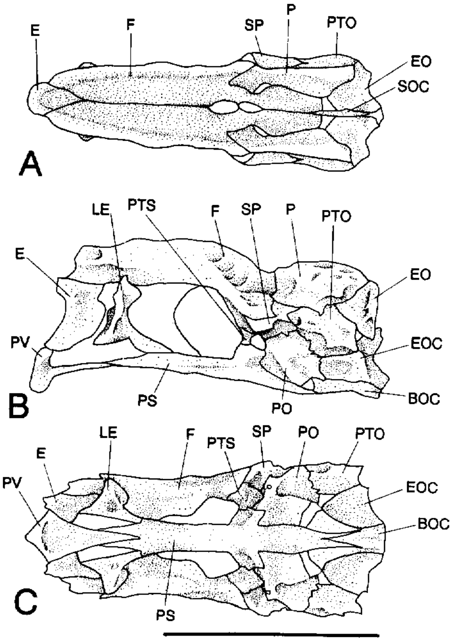

Fig. 28. Neurocranium of *Pataecus fronts*. A, dorsal view; B, left lateral view; C, ventral view.

posterodorsally and the parasphenoid posteriorly. The relationship between the prevomer and lateral ethmoid is noted in the description of the lateral ethmoid.

Pterosphenoid (PTS): The pterosphenoid, a paired, plate-shaped bone associated with the frontal, sphenotics, and prootics, forms the posteroventral face of the orbit.

Basisphenoid (BS): The basisphenoid is a very small, unpaired bone lying at the posteroventral end of the orbit. It is present in most scorpaenoids, including *Setarches* (group 52-0), this bone is present (Figs. 25-27); in the congiopodids *Alertichthys* and *Zanclorhynchus* and pataecids (group 52-1), it is absent (Fig. 28). From an examination of Japanese scorpaenoids that are here included in group 52-1, Matsubara (1943, 1955) stated that the basisphenoid was entirely absent in *Setarches*, but always present in the other scorpaenoids. The conclusion of Eschmeyer and Collette (1966) and Eschmeyer (1984) that the basisphenoid exists in *Setarches* is verified here.

Frontal (F): The frontals, paired bones over the orbit forming the middle roof the neurocranium, articulate dorsomedially, forming a concave, flat or convex interorbital region. The posterolateral edge of the frontal often bears supraorbital, postorbital, and tympanic spines. The frontal articulates with the ethmoid anteromedially, the lateral ethmoid anterolaterally, the sphenotic posterolaterally, the pterosphenoid posteroventrally, the parietal posteriorly, and the supraoccipital posteromedially. The suture between the frontal and supraoccipital is often overlapped by the parietal.

Sphenotic (SP): The sphenotics are paired bones forming the posterolateral processes of the orbit. On the upper part of this bone, a dermosphenotic (DS) is often present (group 56-0) (Fig. 1 A, C). The sphenotic articulates with the frontal dorsomedially, the pterosphenoid anteroventrally, the prootic ventrally, and the pterotic posteriorly.

Pterotic (PTO): The pterotics, paired bones forming the posterolateral face of the neurocranium, bear a spine on the posterolateral margin. Articulation is with the sphenotic anteriorly, the parietal anterodorsally, the epiotic posterodorsally, the prootic anteroventrally, the intercalar, if present, posteroventrally, and the supraoccipital posteriorly. The pterotic and sphenotic form a longitudinal groove articulating with the dorsal margin of the hyomandibular. The relationships between the pterotic, exoccipital, prootic, and intercalar are noted in the description of intercalar.

Epiotic (EO): The epiotic, a paired bone forming the posterodorsal part of the neurocranium, articulates with the supraoccipital dorsally, the parietal anterodorsally, the pterotic anteroventrally, and the exoccipital ventrally. In most scorpaenoids (group 53-0), the epiotics do not meet in the midline, owing to the intervening articulation of the supraoccipital and exoccipital (Figs. 25, 27, 28); in congiopodids (group 53-1), the epiotics meet in the midline, thus separating the supraoccipital and exoccipital (Fig. 26).

Prootic (PO): The prootic, a paired bone forming the otic capsule base, articulates with the pterosphenoid anteriorly, the sphenotic anterodorsally, the pterotic dorsally, the exoccipital posteriorly, the basioccipital posteroventrally, and the parasphenoid ventrally. The relationships between the prootic, pterotic, exoccipital, and intercalar are noted in the description of the intercalar.

Exoccipital (EOC): The exoccipital, a paired bone surrounding the foramen magnum, articulates with the epiotic anterodorsally, pterotic, intercalar, and prootic anteriorly, and the basioccipital ventrally. The exoccipitals and basioccipital together form a condyle for articulation with the first vertebra. The relationship between the exoccipital, supraoccipital, and epiotic are noted in the description of the epiotic, and those between the exoccipital, prootic, pterotic, and intercalar, in the description of the intercalar.

Supraoccipital (SOC): The supraoccipital, an unpaired bone forming the posterior roof of the neurocranium, articulates laterally with the parietals, posterolaterally with the epiotics, and often, anteriorly with the frontals. The relationships between the supraoccipital, exoccipital, and epiotic are noted in the description of the epiotic.

Parietal (P): The parietal, a paired bone forming the posterior roof of the neurocranium, usually forms the parietal ridge bearing parietal and nuchal spines. It articulates with the frontal anteriorly, the pterotic ventrally, the epiotic posteroventrally, and the supraoccipital both medially and posteriorly. The parietals sometimes overlap the anterior surface of the supraoccipital and interdigitate with each other, such a variation being intraspecific, as MATSUBARA (1936: 90, 1943: 75) noted.

Intercalar (IC): The relationships of the intercalar, a paired bone lying on the posterolateral face of the neurocranium, with surrounding bones are variable within scorpaenoids. The intercalar articulates with the exoccipital posteriorly and posteroventrally. In most scorpaenids (group 54-0), it meets the pterotic dorsally and the prootic posteriorly, between the pterotic and exoccipital (Fig. 25); in congiopodids and aploactinids (group 54-1), the intercalar is small, occupying a more posterior position, where it articulates anteriorly with the posterior margin of the pterotic, but is separated from the prootic by the articulation of the pterotic and exoccipital (Figs. 26, 27); in pataecids (group 54-2), the intercalar is absent (Fig. 28).

Supratemporal (ST): The supratemporal, a paired tubular bone lying over the pterotic, forms a part of the sensory canal. It articulates posteriorly with the posttemporal.

Basioccipital (BOC): The basioccipital, an unpaired bone forming the posterior base of the neurocranium, articulates with the prootic anteriorly, the parasphenoid anteroventrally, and the exoccipital dorsally. The basioccipital and exoccipitals together form a condyle for articulation with the first vertebra.

Table 12. Comparison of neurocranial characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Lateral ethmoid and prevomer	Prevomerine teeth	Basisphenoid	Epiotics of both sides	Intercalar and prootic
Sebastidae Setarchidae Neosebastidae Scorpaenidae *Pontinus* *Neomerinthe* *Phenacoscorpius* *Parascorpaena* *Scorpaena* *Iracundus* *Scorpaenopsis* *Scorpaenodes* *Hoplosebastes* Apistidae Tetrarogidae Synanceiidae *Inimicus* *Erosa* *Minous*	meet (50-0)	present (51-0)	present (52-0)	separate (53-0)	meet (54-0)
Scorpaenidae *Pterois* *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois* *Rhinopias*	separate (50-1)				
Scorpaenidae *Taenianotus*		absent (51-1)			
Synanceiidae *Synanceia* *Choridactylus* Gnathanacanthidae	meet (50-0)				
Aploactinidae *Aploactis*		present (51-0)			separate (54-1)
Aploactinidae *Erisphex*					
Aploactinidae *Sthenopus*	separate (50-1)				
Congiopodidae *Cogiopodus*		absent (51-1)		meet (53-1)	
Congiopodidae *Zanclorhynchus*		present (51-0)	absent (52-1)		
Congiopodidae *Alertichthys*		absent (51-1)			
Pataecidae *Pataecus* *Neopataecus*		present (51-0)		separate (53-0)	intercalar is absent (54-2)
Pataecidae *Aetapcus*		absent (51-1)			

Parasphenoid (PS): The parasphenoid is an unpaired, longitudinally elongate bone along the ventral midline below the orbit. The relationship between the parasphenoid, ethmoid, prevomer, and lateral ethmoid is noted in the description of the lateral ethmoid.

2. NASAL AND CIRCUMORBITAL BONES (Figs. 1-3, 24-27; Table 13)

Nasal (N): The nasal, a paired bone lying obliquely on the anterodorsal face of the ethmoid cartilage, is in contact posteriorly with the ethmoid. It often bears a spine.

The circumorbital bones comprise the lachrymal, corresponding to infraorbital 1, infraorbitals 2 to 5, and the dermosphenotic, corresponding to infraorbital 6. These tubular or grooved bones are penetrated by the circumorbital sensory canal associated with the pterotic-supratemporal-posttemporal sensory canal.

Lachrymal (L): The lachrymal is a plate-shaped bone lying anteriorly over the maxillary on the lateral part of the snout. It meets infraorbital 2 posteriorly, and articulates with the lateral ethmoid dorsally and the anterior process of the palatine medially.

Infraorbitals (IO) 2 to 5: Infraorbital 2 is a plate-shaped bone between the lachrymal and the similarly-shaped infraorbital 3. The infraorbital stay is defined as the posterior extension of infraorbital 3 toward the preopercle. In most scorpaenoids (group 55-0), the infraorbital stay is typically formed and may or may not be articulated with the preopercle (Figs. 1A, 1C, 2A, 3A). In pataecids (group 55-1), the infraorbitals are tubular and lack an infraorbital stay (Fig. 3C). Infraorbitals 4 and 5 are posterior to the orbit between infraorbital 3 and the sphenotic. In the sebastids *Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes*, and *Sebastolobus* (group 56-0), both infraorbitals 4 and 5 are present (Fig. 1A); in the sebastids *Trachyscorpia* and *Plectrogenium*, neosebastids, the scorpaenids *Pontinus, Neomerinthe, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis*, and *Scorpaenodes*, the apistid, tetrarogids, synanceiids, the gnathanacanthid, aploactinids, and pataecids (group 56-1), one of these bones is absent (Figs. 2A, 3C); in setarchids, the scorpaenids *Phenacoscorpius, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, and congiopodids (group 56-2), both infraorbitals 4 and 5 are absent (Figs. 1C, 3A). One of infraorbitals 4 or 5 was seen in *Scorpaenodes guamensis*, contrary to MATSUBARA (1943) who reported the absence of both infraorbitals 4 and 5 in that species.

Dermosphenotic (DS): The dermosphenotic, a small, grooved bone lying on the sphenotic, is present in sebastids, neosebastids, and scorpaenids except *Iracundus* (group 57-0) (Figs. 1A, C); in setarchids, the scorpaenid *Iracundus*, the apistid, tetrarogids, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 57-1), it is absent (Figs. 2A, 3A, 3C).

Table 13. Comparison of infraorbital characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Infraorbital stay	Infraorbitals 4 and 5	Dermosphenotic	Infraorbital-neurocranium sensory canal
Sebastidae *Sebastes* *Sebastiscus* *Hozukius* *Helicolenus* *Adelosebastes* *Sebastolobus*	formed (55-0)	both present (56-0)	present (57-0)	present (58-0)
Sebastidae *Trachyscorpia* *Plectrogenium* Neosebastidae		one absent (56-1)		
Scorpaenidae *Pontinus* *Neomerinthe* *Parascorpaena* *Scorpaena* *Scorpaenopsis* *Scorpaenodes* *Rhinopias* *Taenianotus*				absent (58-1)
Scorpaenidae *Iracundus*			absent (57-1)	
Scorpaenidae *Phenacoscorpius* *Hoplosebastes* *Pterois* *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois*		both absent (56-2)	present (57-0)	
Setarchidae			absent (57-1)	
Apistidae Tetrarogidae Synanceiidae Gnathanacanthidae Aploactinidae		one absent (56-1)		present (58-0)
Congiopodidae		both absent (56-2)		
Pataecidae	absent (55-1)	one absent (56-1)		

The circumorbital bones form the circumorbital sensory canal. In sebastids, neosebastids, the apistid, tetrarogids, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 58-0), the canal is present between infraorbital 3 and the temporal part of the neurocranium. In setarchids and scorpaenids (group 58-1), a canal between infraorbital 3 and the neurocranium is absent. In most fishes of group 58-0, the canal from the lachrymal branches in infraorbital 3, one branch extending to the neurocranium through infraorbitals 4 and 5, and the dermosphenotic, and the other, to the preopercle along the infraorbital stay. Among group 58-0, pataecids, which do not have the infraorbital stay (group 55-1), have an unbranched canal from the lachrymal to the neurocranium.

3. JAWS (Figs. 1-3, 5)

The upper jaw comprises the premaxillary and maxillary, and the lower jaw, the dentary, angular, and retroarticular.

Premaxillary (PM): The premaxillary forms the upper margin of the oral cavity. The ascending process of the bone has ligamentous connections with the maxillary and palatine.

Maxillary (M): The maxillary articulates with the anterior process of the palatine behind the lachrymal and has the adductor mandibulae tendinously inserted on its anterodorsal face. The maxillary head has ligamentous connections with the ethmoid and premaxillary.

Dentary (D): The dentary, a large bone forming the lower margin of the oral cavity, articulates with the angular posteriorly. The aw element of the adductor mandibulae develops on its medial face.

Angular (AN): The angular occupies the posterior part of the lower jaw and articulates with the quadrate through a condyle formed on its posterodorsal angle. The medial face of the angular is covered by the aw element of the adductor mandibulae.

Retroarticular (RA): The retroarticular is a small bone on the posteroventral corner of the lower jaw, meeting the posteroventral part of the angular. It is ligamentously connected to the interopercle.

4. SUSPENSORIUM (Figs. 4, 5; Table 14)

The suspensorium comprises seven palatal arch elements: the palatine, quadrate, metapterygoid, ectopterygoid, entopterygoid, hyomandibular, and symplectic, and four opercular elements: the preopercle, opercle, interopercle, and subopercle.

Palatine (PL): The palatine, forming the anteriormost part of the suspensorium, articulates anteriorly with the maxillary head, and meets the entopterygoid posterodorsally and the ectopterygoid posteroventrally. In sebastids, setarchids, the neosebastid *Neosebastes*, the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena*, and *Scorpaena*, the apistid, and tetrarogids except *Liocranium* (group 59-0), the palatine has a villiform tooth band (Fig. 5A, B); in the neosebastid *Maxillicosta*, the scorpaenids *Iracundus, Scorpaenopsis, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, the tetrarogid *Liocranium*, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 59-1), the palatine is not toothed (Fig. 5C-E).

Quadrate (Q): The quadrate, a plate-shaped, triangular bone in the ventral part of the suspensorium, articulates with the ectopterygoid anteriorly, the entopterygoid and metapterygoid dorsally through cartilage, and the anterior end of the preopercle posteroventrally. The medial side of the posterior part of the quadrate is grooved, for insertion of the posterior part of the symplectic. The ventral corner of the quadrate articulates with the angular condyle.

Metapterygoid (MTP): The metapterygoid, a plate-shaped bone articulating with the entopterygoid anteriorly, the quadrate ventrally through cartilage, the symplectic posteroventrally, and the hyomandibular posterodorsally, has the adductor arcus palatini inserted on its dorsomedial face. In most scorpaenoids (group 60-0), a space between the metapterygoid and hyomandibular allows the medial part of the levator arcus palatini fiber bundle to pass through the posteromedial face of the metapterygoid or anteromedial face of the hyomandibular (Fig. 5A, B, D); in the synanceiids *Synanceia, Erosa*, and *Minous*, the congiopodid *Congiopodus*, the gnathanacanthid, aploactinids, and pataecids (group 60-1), the space is closed (Fig. 5C, E).

Ectopterygoid (ECP): The ectopterygoid, a small, crescent-shaped bone with a pointed, ventral end, articulates with the palatine anterodorsally, the entopterygoid dorsally, and the quadrate posteroventrally.

Ectopterygoid (ENP): The entopterygoid is a plate-shaped bone meeting the palatine anteriorly, the ectopterygoid anteroventrally, and the metapterygoid posteriorly. The relationship between the entopterygoid and the adductor arcus palatini is noted in the description of the muscle (groups 7-0, 7-1, 7-2, and 7-3). In group 7-0, the dorsal margin of the entopterygoid is convex, with the adductor arcus palatini covering most of the dorsolateral face of the bone (Fig. 5A); in groups 7-1 and 7-2 the dorsal margin of the bone is straight or slightly concave, with the above muscle covering less than half of its surface or reaching its dorsal margin (Fig. 5B, E); in group 7-3, the muscle fibers extend to a longitudinal ridge present on the medial face of the entopterygoid (Fig. 5C, D).

Hyomandibular (HM): The hyomandibular is a strongly-built bone with a long ventral process. Its relationship with the metapterygoid is noted in the description of the latter. The dorsal margin of the hyomandibular articulates with the capsule formed by the sphenotic and pterotic. Posteriorly the hyomandibular articulates with the opercle. It is

Table 14. Comparison of suspensorial characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Palatine teeth	Space between hyomadibular and metapterygoid
Sebastidae Setarchidae Neosebastidae *Neosebastes* Scorpaenidae *Pontinus* *Neomerinthe* *Phenacoscorpius* *Parascorpaena* *Scorpaena* Apistidae Tetraogidae except *Liocranium*	present (59-0)	open (60-0)
Neosebastidae *Maxillicosta* Scorpaenidae *Iracundus* *Scorpaenopsis* *Scorpaenodes* *Hoplosebastes* *Pterois* *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois* *Rhinopias* *Taenianotus* Tetrarogidae *Liocranium* Synaceiidae *Inimicus* *Choridactylus* Congiopodidae *Alertichthys* *Zanclorhynchus*	absent (59-1)	
Synanceiidae *Synanceia* *Erosa* *Minous* Congiopodidae *Congiopodus* Gnathanacanthidae Aploactinidae Pataecidae		closed (60-1)

overlapped posteroventrally by the preopercle. The ventral process of the hyomandibular is cartilaginous, being connected with the dorsal end of the symplectic.

Symplectic (SY): The symplectic is rod-shaped, with the anteroventral part inserted on the ventromedial groove of the quadrate, and the posterodorsal part articulating with the metapterygoid dorsally and the hyomandibular through cartilage.

Preopercle (POP): The preopercle is a large, crescentic bone lying posterolaterally to the palatal arch. Usually five strong, backwardly or downwardly directed spines are present on the posterior side. The preopercle overlaps the anterior margin of the opercle posterodorsally and the anterodorsal margin of the interopercle posteroventrally. Its dorsomedial and ventromedial faces are firmly attached to the posteroventral face of the hyomandibular and the posteroventral margin of the quadrate, respectively. The al section of the adductor mandibulae and the levator arcus palatini are inserted on the preopercle anterolateral face.

Opercle (OP): The opercle is a large, plate-shaped bone, articulating anteriorly with the hyomandibular. The dilatator operculi is inserted on its anterodorsal margin.

Interopercle (IOP): The interopercle is a plate-shaped bone lying posteroventrally to the preopercle and ligamentously connected to the retroarticular.

Subopercle (SOP): The subopercle is a flat, V-shaped bone lying ventrally to the opercle.

5. HYOID ARCH (Figs. 6-8, 29; Table 15)

The hyoid arch, which corresponds to the second visceral arch, is composed of seven elements: the interhyal, epihyal, ceratohyal, hypohyal, basihyal, urohyal, and branchiostegal ray. Only the basihyal and urohyal are unpaired.

Interhyal (IH): The interhyal is a rod-shaped bone lying at the posterodorsal end of the hyoid arch, and connected with the posterodorsal end of the epihyal ventrally. The dorsal part of the interhyal is cartilaginous and connected with the medial face of the symplectic and the hyomandibular.

Epihyal (EH): The epihyal is a triangular bone connected with the ceratohyal anteriorly through cartilage. The two posteriormost branchiostegal rays are connected with its ventromedial margin.

Ceratohyal (CH): The ceratohyal is a triangular bone connected with the dorsal and ventral hypohyals anteriorly, and the epihyal posteriorly through cartilage. The branchiostegal rays except the two posteriormost are connected with the ventromedial margin of the ceratohyal.

Hypohyal (HH): The hypohyals comprise both dorsal and ventral elements, which are connected to each other and with the ceratohyal through cartilage.

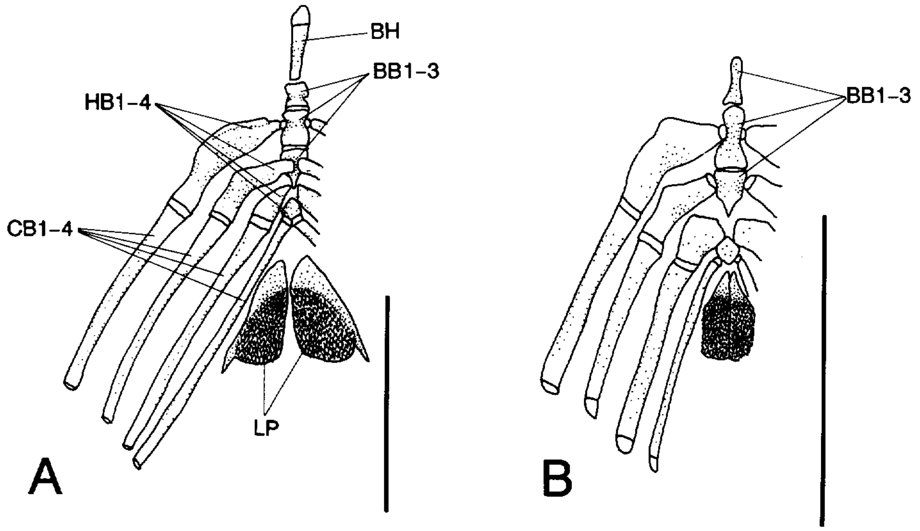

Fig. 29. Dorsal view of ventral branchial arches: A, *Parascorpaena aurita*; B, *Sthenopus mollis*.

Table 15. Comparison of hyoid arch characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Bathyhyal	Number of branchiostegal rays
Sebastidae Setarchidae Neosebastidae Scorpaenidae Apistidae Tetrarogidae Synanceiidae except *Choridactylus*	present (61-0)	7 (62-0)
Congiopodidae *Alertichthys* *Zanclorhynchus* Aploactinidae *Aploactis* *Erisphex*		6 (62-1)
Synanceiidae *Choridactylus* Gnathanacanthidae	absent (61-1)	7 (62-0)
Aploactinidae *Sthenopus* Pataecidae		6 (62-1)
Congiopodidae *Congiopodus*		5 (62-2)

Basihyal (BH): Most scorpaenoids (group 61-0) have a flat, rod-shaped basihyal (Fig. 29A); the synanceiid *Choridactylus*, the congiopodid *Congiopodus*, the gnathanacanthid, the aploactinid *Erisphex*, and pataecids (group 61-1) lack this bone (Fig. 29B).

Urohyal (UH): The urohyal is an unpaired bone, lacking any articulation with the other hyoid arch bones. The sternohyoideus originates from its posterodorsal face.

Branchiostegal ray (BR): The number of branchiostegal rays is variable among scorpaenoids. It is seven in most (group 62-0); six in the congiopodids *Alertichthys* and *Zanclorhynchus*, aploactinids, and pataecids (group 62-1); and five in the congiopodid *Congiopodus* (group 62-2).

6. BRANCHIAL ARCHES (Figs. 29, 30; Table 16)

The branchial apparatus consists of five arches, which correspond to the third to seventh visceral arches. The first to third arches comprise the pharyngobranchial, epibranchial, ceratobranchial, hypobranchial, and basibranchial. The fourth arch comprises the upper pharyngeal, formed by fusion of pharyngobranchials 4 and 5, the epibranchial, and ceratobranchial. The fifth arch comprises the lower pharyngeal, formed by fusion of ceratobranchial 5 and hypobranchial 5. Only the basibranchial is unpaired.

Pharyngobranchial (PB): The pharyngobranchial is the uppermost bone of the first to fourth branchial arches. Pharyngobranchial 1 is rod-shaped and articulates with epibranchial 1 through cartilage. Most scorpaenoids (group 63-0) have pharyngobranchial 1 (Fig. 30A-D); the congiopodids *Alertichthys* and *Zanclorhynchus* (group 63-1) do not (Fig. 30E). Pharyngobranchials 4 and 5 are fused to form the upper pharyngeal bone (UP). Pharyngobranchials 2 and 3, and the upper pharyngeal are connected through cartilage

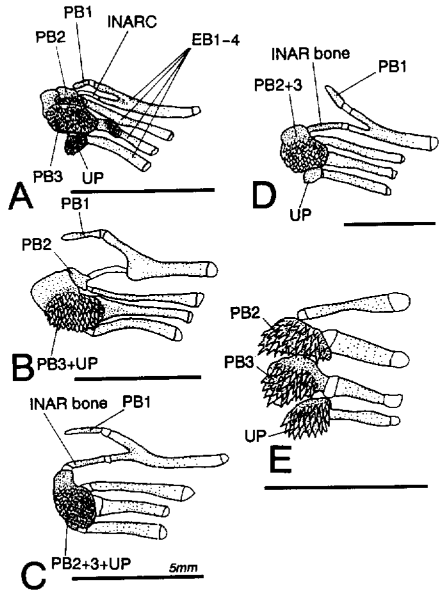

Fig. 30. Ventral view of left side of dorsal branchial arches: A, *Parascorpaena aurita*; B, *Richardsonichthys leucogaster*; C, *Erisphex potti*; D, *Inimicus japonicus*; E, *Zanclorhynchus spinifer*.

with epibranchials 2 to 4, respectively. The relationship between pharyngobranchials 2 and 3, and the upper pharyngeal is variable in scorpaenoids. In most scorpaenoids (group 64-0), pharyngobranchial 2 is separate from pharyngobranchial 3 or its complex with the upper pharyngeal (Fig. 30A, B, E); in the synanceiid *Inimicus* (group 64 - 1), pharyngobranchials 2 and 3 are fused, but pharyngobranchial 2 + 3 and the upper pharyngeal are separate (Fig. 30D); in the synanceiids *Choridactylus* and *Minous*, aploactinids, and pataecids (group 64 - 2), pharyngobranchials 2 and 3, and the upper pharyngeal are fused (Fig. 30C). In most genera of group 64-0 and the synanceiid *Inimicus* (group 65-0), pharyngobranchial 3 and the upper pharyngeal are separate (Fig. 30A, E); in the sebastid *Plectrogenium*, the scorpaenid *Dendrochirus*, the tetrarogids *Liocranium* and *Richardsonichthys*, the synanceiid *Synanceia*, and the gnathanacanthid (group 65 - 1), pharyngobranchial 3 and the upper pharyngeal are fused (Fig. 30B). In sebastids, setarchids, the neosebastid *Neosebastes*, the scorpaenids *Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Rhinopias*, and *Taenianotus*, the apistid, the tetrarogids *Gymnapistes, Centropogon*, and *Notesthes*, and congiopodids (group 66-0), pharyngobranchial 2 is toothed on the ventral face (Fig. 30A, E); in the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius*, and *Parapterois*, the tetrarogids *Neocentropogon, Ocosia, Paracentropogon, Hypodytes, Liocranium, Ablabys*, and *Richardsonichthys*, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 66 - 1), the separated pharyngobranchial 2 is not toothed nor is a separate tooth plate present on the fused pharyngobranchial complex (Fig. 30B-D).

Epibranchial (EB): The epibranchial is a rod-shaped bone between the pharyngobranchial and ceratobranchial, to which it is connected through cartilage. In sebastids, setarchids, neosebastids, scorpaenids, the apistid, and the tetrarogids *Gymnapistes, Centropogon, Notesthes, Neocentropogon*, and *Ocosia* (group 67 - 0), epibranchial 3 is toothed (Fig. 30A); in the tetrarogids *Paracentropogon, Hypodytes, Liocranium, Ablabys*, and *Richardsonichthys*, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 67-1), epibranchial 4 is not toothed (Fig. 30B-E).

Interarcual cartilage (INARC): In most scorpaenoids (group 68 - 0), a process of epibranchial 1 is well developed, with an interarcual cartilage being present between the former and pharyngobranchial 2 or its complex (Fig. 30A - D); in the scorpaenid *Scorpaenopsis* and the aploactinid *Aploactis* (group 68 - 1), this cartilage is absent, epibranchials 1 and 2 being articulated directly (Fig. 30E). In most of group 68-0, the interarcual cartilage is unossified (group 69-0) (Fig. 30A, B); in the synanceiids *Inimicus,*

Table 16. Comparison of branchial arch characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Pharyngobranchial 1	Pharyngobranchials 2,3 and upper pharyngeal		Teeth on pharyngobranchial 2	Teeth on epibranchial 4	Interarcual cartilage	
Sebastidae except *Plectrogenium* Setarchidae Neosebastidae *Neosebastes* Scorpaenidae *Parascorpaena* *Scorpaena* *Iracundus* *Scorpaenodes* *Hoplosebastes* *Pterois* *Ebosia* *Brachypterois* *Rhinopias* *Taenianotus* Apistidae Tetrarogidae *Gymnapistes* *Centropogon* *Notesthes*	present (63-0)	2 and 3 separate (64-0)	3 and upper pharyngeal separate (65-0)	present (66-0)	present (67-0)	prsent (68-0)	unossified (69-0)
Sebastidae *Plectrogenium* Scorpaenidae *Dendrochirus*			3 and upper pharyngeal fused (65-1)				
Scorpaenidae *Scorpaenopsis*			3 and upper pharyngeal separate (65-0)			absent (68-1)	
Neosebastidae *Maxillicosta* Scorpaenidae *Pontinus* *Neomerinthe* *Phenacoscorpius* *Parapterois* Tetrarogidae *Neocentropogon* *Ocosia*				absent (66-1)		present (68-0)	unossified (69-0)
Tetrarogidae *Paracentropogon* *Hypodytes* *Ablabys* Synaceiidae *Erosa*					absent (67-1)		
Tetrarogidae *Liocranium* *Richardsonichthys* Synanceiidae *Synanceia* Gnathanacanthidae			3 and upper pharyngeal fused (65-1)				
Pataecidae		2,3, and upper pharygeal fused (64-2)					
Synanceiidae *Inimicus*		2 and 3 fused (64-1)	3 and upper pharyngeal separate (65-0)				ossified (69-1)
Synanceiidae *Choridactylus* *Minous* Aploatinidae *Erisphex* *Sthenopus*		2,3, and upper pharyngeal fused (64-2)					
Aploactinidae *Aploactis*						absent (68-1)	
Congiopodidae *Congiopodus*		2 and 3 separate (64-0)	3 and upper pharyngeal separete (65-0)	present (66-0)		present (68-0)	unossified (69-0)
Congiopodidae *Alertichthys* *Zanclorhynchus*	absent (63-1)						

Choridactylus, and *Minous*, and the aploactinids *Erisphex* and *Sthenopus* (group 69-1), it is ossified (Fig. 30C, D).

Ceratobranchial (CB): Ceratobranchials 1 to 4 are rod-shaped bones. Ceratobranchials 1 to 3 lying between the epibranchials and the basibranchials of the same arch, connected through cartilage, and ceratobranchial 4 lying between epibranchial 4 and the cartilage posterior to the basibranchial.

Hypobranchial (HB): Hypobranchials 1 to 3 are unpaired, rod-shaped bones lying between the ceratobranchials and the basibranchials.

Basibranchial (BB): Basibranchials 1 to 3 are unpaired rod-shaped bones lying in the ventral midline.

Lower pharyngeal (LP): Ceratobranchial 5 and hypobranchial 5 are fused to form the lower pharyngeal. This bears a villiform tooth band on its dorsal face.

7. VERTEBRAE AND ASSOCIATED BONES (Table 17)

Because of the close association of the anterior abdominal vertebrae and the anterior dorsal proximal pterygiophores, the relationship between these elements is treated in the description of the proximal pterygiophores.

Abdominal vertebrae (AV) and caudal vertebrae (CV): The vertebrae are divided into two groups, abdominal vertebrae and caudal vertebrae, the former being distinguished from the latter by the presence of lateral parapophyses and the absence of a hemal arch. The proximal pterygiophore of the anal spine s inserted between the last abdominal vertebrae and the first caudal vertebrae. In setarchids and scorpaenids except *Phenacoscorpius* (group 70-0), the usual number of vertebrae is 24, although some individual variations are often observed; in sebastids, neosebastids, the scorpaenid *Phenacoscorpius*, the apistid, tetrarogids except *Richardsonichthys*, the synanceiids except *Synanceia*, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 70-1), the usual number of vertebrae is 25 or more. Although the tetrarogid *Richardsonichthys* and the synanceiid *Synanceia* usually have 24 vertebrae, these genera are included in group 70-R, for the reason given under "Character analysis." A few posteriormost vertebrae are described in the section dealing with the caudal skeleton.

Pleural rib (PR): In most scorpaenoids (group 71-0), pleural ribs are present on most abdominal vertebrae except the several anteriormost; in aploactinids (group 71-1), pleural ribs are absent.

Epipleural (EP): The epipleurals are supported by the anteriormost vertebra, the anterior epipleurals being connected to the side of the corresponding vertebra, the middle epipleurals to the corresponding pleural rib, and the posterior epipleurals to the

Table 17. Comparison of vertebral and associated bone characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Usual number of vertebrae	Pleural ribs
	(70-0)	present (71-0)
Setarchidae	24	
Scorpaenidae except *Phenacoscorpius*	24	
	(70-1)	
Sebastidae		
Sebastes	26-30	
Sebastiscus	25	
Hozukius	26	
Helicolenus	25	
Adelosebastes	26	
Sebastolobus	29	
Trachyscorpia	25-26	
Plectrogenium	26	
Neosebastidae		
Neosebastes	27	
Maxillicosta	26	
Scorpaenidae		
Phenacoscorpius	25	
Apistidae	26	
Tetrarogidae		
Gymnapistes	27	
Centropogon	27	
Notesthes	28	
Neocentropogon	25	
Ocosia	28	
Paracentropogon	26	
Hypodytes	26	
Liocranium	25	
Ablabys	28	
Richardsonichthys	24 (see text)	
Synanceiidae		
Inimicus	25	
Synanceia	24 (see text)	
Erosa	25	
Choridactylus	26	
Minous	25-27	
Congiopodidae		
Congiopodus	36	
Alertichthys	32	
Zanclorhynchus	35	
Gnathanacanthidae	29	
Pataecidae		
Pataecus	36	
Aetapcus	36	
Neopataecus	35	
Aploactinidae		absent (71-1)
Aploactis	29	
Erisphex	28	
Sthenopus	26	

parapophyses of the abdominal vertebrae.

8. CAUDAL SKELETON (Fig. 20; Table 18)

The caudal skeleton is composed of five elements: the urostyle, uroneural, epural, parhypural, and hypural. The uroneural only is paired. Preural vertebrae 1 and 2 also support the caudal fin.

Preural vertebra 2 (PV2): Preural vertebra 2 corresponds to preural centrum 3. In sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, the synanceiids *Synanceia* and *Erosa*, and the congiopodids *Congiopodus* and *Zanclorhynchus* (group 72-0), the centrum and hemal spine of preural vertebra 2 are autogenous (Fig. 20A-D); in the synanceiids *Inimicus*, *Choridactylus*, and *Minous*, the congiopodid *Alertichthys*, the gnathanacanthid, aploactinids, and pataecids (group 72-1), these elements are fused (Fig. 20E-H).

Preural vertebra 1 (PV1): Preural vertebra 1 corresponds to preural centrum 2. In most scorpaenoids (group 73-0), the centrum and hemal spine of preural vertebra 1 are autogenous (Fig. 20A-E, G); in the gnathanacanthid and pataecids (group 73-1), these elements are fused (Fig. 20F, H). In sebastids, setarchids, neosebastids, scorpaenids, the apistid, and tetrarogids (group 74-0), the neural spine of preural vertebra 1 is short (Fig. 20A-D); in synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 74-1), the spine is long, extending to the base of the caudal fin rays (Fig. 20E-H).

Urostyle (US): The urostyle is a triangular bone formed by the fusion of preural centrum 1 and several ural centra. In most scorpaenoids (group 75-0), the urostyle and uroneural are autogenous (Fig. 20A-G); in the synanceiids *Inimicus* and *Erosa*, the congiopodids *Congiopodus* and *Alertichthys*, and pataecids (group 75-1), they are fused (Fig. 20H). In most scorpaenoids (group 76-0), the urostyle and parhypural are autogenous (Fig. 20A-E, G); in the gnathanacanthid and pataecids (group 76-1), they are fused (Fig. 20F, H). In sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, the synanceiids *Synanceia*, *Erosa*, and *Choridactylus*, and the aploactinids *Aploactis* and *Sthenopus* (group 77-0), the urostyle and hypurals are autogenous (Fig. 20A-E); in the synanceiids *Inimicus* and *Minous*, congiopodids, the gnathanacanthid, the aploactinid *Erisphex*, and pataecids (group 77-1), they are fused (Fig. 20F-H).

Uroneural (UN): The uroneural is a small, paired bone, lying dorsally to the urostyle.

Epural (EU): The epurals, which have originated from the neural spines of the ural vertebrae, are plate-shaped bones lying dorsally to the uroneural and uppermost hypural. The epurals support the base of the procurrent rays of the upper lobe of the caudal fin. Sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, the synanceiids *Synanceia*, *Choridactylus*, and *Minous*, and aploactinids (group 78-0) have three epurals (Fig. 20A-E, G); the synanceiids *Inimicus* and *Erosa*, congiopodids, and the gnathanacanthid (group 78-1) have two epurals (Fig. 20F); pataecids (group 78-2) have one epural (Fig. 20H).

Table 18. Comparison of caudal skeleton characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Centrum and hemal spine of preural vertebra 2	Centrum and hemal spine of preural vertebra 1	Preural vertebra 1 neural spine	Urostyle and uroneural	Urostyle and parhypural	Urostyle and hypural	Number of epurals	Parhypural and hypurals	Number of hypurals	Caudal fin rays
Sebastidae *Trachyscorpia* *Plectrogenium* Setarchidae Neosebastidae	autogenous (72-0)	autogenous (73-0)	short (74-0)	autogenous (75-0)	autogenous (76-0)	autogenous (77-0)	3 (78-0)	autogenous (79-0)	2+3 (80-0)	branched (81-0)
Scorpaenidae *Pontinus* *Neomerinthe* *Scorpaenodes* *Hoplosebastes* *Pterois* *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois*									1+3 (80-1)	
Sebastidae *Sebastes* *Sebastiscus* *Hozukius* *Helicolenus* *Adelosebastes* *Sebastolobus* Scorpaenidae *Phenacoscorpius* *Parascorpaena* *Scorpaena* *Iracundus* *Scorpaenpopsis* *Rhinopias* *Taenianotus*									1+2 (80-2)	
Apistidae Tetrarogidae except *Richardsonichthys*								fused (79-1)		
Tetrarogidae *Richardsonichthys*									1+1 (80-3)	
Synanceiidae *Choridactylus*	fused (72-1)		long (74-1)						1+2 (80-2)	
Aploactinidae *Aploactis*										unbranched (81-1)
Synanceiidae *Minous*						fused (77-1)				
Aploactinidae *Sthenopus*						autogenous (77-0)			1+1 (80+3)	
Synanceiidae *Synanceia*	autogenous (72-0)									branched (81-0)
Aploactinidae *Erisphex*	fused (72-1)					fused (77-1)				unbranched (81-1)
Synanceiidae *Erosa*	autogenous (72-0)			fused (75-1)		autogenous (77-0)	2 (78-1)			branched (81-0)
Congiopodidae *Zanclorhynchus*				autogenous (75-0)		fused (77-1)				unbranched (81-1)
Congiopodidae *Congiopodus*				fused (75-1)						branched (81-0)
Synanceiidae *Inimicus*	fused (72-1)									
Congiopodidae *Alertichthys*										unbranched (81-1)
Gnathanacanthidae		fused (73-1)		autogenous (75-0)	fused (76-1)					
Pataecidae				fused (75-1)			1 (78-2)			

Parhypural (PHU): The parhypural, corresponding to the hemal spine of preural centrum 1, has the hypurapophysis on its anterolateral face. In sebastids, setarchids, neosebastids, and scorpaenids (group 79-0), the parhypural and lowermost hypural are autogenous (Fig. 20A - C); in the apistid, tetrarogids, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 79-1), they are fused (Fig. 20D-H).

Hypural (HU): The hypurals, which have originated from the hemal spines of the ural vertebrae, are plate-shaped bones with a cartilaginous posterior margin. Hypurals 1 and 2 support the lower lobe, and 3 to 5, the upper lobe of the caudal fin. The hypurals are often fused to one another. The hypural formula, defined as the number of bones supporting the lower lobe + the number of bones supporting the upper lobe of the caudal fin, is 2+3 in the sebastids *Trachyscorpia* and *Plectrogenium*, setarchids, and neosebastids (group 80 - 0)(Fig. 20A); in the scorpaenids *Pontinus, Neomerinthe, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus*, and *Parapterois* (group 80-1), it is 1 + 3 (Fig. 20B); in the sebastids *Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes*, and *Sebastolobus*, the scorpaenids *Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Rhinopias*, and *Taenianotus*, the apistid, tetrarogids except *Richardsonichthys*, the synanceiids *Choridactylus* and *Minous*, and the aploactinid *Aploactis* (group 80-2), it is 1+2 (Fig. 20C-E); in the tetrarogid *Richardsonichthys*, the synanceiids *Inimicus, Synanceia*, and *Erosa*, congiopodids, the gnathanacanthid, the aploactinids *Erisphex* and *Sthenopus*, and pataecids (group 80-3), it is 1+1 (Fig. 20F-H).

Caudal fin (CF): In most scorpaenoids (group 81-0), the principal caudal fin rays are branched; in the synanceiid *Minous*, the congiopodids *Alertichthys* and *Zanclorhynchus*, the gnathanacanthid, aploactinids, and pataecids (group 81-1), all of the caudal fin rays are unbranched.

9. PECTORAL GIRDLE (Fig. 31; Table 19)

The pectoral girdle comprises seven elements: the posttemporal, supracleithrum, cleithrum, postcleithra, scapula, coracoid, and radials. The pectoral fin rays are also described here.

Posttemporal (PT): The posttemporal, a fork-shaped bone articulating with the epiotic anteromedially and the dorsolateral face of the supracleithrum, often meets the supratemporal anteriorly.

Supracleithrum (SCL): The supracleithrum is a plate-shaped bone articulating with the posttemporal dorsolaterally and the cleithrum ventromedially. Baudelot's ligament, if present, is connected to the medial face of the supracleithrum.

Cleithrum (CL): The cleithrum is a large, curved, flat bone, forked dorsally. The lateral face of the base articulates with the supracleithrum. The dorsal postcleithrum articulates with the medial face of the flat posterodorsal arm. The posteroventral face of the cleithrum articulates with the scapula and coracoid. The anteroventral and posterior faces of the cleithrum form the posterior limit of the sternohyoideus and the anterior limit of the hypaxialis, respectively.

Postcleithrum (PCL): In most scorpaenoids (group 82-0), two postcleithra, dorsal and ventral, are present (Fig. 31A, B). The dorsal postcleithrum is flat, articulating with the medial face of the posterodorsal arm of the cleithrum dorsally and the ventral postcleithrum ventrally. The relationship between the ventral postcleithrum and the obliquus inferioris is discussed in the section dealing with the obliquus inferioris. In pataecids (group 82-1), the postcleithrum is absent (Fig. 31C).

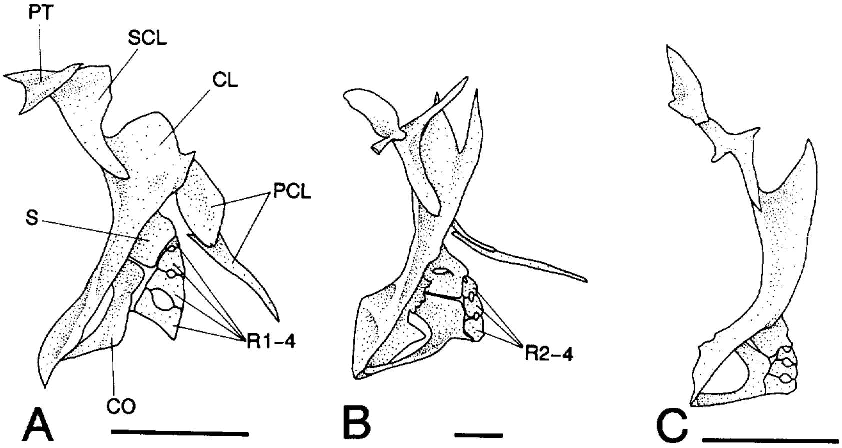

Fig. 31. Left lateral view of pectoral girdle: A, *Phenacoscorpius megalops*; B, *Gnathanacanthus goetzeei*; C, *Neopataecus waterhousii*.

Scapula (S): The scapula is a flat, C-shaped bone articulating with the posteromedial margin of the cleithrum. In the sebastids *Sebastolobus, Trachyscorpia*, and *Plectrogenium*, setarchids, and the scorpaenids *Pontinus, Neomerinthe, Phenacoscorpius, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois*, and *Taenianotus* (group 83-0), the scapula and uppermost radial are autogenous (Fig. 31A); in the sebastids *Sebastes, Sebastiscus, Hozukius, Helicolenus*, and *Adelosebastes*, the neosebastids, the scorpaenids *Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis*, and *Rhinopias*, the apistid, tetrarogids, synanceiids, the congiopodids *Alertichthys* and *Zanclorhynchus*, the gnathanacanthid, aploactinids, and pataecids (group 83-1), the scapula and uppermost radial are fused (Fig. 31B, C). Although in the congiopodid *Congiopodus* the scapula and uppermost radial are autogenous, the genus is included in group 83-R, for the reason given

Table 19. Comparison of pectoral girdle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Postcleithra	Scapula and uppermost radial	Space between coracoid and lowermost radial	Pectoral fin rays
Sebastidae *Sebastolobus* *Trachyscorpia* *Plectrogenium* Setarchidae Scorpaenidae *Neomerinthe* *Phenacoscorpius* *Scorpaenodes* *Hoplosebastes* *Ebosia* *Brachypterois* *Dendrochirus* *Parapterois*	present (82-0)	separate (83-0)	open (84-0)	branched (85-0)
Scorpaenidae *Pontinus* *Pterois* *Taenianotus*				unbranched (85-1)
Sebastidae *Sebastes* *Sebastiscus* *Hozukius* *Helicolenus* *Adelosebastes* Neosebastidae Scorpaenidae *Parascorpaena* *Scorpaena* *Iracundus* *Scorpaenopsis* *Rhinopias* Tetrarogidae Synanceiidae except *Minous*		fused (83-1) (for *Congiopodus* see text)		branched (85-0)
Apistidae			closed (84-1)	
Synanceiidae *Minous* Congiopodidae *Congiopodus* *Alertichthys* *Zanclorhynchus* Aploactinidae			open (84-0)	unbranched (85-1)
Gnathanacanthidae			closed (84-1)	
Pataecidae	absent (82-1)		open (84-0)	

under "Character analysis."

Coracoid (CO): The coracoid is a curved, flat bone articulating anterodorsally and anteroventrally with the posteroventral margin of the cleithrum. In most scorpaenoids (group 84 - 0), a space between the coracoid and lowermost radial is present, accommodating the coracoradialis (Fig. 31A, C); in the apistid and gnathanacanthid (group 84-1), the space is largely closed (Fig. 31B).

Radial (R): The radials are small, flat, perichondral bones arranged along the posterior margins of the scapula and coracoid. The posterior margin of the radials forms the base of the pectoral fin rays. In group 83-0, the number of radials is four; in group 83-1, the number is three owing to the fusion of the uppermost radial with the scapula. The relationship between the lowermost radial and coracoid is noted in the description of the latter.

Pectoral fin (P1F): In sebastids, setarchids, neosebastids, scorpaenids except *Pontinus, Pterois,* and *Taenianotus*, the apistid, tetrarogids, and synanceiids except *Minous* (group 85-0), the middle rays of the pectoral fin are branched; in the scorpaenids *Pontinus, Pterois*, and *Taenianotus*, the synanceiid *Minous*, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 85-1), the pectoral fin rays are unbranched.

10. PELVIC GIRDLE (Fig. 15; Table 20)

The pelvic fins are supported by a pair of pelvic bones.

Pelvis (P2S): The pelvis is a triangular bone, articulating with its opposite number in the ventral midline. The infracarinalis medius is connected to the posterolateral margin of this bone. In scorpaenoids except pataecids (groups 23-0, 24-0, 25-0, 26-0, 28-0, and 29-0), the pelvis is normally developed and supports the muscles serving the pelvic girdle; in pataecids (groups 23-1, 24-1, 25-1, 26-1, 28-1, and 29-1), the pelvis is, small, being flattened anteriorly and conical posteriorly (Fig. 15I).

Pelvic fin (P2F): In most scorpaenoids (group 86-0), the number of pelvic fin rays is five; four in the tetrarogids *Paracentropogon, Hypodytes*, and *Liocranium*, and the synanceiid *Erosa* (group 86-1); three in aploactinids (group 86-2); two in the pataecid *Aetapcus* (group 86 - 3); and one in the pataecids *Pataecus* and *Neopataecus* (group 86 - 4). In most scorpaenoids (group 87-0), some pelvic fin rays are branched; in the synanceiid *Minous*, congiopodids, the gnathanacanthid, aploactinids, and pataecids (group 87-1), the pelvic fin rays are unbranched.

11. DORSAL AND ANAL FIN SUPPORTS (Figs. 32, 33; Tables 21-23)

The median fins are supported by the proximal and distal pterygiophores. The supraneural lies inside the nape in some scorpaenoids.

Table 20. Comparison of pelvic girdle characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Number of pelvic fin rays	Pelvic fin rays
Sebastidae Setarchidae Neosebastidae Scorpaenidae Apistidae Tetrarogidae *Gymnapistes* *Centropogon* *Notesthes* *Neocentropogon* *Ocosia* *Ablabys* *Richardsonichthys* Synanceiidae *Inimicus* *Synanceia* *Choridactylus*	5 (86-0)	branched (87-0)
Synanceiidae *Minous* Congiopodidae Gnathanacanthidae		unbranched (87-1)
Tetrarogidae *Paracentropogon* *Hypodytes* *Liocranium* Synanceiidae *Erosa*	4 (86-1)	branched (87-0)
Aploactinidae	3 (86-2)	unbranched (87-1)
Pataecidae *Aetapcus*	2 (86-3)	
Pataecidae *Pataecus* *Neopataecus*	1 (86-4)	

Supraneural (SN): The supraneural is an elongate, flat bone lying in interneural space 1 (between the neurocranium and neural spine 1). Sebastids except *Plectrogenium*, setarchids, and the scorpaenids *Pontinus*, *Neomerinthe*, and *Phenacoscorpius* (group 88-0) have a supraneural (Fig. 32A); other scorpaenoids (group 88-1) do not (Fig. 32B, C, 33).

Proximal pterygiophore (PP): The proximal pterygiophores are triangular with longitudinal keels on both sides. In the present study, the anterior series of proximal pterygiophores is coded according to the supporting spine: "proximal pterygiophore 1+2" refers to the proximal pterygiophore that supports dorsal spines 1 and 2. Because the

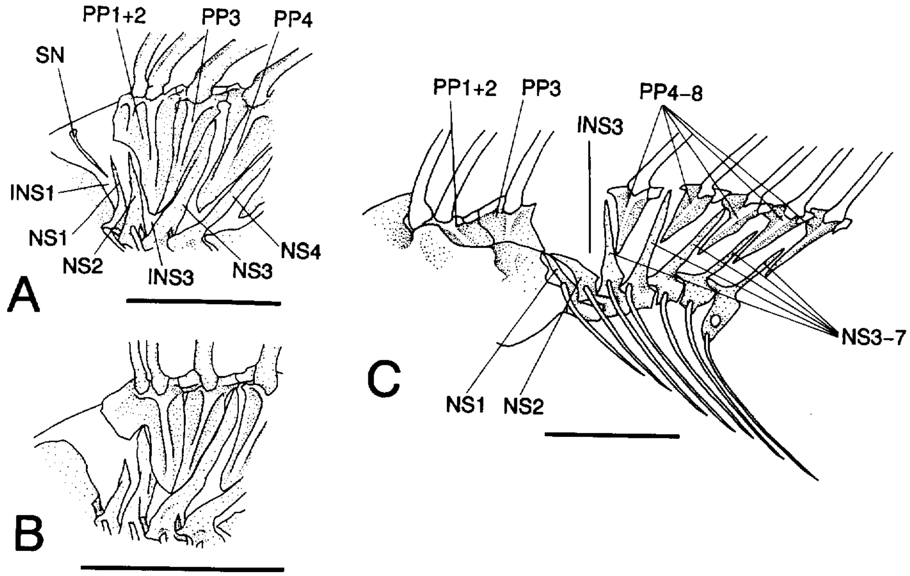

Fig. 32. Left lateral view of anterior vertebrae and dorsal fin supports: A, *Neomerinthe rufescens*; B, *Scorpaenodes kelloggi*; C, *Richardsonichthys leucogaster*.

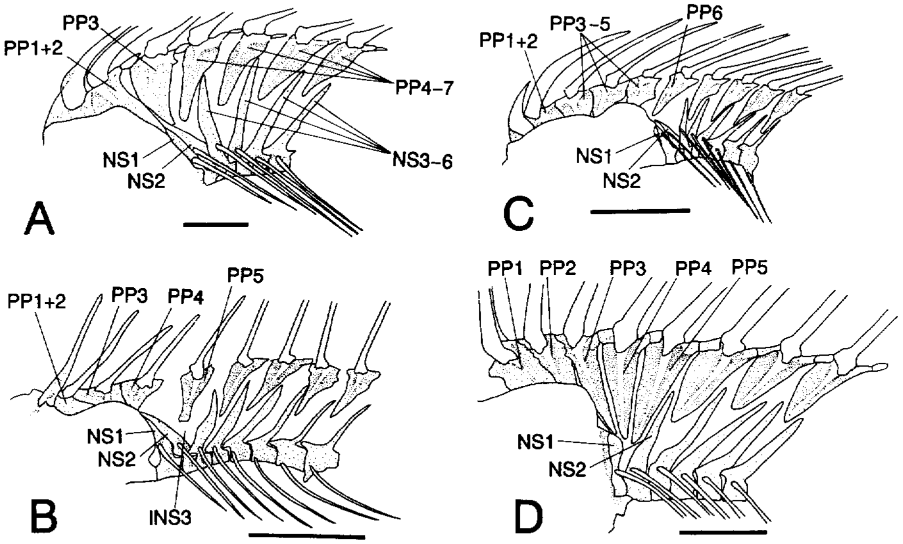

Fig. 33. Left lateral view of anterior vertebrae and dorsal fin supports: A, *Gnathanacanthus goetzeei*; B, *Erisphex potti*; C, *Pataecus fronts*; D, *Congiopodus coriaceus*.

neural spines of the anterior abdominal vertebrae are closely associated with the anterior dorsal pterygiophores, the relationships between these elements are noted below.

In sebastids, setarchids, neosebastids, scorpaenids, and the apistid (group 89-0), neural spine 1 does not articulate with the posterodorsomedial face of the neurocranium, nor does neural spine 2 articulate with neural spine 1 (Fig. 32A, B); in congiopodids (group 89-1), neural spine 1 articulates anteriorly with the posterodorsomedial face of the neurocranium, but neural spine 2 does not articulate anteriorly with neural spine 1 (Fig. 33D); in tetrarogids, synanceiids, the gnathanacanthid, aploactinids, and pataecids (group 89-2), neural spine 1 articulates anteriorly with the posterodorsomedial face of the neurocranium and neural spine 2 articulates anteriorly with neural spine 1 (Figs. 32C, 33A-C). Interneural spaces 1 and 2 are closed in group 89-1 except the gnathanacanthid, in which interneural space 1 is filled by the insertion of proximal pterygiophore 1 + 2 (Fig. 33A). In most scorpaenoids (group 90-0), neural spines 1 and 2 are normally developed compared with the following elements; in synanceiids (group 90-1), the former spines are short. In most scorpaenoids (group 91-0), the anteriormost proximal pterygiophore of the dorsal fin supports dorsal spines 1 and 2 (Figs. 32, 33A-C); in congiopodids (group 91-1), each proximal pterygiophore of the dorsal fin supports a single dorsal spine (Fig. 33D). In sebastids, setarchids, neosebastids, scorpaenids, the apistid, tetrarogids, and synanceiids (group 92-0, 93-0), proximal pterygiophores 1+2 and 3 are inserted in interneural space 3 or on the posterodorsomedial face of the neurocranium, and proximal pterygiophore 4 and succeeding proximal pterygiophores are inserted in the interneural spaces of the same number. In the gnathanacanthid (group 92 - 1), proximal pterygiophore 1 + 2 fills inter neuralspace 1, proximal pterygiophores 3 and 4 occupy interneural space 3, proximal pterygiophores 5 to 8, interneural spaces 4 to 7, respectively, and proximal pterygiophore 8 and succeeding pterygiophores, the interneural spaces of the same number; in the aploactinid *Aploactis* (group 92-2), proximal pterygiophores 1+2 and 3 are attached to the posterodorsomedial face of the neurocranium, proximal pterygiophores 4 to 8 occupy interneural spaces 3 to 7, respectively, and proximal pterygiophore 8 and succeeding pterygiophores, the interneural spaces of the same number; in the aploactinid *Erisphex* (group 92 - 3), proximal pterygiophores 1 + 2, 3, and 4 are attached to the posterodorsomedial face of the neurocranium, proximal pterygiophores 5 to 7 occupy interneural spaces 3 to 5, proximal pterygiophores 8 and 9, interneural spaces 7 and 8, and proximal pterygiophore 10 and succeeding pterygiphores, the interneural spaces of the same number; in the aploactinid *Sthenopus* (group 92-4), proximal pterygiophores 1+2, 3, and 4 are attached to the posterodorsomedial face of the neurocranium, proximal pterygiophores 5 to 8 occupy interneural spaces 3 to 6, proximal pterygiophores 9 and 10, interneural spaces 8 and 9, and proximal pterygiophore 11 and succeeding pterygiophores, the interneural spaces of the same number; in the pataecid *Aetapcus* (group 92 - 5), proximal pterygiophores 1+2, 3, 4, and 5 are attached to the posterodorsomedial face of the neurocranium, proximal pterygiophores 6 to 8 occupy interneural spaces 3 to 5, proximal pterygiophores 9 and 10, interneural spaces 7 and 8, proximal pterygiophores 11 to 13, interneural spaces 10 to 12, and proximal pterygiophore 14 and succeeding pterygiophores, the interneural spaces of the same number; in the pataecid *Pataecus* (group 92-6), proximal pterygiophores 1+2, 3, 4, and 5 are attached to the posterodorsomedial face of the neurocranium, proximal pterygiophores 6 to 9 occupy interneural spaces 3 to 6, proximal pterygiophore 10, interneural space 8, proximal pterygiophores 11 to 13 interneural spaces 10 to 12, and proximal pterygiophore 14 and succeeding pterygiophores, the interneural spaces of the same number; in the pataecid *Neopataecus* (group 92-7), proximal pterygiophores 1+2, 3, 4, 5, and 6 are attached to the posterodorsomedial face of the neurocranium, proximal pterygiophores 7 to 9 occupy interneural spaces 3 to 5, proximal pterygiophore 10, interneural space 7, proximal pterygiophores 11 and 12, interneural spaces 9 and 10, proximal pterygiophores 13 and 14 interneural spaces 12 and 13, and proximal pterygiophore 15 and succeeding pterygiophores, the interneural spaces of the same number. The anterior shift of proximal pterygiophores in congiopodids is described in groups 93-1 and 93-2. In *Alertichthys* and *Zanclorhynchus* (group 93-1), proximal pterygiophores 1 and 2 occupy interneural space 2, and proximal pterygiophore 3 and succeeding pterygiophores, the interneural space of the same number; in *Congiopodus* (group 93-2), proximal pterygiophores 1 and 2 occupy interneural space 2, proximal pterygiophores 6 and 7, interneural spaces 3 and 4, respectively, proximal pterygiophore 8, interneural space 6, proximal pterygiophores 9 to 11, interneural spaces 8 to 10, and proximal pterygiophore 12 and succeeding pterygiphores, the interneural spaces of the same number.

The proximal pterygiophore supporting the anal spines is inserted between the posteriormost abdominal vertebra and the anteriormost caudal vertebra.

Distal pterygiophore (DP): The distal pterygiophores lie posteriorly to the posterodorsal end of the proximal pterygiophores supporting the spines. That supporting the posteriormost dorsal spine is ontogenetically transformed from a soft-ray in scorpaenoids.

Stay (STY): The stay is an unpaired bone lying posteriorly to the posteriormost dorsal and anal pterygiophores.

Dorsal fin (DF): In most scorpaenoids (group 94-0), the dorsal fin rays, except the anteriormost, are branched; in the synanceiid *Minous*, the congiopodids *Alertichthys* and *Zanclorhynchus*, the gnathanacanthid, aploactinids, and pataecids (group 94-1), the dorsal fin rays are unbranched.

Anal fin (AF): In most scorpaenoids (group 95-0), the anal fin rays are branched; in the synanceiid *Minous*, the congiopodids *Alertichthys* and *Zanclorhynchus*, the gnathanacanthid, aploactinids, and pataecids (group 95 - 1), the anal fin rays are unbranched.

Table 21. Comparison of supraneural and the neural spine characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Supraneural	Neural spines 1 and 2	
Sebastidae except *Plectrogenium* Setarchidae Scorpaenidae *Pontinus* *Neomerinthe* *Phenacoscorpius*	present (88-0)	not articulated anteriorly (89-0)	normal (90-0)
Sebastidae *Plectrogenium* Neosebastidae Scorpaenidae except *Pontinus* *Neomerinthe* *Phenacoscorpius* Apistidae	absent (88-1)		
Tetrarogidae		neural spine 1 articulated with neurocranium, neural spine 2 articulated with neural spine 1 (89-2)	
Synanceiidae			short (90-1)
Gnathanacanthidae Aploactinidae Pataecidae			normal (90-0)
Congiopodidae		neural spine 1 articulated with neurocranium (89-1)	

Table 22. Comparison of dorsal proximal pterygiophore and interneural space characters in scorpaenoids. Numerals in parentheses correspond to group numbers. SN: supraneural, which is absent in group 88-1, NC: neurocranium.

Taxon	Dorsal proximal pterygiophores 1 and 2	Dorsal proximal pterygiophores (upper line) and *interneural spaces* (*lower line*)
Sebastidae Setarchidae Neosebastidae Scorpaenidae Apistidae	a single pterygiophore 1+2 supports dorsal spine 1 and 2 (91-0)	SN 1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *1 2 3 4 5 6 7 8 9 10 11 12 13 14 15* (92-0,93-0)
Tetrarogidae Synanceiidae		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-0,93-0)
Gnathanacanthidae		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-1)
Aploactinidae *Aploactis*		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-2)
Aploactinidae *Erisphex*		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-3)
Aploactinidae *Sthenopus*		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-4)
Pataecidae *Aetapcus*		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-5)
Pataecidae *Pataecus*		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-6)
Pataecidae *Neopataecus*		1+2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *3 4 5 6 7 8 9 10 11 12 13 14 15* (92-7)
Congiopodidae *Alertichthys* *Zanclorhynchus*	pterygiophores 1 and 2 support dorsal spines 1 and 2 respectively (91-1)	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 NC *2 3 4 5 6 7 8 9 10 11 12 13 14 15* (93-1)
Congiopodidae *Congiopodus*		12345 6 7 8 9 10 11 12 13 14 15 NC *2 3 4 5 6 7 8 9 10 11 12 13 14 15* (93-2)

Table 23. Comparison of dorsal and anal fin ray characters in scorpaenoids. Numerals in parentheses correspond to group numbers.

Taxon	Dorsal fin rays	Anal fin rays
Sebastidae Setarchidae Neosebastidae Scorpaenidae Apistidae Tetrarogidae Synanceiidae except *Minous* Congiopodidae *Congiopodus*	branched (94-0)	branched (95-0)
Synanceiidae *Minous* Congiopodidae *Alertichthys* *Zanclorhynchus* Gnathanacanthidae Aploactinidae Pataecidae	unbranched (94-1)	unbranched (95-1)

IV. Phylogentic Consideration

1. CHARACTER ANALYSIS

To construct the phylogenetic relationships among the Scorpaenoidei, the cladistic method of Hennig (1966) was adopted. Ninety-five characters were selected following the examination of the muscles and skeletons of 55 scorpaenoid genera, and character polarities are determined primarily by out-group comparison (Watrous and Wheeler 1981, Wiley 1981). Because the Scorpaenoidei has been considered the least morphologically specialized group in the Scorpaeniformes, a suitable out-group within the order is unavailable. Many authors considered the Scorpaeniformes to have evolved from a percoid ancestor because of the similarities in external and internal characters between generalized scorpaenoids and generalized percoids (Matsubara 1943, Quast 1965, Gosline 1971, Lauder and Liem 1983, Washington *et al.* 1984), although most of the above admitted possible derivation from several groups of Perciformes. Other authors have considered the Scorpaeniformes as a pre-perciform group (Greenwood *et al.* 1966, Nelson 1976, 1984). Although a monophyletic versus polyphyletic origin is unclear, this work accept, a percoid origin of scorpaenoids, because most of the scorpaenoid characters recognized here are comparable with those in generalized percoids, with one condition of most characters often being considered the same as that in generalized percoids. Consequently, the out-group comparison was made primarily with generalized percoids (Katayama 1959, Gosline 1966, Greenwood 1976, Zehren 1979, Johnson 1980, 1984). If such was impossible owing to the uniqueness of the character in scorpaenoids, the unquestionably specialized conditions such as absence and fusion, were considered derived. In cases of character polarization still being unclear, the character condition in sebastids and scorpaenids, which have been considered the most morphologically primitive group in scorpaenoids (Matsubara 1943, Quast 1965, Washington *et al.* 1984), was presupposed as primitive (functional out-group, Watrous and Wheeler 1981).

The parenthesized character number and derived character condition are boldfaced before each analysis.

Muscles of the cheek

Although Allis (1909), Dietz (1914), Adamicka (1972), and Yabe (1985) examined the cheek muscles of scorpaenoids, presenting valuable information, the extent of variation in the cheek muscle structures within the scorpaenoids has not been previously shown. Eight derived characters are recognized here.

(1) A1 origin narrow: In generalized percoids, a12 originates broadly from the faces of the upper part of the preopercle and hyomandibular. In scorpaenoids, a1 and a2 are separated by ramus mandibularis 5. In group 1-0, a1 originates broadly from the faces of the upper part of the preopercle and hyomandibular, whereas in group 1-1, the a1 origin is narrow and restricted to the hyomandibular. The condition of group 1-0 is thought to be more easily transformed from that of generalized percoids and is thus considered primitive.

(2) A1 associated with infraorbital 3: In group 2-0, a1 fibers are not associated with the infraorbitals, whereas those in group 2-1 have the dorsolateral portion of the a1 origin from the medial face of infraorbital 3. Because a12 fibers of generalized percoids are not associated with the infraorbitals, that of a1 in group 2-1 is proposed as having evolved with the development of the infraorbital stay.

(3) A1 fibers shortened: In group 3-0, which has the usual mouth structure of scorpaenoids, a1 fibers extend well forward along the primordial ligament between the lower jaw and the maxilla, resulting in a short maxillary tendon; in group 3-1, which has a projecting mouth, a1 fibers do not extend so far forward anteriorly, the maxillary tendon therefore being long. Because a projected mouth is thought to be specialized, the condition of group 3-1 is also considered derived.

(4) A1-maxillary tendon trifid: In generalized percoids and group 4-0, including most scorpaenoids, the a1-maxillary tendon branches anteriorly, resulting in two insertion points; in group 4-1, this tendon branches to three anterior insertion points.

(5) A23 origin shifted medially and dorsally: In group 5-0, a23 lies laterally to the levator arcus palatini; in group 5-1, the a23 origin has shifted to a medial position, sandwiching the levator arcus palatini; in group 5-2, the a23 origin has shifted even more, lying medially to the levator arcus palatini; in group 5-3, the a23 origin has shifted dorsally to the neurocranium. The condition of group 5-0 is thought to be easily transformed from that of generalized percoids. The progressive medial and dorsal shifts of the a23 origin seen in groups 5-0 to 5-3 are regarded as a transformational series.

(6) Levator arcus palatini insertion broad: In generalized percoids and group 6-0, the levator arcus palatini is inserted on the lateral face of the hyomandibular and dorsolateral margin of the metapterygoid; in group 6-1, the insertion of the levator arcus palatini includes the dorsal face of the symplectic.

(7) Adductor arcus palatini insertion shifted medially: In generalized percoids and group 7-0, the adductor arcus palatini is inserted on the posterodorsal face of the palatine and on most of the dorsolateral face of the entopterygoid; in group 7-1, the insertion covers less than half of the dorsolateral face of the crescent-shaped entopterygoid; in group 7-2, the insertion is on the dorsal margin or dorsomedial face of the crescent-shaped entopterygoid; in group 7-3, it is on the longitudinal ridge on the medial face of the entopterygoid. The medial shift of the adductor arcus palatini insertion is thought to represent increasingly derived conditions.

(8) Levator operculi origin shifted posteriorly: In generalized percoids and group 8-0, the levator operculi originates from the ventrolateral face of the pterotic; in group 8-1, its origin is branched, one from the pterotic and the other from the ventral face of the posttemporal; in group 8-2, the muscle originates only from the ventral face of the posttemporal.

Muscles of the ventral surface of the head

Although DIETZ (1914), ADAMICKA (1972), and YABE (1985) examined the muscles serving the ventral surface of the head in scorpaenoids, presenting valuable information, the extent of variation in these muscles in scorpaenoids has not been previously shown. Three derived characters are recognized here.

(9) Protractor hyoidei shortened: The posterior attachment of the protractor hyoidei is on the ventral face of the ceratohyal just anterior to the base of the fourth branchiostegal ray in group 9-0, including most scorpaenoids, the third branchiostegal ray in group 9-1, and the second branchiostegal ray in group 9-2. Group 9-0 includes all sebastids and scorpaenids and is considered the most primitive.

(10) Hyohyoides inferioris reduced: Yabe (1985) examined the muscles of the hyoid arch of scorpaeniforms, classifying the scorpaenoids into three types with regard to the hyohyoides inferioris. Three groups based on this muscle condition 10-0, 10-1, and 10-2 are also recognized here. In group 10-0, the left and right fiber bundles of the hyohyoides inferioris cross over each other; in group 10-1, the left and right origins are tendinous and meet in the midline, from which point the fiber bundles arise; in group 10-2, the hyohyoides inferioris is absent. The muscle is thought to have been reduced as a morphological specialization in scorpaenoids, with the condition of group 10-0 being considered primitive.

(11) Anterior section of hyohyoidei abductores transformed into a raphé; this section reduced and lost: Yabe (1985) recognized three conditions of the anterior section of the hyohyoides abductores in scorpaenoids. However, five morphotypes, 11-0, 11-1, 11-2, 11-3, and 11-4 are recognized here. In group 11-0, the left and right fiber bundles cross over each other between the bases of the first branchiostegal rays; in group 11-1, these elements meet in the midline giving rise posteriorly to fiber bundles, those leading to the left branchiostegal rays being ventral to those from the left side as in group 11-0; in group 11-2, the fibers of the anterior section of the muscle meet those from the opposite side in the midline where they are in broad contact, forming a raphé; in group 11-3, the muscle fibers are absent, with only a pair of tendons remaining. The tendons originate from the midline and are inserted on the medial sides of the first branchiostegal rays; in group 11-4, this muscle section is entirely absent. The condition of group 11-0 is parallels that of generalized percoids and is therefore considered primitive.

Muscles serving the branchial arches

Although Dietz (1914), Adamicka (1972), and Yabe (1985) examined the muscles serving the branchial arches, presenting valuable information, the extent of variation in the muscles serving the branchial arches within scorpaenoids has not been previously shown. Eight derived characters are recognized here.

(12) Levator externus 3 absent: In generalized percoids and group 12-0, including most scorpaenoids, levatores externi 1 to 4 are present; in group 12-1, levator externus 3 is absent.

(13) Levator posterior absent: In generalized percoids and group 13-0, including most scorpaenoids, the levator posterior is present; in group 13-1, it is absent.

(14) Obliquus dorsalis 2 present: In group 14-0, including most scorpaenoids, only obliquus dorsalis 3 is present; in group 14-1, obliquus dorsalis 2, connecting pharyngobranchial 2 and epibranchial 2, is also present. Obliqui dorsales 3 and 4 are known in *Elops*, but many acanthopterygians retain only obliquus dorsalis 3 (WINTERBOTTOM 1974a). Because obliquus dorsalis 2 is thought to be unique among acanthopterygians, the condition of group 14-1 is considered derived.

(15) Levator internus 3 sandwiched by obliquus dorsalis 3: In generalized percoids and group 15-0, obliquus dorsalis 3 lies posteriorly to levator internus 3, but in group 15-1, sandwiches the latter.

(16) Adductores 1 to 3 present: In generalized percoids and group 16-0, including most scorpaenoids, only adductores 4 and 5 are present; in group 16-1, adductores 1 to 5 are present.

(17) Transversus dorsalis anterior insertion unbranched: In generalized percoids and group 17-0, the insertion of the transversus dorsalis is branched into two, one being on the anterodorsal tip of pharyngobranchial 2 or its complex with pharyngobranchial 3 and the upper pharyngeal, and the other on the anterodorsal face of epibranchial 2 and sandwiched by levatores interni 2 and 3; in group 17-1, the insertion is not branched, the latter part only being present.

(18) Rectus ventralis insertion branched: In generalized percoids and group 18-0, the rectus ventralis is inserted on the anteroventral face of ceratobranchial 4; in group 18-1, the insertion of the muscle is branched, being on the anteroventral faces of ceratobranchial 4 and the lower pharyngeal.

Muscles between the pectoral girdle, neurocranium, hyoid arch, and branchial arches

YABE (1985) examined the muscles between the pectoral girdle, neurocranium, hyoid and branchial arches of scorpaenoids. Two derived characters are recognized here.

(19) Pharyngocleithralis externus origin shifted medially: In generalized percoids and group 19-0, the origin of the pharyngocleithralis externus is lateral to the origin of the sternohyoideus; in group 19-1, the origin has shifted medially, being sandwiched by the origin of the sternohyoideus; in group 19-2, the origin is dorsomedial to that of the sternohyoideus.

(20) Pharyngocleithralis internus origin bifid: In generalized percoids and group 20-0, including most scorpaenoids, the origin of the pharyngocleithralis is simple; in group 20-1, the origin is bifid.

Muscles serving the pectoral fin

The muscles serving the pectoral fin of scorpaenoids were examined by YABE (1985), but the extent of variation among scorpaenoids was not sufficiently shown. Two derived characters are recognized here.

(21) Coracoradialis absent: In generalized percoids and group 21-0, including most scorpaenoids, the coracoradialis is present; in group 21-1, it is absent.

(22) Coracoradialis origin shifted to cleithrum: In generalized percoids and group 22-0, the coracoradialis originates only from the posteromedial face of the posterior process of the coracoid; in group 22-1, the origin includes this process, but the posterolateral face of the posteroventral process of the cleithrum is connected with the posteroventral process of the coracoid by a membrane on which rather sparse fibers run from the cleithrum to the coracoradialis; in group 22-2, the coracoradialis is short and remarkably developed between the lowermost radial and the posterolateral face of the cleithrum posteroventral process; in group 22-3, only a short coracoradialis is present.

Muscles serving the pelvic fin

Yabe (1985) examined the muscles serving the pelvic fin in several scorpaenoid genera but extent of variation within scorpaenoids was not shown. Eight derived characters are recognized, seven being concerned with the loss of muscles in pataecids.

(23) Abductor superficialis pelvicus absent: Generalized percoids and group 23-0, including most scorpaenoids, have the abductor superficialis pelvicus. It is lost in group 23-1

(24) Abductor profundus pelvicus absent: Generalized percoids and group 24-0, including most scorpaenoids, have the abductor profundus pelvicus. It is lost in group 24-1.

(25) Arrector ventralis pelvicus absent: Generalized percoids and group 25-0, including most scorpaenoids, have the arrector ventralis pelvicus. It is lost in group 25-1.

(26) Adductor superficialis pelvicus absent: Generalized percoids and group 26-0, including most scorpaenoids, have the adductor superficialis pelvicus. It is lost in group 26-1.

(27) Adductor superficialis pelvicus fibers fused to those of adductor profundus pelvicus: In generalized percoids and group 27-0, including most scorpaenoids, the adductor superficialis pelvicus and adductor profundus pelvicus are separate, but are united in group 27-1.

(28) Adductor profundus pelvicus absent: Generalized percoids and group 28-0, including most scorpaenoids, have the adductor profundus pelvicus. It is lost in group 28-1.

(29) Arrector dorsalis pelvicus absent: Generalized percoids and group 29-0, including most scorpaenoids, have the arrector dorsalis pelvicus. It is lost in group 29-1.

(30) Extensor proprius absent: Generalized percoids and group 30-0, including most scorpaenoids, have the abductor superficialis pelvicus. It is lost in group 30-1.

Muscles serving the dorsal and anal fins

Despite the morphological interest in the anterior shift of the dorsal fin to the neurocranium in scorpaenoids, few studies have been made on the muscles serving the dorsal and anal fins, except RYBACHUK (1979) examining dorsal fin muscles in *Sebastes*. One derived character is recognized here.

(31) Inclinator dorsalis 1 reduced to tendon: In group 31-0, which has the dorsal fin well separated from the posterodorsal end of the neurocranium, fibers of inclinator dorsalis 1 are normally developed as in generalized percoids; in group 31-1, which has the dorsal fin originating above the neurocranium, the fibers of this muscle are reduced, with only a tendon remaining.

Carinal muscles

No comprehensive studies on the carinal muscles of scorpaenoids have been previously made. Two derived characters are recognized here.

(32) Supracarinalis anterior absent: Group 32-0, including most scorpaenoids, have the supracarinalis anterior, which has been lost by group 32-1. This character is apparently associated with the origin of the dorsal fin above the neurocranium, but some tetrarogids with the specialized dorsal fin condition have retained the primitive muscle character.

(33) Lateral branch of infracarinalis medius attached to pelvic girdle: In generalized percoids and group 33-0, the anterior limit of the infracarinalis medius is simple, being connected with the posterior process of the pelvic girdle; in group 33-1, it is divided the medial branch extending to the pelvic girdle as in group 33-0 and the lateral branch being attached to the ventral face of the base of the pelvic girdle or pelvic spine.

Muscles serving the caudal fin

RYBACHUK (1976) and YABE (1985) examined the muscles serving the caudal fin of several scorpaenoid genera. Two derived characters are recognized here.

(34) Flexor ventralis externus absent: In generalized percoids and group 34 - 0, including most scorpaenoids, the flexor ventralis externus is present. It is lost in group 34-1.

(35) Adductor dorsalis absent: Generalized percoids and group 35-0 have the adductor dorsalis. It is lost in group 35-1.

Body muscles

YABE (1985) examined the body muscles of scorpaeniforms, showing the insertion of the obliquus superioris on the posteroventral face of the neurocranium to be primitive. Two further derived characters of the obliquus superioris and three of the obliquus inferioris are recognized here.

(36) Obliquus superioris lying ventrally to Baudelot's ligament, if present: In group 36-0, the obliquus superioris from the posterior face of the neurocranium is penetrated by Baudelot's ligament; in group 36-1, the muscle bypasses the latter, lying ventrally to it. Group 36-0 includes sebastids and those scorpaenids with an apparently non-specialized swimbladder. Accordingly, their condition is considered primitive. Congiopodids have lost Baudelot's ligament.

(37) Obliquus superioris connected with supracleithrum: In group 37-0, including most scorpaenoids, the obliquus superioris from the posterior face of the neurocranium is not directly connected with the supracleithrum, being associated either through Baudelot's ligament or no at all; in group 37-1, the lateral part of the muscle is connected with the supracleithrum; in group 37-2, the entire muscle is connected with the supracleithrum. Because group 37-0 includes sebastids and scorpaenids, its condition is considered primitive.

(38) Plate-shaped element of obliquus inferioris between ventral postcleithrum and coracoid absent: Group 38-0, including most scorpaenoids, has a plate-shaped element of the obliquus inferioris lying laterally to the main muscle between the ventral postcleithrum and coracoid; such an element is absent in group 38-1. The variation of this element in percoids is not clear. Because group 38-0 includes most scorpaenoids, except congiopodids which have an undoubtedly specialized pectoral fin, its condition is considered primitive.

(39) Plate-shaped element of obliquus inferioris between ventral postcleithrum and coracoid tendinous: Group 38-0 is divided into two groups by character 39. In group 39-0, insertion of the above element on the coracoid is by rather broad muscle fibers; in group 39-1, the insertion is tendinous. Group 39-0, including all sebastids and most scorpaenids, is considered primitive.

(40) Anteroventral limit of the obliquus inferioris shifted posteriorly: In generalized percoids and group 40-0, including most scorpaenoids, the anteroventral limit of the main part of the obliquus inferioris is the posteroventral face of the cleithrum, ventral to the abductor profundus; in group 40-1, the anteroventral limit is the ventrolateral margin of the anteroventral arm of the coracoid; in group 40-2, the anteroventral part of the muscle is divided into two branches lying laterally to each other, one extending to the ventrolateral margin of the anteroventral arm of the coracoid and the ventral face of the adductor profundus, and the other to the pelvis. The posterior shift of the anteroventral limit of the obliquus inferioris is undoubtedly a specialized condition.

Swimbladder and associated muscles

MATSUBARA (1943) examined the swimbladder and extrinsic muscle of Japanese scorpaenoids, classifying them into nine types based on the following characters: presence or absence of the swimbladder, its relation to the layer of connective tissue lying outside the peritoneum, shape of the swimbladder, and structure of the extrinsic. HALLACHER (1974) examined the swimbladder muscles in a total of 82 species of *Sebastes*, 23 other scorpaenid genera and nine other scorpaeniform families. He classified swimbladder muscles of *Sebastes* into two morphotypes, the first having the extrinsic attached firmly to the pectoral girdle, at a point between the origin on the occipital cranium and the insertion on the vertebrae, and the second having the extrinsic bypassing the pectoral girdle. YABE (1985) studied the swimbladder muscles of cottoids and other scorpaeniforms, including *Sebastes, Helicolenus, Sebastolobus, Setarches, Pterois, Apistus,* and *Hypodytes*, classifying them into four types based on the following characters: position of the extrinsic insertions, branching condition of the extrinsic, relationship between the extrinsic, and Baudelot's ligament, and presence or absence of the intrinsic. Nine derived characters are recognized here.

(41) Swimbladder absent: The significance of the presence or absence of the swimbladder was difficult to evaluate, owing to the degree of variability in scorpaenoids. Both conditions occur in all scorpaenoid families except pataecids and the monotypic gnathanacanthid. This shows that loss of the swimbladder may have occurred many times in the different phyletic lines. Nevertheless, the absence of a swimbladder is considered as a derived condition for phylogenetic consideration. Group 41-0 has a swimbladder; group 41-1 does not.

(42) Extrinsic lying ventrally to ribs: In group 42-0, the extrinsic lies dorsally to several anterior pleural ribs, but ventrally in group 42-1. Because the extrinsic is evidently transformed from the obliquus superioris, which lies above the pleural ribs, the condition of group 42-0 is considered primitive.

(43) Extrinsic insertions branched: In group 43-0, including most scorpaenoids, each insertion of the extrinsic on the swimbladder or vertebral parapophysis is simple; in group 43-1, the setarchid *Ectreposebastes*, each insertion is branched. The branched condition of group 43-1 is unquestionably derived.

(44) Extrinsic origin restricted to supracleithrum: In generalized percoids and group 44-0, including most scorpaenoids, the origin of the extrinsic includes the occipital face of the neurocranium; in group 44-1, the origin is restricted to the medial face of the supracleithrum.

(45) Extrinsic not connected with supracleithrum: In group 45-0, the extrinsic is connected with the supracleithrum, but not so in group 45-1. A relationship between extrinsic and Baudelot's ligament was not found. Because group 45-0 includes sebastids and scorpaenids which also lack the intrinsic, it is considered primitive.

(46) Extrinsic connected directly with supracleithrum: Most of group 45-0 taxa (group 46-0) had the extrinsic connected with the supracleithrum through Baudelot's ligament; in group 46-1, the extrinsic is connected with the supracleithrum directly, apparently being the derived condition.

(47) Intrinsic present: Group 47-0, including most scorpaenoids does not have the intrinsic; it is present as a derived character in group 47-1.

(48) Intrinsic separated from extrinsic: Among group 47-1, the apistid (group 48-1) has a well developed intrinsic occurring separately from the extrinsic. Undoubtedly this is a unique and specialized condition.

(49) Baudelot's ligament absent: Group 49-0, including most scorpaenoids, retains Baudelot's ligament, being a typical acanthopterygian character; it is absent in group 49-1.

Neurocranium

Many workers have examined the scorpaenoid neurocranium (GILL 1888, EIGENMANN and BEESON 1893, 1894, CRAMER 1895, ALLIS 1909, STARKS 1926, DE BEER 1937, MATSUBARA 1934, 1936, 1943, 1955, ESCHMEYER and COLLETTE 1966, ESCHMEYER 1984, YABE 1985). In particular, MATSUBARA's (1943) detailed descriptions of Japanese scorpaenoids included six characters of the neurocranium: 1) general configuration of the supraoccipital and its relationship with the anterior interneural spines (here termed dorsal proximal pterygiophores), 2) presence or absence of the posterior opening of the myodome, 3) articulation of the epiotic with other cranial elements, 4) presence or absence of the basisphenoid, 5) presence or absence of the basisphenoid ventral process, and 6) relationship of the ectethmoid (ethmoid) to the vomer (prevomer). Five derived characters are recognized here. Of MATSUBARA's characters (above) 1) is discussed under characters 88 to 93, 3) under character 54, 4) under character 52, and 6) under character 50.

(50) Lateral ethmoid separated from prevomer: In group 50-0, the lateral ethmoid meets the prevomer anteroventrally, with the ethmoid and parasphenoid being separate; in group 50-1, the ethmoid and prevomer are separate, with the ethmoid meeting the parasphenoid. The condition of group 50-1 is considered derived because this is thought to have occurred as a result of the prolongation of the ethmoid (MATSUBARA 1943).

(51) Prevomerine teeth absent: In group 51-0, a villiform prevomerine tooth band is present; it is absent in group 51-1, the loss apparently being derived.

(52) Basisphenoid absent: In generalized percoids and group 52-0, including most scorpaenoids, the basisphenoid is present; it is absent in group 52-1.

(53) Epiotics of both sides meeting: In generalized percoids and group 53-0, including most scorpaenoids, the epiotics of each side are separated by the articulation of the supraoccipital and exoccipital; in group 53-1, the epiotics meet.

(54) Intercalar separated from prootic; intercalar absent: In generalized percoids and group 54-0, including most scorpaenoids, the intercalar meets the prootic posteriorly; in group 54-1, the intercalar is comparatively small and is separated from the prootic by the articulation of the pterotic and exoccipital; group 54-2 has lost the intercalar. The posterior shift and reduction of the intercalar are thought to have occurred as a result of specialization of the neurocranium.

Nasal and circumorbital bones

Many ichthyologists have regarded the infraorbital stay as the most important and, in practice, only structure characterizing the Scorpaeniformes. Because of the phylogenetic significance of the infraorbitals, they have been considered by many workers including ALLIS (1909), STARKS (1926), GREGORY (1933), MATSUBARA (1934, 1936, 1943), ESCHMEYER and COLLETTE (1966), and ESCHMEYER (1969). MATSUBARA's (1943) analysis of the infraorbitals of Japanese scorpaenoids, included three structural characters: 1) number of suborbitals (= infraorbitals), 2) degree of development of the infraorbital stay, and 3) extent of the infraorbital sensory canal. Four derived characters are recognized here. Of MATSUBARA's characters (above) 1) is discussed under characters 56 and 57, 2) under character 55, and 3) under character 58.

(55) Infraorbital stay absent: In group 55-0, including most scorpaenoids, an infraorbital stay is typically formed; in group 55-1, an infraorbital stay is absent. Because group 55-0 includes all sebastids and scorpaenids, the absence of the stay is considered derived.

(56) Infraorbitals 4 and 5 reduced: In group 56-0, infraorbitals 4 and 5 are present; in group 56-1, one of these bones is absent; in group 56-2, both infraorbitals 4 and 5 are absent. The condition of group 56-0 is considered primitive because a reduction of bones in fishes is generally believed to indicate specialization.

(57) Dermosphenotic absent: Group 57-0 has a dermosphenotic; it is absent in group 57-1. For the reason given for group 56-0, the former condition is considered primitive.

(58) Infraorbital-neurocranium sensory canal absent: In generalized percoids and group 58-0, a canal between infraorbital 3 and the temporal part of the neurocranium is present; it is absent in group 58-1.

Suspensorium

Allis (1909), Gregory (1933), and Matsubara (1934, 1936, 1940, 1943) examined the suspensorium of scorpaenoids, Matsubara (1943) noting three characters: 1) degree of development of the mesopterygoid (here termed entopterygoid), 2) diminution of the metapterygoid, and 3) diminution of the prepalatine process. Two derived characters are recognized here. Of Matsubara's characters (above) 1) and 2) are discussed under character 60.

(59) Palatine teeth absent: In group 59-0, palatine teeth are present; they are absent in group 59-1, an apparent specialization.

(60) Hyomandibular/metapterygoid space closed: In generalized percoids and group 60-0, including most scorpaenoids, a space is present between the hyomandibular and metapterygoid; in group 60-1, it is closed.

Hyoid arch

Only Matsubara (1943) considered the hyoid arches of Japanese scorpaenoids from a phylogenetic view point, discussing the number of branchiostegal rays. In addition to this character, the presence or absence of the basihyal is discussed here.

(61) Basihyal absent: Generalized percoids and group 61-0, including most scorpaenoids, have a basihyal; it is absent in group 61-1.

(62) Branchiostegal rays reduced in number: In group 62-0, including most scorpaenoids, the branchiostegal rays number seven, as in generalized percoids; group 62-1 is characterized by six branchiostegal rays; in group 62-2 by five.

Branchial arches

No comprehensive study of scorpaenoid branchial arches has been previously made. Seven derived characters are recognized here.

(63) Pharyngobranchial 1 absent: Generalized percoids and group 63-0, including most scorpaenoids, have pharyngobranchial 1; it is absent in group 63-1.

(64) Pharyngobranchials 2 and 3 fused; pharyngobranchials 2 and 3, and upper pharyngeal fused: In generalized percoids and group 64-0, including most scorpaenoids, pharyngobranchials 2 and 3, and the upper pharyngeal are separate; in group 64-1, pharyngobranchials 2 and 3 are fused; in group 64-2, pharyngobranchials 2 and 3, and the upper pharyngeal are fused.

(65) Pharyngobranchial 3 and upper pharyngeal fused: In generalized percoids and group 65-0, including most scorpaenoids, pharyngobranchial 3 and the upper pharyngeal are separate; in group 65-1, they are fused. The fusion of pharyngobranchials 2 and 3, and the upper pharyngeal is noted as character 64-2.

(66) Pharyngobranchial 2 teeth absent: In generalized percoids and group 66-0, pharyngobranchial 2 is toothed; it is toothless in group 66-1.

(67) Epibranchial 3 teeth absent: In generalized percoids and group 67-0, epibranchial 3 is toothed; it is toothless in group 67-1.

(68) Interarcual cartilage absent: Generalized percoids and group 68-0, including most scorpaenoids, have an interarcual cartilage; it is lost in group 68-1.

(69) Interarcual cartilage ossified: In generalized percoids and group 69-0, including most of group 68-0, the interarcual cartilage is unossified; in group 69-1, it is ossified.

Vertebrae and associated bones

MATSUBARA (1940, 1943), HOTTA (1961), and TAKAHASHI (1962) examined the vertebrae and associated bones of scorpaenoids, MATSUBARA (1943) especially presenting detailed information on the structure. and number of vertebrae of Japanese scorpaenids. However, previous studies have lacked any phylogenetic considerations of scorpaenoid vertebrae. Two derived characters are recognized here.

(70) More than 24 vertebrae: The number of vertebrae in fishes is often variable within a species and may change during early development due to temperature influences. However, each species has a given number of vertebrae within a certain range. In scorpaenoids a number of genera (group 70-0) usually have 24 vertebrae, the number usually associated with generalized percoids. Most of the other scorpaenoid genera (group 70-1) always have more than 24 vertebrae, none of those examined having less. Twenty-four vertebrae in scorpaenoids is considered to be the primitive condition, the number increasing with specialization. The tetrarogid *Richardsonichthys* and synanceiid *Synanceia* (group 70-R) usually have 24 vertebrae. This condition is believed to be a secondary reduction from a number greater than 24, because the most parsimonious cladogram of scorpaenoid relationships shows that such a step saves ten or 11 parallelisms.

(71) Pleural ribs absent: Generalized percoids and group 71-0, including most scorpaenoids, have pleural ribs; they are absent in group 71-1.

Caudal skeleton

Although MONOD (1967), YABE (1985), and FUJITA (1990) examined the caudal skeleton of some scorpaenoids, but to date there has been no comprehensive study on the scorpaenoid caudal skeleton, in spite of its phylogenetic importance. Ten derived characters are recognized here.

(72) Centrum and hemal spine of preural vertebra 2 fused: In generalized percoids and group 72-0, the centrum and hemal spine of preural vertebra 2 are autogenous; in group 72-1, they are fused.

(73) Centrum and hemal spine of preural vertebra 1 fused: In generalized percoids and group 73-0, including most scorpaenoids, the centrum and hemal spine of preural vertebra 1 are autogenous; in group 73-1, they are fused.

(74) Neural spine of preural vertebra 1 long: In generalized percoids and group 74-0, the neural spine of preural vertebra 1 is short; in group 74-1, it is long.

(75) Urostyle and uroneural fused: In generalized percoids and group 75-0, including most scorpaenoids, the urostyle and uroneural are autogenous; in group 75-1, they are fused.

(76) Urostyle and parhypural fused: In generalized percoids and group 76-0, including most scorpaenoids, the urostyle and parhypural are autogenous; in group 76-1, they are fused.

(77) Urostyle and hypural fused: In generalized percoids and group 77-0, the urostyle and hypural are autogenous; in group 77-1, they are fused.

(78) Epurals reduced in number: The epurals number is three in generalized percoids and group 78-0, two in group 78-1, and one in group 78-2.

(79) Parhypural and hypural fused: In generalized percoids and group 79-0, the parhypural and lowermost hypural are autogenous; in group 79-1, they are fused.

(80) Hypurals reduced in number: The hypural formula (defined in the description of the hypural) is 2+3 in generalized percoids and group 80-0, 1+3 in group 80-1, 1+2 in group 80-2, and 1+1 in group 80-3.

(81) Caudal fin rays unbranched: In generalized percoids and group 81-0, including most scorpaenoids, the principal caudal fin rays are branched; in group 81-1, they are simple.

Pectoral girdle

Starks (1930) and Matsubara (1943) studied the scorpaenoid pectoral girdle, the latter recognized five significant characters: 1) the form and mode of articulation of the posttemporal with the cranium, 2) relationship of the uppermost actinost (here termed radial) to the hypercoracoid (scapula), 3) form of the upper element of the postclavicle (postcleithrum), 4) width of the actinost, and 5) presence or absence of the postcoracoid process. Four derived characters are recognized here. Matsubara's character 2) is discussed under character 83.

(82) Postcleithrum absent: Generalized percoids and group 82-0 including most scorpaenoids, have both dorsal and ventral postcleithra; they are absent in group 82-1.

(83) Scapula and uppermost radial fused: In group 83-0, the scapula and uppermost radial are autogenous; in group 83-1, they are fused. The autogenous condition is considered primitive because a similar state exists in generalized percoids. In the congiopodid *Congiopodus*, the scapula and uppermost radial are autogenous (83 - R). However, this condition is believed to be secondarily derived, because the most parsimonious cladogram of scorpaenoid relationships, shows that such a step saves four parallelisms.

(84) Space between coracoid and lowermost radial closed: In generalized percoids and group 84-0, including most scorpaenoids, the space between the coracoid and lowermost radial, accommodating the coracoradialis, is present; in group 84-1, it is closed.

(85) Pectoral fin rays unbranched: In generalized percoids and group 85-0, the middle rays of the pectoral fin are branched; in group 85-1, all pectoral fin rays are unbranched.

Pelvic girdle

The only detailed study of scorpaenoid pelvic girdles to date is that of MATSUBARA (1943), who described the pelvic girdles of Japanese scorpaenids in detail. Two derived characters are recognized here.

(86) Pelvic fin rays reduced in number: The pelvic fin rays number five in generalized percoids and group 86-0, including most scorpaenoids, four in group 86-1, three in group 86-2, two in group 86-3, and one in group 86-4.

(87) Pelvic fin rays unbranched: In generalized percoids and group 87-0, including most scorpaenoids, some pelvic fin rays are branched; in group 87-1, all pelvic fin rays are unbranched.

Dorsal and anal fin supports

MATSUBARA (1943) and YABE (1985) studied the dorsal and anal fin supports in scorpaenoids, the former describing the anterior dorsal pterygiophores and neural spines in his discussion of the supraoccipital, and the latter presenting the general arrangement and evolutionary trends shown by these elements in scorpaeniforms. However, to date the structural variations existing in these supports in scorpaenoids have not been sufficiently detailed. Eight derived characters are recognized here.

(88) Supraneural absent: Group 88-0 has one supraneural in interneural space 1; a supraneural is absent in group 88-1. Generalized percoids have two or three supraneurals in interneural space 1 or 2. Because the condition of group 88-0 is more easily transformed from that of generalized percoids, it is considered primitive.

(89) Neural spines 1 and 2 articulating anteriorly: In generalized percoids and group 89-0, the neural spines do not articulate with the anterior bony elements; in group 89-1, neural spine 1 articulates anteriorly with the posterodorsomedial face of the neurocranium; in group 89-2, neural spine 1 articulates anteriorly with the posterodorsomedial face of the neurocranium, and neural spine 2 anteriorly with neural spine 1.

(90) Neural spines 1 and 2 short: In generalized percoids and group 90-0, including most scorpaenoids, neural spines 1 and 2 are normally developed compared with the posterior elements; in group 90-1, the former are short.

(91) Dorsal proximal pterygiophores 1 and 2 separate: In group 91-0, including most scorpaenoids, the dorsal fin anteriormost proximal pterygiophore supports dorsal spines 1 and 2; in group 91-1, each dorsal fin proximal pterygiophore supports a dorsal spine. The condition of group 91-1 is apparently unique in scorpaenoids and is considered the result of the loss of dorsal spine 1.

(92) Dorsal proximal pterygiophores shifted anteriorly, type-1: The anterior shift of the dorsal proximal pterygiophores in the character 92-1 to 92-7 series is believed to have occurred in a different phyletic line from the character 93-1 and 93-2 series, because of the differing in the articulation of the neural spine to the neurocranium and the separation of the anterior pterygiophores supporting dorsal spines 1 and 2. In group 92-0, proximal pterygiophores 1+2 and 3 are inserted in interneural space 3 or on the posterodorsomedial face of the neurocranium, proximal pterygiophore 4 and those following are inserted in the interneural spaces of the same number; in groups 92-1 to 92-7, the dorsal proximal pterygiophores have shifted anteriorly step by step, as explained in the description of the proximal pterygiophore. The condition of group 92-0 is considered primitive because it is thought to be the most easily transformed from that of generalized percoids.

(93) Dorsal proximal pterygiophores shifted anteriorly, type - 2: Group 93-0 is identical to group 92-0; in the series of groups 93-1 and 93-2, the anterior dorsal proximal pterygiophores have shifted anteriorly step by step, as explained in the description of the proximal pterygiophore.

(94) Dorsal fin rays unbranched: In generalized percoids and group 94-0, the dorsal fin soft-rays are branched; in group 94-1, all dorsal fin rays are unbranched.

(95) Anal fin rays unbranched: In generalized percoids and group 95-0, the anal fin soft-rays are branched; in group 95-1, all anal fin rays are unbranched.

The conditions of 95 characters in the 55 scorpaenoid genera examined are summarized in tables 24 (muscles) and 25 (skeletons).

Table 24. Muscles character conditions in 55 scorpaenoid genera. Space indicates the most primitive condition; "—" indicates not applicable.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Sebastidae																																																	
Sebastes			1																																													—	
Sebastiscus			1																																													—	
Hozukius			1																																													—	
Helicolenus			1																																						1							—	
Adelosebastes			1																																						1							—	
Sebastolobus			1																																						1							—	
Trachyscorpia			1																																						1							—	
Plectrogenium			1														1																								1							—	
Setarchidae																																																	
Setarches										2				1																																		—	
Lioscorpius										2				1																						1					1	1			1	—		—	
Ectreposebastes										2				1						1																1					1	1	1					—	
Neosebastidae																																																	
Neosebastes										2		1																														1		1		1		—	
Maxillicosta										2																					1		1						1		1					1		—	
Scorpaenidae																																																	
Pontinus																																																—	
Neomerinthe																																									1							—	
Phenacoscorpius																																																—	
Parascorpaena																																									1							—	
Scorpaena																																									1							—	
Iracundus																																									1							—	
Scopaenopsis																																									1	1						—	
Scorpaenodes																																				1						1			1	—	1		
Hoplosebastes																																				1						1			1	—	1		
Pterois								1																												1						1			1	—	1		
Ebosia								1																									1			1					1	1			1	—	1		
Brachypterois								1										1															1			1					1	1			1	—	1		
Dendrochirus								1																									1			1					1	1			1	—	1		
Parapterois								1																									1			1					1	1			1	—	1		
Rhinopias																																				1			1		1	1						—	
Taenianotus											2							1																		1			1		1	1		1				—	
Apistidae																																																	
Apistus		1			1		1	1		2	1				1		1				1	—									1					1			1			1			1	—	1	1	
Tetrarogidae																																																	
Notesthes		1			2		1	1									1					1									1		1						1		1	1						—	
Centropogon		1			2		1	1									1					1									1		1						1		1	1						—	
Gymnapistes		1			2		1	1									1					1									1		1			1			1			1						—	
Neocentrogon		1			2		1	1														1									1		1			1			1			1						—	
Ocosia		1			2		1	1														1									1		1			1			1		1	1						—	
Paracentropogon		1			2		1	1									1					1									1	1	1						1			1						—	
Hypodytes		1			2		1	1														1									1	1	1			1			1			1						—	
Liocranium		1			2		1	1				1										1									1	1	1			1			1			1			1	—	1	—	
Ablabys		1			2		1	1		1	2											1									1	1	1			1			1			1						—	
Richardsonichthys		1			2		1	1		1	2	1										1									1	1	1			1			1		1	1						—	
Synanceiidae																																																	
Inimicus					1		1	1		1	2	1						1	1			1									1		1		1	1	1		1		1	1						—	
Synanceia					1		3	1		1	2	1							1			1									1		1	1	1	1	1		1			1						—	
Erosa					1		3	1		1	2	1							1			1									1		1	1	1	1	2		1		1	1						—	
Choridactylus					1		1	1		1	2						1		1			1									1		1		1	1	1		1			1						—	
Minous					1		2	1		1	2						1		1			1											1		1	1	1		1			1						—	
Congiopodidae																																																	
Congiopodus			1		1	1	2	2	2	2	3		1			1	1	1	1			3												1	1	—		1	—	1		1				1		—	1
Alertichthys			1		1		2	1	1	2	2		1			1	1	1	2			2					1							1	1	—		1	—	2		1				1		—	1
Zanclorhynchus			1		1	1	3	2	1	2	2		1	1		1	1	1	2			2					1				1			1	1	—		1	—	2	1	1				1		—	1
Gnathanacanthidae																																																	
Gnathanacanthus					1		2		1								1				1	—														1						1						—	
Aploactinidae																																																	
Aploactis		1			2		2	1	1	1	4	1			1				1			1								1	1	1	1		1	1			1		1	1				1		—	
Erisphex					1		2	1	1	1	4	1			1				1			1								1	1	1	1		1	1			1			1				1		—	
Sthenopus					1		1	1	1	1	4	1			1				1			1								1	1	1	1		1	1			1		1	1				1		—	
Pataecidae																																																	
Aetapcus	1			1	3		2		1	1	2	1			1				1			1	1	1	1	1	—	1	1	1	1	1		1	1	1			1			1						—	
Pataecus	1			1	3		2		1	1	2	1			1				1			1	1	1	1	1	—	1	1	1	1	1		1	1	1			1			1						—	
Neopataecus	1			1	3		2		1	1	2	1			1				1			1	1	1	1	1	—	1	1	1	1	1		1	1	1			1			1						—	

Table 25. Osteological character conditions in 55 scorpaenoid genera. Space indicates the most primitive condition; "-" indicates not applicable.

	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
Sebastidae																																															
Sebastes																						1										2			1												
Sebastiscus																						1										2			1												
Hozukius																						1										2			1												
Helicolenus																						1										2			1												
Adelosebastes																						1										2			1												
Sebastolobus																						1										2															
Trachyscorpia							1													1																								
Plectrogenium							1									1					1																		1						
Setarchidae																																															
Setarches							2	1	1																																					
Lioscorpius							2	1	1																																					
Ectreposebastes							2	1	1																																					
Neosebastidae																																															
Neosebastes							1														1													1					1						
Maxillicosta							1			1							1				1													1					1						
Scorpaenidae																																															
Pontinus							1		1								1														1					1										
Neomerinthe							1		1								1														1															
Phenacoscorpius							2		1								1				1										2															
Parascorpaena							1		1																							2			1					1						
Scorpaena							1		1																							2			1					1						
Iracundus							1	1	1	1																					2			1					1						
Scopaenopsis							1		1	1									1												2			1					1						
Scorpaenodes							1		1	1																					1								1						
Hoplosebastes							2		1	1																					1								1						
Pterois	1						2		1	1																					1					1			1						
Ebosia	1						2		1	1																					1								1						
Brachypterois	1						2		1	1																					1								1						
Dendrochirus	1						2		1	1						1															1								1						
Parapterois	1						2		1	1							1														1								1						
Rhinopias	1						1		1	1																					2			1					1						
Taenianotus	1	1					1		1	1																					2					1			1						
Apistidae																																															
Apistus							1	1													1									1	2			1	1				1						
Tetrarogidae																																															
Notesthes							1	1													1									1	2			1					1	2						
Centropogon							1	1													1									1	2			1					1	2						
Gymnapistes							1	1													1									1	2			1					1	2						
Neocentropogon							1	1										1				1									1	2			1					1	2						
Ocosia							1	1										1				1									1	2			1					1	2						
Paracentropogon							1	1										1	1			1									1	2			1			1		1	2						
Hypodytes							1	1										1	1			1									1	2			1			1		1	2						
Liocranium							1	1		1						1	1	1			1									1	2			1			1		1	2						
Ablabys							1	1										1	1			1									1	2			1					1	2						
Richardsonichthys							1	1									1	1	1			R									1	3			1					1	2						
Synanceiidae																																															
Inimicus							1	1		1	1				1		-	1		1	1		1		1	1		1	1	1	3			1					1	2	1					
Synanceia		1					1	1		1	1					1	1	1			R				1					1	3			1					1	2	1					
Erosa							1	1		1							1	1			1				1	1			1	1	3			1			1		1	2	1					
Choridactylus		1					1	1		1		1			2	-	-	1		1	1		1		1					1	2			1					1	2	1					
Minous							1	1		1	1				2	-	-	1		1	1		1		1			1		1	2	1		1		1		1	1	2	1				1	1
Congiopodidae																																															
Congiopodus	1	1		1	1		2	1		1	1	1	2					1			1				1	1		1	1	1	3			R		1		1	1	1		1	-	2		
Alertichthys	1	1	1	1	1		2	1		1			1	1				1			1		1		1	1		1	1	1	3	1		1		1		1	1	1		1	-	1	1	1
Zanclorhynchus	1		1	1	1		2	1		1			1	1				1			1				1			1	1	1	3	1		1		1		1	1	1		1	-	1	1	1
Gnathanacanthidae																																															
Gnathanacanthus		1					1	1		1	1	1				1	1	1			1		1	1	1		1	1	1	1	3	1		1	1	1		1	1	2			1	-	1	1
Aploactinidae																																															
Aploactis					1		1	1		1	1		1		2	-	-	1	1		1	1	1		1					1	2	1		1		1	2	1	1	2			2	-	1	1
Erisphex					1		1	1		1	1		1		2	-	-	1		1	1	1	1		1			1		1	3	1		1		1	2	1	1	2			3	-	1	1
Sthenopus	1				1		1	1		1	1	1	1		2	-	-	1		1	1	1	1		1					1	3	1		1		1	2	1	1	2			4	-	1	1
Pataecidae																																															
Aetapcus	1	1	1		2	1	1	1		1	1	1	1		2	-	-	1			1		1	1	1	1	1	1	2	1	3	1	1	1		1	3	1	1	2			5	-	1	1
Pataecus	1		1		2	1	1	1		1	1	1	1		2	-	-	1			1		1	1	1	1	1	1	2	1	3	1	1	1		1	4	1	1	2			6	-	1	1
Neopataecus	1		1		2	1	1	1		1	1	1	1		2	-	-	1			1		1	1	1	1	1	1	2	1	3	1	1	1		1	4	1	1	2			7	-	1	1

2. RELATIONSHIPS

Figures 34 to 36 show the most parsimonious cladogram of 55 scorpaenoid genera based on 95 characters. The cladogram was constructed by parsimony (minimum number of steps) by hand. Characters were equally weighted. Subsequent character derivations (two or more derived states) were regarded individually for parsimony arguments. Polarity reversals were not hypothesized unless four or more parallelisms were saved, viz. the number of vertebrae (character 70) in *Richardsonichthys* and *Synanceia*, being a secondary reduction, the autogenous scapula and uppermost radial (character 83) in *Congiopodus*, being a secondary separation, and the absence of the infraorbital stay in pataecids, being a secondary reduction. For family ranking, the criterion of equal ranking for sister-groups was not always employed because it would lead to an excessively high rank for taxa branching near the root, for example *Sebastes* and its relatives, and an excessively low rank for taxa which had branched many times from the root, for example, *Neopataecus* and its relatives. Current classification systems were considered in the determination of the family ranking. In this section, the character number is shown in parenthesis.

Position of the Scorpaenoidei among the Scorpaeniformes

The scorpaenoid genera examined here share two derived characters: presence of an infraorbital stay and a single supraneural. These characters are not unique in the scorpaenoids however, but one shared throughout the Scorpaeniformes and have been used in support of the monophyly of the order. In fact, a single character establishing the monophyly of the Scorpaenoidei has not yet to be found. Nevertheless, the Scorpaenoidei is considered a natural group, because the other scorpaeniforms have been shown to be derived from non-scorpaenoid ancestors.

Recently, however, the Scorpaeniformes have been provisionally divided into several suborders: the Scorpaenoidei, Hexagrammoidei, Platycephaloidei, Congiopodoidei, and Cottoidei (LAUDER and LIEM 1983), or the Scorpaenoidei, Platycephaloidei, Anoplopomatoidei, Hexagrammoidei, and Cottoidei (NELSON 1984).

MATSUBARA (1943) hypothesized that the dactylopterid, peristediid, and triglid lineages were branched initially, followed by the cottid, agonid, cyclopterid, and liparidid lineages. Finally, the "generalized scorpaenid", hexagrammid, and anoplopomatid lineages and "specialized scorpaenid", bembrid, platycephalid, and hoplichthyid lineages arose. If his hypothesis was correct, that the Scorpaenidae occupied the basal position of the Scorpaeniformes, from which several derivatives evolved, the former should be considered the paraphyletic group. He stated that the hexagrammids, anoplopomatids, and "generalized scorpaenids" were closely related because the hexagrammid, *Hexagrammos* *otakii*, the anoplopomatid, *Erilepis zonifer*, and the "generalized scorpaenid", *Sebastes glaucus*, strikingly resembled each other in having an unarmed neurocranium and a very wide and roundish interorbital space. However, such resemblances are undoubtedly secondary as QUAST (1965) proposed after comparisons of hexagrammids with other scorpaeniforms. MATSUBARA (1943) suggested that the cottid, agonid, cyclopterid, and liparidid lineage shared with *Setarches* a common ancestor because of two derived characters, the absence of the basisphenoid and intervention of the scapula and coracoid by radials 2 and 3. However, ESCHMEYER and COLLETTE (1966) recognized a basisphenoid in all four species of *Setarches, Lioscorpius*, and *Ectreposebastes*. In addition, setarchids and the other scorpaenoid families, except sebastids, share one derived character (character 56 - 1), the absence of one of infraorbitals 4 and 5, whereas YABE (1985) found both infraorbitals 4 and 5 in some cottoids, being the most primitive condition for the latter. Hence, MATSUBARA's suggestion cannot be seriously entertained.

MATSUBARA (1943) also speculated that *Sebastolobus* was related to *Plectrogenium*, with bembrids, platycephalids, and hoplichthyids having arisen from an ancestor not very unlike *Plectrogenium*. MATSUBARA and OCHIAI (1955) and WASHINGTON *et al.* (1984) supported such a speculation. However, the presence of two supraneurals in the bembrid, *Parabembras*, as well as in generalized percoids, compared with scorpaenoids which have one or no supraneural, suggests that the bembrid, platycephalid, and hoplichthyid lineage was established earlier than the Scorpaenoidei ancestor, the similarity between the former and *Sebastolobus* or *Plectrogenium* being the result of parallelisms or shared primitive characters.

WASHINGTON *et al.* (1984) proposed the Apistinae to be a sister group of the Triglidae and Peristediidae on the basis of the following characters: bilobed swimbladder with intrinsic muscle, elongate pectoral fin rays, one to three free lower pectoral fin rays, and characteristic structure of the head bones, especially the infraorbitals. Although some other authors included the Triglidae and Peristediidae in the Scorpaenoidei (LAUDER and LIEM 1983, NELSON 1984), generalized triglids lack the following derived characters shared by *Apistus* and other scorpaenoids: only one of infraorbitals 4 and 5 reduced (character 56 -1), hypurals numbering 1+3 (80-1), dermosphenotic absent (57), parhypural and hypural fused (79), hypurals numbering 1+2 (80-2), and scapula and uppermost radial fused (83). Of these characters, (56-1) is shared by all scorpaenoids, except sebastids, (80-1) is shared by all scorpaenoids except sebastids, setarchids, and neosebastids, and (57), (79), (80-2), and (83) are shared by *Apistus*, tetrarogids, synanceiids, congiopodids, the gnathanacanthid, aploactinids, and pataecids. Therefore, the Triglidae and Peristediidae are believed to have evolved in a different phyletic line from that of *Apistus* or other scorpaenoids.

Relationships within the Scorpaenoidei

At branching point A, the Scorpaenoidei branches into A1 and A2.

Sebastidae new family (Fig. 35)

Branch A1 comprises eight genera, *Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes, Sebastolobus, Trachyscorpia,* and *Plectrogenium*, which share two derived characters. A1 branches into B1 and B2. The genera of B1, *Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes,* and *Sebastolobus*, share two derived characters. B1 branches

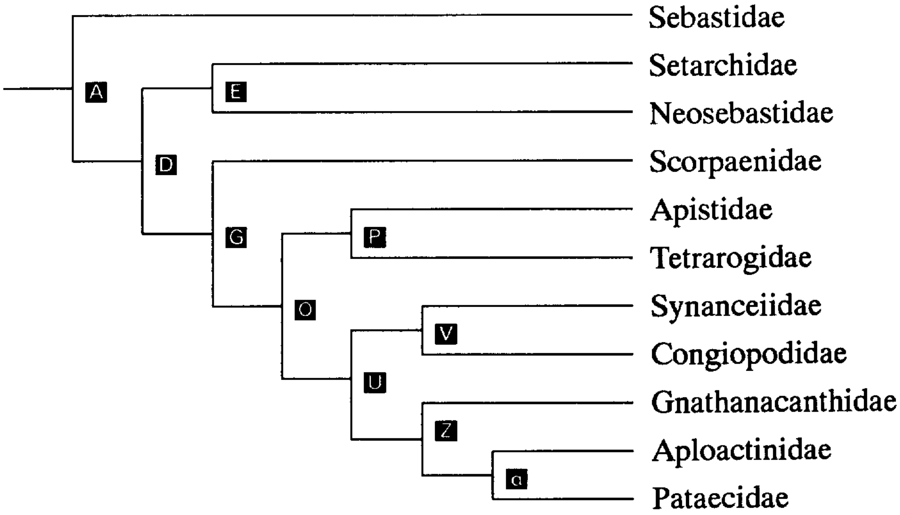

Fig. 34. Cladogram of the families of the suborder Scorpaenoidei. The relationships among the genera are shown in figures 35-36. Letters indicate the branching points.

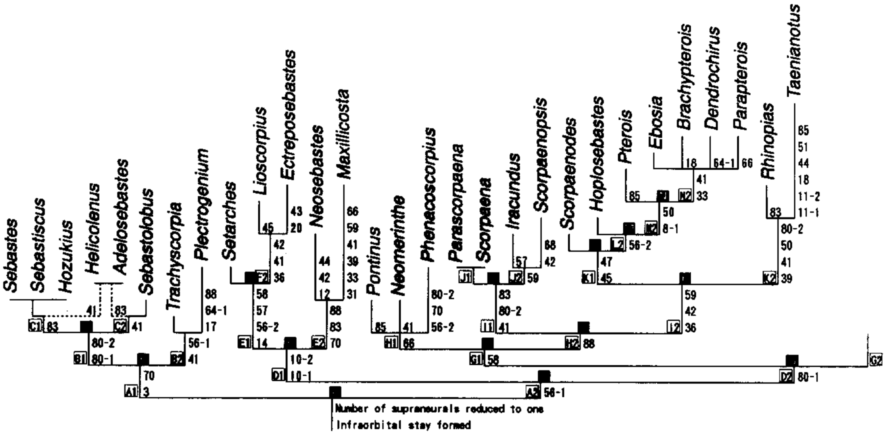

Fig. 35. Cladogram of genera in the Sebastidae (branch A1), Setarchidae (E1), Neosebastidae (E2), and Scorpaenidae (G1). Character numbers are arranged along each branch.

into C1 and *Sebastolobus*. The genera of C1, *Sebastes, Sebastiscus*, and *Hozukius*, share one derived character, (83). *Sebastolobus* has one derived character, (41). On the other hand, *Helicolenus* and *Adelosebastes*, included in B1, have both of (83) and (41), and it is impossible to determine whether these two genera were derived from C1 or from C2. The genera of B2, *Trachyscorpia* and *Plectrogenium*, share two derived characters, (41) and (56 - 1). *Trachyscorpia* has no further derived characters, whereas *Plectrogenium* has three.

Within the Sebastidae, two parallelisms are recognized: (41) in B2 and C2, and (41) in C2 and *Helicolenus-Adelosebastes*, or (83) in C1 and *Helicolenus-Adelosebastes*.

Because A1 branch forms a sister group of all other scorpaenoids, it must be treated as an independent taxon ranked as between suborder and genus. Because two parallelisms, which indicate close relationships between A1 genera, do not support a higher subdivision of the taxon, the new family Sebastidae was established for branch A1.

During his study on the intergeneric relationships in scorpaenoids, MATSUBARA (1943), from his examination of the infraorbitals, suspensorium, hyoid arch, neurocranium, vertebrae, pectoral girdle, pelvic girdle, and swimbladder and its associated muscles in Japanese genera, hypothesized that scorpaenoid specialization followed three directions, forming three generic groups: *Sebastes*-stem, *Scorpaena*-stem, and *Cocotropus*-stem, the last being a sub-branch of the *Scorpaena*-stem. He regarded the *Sebastes*-stem as the most primitive, proposing two subfamilies, the Sebastinae, including the primitive *Sebastes* and *Sebastiscus*, the more specialized *Helicolenus* and *Hozukius*, and the most specialized Neosebastinae. The present findings contradict the above hypothesis in the following respect: *Neosebastes* is not closely related to *Sebastes, Sebastiscus, Hozukius*, or *Helicolenus*, but instead to setarchids and the other scorpaenoids. MATSUBARA also considered the subfamily Sebastolobinae, containing only *Sebastolobus*, as a derivation from the *Scorpaena*-stem. He regarded as closely related to the more highly specialized *Plectrogenium*. These genera were each given monogeneric subfamily status. ESCHMEYER (1969) considered *Trachyscorpia* as a member of the subfamily Sebastolobinae owing to the sharing by *Trachyscorpia* and *Sebastolobus* of a bilobed pectoral fin, fleshy lower pectoral fin rays and pelvic and anal fins, extra large anterior foramina, and median depression on the frontal. ESCHMEYER, ABE, and NAKANO (1979) also considered *Adelosebastes* as belonging to the Sebastolobinae because of the former's sharing the above characters with *Trachyscorpia* and *Sebastolobus*, and the absence of a swimbladder. The relationships shown herein are at odds with MATSUBARA's hypotheses in the following respects: *Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes*, and *Sebastolobus* are closely related, forming the sister group of *Trachyscorpia* and *Plectrogenium*. *Adelosebastes* is possibly closely related to *Helicolenus*, because they share the same derived characters, in spite of two parallelisms. Comparisons of the *Sebastes*-stem and Hexagrammoidei, and *Sebastolobus, Plectrogenium*, and the Platycephaloidei were discussed in the preceding section.

The genera of A2 share one derived character. A2 branches into D1 and D2. The genera of D1 share two derived characters. D1 branches into E1 and E2.

Setarchidae new family (Fig. 35)

Branch E1 comprises three genera, *Setarches, Lioscorpius*, and *Ectreposebastes,* which share four derived characters. E1 branches into *Setarches* and F2, the former having no further derived characters, whereas the F2 genera, *Lioscorpius* and *Ectreposebastes*, share three. *Lioscorpius* has one additional derived character, and *Ectreposebastes* has two, (20) and (43), both being unique in scorpaenoids.

Branch E1 is considered quite distinct from E2, because only a single parallelism (41) (in F2 and *Maxillicosta*) were recognized among the included genera. Although this does not support separate family ranking for branch D1, such status can be accorded for each of E1 and E2. Therefore, the new family Setarchidae was established for the branch E1.

MATSUBARA (1943) regarded the subfamily Setarchinae, including *Setarches* and *Macroscorpius* (synonym of *Lioscorpius*), as a special offshoot from his *Scorpaena*-stem. ESCHMEYER and COLLETTE's (1966) review of Setarchinae sensu MATSUBARA recognized three genera, *Setarches, Lioscorpius*, and *Ectreposebastes*. The relationships shown herein disagree with the hypotheses suggested by MATSUBARA because the Setarchidae is more closely related to the Neosebastidae than to his *Scorpaena*-stem.

Neosebastidae new family (Fig. 35)

Branch E2 comprises two genera, *Neosebastes* and *Maxillicosta*, which share four derived characters. The former has three additional derived characters, and the latter has six.

The new family Neosebastidae was established, because branch E2 is considered quite distinct from E1 as stated earlier.

MATSUBARA (1943) speculated that *Neosebastes* was a highly specialized offshoot from his *Sebastes*-stem, characterized by a T-shaped infraorbital 3 and chained infraorbitals 4 and 5 surrounding the posterior border of the eye. On the other hand, ESCHMEYER and POSS (1976) reviewed *Maxillicosta* and inferred its close relationship with *Neosebastes* on the basis of osteological characters. This study concurs with their conclusion because the two genera share three derived characters, (70), (83), and (88). However, the relationships shown herein are at odds with MATSUBARA's hypotheses in the following respect: *Neosebastes* and *Maxillicosta* are not closely related to sebastids, but instead form the sister group of setarchids. In fact, neosebastids plus setarchids form the sister group of all the remaining scorpaenoids except sebastids.

The genera of D2 share one derived character, (80-1). D2 branches into G1 and G2.

Scorpaenidae (Fig. 35)

Branch G1 comprises 16 genera, *Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias*, and *Taenianotus*, which share one derived character. G1 branches into H1 and H2. The genera of H1 share one derived character. H1 branches into three genera *Pontinus, Neomerinthe*, and *Phenacoscorpius. Pontinus* has one additional derived character, *Neomerinthe* has one, and *Phenacoscorpius* has three. The genera of H2 share one derived character. H2 branches into I1 and I2. The genera of I1 share three derived characters. I1 branches into J1 and J2. J1 comprises *Parascorpaena* and *Scorpaena*, sharing no further derived characters. The genera of J2, *Iracundus* and *Scorpaenopsis*, share one derived character. *Iracundus* has one additional derived character. *Scorpaenopsis* has two. The genera of I2 share three derived characters. I2 branches into K1 and K2. The genera of K1 share two derived characters. K1 branches into *Scorpaenodes* and L2, the former having no further derived characters. The genera of L2 share one derived character. L2 branches into *Hoplosebastes* and M2, the former having no further derived characters. The genera of M2 share two derived characters. M2 branches into *Pterois* and N2, the former having an additional derived character. N2 branches into *Ebosia, Brachypterois, Dendrochirus*, and *Parapterois. Ebosia* has no further derived characters and the remaining genera one each, respectively. The genera of K2 share four derived characters. K2 branches into *Rhinopias* and *Taenianotus*, the former having an additional derived character, and the latter six.

Within the Scorpaenidae, 12 parallelisms are recognized: (66) in H1 and *Parapterois*, (85) in *Pontinus, Pterois*, and *Taenianotus*, (41) in *Neomerinthe*, I1, and N2, (56 - 2) in *Phenacoscorpius* and L2, (80-2) in *Phenacoscorpius*, I1, and K2, (83) in I1 and *Rhinopias*, (59) in *Scorpaenopsis* and I2, (50) in M2 and K2, and (18) in *Brachypterois* and *Taenianotus*.

Matsubara (1943) proposed five subfamilies in his *Scorpaena*-stem: the Scorpaeninae, Pteroinae, Setarchinae, Sebastolobinae, and Plectrogeninae. The relationships shown herein are at odds with Matsubara's hypotheses in the following respects: *Scorpaenodes* and *Hoplosebastes* are closely related to *Pterois, Ebosia, Brachypterois, Dendrochirus*, and *Parapterois*, the latter corresponding to the subfamily Pteroinae sensu Matsubara. If the subfamily Pteroinae was limited so as to include *Pterois, Ebosia, Brachypterois, Dendrochirus*, and *Parapterois, Hoplosebastes* should be also given subfamilial status since it represents the sister group of M2 comprising the above five genera. This being so, *Scorpaenodes*, K2, I1, and H1 should also be treated as subfamilies or higher taxa. Such a subdivision of the Scorpaenidae does not seem practical owing to the following reasons:

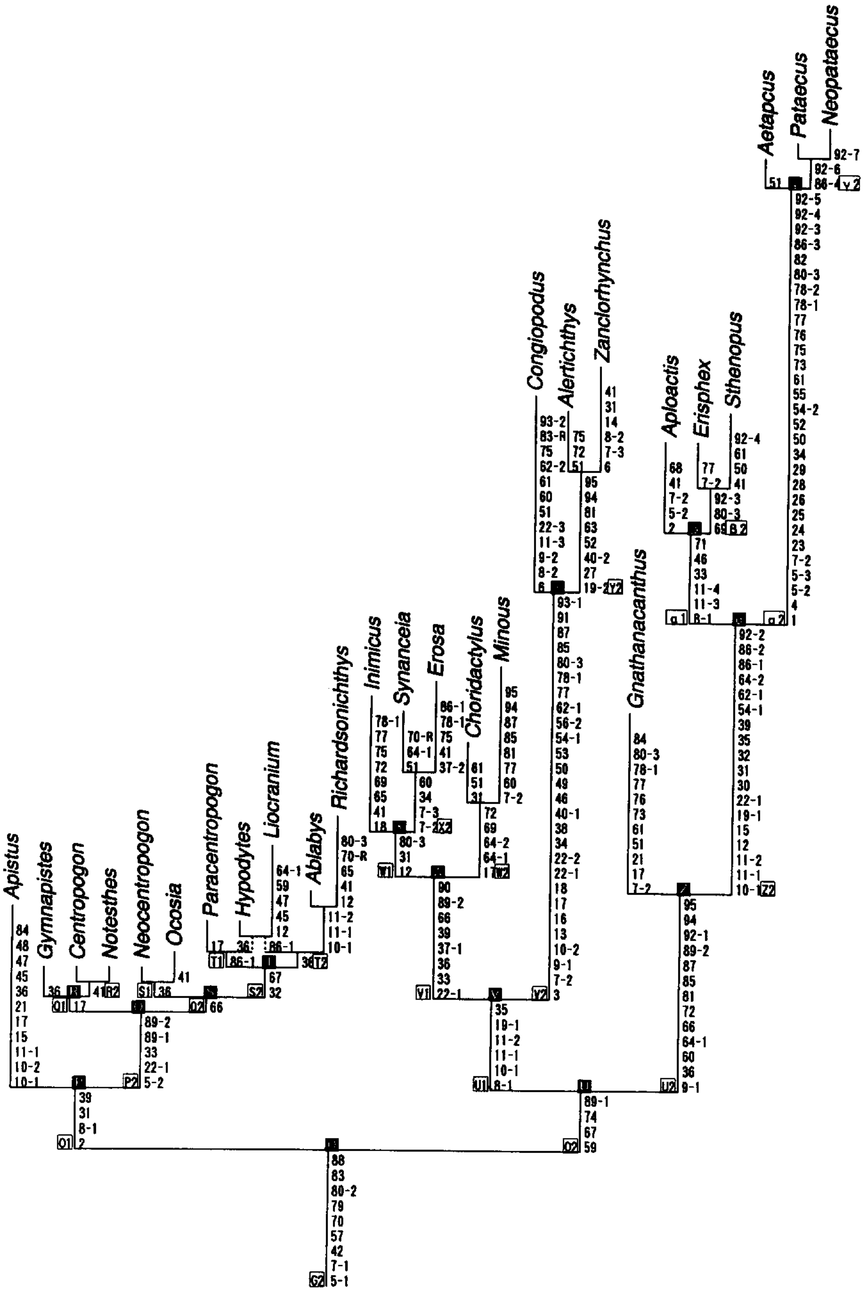

Fig. 36. Cladogram of genera in the Apistidae (*Apistus*), Tetrarogidae (branch P2), Synanceiidae (V1), Congiopodidae (V2), Gnathanacanthidae (*Gnathanacanthus*), Aploactinidae (α1), and Pataecidae (α2). Character numbers are arranged along each branch.

the possibility of future changes in the branching pattern within the Scorpaenidae still remains, since some branches are not firmly supported by uniquely derived characters. This is implied by the 12 parallelisms occurring among only 16 genera. In addition, a derived character unique to *Hoplosebastes* and *Scorpaenodes* was not found. Clearly, additional information is needed for the definition of lower taxa in the Scorpaenidae. The phylogenetic relationships of the following genera remain unrevealed: *Rhinopias*-related genera reviewed by ESCHMEYER *et al.* (1973), *Idiastion*, considered a close relative of *Phenacoscorpius* by ESCHMEYER (1965b), *Sebastapistes*, and *Thysanichthys*.

The genera of G2 share nine derived characters, of which (5-1),(7-1), and (79) are unique in scorpaenoids. G2 branches into O1 and O2.

The genera of O1 share four derived characters. O1 branches at P into the Apistidae and Tetrarogidae.

Apistidae new family (Fig. 36)

Apistus has 11 additional derived characters, of which (48) is unique in scorpaenoids.

Apistus forms the sister group of branch P2, which comprises ten closely related genera. The above 11 derived characters of *Apistus* and five derived characters shared by the P2 genera support the separation of *Apistus* from the latter. Therefore, the new family Apistidae was established.

MATSUBARA (1943) deduced that the *Cocotropus*-stem was a sub-branch of his *Scorpaena*-stem, owing to the well developed infraorbital 3 and reduction of infraorbitals 4 and 5, in the former, which he regarded as the most specialized branch of the three stems. He subdivided the *Cocotropus*-stem into three groups: *Apistus* (the most generalized); *Minous, Erosa*, and *Inimicus*; and *Neocentropogon, Hypodytes, Ocosia, Erisphex, Aploactis*, and *Cocotropus*. The relationships shown herein are at odds with MATSUBARA's hypotheses regarding *Apistus* in the following respects: the swimbladder of *Apistus* is specialized amongst scorpaenoids in having derived characters (36), (45), (47), and (48) as mentioned above. Furthermore, *Apistus* is a sister group of the Tetrarogidae, including *Neocentropogon, Hypodytes*, and *Ocosia*, that were regarded by MATSUBARA as members of the most specialized subdivision. A comparison of *Apistus*, triglids, and peristediids was given earlier.

Tetrarogidae (Fig. 36)

Branch P2 comprises ten genera, *Gymnapistes, Centropogon, Notesthes, Neocentropogon, Ocosia, Paracentropogon, Hypodytes, Liocranium, Ablabys*, and *Richardsonichthys*, which share five derived characters. P2 branches into Q1 and Q2. The genera of Q1 share one derived character. Q1 branches into *Gymnapistes* and R2. *Gymnapistes* has an additional derived character. The genera of R2, *Centropogon* and *Notesthes*, share one derived character, but possess no further derived characters. The genera of Q2 have one derived character. Q2 branches into S1 and S2. The genera of S1, *Neocentropogon* and *Ocosia*, share one derived character, (36), with *Ocosia* having an additional derived character. The genera of S2 share two derived characters. S2 branches into T1 and T2. T1, including *Paracentropogon*, is characterized by one derived character, (86-1). T2, including *Ablabys* and *Richardsonichthys*, is characterized by one derived character, (36). On the other hand *Hypodytes* and *Liocranium* share both characters (36) and (86-1), making impossible the determination of their derivation, being either from T1 or T2. *Paracentropogon* has an additional derived character. *Hypodytes* has no further derived characters, whereas *Liocranium* has five. *Ablabys* and *Richardsonichthys* share three additional derived characters. *Ablabys* has no further derived characters, whereas *Richardsonichthys* has five.

Within the Tetrarogidae, seven parallelisms are recognized: (17) in Q1 and *Paracentropogon*, (36) in *Gymnapistes*, S1, and T2, (41) in R2, *Ocosia*, and *Richardsonichthys*, (12) in *Liocranium* and *Richardsonichthys*, (64-1) in *Liocranium* and *Richardsonichthys*, and either (86-1) in T1, and *Hypodytes-Liocranium* or (36) in *Hypodytes-Liocranium*.

MATSUBARA (1943) defined the family Congiopodidae as the third subdivision of his *Cocotropus*-stem, dividing it into two subfamilies, the Tetraroginae, including *Neocentropogon, Hypodytes*, and *Ocosia*, and the Aploactininae, including *Erisphex, Aploactis*, and *Cocotropus*. He regarded the Tetraroginae as being slightly less specialized than the Aploactininae. POSS and ESCHMEYER (1975) proposed the Tetraroginae, including *Amblyapistus* (synonym of *Ablabys*), *Hypodytes, Liocranium, Ocosia, Paracentropogon, Ptarmus, Snyderina, Tetraroge*, and several other genera of uncertain status. The relationships proposed here indicate that MATSUBARA's Tetraroginae (present Tetrarogidae) is not closely related to his Aploactininae (present Aploactinidae), but instead forms a sister group of *Apistus*. Furthermore, the definition of the Tetraroginae by POSS and ESCHMEYER is upheld, although familial status is given.

The genera of O2 share four derived characters. Of these (74) is unique in scorpaenoids. O2 branches into U1 and U2. The genera of U1 share six derived characters. U1 branches into V1 and V2.

Synanceiidae (Fig. 36)

Branch V1 comprises five genera, *Inimicus, Synanceia, Erosa, Choridactylus*, and *Minous*, which share eight derived characters. Of these (37-1) and (90) are unique in scorpaenoids. V1 branches into W1 and W2. The genera of W1, *Inimicus, Synanceia*, and *Erosa*, share three derived characters. W1 branches into *Inimicus* and X2, the former having eight derived characters. The genera of X2, *Synanceia* and *Erosa*, share four derived characters. *Synanceia* has three additional derived characters. *Erosa* has five additional derived characters. Of these (37 - 2) is unique in scorpaenoids. The genera of W2, *Choridactylus* and *Minous*, share four derived characters. *Choridactylus* has three additional derived characters, whereas *Minous* has eight.

Within the Synanceiidae 11 parallelisms are recognized: (31) in W1 and *Choridactylus*, (41), (75), and (78-1) in *Inimicus* and *Erosa*, (69) and (72) in *Inimicus* and W2, (77) in *Inimicus*and *Minous*, (7-2) and (60) in X2 and *Minous*, (51) in *Synanceia* and *Choridactylus*, and (64-1) in *Synanceia* and W2.

MATSUBARA (1943) placed the family Synanceiidae as the second subdivision of his *Cocotropus*-stem, dividing it into two subfamilies, the Minoinae, including *Minous*, and the Synanceiinae, including *Inimicus* and *Synanceia*. He regarded the Minoinae as less specialized than the Synanceiinae. ESCHMEYER and RAMA-RAO's (1973) review of MATSUBARA's Synanceiinae recognized six genera, including *Synanceia* and *Erosa*. ESCHMEYER, HALLACHER, and RAMA-RAO (1979) and ESCHMEYER, RAMA-RAO, and HALLACHER (1979) later reviewed the Minoinae and Choridactylinae, respectively, including *Minous* in the former and *Choridactylus* and *Inimicus* in the latter. Eleven parallelisms amongst the above five genera indicate their close relationship. The most parsimonious cladogram suggests close relationships between *Synanceia* and *Erosa*, and between *Choridactylus* and *Minous*. The former concurs with ESCHMEYER and RAMA-RAO (1973), but the latter does not agree with ESCHMEYER, RAMA-RAO, and HALLACHER (1979). The close relationships among the synanceiid genera do not support the subdivision of the family.

Congiopodidae (Fig. 36)

Branch V2 comprises three genera, *Congiopodus*, *Alertichthys*, and *Zanclorhynchus*, which share 27 derived characters. Of these characters (9-1), (13), (16), (22-2), (40-1), (49), (53), (91), and (93-1) are unique in scorpaenoids. V2 branches into *Congiopodus* and Y2. The former has 12 additional derived characters, of which (9-2), (22-3), and (93-2) are unique in scorpaenoids. The genera of Y2, *Alertichthys* and *Zanclorhynchus*, share eight derived characters, of which (27), (40-2), and (63) are unique in scorpaenoids, and have three and five additional derived characters.

Within Congiopodidae four parallelisms are recognized: (6) and (8-2) in *Congiopodus* and *Zanclorhynchus*, and (51) and (75) in *Congiopodus* and *Alertichthys*.

MATSUBARA (1943) recognized the Congiopodidae as a group comprising the present Tetrarogidae and Aploactinidae. However, most workers have considered the

Congiopodidae as a group inhabiting only in the Southern Hemisphere (SMITH 1958, QUAST 1965, GREENWOOD *et al.* 1966, HUREAU 1971, NELSON 1984). The present results support this.

The genera of U2 share 13 derived characters, of which (92-1) is unique in scorpaenoids. U2 branches into the family Gnathanacanthidae and Z2.

Gnathanacanthidae (Fig. 36)

The monotypic gnathanacanthid genus *Gnathanacanthus* has 11 additional derived characters.

Although the Gnathanacanthidae has been recognized as a member of the Scorpaenoidei, being treated either as a family (SCOTT *et al.* 1974) or subfamily (of Pataecidae, comprising Pataecinae and Gnathanacanthinae) (NELSON 1984), no phylogenetic study of the family has been previously made. The relationships proposed here indicate that Gnathanacanthidae is a sister group of the Aploactinidae+Pataecidae (=Z2), defined by 13 derived characters. Gnathanacanthidae has further 11 derived characters, whereas Aploactinidae and Pataecidae share another 18, supporting the independent family status of Gnathanacanthidae.

The genera of Z2 share 18 derived characters, of which (30), (86-2), and (92-2) are unique in scorpaenoids.

Z2 branches into $\alpha1$, corresponding to the family Aploactinidae, and $\alpha2$, corresponding to the family Pataecidae.

Aploactinidae (Fig. 36)

Branch $\alpha1$ comprises three genera, *Aploactis, Erisphex*, and *Sthenopus*, which share six derived characters, of which (11-4) is unique in scorpaenoids. $\alpha1$ branches into *Aploactis* and $\beta2$, the former having five additional derived characters. The genera of $\beta2$, *Erisphex* and *Sthenopus*, share three derived characters, and have two and four additional derived characters.

Within the Aploactinidae two parallelisms are recognized: (7-2) in *Aploactis* and *Erisphex* and (41) in *Aploactis* and Sthenopus.

Although MATSUBARA (1943) regarded his Aploactininae as a more specialized sister group of his Tetraroginae, the relationships proposed here show that the former in fact forms a sister group of the Pataecidae.

Pataecidae (Fig. 36)

Branch $\alpha2$ comprises thee genera, *Aetapcus, Pataecus*, and *Neopataecus*, which share 29 derived characters, of which (1), (4), (5-3), (23), (24), (25), (26), (28), (29), (55), (82), (86-3), and

(92-5) are unique in scorpaenoids. $\alpha 2$ branches into *Aetapcus* and $\gamma 2$, the former having one additional derived character. The genera of $\gamma 2$, *Pataecus* and *Neopataecus*, share two derived characters, both (86-4) and (92-6) being unique in scorpaenoids. *Pataecus* has no further derived characters, whereas *Neopataecus* has one additional derived character (92-7), unique in scorpaenoids.

The Pataecidae has been treated both as a family (Scott *et al.* 1974) and as a subfamily (of the Pataecidae with the Gnathanacanthinae) (Nelson 1984). However, no phylogenetic study has been previously made. This study demonstrates the close relationships of the Pataecidae with the Aploactinidae, rather than with the Gnathanacanthidae. Twenty-nine derived characters shared by the three genera support the family status of Pataecidae.

New classification of the Scorpaenoidei

Based on the above relationships, a new classification for the Scorpaenoidei is proposed below. Asterisked genera were not examined during the study.

Suborder Scorpaenoidei

Sebastidae new family

Sebastes, Sebastiscus, Hozukius, Helicolenus, Adelosebastes, Sebastolobus, Trachyscorpia, Plectrogenium

Setarchidae new family

Setarches, Lioscorpius, Ectreposebastes

Neosebastidae new family

Neosebastes, Maxillicosta

Scorpaenidae

Pontinus, Neomerinthe, Phenacoscorpius, Parascorpaena, Scorpaena, Iracundus, Scorpaenopsis, Scorpaenodes, Hoplosebastes, Pterois, Ebosia, Brachypterois, Dendrochirus, Parapterois, Rhinopias, Taenianotus, Idiastion, Sebastapistes*, Thysanichthys*, Hipposcorpaena*, Pogonoscorpius**

Apistidae new family

*Apistus, Cheroscorpaena**

Tetrarogidae

Gymnapistes, Centropogon, Notesthes, Neocentropogon, Ocosia, Paracentropogon, Hypodytes, Liocranium, Ablabys, Richardsonichthys, Coccotropsis, Cottapistus*, Glyptauchen*, Snyderina*, Tetraroge*, Vespicula**

Synanceiidae

Inimicus, Synanceia, Erosa, Choridactylus, Minous, Dampierosa, Pseudosynanceia*, Leptosynanceia*, Trachycephalus**

Congiopodidae,

*Congiopodus, Alertichthys, Zanclorhynchus, Perryena**

Gnathanacanthidae

Gnathanacanthus

Aploactinidae

Aploactis, Erisphex, Sthenopus, Acanthosphex, Adventor*, Aploactisoma*, Bathyaploactis*, Cocotropus*, Eschmeyer*, Kanekonia*, Neoaploactis*, Paraploactis*, Peristrominous*, Prosoproctus*, Ptarmus*, Xenaploactis**

Pataecidae

Aetapcus, Pataecus, Neopataecus

Caracanthidae

*Caracanthus**

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カサゴ亜目魚類の系統分類学的研究

石田　実

カサゴ亜目魚類の系統類縁関係を再構築し、それに基づいた分類体系を提唱するために、55属の全身の筋肉系、骨格系を観察し、95の形質を選択した。

形質の状態は、まず、外群として選んだ一般的なスズキ亜目の状態と一致するものを原始的とした。この比較ができないものは疑いなく特殊なものを派生的とし、それでも決定できないものは、メバル科およびフサカサゴ科に見られるものを原始的とした。系統類縁関係の推定は分岐学的手法を用いた。形質状態は等価と仮定し、原則として形質状態の逆転を認めなかった。分岐図は進化の段階数が最も少なくなるものを選んだ。

カサゴ目の他の分類群がカサゴ亜目に属しない先祖から派生したこと、従ってカサゴ亜目が自然群であることを明らかにした。構築した分岐図から55属について系統類縁関係を推定し、それに基づいて、4新科を含む11科を設定した。これらは以下の順序で派生したと推察された：メバル科、シロカサゴ科＋ヒレナガカサゴ科、フサカサゴ科、ハチ科＋ハオコゼ科、オニオコゼ科＋フエフキオコゼ科、Gnathanacanthidae、イボオコゼ科、および Pataecidae。