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Two New Species of Acanthoclininae (Pisces: Plesiopidae) with a Synopsis and Phylogeny of the Subfamily

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ABSTRACT.—Osteology and soft anatomy were studied to advance a hypothesis of phylogenetic relationships within the previously recognized family Acanthoclinidae in order to determine the correct generic placement of two new species. The following genera are recognized, with the number of their included species given in parentheses: *Acanthoclinus* Jenyns (5), *Belonepterygion* McCulloch (1), *Beliops* Hardy (2) and *Acanthoplesiops* Regan (4). A cladistic analysis based on 33 adult characters resulted in a highly corroborated hypothesis indicating that each of the four genera comprise monophyletic clades ordered in the above phyletic sequence. *Taumakoides* Whitley is a synonym of *Acanthoclinus*.

Beliops batanensis n. sp., known only from the Batan Islands, northern Philippines, shares three unique apomorphies with its allopatric congener. It exhibits a surprisingly large number of derived character states not present in its plesiomorphic sister-species, including short and robust dorsal-fin spines and distinctive body scales with membranous flaps. *Acanthoplesiops echinatus* n. sp., known only from Jolo, Sulu Archipelago and Ambon, Indonesia, is most closely related to the allopatric *A. psilogaster*, and is readily distinguished from its congeners by having most scales on the posterior half of body with one or two membranous flaps supported by elongate ctenii and 6 (versus 3-5) segmented anal-fin rays; the occurrence of minute, pointed papillae on the head of the two Ambon specimens (inexplicably absent in the single Jolo specimen) is unique within the subfamily. [Acanthoclinidae, biogeography, cladistic analysis, osteology, Perciformes, Plesiopidae, scale morphology, systematics]

In April-May of 1987 the authors spent three weeks collecting fishes in the Batanes Province, northern Philippines under the auspices of a Smithsonian Institution sponsored project to sample the biota. Limited transportation facilities and frequent bad weather and sea conditions combined with geographic isolation have all served to inhibit biological exploration in this poorly collected region. The Batanes Province lies at the northern tip of the Philippine Archipelago, between northern Luzon and Taiwan. Most of its dozen islands are of volcanic origin and much of the shoreline consists of rocky ledges and boulders, with coral development relatively

sparse.

Among the fishes collected were two specimens of an enigmatic acanthoclinid that seemingly did not agree with any previously described genus. Subsequently, we discovered an undescribed species of *Acanthoplesiops* in an unsorted collection of fishes from Ambon, Indonesia deposited at the Bernice P. Bishop Museum. Our efforts to place these new taxa led us to re-evaluate the phylogenetic relationships of the Acanthoclinidae as outlined by Hardy (1985). The phylogenetic relationships of the family Acanthoclinidae have been uncertain since it was first established by Günther (1861:297). Although most recent authors have recognized the family as valid, both Regan (1913) and McCulloch (1915) allocated acanthoclinid genera to the Plesiopidae. Mok et al. (1990) treated the Acanthoclinidae and Plesiopidae as sister taxa, although the characters they used to support such a relationship are invalid or were misinterpreted. In his recent revision of the Acanthoclinidae, Hardy (1985) did not consider the possibility of a close relationship between these two groups. Both nominal families share one external feature that we have seen in no other fishes. The third branchiostegal ray (counting posterodorsally) is positioned so that it extends farther posteriorly than adjacent rays resulting in a slight to pronounced notch or rounded projection on the posterolateral margin of the exposed branchiostegal membranes (Fig. 1). This condition can be seen clearly in previously published illustrations of *Plesiops* (Inger 1955:fig. 3a), *Paraplesiops* (Hoese and Kuiter 1984:figs. 3-4), and *Steeneichthys* (Allen & Randall 1985:figs. 1-2). The branchiostegal membranes of *Trachinops*, unlike those of other plesiopids, usually are not exposed in lateral view, but when the opercle is raised the characteristic membrane configuration is readily apparent. The monotypic plesiopid genus *Calloplesiops* is exceptional in lacking notched branchiostegal membranes.

As noted by Mooi (1990), the Plesiopidae has never been satisfactorily defined although three of the seven genera traditionally assigned to the family (*Trachinops*, *Paraplesiops*, and *Fraudella*) have eggs with similar and unique chorionic structures. Furthermore, and of more relevance to this study, no synapomorphy has been found that supports a monophyletic Plesiopidae exclusive of the Acanthoclinidae. The most recent assessment (results of which were presented at the annual meeting of the American Society of Ichthyologists and Herpetologists, Mooi 1990 abstract) of plesiopid relationships has revealed a number of putative synapomorphies that define various monophyletic clades of plesiopid genera + the Acanthoclinidae. We defer discussion of these characters to a future paper by Mooi that is in an advanced state of preparation. Although the monophyly of the fishes treated herein has never been questioned seriously, we believe their cladistic relationships are best expressed by recognizing the Acanthoclinidae as a subfamily within an expanded Plesiopidae[1].

The four genera and 12 species of acanthoclinine fishes, the so-called spiny basslets (Smith & Heemstra 1986), that we recognize occur in depths of 2-73 meters (one trawl collection of *Acanthoclinus marilynae* in 73-91 m) on reefs and along rocky shores in tropical and temperate waters of the Indo-west Pacific (Fig. 3). Our study of these fishes benefited greatly

[1]The Plesiopidae dates from Günther (1861:362) who first recognized the family as the suprageneric taxon Plesiopina; the Acanthoclinidae dates from the same work (p. 297). Past workers either were unaware that both family-group names date from the same source or did not consider it nomenclaturally relevant because they recognized both families as distinct phylogenetic units of equal taxonomic rank. In accordance with article 24 of the *International Code of Zoological Nomenclature* (ICZN 1985), we hereby act as first revisers in selecting the Plesiopidae as taking precedence over the Acanthoclinidae. This action preserves the more commonly cited family name and best serves nomenclatural stability.

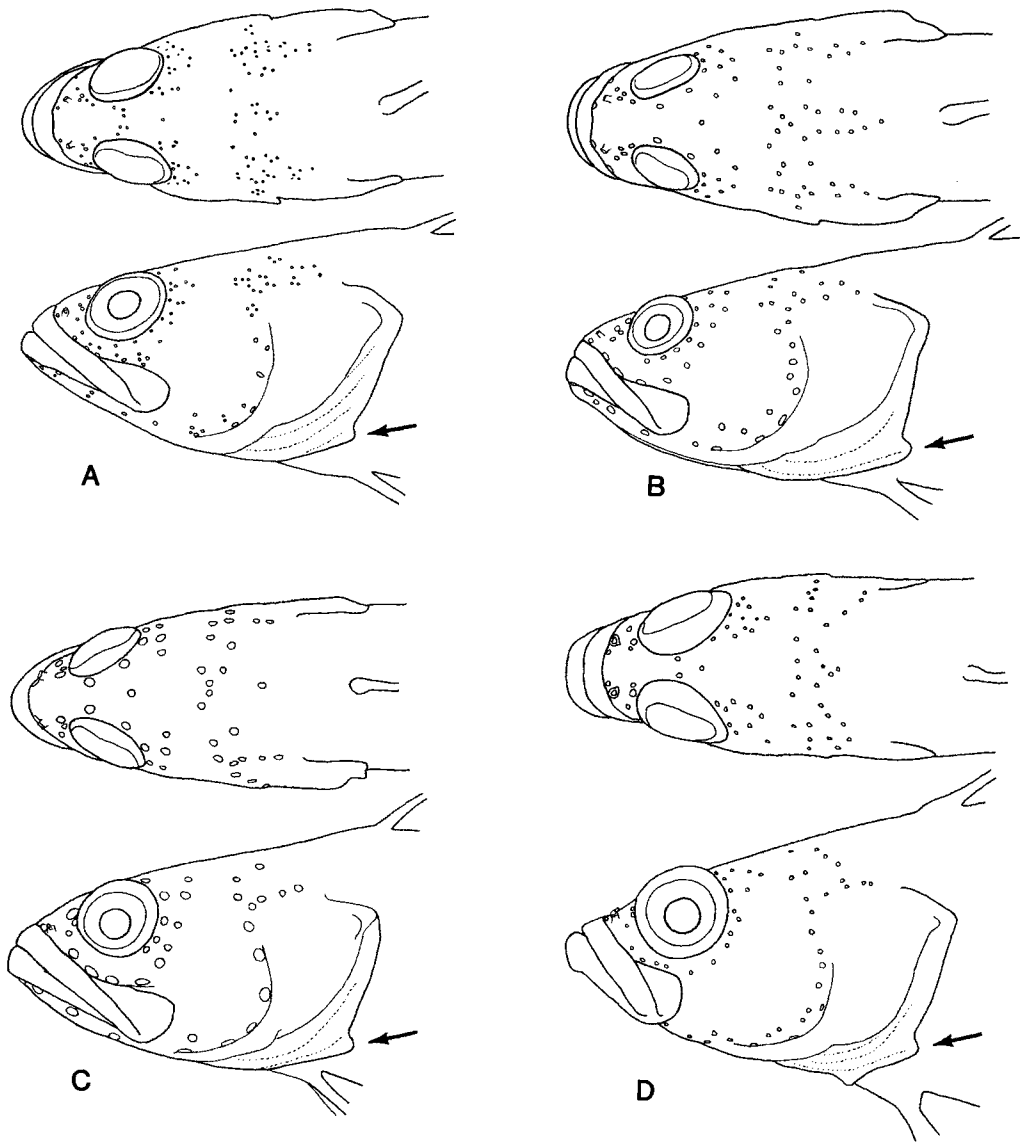


Fig. 1. General physiognomy and cephalic pore patterns in selected species of Acanthoclininae: **A**, *Acanthoclinus fuscus*, ANSP 165085, 57.4 mm SL; **B**, *A. littoreus*, ANSP 165089, 73.3 mm; **C**, *A. rua*, ANSP 165086, 44.8 mm; **D**, *Belonepterygion fasciolatum*, USNM 257883, 35.5 mm. (Small arrows indicate location of rounded projection on posterolateral margin of exposed branchiostegal membrane.)

from Hardy's (1985) revision, and readers should refer to that work for complete synonymies, expanded descriptions, meristic frequency tables and good photographs of all except the two new species described herein. We follow his taxonomic nomenclature, except for our synonymization of *Taumakoides*. In the species accounts all primary synonyms are given but secondary synonymies are selective.

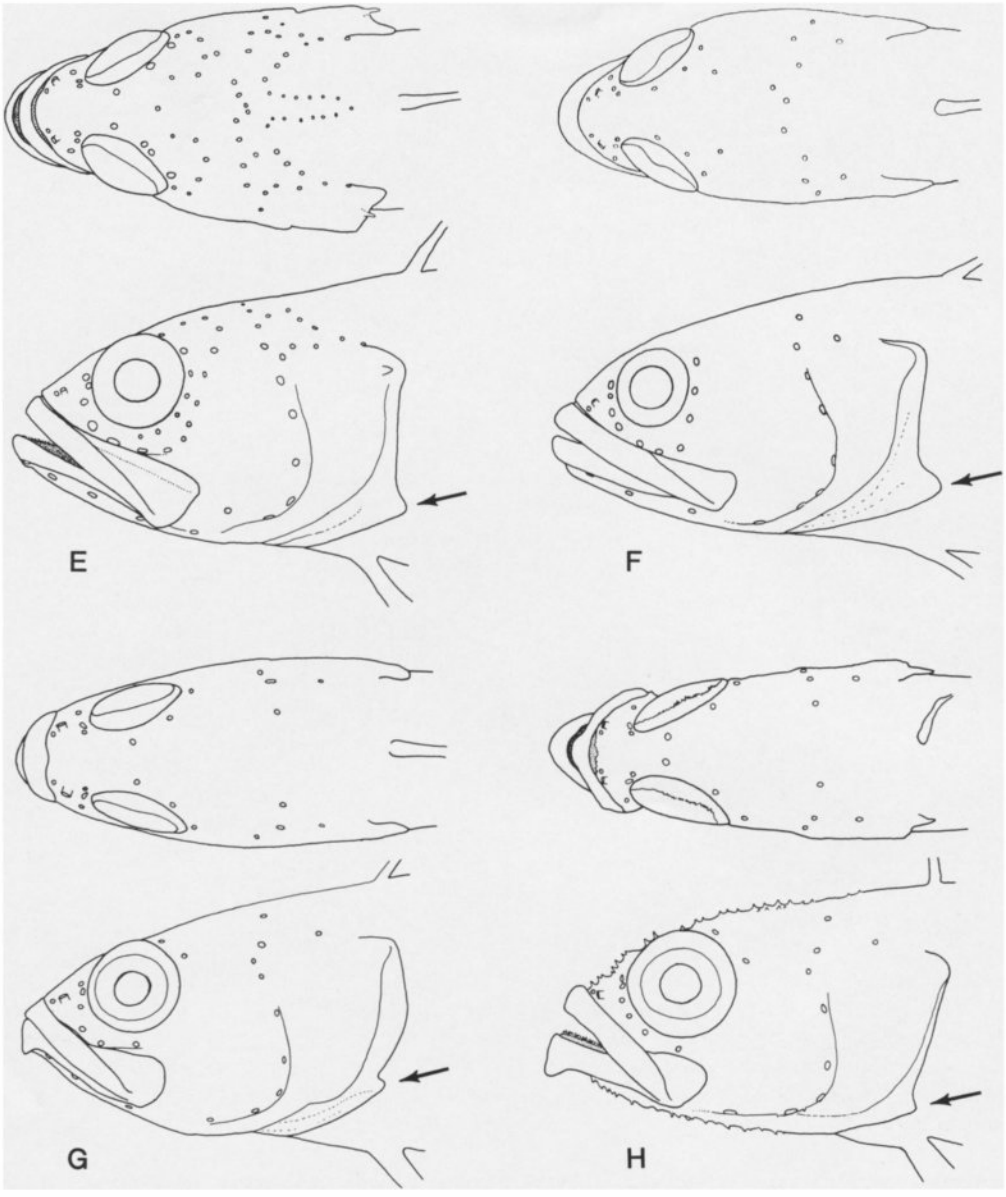


Fig. 1. (continued): **E**, *Beliops xanthokrossos*, ANSP 165557, 25.7 mm SL; **F**, *B. batanensis*, USNM 288976, holotype, 21.0 mm; **G**, *Acanthoplesiops hiatti*, USNM 257631, 18.5 mm; **H**, *A. echinatus*, BPBM 44177, holotype, 19.8 mm.

METHODS AND MATERIALS

Counts.—Counts of dorsal-, anal- and caudal-fin rays and vertebrae were taken from radiographs. The last two elements of the dorsal and anal fins have the "split to base" condition and were counted as one, in accord with the general practice of most authors. The distinction between precaudal and caudal vertebrae, as observed from radiographs, was occasionally difficult to determine with confidence. Except for the

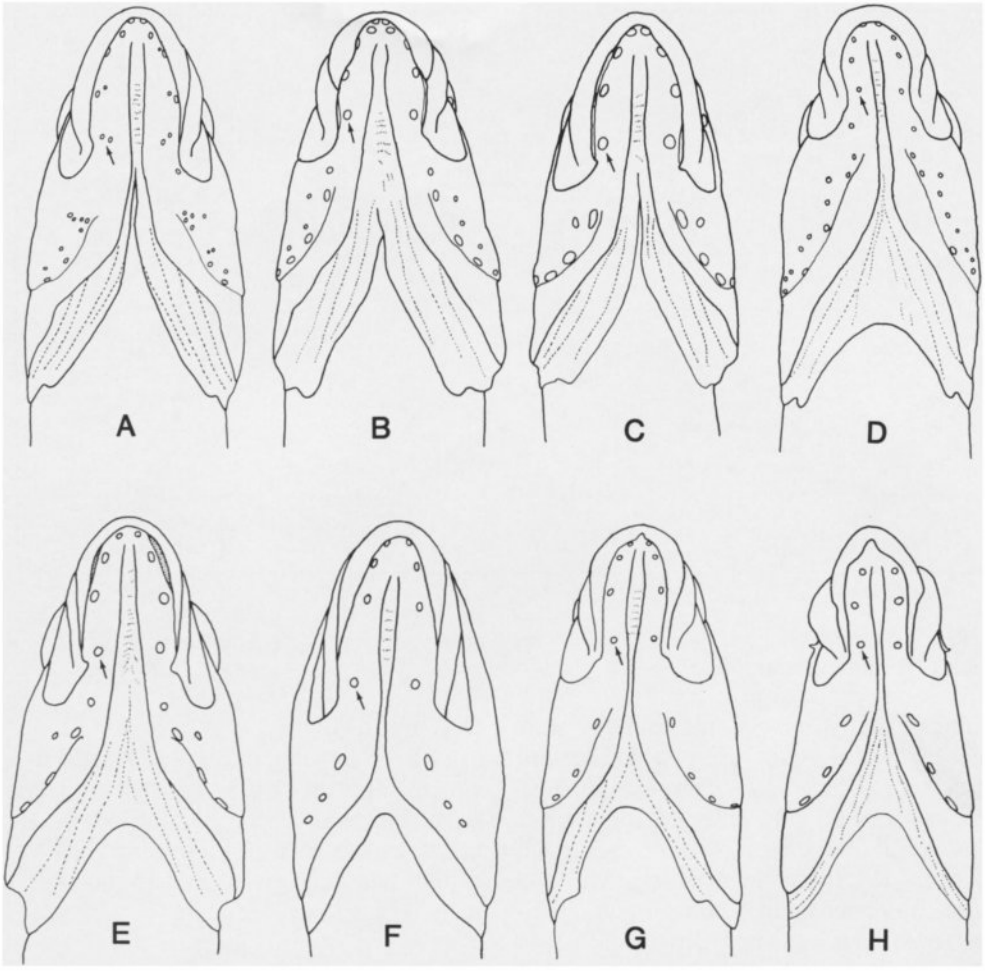


Fig. 2. Ventral views of heads showing general physiognomy and cephalic pore patterns in selected species of Acanthoclininae (data as in Fig. 1.): **A**, *Acanthoclinus fuscus*; **B**, *A. littoreus*; **C**, *A. rua*; **D**, *Belonepterygion fasciolatum*; **E**, *Beliops xanthokrossos*; **F**, *B. batanensis*; **G**, *Acanthoplesiops hiatti*; **H**, *A. echinatus*. (Small arrows indicate location of posteriormost dentary pore position.)

two new species and *Acanthoclinus matti*, for which no cleared and stained whole specimens were available, the number of precaudal and caudal vertebrae was confirmed by examination of C & S specimens. Caudal-fin ray counts include the spinelike dorsal and ventral procurrent rays and the segmented rays. In species of *Acanthoclinus* the posteriormost dorsal and ventral "procurrent" rays are often difficult to distinguish from segmented rays; often a ray will have only one or two segmental joints which can easily be overlooked. For enumeration purposes only rays with at least three segments were counted as "segmented rays." The most important consideration is that the other acanthoclinine genera have fewer total fin elements (18-23, rarely 23 versus 24).

Measurements and illustrations.—All measurements were taken to the nearest 0.1 mm using needle-point dial calipers. Methods of taking measurements were conventional. Except for the two whole fish

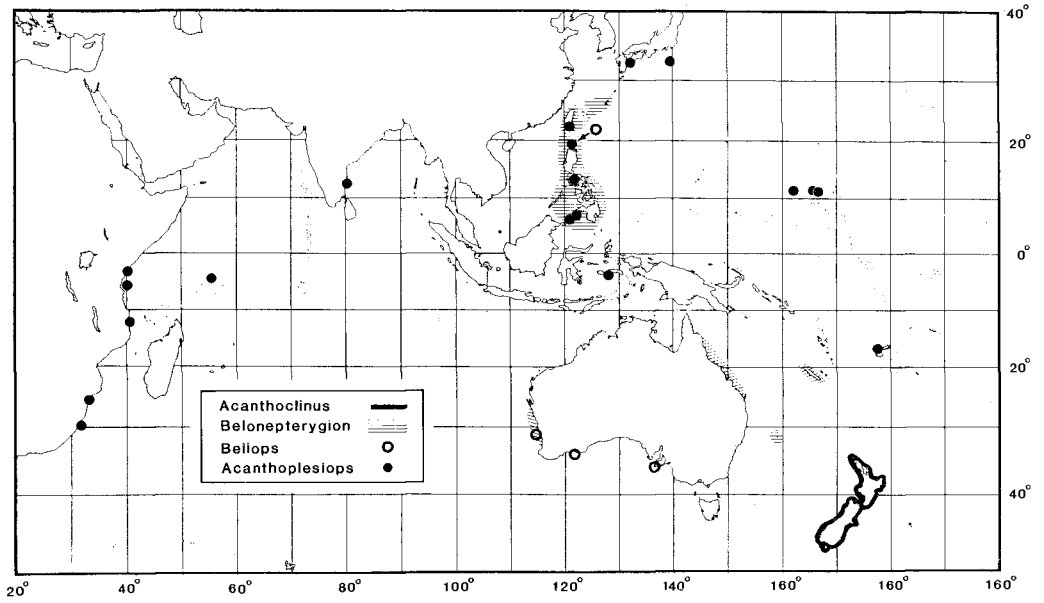


Fig. 3. Distribution of genera of Acanthoclininae; see Fig. 9 for distributions of individual species of *Acanthoplesiops*.

drawings, all specimen illustrations were made by Smith-Vaniz using a microscope and camera lucida. Pore diameters in Figs. 1-2 have been slightly enlarged for clarity.

Material examined.—In the listings of material, C&S designates cleared and stained specimens; the number of specimens and their standard lengths (SL) in mm are given in parentheses. In the species accounts for *Acanthoplesiops* we list all known collections, but do not give lengths unless we have personally examined specimens. Institutional abbreviations for specimen repositories are as follows: Auckland Institute and Museum, Auckland (AIM); Australian Museum, Sydney (AMS); Academy of Natural Sciences of Philadelphia (ANSP); The Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); National Museum of New Zealand, Wellington (NMNZ); Queensland Museum, Brisbane (QM); J.L.B. Smith Institute of Ichthyology, Grahamstown (RUSI); Kyoto University, Seto Marine Biology Laboratory (SMBL); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

The following cleared and stained specimens are the basis for the osteological illustrations and comparative observations noted in the text. If not given below, locality data are given under "material" in individual species accounts.

Plesiopidae

Acanthoclinus fuscus Jenyns, ANSP 165085 (2:44.6-46.5).

Acanthoclinus littoreus (Forster), ANSP 165089 (2:53-69).

Acanthoclinus rua (Hardy), ANSP 165087 (1:46.3).

Acanthoclinus marilynae (Hardy), ANSP 134947 (2:62.8-66.6).

Acanthoclinus matti (Hardy), ANSP 165088 (1:51.0), jaws, suspensorium, gill arches and infraorbitals of right side only.

Acanthoplesiops indicus (Day), ANSP 165570 (1:23.7); ANSP 122483 (1:26.5).

Acanthoplesiops hiatti Schultz, ANSP 165421 (1:18.8); USNM 257874 (2:16.8-21.4).

Acanthoplesiops psilogaster Hardy, USNM 257871 (1:18.8).
Acanthoplesiops echinatus Smith-Vaniz & Johnson, ANSP 166316 (1:21.0), jaws, suspensorium, gill arches, hyoid arch and infraorbitals of right side only.
Assessor macneilli Whitley, ANSP 141752 (4:36.2-36.7) Australia, Great Barrier Reef, One Tree Is.
Belonepterygion fasciolatum (Ogilby), ANSP 142690 (1:30.6); USNM 257875 (3:14.3-28.7).
Beliops batanensis Smith-Vaniz & Johnson, USNM 309905 (1:21.1), jaws, suspensorium, gill arches, hyoid arch and infraorbitals of right side only.
Beliops xanthokrossos Hardy, ANSP 165557 (1:25.9).
Fraudella carassiops Whitley, QM I.19760 (1:42.0), Australia, Great Barrier Reef.
Plesiops coeruleolineatus Rüppell, ANSP 106612 (2:32.7-49), Seychelles, Beacon Is.
Trachinops taeniatus Günther, ANSP 135461 (2:44.7-51.5), Australia, Sydney.

Notograptidae

Notograptus guttatus Günther, ANSP 109653 (4:67.5-81.0), Australia, Queensland, Little Hope Is.

Anatomical abbreviations.—The following abbreviations are used in the text and figures.

A1, A2	separate sections of adductor mandibulae
Af	articular facet
Angart	angulo-articular
Cor	coracoid
Clei	cleithrum
Dent	dentary
Ect	ectopterygoid
Eb	epibranchial
End	endopterygoid
Fl	flange
Hpu	haemal spine of preural centrum
Hyom	hyomandibular
Hypop	hypurapophysis
Intop	interopercle
Io	infraorbital
Max	maxilla
Met	metapterygoid
Nsp	neural spine
Op	opercle
Pal	palatine
Pb	pharyngobranchial (=infrapharyngobranchial)
Pmax	premaxilla
Pop	preopercle
Pp	parapophysis
Ptemp	posttemporal
Quat	quadrate
Rad	radial
Retart	retro-articular
Scap	scapula
Sclei	supracleithrum
Subop	subopercle
Sym	symplectic
Up	uncinate process

Phylogenetic procedures.—Phylogenetic analyses (grouping taxa on the basis of shared derived characters; Wiley 1981) were performed using Hennig-86, version 1.5 (Farris 1988). The outgroup method (Maddison et al. 1984) was used to assign character polarities. Refer to "Character Descriptions and Analysis" and "Phylogenetic Analysis" for specific details.

SYSTEMATIC ACCOUNTS

Acanthoclininae Günther

Description (see also Table 1).—Indo-Pacific marine shorefishes ranging in size from 20-140 mm SL (except 210 mm SL maximum in *Acanthoclinus fuscus*). Dorsal fin XVII-XXVI, 2-6; anal fin VII-XVI, 2-6. Supraneural bones 0-2. Anteriormost proximal pterygiophore (first two in *Acanthoplesiops psilogaster*) of dorsal fin inserted between second and third neural spines. Pterygiophores supporting dorsal- and anal-fin spines with proximal, middle and distal radials fused (distal radials not absent as reported by Mok et al. 1990); distal radials of pterygiophores of dorsal- and anal-fin segmented rays autogenous, middle and proximal radials autogenous or

Table 1. Comparison of selected characters in genera of Acanthoclininae. "N" indicates character states that logically do not apply; number of species in parentheses.

Genus	*Acanthoclinus* (5)	*Belonepterygion* (1)	*Beliops* (2)	*Acanthoplesiops* (4)
Size of adults (maximum mm SL)	64-210	50	21-26	21-26.5
Number of lateral lines	3	3	2	1
Lateral-line scales in upper series	47-97	36-46	24-35	0-13
Infraorbital bones	6	5	5	1
Suborbital shelf	no	yes	yes	N
Vertebrae:				
precaudal	11-12	10-11	10	12-14
caudal	17-23	17-18	16-17	14-17
total	28-35	27-29	26-27	27-30
Dorsal-fin:				
spines	18-26	17-20	18-20	19-21
rays	3-5	4-5	2-4	3-6
Anal-fin:				
spines	9-16	10-12	10-11	7-10
rays	3-5	3-5	2-3	3-6
Gill membranes	separate	united	united	united
Basihyal teeth	yes or no	no	yes	no
Supramaxilla	yes	no	yes or no	no
Primary opercular spine	platelike	platelike	pungent	pungent
Preopercular canal	open	open	tubular	tubular
Neural spine association with 1st precaudal centrum	autogenous	autogenous	fused	fused
2nd and 3rd epurals	separate	separate	fused	fused
Interarcual cartilage	long	long	short	short
Metaptergoid-quadate joint	smooth	smooth	interdigitated	smooth
Secondary opercular spine	no	no	no	yes
Bilobed mid-lateral scales	no	no	no	yes

fused in various species. Ultimate dorsal- and anal-fin pterygiophores each serially supporting two fin elements (last ray split to base). Tips of dorsal- and anal-fin spines with thickened, fleshy pads (spine tips with fleshy tassels in *Beliops xanthokrossos*) that are always pale and contrast conspicuously with heavily pigmented spine shaft and interradial fin membranes (see species account for description of fins in yellow color form of above species). Origin of pelvic fin in advance of vertical from anteriormost insertion of pectoral fin; pelvic fin I, 2; the outermost segmented ray robust basally and deeply bifurcated, the two branches undivided, or very slightly, and with the innermost ray very slender and unbranched or weakly branched distally (Fig. 4). Pectoral fin 15-21. Gill membranes either separate or united across ventral midline; the third branchiostegal ray and immediately adjacent rays positioned so as to produce the distinctive posterolaterally projecting membranous margin (see Fig. 1 and discussion in introduction). At least posterior body scales ctenoid in representatives of all genera but only cycloid scales present in some species (*Acanthoclinus* 2 spp.; *Acanthoplesiops* 1 sp.); head naked except for 1-5 cycloid scales in anterodorsal angle of opercle in three species of *Acanthoclinus*; fins naked except for caudal-fin base. Lateral lines on body in three basic patterns: three essentially complete series (*Acanthoclinus* & *Beloneptery-gion*), except middle lateral line scarcely if at all extending beneath appressed pectoral fin; two incomplete series (*Beliops*), the first from upper angle of opercle to rear of spinous dorsal fin, and the middle from slightly to well behind pectoral fin to caudal-fin base; or one incomplete dorsal series (*Acanthoplesiops*) extending posteriorly to below verticals between origin and about middle of spinous dorsal fin, but with area of the body that is occupied by the middle lateral line in the other genera with a row of scales containing superficial neuromasts (refer to discussion of character 7 in "Character Descriptions and Analysis").

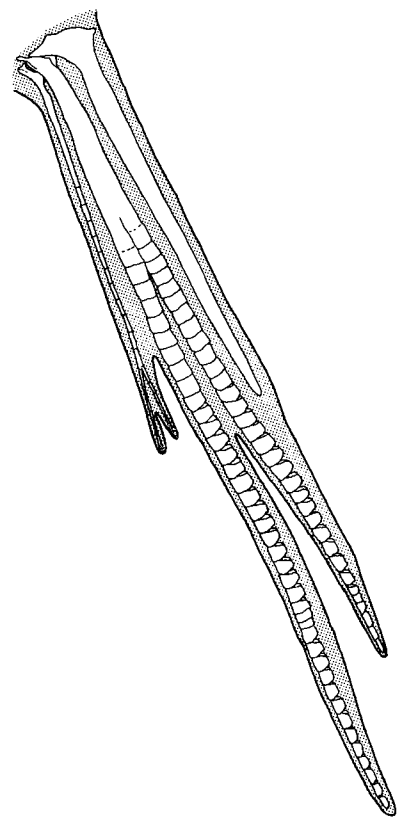


Fig. 4. Ventral view of left pelvic fin of *Acanthoclinus littoreus*, ANSP 165089, 53 mm SL.

Vertebrae 10-14 + 14-23 (total 26-35). Haemal spine of penultimate (second preural) vertebra fused to vertebral centrum (except autogenous in *Acanthoclinus* 3 spp.). Hypurals 1 and 2 and parhypural fused together as autogenous plate; hypurals 3 and 4 fused to each other and to urostylar complex; hypural 5 present and independent. No autogenous uroneurals; 3 epurals, 2nd & 3rd partially fused in *Beliops* & *Acanthoplesiops*). Branched caudal-fin rays 12 or 14, 6-7 + 6-7; total fin elements 18-24. No procurrent spur. Interarcual cartilage present, very small in *Beliops* & *Acanthoplesiops*; infrapharyngobranchial 1 present (toothless) but may be entirely cartilaginous in *Acanthoplesiops hiatti*. Basibranchials 1-3 ossified, 4th present as cartilage. Basibranchial 1 anterior and ventral to basihyal. Urohyal articulating

with ventral surface of basibranchials 1 and 2. Six branchiostegals, anterior 4 on ceratohyal. No ligament connecting ceratohyal and dentary. Dorsal and ventral hypohyals present. Uppermost pectoral-fin ray articulating with scapula. Scapular foramen complete. Dorsal and ventral postcleithra present and usually attached to each other. Basisphenoid present. Vomer toothed; palatine toothed (except in *Belonepterygion*), broadly articulating with anteriorly elongate process of ectopterygoid. Infraorbital bones 1-6; suborbital shelf present or absent. Each eye with one pair of concave sclerotics. One extrascapular (lateral) on each side (supratemporal canal passing only through skin medially). Ectopterygoid and endopterygoid anteriorly elongate, closely associated with palatine. Supramaxilla present or absent. Sesamoid articular (coronomeckelian) present.

At least five readily observed character states (derived) distinguish the Acanthoclininae as a group from all or most of the seven other plesiopid genera:

1. Lower lip with continuous free ventral margin across front of lower jaw (also present in *Calloplesiops* & *Steeneichthys*) versus ventral margin free only laterally, interrupted by isthmus.

2. Head naked (except 2-5 cycloid scales on anterodorsal angle of opercle in *Acanthoclinus* 3 spp.) versus preopercle (scales embedded in some spp.), opercle, and often dorsum of head mostly to completely scaled.

3. Dorsal and anal fins with *higher* numbers of spines (16-26 and 7-16 versus 11-15 and 3, respectively) and concomitant *lower* numbers of segmented rays (2-6 and 2-6 versus 6-21 and 7-23, respectively).

4. Fewer pelvic-fin rays, I,2 (versus I,4).

5. Fewer branched caudal-fin rays in adults, 14 (12 in *Beliops batanensis*) (versus 15-17, rarely 14 in *Steeneichthys*).

Additional characters that bear on the relationship of the Acanthoclininae to other plesiopid genera will be presented elsewhere by Randall Mooi.

The Notograptidae, consisting of two or three species known only from Australia and southern Papua-New Guinea, shares with the Acanthoclininae the combination of pterygiophores supporting dorsal- and anal-fin spines with proximal, middle and distal radials fused, high numbers of dorsal- and anal-fin spines (66-68 and 39-43, respectively), I,2 pelvic-fin rays, scaleless head, and lower lip with continuous free ventral margin (although produced into a barbel at symphysis of lower jaw). Notograptids differ from plesiopids (sensu lato) most notably in absence of the characteristic branchiostegal membrane configuration discussed in the introduction, absence of uncinate process on epibranchial 1 (and associated loss of the interarcual cartilage), absence of infrapharyngobranchial 1, and in having the anterior half of the suspensorium only weakly connected to the posterior half (Gosline 1968:fig. 8d). The precise phylogenetic relationships of the Notograptidae are uncertain and require further investigation, which is beyond the scope of the present study.

Key to the Species of Acanthoclininae

1a. Body with 3 separate lateral lines 2
1b. Body with 1 or 2 lateral lines 7

2a. Gill membranes fused in ventral midline to form a broad free fold across isthmus (Fig. 2D); adults with 9-16 narrow, dark bands on body; palatine teeth absent; 5 infraorbital bones, the 3rd with a well developed suborbital shelf (Fig. 13C) (Western Australia and western Pacific Ocean, excluding New Zealand) . . . . . *Belonepterygion fasciolatum*

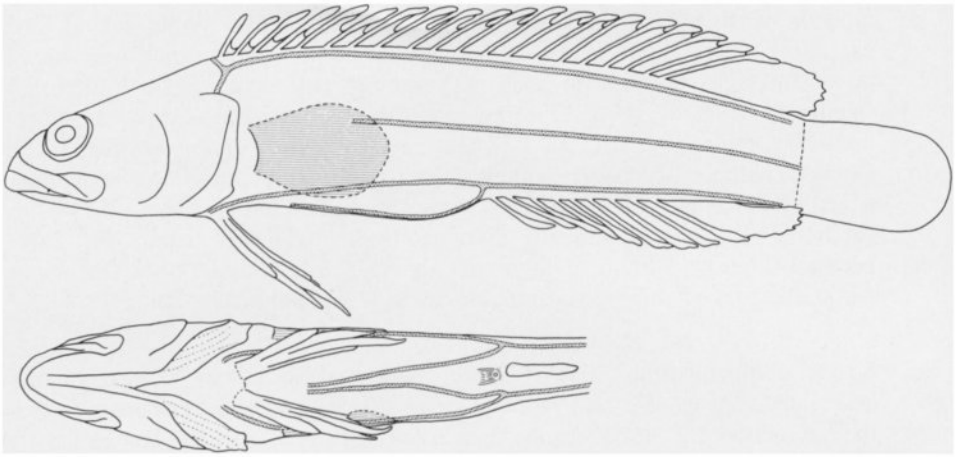


Fig. 5. Lateral line configuration in *Acanthoclinus fuscus*.

2b. Gill membranes separate ventrally, not fused as a continuous fold across isthmus (Figs. 2A-C); adults without narrow, dark bands on body; palatine teeth present; 6 infraorbital bones, the 3rd without a suborbital shelf (Figs. 13A-B) (endemic to New Zealand) . . . . . *Acanthoclinus* . . . 3

3a. Ventral lateral line with branch at anal-fin origin that continues anteriorly on either side of ventral midline (Fig. 5); nape scaled; dorsal- and anal-fin spines 20 and 9, respectively; haemal spine of PU2 fused to centrum . . . . . *Acanthoclinus fuscus*

3b. Ventral lateral line unbranched; nape naked; dorsal- and anal-fin spines 17-26 and 9-16, respectively; haemal spine of PU2 autogenous 4

4a. Body scales all cycloid; innermost pelvic-fin ray branched; dorsal- and anal-fin spines 24-26 and 14-16, respectively; first anal-fin pterygiophore with 1 supernumerary spine; total vertebrae 34-36 . . . . . *Acanthoclinus littoreus*

4b. Body scales ctenoid, at least posteriorly; innermost pelvic-fin ray unbranched; dorsal- and anal-fin spines 18-26 and 9-15, respectively; first anal-fin pterygiophore with 2 supernumerary spines; total vertebrae 28-33 5

5a. Lower jaws anteriorly with a single pair of sensory pores (each dentary with 4 pores, Fig. 2C); dorsal- and anal-fin spines 22-24 and 14-15, respectively . . . . . *Acanthoclinus rua*

5b. Lower jaws anteriorly with two pairs of sensory pores (each dentary with 5 pores); dorsal- and anal-fin spines 18-20 and 9-12, respectively . . . 6

6a. Dark blotch on opercle, head without conspicuous white spots; body without narrow pale stripes; dorsal- and anal-fin spines 19 or 20 and 11 or 12, respectively . . . . . *Acanthoclinus marilynae*

6b. No dark blotch on opercle, head with conspicuous white spots; body with narrow white stripes; dorsal- and anal-fin spines 18 and 9 or 10, respectively . . . . . *Acanthoclinus matti*

7a. Opercle with 1 or 2 secondary spines (Figs. 16F-H); single lateral line extending from upper angle of opercle to no more than half-way along dorsal-fin base; pectoral-fin base with a large pale spot; single infraorbital (lacrimal) bone (Fig. 13F); first anal-fin pterygiophore with 2 supernumerary spines . . . . . *Acanthoplesiops* . . . 9

7b. Opercle without secondary spines; two lateral lines, dorsalmost extending from upper angle of opercle to base of last dorsal-fin ray, the other extending forward a variable distance from middle of caudal-fin base; pectoral-fin base without a large pale spot; 5 infraorbital bones (including lacrimal); first anal-fin pterygiophore with 1 supernumerary spine . . . . . *Beliops* . . . 8

8a. Scales elliptical (Fig. 20F) ; dorsal- and anal-fin spines relatively long and slender (Fig. 8), and with interradial membranes of anterior spines incised about 1/2 to 2/3 spine length; dorsal- and anal-fin spines 18 or 19 and 10, respectively; supramaxilla present (Western and South Australia) . . . . . *Beliops xanthokrossos*

8b. Scales on posterior half of body strongly lanceolate, with membranous flaps (Fig. 20G,); dorsal- and anal-fin spines relatively short and stout, and with interradial membranes of spines very weakly incised; dorsal- and anal-fin spines 22 and 11, respectively; supramaxilla absent (Batan Islands) . . . . . *Beliops batanensis*, n.sp.

9a. Terminal dorsal- and anal-fin rays with broad membranous attachment to caudal fin (Fig. 10); broad white band on base of caudal fin, caudal peduncle and posteriormost rays of dorsal and anal fins; supraneural bones absent (western Indian Ocean and India) . . . . . *Acanthoplesiops indicus*

9b. Terminal dorsal- and anal-fin rays completely free or scarcely membranously attached to caudal peduncle; no broad white band on caudal peduncle and caudal-fin base; 1 or 2 supraneural bones 10

10a. Anterior two thirds of belly naked; first two pterygiophores of dorsal fin inserted between 2nd and 3rd neural spines; 1 supraneural (Japan, Taiwan and Batan Islands) . . . . . *Acanthoplesiops psilogaster*

10b. Belly completely scaled; only first pterygiophore of dorsal fin inserted between 2nd and 3rd neural spines; 2 supraneural bones 11

11a. Symphysis of lower jaws with terminal pair of pores (each dentary with 4 pores, Fig. 2G); segmented anal-fin rays 3-5; posterior profile of scales ovate or bluntly rounded; preopercle occasionally with 2 secondary spines (Sulu Archipelago, Banda Sea, Fiji and Marshall Is.) . . . . . *Acanthoplesiops hiatti*

11b. Symphysis of lower jaws without terminal pair of pores (each dentary with 3 pores, Fig. 2H); segmented anal-fin rays 6; posterior profile of scales lanceolate with membranous flap (Fig. 20J); preopercle with 1 secondary spine; (Sulu Archipelago and Banda Sea) . . . . . *Acanthoplesiops echinatus*, n.sp.

Genus *Acanthoclinus* Jenyns

Acanthoclinus Jenyns, 1842:91 (type species *Acanthoclinus fuscus* Jenyns, 1842, by monotypy, a second species questionably included).

Taumakoides (as a subgenus of *Acanthoclinus*) Whitley, 1955:111 (type species *Acanthoclinus trilineatus* Griffin, 1933, = *Acanthoclinus littoreus* (Forster) *in* Bloch & Schneider, 1801, by original designation and monotypy).

Diagnosis .—A genus of acanthoclinine fishes with five species (maximum size 210 mm SL, in *A. fuscus*, other spp. <135 mm) with the following combination of characters: dorsal fin XVIII-XXVI, 3-5; anal fin IX-XVI, 3-5; pectoral fin 17-21; vertebrae 11-12 + 17-23 = 28-35 total; caudal-fin rays (dorsal/ventral): procurrent 3-4/2-4, segmented 8-9/8-10, middle 14 branched, total elements 24. Body with three lateral lines: dorsal lateral line extends from upper angle of opercle to dorsolateral base of caudal fin (*A. fuscus* sometimes with a short accessory branch on predorsal area); middle lateral line extends from near posterior margin of pectoral fin along horizontal septum to caudal-fin base; ventral lateral line extends from just in front of pelvic fin to ventrolateral base of caudal fin (*A. fuscus* typically has an accessory branch arising at anal-fin origin and continuing forward onto ventral midline). Tubed lateral-line scales: dorsal 47-97, middle 44-81, ventral 51-113; lateral-line scales variable in size compared to adjacent body scales, ranging from scales of all three series noticeably larger (*A. littoreus*) to those of dorsal and ventral series slightly larger and middle lateral-line scales subequal or smaller (*A. matti*); some lateral-line scales typically with a pair of vertically aligned superficial neuromasts (Fig. 20A-D); posterior profiles of non-lateral-line scales ranging from ovate to broadly elliptical. Head entirely naked, except 3 spp. with 2-5 scales in anterodorsal angle of opercle; body and caudal-fin base completely scaled (except predorsal area naked in all species except *A. fuscus*); anterior scales cycloid, becoming ctenoid posteriorly (except cycloid scales basally on caudal fin in *A. rua* and all scales cycloid in *A. fuscus & littoreus*). Sensory pores on head variable in number but postorbital pore positions consistently in multiple series; lower jaws anteriorly with 2 pairs of pores, Figs. 2A-B (except 1 pair in *A. rua*, Fig. 2C); gill membranes separate ventrally, not fused as a continuous fold across isthmus. Infraorbital bones 6, the 3rd infraorbital without a suborbital shelf (Figs. 13A-B). Palatine with teeth; metaptcrygoid with a very well-developed lateral flange; metapterygoid-quadrate joint smooth; preopercular canal open posterolaterally; primary opercular spine broadly rounded and platelike (posterodorsal margin of opercle often fimbriate), no secondary spine present; maxilla moderately broad with a relatively straight posterodorsal margin overlaid by a small supramaxilla (Fig. 14 A-B). Supracleithrum with well-developed supracleithral sensory canal that is continuous anterodorsally with post-temporal canal and posteriorly with lateral-line scales; pectoral girdle with scapulocoracoid joint smooth, posterolateral arm of coracoid relatively slender (Fig. 19A) and with radial formula 2-1-1; hyoid arch with ceratohyal-epihyal suturing medially only. Infrapharyngobranchials 2-4 toothed; interarcual cartilage relatively long (Fig. 15A); basihyal moderately broad to slender, and with or without teeth. Neural spine of first vertebra autogenous; first pterygiophore of anal fin with 2 or 1 (*A. fuscus & littoreus*) supernumerary spines; all but anteriormost pterygiophore of segmented dorsal- and anal-fin rays consisting of autogenous proximal, middle and distal radials; haemal spine of second preural vertebra autogenous (except in *A. fuscus* fused to vertebral centrum). Caudal skeleton with 3 separate epurals, hypural 5 long and wide, and small to moderate hypurapophysis (Fig. 17A). Adductor mandibulae with A1 and A2 sections both visible laterally (Figs. 22A-B).

Remarks.—Hardy (1985) noted that although originally proposed as a subgenus

Table 2. Range of selected counts in species of *Acanthoclinus*[1].

species	total vertebrae	fin spines		lateral-line scales		
		dorsal	anal	dorsal	middle	ventral
A. fuscus	30	20	9	84-97	60-77	100-113
A. littoreus	34-35	24-26	14-16	75-88	68-81	75-91
A. rua	31-33	22-24	14-15	63-75	52-70	63-75
A. marilynae	29-31	18-20	11-12	62-72	54-67	63-74
A. matti	28-29	18	9-10	47-64	44-58	51-64

[1]Data from Hardy (1985).

of *Acanthoclinus*, Whitley (1968) later gave *Taumakoides* full generic rank, and that "its allocation to a separate genus is justified." He listed three new characters that supposedly differentiate these two taxa. Two of these (position of the 5th branchiostegal ray relative to the epi/ceratohyal joint; and the association of the anterior anal-fin spine pterygiophores to the first three haemal spines) are virtually identical in our cleared and stained material of *A. fuscus* & *littoreus*, and the third character (slight difference in gill rakers) we consider to be of trivial significance. Furthermore, as discussed in the section "Acanthoclinine relationships," *A. littoreus* and *fuscus* (the type species of *Taumakoides* and *Acanthoclinus*, respectively) are each others closest relatives; thus, recognition of *Taumakoides* either as a genus or subgenus cannot be justified.

Distribution.—Endemic to New Zealand.

Species comparisons.—The species of *Acanthoclinus* are contrasted in the preceding key, Table 2 and in the following species accounts.

Acanthoclinus fuscus Jenyns
Figs. 1A-2A, 5

Acanthoclinus fuscus Jenyns, 1842:92, pl. 18, fig. 2 (original descr.: Bay of Is., New Zealand); lectotype BMNH 1917.7.14:37); Hardy, 1985:360-364, fig. 1 (redescription; specimen photograph; synonymy; lectotype designation).

Acanthoclinus taumaka Clarke, 1879:293, pl. 15 (original descr.: Jackson's Bay, New Zealand; holotype AIM).

Acanthoclinus quadridactylus [not Bloch & Schneider]. Graham, 1953:320,326, pl on 321 (behavioral observations, including aspects of parental care of eggs); Jillett, 1968:1-7 (aspects of biology: age, growth and food); Jillett, 1968a:1-8 (aspects of biology: breeding & development).

Blennius littoreus [not Forster]. Whitehead, 1969:pl. 30.

Diagnosis.—A species of *Acanthoclinus* with the following autapomorphies: 1) ventral lateral line with an accessory branch at the anal-fin origin (sometimes separate from the ventral lateral line) that continues anteriorly on either side of the ventral midline (Fig. 5), 2) the dorsal lateral line is unique in frequently having an anterior branch arising below base of 2nd dorsal-fin spine and directed obliquely onto predorsal area, but not joined with opposite member at the dorsal midline (often this accessory branch is present on one side only), and 3) haemal spine of second preural vertebra fused to vertebral centrum. *Acanthoclinus fuscus* also has the highest number of lateral-line scales, a unique combination of dorsal- and anal-fin spines (Table 2), and the predorsal area scaled (plesiomorphic character state present in no other species of Acanthoclininae).

Abbreviated description.—Dorsal fin XX, 4; anal fin IX, 4; pectoral fin 17-19; vertebrae 12 + 18 = 30 total; tubed later-

al-line scales: dorsal 84-97, middle 60-77, ventral 100-113 (excluding accessory branch, which has 32-44 scales); lateral-line scales slightly to moderately larger than adjacent scales (Fig. 20A); posterior profiles of non-lateral-line scales somewhat ovate; anterodorsal angle of opercle scaleless; body, including predorsal area, entirely covered with cycloid scales; lower jaws anteriorly with 2 pairs of pores (Fig. 2A), each dentary with 5 pore positions (posterior three positions may each be occupied by one to several pores); basihyal moderately broad and toothed; first pterygiophore of anal fin with a single supernumerary spine; haemal spine of second preural vertebra fused to vertebral centrum.

Color pattern (after Hardy (1985).—When fresh, body and ventral half of dorsal fin olive-greenish, mottled with creamish blotches; broad creamish stripe medially on head and predorsal region; a similar broad stripe anteroventrally angled across cheek, and scattered creamish specks on remainder of head, lips, and opercular region; two or three small, creamish spots on pectoral-fin base; dark blotch posteriorly on dorsal fin over soft rays.

Remarks.—Unlike the other species of *Acanthoclinus*, our specimens of *A. fuscus* all have the same number of dorsal- and anal-fin rays and vertebral counts, the same as those reported by Hardy (1985). Apparently these meristic characters have become genetically fixed in *A. fuscus*.

Maximum size.—Hardy (1985) reported the maximum size as 210 mm SL (250 mm TL). The largest specimens recorded by Jillet (1968) were 200 mm TL and thought to be 10 years old.

Material (all from New Zealand).—ANSP 122745 (1:72), Bay of Islands, Urupukapuka Is.; ANSP 165085 (6:55.8-76, including 2:44.6-46.5 C&S), New Plymouth; USNM 83311 (1:92), "Balabac"; USNM 200547 (6:54.5-82.3), Kaikoura Peninsula; USNM 303548 (3:27.3-28.8), Wellington Harbor, Seaview; USNM 312932 (3:46-89), Auckland, Campbells Bay.

Acanthoclinus littoreus (Forster)
Figs. 1B-2B

Blennius litoreus Forster *in* Bloch & Schneider, 1801:177 (incorrect original spelling; name in synonymy).

Blennius quadridactylus Bloch & Schneider, 1801:177 (original descr.: [New Zealand] based on verbatim description of *Blennius littoreus* in J.R. Forster's unpublished manuscript).

Acanthoclinus trilineatus Griffin, 1933:330, 332-333, fig. 2, pl. 34 (original descr.: Deep Water Cove, Bay of Islands, New Zealand).

Taumakoides trilineatus. Whitley, 1955:111 (type species of new subgenus of *Acanthoclinus*).

Taumakoides littoreus. Hardy, 1985:364-367, fig. 5 (redescription; specimen photograph; synonymy); Mooi, 1990:463, fig. 7 (egg surface morphology).

Nomenclature.—Hardy (1985:359-60) gave a detailed discussion of the nomenclatural confusion that has resulted from use of the name *Acanthoclinus quadridactylus* (Bloch & Schneider) by subsequent authors. We agree with his opinion that the requirements of "first reviser" were fulfilled in essence by Cuvier & Valenciennes (1836), who tacitly implied that Foster's name had priority over that of Bloch & Schneider by including both names under the heading *Clinus littoreus*.

Diagnosis.—*Acanthoclinus littoreus* differs from all other species of *Acanthoclinus* in having 34-35 (versus 28-33) total vertebrae; only it and *A. fuscus* have the first anal-fin pterygiophore with a single supernumerary spine and all body scales cycloid. The combination of high numbers of dorsal- and anal-fin spines and lateral-line scales (Table 2) is shared only with *A. rua*, and the latter counts scarcely overlap.

Abbreviated description.—Dorsal fin XXIV-XXVI, 3-5; anal fin XIV-XVI, 3; pectoral fin 18-20 (rarely 21); vertebrae 12 + 22-23 = 34-35 total; tubed lateral-line

scales: dorsal 75-88, middle 68-81, ventral 75-91; all lateral-line scales noticeably larger than adjacent body scales (Fig. 20B); posterior profiles of non-lateral-line scales appear somewhat ovate; anterodorsal angle of opercle with 1 or 2 partially embedded scales; body, except naked predorsal area, entirely covered with cycloid scales; lower jaws anteriorly with 2 pairs of pores (Fig. 2B), each dentary with 5 pore positions; basihyal slender, toothless; first pterygiophore of anal fin with a single supernumerary spine; haemal spine of second preural vertebra autogenous.

Color pattern.—Back and sides dark reddish brown. Opercle with dark brown blotch outlined by pale pinkish border. Three dark lines, with pale borders, radiating from posterior margin of eye; the 1st from posterodorsal margin of orbital rim along upper surface of head, 2nd from middle of rim towards opercular blotch, sometimes continuous with it, 3rd from ventral margin of rim towards subopercle.

Maximum size.—Hardy (1985) reported the maximum size as 133 mm SL, based on examination of 122 specimens.

Material (all from New Zealand).—ANSP 165089 (6:66.5-95.3, including 2:53-69 C&S), Outer Chetwode Is.; ANSP 122742 (1:104), ANSP 122744 (1:74) and ANSP 122746 (5:27-116), Bay of Islands, vicinity Urupukapuka Is.; USNM 247331 (2:66.5-69), Wellington, Lyall Bay.

Acanthoclinus rua (Hardy)
Figs. 1C-2C

Taumakoides rua Hardy, 1985:367-370, fig. 6 (original descr.: off Barrett's Reef, Wellington Harbour entrance, New Zealand; holotype NMNZ P.13852).

Diagnosis.—*Acanthoclinus rua* differs from all other species of *Acanthoclinus* in having the lower jaws anteriorly with one pair of pores (Fig. 2C), each dentary with 4 pore positions.

Abbreviated description.—Dorsal fin XXIV-XXVI, 3-4; anal fin XIV-XVI, 3-4; pectoral fin 18-21; vertebrae 11 + 20-22 = 31-33 total; tubed lateral-line scales: dorsal 63-75, middle, 52-70, ventral 63-75; lateral-line scales slightly larger than adjacent body scales; posterior profiles of non-lateral-line scales somewhat ovate (Fig. 20C); anterodorsal angle of opercle with 2-4 partially embedded scales; body, except naked predorsal area, covered anteriorly with cycloid scales, that become ctenoid under base of dorsal-fin soft rays and on caudal peduncle, cycloid scales also present basally on caudal fin; lower jaws anteriorly with one pair of pores, each dentary with 4 pore positions; basihyal slender, toothless; first pterygiophore of anal fin with 2 supernumerary spines; haemal spine of second preural vertebra autogenous.

Color pattern (after Hardy (1985).—When fresh, "Body and head uniformly brown, a faintly pale-edged, darker blotch on operculum; white band medially on dorsal surface of snout and predorsal region (may also include 1st dorsal fin spine); dorsal fin webbing almost transparent pale grey, with fleshy appendages on spine tips pale to bright orange; dorsal fin soft rays tipped orange, a very narrow orange margin around caudal fin; anal fin similar to dorsal fin, but appendages on spine tips white; proximal half of pelvic fins greyish, distal half bright orange."

Maximum size.—The smallest species of *Acanthoclinus*; the largest of 37 types of *A. rua* examined by Hardy (1985) is 64 mm SL.

Material (all from New Zealand).—ANSP 165086 (2:44-44.8), Stewart Is.; ANSP 165087 (3:34.3-41.5, 46.3 C&S), Percy Is.

Acanthoclinus marilynae (Hardy)

Taumakoides marilynae Hardy, 1985:370-373, fig. 7 (original descr.: Scorching Bay, Wellington, New Zealand; holotype NMNZ P.14134).

Diagnosis.—A species of *Acanthoclinus* distinguished by the following autapomorphic character state: the lateral lines on opposite sides of the body adjacent to the

dorsal- or anal-fin bases united behind these fins and continuing to caudal-fin base as a single series of tubed scales along the dorsal or ventral ridge of peduncle, respectively.

Abbreviated description.—Dorsal fin XIX-XX, 3-5; anal fin XI-XII, 3-5; pectoral fin 18-21; vertebrae 11 + 18-20 = 29-31 total; tubed lateral-line scales: dorsal 62-72, middle 54-67, ventral 63-74; scales in dorsal and ventral lateral-line series moderately larger than adjacent scales, those in middle series subequal; posterior profiles of non-lateral-line scales broadly elliptical; anterodorsal angle of opercle with 5-6 small scales; body, except naked predorsal area, covered anteriorly with cycloid scales, that become ctenoid dorsally and on sides from behind level of pectoral-fin base, ctenoid scales also basally on caudal fin; lower jaws anteriorly with 2 pairs of pores, each dentary with 5 pore positions; basihyal slender, toothed; first pterygiophore of anal fin with 2 supernumerary spines; haemal spine of second preural vertebra autogenous.

Color pattern (after Hardy (1985).—When fresh (based on several specimens), "body varying from mottled light and dark brown to deep chocolate-brown throughout; head mottled medium brown and dark olive-green to deep chocolate brown (also predorsal and opercular region); dorsal and anal fin webbing dark greyish-brown to black; dorsal and anal fin spine tips pinkish-brown to deep orange; outer margin of dorsal and anal fin soft rays, and caudal fin rays, narrowly lined with bright yellowish-orange; proximal half of pelvic fins medium brown to greyish, distal half medium to deep orange."

Remarks.—Hardy (1985:390) reported the basihyal toothless in *A. marilynae*; all our specimens have this bone distinctly toothed.

Maximum size.—The largest of 70 types of *A. marilynae* examined by Hardy (1985) is 134 mm SL.

Material (all from New Zealand).—ANSP 122743 (3:24.9-60.8) and ANSP 122752 (1:58.2), Bay of Islands, NW of Urupukapuka Is.; ANSP 122747 (2:60.2-65.8), ANSP 122801 (1:49.8), and ANSP 134947 (2:62.8-66.6 C&S), Bay of Islands, SW of Cape Brett.

Acanthoclinus matti (Hardy)

Taumakoides matti Hardy, 1985:373-375, fig. 8 (original descr.: off Sentinel Rock, outer Marlborough Sounds, New Zealand; holotype NMNZ P.15332).

Diagnosis.—*Acanthoclinus matti* differs from all other species of *Acanthoclinus* in its distinctive color pattern (see below), including the absence of dark blotch on opercle; it also has the largest body scales (Fig. 20D) and the lowest number of lateral-line scales (Table 2).

Abbreviated description.—Dorsal fin XVIII, 4-5; anal fin IX-X, 3-5; pectoral fin 19-20; vertebrae 11-12 + 17 = 28-29 total; tubed lateral-line scales: dorsal 47-64, middle 44-58, ventral 51-64; scales in dorsal and ventral lateral lines slightly larger than adjacent body scales, those of middle lateral line subequal or smaller than adjacent scales (Fig. 20D); posterior profiles of non-lateral-line scales broadly elliptical; anterodorsal angle of opercle with about 6 scales; body, except naked predorsal area, covered anteriorly with cycloid scales, that become ctenoid dorsally and on sides from about posterior margin of pectoral-fin base, ctenoid scales also on peduncle and basally on caudal fin; lower jaws anteriorly with 2 pairs of pores, each dentary with 5 pore positions; basihyal slender, toothed; first pterygiophore of anal fin with 2 supernumerary spines; haemal spine of second preural vertebra autogenous.

Color pattern.—Head dark chocolate brown, covered with conspicuous, small, white spots; body scales deep maroon with white upper and lower corners, resulting in a series of about 10 narrow white stripes on sides against a dark background; belly with 7 similar white stripes.

Maximum size.—Attains at least 125 mm SL.

Material.—ANSP 165088 (1:51.0),

Fiordland, mouth of Cunaris Sound, New Zealand.

Genus *Belonepterygion* McCulloch

Belonepterygion McCulloch, 1915:51 (type species *Acanthoclinus fasciolatus* Ogilby, 1889, by original designation and monotypy).

Ernogrammoides Chen and Liang, 1948:32 (type species *Ernogrammoides fasciatus* Chen and Liang, 1948, = *Belonepterygion fasciolatum* (Ogilby), by original designation and monotypy).

Calliblennius Aoyagi, 1954:213 (37) (type species *Calliblennius rubescens* Aoyagi, 1954, = *Belonepterygion fasciolatum* (Ogilby), by original designation and monotypy, preoccupied in fishes by *Calliblennius* Barbour 1912).

Description.—A monotypic acanthoclinine genus (maximum size 50 mm SL), with the following combination of characters: dorsal fin XVII-XX, 4-5; anal fin X-XII, 3-5; pectoral fin 17-19; total vertebrae 10-11 + 17-18 = 27-29 (rarely 29) total; caudal-fin rays (dorsal/ventral): procurrent 3/3, segmented rays 8/8, middle 14 branched, total elements 22. Body with three unbranched lateral lines: dorsal lateral line originates from upper angle of opercle, middle extends from near posterior margin of pectoral fin to caudal-fin base, and ventral (variable) typically extends from just anterior to pelvic fin or from above middle of belly; both the dorsal and ventral lateral lines terminate posteriorly at end of dorsal and anal fins, respectively. Tubed lateral-line scales: dorsal 36-46, middle 23-34, ventral 17-44 (intermediate scales in latter two series may occasionally lack tubes); lateral-line scales no larger than adjacent body scales, some with a pair of vertically aligned superficial neuromasts (not shown in Fig. 20E); posterior profiles of all scales broadly elliptical. Head entirely naked; body and caudal-fin completely scaled, except predorsal area naked; anterior scales cycloid, becoming ctenoid dorsally and on sides from about level of 5th dorsal-fin spine; ctenoid scales also on peduncle and basally on caudal fin. Sensory pores on head (Fig. 1D) variable in number but infraorbital series typically in a single series; lower jaws anteriorly with 1 pair of pores Fig. 2D), each dentary with 4 pore positions; gill membranes fused in ventral midline to form a broad free fold across isthmus. Infraorbital bones 5 (one of four specimens checked for this character with 6 infraorbitals on left side only), 3rd infraorbital with a well-developed suborbital shelf (Fig. 13C). Palatine toothless; metapterygoid with a very slight lateral flange; metapterygoid-quadrate joint not interdigitated; preopercular canal open posterolaterally; primary opercular spine broadly rounded and platelike, no secondary spine present; maxilla very broadly rounded posteriorly (Fig. 14C), supramaxilla absent. Supracleithrum with well developed supracleithral sensory canal that is continuous anterodorsally with posttemporal canal and posteriorly with lateral-line scales; pectoral girdle with scapulo-coracoid joint smooth, posterolateral arm of coracoid relatively slender (Fig. 19B) and with radial formula 2-1-1; hyoid arch with ceratohyal-epihyal suturing medially only. Infrapharyngobranchials 2-4 toothed; interarcual cartilage relatively long (Fig. 15B); basihyal slender, toothless. Neural spine of first vertebra autogenous; first pterygiophore of anal fin with 2 supernumerary spines; all but anteriormost pterygiophore of segmented dorsal- and anal-fin rays consisting of autogenous proximal, middle and distal radials; haemal spine of second preural vertebra fused to vertebral centrum. Caudal skeleton with 3 separate epurals, hypural 5 moderately long, and hypurapophysis very long and slender (Fig. 17B). Adductor mandibulae with A1 section completely covering A2 section laterally, and A1 fibers bundlelike anterodorsally (Fig. 22C).

Distribution.—Australia (east and west coasts), Lord Howe Island, New Caledonia, Philippines, Taiwan and Ryukyu Islands.

Belonepterygion fasciolatum (Ogilby)
Figs. 1D-2D

Acanthoclinus fasciolatus Ogilby, 1889:63, pl. 3, fig. 3 (original descr.: Lord Howe Is.; lectotype AMS I.1876).

Ernogrammoides fasciatus Chen & Liang, 1948: 32, fig. 1 (original descr.: Keelung, Formosa; type species of new genus *Ernogrammoides*); Masuda et al. 1984:141, pl. 126, figs. P,Q (brief description; color photographs).

Calliblennius rubescens Aoyagi, 1954: 213 (37), fig. 1 (original descr.: Kowan, "Okinawa-Honto"; holotype probably destroyed; type species of new genus *Calliblennius*).

Belonepterygion fasciolatum. Hardy, 1985:375-378, fig. 9 (redescription; specimen figure; synonymy; lectotype designation; distribution); Mooi, 1990:463 (egg surface morphology).

Diagnosis.—Belonepterygion fasciolatum differs from all other acanthoclinines in having the combination of three lateral lines and the gill membranes fused in ventral midline to form a broad free fold across isthmus; it also is unique in lacking palatine teeth, in the bundlelike arrangement of adductor mandibulae section A1 anterodorsally, and (in adults) having 9-16 narrow dark bands on body.

Description.—See generic description above.

Color pattern.—Body pale to darkish brown with 9-16 narrow dark brown bands on sides; opercle with an oblong, brownish-black blotch; throat and cheeks with pinkish-red suffusion; lower jaw, snout and upper part of head medium brown, the sharply delimited lower margin of this coloring on a line from inner angle of jaws, extending just above lower margin of eye to opercular blotch; dorsal and anal fins mostly red to dark brown, with fleshy distal tabs on spines white or very pale orange.

Geographic variation.—Hardy (1985) presented frequency tables of selected meristic characters by locality for *B. fasciolatum* and documented geographic variation, especially in number of lateral-line scales. He also noted that the number of bands on the sides varied considerably within and between populations but gave no frequency data.

Maximum size.—Hardy (1985) recorded 50 mm SL as the maximum size of 260 specimens examined.

Material.—ANSP 122316 (1:41.8) and ANSP 142690 (2:39.7 & 30.6 C&S), Queensland, Australia; USNM 257883 (6:33.5-40.6) and USNM 273813 (3:32-36), Taiwan.

Genus *Beliops* Hardy

Beliops Hardy, 1985:378 (type species *Beliops xanthokrossos* Hardy, 1985, by original designation and monotypy).

Description.—A genus of acanthoclinine fishes with two known species (maximum size 26 mm SL), with the following combination of characters: dorsal fin XVIII-XX, 2-4; anal fin X-XI, 2-3; pectoral fin 15-18; pelvic fin I,2 with innermost ray unbranched; vertebrae 10 + 16-17 = 26 or 27 total; caudal fin (dorsal/ventral): procurrent rays 2-4/2-3, segmented rays 7-8/7-8, middle 12 or 14 branched, total elements 18-22 . Body with two unbranched lateral lines: dorsal lateral line extends from upper angle of opercle to below a vertical from near base of last dorsal-fin spine, and middle (= ventral) extends from slightly to well behind posterior margin of pectoral fin to caudal-fin base; tubed lateral-line scales: dorsal 24-35, middle 9-20; lateral-line scales no larger than adjacent body scales; posterior profiles of scales broadly elliptical (Fig. 20F) or distinctly lanceolate with membranous flaps (Fig. 20G). Head with 1-2 cycloid scales in anterodorsal angle of opercle (*B. xanthokrossos*) or entirely naked (*B. batanensis*); body and caudal-fin base completely scaled, except predorsal and prepelvic areas naked (pectoral-fin base also naked in *B. batanensis*); anterior scales cycloid, becoming strongly ctenoid posterior to pectoral

fin (*B. xanthokrossos*) or scales mostly cycloid, some with a few weak ctenii (*B. batanensis*). Sensory pores on head (Figs. 1E-F) variable in number and position but mandibulo-preopercular pores in a single series; lower jaws anteriorly with a single pair of pores, each dentary with 4 pore positions; gill membranes fused in ventral midline to form a broad free fold across isthmus. Infraorbital bones 5, the 3rd infraorbital with a well-developed suborbital shelf (Figs. 13D-E). Palatine teeth present; metapterygoid with a well-developed lateral flange; metapterygoid-quadrate joint interdigitated; preopercular canal tubular, closed posterolaterally; primary opercular spine pungent, not platelike, no secondary spine present; maxilla rather slender posteriorly (Figs. 14D-E), supramaxilla present or absent. Supracleithrum with well developed supracleithral sensory canal that is continuous anterodorsally with posttemporal canal and posteriorly with lateral-line scales; pectoral girdle with scapulo-coracoid joint interdigitated, posterolateral arm of coracoid moderately slender (Fig. 19C) and with radial formula 2-1-1; hyoid arch with ceratohyal-epihyal suturing medially only. infrapharyngobranchials 3-4 toothed; interarcual cartilage relatively short, conical (Figs. 15C-D); basihyal moderately broad and toothed (Figs. 23A-B). Neural spine of first vertebra fused to vertebral centrum; first pterygiophore of anal fin with 1 supernumerary spine; all pterygiophores of segmented dorsal- and anal-fin rays with fused proximal and middle radials; haemal spine of second preural vertebra fused to vertebral centrum. Caudal skeleton with epurals 2-3 fused distally, hypural 5 moderately long, and hypurapophysis relatively short (Fig. 17C). Adductor mandibulae with A1 and A2 sections both visible laterally.

Distribution.—The two species of *Beliops* have allopatric distributions (Fig. 3); *B. xanthokrossos* is an Australian endemic, and *B. batanensis* is known only from the Batan Islands, northern Philippines.

Beliops xanthokrossos Hardy
Figs. 1E-2E, 6, 8

Beliops xanthokrossos Hardy, 1985:378-381, fig. 10 (original descr.: Kingston Reef, Rottnest Is., Western Australia; holotype WAM P.26617-008).

Diagnosis.—The combination of two lateral lines, anterior dorsal-fin spines relatively slender and elongate with deeply incisecd interradial membranes, and scales posterior to the pectoral fin ctenoid and with elliptical profiles readily distinguishes *Beliops xanthokrossos* from all other acanthoclinines. All the character states of *B. xanthokrossos* that are not shared with its congener and that can be polarized with confidence appear to be plesiomorphic (refer to discussion in species account of *B. batanensis*).

Description (see also preceding generic description).—Dorsal fin XVIII-XIX, 2-4; anal fin X, 2-3; pectoral fin 16-18; vertebrae 10 + 16-17; caudal-fin rays (dorsal/ventral): procurrent 2-4/2-3; segmented 8/8, middle 14 branched, total elements 20-22 ; gill rakers on first arch (epibranchial + ceratobranchial) 1-2 + 2-3; tubed lateral-line scales: dorsal 24-31, middle 9-18; body scales elliptical and ctenoid posterior to pectoral fin; sensory pores on head relatively numcrous on dorsum and with pore positions in the infraorbital series mostly bi-pored (Fig. 1E); dorsal- and anal-fin spines with interradial membranes strongly incised, anterior dorsal spines incised to about one-half to two-thirds anteriorly, decreasing thereafter; dorsal- and anal-fin spines relatively long and slender (Fig.8), with elongate fleshy tassels distally; longest dorsal spine 13.5-15.2 percent SL; terminal dorsal- and anal-fin rays without membranous attachment to caudal peduncle. Small supramaxilla present (Fig. 14D). Teeth in both jaws small and conical, curved backward, largest anteromedially; upper jaw with double row of teeth along sides, those in outer row larger; lower jaw similar but only a single row of teeth posteriorly.

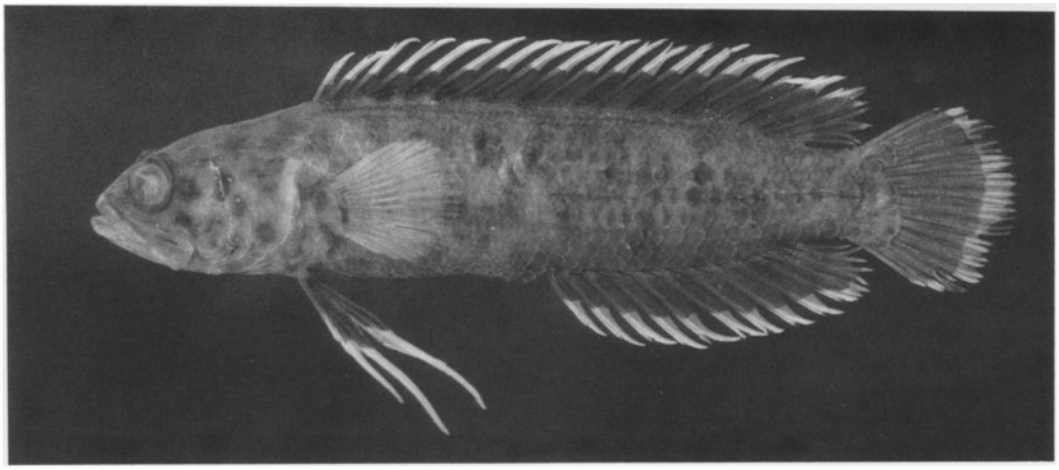


Fig. 6. *Beliops xanthokrossos*, ANSP 165557, 25.7 mm SL, Western Australia, Duke of Orleans Bay.

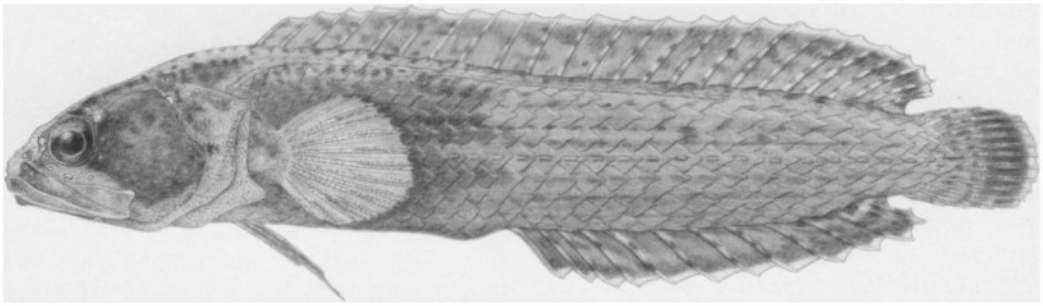


Fig. 7. *Beliops batanensis*, USNM 288976, holotype, 21.0 mm SL, Philippines, Batanes Providence, Batan Island. (Drawn by Penelope K. Hollingsworth.)

Color pattern.—Hardy (1985:379) reported that *B. xanthokrossos* has two color forms, which may indicate sexual dimorphism. He illustrated the yellow form (holotype) and our Fig. 6 shows the mottled morph. His description of the two forms is as follows:

> "Yellow form — head and body yellowish-brown to brownish-yellow, with variable number of small, darker brown spots on sides, each covering 1 or 2 scales; 3 or 4 smaller, brown spots on head, roughly following posterior curve of orbit. Dorsal, anal, pectoral, and caudal fin webbing similar to body, fleshy appendages of dorsal and anal fin spines bright yellow. Pelvic fin yellowish-brown to bright yellow, several dark, brown flecks on proximal half.
>
> "Mottled form — head and body medium brown, densely covered with darker brown blotches, each blotch several scales in extent, with vertical, dark brown band on posterior of caudal peduncle; several smaller, dark brown spots on head and operculum. Dorsal, anal, pectoral, and caudal fin webbing similar to body, a series of dark brown blotches extending length of dorsal and anal fins, close to base. Fleshy appendages of dorsal and anal

fins bright yellow. Proximal half of pelvic fin speckled with brown, distal half pale yellow."

Distribution.—Endemic to Australia (south and west coasts) and collected in depths of 3-15 m.

Maximum size.—Attains at least 25.9 mm SL.

Material.—ANSP 165557 (2:25.7 & 25.9 C&S), Western Australia, Duke of Orleans Bay.

Beliops batanensis, new species
Figs. 1F-2F, 7-8

Diagnosis.—A species of *Beliops* distinctive in having the posterior body scales with membranous flaps (Fig. 20G) and ctenii, if present, very reduced (Fig. 21G), short and robust dorsal-and anal-fin spines (Fig. 8), and the interradial membranes of the spinous dorsal fin very weakly incised.

Description (see also preceding generic description).—The following counts and measurements are given for the holotype first, with values for the paratype, if different, in parentheses. Dorsal fin XX, 2; anal fin XI, 2; pectoral fin 15/15 (16/16); vertebrae 10 + 17; caudal-fin rays (dorsal/ventral): procurrent 2/2; segmented 7/7, middle 12 branched, total elements 18; gill rakers on first arch (epibranchial + ceratobranchial) i,2 + 7,i; tubed lateral-line scales (L/R): dorsal 35/35 (34/33), middle 20/17 (20/20); head, nape, prepelvic area and pectoral-fin base naked, remainder of body including caudal-fin base covered with cycloid scales (some posterior scales with very reduced ctenii); scales lanceolate, those on half of body with membranous flaps; sensory pores on head relatively sparse with all pore positions occupied by single pores (Fig.1F), each dentary with 4 pore positions; dorsal- and anal-fin spines with interradial membranes very weakly incised, and with the spines relatively short and robust (Fig. 8), with distal fleshy tabs poorly developed; terminal dorsal- and anal-fin rays with basal third of ray membranously attached to caudal peduncle. Supramaxilla absent (Fig. 14E). Teeth in both jaws mostly small and conical, curved backward, largest anteromedially; upper jaw anteriorly with three rows of teeth flanked by several much larger teeth, only a single row posteriorly; lower jaw similar but innermost row of large conical teeth not slanted backward.

Measurements as percent standard length: head length 27.6 (29.4); snout tip to dorsal-fin origin 30.5 (31.3); snout tip to anal-fin origin 58.0 (59.2); dorsal-fin base 68.6 (69.0); anal-fin base 38.0 (37.4); pectoral fin 14.5 (13.7); longest pelvic-fin ray 13.8 (14.2); caudal fin 19.5 (20.1); longest dorsal-fin spine 9.3 (10.2); longest anal-fin spine 10.5 (10.4); body depth at dorsal-fin origin 20.7 (19.9); body depth at anal-fin origin 17.1 (17.5); orbit diameter 5.7 (6.2); upper jaw length 15.0 (15.6); postorbital head length 17.6 (19.2).

Color pattern (in alcohol).—Head and body mostly dark, slightly paler on opercle; posterior half of upper jaw and exposed branchiostegal membranes densely covered with small melanophores; dorsum with a poorly defined, pale stripe that extends from origin of dorsal fin across snout and onto upper and lower lips where it widens slightly; dorsal and anal fins mostly uniformly dark with scattered darker flecks, except tips of spines and rays and adjacent interradial membranes pale distally; caudal fin dark except for conspicuous, narrow, white, distal margin; pelvic fin also dark, except spine tip pale.

In life (based on field observations of the freshly collected specimens), the darkly pigmented areas of the body and fins are black, the pale areas white.

Species comparison.—*Beliops batanensis* exhibits a surprisingly large number of apomorphies not present in its closest known relative as follows: 1) distinctive scale type (see diagnosis); 2) reduction in number of total caudal-fin rays (18 vs. 20-22); 3) concomitant reduction in branched caudal-fin rays (12 vs. 14); 4) terminal dorsal- and anal-fin rays membranously attached to caudal peduncle; 5) interradial membranes of dorsal- and anal-fin spines

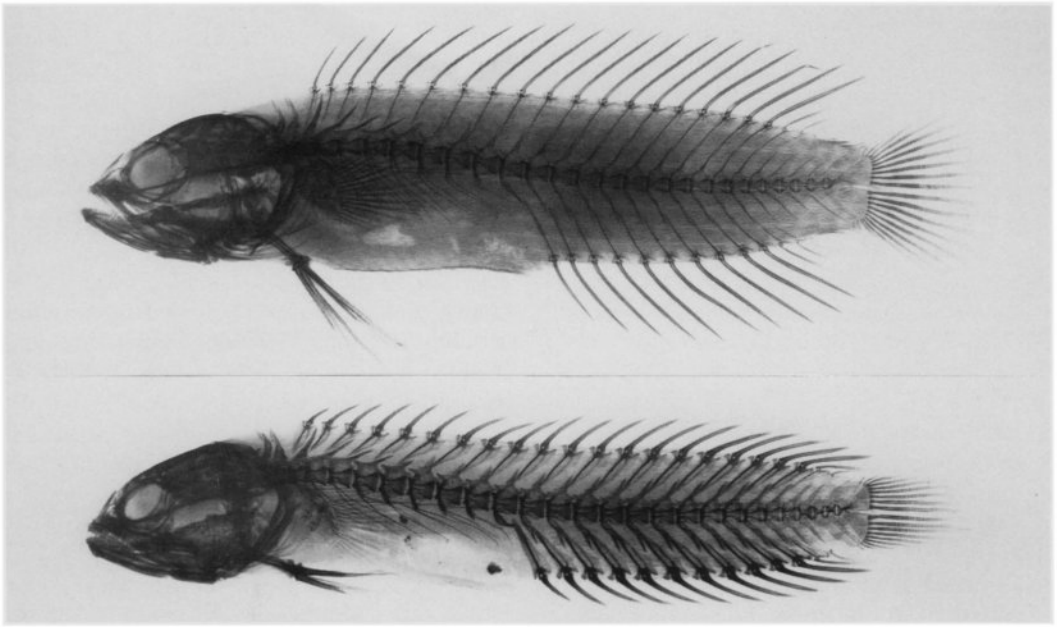


Fig. 8. Radiographs of *Beliops xanthokrossos*, ANSP 165557, 25.7 mm SL (above) and *B. batanensis*, holotype, 21.0 mm (below).

very weakly incised (The first two outgroups and all other species of Acanthoclininae have at least the anterior dorsal-fin spines moderately to strongly incised.); 6) dorsal- and anal-fin spines short and robust (autapomorphy of *B. batanensis*); and 7) supramaxilla absent.

Etymology.—The specific name refers to Batan Island, the type locality, and also acknowledges our appreciation of the friendly and hospitable people of the Batanes Providence.

Distribution.—Known only from the northern Philippines (Batanes Providence), but possibly may occur in Taiwan (refer to discussion in "Biogeography" section).

Material.—Only the two types (21.0-21.1 mm SL), both females, known. HOLOTYPE: USNM 288976 (21.0), Philippine Islands, Batanes Prov., Batan Is., Chawa Point (20°25′45″N, 121°56′40″E); coral encrusted vertical wall and bottom boulders with some soft sediment and sand; 9-12 meters; rotenone; 01 May 1987; G.D. Johnson and W. F. Smith-Vaniz; sta. GDJ 87-13. PARATYPE: USNM 309905 (21.1), taken with the holotype.

Genus *Acanthoplesiops* Regan

Acanthoplesiops Regan, 1912:266 (type species *Acanthoplesiops indicus* Day, 1888:264, by monotypy).

Description.—A genus of acanthoclinine fishes with four known species (maximum size 26.5 mm SL), with the following combination of characters: dorsal fin XIX-XXI,3-6; anal fin VII-X, 3-6; pectoral fin 15-18; pelvic fin I,2, with innermost ray unbranched; vertebrae 12-14 + 14-17 = 27-30 total; caudal-fin rays (dorsal/ventral): procurrent 2-3/2-3, segmented rays 8/8, middle 14 branched, total elements 20-22. Body with single unbranched lateral line that extends from upper angle of opercle to below verticals from 1st dorsal-fin spine to about middle of spinous dorsal fin; tubed lateral-line scales 0-13; lateral-line scales similar in size and shape to other body scales except as noted below; posterior profiles of scales ranging from ovate (*A. hiatti & psilogaster*, Figs. 20H-I), somewhat pyriform, often bi- or trilobed (*A. indicus*) or lanceolate with a flaplike

projection (*A. echinatus*, Fig. 20J); 8-11 bilobed scales typically present (not necessarily consecutive) in midlateral scale row centered on horizontal septum and extending from behind pectoral fin to caudal-fin base; a single, superficial neuromast usually present (immediately adjacent to anterior margin of scale notch) on every 2nd to 4th bilobed scale. Head entirely naked; body and caudal-fin base completely scaled, except predorsal and prepelvic areas, and pectoral-fin base naked (also anterior two thirds of belly in *A. psilogaster*); anterior scales cycloid, becoming strongly ctenoid posterior to pectoral fin, except in *A. indicus* where scale type is uniquely derived (refer to species account). Sensory pores on head (Figs. 1G-H) relatively sparse with pore positions all occupied by single pores, no infraorbital pores behind eye where infraorbital bones 2-5 are missing (see below); lower jaws anteriorly with 1 pair of pores (*A. indicus* & *hiatti*) or this pair of pores absent (*A. psilogaster* & *echinatus*), and each dentary with 4 or 3 pore positions, respectively; gill membranes fused in ventral midline to form a broad free fold across isthmus; free ventral margin of lower lip forming a symphyseal flap. Single infraorbital (lacrimal) bone present (Fig. 13F); Palatine teeth present; metapterygoid without lateral flange; metapterygoid-quadrate joint not interdigitated; preopercular canal tubular, closed posterolaterally; primary opercular spine pungent, a secondary spine (occasionally 2 in *A. hiatti*) also present posterolaterally (Figs. 16F-H); maxilla broadly rounded posteriorly (Fig. 14F); supramaxilla absent. Supracleithral sensory canal absent, posttemporal canal passes laterally over posterodorsal margin of supracleithrum and exits to surface; pectoral girdle with scapulo-coracoid joint smooth, posterolateral arm of coracoid moderately robust (Figs. 19D-E) and with the radial formula 3-0-1; hyoid arch with ceratohyal-epihyal suturing medially and laterally. Infrapharyngobranchials 3-4 (*A. indicus* & *hiatti*) or 2-4 (*A. psilogaster* & *echinatus*) toothed; interarcual cartilage very short (Figs. 15E-F); basihyal broad to slender and toothless (Figs. 23C-F). Neural spine of first vertebra fused to vertebral centrum; first pterygiophore of anal fin with 2 supernumerary spines; all but anteriormost pterygiophore of segmented dorsal- and anal-fin rays consisting of autogenous proximal, middle and distal radials (except all proximal and middle radials fused in *A. hiatti*); haemal spine of second preural vertebra fused to vertebral centrum. Caudal skeleton with epurals 2-3 fused distally, hypural 5 very small, and hypurapophysis absent (Fig. 17D). Adductor mandibulae with A1 section completely covering A2 section laterally (Fig. 22D).

Remarks.—Hardy (1985) listed the absence (lack of ossification) of infrapharyngobranchial 1 as a synapomorphy of *Acanthoplesiops*, apparently based solely of his examination of *A. hiatti*. In the three cleared and stained specimens that we examined, that structure is cartilaginous in the two smallest specimens but well ossified in the largest. Infrapharyngobranchial 1 is fully ossified in our cleared and stained material of the other species of *Acanthoplesiops*.

Distribution.—Broadly distributed throughout most of the tropical Indo-Pacific, with the apparent absence of an Australian representative puzzling, although perhaps due to inadequate sampling (Fig. 9).

Species comparisons.— The known species of *Acanthoplesiops* are contrasted in the preceding key, Table 3 and in the following species accounts.

Acanthoplesiops indicus (Day)

Acanthoclinus indicus Day 1888:264 (original descr.: Madras, India; holotype BMNH 1889.8.17.5); Day 1888a:798-799, fig. unnumbered (description); Day 1889:325, fig. 105 (description).

Acanthoplesiops indicus. Barnard 1948:370-372, fig. 9 (description; Delagoa Bay); Hardy 1985:381-382, fig. 11 (redescription; specimen photograph; synonymy; distribution); Smith & Heemstra 1986:

Table 3. Comparison of selected characters in species of *Acanthoplesiops*. *Denotes autapomorphic characters; **denotes presumed synapomorphic characters.

characters	*hiatti*	*indicus*	*psilogaster*	*echinatus*
1. Sensory pores on dentary	4	4	3**	3**
2. Teeth present on 2nd infrapharyngobranchial	no	no	yes**	yes**
3. Number of supraneurals	2	0*	1*	2
4. Pterygiophores inserted between 2nd and 3rd neural spines	1st only	1st only	1st 2*	1st only
5. Medial radials of segmented dorsal- and anal-fin rays	fused to proximal radials*	proximal radials autogenous	proximal radials autogenous	proximal radials autogenous
6. Preopercle occasionally with 2 secondary spines	yes*	no	no	no
7. Scales on posterior third of body[1]	ctenoid (typical)	"cycloid"*	ctenoid (typical)	ctenoid* (derived)
8. Scales present on belly anteriorly	yes	yes	no*	yes
9. Dorsal and anal rays broadly bound by membrane to caudal fin	no	yes*	no	no
10. Caudal peduncle with broad white band	no	yes*	no	no
11. Minute papillae on head	no	no	no	yes*

[1]Refer to discussion under "Character Description and Analysis."

541, pl. 46, fig. 170.1 (brief description; color illustration).

Diagnosis.—A species of *Acanthoplesiops* with the following autapomorphic character states: 1) distinctive color pattern characterized by a broad white band on caudal peduncle, base of caudal fin, and posteriormost rays of dorsal and anal fins, 2) terminal dorsal- and anal-fin rays with broad membranous attachment to caudal fin, Fig. 10, 3) unique scale type (see below); and 4) no supraneural bones.

Abbreviated description.—Dorsal fin XIX-XX, 3-4; anal fin VIII-X, 3-4; pectoral fin 15-17; vertebrae 12 + 15-16; caudal-fin rays (dorsal/ventral): procurrent 1-2/2 segmented 8/8, total 19-20; no supraneurals; only first pterygiophore of dorsal-fin spines inserted between 2nd and 3rd neural spines; only one secondary opercular spine; tubed lateral-line scales 8-12; belly completely scaled; scales somewhat pyriform, often bi- or trilobed, each lobe supported a single, slender spinule that may or may not be attached to main body of scale (Fig. 21H); terminal dorsal- and anal-fin rays with broad membranous attachment to caudal fin (Fig. 10); lower

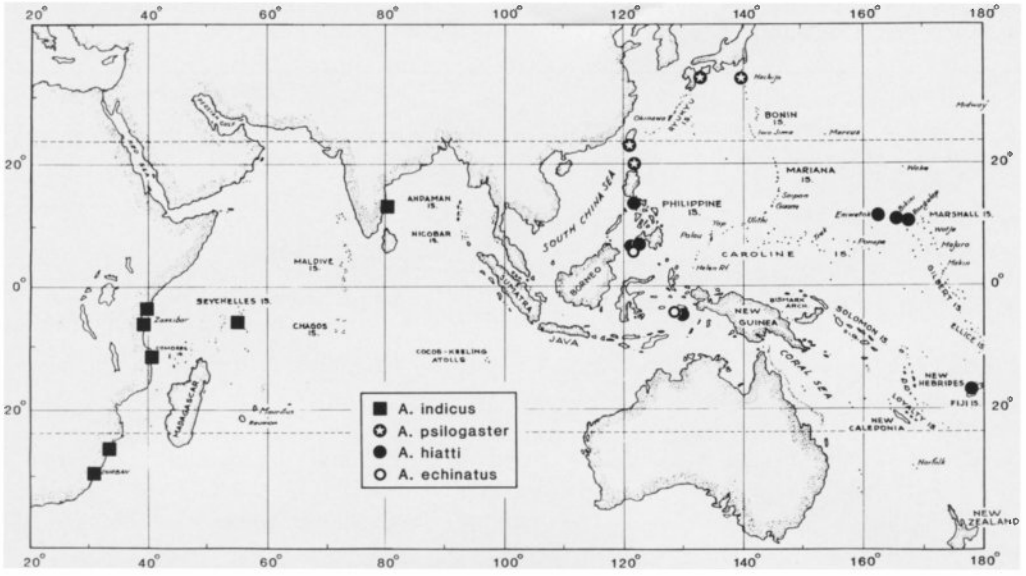


Fig. 9. Distribution of the known species of *Acanthoplesiops*.

jaws with a pair of symphyseal pores, each dentary with 4 pore positions; infrapharyngobranchials 1-2 toothless.

Color pattern (in alcohol).— The broad white band on caudal peduncle, base of caudal fin, and posteriormost rays of dorsal and anal fins is a unique aspect of the color pattern of *A. indicus*; otherwise it agrees with its congeners in being mainly uniformly dark except for a white spot on the pectoral-fin base, a pale stripe on the dorsum extending from the snout to the dorsal-fin origin (also including the first 2-3 spines), and in having the distal margins of dorsal, anal and caudal fins pale or white, and the distal third of the pelvic fin white.

Distribution.—Endemic to the Indian Plate (Fig. 3), and apparently restricted to continental areas or continental crustal fragments (Mahé, Seychelles).

Maximum size.—Largest specimen examined 26.5 mm SL.

Material (*new distributional records).— SOUTH AFRICA: ANSP 165570 (2:23.7 & 24.7 C&S) and RUSI 17291 (8:12.3-24.1), Durban; KENYA: *RUSI 17293 (3), Mombasa; RUSI 17295 (1),

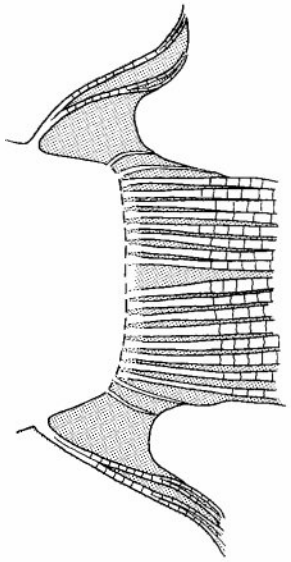


Fig. 10. Caudal peduncle region of *Acanthoplesiops indicus*, RUSI 17291, 24.1 mm, showing broad membranous attachment of terminal dorsal- and anal-fin rays to caudal fin.

Malindi; *MOZAMBIQUE: RUSI 17294 (2), Ibo; *ZANZIBAR: ANSP 122483 (1:26.5 C&S), reef at Mangapwani; ANSP 122484 (1:21.6) Chumbe Is.; SEYCHELLES: RUSI 17292 (2), Mahé; INDIA: BMNH 1889.8.17:5 (1), Madras.

Acanthoplesiops hiatti Schultz
Figs. 1G-2G

Acanthoplesiops hiatti Schultz 1953:407-411, fig. 68 (original descr.; Rongerik Atoll, Eniwetok Is.; holotype USNM 140758); Hardy, 1985:382-384, fig.12 (redescription; specimen photograph; synonymy; distribution).

Diagnosis.—A species of *Acanthoplesiops* with the following autapomorphic character states: 1) preopercle occasionally with 2 secondary spines (see remarks) and 2) pterygiophores of all segmented dorsal- and anal-fin rays with middle and proximal radials fused.

Abbreviated description.—Dorsal fin XIX-XXI (rarely XXI), 3-5; anal fin VIII-X, 3-5; pectoral fin 17; vertebrae 13 + 15-17 (exceptionally 17); caudal-fin rays (dorsal/ventral): procurrent 2-3/2-3, segmented 8/8, total 21-22; 2 supraneurals; only first pterygiophore of dorsal-fin spines inserted between 2nd and 3rd neural spines; 1-2 secondary opercular spines; tubed lateral-line scales 7-11; belly completely scaled; scales typically ctenoid (Fig. 2I) posterior to pectoral fin; terminal dorsal- and anal-fin rays not membranously attached to caudal peduncle or caudal fin; lower jaws with a pair of symphyseal pores, each dentary with 4 pore positions (Fig. 2G); infrapharyngobranchials 1-2 toothless.

Color pattern (after Schultz 1953).—In alcohol, "general background dark brown to blackish; all median rays with tips white, basally brownish black; pelvic fin rays blackish brown with tips white; pectoral fins plain pale; base of pectoral fin with a white spot; a pale band from dorsal surface of snout along dorsal surface of head to dorsal fin origin widest behind orbital region."

Remarks.—Hardy (1985) stated that *A. hiatti* differs from its congeners in having 3 opercular spines (one additional accessory spine). In 21 specimens of *A. hiatti* checked for this character, 13 had 2/2 spines (both sides counted), 5 had 2/3 and 3 had 3/3.

Distribution.—In the tropical Western Pacific known from the Philippines, Banda Sea (Saparua and Ambon), Fiji (Malolo Is.), and nonmarginally on the Pacific Plate only from the Marshall Islands.

Maximum size.—Largest known specimen 21.4 mm SL.

Material.—PHILIPPINES: USNM 135783 (2:15.5-16.0), Sulu Archipelago, Jolo vicinity, Morangas Is., "Albatross"; USNM 164948 (1:17.3), Pilas Is., S. of Zamboanga, "Albatross"; USNM 232049 (1:15.3), Batangas Prov., Sombero Is. INDONESIA: Banda Sea: ANSP 165421 (1:18.8 C&S) and USNM 257874 (9:15.3-21.4, including 2:16.8-21.4 C&S), Saparu Is; USNM 257631 (1:18.5), Ambon. FIJI: USNM 236652 (1:15.3) Malolo Is. MARSHALL IS.: USNM 140758 (16.8), holotype and USNM 140757 (3:13.0-20.3), Rongerik Atoll; USNM 140753 (1), USNM 140754 (1:19.1), USNM 140755 (1:15.5), USNM 140756 (1), Bikini Atoll; USNM 141730 (1:16.0), Rongelap Atoll.

Acanthoplesiops psilogaster Hardy

Acanthoplesiops hiatti (not of Schultz). Masuda et al. 1975:224, color pl. 53, fig. E (description; specimens cited; Japanese distribution records); Masuda et al. 1984:141, pl. 126, fig. R (brief description; color photograph; distribution).

Acanthoplesiops psilogaster Hardy 1985:384-385,387, fig. 13 (original descr.; Taiwan, off Ch'uan-fan-shih; holotype USNM 257872).

Diagnosis.—A species of *Acanthoplesiops* with the following autapomorphic character states: 1) anterior two thirds of belly naked and 2) first two (instead of

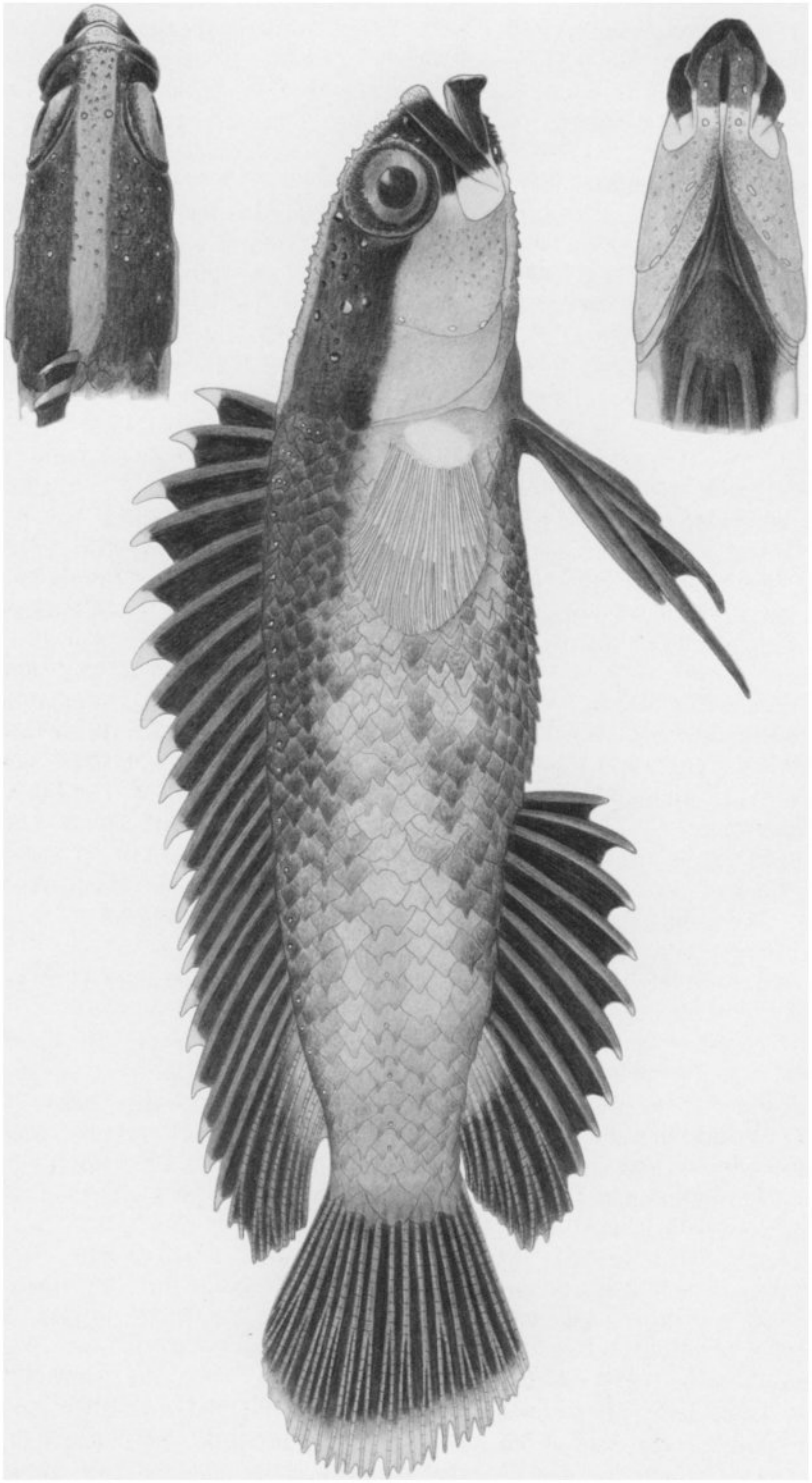


Fig. 11. *Acanthoplesiops echinatus*, BPBM 44177, holotype, 19.8 mm SL, Banda Sea, Ambon Island. (Drawn by Tracy D. Pedersen.)

only the 1st) pterygiophores of dorsal-fin spines inserted between 2nd and 3rd neural spines.

Abbreviated description.—Dorsal fin XIX-XX, 4-5; anal fin VII-VIII, 4-5; pectoral fin 16-17; vertebrae 13-14 + 14; caudal-fin rays (dorsal/ventral): procurrent 2/2, segmented 8/8, total 20; single supraneural; first 2 pterygiophore of dorsal-fin spines inserted between 2nd and 3rd neural spines; only one secondary opercular spine; tubed lateral-line scales 5-10; anterior two thirds of belly naked; scales typically ctenoid posterior to pectoral fin; terminal dorsal- and anal-fin rays with a slight membranous attachment to caudal peduncle; lower jaws without a pair of symphyseal pores, each dentary with 3 pore positions (Fig. 2H); only infrapharyngobranchial 1 toothless.

Color pattern.—In alcohol, head and body uniformly dark brown, with pale stripe from dorsal surface of snout to dorsal-fin origin, widest on nape; dorsal and anal fins uniformly dark brown except tips of each ray white, caudal fin similarly colored except narrow, pale margin; pelvic fin dark with distal third white; small pale spot on pectoral-fin base.

Color plates in Masuda et al. (1975, 1984) show *A. psilogaster* with a dark, greenish-gray body and fins, and bright yellowish-orange tips on dorsal, anal and pelvic fins, and posterior margin of caudal fin.

Maximum size.—The largest of 11 known specimens is 22.6 mm SL.

Distribution.—Known only from southern Japan (where reported as *Acanthoplesiops hiatti*, see above; also reported from Hachijo-jima I., but no specimens available), Taiwan, and the Batan Islands, northern Philippines.

Material (*new distribution record).—JAPAN: SMBL F.73145 (1) and SMBL F.73146 (1), Bansho-zaki Cape, Shirahama, Wakayama Pref.; TAIWAN (all from Ch'uan-fan-shih): USNM 257872 (22.6, holotype); paratypes BPBM 23296 (2), NMNZ P.14813 (1), USNM 257871 (2:18.8 C&S, 20.2), USNM 257873 (1:18.0), USNM 276528 (1:16.9); *PHILIPPINES: USNM 288813 (1:11.8 mm), Batanes Prov., Batan Is., Chawa Point, 20°25′45″N, 121°56′40″E; 9-12 m; 1 May 1987; sta. GDJ 87-13.

Acanthoplesiops echinatus, new species
Figs. 1H, 2H and 11

Diagnosis.—A species of *Acanthoplesiops* with the following autapomorphic characters: 1) most scales on posterior half of body with a flaplike projection (Fig. 20J) supported by elongate ctenii (Fig. 21J) and 2) in the two Ambon specimens (see Remarks) minute, erect, pointed papillae covering much of head. *Acanthoplesiops echinatus* also differs from its congeners in having 6 (versus 3-5) segmented anal-fin rays, and only it and *A. psilogaster* lack symphyseal dentary pores (Fig. 2H).

Description (see also preceding generic description).—Values for the paratypes, if different from the holotype, are given in parenthcses with those of the smaller paratype listed first. Dorsal fin XX (XX, XIX), (5)-6; anal fin VIII, 6; pectoral fin 18/18; vertebrae 13 + 17 (16); caudal-fin rays (dorsal/ventral): procurrent 3/2-(3/3; 3/2), segmented 8/8, middle 14 branched, total elements 21-22; 2 supraneurals; only first pterygiophore of dorsal-fin spines inserted between 2nd and 3rd neural spines; only one secondary opercular spine; tubed lateral-line scales (L/R): 2/0 (2/?; 0/?) (smaller paratype with anterior scales missing on right side, left side with 3 scales anterior to tubed scales missing); lateral line terminates below verticals from 1st to 5th dorsal-fin spines; both sides of holotype with at least 11 bilobed scales in midlateral row centered over horizontal septum; belly completely scaled; most scales on posterior half of body with a flaplike projection (Fig. 20J) supported by elongate ctenii (Fig. 21J); terminal dorsal- and anal-fin rays with very slight membranous attachment to caudal peduncle; lower jaws without a pair of symphyseal

pores, each dentary with 3 pore positions (Fig. 2H); only infrapharyngobranchial 1 toothless (Fig. 15F); both jaws with villiform teeth, 3-4 rows wide anteriorly, tapering posteriorly, inner row of dentary teeth larger than others.

Measurements as percent standard length: head length 31.1 (32.8,32.2); snout tip to dorsal-fin origin 31.3 (33.8,32.8) snout tip to anal-fin origin 29.3 (32.9,33.8); dorsal-fin base 67.2 (63.6,62.2); anal-fin base 28.8 (26.7,24.9); pectoral fin 15.7 (15.2,—); longest pelvic-fin ray 35.1 (36.2,—); caudal fin 26.0 (28.6,28.6); longest dorsal-fin spine 16.2 (18.6,14.6); body depth at dorsal-fin origin 22.2 (23.6,23.2); body depth at anal-fin origin 20.7 (21.7,20.9); orbit diameter 9.3 (9.0,8.9); upper jaw length 12.1 (13.1,13.6); postorbital head length 17.7 (18.3,19.2).

Color pattern (in alcohol).—The most distinctive feature of the color pattern is a dark stripe, about width of eye diameter, that originates on the upper jaw, continues through the eye and then diagonally to middle of spinous dorsal fin; the stripe is much darker on the head and extends only slightly onto the expanded part of the maxilla (which is otherwise conspicuously white), its ventral margin is on a line from just below the pupil to slightly below the posterodorsal angle of the opercle, dorsally the stripe runs from just above the dorsal margin of the orbit to the base of the first dorsal-fin spine; a pale stripe, centered on the nape and dorsum of head, crosses the upper lip and continues, as a much narrower stripe, to tip of symphyseal, dentary flap; the head and body are otherwise light tan, except chin, gular area adjacent to the darkly pigmented lips, gill membranes ventrally, breast and belly dark to dusky; pectoral-fin base with pale spot about half the eye diameter; dorsal and anal fins uniformly dark except tips of spines and rays pale (proximal fourth of fin adjacent to segmented rays also pale in the holotype); caudal fin dark except for narrow, pale distal margin; pelvic fins dark with distal third pale (paratypes) or uniformly dark except for tip of longest ray (holotype), not shown on Fig. 11; pectoral fin transparent except rays outlined with melanophores.

In life (based on a color slide taken by J.E. Randall of the fresh holotype), the dark areas of the body and fins range from nearly black to dark brown and the pale areas of the body and head are straw colored (more yellowish on head) except for the white spot on the pectoral-fin base; the pale margins of the fins and the expanded part of the maxilla and adjacent areas of the lips are white.

Remarks.—The two Ambon specimens both have minute, erect, pointed papillae on the margin of upper lip, snout, interorbital area, dorsal fleshy rim of eyes, dorsum of head (extending posteriorly about half distance between posterior margin of orbits and dorsal-fin origin), preopercle, ventral margin of interopercle and branchiostegal rays, maxillae and dentaries. The single specimen from the Sulu Archipelago inexplicably lacks papillae. The presence of these papillae, which we have observed in no other species of acanthoclinine, apparently is not size related or due to sexual dimorphism.

Etymology.—From the Latin *echinatus* (spiny), in allusion to the papillae that cover much of the head of the Ambon specimens (see above), and that superficially appear spinelike.

Distribution.—Known only from the Banda Sea at Ambon Island and the Sulu Archipelago at Jolo, where at both localities *A. echinatus* occurs sympatrically with *A. hiatti*, although not taken in the same station.

Material.—Only the following three types (19.8-21.3 mm SL) are known. HOLOTYPE: BPBM 34177, probable male (19.8), Indonesia: Molucca Islands, Ambon, Ambon Bay, entrance on NW side, near Cape Batu Badiri (3°43′S, 128°4.5′E); silty sand and mud; 8 m; rotenone coll.; 26 Sept. 1988; J.E. Randall, F. Leatemia and D. Pelasula. PARATYPES: ANSP 166316, gravid female (21.0), taken with the holotype. USNM 146453, sex indeter-

minate (21.3), Sulu Archipelago, Jolo, Cabalian Point (05°51′15″N, 120°58′35″ E); trawled in 34 m; 18 Sept. 1909; "Albatross"; sta. D.5555.

CHARACTER DESCRIPTIONS AND ANALYSIS

On the recommendation of Randall Mooi (see introduction), the plesiopid genera *Plesiops* and *Fraudella* were chosen as the first and second outgroups, respectively. The plesiomorphic character state (0) was determined by the presence of that state in both outgroups, unless otherwise discussed. Characters 1-5 define the subfamily and are discussed on page 220; characters 6-38 (character state matrix given in Table 4) are the basis for the hypothesis of phylogenetic relationships within the Acanthoclininae (Fig. 12). Autapomorphic characters of single species were not used in the numerical analyses and are discussed below only when they are relevant to other considerations; however, they are all described in the individual species accounts.

Character descriptions

1. ***Lower lip configuration***: free ventral margin only laterally, interrupted by isthmus (state 0); continuous free ventral margin across front of lower jaw, Fig. 2 (state 1)

2. ***Squamation***: preopercle, opercle and often dorsum of head completely scaled (state 0); head completely naked (except 2-5 cycloid scales on opercle in some *Acanthoclinus* and nape scaled in *A. fuscus*) (state 1).

3. ***Number of dorsal- and anal-fin elements***: dorsal and anal fins with *lower* number of spines (7-16 and 3, respectively) and *higher* number of segmented rays (6-21 and 7-23, respectively) (state 0); dorsal and anal fins with *higher* number of spines (17-26 and 7-16, respectively) and *lower* number of segmented rays (2-6 and 2-6, respectively) (state 1).

4. ***Number of pelvic-fin rays***: I, 4 (state 0); I, 2, Fig. 4 (state 1).

5. ***Number of branched caudal-fin rays in adults***: 15-17 (state 0); 14 or 12 (state 1).

6. ***Number of total caudal-fin rays***: 27-29 rays (state 0); 24 (rarely 23) rays *Acanthoclinus* only (state 1); 22-18 rays (except infrequently 23 in *Belonepterygion* only) (state 2). In *Fraudella* the total number of rays is 27; *Plesiops* has 26-29 rays, the two species that are successive outgroups to other species have 29 rays, one species has 26 total rays, and all others have 29 (occasionally 27) (Mooi, in litt.). Thus, a reduction in number of total caudal-fin rays is a synapomorphy of the Acanthoclininae and within the subfamily a further reduction in number of rays is a synapomorphy of lineage III.

7. ***Number of lateral lines***: two lateral lines (state 0); three lateral lines (state 1); one lateral line (state 2). All outgroup plesiopids have two lateral lines consisting of a dorsal and middle series, except the diminutive *Steeneichthys* which has only a single lateral-line scale, where the condition is clearly secondarily derived. The Acanthoclininae exhibits a surprisingly diverse array of lateral line types. Both *Acanthoclinus* and *Belonepterygion* have three lateral lines, and within *Acanthoclinus* there are three basic types; two of these involve single species and represent autapomorphic character states. The lateral line pattern of *Acanthoclinus fuscus* (Fig. 5) is characterized by an accessory ventral branch (and frequently a predorsal branch, see species diagnosis). A similar pattern has evolved independently in the congrogadine genus *Halidesmus* (Winterbottom 1982:figs. 2A-B) and in the stichaeid *Ernogrammus hexagrammus* Jordan and Snyder (1902:fig. 23). Refer to diagnosis of *Acanthoclinus rua* for description of its unique lateral-line pattern. The pattern exhibited by the remaining three species of *Acanthoclinus* (and *Belonepterygion*) is essentially identical and represents the three lateral-line pattern that may have characteristized the progenitor of the subfamily. *Acanthoclinus* and *Belonepterygion* differ

Table 4. Character state matrix used in the phylogenetic analysis. "?" indicates character state is unknown for that taxon; "N" indicates character states that logically do not apply. Numbered characters correspond to those used in Fig. 12; see text for description of characters and states.

Characters (6-38) Taxon	6			10						15						20						25						30						35				
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthoclinus fuscus	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0			
A. littoreus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0			
A. rua	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
A. marilynae	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
A. matti	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Belonepterygion fasiolatum	2	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
Beliops xanthokrossos	2	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
B. batanensis	2	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Acanthoplesiops indicus	2	2	2	N	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1					
A. hiatti	2	2	2	N	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1					
A. psilogaster	2	2	2	N	1	1	0	1	2	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1					
A. echinatus	2	2	2	N	1	1	0	1	2	1	1	1	1	1	1	0	0	?	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1					

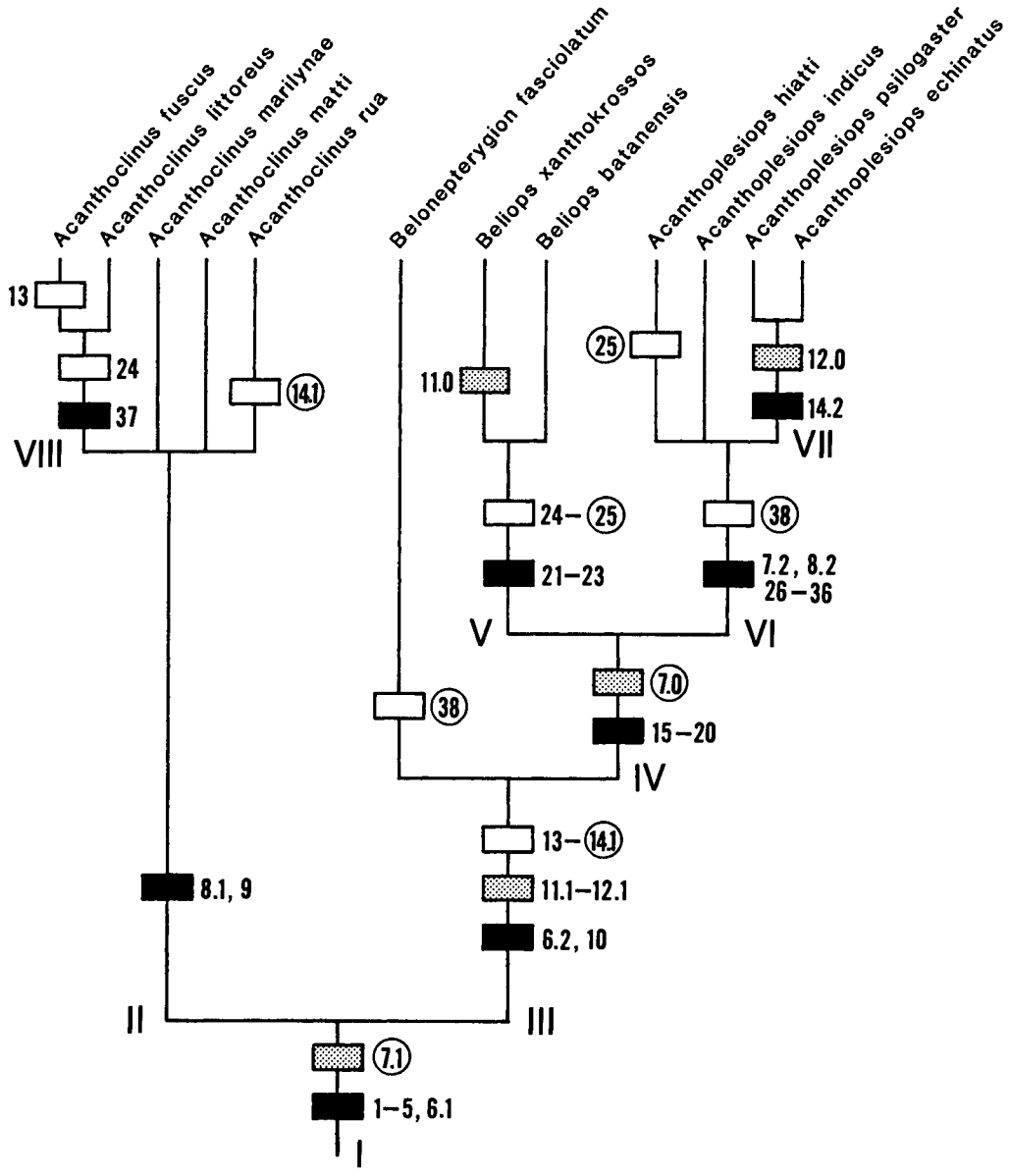


Fig. 12. Phylogenetic relationships among the Acanthoclininae. Roman numbers designate lineages, arabic numbers refer to characters discussed in the section "Character Descriptions and Analysis;" character states for numbers 6-38 are also listed in Table 4. Closed symbols designate uniquely derived unreversed character states; open symbols designate convergent character state changes; shaded symbols designate characters that reverse; numbers with decimals identify multi-state characters, with the number to the right of decimals specifying the character state. Circled numbers identify characters with alternative and equally parsimonious assignments on the cladogram where the placement was arbitrarily selected (see text for discussion).

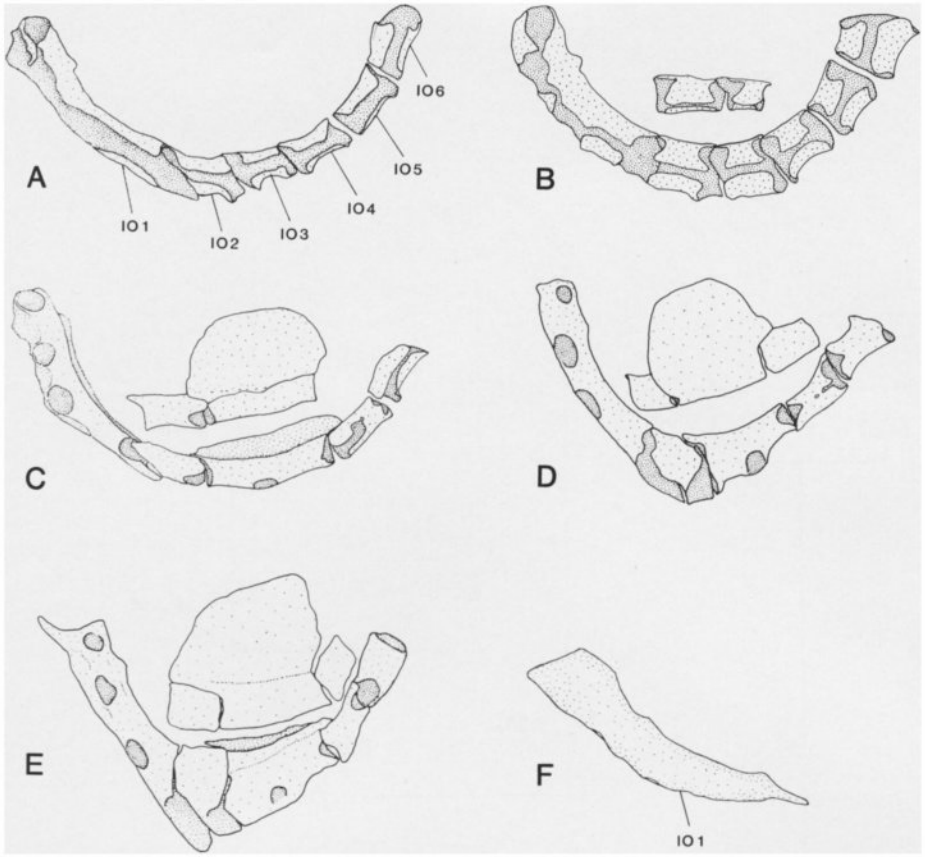


Fig. 13. Infraorbital bones in lateral view (B-E also include dorsal views of infraorbitals 2-3 or 2-4).: A, *Acanthoclinus fuscus*, ANSP 165085; B, *A. littoreus*, ANSP 165089; C, *Belonepterygion fasciolatum*, ANSP 142690; D, *Beliops xanthokrossos*, ANSP 165557; E, *B. batanensis*, USNM 309905; F, *Acanthoplesiops indicus*, ANSP 165570. (B,C = reversed right side views.)

from other acanthoclinines in having lateral-line scales that frequently bear a vertically aligned pair of superficial neuromasts. Although these accessory neuromasts are probable homologues of canal neuromasts (Webb 1990), their phylogenetic significance is unclear.

Beliops lacks a ventral lateral line and, if three lateral lines is plesiomorphic for the subfamily, secondarily acquired the two lateral-line pattern. *Acanthoplesiops* exhibits a further reduction and retains only a single dorsal lateral line, although a series of superficial neuromasts (see discussion of character 38 below) is associated with scales aligned along the horizontal septum.

8. ***Infraorbital bones*** (Fig. 13): five infraorbitals (state 0); six infraorbitals (state 1); one infraorbital (only the lacrimal present) (state 2).

9. ***Suborbital shelf*** (Fig. 13): present (state 0); absent (state 1). In plesiopids, and in most other percoids that have a suborbital shelf, it is typically present on the third infraorbital. Because only the first infraorbital (lacrimal) is present in *Acanthoplesiops*, character 9 can not be evaluated and logically does not apply for that genus.

10. ***Gill membranes***: separate, Figs. 2A-C (state 0); united, Figs. 2D-H (state 1). The gill membranes are fused in

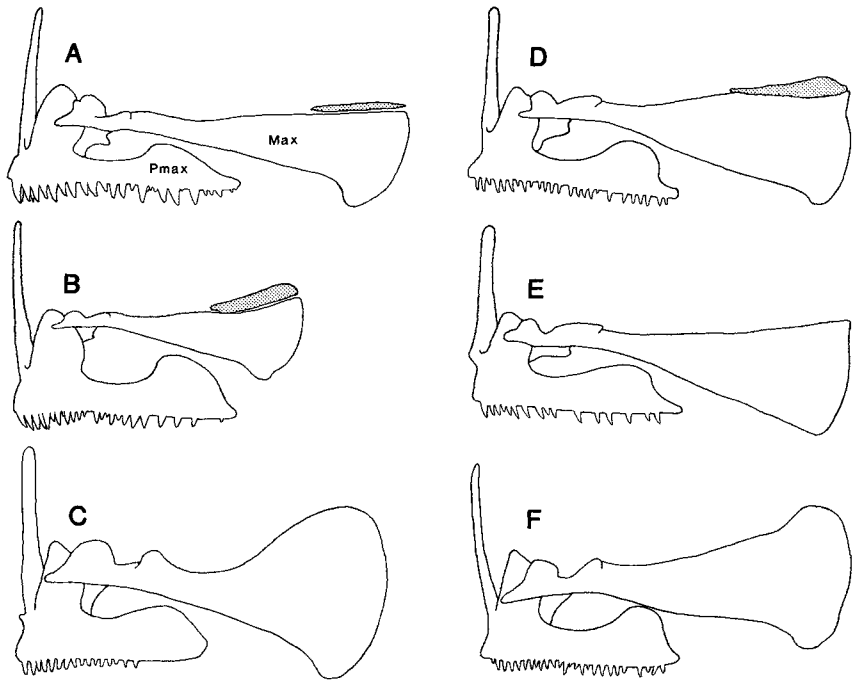


Fig. 14. Upper jaw bones showing relative sizes of maxilla and supramaxilla (stippled): **A**, *Acanthoclinus fuscus*, ANSP 165085; **B**, *A. littoreus*, ANSP 165089; **C**, *Belonepterygion fasciolatum*, ANSP 142690; **D**, *Beliops xanthokrossos*, ANSP 165557; **E**, *B. batanensis*, USNM 309905; **F**, *Acanthoplesiops indicus*, ANSP 165570.

ventral midline to form a broad free fold across isthmus in all members of clade III; they are separate in *Acanthoclinus* and in outgroup plesiopids.

11. ***Supramaxilla***: present, Figs. 14A-B,D (state 0); absent, Figs. 14C,E-F (state 1). The large posteriorly expanded maxilla of *Belonepterygion* suggests that the supramaxilla may have become fused with the maxilla. However, no evidence of such fusion can be seen in our smallest specimen (14.3 mm SL). A developmental series, presently unavailable, might resolve the question.

12. ***Teeth on infrapharyngobranchial 2*** (Fig. 15): present (state 0); absent (state 1). In percoids the tendency to loose teeth on Pb2 is a common pattern. The presence of these teeth in two species of *Acanthoplesiops* (which also share a unique loss of the symphyseal dentary pores) and their absence in all other members of clade III, is most parsimoniously interpreted as a character state reversal.

13. ***Haemal spine of PU2***: autogenous (state 0); fused to vertebral centrum (state 1). In generalized percoids (and in *Fraudella* and *Plesiops*) the haemal spine of preural vertebra 2 is autogenous. It is fused to the vertebral centrum in one species of *Acanthoclinus* (*A. fuscus*) and in the other three acanthoclinine genera.

14. ***Number of dentary pore positions***: five (state 0); four (state 1); three (state 2). In outgroup plesiopids there are five surface pore *positions* (DPP's), that each communicate with separate openings in the dentary bone (including the posteriormost position that shares a common canal connection with both the dentary and preopercle). In three species of *Acanthoclinus* (*A. littoreus*, *marilynae* & *matti*) the two anteriormost pore positions are relatively closely spaced and each is occupied by a

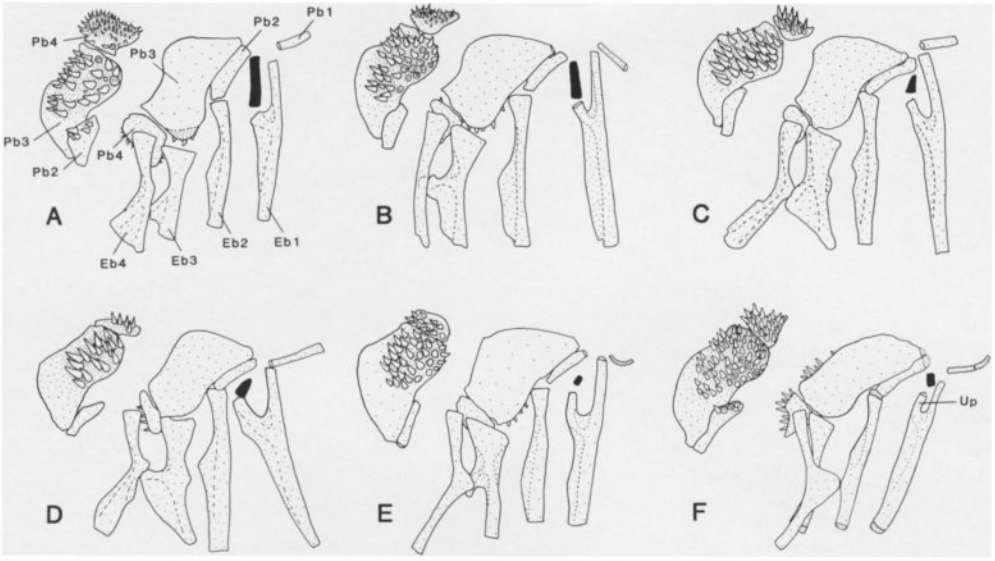


Fig. 15. Pharyngobranchials, right side, dorsal views; also ventral views of Pb2-4; interarcual cartilage (black): **A**, *Acanthoclinus littoreus*, ANSP 165089; **B**, *Belonepterygion fasciolatum*, ANSP 257883; **C**, *Beliops xanthokrossos*, ANSP 165557; **D**, *B. batanensis*, USNM 309905; **E**, *Acanthoplesiops hiatti*, USNM 257874; **F**, *A. echinatus*, ANSP 166316.

single pore; thus the lower jaws appear to have two pairs of symphyseal pores (Fig. 2B); in *A. fuscus* these two pore positions are not as closely spaced and the posterior position may have multiple pores. *Acanthoclinus rua* is exceptional in having only four DPP's (Fig. 2C), with the anterior position occupied by a relatively large pore and DPP2 located in approximately the same position as DPP3 of the three above species. We believe that the reduction in number of pore positions in *A. rua* is the result of ontogenetic consolidation of DPP 1-2, although a developmental series would be required to confirm this hypothesis.

With two exceptions, all members of lineage III have four DPP's, each of which is occupied by a single pore (Figs. 2D-G). *Acanthoplesiops psilogaster* & *echinatus* are exceptional in having only three DPP's (Fig. 2H). In both species the symphyseal dentary pore is absent and DPP1 in located in the same position as DPP2 of congeners.

15. ***Maximum size (mm SL)***: ca. 46-200 (state 0); <27 (state 1). The largest specimen of *Fraudella* is 46.5 mm SL; the three largest species of *Plesiops* attain 100-200 mm, with one species (*P. coeruleolineatus*) rarely attaining 66 mm SL, where small size has probably been independently derived (Mooi, in litt.). Similarly, the relatively small maximum size (64 mm SL) of *Acanthoclinus rua* may be an autapomorphy of that species. The sharp reduction in body size in members of lineage IV (see Table 1) is here interpreted as a synapomorphy.

16. ***Primary opercular spine type***: platelike or fimbriate (state 0); pungent (state 1).

17. ***Preopercular canal***: open posterolaterally, Figs. 16A-C (state 0); tubular, preopercular canal encased in bone for most of its length with a few openings that allow communication with surface sensory pores, Figs. 16D-H (state 1).

18. ***Interarcual cartilage size***: relatively long, Figs. 15A-B (state 0); relatively short, Figs. 15C-F (1).

19. ***2nd & 3rd epurals***: epurals separate, Figs. 17A-B (state 0); epurals fused,

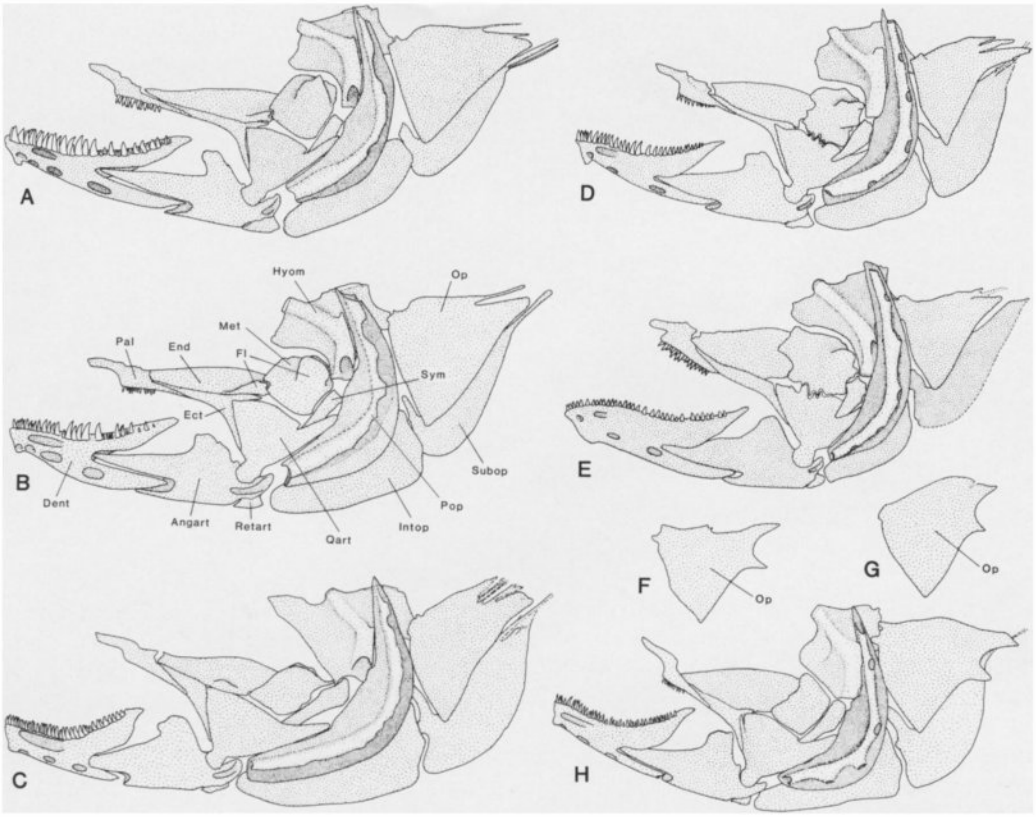


Fig. 16. Lateral view of suspensorium: **A**, *Acanthoclinus fuscus*, ANSP 165085; **B**, *A. littoreus*, ANSP 165089; **C**, *Belonepterygion fasciolatum*, ANSP 142690; **D**, *Beliops xanthokrossos*, ANSP 165557; **E**, *B. batanensis*, USNM 309905; **F**, *Acanthoplesiops hiatti*, ANSP 165421; **G**, *A. echinatus*, ANSP 166316; **H**, *A indicus*, ANSP 165570. (E,G = reversed right side views.)

at least distally, Figs. 15C-D (state 1). Hardy (1985) reported that *Beliops* and *Acanthoplesiops* have only two epurals; all species of both genera have three epurals, but the posterior two are partially or completely fused together.

20. ***First neural spine***: autogenous, Fig. 18A (state 0); neural spine fused to vertebral centrum, Fig. 18B (state 1).

21. ***Interarcual cartilage shape***: rod-shaped, Figs. 15E-F (state 0); cone-shaped, Figs. 15C-D (state 1). The interareual eartilage found in euteleostean fishes typieally is a rod-shaped element (Travers 1981). Although the presence of a cone-shaped interarcual eartilage should be confirmed in additional speeimens, its oeeurrenee in both species of *Beliops* (and absenee in our other eomparative material) leads us to eonelude that it is a valid synapomorphy of the genus.

22. ***Metapterygoid-quadrate joint***: smooth, Figs. 16A-C,H (state 0); interdigitated, Figs. 16D-E (state 1).

23. ***Scapulo-coracoid joint***: smooth, Figs. 19A-B,D-E (state 0); interdigitated, Fig. 19C (state 1). The eharaeter state for *Beliops batanensis* was determined by careful dissection and removal of the pectoral musculature and application of alizarin stain to the seapulo-eoraeoid joint of the non-eleared and stained paratype.

24. ***Supernumerary spines on first anal-fin pterygiophore***: two spines (state 0); one spine (state 1). Hardy (1985) erroneously interpreted the presenee of two spines on the first anal-fin pterygiophore as "apparent fusion" of the first two pterygio-

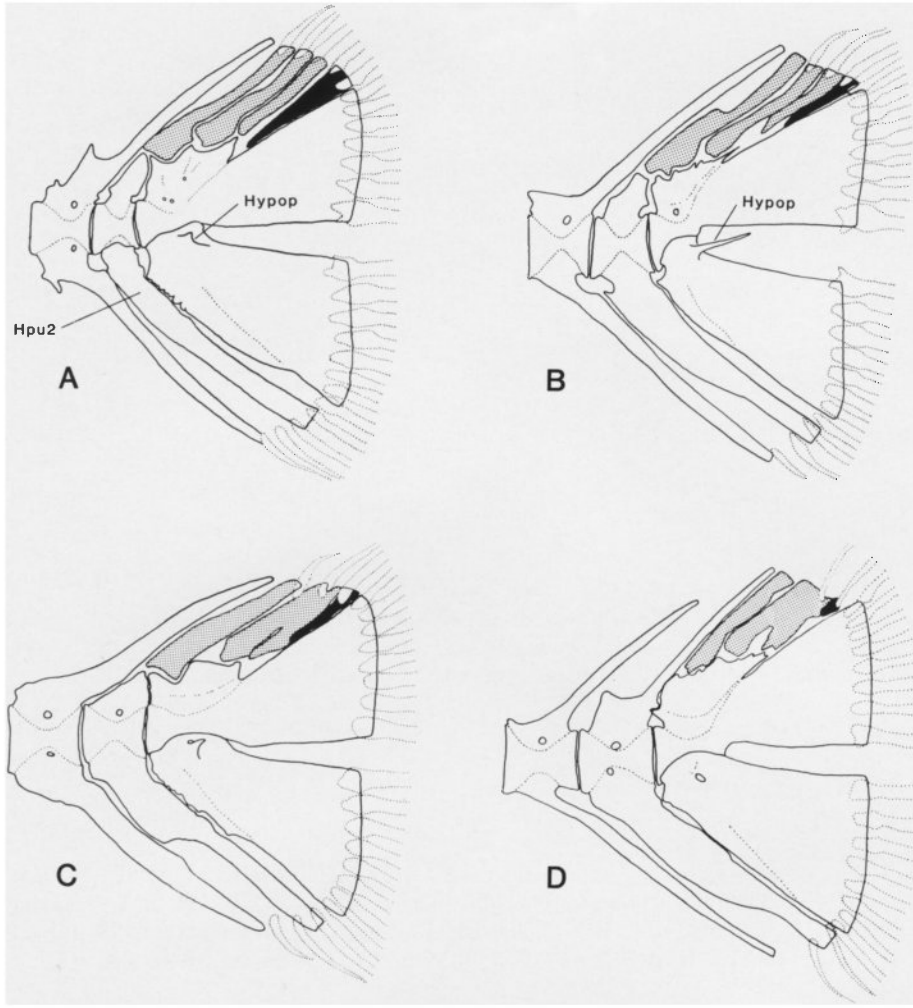


Fig. 17. Caudal skeletons showing epurals (stippled) and hypural 5 (black): **A**, *Acanthoclinus littoreus*, ANSP 165089; **B**, *Belonepterygion fasciolatum*, ANSP 142690; **C**, *Beliops xanthokrossos*, ANSP 165557; **D**, *Acanthoplesiops psilogaster*, USNM 257871.

phores and considered the condition to be derived. As discussed by Johnson (1984:477), the most common condition in percoids is for the first anal pterygiophore to have two spines in supernumerary (non-serial) association and the third in serial association. In addition to the two supernumerary spine condition in outgroup plesiopids, it stands to reason that those species of acanthoclinincs with one supernumerary spine have lost the anterior spine and that the condition is derived. The correct reinterpretation of this character state is especially important because it eliminates the sole putative synapomorphy that might be used to justify recognition of *Taumakoides*.

25. ***Middle radials of segmented dorsal- and anal-fin pterygiophores***: autogenous (state 0); fused to proximal radials (state 1). Johnson (1980:35) discussed the typical trisegmental nature of median fin supports in teleosts. He noted that in acanthopterygians there is a tendency for these supports to become bisegmental through fusion of the proximal and medial

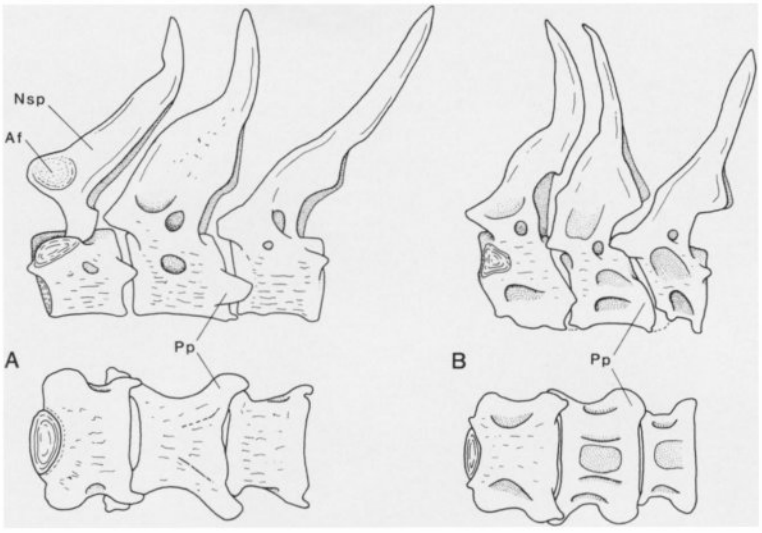


Fig. 18. Lateral and ventral views of first three vertebrae (ribs removed): A, *Acanthoclinus fuscus*, ANSP 165085; B, *Acanthoplesiops indicus*, ANSP 165570. Note condition of first neural spine: autogenous (*Acanthoclinus*) versus fused to centrum (*Acanthoplesiops*); also compare size and shape of parapophysis on 2nd vertebra and relative size of 3rd vertebra.

(= middle) segments.

26. ***Spot on pectoral-fin base***: absent (state 0); present (state 1). Occasionally this spot is difficult to discern in preserved specimens, but in fresh material it is usually conspicuous.

27. ***Symphyseal flap on lower lip***: absent (state 0); ventral margin of lower lip at symphysis produced into a fleshy flap (state 1).

28. ***Uncinate process (Up) of first epibrachial***: not parallel to main arm, so junction between the two arms is "V"-shaped (state 0); parallel to main arm so junction between the two arms is "U"-shaped (Figs. 15E-F) (state 1). The uncinate process can best be seen when the first epibranchial is rotated so that the Up is perpendicular to its long axis. The distinction between the two Up character states as seen in figure 15 can not be fully appreciated because the orientation of Eb1 is not ideal.

29. ***Size of hypural 5***: large to moderate, Figs. 17A-C (state 0); very small, Fig. 17D (state 1).

30. ***Hypurapophysis***: present, small to large, Figs. 17A-C (state 0); absent, Fig. 17D (state 1). Hardy (1985:fig. 14C) illustrated the hypurapophysis as present in *Acanthoplesiops hiatti* and reported it as "small, blunt" for the genus. None of our cleared and stained specimens of *Acanthoplesiops* has a hypurapophysis, and since the single C&S specimen that Hardy examined was also available to us, we conclude that his observation is erroneous. The long and sharp hypurapophysis (Fig. 17B) of *Belonepterygion* is impressive and is virtually identical to that seen in *Plesiops* and *Fraudella*.

31. ***Secondary opercular spine***: absent (state 0); present, Figs. 16F-H (state 1). *Fraudella* has a series of prominent spines on the posterior margin of the opercle; except for the posterodorsally positioned primary opercular spine, this bone is entire in all other outgroup plesiopids and in all acanthoclinines except *Acanthoplesiops*, which typically has one (occasionally two in *A. hiatti*) secondary spine.

32. ***Coracoid arm***: posterolateral arm of coracoid moderately slender, Figs. 19A-C (state 0); robust, Figs. 19D-E (state 1).

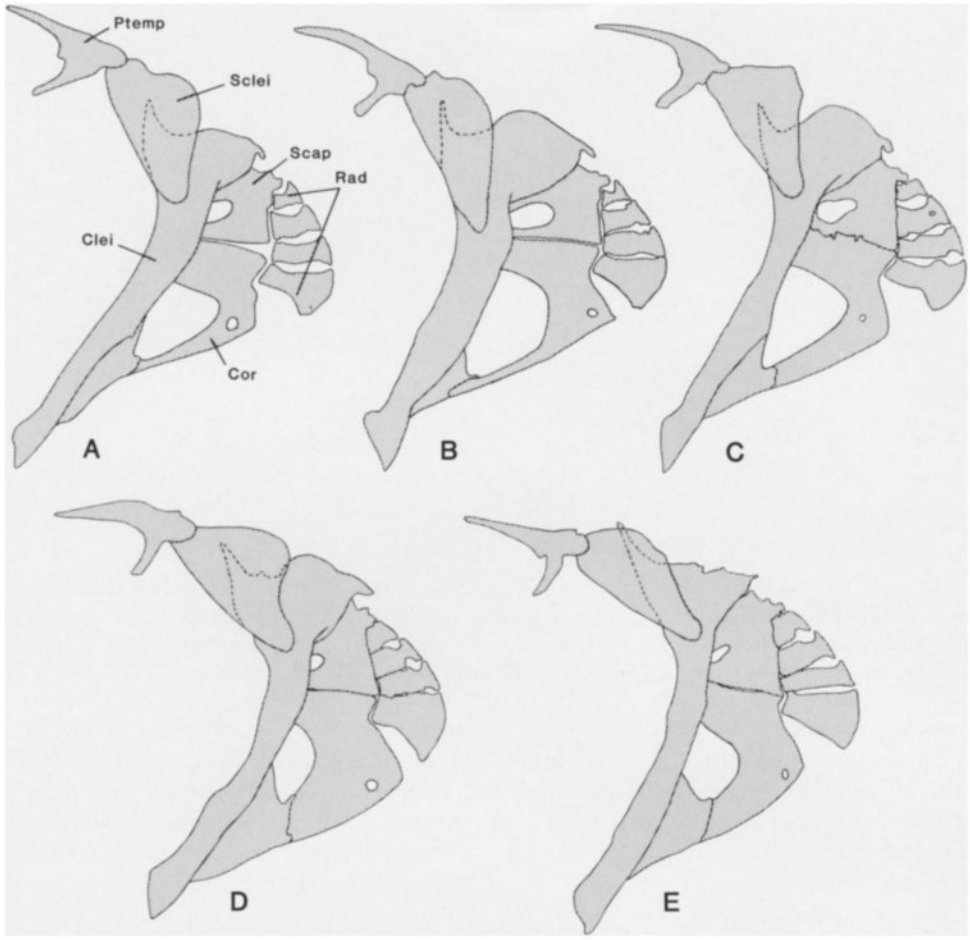


Fig. 19. Lateral view of pectoral girdle: A, *Acanthoclinus fuscus*, ANSP 165085; B, *Belonepterygion fasciolatum*, ANSP 142690; C, *Beliops xanthokrossos*, ANSP 165557; D, *Acanthoplesiops indicus*, ANSP 165570; E, *A. psilogaster*, USNM 257871.

33. ***Pectoral radial formula***: 2-1-1, Figs. 19A-C (state 0); 3-0-1, Figs. 19D-F (state 1). Many generalized percoids, all outgroup plesiopids and three acanthoclinine genera have two pectoral radials articulating with the scapula, one with both the scapula and coracoid (scapulo-coracoid joint) and one with the coracoid (= radial formula 2-1-1); *Acanthoplesiops* is exceptional in having a 3-0-1 radial formula.

34. ***Supracleithral lateral-line canal***: present (state 0); absent (state 1). In *Plesiops*, *Fraudella* and three genera of acanthoclinines the supracleithrum has a well-developed supracleithral sensory canal that is continuous anterodorsally with the posttemporal canal and posteriorly with the lateral-line scales. In *Acanthoplesiops* the supracleithral sensory canal is absent, and the posttemporal canal passes laterally over the posterodorsal margin of the supracleithrum and exits directly to the surface. Loss of the supracleithral lateral-line canal is a common trend in relatively small fishes with a single, reduced lateral line.

35. ***Ceratohyal-epihyal suturing***: suturing joint medial only (state 0); suturing joint on both medial and lateral surfaces (state 1).

36. ***Scales in mid-lateral series***: not

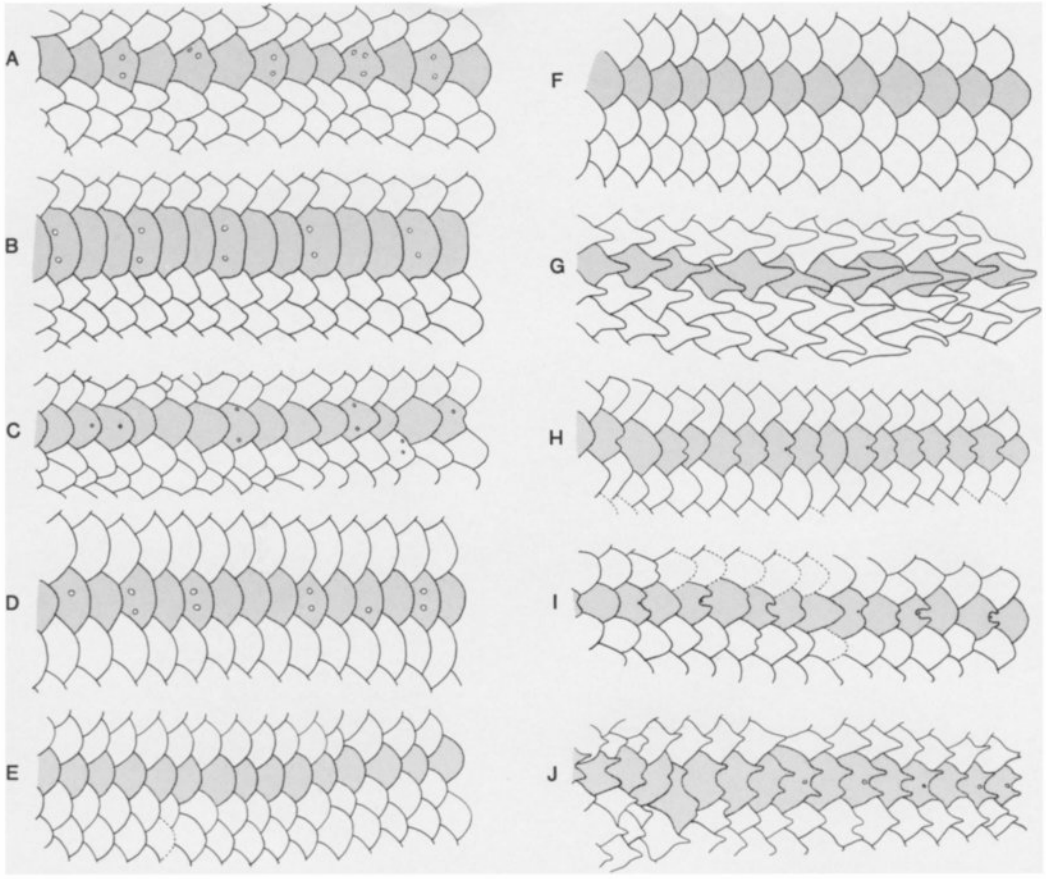
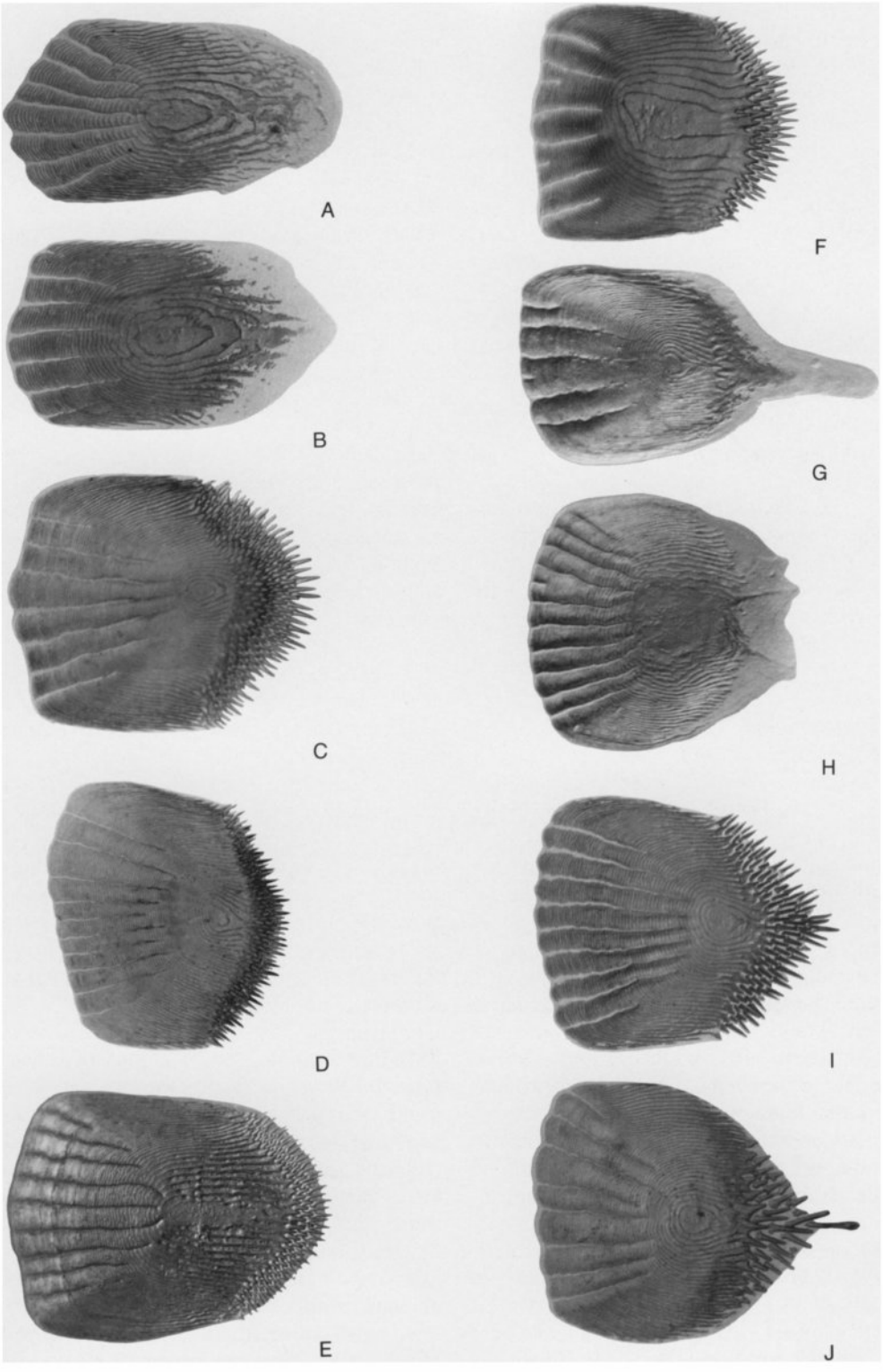


Fig. 20. Scales on mid-side of body; anterior to left (shaded scales are those of middle lateral-line series or scales in the same position normally occupied by them).: **A**, *Acanthoclinus fuscus*, ANSP 165085, 70.3 mm; **B**, *A. littoreus*, ANSP 165089, 65.3 mm; **C**, *A. rua*, ANSP 165086, 41.4 mm; **D**, *A. matti*, ANSP 165088, 51.0 mm; **E**, *Belonepterygion fasciolatum*, USNM 257883, 40.6 mm; **F**, *Beliops xanthokrossos*, ANSP 165557, 25.7 mm; **G**, *B. batanensis*, USNM 309905, 21.1 mm; **H**, *Acanthoplesiops hiatti*, USNM 257874, 18.2 mm; **I**, *A. psilogaster*, USNM 257872, holotype, 22.6 mm; **J**, *A. echinatus*, BPBM 44177, holotype, 19.8 mm. (A,C,D,F,H,J = reversed right side views; tubes on lateral-line scales, if present, not shown).

bilobed (state 0); bilobed, Figs. 20H-J (state 1). Posteriorly bilobed scales centered on the horizontal septum are unique to *Acanthoplesiops* and may be associated with the occurrence of a single, superficial neuromast that is usually present (immediately adjacent to anterior margin of scale notch) on every 2nd to 4th bilobed scale.

37. ***Body scales***: some ctenoid (state 0); all cycloid (state 1). The scales of Acanthoclinines exhibit a remarkable degree of morphological diversity (Figs. 20-21) for such a small group of closely related fishes. Loss of ctenii is a common trend in percoids, with cycloid scales secondarily evolved in most percoids (Johnson 1984). All outgroup plesiopids have ctenoid scales, so the complete absence of ctenoid scales exclusively in *Acanthoclinus fuscus & littoreus* clearly is a synapomorphy. All other acanthoclinines, with two exceptions discussed below, have the posterior region of the body mostly or partially covered with scales


A
B
C
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bearing typical ctenii. Anteriorly some of the scales are cycloid in all species of Acanthoclininae.

The scales of *Beliops batanensis* (Figs. 20F, 22F) and *Acanthoplesiops indicus* (Fig. 21H) (refer to individual species accounts for descriptions) are so highly modified that we are uncertain whether they should be categorized as "ctenoid" or "cycloid" scale types. It is clear, however, that these scales are independently derived and have nothing in common with the typical cycloid scales that characterize the two species of *Acanthoclinus* mentioned above. The scales of *Acanthoplesiops echinatus* (see Figs. 20J, 21J and species account) are also autapomorphic but in this case character evolution involves accentuation of ctenii.

38. ***Adductor mandibulae A2 section***: laterally exposed, Figs. 22A-B (state 0); covered by A1 laterally, Figs. 22C-D (state 1). See also discussion of this character in "Phylogenetic Analysis."

Other Characters

Ectopterygoid Process: Hardy (1985) described the anterior process of the ectopterygoid (best observed in mesial view) as "splint-like" in *Acanthoclinus* (sensu lato) and *Belonepterygion* and "rounded" in other acanthoclinines. Description of this process as splint-like in *Acanthoclinus* and in outgroup plesiopids is accurate but the condition in *Belonepterygion* is equivocal because the entire ectopterygoid is relatively short and ends in a rounded point. In view of the overall shape of this bone in *Belonepterygion*, it might be argued that the anterior process is a short version of "splint-like." However, the intermediate shape of the process in *Belonepterygion* is such that the authors could not agree on how to categorize it. We also observed that while the anterior end of the ectopterygoid is very blunt in some species of *Acanthoplesiops*, in *A. hiatti* it is as sharp as in some *Acanthoclinus* species and in one individual (USNM 257874) the left ectopterygoid has a blunt tip while the right one is sharp. In view of the apparent shape continuum of the ectopterygoid anterior process in acanthoclinines we conclude that this character is not evolutionarily informative.

Basihyals: the basihyals (Fig. 23) range from wide to slender and toothed to toothless in acanthoclinines (see also Table 1). The basihyal is edentate in *Plesiops*, toothed in *Fraudella*, with both conditions also present in other plesiopids (see Hoese and Kuiter 1984). The consecutive outgroup rule of Maddison et al. (1984:89) cannot be used to establish the ancestral acanthoclinine character state for basihyal dentition and a globally parsimonious ingroup cladogram is also equivocal for this character.

PHYLOGENETIC ANALYSIS

Four equally parsimonious tree topologies were inferred using Hennig-86; all have length 45, consistency index 0.82 and retention index 0.93 (Farris 1989). A strict consensus tree (Fig. 12), identical to one of the four maximum parsimony cladograms, was calculated using the "nelsen" option of Hennig-86. Four characters (6-8, 14) each have three character states; all are treated as unordered. Whether these characters are treated as ordered or unordered does not affect the tree topologies. All four trees have the same basic topology differing only in the placement of *Acanthoclinus rua* and *Acanthoplesiops hiatti* in relation to their respective congeners. Character states with alternative and equally parsimonious assignments on

Fig. 21. Individual scales from area between anal fin and mid-lateral scale row; anterior to left (data as in Fig. 20 unless otherwise stated).: **A**, *Acanthoclinus fuscus*; **B**, *A. littoreus*; **C**, *A. marylinae*, ANSP 134947, 62.8 mm; **D**, *A. matti*; **E**, *Belonepterygion fasciolatum*; **F**, *Beliops xanthokrossos*; **G**, *B. batanensis*; **H**, *A. indicus*, ANSP 165570, 24.7 mm; **I**, *A. hiatti*, USNM 257874, 21.4 mm; **J**, *A. echinatus*, ANSP 166316, 21.0 mm.

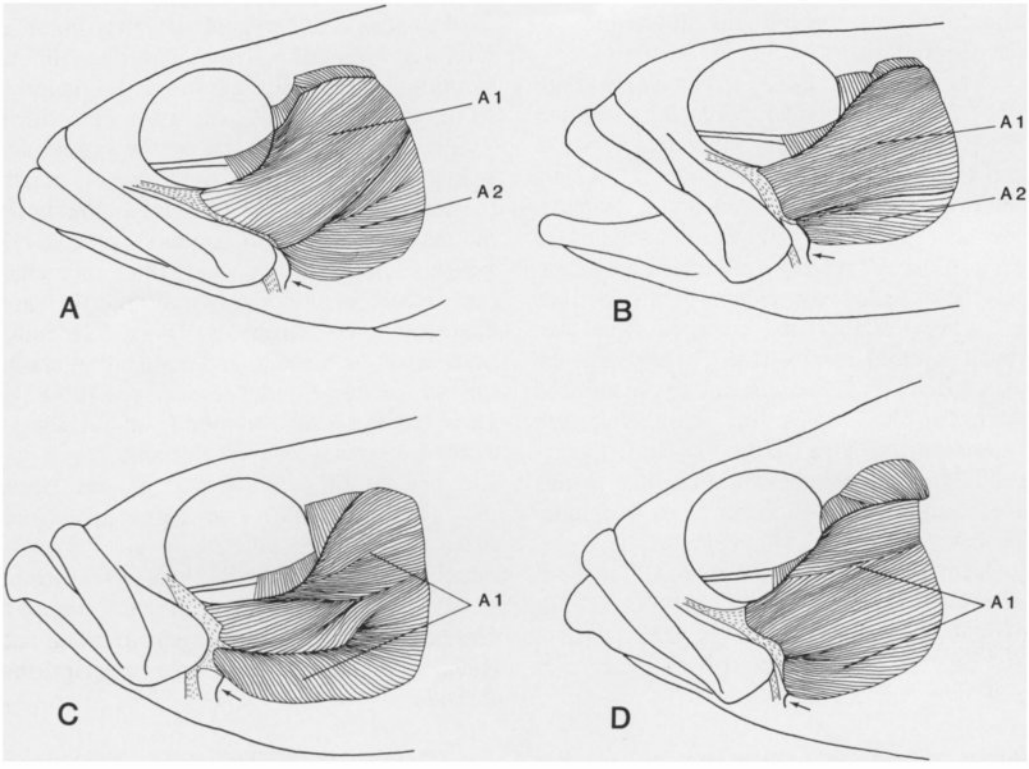

Fig. 22. Lateral view of superficial cheek musculature: **A**, *Acanthoclinus fuscus*, ANSP 165085, 61.2; **B**, *A. matti*, ANSP 165088, 51.0 mm; **C**, *Belonepterygion fasciolatum*, USNM 257883, 36.4 mm; **D**, *Acanthoplesiops indicus*, ANSP 165570, 24.7 mm. (Small arrows denote posteroventral margin of coronoid process of dentary.)

the consensus tree are discussed below.

Characters with ambiguous resolutions

Character 7.—There are three equally parsimonious character state optimizations for number of lateral lines, all requiring three steps. The sequence shown in Fig. 12 assumes a change from two to three lateral lines (7.0 to 7.1) at branch I, a reversal at branch IV to two lateral lines (7.0) and change to a single lateral line (7.2) at branch VI. Alternative scenarios require either: (1) no change (two lateral lines) at branch I, evolution of three lateral lines twice (at branch II and independently in *Belonepterygion*), and with a final change from two to one lateral line at branch IV; or (2) change from two to three lateral lines at branch I, followed by changes from three to two lateral lines at branch V and from three to one lateral line at branch VI.

Character 14.—The placement of *Acanthoclinus rua* is determined by polarity assignment of character 14 (number of dentary pore positions = DPP) at branch I. If 5 DPP's is assumed for branch I, three steps are required to produce the topology depicted in Fig. 12, including independent changes from 5 to 4 DPP's (14.0 to 14.1) in *A. rua* and at branch III. Alternatively, the same number of steps including the identical change from 4 to 3 DPP (14.1 to 14.2) at branch VII, is required if there is a change from 5 to 4 DPP's at branch I with a reversal to 5 DPP's in a lineage leading to a monophyletic grouping of all

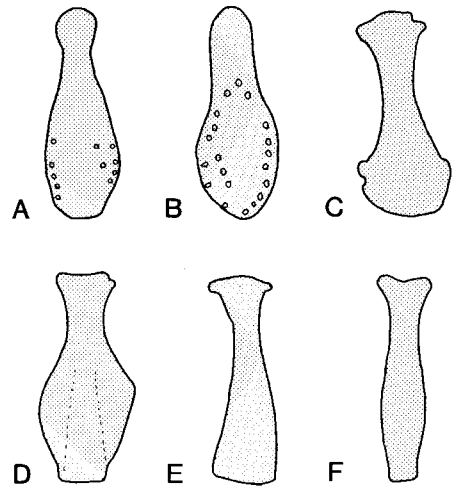

Fig. 23. Dorsal view of basihyals: A, *Beliops xanthokrossos*, ANSP 165557; B, *B. batanensis*, USNM 309905; C, *Acanthoplesiops indicus*, ANSP 165570; D, *A. hiatti*, ANSP 165421; E, *A. psilogaster*, USNM 257871; F, *A. echinatus*, ANSP 166316.

species of *Acanthoclinus* except *A. rua*. The hypothesized, but unproven, ontogenetic character state transformation discussed for character 14 in the previous section favors the first alternative.

Character 25.—The placement of *Acanthoplesiops hiatti* is determined by polarity assignment of character 25 (nature of middle radials of segmented rays) at branch IV. In Fig. 12 the plesiomorphic character state, middle and proximal radials unfused, is assumed for the branch IV lineage with two character state changes to fused radials, once at branch V and as an autapomorphy of *A. hiatti*. Alternatively, change to fused radials at branch IV, with a reversal to autogenous radials in a lineage leading to a monophyletic group including all species of *Acanthoplesiops* except *A. hiatti* requires the same number of steps. The second alternative, if correct, implies that the vicariant event or other factors responsible for the speciation of *A. hiatti* predate the evolutionary bifurcation that separated *A. indicus* from the common ancestor that gave rise to the allopatric sister-species *A. psilogaster* & *echinatus*.

Character 38.—The same two steps are required whether the derived adductor mandibulae character state is hypothesized to have evolved independently in *Belonepterygion* and at branch VI, or initially at branch III followed by reversal to the plesiomorphic state at branch V. We prefer the first alternative (depicted in Fig. 12) because no reversal is required; although the derived condition is found in both *Belonepterygion* (Fig. 22C) and *Acanthoplesiops* (Fig. 22D) the overall adductor mandibulae configuration is clearly different, suggesting the likelihood of convergent evolution of the character state.

Acanthoclinine relationships

In the following discussion numbers given in parentheses correspond to characters or character states described in greater detail in the "Character descriptions" section and plotted on the cladogram (Fig. 12).

Monophyly of *Acanthoclinus* is based on two uniquely derived character states, both involving the infraorbitals: presence of six infraorbitals (8.1) and absence of a suborbital shelf (9). Two additional synapomorphies establish *Acanthoclinus fuscus* & *littoreus* as sister species: all body scales cycloid (37) and first pterygiophore of anal fin with a single supernumerary spine (24), the latter character state also present in *Beliops*. Absence of scales on the anterodorsal angle of the opercle may prove to be an additional synapomorphy of these two species.

Monophyly of a group containing *Belonepterygion*, *Beliops* and *Acanthoplesiops* (lineage III) is supported by the following: one unique synapomorphy, united gill membranes (10); three reductive apomorphies, fewer number of total caudal-fin rays (6.2), absence of supramaxilla (11.1) (reversed in *Beliops xanthokrossos*), and absence of teeth on infrapharyngobranchial 2 (12.1) (reversed in lineage VII); and two homoplastic characters, haemal spine of PU2 fused to vertebral centrum (13) (char-

acter state also present in *Acanthoclinus fuscus*), and four dentary pore positions (14.1) (also present in *Acanthoclinus rua*).

Beliops and *Acanthoplesiops* share the following six uniquely derived characters: small maximum body size (15), primary opercular spine pungent (16), preopercular canal tubular (17), interarcular cartilage relatively short (18), 2nd & 3rd epurals fused, at least distally (19), and first neural spine fused to vertebral centrum (20). If character state evolution for number of lateral lines is as depicted in Fig. 12, the common ancestor of both of these genera had two lateral lines (reversed character state, 7.0); see above for discussion of the ambiguous parsimony resolution of this character on the tree topology.

Monophyly of *Beliops* is based on two homoplastic characters and the following three uniquely derived characters: interarcual cartilage cone shaped (21), metapterygoid-quadrate joint interdigitated (22), and scapulo-coracoid joint interdigitated (23). The two homoplastic characters are: first pterygiophore of anal fin with a single supernumerary spine (24) (character state also present in *Acanthoclinus fuscus*), and pterygiophores of segmented dorsal- and anal-fin rays with fused middle and proximal radials (25) (also present in *Acanthoplesiops hiatti*); the last character has an ambiguous parsimony resolution on the tree topology (see discussion above).

The four species of *Acanthoplesiops* share the following 13 uniquely derived, unreversed characters: one lateral line (7.2), only the first (lacrimal) infraorbital present (8.2), white spot on pectoral-fin base (26), symphyseal flap on lower lip (27), uncinate process on first epibranchial "U"-shaped (28), hypural 5 very small (29), hypurapophysis absent (30), secondary opercular spine present (31), posterolateral arm of coracoid robust (32), pectoral radial formula 3-0-1 (33), supraclethral lateral-line canal absent (34), ceratohyal-epihyal joint suturing on medial and lateral surfaces (35), and posteriorly bilobed scales in mid-lateral series (36). Another synapomorphy of *Acanthoplesiops* (not plotted on Fig. 12 because it is obviously correlated with character 8) is the absence of infraorbital pores behind the eye in the area where infraorbitals 2-5 would normally occur. Additionally, all species of *Acanthoplesiops* have adductor mandibulae A2 section covered by A1 laterally (38); see preceding discussion of this homoplastic character.

Two additional character states of *Acanthoplesiops psilogaster & echinatus* establish them as sister species. The first, symphyseal dentary pore position absent (14.2), is a unique synapomorphy; the second, teeth present on infrapharyngobranchial 2 (12.0), is most parsimoniously interpreted as reversal of the character state, absence of such teeth (12.1), that is one of the synapomorphies of lineage III.

BIOGEOGRAPHY

Exactly when New Zealand became isolated from Australia or the rest of Gondwanaland is uncertain, but as noted by Briggs (1987:66) most biologists agree that its isolation extends back at least to the Cretaceous. This early separation is congruent with our cladogram (Fig. 12) which shows the New Zealand endemic *Acanthoclinus* to be the sister group of all other acanthoclinines, none of which occurs in New Zealand. The sequence of events that produced five species of *Acanthoclinus* will probably never be known, but a combination of sea-level changes associated with glaciation and localized tectonic plate rotational movements (Craw 1988) undoubtedly provided multiple opportunities for allopatric speciation.

The monotypic *Belonepterygion* probably had its genesis on the Indo-Australian plate, with its present northern distribution attained after that plate made contact (ca. 20 m.y.a.) with the Asian plate; with one exception (*Acanthoplesiops hiatti*) no acanthoclinine is known to occur on the Pacific plate. One interesting feature of the distribution of *Belonepterygion* (Fig. 3) is the absence of records between the southern Philippines and the Great Barrier Reef where it is relatively common. If this dis-

junct distribution is not a sampling artifact, then perhaps the same vicariant event that produced the two species of *Beliops* may be the explanation.

The antitropical distributional pattern exhibited by the two species of *Beliops* is probably real. As discussed in the following section, it is likely that the Batan Islands are the southern distributional limit of *B. batanensis*.

Any hypothesis to explain the biogeography of the four species of *Acanthoplesiops* requires too many ad hoc assumptions to be justified, especially in the absence of a fully resolved phylogeny. The broad distribution of the genus as a whole (including the presence of *A. indicus* on the African plate, Fig. 9) and the apparent absence of a species of *Acanthoplesiops* in the Australia-New Guinea region is especially difficult to reconcile.

Batan Islands biogeography.—Although the ichthyofauna of the Batan Islands is still inadequately known (and knowledge of the phylogenetic relationships of individual species is especially poor), it appears likely that historically there may have been a stronger biogeographic connection with Taiwan, the Ryukyu Islands and southern Japan than with the remainder of the Philippine Archipelago. The causative explanation for this relationship is unknown. (Henceforth the above four general localities will be abbreviated B,T,R and SJ.) The following examples, and there are undoubtedly others, are the basis for the above zoogeographic observation:

1. *Acanthoplesiops psilogaster* is known only from B,T,SJ while its sister-species, *A. echinatus*, is known from the Philippines (Sulu Archipelago) and Indonesia (Banda Sea).

2. In a revision of the blenniid genus *Cirripectes*, Williams (1988) recognized a monophyletic trio of allopatric and/or parapatric species, including *C. imitator* Williams (B,T,SJ and the Ogasawara Is.), *C. fuscoguttatus* Strasburg and Schultz (broadly distributed Pacific Plate endemic, sensu Springer 1982, otherwise known only from B,T), and *C. gilberti* Williams (Indian Ocean).

3. Springer (1988), in a revision of the speciose blenniid genus *Ecsenius*, recognized the monophyletic Oculus Group consisting of eight allopatric species, including *E. oculus* Springer (B,T,R) and *E. monoculus* Springer (Ilot du Sud, the Philippines, except B, and the Molucca Is.); several other species of *Ecsenius* are documented from scattered Philippine localities but apparently are absent from B.

4. The pomacanthids, *Holacanthus venustus* Yasuda and Tominaga, *Centropyge ferrugatus* Randall and Burgess, and *Genicanthus semifasciatus* (Kamohara), all previously known with certainty only from T,R,SJ (Allen 1979), were recently discovered at B, the latter species sighted but not collected.

5. Starnes (1988), in a comprehensive revision of the Priacanthidae, reported *Priacanthus zaiserae* Starnes and Moyer from B,R,SJ and the Okinawa Trough. "Probable specimens of *zaiserae*" were said to have been observed by Moyer in Markets at Cebu, Negros, Philippines, which Starnes (pers. comm.) now believes may have been misidentified. Several other species of *Priacanthus* are known from the Philippines including *P. blochii* Bleeker, which has a broad Indo-west Pacific distribution but is unrecorded from B,T,R,SJ.

Numerous marine shorefishes (sensu Springer 1982) have been reported as endemics of the SJ,R,T region (Masuda et al. 1984; Shen 1984), and the proto-Batan Islands may have been geologically connected with that fauna. All of these islands lie on or near the eastern margin of the Philippine Plate. *Beliops batanensis*, *Cirripectes viriosus* Williams and *Cirrisalarias* n.sp. [Blenniidae] are presently known from single localities in the Batan Islands and it would not be surprising if some or all of them are eventually found to occur at T,R or SJ.

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