

Anatomical description and phylogenetic classification of the orbicular velvetfishes (Scorpaenoidea: *Caracanthus*)

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Abstract Anatomical characters for two species of the orbicular velvetfishes (*Caracanthus*) are described, and the phylogenetic position of the genus among the superfamily Scorpaenoidea is estimated cladistically on the basis of morphological characters belonging to 112 transformation series. *Caracanthus* is nested within the family Scorpaenidae, having close relationships with *Taenianotus* and *Pteroidichthys*. Validity of the family Caracanthidae was not supported, *Caracanthus* being included within the Scorpaenidae.

Key words *Caracanthus* · Caracanthidae · Anatomical description · Phylogeny · Classification

The genus *Caracanthus* Krøyer, 1845, containing four species, is the sole member of the scorpaenoid family Caracanthidae (Eschmeyer, 1986), recognized by the uniqueness of its external morphology and habitat (e.g., Gill, 1889; Lindberg, 1971; Nelson, 1976, 1984, 1994; Paxton et al., 1989). The species of *Caracanthus* are distributed in tropical and subtropical waters, all of them being cryptic, living among the branches of corals, such as *Acropora* and *Poecillopora* (Eschmeyer, 1986; Cole, 2003).

Although several studies of *Caracanthus* exist, few considered both anatomical information and phylogenetic position (see Imamura and Shinohara, 1998). Quast (1965) discussed some morphological characters of *Caracanthus* in his phylogenetic study of Hexagrammidae. Although he indicated that Caracanthidae shared three characters (forked posttemporal bone, three pharyngeal tooth plates, and anvil-shaped actinosts) with Hexagrammidae, all are thought to represent primitive conditions of scorpaenoid fishes (Yabe, 1985; Ishida, 1994). Mizuno and Tominaga (1980) reported *Caracanthus unipinna* from Japanese waters, describing osteological and scale characters, but did not discuss its phylogenetic position. Mandrytsa (2001) estimated the phylogenetic relationships of the Scorpaenoidei, including *Caracanthus*, using 93 morphological characters. Although he inferred *Caracanthus* was nested within Scorpaenidae, following his analysis using PAUP version 3.1.1 (fig. 225), he rejected that hypothesis, indicating Caracanthidae to be a sister-group of the Scorpaenidae on the basis of a further analysis by hand (fig. 228). Cole (2003) suggested a close relationship of Caracanthidae and Scorpaenidae following her investigation of the gonad morphology of *Caracanthus*. More recently, Smith and Wheeler (2004) investigated the molecular phylogeny on

69 “scorpaeniform” species including *Caracanthus*. They assumed *Caracanthus* is nested within a monophyletic clade containing the families Scorpaenidae and Sebastidae (sensu Imamura, 2004).

We herein describe the osteological and myological characters of *Caracanthus* and estimate its phylogenetic position among the Scorpaenoidea (sensu Imamura and Yabe, 2002) from a cladistic perspective, with the aim of reflecting that phylogeny in the higher classification of *Caracanthus*.

Materials and Methods

Terminology follows Imamura (2004) for both osteology and myology, the institutional abbreviations following Leviton et al. (1985). The genera *Sebastiscus* and *Sebastes*, which Imamura (2004) recovered as the first and second branches, respectively, from the superfamily Scorpaenoidea, were selected as outgroups (other scorpaenoids, including the *Caracanthus*, being the ingroup) for the phylogenetic analysis of the Scorpaenoidea, so as to infer the phylogenetic position of *Caracanthus* among the superfamily. The data were analyzed using PAUP* version 4.0 (Swofford, 2002), with 1000 heuristic searches involving random addition sequences and tree-bisection-and-reconnection (TBR) branch swapping. Character evolution was assumed as “ordered” (Wagner parsimony), or “unordered” (Fitch parsimony) when the transformation series (TS) contained a derived “loss” or characters were difficult to order because of their many modifications.

Material examined. *Caracanthus maculatus*, USNM 261331 (25.0 mm); *C. unipinna*, NSMT-P 21252 (2 specimens, 20.7–27.7 mm).

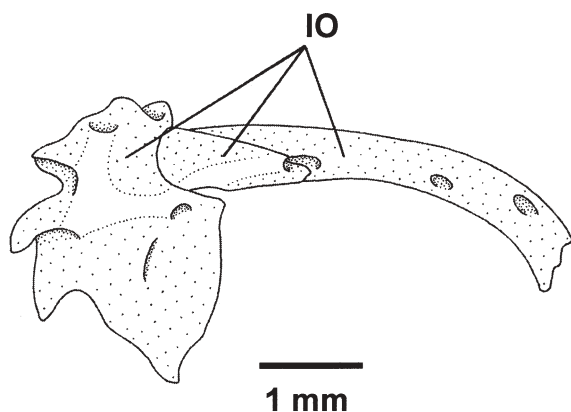


Fig. 1. Lateral aspect of the infraorbitals (IO) of *Caracanthus unipinna*, NSMT-P 21252, 27.7 mm SL

Other material. *Pteroidichtys amboinensis*, BSKU 42479 (41.5 mm).

Other scorpaenoid materials (86 species belonging to 18 families and 59 genera) used for the phylogenetic analysis are listed in Imamura (1996, 2004).

Results

Osteology. *Infraorbitals* (Fig. 1).—The infraorbitals comprise three elements, firmly connected with each other and forming a tubular structure for the infraorbital sensory canal, but not continuous with that of the neurocranium (the canal on posterior to eye completely absent). The fourth and fifth infraorbitals are absent. The sixth infraorbital (=dermosphenotic) is fused with the sphenotic. The suborbital ridge and its spines are absent. The first infraorbital (=lachrymal) articulates with the lateral ethmoid dorsally. The second infraorbital is situated between the first and third infraorbitals and lacks sensory openings in the middle portion. The third infraorbital, being free from the lateral ethmoid, bears three sensory openings anteriorly, ventrally, and slightly forward of the posterior margin, respectively, the sensory canal opening being directed backward. The suborbital stay, situated on the posterior portion of the third infraorbital, is narrowly truncated and connected with the preopercle. A suborbital shelf is absent.

Neurocranium (Fig. 2).—The neurocranium comprises 16 elements, the nasal, prevomer, lateral ethmoid, ethmoid, frontal, parietal, sphenotic, pterosphenoid, parasphenoid, prootic, pterotic, epiotic, intercalar, exoccipital, supraoccipital, and basioccipital. The basisphenoid is absent. The dorsal surface of the neurocranium, including the frontal and parietal, has knoblike processes (*Caracanthus unripinna*) or spines (*C. maculatus*). The nasal is a tubular spined bone, loosely attached to the ethmoid. The nasals on each side are separated from each other. The prevomer lacks teeth. The lateral ethmoid articulates with the dorsal process of the first infraorbital laterally, and also with the prevomer and ethmoid anteriorly. The frontals and parietals on each side are fused, respectively. The parietal bears the supratemporal

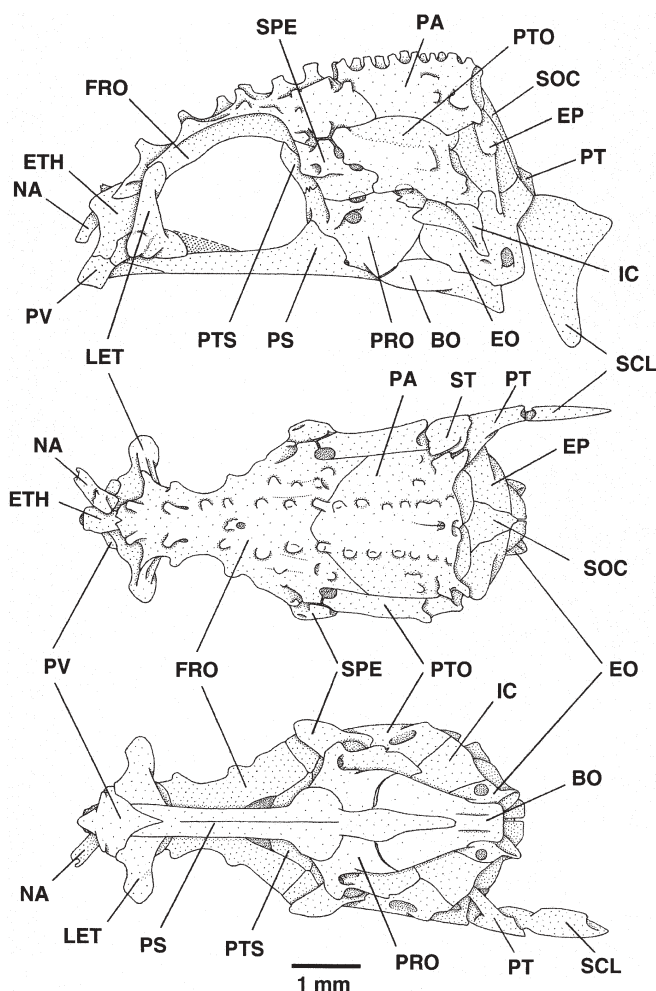


Fig. 2. Lateral (above), dorsal (middle), and ventral (below) aspects of the neurocranium of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. BO, basioccipital; EP, epiotic; EO, exoccipital; ETH, ethmoid; FRO, frontal; IC, intercalar; LET, lateral ethmoid; NA, nasal; PA, parietal; PRO, prootic; PS, parasphenoid; PT, posttemporal; PTO, pterotic; PTS, pterosphenoid; PV, prevomer; SCL, supracleithrum; SOC, supraoccipital; SPE, sphenotic; ST, supratemporal

sensory canal with blunt spines posteriorly, the canals on both sides being continuous. The parasphenoid is separated from the pterosphenoid by the prootic. The pterotic receives the sensory canal, which lacks a lateral opening and is continuous with that in the sphenotic anteriorly, the lateral extrascapular medially, and the preopercle posterolaterally. The intercalar is connected with the prootic anteriorly and the posttemporal dorsally via a ligament. The epiotics are separated by the supraoccipital, which has a low ridgelike crest (supraoccipital crest) in *C. maculatus* and also in a single specimen (27.7 mm SL) of *C. unipinna*.

Jaws (Fig. 3).—The jaws include the premaxilla and maxilla in the upper jaw, and the dentary, anguloarticular, retroarticular, and coronomeckelian in the lower jaw. The premaxilla and dentary both have canine-like teeth. A supramaxilla is absent. The premaxilla has four processes,

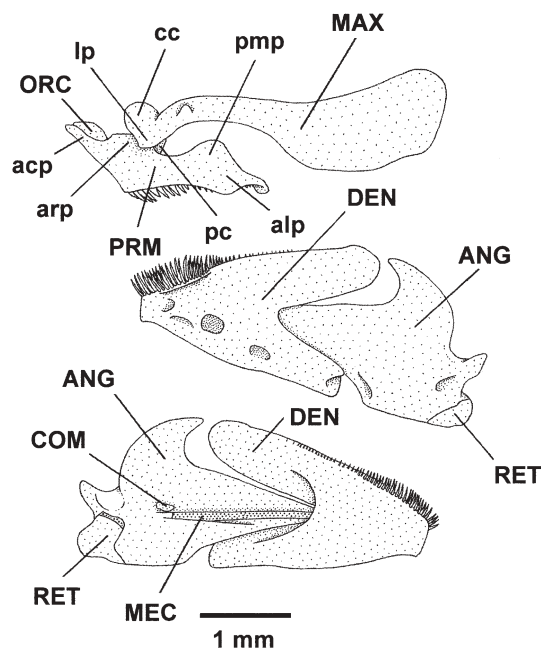


Fig. 3. Lateral aspects of the upper (above) and lower jaws (middle), and medial aspect of the lower jaw (below) of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. ANG, anguloarticular; COM, coronomeckelian; DEN, dentary; MAX, maxilla; MEC, Meckelian cartilage; ORC, ossified rostral cartilage; PRM, premaxilla; RET, retroarticular; acp, ascending process; alp, alveolar process; arp, articular process; cc, cranial condyle; lp, lateral process; pc, premaxillary condyle; pmp, postmaxillary process

the ascending, articular, alveolar, and postmaxillary processes. The ascending process has an ossified rostral cartilage posteriorly. A notch between the ascending process and articular process is absent, both parts being continuous. The maxilla consists of a head bearing a lateral process, premaxillary and cranial condyles, and a long shaft. A slender ligament (ethmo-premaxillary ligament, sensu Stiassny, 1986) connects the lateral process with the anterior process of the ethmoid. The ligamentum primordium is inserted onto a small process on the anterolateral surface of the shaft, and a tendon from the adductor mandibulae section 1 (A1) is inserted onto the posterior surface of the premaxillary condyle. The anterior projection of the anguloarticular is inserted into the deep notch of the dentary. The anguloarticular articulates dorsolaterally with the condyle of the quadrate and is attached to the retroarticular ventrally. The Meckelian cartilage lies on the medial surface of the anguloarticular.

Suspensorium and opercular bones (Fig. 4).—The suspensorium consists of seven elements, the hyomandibula, metapterygoid, quadrate, symplectic, entopterygoid, ectopterygoid, and palatine. The opercular bones include four elements, the preopercle, opercle, interopercle, and subopercle. The metapterygoid bears a prominent lamina (=metapterygoid lamina, sensu Matsubara, 1943) dorsally, separated by a space from the hyomandibula and supporting the levator arcus palatini dorsomedially. The

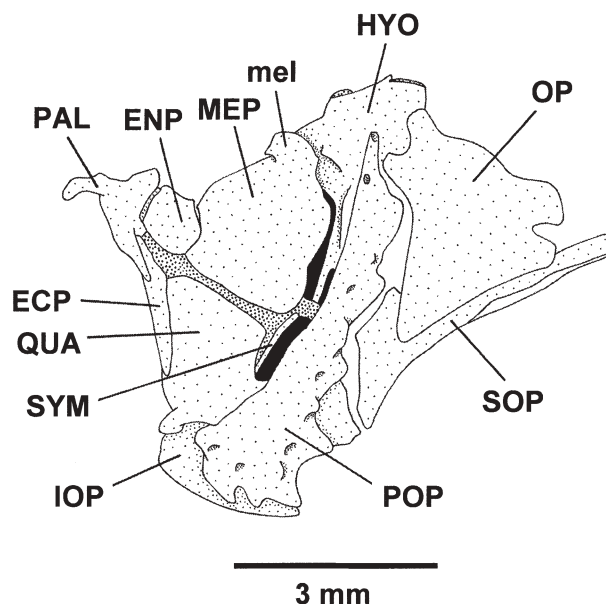


Fig. 4. Lateral aspect of the suspensorium and opercular bones of *Caracanthus unipinna*, NSMT-P 21252, 27.7 mm SL. ECP, ectopterygoid; ENP, entopterygoid; HYO, hyomandibula; IOP, interopercle; MEP, metapterygoid; OP, opercle; PAL, palatine; POP, preopercle; QUA, quadrate; SOP, subopercle; SYM, symplectic; mel, metapterygoid lamina

entopterygoid is small and thin. The palatine lacks teeth ventrally. The ectopterygoid is connected with the palatine anteriorly, quadrate posteriorly and entopterygoid dorsally. The preopercle has spines posteriorly and also a tubelike preoperculomandibular canal along its posterior border. The opercle bears two backwardly-directed spines posteriorly (35-0), and the interopercle a strong spine ventrally. The subopercle is L-shape and thin.

Hyoid and branchial arches (Figs. 5–7).—The hyoid arch consists of seven ossified elements, the basihyal (character 36-0), two hypohyals, ceratohyal, epihyal, interhyal, seven branchiostegal rays, and urohyal, and the branchial arch consists of five, including three basibranchials and three hypobranchials and four ceratobranchials, epibranchials, and pharyngobranchials. The ceratohyal and epihyal are sutured. The urohyal is small and low, and situated below the first basibranchial obliquely. The fifth ceratobranchial, second to fourth pharyngobranchials, and third epibranchial bear small teeth. An interarcual cartilage is present between the second pharyngobranchial and first epibranchial.

Pectoral and pelvic girdles (Figs. 8, 9).—The pectoral girdle is comprises the lateral extrascapular, posttemporal, supracleithrum, cleithrum, scapula, coracoid, and actinosts. The medial extrascapular and postcleithra are absent. The lateral extrascapular bears three openings for the cephalic sensory canal continuous with that on the pterotic, parietal and posttemporal. Three actinosts and the scapula, which is fused to the uppermost actinost, support the pectoral fin rays posteriorly. No lower free rays are present. The middle pectoral fin rays are branched. The cleithrum and coracoid lack a ventromedial connection. The pelvic girdle comprises

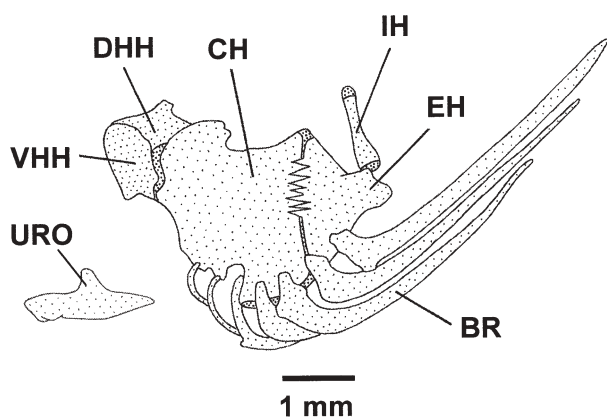


Fig. 5. Lateral aspect of the hyoid arch of *Caracanthus unipinna*, NSMT-P 21252, 27.7 mm SL. BR, branchiostegal ray; CH, ceratohyal; DHH, dorsal hypohyal; EH, epihyal; IH, interhyal; URO, urohyal; VHH, ventral hypohyal

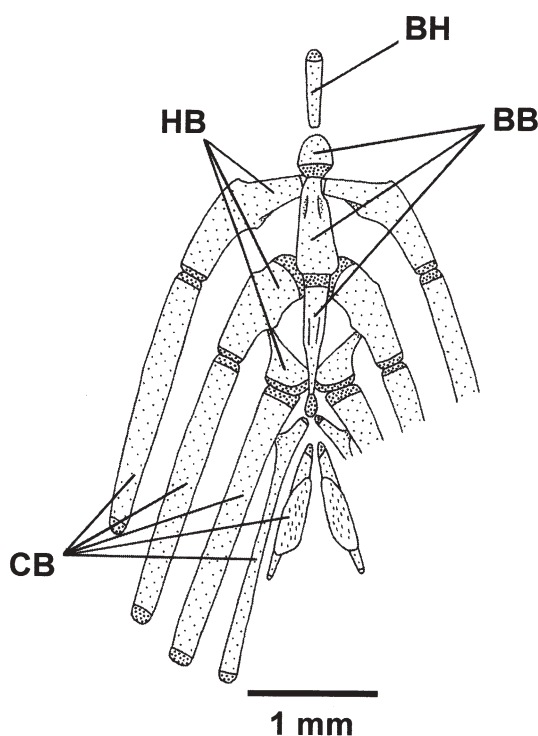


Fig. 6. Dorsal aspect of the lower gill arch of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. BB, basibranchial; BH, basihyal; CB, ceratobranchial; HB, hypobranchial

the pelvis, the opposing elements meeting in the midline where they are fused. The anterior cartilaginous caps of the pelvis on both sides are also fused. The posterodorsal portion of the pelvic girdle does not bear a posterior pelvic fossa (sensu Imamura, 1996). The girdle has an anterior process posteroventrally. A single spine and two or three unbranched soft rays are present. The pelvic spine does not interlock with the pelvis.

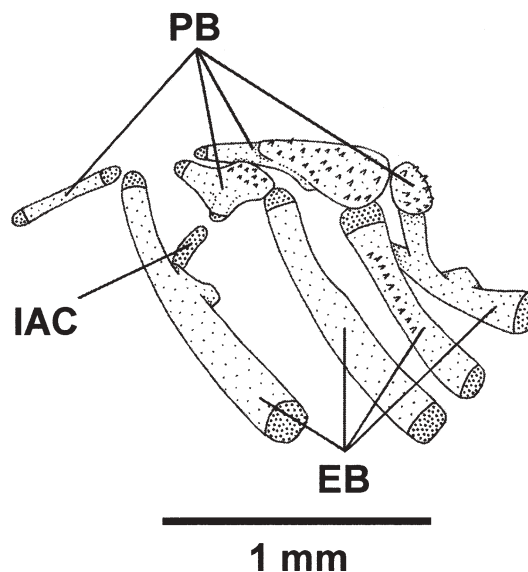


Fig. 7. Medial aspect of the upper gill arch of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. EB, epibranchial; IAC, interarcual cartilage; PB, pharyngobranchial

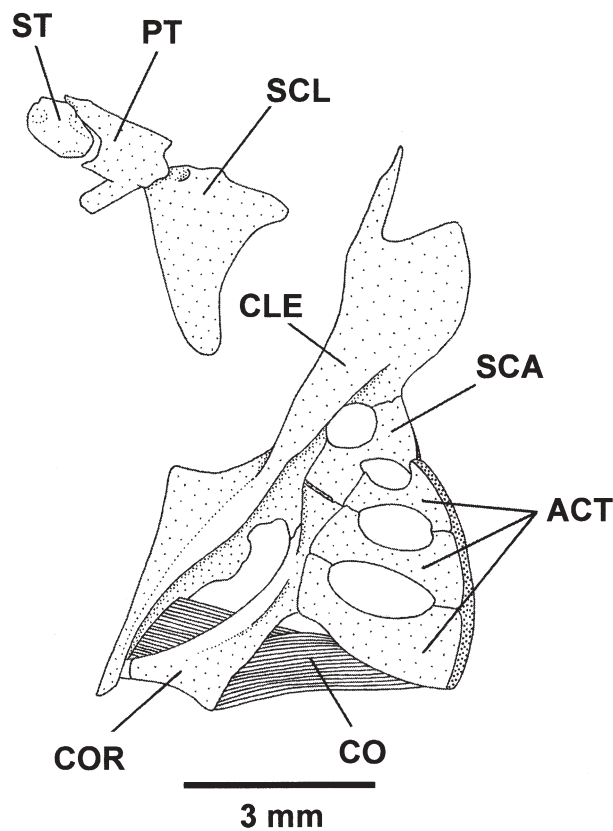


Fig. 8. Lateral aspect of the pectoral girdle of *Caracanthus maculatus*, USNM 261331, 25.0 mm SL. ACT, actinost; CLE, cleithrum; CO, coracoradialis; COR, coracoid; SCA, scapula. Other abbreviations as in Fig. 2

Axial skeleton and median fin supports (Fig. 10).—The axial skeleton comprises the vertebrae and epineurals (sensu Patterson and Johnson, 1995). The former include 10 abdominal and 14 caudal elements (24 in total). The neural spines of the first and second vertebrae are not bent anteriorly, the former being very short. The first and second dorsal proximal pterygiophores are inserted into the space between the second and third neural spines, and the third between the third and fourth neural spines. The median fin supports include both proximal and distal pterygiophores. The dorsal proximal pterygiophores are not exposed laterally. The anterior dorsal proximal pterygiophores are separated from the neurocranium. The first dorsal proximal pterygiophore bears two spines. The first anal proximal pterygiophore supports two spines ventrally, the others

supporting soft rays. The last dorsal and anal proximal pterygiophores each support two rays. All spines are stout and strong, with most dorsal and anal fin soft rays being branched. A single pleural rib was present in *C. maculatus* and a 20.7 mm SL specimen of *C. unipinna*. However, it was absent in a 27.7 mm SL specimen of the latter. The first epineural is stout. The supraneurals, medial pterygiophores, and stays of the dorsal and anal fins are absent.

Caudal skeleton (Fig. 11).—The caudal skeleton consists of two large platelike bones (upper caudal plate formed by the third and fourth hypurals, and the lower plate, the parhypural, and first and second hypurals), fifth hypural, one urostyle, one uroneural, and three epurals, plus the autogenous hemal spines on the second and third preural centra. The lower caudal plate bears the hypurapophysis. The middle 14 to 15 principal caudal fin rays are branched.

Myology. *Cheek muscle* (Fig. 12).—The cheek muscle consists only of the large adductor mandibulae muscle, comprising three sections: A1, A2–3, and Aw, section A3 being poorly differentiated from A2. Section A1, which is not divided into subsections, overlies the dorsolateral part of A2–3 and ventrolateral part of levator arcus palatini, being inserted onto the ligamentum primordium and connected with the preopercle and posterior aspect of the premaxillary condyle via a tendon. The dorsolateral portion of A2–3 is completely covered by levator arcus palatini. Aw lies on the medial surface of the lower jaw, being connected with the medial aspect of the quadrate by a strong tendon.

Cephalic muscles between neurocranium and suspensorium-opercular bones (Figs. 12, 13).—The cephalic muscles in this region consist of the levator arcus palatini, adductor arcus palatini, dilatator operculi, adductor operculi, adductor hyomandibulae, levator operculi, and protractor pectoralis. Levator arcus palatini extends poste-

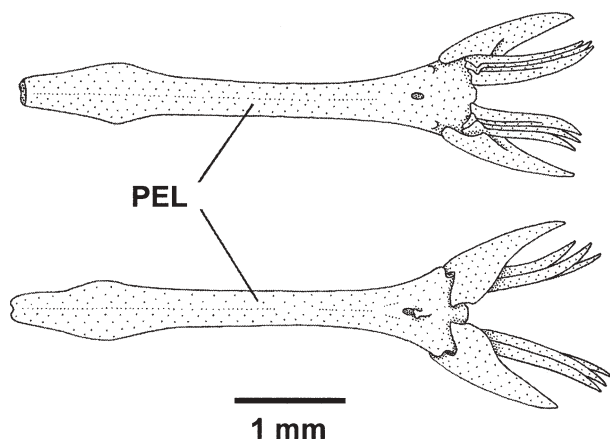
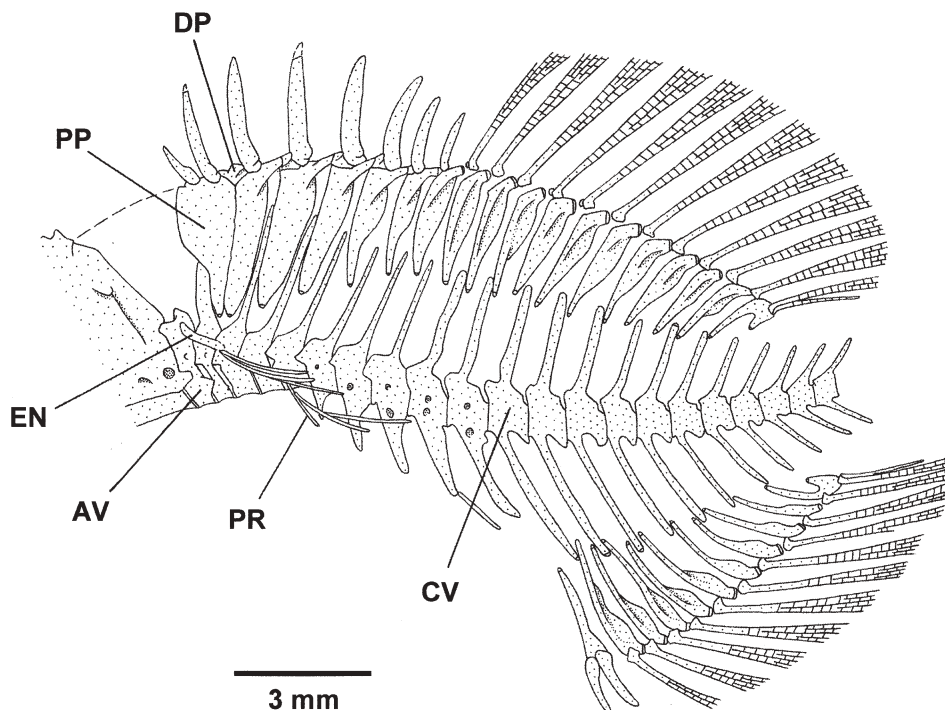


Fig. 9. Dorsal (above) and ventral (below) aspects of the pelvic girdle of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. PEL, pelvis

Fig. 10. Lateral aspect of the axial skeleton and median fin supports of *Caracanthus maculatus*, USNM 261331, 25.0 mm SL. AV, abdominal vertebra; CV, caudal vertebra; DP, distal pterygiophore; EN, epineural; PP, proximal pterygiophore; PR, pleural rib



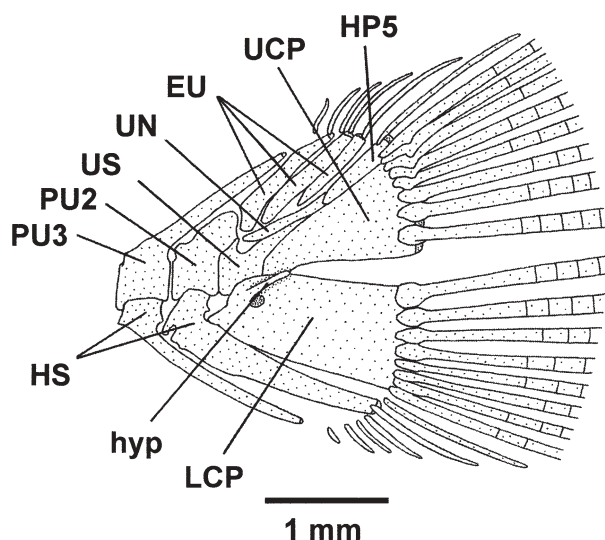


Fig. 11. Lateral aspect of the caudal skeleton of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. *EU*, epural; *HP5*, fifth hypural; *HS*, hemal spine; *LCP*, lower caudal plate; *PU2* (3), preural centrum 2 (3); *UCP*, upper caudal plate; *UN*, uroneural; *US*, urostyle; *hyp*, hypurapophysis

riorly, one branch being situated anterior to A2–3 in *Caracanthus maculatus*. Adductor arcus palatini, occupying the lower region of the orbit, connects the parasphenoid with the ventral surface of the entopterygoid, hyomandibular, and metapterygoid. Levator operculi consists of two elements: the anterior element originates from the posterolateral border of the pterotic and the posterior element from the posttemporal. Protractor pectoralis is single and sheetlike, originating from the posterolateral corner of the neurocranium and inserted onto the posterior portion of the sternohyoideus and cleithrum via sheetlike connective tissue.

Ventral muscles of head (Fig. 14).—The ventral head muscles comprise the intermandibularis, protractor hyoidei, hyohyoidei abductores, hyohyoidei adductores, and sternohyoideus. Hyohyoideus inferioris is absent. The posterior end of protractor hyoidei extends to the base of the fourth branchiostegal ray. Hyohyoidei abductores comprises two sections, section 1 originating from the anteroventral part of the ceratohyal and inserted onto the proximal part of the branchiostegal rays, and section 2 from the anterior part of the hyoid arch onto the first branchiostegal ray on the opposite side. Section 2 on each side cross each other, the right muscle passing medially to the left, with tendinous origins fused in the midline at which point fiber bundles arise. Sternohyoideus originates from the anterior portion of the pectoral girdle and is inserted onto both lateral aspects of the urohyal.

Branchial muscles (Figs. 13, 15).—The branchial muscles consist of the levator internus, levator externus, levator posterior, transversus dorsalis, obliquus dorsalis, retractor dorsalis, rectus communis, pharyngoclavicularis, rectus ventralis, obliquus ventralis, transversus ventralis, sphincter oesophagi, obliquus posterior, and adductor. Obliquus dorsalis II is absent. Levator internus comprises two elements; the

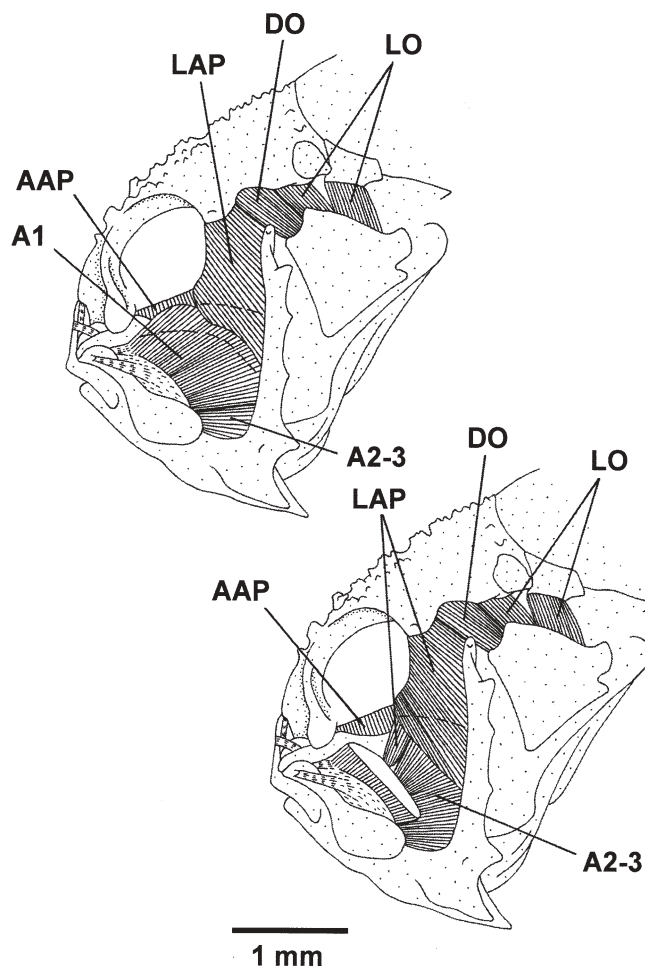


Fig. 12. Lateral aspect of surface (*above*) and after removal of A1 (*below*) of cheek and other cephalic muscles of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. *A1* and *A2–3*, adductor mandibular section 1 and 2–3; *AAP*, adductor arcus palatini; *LAP*, levator arcus palatini; *LO*, levator operculi; *DO*, dilatator operculi

anterior element is inserted onto the dorsal surface of the second pharyngobranchial, and the posterior element onto the dorsal surface of the third pharyngobranchial and lateral to the obliquus dorsalis. Levator externus is composed of four elements, being inserted onto the dorsal aspect of each epibranchial. The transversus dorsalis consists of two elements, the transversus dorsalis anterior and posterior. The former is located on the anterodorsal portion of the upper gill arch, being branched into two anteriorly, viz. the craniopharyngobranchial 2 and transverse epibranchial 2 (*sensu* Anker, 1978). Transversus dorsalis posterior interconnects the third epibranchial and third pharyngobranchial of each side. Retractor dorsalis originates from the posterior margin of third and fourth pharyngobranchials, being inserted onto the ventral face of second to fourth abdominal vertebrae. Pharyngoclavicularis consists of two elements, anterior and posterior. The origin of pharyngoclavicularis externus is lateral to the origin of sternohyoideus. Rectus ventralis is a single unbranched muscle, connecting the third hypobranchial with the fourth cerato-

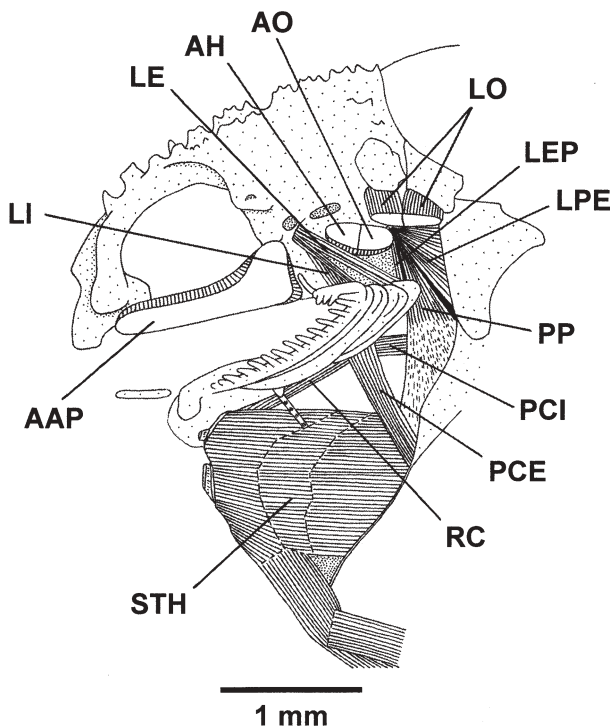


Fig. 13. Lateral aspect of muscles serving the branchial arch of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. AAP, adductor arcus palatini; AH, adductor hyomandibulae; AO, adductor operculi; LE, levator externus; LEP, levator pectoralis; LI, levator internus; LO, levator operculi; LPE, levator posterior; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; PP, protractor pectoralis; RC, rectus communis; STH, sternohyoideus

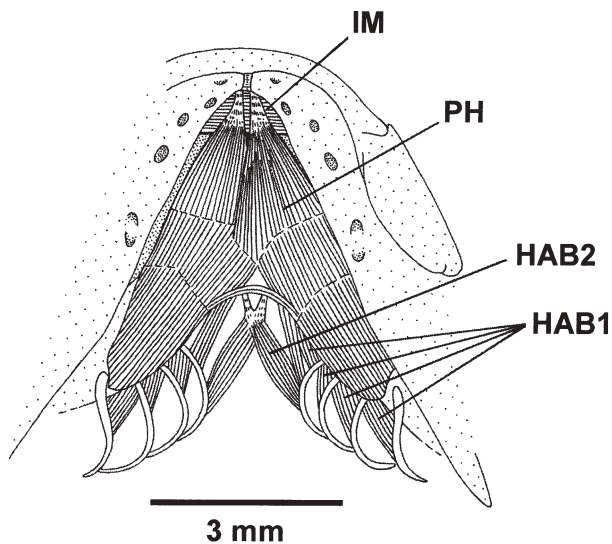


Fig. 14. Ventral aspect of ventral muscles of the head of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. HAB1 (2), hyohyoidei abductor section 1 (2); IM, intermandibularis; PH, protractor hyoidei

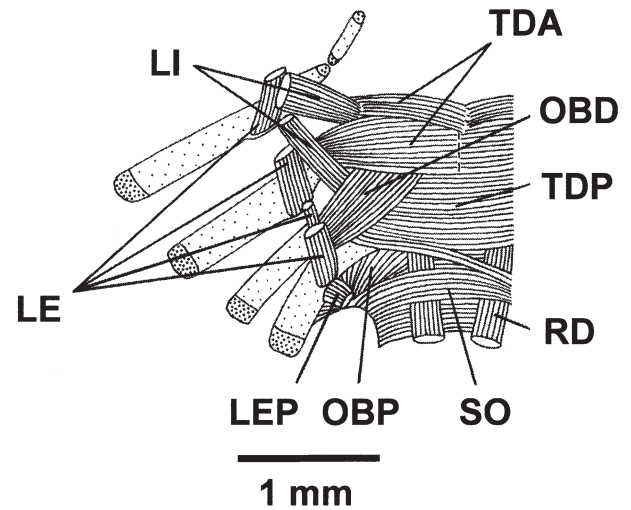


Fig. 15. Dorsal aspect of muscles serving the upper branchial arch of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. OBD, obliquus dorsalis; OBP, obliquus posterior; RD, retractor dorsalis; SO, sphincter oesophagi; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior. Other abbreviations as in Fig. 13

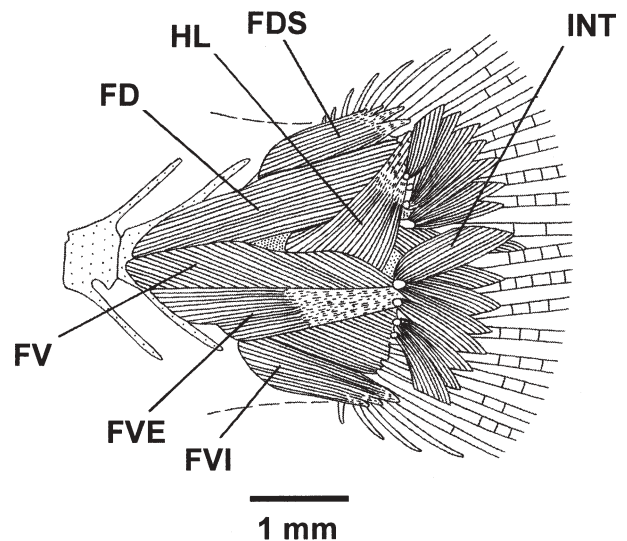


Fig. 16. Lateral aspect of the caudal fin muscles of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. FD, flexor dorsalis; FDS, flexor dorsalis superior; FV, flexor ventralis; FVE, flexor ventralis externus; FVI, flexor ventralis inferior; HL, hypochoyrdal longitudinalis; INT, interradialis

branchial. The adductor muscle comprises two elements, adductores 4 and 5, interconnecting the fourth epibranchial and fourth ceratobranchial, and fourth and fifth ceratobranchials, respectively; other elements (adductores 1–3) are absent. Transversus ventralis comprises two elements, both being separated from each other, with the posterior element bearing a tendon anteriorly.

Pectoral, pelvic, and caudal fin muscles (Figs. 8, 16).—The pectoral fin muscles, serving the pectoral fin rays, consist of

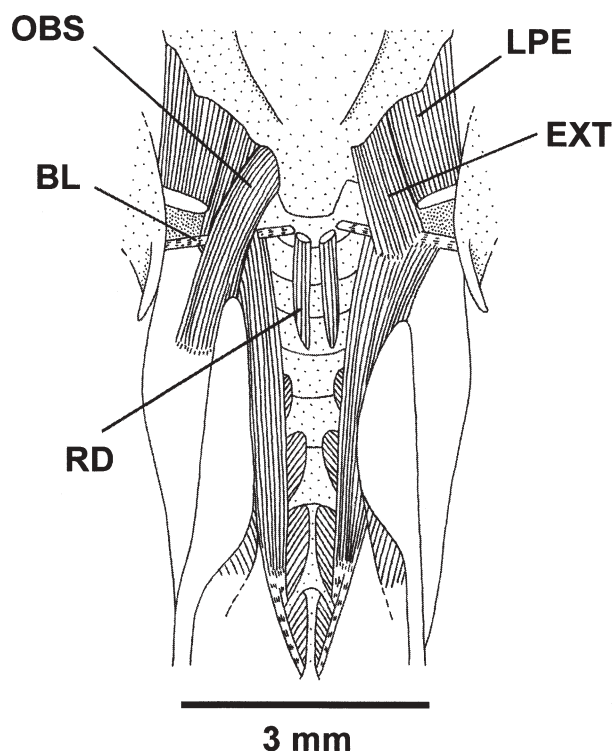


Fig. 17. Ventral aspect of the body cavity muscles of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. *BL*, Baudelot's ligament; *EXT*, extrinsic muscle; *OBS*, obliquus superioris. Other abbreviations as in Figs. 13 and 15

the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, arrector dorsalis, and coracoradialis, the protractor pectoralis and levator posterior also being associated with the cleithrum (Fig. 13). No elements were subdivided. The coracoradialis, originating from the lowermost actinost, extends to the coracoid and cleithrum (96-1).

The pelvic fin muscles, serving the pelvic fin rays, consist of both dorsal and ventral elements. The dorsal elements include the adductor superficialis pelvici, adductor profundus pelvici, and arrector dorsalis pelvici, and the ventral elements the abductor superficialis pelvici, abductor profundus pelvici, and arrector ventralis pelvici. No pelvic fin muscular elements are attached to the pectoral girdle. Extensor proprius is absent.

The caudal fin muscles, serving the caudal fin rays, consist of the interradialis, hypochordal longitudinalis, flexor dorsalis superior, flexor dorsalis, flexor ventralis, flexor ventralis externus, flexor ventralis inferior, and adductor dorsalis.

Body cavity muscles (Fig. 17).—The body cavity muscles consist of the extrinsic muscle and hypaxialis (obliquus superioris and obliquus inferioris). The intrinsic muscle and also swimbladder are absent. The extrinsic muscle originates from the posteroventral border of the neurocranium and is inserted, via a membranous tendon, onto the parapophyses of the abdominal vertebrae, thereby running dorsally to obliquus superioris. The latter is penetrated by

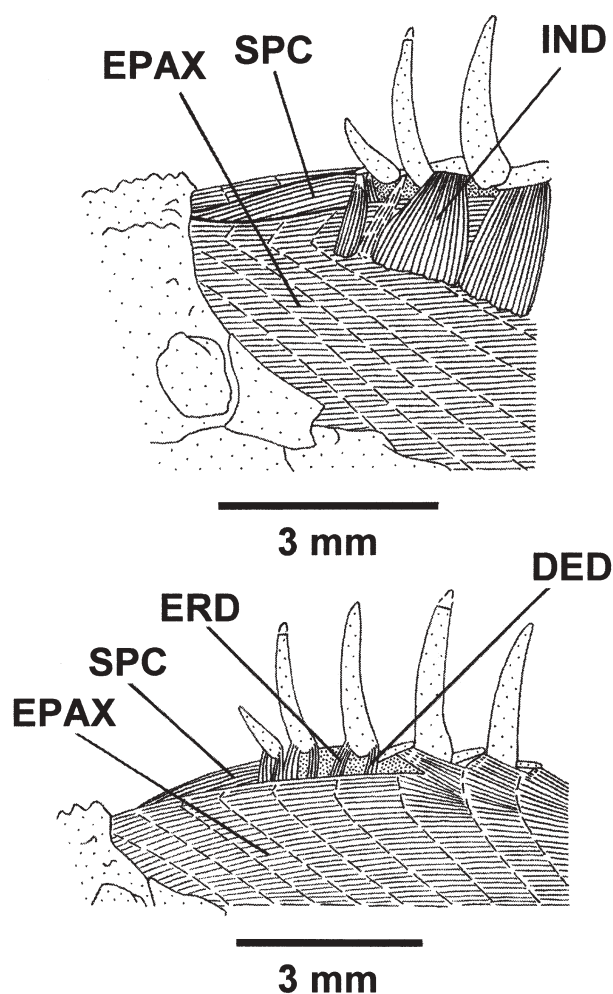


Fig. 18. Dorsolateral (*above*) and lateral (*below*, after removal of *IND*) aspects of the anterior portion of the body of *Caracanthus unipinna*, NSMT-P 21252, 20.7 mm SL. *DED*, depressores dorsales; *ERD*, erector dorsales; *EPAX*, epaxialis; *IND*, inclinatores dorsales; *SPC*, supracranialis anterior

Baudelot's ligament, which interconnects the first vertebra and supracleithrum. Obliquus superioris, extending to the neurocranium, is situated on the ventral portion of Baudelot's ligament, but is not penetrated by it.

Muscles associated with the proximal pterygiophores and median fins (Fig. 18).—The supracranialis anterior, infracranialis medius, supracranialis posterior, and infracranialis posterior are associated with the proximal pterygiophores. Three elements (erector, depressor, and inclinator) occur in both the dorsal and anal fins. Inclinatores dorsales, originating only from the dorsal pterygiophores, are situated between the epaxialis and skin.

Other characters. Gill membranes.—The gill membranes are free from the isthmus, the gill opening being broad.

Scales.—The body scales are restricted to below the dorsal fin base and lateral line. Minute scales with a single spine are also present on the dorsal surface of the head. The dorsal fin base scales have sensory canals, forming a

meshlike sensory system. The spineless lateral line scales are simple and tubelike, being buried under the skin.

Body proportions.—The body is oval and extremely compressed; the spinous and soft dorsal fins are continuous and the pelvic fin very short. The caudal peduncle is short and narrow, bent dorsally. The posterior margin of the caudal fin is rounded.

Discussion

Phylogenetic analysis. A total of 111 transformation series demonstrated by Imamura (2004) and a single new transformation series on the configuration of the caudal peduncle (TS 112) used in this study were recognized and shown in Appendix 1. Characters in TS 3, 8, 24, 34, 47, 54, 65, 68, 69, 93, and 101 were recoded here because outgroups were changed from Imamura (2004) and new taxa (*Caracanthus* and *Pteroidichthys*) were added for the analysis. In TS 112, two characters are included: the caudal peduncle being straight (character 112-0) and it is bent dorsally (112-1). In the scorpaenoids examined, character 112-1 was found in *Caracanthus*, *Taenianotus*, *Gnathanacanthus*, and *Pataecus*, whereas 112-0 occurred in the others, including the two outgroups (*Sebastes* and *Sebastiscus*). These characters were included in the present analysis. On the other hand, autapomorphic characters found only in the terminal taxa were not used in the analysis because they had no influence on the relationships. The character matrix is shown in Appendix 2.

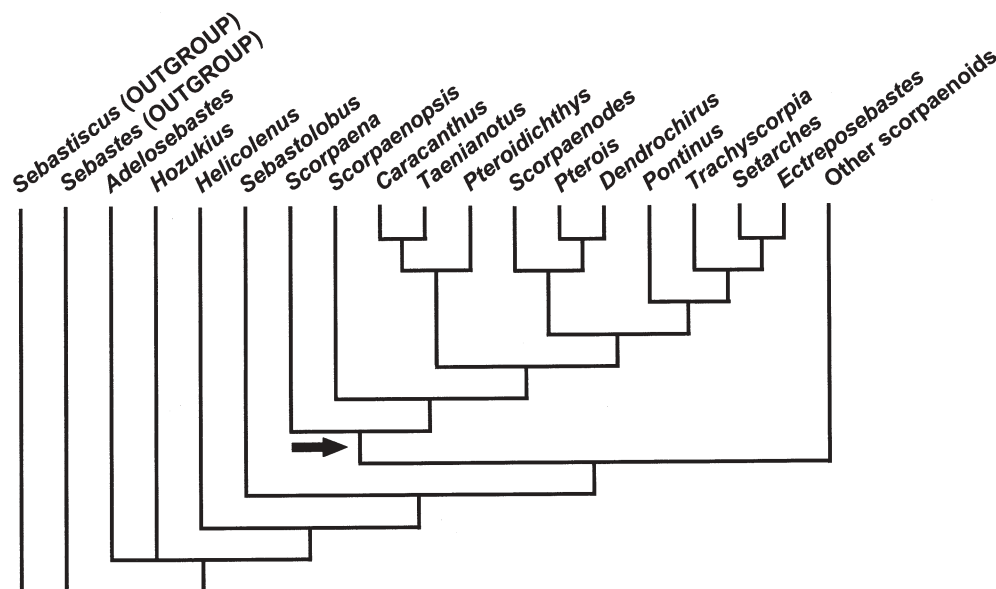
Comparing with the outgroups, the genus *Caracanthus* has the following apomorphies: posterior opening of the third infraorbital backwardly directed (character 6-1); backward opening on third infraorbital anterior to posterior margin (7-1); suborbital stay on the third infraorbital present, its posterior end narrowly truncated (8-1); fourth and fifth infraorbitals absent (9-2); sixth infraorbital fused with the sphenotic (10-1); not continuous with that of neurocranium (11-1 and 12-1); prevomer lacking teeth (16-2); basisphenoid absent (19-2); Baudelot's ligament originating the first vertebra (25-2); notch between the ascending and articular processes absent (27-1); palatine lacking teeth ventrally (30-1); medial extrascapular and postcleithra absent (44-1 and 48-2); anterior cartilaginous caps of the pelvis on both sides fused (51-1); single spine and two or three unbranched soft rays present on pelvic girdle (54-2 and 55-1); first anal proximal pterygiophore supporting two spines ventrally (60-1); supraneurals, medial pterygiophores, and stays of the dorsal and anal fins absent (65-2, 66-3, and 67-3); lower hypural plate (composed of first and second hypurals) and parhypural fused (71-1); hemal spine and third preural centrum fused (72-1); dorsolateral portion of A2–3 completely covered by levator arcus palatini (81-2); adductor arcus palatini connected with ventral surface of entopterygoid (82-2); levator operculi consisting of two elements (83-1); two elements of transversus ventralis separated from each other (92-1); coracoradialis extending to the coracoid and cleithrum (96-1); extensor proprius absent (98-1); extrinsic muscle present, connected with neurocranium

anteriorly and vertebrae posteriorly (101-1); obliquus superioris bypassing and lying ventrally to Baudelot's ligament (104-1); inclinatore dorsales originating only from the dorsal pterygiophores (106-1); lateral line scales tubelike (109-1); body scales restricted to below dorsal fin base (111-1); and caudal peduncle bent dorsally (112-1). However, it is unclear whether character 101-1 found in *Caracanthus* is apomorphic because outgroups have both characters 101-0 (*Sebastiscus*) and 101-1 (*Sebastes*).

The genus *Pteroidichthys*, which was recognized as a sister-group of *Caracanthus* by Mandrytsa's (2001) first analysis, was also examined in this study and found to have the following characters (asterisks indicating shared condition with *Caracanthus*): characters 6-1*, 7-1*, 8-2 (suborbital stay on third infraorbital present, its posterior end broad), 9-1 (fourth infraorbital absent), 11-1*, 25-2*, 30-1*, 31-1 (ectopterygoid and metapterygoid meeting medially), 32-1 (metapterygoid lamina absent), 44-1*, 47-1 (uppermost actinost and scapula separated), 50-1 (branched pectoral fin rays absent), 60-1*, 61-1 (branched dorsal and anal fin rays absent), 65-2, 71-1*, 78-1 (branched caudal fin rays absent), 81-3 (dorsolateral portion of A2–3 not closely associated with levator arcus palatini), 83-1*, 84-1 (hyohyoides inferioris present), 92-1*, 98-1*, and 104-1*. Data for this genus were also analyzed here.

Parsimony analysis for *Caracanthus* and 60 other genera included in Scorpaenoidea on the basis of characters in the 112 transformation series resulted in a most parsimonious tree [tree length (TL) = 443, confidence interval (CI) = 0.35, retention interval (RI) = 0.68] (Fig. 19). The topology of this tree agreed completely with that shown by Imamura (2004), except for the relationships associated with taxa newly added here. According to this tree, *Caracanthus* is nested within the family Scorpaenidae. *Caracanthus* and Scorpaenidae share two unambiguous characters, 6-1 (posterior opening of the third infraorbital, continuous with the sensory canal of the fourth to sixth infraorbitals, backwardly directed) and 11-1 (sensory canal of third infraorbital not continuous with that of infraorbital posterior to eye). Of these, character 6-1 is an autapomorphy of Scorpaenoidea. The genera *Caracanthus* and *Taenianotus* form a monophyletic group defined by the following unambiguous characters: 10-1, 16-2, 66-3, and 112-1 (also 12-1, according to DELTRAN). It was also inferred that the monophyletic group including *Caracanthus* and *Taenianotus* is a sister-group of *Pteroidichthys*. The monophyly of these three genera is supported by the unambiguous characters 25-2, 81-3, 83-1, and 92-1 (also 32-1, 50-1, 60-1, 71-1, and 98-1, according to ACCTAN). These three genera form a monophyletic group with the remaining scorpaenids (excluding *Scorpaenopsis* and *Scorpaena*) in sharing an unambiguous character 47-1 (also 12-1, according to ACCTAN). In addition, *Caracanthus*, *Taenianotus*, and *Pteroidichthys* each have a unique set of unambiguous characters: viz. 8-1, 9-2, 19-2, 27-1, 31-0, 47-0, 48-2, 51-1, 54-2, and 55-1 (also 32-0 and 50-0, according to ACCTAN, and 60-1, 71-1, and 98-1, according to DELTRAN) in *Caracanthus*; 25-1, 33-1, and 101-2 (also 60-0, 71-0, and 98-0, according to ACCTAN, and 32-1 and 50-1, according to DELTRAN)

Fig. 19. Most parsimonious cladogram of the superfamily Scorpaenoidea, showing the phylogenetic position of the genus *Caracanthus*. Arrow indicates clade including *Caracanthus* and family Scorpaenidae (sensu Imamura, 2004)



in *Taenianotus*; and 61-1 and 78-1 (also 12-0, according to ACCTRAN, and 32-1, 50-1, and 60-1, according to DELTRAN) in *Pteroidichthys*. Furthermore, *Caracanthus* has the following autapomorphic characters, which were not included in the analysis: frontals and parietals on both sides fused, respectively; ascending process with an ossified rostral cartilage posteriorly; pelvis on each side fused in mid-line; first epineural stout; and the dorsal fin base scales with sensory canals, forming a meshlike sensory system.

Although Mandrytsa (2001: fig. 225) showed the relationship (((((Caracanthus, Pteroidichthys), Taenianotus), Pteropelor), Rhinopias), Scorpaenopsis), based on an analysis using PAUP version 3.1.1, he rejected it. Our result agrees with Mandrytsa's (2001) first analysis on the phylogenetic position of *Caracanthus* in that the genus is nested within the Scorpaenidae and closely related to *Pteroidichthys* and *Taenianotus*, although he showed *Caracanthus* to have a sister relationship with *Pteroidichthys* (vs. *Taenianotus* in the present hypothesis). However, he did not show the derived characters supporting these relationships. Mandrytsa (2001: fig. 228) subsequently indicated *Caracanthus* to be a sister-group of Scorpaenidae, following a second analysis, showing that they possessed four derived characters in common and that Scorpaenidae lacked synapomorphies. On the other hand, we inferred that the monophyly of *Caracanthus* and *Taenianotus* is supported by four unambiguous characters and failed to find derived characters shared only by Scorpaenidae. Therefore, we do not support a sister relationship of *Caracanthus* and Scorpaenidae. Cole's (2003) expectation of a close relationship of *Caracanthus* to Scorpaenidae is consistent with our result. Smith and Wheeler (2004) indicated *Caracanthus* could be nested within a monophyletic clade including Scorpaenidae and Sebastidae by mitochondrial and nuclear DNA sequence data. In addition, they inferred that *Caracanthus* is a sister-group for a clade including

Iracundus, *Taenianotus*, *Scorpaenodes*, and *Scorpaena*. They did not state anything about the classification of *Caracanthus*. Although our result differs from that of Smith and Wheeler (2004) on the sister-group of *Caracanthus*, it is consistent in both studies that the Scorpaenidae is paraphyletic.

Classification. Based on our results, it is appropriate to synonymize Caracanthidae with Scorpaenidae because Scorpaenidae is rendered paraphyletic if these two families are retained. Based on Imamura's (2004) classification of the Scorpaenoidea, we assign familial rank Scorpaenidae to this clade because it has priority.

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- on third infraorbital—0: present, its posterior end pointed or bluntly pointed; 1: present, its posterior end narrowly truncated; 2: present, its posterior end broad; 3: absent (unordered). **TS 9 fourth and fifth infraorbitals**—0: both present; 1: fourth absent; 2: both absent (ordered as 0-1-2). **TS 10 sixth infraorbital**—0: attached to sphenotic; 1: fused to sphenotic; 2: absent (unordered). **TS 11 sensory canal of third infraorbital**—0: continuous with that of infraorbital posterior to eye; 1: not continuous with that of infraorbital posterior to eye. **TS 12 sensory canal of sixth infraorbital**—0: continuous with that of infraorbital posterior to eye; 1: not continuous with that of infraorbital posterior to eye. **TS 13 tubercles on neurocranium**—0: absent; 1: present. **TS 14 nasal and neurocranium**—0: loosely attached; 1: sutured. **TS 15 nasals on both sides**—0: separated; 1: sutured medially. **TS 16 number of tooth plates on prevomer**—0: one; 1: two; 2: none (unordered). **TS 17 lateral ethmoids**—0: separated; 1: meeting in midline. **TS 18 parasphenoid and pterospheneid**—0: separated; 1: connected. **TS 19 basisphenoid**—0: present, posterior margin connected directly with neurocranium; 1: present, posterior margin free from neurocranium; 2: absent (unordered). **TS 20 prootic and intercalar**—0: in contact; 1: separated. **TS 21 intercalar and posttemporal**—0: ligamentous articulation; 1: sutured. **TS 22 lateral pore on pterotic**—0: absent; 1: present. **TS 23 sensory canal between pterotic and preopercle**—0: present; 1: absent. **TS 24 spines associated with sensory canal on parietal**—0: present; 1: absent. **TS 25 Baudelot's ligament**—0: originating from basioccipital; 1: originating from basioccipital and first vertebra; 2: originating from first vertebra; 3: absent (unordered). **TS 26 ascending process of premaxilla**—0: continuous with remaining part of premaxilla; 1: separated. **TS 27 notch between ascending and articular processes**—0: present; 1: absent. **TS 28 teeth on jaws**—0: present; 1: absent. **TS 29 palatine and ectopterygoid**—0: connected; 1: separated. **TS 30 teeth on palatine**—0: present; 1: absent. **TS 31 ectopterygoid and metapterygoid**—0: separated; 1: meeting medially. **TS 32 metapterygoid lamina**—0: present; 1: absent. **TS 33 space between metapterygoid and hyomandibula**—0: prominent; 1: rudimentary or absent. **TS 34 preopercular margin**—0: with prominent spine; 1: without prominent spines. **TS 35 backwardly directed opercular spine**—0: present; 1: absent. **TS 36 basihyal**—0: ossified; 1: cartilaginous; 2: absent (unordered). **TS 37 branchiostegal rays**—0: seven; 1: six; 2: five (ordered as 0-1-2). **TS 38 interarcual cartilage**—0: present; 1: absent. **TS 39 tooth plate on second epibranchial**—0: absent; 1: present. **TS 40 tooth plate on third epibranchial**—0: present; 1: absent. **TS 41 first pharyngobranchial**—0: ossified; 1: cartilaginous; 2: absent (unordered). **TS 42 tooth plate on second pharyngobranchial**—0: present; 1: absent. **TS 43 second to fourth pharyngobranchials**—0: separated; 1: third and fourth continuous; 2: second to fourth continuous (ordered as 0-1-2). **TS 44 medial extrascapular**—0: present; 1: absent. **TS 45 lateral extrascapular**—0: single element with three sensory openings; 1: two elements (horizontal and longitudinal tubes) with two sensory openings; 2: single element (longitudinal tube) with two sensory openings (unordered). **TS 46 cleithrum and coracoid**—0: without ventromedial connection; 1: with partial ventromedial connection; 2: with complete ventromedial connection (ordered as 0-1-2). **TS 47 uppermost actinost and scapula**—0: fused; 1: separated. **TS 48 number of postcleithra**—0: two; 1: one; 2: zero (ordered as 0-1-2). **TS 49 number of free lower pectoral fin rays**—0: zero; 1: one; 2: two; 3: three or more (ordered as 0-1-2-3). **TS 50 branched pectoral fin rays**—0: present; 1: absent. **TS 51 cartilaginous caps on anterior portion of pelvis**—0: separated; 1: fused. **TS 52 posterior pelvic fossa**—0: absent; 1: present, opposing fossae meeting; 2: present, opposing fossae separated (unordered). **TS 53 opposing posteromedial portions of pelvis**—0: sutured; 1: separated. **TS 54 number of pelvic fin rays**—0: six; 1: five; 2: four to three; 3: none (ordered as 0-1-2-3). **TS 55 branched pelvic fin rays**—0: present; 1: absent. **TS 56 first spine on first dorsal fin proximal pterygiophore**—0: present;

Appendix 1

List of 112 transformation series (TS) and characters. **TS 1 first to third infraorbitals**—0: closely associated; 1: separated. **TS 2 first and third infraorbitals**—0: separated by second infraorbital; 1: attached; 2: separated by second infraorbital and ectopterygoid (unordered). **TS 3 bridge of middle portion of second infraorbital sensory canal**—0: without sensory openings; 1: with a single sensory opening; 2: with more than two sensory openings (ordered). **TS 4 second infraorbital and lateral ethmoid**—0: separated; 1: attached. **TS 5 third and fifth infraorbital**—0: separated by third infraorbital; 1: attached. **TS 6 direction of opening of third infraorbital, continuous with sensory canal of fourth to sixth infraorbitals**—0: upward; 1: backward. **TS 7 position of upward (or backward) opening on third infraorbital**—0: dorsal (or posterior) margin of element; 1: below (or anterior to) margin. **TS 8 suborbital stay**

1: absent. **TS 57** dorsal spines—0: stout; 1: slender. **TS 58** first spine on first anal fin proximal pterygiophore—0: present; 1: absent. **TS 59** second element on first anal fin proximal pterygiophore—0: spine; 1: soft ray; 2: absent (unordered). **TS 60** ray on second anal fin proximal pterygiophore—0: spine; 1: soft ray. **TS 61** branched dorsal and anal fin rays—0: present; 1: absent. **TS 62** number of rays supported by posteriormost proximal pterygiophores—0: two; 1: one. **TS 63** anterior dorsal proximal pterygiophores—0: separated from neurocranium; 1: sutured to neurocranium. **TS 64** dorsal fin proximal pterygiophores—0: not exposed; 1: laterally exposed along first dorsal fin; 2: laterally exposed along both dorsal fins (ordered as 0-1-2). **TS 65** number of supraneurals—0: two; 1: one; 2: zero (ordered as 0-1-2). **TS 66** dorsal fin stay—0: present (separate and ossified); 1: fused with proximal pterygiophore; 2: present (cartilage); 3: absent (unordered). **TS 67** anal fin stay—0: present (separate and ossified); 1: fused with proximal pterygiophore; 2: present (cartilage); 3: absent (unordered). **TS 68** first and second hypurals—0: continuous; 1: separated. **TS 69** third and fourth hypurals—0: continuous; 1: separated. **TS 70** fifth hypural—0: present; 1: absent. **TS 71** lower hypural plate and parhypural—0: separated; 1: fused. **TS 72** hemal spine and third preural centrum—0: separated; 1: fused. **TS 73** hemal spine and second preural centrum—0: separated; 1: fused. **TS 74** urostyle and upper hypural plate—0: separated; 1: fused. **TS 75** urostyle and lower hypural plate—0: separated; 1: fused. **TS 76** uroneural—0: present; 1: absent. **TS 77** number of epurals—0: three; 1: two; 2: one (ordered as 0-1-2). **TS 78** branched caudal fin rays—0: present; 1: absent. **TS 79** posterior end of adductor mandibulae section 1—0: connected with preopercle (and hyomandibula); 1: connected only with hyomandibula; 2: free from posterior bony element(s) (unordered). **TS 80** A1 β —0: absent; 1: present. **TS 81** origin of A2-3—0: lateral to levator arcus palatini; 1: partially medial to levator arcus palatini; 2: completely medial to levator arcus palatini; 3: not closely associated with levator arcus palatini (unordered). **TS 82** position of adductor arcus palatini—0: dorsal surface of entopterygoid; 1: medial margin of entopterygoid; 2: ventral surface of entopterygoid (ordered as 0-1-2). **TS 83** origin of levator operculi—0: pterotic; 1: pterotic and posttemporal; 2: posttemporal (ordered as 0-1-2). **TS 84** hyohyoide inferioris—0: absent; 1: present. **TS 85** anterior portion of transversus dorsalis anterior—0: branched; 1: unbranched. **TS 86** posterior portion of transversus dorsalis anterior—0:

unbranched; 1: branched, not continuous with anterior branch of same muscle; 2: branched, continuous with anterior branch of same muscle, comprising circular muscle elements (ordered as 0-1-2). **TS 87** obliquus dorsalis II—0: absent; 1: present. **TS 88** posterior levator internus—0: lateral to obliquus dorsalis; 1: sandwiched by obliquus dorsalis. **TS 89** levator externus III—0: present; 1: absent. **TS 90** levator posterior—0: present; 1: absent. **TS 91** adductores I-III—0: absent; 1: present. **TS 92** transversus ventralis anterior and posterior—0: overlapped; 1: separated. **TS 93** transversus ventralis posterior—0: with a tendon anteriorly; 1: without a tendon anteriorly. **TS 94** protractor pectoralis—0: sheetlike muscle only; 1: composed of sheetlike anterior and robust posterior elements. **TS 95** division of bundles of adductor superficialis serving free pectoral fin rays—0: absent; 1: present. **TS 96** origin of coracoradialis—0: posteromedial face of posterior process of coracoid; 1: posteromedial face of posterior process of coracoid and posterolateral face of posteroventral process of cleithrum. **TS 97** dorsal elements of pelvic fin muscles—0: not attached to pectoral girdle; 1: attached to pectoral girdle. **TS 98** extensor proprius—0: present; 1: absent. **TS 99** flexor ventralis externus—0: present; 1: absent. **TS 100** adductor dorsalis—0: present; 1: absent. **TS 101** extrinsic muscle—0: present, connected with neurocranium anteriorly and swimbladder posteriorly; 1: present, connected with neurocranium anteriorly and vertebrae posteriorly; 2: present, free from neurocranium anteriorly and connected with vertebrae posteriorly; 3: absent (unordered). **TS 102** intrinsic muscle—0: absent; 1: present. **TS 103** obliquus superioris—0: extending to neurocranium; 1: not extending to neurocranium. **TS 104** obliquus superioris and Baudelot's ligament—0: obliquus superioris penetrated by Baudelot's ligament; 1: obliquus superioris bypassing and lying ventrally to Baudelot's ligament. **TS 105** supracarinalis anterior—0: present; 1: absent. **TS 106** inclinator dorsalis associated with first dorsal spine—0: present; 1: absent. **TS 107** gill membranes—0: free from isthmus; 1: narrowly fused with isthmus, gill opening wide; 2: broadly fused with isthmus, gill opening narrow (ordered as 0-1-2). **TS 108** sensory duct in lateral line—0: simple; 1: with two or more branches. **TS 109** lateral line—0: with scales; 1: with tubelike bones; 2: with bony plates (unordered). **TS 110** spines on lateral line scales—0: absent; 1: present. **TS 111** body scales—0: present; 1: absent, except on dorsal region; 2: entirely absent; 3: present as bony plates (unordered). **TS 112** caudal peduncle—0: straight; 1: bent dorsally.

Appendix 2. Character matrix of superfamily Scorpaenoidea

Taxon	Transformation series																						
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105	106-110	111-112
Outgroup																							
<i>Sebastes</i>	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00001	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
<i>Sebastes</i>	00000	00000	00000	00000	00000	00000	00000	00000	000A0	00000	00000	00000	00001	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
Ingroup																							
<i>Caracanthus</i>	0000?	11121	11000	20020	00002	01001	00000	00000	00010	00200	10021	00001	00002	33000	11000	00000	22100	00000	01000	10100	10010	10010	11
<i>Pterodichthys</i>	00000	11210	10000	00000	00002	00001	11000	00000	00010	01001	00000	00001	10002	00000	10000	00100	30110	0000?	01000	00100	10010	00000	10
<i>Taenianotus</i>	00000	11211	11000	20000	00001	00001	11100	00000	00010	01001	00000	00000	00002	30000	00000	00000	00110	00000	01000	00000	20010	00000	01
<i>Adelosebastes</i>	00000	00100	00000	00000	00000	00000	00000	00000	00010	00000	00000	00000	00001	00000	00000	00000	00010	00000	00000	00000	10000	00000	00
<i>Hozukius</i>	00000	00100	00000	00000	00000	00000	00000	00000	00010	00000	00000	00000	00001	00000	00000	00000	00010	00000	00000	00000	10000	00000	00
<i>Helicolenus</i>	00000	00100	00000	00000	00000	00000	10000	00000	000A0	00000	00000	00000	00001	00000	00000	00000	00010	00000	00000	00000	10000	00000	00
<i>Sebastolobus</i>	00000	01200	00000	00000	00000	00000	10000	00000	00010	01000	00000	00000	00001	00000	00000	00000	00010	00000	00000	00000	10000	00000	00
<i>Scorpaena</i>	00000	11210	10000	00000	00000	00000	10000	00000	00010	00000	00000	00000	00002	00000	00000	00000	00010	00000	00000	00000	10000	00000	00
<i>Scorpaenopsis</i>	00000	11211	10000	00000	00000	00001	10000	00000	00010	00000	00000	00000	00002	00000	00000	00000	00010	00000	00000	00000	10010	00000	00
<i>Scorpaenodes</i>	00200	10210	11000	00000	00000	00001	00000	00000	00010	01000	00000	00000	00002	00010	00000	00000	00000	00000	00?00	00000	00010	00000	00
<i>Pterois</i>	0020?	10220	11000	00000	00002	00001	00001	00000	00010	01001	00000	00000	00002	00010	00000	00000	00010	00000	01000	00000	00010	00100	00
<i>Dendrochirus</i>	0020?	10220	11000	00000	00000	00001	00001	00000	00010	01000	00000	00000	00002	00010	00000	00000	00010	00000	00000	00000	00010	00100	00
<i>Pontinus</i>	00000	11210	11000	00000	00000	00000	00000	00000	00010	01001	00000	00000	00001	00010	00000	00000	00000	00000	00000	00000	10000	00000	00
<i>Trachyscorpia</i>	00000	11210	11000	00010	00000	00000	00000	00000	00010	01000	00000	00000	00001	00110	00000	00000	00000	00000	00000	00000	10000	00000	00
<i>Setarches</i>	0000?	11221	11000	000B0	00000	00000	00000	00000	00010	01000	00000	00000	00001	00110	00000	00000	00000	01000	00000	00000	10010	00000	00
<i>Ectreposebastes</i>	0000?	11221	11000	000B0	00000	00000	00000	00000	0001A	01000	00000	00000	00002	00110	00000	00000	00000	01000	00000	00000	10010	00000	00
<i>Apistus</i>	00000	01211	00100	00020	00000	01000	01000	00000	00010	00010	00000	00000	00002	00000	10000	00000	10101	00100	00100	00000	01010	10000	00
<i>Tetraroge</i>	00000	01211	00000	00000	00000	00000	01100	00001	0101B	00000	00000	00000	01102	33001	1?000	00000	20110	00010	00100	00000	10011	10010	20
<i>Synanceia</i>	00000	01212	00000	00020	00002	00001	01100	00010	01112	00000	00000	00000	00002	33001	10000	01001	12110	00010	00100	00011	101?0	11010	20
<i>Erosa</i>	00000	01211	00000	00000	10002	00001	01100	00001	0111?	00000	00010	00000	00002	00001	11000	01001	12110	00010	00100	00011	101?0	11010	20
<i>Inimicus</i>	00000	01211	00000	00000	00002	00001	01100	00101	01012	00020	00000	00001	01002	33000	11010	1A000	10110	00010	00101	00001	10010	11010	20
<i>Choridactylus</i>	00000	01211	00000	20000	00002	00001	01100	20101	01110	20030	00000	00001	01002	33000	11000	00000	11111	00000	00101	10001	10010	11010	20
<i>Minous</i>	00000	01211	00100	10020	00002	00001	01100	00101	01112	10011	00001	10001	11002	33000	11010	00100	12111	00000	00101	00001	10010	?1010	20
<i>Aploactis</i>	00000	01212	00000	00021	00002	00001	01000	01101	0?212	00001	00021	00101	10002	33000	11000	00100	11111	00?10	00100	10010	10011	10011	00
<i>Eriphex</i>	00000	01211	01000	00001	00102	00001	01000	01101	01112	00001	00021	00101	11102	C2001	11000	00100	11111	00110	00100	10101	10011	10011	00
<i>Congitopodus</i>	0000?	01220	00100	20001	10113	00011	01010	22001	00012	01001	00000	10101	00002	00001	10010	11000	11200	20001	11100	00011	101?0	?2010	20
<i>Alerichthys</i>	0000?	01221	11100	20101	10103	00011	01010	01101	20012	00001	00001	10100	10002	00001	10010	11100	11100	20001	11000	10111	101?0	?2011	00
<i>Gnathacanthus</i>	10000	0121A	00000	200A0	00012	00001	01010	20001	01111	00001	00001	00000	11002	1100A	11101	A0111	11110	20000	01000	0000A	10010	00010	21
<i>Pataetus</i>	10000	00312	00000	00121	00012	00001	01010	21001	01111	00201	0003?	00120	11002	33001	11111	12110	11010	10110	01100	0?111	10011	10010	21
<i>Neosebastes</i>	00100	01210	00000	00000	00000	00000	00000	00000	00010	00000	00000	00000	00002	00110	00000	000?0	00000	00010	00100	00000	20000	00000	00
<i>Maxilliscosta</i>	00100	01210	00000	00000	00000	00000	00000	00000	00010	00000	00000	00000	00002	00110	00000	00001	00000	00000	00100	00000	10000	10000	00
<i>Plectrogenium</i>	00100	01211	00000	00000	00100	00000	00000	00000	00010	01000	01000	00000	00002	22110	00000	00000	00011	00000	00100	00000	10000	00000	00
<i>Bembradium</i>	00100	01210	00000	10A00	00100	00000	00000	00100	10010	01000	01000	00121	00002	22110	00000	00000	00011	00001	00000	00000	10000	00000	00
<i>Parabembras</i>	00100	01200	00000	00000	00000	10000	00000	00000	00010	01000	01000	00000	00000	00110	00000	00000	00000	00000	00100	00000	10000	10000	00
<i>Bembras</i>	00100	01200	00000	00000	00000	00000	00000	00000	00010	01000	02000	00111	00000	00010	00000	00000	00010	00000	00100	00000	10000	00000	00
<i>Chelidonichthys</i>	01111	01200	00110	00000	01001	01001	00000	20110	00010	01130	12000	10111	00022	00101	00010	10020	01011	00000	01001	01011	31010	?0100	00
<i>Lepidotrigla</i>	01011	01200	00110	11001	01000	01001	00000	20110	00010	01130	02000	10111	00022	00000	00010	00020	01011	00000	01001	01011	31010	?0100	00
<i>Pterygotrigla</i>	01011	01200	00110	21000	01002	01001	00000	20110	00010	01130	02000	10111	00012	00100	00010	00020	01011	00000	01001	01011	101?0	?0000	00
<i>Prionotus</i>	01111	01201	00110	10000	01000	01000	00000	00110	00010	01130	12000	10111	00002	001?0	00000	00020	01011	00000	01001	01011	31010	?0000	00
<i>Bellator</i>	01111	01201	00110	01000																			

Numbers assigned to transformation series and to characters correspond to those in the text

Polymorphic characters are coded as follows: 0 and 1, A; 1 and 2, B; 0 and 2, C; 2 and 3, D; 0, 1, and 2, E