

Phylogenetic Relationships and
Revision of the Blennioid Fish Genus
Scartichthys

JEFFREY T. WILLIAMS

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ABSTRACT

Williams, Jeffrey T. Phylogenetic Relationships and Revision of the Blennioid Fish Genus *Scartichthys*. *Smithsonian Contributions to Zoology*, number 492, 30 pages, 20 figures, 4 tables, 1990.—Blennioid fishes of the genus *Scartichthys* Jordan and Evermann comprise a group of marine shore fishes restricted to the tropical and subtropical coasts of western Panama and western South America. *Scartichthys* comprises four species: *S. crapulatus*, new species (northern Chile and vicinity of Valparaiso), *S. gigas* (Panama to northern Chile), *S. variolatus* (San Felix, San Ambrosio, and Juan Fernandez Islands), and *S. viridis* (vicinity of Valparaiso to southern Peru). The four species are quite similar ecologically in being herbivores and detritivores, and inhabiting rocky areas.

The salariin genera *Cirripectes* Swainson, *Scartichthys*, *Exallias* Jordan and Evermann, *Ophioblennius* Gill, *Pereulixia* Smith, *Stanulus* Smith, *Entomacrodus* Gill, and *Istiblennius* Whitley form a monophyletic group within the tribe Salariai. My hypothesized phylogeny indicates that each of the following genera is the sister genus to the combination of all preceding genera: *Scartichthys*, *Ophioblennius*, *Cirripectes*, *Exallias*, *Pereulixia*, *Stanulus*, *Entomacrodus*, and *Istiblennius* (including at least the *I. gibbifrons* species complex).

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Contents

	<i>Page</i>
Introduction	1
Historical Treatment of the Blenniidae	1
Methods	2
Taxonomic Methods	2
Methods of Phylogenetic Analysis	4
Acknowledgments	5
Phylogenetic Analysis	5
Family BLENNIIDAE	6
SALARIINI-PARABLENNIINI Group	7
PARABLENNIINI	8
SALARIINI	8
Salarias Group	9
Node I Group	9
Genus <i>Istiblennius</i>	11
Node II Group	11
Genus <i>Entomacrodus</i>	12
Node III Group	13
Genus <i>Stanulus</i>	14
Node IV Group	14
Genus <i>Pereulixia</i>	15
Node V Group	15
Genus <i>Exallias</i>	17
Node VI Group	17
Genus <i>Cirripectes</i>	17
Node VII Group	18
Genus <i>Ophioblennius</i>	18
Genus <i>Scartichthys</i>	20
Discussion of Phylogenetic Analysis of Genera	20
Genus <i>Scartichthys</i> Jordan and Evermann	21
Key to the Species of <i>Scartichthys</i>	21
<i>Scartichthys crapulatus</i> , new species	23
<i>Scartichthys gigas</i> (Steindachner)	24
<i>Scartichthys variolatus</i> (Valenciennes)	26
<i>Scartichthys viridis</i> (Valenciennes)	27
Literature Cited	30

Phylogenetic Relationships and Revision of the Blenniid Fish Genus *Scartichthys*

Jeffrey T. Williams

Introduction

The blenniid fish tribe Salariae is a group of marine shore-fishes found circumglobally in tropical and subtropical seas. Members of the tribe are quite similar ecologically; most are herbivores or detritivores and inhabit rocky or coralline areas.

The objectives of the present study are to (1) test the preliminary hypothesis proposed by Smith-Vaniz and Springer (1971:49) that the genera *Cirripectes* Swainson, *Scartichthys* Jordan and Evermann, *Ophioblennius* Gill, *Pereulixia* Smith, and *Exallias* Jordan and Evermann comprise a monophyletic group and are each monophyletic; and (2) taxonomically revise *Scartichthys*, and provide complete species descriptions of and distribution maps for each of the included species.

Smith-Vaniz and Springer (1971) gave a synopsis of the Salariae to provide a foundation for future work on the tribe. They pointed out several genera that needed additional study and provided a preliminary hypothesis of the relationships of the 24 genera they recognized in the tribe. Their method was not cladistic, but they did establish the monophyletic nature of the tribe and provided a dendrogram (Smith-Vaniz and Springer, 1971, fig. 51) of the genera showing their preliminary concepts of salariin interrelationships. This dendrogram suggests that the genera *Cirripectes*, *Scartichthys*, *Exallias*, *Pereulixia*, and *Ophioblennius* are more closely related to each other than to other members of the tribe.

Cohen (1956) briefly reviewed the eastern Pacific genus *Scartichthys* Jordan and Evermann. He examined specimens of several nominal species, provided a partial synonymy for the genus, and recognized *S. gigas* and *S. viridis* as valid species.

He did not attempt to treat all of the nominal species, thus leaving the status of many species in doubt. Smith-Vaniz and Springer (1971:54–61) listed thirteen nominal species (Table 1) and estimated that there were only two valid species of *Scartichthys*.

Cirripectes (reviewed by Williams, 1988), *Ophioblennius* (reviewed by Springer, 1962), *Pereulixia*, and *Exallias* (both monotypic), and their individual species, are relatively well defined, but their interrelationships within the Salariae have not been formally hypothesized.

Smith-Vaniz and Springer (1971:20) suggested that *Scartichthys* might be congeneric with *Cirripectes*, but deferred combining them until more detailed studies were made. Their statement (1971:20) about the relationship between these two genera is inconsistent with statements made elsewhere in their paper. They suggested (1971:24) that *Exallias* appeared to be most closely related to *Cirripectes* and (1971:36) that *Ophioblennius* appeared to be most closely related to *Scartichthys*. Later in the paper (their figure 51), they suggested that *Cirripectes* and *Scartichthys* are sister groups, which are together the sister group of *Exallias*, and that these three genera together form the sister group of *Pereulixia*. *Ophioblennius* is then shown as the sister group of all of these genera. This confusion concerning the relationships among these genera illustrates the need for a complete and thorough analysis of their interrelationships.

HISTORICAL TREATMENT OF THE BLENNIIDAE

This discussion is presented to give a framework for the following phylogenetic discussion.

Springer (1968a) reviewed the literature dealing with classification of the Blenniidae. He cited numerous studies of higher level (family or above) relationships, but noted that Norman (1943) provided the only comprehensive intrafamilial classification. Norman (1943) recognized three blenniid subfamilies: Ophioblenniinae, Blenniinae, and Salariae. Springer

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Review Chairman: James G. Mead, Smithsonian Institution. Reviewers: William F. Smith-Vaniz, Academy of Natural Sciences, Philadelphia; Richard Winterbottom, Royal Ontario Museum, Canada.

TABLE 1.—Nominal species of *Scartichthys* with author, publication date, and current identifications (arrangement is alphabetical by species name).

Species	Current identification
<i>Salarias concolor</i> Philippi, 1896	<i>viridis</i>
<i>Scartichthys crapulatus</i> , new species	<i>crapulatus</i>
<i>Salarias cuvieri</i> Günther, 1861	<i>viridis</i>
<i>Salarias eques</i> Steindachner, 1898	<i>gigas</i>
<i>Ophioblennius fernandezensis</i> Clark, 1938	<i>variolatus</i>
<i>Salarias gigas</i> Steindachner, 1876	<i>gigas</i>
<i>Ophioblennius mazorkae</i> Hildebrand, 1946	<i>gigas</i>
<i>Salarias modestus</i> Philippi, 1896	<i>viridis</i>
<i>Salarias petersoni</i> Fowler, 1940	<i>viridis</i>
<i>Salarias rubropunctatus</i> Valenciennes in Cuvier and Valenciennes, 1836	<i>variolatus</i>
<i>Blennophis semifasciatus</i> Kner and Steindachner, 1866	<i>viridis</i>
<i>Salarias variolatus</i> Valenciennes in Cuvier and Valenciennes, 1836	<i>variolatus</i>
<i>Salarias viridis</i> Valenciennes in Cuvier and Valenciennes, 1836	<i>viridis</i>
<i>Ophioblennius xiphodon</i> Clark, 1938	<i>gigas</i>

(1968a) split Norman's Blenniinae into the subfamily Blenniinae, comprised of the tribes Salariini, Blenniini, and Omobranchini, and the subfamily Nemophidinae and noted that Norman's Ophioblenniinae was based on larval stage individuals belonging to several different genera, all but one of which (*Somersia*, now placed in the Labrisomidae) he placed in the tribe Salariini. Springer and Smith-Vaniz (1972) chose not to recognize blenniid subfamilies, preferring instead to recognize five tribes in the family Blenniidae (Blenniini, Salariini, Omobranchini, Nemophini, and Phenablenniini). These tribes are not equivalent to the previously mentioned subfamilies. Springer (1968a:51) proposed that *Blennius* was most closely related to the Omobranchini and Nemophini line. Smith-Vaniz (1976:153), noting that the Blenniini of Springer and Smith-Vaniz (1972) was polyphyletic, removed *Blennius* (which would be the true Blenniini) from the Blenniini, and hypothesized a sister group relationship between *Blennius* and a group comprised of the tribes Omobranchini, Phenablenniini, and Nemophini. Smith-Vaniz (1976) did not propose a hypothesis for the relationship of his monophyletic group (*Blennius* + Omobranchini + Phenablenniini + Nemophini) to the remaining members of the Blenniidae, leaving the relationships of the Salariini and the "Blenniini" unresolved (his figure 88).

In his revision of the tribe Blenniini, Bath (1977:177) commented on the sutured dentaries of *Blennius* but retained it in the tribe Blenniini. Among blenniids, sutured dentaries occur only in *Blennius*, Omobranchini, Phenablenniini, and Nemophini and their presence is a synapomorphy of that group. Bath (1977:213) stated that the tribe was defined by a group of unspecialized characters, thus leaving open the possibility that it was not a natural group.

Springer (1968a:51) stated that the Salariini were either offshoots of the Blenniini or shared a common ancestor with them. Smith-Vaniz and Springer (1971:5) and Springer and

Smith-Vaniz (1972) proposed a close relationship between the tribes Salariini and Blenniini, but did not specify any distinctive characters to support that hypothesis.

Bock and Zander (1986) restricted the tribe Blenniini to the three species they recognized in the genus *Blennius*. All other genera previously included in the Blenniini were assigned to a new tribe, the Parablenniini. Although they provided a name for this problematical group of genera, they did not give any characters that establish the Parablenniini as a monophyletic group. They stated (1968:138) that the Parablenniini "possesses strong relationships to the tribe Salariini," but gave no derived characters to support this hypothesis of relationship. These two tribes were related on the basis of the common possession of unsutured dentaries, a plesiomorphic character.

Smith-Vaniz and Springer (1971:5) provided data supporting the monophyletic nature of the tribe Salariini and discussed in detail the nature of the dentition and jaws. Although the lateral portions of the premaxillary capsule are enclosed in certain genera, all genera of the Salariini share a unique condition in which at least the mesial portion of each premaxilla is an open capsule (i.e., no anteroventral wall of bone). Smith-Vaniz and Springer (1971) diagnosed all genera they recognized in the Salariini and presented their partially intuitive, partially character-based concept of the relationships among the genera in a dendrogram (Smith-Vaniz and Springer, 1971, fig. 51).

METHODS

TAXONOMIC METHODS.—Counts follow Smith-Vaniz and Springer (1971) except as follows: number of vertebrae are presented as a formula, precaudal + caudal = total vertebrae; position of the last three anal-fin pterygiophores is given as a formula representing the number of pterygiophores occupying the last three pterygiophore-occupied interhemal spaces (1-1-2 means there is 1 pterygiophore in each of the 2 anterior spaces and 2 in the last space); nuchal cirri, supraorbital cirri, and nasal cirri counts include all free tips (total of both sides); number of lateral line (LL) tubes includes only unconnected, bipored tubes on the left side (tubes begin at the end of the continuous part of the LL canal); gill raker counts are of the total number of rakers on the first arch; counts of premaxillary and dentary incisors are approximate due to the difficulty of counting these tiny teeth. Counts of the rays of the median fins and characters associated with the vertebral column (i.e., pleural ribs, epipleural ribs, etc.) were taken from radiographs. When the last anal-fin ray was split through its base, yet borne on one pterygiophore, it was counted as 1.

A pore position in a sensory pore series refers to all pores that can be traced back to a single branch from one of the main sensory canals of the cephalic lateralis system (a single position may have from 1 to more than 20 pores).

Species accounts are arranged alphabetically by species. In the "Material Examined" sections, the arrangement is as follows: for type specimens, register number followed by

TABLE 2.—Material used for osteological studies (SL in mm).

Species	Catalog no.	No. of specimens: SL	Species	Catalog no.	No of specimens: SL
	DACTYLOSCOPIIDAE				
<i>Dactylagnus mundus</i>	USNM 200385	(2: 89, 92)	<i>Cirripectes stigmaticus</i>	USNM 223457	(2: 74, 76)
	USNM 270277	(1: 35)	<i>Cirripectes vanderbilti</i>	USNM 142114	(2: 62, 63)
	USNM 270365	(2: 33, 40)	<i>Cirripectes variolosus</i>	USNM 200614	(3: 48–53)
<i>Dactyloscopus crossotus</i>	USNM 270360	(2: 39, 52)	<i>Crossosalarias macrospilus</i>	USNM 205711	(1: 60)
<i>Dactyloscopus tridigitatus</i>	USNM 269550	(2: 45, 47)	<i>Ecsenius bicolor</i>	USNM 211914	(2: 46, 50)
	TRIPTERYGIIDAE		<i>Ecsenius yaeyamaensis</i>	USNM 211924	(2: 34, 45)
<i>Enneanectes altivelis</i>	UF 16179	(2: 26, 29)	<i>Entomacrodus cymatobiotus</i>	USNM 198654	(2: 37, 40)
	CHAENOPSIDAE		<i>Entomacrodus epalzeochilus</i>	USNM 269464	(1: 55, 90)
<i>Hemiblemaria simulus</i>	UF 19112	(1: 65)	<i>Entomacrodus nigricans</i>	UF 17048	(2: 49, 52)
<i>Acanthemblemaria aspera</i>	UF 11881	(2: 22, 27)	<i>Entomacrodus stellifer</i>	USNM 132795	(1: 45)
<i>Emblemariopsis signifera</i>	UF 47329	(1: 22)	<i>Exallias brevis</i>	USNM 224383	(2: 71, 80)
	CLINIDAE			USNM 200544	(1: 39)
<i>Gibbonsia elegans eroli</i>	USNM 200386	(2: 64, 104)	<i>Hirculops cornifer</i>	USNM 200030	(3: 34–47)
	LABRISOMIDAE		<i>Istiblennius gibbifrons</i>	USNM 228313	(2: 74, 82)
<i>Paraclinus nigripinnis</i>	UF 47330	(1: 39)	<i>Istiblennius lineatus</i>	UF 47332	(1: 70)
<i>Labrisomus nuchipinnis</i>	UF 47331	(1: 87)	<i>Litobranchus fowleri</i>	USNM 227798	(1: 29)
	BLENNIIDAE		<i>Mimoblennius atrocinctus</i>	USNM 197980	(1: 22)
	Blenniini			USNM 216676	(2: 24, 25)
<i>Blennius normani</i>	USNM 199533	(2: 57, 57)	<i>Nannosalarias nativitatus</i>	USNM 201369	(1: 33)
<i>Blennius ocellaris</i>	USNM 48387	(1: 111)	<i>Ophioblennius atlanticus</i>	UF 10746	(2: 69, 74)
	USNM 205157	(1: 59)	<i>macclurei</i>		
	Salarini		<i>Pereulixia kosiensis</i>	USNM 197637	(1: 101)
<i>Alloblennius pictus</i>	USNM 203766	(2: 28, 35)	<i>Praealticus</i> sp.	USNM 228318	(2: 74, 78)
<i>Alticus alticus</i>	USNM 227848	(2: 58, 68)	<i>Rhabdoblennius snowi</i>	USNM 228315	(2: 40, 47)
<i>Andamia reyi</i>	USNM 227797	(2: 56, 66)	<i>Salarias fasciatus</i>	UF 47654	(1: 81)
<i>Antennablennius bifilum</i>	USNM 200207	(2: 51, 54)	<i>Scartichthys crapulatus</i>	SIO 87, 140	(1: 82)
<i>Atrosalarias fuscus</i>	USNM 227555	(2: 62, 73)	<i>Scartichthys gigas</i>	USNM 200396	(2: 40, 43)
<i>Cirripectes castaneus</i>	USNM 228189	(2: 64, 81)		USNM 227556	(2: 92, 101)
<i>Cirripectes chelomatus</i>	USNM 258751	(2: 79, 85)		USNM 227981	(2: 103, 116)
<i>Cirripectes filamentosus</i>	USNM 228108	(2: 48, 51)	<i>Scartichthys variolatus</i>	USNM 258770	(3: 47–111)
<i>Cirripectes fuscoguttatus</i>	USNM 198700	(1: 77)	<i>Scartichthys viridis</i>	USNM 258788	(4: 92–141)
	USNM 200612	(1: 66)	<i>Stanulus seychellensis</i>	USNM 228316	(2: 21, 25)
	USNM 227867	(1: 95)			
<i>Cirripectes gilberti</i>	ROM 46597	(1: 79)		Nemophini	
<i>Cirripectes imitator</i>	USNM 227980	(1: 83)	<i>Meiacanthus grammistes</i>	USNM 201363	(1: 59)
<i>Cirripectes jenningsi</i>	USNM 200615	(5: 54, 74)			
<i>Cirripectes obscurus</i>	BPBM 30990	(2: 69, 74)		Omobranchini	
<i>Cirripectes perustus</i>	ROM 46594	(1: 63)	<i>Enchelyurus kraussi</i>	USNM 200609	(1: 29)
<i>Cirripectes polyzona</i>	USNM 227688	(2: 50, 51)	<i>Omobranchus punctatus</i>	USNM 174330	(1: 46)
<i>Cirripectes quagga</i>	USNM 111603	(4: 43, 53)			
	USNM 198751	(2: 63, 70)		Phenablenniini	
	USNM 200605	(2: 38, 54)	<i>Phenablennius heyligeri</i>	USNM 205384	(1: 43)
<i>Cirripectes randalli</i>	BPBM 20165	(1: 77)			
<i>Cirripectes springeri</i>	USNM 228287	(1: 70)		Parablenniini	
	USNM 228294	(1: 51)	<i>Chasmodes bosquianus</i>	UF 28296	(1: 54)
			<i>bosquianus</i>		
			<i>Chasmodes bosquianus</i>	USA 6005	(3: 27–70)
			<i>longimaxilla</i>		
			<i>Chasmodes saburrae</i>	UF 47333	(2: 47, 49)
			<i>Hypoleurochilus geminatus</i>	UF 19621	(1: 78)
			<i>Hypsoblennius hentzi</i>	UF 2584	(1: 82)
			<i>Parablennius marmoreus</i>	UF 11021	(2: 39, 52)
			<i>Scartella cristata</i>	UF 11020	(2: 56, 70)

number of specimens and standard length in parentheses, type status, and collection locality; for nontype material, general locality is followed by register number with the number of specimens in parentheses (standard length in mm is included for those specimens used to obtain meristic and other data).

Specimens used for osteological examination (Table 2) were prepared by clearing and counter-staining with Alizarin-red S and Alcian blue following the method of Dingerkus and Uhler (1977).

I follow Clark (1986:142) in the use of "homoplastic" as the corresponding adjective of the noun "homoplasy."

Institutional abbreviations used in listings of material examined are HL, head length; LL, lateral line; SL, standard length.

METHODS OF PHYLOGENETIC ANALYSIS.—Procedures used to determine relationships between taxa follow the general principles of Hennig (1966). Only monophyletic groups (i.e., a group that includes all descendants and only descendants of a

hypothetical common ancestor) are recognized as valid taxonomic units. Each monophyletic group is diagnosed by shared derived characters (synapomorphies). Polarity of each character (i.e., the character state to which the character is assumed to have evolved in the taxa being analyzed) is determined by outgroup analysis (Maddison et al., 1984). The principle of parsimony is used to resolve cases where derived (apomorphic) characters support conflicting hypotheses of relationship (i.e., homoplastic characters). Although evolution may not proceed in accordance with the principle of parsimony, this approach minimizes the number of assumptions that must be made to explain character transformations.

The result of a phylogenetic analysis is a hierarchical arrangement of increasingly inclusive monophyletic groups. This arrangement, usually illustrated as a branching diagram (cladogram), provides a hypothesis of the phylogenetic relationships of the taxa analyzed. The phylogenetic method is the preferred technique for this study as it provides a clear

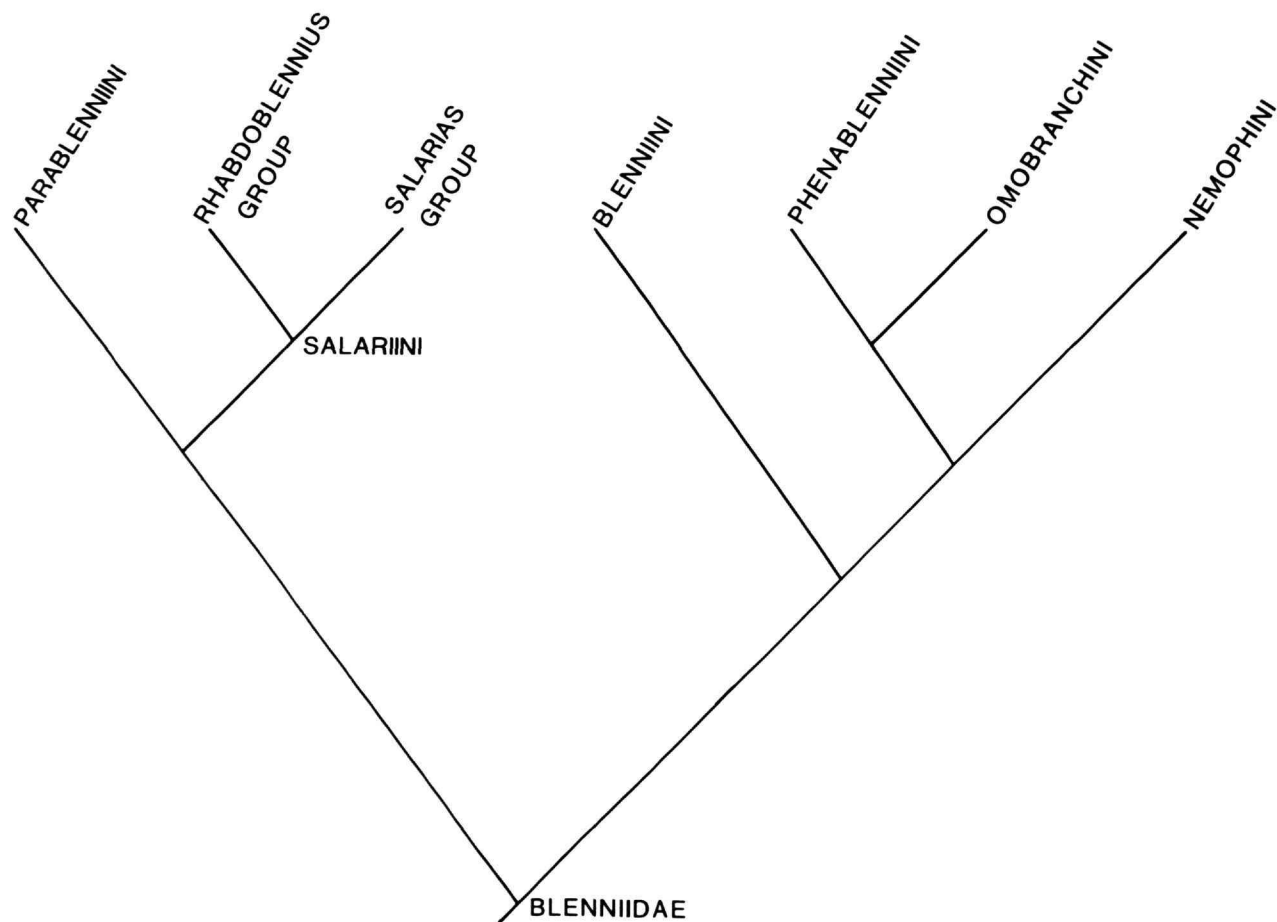


FIGURE 1.—Preliminary hypothesis of the relationships among the blenniid tribes.

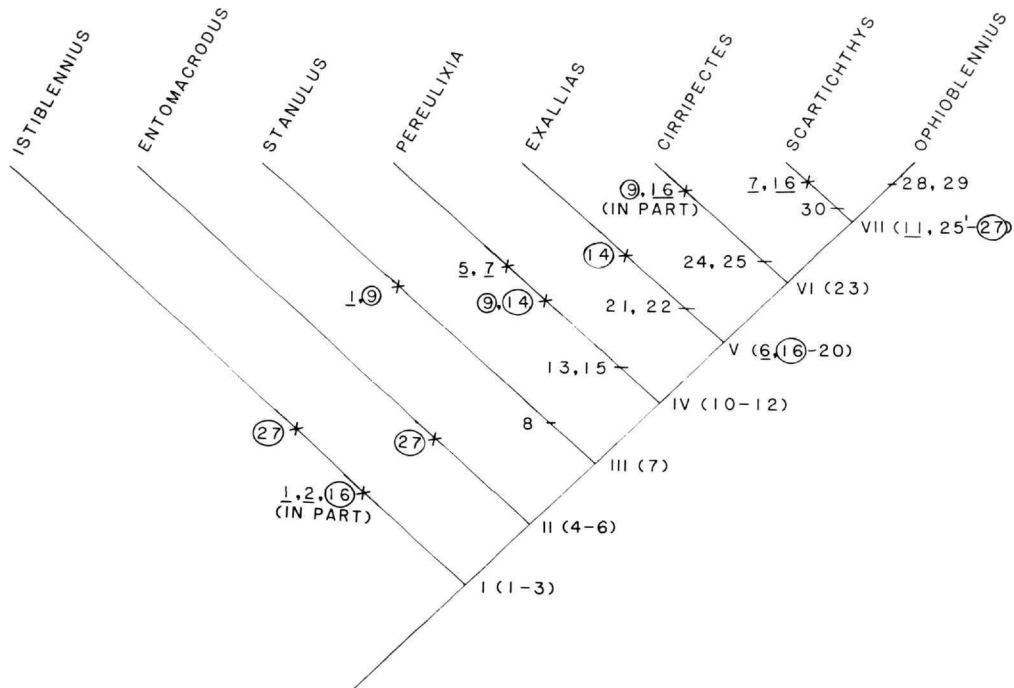


FIGURE 2.—Cladogram depicting the relationships of *Scartichthys* and related genera in the Salarini. Roman numerals indicate nodes, arabic numerals indicate apomorphic characters, and * indicates homoplastic characters (underlined characters are interpreted as reversals, circled characters as independent derivations). Apomorphic characters: 1 = last pleural ribs on caudal vertebra; 2 = terminal anal pterygiophore with two rays; 3 = ophioblennius larvae with two hooked canines on middle of dentary; 4 = males with fleshy anal rugosities; 5 = posterior branchiostegal ray with elongate head; 6 = vomerine teeth present; 7 = large foramen in infrapharyngobranchial plate; 8 = ophioblennius larva with short, robust body; 9 = scale-like flaps on lateral line; 10 = transverse row of nuchal cirri across nape; 11 = premaxillary bone with symphyseal spur; 12 = lacrimal with long slender flange; 13 = nuchal cirri in four overlapping groups; 14 = dentary teeth two to three times as broad as premaxillary teeth; 15 = large crest on skull; 16 = dorsal-fin membrane attached to caudal fin; 17 = fourth epibranchial with two distinct processes; 18 = fifth ceratobranchial with expanded posteroventral flange; 19 = ophioblennius larvae with two to four hooked premaxillary canines; 20 = ophioblennius larvae with two to four hooked dentary symphyseal canines; 21 = lateral cirri progressively shorter than nape cirri; 22 = no dentary canines; 23 = large maxillary prominence; 24 = nuchal cirri in two to four groups of equal length cirri without overlapping bases; 25 = male genital papilla with one or two long filaments; 25' = male genital papilla with two short protuberances; 26 = nuchal cirri in two well-separated groups; 27 = caudal vertebrae 22-26; 28 = LL in two overlapping sections; 29 = greatly elongate dentary canines; 30 = LL tubes 18-21.

groupings outside the assemblage of Figure 2 are shown in Figure 1, but there are relatively few characters used to form the latter phylogenetic hypothesis. The cladogram in Figure 1 will help the reader follow my arguments in the text.

The primary goal of this section is to provide a working phylogenetic hypothesis of blennioid relationships in general and the intergeneric relationships of the genus *Scartichthys* in particular, and should be considered a first step in the dynamic process of phylogenetic analysis.

Family BLENNIIDAE

Springer (1968a) provided an extensive osteological description of the family Blenniidae, based primarily on *Entomacro-*

dus nigricans (Gill). He also discussed three derived characters that distinguish the Blenniidae from all other blennioids: (1) coracoid reduced and fused to cleithrum; (2) distinctive relationship of the interopercle with the epiphyal (= posterior ceratohyal) and interhyal; and (3) distinctive premaxillary and dentary dentition of adults.

In addition to those three characters, the monophyly of the Blenniidae is supported by two other shared derived characters. The first is a distinctive form of the urohyal and its relationship with the dorsal and ventral hypohyals, conditions not found in any other blennioids. The blennioid urohyal has two lateral projections (one dorsal and one ventral) on each side (Figure 3), each with a strong ligamentous attachment to its respective hypohyal(s). There is variation in the positioning of the lateral

projections among the blenniid tribes, but all members have this distinctive urohyal and its association with the hypohyals.

The other derived character shared by the Blenniidae is the presence of fleshy rugosities on the anal-fin spines of adult males. As anal-fin spine rugosities are not found in other blennioid (sensu George and Springer, 1981:4), or perciform fishes, the presence of these fleshy rugosities is hypothesized to be an apomorphic condition. The Omobranchini-Phenablenniini group of Smith-Vaniz (1976) and certain genera of the Salariaiini are the only Blenniidae not having anal-fin spine rugosities. The most parsimonious explanation (based on Smith-Vaniz's (1976, fig. 88) cladogram, as modified in the following discussion of the Salariaiini-Parablenniini group) of this character's distribution among blenniid taxa is that the absence of anal-fin spine rugosities represents two independent reversals (losses), one in the Omobranchini-Phenablenniini group and one in the ancestral line giving rise to the Salariaiini, with a secondary derivation of the rugosities in one lineage within the Salariaiini.

SALARIINI-PARABLENNIINI Group

Springer (1968a) and Smith-Vaniz and Springer (1971) proposed a close relationship between the Salariaiini and Blenniini, but did not provide a character to support this relationship. I follow Smith-Vaniz (1976) in separating *Blennius*, which is now the only member of the true Blenniini, from the remaining genera of the tribe, which I will refer to as the Parablenniini. A thorough study of the Parablenniini is needed to determine whether it is monophyletic (see "Parablenniini" below for two possible synapomorphies for the tribe).

The hypothesized sister-group relationship between the Parablenniini and Salariaiini is supported by two apparent synapomorphies: (1) premaxillary ascending process only weakly attached to main body of bone, and (2) 2-0-2 pectoral radial formula (the formula is presented as the number of radials on the scapula—number of radials attached to the coracoid and the scapula—number of radials borne on the coracoid; remember that the coracoid is completely fused to the cleithrum in blenniids).

Springer (1968a:30) stated that the blenniid ascending process was weakly joined (ossified connection) at two points, anteriorly and posteriorly, to the ventral portion of the premaxilla. Although this is true of the Salariaiini-Parablenniini line, other blenniids and blennioids have the entire base of the ascending process weakly or strongly connected by bone to the main body of the premaxilla. The ascending process of the premaxilla in the Parablenniini and Salariaiini has an ossified connection to the main body of the bone only at the anteriormost and posteriormost edges, while the middle part is loosely attached by connective tissue as a further reduction of those attachments. The ascending process is an independent ossification in *Pereulixia* and *Scartichthys*, where the anterior and posterior connections to the main body of the premaxilla

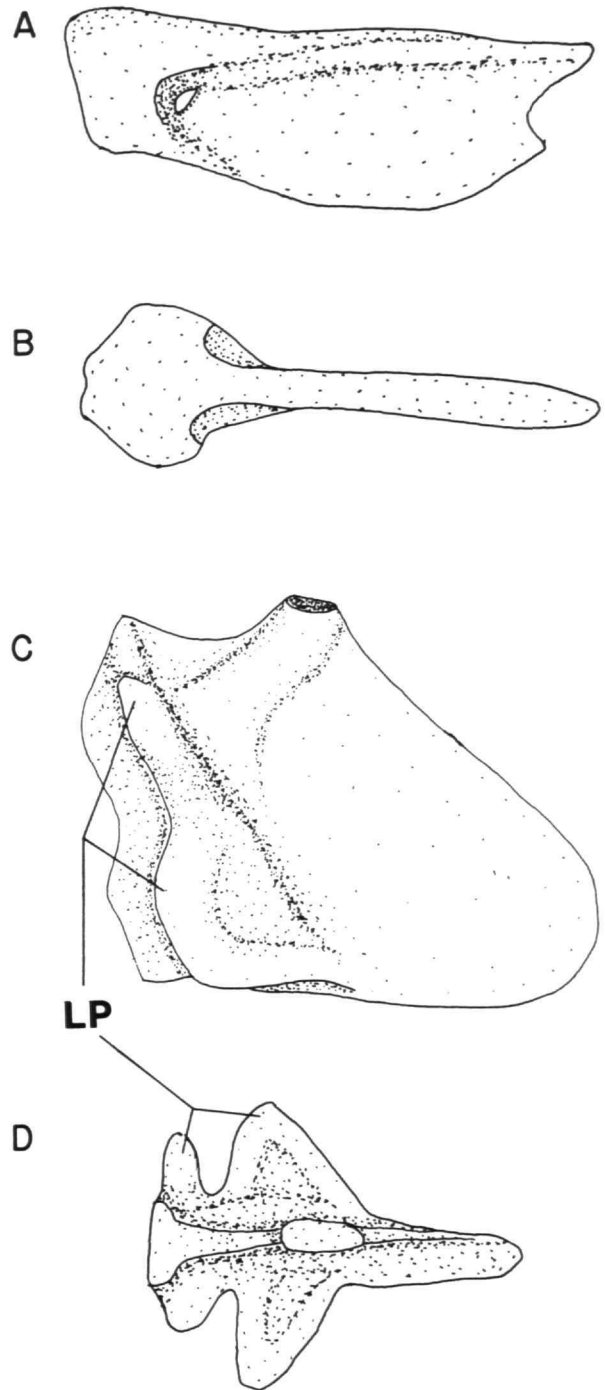


FIGURE 3.—Urohyal bone (anterior toward left): A and C, left lateral views; B and D, dorsal views; A and B, no developed lateral processes (*Acanthemblemaria aspera*); C and D, well-developed lateral processes (*Chasmodes saburrae*). (LP = lateral process.)

have been replaced by connective tissue (process is independent in both juveniles and 120 mm SL adults of the later genus). *Alticus* and *Praealticus* have an intermediate condition in that a bony anterior connection has been lost, but the posterior connection has been retained.

Springer (1968a:60) hypothesized that the most primitive pectoral radial formula for blenniids is 2-1-1 (occurs in most Tripterygiidae, Chaenopsidae, Labrisomidae, and Clinidae; some species of the last two families have 3-0-1) and that the "evolutionary trend" (i.e., increasingly derived condition) is a decrease in the number of radials attached to the scapula by a downward movement (in an evolutionary context) of the radials. Therefore, the 2-0-2 formula (shared by most Salariaiini and Parablenniini) is considered to be a derived condition. Some members of both tribes have the 2-1-1 formula, which I interpret as a secondary reversion to the 2-1-1 condition based on the presence of other derived characters in these taxa that they share with other Parablenniini and Salariaiini. Further derived formulas are exhibited by the Nemophini and Omobranchini, which have 1-1-2, and the Phenablenniini, which has 1-0-3.

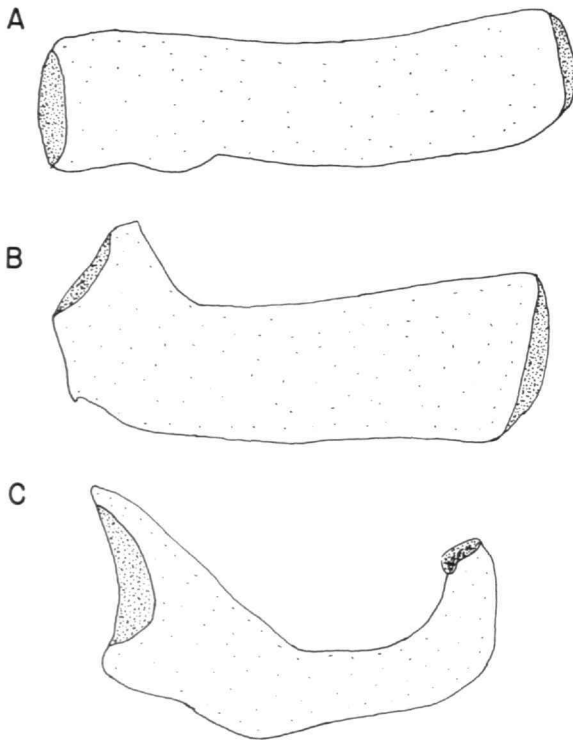


FIGURE 4.—Left lateral view of basibranchial bone (anterior toward left; dense stippling indicates cartilage): A, plesiomorphic rod-shape structure (*Cirripectes filamentosus*); B, slightly upturned anterior end (*Atrosalarias fuscus*); C, derived shallow U-shape of Parablenniini (*Chasmodes saburrae*).

PARABLENNIINI

The Parablenniini referred to here comprises those genera included in the tribe by Bath (1977), but excluding *Blennius*.

Monophyly of the Parablenniini is supported by two synapomorphies. The first character is the first basibranchial shaped like a broad, shallow U, curving downward between the posterior end of the basihyal and the anteroventral edge of the second basibranchial (Figure 4C). I have not found a similarly shaped basibranchial in any other blennioids examined and consider this condition as derived. In most other blenniid genera the basibranchial is straight in lateral aspect (Figure 4A), and in a few (*Istiblennius*, *Antennablennius*, *Atrosalarias*, *Ecsenius*, *Entomacrodus*, and *Litobranchus*) the anterior end is slightly upturned (Figure 4B).

The second character uniting the Parablenniini is a distinctively shaped fourth epibranchial bone (Figure 5B). The parablenniin fourth epibranchial is a relatively smooth bone with a flattened longitudinal bony flange projecting dorsally from the lateral half of the shaft of the bone. All other blennioids examined have a fourth epibranchial bone with one or two dorsally directed bony projections situated dorsally on the shaft slightly before the articulation of the epibranchial shaft with the infrapharyngobranchial plate (Figure 5A,C). These projections are lacking in the Parablenniini.

These characters have been examined in only a small percentage of parablenniin species. Thus, this hypothesis of monophyly for the tribe needs to be further tested.

SALARIINI

Two characters support monophyly of the Salariaiini: (1) premaxilla an open capsule and (2) distinctively shaped infrapharyngobranchial plate (Figure 6F-K). The first character was discussed in detail by Smith-Vaniz and Springer (1971:5, figs. 2-4). The highly modified premaxilla of the Salariaiini has a band of connective tissue in place of the anteroventral bony wall present in all other blennioid fishes.

The infrapharyngobranchial plate of the Salariaiini has a broad, flattened bony flange projecting medially from the tooth-bearing portion of the bone (Figure 6F). This flange extends anteriorly to articulate with the medial tip of the second epibranchial. In the immediate outgroup (Figure 1), Parablenniini (Figure 6C), all other groups in the family Blenniidae (Figure 6D and E), and in the family Tripterygiidae (Figure 6A) the infrapharyngobranchial plate is composed primarily of a broad tooth-bearing portion with a narrow medial flange of bone that has an anterior protuberance articulating with the second epibranchial. The families Dactyloscopidae, Chaenopsidae, Clinidae, and Labrisomidae also have an infrapharyngobranchial plate with a large bony flange projecting anteromedially from the tooth-bearing portion (Figure 6B), but the lateral edge of the flange is developed as a rod-shaped cartilaginous swelling, which is probably a synapomorphy of

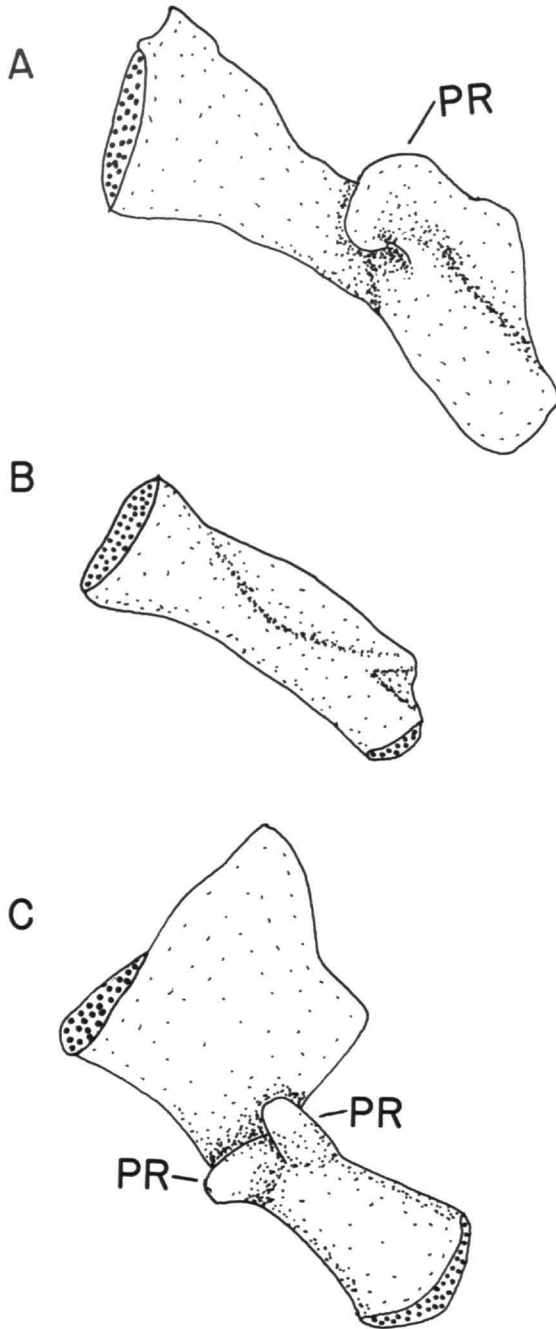


FIGURE 5.—Left dorsolateral view of fourth epibranchial bone (anterior toward left; large stipples indicate cartilage): A, single, broad, mid-shaft process (*Atrosalarias fuscus*); B, no mid-shaft process (*Chasmodes saburrae*); C, two mid-shaft processes (*Cirripectes filamentosus*). (PR = mid-shaft process.)

these families. The expanded bony flange appears to have developed independently in the two groups and, thus, is considered a synapomorphy of the Saliariini.

I recognize two major groups within the Saliariini, which I refer to as the Salaris group and the Rhabdoblennius group.

Salaris Group

The Salaris group comprises the genera *Ecsenius*, *Andamia*, *Alticus*, *Dodekablennios*, *Praealticus*, *Istiblennius*, *Ophioblennius*, *Pereulixia*, *Exallias*, *Cirripectes*, *Scartichthys*, *Stanulus*, *Entomacrodus*, *Nannosalarias*, *Crossosalarias*, *Atrosalarias*, *Salaris*, and *Glyptoparus*. Representatives of these genera have a highly modified dentary (Smith-Vaniz and Springer, 1971:5, fig. 5) that forms an open capsule as a result of the loss of the anterodorsal bony wall. The anterodorsal bony wall of the dentary is present in all other blennioid fishes, but is only poorly developed (Smith-Vaniz and Springer, 1971, fig. 6) in two genera, *Hirculops* and *Rhabdoblennius*, of the Rhabdoblennius group. With the exception of 1 of 46 species of *Ecsenius* (see V.G. Springer, 1988:1), members of the Salaris group have a very high number of premaxillary teeth (55 to almost 400, but only four genera with fewer than 100) and dentary teeth (39 to about 300) as adults (Smith-Vaniz and Springer, 1971, table 2). The remaining salariini genera have 17–50 premaxillary teeth and 16–38 dentary teeth. All other blenniids typically have tooth counts less than or in the lower end of the range found in the Saliariini. Although the presence of a high number of teeth is difficult to interpret phylogenetically, no other blennioid fishes have such a high number of teeth and I tentatively accept the high numbers as derived for this group.

The relationships of the remaining salariini genera (the Rhabdoblennius group), *Cirrisalarias*, *Medusablennius*, *Mimoblennius*, *Litobranchius*, *Antennablennius*, *Alloblennius*, *Hirculops*, and *Rhabdoblennius*, are unresolved, although Bath (1983, fig. 27) recognized *Hirculops* and *Rhabdoblennius* as a monophyletic group that together form the sister group to *Mimoblennius*, *Alloblennius*, and *Antennablennius*, which were associated in an unresolved trichotomy. The occurrence of lower tooth counts in these genera than in the Salaris group cannot be used to infer relationships, as this is the plesiomorphic condition. It is not known whether the Rhabdoblennius group is monophyletic. A comprehensive analysis of the interrelationships of all salariini genera is needed.

Node I Group

Although generic interrelationships within the Salaris group are unresolved, the genera referred to here as the node I group appear to represent a monophyletic unit. Relationships within the node I group are presented in the cladogram in Figure 2 (synapomorphies are numbered in the text to correspond with the numbered synapomorphies of Figure 2).

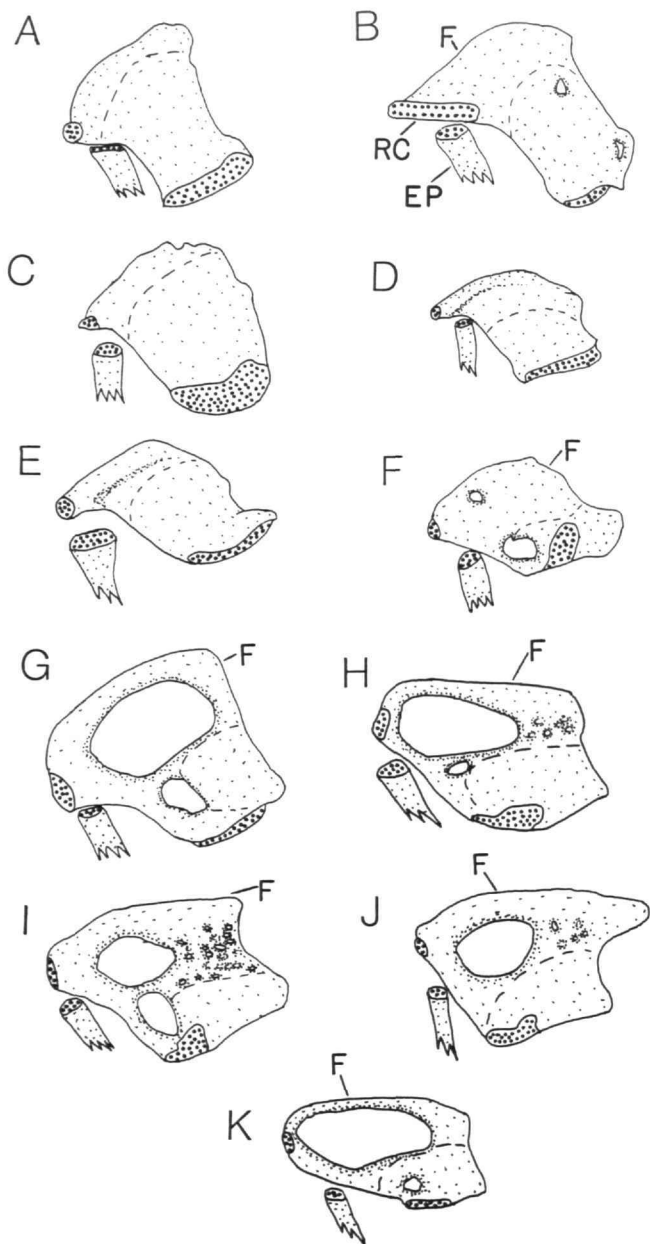


FIGURE 6.—Dorsolateral view of left infrapharyngobranchial plate (anterior toward left): A, *Enneanectes altivelis*; B, *Acanthemblemaria aspera*; C, *Chasmodes saburrae*; D, *Omobranchus punctatus*; E, *Meiacanthus grammistes*; F, *Atrosalarias fuscus*; G, *Stanulus seychellensis*; H, *Ophioblennius atlanticus*; I, *Cirripectes perustus*; J, *Cirripectes polyzona*; K, *Cirripectes quagga*. (Dashed line indicates anteriormost limit of tooth-bearing portion of bone; large stipples indicate cartilage; EP = second epibranchial; F = medial flange; RC = rod-shaped cartilage.)

Monophyly for this group, comprising the genera *Istiblennius*, *Entomacrodus*, *Stanulus*, *Pereulixia*, *Exallias*, *Cirripectes*, *Scartichthys*, and *Ophioblennius*, is supported by three derived characters at node I.

1. Last pleural ribs borne on first or second caudal vertebral centrum (usually centrum 11 or 12).

The node I group, with the exception of *Stanulus*, consistently has the last pleural ribs borne on the first or second caudal vertebra. *Stanulus* (some specimens rarely have them on the first caudal vertebra), the Parablenniini, and other blenniids typically have the last pleural ribs borne on the last precaudal vertebra. Among other salariini genera, only *Alticus*, *Atrosalarias*, and *Salarias* contain one or more species that usually have the last pleural ribs borne on a caudal vertebra, but each of these genera also has members with the last pleural ribs borne on a precaudal vertebra. *Dodekablennios* (of the *Salarias* group) also has the last pleural ribs borne on a caudal vertebra and may be the sister group to the node I group, but the unavailability of cleared and stained material leaves its status uncertain. Presence of the last pleural ribs on a caudal vertebra is considered apomorphic, whereas their presence on a precaudal vertebra is plesiomorphic. Although *Stanulus* typically has the last pleural ribs on the last precaudal vertebra (Springer, 1968b:112), additional characters at node II support its inclusion in this clade on the basis of parsimony. Some species of *Istiblennius* have the last pleural ribs borne on a precaudal vertebra. This and other characters suggest that *Istiblennius*, as presently defined, may be polyphyletic. A complete revision of *Istiblennius* is needed to define its limits.

2. Terminal anal pterygiophore bearing two rays.

Springer (1968a:58) noted the presence of two rays on the terminal anal proximal pterygiophore (= pterygiophore in the following discussion) of these genera. Although Smith-Vaniz and Springer (1971:71) stated that *Praealticus* "frequently" has the last anal-fin ray divided through the base, I found this to be a rare and probably exceptional condition in *Praealticus*. *Istiblennius* shows variation in this character that appears to be species specific. Many *Istiblennius* species have the last two anal-fin rays on one pterygiophore, whereas other species have the last two rays borne on separate pterygiophores. Most genera in the node I group show some variation in this character, as discussed by Springer (1967:5), but they usually have the last anal pterygiophore bearing two distinct rays. Other blenniids and many blennioids (including the Chaenopsidae, Labrisomidae, and Ophiclinini) have the last anal pterygiophore bearing a single ray. The presence of two rays on the last anal pterygiophore is considered the derived condition for blennioid fishes, and supports monophyly for the node I group. I should note that a last anal-fin ray split to its base is plesiomorphic for the Perciformes. Among blennioids, at least the Blenniidae (except the node I group) and Chaenopsidae do not have the last ray split. The simplest explanation for the presence of the split

ray in the node I group is that it is a reversal and, thus, is apomorphic at this node.

3. Large recurved canine positioned midlaterally on each dentary of ophioblennius-stage larvae.

The ophioblennius-stage (= prejuvenile pelagic; Matarese et al., 1984:565) larvae of each of the genera in the node I group have two posterolaterally directed, large, recurved canines located about midlaterally on each dentary (larvae have not been found for *Pereulixia*). *Istiblennius* is problematical in that an ophioblennius larval stage (or any larval stage) is known only for members of the *I. gibbifrons* species complex (Smith-Vaniz and Springer, 1971:50) and for *I. zebra* (Matarese et al., 1984:570), but the hooked canines are present in larvae of both these taxa. If other *Istiblennius* species do not have these hooked canines at a similar stage of larval development, then the genus as presently defined may not be monophyletic. No other blennioid larvae possess these hooked canines midlaterally on each dentary. Larval Nemophini have large anterior canines in the jaws, but these teeth are not hooked. The prejuveniles of *Aspidontus* lack the anterior and midlateral canines (Smith-Vaniz, 1976:54), but have strongly hooked posterior canines (homologous to the posterior canines present in many other blennioid genera). The presence of hooked anterior and midlateral canines is considered a derived condition and is evidence for monophyly of the node I group. Although larval *Pereulixia* are not known, the presence of several additional characters (see node II and node IV discussions) places this genus in the node I group on the basis of parsimony.

Genus *Istiblennius* Whitley

The genus *Istiblennius* as defined by Smith-Vaniz and Springer (1971:25) (or some part of the genus including the *Istiblennius gibbifrons* species complex) appears to be the sister group of the remaining members of the node I group. I know of no character that supports a hypothesis of monophyly for the species included in *Istiblennius*. The genus is presently being revised by V.G. Springer and the author.

Node II Group

This group of genera (*Entomacrodus*, *Stanulus*, *Pereulixia*, *Exallias*, *Cirripectes*, *Scartichthys*, and *Ophioblennius*) shares three derived characters.

4. Each anal-fin spine of adult males enveloped in fleshy rugosity (bulbous mass of deeply folded skin).

The fleshy rugosities common to the node II group, occur elsewhere in the Salariai only in adult males of *Nannosalarias* (also a member of the *Salarias* group). As discussed in the section on the Blenniidae, the presence of fleshy rugosities is a synapomorphy of that family. Based on my hypothesis of

relationships within the Salariaiini, the occurrence of fleshy anal-fin spine rugosities in the node II group is most parsimoniously considered a secondary derivation because the rugosities have been lost in the basal Salariaiini. Inasmuch as the genera of the node II group and *Nannosalarias* do not exhibit other characters shared by the Parablenniini (the phylogenetically closest group having rugosities; Figure 1), the most parsimonious explanation is that this apomorphic character is secondarily derived in *Nannosalarias* and the node II group. Within the Salariai group, the rugosities appear to have been independently derived in *Nannosalarias*, which does not share the other characters defining the node I group. I thus interpret the presence of fleshy anal-fin spine rugosities as a synapomorphy of the node II group.

5. Posteriormost (sixth) branchiostegal ray with elongated proximal portion extending well onto anterior ceratohyal and passing dorsad of proximal end of preceding (fifth) branchiostegal ray (Figure 7C).

The sixth (= posteriormost) branchiostegal ray, although variously shaped among blennioid genera, has two distinctive conditions involving the degree of development of the proximal portion (herein referred to as the head) that overlaps the posterior and anterior ceratohyals: (1) head of posteriormost (sixth) and preceding (fifth) branchiostegal rays overlapping the posterior and anterior ceratohyals to the same degree (Figure 7A) or (2) head of sixth ray extending up to three to four times as far onto anterior ceratohyal as fifth ray (Figure 7C). Condition 1 is the typical condition found in other salariini and blennioid fishes and is considered the plesiomorphic state. The node II genera, except *Pereulixia*, which has condition 1, have condition 2. The most parsimonious explanation for the occurrence of condition 1 in *Pereulixia* is that it is a reversal to the plesiomorphic condition.

In condition 2, the elongate head of the sixth branchiostegal ray has an anterodorsally directed component projecting onto the anterior ceratohyal over the dorsal tip of the preceding ray(s) and a posterodorsally directed spur (Figure 7C), which sometimes extends along a slight groove in the posterior ceratohyal. There is a ligamentous connection of the elongate portion of the sixth branchiostegal head to the anterior and posterior ceratohyals. Condition 2 does not occur in other blennioid fishes and, thus, is considered a synapomorphy of the node II genera.

The head of the sixth branchiostegal ray in *Stanulus* is not as extensively developed as in the other node II genera. In *Stanulus*, the head is only slightly elongate in an anterodorsal direction, reaching a point just above the preceding (fifth) ray (Figure 7B). The species of *Stanulus* are typically of small body size, and the reduction in the length of the head of the sixth ray in *Stanulus* might be related to small body size. This condition is interpreted as being a reduction of condition 2.

6. Vomerine teeth present.

The genera *Entomacrodus*, *Stanulus*, and *Pereulixia* have

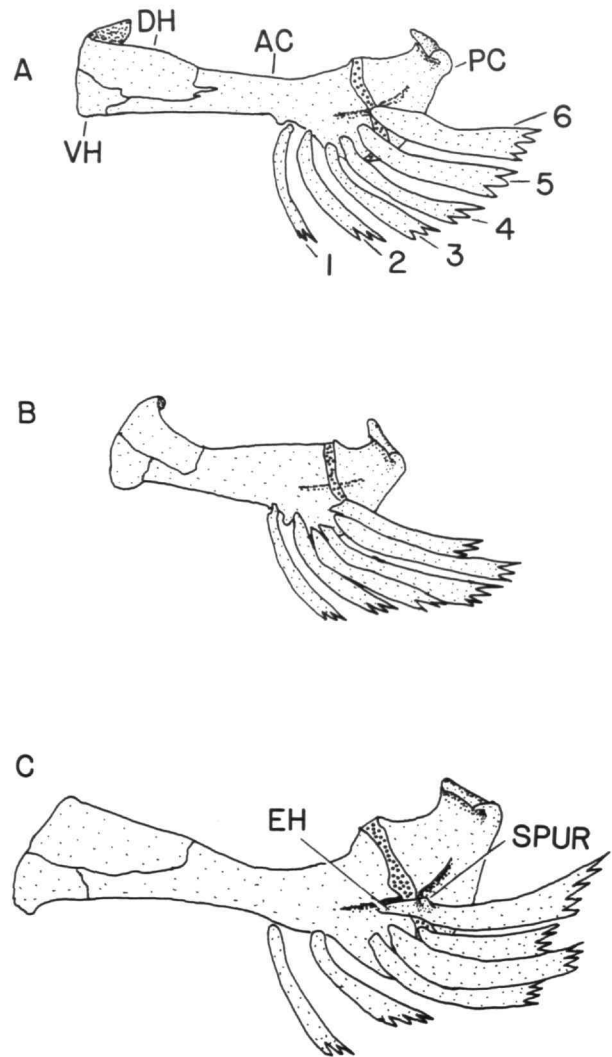


FIGURE 7.—Left lateral view of branchiostegals and associated bones (anterior toward left; large stipples indicate cartilage): A, fifth and sixth branchiostegal rays extending about equally onto ceratohyals (*Crossosalarias macrospilus*); B, sixth branchiostegal ray extending slightly dorsad of fifth (*Stanulus seychellensis*); C, sixth branchiostegal extending dorsad of and anterior to fifth (*Cirripectes perustus*). (AC = anterior ceratohyal; DH = dorsal hypohyal; EH = elongate head of sixth ray; PC = posterior ceratohyal; SPUR = posterodorsally directed spur on sixth ray; VH = ventral hypohyal.)

vomerine teeth, but the node V genera do not (hypothesized reversal at node V). The presence of vomerine teeth is homoplastic, occurring in other members of the Salariaiini (see below). I tentatively accept it as derived for the node II group.

Genus *Entomacrodus* Gill

I know of no uniquely derived character that will diagnose the genus *Entomacrodus* as a monophyletic taxon. *Entomacro-*

dus has vomerine teeth, but vomerine teeth are also present in *Pereulixia* and some *Stanulus* in the node I group, and elsewhere in the Salariaiini in some *Alticus*, some *Praealticus*, *Nannosalarias*, *Rhabdoblennius*, and *Hirculops*.

Smith-Vaniz and Springer (1971:23) and Springer (1967:12, 1968b:113) stated that *Entomacrodus* is most closely related to *Stanulus*, based on their similarity in overall appearance. I have found no synapomorphy to support this hypothesis.

Node III Group

This group comprises the genera *Stanulus*, *Pereulixia*, *Exallias*, *Cirripectes*, *Scartichthys*, and *Ophioblennius*. I have found only one character that defines this assemblage.

7. Infrapharyngobranchial bone with one or two large foramina (Figure 6G–K).

The anteromedially positioned flange of the infrapharyngobranchial plate (either a fused complex of one or more of

infrapharyngobranchial bones 2, 3, and 4, or a loss of one or two of these bones) has one or two large foramina, giving the bone a doughnut-shaped appearance (Figure 6G–K). This condition appears to be unique and defines these genera as a monophyletic group.

The infrapharyngobranchial plate of *Pereulixia* and *Scartichthys* is typical of other salariini genera (Figure 6F; see previous discussion for the Salariaiini) and does not show the large foramina, although there may be small foramina as in Figure 6F present in the other members of this group. The loss of the large foramina in *Pereulixia* and *Scartichthys* is interpreted, based on parsimony, as two independent reversals.

An equally parsimonious, alternative explanation is that the presence of the large foramen was independently derived in *Stanulus* and the node V taxa and secondarily lost in *Scartichthys*. This hypothesis results in the collapse of node III to node II forming an unresolved trichotomy among *Entomacrodus*, *Stanulus*, and the node IV group. I have not illustrated this alternative cladogram as it is easily visualized and does not

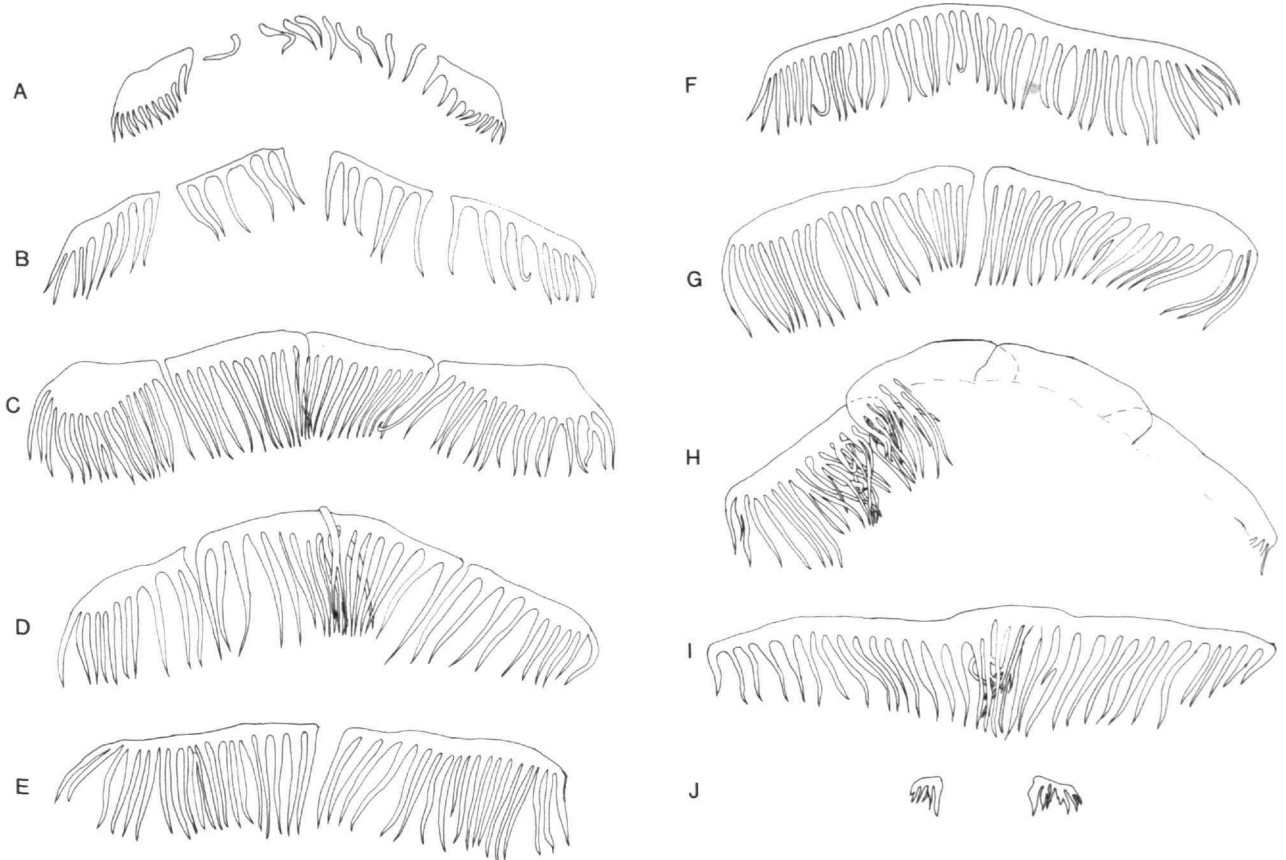


FIGURE 8.—Dorsal view of nuchal cirri (anterior toward top): A, type A, *Cirripectes kuwamurai*; B, type B, *C. variolosus*; C, type C, *C. gilberti*; D, type D, *C. perustus*; E, type E, *C. alboapicalis*; F, type F, *C. jenningsi*; G, type G, *C. vanderbilti*; H, *Pereulixia kosiensis* (dashed line indicates cirri not illustrated); I, *Exallias brevis*; J, *Scartichthys viridis*.

alter the polarity assessment of the other characters.

Genus *Stanulus* Smith

Adult *Stanulus* are smaller than other members of this group (except *Entomacrodus thalassinus* and *E. strasburgi*).

8. Ophioblennius-stage larva with short, robust body.

Stanulus has a distinctive ophioblennius-stage larva that is much smaller than the larvae (at an equivalent stage of development) of other genera in the node I group (larvae unknown for *Pereulixia*).

9. Scale-like flaps present along anterior portion of lateral line.

Stanulus, *Pereulixia*, and three species of *Cirripectes* have similar scale-like flaps associated with the anterior lateral line pores. *Pereulixia* and *Cirripectes* possess additional characters that argue for an independent derivation of the flaps in each genus. An alternative, equally parsimonious, interpretation is that the flaps are a node III synapomorphy, are lost at node V, and are secondarily regained by some *Cirripectes*.

Node IV Group

The node IV group comprises *Pereulixia*, *Exallias*, *Cirripectes*, *Scartichthys*, and *Ophioblennius*. These genera share three derived characters.

10. Transverse row of cirri extending across nape (Figure 8).

A distinctive transverse row of cirri across the nape manifests itself variously in the node IV genera. All other Blenniidae either lack nape cirri, or have a single cirrus on either side of the nape (both conditions are considered plesiomorphic relative to the condition in the node IV taxa). Although some genera of the Labrisomidae (sensu George and Springer, 1981:4) also have a transverse row of nuchal cirri, this character is considered to be convergent, as the Labrisomidae is not closely related to the node IV taxa. The different patterns of this transverse row of cirri (Figure 8A-I) are discussed by Williams (1988).

11. Premaxillary bone with symphyseal spur.

The symphyseal portion of the premaxilla is connected to the remainder of the premaxilla by a slender bridge of bone beneath the anterior edge of the base of the ascending process, with the symphyseal portion (symphyseal spur) free posteriorly (Figure 9B).

The distinctive shape of the body of the premaxilla in the node IV group (Figure 9B) appears to have resulted from a loss of bone in the concavity beneath the base of the ascending process. In the node IV group, the posterior tip of the free symphyseal portion (symphyseal spur) is tightly connected by ligaments to the posterior edge of the base of the premaxillary ascending process and the anterior edge of the maxilla. The base of the ascending process straddles the unossified concavity in the body of the premaxilla and appears to serve as

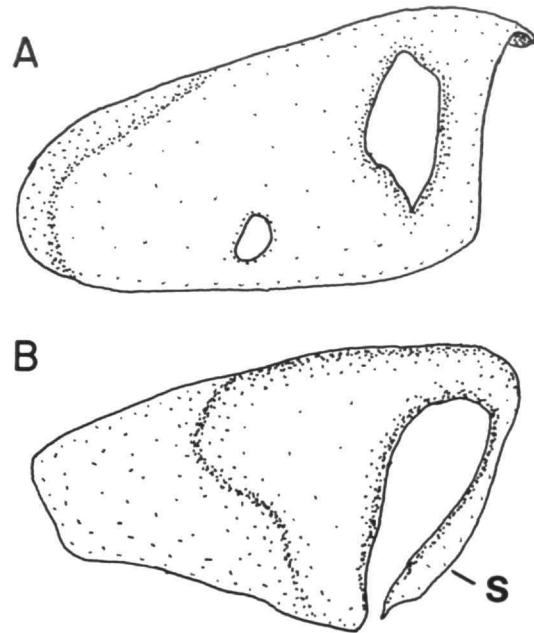


FIGURE 9.—Dorsal view of left premaxilla, ascending process removed from each bone (anterior toward top; medial toward right): A, *Alticus alticus*; B, *Scartichthys gigas*. (S = free symphyseal spur.)

a point of attachment for connective tissue holding the teeth in place. *Scartichthys* and *Ophioblennius* exhibit the plesiomorphic condition (Figure 9A), which, based on parsimony, is considered a secondary derivation. Other genera of the Blenniidae either do not have an open gap in the body of the premaxilla, or, if there is an opening, there is an anterior and posterior bony connection to the main body of the premaxilla (Figure 9A). The loss of the posterior bony connection between the symphyseal portion and the main body of the premaxilla is thus considered a synapomorphy of the node IV group.

12. Lacrimal with elongate anteroventral extension reaching ventrally to lower edge of maxilla. Sensory canal opening at or near lacrimal's ventral edge (Figure 10B).

The distinctively shaped lacrimal (Figure 10B) of the node IV group is not found elsewhere in the Blenniidae. In other salariin genera, except *Ecsenius*, the lacrimal is much shorter and broader than it is in the node IV group, and the ventrally directed sensory canal(s) exits from the bone at a point relatively close to the main infraorbital canal. The slender, vertically elongate, anteroventrally directed extension of the lacrimal is a synapomorphy of the node IV genera. Among the outgroups, only *Ecsenius* has an elongate lacrimal (Springer, 1968a, pl. 9), but the ventral sensory canal exits relatively close to the main infraorbital canal. As *Ecsenius* does not share other derived characters with any of the node I taxa, I interpret the elongate lacrimal in the two groups as independent derivations.

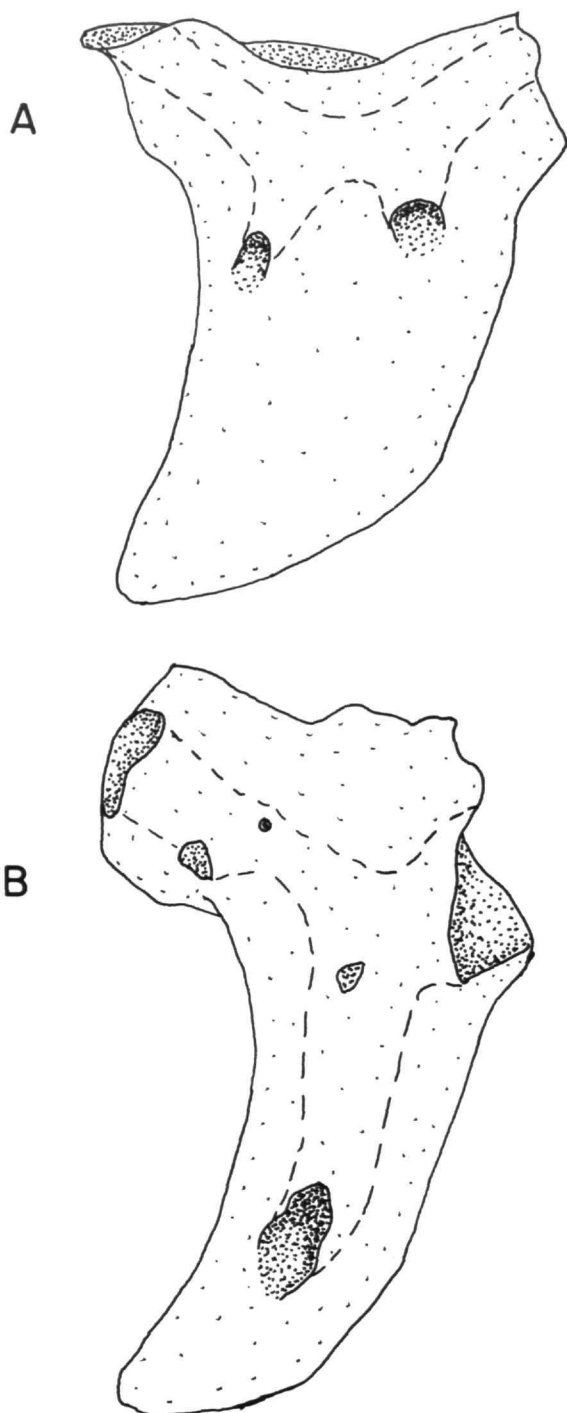


FIGURE 10.—Left lateral view of left lacrimal (anterior toward left): A, pores exit near main canal (*Alticus alticus*); B, branch of canal almost reaches ventral margin of bone (*Scartichthys gigas*).

Genus *Pereulixia* Smith

The genus *Pereulixia* forms the sister group of the node V group. It has three derived characters.

13. Nuchal cirri row comprised of four slightly overlapping groups of cirri.

The nuchal cirri arrangement is unique to *Pereulixia*. The cirri are frequently complex, with multiple branches arising from a single base (Figure 8H).

14. Dentary incisors larger (thus fewer) than premaxillary incisors.

Exallias has dentition similar to *Pereulixia*, but *Exallias* has more incisors in both jaws. *Ecsenius* (of the *Salarias* group) also has dentary incisors larger than premaxillary incisors, but has fewer incisors. This character of dentary incisors larger than premaxillary incisors is considered to be a derived condition as all other Salariini have similar sized maxillary and dentary incisors. Based on the characters defining the node IV and V groups, I hypothesize independent derivations in *Ecsenius*, *Exallias*, and *Pereulixia*. An equally parsimonious alternative explanation is the gain of the character at node IV and its loss at node VI, but this does not alter the branching sequence.

15. Skull with high bony crest.

The skull of *Pereulixia* has a high bony crest extending anteriorly from the dorsalmost edge of the supraoccipital bone to a point above the posterior edge of the orbits (Figure 11). The crest is formed from dorsal expansions of the frontal and parietal bones, each of which comprises about half of the crest and which are firmly sutured to each other. Other Salariini may have short bony crests on the skull, but the crest does not reach the height of the dorsalmost tip of the supraoccipital bone. Even salariini taxa with well-developed fleshy crests have only low bony crests on the skull. In other blennioid tribes, a large bony crest is present in large *Hypoleurochilus* (Parablenniini), *Omobranchus aurosplendidus* (Omobranchini), and *Petroscirtes* (Nemophini). These occurrences are considered independent derivations.

Node V Group

The node V group includes *Exallias*, *Cirripectes*, *Scartichthys*, and *Ophioblennius*. This assemblage shares five synapomorphies.

16. Dorsal-fin membrane attached to caudal fin.

Most members of the node V group have the dorsal-fin membrane attached to the caudal fin at a point dorsal or posterior to the caudal-fin base as adults. Most salariini genera have the dorsal-fin membrane attached to the caudal peduncle anterior to the caudal-fin base. Although the dorsal fin is attached to the caudal fin in many other blennioids, the attachment to the caudal fin is considered to be apomorphic for the node V group, inasmuch as the dorsal fin is not attached to

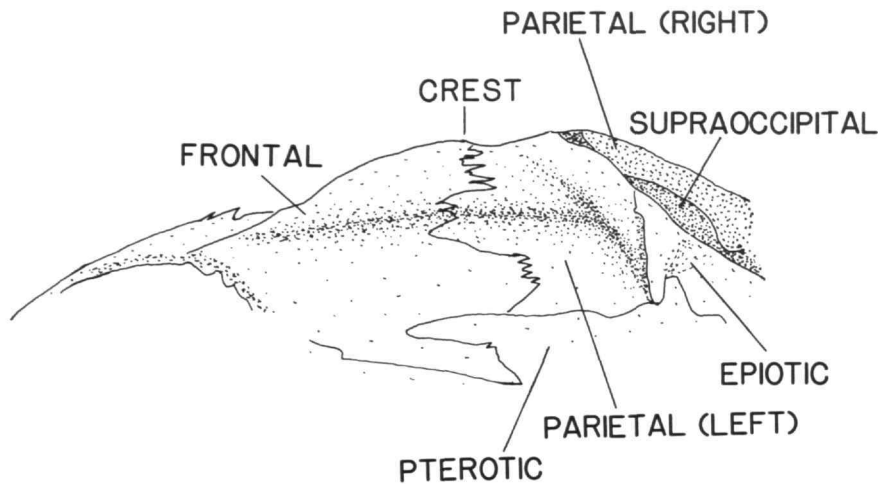


FIGURE 11.—Left lateral view of supraoccipital region of skull of *Pereulixia kosiensis* illustrating well-developed crest.

the caudal fin in other node I genera (except some species of *Istiblennius*). Although the dorsal-fin membrane is not attached to the caudal fin in *Scartichthys* and a few species of *Cirripectes*, I consider this condition to be a secondary derivation. An equally parsimonious hypothesis is that the attachment to the caudal fin was independently derived in *Exallias*, *Ophioblennius*, and some *Cirripectes*. The latter scenario does not alter the branching sequence.

17. Fourth epibranchial with two distinct processes.

The two processes are located on the dorsal surface of the fourth epibranchial near the midpoint of the shaft of the bone. One process is directed anterodorsally and the other posterodorsally (Figure 5C). The presence of two distinct processes on the fourth epibranchial is unique to the node V taxa. The plesiomorphic condition in the outgroups is a single broad dorsal projection (Figure 5A) in this position on the fourth epibranchial and occurs in all blennioids except the Parablenniini and node V group. There appear to be two derived conditions for these features of the fourth epibranchial: two projections (Figure 5C) or no projections (Figure 5B). The former condition is a synapomorphy of the node V group and the latter a synapomorphy of the tribe Parablenniini.

18. Fifth ceratobranchial with expanded, posteroventrally directed flange.

In the node V group, the fifth ceratobranchial has a distinctive, unconstricted, posteroventrally directed flange (Figure 12F) that extends posteriorly to a point beyond the main body (tooth-bearing portion) of the bone. The ventral margin of the flange meets the posterior margin to form an acute angle. *Alloblennius*, *Mimoblennius*, *Hirculops*, and *Litobranchius* (all members of the Rhabdoblennius group) also have a posteriorly directed flange, but, in these genera, the flange is distinctive in

having a rounded extension at the posterior edge and a constriction separating it from an angular process on the ventral edge (Figure 12C, D). Other salariin genera have a small posterior flange that does not project posteriorly beyond the dorsal limb of the fifth ceratobranchial (Figure 12E). Genera of the Parablenniini have a rounded flange of bone on the posterior edge of the dorsal limb of the fifth ceratobranchial, another flange located ventrally below the tooth-bearing portion of the bone, and a distinct constriction between the flanges at the dorsoposterior edge of the tooth-bearing portion (Figure 12B). All other blennioids have a slender fifth ceratobranchial bone with a very narrow flange of bone on the ventromedial edge of the tooth-bearing portion (Figure 12A). The slender fifth ceratobranchial with a very narrow flange of bone is considered the plesiomorphic condition. The unconstricted, extensively developed flange of bone (presumably derived from the constricted condition of the close outgroups shown in Figure 12B–D) on the fifth ceratobranchial is a synapomorphy of the node V group.

19. Each premaxilla of ophioblennius-stage larvae with one or two large, recurved canines near symphysis of premaxillae.

20. Each dentary of ophioblennius-stage larvae with one or two large, recurved canines at symphysis of dentaries.

The last two synapomorphies for the node V group are characters of the dentition of the ophioblennius-stage larvae. The first of these is the presence of large, hooked canines at the symphysis of the premaxillae. The second character is the presence of large, hooked canines at the symphysis of the dentaries. Watson (in Leis and Rennis, 1983:192) distinguished larvae of the genera *Exallias*, *Entomacrodus*, *Cirripectes*, and *Stanulus* from larvae of the Nemophini by their large, hooked

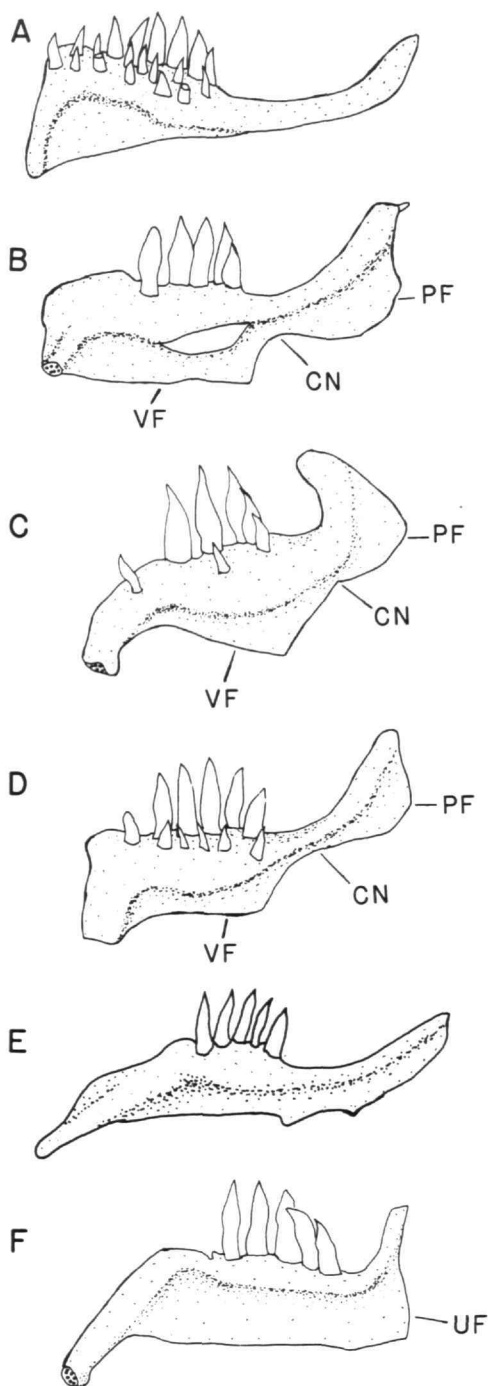


FIGURE 12.—Left lateral view of left fifth ceratobranchial (anterior toward left; large stipples indicate cartilage): A, *Acanthemblemaria aspera*; B, *Chasmodes saburrae*; C, *Mimoblennius atrocinctus*; D, *Hirculops cornifer*; E, *Alticus alticus*; F, *Scartichthys gigas*. (CN = constriction; PF = posterior flange; UF = unconstricted flange; VF = ventral flange.)

canines at the symphyses of the jaws. Although Watson suggested that the hooked canines serve to identify salariin larvae, they actually diagnose only the node I genera. All node I genera have a large hooked canine midlaterally on each dentary, but hooked symphyseal canines are unique to the node V genera and, thus, are a synapomorphy for the group.

Characters 17 through 20 are present in all node V genera and are unique synapomorphies of the group. Character 16 is derived, but is homoplastic.

Genus *Exallias* Jordan and Evermann

Exallias, a monotypic genus, is the sister group of the node VI group.

21. Lateralmost nuchal cirri very short; cirri increasing in length toward nape (Figure 8I).

The distinctive nuchal cirri morphology of *Exallias* is unique among blennioids.

22. Adults (both sexes) lacking posterior dentary canines.

Although adults of some species of *Istiblennius* also lack posterior dentary canines, adults of all other genera in the node I group have them. The most parsimonious explanation is that the lack of dentary canines in *Exallias* is apomorphic.

Exallias differs from other members of the node V group in having enlarged dentary incisors. *Exallias* usually has about three or four times as many premaxillary incisors as dentary incisors. *Pereulixia* has enlarged dentary incisors, but has fewer incisors on both jaws (Smith-Vaniz and Springer, 1971, table 2). Other members of the Salariini (see discussion of *Ecsenius* in "Genus *Pereulixia*") have incisors of similar size in each jaw with up to twice as many premaxillary incisors as dentary incisors.

Node VI Group

This group comprises *Cirripectes*, *Scartichthys*, and *Ophioblennius* and is diagnosed by one synapomorphy.

23. Large prominence (Figure 13B) at about midpoint of posteromedial margin of maxilla.

The well-developed maxillary prominence (Figure 13B), which serves as the point of insertion for the primordial ligament, is not present in other blennioid fishes, although, occasionally a slender flange in approximately the same position, or slightly anterior to this position, is present in other salariin genera. The presence of a well-developed maxillary prominence is a synapomorphy of the node VI group.

Genus *Cirripectes* Swainson

Cirripectes, sister group of the node VII group, contains a diverse assemblage of 21 species. I have found only two synapomorphies that diagnose *Cirripectes*.

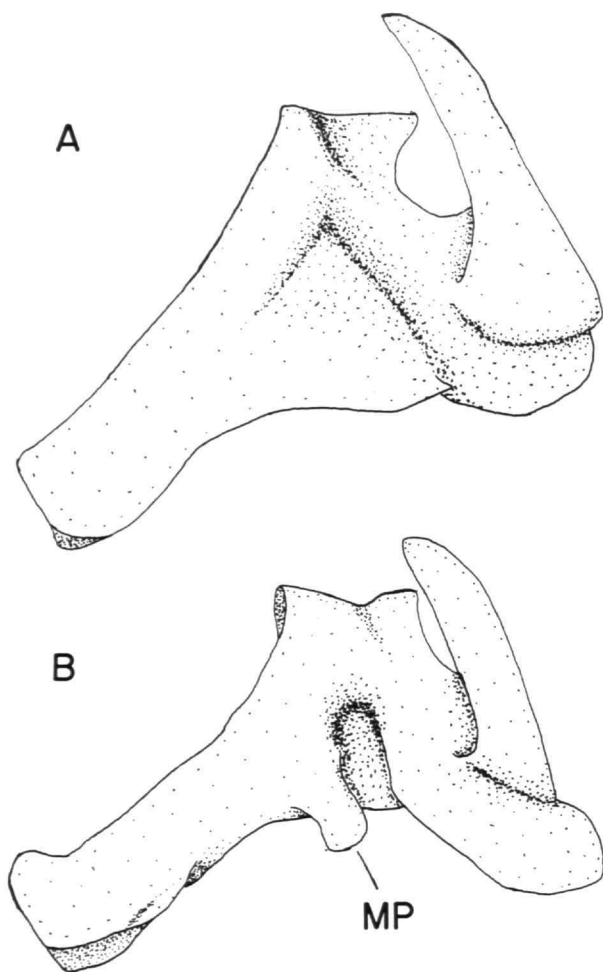


FIGURE 13.—Posterodorsal view of left maxilla: A, *Alticus alticus*; B, *Scaritichthys gigas*. (MP = maxillary prominence.)

24. Nuchal cirri arrangement (Figure 8A–G) consisting of one to four groups of cirri with non-overlapping bases; cirri approximately equal in length.

Other members of the node VI group have variously modified nuchal cirri morphologies (Figure 8H–J), each condition unique within the Blenniidae.

25. Adult male urogenital papilla with one or two tapering filaments associated with gonopore (Figure 14A–D).

The genera *Istiblennius*, *Entomacrodus*, *Stanulus*, *Pereulixia*, and *Exallias* have the gonopore positioned distally on a short, rounded papilla (the papilla is slightly larger in *Exallias*, but does not have tapering filaments). The papilla of the node VII group (Figure 14E) differs from that of *Cirripectes* in having two short, flattened projections, which are broadly rounded distally, on either side of the gonopore. I hypothesize

that the filamentous form of the papilla (*Cirripectes*) has been derived from the node VII condition, but it could be argued that the polarity should be reversed. Whatever the correct polarity, each morphology is unique among blennioids and the polarity assignment does not alter the branching sequence.

These characters are discussed more thoroughly by Williams (1988).

Node VII Group

Scaritichthys and *Ophioblennius* are included in the node VII group. Three synapomorphies are shared by this group.

- 25'. Male genital papilla flattened anteroposteriorly, with one short, blunt projection on either side of gonopore (Figure 14E).

The distinctive shape of the male genital papilla is unique among blennioids and I consider it to be a derived condition (see "Genus *Cirripectes*").

26. Transverse row of nuchal cirri in two widely separated groups (Figure 8J).

The nuchal cirri arrangement in these two genera varies among species, but always consists of a group of cirri (as few as two in some *Ophioblennius*) on each side of the nape with a broad gap between the groups. This condition is hypothesized to be a secondary modification of the condition characterizing the node IV group and, as such, is a synapomorphy for the node VII group.

27. High number of caudal vertebrae (22–26).

Although other blenniids have a high number of caudal vertebrae, of the node I taxa, only *Istiblennius*, *Entomacrodus*, and the node VII taxa have 23 or more caudal vertebrae; other node I taxa have 19 to 22 caudal vertebrae (only a few species of *Cirripectes* have as many as 22). At this level of analysis, I consider the high number of caudal vertebrae (22–26) to be a synapomorphy for the node VII group.

Genus *Ophioblennius* Gill

Two characters are synapomorphies of the species of *Ophioblennius*.

28. Lateral line with disconnected overlapping portions.

The anterior section of the lateral line ends at a point above the posterior section of the lateral line near the middle of the body. The posterior section of the lateral line begins slightly anterior to and beneath the end of the anterior section of the lateral line and continues to the caudal-fin base (frequently as a series of short tubes). Among blenniids, this condition is unique to *Ophioblennius*.

29. Elongated dentary canines.

As discussed by Smith-Vaniz and Springer (1971:36), adults of this genus have dentary canines that are as long as or longer

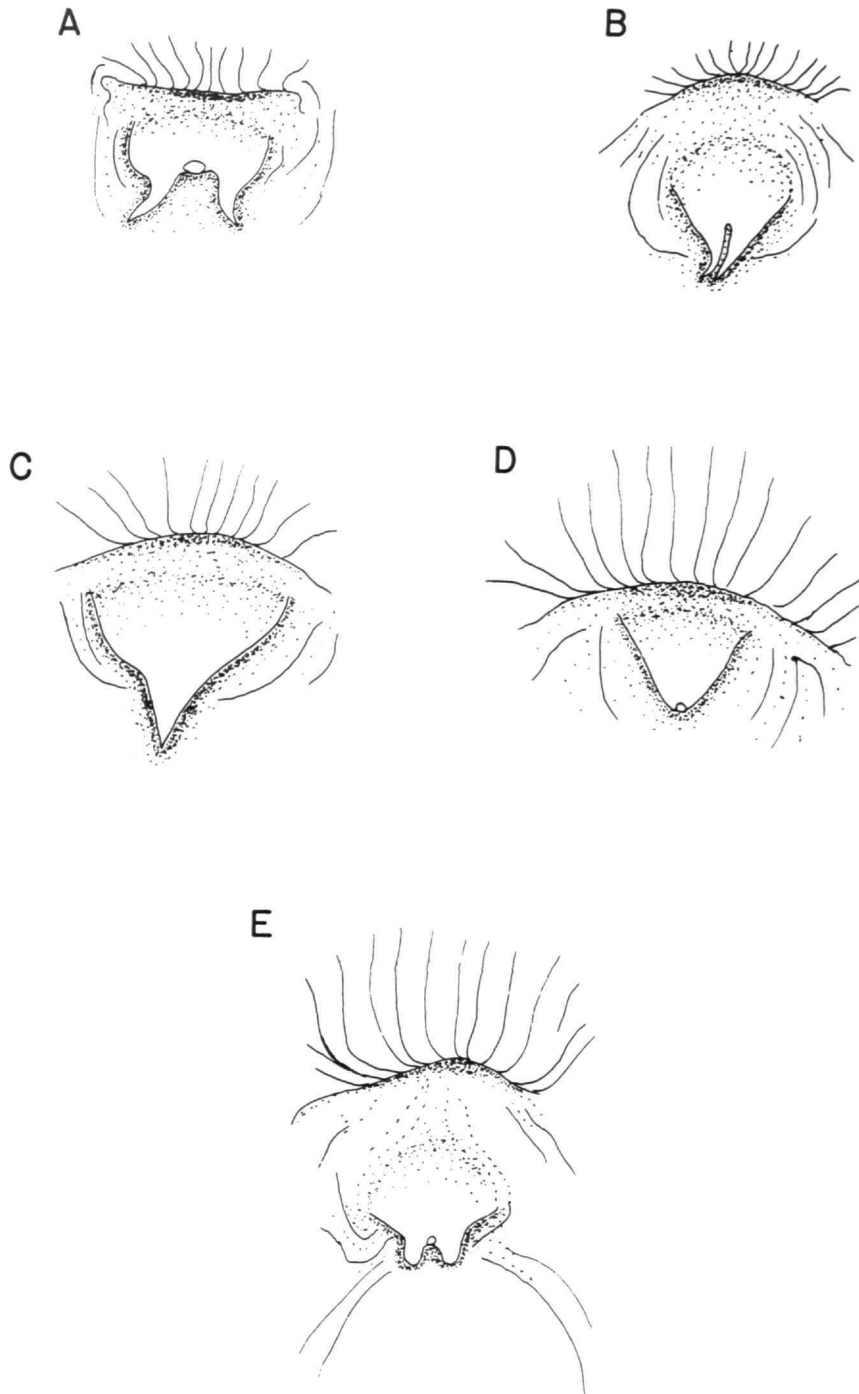


FIGURE 14.—Ventral view of male urogenital papilla (anterior toward top): A, type I, *Cirripectes perustus*; B, type II, *C. vanderbilti*; C, type III with posteriorly positioned gonopore, *C. alboapicalis*; D, type III with distally positioned gonopore, *C. obscurus*; E, *Scartichthys viridis* (type numbers defined in Williams, 1988).

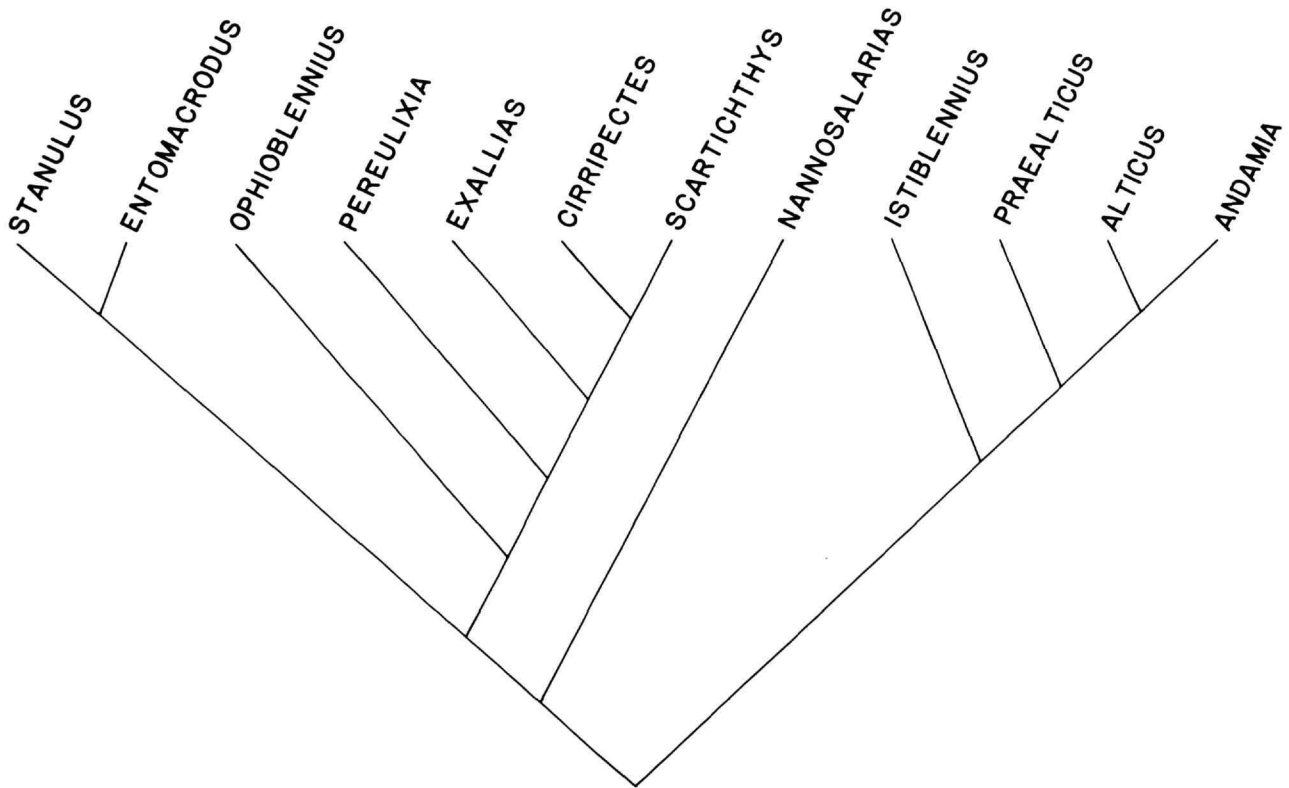


FIGURE 15.—Modified dendrogram of interrelationships of *Scartichthys* and allies proposed by Smith-Vaniz and Springer (1971, fig. 51).

than the pupil diameter. Other adult members of the node I group have much shorter canines (or none at all in *Exallias*).

Genus *Scartichthys* Jordan and Evermann

30. Lateral line with 18–21 tubes.

The genus *Scartichthys* is distinctive in that the posterior part of the lateral line consists of about 18–21 (typically 21) short tubes, each with a pore at either end. Other members of the node I group have from 0 to 10 lateral line tubes, although a few species of *Istiblennius* have high numbers of lateral line tubes. The high number of lateral line tubes is a synapomorphy of this genus.

Discussion of Phylogenetic Analysis of Genera

The results of my study of this group of genera permit the advancement of a hypothesis of phylogenetic relationships within this clade. In many cases, additional information will be necessary to determine the robustness of the hypothesis. Nonetheless, the presented data do set forward an explicit hypothesis based on concisely described morphological features. As this study is the first attempt to provide a phylogenetic

analysis of this group of salariin genera, it is possible that my hypothesis of relationships will be altered as the related taxa are analyzed in greater depth.

My hypothesis of phylogenetic relationships (Figure 2) is similar to Smith-Vaniz and Springer's (1971, fig. 51) dendrogram (reproduced here as Figure 15), essentially differing only in the placement of *Istiblennius* and *Ophioblennius*. In my analysis, *Istiblennius* (based primarily on the *I. gibbifrons* species complex) is included in the node I group, whereas Smith-Vaniz and Springer (1971) placed it with *Praealticus*, *Alticus*, and *Andamia*. It seems likely that this difference results from the particular species of *Istiblennius* used in each analysis. I agree with Smith-Vaniz and Springer (1971:50) who state that *Istiblennius* might be polyphyletic and, thus, both placements could be correct for a different subset of *Istiblennius* species. A revision and phylogenetic analysis of *Istiblennius* is needed before its relationships can be assessed adequately.

Smith-Vaniz and Springer (1971, fig. 51) regarded *Ophioblennius* as the sister group of the other genera in my node IV group. They placed it in this position because it possesses a combination of unique and distinctive characters that they felt isolated it from the other genera. In a cladistic

analysis, unique characters (autapomorphies) cannot be used to infer relationship or lack of relationship with taxa not possessing these characters. In my analysis, *Ophioblennius* and *Scartichthys* are sister genera, which together are the sister group of *Cirripectes*.

Smith-Vaniz and Springer (1971, fig. 51) considered *Nannosalarias* to be the sister group of my node II group. As I did not treat the interrelationships of the members of my *Salarias* group, outside of my node I group, it is possible that *Nannosalarias* is the sister group of the node I group. Further study of the *Salariini* is needed to determine the interrelationships of the remaining genera in the *Salarias* group.

Smith-Vaniz and Springer (1971, fig. 51) considered *Stanulus* and *Entomacrodus* to be sister genera that together form the sister group of my node IV group. They grouped *Entomacrodus* and *Stanulus* on the basis of overall similarity, but did not provide a specific character to support the hypothesized sister group relationship. In my analysis, *Entomacrodus* is the sister group of the node III group, which includes *Stanulus* and whose members share the presence of a large foramen in the infrapharyngobranchial plate. Thus, *Stanulus* might be more closely related to the node IV group than to *Entomacrodus*, but this result is tentative as the PAUP analysis suggests that the placement of these two genera in an unresolved trichotomy with the node IV group forms an equally parsimonious hypothesis. As the node I group is monophyletic and the different arrangements of *Stanulus* and *Entomacrodus* on the cladogram do not alter my polarity statements for the characters of the node IV taxa, I will not discuss these different hypotheses of relationship among *Entomacrodus* and *Stanulus*.

Although many of the characters I used to determine relationships among the genera in my node I group are homoplastic (PAUP consistency index = 0.694), a cladistic

analysis is preferable because it specifies how a character is distributed and clearly illustrates weak and strong components of the hypothesis. A cladistic hypothesis is based on a specific distribution of characters among taxa and can be tested by adding additional characters or reassessing the original characters. Thus, it is possible that any given hypothesis of relationships will change when additional characters are added to the analysis. Because of the potential for a given cladogram to change when additional characters are added, formal taxonomic names should be applied with care in order to minimize future nomenclatural confusion.

Genus *Scartichthys* Jordan and Evermann

Scartes Jordan and Evermann, 1896:471 [type species: *Salarias rubropunctatus* Valenciennes in Cuvier and Valenciennes, 1836, by original designation; a junior homonym of *Scartes* Swainson, 1835, Mammalia].

Scartichthys Jordan and Evermann, 1898:2395 [type species: *Salarias rubropunctatus* Valenciennes in Cuvier and Valenciennes, 1836, by original designation].

DIAGNOSIS.—*Scartichthys* are salariin blennies with the posterior section of the lateral line comprising 18–21 short bi-pored tubes (continuous section and tubed section of lateral line not in disconnected overlapping portions). Specimens of *Scartichthys*, with adults often exceeding 180 mm SL (up to 300 mm total length), are the largest (referring to a combination of length and weight) in the Blenniidae (the nemophin genus *Xiphasia* reaches 550 mm SL, but has an extremely slender body).

Selected counts for the species of *Scartichthys* are provided in Table 4.

DISTRIBUTION.—The genus *Scartichthys* is restricted to the eastern Pacific Ocean, where it occurs from Panama to Chile (Figure 16).

Key to the Species of *Scartichthys*

(For specimens greater than 45 mm SL)

1. Dentary incisors 57–93; body coloration mottled with brown and white, or with white (red in life) spots 2
 Dentary incisors 92–131; body uniformly brown, occasionally with pupil-size, dark-brown, midlateral stripe, or with tiny, dark-brown (brownish orange in life) spots on posterior half of body 3
2. Dentary incisors 80–93; typically 18 segmented dorsal-fin rays; pupil-size black spot on first (sometimes on second also) interspinal membrane of dorsal fin; pupil-size white spots over head and body; offshore islands of Chile *S. variolatus*
 Dentary incisors 57–69; typically 17 segmented dorsal-fin rays; no pupil-size black spot on first interspinal membrane of dorsal fin; body mottled with brown and white; Panama to northern Chile *S. gigas*
3. Tiny, dark-brown (rarely pale) spots on posterior half of body; known only from northern Chile and from the vicinity of Valparaiso
 *S. crapulatus*, new species
 Body coloration uniformly brown, without spots posteriorly, occasionally with dark-brown stripe (its width about equal to diameter of pupil); southern Peru to vicinity of Valparaiso, Chile *S. viridis*

TABLE 4.—Frequency distributions for selected meristic characters of the species of *Scartichthys*.

Species	Segmented dorsal fin rays				Segmented anal fin rays			Vertebral centrum bearing last pleural rib		Caudal vertebrae		
	16	17	18	19	18	19	20	11	12	23	24	25
<i>crapulatus</i>			14	1		7	8		12			12
<i>gigas</i>	8	216	11		32	140	1	163	1	3	157	6
<i>variolatus</i>		6	62			41	31	68		1	65	3
<i>viridis</i>		5	22	1		16	18	7	16	1	19	3

Species	Vertebral centrum bearing last epipleural rib						Dorsal branches of LL					
	15	16	17	18	19	20	21	11-14	15-19	20-24	25-29	30-34
<i>crapulatus</i>	1		2	3	6			6	5			
<i>gigas</i>	2	4	60	60	25	5		9	5			
<i>variolatus</i>		3	32	30	3					7	6	11
<i>viridis</i>		2	3	9	3	4	3	5	11			

Species	Left + right nasal cirri								
	6-8	9-11	12-14	15-17	18-20	21-23	/	27-29	30-31
<i>crapulatus</i>	11	3							
<i>gigas</i>	10	12		1					
<i>variolatus</i>	1	4	8	6	6	3		1	1
<i>viridis</i>	8	7	1	2					

Species	Left + right supraorbital cirri									
	17-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	/	60-116
<i>crapulatus</i>	4	6	5	1						
<i>gigas</i>	1	3	6	2	2					
<i>variolatus</i>		3	1	2	3	1	2	1		7
<i>viridis</i>		3	6	5		1		1		

Species	Total nuchal cirri									
	5-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	/	95
<i>crapulatus</i>	5	6	3							
<i>gigas</i>	4	12								
<i>variolatus</i>			5	2	5	3	2	3		1
<i>viridis</i>	1	2	5	5	1	1	1			

Species	Dentary teeth of specimens longer than 45 mm SL									
	57-59	60-69	/	80-84	85-89	90-94	95-99	100-109	110-113	114-131
<i>crapulatus</i>						1	5	7	4	
<i>gigas</i>	6	24								
<i>variolatus</i>				6	19	5				
<i>viridis</i>								2	5	15

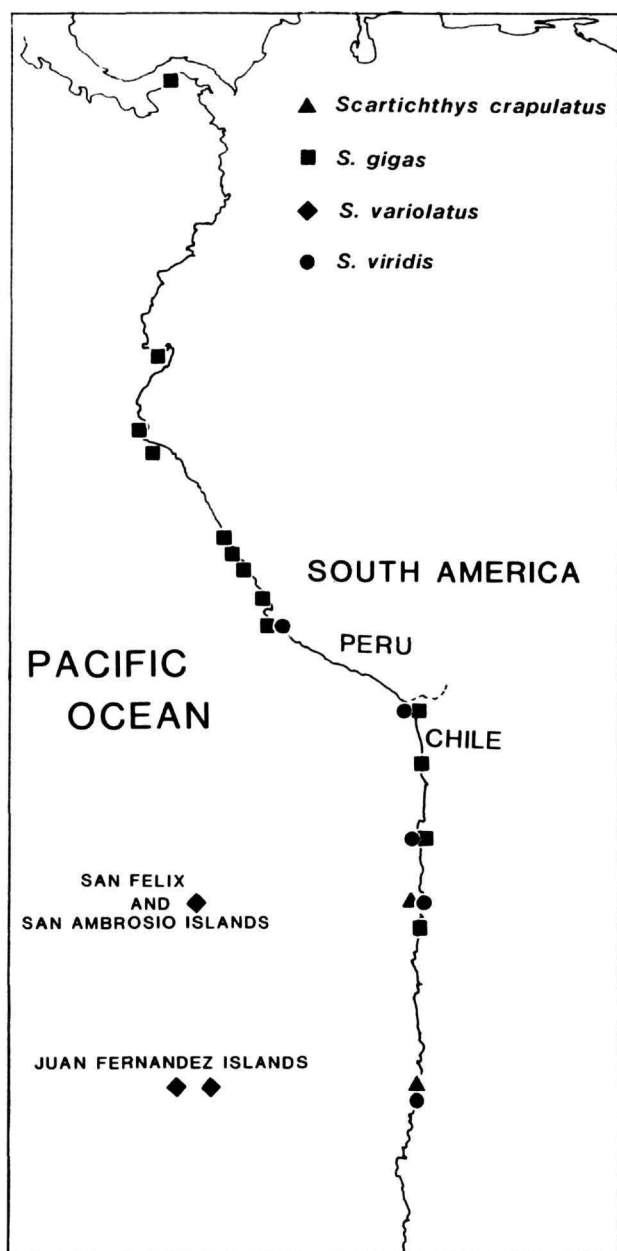


FIGURE 16.—Geographic distribution of *Scartichthys* (dashed line indicates the border between Peru and Chile).

Scartichthys crapulatus, new species

FIGURES 16, 17

DIAGNOSIS.—A species of *Scartichthys* with more than 95 dentary incisors and small dark-brown or pale (brownish orange in life) spots on posterior half of body.

DESCRIPTION.—Dorsal fin XII,18-19 (18 in 14 of 15 specimens); anal fin II,19-20; total procurrent caudal-fin rays 14-15; pelvic fin I,4; vertebrae 10 + 24 = 34; last pleural ribs on vertebral centrum 12; last epipleural rib on vertebral centrum 15-19 (17-19 in 11 of 12); anal pterygiophores 2-1-1 or 1-2-1 (1-2-1 in 9 of 12); nuchal cirri 6-33 (6-12 in 11 of 15); supraorbital cirri 17-32; nasal cirri 6-11; LL tubes 20-22 (21 in 14 of 16); last LL tube at base of caudal fin; no scale-like flaps along LL; lower lip smooth mesially (plicate laterally); gill rakers 22-27 (based on 5 specimens); pseudo-branchial filaments on one side 10-12 (based on 7 specimens); premaxillary teeth 205-220 (based on 3 specimens); dentary teeth 92-113 (95-111 in 15 of 18; fewer than 95 only in specimens less than 50 mm SL); upper lip crenulae approximately 28-36; nuchal cirri in 2 groups widely separated across nape (Figure 8j); first dorsal-fin spine of adults approximately equal in length to second in both sexes; dorsal-fin membrane deeply incised above last dorsal-fin spine; dorsal-fin membrane attached to caudal peduncle in advance of caudal fin in adults; cephalic pore system relatively simple (less than 3 pores at most positions; number of pores increases with increasing SL); male genital papilla with urogenital orifice located basally between 2 small protuberances on a fleshy swelling behind anus (Figure 14E); testes elongate, length equals about twice width; maximum SL may reach 300 mm (Rosenblatt, pers. comm.), but the largest specimen collected measures 116 mm SL.

No mature females of this species have been examined, but the female holotype (~110 mm SL) has well-developed ovaries and females less than 70 mm SL do not. Males are mature at 116 mm SL, but not at 75 mm SL.

COLOR IN ALCOHOL.—Juveniles have a brown pupil-size stripe on paler background midlaterally on body, 9 to 11 saddle-like blotches (sometimes connected to form a continuous dark stripe) along dorsal surface of body, posterior half of body speckled with tiny black spots; head brown with small black spot, its diameter equal to about half diameter of pupil, behind posterior margin of eye; anterior 1 to 3 interspinal membranes of dorsal fin with black pupil-size spot, remainder of fins dusky; all cirri black.

Adult females (Figure 17) and males with brown background color on head and body, faint eye-size dark stripe midlaterally on body (breaking into blotches and becoming fainter with increasing size), posterior half of body with small dark or pale spots; dorsal and anal fins with narrow pale distal margins. A female 101 mm SL has a uniform pale brown body with small pale spots on posterior half of body. Adult males have pale rugosities covering the 2 anal-fin spines. Other colors as for juveniles.

COLOR IN LIFE.—Freshly killed specimens taken near Quintero, Chile, were highly variable in color. Body colors ranged from green or reddish brown to golden with small brownish orange or brown spots on posterior half of body and on segmented-ray portion of dorsal fin. Elongate, iridescent

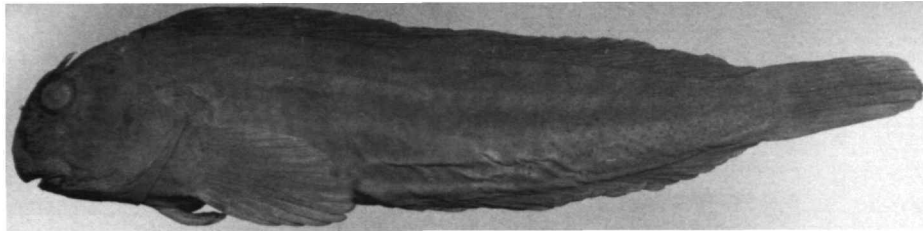


FIGURE 17.—*Scartichthys crapulatus*, USNM 276344, holotype, female, 110 mm SL, Chile.

pale-green spot located dorsally on pectoral-fin base and another covering bases of ventralmost rays. Orbital cirri iridescent blue. Adult males with pale-green anal-fin spine rugosities. Other colors as in alcohol.

COMPARISONS.—*Scartichthys crapulatus* is the only member of the genus with small dark-brown spots on the posterior half of the body. It is most similar in meristics and other counts (Table 4) to *S. viridis*, but is easily distinguished by color pattern (the latter has a uniformly brown body).

DISTRIBUTION.—*Scartichthys crapulatus* is known only from the coast in the vicinity of Valparaiso, Chile (33°S), and from a power plant trap in the northern Chilean town of Barquito (26°S), where it was collected with specimens of *S. gigas* (Figure 16). It lives on rocky bottoms and has been collected at depths of 1–15 m.

ETYMOLOGY.—The specific epithet, from the Latin *crapulatus* (drunk), refers to the purported sleepy or drunken feeling experienced when the flesh of *Scartichthys* is eaten (Koeppke, 1955:67).

MATERIAL EXAMINED.—20 specimens, 37–116 mm SL.

Holotype: USNM 276344 (female: 110 mm SL), Montemar Biological Station, field number BBC 1155, collected by B.B. Collette and R.H. Gibbs, Jr., 14 Feb. 1966.

Paratypes: ANSP 158678 (4 specimens: 42–64 mm SL), Barquito, Chile, power plant trap, 28 Apr. 1955; BMNH 1850.6.14.20 (1: 67), South America (probably Chile), collected by Mr. Bridges; MNHC P.6.411 (8: 37–78), El Quisco, Chile, 32°23'S, 71°42'W, 14 Sep. 1952; SIO 87-133 (1: 101), Los Farallones de Quintero, Chile, shoaling rocks ~1 mile offshore, 32°47'S, 71°32'W, 10–45 ft. (3–13.5 m), collected by R. McConnaughey, 7 Aug. 1987; SIO 87-136 (2: 72, 116), Los Farallones de Quintero, Chile, ~1 mile offshore, 15–50 ft. (4.5–15 m), R. Rosenblatt et al., 20 Aug. 1987; SIO 87-140 (3: 75–116), Bahía Quintero, Chile, between La Ventana and village of Ventana, collected by R. McConnaughey, 26 Aug. 1987.

Scartichthys gigas (Steindachner)

Salaria gigas Steindachner, 1876:220 [Callao, Peru; syntypes NMW 73438:1 and 73438:2].

Salaria eques Steindachner, 1898:307 ["Cavanchabai bei Iquique"; holotype ZMB 15658].

Ophioblennius xiphiodon Clark, 1938:183 [Callao, Peru; holotype CAS 5543] [new synonymy].

Ophioblennius mazorkae Hildebrand, 1946:384 [Mazorka Island, Huaura Group, Peru; holotype USNM 128188] [new synonymy].

DIAGNOSIS.—A species of *Scartichthys* with fewer than 70 dentary incisors and a reticulated color pattern.

DESCRIPTION.—Dorsal fin XI–XIII (XII in 96.6% of specimens), 16–18 (17 in 91.9%); anal fin II, 18–20 (19 in 80.9%; 18–19 in 99.4%); total procurent caudal-fin rays 10–16; pelvic fin I, 4; vertebrae 10–11 (10 in 99.4%) + 23–25 (24 in 94.6%) = 33–35 (34 in 94.6%); last pleural ribs on vertebral centrum 11–12 (11 in 99.4%); last epipleural rib on vertebral centrum 15–20 (17–19 in 92.9%); anal pterygiophores 2–1–1, 1–2–1, or 1–1–2 (1–2–1 in 75.6%); nuchal cirri 8–19; supraorbital cirri 19–53 (23–39 in 80.0%); nasal cirri 7–15 (7–11 in 95.7%); LL tubes 18–22 (19–21 in 87.5%); last LL tube on caudal-fin base; no scale-like flaps along LL; lower lip smooth mesially (plicate laterally); gill rakers 16–20 (based on 10 specimens); pseudobranchial filaments on one side 9–13 (based on 12 specimens); premaxillary teeth 108–146 (based on 10 specimens); dentary teeth 57–69 (based on 30 specimens); upper lip crenulae approximately 24–31; nuchal cirri in two irregular groups on either side of nape, distance between them approximately equal to diameter of eye; length of first dorsal-fin spine of adults about equal to second in both sexes; dorsal-fin membrane deeply incised above last dorsal-fin spine; dorsal-fin membrane attached to caudal peduncle in advance of caudal fin in adults; cephalic pore system complex (4 or more pores at most positions; number of pores increases with increasing SL); male genital papilla with urogenital orifice located basally between 2 small protuberances on a fleshy swelling behind anus (Figure 14E); maximum SL about 222 mm; ophioblennius larvae with 2–3 canines posteriorly on each dentary; no spots on membrane between anterior dorsal-fin spines.

The smallest mature female (ova ~0.6 mm diameter) examined is ~126 mm SL. Males mature by ~90 mm SL.

COLOR IN ALCOHOL.—Ophioblennius-stage larvae pale with 11 to 13 saddle-like blotches of pigment along dorsal surface of body; distal half of pectoral fin with numerous melanophores on rays and membranes; scattered melanophores at tips of spinous dorsal-fin rays; remainder of fins pale; small pupil-size

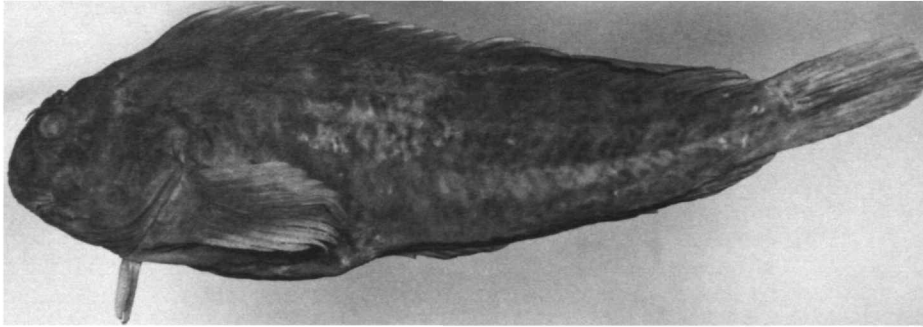


FIGURE 18.—*Scartichthys gigas*, GCRL 12635, female, 140 mm SL, Peru.

cluster of melanophores behind midpoint of posterior margin of eye.

Juveniles with about 8 to 10 irregular dark-brown bars separated by pale interspaces along body; head irregularly covered with pale spots and dark-brown bars, large black spot behind posterior margin of orbit, size of spot about half to three-quarters size of eye; dorsal and anal fins dark brown with pale-tipped fin elements; other fins dusky.

Adult color pattern (Figure 18 shows a female) similar to that of juveniles except that the bars on the head and body break up into a reticulated pattern.

COLOR IN LIFE.—A recently collected adult male in alcohol retained some orange color at the distal tips of the dorsal-fin elements. Other colors are unknown.

COMPARISONS.—*Scartichthys gigas* differs from all other *Scartichthys* in having fewer than 70 dentary teeth (versus 74 or more) and in having a vermiculated color pattern over head and body (all others have spots or a uniformly pigmented body).

DISTRIBUTION.—*Scartichthys gigas* occurs from the Pacific coast of Panama (9°N) to Antofagasta, Chile (23°S; Figure 16). It is sympatric with *S. viridis* in southern Peru and northern Chile, and with *S. crapulatus* in northern Chile. It has been collected from rocky bottom and artificial hard bottom areas at depths of 1–5 m.

ETYMOLOGY.—The specific epithet, from the Latin *gigas* (giant), refers to the relatively large size of adults.

NOMENCLATURE DISCUSSION.—Steindachner (1876) described *Salarias gigas* based on two specimens from Callao, Peru, but gave no catalog numbers. The two syntypes of *S. gigas* are cataloged as NMW 73438:1 (female) and NMW 73438:2 (male).

Salarias eques was described by Steindachner (1898:307) based on a single specimen from “Cavanchabai bei Iquique.” Steindachner treated *S. gigas* and *S. viridis* on the pages following the description of *S. eques*, but failed to recognize *S. eques* as a sub-adult specimen of *S. gigas*. The holotype of *S. eques* is cataloged as ZMB 15658 (female, 86 mm SL). Although the holotype is a sub-adult, it retains the striped

pigmentation pattern frequently found on much smaller specimens. The low number of dentary teeth and the lack of a spot anteriorly in the dorsal fin are characteristic of *Scartichthys gigas*. *Salarias eques* is thus considered a junior synonym of *S. gigas*.

Clark (1938:183) described *Ophioblennius xiphiodon* based on ophioblennius-stage post-larval specimens from Peru and Chile. As discussed in the account of *Scartichthys viridis*, the paratypes from Valparaiso, Chile, are referable to *S. viridis*, and the other specimens belong to *S. gigas*. The Peruvian holotype (on loan) was not available for examination, but, as the Peruvian paratypes are post-larvae of *S. gigas* and the collection locality (Callao) of the holotype is the same as that of the types of *S. gigas*, I tentatively consider *Ophioblennius xiphiodon* to be a junior synonym of *S. gigas*.

Ophioblennius mazorkae was described by Hildebrand (1946:384) based on ophioblennius-stage post-larval specimens of *Scartichthys gigas* and, thus, is a junior synonym of the latter.

MATERIAL EXAMINED.—482 specimens, 30–222 mm SL.

Types: NMW 73438:1 (female: 150 mm SL) and NMW 73438:2 (male: 185), syntypes of *Salarias gigas*, Callao, Peru; ZMB 15658 (1: 84), holotype of *Salarias eques*, Iquique, Chile; CAS 5544–5550 (3 of 7 examined: 33–41), paratypes of *Ophioblennius xiphiodon*, Callao, Peru; CAS 5553–5556 (2 of 4 examined: 31, 32), Chinchas, Peru; USNM 128188 (1: 33), holotype of *Ophioblennius mazorkae*, Mazorka Island, Huaru Group, Peru; USNM 128189 (20 of 60+ examined: 30–36), paratypes of *Ophioblennius mazorkae*, Mazorka Island, Huaru Group, Peru.

Nontypes: West Coast of South America (exact locality unknown): BMNH 1908.12.5.32–3 (2: 54, 57). Panama: USNM 144797 (72: 30–58). Ecuador: USNM 88796 (3: 106–120). Peru: GCRL 12492 (1), GCRL 12513 (3: 127–159), GCRL 12628 (9), GCRL 12633 (6), GCRL 12635 (25), NMW 20516 (1), NMW 22184 (1), NMW 73244 (2: 102, 103), NMW 73425 (2: 117–141), RMNH 11283 (1: 193), RMNH 11462 (1: 167), SIO 65-602 (12), UF 21437 (1: 136), USNM 102009 (1:

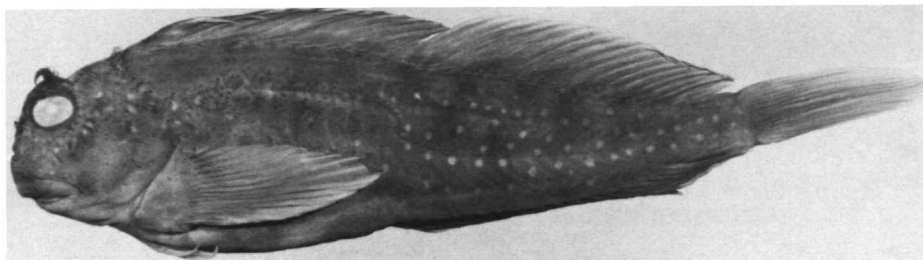


FIGURE 19.—*Scartichthys variolatus*, MNHNC P.6.227, female, 103 mm SL, Juan Fernandez Islands, Chile.

50), USNM 102010 (1: 65), USNM 128192 (2: 30, 52), USNM 128195 (1: 43), USNM 200396 (1: 45), USNM 227556 (57 of 100+ examined: 47–108), USNM 227981 (100+), USNM 273064 (5: 120–153); USNM 280209 (1: 63), USNM 280210 (4: 37–55), USNM 280211 (4: 33–57), USNM 280218 (2: 135, 135), ZMB 9058 (1: 220), ZMB 9107 (1), ZMB 13740 (4), ZMB 13741 (6). Chile: BMNH 1871.4.13.26–7 (2: 138–222), MNHNC P.6.434 (1), USNM 76389 (1: 71), USNM 122571 (7: 40–126), USNM 175368 (1: 78), ZMB 15659 (1), ZMB 15660 (3), ZMB 15662 (5).

Scartichthys variolatus (Valenciennes)

Salaris variolatus Valenciennes in Cuvier and Valenciennes, 1836:346 [Juan Fernandez Island; holotype MNHN 4410].

Salaris rubropunctatus Valenciennes in Cuvier and Valenciennes, 1836:348 [Juan Fernandez Island; lectotype MNHN A.2038, new designation] [new synonymy].

Ophioblennius fernandezensis Clark, 1938:184 [San Juan Bautista [Cumberland] Bay, Juan Fernandez Islands] [new synonymy].

DIAGNOSIS.—A species of *Scartichthys* with the following combination of characters: 80–93 dentary incisors, 18 segmented dorsal-fin rays, pupil-size black spot on first and sometimes second interspinal membrane, and pupil-size white spots (brownish red in life) on head and body.

DESCRIPTION.—Dorsal fin XI–XII (XII in 98.6% of specimens), 17–18 (18 in 91.2%); anal fin II, 19–20 (19 in 56.9%); total procurrent caudal-fin rays 12–14 (1 specimen with 16); pelvic fin I, 4; vertebrae 10 + 23–25 (24 in 94.2%) = 33–35 (34 in 94.2%); last pleural ribs on vertebral centrum 11; last epipleural rib on vertebral centrum 16–19 (17–18 in 91.2%); anal pterygiophores 2–1–1, 1–2–1, or 1–1–2 (1–1–2 in 76.8%); nuchal cirri 20–95 (20–77 in 95.2%); supraorbital cirri 22–116 (19–74 in 91.7%); nasal cirri 8–31 (10–23 in 90.0%); LL tubes 19–21 (20–21 in 90.0%); last LL tube on base of caudal fin; no scale-like flaps along LL; lower lip entire mesially (plicate laterally); gill rakers 21–28 (based on 16 specimens); pseudobranchial filaments on one side 10–15 (based on 16 specimens); premaxillary teeth 200–223 (based on 2 specimens); dentary teeth 80–93 (based on 30 specimens); upper lip crenulae approximately 35–43; nuchal cirri in 2

widely separated transverse rows on either side of nape; first dorsal-fin spine of adults approximately equal to second in males and females; dorsal-fin membrane deeply incised above last dorsal-fin spine; dorsal-fin membrane attached to caudal peduncle in advance of caudal fin in adults; cephalic pore system complex (3 or more pores at most positions; number of pores increases with increasing SL); male genital papilla with urogenital orifice located basally between 2 short protuberances on a fleshy swelling behind anus (Figure 14E); testes elongate, length more than twice width; maximum SL about 150 mm; pupil-size black spot on distal portion of membrane between first and second dorsal-fin spines (93.5% of specimens) and occasionally a second spot on membrane between second and third spines (6.5%).

The smallest mature female (ova ~0.8 mm diameter) examined is ~100 mm SL. Males mature by ~100 mm SL.

COLOR IN ALCOHOL.—Subadults and adults of both sexes (Figure 19 shows a female) have a dark brown background coloration with pupil-size pale spots over head and body, and 7 to 9 broad, faint, dark-brown bars on body; dorsal fin with pupil-size black spot on first interspinal membrane, remainder of fin dusky with small pale spots, dorsal and anal fins with distal ends of elements pale tipped; caudal fin brown with small pale spots; black spot about half diameter of pupil on head behind posterior margin of eye.

COLOR IN LIFE.—I have not seen the life colors of this species, but Valenciennes in Cuvier and Valenciennes (1836:347) described (based on a drawing “made by Gay”) the spots on the body as brownish red. A color illustration (presumably the one rendered by Gay) in the Cuvier and Valenciennes manuscript material in the library of the Muséum National d’Histoire Naturelle, Paris, clearly shows the brownish red spots described in their 1836 publication. Other colors are the same as described for specimens in alcohol.

COMPARISONS.—*Scartichthys variolatus* differs from other *Scartichthys* in that adults have 80–93 dentary teeth. *Scartichthys variolatus* also differs from *S. gigas* in typically having 18 segmented dorsal-fin rays (versus 17 modally). The distinctive color pattern of *Scartichthys variolatus* comprising pale (brownish red in life) spots on a dark background will

distinguish this form from all other *Scartichthys*.

DISTRIBUTION.—*Scartichthys variolatus* is an island endemic known only from San Felix and San Ambrosio Islands (26°S), and Juan Fernandez Islands (33°S; Figure 16). It has been collected from rocky bottoms at depths of 1–9 m.

ETYMOLOGY.—The specific epithet, derived from the late Latin *variola* (smallpox or spotted), refers to the pattern of spots on the head and body.

NOMENCLATURE DISCUSSION.—Valenciennes in Cuvier and Valenciennes (1836:346, 348) described specimens belonging to *Scartichthys variolatus* under two species names, *Salarias variolatus* and *S. rubropunctatus*. The former description was based on an adult specimen and the latter on five young individuals from the same island. The syntypic series of *S. rubropunctatus*, also from the same island, comprises four specimens belonging to *Scartichthys variolatus* and one specimen with supraorbital and nuchal cirri morphologies similar to *S. viridis* and number of dentary teeth in the range for *S. variolatus*. As no other specimens of *S. viridis* have been collected from the Juan Fernandez Islands, I consider the last specimen to be an aberrant specimen of *S. variolatus*. It is possible, however, that Valenciennes inadvertently mixed some of his mainland Chile and Juan Fernandez Islands collections. To avoid future confusion, I designate a 43 mm SL male (MNHN A.2038) as lectotype of *Salarias rubropunctatus*. The name *S. variolatus* is the senior synonym, based on page priority, of *S. rubropunctatus*.

Clark (1938:184) described *Ophioblennius fernandezensis* based on eight specimens from the Juan Fernandez Islands. I have not examined the holotype (CAS 5557), but my examination of 3 of the 7 paratypes, the original description, and data taken from the holotype by V.G. Springer clearly indicates that this species was described based on ophioblennius-stage larval specimens of *Scartichthys variolatus*. Thus, *Ophioblennius fernandezensis* is a junior synonym of *Scartichthys variolatus*.

MATERIAL EXAMINED.—167 specimens, 40–163 mm SL.

Types: MNHN 4410 (1 specimen: 133 mm SL), holotype of *Salarias variolatus*, Ile Juan Fernandez; MNHN A.2038 (1: 43), lectotype of *Salarias rubropunctatus*, Ile Juan Fernandez; MNHN 1986-634 (3: 43–59), paralectotypes of *Salarias rubropunctatus*, Ile Juan Fernandez; MNHN B.2965 (1: 58), paralectotype of *Salarias rubropunctatus*, Ile Juan Fernandez; CAS 5558–5564 (examined 3 of 7 specimens: 40–42), paratypes of *Ophioblennius fernandezensis*, Juan Bautista Bay, Juan Fernandez Island.

Nontypes: Juan Fernandez Islands: BMNH 1935.9.10.19 (1: 117), MNHNC P.6.073 (4), MNHNC P.6.212 (1: 163), MNHNC P.6.230 (1), MNHNC P.6.408 (1), NMW 73428 (1), SIO 65-638 (41), USNM 176540 (1: 60), USNM 176546 (11: 45–97), USNM 280195 (1: 67), ZMB 15661 (3), ZMB 15663 (4). Isla San Felix: MNHNC P.6.406 (1), SIO 65-624 (65: 42–148). San Ambrosio Island: MNHNC P.6.166 (2), MNHNC P.6.227 (20).

Scartichthys viridis (Valenciennes)

Salarias viridis Valenciennes in Cuvier and Valenciennes, 1836: 344 [Valparaiso; holotype MNHN A.2128].

Salarias cuvieri Günther, 1861:248 [Chile; lectotype BMNH 1850.6.14.19 and paralectotype 1850.6.14.21, new designations] [new synonymy].

Blennophis semifasciatus Kner and Steindachner, 1866:369 [near Iquique, west coast of South America; neotype USNM 194480, new designation] [new synonymy].

Salarias concolor Philippi, 1896:380 [Valparaiso, Chile; type specimen not located, no depository listed] [new synonymy].

Salarias modestus Philippi, 1896:381 [not specified but presumably in Chile; type specimen not located, no depository listed] [new synonymy].

Salarias petersoni Fowler, 1940:189 [Antofagasta, Chile; holotype ANSP 69150] [new synonymy].

DIAGNOSIS.—*Scartichthys viridis* is distinctive in having a relatively uniformly pigmented body without spots. It is further differentiated from *S. gigas* and *S. variolatus* in having a high number of dentary teeth, 106–131 (versus 93 or fewer).

DESCRIPTION.—Dorsal fin XII,17–19 (18 in 78.6% of specimens); anal fin II,19–20; total procurrent caudal-fin rays 13–16; pelvic fin I,4; vertebrae 10 + 23–25 (24 in 82.6%) = 33–35 (34 in 82.6%); last pleural ribs on vertebral centrum 11–12 (12 in 69.6%); last epipleural rib on vertebral centrum 16–21; anal pterygiophores 1–1–2, 1–2–1, or 2–1–1 (1–2–1 in 65.2%); nuchal cirri 6–60 (6–40 in 88.9%); supraorbital cirri 20–51 (20–32 in 87.5%); nasal cirri 6–15 (6–12 in 88.9%); LL tubes 20–22 (21 in 63.6%); last LL tube on base of caudal fin; no scale-like flaps along LL; lower lip smooth mesially (plicate laterally); gill rakers 20–26 (based on 13 specimens); pseudobranchial filaments on one side 9–14 (based on 14 specimens); premaxillary teeth 226–268 (based on 5 specimens); dentary teeth 106–131 (based on 26 specimens; 93 in a 47 mm SL specimen); upper lip crenulae ~30–42; nuchal cirri in 2–4 groups of irregularly shaped cirri with broad separation across nape (Figure 8j); first dorsal-fin spine of adults approximately equal to second in both sexes; dorsal-fin membrane deeply incised above last dorsal-fin spine; dorsal-fin membrane attached to caudal peduncle in advance of caudal fin in adults; cephalic pore system relatively simple (less than 3 pores at most positions); male genital papilla with urogenital orifice located basally between 2 small protuberances on a fleshy swelling behind anus (Figure 14E); testes elongate, length more than twice width; maximum SL ~200 mm; pupil-size black spot on distal portion of membrane between first and second dorsal-fin spines and usually a second spot on membrane between second and third spines.

The smallest mature female (ova ~0.8 mm diameter) examined is ~170 mm SL, but females have fully developed ovaries by ~100 mm SL. Males mature by ~100 mm SL.

COLOR IN ALCOHOL.—Diffuse pupil-size black spot behind middle of posterior margin of eye at all sizes (often difficult to discern in dark specimens). Ophioblennius-stage larvae pale with 9 or 10 blotches on dorsum, pectoral fin with distal half black and proximal half pale. Adults of both sexes (Figure 20 shows a female) uniformly dark brown dorsally, becoming

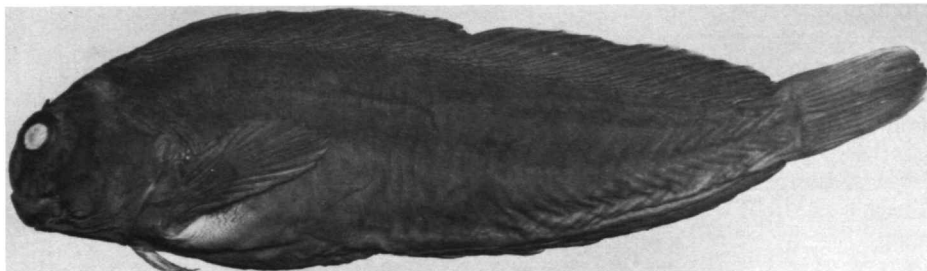


FIGURE 20.—*Scartichthys viridis*, GCRL 12618, female, 121 mm SL, Chile.

paler ventrally, and sometimes with midlateral dark-brown stripe (width about equal to eye diameter); all fins dusky; dorsal fin with pale area over distal tips of anterior 3 or 4 spines, other spines pale tipped, black pupil-size spot on each of first two or three interspinal membranes, spots located ventral to pale area.

COLOR IN LIFE.—Valenciennes in Cuvier and Valenciennes (1836:345) describes the life colors (from a drawing “made by Gay”) as dark green on the back and somewhat paler green on the stomach.

DISTRIBUTION.—*Scartichthys viridis* occurs from Independencia Bay, Peru (14°S), southward to Valparaiso, Chile (33°S) (Figure 16). Specimens have been collected from tidepools and rocky shore areas from depths of 0–10 m.

ETYMOLOGY.—The specific epithet, from the Latin *viridis* (green), refers to the green color of the body in life.

NOMENCLATURE DISCUSSION.—Valenciennes in Cuvier and Valenciennes (1836) described *Salarias viridis* based on a single specimen (MNHN A.2128) from Valparaiso, Chile.

The description of *S. cuvieri* by Günther (1861:248) is problematical in that it appears to be based on two species. He cited data in Valenciennes’ description of *S. variolatus*, which he placed in the synonymy of *S. cuvieri*, but based the description on two specimens (BMNH 1850.6.14.19 and 1850.6.14.21). The specimens he listed as material of *S. cuvieri* are referable to *Scartichthys viridis*. Smith-Vaniz and Springer (1971:55) listed these specimens as primary types of *S. cuvieri*. As there are type specimens for *S. cuvieri*, I consider the description to apply to these specimens. To avoid future confusion, I designate one of these (BMNH 1850.6.14.19, 196 mm SL male) as the lectotype of *Salarias cuvieri*, and consider the species name a junior synonym of *S. viridis*.

Kner and Steindachner (1866) described *Blennopterus semifasciatus* based on an ophioblennius-stage larva. Although Smith-Vaniz and Springer (1971) correctly placed it in the genus *Scartichthys*, the characters given in the original description are not sufficient to assign the specimen to a particular species of *Scartichthys*, but the figure of the type generally resembles ophioblennius larvae of *Scartichthys viridis*. I searched the collection of fishes in the Naturhistorisches Museum, Vienna, the type depository, but was unable to

locate the specimen. In addition, the type specimen was not found by V.G. Springer (pers. comm.) in the Hamburg Museum, where many Godeffroy types are located, thus it appears to be lost. To avoid future confusion, I have selected a neotype (USNM 194480, an ophioblennius larva of *S. viridis* from northern Chile) for *Blennopterus semifasciatus* and consider *Blennopterus semifasciatus* a junior synonym of *S. viridis*.

The type specimens (Philippi mentioned no depository in the original description) of *Salarias concolor* and *S. modestus*, described by Philippi (1896:380–382), could not be located (may be lost) but appear to be referable to *Scartichthys viridis*, based on Philippi’s descriptions. *Salarias concolor* was described by Philippi (1896) from Algarrobo and Valparaiso, Chile. This distribution limits the number of species to which it can belong and, combined with Philippi’s (1896) description, clearly places this species with *S. viridis*. Philippi (1896) did not give the geographic distribution of *S. modestus*. He compared his specimens with *S. variolatus*, but the color pattern he described clearly fits *S. viridis*. Thus, I place *S. modestus* in the synonymy of *S. viridis*.

Clark (1938:183) described *Ophioblennius xiphiodon* based on a mixture of specimens belonging to *Scartichthys gigas* and *S. viridis*. Based on the collection locality (Callao, Peru) of the holotype (specimen has been on loan and not available for my examination), I place *O. xiphiodon* in the synonymy of *S. gigas*. The two paratypes from Valparaiso, Chile, are referable to *S. viridis*, but all other type specimens are *S. gigas*.

Fowler (1940:189) described *Salarias petersoni* based on a metamorphosing specimen from Antofagasta, Chile, that is referable to *Scartichthys viridis*. The holotype (ANSP 69150) has lost the large canines typical of ophioblennius-stage larvae, but retains the larval pigmentation pattern consisting of dark blotches along the dorsum.

MATERIAL EXAMINED.—48 specimens, 38–197 mm SL.

Types: MNHN A.2128 (1 specimen: 197 mm SL), holotype of *Salarias viridis*, Valparaiso, Chile; BMNH 1850.6.14.19 (1: 196), lectotype of *Salarias cuvieri*, South America; BMNH 1850.6.14.21 (1: 142), paralectotype of *Salarias cuvieri*, South America; USNM 194480 (1: 45), neotype of *Blennopterus semifasciatus*, Atlantis Cruise 221,

24°54'S, 71°26'W, dip netted under a night light by S. Bray, 10 Dec. 1955; CAS 5552 (1: 40), paratype of *Ophioblennius xiphodon*, Valparaiso Harbor, Chile; ANSP 69150 (1: 46), holotype of *Salaria petersoni*, Antofagasta, Chile.

Nontypes: Chile: NMW 73462 (1: 128), RMNH 1810 (2: 188, 193), ZMB 1964 (1: 134). Chile, Algarrobo: GCRL 12618 (1: 122), GCRL 12619 (5: 154–167), USNM 273065 (2: 122,

158). Chile, Arica: MNHNC P.6.433 (1). Chile, Valparaiso and vicinity: MNHNC P.6.067 (2: 118, 156), MNHNC P.6.405 (3: 47–167), MNHNC P.6.407 (4), USNM 258788 (14: 38–181), USNM 276345 (3: 100–111), USNM 280217 (1: 35). Peru: BMNH 1868.1.11.22–3 (2: 169, 179), CAS-SU 48836 (1: 126).

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