The Indo-West Pacific Blenniid Fish Genus *Istiblennius* Reappraised: A Revision of *Istiblennius*, *Blenniella*, and *Paralticus*, New Genus

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ABSTRACT

Springer, Victor G., and Jeffrey T. Williams. The Indo-West Pacific Blenniid Fish Genus *Istiblennius* Reappraised: A Revision of *Istiblennius, Blenniella,* and *Paralticus,* New Genus. *Smithsonian Contributions to Zoology,* number 565, 193 pages, 73 figures, 45 tables, 1994.—*Istiblennius* Whitley, as most recently defined (Smith-Vaniz and Springer, 1971), comprises 2 monophyletic groups of species, which we recognize as separate genera, *Blenniella* Reid (9 species) and *Istiblennius* (14 species). A cladistic analysis supports the hypothesis that *Blenniella* and *Istiblennius* form a clade. The 14 species of *Istiblennius* include 2 new species: *I. pox,* from southernmost Red Sea, Persian Gulf, Gulf of Oman, and *I. spilotus,* from most of East African coast, Comoro Islands, Madagascar, Gulf of Oman, and Pakistan. A monotypic new genus, *Paralticus,* is described for *Salarias amboninensis* Bleeker, which had been assigned most recently (Smith-Vaniz and Springer, 1971) to *Praealticus* Schultz and Chapman. Although superficially similar to *Istiblennius* species, *P. amboinensis* is a member of a clade that also comprises *Praealticus, Alticus,* and *Andamia.*

Most of the species we revise exhibit statistically significant meristic sexual dimorphism, as well as noticeable geographic variation. All species are illustrated, including both sexes, individual and geographic variants, and ophioblennius stage prejuveniles (for all 5 species for which these stages are known). Distribution maps for all species are presented.

Cladistic analyses are given for a subset of the genera of the tribe Salariini, to which the 3 genera we revise belong, and for the species of *Blenniella* and *Istiblennius.* The generic level analysis corroborates a major portion of the analysis proposed by Williams (1990). Because of character variability, we consider the results of the generic analyses highly tentative.

Discussions of the biogeography of the genera and species are presented. The Philippine Islands are noted as a general area of endemism for fishes and an explanation is proposed. The pattern of east-west disjunctly distributed species, or sister species, first noted by Springer and Williams (1990), is modified slightly and shown to be common one for fishes. The western portion of the disjunct distributions appears to be restricted to the western Indian Ocean south of the equator and west of the mid-Indian Ocean Ridge. Some species that are not disjunctly distributed are limited in distribution to the same area of the Indian Ocean as the western disjunct portions of other species. The area of disjunction almost always includes, at least, the Gulf of Thailand and the southern half of the South China Sea.

Contents

"The secret of life is to have a task...And the most important thing is—it must be something you cannot possibly do!"

Henry Moore, sculptor

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Introduction

The original purpose of our study was to revise the genus *Istiblennius* Whitley as currently accepted and as essentially defined by Smith-Vaniz and Springer (1971). Springer began work on the revision as a secondary project shortly after 1971, and progressed slowly until 1984, when he began phasing it in as his primary project and Williams joined in the effort. A preliminary assessment of museum holdings of *Istiblennius* specimens indicated that it was the most abundantly represented genus of Salariini, if not all blenniids, and that the time required to examine the material and to record and analyze data taken from it, conceivably could extend beyond that remaining to the senior author.

For our study, we recorded and analyzed detailed data from over 9000 specimens, which emanated from 35 museums and one private collection, almost all of which we visited. We estimate that we encountered many thousands more museum specimens of *Istiblennius* and *Blenniella* on which we recorded little or no data. The specimens we excluded were those of species from localities for which we deemed we had examined adequate numbers. With relatively few exceptions, all our study specimens were radiographed, and we made a variety of counts of meristic elements from the radiographs. Using roughly average numbers for each count, we conservatively estimate that we counted to well over one million, one skeletal element at a time, but in reality we probably counted to two million, considering fin-ray, pore, and cirri counts made on whole

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specimens, and thousands of repeat counts made for purposes of verification. Numerous radiographed specimens were counted independently by one of us and an assistant, and where counts for the same specimen differed, they were repeated one or more times to rectify the differences.

It was not until we had essentially completed the routine examination and analysis of our material, prepared the species descriptions, and begun to prepare summary tables of characters (Tables 1–3), that we became convinced we were dealing with at least three clearly different groups of species. Further examination of the species, including skeletal preparations of all but one species, convinced us that the groups should be recognized generically. We also found indications that the genera probably formed a polyphyletic group.

The obvious next step in our study would have been a phylogenetic analysis of all currently recognized genera (28) and species (estimated at over 200) of Salariini. Fortunately, Williams (1990) had already hypothesized characters for a node that split the known genera into two monophyletic groups, and all our species fell into the clade to which he had devoted most of his attention. At this point, however, the cladistic analysis took a much more complicated turn because of the necessity to find and evaluate ever more characters and because almost none of the characters we could find were "black or white." This necessitated our introducing some rationalizations into the analysis in order to proceed with it. The same problems developed, and were treated similarly, in the phylogenetic analyses of our three genera. Orthodox practitioners of cladistics, predictably, will object, but that will have to be. To have proceeded otherwise would have delayed the appearance of the revisionary aspects of the study longer than we believe is reasonable (perhaps forever). Nevertheless, we believe we have drawn attention to some of the spoor that lead to the true phylogenies and that the defects of the phylogenies we present are possibly irrelevant ("right for the wrong reasons").

Harkening to the words of Ecclesiastes, "The making of many books is without end, and much study is a weariness of the flesh," we present the results of our study, and hope that a new generation will be inspired to improve on them.

METHODS

OSTEOLOGICAL PREPARATIONS.—Specimens were cleared with trypsin and stained with Alizarin-red S only or counter stained with Alcian blue, following the methods of Dingerkus and Uhler (1977).

COUNTS.—Most specimens were radiographed and counts of *dorsal-, anal-,* and *caudal-fin elements, precaudal* and *caudal vertebrae, pleural ribs,* and *epineurals* were made from radiographs. Occasional specimens lacked a dorsal-fin element or segmented anal-fin ray. A missing fin-ray element is recognizable by the presence of a pterygiophore without an associated fin ray. Missing fin elements were counted as if they were present. The status of the last anal-fin element, whether simple or split to base, was also determined from radiographs, but it was often necessary to verify determinations by direct examination of specimens.

Precaudal vertebrae are those anterior vertebrae lacking a hemal spine; all other vertebrae are *caudal vertebrae.* The anteriormost vertebra with a hemal spine was often impossible to determine from a radiograph because of shadows cast by other structures. In some species (e.g., *Istiblennius edentulus*), the first hemal spine is variously developed, ranging from a questionable, slight projection to a relatively long spine. When we were in doubt, only total vertebral counts were recorded. Total or caudal vertebral counts were not recorded for specimens in which there appeared to be vertebral fusions; we encountered no instances of fusions among the precaudal vertebrae. The penultimate caudal vertebra (pu2) varies in length among specimens of a species from any given locality. Pu2 may be about the same length as the next vertebra anteriorly or noticeably longer, and if longer it may or may not have a forked hemal spine and/or a long neural spine. Pu2 was always counted as a single vertebra whatever its condition; we found no obvious correlation between condition of pu2 and the total number of vertebrae present (for a case of similar variation in the structure of pu2, but with a correlation with vertebral count see Munroe and Mahadeva, 1989:464–465).

The *pleural rib* count is the number of the posteriormost vertebra, counting from the first precaudal vertebra, bearing a pleural rib or fragment of a rib, whether on one or both sides. Based on cleared and stained specimens, the anteriormost pleural ribs begin on the third vertebra, although it is usually not possible to ascertain this from a radiograph. Pleural ribs are associated with each succeeding precaudal vertebra and usually the first caudal vertebra, but occasionally they may be associated with the second caudal vertebra as well, but no others. The pleural ribs are usually bilaterally paired, but the posteriormost rib-bearing vertebra may bear a rib only

unilaterally, or the posteriormost pleural ribs may be represented only by disconnected fragments of bone.

The *epineural* (formerly epipleural; Johnson and Patterson, 1993:557, "the bones conventionally called epipleurals...are homologous with the epineurals, not epipleurals, of non-acanthomorph teleosts.") count is the number of the posteriormost vertebra, counting from the first precaudal vertebra, bearing an epineural. The anteriormost epineurals are always on the first vertebra and they continue posteriorly to at least the second caudal vertebra. Epineurals may be present only unilaterally on a few caudal vertebrae, and as many as two consecutive caudal vertebrae anterior to the posteriormost epineural-bearing vertebra may completely lack epineurals. Epineurals often decrease in size serially as they proceed posteriorly on the vertebrae, and it may be difficult to ascertain the presence of the posteriormost epineural. An individual count may be subject to an error of ±2, but the overall range of counts for a species is probably no greater than ±1.

Cirri, whether nasal, orbital (or supraorbital), or nape (or nuchal), were counted as the number of free cirri tips (or branches). Nape cirri, when present, are normally simple, but may bear one or two short branches in large individuals of a species. Individual specimens of species that typically have simple orbital cirri may have cirri with branches, although the presence of more than three branches, including the main branch, is rare.

Infraorbital pores, with the exception of the dorsalmost pore, are the external sensory pores issuing from openings in the sensory canals of the infraorbital bones. The dorsalmost pore of the infraorbital series is positioned at about one o'clock on the postorbital margin. This pore usually lies lateral to the junction of the dorsalmost infraorbital bone with the frontal, but the internal canal leading to the pore actually issues from an opening in the frontal bone. Because of difficulty in ascertaining this fact without dissection, we treat this frontal pore as an infraorbital pore. We term each internal canal opening of the infraorbital series a sensory pore position. The number of external pores representing a sensory pore position may vary from one to many (when there is more than one pore at a position, the pores at that position are connected to a common canal in the skin). Our counts of infraorbital sensory pore positions refer only to those pore positions between one and five o'clock on the postorbital margin. Our counts of pore positions with pairs or multiples of pores refer only to those same pore positions. The count of the infraorbital pores in Figure 12*b,* for example, is six with two pore positions with paired pores. The number and complexity of the sensory pores in *Blenniella gibbifrons* precluded our making reasonably accurate counts of pore positions.

Dentary pores (= mandibular pores of Smith-Vaniz and Springer, 1971, fig. 16) are the external sensory pores issuing from openings in the sensory canal of the dentary bone. The most posterior pore is the external opening in the sensory canal between the anterior end of the preopercle and the posterior end

of the dentary. This portion of the sensory canal is not enclosed in bone and, in most species, two pores are connected to this segment of the canal and the two pores are positioned at the posterior corner of the mouth (typical disposition of the mandibular pores in a species with two pores at the corner of the mouth is shown in Figure 19e; total complement of six mandibular pores shown).

Vertical pairs of lateral-line pores. These pores issue from vertically paired, short canal branches connected to the continuous portion of the lateral line (Figures 26, 29). Although an occasional branch may not be paired in one of the two species that are characterized by having paired vertical branches, counts are based on the number of dorsally directed branches.

MEASUREMENTS.—Specimens were measured with needle-point dial calipers reading directly to the nearest 0.1 millimeter.

Standard length (SL) is the distance between the midtip of the upper lip and the midlateral margin of the the hypural fan as indicated externally on the specimens (the latter point is actually opposite the diastema between the dorsal and ventral hypural plates, Springer, 1968:37, fig. 15). Variably, the anteriormost point of the head is in the predorsal area directly anterior to the orbit, and is in advance of the upper lip, but this anteriormost point of the head was not used in determining standard length. Standard lengths for specimens over 100 mm were rounded to the nearest whole mm, and, depending on usage (general discussion vs. particular specimens; distorted specimens vs specimens in good condition), were similarly rounded for smaller specimens.

Head length (HL) is the distance between the midtip of the upper lip and the dorsoposterior junction of the skin of the opercle with the body.

Caudal-fin length is the length of the longest caudal-fin ray measured from its base to its tip.

Orbital cirrus length is the greatest distance from the base of the cirrus where it joins the eye to the tip of the cirrus, if simple, or tip of the longest branch when inclined dorsally, if the cirrus is branched.

A *head crest* is a thin, blade-like flap that occurs dorsally on the head. Head crest height was measured as a perpendicular from the base of the crest to the highest point on the margin of the crest. Head crests occur in males of all species of *Istiblennius* and some species of *Blenniella*, but not in *Paralticus*. Males of *Paralticus* and those of *Blenniella* that lack head crests may have a rounded ridge in place of a crest, or the head may be somewhat inflated with a hump-like swelling dorsally. Females variably have or lack crests, but in no species in which the male lacks a crest does a female have one. The appearance of a head crest is closely correlated with standard length, and females tend to develop head crests at much larger sizes than do conspecific males. Preservatives often cause the skin on the top of the head to shrink, resulting in formation of a shrinkage ridge that is easily confused with the ridge-like precursor of a crest. Shrinkage ridges, unlike precursor ridges,

often veer sharply right or left from the median anteriorly, and may be stretched flat with one's fingers. Ridge precursors are often delineated by a dark, mid-longitudinal line of pigment.

Depth of dorsal-fin notch was measured from the tip of the first segmented dorsal-fin ray, which is usually somewhat curved distally, to the dorsal point of attachment on the ray of the interradial membrane from the next one or two elements (spines) anteriorly. Often, the membrane from the penultimate dorsal-fin spine exends posteriorly over the distal tip of posteriormost spine to attach to the first segmented ray (the posteriormost spine is completely imbedded in the membrane or applied closely to the anterior margin of the first segmented ray).

Posterior attachment of membrane from last dorsal-fin ray to caudal fin was measured as the distance between verticals, ascertained visually, at the posterior midlateral margin of the hypural fan and at the posteriormost attachment of the membrane to the dorsal edge of the caudal fin. This measurement is reported as percent caudal-fin length. Although not analyzed in detail, we observed that in those species in which the dorsal fin may be attached well out on the caudal fin, the extent of the attachment is generally more posterior in males than in comparably sized females, and in larger specimens than in smaller specimens.

OTHER CHARACTERS.—The *lateral line* consists of a dorsoanterior continuous canal and a posterior series of tiny tubes, each of which has a pore at both ends. The continuous canal may be interrupted once or twice forming up to three relatively long segments. The tubes roughly correspond with the body myomeres, but the spaces separating the tubes may be irregular and widely separated. The position of the end of the continuous portion of the lateral line relative to a dorsal element was determined by drawing the end of a probe perpendicularly, as judged visually, from the end of the lateral line to the base of the dorsal fin. The number of the dorsal-fin element base touched by the probe was recorded, the anteriormost spine being element number one. If the probe fell between the bases of two elements, this fact was recorded, but in tabulating frequencies, the more posterior element number was recorded. Position of the posteriormost bi-pored tube relative to a dorsal-fin element was determined and recorded similarly.

Posterior dentary canines are relatively large teeth, (usually only one on each side when present) compared to the numerous, fine, comb-like teeth in the lower jaw. The canines are positioned well posterior on the dentaries and may be difficult to locate if the mouth of a specimen has been fixed in a fully closed position. The first appearance of dentary canines varies ontogenetically: they are relatively much larger and appear much earlier in *Blenniella* species than in those two *Istiblennius* species that have them. There is no ontogenetic information on the appearance of dentary canines in *Paralticus*, which occur only in males.

Lip margins. The free margins of the upper and lower lips,

depending on the species, may be entire or crenulate (Figure 52, lower right) If the upper lip is crenulate, the lower lip may be crenulate or entire, but if the upper lip is entire, the lower lip is also, with the exception of some specimens of *Istiblennius zebra*. The crenulae may be faintly developed and irregular in size, less well developed laterally than medially, or vice versa. In some specimens of species with normally crenulate upper lips, the crenulae may border on the imperceptible, but will be represented by a series of small mucosal pads on the inner surface of the lip.

Last segmented anal-fin ray simple (N) or split to base (S). We did not distinguish between these two conditions when counting number of segmented anal-fin rays (method A counts of Springer, 1967:5). Often, the posterior element of the split-ray condition is represented only by a nubbin of bone that is discernible only on radiographs or in osteological preparations. Among a group of specimens of a species from a single locality there is no obvious correlation between the N or S conditions and the number of rays, except that occasionally we noted that a high or extreme count might be exhibited by a specimen with the N condition. Among the species of *Blenniella* and *Istiblennius,* the unusual state of the posteriormost anal-fin ray being attached by membrane to the caudal peduncle occurs only in specimens that exhibit the N condition. All *Paralticus* specimens exhibit the N condition, and the posteriormost ray is attached by membrane to the caudal peduncle in all specimens.

The S condition is characteristic of a group of genera in the blenniid tribe Salariini (henceforth referred to adjectivally as salariinin) that Williams (1990:11) hypothesized to form a monophyletic group, and which includes *Istiblennius* and *Blenniella.* The character state is quite variable within a genus, with some species or populations of some species having the N state as the modal condition.

Anterior ceratohyal process (ACP; Figure 1*b*). The ACP is a hook-like process on the dorsal margin of the anterior ceratohyal. The hook, when present, can take several different forms, for example, slender based, or broad based, somewhat triangular with a disconnected needle-like filament of bone extending to or toward the dorsal hypohyal. Occasionally, the process may be present on the anterior ceratohyal of one side, but not the other.

Infraorbital bones (Figure 2). The general structure of the infraorbital bones can be described as slender (Figure 2*a*) or stout (Figure 2*b,c*). Slender infraorbital bones are weakly attached dorsoposteriorly to the frontal, the depth of the joint between the second infraorbital and the first (lacrimal) is less than half the depth of the first infraorbital, and the dorsal margin of the first infraorbital is notched where it joins the lateral process of the lateral ethmoid. Stout infraorbital bones are strongly attached dorsoposteriorly to the frontal, the depth of the joint between the second infraorbital and first is half or more than the depth of the first infraorbital, and the dorsal margin of the first infraorbital is not notched where it joins the
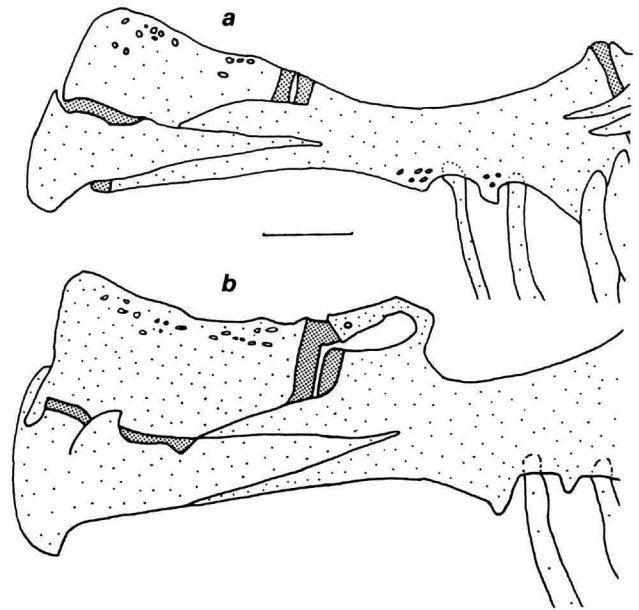
FIGURE 1.—Lateral views of anterior portions of 2 left hyoid bars (cartilage shown as dense stippling): *a, Istiblennius bellus,* USNM 293738, 42 mm SL, no process on dorsal margin of anterior ceratohyal; *b, Istiblennius edentulus,* USNM 296214, 52 mm SL, process on dorsal margin of anterior ceratohyal. (Scale bar represents 0.5 mm.)

lateral process of the lateral ethmoid. The two types of infraorbitals clearly distinguish *Istiblennius* and *Paralticus* (slender) from *Blenniella* (stout), but are not always clearly descriptive of other salariinin genera.

Ophioblennius-stage specimens (Figures 3–6). Ophioblennius-stage specimens are larval, postlarval, or prejuvenile specimens that are characteristic of some genera and species of salariinin blennies that Williams (1990:11) hypothesized to form a monophyletic group, and which includes, among other genera, *Blenniella* and *Istiblennius.* One monotypic genus, *Pereulixia* Smith, and several species of the genera Williams included are not known to have ophioblennius stages, but these circumstances may be due to artifacts of collection.

Ophioblennius-stage specimens are characterized by having one or two enlarged, laterally projecting, recurved canine teeth about mid-laterally on each dentary and one or more smaller anteriorly projecting canines on either side of the dentary symphysis (Figure 3). None of these canines are homologous with the posterior dentary canines of adults. There are no canines in the upper jaw, as there are in the ophioblennius stages of some other salariinin genera (e.g., *Ophioblennius;* Labelle and Nursall, 1985). Most, perhaps all, ophioblennius stages also have a distinctive pattern of melanophores on the pectoral fin (Figure 6). Ophioblennius stages may be planktonic, but most of those we examined were taken in shore collections with transformed juveniles and adults.
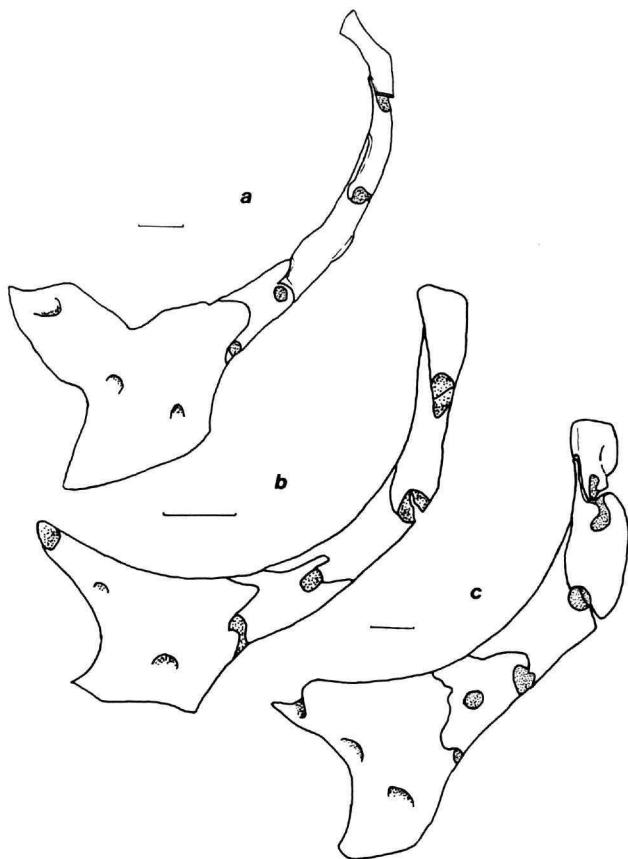
FIGURE 2.—Lateral views of left infraorbital bones: *a*, slender, with notch on dorsal margin of first infraorbital (*Istiblennius edentulus*, USNM 296214, male, 50 mm SL), characteristic of the species of *Istiblennius* and *Paralticus; b,c*, stout, without notch on dorsal margin of first infraorbital (*b, Blenniella caudolineata*, USNM 283142, male, 52 mm SL; *c, B. chrysospilos*, USNM 296309, male, 60 mm SL), characteristic of the species of *Blenniella*. (Scale bars represent 0.5 mm.)

FIGURE 3.—View of snout region of 11.0 mm SL ophioblennius-stage specimen of *Istiblennius zebra* (reproduced from Miller et al., 1979, fig. 92).

During our study, we identified ophioblennius stages for five species, and tentatively for one other (*Blenniella paula*, not illustrated): *Istiblennius dussumieri* (Figures 4*b*, 6*c*), *I. lineatus* (Figures 4*c*, 6*d*), *I. meleagris* (Figures 4*d*, 6*e*), *I. zebra* (Figures 3, 5, 6*f*), *Blenniella gibbifrons* (Figures 4*a*, 6*a*). We also encountered a prejuvenile stage of *Istiblennius edentulus* with darkly pigmented pectoral fins (Figure 6*b*), but lacking the dentary canines, which might indicate that it had just transformed (metamorphosed) from an ophioblennius stage and lost the canines. Based on juveniles of those species with ophioblennius stages, the stages lose the dentary canines first and then the dark pectoral-fin pigment, although the two losses appear to follow each other rapidly. Very few specimens of *Paralticus* are available and all are adults. The absence of an ophioblennius stage for *Paralticus* would be consistent with our hypothesis (see discussion in section on phylogenetic

analysis) that *Paralticus* is closely related to a group of genera including *Praealticus, Alticus,* and *Andamia,* which are not part of the clade Williams (1990) characterized as having an ophioblennius stage.

Color pattern. Stripes refer to longitudinal markings, which may be oriented diagonally; bands or bars refer to vertical markings

STATISTICAL TESTS.—The Student's t-test was used to test meristic data for sexual dimorphism when at least three cells contained data for one sex and at least two for the other. The t-tests were run at least twice, for verification, on a programmatically hard-wired Compucorp 344 Statistican calculator. Fisher's test (R. Langley, *Practical Statistics,* Dover Publications, Inc., 1971) was used for 2×2 cell comparisons when n ≤ 50. The Chi-square test, with Yates correction, was used to test meristic data when conditions for the t or Fisher's tests were not met. Differences between means for meristics of the sexes were considered significant when p ≤ .05.

PHYLOGENETIC ANALYSIS.—Procedures used to determine relationships among taxa follow the general principles of Hennig (1966). Each monophyletic group is diagnosed by synapomorphies. Character polarity is determined by outgoup analysis (Maddison et al., 1984), and parsimony is used to resolve cases where apomorphies support conflicting hypothe-
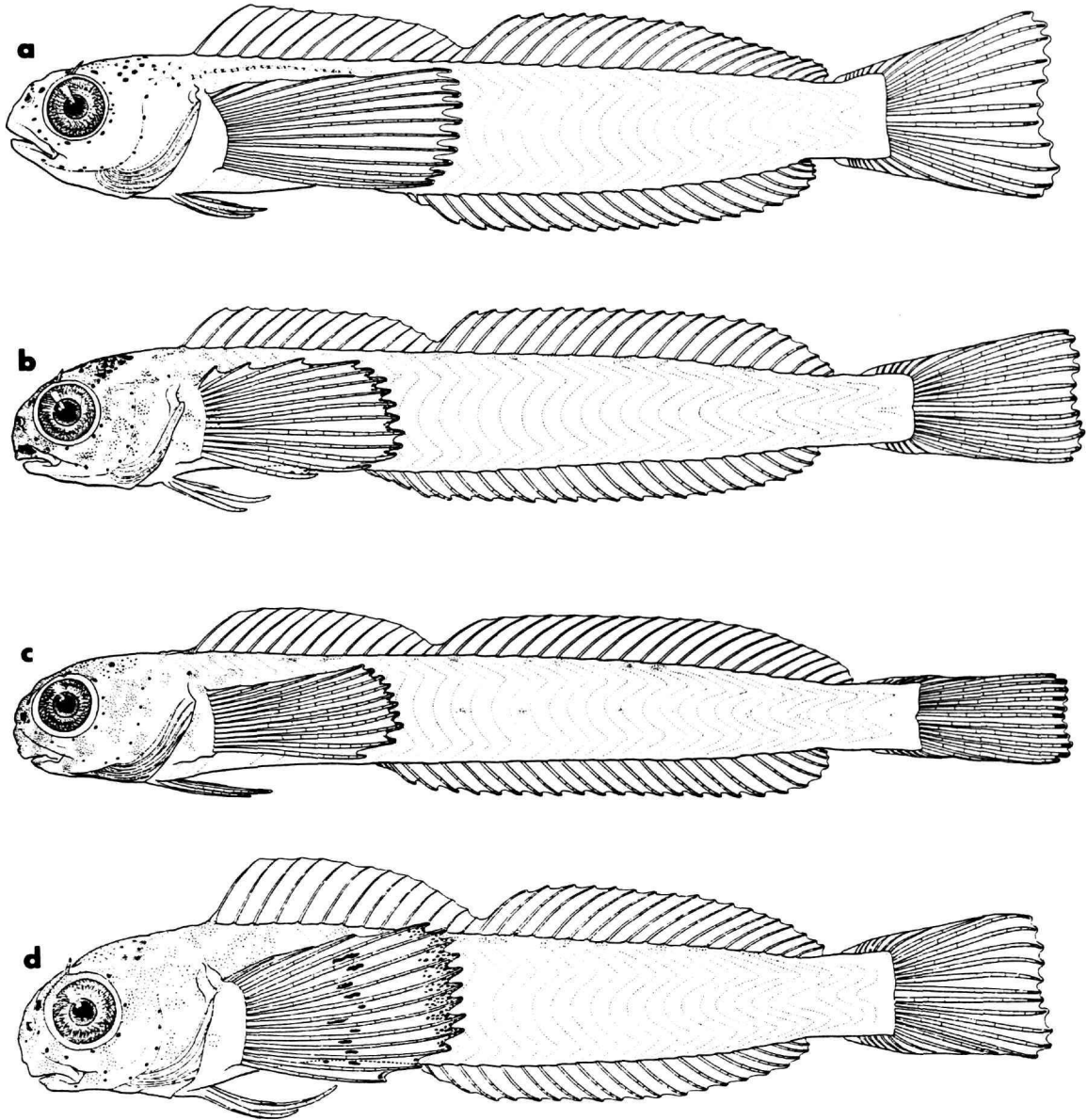
FIGURE 4.—Ophioblennius stage specimens: *a*, *Blenniella gibbifrons*, USNM 164994, 22.8 mm SL, Molokai, Hawaii; right pectoral fin illustrated in place of left (see also Figure 6*a*); *b*, *Istiblennius dussumieri*, UF 31308, 18.9 mm SL, Pulau Babi, Flores Island, Indonesia (see also Figure 6*c*); *c*, *I. lineatus*, USNM 317505, 19.8 mm SL, Mioko Island, Duke of York Group, off Rabaul, New Britain (see also Figure 6*d*); *d*, *I. meleagris*, USNM 174359, 16.1 mm SL, Yirrkala, Northern Territory, Australia (see also Figure 6*e*). (Drawings by T.B. Griswold).

ses of relationship.

SYNONYMIES.—With few exceptions, the synonymies include only strict synonyms. Table 4 provides an alphabetized listing of all nominal species of the three genera we treat and our current identifications of the nominal species.

INSTITUTIONAL ABBREVIATIONS.—In citing specimens, we follow Leviton et al. (1985) for the following institutional abbreviations:

AMNH   American Museum of Natural History, New York
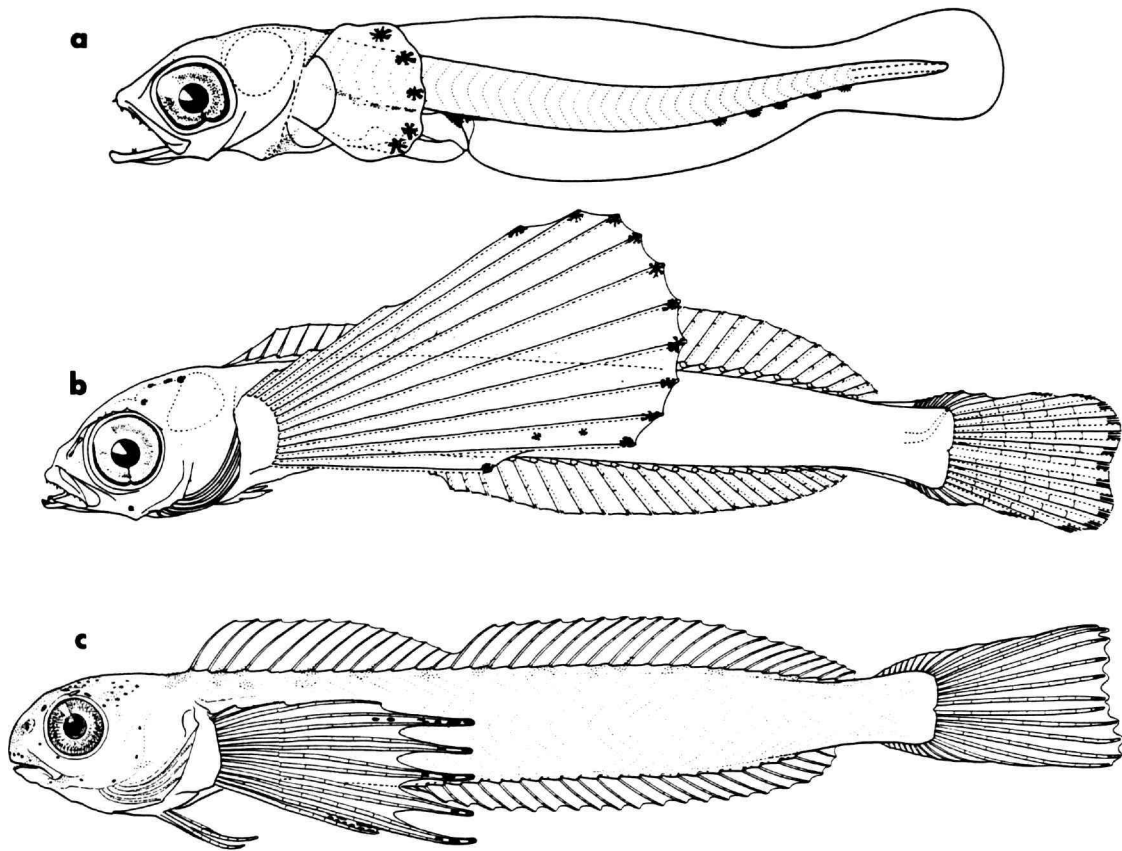
FIGURE 5.—*Istiblennius zebra*, ophioblennius stages: *a,b*, 3.3 and 11.0 mm TL (from Miller et al., 1979); *c*, USNM 292829, 21.4 mm SL, Oahu (see also Figure 6*f* and discussion under species account; drawing by T.B. Griswold).

AMS	Australian Museum, Sydney	RMNH	Nationaal Natuurhistorisch Museum, Leiden, Netherlands
ANSP	Academy of Natural Sciences of Philadelphia	ROM	Royal Ontario Museum, Toronto
BMNH	The Natural History Museum, London	RUSI	J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa
BPBM	Bernice P. Bishop Museum, Honolulu		
CAS	California Academy of Sciences, San Francisco; when followed by SU indicates specimens formerly cataloged in the collections of Stanford University, which retain their original catalog numbers.	SAM	South African Museum, Cape Town
		SMF	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt
		SMNS	Staatliches Museum für Naturkunde in Stuttgart
FAKU	Kyoto University, Department of Fisheries, Faculty of Agriculture, Maizuru	TAU	Tel Aviv University, Israel
		UAZ	University of Arizona, Department of Ecology and Evolutionary Biology, Tucson
FMNH	Field Museum of Natural History, Chicago		
HUJ	Hebrew University, Department of Zoology, Jerusalem	UF	Florida Museum of Natural History, Gainesville
IRSM	Institut Royal des Sciences Naturales de Belgique, Brussels	UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts	USNM	National Museum of Natural History, Washington
		VMM	Vanderbilt Marine Museum, Long Island, New York
MNHN	Museum National d'Histoire Naturelle, Paris	WAM	Western Australian Museum, Perth
MSNG	Museo Civico di Storia Naturale di Genova "Giacomo Doria"	ZMA	Zoologisch Museum, Universiteit van Amsterdam
NMNZ	National Museum of New Zealand, Wellington	ZMB	Museum für Naturkunde, Universitat Humbolt, Berlin
NMW	Naturhistorisches Museum, Vienna	ZMH	Zoologisches Institut und Museum, Universitat Hamburg
NTM	Northern Territory Museum of Arts and Sciences, Darwin	ZMUC	Kobenhavns Universitet Zoologisk Museum, Copenhagen
QM	Queensland Museum, Brisbane	ZSI	Zoological Survey of India, Calcutta
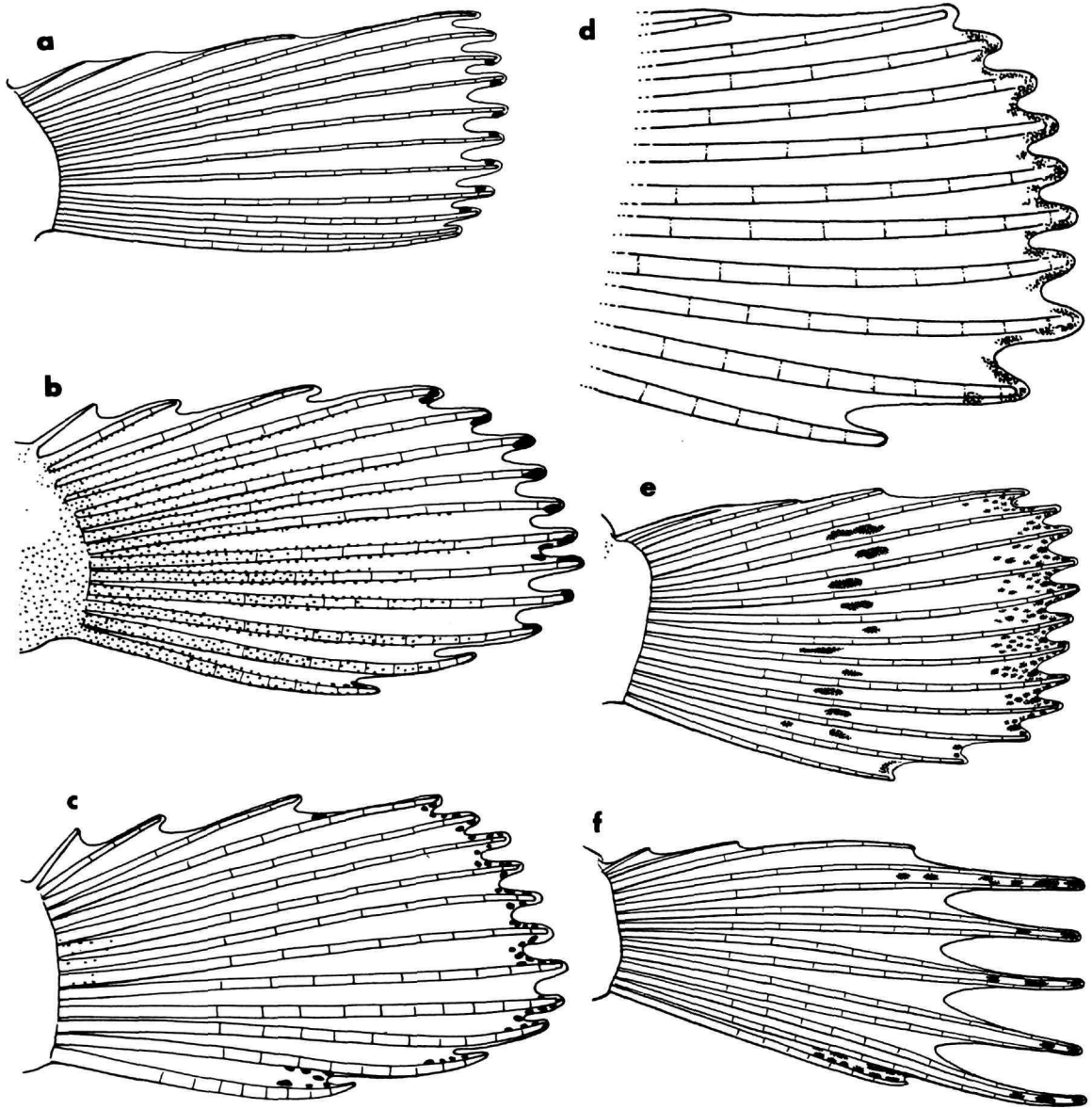
FIGURE 6.—Pectoral-fin pigment patterns for ophioblennius-stage specimens: a, Blenniella gibbifrons, USNM 164994, 22.8 mm SL (enlarged from Figure 4a); b, Istiblennius edentulus, UF 31308, 17.6 mm SL, Pulau Babi, Flores Island (specimen possibly just metamorphosed from ophioblennius stage; see discussion under species account); c, I. dussumieri, UF 31308, 18.9 mm SL (enlarged from Figure 4b); d, I. lineatus, USNM 317505, 19.8 mm SL (fin truncated and enlarged from Figure 4c, dorsalmost 2 rays not shown); e, I. meleagris, USNM 174359, 16.1 mm SL (enlarged from Figure 4d); f, I. zebra, USNM 292829, 21.4 mm SL (enlarged from Figure 5c). (Drawings by T.B. Griswold).

OTHER ABBREVIATIONS.—Most other abbreviations are clear from the context in which they are used. In giving localities, particularly in the tables, to accommodate limited space, and the material lists, to save space, the following

abbreviations are often used:

Arch	Archipelago
Aust	Australia
G	Gulf

GBR	Great Barrier Reef
Id	Island
IO	Indian Ocean
Is	Islands
NSW	New South Wales
O	Ocean
PNG	Papua New Guinea
PO	Pacific Ocean
Qd	Queensland
WA	Western Australia

PRESENTATION OF ACCOUNTS OF THE GENERA AND SPECIES.—The genera are presented in alphabetic order. Within a genus, the species accounts are presented in phylogenetic order as they appear in the cladograms (Figures 59 and 60). The species accounts may be presented separately or in groups under accounts of putatively monophyletic species complexes. The species complexes were actually conceived prior to our phylogenetic analyses based primarily on our subjective impressions (e.g., our partitioning a previously recognized species into 2 or 3 species, each differing from the other only slightly, even though consistently). In some instances we give combined descriptions for closely related species, followed by description of the differences that define the species.

ACKNOWLEDGMENTS

Joint Nomenclatural Discussion of *Blenniella, Istiblennius,* and *Paralticus*

Because of their intertwined nomenclatural history, we discuss the generic synonymies of *Blenniella, Istiblennius,* and *Paralticus* together. A key and the descriptive accounts of the 3 genera and the species within each follow this section.

The species covered by our study have always been included in the family Blenniidae, which in older literature comprised many groups that we no longer consider to be closely related. Norman (1943) published the first modern classification of the Blenniidae. He was also the first to recognize a subfamily Salariinae, with essentially the same composition we currently recognize, but only as a tribe (we do not recognize subfamilies within the Blenniidae). Norman, however, was uncertain what to do with certain taxa that he thought might be postlarval stages, and he assigned them to a subfamily Ophioblenniinae. Except for one taxon, *Somersia furcata* Beebe and Tee Van,

Table 1.—Summary table for some characters of species of Blenniella, Istiblennius, and Paralticus. (A = absent; Acp = anterior ceratohyal process; C = crenulate; c = commonly occurring state; Cteeth = posterior dentary canine teeth; Dfs = dorsal-fin spines; E = entire; Hdcrst = blade-like head crest; Llm = lower-lip margin; M = modal state, which maybe only state; N = not split to base; Napcir = nape cirri; P = present; Pecfr = pectoral-fin rays; S = split to base; Sgcaudfr = segmented caudal-fin rays; Sgpelfr = segmented pelvic-fin rays; Tafr = terminal anal-fin ray; u = uncommon state, usually less than 5% of specimens; Ulm = upper-lip margin; - = state not observed.)

Genus/Species	Dfs 12	13	14	Total dorsal-fin elements 29	30	31	32	33	34	35	36	37	38	Segmented anal-fin rays 16	17	18	19	20	21	22	23	24	25	26	Tafr N	S
BLENNIELLA																										
cyanostigma	u	M	u	-	-	-	-	u	c	c	c	-	-	-	-	-	u	c	c	c	-	-	-	-	M	c
caudolineata	u	M	u	-	-	-	-	c	c	c	c	-	-	-	-	-	-	c	c	c	u	-	-	-	M	c
interrupta	u	M	u	-	-	u	c	c	c	c	u	-	-	-	-	-	u	c	c	c	-	-	-	-	M	u
leopardus	u	M	u	-	u	c	c	c	c	-	-	-	-	-	-	-	-	c	c	c	u	-	-	-	M	-
bilitonensis	u	M	u	-	-	-	c	c	c	u	-	-	-	-	-	u	c	c	c	c	-	-	-	-	M	u
periophthalmus	u	M	u	-	-	u	c	c	c	u	-	-	-	-	-	-	u	c	c	c	-	-	-	-	c	M
paula	u	M	u	-	-	-	c	c	c	u	-	-	-	-	-	-	u	c	c	c	-	-	-	-	c	M
gibbifrons	u	M	u	-	-	c	c	c	c	-	-	-	-	-	-	u	c	c	c	u	-	-	-	-	c	M
chrysospilos	u	M	u	-	-	u	c	c	c	c	-	-	-	-	-	-	-	c	c	c	c	-	-	-	M	c
ISTIBLENNIUS																										
pox	u	M	u	-	-	-	-	c	c	c	-	-	-	-	-	-	-	-	c	c	c	-	-	M	c	
steindachneri	u	M	c	-	-	-	-	-	-	c	c	u	-	-	-	-	-	-	-	c	c	c	-	M	u	
lineatus	u	M	c	-	-	-	-	u	c	c	c	u	-	-	-	-	u	c	c	c	c	u	M	c		
rivulatus	u	M	u	-	-	-	u	c	c	-	-	-	-	-	-	u	c	c	u	-	-	-	M	c		
edentulus	u	M	u	-	-	u	c	c	c	c	u	-	-	-	-	u	c	c	c	c	-	-	c	M		
meleagris	u	M	u	u	u	u	c	c	c	u	-	-	-	-	u	u	c	c	c	-	-	-	c	M		
dussumieri	u	M	u	-	-	-	u	c	c	c	c	c	u	-	-	-	c	c	c	c	c	-	c	c		
zebra	u	M	u	-	-	-	-	-	c	c	c	-	-	-	-	-	-	c	c	c	-	-	-	M		
bellus	u	M	u	-	-	-	-	c	c	c	-	-	-	-	-	-	-	c	c	c	-	-	u	M		
muelleri	u	M	u	-	-	-	c	c	c	-	-	-	-	-	-	-	-	c	c	u	-	-	c	M		
unicolor	-	M	-	-	c	c	-	-	-	-	-	-	-	-	u	c	c	-	-	-	-	-	c	c		
spilotus	-	M	u	u	c	c	c	-	-	-	-	-	-	-	u	c	c	-	-	-	-	-	c	c		
flaviumbrinus	-	M	u	c	c	-	-	-	-	-	-	-	c	c	-	-	-	-	-	-	-	-	u	M		
colei	-	c	M	-	-	-	c	c	u	-	-	-	-	-	-	-	c	c	c	-	-	-	c	M		
PARALTICUS																										
amboinensis	-	-	M	-	-	-	u	c	c	-	-	-	-	-	-	u	c	c	-	-	-	-	M	-		

Genus/Species	Pecfr 12	13	14	15	Sgpelfr 2	3	4	Sgcaudfr 11	12	13	14	15	Napcir P	A	Hdcrst[1] ♂♂	♀♀	Cteeth ♂♂	♀♀	Ulm C	E	Llm C	E	Acp
BLENNIELLA																							
cyanostigma	-	u	M	u	-	M	-	-	-	M	-	-	-	M	P	P	P	P	-	M	-	M	P
caudolineata	u	u	M	u	-	M	-	-	-	M	-	-	-	M	P	P	P	P	-	M	-	M	P+A
interrupta	u	u	M	u	-	M	-	-	-	M	-	-	c	M	A	A	P	P	-	M	-	M	P+A
leopardus	-	u	M	u	-	M	-	-	u	M	-	-	M	-	A	A	P	P	-	M	-	M	A
bilitonensis	-	u	M	u	-	M	-	u	u	M	-	-	u	M	P	A	P	P	-	M	-	M	P
periophthalmus	-	u	M	u	-	M	-	-	u	M	-	-	M	-	A	A	P	P	M	-	-	M	A
paula	-	u	M	u	-	M	-	-	-	M	-	-	M	-	A	A	P	P	M	-	-	M	A
gibbifrons	-	u	M	u	-	M	-	-	-	M	-	-	c	c	A	A	P	P	-	M	-	M	A
chrysospilos	u	u	M	u	-	M	-	-	-	M	-	-	M	c	A	A	P	P	M	-	-	M	A
ISTIBLENNIUS																							
pox	-	u	M	u	-	M	-	-	-	M	-	-	-	M	P	A,P[2]	A	A	M	-	-	M	P
steindachneri	-	u	M	u	-	M	-	-	-	M	-	-	-	M	P	A	A	A	M	-	-	M	
lineatus	-	u	M	u	-	M	-	-	-	M	u	-	-	M	P	A	A	A	M	-	-	M	P
rivulatus	M	u	-	-	-	M	-	-	-	M	-	-	M	u	P	A	A	A	-	M	-	M	P
edentulus	-	u	M	-	-	M	-	-	u	M	-	-	M	-	P	P,A	A	A	u	M	-	M	P
meleagris	u	u	M	u	-	M	-	-	-	M	c	u	c	c	P	P,A	A	A	M	-	u	M	P
dussumieri	-	u	M	u	-	M	-	-	u	M	u	-	-	M	P	A	P,A	P,A	-	M	-	M	P
zebra	-	u	M	-	-	M	-	-	-	M	u	-	-	M	P	P	A	A	-	M	M	-	A
bellus	-	u	M	-	-	M	-	-	-	M	-	-	-	M	P	A	A	A	M	-	M	-	A
muelleri	-	u	M	u	-	M	-	-	u	M	-	-	-	M	P	P	A	A	-	M	-	M	A
unicolor	-	-	M	-	-	-	M	-	-	M	-	-	-	M	P	A	A	A	M	-	M	-	
spilotus	-	u	M	-	u	c	c	-	-	M	-	-	-	M	P	A	A	A	M	-	M	-	P
flaviumbrinus	u	u	M	u	u	M	-	-	-	M	u	-	-	M	P	A,P[2]	P,A	A	M	-	u	M	P
colei	-	-	M	u	-	-	M[3]	-	-	-	M	-	-	M	P	A	A	A	-	M	u	M	P
PARALTICUS																							
amboinensis	-	u	M	-	-	M	-	-	-	-	M	-	-	M	A	A	P	A	M	-	M	-	P

[1] In adults and blade-like, as opposed to absent, ridge-like, or hump-like.
[2] Present only uncommonly.
[3] Only 3 rays visible externally; innermost segmented ray greatly reduced, visible only in cleared and stained specimens.

Table 2.—Summary table of some characters of species of _Blenniella_, _Istiblennius_, and _Paralticus_. (Terminal pleural rib and terminal epineural refer to number of vertebra, counting anterior to posterior, with which posteriormost element articulates; c = commonly occurring state; Ifro = infraorbitals; M = modal state, which may be only state; S = stout; u = uncommon state, usually in less than 5% of specimens; W = weak; - = state not observed. With regard to epineurals, a "u" at the extreme high or low end of the range for any species, may indicate a state that actually does not exist, as epineural counts, made from radiographs, are often subject to an error of ± 2.)

Genus/Species	Precaudal vertebrae				Total vertebrae												Terminal pleural rib				
	10	11	12	13	34	35	36	37	38	39	40	41	42	43	44	45	10	11	12	13	14
BLENNIELLA																					
cyanostigma	-	M	u	-	-	-	-	-	-	c	c	c	-	-	-	-	-	-	M	u	-
caudolineata	u	M	u	-	-	-	-	-	u	c	c	c	-	-	-	-	-	u	M	u	-
interrupta	-	M	u	-	-	-	-	-	-	c	c	c	u	-	-	-	-	u	M	u	-
leopardus	-	M	u	-	-	-	-	-	-	c	c	-	-	-	-	-	-	-	M	-	-
bilitonensis	-	M	u	-	-	-	-	-	-	c	c	c	u	-	-	-	-	-	M	-	-
periophthalmus	-	u	M	u	-	-	-	-	-	c	c	c	u	-	-	-	-	u	c	c	-
paula	-	u	M	u	-	-	-	-	u	c	c	u	-	-	-	-	-	u	c	c	-
gibbifrons	-	u	M	u	-	-	c	c	c	c	-	-	-	-	-	-	-	-	u	M	u
chrysospilos	-	u	M	u	-	-	-	u	c	c	c	-	-	-	-	-	-	-	c	M	-
ISTIBLENNIUS																					
pox	M	u	-	-	-	-	-	-	-	c	c	c	-	-	-	-	u	M	u	-	-
steindachneri	c	M	-	-	-	-	-	-	-	-	-	c	c	c	-	u	u	c	c	-	-
lineatus	c	c	-	-	-	-	-	-	-	c	c	c	c	c	-	-	-	c	c	-	-
rivulatus	-	M	-	-	-	-	-	-	-	u	c	c	-	-	-	-	-	-	M	u	-
edentulus	c	c	-	-	-	-	u	c	c	c	-	-	-	-	-	-	-	c	c	u	-
meleagris	-	M	u	-	-	u	u	c	c	u	-	-	-	-	-	-	-	u	M	-	-
dussumieri	M	u	-	-	-	-	-	u	c	c	c	c	c	-	-	-	u	M	u	-	-
zebra	c	M	-	-	-	-	-	-	-	c	c	c	-	-	-	-	-	c	c	u	-
bellus	u	M	u	-	-	-	-	-	c	c	c	-	-	-	-	-	-	c	c	-	-
muelleri	M	-	-	-	-	-	-	c	c	c	u	-	-	-	-	-	-	M	-	-	-
unicolor	M	-	-	-	-	c	-	-	-	-	-	-	-	-	-	-	-	M	u	-	-
spilotus	M	u	-	-	-	u	c	u	-	-	-	-	-	-	-	-	-	M	u	-	-
flaviumbrinus	-	M	u	-	u	c	-	-	-	-	-	-	-	-	-	-	-	M	u	-	-
colei	-	M	u	-	-	-	-	c	c	c	-	-	-	-	-	-	-	u	M	-	-
PARALTICUS																					
amboinensis	-	M	-	-	-	-	-	c	c	c	-	-	-	-	-	-	-	M	-	-	-

Genus/Species	Terminal epineural																				Ifro	
	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	S	W
BLENNIELLA																						
cyanostigma	-	-	-	-	-	-	-	-	-	-	-	u	c	c	c	c	u	u	-	-	M	-
caudolineata	-	-	-	-	-	-	-	-	-	u	u	u	c	c	c	c	c	u	u	-	M	-
interrupta	-	-	-	-	-	-	-	-	u	u	-	u	c	c	c	c	c	u	-	-	M	-
leopardus	-	-	-	-	-	-	-	-	-	u	-	c	c	c	c	-	-	-	-	-	M	-
bilitonensis	-	-	-	-	-	-	-	-	u	u	c	c	c	c	c	u	u	u	-	-	M	-
periophthalmus	-	-	-	-	-	-	-	-	-	u	u	c	c	c	c	c	u	-	-	-	M	-
paula	-	-	-	-	-	-	-	-	u	u	c	c	c	c	u	u	-	-	-	-	M	-
gibbifrons	-	-	-	-	-	-	-	-	-	u	c	c	c	c	c	c	u	-	-	-	M	-
chrysospilos	-	-	-	-	-	-	-	-	-	-	-	-	u	c	c	c	c	c	u	-	M	-
ISTIBLENNIUS																						
pox	-	-	-	u	c	c	c	c	c	u	-	-	-	-	-	-	-	-	-	-	-	M
steindachneri	-	-	-	-	u	c	c	c	c	c	-	-	-	-	-	-	-	-	-	-	-	M
lineatus	-	u	u	c	c	c	c	c	c	u	u	-	-	-	-	-	-	-	-	-	-	M
rivulatus	-	-	-	c	c	c	c	c	-	-	-	-	-	-	-	-	-	-	-	-	-	M
edentulus	-	-	u	c	c	c	c	c	c	c	u	-	-	-	-	-	-	-	-	-	-	M
meleagris	-	-	u	c	c	c	c	c	u	-	-	-	-	-	-	-	-	-	-	-	-	M
dussumieri	-	-	u	c	c	c	c	c	u	u	-	-	-	-	-	-	-	-	-	-	-	M
zebra	-	-	c	c	c	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M
bellus	-	u	c	c	c	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M
muelleri	-	-	-	u	c	c	c	u	-	-	-	-	-	-	-	-	-	-	-	-	-	M
unicolor	c	M	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M
spilotus	c	M	c	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M
flaviumbrinus	c	M	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M
colei	-	-	u	c	c	c	c	u	-	-	-	-	-	-	-	-	-	-	-	-	-	M
PARALTICUS																						
amboinensis	-	-	-	c	c	c	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M

Table 3.—Summary table for some characters of the species of <u>Blenniella</u>, <u>Istiblennius</u>, and <u>Paralticus</u> (A = absent, c = common; Inforbpors = number of infraorbital pore positions with pairs or multiples of pores; LL = lateral line; Mafcp = membrane attaching anal fin to caudal peduncle, excluding ophioblennius stages; Mndsenpor = unilateral number of mandibular sensory pores; P = present; Pstcl = dorsal and ventral postcleithra; - = character state not observed; u = uncommon state, ususally less than 5% of specimens.)

Genus/Species	Mafcp P	Mafcp A	Pstcl P	Pstcl A	Mndsenpor 3 4 5 6 7	Inforbpors 0 1 2 3 4 5	LL continuous portion extends to below base of dorsal-fin element[1] 3 4 5 6 7 8 9 10 11 12 13 14 15 16
BLENNIELLA							
<u>cyanostigma</u>	u	M	M	-	- u M c -	u c M - - -	
<u>caudolineata</u>	u	M	M	-	u u c M u	u c M - - -	
<u>interrupta</u>	u	M	M	-	- u u M -	u c M u - -	
<u>leopardus</u>	-	M	M	-	- - u M -	- u M - - -	
<u>bilitonensis</u>	u	M	M	-	- - u M -	u c M - - -	
<u>periophthalmus</u>	u	M	M	-	- - u M u	- u M c - -	
<u>paula</u>	u	M	M	-	- - u M u	- - M c - -	
<u>gibbifrons</u>	u	M	M	-	- - u M u	- - - - - -[2]	
<u>chrysospilos</u>	u	M	M	-	- - u M -	- - u u c c	
ISTIBLENNIUS							
<u>pox</u>	u	M	M	-	u u M c -	M - - - - -	
<u>steindachneri</u>	-	M	M	-	- u c M -	M - - - - -	
<u>lineatus</u>	u	M	M	-	- u c M u	M - - - - -	
<u>rivulatus</u>	-	M	M	-	- u M - -	u c c - - -	
<u>edentulus</u>	u	M	M	-	- - c M -	u c c c c c	
<u>meleagris</u>	-	M	M	-	- u c M -	c M c - - -	
<u>dussumieri</u>	u	M	M	-	- u M u -	c M c u - -	
<u>zebra</u>	-	M	M	-	- u c M -	M c c - - -	
<u>bellus</u>	-	M	M	-	u u c M u	M c c - - -	
<u>muelleri</u>	u	M	M	-	u c M - -	M u - - - -	
<u>unicolor</u>	-	M	M	-	- - M - -	M - - - - -	
<u>spilotus</u>	-	M	M	-	- u M - -	M c - - - -	
<u>flaviumbrinus</u>	-	M	M	-	- u M u -	M - - - - -	
<u>colei</u>	-	M	M	-	- u c M u	c M u - - -	
PARALTICUS							
<u>amboinensis</u>	M	-	-	M	u M - - -	M - - - - -	

Genus/Species	Number of bi-pored lateral-line tubes[3] 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26	Longest (SL) ♂	Longest (SL) ♀
BLENNIELLA			
<u>cyanostigma</u>		81	60
<u>caudolineata</u>		82	68
<u>interrupta</u>		60	51
<u>leopardus</u>		60	50
<u>bilitonensis</u>		91	87
<u>periophthalmus</u>		118	101
<u>paula</u>		125	131
<u>gibbifrons</u>		102	90
<u>chrysospilos</u>		114	97
ISTIBLENNIUS			
<u>pox</u>		119	101
<u>steindachneri</u>		131	120
<u>lineatus</u>		140	112
<u>rivulatus</u>		86	93
<u>edentulus</u>		·144	132
<u>meleagris</u>		118	106
<u>dussumieri</u>		109	98
<u>zebra</u>		150	141
<u>bellus</u>		128	131
<u>muelleri</u>		70	55
<u>unicolor</u>		102	92
<u>spilotus</u>		121	97
<u>flaviumbrinus</u>		90	72
<u>colei</u>		118	103
PARALTICUS			
<u>amboinensis</u>		141	106

[1] Counting posteriorly from first spine; may extend to point between bases of two elements; thin line delimits range; heavy line denotes most frequent occurrences.
[2] Pores too numerous to determine number and nature of pore positions.
[3] Thin line delimits range; heavy line denotes most frequent occurrences.

Table 4.—Allocation of the Nominal Species-group Taxa of _Blenniella_, _Istiblennius_, and _Paralticus_ arranged alphabetically by species.

Nominal species-group taxa	Allocation in present study
Istiblennius afilinuchalis Schultz and Chapman, 1960:350	_Blenniella gibbifrons_
Salarias amboinensis Bleeker, 1857a:67	_Paralticus amboinensis_
Salarias andamanensis Day, 1876:332	_Blenniella cyanostigma_
Salarias andamensis Day, 1870:611	_Blenniella cyanostigma_
Salarias atratus Macleay, 1882:361	_Istiblennius edentulus_
Salarias atrimarginatus Fowler, 1946:182	_Istiblennius edentulus_
Salarias aureopuncticeps Fowler, 1946:179	_Blenniella chrysospilos_
Salarias auridens Alleyne and Macleay, 1877:338	_Istiblennius dussumieri_
Salarias azureus Seale, 1906:87	_Istiblennius edentulus_
Salarias barbatus Gilchrist and Thompson, 1908:108	_Istiblennius dussimieri_
Scartichthys basiliscus Fowler, 1904:552	_Istiblennius edentulus_
Salarias beani Fowler, 1928:441	_Blenniella caudolineata_
Salarias belemites DeVis, 1884:695	_Blenniella chrysospilos_
Salarias bellus Günther, 1861:256	_Istiblennius bellus_
Istiblennius bellus impudens J.L.B. Smith, 1959:242	_Istiblennius bellus_
Salarias bilitonensis Bleeker, 1858a:231	_Blenniella bilitonensis_
Salarias biseriatus Valenciennes _in_ Cuvier and Valenciennes, 1836:3	_Blenniella periophthalmus_
Salarias bleekeri Chapman, 1951:338	_Blenniella leopardus_
Salarias brevoorti Fowler, 1946:177	_Blenniella bilitonensis_
Salarias bryani Jordan and Seale, 1906:430	_Blenniella chrysospilos_
Entomacrodus calurus Fowler, 1904:555	_Blenniella cyanostigma_
Salarias caudolineatus Günther, 1877:209	_Blenniella caudolineata_
Salarias cervus Cuvier and Valenciennes _in_ Sauvage, 1880:218	_Istiblennius flaviumbrinus_
Salarias cheverti Macleay, 1881:12	_Istiblennius dussumieri_
Salarias chrysospilos Bleeker, 1857a:66	_Blenniella chrysospilos_
Istiblennius chrysospilos insulinus J.L.B. Smith, 1959:243	_Blenniella chrysospilos_
Blennius cinereus Castelnau, 1875:26	_Istiblennius edentulus_
Salarias colei Herre, 1934:96	_Istiblennius colei_
Salarias coronatus Günther, 1872:424	_Blenniella chrysospilos_
Salarias cristiceps Alleyne and Macleay, 1877:338	_Istiblennius dussumieri_
Salarias cyanostigma Bleeker, 1849:18	_Blenniella cyanostigma_
Salarias cypho Jenkins, 1903:506	_Istiblennius zebra_
Blennius dama Hemprich and Ehrenberg, 1899:3	_Istiblennius flaviumbrinus_
Salarias dama Valenciennes _in_ Cuvier and Valenciennes, 1836:366	_Istiblennius flaviumbrinus_
Salarias deani Jordan and Seale, 1905:799	_Blenniella bilitonensis_
Salarias diproktopterus Bleeker, 1857b:69	_Istiblennius edentulus_
Salarias doliatus Sauvage, 1880:217	_Istiblennius dussumieri_
Salarias dussumieri Valenciennes _in_ Cuvier and Valenciennes, 1836:310	_Istiblennius dussumieri_
Blennius edentulus Schneider _in_ Bloch and Schneider, 1801:172	_Istiblennius edentulus_
Scartichthys enosimae Jordan and Snyder, 1902:460	_Istiblennius edentulus_
Alticus evermanni Jordan and Seale, 1906:422	_Blenniella chrysospilos_
Salaris [sic] _flaviumbrinus_ Rüppell, 1830:113	_Istiblennius flaviumbrinus_
Salarias flavoumbrinus Rüppell, 1838:135	_Istiblennius flaviumbrinus_
Salarias fluctatus Fowler, 1945:70	_Istiblennius edentulus_
Salarias forsteri Valenciennes _in_ Cuvier and Valenciennes, 1836:315	_Istiblennius dussumieri_
Salarias fronto Günther, 1861:255	_Blenniella cyanostigma_
Salarias garmani Jordan and Seale, 1906:429	_Istiblennius edentulus_
Salarias geminatus Alleyne & Macleay, 1877:336	_Istiblennius dussumieri_
Salarias gibbifrons Quoy and Gaimard, 1824:253	_Blenniella gibbifrons_
Istiblennius gibbifrons insolitus J.L.B. Smith, 1959:242	_Blenniella gibbifrons_
Salarias gilberti Bryan and Herre, 1903:135	_Istiblennius edentulus_
Salarias goesii Bleeker, 1859a:19	_Istiblennius amboinensis_
Salarias hasseltii Bleeker, 1851:257	_Istiblennius lineatus_
Salarias hendriksii Bleeker, 1858a:233	_Blenniella bilitonensis_

Table 4.—continued

Istiblennius impudens (see Istiblennius bellus impudens)	
Istiblennius insolitus (see Istiblennius gibbifrons insolitus)	
Salarias insulae Ogilby, 1899:741	Istiblennius edentulus
Istiblennius insulinus (see Istiblennius chrysospilos insulinus)	
Salarias interruptus Bleeker, 1857b:68	Blenniella interrupta
Salarias kellersi Fowler, 1932:6	Istiblennius bellus
Salarias kingii Valenciennes in Cuvier and Valenciennes, 1836:334	Istiblennius lineatus
Entomacrodus leopardus Fowler, 1904:554	Blenniella leopardus
Salarias leopardus Fowler, 1938:82	Istiblennius bellus
Salarias lineatus Valenciennes in Cuvier and Valenciennes, 1836:314	Istiblennius lineatus
Salarias lividus Thiollière in Montrouzier, 1856:463	Istiblennius lineatus
Salarias marcusi Bryan and Herre, 1903:136	Istiblennius edentulus
Salarias martini Herre, 1942:2	Istiblennius colei
Salarias mccullochi Fowler and Bean, 1923:25	Istiblennius lineatus
Salarias melanocephalus Bleeker, 1849:18	Istiblennius edentulus
Salarias meleagris Valenciennes in Cuvier and Valenciennes, 1836:332	Istiblennius meleagris
Salarias muelleri Klunzinger, 1880:388	Istiblennius muelleri
Salarias multilineatus Fowler, 1945:68	Istiblennius lineatus
Salarias muscarus Snyder, 1908: 109	Blenniella periophthalmus
Alticus novemmaculosus Snyder, 1908:107	Blenniella bilitonensis
Salarias olivaceus Blyth, 1859:271	Istiblennius dussumieri
Salarias oryx Ehrenberg in Cuvier and Valenciennes, 1836:335	Istiblennius rivulatus
Blennius pardalis Castelnau, 1875:26	not Istiblennius
Salarias paulus Bryan and Herre, 1903:136	Blenniella paula
Salarias percophthalmus Swainson, 1839:274 [misspelling]	Blenniella periophthalmus
Salarias periophthalmus Valenciennes in Cuvier and Valenciennes, 1836:311	Blenniella periophthalmus
Salarias periophthalmus visayanus Herre, 1934:97	Blenniella bilitonensis
Salarias personatus Fowler, 1945:71	Istiblennius zebra
Istiblennius pox Springer and Williams, present study	Istiblennius pox
Salarias quadricornis Valenciennes in Cuvier and Valenciennes, 1836:329	Istiblennius edentulus
Salarias quadricornis status coloratus Klunzinger, 1871:488	inadmissible name
Salarias quadricornis status hyalinus Klunzinger, 1871:487	inadmissible name
Salarias quadricornis status transiens Klunzinger, 1871:488	inadmissible name
Salarias quadricornis status unitus Klunzinger, 1871:488	inadmissible name
Salarias rechingeri Steindachner, 1906:1411	Istiblennius edentulus
Blenniella rhessodon Reid, 1943:383	Blenniella gibbifrons
Salaris [sic] rivulatus Rüppell, 1830:114	Istiblennius rivulatus
Istiblennius rodenbaughi Schultz and Chapman, 1960:358	Blenniella gibbifrons
Salarias rutilus Jenkins, 1903:509	Blenniella gibbifrons
Salarias saltans Jenkins, 1903:508	Blenniella gibbifrons
Salarias schultzei Bleeker, 1859b:345	Blenniella periophthalmus
Salarias siamensis H.M. Smith, 1934:320	Istiblennius dussumieri
Salarias sindonis Jordan and Seale, 1906:427	Istiblennius edentulus
Istiblennius spilotus Springer and Williams, present study	Istiblennius spilotus
Salarias steindachneri Pfeffer, 1893a:143; 1893b:15	Istiblennius steindachneri
Istiblennius steinitzi Lotan, 1970:367	Istiblennius flaviumbrinus
Scartichthys stigmatopterus Fowler, 1904: 553	Istiblennius dussumieri
Salarias striatomaculatus Kner and Steindachner, 1866:368	Istiblennius dussumieri
Salarias striolatus Day, 1876:333	Blenniella cyanostigma
Salarias sumatranus Bleeker, 1851:256	Istiblennius edentulus
Blennius truncatus Forster, 1844:231	Istiblennius edentulus
Salarias tubuensis Seale, 1906:87	Blenniella paula
Salarias unicolor Rüppell, 1838:136	Istiblennius unicolor
Salarias unimaculatus Aoyagi, 1954:215	Blenniella chrysospilos
Salarias visayanus (see Salarias periophthalmus visayanus)	
Blennius vittipinnis Castelnau, 1875:25	Istiblennius meleagris
Salarias zamboangae Evermann and Seale, 1906:512	Istiblennius dussumieri
Salarias zebra Vaillant & Sauvage, 1875:281	Istiblennius zebra

which was subsequently assigned to the Labrisomidae (Springer, 1959:291, as Labrisomini), Norman's Ophioblenniinae contained only species that should have been included in his Salariinae.

Springer (1968) reappraised Norman's Blenniidae and hypothesized the monophyly of the Blenniidae and, among others, a tribe Salariini, which was essentially equivalent to the corrected Norman's Salariinae. Springer included tribal assignments of all nominal blenniid genera, and the composition of his Salariini for the time was complete, except for the omission of *Medusablennius* Springer, which he erroneously assigned to the Blenniini.

Smith-Vaniz and Springer (1971) expanded on Springer's (1968) definition of the Salariini (in which they included *Medusablennius*) and made the first attempt to assign all of the approximately 350 nominal species of the tribe to genera. Of the 94 nomenclaturally valid species-group taxa they allocated to *Istiblennius* (under which, among other genera, they synonymized *Blenniella*), 1 species (*Salarias oortii* Bleeker) should have been assigned to *Praealticus* Schultz and Chapman (Bath, 1992). Three species they assigned to *Praealticus* (*S. colei, S. goesii, S. mccullochi*) should have been assigned to *Istiblennius*, and 1 species, *S. amboinensis*, which they assigned to *Praealticus*, did not fit with any of their genera, keying out to their key couplet separating *Istiblennius* from *Salarias*.

Prior to 1943, the species we include in *Blenniella, Istiblennius*, and *Paralticus* (Table 4) were predominantly, or only, included by authors in the genus *Salarias* Cuvier, 1816, a currently valid senior synonym. Authors occasionally included species in *Alticus* Lacepède, *Blennius* Linnaeus, *Entomacrodus* Gill, and *Scartichthys* Jordan and Evermann, all of which are also currently valid senior synonyms (Smith-Vaniz and Springer, 1971; Eschmeyer, 1990).

Whitley (1943) described *Istiblennius* based on *Salarias muelleri* Klunzinger. He included *Entomacrodus calurus* Fowler (= *Blenniella cyanostigma*) as the only other species in *Istiblennius*, but questioned the inclusion because *Entomacrodus calurus* was described as having canine teeth in the lower jaw and Whitley used the absence of canine teeth as a distinguishing character of *Istiblennius*.

Shortly after Whitley's description of *Istiblennius*, Norman (1943) published the first modern synopsis of the Blenniidae. Norman recognized *Istiblennius*, in which he included several species that we currently assign to *Istiblennius, Blenniella* Reid, 1943 (understandably missed by Norman), *Entomacrodus* Gill, 1859, and *Praealticus* Schultz and Chapman, 1960. Norman also recognized *Entomacrodus*, in which he included three species, all correctly assigned.

Shortly after, or concurrently with, Norman's synopsis, Reid (1943) described a monotypic genus, *Blenniella*, based on ophioblennius-stage specimens of *Blenniella gibbifrons*. Reid failed to recognize the correct specific affinities of his specimens and described them as a new species, *B. rhessodon*.

The next study relevant to the present discussion is that of J.L.B. Smith (1948:340), who was concerned with South African fishes. Smith recognized that Norman's *Istiblennius* was a mixture of species with diverse affinities. He further believed that none of the South African species were allied to *Istiblennius muelleri*, type species of *Istiblennius*, and described *Alticops* and *Halmablennius* to accommodate the species that he believed did not belong in *Istiblennius*. Smith made no mention of *Blenniella* or Reid's (1943) study.

Smith (1948:340) distinguished his *Alticops* and *Halmablennius* from *Istiblennius* because the dorsal fins of the 2 genera were supposedly "more-or-less uniform, united with caudal at most basally," as opposed to *Istiblennius*, in which the dorsal fin was supposedly "elevated [and] united with whole of upper margin of caudal." With regard to this character, Smith was following Whitley (1943). Whitley had illustrated the holotype of *Salarias muelleri*, which appears to have an abbreviated (malformed?) caudal fin; hence, the attachment of the dorsal fin on the caudal fin appears to be relatively much further posteriorly than it is normally. Normal specimens of *muelleri* have the dorsal fin attaching out on the caudal fin no more than 18% of the length of the caudal fin. Smith was correct, nevertheless, in indicating that the dorsal fin was essentially free from the caudal fin in the type species of each of his 2 new genera. Some of the species Smith included in each of the genera, however, have the dorsal fin attaching out on the caudal fin, up to 20% or more of the length of the fin. One species (*Salarias oortii* Bleeker) Smith included in *Halmablennius* is currently (Bath, 1992) assigned to *Praealticus*, which was still undescribed at the time of Smith's publication.

Smith (1948:340) distinguished *Alticops* from *Halmablennius* only by the nature of the orbital cirrus: simple in *Alticops*, fringed in *Halmablennius*. Although the difference holds for those species that Smith examined, and even for an expanded *Alticops* (to include all the other species of our *Blenniella*), the character fails for *Halmablennius*, which is a synonym of *Istiblennius* and which includes forms with both simple and fringed cirri. Except for *Praealticus oortii*, Smith's *Alticops* included species we assign to *Blenniella* and *Istiblennius*. His *Halmablennius* included only species we assign to *Istiblennius*. Later, Smith (1959:241) included his *Alticops* as a junior synonym of *Istiblennius*, but continued to recognize *Halmablennius*, which he again distinguished from *Istiblennius* only by the nature of the orbital cirrus.

In his extensive revision of Indo-Australian Blenniidae, Chapman (1951) cited the Norman (1943) and Whitley (1943) publications, but made no reference to Reid (1943) or J.L.B. Smith (1948). Chapman (1951) returned *Istiblennius* to the synonymy under *Salarias*. Chapman's *Salarias* comprised species currently included in *Blenniella, Istiblennius, Paralticus* (new genus we describe below), *Salarias*, and *Praealticus* (the last still undescribed). Chapman acknowledged the "heterogeneous origin" of the species he included in *Salarias*, but wrote, presciently, "To accept a less broad taxonomic

category than that here considered would require the use of a considerable number of genera, not only those proposed by Whitley but several new ones. At the present stage of our knowledge...such splitting would not appear to serve any useful purpose" (Chapman, 1951:288–289).

Among the species Chapman recognized in his *Salarias*, is *S. goesii* Bleeker, under which he synonymized *S. colei* Herre and *S. martini* Herre. Chapman (1951:325) based his description of *goesii* on the latter two species because, "The type [of *goesii*] is in poor shape...." From our examination of the holotypes of all three of these species, we find that *S. colei* and *S. martini* are synonymous and assignable to *Istiblennius*, and that *S. goesii* is a synonym of *Paralticus amboinensis*. Chapman (1951:306), as *Salarias unicolor amboinensis* Bleeker, clearly recognized *amboinensis*, although he gave an incorrect count, XIII, for the number of dorsal-fin spines, which invariably, and distinctively, number XIV in this species (our study material includes most of the specimens Chapman examined). Chapman (1951:307) believed erroneously that his *S. unicolor amboinensis* was the Indo-Australian "cognate of *S. unicolor* [*unicolor*]... of the Indian Ocean," and went on to describe the color pattern of the latter subspecies, but which in reality is the color pattern of *Istiblennius spilotus*, a western Indian Ocean species we describe as new below, and which we discuss as the probable sister group of the Red Sea endemic *I. unicolor*!

Moving our discussion ahead a little, Schultz and Chapman (1960:368) described the genus *Praealticus*, in which they included, among other taxa, "*P. amboinensis amboinensis* (Bleeker)" and two other subspecies of *amboinensis*, but they made no mention of *unicolor*. They must have decided to include *amboinensis* in *Praealticus* based on data taken from misidentified specimens, as the characters of Bleeker's *amboinensis*, clearly recognized earlier by Chapman (1951), would have excluded it from *Praealticus*. In Schultz and Chapman's (1960:302–305) key to the genera of Salariinae, true *amboinensis* will not key to *Praealticus*. It keys to a couplet separating *Istiblennius* and *Negoscartes* Whitley, 1930 (= *Salarias*; Smith-Vaniz and Springer, 1971:38), and, based only on the first character in this couplet (last anal ray wholly or partly membranously attached to caudal peduncle), true *amboinensis* would key out to *Negoscartes*. Other characters in the couplet, however, would place *amboinensis* in *Istiblennius*.

Schultz and Chapman's mistake is surprising, but, perhaps, no more so than that of Smith-Vaniz and Springer (1971), who examined among others, the holotypes of *S. amboinensis* and its junior synonym, *S. goesii*, and those of *S. colei* and its junior synonym, *S. martini*. Smith-Vaniz and Springer assigned the first 3 of these species to *Praealticus*, and the fourth to *Istiblennius*. Smith-Vaniz and Springer (1971:26, 37) noted the difficulties of distinguishing *Praealticus* from *Istiblennius*: "Several species of *Istiblennius*, as here defined, show a remarkable resemblance to species of *Praealticus*, and there appears to be no single character...that will distinguish all

species of either genus...We urge future workers to consider carefully all the nominal species in both genera before describing additional species [of either]" (p. 26), and (p. 37), "species of *Istiblennius* are most often confused with *Praealticus* and are the most difficult to distinguish from it."

In their defense (made here by VGS), Smith-Vaniz and Springer were not revising *Istiblennius* and *Praealticus*, but were presenting a comprehensive synopsis of all the genera and species of Salariini, which, at that time, were in a complex and confused state, to serve as a basis for future generic revisions. Since 1971, the only major shift in the generic assignments of the several hundred nominal species they assigned to genera, are those made by us in the present study. (Note: H. Bath, 1992, at the suggestion of VGS, revised *Praealticus* and excluded consideration of *amboinensis*, *colei*, and *martini* based on VGS' informing him that we would be treating those species in our revision of *Istiblennius*; Bath, 1992:238.)

Returning to Chapman's (1951) study, it is relevant to the following discussion that Chapman recognized no junior subjective synonyms of *Salarias gibbifrons* in his extensive synonymy of that species.

Chapman's (1951) treatment of *Salarias* is additionally interesting because earlier, in manuscript, he had essentially completed a revision of the species we assign to *Blenniella*, and which he was clearly intending to be part of his 1951 publication (letter, 31 Oct 1946, to L.F. de Beaufort; copy in Chapman file of VGS). Although Chapman, in manuscript, retained these species in *Salarias*, he provisionally assigned them a new subgeneric name (same letter previously cited). It is doubtful that Chapman suppressed the subgenus in publication because he had become aware of Reid's *Blenniella* or J.L.B. Smith's *Alticops*. This is evidenced by Schultz and Chapman's (1960) extensive revision of Marshall and Marianas islands blenniids, in which they resurrected *Istiblennius*, but made no mention of *Blenniella* or *Alticops*, or the type species of these two genera. Schultz and Chapman (1960: 347) also recognized "*Istiblennius*" *gibbifrons* (quotation marks ours) and described two new species, both of which we have synonymized under *Blenniella gibbifrons*.

Schultz and Chapman apparently failed to recognize that *Blenniella rhessodon* Reid, 1943, is the ophioblennius stage of *B. gibbifrons*, even though Chapman (1951:246–247) was the first to recognize ophioblennius-stage specimens as the distinctive "larvae" (probably postlarvae or prejuveniles) of certain salariiins. He did so when he synonymized *Gloriella* Schultz, 1941, based on an ophioblennius stage, with *Cirripectes* Swainson, 1839, and stated that *Ophioblennius* Gill, 1860, had a similar "larva" to that of *Cirripectes*.

That Schultz and Chapman missed *Blenniella* is all the more surprising because Earl D. Reid (1943) did his work on *Blenniella* while employed as a museum aide under the supervision of L.P. Schultz (Schultz, 1961:121, and VGS, personal conversation with Schultz many years ago; also,

following Reid's name as author of the 1943 paper is the following: "(Communicated by Leonard P. Schultz.)"). Our recognition of *Blenniella* was arrived at independently of Chapman's manuscript, and is based primarily on characters—infraorbital bones, epineurals, bi-pored lateral-line tubes, etc, that Chapman did not consider; we also recognize 2 more species and some different synonyms.

The most recent substantive contribution to the classification of *Blenniella* and *Istiblennius* is that of Smith-Vaniz and Springer (1971), already alluded to. They published a synopsis of the genera of Salariini in which they included synonymies and definitions of all the nominal genera and a list of all the nominal species with assignments to genera. Smith-Vaniz and Springer synonymized *Alticops, Blenniella*, and *Halmablennius* under *Istiblennius*, but mistakenly assigned some species of *Istiblennius* to *Praealticus* and failed to recognize the distinctiveness of *Salarias amboinensis*, which they also assigned to *Praealticus*.

RELATIONSHIPS.—Williams (1990) corroborated the monophyly of the Salariini and hypothesized that the tribe comprised two monophyletic groups: *Rhabdoblennius* group and *Salarias* group. Within the *Salarias* group he hypothesized that some of the species previously included in *Istiblennius* appeared to be the sister group of all the other genera in a clade of eight genera. Relative to the genera we treat in the present study, Williams' decisions concerning the relationships of *Istiblennius* were based primarily on only 2 species, 1 each of *Istiblennius* and *Blenniella*. A few new characters, which we will discuss, tend either to place *Blenniella* and *Istiblennius* as sister genera in a clade that is the sister group of a clade of 4 genera, including *Paralticus*, that Williams (1990) did not analyze, or as 2 monophyletic groups in an unresolved polytomy of 8 monophyletic groups, one of which is *Paralticus* (see discussion in our section on Phylogenetic Analysis).

Key to the Species of *Blenniella, Istiblennius,* and *Paralticus*

(This key will probably serve to identify most specimens over 30 mm SL; difficulty can be expected with many specimens less than 30 mm SL; some species key out in more than 1 couplet)

1. Pectoral-fin rays strongly modally 12; dorsal fin notched from slightly less to sightly more than half length of first segmented ray; nasal cirrus usually simple; orbital cirrus usually simple, often longer than eye diameter; nape cirrus present; dark or dusky spot distally between interradial membranes of at least first two dorsal-fin spines; free margins of both lips entire; dentary canines absent . . . .
. . . . ***Istiblennius rivulatus***
(Red Sea and Gulf of Aqaba)
Pectoral-fin rays 13 to 15, strongly modally 14; dorsal fin notched more (usually much more) than half length of first segmented ray; nasal cirrus simple or multifid; orbital cirrus simple or branched, frequently shorter than eye diameter; nape cirrus present or absent; dark or dusky spot present or absent distally between interradial membranes of first two dorsal-fin spines; free margins of one or both lips entire or crenulate; dentary canines present or absent 2

2. Dorsal-fin spines 14 or 15 (rarely 13); posteriormost dorsal-fin ray attached by membrane at or anterior to caudal-fin base 3
Dorsal-fin spines 12 or 13 (rarely 14); attachment point of posteriormost dorsal-fin ray variable, extending as far posteriorly as one-third distance along dorsal edge of caudal fin 5

3. Segmented caudal-fin rays 14; posteriormost anal-fin ray bound by membrane to caudal peduncle; dorsal margin of lower lip crenulate; males with posterior dentary canine teeth, without blade-like crest on head (swollen rounded hump variably present) . . . . . ***Paralticus amboinensis,*** new genus, new combination
(eastern Indonesia)
Segmented caudal-fin rays 13; posteriormost anal-fin ray usually or always free from caudal peduncle; dorsal margin of lower lip entire; males without posterior dentary canine teeth, with blade-like crest on head 4

4. Ventral margin of upper lip entire . . . . ***Istiblennius colei***
(Philippines)

Ventral margin of upper lip crenulate 17

5. Anterior, continuous portion of lateral line with five or more vertically paired branches [Figures 26, 29]; posteriormost dorsal-fin ray attached by membrane at or, usually, anterior to caudal-fin base; well-developed blade-like crest mid-dorsally on head rarely present in males (never in females) 6

Anterior, continuous portion of lateral line with at most one or two vertically paired branches (restricted to anteriormost portion of lateral line); posteriormost dorsal-fin ray attachment variable, attached as far posteriorly as one-third distance along dorsal edge of caudal fin; well-developed blade-like crest present or absent mid-dorsally on head 7

6. Ventral margin of upper lip crenulate; preopercular sensory canal with single pore at each pore position; all or most dorsal-fin spines with conspicuous black tips; no large black spots in anteriormost interspinous membranes of dorsal fin; midlateral dark spot on body often present in males . . . .
. . . . **Blenniella chrysospilos,** new combination
(Indo-West and central Pacific)

Ventral margin of upper lip entire; preopercular sensory canal with pairs of pores at each pore position; few or no dorsal-fin spines with black tips; one or more black spots often present in anteriormost interspinous membranes of dorsal fin; no midlateral dark spot on body in males . **Blenniella gibbifrons,** new combination
(Pacific plate islands; Western Indian Ocean)

7. Segmented anal-fin rays 16 to 19; dorsal margin of lower lip partially to completely crenulate (crenulae may be less distinct than those of upper lip); orbital cirrus bush- or tree-like (branched laterally and medially); mandibular pores 4 or 5; distribution: Red Sea, western Indian Ocean, Gulf of Oman 8

Segmented anal-fin rays 17 to 26 (rarely 17 or 18); dorsal margin of lower lip crenulate or entire; orbital cirrus variable; mandibular pores 4 to 7; distribution varies with species, but all except *I. pox* and *I. steindachneri* (which have 22 to 24 and 23 to 25 segmented anal-fin rays, respectively) include at least Pacific and eastern Indian oceans 10

8. Dorsal margin of lower lip entire; segmented anal-fin rays 16 or 17; segmented dorsal-fin rays 16 or 17; segmented pelvic-fin rays 2 or 3 (rarely 2); caudal fin without columns of distinct, dark spots; continuous portion of lateral line terminating at vertical from 5th to 9th dorsal-fin spine (rarely as far posteriorly as 8th spine); disjunct, bi-pored, lateral-line tubes 3 to 11 (rarely more than 8); males often with small, posterior canine tooth on dentary; precaudal vertebrae 11 to 12 (rarely 12) . . . . **Istiblennius flaviumbrinus**
(Red Sea)

Dorsal margin of lower lip crenulate (sometimes only laterally); segmented anal-fin rays 17 to 19 (rarely 17); segmented dorsal-fin rays 16 to 19 (rarely 16); segmented pelvic-fin rays 2 to 4 (commonly 4, innermost, often difficult to see); caudal fin with or without columns of distinct dark spots; continuous portion of lateral line terminating at vertical from 7th to 10th dorsal-fin spine (usually posterior to 7th); disjunct, bi-pored lateral-line tubes 6 to 20 (usually more than 9); males never with posterior canine tooth on dentary; precaudal vertebrae 10 or 11 (rarely 11) 9

9. Upper lip with up to 12 slender, dark bands (lateralmost bands continuing dorsally to ventral margin of orbit [Figure 51]; body with irregular, dark bands (no reticulations) interrupted by irregular, slender, pale stripes; obvious segmented pelvic-fin rays 4; total vertebrae 35 . . . . *Istiblennius unicolor*
(Red Sea, gulfs of Aqaba and Suez)

Upper lip with small, dark or pale spots, which also occur on head and body (less obvious on females than males; [Figures 52, 54]; body with irregular, dark bands (males) or reticular pattern (females), not interrupted by slender, pale stripes; obvious segmented pelvic-fin rays 2 to 4; total vertebrae 35 to 37 (35 in only 2%

positions with paired pores in 93% of specimens; posteriormost bi-pored
lateral-line tube usually posterior to vertical from 9th segmented ray; nape cirri
present or absent . . . . *Istiblennius meleagris*
(Australia, from Perth, Western Australia, north around to
Sydney, New South Wales)
Segmented anal-fin rays 21 to 26 (rarely 21); all infraorbital sensory pore positions
with simple pores; posteriormost bi-pored lateral-line tube rarely posterior to
vertical from base of third segmented dorsal-fin ray, never posterior to 5th ray;
nape cirri absent 17

17. Males with more or less uniformly dusky or banded crest on head . . . .
. . . . *Istiblennius lineatus*
(Laccadive and Maldive islands, Indian Ocean, east to Mangareva,
Pacific Ocean)
Males with spotted crest on head 18
(Indian Ocean, from Pakistan west to east African coast,
including southernmost Red Sea)

18. Females with numerous dark spots on caudal peduncle; total dorsal-fin elements 36
to 38 . . . . *Istiblennius steindachneri*
(Western Indian Ocean south of Horn of Africa)
Females with fine lines or dashes on caudal peduncle; total dorsal-fin elements 33
to 36, uncommonly 36 . . . . *Istiblennius pox,* new species
(Western Indian Ocean north of Horn of Africa east to Laccadive
and Maldive islands)

19. Orbital cirrus branched; nape cirri absent; mandibular pores modally 5 (bilaterally
in 91% of specimens; unilaterally in 7%) . . . .
. . . . *Istiblennius dussumieri*
(Indo-west Pacific—absent from Pacific plate)
Orbital cirrus simple (occasionally with small side branch or tiny branches at tip);
nape cirri present or absent; mandibular pores modally 5 or 6 20

20. Posterior dentary canines absent 21
Posterior dentary canines present 23

21. Nape cirri present . . . . *Istiblennius edentulus*
(Indian and central and western Pacific oceans)
Nape cirri absent 22

22. Bi-pored lateral-line tubes 1 to 5, posteriormost tube lying between verticals from
bases of 9th and 12th dorsal-fin spines; mandibular pores modally 3 to 5 (always
5, at least unilaterally); segmented dorsal-fin rays 19 to 21; precaudal vertebrae 10
. . . . *Istiblennius muelleri*
(southeastern Taiwan SSE to Moluccas)
Bi-pored lateral-line tubes 4 to 15, posteriormost tube lying between verticals from
bases of 10th dorsal-fin spine and 21st segmented ray; mandibular pores 4 to 6 (6
bilaterally in 81%, and unilaterally in 12%, of specimens); segmented anal-fin rays
21 to 23); precaudal vertebrae 11 . . . . *Istiblennius zebra*
(Hawaiian Islands: Laysan SE to Hawaii)

23. Males: caudal and segmented-ray portion of dorsal fin usually without distinct, dark
spots; dark spot often present dorsally on opercle; 1 or more vertical pairs of pale
or dark ocelli usually present on posterior half of body; 2 anal-fin spines visible
externally (see also Table 5) 24
Females: caudal and segmented-ray portion of dorsal fin with numerous distinct,
dark spots; dark spot never present dorsally on opercle; no, or only faint, pale
ocelli on body; usually only 1 anal-fin spine visible externally (anterior spine
embedded in fleshy urogenital swelling) 28

24. Nape cirri present (absent in 1 of 18 available males); fleshy head crest ridge-like;
1 or 2 dark ocelli on body dorsal to midline (ocelli may border dorsal portion of

subquadrate, dark bands); 1 or both dorsal ocelli usually intensified, larger than pupil diameter . . . . *Blenniella leopardus,* new combination
(easternmost Indian Ocean: Andaman Islands south to Sumatra)
Nape cirri rarely, if ever, present; fleshy head crest varying with species, flap-like or low fold; up to 6 dark ocelli on body dorsal to midline (ocelli often incorporated in, or border, dark body bands); dorsal ocelli same size or smaller than pupil 25

25. Fine, dark spots usually present on distal half of pectoral fin; dark spot always present dorsally on opercle; up to 9 faint, dusky pinstripes on body (usually more than 4); stripes, when present, often extend posteriorly well beyond vertical from base of 6th segmented dorsal-fin ray; 5 or 6 (usually 5) dusky bands on body midside posterior to vertical from base of first segmented dorsal-fin ray (bands variably forked dorsally; band on caudal peduncle often faint or absent); vertical pair of fine, dark slashes present slightly posterior to orbit, dorsal slash extending dorsal to mid-orbital level; nuchal cirri absent . . . .
. . . . *Blenniella bilitonensis,* new combination
(western Pacific: Riu Kius south to Northern Territory, Australia)
Fine, dark spots rarely present on pectoral fin; dark spot present or absent dorsally on opercle; 0 to 4 dusky pinstripes on body; pinstripes, when present, extend no farther posteriorly than to vertical from base of 6th segmented dorsal-fin ray (usually failing to reach 6th ray base); 6 or 7 dusky bands on body midside posterior to vertical from base of first segmented dorsal-fin ray (bands variably forked dorsally, band on caudal peduncle and band just anterior to it, often faint or absent); small dark spot slightly posterior to orbit, if present, situated ventral to mid-orbital level; nuchal cirri present or absent 26

26. Fleshy head crest ridge-like; dark-margined pale spots on body slender, most slender spot (in ventral row) more than twice as long as deep; no dusky pinstripes on body; dark spot always present dorsally on opercle; nuchal cirri rarely present
. . . . *Blenniella interrupta,* new combination
(northeasternmost Indian Ocean east to New Hebrides)
Fleshy head crest blade- or flap-like; dark-margined pale spots on body ovoid, most slender spot less than twice as long as deep; 0 to 4 dusky pinstripes on body anteriorly; dark spot present or absent dorsally on opercle; nuchal cirri never present 27

27. Total mandibular pores 8 to 12 (rarely 12; Table 8), strongly modally 10 (5 on each side); dark spot on opercle frequently absent in specimens of some populations
. . . . *Blenniella cyanostigma,* new combination
(Indian Ocean east to Sumatra, Java, and Bali)
Total mandibular pores 9 to 13 (rarely 9 or 10), strongly modally 12 (6 on each side); dark spot on opercle rarely absent (may be small and faint) . . . .
. . . . *Blenniella caudolineata,* new combination
(southern Japan south to Moluccas, east to Tuamotus)

28. Posterior half of body with dusky blotches and bands, but no intensely dark spots, dashes or pinstripes; fine, dark spots usually present on distal half of pectoral fin; nuchal cirri absent; low, blade-like head crest absent, but low, rounded ridge usually present . . . . *Blenniella bilitonensis,* new combination
(Western Pacific from Riu Kius south to Northern Territory, Australia)
Posterior half of body with intensely dark spots, dashes, and/or pinstripes; fine, dark spots rarely present on distal half of pectoral fin; nuchal cirri present or absent; low, blade-like head crest present or absent 29
(Indo-Pacific, excluding Australia)

29. Nuchal cirri present (bilaterally); no fleshy crest or ridge on head; no pinstripes on body . . . . *Blenniella leopardus,* new combination
(easternmost Indian Ocean: Andaman Islands south to Sumatra)

Table 5.—Comparison of characters of males of five similar species of _Blenniella_.

Character	bilitonensis	caudolineata	cyanostigma	interrupta	leopardus
Crest on head	blade-like up to 2.6 mm high	blade-like up to 2.2 mm high	blade-like up to 2.8 mm high	low, fleshy ridge 0.0-0.7 mm high	low, fleshy ridge 0.0-0.6 mm high
	no narrow, pale submarginal stripe	pale, submarginal stripe often present	pale, submarginal stripe rarely present	not applicable	not applicable
Nape cirri	absent (present on one side of one specimen)	absent	absent	absent (present in 4% of specimens, usually only on one side)	present in 18 of 19 specimens (absent in one specimen)
Pectoral fin	dark spots usually present	dark spots rarely present	dark spots rarely present	dark spots rarely present	dark spots rarely present
Dorsal fin attached on caudal fin	often; up to 15% length of fin	often; up to 25% length of fin	often; up to 22% length of fin	uncommonly; up to 12% length of fin	uncommonly; up to 10% length of fin
Orbital cirrus	often longer than orbit	often longer than orbit	often longer than orbit	rarely equal to or longer than orbit	shorter than orbit in all but 1 specimen
Body pinstripes number	0 to 9	0 to 4	0 to 4	absent	absent
may extend posteriorly	well past vertical from base of 6th segmented dorsal-fin ray	as far as vertical from base of 6th segmented dorsal-fin ray	as far as vertical from base of 6th segmented dorsal-fin ray	not applicable	not applicable
Dark body bands[1]	rarely more than 5	frequently 6 or 7	frequently 6 or 7	usually 6	faint indications of up to 6
Ocelli on body	up to 3 vertical pairs; ventral ocelli often poorly developed	up to 4 vertical pairs, ventral ocelli often well developed	up to 4 vertical pairs; ventral ocelli often well developed	up to 5 vertical pairs, ventral ocelli often well developed	1 or 2 vertical pairs; ventral ocelli often well developed
Ocelli in ventral row	up to 4, usually 0 to 2	up to 5, usually 3 or 4	up to 5, usually 3 or 4	up to 6, usually 4 or 5	up to 6, usually 4 or 5
Mandibular sensory pores	strongly modally 6	strongly modally 6	strongly modally 5	strongly modally 6	strongly modally 6
Longest body ocellus	up to 2.5X longer than deep	up to 2.5X longer than deep	up to 2.5X longer than deep	up to 4X longer than deep	up to 4X longer than deep
Ocellus below 10-12th dorsal-fin segmented rays	absent or smaller than pupil, inconspicuous	absent or smaller than pupil, inconspicuous	absent or smaller than pupil, inconspicuous	less deep than pupil, usually conspicuous	may be much larger than pupil, usually conspicuous, very dark
Dark post-orbital markings (when present)	vertical pair of slashes, dorsalmost extending dorsal to mid-orbital level (slashes often joined)	dark spot ventral to mid-orbital level, often inconspicuous	dark spot ventral to mid-orbital level often inconspicuous	dark spot ventral to mid-orbital level, rarely another dorsal to midorbital level	dark spot ventral to mid-orbital level
Dark spot dorsally on opercle	always present	rarely absent	frequently absent	always present	always present
Dark spot just dorsal to opercle	present or absent	absent	absent	present or absent	present or absent
Largest specimen	91 mm SL (n = >150)	82 mm SL (n = >150)	81 mm SL (n = 91)	60 mm SL (n = >150)	60 mm SL (n = 19)

[1]when present, on mid-side posterior to vertical at base of first segmented dorsal-fin ray

Nuchal cirri rarely present (when present, almost always only unilaterally); fleshy crest or ridge present or absent on head; pinstripes present or absent on body 30

30. No fleshy crest or ridge on top of head; no dark pinstripes on body (body pattern of intensely dark spots and dashes); nape cirri rarely present (<5% of specimens) . . . . *Blenniella interrupta*, new combination (Western Pacific east to New Hebrides)

Fleshy crest or ridge present dorsally on head; 3 to 6 dark pinstripes present on body; nape cirri absent 31

31. Body with 5 or 6, more or less evenly spaced, dark pinstripes; total mandibular pores 8 to 12 (rarely 12; Table 8), strongly modally 10 (5 on each side) . . . . *Blenniella cyanostigma*, new combination (Western Indian Ocean east to Sumatra, Java, and Bali)

Body with 3 or 4 dark pinstripes, stripe ventral to body midline separated by space about twice that separating stripes above body midline (occasionally, faintly to darkly dusky dashes present in space above ventral stripe; second from dorsalmost stripe occasionally represented by dashes); total mandibular pores 9 to 13 (rarely 9 or 10), strongly modally 12 (6 on each side) . . . . *Blenniella caudolineata*, new combination (Southern Japan south to Moluccas, east to Tuamotus)

Blenniella Reid

Blenniella Reid, 1943:383 [type species: *Blenniella rhessodon* Reid, 1943 = *Salarias gibbifrons* Quoy and Gaimard, 1824, by original designation].
Alticops J.L.B. Smith, 1948:340 [type species: *Salarias periophthalmus* Valenciennes in Cuvier and Valenciennes, 1836, by original designation].

DIAGNOSIS (see also Tables 1 to 3).—A genus of Salariini (Smith-Vaniz and Springer, 1971) with stout infraorbital bones (Figure 2b,c) strongly attached to cranium, deepest portion of second infraorbital (usually at junction with first infraorbital) one-half or more depth of first, dorsal margin of first infraorbital without notch (Figure 2b,c); dorsal and ventral postcleithra normal and in contact (Smith-Vaniz and Springer, 1971, fig. 15d); vomer edentate; anterior dentary canines absent; posterior dentary canines present in males and females; more than 100 teeth in entire upper jaw, more than 75 in entire lower jaw; pectoral-fin rays strongly modally 14; segmented pelvic-fin rays 3; dorsal fin: XII to XIV,17 to 22 = 30 to 35 (strongly modally XIII in all species; segmented rays rarely 17; total elements rarely 30); membrane between last spine and first segmented ray notched more than half length of first segmented ray; posteriormost segmented ray bound by membrane to caudal peduncle, or, depending on species, sex, and SL, to point out on dorsal edge of caudal fin up to 25% length of fin; membrane attaching terminal anal-fin ray to caudal peduncle modally absent in all species; terminal anal-fin ray modally split to base or not split to base, depending on species; segmented caudal-fin rays modally 13, branched rays modally 9; lateral line consisting of continuous anterior portion followed posteriorly by series of 0 to 7 (usually 1 to 5) short, horizontally bi-pored tubes in skin; no scale-like flaps in continuous portion of lateral line; preoperculomandibular pores without cirri; fleshy blade-like crest present dorsally on head of males of only three species (*bilitonensis, caudolineata, cyanostigma*), and on head of females of only two species (*caudolineata, cyanostigma*); supraorbital cirrus present, usually simple or with tiny branches at tip; nape cirrus present or absent; upper lip without free dorsal margin; ventral margin of upper lip crenulate or entire; dorsal margin of lower lip entire; no cup-shaped fleshy disk or appendage posterior to lower lip; precaudal vertebrae modally 11 or 12; posteriormost epineural articulating with 20th to 31st vertebra from anteriormost (rarely on 20th, 21st, or 31st).

Blenniella cyanostigma (Bleeker), new combination

FIGURE 7

Salarias cyanostigma Bleeker, 1849:18 [Pagotang, Javae meridionalis; lectotype, RMNH 4794, designated below].
Salarias fronto Günther, 1861:256 [Java; lectotype BMNH 1845.6.22.196, designated below].
Salarias andamensis Day, 1870:611 [Andaman Islands; neotype USNM 112032, designated below].
Salarias striolatus Day, 1876:333 [Andamans; several syntypes presumably at ZSI; lectotype designation below, ZSI 2011].
Salarias andamanensis Day, 1876:332 [inadmissible emendation of *Salarias andamensis* Day, 1870].
Entomacrodus calurus Fowler, 1904:555 [Padang, Sumatra; holotype, ANSP 27807].

DESCRIPTION.—Dorsal fin (Tables 6 and 7). XII to XIV,19 to 22 = 32 to 35 (XIII in 93% of 168 specimens examined for character; 19 segmented rays and 32 total elements in only 2 specimens); mean numbers of total elements higher for males than for females from all 5 localities where means for both sexes are available (statistically significantly higher for 2 of the

localities); membrane between spinous and segmented-ray portions notched 60% to more than 75% length of first segmented ray (usually more than 75% length); membrane from posteriormost ray attaching to point ranging from slightly in advance of caudal-fin base to out on dorsal edge of caudal fin (out up to 22% length of fin in males, up to 9% in females; usually attached at or anterior to origin of caudal-fin base in both sexes).

Anal fin (Tables 6 and 7). II,19 to 22 (19 in only one, female, specimen); mean numbers of segmented elements higher for males than for females from all 5 localities where means for both sexes are available (statistically significantly higher for 2 of the 5 localities); posteriormost element usually not split to base (89% of 145 specimens examined for this character); fin bound by membrane to caudal peduncle in only 1 specimen. Skin covering distal half of anterior segmented anal-fin rays of few[1] large or mature males thickened or inflated, weakly crinkled along edges.

Pectoral-fin rays 10, 13 to 15 (14 bilaterally in 90% of 80 specimens examined for this character; 10 only unilaterally and in only one specimen (probably aberrant), 15 only unilaterally and in only two specimens.

Pelvic-fin rays I,3.

Caudal fin. Dorsal procurrent rays 4,6 or 7, ventral procurrent rays 5 to 7, total procurrent rays (Table 8) 10 to 14 (6/6, 7/6, or 7/7 in 93% of 145 specimens examined for this character); segmented rays 13 in all 84 specimens examined for this character.

Vertebrae (Tables 6 to 8). 11 to 12+27 to 29 = 38 to 40 (11 precaudal vertebrae in 98% of 132 specimens examined for this character), mean numbers of total (and caudal) vertebrae higher for males than for females for 4 of 5 localities where means for both sexes are available (statistically significantly higher for 2 of the 4 localities); posteriormost pleural rib on 12th or 13th from anteriormost centrum (on 12th in 97% of 133 specimens examined for this character); posteriormost epineural on 23rd to 29th from anteriormost centrum (on 24th to 29th in 98 of 99 specimens examined for this character).

Cirri. Nape cirrus absent. Orbital cirrus a simple filament, always shorter than orbital diameter in females, occasionally equal to or slightly longer than orbital diameter in males. Nasal cirri short, simple to palmate, with 2 to 6 branches (rarely simple or with 6 branches).

Lateral line. Continuous canal anterodorsally with simple pores extending posteriorly to point between vertical from between bases of 6th and 7th dorsal-fin spines to vertical between bases of 9th and 10th spines (extending posterior to

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[1] Most authors date this publication 1869. Duncan (1937) published a listing of the dates of publication of the *Proceedings of the Zoological Society of London*, 1859–1926, in which he gives the date of April 1870. According to information in the third part of the published *Proceedings of the Zoological Society of London for the Year 1869*, in which Day's paper was published, the proceedings were held on 9 December 1869. It would hardly seem possible for Day's paper to have been published before 1870.

vertical from base of 7th spine in 92% of specimens examined for this character), then continuing posteroventrally and posteriorly as series of 1 to 6 short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area between vertical from base of 7th spine and vertical from between bases of 12th and 13th spines (posterior to vertical from 9th spine in 85% of specimens).

Mandibular pores 4 to 6 (Table 8; 5 bilaterally in 69% of 169 specimens examined for this character, and at least unilaterally in 90% of the specimens).

Six or 7 sensory pore positions between 1 and 5 o'clock on postorbital margin (6 in 84 of 86 specimens examined for this character), 0 to 2 positions occupied by pairs of pores (2 positions in 87% of specimens; no pairs in only 2 specimens).

Posterior canines present in specimens longer than 26 mm SL, variably present in specimens as small as 25.0 mm SL.

Margins of both lips entire.

Crest. Males ≥25.1 mm SL with well-developed blade-like crest; only smaller male, 18.8 mm, with definite, dark, raised ridge where crest would form; highest crest, 2.9 mm, but crests uncommonly higher than 2.2 mm. Females ≥24.9 mm SL with distinct crest, except one female, 28.1 mm, with scarcely noticeable raised line in place of crest; highest crest 1.0 mm, but most crests <0.6 mm; crests lower than those of males of comparable SL.

Color pattern (in preservative). Males (Figure 7a). Head: variably dusky, usually without distinct dark markings; opercle uncommonly with small, faintly-to-darkly dusky spot dorsally; small, faintly-dusky, elliptical or almond-shaped spot just posteroventral to orbit often present, often almost unnoticeable; ventral surface often with pale areas, particularly anteriorly; upper lip occasionally with 3 barely recognizable, dusky bands; crest more or less uniformly dusky, never with well-delineated, narrow, pale distal margin. Body: well-preserved specimens with up to 9 dusky bands on midside, 6 or 7 bands posterior to vertical at dorsal-fin notch; bands anterior to notch and on caudal peduncle frequently faint or missing; dorsal body contour with several dusky saddles extending onto dorsal fin basally; saddles sometimes paired and connected to body bands; anterior 4 body bands below segmented-ray portion of dorsal fin may each incorporate vertical pair of small, dark ocelli (rarely more than 3½ ocelli pairs total, with half pair represented by ventral member), ventral member of each pair at ventral margin of band, dorsal member usually completely enveloped by band; additional ocellus occasionally present above dorsal member of each ocelli pair; other ocelli, barely noticeable, sometimes at mid-left and mid-right margins of 1 or 2 bands; occasionally up to 4 short, very fine, faintly dusky pinstripes in region below posteriormost 4 dorsal-fin spines and anteriormost 2 segmented dorsal-fin rays. Dorsal fin: spinous portion dusky, darker distally, occasionally with interrupted, very fine, dark, distal edge or subdistal stripe and/or pale distal edge; segmented-ray portion irregularly dusky, with fine, dark, interrupted pinstripes coursing through basal third of fin.

FIGURE 7.—*Blenniella cyanostigma: a,* H. Bath personal collection, male, 61 mm SL, Galle, Ceylon, right side reversed (note: dark spot dorsally on opercle variably present or absent in males); *b,* H. Bath personal collection, female, 60 mm SL, Hikkaduwa, Ceylon, typical 5-striped pattern; *c,* USNM 296020, female, 46 mm SL, Malindi, Kenya, uncommon 6-striped pattern (photographs by T.B. Griswold).

Caudal fin: several faint, fine, dusky spots on each ray of dorsal half (but distal margin unmarked dorsally) forming up to about 6 irregular bands; ventral half dusky with small, pale spots sometimes in membranes between rays. Pectoral and pelvic fins unremarkable, except one specimen with 4 or 5 fine, dark spots on each pectoral fin.

Remarks: J.L.B Smith (1959, fig. 5, as *Istiblennius andamanensis*) gives a drawing of a male that must have been based on a fresh specimen. It exhibits several more stripes on the side, each extending for a greater length of the body than those of preserved specimens, and also numerous pale spots posteriorly on the body. The fainter of the stripes (2 on body dorsally, 3 ventrally) and the pale spots (but not the ocelli in the bands) apparently fade in preservation, as evidenced by a color photograph, in our possession, of a fresh specimen from Kenya, which shows similar stripes and spots to those in Smith's illustration, but which are not in evidence in the same specimen preserved.

Based on a color slide, a freshly dead male from Ras Iwetme, Kenya, exhibits a complex color pattern: Several reddish orange spots posterior to eye, on cheek, and surrounding dark-blue spot on opercle; iris bright yellow ventrally, with

Table 6.—Frequency distributions for certain meristic characters in male specimens of *Blenniella cyanostigma* and *B. caudolineatus* from various localities. Underlining of means indicates significant differences between means of sexes from same locality (p ≤ .05).

Locality	Total dorsal-fin elements					Segmented anal-fin rays					Total vertebrae				
	32	33	34	35	x̄	20	21	22	23	x̄	37	38	39	40	x̄
cyanostigma															
Kenya	1	10	34	2	33.8	2	33	12	-	21.2	-	13	32	2	38.8
Zanzibar	-	-	2	-	34.0	-	1	1	-	21.5	-	-	2	-	39.0
Mozambique	-	2	4	-	33.7	1	3	2	-	21.2	-	4	2	-	38.3
Grand Comore Island	-	-	1	-		-	1	-	-		-	-	1	-	
Madagascar	-	-	6	2	34.3	-	5	3	-	21.4	-	-	7	1	39.1
Ceylon	-	1	15	4	34.2	-	13	7	-	21.4	-	1	17	2	39.0
Andaman Islands	-	-	1	-		-	-	1	-		-	-	1	-	
Sumatra	-	2	1	-	33.3	-	3	-	-	21.0	-	3	-	-	38.0
Java	-	-	2	-	34.0	-	2	-	-	21.0	-	-	-	-	
Christmas Island, IO	-	-	2	-	34.0	-	1	1	-	21.5	-	1	1	-	38.5
Bali	-	-	1	-		-	1	-	-		-	-	1	-	
caudolineatus															
Okinawa	-	-	1	-		-	1	-	-		-	-	1	-	
N Philippines*	-	1	7	-	33.9	1	4	3	-	21.2	-	1	7	-	38.9
S Philippines**	-	6	4	-	33.4	-	8	2	-	21.2	-	6	4	-	38.4
Ambon	-	4	4	-	33.5	1	5	1	-	21.0	-	3	5	-	38.6
Saipan	1	15	-	-	32.9	4	12	-	-	20.7	1	10	4	-	38.2
Rota	1	20	1	-	33.0	3	20	-	-	20.9	-	13	10	-	38.4
Guam	1	28	2	-	33.0	2	28	-	-	20.9	-	18	13	-	38.4
Palau	-	1	1	-	33.5	-	1	1	-	21.5	-	-	2	-	39.0
Ninigo Islands	-	-	1	-		-	-	1	-		-	-	-	1	
Trobriand Islands	-	-	2	-	34.0	-	-	2	-	22.0	-	-	2	-	39.0
Solomon Islands	-	-	1	-		-	-	1	-		-	-	1	-	
New Hebrides	-	2	18	10	34.3	1	5	19	4	21.9	-	2	17	8	39.2
Fiji	-	-	12	2	34.1	-	7	7	-	21.5	-	-	10	4	39.3
Rotuma	-	4	14	1	33.8	-	13	6	-	21.3	-	-	17	2	39.1
Gilbert Is, Tarawa	-	-	1	-		-	-	1	-		-	-	1	-	
Howland Island	-	7	3	-	33.3	-	10	-	-	21.0	-	3	7	-	38.7
Western Samoa, Apia	-	2	17	-	33.9	-	13	5	-	21.3	-	4	13	2	38.9
Amer Samoa, Tutuila	-	4	7	-	33.6	-	5	6	-	21.5	-	2	8	1	38.9
American Samoa, Tau	-	3	12	-	33.8	-	8	6	-	21.4	-	1	12	1	39.0
Palmerston Island	-	-	2	-	34.0	-	-	2	-	22.0	-	-	2	-	39.0
Rarotonga	-	-	3	-	34.0	-	-	3	-	22.0	-	-	2	1	39.3
Society Islands	-	1	3	-	33.8	-	1	3	-	21.8	-	-	4	-	39.0
N Tuamotu Arch	-	7	18	-	33.7	1	8	15	-	21.6	-	1	21	1	39.0

*Babuyan and Batanes islands **Southern Luzon to Negros

reddish brown spots separated by small, pale-bluish spots dorsally; reddish brown spot present just dorsoposterior to orbit; orbital cirrus pink; crest variably tinted, with broad, pale, subdistal margin and narrow, reddish brown distal margin; remainder of head toned dark greenish brown dorsally, faintly pale yellowish ventrally. Anterior half of body dark-greenish gray-blue dorsally, gray ventrally, dorsal area forming diffuse broad bands, ventral area interrupted by paler areas, forming several alternating pale and grayish stripes; two short, fine, black pinstripes present; anterior body color grading into brown on posterior half of body, darker bands and numerous small, white or pale-bluish spots, including ocelli, incorporated in bands. Both dorsal fins dark brown basally, segmented-ray portion with black, oblique pinstripes; dorsal to basal area, spinous portion anteriorly with variegated reddish brown spots grading into greenish brown spots posteriorly, distal margin narrowly bright white; segmented-ray portion, dorsal to dark basal area, tones of complex green broken into spots by irregular, slender, pale stripes; fin becoming reddish distally with narrow, pale distal margin. Caudal fin variably brownish and greenish, interrupted by numerous pale spots basally, spots gradually coalescing posteriorly, forming all pale distal margin. Anal fin darkly toned basally with interrupted bright-pale subdistal stripe and dark distal membranes; fin paler posteriorly with greenish tones.

Females (Figure 7b,c). Head: variably dusky, usually without distinctive marks; small, dusky spot occasionally ventroposterior to orbit; corner of mouth and adjacent area between mouth corner and ventral orbital margin occasionally noticeably pale, set off by dorsal, dusky area above corner of mouth and diffuse, dusky band extending from ventral orbital margin across upper lip. Body: most noticeable markings 5 or,

Table 7.—Frequency distributions for certain meristic characters in female specimens of
Blenniella cyanostigma and B. caudolineatus from various localities. Underlining of means
indicates significant differences between means of sexes from same locality (p ≤ .05).

Sex/Locality	Total dorsal-fin elements					Segmented anal-fin rays						Total vertebrae				
	32	33	34	35	x̄	19	20	21	22	23	x̄	37	38	39	40	x̄
cyanostigma																
Kenya	1	26	6	-	33.2	1	11	18	1	-	20.6	-	17	12	-	38.4
Zanzibar	-	3	1	-	33.2	-	-	4	-	-	21.0	-	3	1	-	38.2
Mozambique	-	2	2	-	33.5	-	-	3	-	-	21.0	-	1	3	-	38.8
Aldabra	-	1	-	-		-	1	-	-	-		-	-	1	-	
Grand Comore Island	-	-	2	-	34.0	-	-	-	2	-	22.0	-	-	2	-	39.0
Madagascar	-	1	2	-	33.7	-	1	1	1	-	21.0	-	1	2	-	38.7
Ceylon	-	16	11	1	33.5	-	9	16	4	-	20.8	-	9	18	-	38.7
Sumatra	-	1	-	-		-	1	-	-	-		-	1	-	-	
Java	-	1	-	-		-	1	-	-	-		-	-	1	-	
caudolineatus																
Japan, Tanegashima	-	1	-	-		-	-	1	-	-		-	1	-	-	
Taiwan	-	2	-	-	33.0	-	1	1	-	-	20.5	-	1	1	-	38.5
N Philippines*	-	4	3	-	33.4	-	-	7	-	-	21.0	-	3	4	-	38.6
S Philippines**	1	8	-	-	32.9	-	1	8	-	-	20.9	-	7	1	-	38.1
Ambon	-	5	2	-	33.3	-	-	7	-	-	21.0	-	2	4	-	38.7
Saipan	2	10	-	-	32.8	-	5	7	-	-	20.6	-	11	1	-	38.1
Rota	10	15	-	-	32.6	-	15	10	-	-	20.4	3	17	4	-	38.0
Guam	12	18	-	-	32.6	-	24	5	1	-	20.2	3	26	1	-	37.9
Palau	-	-	1	-		-	-	1	-	-		-	-	1	-	
Trobriand Islands	-	1	-	-		-	-	1	-	-		-	-	1	-	
New Britain	-	1	-	-		-	-	1	-	-		-	-	1	-	
New Hebrides	-	8	12	-	33.6	-	-	12	8	-	21.4	-	-	18	1	39.0
Fiji	-	10	4	-	33.3	-	1	10	2	-	21.1	-	5	9	-	38.6
Tongatapu	-	-	2	-	34.0	-	-	2	-	-	21.0	-	-	2	-	39.0
Rotuma	-	4	2	-	33.3	-	1	4	2	-	21.1	-	4	2	1	38.6
Gilbert Is, Tarawa	1	1	-	-	32.5	-	1	1	-	-	20.5	-	1	1	-	38.5
Howland Island	1	4	-	-	32.8	-	2	3	-	-	20.6	-	5	-	-	38.0
Western Samoa, Apia	-	15	1	-	33.1	-	5	11	-	-	20.7	-	9	7	-	38.4
Amer Samoa, Tutuila	-	4	2	-	33.3	-	-	5	-	-	21.0	-	2	4	-	38.7
American Samoa, Tau	1	7	4	-	33.2	-	2	7	3	-	21.1	-	4	8	-	38.7
Palmerston Island	-	1	-	-		-	-	1	-	-		-	-	1	-	
Rarotonga	-	-	5	-	34.0	-	-	3	2	-	21.4	-	-	4	-	39.0
Society Islands	-	1	5	-	33.8	-	-	3	3	-	21.5	-	-	6	-	39.0
N Tuamotu Arch	-	6	13	-	33.7	-	-	19	-	-	21.0	1	-	15	2	39.0

*Babuyan and Batanes islands   **Southern Luzon to Negros

uncommonly, 6 more or less evenly spaced, dark pinstripes extending posteriorly from area below 5 posteriormost dorsal-fin spines for varying distances to area below posterior third or fourth of base of segmented-ray portion of fin, there breaking up into numerous dark spots and dashes; stripe along body midline and 2 stripes above it, always present and darkest; up to 6 or 7 faintly dusky bands on midside anterior to and underlying dark pinstripes; bands occasionally forked ventrally, with disjunct small, paired saddles along dorsal body contour. Dorsal fin: spinous portion irregularly dusky, usually darkest distally, occasionally with 1 or 2 rows of diffuse, irregularly shaped, dusky spots distally; segmented-ray portion varying from almost unmarked (uncommonly) to, usually, bearing 2 or 3 rows of dark spots centered on rays. Anal fin faintly dusky, darkest distally. Caudal fin with up to about 8 irregular, vertical columns of dark spots centered on rays. Pectoral and pelvic fins essentially unmarked.

J.L.B. Smith (1959, pl. 16: fig. 7) provides a color illustration (painting) of a fresh female from Ibo, Mozambique. The illustration indicates brownish purple stripe on body dorsal to dorsalmost (3rd) dark pinstripe, slender reddish bands dorsally on head, bluish spot on cheek, another spot ventroposterior to orbit. All these marks, except occasionally the last, are not indicated by preserved specimens.

Size. Largest available specimen: male, 81 mm SL; males commonly exceeding 60 mm SL; largest female, 60 mm SL, few females exceeding 55 mm. Smallest available specimens: male, 18.8 mm SL; female, 24.9 mm SL; ophioblennius-stage specimens unknown.

COMPARISONS AND RELATIONSHIPS.—Based on overall similarity, (and our phylogenetic analysis, q.v.) *Blenniella cyanostigma* appears to be the sister species of the allopatric *B. caudolineata*. The latter species has long been considered a junior synonym of the former. J.L.B. Smith (1959:242) first

Table 8.—Frequency distributions for certain characters of specimens of _Blenniella cyanostigma_ and _B. caudolineata_ from various localities (total mandibular pores = right + left sides*; total procurrent caudal-fin rays = dorsal + ventral rays).

Locality	Total mandibular pores							Terminal epineural on vertebra #											Total procurrent caudal-fin rays							
	8	9	10	11	12	13	$\bar{x}$	21	22	23	24	25	26	27	28	29	30	$\bar{x}$	10	11	12	13	14	15	16	$\bar{x}$
cyanostigma																										
Kenya	1	4	46	19	9	-	10.4	-	-	-	5	8	17	7	6	1	-	26.1	1	4	44	19	3	-	-	12.3
Mozambique	-	-	7	2	2	-	10.5	-	-	-	1	-	3	1	2	-	-	26.4	-	2	2	1	-	-	-	11.8
Zanzibar	-	-	5	1	-	-	10.2	-	-	-	-	-	2	-	-	-	-	26.0	-	-	6	-	-	-	-	12.0
Aldabra	-	-	-	1	-	-		-	-	-	-	-	-	1	-	-			-	-	-	1	-	-	-	
Grand Comore Island	-	-	3	-	-	-	10.0	-	-	-	-	-	1	2	-	-	-	26.7	-	-	3	-	-	-	-	12.0
Madagascar	-	-	8	2	1	-	10.4	-	-	1	-	-	5	3	-	1	-	26.3	-	1	5	2	3	-	-	12.6
Ceylon	-	3	33	10	2	-	10.2	-	-	-	4	5	8	3	1	2	-	25.9	-	-	16	12	14	-	-	13.0
Andaman Islands	-	-	1	-	-	-		-	-	-	-	-	-	-	1	-			-	-	-	1	-	-	-	
Sumatra & Benkoelen Is	-	1	3	-	-	-	9.8	-	-	-	1	-	1	1	-	1	-	26.5	-	-	-	1	-	-	-	
Java	-	-	1	-	1	-	11.0	-	-	-	1	-	-	-	-	-	-		-	-	-	-	1	-	-	
Christmas Island, IO	-	-	2	-	-	-	10.0	-	-	-	-	-	-	-	1	1	-	26.5	-	-	2	-	-	-	-	12.0
Bali	-	-	1	-	-	-		-	-	-	-	-	1	-	-	-			-	-	1	-	-	-	-	
caudolineata																										
Japan, Tanegashima	-	-	-	-	1	-		-	-	-	-	-	1	-	-	-			-	-	-	1	-	-	-	
Okinawa	-	-	-	1	-	-		-	-	-	-	-	1	-	-	-			-	-	-	-	1	-	-	
Taiwan	-	-	-	1	1	-	11.5	-	-	-	-	1	1	-	-	-	-	25.5	-	-	-	2	-	-	-	13.0
N Philippines	-	-	-	2	12	-	11.8	-	-	-	-	-	11	3	2	1	-	26.6	-	-	4	3	7	1	-	13.3
S Philippines	-	-	1	-	15	-	11.9	-	-	1	1	-	4	1	1	-	-	25.8	-	1	2	9	5	-	-	13.0
Ambon	-	-	-	1	11	-	11.9	-	-	-	-	-	4	1	1	-	-	26.5	-	-	-	4	6	-	-	13.6
Saipan	-	-	1	3	23	-	11.8	-	-	-	2	5	8	3	1	-	-	25.8	-	-	1	5	14	3	1	13.9
Rota	-	-	-	6	44	-	11.9	-	2	1	9	7	15	1	3	-	-	25.2	-	-	2	18	21	3	1	13.6
Guam	-	-	-	3	60	-	12.0	-	-	1	11	9	25	2	6	-	-	25.6	-	-	8	16	26	4	2	13.6
Palau	-	-	-	-	3	-	12.0	-	-	-	-	-	-	1	1	-	1	28.3	-	-	2	1	-	-	-	12.3
Ninigo Islands	-	-	-	-	1	-		-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	
Trobriand Islands	-	-	-	-	3	-	12.0	-	-	-	-	-	-	-	2	-	-	28.0	-	-	-	-	2	1	-	14.3
New Britain	-	-	-	-	1	-		-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	
Solomon Is, New Georgia	-	-	-	-	1	-		-	-	-	-	-	-	-	-	1	-		-	-	-	-	1	-	-	
New Hebrides	-	1**	3	3	41	-	11.8	-	-	-	-	1	9	5	14	4	2	27.5	-	-	5	6	27	3	2	13.8
Fiji	-	-	2	3	16	1	11.7	-	-	-	2	2	3	4	-	1	-	26.1	-	-	-	3	11	5	-	14.1
Tonga, Tongatapu	-	1	-	-	1	-	10.5	-	-	-	-	1	1	-	-	-	-	25.5	-	-	-	-	2	-	-	14.0
Rotuma	-	-	1	2	23	-	11.8	-	-	-	-	3	2	4	2	-	-	26.4	-	-	7	3	13	2	-	13.4
Gilbert Islands, Tarawa	-	-	-	-	3	-	12.0	-	-	-	-	1	3	-	1	-	-		-	-	-	1	2	-	-	13.7
Howland Island	-	-	-	1	14	-	11.9	-	-	1	1	2	4	-	-	-	-	25.1	-	-	1	7	6	1	-	13.5
Apia, Western Samoa	-	-	1	2	32	-	11.9	-	-	-	1	2	15	3	2	-	-	26.1	1	-	3	5	20	1	-	13.5
Tutuila, American Samoa	-	-	1	1	15	-	11.8	-	-	-	1	1	5	4	3	-	-	26.5	-	-	3	6	7	1	-	13.4
Tau I, American Samoa	-	-	-	1	26	-	12.0	-	-	-	1	2	3	1	9	1	-	27.0	-	-	-	7	15	2	-	13.8
Palmerston Island	-	-	-	-	3	-	12.0	-	-	-	1	-	-	1	-	-	-	25.5	-	-	-	-	2	1	-	14.3
Rarotonga	-	-	1	-	8	-	11.8	-	-	-	1	1	1	2	1	-	-	26.2	-	-	-	-	7	1	-	14.1
Society Islands	-	-	-	-	8	-	12.0	1	-	-	1	1	3	1	-	-	-	25.0	-	-	-	-	8	-	-	14.0
N Tuamotu Archipelago	-	-	2	7	32	1	11.8	-	-	1	3	3	12	2	3	-	1	26.0	-	-	3	4	24	6	3	14.0

*Combinations are (frequency of occurrence for some in parentheses): 4/4 (1), 3/6 (1), 4/5, 6/4 (2), 5/5, 5/6, 6/6, 6/7 (1).
**Three on one side 6 on the other, probably aberrant.

recognized two species in the complex based on differences in the color patterns of the females. Smith, however, believed that "*andamanensis*" (a junior synonym of *cyanostigma*), applied to the Indian Ocean species and *cyanostigma* to the Pacific species. He apparently included Java as a Pacific Ocean locality.

The most apparent difference between *B. cyanostigma* and *B. caudolineata* is in the color pattern of the females (see Table 5 for comparison of males with those of similar species). Female *cyanostigma* have 5 or 6 more or less equally spaced, fine, dark stripes on the side of the body, whereas female *caudolineata* only have 3 or 4, the ventralmost of which is separated from the next more dorsal stripe (at the body midline) by a space about twice as deep as each of the two spaces separating the three stripes dorsal to the ventralmost stripe. The two species are further distinguished in that *cyanostigma* has strongly modally 5 mandibular sensory pores on each side and *caudolineata* has strongly modally 6 (Table 8, presented as total mandibular pores, right + left sides). There is also a strong tendency for *cyanostigma* to have modally fewer dorsal + ventral procurrent caudal-fin rays than *caudolineata* (Table 8), a reflection of the occurrence of modally 6 dorsal procurrent rays in *cyanostigma* and modally 7 in *caudolineata*.

Many male specimens of *cyanostigma* lack any indication of a dark spot on the opercle and the spot, when present, is usually small; however, the lectotype of *cyanostigma*, at least, has a relatively large spot (see also nomenclatural discussion). In *caudolineata*, the opercle spot varies from absent (uncommonly) to well-developed, occupying most of the opercular surface dorsally.

DISTRIBUTION (Figure 65).—*Blenniella cyanostigma* is essentially restricted to the Indian Ocean, extending from the east coast of Africa to the west coast of Sumatra, and from there to Java and Bali. J.L.B.Smith (1959:242) stated that the distribution included the Seychelles, but we have seen no specimens from those islands. He also reported the species from as far south as Bazaruto (~22.5°S), Mozambique, on the African coast, but we have seen no specimens from farther south than Pinda (~17°S). The Bazaruto record seems reasonable, and we have included it on the distribution map. There is an apparent distributional gap in the central Indian Ocean (Seychelles, Laccadive, Maldive, Chagos islands), which separates the distribution into western and eastern sections. There is little evidence that the gap serves as a barrier to gene flow between the sections.

NOMENCLATURAL DISCUSSION.—Based on a range of variation for some characters, it appears that Bleeker (1849:18) had more than one specimen (syntypes) on which he based his description of *Salarias cyanostigma*, but only one specimen, the largest, 81 mm TL, was specified ("Longitudo *speciminis maximi* 81 millimetr." Italics Bleeker's). The auction catalog of Bleeker specimens (reproduced in Lamme, 1973) indicates that there were 10 specimens of *Salarias cyanostigma*, among which one or more of the syntypes were presumably included.

The description appears to have been based only on male specimens.

Prior to our study, there were four lots of specimens identified as *Salarias cyanostigma* at RMNH (4794, 17946, 17948, 17949), comprising a total of 7 specimens, that apparently emmanated from the Bleeker auction (Whitehead et al., 1966, discuss discrepancies between the numbers of specimens available and the number listed in the catalog, as well as other problems in determining Bleeker types). Among these lots, only RMNH 4794, which contains three specimens, males (~77, 81, 92 mm TL), has a specimen that is approximately 81 mm TL. The four specimens in the other three lots are much smaller than 81 mm TL; hence, all but the 92 mm specimen, which is ostensibly longer than Bleeker's largest specimen, could be syntypes of *Salarias cyanostigma*.

The three specimens in RMNH 4794 appear to be conspecific and different from those in the other three lots. The 81 mm TL specimen agrees closely, but not completely, with Bleeker's description, and, although in poor condition (poorer than the other two specimens in the same jar), is identifiable (see Chapman, 1951:335, who reports features of the color pattern of this specimen that are no longer visible). Chapman believed that the 81 mm specimen "is undoubtedly the type," and we concur in believing that it is probably the 81 mm specimen that Bleeker listed. Assuming that the 81 mm specimen is one of the syntypes, we designate it lectotype of *Salarias cyanostigma*. The lectotype retains the catalog number RMNH 4794, but the other two specimens formerly with the lectotype are now cataloged as RMNH 26062. The lectotype bears a large, dark, opercle spot, which is lacking in both specimens in RMNH 26062.

Aside from female color pattern, the best character for distinguishing *Blenniella cyanostigma* from *B. caudolineata* is the mandibular pore count (strongly modally 5 in the former and 6 in the latter). The lectotype is in poor condition and we were able to obtain a mandibular pore count, 5, only on the left side. Both of the specimens in RMNH 26062 have 5 mandibular sensory pores on each side. As we are uncertain that these two specimens originated from Java, however, we have not included information on them in Tables 6 to 8 (Table 8 presents mandibular pores as total pores on both sides and, therefore, does not include data on this character from the lectotype).

The dorsal and anal-fin ray counts (XII,20; II,20) obtainable from the illustration of *Salarias cyanostigma* in Bleeker (1983, pl. 444: fig. 9), which appears to represent an adult male of that species, indicate that the illustration probably was based on a specimen other than the lectotype, in which the counts are XIII,21 and II,21.

A single male specimen appears to have been the basis of Günther's (1861) description of *Salarias fronto*. Immediately following the description is the statement: "Molucca Sea," which appears to indicate the source of the specimen upon

which the description is based. Immediately following that locality, however, are two localities: "*a.* Java" (which is distant from the Molucca Sea) and "*b.* Moluccas," which indicates Günther had more than one specimen he was ascribing to his species. Furthermore, following these two localities, Günther gave three measurements (total length, head length, body height), undoubtedly based on a single specimen.

We found only one specimen, BMNH 1845.6.22.196, that might have been included among Günther's type material. It is labeled as *Salarias fronto* and as having come from Java. It agrees moderately well with both the description and the measurements given by Günther. Information obtainable from this specimen is inadequate to decide conclusively if the specimen is *Blenniella cyanostigma*, which occurs in Java, or its very similar allopatric sister species, *B. caudolineata*, which occurs in the Moluccas.

The specimen has 6 mandibular sensory pores on each side, the modal count for *caudolineata*, but no evidence of a dark opercular spot, which is rarely, if ever, absent in *caudolineata*, but commonly absent in *cyanostigma*. In any event, we designate this specimen lectotype of *Salarias fronto*, and restrict the type locality to Java with the same action. Our actions may cause a problem if it is later determined that the lectotype emanated from the Moluccas; however, as Günther's name is junior to both of those of the two species with which it might be associated, the problem may be moot.

Günther (1861) did not compare *Salarias fronto* with any other species. Chapman (1951:335), giving no reasons, considered *S. fronto* to be a junior synonym of *S. bilitonensis*. The lectotype of *fronto* is a male, which exhibits the following important features of the color pattern: small, dark, oblong spot restricted to area ventral to mid-postorbital level (2 dusky slashes, 1 at or above mid-postorbital level in *bilitonensis*), 3 distinct, small, oblong ocelli on ventral half of body (0 to 2 in *B. bilitonensis*), no spots on pectoral fin (usually present in *B. bilitonensis*), and no dorsal, dark opercular spot. A dark opercular spot is frequently absent in *B. cyanostigma*, but never absent in *B. bilitonensis* (or in any of our specimens of *B. caudolineata* from the Moluccas). The combination of these color-pattern characters are most descriptive of male *B. cyanostigma* among the species with which the lectotype might be confused. Possibly contradicting our identification is the presence, as noted, of 6 mandibular sensory pores on each side.

Day's (1870) description of *Salarias andamensis* clearly was based on 3 crested male specimens (syntypes) of *Blenniella cyanostigma*, 2 of which were "up to 4 inches" and one was 3 inches long. When Day (1870:612) cited his material he mentioned a fourth specimen (italicized by us as follows), "One specimen, 3 inches long, from the same locality [Andaman Islands, as the two previously mentioned,] was presented by Capt. Hodges, *who also gave what appears to be the same species 1⁷/₁₀ inch long, but wanting both the crest and orbital tentacle.*" The fourth specimen, unfortunately, must also be considered a syntype. If it is a male, it is not the same species

as the other 3 specimens. If it is a female *B. cyanostigma*, one would expect that Day would have noted the marked and radically different color pattern of that sex. The identity of the fourth specimen is unknown, hence, the names of currently valid, more recently described species of blenniids, including *Blenniella leopardus* (Fowler), that occur in the Andamans, are in jeopardy. Designation of 1 of the 3 specimens upon which Day based his description would solve this problem, but it appears that none of these exist.

Whitehead and Talwar (1976) attempted to locate all of Day's types, or possible types. For *Salarias andamensis* Day, they reported (p. 161) 2 lots at the Calcutta museum (A 285, A 287; both lost) and 1 at BMNH (1889.2.1.3606). The latter specimen exists and is identifiable as *Blenniella leopardus*. The specimen is 33.0 mm SL and 39.1 mm TL, or approximately 1.3 and 1.5 inches, respectively, and on this basis conceivably could be Day's fourth specimen. It is a female and has no head crest, but unlike Day's fourth specimen, it does have a cirrus (simple) on each eye (and one on each side of the nape, which Day did not mention). For these reasons, and its spotted color pattern, we do not believe that this specimen is a syntype of *Salarias andamensis*, and we know of no other specimen that might be. (Dor, 1984:230, as *Salarias andamanensis* Day, seems to have accepted Whitehead and Talwar's listing of possible type specimens and gave BMNH 1889.2.1.3606 as "type" of that species.) In order to solve the nomenclatural problem concerning the identity of *Salarias andamensis* Day, we designate a neotype for the species: USNM 112032, male, 50.8 mm SL, Mundakhari Bay, Andaman Islands, collected by K. Misra, 17 Dec 1934, originally cataloged as ZSI ⁵⁴. Characters of the neotype: dorsal fin XIII,21; anal fin II,22, last ray not split to base; pectoral fins 14/14; vertebrae 39; caudal-fin dorsal/ventral procurrent rays 6/6, segmented rays 13; orbital cirri 1, on each eye; nape cirri absent; nasal cirri 3-2; mandibular pores 5-5.

The description of *Salarias striolatus* Day (1876) was clearly based on female *B. cyanostigma*. Day stated that there were "several specimens in the Calcutta Museum." Whitehead and Talwar (1976) reported the existence of only 1 putative type: ZSI 2011. Dr. W.F. Smith-Vaniz, who examined the specimen in 1969, recorded that it is a female, 40 mm SL, with a low crest on the head, no nape cirri, and 14 pectoral-fin rays, which characters agree with Day's description. The specimen, although in alcohol, appeared to be badly dessicated, and it was not possible to record other fin-ray counts. Information with the specimen indicated that it was from the Andamans and was purchased from F. Day. Despite its condition, we designate this specimen lectotype and, if it can be determined that no specimen of the syntypic series exists, recommend that it be designated neotype of *Salarias striolatus*. It can be deduced from the description that this species is the same as *Blenniella cyanostigma*.

Salarias andamanensis was substituted by Day (1876) for *S. andamensis* without comment. Although "andaman-" would

have been the proper stem for Day's (1870) species, his emendation is inadmissible under the current rules of nomenclature.

Fowler (1904) described *Entomacrodus calurus* from a "type," which he believed to be a male, and five "cotypes," which he believed to be females. His type is a male *B. cyanostigma*, but his cotypes are male *B. leopardus* (q.v.). He was confused by the much lower crest in the latter species, which may be represented only as an inconspicuous fold.

MATERIAL EXAMINED.—Kenya: Mombasa, CAS-SU 31476 (3), 31478 (4); Malindi, RUSI 39513 (16), 39533 (5), SMNS 13132 (2), USNM 296020 (13); Ras Iwetme (1); Shimoni, RUSI 39512 (20), 39535 (15). Zanzibar: RUSI 39522 (2), 39536 (4). Mozambique: Cape Delgado, RUSI 39529 (1); Nangata, RUSI 39523 (1); Pinda, RUSI 39515 (1), 39516 (1), 39531 (1); Port Amelia, RUSI 9276 (1); Querimba Arch, RUSI 39518 (1), 39519 (1), 39527 (1); Rongui Id, RUSI 39525 (1); Tekomaji Id, RUSI 39521 (1). Aldabra: USNM 285274 (1). Comoros Is: Grand Comore, CAS 33691 (3). Madagascar: Ambatoleaka, HUJ 4711 (2); Nosy-Bé, USNM 291298 (3), 307716 (1), 308005 (1), 308014 (1); 13°28'38" S, 048°14'48"E, USNM 285395 (3). Ceylon: Bentota, H. Bath personal collection (3); Galle, H. Bath personal collection (25), USNM 296019 (8, including 2 cleared and stained); Trincomalee, H. Bath personal collection (6), USNM 285396 (1), 296102 (1); Hikkaduwa, H. Bath personal collection (5). Andaman Islands: Mundakhari Bay, USNM 112032 (neotype of *Salarias andamensis*); South Point, CAS-SU 14756 (1). Christmas Id (IO): WAM P.26114-009 (1), P.26088-037 (1). Indonesia: Sumatra: Benkoelen, USNM 88017 (1), 143783 (1); Padang, ANSP 27807 (holotype of *Entomacrodus calurus*), CAS-SU 8061 (1); Java: BMNH 1845.6.22.196 lectotype of *Salarias fronto*); Pagotang, RMNH 4794 (lectotype of *Salarias cyanostigma*); Triperwageram, USNM 72728 (1); Bali: Tanah Lot, H. Bath personal collection (1).

Blenniella caudolineata (Günther), new combination

FIGURES 8, 9

Salarias caudolineatus Günther, 1877:209 [Otaheiti (= Tahiti); lectotype BMNH 1873.4.3.177, designated below].
Salarias beani Fowler, 1928:441 [Faté, New Hebrides; holotype BPBM 1063].

DESCRIPTION.—Dorsal fin (Tables 6 and 7). XII to XIV,19 to 22 = 32 to 35 (XIII in 97% of 475 specimens examined for character); mean numbers of total elements higher for males than for females for 13 of 16 localities for which means for both sexes are available (statistically significantly higher for 8 of the 13 localities, means identical for 3 localities); membrane between spinous and segmented-ray portions notched $^1/_2$ to more than $^3/_4$ length of first segmented ray (usually more than $^3/_4$ length); membrane from posteriormost ray attaching to point ranging from slightly in advance of caudal-fin base to on dorsal edge of caudal fin (out on fin up to 25% length of fin in males,

up to 6% in females, usually no more than slightly posterior to fin base in both sexes).

Anal fin (Tables 6 and 7). II or III,20 to 23 (III in only 3 of 466 specimens examined for this character); mean numbers of segmented elements higher for males than for females from all 16 localities for which means for both sexes are available (statistically significantly higher for 6 localities); posteriormost element usually not split to base (85% of 439 specimens examined for this character), posterior element of split ray often present as nubbin of bone visible only on radiographs; fin bound by membrane to caudal peduncle in only 2 of over 114 specimens examined for this character. Skin covering distal half of anterior segmented anal-fin rays of large or mature males thickened or inflated and weakly crinkled along edges.

Pectoral-fin rays 12 to 15 (14 bilaterally in 90% and unilaterally in 9% of 142 specimens examined for this character).

Pelvic-fin rays I,3.

Caudal fin. Dorsal procurrent rays 6 to 8, ventral procurrent rays 4 to 8 (rarely 4 or 5), total procurrent rays (Table 8) 10 to 16 (14 in 55% of 417 specimens examined for this character; dorsal/ventral rays 6/6, 7/6, or 7/7 in 86% of specimens); segmented rays 13 in all 323 specimens examined for this character.

Vertebrae (Tables 6 and 7). 10 to 12+26 to 29 = 37–40 (11 precaudal vertebrae in 404 of 411 specimens examined for this character), mean numbers of total (and caudal) vertebrae usually higher for males from any locality than for females from same locality, higher at 13 of 16 localities for which means for both sexes are available, statistically significantly higher at 5 of the 13 localities); posteriormost pleural rib on 11th to 13th from anteriormost centrum (on 12th in 372 of 376 specimens examined for this character); posteriormost epineural on 21st to 30th from anteriormost centrum (on 24th to 29th centrum in 96% of 320 specimens examined for this character).

Cirri. Nape cirrus absent. Orbital cirrus a simple filament, always shorter than orbital diameter in females, length occasionally equal to or slightly exceeding orbital diameter in males. Nasal cirri short, simple to palmate, with 2 to 7 branches (rarely more than 4 branches; anomalously, one specimen with 8 branches on 1 side, 13 on the other).

Lateral line. Continuous canal anterodorsally with simple pores extending posteriorly to point between vertical from between bases of 6th and 7th dorsal-fin spines to vertical from base of 10th spine (to 10th in only one specimen; extending posterior to vertical from base of 7th spine in 98% of 124 specimens examined for this character), then continuing posteroventrally and posteriorly as series of 1 to 6 short, disconnected, horizontally bi-pored canals (tubes) in skin (2 to 5 in 97% of specimens); posteriormost tube in area between vertical from between bases of 9th and 10th spines and vertical from base of 13th spine (posterior to vertical from 9th spine in 94% of specimens).

Mandibular pores 3 to 7 (Table 8; 6 bilaterally in 88% of 454
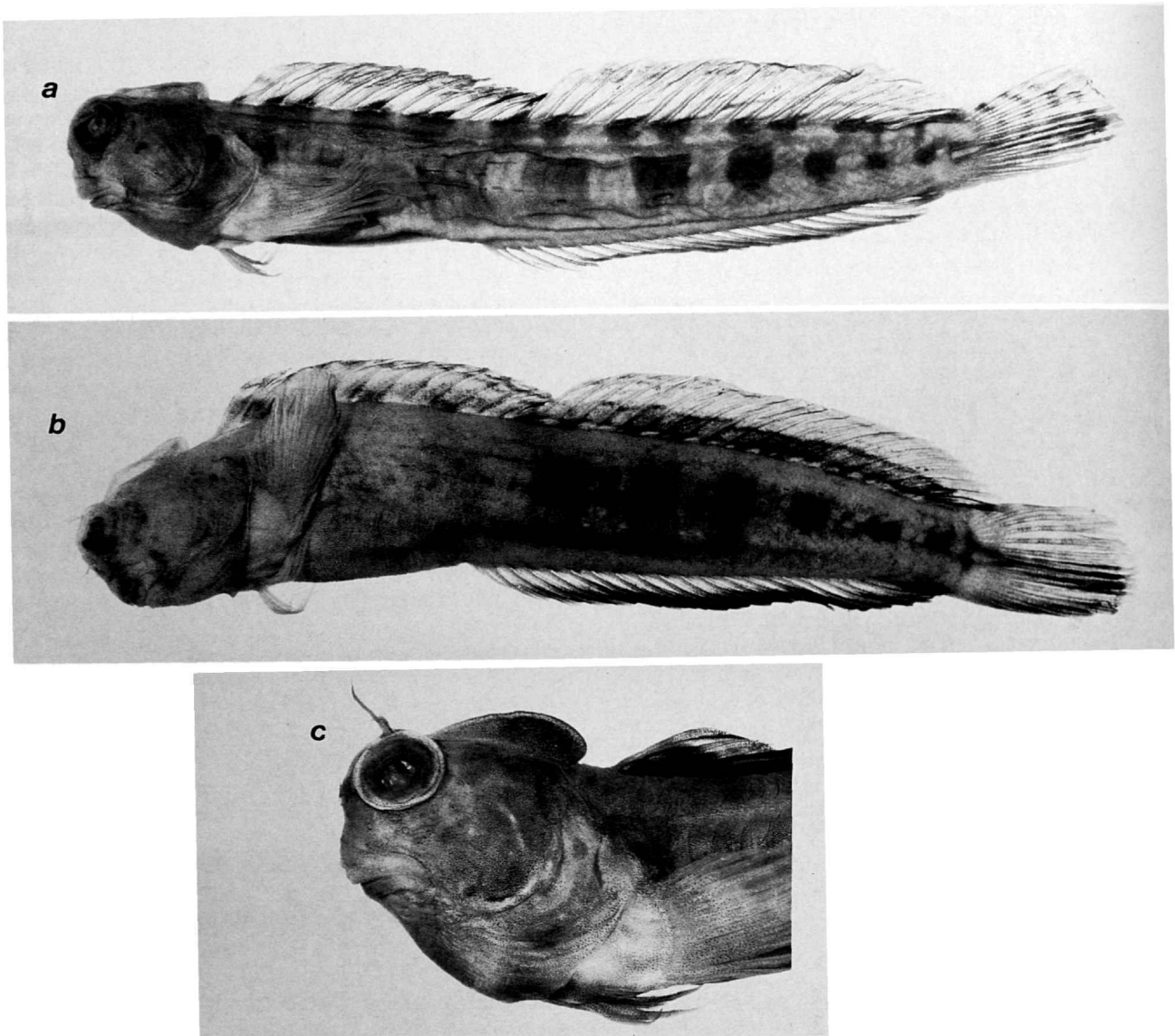
FIGURE 8.—*Blenniella caudolineata*, males: *a*, USNM 259188, 51 mm SL, SE of Maloh, Negros, Philippines (large spot on opercle); *b*, USNM 283142, 50 mm SL, Rotuma (small spot on opercle); *c*, NMNZ P.15706, 48 mm SL, Palmerston Island, note pale submarginal stripe on fleshy head crest (photographs by T.B. Griswold).

specimens examined for this character, and at least unilaterally in 97% of specimens). Six or 7 sensory pore positions between 1 and 5 o'clock on postorbital margin (6 in 97% of 117 specimens examined for this character), 0 to 2 positions occupied by pairs of pores (2 positions in 94% of specimens; no pairs in only 3 specimens).

Posterior canines present in specimens longer than 26 mm SL, variably present in specimens as small as 21 mm SL.

Margins of both lips entire.

Crest. Recognizable crest-like ridge or well-developed blade-like crest present dorsally on head of all male specimens ≥19 mm SL; crest-like ridge occasionally present in males as small as 18 mm; highest crest 2.9 mm. Distinct crests or crest-like ridges present in all female specimens ≥21 mm SL, crests and ridges essentially absent in smaller females, but several sex- indeterminate specimens about 19 to 20 mm SL with definite crest-like ridges, and one 17 mm female with slight ridge; highest crest only 1.3 mm, but most <0.7 mm.

Color pattern (in preservative). Males (Figure 8). Head: variably dusky, without prominent, dark markings at many

localities, except commonly with small-to-large, faintly-to-darkly dusky spot dorsally on opercle, and small, faintly-to-darkly dusky, elliptical or almond-shaped spot just posteroventral to orbit; upper lip occasionally with 3 barely recognizable, dusky bands, those at corners of mouth extending posteroventrally onto ventral surface; crest more or less uniformly dusky, often with well-delineated, narrow, pale distal edge. Body: well-preserved specimens with up to 9 dusky bands on midside, 6 or, occasionally, 7 posterior to vertical at dorsal-fin notch; anterior 3 bands and band on caudal peduncle frequently faint or missing; several dusky saddles, often paired and connected to bands, present along dorsal body contour, extending onto dorsal fin basally; each of anterior 4 bands below segmented-ray portion of dorsal fin variably incorporating vertical pair of small, dark ocelli (rarely more than $3^1/2$ pairs total, with half pair represented by ventral member), ventral member of each pair at or near ventral margin of band, dorsal member usually completely enveloped by band; smaller, additional ocelli occasionally present above dorsal member of each ocelli pair, and at mid-left and mid-right margins of bands; occasionally numerous, tiny, pale spots posteriorly on body, giving speckled appearance to body; occasionally up to 4 short, very fine, faintly dusky pinstripes in region below posteriormost 4 dorsal-fin spines and anteriormost 2 segmented dorsal-fin rays (visible only in well-preserved specimens). Dorsal fin: spinous portion dusky, darker distally, occasionally with interrupted, very fine, dark, distal edge or subdistal stripe and/or pale distal edge; segmented-ray portion irregularly dusky; fine, dark, interrupted pinstripes coursing through basal third of fin, rarely combining with dusky interspace between stripes to form broad, basal stripe. Caudal fin: several faint, fine, dusky spots on each ray of dorsal half (but distal margin unmarked dorsally) forming up to about 6 irregular bands; ventral half dusky with small, pale spots sometimes in membranes between rays. Pectoral and pelvic fins unremarkable.

Color slide of freshly dead male from Rotuma indicates following: most dusky areas on head, body, and vertical fins of preserved specimens represented by shades of brown or greenish brown; faintly blue ocelli on body; numerous small, pale spots present ventrally, between body bands, and covering caudal peduncle; row of large, slender, cream-colored spots just below dorsal body contour; 3 short, dark sections of pinstripes on midside below posterior end of spinous dorsal fin; caudal fin olive-brown with few small, pale spots subdistally and broad, pinkish, distal margin.

Schultz and Chapman (1960, pl. 117: fig. E), as *I. cyanostigma*, present a black an white illustration of a male.

Females (Figure 9). Head: variably dusky, usually without distinctive marks; small, faintly dusky spot occasionally ventroposterior to orbit; corner of mouth and adjacent area between corner and ventral orbital margin occasionally noticeably pale; crest dusky, often with narrow, pale, distal margin. Body: most noticeable markings consist of 3 or 4 dark pinstripes extending posteriorly from area below 5 posteri-

ormost dorsal-fin spines for varying distances to area below posterior third or fourth of base of segmented-ray portion of fin, there breaking up into numerous dark spots and dashes; only 1 pinstripe below body midline, separated from stripe at body midline by space about twice depth of spaces separating stripes above midline; space between ventral stripe and midline stripe either without markings or with row of well-separated, fine, dark dashes; when only 1 pinstripe exists above midline stripe, interspace between these 2 stripes contains row of dark dashes (Shen, 1984, fig. 392-16a, and Shen et al., 1986, fig. 42a, as *Istiblennius cyanostigma*, present a photograph of a specimen with only the ventral and midline pinstripes; the 2 stripes dorsal to the midline are broken into long dashes; Myers, 1989:211, fig. 5d, as *I. lineatus*, provides a good photograph of a more typical female); up to 6 or 7 faintly dusky bands on midside in advance of and underlying dark pinstripes; bands occasionally forked ventrally, with disjunct small, paired saddles along dorsal body contour. Dorsal fin: Spinous portion usually with 1 or 2 rows of dark spots distally and diffuse dusky markings basally, distal dark markings occasionally irregularly shaped; segmented-ray portion with 2 or 3 rows of dark spots centered on rays. Anal fin faintly dusky, darkest distally, row of dark spots often present posterobasally. Caudal fin with up to about 8 irregularly vertical columns of dark spots centered on rays. Pectoral and pelvic fins essentially unmarked, except several specimens from New Hebrides with few fine, dark spots on each pectoral fin.

Size. Largest specimen, male, 82 mm SL, males commonly exceeding 70 mm SL; largest female, 68 mm SL, few females exceeding 55 mm. Smallest specimen, juvenile, sex indeterminate, 14 mm SL. No ophioblennius-stage specimens known.

COMPARISONS AND INTERRELATIONSHIPS.—See this section under *Blenniella cyanostigma* species account; also Table 5 for comparisons of males with those of similar species.

DISTRIBUTION (Figure 65).—Southern Japan south to Moluccas, east to Marianas Islands, east and south to Tonga, and east to Tuamotu Archipelago; Tarawa, Kiribati (= Gilbert Islands), Howland Island.

NOMENCLATURAL DISCUSSION.—Günther (1877) based his description of *Salarias caudolineatus* on two syntypes, which have not been reported in the literature since the original description. We found them cataloged as BMNH 73.4.3.177 and 179 in the same jar. Both are females, approximately 50 mm SL. We select one here as the lectotype and assign it to BMNH 73.4.3.177. The lectotype can be distinguished from the paralectotype in having 14 rays in both pectoral fins. The paralectotype has 15 rays in the left pectoral fin and 14 in the right. Other characters of the lectotype: dorsal fin XIII,21 attached at base of caudal fin; anal fin II,21 (not split to base; paralectotype, II,22, also not split); orbital cirri, 1 on each eye; nape cirri absent; nasal cirri: left side 3, right side 2 (paralectotype, 4/3); long, low median crest on head.

Fowler (1928) compared his *Salarias beani* with *S.*
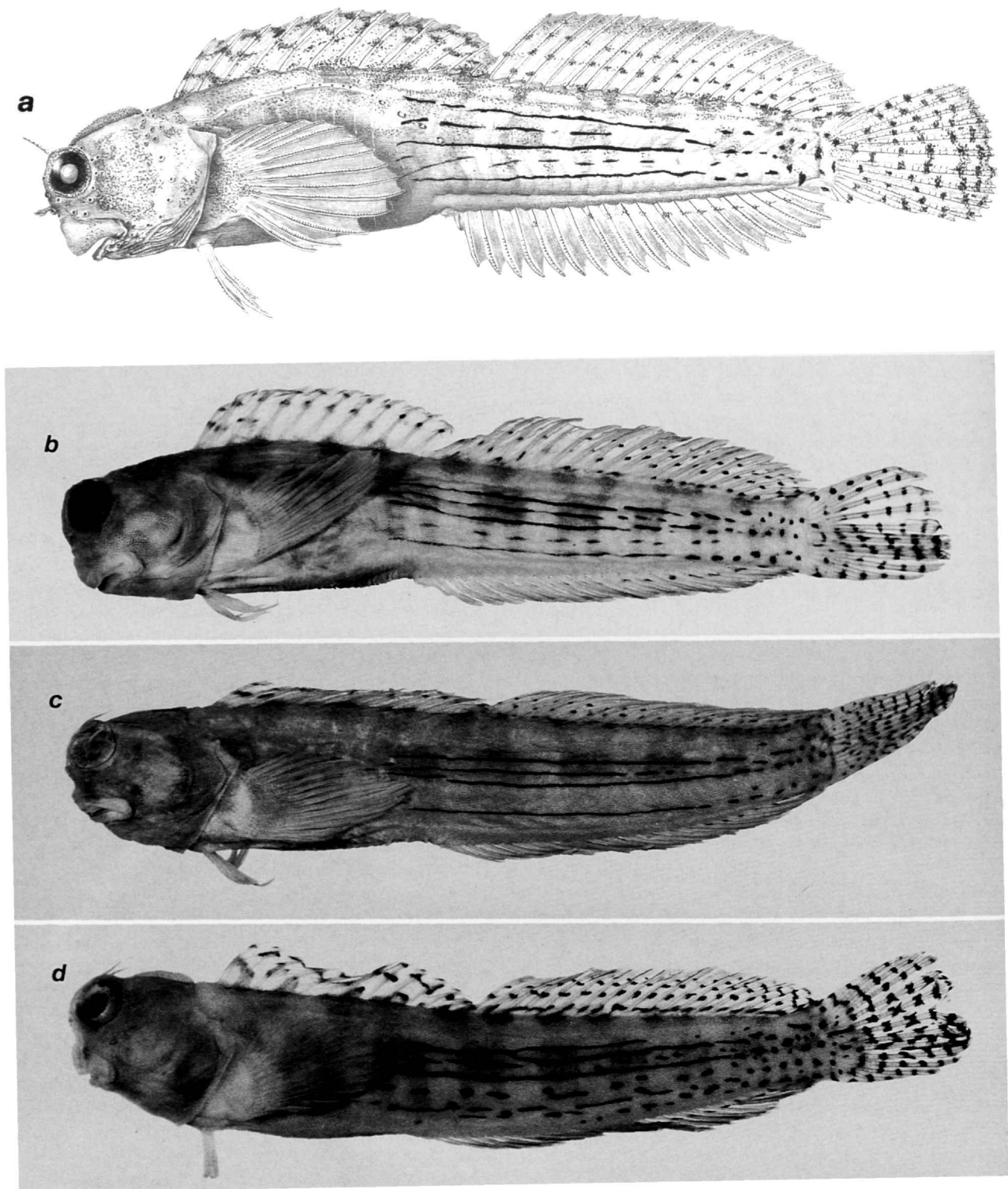
FIGURE 9.—*Blenniella caudolineata*, females: *a*, USNM 259188, 53 mm SL, SE of Maloh, Negros, Philippines (modified 4-striped pattern; note dark dashes in interspace between lower two stripes and interrupted third stripe above body midline); *b*, USNM 277964, 44 mm SL, Ambon, Moluccas (4-striped pattern with dark dashes between lower 2 stripes); *c*, USNM 256541, 49 mm SL, Malolo Lailai, Fiji (4-striped pattern); *d*, USNM 283142, 38 mm SL, Rotuma (unusually modified 4-striped pattern) (drawing by P.K. Hollingsworth; photographs by T.B. Griswold).

Table 9.—Frequency distributions for certain meristic characters in male and female specimens of *Blenniella leopardus* and *B. interrupta* from various localities. Underlining of means indicates significant differences between means of sexes from same locality (p ≤ .05).

Species/Locality	Total dorsal-fin elements							Segmented anal-fin rays					Total vertebrae				
	30	31	32	33	34	35	x̄	19	20	21	22	x̄	37	38	39	40	x̄
MALES																	
leopardus	-	-	11	8	-	-	32.4	-	10	7	1	20.5	6	12	-	-	37.7
interrupta																	
Taiwan	-	-	1	1	-	-	32.5	-	-	2	-	21.0	-	2	-	-	38.0
Luzon, Philippines	-	-	4	19	2	-	32.9	-	4	20	1	20.9	2	15	5	-	38.1
Negros, Philippines	-	-	8	21	2	-	32.8	1	8	22	-	20.7	5	22	3	-	37.9
Palau	-	-	1	1	2	-	33.2	-	1	1	1	21.0	-	2	2	-	38.5
Bali, Indonesia	-	-	-	1	1	-	33.5	-	-	1	1	21.5	-	1	1	-	38.5
Flores, Indonesia	-	-	-	4	1	-	33.2	-	-	5	-	21.0	-	4	1	-	38.2
G of Bone, Sulawesi	-	-	1	-	-	-		-	-	1	-		-	1	-	-	
Halmahera & Morotai	-	-	2	5	-	-	32.7	-	3	4	-	20.6	2	4	1	-	37.8
Ambon to Nusa Laut	-	-	-	4	2	-	33.3	-	-	5	1	21.2	-	4	1	-	38.2
Hermit & Ninigo Is	-	-	4	23	3	-	33.0	-	3	19	8	21.2	2	22	6	-	38.1
Misool Id, Indonesia	-	-	1	4	-	-	32.8	-	1	4	-	20.8	1	4	-	-	37.8
Mushu Id, PNG	-	-	1	-	-	-		-	-	1	-		-	1	-	-	
Madang, PNG	-	-	-	6	1	-	33.1	-	-	6	1	21.4	-	5	2	-	38.3
Trobriand Is, PNG	-	-	-	7	4	-	33.4	-	1	7	2	21.1	-	6	1	-	38.1
New Britain, PNG	-	-	1	7	1	1	33.2	-	1	6	3	21.2	-	7	3	-	38.3
Bonarua Id, PNG	-	-	1	-	-	-		-	-	1	-		-	1	-	-	
Solomon Is	-	-	3	16	6	-	33.1	-	3	14	8	21.2	2	12	5	2	38.3
New Hebrides	-	-	-	10	8	1	33.5	-	-	9	9	21.5	-	7	9	1	38.6
FEMALES																	
leopardus	1	4	10	3	-	-	31.8	4	13	1	-	19.8	9	9	-	-	37.5
interrupta																	
Taiwan	-	-	2	2	-	-	32.5	-	3	1	-	20.2	1	3	-	-	37.8
Luzon, Philippines	-	-	4	7	-	-	32.6	-	6	5	-	20.4	2	9	-	-	37.8
Negros, Philippines	-	1	14	11	-	-	32.4	1	13	13	-	20.4	5	21	-	-	37.8
Palau	-	-	1	3	-	-	32.8	-	1	3	-	20.8	1	3	-	-	37.8
Bali, Indonesia	-	-	-	1	-	-		-	-	1	-		-	1	-	-	
Flores, Indonesia	-	-	-	1	-	-		-	-	-	1		-	1	-	-	
Buton Id, Indonesia	-	-	3	-	-	-	32.0	-	3	-	-	20.0	2	-	1	-	37.7
Halmahera & Morotai	-	-	4	3	-	-	32.4	-	5	2	-	20.3	1	6	-	-	37.8
Ambon to Nusa Laut	-	-	4	3	-	-	32.4	-	3	4	-	20.6	2	5	-	-	37.7
Buru Id, Indonesia	-	-	1	-	-	-		-	-	1	-		-	1	-	-	
Biak Id, Indonesia	-	-	1	-	-	-		-	1	-	-		-	1	-	-	
Hermit & Ninigo Is	-	-	7	11	-	-	32.6	-	9	9	-	20.5	3	15	-	-	37.8
Madang, PNG	-	-	3	2	-	-	32.4	-	2	3	-	20.6	-	5	-	-	38.0
Trobriand Is, PNG	-	-	1	10	-	-	32.9	-	4	7	-	20.6	-	9	-	-	38.0
New Britain, PNG	-	-	5	7	-	-	32.6	-	7	5	-	20.4	1	10	1	-	38.0
Bonarua Id, PNG	-	-	1	3	-	-	32.8	-	3	1	-	20.2	1	3	-	-	37.8
Solomon Is	-	-	7	5	1	-	32.5	-	7	5	1	20.6	4	8	1	-	37.8
New Hebrides	-	-	3	9	1	-	32.8	-	3	9	2	20.9	-	8	4	-	38.3

(11.8%) have cirri bilaterally; single collection of 59 specimens from Maloh, Negros, about 50 km down coast from Dumaguete, includes only two specimens with nape cirri (3.4%), both unilaterally; single collection of 25 specimens from nearby Siquijor Island includes only 1 specimen (4.0%) with nape cirri, bilaterally. Orbital cirrus a simple filament (3 specimens with cirrus on one side with short branch, fourth specimen with cirrus on 1 side with 3 short branches), always shorter than orbital diameter in females, rarely equaling or slightly exceeding orbital diameter in males. Nasal cirri short, simple to palmate, with 2 to 6 branches (rarely 6, rarely simple in specimens over 25 mm SL).

Lateral line. Continuous canal anterodorsally with simple pores (1 specimen of 173 examined for character with single vertical pair of pores near origin of lateral line), extending posteriorly to point between verticals from bases of 4th and 10th dorsal-fin spines (extending posterior to base of 7th spine in 93% of specimens examined; terminating before base of 6th spine in only 1 specimen), then continuing posteroventrally and posteriorly as series of 0 to 5 short, disconnected, horizontally bi-pored canals (tubes) in skin (only 1 specimen lacked tubes); posteriormost tube in area between vertical from between bases
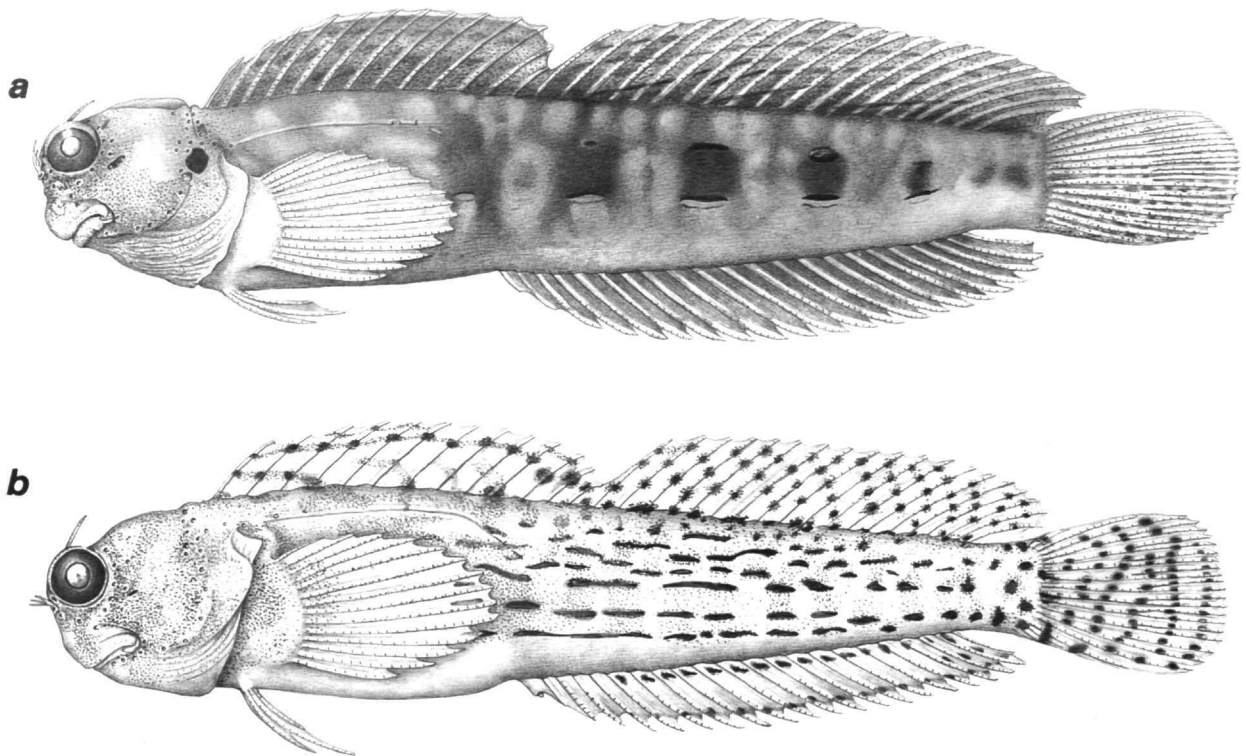
FIGURE 10.—*Blenniella interrupta: a*, USNM 220914, male, 49 mm SL, southern tip of Negros Island, Philippines; *b*, USNM 221172, female, 42 mm SL, Tandjung Paprekama, Teluk Buton, Buton Island, Indonesia (drawings by J.R. Schroeder).

of 7th and 8th spines and vertical from between bases of 12th and 13th spines (posterior to vertical from base of 9th spine in 92% of specimens examined).

Mandibular pores 4 to 6 (6 bilaterally in 87% of 181 specimens examined for character, and at least unilaterally in all but 2 specimens).

Five to 7 sensory pore positions between 1 and 5 o'clock on postorbital margin (6 in 93% of 173 specimens examined for character), 0 to 3 positions occupied by pairs of pores (2 positions in 89% of specimens examined; no pairs in only 3 specimens).

Posterior canines present in all specimens >25.0 mm SL, variably present in specimens as small as 20.0 mm SL.

Margins of both lips entire.

Crest. Females lack any indication of crest. Males up to 58 mm SL exhibit little or no indication of crest, but most males >34 mm SL with distinct, low, rounded, longitudinal ridge on top of the head; crests most highly developed in males >50 mm SL; highest crests only 0.7 mm high (2 males 60 and 62 mm SL).

Color pattern (in preservative). Highly variable. Males (Figures 10a, 11a). Head: variably dusky with prominent small,

dark spot (sometimes appearing silvery white) just posterior and ventral to mid-level of orbit; rarely, small, indistinct spot just dorsal to previous spot; another small, dark spot often present just dorsoposterior to pore at about 1 o'clock on postorbital margin; large, prominent dark spot always present dorsoanteriorly on opercle, encroaching on preopercular margin; small, dark spot often present just dorsal to opercular spot; short, irregular bar, slightly paler than dusky surrounding area, extending ventrally from orbit across corner of upper lip, occasionally narrowing and extending across ventral surface of head just posterior to edge of lower lip, continuous with similar marking from opposite side of head, sometimes followed posteriorly on ventral head surface by broad, dusky band and another pale area. Body: side irregularly dusky below spinous portion of dorsal fin, with up to 3 dusky bands, posteriormost darkest, sometimes forked ventrally, occasionally incorporating tiny, pale or dark ocellus in portion below body midline; row of up to 5 small-to-large, often diffuse, dark bars or blotches on midside below segmented-ray portion of dorsal fin, posteriormost 1 or 2 blotches often absent, indications of another blotch occasionally present on caudal peduncle; dorsal and/or ventral ends of some or all blotches, except those on
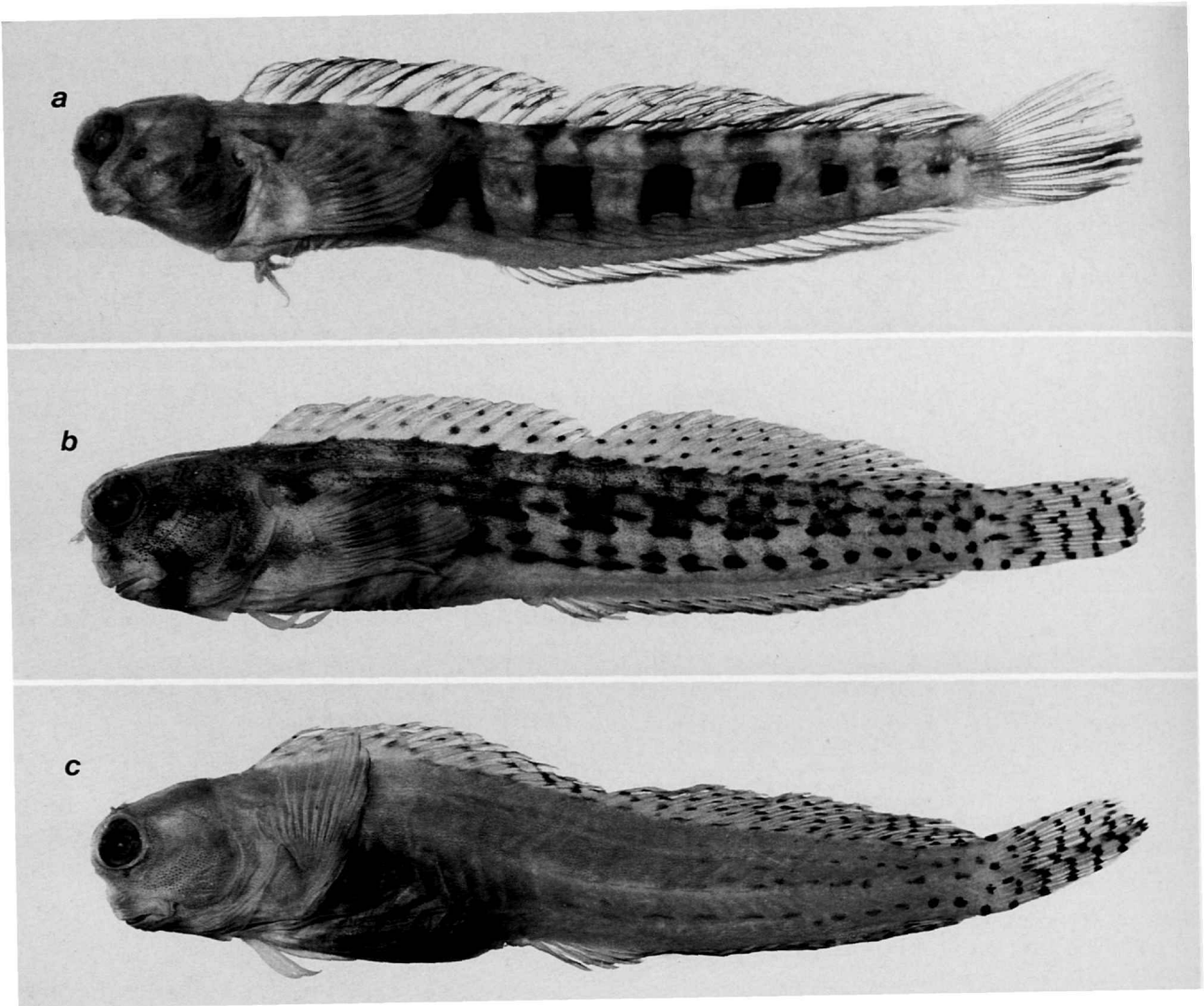
FIGURE 11.—*Blenniella interrupta: a,* USNM 295128, male, 43 mm SL, SE of Maloh, Negros, Philippines; *b,* USNM 293997, female, 38 mm SL, Siquijor Island, Philippines; *c,* USNM 296137, female 45 mm SL, Kiriwina, Trobriand Islands, extremely pale variant (photographs by T.B. Griswold).

peduncle, with dark-margined, white spot (ocellus); dorsal ocelli usually fewer in number than ventral ocelli; dorsal ocellus of each pair less elongate than ventral ocellus, depth ≤ that of pupil, none especially prominent; ventral ocelli usually very slender, up to 4 times as long as deep, usually more prominent than dorsal ocelli. Dorsal fin: spinous portion varying from overall dusky to basally dark dusky becoming less dark distally with diffuse, dusky spots; segmented-ray portion somewhat similar to spinous portion but usually with more spots and few, dark pinstripe-like marks radiating dorsoposteriorly across basal half of fin. Anal fin dusky, slightly darker distally. Caudal fin with dusky interradial

membranes often interrupted by rows of small, diffuse, pale spots; dorsoposterior portion of fin generally paler or unmarked; dusky bands variably present on caudal fin of males <25 mm SL. Pectoral and pelvic fins unmarked.

Features of fresh color, based on slide of 47 mm SL specimen from Savo, Solomon Islands (head and body mostly faded). Iris with rusty-brown patches; fleshy ridge on top of head rusty brown anteriorly and dorsally; slender, rusty-brown bar extending dorsoposteriorly from dark postorbital spot across fleshy ridge on top of head, another, similar bar extending dorsally from anterior margin of dark opercle spot almost to fleshy ridge; tips of dorsal-fin spines and 3

anteriormost segmented rays bright white, margins of interradial membranes rusty brown; anteriorly, subdistal half of each interradial membrane of segmented-ray portion with 3 dusky-margined, rusty-brown blotches separated by wavy, pale pinstripes, blotches becoming olive brown posteriorly; 4 or 5 brown pinstripes on basal half of segmented-ray portion; anal fin interradial membranes bright white distally; caudal fin pale distally, darker brown proximally with rows of up to 7 or 8 fine, white spots; caudal peduncle covered with fine, white spots.

Females (Figures 10c, 11b,c). Head: variably pale and dusky, markings paler than those of males; small, dusky spot often present just posterior and ventral to mid-level of orbit; broad, dusky band extending across ventral surface from corners of mouth; band may be interrupted mid-ventrally by pale area, separated from dark lower lip by pale area; another dusky band extending ventrally from mid-ventral margin of orbit across upper lip. Body: up to 6 slightly irregular rows of dark spots and dashes covering posterior half to two-thirds of body, occasionally up to 6 faintly dusky H-shaped bands incorporating dark spots and dashes. Dorsal fin: pale with dark spots on spines and rays or adjacent to rays; spots arranged in more or less curved rows. Anal fin with 1 or 2 rows of faintly to darkly dusky spots, interradial membranes dusky distally, tips of rays pale. Caudal fin with up to about 7 columns of dark spots mostly restricted to rays. Pectoral and pelvic fins essentially immaculate.

Bath and Patzner (1991, fig. 16) reproduce a useful black-and-white photograph of a male specimen from Bali. The only published illustrations of fresh coloration of B. interrupta are those of Shen et al. (1986, figs. 43a, female, and 43b, male), from which the following description is taken: female coloration little different from that of female in our Figure 10b. Male mostly dark brown interspersed with paler brown areas; dark opercular spot with slight bluish cast; pale slashes of body ocelli also bluish; numerous fine, whitish spots posteriorly on body (rarely evident in long-preserved specimens).

Bleeker (1983, pl. 444: fig. 11, as Salarias interrupta, and pl. 44: fig. 2, as Salarias hendriksi, a synonym of Blenniella bilitonensis) illustrated, in color, 2 females of B. interrupta. Neither offers much information over that of Shen et al. The first Bleeker figure shows a slight yellowish cast to the fins and iris, and the second, a reddish brown cast to the same features.

Size. Largest male and female specimens about 60 mm and 51 mm SL, respectively; few males exceed 55 mm SL, few females, 45 mm SL. Smallest specimen identifiable as male, 17.5 mm SL (BPBM 5713), exhibits opercle spot and beginning formation of ocelli on body. Smallest specimen identifiable as female, 20.0 mm SL, exhibits female color pattern, urogenital papilla; specimens <19 mm SL usually not assignable with certainty to sex based on urogenital papilla or color pattern. Specimen, 12.5 mm SL, taken with large sample of juvenile interrupta, 15.6 mm and larger (BPBM 5713), has color pattern unlike that of any larger specimen: 5^1/2 pairs of slender bands on body, 10 saddles along dorsal body contour; based on size series of specimens taken with it, 12.5 mm

specimen is probably B. interrupta; none of these small specimens have ophioblennius-stage dentition.

GEOGRAPHIC VARIATION.—There appears to be a slight trend for means of meristics (Table 9) to increase as one progresses from the northern end of the range south and east to the southern end of the range of the species.

ECOLOGY.—Habitat data indicate that B. interrupta is an inhabitant of near-shore rocky areas, including tide pools and at depths usually under 1 m.

COMPARISONS AND INTERRELATIONSHIPS.—Blenniella interrupta is the sister species to B. leopardus (see Phylogenetic Analysis section), from which it differs primarily in lacking nape cirri and males not having one of the dorsal body ocelli enlarged and melanistic; female interrupta often have several dark slashes on body, probably formed by fusions of spots, whereas slashes are essentially absent in leopardus females (see also Table 5 for comparisons of males with those of similar species).

DISTRIBUTION (Figure 63).—Bali and Flores, Indonesia, north to Taiwan, east to New Britain, and south to Efate, New Hebrides; absent from nonmarginal Pacific plate.

NOMENCLATURAL DISCUSSION.—Bleeker's (1857b) description of Salarias interruptus was based on a single female specimen from Kajeli, Boero. The Bleeker auction catalog (reproduced in Lamme, 1973), however, indicates the presence of two specimens of Salarias interruptus in the Bleeker collection. There are only two female specimens, both attributed to Bleeker and labeled as having come from Kajeli, Boero, in the RMNH collection (RMNH 4787). The holotype was reported to be 58 mm. The larger of the two specimens in RMNH 4787 is about 55 mm TL, the other specimen is 44 mm TL. Clearly, only the larger of these two could be the holotype, and its fin formulae agree closely with those given by Bleeker (the other specimen does not agree closely). Hence we accept the larger specimen as holotype. We are unaware of the provenance of the second specimen, which is in better condition than the presumptive holotype. Bleeker never reported obtaining a second specimen of his Salarias interruptus.

MATERIAL EXAMINED.—Taiwan: Ta Fan Lieh, USNM 285386 (2); Su Ao, USNM 296086 (1), 296473 (1); Ho Wan Li, USNM 296033 (1); Chenkong Taitung, USNM 302353 (1). Philippines: Babuyan Is, Maybag Is, USNM 317887 (1), Fuga Is, USNM 317884 (1); Luzon, Santa Ana, USNM 309363 (3), Maculabo, 138316 (3), Batan Is, USNM 138314 (6), near Daet, USNM 138317 (2), Nasugbu, CAS-SU 38251 (1), 128433 (25), Gubat Bay, USNM 291679 (1); Sombrero Is, USNM 296087 (3), 296122 (7); Mindoro, Sablayan, USNM 320102 (1); Panay, Nogas Point, USNM 122501 (4), 139678 (6); Mactan Is, USNM 138313 (2); Negros, Bais Bay, USNM 296031 (2), Dumaguete, CAS-SU 28431 (17), Bonbonon Point, USNM 220914 (11), Maloh, USNM 295128 (59); Siquijor Is, USNM 293997 (25); Mindanao, Kolambugan, CAS-SU 38252 (1). Indonesia: Bali, Menjangan Is, SMF 10850 (1), Sanur, UF 31305 (1), 31315 (1); Flores, UF 18382 (2), 31293 (3), 31297

(1); Sulawesi, G of Bone, USNM 308105 (1), Buton Id, USNM 221172 (7); Buru, Kajeli, RMNH 4787 (2, including holotype of *Salarias interruptus*); Halmahera, Morotai Id, USNM 147727 (3), Ternate, USNM 285383 (10); Ambon, USNM 295869 (8); Saparua, USNM 210932 (1); Haruku, USNM 209622 (1), 296171 (1); Nusa Laut, USNM 210951 (1), 210954 (2); Biak, RMNH uncat. (1); Irian Jaya, Misool Id, USNM 296352 (5). Palau: Angaur CAS 67790 (8). Papua New Guinea: Hermit Is, USNM 296025 (3), 296028 (2), 296034 (3); Ninigo Is, USNM 296026 (27), 296027 (1), 296030 (9), 296032 (3); Madang, USNM 285385 (7), 296158 (5); Trobriand Is, Kiriwina, USNM 296137 (11), 313272 (11); Muschu Is, USNM 283627 (1); Bonarua Id, USNM 279843 (5); Nissan Is, Pinipel, USNM 144711 (1); New Britain, Rabaul, USNM 285278 (5, including 1 cleared and stained), 285382 (8), 296029 (9, including 1 cleared and stained). Solomon Is: New Georgia, BPBM 16106 (1), BPBM 16112 in part (1), USNM 144287 (1), 144288 (5), 144712 (13), 144713 (8), 144714 (6), 195772 (1); Guadalcanal, AMS I.17490-007 (2), BPBM 5713 (40). New Hebrides: AMS I.14282 (2), I.14283 (2), I.14284 (2), I.14285 (2), I.14288 (2), I.14289 (2), I.14290 (4); Wala Id, CAS-SU 25104 (12, the smallest specimens in this lot might be *Blenniella cyanostigma*); Efate, UAZ 82-8 (13).

Blenniella leopardus (Fowler), new combination

FIGURES 12, 13

Entomacrodus leopardus Fowler, 1904:554 [Padang, Sumatra; holotype ANSP 27805].

Salarias bleekeri Chapman, 1951:338 [Port Blair, South Andamans; holotype CAS-SU 37136].

DESCRIPTION.—Dorsal fin (Table 9). XII to XIV,17 to 20 = 30 to 33 (XIII,19 or 20 in 31 of 37 specimens examined for character); mean number of total elements statistically significantly higher for males than for females; membrane between spinous and segmented-ray portions notched $3/4$ or more length of first segmented ray (usually more than $3/4$ length); membrane from posteriormost ray attaching to point ranging from slightly in advance of caudal-fin base to out on dorsal edge of caudal fin up to 10% length of fin in males (rarely more than 6%, usually not attached on fin), up to 5% in females (rarely attached on fin).

Anal fin (Table 9). II,19 to 22 (22 in only 1 of 18 males); mean number of segmented elements statistically significantly higher for males than for females; posteriormost element not split to base, not bound by membrane to caudal peduncle in any of 37 available specimens. Skin covering anal-fin spines and distal half of segmented rays of large or mature males occasionally thickened or inflated, but not rugose or crinkled along edges (relatively few males available).

Pectoral-fin rays 13 to 15 (14 bilaterally in 33 of 37 available specimens).

Pelvic-fin rays I,3.

Caudal fin. Dorsal procurrent rays 5 to 7 (6 or 7 in 31 of 32 specimens examined for character), ventral procurrent rays 5 to 7 (6 or 7 in 30 of 32 specimens examined for character), total procurrent rays 11 to 14; segmented rays 12 or 13 (12 in only 1 of 34 specimens examined for this character).

Vertebrae (Table 9). 11 or 12+26 or 27 = 37 or 38 (12 in only one of 36 specimens examined for character), mean number of total (and caudal) vertebrae higher for males than for females (difference not statistically significant); posteriormost pleural rib on 12th from anteriormost centrum in all 27 specimens examined for character; posteriormost epineural on 22nd, or 24th to 27th from anteriormost centrum (on 22nd in only 1 of 29 specimens examined for character).

Cirri. Nape cirrus present bilaterally in 36 of 37 specimens examined for character (absent bilaterally in one specimen). Orbital cirrus a simple filament in all specimens; shorter than orbital diameter in all but 1 specimen, male, with cirrus slightly longer than orbital diameter. Nasal cirri short, palmate, with 2 to 5 branches in specimens over 25 mm SL.

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between vertical from between bases of 7th and 8th dorsal-fin spines and vertical from base of 10th spine (between verticals from bases of 8th and 9th spines in 29 of 33 specimens examined for character), then continuing posteroventrally and posteriorly as series of 2 to 5 short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area between vertical from base of 9th spine and vertical between bases of 12th and 13th spines.

Mandibular pores 5 or 6 (6 bilaterally in 27 of 29 specimens examined for character).

Six or 8 sensory pore positions between 1 and 5 o'clock on postorbital margin (6 in 28 of 29 specimens examined for character); 2 or 3 positions each occupied by pair of pores (2 positions in 28 of 29 specimens).

Posterior canines present in both sexes (visible in smallest specimen, 25.7 mm SL, available.

Margins of both lips entire.

Well-developed fleshy crest absent in all specimens, but males >29 mm SL with distinct, low, fleshy, median predorsal ridge dorsally on head; males 27 to 29 mm (smallest available) with faint indication of ridge; females always lack indication of ridge.

Color pattern (in preservative). Males (Figures 12a, 13a). Head: variably dusky with prominent small, dark spot (sometimes appearing silvery white) just posterior and ventral to mid-level of orbit; another small, dark spot often present just dorsoposterior to pore at about 1 o'clock on postorbital margin; large, prominent, dark spot always present dorsoanteriorly on opercle, encroaching on preopercular margin; small, dark spot sometimes present just dorsal to opercular spot; short, irregular bar, slightly paler than dusky surrounding area, extends ventrally from orbit across corner of upper lip, occasionally narrowing and extending across ventral surface of head just posterior to edge of lower lip, continuous with similar marking
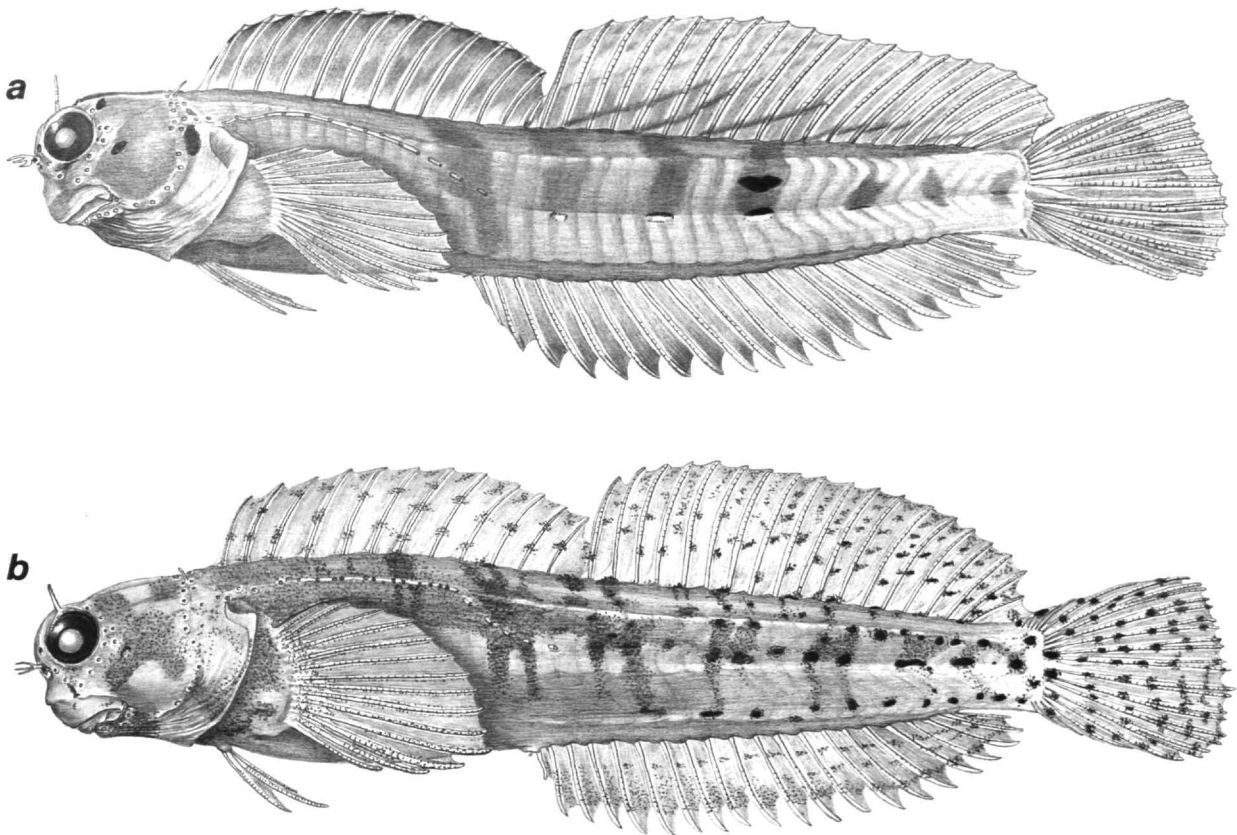
FIGURE 12.—*Blenniella leopardus*, USNM 285227, Pulau Tanga, Thailand, 06°34′N, 99°28′E: *a*, male, 44 mm
SL; *b*, female, 50 mm SL, note atypical lack of 13th dorsal-fin spine (drawings by P.K. Hollingsworth).

from opposite side of head. Body: side irregularly dusky below spinous portion of dorsal fin; row of up to 4 small-to-large, often diffuse, dark bars or blotches on midside below segmented-ray portion of dorsal fin, usually only 2 or 3 blotches recognizable, indications of another blotch occasionally present on caudal peduncle; ventral margin of each blotch frequently with slender, white area with dark dorsal margin (ocellus); 1 or 2 middle blotches with moderately large, dark, oblong spot (ocellus) dorsally (spot may have paler center); dorsal ocellus below 10th to 12th segmented rays usually prominent, diameter greater than that of pupil. Dorsal fin: spinous portion overall dusky with narrow, pale area just above dorsal body contour, followed dorsally by wide, diffuse, dark area, wide, slightly less dark area, and narrow, darker distal margin to fin interrupted by unpigmented tips of spines; segmented-ray portion somewhat similar to spinous portion but less evenly dusky, occasionally with few, faintly dusky pinstripes radiating dorsoposteriorly across basal half of fin. Anal fin dusky, slightly darker distally. Caudal fin with dusky

interradial membranes often interrupted by rows of small, diffuse, pale spots; dorsoposterior portion of fin generally paler or unmarked. Pectoral fin unmarked, except 1 specimen with 4 or 5 small, diffusely dusky spots on each fin. Pelvic fins unmarked.

Females (Figures 12*b*, 13*b*). Head: variably pale and dusky, markings paler than in male; small, dusky spot sometimes present just posterior and ventral to mid-level of orbit; broad, dusky band extending across ventral surface from corners of mouth; band partially interrupted mid-ventrally by pale area, separated from dark lower lip by narrow, pale area. Body: irregular, faint, dusky band-like markings anteriorly grading posteriorly into numerous small, dark spots, mostly restricted to side below segmented-ray portion of dorsal fin; spots more or less arranged in pairs and rows, especially on midside and just dorsal to ventral body contour (dark dashes or pinstripes not present, although, infrequently, spots of a horizontal pair may coalesce). Dorsal fin: pale with dark spots on spines and rays, or adjacent to rays; spots arranged in more or less curved
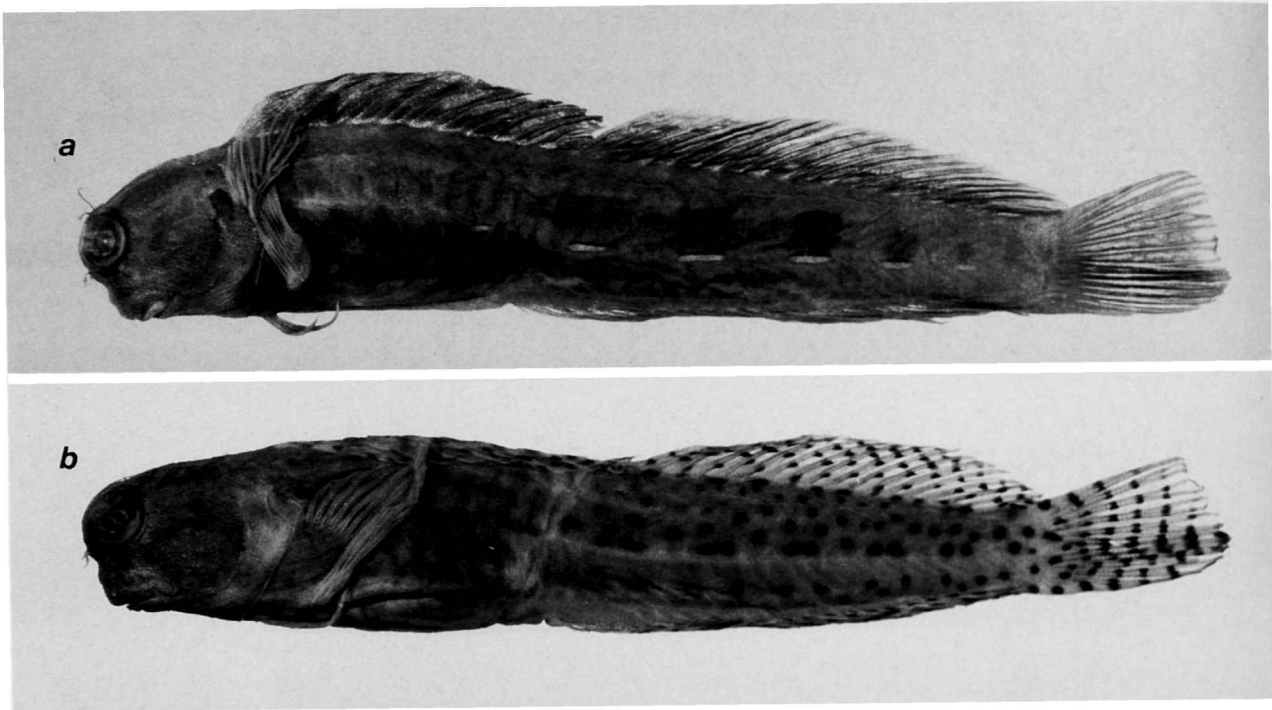
FIGURE 13.—*Blenniella leopardus*, USNM 285227, Pulau Tanga, Thailand, 06°34′N, 99°28′E: *a*, male, 42 mm SL, unusually darkly pigmented (compare with Figure 12*a*); *b*, female, 44 mm SL (photographs by T.B. Griswold).

rows. Anal fin with 1 or 2 rows of faintly to darkly dusky spots, interradial membranes dusky distally, tips of rays pale. Caudal fin with up to about 7 columns of dark spots mostly restricted to rays. Pectoral and pelvic fins essentially immaculate.

The only previously published illustration of *Blenniella leopardus*, is that of Fowler's (1904, pl. 27, upper figure) rather stylized drawing of the female holotype, which captures the essence of the color pattern.

Size. Largest available male and female specimens about 60 mm and 50 mm SL, respectively; smallest specimens 27.0 mm and 25.7 mm SL. No ophioblennius-stage (if they occur) or sex-indeterminate specimens available.

ECOLOGY.—Habitat data are available for only 1 lot of specimens (USNM 285227): collected from inner portion of reef flat in small, irregular sand pool, about 2 × 3 m, between limestone outcrops with coral fragments, at depth of 0.1 m.

COMPARISONS AND INTERRELATIONSHIPS.—Sister species to *B. interrupta* (see Phylogenetic Analysis section), from which it differs most obviously in having nape cirri; females differ in that those of *interrupta* usually have several dark slashes on body, probably formed by fusions of spots, whereas slashes are essentially absent in female *leopardus* (see Table 5 for comparison of males with those of other species).

DISTRIBUTION (Figure 63).—Northeasternmost Indian

Ocean from Andaman Islands south to Bengkulu, Sumatra.

NOMENCLATURAL DISCUSSION.—*Entomacrodus leopardus* and *E. calurus* were described by Fowler (1904) in the same paper. The holotype and paratype of *E. leopardus* are females of the species, and the paratypes of *E. calurus* represent the male (the holotype of *E. calurus* is a male specimen of *B. cyanostigma*). For *Entomacrodus leopardus*, Fowler (1904:554) reported, "Type No. 27,805, A.N.S.P. Padang," and that he had 2 specimens. He did not provide a catalog number for the second specimen (paratype). The jar at ANSP bearing the catalog number 27805 also bears the number 27806, and contains 2 conspecific female specimens. The holotype of *E. leopardus* is readily identifiable as it alone must have formed the basis for Fowler's description, which indicated no variation in counts. The holotype has 19 segmented dorsal-fin rays and 20 segmented anal-fin rays, whereas the paratype has 20 and 21, respectively. See also the nomenclatural discussion of *Salarias andamensis* Day under the account of *Blenniella cyanostigma*.

Fowler considered the 6 paratypes of *E. calurus* to be females of that species; however, they are all males and are not conspecific with the male holotype of *E. calurus*.

Chapman (1951:335), without explanation, erroneously treated *Entomacrodus leopardus* Fowler as a junior synonym

of *Salarias bilitonensis* Bleeker (= *Blenniella bilitonensis*). He also erroneously considered the paratypes of *Entomacrodus calurus* Fowler to be identifiable as *S. bilitonensis*. Chapman, therefore, must have believed that the specimens he would describe as *Salarias bleekeri* belonged to an undescribed species. In his defense, we note that one of the 6 paratypes of *Entomacrodus calurus* uniquely lacks nuchal cirri and has a few dark spots on each pectoral fin, and might be misidentified as *B. bilitonensis*. The same specimen, however, exhibits a relatively large, black area surrounding one of the dorsal ocelli on the body, a distinctive character of *B. leopardus,* and a character that Chapman used to distinguish his *S. bleekeri*.

MATERIAL EXAMINED.—Andaman Is: BMNH 1889.2.1.3606 (1 specimen), USNM 195815 (1); South Andaman Id, Port Blair, CAS-SU 37136 (holotype of *Salarias bleekeri*); Long Id, USNM 144428 (1). Thailand, Pulau Tanga, 06°34′N, 99°28″E, USNM 285227 (25, including 2 C&S). Sumatra: Padang, ANSP 27805 (holotype of *Entomacrodus leopardus*), 27806 (1), 27808-12 (5, paratypes of *Entomacrodus calurus* not conspecific with holotype of *E. calurus*); Bengkulu, USNM 88014 (1).

Blenniella bilitonensis (Bleeker), new combination

FIGURES 14, 15

Salarias bilitonensis Bleeker, 1858a:231 [Biliton, occident.; lectotype, RMNH 4792, largest specimen, designated below, same specimens as neotype of *Salarias hendriksii* Bleeker].

Salarias hendriksii Bleeker, 1858a:233 [Biliton occidentalis; neotype, RMNH 4792, largest specimen, designated below, same specimen as lectotype of *Salarias bilitonensis* Bleeker].

Salarias deani Jordan and Seale, 1905:799 [Negros, Philippine Islands; holotype, USNM 51950].

Alticus novemmaculosus Snyder, 1908:109 [Naha, Okinawa; holotype, USNM 62244].

Salarias periophthalmus visayanus Herre, 1934:97 [Philippine Islands, Oriental Negros, Dumaguete; neotype, CAS-SU 28435, designated below].

Salarias brevoorti Fowler, 1946:177 [Aguni Shima, Riu Kiu Islands; holotype ANSP 72048].

DESCRIPTION.—Dorsal fin (Table 10). XII to XIV,19 to 22 = 32 to 35 (XIII in 94% of 226 specimens examined for character; 22 and 35 in only one male, of 35, from Okinawa); mean numbers of total elements tending to be higher for males from any locality than for females from the same locality (higher at 7 of 8 localities where means for both sexes are available, statistically significantly higher at 4 of the 7 localities); membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray (usually more than three-fourths length); membrane from posteriormost ray attaching to point ranging from well in advance of caudal-fin base to out on dorsal edge of caudal fin up to 15.4% length of fin in males (rarely more than 11%), up to 7.7% in females (rarely attached on fin in females).

Anal fin (Table 10). II,18 to 22 (18 only in 1 female); mean numbers of segmented rays higher for males from any locality

than for females from same locality (higher at all 8 localities where means for both sexes are available, statistically significantly higher at 2 localities); posteriormost element split to base in only 4.5% of 223 specimens examined for character; posterior element of split ray usually visible externally; fin not bound by membrane to caudal peduncle in 98% of 293 specimens examined for character. Skin covering anal-fin spines and distal half of segmented rays of large or mature males rarely thickened or inflated, never rugose or crinkled along edges.

Pectoral-fin rays 13 to 15 (14 bilaterally in 91% of 174 specimens examined for character; 15 only unilaterally, in only 4 specimens).

Pelvic-fin rays I,3.

Caudal fin. Dorsal procurrent rays 4,6 or 7 (6 or 7 in 99% of specimens examined for character); ventral procurrent rays 6 or 7 (7 in 78% of specimens), total procurrent rays 10, or 12 to 15; (modally 14; 10 or 15 total procurrent rays in only 1 specimen each); segmented rays 11 to 13 (1 with 11, 2 with 12 of 185 specimens examined for character).

Vertebrae (Table 10). 11 or 12+26 to 29 = 37 to 40 (12 in only 7 of 198 specimens examined for character, 40 in only 1 specimen, female), mean numbers of total (and caudal) vertebrae tending to be higher for males from any locality than for females from same locality (higher at 6 of 8 localities where means for both sexes are available, statistically significantly higher at 1 of the 6 localities); posteriormost pleural rib on 12th or 13th from anteriormost centrum (on 13th in only 1 of 195 specimens examined for character); posteriormost epineural rib on 20th to 30th from anteriormost centrum (on 23rd–30th in 96% of 142 specimens).

Cirri. Nape cirrus absent in 307 of 314 specimens examined for character (present unilaterally in 2 specimens from Ambon). Orbital cirrus a simple filament in 197 of 203 specimens (with 2 or 3 short branches distally in 3 specimens); absent on 1 side in 1 specimen, almost always shorter than orbital diameter in females, ranging from shorter than to slightly longer than orbital diameter in males. Nasal cirri short, palmate, with 2 to 6 branches in specimens over 25 mm SL (usually 3 or 4 branches in specimens over 30 mm).

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between vertical from between bases of 6th and 7th dorsal-fin spines and vertical between bases of 9th and 10th spines (posterior to vertical from 7th spine in 98% of 163 specimens examined for character), then continuing posteroventrally and posteriorly as series of 1 to 7 short, disconnected, horizontally bi-pored canals (tubes) in skin (2 to 5 tubes in 93% of specimens; 7 in only 1 specimen); posteriormost tube in area between verticals from 9th spine and 1st segmented dorsal-fin ray (posterior to 10th spine in 89% of specimens).

Mandibular pores 5 to 7 (6 bilaterally in 92%, and unilaterally in 5%, of 166 specimens examined for character).

Table 10.—Frequency distributions for certain characters of male and female specimens of *Blenniella bilitonensis* from various localties. Underlined means indicate significant differences between means of sexes from same locality (p ≤.05).

Sex/Locality	Total dorsal-fin elements					Segmented anal-fin rays						Total vertebrae				
	32	33	34	35	x̄	18	19	20	21	22	x̄	37	38	39	40	x̄
MALES																
Okinawa & vicinity	1	18	15	1	33.4	-	-	6	24	5	21.0	-	20	16	-	38.4
Taiwan	-	6	-	-	33.0	-	-	-	6	-	21.0	-	5	1	-	38.2
Philippines																
Batanes Is	-	-	1	-		-	-	-	1	-		-	-	1	-	
Babuyan Is	1	1	-	-	33.5	-	-	1	1	-	20.5	1	1	-	-	37.5
Luzon & vicinity	-	7	-	-	33.0	-	-	1	6	-	20.8	-	5	1	-	38.2
Masbate Id	1	-	-	-		-	-	1	-	-		-	1	-	-	
Negros Id	-	9	5	-	33.4	-	-	3	11	-	20.8	1	5	3	-	38.2
N Gulf of Thailand	2	13	2	-	33.0	-	1	10	6	-	20.3	5	11	1	-	37.8
Malaysia	-	8	-	-	33.0	-	-	5	3	-	20.4	1	7	-	-	37.9
Sabah	-	8	-	-	33.0	-	-	6	2	-	20.2	1	7	-	-	37.9
Indonesia																
Biliton	-	2	-	-	33.0	-	-	1	1	-	20.5	-	-	-	-	
Sulawesi, G of Bone	-	-	-	-		-	-	-	1	-		-	-	1	-	
Bali	-	1	-	-		-	-	-	1	-		-	1	-	-	
Moluccas	-	10	-	-	33.0	-	-	-	10	-	21.0	-	8	1	-	38.1
Northern Territory	1	5	4	-	33.3	-	-	2	6	2	21.0	-	8	2	-	38.2
FEMALES																
Okinawa & vicinity	-	25	7	-	33.2	-	2	7	20	2	20.7	-	18	9	1	38.4
Taiwan	2	1	-	-	32.3	-	-	3	-	-	20.0	-	3	-	-	38.0
Philippines																
Batanes Is	1	4	1	-	33.0	-	-	3	2	1	20.7	1	6	1	-	38.0
Babuyan Is	-	1	-	-		-	-	1	-	-		-	-	1	-	
Luzon & vicinity	-	3	-	-	33.0	-	-	2	1	-	20.3	-	3	-	-	38.0
Masbate Id	-	2	-	-	33.0	-	-	2	-	-	20.0	-	-	-	-	
Negros Id	1	9	-	-	32.9	-	-	4	6	-	20.6	1	6	1	-	38.0
N Gulf of Thailand	6	2	-	-	32.2	-	-	8	-	-	20.0	6	1	-	-	37.1
Maylasia	3	3	-	-	32.5	-	1	4	1	-	20.0	3	3	-	-	37.5
Sabah	7	4	-	-	32.4	1	3	6	1	-	19.6	5	6	-	-	37.5
Indonesia																
Bali	2	1	-	-	32.3	-	1	2	-	-	19.7	2	-	1	-	37.7
Flores	-	1	-	-		-	-	1	-	-		-	1	-	-	
Moluccas	7	8	-	-	32.5	-	-	8	7	-	20.5	4	8	1	-	37.7
Northern Territory	3	4	-	-	32.6	-	-	5	2	-	20.3	2	5	-	-	37.7

Five to 7 sensory pore positions between 1 and 5 o'clock on postorbital margin (6 in 92% of 165 specimens examined for character); 0 to 2 positions occupied by pair of pores (2 positions in 90% of specimens).

Posterior canines present in both sexes (visible in specimens as small as 28 mm SL, but usually not obvious in specimens less than 30 mm SL).

Margins of both lips entire.

Males >32 mm SL either with well-developed crest on head (highest crest 19.7% HL, but crest height usually <15% HL) or noticeable ridge-like crest precursor; males 27 to 31 mm SL with or without indications of ridge development, but shorter males exhibit no indication; highest male crest, 2.6 mm, crests ≥2.0 mm present only in males >60 mm SL. Well-developed crests absent in females, but females ≥40 mm SL may exhibit faint indications of ridge-like crest precursor, and few females >50 mm have well-developed ridge up to 0.6 mm high (up to 5% head length).

Color pattern (in preservative). Males (Figures 14a, 15a–c). Head: variably dusky, diffuse band between ventral margin of orbit and upper lip, occasionally discontinuous across ventral surface of head; ventral usually lacking distinct markings; similar band at corner of mouth, also occasionally continuing across ventral surface of head; dark, vertical pair of small slashes just posterior to orbit, dorsal slash extending dorsally above mid-level of orbit, ventral slash extending below mid-level, slashes sometimes connected, ventral slash sometimes forming tiny ocellus; small, faintly dusky mark some-
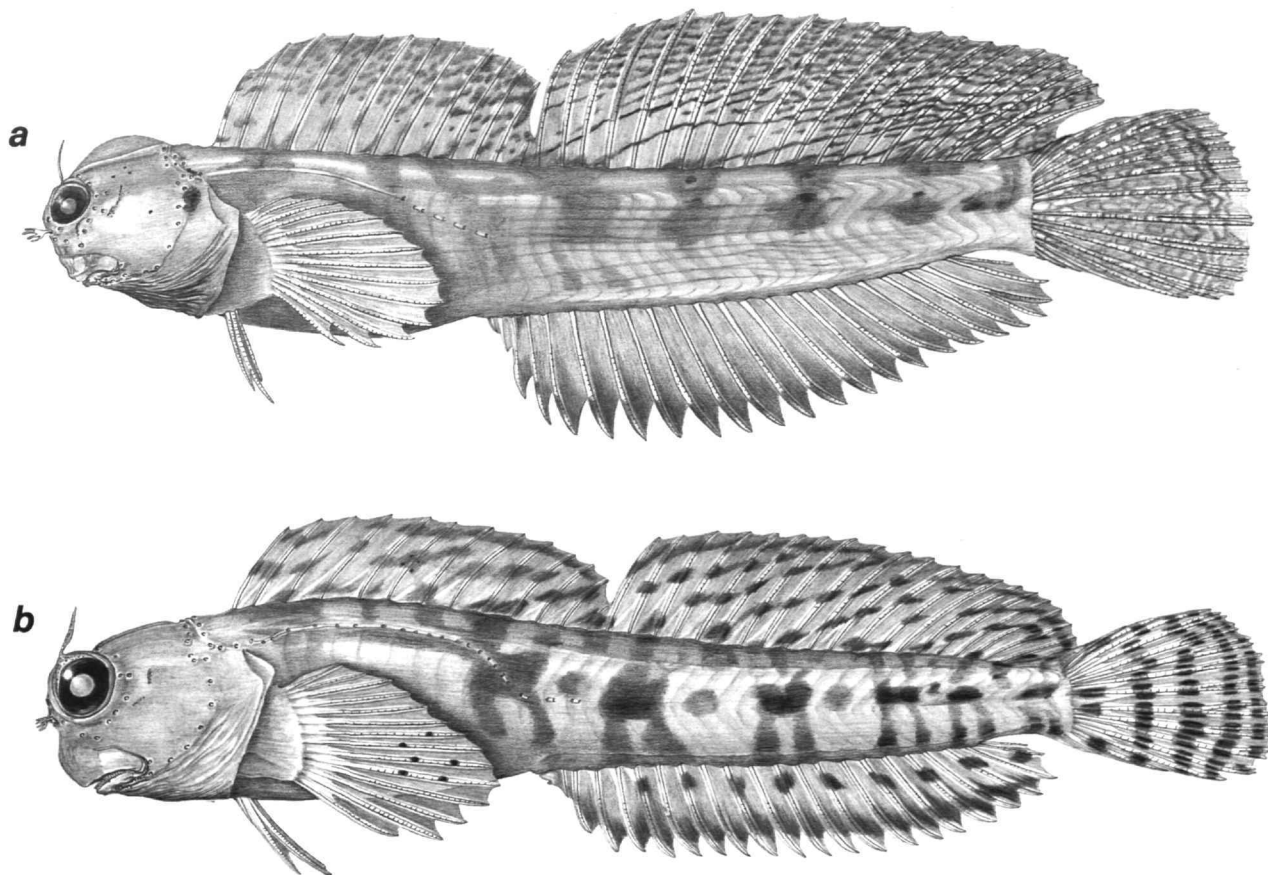
FIGURE 14.—*Blenniella bilitonensis: a*, USNM 297897, male, 82 mm SL, Okinawa, Ryukyu Islands, caudal fin partially reconstructed, pectoral fin lacks small, dark spots, which most specimens have; *b*, USNM 277965, female, 48 mm SL, Ambon, Indonesia (drawings by P.K. Hollingsworth).

times present near pore at 2 o'clock on postorbital margin; large, dark spot dorsally on opercle (most consistent and prominent of all head markings), much smaller dark spot occasionally just dorsal to opercle; diffuse, dusky spot occasionally on preopercular area ventrally. Body: dusky band on side in area below anteriormost 4 dorsal-fin spines, another below posterior half of spinous portion, 4 or 5 bands in area below segemented-ray portion of fin (60% of specimens have 4 bands bilaterally, 13% have 5 bands bilaterally, 27% have 4 bands on one side, 5 on other), and 1 band on caudal peduncle (peduncular band faint or absent in many specimens); bands may fork at dorsal body contour (appear as series of small saddles) or be restricted to sides mid-laterally; vertical pair of small, dark-margined ocelli variably present in mid-portions of anteriormost 1 to 3 bands below segmented-ray portion of fin, dorsal or ventral ocellus of pair variably absent in as many as 4

bands (maximally 7 ocelli); variably, small, dark spot included in dorsal extension of any band; up to 9 diffuse to relatively well-marked pinstripes variably present on some portion of side below and between mid-spinous portion of dorsal fin and posterior third of segmented-ray portion, stripes becoming more diffuse posteriorly, changing into pattern of small, diffuse, pale spots that extend onto caudal fin. Dorsal fin spinous portion variably dusky or with numerous, diffuse, dusky spots in distal half; segmented-ray portion with up to 6 well-spaced, dark pinstripes in anterobasal half (pair of stripes radiating dorsoposteriorly from each of 3 anteriormost body bands below segmented-ray portion), remainder of fin with numerous dusky dashes more or less aligned in rows (number increasing with size). Anal fin uniformly dusky, gradually darkening distally. Caudal fin dusky with rows of diffuse, pale spots; dorsoposterior margin noticeably paler. Pectoral fin with
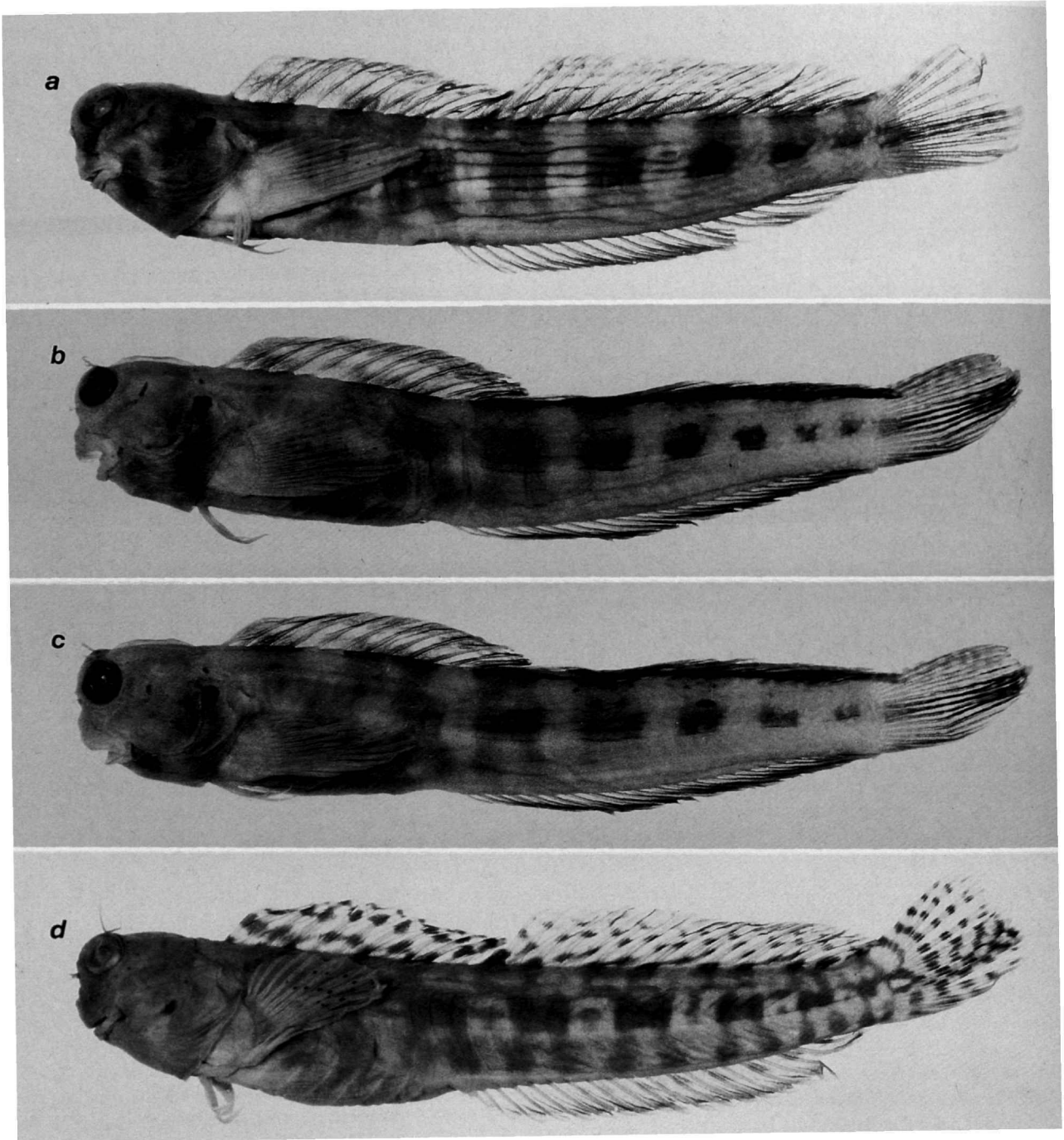
FIGURE 15.—*Blenniella bilitonensis: a,* USNM 295127, male, 40 mm SL, Negros Island, Philippines (note body pinstriping extends posterior to vertical at base of 6th segmented dorsal-fin ray, modal number of 5 bands on body posterior to vertical at base of first segmented dorsal-fin ray); *b,c,* USNM 317931, male, 56 mm SL, Babuyan Islands, Philippines, left and right sides (right side reversed), exhibiting 6 and 5 bands on body posterior to vertical at base of first segmented dorsal-fin ray; *d,* USNM 296049, female, 59 mm SL, Okinawa (photographs by T.B. Griswold).

up to 5 fine, dark spots on distal half of each ray in specimens over 25 mm SL (no more than 25, usually fewer than 15, spots on a fin); about 5% of specimens without spots (except 5 of 9 males from Northern Territory lacked pectoral-fin spots). Pelvic fins immaculate.

Females (Figures 14b, 15d). Head varying from lacking distinct marks to having short, dusky stripe at mid-tip of upper lip, dusky stripe extending ventrally from mid-orbit across upper lip, faintly dusky pair of small slashes posterior to orbit, dusky spot ventrally on preopercular area. Body with 1 to 3 dusky bands on midside below spinous dorsal fin, anterior band faintest, bands may fork at dorsal body contour, posteriormost band usually forks ventrally; 5 dark bands on midside below segmented-ray portion of dorsal fin, bands usually forking dorsally and ventrally, forked portions occasionally disjunct from central, darkest, portion of each band, dusky blotch in pale area between each pair of bands. Dorsal fin with diagonal rows of dark spots. Anal fin with sub-basal row of dusky spots and diffusely dusky interradial membranes distally. Caudal fin with up to 7 dark spots on each ray, spots forming irregular bands. Pectoral fin rays each with up to 5 tiny, dark spots (maximum spots per fin, 27, usually fewer than 15, spots rarely absent). Pelvic fins immaculate.

Fresh coloration (based on color photographs taken by J.E. Randall at Okinawa and Tioman Island, Malaysia). Male, 59 mm SL. Head: crest pale dusky with 2 brownish bands, anterior band extending ventrally to dorsal orbital margin, posterior band extending ventrally posterior to orbit to level opposite ventral orbital margin; dark slash-like mark with slender, bright-white margin bordering previous band posteriorly opposite level of orbit; short, dusky band with slender, bright-white margin posteriorly extending ventrally from ventral orbital margin; 2 white spots on upper lip posteriorly; iris with alternating pink and pale dusky spokes; blackish spot with narrow, orange posterior margin on opercle dorsally. Body: bands olive brown dorsally separated by paler olive-brown interspaces; bands dusky ventrally with bright-white interspaces; pair of ocelli in third from posteriormost band, dorsal ocellus of pair oblong, dark gray with pale-blue margin surrounded by diffuse, dull-orange halo; ventral ocellus smaller, more elongate, consisting of slender, dark, dorsal and slightly wider, white, ventral portions; dark olive-brown pinstripes anteriorly, widening and becoming paler brown posteriorly; pinstripes separated posteriorly by bright-white areas, stripes broaden and coalesce to form area punctuated with small, white spots, which extend onto and cover most of caudal fin. Dorsal-fin spines with tips and adjacent margins of interradial membranes bright white; 3 rows of dark-brown spots distally in posterior half of spinous dorsal; anterior 8 segmented dorsal-fin rays with white tips, margin of interradial membranes of succeeding rays pinkish orange; distal third of segmented-ray portion of dorsal with bright-white pinstripes separating brownish, subquadrate blotches; 7 dark pinstripes

radiating obliquely from dark body bands into dark-brown basal half of fin. Caudal fin mostly dusky with small, pale spots, except for moderately wide, pinkish, distal margin. Pelvic fin white. Pectoral fin unmarked except for fine, dark spots on rays. Schultz and Chapman (1960, pl. 117: fig. D), as *I. coronatus,* present a useful black and white illustration of male.

Female, 45 mm SL (much faded): Most obvious features: 2 brownish orange stripes on head similar to those arising from crest in male, also similar spokes in iris; moderately large, diffuse, brownish orange spots with diffuse, dusky halos in spinous dorsal fin, spots arranged in more or less curving pattern, distal tips of spines bright white; distal tips of segmented anal-fin rays and adjacent interradial membranes bright white; bright-white spots on segmented-ray portion of dorsal fin and caudal fin more prominent than dark spots separating them (other dark or dusky markings on body and fins similar to those of preserved specimens).

SIZE.—Largest male slightly longer than largest female (90.8 mm SL vs 87.1 mm SL), males usually largest specimens in large samples from any locality. Ophioblennius-stage specimens unknown for *B. bilitonensis.* Several small specimens, 15.3 to 23.4 mm SL, from widely scattered localities, with relatively well-developed color patterns; males as small as 20 mm distinguishable from females by having a large, dusky blotch on opercle.

GEOGRAPHIC VARIATION.—Means for meristic characters (Table 10) tend to be highest for specimens from northernmost distributional areas of species (Okinawa and vicinity), and lowest for Gulf of Thailand. Southernmost specimens, from Northern Territory, exhibit very little color pattern on body, and 4 of 7 available males lack pectoral-fin spots; 2 other males have only a few poorly developed spots, but all females have well-developed pectoral-fin spots.

The pattern of conspecific populations in the Gulf of Thailand and Northern Territory varying from other populations resembles the situation discussed by Williams (1988:36) for *Cirripectes filamentous. Cirripectes filamentosus* is the only species of *Cirripectes* that occurs in both the northern Gulf of Thailand and Northern Territory, and specimens from these 2 areas are noticeably divergent from all others. Both areas are characterized by high river runoff and it is possible that environmental factors, such as low salinity, influence the expression of certain characters.

ECOLOGY.—*Blenniella bilitonensis* is a shallow, near-shore inhabitant, taken often in tidepools.

COMPARISONS AND RELATIONSHIPS.—*Blenniella bilitonensis* appears to be closely related to the 2 sister-species pairs, *B. cyanostigma* and *B. caudolineata,* and *B. interrupta* and *B. leopardus,* either as the sister group to both pairs of sister species, or as the sister group of the second pair of sister species (see Phylogenetic Analysis section). Although differing in several respects, the males of these species are superficially

quite similar, and it is necessary to use a complex of characters (often their modal expression) in order to distinguish them (Table 5). Females, in contrast, are easily separated. Those of the 2 sister-species pairs are distinguished by having dark (almost black) spots, dashes, or pinstripes on the body, whereas such markings are absent from the body of female *B. bilitonensis*. Both sexes of *B. bilitonensis* are modally distinguishable from those of the other 4 species in having small, dark spots on the pectoral fins.

DISTRIBUTION (Figure 62).—Between 100°–135° E longitude, from Riu Kiu Islands south to McClure and New Year islands, Northern Territory, Australia.

NOMENCLATURAL DISCUSSION.—Bleeker's description of *Salarias bilitonensis* was based on 2 conspecific male specimens 94 and 99 mm TL. There are 2 male specimens in RMNH 4792, 91 and 97 mm TL (75.0 and 79.5 mm SL, respectively) that appear to be the syntypes. We designate the larger of these as lectotype of *S. bilitonensis*. Aside from size, the lectotype can be distinguished from the paralectotype in having 20 segmented anal-fin rays (as opposed to 21).

Bleeker's (1858a) description of *Salarias hendriksii*, which appeared in the same publication as his description of *S. bilitonensis*, was based on a single specimen, not mentioned in the auction catalog of his collections and now apparently lost. Bleeker's description of the color pattern agrees well with that of a female *Blenniella bilitonensis*, or less possibly a female *B. interrupta* or *B. leopardus* (neither of the latter 2 species has been reported from Biliton, and only 1 would be expected to occur there in any case). The reported size, 76 mm TL, of the holotype is within the size range of female *B. bilitonensis*, but is at least 16 mm longer than any female *B. interrupta* or *B. leopardus* we have seen. Furthermore, Bleeker's comment that the pectoral fin was sparsely spotted ("pectoralibus dimidio libero punctis sparsis fuscis") would tend to apply to *B. bilitonensis*, rather than either of the other 2 species, in which the pectoral fin rarely bears spots, and then no more than 2 or 3 fine and almost unnoticeable ones.

The identification of *Salarias hendriksii* is confused because the color pattern of Bleeker's illustration (1983, pl. 445: fig. 2) of *S. hendriksii* is diagnostic of a female *B. interrupta* or *B. leopardus*. The illustration, however, probably was not based on the holotype of *S. hendriksi*, as the illustrated numbers of dorsal- and anal-fin rays (D.XIII,21; A.20—the anal-fin spines of females are not obvious) are at odds with the description ("13/20 or [perhaps] 13/19"; "21"), and the pectoral fin is not spotted. It is surprising that Bleeker (1858a) compared his *Salarias hendriksii* only with his *S. sumatranus* (= *I. edentulus*), considering the close similarity of his illustrations of *S. hendriksii* and the older *S. interruptus*.

Because *hendriksii* is one of the older names available in *Istiblennius* and *Blenniella* and could place younger, currently recognized senior synonyms in nomenclatural jeopardy, and

because we consider *S. hendriksii* to be the same as *S. bilitonensis*, which was described in the same publication, thus raising the issue of page priority, we believe it desirable to designate a neotype for *S. hendriksii*. We designate RMNH 4792, lectotype of *S. bilitonensis*, as neotype of *S. hendriksii*. We do this in spite of the fact that the neotype is a male specimen, whereas the description was based on a female specimen. We, furthermore, use page priority as the basis for accepting *S. bilitonensis* as the oldest name for the species. The result of our actions is to make *S. hendriksii* a junior objective synonym of *S. bilitonensis*.

Jordan and Seale (1905) did not compare their *Salarias deani* with any other species. Their holotype is a female specimen of *B. bilitonensis*.

Snyder (1908) did not compare his *Salarias novemaculosus* with any other species. His holotype is a male *Blenniella bilitonensis*. Snyder was the first to recognize the remarkable sexual dimorphism in color pattern exhibited by this species.

Herre (1934) neither distinguished the holotype nor reported the total number of specimens in the type series of his *Salarias periophthalmus visayanus*. The holotype and some of the paratypes were indicated to have been collected at Dumaguete, Negros, Philippines; other paratypes were from the island of Culion. The Dumaguete series was originally deposited in the Stanford University collections, which were transferred later to CAS. Böhlke (1953) reported that CAS-SU 28435 contained the holotype and 7 paratypes (6 more specimens, representing other species, were originally included in this lot, but had been removed). We found a total of only 7 specimens (female and 6 males) in CAS-SU 28435, and these are all identifiable as *B. bilitonenis*. The original description also appears to have been based primarily on *B. bilitonensis*. We were unable to establish which, if any, of the specimens in CAS-SU 28435 might be the holotype, and, therefore, consider the holotype to be lost. In order to stabilize the application of Herre's subspecies, we select as neotype from CAS-SU 28435, a male, 49.8 mm SL, with the following characteristics, which will distinguish it from the other specimens in the lot: dorsal-fin XIII,20; anal fin II,21 (last ray not split to base), pectoral fins 14/13; nasal cirri 3/3. The neotype retains the original catalog number.

Fowler (1946) did not compare his *Salarias brevoorti* with any other species. His holotype, and only specimen, is a male *B. bilitonensis*.

MATERIAL EXAMINED.—Riu Kiu Is: Aguni Shima, ANSP 72048 (holotype of *Salarias brevoorti*); Okinawa, USNM 62244 (holotype of *Alticus novemmaculosus*), 74546 (92), 74587 (72 specimens), 280194 (3), 285012 (1), 285013 (2), 285014 (6), 285015 (1), 296036 (2), 296037 (3), 296039 (1), 296040 (7), 296041 (2 cleared and stained), 296044 (1), 296045 (14), 296046 (3), 296047 (1), 296048 (1), 296049 (4), 296160 (6), 296247 (4), 297897 (1); Oki Erabu Jima, USNM 285011 (1), 296038 (3). Taiwan: USNM 296326 (3), 296330

(1), 298913 (1), 322569 (1). Lanyu Id: USNM 296042 (1), 296043 (1), 296050 (1). Philippines: Batan Is, USNM 139681 (1), 226718 (1), 226726 (2), 226750 (1), 283962 (1) 283972 (3), 296035 (4); Babuyan Is, CAS-SU 20650 (1), USNM 317926 (1), 317931 (1); Luzon, Cagayan Province, USNM 309356 (2), 309362 (1), Gubat Bay, USNM 99389 (6); Masbate, Port Cataingan, USNM 99380 (1); Mactan Id, USNM 139679 (1), 139682 (1); Maculabo Id, USNM 139680 (1); Samar Id, CAS-SU 40645 (1); Negros Id, CAS-SU 14827 (1), 28435 (neotype of *Salarias periophthalmus visayanus*), 69690 (6 paralectotypes of previous taxon), 67677 (2), 69697 (5); USNM 51950 (holotype of *Salarias deani*), 51998 (1), 295127 (7). G of Thailand: Koh Kra, CAS 67681 (1), 68069 (1); Koh Samet, CAS 67678 (1), 67689 (1); Hinsonchakam, CAS 67679 (2); Goh Kram, CAS-SU 62086 (12), CAS 67680 (6); Goh Kram Noi, CAS 67676 (1). Malaysia: Tioman Id, BPBM 21952 (7), 21953 (6); Pulau Rawa, AMS I.29688-001 (1). Sabah: Manukan Id, off Kota Kinabalu, WAM P.30400-002 (19). Indonesia: Biliton, RMNH 4792 (lectotype and paralectotype of *Salarias bilitonensis*, lectotype is also neotype of *Salarias hendriksii*); Flores, UF 92359 (1); Sulawesi, G of Bone, USNM 122443 (1), 138318 (1); Bali, UF 31306 (3), NTM S.11127-001 (1), Hans Bath, personal collection (2, formerly part of NTM S.11127-009); Ambon, USNM 277965 (33); Saparua, USNM 293744 (1); Haruku, USNM 209613 (1). Australia: Northern Territory, McClure Id, NTM S.10595-011 (11); New Year Id, NTM S.10600-033 (4).

Periophthalmus Species Complex

We had considerable difficulty in deciding whether to treat the Periophthalmus species complex as a single, highly variable species or as 2 or more species with several exceptional populations and specimens. We do not believe our difficulties result from lack of adequate numbers of specimens or geographic coverage. Rather, they are the result of perceptual and philosophical limitations, the limitations of gross morphology as the sole basis for species recognition, and a need to limit the amount of time spent on the problem. With less than conviction, we recognize only 2 species in the complex. We base our decision primarily on female color pattern and, secondarily, on less consistent aspects of male color pattern and the modal serial position of the posteriormost pleural rib. All of these characters are correlated with geography.

Similar problems in species recognition surfaced during our investigations of two other taxa that we treat as single species: *Istiblennius edentulus*, in which population and individual variation presents even more perplexing problems, and *Blenniella gibbifrons*, in which such variation is, perhaps, less confusing than that which we encountered in the Periophthalmus complex.

Because of the intertwined nature of the two species we

recognize in the Periophthalmus complex, we treat the two species together, first presenting a combined descriptive account and some discussions (meristic characters, for example, overlap completely), and follow these with the synonymies and nomenclatural discussions of both species, In the discussions, for the sake of simplicity, we often refer to *B. periophthalmus* as "color-pattern Type I" (or variously, Types Ia to c), or just as "Type I," and *B. paula*, the other species in the Periophthalmus complex, as "type II."

COMPOSITE DESCRIPTION OF PERIOPHTHALMUS SPECIES COMPLEX.—Dorsal fin (Tables 11 and 12). XII to XIV,18 to 22 = 31 to 35 (XIII in over 98% of specimens; 18 segmented and 31 total elements in no males and only 2 of over 700 female specimens examined; 22 segmented rays and 35 total elements in only 9 of over 1500 specimens of both sexes combined); mean number of total elements tending to be higher for males from any locality than for females from same locality (higher for 47 of 61 localities for which means for both sexes are available, statistically significantly higher for 14 of the 47 localities); membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle well anterior to caudal-fin base to point on dorsal edge of caudal fin just distal to caudal-fin base (rarely on caudal fin).

Anal fin (Tables 11 and 12). II,19 to 23 (19 in only 1 male and 5 females, 23 in only 1 female in over 1500 specimens examined); mean number of segmented rays tending to be higher for males from any locality than for females from same locality (higher for 51 of 61 localities for which means for both sexes are available, statistically significantly higher for 16 of the 51 localities); posteriormost ray predominantly split to base in all populations, posteriormore element of paired ray usually well developed, readily discernible externally, but often represented by nub of bone recognizable only on radiograph or by dissection; terminal ray bound by membrane to caudal peduncle in less than 2% of over 500 specimens examined for character. Skin covering anal-fin spines and distal half of rays of large or mature males occasionally thickened or slightly inflated, never rugose or crinkled along the edges.

Pectoral-fin rays 13 to 15 (14 bilaterally in 91%, unilaterally in 7.5% of 291 specimens examined for character).

Pelvic-fin segmented rays 3.

Caudal fin. Dorsal procurrent rays 6 to 9 (9 in only 2 of 722 specimens examined for character; 7 in 70% of specimens), ventral procurrent rays 5 to 8 (5 in only one specimen, 7 in 77% of specimens), combination of 7 dorsal and 7 ventral procurrent rays in 62% of specimens; segmented rays 12 or 13 (12 in only 2 of 489 specimens examined for character, both from Cargados Carajos).

Vertebrae (Tables 11 and 12). 11 to 13+25 to 28 = 37 to 40 (12+25 to 27 = 37 to 39 in over 99% of specimens examined for

Table 11.—Frequency distributions for certain characters of male specimens of *Istiblennius periophthalmus* (Types Ia–c) and *I. paula* (Type II) from various localties. Underlining indicates significant differences between means of sexes from same locality (p ≤.05).

Type/Locality	Total dorsal-fin elements						Segmented anal-fin rays					Total vertebrae				
	31	32	33	34	35	x̄	19	20	21	22	x̄	37	38	39	40	x̄
TYPE Ia (E Indian & W Pacific Oceans)																
Maldive Islands	-	-	22	7	-	33.2	-	6	21	2	20.9	1	27	1	-	38.0
Cocos-Keeling Islands	-	-	15	13	-	33.5	-	1	25	2	21.0	-	23	5	-	38.2
Christmas Island	-	-	1	-	-		-	-	1	-		-	-	-	-	
Ashmore Reef, IO	-	1	9	2	-	33.1	-	1	10	1	21.0	-	9	3	-	38.2
Seringapatnam Reef	-	-	1	-	-		-	-	1	-		-	1	-		
North Reef, IO	-	-	2	-	-	33.0	-	1	1	-	20.5	-	2	-	-	38.0
Scott Reef	-	-	2	1	-	33.2	-	-	3	-	21.0	1	1	1	-	38.0
Rowley Shoals	-	-	5	1	-	33.2	-	-	6	-	21.0	-	4	1	-	38.2
Dampier Archipelago	-	-	2	-	-	33.0	-	-	2	-	21.0	-	2	-	-	38.0
Philippines																
Batanes Islands	-	-	4	1	-	33.2	-	-	5	-	21.0	-	4	-	-	38.0
S Luzon	-	-	1	2	-	33.7	-	-	3	-	21.0	-	2	1	-	38.3
Panay	-	-	1	-	-		-	-	1	-		-	-	-	-	
Siquijor & Negros	-	1	3	-	-	32.8	-	1	3	-	20.8	1	3	-	-	37.8
Indonesia																
Pulo Mega	-	-	1	-	-		-	-	1	-		1	-	-	-	
Bali	-	-	3	-	-	33.0	-	-	3	-	21.0	-	3	-	-	38.0
Moluccas	-	1	3	-	-	32.8	-	2	2	-	20.5	-	4	-	-	38.0
Papua New Guinea																
Ninigo Islands	-	-	1	2	-	33.7	-	-	1	2	21.7	-	1	2	-	38.7
Trobriand Islands	-	1	13	3	-	33.1	-	3	9	6	21.2	2	13	-	-	37.9
Pinipel	-	1	4	1	-	33.0	-	2	4	-	20.7	1	4	1	-	38.0
TYPE Ib (W Indian Ocean)																
Kenya	-	-	1	1	-	33.5	-	-	1	1	21.5	-	1	1	-	38.5
Zanzibar	-	-	1	1	-	33.5	-	-	2	-	21.0	-	2	-	-	38.0
South Africa	-	-	2	-	-	33.0	-	-	2	-	21.0	-	1	1	-	38.5
Comores Islands	-	-	4	7	-	33.6	-	-	6	5	21.4	1	5	5	-	38.4
Aldabra	-	-	15	11	-	33.4	-	-	20	5	21.2	-	17	9	-	38.3
Madagascar, Nossi Be	-	-	1	3	-	33.8	-	-	3	1	21.2	-	2	2	-	38.5
Madagascar, Tulear	-	-	6	9	-	33.6	-	1	9	5	21.3	-	8	7	-	38.5
Agalega	-	-	8	3	-	33.3	-	3	8	-	20.7	-	8	3	-	38.3
Chagos Islands	-	-	18	5	-	33.2	-	6	16	2	20.8	2	16	1	-	37.9
Cargados Carajos	-	-	-	20	3	34.1	-	-	7	18	21.7	-	1	22	2	39.0
Mauritius & Reunion	-	-	-	4	-	34.0	-	-	-	4	22.0	-	-	3	1	39.2
TYPE Ic (Red Sea, Oman)																
Gulf of Tadjourah	-	4	-	-	-	32.0	-	2	2	-	20.5	1	3	-	-	37.8
W Gulf of Aden	-	-	4	-	-	33.0	-	2	2	-	20.5	-	4	-	-	38.0
Egypt	-	3	11	-	-	32.8	-	3	11	-	20.8	1	13	-	-	37.9
Saudi Arabia	-	1	1	1	-	33.0	-	3	1	-	20.2	-	4	-	-	38.0
Sudan	-	4	6	-	-	32.6	-	7	3	-	20.3	-	10	-	-	38.0
Difnein Id (Ethiopia)	-	2	11	-	-	32.8	-	6	7	-	20.5	-	13	-	-	38.0
Cundabilu (Ethiopia)	-	-	2	-	-	33.0	-	1	1	-	20.5	-	2	-	-	38.0
Zubayr Id (Yemen)	-	5	2	-	-	32.3	-	5	2	-	20.2	2	4	-	-	37.7
Oman	-	4	1	-	-	32.2	1	3	1	-	20.0	2	3	-	-	37.6

character); mean number of total vertebrae tending to be higher for males from any locality than for females from same locality (male means higher at 44 of 61 localities for which means for both sexes are available; statistically significantly higher for only 6 of the 44 means; female means higher at 6 of the 61 localities, statistically significantly higher at 1 of the 6 localities, 11 means are identical); posteriormost pleural rib on 11th to 13th from anteriormost vertebra (rarely on 11th; Tables 13 and 14), rib often present only as small, bony fragment; posteriormost epineural on 20th to 28th from anteriormost centrum (on 22nd to 27th in 98% of specimens examined for character); mean serial number of vertebra bearing posteriormost epineural statistically significantly higher by about 1 vertebra for males than for females from a few localities (Maldive, Cocos-Keeling, Palmyra islands—note: accuracy of determination of posteriormost epineural from radiographs

Table 11.—continued.

Locality	Total dorsal-fin elements						Segmented anal-fin rays					Total vertebrae				
	31	32	33	34	35	x̄	19	20	21	22	x̄	37	38	39	40	x̄
TYPE II (Pacific Plate, S GBR, Coral Sea)																
Wake Island	-	-	2	5	-	33.7	-	1	2	4	21.4	-	5	2	-	38.3
Saipan	-	-	2	2	-	33.5	-	-	3	1	21.2	-	2	2	-	38.5
Guam	-	1	16	2	-	33.0	-	1	16	1	21.0	-	16	3	-	38.2
Ulithi	-	-	1	-	-		-	-	1	-		-	1	-	-	
Yap	-	-	2	-	-	33.0	-	-	2	-	21.0	-	1	1	-	38.5
Fais	-	1	5	2	-	33.1	-	2	6	-	20.8	1	5	2	-	38.1
Palau	-	-	18	9	-	33.3	-	3	20	4	21.0	-	17	10	-	38.4
Marshall Islands																
Enewetak	-	-	4	-	-	33.0	-	-	4	-	21.0	-	4	-	-	38.0
Bikini	-	-	25	-	-	33.0	-	2	23	-	20.9	-	22	3	-	38.1
Rongerik	-	-	12	1	-	33.1	-	3	10	-	20.8	-	12	1	-	38.1
Kwajelein	-	1	2	2	-	33.2	-	2	3	-	20.6	-	4	1	-	38.2
Arno	-	1	17	1	-	33.0	-	3	16	1	20.9	1	14	1	-	38.0
Onotoa	-	-	1	-	-		-	-	1	-		-	1	-	-	
Tuvalu (=Ellice Is)	-	-	3	-	-	33.0	-	-	3	-	21.0	-	3	-	-	38.0
Herald Cay	-	-	15	3	-	33.2	-	3	13	2	20.9	-	17	1	-	38.0
Kenn Reef	-	-	1	1	-	33.5	-	-	1	1	21.5	-	1	1	-	38.5
Lihou Reefs	-	-	4	-	-	33.0	-	1	3	-	20.8	-	3	1	-	38.2
Chesterfield Bank	-	-	-	4	-	34.0	-	-	3	1	21.2	-	2	2	-	38.5
Heron Island, GBR	-	-	1	3	-	33.8	-	-	3	1	21.2	-	1	3	-	38.8
Fiji	-	-	13	9	-	33.4	-	-	18	3	21.1	-	12	10	-	38.4
Rotuma	-	-	4	1	-	33.2	-	-	4	1	21.2	-	3	2	-	38.4
Samoa	-	-	-	1	-		-	-	1	-		-	1	-	-	
Rose Island	-	-	20	5	-	33.2	-	1	24	-	21.0	-	18	6	-	38.2
Niue	-	-	4	1	-	33.2	-	-	5	-	21.0	-	4	1	-	38.2
Tongareva (=Penrhyn)	-	-	10	-	-	33.0	-	-	10	-	21.0	-	10	-	-	38.0
Palmerston Island	-	-	2	13	1	33.9	-	-	7	9	21.6	-	2	14	-	38.9
Rarotonga	-	-	-	5	-	34.0	-	-	-	5	22.0	-	1	3	-	38.8
Society Islands	-	-	1	7	-	33.9	-	-	3	5	21.8	-	1	5	-	38.8
Tikahau	-	-	1	2	-	33.7	-	-	1	2	21.7	-	1	2	-	38.7
Rangiroa	-	-	11	11	-	33.5	-	-	18	4	21.2	-	4	18	-	38.8
Makatea	-	-	-	8	1	34.1	-	3	6	1	21.8	-	1	7	1	39.0
Makerno	-	1	-	-	-		-	-	1	-		-	-	1	-	
Ducie	-	-	-	1	-		-	-	-	1		-	-	1	-	
Marquesas Islands	-	-	-	1	-		-	-	-	1		-	-	1	-	
Canton Island	-	1	24	-	-	33.0	-	5	19	1	20.8	1	23	1	-	38.0
Hull(=Orona) Island	-	1	21	3	-	33.1	-	4	21	-	20.8	-	18	6	-	38.2
Atafu	-	-	10	2	-	33.2	-	1	10	1	21.0	-	10	1	-	38.1
Nukuonu	-	-	4	1	-	33.2	-	-	5	-	21.0	-	5	-	-	38.0
Fakaofo	-	-	23	1	-	33.0	-	3	20	1	20.9	-	20	3	-	38.1
Howland Island	-	-	21	4	-	33.2	-	1	22	2	21.0	-	17	6	-	38.3
Caroline Island	-	1	23	1	-	33.0	-	3	22	-	20.9	-	21	4	-	38.2
Starbuck	-	-	2	2	-	33.5	-	-	4	-	21.0	-	2	2	-	38.5
Christmas Island, PO	-	-	-	1	-		-	-	1	-		-	-	1	-	
Jarvis	-	-	-	1	-		-	-	-	1		-	-	1	-	
Fanning Island	-	-	1	1	-	33.5	-	-	1	1	21.5	-	-	2	-	39.0
Palmyra Island	-	-	11	18	-	33.6	-	-	15	15	21.5	-	2	28	-	38.9

often in realm of ±2).

Cirri. Nape cirrus present, occasionally missing unilaterally, small, usually simple, sometimes with ragged edge or tiny, single branch; largest specimen, unilaterally, with tip of cirrus bearing 5 minute branches. Orbital cirrus slender, usually simple, occasionally with short, lateral branch, less often with up to 4 tiny branches, main cirrus usually shorter than diameter of orbit, rarely slightly longer than diameter, but only in males. Nasal cirri short, palmate, rarely with more than 6 free tips.

Lateral line. Continuous canal anterodorsally with simple pores (infrequently with 1 or 2 vertical pairs of pores anteriorly), extending posteriorly to point between verticals

Table 12.—Frequency distributions for certain characters of female specimens of Istiblennius periophthalmus (Types Ia–c) and I. paula (Type II) from various localties. Underlining indicates significant differences between means of sexes from same locality (p ≤.05).

Type/Locality	Total dorsal-fin elements						Segmented anal-fin rays						Total vertebrae				
	31	32	33	34	35	x̄	19	20	21	22	23	x̄	37	38	39	40	x̄
TYPE Ia (E Indian & W Pacific Oceans)																	
Maldive Islands	-	3	34	1	-	32.9	-	14	23	-	-	20.6	6	29	1	-	37.9
Cocos-Keeling Islands	-	1	17	2	-	33.0	-	6	13	1	-	20.7	2	15	2	-	38.0
Christmas Island, IO	-	1	1	-	-	32.5	-	2	-	-	-	20.0	-	2	-	-	38.0
Similan Island, IO	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Ashmore Reef, IO	-	1	7	-	-	32.9	-	4	4	-	-	20.5	1	7	-	-	37.9
Seringapatnam Reef	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
North Reef, IO	-	-	2	-	-	33.0	-	2	-	-	-	20.0	-	2	-	-	38.0
Scott Reef	-	-	1	-	-		-	-	1	-	-		-	-	1	-	
Rowley Shoals	-	-	4	-	-	33.0	-	-	4	-	-	21.0	-	4	-	-	38.0
Dampier Arch.	-	-	2	-	-	33.0	-	1	1	-	-	20.5	-	2	-	-	38.0
Philippines																	
Batanes Islands	-	-	1	-	-		-	1	-	-	-		-	1	-	-	
S Luzon	-	1	3	-	-	32.8	-	4	-	-	-	20.0	1	2	-	-	37.7
Siquijor & Negros	-	1	4	-	-	32.8	-	2	4	-	-	20.7	-	6	-	-	38.0
Indonesia																	
Pulo Mega, IO	-	2	-	-	-	32.0	-	2	-	-	-	20.0	-	2	-	-	38.0
Bali	-	1	-	-	-		-	1	-	-	-		1	-	-	-	
Moluccas	-	-	2	-	-	33.0	-	1	1	-	-	20.5	-	2	-	-	38.0
Papua New Guinea																	
Ninigo Islands	-	3	1	-	-	32.2	-	2	2	-	-	20.5	1	3	-	-	37.8
Madang	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Trobriand Islands	-	3	14	-	-	32.8	-	5	11	-	-	20.7	2	12	-	-	37.8
Pinipel	-	1	-	-	-		-	1	-	-	-		-	1	-	-	
Solomon Islands	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Taiwan	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Okinawa	-	-	1	-	-		-	-	1	-	-		-	-	1	-	
TYPE Ib (W Indian Ocean)																	
South Africa	-	-	1	3	-	33.8	-	-	4	-	-	21.0	-	2	2	-	38.5
Mozambique	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Comores Islands	-	-	13	4	-	33.2	-	3	12	2	-	20.9	1	12	4	-	38.2
Aldabra	-	1	18	6	-	33.2	-	2	22	-	-	20.9	-	20	5	-	38.2
Madagascar, Nossi Be	-	-	1	1	-	33.5	-	-	2	-	-	21.0	-	1	1	-	38.5
Madagascar, Tulear	-	1	15	4	-	33.2	-	2	17	1	-	21.0	-	15	5	-	38.2
Agalega	1	1	8	3	-	33.0	1	1	10	1	-	20.8	1	8	3	1	38.3
Chagos Islands	-	3	20	-	-	32.9	-	9	14	-	-	20.7	3	19	-	-	37.9
Cargados Carajos	-	-	5	11	3	33.9	-	-	11	9	-	21.4	-	5	12	1	38.8
Mauritius	-	-	-	2	1	34.3	-	-	1	1	1	22.0	-	-	2	1	39.3
TYPE Ic (Red Sea, Oman)																	
Gulf of Tadjourah	-	5	2	-	-	32.3	1	6	-	-	-	19.8	2	5	-	-	37.7
W Gulf of Aden	-	8	-	-	-	32.0	-	8	-	-	-	20.0	1	7	-	-	37.9
Egypt	-	4	8	-	-	32.7	-	7	5	-	-	20.4	2	10	-	-	37.8
Saudi Arabia	-	2	3	-	-	32.6	-	3	2	-	-	20.4	1	4	-	-	37.8
Sudan	-	3	2	-	-	32.4	-	5	-	-	-	20.0	1	4	-	-	37.8
Difnein Id (Ethiopia)	-	5	2	-	-	32.3	1	5	1	-	-	20.0	2	4	-	-	37.7
Zubayr Id (Yemen)	-	1	1	-	-	32.5	-	1	1	-	-	20.5	-	2	-	-	38.0
Oman	-	3	1	-	-	32.2	1	3	-	-	-	19.8	3	1	-	-	37.2

from 8th and 12th dorsal-fin spines (from 8th only in Type Ic, from 9th commonly only in Type Ic; rarely as far as 12th), then continuing as 1 to 5 (rarely 1; modally 3 in most populations) short, disconnected, horizontally bipored canals (tubes) in skin to point between verticals from 10th dorsal-fin spine and 4th segmented ray (rarely only to vertical from 10th spine or posterior to vertical from second segmented ray); lateral line, including tubes, sometimes descending to body midline, but often failing to continue posteriorly after reaching midline.

Mandibular pores 5 to 7, 6 bilaterally in 95%, unilaterally in 4.9% of 234 specimens examined for character (5 or 7 pores only unilaterally).

Table 12.—continued.

Type/Locality	Total dorsal-fin elements						Segmented anal-fin rays						Total vertebrae				
	31	32	33	34	35	x̄	19	20	21	22	23	x̄	37	38	39	40	x̄
TYPE II (Sulawesi, Pacific Plate, S Great Barrier Reef, Coral Sea)																	
Indonesia, Sulawesi	-	-	3	-	-	33.0	-	2	1	-	-	20.3	1	2	-	-	37.7
Marcus	-	-	1	-	-		-	-	1	-	-		-	-	-	-	
Wake Island	-	-	4	-	-	33.0	-	-	4	-	-	21.0	-	4	-	-	38.0
Saipan	-	1	1	-	-	32.5	-	1	1	-	-	20.5	-	2	-	-	38.0
Guam	-	1	5	1	-	33.0	-	3	4	-	-	20.6	-	6	1	-	38.1
Yap	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Fais	-	-	4	-	-	33.0	-	3	1	-	-	20.2	-	4	-	-	38.0
Palau	-	4	15	1	-	32.8	-	9	12	-	-	20.6	4	16	1	-	37.8
Ponape	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Marshall Islands																	
Enewetak	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Bikini	-	3	21	-	-	32.9	-	7	17	-	-	20.7	1	23	-	-	38.0
Rongerik	-	3	13	-	-	32.8	-	7	9	-	-	20.6	2	11	1	-	37.9
Kwajelein	-	1	1	-	-	32.5	-	2	-	-	-	20.0	1	1	-	-	37.5
Arno	-	3	17	-	-	32.8	-	12	8	-	-	20.4	3	13	2	-	37.9
Abaiang	-	-	2	-	-	33.0	-	-	2	-	-	21.0	-	2	-	-	38.0
Onotoa	-	-	3	-	-	33.0	-	2	1	-	-	20.3	-	3	-	-	38.0
Herald Cay	-	5	35	8	-	33.1	-	16	31	1	-	20.7	3	40	4	-	38.0
Lihou Reefs	-	-	5	-	-	33.0	-	1	4	-	-	20.8	-	5	-	-	38.0
Chesterfield Bank	-	-	5	-	-	33.0	-	1	4	-	-	20.8	-	3	2	-	38.4
Middleton Reef	-	-	2	-	-	33.0	-	-	2	-	-	21.0	-	2	-	-	38.0
Heron Island, GBR	-	-	2	-	-	33.0	-	-	2	-	-	21.0	-	2	-	-	38.0
Fiji	-	-	9	2	-	33.2	-	-	10	-	-	21.0	-	8	3	-	38.3
Rotuma	-	1	4	1	-	33.0	1	2	3	-	-	20.3	-	5	1	-	38.2
Rose Island	-	1	23	1	-	33.0	-	7	18	-	-	20.7	-	23	2	-	38.1
Niue	-	-	4	-	-	33.0	-	-	4	-	-	21.0	-	4	-	-	38.0
Tongareva (= Penrhyn)	-	3	15	-	-	32.8	-	7	11	-	-	20.6	-	17	1	-	38.0
Palmerston Island	-	-	2	7	-	33.8	-	-	7	2	-	21.2	-	3	5	-	38.6
Rarotonga	-	-	1	1	-	33.5	-	-	2	-	-	21.0	-	-	2	-	39.0
Society Islands	-	-	2	-	-	33.0	-	-	2	-	-	21.0	-	1	1	-	38.5
Tikahau	-	1	1	-	-	32.5	-	-	2	-	-	21.0	-	-	2	-	39.0
Rangiroa	-	-	14	1	-	33.1	-	-	16	1	-	21.0	-	9	8	-	38.5
Makatea	-	-	3	3	-	33.5	-	-	4	2	-	21.3	-	2	4	-	38.7
Tubuai	-	-	-	1	-		-	-	1	-	-		-	-	-	-	
Mangareva	-	-	-	1	-		-	-	1	-	-		-	-	1	-	
Ducie	-	-	-	1	-		-	-	-	1	-		-	-	1	-	
Canton Island	-	-	25	-	-	33.0	-	9	16	-	-	20.6	-	17	7	-	38.3
Hull Island	-	1	24	-	-	33.0	-	10	15	-	-	20.6	1	22	1	-	38.0
Atafu	-	-	5	-	-	33.0	-	-	5	-	-	21.0	-	5	-	-	38.0
Nukuonu	-	-	1	-	-		-	-	1	-	-		-	1	-	-	
Fakaofo	-	1	15	-	-	32.9	-	7	9	-	-	20.6	-	16	-	-	38.0
Howland Island	-	3	25	-	-	32.9	-	11	16	1	-	20.6	-	24	3	-	38.1
Caroline Island	-	4	21	-	-	32.8	-	9	16	-	-	20.6	2	23	-	-	37.9
Starbuck	-	2	7	-	-	32.8	-	1	8	-	-	20.9	-	7	2	-	38.2
Christmas Island, PO	-	-	1	-	-		-	-	1	-	-		-	-	1	-	
Fanning Island	-	-	1	1	-	33.5	-	-	2	-	-	21.0	-	1	1	-	38.5
Palmyra Island	-	-	4	3	-	33.4	-	-	7	-	-	21.0	-	2	5	-	38.7

Five to 10 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (rarely 5 or 10 positions, 7 or 8 positions in 84% of 323 specimens examined for character); 1 to 4 positions with paired pores (2 positions with paired pores in 83% of specimens examined for character).

Ventral margin of upper lip crenulate; crenulae often shallow, irregular, occasionally appearing to be absent in large or poorly preserved specimens; dorsal margin of lower lip entire.

Posterior dentary canines present in both sexes.

Males lack blade-like fleshy crest on head dorsally, although few large Type-II males with relatively thin ridge up to 1.8 mm
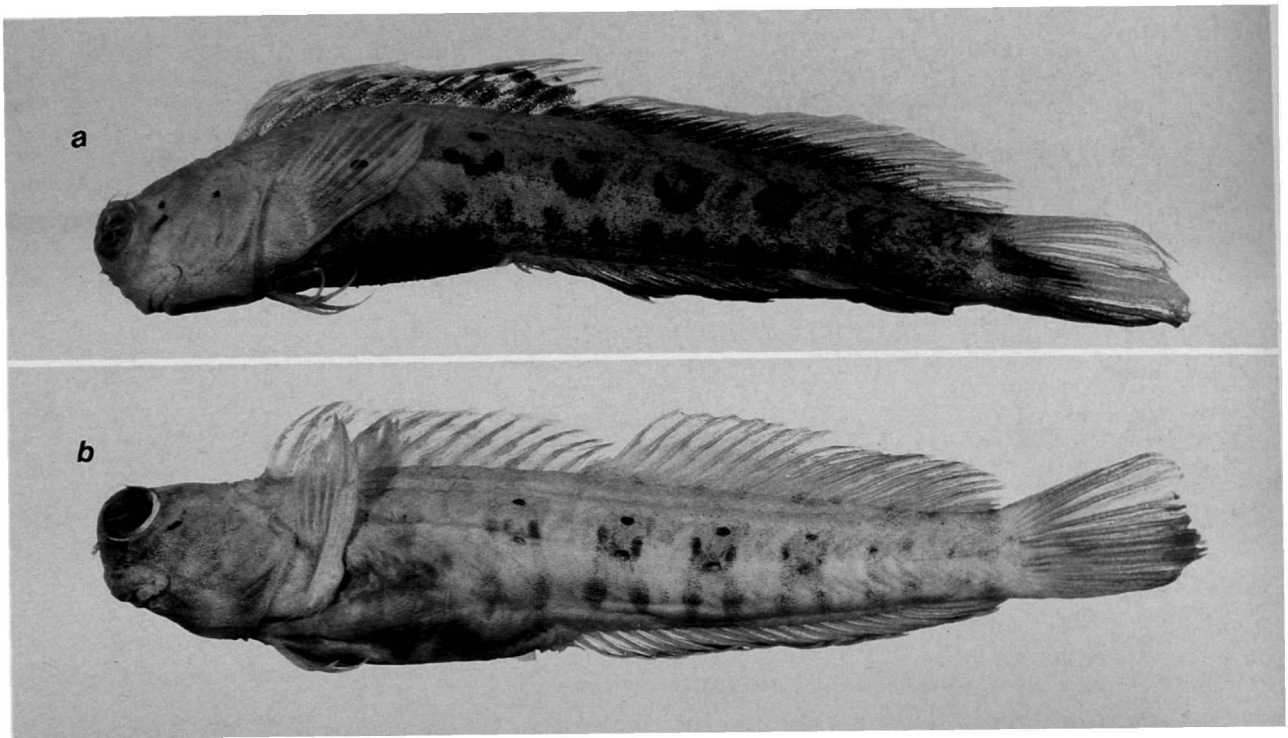
FIGURE 16.—*Blenniella paula*, USNM 291924, Caroline Island, Line Islands: *a*, male, 52 mm SL; *b*, female, 54 mm SL (photographs by T.B. Griswold).

high; head of males dorsally usually with low, broadly rounded, mid-longitudinal ridge or swelling, first noticeable at 47 to 65 mm SL, although males >100 mm may exhibit little or no ridge development. Females always lacking crest or ridge on head.

Color pattern (in preservative; only features shared by Type II and at least 1 of the 3 subtypes of Type I are given here; not every specimen will exhibit all features; for more details see discussion of color pattern in section on geographic variation). Head: 1 or 2 small, slender, dark spots (as vertical pair when 2) posterior to eye, spots separated by broader, pale area from posterior margin of orbit; irregular, faintly dusky band extending from midventral margin of orbit across upper lip; small, faintly to darkly dusky spot at ventroposterior end of preopercular area; ventral surface of head varying from uniformly pale or dark dusky to having highly variable, irregular, complete or ventromedially interrupted dusky cross-band, chevron, or U-shaped marking begining on each side of head just posterior to corner of mouth; occasionally another dusky area ventrally in opercular area extending broadly or narrowly along posterior margin (or narrowly in advance of margin) of gill membrane across ventral surface of head to

opposite side; upper lip often with 1 or 2 dusky bands separated by paler interspaces; anterior nostril occasionally surrounded by dusky spot.

Body: up to 7 dusky bands on sides, usually bifurcated ventrally, sometimes dorsally also; bands often interrupted dorsally and ventrally so that bifurcations appear as separate markings; vertical pair of dark-margined, pale, oblong to elongate-oblong ocelli incorporated in up to 6 bands (dorsal or ventral member of ocelli pair variably absent); ocelli pairs aligned, forming 2 longitudinal rows; male ocelli much more prominent than female ocelli, which may be faint or entirely lacking; 1 to several similar, usually smaller, ocelli variably occurring on body, particularly in large males; smaller specimens with solid, dark spot variably present on either side of each vertical pair of ocelli (Figure 16).

Head and/or body of many specimens, particularly females (Figures 9a, 17a), variously covered with small, diffuse, pale spots.

Spinous dorsal-fin of males with subdistal row of dark spots, mostly centered on spines, arranged in oblique rows, which may extend into irregularly pale and dark-dusky, broad, basal stripe (stripe composed of discontinuous dorsal extensions of

FIGURE 17.—*Blenniella paula: a,* USNM 242051, female, 81 mm SL, Viwa, Fiji; *b,c,* USNM 256542, Malolo Lailai, Fiji, *b,* female, 82 mm SL (see also Figure 18*c*), *c,* male, 89 mm SL; *d* (right side reversed), USNM 296060, male, 66 mm SL, Howland Island (photographs by T.B. Griswold).
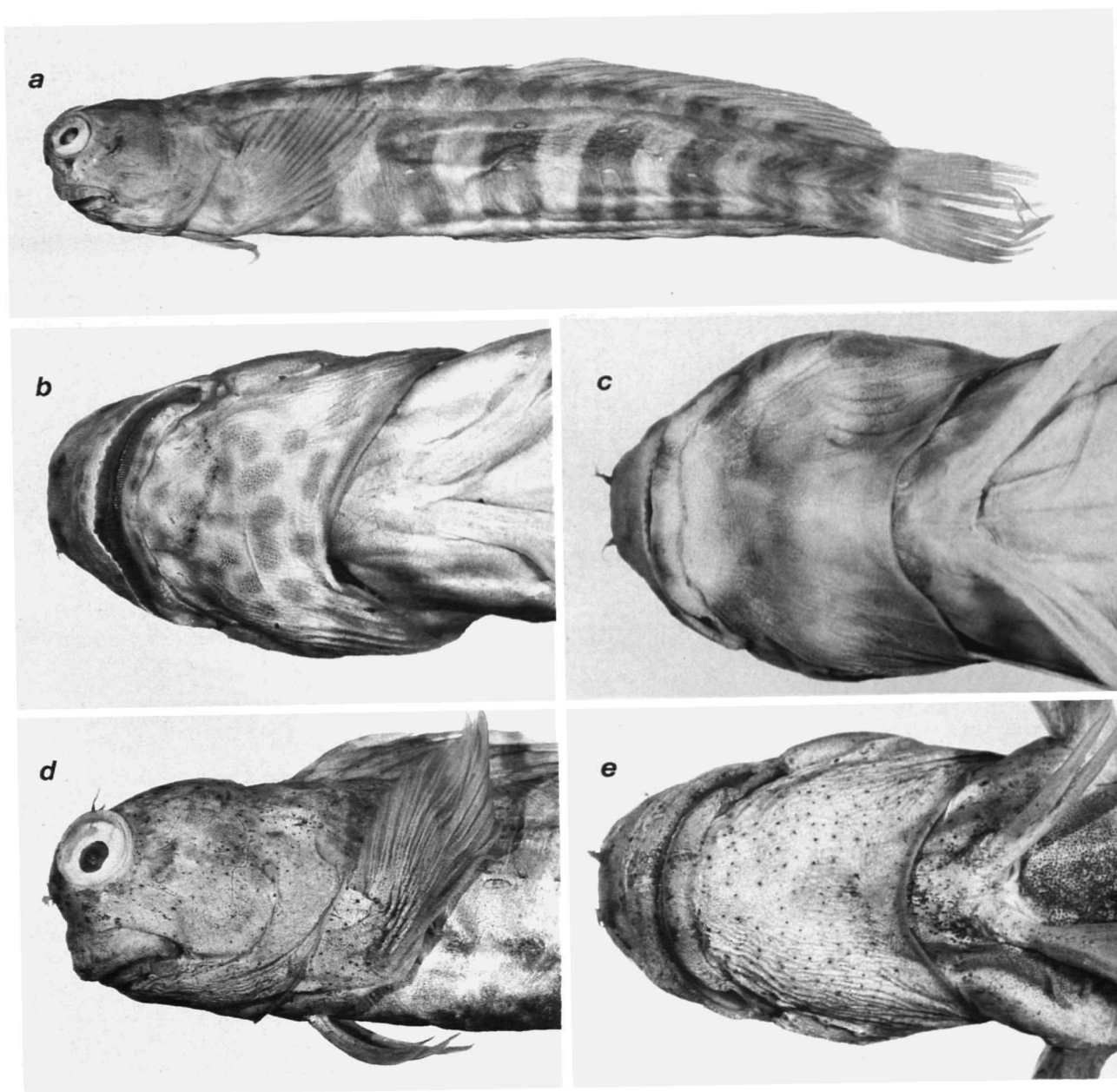
FIGURE 18.—*Blenniella paula: a,b*, USNM 137773, female, 69 mm SL, Gulf of Bone, Sulawesi, Indonesia; *c*, USNM 256542, female, 82 mm SL, Malolo Lailai, Fiji (see also Figure 17*b*); *d,e*, USNM 142212, male, 86 mm SL, Kwajalein, Marshall Islands; *b,c*, and *e* show the ventral surface of the head (photographs by T.B. Griswold).

dark body bands); basal half of segmented-ray portion dusky, variably marked, distal half abruptly paler with less distinct markings. Dorsal fin of females similarly, but less contrastingly, marked to that of males. Both portions of fin of females and, less often males, commonly with faint or almost no markings.

Anal fin more or less uniformly dark or darker distally in males, uniformly pale dusky in females, or with slightly darker diffuse areas basally and distally.

Caudal fin of males dark ventrally, much paler dorsally; that of females generally pale with small, faintly dusky, vertical pair of elongate markings entering middle of fin basally (similar

marks sometimes exhibited by males). Pectoral fins in most populations without distinct markings (however, see discussion of color pattern in section on geographic variation). Pelvic fins pale, without distinctive markings.

Live or fresh coloration. Following markings exhibited by both Types I and II. Males: dark blotch with incomplete, slender, bright-white posterior margin posterior to eye; small, bright-white spot ventral to eye; 2 rows of dark-margined, whitish or bluish spots on body incorporated in brownish bands, bands separated by whitish interspaces containing irregular, pale-brown or yellow-brown blotches; caudal fin variably tinged with pink, yellow, and/or orange posteriorly; brown markings on basal half of dorsal fin, pinkish or brownish orange on dorsal half. Female markings similar to those of males, but markings less strong.

Type-I specimens generally incorporate much red pigment on head, body and vertical fins, often in form of tiny red spots, which may extend onto pectoral fins and body anteriorly; females, in particular, may have red spotting covering entire body and dorsal fin. Type-II specimens may exhibit none of the red pigment or have, at most, rusty brown spots.

Published reproductions of color photographs taken of living or freshly dead specimens of *B. periophthalmus* have appeared in Allen (1985, fig. 393, male, Type Ia); Allen and Steene (1987, pl. 107: fig. 2, same male as Allen, 1985, poorer reproduction); Allen and Steen (1988, fig. 411, female, Type Ia); Masuda et al. (1975:88, fig. L, male, Type Ia and 1984, pl. 268: figs. L, same male, and M, female, Type Ia); Randall (1982, fig. 276, female, Type Ic), and Randall (1983:154, fig. 276, same as Randall, 1982, better reproduction, and p. 153, upper right, unnumbered figure, 2 individuals, probably males, Type Ic); Shen (1984, fig. 392-14) and Shen et al. (1986, fig. 35a, male, Type Ia, the 1986 reproduction of the figure is better). The only colored illustration of a Type-Ib specimen is a drawing of a male, which appeared in Smith (1949, pl. 75: fig. 970).

The only published color illustrations of *B. paula* we have seen are those of an apparent male (Myers, 1989, pl. 115: fig. d, Guam) and an apparent female (Randall et al., 1990:385, bottom fig., Great Barrier Reef). Myers (1989:211, fig. 5e, as *I. periophthalmus*) provides a nice black-and-white halftone illustration of a male *B. paula,* and Schultz and Chapman (1960, pl. 117: figs. *b,c*) present a drawing of a female and a photograph of a male.

Available, unpublished color photographs of fresh specimens are listed at the end of the material examined section.

Size. In large samples from any locality, largest specimen usually a male; in general, males attain larger size than females in both species, although 2 largest specimens of *B. paula* (128, 131 mm SL) are both females and only specimens available from Middleton Reef. Largest specimens of each type as follows: Type Ia: male 99 mm SL, female 79 mm; Type Ib: male 118 mm, female 101 mm; Type Ic: male 81 mm, female 80 mm; Type II: male 125 mm, female 131 mm.

Ophioblennius stage. This stage identified only tentatively for *Blenniella paula.* One series of specimens (USNM 143789) from Tau Island, American Samoa, containing 25 juveniles, about 12 to 56 mm SL, includes 2 specimens 14.4 and 14.6 mm SL lacking pigmentation except for scattered large melanophores covering dorsal portion of head above brain; tiny, laterally placed, ophioblennius-type recurved canine on each side of lower jaw present in 14.4 mm specimen, lacking in 14.6 mm specimen; both specimens have orbital and nasal cirri, but lack nape cirri and lip crenulae; other juveniles, about 12 to 18 mm SL, in same series appear metamorphosed, lacking ophioblennius-stage and posterior canines, but having strong patterns of 8 to 10 dark bands on body and dark pigmentation on head, all also lack nape cirri, and only largest exhibit beginnings of lip crenulae; specimens larger than 18 mm in series with well-developed nape cirri and lip crenulae; posterior dentary canines only become noticeable in specimens about 28 to 30 mm SL.

We believe all the specimens in USNM 143789 are probably conspecific, and the larger specimens are clearly identifiable as *B. paula.* Lack of dark melanophores on pectoral fins is distinctive for the ophioblennius-stage specimen described above (however, see discussion of ophioblennius stage under *B. gibbifrons*), but may be true of other species for which we have not identified ophioblennius stages.

GEOGRAPHIC VARIATION.—Meristic variation (Tables 11 and 12). Means for total numbers of dorsal-fin elements, segmented anal-fin rays, and vertebrae are lowest at localities from the Red Sea to Gulf of Oman (color-pattern Type Ic) and generally highest at the Cargados Carajos and Mauritius (color-pattern Type Ib) and in southern Oceania (color-pattern Type II). Otherwise, means are generally high at western Indian Ocean localities (color-pattern Type Ib) and intermediate at localities in the eastern Indian-western Pacific oceans (color-pattern Type Ia) and central Pacific Ocean (color-pattern Type II).

Means for serial number of vertebra bearing the terminal pleural rib (Tables 13 and 14) overlap considerably among the color-pattern types. The means range from 12.0 to 12.8 for color-pattern Types Ia to c, and 12.5 to 13.0 for Type II. There is a noticeable difference between the means of Types I and II, however, if only means based on 10 or more specimens are considered (Table 14). The 15 such means in the area comprising Types Ia to Ic vary from 12.0 to 12.6, whereas the 21 such means in the area comprising Type II vary from 12.7 to 13.0, with only the mean for Fiji (12.7) less than 12.8. To summarize, in specimens from areas with color-pattern Types Ia to c, the serial position of the terminal pleural rib is usually (27 of 35 means) on the 12th (posteriormost precaudal) vertebra, and in specimens from the area with color-pattern Type II, the terminal rib is almost always (42 of 44 means) on the 13th (first caudal) vertebra.

Color-pattern variation (preserved). There are two main

Table 13.—Frequency distributions for serial number of vertebra bearing terminal pleural rib in specimens of *Istiblennius periophthalmus* (Types Ia–c) and *I. paula* (Type II) from various localities.

Type/Locality	Terminal pleural rib on vertebra #				Type/Locality	Terminal pleural rib on vertebra #			
	11	12	13	x̄		11	12	13	x̄
TYPE Ia (E Indian & W Pacific Oceans)					**TYPE II (Pacific Plate, S GBR, Coral Sea)**				
Maldive Islands	-	52	13	12.2	S Sulawesi	-	-	3	13.0
Cocos-Keeling Ids	-	24	17	12.4	Wake Island	-	-	9	13.0
Christmas Island	-	3	-	12.0	Saipan	-	-	5	13.0
Ashmore Reef, IO	-	18	2	12.1	Guam	-	2	20	12.9
Seringapatnam Reef	-	1	-		Ulithi	-	-	1	
North Reef, IO	-	3	-	12.0	Yap	-	-	3	13.0
Scott Reef	-	2	2	12.5	Fais	-	1	11	12.9
Rowley Shoals	-	9	1	12.1	Palau	-	3	36	12.9
Dampier Arch.	-	4	-	12.0	Ponape	-	-	1	
Pulo Mega	-	3	-	12.0	Enewetak	-	1	4	12.8
Bali	-	3	-	12.0	Bikini	-	1	44	13.0
Moluccas	-	1	1	12.5	Rongerik	-	1	23	13.0
Ninigo Islands	-	3	1	12.2	Kwajelein	-	1	5	12.8
Batanes Islands	-	4	1	12.2	Arno	-	3	19	12.9
S Luzon	-	2	3	12.6	Abaiang	-	1	1	12.5
Panay	-	-	1		Onotoa	-	1	3	12.8
Siquijor & Negros	-	4	6	12.6	Tuvalu (=Ellice Is)	-	-	3	13.0
Madang	-	-	1		Herald Cay	-	8	41	12.8
Trobriand Islands	-	23	8	12.2	Kenn Reef	-	-	2	13.0
Pinipel	-	1	3	12.8	Lihou Reefs	-	-	9	13.0
Taiwan	-	1	-		Chesterfield Bank	-	-	5	13.0
Okinawa	-	-	1		Middleton Reef	-	-	2	13.0
					Heron Island, GBR	-	-	5	13.0
					Fiji	-	9	19	12.7
TYPE Ib (W Indian Ocean)					Rotuma	-	1	9	12.9
Kenya	-	2	-	12.0	Rose Island	-	5	38	12.9
Zanzibar	-	2	-	12.0	Niue	-	1	8	12.9
South Africa	-	2	4	12.7	Tongareva	-	3	23	12.9
Mozambique	-	-	1		Palmerston Island	-	5	19	12.8
Comores Islands	-	17	10	12.4	Rarotonga	-	3	4	12.6
Aldabra	-	30	17	12.4	Society Islands	-	-	7	13.0
Madagascar, Nossi Be	-	2	2	12.5	Rangiroa	-	4	30	12.9
Madagascar, Tulear	-	19	13	12.4	Makatea	-	1	14	12.9
Agalega	-	18	5	12.2	Tikahau	-	-	5	13.0
Chagos Islands	-	21	12	12.4	Makerno	-	-	1	
Cargados Carajos	-	25	15	12.4	Mangareva	-	-	1	
Mauritius	-	2	4	12.8	Ducie	-	-	2	13.0
					Canton Island	-	4	38	12.9
					Hull Island	-	1	36	13.0
					Atafu	-	1	6	12.8
TYPE Ic (Red Sea, G Aden & Tadjourah, Oman)					Nukuonu	-	-	3	13.0
Aden & Tadjourah gulfs	-	7	2	12.2	Fakaofo	-	4	23	12.8
Egypt	-	21	3	12.1	Howland Island	-	2	42	13.0
Saudi Arabia	1	3	5	12.4	Caroline Island	-	6	41	12.9
Sudan	-	11	1	12.1	Starbuck	-	1	10	12.9
Difnein Id (Ethiopia)	-	19	-	12.0	Christmas Island	-	1	1	12.5
Cundabilu Id (Ethiopia)	-	1	-		Jarvis	-	-	1	
Zubayr Id (Yemen)	-	7	2	12.2	Fanning	-	1	3	12.8
Oman	-	8	1	12.1	Palmyra Island	-	4	29	12.9

types (I, II) of color pattern exhibited by the various populations of the Periophthalmus complex. These color-pattern types are, for the most part, correlated with the position of the terminal pleural rib (thus, also correlated with geography). Although it is usually possible to assign a series of specimens comprising adults of both sexes from a single locality to 1 or the other of the 2 main color-pattern types, some specimens can be confusing. We also recognize 3 main, geographically differentiated color-pattern subtypes (Types a,b,c) within the Type I-color pattern, but there is overlap

Table 14.—Frequency distributions for means reported in Table 13; upper half of table includes all means; lower half includes only means based on 10 or more specimens.

Color pattern	Means										
	12.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	13.0
Type Ia	5	2	4	-	1	2	2	-	1	-	-
Type Ib	2	-	1	-	5	1	-	1	1	-	-
Type Ic	1	3	2	-	1	-	-	-	-	-	-
Type II	-	-	-	-	-	2	1	1	8	14	18
Type Ia	-	2	2	-	1	-	1	-	-	-	-
Type Ib	-	-	1	-	5	-	-	-	-	-	-
Type Ic	1	2	-	-	-	-	-	-	-	-	-
Type II	-	-	-	-	-	-	-	1	3	13	4

among the subtypes. We first give a brief, general summary of the color-pattern types, and then discuss the patterns in detail.

Summary description. Type-I color pattern (*B. periophthalmus*): body of adult females sprinkled with fine, dark spots; dark opercle spot, if present, located entirely, or almost entirely, dorsal to widest portion of opercle. Type-Ia pattern (Figures 20a,b): dark opercle spot often present, rarely extending ventrally onto widest portion of opercle; no dark spots on pectoral fin; body of males without sprinkling of fine, dark spots. Type-Ib pattern (Figures 19, 21): dark opercle spot usually lacking, usually faint when present, similar to that of Type Ia when most fully developed; few small pale spots on opercle when no dark spot present; no dark spots on pectoral fin; some portion of body of males often with sprinkling of fine, dark spots. Type-Ic pattern (Figures 20c,d, 22): dark opercle spot usually present, occasionally extending ventrally onto widest portion of opercle; dark spots usually present on pectoral fin; body of male usually sprinkled with fine, dark spots. Type-II color-pattern (*B. paula*; Figures 16 to 18): no sprinkling of fine, dark spots on body of either sex; dark opercle spot, if present, at least partially, if not completely, located at level of widest portion of opercle; no dark spots on pectoral fin.

Detailed description. Several color-pattern markings may occur only in specimens of one or the other of the color-pattern types, but the most consistent characteristic for separating Types I and II involves only females. In most adult Type-I females, there is a sprinkling of tiny dark spots that covers some to all of the body (but not the head, except for some specimens from the east African coast, which are like some Type-II specimens from Kwajelein, Marshall Islands (compare Figure 18d with head of specimen in Figure 21d). The spots appear to lie in a superficial layer of the skin, and overlie other dark markings on the body (e.g., the body bands). At some localities (e.g., Agalega, Type Ib), however, many females have these spots so reduced in number or so faintly expressed as to be almost unnoticeable, if not actually absent Figure 19a). Such

Type-Ib females can be confused easily with Type-II females, which never exhibit fine spotting on the body. In small (size varies considerably) Type-II females, the developing body ocelli or developing posterior dark body bands are spot-like, and may superficially resemble the spots of Type-I females. The body spots of Type-Ic specimens are often slightly larger and more prominent than those of Types Ia and b.

At one locality, Gulf of Bone, southern Sulawesi, essentially within the Type-Ia area, females (only 3 available) lack body spots (Figure 18a,b) and, except for a unique pattern of large, dusky spots on the ventral surface of the head, are remarkably similar in color pattern to Type-II females (males from Gulf of Bone unavailable). With reservation, we have identified the Gulf of Bone specimens (Figure 61) as belonging to Type II.

Many Types Ib and c, but few Type-Ia, males also exhibit female-type body spotting, particularly males from the Red Sea (Type Ic), where the spots are often prominent and may cover almost the entire body, Figure 22d). In contrast to the Red Sea males, males from the Gulf of Oman and Strait of Hormuz (also Type Ic, Figure 20c) have few to no dark body spots. In Comores and Chagos islands and southern Madagascar males (Type Ib), the spots are not prominent and may be restricted to the body ventrally (Figure 21b). In the Type-Ia area, sparsely spotted males are known only from the main islands of the Philippines. At most of these localities there are males with few or no fine, dark body spots, and these males might be confused with Type-II males (see also following).

Type-Ia and Type-Ic specimens usually have a dusky-to-dark ovoid spot (often partially surrounded by a diffuse, unpigmented margin) that covers some to almost all of the dorsalmost area of the opercle (dorsal to the widest portion of the opercle, Figures 20, 22). In Type-Ic (but not Ia) specimens, the spot may extend ventrally onto the widest portion of the opercle and touch or surround a sensory pore of the preopercle canal (the ventral portion of the spot appears to be a homologue of one of the Type-II opercle spots). Type-Ib specimens at most localities have no recognizable dark spot on the opercle, but in exceptional specimens, a spot similar to that of Types Ia and Ic does occur (but does not extend onto the widest portion of the opercle). For instance, among more than 25 specimens of each sex available from Aldabra (see material examined), 4 males, but no females, have a dark opercle spot: 2 have a large, dark spot and 1 a moderately dark spot, and the fourth has only a faintly dusky spot.

A somewhat intermediate state for opercle spot occurs on specimens from the Chagos Islands, which are geographically intermediate between the Maldive Islands, where all specimens have a well-developed opercle spot, and the western Indian Ocean, where few specimens have a well-developed opercle spot. Among 39 adult specimens in a single collection from the Chagos Islands (ROM 43907), 4 males and 2 females have moderately well-developed opercle spots, 10 males and 8 females have faint, but noticeable spots, and 3 males and 12 females show no evidence of opercle spots. Among 18 small,
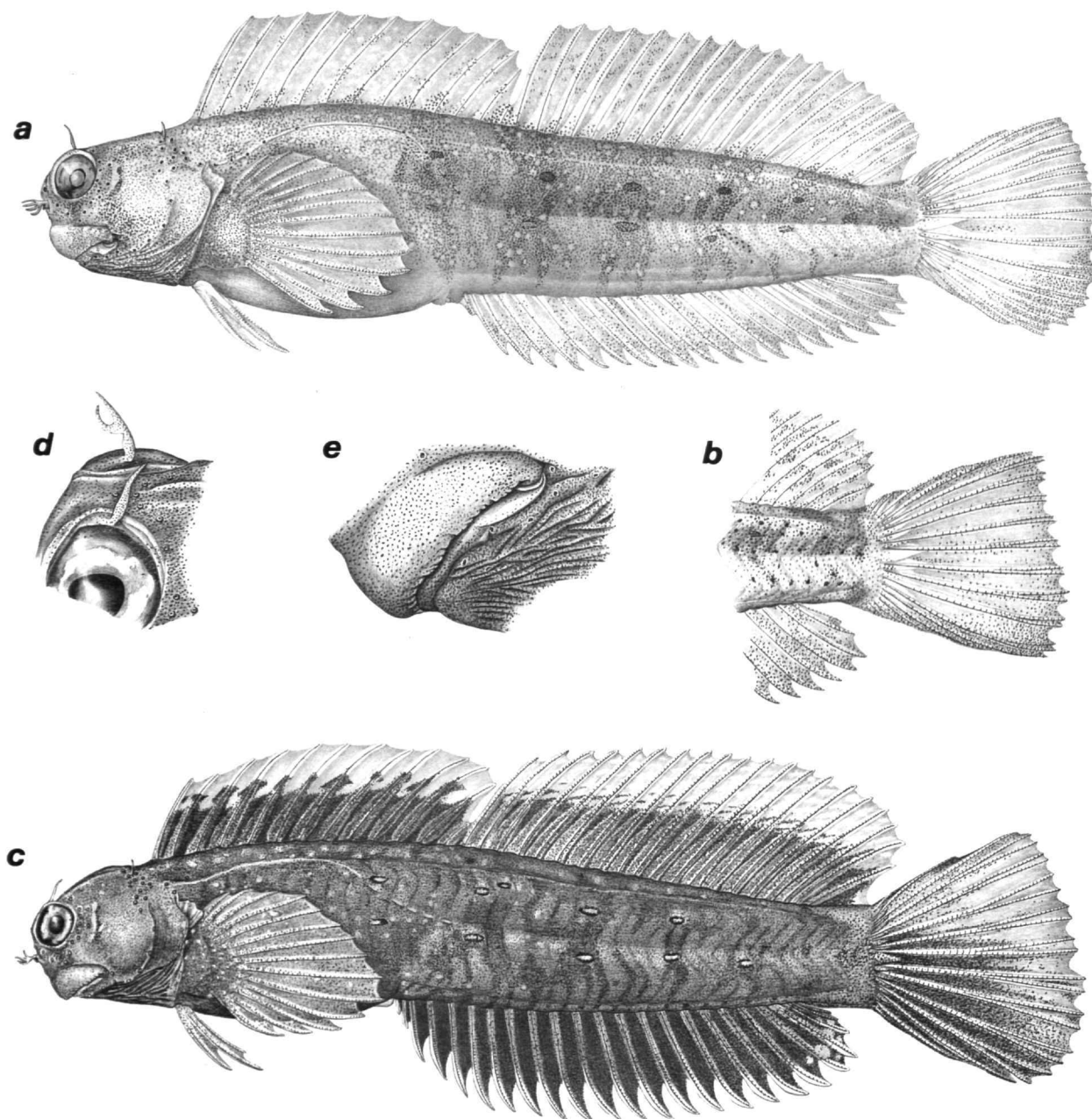
FIGURE 19.—*Blenniella periophthalmus*, color-pattern type Ib (see also Figure 21), USNM 224888, Agalega: *a*, female, 70 mm SL; *b*, female, 58 mm SL, posterior end of body; *c-e*, male, 73 mm SL (drawing by P.K. Hollingsworth).
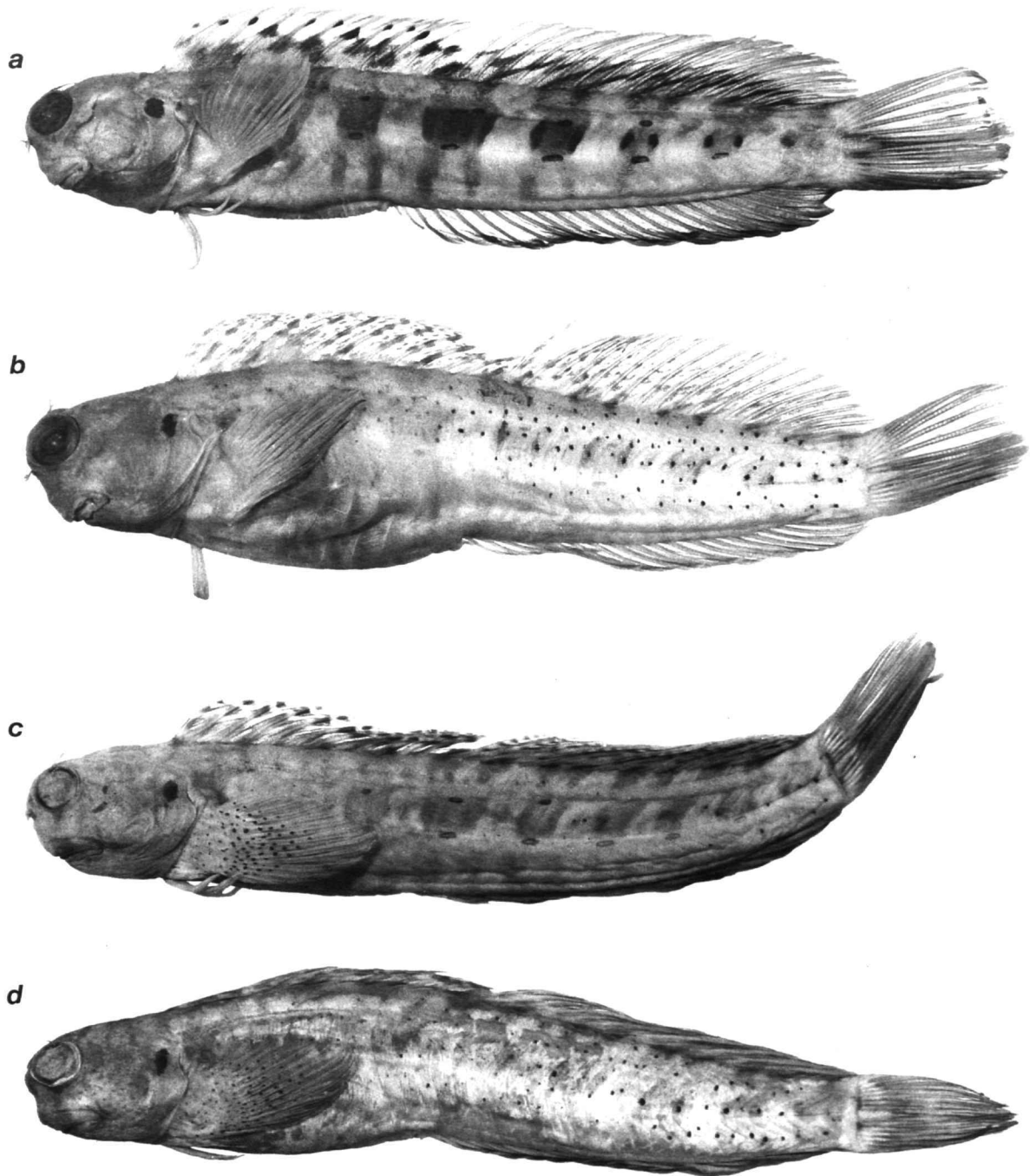
FIGURE 20.—*Blenniella periophthalmus: a,b,* color-pattern type Ia, USNM 296167, Kiriwina, Trobriand Islands, *a,* male, 71 mm SL, *b,* female, 62 mm SL; *c,d,* color-pattern type Ic (see also Figure 22), USNM 217356, S of Sidab, Gulf of Oman, *c,* male, 66 mm SL, *d,* female 66 mm SL (photographs by T.B. Griswold).
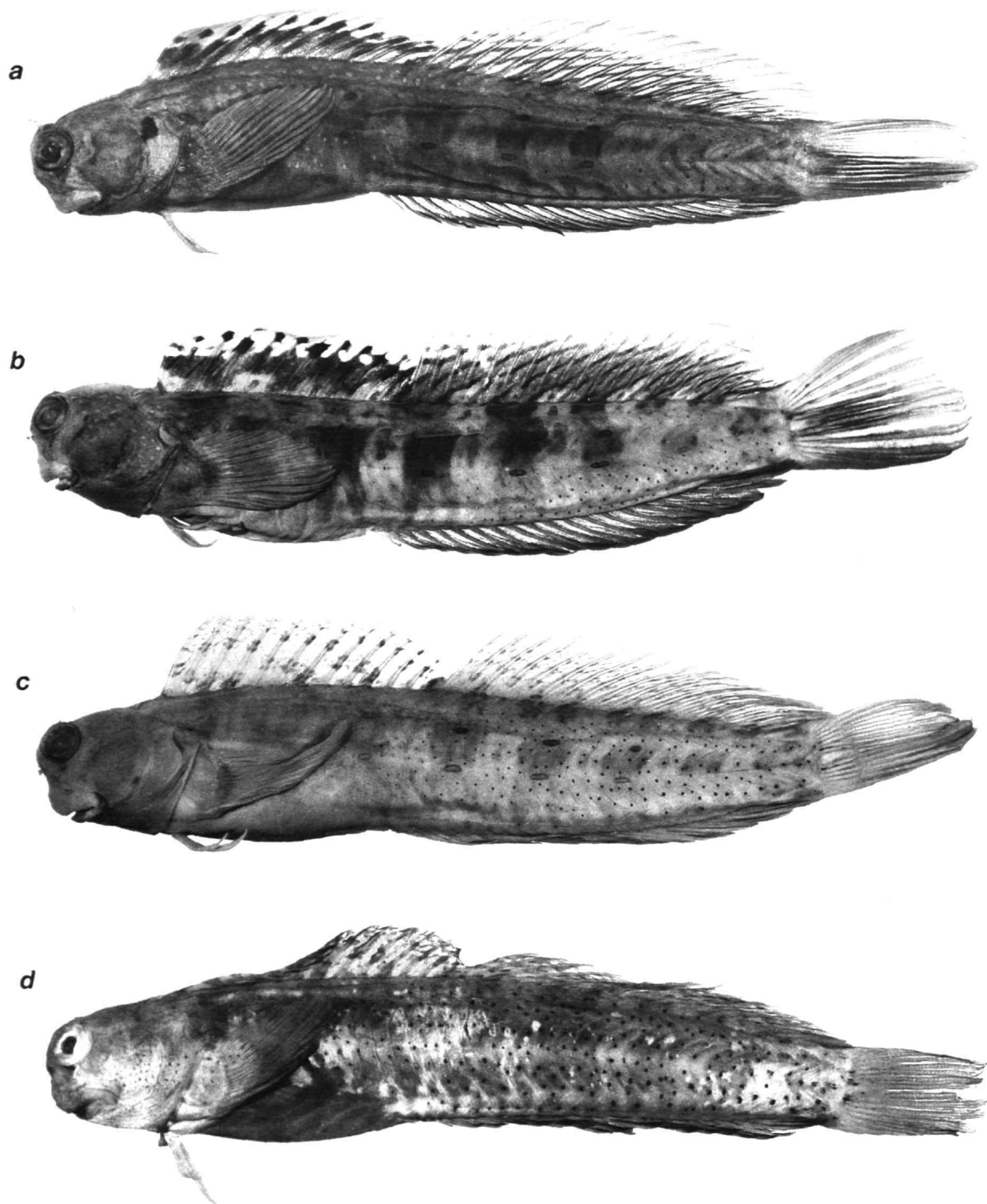
FIGURE 21.—*Blenniella periophthalmus*, color-pattern type Ib (see also Figure 19): *a*, USNM 296055, male, 66 mm SL, Aldabra (dark opercle spot is uncommon variation); *b,c*, UMMZ 186188, Tulear, Madagascar, *b*, male, 82 mm SL, *c*, female, 86 mm SL; *d* (right side reversed), USNM 227346, female, 67 mm SL, Kwazulu, South Africa (photographs by T.B. Griswold).
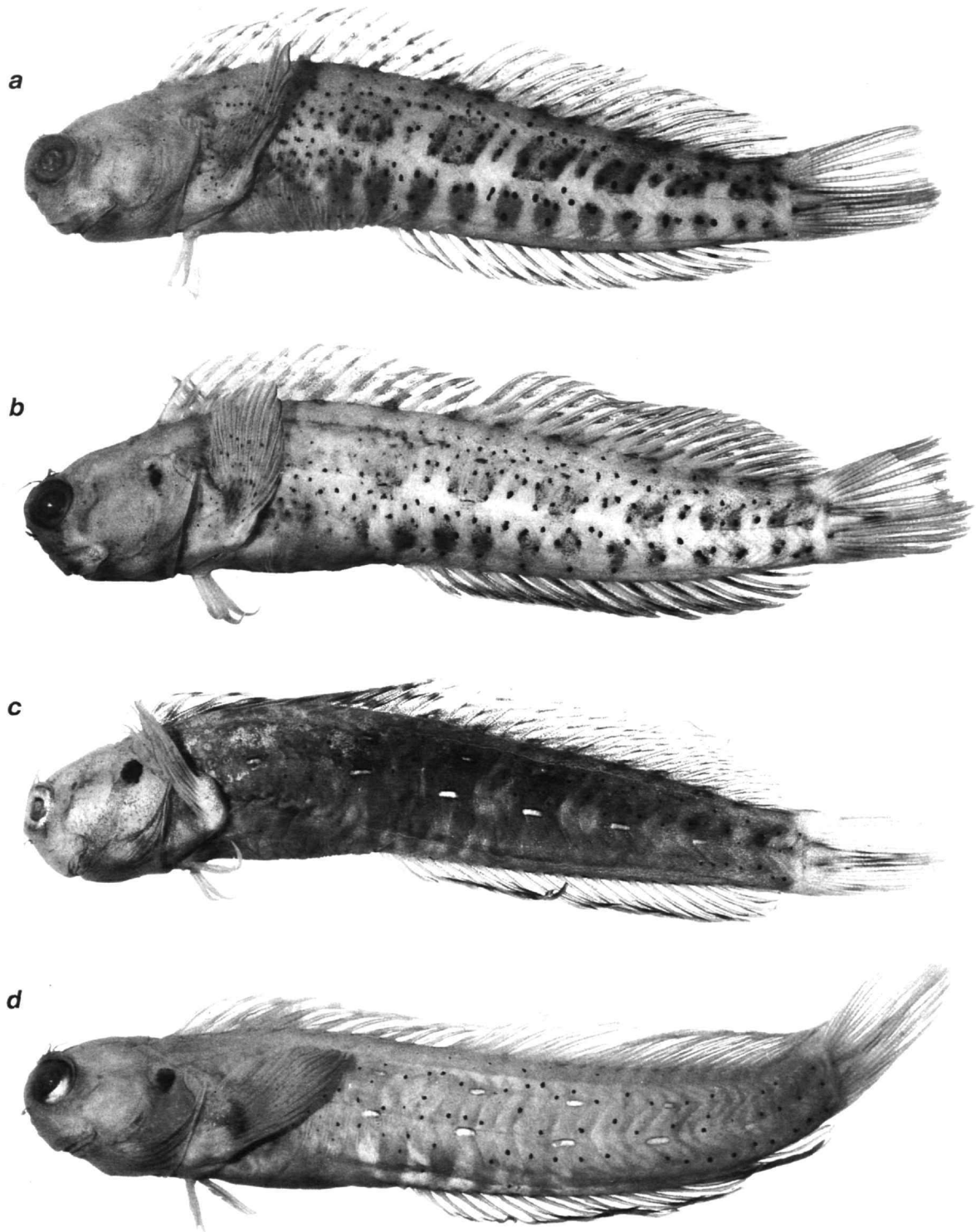
FIGURE 22.—*Blenniella periophthalmus*, color-pattern type lc (see also Figures 20*c,d,*), USNM 204505, Difnein Island, Red Sea: *a*, female, 43 mm SL; *b*, female, 48 mm SL; *c*, male, 53 mm SL; *d*, male, 52 mm SL (photographs by T.B. Griswold).

sex-indeterminate specimens from the same collection, 9 have small or faint opercle spots and 9 show no evidence of spots. The Chagos Islands specimens are assigned to Type Ib, rather than Ia, because none exhibit as well-developed an opercle spot as occurs in Type Ia, and most of the adult males have some portion of the body sprinkled with fine, dark spots, which are present only in some Type-Ia males from the Philippines.

Based on the proportion of specimens with an opercle spot, the Type-Ia distribution can be divided into two sub-areas, which correspond to the Pacific Ocean and Indian Ocean portions of the distribution. With only the rarest of exceptions (e.g., none of 66 specimens from the Maldive Islands, in only 1 of 49 specimens from Cocos-Keeling Islands) is a well-developed opercle spot lacking on Type-Ia specimens from the Indian Ocean. None to about half the Type-Ia specimens from any Pacific Ocean locality lack opercle spots.

Type-II specimens may also have a dark or dusky opercle spot, but it is usually much smaller than the Type-I spot and all or part of the spot is located more ventrally—at the level of the widest portion of the opercle. The Type-II spot almost always touches or partially surrounds a pore of the preopercular sensory canal, and the spot, when restricted to the widest portion of the opercle, scarcely impinges on the opercle (this portion of the opercle spot appears to be a homologue of a portion of the Type-Ic opercle spot). The Type-II spot often appears as a small, black dot (Figures 16a, 17c); however, a pale spot may be in the position where a dark spot might be expected. A second small, dusky opercle spot also may be present just posterodorsal to the widest portion of the opercle, and the two spots may fuse and appear as a single, more or less vertically elongate spot. When vertically elongate, the marking may be more or less uniformly dark, or pale with a narrow, dark margin (Figure 17d). We believe that the pale variations of the dark opercle spots are artifacts of preservation and the result of light diffraction: in life these spots are whitish or bluish and may become dark only after preservation (the opercle spot of Type-I specimens also appears as a pale area in color photographs of living or freshly dead specimens).

The opercle spot of Type-II specimens is predominantly restricted in occurrence to males. Poorly developed opercle spots occasionally occur in Types Ia and Ic specimens, and these spots can closely resemble those of Type-II specimens, but they are positioned more dorsally. Some male specimens from the northeastern portion of the Type-Ia distribution area lack all indications of opercle spots and these males are virtually impossible to distinguish externally from Type-II males that lack opercle spots.

Klausewitz (1963, as *Istiblennius periophthalmus*) recognized two subspecies of *Blenniella periophthalmus*, based on the presence or absence of the opercle spot. He believed that the spot was present in his Indian Ocean subspecies (*I. p. biseriatus*) and absent in his Pacific Ocean subspecies (*I. p. periophthalmus*). He was only partially correct, because his conclusions were based on incomplete data and an erroneous interpretation of the identities of the holotypes of his two nominal subspecies (*biseriatus* is a synonym of *periophthalmus*). Additionally, his *I. p. periophthalmus* comprises both of the species that we recognize in the Periophthalmus complex. In Type-I males, the segmented-ray portion of the dorsal fin frequently bears slender, dark, posteriorly inclined pinstripes that course through, at least, the dusky basal half of the fin (Figures 20a, 21a,b, 22c; see also Smith, 1959, pl. 14: fig. B, Type-Ib male from Mozambique, or Springer, 1986, fig. 235.22, same illustration as Smith). In Type-II males, the dusky basal half of the segmented-ray portion of the dorsal fin rarely incorporates distinctive markings, although faint indications of inclined pinstripes are sometimes noticeable just dorsal to the basal dusky area similar to the pattern shown in the drawing of the male from Agalega (Type Ib, Figure 19c). Irregular, inclined dorsal extensions of the body bands may enter the segmented-ray portion of the dorsal fin of males from any locality.

Type-I females often have noticeable dusky spots and irregular markings in the segmented-ray portion of the dorsal fin, whereas, Type-II females rarely have such markings, the fin usually appearing to be almost immaculate.

Type-Ic specimens (both sexes) usually have the basal half of the pectoral fin covered with fine, dark spots (Figures 20c,d, 22). Similar, but much less numerous and less conspicuous spots occur in some Type-Ib females (Figure 21d) from the east African coast, and some specimens of both sexes of Type II from Kwajelein, Marshall Islands (Figure 18d).

Winterbottom et al. (1989, fig. 387) provide a halftone photograph of a female Type Ib from the Chagos Islands. The head and basal third of the pectoral fin of the specimen appears to bear numerous, fine, dark spots. The original photograph, however, was in color, and the spots were red; they have completely faded from the preserved specimen. Many of the dark spots on the head and body of preserved Type-I specimens were surrounded by red chromatophores in life. The red spots of live or fresh specimens of both Types I and II (especially, females of Type II) fade in preservation and leave no evidence unless they occurred in a dusky area, in which case they are replaced by pale spots (Figures 17a, 19a). Often, each red spot surrounds a fine, black spot on the body of females. When the red pigment fades the dark spot remains.

COMPARISONS AND RELATIONSHIPS.—*Blenniella periophthalmus* and *B. paula* form a sister group which is the sister group of the sister-species pair *B. gibbifrons* and *B. chrysospilos* (see section on Phylogenetic Analysis). The 4 species share a general similarity in morphology and, uniquely in *Blenniella* (and *Istiblennius*), predominantly 12 precaudal vertebrae. Less exclusively, they all lack a well-developed head crest in males and share a habitat preference for clear, subtidal, fully marine waters in the vicinity of rocky or coral reefs, although *B. paula* and *B. periophthalmus* are often collected in tidepools, whereas

the other two species are not. *Blenniella periophthalmus* and *B. paula* can be readily distinguished from *B. gibbifrons,* and *B. chrysospilos,* with which they are extensively sympatric, in lacking paired dorsal and ventral branches extending from the lateral line.

DISTRIBUTION.—The distribution of the Periophthalmus species complex was discussed in the section on geographic variation, and is given in Figure 61.

Blenniella paula (Bryan and Herre), new combination

FIGURES 16–18

Salarias paulus Bryan and Herre, 1903:136 [Marcus Island; holotype BPBM 2455]. [Type II.]

Salarias tubuensis Seale, 1906:87 [Tubuai, Austral Ids.; holotype BPBM 784]. [Type II.]

NOMENCLATURAL DISCUSSION.—Seale (1906) did not compare his *Salarias tubuensis* with any species. He reported that the holotype lacked nape cirri and dentary canines. We have examined the holotype and find that it has small dentary canines. The nape cirri are not missing, but are represented by small, inconspicuous nubbins. The specimen is identifiable as *B. paula.*

MATERIAL EXAMINED.—Type II. Indonesia: Sulawesi, G of Bone, USNM 137773 (3). Marcus Id: BPBM 2455 (holotype of *Salarias paulus*). Wake Id: BPBM formerly part of 4938 (1), CAS 68011 (3), 68058 (7). Guam: USNM 111884 (19), 123935 (3), 124008 (1), 124195 (1), 139903 (1), 291629 (1). Micronesia: Yap, CAS 68043 (1), 68044 (1), 68056 (1); Ulithi, CAS 68012 (1); Fais Id, CAS 68047 (12). Palau: CAS 67300 (64), 68053 (1). Mariana Is: Saipan, CAS 67298 (2), 68008 (1), 68045 (3). Ponape: USNM 223401 (1). Marshall Is: Enewetak, USNM 296624 (5); Rongerik, USNM 142210 (29); Bikini, USNM 142202 (65); Kwajelein, BPBM 296115 (2), USNM 142212 (6), 296115 (2); Arno, USNM 166801 (40). Kiribati (= Gilbert Is): Abaiang, AMS I.18052-026 (2); Onotoa, USNM 167339 (7). Coral Sea: Diamond Islet, AMS I.18488-001 (1); Kenn Reef, AMS IB.4898 (1), IB.4899 (1); Herald Cay, AMS IB.5029 (1), IB.5030 (1), QM I.29520 (9), 29523 (21); WAM P.28536-023 (32); Lihou Reefs, QM I.25911 (10); Chesterfield Bank, BPBM 33707 (9). Tasman Sea: Middleton Reef, QM I.2290 (2). GBR: Heron Island, USNM 296098 (2), 296145 (3), 315311. Tuvalu: Funafuti, AMS I.4165 (1), I.4166 (1); Vaitupu, AMS I.4691 (1). Fiji: Makaluva, ANSP 93917 (3), 93961 (5), 114790 (2), USNM 315368 (1); Viti Levu, BPBM 35050 (3); Viwa Id, USNM 242051 (7), 257644 (3); Malolo Lailai, USNM 256542 (11). Rotuma: USNM 283140 (11). Samoa Is: Upolu, USNM 124336 (1); Tutuila, USNM 301961 (1); Tau Id, USNM 143789 (25); Rose Id, USNM 115473 (115); Swains Id, USNM 115471 (15, including 2 cleared and stained). Niue: NMNZ 12377 (1), 15682 (5), formerly part of 15688 (3). Cook Is: Palmerston, NMNZ P.15706 (25); Rarotonga, 296058 (7); Tongareva (=Penrhyn): USNM 296622

(27), 296623 (1). Society Is: Tahiti, USNM 87626 (3); Moorea, USNM 296379 (1), 296395 (2), 296398 (3); Huahine, USNM 296100 (1). Austral Is: Tubuai, BPBM 784 (holotype of *Salarias tubuensis*). Phoenix Is: Hull, USNM 115460 (339); Canton, USNM 115463 (84); Enderbury, USNM 115469 (>50; only for distribution); Mckean, USNM 291916 (21; only for distribution). Tokelau Is: Atafu, USNM 296054 (18); Fakaoto, USNM 291921 (6), 296094 (14), 296165 (20); Nukuono, USNM 296090 (6). Tuamotu Arch: Rangiroa, USNM 300439 (44); Tikahau, USNM 296120 (5); Makatea, CAS 67301 (4), USNM 296399 (6), 301774 (3), 315313 (3); Makemo, USNM 65724 (1). Gambier Is: Mangareva, USNM 65410 (1). Marquesas Is: Nukuhiva, ANSP 81989 (1). Ducie Is: BPBM 17128 (2). Howland Island: USNM 198692 (5), 198708 (8), 198730 (45), 198703 (1), 296060 (59). Line Is: Palmyra, CAS 68037 (17), 68038 (4), 68039 (4), 68040 (12); Fanning, USNM 278395 (4); Christmas, CAS 68013 (2); Jarvis, USNM 296621 (1); Starbuck, USNM 291918 (13); Caroline, USNM 291924 (49), 296109 (72).

Color slides: Males, only, from Tahiti, Tutuila, Enewetak, and Vauvau, Tonga (BPBM), and Guam (R.F. Myers).

Blenniella periophthalmus (Valenciennes), new combination

FIGURES 19, 22

(See geographic variation section for discussion of color-pattern types indicated in synonymy.)

Salarias periophthalmus Valenciennes in Cuvier and Valenciennes, 1836:311 [Ticopia, archipel de Santa Cruz; lectotype designation by inference, MNHN 857, Vanikoro, Santa Cruz Islands, in Bauchot, 1967:30; see nomenclatural discussion below]. [Color-pattern Type Ia.]

Salarias biseriatus Valenciennes in Cuvier and Valenciennes, 1836:316 [archipel des Indes; putative holotype, MNHN A.2150, designated neotype in nomenclatural discussion below]. [Color-pattern Type Ia.]

Salarias percophthalmus Swainson, 1839:274 [misspelling of *periophthalmus*].

Salarias schultzei Bleeker, 1859b:345 [Karangbollong, Java; holotype lost]. [Type Ia.]

Salarias muscarus Snyder, 1908:109 [Naha, Okinawa; holotype USNM 62245]. [Type Ia.]

NOMENCLATURAL DISCUSSION.—Valenciennes (in Cuvier and Valenciennes, 1836) appears to imply that his description of *Salarias periophthalmus* was based on a single specimen collected by Quoy and Gaimard at Tikopia, Santa Cruz Islands, during an *Astrolabe* expedition. It is unclear, however, whether Valenciennes took his description from an actual specimen and/or from a manuscript and colored drawing, to which he referred, that was prepared by Quoy and Gaimard during the expedition. It is also unclear, if, indeed, Valenciennes took his description from a specimen, if that specimen was the same as the one on which Quoy and Gaimard based their manuscript description and drawing (for which they used the manuscript name "*Periophthalmus elegans*" (not to be considered nomen-

Table 15.—Comparison of various characters putatively derived from the holotype of <u>Salarias</u> <u>periophthalmus</u> (see nomenclatural discussion section under <u>Blenniella</u> <u>periophthalmus</u>).

	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Nape cirri	Opercular ocellus
Salarias periophthalmus Val.						
published description	XII,20	21	13	11	no mention	no mention
published figure (left side)	XII,20	23	13	13 or 14?	none	none
"Periophthalmus elegans" Q&G ms						
description	XII,20	23	14	"12?"	no mention	no mention
Sophie's figure (left side)	XII,20	23	14	12	none	none
Specimen in MNHN 857	XIII,20[1]	II,21	14	damaged	left absent right present	present

[1]Only XII obvious.

claturally available from us as a published name).

There is no specimen of *Blenniella periophthalmus* from Tikopia in the MNHN collections, and M.L. Bauchot informs us that she knows of no fish specimens indicated in the MNHN catalog as having come from Tikopia. She believes that all the *Astrolabe* specimens obtained in the Santa Cruz Islands were cataloged as having come from Vanikoro, which the *Astrolabe* also visited during the expedition. It is possible, therefore, that some of the Vanikoro locality records in the catalog could be in error.

Quoy and Gaimard's colored drawing probably served as the basis for the colored figure (#328) of *Salarias periophthalmus* published with Valenciennes' description, despite a possible discrepancy that exists between the two illustrations. The disposition of Quoy and Gaimard's original colored figure is unknown; however, a freehand copy of the figure (prepared [calgré] by "Mlle. Sophie," whom M.L. Bauchot informs us was Cuvier's daughter from a first marriage), is available. Through the courtesy of M.L. Bauchot, we have obtained photocopies of Sophie's drawing and Quoy and Gaimard's manuscript description (MS 502 of volume 11 of *HNP*, General Library, MNHN) of the species. "Ile Tikopia" is inscribed on the margins of both the manuscript and the drawing.

The published description and illustration differ from the unpublished material in indicating 13 rather than 14 rays in the pectoral fin.

The above discussion is necessitated, in part, because Bauchot (1967:30), in her type catalog of the blenniids in the MNHN collection, considered MNHN 857 to be the holotype of *Salarias periophthalmus* and (erroneously?) assigned the locality Tikopia to the specimen. However, the MNHN catalog and the label on the bottle containing the specimen in MNHN 857, both indicate that the specimen is from Vanikoro, and there is no way to confirm which locality is correct.

In spite of this information, it is possible that the specimen in

MNHN 857 served as a basis for part of the description of *Salarias periophthalmus*. A comparison of data presented in the descriptions and illustrations of *Salarias periophthalmus* and "Periophthalmus elegans," and taken from the specimen in MNHN 857 is informative (Table 15). The published and manuscript materials give no indication that nape cirri were present, and this agrees with the left side of the specimen in MNHN 857. The coincidence is surprising. Only 14 of 150 specimens (9.3%) of *B. periophthalmus,* for which we recorded condition of the nape cirri, lacked a nape cirrus on 1 side, and none lacked cirri on both sides (many more were examined for nape cirri, but data were not recorded; however, none of these had a bilateral absence of nape cirri).

Other surprising differences exist between Valenciennes' published description and Quoy and Gaimard's manuscript account of *Salarias periophthalmus*.

Why, for instance, did Valenciennes report 21 anal-fin elements, when all the Quoy and Gaimard evidence indicates 23? Could it have been that he examined MNHN 857 and, as was common with early authors who described blenniids, overlooked the small, closely spaced anal-fin spines?

Valenciennes' color-pattern description agrees well with Quoy and Gaimard's, and both disagree with certain important aspects of the pattern exhibited by MNHN 857. Neither Quoy and Gaimard nor Valenciennes made mention of the conspicuous, large, dark ocellus that is present dorsally on the opercle of the specimen in MNHN 857. Even today, the bands and dark-margined ocelli on the body are prominent, yet these characters are not stressed in the descriptions and figures.

The foregoing discussion provides sufficient justification to conclude that Valenciennes' original description of *Salarias periophthalmus* was probably based on at least 2 specimens (syntypes): the specimen from Tikopia that was illustrated and described by Quoy and Gaimard and the Vanikoro specimen, MNHN 857. As it cannot be determined that Valenciennes

based his description on a single specimen, Bauchot's (1967:30) designation of MNHN 857 as the "holotype" fixes that specimen as lectotype by inference, as dictated by Article 74(b) of the *International Code of Zoological Nomenclature* (Ride et al., 1985:155). The type locality becomes, then, Vanikoro, Santa Cruz Islands.

The lectotype is a male, approximately 85 mm SL (approximately 105 mm including the length of the damaged caudal fin), and has only the right-side nape cirrus.

The putative holotype of *Salarias biseriatus* (MNHN A.2150) is a small female (35.2 mm SL, 42.5 mm TL). It is almost completely faded and in poor condition. The specimen agrees generally with the original description, but differs notably in having dentary canine teeth (lacking according to the description) and simple supraorbital cirri (forked according to the description). Nape cirri are present, the upper lip is partially crenulate, and there is a faded, but noticeable, large, dark ocellus dorsally on the opercle on each side (no mention of these characters in the description). The presence of a dark opercle spot in a female is a character that occurs only in *B. periophthalmus* among all the species of *Blenniella*, and the other characters exhibited by the putative holotype of *S. biseriatus* are also in agreement with our synonymization of the latter species under the former.

The type locality of *S. biseriatus* was given only as "archipel des Indes," or Indian Archipelago (also East Indies, Malay Archipelago), an old term that included the Sunda Islands, Moluccas, New Guinea, and Philippine Islands (*The Encyclopaedia Britannica*, 11th edition, 1911, vol. 17:466). Western Indian Ocean specimens of *B. periophthalmus* rarely, if ever, have a dark ocellus on the opercle, whereas specimens from the Indian Archipelago (and the Red Sea and Persian Gulf) frequently do. The presence of an ocellus on the opercle of the putative holotype is, thus, consistent with the reported type locality. Nevertheless, the differences between characters given (and not given) in the original description of *Salarias biseriatus* and characters exhibited by the putative holotype leave doubt as to the type status of the putative holotype. If the putative holotype is not the actual type, we know of no other specimen that might be. *Salarias biseriatus*, dating from 1836, is one of the older names for a salariiin and its identity, if different from that which we accord it, could place another, accepted, younger name in jeopardy. In the event that it is determined that the putative holotype is not the actual holotype, we recommend that the putative holotype be designated as the neotype of *Salarias biseriatus*.

Bleeker (1859b) described *Salarias schultzei* from a single specimen, which is now missing (not mentioned in auction catalog of Bleeker collections), from Karangbollong (= Ujung Karangbolong, 07°46'S, 109°02"E). Bleeker, during his lifetime, never mentioned the species subsequent to its description and there are no specimens in his collections bearing this identification. The species was illustrated under Bleeker's direction and published posthumously (Bleeker, 1983, pl. 445:

fig. 7), and the drawing is presumably based on the holotype.

Bleeker (1859b) provided the following important characters for *S. schultzei*: no crest on head, no nape cirri, orbital cirrus short and simple, nasal cirrus with 4 branches, upper lip without crenulae, posterior canines conspicuous, lateral line inconspicuous posterior to anus, dorsal fin not united with caudal fin, total length 98 mm. The illustration shows a large blue spot on the opercle, 2 rows of small, elongate dark-margined, blue spots (8 in upper row, at least 7 in lower row) that, except for the caudal peduncle, extend the length of the body, numerous large, red spots dorsally on the head and body, and a peppering of fine, dark spots on the caudal peduncle. The caudal and pectoral fins are not spotted and the dorsal fin shows no definite pattern of spots, such as form stripes.

Based on the blue opercle spot, all species of *Istiblennius* can be excluded from consideration as possibly conspecific with *S. schultzei*. Based on the published data, it is not possible to positively identify *Salarias schultzei* with any of the nominal species of *Blenniella*.

Among the species of *Blenniella* that might be expected to occur in Java and thus might be synonyms of *S. schultzei*, 2 rows of dark-margined blue spots on the body, as indicated for *S. schultzei*, occur only in *B. periophthalmus*, and males of *B. cyanostigma*, *B. interrupta*, *B. leopardus*, and *B. bilitonensis*.

Blenniella periophthalmus might be excluded as a possible synonym of *S. schultzei* because *B. periophthalmus* has a crenulate upper lip and nape cirri. The red head and body spots and peppering of dark spots on the caudal peduncle of *S. schultzei*, however, occur only in *B. periophthalmus* among the 5 relevant species.

The size of the holotype of *S. schultzei* is larger than that known for *B. cyanostigma*, which, also unlike the holotype, has a crest on the head. These discrepancies tend to exclude *B. cyanostigma* from consideration as being identical with *S. schultzei*. Size also excludes *B. interrupta* and *B. leopardus* from consideration; the lack of nape cirri excludes *B. leopardus* (which does not occur in Java in any event), and the lack of a high crest and presence of the two rows of spots anteriorly on the body would exclude *B. bilitonensis* from consideration.

In spite of the inadequacies of the original description, we believe, that the available information on *S. schultzei*, particularly the color pattern, best fits a specimen of *B. periophthalmus* with color-pattern Type Ia. We, therefore, assign *S. schultzei* to the synonymy of *B. periophthalmus*.

Of the five species that appear to be possible candidates as synonyms of *Salarias schultzei*, all are senior to *S. schultzei*, except *Salarias leopardus* Fowler, which is a much smaller species, has nape cirri, and probably does not occur in Java. None of the five names is, therefore, in jeopardy and there is no need to designate a neotype for *Salarias schultzei* at this time.

The name *Salarias schultzei* has rarely appeared in the literature since the original description, and then only in listings or, most recently (Chapman, 1951:340; Herre, 1953:806), as an undefended junior synonym of *Salarias interruptus*.

Snyder (1908) did not compare his *Salarias muscarus*, of which he had only the holotype, with any other species. We have examined the holotype and find it to be a female *B. periophthalmus* of Type Ia, in which the body is spattered with fine, dark spots and there is a large, dark spot on the opercle (somewhat larger and more prominent than in Snyder's illustration of the holotype (1912, pl. 70: fig. 1).

MATERIAL EXAMINED.—*Blenniella periophthalmus* Type Ia. Maldive Islands: CAS 58746 (51), USNM 197596 (15). Thailand: Similan Island, Andaman Sea, BPBM 22786 (1). Cocos-Keeling Islands: WAM P.29905-036 (4), P.29907-034 (35), P.29913-035 (9). Christmas Island (IO): WAM P.20088-039 (2), P.28998-017 (1). Ashmore Reef, Timor Sea: AMS I.26750-014 (1), WAM P.29041-001 (19). Seringapatnam Reef, Timor Sea: NTM S.11388-014 (2). Scott Reef: NTM S.11374-063 (4). North Reef, Timor Sea: NTM S.11386-033 (3), S.11386-034 (1). Rowley Shoals: WAM P.27667-030 (9), P.28032-014 (1). Western Australia: Dampier Archipelago: WAM P.24324-6 (3), P.25112-026 (1). Philippines: Batanes Islands, USNM 133772 (1), 137774 (3), 226747 (2), 284055 (1); Babuyan Islands, USNM 320100 (1); S Luzon, USNM 137775 (6), 291680 (2); Panay, Nogas Pt., USNM 323482 (1); Negros, Duamaguete, CAS-SU 32307 (3); Siquijor, USNM 296061 (7). Indonesia: Sumatra, Pulo Mega, USNM 291919 (3); Bali, NTM S.10689-028 (2), S.11081-014 (1), UF 31304 (1); Moluccas: Nusa Laut, USNM 290586 (1); Ambon, USNM 277967 (22). Papua New Guinea: Madang, USNM 296116 (1); Ninigo Islands, USNM 303676 (7); Trobriand Islands, USNM 296167 (35). Solomon Islands: Pinipel Island, USNM 144284 (7); New Georgia, USNM 195773 (1); Rennell Island, ANSP 99504 (1). Santa Cruz Islands: Vanikoro, MNHN 857 (lectotype of *Salarias periophthalmus*). Taiwan: USNM 303677 (1). Okinawa: USNM 62245 (holotype of *Salarias muscarus*). Archipel des Indes, MNHN A.2150 (putative holotype of *Salarias biseriatus*).

Blenniella periophthalmus Type Ib. Kenya: Malindi, USNM 296063 (1); Mombasa, USNM 296505 (1). Zanzibar: USNM 296510 (2). Mozambique: Ibo, RUSI 5640 (1). South Africa: Kwazulu Reef, USNM 227346 (5); Durban, CAS-SU 31294 (1). Cargados Carajos: USNM 296053 (17), 296059 (1), 296221 (29). Seychelles, Mahe: BPBM 35520 (1), ROM 56235 (3). Chagos Is: ROM 43907 (57), USNM 279839 (2), 279856 (2), 296056 (7), 296125 (8), 296504 (9), 296536 (4), 296543 (19). Mauritius: RUSI 32509 (3), 32511 (1), 32516 (2). Reunion: MNHN 836 (1). Comores Is: CAS 33048 (5), 33247 (5), 33773 (14), 68015 (1), ROM 60522 (4). Aldabra: USNM 270001 (1), 296055 (25), 296502 (12, including 2 cleared and stained), 296503 (26), 296506 (4), 296515 (3), 296517 (1), 296525 (2). Madagascar: Tulear, MNHN 1965-428 (9), UMMZ 186188 (26); Nossi Be, USNM 296509 (1), 296512 (1), 296513 (1), 307998 (2), 308414 (1). Agalega Is: USNM 224888 (33).

Blenniella periophthalmus Type Ic. Egypt: G of Aqaba, N of Ras Burka, USNM 291915 (1); Ras Muhammad, USNM 291922 (8); Giften al Kebir Id, USNM 296299 (8); Koseir,

UMMZ 211766 (1), USNM 296526 (7); Shab al Fanadir, USNM 296508 (1). Saudi Arabia: Djidda, USNM 147582 (1), 147585 (8). Sudan: Port Sudan, SMF 8233 (15). Ethiopia: Dahlak Arch, Cundabilu, HUJ 12374 (2); Difnein Id, USNM 204505 (20). Yemen: Zubayr Id, HUJ 4265 (9). G of Aden: [Seven Brothers Is, J.E. Randall, pers. comm.], MNHN 1977-739 (13). G of Tadjourah: MNHN 1977-740 (14). Oman: Strait of Hormuz, Musandam, BPBM 33473 (5); G of Oman, S of Sidab, BPBM 21351 (1), USNM 217356 (3).

Color slides: Type-Ic male and female from Musandam, Oman; Type-Ic female from Sudan, Red Sea (BPBM); Type-Ib males and females from Chagos Islands (ROM); Type-Ib female from Comores (ROM); Type-Ia male and female from Maldive Islands (BPBM); Type-Ia female from Similan Island, Andaman Sea (BPBM).

Blenniella gibbifrons (Quoy and Gaimard), new combination

FIGURES 23–27

Salarias gibbifrons Quoy and Gaimard, 1824:253 [Îles Sandwich; holotype MNHN 4002].

Salarias saltans Jenkins, 1903:508 [Hawaiian Islands: Honolulu; holotype USNM 50696].

Salarias rutilus Jenkins, 1903:509 [Hawaiian Islands: Honolulu; holotype USNM 50695].

Blenniella rhessodon Reid, 1943:383 [*Albatross* Station 3921, off Honolulu, T.H. Diamond Head Light, S. 62°, E. 3.9'; holotype USNM 118029, apparently lost].

Istiblennius gibbifrons insolitus J.L.B. Smith, 1959:242 [Assumption (western Indian Ocean); holotype RUSI 247].

Istiblennius afilinuchalis Schultz and Chapman, 1960:350 [Hull Island (= Orona, Phoenix Islands); holotype 115421].

Istiblennius rodenbaughi Schultz and Chapman, 1960:358 [Bikini Atoll, Namu Island; holotype USNM 142067].

DESCRIPTION.—Dorsal fin (Table 16). XII to XIV,17 to 21 = 31 to 34 (XIII in 98% of specimens; 18 to 20 in 99%), mean number of total elements usually higher for males from any locality than for females from same locality (higher for 13 of 17 localities for which means for both sexes are available, statistically significantly higher for 3 of the 13 localities); membrane from posteriormost ray attaching to point on dorsal edge of caudal peduncle just anterior to caudal-fin base.

Anal fin (Table 16). II,18 to 22, mean number of segmented rays usually higher for males from any locality than for females from same locality (higher for 12 of 17 localities for which means for both sexes are available, statistically significantly higher for 6 of the 12 localities); posteriormost ray usually split to base, (posterior element of split ray well developed, easily discernible externally); posteriormost ray predominantly not bound by membrane to caudal peduncle (bound by membrane in only 2 of 117 specimens examined for character); skin covering anal-fin spines and distal half of segmented rays slightly inflated or expanded laterally in large and/or mature

Table 16.—Frequency distributions for certain meristic characters in specimens of _Blenniella gibbifrons_ from various localties. Underlining indicates significant differences between means of sexes (p = ≤ .05).

Locality/Sex	Total dorsal-fin elements					Segmented anal-fin rays						Total vertebrae				
	31	32	33	34	x̄	18	19	20	21	22	x̄	36	37	38	39	x̄
Midway																
males	-	1	4	1	33.0	-	-	1	6	1	21.0	-	1	5	2	38.1
females	-	1	8	4	33.2	-	-	1	10	2	21.1	-	1	7	6	38.4
Hawaiian Islands (excluding Midway)																
males	-	9	30	1	32.8	-	-	8	30	2	_20.8_	-	5	34	1	37.9
females	-	10	29	2	32.8	-	-	15	26	-	_20.6_	-	2	39	-	38.0
Johnston Island																
males	-	2	5	-	32.7	-	-	3	5	-	_20.6_	-	1	7	-	37.9
females	-	4	-	-	32.0	-	-	5	-	-	_20.0_	-	1	4	-	37.8
Marcus Island																
males	-	9	13	-	32.6	-	-	9	13	-	_20.6_	-	1	20	2	38.0
females	-	14	9	-	32.4	-	-	16	6	-	_20.3_	-	2	19	1	38.0
Wake Island																
males	1	6	6	1	32.5	-	-	8	6	-	20.4	-	3	9	-	37.8
females	-	12	4	-	32.2	-	-	12	4	-	20.2	-	7	7	-	37.5
Mariana Islands																
males	2	2	-	-	31.5	-	2	2	-	-	19.5	-	-	4	-	38.0
Line Islands																
males	16	52	-	-	31.8	-	18	49	-	-	_19.7_	2	65	2	-	37.0
females	17	50	-	-	31.7	2	26	39	-	-	_19.6_	5	62	1	-	36.9
Marquesas Islands																
males	-	3	4	-	32.6	-	1	6	-	-	19.9	-	-	6	1	38.1
females	-	3	2	-	32.4	-	3	2	-	-	19.4	-	1	4	-	37.8
Pitcairn Islands																
males	3	20	2	-	32.0	-	3	21	1	-	19.9	5	19	1	-	36.8
females	2	13	-	-	31.9	-	2	13	-	-	19.9	1	13	-	-	36.9
Tuamotu Archipelago																
males	1	14	-	-	31.9	-	1	15	-	-	19.9	1	14	1	-	37.0
females	5	40	1	-	31.9	-	12	35	-	-	19.7	4	42	1	-	36.9
Society Islands																
females	-	1	-	-		-	-	1	-	-		-	-	1	-	
Cook Islands																
males	-	18	1	-	32.0	-	-	19	1	-	20.0	-	18	2	-	37.1
females	3	20	1	-	31.9	-	1	23	1	-	20.0	1	21	2	-	37.0
Niue Island																
males	-	5	-	-	32.0	-	-	5	-	-	20.0	-	5	-	-	37.0
females	-	3	-	-	32.0	-	-	3	-	-	20.0	-	3	-	-	37.0
Swains Island																
males	-	4	1	-	32.2	-	1	4	-	-	19.8	-	5	-	-	37.0
females	2	4	-	-	31.7	-	2	4	-	-	19.7	1	5	-	-	36.8
Phoenix Islands																
males	18	46	-	-	_31.7_	-	21	43	-	-	19.7	2	61	1	-	37.0
females	27	37	-	-	_31.5_	1	22	39	-	-	19.6	2	59	2	-	37.0
Howland Island																
males	1	11	1	-	_32.0_	-	2	11	-	-	_19.8_	-	11	2	-	_37.2_
females	7	1	-	-	_31.1_	-	7	1	-	-	_19.1_	2	6	-	-	_36.8_
Gilbert Islands																
males	1	-	-	-		-	1	-	-	-		-	1	-	-	
females	1	-	-	-		-	1	-	-	-		-	1	-	-	
Marshall Islands																
males	9	51	4	-	_31.8_	-	10	52	1	-	_19.8_	4	53	7	-	37.0
females	15	24	-	-	_31.6_	-	19	21	-	-	_19.5_	4	31	4	-	37.0
Caroline Islands																
males	1	11	-	-	31.9	-	3	8	-	-	19.7	1	9	1	-	37.0
females	9	31	-	-	31.8	-	9	31	-	-	19.8	-	34	6	-	37.1
Western Indian Ocean																
males	4	37	5	-	32.0	-	8	35	2	-	19.9	1	40	5	-	37.1
females	9	25	3	-	31.8	-	8	28	1	-	19.8	2	33	2	-	37.0

Table 17.—Frequency distributions for position of epineurals (modes underlined) and nape cirri in specimens of _Blenniella gibbifrons_ from various localties.

Locality	Terminal epineural on vertebra number									Nape cirri[1]		
	21	22	23	24	25	26	27	28	x̄	0	1	2
Midway	1	2	_6_	5	_6_	1	-	-	23.8	22	-	-
Hawaiian Islands (except Midway)	1	6	17	_33_	21	25	4	1	24.5	67	-	1
Johnston Island	-	1	2	_5_	1	3	1	-	24.5	13	-	-
Marcus Island	-	1	9	10	_20_	4	1	-	24.4	45	-	-
Wake Island	-	-	1	2	_10_	8	4	-	25.5	26	1	-
Mariana Islands	-	1	1	1	_1_	-	-	-	23.5	4	-	-
Line Islands	-	15	_44_	33	28	10	-	-	23.8	14	37	60
Marquesas Islands	-	-	-	-	-	_6_	2	1	26.4	12	-	-
Pitcairn Islands	-	-	3	6	_17_	6	6	-	25.2	2	8	31
Tuamotu Archipelago	-	1	14	_20_	17	5	5	-	25.6	7	16	39
Society Islands	-	-	-	-	_2_	-	-	-	25.0	-	-	2
Cook Islands	-	1	4	3	_15_	11	4	-	25.1	8	16	21
Niue Island	-	-	1	_3_	_3_	1	-	-	24.5	2	-	6
Swains Island	-	-	_5_	1	1	2	1	-	24.3	3	3	5
Phoenix Islands	2	8	19	_33_	26	22	8	-	24.3	14	19	41
Howland Island	-	-	2	_10_	6	3	-	-	24.5	5	6	10
Gilbert Islands	-	1	1	-	-	-	-	-	22.5	-	-	2
Marshall Islands	-	5	15	23	_42_	23	6	1	24.7	58	5	5
Caroline Islands	1	-	4	7	_14_	13	10	3	25.4	48	-	5
Western Indian Ocean	3	8	17	_19_	17	10	3	-	24.0	83	-	-

[1]0 = absent; 1 = present on one side; 2 = present on both sides

Table 18.—Frequency distributions for number of dorsally directed lateral-line pores in specimens of _Blenniella gibbifrons_ from various localties.

Locality	Number of dorsally directed pores																											x̄
	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	
Midway	-	-	1	2	-	3	-	3	-	2	1	2	3	3	-	-	2	-	-	-	-	-	-	-	-	-	-	38.1
Hawaiian Islands (excluding Midway)	-	-	-	2	2	4	6	7	7	12	11	6	7	1	1	1	1	-	-	-	-	-	-	-	-	-	-	37.8
Johnston Island	1	-	-	1	-	-	2	1	4	1	-	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	37.0
Marcus Island	-	-	-	-	-	-	-	-	1	-	1	3	3	4	4	8	4	6	5	1	1	-	3	-	-	-	1	45.6
Wake Island	-	-	-	-	-	-	-	-	1	-	-	2	-	3	6	2	1	2	2	3	-	-	1	-	1	-	-	45.0
Mariana Islands	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	1	-	-	-	-	-	-	-	-	45.5
Line Islands	-	-	-	-	-	-	1	-	2	7	6	6	3	8	6	4	4	3	1	-	-	1	-	-	-	-	-	41.5
Marquesas Islands	-	-	-	-	-	-	-	-	2	-	-	3	1	-	2	4	2	2	1	-	1	-	-	-	-	-	-	43.0
Pitcairn Islands	-	-	-	-	-	-	-	-	-	1	1	-	3	6	3	2	4	6	2	3	1	1	3	1	1	-	-	46.3
Tuamotu Archipelago	-	-	-	-	-	-	-	-	-	1	-	1	5	2	4	3	5	5	10	7	5	6	4	4	-	-	-	46.6
Cook Islands	-	-	-	-	-	-	-	-	1	-	-	1	3	2	1	2	6	5	6	1	-	1	1	-	-	-	1	46.2
Niue Island	-	-	-	-	-	-	-	-	-	-	1	1	-	-	2	1	1	-	2	-	-	-	-	-	-	-	-	46.5
Swains Island	-	-	-	-	-	-	-	-	-	1	1	2	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	40.8
Phoenix Islands	-	-	-	-	-	-	1	2	3	5	3	8	13	7	5	6	1	2	3	1	1	-	-	-	-	-	-	42.4
Howland Island	-	-	-	-	-	-	-	-	1	1	2	2	-	1	3	2	3	2	3	-	1	-	-	-	-	-	-	43.3
Gilbert Islands	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	43.5
Marshall Islands	-	-	-	-	-	-	2	-	-	6	4	5	4	8	5	4	5	4	4	1	-	-	-	-	-	-	-	42.7
Caroline Islands	-	-	-	-	1	-	-	4	3	2	4	4	3	6	9	5	1	2	5	2	-	1	-	-	1	-	-	42.1
Western Indian Ocean	-	-	-	-	-	2	2	6	11	11	14	5	9	9	3	6	4	-	2	-	-	-	-	-	-	-	-	39.8

males, never crinkled along edges.

Pectoral-fin rays 13 or 14 (14 bilaterally in 61 and unilaterally in 3 of 65 specimens examined for character).

Pelvic-fin segmented rays 3.

Caudal-fin. Dorsal procurrent rays 5 to 9 (7 in 59% of specimens), ventral procurrent rays 5 to 9 (7 in 76% of specimens), segmented rays 13.

Vertebrae (Table 16). 11 to 13+24 to 27 = 36 to 39 (12 in 877 of 879 specimens examined for character; 25 or 26 in 94%), mean numbers of total vertebrae apparently not sexually dimorphic, although mean for males of 1 population (Howland Island) significantly higher than mean for females; posteriormost pleural rib on 12 to 14th from anteriormost centrum (on 13th in 99% of specimens); posteriormost epineural on 21st to 28th from anteriormost centrum (Table 17), modally 23 to 26, depending on population (range and mean varying with population, with Marquesas Islands population having noticeably highest mean).

Cirri. Nape cirri present or absent, varying with population (Table 17). Orbital cirrus slender, usually simple, rarely with 1 to few tiny branches near tip; male cirrus length about 0.75 to 1.0 eye diameter; female about 0.50 to 0.75 eye diameter. Nasal cirri short, slender, with 1 to 17 free tips, usually only 4 or 5.

Lateral line (Table 18). Continuous canal anterodorsally with 29 to 55 vertical pairs of pores, extending posteriorly to point between verticals from 10th and 13th dorsal-fin spines, then descending to midside and continuing posteriorly as 0 to 3 separated bi-pored tubes (canals) to point between verticals from 11th and 13th dorsal-fin spines.

Mandibular pores 5 to 7 (6 bilaterally in 93% of specimens examined for character; 5 or 7 usually only unilaterally).

Sensory pore positions along postorbital margin numerous, difficult to count, forming complex series of radiating canals with small pores, at least, along mid-postorbital margin where pore positions fuse together (particularly in specimens larger than about 45 mm SL).

Posterior dentary canines present in both sexes.

Ventral margin of upper lip and dorsal margin of lower lip entire.

Crest on head absent in both sexes; adult males with head fleshy, swollen, often with very low, broad, longitudinal ridge on nape.

Color pattern (in preservative). Males (Figures 23, 24, 27a). Head, pectoral-fin base, and anterior portion of body with closely spaced, small, dark spots on pale background; underside of head spotted, transversely barred, or uniformly pigmented (geographically variable, Table 19); posterior two-thirds of body with 6 or 7 faintly to darkly dusky, broad bands, and widely and randomly spaced, elongate, white spots that diminish in size and become rounded on caudal peduncle and basal half of caudal fin; spinous and segmented-rayed dorsal fins dusky with indistinct, small, dark or pale spots; large, black spot variably present on anterior 1 or 2 interspinous

membranes (geographically variable; Table 19), segmented rays with dark, distal tips; Indian Ocean males often have slightly darkened distal tips; anal fin dusky; margin of lower lip dark; pelvic fins dusky; pectoral fins dusky with tiny, pale or dark spots basally; caudal fin dusky with small, faint, pale spots on basal and central portions. Females (Figures 25, 26, 27b,c). Similar to males except as follows: dark spot always present on first interspinous membrane of dorsal fin; sometimes also present on second and third membranes; distinct, small, dark spots on pectoral fin, segmented-ray portion of dorsal fin, and caudal fin; no large, pale spots on body posteriorly; body bands distinct (dorsal portions sometimes faint), with ventral portion of each band divided into 2 vertically parallel lines, each almost or completely separated by pale area from dorsal portion of band; anterior portion of body frequently with reticulated pattern of dark streaks and spots.

Randall et al. (1985, fig. 51) present an excellent black-and-white halftone (converted from a color photograph) of a male and female taken at Johnston Island, and Randall et al. (1993, fig. 77) and Winterbottom et al. (1989, fig. 386) present, respectively, similarly converted illustrations of a female from Midway and a male from the Chagos Archipelago.

Color of freshly dead specimens. J.L.B. Smith (1959, pl. 16: fig.2; reproduced in J.L.B. Smith and M.M. Smith, 1963, pl. 92: fig. 2) presents a colored painting of a fresh male from the Seychelles, and Springer (1986, pl. 116: fig. 235.20) presents a color photograph of a large, fresh female from Mauritius. Based on these illustrations and color photographs of fresh specimens from the Chagos Archipelago (by R. Winterbottom and A.R. Emery) and Johnston, Marquesas, and Marcus islands (by J.E. Randall): pale spots over the head and body of males bluish white; background color of the head reddish brown; bars on body brown; streaks in the dorsal fin red. Females have: small red spots on whitish background on head, reddish streaks in spinous dorsal fin, all other dark markings brown to reddish brown.

Size: Largest male 102 mm SL, largest female 90 mm; specimens over 90 mm uncommon; smallest metamorphosed specimen examined 21.5 mm SL.

Ophioblennius-stage specimens (Figure 4a) 22.0–23.0 mm SL, with large, laterally directed, posteriorly recurved canine medially on each dentary (usually covered by lower lip); no symphyseal canines in upper or lower jaws; 22.8 mm SL ophioblennius stage with melanophores scattered over cranium, most pectoral-fin rays with small melanophore in membrane near tip of each ray (Figure 6a), no other pigmentation evident; other ophioblennius-stage specimens of about same size lack melanophores at pectoral-fin ray tips. Reid (1943:383 and 377, fig. 4) neither illustrates nor reports the existence of melanophores at the tips pectoral-fin rays in ophioblennius-stage types of *Blenniella rhessodon*.

GEOGRAPHIC VARIATION.—Several color-pattern and meris-

Table 19.—Frequency distributions for certain color-pattern characters in specimens of <u>Blenniella gibbifrons</u> from various localties. For dorsal fin: S = broad, dark, distal stripe; U = uniform (no large, anterodistal, dark spot or broad stripe); 1-2-3 = number of interspinous membranes, beginning anteriorly, bearing large, dark spots distally. For chin: S = spotted; U = uniform; B = barred.

Locality/Sex	Dorsal fin					Chin		
	U	1	2	3	S	S	U	B
Midway								
males	-	8	-	-	-	-	8	-
females	-	14	-	-	-	6	8	-
Hawaiian Islands (less Midway)								
males	-	32	7	-	-	10	29	-
females	-	23	6	-	-	26	3	-
Johnston Island								
males	-	8	-	-	-	1	7	-
females	-	5	-	-	-	1	4	-
Marcus Island								
males	20	3	-	-	-	-	23	-
females	-	-	21	1	-	-	2	20
Wake Island								
males	9	3	-	-	-	-	12	-
females	-	3	11	-	-	-	1	13
Mariana Islands								
males	-	4	-	-	-	-	3	1
Line Islands								
males	-	54	3	-	-	-	56	1
females	-	43	11	-	-	-	7	47
Marquesas Islands								
males	-	-	-	-	9	-	7	-
females	-	-	9	-	-	-	-	5
Pitcairn Islands								
males	-	24	-	-	-	-	25	-
females	-	9	5	-	-	-	1	14
Tuamotu Archipelago								
males	-	15	-	-	-	-	15	-
females	-	22	25	-	-	-	-	46
Cook Islands								
males	-	21	3	-	-	-	24	-
females	-	4	11	1	-	-	-	17
Niue Island								
males	-	5	-	-	-	-	5	-
females	-	1	2	-	-	-	-	3
Swains Island								
males	-	5	-	-	-	-	4	1
females	-	5	1	-	-	-	-	6
Phoenix Islands								
males	-	32	5	-	-	1	4	23
females	-	18	16	-	-	-	-	31
Howland Island								
males	-	13	-	-	-	-	13	-
females	-	8	-	-	-	-	-	8
Gilbert Islands								
females	-	1	-	-	-	-	-	1
Marshall Islands								
males	28	17	-	-	-	-	43	2
females	-	1	22	-	-	-	4	19
Caroline Islands								
males	8	4	-	-	-	-	11	1
females	-	1	39	-	-	-	2	38
Western Indian Ocean								
males	45	1	-	-	-	-	43	2
females	-	-	38	-	-	-	23	15

tic characters vary geographically. Pigmentation pattern on the chin (Figure 27) and spinous-dorsal fin vary among, and sometimes within, populations (Table 19). Although most mature males from all localities have a uniform distribution of melanophores over the chin, young males and most females have either small spots or narrow bars in this area.

Females and about one-fourth of the males from Midway, Hawaiian, and Johnston islands (MHJ) have small, dark spots, which are most prominent in females, on the chin. The only other incidence of chin spots is in a single Phoenix Islands male, which has small, white spots on the chin, but all other specimens from this locality have either barred or uniform chin pigmentation. None of the MHJ specimens have bars.

Non-MHJ females typically have 2 or 3 bars on the chin, but some have uniformly pigmented chins. Occasionally melanophores fill the space between the 2 anterior bars to form a single broad band. Some non-MHJ males also have the chin barred.

Variation in pigmentation of the spinous-dorsal fin is most pronounced in males (Table 19, Figures 23, 24). Marquesas Islands males have a distinctive, broad, dark stripe extending along the complete distal edge of the fin; females have 2 large, black spots, 1 each on the 2 anteriormost interspinous membranes. Some males from the Hawaiian Islands have a faintly dusky spinous dorsal-fin stripe faintly similar to that of Marquesas males, but most Hawaiian males (and females) are characterized by having 1 (sometimes 2), black, anterior interspinous dorsal-fin spot. Males from Marcus, Wake, Caroline, and Marshall islands (71%), and from the western Indian Ocean (98%), typically lack anterior interspinous dorsal-fin spots (none have more than 1 spot). At these same localities, females typically have 2 spots (1 or 3 in about 4% of specimens). Both sexes at other Pacific localities have at least 1 dorsal-fin spot and females often have 2 spots, but no locality has the distinctive dichotomy of males with no spots and females with 2 spots.

The Johnston, Hawaiian, Midway, Marcus, Wake, and Marquesas islands specimens have the highest modal and mean numbers of total dorsal-fin elements and total vertebrae (Mariana Islands specimens have only high vertebral counts, Table 16). The same islands, less the Marquesas, tend to have the highest modal and mean numbers of segmented anal-fin rays (Table 16).

The presence or absence of nuchal cirri varies both within and among the various populations, with a strong tendency to lack cirri exhibited by the Hawaiian, Johnston, Midway, Marcus, Wake, Mariana, Marquesas, Caroline, and Marshall islands and the Western Indian Ocean populations (Table 17).

Mean numbers of lateral-line pores (Table 18) tend to be similar in certain geographic areas. The lowest means occur among specimens from Midway, Hawaiian, and Johnston islands. The highest means occur among the southern Oceania populations (Niue, Cook, Tuamotu, Pitcairn islands), on the
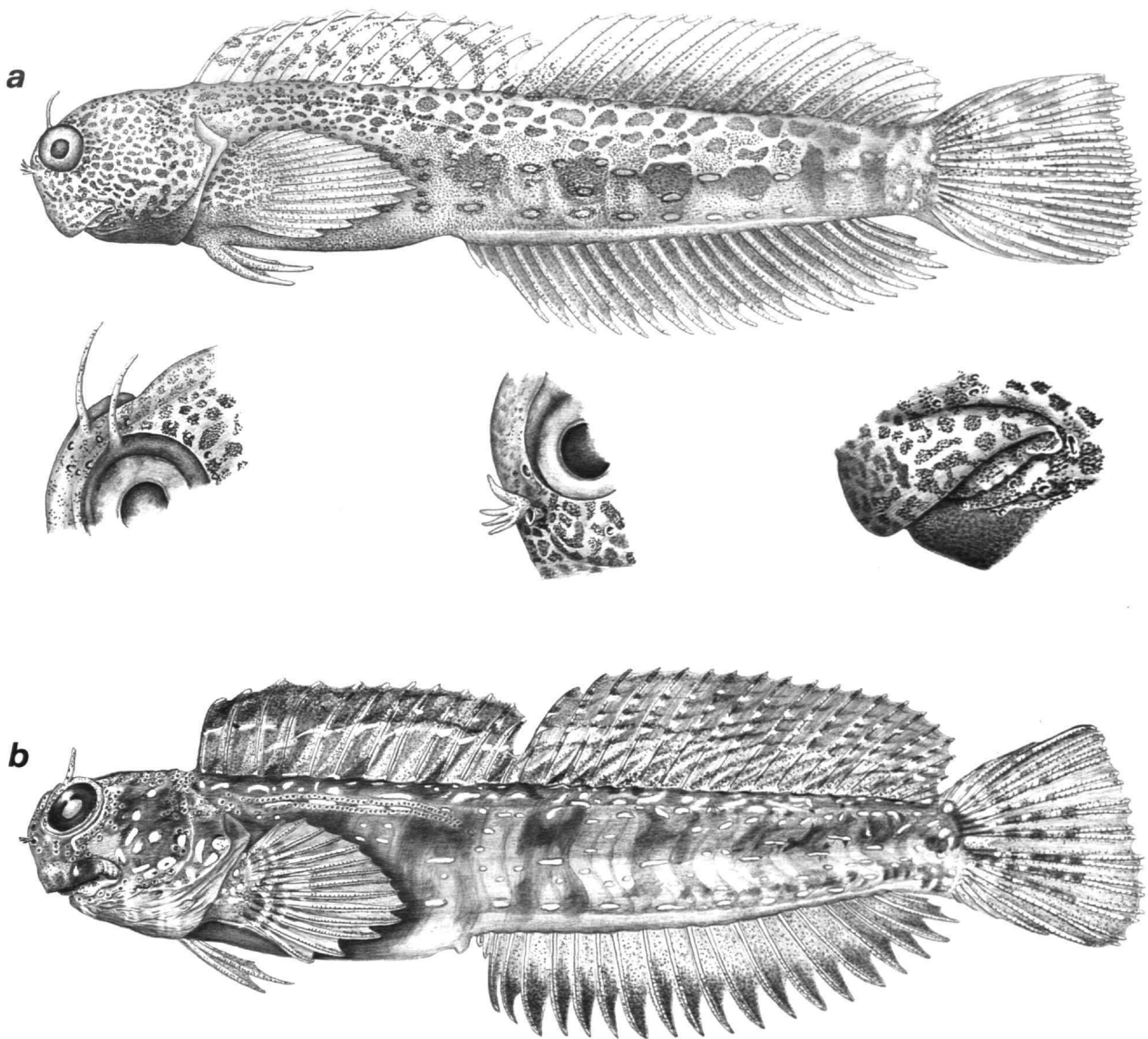
FIGURE 23.—*Blenniella gibbifrons*, males: *a*, USNM 142058, 65 mm SL, Bikini Atoll, Marshall Islands, with enlarged views of orbital and nasal cirri and lips (drawing by J.R. Schroeder); *b*, BPBM 12141, 60 mm SL, Ua Pou, Marquesas Islands (depicted color pattern contains elements of both preserved and fresh patterns: pale spots of fresh pattern, fade to dusky in preservative) (drawing by P.K. Hollingsworth).

one hand, and the northwestern populations (Marcus, Wake, Mariana islands), on the other. Means for the more central Pacific island populations and that from the Western Indian Ocean, tend to be intermediate.

The Midway, Hawaiian, and Johnston islands populations, as a group, are the most distinctive. They exhibit only one character, however, that separates them from the other populations: the spotted chin pigmentation pattern of most
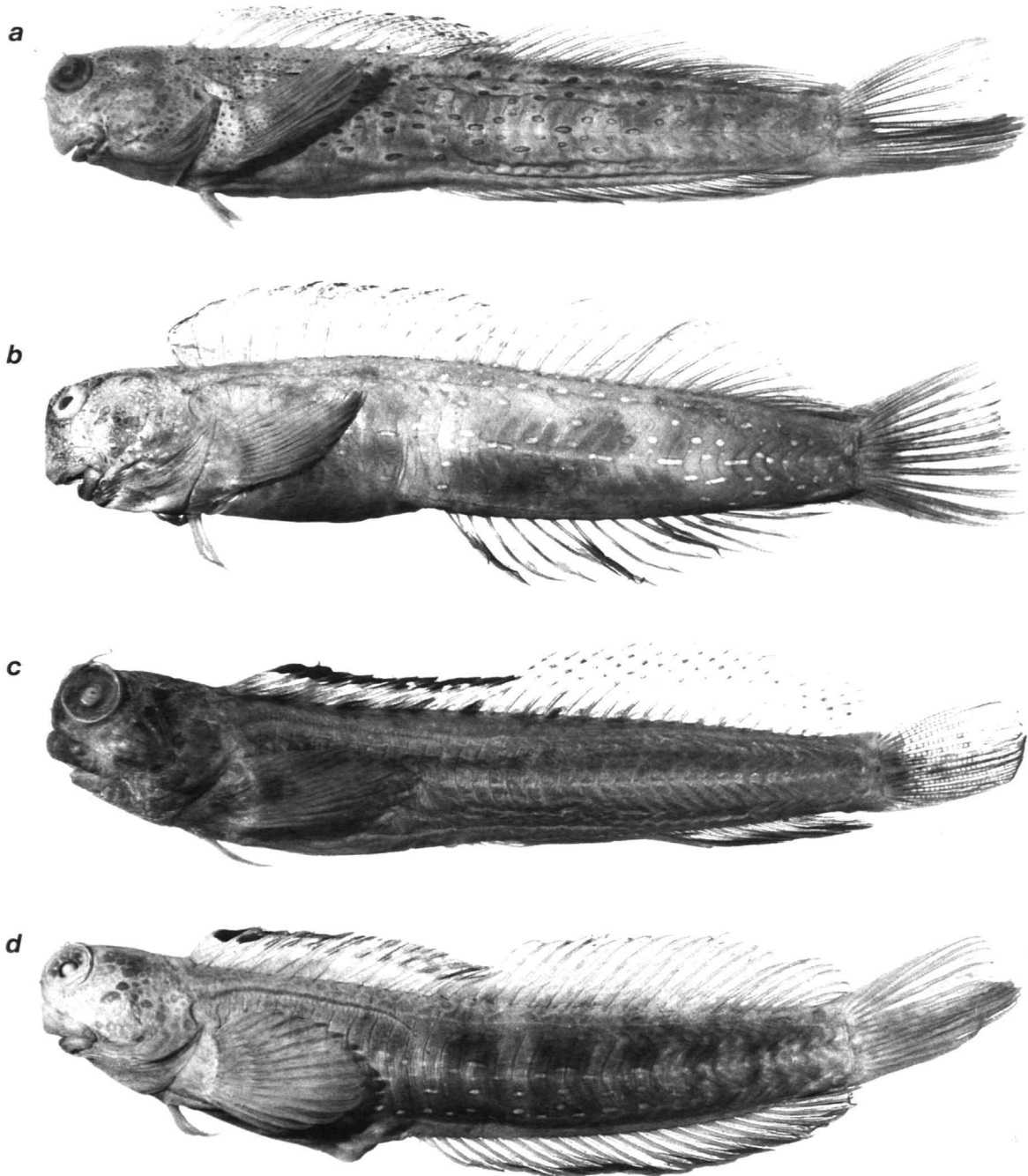
FIGURE 24.—*Blenniella gibbifrons*, males: *a*, USNM 265051, 74 mm SL, Chagos Archipelago; *b*, ROM 43910, 86 mm SL, Chagos Archipelago; *c*, BPBM 12415, 53 mm SL, Ua Huka, Marquesas Islands; *d*, CAS-SU 8399, 73 mm SL, Oahu, Hawaiian Islands (photographs by T.B. Griswold).
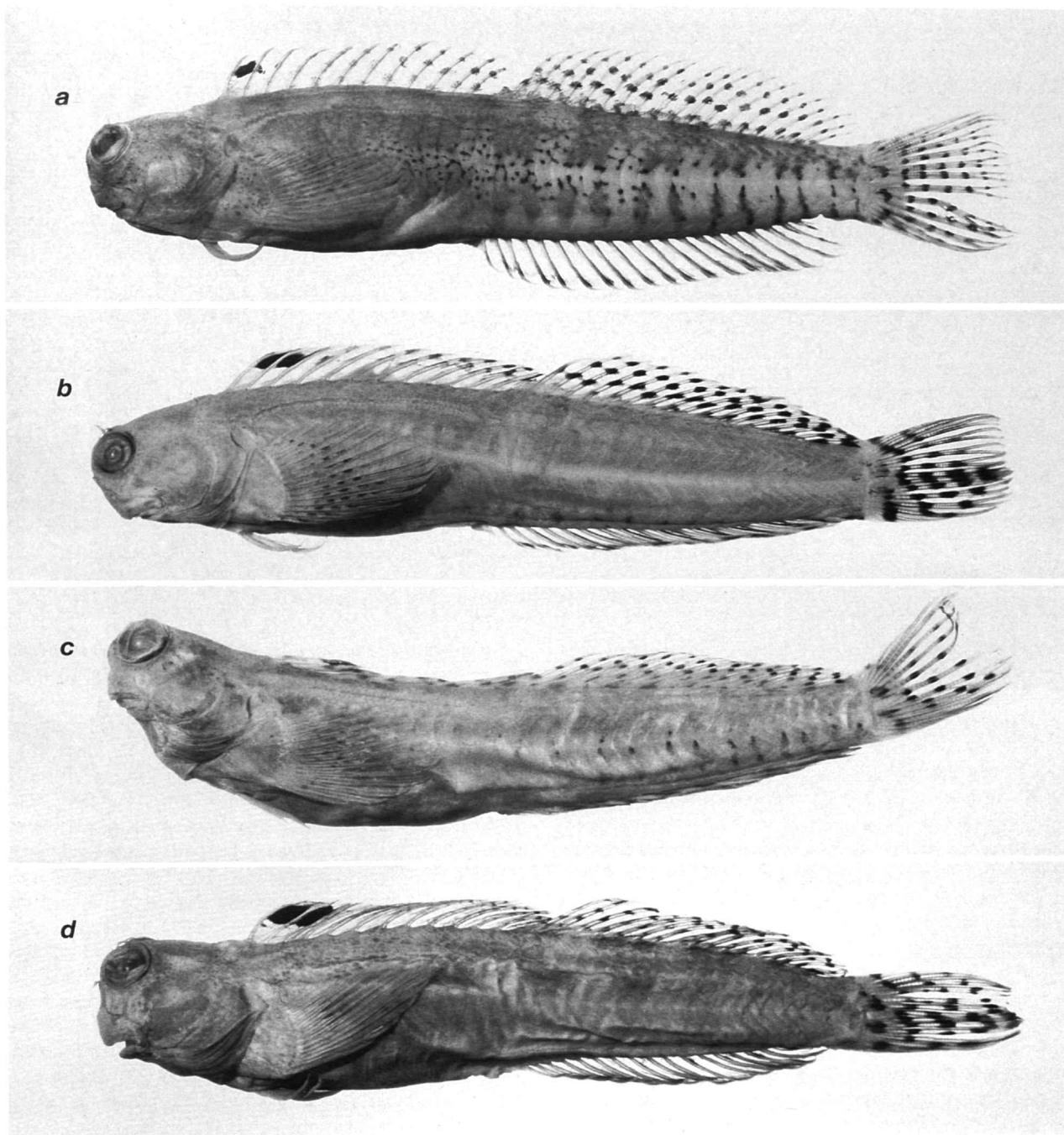
FIGURE 25.—*Blenniella gibbifrons*, females: *a*, BPBM 29588, 78 mm SL, Johnston Island; *b*, USNM 228313, 62 mm SL, Jarvis Island; *c*, BPBM 12098, 53 mm SL, Hiva Oa, Marquesas Islands; *d*, USNM 265051, 65 mm SL, Chagos Archipelago (photographs by T.B. Griswold).
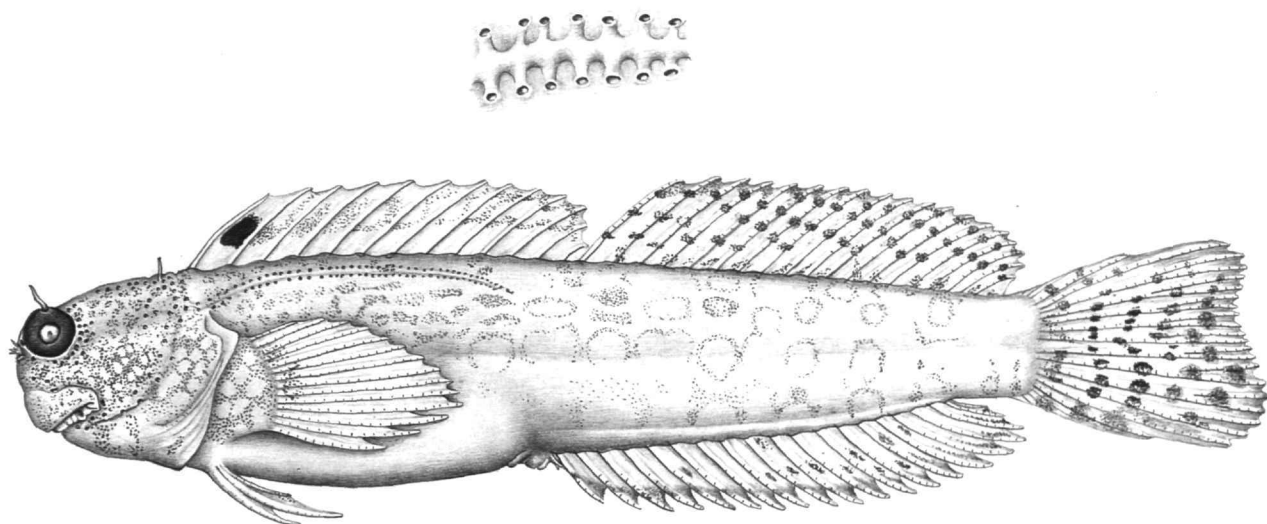
FIGURE 26.—*Blenniella gibbifrons*, USNM 224889, 68 mm SL, female, Vostok, Line Islands, includes enlargement of section of lateral line (drawings by J.R. Schroeder).

females and some males. Specimens with uniform chin pigmentation from these three localities, therefore, may not be recognizably different from similarly pigmented specimens from other localities where *B. gibbifrons* occurs. Somewhat similarly, males from the Marquesas Islands are distinguished from all other males by the broad, dark stripe in the spinous dorsal fin (faintly suggested in some males from the Midway, Hawaiian, and Johnston islands). Females from the Marquesas, however, are undistinguished, and cannot be localized based on morphology. There is considerable overlap among the various populations in all the other characters. For these reasons, we recognize only one taxon for all the populations of *B. gibbifrons*.

COMPARISONS AND RELATIONSHIPS.—*Blenniella gibbifrons* appears to be most closely related to *B. chrysospilos*, with which it alone shares in having numerous vertical pairs of pores in the lateral line and numerous multipored infraorbital pore positions (see Phylogenetic Analysis section). In *B. chrysospilos* there are many fewer paired pores and there is a dark spot at the tip of each dorsal-fin spine. The 2 species differ most prominently in the presence of upper-lip crenulae and bifurcated tips of the orbital cirri in *B. chrysospilos* and their absence in *I. gibbifrons*. These 2 species, together with *B. periophthalmus* and *B. paula*, share, to the exclusion of the other species of *Blenniella*, in having strongly modally 12 precaudal vertebrae and the terminal pleural rib strongly modally or commonly on the 13th vertebra.

Possible confusion may occur in distinguishing the ophioblennius stages of *Blenniella gibbifrons* and the endemic

Istiblennius zebra, the only species of these genera that occur in the Hawaiian Islands. *Blenniella gibbifrons* usually has lower total numbers of dorsal-fin elements (32 to 34, uncommonly 34), segmented anal-fin rays (20 to 22, uncommonly 22), and total vertebrae (37 to 39—rarely 39, except at Midway) than *I. zebra* (34 to 36, 21 to 23—uncommonly 21, and 39 to 41, respectively; not known to occur at Midway). Furthermore, *B. gibbifrons* has 12 precaudal vertebrae (over 99% of specimens) and *I. zebra* has 10 or 11 (usually 11). The unique condition of joined tips of pairs of pectoral-fin rays of the larger *I. zebra* ophioblennius stages is unequivocal for recognition of that species.

DISTRIBUTION.—*Blenniella gibbifrons* occurs in shallow, subtidal areas and, with the exception of the east African coast, is limited in distribution to islands. It has a disjunct distribution pattern including the Pacific plate and the western Indian Ocean (Figure 62). It is found at most Pacific plate islands, east to Ducie Atoll, but appears to be conspicuously absent from Samoa, which has been sampled intensively over the past 30 years. It has a spotty distribution in the western Indian Ocean, where it appears to be absent from the Red Sea, Persian Gulf, and other localities north of the equator, many of which have been intensively sampled (this distributional pattern will be discussed further in the Biogegographic Discussion section. Springer and Williams (1990) have proposed that Recent, glacially influenced extinction of populations in the Indo-Malaysian area accounts for disjunct distribution patterns such as that exhibited by *B. gibbifrons*. Although this may be true, and Recent glacial sea-level changes probably did influence
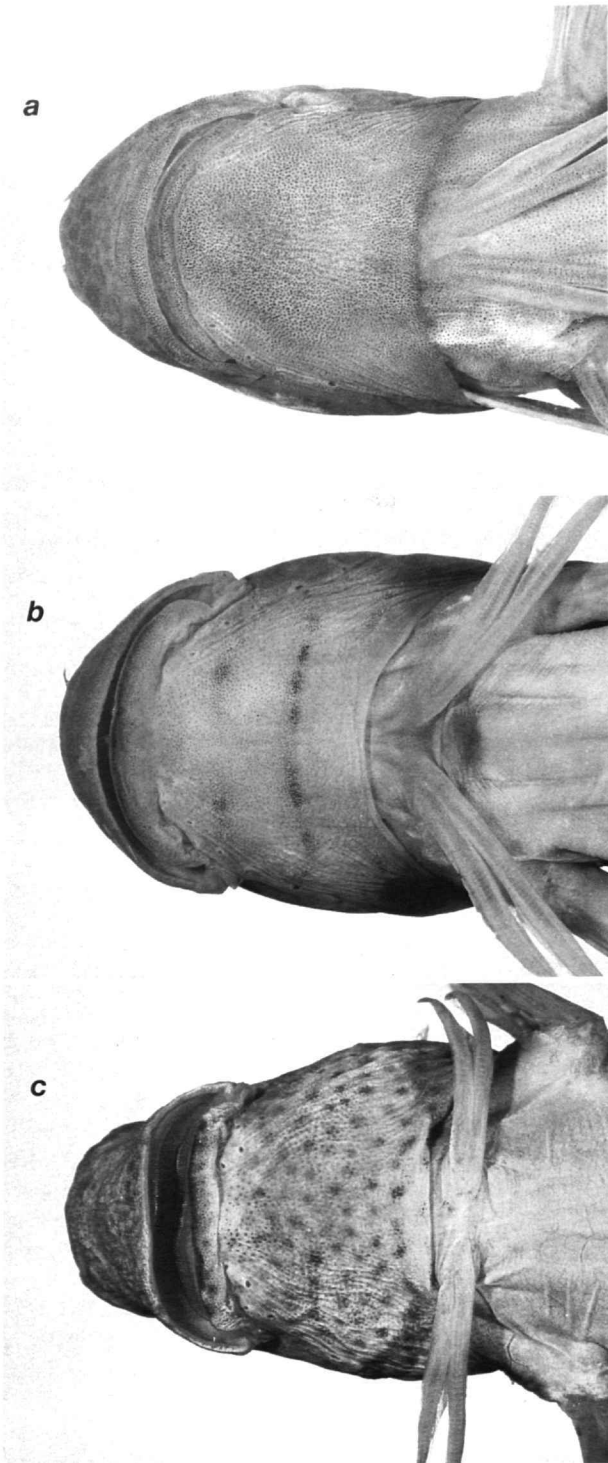
FIGURE 27.—*Blenniella gibbifrons*, ventral views of underside of head: *a*, male, 68 mm SL, and *b*, female, 72 mm SL, both CAS 66811, Cook Islands; *c*, USNM 55399, female, 66 mm SL, Oahu, Hawaiian Islands (photographs by T.B. Griswold).

distribution patterns (see discussion in account of *Istiblennius meleagris* and Biogeographic Discussion section), we now believe that its distribution pattern probably is the result of influences that existed prior to the Recent.

It is, perhaps, noteworthy that *Blenniella gibbifrons* is the only species of *Blenniella* or *Istiblennius* that occurs at Johnston Island (Randall et al., 1985). Johnston Island is geographically intermediate in position between the Hawaiian Islands and other islands on the Pacific plate. One species each of *Istiblennius* and *Blenniella* occur in the Hawaiian Islands and at least 2 of each genus occur at the islands closest to Johnston on the Pacific plate. Few, if any, other localities more or less surrounded by localities harboring several species of these 2 genera harbor only 1 species of the 2 genera. Randall et al. (1985) discussed the depauperate nature of the Johnston Island fish fauna, which they attributed, in part, to the small size of the island and its low diversity of habitats.

NOMENCLATURAL DISCUSSION.—Jenkins (1903) did not compare his *Salarias saltans* and *S. rutilus*, described in the same publication, with each other or any other species. The holotypes represent the male and female, respectively, of *Blenniella gibbifrons*. Springer et al. (1991:20) discussed problems in establishing which of Jenkins' specimens is the holotype of *Salarias saltans*, but concluded that the problem was inconsequential as all specimens in the type series are conspecific.

Reid's (1943) *Blenniella rhessodon* was an ophioblennius-stage specimen taken at the surface under an electric light. Strasburg (1956:254) examined the holotype (USNM 118029) of *Blenniella rhessodon* and stated that it was "a late larval stage of *I. gibbifrons*." Although Smith-Vaniz and Springer (1971:59) reported examining the holotype, we found the holotype missing from its jar on 22 Feb 1977. There is no record that the paratypes, USNM 120031, were examined subsequent to Reid's publication, and they were not present in the collection in 1977. In 1943, Leonard P. Schultz, then curator-in-charge, entered a note in the catalog book beside USNM 120033, a provisional Reid type, that 11 lots were stolen (and lost) for alcohol by a laborer. Possibly USNM 120031 was among the 11 lots.

J.L.B. Smith (1959) reported that his *Istiblennius gibbifrons insolitus* differed from the nominal subspecies (Hawaiian) in having fewer dorsal- and anal-fin rays and a shorter pectoral fin, and in lacking spots on the pectoral fin. Although western Indian Ocean specimens typically have 18 or 19 segmented dorsal- fin rays (vs. 19 or 20 in Hawaiian specimens) and 19 or 20 segmented anal-fin rays (vs. 20 or 21), these counts do not differ from those of specimens at most other Pacific localities (Table 16). We find no apparent variation in the pectoral-fin length. Spotting on the pectoral fin is highly variable within populations and between sexes (often exhibited only by females) and is not useful taxonomically.

Schultz and Chapman (1960:346–347) claimed their *Istiblennius afilinuchalis* and *I. rodenbaughi* differed from *B. gibbifrons* in usually having 1 less dorsal- and 1 less anal-fin

ray and in details of the color pattern. Because of the geographic variability in dorsal- and anal-fin ray counts, presence or absence of nuchal cirri, and presence of spots or bars on the chin (discussed in the geographic variation section above), we do not recognize these forms taxonomically. Schultz and Chapman (1960:347) distinguished their *I. afilinuchalis* (Swains and Phoenix islands) from *I. rodenbaughi* (Marshall Islands) primarily by the absence of chin bars in the latter species. Chin bars are typically present on females from all three of these island groups, but are often absent on males from Swains Island and the Marshall Islands.

MATERIAL EXAMINED.—Pacific Ocean. Marcus Id: BPBM 2457 (1), 7162 (24), USNM 264370 (20). Wake Id: BPBM 4938 (1), 15364 (15), 15378 (11), CAS-SU 50163 (1). Midway Island: BPBM 15234 (23). Hawaiian Is: CAS-SU 7680 (1), MNHN 4002 (holotype of *Salarias gibbifrons*), USNM 55400 (3); Hawaii, USNM 126682 (1), 126684 (1), 160686 (1); Molokai, USNM 164994 (4); Oahu, CAS-SU 8399 (37), USNM 34819 (1), 50695 (holotype of *Salarias rutilus*), 50696 (holotype of *Salarias saltans*), 51162 (1), 55399 (20), 55405 (4), 123377 (1), 126080 (2), 142058 (61), 149992 (1), 149993 (1), 196737 (1). Johnston Id: BPBM 4937 (1), 8948 (2), 15250 (1), 15253 (1), 29588 (7), USNM 142061 (3). Jarvis Id: USNM 228313 (36, including 2 cleared and stained). Line Is: Palmyra, CAS 68039 (in part, 1); Malden, USNM 199459 (47); Starbuck, USNM 264365 (4); Vostok, USNM 224889 (68). Marquesas Is: Nuku Hiva, BPBM uncat. (6); Hiva Oa, BPBM 12098 (6); Ua Pou, BPBM 12141 (4); Ua Huka, BPBM 12415 (3). Pitcairn Is: Pitcairn, BPBM 16733 (4), 17010 (10); Henderson, BPBM 17095 (16); Ducie, BPBM 17147 (11). Tuamotu Archipelago: Raroia, CAS 56331 (22), 56332 (26), 56339 (32), 64229 (33), 66799 (1); Tikahau, USNM 264363 (1). Society Is: Tahiti, BPBM 10812 (1); Moorea, CAS 66796 (1), MNHN 1984-318 (2). Cook Is: Rarotonga, BPBM 10827 (3); Mangaia, CAS 66811 (190; 40 used in analysis); Tongareva, USNM 264368 (2). Niue: NMNZ uncat. (1), NMNZ P.15674 (1), P.15675 (1), P.15676 (1), P.15679 (1), P.15685 (1), P.15687 (1), P.15688 (1). Swains Id: USNM 115422 (9), 144718 (2). Phoenix Is: Orona, USNM 111886 (28), 115419 (33), 115421 (holotype of *Istiblennius afilinuchalis*); Enderbury, USNM 115420 (53); McKean, USNM 264360 (100+; 60 specimens used in analysis; total count not confirmed); Rawaki, USNM 264362 (3); Birnie, USNM 264364 (1), 264369 (4); Baker, USNM 264366 (1). Howland Id: USNM 198704 (6), 198705 (6), 264367 (9). Kiribati (= Gilbert Is): Onotoa, USNM 167335 (1), 167336 (1). Marshall Is: Enewetak, BPBM 29049 (1), USNM 142083 (2), 142084 (7); Bikini, USNM 142067 (holotype of *Istiblennius rodenbaughi*), 142068 (13), 142069 (42), 142070 (1), 142071 (2), 142072 (1), 142073 (2), 142074 (3), 142075 (3), 142076 (10), 142077 (15), 142078 (23), 142079 (16); Rongrik, USNM 142080 (21); Rongelap, USNM 142081 (2), 142082 (3); Bikar, Taka, or Kwajelein, USNM 200545 (14, including 2 cleared and stained). Caroline Is: Kapingamarangi, CAS 56336 (4),

66813 (11); Ifaluk, CAS 56333 (36), 56334 (13), 56335 (4). Mariana Islands: Saipan, CAS 66798 (3); Guam, CAS 66800 (1).

Indian Ocean. Chagos Arch: Saloman Is, ROM 43909 (3), 43910 (20); Diego Garcia, USNM 265049 (8), 265051 (10), 265052 (1), 265054 (3), 265055 (9). Republic of Seychelles: Aldabra, RUSI 22478 (1), 22482 (1), USNM 232648 (1), 265053 (3). Agalega Is: USNM 266768 (3). Comoros: Grande Comore Id, CAS 33773 (in part; 1). Mauritius: RUSI 74-94 (1), 74-98 (2), BPBM 20169 (6). Madagascar: Nosy Be, USNM 308001 (1). Tanzania: Latham Id, USNM 265050 (7). Mozambique: Inhambane, RUSI 22479 (2); Baixo Pinda, RUSI 22480 (1); Ilha de Mozambique, RUSI 22481 (1); Bassas da India Id, RUSI 43072 (1). South Africa: Natal, Sodwana Bay, RUSI 74-352 (1), 9159 (1).

Blenniella chrysospilos (Bleeker), new combination

FIGURES 28, 29

Salarias chrysospilos Bleeker, 1857a:66 [Amboina; lectotype RMNH 4788 designated below].

Salarias coronatus Günther, 1872:424 [Saloman Islands; holotype BMNH 1871.3.29.42].

Salarias belemites De Vis, 1884:695 [Queensland Coast; holotype QM 1.224].

Alticus evermanni Jordan and Seale, 1906:422 [Apia; holotype USNM 51789].

Salarias bryani Jordan and Seale, 1906:427 [Apia; holotype USNM 51794].

Salarias aureopuncticeps Fowler, 1946:179 [Aguni Shima, Riu Kiu Islands; holotype ANSP 72050].

Salarias unimaculatus Aoyagi, 1954:215 [Ishigaki Island; Kowan, Okinawa-Honto; three syntypes, all apparently lost].

Salarias chrysospilus Chapman, 1951:290; Bleeker, 1983:14, 20, pl. 444: fig. 8 [misspelling].

Istiblennius chrysospilos insulinus J.L.B. Smith, 1959:243 [Aldabra; holotype RUSI 244].

DESCRIPTION.—Dorsal fin (Table 20). XII to XIV,18 to 22 = 31 to 35 (XIII,19 to 21 in 96% of specimens); mean numbers of total elements slightly higher for males from any locality than for females from same locality (higher for all 14 localities for which means for both sexes are available, but statistically significantly higher for only 1 locality—Queensland, essentially the southern Great Barrier Reef); membrane between spinous and segmented-ray portions incised $^2/_3$–$^3/_4$ length first segmented ray; membrane from posteriormost ray attaching to point on dorsal margin of caudal peduncle just anterior to caudal-fin base.

Anal fin (Table 20). II,20 to 23 (20 to 22 in 97% of specimens); mean numbers of segmented rays tending to be slightly higher in males from any locality than for females from same locality (higher for 12 of 14 localities for which means for both sexes are available; statistically significantly higher for 4 of the 12 localities); posteriormost ray split through base in 44% of specimens, not bound by membrane to caudal peduncle in all but 1 specimen. Some large and/or mature males with skin covering anal-fin spines and distal half of anterior segmented rays slightly inflated or expanded laterally, never

Table 20.—Frequency distributions for certain meristic characters in male and female specimens of _Blenniella_ _chrysospilos_ from various localities. Underlining indicates significant differences between means of sexes from same locality (p ≤ .05).

Sex/Locality	Total dorsal-fin elements						Segmented anal-fin rays					Total vertebrae				
	31	32	33	34	35	x̄	20	21	22	23	x̄	37	38	39	40	x̄
MALES																
Eastern Africa	-	1	9	-	-	32.9	-	10	1	-	_21.1_	-	8	2	-	38.2
Comoro Islands	-	-	4	-	-	33.0	-	4	-	-	21.0	-	3	1	-	38.2
Madagascar	-	-	1	-	-		-	1	-	-		1	-	-	-	
Mauritius	-	-	-	1	-		-	-	1	-		-	-	1	-	
Seychelles	-	7	18	1	-	32.8	9	17	-	-	20.7	-	22	4	-	38.2
Maldive Islands	-	1	2	-	-	32.7	1	2	-	-	20.7	-	3	-	-	38.0
Cocos-Keeling	-	-	9	13	-	33.6	-	9	13	-	_21.6_	-	-	18	4	_39.2_
Rowley Shoals	-	-	-	1	-		-	-	1	-		-	-	1	-	
Montebello Id, WA	-	-	1	2	-	33.7	1	-	2	-	21.3	-	-	3	-	39.0
Riu Kiu Islands	-	-	-	1	-		-	1	-	-		-	-	1	-	
Taiwan, Lanyu Island	-	-	-	1	-		-	1	-	-		-	-	1	-	
Philippines	-	-	3	-	-	33.0	-	3	-	-	21.0	-	3	-	-	38.0
Vietnam	-	-	1	1	-	33.5	-	-	2	-	22.0	-	-	2	-	39.0
Indonesia	-	1	-	-	-		1	-	-	-		1	-	-	-	
Papua New Guinea	-	-	-	3	-	34.0	-	-	3	-	22.0	-	-	3	-	39.0
Queensland	-	-	3	23	4	_34.0_	-	8	20	2	_21.8_	-	3	25	3	39.0
Solomon Islands	-	-	1	-	-		-	1	-	-		-	-	1	-	
Vanuatu	-	-	-	2	-	34.0	-	1	1	-	21.5	-	-	2	-	39.0
Loyalty Islands	-	-	1	-	1	34.0	-	1	-	1	22.0	-	-	2	-	39.0
Fiji	-	-	-	17	6	34.3	-	-	17	6	_22.3_	-	-	17	6	39.3
Rotuma	-	-	1	5	-	33.8	-	1	5	-	21.8	-	-	6	-	39.0
Samoa	-	-	1	3	-	33.8	-	1	3	-	21.8	-	-	4	-	39.0
Caroline Islands	-	-	3	3	-	33.5	-	3	3	-	21.5	-	3	3	-	38.5
Palau	-	3	11	4	-	33.0	5	10	3	-	20.9	-	8	10	-	38.6
Mariana Islands	-	-	-	1	-		-	1	-	-		-	-	1	-	
Marshall Islands	-	-	14	6	-	33.3	-	13	7	-	21.4	-	5	15	-	38.8
Society Ids, Tahaa	-	-	1	-	-		-	1	-	-		-	-	1	-	
FEMALES																
Eastern Africa	1	2	5	1	-	32.7	3	7	-	-	_20.7_	1	8	1	-	38.0
Comoro Islands	-	1	3	-	-	32.8	1	3	-	-	20.8	-	3	1	-	38.2
Seychelles	2	10	16	-	-	32.5	12	16	-	-	20.6	2	21	4	-	38.1
Maldive Islands	-	6	-	-	-	32.0	6	-	-	-	20.0	2	4	-	-	37.7
Cocos-Keeling	-	-	15	7	-	33.3	1	15	6	-	_21.2_	-	4	19	-	_38.8_
Rowley Shoals	-	-	1	-	-		-	1	-	-		-	-	1	-	
Montebello Id, WA	-	-	4	-	-	33.0	1	3	-	-	20.8	-	3	1	-	38.2
Philippines	-	-	1	-	-		-	1	-	-		-	1	-		
Indonesia	-	2	-	-	-	32.0	2	-	-	-	20.0	1	-	-	-	
Irian Jaya, Biak	-	-	-	1	-		-	1	-	-		-	-	1	-	
Papua New Guinea	-	-	3	1	-	33.2	-	3	1	-	21.2	-	2	2	-	38.5
Queensland	-	1	18	5	-	_33.2_	-	14	9	-	_21.4_	-	4	20	-	38.8
Solomon Islands	-	-	-	-	-		-	-	1	-		-	-	-	-	
Fiji	-	-	1	19	2	34.0	-	2	19	1	_22.0_	-	-	16	6	39.3
Rotuma	-	-	3	2	-	33.4	-	2	3	-	21.6	-	-	5	-	39.0
Samoa	-	-	2	3	-	33.6	-	1	4	-	21.8	-	-	5	-	39.0
Caroline Islands	-	2	4	1	-	32.9	-	6	1	-	21.1	-	3	4	-	38.6
Palau	-	2	11	-	-	32.8	-	12	1	-	21.1	-	6	7	-	38.5
Mariana Islands	-	-	2	-	-	33.0	-	2	-	-	21.0	-	1	1	-	38.5
Marshall Islands	-	2	9	4	-	33.1	-	10	5	-	21.3	-	7	8	-	38.5

crinkled along edges.

Pectoral-fin rays 12 to 15, 14 bilaterally in 95% of specimens, at least unilaterally in 98% (1 specimen with 12/13, 3 with 15/15).

Pelvic-fin segmented rays 3.

Caudal-fin elements. Total (dorsal + ventral) procurrent rays 11 to 18 (14 to 16 in 91% of specimens); segmented rays 13.

Vertebrae (Table 20) 11 to 13+25 to 28 = 37 to 40 (12 precaudal vertebrae in 99% of specimens; 26 or 27 caudal vertebrae in 93% of specimens); mean number of total

vertebrae tending to be higher for males from any locality than for females from same locality (higher for 9 of 14 localities for which means for both sexes are available; statistically significantly higher for only 1 of the 9 localities); posteriormost pleural rib on 12th or 13th from anteriormost centrum (13th in 74% of specimens; Table 21); posteriormost epineural on 25th to 31st from anteriormost centrum (rarely on 25th or 31st; on 27th to 30th in 95% of specimens; Table 21).

Cirri. Nape modally with single, small cirrus on each side, frequently missing unilaterally or bilaterally. Orbital cirrus consisting of elongate basal section with distal end branching into 2 to 11 tiny filaments (usually with 2 to 4; simple bilaterally in 3% and unilaterally in 15% of specimens; 9 or 11 distal cirri in only 2 of 240 specimens examined). Nasal cirri short, palmate, rarely with more than 6 free tips.

Lateral line. Continuous canal anterodorsally with 1 to 25 vertical pairs of pores (varying with population, Table 21), extending posteriorly to point between verticals from bases of 9th and 12th dorsal-fin spines, ending there or continuing posteriorly and ventroposteriorly along body midline as series of 0 to 7 (usually 1 to 4) bi-pored canals (tubes) in skin to point no further posteriorly than vertical from base of third segmented dorsal-fin ray. Mandibular pores 6 (rarely 5, and only unilaterally).

Up to at least 11 (usually 9 or more) sensory pore positions between 1 and 5 o'clock on postorbital margin; 2 to 5 (usually 4 or 5) positions occupied by pairs or multiples of pores.

Posterior dentary canines present in both sexes (rarely absent).

Ventral margin of upper lip crenulate medially; crenulae becoming weak or absent laterally; dorsal margin of lower lip entire. Crest on head of large, adult males consisting of low, longitudinal, fleshy fold or ridge originating anteriorly at level of posterior edge of interorbital space; large females often with very low, longitudinal ridge on nape.

Color pattern (in preservative). Males (Figures 28a, 29a). Two basic forms, dark and pale, with considerable variation within each, probably the result of preservation and handling. Dark form (Figure 28a): body generally brown with tan area ventrally and, sometimes, dorsally; small, dark or pale spots (or narrow stripes, western Indian Ocean specimens) cover posterior half to two-thirds of body; pupil-sized, black spot (rarely 2 spots) in middle of body below first few segmented dorsal-fin rays (usually absent on western Indian Ocean specimens); anterordorsal half of body with scattered small, dark spots. Pale form (Figure 29a): body with series of alternating dark and pale bars, with dark bars occasionally restricted to dorsal half of body; spotting pattern overlying bars similar to that of dark form. Head (both forms): narrow, dark bar usually crossing head behind eyes, followed posteriorly by wide, pale bar bordered posteriorly by another narrow, dark bar, which crosses nape immediately anterior to dorsal-fin origin; small, pale or dark spots variously scattered over head and branchiostegal membranes, which may be barred, spotted,

or mixture of both; pigment of ventral portion of dark bar immediately posterior to orbit intensified as contrasting, often crescent-shaped, dark spot, typically persisting in preservative even when remainder of bar not evident; background pattern on head often bicolored, tan over dorsal half, whitish over ventral half. Pectoral-fin base with broken bar, best developed ventrally; fin either spotted (Pacific) or more or less plain dusky (western Indian Ocean). Each dorsal-fin spine usually with black spot at tip; remainder of spinous dorsal fin dusky with small, dusky spots and/or faint, diagonal streaks; segmented-ray portion of fin with basal half to $^3/_4$ covered with dark reticulations and spots, distal half pale, often with faint, slender, diagonal streaks. Anal fin more or less uniformly dark. Pelvic fin dusky. Caudal fin: ventral half dusky, dorsal half mostly pale with dusky margin.

Females (Figures 28b, 29b). Similar to pale-form males, except: dark bars on body irregularly H-shaped with ventral legs of H distinct, separated by pale area; bars usually formed by, or include, small, black spots (Figure 29b); crossbar and adjacent middle part of H often lacking, resulting in series of vertically paired blotches or spots; black pupil-sized spot on midside of body below anterior segmented dorsal-fin rays usually lacking, poorly developed when present; dorsal fin with distinct, small, black spot usually present near base of every second to fourth element, segmented rayed portion of dorsal fin pale or dusky with faint, dark spots and slender streaks; anal fin dusky with dark distal margin.

Fresh coloration. Smith (1959, pl. 16-4, 16-5; Aldabra) published colored illustrations of fresh female and male. Randall (1992b, fig. 314, Maldives) published a colored illustration of a fresh male. Allen and Swainston (1988, pl. 56-851; Western Australia) and Allen (1985, fig. 387, Kendrew Island) published colored illustration and underwater photograph, respectively, of females. Masuda et al. (1984, pl. 269 A,B) published photographs of fresh male and female specimens from Japan. Underwater photographs of live specimens were published by Myers (1989, pl. 115-A; male; Guam) and Randall et al. (1990:383, female; Great Barrier Reef). R. Winterbottom provided us with a photograph of fresh male from Comoros and G. Allen a photograph of a fresh male from Cocos-Keeling. J. Randall provided photographs of living specimens from Fiji (female) and Bougainville Reef, Coral Sea (male), and fresh specimens from Kendrew Island (male and female), Fiji (female), Samoa (female), and Enewetak, Marshall Islands (males; one photograph published in Burgess and Axelrod, 1973, fig. 375). One of us (JTW) photographed fresh male at the Loyalty Islands and male and female at Rotuma.

Males from Comoros and Aldabra have head olive with small, red spots on snout, becoming orange on opercle; ventral and posteroventral edges of orbit and upper end of preopercle with black spots, each of which has iridescent-blue crescent along posteroventral margin; body olive with about 7 or 8 longitudinal stripes extending from beneath appressed pectoral fin to caudal-fin base; proximal half of dorsal fin with reddish
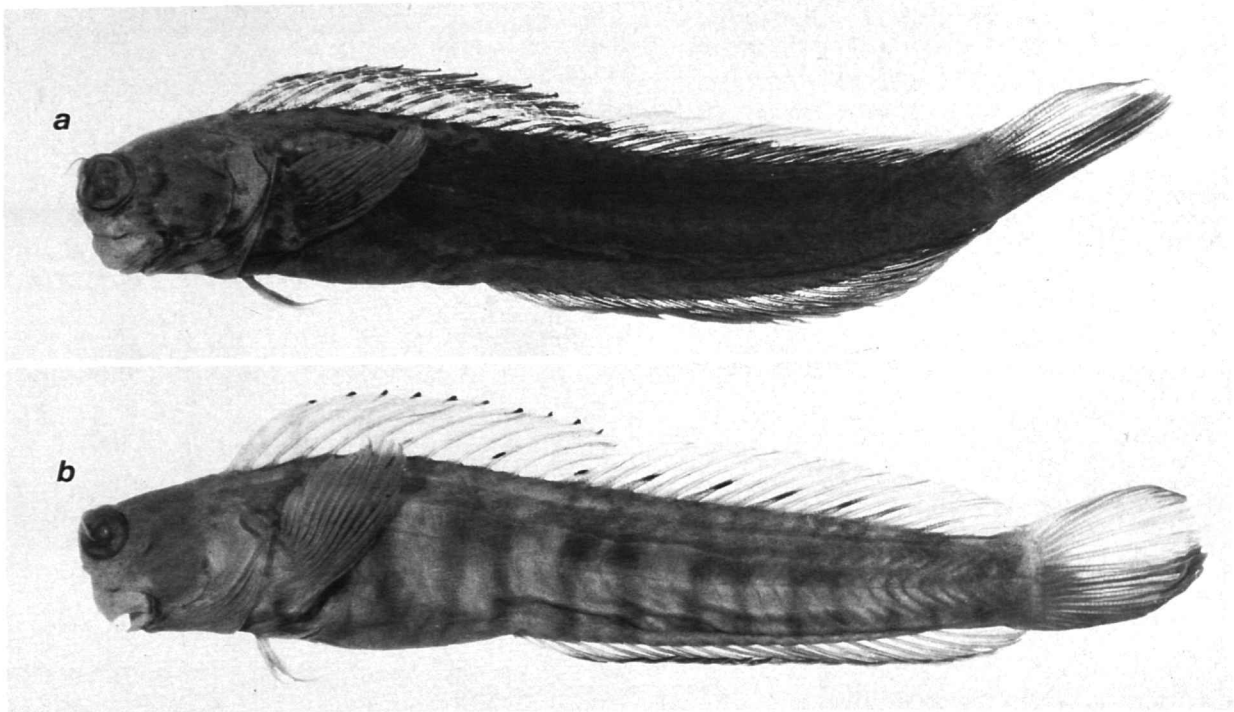
Table 21.—Frequency distributions for certain characters in specimens of <u>Blenniella</u> <u>chrysospilos</u> from various localities. A = absent, P = present, S = spotted, U = unspotted. Underlining indicates significant difference between frequency distributions for males and females from same locality (p ≤ .05).

Locality	Pleural ribs			Epineurals								Pectoral fin		Lateral body spot ♂♂		♀♀	
	12	13	x̄	25	26	27	28	29	30	31	x̄	U	S	P	A	P	A
Eastern Africa	15	5	12.3	-	1	7	10	1	-	-	27.6	20	-	-	10	-	10
Comoro Islands	3	5	12.6	-	-	3	4	1	-	-	27.8	4	2	-	4	1	3
Madagascar	1	-		-	-	-	1	-	-	-		1	-	-	1	-	-
Mauritius	-	1		-	-	-	-	-	1	-		1	-	-	1	-	-
Seychelles	27	24	12.5	1	5	16	26	5	-	-	27.5	38	2	<u>10</u>	<u>15</u>	-	<u>26</u>
Maldive Islands	8	1	12.1	-	2	1	3	3	-	-	27.8	9	-	-	<u>3</u>	-	<u>6</u>
Cocos-Keeling	4	41	12.9	-	1	3	13	17	9	1	28.8	2	32	<u>10</u>	<u>9</u>	-	<u>15</u>
Rowley Shoals	-	2	13.0	-	-	1	-	1	-	-	28.0	2	-	-	1	-	1
Montebello Id, WA	2	5	12.7	1	-	-	5	-	-	1	28.0	-	7	3	-	1	3
Riu Kiu Islands	-	1		-	-	-	1	-	-	-		-	1	1	-	-	-
Taiwan, Lanyu Island	-	1		-	-	-	1	-	-	-		-	1	1	-	-	-
Philippines	1	3	12.8	-	-	-	3	1	-	-	28.2	-	4	3	-	1	-
Vietnam	1	1	12.5	-	-	-	1	1	-	-	28.5	-	2	1	1	-	-
Indonesia	-	2	13.0	-	-	1	1	-	-	-	27.5	-	3	1	-	-	2
Irian Jaya, Biak Id	-	1		-	-	-	-	1	-	-		-	1	-	-	-	1
Papua New Guinea	-	7	13.0	-	-	1	4	2	-	-	28.1	-	7	3	-	2	2
Queensland	6	48	12.9	-	1	10	17	15	8	-	28.4	-	32	<u>24</u>	-	<u>10</u>	<u>6</u>
Solomon Islands	1	-		-	-	-	1	-	-	-		-	1	1	-	-	-
Vanuatu	-	2	13.0	-	-	-	2	-	-	-	28.0	-	2	2	-	-	-
Loyalty Islands	1	1	12.5	-	-	-	2	-	-	-	28.0	-	2	2	-	-	-
Fiji	4	41	12.9	-	-	1	11	17	14	-	29.0	-	24	<u>10</u>	-	<u>8</u>	<u>6</u>
Rotuma	2	9	12.8	-	-	-	5	4	2	-	28.7	-	11	6	-	2	3
Samoa	1	8	12.9	-	1	-	3	4	1	-	28.3	-	9	4	-	2	3
Caroline Islands	2	11	12.8	-	-	1	4	8	-	-	28.5	1	12	<u>6</u>	-	<u>2</u>	<u>5</u>
Palau	8	22	12.7	-	-	4	14	6	5	1	28.5	1	29	<u>16</u>	-	<u>2</u>	<u>10</u>
Mariana Islands	-	3	13.0	-	-	-	2	-	1	-	28.7	-	3	1	-	-	2
Marshall Islands	-	34	13.0	-	-	3	9	16	5	1	28.8	1	26	<u>16</u>	-	<u>1</u>	<u>10</u>
Society Is, Tahaa	-	1		-	-	-	1	-	-	-		-	1	1	-	-	-

Locality	Number of vertical pairs of pores in lateral line																									x̄
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Eastern Africa	1	1	5	1	1	2	1	-	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	5.3
Comoro Islands	-	-	2	1	-	4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.2
Madagascar	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	
Mauritius	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.5
Seychelles	-	4	11	3	10	3	4	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	4.7
Maldive Islands	-	2	4	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4
Cocos-Keeling	-	-	-	-	-	1	-	-	4	4	4	7	1	3	3	2	-	2	2	-	-	-	-	-	-	12.6
Rowley Shoals	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	13.5
Montebello Id, WA	-	-	-	-	-	-	1	-	-	2	-	-	1	1	-	-	-	-	-	2	-	-	-	-	-	14.4
Riu Kiu Islands	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Taiwan, Lanyu Island	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Philippines	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1	-	1	-	-	-	-	-	1	-	16.8
Vietnam	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1	-	-	-	-	-	-	-	-	15.0
Indonesia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	18.0
Irian Jaya, Biak Id	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Papua New Guinea	-	-	-	1	-	-	-	-	-	-	-	1	1	-	-	1	-	2	-	-	-	-	-	-	-	14.7
Queensland	-	-	-	-	-	-	1	1	2	-	2	2	6	5	4	2	4	4	1	-	2	-	-	1	-	15.7
Solomon Islands	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
Vanuatu	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.0
Loyalty Islands	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.0
Fiji	-	-	-	-	-	-	2	1	-	2	-	3	2	1	4	-	3	2	1	3	-	-	-	-	-	16.3
Rotuma	-	-	-	-	-	3	1	-	3	-	-	1	-	1	-	1	1	-	-	-	-	-	-	-	-	11.1
Samoa	-	-	-	-	-	-	2	-	-	1	-	2	1	-	1	-	1	1	-	-	-	-	-	-	-	14.3
Caroline Islands	-	-	-	-	-	1	-	1	-	2	-	1	2	1	-	1	-	-	1	-	-	-	-	-	-	14.1
Palau	-	-	-	-	1	1	2	-	2	1	2	-	2	2	2	1	-	1	-	-	-	-	-	-	-	12.4
Mariana Islands	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	1	-	1	-	-	-	20.0
Marshall Islands	-	-	-	-	-	1	1	-	-	3	-	2	3	3	-	2	1	1	3	1	2	-	1	-	-	15.9
Society Is, Tahaa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	

FIGURE 28.—*Blenniella chrysospilos*, USNM 296215, Aldabra, western Indian Ocean: *a*, male 54 mm SL, dark-form coloration obscuring underlying pattern of bars and spots (one of few specimens from western Indian Ocean with spots on pectoral fin); *b*, female, 59 mm SL (photographs by T.B. Griswold).

spots and reticulations, spots becoming pale yellow on distal portion of segmented rays. The Maldives male is similar to previous males, but ventral half of head pale with oriange spots, only 2 regular and 2 or 3 irregular orange stripes on body. Males from Cocos-Keeling, Kendrew Island, and all Pacific localities lack orange stripes and have pale-greenish head and body that are abruptly paler on their ventral halves, giving slightly bicolored appearance; small, orangish-tinted, tan spots present on head and body anteriorly; posterior half of body with small, round to dorsoventrally depressed, pale-blue spots; dorsal fin with reticulate pattern of brown streaks and pale-greenish spots basally, reticulations becoming red, merging into yellow-edged distal margin on segmented-ray portion of fin.

Colored illustration of Aldabra female specimen shows olive ground color with orange spots on head and body, spots on body large, oval shaped; 2 orange spots posterior to orbit each with dark-blue, crescent-shaped posterior margin; all vertical fins yellowish with scattered reddish spots on spinous dorsal fin, row of reddish spots suprabasally on the segmented-ray dorsal fin. Females from Western Australia, Great Barrier Reef, and Fiji have pale body with only slight greenish tint; spots on head and body about same size; spots on head and anteriorly on body orangish brown, those posteriorly becoming brown; distal

border of spinous dorsal fin edged in white between black-tipped spines.

Pupil of the eye in all specimens incorporated in pair of orange bars, separated by narrow, pale-blue area; iris pale-blue dorsal and ventral to orange bars.

Size. Largest male 114 mm SL, largest female 97 mm SL, smallest specimen, 24 mm SL. No ophioblennius-stage specimens known.

GEOGRAPHIC VARIATION (Tables 20, 21).—Meristic, color-pattern, and lateral-line pore characters in *Blenniella chrysospilos* vary considerably geographically. Specimens from neighboring groups of localities may be generally or almost completely recognizable from specimens at other localities based on one or more characters. The geographic distribution of other characters, however, may conflict with such recognition, and there are varying degrees of overlap in most characters between groups of localities. Cocos-Keeling appears to be an area of transition for meristic and some color-pattern characters. Specimens from Cocos-Keeling tend to be intermediate between the low counts in the western Indian Ocean and the high counts in the Pacific. Because of intermediacy and overlaps in characters, we do not believe that nomenclatural recognition of specimens from any grouping of localities is warranted.
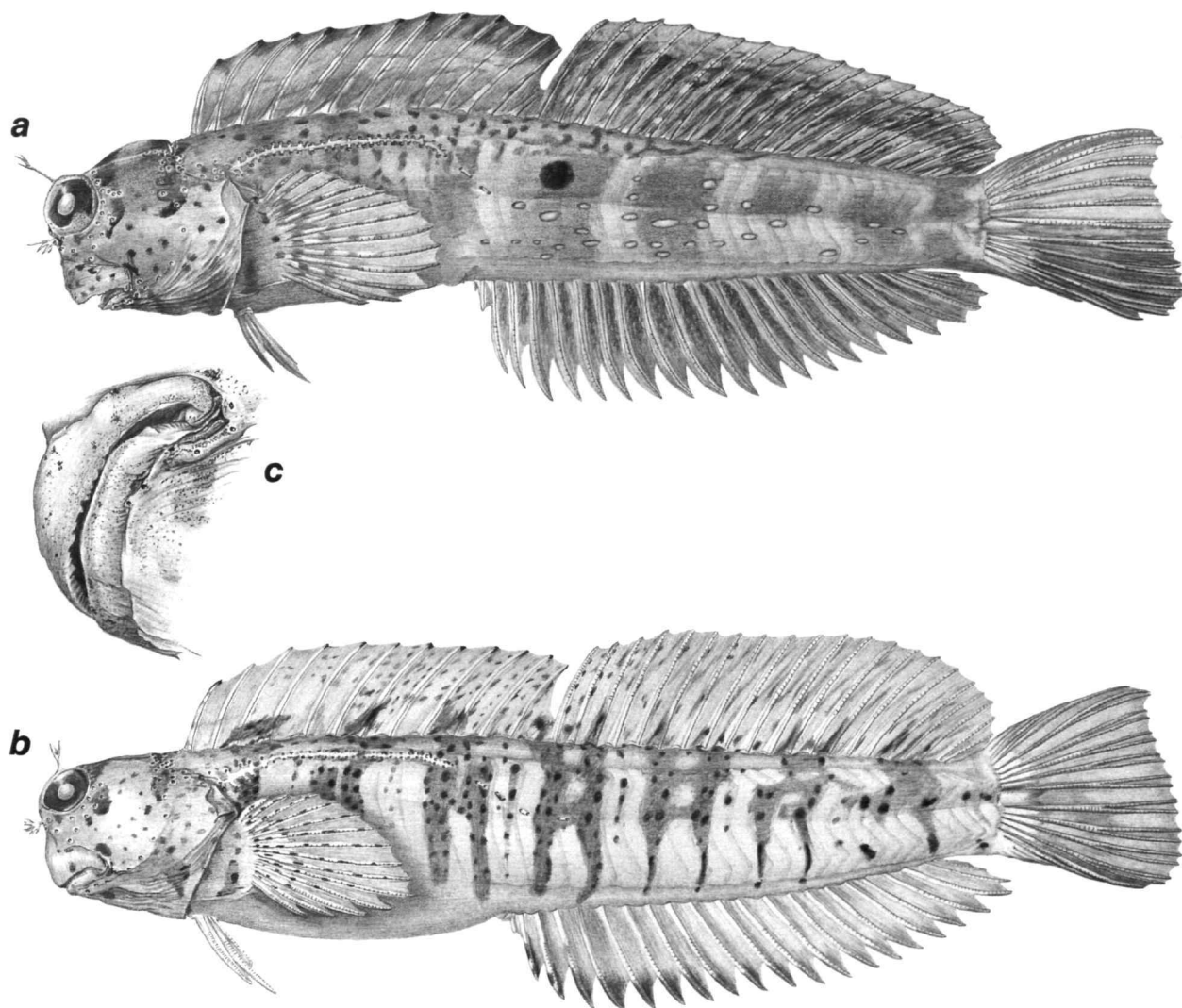
FIGURE 29.—*Blenniella chrysospilos*, western Pacific color pattern: *a*, USNM 265394, male, 76 mm SL, One Tree Island, Great Barrier Reef, pale-form male with spots and bars (13 pectoral-fin rays unusual); *b,c*, USNM 256543, female, 78 mm SL, Malolo Lailai, Fiji (*c* is enlarged, view of mouth, rotated dorsally about 45° to show weakly crenulate medial portion of upper lip; note disposition of 6 mandibular sensory pores) (drawings by P.K. Hollingsworth).

Specimens from western Indian Ocean localities (east Africa east to the Maldives) are almost completely distinguishable from those from more eastern localities in having an unspotted pectoral fin and low numbers of vertical pairs of lateral-line pores (Table 21). Western Indian Ocean specimens also tend to have the lowest means for all 5 meristic characters (total dorsal-fin elements, segmented anal-fin rays, total vertebrae, pleural ribs, and epineurals).

The clustering of specimens from western Indian Ocean localities is similarly indicated by the state of the midlateral body spot, whether present or absent. The spot is absent in all males from the western Indian Ocean, except those from Seychelles, in which it is present in 40% of the males. The spot is present in 53% of the males from Cocos-Keeling, eastern Indian Ocean, and in 98% (102 of 104) of males from localities east of Cocos-Keeling. The Seychelles and Cocos-Keeling are transitional areas where males are almost equally likely to have or lack the spot. Females show a different, but similar,

distribution of the body spot. The spot is absent in 64 of 66 (97%) females from localities extending from the eastern Indian Ocean to the Philippines, but is present in 9% to 62% of the females from any locality east and south of the Philippines, except for the only 2 females from the Mariana Islands and the only female from Irian Jaya, which all lack the spot.

Although live coloration of males is known for only 2 western Indian Ocean localities, they differ from males from other localities in having distinctive orange pinstripes on the body. Female coloration does not exhibit geographic variation.

A second pattern, though less pronounced, is discernible from the meristic data. The male specimens from Palau, Philippines, and Marshall Islands have low meristics, more similar to those of western Indian Ocean localities than to those of neighboring western Pacific localities. Among males, Palau specimens completely overlap western Indian Ocean specimens (except those from Madagascar) in dorsal-fin, anal-fin, and vertebral counts. The pattern of variation wherein western Indian Ocean and Caroline-Marshall islands specimens have similar meristic counts is reflective of the pattern for *B. gibbifrons* (although the intermediate eastern Indian Ocean-western Pacific component is lacking for *B. gibbifrons*). In both groups, these areas tend to exhibit greater agreement with each other than either does with its closest neighboring populations.

In general, means for meristics are highest for specimens from Fiji, which is in an area where means generally tend to be high for populations of species of *Blenniella* and *Istiblennius* that occur there.

ECOLOGY.—*Blenniella chrysospilos* dwells in shallow water on reef crests or fringing reefs. It appears to prefer a high-energy surge environment on exposed reefs.

COMPARISONS AND RELATIONSHIPS.—(See this section under *Blenniella gibbifrons*). *Blenniella chrysospilos* is most easily distinguished from all other *Blenniella* and *Istiblennius* species by the presence of black-tipped dorsal-fin spines.

DISTRIBUTION (Figure 64).—Known from the Society Islands in the south-central Pacific to the east coast of Africa, and from the Riu Kiu Islands in the north to about 24° S latitude in the Pacific and Indian oceans.

Seale (1906:86), followed by Fowler (1928:437), reported *Salarias coronatus* Günther (a junior synonym of *Salarias chrysospilos* Bleeker) from Nukuhiva, Marquesas Islands, based on two specimens. Seale's specimens, however, are identifiable as *Blenniella paula* (one of Seale's two specimens is now ANSP 81989). Chapman (1951:308), who did not see Seale's specimens, appears to have based his report of *Salarias chrysospilos* from Nuku Hiva on Seale and Fowler's reports. *Blenniella chrysospilos* is not known from the Marquesas.

NOMENCLATURAL DISCUSSION.—Bleeker (1857a) based *Salarias chrysospilos* on two specimens, 60 and 66 mm (TL). There are, however, three specimens in the jar (RMNH 4788) containing the putative syntypes, and three specimens were listed in the 1879 auction catalog of Bleeker's collections (reproduced in Lamme, 1973). These specimens are ~58, 64,

and 72 mm TL. The longest specimen appears to be too long to have been one of the syntypes and is here excluded from the syntypic series. We designate the shortest specimen, a female, as lectotype of *Salarias chrysospilos*. The dorsal- and anal-fin formulae (XIII,19; II,20 last ray split to base) also distinguish the lectotype from the 64 mm paralectotype. The lectotype agrees closely with Bleeker's (1983, pl. 444: fig. 8) illustration of this species, except that there is no membrane attaching the last anal-fin ray to the caudal peduncle. This is apparently an artist's error as some of the other species of *Blenniella* and *Istiblennius* illustrated in the atlas exhibit the same error. For a discussion of the problems surrounding the recognition of Bleeker types see Whitehead et al. (1966).

Günther (1872) did not compare his *Salarias coronatus* with any other species. We have examined the holotype and find it identifiable as *B. chrysospilos*.

De Vis (1884) did not compare his *Salarias belemites* with another species. Both the description and the holotype, which is in very poor condition, are identifiable as *B. chrysospilos*.

Jordan and Seale (1906) reported that they had 21 specimens (including the holotype?) of their *Alticus evermanni*, and that the holotype was cataloged as USNM 51789; no other catalog numbers were indicated. In the USNM catalog, the remarks section by USNM 51789 indicates that, initially, "1" specimen was in this lot. The 1 is crossed out and a "5" written above it. An inventory of USNM fish types completed in the 1980s noted that the jar bearing catalog number 51789 contained only four specimens. One of these, in very good condition, has the metal tag with the catalog number tied to it. The other three specimens, in poor condition, appear to have been preserved differently from the fourth, which Springer et al. (1991:8) list as the holotype. We have recataloged the three specimens as USNM 292586. Additionally, the catalog lists USNM 52308 (4 specimens), 126334 (formerly in U.S. Bureau of Fisheries collection; 4 specimens), and 126602 (also formerly USBF; 3 specimens) as paratypes of *S. evermanni*. A card in the USNM type card file states that 2 specimens were exchanged to the Bishop Museum in 1939, where they are now cataloged as BPBM 5322. There are 9 specimens (CAS-SU 8699) labeled as paratypes at CAS. The USNM and CAS specimens total 23 paratypes, 3 more than the 20 indicated in the original description. The 3 specimens in USNM 292586 may not have been included among the 20 in the original description. We have not been able to account for the missing paratypes.

Jordan and Seale (1906) compared their *A. evermanni* only with *B. periophthalmus*. We have examined their putative holotype and the 14 USNM paratypes and find all identifiable as *B. chrysospilos*.

Jordan and Seale (1906) did not compare their *Salarias bryani*, of which they had only the juvenile holotype, with any other species. We have examined the holotype (USNM 51794, erroneously listed in their publication as USNM 31794) and find it identifiable as *B. chrysospilos*.

Fowler (1946) compared his holotype (only specimen) of

Salarias aureopuncticeps with *Salarias coronatus* (= *B. chysospilos*), from which he believed his species differed "markedly in coloration and the rounded caudal fin." He made the contradictory statement that his specimen had the "soft dorsal" with a black border and the "second dorsal" with a white border. Fowler's use of the term "soft dorsal" was probably an error as his use of the term black border undoubtedly refers to the black-tipped spines of the first dorsal fin. In preservative, the second dorsal has an immaculate distal margin and would agree with Fowler's use of the term white border to describe it. We have examined the holotype and find it identifiable as *B. chrysospilos*.

Aoyagi (1954) compared his *Salarias unimaculatus* only with *B. periophthalmus*. His illustration clearly depicts *B. chrysospilos*. During his career, Aoyagi described many species, but the disposition of many of his types is unknown.

J.L.B. Smith (1959:244) distinguished his western Indian Ocean subspecies, *Istiblennius chrysospilos insulinus*, from the central Pacific form based on *insulinus*: always having a nuchal cirrus, males having a deep anal fin ("at least body depth"), pectoral fins lacking spots, only rarely having traces of a black spot on the side, and the upper lip being very feebly crenulate. We found that the central Pacific form commonly exhibits 3 of these 5 characters. Only the lack of pectoral-fin spots and the black spot on the side are useful in distinguishing the two forms. Although Smith (1959) stated that his form lacks pectoral-fin spots, his illustration of the male (1959, pl. 16-5) depicts a heavily spotted pectoral fin, and the female on the same plate (pl. 16-4) has a few spots basally on the fin. Nevertheless, we find that the presence of pectoral-fin spotting is rare in Indian Ocean specimens. Of 39 male and 40 female specimens available from the western Indian Ocean, only 4 males have spotted pectoral fins. All but 2 males and 5 females from the eastern Indian Ocean and Pacific have spotted pectoral fins. Except for 10 of 25 males from the Seychelles and 1 of 4 females from Comoros Islands, the black spot on the midside of the body is lacking on both sexes from the western Indian Ocean, but is generally present on males from the eastern Indian Ocean, almost always present in males from the Pacific, and present or absent on females from the Pacific (Table 21).

MATERIAL EXAMINED.—Indian Ocean. Kenya: Malindi, RUSI 22485 (1 specimen). Tanzania: Latham Id, USNM 296010 (15), 296240 (2); Zanzibar, USNM 296264 (1). Mozambique: Pinda, RUSI 22483 (1). Madagascar: Nosi Be, USNM 308415 (1). Comoros Is: Grand Comore, CAS 68017 (9), 33597 (6), USNM 296235 (1); Mayotte, USNM 296236 (1). Mauritius: BPBM 21030 (1). Seychelles: Aldabra, RUSI 271 (1), 22482 (1), USNM 265056 (1), 276007 (8), 296215 (32), 296265 (2); Assumption, RUSI 22487 (4); Arros, USNM 296226 (2), La Digue, RUSI 22484 (1), Mahé, RUSI 22486 (1). Maldives: Male, CAS 58690 (2), 58692 (7). Cocos-Keeling: Horsburgh, WAM P.29907-042 (2); Direction, ANSP 134749 (114). Rowley Shoals: WAM P.27667-042 (2). Australia: Montebello Is, Daisey, WAM P.27978-028 (2); South East Id,

WAM P.27980-060 (5).

Pacific Ocean. Indonesia: Amboina, RMNH 4788 (lectotype and paralectotype of *Salarias chrysospilos*); Lucipara Group, Maisel, CAS 62523 (1); Banda Sea area, USNM 296237 (1); Irian Jaya, Biak, USNM 296410 (1). Riu Kiu Is: Aguni Shima, ANSP 72050 (holotype of *Salarias aureopuncticeps*). Taiwan: Lanyu (Orchid Id), USNM 296016 (1). Philippines: Cocoro Island, USNM 296012 (1); Apo Id, USNM 296015 (1); Mindanao, Aliguay Id, USNM 225130 (1), 296011 (1). Vietnam: Ilot du Sud, CAS 67774 (2). Papua New Guinea: Trobriand Is, USNM 301311 (5); Madang, USNM 296239 (1); Bagabag Island, USNM 296411 (1). Australia, Qd: Keeper Reef (off Townsville), QM I.6289-92 (4); Escape Reef, AMS I.22600-065 (2); Heron Id, USNM 315727 (1), 296017 (5), 296014 (1), 296314 (4); One Tree Id, USNM 265394 (33), 296323 (7); Queensland coast, QM I.224 (holotype of *Salarias belemnites*). Solomon Is: Savo, BMNH 1871.3.29.42 (holotype of *Salarias coronatus*), BPBM 16112 (1). Vanuatu: Efate, USNM 322411 (2). Loyalty Is: Ouvéa, USNM 322409 (1), 322410 (1). Fiji: USNM 82804 (2); Malolo Lailai, USNM 256543 (44); Kandavu, USNM 256539 (1), USNM 296013 (1); Viti Levu, BPBM 11388 (2). Rotuma: USNM 283138 (10), 284373 (1). Samoa Is: Apia, BPBM 5322 (2), 11319 (2), USNM 51794 (holotype of *Salarias bryani*), 51789 (holotype of *Alticus evermanni*), 292586 (3), 296233 (2). Mariana Is: Guam, USNM 124232 (1), 296228 (1); Saipan, BPBM 35035 (1). Caroline Is: Palau, CAS 49002 (2), 67684 (19), 67686 (9), 76096 (1); Ulithi, CAS 49047 (1), 56338 (6), 66854 (1); Pohnpei, USNM 223450 (4), 224377 (1). Marshall Is: Bikini, USNM 142093 (24); Arno, USNM 314254 (1); Rongelap, USNM 142082 (2), 142086 (1); Rongerik, USNM 142088 (7); Enewetak, USNM 296309 (18, including 2 cleared and stained); Kwajelein, USNM 200611 (3, including 1 cleared and stained). Society Is: Tahaa, USNM 133864 (1).

Istiblennius Whitley

Istiblennius Whitley, 1943:185 [type species: *Salarias muelleri* Klunzinger, 1880, by original designation].

Halmablennius J.L.B. Smith, 1948:340 [type species: *Salarias unicolor* Rüppell, by original designation].

DIAGNOSIS (see also Tables 1 to 3).—A genus of Salariini (Smith-Vaniz and Springer, 1971) with weak infraorbital bones, weakly attached to cranium, deepest portion of second infraorbital (usually at junction with first infraorbital) less than half depth of first infraorbital, dorsal margin of first infraorbital slightly to deeply notched (Figure 2a); dorsal and ventral postcleithra normal and in contact (Smith-Vaniz and Springer, 1971, fig. 15d); vomer edentate; anterior dentary canines absent; posterior dentary canines absent in females of all but 1 species (present or absent in *dussumieri*); posterior dentary canines absent in males of all but 2 species (present or absent in *dussumieri* and *flaviumbrinus*); more than 100 teeth in entire upper jaw, more than 75 in entire lower jaw; pectoral-fin rays

strongly modally 14 in all but 1 species (modally 12 in *rivulatus*); segmented pelvic-fin rays 2 to 4, strongly modally 3 in all but 3 species (3 or 4 in *spilotus*, 4 in *unicolor* and *colei*—but only 3 obvious in *colei*); dorsal-fin: spines strongly modally XIII in all but one species (strongly modally XIV in *colei*); segmented rays 16 to 25 (rarely 25); total elements 29 to 38 (rarely 38); membrane between last spine and first segmented ray notched half or more length of first segmented ray; posteriormost segmented ray bound by membrane to caudal peduncle, or, depending on species, sex, and SL, to point out on dorsal edge of caudal fin up to 25% length of fin; membrane attaching terminal anal-fin ray to caudal peduncle modally absent; terminal anal-fin ray modally split to base or not split to base, depending on species; segmented caudal-fin rays modally 13, of which modally 9 branched; lateral line consisting of continuous anterior portion followed posteriorly by series of 1 to 26 short, horizontally bi-pored tubes in skin (highly variable within and among species, Table 3); no scale-like flaps in continuous portion of lateral line; preoperculomandibular pores without cirri; fleshy blade-like crest present dorsally on head of males of all species, present or absent in females (varying among species and within a species); supraorbital cirrus present, varying from simple filament to palmate flap to highly branched stalk; nape cirrus present in only 3 species (typically in *edentulus* and *rivulatus*, variably, depending on population, in *meleagris*); upper lip without free dorsal margin; ventral margin of upper lip crenulate or entire; dorsal margin of lower lip crenulate or entire; no cup-shaped fleshy disk or appendage posterior to lower lip; precaudal vertebrae modally 10 or 11; posteriormost epineural articulating with 12th to 22nd vertebra from anteriormost (rarely to 22nd).

Lineatus Species Complex

The most obvious character defining the Lineatus species complex is the well-developed dark or dusky striping that occurs on the bodies of both sexes (well-preserved specimens). Current literature accords only one name, *Istiblennius lineatus*, to specimens in this complex. Among the species of *Istiblennius*, similar, but much fainter, striping occurs only in *Istiblennius rivulatus*, which also shares only with the Lineatus complex in having the last anal-fin ray strongly modally not split to the base. This last character is highly variable among the other *Istiblennius* species, in which the unsplit condition may be common, but never clearly modal. *Istiblennius rivulatus* is readily distinguished from the Lineatus complex by many characters, including, but not limited to, having 12 (versus 14) pectoral-fin rays, simple (versus branched) orbital cirri, and nape cirri (versus nape cirri absent). Other distinguishing characters of the Lineatus complex include: crenulate upper lip and all infraorbital pore positions occupied by simple pores.

We recognize three closely related, allopatric species in the Lineatus complex, *I. lineatus*, *I. pox*, new species, and *I. steindachneri*. The three species are separable only on the basis of a sexually associated combination of color-pattern and meristic characters, although *I. pox*, in general, has the lowest means for meristics (Tables 22 and 23). A first separation of the species is based on the color pattern of the head crest of males. In *I. lineatus* the crest is more or less uniformly dusky, or dusky with an irregular, often bar-shaped, central pale area; in *I. pox* and *I. steindachneri*, the crest in well-preserved specimens always bears several noticeable small, dark spots (Figures 30a, 31a). We believe that the spotted head crest of males is probably a synapomorphy for a *pox-steindachneri* clade because this color pattern does not occur in any other *Istiblennius* or *Blenniella* species, whereas, the *lineatus*-type crest color pattern (uniform or with a pale central area) is the type found, at least, among the other *Istiblennius* species (see Phylogenetic Analysis section, particularly discussion of crest color pattern in *I. colei*).

A complete separation of *I. pox* from *I. steindachneri* is only possible based on females. In female *I. pox*, the body striping is similar to that of males, and the stripes on the caudal peduncle are only slightly interrupted to form dashes or squiggles (Figure 30b). Total dorsal-fin elements in female *I. pox* range from 33 to 35, total vertebrae from 39 to 41, uncommonly 41. Female *I. steindachneri* differ from males (and *I. pox*) in that the color pattern on the caudal peduncle consists of several dark spots or dots (Figure 31b); total dorsal-fin elements are 35 to 38 and total vertebrae 41 to 43. In female *I. lineatus*, the color pattern on the caudal peduncle, although highly variable, differs from that of males. It is usually noticeably spotted, and when males at a locality also have spotted caudal peduncles, the area of the spotting is much more restricted than it is in females from the same locality. Sexual dimorphism involving spotting on the caudal peduncle of females, but not males, is present in several species of *Istiblennius* (e.g., *dussumieri*, *edentulus*) and *Blenniella* (e.g., *periophthalmus*, *cyanostigma*, *interruptus*), but no other salariinin genera, and is possibly a synapomorphy for these 2 genera. Total numbers of dorsal-fin elements and vertebrae in female *I. lineatus* range from 34 to 38 and 39 to 43, respectively.

The body striping of *I. steindachneri* usually distinguishes that species from *I. pox* and often from *I. lineatus*. In *I. steindachneri*, the stripes are restricted to the posterior (roughly 40%) of the body, whereas in the other 2 species the stripes may extend almost the entire length of the body.

The following composite description applies to all 3 species of the Lineatus complex. Data for the 3 species are, however, distinguished in Tables 22–26. After the composite description, we provide brief diagnostic characters and general discussions for each of the species.

COMPOSITE DESCRIPTION OF LINEATUS COMPLEX.—Dorsal fin (Tables 22–24). XII to XIV,20 to 24 = 33 to 38 (formulae XII,20 or 21 or XIV,20 not observed, XIII,20 present only in females; spines modally XIII at all localities, up to 26% of

Table 22.—Frequency distributions for certain characters of male specimens of species of the Lineatus species complex from various localties. Underlined means indicate significant differences between means of sexes from same locality (p ≤.05).

Species/Locality	Total dorsal-fin elements						Segmented anal-fin rays						Total vertebrae							
	34	35	36	37	38	x̄	22	23	24	25	26	x̄	39	40	41	42	43	44	45	x̄
Istiblennius steindachneri																				
Mauritius	-	-	-	2	3	37.8	-	-	1	4	-	24.8	-	-	-	1	4	-	-	42.8
N Madagascar	-	-	3	16	1	36.9	-	-	11	9	-	24.4	-	-	3	13	2	-	1	42.1
Juan de Nova Id	-	-	1	1	-	36.6	-	-	1	1	-	24.5	-	-	-	1	1	-	-	42.5
Zanzibar	-	-	1	-	-		-	-	1	-	-		-	-	-	1	-	-	-	
Kenya	-	-	-	2	-	37.0	-	-	1	1	-	24.5	-	-	-	1	1	-	-	42.5
Istiblennius pox																				
Gulfs of Aden & Tadjoura	1	3	-	-	-	34.8	-	2	2	-	-	23.5	-	4	-	-	-	-	-	40.0
Persian Gulf	9	11	2	-	-	34.7	-	15	7	-	-	23.3	1	15	4	-	-	-	-	40.1
Muscat, G Oman	3	4	-	-	-	34.6	-	4	3	-	-	23.4	-	5	2	-	-	-	-	40.3
Pakistan	1	12	2	-	-	35.1	-	8	7	-	-	23.5	2	9	3	-	-	-	-	40.1
Istiblennius lineatus																				
Maldive Is	-	4	6	1	-	35.7	-	-	7	4	-	24.4	-	5	5	1	-	-	-	40.6
S India & Ceylon	-	6	10	1	-	35.7	-	5	11	1	-	23.8	-	6	10	1	-	-	-	40.7
Moscos Is, Myanmar	-	1	-	-	-		-	-	1	-	-		-	1	-	-	-	-	-	
Nicobar Is	-	2	-	-	-	35.0	-	-	2	-	-	24.0	-	-	2	-	-	-	-	41.0
Cocos-Keeling Is	-	-	10	4	-	36.3	-	11	4	-	-	23.3	-	1	8	5	-	-	-	41.3
Christmas I, Indian O	-	3	8	4	-	36.1	-	4	11	-	-	23.7	-	2	9	4	-	-	-	41.1
Cartier I, Timor Sea	-	2	2	-	-	35.5	-	-	4	-	-	24.0	-	1	3	-	-	-	-	40.8
W Australia, 20-23°S	-	1	21	10	-	36.3	-	-	13	17	2	24.6	-	1	20	9	-	-	-	41.3
Toyohama-ku, Japan	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	-	-	
Tanegashima "	-	-	2	-	-	36.0	-	1	1	-	-	23.5	-	-	1	1	-	-	-	41.5
Okinawa	-	-	3	1	-	36.2	-	-	4	-	-	24.0	-	1	1	1	-	-	-	41.0
N Taiwan	-	-	3	1	-	36.2	-	-	2	2	-	24.5	-	-	3	-	1	-	-	41.5
S Taiwan	-	8	8	3	-	35.7	-	1	16	2	-	24.0	-	4	14	1	-	-	-	40.8
Saipan	-	5	23	-	-	35.8	-	20	8	-	-	23.3	-	4	21	1	-	-	-	40.9
Guam	-	4	1	1	-	35.5	1	4	1	-	-	23.0	-	2	4	-	-	-	-	40.7
Palau	-	1	4	1	-	36.0	-	4	2	-	-	23.3	-	1	3	1	-	-	-	41.0
Philippines, Batan Id	-	2	2	4	-	36.2	-	-	5	3	-	24.4	-	2	4	2	-	-	-	41.0
" Maricaban & Mindoro Is	-	-	6	-	-	36.0	-	-	3	3	-	24.5	-	1	4	1	-	-	-	41.0
" Negros Id	-	10	20	1	1	35.8	-	1	23	8	-	24.2	-	9	20	1	-	-	-	40.7
" Pilas & Simulac Is	-	-	2	-	-	36.0	-	-	1	1	-	24.5	-	-	2	-	-	-	-	41.0
Indonesia bet. 100-135°E	-	3	10	-	-	35.8	-	2	8	3	-	24.1	-	2	8	2	-	-	-	41.0
Madang & vicinity, PNG	-	1	5	-	-	35.8	-	1	5	-	-	23.8	-	1	6	-	-	-	-	40.8
Brumer Id, PNG	-	1	4	-	-	35.8	-	-	3	2	-	24.4	-	1	4	-	-	-	-	40.8
New Britain, PNG	-	-	2	-	-	36.0	-	-	1	1	-	24.5	-	-	1	1	-	-	-	41.5
Pinipel Id, PNG	-	2	1	-	-	35.3	-	1	1	1	-	24.0	-	1	2	-	-	-	-	40.7
Trobriand Is, PNG	-	8	21	1	-	35.8	-	3	22	5	-	24.1	-	5	23	1	-	-	-	40.9
Queensland, 10-18°S	-	3	6	-	-	35.7	-	1	7	1	-	24.0	-	2	7	-	-	-	-	40.8
Guadalcanal	-	8	14	2	-	35.8	-	3	18	3	-	24.0	-	8	14	1	-	-	-	40.7
Santa Cruz Is	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	-	-	
Efate, New Hebrides	-	-	4	12	1	36.8	-	-	12	5	-	24.3	-	-	1	13	2	-	-	42.1
Viti Levu, Fiji	-	-	13	13	-	36.5	-	-	8	14	4	24.8	-	-	8	14	3	-	-	41.8
Niuaf'ou, Tonga	-	-	4	11	1	36.8	-	1	13	2	-	24.1	-	-	4	12	-	-	-	41.8
Tongatapu "	-	-	1	8	-	36.9	-	1	6	2	-	24.1	-	-	2	5	1	-	-	41.9
New Caledonia	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	-	-	
Niue	-	-	-	1	-		-	-	1	-	-		-	-	1	-	-	-	-	
Enewetak, Marshall Is	-	-	3	-	-	36.0	-	1	1	1	-	24.0	-	-	1	-	-	-	-	
Bikini " "	-	-	13	13	-	36.5	-	4	12	10	-	24.2	-	-	14	12	-	-	-	41.5
Rongelap " "	-	-	1	1	-	36.5	-	1	1	-	-	23.5	-	-	1	1	-	-	-	41.5
Arno " "	-	-	14	5	1	36.4	-	1	11	7	1	24.4	-	2	13	5	-	-	-	41.2
Jaluit " "	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	-	-	
Majuro " "	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	-	-	
Onotoa, Gilbert Is	-	-	3	4	-	36.6	-	2	4	1	-	23.8	-	-	4	2	1	-	-	41.6
Funafuti, Tuvalu	-	-	1	-	-		-	-	1	-	-		-	1	-	-	-	-	-	
Swains Id	-	-	2	1	-	36.3	-	2	1	-	-	23.3	-	-	2	1	-	-	-	41.3
Upolu, W Samoa	-	-	2	1	1	36.8	-	-	1	2	1	25.0	-	-	-	4	-	-	-	42.0
Tutuila	-	-	-	3	-	37.0	-	-	-	2	1	25.3	-	-	-	3	-	-	-	42.0
Howland Id	-	-	2	3	-	36.6	-	1	4	-	-	23.8	-	-	4	1	-	-	-	41.2
Phoenix Is	-	-	21	12	-	36.4	-	11	21	1	-	23.7	-	1	25	5	-	-	-	41.1
Tokelau Is	-	-	7	2	-	36.2	-	4	5	-	-	23.6	-	1	8	-	-	-	-	40.9
Caroline, Line Is	-	2	8	8	-	36.3	-	7	12	-	-	23.6	-	1	14	3	-	-	-	41.1
Penrhyn	-	-	9	1	1	36.3	-	6	5	-	-	23.4	-	1	8	2	-	-	-	41.1
Tuamotu Arch	-	-	4	6	-	36.6	-	-	8	2	-	24.2	-	-	2	6	1	-	-	41.9
Mangareva, Gambier Is	-	-	-	1	-		-	-	1	-	-		-	-	1	-	-	-	-	

Table 23.—Frequency distributions for certain characters of female specimens of species of the Lineatus species complex from various localties. Underlined means indicate significant differences between means of sexes from same locality (p ≤.05).

Species/Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae					
	33	34	35	36	37	38	x̄	21	22	23	24	25	x̄	39	40	41	42	43	x̄
Istiblennius steindachneri																			
Mauritius	-	-	-	-	1	2	37.7	-	-	-	-	3	25.0	-	-	-	1	2	42.7
N Madagascar	-	-	-	7	4	-	_36.4_	-	-	3	7	1	_23.8_	-	-	7	3	1	_41.4_
Juan de Nova Id	-	-	1	2	4	-	36.4	-	-	3	2	2	23.8	-	-	2	5	-	41.7
Zanzibar	-	-	-	2	-	-	36.0	-	-	2	-	-	23.0	-	-	1	1	-	41.5
Kenya	-	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	
Seychelles, La Digue	-	-	1	1	-	-	35.5	-	-	1	1	-	23.5	-	-	1	-	-	
Istiblennius pox																			
Dahlak Arch, Red Sea	-	-	2	-	-	-	35.0	-	-	1	1	-	23.5	1	1	-	-	-	39.5
Gulfs of Aden & Tadjoura	-	5	2	-	-	-	34.3	-	1	6	-	-	_22.8_	3	4	-	-	-	39.6
Persian Gulf	2	8	5	-	-	-	_34.2_	-	4	11	-	-	_22.7_	4	9	2	-	-	39.9
Muscat, Gulf of Oman	3	8	2	-	-	-	_33.9_	-	5	6	2	-	_22.8_	6	7	-	-	-	_39.5_
Pakistan	-	5	5	-	-	-	_34.5_	-	1	9	-	-	22.9	4	6	-	-	-	39.6
Istiblennius lineatus																			
Maldive Is	-	-	2	3	-	-	35.6	-	-	2	3	-	_23.6_	-	1	4	-	-	40.8
S India & Ceylon	-	-	7	3	-	-	35.3	-	-	5	5	-	_23.5_	-	6	4	-	-	40.4
NE India	-	-	1	-	-	-		-	-	1	-	-		-	1	-	-	-	
Nicobar Is	-	-	2	-	-	-	35.0	-	-	1	1	-	23.5	-	1	1	-	-	40.5
Andaman Is	-	2	7	1	-	-	34.9	-	-	8	2	-	23.2	-	8	2	-	-	40.4
Cocos-Keeling Is	-	-	14	12	-	-	_35.5_	-	4	20	2	-	_22.9_	-	9	16	-	-	40.6
Christmas Id, IO	-	-	10	6	-	-	_35.4_	-	2	14	-	-	_22.8_	-	4	11	-	-	40.7
Cartier Id, Timor Sea	-	-	2	-	-	-	35.0	-	-	1	1	-	23.5	-	1	1	-	-	40.5
W Australia, 20-23°S	-	-	8	25	2	-	35.8	-	-	8	23	4	23.9	-	4	28	2	-	_40.9_
Tanegashima, Japan	-	-	-	3	-	-	36.0	-	-	1	2	-	23.7	-	1	2	-	-	40.7
Okinawa	-	-	3	8	-	-	35.7	-	-	2	7	2	24.0	-	2	6	1	-	40.9
N Taiwan	-	-	5	3	-	-	_35.4_	-	-	4	3	1	23.6	1	4	3	-	-	_40.2_
S Taiwan	-	-	14	6	-	-	_35.3_	1	1	7	11	-	_23.4_	-	10	10	-	-	_40.5_
Saipan	-	2	13	4	-	-	_35.1_	2	7	7	-	-	22.4	-	12	4	-	-	_40.2_
Rota	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Guam	-	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	
Palau	-	-	9	2	-	-	_35.2_	-	4	7	-	-	22.6	-	6	5	-	-	40.4
Philippines: Batan Id	-	-	8	6	-	-	_35.4_	-	-	5	9	-	_23.6_	-	8	5	-	-	_40.4_
" Maricaban & Mindoro Is	-	-	2	5	1	-	35.9	-	-	5	3	-	_23.4_	-	2	6	-	-	40.8
" Panay Id	-	-	1	2	-	-	35.7	-	-	1	1	1	24.0	-	1	2	-	-	40.7
" Negros Id	-	-	14	16	1	-	35.6	-	-	9	21	1	23.7	-	12	17	2	-	40.7
Indonesia bet. 100-135°E	-	-	9	3	-	-	_35.2_	-	1	4	6	1	23.6	-	5	6	1	-	40.7
Madang & vicinity, PNG	-	-	4	-	-	-	35.0	-	-	1	3	-	23.8	-	3	1	-	-	40.2
Brummer Id, PNG	-	-	2	3	-	-	35.6	-	-	1	4	-	23.8	-	2	3	-	-	40.6
Trobriand Is, PNG	-	-	18	10	-	-	_35.4_	-	1	4	23	-	23.8	-	12	15	1	-	40.6
Pinipel Id, PNG	-	-	1	-	-	-		-	-	-	1	-		-	1	-	-	-	
Port Moresby area, PNG	-	-	-	1	-	-		-	-	-	1	-		-	-	1	-	-	
Queensland, 10-18°S	-	-	6	9	-	-	35.6	-	-	4	11	-	23.7	-	4	11	-	-	40.7
Guadalcanal	-	-	14	10	1	-	35.5	-	-	9	16	1	_23.7_	-	13	12	-	-	40.5
Santa Cruz Is	-	-	3	-	-	-	35.0	-	-	1	2	-	23.7	-	3	-	-	-	40.0
Efate, New Hebrides	-	-	2	33	4	-	_36.0_	-	1	26	11	1	_23.3_	-	1	27	7	-	_41.2_
Viti Levu, Fiji	-	-	3	19	5	-	_36.1_	-	-	2	13	11	_24.3_	-	1	19	7	-	_41.2_
Niuaf'ou, Tonga	-	-	1	6	3	1	36.4	-	-	4	6	1	23.7	-	1	5	4	1	41.4
Tongatapu "	-	-	-	5	4	1	36.6	-	-	1	7	2	24.1	-	-	4	6	-	41.6
Rotuma	-	-	-	1	-	-		-	-	-	1	-		-	-	1	-	-	
Enewetak, Marshall Is	-	-	-	-	1	-		-	-	-	1	-		-	-	-	1	-	
Bikini " "	-	-	2	22	5	-	_36.1_	-	1	20	5	4	_23.4_	-	2	21	7	-	_41.2_
Arno " "	-	-	3	14	2	-	_35.9_	-	-	5	10	4	_23.9_	-	2	13	4	-	41.1
Onotoa, Gilbert Is	-	-	3	5	1	-	_35.8_	-	-	7	2	-	_23.2_	-	3	5	1	-	40.8
Funafuti, Tuvalu	-	-	-	1	-	-		-	1	-	-	-		-	-	1	-	-	
Swains Id	-	-	-	1	-	-		-	-	-	1	-		-	-	1	-	-	
Upolu, W Samoa	-	-	1	3	1	-	36.0	-	-	2	1	2	24.0	-	-	4	1	-	41.2
Howland Id	-	-	1	-	-	-		-	-	1	-	-		1	-	-	-	-	
Phoenix Is	-	-	8	23	2	-	_35.8_	-	1	24	8	-	_23.2_	-	4	24	3	-	41.0
Tokelau Is	-	-	-	7	2	-	36.2	-	1	5	3	-	23.2	-	1	8	-	-	40.9
Caroline, Line Is	-	-	1	7	1	-	36.0	-	1	7	1	-	_23.0_	-	1	7	1	-	41.0
Manihiki	-	-	-	2	-	-	36.0	-	-	-	2	-	24.0	-	1	1	-	-	40.5
Penrhyn	-	-	4	5	-	-	_35.6_	-	2	7	1	-	_22.9_	-	2	6	1	-	40.9
Motu One, Society Is	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Tahiti " "	-	-	-	2	-	-	36.0	-	-	1	-	1	24.0	-	-	1	1	-	41.5
Tuamotu Arch	-	1	2	21	4	-	_36.0_	-	2	16	10	-	_23.3_	-	2	19	7	-	_41.2_
Mangareva, Gambier Is	-	-	-	1	1	-	36.5	-	-	1	1	-	23.5	-	-	-	2	-	42.0

Table 24.—Frequency distributions for certain characters of specimens of the Lineatus species complex from various localities.

Species/Locality	Dorsal-fin spines 12	13	14	Precaudal vertebrae 10	11	Pleural ribs 10	11	12	Dorsal + ventral procurrent caudal-fin rays 10	11	12	13	14	15	16	17	x̄
Istiblennius steindachneri																	
Mauritius	-	5	3	2	6	-	3	5	-	-	5	1	2	-	-	-	12.6
N Madagascar	2	24	5	7	21	1	12	13	-	1	4	5	6	2	-	-	13.2
Juan de Nova Id	-	7	2	2	3	-	2	3	-	-	1	1	6	-	-	-	13.6
Zanzibar	-	3	-	2	-	-	2	-	-	-	-	-	3	-	-	-	14.0
Kenya	1	2	-	1	2	-	1	2	-	-	-	1	2	-	-	-	13.7
Seychelles, La Digue	1	1	-	2	-	-	1	1	-	-	-	1	1	-	-	-	13.5
Istiblennius pox																	
Red Sea	-	2	-	-	2	-	1	1	-	-	-	-	1	1	-	-	14.5
Gulfs of Aden & Tadjoura	-	11	-	10	-	-	10	-	-	-	-	7	3	-	-	-	13.3
Persian Gulf	2	35	-	28	-	-	24	-	-	1	8	14	14	-	-	-	13.1
Muscat, Gulf of Oman	-	19	1	16	3	-	16	2	-	-	7	6	6	-	-	-	12.9
Pakistan	-	25	-	19	-	1	15	2	-	-	3	3	12	-	-	-	13.5
Istiblennius lineatus																	
Maldive Is	1	12	2	9	4	-	12	1	-	-	1	3	7	1	1	-	13.8
India & Ceylon	1	25	2	20	5	-	20	4	-	-	1	12	9	2	-	-	13.5
Moscos Is, Myanmar	-	1	-	1	-	-	1	-	-	-	-	-	-	1	-	-	
Nicobar & Andaman Is	-	13	1	10	2	-	8	1	-	-	2	3	7	-	-	-	13.4
Cocos-Keeling Is	-	36	5	-	34	-	5	31	-	-	-	-	16	12	9	-	14.8
Christmas Id, Indian O	-	32	1	7	20	-	10	17	-	-	-	2	16	7	7	-	14.6
Cartier Id, Timor Sea	-	5	1	1	1	-	5	-	-	-	2	2	2	-	-	-	13.0
W Australia, 20-23°S	-	66	1	42	6	-	38	6	1	3	18	14	29	1	-	-	13.1
Toyohama-ku, Japan	-	1	-	1	-	-	1	-	-	-	-	1	-	-	-	-	
Tanegashima "	-	5	-	1	3	-	1	3	-	-	3	1	1	-	-	-	12.6
Okinawa	1	12	2	4	3	-	6	1	-	-	5	5	9	-	-	-	13.2
N Taiwan	-	11	1	8	3	-	10	1	-	1	1	2	7	-	-	-	13.4
S Taiwan	1	37	2	25	6	-	29	2	-	-	5	7	20	1	-	-	13.5
Saipan	-	48	5	9	32	-	9	23	-	-	-	4	24	9	2	-	14.2
Guam & Rota	-	8	-	-	6	-	6	2	-	-	-	-	4	1	3	-	14.9
Palau	-	16	1	3	13	-	6	8	-	-	-	-	10	3	1	-	14.4
Philippines: Batan Id	-	21	1	13	4	-	12	3	-	-	2	3	15	1	-	-	13.7
" Maricaban & Mindoro Is	1	10	3	6	6	-	8	3	-	-	1	4	9	-	-	-	13.6
" Panay Id	-	3	-	1	-	-	1	-	-	1	-	1	1	-	-	-	12.7
" Negros Id	-	61	2	36	15	-	43	7	-	-	12	13	32	-	1	-	13.4
" Pilas & Simalac Is	-	2	-	2	-	-	2	-	-	-	-	1	1	-	-	-	13.5
Indonesia	-	27	1	19	4	-	18	1	-	-	2	1	12	1	1	-	13.9
Papua New Guinea	3	80	2	49	14	-	58	11	-	-	6	11	51	9	3	-	13.9
Queensland, 10-18°S	1	22	1	8	3	-	6	2	-	1	2	3	13	3	-	-	13.7
Guadalcanal	4	43	2	26	7	-	26	2	-	-	2	6	19	4	-	-	13.8
Santa Cruz Is	-	4	-	4	-	-	4	-	-	-	-	-	3	-	1	-	14.5
Efate, New Hebrides	-	42	14	5	42	-	8	43	-	-	1	5	32	11	6	-	14.3
Viti Levu, Fiji	1	48	3	31	10	-	32	10	-	-	4	11	31	3	3	-	13.8
Tonga	-	34	12	3	24	-	7	24	-	-	-	4	26	6	4	-	14.2
New Caledonia	-	1	-	1	-	-	1	-	-	-	-	-	-	-	-	-	
Niue	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	
Rotuma	-	1	1	1	-	-	1	-	-	-	-	1	-	-	-	-	
Enewetak, Marshall Is	-	3	1	-	2	-	1	3	-	-	-	-	3	-	1	-	14.5
Bikini " "	-	48	8	13	41	-	17	37	-	-	5	5	21	11	11	-	14.3
Rongelap " "	-	1	1	-	2	-	1	1	-	-	-	-	1	1	-	-	14.5
Arno " "	1	34	4	10	11	-	13	11	-	-	7	5	22	3	1	-	13.6
Jaluit " "	-	1	-	1	-	-	1	-	-	-	-	-	1	-	-	-	
Majuro " "	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	
Onotoa, Gilbert Is	-	16	-	-	16	-	1	15	-	-	-	2	9	3	1	-	14.2
Funafuti, Tuvalu	-	2	-	-	2	-	2	-	-	-	-	-	-	2	-	-	15.0
Swains Id	-	3	1	-	2	-	1	1	-	-	-	-	1	1	2	-	15.2
Upolu, W Samoa	-	9	2	4	3	-	4	4	-	-	-	1	5	3	-	-	14.2
Tutuila	-	2	1	1	2	-	1	2	-	-	-	1	2	-	-	-	13.7
Howland Id	-	6	-	1	3	-	2	3	-	-	-	-	2	2	2	-	15.0
Phoenix Is	2	57	7	2	47	-	7	36	-	-	-	1	21	24	10	-	14.8
Tokelau Is	-	18	-	1	11	-	2	10	-	-	-	-	7	7	2	-	14.7
Caroline, Line Ids	-	26	2	2	24	-	9	17	-	-	-	1	14	12	1	-	14.5
Manihiki	-	2	-	-	1	-	-	1	-	-	-	-	-	2	-	-	15.0
Penrhyn	-	18	3	2	12	-	2	13	-	-	-	1	6	4	5	-	14.8
Motu One, Society Is	-	2	1	1	2	-	1	2	-	-	-	1	-	1	-	-	14.0
Tuamotu Archipelago	-	29	9	2	30	-	5	28	-	-	-	3	15	11	4	1	14.6
Mangareva	-	3	-	-	3	-	-	2	-	-	-	2	1	-	-	-	13.3

Table 25.—Frequency distributions for condition of posteriormost anal-fin ray in specimens of the Lineatus species complex from various localities or areas; (N = simple; S = split to base).

Species/locality or area	Anal-fin ray		%S
	N	S	
Istiblennius steindachneri			
Mauritius	8	-	0
N Madagascar	20	2	9.1
Juan de Nova Id	8	1	11.1
Zanzibar	3	-	0
Kenya	3	-	0
Seychelles, La Digue	2	-	0
Istiblennius pox			
Red Sea	2	-	0
Gulfs of Aden & Tadjoura	8	3	27.3
Persian Gulf	25	11	30.6
Muscat, Gulf of Oman	16	4	20.0
Pakistan	20	5	20.0
Istiblennius lineatus			
S India & Ceylon	14	1	6.7
Maldive Is	14	-	0
Nicobar Is	4	-	0
Andaman Is	8	2	20.0
Cocos-Keeling Is	39	0	0
Christmas Id, Indian O	27	5	15.6
Cartier Id, Timor Sea	6	0	0
Western Australia	61	6	9.0
Japan	5	1	16.7
Okinawa	14	1	6.7
Taiwan	46	4	8.0
Saipan	41	5	10.9
Guam	6	1	14.3
Palau	15	2	11.8
Philippines	85	6	6.6
Irian Jaya, Indonesia	2	-	0
Sulawesi "	2	-	0
Bali "	1	-	0
Morotai "	2	-	0
Ambon & Nusa Laut "	4	3	42.8
Flores "	3	-	0
Timor "	3	-	0
Bengkulu, Sumatra "	-	2	100
Papua New Guinea	75	8	9.6
Queensland	20	2	9.1
Guadalcanal	42	4	8.7
Santa Cruz Is	4	-	0
Efate, New Hebrides	47	8	14.5
Viti Levu, Fiji	44	4	8.3
Tonga Is	38	8	17.4
New Caledonia	1	-	0
Niue	1	-	0
Rotuma	1	-	0
Marshall Is	93	9	8.8
Onotoa, Gilbert Is	13	3	18.8
Funafuti	2	-	0
Swains Id	3	1	25.0
Upolu, W Samoa	9	-	0
Tutuila	3	-	0
Howland Id	6	-	0
Phoenix Is	65	5	7.1
Tokelau Is	18	1	5.3
Caroline (Line Is)	27	1	3.6
Manihiki	2	0	0
Penrhyn	14	3	17.6
Society Is	3	-	0
Tuamotu Arch	30	6	16.7
Mangareva	3	-	0

Table 26.—Frequency distributions for total number of mandibular sensory pores[1] in specimens of the Lineatus species complex from various localities.

Species/Locality	Total mandibular pores							Locality	Total mandibular pores						
	8	9	10	11	12	13	$\bar{x}$		8	9	10	11	12	13	$\bar{x}$
Istiblennius steindachneri								I. lineatus continued							
Mauritius	-	-	-	-	8	-	12.0	Indonesia	-	-	1	5	17	-	11.7
N Madagascar	-	1	4	5	21	-	11.5	Papua New Guinea	-	-	3	13	64	-	11.8
Juan de Nova Id	-	-	-	2	6	-	11.8	Queensland	-	-	-	2	22	-	11.9
Zanzibar	-	-	-	-	2	-	12.0	Guadalcanal	-	-	-	9	41	-	11.8
Kenya	-	-	-	1	2	-	11.7	Santa Cruz Is	-	-	-	2	2	-	11.5
Seychelles, La Digue	-	-	1	1	-	-	10.5	Efate, New Hebrides	-	-	1	4	32	-	11.8
Istiblennius pox								Viti Levu, Fiji	-	2	3	9	38	-	11.6
Red Sea	-	-	-	2	-	-	11.0	Tonga Is	-	-	-	3	37	-	11.9
Gulfs of Aden & Tadjoura	-	1	1	2	7	-	11.4	New Caledonia	-	-	-	-	1	-	
Persian Gulf	2	2	17	6	10	-	10.5	Niue	-	-	-	1	-	-	
Muscat, Gulf of Oman	-	1	5	8	4	-	10.8	Pakistan	-	3	8	6	8	-	10.8
Pakistan	-	3	8	6	8	-	10.8	Rotuma	-	-	-	1	-	-	
Istiblennius lineatus								Enewetak, Marshall Is	-	-	-	1	3	-	11.8
S India & Ceylon	-	-	-	2	15	1	11.9	Bikini, Marshall Is	-	1	1	7	47	-	11.8
Maldive Is	-	-	-	3	12	-	11.8	Rongelap, Marshall Is	-	-	-	-	2	-	12.0
Moscos Is, Myanmar	-	-	-	-	1	-		Arno, Marshall Is	-	1	4	10	20	-	11.4
Nicobar Is	-	-	-	1	2	-	11.7	Jaluit, Marshall Is	-	-	-	-	1	-	
Andaman Is	-	-	-	2	8	-	11.8	Majuro, Marshall Is	-	-	-	-	1	-	
Cocos-Keeling Is	-	-	-	1	40	-	12.0	Onotoa, Gilbert Is	-	-	-	2	14	-	11.9
Christmas Id, Indian O	-	-	-	1	29	1	12.0	Funafuti	-	-	-	-	2	-	12.0
Cartier Id, Timor Sea	-	-	-	1	5	-	11.8	Swains Id	-	-	-	-	4	-	12.0
Western Australia	-	-	4	8	55	-	11.8	Upolu, W Samoa	-	-	-	1	7	-	11.9
Toyohama-ku, Japan	-	-	-	-	1	-		Tutuila	-	-	-	-	3	-	12.0
Tanegashima, Japan	-	-	-	-	4	-	12.0	Howland Id	-	-	-	-	6	-	12.0
Okinawa	-	-	1	1	13	-	11.9	McKean, Phoenix Is	-	-	-	-	1		
N Taiwan	-	1	1	1	9	-	11.5	Canton, Phoenix Is	-	-	-	-	14	-	12.0
S Taiwan	-	-	2	4	33	-	11.8	Enderbury, Phoenix Is	-	-	-	-	2	-	12.0
Saipan	-	-	-	2	32	-	11.9	Orona, Phoenix Is	-	-	1	6	39	-	11.8
Rota	-	-	-	-	1	-		Tokelau Is	-	-	-	1	17	-	11.9
Guam	-	-	-	-	7	-	12.0	Line Is (Caroline)	-	-	-	-	28	-	12.0
Palau	-	-	-	2	14	-	11.9	Manihiki	-	-	-	1	1	-	11.5
Philippines: Batan Id	-	-	2	-	20	-	11.8	Penrhyn	-	-	-	1	20	-	11.9
" Maricaban & Mindoro Is	-	-	1	1	19	-	11.8	Motu One, Society Is	-	-	-	-	1	-	
" Panay Id	-	-	-	-	3	-	12.0	Tahiti, Society Is	-	-	-	-	2	-	12.0
" Negros Id	-	-	1	6	31	-	11.8	Tuamotu Archipelago	-	-	1	3	44	-	11.9
" Pilas & Simalac Is	-	-	-	-	2	-	12.0	Mangareva	-	-	-	-	3	-	12.0

[1]right + left sides; combinations, independent of side, are: 3/5, 4/4, 4/5, 4/6, 5/5, 5/6, 6/6, 6/7

specimens from some localities with spines XIV); mean number of total elements usually higher for males than for females (higher for 38 of 42 localities for which means for both sexes are available, statistically significantly higher for 22 of the 38 localities); membrane between spinous and segmented-ray portions notched deeper than half, usually more than three-fourths, length first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle well anterior to caudal-fin base (usually in specimens <50mm SL) to point on dorsal edge of caudal fin well distal to base of fin (up to 28% length of fin in males, 15% in females).

Anal fin (Tables 22, 23, 25). II or III,21 to 26 (III in only 2 specimens of I. lineatus of over 1000 examined for character); mean number of segmented anal-fin rays usually higher for males than for females (higher for 37 of 42 localities for which

means for both sexes are available, statistically significantly higher for 26 of the 37 localities); posteriormost ray usually not split to base, when split, posterior element of split ray well developed; terminal ray bound by membrane to caudal peduncle in only 2.8% of 657 specimens examined for character. Skin covering anal-fin spines and distal half of rays of presumably mature males slightly swollen subdistally (only 3 males with anteriormost segmented rays both swollen distally and with faintly crinkled edges: Christmas Island, Indian Ocean, 96 mm SL; Sri Lanka, 111 mm SL; Tongatapu, Tonga, 117 mm SL).

Pectoral-fin rays 13 to 15, rarely 15 (14 bilaterally in 90%, unilaterally in 8%, of 449 specimens examined for character; 15 bilaterally in only 1 specimen).

Pelvic-fin segmented rays 3.

Caudal fin. Dorsal procurrent rays 5 to 9, ventral procurrent

rays 4 to 9 (4,5, or 9 dorsal or ventral rays in less than 1% of over 1,100 specimens examined for these characters; combination of 7 dorsal and 7 ventral procurrent rays in 52% of specimens), total procurrent rays 10 to 17 (modally 13 or 14 at almost all localities, Table 24); segmented rays 13 (14 in 1 specimen of over 340 examined for character).

Vertebrae (Tables 22-24). 10 or 11+29 to 34 = 39 to 43,45 (combination of 10+33 only in *I. lineatus* males; 11+34 only in 1 *I. steindachneri* male; 10+29 not present in *I. lineatus* or *I. steindachneri* males; 11+32 not in females of *I. pox* or *I. steindachneri*); mean number of total vertebrae usually higher for males than for females (higher for 39 of 42 localities for which means for both sexes are available, statistically significantly higher for 13 of the 39 localities); posteriormost pleural rib on 10th to 12th from anteriormost vertebra (10th in only 1 specimen each of *I. pox* and *I. steindachneri*), rib often present only as small bony fragment; posteriormost epineural on 13th to 22nd from anteriormost vertebra (on 13th or 22nd centrum in only 1 specimen each of over 800 specimens of *I. lineatus* examined for character; on 16th to 19th vertebra in 76 to 89% of specimens of each species examined for character).

Cirri. Nape cirrus absent. Orbital cirrus variable, usually short-to-elongate triangular flap with short branches on lateral and medial edges (branches few or absent in specimens <40 mm SL), rarely as long as orbital diameter (usually <half diameter). Nasal cirrus short, palmate, usually with fewer than 8 branches (usually simple in specimens <40 mm SL).

Lateral line. Continuous canal anterodorsally with simple pores, extending posteriorly to point between verticals from 4th and 9th dorsal-fin spines (to between 6th and 8th spines in 95% of 576 specimens examined for character), then continuing as 1 to 12 short, disconnected, horizontally bi-pored canals (tubes) in skin to point between verticals from 6th dorsal-fin spine and 5th dorsal-fin ray (rarely as few as 1 or more than 9 tubes, 4 to 8 tubes in 90% of 569 specimens examined for character); posteriormost tube in area between verticals from 10th spine and 2nd segmented ray in 89% of 583 specimens examined for character); lateral line, including tubes, variably descending to midline of body, but often failing to continue posteriorly after reaching midline.

Mandibular pores 3 to 7 (rarely 3 or 7 and only unilaterally; 6 bilaterally in 81% of 1188 specimens examined for character); total mandibular pores 8 to 13 (rarely 8 or 13; Table 26).

Five to 7 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (6 pore positions in 88% of 165 specimens examined for character); all positions with simple pores (no pairs of pores at any position).

Ventral margin of upper lip crenulate; dorsal margin of lower lip entire.

Posterior dentary canines absent in both sexes.

Blade-like fleshy crest on head dorsally of males (smallest available *I. pox* male, 26.5 mm SL, lacks crest, next smallest,

39.5 mm, has crest; smallest available *I. steindachneri* male, 41.7 mm SL, and all others have crest; crest recognizable in *I. lineatus* males as small as 26.1 mm SL, although males as large as 31.6 mm SL may show little or no indication of crest). Females lack well-developed crests, but some *I. pox* females >70 mm SL exhibit thin, median ridge up to 1.2 mm high on head dorsally, and some *I. lineatus* females >64 mm SL have low crest-like ridges, although never so well developed as may occur in *I. pox*.

Color pattern (in preservative). Males (Figures 30a, 31a, 32a, 33a,b). Head: varying from irregularly dusky without distinct marks to bearing various dark markings, including: diffuse spot on midposterior border of orbit; 1 or 2 fine, long, more or less vertical lines or columns of slashes on cheek anterior to opercular region; 1 or 2 lines extending from below orbit across corner of upper lip; fine marks on opercle; 1 or 2 incomplete, diffusely indicated chevrons restricted laterally on ventral surface of head; 2 small, faint, diffuse spots on anterior margin or orbit (seen in frontal view of snout), another slightly mesial to anterior nostril, and ∩-shaped mark surrounding bright, pale area (usually only ∩ present, faintly indicated); fleshy occipital crest with noticeable dusky spots (*pox* and *steindachneri*) or more or less uniformly dusky, often paler centrally (*lineatus*)[2].

Body. "Lineatus" type pattern (applies to all three species). Up to 9 dark stripes (usually fewer than 8) present; stripes absent on anterior half of body in *steindachneri*, variably absent on anterior half in *lineatus* and *pox;* stripes often coalescing, separating, and breaking into dashes, spots, or squiggles on caudal peduncle of *lineatus*, usually more consistent in *pox* and *steindachneri*. Up to 6 pairs of distinct or diffuse, dark saddles along dorsal body contour (2 pairs below spinous portion of dorsal fin, 4 pairs below segmented-ray portion), faint, disconnected continuations of saddles variously present along midside. "Hasselti" type pattern (applies only to *lineatus* and *pox*): similar to "lineatus" type pattern, but stripes broader, sometimes comprising dusky middle portion with slightly darker dorsal and ventral margins; all markings less discrete than in "lineatus" type pattern.

Fins. Dorsal fin varying from variably dusky with indistinct markings to having several oblique, dark stripes, those in spinous portion and basal half of segmented-ray portion relatively widely spaced, becoming closely spaced in distal third of segmented-ray portion; occasionally, dark, narrow, subdistal stripe, margined by pale, distal tips of rays, in segmented-ray portion of fin. Anal fin diffusely dusky, paler ventrally, darker distally. Pectoral fin unmarked, fleshy base with slender, dark, irregularly vertical mark, another, smaller,

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[2]Observations based on photographs of freshly collected specimens and on the same specimens years later, indicate that in many old or poorly preserved specimens (particularly those maintained in isopropanol) the crest spots of *I. pox* and *I. steindachneri* may become faint and disappear, leaving the crest more or less uniformly dusky, hence, inseparable from that of *I. lineatus*.
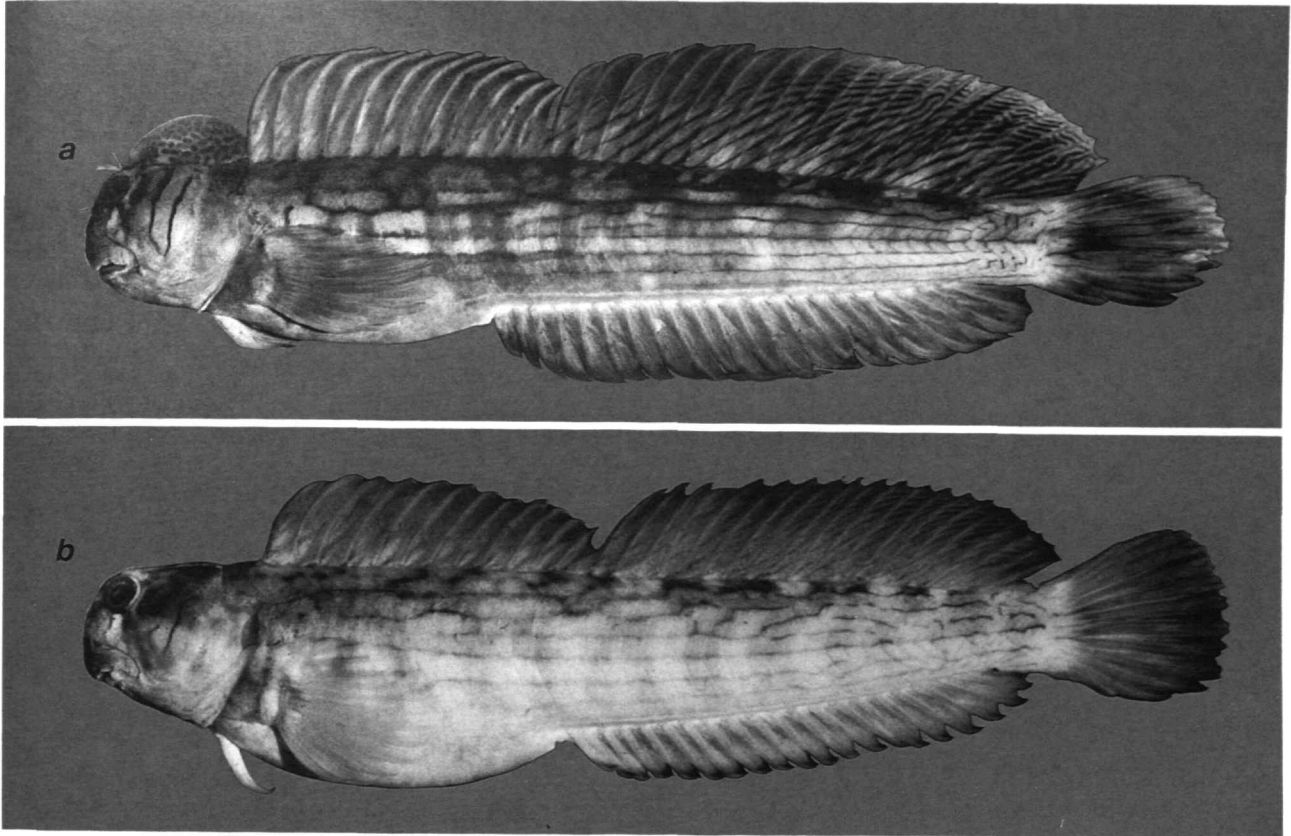
FIGURE 30.—*Istiblennius pox*, new species, BPBM 30428, Jana Id, Persian Gulf: *a*, male, 104 mm SL; *b*, female, 87 mm SL (made from color photograph of fresh specimens taken by L. McCarthy).

at bases of central fin rays. Pelvic fin dusky, unmarked. Caudal fin with 2 narrowly, vertically separated, dark, variably diffuse stripes originating at central base of fin, extending about one-third to one-half fin length before converging; diffuse subdistal dusky area on dorsal half of fin, curving ventrally around posterior end of fin, continuing length of ventral portion of fin; subdistal dusky area occasionally broken into vermiculations.

Females (Figures 30*b*, 31*b*, 32*e*, 33*c*). Generally similar to males except dark markings often less distinct, variably absent. Other noticeable differences from males: body stripes less coherent posteriorly in *lineatus* and *steindachneri*, usually broken into rows of spots well anterior to caudal peduncle; almost no indications of stripes in *steindachneri*; oblique stripes in segmented-ray portion of dorsal fin rarely crowded distally; dorsal subdistal portion of caudal fin rarely vermiculated; *steindachneri* females >98 mm SL from Juan de Nova Island with numerous, small, irregularly shaped black spots on head dorsally and body anteriorly, spots most dense in largest females (spots also present in males from same locality, but so

reduced in size and number as to be almost not visible).

Useful published illustrations include the following. *Istiblennius lineatus:* Allen and Steene (1988, fig. 410, male, Christmas Island, Indian Ocean), Masuda et al. (1975:88, fig. J, male, southern Japan), Masuda et al. (1984, pl. 269: fig. E, male, southern Japan), McCulloch and McNeill (1918, pl. 4: fig. 1, male, New Hebrides), Randall et al. (1990:285, male [Cape Croisilles, Papua New Guinea]), Schultz and Chapman (1960, pl. 117A, male, no locality), Shen (1984, figs. 392-12a,c males; fig. 392-12b, female, Taiwan), Shen et al. (1986, fig. 36a, male; fig. 36b, female, Taiwan); *I. steindachneri:* Pfeffer (1893a, pl. 3: fig. 3; 1893b, pl. 3: fig. 3, male, Zanzibar), Smith, J.L.B. (1959:245, fig. 8, male, Isla Juan de Nova; fig. 9, female, Delagado, Mozambique).

Live coloration. Based on color photographs published by Allen (1985, fig. 391, males and females, *I. lineatus,* Kendrew Island, Dampier Archipelago, Western Australia), Myers (1989, pl. 115, *I. lineatus,* as "*Istiblennius* sp.," male, Guam), and Stanaland (1991:48, bottom figure, *I. pox,* as "*Istiblennius lineatus,*" male and female, [Jana Island, Arabian Gulf,

FIGURE 31.—*Istiblennius steindachneri:* USNM 296472, Nossi Be, Madagascar: *a*, male, 82 mm SL; *b*, female, 68 mm SL (photographs by T.B. Griswold).

Stanaland, pers. comm.]). Dark and dusky markings on body and fins mostly tones of brown or brownish purple; pale markings on head and body often brilliant white, of which following especially obvious: white spot anterior to each nostril (diagnostic for complex), wide, white bar below eye, pale bar on fleshy pectoral-fin base; small, coppery-brown spots in interorbital region; interradial membranes of dorsal and pectoral fins, pinkish-tinged, except slender, pale distal margin of dorsal fin; pelvic fins white (anal fin not visible in illustrations); caudal fin variably pale dusky, similar to preserved pattern, and/or with pinkish tinged membranes; based on several color slides taken of freshly preserved specimens of both species, pale areas on body and fins tinged with yellow.

Size. In large samples from any locality, largest specimen usually male; males attaining larger size than females. Largest male *I. lineatus*, 140 mm SL, from Niue, next largest, 122 mm SL, from Tongatapu, only 15 males ≥100 mm available; largest female, 112 mm SL, from Bikini, only 6 females ≥100 mm available. Largest male *I. pox*, 119 mm SL, from Jana Island, Arabian Gulf, only 6 males ≥100 mm available; only 2 females, both 101 mm, over 100 mm SL, from Jana Island. Largest male *I. steindachneri*, 131 mm SL, from Juan de Nova Island, only 3 other males >99 mm available; largest female, 120 mm SL, from Juan de Nova.

Ophioblennius and early metamorphosed stages (Figures 4c, 6d). Only 3 ophioblennius-stage specimens known (17.8, 19.6, 19.8 mm SL), all *Istiblennius lineatus*, part of lot (USNM 317505) comprising 47 small specimens, 17.3 to 39.2 mm SL, obtained near Rabaul, New Britain. Ophioblennius stages with crenulae on upper lip, single, relatively tiny, laterally recurved canine on each side of lower jaw, narrow, darkly pigmented distal margin on pectoral fin (Figure 6d), diffuse indications of pattern of dusky markings on head, and faint indications of pairs of dusky saddles on dorsal body contour. Among other specimens in lot, 12 specimens, 18.4 to 20.2 mm SL, appear newly metamorphosed in lacking recurved canines, but having various amounts of dark pigment on distal margin of pectoral fin and very little color pattern on body. Remaining 28 specimens in same lot, 17.3 to 39.2 mm, lack canines and dark marginal pigment on pectoral fins, but vary from having little to considerable body pigmentation in form of irregular bands; 39.2 mm specimen, male, with faint indications of 2 or 3 stripes on body; specimens ≤25 mm SL of indeterminable sex.

Many apparently recently metamorphosed specimens (no canines, but pigmented pectoral fins) are available from widely separated Pacific localities. These range in size from 17.1 to 20.5 mm SL. The smallest specimens without pigmented pectoral fins are 17.3 mm SL. In contrast to the specimens from Rabaul, one non-ophioblennius-stage specimen (UF 31296),
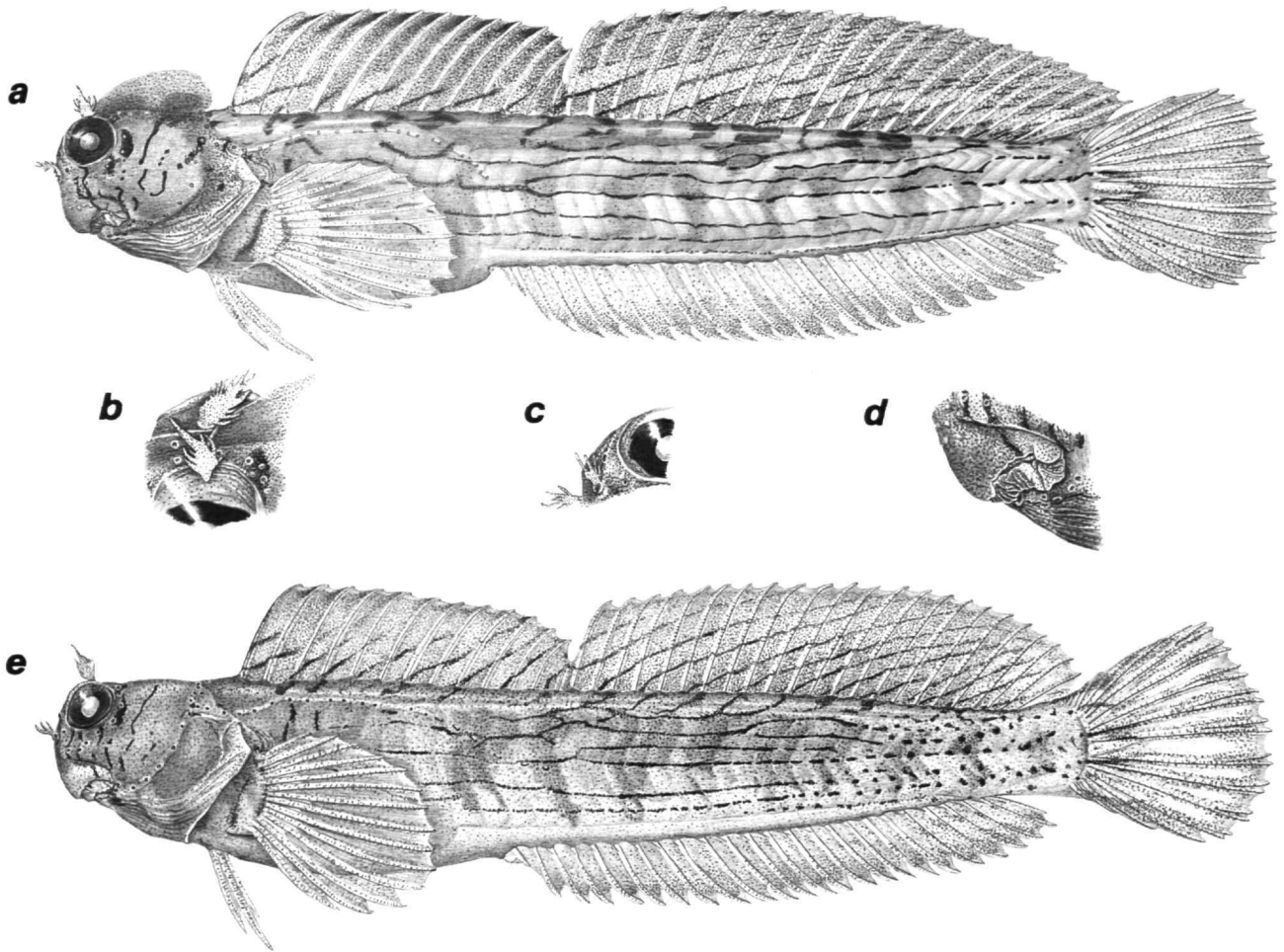
FIGURE 32.—*Istiblennius lineatus*, USNM 227347, Bonarua Id, Brumer Is, Papua New Guinea: *a-d*, male, 71 mm SL, lateral view and details of orbital and nasal cirri and upper lip; *e*, female, 65 mm SL (drawing by P.K. Hollingsworth).

18.4 mm SL, from Flores, Indonesia, has well-developed melanic pigment distally in the pectoral fins, the head almost uniformly dusky, and numerous dusky bars on the body midside and along the dorsal body contour.

ECOLOGY.—All three species appear to have similar ecological preferences, occurring primarily intertidally and at depths less than 1 m. Stanaland (1991:48) reported that *I. pox* (as *I. lineatus*) can forage on land at night, which he documented with a photograph. Similar behavior probably holds for both *I. lineatus* and *I. steindachneri*.

COMPARISONS AND INTERRELATIONSHIPS.—The species of the Lineatus complex are compared under the general account of the complex at the beginning of this section. We do not have a strong suggestion as to what the probable sister group

(species) of the complex might be and our phylogenetic analysis (Figure 60; see discussion under this section) was similarly inconclusive. Pfeffer (1893a,b) included a specimen of *I. dussumieri* among the syntypes of his *Salarias steindachneri*, with a comment that the specimen was probably a variety (or variant). Before we were aware of the identity of Pfeffer's "variety," we intuited that *I. dussumieri* might be the sister species to the Lineatus complex, but we had only vague color-pattern characters that might support our intuition. The color-pattern of the caudal fin of many mature males of the complex and that of mature males of *I. dussumieri* are similar and not shared with males of other species (compare descriptions in the two pertinent accounts; also compare uppermost figures on facing pages 384 and 385 in Randall et
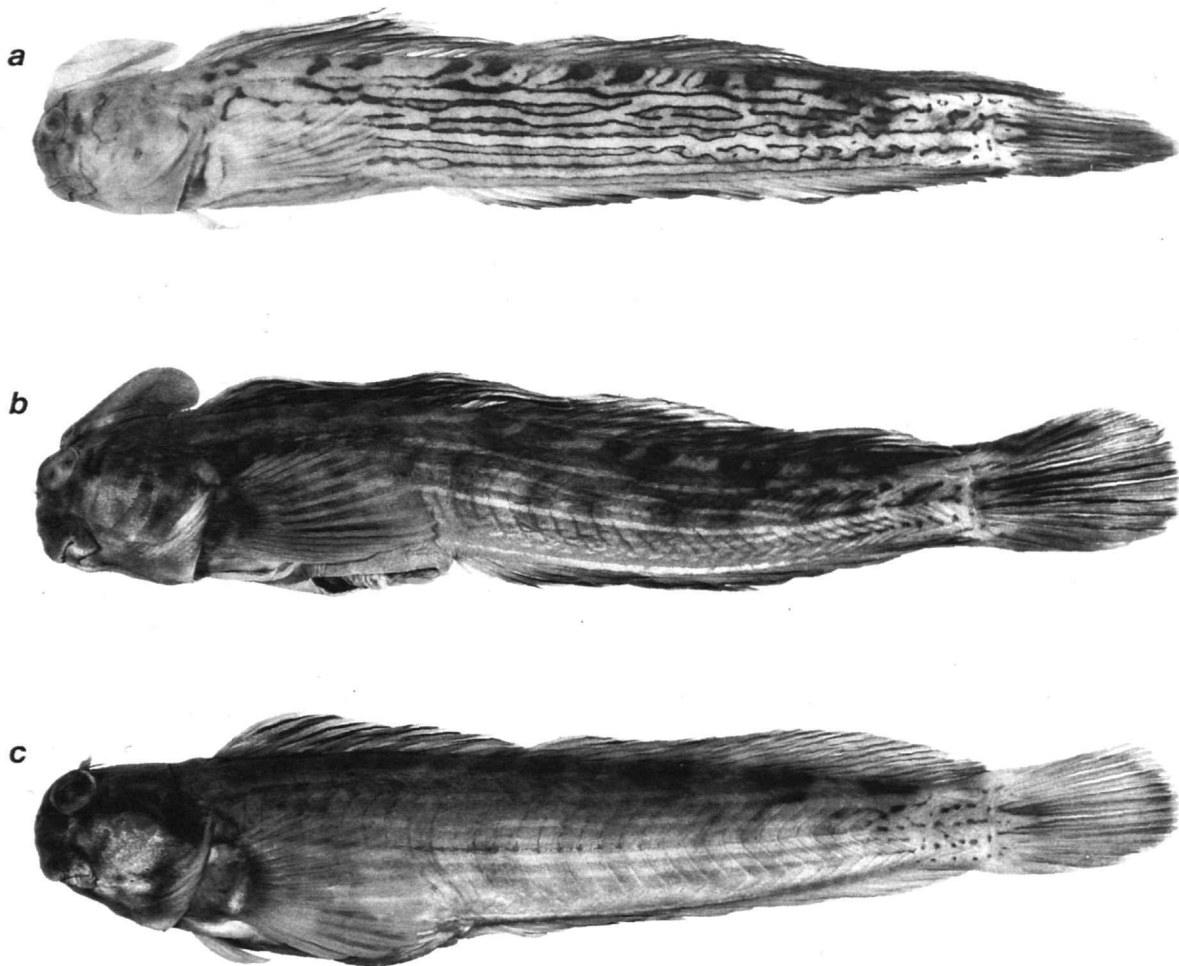
FIGURE 33.—*Istiblennius lineatus: a,* USNM 256439, male, 88 mm SL, Yangasa, Lau Is, Fiji (example of extreme complexity of striping); *b,c,* Christmas Island, Indian Ocean, *hasselti*-type color pattern: *b,* WAM P.28989-007, male, 81 mm SL, right side reversed; *c,* WAM P.29014-002, female, 76 mm SL (photographs by T.B. Griswold).

al., 1990), but are difficult to equate objectively. Partially faded Lineatus complex females that have lost the stripes on the body are somewhat similar in appearance to female *dussumieri*. The only species of *Istiblennius* that exhibits similar longitudinal stripes on the body, and these are only faintly manifested, is *I. rivulatus.* The caudal-fin color pattern and body stripes ultimately may be useful in hypothesizing the interrelationships of the species of *Istiblennius.*

Istiblennius pox, new species

FIGURE 30

DIAGNOSIS (see also Tables 22 to 26).—A species of the Lineatus complex in which males have spotted occipital crest; females lack crest or, rarely, have low ridge-like crest; color pattern on caudal peduncle of both sexes consisting of fine, dark lines, dashes, and/or squiggles; dark stripes usually

present on anterior half of body of both sexes; total dorsal-fin elements of males 34 to 36 (usually 34 or 35), of females 33 to 35; total vertebrae 39 to 41 (usually 40 or 41 in males, 39 or 40 in females).

HOLOTYPE.—USNM 296480, male, ~98 mm SL, tidepools at Boleiji Pt (Karachi), Pakistan, 3 March 1978, S.M. Shamsul Hoda. Dorsal fin XIII,22, attached to point out on dorsal edge of caudal fin 23.3% length of fin; anal fin II,24, last ray not split to base, free from caudal peduncle; pectoral fins 14/14; vertebrae 10+31; caudal fin 13, dorsal and ventral procurrent rays each 7; terminal pleural rib on 11th vertebra; terminal epineural on 19th vertebra; continuous portion of lateral line extending posteriorly to vertical from between 7th and 8th dorsal-fin spines; 6 bi-pored lateral-line tubes in skin, posteriormost below vertical from 12th dorsal-fin spine; mandibular pores 5/5.

ETYMOLOGY.—Pox is a varietal spelling of the English pocks, an eruptive disease such as chicken pox, referring also to spots resembling the disease eruptions, and, in the present case, to the spots on the occipital crest of males of the species; here used as a noun in apposition.

COMPARISONS.—See discussion beginning with second paragraph in introductory section on Lineatus species complex.

DISTRIBUTION (Figure 68).—*Istiblennius pox* is distributed from the Persian Gulf, southeastern Pakistan, and northern Arabian Gulf, westward to the gulfs of Aden and Tadjoura and into the southernmost Red Sea. Day (1876:332, as *Salarias lineatus*) reported *I. pox* from the Red Sea, without specific locality, and Giglioli (1888:70, also as *S. lineatus*) reported it from Assab, which is just northwest of the entrance to the Red Sea. We have seen only two specimens (both females) from the Red Sea, Dahlak Archipelago, off the coast of Eritrea. In the Red Sea, the species appears to be restricted to the southernmost portion, and is possibly a recent immigrant. Of possible significance is its replacement in the northern half of the Red Sea by the possibly related *I. rivulatus*, which is restricted to that area.

Day (1876:332 and pl. 70: fig. 8) reported *Istiblennius pox* (as *Salarias lineatus*) from the Andaman Islands and Red Sea, and illustrated a male with a spotted crest, which he claimed was from the Andamans. The lowest count he reported for number of segmented dorsal-fin rays in his specimens occurs only in female *I. pox*, among specimens of the species in the Lineatus complex. He also reported *I. lineatus* (as *Salarias hasselti*) from the Andamans, and the fin formulae he provides are similar to those of the female specimens of *I. lineatus* that we examined from the Andamans (we saw no males of the Lineatus complex from the Andamans). We believe that the Andaman Islands locality Day reported for *I. pox* is erroneous, and possibly based on his Red Sea specimens, although, as far as we know, the distribution of *I. pox* in the Red Sea is restricted to the southernmost coasts.

MATERIAL EXAMINED.—(Holotype indicated, all other specimens are paratypes). G of Aden: Djibouti, BPBM 21560 (2), MNHN 1904-320-22 (3); just outside G of Tadjoura, MNHN 1977-738 (1); Mait Id, Somalia, USNM 287031 (2). G of Tadjoura: MNHN 1897-317 (1), 1960-69 (1), 1977-703 (1). G of Oman: Khor Fakkan, USNM 217344 (13); Musandam, BPBM 34466 (1); Muscat, BMNH 1988.12.29.154-61,163-65 (11), MNHN 1987-132-8 (7), USNM 217352 (1); S Sidab, BPBM 21352 (1). Persian G: Farur Id, ZMUC CN6-9 (4); Henjam Id, BMNH 1932.2.18.35-7 (3); Jana Id, BPBM 30428 (16). Pakistan: Astola Id, USNM 200206 (19, including 1 cleared and stained), 216127 (1); Boleji Pt, USNM 296477 (1), 296480 (holotype), 296481 (3).

Istiblennius steindachneri (Pfeffer), new combination

FIGURE 31

Salarias steindachneri Pfeffer, 1893a:143; 1893b:15 [ZMH 410, Insel Baui, ♂ and 2 ♀♀ (conspecific), and ZMH 18076, Tumbatu, ♀ (= *I. dussumieri*); lectotype, ♂, ZMH 410, Insel Baui, designated below].

DIAGNOSIS (see also Tables 22 to 26).—A species of the Lineatus complex in which: males have spotted occipital crest; females lack crest; color pattern on caudal peduncle of males consisting of dark stripes, which are restricted to posterior 45% of body; pattern on peduncle of females consisting of dark spots, which may also be present anterior to peduncle; dark pinstripes of females restricted to posterior 45% of body excluding spotted area; total dorsal-fin elements of males 36 to 38, of females 35 to 38; total vertebrae 41 to 43,45 (both sexes; 45 in only one male).

DISTRIBUTION (Figure 68).—*Istiblennius steindachneri* is distributed from Kenya south to Mozambique, on the east African coast. It also occurs at Juan de Nova (island off midwestern Madagascar), northern Madagascar, Mauritius, and La Digue, Seychelles. It, like *I. lineatus*, is also notably absent from the Chagos Islands, which are intermediate between the distributions of *steindachneri* and *lineatus*. Smith (1959:245, as *Halmablennius lineatus*) reported that *I. steindachneri* was rare in the western Indian Ocean, and, except for northern Madagascar, his observations seem to hold.

NOMENCLATURAL DISCUSSION.—Pfeffer's description of *Salarias steindachneri* appeared twice in 1893. The descriptions are identical, not only in content and organization, but also in layout on the journal pages. We do not know which description appeared first. The description we list as 1893a, bears the page numbers (143-145) in large type in the upper corners of the pages and, additionally, the numbers 14-16 at the bottom center of the pages in smaller type. The 1893b description lists only the numbers 14-16 in large type in the upper corners of the pages. For nomenclatural purposes, it does not matter which description appeared first, and we arbitrarily

assign priority to the one we list as 1893a.

Pfeffer based his description on a male, which he illustrated, and three females. Two females and the male were collected at Insel Baui (Zanzibar) and are cataloged as ZMH 18076. The other female was collected at Tumbatu, a small island adjacent to Zanzibar, and is cataloged as ZMH 410. Pfeffer believed that the Tumbatu specimen was a variety of *I. steindachneri*; it is, however, identifiable as *I. dussumieri*. We herewith designate the male, 110 mm SL, from Insel Baui, as lectotype of *Salarias steindachneri*.

MATERIAL EXAMINED.—Seychelles: La Digue, RUSI 37079 (2). Mauritius: MNHN 1990-700 (1), RUSI 33236 (7). Madagascar: Nossi-Be and vicinity, USNM 296464 (18), 296469 (1), 296472 (11), 308412 (1). Juan de Nova: RUSI 37075 (1), 37076 (6), 37077 (2). Zanzibar: Insel Baui, ZMH 410 (3: 2 ♀♀, ♂ lectotype of *Salarias steindachneri*). Kenya: Mombasa, BMNH 1938.10.18.8 (1); Malindi, USNM 296066 (1), 296068 (1).

Istiblennius lineatus (Valenciennes)

FIGURES 4c, 32, 33

Salarias lineatus Valenciennes in Cuvier and Valenciennes, 1836:314 [Java; holotype MNHN 1396].

Salarias kingii Valenciennes in Cuvier and Valenciennes, 1836:334 [Côte nord-ouest de la Nouvelle-Hollande (Australia); holotype MNHN A.2048].

Salarias hasseltii Bleeker, 1851:257 [Tjilankahan, Java; neotype MNHN 1396, holotype of *Salarias lineatus* Valenciennes, designated below].

Salarias lividus Thiollière in Montrouzier, 1856:463 [Woodlark Island, holotype lost; neotype USNM 203749, Trobriand Islands, Kuia Island; designated below].

Salarias mccullochi Fowler and Bean, 1923:25 [Billingshausen Island; holotype USNM 83293].

Salarias multilineatus Fowler, 1945:68 [Saipan Island; holotype ANSP 71602].

DIAGNOSIS (see also Tables 22 to 26).—A species of the Lineatus complex in which: crest of males uniformly pigmented or with pale central area; females lack crest; color pattern on caudal peduncle of males usually of dark stripes or dashes, occasionally including squiggles, occasionally dark spots, which are restricted to peduncular area; pattern on caudal peduncle of females infrequently like male pattern, usually of dark spots (dots), which also occur well anterior to peduncle; dark stripes often present on anterior half of body of both sexes; total dorsal-fin elements of males 35 to 38 (rarely 38), of females 34 to 38 (rarely 38); total vertebrae 39 to 43 (usually 40 to 42, both sexes).

DISTRIBUTION (Figure 68).—*Istiblennius lineatus* is distributed from the Laccadive (Jones and Kumaran, 1980:530) and Maldive islands, central Indian Ocean, east to Mangareva, Gambier Islands, Pacific Ocean. It occurs as far north as Toyohama, Japan (about 200 km farther WNW than reported by Yoshino in Masuda et al., 1984:300). It is notably absent from the Chagos Islands (Indian Ocean) and Wake, Marcus, Hawaiian, Johnston, and northern Line islands, although it has been reported from Fanning based on sight records (Chave and Eckert, 1974:306; record not included on Figure 68). The Paracel Islands, South China Sea, record indicated in Figure 68 is based on an illustrated report in Anonymous (1979:423).

GEOGRAPHIC VARIATION.—Means for meristics of *I. lineatus* (Tables 22 and 23) vary widely and seemingly randomly, but there is a tendency for specimens from New Hebrides, Fiji, Tonga (all marginally off the Pacific plate), and Pacific-plate localities to exhibit higher means than do specimens from other localities. Similarly, the New Hebrides, Tonga (but not Fiji!), and Pacific-plate localities appear to include a greater percentage of specimens with 14 dorsal-fin spines than do the other localities (except Maricaban and Mindoro islands in the Philippines; Table 24). Modal frequencies for number of precaudal vertebrae (10 or 11), which is closely correlated with position of posteriormost pleural rib (usually on first caudal vertebra), vary irregularly in specimens from non-Pacific-plate localities, but tend to be 11 at Pacific-plate localities (i.e., noncontinentally influenced islands).

Specimens from the 28 localities where more than 10 specimens are available vary from having 0 to 20% of specimens with the split-ray condition for the last anal-fin ray (Table 25), but at almost half of these localities (13), the percentage is greater than 10%. Means for total number of mandibular sensory pores (Table 26) tend to fall between 11.8 to 12.0 at almost all localities, but the means at Fiji (11.4), Arno, Marshall Islands (11.6), and Indonesia (11.7) are noticeably lower, considering localities where counts from 10 or more specimens are available. Considering all characters, the Fiji specimens tend to be the most divergent, with specimens from relatively nearby New Hebrides and Tonga exhibiting similar (to each other), and almost as much, divergence.

NOMENCLATURAL DISCUSSION.—Chapman (1951) appears to have been the first reviser to use page priority as a basis for recognizing *Salarias lineatus* Valenciennes as a senior synonym of *Salarias kingii* Valenciennes. Valenciennes differentiated his *S. kingii* only from *Salarias meleagris* Valenciennes.

Bleeker (1851) based his description of *Salarias hasseltii*, which he did not compare with any other species, on a Kuhl and Van Hasselt drawing, which showed no head cirri or color pattern. Considering the type locality (Java), the number of segmented dorsal- and anal-fin rays shown in the drawing (22 and 23, respectively) would only be expected to occur in specimens of *I. dussumieri* or *I. lineatus*. The length, 112 mm, of the specimen drawn is infrequently attained by *I. dussumieri*, but frequently attained by *I. lineatus*. For that reason, we identify *S. hasseltii* with *I. lineatus*. In any event, in order to stabilize the nomenclature of the name *Salarias hasseltii*, we believe a neotype should be designated for the species. We designate the holotype of *Salarias lineatus* (MNHN 1396, from "Java," as neotype of *S. hasseltii*. In doing this, *S. hasseltii* becomes a junior objective synonym of *S. lineatus*.

Chapman (1951) recognized *S. hasseltii* as a valid species

that could only be differentiated from *S. lineatus* on the basis of color pattern, mainly (Chapman, 1951:314): *"hasseltii* has the black horizontal lines [of *lineatus*] on the sides subdued or quite absent while in their place are pale horizontal lines of equal prominence." In doing so, Chapman accepted Bleeker's then unpublished (published in Bleeker, 1983) colored illustration of *S. hasseltii,* which was not based on the holotype of *S. hasseltii,* but on Bleeker's interpretation of the species that Kuhl and Van Hasselt had drawn only in outline. Chapman, furthermore, noted that both color-pattern types were widely distributed, occurring in the same geographic areas, but did not mention or realize that both types are taken together in collections. The differences between the two types are not absolute, and we do not believe they represent different taxa.

Thiollière's (in Montrouzier, 1856) description of *Salarias lividus* was based on even more scanty information than Bleeker's *S. hasseltii.* The holotype of *S. lividus* was not available to Montrouzier, having been lost before he prepared the description based on Thiollière's notes. It is described as being 4 inches long and having short, simple supraorbital cirri, a head crest, dorsal fin attached to caudal fin, 22 rays in the second dorsal fin, and 23 in the anal fin. There is no species of *Istiblennius* that might be expected to occur in the Woodlark Island area that has this combination of characters. Except for the simple supraorbital cirri, which might indicate *Istiblennius edentulus,* the description best fits *I. lineatus* or *I. dussumieri.* The size of the specimen seems to favor *I. lineatus.* Although we do not have specimens of either *I. lineatus* or *I. dussumieri* (or *I. edentulus*) from Woodlark (~09°06'S, 152°50'E), we have a large series of *I. lineatus* from nearby Kuia (= Kuyau) Island (~08°37'S; 150°50'E) in the Trobriand Islands. To stabilize the name *Salarias lividus,* we designate USNM 293749, male, from NE side of Kuia Island, neotype. The neotype (97.3 mm SL, 117 mm TL) has the following characters: dorsal fin XIII,23; anal fin II,24N; dorsal fin attached to base of caudal fin (now ripped); crenulate upper lip; smooth lower lip; broad, branched supraorbital cirri; branched nasal cirri (the left cirrus malformed); no nape cirri; no canines.

Fowler and Bean (1923), in differentiating their *Salarias mccullochi,* merely stated that it differed from other Polynesian species in coloration. Their holotype is identifiable as *I. lineatus.* Fowler (1945) compared his *Salarias multilineatus* only with *Salarias caudolineatus* Günther (= *Blenniella caudolineata*). His holotype is identifiable as *I. lineatus.* Böhlke (1984) called attention to the discrepancy involving Fowler's report that he had only a single specimen ("type") of *S. multilineatus* (ANSP 71602). Fowler's description was clearly based on more than 1 specimen and he cataloged a paratype (ANSP 71601) with the same locality data.

MATERIAL EXAMINED.—Indian Ocean area. Maldive Is: Kandooma-fushi Id, SMNS 8459 (1); Rasdu Atoll, SMF 10437 (1), 13589 (10), 23186 (1), USNM 290934 (3). India: Konival, CAS-SU 14826 (1), 41343 (14); Waltair, CAS-SU 41345 (1).

Ceylon: Bentota, USNM 296478 (2); Galle, NTM S.11245-001 (2); Tangalle, USNM 296468 (5); Weligama, SMF 11640 (3). Myanmar: S Moscos Id, CAS-SU 39494 (1). Andaman Is: CAS-SU 37128 (1), 37129 (1), 37130 (2), 37135 (1), USNM 144433 (1), 144516 (1), 144545 (2), 195771 (1). Nicobar Is: Tillongchong, SMF 18020 (1), Trinculle, SMF 112 (1), 118 (1), 121 (1). Cocos-Keeling Is: BMNH 1949.11.29.544-72 (29), WAM P.29907-041 (1), P.29913-036 (11). Christmas Id: BMNH 1909.3.4.69 (3), 1934.6.29.24-6 (3), WAM P.10683-001 (1), P.10468-001 (1), P.26088-041 (2), P.26114-008 (6), P.28988-007 (5), P.28989-007 (8), P.29014-002 (4). Cartier Id, Timor Sea: WAM P29062-013 (6). WA: Kendrew Id, BPBM 17420 (4), WAM P.24103-001 (5); Montebello Is, BMNH 1861.8.16.106-116 (11), WAM P.4851-001 (2), P.23137-001 (11); Northwest Cape, AMS IB.5182-87 (6), WAM P.6641-001 (23); Point Cloates, WAM P.2810-001 (3); Point Samson, WAM P.22671-001 (1); South Muiron Id, WAM P.25822-002 (1); Thevenard Id, WAM P.11242-001 (1).

Pacific Ocean area. Japan: Okinawa, USNM 71486 (7), 296161 (2), 296452 (2), 296486 (1), 296529 (2), 298932 (1), 313575 (1); Tanegashima, USNM 71427 (5); Toyohama-ku, Chiita Hanto, CAS 27448 (1). N Taiwan: Ken Tzu Liao, USNM 296530 (1); Shen-Ao, USNM 205312 (3); Shih-Cheng, USNM 296531 (1); Su-Ao, USNM 205318 (1), 205329 (4); S Taiwan: Ch'uan-Fan-Shih, USNM 205330 (3), 296462 (1); K'en-Ting, USNM 296542 (1); Lan-Yu, USNM 179324 (1); Nan-Wan, USNM 137804 (14), 205317 (1), 205328 (1); Sha-Toa, USNM 296507 (1); SE end, USNM 279872 (1); SW tip, USNM 296541 (8); Ta-Fan-Lieh, USNM 296516 (1), 296535 (2); Wan-Li-Tung, USNM 205310 (2), 205313 (1); Yeh-Liu, USNM 205319 (1), 205331 (1). Saipan: ANSP 71601 (1), 71602 (holotype of *Salarias multilineatus*), USNM 123836 (3), 132846 (1). Rota: USNM 150589 (1). Guam: CAS 68020 (8). Saipan: BPBM 34604 (27), USNM 320334 (27) Palau Is: CAS 68621 (23). Philippines: Batanes Is, USNM 226735 (1), 226740 (1), 226763 (2), 226764 (5). 226766 (11), 226713 (4); Babuyan Is, USNM 320101 (1); Cabagan Id, Leyte, USNM 137800 (1); Liloan Pt, Cebu, USNM 296069 (3); Mactan Id, USNM 137799 (1); Maloh, Negros Id, USNM 303679 (63); Maricaban Id, USNM 137797 (8); Nogas Pt, Panay, USNM 137803 (3); Pilas Id, USNM 137801 (1); Sablayan, Mindoro, USNM 137802 (6); Simaluc Id, USNM 137798 (1); Siquijor Id, USNM 296065 (1). Indonesia: Sumatra: Benkoelen, USNM 88016 (2); Java: RMNH 17272, Paeloboean Ratu, USNM 72727 (1), 72736 (1); Bali, UF 47332 (1 cleared and stained); Koepang, Timor, RMNH 20674 (3); Flores, UF 31296 (3), 31301 (1); Ambon, BPBM 32297 (3), USNM 277968 (1), 296467 (5); Nusa Laut, USNM 296405 (1); Morotai, RMNH 19951 (1); Sulawesi: Lembeh Strait, CAS-SU 28840 (1), Paleleh, RMNH 20223 (1); Waigeo, CAS-SU 28042 (2); Sorong, West Irian, ANSP 81586 (2). PNG: Port Moresby & vicinity, USNM 304673 (1); Brummer Is, Bonarua Id, USNM 296142 (2), 227347 (10); Trobriand Is, Kuia, USNM 293748

(247), 293749 (neotype of *Salarias lividus*), 296133 (8); Madang, USNM 296142 (2), 296149 (1), 296150 (1); Cape Croisilles [N of Madang], USNM 298708 (8); Rabaul & vicinity, New Britain, USNM 296471 (2), 317505 (47, including 1 ophioblennius stage cleared and stained); Nissan Is, Pinipel, USNM 144710 (4). Qd: Lizard Id, AMS I.21344-012 (2), I.21598-027 (6); N Barnard Id, AMS IA.2185 (2); High Id, AMS IA.2186 (3), IA.2287 (3); Low Isles, BMNH 1933.1.25.198; Murray Id, AMS I.11796 (1), I.11797 (1), I.11798 (1), I.11799 (5). Solomon Is: Guadalcanal, USNM 315312 (50). Santa Cruz Is: Santa Cruz, AMS I.2931 (2), I.2932 (2). New Hebrides: Efate, USNM 296067 (23), 296071 (115); Venui Islet, Santo, ANSP 105234 (1). New Caledonia: MNHN 1505 (1). Fiji: Viti Levu, BPBM 5716 (16), 5727 (40), USNM 236027 (1); Yangasa, Lau Is, 256439 (6). Tonga Is: Niuafo'ou, USNM 91914 (4), 91929 (3), 91933 (1), 91945 (2), 91949 (2), 91957 (1), 91960 (2), 91967 (1), 91968 (1), 92001 (1), 92002 (3), 92003 (1), 92004 (1), 92006 (1), 92007 (1), 137822 (1); Tongatapu, BPBM 34540 (3), USNM 296072 (16). Rotuma: USNM 296476 (1). Niue: NMNZ P12376 (1). Marshall Is: Arno, BPBM 15214 (34), USNM 166798 (7), 166799 (1), 166800 (1); Bikini, USNM 142191 (6), 142192 (36), 142193 (14, including 2 cleared and stained), 313768 (1); Enewetak, USNM 142195 (2), 144424 (2); Jaluit [=Bonham Id], BMNH 1873.4.3.189; Majuro, USNM 195841 (1); Rongelap, USNM 142194 (2). Kiribati (= Gilbert Is): Onotoa, USNM 167337 (6), 296291 (10); Tarawa, USNM 259644 (3). Tuvalu: Funafuti, AMS I.4163 (1), I.4164 (1). Swains Id: BPBM 10136 (1), USNM 115425 (3). Samoa Is: Upolu, BPBM 5726 (11), 5731 (1), 5738 (2), USNM 52192 (3); Tutuila, CAS-SU 8997 (3). Howland Id: USNM 198689 (1), 198706 (5). Phoenix Is: Canton, USNM 115426 (1), 115428 (3), 115429 (10); Enderbury, USNM 115424 (2); Hull, USNM 115423 (48), 296448 (1); McKean, USNM 198710 (1). Tokelau Is: Atafu, USNM 296487 (8), USNM 313474 (1); Fakaofo, USNM 296163 (9), 313472 (1); Manihiki, CAS 68171 (2). Line Is: Caroline, USNM 296475 (28). Cook Is: Penrhyn (= Tongareva), ANSP 64325 (1), 64326 (2), 65370 (1), BPBM 4979-80 (5), USNM 296466 (12). Society Is: Motu One (= Bellingshausen): USNM 83293 (holotype of *Salarias mccullochi*); Tahiti, CAS 68019 (1), USNM 304674 (1). Tuamotu Arch: Fakarava, USNM 66011 (3); Makatea, CAS-SU 14819 (4), USNM 296383 (3), 301775 (3); Rangiroa, USNM 300401 (21); Raroia, CAS 64230 (6), 68166 (1). Gambier Is: Mangareva, ANSP 101019 (1), USNM 65646 (2).

Istiblennius rivulatus (Rüppell)

FIGURES 34, 35

Salaris [sic] *rivulatus* Rüppell, 1830:114 [Tor 9SW coast Sinai Peninsula); holotype or lectotype SMF 1843; see nomenclatural discussion section below].

Salarias oryx Ehrenberg in Cuvier and Valenciennes, 1836:335 [mer Rouge; lectotype designated in present study from among MNHN A.1804].

DESCRIPTION.—Dorsal fin. XII to XIV,20 to 23 = 33 to 35 (XII in only 8, and XIV in only 1 of 111 specimens examined for character; 20 in only 5, and 23 in only 2 of 103 specimens; 33 in only 2 of 53 males and 3 of 49 females); mean number of total elements significantly higher for males than for females (34.3 vs. 34.1, $p = .02$); membrane between spinous and segmented-ray portions notched about one-third to two-thirds length of first segmented ray; membrane from posteriormost ray usually attaching to point on dorsal edge of caudal fin posterior to caudal-fin base in specimens over 45 mm SL, attachment rarely extending out along edge more than 20% caudal-fin length (at most 25%).

Anal fin. II,20 to 23 (rarely 20 or 23); mean number of segmented elements significantly higher for males than for females (21.6 vs. 21.2, $p = .05$); posterior element split to base in about 25% of specimens; posterior element of split ray usually visible externally; fin not bound by membrane to caudal peduncle. Skin covering anal-fin spines and distal half of rays not modified in males.

Pectoral-fin rays 12 or 13 (13, only unilaterally, in 1 of 75 specimens examined for this character).

Pelvic-fin segmented rays 3.

Caudal fin. Dorsal procurrent rays 5 to 7 (rarely 5, modally 6), ventral procurrent rays 5 to 8 (rarely 5 or 8, modally 6), procurrent rays 6/6 and 7/7 in 89% of specimens; segmented rays 13.

Vertebrae. 11+27 to 29 = 38 to 40 (rarely 11+27), mean 39.0 in both sexes; posteriormost pleural rib on 12th or 13th from anteriormost centrum (on 12th in 30 of 34 specimens examined for character); posteriormost epineural on 15th to 19th from anteriormost centrum (on 17th in 50% of specimens).

Cirri. Nape cirri simple, occasionally absent unilaterally. Orbital cirri usually simple, occasionally with single branch, length greater than (up to almost twice) orbital diameter in males ≥40 mm SL, slightly less than to slightly more than orbital diameter in females; nasal cirri simple, occasionally with single branch.

A single female (BMNH 1967.5.13.18), abnormally, lacked both nape cirri and had orbital cirri with numerous small side branches and palmately branched nasal cirri; 1 nasal and 1 orbital cirrus of each pair appeared malformed, but others, except for branching, appeared normal; nasal and orbital cirri darkly pigmented (cirri uniformly pale in normal specimens).

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between verticals from bases of 7th and 10th dorsal-fin spines (usually posterior to base of 8th spine), thence continuing posteriorly as series of 1 to 8 (usually 4 to 6) short, disjunct, horizontally bi-pored tubes (canals) in skin; posteriormost tube

on body in area between verticals from bases of 9th dorsal-fin spine and 3rd segmented ray (usually between bases of 12th spine and 1st segmented ray).

Mandibular pores 4 or 5 (4 only unilaterally, in 4 of 48 specimens checked for character).

Six or 7 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (6 in 90% of 62 specimens examined for character); 0 to 2 positions occupied by pair of pores (rarely 0 pairs in specimens over 50 mm SL).

Mandibular posterior canine teeth absent.

Ventral margin of upper lip and dorsal margin of lower lip entire, without crenulae.

Well-developed fleshy crest on head present or absent in males 31 to 40 mm SL, present in larger males; no crest noticeable in most females, but ridges or low crests common in females >57 mm SL; 2 largest females, 88 to 93 mm SL, lacked crests.

Color pattern (in preservative; Figures 34, 35). Males and females essentially the same. Head with dusky band posterior to eye, pale band below eye extending across corner of mouth; other dusky markings on upper lip and head posteriorly; crest of male with dusky band at each end, separated by broader, pale area. Body varying from unmarked to bearing up to 9 irregular to regular dusky bands, middle 2 or 3 bands represented by paired elements; bands extending dorsally well out on dorsal fin, breaking up into slender, dusky, diagonal streaks; posterior body variably with several pairs of faintly dusky, wavy pinstripes with slightly more faintly dusky areas between members of each pair (reminiscent of pattern in *I. lineatus*). Dorsal fin with black mark distally on membrane between first two spines, occasionally continuing to between third and fourth spines, then continuing as fainter, dusky, distal or subdistal margin on remainder of spinous dorsal fin. Anal fin faintly dusky with darker dusky subdistal margin; ray tips noticeably pale. Pectoral, pelvic, and caudal fins plain.

Size. Largest male 86 mm SL, largest female 93 mm SL; smallest specimen 25.3 mm SL, sex indeterminate. Ophioblennius-stage specimens unknown.

COMPARISONS AND RELATIONSHIPS.—*Istiblennius rivulatus* is unique in *Istiblennius* and *Blenniella* in having 12 pectoral-fin rays; all other species have strongly modally 14 rays. Also noteworthy are its simple cirri, particularly the long orbital cirrus, and the relatively shallow notch in the dorsal fin. Our phylogentic analysis of *Istiblennius* (Figure 60; see discussion in Phylogenetic Analysis section) was unsatisfactory in fully resolving the relationships of *I. rivulatus*. Although placed in a polytomous clade of 4 species, the clade is only weakly supported. Possible evidence of its relationships to other species in the genus is the presence of a configuration of striping on the body that it shares with the Lineatus complex of species, which, interestingly, is widely distributed in the Indo-Pacific, but absent from the Red Sea, except for a record

from just inside its entrance. The presence of a dark spot anteriorly in the dorsal fin of both sexes of *I. rivulatus* is, perhaps indicative of a relationship with *I. dussumieri*, in which, however, only the male exhibits the dark spot.

Distribution (Figure 71).—Southern Gulf of Suez; Gulf of Aqaba; northern Red Sea south only to Mersa Ar-rakiyai, Sudan (~20°12'N). Extremely common in very shallow water (as little as 10 cm) on rocky shores.

NOMENCLATURAL DISCUSSION.—Rüppell's (1830) brief description of *Salaris rivulatus* included no mention of variation in the characters and only 1 length (5 inches) for the species. It is possible, therefore, that only 1 specimen, a holotype, was the basis for the description. There are 2 specimens at Frankfurt, SMF 1843 and 6445, that could be the holotype or syntypes of *S. rivulatus*. SMF 6445 is too short to have been the basis of Rüppell's description, but SMF 1843, approximately 4.5 inches TL, could have been. Klausewitz (1964) designated SMF 1843 as lectotype of *S. rivulatus*. In view of the questionable status of the 2 specimens, we recognize both as syntypes and reconfirm Klausewitz' action.

Dor (1984:231) erroneously listed SMF 6446, Et Tur, as "paralectotype" of *S. rivulatus*. SMF 6446 comprises 10 specimens collected at Ghardaqa, and have no status as types. There is, however, in Leiden, a specimen (RMNH 1808) that is indicated as having been collected by Rüppell in the Red Sea. This specimen may have been among Rüppell's specimens when he described *S. rivulatus*, but we are unable to establish this.

Ehrenberg (in Cuvier and Valenciennes, 1836) stated that he had 4 specimens of his *Salarias oryx*, which he did not differentiate from *S. rivulatus*. Bauchot (1967:29–30) reported that MNHN had 6 specimens (MNHN A.1803, A.1804) of *S. oryx* that were labeled as types. She noted, furthermore, that there were three specimens (ZMB 1954; erroneously listed as 1945 by Dor, 1984:231) in the Berlin Museum that were also indicated as types of *S. oryx*, and we examined 3 more (ZMB 1955) that were similarly indicated. All 12 specimens conform with the original description and are identifiable as *I. rivulatus*. We designate a male, approximately 79 mm SL, the longest of the 3 specimens in MNHN A.1804, as lectotype of *Salarias oryx*. The lectotype is further distinguished from the other 2 specimens (~64 and 70 mm SL) in having the catalog number attached to it.

MATERIAL EXAMINED.—Gulf of Aqaba: Israel: Elat, USNM 191727 (2), BMNH 1967.5.13.18 (1); ~10 km S of Elat, USNM 232653 (7); Egypt: Marsa Muqabila, USNM 298471 (10); Ras Burka, ROM 43605 (5); Abu Zabed, BMNH 1951,16,583-593 (11); Sharm el Sheikh, HUJ F-4780 (1), USNM 293842 (5). Red Sea: MNHN A.1804 (3, of which largest is lectotype of *Salarias oryx*), A.1803 (3), SMF 1843 (holotype and/or lectotype of *Salaris rivulatus*), 6445 (1), ZMB 1954 (3), 1955 (3); Egypt: near Ghardaqa, USNM 200303 (291, including 3
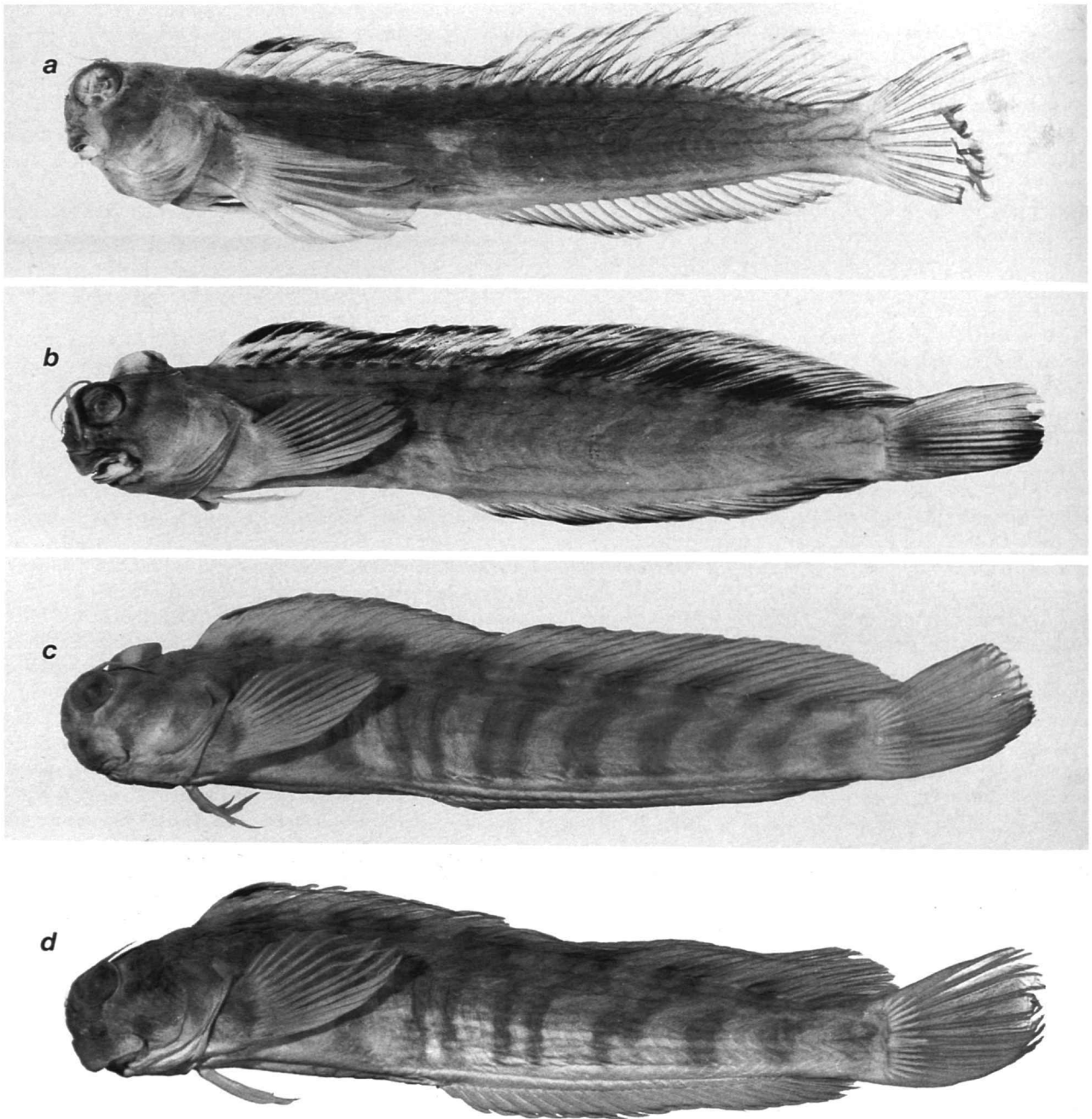
...., ... *a,b,* BMNH 1931.1.10.585-593, Abu Zabad, *a,* female, 51 mm SL; *b,* male, 58 mm SL; *c,d,* USNM 293842, Sharm al Sheikh, *c,* male, 72 mm SL; *d,* female, 71 mm SL (photographs by T.B. Griswold).
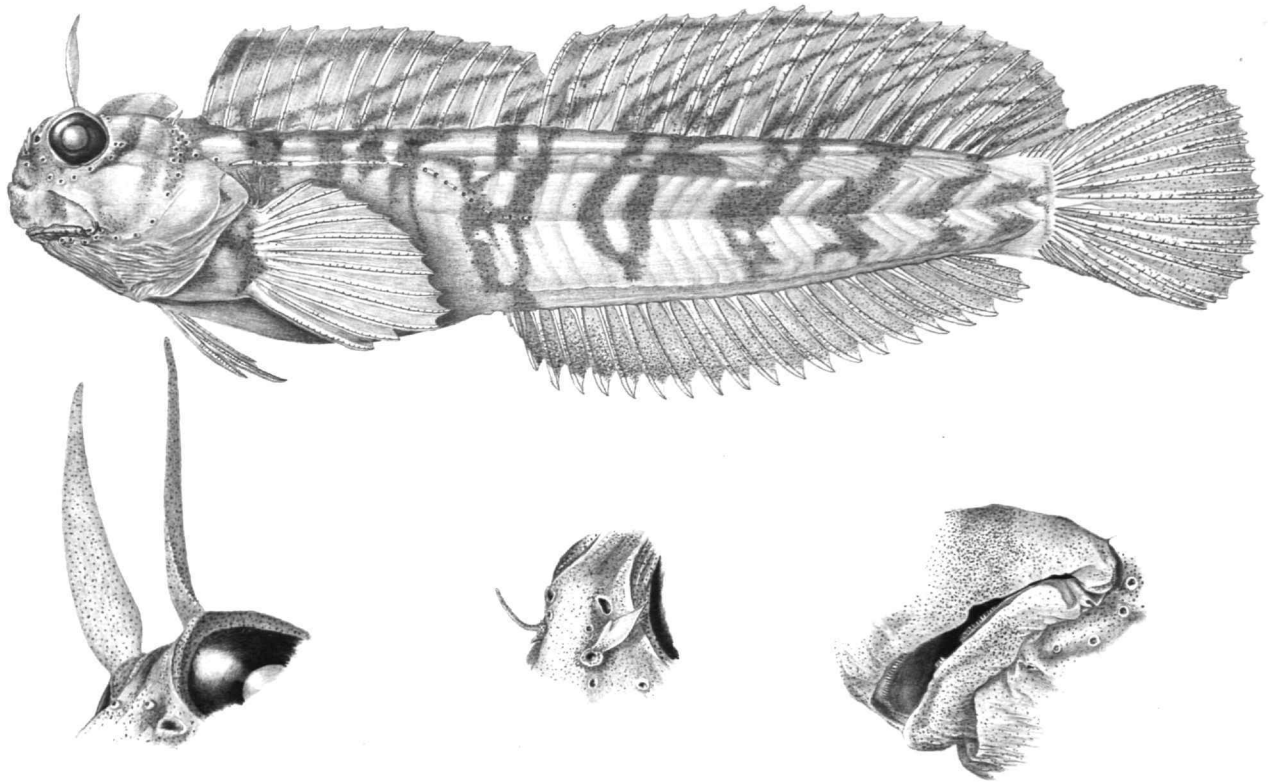
FIGURE 35.—*Istiblennius rivulatus*, USNM 232604, male, 54 mm SL, Gubat Ashra, Saudi Arabia, lateral view and enlarged views of orbital and nasal cirri and lips (drawing by P.K. Hollingsworth).

cleared and stained); Saudi Arabia: Gubat Ashra, USNM 232604 (1); Sudan: Mersa Bela, BMNH uncataloged (1), Mersa Arrakiyai, BMNH uncataloged (2).

Istiblennius edentulus (Schneider)

FIGURES 36–42

Blennius edentulus Schneider in Bloch and Schneider, 1801:172 [Society Islands, Tahiti; neotype, USNM 292529, designated below in nomenclatural discussion section].

Salarias quadricornis Valenciennes in Cuvier and Valenciennes, 1836:329 [type locality restricted to Isle-de-France and lectotype, MNHN A.2003, designated below in section on nomenclatural discussion].

Blennius truncatus Forster, 1844:231 [Society Islands, Tahiti; neotype, USNM 292529, designated below in section on discussion to be same specimen as neotype of *Blennius edentulus*].

Salarias melanocephalus Bleeker, 1849:18 [Pagotang, Javae; RMNH 6297, 14 specimens, probably syntypes, largest, 94.4 mm TL, possible holotype, designated lectotype below in section on nomenclatural discussion].

Salarias sumatranus Bleeker, 1851:256 [Sumatra occidentalis; location of holotype unknown].

Salarias diproktopterus Bleeker, 1857b:69 [Kajeli, Boeroe; holotype RMNH 4468].

Blennius cinereus Castelnau, 1875:26 [Queensland, One Tree Island; neotype,

USNM 291700, designated below in section on nomenclatural discussion].

?*Salarias atratus* Macleay, 1882:361 [Port Moresby, New Guinea; 2 putative syntypes, MAMU F1047, apparently lost].

Salarias insulae Ogilby, 1899:741 [Lord Howe Island; holotype apparently lost].

Scartichthys enosimae Jordan and Snyder, 1902:460 [Misaki, Japan; holotype, CAS-SU 7068].

Salarias gilberti Bryan and Herre, 1903:135 [Marcus Island; holotype included in BPBM 2454].

Salarias marcusi Bryan and Herre, 1903:136 [Marcus Island; holotype, BPBM 2456].

Scartichthys basiliscus Fowler, 1904:552 [Padang, Sumatra; holotype, ANSP 27802].

Salarias azureus Seale, 1906:87 [Tubai, Austral Ids.; holotype, BPBM 783].

Salarias sindonis Jordan and Seale, 1906:427 [Pago Pago, Samoa; neotype, USNM 51793, designated below in section on nomenclature].

Salarias garmani Jordan and Seale, 1906:429 [Apia, Samoa; holotype, USNM 51792].

Salarias rechingeri Steindachner, 1906:1411 [Western Samoa, Upolu; neotype, USNM 293747, designated below in section on nomenclatural discussion].

Salarias fluctatus Fowler, 1945:70 [Saipan Island; holotype, ANSP 71603].

Salarias atrimarginatus Fowler, 1946:182 [Aguni Shima, Riu Kiu Islands; holotype, ANSP 72052].

Istiblennius edentululus.—Allen and Swainston, 1988:130 [Northwestern Australia; misspelling].

DESCRIPTION.—Dorsal fin (Tables 27 and 28). XII to XIV,18

Table 27.—Frequency distributions for certain meristic characters of male specimens of <u>Istiblennius</u> <u>edentulus</u> from various localties. Underlining indicates significant differences between means of sexes from same locality (p ≤ .05).

Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae					
	31	32	33	34	35	36	x̄	20	21	22	23	24	x̄	36	37	38	39	40	x̄
Gulf of Aqaba	-	2	2	-	-	-	32.5	-	3	1	-	-	21.2	-	-	4	-	-	38.0
Red Sea, Kosseir, Egypt	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Red Sea, Sudanese coast	-	6	19	-	-	-	<u>32.8</u>	-	13	12	-	-	<u>21.5</u>	-	5	20	-	-	<u>37.8</u>
Red Sea, Difnein Island	-	5	19	1	-	-	32.8	2	11	12	-	-	21.4	-	11	13	1	-	37.6
Gulf of Aden	-	1	5	2	-	-	33.1	-	1	6	1	-	22.0	-	1	6	1	-	38.0
Oman	-	-	4	-	-	-	33.0	-	1	3	-	-	21.7	-	-	3	-	-	38.0
Chagos Islands	-	1	21	3	1	-	33.2	-	4	21	1	-	<u>21.9</u>	-	3	22	1	-	37.9
Aldabra	-	3	16	6	-	-	33.1	-	6	17	2	-	21.8	-	4	18	3	-	38.0
Agalega	-	-	13	3	1	-	33.3	-	-	15	2	-	<u>22.1</u>	-	-	15	1	-	<u>38.1</u>
St. Brandon's Shoals	-	-	-	18	10	-	<u>34.4</u>	-	-	10	16	2	22.7	-	-	1	22	5	39.1
Mauritius	-	-	-	10	8	2	34.6	-	-	2	13	5	23.2	-	-	1	12	6	39.3
Reunion	-	-	-	3	3	-	34.5	-	-	-	5	1	23.2	-	-	-	5	1	39.2
NW Madagascar	-	-	9	15	1	-	<u>33.7</u>	-	1	20	3	1	22.2	-	1	19	4	1	38.2
Kenya	-	-	1	3	1	-	34.0	-	-	3	2	-	22.4	-	-	1	3	-	38.8
Zanzibar	-	-	1	6	1	-	34.0	-	-	4	4	-	22.5	-	-	4	4	-	38.5
South Africa, Natal coast	-	1	6	7	-	-	33.4	-	-	10	4	-	<u>22.3</u>	-	1	7	5	-	<u>38.3</u>
Cocos-Keeling Islands	-	-	20	5	-	-	<u>33.2</u>	-	1	21	3	-	22.1	-	-	22	3	-	38.1
Japan																			
Misaki & Enoshima ca. 35°N	-	-	5	16	-	-	33.8	-	10	10	-	-	21.5	-	-	4	15	-	38.8
Chiba Prefecture 35-36°N	-	-	-	6	-	-	34.0	-	2	4	-	-	21.7	-	-	-	6	-	39.0
Shirahama 33°30'N (Fukao, 1985)	-	1	13	8	-	-	33.3	-	6	15	1	-	21.8						
Shirahama (present study)	-	-	1	6	-	-	33.8	-	1	6	-	-	<u>21.8</u>	-	-	1	6	-	<u>38.8</u>
Iki 33°45'N (Fukao, 1985)	-	-	-	1	-	-		-	-	1	-	-							
Tanegashima 30°30'N	-	1	5	4	1	-	33.4	-	2	8	-	-	21.8	-	1	8	2	-	38.1
Ryukyu Islands																			
Takarajima 29°15'N (Fukao, 1985)	-	-	-	1	-	-		-	-	1	-	-							
Okinawa 26°30'N																			
Fukao, 1985	-	1	8	6	-	-	<u>33.3</u>	-	3	12	2	-	<u>21.9</u>						
present study	-	2	21	6	-	-	33.1	-	5	20	4	-	22.0	-	3	21	5	-	<u>38.1</u>
Ishigaki 24°15'N (Fukao, 1985)	-	-	10	4	-	-	33.3	3	9	2	-	-	20.9						
Iriomote 24°15'N (Fukao, 1985)	-	-	-	1	-	-		1	-	-	-	-							
Goh Samet Island, Gulf of Thailand	-	1	14	9	-	-	<u>33.3</u>	-	5	15	4	-	<u>22.0</u>	-	-	14	10	-	<u>38.4</u>
Ko Kra Island, Gulf of Thailand	-	-	12	3	-	-	33.2	-	2	11	2	-	22.0	-	1	9	4	-	38.2
Batanes Islands, Philippines	-	4	22	4	-	-	33.0	-	3	25	2	-	<u>22.0</u>	-	4	20	6	-	<u>38.1</u>
Mindoro Island, Philippines	-	1	9	3	-	-	33.2	-	2	10	1	-	21.9	-	2	11	-	-	37.8
Siquijor, Philippines	-	-	4	-	-	-	33.0	-	-	4	-	-	22.0	-	-	4	-	-	38.0
Bonin Islands (Ogasawara)																			
Fukao, 1985	-	-	-	8	1	-	34.1	-	-	8	1	-	22.1						
present study	-	-	-	-	2	-	35.0	-	-	2	-	-	22.0	-	-	-	-	2	40.0
Marcus Island	-	-	1	14	16	-	<u>34.5</u>	-	-	5	25	1	22.9	-	-	3	27	1	38.9
Saipan, Marianas Islands	-	-	2	-	-	-	33.0	-	-	2	-	-	22.0	-	-	2	-	-	38.0
Guam, Marianas Islands	-	-	5	2	-	-	<u>33.3</u>	-	2	5	1	-	21.9	-	1	6	1	-	38.0
Sumatra (Padang), Indonesia	-	1	-	-	-	-		-	-	1	-	-		-	-	1	-	-	

to 23 = 31 to 36 (XIII in 95% of specimens); segmented rays rarely 18 or 23; total elements rarely 31 or 36); mean number of total elements usually higher for males from any locality than for females from same locality (higher for 55 of 61 localities for which means for both sexes are available, statistically significantly higher for 14 of the 55 localities); membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; fin membrane from posteriormost ray attaching to point on dorsal edge of caudal fin posterior to vertical through bases of central segmented caudal-fin rays in specimens >25 to 40 mm SL, attachment extending along edge up to 25% caudal-fin length; in general, attachment extending farthest posteriorly in largest specimens.

Anal fin (Tables 27 and 28). II,20 to 24; mean number of segmented rays usually higher for males from any locality than for females from same locality (higher for 55 of 61 localities for which means for both sexes are available, statistically significantly higher for 20 of the 55 localities); posteriormost ray usually split to base, (posterior element of split ray often represented only by a basal nub of bone visible only in radiographs or cleared and stained specimens); posteriormost ray usually not bound by membrane to caudal peduncle (bound in 0 to 10% specimens examined for character from any locality). Skin covering anal-fin spines and distal half of several rays expanded and wrinkled along lateral edges in large, apparently sexually mature males (similar to condition in

Table 27.—continued

Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae					
	31	32	33	34	35	36	x̄	20	21	22	23	24	x̄	36	37	38	39	40	x̄
Java, Indonesia	-	-	1	-	-	-		-	-	1	-	-		-	-	-	-	-	
Flores, Indonesia	-	-	4	-	-	-	34.0	-	1	3	-	-	21.8	-	1	3	-	-	37.8
Halmahera, Indonesia	-	-	2	-	-	-	33.0	-	-	1	-	-		-	-	2	-	-	38.0
Moluccas, Indonesia	-	-	11	1	-	-	33.1	-	1	8	2	-	22.1	-	-	10	1	-	38.1
Trobriand Islands	-	4	18	6	-	-	33.1	-	7	19	2	-	21.8	-	5	20	2	-	37.9
Cape Range Nat. Pk., W Australia	-	-	-	2	-	-	34.0	-	-	1	1	-	22.5	-	-	-	2	-	39.0
Point Quobba, W Australia	-	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-	
Lizard Island, Queensland	-	1	7	1	-	-	33.0	-	1	6	2	-	22.1	-	3	5	-	-	37.6
One Tree Island, Queensland	-	-	12	12	2	-	33.6	-	1	16	8	-	22.3	-	-	20	5	1	38.3
Byron Bay, New South Wales	-	-	12	10	-	-	33.4	-	3	15	2	-	22.0	-	-	17	5	-	38.2
Minnie Water, New South Wales	-	-	1	1	-	-	33.5	-	-	2	-	-	22.0	-	-	1	1	-	38.5
Warrell Creek, New South Wales	-	1	1	-	-	-	32.5	-	-	2	-	-	22.0	-	-	2	-	-	38.0
Newcastle, New South Wales	-	-	3	1	-	-	33.3	-	-	3	1	-	22.3	-	-	4	-	-	38.0
Middleton Reef	-	-	-	-	1	-		-	-	-	1	-		-	-	-	1	-	
Lord Howe Island	-	-	3	3	-	-	33.5	-	-	6	-	-	22.0	-	-	4	2	-	38.3
Fiji	-	-	8	2	-	-	33.2	-	-	8	2	-	22.2	-	-	8	2	-	38.2
Rotuma	-	-	18	7	-	-	33.3	-	-	20	5	-	22.2	-	-	19	6	-	38.2
Western Samoa	-	1	28	20	-	-	33.4	-	-	34	13	-	22.3	-	3	39	6	-	38.1
Niue	-	-	-	6	2	-	34.2	-	-	1	7	1	23.0	-	-	1	7	1	39.0
Penrhyn (=Tongareva), Cook Ids	-	-	6	21	-	-	33.8	-	1	7	19	-	22.7	-	1	9	16	-	38.6
Aitutaki, Cook Islands	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Rarotonga, Cook Islands	-	-	-	8	1	-	34.1	-	-	5	4	-	22.4	-	-	2	6	1	38.9
Palmerston, Cook Islands	-	-	-	2	-	-	34.0	-	-	2	-	-	22.0	-	-	2	-	-	38.0
Tahiti & Moorea, Society Islands	-	-	11	14	1	-	33.6	-	-	14	12	-	22.5	-	-	13	12	-	38.5
Howland Island	-	-	20	5	-	-	33.2	-	5	20	1	-	21.8	-	-	20	6	-	38.2
Baker Island	-	-	1	6	-	-	33.8	-	-	2	5	-	22.7	-	-	3	4	-	38.6
Enderbury, Phoenix Islands	-	-	11	13	1	-	33.6	-	-	14	11	-	22.4	-	-	12	13	-	38.5
McKean, Phoenix Islands	-	-	1	17	1	-	34.0	-	-	2	17	-	22.9	-	-	1	17	1	39.0
Caroline, Line Islands	-	-	10	6	-	-	33.4	-	-	11	5	-	22.3	-	-	13	3	-	38.2
Christmas, Line Islands	-	-	21	4	-	-	33.2	-	2	20	3	-	22.0	-	-	19	5	-	38.2
Palmyra, Line Islands	-	-	10	3	-	-	33.2	-	-	11	2	-	22.2	-	-	10	3	-	38.2
Rangiroa, Tuamotu Archipelago	-	-	7	13	-	-	33.6	-	-	11	9	-	22.4	-	-	10	9	-	38.5
Marquesas Islands	-	2	23	4	-	-	33.1	-	3	23	3	-	22.0	-	-	26	4	-	38.1
Mangareva, Gambier Islands	-	-	1	9	4	-	34.2	-	-	3	11	-	22.8	-	-	3	11	-	38.8
Rapa	-	-	-	3	2	-	34.4	-	-	-	5	-	23.0	-	-	-	5	-	39.0
Pitcairn	-	-	-	2	-	-	34.0	-	-	-	2	-	23.0	-	-	-	2	-	39.0
Wake Island	-	1	9	12	-	-	33.5	-	1	13	8	-	22.3	-	-	13	9	-	38.4
Onotoa, Gilbert Islands	-	-	10	1	-	-	33.1	-	1	10	-	-	21.9	-	2	8	1	-	37.9
Abaiang, Gilbert Islands	-	-	5	3	-	-	33.4	-	1	7	-	-	21.9	-	-	7	1	-	38.1
Arorae, Gilbert Islands	-	-	2	3	-	-	33.6	-	-	2	3	-	22.6	-	-	1	4	-	38.6
Bikini, Marshall Islands	-	-	21	7	-	-	33.2	-	-	26	2	-	22.1	-	-	25	3	-	38.1
Enewetok, Marshall Islands	-	-	6	1	-	-	33.1	-	2	4	1	-	21.8	-	2	5	-	-	37.7
Kwajalein, Marshall Islands	-	-	5	-	-	-	33.0	-	-	5	-	-	22.0	-	-	5	-	-	38.0
Kapingamarangi	-	-	4	-	-	-	33.0	-	2	2	-	-	21.5	-	-	4	-	-	38.0

mature males of *Entomacrodus* species; Springer, 1967, especially pl. 24f).

Pectoral-fin rays 13 or 14 (14 bilaterally in 90 and unilaterally in 4 of 94 specimens examined for character).

Pelvic-fin segmented rays 3.

Caudal fin. Dorsal procurrent rays 6 to 8 (7 in 78% of 278 specimens examined for character), ventral procurrent rays 6 to 8 (7 in 71% of specimens), combination of 7 dorsal with 7 ventral procurrent rays in 58% of specimens; segmented rays 12 or 13 (12 in <1% of specimens).

Vertebrae (Tables 27 and 28). 10 or 11+26 to 30 = 36 to 40 (modally 11 precaudal vertebrae at most localities; however modally 10 in Red-Sea specimens; 10 also common or modal count at several Indian Ocean localities and Okinawa, Philippines, and Trobriand Islands, but more data needed for these localities); mean number of total vertebrae usually higher for males from any locality than for females from same locality (higher for 53 of 61 localities for which means for both sexes are available, statistically significantly higher for 14 of the 53 localities); posteriormost pleural rib on 11th to 13th from anteriormost vertebra (predominantly on 12th vertebra at all localities, except commonly on 11th in Red Sea specimens); posteriormost epineural on 14th to 22nd from anteriormost vertebra (Table 29), modal occurrence varying among localities

Table 28.—Frequency distributions for certain meristic characters of female specimens of _Istiblennius edentulus_ from various localties. Underlining indicates significant differences between means of sexes from same locality (p ≤ .05).

Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae					
	31	32	33	34	35	36	x̄	20	21	22	23	24	x̄	36	37	38	39	40	x̄
Gulf of Aqaba	-	-	6	-	-	-	33.0	1	4	1	-	-	21.0	-	3	3	-	-	37.5
Red Sea, Sudanese coast	1	18	6	-	-	-	32.2	2	23	-	-	-	20.9	2	15	8	-	-	37.3
Red Sea, Difnein Island	1	11	11	2	-	-	32.6	4	16	5	-	-	21.0	1	12	12	-	-	37.4
Gulf of Aden	-	4	4	-	-	-	32.5	1	3	4	-	-	22.0	-	2	5	-	-	37.7
Oman	-	2	6	-	-	-	32.8	-	3	5	-	-	21.6	-	3	4	1	-	37.8
Chagos Islands	-	2	20	1	-	-	33.0	1	10	13	-	-	21.5	-	3	21	-	-	37.9
Seychelles	-	1	2	-	-	-	32.7	-	2	1	-	-	21.3	-	2	1	-	-	37.3
Aldabra	-	1	23	1	-	-	33.0	-	3	21	-	-	21.9	-	4	19	1	-	37.9
Agalega	-	5	13	5	-	-	33.0	-	10	13	-	-	21.6	-	6	15	1	-	37.8
St. Brandon's Shoals	-	-	3	19	4	-	34.0	1	1	13	10	1	22.3	-	-	2	21	3	39.0
Mauritius	-	-	-	7	3	-	34.3	-	-	2	7	1	22.9	-	-	1	9	-	38.9
Reunion	-	-	2	6	4	-	34.2	-	-	3	7	1	22.8	-	-	2	9	1	38.9
NW Madagascar	-	1	15	10	-	-	33.3	-	5	19	2	-	21.9	-	3	19	4	-	38.0
Kenya	-	-	3	1	-	-	33.2	-	2	1	2	-	22.0	-	1	3	1	-	38.0
Zanzibar	-	-	11	2	-	-	33.2	-	4	8	-	-	21.7	-	4	8	1	-	37.8
South Africa, Natal coast	-	-	11	4	-	-	33.3	-	2	13	-	-	21.9	-	2	12	-	-	37.8
Cocos-Keeling Islands	-	2	21	-	-	-	32.9	-	2	22	-	-	21.9	-	4	19	1	-	37.9
Japan																			
Misaki & Enoshima ca. 35°N																			
enosimae form	-	-	5	18	-	-	33.8	-	16	6	1	-	21.3	-	-	10	13	-	38.6
Chiba Prefecture 35-36°N																			
enosimae form	-	-	1	5	-	-	33.8	-	5	1	-	-	21.2	-	-	3	2	-	38.4
Shirahama 33°30'N																			
enosimae form (Fukao, 1989)	-	-	4	12	1	-	33.8	1	10	6	-	-	21.3						
edentulus form (Fukao, 1989)	-	-	5	-	-	-	33.0	-	1	4	-	-	21.8						
enosimae form (present study)	-	-	2	2	-	-	33.5	-	4	-	-	-	21.0	-	-	3	1	-	38.2
Nomozaki 32°30'N (Fukao, 1985)																			
enosimae form	-	-	1	1	-	-	33.5	-	2	-	-	-	21.0						
Tanegashima 30°30'N																			
enosimae form	-	1	6	3	-	-	33.2	-	7	3	-	-	21.3	-	2	6	2	-	38.0
Ryukyu Islands																			
Yoronto 27°00'N (Fukao, 1985)	-	-	1	-	-	-		-	-	1	-	-							
Okinawa 26°30'N																			
Fukao, 1985	-	3	7	1	-	-	32.8	2	4	5	-	-	21.3						
present study	-	4	19	3	-	-	33.0	-	11	13	1	-	21.6	-	10	15	1	-	37.6
Ishigaki 24°15'N (Fukao, 1985)	-	1	8	2	-	-	33.1	1	5	5	-	-	21.4						
Iriomote 24°15'N (Fukao, 1985)	-	1	1	-	-	-	32.5	-	1	1	-	-	21.5						
Agunishima	-	-	1	-	-	-		-	-	1	-	-		-	1	-	-	-	
Goh Samet Island, Gulf of Thailand	-	3	23	-	-	-	32.9	-	10	16	-	-	21.6	-	6	20	-	-	37.8
Batanes Islands, Philippines	-	6	14	1	-	-	32.8	-	12	9	-	-	21.4	-	7	13	1	-	37.7
Mindoro Island, Philippines	-	4	11	3	-	-	32.9	-	6	11	1	-	21.7	-	5	12	1	-	37.8
Siquijor Island, Philippines	-	1	3	-	-	-	32.8	-	2	2	-	-	21.5	-	1	3	-	-	37.8
Bonin Islands (Ogasawara)																			
Fukao, 1985	-	-	-	4	1	-	34.2	-	-	5	-	-	22.0						
present study	-	-	-	3	-	-	34.0	-	2	1	-	-	21.3	-	-	-	3	-	39.0
Marcus Island	-	-	2	19	6	-	34.1	-	1	5	21	-	22.7	-	-	2	25	-	38.9

from on 16th to on 20th vertebra.

Cirri. Nape cirrus present on each side, relatively long (compared with that of other species of _Istiblennius_ or _Blenniella_), usually simple, occasionally with short side branch or ragged edges, particularly in large specimens. Orbital cirrus slender, transversely flattened, tapering distally, usually simple, occasionally with 1 to 8 long or short branches along edges or at tip, particularly in large specimens or specimens in which cirrus appears deformed and/or regenerating after damage. Nasal cirri usually 3 to about 20 in specimens >35 mm SL, number generally increasing with increasing SL.

Lateral line (based on 181 specimens ≥30 mm SL; Table 30). Continuous canal anterodorsally with simple pores (no vertical pairs of pores; rarely, vertical pair near lateral-line origin), extending posteriorly to point between verticals from 9th dorsal-fin spine and 3rd segmented ray (to or beyond vertical from 11th spine in 85% of specimens), usually descending to or near midline of body, then continuing posteriorly along midline as series of 2 to 18 short, disconnected, horizontally bi-pored canals (tubes) in skin (more than 5 tubes in 89% of specimens); posteriormost bi-pored tube at point between verticals from bases of 13th dorsal-fin spine and 15th segmented ray

Table 28.—continued.

Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae					
	31	32	33	34	35	36	x̄	20	21	22	23	24	x̄	36	37	38	39	40	x̄
Guam, Marianas Islands	-	4	6	-	-	-	32.6	-	4	6	-	-	21.6	-	1	9	-	-	37.9
Bali, Indonesia	-	-	2	-	-	-	33.0	-	1	1	-	-	21.5	-	-	2	-	-	38.0
Flores, Indonesia	-	2	3	1	-	-	32.8	-	3	2	1	-	21.7	-	2	3	1	-	37.8
Halmahera, Indonesia	-	1	1	2	-	-	33.2	-	1	3	-	-	21.8	-	1	2	-	-	37.7
Moluccas, Indonesia	-	2	6	1	-	-	32.9	1	2	6	-	-	21.6	-	2	6	-	-	37.8
Trobriand Islands	-	5	18	3	-	-	32.9	-	10	16	-	-	21.6	-	6	19	1	-	37.8
New Georgia	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Point Quobba, W Australia	-	-	-	5	-	-	34.0	-	-	2	3	-	22.6	-	-	-	5	-	39.0
Lizard Island, Queensland	-	3	10	-	-	-	32.8	-	3	10	-	-	21.8	-	3	8	-	-	37.7
One Tree Island, Queensland	-	1	14	9	-	-	33.3	-	3	20	2	-	22.0	-	1	17	7	-	38.2
Byron Bay, New South Wales	-	1	15	-	-	-	32.9	-	7	9	-	-	21.6	-	-	16	-	-	38.0
Minnie Water, New South Wales	-	-	2	1	-	-	33.3	-	-	3	-	-	22.0	-	-	2	1	-	38.3
Sydney, New South Wales	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Lord Howe Island	-	-	4	-	-	-	33.0	-	1	3	-	-	21.8	-	-	4	-	-	38.0
New Caledonia	-	1	-	-	-	-		-	1	-	-	-		-	1	-	-	-	
Loyalty Islands, Ouvea	-	-	1	-	-	-		-	-	1	-	-		-	-	-	-	-	
Fiji	-	-	6	3	-	-	33.3	-	-	9	-	-	22.0	-	2	5	2	-	38.0
Rotuma	-	2	22	1	-	-	33.0	-	2	21	2	-	22.0	-	1	23	1	1	38.1
Western Samoa	-	10	37	1	-	-	32.8	-	8	38	1	-	21.8	-	13	33	2	-	37.8
Niue	-	-	1	1	-	-	33.5	-	-	1	1	-	22.5	-	-	1	1	-	38.5
Penrhyn (=Tongareva), Cook Is	-	1	7	8	-	-	33.4	-	2	9	5	-	22.2	-	-	8	7	-	38.5
Rarotonga, Cook Islands	-	-	3	3	1	-	33.7	-	-	3	4	-	22.6	-	-	4	3	-	38.4
Palmerston, Cook Islands	-	-	1	-	-	-		-	-	1	-	-		-	-	-	1	-	
Tahiti & Moorea, Society Islands	-	1	18	6	1	-	33.3	-	3	15	8	-	22.2	-	2	19	5	-	38.1
Howland Island	-	-	20	2	-	-	33.1	1	5	16	-	-	21.7	-	1	19	1	-	38.0
Baker Island	-	-	3	2	1	-	33.7	-	1	4	1	-	22.0	-	-	4	1	1	38.5
Enderbury, Phoenix Islands	-	-	13	11	1	-	33.5	-	1	14	10	-	22.2	-	1	14	10	-	38.4
McKean, Phoenix Islands	-	1	4	14	-	-	33.7	-	1	11	7	-	22.3	-	-	5	14	-	38.7
Caroline, Line Islands	-	1	8	2	-	-	33.1	-	1	9	1	-	22.0	-	1	8	1	-	38.0
Christmas, Line Islands	-	5	15	4	⊣	-	33.0	-	7	17	1	-	21.8	-	4	21	-	-	37.8
Palmyra, Line Islands	-	-	2	-	-	-	33.0	-	-	2	-	-	22.0	-	-	2	-	-	38.0
Rangiroa, Tuamotu Archipelago	-	2	12	12	-	-	33.4	-	-	22	4	-	22.2	-	2	20	4	-	38.1
Marquesas Islands	-	6	21	-	-	-	32.8	-	8	19	-	-	21.7	-	4	22	-	-	37.8
Mangareva, Gambier Islands	-	-	2	19	1	-	34.0	-	-	11	11	-	22.5	-	-	6	16	-	38.7
Pitcairn	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Wake Island	-	1	8	3	-	-	33.3	-	3	8	-	-	21.7	-	3	8	1	-	37.8
Onotoa, Gilbert Islands	-	-	5	-	-	-	33.0	-	-	5	-	-	22.0	-	1	3	1	-	38.0
Abaiang, Gilbert Islands	-	-	10	1	-	-	33.1	-	1	9	1	-	22.0	-	-	9	2	-	38.2
Arorae, Gilbert Islands	-	-	2	-	-	-	33.0	-	-	2	-	-	22.0	-	-	1	1	-	38.5
Bikini, Marshall Islands	-	4	20	5	-	-	33.0	1	8	19	1	-	21.7	-	6	21	2	-	37.9
Enewetok, Marshall Islands	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-	
Kapingamarangi	-	-	4	-	-	-	33.0	-	2	2	-	-	21.5	-	-	4	-	-	38.0

(posterior to vertical from 3rd segmented ray in 93% of specimens; mean position of posteriormost tube tending to increase with increasing SL, Table 30).

Mandibular pores 5 or 6 (bilaterally 6 in 88%, and at least unilaterally in 98% of specimens examined for character).

Five to 7, predominantly 5, sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin; 0 to 5 positions with pairs or multiples of pores (see Table 31 and discussion of infraorbital pores under section on geographic variation).

Posterior dentary canines absent.

Ventral margin of upper lip and dorsal margin of lower lip entire (for exception, see subsection "Western Australian specimens" in section on geographic variation).

Males with fleshy, blade-like crest on head; females with or without crest (see geographic variation section). Sexual dichromatism present or absent (see geographic variation section).

Size. Largest male, 144 mm SL; largest female 132 mm SL; specimens >120 mm uncommon, mostly females. Ophioblennius-stage specimens unknown, but smallest specimen examined, 17.6 mm SL (UF 31309, Flores, Indonesia), perhaps recently metamorphosed: pectoral fins with distinctive pattern of black pigment distally (Figure 6b), patch of moderate-sized melanophores distally in membrane between 2 ventralmost rays, none between next 2 rays, then melanophores at tips and/or in membranes between next 9 rays, no melanophores dorsal to these rays; proximal $2/3$ of fin bears sprinking of very fine melanophores, mostly restricted to fin rays (these melanophores possibly not present in unmetamorphosed specimens). Next smallest available specimens, 17.8 to 19.2

Table 29.—Frequency distributions for location of posteriormost epineural relative to a vertebra, counting anteriorly to posteriorly, in specimens of *Istiblennius edentulus* from various localities (modes are underlined).

Localities	Posteriormost epineural on vertebra number										Localities	Posteriormost epineural on vertebra number									
	14	15	16	17	18	19	20	21	22	x̄		14	15	16	17	18	19	20	21	22	x̄
Gulf of Aqaba	-	-	1	4	4	-	-	-	-	17.3	Australia										
Red Sea											One Tree Island GBR	-	1	8	12	12	17	6	1	-	18.0
Sudanese Coast	2	2	13	6	4	-	-	-	1	16.8	Minniewater NSW	-	1	1	-	1	1	-	-	-	17.0
Difnein Island	-	3	14	17	9	4	2	-	1	17.2	Warrell Creek NSW	-	-	-	2	-	-	-	-	-	17.0
Gulf of Aden	-	-	-	-	2	-	1	-	-	18.7	Newcastle NSW	-	-	-	-	1	2	-	-	-	18.7
Oman	-	-	2	3	3	4	-	-	-	17.8	Byron Bay NSW	-	1	3	7	10	7	3	-	-	17.9
Chagos Islands	-	-	1	11	21	13	1	-	-	18.0	Middleton Reef	-	-	-	-	-	-	1	-	-	
Seychelles	-	-	2	1	1	-	-	-	-	16.8	Lord Howe Island	-	1	1	4	1	1	2	-	-	17.6
Aldabra	-	-	1	4	12	17	2	1	-	18.5	Fiji	-	1	6	3	6	2	1	-	-	17.3
Agalega	-	-	2	2	5	16	7	3	-	18.9	Rotuma	2	2	2	12	7	5	1	-	-	17.2
St. Brandon's Shoals	-	1	-	5	10	15	12	9	1	19.2	Western Samoa	2	4	19	23	28	13	3	-	-	17.3
Mauritius	-	-	2	-	2	17	11	1	-	19.2	Niue	-	-	1	4	4	1	-	-	-	17.5
Reunion	-	-	-	3	3	6	3	-	-	18.6	Cook Islands										
NW Madagascar	-	-	1	3	9	5	14	1	3	19.2	Penrhyn	-	1	2	9	12	11	-	-	-	17.8
Kenya	-	-	-	1	2	1	-	-	-	18.0	Aitutaki	-	-	-	-	-	1	-	-	-	
Zanzibar	-	-	-	2	12	1	6	-	-	18.5	Rarotonga	-	-	3	3	4	2	1	1	-	17.8
South Africa, Natal	-	-	-	5	10	8	3	2	-	18.5	Palmerston	-	-	1	-	1	1	-	-	-	17.7
Cocos-Keeling Islands	-	1	8	14	10	9	5	1	-	17.8	Tahiti & Moorea	-	3	7	15	9	10	2	-	-	17.5
Japan											Howland Island	-	1	4	13	7	9	3	-	1	17.8
Misaki & Enoshima	2	7	10	16	3	-	1	-	-	16.4	Baker Island	-	-	-	7	4	1	1	-	-	17.7
Chiba Prefecture	-	-	-	4	1	-	-	-	-	17.2	Marshall Islands										
Shirahama	1	1	2	3	3	1	-	-	-	17.1	Bikini	-	2	5	14	11	7	-	-	-	17.4
Tanegashima	-	5	5	8	3	2	-	-	-	16.6	Enewetok	-	2	2	2	2	-	-	-	-	16.5
Okinawa	1	2	6	15	17	3	2	-	-	17.3	Kwajelein	-	1	1	1	1	1	-	-	-	17.0
Gulf of Thailand											Kapingamarangi	-	1	2	5	1	2	-	-	-	17.1
Goh Samet Island	-	2	13	16	12	-	2	-	-	17.0	Phoenix Islands										
Ko Kra Island	-	2	6	3	-	3	-	-	-	16.7	Enderbury	-	-	1	17	16	11	3	2	-	18.1
Philippines											McKean	-	-	5	16	9	4	-	-	-	17.4
Batanes Islands	-	3	8	10	12	7	1	-	-	17.4	Line Islands										
Mindoro Island	-	1	2	9	10	6	-	-	-	17.6	Caroline	-	-	2	9	1	2	-	-	-	17.2
Siquijor Island	-	-	2	2	2	2	-	-	-	17.5	Christmas	-	-	4	11	10	18	3	-	-	18.1
Bonin Islands	-	1	-	-	-	1	-	-	-	17.0	Palmyra	-	-	-	2	5	5	1	-	-	18.4
Marcus Island	-	13	18	15	5	1	-	-	-	16.3	Rangiroa	-	1	13	13	6	3	1	-	-	17.0
Guam	-	-	6	10	1	-	-	-	-	16.7	Marquesas Islands	-	-	1	11	20	7	1	-	-	17.9
Sumatra	-	-	-	1	-	-	-	-	-		Mangareva	-	-	-	6	12	3	2	-	-	18.0
Halmahera	-	1	1	2	-	-	-	-	-	16.2	Rapa	-	-	-	2	-	3	-	-	-	18.2
Flores	-	-	-	4	-	-	-	-	-	17.0	Pitcairn	-	-	-	-	2	1	-	-	-	18.3
Trobriand Islands	-	1	3	12	10	16	6	4	-	18.4	Wake Island	-	1	3	5	15	2	3	-	-	17.8
Australia											Gilbert Islands										
Point Quobba, WA	-	-	-	1	1	2	-	-	-	19.0	Onotoa	-	-	4	5	3	7	-	-	-	17.7
Cape Range WA	-	-	-	1	-	1	-	-	-	18.0	Abaiang	-	-	1	3	2	3	-	-	-	17.8
Lizard Island GBR	-	1	1	5	5	3	3	3	-	18.4	Arorae	-	-	3	2	-	1	-	-	-	17.8

Table 30.—Frequency distributions for certain lateral-line characters in specimens of Istiblennius edentulus ≥30 mm SL.

	Continuous portion extends to vertical from base of dorsal-fin element[1]							
	9	10	11	12	13	14	15	16
Frequencies	1	14	34	43	50	19	1	2

	Number of disconnected bi-pored tubes																
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Frequencies	1	4	5	10	15	21	31	32	10	23	14	6	1	4	1	-	3

	Posteriormost bi-pored tube at vertical from base of dorsal-fin element[1]																	
SL (mm)	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	x̄	SD
30-39	-	1	1	3	2	2	2	3	1	-	-	1	-	-	-	-	18.1	2.6
40-49	-	-	-	-	2	2	2	5	8	3	2	-	-	1	-	-	20.3	1.6
50-59	-	-	2	-	3	1	7	3	4	-	1	3	-	-	-	-	19.6	2.5
60-69	-	-	1	-	3	-	5	6	5	3	2	-	-	-	-	-	19.9	2.0
70-79	1	-	-	-	-	1	4	1	2	2	6	4	-	-	-	-	21.3	2.7
80-89	-	-	1	1	-	-	1	2	-	-	1	1	-	1	-	2	21.9	4.6
90-99	-	-	-	-	-	1	3	3	1	1	1	2	1	-	-	-	21.1	2.3
100+	-	1	-	-	1	2	5	2	3	8	4	4	4	1	3	1	22.2	3.1
totals	1	2	5	4	11	9	29	25	24	17	17	15	5	3	3	3		

[1]Counting posteriorly from anteriormost element (spine). If position was below interspace between two elements, more posterior element is tallied in table.

mm SL (various localities), lack black pigment distally on pectoral fins.

GEOGRAPHIC VARIATION.—We address here why we treat *I. edentulus* as a single species rather than as a complex of species with allopatric distributions. In summary, the decision is mainly an arbitrary and pragmatic one, not necessarily consistent with the way we treat other putatively monophyletic groups in *Istiblennius* and *Blenniella*. Our decision was influenced by the fact that males from the various *I. edentulus* populations are, in general, indistinguishable, with differences manifested mainly by shifts in modes and means for meristic characters (Tables 27 to 29). Female specimens from some localities, however, are, or are almost, completely separable from those from some other localities based on color pattern, development of a fleshy head crest, number of infraorbital pores, or meristics, or on some combination of these characters; however, more than one type of female can occur at a particular locality, but only one type of male.

The development of the female head crest and color pattern is complex and may vary individually and apparently ontogenetically among specimens from a single locality. Method and state of preservation of museum specimens also may strongly affect the appearence of specimen color pattern, which is conceivably influenced as well by season, sexual maturity, and general coloration of the bottom on which the specimens were inhabiting when collected. In the discussion that follows, we may have biased our findings by excluding from consideration numerous specimens that we believe are faded or otherwise artifactually discolored.

In spite of the abundance of representative specimens from a great number of localities, we did not have enough specimens of the proper size or condition on which to fully characterize the populations from each of the localities represented by our samples.

Following is a summary discussion of some of the main population variations represented by our material. The discussion concentrates first on color pattern, followed by discussions

Table 31.—Frequency distributions for number of infraorbital pore positions occupied by more than one pore (IPPMP) between 2 and 4 o'clock on postorbital margin in specimens of *Istiblennius edentulus* from various localities.

Standard length class (mm)	30					40					50					60						70						80					≥90				
Number of IPPMP	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	5	0	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Sudan coast, mid-Red Sea	-	3	5	-	-	-	6	5	-	-	-	5	3	1	-	-	2	3	2	-	-	-	1	1	2	-	-	3	5	1	-	-	-	1	2	-	-
Difnein Island, south Red Sea	1	8	4	-	-	-	9	10	1	-	-	8	8	-	-	-	3	1	1	1	-	-	1	1	1	-	-	-	-	1	-	-	-	-	-	-	-
Diego Garcia, Chagos Arch.	-	10	-	-	-	1	10	1	-	-	-	12	4	-	-	-	7	2	1	-	-	-	2	2	-	-	-	3	-	-	-	-	2	-	2	-	-
St. Brandon's Shoals	-	10	-	-	-	-	10	-	-	-	-	6	2	-	-	-	8	1	-	1	-	-	4	-	-	-	-	3	1	-	1	-	3	3	1	-	-
Maldives Islands	-	6	3	-	-	-	8	1	-	-	-	4	-	-	-	-	2	2	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Misaki and Enoshima, Japan	4	7	1	-	-	1	3	1	-	-	-	1	-	-	-	-	1	-	1	-	-	-	4	-	-	-	-	3	1	-	-	-	3	3	5	2	-
Okinawa	-	9	1	-	-	1	10	-	-	-	1	5	1	-	-	-	8	-	2	-	-	-	7	1	-	-	-	1	4	1	-	-	3	-	1	1	-
Gulf of Thailand[1]	-	11	3	-	-	-	7	3	1	-	-	1	1	-	-	-	3	1	1	-	-	-	6	2	4	-	-	5	2	1	1	-	1	3	6	1	-
Batanes Islands, Philippines	-	17	-	-	-	-	4	4	2	-	-	4	1	2	-	-	2	2	2	-	-	-	1	1	-	-	-	2	2	1	-	-	3	-	1	-	-
Papua New Guinea[2]	-	6	1	-	-	-	24	-	-	-	1	14	1	1	-	-	9	7	1	-	-	1	5	-	-	-	-	1	-	-	-	-	-	1	-	-	-
One Tree Id, Qd, Australia	-	-	-	-	-	-	9	1	-	-	-	4	5	1	-	-	5	7	2	-	-	1	2	2	3	1	1	4	2	3	-	-	1	-	-	1	-
Bikini, Marshall Islands	-	15	1	-	-	-	10	-	-	-	-	7	2	-	-	-	3	3	2	-	-	-	5	1	4	-	-	3	3	2	-	-	2	-	2	-	-
Rotuma	4	9	1	-	-	-	9	-	-	-	1	16	1	-	-	-	5	2	1	-	-	-	3	-	1	-	-	-	-	-	-	-	1	-	-	-	-
Marcus Island	1	3	-	-	-	2	11	1	-	-	-	5	-	-	-	-	14	2	-	-	-	-	3	5	2	-	-	-	-	1	1	-	-	-	2	7	5
Wake Island	-	1	1	-	-	-	-	3	-	-	-	-	2	-	-	1	4	1	2	-	-	-	3	-	-	-	-	1	2	1	1	-	2	-	2	-	-
McKean Island	-	-	-	-	-	-	4	-	-	-	1	-	1	-	-	-	5	-	-	-	-	-	7	3	2	-	-	2	3	1	-	-	-	2	4	3	-
Palmyra, Line Islands	-	-	-	-	-	-	5	1	-	-	-	4	-	-	-	-	3	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Caroline, Line Islands	1	7	-	-	-	-	10	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marquesas Islands	-	4	9	7	1	-	-	1	8	5	-	-	-	3	9	-	-	-	2	9	-	-	-	-	-	5	2	-	-	-	-	1	-	-	-	1	1
Rangiroa, Tuamotus	-	11	-	-	-	-	10	1	-	-	-	6	2	-	-	-	2	-	-	-	-	-	3	1	1	-	-	4	1	-	-	-	-	-	-	1	1
Mangareva, Gambier Islands	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-	3	4	4	2	1	-	1	1	7	1	1	-	-	-	1	-	-	-	-	3	-

[1] One specimen with 0 IPPMP in ≥90 mm class not entered in table.
[2] Here includes only Trobriand and Bonarua islands and Madang.

of crest development, meristics, and infraorbital pores.

Color Pattern. At all localities, except the Line Islands, where *I. edentulus* occurs, the color pattern of females smaller than about 50 mm is indistinguishable from that of males. The pattern on the body consists mainly of paired, dark bands. This pattern persists throughout life in males (Figures 40, 41), but may change in females. At most localities, females 55 to 60 mm SL begin to exhibit a pattern of small, dark spots posteriorly on the body (e.g., Figure 36*a,b*). With increase in SL, the distribution of spots expands to include the dorsal and anal fins, posterior half of the body, and, occasionally, the base of the caudal fin (e.g., Figures 36*c*, 37*a*). The first spots appear distally in the segmented-ray portion of the dorsal fin. Prior to the appearance of these spots, the dorsal fin appears to be uniformly blackish or exhibits oblique, blackish, streak-like markings.

Grant (1987:335, fig. 715) provides an excellent color photograph of a large, fresh female specimen from Queensland that exhibits a fully developed adult color pattern. Yoshino (in Masuda et al., 1984, pl. 268: fig. J) provides an excellent color photograph of a large, fresh male specimen from Japan (probably Okinawa) with fully developed adult color pattern (compare also Grant's figure of the female with Yoshino's, pl. 268: fig. K). Myers (1989:211, fig. 5c) presents a good black-and-white halftone of a male and female from Guam.

Female specimens from Papua New Guinea and neighboring islands may be heavily spotted by 55 mm SL. Females from Christmas and Caroline islands (both Line Islands) are unique in having a heavily spotted pattern manifested by 43 and 38 mm SL respectively (Figure 38*d*).

At McKean Island (Phoenix Islands), large, comparably sized females may exhibit either spotted female or nonspotted male-type patterns (Figures 38*a,b*). Other Phoenix Islands' females and those at more remote Howland and Baker islands exhibit normal female spotting.

Large females from Penrhyn, Cook Islands (Figure 38*c*), most localities in Japan north of about 32°N (36*c*), and the Bonin Islands have male-like body coloration. An extended discussion of the Japanese specimens is presented at the end of this section.

Females 49 to 74 mm SL from the Marquesas Islands may exhibit spotting, which, on the body, is usually restricted to the ventral half of the caudal peduncle (Figure 37*c*). Although larger females, up to 91 mm, were available, they were from a collection in which the color pattern of all specimens, both males and females, was uniformly dark. We are uncertain whether this pattern accurately reflects the pattern of these specimens when fresh, or if it is an artifact, the result of poor preservation in isopropyl alcohol.

Females from Elat (Gulf of Aqaba–north end Red Sea), Sudan coast (middle Red Sea), and Difnein Island (southern Red Sea) either have a male-like pattern or bear a few relatively large spots on the caudal peduncle (Figure 39*a,b*). Randall (1983, figure on page 154) illustrates a fresh Red Sea female

specimen of unspecified size that shows a complete absence of body spots.

Two small (52 to 56 mm SL) females (only ones available) from Mait, Somalia (in the Gulf of Aden, into which the Red Sea opens), exhibit well-developed spots on the caudal peduncle. Two females, 63 and 85 mm SL, from Mahé (Seychelles, Indian Ocean) have a few indistinct spots on the caudal peduncle, and another, 72 mm, is unspotted and male-like in pattern, whereas a female, 71 mm, from nearby Curieuse, has well-developed spotting (and a fleshy crest—see next section). Females from the Comoros Islands, including one of the largest specimens of *I. edentulus* examined, 132 mm SL, have indistinct spots on the caudal peduncle (as do the 63 and 85 mm Seychelles females) and, variably, in the dorsal fin. At similar sizes, females from Aldabra, Agalega, and St. Brandons (islands scattered throughout the western Indian Ocean) are typically very pale, but the darker specimens among these appear to have patterns closely similar to the most common Pacific female pattern (Figure 39*c,d*). Females, 51 to 88 mm SL, from Mauritius and Reunion, however, have a male-like in color pattern. Fleshy Head Crest. With rare exception, male specimens 30 mm SL and larger from all localities have either well-developed crests or clear indications of a ridge-like crest precursor.

At all but a few localities (i.e., Marquesas Islands, Bonin Islands, main islands of Japan, Red Sea, Enderbury, Mangareva, Marcus) where sizable numbers of females are available, females of all sizes usually lack any indication of a crest or its ridge-like precursor. When a crest or its precursor is present in females, it is usually restricted to specimens larger than about 70 mm SL. In particular, a precursor ridge or crest was not present in any Gulf of Thailand female, including many large specimens, that we examined. An inconspicuous crest precursor, at most, is present in large Indian Ocean females, with the notable exception of a 71 mm spotted female from Curieuse, Seychelles, which has a low but distinct crest (0.8 mm high).

At the exceptional localities, all or almost all females at or larger than a certain size bear a crest or precursor ridge, and at all these localities, except Japan, the size (length, height) of the female crest is always smaller than that of males of comparable SL. In Japan, the female crest may be equal to or larger than the crest of males of comparable SL.

All females longer than 37 mm SL from the Marquesas, longer than about 57 mm SL from Mangareva, longer than about 70 mm SL from Marcus, and longer than 35 mm from the main islands of Japan, have crests or definite ridge-like precursors. At the Bonin Islands (= Ogasawara), the smallest females available were about 50 mm SL (also includes data reported by Fukao, 1985), and all had small crests. Most females longer than about 60 mm SL from the Red Sea (including Gulf of Aqaba), 70 mm SL from Mangareva (Gambier Islands), and 65 mm SL from Enderbury (Phoenix Islands) have ridge-like precursors or low crests.

The presence of precursor ridges or crests in females from
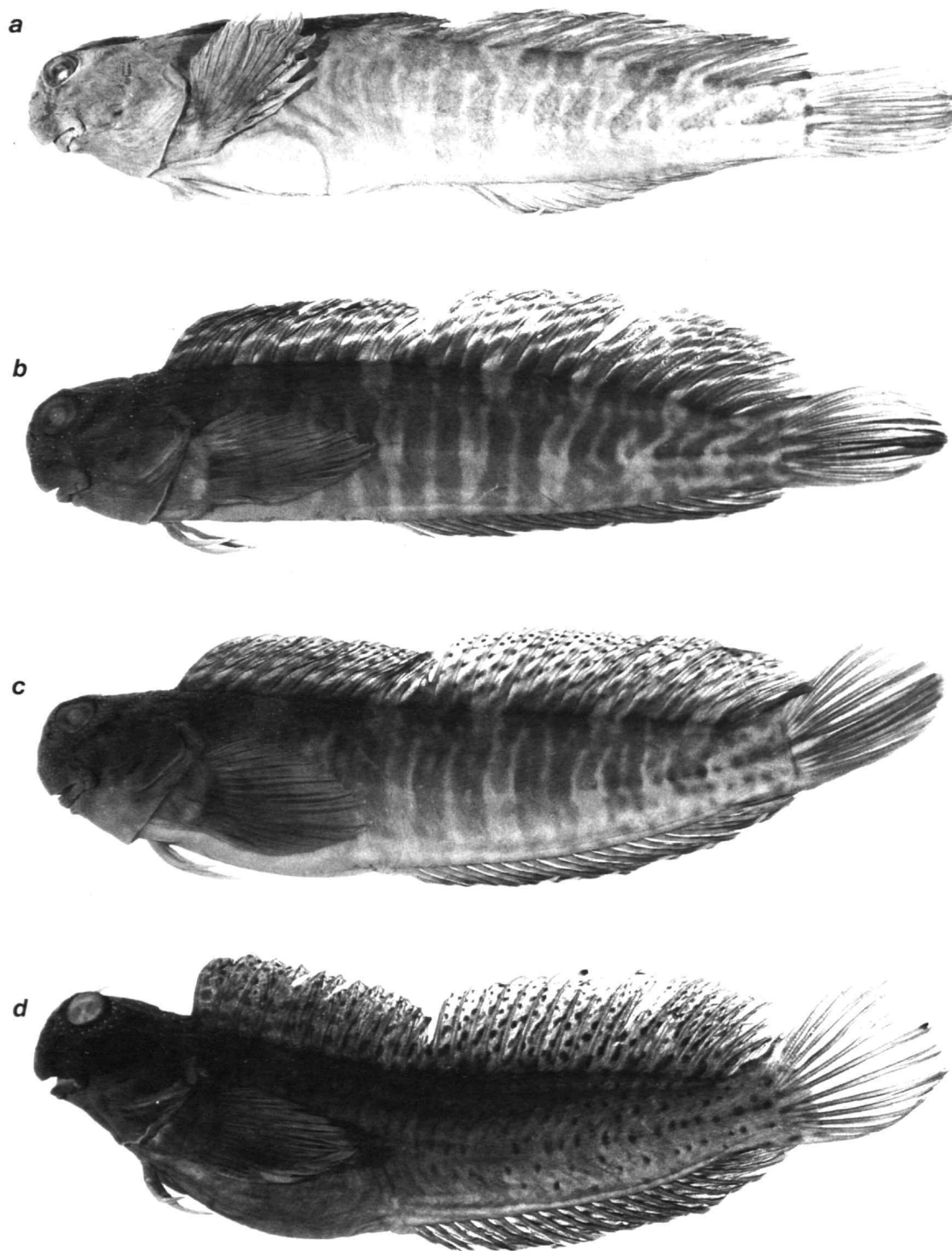
FIGURE 36.—*Istiblennius edentulus*, females: *a*, USNM 71115, 99 mm SL, Misaki, Sagami, Japan (right side reversed; head crest only partially visible); *b–c*, USNM 296266, 56 and 74 mm SL, Okinawa; *d*, USNM 203560, 81 mm SL, Okinawa (photographs by T.B. Griswold).
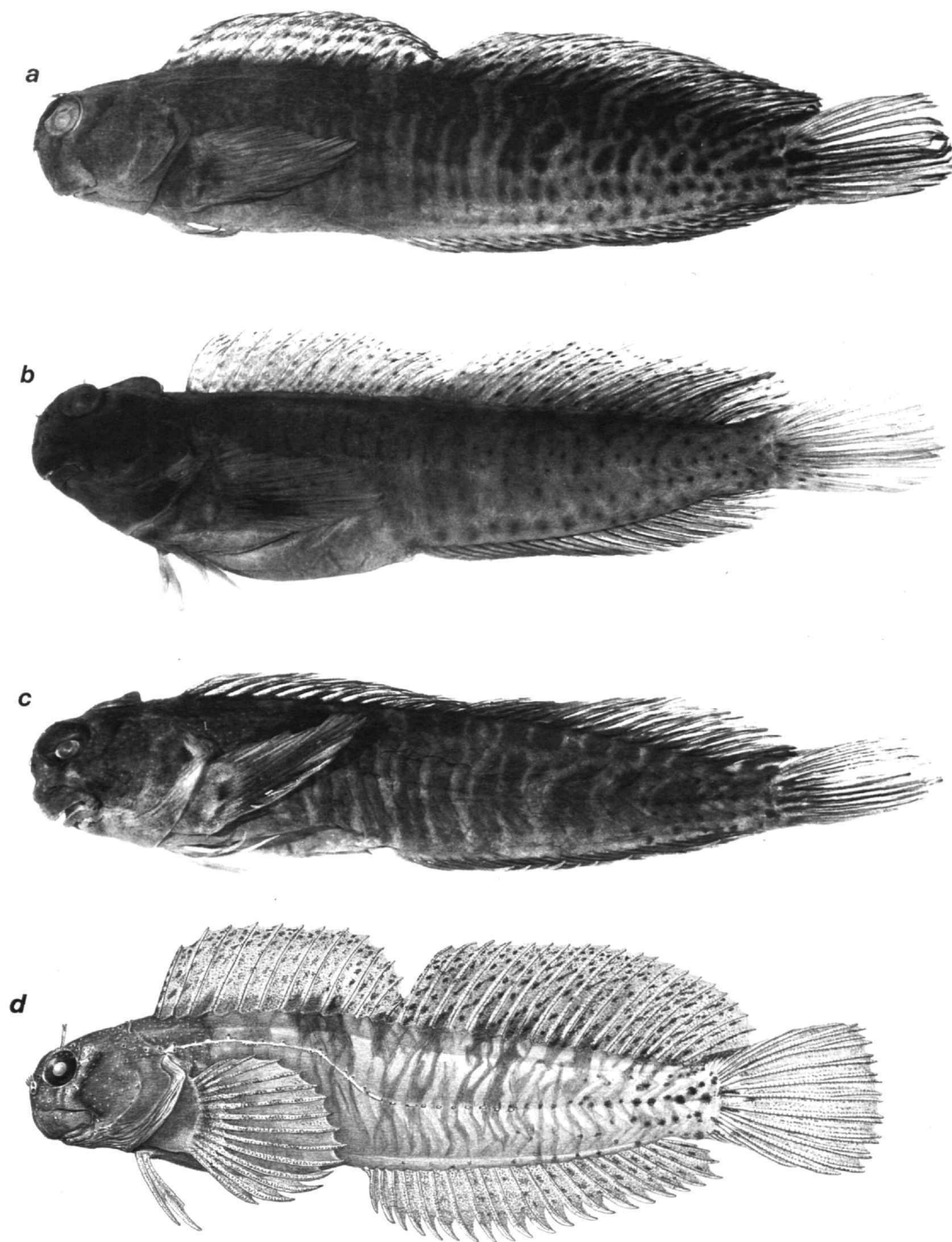
FIGURE 37.—*Istiblennius edentulus*, females: *a*, USNM 283164, 70 mm SL, Rotuma (for male see Figure 40*a*); *b*, NMNZ P.15705, 72 mm SL, Palmerston, Cook Islands (for male see Figure 40*b*); *c*, AMS I.21773-001, 56 mm SL, Nuku Hiva, Marquesas; *d*, USNM 229909, 94 mm SL, Taiwan (for male see Figure 40*c*) (photographs by T.B. Griswold; drawing by P.K. Hollingsworth).
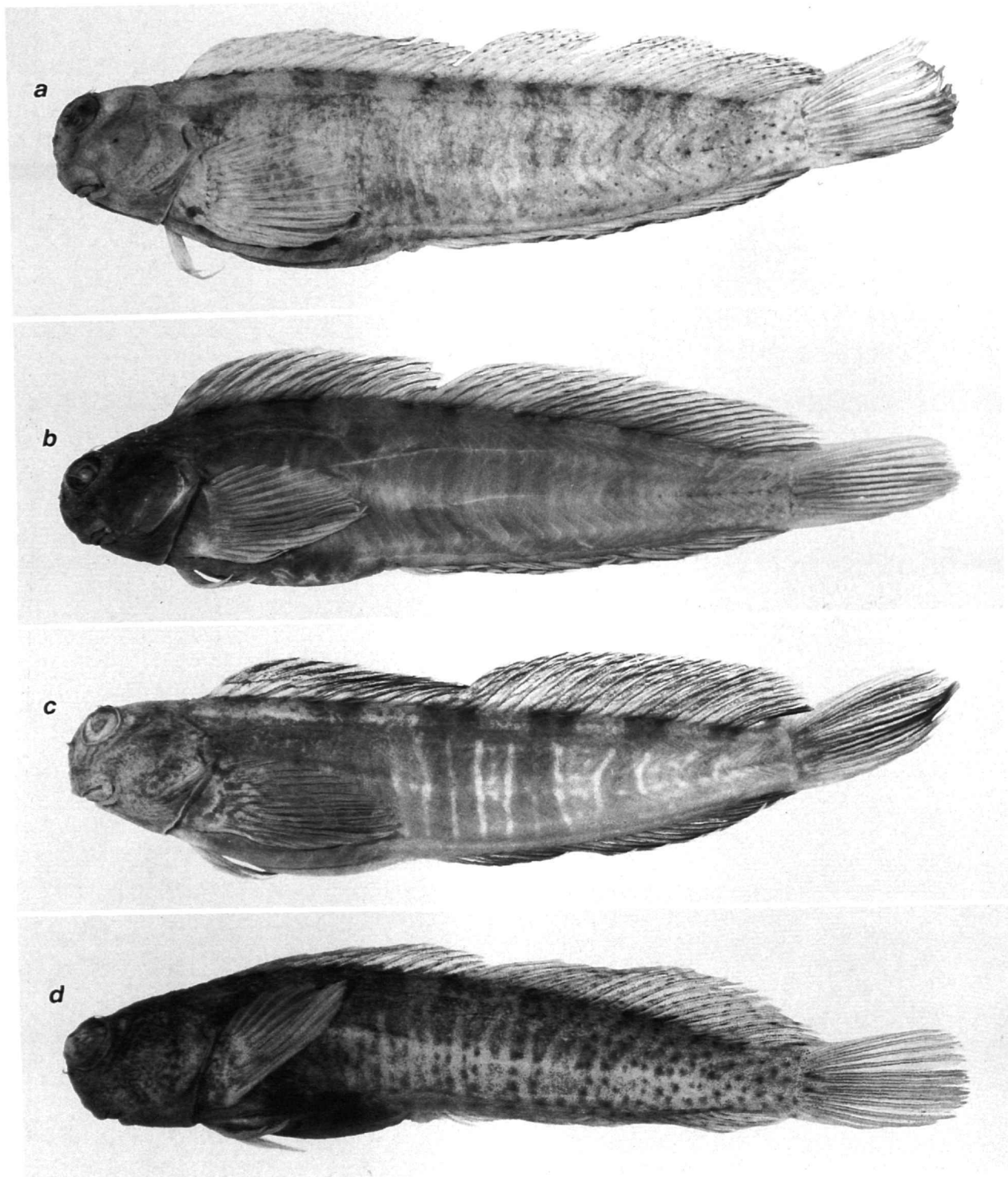
FIGURE 38.—*Istiblennius edentulus*, females: *a*, USNM 296219, 90 mm Sl, McKean, Phoenix Islands; *b*, USNM 278399, 89 mm SL, McKean, Phoenix Islands; *c*, USNM 296211, 75 mm SL, Penrhyn (= Tongareva), Cook Islands (for male see Figure 41*c*); *d*, USNM 296117, 44 mm SL, Caroline, Line Islands (for male see Figure 41*d*) (photographs by T.B. Griswold).
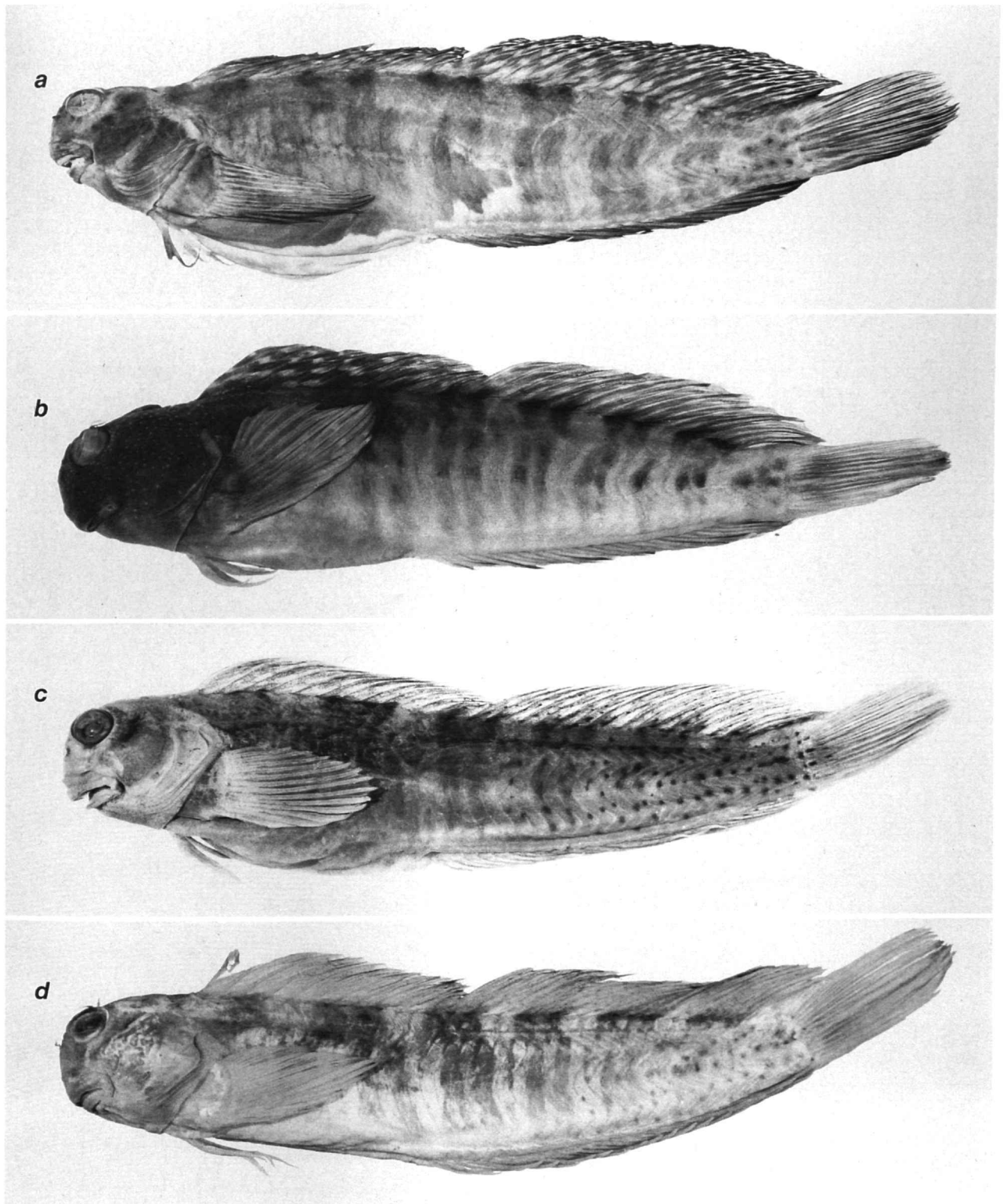
FIGURE 39.—*Istiblennius edentulus*, females: *a*, HUJ F-4797, 106 mm SL, Elat, Israel; *b*, USNM 204514, 68 mm SL, Difnein Island, Ethiopia (for male see Figure 41*a*); *c*, USNM 296412, 89 mm SL, Aldabra; *d*, USNM 292532, 93 mm SL, St. Brandon's Shoals (photographs by T.B. Griswold).
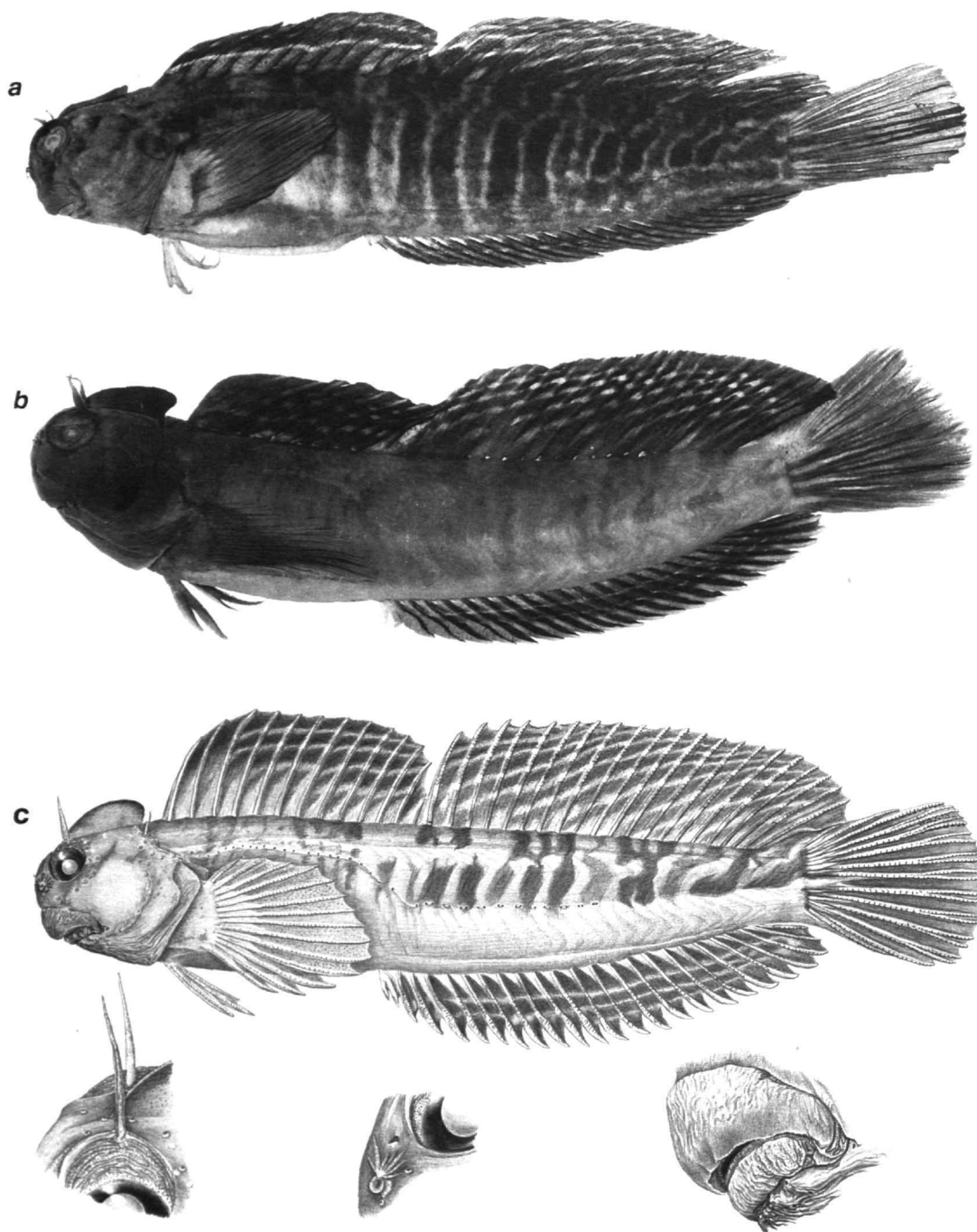
FIGURE 40.—*Istiblennius edentulus*, males: *a*, USNM 283164, 64 mm SL, Rotuma (for female see Figure 37*a*); *b*, NMNZ P.15705, 63 mm SL, Palmerston, Cook Islands (for female see Figure 37*b*); *c*, USNM 229910, 89 mm SL, Taiwan, with enlarged views of orbital and nasal cirri and lips (for female see Figure 37*d*) (photographs by T.B. Griswold; drawings by P.K. Hollingsworth).
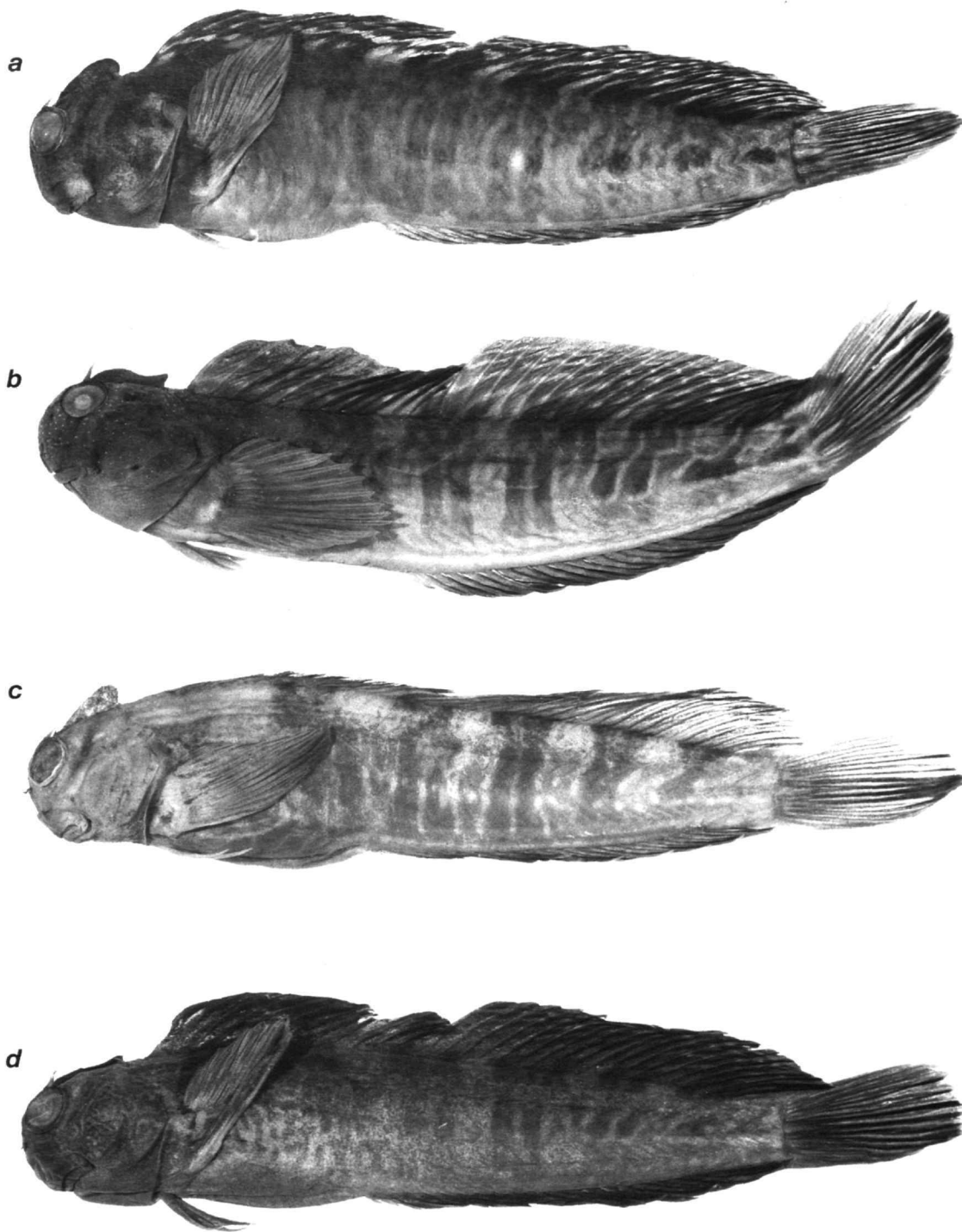
FIGURE 41.—*Istiblennius edentulus*, males: *a*, USNM 204514, 67 mm SL, Difnein Island, Ethiopia (for female see Figure 39*b*); *b*, USNM 278385, 77 mm SL, Okinawa (for females see Figures 36*b*–*d*); *c*, USNM 296211, 62 mm SL, Penrhyn, Cook Islands (right side reversed; for female see Figure 38*c*); *d*, USNM 296117, 59 mm SL, Caroline, Line Islands (for female see Figure 38*d*) (photographs by T.B. Griswold).

other localities is considerably variable, but a ridge is not usually present in females under 60 mm SL and a crest in females under 80 mm SL (but note 72 mm SL female from Palmerston Island, Figure 37b).

Dorsal- and anal-fin elements. Means and modes for dorsal-and anal-fin elements and vertebrae (Tables 27, 28) vary considerably and somewhat irregularly throughout the distribution of *Istiblennius edentulus*. Notable are the very low means for Gulf of Aqaba and Red Sea specimens and the very high means for western Indian Ocean specimens (particularly St. Brandons Shoals, Mauritius, Reunion), and specimens from Bonin, Marcus, McKean, Niue, Mangareva, Rapa, Penrhyn, and Pitcairn islands, Western Australia, and the more northern Japanese localities. Several of these localities were noted above for their variations in color pattern and possession of a head crest in females. Most notably absent from the localities where specimens have either low or high means are the Marquesas Islands, where means, although intermediate, are somewhat lower than those for specimens from the nearby Tuamotus.

Epineurals. Means for the serial number of the posteriormost vertebra bearing an epineural (Table 29) also vary considerably geographically and usually parallel means for the other meristic characters. Mean number of epineural ribs for specimens from northern Japan and Marcus Island, however, are low, and those for specimens from NW Madagascar are high, whereas means for the other meristics of specimens from these localities are just the opposite.

Infraorbital pores. Although not studied for all populations, there is evidence that geographic variation exists in the nature of the infraorbital sensory pore positions (Table 31). This variation, which is independent of sex, is complex, masked by ontogeny, and may not be obvious in specimens less than 30 mm or more than 80 mm SL.

Between 1 o'clock and 5 o'clock on the postorbital margin, there are normally 6 (rarely 5 or 7) regularly placed sensory pore positions adjacent to the margin. In almost all specimens over 25 mm SL, the third from dorsalmost pore (at 3 o'clock) is connected posteriorly by a horizontal subcutaneous canal to one or more pores. Depending on SL and population, each of the other pore positions is occupied by 1 or more pores, with multiple pores at a position connected by a subcutaenous canal, which may be quite short and directed horizontally, obliquely, or vertically (when 2 pores are present at the 2 o'clock position, the canal is very short and may be vertical). With the exception of Marquesas Islands specimens, it is uncommon to find multiple pores at more than 2 pore positions in specimens less than 60 mm. At more than 59 mm, it is common to find multiple pores at 3 or more positions.

The Marquesas specimens are distinctive in usually having more than 2 multipored positions (up to 4) at sizes less than 60 mm SL, and all size classes tend to have more multipored positions than those of other populations. In the largest size class, ≥90 mm, specimens from Marcus, Marquesas, Rangiroa,

and Mangareva tend to have relatively more individuals with 4 or 5 positions with multiple pores than do specimens from other localities.

From the information presented on variation in meristics, color pattern, head crest, and pores, several distinctive populations can be discerned from among those studied: Marquesas Islands, main Islands of Japan, Bonin Islands (= Ogasawara), Marcus Island, Red Sea, St. Brandon's-Mauritius-Reunion, northwest Madagascar, McKean Island, Mangareva, etc. For most of these populations, a male specimen is usually inadequate for recognition of the specimen's locality of origin. If the specimen is a female, the chances for recognizing its provenance are better, but, even so, the specimen must be of a certain size and its color pattern well preserved. Even with these conditions satisfied, assignment of most individual females would probably be uncertain. Building a satisfactory key to the *I. edentulus* populations is, therefore, not possible.

There are many localities from which adequate numbers of specimens of *I. edentulus* are unavailable or, if available, were not studied (see "Material examined"). These localities might also harbor populations with reasonably distinctive characteristics. Even for those populations studied in most detail, other taxonomic characters probably exist that would extend the number of recognizable populations. At the risk of erring on the side of conservatism, we have chosen to recognize only one species-group name for the *I. edentulus* complex of populations.

The most readily recognizable population in the complex is that from the Marquesas, which is prominent in having an increased number of multipored infraorbital pore positions (in both sexes), particularly in small specimens, and in having a head crest in all females over 37 mm SL. The main islands of Japan are the only other areas where females exhibit evidence of crests at sizes less than 40 mm SL (as small as 35 mm).

As a final comment, females with well-developed head crests are almost entirely restricted to the Red Sea, Japan (including Bonin Islands), and Pacific-plate islands; male type color pattern in large females is restricted to the same localities and Mauritius and, adjacently, Reunion.

THE *Istiblennius enosimae* PROBLEM

Istiblennius enosimae has long been recognized by students of the Japanese biota as distinct from and allopatric to *I. edentulus*. The characters given for distinguishing these two forms are that female *I. enosimae* have a head crest and color pattern like those of males, whereas female *I. edentulus* lack a head crest and have a different color pattern from that of males. For Japan, we have seen specimens of the *enosimae*-form female only from the main islands, from Chiba Prefecture, Honshu (~35°30′N), south to Tanegashima (~32°30′N), and from the Bonin Islands. Until recently, the *edentulus* form had not been reported to occur north of Tanegashima.

Yoshino (in Masuda et al., 1984:300) reported that *I. edentulus* occurs in Japan as far north as Wakayama Prefecture (~34°N), but delimited the distribution of *I. enosimae* only generally: southern Japan. Fukao (1985:104–108) reported two types of female *I. edentulus* in his collections from Shirahama, (~33° N), Wakayama Prefecture: those that resemble males in color pattern (unspotted) and have a crest (*enosimae*-form) and those that differ from males in having a spotted color pattern and lack a crest (*edentulus*-form). He had 17 *enosimae*-form females, but only 5 *edentulus*-form females. The mean number of dorsal-fin elements of his *edentulus* females was 0.82 less (.005>p>.002) and the mean number of segmented anal-fin rays 0.51 more (.10>p>.05) (Table 28) than for the *enosimae*-form females.

Fukao could find no basis for recognizing more than one type of male in his Shirahama specimens. The mean number of dorsal-fin elements for the Shirahama males (both forms together?) was much lower than that of the Shirahama *enosimae*-form females and slightly higher than that of the Shirahama *edentulus*-form females. The mean number of anal-fin elements for the males was, conversely, much higher than the mean for the *enosimae* females, but slightly lower than the mean for the *edentulus* females. Males of the *I. edentulus* species complex almost always have higher mean numbers of fin elements (and vertebrae) than do females. The Shirahama males and Shirahama *edentulus* females have fin-element means closely similar to those of "pure" *I. edentulus* females from Okinawa.

Based on the means of "pure" *enosimae*-form specimens from other Japanese localities, and "pure" *I. edentulus*-form specimens from Okinawa (compare in Table 28), it appears that Fukao's Shirahama males are probably assignable to the *edentulus* form, rather than the *enosimae*-form, as he suggested. This conclusion is only partially supported by data from our Shirahama specimens. The mean for dorsal-fin elements for the males we examined is very similar to the means of males from more northern Japanese localities, and is significantly different (.05>p>.02) from that of Fukao's males (Table 27). The segmented anal-fin ray mean of the Shirahama specimens we examined, however, is identical to that of both Fukao's males and males from more northern Japanese localities, and, thus, is neutral in its bearing on our conclusion.

It may be, as Fukao (1985:106) proposed, that the Shirahama *edentulus*-form specimens originated as the pelagic larvae of southern populations and were transported north into *enosimae*-form territory by the Kuroshio current. The *edentulus* form is not known otherwise from further north than about 27°N in the chain of islands extending from Okinawa north to Chiba Prefecture. On the other hand, the *enosimae* form is known at least as far south as 32°30′N. It would be of interest to know if the two forms are reproductively isolated, or if not, whether "swamping" may mask expression of the *edentulus* female form in *enosimae*-form territory.

Fukao (1985) was ambivalent about whether to recognize *I. enosimae*, and also mentioned that the Bonin Islands' specimens appeared to represent a third form. We appreciate his difficulties.

WESTERN AUSTRALIAN SPECIMENS OF *Istiblennius edentulus*

We have 11 specimens of *Istiblennius edentulus* from Western Australia (see material examined section): 2 males (73 and 98 mm SL) from Cape Range National Park, 2 km S Yardie Creek, 22°21′S, 113°48′E; male (44 mm) and 2 females (76 and 108 mm), Rosemary Id, Dampier Arch.; 5 females (85 to 113 mm) and 1 male (111 mm), Point Quobba, 24°29′S, 113°25′E.

The 2 males from Cape Range National Park, have well-branched (4 to 6 free tips) cirri on each eye. Of the other 9 specimens, 2 females (1 each from Rosemary Island and Point Quobba) have branched cirri (2 or 3 tips) on each eye; the other 7 specimens have simple cirri. Additionally, the larger male from Cape Range National Park has very fine, but noticeable, crenulations on the ventral margin of the upper lip at the corners of the lip. The 11 specimens are otherwise unremarkable for the species. The females are spotted and 2 have low, but distinct, crests and one has a low ridge on the head dorsally.

Although branched orbital cirri occur occasionally in *Istiblennius edentulus*, particularly in large specimens, we find the proportion of specimens (4 of 11) from Western Australia with branched cirri unusual. Additionally, we have not found lip crenulae in any other specimen of the species, although fine, fleshy pads may be present on the hidden, buccal surface of the upper lip.

COMPARISONS AND RELATIONSHIPS.—We have no intuitive opinion about the interrelationships of *I. edentulus*. If *I. enosimae* should prove to be valid, we would believe that it and *I. edentulus* would be sister groups. Our phylogenetic analysis indicates that *I. edentulus* forms a clade with *I. rivulatus*, *I. meleagris*, and *I. dussumieri*, but this clade is only weakly supported and we are not convinced of its monophyly.

Most recently, Strasburg (1955) suggested that *I. zebra* was the Hawaiian form of *I. edentulus*. He treated the 2 species as 1 in discussing the effects of temperature and latitude on meristics of the combined species. Although *I. edentulus* does not occur in Hawaii, we believe Strasburg combined the wrong 2 species, even though his conclusions may have been correct.

Strasburg (1955), who lacked data for Japanese specimens of *I. edentulus* (the *I. enosimae* of authors), noted that *I. zebra* differed from *I. edentulus* mainly in lacking nape cirri. He missed some other important characters: the crenulate lower lip, shorter continuous portion of the lateral line, and the often simple nasal cirrus of *I. zebra*. We believe that these characters indicate that *I. zebra* is more probably the sister species of *I. bellus*, which occurs sympatrically with *I. edentulus*, and, as does *I. edentulus*, has lower meristics than *I. zebra* (hence,

would have supported Strasburg's correlations of temperature and latitude with meristics).

DISTRIBUTION (Figure 67, based almost entirely on specimens we examined; a few localities entered based on literature).—*Istiblennius edentulus* is distributed along most of the warm, rocky shores of the Indo-west and central Pacific oceans, including the Red Sea and Persian Gulf, as far north as about 35°N on the coast of Japan, south to about 30°S on the east coast of South Africa and 33°51'S on the east coast of Australia, east to Pitcairn Island, but excluding Hawaiian, Johnston, and Easter islands, where it is notably absent.

Common on rocky flats in intertidal areas (a type of habitat notably absent at Johnston Island). *Istiblennius zebra*, which is not a sister group of *I. edentulus*, occupies the ecological niche in the Hawaiian Islands that *I. edentulus* would occupy. *Istiblennius zebra* is also absent from Johnston Island. According to Grant (1987:435), *I. edentulus* is often found in the company of *I. meleagris*, an Australian endemic, in the intertidal area on the Queensland cost.

NOMENCLATURAL DISCUSSION.—The oldest name for a species of *Istiblennius*, *Blenniella*, or *Paralticus* is *Blennius edentulus* Schneider (in Bloch and Schneider, 1801:172), described from Huahine (variably spelled Huaheine and Huahaine in the literature), Society Islands. Because Schneider's name has priority over more than 100 nominal species of these genera, it is important to establish the identity of the form to which his name applies.

Schneider clearly indicated that his description of *Blennius edentulus* was taken from J.R. Forster's unpublished manuscript description of *Blennius truncatus*. No type material was specified in either description, and there is no specimen that can be considered unequivocally as a type of either nominal species. Furthermore, because the first published appearance of *Blennius truncatus* must be considered as a junior synonym, this name was unavailable in 1801.

It is not possible to identify the species to which Schneider's and Forster's descriptions refer solely on the basis of their descriptions, which are incomplete and misleading. Given the type locality of *Blennius edentulus*, however, together with the heretofore unpublished illustration (Figure 42) of *Blennius truncatus* prepared by Forster, one can be reasonably certain that the species they described is a species of *Istiblennius* and the one that is commonly identified as *Istiblennius edentulus*. The illustration depicts a female, and although the description reports the orbital cirrus as simple, the illustration, interestingly, shows the cirrus with a fine, tiny branch, such as occurs occasionally in *I. edentulus*. One might interpret this branch as a slip of the artist's brush. The small nape cirrus, which is characteristic of current concepts of *I. edentulus*, is not illustrated, but could well have been overlooked by Forster. (The illustration of *Blennius truncatus* has not been generally referred to; see Whitehead, 1978, for an historical discussion of Forster's illustrations).

In order to avoid possible future confusion and to stabilize the nomenclatural application of *Salarias edentulus* and other names applicable to *Istiblennius*, we believe that a neotype should be designated for *Salarias edentulus*. There are no good specimens from Huahine that might serve this purpose. We, therefore, designate USNM 292529, female, 78.5 mm SL, from Tahiti, Society Islands, neotype of *Blennius edentulus*. The following is a brief description of the characters of this specimen: dorsal fin XIII,20; anal fin II,22, last ray split to base; pectoral fins 14/14, nape cirri 1/1; orbital cirri 1/1; occipital crest, upper-lip crenulae, and dentary canines absent; body posteriorly with few distinct spots and indications of others beginning to form; segmented-ray portion of dorsal fin dark with only faintest hint of fine spots starting to appear distally.

Valenciennes (in Cuvier and Valenciennes, 1836:315) described *Salarias forsteri*, which he believed to be the same as Forster's *Blennius truncatus* (a name still unavailable in 1836) and Schneider's *Blennius edentulus*. In his discussion of *Salarias forsteri*, Valenciennes (loc. cit.), included the following remarks, which we have translated (bracketed remarks are ours):

I have seen in the Berlin Cabinet one of the salarias [sic] Forster had described previously, but Bloch failed to recognize.... These specimens are only three inches [long]. They come from the Pacific Ocean and were deposited in Bloch's Cabinet with the label *blennius* [sic] *fasciatus* [Bloch, 1786], but it has been easy for us to recognize, to the contrary, the species that Forster illustrated and described under the name *blennius* [sic] *truncatus* and which has become the *blennius* [sic] *edentulus* of the posthumous Systema [= Bloch and Schneider, 1801], p. 172, no. 19. Its description and illustration, conserved in Banks' library, are equally in agreement....

Forster had taken this fish at Huaheine, one of the Society Islands; perhaps the specimens conserved by Bloch came from him.

The type series of *Salarias forsteri*, thus, can be considered to include those specimens that Valenciennes mentioned as being in Bloch's Cabinet, and probably that (or those) on which Forster based *Blennius truncatus* and, hence, Schneider based *Blennius edentulus*. All subsequent published appearances of Valenciennes' *forsteri* have been in lists or as a junior synonym of *Blennius edentulus*.

One of us (VGS) has examined two specimens (cat. no. ZMB 1942; C. Karrer in Bauchot, 1967:35) that appear to be those Valenciennes reported as existing in Bloch's Cabinet. These specimens are in essential agreement with Valenciennes' description of *Salarias forsteri*, except for having branched, rather than simple, orbital cirri. Possibly, Valenciennes overlooked the tiny branches on the orbital cirri. The two specimens differ in the same way from Schneider's and Forster's descriptions, but also, and importantly, in that the longer of the two (65.3 mm SL) is about 11 mm shorter than both Schneider and Forster reported for their specimen ($3^7/8$ inches = 98.4 mm, TL?, = ~77 mm SL). The difference from the reported length is sufficient for us to exclude either of these two specimens as possible types of Schneider's and Forster's species.

Valenciennes' specimens of *S. forsteri* are identifiable as *Salarias dussumieri* Valenciennes, which was described on an
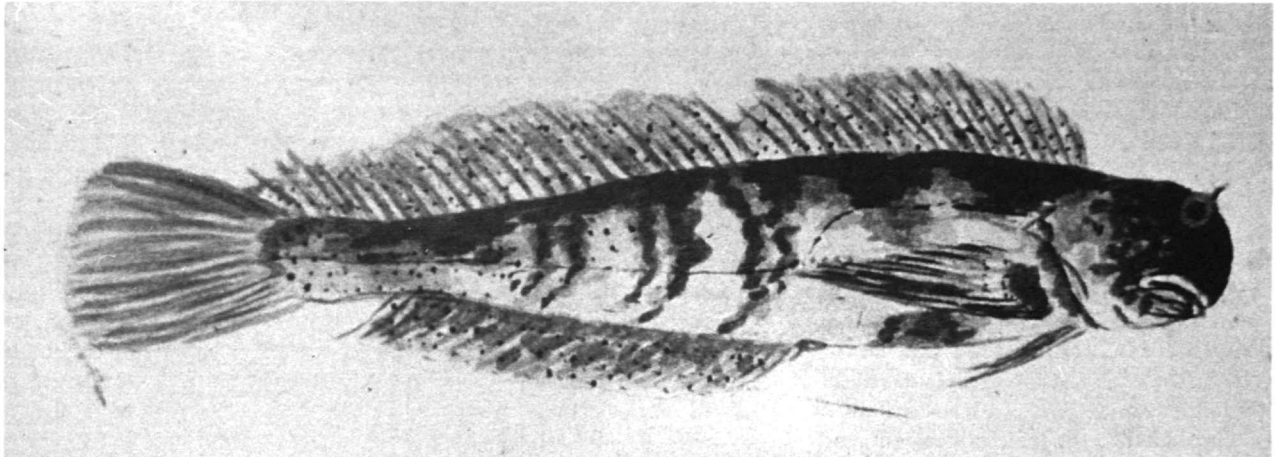
FIGURE 42.—Copy of original unpublished colored illustration of holotype of *Blennius truncatus* Forster (= *Istiblennius edentulus*), made from a color slide. The fine branch on the orbital cirrus, apparent in the original, is, at best, barely perceptible in the copy. See nomenclatural discussion section under *Istiblennius edentulus* species account.

earlier page of the same work as his description of *S. forsteri. Salarias dussumieri* is, considering page priority, the oldest name available for, and the one generally applied to, a species of *Istiblennius* different from that which is almost universally identified as *Istiblennius edentulus. Salarias forsteri*, however, has never been considered to be a synonym of *S. dussumieri*. In order to assure the seniority of *S. dussumieri*, we, as first revisers, assign it priority over *S. forsteri*. As an additional precaution, we designate as lectotype of *S. forsteri*, the largest specimen (65.3 mm SL; the smaller is 60.7 mm) in ZMB 1942. As defined in the present study, *Istiblennius dussumieri* is restricted to continental lithospheric plates and their margins; it has not been reported reliably from the Pacific plate, on which the Society Islands are situated far distant from the plate margin. Thus, the collection locality for the types of *S. forsteri*, as suggested by Valenciennes, was probably in error.

In 1844, Forster's manuscript, edited by H. Lichtenstein, was published. The publication included the description of *Blennius truncatus* (indicated as having come from Huahaine), with a footnote added by Lichtenstein that indicated Forster's species was the same as *Blennius edentulus* (which he credited to Bloch and Schneider) and *Salarias forsteri* (which he credited to Cuvier and Valenciennes). Because of Schneider's (in Bloch and Schneider, 1801:172) original treatment of *Blennius truncatus*, publication by Forster (1844) does not change the status of this name as a junior synonym of *Blennius edentulus*. To insure that this circumstance persists, we designate the neotype of *B. edentulus*, USNM 292529, as the neotype of *Blennius truncatus* Forster.

Valenciennes (in Cuvier and Valenciennes, 1836:329) described *Salarias quadricornis* from specimens from Mauritius and the Seychelles. Dorsal- and anal-fin ray counts and vertebral numbers of specimens of *I. edentulus* from these two localities are recognizably different (Tables 27 and 28). For these reasons, we restrict the type locality of *S. quadricornis* to Mauritius, and select as lectotype for the species, MNHN A.2003, male, 110.7 mm SL, but do not elect to recognize the species (see remarks in section on geographic variation).

Bleeker's (1849:18) description of *Salarias melanocephalus* indicated variation in the characters he reported, but he gave a single measurement, 95 mm, for the length of the species. It is possible Bleeker was giving only the length of his largest specimen. The description agrees with *I. edentulus*, except for failing to mention the presence of nape cirri. Similarly, the nape cirrus is lacking in Bleeker's (1983, pl. 445: fig. 5) illustration of *Salarias melanocephalus*, which is otherwise readily identifiable as a male *I. edentulus*. (The illustration, interestingly, is 147 mm TL; unless he indicated otherwise, Bleeker's *Atlas* illustrations all appear to be 1:1.)

There is a jar (RMNH 6297) labeled *Salarias melanocephalus* that bears a clipping from the 1879 auction catalog of Bleeker's collections (catalog reproduced in Lamme, 1973), which contains 14 specimens, all identifiable as *I. edentulus*. Although the auction catalog lists 18 specimens, it is probable that RMNH 6297 contains Bleeker's types of *S. melanocephalus*. Only one of these specimens, 95.4 mm TL (79.0 mm SL), approximates 95 mm; the other specimens are much smaller or much larger. We designate this specimen, which has nape cirri, as lectotype of *Salarias melanocephalus*. Whitehead et al. (1966) discussed problems surrounding recognition of Bleeker types.

Bleeker (1851:256) described *Salarias sumatranus* from a single specimen from western Sumatra. The type appears to be lost, but the description and illustration (Bleeker, 1983, pl. 445:

fig. 1) of the species are readily recognizable as that of a female *I. edentulus.* Bleeker's holotype was 85 mm, whereas the *Atlas* illustration was of a specimen 135 mm TL, 105 mm SL.

Bleeker (1857b:69) described *Salarias diproktopterus* from a single specimen, 94 mm TL. The description is identifiable as that of a female *I. edentulus,* except for the dorsal-fin formula ("11/17" or "12/17," Bleeker was uncertain) and in having a two-parted anal-fin. Bleeker (1983, pl. 444: fig. 12) figured a specimen that, except for lacking a nape cirrus, conformed with his description. A specimen, which we believe is the holotype, in the Leiden museum (RMNH 4468) conforms in all respects with Bleeker's description and also his figure, except for having nape cirri. The dorsal fin is damaged, which accounts for the unusual formula, and the anal fin is malformed, a condition that Bleeker apparently did not recognize.

Castelnau (1875:26) described *Blennius cinereus* from Queensland. The holotype is apparently lost. The description is lacking in details, but by the process of elimination, best fits the genus *Istiblennius.* The pectoral-fin count of 15 is exceptional in *Istiblennius,* as is a dorsal-fin spine count of 12 (most workers in the 19th century missed the reduced, terminal 13th spine in *Istiblennius*). The presence or absence of nape cirri or crenulae on the upper lip, which would have enabled more certain identification of *B. cinereus,* were not discussed. The indicated presence of a nuchal crest, simple orbital cirri, and 19 segmented dorsal-fin rays, and the absence of canines, however, appears to restrict the identification of the species to a male *I. edentulus.* In order to stabilize the name, we designate USNM 291700, male, 48.3 mm SL (60.8 mm TL), from One Tree Island, Queensland, as neotype of *Blennius cinereus* Castelnau. Other characters of the neotype: dorsal fin XIII,20; anal fin II,22, last ray split to base; pectoral fins 14/14; left supraorbital cirrus bifurcate, right simple; simple cirrus on each side of nape; fleshy crest on occiput.

Macleay's (1882:361) description of *Salarias atratus,* from Port Moresby, Papua New Guinea, is so brief that it is not possible to assign it with certainty even to *Istiblennius,* much less *I. edentulus.* The description mentions 2 specimens that were all black (poorly preserved?), which is descriptive of some *Enchelyurus* species, and probably explains why Fowler (1928) synonymized *S. atratus* with *Enchelyurus ater* (Günther). Macleay, however, noted that the dorsal fin was deeply notched, which it is not in *Enchelyurus.* Macleay also gave the dorsal-fin formula as "12/20," which could refer to *I. edentulus,* but denotes 2 more spines and 2 less rays than occur in *E. ater,* a species that is not known or expected to occur at Port Moresby. *Enchelyurus kraussi,* which might be expected to occur at Port Moresby, has at most 9 dorsal-fin spines and at least 21 segmented rays.

Munro (1956:250), who may have seen the syntypes, placed *S. atratus* in synonymy with *I. edentulus,* and there is nothing in the description that would contraindicate such an action. The types of *S. atratus* were not present in the Macleay Museum (MAMU) in 1966 or 1969 when either we or W.F. Smith-Vaniz

examined the collections. Stanbury (1969:209) reported the types were present, but later indicated (see Smith-Vaniz and Springer, 1971:53–54) that he had not seen the specimens, but merely listed them because they were supposed to be present according to a MAMU catalog entry dated 1965. The catalog entry also indicated that they were in poor condition and had been re-identified as *Salarias rivulatus* (= *I. rivulatus*), a Red Sea endemic, but a name that in older literature was frequently misapplied to *I. edentulus* specimens. The Macleay collection was transferred to AMS several years ago, but we did not find the types of *S. atratus* during a recent search of the collection (Nov, 1989). Accordingly, we assign *Salarias atratus* to the synonymy of *I. edentulus,* but as we have no specimens of *I. edentulus* from (or near) Port Moresby, we hesitate at this time to designate a neotype for *S. atratus,* but suggest that this be done when specimens are available.

Ogilby (1899:741) described *Salarias insulae* from a single specimen. There is a jar (QM I.862) in the Queensland Museum labeled as the "type" of *Salarias insulae* Ogilby. The jar contains 2 specimens, both identifiable as *I. edentulus* and both too long (~108 snf 130 mm SL) to be the holotype, which was described as being 65 mm (total length?). The holotype, therefore, appears to be lost, but the description is clearly based on a female specimen of *I. edentulus.* The only other species of *Istiblennius* known to occur at Lord Howe Island is *I. dussumieri,* which lacks nape cirri, which Ogilby reported were present in the holotype of *Salarias insulae.*

Jordan and Snyder (1902:460) did not compare their *Scartichthys enosimae* (described from Misaki, Japan, ~35°N) with any other species. If they had, they would have been unable to distinguish their male specimens (includes holotype) from males of other populations of *Istiblennius edentulus* (meristics excluded). All or most female specimens, depending on specific locality, of *I. edentulus* from the main islands of Japan, however, differ from females of *I. edentulus* from non-Japanese localities. Our decision not to recognize *enosimae* is discussed above in the section on geographic variation: the *Istiblennius enosimae* problem.

The holotype of *Scartichthys enosimae* was originally deposited in the Stanford University collections. These collections have been incorporated at CAS, where they retain their original Stanford catalog numbers prefixed CAS-SU. Jordan and Snyder had specimens from Misaki and Enoshima (both ~35°N, 139°30′E). They stated that the holotype was from Misaki, but did not specify the locality of the single paratype, which is cataloged as having come from Enoshima. They reported other specimens from both localities, but did not designate them as type material.

Bryan and Herre (1903:136) indicated that they had more than 1 specimen of their new species, *Salarias gilberti,* but that BPBM 2454 "is the type." There are 2 specimens (male, female) in the jar labeled BPBM 2454. No information was given in the description that might distinguish the holotype from any other specimen, although the species was described as

having a fleshy crest on the head. Ordinarily, this would indicate that the description was based on a male, but some female *I. edentulus* from Marcus Island bear a low, but recognizable crest. Both specimens are conspecific and remain in BPBM 2454, undistinguished as to the type status of each. Bryan and Herre did not attempt to differentiate their species from any other.

Bryan and Herre's (1903:136) *Salarias marcusi*, described in the same paper as their *S. gilberti*, is a large female specimen of *I. edentulus*. The specimen also bears a low fleshy crest on the head. Bryan and Herre made no statements as to how their *S. gilberti* and *S. marcusi* differed from any other species or each other.

Fowler (1904:552) compared his *Scartichthys basiliscus* only with *Salarias oorti*, which is a junior synonym of *I. dussumieri*. Fowler reported that his holotype had XIV,8 dorsal-fin rays, whereas, his figure shows XIV,18, indicating a probable typographical error. Our count of the dorsal fin is XIII,19. Fowler did not describe the nature of the supraorbital cirrus, but his illustration shows it as simple. The holotype, however, has two small branches at the tip of one cirrus and one branch at the tip of the other. Although the supraorbital cirri are usually simple in *I. edentulus*, it is common, particularly in specimens over 75 mm SL, for them to have side branches. The specimen is clearly identifiable as *I. edentulus*.

Seale (1906:87) did not compare his *Salarias azureus* with any species, other than to say that it was "nearly related to *S. quadricornis.*" We agree with Seale, but find his holotype to be a typical specimen of *I. edentulus* as we recognize the species. In Seale's time, *S. quadricornis* included specimens from both Mauritius and the Seychelles. Although few specimens are available from the Seychelles, it appears that the meristics of specimens from these two areas are quite different (Tables 27 and 28).

Jordan and Seale (1906:427) indicated that the "type" of their *Salarias sindonis* was 0.99 inch long, cataloged as USNM 51792, and that there were "numerous specimens (50) collected at Pago Pago...." The correct catalog number is USNM 51793, and is recorded in the catalog ledger as containing 20 specimens (USNM 51792 is the holotype of *Salarias garmani*, described in the same study as *Salarias sindonis*). About 1975, the contents of USNM 51793 were radiographed; the number of specimens was then 18. In December 1987, there were only 17 specimens. It is not possible to determine which, if any, of these specimens, all of which are juveniles, is the holotype. Fifteen of the specimens are identifiable as *Istiblennius* and 2 are identifiable as *Praealticus*. Because 2 genera and at least 2 species are represented in the type series and it is not possible to determine which genus pertains to the holotype, we believe that designation of a neotype is necessary to fix the identity of *Salarias sindonis*.

We designate the largest specimen, 23.2 mm SL, in USNM 51793 as neotype of *Salarias sindonis*. It retains the catalog

number USNM 51793. The neotype is a juvenile *Istiblennius edentulus*. The two smallest paratypes (~13 mm SL) are identifiable as *Praealticus* and are recataloged USNM 307577. The 14 remaining paratypes are recataloged as USNM 291686.

Jordan and Seale (1906:429) described *Salarias garmani* from a small specimen ("1.2 inches"), which has simple orbital cirri, II,23N anal-fin rays, and no canines, nape cirri, or lip crenulae. Except for the lack of nape cirri, the specimen appears to be a juvenile *I. edentulus*. The holotype conforms less well with the other species of *Istiblennius* that occur at Samoa. The holotype is similar to, and might be conspecific with, *I. dussumieri*, except that *I. dussumieri* has not been reliably reported from any Pacific plate locality. Borodin (1932:97) and Wass (1984:25, compiled), reported *I. dussumieri* from Samoa. We have examined Borodin's specimen and find it to be identifiable as *Entomacrodus striatus*, as is Borodin's (ibid.) specimen reported as *I. dussumieri* from Tahiti. (Other species, *Blenniella bilitonensis*, restricted to the western Pacific, and *Istiblennius unicolor*, Red Sea and western Indian Ocean, reported by Borodin from Pacific plate localities are also undoubtedly misidentifications.)

Steindachner (1906:1411) described *Salarias rechingeri* from a specimen, 35 mm (total length), from Savaii, Samoa Islands. It is unclear from Steindachner's statements whether he acquired (permanently?) the holotype from the Museum Godeffroy (Hamburg) or if it was sent to him for identification only (but retained for the Stuttgart Museum?). In any case, we failed to locate the specimen at the Vienna, Hamburg, or Stuttgart museums. The main characters given by Steindachner are: dorsal fin XIII,19, moderately deeply incised, bound to caudal; anal fin 24; simple orbital cirrus; no canine teeth; an extremely weak hint of a crest on the head; body with 6 crossbands, each divided by 2 or 3 bright crosslines; 2 or 3 bright stripes in dorsal fin; wiggly lines on cheeks. Although the description appears to apply to a species of *Istiblennius*, it is not possible to determine which (*Blenniella* species can be excluded because they exhibit well-developed canine teeth at 35 mm TL).

There are only 3 species of *Istiblennius* known from Samoa: *I. bellus*, *I. edentulus*, and *I. lineatus*, all of which were described before *S. rechingeri*. *Istiblennius bellus* can be excluded from consideration because its females, which lack a crest, exhibit a highly distinctive pepper-spotted body color pattern, and its males have a well-developed crest at 35 mm TL. *Istiblennius lineatus* can probably be excluded from consideration because it has branched supraorbital cirri and a noticeably crenulate lip in specimens even smaller than 35 mm TL; however, it is the only one of the 7 species that has what might be considered to have wiggly lines on the cheeks, and a segmented anal-fin ray count of 24 is more typical of *I. lineatus* than any of the other species, if Steindachner was reporting only segmented rays. He may well have mistaken the nature of the anal-fin spines, as did most workers in his day, in which case his specimen may have had an anal-fin count of II,22. The

color pattern described for the body of *S. rechingeri*, however, is quite different from that of *I. lineatus*, and the low number (19) of segmented dorsal-fin rays given by Steindachner is 2 less than is known to occur in *I. lineatus*, and 3 less than for specimens from the vicinity of Samoa.

Samoan specimens of *I. edentulus* also rarely, if ever, have as many as 24 segmented anal-fin rays (but Steindachner may have been giving total elements). *I. edentulus* has prominent nape cirri, which were not mentioned for *S. rechingeri*, but, nevertheless, may have been overlooked.

Fowler (1928) thought that *S. rechingeri* might be a species of *Cirripectes*, but no species of *Cirripectes* has as many as 13 dorsal-fin spines, 19 segmented dorsal-fin rays, or 24 (total?) anal-fin elements as Steindachner reported for *S. rechingeri*.

In order to stabilize the identification of *Salarias rechingeri*, we believe that designation of a neotype is desirable, and that *I. edentulus* best conforms with Steindachner's description. We have no specimens of *I. edentulus* from Savaii, but we have several from nearby Upolu (about 10 km east of Savaii), and we here designate one of these, USNM 293747, from Plum Pudding Rock, Upolu, Western Samoa, as neotype. The neotype is a male, 31.3 mm SL, 38.2 mm TL, with the following characters: dorsal fin XIII,21, attached on caudal fin; anal fin II,23, last ray not split to base; 14 pectoral-fin rays; simple nape and orbital cirri; nasal cirri simple with 1 or 2 side branches beginning to form.

Fowler (1945:71) believed his *Salarias fluctatus* was unique in color pattern and in having a fleshy occipital crest. We have examined the holotype (ANSP 71603; there were no paratypes) and find it to be identifiable as *I. edentulus*.

Fowler (1946:183) compared his *Salarias atrimarginatus* only with *Salarias muscarus* Snyder (= *Blenniella chrysospilos*). We have examined the Fowler's holotype (ANSP 72052, there were no paratypes) and find it to be identifiable as *I. edentulus*.

MATERIAL EXAMINED.—There is an extraordinary number of lots and specimens of *Istiblennius edentulus* available in museum collections. USNM alone has over 300 lots containing about 3000 specimens. We did not attempt to record data on all available material for our study. We estimate that we examined about 500 lots (we have records from over 400 lots), but in many instances we did not examine all specimens in a lot, and we did not take complete data on every specimen we examined. Examinations varied from taking complete data on specimens to only verifying their identification or recording data on a single character for a series of specimens or single specimen. Relatively complete data were recorded from over 2000 specimens. Considering the ubiquity of the species, we do not believe it useful to cite all our material here. The material we do cite, either formed the bases for the data reported in Tables 27-31, or served as the basis for plotting the distribution map (Figure 67).

Indian Ocean. Zanzibar: USNM 12673 (3), 296220 (21). Kenya: Malindi, SMNS 13134 (1), USNM 296339 (5);

Bamburi, USNM 278379 (2), 296284 (2). Mozambique: Porto Amelia, RUSI 5629 (1). South Africa: Natal coast, CAS-SU 14830 (12), RUSI 74-70 (4), 74-346 (1), 74-347 (2), 74-349 (2), 74-350 (3), 74-351 (4), 74-355 (5), 77-13 (1), 77-17 (2). Seychelles: MNHN 767 (1); Mahe, USNM 267200 (3); Farquar Is, USNM 296279 (1); Aldabra, MNHN 1954-31 (2), USNM 296212 (77), 296262 (1), 296272 (9), 296274 (6), 296286 (1), 296325 (7), 296327 (1), 296328 (1). Comoros Is: Grande Comore, USNM 296223 (1); Pamanzi, USNM 296278 (7). Agalega: USNM 292531 (45). Cargados Carajos (= St. Brandon's Shoals): USNM 291699 (1), 292532 (101), 292534 (4), 292533 (4). Oman: Masirah, MCZ 90343; Muscat, 2-3 mi S of Sidab, USNM 217534 (3); Sur, ROM 40201 (11). Reunion: MNHN 1988-447, in part (11), RUSI 10654 (4), USNM 28529 (3), Hans Bath personal collection (1). Mauritius: MNHN A.2002 (5), A.2003 (lectotype of *Salarias quadricornis*), A.2004 (1), A.2005 (1), A.2007 (1), 846 (1), MCZ 5790 (7), 5790 [sic] (1), 6082 (3) 12551 (1), RUSI 1274 (4), 74-95 (2), 74-312 (2). Madagascar: Nossi Be, USNM 278403 (17), 296009 (25), 296277 (1), 296288 (28); Tankely, USNM 296007 (2). Maldive Is: Male Atoll and vicinity, CAS 56676 (19), 58688 (5), 58693 (4), 58736 (5), 58739 (5), FMNH 90619 (1), 101058 (1); Rasdu Atoll, USNM 290935 (2). Sri Lanka: NTM S.11247-001 (1), USNM 278386 (2). Gulf of Aden: Seven Brothers Is (entrance to Red Sea), MNHN 1977-737 (22: locality from J.E. Randall, pers. comm.), USNM 224117 (7); Somalia: Mait Id, USNM 278033 (10); Berbera, BMNH 1954.4.26.133-5 (2). Red Sea (non Gulf of Aqaba): Egypt: Kosseir, SMNS 3634 (1); Ethiopia: Difnein Id, USNM 204514 (135), 292546 (1); Isola Delemme, USNM 204496 (1); Massawa, USNM 204483 (3); Sudan: Mersa Ar-rakiya, Mersa Fijab, and Suakin, BMNH 1960.3.15.1529-88 (>50); Saudi Arabia: Jidda (= Djetta), USNM 147581 (1), 147587 (2), 147588 (5). Gulf of Aqaba: Israel: Elat, HUJ F.4797 (1); Egypt: Ras Burka, ROM 43605, in part (2); Marsa Muaqbila, USNM 278358 (8), 300327 (1). Aden Peninsula: BMNH 1935.7.11.1 (1). Seychelles: Mahe, USNM 267200 (3). Chagos Is: Diego Garcia, USNM 278376 (19), 296118 (2), 296213 (>100), 296214 (>100, including 2 cleared and stained), 296269 (7), 296276 (1), 296283 (3). Andaman Is: Port Blair, USNM 112036 (2). Burma: Maungmagan Bay, USNM 195777 (1). Pakistan: Astola Id, USNM 278404 (1). India: Maharanipita Beach, Vizagapatam, ZSI 407/2 (1); Cocos-Keeling Is: ANSP 130775 (5), 130776 (3), 130777 (6), 130778 (4), 130868 (35), 130891 (3). Cocos-Keeling Is: ANSP 130775 (5), 130776 (3), 130777 (6, 130778 (4), 130868 (29) 130891 (3) Australia: Western Australia, Dampier Is, Rosemary Id, NTM S.10811-016 (1), S.10811-017 (2); Cape Range National Park, AMS I.25503-003 (1), I.25504-004 (1); Point Quobba, WAM P.8728-001 (3), P.8733-001 (1), P.8740-001 (2).

Western Pacific area. Bonin Is (= Ogasawara): USNM 5896 (2), UMMZ 144779 (3); Chichijima, FAKU 48179 (2). Japan: Tanegashima, USNM 71243 (4), 71473 (19), 139676 (2); Chiba Pref.: Awa, USNM 195775 (8); Tateyama, USNM

195776 (2); Boshyu, UMMZ 144780 (2); Kanagawa Pref.: Misaki, USNM 75842 (1), 71115 (24), UMMZ 144783 (12), CAS-SU 7105 (3), 7068 (holotype of *Salarias enosimae*); Enoshima, USNM 50297 (2); Sagami Bay, Manazuru, UMMZ 144782 (1); Kagoshima Pref.: Akune, USNM 71243 (4); Wakayama Pref.: Shirahama, CAS 66851 (11), FAKU 48350 (4), 48353 (5). Ryukyu Is: Aguni Shima, ANSP 72052 (holotype of *Salarias atrimarginatus*); Okinawa, USNM 71242 (46), 132813 (1), 203560 (1), 278377 (1), 278380 (1 cleared and stained), 278385 (1), 278388 (1), 278402 (7), 296008 (3), 296112 (1), 296121 (1), 296134 (2), 296135 (1), 296136 (1), 296162 (4), 296159 (2), 296260 (5), 296266 (3), 296287 (1 cleared and stained), 298943 (4). Taiwan and vicinity: Lanyu Id, USNM 179325 (2); Tai Fan Lieh, USNM 296267 (1); S end, USNM 278391 (2), 278359 (1); SE end, USNM 229909 (5); Shih Cheng, USNM 229910 (1); N end, 261172 (2); Sha Toa, USNM 278360 (1). Thailand: Gulf of Thailand: Prachuap Goh Luem, CAS GVF reg. no. 2648 (7); Goh Samet Id, CAS 64177 (>50); Ko Kra Id, CAS 64176 (15), and many other CAS G of Thailand specimens from which sundry data were recorded: GVF reg. no. 2037, 2206, 2645, sta 11, sta 114, sta 128. Philippines: Batanes Is, USNM 137794 (4), 226745 (1), 226746 (44), 283969 (1), 284052 (6), 284059 (6), 284060 (1), 287089 (1), 289947 (3); Camiguin Id, USNM 137791 (1); Cuyo Is, USNM 301869 (1); Luzon, Maricaban Id, USNM 137795 (2); Mindoro, USNM 137796 (31); Negros, USNM 301873 (15); Pilas Id, USNM 137784 (4); Siquijor, USNM 292564 (10). Indonesia: Bali: Sanur Reef, UF 31316 (2), NTM S.11127-038 (2); Buru (= Boeroe): Kajeli, RMNH 4468 (holotype of *Salarias diproktopterus*); Java: Pagotang, RMNH 6297 (14 specimens of which largest, 95.4 mm TL, 79.0 mm SL, male, is lectotype of *Salarias melanocephalus*); Pelaboean Rotoe, USNM 72729 (1); Flores: UF 31295 (20), 31300 (3), 31309 (1); Molucca Is: Ambon, IRSNB 1809 (2), USNM 277966 (31), Haruku, USNM 209617 (2), 209623 (6); Nusa Laut, 210943 (2); Sumatra: Padang, ANSP 27802 (holotype of *Scartichthys basiliscus*); Ternate: USNM 309869 (6). Australia: Qd: Lizard Id, AMS I.19477-012 (1), I.21538-011 (21), I.22732-004 (1); One Tree Id, USNM 291700 (neotype of *Blennius cinereus*), 296210 (>100). NSW, Byron Bay, AMS I.18063-001 (38), Minnie Water, AMS IB.6853 (1), I.15899-013 (3), NMNZ P.20629 (1), P.20637 in part (1), ROM 38271 (3); Newcastle area, AMS I.17343-008 (4); Warrell Creek, AMS I.15907-012 (2); Sydney, Clovelly Pool, AMS I.16915-010 (1). Lord Howe Id: AMS I.4276-77 (2), I.17359-003 (6), IA.2646 (1), IB.5757 (1). Lord Howe Rise: Middleton Reef, AMS I.27141-016 (1). New Caledonia: Noumea, USNM 144706 (1); Port de Goro, ROM 64633 (1). Loyalty Islands: Ouvea, USNM 319700 (1). PNG: Bonarua Id, USNM 279895 (34); Hermit Id, USNM 296340 (2); Madang, USNM 296151 (4); New Britain, Loloho, WAM P.28166-010 (6); Ninigo Is, USNM 296401 (16); Nissan Is, Pinipel, USNM 144285 (5); Trobriand Is, Kuia, USNM 296127 (2), 296147 (2), 296224 (40), 296285 (19). Solomon Is: Bougainville, USNM 122989

(1); Guadalcanal, USNM 292547 (30); New Georgia, USNM 144442 (1), 144705 (4). Santa Cruz Is: Pileni, AMS IA.2897 (1); Tikopia, USNM 278392 (1). New Hebrides: Efate, USNM 296595 (41); Santo, USNM 287471 (1). Fiji: Kandavu, USNM 256538 (7); Viti Levu, UF 31314 (9); Viwa, USNM 257646 (3). Tonga Is: Niuafo'ou, USNM 91924 (1), 91952 (1). Mariana Is: Guam, USNM 123899 (3), 123955 (2), 132463 (1), 150588 (2), 198171 (1), 278381 (5), 278383 (5); Rota: USNM 139842 (4); Saipan: ANSP 71603 (holotype of *Salarias fluctatus*), CAS 56337 (1).

Pacific plate area. Marcus Id: BPBM 2454 (holotype and paratype of *Salarias gilberti*), 2456 (holotype of *Salarias marcusi*), 7163 (10), USNM 278394 (17), 296218 (40). Wake Id: BPBM 4944 (2), 15209 (17), CAS 40699 (6), 66855 (1), UF 12051 (9). Kapingamarangi: CAS 66853 (12). Ponape: USNM 223370 (3), 224375 (2). Marshall Is: Arno, USNM 166794 (3); Bikini, USNM 142199 (1), 142200 (32), 142201 (49); Enewetak, USNM 142196 (8); Kwajalein, USNM 142198 (5); Majuro, USNM 179445 (1). Kiribati (= Gilbert Is): Abaiang, AMS I.18049-007 (9), MCZ 12536 (10); Arorae, AMS IB.6621-5 (5), IB.6627-28 (2); Onotoa, USNM 167325 (1), 167334 (2), 296316 (13); Tarawa, USNM 259643 (3). Tokelau Is: Atafu, USNM 278398 (11); Fakaofo, USNM 296153 (4). Rotuma: USNM 226584 (30), 283146 (5), 283164 (14), 296280 (7). Samoa Is: Rose, USNM 115439 (6); Swains, USNM 115431 (3); Tutuila, USNM 51793 (neotype of *Salarias sindonis*), 115435 (38), 115440 (24), 126289 (9), USNM 291686 (14); Upolu, USNM 52512 (3), 52526 (22), 115433 (2), 51792 (holotype of *Salarias garmani*), 293746 (38), 293747 (neotype of *Salarias rechingeri*), 296273 (3). Phoenix Is: Birnie, USNM 278393 (1); Canton, USNM 115438 (>50); Enderbury, USNM 115434 (>50); Hull (= Orona), USNM 115441 (26); McKean, USNM 198696 (2), 278387 (4), 278399 (6), 296126 (2), 296127 (5), 296219 (14), 296282 (5). Howland Is: USNM 198694 (7), 198702 (28), 198707 (1), 198712 (12), 198725 (4). Baker Id: MCZ 26386 (10), USNM 278401 (2), 296275 (1). Niue Id: NMNZ P.12374 (1), P.12375 (1), P.15648 (1), P.15678 (1), P.15681 (1), P.15684 (1), P.15689 (1), P.15690 in part (1), P.15691 (1), P.20526 (1), P.20533 (1). Cook Is: Aitutaki, NMNZ P.15692 (1); Palmerston, NMNZ P.15705 (2); Penrhyn, USNM 296211 (43, including 2 cleared and stained); Rarotonga, NMNZ P.15707 (2), ROM 38244 (14). Austral Is: Rapa, BPBM 12879 (5); Tubai, BPBM 783 (holotype of *Salarias azureus*). Society Is: Moorea, USNM 278396 (1), 296304 (7), 296315 (2); Raiatea, BPBM 1680 (1); Tahiti, BPBM 5724 (5), 5728 (22), 6943, 11571 (9), IRSNB 6504 (19), USNM 87624 (2), 87637 (1), 292529 (neotype of *Blennius truncatus*), 296310 (7), 296402 (2). Marquesas Is: Fatu Hiva, BPBM 11790 (9), USNM 301867 (26); Hivaoa, BPBM 12077 (7); Nuku Hiva, AMS I.21773-001 (33), I.22124-008 (6), BPBM 12404 (37), 12805 (2), 26243 (7), CAS-SU 19028 (1); Ua Huka, USNM 89778 (3). Line Is: Caroline, USNM 296117 (27); Christmas, USNM 297384 (68); Fanning, USNM 296263 (1); Palmyra, AMS I.20656-001 (15).

Tuamotu Arch: Fakarava, USNM 66007 (1); Hereheretue, USNM 133863 (1); Makatea, CAS 67301, in part (1); Makemo, USNM 66008 (3); Rangiroa, USNM 300438 (60); Tikehau, USNM 296099 (1). Gambier Is: Mangareva: MCZ 29422 (9), USNM 65645 (29). Pitcairn Id: BPBM 17021 (3).

Istiblennius meleagris (Valenciennes)

FIGURES 43, 44

Salarias meleagris Valenciennes in Cuvier and Valenciennes, 1836:332 [terre de Van-Diemen; lectotype designated below: MNHN A.1808].

Blennius vittipinnis Castelnau, 1875:25 [Dampier's Archipelago, West Coast of Australia; 7 syntypes MNHN A.2120 [3] and A.2121 [3], BMNH 1883.7.4.5.6 [1]].

DESCRIPTION.—Dorsal fin (Table 32). XII to XIV,17 to 21 = 29 to 34 (XIII in 94% of specimens; 17 segmented rays in only 1 of several hundred specimens examined for this character); mean number of total elements usually higher for males from any locality than for females from same locality (higher for 15 of 16 localities where means for both sexes are available, statistically significantly higher for 6 of the 15 localities); membrane between spinous and segmented-ray portions notched more than three-fourths length first segmented ray; posterior membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle anterior to caudal-fin base to point out on dorsal edge of caudal fin <15% caudal-fin length (attachment usually on caudal peduncle, rarely posterior to vertical at caudal-fin base).

Anal fin (Table 32). II,17 to 21 (rarely 17 or 18); mean number of segmented rays usually higher for males from any locality than for females from same locality (higher for 15 of 16 localities where means for both sexes are available, statistically significantly higher for 4 of the 15 localities); posteriormost ray usually split to base (about 65% of specimens); posterior element of split ray usually well developed, readily discernible externally, not bound by membrane to caudal peduncle in any of 50 specimens examined for character (bound, however, in single available ophioblennius-stage specimen). Mature males with skin covering anal-fin spines and distal half of rays expanded slightly, crinkled slightly along lateral edges.

Pectoral-fin rays 12 to 15 (12 only unilaterally, in 1 of 125 specimens examined for character; 14 bilaterally in 93% of specimens). Pelvic-segmented rays 3.

Caudal fin. Dorsal procurrent rays 4 to 7 (6 or 7 in 97% of specimens examined for character), ventral procurrent rays 5 to 8 (6 or 7 in 95% of specimens), modal combination of 6 dorsal with 6 ventral procurrent rays in 36% of specimens (7/6 in 32%, 7/7 in 21%); segmented rays 13 to 15, strongly modally 13 (Table 33).

Vertebrae (Table 32). 11 or 12+24 to 28 = 35 to 39 (12 in only 3 specimens, 24 in only 1 specimen of 309 specimens examined for characters; total vertebrae 37 or 38 in 95% of specimens); mean number of total vertebrae tending to be higher for males from any locality than for females from same locality (higher for 11 of 16 localities where means for both

sexes are available, statistically significantly higher for 2 of the 11 localities); posteriormost pleural rib on 11th to 13th from anteriormost centrum (on 12th in 98% of specimens examined for character); posteriormost epineural on 15th to 21st from anteriormost centrum (rarely on 15th); mean number of vertebra bearing posteriormost epipneural tending to be higher (more posterior) for males from any locality than for females from same locality (higher for 8 of 14 localities where means for both sexes are available, statistically significantly higher for 3 of the 8 localities).

Cirri. Nape cirrus present or absent (Table 33) bilaterally or unilaterally, varying somewhat depending on population; cirri predominantly simple, occasionally forked or with up to 4 branches. Orbital cirrus tree-like with medial and lateral branches (specimens as small as 26 mm SL with up to 6 branches), varying from slightly shorter than to much longer than orbital diameter, number of branches and relative length increasing with increase in SL. Nasal cirri short, palmate, with 2 to 8 branches (usually less than 6) on rim of each anterior nostril.

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between verticals from 8th and 13th (rarely only to 8th) dorsal-fin spines, descending to midside and, in specimens >30 mm SL, continuing posteriorly as series of 6 to 26 short, disconnected, horizontally bi-pored canals (tubes) in skin; number of tubes usually more than 10, tending to increase in number with increase in SL; posteriormost tube in area between vertical from base of 2nd segmented dorsal-fin ray and caudal-fin base, usually posterior to vertical from base of 9th segmented ray; position tending to be more posterior in larger specimens.

Mandibular pores 4 to 6 (6 pores bilaterally in 88%, unilaterally in 9% of specimens examined for character; 4 pores, unilaterally, in only 1 specimen).

Five to 8 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (6 in 93% of specimens examined for character); 0 to 2 positions with paired pores (0 in 7%, 1 in 74%, 2 in 19% of specimens examined for this character).

Posterior canines absent.

Ventral margin of upper lip crenulate; dorsal margin of lower lip usually entire, often weakly, irregularly scalloped, usually restricted to corners of mouth (only 2 of several hundred specimens examined with well-developed crenulae along entire lip margin).

Males with fleshy, blade-like crest dorsally on head; earliest indication of beginning crest a darkly pigmented, longitudinal line dorsally on head, indication variably present in males as small as 28 mm SL; however, definite ridge or crest first apparent only in specimens >30 mm SL, but usually not before 35 mm SL; total absence of crest or ridge may occur in rare males up to 59 mm SL, but almost all males >45 mm SL have noticeable crest. Crest or ridge-like precursor absent in females <50 mm SL, rarely indicated in females <70 mm SL; females

Table 32.—Frequency distributions for certain meristic characters of specimens of *Istiblennius meleagris* from various localties (arranged by sex and more-or-less linearly around the northern Australian coast from Scarborough, WA, to Sydney, NSW). Underlining indicates significant differences (p ≤.05) between means of sexes from same locality.

Sex/Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae						Posteriormost epineural on vetebra number[1]							
	29	30	31	32	33	34	x̄	17	18	19	20	21	x̄	35	36	37	38	39	x̄	15	16	17	18	19	20	21	x̄
MALES																											
Western Australia																											
Scarborough	-	-	-	2	-	-	32.0	-	-	-	2	-	20.0	-	-	-	2	-	38.0	-	-	-	1	-	-	-	
Port Denison	-	-	-	-	1	-		-	-	-	1	-		-	-	-	1	-		-	-	-	1	-	-	-	
Houtman Abrolhos	-	-	-	1	1	-	32.5	-	-	-	1	1	20.5	-	-	1	-	1	38.0	-	-	2	-	-	-	-	17.0
Murchison River	-	-	-	3	5	-	32.6	-	-	-	8	-	20.0	-	-	2	5	1	37.9	-	1	2	3	1	-	-	17.6
False Entrance	-	-	-	2	1	-	32.3	-	-	1	2	-	19.7	-	-	1	2	-	37.7	-	-	-	3	-	-	-	18.0
Dirk Hartog Island	-	-	-	5	4	-	32.4	-	-	1	7	1	20.0	-	-	3	6	-	37.7	-	-	3	4	2	-	-	17.9
Shark Bay	-	-	-	10	6	-	32.4	-	-	4	12	-	19.8	-	-	5	11	1	37.8	-	-	-	1	6	-	1	19.1
Rosemary Island	-	-	-	5	4	-	32.4	-	-	2	6	-	19.8	-	-	1	6	-	37.8	-	-	-	1	1	3	1	19.7
Lacepede Islands	-	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-		-	-	-	1	-	-	-	
Fenelon Island	-	-	1	3	-	-	31.8	-	-	1	3	-	19.8	-	-	3	1	-	37.2	-	-	-	1	1	1	-	19.0
Northern Territory																											
McCluer Island	-	1	2	11	-	-	31.7	-	-	7	8	-	19.5	-	2	10	1	-	36.9	-	-	3	2	5	2	-	18.5
New Year Island	-	-	2	5	-	-	31.7	-	-	3	4	-	19.6	-	1	5	1	-	37.0	-	-	2	3	2	-	-	18.0
Yirrkala	-	-	8	14	3	-	31.8	-	-	17	9	-	19.3	-	-	20	6	-	37.2	-	-	3	8	7	3	-	18.5
Groote Eylandt	-	-	5	18	4	-	32.0	-	-	13	13	1	19.6	-	-	18	7	-	37.3	-	1	7	8	5	5	1	18.3
Queensland																											
Prince of Wales Id	-	-	-	1	-	-		-	1	-	-	-		-	-	-	1	-		-	-	-	-	-	-	1	
Lizard Island	-	-	-	5	1	-	32.3	-	-	2	3	1	20.0	-	-	2	4	-	37.7	-	-	-	1	1	1	-	19.0
Cairns	-	-	-	1	3	-	32.8	-	-	-	4	-	20.0	-	-	-	3	-	38.0	-	-	-	-	1	-	-	19.0
Townsville	-	-	-	2	6	-	32.8	-	-	1	6	1	20.0	-	-	2	6	-	37.8	-	-	-	1	4	1	1	19.3
Heron Island	-	-	-	18	10	2	32.5	-	-	2	22	6	20.1	-	-	2	24	1	38.0	-	-	9	4	4	5	1	18.3
New South Wales																											
Broken Head Beach	-	-	-	4	2	-	32.3	-	-	-	6	-	20.0	-	-	-	6	-	38.0	-	-	2	2	2	-	-	18.0
Arrawarra	-	-	-	3	2	-	32.4	-	-	1	4	-	19.8	-	-	2	3	-	37.6	-	-	1	1	3	-	-	18.4
Sydney	-	-	1	-	-	-		-	-	-	1	-		-	-	-	1	-									
FEMALES																											
Western Australia																											
Port Denison	-	-	-	1	-	-		-	-	1	-	-		-	-	1	-	-		-	1	-	-	-	-	-	
Houtman Abrolhos	-	-	1	1	-	-	31.5	-	1	-	1	-	19.0	-	-	1	1	-	37.5	-	2	-	-	-	-	-	16.0
Murchison River	-	-	2	5	3	-	32.1	-	-	4	5	1	19.7	-	-	3	5	1	37.8	-	-	2	4	-	1	-	18.0
False Entrance	-	-	1	-	-	-		-	-	1	-	-		-	-	1	-	-		-	1	-	1	-	-	-	
Dirk Hartog Island	-	-	-	9	1	-	32.1	-	-	4	5	1	19.7	-	-	3	7	-	37.7	-	1	1	1	4	1	1	18.7
Shark Bay	-	-	3	19	-	-	31.9	-	-	13	7	-	19.4	-	1	9	10	-	37.4	-	-	3	3	3	-	-	18.0
Rosemary Island	-	-	4	12	3	-	31.9	-	-	7	11	1	19.7	-	-	8	9	-	37.5	-	-	4	3	4	1	1	18.4
Lacepede Islands	-	-	-	1	-	-		-	-	-	1	-		-	-	-	1	-		-	-	-	-	1	-	-	
Fenelon Island	-	-	1	3	-	-	31.8	-	-	3	1	-	19.2	-	-	2	2	-	37.5	-	-	-	-	2	1	-	19.3
Northern Territory																											
McCluer Island	-	1	6	7	-	-	31.4	-	-	11	3	-	19.2	-	2	9	3	-	37.1	-	-	-	6	5	1	-	18.6
New Year Island	1	-	8	6	-	-	31.3	1	-	11	2	-	19.0	1	-	14	-	-	36.9	-	-	-	1	3	-	-	18.8
Yirrkala	-	1	15	8	-	-	31.3	-	2	17	5	-	19.1	-	4	15	3	-	37.0	-	2	3	8	4	-	1	18.0
Groote Eylandt	-	-	19	9	-	-	31.3	-	-	26	2	-	19.1	-	-	26	2	-	37.1	1	2	10	6	6	-	-	17.6
Queensland																											
Prince of Wales Id	-	-	-	2	-	-	32.0	-	-	-	2	-	20.0	-	-	-	2	-	38.0	-	-	-	-	1	-	-	
Lizard Island	-	-	-	6	-	-	32.0	-	-	4	3	-	19.4	-	-	1	6	-	37.8	-	1	-	-	3	-	-	18.2
Cairns	-	-	1	7	-	-	31.9	-	-	2	6	-	19.8	-	-	3	5	-	37.6	-	-	2	3	2	-	-	18.0
Townsville	-	-	-	1	1	-	32.5	-	-	-	2	-	20.0	-	-	1	1	-	37.5	-	-	1	-	-	1	-	18.5
Heron Island	-	-	2	25	5	-	32.1	-	-	18	13	-	19.4	-	-	11	19	1	37.7	1	1	8	11	7	-	-	17.8
New South Wales																											
Broken Head Beach	-	-	-	9	-	-	32.0	-	-	5	4	-	19.4	-	-	2	7	-	37.8	-	1	4	-	4	-	-	17.8
Minnie Water	-	-	-	2	-	-	32.0	-	-	-	2	-	20.0	-	-	-	1	1	38.5	-	-	-	1	1	-	-	18.5
Arrawarra	-	-	-	3	-	-	32.0	-	-	2	1	-	19.3	-	-	1	2	-	37.7	-	1	-	-	2	-	-	18.0

[1] Counting anterior to posterior.

>70 mm SL usually show indications of ridge formation, but definite crests present only in females ≥89 mm SL; however, indications variably absent in females as large as 106 mm SL.

Color pattern (in preservative; Figures 43, 44). Head variably dusky with dark spot posterior to eye; dark area just posterior to corner of jaws. Body pale to dark dusky, often with indications of up to 6½ dark, irregular, more or less paired, broken bands; bands contrasting more strongly with body ground color in

Table 33.—Frequency distributions for occurrence of nuchal cirri and number of segmented caudal-fin rays in specimens of Istiblennius meleagris from various localities (arranged more-or-less linearly around the northern Australian coast Scarborough, WA, to Sydney, NSW).

Locality	Nuchal cirri[1]			Caudal-fin rays		
	0	1	2	13	14	15
Western Australia						
Scarborough	-	2	-	1	-	-
Port Denison	1	1	-	2	-	-
Houtman Abrolhos	3	1	-	3	1	-
Murchison River	17	1	-	12	1	-
False Entrance	4	-	-	3	1	-
Dirk Hartog Island	21	-	-	14	2	1
Shark Bay	35	3	1	9	1	-
Rosemary Island	27	-	-	21	-	-
North Turtle Island	1	-	-	-	-	-
Lacepede Islands	2	-	-	2	-	-
Fenelon Island	8	-	-	3	-	-
Northern Territory						
McCluer Island	35	6	5	27	1	-
New Year Island	12	8	2	22	-	-
Yirrkala	52	4	5	13	-	-
Groote Eylandt	45	8	7	35	1	-
Queensland						
Prince of Wales Id	-	-	3	3	-	-
Lizard Island	-	1	12	11	-	-
Cairns	-	3	26	7	-	-
Townsville	-	-	10	10	-	-
Heron Island	2	6	55	51	-	-
New South Wales						
Broken Head Beach	1	3	11	15	-	-
Minnie Water	-	1	1	2	-	-
Arrawarra	1	2	5	8	-	-
Sydney	-	-	1	1	-	-

[1] 0 = absent on both sides; 1 = present unilaterally; 2 = present bilaterally.

females than in males; dark dorsal extensions of bands positioned on dorsal body contour, entering dorsal fin basally; numerous small, pale spots on body (spots often absent in long-preserved specimens) arranged, more or less, in unmatched rows. Spinous- and segmented-ray portions of dorsal fin faintly to darkly dusky, often bearing dark, slender, oblique stripes (particularly males) or dark spots (particularly females); fin dusky with pale, slender, oblique stripes in some males. Anal fin faintly to darkly dusky, variably with pale spots in interradial membranes. Caudal fin faintly to darkly dusky, with vertical pair of darker dusky spots centrally at base, more distinct in females than males; darker caudal fins with small, pale spots in interradial membranes. Pectoral fins variably dusky. Pelvic fins uniformly pale or dark dusky.

Freshly preserved specimens with pale spots very conspicuous, variably present on the head. Randall et al. (1990:385, middle fig.) provide color photograph of fresh male specimen, but color seems faded. Grant (1987:333, fig. 713) provides color photograph of fresh female specimen, very similar to preserved specimens, except: pale spots on head and body white or pale blue; dark spot distally in interradial membranes between first 2 dorsal-fin spines; anal fin and segmented-ray

portion of dorsal fin darkest just subdistally; Grant describes life color as, "head, face and lips are peacock-purple...shading through to the dull purple of the body."

Ophioblennius stage. Only 1 ophioblennius-stage specimen, 16.1 mm SL (Figure 4d), available: 4 tiny canines anteriorly in lower jaw; enlarged, posterolaterally projecting canine on only 1 side of lower jaw; head with small melanophores dorsally; few faint bands beginning to form dorsally on body below anterior spinous dorsal fin; pectoral fin (Figure 6e) with column of elongate melanophores in interradial membranes at about mid-length of fin and distal band of much smaller melanophores. Specimens ≥16.3 mm SL are all metamorphosed.

Size. Largest male 118 mm SL, largest female, 106 mm SL.

GEOGRAPHIC VARIATION.—Specimens from different localities exhibit noticeable variation in mean numbers of meristic elements (Table 32), numbers of segmented caudal-fin rays, and in presence of nuchal cirri (Table 33).

Means for meristic elements appear to be highest along the western and eastern coasts of Australia, and lowest along the northernmost coast. Nape cirri appear to show a progression from cirri being absent on one or both sides in Western Australian specimens, to occasionally being present on both sides in Northern Territory specimens, to usually being present on both sides in Queensland and New South Wales specimens. The presence of 14 or 15 segmented caudal-fin rays occurs only in some specimens from Western Australia and Northern Territory, with slight indication that presence is more common in the former area than the latter.

The transition area, where nape cirri change from being usually absent to being usually present, is relatively narrow. It occurs somewhere between the eastern Gulf of Carpentaria and Prince of Wales Island off the northwest tip of the York Peninsula, northern Queensland. Northern Australia was connected to southern New Guinea during the last glaciation, about 18,000 years ago, when sea level was over 100 m lower (Myers, 1989, fig. 8; Springer and Williams, 1990). This connection probably isolated populations of *I. meleagris* on either side and permitted them to diverge. Gradual rise in sea level has inundated the connection and allowed the separated populations to become reproductively connected once again.

The partial barrier formed by the Cape York Peninsula, perhaps, still limits interbreeding between populations on either side, and this is manifested by the relatively narrow area where intergrades in nape cirri occur.

COMPARISONS AND RELATIONSHIPS.—We have no intuitive suggestion as to what the sister group of *Istiblennius meleagris* might be, although our phylogenetic analysis places it in a weakly supported polytomous clade with *I. edentulus, I. rivulatus,* and *I. dussumieri* (Figure 60; see Phylogenetic Analysis section). It is easily distinguished from all other *Istiblennius* species in having the following combination of characters: 14 pectoral-fin rays; crenulate upper lip; highly complex (tree-like) orbital cirrus; usually more than 10 (up to 26) bi-pored lateral-line tubes, which usually extend posteriorly
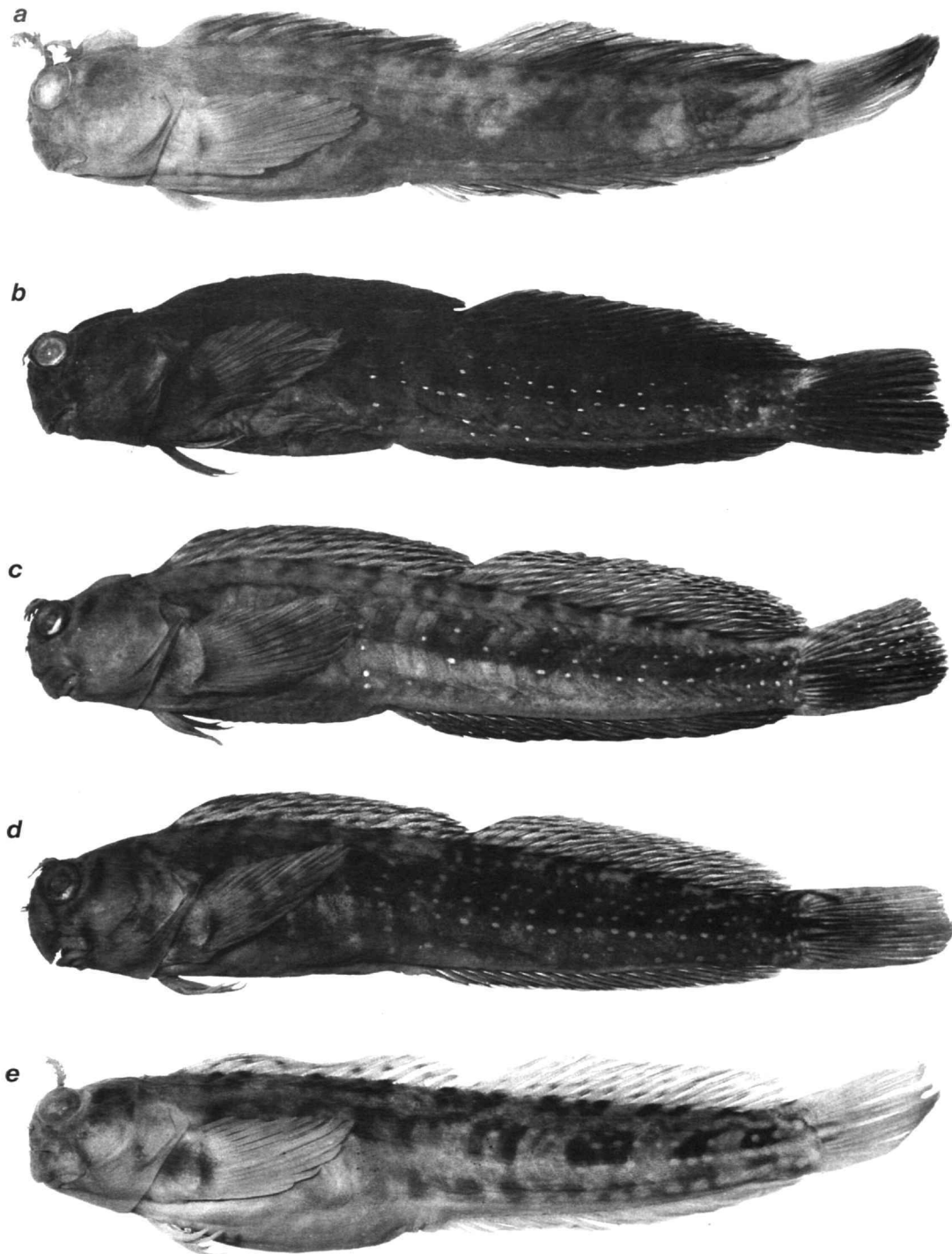
FIGURE 43.—*Istiblennius meleagris: a,b,* NTM S-11951-008, males, 64 and 66 mm SL, Fenelon Island, Western Australia; *c,* male, USNM 293844, 56 mm SL, Heron Island, Queensland (orbital cirrus on right side arching anteriorly, left side, posteriorly); *d,* NTM S-11951-008, female, 49 mm SL, Fenelon Island, Western Australia; *e,* USNM 293844, female, 70 mm SL, Heron Island, Queensland (photographs by T.B. Griswold).
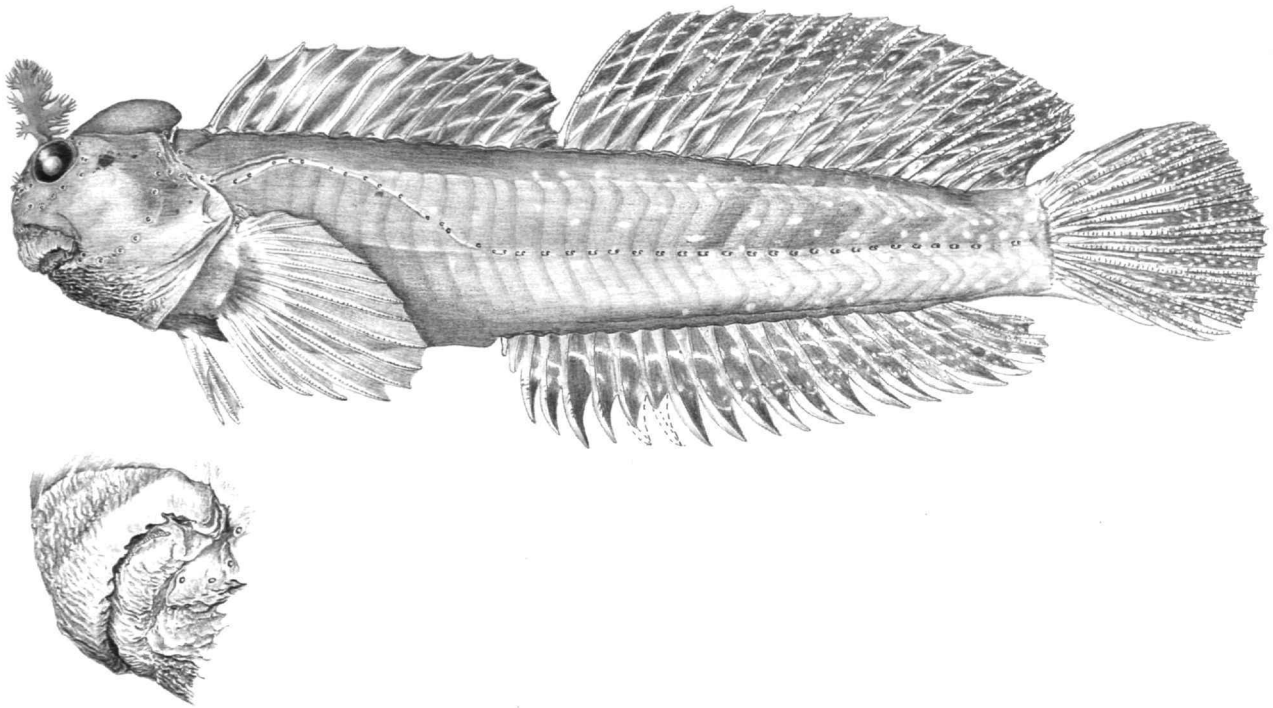
FIGURE 44.—*Istiblennius meleagris*, USNM 246426, male, 107 mm SL, Townsville, Queensland, lateral view and enlarged view of lips (drawing by P.K. Hollingsworth).

beyond vertical from 10th segmented dorsal-fin ray (as far as caudal-fin base); dorsal fin rarely attached posterior to caudal peduncle; no posterior canines in lower jaw.

DISTRIBUTION (Figure 69).—Known only from Australia, ranging from Scarborough (vicinity of Perth), Western Australia, north around the top of the continent, then east, and south to Sydney, New South Wales. Occurs close to shore at very shallow depths and, perhaps, under brackish or freshwater conditions. One lot of specimens (WAM P.15850-001) was taken near the mouth of the Murchison River, and two others (WAM P.5918-001, P.6581-001) were taken about 15 km upstream in that river. No other species of *Istiblennius* is reported to occur so far from the sea, and few, if any, of the others are known to occur under brackish conditions. Grant (1987:333) reported that groups of up to 20 individuals may occur together beneath flakes of rock and dead coral clinker well above low-tide area. According to Grant, *I. meleagris* often occurs closely together with *I. edentulus*.

NOMENCLATURAL DISCUSSION.—The type locality of *Salarias meleagris*, "terre de Van-Diemen" (an old name for Tasmania), is undoubtedly incorrect. No species of *Istiblennius* has been reported during the 20th Century to occur south of Sydney, New South Wales, in eastern Australia, and the only pre-20th century report we know of is the clearly erroneous one for the holotype of *Istiblennius muelleri*, which was supposedly taken in Victoria.

The description of *Salarias meleagris* indicates neither the number of type specimens nor their sizes, although 2 specimens were discussed, one with a crest (hence, a male) and the other a female without a crest, but with well-developed ovaries. The female apparently no longer exists. Two conspecific males, MNHN A.1808 and A.2042, both purportedly collected from Van Diemen's Land by Péron, were reported by Bauchot (1967) as syntypes. We designate MNHN A.1808 (77.7 mm SL), which is in better condition, as lectotype.

Castelnau (1875) did not compare his *Blennius vittipinnis* with any other species, nor did he indicate how many specimens he had, other than to state "many." His description states that there are 15 pectoral-fin rays, whereas we record 14 for putative syntypes. Otherwise Castelnau's description clearly pertains to the (larger) specimens we list as syntypes of *B. vittipinnis*. The BMNH syntype is registered as having been received from the "Paris Museum."

MATERIAL EXAMINED.—WA: Dampier's Arch, BMNH 1883.7.4.5.6 (syntype of *Blennius vittipinnis*), MNHN A.2120 (3 syntypes of *Blennius vittipinnis*), A.2121 (3 syntypes of *Blennius vittipinnis*); Scarborough, WAM P.2333-001 (1), P.2334-001 (1); Port Denison, WAM P.10356-001 (2);

Murchison River, WAM P.15850-001 (1), P.5918-001 (1), P.6581-001 (6); Houtman Abrolhos, WAM P.25853-001 (2), P.30063-001 (2); False Entrance, WAM P.4667-001 (4); Dirk Hartog Id, WAM P.26675-002 (21); Shark Bay, WAM P.4668-001 (27), P.6699-001 (2), P.7323-001 (4), P.7343-001 (7); Rosemary Id, NTM S.10811-015 (27 specimens); North Turtle Id, NTM S.10831-001 (1); West Lacepede Id, WAM P.27671-016 (2); Fenelon Id, NTM S.11951-008 (8). NT: New Year Id, NTM S.10601-001 (22); McCluer Id, NTM S.10595-013 (46); Yirrkala, USNM 174359 (63); Groote Eylandt, USNM 174358 (41), 174362 (19, including 2 cleared and stained). Qd: Prince of Wales Id, AMS I.19356-026 (3); Lizard Id, AMS I.21344-051 (3), I.22726-009 (4), I.22732-004 (2), NTM S.11446-007 (4); Cairns, USNM 308830 (18), 308833 (12); Townsville, USNM 264246 (10); Heron Id, USNM 293844 (25), 296002 (3), 296085 (29), 296101 (13). NSW: Broken Head Beach, AMS I.18064-005 (15); Arrawarra Headland, AMS I.20095-005 (8); Minnie Water, AMS I.16467-027 (2); Parsley Bay, Sydney Harbor, AMS I.17661-007 (1). Terre de Van-Diemen, MNHN A.1808 (lectotype of *Salarias meleagris*), A.2042 (possibly a paralectotype of *Salarias meleagris*).

Istiblennius dussumieri (Valenciennes)

FIGURES 4*b*, 45, 46

Salarias dussumieri Valenciennes in Cuvier and Valenciennes, 1836:310 [Malabar; lectotype, designated in nomenclatural discussion section below, larger of 2 syntypes in MNHN A.1740]).

Salarias forsteri Valenciennes in Cuvier and Valenciennes, 1836:315 [Pacific Ocean; designated in nomenclatural discussion section under *Istiblennius edentulus*, larger of 2 syntypes in ZMB 1942].

Salarias olivaceus Blyth, 1859:271 [Port Blair, eastern coast of the southern island of Great Andaman; neotype, USNM 242052, designated in nomenclatural discussion section below].

Salarias striatomaculatus Kner and Steindachner, 1866:366 [Mauritius; holotype, apparently lost].

Salarias geminatus Alleyne and Macleay, 1877:336 [Torres Straits; AMS I.16416-001, 2 presumable syntypes].

Salarias auridens Alleyne and Macleay, 1877:338 [Darnley Island; AMS I.16418-001, holotype].

Salarias cristiceps Alleyne and Macleay, 1877:338 [Darnley Island; AMS I.16417-001, holotype].

Salarias doliatus Sauvage, 1880:217 [Océan atlantique; MNHN 2548, holotype].

Salarias cheverti Macleay, 1881:12 [Darnley Island; AMS I.16419-001, presumed syntypes].

Scartichthys stigmatopterus Fowler, 1904:553 [Padang, Sumatra; ANSP 27803, holotype].

Salarias zamboangae Evermann and Seale, 1906:512 [Zamboanga, Mindanao; USNM 55623, holotype].

Salarias barbatus Gilchrist and Thompson, 1908:108 [Bluff, Durban; 2 syntypes, SAM 9891].

Salarias siamensis H.M. Smith, 1934:320 [Koh Tao, Gulf of Siam; holotype apparently lost].

Salarias oortii [not Bleeker], Chapman, 1951:325,328 [misidentification].—Smith-Vaniz and Springer, 1971:58 [misidentification].

DESCRIPTION.—Dorsal fin (Table 34). XII to XIV,19 to 24 =

32 to 37 (XIII in 93% of specimens; 19 in only 5 of over 600 specimens examined for character); mean number of total elements for males from any locality usually higher than that of females from same locality (higher for 17 of 20 localities where means for both sexes are available, statistically significantly higher for 11 of the 17 localities); membrane between spinous and segmented-ray portions notched more than half length of first segmented ray (usually more than two-thirds length); membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle anterior to caudal-fin base to point less than 21% caudal-fin length out on dorsal edge of caudal fin (attachment usually on caudal fin in specimens >40 mm SL, usually out on fin <16% fin length).

Anal fin (Tables 34 and 35). II,21 to 25; mean number of segmented rays for males from any locality usually higher than that of females from same locality (higher for 16 of 20 localities where means for both sexes are available, statistically significantly higher for 7 of the 16 localities); posteriormost ray split to base or simple (modal condition varying with population; see section below on geographic variation; posterior element of split ray often difficult to determine externally), not bound by membrane to caudal peduncle in more than 96% of specimens. Mature males with skin covering anal-fin spines and distal half of rays rarely, if ever, expanded, never crinkled along lateral edges.

Pectoral-fin rays 13 to 15 (13 only unilaterally; 14 bilaterally in 94%, unilaterally in 5%, of specimens examined for character).

Pelvic-fin segmented rays 3.

Caudal fin (Table 36). Dorsal procurrent rays 5 to 9 (rarely 5 or 9), ventral procurrent rays 5 to 8 (rarely 5), modal combination 6/6, 7/6, or 7/7, depending on population (see section below on geographic variation); segmented rays 12 to 14 (13 in 99% of specimens).

Vertebrae (Table 34). 10 or 11+27 to 32 = 38 to 42 (10 in 92% of specimens examined for character; 27 in only 2 of 420 specimens examined for character); mean number of total vertebrae usually higher for males from any locality than for females from the same locality (higher for 17 of 20 localities where means for both sexes are available, statistically significantly higher for 7 of the 17 localities); posteriormost pleural rib on 10th to 12th from anteriormost centrum (on 11th in 94% of specimens); posteriormost epineural on 14th to 21st from anteriormost centrum (rarely on 14th or 21st).

Cirri (specimens over 40 mm SL). Nape cirri absent. Orbital cirrus highly variable within and among populations, often appearing damaged or malformed; normal appearing cirri branched, usually comprising elongate, transversely placed pennant with usually no more than 5 branches (cirri) on each medial and lateral edge; cirri of males generally longer than those of females, often longer than orbital diameter; female cirrus rarely as long as orbital diameter; pennant of some specimens from New Caledonia with additional branches arising from low, median keel on anterior surface, other

Table 34.—Frequency distributions for certain meristic characters in male and female specimens of _Istiblennius dussumieri_ from various localities. Underlining indicates significant differences between means of sexes from same locality (p ≤ .05).

Sex/Locality	Total dorsal-fin elements							Segmented anal-fin rays						Total vertebrae						
	32	33	34	35	36	37	x̄	21	22	23	24	25	x̄	37	38	39	40	41	42	x̄
MALES																				
South Africa	-	1	5	4	1	-	34.4	-	1	8	2	-	22.1	-	-	5	5	1	-	39.6
Kenya	-	-	-	4	-	-	35.0	-	-	2	2	-	22.5	-	-	1	3	-	-	39.8
Comoro Islands	-	-	-	1	-	-		-	-	1	-	-		-	-	-	1	-	-	
NW Madagascar	-	1	15	10	-	-	34.3	-	1	20	5	-	23.2	-	-	11	15	-	-	39.6
Seychelles (Mahé)	-	-	21	8	-	-	34.3	-	-	22	7	-	23.2	-	-	11	18	-	-	39.6
Ceylon	-	-	6	-	-	-	34.0	-	-	5	-	-	23.0	-	-	4	1	-	-	39.2
Pakistan & NW India	-	1	10	5	-	-	34.2	-	2	9	5	-	23.2	-	1	9	5	-	-	39.3
NE India	-	-	3	-	-	-	34.0	-	1	2	-	-	22.7	-	-	2	1	-	-	39.3
Myanmar	-	4	2	-	-	-	33.3	-	4	2	-	-	22.3 ·	-	2	4	-	-	-	38.7
Andaman Islands	-	-	1	-	-	-		-	-	1	-	-		-	-	-	1	-	-	
Thailand, Andaman Sea	-	3	6	4	-	-	34.1	1	5	4	3	-	22.7	-	1	6	5	1	-	39.5
Sumatra, Indian O coast	-	-	1	1	-	-	34.5	-	-	2	-	-	23.0	-	-	1	1	-	-	39.5
Gulf of Thailand	-	9	22	1	-	-	33.8	-	17	15	-	-	22.5	-	5	23	4	-	-	39.0
Taiwan	-	1	3	-	-	-	33.8	-	1	3	-	-	22.8	-	-	4	-	-	-	39.0
Hong Kong	-	1	1	-	-	-	33.5	-	1	1	-	-	22.5	-	-	2	-	-	-	39.0
Palau	-	-	1	-	-	-		-	1	-	-	-		-	-	1	-	-	-	
Philippines	-	3	19	1	-	-	33.9	-	6	15	2	-	22.8	-	2	15	4	-	-	39.1
Java (Pulau Edam)	1	-	-	-	-	-		1	-	-	-	-		1	-	-	-	-	-	
Flores	-	9	8	2	2	-	33.8	-	10	8	2	1	22.7	-	6	9	1	2	-	38.9
Boeton (= Bouton)	-	1	1	-	-	-	33.5	-	-	2	-	-	23.0	-	1	1	-	-	-	38.5
Ambon	-	1	-	-	-	-		-	1	-	-	-		-	1	-	-	-	-	
Halmahera	-	14	13	2	-	-	33.6	1	18	10	-	-	22.3	-	5	17	4	-	-	39.0
Western New Guinea	-	-	1	-	-	-		-	1	-	-	-		-	1	-	-	-	-	
Eastern New Guiea	-	-	8	7	-	-	34.5	-	-	11	4	-	23.3	-	-	4	11	-	-	39.7
N Great Barrier Reef	-	-	2	3	-	-	34.6	-	2	3	-	-	22.6	-	-	-	2	-	-	40.0
New Caledonia	-	-	1	5	12	-	35.6	-	-	4	11	3	23.9	-	-	-	8	9	-	40.5
Lord Howe Island	-	-	-	1	-	-		-	-	-	-	1		-	-	-	-	1	-	
Indies Orientales[1]	-	-	-	2	1	1	35.8	-	-	1	2	1	24.0	-	-	-	1	2	1	41.0
Fiji	-	-	7	12	-	1	35.0	-	-	9	11	-	23.6	-	-	2	15	1	1	40.0
FEMALES																				
South Africa	-	2	4	1	-	-	33.8	-	3	4	-	-	21.6	-	1	3	3	-	-	39.3
Kenya	-	1	1	-	-	-	33.5	-	2	-	-	-	21.0	-	-	2	-	-	-	39.0
Comoro Islands	-	2	2	-	-	-	33.5	-	2	2	-	-	21.5	-	-	3	1	-	-	39.2
NW Madagascar	-	7	22	3	-	-	33.9	2	10	19	1	-	22.6	-	4	22	5	-	-	39.0
Seychelles (Mahé)	-	6	20	1	-	-	33.4	-	8	17	2	-	22.8	-	2	18	2	1	-	39.1
Ceylon	-	3	-	-	-	-	33.0	-	3	-	-	-	22.0	-	2	1	-	-	-	38.3
Pakistan & NW India	-	4	11	1	-	-	33.8	-	3	13	-	-	22.8	-	2	11	2	-	-	39.0
NE India	-	2	-	-	-	-	33.0	-	2	-	-	-	22.0	-	1	1	-	-	-	38.5
Myanmar	-	3	3	-	-	-	33.5	-	4	2	-	-	22.3	-	1	4	1	-	-	39.0
Andaman Islands	-	1	2	-	-	-	33.7	-	1	2	-	-	22.7	-	1	2	-	-	-	38.7
Thailand, Andaman Sea	-	8	7	-	-	-	33.5	-	11	4	-	-	22.3	-	2	12	-	-	-	38.8
Sumatra, Indian O coast	1	2	-	-	-	-	32.7	2	1	-	-	-	21.3	1	2	-	-	-	-	37.7
Gulf of Thailand	3	15	9	-	-	-	33.3	4	18	5	-	-	22.0	-	9	17	-	-	-	38.6
Taiwan	-	-	2	-	-	-	34.0	1	-	1	-	-	22.0	-	-	2	-	-	-	39.0
Hong Kong	-	-	1	-	-	-		-	1	-	-	-		-	-	-	1	-	-	
Palau	-	1	-	-	-	-		-	1	-	-	-		-	-	1	-	-	-	
Philippines	1	24	35	3	-	-	33.6	2	40	20	1	-	22.3	-	14	41	4	-	-	38.8
Java (Pulau Edam)	-	2	-	1	-	-	33.7	-	2	-	1	-	22.7	-	-	2	1	-	-	39.3
Flores	1	13	9	2	-	-	33.5	1	18	6	-	-	22.2	-	12	8	3	-	-	38.6
Timor	-	1	-	-	-	-		-	1	-	-	-		-	-	1	-	-	-	
Boeton (= Bouton)	-	1	5	-	-	-	33.8	1	4	1	-	-	22.0	-	1	5	-	-	-	38.8
Ambon	-	-	1	-	-	-		-	1	-	-	-		-	-	1	-	-	-	
Halmahera	-	15	11	-	-	-	33.4	1	24	1	-	-	22.0	-	11	15	-	-	-	38.6
Western New Guinea	-	2	1	-	-	-	32.3	-	2	1	-	-	22.3	-	1	2	-	-	-	38.7
Eastern New Guinea	-	3	12	1	-	-	33.9	-	10	5	1	-	22.4	-	1	14	1	-	-	39.0
N Great Barrier Reef	-	1	6	-	-	-	33.8	-	3	4	-	-	22.6	-	-	4	-	-	-	39.0
New Caledonia	-	-	4	8	3	-	34.9	-	-	4	9	2	23.9	-	-	3	8	5	-	40.1
Fiji	-	-	7	4	-	-	34.4	-	1	7	3	-	23.2	-	-	5	5	1	-	39.6

[1] Probably New Caledonia; see section on geographic variation under _Istiblennius dussumieri_.

Table 35.—Frequencies for condition of posteriormost anal-fin ray in specimens of Istiblennius dussumieri from various localities (modes underlined; N = anal-fin ray simple; S = anal-fin ray split to base).

Locality	N	S	%S
INDIAN OCEAN			
South Africa	6	9	60.0
Kenya	3	4	57.1
Comoro Islands	4	1	20.0
Madagascar (NW)	19	29	60.4
Seychelles (Mahé)	33	23	39.0
Ceylon	1	6	85.7
Pakistan & NW India	8	19	70.4
Myanmar	3	9	75.0
Andaman Islands	2	2	50.0
Thailand (Andaman Sea)	7	20	74.1
Sumatra (Indian Ocean)	-	2	100
PACIFIC OCEAN			
Gulf of Thailand	30	27	47.4
Taiwan	4	1	20.0
Hong Kong	2	1	33.3
Palau	1	1	50.0
Philippines	50	29	36.7
Java (Pulau Edam)	1	2	66.7
Flores	31	15	67.4
Boeton (= Bouton)	5	3	37.5
Ambon	1	1	50.0
Halmahera	27	24	40.1
New Guinea (western)	3	1	25.0
New Guinea (eastern)	16	12	42.9
Great Barrier Reef (N)	9	2	18.2
New Caledonia	22	5	18.5
Lord Howe Island	1	-	100
Indies Orientales[1]	4	-	100
Fiji	17	9	34.6

[1] Probably New Caledonia; see geographic variation section under Istiblennius dussumieri.

branches arising from posterior surface. Nasal cirri short, variable, usually irregularly palmate with less than 7 finger-like branches, variably a simple flap or broad, folded flap with up to at least 16 tiny branches.

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between verticals from 4th and 10th dorsal-fin spines (between 7th and 9th spines in 93% of specimens examined for character), continuing posteriorly and descending to midside in specimens >30 mm SL, as series of 1 to 11 (3 to 7 in 92% of specimens) short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area between verticals from 9th dorsal-fin spine and 3rd segmented ray (between 9th spine and 1st ray in 95% of specimens).

Mandibular pores 4 to 6 (5 pores bilaterally in 91%, unilaterally in 7% of specimens; 6 pores only unilaterally (in only 4 of 202 specimens examined for character).

Five to 8 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (6 in 88% of over 200 specimens examined for character); 0 to 3 positions with paired pores (0 in 32%, 1 in 48%, 2 in 18%, and 3 in only 1 of over 200 specimens examined for character). Posterior canines present or absent (on one or both sides), often tiny, inconspicuous; smallest male (of 196 examined for character) with canines, 26 mm SL (canines barely evident), but canines present in only 19% of 75 males <50 mm SL, and 68% of 121 males >49 mm; smallest female (of 181 examined for character) with canines, 50 mm SL, but canines present in only 9% of 114 females >49 mm SL.

Ventral margin of upper lip and dorsal margin of lower lip entire.

Males with fleshy, blade-like crest dorsally on head; earliest indication of beginning crest a darkly pigmented, longitudinal line mid-dorsally on head; definite ridge or crest variably present in males as small as 23 mm SL, but usually absent at lengths <29 mm SL; crests present in all males >30 mm, except those from South Africa; crests absent in males <38 mm SL from South Africa. Crests absent in all females, but almost unnoticeable mid-dorsal ridge present in few large females.

Color pattern (in preservative). Males (Figures 45a, 46a,b). Head dark dusky, without distinct markings. Body dark dusky anteriorly with 1 or 2 slightly darker bands dorsally in area below anterior 8 dorsal-fin spines, followed posteriorly with up to 5+ pairs of dusky bands, posteriormore bands sometimes composed of small, dusky spots on ventral half of body, particularly in small males. Spinous dorsal fin usually with dark spot covering some portion of interradial membranes between first and third spines; several wavy, dusky stripes coursing through spinous dorsal fin, or fin generally dark dusky, except pale basally and distally; segmented-ray portion of dorsal fin with slender, pale distal margin and broad, dusky, submarginal stripe or series of dark dashes forming submarginal stripe or stripes; paler, variably marked area below submarginal stripe, subtended by basal dusky area into which body bands diffusely enter. Anal fin dusky overall, darker distally. Caudal fin variably marked, often with pale, distal, dorsoposterior edge, followed proximally by distinctive, broad, dusky, crescentic margin on remainder of fin; crescentic marking continuous with central, dusky stripe originating basally on fin as vertical pair of dusky spots (this pattern not clearly discernible in our illustrations; Randall et al., 1990:384, top fig.; J.L.B. Smith, 1959, fig. 7; and H.M. Smith, 1934, pl. 14 present reasonable renderings of the male color pattern, particularly the caudal fin); dorsal portion of dusky crescentic marking often broken into several dark spots, which appear to be continuations of dorsal-fin spotting. Fleshy pectoral-fin base often with one or two irregular, diagonal, dusky bands; large, diffusely dusky area basally on central rays often present; sometimes 1 or 2 intensely dark spots also present. Pelvic fins dusky without distinctive markings.

Allen and Steene (1987, pl. 107: fig. 3) provide color photograph of head and anteriormost part of body of living male: head generally pale with brownish markings in interorbi-

Table. 36—Frequency distributions for numbers of procurrent caudal-fin rays in specimens of _Istiblennius dussumieri_ from various localities.

Locality	Dorsal procurrent caudal-fin rays						Ventral procurrent caudal-fin rays					Total procurrent caudal-fin rays								
	5	6	7	8	9	x̄	5	6	7	8	x̄	10	11	12	13	14	15	16	17	x̄
WESTERN INDIAN OCEAN																				
South Africa	-	1	10	5	-	7.2	-	8	6	2	6.6	-	-	1	5	6	3	1	-	13.9
Kenya	-	-	3	4	-	7.6	-	1	5	1	7.0	-	-	-	3	3	1	-	-	13.7
Comoro Islands	-	-	3	1	-	7.2	-	-	4	-	7.0	-	-	-	-	3	1	-	-	14.2
Madagascar (NW)	-	1	32	13	1	7.3	-	10	34	3	6.8	-	-	1	9	22	13	1	1	14.1
Seychelles (Mahé)	-	4	44	7	-	7.0	2	40	13	-	6.2	-	1	4	34	12	4	-	-	13.2
Ceylon	-	-	6	1	-	7.1	-	2	5	-	6.7	-	-	-	2	4	1	-	-	13.8
Pakistan & NW India	1	4	16	5	-	7.0	-	16	9	1	6.4	-	-	5	11	6	3	1	-	13.4
EASTERN INDIAN OCEAN																				
Myanmar	-	-	7	3	-	7.3	-	4	6	-	6.6	-	-	-	4	3	3	-	-	13.9
Andaman Islands	-	-	-	1	-		-	-	1	-		-	-	-	-	-	1	-	-	
Thailand																				
Andaman Sea coast	-	3	18	2	-	7.0	-	11	12	-	6.5	-	-	2	10	9	2	-	-	13.5
Sumatra																				
Indian Ocean coast	-	-	4	-	-	7.0	-	4	-	-	6.0	-	-	-	4	-	-	-	-	13.0
PACIFIC																				
Thailand																				
Gulf of Thailand	-	8	42	5	-	6.9	-	29	16	-	6.4	-	-	8	29	15	3	-	-	13.2
Taiwan	-	2	4	-	-	6.7	-	5	1	-	6.2	-	-	2	3	1	-	-	-	12.8
Hong Kong	-	-	2	-	-	7.0	-	-	2	-	7.0	-	-	-	-	2	-	-	-	14.0
Palau	-	-	1	-	-		-	1	-	-		-	-	-	1	-	-	-	-	
Philippines	-	13	52	6	-	6.9	2	46	23	-	6.3	-	2	11	35	17	6	-	-	13.2
Java (Pulau Edam)	-	-	2	-	-	7.0	-	2	-	-	6.0	-	-	-	2	-	-	-	-	13.0
Flores	-	4	27	4	-	7.0	-	17	18	-	6.5	-	-	4	12	16	3	-	-	13.5
Boeton (= Bouton)	-	-	7	-	-	7.0	-	1	6	-	6.8	-	-	-	1	6	-	-	-	13.8
Ambon	-	1	1	-	-	6.5	-	-	2	-	7.0	-	-	-	1	1	-	-	-	13.5
Halmahera	1	10	32	5	-	6.8	-	25	23	-	6.5	-	1	9	16	17	5	-	-	13.2
New Guinea																				
Western	-	-	4	-	-	7.0	-	3	1	-	6.2	-	-	-	3	1	-	-	-	13.2
Eastern	-	5	22	2	-	6.9	-	19	10	-	6.3	-	-	5	14	8	2	-	-	13.2
Great Barrier Reef (N)	-	-	4	-	-	7.0	-	4	-	-	6.0	-	-	-	4	-	-	-	-	13.0
New Caledonia	-	10	11	-	-	6.5	-	12	9	-	6.4	-	-	9	4	8	-	-	-	13.0
Lord Howe Island	-	-	1	-	-		-	-	1	-		-	-	-	-	1	-	-	-	
Fiji	-	10	16	-	-	6.6	1	19	6	-	6.2	-	1	4	8	12	1	-	-	12.3
INDES ORIENTALES[1]	1	3	-	-	-	5.8	1	3	-	-	5.8	1	-	3	-	-	-	-	-	11.5

[1] Probably New Caledonia; see section on geographic variation under _Istiblennius dussumieri_.

tal region and posterior to eye; iris of eye with coppery brown marks; fleshy crest, dusky brown with pale central band; 2 brown bands separated by pale area on fleshy pectoral-fin base.

Female (Figures 45e, 46c,d). Head similar to male, but often with series of broad, alternating, pale and dusky bands on upper lip (beginning with pale corners of lip). Body bands of same number as in males; anterior bands indistinct, others often composed in whole or in part of (or superimposed with) dark spots. Spinous dorsal fin with 3 or 4 rows of dark spots on spines or with wavy, dark stripes; small, dark spot sometimes present on membrane between first 2 spines; segmented-ray portion of dorsal fin spotted or striped. Anal fin faint to dark dusky, paler basally; caudal fin varying from almost unspotted (particularly ventral half of fin in some Indian Ocean females) to having 3 or 4 irregular columns of distinct, dark spots on rays; vertical pair of elongate, dark spots usually present at

central base of fin. Pectoral and pelvic fins similar to those of males.

Allen and Steene (1987, pl. 107: fig. 4) present in-habitat color photograph of live or freshly dead female with distinctive pale markings on head, body, and pectoral-fin base, and dark spots on anterior dusky body bands; dusky markings on head and body various shades of brown or gray.

Ophioblennius-stage specimens. Only 1 ophioblennius-stage specimen available (UF 31308, 18.5 mm SL from Flores, tide pools; Figures 4b, 6c): 1 enlarged, laterally recurved canine tooth on each side of lower jaw; immediately anterior to canine tooth on right side (only), 2 pointed, anteriorly directed teeth, about half size of canine; pectoral fins bear dark melanophores near tips of rays and/or between rays; small, round cluster of fainter melanophores near proximal ends of central pectoral-fin rays; other pigment consisting mostly of large, faint, expanded
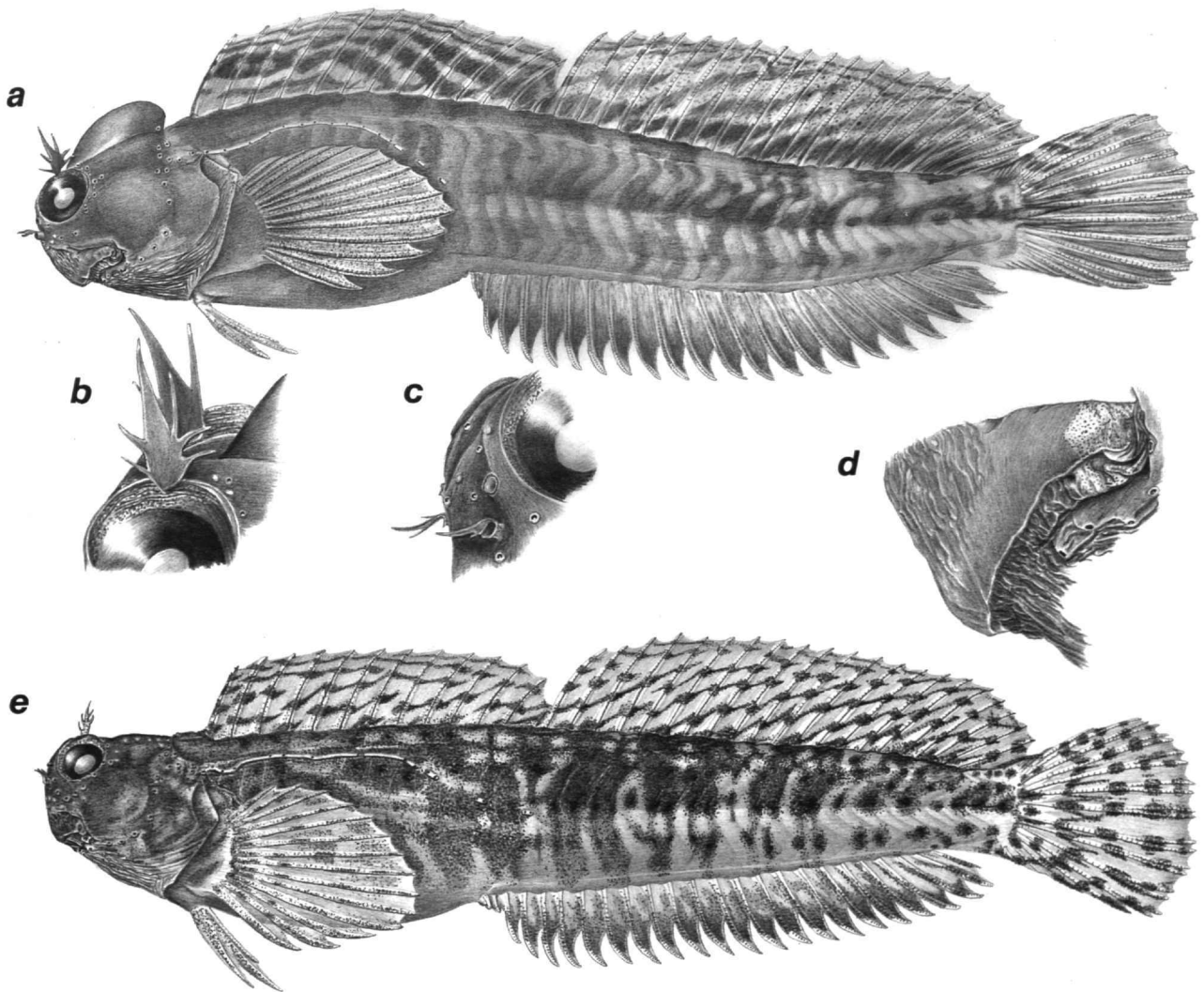
FIGURE 45.—*Istiblennius dussumieri*, USNM 229346, Halmahera, Indonesia: *a-d*, male, 55 mm SL, lateral view with enlarged views of orbital and and nasal cirri and ventral margin of upper lip; *e*, female, 64 mm SL (drawings by P. K. Hollingsworth).

melanophores covering brain area.

The ophioblennius-stage specimen was taken in the same collection with a metamorphosed juvenile 18.9 mm SL (UF 92360) and several other specimens 28.2 to 59.7 mm SL (UF 31299). The ophioblennius-stage specimen is the only specimen smaller than 18.9 mm among our material.

Size. Largest male, 109 mm SL; males commonly >90 mm; 4 largest females available, 80 to 98 mm SL, all other females <76 mm SL.

GEOGRAPHIC VARIATION.—There is considerable variation in mean numbers of dorsal- and anal-fin ray and vertebral numbers among specimens from different localities (Table 34).

In general, means for these counts are highest at localities in the southwest Pacific, intermediate in the western Indian Ocean, and lowest in the central, western Pacific. On the other hand, mean numbers of procurrent caudal-fin rays (Table 36) are generally higher at western Indian Ocean localities, and lower at other localities. There is a tendency for the modal condition for the terminal anal-fin ray (Table 35) to be split in Indian Ocean specimens and simple (unsplit) in Pacific Ocean specimens. See also color pattern description of females.

Four male specimens (MNHN 4771), which were originally cataloged as having been collected by Banaré from "Indes Orientales," have higher mean numbers of dorsal and anal-fin
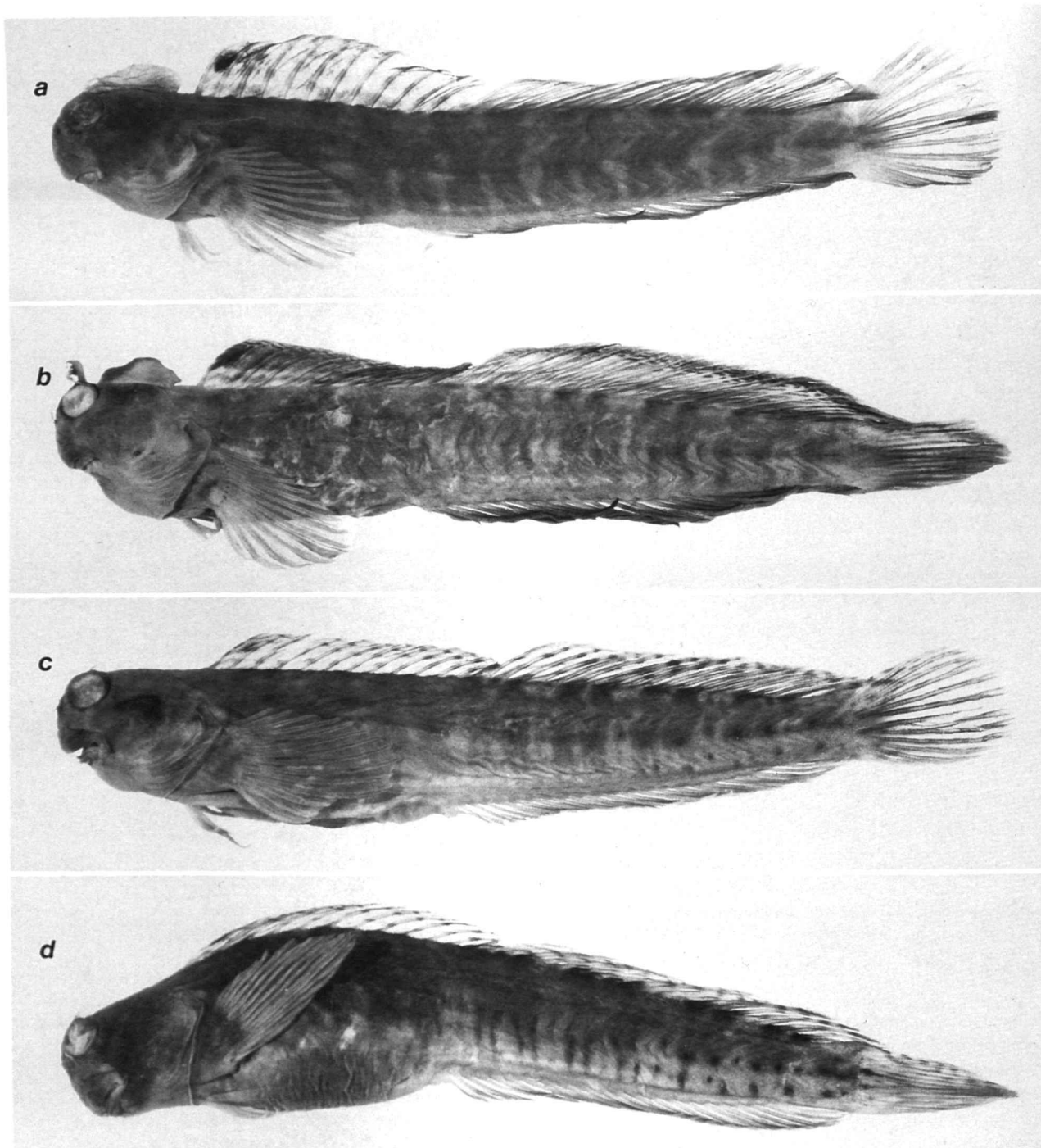
FIGURE 46.—*Istiblennius dussumieri: a,* UMMZ 214578, male, 65 mm SL, Ko Lan, Gulf of Thailand; *b,c,* USNM 291931, male, 76 mm SL, female, 65 mm SL, Nossi Bé, Madagascar; *d,* USNM 296403, female, 77 mm SL, Pamanzi Island, Comoro Islands (photographs by T.B. Griswold).

rays and total vertebrae than do males from other localities. In general, these means agree most closely with those of male specimens from New Caledonia and Fiji, in the southwest Pacific (Table 34), and we believe it probable that they were taken in that area. Considering that, we wrote Dr. M.-L. Bauchot, MNHN, to determine if more data were available that might have bearing on the provenance of the specimens. In response, she wrote us that the specimens were sent by "Armand, Aubin Banaré, né le 1.03.1836 à la Martinique, est embarqué comme lieutenant de vaisseau en 1863 sur 'la Fine,' en Novelle-Calédonie. Il sert sur divers bâtiments de 1863 à 1866 dans cette même région et on le retrouve encore en 1867 en Nouvelle-Calédonie où il fait des travaux d'hydrographie." The specimens were registered 20 Sep 1867. Bauchot feels certain that the originally assigned locality was erroneous and "qu'il n'y a plus de doute sur l'origine [= New Caledonia] de nos poissons envoyés par Banaré." It is noteworthy that all 4 of the males, which range in size from 52–76 mm SL, have a simple cirrus on each anterior nostril, an unusual condition for such large specimens of *I. dussumieri*, and not duplicated in our other specimens from New Caledonia.

COMPARISONS AND RELATIONSHIPS.—We have no strong intuitive suggestion as to what the sister group of *I. dussumieri* might be, although our phylogenetic analysis places it in a polytomous monophyletic clade with *I. edentulus*, *I. meleagris*, and *I. rivulatus* (Figure 60; see Phylogenetic Analysis section). The distinctive color pattern on the caudal-fin of many males (see color-pattern description above) appears to occur otherwise only in males of *I. lineatus* (see Comparisons and relationships section under Lineatus Species Complex). Other characters of *I. dussumieri* occur in various combinations in other species of *Istiblennius*. The combination of: smooth lips, branched orbital cirri, no nape cirri, posteriormost bi-pored lateral-line tube anterior to vertical from 3rd dorsal-fin spine, and modally 5 mandibular pores, 13 dorsal-fin spines, and posterior canine teeth present (occasionally) on the dentaries, distinguishes *I. dussumieri* from all other species of *Istiblennius*.

DISTRIBUTION (Figure 70).—*Istiblennius dussumieri* is distributed throughout much of the Indo-west Pacific, purportedly even entering the southeasternmost Atlantic Ocean marginally at the Cape of Good Hope (based on a specimen reported by Günther, 1861:562; we believe its occurrence at the Cape of Good Hope is rare, probably only as the result of straggling). Well-documented collections of *I. dussumieri* have been made from southern Africa east to Palau, northwest to northern Taiwan and southeast to Fiji. A single specimen, in poor condition, is available from Lord Howe Island, the southernmost occurrence in the the Pacific Ocean. The species appears to be absent (although not necessarily unreported) from the Red Sea, Persian Gulf, Sri Lanka, and Christmas, Cocos-Keeling (Smith-Vaniz, pers. comm.), Chagos, and Mariana islands, all of Australia except the northern Great Barrier Reef, and all islands on the Pacific plate.

Borodin (1932) reported *I. dussumieri*, as *Salarias dussumieri*, from Apia, Samoa, and Huahine, Society Islands, both on the Pacific Plate. We have examined these 2 specimens, which are housed in the Vanderbilt Marine Museum, and find them both to be *Entomacrodus striatus*. Fowler (1938) reported *I. dussumieri*, also as *S. dussumieri*, from Palmyra, Line Islands, on the Pacific plate. Fowler's record is based on 2 small specimens in poor condition (ANSP 82162, ~ 22.6 and 25.5 mm SL). These specimens are referable to *Istiblennius*, but we are unable to identify the species. We believe it highly unlikely that they represent *I. dussumieri*.

Istiblennius dussumieri is a shallow-dwelling species, often taken intertidally and at depths less than 1 m in rocky areas. It may occur together with *I. edentulus*.

NOMENCLATURAL DISCUSSION.—It is clear from Valenciennes' (in Cuvier and Valenciennes, 1836) description of *Salarias dussumieri* that his type series comprised more than 1 specimen. Apparently, only 2 specimens were involved, and these are cataloged as MNHN A.1740. The specimens are conspecific and both are females. We designate the smaller specimen (~68 mm SL vs. ~77 mm), which is in better condition, lectotype of the species.

Blyth's (1859) description of *Salarias olivaceus* from the Andaman Islands seems to pertain to a crested male specimen of *Istiblennius* or *Blenniella*, although it is impossible to tell to which species it belongs. Blyth did not indicate where the holotype of *S. olivaceus* was deposited, and no one has reported seeing it subsequent to its description. W.F. Smith-Vaniz (pers. comm.) did not find the holotype in the museum at Calcutta, where one might expect to find Blyth holotypes.

There are 3 species of *Istiblennius* and 1 crested species of *Blenniella* known from the Andaman Islands (no others are expected to occur there): *I. edentulus*, *I. dussumieri*, *I. lineatus*, and *B. cyanostigma*. The segmented dorsal-fin ray count, 19, given by Blyth, does not occur in *I. lineatus* or males of *I. dussumieri* and would not be expected for males of *I. edentulus* and *B. cyanostigma* from Andaman Islands or vicinity. All 4 of these species' names predate that of *Salarias olivaceus* and are not in jeopardy. We believe it desirable, nevertheless, to settle the identity of *Salarias olivaceus* by designating a neotype for it.

Other than listings, the only published citations (Chapman, 1951; Herre, 1953) of *Salarias olivaceus* we have found have been as junior synonyms of *Istiblennius dussumieri*. No explanation for the synonymy was provided by either author. In view of Chapman's (1951) and Herre's (1953) precedents, we believe it best to firmly establish *Salarias olivaceus* as a junior synonym of *I. dussumieri*.

We are fortunate to have specimens of *I. dussumieri* from the type locality of *Salarias olivaceus*, and here designate as neotype of *Salarias olivaceus* Blyth, USNM 242052, a female, 55 mm SL, which is indicated in the USNM catalog as having been collected by H.S. Rao from "about south point, Pt. Blair, Andaman Islands," 12 Apr 1930. This specimen, which has a

metal tag reading F82—tied through the caudal peduncle, was undoubtedly deposited originally in the collection of the Zoological Survey of India at Calcutta, in which collection similar metal tags are common.

Kner and Steindachner (1866) believed their *Salarias striatomaculatus* from Mauritius, was closely related to both *S. dussumieri* and *S. sumatranus* Bleeker (= *I. edentulus*). They even questioned whether their species was different. They did not indicate how many specimens they had, and no range of variation is indicated in the description, which is based on a female. Their type material, originally cataloged "Nr. 1554" (Godeffroy Museum, Hamburg?) is apparently lost, but the description and illustration are adequate to identify their species as *I. dussumieri*. There are no other specimens of *I. dussumieri* available from Mauritius, and it would be desirable to verify the occurrence of this species at that island.

J.L.B. Smith (1959:244) recognized both *dussumieri* and *striatomaculatus*, believing that the former did not occur on the African coast, to which he believed the latter was restricted. He differentiated *dussumieri* from *striatomaculatus* on the supposed basis that *dussumieri* has a more prominent forehead, and that male *dussumieri* were more strongly marked than males of *striatomaculatus*, particularly the "[broad] black edged wine-red vertical fins." We did not perceive a qualitative difference in the shape of the forehead among specimens from any locality. Our specimens from the African coast are all somewhat faded, but appear to be similar to those from other areas, and at least one male from Kenya has the vertical fins with broad, dark margins like those in Smith's figure 7, based on a specimen from the Seychelles. On the other hand, as we note in our description of the female color pattern, Indian Ocean females tend to be less strongly marked than those of the Pacific, especially, the caudal fin of the former often lacks . distinct, dark spots, particularly on its ventral half, which is rarely, if ever, absent in Pacific females.

Alleyne and Macleay (1877) did not compare their *Salarias geminatus* with any other species nor indicate how many specimens they had. Two specimens in the former Macleay Museum (MAMU F1050; now AMS I.16416-001) were labeled as types of *S. geminatus*. Although the dorsal-fin formula (12/23) given in the original description agrees with neither of the putative types, 1 of the 2 has the unusual spine count of 12. Both these specimens are identifiable as *I. dussumieri*.

Alleyne and Macleay (1877) also did not compare their *Salarias auridens* and *S. cristiceps* with any other species in their exceedingly brief descriptions. They indicated that they had only 1 specimen of *S. auridens*, but did not mention the number for *S. cristiceps*. The putative types of these 2 species each consist of a single specimen: AMS I.16418-001 (formerly MAMU F1051) for *S. auridens* and AMS I.16417-001 (formerly MAMU F1050B) for *S. cristiceps*. The two specimens are identifiable as *I. dussumieri*.

Sauvage (1880) did not compare his *Salarias doliatus* with any other species. As Bauchot (1967) noted, Sauvage was in error in according "Océan atlantique" as the type locality of *Salarias doliatus*, which Bauchot correctly identified as *Halmablennius* (= *Istiblennius*) *dussumieri*. Springer (1963) reported a similar error made by Sauvage in the same 1880 paper, wherein Sauvage reported that Sainte Catherine, Brésil, was the type locality of his *Salarias brasiliensis* (= *Salarias fasciatus*), a species restricted otherwise to the Indo-Pacific.

Macleay (1881) briefly described *Salarias cheverti* without comparing it to any other species and failing to mention how many specimens he had or a specimen length. In the early 1960s, there was a jar (MAMU F1051A) in the Macleay Museum collection labeled as cotypes of *Salarias cheverti*. That jar contained 10 specimens, all female, identifiable as *I. dussumieri*. The jar has been recataloged as AMS I.16419-001, but now contains only 9 specimens.

The holotype and paratype of *Scartichthys stigmatopterus* Fowler (1904), from Padang, Sumatra, were believed to be lost (Smith-Vaniz and Springer, 1971; Böhlke, 1984). During the course of our study, we examined the type series of *Entomacrodus calurus* Fowler (1904), also from Padang, and found that the series contained 2 species and 2 more than the 6 specimens that Fowler reported. Two of the specimens are *I. dussumieri* and 6 are *B. cyanostigma*. Comparison of the 2 specimens with Fowler's description of *Scartichthys stigmatopterus* convinces us that these are Fowler's missing types. The only difference between the specimens and the description is that the specimens have branched supraorbital cirri, whereas Fowler illustrated the cirri as simple. We have removed the 2 specimens from the type series of *E. calurus* and accorded them their original catalog numbers (holotype, ANSP 27803; paratype, ANSP 27804).

Evermann and Seale (1906) compared their *Salarias zamboangae* only with *I. meleagris*. We have examined their type series and find all 3 specimens to be *I. dussumieri*. Although Evermann and Seale reported that the holotype and 2 paratypes were each assigned different catalog numbers (a paratype, each, in the Stanford University and U.S. Bureau of Fisheries collections), all 3 specimens were cataloged as USNM 55623. We have segregated the holotype as USNM 55623 and the 2 paratypes as USNM 291687).

Gilchrist and Thompson (1908) reported that the upper and lower lips of their *Salarias barbatus* had patches of hairlike filaments on them. They did not compare their species with any other. We have examined 1 of the 2 syntypes, and the other was examined for us by Dr. P.A. Hulley. Neither syntype bears the putative filaments, and both are identifiable as *I. dussumieri*. It is possible for the upper lip, at least, that the hairlike filaments were actually the cirri on the anterior nostrils.

Hugh M. Smith (1934) did not compare his *Salarias siamensis* with any other species. Although we are uncertain if his holotype exists, his description and illustration are clearly identifiable as *I. dussumieri*.

Chapman (1951) mistakenly accepted RMNH 4791 as the type series of *S. oortii* Bleeker (1851), and on the basis of these specimens synonymized *S. oortii* with *S. dussumieri*. Bleeker's

description of *Salarias oortii* was based on a Kuhl and Van Hasselt drawing for which the specimen was unavailable. Bleeker (1858b) redescribed *S. oortii* based on specimens (RMNH 4791) that he apparently thought belonged to the same species that Kuhl and Van Hasselt had depicted. Based on the distinctive shape of the caudal fin in the Kuhl and Van Hasselt drawing, the depiction of 15 pectoral-fin rays (an uncommon count in *I. dussumieri*), and the relatively low number of segmented dorsal- and anal-fin rays (19 each), we believe that *S. oortii* should be assigned to the genus *Praealticus*, and it has been treated there by Bath (1993).

MATERIAL EXAMINED.—South Africa: Cape of Good Hope, BMNH 1861.11.7.27 (1 specimen); Durban, SAM 9891 (one of two syntypes of *Salarias barbatus*), USNM 195766 (1); Transkei, USNM 227344 (10); Natal, BPBM 21696 (1), RUSI 77-13 (3); Kwazulu, RUSI 76-16 (1). Zanzibar: Tumbatu, ZMH 18076 (1, originally a syntype of *Salarias steindachneri* Pfeffer, now a paralectotype; not conspecific with lectotype or other paralectotypes; see discussion under Lineatus Species Complex); Kenya: Malindi, SMNS 13138 (1), USNM 296081 (1), 296082 (1), 296083 (1), 302632 (2); Bamburi, USNM 296331 (1). Comoro Is: Pamanzi, USNM 296324 (1), 296403 (4). Madagascar: Nossi Be, USNM 200209 (97, including 3 cleared and stained), 291929 (1), 291931 (38), 291932 (22), 296096 (3), 296110 (34), 298911 (1), 323671 (1). Seychelles: Mahé: ANSP 126980 (37), 127006 (20), CAS 58572 (1), 58574 (5). Pakistan: Astola Id, USNM 305208 (4); W Karachi, USNM 296172 (5). W India: Okha Point, USNM 291926 (2), 291927 (20), 291930 (1); Malabar, MNHN A.1740 (lectotype and paralectotype of *Salarias dussumieri*). Ceylon: Hans Bath, personal collection, collected 1980-84, Galle (1), Marissa (1), Trincomalee (7). E India: Vizagapatam, ZSI F403/2 (3), F404/2 Andaman Is, USNM 195767 (1), Pt. Blair, USNM 144379 (2), 242052 (neotype of *Salarias olivaceus*). Myanmar (= Burma): Maungmagan, USNM 112033 (1); Akyab, USNM 144377 (1); Sandoway, UF 30228 (11). Indonesia: Sumatra, Padang, ANSP 27803 (holotype of *Scartichthys stigmatopterus*), 27804 (1); Benkoelen, USNM 88015 (1), 315777 (2); Pulau Edam (N of Jakarta), CAS 67744 (4); Timor, UF 31303 (1); Flores, UF 18323 (1), 31294 (32), 31299 (31), 31308 (1), 92360 (1); Boeton, USNM 293341 (17); Ambon, USNM 296073 (4), 296078 (1); Halmahera, USNM 229346 (>35), 278253 (2), 296080 (12), 296155 (3), 296170 (2); Ternate, USNM 296143 (3) Irian Jaya [W New Guinea]: Misool Id, USNM 296140 (4). Taiwan: SW Yeh-Liu, USNM 296077 (2), 296164 (1); Wan-Li-Tung, USNM 296329 (1); Ma-Kong, USNM 201906 (2). Hong Kong: CAS 68111 (2), 69649 (1). PNG [E New Guinea]: Milne Bay, USNM 296088 (1); Port Moresby Harbor, USNM 296141 (5); Ravao Id (= Yule Id.), USNM 296079 (13), 296169 (12). Palau: CAS 68103 (1), 68112 (1). Philippines: Luzon, Batan Id, USNM 99384 (2); Mactan Id, USNM 122429 (1), 122441 (2); Panay Id, USNM 122428 (3), 122430 (1); Negros Id, USNM 143786 (1), 296074 (2), 302630 (27), 302633 (9); Siquijor Id, USNM 302638 (11); Masbate Id, USNM 99385 (8), 122329 (1), 122440 (5); Pilas Is [SW

Mindanao], USNM 122427 (3), 122437 (7); Maculabo Id, USNM 122434 (1). Thailand: W coast (Andaman Sea): Phuket, UMMZ 214580 (3), USNM 291925 (9), 291933 (2), 296095 (7), Pulo Tenga, Butang Ids., USNM 296231 (9); E coast (G of Thailand): Ko Lan, off Bon Patthaya, UMMZ 214578 (8); Ko Samed (= Goh Samet), UMMZ 214577 (5); Ko Phai, UMMZ 214581 (1); Ban Pe, USNM 179816 (3); Ko Kut, USNM 119662 (2); Goh Kram No, CAS 67750 (91). Australia: Lizard Id, AMS I.19477-011 (1), I.21536-001 (1), I.21538-026, (4); Torres Straits, AMS I.16416-001 (2 syntypes of *Salarias geminatus*); Darnley Id, AMS I.16417-001 (holotype of *Salarias cristiceps*), I.16418-001 (holotype of *Salarias auridens*); I.16419-001 (10 presumed syntypes of *Salarias cheverti*). New Caledonia: ROM 64494 (4), USNM 114688 (1), 144279 (1), 144280 (1), 144378 (1), 144709 (21), 144717 (1), 216924 (2), 296075 (1). Lord Howe Id: ANSP 75302 (1). Fiji: BPBM 5259 (1), NMNZ P.15701 (2), SMNS 12138 (1), UF 31302 (15), USNM 82937 (1), 236026 (7), 296076 (1). Pacific Ocean: ZMB 1942 (lectotype and paralectotype of *Salarias forsteri*). Atlantic Ocean [erroneous]: MNHN 2548 (holotype of *Salarias doliatus*). Indes Orientales: MNHN 4771 (4).

Istiblennius zebra (Vaillant and Sauvage)

FIGURES 5, 47

Salarias zebra Vaillant and Sauvage, 1875:281 [Iles Sandwich; lectotype, MNHN 8917, designated below].
Salarias cypho Jenkins, 1903:506 [Hawaiian Islands, Honolulu; holotype, USNM 50697].

DESCRIPTION.—Dorsal fin (Table 37). XII to XIV,20 to 23 = 34 to 36 (XIII in 94% of specimens; 20—associated with XIV spines—in only 1 of 109 specimens examined; Miller et al., 1979:91, reported XIII,20 = 33, a combination and total count not observed by us); males tending to have higher mean numbers of total elements than females; membrane between spinous- and segmented-ray portions notched more than half length of first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle to point out on dorsal edge of caudal fin up to 12% caudal-fin length in specimens <70 mm SL, attachment 10% to 33% (rarely more than 22%) caudal-fin length in specimens >70 mm, attachment generally farthest posteriorly in largest specimens.

Anal fin (Table 37). II,21 to 23 (Miller et al., 1979:91, reported as few as 20 segmented anal-fin rays, a number not observed by us in any of 109 specimens examined); males tending to have higher mean numbers of segmented rays than females; posteriormost ray almost always split to base, posterior element of split ray almost always visible externally; fin not bound by membrane to caudal peduncle in any of 43 specimens examined for character (bound, however, in ophioblennius-stage specimens). Skin covering anal-fin spines and distal half of rays not expanded or wrinkled along lateral edges in large and/or mature males.

Pectoral-fin rays 13 to 15 (14 bilaterally in 59, and

Table 37.—Frequency distributions for certain meristic characters of specimens of *Istiblennius zebra* from various islands of Hawaii. Underlining indicates significant difference between means of sexes from same locality (p ≤ .05).

Locality	Total dorsal-fin elements				Segmented anal-fin rays				Total vertebrae			
	34	35	36	x̄	21	22	23	x̄	39	40	41	x̄
Laysan												
males	3	8	1	34.8	-	9	3	22.2	5	6	1	39.7
females	9	10	-	34.5	1	16	4	22.1	10	9	-	39.5
Necker												
males	2	7	3	_35.1_	1	6	5	22.3	2	7	2	40.0
female	10	6	-	_34.4_	2	12	2	22.0	4	11	-	39.7
Oahu												
males	-	12	3	_35.2_	-	7	8	_22.5_	1	13	-	39.9
females	3	20	-	_34.9_	2	17	4	_22.1_	2	20	-	39.9

Locality	Terminal pleural rib on centrum #			Dorsal procurrent caudal-fin rays				Ventral procurrent caudal-fin rays		Total procurrent caudal-fin rays			
	11	12	13	5	6	7	8	6	7	12	13	14	15
Laysan	21	5	-	-	16	7	-	13	10	12	5	6	-
Necker	10	11	1	-	2	19	2	4	19	1	4	16	2
Oahu	11	19	-	1	3	27	3	7	27	3	6	22	3

unilaterally in 5, of 65 specimens examined for character; 15 only unilaterally, in 1 specimen).

Pelvic-fin segmented rays 3.

Caudal fin. Dorsal procurrent rays 5 to 8, ventral procurrent rays 6 or 7, total procurrent rays 12 to 15 (Table 37), segmented rays 13 or 14 (14 in 3 of 80 specimens examined for character).

Vertebrae (Table 37). 10 or 11+28 to 30 = 39 to 41 (11 in 88% of 75 specimens examined for character); males tending to have higher mean numbers of total vertebrae than females; posteriormost pleural rib on 11th to 13th from anteriormost centrum (about equally divided between 11th and 12th, on 13th in only 1 of 77 specimens examined for character); posteriormost epineural on 14th to 17th from anteriormost centrum (modally on 15th).

Cirri. Nape cirrus absent. Orbital cirrus slender, stalk-like, tapering distally, usually simple, occasionally with tiny branches at tip, longer than eye diameter (up to 2.5× diameter) in males >50 mm SL, varying from slightly less to slightly greater in length than eye diameter in females >50 mm SL (generally proportionately longer in largest specimens of either sex). Nasal cirri short, usually simple flap in specimens under 50 mm SL, highly variable in larger specimens, ranging from simple flap to irregularly palmate or pinnate, rarely with as many as 10 distinct tips.

Lateral line. Continuous canal anterodorsally with simple, nonvertically paired pores, extending posteriorly to point between verticals from 7th and 10th (usually between 8th and 9th) dorsal-fin spines, then descending to midside and continuing posteriorly up to little more than half distance to

caudal-fin base as series of 2 to 15 (usually 4 to 13) short, disconnected, horizontally bi-pored canals (tubes) in skin (posteriormost tube lying between verticals from 10th dorsal-fin spine and 11th segmented ray); usually fewer than 7 tubes in specimens under 70 mm SL.

Mandibular pores 4 to 6 (6 pores bilaterally in 81%, and unilaterally in 12% of specimens examined for character; 4 pores, unilaterally, in only 1 specimen).

Four to 8 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (6 in 74%, 7 in 18% of 74 specimens examined for character); 0 to 2 positions with paired pores (0 in 59%, and 1 in 35% of specimens examined for character).

Posterior dentary canines absent.

Ventral margin of upper lip generally entire, often with crenulae-like pads on inner (buccal) surface; margin sometimes finely crenulate laterally; dorsal margin of lower lip crenulate, crenulae sometimes restricted to lateral margins, often absent in specimens <35 mm SL.

Males and females with fleshy, blade-like crest dorsally on head; male crest first apparent in specimens about 35 mm SL; females with crest first apparent in specimens about 50 mm SL; crest in females much smaller than that of comparably sized males.

Color pattern (in preservative; Figure 47). Most specimens over about 60 mm SL generally dark overall with few distinctive markings; diffuse indications of bands variably noticeable on body. Females variably exhibiting somewhat vermiculated pattern on caudal peduncle, fine dark pinstriping
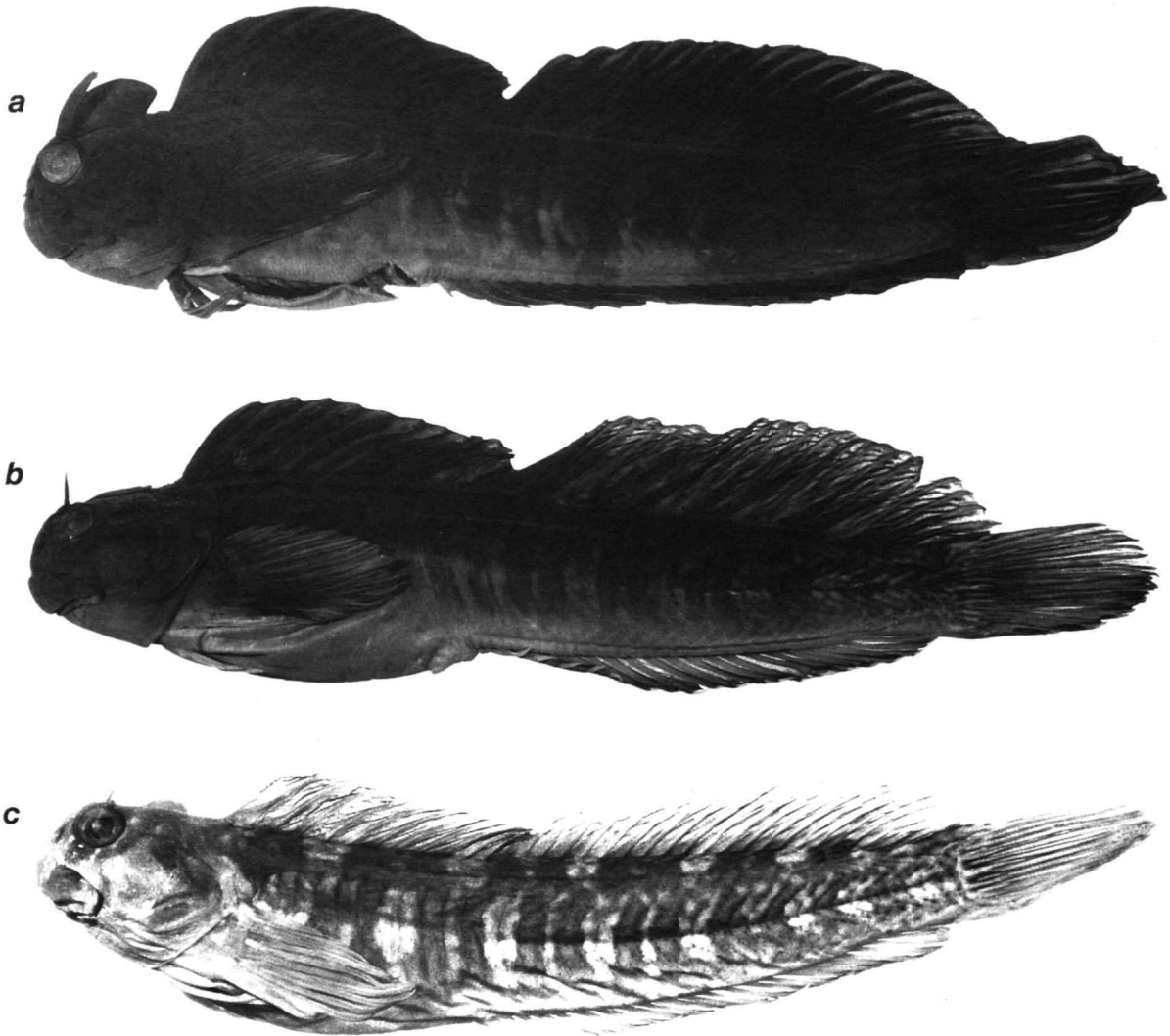
FIGURE 47.—*Istiblennius zebra*, Hawaiian Islands, Oahu: *a,b*, USNM 296594, male, 88 mm SL (right side reversed), female, 101 mm SL; *c*, USNM 292829, female, 75 mm SL (photographs by T.B. Griswold).

in segmented-ray portion of the dorsal fin. Contrastingly marked adults and juveniles <50 mm SL with up to 7 pairs of irregular, dark bands on body, extensions from bands entering dorsal fin basally. Females, especially, with mid-longitudinal area of body bearing dense scattering of fine, almost pinpoint melanophores appearing to lie deep in skin; melanophores on caudal peduncle appearing to follow myosepta, producing chevron-like markings.

Strasburg (1956:254) briefly described the life coloration of adults, "varies from bluish black through gray to yellowish brown, the sides commonly being marked with a series of gray or tan vertical bars. In large specimens the fins may be irregularly blotched with red, and in males the cheeks may be dull orange." Phillips (1977:3) described *I. zebra* as predominantly charcoal grey, with mature specimens having a line of small, bright-blue dots under their eyes.

A useful color photograph of a freshy preserved male specimen of *I. zebra* appears in Randall (1981, fig. 150) and Randall (1985, fig. 150).

Size. Largest male, 150 mm SL; largest female, 141 mm SL,

both from Laysan. Phillips (1977:2), who studied behavior of *I. zebra* at Oahu, reported that the mean SL of adult males was 110 mm, of adult females 99 mm.

DISCUSSION OF OPHIOBLENNIUS-STAGE SPECIMENS (Figures 3, 5, 6*f*).—Miller et al. (1979:88-91) described and illustrated planktonic specimens 3.3 and 11.0 mm SL of *I. zebra* (the illustrations of the larvae were reproduced in Matarese et al., 1984:570, and here as Figure 5*a,b*). The 11 mm larva was an ophioblennius stage with a large, horizontally projecting, recurved canine on each side of the lower jaw (Figure 3) and 2 or 3 smaller, anteriorly projecting, sinuous canines on each side of the lower jaw symphysis. The pectoral fin is large, all 14 of the rays are developed, and each, except the 3 dorsalmost, has a melanophore at its distal tip; there are no incisions in the membranes between any of the rays.

We examined a large shore collection (USNM 292829, Oahu) of *I. zebra* that contained 1 ophioblennius-stage specimen, 20.4 mm SL (Figure 5*c*), several, apparently just metamorphosed juveniles of about the same size and slightly larger, and other specimens up to 75 mm SL. In contrast to the 11 mm ophioblennius stage, the 20 mm specimen (Figure 5*c*) has a pair of horizontally projecting, posteriorly recurved canine teeth on each side of the lower jaw and 2 tiny, very fine, upright, pointed teeth on each side of the symphysis; several similar tiny teeth are present in the upper jaw. The pectoral fins are similarly large, but the distal tips of 5 pairs of rays (2nd and 3rd, 4th and 5th, 6th and 7th, 8th and 9th, 10th and 11th from ventralmost pectoral-fin ray) are fused (unique condition in our experience and that of G.D. Johnson and J.M. Leis, pers. comms.), and there is a deep incision in the fin membrane between each pair of rays with fused tips. Melanophores are present in the membrane between the tips of the 2 ventralmost rays, in the distal half of the membrane between the 4th and 5th from dorsalmost rays, and at the joined tips of the paired rays. Many other melanophores are present, but most noticeable are 7 melanophores that form a mustache on the upper lip, a median melanophore posteriorly at the base of each anal-fin element, and another on the body contour between each pair of segmented rays.

In apparently just metamorphosed specimens of the same size as the 20.4 mm ophioblennius stage, the horizontal canines and fine pointed teeth in both jaws have been lost, and fine comb-like teeth are present in both jaws. The pectoral fin has shortened considerably, but some of the ray pairs are still fused at their tips and marked with melanophores. The upper lip is faintly dusky without a discrete mustache; pairs of dusky bands are beginning to form on the body; and the series of anal-fin melanophores are still present. In slightly larger specimens, the pectoral-fin rays are much shorter proportionately and the tips are all free. There is no evidence of the former deep incisions in the interradial membranes, and the margins of the membranes between the members of a pair of formerly fused rays may exhibit small thickenings of tissue, which appear to be the remnants of the fused ray tips.

There appears to be variation in the size at which the joined pectoral-ray tips are lost. One specimen, 18.9 mm SL (CAS-SU 7682) had only the dorsalmost pair of rays joined at the tips.

For a comparison of the ophioblennius stages of *I. zebra* and *Blenniella gibbifrons*, the only 2 species of the 2 genera in the Hawaiian Islands, see comparisons section under *B. gibbifrons*.

GEOGRAPHIC VARIATION.—Modal counts for position of the terminal pleural rib and numbers of procurrent caudal-fin rays of specimens from Laysan, westernmost island in the distribution of *I. zebra*, are at the lower ends of the ranges for these elements compared with modes for the same characters for other, more eastern, islands (Table 37).

COMPARISONS AND RELATIONSHIPS.—*Istiblennius zebra* subjectively appears to us to be most closely related to the allopatric *I. bellus*, with which it falls into a weakly supported polytomous clade, which also includes *I. muelleri*, in our phylogenetic anyalysis (Figure 60, see Phylogenetic Analysis section). The highly variable and irregularly formed nasal cirrus (difficult to describe precisely), often consisting only of a simple flap (always simple in *muelleri*), is a character shared by these 2 species. The 2 species differ most noticeably in the strikingly different color patterns of the females as well as in the presence of a fleshy head crest in females of *I. zebra* and its absence in *I. bellus*. Additionally, in *I. zebra* the upper lip crenulae are absent or scarcely noticeable (in contrast to well developed in *I. bellus*) and the orbital cirrus is relatively longer, the dorsal fin connected relatively farther out on the caudal fin, and means for numbers of dorsal- and anal-fin elements and total vertebrae are much higher than in *I. bellus*.

DISTRIBUTION (Figure 66).—Known only from the Hawaiian Islands, from Hawaii northwestward only to Laysan. Generally restricted to supra- or inter-tidal pools on rocky shores; rarely taken from submerged reefs (Strasburg, 1956:254; Phillips, 1977:1-2); standing out of water on spray-wetted rocks at night (Phillips, 1977:21).

NOMENCLATURAL DISCUSSION.—Vaillant and Sauvage (1875) did not indicate the material upon which they based their description of *Salarias zebra*. The description indicates variation in the number of segmented dorsal-fin rays, 22 or 23, so more than one specimen must have been available. Bauchot (1967) indicated that there are 2 syntypes, MNHN 8917 and 8918. We have examined both specimens. The former is a male in reasonably good condition, and the color pattern is well preserved. The latter is a female in better condition, but the color pattern is mostly faded. We designate the male, MNHN 8917, lectotype of the species.

Jenkins (1903) did not compare his *Salarias cypho*, which is based on a male *I. zebra*, with any other species.

MATERIAL EXAMINED.—Hawaiian Is: CAS-SU 7682 (4), MNHN A8917 (lectotype of *Salarias zebra*), A8918 (paralectotype); Laysan, CAS 67304 (15), USNM 55136 (10), 55310 (21); Necker, USNM 55308 (31); between Maui and Molokai, USNM 55307 (10); Oahu, USNM 50697 (holotype of *Salarias*

cypho), 200566 (2 cleared and stained), 292570 (numerous embryos and fry: ~4 mm SL), 292829 (>50, includes ophioblennius and newly metamorphosed stages), 296292 (21), 296594 (18); Hawaii USNM 49134 (1).

Istiblennius bellus (Günther)

FIGURES 48, 49

Salarias bellus Günther, 1861:256 [type locality: "China seas" or "Chinese seas," probably erroneous; lectotype, BMNH 1848.3.16.1, 123 mm SL specimen, designated in nomenclatural discussion below].

Salarias kellersi Fowler, 1932:6 [Niuafoou, Tonga Group; holotype, USNM 91944].

Salarias leopardus Fowler, 1938:82 [Nukuhiva, Marquesas Islands; holotype, ANSP 68305].

Salarias personatus Fowler, 1945:71 [Saipan Island, holotype, ANSP 71604].

Istiblennius bellus impudens J.L.B. Smith, 1959:242 [St. Pierre Isl. [Seychelles], holotype, RUSI 270].

DESCRIPTION.—Dorsal fin (Table 38). XII to XIV,20 to 22 = 33 to 35 (XIII in 93% of specimens); males from any locality tending to have higher mean number of total elements than females from same locality (higher for 6 of 7 localities where means for both sexes are available; statistically significantly higher for 4 of the 6 localities); membrane between spinous and segmented-ray portions notched deeper than half length first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle just anterior to caudal-fin base to point <20% caudal-fin length out on dorsal edge of caudal fin (out on caudal-fin >10% fin length in only 1 of more than 125 specimens examined for character).

Anal fin (Table 38). II,20 to 22; males from any locality have higher mean number of segmented rays than females from same locality (higher for all 7 localities where means for both sexes are available; statistically significantly higher for 3 localities); posteriormost ray usually split to base, (posterior element of split ray usually well developed, readily discernible externally); last ray attached by membrane to caudal peduncle in only 4 of 57 specimens examined for character. Skin covering anal-fin spines and distal half of rays scarcely expanded, at most only slightly crinkled along lateral edges in large and/or mature males.

Pectoral-fin rays 13 or 14 (14 bilaterally in 94%, unilaterally in 6% of 103 specimens examined for character).

Pelvic-fin segmented rays 3.

Caudal fin. Dorsal procurrent rays 6 to 8 (7 in 77% of 102 specimens examined for character), ventral procurrent rays 5 to 8 (7 in 66% of specimens), combination of 7 dorsal with 7 ventral procurrent rays in 57% of specimens; segmented rays 13.

Vertebrae (Table 38). 10 to 12+27 to 29 = 38 to 40 (11 precaudal vertebrae in 91% of specimens); males from any locality tending to have higher mean number of total vertebrae than females from same locality (higher for 6 of 7 localities where means for both sexes are available; statistically significantly higher for only 1 of the 6 localities); posteriormost

pleural rib on 11th or 12th from anteriormost centrum (about equally divided between these centra); posteriormost epineural on 13th to 17th from anteriormost centrum (rarely on 13th; on 15th in 59% of specimens).

Cirri. Nape cirrus absent. Orbital cirrus slender, usually simple, occasionally with lateral branch or few, tiny branches near tip, length ≤half orbital diameter in females, slightly <diameter in males. Nasal cirri short, varying from flap-like with ragged edge or with 1 or 2 branches in specimens <75 mm SL to palmate with up to about 10 branches of variable length in larger specimens.

Lateral line. Continuous canal anterodorsally with no vertical pairs of pores, extending posteriorly to point between verticals from 5th and 10th dorsal-fin spines (to point between 8th and 9th spines in 77% of specimens examined for character), then descending to midside and continuing posteriorly up to half distance to caudal-fin base (varying with locality, Table 39) as series of 1 to 16 short, disconnected, horizontally bi-pored canals (tubes) in skin (number of tubes varying with locality, Table 28; posteriormost tube lying between verticals from 9th dorsal-fin spine and 13th segmented ray).

Mandibular pores 3 to 7 (rarely 3,4 or 7, and only unilaterally; 5, at least unilaterally, in 16%, and 6, at least unilaterally, in 81% of 117 specimens examined for character).

Five to 7 (commonly 5 or 6, rarely 7) sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin; 0 to 2 positions with paired pores (0 in 58% of specimens, 1 in 36%, 2 in 6% of 163 specimens examined for character).

Posterior dentary canines absent.

Ventral margin of upper lip and dorsal margin of lower lip noticeably crenulate in most specimens >60 mm SL, variably crenulate or entire in smaller specimens (upper lip crenulae granular, visible only on internal surface of lip in some specimens; crenulae scarcely noticeable in some poorly preserved specimens).

Males with fleshy, blade-like crest on head dorsally, definitely noticeable at about 35 mm SL, ridge-like crest precursor noticeable at 33 mm; females without crest, but short, low, rounded ridge (crest precursor) in largest females from Pacific localities.

Color pattern (in preservative). Males (Figure 48). Head dark dusky, usually with darker spots on snout, bordering eye and upper lip, along preopercular pore series, and on opercle (position of each spot apparently consistent among all specimens, although all positions not spotted in all specimens, spots of variable darkness; males from Christmas Island, Indian Ocean, usually lack dark spots, possibly artifact of preservation). Body dark dusky with up to 7 irregular bands (4 anteriormost bands each variably split vertically into band pair), bands variably restricted to mid-longitudinal axis of body or continuing dorsally into basal portion of dorsal fin; faint-dusky spots or rings scattered on body, spots most apparent posteriorly (spots may fade completely in long-

Table 38.—Frequency distributions for certain characters of specimens of *Istiblennius* bellus from various localties. Underlining indicates significant differences between means of sexes from same locality (p ≤ .05).

Locality	Total dorsal-fin elements				Segmented anal-fin rays				Total vertebrae			
	33	34	35	x̄	20	21	22	x̄	38	39	40	x̄
Somalia, Muqdisho												
males	-	5	2	**34.3**	-	3	4	21.6	-	5	1	39.2
females	2	5	-	**33.7**	1	5	1	21.0	-	5	1	39.2
Kenya												
females	-	2	-	34.0	2	-	-	20.0	1	1	-	38.5
Zanzibar												
females	-	1	-		-	1	-					
Northern Mozambique												
males	-	3	-	34.0	-	3	-	21.0	-	3	-	39.0
South Africa												
females	-	3	-	34.0	-	3	-	21.0	-	3	-	39.0
Madagascar												
females	-	7	-	34.0	3	3	1	20.7	1	5	-	38.8
Juan de Nova												
males	-	3	-	34.0	-	2	1	21.3	-	2	1	39.3
St. Pierre												
males	1	1	1	34.0	-	2	1	21.3	-	2	1	39.3
Mauritius & Reunion												
males	-	3	2	34.4	-	4	1	21.2	-	4	1	39.2
females	-	1	-		-	1	-		-	1	-	
Christmas Id, IO												
males	4	14	-	**33.8**	2	16	-	**20.9**	6	12	-	38.7
females	8	5	-	**33.4**	8	5	-	**20.4**	7	6	-	38.5
Saipan												
males	1	8	-	**33.9**	1	6	2	21.1	5	4	-	38.4
females	4	2	-	**33.3**	3	3	-	20.5	4	2	-	38.3
New Hebrides, Efate												
males	5	16	4	34.0	2	18	5	21.1	2	19	3	**39.0**
females	9	21	3	33.8	10	18	5	20.8	11	19	2	**38.7**
New Hebrides, Venui												
females	-	-	1		-	1	-		-	1	-	
Niuafo'ou												
males	2	12	1	33.9	1	10	4	**21.2**	1	10	4	39.2
females	3	14	-	33.8	3	14	-	**20.8**	2	13	-	38.9
Samoa, Upolu												
males	-	17	3	**34.2**	-	14	6	**21.3**	-	17	2	39.1
females	6	15	1	**33.8**	-	21	1	**21.0**	5	14	2	38.9
Samoa, Tutuila												
males	-	-	1		-	-	1		-	-	1	
females	1	1	-	33.5	2	-	-	20.0	1	1	-	38.5
Niue												
males	1	-	-		-	1	-		1	-	-	
females	-	1	-		-	-	1		-	1	-	
Marquesas												
males	-	2	-	34.0	-	1	1	21.5	-	2	-	39.0
females	-	6	1	34.1	-	6	1	21.1	-	6	1	39.1

preserved specimens; not present on Christmas Island males). Fins dark dusky, dorsal fin occasionally with pale streaks, anal occasionally with pale spots. Body more or less uniformly pigmented, head without spots at 35 mm SL; body faintly spotted at 33 mm SL.

Females. Head faint to dark dusky with densely distributed, small, diffuse dark spots variably present; spots occasionally appearing to occupy positions similar to those on heads of males. Body with up to 7 dusky bands; body and fins, except uniformly pale-dusky pelvics, densely covered with dark spots (see section on geographic variation for modification of this description). Pattern recognizable in specimens at least as small as 38 mm SL.

Two smallest available specimens, both 22 mm SL (Éfaté, New Hebrides), sex indeterminate, with diffuse spots on body; spots relatively larger in 1 specimen than in other, possibly indicating sexual difference, but specimens not otherwise sexually differentiated.

Table 39.—Frequency distributions for lateral-line characters in specimens of Istiblennius bellus from various localities.

Locality	Posteriormost lateral-line tube below dorsal-fin element # (specimens ≥45mm SL)																	
	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	x̄
Somalia, Muqdisho	-	-	-	3	2	1	-	1	-	-	-	-	-	-	-	-	-	13.1
Kenya	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	15.0
Zanzibar	-	-	(before 14)		-	-	-	-	-	-	-	-	-	-	-	-	-	
Northern Mozambique	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	12.0
South Africa, Natal	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	15.3
Madagascar	-	-	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	12.0
Juan de Nova	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	14.1
St. Pierre	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	12.3
Mauritius & Reunion	-	-	-	2	2	1	1	-	-	-	-	-	-	-	-	-	-	13.2
Christmas Id, IO	1	5	5	7	5	2	2	3	1	-	-	-	-	-	-	-	-	12.4
Saipan	-	-	2	1	8	1	1	1	-	-	-	1	-	-	-	-	-	13.5
New Hebrides, Efate	-	-	2	11	5	2	-	-	-	-	-	-	-	-	-	-	-	12.4
New Hebrides, Venui	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	
Niuafo'ou	-	-	1	1	3	1	5	4	7	1	2	1	3	-	1	1	-	16.8
Samoa, Upolu	-	-	-	-	-	1	1	2	4	3	4	6	-	2	-	2	1	19.1
Samoa, Tutuila	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	20.0
Niue	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	
Marquesas	-	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	17.5

Locality	Number of lateral-line tubes (specimens ≥45mm SL)																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	x̄
Somalia, Muqdisho	-	-	1	1	2	2	1	-	-	-	-	-	-	-	-	-	5.1
Kenya	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	6.0
Northern Mozambique	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	5.3
South Africa, Natal	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	4.7
Madagascar	-	1	-	1	2	1	1	-	-	-	-	-	-	-	-	-	4.8
Juan de Nova	-	-	4	-	-	-	-	1	1	-	-	-	-	-	-	-	7.0
St. Pierre	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	5.7
Mauritius & Reunion	-	1	-	-	1	3	-	1	-	-	-	-	-	-	-	-	5.5
Christmas Id, IO	2	4	3	1	8	8	3	1	-	1	-	-	-	-	-	-	4.8
Saipan	-	-	1	1	1	5	5	1	-	-	-	1	-	-	-	-	6.5
New Hebrides, Efate	-	2	-	4	7	4	2	-	1	-	-	-	-	-	-	-	5.1
New Hebrides, Venui	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
Niuafo'ou	-	-	-	2	-	4	2	4	5	2	3	-	3	-	1	-	8.8
Samoa, Upolu	-	-	-	-	1	1	2	3	3	5	5	4	1	-	-	1	9.9
Samoa, Tutuila	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	12.3
Niue	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	6.0
Marquesas	-	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	9.5

Live or fresh color. Springer (1986, pl. 114: figs. 235.21(A),(B)) illustrates colored paintings prepared by M.M. Smith from large, fresh specimens (male holotype from St. Pierre Island; female from southern Mozambique): Male. Dark spots and streaks on body and fins of preserved males appear blue, segmented-rayed fins pinkish; spinous dorsal fin, head, and body with dark dusky-brown markings, body pale ventrally.

Female. Yellowish overall, with fine, reddish spots. Fine spots in spinous dorsal, anal, and pectoral fins, contrasting somewhat with pattern of western Indian Ocean females; see section on geographic variation. We could not verify the accuracy of the painting as the specimen upon which it is based was not available; P.C. Heemstra, in litt., wrote that no [female] specimens from Mozambique are present in the RUSI collection.

Size. Largest male, 128 mm SL; largest female, 131 mm SL; specimens >100 mm uncommon.

GEOGRAPHIC VARIATION.—Geographic variation is expressed primarily in color-pattern differences among females (no differences among males, except possibly Christmas Island males; see color pattern description above) and secondarily by the position of the posteriormost lateral-line tube relative to a dorsal-fin element (both males and females, Table 39), which is related to the number of lateral-line tubes (Table 39).

In females from the western Indian Ocean (Figure 49c,d), the
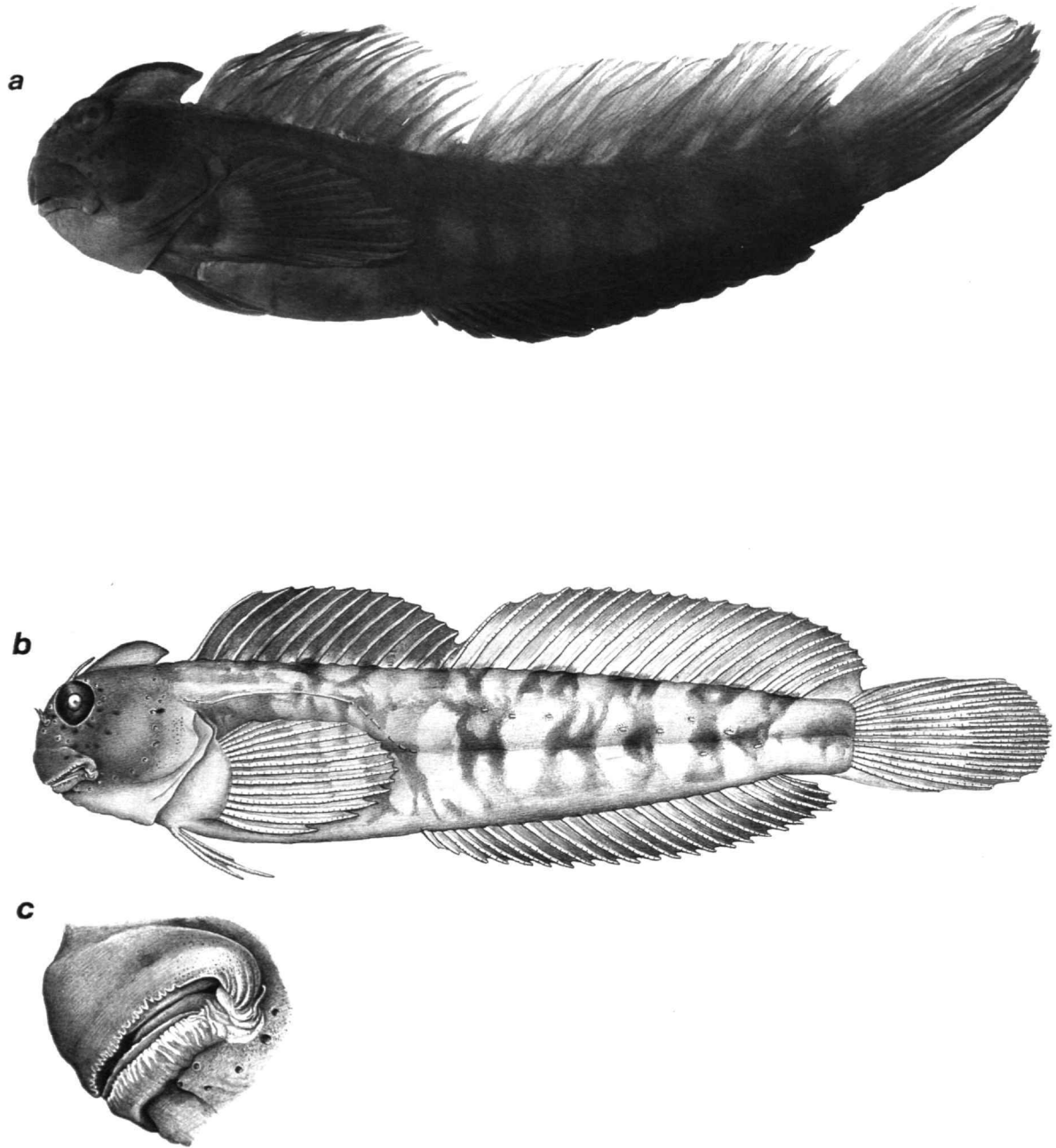
FIGURE 48.—*Istiblennius bellus*, males: *a*, NMNZ P.15690, 83 mm SL, Niue (photograph by T.B. Griswold); *b,c*, USNM 293738, 78 mm SL, Efate, New Hebrides, lateral view and enlarged view of lips (drawings by J.R. Schroeder).
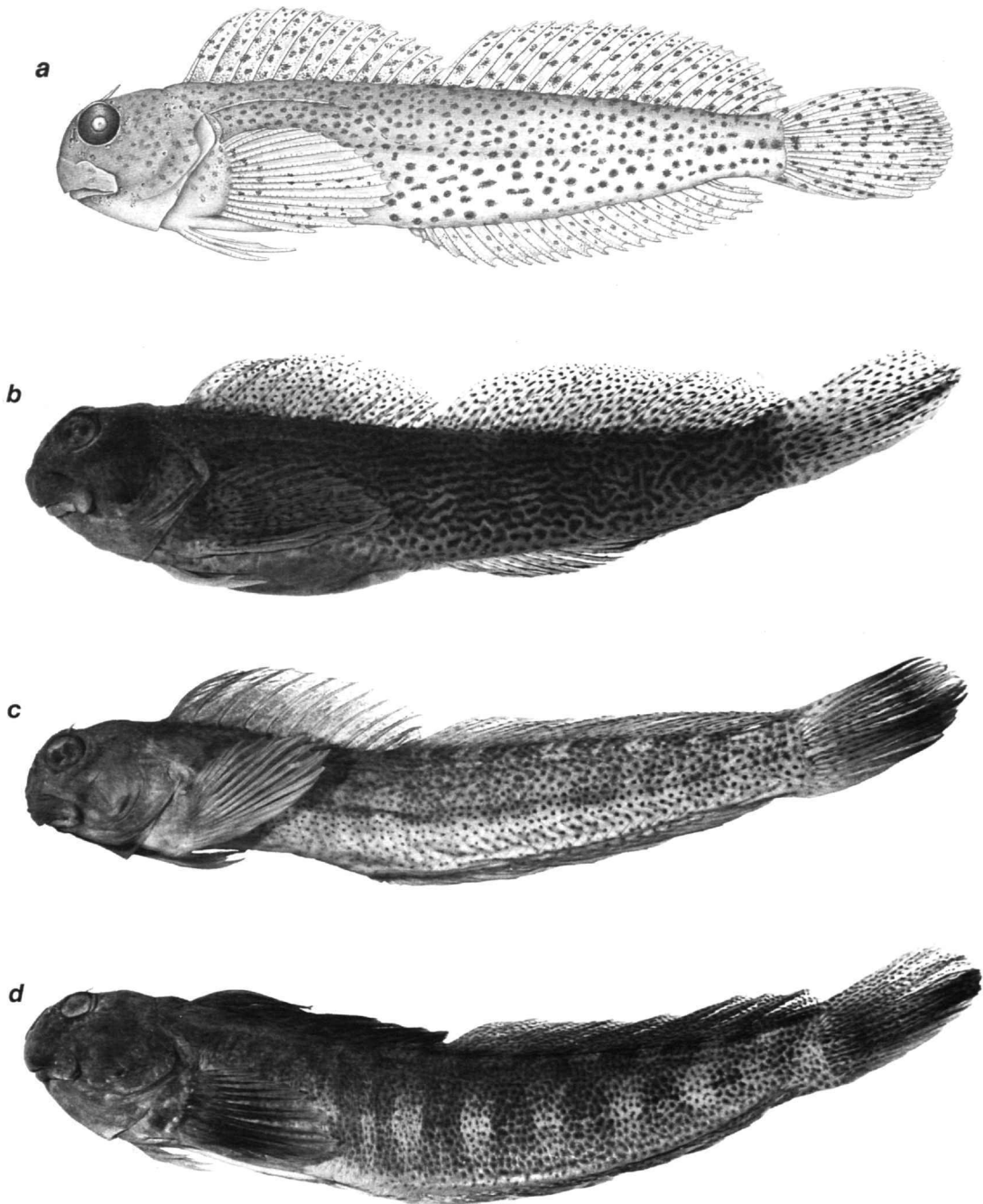
FIGURE 49.—*Istiblennius bellus*, females: *a*, USNM 224887, 59 mm SL, Efate, New Hebrides (drawing by J.R. Schroeder); *b*, NMNZ P.15690, 88 mm SL (right side reversed), Niue; *c*, USNM 293843, 81 mm SL, Malindi, Kenya; *d*, RUSI 74-69, 122 mm SL, Ballito Bay, Natal, South Africa (photographs by T.B. Griswold).

pectoral fins are more or less uniformly dusky (not spotted), the spinous dorsal fin is variable: with fine, dark spots, or dusky with indistinct, irregular, pale streaks or diffuse dark spots that can be seen only with transmitted light; the anal fin of large females, at most, bears faint spots (but heavily spotted in small females), and the spots on the body maintain their integrity even in the largest females. In females from Christmas Island (eastern Indian Ocean) and the Pacific (Figure 49a,b), the pectoral, spinous dorsal, and anal fins are distinctly dark spotted (but fewer spots in Christmas Island females than in others). In females from Christmas Island and the New Hebrides (Figure 49a), the body spots also maintain their integrity, but in females from Pacific-plate islands (Figure 49b), the spots on the body begin to fuse and form vermiculations at sizes over 70 mm SL, and the pattern is completely vermiculated at about 85 mm SL.

Specimens from Niuafo'ou, Samoa, and possibly the Marquesas, tend to have the posteriormost lateral-line tube positioned further posteriorly than in specimens from other localities.

COMPARISONS AND RELATIONSHIPS.—*Istiblennius bellus* subjectively appears to us to be most closely related to *I. zebra*, endemic to the Hawaiian Islands, with which it falls into a weakly supported polytomous clade, which also includes *I. muelleri* (Figure 60, see Phylogenetic Analysis section). The two species differ most obviously in that the females of *Istiblennius bellus* do not have a crest on the head and have a strikingly different color pattern from that of males (crest present and color pattern more or less similar to that of males in *I. zebra* and *I. muelleri*). Additionaly, means for numbers of dorsal- and anal-fin elements and total vertebrae are lower for *I. bellus* than for *I. zebra*.

DISTRIBUTION (Figure 66).—Western Indian Ocean from 3 miles (5km) north of Muqadisho, Somalia, south to Balito Bay, Natal, South Africa; St. Pierre (SW Seychelles); Nossi Be, Madagascar; Juan de Nova Island; Mauritius; Eastern Indian Ocean only from Christmas Island; Pacific Ocean from New Hebrides, Niuafo'ou (but not more southern islands of Tonga), Samoa, Niue, Marquesas, Saipan islands. The large distributional gap between the Indian Ocean and islands on and along the western margin of the Pacific plate appears to be real (as do other large gaps in its Indian and Pacific oceans distributions), and is evidence favoring extinction of *I. bellus* in the gap area (Springer and Williams, 1990). Saipan, Mariana Islands, is well removed from all other known occurrences of *I. bellus*, which is otherwise known essentially only from south of the equator. Large shorefish collections are available from, at least, nearby Guam, but no specimens of *I. bellus* have been taken at the other Mariana Islands.

NOMENCLATURAL DISCUSSION.—Günther (1861:256) indicated that he had 8 specimens on which he based his description of *Salarias bellus*. Five specimens were obtained from Captain E. Belcher, and listed in the material as from "China Seas," whereas the locality given in the description is "Chinese Sea."

No locality is provided for the other 3 specimens, which are mentioned only as having come from the Haslar Collection. The Haslar Collection refers to the Royal Naval Hospital of Haslar (Günther, 1859:v), located in Portsmouth, Hampshire, England. All 8 specimens, thus are syntypes.

Chapman (1951:305–306) stated that the type series of *Salarias bellus* was cataloged as BMNH 1848.3.16, "contained" three species, and that the description was "obviously" drawn from the largest specimen, a male, 121 mm SL, 5.8 inches TL. The description was certainly based on a male or males, as the head is described as having a crest, the body as having bluish white spots that are most conspicuous posteriorly, and the dorsal and anal fins as being dark with white streaks or spots; none of these characters is present in females. Additionally, no mention is made in the color-pattern description of the strikingly dense spotting that is so characteristic of females. The description is at least partially based on more than one specimen because a range of counts is given for the dorsal and anal fins; however, the measurements of only one specimen are given: total length 5 inches 10 lines.

Chapman's reference to "contained" would seem to indicate that the type series was split and reidentified, but we have no information on the details of the split (how many specimens of each species, their identifications and sizes, and the catalog numbers assigned to them).

The catalog number Chapman gave for the type series is incomplete; after 1848.3.16 there should be a period and one or more numbers. We located two lots of blenniids at BMNH with the prefix 1848.3.16. One lot, 1848.3.16.14, is labeled as *Blennius sinensis*, and it undoubtedly represents the holotype of *B. sinensis* (= *Parablennius sanguinolentus*, H. Bath, in litt., a Mediterranean species of the Tribe Parablenniini). The other lot, 1848.3.16.1, is labeled *Istiblennius oortii* (*oortii* is a species of *Praealticus*), and contains two large male *I. bellus* (94 and 123 mm SL) and one small male *I. edentulus* (69 mm SL). The 123 mm specimen measures 5.9 inches TL and, uniquely, has a shiny metal tag bearing the numbers 3/16.1 tied to it. Both of these lots were collected by Belcher and are reputed to have come from "China Seas," but the holotype of *B. sinensis* clearly did not come from the Indo-Pacific, and the other lot probably did not come from the sea bordering China. All three of the specimens labeled *oortii* probably are part of the syntypic series of *S. bellus*, and the close agreement of the total length and color pattern of the largest specimen with those given by Günther indicate that this was probably the specimen upon which he mainly based his description. We, therefore, designate the 123 mm SL specimen in BMNH 1848.3.16.1 lectotype of *Salarias bellus* Günther.

Another lot, BMNH 1855.9.19.700, is labeled as the holotype of *Salarias bellus*. It is derived from the Haslar Collection and contains a male, 113 mm SL, of that species. This specimen is probably part of the syntypic series of *S. bellus*, but it is not a holotype and, to our knowledge, has not been designated as a lectotype.

It is important to note that the China seas locality assigned to Belcher specimens may be in error. Aside from the holotype of *Blennius sinensis,* Winterbottom (1976) has shown that the type locality of *Clinus nematopterus* Günther, based on a Belcher "China seas" specimen, is most probably South Africa.

We are unable to determine the locality of origin of Belcher's (or Haslar) specimens of *Istiblennius bellus.* During his two major expeditions to the Indo-Pacific (Belcher, 1843; 1848), Belcher visited, and possibly made collections at, most of the localities where *I. bellus* is known to occur. It is also possible that he obtained the specimens at a locality from where no other specimens of *I. bellus* are known. Had Belcher's material included females, we would have been able to assign a more restricted locality to them, but we have not found noteworthy differences among males from different localities.

Fowler (1932:7) compared his *Salarias kellersi* only with a specimen he erroneously accepted as *Salarias guttatus* Valenciennes, 1836, but which was then an undescribed genus and species, *Glyptoparus delicatulus* J.L.B. Smith, 1959. The holotype and 19 paratypes of *S. kellersi* are all females. Fowler (1932:7) misidentified the males of his species as *Salarias edentulus.*

Fowler (1938:82) compared his *Salarias leopardus* with his *Salarias kellersi,* stating that it was similar, but with much larger dark spots. The holotype of *S. leopardus* is considerably shorter than that of *S. kellersi.* It is not that the spots of the former are larger, but that they are more distinct, circumstances typical of smaller female specimens of *I. bellus.* As the females increase in size, the spots, in some populations, tend to coalesce into vermiculations. Fowler (1938:83) again misidentified the males of his species as *Salarias edentulus.* In any event, *Salarias leopardus* Fowler (1938) is a junior primary homonym of *Salarias leopardus* Day (1876) (= *Exallias brevis* (Kner)) and is to be rejected.

Fowler (1945:71) did not compare his *Salarias personatus* with any other species. Both the holotype and paratype are males, faded, and in poor condition, but they exhibit remnants of the spots on the anterior part of the head that typify males of *I. bellus.*

J.L.B. Smith (1959:242) differentiated his *Istiblennius bellus impudens* from *I. bellus* [*bellus*] by stating only that the 2 forms "differ somewhat." Although western Indian Ocean females do exhibit slight differences in color pattern from that of eastern Indian and Pacific ocean females, we find no differences among males and refrain from recognizing different taxa for specimens from the two areas.

MATERIAL EXAMINED.—Belcher collection, China Seas: BMNH 1848.3.16.1 (3, including lectotype, 123 mm SL, of *Salarias bellus*); Haslar Collection: BMNH 1855.9.19.700 (1). Somalia: 3 miles (5km) N of Muqadisho, MCZ 41710 (3), 41713 (1), 41714 (3) 41715 (7, including two cleared and stained), Zanzibar: MSNG 38952. Kenya: Mombasa, USNM 296003 (1); Malindi, USNM 293843 (1). Mozambique: Cape Delgado, RUSI 30143 (3). South Africa: Natal, Bolito Bay (2).

Madagascar: Nossi Be, USNM 200610 (5, including 1 cleared & stained), 296004 (2). Seychelles: St. Pierre, RUSI 30144 (3). Juan de Nova Id, RUSI 30146 (3). Mauritius: H. Bath, personal collection (2), RUSI 1274 in part (1). Reunion: MNHN 1988-447, in part (3). Christmas Id (IO): WAM P.28989-001 (21), P.29014-001 (10). Mariana Is: Saipan, ANSP 71604 (holotype of *Salarias personatus*), 71605 (1), 114812 (1), 167398 (1), BPBM uncataloged (2), USNM 316690 (9). New Hebrides: Venui Id (off S. Espiritu Santo), ANSP 105237 (1); Éfaté, USNM 224887 (5), 293738 (51, including 1 cleared and stained), 296005 (3). Tonga Is: Niuafo'ou, USNM 91905 (1), 91913 (2), 91918 (1), 91922 (2), 91927 (2), 91938 (1), 91939 (3), 91942 (1), 91944 holotype of *Salarias kellersi*), 91951 (1), 91956 (1), 91958 (4), 91959 (4), 91962 (2), 91964 (1), 91997 (1), 91998 (1), 91999 (1), 138299 (1), 92000 (1). Samoa Is: Upolu, BPBM 12541 (44); Tutuila, USNM 152297 (1), 221475 (2). Niue: NMNZ P.15690 (2). Marquesas Is: Nukuhiva, ANSP 68305 (holotype of *Salarias leopardus* Fowler), 68306-7 (2); Fatu Hiva, BPBM 32854 (1); Eiao, USNM 89777 (1), 89779 (4).

Istiblennius muelleri (Klunzinger)

FIGURE 50

Salarias muelleri Klunzinger, 1880:388 [Australian, Hobsons Bay (Victoria; erroneus locality); holotype SMNS 1519].

DESCRIPTION.—Dorsal fin. XII to XIV,19 to 21 = 32 to 34 (XIII in 44 of 47 specimens examined for character; 34 total elements only in males, which have statistically significant higher mean number of total elements than females); membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle at caudal-fin base (rarely) to point out on dorsal edge of caudal fin up to 18% caudal-fin length in specimens ≥30 mm SL.

Anal fin. II,21 to 23 (23 only in males; Shen et al., 1986:40, reported II,20 and 21 for 2 specimens from Taiwan); posterior element usually not split to base (split in <33% of specimens); posteriormore element of split ray variably well developed or vestigial and visible only on radiographs; fin usually not bound by membrane to caudal peduncle; when bound, membranous attachment almost unnoticeable, extending along basal portion of posteriormost ray no more than 10% length of ray. Skin covering anal-fin spines and distal half of rays not modified in any of 21 males available (32 to 59 mm SL).

Pectoral-fin rays 13 or 14 (14 bilaterally in 34 of 36 specimens examined for character).

Pelvic-fin rays I,3.

Caudal fin. Dorsal procurrent rays 6 or 7, ventral procurrent rays 5 to 7, total procurrent rays 11 to 14, segmented rays 12 or 13 (13 in 40 of 41 specimens examined for character).

Vertebrae. 10+27 to 30 = 37 to 40 (40 in only one specimen,

male); posteriormost pleural rib on 11th from anteriormost centrum; posteriormost epineural on 15th to 19th from anteriormost centrum.

Cirri. Nape cirrus absent. Orbital cirrus simple, rarely a single branch or a few short, fine filaments at tip, shorter than orbital diameter in females, usually shorter than orbital diameter in males. Nasal cirrus simple, relatively long (usually about half orbital diameter).

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between verticals from bases of 6th and 9th dorsal-fin spines (usually to between verticals from 7th and 8th spines), then continuing posteriorly and posteroventrally as series of 1 to 6 (rarely 1 or 6) short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area below and between verticals from bases of 7th spine and second segmented dorsal-fin ray (rarely posterior to vertical from 12th spine).

Mandibular pores 3 to 5 (always 5 pores, at least unilaterally; 5 bilaterally in 22 of 41 specimens examined for character).

Five to 7 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (usually 6 pores); no more than 1 position occupied by a pair of pores (all positions with single pores in 40 of 41 specimens examined for character).

Posterior canines absent.

Ventral margin of upper lip and dorsal margin of lower lip entire.

Well-developed, fleshy, blade-like crest dorsally on head of both males and females (at least at sizes ≥ 30 mm SL); crest of female relatively smaller than that of males of comparable size.

COLOR PATTERN (in preservative; Figure 50).—Males and females basically similar, but male color pattern more strongly delineated. Head more or less uniformly dusky, except crest darkest posterodorsally and with central, diffuse pale area separating dusky anterior and posterior regions. Body with up to about 10 pairs of slender, almost vertical, dusky bands; dusky band pairs separated by slender, pale interspaces, each of which may appear as pair of pale bands separated by interrupted, slender, dusky band; dusky band pairs least distinct anteriorly on body, breaking up into fine, dusky specks or reticulation of small pale spots with dusky margins on caudal peduncle. Dorsal fin: spinous portion dusky, crossed by several diagonal, paler-dusky stripes with dark margins; segmented-ray portion faint dusky with numerous dark pinstripes coursing length of fin, stripes coalescing into reticular pattern posteriorly. Anal fin: more or less uniformly dusky, or dusky with very faint, small, pale spots basally. Caudal fin dusky, with dusky reticular pattern of small, pale spots (especially males). Pelvic and pectoral fins unmarked.

Chapman (1951:323) provides a reasonable illustration of a male specimen.

Size. Largest male, approximately 70 mm SL; largest female, approximately 55 mm; smallest specimen, ~30 mm (female).

COMPARISONS AND RELATIONSHIPS.—We have no subjec-

tive impression as to what the sister group of *I. muelleri* might be, although it falls into a weakly supported polytomous clade that also includes *I. bellus* and *I. zebra* in our phylogenetic analysis (Figure 60, see Phylogenetic Analysis section). *Istiblennius muelleri* differs from all other *Istiblennius* species in its color pattern, and all except *I. rivulatus*, in having a simple nasal cirrus at all sizes. It differs most conspicuously from *I. rivulatus* in having 14 (as opposed to 12) pectoral-fin rays, in lacking nape cirri (as opposed to having nape cirri), and in having the orbital cirrus length equal to (usually) or shorter than the orbital diameter, whereas it usually exceeds the orbital diameter in *I rivulatus*. *I. muelleri* differs from *I. bellus* in that *I. muelleri* females have a blade-like crest on the head and a color pattern similar to that of males. It shares the latter 2 characters with *I. zebra* in the clade, but differs from *I. zebra* in having, among other characters, the dorsal margin of the lower lip entire, as opposed to crenulate. Although the ventral margin of the upper lip is entire in both *I. muelleri* and *I. zebra*, *I. zebra* often exhibits indications of fine lip crenulae laterally or as crenulae-like pads on the buccal surface of the lip.

DISTRIBUTION (Figure 69).—Known definitely only from Hsiao-liu-chiu Island, off southwest Taiwan, south to Kur Island, Indonesia. Occurs in tidepools, also close to edge of rocky shores at low tide. The type locality of *Istiblennius muelleri*, Hobson's Bay, Victoria, Australia, is clearly an error. As Whitley (1943:186) noted, no species of *Istiblennius* is found so far south as Victoria, in fact, no further south than Sydney, New South Wales (~33°51'S) on the east Australian coast. Müller, the collector of the holotype of *I. muelleri*, made collections at various localities between Port Darwin and southern Queensland along the warm coast of Australia, and possibly (although improbably) obtained the specimen in that area. Whitley remarked that the specimen may have come from Port Darwin, probably because that is the Australian locality most proximate to localities (in Indonesia) from whence *I. muelleri* is definitely recorded. The only problem with such an assumption is that there is no well-documented record of *I. muelleri* from Australia.

The record of *Istiblennius muelleri* from Taiwan, plotted on the distribution map, is based on the well-documented record in Shen et al. (1986:40 and fig. 54i).

MATERIAL.—Australia, Hobson's Bay [probably erroneous; see previous discussion]: SMNS (holotype of *Salarias muelleri*). Indonesia: Nusa Laut, USNM 210953 (5, including 2 cleared and stained); Ambon, ZMA 120.378 (1); Haruku, RMNH 20338 (2), 20763 (7); Kur Id, ZMA 120.379 (1); Karakelang Id, ZMA 120.375 (3); Sula Besi Id, ZMA 120.377 (1); Salebabu Id, ZMA 120.376 (3); Sorong, Irian Jaya, ANSP 168866 (1). Philippines: Homonhon Id, USNM 123361 (1); Simaluc Id, USNM 122435 (7); Negros: Dumaguete, CAS 46498 (2), Ciagba Bay, CAS 66856 (2); Mindoro, Calapan, CAS-SU 32304 (1); Iba Id, CAS-SU 32305 (1); Tataan, Tawi Tawi Group, USNM 122436 (2). No locality [Bleeker specimens, probably Indonesia), RMNH 30339 (6).
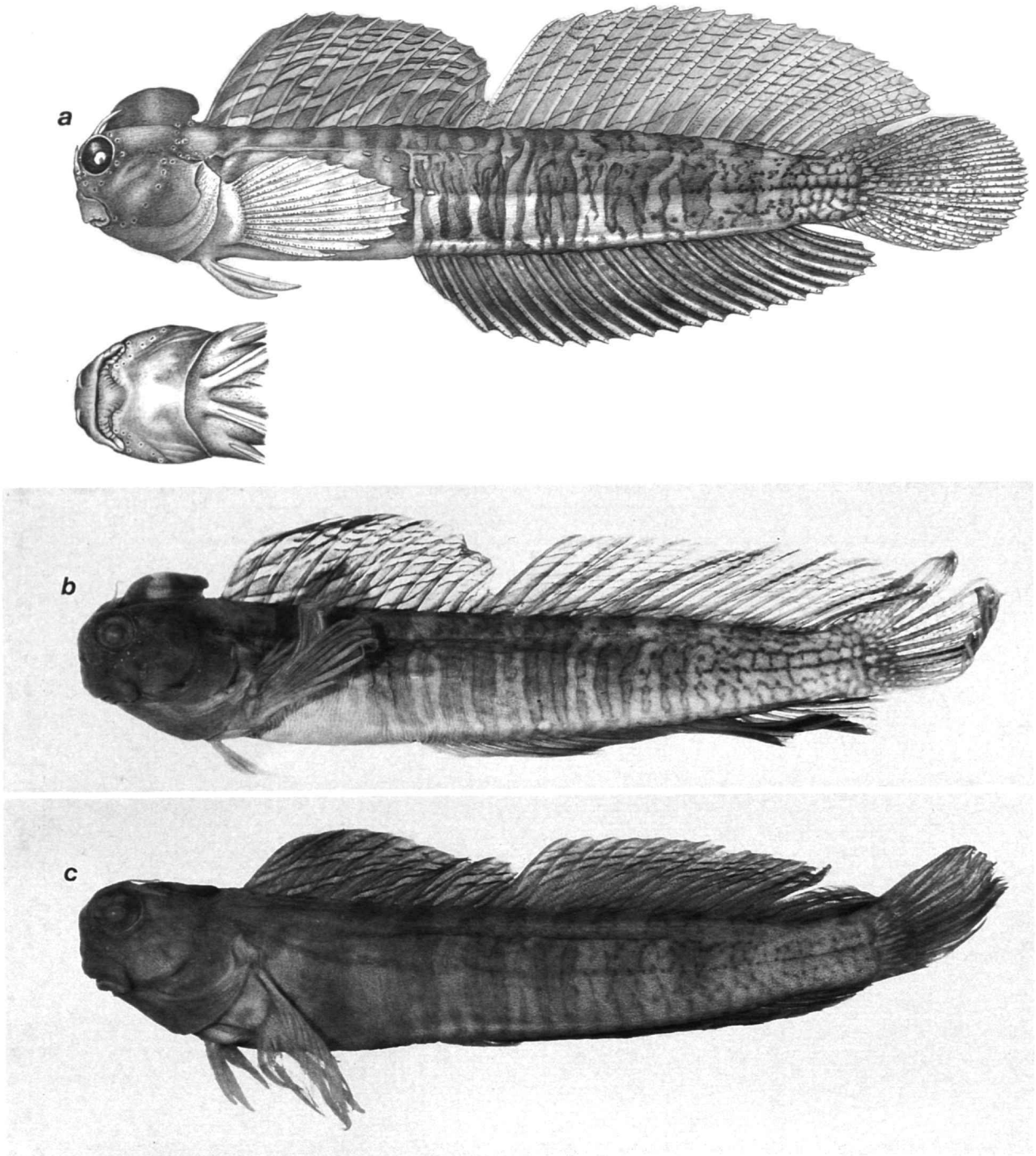
FIGURE 50.—*Istiblennius muelleri*, USNM 210953, Indonesia, Moluccas, Nusa Laut: *a* (left side), *b* (right side reversed), male, 56 mm SL; *c*, female, 38 mm SL (drawings by J.R. Schroeder; photographs by T.B. Griswold).

Istiblennius unicolor (Rüppell)

FIGURE 51

Salarias unicolor Rüppell, 1838:136 [Massaua; holotype, SMF 1866].

DESCRIPTION (based on 6 males and 4 females).—Dorsal fin (Table 40). XIII,17 or 18 = 30 or 31; membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle anterior to caudal-fin base to on dorsal edge of caudal fin very slightly posterior to caudal base.

Anal fin (Table 40). II,17 to 19; posterior element split to base in 4 specimens and not split in 5, of 9 specimens checked for character; posterior element of split ray visible externally; last ray not attached by membrane to caudal peduncle. Skin covering anal-fin spines and distal half of rays not modified in males.

Pectoral-fin rays 14.

Pelvic-fin segmented rays 4, tip of innermost ray not free, but externally visible in all specimens.

Caudal fin. Dorsal procurrent rays 5 to 7, ventral procurrent rays 5 to 7, total procurrent rays 10 to 14 (Table 41), segmented rays 13.

Vertebrae (Tables 40 and 41). 10+25 = 35; posteriormost pleural rib on 11th or 12th from anteriormost centrum (on 12th in only 1 specimen); posteriormost epineural on 12th to 14th from anteriormost centrum (on 13th in 8 specimens).

Cirri. Nape cirrus absent. Orbital cirrus variable, usually shorter than orbital diameter, consisting of central stalk with side branches. Nasal cirrus small, palmate with 4 to 7 separate tips.

Table 40—Frequency distributions for certain characters of specimens of *Istiblennius flaviumbrinus*, *I. unicolor*, and *I. spilotus* from various localities. Underlining indicates significant differences between means of sexes from same locality (p ≤ .05).

Species/Locality	Total dorsal-fin elements					Segmented anal-fin rays					Total vertebrae				
	29	30	31	32	x̄	16	17	18	19	x̄	34	35	36	37	x̄
flaviumbrinus															
Red Sea															
males	8	25	-	-	29.8	7	26	-	-	16.8	1	27	-	-	35.0
females	20	11	-	-	29.4	16	14	-	-	16.5	1	26	-	-	35.0
unicolor															
Red Sea[1]															
males	-	3	3	-	30.5	-	-	5	1	18.2	-	6	-	-	35.0
females	-	3	1	-	30.2	-	1	3	-	17.8	-	4	-	-	35.0
spilotus															
Abd al Kuri & Samhah															
males	-	1	6	-	30.8	-	-	4	3	18.4	-	-	4	2	36.3
females	-	-	4	-	31.0	-	-	4	-	18.0	-	-	4	-	36.0
?Henjam Island															
males	-	-	1	-		-	-	-	1		-	-	1	-	
females	-	-	1	-		-	-	-	1		-	-	1	-	
Gulf of Oman															
males	-	-	1	-		-	-	1	-		-	-	1	-	
females	1	6	3	-	30.3	-	2	8	-	17.8	-	1	9	-	35.9
Pakistan & NW India															
males	-	1	10	4	31.2	-	-	8	7	18.5	-	-	13	-	36.0
females	-	3	19	5	31.1	-	-	17	10	18.4	-	1	27	1	36.0
Grand Comore															
males	-	1	17	1	31.0	-	-	17	1	18.2	-	-	18	-	36.0
females	-	7	17	-	30.7	-	1	23	1	18.0	-	2	18	1	36.0
Somalia, Muqdisho															
males	-	-	2	-	31.0	-	-	2	-	18.0	-	-	2	-	36.0
females	-	-	1	-		-	-	1	-		-	-	1	-	
Kenya															
males	-	-	5	-	31.0	-	-	5	-	18.0	-	-	5	-	36.0
females	-	-	7	-	31.0	-	-	6	1	18.1	-	-	7	-	36.0
South Africa															
males	-	-	2	1	31.3	-	-	1	2	18.7	-	-	3	-	36.0
females	-	-	4	-	31.0	-	-	4	-	18.0	-	-	4	-	36.0
Madagascar															
males	-	-	18	5	31.2	-	-	9	14	18.6	-	-	21	1	36.0
females	-	-	23	3	31.1	-	1	19	6	18.2	-	-	24	2	36.1

[1] Including Gulfs of Aqaba and Suez

Table 41.—Frequency distributions for certain characters of specimens of _Istiblennius flaviumbrinus_, _I. unicolor_, and _I. spilotus_ from various localities.

Species/Locality	Precaudal vertebrae			Total segmented pelvic-fin rays[1]					Total procurrent caudal-fin rays[2]							Continuous portion of lateral line extends to vertical from dorsal-fin spine[3]										
	10	11	12	4	5	6	7	8	10	11	12	13	14	15	16	4-5	5	5-6	6	6-7	7	7-8	8	8-9	9	9-10
flaviumbrinus																										
Red Sea	-	49	1	-	2	55	-	-	-	-	1	4	46	6	1	4	4	7	16	10	8	2	-	1	-	-
unicolor																										
Red Sea, G Suez & G Aqaba	10	-	-	-	-	-	-	10	1	2	2	2	1	-	-	-	-	-	-	-	1	-	2	2	2	1
spilotus																										
Abd al Kuri & Samhah	10	-	-	-	-	6	4	1	-	-	-	2	-	-	1	-	-	-	-	-	-	1	4	2	1	-
?Henjam Island	2	-	-	-	-	-	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-	1	-	1	-	-
Gulf of Oman	11	-	-	-	-	6	2	4	-	-	3	6	1	-	-	-	-	-	-	-	-	4	-	2	-	-
Pakistan-NW India	41	1	-	-	1	24	2	9	-	1	13	15	7	-	-	-	-	-	-	-	2	12	12	10	3	1
Grand Comore	33	-	-	-	2	2	10	31	-	-	3	13	24	1	-	-	-	-	-	-	1	7	7	9	4	-
Somalia, Muqdisho	3	-	-	-	-	-	1	1	-	-	-	2	-	-	1	-	-	-	-	-	-	1	2	-	-	-
Kenya	12	-	-	1	-	1	4	6	-	-	1	3	1	-	-	-	-	-	-	-	-	1	7	1	-	-
South Africa, Natal	6	-	-	-	-	-	2	6	-	-	-	-	4	1	-	-	-	-	-	-	1	1	4	-	1	-
Madagascar	44	2	-	-	-	7	16	25	-	-	1	17	23	1	-	-	-	-	-	-	-	3	5	1	2	-

	Posteriormost bi-pored lateral-line tube at vertical from dorsal-fin element number																		Number of lateral-line tubes																	
	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
flaviumbrinus	2	5	8	21	9	2	2	1	3	-	-	-	-	-	-	-	-	-	1	1	5	13	16	7	5	1	1	-	1	-	-	-	-	-	-	-
unicolor	-	-	-	-	-	-	1	-	2	-	-	3	1	-	1	-	-	-	-	-	-	-	-	-	-	1	1	2	2	1	1	-	-	-	-	-
spilotus	-	-	-	-	3	5	1	5	18	22	12	19	12	14	6	2	2	2	-	-	-	2	5	3	8	18	21	26	11	12	5	2	3	-	2	1

[1] Apparent rays, both fins added together; combinations are: 2/2, 2/3, 3/3, 3/4, 4/4
[2] Dorsal and ventral rays added together; combinations are: dorsal-ventral 5/5, 6/5, 6/6, 6/7, 7/6, 7/7, 8/6, 8/7, 8/8
[3] Vertical may occur between two spines.
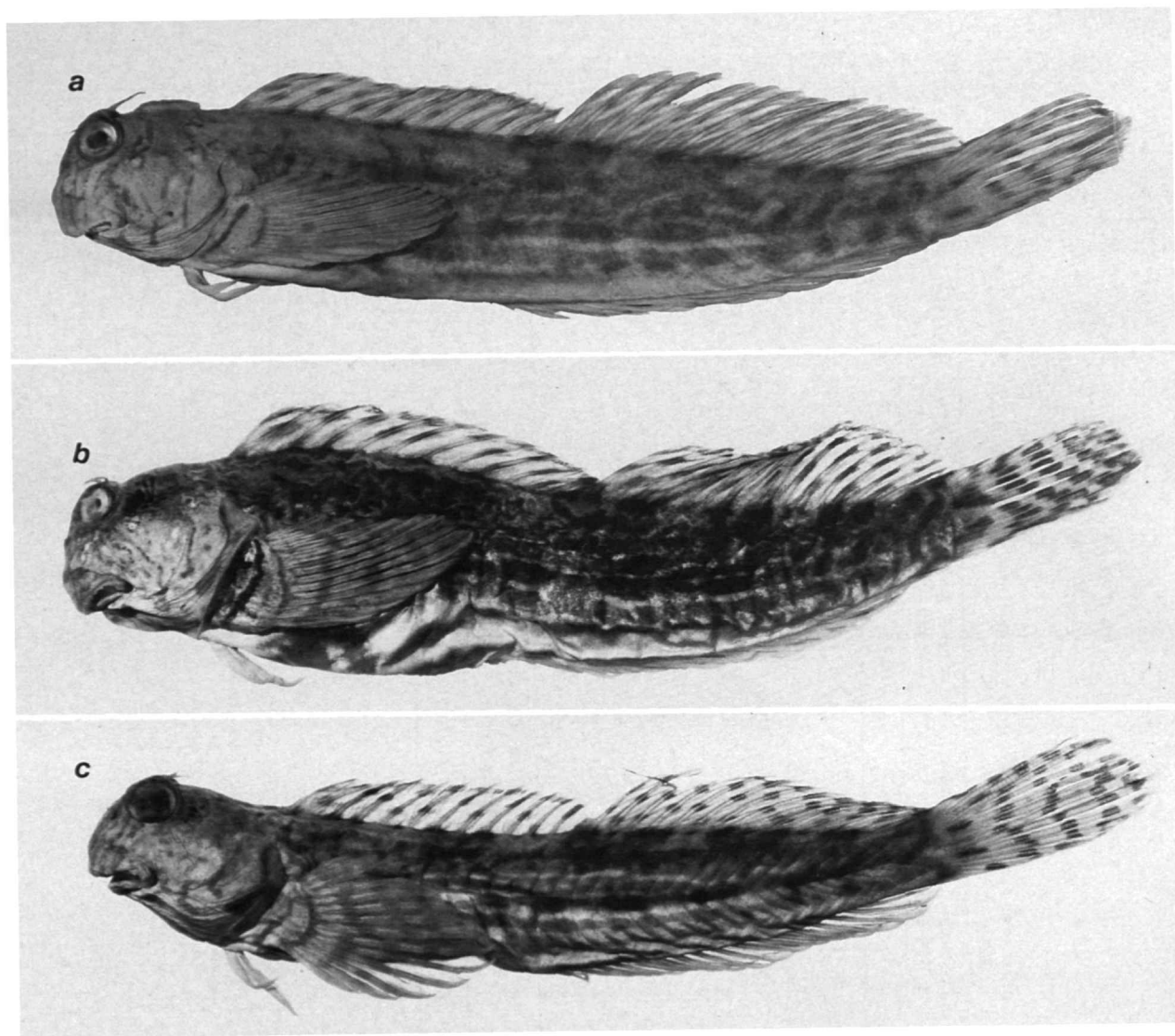
FIGURE 51.—*Istiblennius unicolor: a,* USNM 325430, El Tur, Egypt, male, 82 mm SL, (head crest depressed); *b,* HUJ 12779, Romia, Dahlak Archipelago, female, 77 mm SL; *c,* HUJ 12377, Elat, Gulf of Aqaba, female, 66 mm SL (photograph *a* by R. Gibbons; *b,c* by T.B. Griswold).

Lateral line (Table 41). Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between vertical from interspace between bases of 6th and 7th dorsal-fin spines and vertical from base of 9th spine (probably only rarely failing to reach posterior to vertical from base of 7th spine), thence continuing posteriorly as series of 9 to 14 short, disjunct, horizontally bi-pored canals (tubes) in skin; posteriormost tube on body in area between verticals from bases of 2nd and 10th segmented dorsal-fin rays.

Mandibular pores 5.

Six sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (dorsalmost pore somewhat removed from margin); all pore positions with simple pores (no pore pairs).

Posterior canines absent in both sexes.

Ventral margin of upper lip crenulate; dorsal margin of lower lip completely or partially crenulate.

All males, including smallest, 57 mm SL, have small, but well-developed crests; females, including largest, 92 mm SL, lack all evidence of crest formation.

Color pattern (in preservative; Figure 51). Well-preserved specimens of both sexes, with dark, posteriorly rounded blotch (apparently bluish in life), often separated posteriorly by narrow, pale area from paler, anteriorly facing crescent, just posterior to orbit; second crescent variably present just posterior to first; several specimens with small, pale spot just ventral to dark blotch; about 12 more or less evenly spaced fine, dark, bands extending from area below middle of eye around snout to middle of other eye. Very faint indications of similar marks noticeable in most specimens. Both sexes with up to 4 irregular, fine, pale stripes on body coursing through dark, mottled background, each stripe with several darkenings vertically aligned with darkenings of other stripes, giving appearance of bands.

Slender, dark band present on fleshy pectoral-fin base; second band, not as dark, curves around bases of fin rays; 3 or 4 faint-dusky, irregular bands cross fin distal to curving band. Females have dark spots or streaks on dorsal fin, dark spots on caudal fin; males also have dark spots on these fins, but spots may be more diffuse than those of females; vertical pair of prominent dark spots at bases of caudal-fin rays.

Size. Largest specimen, male, 102 mm SL; largest female, 92 mm SL; smallest specimen, male, 57 mm SL.

COMMENT.—*Istiblennius unicolor* is the least common species of *Istiblennius* in collections. Nothing is known of its habits or habitat preferences. Such rarity is unexpected, as highly restricted endemic fish species, such as this species, are usually very common (Randall, 1992b:56). *Istiblennius rivulatus*, which, like *I. unicolor* is also endemic to the Red Sea, is extremely common.

COMPARISONS AND RELATIONSHIPS.—See discussion in this section under *Istiblennius spilotus*.

DISTRIBUTION (Figure 69).—Northernmost Gulf of Aqaba south to Dahlak Archipelago, southern Red Sea.

MATERIAL EXAMINED.—G of Aqaba: Israel, Elat, HUJ 12377 (1), TAU 10315 (1). Gulf of Suez: Egypt, Et Tur, HUJ 9553 (1), USNM 325430 (1). Red Sea: NMW 73248 (1 specimen), NMW 73249 (1); Dahlak Archipelago, Romia, HUJ 12779 (3); Ethiopia, Massawa, SMF 1866 (holotype of *Salarias unicolor*).

Istiblennius spilotus, new species

FIGURES 52–54

DESCRIPTION.—Dorsal fin (Table 40). XIII or XIV,16 to 19 = 29 to 32 (XIV in only 3, 16 in only 1, 29 in only 1 of 186 specimens examined for these characters); mean number of total elements tending to be higher for males from any locality than for females from same locality (higher at 4 of 7 localities where means for both sexes are available, statistically significantly higher at 1 of the 4 localities); membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; posterior membranous attach-ment usually on dorsal edge of caudal peduncle anterior to caudal-fin base, occasionally at base or on dorsal edge of caudal fin very slightly posterior to base.

Anal fin (Table 40). II,17 to 19; mean number of segmented rays tending to be higher for males from any locality than for females from same locality (higher for 5 of 6 localities where means for both sexes are available, statistically significantly higher for 1 of the 5 localities); posterior element split to base in about half of specimens; posterior element of split ray usually visible externally; fin bound by membrane to caudal peduncle in only 1 of 30 specimens examined for character. Skin covering anal-fin spines and distal half of rays not modified in males.

Pectoral-fin rays 13 or 14 (13, only unilaterally, in 2 of 100 specimens examined for character).

Pelvic-fin segmented rays 2 to 4 (Table 41), probably only aberrantly 2; 4th (innermost) ray, when present, ranging from well developed, obvious, to short, fine splint closely applied to third ray, not visible externally; bilateral asymmetry in number of rays common; tip of innermost ray, whether third or fourth, not free.

Caudal fin. Dorsal procurrent rays 6 to 8 (predominantly 6 or 7), ventral procurrent rays 5 to 8 (rarely 5 or 8), total procurrent rays 11 to 16 (rarely 11, 15, or 16; Table 41), segmented rays 13.

Vertebrae (Tables 40 and 41). 10 or 11+25 to 27 = 35 to 37 (10 in 98% of specimens; 36 in 94%), means for males and females not statistically different; posteriormost pleural rib on 11th or 12th from anteriormost centrum (on 12th in only 2 of 140 specimens examined for character); posteriormost epineural on 12th to 15th from anteriormost centrum (on 13th in 107, on 15th in only 1, of 144 specimens examined for character).

Cirri. Nape cirrus absent. Orbital cirrus highly variable, usually shorter than orbital diameter in males less than about 70 mm SL and females, often much longer than orbital diameter in larger males, consisting of central stalk with side branches, becoming highly complex in large males. Nasal cirrus small, palmate with up to 14 separate tips, but rarely more than 8.

Lateral line (Table 41). Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between vertical from interspace between bases of 6th and 7th dorsal-fin spines and vertical from interspace between 9th and 10th spines (rarely anterior to 7th or posterior to 9th spines), thence continuing posteriorly as series of 6 to 20 (usually >than 9) short, disjunct, horizontally bi-pored canals (tubes) in skin; posteriormost tube on body in area between verticals from bases of 13th dorsal-fin spine and 13th segmented ray (usually posterior to 3rd ray).

Mandibular pores 4 or 5 (5 pores bilaterally in 90% of 133 specimens examined for character, unilaterally in 9% of specimens; only 1 specimen with 4 pores bilaterally).

Five to 7 sensory pore positions between 1 o'clock and 5 o'clock on postorbital margin (6 in 86% of 108 specimens examined for character); 0 or 1 position occupied by pair of
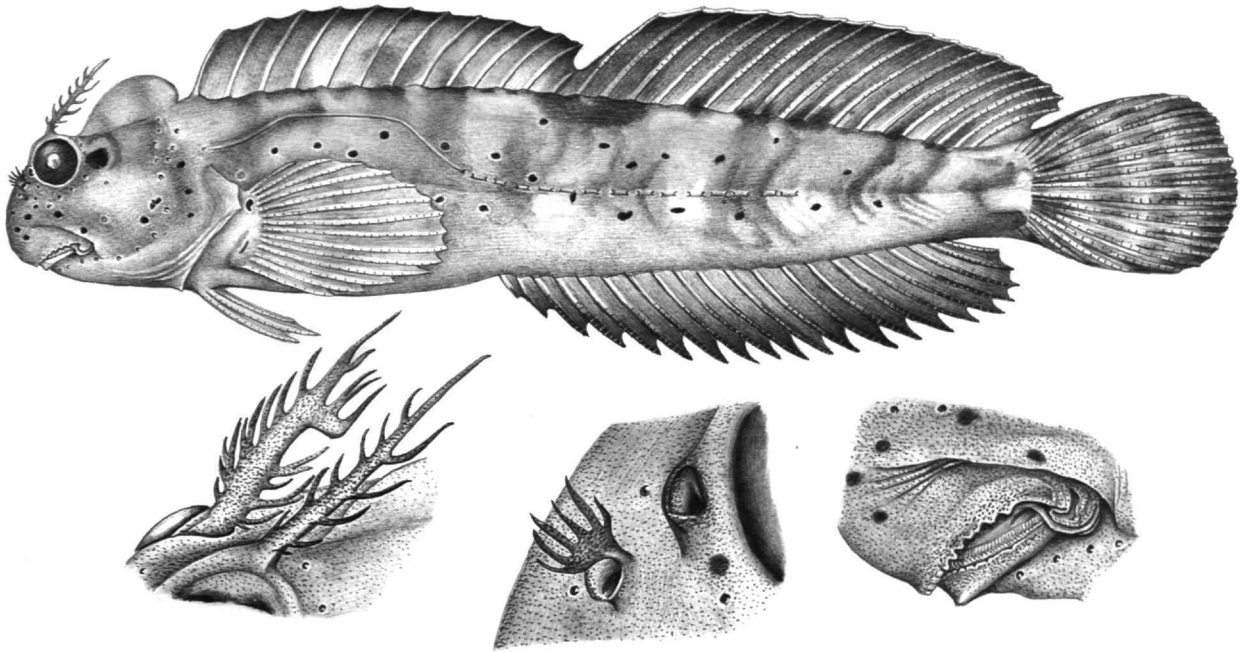
FIGURE 52.—*Istiblennius spilotus*, new species, USNM 220913, holotype, male, 88 mm SL, Boleji Point, Pakistan: *Upper*, lateral view; *Lower left*, orbital cirri enlarged; *Lower center*, nasal cirrus enlarged; *Lower right*, enlarged lateral view of lips (drawings by J.R. Schroeder).
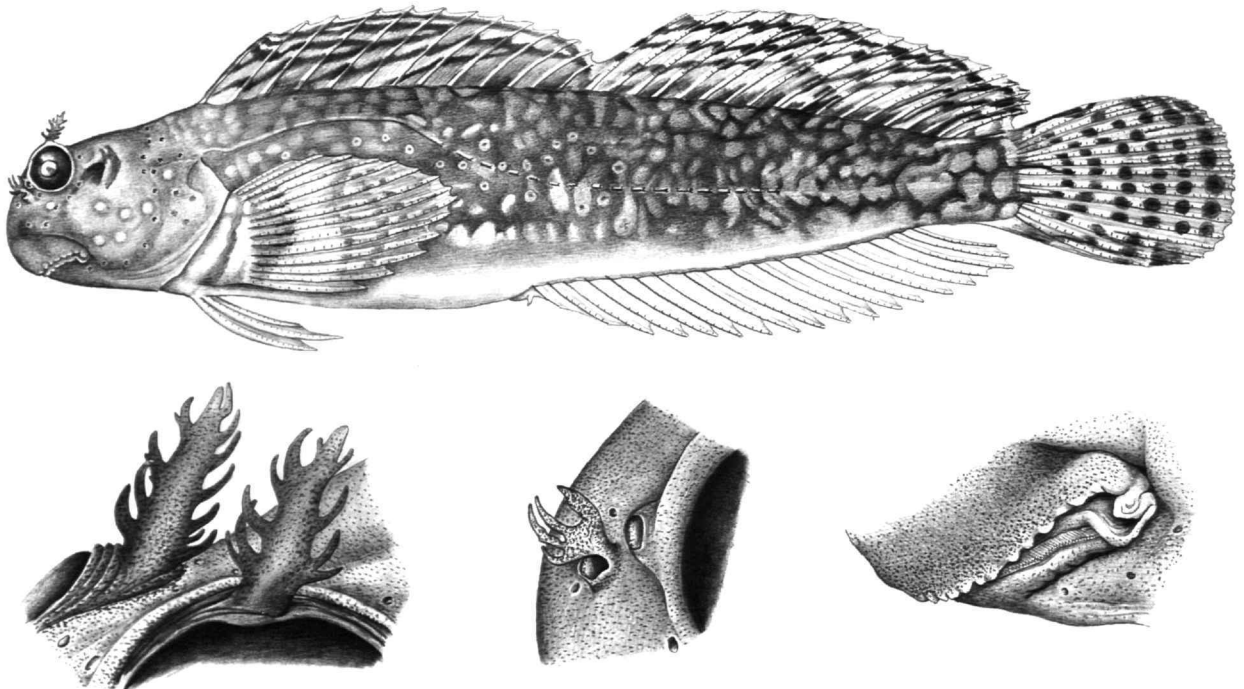
FIGURE 53.—*Istiblennius spilotus*, new species, USNM 325131, female, 84 mm SL, Boleji Point, Pakistan: *Upper*, lateral view; *Lower left*, orbital cirri enlarged; *Lower center*, nasal cirrus enlarged; *Lower right*, enlarged lateral view of lips (drawings by J.R. Schroeder).
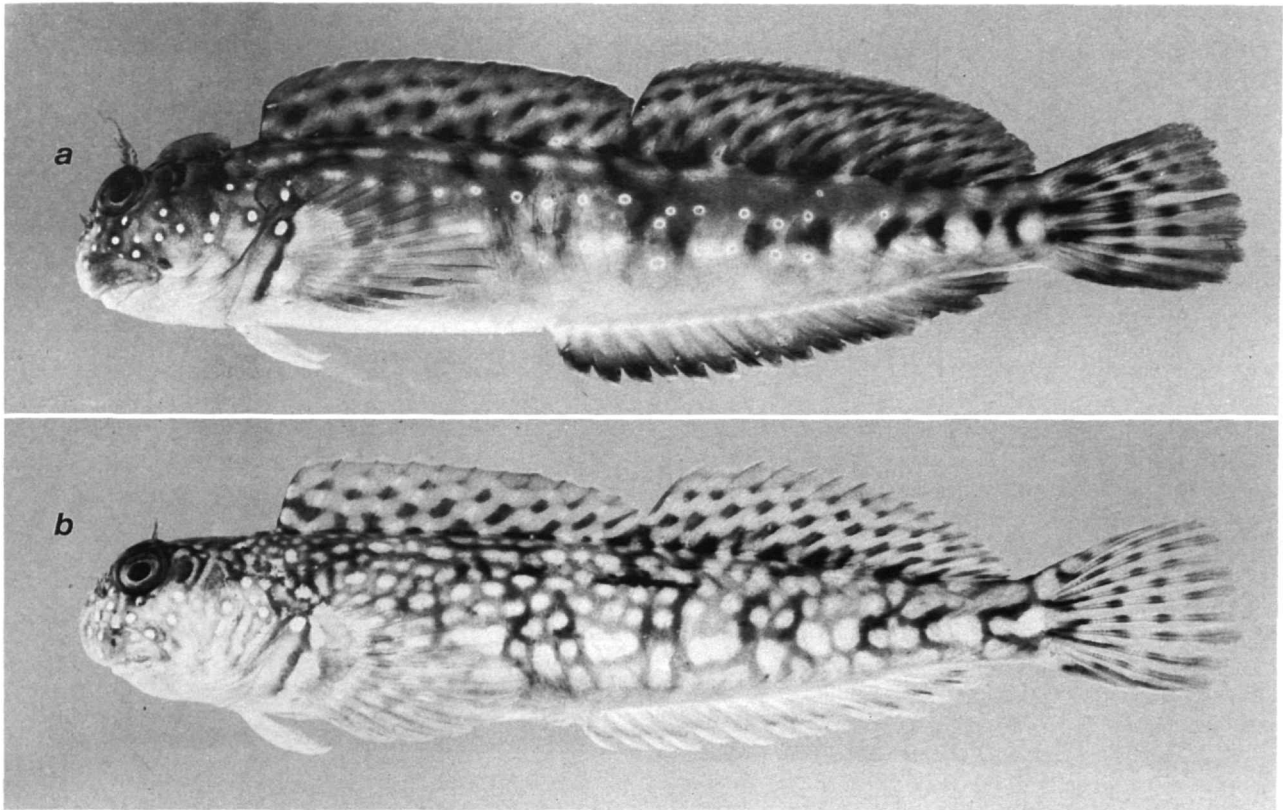
FIGURE 54.—*Istiblennius spilotus*, new species: *a,b*, BPBM 21353, male and female, 57 and 54 mm SL, islet –3 to 5 km south of Sidab, Oman (from color photograph of fresh specimens by J.E. Randall).

pores (90% of specimens with only simple pores at each position).

Posterior canines absent in both sexes.

Ventral margin of upper lip crenulate (specimens as small as 15 mm SL); dorsal margin of lower lip completely or partially crenulate in specimens at least as small as 28 mm SL.

Males first show faint indications of fleshy crest development on head at 44 to 65 mm SL. Well-developed crests, at least 0.5 mm high, absent in specimens less than about 55 mm SL. Largest female, 97 mm SL, with low, ridge-like fold (artifactual?) where crest expected to form in male, 2 next largest females, 90 and 92 mm, and all smaller females, lack indications of crest formation.

Color pattern (in preservative; Figures 52, 53). Well-preserved specimens of both sexes with dark, posteriorly rounded blotch (apparently bluish in life), often separated posteriorly by narrow, pale area from less dark, anteriorly facing crescent, present just posterior to orbit; second crescent variably present just posterior to first. Indications of small, pale spots usually present on head and body; spots variably with dusky margins and/or darker centers (spots bright bluish or whitish in life); either no distinct markings in snout region, or only diffuse indications of dusky and pale bands on lips. Based on photographs of fresh males, row of spots present dorsally on body, extending most of body length; most preserved specimens, however, appear faded and lack all traces of spots.

Body of females generally more complexly patterned than that of males; fresh females (Figure 54*b*) have dusky reticular pattern on body with about 5 portions of network darkened and resembling bands. Body of males more uniform in pattern, but exhibiting indications of dusky bands.

Slender, dark band present on pectoral-fin base of most specimens. Females from all localities have dark spots or streaks on dorsal fin and dark spots on caudal fin. Dorsal and caudal fins of males with only faint indications of spots, which are readily recognizable only in fresh specimens (Figure 54*a*).

Useful illustrations of the species appear in Day (1876, pl. 70: figs. 5 and 6, as *Salarias unicolor*) and Springer (1986, pl. 116: fig. 235.19, as *Istiblennius flaviumbrinus*).

Size. Largest male, 121 mm SL; largest female, 97 mm SL;

smallest specimen, sex indeterminate, 15.3 mm SL, lacks enlarged canine teeth anteriorly in jaws (not an ophioblennius stage).

GEOGRAPHIC VARIATION.—Specimens from the Gulf of Oman have low total dorsal-fin element and segmented anal-fin ray counts relative to specimens from other localities. Specimens from the Gulf of Oman and from Pakistan-NW India tend to have lower total numbers of apparent segmented pelvic-fin rays and procurrent caudal-fin rays (Table 41) than do specimens from other localities.

COMPARISONS AND RELATIONSHIPS.—*Istiblennius spilotus* is the Indian Ocean sister group of the Red Sea endemic, *I. unicolor*, and these 2 species are the sister group of the Red Sea endemic, *I. flaviumbrinus* (Figure 60, see Phylogenetic Analysis section). The 3 species share in having the lowest numbers of dorsal- and anal-fin elements, total vertebrae, and epineurals of all *Istiblennius* (and *Blenniella*) species. In some specimens of *flaviumbrinus*, there is an indication of the dark spot and associated crescentic mark posterior to the eye that is otherwise unique to *I. unicolor* and *I. spilotus*. The 3 species also share other characters that, although not unique in *Istiblennius*, are found only in some of the other species: crenulate lips (although the lower lip of *flaviumbrinus* is almost always entire and only occasionally exhibits a few broad, shallow scallops), branched orbital cirri, restriction of the posterior attachment of the membrane of the dorsal-fin primarily to the caudal peduncle, modally 5 mandibular pores.

Istiblennius spilotus and *I. unicolor* share, to the exclusion of *I. flaviumbrinus*, in having 10 precaudal vertebrae and exclusively (*unicolor*) or commonly (*spilotus*) 4 segmented pelvic-fin rays (present in *Istiblennius* otherwise only in *I. colei*). They also share in generally having more bi-pored lateral-line tubes, the posteriormost of which is generally situated much farther posteriorly on the body, and in never having posterior dentary canine teeth, which are present in some male specimens of *I. flaviumbrinus* (present otherwise in *Istiblennius* only in some specimens of both sexes of *I. dussumieri*).

Istiblennius spilotus and *I. unicolor* are distinguished primarily on the basis of color pattern and number of total vertebrae (see key couplet 9 and Table 40).

DISTRIBUTION (Figure 69).—Western Indian Ocean from Gulf of Oman (and probably entrance to Persian Gulf) south to northern South Africa.

ETYMOLOGY.—The specific epithet is derived from the Greek *spilotos* (spotted) and refers to the small, brilliant white or blue spots on the head and body, particularly of males.

HOLOTYPE.—USNM 220913, male, 88 mm SL, Pakistan, tidepools at Boleji Point (Karachi), 24 March 1978, S.M.S. Hoda.

PARATYPES.—G of Oman: Oman, Muscat, BMNH 1888.12.29.150-153 (4); S. of Sidab, BPBM 21353 (4), USNM 217331 (4). Pakistan: near Karachi, CAS 35597 (11), USNM 199617 (2), 325131 (7, collected with holotype), 296479 (4),

Astola Id, USNM 296463 (3), 296465 (1). India: G of Kutch, Okha Point, USNM 296450 (3), 296451 (5), 296470 (3). Abd al Kuri Id: BMNH 1899.12.29.30-39 (10). South Africa: Boteler Point, 27°01'S, 32°52'E, RUSI 8648 (3). Kenya: Malindi, SMNS 13136 (1).

ADDITIONAL MATERIAL.—"?Henjam Island, Persian Gulf" BMNH 1932.2.18.38-39 (2). Pakistan: Sind, NMW 11646 (2), RMNH 1814 (1), 1815 (1). Samhah Id [between Socotra and Abd al Kuri], NMW 11645 (1). Somalia: Muqdisho, MCZ 41711 (2). Kenya: Malindi, USNM 288490 (2), 288492 (1), 288493 (1), 288494 (4), 288495 (2), 288496 (1). Grande Comore: CAS 32579 (4), 33020 (1), 33045 (3), 33428 (8), 33771 (17), USNM 201872 (14). Madagascar: Nosy Be (also Nossi Bé), SMF 1837 (2, data supplied by H. Bath), USNM 200208 (45, including 2 cleared and stained), 288491 (1), 296051 (13), 296052 (10). South Africa: Natal coast, Sodwana Bay, BPBM 21073 (5).

Istiblennius flaviumbrinus (Rüppell)

FIGURE 55

Salaris [sic] *flaviumbrinus* Rüppell, 1830:112 [Mohila (Saudi Arabia); holotype or lectotype, SMF 1893; see nomenclatural discussion below].

Salarias dama Valenciennes in Cuvier and Valenciennes, 1836:366 [based on illustration by C.G. Ehrenberg, which was probably based on ZMB 1957 from Red Sea, accepted as holotype in present study; see nomenclatural discussion below and *Blennius dama* in synonymy below].

Salarias flavo-umbrinus Rüppell, 1838:135 [misspelling].

Salarias cervus Cuvier and Valenciennes in Sauvage, 1880:218 [Mer Rouge; holotype, MNHN 2208].

Blennius dama Hemprich and Ehrenberg, 1899:3 [mari rubro; probably based on ZMB 1957, accepted as holotype in present study, see *Salarias dama* in synonymy above].

Halmablennius steinitzi Lotan, 1970:367 [Entedebir islet, Dahlak Archipelago; holotype, HUJ 13930].

DESCRIPTION.—Dorsal fin (Table 40). XIII or XIV,16 or 17 = 29 or 30 (XIV in only 2 of 64 specimens examined for character); males have significantly (p = <.001) higher mean number of total elements than females; membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; membrane from posteriormost ray attaching on dorsal edge of caudal peduncle anterior to caudal-fin base in specimens <80 mm SL, at caudal-fin base or on dorsal edge of fin slightly posterior to fin base in specimens >80 mm.

Anal fin (Table 40). II,16 or 17; males have significantly (p = <.005) higher mean number of segmented rays than females; posterior element split to base in only 4 of 50 specimens examined for character; posterior element of split ray visible externally in 3 specimens, present vestigially in 1; fin not bound by membrane to caudal peduncle in any of 32 specimens examined for character. Skin covering anal-fin spines and distal half of rays not modified in any of 33 males available (31 to 90 mm SL).

Pectoral-fin rays 12 to 15, 14 bilaterally in 52 of 55
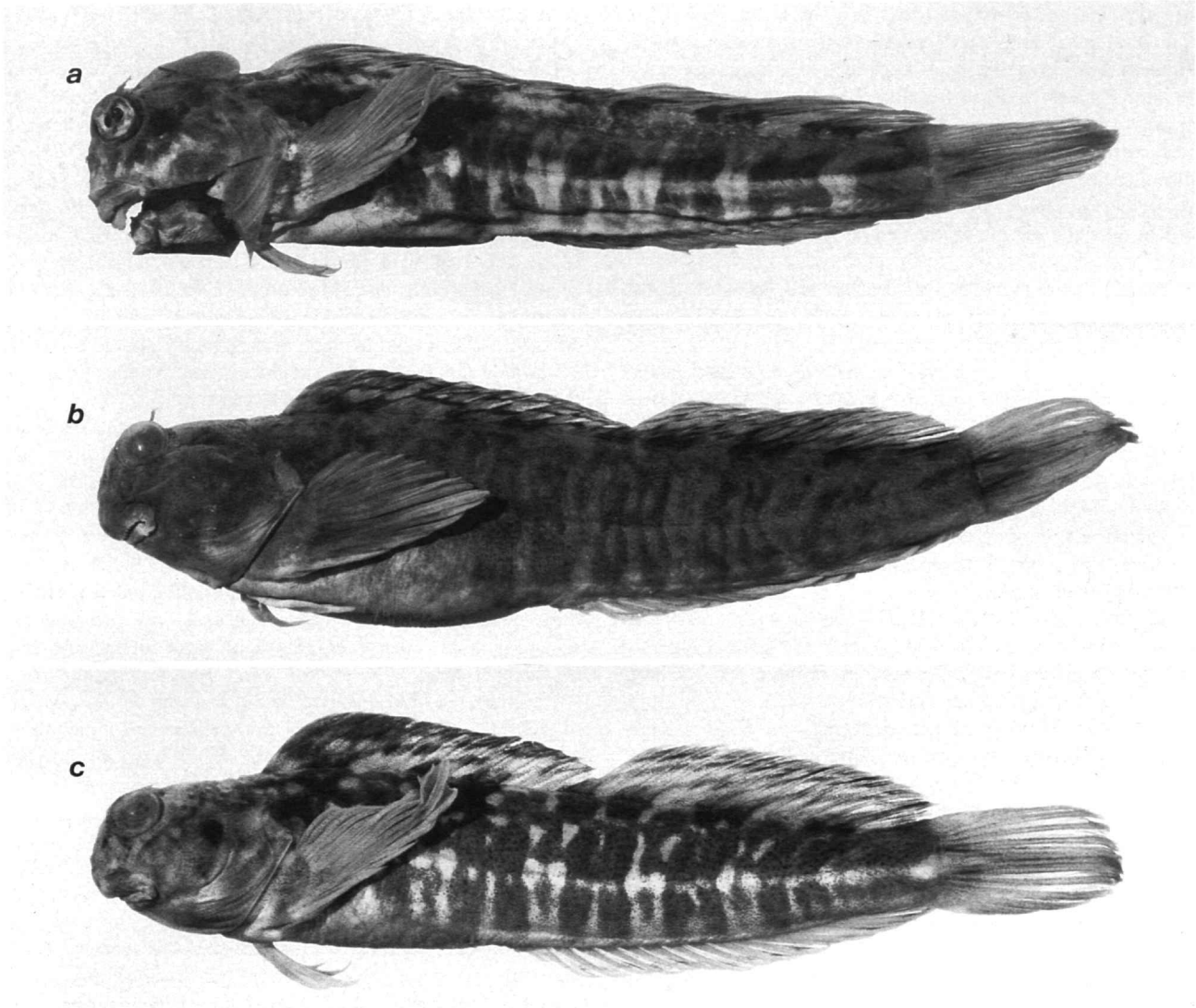
FIGURE 55.—*Istiblennius flaviumbrinus: a*, male, HUJ E62/406b, 60 mm SL, Cundabilu, Dahlak Archipelago (damaged lower jaw; dark mark in crest is pin used as prop); *b,c*, females, USNM 204509, Massawa, Ethiopia, *b*, 50 mm SL; *c*, 69 mm SL (photographs by T.B. Griswold).

specimens examined for character (rays 12/14, 13/14, and 14/15 in 1 specimen each).

Pelvic-fin rays I,2 or 3 (2 only unilaterally, in only 2 specimens).

Caudal fin. Dorsal procurrent rays 6 to 8 (predominantly 7), ventral procurrent rays 6 to 8 (predominantly 7), total procurrent rays 12 to 16 (predominantly 14, Table 41), segmented rays 13 or 14 (14 in only 3 of 61 specimens examined for character).

Vertebrae (Tables 40 and 41). 11 or 12+23 or 24 = 34 or 35 (only 1 specimen with 12, 2 with 34, and 3 with 23 in 64 specimens examined for these characters); posteriormost pleural rib on 11th or 12th from anteriormost centrum (on 12th in only 2 of 47 specimens); posteriormost epineural on 12th to 14th from anteriormost centrum (on 13th in 34 of 49 specimens examined).

Cirri. Nape cirrus absent. Orbital cirrus shorter than orbital diameter, variable in shape, often consisting of central stalk with 2 short branches or points on lateral and medial edges, tip often notched. Nasal cirrus short, palmate, with 3 to 8 branches

in specimens >45 mm SL.

Lateral line (Table 41). Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between verticals from bases of 5th and 9th dorsal-fin spines (usually to between 6th and 7th spines), then continuing posteriorly as series of 3 to 13 (usually 5 to 8) short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area between verticals from bases of 9th dorsal-fin spine and 4th segmented ray (usually anterior to 3rd ray).

Mandibular pores 4 to 6 (always 5 pores, at least unilaterally; 4 and 6 pores only unilaterally and in only 1 specimen each of 54 specimens examined for character).

Five or 6 sensory pore postions between 1 o'clock and 5 o'clock on postorbital margin (6 in 26 of 43 specimens examined for character); all positions occupied by single pores.

Posterior canines tiny, inconspicuous (often present only unilaterally) in 20 males 38 to 90 mm SL, absent in 10 males 30 to 60 mm SL and in all females.

Ventral margin of upper lip crenulate (in specimens as small as 30 mm SL); dorsal margin of lower lip entire, sometimes with few broad, shallow scallops.

Males ≥38 mm SL with fleshy, blade-like crest dorsally on head; males 30 to 38 mm with scarcely noticeable ridge; 30 females, 29 to 72 mm SL, without crest or ridge, and 1 female, 72 mm, with well-developed crest (abnormal?).

Color pattern (in preservative; Figure 55). Head variably dusky with diffuse markings; sometimes with dark reversed-C or reversed double-C arrangement of small, dark spots posterior to orbit (see small female, Figure 55c); body with up to 5^1/2 pairs of irregular, dusky bands, which extend dorsally onto dorsal fin, become slender, and extend dorsoposteriorly as stripes; tiny, dark spot often present on side between lateral line and proximal base of dorsalmost pectoral-fin ray (spot external to dorsalmost extension of cleithrum); fins, except dorsal, indistinctly marked, except for dorsoventral pair of diffusely dusky spots basally on caudal fin.

Size. Largest male, 90 mm SL; largest female, 72 mm; smallest specimen available 29.5 mm SL, not an ophioblennius stage.

COMPARISONS AND RELATIONSHIPS.—See discussion in this section under *I. spilotus*.

DISTRIBUTION (Figure 69).—Restricted to the Red Sea. All but one specimen, from Mohila, northeastern Red Sea, have come from the southern Red Sea.

NOMENCLATURAL DISCUSSION.—Rüppell's (1838:112) description of *Salaris flaviumbrinus* mentions no variation in characters and, thus, appears to have been based on a single specimen, 4 inches long (~101 mm; TL?). Smith-Vaniz and Springer (1971:56), however, indicated that the type material for this nominal species included 4 specimens SMF 1893 and SMF 8053-6, mainly because these specimens were all labeled as types at SMF. Only 1 of these specimens, SMF 1893, approximates 4 inches TL (the others are much shorter), and we

believe it is the holotype, as, apparently, did W. Klausewitz (*in* Lotan, 1970:367).

Dor (1984:230) listed SMF 1893 as the lectotype of *Salarias* [sic] *flaviumbrinus*, and assigned paralectotype status to the three specimens in SMF 8053-6. We doubt that the latter 3 specimens have status as types.

We found it difficult to locate the geographic position of Mohila, the type locality of *Salaris flaviumbrinus*. Rüppell entered this name on the map he made of his travels during 1826. The map is reproduced in Klausewitz (1984, fig. 6). Using a magnifying glass, Mohila can be seen as the lowermost locality on the right-hand side of the map. Mohila is currently denoted Al Muwaylih in some atlases; its location is 27°41'N, 35°28'E, near the northeasternmost end of the Red Sea (excluding the gulfs of Suez and Aqaba).

Bauchot (1967:36) discussed the putative types of *Salarias dama* Valenciennes, 1836, which was described from an Ehrenberg illustration. The species was figured and redescribed as *Blennius dama* by Hemprich and Ehrenberg (1899:3), in which publication *B. dama* was indicated as a junior synonym of *Salarias flavoumbrinus* (sic). Bauchot concluded, and we agree, that ZMB 1957 is probably the [holo]type of *S. dama*, hence, also of *B. dama*. Valenciennes did not compare his species with any other; the probable holotype identifiable as *I. flaviumbrinus*.

Bauchot (1967:26) discussed problems with the description of *Salarias cervus* Sauvage, which was not differentiated from other species, and she recognized MNHN 2208 as the holotype. Bauchot identified Sauvage's species as *I. flaviumbrinus*. We agree with Bauchot's actions.

Lotan (1970:367) erroneously distinguished her *Halmablennius steinitzi* from *I. flaviumbrinus* in her key by stating that the upper lip of the former was smooth and of the latter, crenulate. Both nominal species have crenulate upper lips. In the description of *H. steinitzi*, she distinguished this species from *I. flaviumbrinus*, stating that the former had fewer gill rakers (14 vs. 24), a different head crest (beginning between eyes vs at middle of head), and a smooth lower (sic) lip (vs. crenulate). We find no differences in these characters between the two nominal species. Part of Lotan's problem was that the specimens she identified as *flaviumbrinus* are *I. unicolor*, which does have a crenulate lower lip; however, these two species do not differ in number of gill rakers or the point of origin of the head crest.

MATERIAL EXAMINED.—Red Sea: BMNH 1845.19.29.112 (1 specimen), MNHN 2208 (holotype of *Salarias cervus*), ZMB 1957 (probable holotype of *Salarias dama* and *Blennius dama*). Ethiopia: Massawa, SMF 8053-6 (4), USNM 204509 (5), 296114 (1 cleared and stained); Difnein Id, USNM 303423 (2); Dahlak Arch: 15°48'N, 40°05'E, USNM 296474 (8, including 1 cleared and stained); Entedebir, HUJ 13931 (1), 13930 (holotype of *Halmablennius steinitzi*), 12123 (1); Cundabilu, HUJ 13932 (7), 12107 (2), 12124 (10); Nocra, HUJ 12288 (10), MSNG 42928 (1); Um Aabak, HUJ 12289 (7).

Table 42.—Frequency distributions for certain characters of specimens of _Istiblennius colei_. Underlining indicates significant differences between means of sexes (p ≤ .05).

Sex	Dorsal-fin spines			Total dorsal-fin elements				Segmented anal-fin rays				Total vertebrae			
	13	14	15	32	33	34	x̄	19	20	21	x̄	37	38	39	x̄
males	-	34	1	10	23	2	32.8	1	27	7	20.2	6	25	3	37.9
females	4	31	2	24	7	-	32.2	15	16	-	19.5	11	19	-	37.6

	Procurrent caudal-fin rays[1]						Epipleural ribs						Total mandibular pores[2]				
	6/6	6/7	7/6	7/7	7/8	8/7	14	15	16	17	18	19	9	10	11	12	13
both	1	-	9	37	1	3	2	12	28	15	5	1	3	6	17	24	1

	Bi-pored lateral-line tubes end at vertical from dorsal-fin element number											Number of lateral-line tubes									
	11	12	13	14	15	16	17	18	19	20	x̄	3	4	5	6	7	8	9	10	11	12	x̄
males	-	3	6	11	5	-	3	-	-	-	14.1	-	-	9	4	11	-	4	-	-	-	6.5
females	1	2	2	3	5	4	3	2	1	1	15.3	1	2	3	-	6	7	1	1	1	2	7.4

[1] Dorsal/ventral
[2] Both sides; combinations are: 4-5, 4-6, 5-5, 5-6, 6-6, 6-7

Saudi Arabia: Mohila, SMF 1893 (holotype or lectotype of _Salaris flaviumbrinus_).

Istiblennius colei (Herre)

FIGURE 56

Salarias colei Herre, 1934:96 [Philippines, reef in Culion Harbor; holotype CAS-SU 25520].
Salarias martini Herre, 1942:2 [Estancia, Panay, Philippine Islands; holotype CAS-SU 28253].

DESCRIPTION.—Dorsal fin (Table 42). XIII to XV,18 to 20 = 32–34 (XIV in 91% of specimens; 20 in only one male of 36 males examined), mean number of total elements statistically significantly higher for males than for females; membrane between spinous and segmented-ray portions notched deeper than half length of first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle well in advance of caudal-fin base to point on dorsal edge of caudal fin just posterior to base (usually anterior to caudal-fin base).

Anal fin (Table 42). II,19 to 21, mean number of segmented elements statistically significantly higher for males than for females; posterior element split to base in more than half of specimens; posterior element of split ray usually visible externally; fin not bound by membrane to caudal peduncle in any of 53 specimens examined for character. Skin covering anal-fin spines and anterior segmented rays not modified in adult males. Pectoral-fin rays 14 or 15 (15 only unilaterally, in only 2 of 46 specimens examined for character).

Pelvic-fin rays I,4, but only 3 segmented rays visible externally; innermost ray greatly reduced, but retaining segmentations, completely imbedded in skin; visible only in 2 available cleared-and-stained specimens, but presumably present in all other specimens.

Caudal fin (Table 42). Dorsal procurrent rays 6 to 8 (7 in 92% of specimens examined for character), ventral procurrent rays 6 to 8 (7 in 78% of specimens), total procurrent rays 12 to 15 (14 in 92% of specimens), segmented rays 13.

Vertebrae (Table 42). 11 or 12+26 to 28 = 37 to 39 (12 in only 2 of 62 specimens examined for character), mean number of total (and caudal) vertebrae statistically significantly higher for males than for females; posteriormost pleural rib on 11th or 12th from anteriormost centrum (on 11th in only 1 of 58 specimens); posteriormost epineural rib on 14th to 19th from anteriormost centrum (on 19th in only 1 of 63 specimens).

Cirri. Nape cirrus absent. Orbital cirrus consisting of flattened central stalk with up to 7 branches on each lateral and medial margin; <orbital diameter in females, ranging from < to
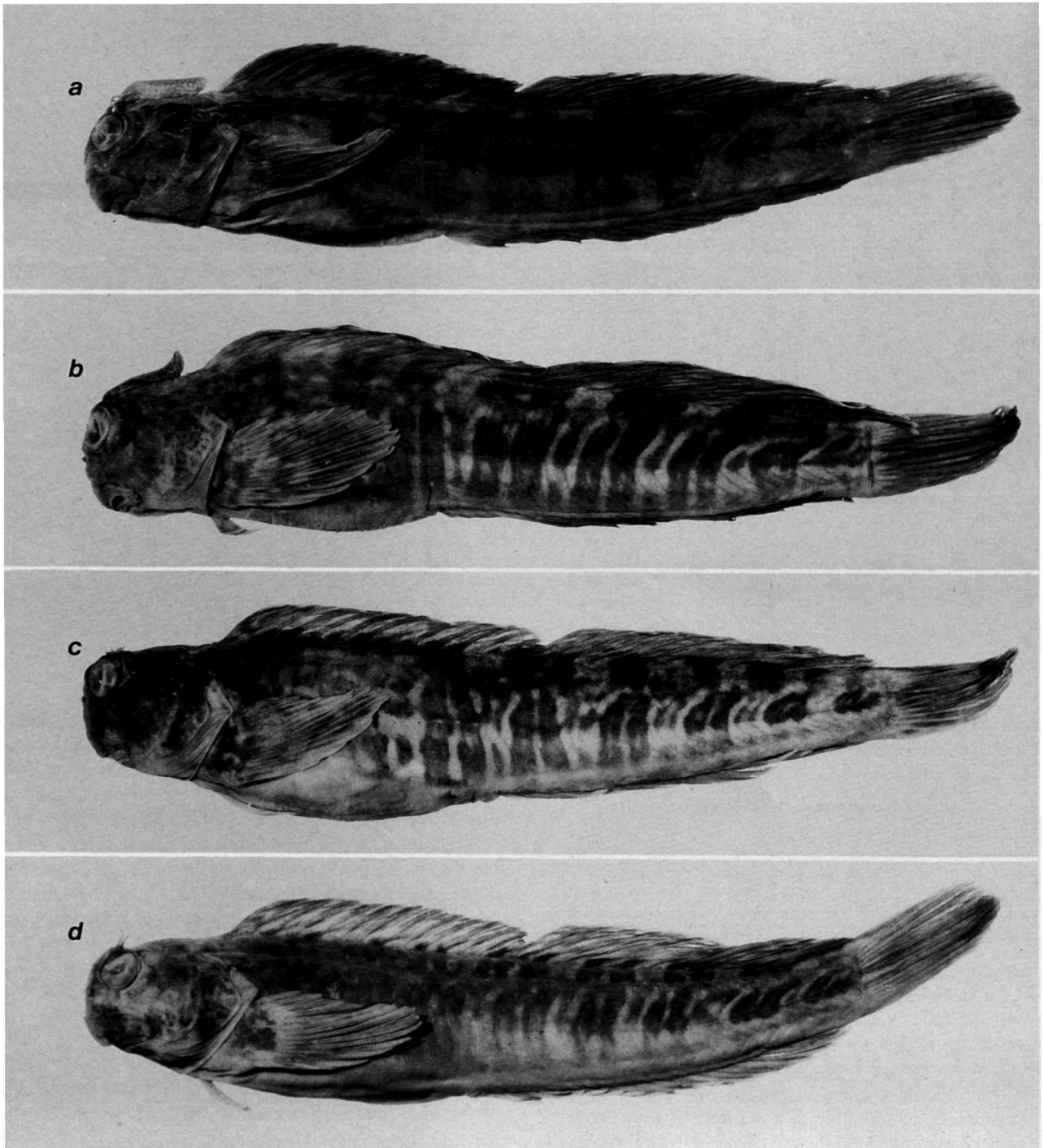
FIGURE 56.—*Istiblennius colei*, Estancia Bay, Philippine Islands: *a*, USNM 123655, male, 78 mm SL; *b*, CAS-SU 38249, male, 81 mm SL; *c*, CAS-SU 38249, female, 85 mm SL; *d*, USNM 123655, female, 80 mm SL (photographs by T.B. Griswold).

slightly >orbital diameter in males. Nasal cirrus short, ranging from ragged-edged flap to palmate flap with up to 16 irregular branches.

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between vertical from between bases of 7th and 8th dorsal-fin spines and vertical from base of 10th spine (usually to vertical from, or between, 8th or 9th spines), then continuing posteroventrally and posteriorly as series of 3 to 12 short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area between verticals from 11th and 20th from anteriormost dorsal-fin element (i.e., no farther posteriorly than 6th segmented ray; mean number of element significantly higher in females than males, Table 42).

Mandibular pores 4 to 7 (6, at least unilaterally, in 84% of specimens; modally 6 bilaterally, 47% of specimens; Table 42).

Six to 8 sensory pore positions between 1 and 5 o'clock on postorbital margin; 0 to 2 positions occupied by pair of pores (modally 1).

Posterior canines absent.

Ventral margin of upper lip entire; dorsal margin of lower lip varying from entire to weakly, irregularly, and almost unnoticeably crenulate (irregularities almost entirely restricted to corners of lip).

Males with well-developed, blade-like crest on head (smallest male available, 49 mm SL); females lack crest (largest available, 103 mm SL), but several females 68 to 86 mm SL with faint, ridge-like crest precursors, and 1 female, 71 mm, with definite slender crest, 1.0 mm high, and another, 85 mm SL, with well-developed fleshy ridge, 0.9 mm high (both much lower than that of any male examined).

Color pattern (in preservative; Figure 56). Male and female color patterns generally similar, but that of female usually more contrasty; male crest uniformly dusky or covered with dusky spots or granular vermiculations; remainder of head either almost uniformly dusky or with fine, dusky spots on opercle; up to about 6 pairs of dark, irregular bands on body, bands extending from above anal-fin base to dorsal body contour, variably entering dorsal fin basally; all fins darkly, irregularly pigmented, except tips of dorsal- and anal-fin elements tend to be pale.

Size. Largest male, 118 mm SL; largest female, 103 mm SL; smallest specimen available, 36 mm SL, not an ophioblennius stage.

COMPARISONS AND RELATIONSHIPS.—We have no subjective opinion on what the interrelationships of *Istiblennius colei* might be. Our phylogenetic analysis places it as the sister group of all other *Istiblennius* species (Figure 60, see Phylogenetic Analysis section). Superficially, *Istiblennius colei* resembles *Paralticus amboinensis* and is different from all other *Istiblennius* and *Blenniella* species in having modally 14 dorsal-fin spines. The two species differ in many characters (see Comparisons and Relationships section under *P. amboinensis*) and there is no reason to believe they are closely

related. In possessing 4 segmented pelvic-fin rays (but only 3 obvious), *I. colei* resembles only *I. unicolor* and *I. spilotus* (only some of the specimens of *spilotus* have 4 segmented pelvic-fin rays), but, among many characters, differs from these two species in having the ventral margin of the upper lip entire (crenulate in the other 2 species).

DISTRIBUTION (Figure 66).—*Istiblennius colei* is known only from Culion and Panay islands in the Philippines, and, thus, has the most restricted distribution of all the species of *Istiblennius* and *Blenniella*. This species is known only from the type series of its 2 nominal synonyms, collected more than 50 years ago. Considering all the collecting that has occurred in the Philippines in the past 20 years, it seems amazing that this clearly shallow-dwelling, once-common species has not been re-collected. We fear that it may be extinct.

NOMENCLATURAL DISCUSSION.—The holotypes of both synonyms of *Istiblennius colei* were originally deposited in the Stanford University collections. These collections were transferred to the CAS, where they retain their original Stanford catalog numbers prefixed with SU.

Herre (1942) thought his *Salarias martini* was most closely related to *I. edentulus* and *I. dussumieri*, from which he differentiated it. He also gave a key, in which he included *colei*, to all the Philippine species of "*Salarias*." The character in the key that separates *colei* from the other species belonging in *Istiblennius* (and *Blenniella*) is the presence of 14 or 15 dorsal-fin spines. The other species were said to have 12 or 13, exceptionally 11 or 14. Thirteen, "rarely" 12 spines was specified for *martini*. The reduced, terminal dorsal-fin spine of *Istiblennius* was frequently overlooked by ichthyologists, particularly those working before the advent and common use of radiography as an aid in counting vertical-fin elements and vertebrae.

We did not find 12 dorsal-fin spines in any of the 69 specimens of *I. colei* we examined for number of spines; however, there are probably more than 150 specimens available that we did not examine for the character.

The type series of *Salarias martini* consists of a holotype and 226 other specimens. All of these must be considered as paratypes of *S. martini*, although only 10 (CAS-SU 38254) are listed as such by Böhlke (1953:94) and maintained as such at CAS. All other specimens of the species at CAS are not labeled as types and are shelved in the regular collection. The 6 specimens at USNM (123655) and the 7 at FMNH (Ibarra and Stewart, 1987:77) are labeled as paratypes, but the 6 specimens at AMS (IB.3444) are not labeled as paratypes. It is possible that other specimens of the paratypic series of *S. martini* are deposited in other museums.

MATERIAL EXAMINED (all Philippine Islands).—Panay, CAS-SU 38253 (holotype of *Salarias martini*), 38254 (10), 38249 (73), USNM 123655 (6), 323836 (2 cleared & stained), AMS IB.3444 (6); Culion, CAS-SU 25520 (holotype of *Salarias colei*), 25521 (1).

Paralticus, new genus

TYPE SPECIES.—*Salarias amboinensis* Bleeker, 1857a.

DIAGNOSIS (see also Tables 1 to 3).—A genus of Salariini (Smith-Vaniz and Springer, 1971) with weak infraorbital bones, weakly attached to cranium, deepest portion of second infraorbital (usually at junction with first infraorbital) <half depth first infraorbital, dorsal margin of first infraorbital slightly to deeply notched (Figure 2a); dorsal and ventral postcleithra lacking; vomer edentate; anterior dentary canines absent; posterior dentary canines present in males, absent in females; >100 teeth in entire upper jaw, >75 in entire lower jaw; pectoral-fin rays strongly modally 14 (otherwise 13, only unilaterally, only in 1 specimen); segmented pelvic-fin rays 3; dorsal fin: XIV,18 to 20, membrane between last spine and first segmented ray notched >half length first segmented ray, posteriormost segmented ray bound by membrane to point ranging from on dorsal edge of caudal peduncle just in advance of caudal-fin base to point on dorsal edge of caudal fin just posterior to origin of caudal fin; terminal anal-fin ray attached by membrane to caudal peduncle, not split to base; segmented caudal-fin rays 14, including 9 branched; lateral line consisting of continuous anterior portion followed posteriorly by series of 6 to 12 short, horizontally bi-pored tubes in skin; no scale-like flaps in continuous portion of lateral line; preoperculomandibular pores without cirri; fleshy blade-like crest not present dorsally on head of either sex; supraorbital cirrus present, large, broad, palmate flap; nape cirrus absent; upper lip without free dorsal margin; ventral margin of upper lip crenulate; dorsal margin of lower lip crenulate; no cup-shaped fleshy disk or appendage posterior to lower lip; precaudal vertebrae 11; posteriormost epineural articulating with 15th to 18th vertebra from anteriormost.

COMPARISONS AND RELATIONSHIPS.—*Paralticus* differs from all other Salariini, except some species of *Alticus* Lacépède and *Andamia* Blyth, in lacking both dorsal and ventral postcleithra. All species of the latter two genera lack one or both postcleithra, and when postcleithra are present, they are much reduced and represented only by fragments of bone; individual specimens may vary bilaterally. Inasmuch as only one specimen of *Paralticus* was available for osteological preparation, it is possible that additional skeletal material will exhibit the presence of fragmental postcleithra.

Reduction in postcleithra is otherwise exhibited in the Salariini only by the species of *Praealticus* Schultz and Chapman. In *Praealticus*, the dorsal postcleithrum is always present (although it is much reduced in size and may be represented only by a thin, dorsal plate of bone attached to the inner surface of the dorsal end of the cleithrum). The ventral postcleithrum in *Praealticus* also is always reduced and ranges from being absent to being a long, slender piece of bone, but when present, is always separated from the dorsal postcleithrum and never overlaps the ventral end of the dorsal postcleithrum (Smith-Vaniz and Springer, 1971, fig. 15), as is

the normal condition in other blenniids and perciforms generally.

Paralticus differs most obviously from *Alticus* and *Andamia* in having 14 caudal-fin rays, as opposed to 11 to 13, and in having several branched caudal-fin rays, as opposed to all caudal-fin rays simple. It further differs from these two genera in having a hook-like process on the antero-dorsal edge of the anterior ceratohyal (Figure 1b). It differs from *Andamia* in lacking the cup-shaped fleshy disc on the ventral surface of the head posterior to the lower lip, and from *Alticus* in lacking a fleshy blade-like crest on top of the head of males and in having the last anal-fin ray attached by membrane to the caudal peduncle.

Paralticus differs most obviously from *Praealticus* in having 14 pectoral-fin rays, as opposed to strongly modally 15 rays, 14 dorsal-fin spines, as opposed to strongly modally 13, in lacking a blade-like crest on the head of males, and in having the last anal-fin ray attached by membrane to the caudal peduncle. It further differs from *Praealticus* in having 11 precaudal vertebrae (versus 10), the posteriormost pleural rib on centrum 11 (versus 10), and the posteriormost epineural on centrum 15 to 18 (versus 11 to 13).

In our phylogenetic analysis of the relevant genera of Salariini (Figure 58, see Phylogenetic Analysis section), interrelationships based on polarizable characters resulted in a cladogram that included a clade with the following construction (*Praealticus* (*Paralticus* (*Alticus*, *Andamia*))). The only non-homoplastic specialization supporting this clade is the reduction or absence of the postcleithra. More such synapomorphies in support of this clade would be highly desirable.

ETYMOLOGY.—*Paralticus* is derived from the Latin prefix *par* (near) plus *Alticus*, a genus of Salariini, and is intended to indicate our belief that *Paralticus* is closely related to a group of genera that includes *Alticus*. Gender: masculine.

Paralticus amboinensis (Bleeker), new combination

FIGURE 57

Salarias amboinensis Bleeker, 1857a:67 [Amboina; holotype, RMNH 4781, largest of 3 specimens].

Salarias goesii Bleeker, 1859a:19 [Doreh, Nieuw-Guinea; holotype, RMNH 4659].

DESCRIPTION.—Dorsal fin. XIV,18 to 20 = 32 to 34 (32 in only 1 of 15 specimens examined for character); membrane between spinous and segmented-ray portions notched deeper than half length first segmented ray; membrane from posteriormost ray attaching to point ranging from on dorsal edge of caudal peduncle just in advance of caudal-fin base to dorsal edge of caudal fin just posterior to base. One specimen (ZMA 120.372) with apparently aberrant dorsal-fin formula XIII,20, notch depth noticeably < half length first segmented ray; radiograph indicates last spine not reduced in length, as in other specimens, and first 2 segmented rays supported by same
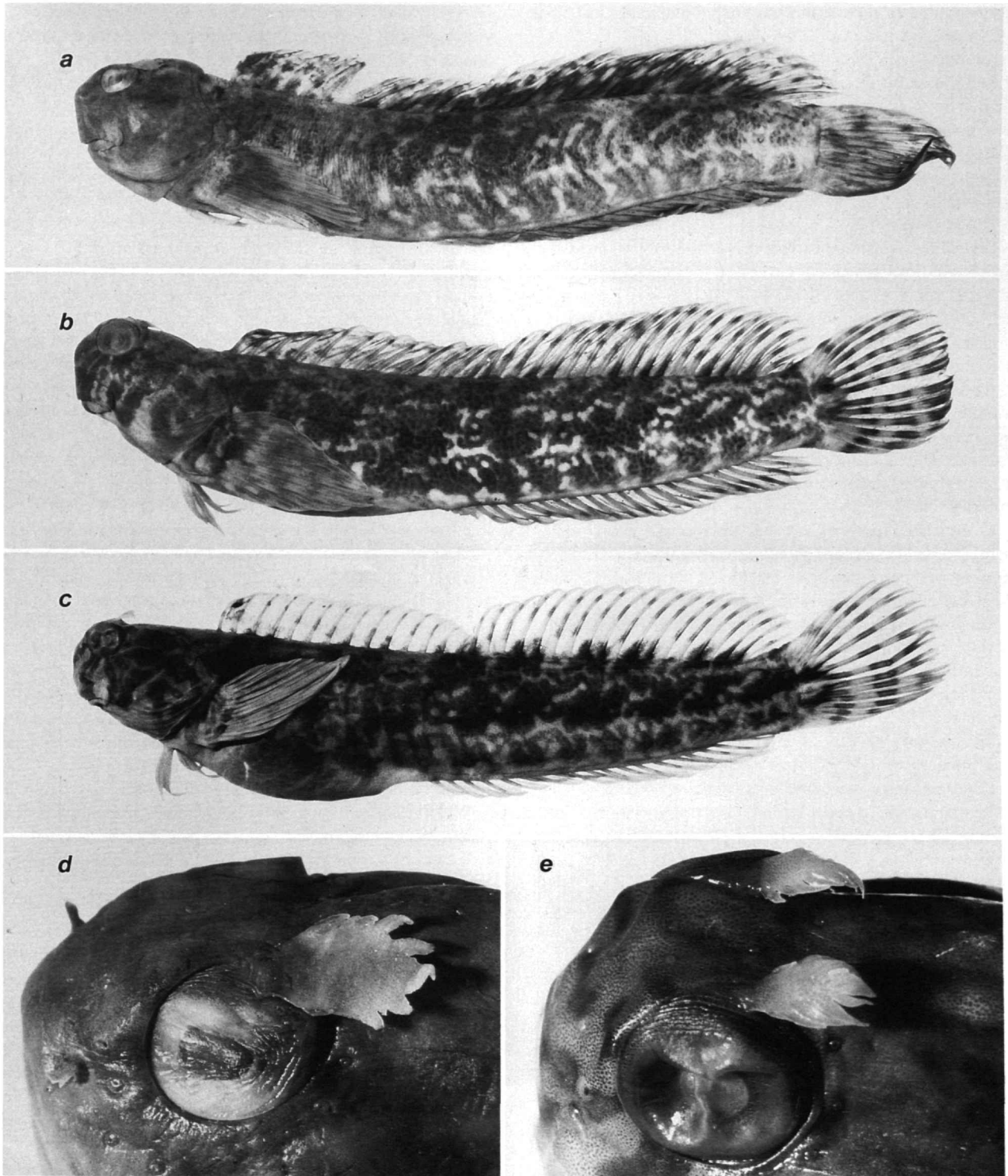
FIGURE 57.—*Paralticus amboinensis*, Indonesia: *a,d*, ZMA 120.373, male, ~86 mm SL, Ambon (right side reversed; damaged dorsal fin); *b*, ZMA 120.372, female, 88 mm SL, Saonek, Waigeo; *c,e* USNM 293299, female, Korido Bay, Soepiori, Biak; *d,e*, orbital cirri (note absence of cirrus on right eye in *d*) (photographs by T.B. Griswold).

pterygiophore in relationship normally comprising last spine and first segmented ray.

Anal fin. II,19 to 21 (only 1 of 15 specimens with 19); posterior element simple, never split to base; last ray bound by membrane to caudal peduncle for at least half length of ray. Skin covering anal-fin spines and anterior segmented rays in adult males not modified (only 4 males available).

Pectoral-fin rays 13 or 14 (13 only unilaterally, in only 1 specimen).

Pelvic-fin rays I,3.

Caudal fin. Dorsal procurrent rays 7 or 8, ventral procurrent rays 5 or 6, total procurrent rays 12 to 14, segmented rays 14.

Vertebrae. 11+26 to 28 = 37 to 39; posteriormost pleural rib on 11th from anteriormost centrum (= posteriormost precaudal centrum); posteriormost epineural on 15th to 18th from anteriormost centrum.

Cirri. Nape cirrus absent. Orbital cirrus (Figure 57d,e) usually broad, flap-like, with up to 12 secondary cirri on perimeter, much shorter than orbital diameter in females, about equal to orbital diameter in males. Nasal cirrus short, fine, usually simple, sometimes with ragged edge or few very fine branches.

Lateral line. Continuous canal anterodorsally with simple pores (no vertical pairs of pores), extending posteriorly to point between verticals from bases of 3rd and 6th dorsal-fin spines, then continuing posteriorly and posteroventrally as series of 6 to 12 short, disconnected, horizontally bi-pored canals (tubes) in skin; posteriormost tube in area between verticals from 8th and 14th dorsal-fin spines.

Mandibular pores 3 or 4 (3 only unilaterally, in only 1 specimen).

Five sensory pore positions between 1 and 5 o'clock on postorbital margin; all positions occupied by single pores.

Posterior canines well developed in males, absent in females.

Ventral margin of upper lip crenulate; dorsal margin of lower lip varying from weakly to strongly crenulate.

Both sexes lack blade-like crest on head; swollen, fleshy hump dorsally on head variably present in males.

Color pattern (in preservative; Figure 57a–c). Sexes apparently similar. Pattern complex, head dark, with irregular, pale and dark bands radiating ventrally from orbit onto lip, remainder of head with irregular, broad, dark patches separated by smaller, pale spaces; body with more or less uniformly positioned, irregular, dark markings, separated by narrower, pale areas; dark patches sometimes embracing numerous darker specks; dark patches faintly resembling about 5 to 7 pairs of bands, which extend onto dorsal fin basally; dorsal- and caudal-fin rays with regular rows of dark spots; membranes between first 2 or 3 dorsal-fin spines with conspicuous dark spot; vertical pair of dark spots basally on caudal fin; anal fin dusky or with faint spots on rays only; fleshy pectoral-fin base with irregular dark bands or spots, fin itself irregularly dusky, or dusky spotted; pelvic fin immaculate.

Color pattern of fresh specimen (based on color slide).

Generally dark, olive green with irregular, pale-yellow or white vermiculations segregating patches of green color embracing numerous dark specks.

Size. Largest male, 141 mm SL; largest female, 106 mm SL; smallest specimen available, female, 70 mm SL.

COMPARISONS AND RELATIONSHIPS.—See this section under the generic account of *Paralticus*.

Paralticus amboinensis differs from all *Blenniella* and *Istiblennius* species in lacking dorsal and ventral postcleithra (both present in the other genera) and in having modally 4 mandibular pores (versus modally 5 or 6); modally 5 pore positions between 1 and 5 o'clock on the postorbital margin (versus modally 6 or more in the other species); 14 segmented caudal-fin rays (versus strongly modally 13 in the other species); and in always having the last anal-fin ray bound by membrane to the caudal peduncle (versus having the ray free in at least 95% of the specimens of each of the other species). Among the *Istiblennius* species, it superficially resembles *I. colei* in having modally 14 dorsal-fin spines, but is readily distinguished from that species by many characters (two easily accessible characters: last anal-fin ray attached by membrane to caudal peduncle and lip margins crenulate in *amboinensis*; ray free from caudal peduncle and lip margins entire in *colei*).

The only species of *Istiblennius* that commonly exhibits 14 segmented caudal-fin rays is the Australian endemic *I. meleagris*. In *I. meleagris,* 14 rays occurs only in some specimens from localities west of Torres Strait. The normal condition for segmented caudal-fin rays in *I. meleagris,* and all other species of *Istiblennius* and *Blenniella*, is to have 7 rays in the dorsal half of the fin and 6 in the ventral half. When a 14th ray is present in *I. meleagris,* the additional ray is usually in the dorsal half of the fin, so that there are 8 dorsal and 6 ventral segmented rays. In *P. amboinensis*, there are 7 segmented rays in both the dorsal and ventral halves of the fin.

DISTRIBUTION (Figure 66).—Known only from northeastern Sabah east to western New Guinea at Biak Island and Geelvink (= Sarera or Cenderawasih) Bay, in depths as little as 0.3 m, often near mangroves.

NOMENCLATURAL DISCUSSION.—Bleeker (1857a) described *Salarias amboinensis* from a single specimen 127 mm TL. The Bleeker auction catalog (reproduced in Lamme, 1973) lists 3 specimens with this name, and 3 specimens, presumably including the holotype, are included in RMNH 4781. The largest specimen, which we believe is the holotype, is 126 mm TL; the other two specimens are 114 and 84 mm TL.

Bleeker (1859a) described *Salarias goesii* from a single specimen, 113 mm TL. He never reported obtaining additional specimens of *S. goesii*, and there is only 1 specimen identified as this species among his collections.

Bleeker believed that *S. goesii* was most closely related to his *S. amboinensis,* and was distinguished from the latter by having a slenderer body, a noncrenulate upper lip, 1 more ray in the dorsal fin, an unspotted anal fin, only 3 bands in the caudal fin (as opposed to 4), and other, unspecified, color markings on the

body. We have examined the holotype, which we measured as approximately 119 mm TL. A relatively recently collected specimen from Biak, not far from Doreh, is very similar to Bleeker's illustration of *Salarias amboinensis,* and other specimens from Ambon. We believe that the differences Bleeker noted are well within the range of intraspecific variation. There are few specimens available, however, so we cannot be certain that population variation does not exist.

The degree of development of the crenulae on the lips is variable, ranging from clearly present to debatably absent, but we did note a few crenulae on the upper lip of the holotype of *S. goesii.*

MATERIAL EXAMINED (all Indonesia).—Sabah: Bohaydulong Id, Bodgaya Is, off Semporna, WAM P.30412-005 (1 specimen). Indonesia: Sangi Id, ZMA 120.374 (1); Moluccas, NMW 73245 (1), Ambon, BPBM 19277 (3, including 1 cleared and stained), RMNH 4781 (3, including probable holotype of *Salarias amboinensis*), ZMUC P.75494 (1), ZMA 120.373 (1); Irian Jaya, Waigeo, ZMA 120.372 (1); Doreh, RMNH 4659 (probable holotype of *Salarias goesii*); Salawati, ANSP 81567 (1); Biak, MSNG 39681 (1), USNM 293299 (1); Geelvink Bay, MSNG 38359 (1).

Phylogenetic Analysis

Relationships among and within genera were analyzed using D. Swofford's PAUP version 3.1.1. The analyses are based on the data in Tables 43 to 45. Williams (1990) provided a hypothesis of the relationships among the blenniid tribes and recognized two subgroups (which we call the *Rhabdoblennius* and *Salarias* groups) within the tribe Salariini. All of the species we treat belong to genera in the *Salarias* group. With the exception of the *Cirripectes* clade (*Cirripectes, Exallias, Ophioblennius, Pereulixia, Scartichthys*), treated by Williams (1990), the generic interrelationships for the *Salarias* group have not been hypothesized cladistically. As the interrelationships remain unresolved for most of the genera in the *Salarias* group, we polarized the characters for our generic analysis using the 6 genera (*Atrosalarias, Salarias, Crossosalarias, Nannosalarias, Glyptoparus,* and *Dodekablennos*) of the *Salarias* group that we hypothesize as being excluded from the nested clades that include *Istiblennius, Blenniella,* and *Paralticus.* We present characters to support the monophyly of the nested clades that include *Istiblennius, Blenniella,* and *Paralticus,* but are unable to corroborate monophyly of these clades and the *Cirripectes* clade (*Stanulus, Pereulixia, Exallias, Cirripectes, Scartichthys,* and *Ophioblennius*) to the exclusion of the 6 outgroup genera (it is possible, therefore, that 1 or more of the ingroup clades is paraphyletic). We treated the 6 outgroup genera as an unresolved polytomy for the purposes of polarizing characters. The result is that 8 of our 29 characters have equivocal polarities. This situation illustrates the high degree of homoplasy for characters of these closely related taxa. For 4 of the 8 equivocal characters, only 1 of the 6

outgroup genera had a character state differing from that of the others, and 2 characters had 2 genera with a different condition. The remaining 2 characters were more variable, with 3 of the 6 genera having a variety of different states. For the other 21 characters, all 6 outgroup genera and the *Rhabdoblennius* group had the same state.

We found very few characters for use in phylogenetic analyses of these groups, particularly for intrageneric analyses. Most of the characters used in the analyses show variation within a taxon. We used the modal condition (which is usually strongly modal) for the purposes of coding characters. Some characters are bimodal for some species (different populations with different modes). For intrageneric analyses, we used the unordered and polymorphism options of PAUP for the bimodal characters and the results were the same in both analyses. Based on our previous work with blenniids, we believe these characters are phylogenetically meaningful despite their variability.

We ran the cladistic analysis 2 ways, first excluding the equivocal characters and second using the common condition among the 6 outgroup genera and the *Rhabdoblennius* group as plesiomorphic, which enabled us to polarize 6 of the 8 equivocal characters (we are well aware of the pitfalls of "common = plesiomorphic" assumption). All multistate characters were treated as unordered. Both ACCTRAN (accelerated transformation, which optimizes for character reversal) and DELTRAN (delayed transformation, which optimizes for independent derivation of characters) optimizations were used in the PAUP analyses. We discuss the results of these analyses.

Our goal was to hypothesize the phylogenetic relationships among *Blenniella, Istiblennius,* and *Paralticus* (species of all 3, we had previously placed in the genus *Istiblennius*), and to attempt resolution of the intrageneric relationships of *Blenniella* and *Istiblennius.* Character polarity for intrageneric analyses was based on the phylogeny hypothesized for the genera (Figure 58a). Unfortunately, the available characters for intrageneric analyses are predominantly homoplastic, and our hypothesized intergeneric relationships are highly tentative, making character polarity assessments difficult to corroborate. Our analyses of intergeneric relationships produced mixed results. The analysis excluding all equivocal characters yielded 17 trees of 38 steps and a strict consensus tree generated from these 17 trees resolves only 2 clades, the *Cirripectes* clade and an *Andamia-Alticus* sister group. All other generic relationships and the interrelationships of the 2 resolved clades are associated in an unresolved basal polytomy. Analysis of the data set using the 6 equivocal characters produced 1 tree for the intergeneric relationships (Figure 58a). We obtained 14 equally parsimonious trees, which were used to generate a strict consensus tree, for the species of *Istiblennius* (Figure 60), and 2 trees for the species of *Blenniella* (Figure 59a and b).

Table 43.—Character matrix for phylogenetic analysis of the _Salarias_ group of taxa. Missing or unknown character states are indicated by a question mark; asterisk indicates one or more of included species has different condition.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
																					Characters								
Scartichthys	0	1	0	1	1	1	1	1	1	0	1	2	0	0	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0
Ophioblennius	0	1	0	1	1	1	1	1	1	0	1	2	0	1	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0
Cirripectes	0	1	0	1	1	1	1	1	1	0	1	2	0	0*	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0
Exallias	0	1	0	1	1	1	1	1	1	0	1	2	0	1	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0
Pereulixia	0	1	0	?	1	1	0	1*	0	1	0	1	0	1	1	1	1	0	1	1	0	?	?	0	0	0	1	0	0
Stanulus	0	1	0	1	1	1	0	0	0	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Entomacrodus	0	1	2	1	2	1	1*	1	1	2	2	1	0	0	1*	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Blenniella	2	0	2	1	2	1	1*	2	1	0	0	0	0	0	1*	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Istiblennius	1	2	2	1	2	1	1*	2	1*	2	0	0	0	0	1*	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Andamia	3	1	0	?	0	2	1*	0	3	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	1	1	1	2	0
Alticus	1	2	0	?	0	1	1*	2	3*	0	0	2	0	0	0	0	0	0	0	0	0	?	?	0	1	1	1	2	0
Paralticus	0	0	1	?	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	1	1	0	0
Praealticus	1	2	1	?	2	1	1*	0	1	0	2	2	0	0	0	0	0	0	0	0	0	?	?	0	0*	1	1	1	0
Atrosalarias	0	0	0	?	0	0	1	2	2	1	0	0	0	0	1	0	0	0	0	0	0	?	?	0	1	0	1	0	0
Salarias	2	0	0	?	0	0	2	2	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	0	0	0	1	0	0
Dodekablennos	1	0	0	?	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0
Crossosalarias	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	0	0	0	1	0	0
Nannosalarias	0	0	0	?	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	?	?	0	0	0	0	0	0
Glyptoparus	1	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	0	0	0	0	0	0
Rhabdoblennius group	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 44.— Character matrix for <u>Blenniella</u>. Asterisk indicates some specimens have different condition.

	Characters												
Taxon	30	31	32	33	34	35	36	37	38	39	40	41	42
<u>cyanostigma</u>	0	0	0	1	0	1	1	1	0	2	0	1	0
<u>caudolinieta</u>	0	0	0	1	0	1	1	1	0	1	0	1*	0
<u>interrupta</u>	0	0	0	1	0	1	0	1	1	1	1*	1*	0
<u>leopardus</u>	0	0	0	1	0	1	0	1	1	1	1*	0	0
<u>bilitonensis</u>	0	0	0	1	1	0	0	1	0	1	1*	1	0
<u>paula</u>	0	1	1	0	1	0	0	1	0	2	0	0	1
<u>periophthalmus</u>	0	1	1	0	1*	0	0	1	0	2	0	0	1
<u>chrysospilos</u>	1	1	1	0	1*	0	0	0	0	0	0	0	0
<u>gibbifrons</u>	1	1	0	0	1	0	0	0	0	0	0	0	0

Table 45.— Character matrix for <u>Istiblennius</u>. Asterisk indicates some of specimens have different condition.

	Characters												
Taxon	43	44	45	46	47	48	49	50	51	52	53	54	55
<u>pox</u>	1	1	1	1	0	0	1	0	1	0	0	1	1
<u>lineatus</u>	1	1	1	1	0	0	0	0	1	0	0	0	1
<u>steindachneri</u>	1	1	1	1	0	0	0	0	1	0	0	1	1
<u>rivulatus</u>	1	1	0	1	0	1	1	1	1	0	1	0	1
<u>zebra</u>	0	0	1	1	1	0*	0	1	1	0	0	0	0
<u>bellus</u>	0	0	1	1	0	0*	0	1	1	0	0	0	0
<u>edentulus</u>	1	1	0	1	0*	1	0	1	1	0	0	0	0
<u>meleagris</u>	1	1	0*	1	1*	1	0	0	1	0	0	0	0
<u>dussumieri</u>	1	1	1	1	0	1	1	0	1	0	1	0	0
<u>muelleri</u>	1	0	1	1	1	0	1	1	1	0	0	0	0
<u>colei</u>	1	1	1	0	0	0*	0	0	0	0	0	0	0
<u>unicolor</u>	0	?	1	0	0	0	1	0	0	1	0	0	0
<u>spilotus</u>	0	1	1	1*	0	0	1	0	0	1	0	0	0
<u>flaviumbrinus</u>	1	1	1	1	0	0	1	0	0	0	0	0	0

INTERGENERIC RELATIONSHIPS

Character Analysis (numbers in parentheses following a trait indicate the symbol assigned to each character state; character numbers correspond to those in Table 43; characters with equivocal polarity are treated as unordered):

Crest on head (CHARACTER 1). A fleshy, blade-like crest on the nape of males is present (1) in many salariinin genera, but has been lost (0) in the *Cirripectes* clade and in *Paralticus*. This character is difficult to interpret as 3 of the 6 outgroup genera lack the crest. A blade-like crest may be present or absent (2) in *Blenniella*. *Andamia* has a distinctive bulbous crest (3) that is quite different from the typical blade-like crest. The variable presence or absence of a crest in outgroup genera results in an equivocal polarization. This character could not be polarized.

Pelvic-fin rays (CHARACTER 2). Springer (1968:61), in a discussion of the pelvic fin of blenniids, concluded that 3 rays is the primitive blennioid condition and the addition of a fourth ray is derived. Presence of 3 rays (0) is considered plesiomorphic and 4 rays (1) is the derived condition at the level of our analysis. *Istiblennius*, *Alticus*, and *Praealticus* may have 3 or 4 rays (2).

Ceratohyal process (CHARACTER 3). Outgroup genera have a smooth anterodorsal margin of the ceratohyal (0). *Paralticus* and *Praealticus* have a bony hook-like process (Figure 1*b*) arching anteriorly toward the dorsal hypohyal, and merging with the cartilage at the cera-tohyal-hypohyal joint (1). The hook-like process may be present or absent within a genus (2), but when present it occurs in most of the species in the genus. The process is often broken or absent on 1 or both sides of a specimen, suggesting that it is susceptible to loss and might appear absent in certain specimens that lose it through damage early in development (it is also possible that there is unossified connective tissue in place of the bone in these specimens).

Canine tooth present midlaterally on dentary of postlarvae (CHARACTER 4). Postlarvae with these (and other similar) teeth have been termed ophioblennius larvae or postlavae in the literature. A distinctive, laterally recurved canine is present on the dentary of postlarvae (1) of at least some species of *Blenniella*, *Istiblennius*, and the *Cirripectes* clade (known for all but one genus, *Pereulixia*, of the clade). The known postlarvae of all other genera of Salariini appear to lack a midlateral canine (0). As the larval development is unknown for species of most of the other genera, including *Paralticus*, in the Salariini, this character is used with caution, but we believe it unlikely that the postlarvae of any species in the other genera of Salariini have a similar canine in the lower jaw. (See also characters 21 and 22 below.)

Terminal anal-fin ray split through base (CHARACTER 5). The 6 outgroup genera and the *Rhabdoblennius* group have an unsplit terminal anal-fin ray (0). The split condition (1) is characteristic of the *Cirripectes* group. Both the split and unsplit conditions (2) are found in *Praealticus*, *Istiblennius*, and *Blenniella*.

Terminal anal-fin ray bound to caudal peduncle by membrane (CHARACTER 6). All of the outgroup genera, except *Dodekablennos*, have the ray bound to the peduncle (0). The last ray is free from the peduncle (1) in *Blenniella*, *Istiblennius*, *Entomacrodus*, *Alticus*, *Praealticus*, and the *Cirripectes* group, although it may be bound in a small percentage of specimens of any species. The last ray is bound to the peduncle in *Paralticus*. The last ray may be free or bound (2) in *Andamia*. The polarity is equivocal and the character is treated as unordered.

Upper-lip crenulae (CHARACTER 7). The absence (0) or presence (1) of crenulae on the upper lip is highly variable. Many of the genera that typically have lip crenulae will contain one or more species that lack lip crenulae. Crenulae may be present or absent (2) in *Salarias*. The variation exhibited results in this character being of equivocal polarity at the generic level, although the lack of crenulae in 4 of the 6 outgroup genera and in the *Rhabdoblennius* group indicate that the presence of upper-lip crenulae is derived for this group.

Last pleural ribs borne on 1 or more caudal vertebral centra (CHARACTER 8). There is considerable variation in this character. Although 3 of the outgroup genera lack pleural ribs on caudal vertebrae (0), *Dodekablennos* has them (1) and *Salarias* and *Atrosalarias* may have them or lack them (2). Some specimens of *Pereulixia* lack them, but they are typically present. The polarity of this character is equivocal and it could not be polarized.

Dorsal-fin spines (CHARACTER 9). All of the outgroup genera, except *Atrosalarias*, have modally 12 spines (0); *Atrosalarias* has 10 or 11 spines (2). Most other blenniids have 12 or fewer spines. The presence of 13 spines (1) or 14 or more spines (3) is considered derived for each condition. This character may vary among the species within a genus (e.g. *Alticus*, *Istiblennius*), but rarely more than 1 or 2 species within a genus have a count different from that of the other species. This character is treated as unordered.

Anal-fin rugosities (CHARACTER 10). Outgroup salarii-nin genera, except *Atrosalarias*, lack fleshy rugose swellings at the tips of male anal-fin spines (0). The presence of well-developed rugosities at the tips of male anal-fin spines (1) is found in the *Cirripectes* group as well as in the tribe Parablenniini (considered to be an independent derivation). *Entomacrodus* and *Istiblennius* may have slightly rugose tissue on the anal-fin spines and also on the distal half or less of the anterior segmented

anal-fin rays.

Sixth branchiostegal ray (CHARACTER 11). Williams (1990, fig. 7) discussed this character. The proximal portion of the sixth branchiostegal ray that overlaps the ceratohyals can be equal in length to that of the fifth and preceding rays (0), slightly elongated (1), or greatly elongated and extending anterodorsally over the proximal end of the fifth branchiostegal ray (2) as occurs in the *Cirripectes* group and in *Praealticus*.

Vomerine teeth (CHARACTER 12). Vomerine teeth may be absent (0), present (1), or present or absent (2). The vomerine teeth are present in *Entomacrodus* and *Nannosalarias*. The vomerine teeth may be present or absent in certain species of *Stanulus*, *Alticus*, and *Praealticus*.

Infrapharyngobranchial 3 (CHARACTER 13). The outgroup genera have a well-developed bony flange with no, or only a tiny foramen (Williams, 1990, fig. 6) (0). The presence of a large foramen in the middle of the flange (1) is characteristic of *Stanulus*, and the *Cirripectes*-group genera.

Scale-like flaps covering lateral-line pores (CHARACTER 14). The plesiomorphic condition is to lack these flaps (0). Scale-like flaps are present (1) in *Stanulus* and *Pereulixia*, and in 3 of the 22 *Cirripectes* species.

Nape cirri (CHARACTER 15). The presence (1) or absence (0) of a single cirrus on either side of the nape has an equivocal polarization. Among the outgroup genera, the cirrus is lacking in *Dodekablennos*, but present in the others, suggesting that the loss of the cirri may be derived for this group.

Row of nape cirri (CHARACTER 16). The presence of a row of cirri (1) across the nape in the *Cirripectes* group is considered derived as opposed to the lack of a row of cirri (0). The presence (1) or absence (0) of cirri on the nape was evaluated independently as character 15. Williams (1990) treated the cirri patterns in detail.

Nape cirri in 2 separate groups (ChARACTER 17). Williams (1990:18) described the widely separated groups of cirri (1) as a secondary specialization for *Ophioblennius* and *Scartichthys*, versus closely spaced or continuous groups of cirri (0, character 16).

Symphysial premaxillary spur (CHARACTER 18). The premaxillary spur was discussed by Williams (1990:14). The presence of the spur (1) is considered to be derived.

Elongate lacrimal (CHARACTER 19). The ventral elongation of the lacrimal discussed by Williams (1990:15) is traversed over most of its length by a ventral branch of the infraorbital sensory canal (1). The plesiomorphic condition has the sensory canal terminating near the dorsal edge of the lacrimal (0).

Fourth epibranchial (CHARACTER 20). Williams (1990:8-9) discussed the presence of 2 dorsally directed processes (1) on the fourth epibranchial as being derived over the presence of 1 process or none (0).

Dentition of ophioblennius-stage postlarvae (CHARACTERS 21, 22). Character 21: the presence of large premaxillary symphysial canines (1) or their absence (0). Character 22: the presence of large dentary symphyseal canines (1) or their absence (0). The dentary symphysial canines are present in all ophioblennius-stage postlarvae. Ophioblennius-stage post larvae are unknown for many genera, but the presence of the well-developed canines is considered derived.

Maxillary process (CHARACTER 23). Williams (1990:17-18) discussed the distinctive process (1) on the posteromedial face of each maxilla. A smooth posterior margin (0) of the maxillary is the typical blenniid condition.

Male genital papilla (CHARACTER 24). The presence of 1 or 2 filaments associated with the gonopore (1) is derived over their absence (0) (Williams, 1990:19).

Branched caudal-fin rays (CHARACTER 25). The lack of branched caudal-fin rays (1) is considered derived over the presence of branched rays (0).

Postcleithra (CHARACTER 26). The reduction or loss of postcleithra (1) is derived compared to the presence of well-developed postcleithra (0). *Paralticus* has lost both postcleithra. *Alticus*, *Andamia*, and *Praealticus* may either lack postcleithra or have them reduced in size and not overlapping.

Number of premaxillary teeth (CHARACTER 27). The presence in adults of more than 100 premaxillary teeth (1) is the derived condition. The other Salariini have 17-80 teeth (0).

Caudal-fin shape (CHARACTER 28). The ventralmost caudal-fin rays have been reduced in length, giving the ventral edge of the fin a slightly (1) or strongly (2) "clipped" appearance. The latter condition is known only for *Alticus*, *Andamia*, and *Praealticus*. All other Salariini have the ventral caudal-fin rays similar in length to, or longer than, the corresponding rays on the dorsal half (0) of the fin.

Caudal peduncle spots (CHARACTER 29). Females of all but 1 species of *Blenniella* and 8 of 14 species of *Istiblennius* typically have distinctive small, black spots on the caudal peduncle (1). Females of other Salariini lack peduncle spots (0). The presence of the distinctive spots is considered derived.

Character analysis. An analysis utilizing all polarized characters (Table 43; characters 1 and 8 excluded) produced 1 tree with 53 steps and a consistency index of 0.667 (Figure 58a). Analysis of the generic relationships excluding all characters of equivocal polarity yields 17 trees each with 38 steps. A strict consensus tree generated from these 17 trees is shown in Figure 58b. Both trees resolve the *Cirripectes* group and the *Alticus-Andamia* sister group as monophyletic clades, but figure 58b provides no other resolution, and all of the

NODES	SUPPORTING CHARACTERS
1	1, 2, 4, 5, 6, 27
2	3, 9, 7, 11, 5
3	1, 2,
4	8, 29
5	3, 15, 26
6	5, 9
7	2, 3, 25, 28
8 to 12	see Williams (1990)
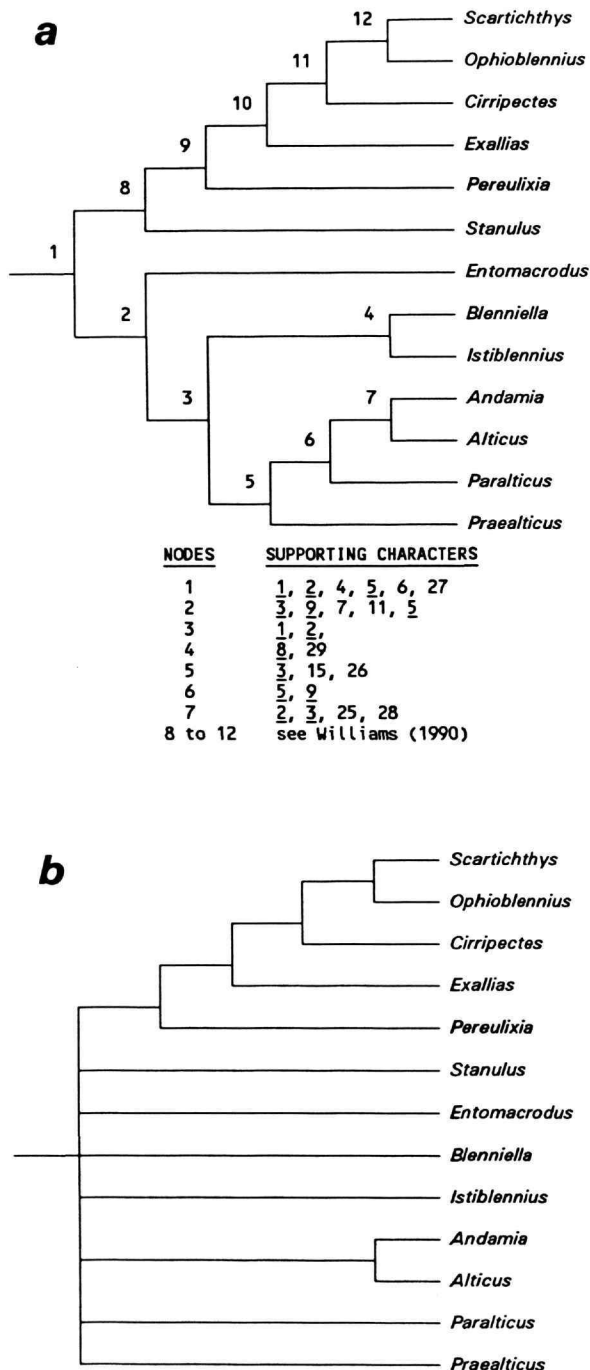
FIGURE 58.—Phylogenetic hypotheses of intergeneric relationships: *a*, cladogram based on polarized characters, characters supporting each node listed, homoplastic characters underlined; *b*, consensus tree resulting from analysis excluding equivocal characters.

groups are associated in an unresolved basal polytomy. The relationships among the *Stanulus*-group genera (nodes 8–12 in Figure 58*a*) have been discussed by Williams (1990) and are not treated here. The only difference in character changes under the DELTRAN and ACCTRAN optimizations was in 2 equally parsimonious interpretations of the split anal-fin ray character (character 5). The split condition develops at node 1 if reversals are optimized, whereas the split condition develops at node 8 if independent derivations are optimized. In both optimizations, the split condition may be present or absent at node 2 and is lost at node 6.

It is uninformative to discuss the results indicated by the tree (Figure 58*b*) generated when all equivocal characters are deleted. We, therefore, discuss only the results indicated by the tree (Figure 53*a*) generated when all characters are included. Although the latter tree can be considered as a possible relationship scenario, we recognize the high degree of homoplasy in our characters, and expect that the tree will change when additional characters are found.

Node 1. Node 1 is supported by an increase in the number of pelvic-fin rays from 3 to 4 (character 2), and the presence of a midlateral canine tooth (character 4) in the lower jaw of ophioblennius-stage postlarvae (at least for those taxa known to have this stage; none of the node-5 genera are known to have ophioblennius-stage postlarvae). As mentioned above, the development of the split anal-fin ray (character 5) is placed at this node if reversals are optimized. Among the equivocal characters at node 1, the crest on the head (character 1) is lost, the anal fin loses its membranous attachment to the caudal peduncle (character 6, secondarily derived in *Paralticus* and some *Andamia*), and the number of premaxillary teeth increases to over 100 (character 27).

Node 2. The ceratohyal hook (character 3) may be present or absent at this level. The variable genera include only *Entomacrodus, Istiblennius,* and *Blenniella,* each of which includes species with or without the hook. The split anal-fin ray (character 5) may also be present or absent in these same genera and *Praealticus.* Node 2 is supported by an increase in the number of dorsal-fin spines (character 9) from 12 to 13 or more. One equivocal character, the development of lip crenulae (character 7) also supports node 2. Some of the species of *Entomacrodus* have independently developed an expanded proximal portion of the sixth branchiostegal ray (character 11), although other conspecifics have not.

Node 3. There is a partial reversal in the number of pelvic-fin rays (character 2) at this node, with some of the genera having either 3 or 4 rays. The pelvic-fin ray character is weak, exhibiting a high level of homoplasy. The crest on the head (character 1) is gained secondarily at this node, but it may be present or absent in *Blenniella* and is lost in *Paralticus.*

Node 4. The sister-group relationship of *Blenniella* and *Istiblennius* is supported by the presence of small spots on the caudal peduncle of females (character 29). *Blenniella* has secondarily reverted to 3 pelvic-fin rays (character 2). As the

peduncle spots are lacking in 6 of the 14 *Istiblennius* species, this character is considered to provide weak support at most for the sister-group relationship. If this character is removed, nodes 2, 3, 4, 5, and 8 collapse to node 1, yielding a large basal polytomy. Although we provisionally accept character 29 as valid for the node-4 genera, we recognize its weakness. The last pleural rib borne on the first caudal vertebral centrum (character 8), an equivocal character, may be present or absent at node 4.

Node 5. Node 5 is characterized by a reduction in size or loss of the postcleithra (character 26). The reduction or loss of postcleithra is found only in the node-5 genera among the Salariini. Node 5 is weakly supported by the presence of a ceratohyal hook (character 3) and by the loss of nape cirri (character 15), but both of these characters are homoplastic. The secondary loss of nape cirri (character 15), an equivocal character, is placed at node 5. *Praealticus* has secondarily derived an expanded sixth branchiostegal (character 11), vomerine teeth (character 12), and a slightly "clipped" caudal fin (character 28). The node-5 genera and *Pereulixia* are the only node-1 genera not known to have an ophioblennius-stage postlarva. The absence of an ophioblennius-stage postlarva is inferred to be a secondary loss, and provides support for the monophyly of the node 5-group (we assume the loss is independent in *Pereulixia*).

Node 6. The presence of 14 or more dorsal-fin spines (character 9) supports monophyly for the node-6 group. *Paralticus* has independently lost the crest on the head (character 1) and has lost a pelvic-fin ray (character 2). *Paralticus* also has the anal fin membranously bound to the caudal peduncle (character 6). The node-6 group has secondarily lost the split anal-fin ray (character 5).

Node 7. The sister group relationship between *Alticus* and *Andamia* is supported by the secondary loss of the ceratohyal hook (character 3), by having all caudal-fin rays simple (character 25), and by the strongly "clipped" shape of the ventral margin of the caudal fin (character 28). *Andamia* and most *Alticus* have 4 pelvic-fin rays (character 2), but *Alticus simplicirrus* and a group of species related to *A. kirkii* have only 3.

Nodes 8–12. As explained above, these nodes were discussed by Williams (1990).

Blenniella INTRARELATIONSHIPS

Character analysis for *Blenniella* (numbers in parentheses indicate the symbol assigned to each character state; character numbers follow numbering in Table 44):

Lateral line (CHARACTER 30). Anteriorly, the lateral line may be formed by pores along a straight tube (0) or there may be dorsal and ventral branches with terminal pores extending from the tube (1). The branched lateral line is found only in 2 species among the node 2 genera

and is considered derived.

Precaudal vertebrae (CHARACTER 31). The number of precaudal vertebrae is 10 for most of the Salariini, but several genera have 11 (0). The presence of 12 precaudal vertebrae is considered derived in the Salariini (1). Some *Ecsenius pulcher* specimens have as many as 12 precaudal vertebrae, but the modal value for the species is 11.

Upper lip crenulae (CHARACTER 32). As mentioned in the discussion of generic relationships, crenulation of the upper lip is variable. Related genera in the node 1 group typically have upper lip crenulae (0). At the present level of analysis, there has been a character reversal and the lack of upper lip crenulae (1) is considered to be the derived condition for *Blenniella*.

Posterior attachment of dorsal fin (CHARACTER 33). The membranous attachment of the dorsal fin to the caudal peduncle in advance of the caudal-fin base (0) is typical of closely related genera. The attachment of the dorsal fin to the uppermost caudal-fin rays posterior to the caudal-fin base (1) is considered derived at node 4 of Figure 58.

Caudal-peduncle color pattern of females (CHARACTER 34). Female *Blenniella* may have well-developed black spots (0) on the caudal peduncle, or the spots may be reduced or absent (1). *Blenniella bilitonensis* lacks the black spots. We consider the absence of black spots to be a character reversal at this level and, thus, derived.

Dark dashes or lines anteriorly on body of females (CHARACTER 35). Females of related genera typically have a barred or mottled (0) color pattern on the body. The development of distinctive dark dashes or lines arranged in more or less regular rows, at least anteriorly, on the body (1) is considered to be a derived pattern.

Dark stripes on females (CHARACTER 36). A further derivation of the dashed pattern (0) is for the dashes to form distinctive dark (essentially black) stripes (1) on the body. The distinctive dark stripes on females of *Blenniella cyanostigma* and *B. caudolineata* are considered derived for the genus.

Vertical pairs of ocelli on body (CHARACTER 37). Males of related genera lack vertical pairs of ocelli on the body (0). The presence of vertical pairs of ocelli (white or blue in life) on the body (1) of males is a derived condition.

Elongate body ocelli (CHARACTER 38). Body ocelli of males are typically rounded or oblate (0). A derived condition is found in *Blenniella* males (except *B. gibbifrons* and *B. chrysospilos*, which lack ocelli) wherein the most slender body ocelli are up to 4 times as long as deep (1).

Spot on opercle (CHARACTER 39). Males may either lack (0) or possess (1) a dark spot on the dorsal portion of the opercle. In some species, the males may have the spot

NODES	SUPPORTING CHARACTERS
13	<u>34</u>, <u>37</u>
14	31, 32, <u>34</u>
15	<u>37</u>, <u>39</u>, 42
16	30, <u>37</u>
17	33, <u>37</u>, <u>39</u>, <u>40</u>, <u>41</u>
18	<u>34</u>, 35
19	38, <u>40</u>
20	36, <u>40</u>

NODES	SUPPORTING CHARACTERS
13	<u>37</u>
14	31, 32, <u>34</u>
15	<u>37</u>, <u>39</u>, <u>42</u>
16	30, <u>37</u>
17	33, <u>37</u>, <u>39</u>, <u>40</u>, <u>41</u>
18	40
19	<u>35</u>, 38
20	<u>35</u>, 36
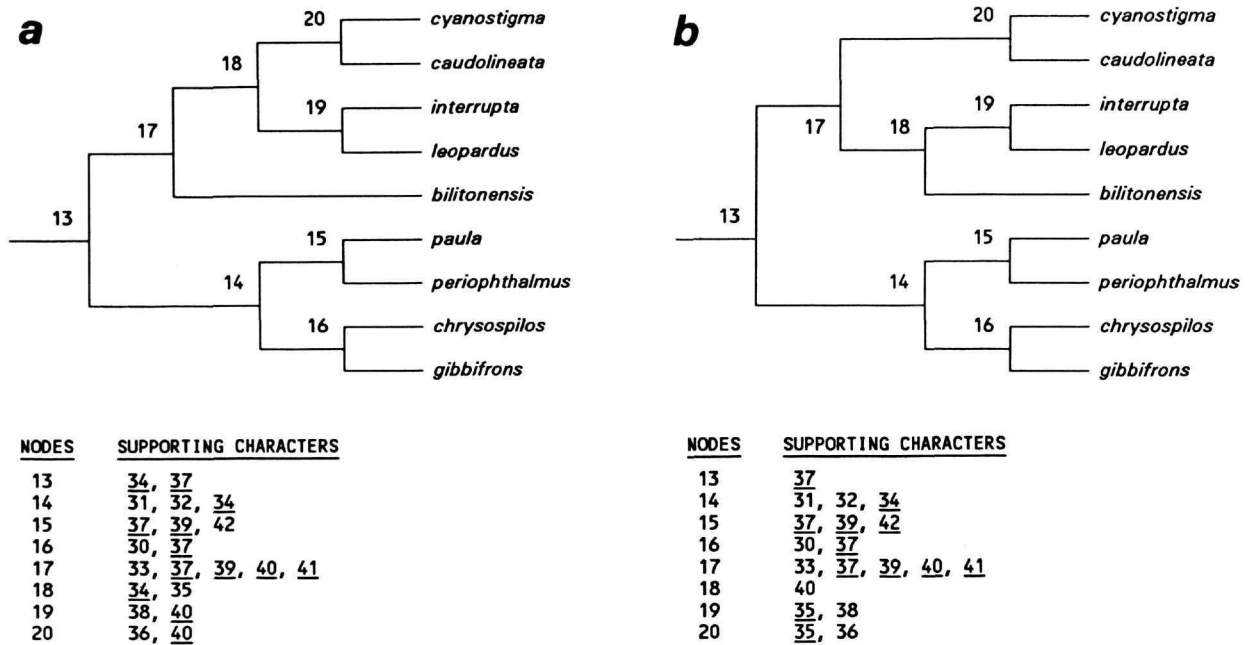
FIGURE 59.—Two equally parsimonious phylogenetic hypotheses (cladograms) of the intrageneric relationships of *Blenniella*. Supporting characters listed below each cladogram, homoplastic characters underlined.

variably present or absent (2). Males of related genera lack the spot, so its presence is considered to be derived.

Dark spot above opercle (CHARACTER 40). Males may have (1) or lack (0) a dark spot on the side of the head immediately above the opercle. We consider the presence of the spot to be derived.

Ceratohyal process (CHARACTER 41). The ceratohyal process was discussed as character 3 in the generic analysis. The hook is absent (0) or present (1) in *Blenniella*. This character is difficult to polarize because of the high level of homoplasy, but we tentatively consider the secondary loss of the process to be plesiomorphic at node 4 based on the hypothesized generic phylogeny.

Dorsal-fin coloration (CHARACTER 42). The dorsal fin is variably pale, mottled or spotted (0) in *Blenniella*, but only *B. periophthalmus* and *B. paula* have a bicolored pattern with the distal half pale and the basal half darkly mottled (1). The bicolored pattern is considered derived.

Phylogenetic analysis. The 13 characters for the 9 species of *Blenniella* yield 2 trees (Figure 59a,b) of 21 steps with a consistency index = 0.714. The 2 trees differ at node 18, with 1 tree having the node-19 group as the sister group to the node-20 group (Figure 59a), and the other tree placing the node-19 group as the sister of *B. bilitonensis* (Figure 59b).

One of the 13 characters employed in the analysis may be interpreted in 2 equally parsimonious patterns on both trees in Figure 59, and 3 characters may be interpreted in 2 equally parsimonious patterns on only 1 of the 2 trees. Dark lines or dashes anteriorly on the body of females (character 35), loss of caudal-peduncle spots (character 34), and the character of males having a dark spot just dorsal to the opercle (character 40) appear at different nodes on 1 of the 2 trees in Figure 59 depending on whether they are optimized for reversal or parallelism. The presence of vertically paired ocelli (character 37), appears at different nodes on both trees in Figure 59. Character 37 can either develop at node 13 and be lost at node 16 (Figure 59a,b), or it can be derived independently at nodes 15 and 17. Character 34 can either appear at node 13 and be reversed at node 18 (Figure 59a), or it can appear independently at node 14 and in *B. bilitonensis* (Figure 59a,b). Character 40 can be derived at node 17 and then lost at node 20, or be independently derived at node 19 and for *B. bilitonensis* (both in Figure 59a). Dark lines or dashes anteriorly on the body of females (character 35) appears at different nodes only on the tree in Figure 59b. Depending on type of character optimization, character 35 can either be derived at node 17 and lost in *B. bilitonensis*, or independently derived at node 19 and node 20.

Node 13. In both trees, vertically paired ocelli (character 37) develop at node 13 and are subsequently lost at node 16 when reversals are optimized. The tree in figure 59a also has

the loss of caudal-peduncle spots (character 34) at node 13 when reversals are optimized (i.e., the ACCTRAN analysis for Figure 59a; see also node 14).

Node 14. Node 14 is supported in both trees by the presence of 12 precaudal vertebrae (character 31) and by lacking upper-lip crenulae (character 32). The loss of caudal-peduncle spots (character 34) appears at node 14 and independently in *B. bilitonensis* in the ACCTRAN analysis for Figure 59b and in both DELTRAN analyses.

Node 15. For both trees, the development of a distinctive dorsal-fin color pattern (character 42) characterizes the sister-group relationship between *Blenniella periophthalmus* and *B. paula;* the males may have or lack a dark spot on the opercle (character 39); and, if the presence of vertically paired ocelli (character 37) is optimized for independent derivation, the gain of the paired ocelli is derived at node 15.

Node 16. For both trees, the presence of dorsal and ventral branches from the lateral line (character 30) characterizes *Blenniella gibbifrons* and *B. chrysospilos*. If the paired ocelli in males (character 37) are optimized for reversals, the loss of the ocelli is derived at node 16.

Node 17. Node 17 is supported by several characters in both optimizations of both trees: males may have the dorsal-fin membrane attached well out on the caudal fin (character 33), males with a dark spot dorsally on opercle (character 39), and the secondary development of a well-developed ceratohyal process (character 41; subsequently lost in *Blenniella leopardus*). If optimized for reversal, character 40 (males with dark spot just dorsal to opercle) supports node 17 in the tree in Figure 59a, but in the tree in Figure 59b, character 35 (presence of dark lines on dashes on the body of females) supports node 17. If optimized for independent derivation, character 37 (vertically paired ocelli in males) is derived at node 17 in both trees.

Node 18. In the tree in Figure 59a, node 18 joins nodes 19 and 20 and is supported by the presence of dark lines or dashes anteriorly on the body of females (character 35) and, if reversals are optimized, by the secondary gain of dark spots on the caudal peduncle of females (character 34). In the tree in Figure 59b, node 18 joins node 19 and *B. bilitonensis* and is supported by character 40 (males with dark spot just dorsal to opercle).

Node 19. In both optimizations of both trees, males of node 19 (*Blenniella interrupta* and *B. leopardus*) have the slenderest body ocelli, which are up to 4 times as long as they are deep (character 38). If optimized for independent derivation, character 40 will support node 19 in tree 59a and character 35 supports it in tree 59b.

Node 20. *Blenniella cyanostigma* and *B. caudolineata* females have well-developed, narrow, dark stripes on the body anteriorly (character 36). *Blenniella cyanostigma* males may have the dark opercle spot (character 39) present or absent. In tree 59a, optimizing for reversals places character 40 at this node as a secondary loss. In tree 59b, character 35 is independently derived at node 20 when optimized for independent derivations.

Istiblennius INTRARELATIONSHIPS

Character analysis for *Istiblennius* (numbers in parentheses indicate the symbol assigned to each character state; character numbering corresponds with numbered characters in Table 45):

Lower-lip crenulae (CHARACTER 43). The outgroup genera and most of the node-1 genera typically lack crenulae on the lower lip (0). Lower-lip crenulae (1) are present in some species of *Cirripectes* and *Istiblennius*. At this level of analysis, the presence of lower-lip crenulae is considered to be derived within *Istiblennius*.

Ceratohyal process (CHARACTER 44). The ceratohyal process was discussed above in the generic analysis and for *Blenniella*. The hook is either absent (1) or present (0) in *Istiblennius*. The process is present in all *Istiblennius* species except *I. rivulatus, I. muelleri,* and *I. bellus*. We tentatively consider the loss of the process to be secondary and, thus, derived for this group of 3 species of *Istiblennius*.

Nape cirri (CHARACTER 45). The outgroup genera typically have nape cirri (0). The loss (1) of nape cirri in a few species of *Istiblennius* is considered to be derived.

Pelvic-fin rays (CHARACTER 46). The species of *Istiblennius* have either 3 (1) or 4 (0) segmented pelvic-fin rays. As the immediate outgroups have 4 rays, the presence of 3 rays is considered a secondary loss and, thus, derived within *Istiblennius*.

Blade-like crest on female (CHARACTER 47). Females of most Salariini lack (0) a crest on the head. The presence (1) of a crest on the head of females is derived within *Istiblennius*, based on the hypothesized phylogeny for the node-1 group.

Infraorbital pores (CHARACTER 48). Many of the closely related genera have at least one infraorbital pore position with a pair of pores (1), but others have a single pore (0) at each position. Outgroup analysis based on the node 1 group indicates that the paired-pores state is derived within *Istiblennius*.

Mandibular sensory pores (CHARACTER 49). The species of *Istiblennius* have either 5 (1) or 6 (0) pores on each side. The presence of 5 pores is derived within *Istiblennius*.

Supraorbital cirrus (CHARACTER 50). The supraorbital cirrus may be branched (0) or simple (1). The simple cirrus is derived within *Istiblennius*.

Posterior attachment of dorsal fin (CHARACTER 51). As discussed for *Blenniella*, the membranous attachment of the dorsal fin to the caudal peduncle in advance of the caudal-fin base (0) is typical of closely related genera.

NODES	SUPPORTING CHARACTERS
21	45
22	46
23	49
24	43, 52
25	51
26	44, 47, 50
27	45, 48
28	55
29	54
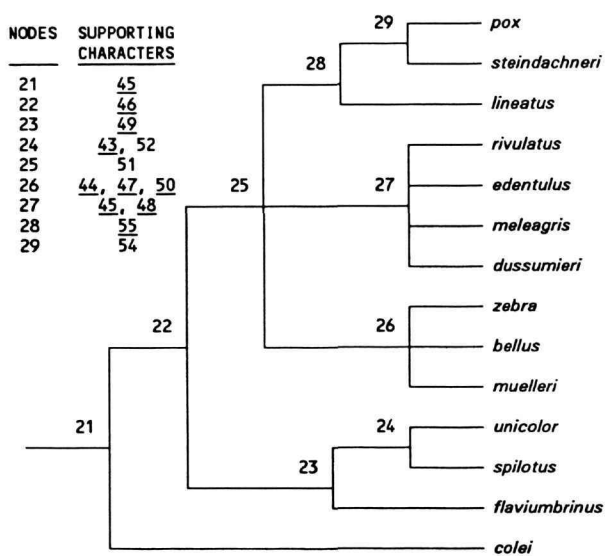
FIGURE 60.—Phylogenetic hypothesis (cladogram) of the intrageneric relationships of *Istiblennius*. Supporting characters listed, homoplastic characters underlined.

The attachment of the dorsal fin to the uppermost caudal-fin rays posterior to the caudal-fin base (1) is considered derived within *Istiblennius*.

Caudal-fin color pattern of males (CHARACTER 52). Males typically have a more or less evenly pigmented caudal fin (0). The presence of columns of dark spots (1) on the fin is derived within *Istiblennius*.

Dorsal-fin spot (CHARACTER 53). Males typically lack a spot anteriorly in the spinous dorsal fin (0). The presence of a dark spot (1) at the anterior end of the dorsal fin of males is derived within *Istiblennius*.

Color pattern of male crest (CHARACTER 54). Males typically have uniformly pigmented crests (0), but the crest may have dark spots (1). The presence of dark spots on the crest is derived within *Istiblennius*. *Istiblennius colei* is unusual in that the crest color is variable, specimens may have it uniformly pigmented, mottled with grainy reticulations, or with fine, small spots (coded as uniform for this species as the variable pattern would otherwise have to be treated as an autapomorphy).

Male body color (CHARACTER 55). Body color of males is variably patterned with bars, mottled, or uniformly colored (0). The presence of dark stripes on the body (1) is considered derived within *Istiblennius*.

Phylogenetic analysis. The 13 characters yield 14 equally parsimonious trees, each with 25 steps and a consistency index of 0.520. A strict consensus analysis of the 14 trees results in

the tree illustrated in Figure 60. The characters were mapped onto the consensus tree to show how the nodes are supported and the results are discussed below for each of the nodes in Figure 60. The relationships among the species of *Istiblennius* remain poorly resolved. There is a high degree of homoplasy for the characters used in the analysis and the results should be considered merely as the first step in resolving the intrageneric relationships of *Istiblennius*.

Node 21. The loss of nape cirri (character 45) occurs at node 21. Cirri are subsequently regained at node 27 and then lost again in *I. dussumieri*. As the position of *I. dussumieri* is not resolved, an alternative scenario for character 45 could exclude *I. dussumieri* from the clade and have character 45 appear at a node linking *I. rivulatus*, *I. edentulus*, and *I. rivulatus*.

Node 22. Node 22 is supported by the loss of a pelvic-fin ray (character 46) to yield 3 rays. *Istiblennius unicolor* has secondarily gained a fourth ray; *I. spilotus* may have 3 or 4 rays.

Node 23. One character, the mandibular sensory pores (character 49), supports node 23. The node-23 group has only 5 pore positions on each side. *Istiblennius muelleri* and *I. pox* have independently lost a pore and each of them has 5.

Node 24. *Istiblennius unicolor* and *I. spilotus* have a crenulate lower lip (character 43) and columns of dark spots on the caudal fin of adult males (character 52). A crenulate lower lip is independently developed in *I. zebra* and *I. bellus*.

Node 25. The node-25 group may have the dorsal fin of males attached to the upper edge of the caudal fin well posterior to the caudal-fin base (character 51). Node 25 comprises an unresolved trichotomy of the node-26, -27, and -28 groups.

Node 26. The presence of a simple supraorbital cirrus (character 50) is found in *Istiblennius zebra*, *I. bellus*, and *I. muelleri*, and is secondarily derived in *I. rivulatus* and *I. edentulus*. The node-26 trichotomy is also supported by the secondary loss of the hook-like ceratohyal process (character 44) and the development of a crest on females (character 47). The female crest has been lost in *I. bellus*. A crest on females can be present or absent in *I. edentulus* and *I. meleagris*.

Node 27. The node-27 polytomy is supported by a secondary gain of nape cirri (character 45) in all node-27 species except *I. dussumieri*. Node 27 is also supported by the presence of paired pores in the infraorbital series (character 48); *I. zebra* and *I. bellus* may have paired or simple pores (*I. colei* may also have paired pores).

Node 28. The node-28 group has dark stripes on the body of males (character 55). The dark stripes are independently developed in *I. rivulatus*.

Node 29. Dark spots on the crest of males (character 54) characterizes *I. pox* and *I. steindachneri*. No other *Istiblennius* species have similar spots.

Biogeographic Discussion

Paralticus

Of the 3 genera, the monotypic *Paralticus* appears to have the most restricted distribution (Figure 66): northern and eastern Indonesia. Its distribution is by far the most restricted of any of the 14 genera of the clade of Salariini with high numbers of teeth (see section on cladistic analysis). Among the other genera (also 14 in number) of Salariini, only *Dodekablennos*, known only from Mauritius and Reunion islands (southwest Indian Ocean), *Medusablennius*, known only from Raroia Atoll (Tuamotu Archipelago, southeastern Pacific plate), and, perhaps, *Litobranchus*, known only from Negros Island (Philippines), Lombok and Waigeo islands (Indonesia), and the Palau Islands, are more or comparably restricted in distribution.

Of the 3 genera that appear in our cladistic analyses to form a monophyletic group with *Paralticus: Alticus* ranges across most of the Indo-west and central Pacific (J.T. Williams unpublished); *Praealticus* ranges from the easternmost Indian Ocean east to the eastern margin of the Philippine plate, then south along the Pacific plate eastern margin and out along the southern Pacific plate island chains to the Pitcairn Island group (Bath, 1992); and *Andamia* ranges from the Andaman and Christmas islands (eastern Indian Ocean) east to the Philippines and western Irian Jaya and south along the western margin of the Pacific plate to Vanuatu and neighboring Matthew and Hunter islands (J.T. Williams, unpublished).

The ranges of these four genera form a nested pattern with that of *Alticus* encompassing the ranges of the other three genera; that of *Praealticus* encompassing those of *Andamia* and *Paralticus*, and that of *Andamia* encompassing the range of *Paralticus*. The significance of this nested pattern is unknown and does not clearly relate to interrelationships within the clade, in which *Alticus* and *Andamia* form a sister group. We believe that the distribution of *Paralticus*, like many other fishes, reflects the effects of sea-level lowering during the last glacial period (18,000 B.P.) when the distribution of marine waters in SE Asia was much more restricted than presently (Figure 72). The present distribution of *Paralticus amboinensis*, like that of many other fishes, is essentially restricted to an area that we believe comprised a group of small isolated seas during the last glacial sea-level low (discussed further in the following section on *Blenniella* and *Istiblennius*).

Alticus and *Andamia* have similar habits and ecological niches. Both are found along open rocky shores, essentially at the shoreline or in tidepools, and they frequently leave the water and cling to rocks. *Praealticus* is also a close-shore form in rocky areas, but we have not seen it leave the water. All three of these genera are either seen or occasionally taken in large numbers at a single collection site. *Paralticus*, which attains a much larger size and has a more robust body than that exhibited by any of the other genera, is poorly known, but appears to be associated with mangroves. Its general rarity in collections suggests that it does not occur in dense concentrations.

Blenniella and Istiblennius

The overall distributions of *Blenniella* (Figures 61 to 65) and *Istiblennius* (Figures 66 to 71), which appear to form a sister group, are closely similar and extend over the entire tropical Indo-west and central Pacific. The major differences in their distributions is that *Blenniella* appears to be essentially absent from the Persian Gulf and Northern Territory coast of Australia, and its distribution does not extend as far south or north as that of *Istiblennius*, which occurs widely in the Persian Gulf and along the entire north coast of Australia. *Istiblennius*, on the other hand, is absent from Johnston Island, where one species of *Blenniella* occurs, and does not extend quite as far east as *Blenniella*.

Within *Blenniella* and *Istiblennius*, the nature of the species distributions is considerably different. The species of *Istiblennius* are, in general, much more localized in distribution than those of *Blenniella*. Of the 14 species of *Istiblennius*, 3 are endemic to the Red Sea (*rivulatus, unicolor, flaviumbrinus*), 1 to Hawaii (*zebra*), 1 to Australia (*meleagris*), 1 to the mid-Philippines (*colei*), 1 to the gulfs of the northwestern Indian Ocean (*pox*), 2 to the western Indian Ocean (*spilotus, steindachneri*), and 1 from Taiwan south to Indonesia (*muelleri*). Only 4 species of *Istiblennius* are distributed across the disconnected island coastlines from the Pacific to the Indian Ocean (*edentulus, lineatus, bellus, dussumieri*).

Of the 9 species of *Blenniella*, only 3 species exhibit relatively localized distributions (*leopardus*—Andaman Islands south to Sumatra; *interrupta*—Taiwan south to New Hebrides; *bilitonensis*—Taiwan and Thailand south to islands along the Northern Territory, Australia). Three others are confined to either the Pacific or Indian oceans, but are widely distributed within these oceans (*paula, cyanostigma, caudolineata*), and 3 species are broadly distributed across the Pacific and Indian oceans (*periophthalmus, gibbifrons, chrysospilos*).

Although 5 species of *Istiblennius* occur in the Red Sea (the Red Sea portion of the distribution of one, *pox*, includes only the southernmost end of that body), and 3 are endemic, only 1 species of *Blenniella* occurs in the Red Sea, and it also occurs widely in the Indo-west Pacific.

It is unclear if there is a correlation between widely distributed species and the possession of ophioblennius stages, which are often taken pelagically (also inshore), during ontogeny. We have identified ophioblennius stages for only one species of *Blenniella* (*gibbifrons*) and 4 species of *Istiblennius* (*dussumieri, lineatus, meleagris, zebra*), and we have tentatively identified this stage for *Blenniella paula*. There is also evidence that an ophioblennius stage may exist for *Istiblennius edentulus*. Of these seven species, all but *I. zebra*,
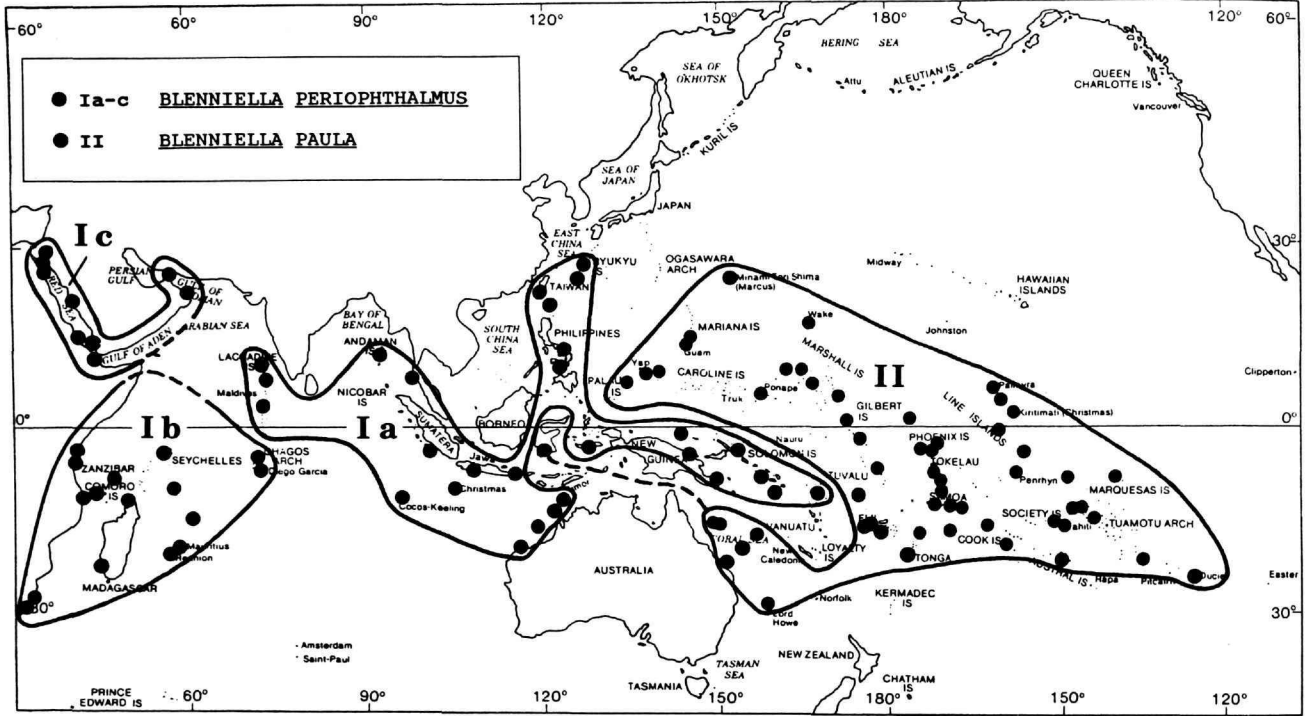
FIGURE 61.—Distribution of the Periophthalmus species complex, comprising *Blenniella paula* and *B. periophthalmus*. Records of *B. paula* from Tonga are based on recently acquired, uncataloged USNM specimens. Records of *B. periophthalmus* from Laccadive, Andaman, and Takarajima islands are based on Jones and Kumaran (1980:532), Day (1875–1878:333 and pl. 69: fig. 5), and Kamohara (1954:298).
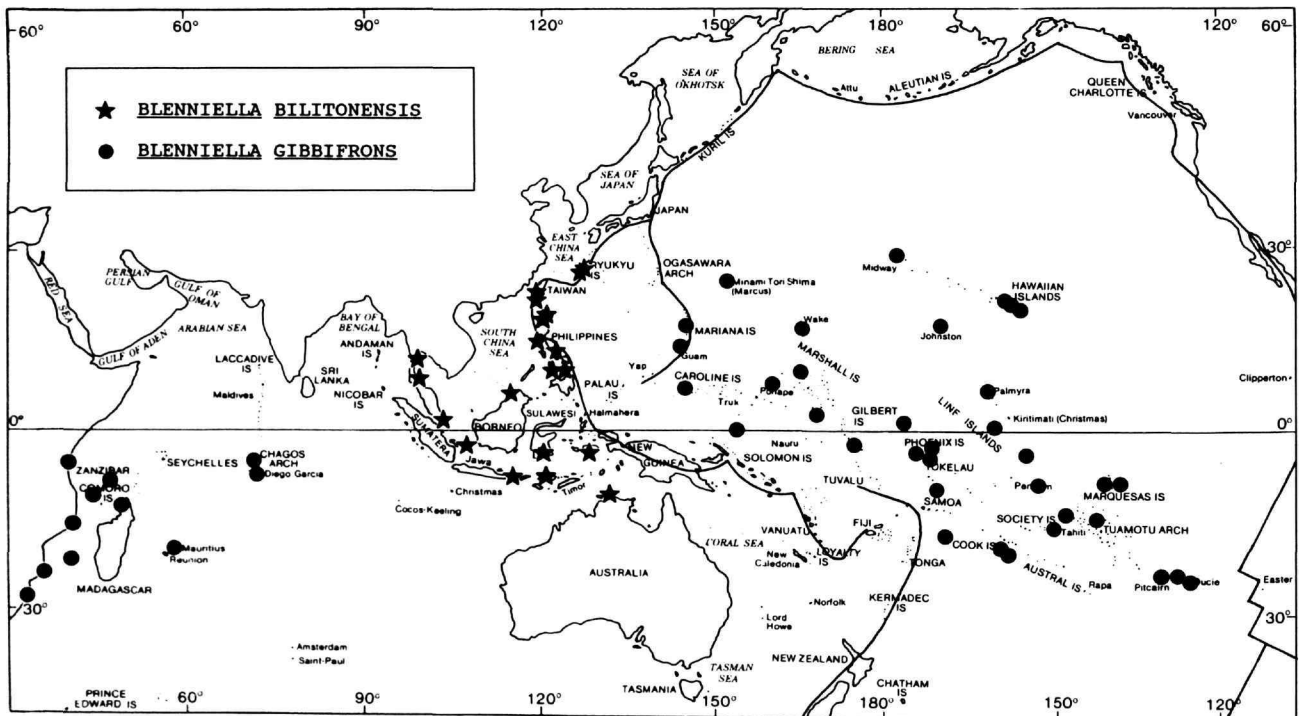

FIGURE 62.—Distribution of *Blenniella gibbifrons* and *B. bilitonensis* (delineation of Philippine and Pacific lithospheric plates indicated).

FIGURE 63.—Distributions of *Blenniella interrupta* (dots) and *B. leopardus* (stars).

FIGURE 64.—Distribution of *Blenniella chrysospilos* (Tongan records based on recently acquired, uncataloged USNM specimens).

FIGURE 65.—Distribution of *Blenniella caudolineata* and *B. cyanostigma* (southernmost record on African coast based on J.L.B. Smith, 1959:242, Bazaruto, Mozambique; northern Tongan record based on recently acquired, uncataloged USNM specimens).

FIGURE 66.—Distribution of *Paralticus amboinensis*, *Istiblennius bellus*, *I. colei*, and *I. zebra* (delineation of Philippine and Pacific lithospheric plates indicated).

FIGURE 67.—Distribution of *Istiblennius edentulus*. Records from Christmas and Laccadive islands, Indian Ocean, based on Allen and Steene (1987, fig. 409) and Jones and Kumaran (1980:531), and Paracel Islands, South China Sea, on Anonymous (1979:420–421). Records from Tonga based on recently acquired, uncataloged USNM specimens.
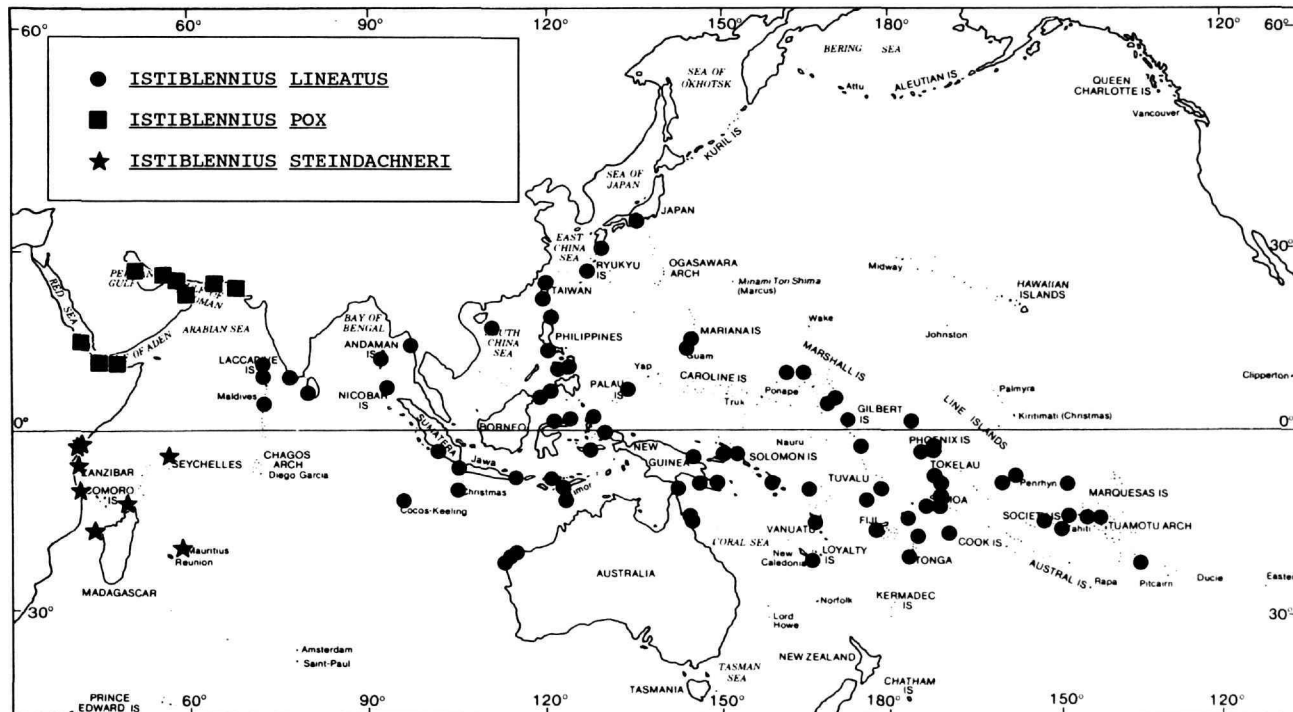
FIGURE 68.—Distribution of the Lineatus Species Complex; open symbols indicate acceptable literature reports (Anonymous, 1979:424; Jones and Kumaran, 1980:530; J.L.B. Smith, 1959:245). Record from northern Tonga based on recently acquired, uncataloged USNM specimens.
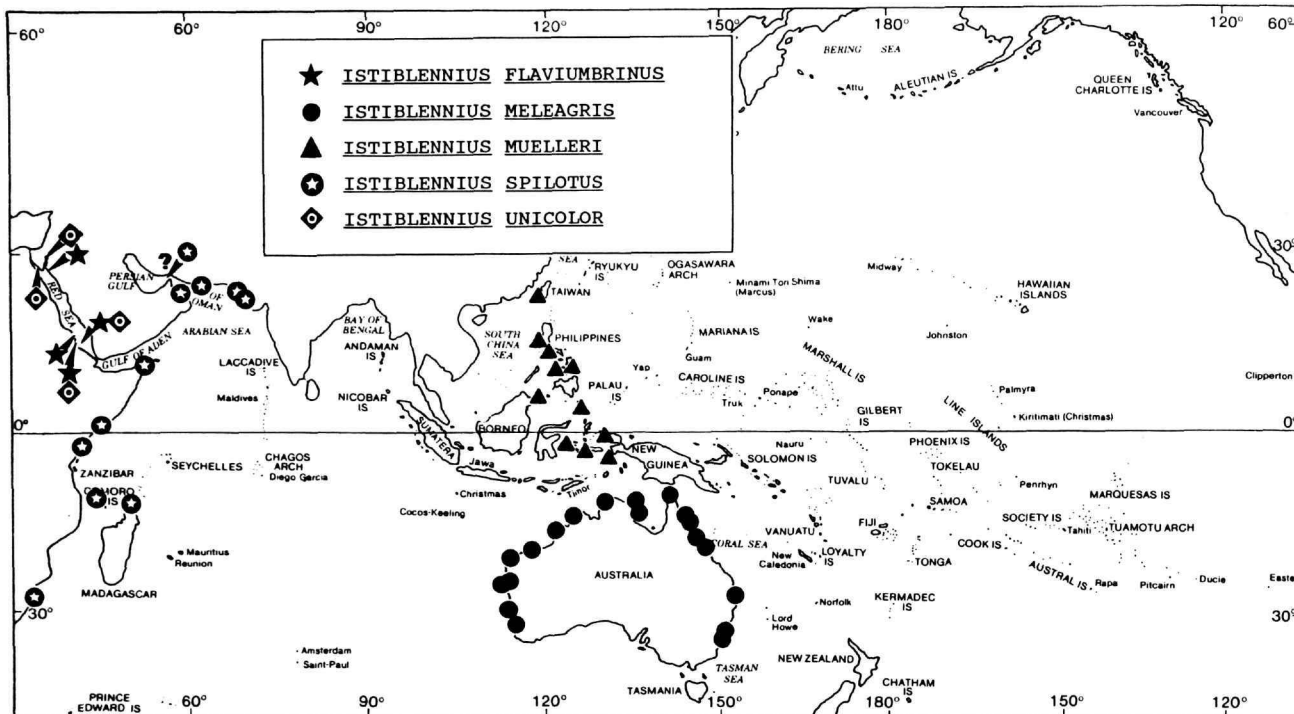
FIGURE 69.—Distribution of *Istiblennius flaviumbrinus, I. meleagris, I. muelleri* (record from Taiwan based on Shen et al. (1986:40), *I. spilotus,* new species, and *I. unicolor.* Arrows point from symbols to localities in the Red Sea.
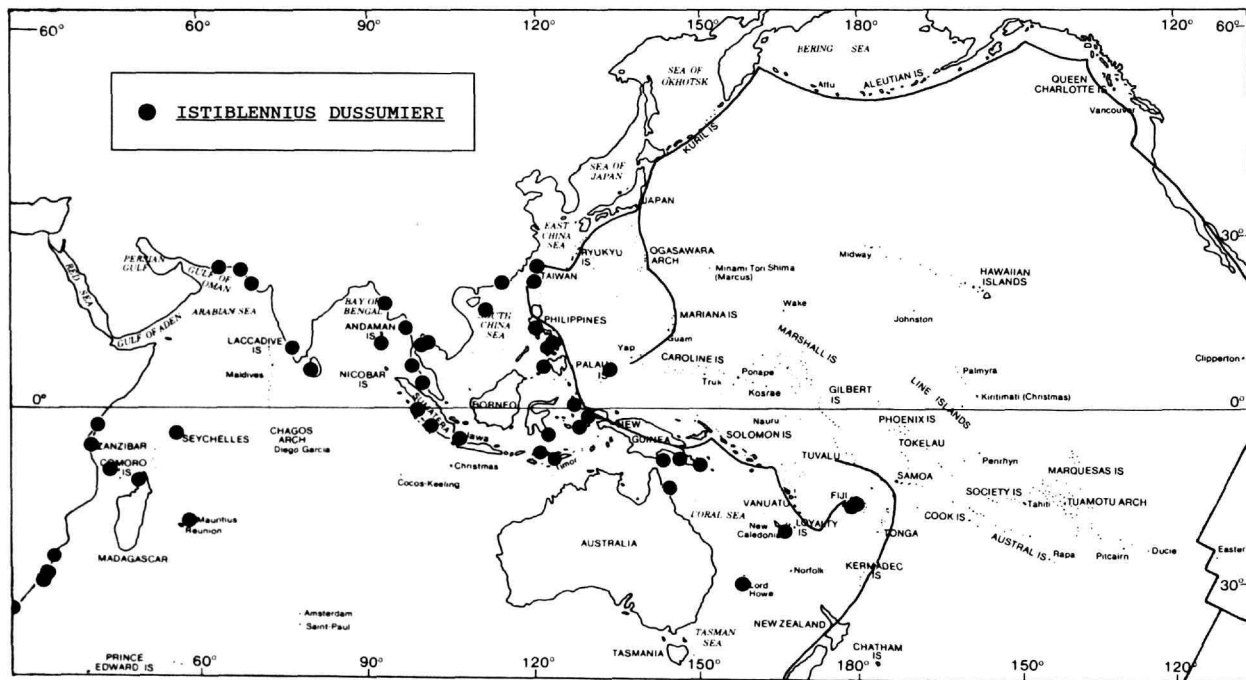
FIGURE 70.—Distribution of *Istiblennius dussumieri* (delineation of Philippine and Pacific lithospheric plates indicated). Record from Mauritius based on lost holotype of *Salarias striatomaculatus;* record from Paracel Islands, South China Sea, based on Anonymous (1979:422–423), and that from Inhaca, Mozambique, on Sanches (1963:145).
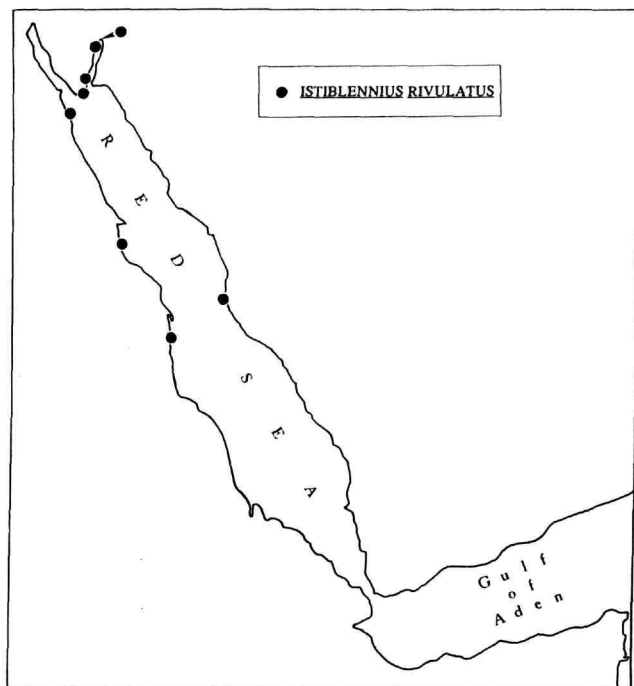
FIGURE 71.—Distribution of *Istiblennius rivulatus*.

endemic to Hawaii, and *I. meleagris*, endemic to Australia, are widely distributed among the islands in both the Indian and, at least, western Pacific oceans. *Istiblennius dussumieri*, however, is predominantly a continental coastal species, and has been unable to transgress the Pacific plate margin. On the other hand, *Blenniella chrysospilos*, which is widely distributed across the Indo-Pacific (Figure 64), *B. caudolineata* (widely distributed in the Pacific), and *B. cyanostigma* (widely distributed in the Indian Ocean; both Figure 65) are not known to have ophioblennius stages.

Perhaps relevant to the present discussion are the 8 species of Salariini that occur in the Hawaiian Islands (1 *Blenniella*, 3 *Cirripectes*, 2 *Entomacrodus*, 1 *Exallias*, 1 *Istiblennius*). All have ophioblennius stages in their ontogeny, yet 5 are endemic to Hawaiian Islands and 3 are distributed throughout the Indo-Pacific. The high degree of isolation of the Hawaiian Islands would seem to require that colonizing fishes be pelagic at some stage. Once reaching the islands, the operation of founder principle could result in the formation of endemics. But why not for all 8 of the salariinins? There are 3 possible explanations that we can think of. The first 2 are obvious: different rates of evolution and different times of colonization. The third is less obvious and might be considered a modification of the second: continual colonization.

The 3 non-endemic salariinins, all of which occur at one or

more island groups between the Hawaiian Islands and southern Japan, may be continually resupplying the Hawaiian Islands with propagules carried in by the oceanic current gyres arising from the eastward flowing surface currents originating in the Pacific northwest, as elegantly proposed for corals by Grigg (1988). A problem with the continual colonization explanation is why only 3 wide-ranging salariinins are present in the Hawaiian Islands. Wide-ranging salariinins, of which there are many, such as *Blenniella chrysospilos* (Figure 64), *Cirripectes variolosus* (Williams, 1988, fig. 12; ophioblennius stage known), and *Entomacrodus striatus* (Springer, 1967, fig. 7) co-occur at scattered and well-separated western Pacific islands with the 3 non-endemic salariinins that reach the Hawaiian Islands. The causal factors contributing to Hawaiian Islands' endemism are undoubtedly complex and remain to be elucidated.

Our attempts to find comparable distributions in *Blenniella* and *Istiblennius* by comparing distributions of putative monophyletic groups evinces the following. The overall distribution of the Periophthalmus species complex (Figure 61) of *Blenniella*, which comprises only *B. periophthalmus* (with 3 incompletely differentiated forms) and *B. paula* (Figure 61), is closely similar to the distributions of *I. edentulus* (Figure 67) and the Lineatus species complex of *Istiblennius*, which comprises 3 species: *I. lineatus*, *I. pox*, *I. steindachneri* (Figure 68). The distribution of form Ic of *B. periophthalmus* is essentially the same as that of *I. pox;* the distribution of form Ib is essentially the same as that of *I. steindachneri*, and the combined distribution of form Ia and *B. paula* is essentially the same as that of *I. lineatus*. Although it is questionable whether the taxonomic level of the 3 forms of *B. periophthalmus* are comparable to the species-level taxa of the Lineatus species complex, one can infer that the ancestor of each complex has responded to, or is responding to, some or all of the same historical events leading to their current taxonomic fractionation. If the rates of divergence of the ancestral forms were equivalent, one would assume that the split between *B. periophthalmus* and *B. paula* predated the apparently incomplete speciation of the three *B. periophthalmus* forms. Otherwise, one would expect that *I. lineatus* would be represented currently by 2 forms with distributions comparable to those of *B. periophthalmus* form Ia and *B. paula* (and, as A.C. Gill has suggested to us, leads to the conclusion that the area occupied by *B. periophthalmus* form Ia is a composite). Some of the factors that may have contributed to speciation of these 2 species groups will be discussed below.

The overall distribution of *B. periophthalmus*, although apparently absent from the Gulf of Thailand and South China Sea, is similar to that of *I. dussumieri* (Figures 61 and 70): widely distributed in the Indo-west Pacific, but limited to continental plate areas west of the western margin of the Pacific plate. Springer (1982) presented abundant evidence that the western margin of the Pacific plate delineated a major barrier to dispersal for marine forms. Many more taxa have their eastern
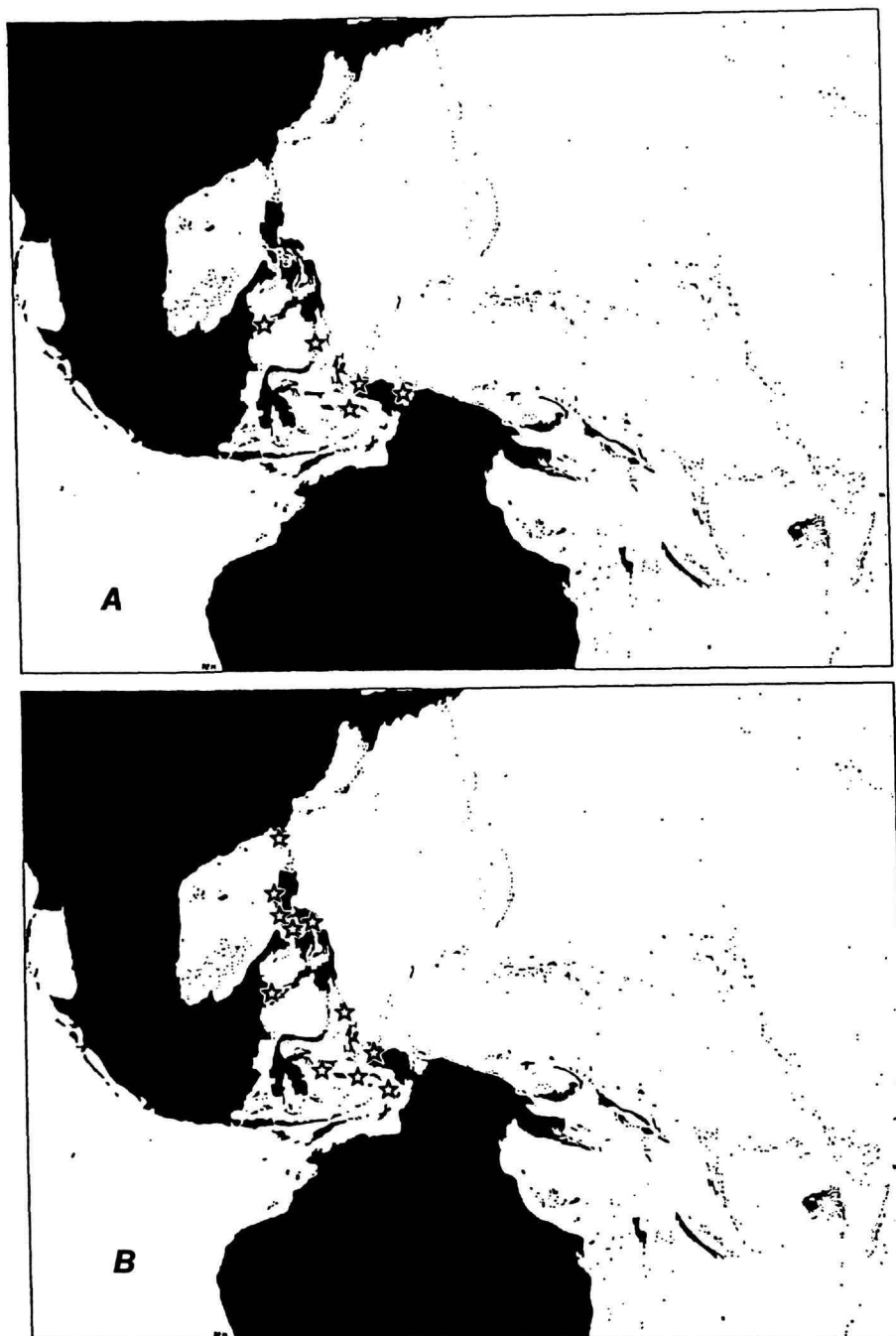
FIGURE 72.—Present-day distributions of *a, Paralticus amboinensis,* and *b, Istiblennius muelleri,* plotted on maps showing distribution of land and sea in part of Indo-Pacific during last glacial sea-level low, about 18,000 years ago (map after Myers, 1989, fig. 8; compare with plots on present-day maps for same species, Figures 66 and 69).
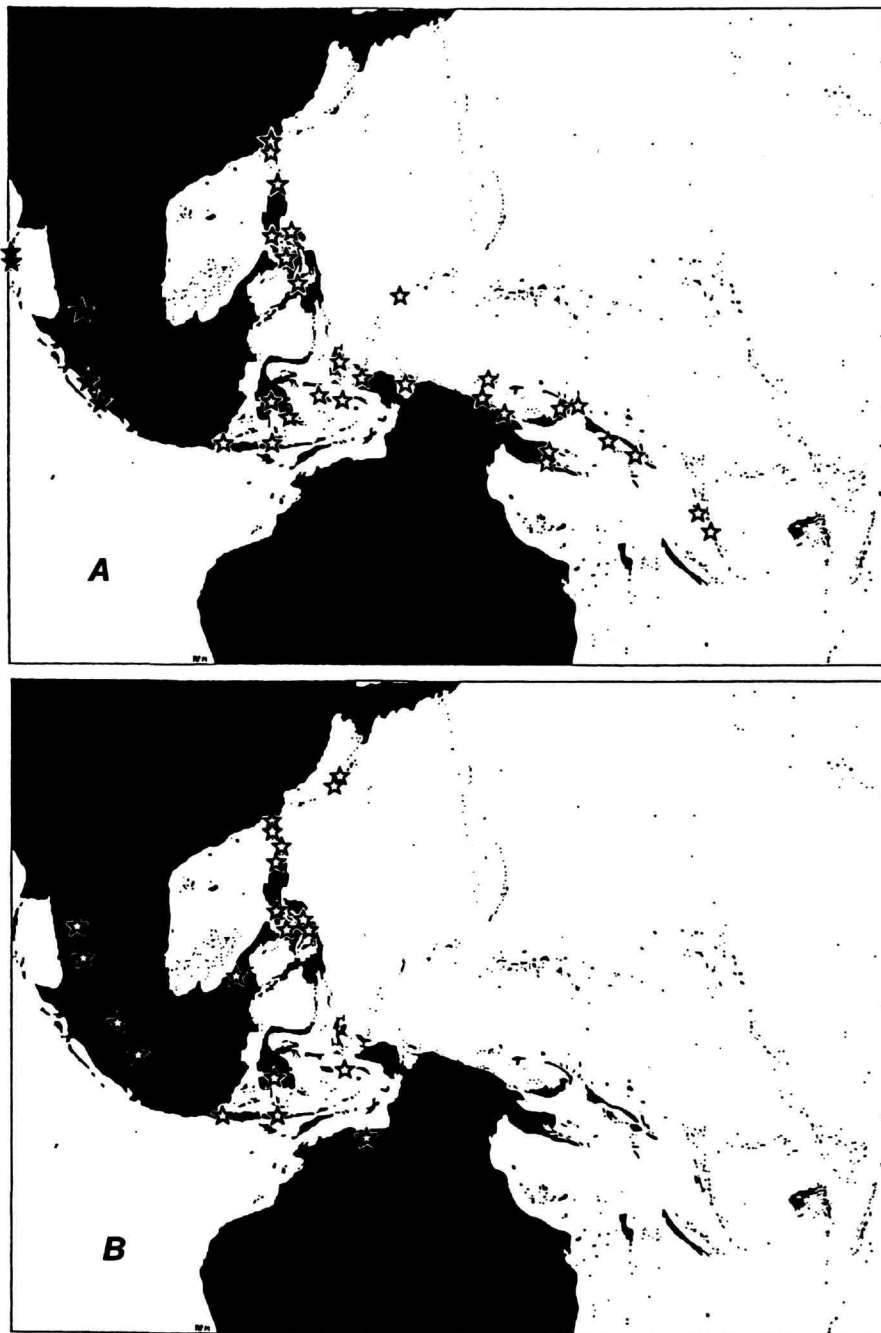
FIGURE 73.—Present-day distributions of *a*, *Blenniella interrupta* (open stars) and *B. leopardus* (solid stars), sister species, and *b*, *Blenniella chrysospilos*, plotted on maps showing distribution of land and sea in part of Indo-Pacific during last glacial sea-level low, about 18,000 years ago (map after Myers, 1989, fig. 8; compare with plots on present-day maps for same species, Figures 63 and 64). Inland distributions shown for *B. leopardus* and *B. chrysospilos* would not have been possible during sea-level low, thus, indicate subsequent eastward dispersal of former and westward dispersal of latter species.

distributional limits at, or to the west of, the western margin of the Plate than have their western limits at or to the east of the western margin. Springer (1982) was unable to explain the nature of the barrier and suggested that physical evidence of its origin may have been lost (subducted) during the passage of time.

Springer and Williams (1990) suggested that in some cases, the extinction of the Indo-west Pacific portion of the distribution of a species originally distributed across the Indo-Pacific could result in a Pacific plate endemic species. Among several examples they offered as evidence for this possibility, Springer and Williams mentioned the distributions of *Blenniella gibbifrons* (Figure 62) and *Istiblennius bellus* (Figure 66).

Blenniella gibbifrons presents the clearer case. Its distribution consists of two widely distributed, disjunct portions, one on the Pacific plate and the other in the western Indian Ocean. The extensive distributional gap between the 2 portions probably acts as a barrier to gene flow, which, if operational long enough, should result in evolutionary divergence of the populations, thus resulting in a pair of sister species with allopatric disjunct distributions. Extinction of one of the 2 species (or in 1 of the 2 disjunct areas, if divergence did not occur) would result in either a Pacific plate endemic or a western Indian Ocean endemic species. Springer (1982 and presently), however, believes that many taxa distributed like *Istiblennius dussumieri* (Figure 70; widely distributed Indo-west Pacific) are continental plate forms that never were present on the Pacific plate and are unable to disperse onto it. Springer (1982) did present evidence that the plate-margin barrier may be breaking down in certain areas (e.g., "Caroline Islands Conduit," resulting from the formation of the east-west Caroline Islands chain).

East-west disjunctly distributed species or sister groups are much more common than Springer and Williams (1990) indicated. A few additions to the examples they gave, based on fishes, include *Synodus binotatus* (Synodontidae; Cressy, 1981, fig. 39), *Apogon taeniopterus* (Apogonidae; Fraser and Lachner, 1985, fig.10), *Eviota distigma* (Gobiidae; Lachner and Karnella, 1980, fig. 24), *Stegastes albifasciatus* (Pomacentridae; Allen and Emery, 1985, fig. 1), *Calotomus carolinus* (Scaridae; Bruce and Randall, 1985, fig. 1), *Plagiotremus tapeinosoma, P. isodon* (Blenniidae; Smith-Vaniz, 1976, figs.78, 79), *Cephalopholis sexmaculata, Epinephelus chlorostigma, E. hexagonatus, E. tauvina, Plectropomus laevis* (Serranidae; Randall and Heemstra, 1991, figs. 25, 58, 80, 144; Randall and Hoese, 1986, fig. 1), and the sister species *Blenniella cyanostigma-B. caudolineata* (Figure 65) and, possibly, *B. interrupta-B. leopardus* (Figure 63).

The extent of the "vacant" area separating the eastern and western portions of disjunct distributions is highly variable, but always includes all or some of the fragmented seas and associated coastlines of SE Asia (South China Sea, Gulf of Thailand, Java, Sulu, Celebes, Banda, Molucca and associated lesser seas, bays, and straits) and among these, usually includes, at least, the Gulf of Thailand and southern half of the South China Sea. Both of the last two areas were subaerial (did not exist) during the last glacial sea-level lowering (18,000 BP; Myers, 1989, fig. 8). The distribution of *Blenniella periophthalmus* (Figure 61) shows a disjunction whose gap appears only to comprise the Gulf of Thailand and South China Sea. Even today, many marine organisms that are essentially continuously distributed across the the Indo-west Pacific, are noticeably absent from the Gulf of Thailand and southwestern South China Sea (e.g., *Istiblennius lineatus*, Figure 68).

The SE Asian portion of the distributional void, interestingly, is almost exactly defined by the current distribution of *Blenniella bilitonensis* (Figure 62) if the Australian and Ryukyu Islands records are ignored. It is clear, however, that the western portion of the distribution of *B. bilitonensis* represents a western dispersal since the last glacial sea-level low (Figure 73*b*). But it is unclear whether species (e.g., *I. muelleri*, Figure 72*b*; *B. interrupta*, Figure 73*a*) that are currently absent from the Gulf of Thailand-southern South China Sea area, were present in this area prior to the last sea-level low and have been unable to re-enter it.

Cold upwelling enforced the barrier to marine dispersal created by the emergent SE Asian lands of the glacial sea-level low (Fleminger, 1986). In particular, sea-surface temperatures were greatly depressed in the easternmost extension of the Indian Ocean—in the area between Australia and what today comprises the Indonesian islands extending from Bali to Timor (Fleminger, 1986, fig. 5). The depressed temperatures would have eliminated populations of warm-water species in this arm of the Indian Ocean and created an area of disjunction in the distributions of previously continuously distributed species extending from the Indonesian islands west and north along the Indian Ocean coast of the expanded Malaya-Thailand Peninsula (appears as a massive fish hook in Figures 72–73). Such conditions may well have divided the common ancestor of each of the sister-species groups *Blenniella leopardus-B. interrupta* and *B. cyanostigma-B. caudolineata* into two disjunct populations and allowed them to diverge (Figures 63 and 73*a*; Figure 65).

As a result of glacial sea-level lowering, some of the small seas and bays of the SE Asian area probably became landlocked, and small populations of more widely distributed species may have been isolated in them. Small isolated populations are most subject to genetic drift and selection and might diverge quickly, giving rise to highly localized endemics. McManus (1986) gives an extended discussion of isolation and endemism in SE Asia, as initiated by sea-level and tectonic changes and Nishimura (1992) provides evidence that the tropical Indian and Pacific oceans (surface circulation) were isolated between about 8 and 16 Mya as a result of tectonic changes in the Indonesian region. It is possible, therefore, that the isolation of the faunal gap we descibe (also in Springer and Williams, 1990) may have been initiated much earlier than we

propose, only to be reinforced by more recent glacially affected events.

A few examples of localized fish species, all endemic to the Philippines-Sulu Sea area, that may be the result of divergence of population isolates in small bays include *Istiblennius colei* (Figure 66), *Ecsenius kurti*, *E. dilemma*, and *E. bimaculatus* (all Blenniidae; Springer, 1988, figs. 11 to 13), *Salarias obscurus* (Blenniidae; Bath, 1992:225), *Meiacanthus abditus*, *M. geminatus* (Blenniidae; Smith-Vaniz, 1987, figs. 6, 13), *Congrogadus hierichthys* (Pseudochromidae; Winterbottom, 1985, fig. 11), *Pseudochromis colei*, *P. fowleri*, *P.* new species (Pseudochromidae; A.C. Gill, pers. comm.), *Pomacentrus stigma* (Pomacentridae; Allen, 1991:158), *Stonogobiops nematodes* (Gobiidae; Hoese and Randall, 1982, fig. 1), *Pandaka pygmaea* (Gobiidae; H.K. Larson, pers. comm.), *Callionymus acutirostris*, *C. hildae*, *C. umbrithorax*, *C. platycephalus*, *Synchiropus grinelli* (Callionymidae; Fricke, 1983, figs. 10, 16, 30, 95, 175). All or most of these species are small and shallow-dwelling, and are probably annuals. Annual species would be most prone to speciate rapidly. With postglacial rise in sea level, newly evolved, isolated species such as these could be expected to expand their ranges, but these species appear to have moved little. Perhaps, species such as *Istiblennius muelleri* (Figure 72a) and *Paralticus amboinensis* (Figure 72b) were originally highly restricted and expanded their ranges after rise in sea level.

There is also evidence of isolation of some of the deep basins in the SE Asian area, particularly the Sulu Sea. Gibbs, et al. (1983, fig. 42) described *Eustomias suluensis* (Melanostomiidae), which is known only from the Sulu Sea. Gilbert and Hubbs (1920) reported 36 species of grenadiers (Macrouridae, Bathygadidae) from the Sulu Sea basin, including such lesser Philippine seas as the Bohol, Samar, Visayan, and Sibuyan, and associated straits. Of the 36, T. Iwamoto (in litt., 19 August 1993) informs us that about one-third are endemic. There are an additional 24 species reported from the combined Sulu and Celebes basins, of which 5 or 6 are endemic.

Nishimura (1992) called attention to an unpublished study by H. Shibuya, D. Merrill, and V. Hsu that indicated that the Celebes Sea is trapped old ocean basin. Sister-group relationships of the deeper dwelling biota of the Celebes Sea could well provide evidence of, or confirmation for, the historic origin of the Celebes Sea.

Blenniella periophthalmus and *B. paula* are allopatric sister species whose distributions (Figure 61) are separated for the most part by the western margin of the Pacific plate. The ancestor of these two species was probably widely distributed across the Indo-Pacific and its distribution was split by Springer's (1982) hypothesized barrier along the western margin of the Pacific plate. The southwestern disjunct extension of the distribution of *B. paula* westward across the Pacific plate margin to the Great Barrier Reef and Coral Sea (ignoring here the peculiar disjunct distribution in the Gulf of Bone, Sulawesi) represents either a relictual disjunct remnant

of a more continuous distribution or a recent range expansion by dispersal. We favor the relictual explanation as there is evidence for the presence of a barrier in the SW Pacific that is splitting or has split the distribution of *B. paula* into its two disjunct portions. The barrier is represented by a distributional gap in the area occupied by the New Hebrides, Loyalty, and New Caledonia islands. The gap appears to be real as both species are relatively common wherever they occur and there has been considerable collecting recently, at least in New Caledonia and the Loyalties. The absence of *B. paula* (or *B. periophthalmus*!) in the area is remarkable and indicates the presence of a barrier to distribution that we have not found duplicated for other species or sister groups of fishes. Although the New Hebrides have not been well sampled, New Caledonia and/or the Loyalties often appear to be just at or outside the limits of distribution of many fish species (besides *B. periophthalmus* and *B. paula*, see also *B. caudolineata*, Figure 65; *B. interrupta*, Figure 63).

Springer (1988:122–131) reviewed recent literature pertaining to endemism in the western Indian Ocean and Red Sea (including the Gulf of Aqaba). He proposed some scenarios based on the geophysical history of the area to account for various distribution patterns in the blenniid genus *Ecsenius*. The following discussion will expand on that of Springer as it treats mostly species groups with different Indo-Pacific distributions than those of *Ecsenius*.

As a whole, the consensus cladogram of *Istiblennius* species is not well supported, but we believe that 2 clades are well supported and particularly relevant to a discussion of western Indian Ocean endemism: 1—the Lineatus Species Complex: *pox* is the sister group of *steindachneri*, and *lineatus* is the sister group of the other 2 species; 2—the clade with *unicolor* as the sister group of *spilotus*, and *flaviumbrinus* as the sister group to the other 2 species.

The distribution patterns shown by the species of the Lineatus Complex (Figure 68) and those of the 3 forms of *Blenniella periophthalmus* (Figure 61) are very similar. The distributions of 2 of the Lineatus Complex of species, *Istiblennius pox*, Red Sea to Persian Gulf, and its sister species, *I. steindachneri*, western Indian Ocean south of the Horn of Africa (Figure 68) are common and well-known (Cohen, 1973; Klausewitz, 1974, 1978, 1989). Although highly suggestive, we are unable to defend an hypothesis that *Blenniella periophthalmus* forms Ic and Ib, which are distributed almost identically as are *I. pox* and *I. steindachneri* (Figure 61), are sister forms. Furthermore, we are unaware of other cladistically hypothesized sister-group relationships that would indicate that the two areas occupied by *I. pox* and *I. steindachneri* are sister areas, but predict that such will be corroborated by future cladistic studies.

We offer the following scenario to explain the distribution of the Lineatus Complex of species. We begin with an ancestral species that was widely distributed in the Indian and Pacific oceans, but probably not in the Red Sea, where the distribution

of the present-day *I. pox* barely extends north of the Red Sea's entrance. As Springer (1988) proposed, the movement of India north created a barrier that split the distribution of the ancestral species into two portions: western Indian ocean and eastern Indian Ocean-Pacific Ocean. India persists as a barrier to reef fishes because most of its peninsular coasts are inhospitable: presence of numerous river deltas and extensive sandy coasts, and few or no reefs (Springer, 1988:122).

Blum (1989, fig. 11, Barrier D) indicated that an unspecified barrier to dispersal for butterflyfishes existed between the Gulf of Aden to the north and the western Indian Ocean to the south. Klausewitz (1989:318) proposed that cold upwelling, with surface temperatures of 13°-15°C (Currie et al., 1973, fig. 10), south of Ras Hafun (= Raas Xaafuun, ~150 km S of the tip of the Horn of Africa) constituted a barrier to dispersal between the Gulf of Aden and the east coast of Africa. This upwelling, presumably, would have split the distribution of the common ancestor of *pox-steindachneri* and allowed the populations on either side to diverge. Cold upwelling in the relevant area, however, is restricted to the period of the southwest monsoon (Currie et al., 1973), which occurs during the summer months. We question, therefore, if it affects water temperatures against the shore and in the intertidal, habitats occupied by the Lineatus Species Complex. On the other hand, if these species have an offshore planktonic larva, cool temperatures might be limiting. Wyrtki (1973, fig. 1, based on other sources) provides a current scheme for the western Indian Ocean in winter that might reinforce cold upwelling. In winter, there is a strong westward flowing current across the Indian Ocean that splits at the Horn of Africa into a northward flowing current, which enters the Red Sea, and a southward flowing current, which reverses to the east just south of the Horn. The presence of *I. pox* just inside the entrance to the Red Sea represents a recent invasion, probably reflecting the effects of the north branch of the westward flowing current.

If a more resolved cladogram of *Istiblennius* species relationships should show that *I. rivulatus*, which has a faintly striped color pattern reminiscent of that of the Lineatus Complex, is the sister group of the 3 species of the Lineatus Complex, the previous scenario could be modified to include isolation of a Red Sea population of a more widely distributed ancestor. *Istiblennius rivulatus* is currently restricted to the northern half of the Red Sea (Figure 71).

We are unable to propose a well-defended scenario to explain the distribution of the (*flaviumbrinus* (*unicolor, spilotus*)) clade. It would be helpful if we had a stronger indication for the sister group of the clade. Starting our scenario with a widely distributed ancestral species limited to the western Indian Ocean, including the Red Sea and the gulfs of Oman and Aden, it would appear that a barrier formed between the Red sea and Indian Ocean isolating a Red Sea population that evolved into *flaviumbrinus* and a western Indian Ocean population, which was ancestral to *unicolor-spilotus*. If the Red Sea were to reopen, become invaded by this latter ancestor, and then close again, a second Red Sea endemic (*unicolor*) could have formed. Klausewitz (1989:318-322) discussed the physical evidence for complete isolation, including repeated isolations, of the Red Sea from the Gulf of Aden and concluded that these "are still matters of controversy."

As a final observation, we mention an Indian Ocean distributional pattern that is repeated by several species of *Blenniella* and *Istiblennius* that is probably of more general occurrence. The distributions of the following species, or a disjunct portion of an individual species distribution, are restricted entirely, or nearly so, to the western Indian Ocean south of the equator and west of the Carlsberg-Mid-Indian Ridge: *Blenniella cyanostigma* (Figure 65), *B. bilitonensis* (Figure 62), *B. chrysospilos* (Figure 64), *B. periophthalmus* form Ib (Figure 61), *Istiblennius dussumieri* (Figure 70), *I. steindachneri* (Figure 68), *I. bellus* (Figure 66).

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Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "...Jones (1910:122)." If bibliographic footnotes are

required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number):pagination: "10(2):5–9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

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