The Indo-Pacific Blenniid Fish Genus *Ecsenius*

VICTOR G. SPRINGER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 465

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SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1988

ABSTRACT

Springer, Victor G. The Indo-Pacific Blenniid Fish Genus *Ecsenius*. *Smithsonian Contributions to Zoology*, number 465, 134 pages, 68 figures, 14 color plates, 30 tables, 1988.—*Ecsenius* McCulloch is defined and its major specializations illustrated. It is not possible to propose its sister group unequivocally within the tribe Salariini.

Ecsenius comprises 12 species groups, most hypothesized to be monophyletic based on a few heavily weighted characters; a few groups are possibly paraphyletic. The groups contain from one to nine species. Interrelationships of some groups, and some species within some groups, are hypothesized based on heavily weighted characters and/or distribution patterns.

Ecsenius comprises 46 species, 20 here described as new. The new species are: *E. aequalis* (Great Barrier Reef; Trobriand Islands), *E. alleni* (Rowley Shoals and Scott Reef, Western Australia), *E. australianus* (Great Barrier Reef), *E. axelrodi* (Hermit Islands; New Britain; Solomon Islands), *E. bathi* (Java; Komodo), *E. dentex* (Gulf of Aqaba), *E. dilemma* (Philippines), *E. fijiensis* (Fiji: Viti Levu south to Vatoa, Lau Islands), *E. kurti* (Philippines), *E. lubbocki* (Phuket, Thailand, Indian Ocean), *E. monoculus*, (Philippines; Ilot du Sud, Viet Nam; Moluccas), *E. oculatus* (Christmas Island, Indian Ocean; Western Australia), *E. pardus* (Fiji), *E. paroculus* (Phuket, Thailand; Malacca, Malaysia; Mentawei, Bawean, Seribu islands, Indonesia), *E. portenoyi* (Rotuma; American Samoa), *E. sellifer* (Umboi Island and Trobriand Islands, Papua New Guinea; Solomon Islands; Palau Islands), *E. stictus* (Great Barrier Reef), *E. taeniatus* (Basilaki and Goodenough islands, western Papua New Guinea), *E. tessera* (New Caledonia; New Hebrides), and *E. tigris* (Osprey and Bougainville reefs, Coral Sea). *Ecsenius minutus* Klausewitz, formerly synonymized with *E. nalolo* Smith, is resurrected. Several of the species have two or three strikingly different color-pattern forms, which are not associated with size or sex.

A key is given to all species, all are illustrated in black-and-white halftones, and most are illustrated live in color photographs. Distribution maps are provided for all the species groups and species.

Of the 12 species groups, all the species within each of five groups, containing from three to nine species, are allopatric. Two of these five groups, one with five and one with eight species, are hypothesized to form a clade. Of the 13 species in this clade, 12 are allopatric. One of the five species in one group is broadly sympatric with six of the eight species in the other group. The overall distribution of the two groups, and the distributions of the species in each of them, are used as the basis for a speculative vicariance biogeographic discussion, in which the tectonic history of India is proposed as the primary physical barrier that isolated biotas in the western Indian Ocean and allowed them to diverge.

Species within a group usually exhibit sharply delimited distributions with respect to each other. For instance, one species of a group may have an extremely broad distribution with islandless voids of hundreds of kilometers separating its populations. Populations of the same species, however, may be separated from populations of another species in the same group at other islands by distances of only a few tens of kilometers. Such distribution patterns appear to be better explained by the tectonic history of the pertinent areas than by dispersal.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging-in-Publication Data
Springer, Victor Gruschka, 1928–
The Indo-Pacific blenniid fish genus Ecsenius.
(Smithsonian contributions to zoology ; no. 465)
Bibliography: p.
Supt. of Docs. no.: SI 1.27:465
1. Blenniidae—Classification. 2. Blenniidae—Geographical distribution. 3. Fishes—Classification. 4. Fishes—Geographical distribution. I. Title. II. Series.
QL1.S54 no.465 [QL638.B6] 591 s 88-600023 [597'.58]

Contents

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Introduction

This is the fourth study I have published (Springer, 1971, 1972; McKinney and Springer, 1976) on the systematics of *Ecsenius*. In the first study I recognized 18 species, but the material actually comprised 26 species. Of the eight species that I did not recognize nomenclaturally, seven were described as variations within other species of *Ecsenius*, and one (*Ecsenius minutus* Klausewitz), known from a single juvenile specimen, was incorrectly synonymized. Since 1971, seven more species of *Ecsenius* have been described (Springer, 1972; McKinney and Springer, 1976). Herein, I describe 20 new species and resurrect *E. minutus*, bringing the total number of species in *Ecsenius* to 46. For all the species, I propose 12 species groups (most hypothesized as monophyletic based on a few heavily weighted characters) and some intragroup relationships and vicariance scenarios that are compatible with the distributions of some species in certain groups.

The increased number of species in *Ecsenius* results from the great amount of collecting in the Indo-Pacific during the past ten years. Approximately 3,500 specimens, more than twice the number included in my three previous reports, form the basis of the present study (I excluded from consideration many other specimens of the more common *Ecsenius* species).

Not only does the post-1976 material include species previously unrepresented in collections, but it also permitted me to reassess several of my earlier taxonomic conclusions.

Ecsenius is among the most speciose genera of fishes for which monophyly can be hypothesized unequivocally, and it is the most speciose genus of blenniids. Otherwise, the blenniid genus with the most reported species is *Entomacrodus*, with 22 (Springer, 1967). That genus should be reassessed in light of newly available material. I doubt, however, that *Entomacrodus* or any other blenniid genus will be found to approach *Ecsenius* in numbers of species. There is even a reasonable possibility that some of the *Ecsenius* species I recognize will warrant subdivision when more complete geographical samples are available (e.g., *E. opsifrontalis*, *E. lineatus*), or when more is known about their genetics (e.g., *E. frontalis*). There is also a good possibilty that undescribed species of *Ecsenius* for which no material is available lurk in various parts of Indonesia, the New Hebrides, and islands off eastern and western Australia—areas that have not been sampled well.

Ecsenius juveniles and adults are restricted almost entirely to subtidal habitats with living coral. This contrasts with other speciose genera of blenniids, such as *Entomacrodus*, *Istiblennius*, and *Omobranchus*, which, as juveniles and adults, occur only in the shallowest areas, often intertidally or in mangrove swamps, but usually not among corals. Several species of *Ecsenius* occur at depths over 30 m (to 39 m), much greater than known for the other three genera.

Little information is available on the reproductive habits and early life history of *Ecsenius* species. The smallest specimens (about 12 mm SL, but rarely less than 15 mm) collected in the wild using ichthyocides are nonplanktonic and essentially adult-like in color pattern and morphology, although dentition may be incompletely developed. I have examined blenniid specimens ranging from ~12 to ~14 mm SL, taken well offshore at the surface around a light at night, that I tentatively identified as *Ecsenius*. These specimens are also essentially adult-like, although no color pattern remained, if, indeed, any was present originally (specimens, sorted only to family, at USNM, are from the 1907–1910 Philippine collections made by the United States Fish Commission Steamship *Albatross*).

Wickler (1965) described breeding, hatching, newly hatched larvae, and initial larval activity of *E. bicolor* in aquaria. The newborn larvae were 3.5 mm TL, toothless, lacked spines on the head, and swam immediately to the surface of the aquarium, but failed to eat.

Unlike *Ecsenius*, at least some species of *Entomacrodus*, *Istiblennius*, and *Omobranchus*, which occurred in the same night-light collections with *Ecsenius*, have modified planktonic

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Review chairman: Richard L. Zusi.

larval stages with, variably, spines on the head, enlarged, deciduous fangs, and/or heavy black pigmentation of the pectoral fins.

Because the habitat of *Ecsenius* is less easily sampled than that of *Entomacrodus, Istiblennius,* and *Omobranchus,* it would seem that the species of *Ecsenius* are less likely to be collected. Thus the distributions of those species would be less well known than those of the species of the other three genera. The facts seem to support this assumption. Although a reassessment of *Entomacrodus* will probably show that one or two of the species I (Springer, 1967) recognized comprise complexes, only one form has been collected subsequently that was not represented in my 1967 material. Similarly, since the revision of *Omobranchus* (Springer and Gomon, 1975) appeared, only one species not included in the material has been collected. *Istiblennius* has not been revised and, therefore, cannot be compared as completely with *Ecsenius* as can the other two genera.

The apparent presence of a planktonic stage suggests that species of *Ecsenius* should, in general, have distributions no less restricted than those of the species of *Entomacrodus, Omobranchus,* and *Istiblennius.* The facts, however, only partially support this presumption. As a whole, *Entomacrodus* and *Istiblennius* are each distributed much more widely in the Indo-Pacific than is *Ecsenius* (even circumtropically in the case of *Entomacrodus*), but *Omobranchus* is about equal in overall distribution (excluding an Indo-west Pacific species putatively introduced into the Caribbean; Springer and Gomon, 1975:59–63).

In the Indo-Pacific, *Ecsenius* ranges from the east coast of Africa eastward only to the Marquesas (140°W), whereas *Entomacrodus* reaches Easter Island (110°W) and the west coast of Middle America. *Istiblennius* extends eastward as far as Ducie Island (125°W). Although *Omobranchus* occurs only as far east as the Line Islands (155°W), it, *Entomacrodus,* and *Istiblennius* inhabit the relatively isolated Hawaiian Islands, where *Ecsenius* apparently does not exist (collected there once, under peculiar circumstances; Springer, 1971). Somewhat in contrast, *Ecsenius* is common in the Red Sea, as is *Istiblennius* and, to a lesser degree, *Omobranchus,* but *Entomacrodus* has been collected there only once. Clearly, there is more involved in these distributions than simply ecology and/or the presence or absence of a planktonic stage. I believe that the explanations of many of these distribution patterns reside in the tectonic history of the Indo-Pacific, which is only just being unraveled.

Methods

Measurements.—Specimens were measured with needle-point dial calipers reading directly to the nearest tenth millimeter; measurements agree with those described in Springer (1971). Standard length, often rounded to the nearest whole mm, was taken from the midtip of the upper lip to the midlateral posterior margin of the hypurnal fan as indicated externally on the specimens. 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 portion of the head was not used in determining standard length.

I have not used measurements as extensively as I did in my 1971 study. To have made and analyzed detailed measurements in *Ecsenius* would have delayed inordinately the completion of my study, which has taken more years to complete than I anticipated when I started. Measurements are more time consuming to make and analyze, and are more difficult to make accurately, than counts. Measurements are seemingly more variable individually, and may be less accurate owing to the vagaries of preservation and damage to specimens from handling. Many measurements, unlike numerical characters in *Ecsenius,* regress positively or negatively during ontogeny, and many, like some numerical characters in *Ecsenius,* are additionally variable geographically or sexually. All species of *Ecsenius* can be distinguished without measurements. The usefulness and meaning of measurements in *Ecsenius* can be gleaned from my 1971 study: for most species, the proportionately longest nasal cirri and segmented dorsal-and caudal-fin rays occur in males, and males attain a greater standard length than females.

Counts.—With few exceptions, specimens were radiographed and counts of the dorsal-, anal-, and caudal-fin elements and precaudal and caudal vertebrae were taken from the radiographs. Occasional specimens lacked a dorsal-fin spine or ray or anal-fin ray. A missing dorsal-fin spine is recognizable when a pterygiophore in the spinous portion of the fin supports no element. A missing segmented ray in either fin is recognizable when the posterodistal end of a fused proximal plus middle pterygiophore (proximal pterygiophore of Springer, 1968: fig. 10) does not articulate with a ray). Missing fin elements were counted as if they were present.

Dentary incisor teeth include the total number of teeth on both dentaries, except for the posterior canines, and in all species except *E. midas,* in which the anterior canines are uniquely well differentiated and easily recognizable (to make dentary tooth counts comparable, either add two to each count for *E. midas* or subtract two from each count for the other species).

I have not included counts for procurrent caudal-fin rays, gill-rakers, pseudobranchial filaments, or epipleural ribs. In my 1971 study I included these counts, which although of interest are difficult to make accurately or with confidence, and do not affect the conclusions based on other information.

The meristic characters of all the species are summarized in Tables 1–4. Because many of the characters vary sexually or geographically within a species, actual frequency distributions are given in tables accompanying the species-group accounts.

Termination of Lateral Line.—The dorsal-fin element under which the lateral line terminated was recorded. Fin elements were numbered anteriormost to posteriormost without distinguishing spines from rays. If the lateral line terminated

TABLE 1.—Dorsal-fin element counts in the species of *Ecsenius* (X = modal count; more than one mode indicated where population or sexual differences or no definite mode exist; + = non-modal count). Actual frequencies for most species given in tables accompanying species-group accounts.

Species group and species	Spines					Segmented rays										Total elements										
	10	11	12	13	14	12	13	14	15	16	17	18	19	20	21	24	25	26	27	28	29	30	31	32	33	34
Pulcher Group																										
aroni			+	X						+	X	X									+	X	X			
gravieri			+	X	+					+	X	X	+								+	X	X	+		
pulcher			+	X	+							+	X	+									+	X	+	+
Stigmatura Group																										
lividanalis		+	X			+	X	+								+	X	+								
melarchus		+	X						+	X	+								+	X	+					
midas			+	X	+							+	X	X	+								+	X	X	+
stigmatura			X	+					+	X	+								+	X	+					
Frontalis Group																										
frontalis	+	+	X	+							+	X	X	X	+					+	+	X	X	X	+	
Bicolor Group																										
bicolor		+	X						+	X	X	X							+	X	X	X				
namiyei		+	X									X	X	X	+							X	X	X	+	
Lineatus Group																										
lineatus			X	+						+	X	X								+	X	X				
Oculus Group																										
monoculus		+	X			+	X	+								+	X	+								
oculatus			X				X	X	+								X	X	+							
oculus			X			+	X	X	+							+	X	X	+							
pardus			X				+	X	+								+	X	+							
paroculus			X			+	X	+								+	X	+								
portenoyi			X				+	X	+								+	X	+							
sellifer			X				X	X									X	X								
tessera			X					X	+									X	+							
Yaeyamaensis Group																										
dentex		+	X	+			+	X	+								+	X	+							
minutus			X	+			+	X									+	X								
nalolo		+	X	+		+	X	X								+	X	X	+							
stictus			X	+			+	X	+								+	X	+							
yaeyamaensis		+	X	+			+	X	+								+	X	+							
Opsifrontalis Group																										
alleni			X				X	+									X	+								
australianus			X				+	X	+								+	X	+							
axelrodi			X			+	X	+								+	X	+								
bathi		+	X			+	X	+								+	X	+								
dilemma			X			+	X									+	X									
fijiensis			X				X	+									X	+								
fourmanoiri			X					+	X									+	X							
opsifrontalis			X			+	X	+								+	X	+								
tigris			X				+	X									+	X								
Isos Group																										
isos			X					X	+									X	+							
lubbocki		+	X				+	X									+	X								
trilineatus		+	X				+	X	+								+	X	+							
Prooculis Group																										
bandanus		+	X	+			+	X	+								+	X	+							
bimaculatus			X	+			+	X									+	X								
collettei			X					X	+									X	+							
prooculis			X	+			+	X	+								+	X	+							
taeniatus			X					X										X								
Pictus Group																										
pictus			X				X	X	X									X	X	X						
Mandibularis Group																										
aequalis			X	+			+	X	+								+	X	+							
kurti			X				+	X	+								+	X	+							
mandibularis		+	X					+	X	+								+	X	+						
schroederi		+	X	+			+	X										+	X							

TABLE 2.—Certain fin-ray counts in the species of *Ecsenius* (X = modal count; more than one mode indicated where population or sexual differences or no definite mode exist; + = non-modal count). Actual frequencies for most species given in tables accompanying species-group accounts.

Species group and species	Segmented anal-fin rays											Pectoral-fin rays					Segmented caudal-fin rays			
	13	14	15	16	17	18	19	20	21	22	23	12	13	14	15	16	12	13	14	15
Pulcher Group																				
aroni							+	X					+	X	+			X		
gravieri						+	X	X	+				+	X	+			X		
pulcher							+	+	X	X	+		+	X	+			X	+	
Stigmatura Group																				
lividanalis	X	X										+	X	+				+	X	+
melarchus					+	X	+						+	X	+			+	X	
midas								+	X	X	+	+	X	+				+	X	+
stigmatura					+	X	+						+	X	+			+	X	
Frontalis Group																				
frontalis					+	+	X	X	+	+				+	X	+		X	+	
Bicolor Group																				
bicolor					+	X	X	X	+			+	X	+				+	X	
namiyei							+	X	X	X		+	X	+				+	X	
Lineatus Group																				
lineatus						+	X	X				+	X	+				X		
Oculus Group																				
monoculus		+	X	+									X	+				X	+	
oculatus			X	X	+								X					X		
oculus			+	X	+								X					X	+	
pardus				X	X							+	X	+				X	+	
paroculus		+	X	+								+	X	+				X		
portenoyi		+	+	X								+	X					X		
sellifer			X	+									X					X		
tessera				X	X								X					X		
Yaeyamaensis Group																				
dentex			+	X	+							+	X	+				X		
minutus			X	X								+	X	+				X		
nalolo		+	X	X	+							+	X	+				X	+	
stictus			+	X	+							+	X	+				X		
yaeyamaensis		+	+	X	+							+	X					X		
Opsifrontalis Group																				
alleni		+	X	+									X					X		
australianus			+	X	+								X	+				X		
axelrodi		+	X	+								+	X					X		
bathi		X	X										X	+				X		
dilemma		+	X									+	X	+				X		
fijiensis			X	X									X	+				X		
fourmanoiri				+	X							+	X					X		
opsifrontalis		+	X	+								+	X	+				X		
tigris			+	X								+	X	+			+	X		
Isos Group																				
isos				X	+								X	+				X		
lubbocki			+	X									X					X		
trilineatus			+	X	+							+	X	+				X		
Prooculis Group																				
bandanus			+	X	+							+	X	+				X	+	
bimaculatus			+	X	+							+	X					X		
collettei				X									X					X		
prooculis			+	X	+							+	X	+				X		
taeniatus				X									X					X		
Pictus Group																				
pictus			+	X	X							+	X	+				X		
Mandibularis Group																				
aequalis		+	+	X	+							+	X	+				X		
kurti		+	+	X	+								X	+				X		
mandibularis				+	X	+						+	X					X		
schroederi			+	X									X	+				X		

TABLE 3.—Vertebral counts in the species of *Ecsenius* (X = modal count; more than one mode indicated where population or sexual differences or no definite mode exist; + = non-modal count; PCV = precaudal vertebrae). Actual frequencies for most species given in tables accompanying species-group accounts.

Species group and species	PCV				Caudal vertebrae												Total vertebrae											
	9	10	11	12	18	19	20	21	22	23	24	25	26	27	28	29	29	30	31	32	33	34	35	36	37	38	39	40
Pulcher Group																												
aroni		+	X							+	+	X	+									+	+	X	+			
gravieri		+	X								+	X	+										+	X	+			
pulcher		+	X	+									X	X	+										X	X	+	
Stigmatura Group																												
lividanalis			X		+	X											+	X										
melarchus		X	+						+	X	+									+	X	+						
midas		+	X												X	X	X									X	X	X
stigmatura		X							+	X	+									+	X	+						
Frontalis Group																												
frontalis		+	X							+	X	X	+									+	X	X	+			
Bicolor Group																												
bicolor		X	+						+	X	X	X								+	X	X	X					
namiyei		X	X								X	X	X	X	+							X	X	X	X	+		
Lineatus Group																												
lineatus		X	X								X	X	+									X	X	X				
Oculus Group																												
monoculus	+	X						+	X	+									+	X	+							
oculatus		X						+	X	+									+	X	+							
oculus		X						+	X	X	+								+	X	X	+						
pardus		X							+	X	+									+	X	+						
paroculus		X					+	X	X									+	X	X								
portenoyi		X						+	+	X	+								+	+	X							
sellifer		X						+	X										+	X								
tessera		X								X											X							
Yaeyamaensis Group																												
dentex		X						+	X	+									+	X	+							
minutus		X						+	X										+	X								
nalolo		X						X	X	+									X	X	+							
stictus		X						+	X	+									+	X	+							
yaeyamaensis		X						+	X	+									+	X	+							
Opsifrontalis Group																												
alleni		X						+	X										+	X								
australianus		X						+	X	+									+	X	+							
axelrodi		X						+	X	+									+	X	+							
bathi		X					+	X	X									+	X	X								
dilemma		X					+	X	+									+	X	+								
fijiensis		X						+	X	+									+	X	+							
fourmanoiri		X								X	+										X	+						
opsifrontalis		X						+	X	+									+	X	+							
tigris		X							X											X								
Isos Group																												
isos		X							X											X	+							
lubbocki		X						+	X										+	X								
trilineatus		X						+	X	+									+	X	+							
Prooculis Group																												
bandanus		X						+	X	+									+	X	+							
bimaculatus		X						+	X										+	X								
collettei		X						+	X										+	X								
prooculis		X						+	X	+									+	X	+							
taeniatus		X							X	+										X	+							
Pictus Group																												
pictus		X						X	X	+									X	X	+							
Mandibularis Group																												
aequalis		X						+	X	+									+	X	+							
kurti		X						+	X	+									+	X	+							
mandibularis		X	+					+	+	X	+								+	+	X	+						
schroederi		X	+					+	X	+									+	X	+							

Table 4.—Dentary incisor teeth counts in the species of *Ecsenius* (X = common count; + = uncommon count; - = no information). Anterior canines included in counts except for *E. midas*. Actual frequencies for most species given in tables accompanying species-group accounts.

	Dentary incisor teeth																																							
Species group and species	11	12	13	14	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	56	57	58	59	60	61	62	63	64
Pulcher Group																																								
aroni																						+	-	-	+	+	X	X	X	X	X	X	+							
gravieri																				+	-	+	X	X	X	X	X	+	+	+										
pulcher																				X	X	X	X	X	X	X	X	+	+											
Stigmatura Group																																								
lividanalis					+	X	X	X	X	X	X	X	+																											
melanchus												+	+	X	X	X	+	+																						
midas	+	+	+	X																																				
stigmatura										+	+	X	X	X	+	+																								
Frontalis Group																																								
frontalis																+	+	+	+	X	X	X	X	X	X	X	X	X	+											
Bicolor Group																																								
bicolor								+	-	-	+	+	+	+	X	X	X	X	X	X	+	+																		
namiyei										X	X	X	X	X	X	X	X	X	X	X	X																			
Lineatus Group																																								
lineatus																					X	X	X	X	X	-	+													
Oculus Group																																								
monoculus																		+	-	+	+	X	X	X	X	X	X	X	X	+	-	+								
oculatus																							+	+	-	X	X	X	X	X	X	X	X	X	-	+				
oculus																														+	+	X	X	X	X	X	X	X	+	+
pardus																								+	+	X	X	X	X	X	X	X	X							
paroculus																							+	X	X	X	X	X	X	X	X	X	+	+						
portenoyi																						+	+	+	+	X	X	X	X	X	X	X	X	+						
sellifer																							+	+	+	X	X	X	X	+										
tessera																										X	X	X	X	X										
Yaeyamaensis Group																																								
dentex																											+	X	X	X	X	X	X	X	X	X	X	+	+	
minutus																						X	X	X	X	X	X	+	+											
nalolo																		+	+	+	X	X	X	X	X	X	X	X	+	+										
stictus																						X	X	X	X	X	X	X	X	X	+	+								
yaeyamaensis																	+	+	+	X	X	X	X	X	X	X	X	X	X	+										
Opsifrontalis Group																																								
alleni																	X	X	X	X	X	X	+	-	-	+														
australianus																				+	-	X	X	X	X	X														
axelrodi														+	-	X	X	X	X	X	+	+																		
bathi											X	-	X	X	X	X	X	-	X																					
dilemma															X	X	X	X	X	+																				
fijiensis												+	-	-	-	-	+	+	+	+	X	X	X	X	X	+														
fourmanoiri																					+	X	X	X	X															
opsifrontalis																	+	+	X	X	X	X	X	X	X	X														
tigris																			X	-	X	X																		
Isos Group																																								
isos																	X	-	X	X	-	-	-	X	X															
lubbocki													X	-	-	-	-	X	-	X	X	-	X	X																
trilineatus																X	X	X	X	X	X	+																		
Procculis Group																																								
bandanus															+	X	X	X	X	X	X	X	+																	
bimaculatus															X	X	X	X	X	X	X																			
collettei																					X	X	-	X	X	X														
procculis																	+	X	X	X	X	X	X	X	+															
taeniatus																				X	-	X	X																	
Pictus Group																																								
pictus																X	X	X	X	X	X	X	X	X																
Mandibularis Group																																								
aequalis																		+	+	+	+	X	X	X	X	X	+													
kurti																		+	X	X	X	X																		
mandibularis																					X	X	X	X	X	X	X	+	+											
schroederi																	+	-	+	X	X	X	-	X	X	-	-	-	+											

below the space between two elements, the number of the more posterior element was recorded (this method is different from that of Springer, 1971).

DORSAL-FIN NOTCH.—The dorsal fin varies from entire to deeply notched in the area above the last spine. The following terms were used to describe notching: entire = unnotched; slightly notched = incised less than half height of fin; moderately notched = notched about half height of fin; deeply notched = notched more than half height of fin.

COLOR PATTERN.—Stripes refer to markings aligned with the longitudinal axis of the body; bands or bars refer to markings aligned with the vertical axis of the body.

Most of the species of *Ecsenius* can be identified on color pattern alone, and I believe relationships are reflected to a great extent by color-pattern similarities. For these reasons I devote most of my species descriptions to color pattern, even though I provide numerous illustrations, both halftone and color. Often, color pattern characteristics are unclear in printed illustrations, and published color may be greatly different from that of the original color photograph. It is rarely possible to give the full range of variation in color pattern that any species exhibits. I have tried, therefore, to err (if error it is), on the side of over-illustrating.

Because seawater rapidly absorbs color at the red end of the spectrum, most close-up underwater color photographs are taken with electronic flash, which can illuminate sufficiently to overide the light absorption of the water. The colors of the images obtained, therefore, do not appear in the photographs as they would to an underwater observer under natural conditions. These factors should be considered when reading my descriptions of live coloration or when viewing the color plates.

With the exception of *E. bicolor*, and unless indicated otherwise, the species descriptions are based on all the specimens in the material lists. New material that I have not previously reported is noted with an asterisk (*). The available material of *E. bicolor* is so extensive that I have only listed the new material (without asterisks) in the material list, but the description and discussion also include that on which I have published previously.

PHILOSOPHY OF CLASSIFICATION.—I subscribe to the principles of phylogenetic classification (cladistics), but have found insurmountable obstacles in the practical application of these principles, particularly when trying to relate blenniid genera and the species within genera. For *Ecsenius*, I can only propose one outgroup, the Salariini less *Ecsenius*. Because the phylogeny of the Salariini is unresolved, I am unable to polarize characters unequivocally for *Ecsenius* species. Furthermore, many of the characters I had for consideration, especially at the species level, are modal states for meristic characters, which I find impossible to polarize unequivocally (one exception: number of segmented caudal-fin rays). Populations of some species exhibit variation in modal states for meristic characters, even for such an ordinarily invariable character as number of precaudal vertebrae.

One reviewer disagrees with me, apparently proposing that only the modal state for a meristic character of a species be used in polarizing the character, without considering all other states exhibited for the character by the species. If the reviewer's reasoning is valid, could not the same reasoning be used to characterize a genus by selecting from among the species only the modal state for each character?

In establishing the species groups of *Ecsenius*, I used ingroup analysis, wherein I heavily weighted selected uncommon character states, at the same time recognizing the fallacy of such a basis. In some instances the groups so defined were established in earlier studies, particularly McKinney and Springer (1976), based on intuitive or other non-cladistic assessment. In spite of problems in formal methodology, I believe most of the species groups I recognize are monophyletic, but a few are possibly paraphyletic.

In several of the groups established early in the study, all the species were allopatric. Later in the study, I found additional species assignable to these groups. In each group, the newly added species were also allopatric. Although this information has no bearing on the formulation of cladistic hypotheses of relationships, I consider these circumstances interestingly coincidental, and what one might expect if strict vicariance (without subsequent dispersal) was the main or only mechanism of speciation in a monophyletic group.

ABBREVIATIONS.—Symbolic codes (Leviton et al., 1985) are used to identify the institutions that made available the specimens incorporated in my study. The same codes are used to designate the institutional affiliations of persons acknowledged for assistance.

SL = standard length
m.y.a. = million years ago

Other abbreviations are clear in context.

ACKNOWLEDGMENTS

Numerous individuals have assisted me during the long course of preparing this study. Without their help, my work would not have been completed: K.A. Bruwelheide, J. Clayton, A. Gerberich, V. Krantz, and J.T. Williams, USNM, and E.O. Murdy, formerly USNM; L.K. Knapp, Smithsonian Oceanographic Sorting Center; J. Libbey, Smithsonian Diving Officer; T. Iwamoto and W.N. Eschmeyer, CAS; D.F. Hoese and J. Paxton, AMS; G.R. Allen and J.B. Hutchins, WAM; B.C. Russell, NTM; R. Winterbottom, ROM; J.E. Randall and A. Susumoto, BPBM; W. Saul and W.F. Smith-Vaniz, ANSP; W. Klausewitz, SMF; H. Bath, Pirmasens, W. Germany; R. Patzner, Universität Salzburg, Austria; staff, AMNH; A.D. Lewis and fisheries staff, Ministry of Primary Industries, Suva, Fiji; M. Gawel, formerly University of the South Pacific, Fiji; R. Croft, formerly fisheries officer, State of Pohnpei; M.L. Bauchot, MNHN; A. Ben-Tuvia, HUJ; L. Fishelson, TAU; A.C. Wheeler and P. Whitehead, BMNH; R. Myers, UGM; staff, KFRS; staff, FMRI; P.C. Heemstra and M.M. Smith,

RUSI; R.K. Johnson, formerly FMNH; R.C. Wass, Office of Marine Resources, American Samoa; B.A. Carlson, Waikiki Aquarium, Honolulu; C.H. Hocutt, Horn Point Environmental Laboratories, Cambridge, Maryland.

Most of the half-tone drawings, and some of the half-tone photographs, of fishes were published and acknowledged in my previous studies, but all are individually acknowledged parenthetically in the illustration captions.

I am most grateful for the extreme generosity of J.E. Randall (BPBM), who permitted me to use a very large number of his original color photographs, and G.R. Allen, who permitted me to use some of his photographs awaiting publication elsewhere. R.C. Steene, Cairns, Queensland, provided several fine duplicates of his color slides for my use. Other color slides reproduced among my plates were provided by H.R. Axelrod and W.E. Burgess from the files of T.F.H. Publications, Inc., which generously provided the color separations and printed and donated the color plates for inclusion in the final publication.

Portions of early drafts of this manuscript were discussed with or read by several persons, especially R.H. Gibbs, Jr., and G. David Johnson, whose valued suggestions materially improved the final draft. Entire drafts of a complete ms were read and constructively criticized by J.T. Williams (USNM), G. Nelson (AMNH), and R. Winterbottom (ROM), an arduous task at best, and one for which I am greatly appreciative. I especially thank my editors, T.J. Slowik and J. Horn, for the great effort they expended in improving format and text and bringing the whole to a printable state.

Important new material, added since McKinney and Springer (1976), resulted from my fieldwork in Fiji, Philippines, Rotuma, Papua New Guinea, Pohnpei, and Cargados Carajos. My fieldwork in these places was supported by grants from the Dreyfus Foundation and the Lewis L. and Rosa Strauss Memorial Foundation.

Ecsenius McCulloch

Ecsenius McCulloch, 1923:121 [type-species: *E. mandibularis* McCulloch, 1923, by original designation].

Pescadorichthys Tomiyama, 1955:8 [type-species: *Salarias namiyei* Jordan and Evermann, 1902, by original designation].

Anthiiblennius Starck, 1969:1 [as a subgenus of *Ecsenius;* type-species: *Ecsenius* (*Anthiiblennius*) *midas* Starck, 1969, by original designation].

DESCRIPTION AND RELATIONSHIPS.—*Ecsenius* is a member of the family Blenniidae, tribe Salariini. Springer (1968) implicitly hypothesized the monophyly of the Blenniidae, and I reassert that the three main characters used to define the family are synapomorphies. Springer (1968) and Smith-Vaniz and Springer (1971) implicitly hypothesized the monophyly

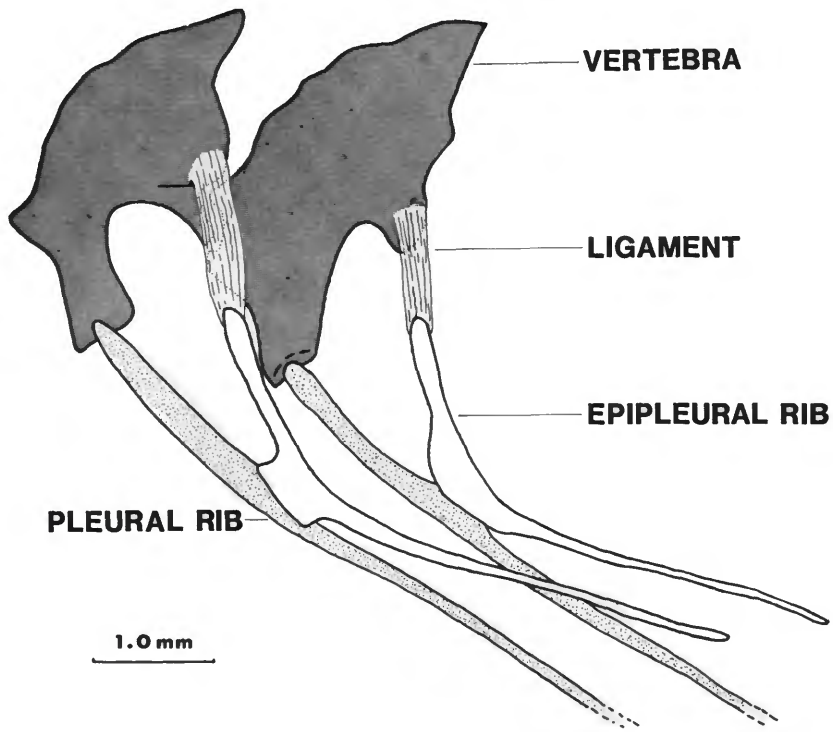


FIGURE 1.—Epipleural ribs attached to third and fourth from anteriormost vertebrae in *Ecsenius stigmatura,* USNM 221238, anterior toward left, left side rotated about 20° dorsally.

of the Salariini, and I reassert that the main character used to define the tribe is a synapomorphy. Springer (1971) and Smith-Vaniz and Springer (1971) defined *Ecsenius*, implicitly hypothesizing monophyly of the genus, which is characterized by a number of specializations, at least two of which are unique among blennioids (sensu George and Springer, 1980) and which I reassert are synapomorphies: (1) absence of an ossified median ethmoid bone (little or no ethmoid cartilage is present) (Figure 3); (2) dorso-medial extension of the proximal end of one or more of the anteriormost epipleural ribs from their point of contact with the pleural ribs, and with a ligament connecting the proximal end of the extension to the associated neural arch (Figure 1).

Springer and Smith-Vaniz also implicitly hypothesized a third synapomorphy of *Ecsenius:* presence on dentary of both posterior and anterior canine teeth (Figure 2). While the presence in combination of both types of dentary canines is unique to *Ecsenius* among the Blenniidae, each type of canine should be treated as a separate character.

Among the Salariini, anterior dentary canine teeth are present only in *Ecsenius* (all species). Among the other blenniid tribes, anterior dentary canines are present in all species except some species of the Parablenniini (Bock and Zander, 1986; = "Blenniini" of Smith-Vaniz, 1976), which is probably polyphyletic, but presumably contains the most plesiomorphic blenniids and the presently unknown sister group of the Salariini. Superficially, the presence of anterior canines in *Ecsenius* would appear to indicate that *Ecsenius* is the sister group of all other Salariini and that it is plesiomorphic for anterior canines. The polarity of the anterior canines in *Ecsenius* is equivocal, however, because the Parablenniini exhibits both states for the character.

Except for *Ecsenius midas*, which has well differentiated anterior dentary canines, the anterior canines in nonskeletonized preparations of *Ecsenius* species are either so modified that they superficially appear to be incisors, or they are only just recognizably differentiated from the incisors (Figure 2 illustrates skeletonized mandible of *E. bicolor*, in which canines are slightly differentiated; Figure 4 illustrates *E. yaeyamaensis*, in which the canine is recognizable only because it is ankylosed to the dentary). In other blenniids that have them, the anterior canines are clearly differentiated from

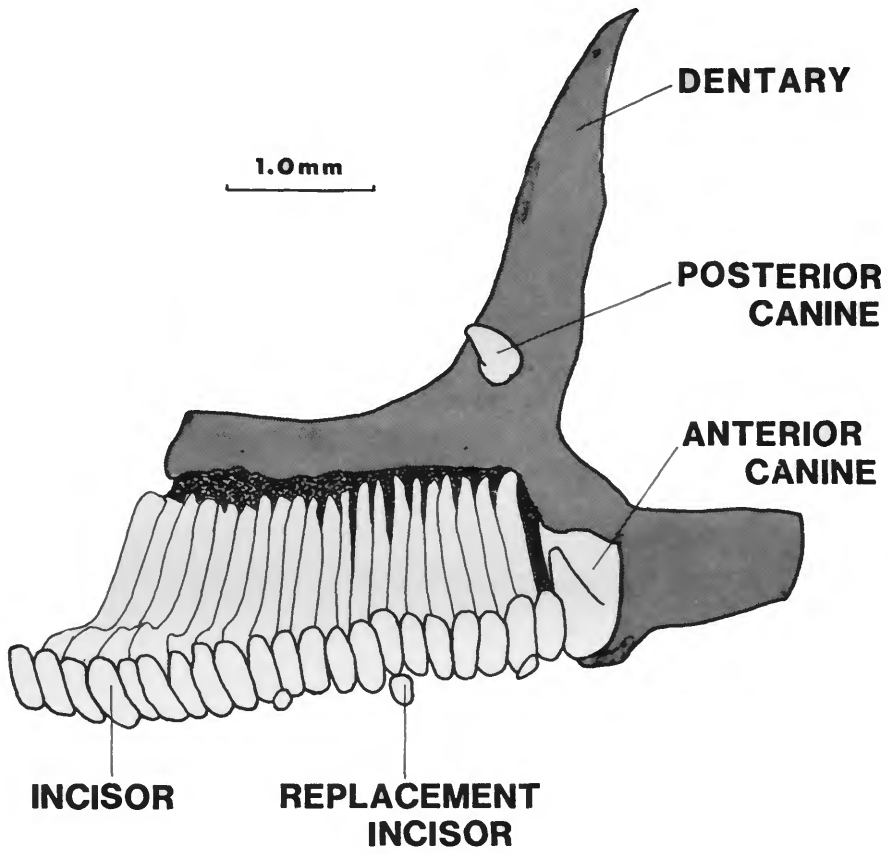


FIGURE 2.—Anterior view of left dentary bone of *Ecsenius bicolor*, USNM 201368. Anterior canine tooth is often more bluntly rounded.

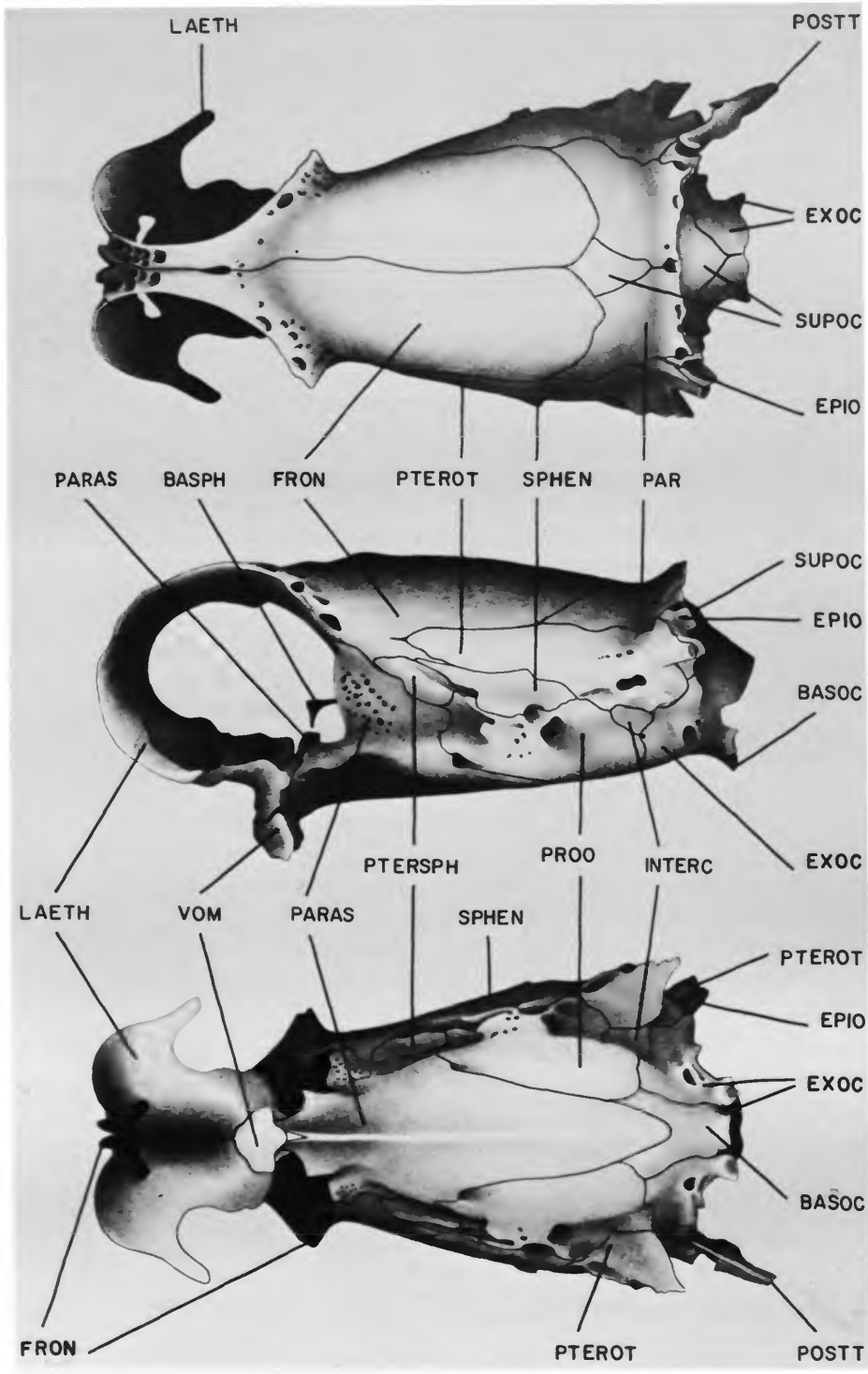


FIGURE 3.—Dorsal, lateral, ventral views of cranium of *Ecsenius yaeyamaensis*, USNM 200428. BASPH = basisphenoid; BASOC = basioccipital; EPIO = epioccipital; EXOC = exoccipital; FRON = frontal; INTERC = intercalar; LAETH = lateral ethmoid; PAR = parietal; PARAS = parasphenoid; POSTT = posttemporal; PROO = prootic; PTEROT = pterotic; PTERSPH = pterosphenoid; SPHEN = sphenotic; SUPOC = supraoccipital; VOM = vomer (drawn by S. L. Chambers).

the incisors. It might appear, therefore, that the clearly differentiated condition of the anterior canines in *E. midas* is plesiomorphic. The possiblility, however, that the presence of anterior canines in *Ecsenius* is a homoplasious condition, precludes an unequivocal hypothesis of the primitive state of these canines in *Ecsenius*.

Posterior dentary canine teeth are present in the Blenniidae only in 17 of the 21 genera of Salariini, but they may not be present in all species of a genus or in both sexes of a species. The argument that posterior canines are a synapomorphy of *Ecsenius* plus the other genera of Salariini that have them appears at first to be parsimonious. I believe, however, that the canines are a synapomorphy of the Salariini, having been lost secondarily in the four, otherwise highly specialized, genera comprising five species that lack them. In any event, even if I were to narrow the sister group of *Ecsenius* to the 17 genera with about 125 species exhibiting the canines, problems of polarizing characters in *Ecsenius* would not be facilitated.

Two synapomorphies of *Ecsenius*—loss of the lateral extrascapulars (or their fusion with the pterotics, Figures 3 and 4) and filamentous caudal-fin lobes—occur variously in some genera of the tribes Omobranchini and Nemophini, which are not sister groups of the Salariini (Smith-Vaniz, 1976).

Characters exhibited by *Ecsenius* that are probably plesiomorphic for the Salariini or cannot be polarized unequivocally are all caudal-fin rays simple; four infraorbital bones; restriction of the lateral-line to the anterodorsal portion of the body (rarely extends posteriorly beyond a vertical from the last dorsal-fin spine and never beyond the first dorsal-fin segmented ray); anal-fin spines of mature males not enveloped by fleshy or rugose swellings; nape and orbital cirri lacking; simple cirrus present on posterior rim of anterior nostril; fleshy nuchal crest absent; gill opening continuous across throat; lips entire (not crenulate); sensory pore positions on head simple; median, dorsal supraoccipital pore present; dorsal-fin spines 10–14 (strongly modally 12 or 13 in all species); segmented

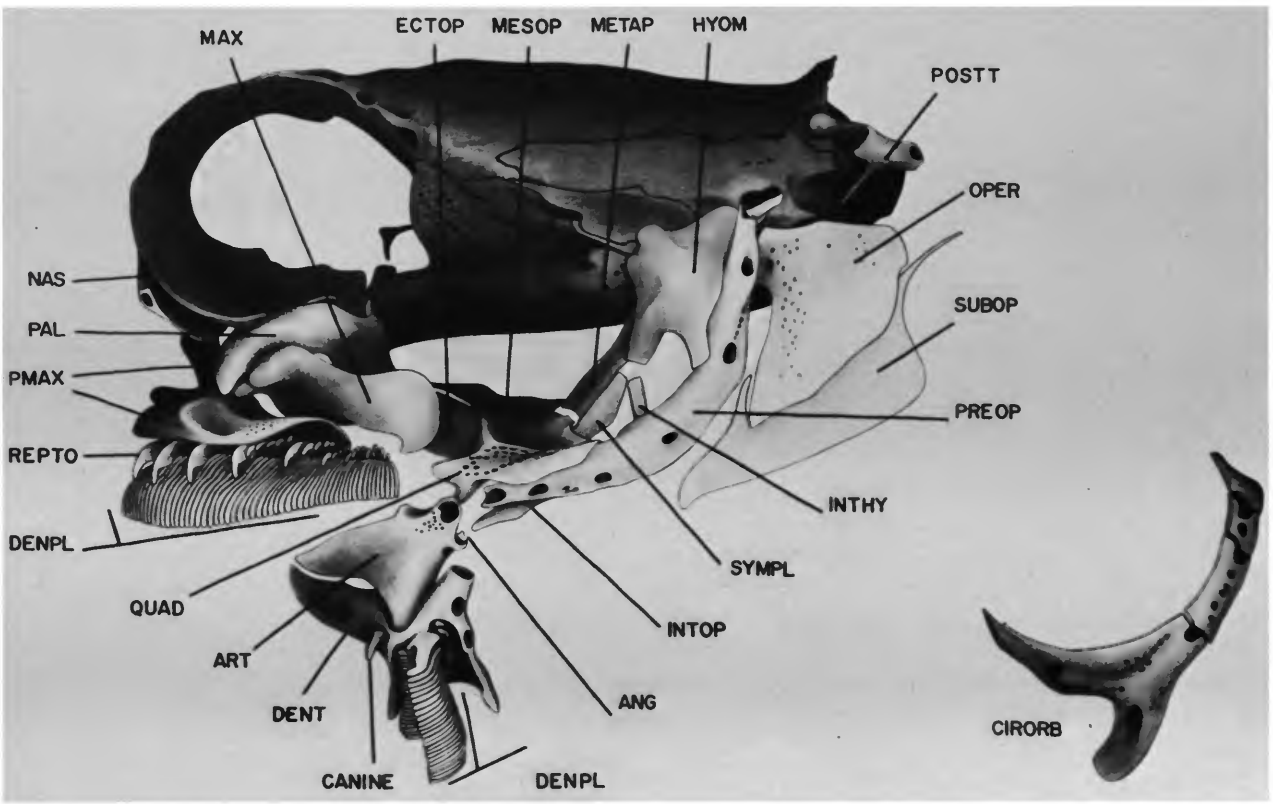


FIGURE 4.—Lateral view of skull of *Ecsenius yaeyamaensis* with infraorbital bones separated (lower right). ANG = retroarticular; ART = articular; CANINE = posterior canine tooth (anterior not labelled); CIRORB = infraorbitals; DENPL = dental plate; DENT = dentary; ECTOP = ectopterygoid; HYOM = hyomandibula; INTHY = interhyal; INTOP = interopercle; MAX = maxillary; MESOP = mesopterygoid; METAP = metapterygoid; NAS = nasal; OPER = opercle; PAL = palatine; PMAX = premaxilla; POSTT = posttemporal; PREOP = preopercle; QUAD = QUADRATE; REPTO = replacement tooth; SUBOP = subopercle; SYMPL = symplectic (drawn by S.L. Chambers).

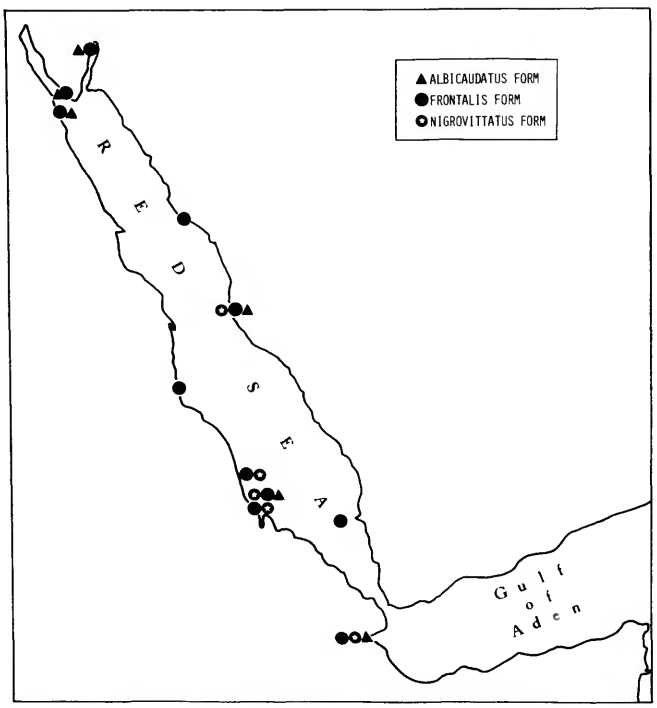


FIGURE 5.—Distribution of the three color-pattern forms of *Ecsenius frontalis*, only member of the Frontalis Group.

dorsal-fin rays 12–21; segmented anal-fin rays 13–23; last anal-fin pterygiophore supports single ray (as opposed to two rays, a condition occurring only in some individuals of some genera of Salariini); last anal-fin ray bound to caudal peduncle by membrane; precaudal vertebrae modally 10 or 11; caudal vertebrae 18–29; total vertebrae 29–40; pectoral-fin rays 12–16 (strongly modally 13–15 depending on species); segmented pelvic-fin rays 3; innermost pelvic-fin ray greatly reduced and often inapparent; segmented caudal-fin rays 13–15 (modally 13 or 14 depending on species); dentary incisor teeth 11–16 or 29–64; premaxillary teeth 26–34 or ~95–150; vomer edentate; membrane from posteriormost dorsal-fin ray attaches to caudal peduncle anterior to bases of segmented caudal-fin rays; larvae apparently lacking an ophioblennius stage, head spines, or darkly pigmented pectoral-fin rays.

Generalized frequency distributions for several meristic characters and numbers of dentary incisor teeth for the *Ecsenius* species are given in Tables 1–4 (actual frequencies for most characters are given in tables accompanying each species-group account).

TABLE 5.—Distribution of numbers of species and species groups in *Ecsenius*.

	Species		Species groups	
Distribution	Total	Endemic	Total	Endemic
Indo-west and central Pacific	46	46	12	12
W. Indian Ocean	7	5	4	1
Red Sea	6	4	4	1
E. Africa	2	0	2	0
N. Arabian Sea	1	1	1	0
Central Indian Ocean	5*	1	4*	0
W. Pacific & E. Indian oceans	39	33	9	5
W. Pacific Ocean	36	28	9	2
Java and vicinity	5	1	5	0
Philippines (less Batan Id)	13	3**	9	0
Mariana & Palau islands	4	0	4	0
Taiwan, Ryukyus, & Batan Ids	4	1	4	0
New Guinea	12	2	7	0
Solomon Islands	10	0	8	0
New Caledonia & New Hebrides	4	2	4	0
Fiji	5	2	5	0
Great Barrier Reef	6	3	5	0
Coral Sea	2	1	2	0
Pacific Plate	4	2	4	0
Samoa & Rotuma	3	1	3	0

*Includes one species and one group expected.
**Includes one species also known from NW corner of Borneo.

GENERAL BIOGEOGRAPHICAL COMMENTS.—The distribution of many of the species and species groups of *Ecsenius* are tightly delimited (Figures 5–13). Within each of several species groups no two species occur sympatrically. The most isolated population of a species may be separated from its geographically closest possible conspecific population by a distance far greater than that separating the isolated population from that of another species in the same species group (for instance, Figures 40 and 41). This circumstance exists even though the geographically closer species may not be the sister group of the species in question.

More species (13) and species groups (9) of *Ecsenius* are known from the Philippines than any other area of comparable size. Only three species groups are missing from the Philippines: the two confined to the Red Sea and Persian Gulf areas (Frontalis, Pulcher) and the Isos Group. A generalized breakdown of the distribution of the species and species groups is given in Table 5. Distribution maps, each incorporating all the species of one or more species groups, are given in Figures 5–13. The base maps for all but one of these figures are slightly modified from those used by Springer (1982), which include dashed lines indicating generalized margins of the major lithospheric plates.

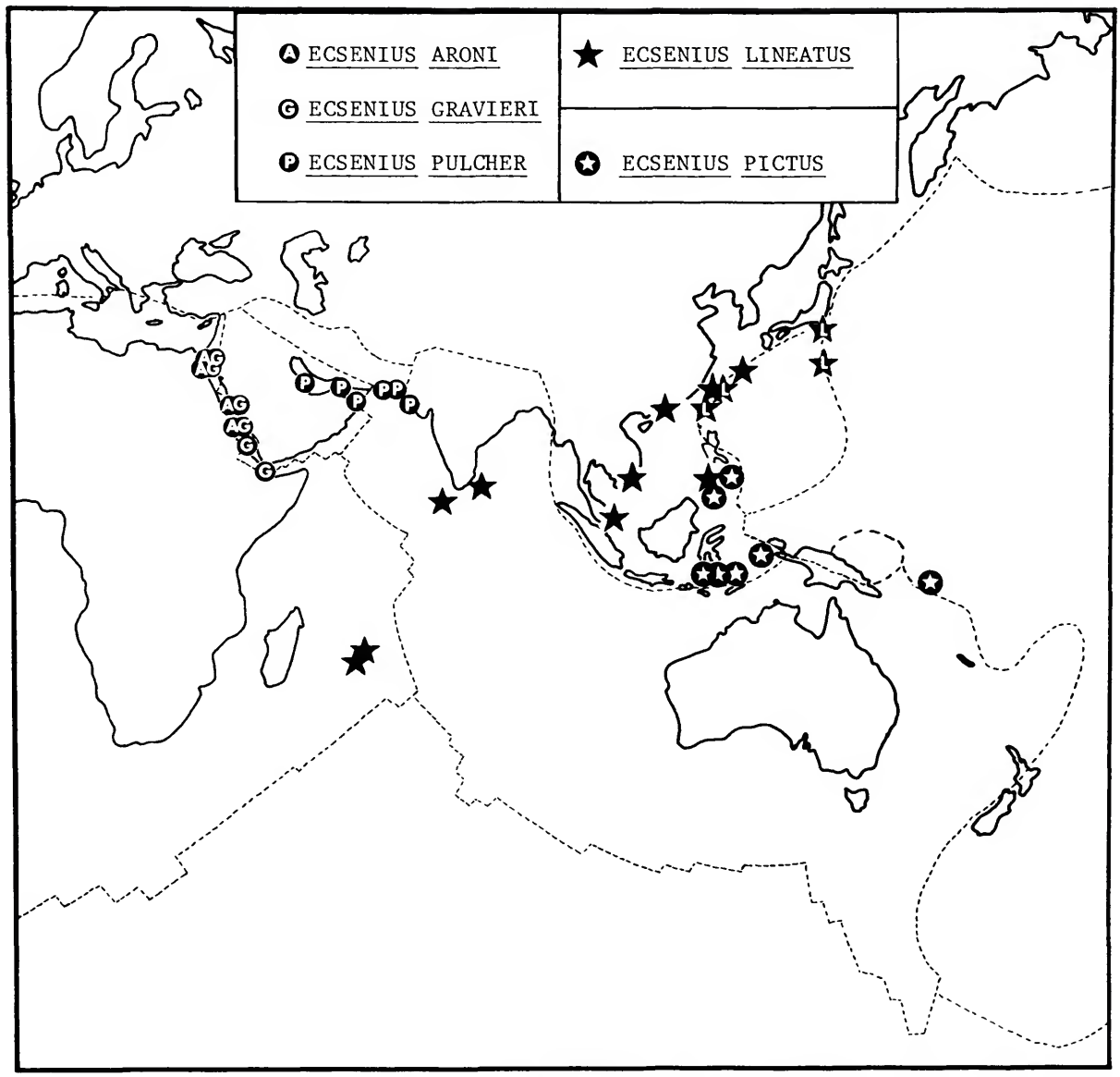


FIGURE 6.—Distribution of the species in the Pulcher (A,G,P), Lineatus, and Pictus groups ("L" in symbol for *Ecsenius lineatus* represents acceptable distribution record based on the literature).

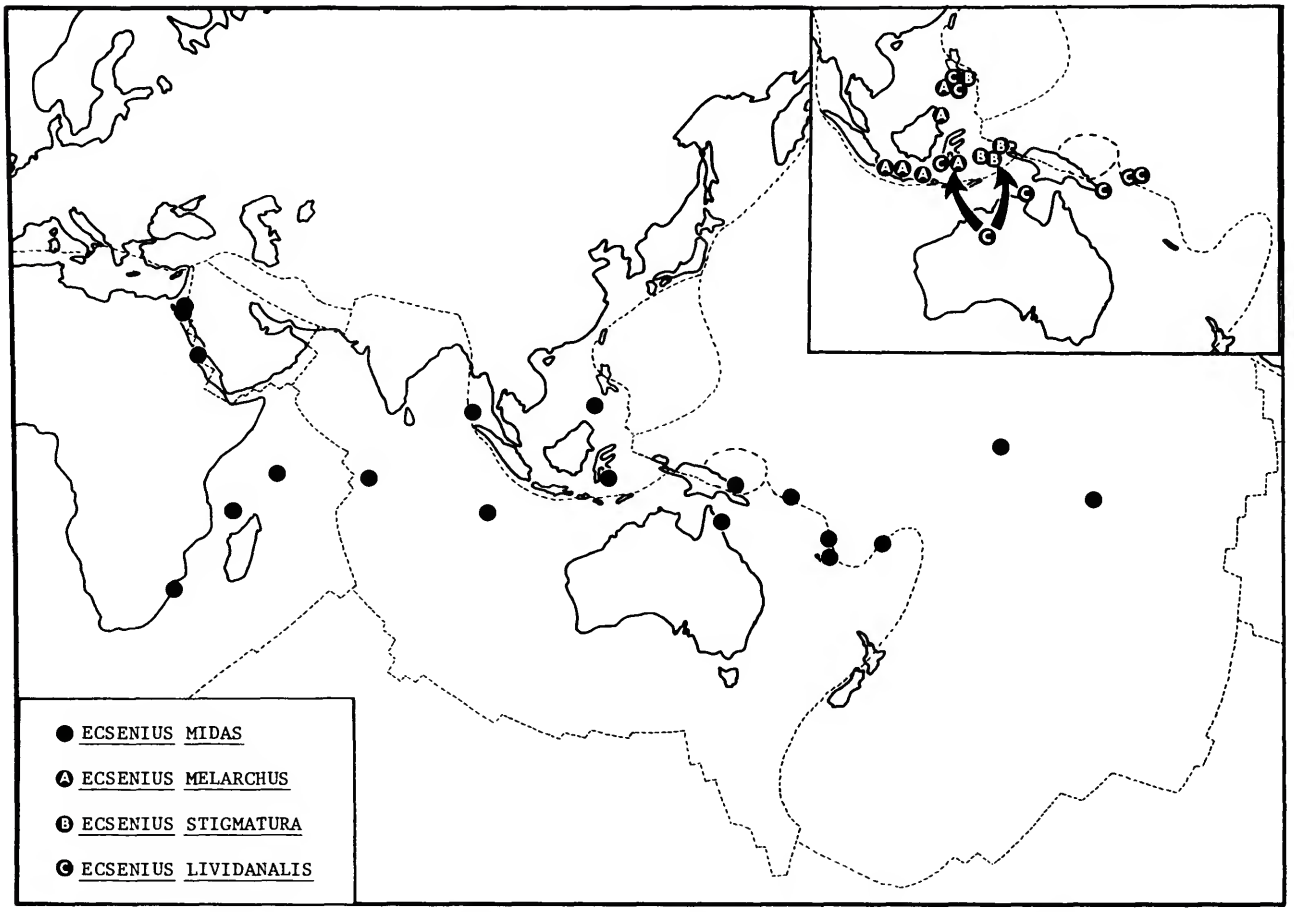


FIGURE 7.—Distribution of the species in the Stigmatura Group. Arrows point to two localities where *Ecsenius lividanalis* is sympatric with either *E. melarchus* or *E. stigmatura* (the symbol for *E. lividanalis* in inland Australia is not meant to indicate presence of *E. lividanalis* at that spot). A recently received record for *E. melarchus* based on a photograph taken at Flores (just south of Sulawesi) is not indicated.

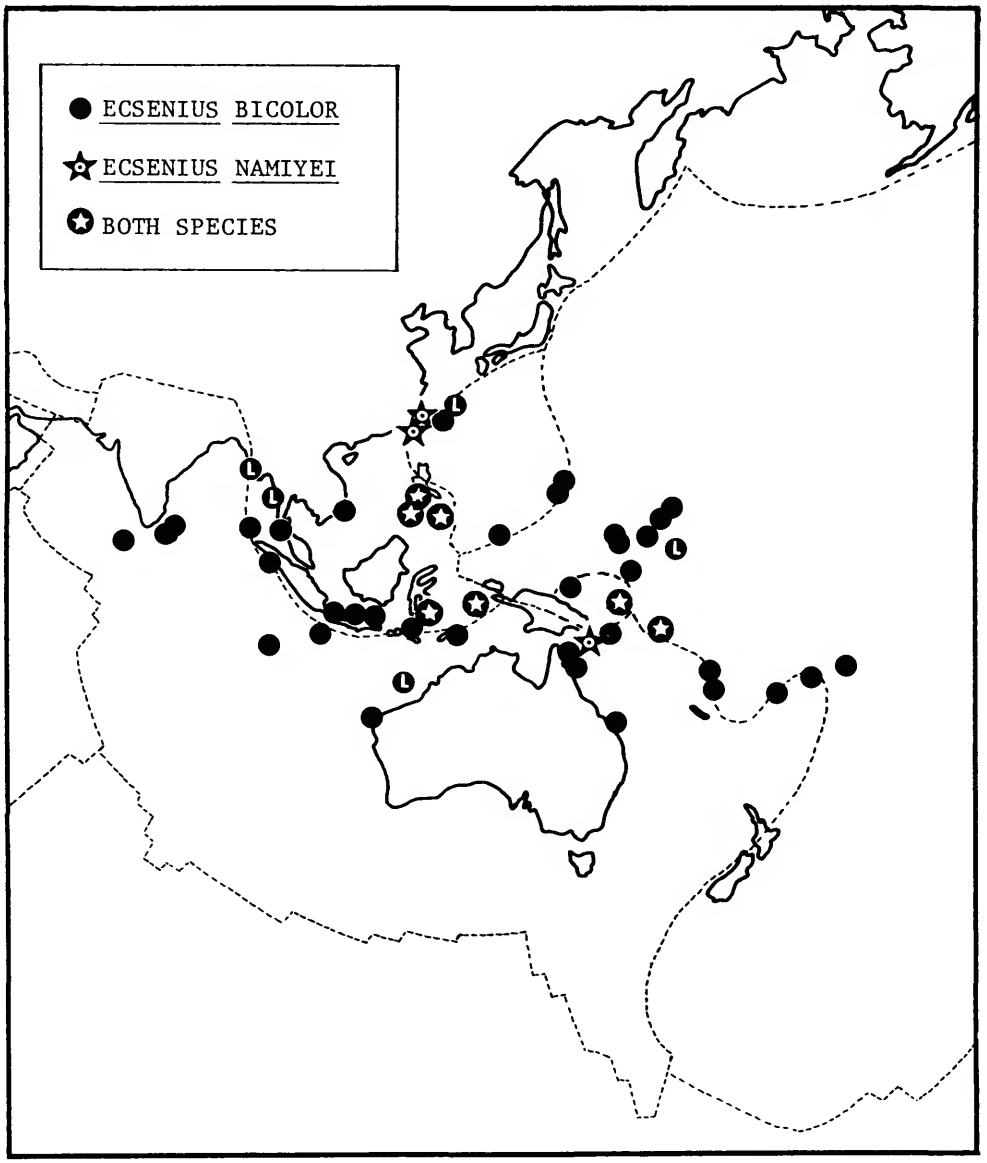


FIGURE 8.—Distribution of the species of the Bicolor Group ("L" in symbol for *Ecsenius bicolor* indicates acceptable distribution record based on literature, or, in the case of Rowley Shoals, Western Australia D.F. Hoese, in litt.).

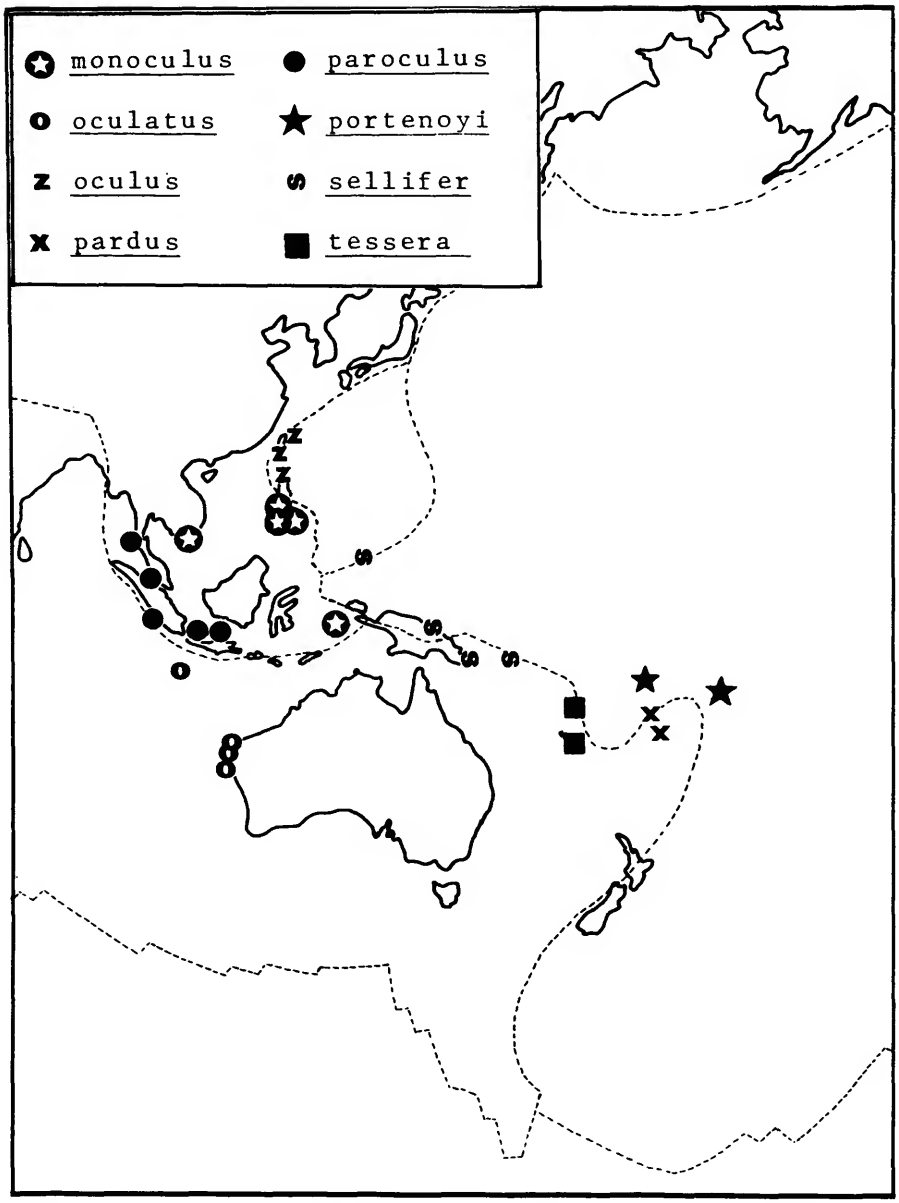


FIGURE 9.—Distribution of the species in the Oculus Group.

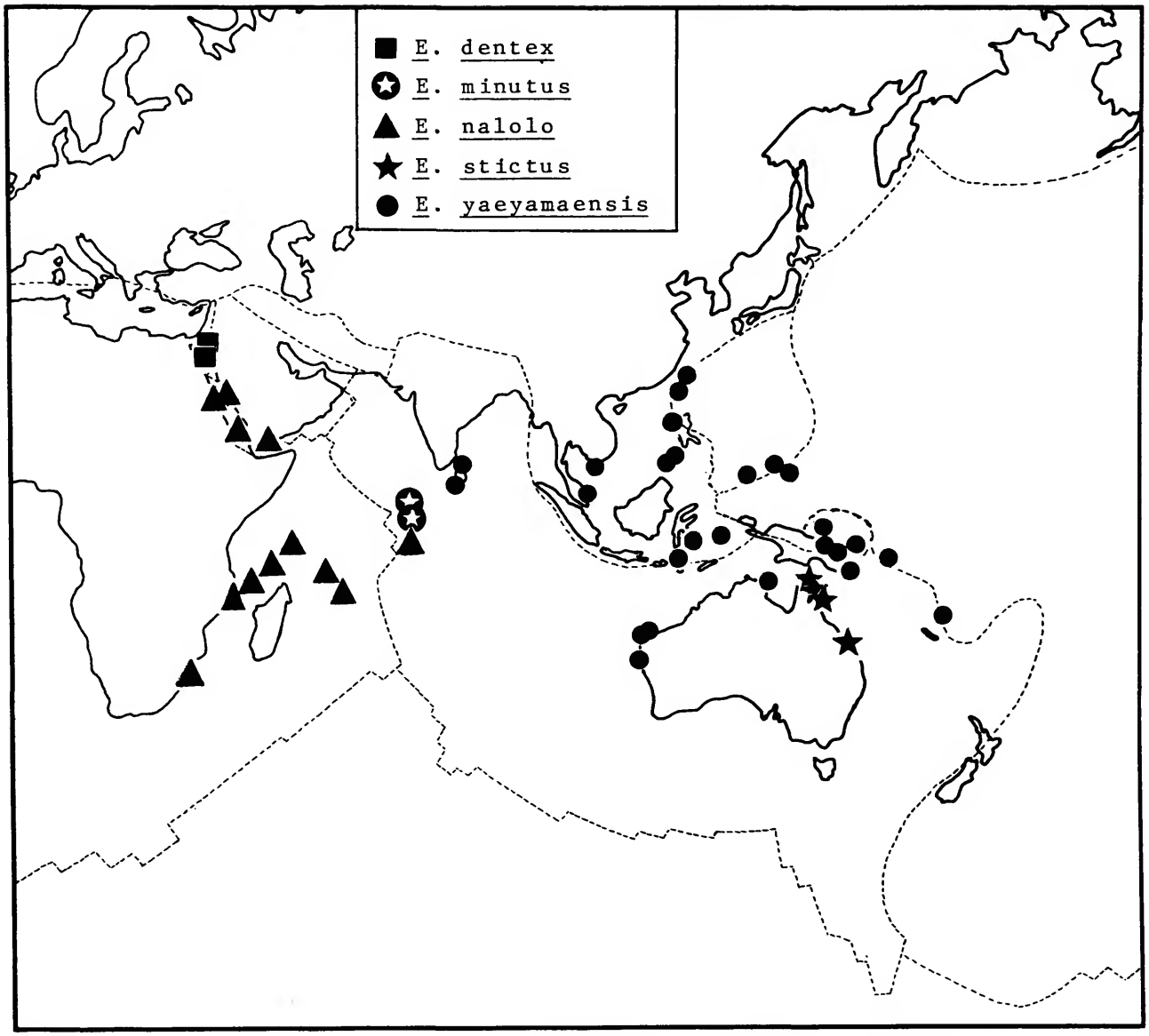


FIGURE 10.—Distribution of the species in the Yaeyamaensis Group.

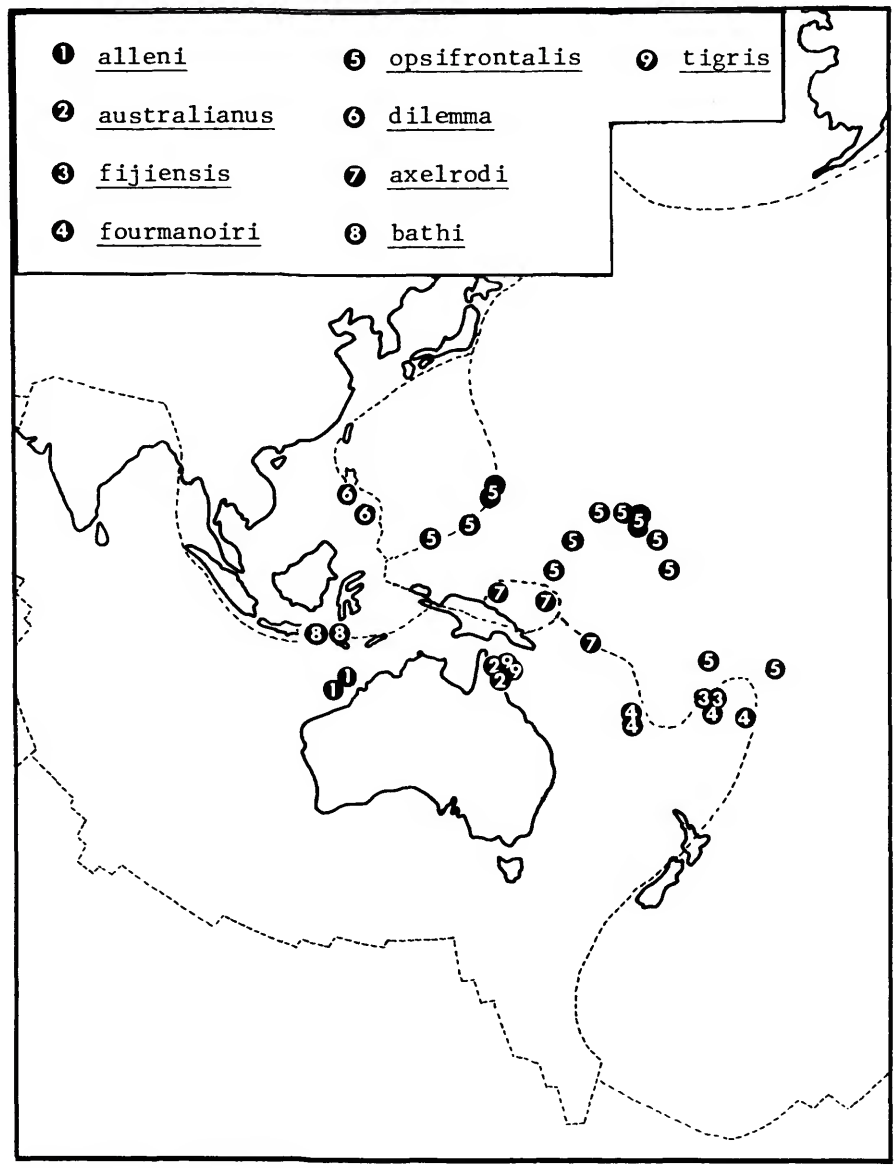


FIGURE 11.—Distribution of the species in the Opsifrontalis Group (see also Figures 40 and 41).

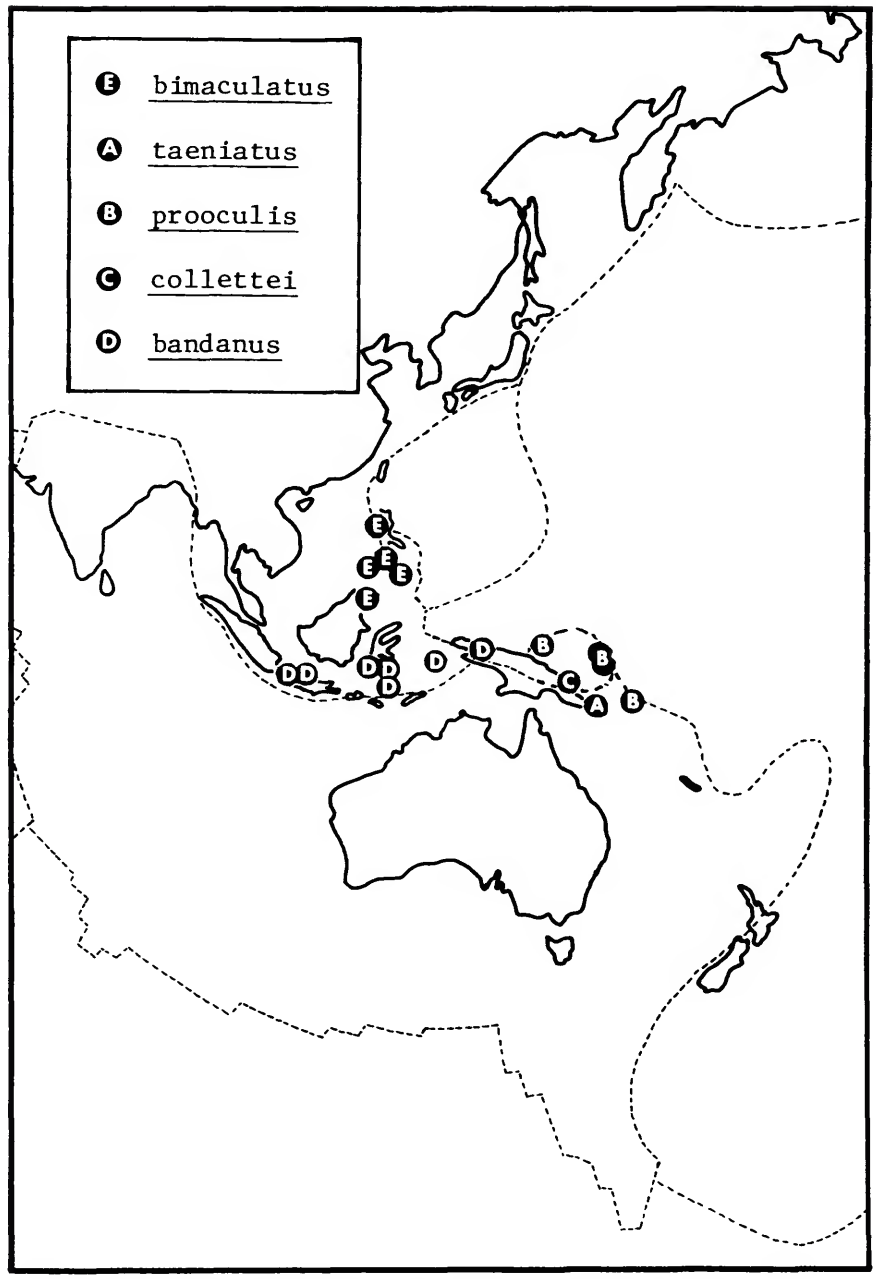


FIGURE 12.—Distribution of the species in the Prooculis Group (includes plot based on photograph of *E. bandanus* taken at Bone Rate, south of Sulawesi).

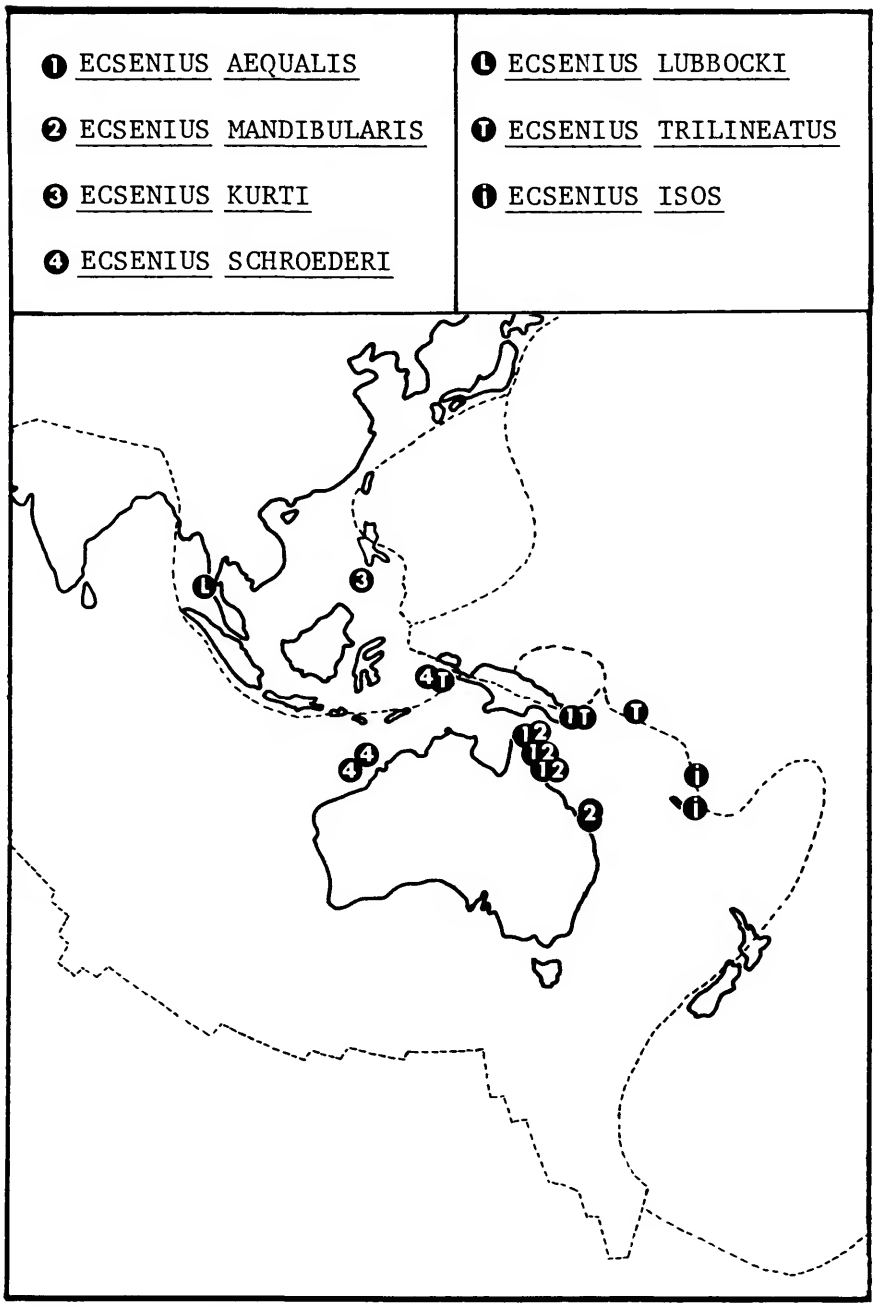


FIGURE 13.—Distribution of the species in the Mandibularis (numbered) and Isos (lettered) groups.

Key to the Species of *Ecsenius*

1. Pectoral-fin rays 14–16 (15 or 16 in 95% of specimens); dorsal fin entire (no notch between spinous and segmented ray portions) (Frontalis Group) . . . ***E. frontalis***
(Red Sea and adjacent gulfs)

   Pectoral-fin rays 12–15 (12–14 in 95% of specimens); dorsal fin entire or notched 2

2. Large, dark spot in skin present just anterior to anus; segmented caudal-fin rays usually 14; dentary incisor teeth 13–42, rarely more than 40 (Stigmatura Group) . 3

   No dark spot present in skin anterior to anus; segmented caudal-fin rays usually 13 or 14 (most species with 13); dentary incisor teeth 32 or more 6

3. Anterior dentary canines enlarged and obvious; total incisor teeth in lower jaw 13–16; dorsal fin entire, spines usually 13, origin anterior to vertical from middle preopercular pores . . . . . ***E. midas***
(Indo-Pacific)

   Anterior dentary canines not enlarged or obvious; total incisor teeth in lower jaw 29–42; dorsal fin notched slightly to deeply, spines usually 12, origin posterior to vertical from middle preopercular pores 4

4. Total dorsal-fin elements 24–26; dorsal fin notched slightly at most; segmented anal-fin rays 13 or 14; pectoral-fin rays usually 13 . . . . . ***E. lividanalis***
(Philippines S to N Australia, W to Solomon Islands)

   Total dorsal-fin elements 27–29; dorsal fin notched deeply; segmented anal-fin rays 17–19; pectoral-fin rays usually 14 5

5. Large, dark spot on caudal peduncle . . . . . ***E. stigmatura***
(eastern Philippines S to Moluccas)

   No dark spot on caudal peduncle . . . . . ***E. melarchus***
(western Philippines S to Sulawesi, W to Java)

6. Cirrus present on both anterior and posterior rims of anterior nostril; lateral line frequently with vertical pairs of pores; dorsal fin entire or with shallow notch; segmented caudal-fin rays usually 14 (Bicolor Group) 7

   Cirrus present only on posterior rim of anterior nostril; lateral-line pores unpaired; dorsal fin deeply notched; segmented caudal-fin rays usually 13 8

7. Dorsal fin entire, origin at or anterior to vertical from middle preopercular pores, total elements 30–33 . . . . . ***E. namiyei***
(Ryukyu Islands S to Indonesia, E to Solomon Islands)

   Dorsal fin notched, origin posterior to vertical from middle preopercular pores, total elements 27–30 . . . . . ***E. bicolor***
(Maldive Islands E to Samoa Islands)

8. Posterior canine teeth 0–2 (usually 1) on each side 12

   Posterior canine teeth 4–8 on each side (Mandibularis Group) 9

9. Body without indications of dark stripes on side; segmented dorsal-fin rays 14–16 (usually 15); segmented anal-fin rays 16–18 (usually 17); size to 51 mm SL . . . . . ***E. mandibularis***
(Great Barrier Reef)

   Body with indications of three dark stripes on side; segmented dorsal-fin rays 13–15 (usually 14); segmented anal-fin rays 14–17 (usually 16); size to 33 mm SL 10

10. Anteriorly on body, middle stripe spaced about equidistant from upper and lower stripes 11

    Anteriorly on body, middle stripe about twice as close to lower stripe as to upper stripe . . . . . ***E. schroederi***
(islands off Western Australia; Moluccas)

11. Three to 6 well-defined, dark spots in line with posterior end of each middle and lower body stripe (occasionally upper stripe also); posteriormost spot exactly at

caudal-fin base; pair of well-defined, dusky stripes on ventral surface of head usually present; dusky stripe often present on fleshy pectoral-fin base . . ***E. kurti***
(Philippines)

Zero to 5 (rarely more than 2) diffuse, usually dash-like, dark spots in line from posterior end of each middle or lower body stripe; posteriormost spot noticeably anterior to caudal-fin base; pair of dusky stripes on ventral surface of head usually absent, poorly represented when present; no dusky stripe present on fleshy pectoral-fin base . . . . . ***E. aequalis***
(Great Barrier Reef; Trobriand Islands)

12. Segmented dorsal-fin rays 16–20, total elements 28–34; segmented anal-fin rays 18–23 13

Segmented dorsal-fin rays 12–15, total elements 24–27; segmented anal-fin rays 13–16 16

13. Dorsal-fin spines 12 or 13 (rarely 13); pectoral-fin rays 12–14 (rarely 14) (Lineatus Group) . . . . . ***E. lineatus***
(mid-Indian Ocean E to Japan, S to Sumatra and Philippines)

Dorsal-fin spines 12–14 (rarely 12); pectoral-fin rays 13–15 (rarely 13) (Pulcher Group) 14

14. Mid-portion of distal half of at least spinous dorsal fin black or with black spots in interradial membranes; dorsal and ventral lobes of caudal fin darker than remainder of fin; body usually with several small, black spots on posterior third and slender, black stripe on dorsoanterior portion . . . . . ***E. gravieri***
(Red Sea and adjacent gulfs)

No black marks in dorsal fin; caudal-fin lobes not darker than remainder of fin; body without black spots or black stripe 15

15. Body uniformly dark with dusky spot at caudal-fin base; segmented dorsal-fin rays 16–18; segmented anal-fin rays 19 or 20 . . . . . ***E. aroni***
(Red Sea)

Body uniformly dark or posterior half pale with contrasting dark bars; segmented dorsal-fin rays 18–20 (usually more than 18); segmented anal-fin rays 19–23 (rarely less than 21) . . . . . ***E. pulcher***
(Persian Gulf, Gulf of Oman, and N Arabian Sea)

16. Anterior three-fourths of body dusky with 5–8 (usually more than 6) slender, pale stripes; posterior quarter of body pale with three irregular, dusky bars (Pictus Group) . . . . . ***E. pictus***
(Philippines SE to Solomon Ids.)

Anterior body color pattern variable, but pale stripes, if present, fewer than 4; posterior body color pattern variable, with or without dusky bars 17

17. Following combination of characters present: one or more pale-ringed or pale-margined, large, dark spots present on body posterior to vertical at anal-fin origin (may be present anteriorly as well; if only one spot is present it appears as saddle dorsally on caudal peduncle; vertical pair of posteriorly converging, dark, tapered, stripe-like markings extending from caudal peduncle onto caudal fin; ventral lip (exclusive of corners of mouth) and small area just posterior to lip immaculate (occasionally a fine line of melanophores outline lip margin anteriorly) (Oculus Group) 18

Pale-ringed or margined, large, dark spots not present on body posterior to vertical at anal-fin origin (dark, saddle on caudal peduncle never present); converging, dark, tapered, stripe-like markings extending from caudal peduncle onto caudal fin present or absent; ventral lip varying from almost black to pale; immaculate area just posterior to lip present or absent 25

18. Large, pale-margined, intensely dark spots (exclusive of dark markings at caudal-fin base) present both above and below midline of body (some ventral body spots, exclusive of spots at caudal-fin base, as intensely pigmented as most intensely pigmented dorsal body spots) 19

Large, pale-margined, intensely dark spot or spots (exclusive of dark spots at caudal-fin base) present only above midline of body (ventral body spots, exclusive of spots at caudal-fin base, never as intensely pigmented as most intensely pigmented dorsal body spots) 21

19. Dark spots on posterior half of body tile-like, surrounded and separated from each other only by pale, grout-like (interconnected) network . . . . . ***E. tessera***
(New Caledonia; New Hebrides)

Dark spots on posterior half of body not tile-like, each spot usually surrounded by discrete, pale ring or broad, pale, diffuse area, with darker ground color of body between pale rings or areas 20

20. Dorsal row of dark spots below segmented-ray portion of dorsal fin usually not saddle-like; space between pair of dorsal dark body spots just posterior to vertical from anteriormost (of 3) dark spot of ventral row about equal to space between second spot of pair and next spot posteriorly; no pale stripe extending most of midbody length; dark spots on posterior half of body surrounded by conspicuous, discrete, pale rings . . . . . ***E. pardus***
(Fiji)

Dorsal row of dark spots below segmented-ray portion of dorsal fin usually saddle-like; space between pair of dorsal dark body spots just posterior to vertical from anteriormost (of 3) dark spot of ventral row narrower than space between second spot of pair and next spot posteriorly; slender, pale stripe extending most of midbody length usually present; dark spots on posterior half of body often not surrounded by conspicuous, discrete, pale rings (diffuse or faintly pale rings often present around spots) . . . . . ***E. portenoyi***
(Samoa; Rotuma)

21. One to 5 (rarely 5) intensely dark spots on body (exclusive of vertical pair at caudal-fin base), all of which are saddle-like, reaching dorsal body contour (pale margins not surrounding spots dorsally) 22

Five to 11 intensely dark spots on body (exclusive of vertical pair at caudal-fin base), all or most of which are not saddle-like, not reaching dorsal body contour (pale margins completely surrounding spots) 23

22. Three to 5 (rarely 5) large, dark, saddle-like spots on body; transverse pair of conspicuous dark spots on nape; melanophores of interradial membranes of spinous dorsal fin ascending spines but not forming stripe . . . . . ***E. sellifer***
(New Guinea; Solomon Islands)

One large, dark, saddle-like spot on body; no conspicuous dark spots on nape (pair of dusky spots may be present); melanophores of interradial membranes of spinous dorsal fin ascending spines and forming fine, dusky, suprabasal stripe . . . . . ***E. monoculus***
(Viet Nam; Philippines; Moluccas)

23. Nape without transverse pair of conspicuous, small, dark or dusky spots; ocellus, if present on body below fifth to sixth dorsal-fin spines positioned in line with postorbital head stripe; distance between midline of body (in area below segmented dorsal-fin rays) and ventral edge of dark portion of each ocellus less than distance between dorsal edge of dark portion and dorsal body contour; pairs of distinct, small, dark spots on dorsal body contour dorsal to ocellated spots; dentary incisors 54–64 (rarely less than 56) . . . . . ***E. oculus***
(Taiwan S to Batan Islands—northernmost Philippines)

Nape usually with transverse pair of conspicuous, small, dark or dusky spots; ocellus, if present on body below fifth to sixth dorsal-fin spines, positioned slightly dorsal to level of postorbital head stripe; distance between midline of body (in area below segmented dorsal-fin rays) and ventral edge of dark portion of each ocellus equal to or greater than distance between dorsal edge of dark portion and dorsal body contour; distinct, small, dark spots rarely present on dorsal body contour dorsal to

ocellated spots, never paired when present; dentary incisors 47–60 (rarely more than 58) 24

24. Anteriormost ocellated, dark spot of linear series on dorsal portion of body usually at or anterior to vertical at midbase of spinous dorsal fin; linear series of ocellated, dark body spots (excluding vertical pair at caudal-fin base) 7–11 (rarely 7; average 8.0–9.5 depending on population); round or horizontally oblong ocellus often present on body just posterodorsal to pectoral-fin axil (occasionally represented only by an intensification of the postorbital stripe as it extends onto the body) . . . . . ***E. paroculus***
(Thailand to Sumatra and Java)

Anteriormost ocellated, dark spot of linear series on dorsal portion of body usually posterior to vertical at midbase of spinous dorsal fin (usually at or posterior to dorsal-fin notch); ocellated, dark body spots (excluding vertical pair at caudal-fin base) 5–8 (rarely 8; average 5.7–6.5 depending on population); no ocellus or intensification of pigment on body in area just posterodorsal to pectoral-fin axil (extension of postorbital stripe on body unremarkable) . . . . . ***E. oculatus***
(Christmas Island, Indian Ocean, S to Western Australia)

25. Combination of characters usually present: conspicuous, immaculate, pale area on chin bordered anteriorly by dark ventral lip and posteriorly by darkly dusky area; dark stripe extending posteriorly from mid-postorbital margin (possibly absent in Maldive Islands specimens); dark stripe or Y-shaped mark on fleshy pectoral-fin base; diffuse pale spots on body in more than one row; no transverse pair of dark spots on nape; no dark or dusky stripe-like marks extending from caudal peduncle onto caudal fin . . . . . 26 (Yaeyamaensis Group)

Above characters never present in combination; pale area on chin, if present, unremarkable, usually associated with species lacking dark postorbital stripe; dark markings on pectoral-fin base never Y-shaped; diffuse, pale spots, when present, often in a single row; transverse pair of dark spots on nape present only in ***E. lubbocki*** (key couplet 30); stripe-like marks extending onto caudal fin present or absent 30

26. Fleshy pectoral-fin base with distinct, dark Y-shaped mark (shank of Y directed anteriorly) 27

Fleshy pectoral-fin base with dark stripe, stripes, or various dark markings, never distinctly Y-shaped 28

27. Posterior portion of body with sparse peppering of fine, dark spots . . . . ***E. stictus***
(Great Barrier Reef)

Posterior portion of body without sparse peppering of fine, dark spots . . . . . ***E. yaeyamaensis***
(Sri Lanka E to New Hebrides, N to Ryukyus, Western Australia, Northern Territory, not Great Barrier Reef)

28. Distinct, dark stripe on pectoral-fin base entering fin between seventh and eighth from dorsalmost rays; dark, curving stripe on opercle extending dorsally to, or almost to, dark spot (remnant of a dark postorbital stripe) at dorsal margin of opercle . . . . . ***E. minutus***
(Maldive Ids.)

Dark stripe on pectoral-fin base, if distinct, entering fin between fifth and sixth from dorsalmost rays; dark, curving line on opercle extending dorsally to point well ventral to dorsal margin of opercle (dark postorbital stripe usually present along dorsal opercular margin) 29

29. Dentary incisor teeth of males 49–59 (rarely less than 52), females 53–63; only distinct marking on pectoral-fin base is a dark stripe . . . . . ***E. dentex***
(Gulf of Aqaba and Red Sea coast of Egypt S to about Ghardaqa)

Dentary incisor teeth of males 41–52 (rarely 52), females 45–54; pectoral-fin base with dark stripe and/or other dark markings . . . . . ***E. nalolo***
(Red Sea S of Egypt and western Indian Ocean)

30. Fleshy pectoral-fin base with two faintly to darkly dusky stripes: dorsal stripe usually entering fin between dorsalmost two rays, ventral stripe usually entering fin at about midlevel; transverse pair of dark spots present or absent on nape; no dark or dusky postorbital stripe on head; no dark bars on body (faint bars may be present); ventroanteriorly curving, faintly or darkly dusky line on opercle present (two species) or absent (one species) . . . . . 31 (Isos Group)

    Fleshy pectoral-fin base marked variously, but never more than one dark stripe, which, when present, enters fin at about midlevel; no transverse pair of dark spots on nape; dark or dusky postorbital stripe present or absent on head; dark bars present or absent on body; ventroanteriorly curving darkly dusky line on opercle present (one species) or absent (12 species) 33

31. Transverse pair of distinct, dark spots present on nape; no rows of distinct, dark spots, dashes, or pinstripes present on body posteriorly . . . . . ***E. lubbocki***
    (Indian Ocean coast of Thailand)

    No dark spots present on nape; two rows of distinct dark spots, dashes, or stripes present on body 32

32. Pair of distinct, dark stripes present on fleshy pectoral-fin base; two rows of distinct dark stripes, dashes, and spots extend length of body; ventroanteriorly curving darkly dusky line on opercle . . . . . ***E. trilineatus***
    (Moluccas E to Solomon Islands)

    Pair of faintly dusky stripes present on fleshy pectoral-fin base; two rows of distinct, dark spots present only on posterior half of body; two dusky spots present on opercle . . . . . ***E. isos***
    (New Caledonia; New Hebrides)

33. Lateral line terminates posteriorly between verticals from eighth and tenth from anteriormost dorsal-fin element (rarely posterior to ninth); one or two pairs of dark spots present or absent on ventral surface of head; segmented dorsal-fin rays modally 14 . . . . . 34 (Prooculis Group)

    Lateral line terminates posteriorly between verticals from ninth and 13th from anteriormost dorsal-fin element (rarely anterior to tenth); ventral surface of head more or less uniformly pigmented, except one species with dark line on each side (lines originate on opercle); segmented dorsal-fin rays modally 13–15 (13 in six species, 14 in two, and 15 in one) (Opsifrontalis Group) 38

34. Body with two rows of large, dark spots extending for most of body length (four spots on caudal peduncle) . . . . . ***E. collettei***
    (Madang Harbor, Papua New Guinea)

    Body striped, or with two dark spots on abdomen, or lacking distinct, dark markings 35

35. Body with two dark spots on side in abdominal region . . . . . ***E. bimaculatus***
    (Philippines SW to N Borneo)

    Body striped or lacking distinct, dark markings 36

36. Body lacking distinct, dark markings . . . . . ***E. bandanus***
    (islands off NW Java E to NW New Guinea)

    Body with alternating dark and pale stripes 37

37. Dorsal pale stripe on body ventral to level of lateral line; ventral pale stripe well ventral to body midline . . . . . ***E. prooculis***
    (Western Admiralty Islands E to Solomon Islands)

    Dorsal pale stripe on body just dorsal to lateral line; ventral pale stripe on body midline . . . . . ***E. taeniatus***
    (Milne Bay area SE Papua-New Guinea)

38. Conspicuous dark line originating along posterior margin of opercle and extending ventroanteriorly to ventral surface of head; distinct, dark stripe on fleshy pectoral-fin base; segmented dorsal-fin rays 14 or 15 (15 in 88% of specimens) . . . . . ***E. fourmanoiri***
    (Loyalty Islands and New Caledonia E to Tongatabu)

No dark line on posterior margin of opercle; distinct, dark stripe on fleshy pectoral-fin base rarely present (large, dark spot may be present); segmented dorsal-fin rays 12 to 15 (15 only in 4% of specimens of 1 of 7 species) 39

39. Large, round, black spot on fleshy pectoral-fin base, another, smaller spot in pectoral axil . . . . . ***E. alleni***
(Scott Reef and Rowley Shoals off Western Australia)

Markings on fleshy pectoral-fin base diffuse and unremarkable, or dusky spot- or stripe-like; no black spot in pectoral axil 40

40. Six to 8 more-or-less vertical pairs of dark spots (round or vertically elongate) on body posterior to vertical at dorsal-fin notch 41

Dark markings, when present, on body posterior to vertical at dorsal-fin notch, in form of stripes, bands, or unpaired spots 42

41. Four to six conspicuous, dark spots on dorsal body contour at base of spinous dorsal fin; two vertical pairs of dark spots on caudal peduncle . . . . . ***E. tigris***
(Osprey and Bougainville reefs, Coral Sea)

Zero to two (usually zero) dark spots on dorsal body contour at base of spinous dorsal fin; three vertical pairs of dark spots on caudal peduncle . . . . ***E. fijiensis***
(Fiji, except Rotuma, S to Vatoa, Lau Islands)

42. Two intensely dark stripes most conspicuous dark markings on body 43

Dark spots or bands or equally dark, diffusely dusky stripes and bands most conspicuous markings on body 45

43. Oblong, obliquely inclined, black spot just dorsal to dorsal insertion of pectoral fin (marking may be continuous or only slightly discontinuous with dorsal dark body stripe, or postorbital stripe) . . . . . ***E. axelrodi***
(Western Admiralties E to Solomon Islands)

No obvious dark spot in area above dorsal insertion of pectoral fin (dorsalmost dark body stripe continuous and unremarkable in this area) 44

44. Philippines (cheeks in life pinkish, as far as known) . . . . . ***E. dilemma***

Bali and Komodo, Indonesia (cheeks in life yellowish, as far as known) . . . . . ***E. bathi***

45. Four or 5 round, dark spots on dorsal body contour below base of spinous dorsal-fin; round, dark spot on midside of body in area below third or fourth from posteriormost dorsal-fin spine; black, obliquely inclined spot just dorsal to dorsal insertion of pectoral fin (marking may be continuous with dark postorbital stripe) . . . . . ***E. axelrodi***
(Western Admiralties SE to Solomon Ids.)

Dark markings on dorsal body contour below spinous dorsal-fin base, if present, consisting of 3 or 4 slender bands that extend ventrally almost to midline of body; no dark spot on midside of body in area below third or fourth from posteriormost dorsal-fin spine (dark spot may be present in area below third or fourth from anteriormost spine); no dark spot just dorsal to dorsal insertion of pectoral fin . 46

46. Seven to 9 slender, intensely dark bands on body . . . . . ***E. dilemma***
(Philippines)

No intensely dark bands on body (broad or slender diffusely to darkly dusky bands may be present; usually restricted to body posteriorly) 47

47. Bands on body darkest in area below spinous dorsal fin; dentary incisor teeth 35–43 . . . . . ***E. bathi***
(Bali and Komodo, Indonesia)

Bands aon baody of about equal darkness or darkest in area below segmented-ray portion of dorsal fin; dentary incisor teeth 41–50 48

48. Segmented anal-fin rays 15–17 (16 or 17 in 96% of specimens); segmented dorsal-fin rays 13–15 (14 or 15 in 88% of specimens); specimens over 30 mm SL occasionally with broad, darkly dusky stripes and bands setting off pale spots on body; dark

postorbital stripe always present; distinct, dark spots never present posteriorly on body . . . . . ***E. australianus***
(Great Barrier Reef)

Segmented anal-fin rays 14–16 (16 in 8% of specimens); segmented dorsal-fin rays 12–14 (14 in 13% of specimens); specimens over 30 mm never with with broad, darkly dusky stripes and bands (broad, faintly dusky stripes and bands or slender, darkly dusky bands may be present); postorbital stripe varying from very faint to dark; distinct, dark spots present or absent posteriorly on body . . . . . ***E. opsifrontalis***
(Marianas Islands S to Palau; islands of the mid-western Pacific lithospheric plate)

Pulcher Group

The Pulcher Group comprises three species (*E. pulcher, E. gravieri,* and *E. aroni*) that share the following unique combination of characters within *Ecsenius:* modally 13 dorsal-fin spines, modally 14 pectoral-fin rays, and modally 11 precaudal vertebrae. None of these three characters is unique to the Pulcher Group, but of the four other groups in which these characters variously occur, three groups are defined by unique characters, and one, monotypic, has only one of several of its populations exhibiting one of the characters. For instance, a modal dorsal-fin spine count of 13 is found otherwise in *Ecsenius* only in *E. midas* of the Stigmatura Group, which group is unique among all blenniids in having a large, black spot anterior to the anus. Besides the Pulcher Group and *E. midas,* all other species of *Ecsenius* have modally 12 dorsal-fin spines.

A modal pectoral-fin ray count of 14 occurs otherwise in *Ecsenius* only in *E. stigmatura* and *E. melarchus,* both also in the Stigmatura Group. All other species of *Ecsenius* have modally 13 pectoral-fin rays, except *Ecsenius frontalis,* Frontalis Group (monotypic), which is unique in having 15 rays modally. The 15-rayed state of *E. frontalis* is possibly a specialized state that evolved from a 14-rayed ancestral state, such as occurs in the Pulcher Group (another possibility: the 15-rayed state is the primitive state ancestral to the 14-rayed state). *Ecsenius frontalis* also shares its modal precaudal vertebral count of 11 with the Pulcher Group, but *E. frontalis'* dorsal-fin spine count of 12, three types of color pattern, and unnotched dorsal fin might relate it more closely to the Bicolor Group.

A precaudal vertebral count of 11 occurs otherwise in *Ecsenius* only in *E. midas, E. lividanalis* (both Stigmatura Group), and a single population each of *E. lineatus* (Lineatus Group) and *E. namiyei* (Bicolor Group). All other species of *Ecsenius* have modally 10 precaudal vertebrae in all populations. The Bicolor Group exhibits two apparent synapomorphies (paired cirri on anterior nostril, vertical pairs of pores in lateral line), and share a possible third (modally 14 segmented caudal-fin rays) only with the Stigmatura Group. *Ecsenius lineatus* has no features that are more clearly similar to those of the Pulcher Group than to any of several other groups, although in having high numbers of meristic characters, it is similar to the Pulcher, Stigmatura, Frontalis, and Bicolor groups.

Ecsenius pulcher exhibits two characters (meristic sexual dimorphism, uniform and bicolored color-pattern forms) that are of limited distribution among *Ecsenius* species. Males of *E. pulcher* have significantly higher average numbers of segmented dorsal-fin rays than do females. Sexually dimorphic numbers of segmented dorsal-fin rays are otherwise known to occur in *Ecsenius* only in the two species of the Bicolor Group, in which the dimorphism also occurs in numbers of segmented anal-fin rays and caudal vertebrae. The two color-pattern forms found in *E. pulcher* occur also in *E. lividanalis* and *E. namiyei* (Bicolor Group) and *E. bicolor,* and *E. frontalis* (but as noted, the last two species also have a third color pattern). Some species of the Opsifrontalis Group also have two different color patterns (striped and banded), but these are not comparable to the two discussed here.

Two of the Pulcher Group species (*E. gravieri, E. aroni*), like *E. frontalis,* are restricted to the Red Sea and easternmost portion of the Gulf of Aden, probably indicating that *E. frontalis* evolved in close geographic, if not close genetic, association with these species (genetically, if the 15-rayed pectoral fin of *E. frontalis* is derived from a 14-rayed ancestor common to *E. frontalis* and the Pulcher Group species). The third species, *E. pulcher,* of the Pulcher Group, is restricted to the Arabian Gulf and adjacent coasts just outside the Gulf.

Based on other fishes, the relatively restricted geographic range occupied by the Pulcher Group (Figure 6) has been recognized by Klausewitz (1983) as a biogeographic unit: Arabian Subprovince (of the Indian Ocean Province). He divided the subprovince into three sections: Erythrean (comprising the Red Sea, with some "leakage" into the westernmost Gulf of Aden), South Arabian (comprising the Gulf of Aden and southern Arabian coast), Persian (comprising the Persian Gulf and Gulf of Oman). The distribution of *E. gravieri* and *E. aroni* is defined essentially by the Erythrean Section, and the distribution of *E. pulcher* is defined by the Persian Section. No species of *Ecsenius* is known from the South Arabian Section, which connects the other two sections. The distribution of *E. frontalis* (Figure 5) also is defined by the Erythrean Section. Klausewitz contended that the Red Sea has never been

isolated physiographically from the Indian Ocean, but that on various occasions it has been physicochemically (ecologically) isolated. These periods of isolation presumably were the major factors leading to the formation of Erythrean and Persian endemic species.

The Pulcher Group species are strikingly different from each other in color pattern, and to some degree in anatomy and behavior. The filamentous caudal-fin rays of *E. gravieri* are undifferentiated sexually, whereas the rays attain much greater lengths in males of the other two species (Springer, 1971). *Ecsenius pulcher* exhibits two quite different color patterns, whereas the other two species exhibit but one pattern. *Ecsenius gravieri* spends considerable time swimming above the bottom, whereas the other two species appear to be almost exclusively benthic. The caudal-fin ray, color-pattern, and behavioral differences of *E. gravieri* are probably the result of its close Batesian mimetic association (Springer and Smith-Vaniz, 1972) with the nemophin blenniid *Meiacanthus nigrolineatus*. *Ecsenius pulcher* has higher numbers of segmented dorsal-and anal-fin rays and caudal vertebrae than the other two species and, uniquely in the group, exhibits sexual dimorphism in number of segmented dorsal-fin rays. I have found no characters that might relate two of the species more closely than either is to the third.

Ecsenius aroni Springer

FIGURE 14; PLATE 2: FIGURE 1; TABLE 6

Ecsenius (Ecsenius) aroni Springer, 1971:24 [El Himeira, Sinai Peninsula, Gulf of Aqaba; holotype, USNM 204468].

DESCRIPTION.—Dorsal fin XII or XIII (rarely XII),16–18 (rarely 18), deeply notched between spinous and segmented-ray portions. Anal fin II,19 or 20. Pectoral fin 13–15 (usually 14). Segmented caudal-fin rays 13. Vertebrae 10 or 11 (rarely 10) + 23–26 (usually 24 or 25) = 34–37 (rarely 34). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 46–57; posterior dentary canines 0 or 1 (rarely 0) on each side. Lateral line without pairs of pores, terminating posteriorly at a point between verticals from dorsal-fin spines 8 and 10. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, head and body darkly dusky, except for pale ventral surface of head and large, diffuse, slightly darker spot extending from caudal peduncle onto caudal fin basally. Dorsal fin with fine, dusky, suprabasal stripe. Anal fin generally dusky, but tips of rays pale in mature males. Pectorals and pelvics unmarked.

Live Color (based on underwater observations in Gulf of Aqaba): Head dark brown. Body generally dark tan with black spot with blue overtones at base of, and on, caudal fin. Some individuals exhibited a bright orange stripe along the dorsal body contour. Anal fin dark brown, other fins pale or unmarked. Photographs (Plate 2: figure 1) taken in life of a specimen off the coast of Sudan shows the head orange brown with a faint bluish overtone anteriorly; the body is orange brown.

REMARKS.—*Ecsenius aroni* is one of the deeper dwelling species in the genus, most commonly occurring at depths greater than 10 m, and has been recorded as occuring as deep as about 37 m.

DISTRIBUTION.—Known only from the Gulf of Aqaba and the Red Sea, as far south as Djetta, Saudi Arabia, and Towartit Reef, Sudan.

MATERIAL (* = new material).—*Gulf of Aqaba:* USNM 204468 (holotype: 37 mm SL), 204690 (12 specimens: 18–41), 204560 (21:19–32), 204550 (2:21, 27), 204558 (1:25), 204557 (2:21, 35), 204556 (1:33). *Red Sea:* Ras Muhammad, USNM 204561 (1:41), 204562 (7: 26–40); Djetta and vicinity, ANSP 158833* (1:39), USNM 217725* (2:28, 36); Towartit Reef, BPBM 27436* (4:35–41).

Ecsenius gravieri (Pellegrin)

FIGURES 15, 16; PLATE 1: FIGURES 1–3; TABLE 6

Salarias gravieri Pellegrin, 1906:93 [Bay of Tadjourah; holotype, MNHN 04-319].

Ecsenius klausewitzi Lotan, 1969:371 [Entedebir, Dahlak Archipelago;

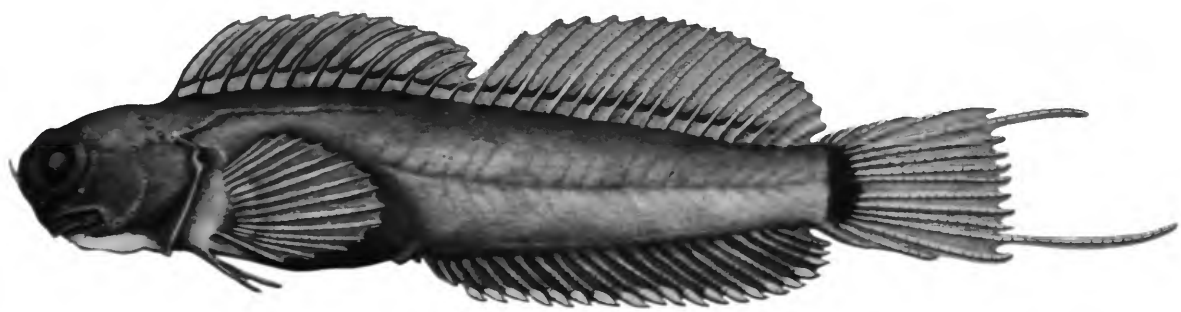


FIGURE 14.—*Ecsenius aroni*, USNM 204468, male, 37 mm SL, Gulf of Aqaba (drawn by J.R. Schroeder).

TABLE 6.—Frequency distributions for certain characters in the species of the Pulcher Group.

Species	Segmented dorsal-fin rays						Segmented anal-fin rays							Caudal vertebrae						
	16	17	18	19	20	$\bar{x}$	18	19	20	21	22	23	$\bar{x}$	23	24	25	26	27	28	$\bar{x}$
aroni	1	28	26			17.4		15	39				19.7	1	13	36	4			24.8
gravieri	3	51	41	1		17.4	2	46	44	3			19.5		5	56	33			25.3
pulcher																				
Iran to India																				
males			3	10	9	19.3		1	-	6	14	1	21.6				1	14	3	27.1
females			6	14	2	18.8			1	9	11		21.5				2	8	2	27.0
Oman																				
males			4	9	1	18.8			1	7	5		21.3				7	5	1	26.5
females			7	20	3	18.9			4	15	11		21.2				14	12	2	26.6

Species	Dentary incisor teeth														
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	$\bar{x}$
aroni			1	-	-	1	2	6	9	9	9	4	4	1	52.9
gravieri	2	-	3	9	10	11	14	13	3	4	1				49.3
pulcher															
Iran to India	2	3	4	6	8	3	6	7	2	1					48.4
Oman	3	3	16	3	7	2	1	1							46.6

holotype, HUJ E-62/3708].

Ecsenius (Ecsenius) gravieri.—Springer, 1971:22.

Ecsenius gravieri.—Springer and Smith-Vaniz, 1972:2.

DESCRIPTION.—Dorsal fin XII–XIV (modally XIII),16–19 (rarely 16 or 19), moderately notched between spinous and segmented-ray portions. Anal fin II,18–21 (rarely 18 or 21). Pectoral fin 13–15 (rarely 13, modally 14). Segmented caudal-fin rays 13. Vertebrae 10 or 11 (rarely 10) + 24–26 (rarely 24) = 35–37 (rarely 35). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 44–54; posterior dentary canines 0 or 1 (modally 1) on each side. Lateral line without pairs of pores, terminating posteriorly at a point between verticals from dorsal-fin spines 8 and 11 (rarely as far anteriorly as 8). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Color Pattern: There are two color patterns: pale (northern) and dark (southern), the difference being the intensity and area covered by the dark markings. There is no problem recognizing the two types (see Figures 15 and 16) from Ras Muhammad, Sinai Peninsula, north, or from Massawa, Ethiopia, south, but the few available specimens from intermediate geographic areas are somewhat intermediate in their markings.

Preserved Color: In preservative, specimens of the northern type have the head relatively darkly dusky with the intensity of the pigment decreasing gradually on the body and becoming quite pale posteriorly; however, the abdominal area is dark gray. At about the midposterior margin of the orbit of

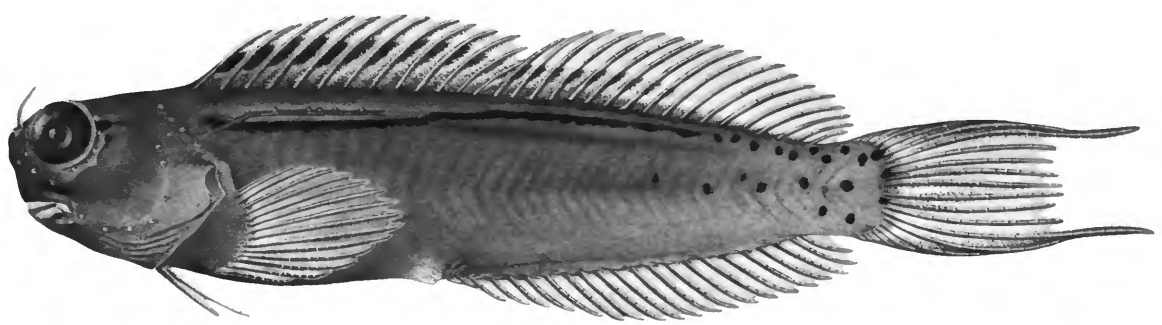


FIGURE 15.—*Ecsenius gravieri*, northern (pale) form, HUJ F-4382, male, 39 mm SL, Gulf of Aqaba coast, Sinai Peninsula (drawn by S.L. Chambers).

most specimens there is a dark, almost black, stripe, or diffuse evidence of one, that extends posteriorly across the head, darkens greatly on the body, and usually continues at least to below the middle of the spinous dorsal fin, but terminates anterior to the caudal peduncle. On the body posterior to the termination of the stripe are several variably placed small black spots. There may also be a few small dark spots on the body ventroanterior to the termination of the stripe. Occasional specimens may lack the dark stripe or spots, but not both. The spinous dorsal fin bears a row of jet-black spots restricted mostly to the interspinous membranes. These spots decrease in size and intensity and disappear at some point along the segmented-ray portion of the fin. The dorsal and ventral caudal-fin lobes are darkly dusky; there are no other noticeable markings on the fins.

Specimens of the southern type differ from those just described in having the dark pigment generally blacker and covering a larger area. The stripe on the body may be almost completely obscured anteriorly by the body pigment (the stripe is absent in the holotype of *E. gravieri*, see Smith, 1959, for reasonably good illustration of the holotype). In addition, some specimens exhibit dark pigment at the tips of some dorsal- and anal-fin rays.

Live Color (based on color photographs of living specimens, Plate 1, taken in the Gulf of Aqaba): The head and body anterior to the anal-fin origin are generally blue gray; the remainder of the body is bright yellow. The iris of the eye is divided diagonally by a dark stripe into equal anterodorsal and posteroventral sections; except for the dark (black) stripe, which is interrupted by the pupil, the iris is blue gray with two short, fine, bright yellow arcs margining the pupil. The animal is able to rotate the eyes somewhat, but often, the dark stripe is positioned as a continuation of the black postorbital stripe. The black and dusky markings of the dorsal and caudal fins, and a suffusion of yellow along the dorsal-fin base, represent the only fin pigmentation. Other black marks on the head and body are the same as in preserved specimens.

Sexual Dimorphism.—Primarily restricted to size: the largest males are about 15 mm (or about one-third) longer than the largest females. It is noteworthy that there is essentially no distinction between the sexes in the relative lengths of the longest caudal-fin ray (Springer, 1971: table 9), although the ray is usually long and filamentous. In all the other species of *Ecsenius* the longest ray, when filamentous, is relatively longer in males.

Geographic Variation.—The main such variation noted is described in the above section on color pattern.

Remarks.—Springer and Smith-Vaniz (1972) published an extensive study of the mimetic association involving *E. gravieri*, *Meiacanthus nigrolineatus* Smith-Vaniz, and *Plagiotremus townsendi* (Regan), in which considerable information on the natural history of each of the species is given. *Ecsenius gravieri* is an extremely close Batesian mimic of *M. nigrolineatus*.

Distribution.—Gulf of Aqaba, Red Sea south to westernmost Gulf of Aden.

Material (* = new material).—*Gulf of Aqaba:* TAU NS-3580 (3 specimens: 20–48 mm SL); HUJ F-4382 (1:39), F-4377 (2:20, 21), E-64/30A (2:20, 32); USNM 204542 (9:32–56), 204555 (15:19–33), 204546 (9:18–23), 204544 (22:20–53), 204543 (3:20–61), 227982* (7:22–33), 204697* (7:20–45). *Gulf of Suez:* USNM 204548 (3:50–55). *Red Sea:* Ras Muhammad, Sinai Peninsula, USNM 204545 (9:28–44), 204547 (2:28, 41); Egypt, Al Ghardaqa, SMF 5122-23 (2:30, 35); Saudi Arabia, Jiddah, USNM 217730* (1:28), 217723* (1:26); Sudan, Suakin, BPBM 19739* (1:37); Dahlak Archipelago, HUJ E-62/3708 (holotype of *Ecsenius klausewitzi:* 15); Isola Delemme, USNM 204479 (1:56); Sheikh el Abu, USNM 204480 (3:30–40). *Bay of Tadjourah:* MNHN 04-319 (holotype of *Salarias gravieri:* 54).

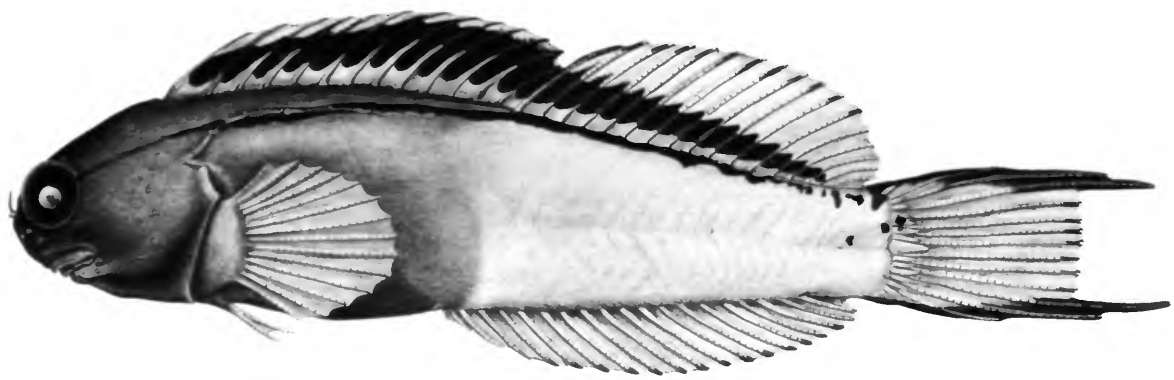


Figure 16.—*Ecsenius gravieri*, southern (dark) form, USNM 204480, female, 40 mm SL, Sheikh el Abu, Ethiopia, Red Sea, (drawn by S.L. Chambers).

Ecsenius pulcher (Murray)

FIGURE 17; PLATE 2: FIGURES 2–4; TABLE 6

Salarias pulcher Murray, 1887:47 [Manora Rocks, Karachi; lectotype, BMNH 1887.9.22.59–60, male].

Salarias phntasticus Boulenger, 1897:422 [typographical error; Mekran Coast, Persia; syntypes, BMNH 1897.9.22.20-21].

Salarias anomalus Regan, 1905:327 [Mekran Coast, Persian Gulf; syntypes, BMNH 1900.5.9.47-56].

Ecsenius (Ecsenius) pulcher.—Springer, 1971:20.

DESCRIPTION.—Dorsal fin XII–XIV (rarely XII or XIV),18 to 20, moderately notched between spinous and segmented-ray portions. Anal fin II,19–23 (rarely 19, 20 or 23). Pectoral fin 13–15 (rarely 13 or 15). Segmented caudal-fin rays 13 or 14 (rarely 14). Vertebrae 10–12 (rarely 10 or 12) + 26–28 (modally 26 or 27) = 37–39. Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 44–53; posterior dentary canines 0–2 (modally 1) on each side. Lateral line without pairs of pores, terminating posteriorly at a point between verticals from dorsal-fin spines 8 and 12 (rarely 8, 11, or 12). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Color Pattern: There are two strikingly different, non-sex linked color patterns found in preserved adult and young adult specimens. The most common pattern, based on museum specimens, is that in which the head and body are generally uniformly dark or dusky brown, sometimes paling slightly posteriorly on the body. There is a small, slightly darker spot (unpaired) on the snout between, and sometimes just posterior to, the posterior nostrils, two small, darker spots on the anterior orbital rim, and two (one at the one o'clock and another at the three o'clock positions) fine, short, diagonally upward dark lines on the postorbital margin. The spinous dorsal fin bears a broad dusky basal stripe that extends onto the segmented-ray portion of the fin, where it becomes suprabasal in position; extensions from the stripe may extend along the rays. The anal fin is almost uniformly pale dusky; the other fins are variably marked with dusky areas.

The other color pattern (banded or bicolor) is similar to the first, except that the posterior half of the body bears a pigmentless area with 5–8 dark barlike inclusions. The smallest specimen examined that had this pattern was 33 mm SL. Below about 20 mm SL, specimens may be uniformly dark or bear 7 or 8 pairs of diffusely dusky bands on each side.

Live Color (Plate 2: figures 2–4): There are three color phases, two of which correspond to the two preserved patterns, and a third (horizontally bicolored), which in preservative reverts to the uniformly colored phase (and thus may represent a transient, emotionally produced pattern).

The uniform phase in life is almost uniformly dark brownish purple with fine, faint yellow marks in the position of the dark marks at the one and three o'clock positions on the orbital margin (see preserved color pattern) and a bright yellow ring, which gives rise to 5 low, equally-spaced points, around the pupil.

Anteriorly, the banded (or "true" bicolored) phase is tinted similarly to the uniform phase, but the pigmentless (in preservative) areas surrounding the dark bands are bright yellow, the color extending onto and covering most of the anal fin, and tapering well out onto the caudal fin, where the basal yellow color becomes red-orange posteriorly. An additional color photograph of a specimen exhibiting the banded pattern was published by Axelrod and Emmens (1969:353). In the published illustration the yellow color does not change to red-orange posteriorly. The banded phase is comparable to the bicolored phases of *E. frontalis, E. lividanalis, E. namiyei,* and, particularly, *E. bicolor.* In *E. bicolor,* the pale (yellow-orange in life) area posteriorly may occasionally contain one or two faint, dusky bands.

The head and body of specimens of *E. pulcher* exhibiting the horizontally bicolored pattern are dark brown dorsal to the level of a line extending along the ventral margin of the orbit and midside of the body from the snout tip posteriorly to the caudal fin. Below this line the head and body are white. There are yellow markings in the orbital region that are similar to those of the other two patterns. Just posterior to the ventral

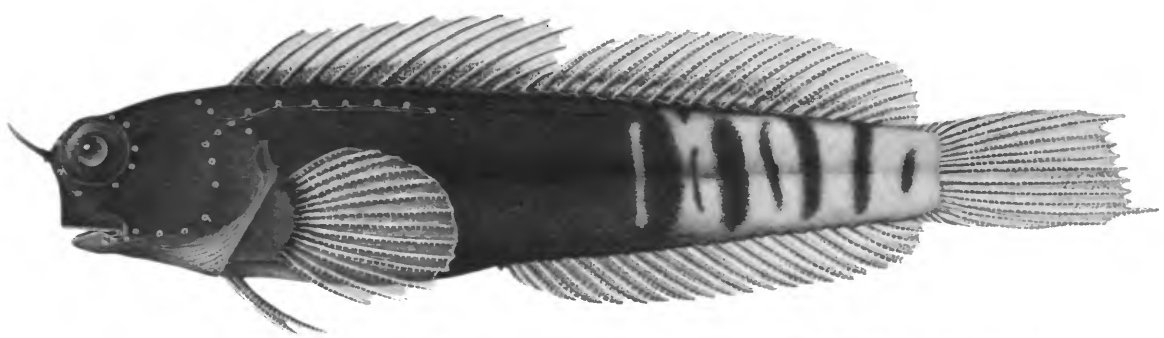


FIGURE 17.—*Ecsenius pulcher,* banded form, USNM 201571, male, 33 mm SL, Tarut Bay, Ras Tanura, Persian Gulf (drawn by M.H. Lester).

half of the eye is a relatively large, dull orange-brown spot.

SEXUAL DIMORPHISM.—Sexual dimorphism is apparently limited primarily to the relative length of the caudal fin, which is greater in males (see Springer, 1971:26, fig. 11), and possibly the number of segmented dorsal-fin rays in specimens from the coasts of Iran to India (combined), which average significantly more in males, 19.3 versus 18.8 for females ($t = 2.33$; $0.05 > p > 0.02$; df = 42). The averages for number of segmented dorsal-fin rays in the two sexes for specimens from the coast of Oman are not significantly different.

REMARKS.—The type material of *Salarias pulcher* (see "Material" section) consists of two syntypes, a male and a female, each 44 mm SL. I here designate the male as the lectotype. The lectotype is most readily distinguishable from the paralectotype in having the caudal-fin lobes elongated.

Comparisons of averages for numbers of meristic elements and incisor teeth are higher in the grouped Iran-to-India specimens than in the Oman specimens (Table 6). Average numbers of teeth, which are not sexually dimorphic, are highly significantly different ($t = 3.897$; $p < 0.001$; df = 76). Average numbers of segmented dorsal-fin rays for males, but not females, from the two areas are signifcantly different ($t = 2.164$, $0.05 > p > 0.02$, df = 34). Similarly, average numbers of caudal vertebrae of males, but not females, are significantly different (males × males: $t = 2.822$, $p = < 0.01$, df = 29).

DISTRIBUTION.—This species is known only from the Persian Gulf, Gulf of Oman coast of Oman, and northwestern coast of the Indian subcontinent as far south as the Gulf of Kutch.

MATERIAL (* = new material).—*Persian Gulf:* USNM 201572 (1 specimen: 36 mm SL, cleared and stained), 201571 (1:33), 196505 (2:42, 52), 196506 (1:52), 265625* (1:70), BMNH 1900.5.9.47-56 (16:31–46, syntypes of *Salarias anomalus*), 1898.6.29.163 (1:57), 1932.2.18.43 (1:40). *Gulf of Oman* (Makran coast): BMNH 1899.5.8.94 (2:29, 34), 1897.9.22.20-21 (2:54, 58, syntypes of *Salarias phntasticus* [sic]). *Oman:* Muscat, BMNH 1912.11.26.1 (1:51), USNM 217728* (1:40); vicinity of Sur or Qalhat, ROM 40119* (3:37–56), 40121* (6:42–54), 40179* (4:34–54), 40184* (7:38–51), 40185* (1:53), 40186* (3:53–57), 40187* (1:38), 40188* (4:16–68), 40189* (10:15–57), 40190* (10:18–51), 40195* (1:46), 40199* (1:42), several other lots at ROM not included in my study. *Pakistan:* BMNH 1887.9.22.59-60 (2: each 44, lectotype and paralectotype of *Salarias pulcher*), USNM 201867 (3:39–58), 201816 (1:48), SMF 8239 (1:37). *India:* SMF 5120 (9:22–55); Rupan Coast, FMRI uncataloged (4:18–31, in three lots); Gulf of Kutch, USNM 201863 (1:17).

STIGMATURA GROUP

This species group comprises *E. stigmatura, E. melarchus, E. midas,* and *E. lividanalis,* which exhibit the following synapomorphy: a black spot extending anteriorly from the anus. The group also shares in having generally the lowest numbers of dentary incisor teeth (Table 4) and in having modally 14 segmented caudal-fin rays. Low numbers of teeth and modally 14 segmented caudal-fin rays are characteristic otherwise in *Ecsenius* only of the Bicolor Group. Although low tooth counts are found in some species among the other species groups of *Ecsenius,* no other species of blenniid (blennioid?) has more than modally 13 segmented caudal-fin rays, a number often found in other blennioid families. I therefore consider modally 14 rays to be a specialization in *Ecsenius,* but I am uncertain that it is a synapomorphy uniting the Stigmatura and Bicolor groups. Two of the four species of the Stigmatura group, for instance, share an apparent specialization, 14 pectoral-fin rays, only with species of the Pulcher Group, thus providing possibly contradictory evidence of relationship. (See also discussion under account of Pulcher Group.)

Within the Stigmatura Group, *E. stigmatura* and *E. melarchus* alone share in having a similar and unique color pattern (a complex character) on the head, 10 precaudal vertebrae, a modal pectoral-fin ray count of 14, and a deeply notched dorsal-fin. These similarities and the allopatric (almost parapatric) distributions of the two species, bias me strongly in favor of the hypothesis of a monophyletic group comprising *E. stigmatura* and *E. melarchus.*

Ecsenius lividanalis and *E. midas* share in having 11 precaudal vertebrae, a modal pectoral fin-ray count of 13, and the dorsal fin at most only slightly notched. They do not share any color-pattern characters to the exclusion of the the other two species, nor does either share a color-pattern character with one or both of the other two species to the exclusion of the remaining species. Over its entire, relatively restricted range, *Ecsenius lividanalis* is generally sympatric with the widely distributed *E. midas,* and the range of both these species variously includes portions of the ranges of the other two species in the Stigmatura Group (Figure 6). How *E. lividanalis* and *E. midas* relate to each other and to the *stigmatura-melarchus* clade in a cladogram is uncertain, but there are only three possibilities: first, that they form a monophyletic group, which would be the sister group of the *stigmatura-melarchus* clade; second and third, that one or the other is the sister group of the *stigmatura-melarchus* clade, and the remaining species is the sister group of all the others.

Ecsenius lividanalis Chapman and Schultz

FIGURE 18; PLATE 2: FIGURES 5, 6; TABLE 7

Ecsenius lividanalis Chapman and Schultz, 1952:517 [Munda, New Georgia, Solomon Islands; holotype, USNM 144723].

Ecsenius (Ecsenius) lividinalis [sic].—Springer, 1971:32.

Ecsenius lividinalis [sic].—Springer, 1972:9.—McKinney and Springer, 1976:7.

DESCRIPTION.—Dorsal fin XI or XII,12–14 (rarely XI or 14), moderately notched between spinous and segmented ray portions (notch depth less than half length of first dorsal segmented ray). Anal fin II,13 or 14. Pectoral fin 13 or 14 (uncommonly 14). Segmented caudal-fin rays 13–15 (modally 14, commonly 13; note: segmentations of ventralmost segmented ray frequently discernible only with transmitted light,

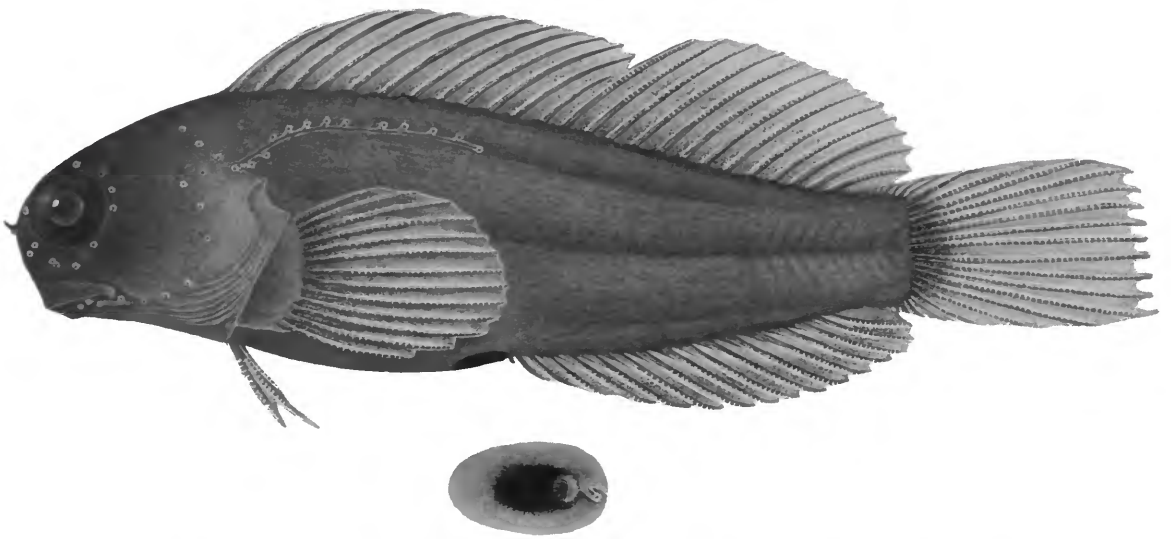


FIGURE 18.—*Ecsenius lividanalis*, USNM 144292, male, 26 mm SL, Munda Lagoon, New Georgia, Solomon Islands (small figure shows ventral view of area surrounding anus; drawn by M.H. Lester).

and specimen immersed in liquid). Vertebrae 11 + 18 or 19. Dentary incisor teeth 29 to 37 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior dentary canines 1 on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8 and 11. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, variably uniformly dark brown or darker brown anteriorly than posteriorly, and with ventral surface of head very pale. The two specimens from off

TABLE 7.—Frequency distributions for certain characters in populations of *Ecsenius lividanalis*.

	Segmented dorsal-fin rays			Segmented anal-fin rays		Caudal vertebrae		Lateral line ends below dorsal-fin spine			
Population	12	13	14	13	14	18	19	8	9	10	11
Philippines	1	7		2	6	3	4			2	3
Indonesia											
off Ujung Padang		2		2			2			2	
Boeton	1	4		1	3	4			2	-	3
Saparua	2	1		1	2	3				3	
Australia (N.T.)		5		2	2	2	2		1	2	2
Papua-New Guinea		3			3	1	2		1	1	1
Solomon Islands	2	8	1	3	8	1	10	1	4	5	1

	Dentary incisor teeth								
Population	29	30	31	32	33	34	35	36	37
Philippines		1	-	-	2	2			
Indonesia									
off Ujung Padang			1	-	1				
Boeton		3	-	2					
Saparua	1	-	-	2					
Australia (N.T.)					1	1	1	2	
Papua-New Guinea				2	1				
Solomon Islands				2	1	4	3	-	1

Ujung Pandang, Sulawesi, were abruptly paler on the caudal peduncle (bicolor form). A black spot, usually with a pale margin, extends anteriorly from the anus. The dorsal and anal fins usually are almost entirely dusky brown, but dorsal fin pales distally and posteriorly. Other fins, and occasionally dorsal, mostly clear, variably with dark pigment distributed along rays.

Live and Fresh Colors (Plate 2: figures 5, 6): Underwater color photographs (Plate 2: figure 5) taken at Ujung Pandang show the head and body, except posterior one-sixth, to be uniformly dark brownish purple with faint bluish suffusions (region around anus not visible); iris of eye bright white. Posterior one-sixth of body, spinous dorsal fin, basal third of segmented-ray portion of dorsal fin, and base of caudal fin orange yellow. Anal fin dusky basally; other fins untinted. A freshly preserved specimen (Plate 2: figure 6) from the same locality retained the orange-yellow coloration, but the head and body were slate gray except ventrally, where they were white; the black spot with a white margin situated near the anus was evident. A photograph of a freshly dead specimen from Saparua, Moluccas (Plate 2: figure 6), had the head and body almost entirely orange yellow (head darker, almost brown, venter paler, almost yellow). A freshly dead specimen from Florida Island, Solomons, had the top and sides of the head dark brown, underside of head paler with metallic blue tint; body beneath spinous dorsal fin brown, grading into dusky yellow posteriorly; belly and ventrolateral portion of body yellow; basal halves of dorsal and anal fins yellow, distal portions untinted; lower two or three pectoral-fin rays black-tipped; scattered dark pigment along pectoral- and caudal-fin rays; pelvic fins creamy white. The pale-margined black spot in the region of the anus was present in both the Saparua and Florida islands specimens.

GEOGRAPHIC VARIATION.—Inadequate material is available to determine if such variation exists, but there are possible indications that specimens from the Philippines, Solomon Islands, and Northern Territory, Australia, have more dentary incisors, and specimens from Saparua and Boeton, Indonesia, have fewer caudal vertebrae, than specimens from the other localities (Table 7).

REMARKS.—Only *E. lividanalis* among the Stigmatura Group species has a bicolored form. The bicolored form in *E. lividanalis* is most similar to that of *E. namiyei*, Bicolor Group. Bicolored forms also occur in *E. bicolor* (Bicolor Group), *E. pulcher* (Pulcher Group), and *E. frontalis* (Frontalis Group), and may be indicative of relationships.

I have consistently and erroneously referred to *E. lividanalis* in all my previous studies (including those as second author) as *E. lividinalis*.

DISTRIBUTION (Figure 5).—Mindoro and Siquijor islands, Philippines; Sulawesi, Boeton, and Saparua, Indonesia; North Oxley Island, N.T., Australia; Basilaki Island, Papua-New Guinea; Solomon Islands.

MATERIAL (* = new material).—*Solomon Islands:* New Georgia, USNM 144723 (holotype: 33 mm SL), 144292 (6 specimens: 22–27, including one cleared and stained); Florida Island, BPBM 16141 (1:21). *Papua-New Guinea:* Milne Bay District, Basilaki Island, USNM 217565* (3:30–35, including one cleared and stained). *Indonesia:* Saparua Island, USNM 209992 (2:18, 26), 210105 (1:22); Boeton [Buton], USNM 211966* (5:28–37); Sulawesi, off Ujung Padang, BPBM 26795* (2:25, 29). *Australia:* Northern Territory, North Oxley Island, NTM S.10605-028* (5:26–35). *Philippine Islands:* ANSP 109211 (1:26); Mindoro, Puerto Galera, LACM 42490* (1:22); Siquijor Island (off Negros), USNM 219313* (5:16–36).

Ecsenius melarchus McKinney and Springer

FIGURES 19, 20; PLATE 3: FIGURES 1, 2; TABLE 8

Ecsenius stigmatura.—Springer, 1971:30 [in part not Fowler; fig. 25].
Ecsenius melarchus McKinney and Springer, 1976:9 [Karimundjawa, Indonesia; holotype, USNM 212229].

DESCRIPTION.—Dorsal fin XI or XII (rarely XI),15–17

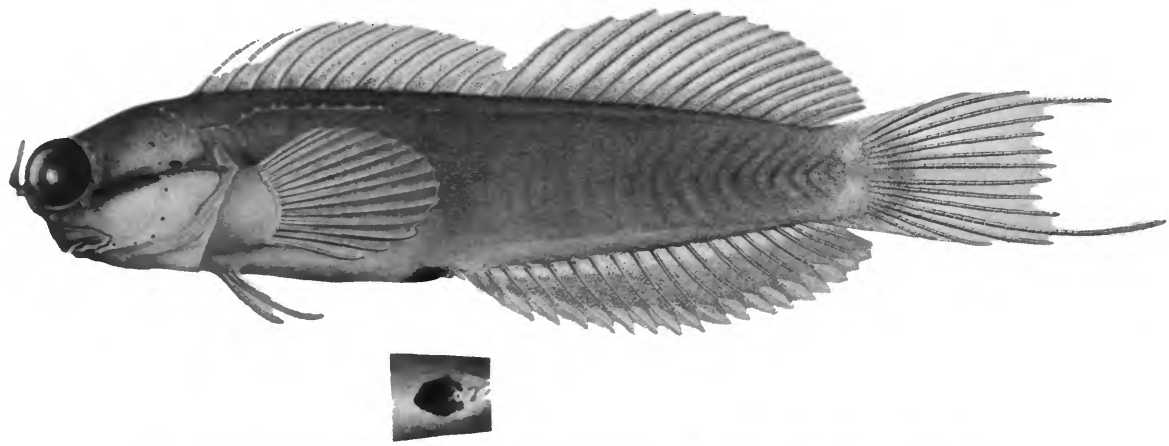


FIGURE 19.—*Ecsenius melarchus*, USNM 201815, male, 38 mm SL, Pulau Gaya, Dravel Bay, Borneo (small figure shows ventral view of area surrounding anus; drawn by S.L. Chambers).

(rarely 17), deeply notched between spinous and segmented-ray portions. Anal fin II,17–19 (rarely 19). Pectoral fin 13 to 15 (rarely 13 or 15). Segmented caudal-fin rays 13 or 14 (usually 14). Vertebrae 10 or 11 (rarely 11) +22–24 (usually 23) = 32–34 (usually 33). Dentary incisor teeth 36–42 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior dentary canines 0–2 on each side (rarely 0 or 2). Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8–10 (rarely 10). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, head and body varying from pale to dark dusky, with head darker than body. Dorsal half of head often darker than ventral half, with 0–2 slender, pale stripes (pale stripes separated by slender dark stripe) separating dorsal and ventral portions of color pattern;

FIGURE 20.—*Ecsenius melarchus: a,* pale form, BPBM 29567, male, 43 mm SL, Pulo Menjangan, Bali, Indonesia (note unusual dark spot at dorsal postorbital margin); *b,* pale spotted form, USNM 211897, male, 33 m SL Kabaena Island, Indonesia; *c,* USNM 222137, male, 39 mm SL, Palawan, Philippines (note two pale stripes below level of orbit); *d,* USNM 211894, male, 34 mm SL, Karimundjawa, Indonesia (note single pale stripe on head; photographs by J.T. Williams).

TABLE 8.—Frequency distributions for certain characters in *Ecsenius melarchus* and *E. stigmatura*.

	Segmented dorsal-fin rays				Segmented anal-fin rays				Caudal vertebrae			
Species	15	16	17	$\bar{x}$	17	18	19	$\bar{x}$	22	23	24	$\bar{x}$
melarchus	17	64	2	15.8	17	63	2	17.8	8	58	8	23.0
stigmatura	1	26	7	16 2	5	22	7	17.0	4	27	3	23.0

	Dentary incisors									
Species	34	35	36	37	38	39	40	41	42	$\bar{x}$
melarchus			4	6	16	12	13	9	7	39.2
stigmatura	3	2	5	3	7	3	1			38.5

dorsalmore of two pale stripes in Palawan specimens occasionally continuing on body for up to half body length (pale stripes present in living specimens are often completely lost after preservation). Specimens from Bali and Kabaena exhibit a faint to prominent dark spot just posterior to the eye at the one o'clock postion. One male specimen from Kabaena (Figure 20*b*) exhibits two rows of pale spots on the body, and another male, also from Kabaena, has irregularly distributed pale spots on the body. A prominent dark spot extends anteriorly from the anus of all specimens. Dorsal fin dusky basally and along margins of rays; interradial membranes clear. Anal fin dusky with indistinct pale stripe basally. Basal portions of all caudal-fin rays and and entire length of middle two to four rays dusky; remainder of fin unmarked. Pectoral and pelvic fins with dark pigment along rays; membranes clear.

Live Color: Specimens in life exhibit great variation in color. Specimens from Bali (Plate 3: figures 1, 2) appear to be of two types. In one type the head is dark brown, or slate gray with bluish overtones, dorsal to the ventral level of the orbit; at the ventral level of the orbit is a fine, bright, white pinstripe that extends posteriorly to the preopercular margin; the snout and ventral portion of the head are slate gray with bluish overtones; the iris is bright yellow, and the body is yellow brown. The second type pattern is similar to the first type dorsal to the level of the bright, white pinstripe, but ventral to this level, the head and body are abruptly paler, almost white (this horizontally bicolored phase is not evident in preserved specimens and may reflect a transient emotional state). Specimens from the Seribu Islands (off Djakarta, Indonesia) may have the bright pinstripe extending posteriorly to the pectoral-fin base, and there is a faint orange stripe, apparently lacking in the Balinese specimens, below the pinstripe posteriorly. Schroeder (1980:174, questionably identified as *Ecsenius bicolor*) illustrates a specimen from Palawan that has the bright, white pinstripe extending posteriorly almost half the body length, with the body dark, purple brown anteriorly and yellow brown posteriorly; a bright orange stripe is present just below the white pinstripe posteriorly.

GEOGRAPHIC VARIATION.—I note no geographic variation among populations other than the color-pattern differences described above. It seems possible that much, if not all, of this variation is artifactual, resulting from differences in methods of collecting and preserving. Live color pattern differences were based on relatively few specimens, and degree of consistency is not ascertainable.

REMARKS.—*Ecsenius melarchus* has been collected at depths ranging from 1 to 30.5 m, but most frequently from depths less than 15 m.

Ecsenius melarchus differs most obviously from *E. stigmatura*, its presumed sister species, in lacking a large, dark, spot at the caudal-fin base and in having lower average numbers of segmented dorsal- and anal-fin rays and higher average numbers of dentary incisor teeth (Table 8). It shares only with *E. stigmatura* the fine, white pinstripe at the ventralmost level of the orbit margined ventrally and posteriorly by a bright orange stripe (other species of *Ecsenius* may have a fine, white pinstripe slightly dorsal to the ventralmost level of the orbit, but lack an orange stripe).

DISTRIBUTION.—Seribu Islands (off Djakarta), Karimunjawa, Bali, and Kabaena (all Indonesia); Darvel Bay, Sabah; Palawan, Philippine Islands. I have seen a photograph of the species taken by R. Kuiter at Flores.

MATERIAL (* = not previously reported).—*Philippine Islands:* Palawan, N. end Rita Island, Ulugan Bay, USNM 222137* (7 specimens: 22–40 mm SL). *Indonesia:* Bali, Pulau Menjangan, BPBM 29567* (3:36–47); Karimunjawa, USNM 212229 (holotype, 39 mm SL), 211896 (12:16–44), 211894 (8:24–38); Seribu Islands, USNM 212893 (32:18–36), BPBM 18053 (4:22–25), CAS 34244 (3:30–32); Kabaena, USNM 211897 (6:24–36), AMS I.18491-001 (6:25–45). *Sabah* (North Borneo): USNM 201815 (1:38).

Ecsenius midas Starck

FIGURE 21; PLATE 3: FIGURES 3–6; TABLE 9

Ecsenius (Anthiiblennius) midas Starck, 1969:1 [D'Arros Island, Amirante Islands; holotype, ANSP 111148].—Springer, 1971:13; Springer, 1972:1.
Ecsenius midas.—McKinney and Springer, 1976:10.

DESCRIPTION.—Dorsal fin XII–XIV (usually XIII),18–21 (usually 19 or 20), without notch between spinous and segmented-ray portions. Anal fin II,20–23 (rarely 20). Pectoral fin 12–14 (usually 13). Segmented caudal-fin rays 13 to 15 (usually 14). Vertebrae 10–11 (rarely 10) +27–29 = 38–40. Dentary incisor teeth (does not include anterior canine teeth, which are greatly enlarged and conspicuous) 11–14 (modally 14, rarely 11 or 12); posterior dentary canines 0–2 (usually 1) on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 7–9. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, head and body usually dark dusky anteriorly, paling gradually posteriorly and becoming unpigmented on caudal peduncle and much of caudal fin, but some specimens more or less uniformly pale dusky. One or two diffuse, dusky markings occasionally present on head, one of which is a small spot at 11 o'clock position on orbital margin, the other a stripe beginning just posterior to ventroposterior orbital margin and extending diagonally upward across cheek. Lips and cirri dark. One specimen had some diffuse vertical bands on body; most exhibit several faint, fine dusky lines outlining myomeres. Most consistent and conspicuous marking is black spot extending anteriorly from anus. Dorsal fin varying from almost black to faintly dusky anteriorly; specimens with darkest fins with fine pale edging on posterior half of fin; specimens with palest fins with darker distal edging to spinous portion, edging continuing onto less dark segmented-ray portion as slightly subdistal stripe; distal edge of segmented-ray portion immaculate. Anal fin varying from uniformly dark dusky to pale dusky with slightly darker fine distal edging. Caudal fin more-or-less pale with duskier dorsal and ventral lobes, or lobes only with fine, dusky edging. Pectoral-fin rays dusky, interradial membranes immaculate. Pelvic fins dusky.

Live Color: Coloration of *E. midas* is extremely variable. Starck (1969) reported life color to be golden yellow. A freshly dead specimen from the Gulf of Aqaba (Springer, 1971) had the head pale dusky orange with narrow, pale yellow-green stripe extending posteriorly from orbit to opercle; underside of head white; side of body pale dusky purple overlying orange; venter chartreuse; dorsal, anal, and caudal fins orange yellow; pectoral fin pale yellow green. Dr. L. Fishelson (pers. comm.) described the color of live Gulf of Aqaba specimens as very similar to that of [female] *Anthias squamipinnis* Peters, with which it was swimming. A color photograph (Plate 3: figure 6) of a Sudan (Red Sea) specimen in the wild swimming with *Anthias squamipinnis*, shows it to be overall yellow, more yellow than the *A. squamipinnis*. Photographs (by A. Norman; in files of TFH Publications, Inc.) of a live Red Sea specimen in an aquarium (in New York), show an individual very similar to *A. squamipinnis* in its overall yellow-orange color.

Photographs (Plate 3: figures 3, 4) of living specimens in the wild at Christmas Island, Indian Ocean, are variably bright yellow dorsally, grayish white laterally or posteriorly, with yellow dorsal and ventral caudal-fin lobes, or brownish anteriorly with brownish or yellowish-brown bands on the body.

Photographs (Plate 3: figure 5) taken in the wild of a live specimen at Mauritius show an individual exhibiting a complex pattern that is quite different from that of any other specimens. The dusky markings on the head of the Red Sea specimens are present as brilliant yellow spots on the Mauritius specimen; the dusky anterior portions of the head and dorsal fin exhibit a faint

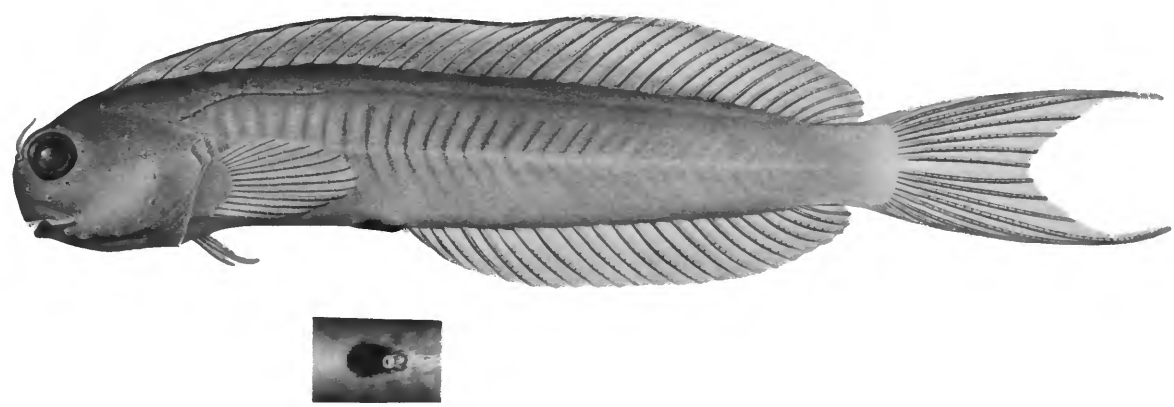


FIGURE 21.—*Ecsenius midas*, ANSP 111148, holotype, male, 74 mm SL, D'Arros Island, Amirante Islands, Seychelles (small figure shows ventral view of area surrounding anus; drawn by S.L. Chambers).

TABLE 9.—Frequency distributions for certain meristic characters of specimens of *Ecsenius midas* from different localities. Some regional groups of localities are set off by horizontal lines.

	Dorsal-fin rays				Anal-fin rays				Caudal vertebrae		
Locality	18	19	20	21	20	21	22	23	27	28	29
Gulf of Aqaba		3	1		1	3			3		
Port Sudan, Red Sea		1			1				1		
Amirante Islands		1	2	1			2	2		2	2
Grand Comore Island			1				1			1	
Chagos Islands		4	10	2		3	11	2	4	7	5
Mauritius			5	1			4	2		4	2
Zululand, South Africa			4	1			4	1		3	2
Nicobar Islands		1	1			1	1			2	
Cocos-Keeling Islands		1	1			1	1			2	
Palawan, Philippines		2				2			1	1	
Kabaena Island, Indonesia	1				1				1		
Madang, Papua-New Guinea			1				1		1		
Port Moresby, Papua-New Guinea		1	1				2			2	
Northern Escape Reef, GBR		2	1			1	2		2	1	
Solomon Islands			1			1				1	
New Hebrides Islands			1				1			1	
Loyalty Islands		3	4	1	1	1	6		2	5	
Fiji			1				1			1	
Marquesas Islands		2	10	5			10	7	1	8	8
Christmas Island, Line Ids.	1				1				1		

yellow suffusion; the fine dusky stripes outlining the myomeres, which are scarcely noticeable in Red Sea specimens, are black in the Mauritius specimen, and there is a fine, black stripe that begins anteriorly on the lateral line and continues on to the caudal peduncle (absent in Red Sea specimens); the ventral portions of the body and head are pearly white; the dorsal fin bears a fine immaculate distal edge below which is a fine, blackish area that becomes deeper posteriorly and grades into a complex dark and pale vermiculated pattern covering the entire segmented-ray portion of the fin, and extending diffusely onto the dorsalmost portions of the body. The dorsal edge of the dorsal lobe of the caudal fin is white, the lobe is otherwise dusky with a faintly yellow tip; the ventral lobe is dusky, but the ventral edge and tip are not visible. According to J.E. Randall (pers. comm.), the generally orange type coloration found in specimens from other localities also occurs at Mauritius. I am unable to differentiate preserved specimens from Mauritius and other localities based on color pattern.

GEOGRAPHIC VARIATION.—Based on the limited samples available, it appears that statistically significant geographic variation may occur in numbers of segmented dorsal- and anal-fin rays and caudal vertebrae. Specimens from the Gulf of Aqaba and western Pacific appear to have fewer of these elements than specimens from the Indian Ocean and Marquesas (Table 9).

REMARKS.—*Ecsenius midas* is the most widely distributed of the species of *Ecsenius*, its range over longitude encompassing and exceeding that of all the other species together. Its latitudinal range fails only by about 10° in the north from encompassing that of all the other species together. Perhaps not surprisingly, it is also the most pelagic of the species, rising several feet above coral heads and swimming among groups of *Anthias squamipinnis*, which it reportedly mimics (Starck, 1969; L. Fishelson, pers. comm.). Its status as a mimic, at least of *A. squamipinnis*, must not be obligatory, because the latter species does not occur as far east into the Pacific as does *E. midas*. Also, the life colors described above for Mauritius and Christmas Island do not resemble those of *A. squamipinnis*, which, except for sexual dimorphism, is relatively invariable.

In its general morphology, *E. midas* is strikingly distinctive within *Ecsenius:* it is the largest species, attaining almost 100 mm SL; it has many fewer teeth in each jaw than any other species of *Ecsenius;* the anterior canines are greatly enlarged; the caudal fin is lyre-shaped and gives the impression that the long upper and lower lobes are the result, at least in part, of a shortening of the central rays, whereas in the other species of *Ecsenius*, the longer upper and lower lobes, when present,

appear to be the result solely of elongation without concomitant shortening of the central rays; it has the highest numbers of pseudobranchial filaments (Springer, 1971: table 6), and dorsal-fin, anal-fin, and vertebral elements, and one of the shortest lateral lines; it is one of two species (the other, *E. namiyei*) with the dorsal fin originating anterior to a vertical from the anterior margin of the opercle; one of three species (the others, *E. namiyei, E. frontalis*) in which the dorsal fin is not incised between the spinous and segmented-ray portions.

Because of its numerous, unique differences, which are probably autapomorphies, *E. midas* has been accorded its own subgenus, *Anthiiblennius*. The problem with recognizing this subgenus is that there is no obvious synapomorphy that defines all the other species of *Ecsenius* to the exclusion of *E. midas*. The black spot in the anal region, found among blennioids only in the four species of the Stigmatura Group, and possibly the modal number of segmented caudal-fin rays (14, found otherwise only in the two species of the Bicolor Group), are evidence for the monophyly of the group, which could take the subgeneric name *Anthiiblennius*. If the Stigmatura Group is not the sister group of all other *Ecsenius* species groups, assigning the Stigmatura Group a subgeneric name would require at least two, probably more, other subgeneric names be accorded to the remaining species groups of *Ecsenius*, if nomenclatural consistency is to be maintained. Until interrelationships of the groups have been resolved, it is best not to recognize subgenera in *Ecsenius*.

DISTRIBUTION.—From the Gulf of Aqaba and southeast coast of Africa east to the Marquesas Islands. Specimens or reports are notably lacking from the west coast of Australia and from north of the Philippines in the Pacific.

MATERIAL (* = new material).—*Egypt:* Sinai coast, UTAI 4221 (1 specimen: 71 mm SL), USNM 204707 (1:77), 204559 (1:45), 204551 (1:69). *Sudan:* Port Sudan, BPBM 20419* (1:58). *Amirante Islands:* ANSP 134980* (1:72), 111148 (holotype: 74), 111149 (1:49), 111854 (1:34, cleared and stained), USNM 202422 (1:56). *Grand Comore Island:* CAS 34384 (1:39). *Chagos Islands:* ROM 43805* (3:44–53), 43806* (4:41–50), 43807* (2:46,50), 43808* (2:37,48), 43809* (5:43–57). *Mauritius:* BPBM 15945 (1:86), 15944 (3:35–77), 21844* (1:66), RUSI 7166* (1:74). *South Africa:* Zululand, Sodwana Bay, RUSI 9180* (5:63–98). *Nicobar Islands:* SMF 9579 (1:83), 9577 (1:44). *Cocos-Keeling Islands:* ANSP 128011 (2:42,49). *Philippines:* Palawan, USNM 227402* (2:75,84). *Indonesia:* Kabaena Island, USNM 211913 (1:46). *Papua-New Guinea:* Madang, BPBM 15866* (1:63); Port Moresby, ANSP 158830* (2:47,64). *Australia:* Great Barrier Reef, Northern Escape Reef, ANSP 109686 (2:28,29), AMS I.22638-100* (1:63). *Solomon Islands:* AMS I.17532-001 (1:76). *New Hebrides:* USNM 214736 (1:53). *Loyalty Islands:* USNM 213727 (3:34–36, including one cleared and stained), BPBM 19701 (5:31–40). *Fiji:* USNM 214786 (1:67). *Marquesas Islands:* BPBM 10866 (6:29–67), 11934* (8:34–84), 12104* (2:37,47), 12400* (1:68). *Line Islands:* Christmas Island, BPBM 30656* (1:60).

Ecsenius stigmatura Fowler

FIGURES 22, 23; PLATE 4: FIGURES 1, 2; TABLE 8

Ecsenius stigmatura Fowler in Chapman and Schultz, 1952:514 [Dammi Island; corrected by Springer, 1971, to Tomahu Island, Indonesia; holotype, USNM 99379].—McKinney and Springer, 1976:22.

Ecsenius (Ecsenius) stigmatura.—Springer, 1972:50 [right column of text only].

DESCRIPTION.—Dorsal fin XII or XIII (rarely XIII),15 or 17 (rarely 15), deeply notched between spinous and segmented-ray portions. Anal fin II,17–19. Pectoral fin 13–15 (usually 14). Segmented caudal-fin rays 13 or 14 (rarely 13). Vertebrae 10 + 22–24 (rarely 22 or 24). Dentary incisor teeth 34–40 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior dentary canines 1 on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 7 and 10 (usually between 8 and 9). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, head and body generally dark brown, gradually becoming paler on posterior half of body. Fine dark stripe extending posteriorly from near posteroventral margin of orbit to posterior opercular margin; short, broader, immaculate stripe on opercle slightly ventral to fine dark stripe; continuation of pale stripe on body limited to small area just dorsal to pectoral-fin axil. Dark spot extending anteriorly from anus, and another, much larger dark spot on caudal peduncle and bases of caudal-fin rays; peduncular spot often with broad, pale, encircling margin, or pale margin present only anteriorly. Dorsal-fin with broad, pale dusky stripe basally; stripe often with dusky extensions along spines. Anal fin almost uniformly dusky. Other fins, except as noted for caudal, scarcely marked.

Live Color (Plate 4: figures 1, 2): The head and anterior half of the body are generally brown, grading into salmon orange posteriorly on the body, with a bright white margin anteriorly to the black peduncular spot; a slender, salmon-orange stripe extends along the dorsal body contour at the base of the dorsal fin; a juxtaposed pair of very fine stripes, black stripe dorsally, white stripe ventrally, extends posteriorly from the ventroposterior margin of the orbit to a point on the body above the insertion of the dorsalmost pectoral-fin ray. Just ventral to this pair of stripes, and only narrowly separated from them, is a deeper, brilliant orange stripe that extends from about the preopercular margin to the insertion of the dorsalmost pectoral-fin ray. The fins are inconspicuously pigmented. The iris of eye is dark brown, with a slender orange ring peripherally, and faintly orange ring around pupil. A color photograph of a freshly dead specimen from the Moluccas indicates the following differences: iris of eye with broad orange outer ring, slender black middle ring, and broad yellow inner ring. (Note: see color described by Springer, 1972:31, based on a colored painting.)

REMARKS.—Springer (1971:31) corrected the originally reported collection locality of the holotype and one paratype

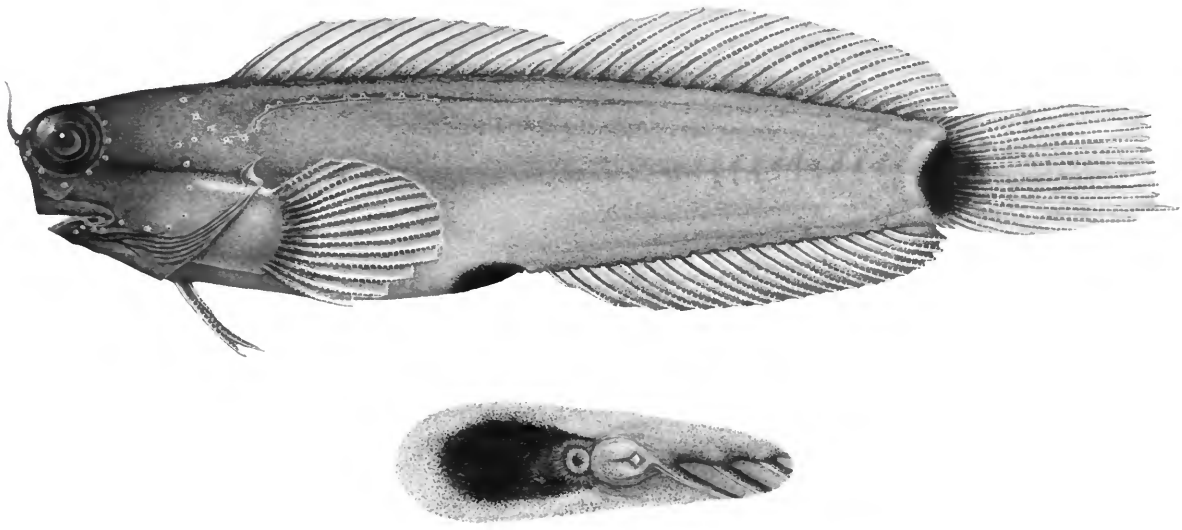


FIGURE 22.—*Ecsenius stigmatura*, USNM 11878, female, 37 mm SL, Tomahu Island, Indonesia (small figure shows ventral view of area surrounding anus; drawn by M.H. Lester).

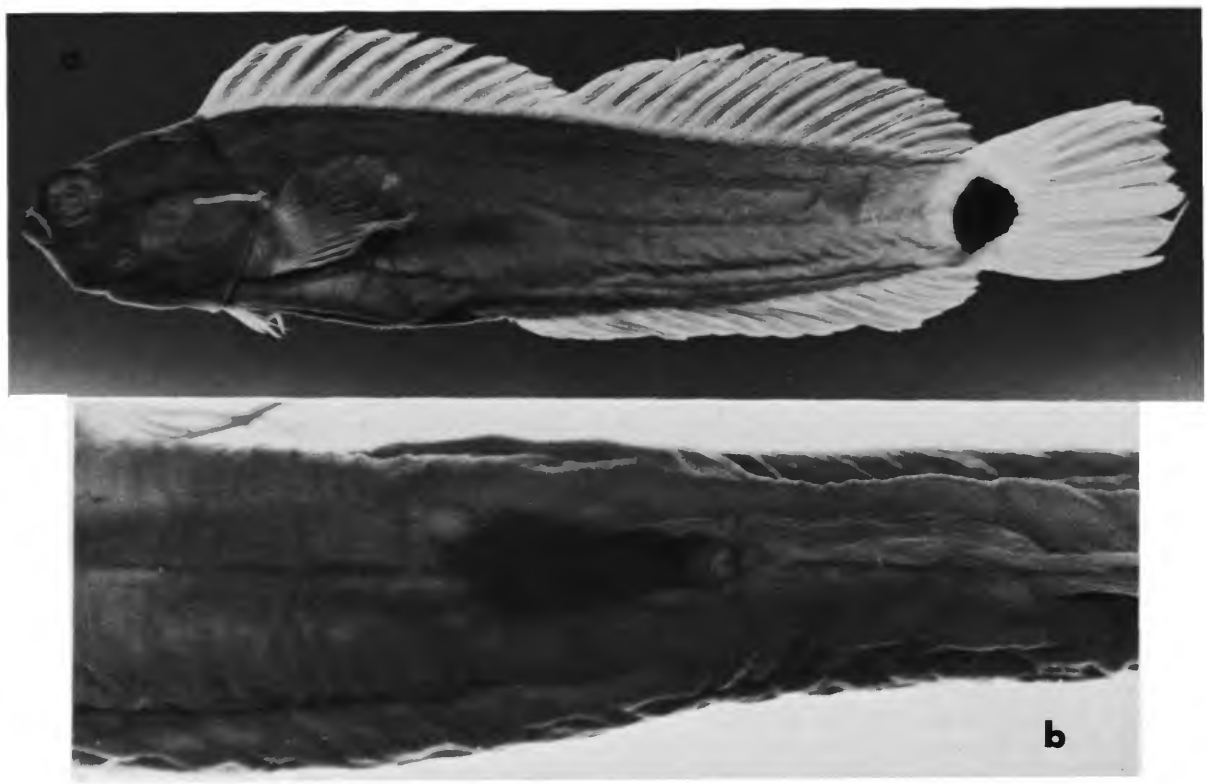


FIGURE 23.—*Ecsenius stigmatura*, USNM 210445, male, 43 mm SL, Ambon, Indonesia: *a*, lateral view; *b*, ventral view of area extending from about midbelly posteriorly to anterior anal-fin rays (photograph by J.T. Williams).

of *E. stigmatura* (Dammi Island, between Jolo and Tawi Tawi Straits, Philippine Islands) to: Tomahu Island, off the west coast of Buru, Indonesia. He had no reason to question the locality accorded the second paratype (Cataingan Bay, east side of Masbate Island, Philippine Islands). The only other records of *E. stigmatura* from the Philippines are based on photographs. An underwater photograph (Plate 4: figure 2) in the files of T.F.H Publications, Inc., is noted as having been taken by Roger Lubbock at Cebu [if so, probably Mactan Island near Cebu City]. Guiuan, Samar, is inscribed on the reverse of a print in my possession of a color photograph of a specimen (source now forgotten). The three Philippine records are from localities close together and well removed from the Moluccan Sea localities (Figure 6), whence all subsequent specimens of *E. stigmatura* have come. The Philippine localities are also closer to a Philippine collecting site (Palawan) of *E. melarchus*, which I believe is the sister group of *E. stigmatura*, than to the Moluccas. It is surprising that there are so few palpable records of *E. stigmatura* from the central Philippines, given the intensive collecting in that area in recent years.

Additional confirmation of the occurrence of *E. stigmatura* in the Philippines, as well as other localities between the Moluccas or Palawan and the central Philippines, would be worthy of report. More complete distributional information on *E. stigmatura* and *E. melarchus* would be helpful in hypothesizing the vicariant event that inaugurated the evolution of these two species, which appear to form a sister group, from a common ancestor.

Springer (1971:30) gave two species accounts with identical headings: *Ecsenius (Ecsenius) stigmatura* Fowler. The first such heading, in the left-hand column of the page, is an error, and pertains to *Ecsenius lineatus* Klausewitz.

DISTRIBUTION.—Philippine Islands; Tomahu, Ambon, Saparua, and western Ceram, Molucca Islands.

MATERIAL (* = new material).—*Indonesia:* Tomahu Island, USNM 99379 (holotype: 45.9 mm SL); Ambon, BPBM 18613 (1 specimen: 25), USNM 210445 (1:43); Ceram, USNM 209696 (2:20, 22), 209851 (12:16–32); Saparua, USNM 209993 (1:24), 210146 (5:26–37); Irian Jaya, Batanta Island, USNM 221238* (9:22–43, including 2 cleared and stained). *Philippine Islands:* Cataingan Bay, USNM 111878 (1:37).

FRONTALIS GROUP

The Frontalis Group comprises only *E. frontalis*, which is distinctive for having modally 15 pectoral-fin rays, more than any other species of *Ecsenius*. Other distinctive characters, shared with relatively few species of *Ecsenius*, are: an unnotched dorsal fin (present also in *E. namiyei*, of the Bicolor Group, and *E. midas*, of the Stigmatura Group; only slightly notched in *E. lividanalis*, Stigmatura Group; moderately to deeply notched in all other species); modally 11 precaudal vertebrae (present also in the four species of the Pulcher Group, *E. midas* and *E. lividanalis*, Stigmatura Group, and one population of *E. lineatus*, Lineatus Group); presence of three different color patterns: uniform, striped, and bicolored (all three present otherwise only in *E. bicolor* of the Bicolor Group); and relatively high numbers of segmented dorsal- and anal-fin rays and caudal vertebrae (also characterize Pulcher, Stigmatura, except *E. lividanalis*, Bicolor, and Lineatus groups).

Ecsenius frontalis is possibly most closely related to the Pulcher and/or Stigmatura groups (see discussion under Pulcher Group account), which also tend to have high numbers of pectoral fin rays. All the species of the Pulcher Group and two of the four species of the Stigmatura Group have modally 14 pectoral-fin rays, one less than *E. frontalis*, but one more than all the other species of *Ecsenius*, which might indicate presence of a transformation series from the other species to the Pulcher and Stigmatura groups to *E. frontalis* (the reverse or bi-directional transformation sequences may also be possible). It is, perhaps, of interest that the Pulcher Group species are restricted to the Red Sea-Persian Gulf area; *E. frontalis* is restricted to the Red Sea and adjacent gulfs, and three of the four Stigmatura Group species occur only in the western Pacific, whereas, the fourth ranges over most of the Indo-Pacific.

I am unable to polarize the characters that seem to be of importance for hypothesizing parsimoniously, or reasonably unequivocally, the sister group of *E. frontalis*.

Ecsenius frontalis (Ehrenberg)

FIGURES 24–26; PLATE 4: FIGURES 3–5; TABLE 10

Salarias frontalis Ehrenberg in Cuvier and Valenciennes, 1836:328 [Massawa, Red Sea; 5 syntypes in poor condition, ZMB 1947].

Salarias nigrovittatus Rüppell, 1838:136 [Massawa, Red Sea; holotype, SMF 1680].

Ecsenius albicaudatus Lotan, 1969:372 [Marsa Murach, Gulf of Aqaba; holotype, HUJ F-3540].

Ecsenius (Ecsenius) frontalis.—Springer, 1971:14.

DESCRIPTION.—Dorsal fin X–XIII (XII in 95% of specimens), 18–21 (rarely 21), not incised between spinous and segmented-ray portions. Anal fin II,17–22 (19–21 in 96% of specimens). Pectoral fin 14–16 (15 in over 80% of specimens of any population). Segmented caudal-fin rays 13 or 14 (rarely 14). Vertebrae 10 or 11 (rarely 10) + 23–26 (rarely 23) = 34 to 37 (rarely 34). Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 40–53 (rarely less than 44); posterior canines 0 or 1 (usually 1) on each side. Lateral line without vertical pairs of pores, extending posteriorly to point between verticals from 8th and 12th from anteriormost dorsal-fin spine (usually past vertical from 8th). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Color Pattern: There are three basic color patterns found in *E. frontalis:* (1) more-or-less uniformly brown, except body paling slightly and gradually in area slightly anterior to caudal peduncle posteriorly (frontalis form); (2) more-or-less uni-

formly dark brown or black, except most intensely dark slightly anterior to caudal-fin base and abruptly pigmentless from this darkest area posteriorly (albicaudatus, or bicolor, form); (3) generally brownish with darker stripe dorsally on body extending from anterior portion of body onto anterior portion of caudal fin; narrow paler areas margining dark stripe dorsally and/or ventrally (nigrovittatus form). In life the frontalis form is generally brown anteriorly, changing gradually posteriorly into yellow orange, with a bright yellow-orange caudal fin. One color slide of a frontalis form showed the fish as generally faint dusky-olive with the caudal peduncle, caudal fin, and a narrow distal edging of the dorsal fin faintly yellow orange. The albicaudatus form is generally black or brown with the narrow, pale area on the caudal peduncle white and the caudal fin immaculate or tinged with pink. The nigrovittatus form is generally gray brown with the dark body stripe almost black

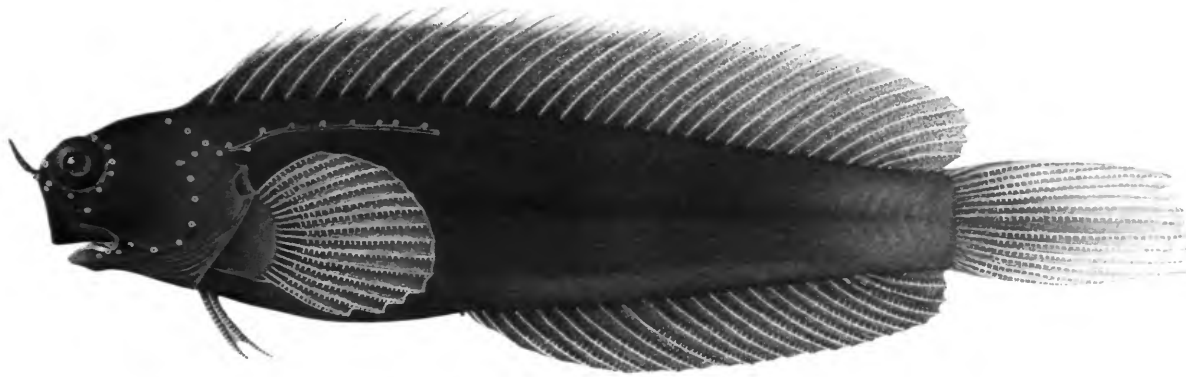


FIGURE 24.—*Ecsenius frontalis*, frontalis form, USNM 200613, male 59 mm SL, Red Sea, Strait of Jubal, Egypt (drawn by M.H. Lester).

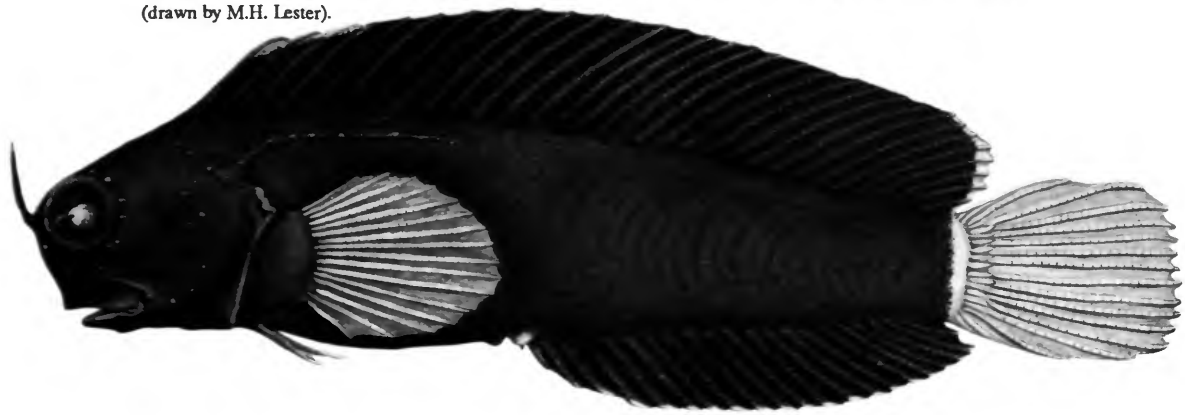


FIGURE 25.—*Ecsenius frontalis*, albicaudatus form, USNM 204650, female, 37 mm SL, Gulf of Aqaba coast, Sinai Peninsula (drawn by J.R. Schroeder).

FIGURE 26.—*Ecsenius frontalis*, nigrovittatus form, USNM 204490, male, 39 mm SL, Sheikh el Abu, Ethiopia, Red Sea (drawn by J.R. Schroeder).

TABLE 10.—Frequency distributions for certain characters in Ecsenius frontalis indicating geographic variation (Gulf of Aqaba also includes Red Sea north of Ghardaqa, Egypt; Middle Red Sea includes Djeddah, Saudi Arabia, and Sanganeb Reef, Sudan; southern Red Sea includes Ethiopia and proprietary islands).

Locality	Segmented dorsal-fin rays						Segmented anal-fin rays						Caudal vertebrae				
	17	18	19	20	21	$\bar{x}$	18	19	20	21	22	$\bar{x}$	23	24	25	26	$\bar{x}$
Gulf of Aqaba		7	59	58	3	19.4		4	72	44	1	20.4		5	91	28	25.2
Red Sea																	
Middle		3	10			18.8		3	9	1		19.8		3	7	3	25.0
Southern	3	100	41			18.3	9	93	40			19.2	2	75	65	2	24.5
Gulf of Aden			12	1		19.1		3	9			19.8			11	2	25.2

Locality	Pectoral-fin rays				Dentary incisor teeth													
	14	15	16	$\bar{x}$	40	41	42	43	44	45	46	47	48	49	50	51	52	53	$\bar{x}$
Gulf of Aqaba	4	101	24	15.2				1	-	-	3	13	19	16	30	9	12	3	49.3
Red Sea																			
Middle	2	11		14.8					1	-	5	4	1	2					46.8
Southern	11	129	3	14.9	1	1	1	3	9	21	35	24	31	12	2				46.5
Gulf of Aden		13		15.0						1	2	5	2	1					47.0

and the caudal fin tinged with orange; the head is occasionally yellow orange anterior to the orbits, changing to orange brown posterolaterally. All three forms have a horizontally parallel pair of slender, yellow or white stripes, which sandwich the pupil and extend from the anterior to the posterior orbital margin. A 15 mm postlarva had a preserved pattern of irregular vertical bands composed of dark spots. Small, bright-yellow specimens identified by Springer (1971) as *E. frontalis* were more probably the young of *Atrosalarias fuscus*, which superficially resembles *E. frontalis*, occurs with it in the same habitat, and has bright yellow juveniles.

SEXUAL DIMORPHISM.—Springer (1971) erroneously reported that Ethiopian frontalis-form males have a statistically significant higher average number of segmented dorsal-fin rays than females; however, these males do have a significantly higher average number of caudal vertebrae than females (Springer, 1971, table 11; two-tailed $t = 2.38$; $0.02 > p > 0.01$; df = 86). No other meristic character exhibits sexual dimorphism when tested by color pattern and geographic location, and it seems possible that the significant difference in caudal vertebrae is, nevertheless, the result of chance. Tests for differences in meristics among color-pattern forms from the same locality are also not significant. I have, therefore lumped the sexes and color patterns in tabulating the data for Table 10.

GEOGRAPHIC VARIATION.—Specimens from the northern end of the distribution have significantly higher average numbers of dorsal-, anal-, and pectoral-fin rays, caudal vertebrae, and dentary incisor teeth ($p = < 0.001$) than do specimens from the southern Red Sea. Specimens from the middle part of the Red Sea have averages for these counts that tend to be intermediate between those of the other two areas, and averages of specimens from the Gulf of Aden tend to be slightly higher than those for the middle Red Sea (Table 10).

REMARKS.—Collections from the northern part of the range indicate that the albicaudatus form tends to be more abundant in deeper collections and that the frontalis form tends to be more abundant in shallower collections. The tabulation that follows lists the greatest depth collected (using rotenone) in each of 11 collections I made, and the number of specimens of each of the forms taken in the collection:

Form	*Depth (m)*										
	3	3.5	7.5	9	10	10.5	12	15	16	18	27
frontalis	37	8	0	9	31	1	1	9	2	3	0
albicaudatus	10	1	3	0	1	4	18	5	14	11	3

Only the frontalis and albicaudatus forms occur in the northern part of the range (north of about 26°N), whereas all three forms occur in the southern part of the range (south of about 22°N). Only one specimen is available between 22° and 26°. Other than the depth associated separation, which is not absolute, the forms do not appear to be ecologically separated. I have seen all three forms together on the same small coral head in the southern Red Sea. The three forms are more-or-less comparable with the three forms found in *Ecsenius bicolor*, but differ in that all the forms of *E. bicolor* occur throughout the range of the species, and the striped form is the least common of the three (the albicaudatus form of *E. frontalis* is the least common where all three forms occur). I have no explanation for absence of the nigrovitattus form of *E. frontalis*

in the northern part of the species' range. Experimental inter-and intra-form breeding experiments using all three forms would make an excellent research project.

DISTRIBUTION.—Known only from Red Sea (including Gulfs of Aqaba and Suez) and the westernmost portion (Bay of Tadjourah) of the Gulf of Aden.

MATERIAL (* = new material).—*Gulf of Aqaba:* USNM 204534 (19 specimens: 17–37 mm SL), 204535 (3:25–30), 204536 (4:16–24), 204650 (14:18–48), 204685 (9:29–52), 204684 (46:17–44), HUJ F-3540 (1:43, holotype of *Ecsenius albicaudatus*), E-60/90.16 (1:47), F-4375 (2:19, 21), F-3544 (2:40, 42), E-64/34 (4:32–41), E-64/3013 (1:40), TAU NS-3582 (1:44). *Gulf of Suez, Et Tor:* USNM 204651 (9:30–45). *Egypt:* Strait of Jubal, USNM 200613 (7:24–50, including one cleared and stained); Al Ghardaqa, SMF 5118 (1:44). *Saudi Arabia:* Jeddah, USNM 217727* (10:42–73); Yanbu, BPBM 30380* (1:41). *Sudan:* Sanganeb Reef, SMF 8236 (3:41–47). *Ethiopia:* Massawa, ZMB 1947 (5: damaged syntypes of *Salarias frontalis*), SMF 1680 (1:29, holotype of *Salarias nigrovittatus*), USNM 204517 (12:21–36); Harat Island, USNM 204490 (86:20–61); Dahlak Islands, HUJ E-62/424A (21:16–47), E-62/1280 (2:32, 34), E-62/428 (2:19, 40), E-62/604 (1:39), E-62/3678A 1:40), E 62/1280A (8:31–43), E-62/417H (18:17–38), SMF 8757 (7:24–44); Zubair Island, HUJ F4628 (4:29–35). *Gulf of Aden:* Bay of Djibouti, MNHN 04-318 (3:38–47), USNM 223713* (10:20–44). Additional USNM material, some uncataloged, from Delemme, Sciumma, and Difnein islands, and Melita Bay, Ethiopia, were used by Springer (1971) to obtain data on frequencies of occurrence of the color pattern forms.

BICOLOR GROUP

The Bicolor Group comprises *E. bicolor* and *E. namiyei*. These two species are distinguished from all other species of *Ecsenius* in having cirri on both the anterior and posterior rims of the anterior nostril (versus on the posterior rim only) and in commonly having more than one (up to 10) vertical pairs of pores in the lateral line (many specimens of *E. namiyei* lack vertical pairs of pores, which I propose is a secondary loss). I consider these two characters to be synapomorphies. Furthermore, *E. bicolor* and *E. namiyei* exhibit sexual dimorphism in average numbers of caudal vertebrae and segmented dorsal-and anal-fin rays. Such sexual dimorphism is known otherwise in *Ecsenius* only for two other species: *E. pulcher* (Pulcher Group), in which the dimorphism affects only the number of segmented dorsal-fin rays, and the Ethiopian population of the frontalis form of *E. frontalis* (Frontalis Group), in which the dimorphism affects only the number of caudal vertebrae (see section on sexual dimorphism under *Ecsenius frontalis* species account, where this dimorphism is considered as possibly due to chance).

Ecsenius bicolor and *E. namiyei* specimens almost always have 14 segmented caudal-fin rays, a number that occurs modally in *Ecsenius* otherwise, only in the four species of the Stigmatura Group. No other blenniids have as high a modal number of segmented caudal-fin rays as these species, and it is possible that 14 segmented caudal-fin rays is a synapomorphy of the Bicolor and Stigmatura groups. For further discussion of relationships, see discussion in accounts of the Pulcher and Stigmatura groups.

Because the distribution of *E. bicolor*, which is one of the most broadly distributed species of *Ecsenius*, essentially envelops that of *E. namiyei*, it is not possible to hypothesize the vicariant scenario that split the ancestral population that gave rise to the two species.

Ecsenius bicolor (Day)

FIGURES 27, 28; PLATE 4: FIGURE 6, PLATE 5: FIGURES 1–4; TABLES 11, 12

Salarias bicolor Day, 1888:798 [Saddle Island, off Kyoukphyoo, Arakan, Burma; holotype discarded].

Salarias furcatus Johnstone [not of De Vis], 1904:213 [Chilaw Paar, Ceylon; location of holotype unknown].

Salarias melanosoma Regan, 1909:406 [Christmas Island, Indian Ocean; syntypes, BMNH 1909.3.4.52-57, USNM 157373].

Salarias burmanicus Hora and Mukerji, 1936:34 [Maungmagan, Tavoy District, Lower Burma; holotype, ZSI F11872/1, type 429].

Ecsenius hawaiiensis Chapman and Schultz, 1952:526 [Pearl Harbor, Oahu, Hawaii; a possible introduction from Guam; holotype, USNM 112293].

Ecsenius (Ecsenius) bicolor.—Springer, 1971:25.

Ecsenius bicolor.—McKinney and Springer, 1976:4.

DESCRIPTION.—Dorsal fin XI or XII, 15–18 (rarely XI or 15), incised about half length of first dorsal-fin ray between spinous and segmented ray portions; origin posterior to vertical from middle (posteriormost) pores of preopercular series. Anal fin I or II, 17–21 (rarely I - and only in females; rarely 17). Pectoral fin 12–14 (13 in 97% of specimens). Segmented caudal-fin rays 13 or 14 (14 in 99% of specimens). Vertebrae 10 or 11 + 22–25 (10 in over 99% of specimens; 22 in less than 1% of specimens) = 32–35 (rarely 32). Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 32–46 (only 1 specimen of over 200 checked with less than 35); posterior canines 0 or 1 (usually 1). Lateral line with vertical pairs of pores along one-quarter or more of its length, extending posteriorly to point between verticals from 10th and 13th from anteriormost dorsal-fin element. Cirrus present on both posterior and anterior rims of anterior nostril (anterior cirrus frequently inapparent in specimens less than 25 mm SL).

Color Pattern: Ecsenius bicolor is one of the more variably pigmented species of *Ecsenius*. There are three basic color patterns that specimens exhibit, both in life and in preservation: (1) uniform pattern, more-or-less uniformly dark head and body with dark pigment extending as triangle onto caudal fin; (2) bicolored pattern, more-or-less uniformly dark head and anterior half (rarely more) of body, posterior half of body and caudal fin contrastingly pale; (3) striped pattern, head and dorsal portion of body dark with darker stripe on body side, ventral portion of body paler than dorsal portion, posterior

FIGURE 27.—*Ecsenius bicolor*, bicolored form, USNM 201368, male, 66 mm SL, One Tree Island, Queensland, Australia (drawn by S.L. Chambers).

TABLE 11.—Frequency distributions for certain meristic characters in specimens of *Ecsenius bicolor* from selected localities. * = $\bar{x}$ for males is significantly different (i.e. higher) from $\bar{x}$ for females (p = <0.05; 2-tailed t-test). ** = corrected from Springer, 1971, table 15.

	Dorsal-fin rays					Anal-fin rays						Caudal vertebrae				
Locality	15	16	17	18	$\bar{x}$	17	18	19	20	21	$\bar{x}$	22	23	24	25	$\bar{x}$
Queensland (GBR)																
males	-	-	21	20	17.5*	-	-	12	28	1	19.7*	-	-	7	28	24.8*
females	-	2	32	2	17.0	-	1	29	6	-	19.1	-	-	20	14	24.4
Western Australia																
males	-	-	6	2	17.2	-	-	3	5	-	19.6*	-	-	3	5	24.6
females	-	1	4	-	16.8	-	1	4	-	-	18.8	-	-	4	1	24.2
Fiji																
males	-	1	18	4	17.1	-	-	11	12	-	19.5*	-	2	5	15	24.6*
females	-	3	21	2	17.0	-	2	21	3	-	19.0	-	1	22	3	24.1
New Hebrides																
males	-	1	4	1	17.0*	-	-	4	2	-	19.3	-	-	2	4	24.7
females	-	4	1	-	16.2	-	-	5	-	-	19.0	-	1	4	-	23.8
Kapingamarangi																
males	-	4	21	1	16.9*	-	-	23	3	-	19.1*	-	-	16	8	24.3*
females	-	9	8	-	16.5	-	4	13	-	-	18.8	-	-	16	-	24.0
Ponape																
males	-	3	12	-	16.8*	-	2	10	3	-	19.1*	-	-	13	2	24.1*
females	-	13	8	-	16.4	-	16	5	-	-	18.2	-	7	14	-	23.7
Marshall Islands																
males**	-	3	24	-	16.9*	1	-	23	2	-	19.0*	-	-	15	10	24.4
females	1	9	2	-	16.1	-	6	6	-	-	18.5	-	-	10	1	24.1
South China Sea																
males**	-	-	1	5	17.8	-	-	1	5	-	19.8	-	-	2	4	24.7
females	-	-	2	1	17.3	-	-	-	3	-	20.0	-	-	1	2	24.7
Malacca Straits (Phuket, Thailand)																
males**	-	1	1	-	16.5	-	-	2	-	-	19.0	-	-	2	-	24.0
females**	-	1	2	-	16.7	-	1	2	-	-	18.7	-	-	3	-	24.0
Philippine Islands																
males	-	1	6	-	16.8	-	1	5	1	-	19.0	-	1	4	2	24.1
females	-	4	2	-	16.3	-	3	3	-	-	18.5	-	-	6	-	24.0
Kabaena Island (Indonesia)																
males	-	4	4	-	16.5*	-	2	6	-	-	18.8*	-	2	6	-	23.8*
females	2	13	1	-	15.9	-	13	3	-	-	18.2	1	10	5	-	23.2
Christmas Island (Indian Ocean)																
females	-	-	5	-	17.0	-	-	4	1	-	19.2	-	-	3	1	24.2
Ceylon																
males	-	3	21	2	17.0*	-	-	22	4	-	19.2*	-	1	20	5	24.2
females	-	9	14	-	16.6	-	7	15	1	-	18.7	-	5	15	3	23.9

FIGURE 28.—*Ecsenius bicolor: a,* bicolored form, USNM 214812, female, 43 mm SL, Efate, New Hebrides; *b,* unicolored form, WAM 25111-008, male, 54 mm SL, Dampier Archipelago, Western Australia; *c,* stri ed form, ANSP 128012, male, 43 mm SL, Horsburgh Island, Cocos Keeling Islands (photographs by J.F. McKinney).

TABLE 12.—Frequency distributions for numbers of dentary teeth in two populations of *Ecsenius bicolor.* Sexually associated differences in averages are statistically significant (two-tailed *t* test) for both populations.

	Dentary teeth								
Population	37	38	39	40	41	42	43	44	$\bar{x}$
Kapingamarangi (Caroline Islands) [t = 3.28; .005> p >.002]									
males	1	-	3	15	4	3	-	-	40.2
females	-	-	1	4	4	5	3	-	41.3
One Tree Island (Great Barrier Reef) [t = 5.48; p = <.001]									
males	-	-	4	11	9	13	1	-	40.9
females	-	-	1	2	3	12	7	9	42.4

Note: population differences between averages for males vs males and for females vs females are statistically significant. For males, t = 2.72, .01> p >.005. For females, t = 3.02, .005> p >.002.

portion of body and caudal fin pale. A black spot is variably present at the anterior end of the spinous dorsal fin of any of the color pattern types.

The striped pattern, although not rare, is by far the least common, and is never the most abundant pattern at any locality. Usually no more than one or two individuals with a striped pattern are taken in a single collection, whereas more than 25 of either of the other two forms may be taken in a single collection. One or the other of the uniform or bicolored patterns is dominant at any locality, although both types may predominate within a relatively restricted area. All three types may be taken in a single collection, and there is no correlation of the color-pattern types with sex or size. Comparable color-pattern types also occur in *E. frontalis*, and the first two patterns are somewhat duplicated in *E. lividanalis*, *E. namiyei* and *E. pulcher*.

Live Color: The uniformly dark form of *E. bicolor* is generally dark brown or purple brown; the bicolored form is deep slate-blue gray to brownish gray anteriorly and orange yellow posteriorly; the striped form is dark brownish gray dorsoanteriorly, orange yellow dorsoposteriorly, the stripe is almost black, and the area below the level of the stripe is bright white, often with a more brilliant white stripe bordering the dark one ventrally. The cheeks in any form may have a pinkish tinge.

Springer (1971) described some of the variation exhibited by both preserved and live specimens and referred to literature containing information on coloration and pattern in *E. bicolor*. Color photographs of living *E. bicolor* have been published by Debelius (1985, 1986). The photographs of *E. bicolor* in Allen (1985) appear to be posed freshly dead specimens.

Sexual Dimorphism.—Males generally have higher average numbers of meristic elements than do females, and where large numbers of specimens are available, the differences are usually statistically significant (Table 11). Females, as is often true among blenniids, have statistically significant higher average numbers of dentary incisor teeth than do males (only two populations tested; Table 12).

Geographic Variation.—Obvious differences in average numbers of meristic elements occur among specimens from various localities (Table 11). Similarly, statistically significant differences in average numbers of dentary incisor teeth exist among specimens from different localities (males versus males, females versus females), although only two localities were tested for this possibility.

Remarks.—Springer and Smith-Vaniz (1972) and Losey (1972) reported on the possible mimetic association of the bicolored form of *E. bicolor* with two other blenniids: *Meiacanthus atrodorsalis* (Günther) and *Plagiotremus laudandus* (Whitley). In the bicolored form of *E. bicolor*, the posterior portion of the body is orange yellow, whereas in the other two species it is lemon yellow. It has not been reported if these pigmentation differences are masked by the spectral absorption characteristics of seawater at the relatively shallow depths (usually less than 6 m) at which the species occur, but I believe that the mimetic relationship excludes *E. bicolor*. In Fiji and Tonga, *M. atrodorsalis* and *P. laudandus* are each replaced by essentially all-yellow species, a circumstance that occurs nowhere else. In contrast, *E. bicolor* exhibits the same coloration at Fiji and Tonga as it does at other localities, and an all-yellow (or orange-yellow) form is unknown. If *E. bicolor* were a mimic of the other two species, an all-yellow form of *E. bicolor* could reasonably, though not necessarily, be expected to occur at Fiji and Tonga. Parallel geographic variation of mimics with models is one of the best pieces of circumstantial evidence favoring interpretations of mimetic relationships. Such variation was reported by Springer and Smith-Vaniz (1972) for the mimetic association involving *Ecsenius gravieri* and *Meiacanthus nigrolineatus* Smith-Vaniz.

Distribution.—*Ecsenius bicolor* ranges from the Maldive Islands, central Indian Ocean, westward to Samoa, in the Pacific, and from the southern Ryukyu Islands in the north to the Capricorn Group of islands at the southern end of the Great Barrier Reef. The species distribution map (Figure 8) includes a few records based on the literature (most cited in Springer, 1971; additionally, Eldredge et al., 1979).

Springer (1971) discussed the peculiar circumstances under which the type specimens of *Ecsenius hawaiiensis* Chapman and Schultz (= *E. bicolor*) were taken at the Hawaiian Islands. The species has not been taken again in the Hawaiian Islands, and in view of the large arount collecting and ichthyological observations made in the Hawaiian Islands, especially in recent years, I doubt that it occurs there.

Material.—Extensive material of *E. bicolor* is listed in Springer, 1971:29, and McKinney and Springer, 1976:5. Only new material is listed here, and even this does not include all the previously uncited material known from many of the same general localities; large uncited collections are available at USNM and ROM. *Fiji:* USNM 243360 (2 specimens: 53, 53 mm SL), 243987 (21:34–58), 256466 (28:23–62). *New Hebrides:* Efate, USNM 214812 (1:44), [Espiritu?] Santo, 219924 (1:60). *Australia:* Queensland, Tijou Reef, AMS I.20779-171 (1:29); Lizard Island, USNM 218088 (2:22, 45); Escape Reef, AMS I.22578-047 (1:56), I.22619-010 (1:52); Western Australia, Kendrew Island, WAM P.25111-008 (2:39, 44; nine other specimens previously reported). *Papua-New Guinea:* Hermit Islands, USNM 227359 (1:44), 227399 (1:53); Ninigo Islands, USNM 222967 (2:29, 33). *Indonesia:* Toko Toko Rock (N of NE corner of Komodo), BPBM 31534 (1:44). *Philippine Islands:* Apo Island, BPBM 26435 (1:29); Negros, USNM 225139 (1:24); Batangas, Sombrero Island, USNM 225047 (6:24–47), 225048 (4:39–51), 228924 (1:50); Palawan, Puerto Princessa, USNM 227400 (1:48). *Caroline Islands:* Ponape, USNM 223485 (5:32–42), 223547 (1:28), 223613 (1:50), 224348 (19:16–51), 224374 (7:26–57). *Samoa:* USNM 227398 (2:52, 53). *Thailand:* Phuket, BPBM 22581 (1:61).

Ceylon: USNM 206666 (3:43–45), 206667 (1:61), 206668 (4:37–44), 272585 (4:18–34), 272586 (17:16–46).

Ecsenius namiyei (Jordan and Evermann)

FIGURE 29; PLATE 5: FIGURES 5, 6; PLATE 6: FIGURE 1; TABLES 13, 14

Salarias namiyei Jordan and Evermann, 1903:362 [Pescadores Islands; holotype, ZUMT 5726].
Ecsenius (Ecsenius) namiyei.—Springer, 1971:29.
Ecsenius namiyei.—McKinney and Springer, 1976:11.

DESCRIPTION.—Dorsal fin XI or XII,18–21 (rarely XI or 21), not incised between spinous and segmented ray portions, origin over or anterior to vertical from middle (posteriormost) pores of preopercular series. Anal fin II,19–22. Pectoral fin 12 to 14 (rarely 12 or 14). Segmented caudal-fin rays 13 or 14 (rarely 13). Vertebrae 10 or 11 + 24–28 = 34–38. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 34–45; posterior canines 0 or 1 on each side (rarely 0, and only unilaterally). Lateral line with 0–10 vertical pairs of pores, extending posteriorly to point between verticals from 10th and 13th elements from anteriormost dorsal-fin element (usually posterior to 10th element). Cirrus present on both posterior and anterior rims of anterior nostril.

Preserved Color: Body, head, and dorsal and anal fins dark brown, with caudal peduncle often noticeably pale (bicolor color pattern). Body occasionally with three or four widely separated, short, narrow, pale, vertical marks on each side, similar to marks found in some specimens of *E. bicolor;* other specimens with row of microscopic pale spots along midside; still others with a few small, oblong, intensely dark spots that underlie surface pigment. Spinous dorsal fin occasionally with slender, diagonal, deeply pigmented stripes below dark surface pigment. Anal fin occasionally with indistinct dark stripe along midlength. Caudal, pelvic, and pectoral fins dusky, with greater concentration of pigment along rays.

Live Color: A female specimen from Taiwan, which had been in an aquarium for a few weeks, had the head and body dark brown, grading on the caudal peduncle into amber yellow and then orange on the proximal portion of the caudal fin . Body with eight small, midlateral, blue-white spots beginning in pectoral-fin axil and extending to area below last dorsal-fin rays. Similar spots on pectoral-fin base and dorsal body contour, where they were less obvious than midlateral spots. Upper lip with blue-white bands separated by dark interspaces. Pale stripe extending from postorbital region to lip; some pale blue dashes on cheek.

The photograph, taken in the wild in the Philippines, reproduced in Plate 6: figure 1, shows an almost black fish with a gray caudal peduncle. The fish does not exhibit the blue-white spots and bands I observed in the aquarium specimen. Another photograph taken by R.C. Steene at Mactan Island (presently in his files), shows a specimen that is generally grayish brown suffused with yellow, with pale buff and yellowish-buff spots and irregular markings on the head (fright pattern?) and anteriorly on the body. There is a midlateral row of 4 or 5 small pale spots on the body posteriorly. The caudal-fin and peduncle are yellow and the yellow pigment continues broadly onto the segmented-ray portion of the dorsal fin, where it narrows gradually as it extends anteriorly to form a fine distal margin on the fin. The anterior rays of the anal fin are outlined in dusky yellow. In the files of T.F.H. Publications, Inc., are photographs of two freshly dead specimens from the Solomon Islands. One specimen (similar in appearance to Plate 5: figure 5) is dark brown, except for the caudal peduncle and central portion of the caudal fin, which are lemon yellow; the remainder of the fin is immaculate. The head and entire body of the other specimen are dark brown, the caudal-fin rays are darkly pigmented, and the interradial membranes are immaculate.

I am not certain of the extent to which live color pattern varies geographically, but I only recall seeing the posteriorly orange form in Taiwan. There are obviously two forms in the Solomon Islands and Philippines.

SEXUAL DIMORPHISM.—Males tend to have higher average

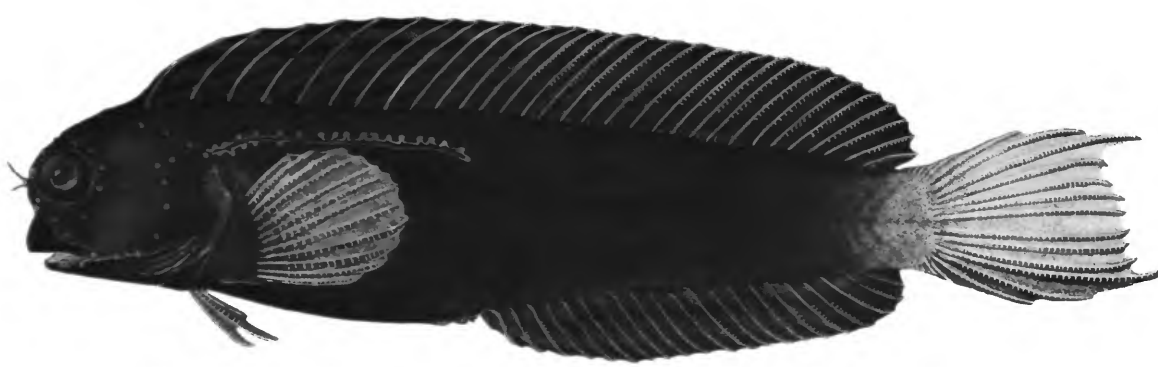


FIGURE 29.—*Ecsenius namiyei*, bicolored form, USNM 203125, female, 64 mm SL, north end of Taiwan (drawn by M.R. Davis).

TABLE 13.—Frequency distributions for certain characters in populations of *Ecsenius namiyei*.

Population	Segmented dorsal-fin rays					Segmented anal-fin rays					Precaudal vertebrae			Caudal vertebrae						Total vertebrae					
	18	19	20	21	$\bar{x}$	19	20	21	22	$\bar{x}$	10	11	$\bar{x}$	24	25	26	27	28	$\bar{x}$	34	35	36	37	38	$\bar{x}$
Taiwan and Pescadores																									
males	-	3	15	1	19.9	-	-	6	13	21.7	17	2	10.1	-	1	8	9	1	26.5	-	-	8	10	1	36.1
females	-	9	2	-	19.2	-	-	10	1	21.1	9	2	10.2	-	2	9	-	-	25.8	-	-	11	-	-	36.0
Philippine Islands																									
males	1	3	1	-	19.0	-	1	4	1	21.0	5	-	10.0	-	1	4	-	-	25.8	-	1	4	-	-	35.8
females	1	1	-	-	18.5	-	2	-	-	20.0	2	-	10.0	-	2	-	-	-	25.0	-	2	-	-	-	35.0
Indonesia																									
Celebes																									
males	4	16	2	-	18.9	1	9	12	-	20.5	19	3	10.1	1	15	6	-	-	25.2	1	12	9	-	-	35.4
females	11	1	-	-	18.1	1	9	2	-	20.1	9	-	10.0	-	8	1	-	-	25.1	-	9	1	-	-	35.1
Moluccas																									
males	2	3	1	-	18.8	-	4	2	-	20.3	5	1	10.2	-	4	2	-	-	25.3	-	3	3	-	-	35.5
females	3	-	-	-	18.0	1	2	-	-	19.7	3	-	10.0	1	2	-	-	-	24.7	1	2	-	-	-	34.7
Papua-New Guinea																									
Port Moresby																									
males	-	1	1	-	19.5	-	1	-	1	21.0	2	-	10.0	-	1	1	-	-	25.5	-	1	1	-	-	35.5
females	-	3	-	-	19.0	-	1	2	-	20.6	2	-	10.0	-	2	-	-	-	25.0	-	2	1	-	-	35.3
New Britain																									
males	-	2	-	-	19.0	-	1	1	-	20.5	1	1	10.5	-	1	1	-	-	25.5	-	-	2	-	-	36.0
females	1	1	-	-	18.5	-	1	-	-		2	-	10.0	-	2	-	-	-	25.0	-	2	-	-	-	35.0
Solomon Islands																									
males	2	5	-	-	18.7	-	3	4	-	20.6	1	6	10.8	2	4	1	-	-	24.8	-	2	5	-	-	35.7
females	2	1	-	-	18.3	-	2	1	-	20.3	-	3	11.0	3	-	-	-	-	24.0	-	3	-	-	-	35.0

TABLE 14.—Frequency distributions for certain characters in populations of *Ecsenius namiyei*.

Population	Dentary incisor teeth														Lateral-line pore pairs											
	34	35	36	37	38	39	40	41	42	43	44	45	$\bar{x}$	0	1	2	3	4	5	6	7	8	9	10	$\bar{x}$
Taiwan and Pescadores																										
males	-	1	-	1	-	1	4	6	2	4	-	-	40.7	-	1	3	3	5	4	1	-	-	1	1	4.3
females	-	-	-	-	-	1	1	1	2	-	4	2	42.7	-	-	1	4	-	1	2	-	1	-	-	4.3
Philippine Islands																										
males	-	-	1	-	2	2	-	-	-	-	-	-	38.0	1	1	1	1	-	-	-	-	-	-	-	1.5
females	-	-	-	1	-	1	-	-	-	-	-	-	38.0	2	-	-	-	-	-	-	-	-	-	-	0.0
Indonesia																										
Celebes																										
males	2	3	4	4	2	3	2	-	-	-	-	-	36.9	10	6	-	1	-	-	1	-	-	1	-	1.3
females	-	1	4	2	3	1	1	-	-	-	-	-	37.2	9	2	1	-	-	-	-	-	-	-	-	0.3
Moluccas																										
males	-	-	2	3	1	-	-	-	-	-	-	-	36.8	6	-	-	-	-	-	-	-	-	-	-	0.0
females	-	-	-	1	1	-	-	-	-	1	-	-	39.3	2	-	-	1	-	-	-	-	-	-	-	1.0
Papua-New Guinea																										
Port Moresby																										
males	-	-	1	1	-	-	-	-	-	-	-	-	36.5	2	-	-	-	-	-	-	-	-	-	-	0.0
females	-	-	1	-	1	-	1	-	-	-	-	-	38.0	1	1	-	1	-	-	-	-	-	-	-	1.3
New Britain																										
males	-	-	-	1	1	-	-	-	-	-	-	-	37.5	1	-	1	-	-	-	-	-	-	-	-	1.0
females	-	-	1	-	1	-	-	-	-	-	-	-	37.0	1	-	-	1	-	-	-	-	-	-	-	1.5
Solomon Islands																										
males	-	-	2	4	1	-	-	-	-	-	-	-	36.8	5	1	-	1	-	-	-	-	-	-	-	0.6
females	-	-	-	1	2	-	-	-	-	-	-	-	37.7	1	-	-	-	-	1	-	1	-	-	-	4.0

numbers of meristic elements than do females (Table 13), which in some cases are statistically significantly different (McKinney and Springer, 1976). Females from Taiwan have a higher average number of dentary incisor teeth than do males (Table 14; highly significant statistically; McKinney and Springer, 1976).

GEOGRAPHIC VARIATION.—The Taiwan population has the highest averages for numbers of dentary teeth, pairs of lateral-line pores, and all meristic characters except precaudal vertebrae (Tables 13 and 14). The remaining populations all appear to have about the same averages for these characters, with the exception of the Solomon Islands' population, which has the highest average number of precaudal vertebrae (population shifts in average numbers of precaudal vertebrae also occur in *Ecsenius lineatus*, but otherwise among blenniids have been reported only in the blenniid tribe Omobranchini, genus *Omobranchus*, by Springer and Gomon, 1975).

The higher averages in *E. namiyei* occur in a highly restricted geographic area, with the shift to lower averages occurring over a narrow geographic area (between Taiwan and the Philippines). The lower averages occur in populations scattered over a broad geographic range. These circumstances indicate, perhaps, that the Taiwan population is isolated from the other populations, and that the two groups are in the process of diverging (probably also true of the Solomon Islands' population). It would be useful to have collections of *E. namiyei* from the northernmost Philippines and the few islands between the Philippines and Taiwan to determine if specimens from these intervening areas are intermediate for the pertinent character averages. Observations on live color pattern at various localities are also of importance.

REMARKS.—*Ecsenius namiyei* occurs at depths of from one to three meters in Taiwan (and Pescadores?). Specimens from other localities, although occasionally taken at equally shallow depths, more often come from greater depths, to about 30 m.

DISTRIBUTION.—Western Pacific, from Taiwan in the northwest to the Solomon Islands in the southeast.

MATERIAL (* = new material).—*Pescadores Islands:* ZUMT 5726 (holotype: 50 mm SL, radiograph of *Salarias namiyei*). *Taiwan* (northern end): USNM 203125 (1:64, cleared and stained), 203126 (2:58–63), 203127 (5:62–80), 203128 (5:55–82), 204478 (9:59–76). *Philippine Islands:* Batangas, Caban Island, AMS I.21914-038* (2:39, 48), USNM 228921* (1:44); Cebu, USNM 219304* (1:61), USNM 267268* (1:84), 267269* (1:21); Cuyo Islands, USNM 219307* (1:56); Palawan, USNM 270837* (1:42). *Indonesia:* Celebes (= Sulawesi), Boeton, USNM 211969 (14:17–63), Kabaena, USNM 211904 (3:33–48), 211915 (18:26–60); Moluccas, Ambon, USNM 209736 (1:44), 211951 (1:52), 211957 (1:52), Saparua, USNM 210088 (2:22, 34), 210345 (4:23–51). *Papua-New Guinea:* Port Moresby, BPBM 15930 (1:56), KFRS uncataloged (4:46–63); New Britain, AMS I.17503-005* (2:37, 41), USNM 201866 (1:49), 201865 (1:49). *Solomon Islands:* Florida Island, AMS I.17500-002 (2:46, 53), BPBM 15644 (4:49–61); Guadalcanal, ROM 42338* (1:41), 42646* (1:20), USNM 212038 (1:32), 212040 (1:51).

LINEATUS GROUP

This group comprises a single species, *Ecsenius lineatus*. I am unable to hypothesize unequivocally its sister group, which is probably among those species groups that, like *E. lineatus*, are characterized by having a dark postorbital stripe and a deeply incised dorsal fin: Mandibularis, Oculus, Opsifrontalis, Pictus, Prooculis, Yaeyamaensis. In contrast to *E. lineatus*, all these groups have relatively low numbers of fin-rays and caudal vertebrae. The color pattern of *E. lineatus* is distinctive and sets it apart from the species in all the other species groups in *Ecsenius*. It is of interest, perhaps, that among these six groups, *E. lineatus* comes closest to being allopatric to the Pictus Group, which is the only one of the six that is monotypic. I find no character that would indicate that *E. lineatus* might be more closely related to *E. pictus* than to another of the six species groups.

Ecsenius lineatus Klausewitz

FIGURES 30, 31; PLATE 6: FIGURES 2–6; TABLE 15

Ecsenius lineatus Klausewitz, 1962:145 [Madewaru Island, Fadiffulu Atoll, Maldive Islands; holotype, SMF 5532].—McKinney and Springer, 1976:7.
Ecsenius (Ecsenius) stigmatura Fowler.—Springer, 1971:30 [*lapsus calami*, first column only; non Fowler].

DESCRIPTION.—Dorsal fin XII or XIII,16–18 (XIII in only one of 41 specimens), deeply notched between spinous and segmented ray portions. Anal fin II,18–20. Pectoral fin 12 to 14 (rarely 12 or 14 and only unilaterally). Caudal fin 13. Vertebrae 10 or 11 (usually 10 at most localities) + 24–26 = 34–36. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 45 to 51; posterior canines one on each side. Lateral line without vertically paired pores, extending posteriorly to point between vertical from interspace between dorsal-fin spines 9 and 10 and vertical from spine 11 (one specimen, of 32 examined for this character, had the lateral line terminating on one side at the vertical from spine 8). Cirrus (occasionally with one branch) present on posterior rim of anterior nostril, none on anterior rim, noticeably long (usually more than 4% SL), reaching, when depressed, to, or most of the way to, ventral margin of upper lip.

Preserved Color: In preservative, head generally darker above level of ventral third of eye; cheeks below this level more-or-less evenly dusky, except some specimens with pale, somewhat triangular area extending ventrally from orbit; ventral surface dusky with noticeable pale area anteriorly; deep, dark stripe usually extending posteriorly from midpostorbital margin, crossing head, and entering body, where it broadens and continues out onto caudal fin, or decomposes into series of up to 9 disconnected, dark, round, rectangular, or squarish

FIGURE 30.—*Ecsenius lineatus*, USNM 203129, male, 48 mm SL, just SW of Yeh-Liu, north end of Taiwan (drawn by M.R. Davis).

blotches, the last of which is often tear-shaped (apex posteriorly) and extends onto central caudal-fin rays; short, slender, pale stripe on head margining dark stripe dorsally; another slender, pale stripe margining dark stripe ventrally, extending posteriorly, crossing head, and reaching as far posteriorly as caudal-fin base, usually becoming inapparent on body; area above short, pale stripe dusky, margined dorsally by another slender, pale stripe, which extends well out on body, becoming diffuse posteriorly; slender, pale, mid-predorsal stripe variably present. Dorsal fin with dusky, slender, basal stripe, remainder of fin undistinctive. Anal fin dusky overall except for pale tips of rays; pigment intensifies slightly subdistally. Pectoral fin faintly dusky, except most rays and more dorsal interradial membranes immaculate. Pelvic fins pale with sprinkling of fine melanophores. Caudal fin with dark central extension of posteriormost body blotch, extension narrowing and decreasing in intensity posteriorly.

Live Color (based on photographs taken in wild at Maldive Islands, Mauritius, and Taiwan; Plate 6: figures 2, 3, 5, 6): In life the three postorbital stripes of preserved specimens are brilliant white (Maldives), brilliant yellow (Taiwan), or dorsal two are brilliant yellow and ventral one is brilliant white (Mauritius); ventral to these stripes, the head is sharply, pearly gray or white; the dark head stripes of preserved specimens are shades of brown or purple brown; the ventral 40% of the iris is brilliant white (Maldives, Mauritius) or yellow (Taiwan), the upper 60% is dark brown, interrupted by up to three white (Maldives) or yellow (Mauritius, Taiwan) spokes; ventral surface of lower lip yellow (Maldives, Taiwan) or pearly gray (Mauritius). Dorsal pale body stripe yellow (Mauritius, Taiwan) or white (Maldives), ventral stripe brilliant white (Maldives, Mauritius) or yellow (Taiwan); area below stripe pearl gray. Dark body blotches almost black, with brownish area dorsal to anterior blotches; posteriorly, dorsal body area and interspaces between blotches largely yellow (Maldives), dusky yellow (Mauritius), or brownish (Taiwan). A photograph taken in the wild at Okinawa (Plate 6: figure 4) shows an individual that is almost blackish dorsally and gray-brown ventrally, with faint indications of yellowish stripes on the head. I believe that this is probably a transitional pattern representing a state of fright.

None of several color photographs of *E. lineatus* that I have seen show individuals with a dark, uninterrupted stripe on the body as occurs in some preserved specimens.

GEOGRAPHIC VARIATION.—The dark body blotches of Mauritius (and, questionably Reunion; only a juvenile available) specimens usually reach the dorsal body contour, decreasing in intensity dorsal to interruption by the dorsal pale

FIGURE 31.—*Ecsenius lineatus*, USNM 219315, female, 54 mm SL, Bararin Island, Cuyo Islands, Philippines (photograph by J.M. Clayton).

TABLE 15.—Frequency distributions for certain characters in populations of *Ecsenius lineatus*.

Population	Segmented dorsal-fin rays				Segmented anal-fin rays				Dentary incisor teeth							
	16	17	18	$\bar{x}$	18	19	20	$\bar{x}$	45	46	47	48	49	50	51	$\bar{x}$
Okinawa			2	18.0			2	20.0		1	-	1				47.0
Taiwan		11	2	17.2		4	9	19.7	3	2	2	3	3			47.1
Pratas Reef			1				1					1				
Viet Nam			1			1			1							
Malaysia	1	3		16.8		4		19.0		1	1	1	1			47.5
Philippine Islands	1	1		16.5	1	1		18.5			1	1				47.5
Western Australia		1	1	17.5		1	1	19.5	1	-	1					46.0
Ceylon		3	1	17.3		1	3	19.8	1	-	1	1	1			47.3
Maldive Islands		2		17.0		1	1	19.5		1	-	1				47.0
Mauritius		3	6	17.7		1	8	19.9			2	2	1	-	1	48.3
Reunion			1				1									

Population	Precaudal vertebrae			Caudal vertebrae				Total vertebrae			
	10	11	$\bar{x}$	24	25	26	$\bar{x}$	34	35	36	$\bar{x}$
Okinawa	2		10.0		1	1	25.5		1	1	35.5
Taiwan	13		10.0	2	11		24.8	2	11		34.8
Pratas Reef	1					1				1	
Viet Nam	1				1				1		
Malaysia	4		10.0	3	1		24.2	3	1		34.2
Philippine Islands	2		10.0	2			24.0	2			34.0
Western Australia	2		10.0	1	1		24.5	1	1		34.5
Ceylon	4		10.0		4		25.0		4		35.0
Maldive Islands	2		10.0		2		25.0		2		35.0
Mauritius*	3	6	10.7		6	3	25.3			9	36.0
Reunion	1					1				1	

*Separation of precaudal from caudal vetebrae is often questionable; only ranges and total vertebral counts are certain.

stripe; the posteriormost, tear-shaped blotch is almost as large as the largest anterior blotches. These blotches in specimens from other localities do not reach the dorsal body contour and the tearshaped blotch is usually noticeably smaller than the anterior blotches.

Specimens from the higher latitudes tend to have higher averages for certain meristic characters (Table 15). This tendency is particularly obvious for total vertebrae for Mauritius-Reunion specimens. Additionally, there is a tendency for Mauritius specimens to have 11 precaudal vertebrae. There is difficulty in determining precaudal vertebral number (from radiographs), however, and, although some specimens from Mauritius definitely have 11, I am not certain that all six of the specimens so indicated in Table 15 do in fact have 11.

REMARKS.—*Ecsenius lineatus* is often taken at depths of less than 1 m in the northernmost parts of its range, but appears to occur more deeply (to 28 m) further south, and rarely more shallow than 5 m.

Although filamentous or strongly exserted caudal-fin lobes develop in males (and less commonly in females) of most species of *Ecsenius*, such development is uncommon in *E. lineatus* (see also *E. lividanalis*).

DISTRIBUTION.—From widely separated localities in the Indian and Western Pacific Oceans; also reliably reported from Miyakejima (Izu Islands), Bonin Islands, and Taketomi (Ryukyu Islands) by Masuda, Araga, and Yoshino (1975) and Yoshino (1984), and southeastern Taiwan (Shen, 1984).

MATERIAL (* = new material).—*Taiwan* (north end): USNM 203129 (4 specimens: 42–48, incl. one cleared and stained), 203130 (2:49, 55), 203131 (1:55), 203132 (2:45, 50), 204477 (1:60), BPBM 23078* (3:45–64). *Okinawa:* BPBM 22281* (2:27, 33 mm SL). *Viet Nam:* Bay of Nahtrang, CAS 24489 (1:47). *South China Sea:* Pratas Reef, CAS 24477 (1:20). *Philippines:* Cuyo Islands, Bararin Island, USNM 219315* (2:54, 56). *Malaysia:* Pulau Tulai, BPBM 21940* (3:34–45); Pulau Chebeh, BPBM 21956* (1:44). *Ceylon:* BPBM 18056

(3:35–40), USNM 213493 (1:20). *Maldive Islands:* Fadiffulu Atoll, SMF 5532 (1:66, holotype); Villingili, BPBM 22591* (1:50). *Mauritius:* BPBM 15943 (4:45–54), 15946 (1:26), 15947 (2:20, 56), BPBM 21823* (1:62), RUSI 11088* (1:57). *Reunion:* BPBM 16276 (1:22). *Western Australia:* Northwest Cape, WAM P.25371-006 (2: 45, 54).

Oculus Group

This group, now consisting of eight species, was treated by Springer (1971, 1972) and McKinney and Springer (1976) as a single species comprising six allopatric color-pattern types. Among these six types were two others, also allopatric, that were not recognized at the time, but are recognized here. New material of all the color-pattern types has become available since 1976. The new material corroborates previous findings that the color-pattern types are all allopatric, relatively widely distributed geographically, and each is readily recognizable as different from all the others. In a change of philosophy from that stated by McKinney and Springer (1976:14–15), who elected not to recognize the various color-pattern types nomenclaturally, I have decided to name them here.

The hypothesized synapomorphy uniting the species of the Oculus Group resides in the color pattern: the presence on the side of the body of large, dark spots and/or saddles, each usually with a conspicuous pale ring or margin, and, in living or fresh specimens, a brilliant white spot just dorsal to the pectoral-fin axil and one or two more on the pectoral-fin base. Pale-margined or ringed spots on the side of the body are present in *Ecsenius* otherwise in only one of the four species of the Stigmatura Group, *E. stigmatura,* and one of the five species in the Prooculis Group, *E. bimaculatus.*

Ecsenius stigmatura has but one such spot (occupying almost the entire side of the caudal peduncle) on each side, and the width of the pale margin is relatively much broader than in any species of the Oculus Group. As there are several synapomorphies that distinguish the Stigmatura Group from the Oculus Group, I consider the pale-margined spot in *E. stigmatura* to be an autapomorphy. Freshly collected specimens of *Ecsenius bimaculatus* exhibit a pair of elongate-oblong dark spots, which are jointly enveloped by a pale margin, anteriorly on each side of the abdomen. These spots are not duplicated in position or shape among the species of the Oculus Group. As the Prooculis Group species have a unique sexual dichromatism, I consider the spots of *E. bimaculatus* to be autapomorphous. Furthermore, neither *E. stigmatura* nor *E. bimaculatus* has any of several other, probably synapomorphic, color-pattern characters present in the Oculus Group species (e.g., dark pelvic fins, bright-white spots dorsal to the pectoral-fin axil and on the pectoral-base, dark marks extending onto the caudal fin, etc).

Freshly collected specimens of *E. lividanalis* (Stigmatura Group) exhibit a pale margin around the dark spot anterior to the anus (Plate 2: figure 6), but the pale margin appears to be autapomorphic; a dark preanal spot is a synapomorphy of the Stigmatura Group.

Within the Oculus Group, only *E. monoculus* has but one pale-ringed spot, in the form of a saddle located dorsally on the caudal peduncle. *Ecsenius sellifer* has three or four saddles on the dorsal body contour, but no other pale-margined dark spots on the body. The saddles in *E. monoculus* and *E. sellifer* lack the dorsal portions of the pale margins. The other species in the Oculus Group may have saddles, but all have pale-margined dark spots on the body sides. The pale margins vary from obvious to absent in *E. portenoyi,* depending sometimes, at least, on the specimen's state of preservation. In general, the pale rings are less pronounced in *E. portenoyi* than in other species of the group.

Other markings characteristic of most or all of the Oculus Group species are: one or a pair of vertical, large, posteriorly converging, dark blotches (often with conspicuous pale margins anteriorly) on the caudal peduncle that extend well out on the caudal fin, often enclosing a small, conspicuous, pale spot on the fin basally; a darkly pigmented middle (longest) pelvic-fin ray; a small, dark spot on the inner surface of the fleshy pectoral-fin base (often diffuse and indistinct); a dark, curving line originating dorsally on, or very close to, the posterior margin of the opercle at about the opercle's midlevel, and extending ventroanteriorly to some point posterior to the lower lip; and, in preservation, a pale spot on the chin, which, so far as is known, is salmon-pink or orange in life.

Dark or dusky peduncular markings (never with conspicuous pale margins) extending onto the caudal fin occur also in some species of the Opsifrontalis Group, where they are often continuations of stripes on the body, and the Isos Group, in which the extensions are small and faint. Darkly pigmented middle pelvic-fin rays occur also in the species of the Yaeyamaensis Group, except possibly *E. minutus* (well-preserved specimens unavailable), and at least males of two of the three species of the Isos Group. A small, dark spot on the inner surface of the fleshy pectoral-fin base is also present in the Yaeyamaensis Group and, at least, *E. trilineatus* of the Isos Group, where it may be much more discrete than in the Oculus Group. *Ecsenius alleni* (Opsifrontalis Group) has a large, dark spot on the inner surface of the fleshy pectoral-fin base that corresponds to another on the external base; these spots appear to be autapomorphic for *E. alleni.* A dark, curving opercular line, more-or-less identical in position to that of the Oculus Group, occurs otherwise in *Ecsenius* only in *E. fourmanoiri* (Opsifrontalis Group; faint, almost unnoticeable stripe may occur in *E. australianus,* same group). An opercular line superficially similar to that of the Oculus Group is present in the Yaeyamaensis and Isos groups, but the line in the latter two groups originates slightly to much more anteriorly on the opercle, often at or in advance of the horizontal midlength of the opercle.

A pale spot on the chin, similar to that in the Oculus Group, is present in preserved specimens of the Isos, Pictus, and Yaeyamaensis groups, but only in the Oculus and Yaeya-

FIGURE 32.—*a, Ecsenius oculus,* USNM 203140, holotype, male, 54 mm SL, Taiwan; *b, Ecsenius paroculus,* USNM 211995, male, 34 mm SL, Pulau Seribu, Indonesia; *c, Ecsenius oculatus,* WAM P25374-018, female, 30 mm SL, North West Cape, Western Australia; *d, Ecsenius monoculus,* USNM 209577, male, 49 mm SL, Haruku Island, Molucca Islands, Indonesia; *e, Ecsenius sellifer,* USNM 261462, holotype, male, 37 mm SL, Kiriwina Island, Trobriand Islands, Papua New Guinea, reversed photograph of right side (photographs by J.F. McKinney).

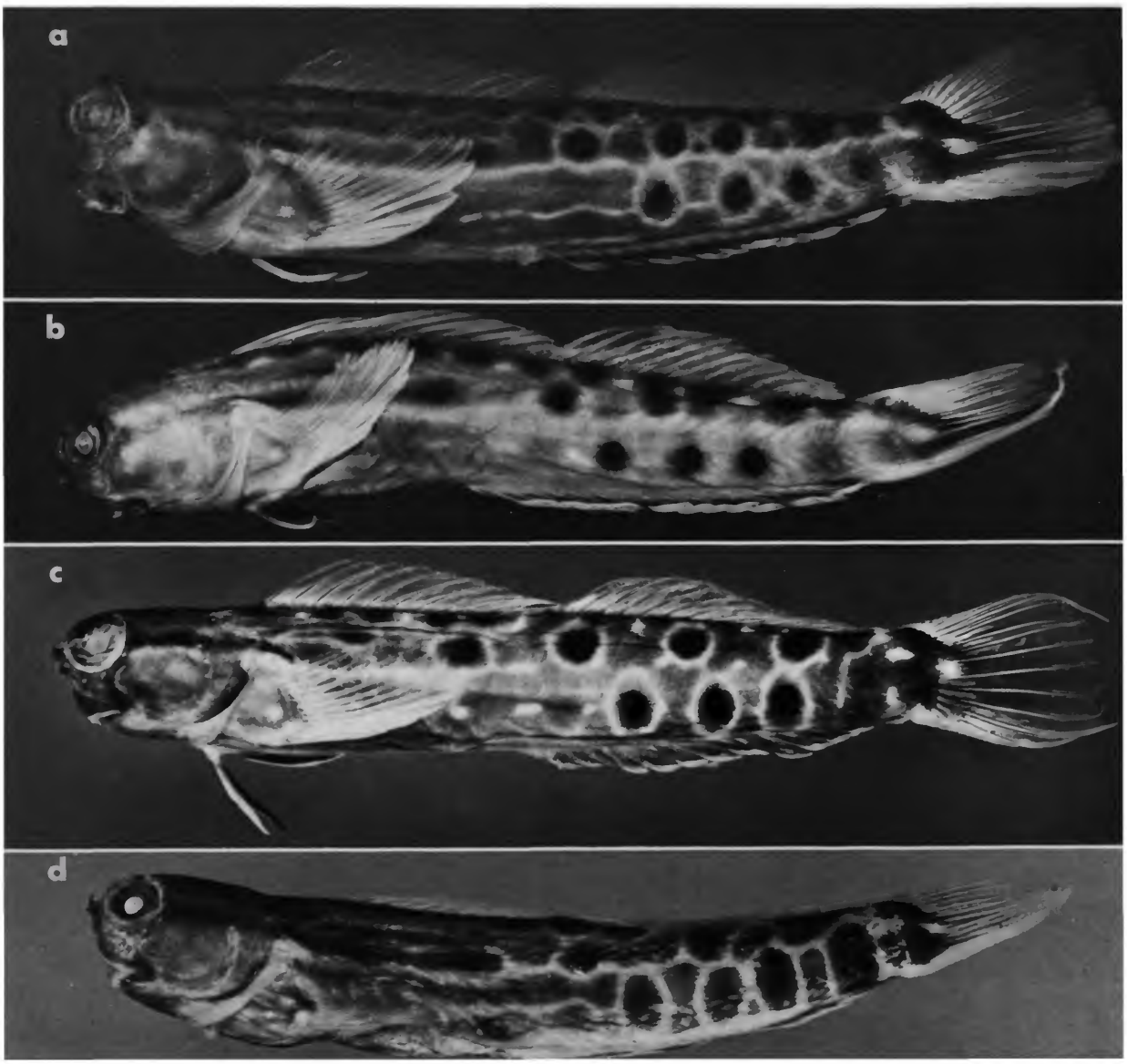


FIGURE 33.—*a, Ecsenius portenoyi,* USNM 278914, female, 38 mm SL, Rotuma; *b, Ecsenius portenoyi,* USNM 276370, male, 38 mm SL, Tutuila, American Samoa; *c, Ecsenius pardus,* USNM 214520, male 38 mm L, V ti Levu, Fiji; *d, Ecsenius tessera,* MNHN 1980-964, holotype, female, 41 mm SL, New Caledonia (photograph *a* by T.B. Griswold, *b* and *d* by K.A. Bruwelheide, *c* by J.F. McKinney).

maensis groups is the spot salmon-pink in life. The pale spot is unremarkable in the other groups.

Some species of the Oculus Group, and particularly *E. monoculus,* exhibit a pattern of regularly distributed pale spots over the body, recalling a similar characteristic that occurs otherwise only in the Yaeyamaensis Group. Weighting heavily the shared salmon-pink spot on the chin and, to lesser degree, the pattern of pale spots on the body, shared only by the Oculus and Yaeyamaensis groups, I believe that the two groups form a clade.

Aside from lacking pale-margined ocelli, the distinct, dark anterior margin of the lower lip distinguishes the Yaeyamaensis-group species from the Oculus Group species, in which the lip margin is either immaculate or with a very fine line of melanophores. Of considerable interest is that if one excludes *E. yaeyamaensis,* all 12 of the remaining species composing

TABLE 16.—Frequency distributions for certain meristic characters in species of the Oculus Group.

Species/locality	Segmented dorsal-fin rays					Segmented anal-fin rays					Caudal vertebrae					
	12	13	14	15	$\bar{x}$	14	15	16	17	$\bar{x}$	20	21	22	23	24	$\bar{x}$
Ecsenius monoculus																
Ilot du Sud			1					1						1		
Philippine Islands																
Bolinao		3	3		13.5		3	3		15.5				5	2	22.3
Batangas		9	3		13.2		9	3		15.2		1	11			21.9
Negros	2	42	6		13.1		37	13		15.3		13	37			21.7
Cuyo Islands	1	22	10		13.3		20	13		15.4		5	25	3		21.9
Molucca Islands		14	7		13.3	1	14	4		15.2		3	17			21.8
Ecsenius oculatus																
Christmas Island		20	6		13.2		21	4		15.2		3	18			21.8
North West Cape		2	13	2	14.0			16	2	16.1			15	4		22.2
Point Quobba		1	1		13.5		1	1		15.5			2			22.0
Dirk Hartog Island			3		14.0			3		16.0			2	1		22.3
Ecsenius oculus																
Ryukyu Islands			13	2	14.1			12	3	16.2			4	10	1	22.8
Taiwan	1	3	12		13.7		3	13		15.8		1	11	3		22.1
Batan Islands			1					1					1			
Ecsenius pardus																
Fiji																
Viti Levu			36	2	14.0			32	6	16.2			6	28	4	22.9
Kandavu		2	7	4	14.2			4	9	16.7				11	2	23.2
Moala			3	1	14.2			3	1	16.2				5		23.0
Ono-ilau			8	2	14.2			10	1	16.1				9	1	23.1
Ecsenius paroculus																
Phuket area		5	3		13.4		5	3		15.4		1	7			21.9
Malacca Strait	1	1			12.5	1	1			14.5		1	1			21.5
Mentawei Islands		3			13.0		3			15.0		1	2			21.7
Seribu Islands		16	3		13.2	1	16	2		15.0		8	8			21.5
Bawean	1	22	1		13.0	4	19	1		14.9	1	12	7			21.3
Ecsenius portenoyi																
Samoa		2	14	2	14.0		3	15		15.8			2	16		22.9
Rotuma		2	61	1	14.0	1	7	55		15.8		1	5	56	1	22.9
Ecsenius sellifer																
Palau		1					1						1			
New Guinea		10			13.0		10			15.0		1	8			21.9
Solomon Islands			2		14.0		1	1		15.5			2			22.0
Ecsenius tessera																
New Hebrides			4		14.0			4		16.0				4		23.0
New Caledonia			2	1	14.3			1	2	16.7				3		23.0

the two groups are allopatric (Figures 9 and 10). Although all the species of the Yaeyamaensis Group are allopatric, *E. yaeyamaensis* is sympatric with six of the eight species of the Oculus Group. A discussion of the biogeographic implications of an Oculus-Yaeyamaensis sister group is given in Appendix I.

Because I am unable to hypothesize the primitive state of the color pattern of the Oculus Group, I am unable to provide a set of unequivocal hypotheses of the interspecific relationships within the group. Some of the intragroup relationships seem obvious, based on a partially intuitive assessment of color-pattern characters.

Within the Oculus Group, *Ecsenius paroculus* and *E. oculatus* appear to be sister species based on similarities of color pattern. The patterns differ only in an abrupt shift in the average number of pale-ringed ocelli, from 9.5–6.5 in adjacent populations (Table 18). Within *E. oculatus*, specimens from Christmas Island (Indian Ocean) exhibit greater meristic similarity to specimens of *E. paroculus* than to other specimens of *E. oculatus*. I weighted color pattern over meristics in this instance, because color pattern in *Ecsenius* generally appears to provide the most important evidence of relationships. *Ecsenius paroculus* and *E. oculatus* are parapatric in distribution with the joint margin of the the Indian-Australian and

Asian lithospheric plates demarcating their separation (Figure 9).

Ecsenius oculus is possibly the sister group of *E. paroculus* and *E. oculatus*, from which it differs primarily in the slightly, but consistently lower position of the ocelli on its body and the lack of dark nape spots, which, in the Oculus Group, are present only in *E. oculatus*, *E. paroculus*, and *E. sellifer*. The average number of ocelli (Table 18) in *E. oculus* is intermediate between the averages for *E. paroculus* and *E. oculatus;* however, the distribution of *E. oculus* is separated from that of the other two species by a large geographic area in which a markedly different appearing Oculus Group species, *E. monoculus*, occurs. I believe the presence of *E. monoculus* in that area to be evidence of a vicariant event as yet undeciphered.

Ecsenius monoculus and *E. sellifer* appear to be sister species based on their unique, dark, saddle-like markings with incomplete pale rings, together with a lack of pale-margined dark spots on the lower half of the body. *Ecsenius tessera* has saddles similar to those of *E. sellifer*, but also has pale-margined dark spots on the lower half of the body, present otherwise in the Oculus Group only in *E. pardus* and *E. portenoyi*.

Ecsenius pardus and *E. portenoyi* appear to be sister species based on overall similarity of the distribution of the ocelli on the body. *Ecsenius portenoyi* differs from *E. pardus* mainly in that the dorsal row of dark spots below the segmented-ray portion of the dorsal fin of *E. portenoyi* is almost always along the dorsal body contour (therefore, more saddle-like) and less intensely pigmented, and the middle two saddles are closer together than either is to its next adjacent saddle. In *E. pardus* the spots of the dorsal row below the segmented-ray portion of the dorsal fin usually do not impinge on the dorsal body contour (therefore, are not saddle-like), are quite intensely pigmented, and are about equally spaced. Furthermore, as noted above, the pale margins of the spots in *E. portenoyi* are generally less distinct compared with the bright, pale rings that are always apparent in *E. pardus*.

The presumptively monophyletic *pardus-portenoyi* group is probably the sister group of *E. tessera*. One can visualize the dark spots and pale rings of *E. tessera* becoming reduced in size, with the new areas on the body being covered by a generally darkish ground color, thus producing a pattern like that of *E. pardus* (or beginning with a pattern similar to that of *E. pardus* and reversing the changes to produce a pattern like that of *E. tessera*). The differences in color pattern between *E. pardus* and *E. portenoyi* subjectively appear to be of lesser magnitude than the differences between these two species and *E. tessera;* hence, my decision to favor them as the sister group of *E. tessera*.

Several populations of various Oculus Group species exhibit sexual dimorphism in average numbers of dentary incisor teeth, with females usually having higher averages than males (Table 17). Statistical tests comparing male vs. female averages do not always give significant results, but the trends in the averages are apparent even so.

Ecsenius monoculus, new species

FIGURE 32*d;* PLATE 7: FIGURE 4; TABLES 16, 17

Ecsenius (Ecsenius) oculus Springer.—Springer, 1971:35 [paratypes, in part: Ilot du Sud, South China Sea].

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type D; Ilot du Sud and Indonesia: Bawean, Ambon, Saparua, and Haruku, Molucca Islands].

DESCRIPTION.—Dorsal fin XI–XII (rarely XI), 12–14 (rarely 12) deeply notched between spinous and segmented-ray portions. Anal fin II,14–16 (rarely 14). Pectoral fin 13 to 14 (rarely 14, and only unilaterally). Segmented caudal-fin rays 13 or 14 (rarely 14). Vertebrae 9–10 (rarely 9) + 21–23 = 31–33. Dentary incisor teeth 42–59 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from interspace between dorsal-fin spines 10 and 11 and vertical from first segmented ray (usually between spines 11 and 12). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Important features include: No pair of dark spots present dorsally on nape; nape usually with 2–4 dark stripes separated by pale interspaces. Dark stripe extending from postorbital margin across opercle often indistinct or absent; stripe, when present, continuing onto body anteriorly; no deep, short, dark stripe present just ventral to dorsal opercular portion of postorbital stripe. Conspicuous blackish pigment present ventroanteriorly to corners of mouth. Body sides usually darkly dusky with 4 or 5 rows of pale spots; single, conspicuous, pale-margined, large, dark, saddle-like spot on dorsal body contour at posterior end of dorsal fin; occasionally 1–3 irregular, large, dark, pale-margined spots at ventroposterior end of body (not including ventral dark spot that extends onto caudal fin), but these spots not as intensely dark as dark saddle-like spot at posterior end of dorsal fin. Venter of large or sexually mature males sprinkled with fine melanophores; venter of females and immature males unpigmented. Spinous dorsal fin of males only occasionally with faint, fine, dusky suprabasal stripe.

Live Color: An underwater photograph (Plate 7: figure 4), taken in the Philippines, of a living specimen, shows the dark areas on the body to be various shades of olive brown, except for the dark saddle-like spot, which is black, on the dorsal body contour at the posterior base of the dorsal fin. A vertical pair of spots at the caudal-fin base is dark brown. A brilliant white spot is present immediately anterior to the saddle-like spot, and another is present between the vertical pair of dark spots. Most of the pale markings on the head and body are pale gray or cream colored, but on the fleshy pectoral-fin base there is a vertical pair of yellow spots, followed in line posteriorly on the body by two rows of pale yellow spots or

TABLE 17.—Frequency distributions for numbers of dentary incisor teeth in species of the Oculus Group.

Species/locality/sex	Number of teeth																							
	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	$\bar{x}$
Ecsenius monoculus																								
Philippines																								
Bolinao																								
males						1	-	2	-	1														49.0
females				1	-	-	-	-	-	-	1													48.5
Batangas																								
males							1	2	4	2														49.8
females								1	-	1	-	1												51.0
Cuyo Islands																								
males	1	-	-	-	1	-	2	1	1	1	1	-	1											48.9
females			1	-	-	-	2	1	1	5	1	2	-	-	1									50.6
Negros																								
males				1	2	3	2	2	6	2														48.6
females					1	5	3	4	2	3	1	1												49.0
Ilot du Sud																								
females																		1						
Moluccas																								
males							1	-	-	1	1													50.3
females						1	-	1	2	-	-	1												49.8
Ecsenius oculatus																								
Christmas Island																								
males						1	2	-	2	-	-	1	1											50.0
females										2	1	2	2											52.6
North West Cape																								
males									1	3	2	1	1	1										52.1
females												2	2	2	1	1	2	-	1					55.7
Point Quobba																								
males														1										
females															1									
Dirk Hartog Island																								
males										2														51.0
females														1										
Ecsenius oculus																								
Ryukyu Islands																								
males													1	-	-	-	1	2	1	1				58.5
females																	2	-	-	-	2	1	1	61.2
Taiwan																								
males														1	2	1	-	1						56.6
females															1	2	2	1	3	1	1			58.9
Batan Islands																								
males																			1					

TABLE 17.—Continued.

Species/Locality/Sex	Number of teeth																						
	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	$\bar{x}$
Ecsenius pardus																								
Fiji																								
Viti Levu																								
males								1	1	1	4	2	3	3	2	1								53.3
females										3	2	5	4	2	1	-	1							53.4
Kandavu																								
males							1	-	1	2	1	1	2	-	1									52.1
females						1	-	-	-	1	-	1	1											51.2
Moala																								
males											1	1												52.5
females													1	-	1									55.0
Ono-i-Lau																								
males													1	1	-	1								55.3
females											2	-	2	2	1									54.0
Ecsenius paroculus																								
Phuket area																								
males							2	-	1	1	-	2												50.5
females											1	-	1											53.0
Malacca Strait																								
males						1	-	1																48.0
Mentawei Islands																								
males									1	-	-	-	1											52.0
Seribu Islands																								
males									1	4	3													51.2
females									1	1	1	1	1											52.0
Bawean																								
males							1	1	-	4	3	1	1											51.3
females											1	2	2	3	3	1	1							54.9
Ecsenius portenoyi																								
Samoa																								
males								2	-	1	3	2	-	5										52.8
females											1	3	-	-	1	1								54.0
Rotuma																								
males									2	2	7	5	11	3	2									53.2
females							1	1	-	4	5	3	8	5	2	3								53.4
Ecsenius sellifer																								
Palau																								
males											1													
New Guinea																								
males									3	-	1													50.5
females									2	1	2	-	1											51.5
Solomon Islands																								
males											1	1												52.5
Ecsenius tessera																								
New Hebrides																								
males												1	1											53.5
females									1	-	-	1												51.5
New Caledonia																								
males											1													
females											1	1												52.5

dashes, which gradually become fainter posteriorly. There is a narrow, faint-yellow ring around the pupil; the remainder of the iris is olive brown interrupted by yellow vermiculations.

REMARKS.—Although there is no unequivocal geographic variation or sexual dimorphism indicated for any of the meristic characters, the exceedingly high number of dentary incisor teeth in the single specimen (a female, erroneously recorded as a male in McKinney and Springer, 1976: table 9) from Ilot du Sud (Table 17) indicates that geographic variation in number of teeth probably exists.

Ecsenius monoculus is one of the shallowest dwelling species in the genus. Most collections were made a depths under 5 m.

DISTRIBUTION.—Known only from the Philippine Islands, Ilot du Sud (10°29′15″N, 108°57′30″E, off South Viet Nam), and the Molucca Islands. The distribution of *E. monoculus* is bounded by that of *E. oculus* to the north, *E. paroculus* to the west, and *E. sellifer* to the east. There are gaps, from which no species of the Oculus Group are known, between the distributions of *E. monoculus* and the other Oculus-group species. It would be important to know what species of the Oculus Group occur on the coasts of Borneo, Sulawesi, Halmahera, western New Guinea, southeastern China, and North Viet Nam, before hypothesizing vicariance scenarios to explain the distributions of the species.

COMPARISONS.—The presence of a single, large, saddle-like dark spot on the dorsal body contour (on the caudal peduncle) distinguishes *E. monoculus* from all other members of the Oculus Group. I am unable to hypothesize its closest relative unequivocally, but I believe that it is *E. sellifer*, as these two species uniquely share in having dark saddles together with a lack of ocelli on the body. Within the Oculus Group, however, *Ecsenius sellifer* shares a character (transverse pair of dark spots on the nape) only with *E. paroculus* and *E. oculatus*, which two species appear otherwise to form a monophyletic group. I believe that the nape spots are either a synapomorphy of the Oculus Group or homplastic in *E. sellifer*, especially as I believe that *E. oculus*, which lacks the spots, is the sister group of *E. paroculus* and *E. oculatus*.

ETYMOLOGY.—The specific name is from the Greek *"monos,"* meaning "one," plus *"oculus,"* Latin for "eye," in reference to the characteristic single, dark, saddle-like spot on each side of the body.

HOLOTYPE.—USNM 261243, male, 36 mm SL, NW side Putic Island, Cuyo Islands, Philippine Islands (10°55′05″N, 121°02′03″E), 0–4.6 m, V.G. Springer et al., 22 May 1978.

PARATYPES.—*Philippine Islands:* USNM 219309 (18 specimens: 16–42 mm SL) and USNM 226575 (6:13–38), both collected with holotype; USNM 226581 (7:23–49), Cocoro Island, Cuyo Islands, 0–3 m, V.G. Springer et al., 26 May 1978; USNM 219308 (1:43), Tagauayan Island, Cuyo Islands, 0–2.4 m, V.G. Springer et al, 25 May 1978; USNM 226577 (5:15–30), Maloh, Negros Oriental, 0–3.1 m, H.A. Fehlmann et al., 18 May 1979; USNM 226579 (31:22–38), near Maloh, Negros Oriental, L. Knapp et al., 24 April 1979; USNM 227537 (1:24) and 226578 (15:14–35), near Giligaon, north of Maloh, Negros Oriental, 0–1.8 m, L. Knapp et al., 26 April 1979; USNM 228928 (1:30), USNM 228926 (2:27,41), and USNM 225049 (5:27–43), all Sombrero Island, Batangas, 0–5 m, C.J. Ferraris, 23 April 1980; USNM 226580 (1:28), Sombrero Island, Batangas, C.J. Ferraris and E.O. Murdy, 30–31 January 1980; AMS I.21909-001 (2:43 each), Sombrero Island, Batangas, 0–1 m, C.J. Ferraris, 25 April 1980; USNM 225050 (7:16–33), Bolinao, Pangasinan, 0–2 m, C.J. Ferraris and E.O. Murdy, 17 April 1980. *Indonesia, Molucca Islands:* BPBM 18046 (1:27), 18048 (1:20), 18049 (1:28), 18052 (4:19–32), all from Ambon; USNM 211925 (7:13–17), SE tip of Haria Bay, Saparua, 1.5–4.6 m, V.G. Springer and M.F. Gomon, 5 March 1974; USNM 209577 (7:13–49), point E of Tandjung Naira, Haruku, 4.6 m, V.G. Springer and M.F. Gomon, 15 January 1973.

OTHER MATERIAL.—*South China Sea:* CAS 13464 (1:41; previously CAS GVF-2113, paratype of *Ecsenius oculus*), W shore Ilot du Sud (off S tip of Poulo Cecir de Mer), 0–7 m, R. Bolin et al., 10 March 1960.

Ecsenius oculatus, new species

FIGURE 32*c*; PLATE 7: FIGURE 1; TABLES 16–18

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type C, North West Cape, Western Australia].

DESCRIPTION.—Dorsal fin XII,13–15, deeply notched between spinous and segmented ray portions. Anal fin II,15–17. Pectoral fin 13. Segmented caudal-fin rays 13. Vertebrae 10 + 21–23. Dentary incisor teeth 47–60 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between vertical from interspace between dorsal-fin spines 10 and 11 and vertical from first segmented ray (rarely anterior to spine 11). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Important features include transverse pair of dark spots present on nape. Dark stripe extending from postorbital margin across opercle dorsally, often continuing on body anteriorly; no deep, short, dark stripe present just ventral to dorsal opercular portion of postorbital stripe. Dusky pigment ventroanterior to corners of mouth not blackish or remarkable. Side of body with 5–8 (modally 5–7) dark, pale-margined spots (ocelli), usually arranged in pairs; pale margin of each ocellus usually distinct, not coalesced with that of its fellow. Anteriormost ocellus usually positioned at or posterior to vertical from midbase of spinous dorsal fin. Distance between midline of body side (in area below segmented dorsal-fin rays) and ventral edge of dark portion of each ocellus equal to or greater than distance between dorsal edge of dark portion and dorsal body contour. Dark saddle-like spot at posteriormost end of dorsal fin often ocellus-like in appearance. Conspicuous, smaller ocelli not present on dorsal

TABLE 18.—Numbers of ocelli on body side of specimens of populations (arranged north to south) of three species of the Oculus Group.*

Species/locality	Number of spots							
	5	6	7	8	9	10	11	$\bar{x}$
Ecsenius oculus								
Ryukyu Islands		1	10	2				7.1
Taiwan	1	1	9	5				7.1
Batan Islands**		1	-	1				7.0
Ecsenius paroculus								
Thailand								
Phuket and vicinity			1	6	1			8.0
Malaysia								
Malacca				2				8.0
Indonesia								
Mentawai Islands				1	1	1		9.0
Bawean			1	3	29	15	2	9.3
Seribu Islands				1	8	11		9.5
Ecsenius oculatus								
Christmas Island	1	13	8	3				6.5
Western Australia								
North West Cape & vicinity	4	6	9	1				6.4
Point Quobba	1	-	1					6.0
Dirk Hartog Island	2	-	1					5.4

*If there was doubt that a particular marking should be included in a count, it was included.
**One specimen, both sides counted.

body contour dorsal to body ocelli. Venter of large or sexually mature males sprinkled with fine melanophores; venter of females and immature males unpigmented. Spinous-dorsal fin with fine, dusky suprabasal stripe.

Live Color (Plate 7: figure 1): Photographs in the files of T.F.H. Publications, Inc., of a live specimen at Christmas Island shows most of the dark areas on the head and body to be shades of olive brown, but the ocelli on the body range to almost black; pale areas (mostly dash-like) on body are white, mostly brilliant white dorsally and ventrally, with the most conspicuous such marks a spot at the posterior end of the dorsal fin and the area between the vertical pair of dark spots at the caudal-fin base; pale markings on the head vary from spot-like to stripe- and band-like, and are pearly white. The lower portion of the iris is bright white, most of the remainder is brown interrupted by yellow dashes, and there is a narrow yellow ring around the pupil. One specimen has the color pattern much paler, almost blanched. Allen (1985: fig. 383) gives a colored photograph of a freshly dead specimen from North West Cape. The color of this specimen is much like that of the Christmas Island specimen, but the dark spots on the body of the North West Cape specimen are much lower on the body—similar in position to the spots of *E. oculus*—than any specimen of *E. oculatus* I have examined or seen pictures of.

REMARKS.—There are indications that *E. oculatus* manifests both sexual and geographic variation. Females have higher average numbers of dentary incisor teeth than do males (Table 17). Specimens from Christmas Island have lower average numbers for meristic characters (Table 16) than do specimens from Western Australia.

DISTRIBUTION.—Known only from Christmas Island (Indian Ocean) and the middle coast of Western Australia.

COMPARISONS.—See section under *Ecsenius paroculus*.

ETYMOLOGY.—The specific name is a Latin word meaning "having eyes," and refers to the dark, eye-like spots on the body.

HOLOTYPE.—WAM P.25368-023, male, 44 mm SL, lagoon reef off Tantabiddi Creek, North West Cape, Western Australia, 2–3 m, G.R. Allen, 25 June 1975.

PARATYPES.—*Western Australia:* WAM P.25368-023 (3 specimens: 32–37 mm SL), collected with the holotype; WAM P.25813-050 (1:24), South Muiron Island [NNW of North West Cape], [J.] B. Hutchins, 5 June 1977; USNM 261219 (4:30–41), N of Mangrove Bay, North West Cape, 21°57′S, 113°55′E, G.[R.] Allen and P. Berry, 26 May 1980; WAM P.27970–041 (1:39), off NW side of Isd., Pt. Quobba, 24°29′S, 113°25′E, 10–12 m, J.B. Hutchins et al., 26 April 1983; WAM P.26670-006 (3:39–47), bombie on inner side of Surf Point, Dirk Hartog Island, 26°08′S, 113°10′E, 2 m, [J.]B. Hutchins and N. Sarti, 14 April 1979; WAM P.27961.014 (1:53), S end of shallow reef area, Pt. Quobba, 24°29′S, 114°25′E, J.B. Hutchins, 20 April 1983; WAM P.25374-018 (9:26–33), lagoon off Tantabiddi Creek, North West Cape, 3–4 m, G.R. Allen, 2 July 1975; AMS I.19641-016 (2:35–38), North West

Cape; G.[R.] Allen, 27 June 1975. *Christmas Island (Indian Ocean):* WAM P.26110-004 (24:18–36), Smith Point, 7–10 m, G.R. Allen and R. Steene, 4 June 1978; WAM P.26102-005 (1:26), Flying Fish Cove, 6–8 m, G.R. Allen and R. Steene, 30 May 1978.

Ecsenius oculus Springer

FIGURE 32*a;* PLATE 7: FIGURE 3; TABLES 16–18

Ecsenius (Ecsenius) oculus Springer, 1971:35 [holotype, USNM 203140, and paratypes, in part; south end of Taiwan; Ishigaki Island, Ryukyu Islands].

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type A; same localities as above].

DESCRIPTION.—Dorsal fin XII,12–15, deeply notched between spinous and segmented-ray portions. Anal fin II,15–17. Pectoral fin 13. Segmented caudal-fin rays 13 or 14 (rarely 14). Vertebrae 10 + 21–24 (rarely 21). Dentary incisor teeth 54 to 64 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior dentary canines 1 on each side (rarely missing unilaterally). Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spine 11 and first segmented ray. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Important features include no pair of dark spots present dorsally on nape. Dark stripe extending from postorbital margin across opercle dorsally, often continuing on body anteriorly; no deep, short, dark stripe present just ventral to dorsal opercular portion of postorbital stripe. Dusky pigment ventroanterior to corners of mouth not blackish or remarkable. Side of body with 5–8 (modally 6 or 7) large, pale-margined dark, ocelli, usually arranged in pairs; pale margin of each ocellus in each pair coalesced with that of its fellow. Distance between midline of body side (in area below segmented dorsal-fin rays) and ventral edge of dark portion of each ocellus less than distance between dorsal edge of dark portion and dorsal body contour. Ocellus at vertical just anterior to posterior end of dorsal fin occasionally absent or lacking pale margin, and often appearing similar to dark saddle-like spot at posterior end of dorsal fin (difficulty in counting ocelli is most often encountered when deciding how to treat posteriormost "ocellus" and saddle). Two to 4 pairs of conspicuous, but smaller, slightly less dark, paired spots on dorsal body contour just dorsal to body ocelli. Venter of large or sexually mature males sprinkled with fine melanophores; venter of females and immature males unpigmented. Spinous dorsal fin with fine, dusky suprabasal stripe.

Live Color (Plate 7: figure 3): A photograph in the wild of a specimen from Taiwan shows the head and ventrolateral portion of the abdomen suffused with pink; postocular stripe and general tone of body olive brown; pale-margined ocelli almost black; whitish spots on body dorsally and ventrally, brightest white spots on fleshy pectoral-fin base, midlateral abdomen, and caudal peduncle; iris of eye brownish with pale vermiculations and yellow ring around pupil; fin rays pinkish, except pelvics, which are untinted.

REMARKS.—There are indications that *E. oculus* manifests both sexual and geographic variation. Females have higher average numbers of dentary incisor teeth than do males (Table 17). Specimens from the Ryukyu Islands have higher average numbers of fin rays, vertebrae, and teeth than do specimens from Taiwan (Tables 16 and 17).

DISTRIBUTION.—Known definitely only from Ishigaki Island (southern Ryukyu Islands), southern Taiwan, and the Batan Islands, which lie between northernmost Luzon and southernmost Taiwan. Masuda, Araga, and Yoshino (1975) illustrate (in color) and report *E. oculus* from the Ryukyu Islands, probably based on material obtained at Okinawa (as well as specimens reported by Aoyagi, 1954, from Yaeyama, which includes Ishigaki). Springer (1971: fig. 3) and McKinney and Springer (1976: fig. 7) erroneously indicated that *E. oculus* occurs in the northern Ryukyu Islands. While the species may occur that far north, there are no specimens or reports from there.

The Batan Islands are politically part of the Philippines, but, based on the presence of *E. oculus*, they belong to Taiwan biogeographically. For that reason I have not included *E. oculus* among the 13 species noted as being present in the Philippines (Table 5). The northernmost record of an Oculus Group species in the Philippines proper is for *E. monoculus* from Bolinao, about halfway up the west coast of Luzon. If, as should be expected, the distribution of *E. monoculus* extends to northernmost Luzon, there would be a maximum of 200 km separating the distributions of *E. oculus* and *E. monoculus*. The Babuyan Islands (from which no collections are available) are stepping-stones between Luzon and the Batan Islands, however, and it would appear that the two species probably are no more separated than about 50 km. On the other hand, there is an islandless void of 150 km between the northernmost of the Batan Islands and southernmost Taiwan. Obviously distance has little to do with the distributions of these species.

As noted below, I do not believe that *E. oculus* and *E. monoculus* form a monophyletic group. The geographic distribution of *E. monoculus* forms a wedge (Figure 9) between the distributions of *E. oculus* and the pair of species (*E. paroculus, E. oculatus*), which I believe is the sister group of *E. oculus*.

COMPARISONS.—*Ecsenius oculus* is most, and closely, similar to *E. paroculus* and *E. oculatus*, in color pattern. These three species share in having the pale-margined dark spots on the body usually arranged in pairs, eye-like, and restricted to the upper half of the body. *Ecsenius oculus* differs from *E. paroculus* and *E. oculatus* most obviously in lacking a transverse pair of dark spots on the nape and in having the pale-margined dark spots positioned slightly lower on the body: the anterior spots below the spinous dorsal are aligned with the mid-postorbital stripe and the ventral edges of the dark portion of the spots below the segmented-ray portion of the dorsal fin are closer to the body midline than the dorsal

edges of the spots are to the dorsal body contour. In *E. paroculus* and *E. oculatus*, the spots below the spinous dorsal (when spots are present in this region) are slightly dorsal to the level of the mid-postorbital stripe and the dorsal edges of the spots are closer to the dorsal body contour than the ventral edges are to the body midline.

MATERIAL (* = new material).—*Taiwan:* USNM 203140 (holotype: 54 mm SL), 203139 (3 paratypes: 41–43), 203141 (paratype: 46), 203142 (4 paratypes: 44–50), 203923 (7 paratypes: 38–52). *Ryukyu Islands:* Ishigaki Island, BPBM 7464 (paratype: 20), 7468 (13 paratypes: 20–48), 8694 (1 specimen: 18). *Philippines:* Batan Islands, Baludgn Bay, near Desquid Point, 20°26'N, 121°59'E, USNM 283648* (1:26).

Ecsenius pardus, new species

FIGURE 33*c*; PLATE 7: FIGURE 6, PLATE 8: FIGURE 1; TABLES 16, 17

Ecsenius (Ecsenius) oculus.—Springer, 1972:4 [in part, Viti Levu, Fiji].
Ecsenius oculus.—McKinney and Springer, 1976:12 [Type F, in part, Fiji].

DESCRIPTION.—Dorsal fin XII,13–15 (usually 14), deeply notched between spinous and segmented-ray portions. Anal fin II,16 or 17. Pectoral fin 12–14 (predominantly 13). Segmented caudal-fin rays 13 or 14 (rarely 14). Vertebrae 10 + 22–24 (usually 23). Dentary incisor teeth 47–58 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between vertical from interspace between dorsal-fin spines 10 and 11 and vertical from spine 12 (rarely anterior to spine 11). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: No pair of dark spots present dorsally on nape; nape with 2–4 diffusely dusky stripes; dorsalmost one or two stripes each sometimes with slight spot-like intensification, but intensifications not forming discrete spots as in Figure 34*b*. Dark stripe extending from postorbital margin across opercle dorsally, intensifying for short distance as it continues on body anteriorly, terminating at vertical from mid-spinous portion of dorsal fin. Diffuse, pale stripe margining dark postorbital stripe ventrally, may extend on body but not further than half body length. No deep, short, dark stripe present just ventral to dorsal opercular stripe. Blackish pigment in area ventroanterior to corners of mouth usually not conspicuous (occasionally conspicuous in some males); lower lip immaculate except for some fine melanophores along edge. Body sides generally dark dusky, with two rows of intensely dark ocelli, 4 or 5 (more-or-less equally spaced) in dorsal row and 2 to 4 (usually 3) in ventral row; distinct pale rings usually completely encircling ocelli (dark portions of ocelli usually not saddle-like); 0–5 intensely dark spots, much smaller than ocelli, along dorsal body contour in region below spinous dorsal fin; pale lines and dashes variously present. Pectoral-fin axil moderately dusky, without discrete, dark spot. Venter of large males with sprinkling of fine melanophores, except for longitudinal midventral immaculate area; venter of females and small males immaculate. Spinous dorsal fin without fine dusky suprabasal stripe.

Live Color (based on freshly collected specimens): Ground color of head and body brownish; head suffused with reddish; lower lip and small adjacent area posteriorly, pink; ocellated spots blackish brown with whitish rings; a few brilliant white spots on pectoral-fin base, ventral portion of sides, and along dorsal body contour; dark postocular stripe with pale, slender, bordering stripe ventrally, becoming white on body; outer margin of pelvic-fin white; white spot centrally near caudal-fin base.

DISTRIBUTION.—Known only from Fiji (Viti Levu south to Ono-i-Lau). Although one would expect *E. pardus* to occur along the northern barrier islands of Fiji, it would be desirable to substantiate this expectation.

COMPARISONS.—*Ecsenius pardus* appears to be most similar in color pattern to *E. portenoyi*, with which I believe it forms a monophyletic group. It differs from *E. portenoyi* primarily in having the large body spots encircled with distinct pale rings (pale margins often diffuse in *E. portenoyi*), the dorsal body ocelli equally spaced (in *E. portenoyi*, dorsal two ocelli, or spots, posterior to vertical from third from posteriormost ocellus in ventral row, closer together than either is to its next adjacent ocellus), and the pale stripe, when present, on the midside of the body extending less than half the body length (often extending entire body length in *E. portenoyi*). In *E. pardus* there are two or three completely free, nonsaddle-like, dark spots on the dorsal half of the body in the area below the segmented-ray portion of the dorsal fin, whereas in *E. portenoyi* only rarely is there more than one (Figure 33*a* is exceptional; 33*b* is more typical). Although both species have modally 16 segmented anal-fin rays, in *E. pardus* there are 16 or 17 (commonly 17), whereas in *E. portenoyi* there are 14–16 (commonly 15). Relationships are also discussed under the account of the Oculus Group.

ETYMOLOGY.—The specific name *pardus* is from the Greek *pardos*, meaning leopard, and refers to the leopard-like ocelli on the body of the new species.

HOLOTYPE.—USNM 263113, male, 33 mm SL, Fiji, Kandavu, just S of NE point at entrance to Ndaku Bay, 0 to ~2.4 m, V.G. Springer et al., 11 May 1982.

PARATYPES (all Fiji).—USNM 230618 (12 specimens: 27–40 mm SL), collected with the holotype. *Lau Group:* USNM 236017 (11:20–38), Ono-ilau, Yanutha Islet, ~0.6–4.6 m, V.G. Springer et al, 30 April 1982; USNM 279471 (7:31–48), Vatoa, outer reef on NW side, 4.5–9.4 m, A.D. Lewis et al., 14 June 1986; USNM 214788 (4:32–40), Moala, N coast, 6.1–9.1 m, B. Carlson et al., November, 1974. *Viti Levu:* USNM 214520 (3:32–38), mouth of Rat-Tail Passage, 0–7.6 m., B. Carlson et al., 21 July 1975; USNM 214787 (1:18), W side of Suva Harbor entrance, ~3.0–6.1 m, B. Carlson, 18 August 1973; BPBM 11270 (3:34–43), W side Rat-Tail Passage, ~2.4–6.1

m, J.E. Randall et al., 7 August 1971; AMS I.18354-071 (19:30–46), Bird Is., Suva, B. Russell and B. Goldman, 9 July 1974; ROM 42510 (29:27–42), Suva Harbor, Rat-Tail Pass[age], tip of entrance on W side, 6–10 m, A. Emery et al., 14 April 1983; BPBM 14584 (2:45–46), Mbengga, outside barrier reef near E end of Frigate Pass, 15 m, J.E. Randall et al., 11 March 1973.

ADDITIONAL MATERIAL.—Viti Levu, Suva Harbor, ROM 42508 (13 specimens), 42511 (3); Kandavu, Great Astrolabe Reef, ROM 42509 (5).

Ecsenius paroculus, new species

FIGURES 32*b*, 34; PLATE 7: FIGURE 2; TABLES 16–18

Ecsenius (Ecsenius) oculus.—Springer, 1971:35 [paratypes, in part: Goh Huyong, Similan Island, Thailand; Pulo Jarak, Strait of Malacca, Indonesia; Pulo Mega, Mentawei Islands, Indonesia].

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type B; same localities as above and Seribu Islands, Indonesia].

DESCRIPTION.—Dorsal fin XII,12–14 (rarely 12), deeply notched between spinous and segmented ray portions. Anal fin II,14–16 (usually 15). Pectoral fin 13 (11 or 14, unilaterally, in 2 of 30 specimens). Segmented caudal-fin rays 13. Vertebrae 10 + 20–22 (rarely 20). Dentary incisor teeth 47–58 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spine 10 and first segmented ray (rarely anterior to spine 11). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Important features include: Transverse pair of dark spots present dorsally on nape. Dark stripe extending from postorbital margin across opercle dorsally, often continuing on body anteriorly or becoming interrupted on body and appearing as dark, oblong, ocellus anteroventrally offset from next ocellus posteriorly; no deep, short, dark, stripe present just ventral to opercular portion of postorbital stripe. Dusky pigment ventroanterior to corners of mouth not blackish or remarkable. Side of body with 7–11 (modally 8–10) dark, ocelli, usually arranged in pairs; pale margin of each ocellus usually distinct, not coalesced with that of its fellow. Distance between midline of body side (in area below segmented dorsal-fin rays) and ventral edge of dark portion of each ocellus equal to or greater than distance between dorsal edge of dark portion and dorsal body contour. Dark, saddle-like spot at posteriormost end of dorsal fin often ocellus-like in appearance (difficulty in counting ocelli is most often encountered when deciding whether to include posteriormost "ocellus" and/or disconnected, ocellus-like portion of postorbital stripe in count). Conspicuous, smaller dark spots or ocelli not present on dorsal body contour dorsal to body ocelli. Venter of large or sexually mature males sprinkled with fine melanophores; venter of females and immature males unpigmented. Spinous dorsal fin with fine, dusky, suprabasal stripe.

Live Color (Plate 7: figure 2): A specimen photographed in the wild at Similan Island, Andaman Sea, was generally tinted various tones of brown; postocular stripe, opercle margin, dorsal body ocelli, and abdomen laterally, dark brown; other markings paler; body with pale-white spots, brightest of which are anteriorly on body above pectoral-fin base, ventrally on pectoral-fin base, and midlaterally on caudal peduncle; snout suffused with pink; iris pale ventrally, dark brown dorsally with pale spots included; yellow ring around pupil.

REMARKS.—There are indications that *E. paroculus* manifests both sexual and geographic variation. Females have higher average numbers of dentary incisor teeth than do males (Table 17). Specimens from the Phuket area of Thailand, in general, have higher averages for meristic characters (Table 17) and fewer body ocelli (Table 18) than do specimens of most other populations of *E. paroculus*.

DISTRIBUTION.—Known from the west coast of Thailand, Malacca Strait, Mentawai (= Mentawei) Islands (off NW Sumatra), and Seribu Islands and Bawean Island, off NW and N central Java, respectively.

COMPARISONS.—*Ecsenius paroculus* appears to be most closely related to *E. oculatus*, from which it differs primarily in having about three more ocelli on the side of the body. Although these two species overlap in the number of ocelli present, only minimal overlap is exhibited by the populations on either side of the narrow geographic gap that separates their distributions (compare Figure 9 with Table 18). *Ecsenius paroculus*, *E. oculatus*, and *E. sellifer* are the only species of the Oculus Group that have a transverse pair of dark spots on the nape. *Ecsenius sellifer* differs from the other two species in having dark saddle-like markings on the dorsal body contour and lacking pale-margined dark spots on the body proper. The shared presence of nape spots in these three species might be evidence of common ancestry, and if so, my proposed sister-group relationship (see Oculus Group account) between *E. oculatus* and *E. paroculus*, on the one hand, and *E. oculus*, on the other, would be incorrect. My subjective opinion is that the nape spots are either synapomorphic for the Oculus Group or homoplasious in *E. sellifer*.

ETYMOLOGY.—Named paroculus from the Latin "par," meaning "near," plus *oculus*, in reference to the superficial similarity of its color pattern to that of *E. oculus*.

HOLOTYPE.—USNM 260389 (previously a paratype of *E. oculus*), male, 31 mm SL, live reef off NW side Pulau Tikus, Pulau Pari Group, Pulau Seribu, Indonesia (~05°51′25″S, ~106°34′15″E), depth to 4.6 m, V.G. Springer et al., 5 April 1974.

PARATYPES.—USNM 211995 (19 specimens: 14–34 mm SL, previously paratypes of *E. oculus*), collected with holotype; USNM 201811 (4:26–32, previously paratypes of *E. oculus*), Goh Huyong, Similan Island, Thailand; USNM 259240 (4: 32–37), Laem Sai off Kata Beach, Phuket Island, Thailand; USNM 211975 (86:13–38), first bay west of Sangkapura, Bawean Island, Indonesia; USNM 201522 (3:32–40, previ-

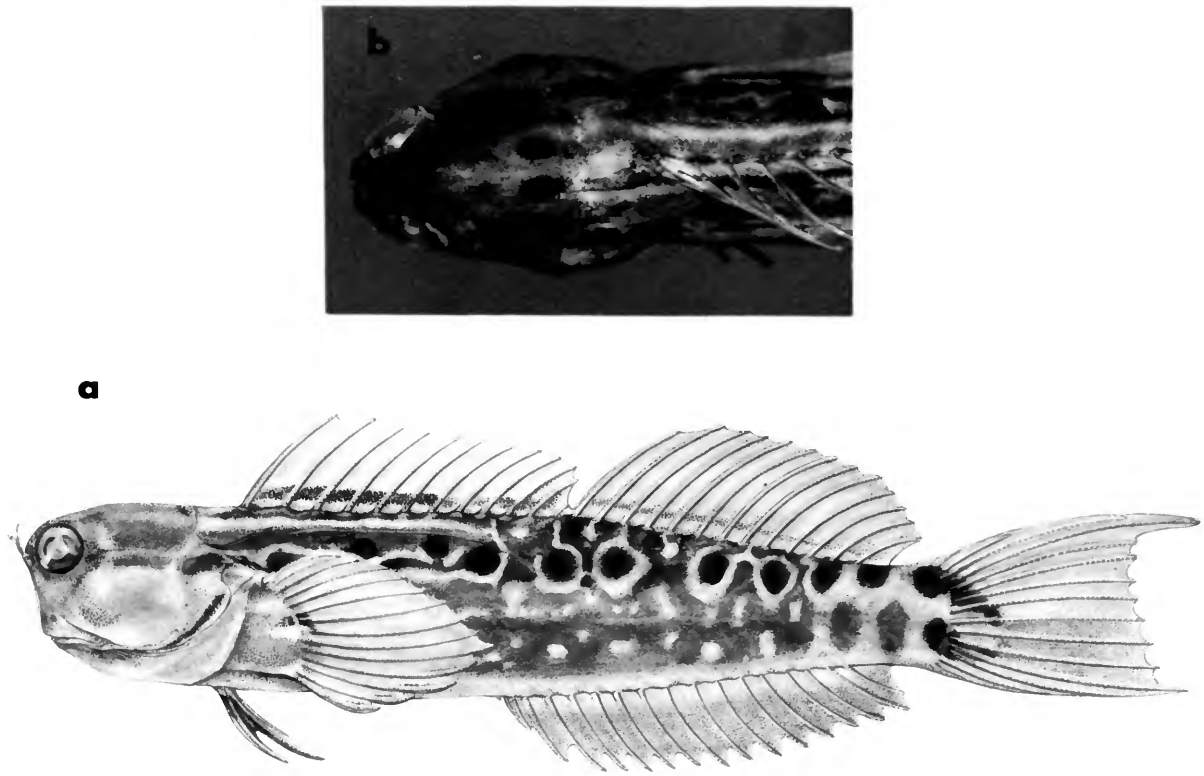


FIGURE 34.—*Ecsenius paroculus: a,* USNM 201522, male, 40 mm SL, Pulo Mega, Mentawei Islands, Indonesia (forked nasal cirrus is atypical; drawn by A. Schreitz); *b,* USNM 259240, Phuket Island, Thailand, dorsal view of head region illustrating transverse pair of dark spots (photograph by K.A. Bruwelheide).

ously paratypes of *E. oculus*), Pulo Mega, Mentawei [= Mentawai] Islands, Indonesia; USNM 201560 (2: both 30, previously paratypes of *E. oculus*), Pulo Jarak, Strait of Malacca, Maylasia.

Ecsenius portenoyi, new species

FIGURE 33*a*; PLATE 8: FIGURES 2, 3; TABLES 16, 17

Ecsenius (Ecsenius) oculus.—Springer, 1971:35 [paratypes, in part, ascribed to Banda Islands].

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type F, in part, Samoa].

DESCRIPTION.—Dorsal fin XII,13–15 (usually 14), deeply notched between spinous and segmented-ray portions. Anal fin II,14–16 (usually 16). Pectoral fin 12 or 13 (usually 13). Segmented caudal-fin rays 13. Vertebrae 10 + 21–24 (usually 23). Dentary incisor teeth 48–57 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 0 or 1 on each side (rarely 0). Lateral line without vertical pairs of pores, terminating posteriorly at point between vertical from interspace between dorsal-fin spines 10 and 11 and vertical from spine 12 (rarely anterior to spine 11). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: No pair of dark spots present dorsally on nape; nape with up to 4 diffusely dusky stripes. Dusky stripe extending from postorbital margin across opercle dorsally, intensifying for short distance as it continues on body anteriorly, terminating below spinous-dorsal fin; pale stripe margining dusky postorbital stripe ventrally, often extending posteriorly almost entire body length; one or two pale stripes often on body dorsal to dusky postorbital stripe. No deep, short, dark stripe present just ventral to dorsal opercular stripe. Lower lip immaculate except for few fine melanophores along edge; blackish pigment in area ventroanterior to corners of mouth usually conspicuous in fresh specimens. Body sides generally dusky, with small, dark saddle-like spots on dorsal body contour (pair below middle of segmented-ray portion of dorsal fin closer together than either member of pair is to next adjacent spot of row); spots in dorsal row below segmented-ray portion of dorsal fin rarely free (not impinging on dorsal body contour) or pale ringed (see Figure 33*a* for exception); ventral half of body in region below segmented-ray portion of dorsal fin with row of 3 or 4 dark spots; one dark spot on body in area below anterior segmented dorsal-fin rays and between dorsal and ventral rows of dark body spots; pale rings, often indistinct, sometimes margining dark spots. Spinous-dorsal fin

without fine, dusky, suprabasal stripe. Pectoral-fin axil moderately dark dusky, without distinct spot.

Live Color (based on photograph taken at Tutuila, Plate 8: figure 2): Ground color of head and body brownish. Head suffused with pink below midorbital level; postorbital stripe and crescentic stripe on opercle blackish; dorsal half of iris blackish with four or five pale spokes, ventral half bright white, aligning with faint, pale ventral margin of blackish postorbital stripe and continuing as bright-white stripe for most of body length. Body spots black; line of white dashes on ventral third of body; one or two bright white-spots on fleshy pectoral-fin base. Freshly collected specimens from Rotuma exhibit a salmon-pink, half-moon area enveloping the lower lip and small adjacent area posteriorly (not visible in photo taken at Tutuila).

REMARKS.—This species was most commonly taken on reefs formed of predominantly rock and dead coral and at depths of 9 m or more, although it occurred as shallow as about 2 m and, perhaps, as deep as about 18 m (rotenone used in making collections was usually dispensed near the bottom of collecting areas, but it usually dispersed into shallower areas). Although both *E. portenoyi* and *E. opsifrontalis* (Opsifrontalis Group) were taken together in some collections, where *E. portenoyi* was common, *E. opsifrontalis* was not, usually preferring areas with relatively more live coral.

In the largest collection of *E. portenoyi,* 114 specimens were taken, of which 57 were males and 57 females, indicating that the sex ratio is 1:1. The largest female was 39 mm SL, with only two specimens of more than 37 mm. The largest male was 44 mm, with ten specimens more than 37 mm, indicating, as is normally true of blenniids, that males attain a greater length than females.

DISTRIBUTION.—Known only from Rotuma and Tutuila, American Samoa.

COMPARISONS.—See comparisons section under *Ecsenius pardus* and discussion of relationships under account of Oculus Group.

ETYMOLOGY.—This species is named in honor of Norman S. Portenoy, Bethesda, Maryland, in recognition of his many years of support of ichthyological exploration by the staff of the National Museum of Natural History, Smithsonian Institution.

HOLOTYPE.—USNM 226576, male, 37.6 mm SL, Rotuma, north coast (slighty east of vertical from Sumi, which is on south coast), ocean side of reef crest about 100 m from shore; rock and dead coral with some live coral; depth to 9 m. V.G. Springer, et al., 9 May 1986.

PARATYPES.—*Rotuma:* USNM 278914 (113 specimens: 21–43 mm SL, collected with the holotype); USNM 283103 (32:18–36), east side, just north of Afnaha Island, 0–13.7 m, V.G. Springer et al., 21 May 1986. *American Samoa:* Tutuila, BPBM 17514 (5:22–37, lost in mail), USNM 276370 (9:19–45).

ADDITIONAL MATERIAL.—USNM 195716 (3 specimens: 31–38 mm SL, paratypes of *Ecsenius oculus* Springer), originally believed to have come from the Banda Sea; later, McKinney and Springer (1976:15–16) proposed as probably having come from Samoa. *Rotuma:* USNM 283102 (54 specimens), 283100 (1), 283101 (2).

Ecsenius sellifer, new species

FIGURE 32*e;* TABLES 16, 17

Ecsenius (Ecsenius) oculus.—Springer, 1971:35 [paratypes, in part; Palau Islands].—Springer, 1972:4 [Trobriand Islands, New Guinea].

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type E; Palau, Trobriand, and Savo, Solomon islands].

DESCRIPTION.—Dorsal fin XII,13 or 14, deeply notched between spinous and segmented-ray portions. Anal fin II,15 or 16 (rarely 16). Pectoral fin 13. Segmented caudal-fin rays 13. Vertebrae 10 + 21 or 22. Dentary incisor teeth 50–54 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at between vertcials from dorsal-fin spine 11 and and first segmented ray. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Important features include: Pair of dark spots present dorsally on nape. Stripe extending from postorbital margin faint or absent anteriorly; when present, becoming abruptly darker on dorsal portion of opercle and anterior portion of body above pectoral-fin base; stripe decreases in intensity as it continues along body. Second, slightly deeper, short, dark stripe on opercle below previously described dark stripe; stripes separated by fine, pale stripe. No conspicuous blackish pigment present ventroanteriorly to corners of mouth (pigment in this area darkly dusky, however).

VARIATION.—Specimens from the Solomon Islands have one more segmented dorsal-fin ray than do specimens from Papua New Guinea and the Palau Islands (Table 16).

DISTRIBUTION.—Umboi Island, Papua New Guinea; Kiriwina Island (Trobriand Islands), Papua New Guinea; Savo and Guadalcanal, Solomon Islands; Nardueis Island, Palau Islands.

COMPARISONS.—*Ecsenius sellifer* is distinguished from all other species of the Oculus Group by the combination of having more than one pale-margined dark saddle on the dorsal body contour and lacking pale-margined dark spots on the body proper. In possessing a transverse pair of dark spots on the nape, it is similar only to *E. paroculus* and *E. oculatus* in the Oculus Group. See comparisons section under *E. monoculus* for comments on possible intragroup relationships.

ETYMOLOGY.—From the Latin *"sella,"* meaning "saddle," and "-fer," meaning "carry" or "bear," in reference to the distinctive large, saddle-like markings on the body.

HOLOTYPE.—USNM 261462, male, 37 mm SL, Papua New Guinea, Trobriand Islands, Kiriwina Island, surge channels and shallow flats, 0–3.7 m, B.B. Collette and B. Goldman, 17 June 1970.

PARATYPES.—USNM 206431 (8 specimens: 27–37 mm SL, collected with the holotype); USNM 221237, 32 mm SL, Papua

New Guinea, Umboi Island, in lee of Higgins Point, 0–4.5 m, B.B. Collette et al., 18 June 1979; AMS I.17490-001, 40 mm SL, Solomon Islands, SW corner of Savo Island, J.E. Randall et al., 18 July 1973; AMS I.17486-033, 29 mm SL, Solomon Islands, Guadalcanal, Honiara, G. Allen and J.E. Randall, 11 July 1973; CAS 13463, 41 mm SL, Palau Islands, edge of reef off Nardueis Island, vicinity of Garudowaishi Point (GVF Register no. 880), ~1–5.5 m, Sumang et al., 4 September 1956 (previously paratype of *Ecsenius oculus*).

Ecsenius tessera, new species

FIGURE 33*d*; PLATE 7: FIGURE 5; TABLES 16, 17

Ecsenius (Ecsenius) oculus.—Springer, 1971:35 [paratypes, in part, New Hebrides].

Ecsenius oculus.—McKinney and Springer, 1976:12 [Type F, in part; New Hebrides].

DESCRIPTION.—Dorsal fin XII,14 or 15, deeply notched between spinous and segmented-ray portions. Anal fin II,16 or 17.

Pectoral fin 13. Segmented caudal-fin rays 13. Vertebrae 10 + 23. Dentary incisor teeth 50–54 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at some point between vertical from interspace between dorsal-fin spines 10 and 11 and vertical from first segmented ray. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Important features include the following: No pair of dark spots present dorsally on nape; nape with 2 dusky stripes (may be faint) separated by pale interspace. Dark stripe extending from postorbital margin across opercle dorsally, intensifying for short distance as it continues on body anteriorly, terminating below spinous-dorsal fin, where it may be continuous with an elongate, partly pale-margined, dark spot. No, deep, short, dark stripe present just ventral to dorsal opercular stripe. Blackish pigment in area ventroanterior to corners of mouth conspicuous in males, less so in females. Sides of body anteriorly with irregular, dusky, broad stripes separated by paler, slenderer stripes; posteriorly with two rows of irregularly shaped, variably-dark polygons surrounded by network of narrow, pale, grout-like areas. Venter of males with sprinkling of fine melanophores, except for narrow, midventral area; that of females immaculate.

Live Color (based on a freshly dead specimen): Dorsal-, pectoral-, and caudal-fin rays tinged with pink; anal fin with broad, orange-brown stripe; brilliant white spot just dorsal to pectoral-fin base, one or two on base, one on caudal peduncle dorsally, and one on caudal fin basally and centrally; pelvic fins mostly black, with white base and outer margin.

REMARKS.—The apparent restriction of *E. tessera* to New Caledonia and New Hebrides is duplicated in *Ecsenius* by the distribution of *E. isos*. It is possible that the distribution of these two species is indicative of an area of marine endemism that merits closer examination by systematists.

DISTRIBUTION.—New Caledonia and New Hebrides.

COMPARISONS.—*Ecsenius tessera* is distinguished from other species in the Oculus Group by its unique tile-like color pattern of dark polygonal spots separated by a pale, grout-like network. For possible relationships see discussion under account of the Oculus Group.

ETYMOLOGY.—The specific name tessera is from Latin, meaning "paving tile," in reference to the tile-like appearance of the color pattern on the body. The name is used here as a noun in apposition.

HOLOTYPE.—MNHN 1980-964, female, 41 mm SL, New Caledonia, S end of island: outside barrier reef W of Mato Pass, 6–10 m, J.E. Randall and L. Maugé, 13 January 1979.

PARATYPES.—BPBM 27126 (2 specimens: 38–45 mm SL), collected with the holotype. AMS I.6521-24 (4:35–42), New Hebrides (originally paratypes of *E. oculus*).

YAEYAMAENSIS GROUP

This group comprises five species: *E. yaeyamaensis*, *E. stictus*, *E. nalolo*, *E. dentex*, and *E. minutus*. These species are united by a complex of color-pattern characters. The most distinctive portion of the pattern occurs on the ventral surface of the head. The lower lip is dusky to almost black, followed posteriorly by a roughly bell-shaped or semicircular area that is devoid of melanophores (area salmon-pink in life in *E. dentex*, *E. stictus*, and *E. yaeyamaensis*; not recorded for other two species) and usually extends posteriorly to the level of the posterior end of the jaw (in *E. minutus* the immaculate area may contain a few melanophores and commonly terminates anterior to the level of the posterior end of the jaw). The immaculate area is bounded laterally and posteriorly by dusky to almost black pigment, and there is a ventroanteriorly curving dark line[1] that originates on the opercle slightly to well anterior to the opercle's posterior margin (as far anteriorly as the posterior preopercular margin in *E. minutus*) and ends at or near the immaculate area. The dark curving line occasionally extends across the posterior margin of the immaculate area to join the line's contralateral twin. The underside of the head is darkest in males, and the immaculate area in males may be reduced greatly in size, but some manifestation is invariably present.

Some specimens of *E. pictus* (only member of the Pictus Group) and female specimens of *E. trilineatus* and *E. isos* (Isos Group) have a similar color pattern on the ventral surface of the head. In these species, however, the pigmented portion is

[1]The position of the dorsal end of this line along the horizontal length of the opercle is variable within a species, and often difficult to assess unless a variety of species and well-preserved specimens are available for comparisons. With such material amassed for the present study, I have been able to convince skeptical colleagues of the validity of my assessments of the relative constancy of the character within species groups, particularly the Yaeyamaensis, Oculus, and Isos groups and *Ecsenius fourmanoiri* of the Opsifrontalis Group. In spite of this caveat, there are many specimens that are readily and unequivocally assessable for the character.

usually not very dark, and the immaculate area is usually narrow, terminating well in advance of the level of the posterior end of the jaw. The life color of the immaculate area in these species, except *E. pictus,* is not tinted with pink. In some specimens of *E. pictus,* there is a general dull pinkish cast to the entire ventroanterior end of the mandible. In addition to these differences, the dark curving opercular line is absent in *E. pictus.*

A dark, curving opercular line superficially similar to that of the Yaeyamaensis and Isos groups also exists in the Oculus Group and *E. fourmanoiri* (Opsifrontalis Group). The line in these latter species differs from that of the Yaeyamaensis and Isos groups in that dorsally it originates and courses close to or along the posterior margin of the opercle, rather than anterior to the opercle's posterior margin.

The pattern on the ventral surface of the head of various other *Ecsenius* species, particularly the species of the Oculus Group, resembles that of the Yaeyamaensis Group. In the Oculus Group the lower lip has at most a fine edging of melanophores, and the dark area posterior to the pale area on the chin, which, like *E. dentex, E. stictus,* and *E. yaeyamaensis,* is salmon pink in life, does not become so intensely dark as it does in some males of the Yaeyamaensis Group. Some species of the Prooculis Group may have spot-like areas devoid of melanophores on the ventral head surface, but these spots are bilaterally arranged and circular or crescentic in shape.

The Yaeyamaensis Group species, except some specimens of the Cargados Carajos population of *E. nalolo,* have a distinct, dark mark on the fleshy pectoral-fin base. In *E. yaeyamaensis* and *E. stictus* the mark is roughly Y-shaped, with the arms of the Y directed posteriorly and extending onto the fin rays. The dorsal arm of the Y enters the fin at a point along a vertical connecting the bases of the third and fourth from dorsalmost fin rays (usually enters between the third and fourth rays) and the ventral arm enters the fin at a point along a vertical connecting the bases of the sixth and seventh rays (usually enters at the seventh ray).

In the other three species of the Yaeyamaensis Group, there is a dark stripe on the pectoral-fin base of most specimens. In *E. minutus* the stripe broadens considerably anteriorly; posteriorly, the stripe enters the pectoral fin at a point along the vertical connecting the bases of the seventh and eighth from dorsalmost pectoral-fin rays (usually at the 8th), and there are no prominent dark marks, other than the stripe, on the fleshy base or fin. In *E. dentex* and most specimens of *E. nalolo* (including all those from the Red Sea), the dark stripe does not broaden noticeably anteriorly, and posteriorly the stripe enters the pectoral fin at some point along the vertical connecting the bases of fifth and sixth from dorsalmost pectoral-fin rays.

In *E. dentex* and specimens of *E. nalolo* from the Red Sea there are no prominent dark marks, other than the stripe, on the pectoral-fin base. Most specimens from the Indian Ocean populations of *E. nalolo* exhibit additional dark marks on the pectoral-fin base and rays. The most common mark is a dark spot on the proximal portion of the eighth from dorsalmost pectoral-fin ray. The Cargados Carajos population also frequently has a spot of lesser intensity on the 2nd and 3rd from dorsalmost rays, and the stripe on the pectoral-fin base may often be obscured, or even appear diffusely forked (Y-shaped) anteriorly, as if the dark anterior portion of the stripe, as occurs in *E. minutus,* has been excavated.

The differences in color pattern of the pectoral fin and its base, as exhibited by the Red Sea population of *E. nalolo,* might warrant recognition of that population as a separate taxon from the Indian Ocean populations (true *nalolo*). The narrow entrance (30–40 km) to the Red Sea from the Gulf of Aden is less than 200 m deep and could have been closed off and/or greatly restricted during periods of glaciation, causing the initiation of divergence of Red Sea and Indian Ocean populations of conspecifics (see similar discussion in Appendix II regarding the Gulf of Aqaba endemic *E. dentex* and Red Sea *E. nalolo*). I am reluctant to name the Red Sea form, however, because there is an extensive area of coastline between the Red Sea and Mozambique from which there are no specimens and along which gradual change from the Red Sea to Indian Ocean color patterns might occur.

A single pectoral-fin base stripe is also present in *E. fourmanoiri,* and a pair of dark stripes, superficially resembling the arms of a Y, are present in *E. trilineatus.* In *E. fourmanoiri* the stripe broadens as it enters the pectoral fin and covers one or more of the bases of the fourth to sixth from dorsalmost rays. In *E. trilineatus* the dorsal stripe enters the pectoral fin at a point along the vertical connecting the interspace between the dorsalmost two rays and the base of the third ray. The ventral stripe enters the pectoral fin between the bases of the sixth and seventh from dorsalmost rays, and anteriorly often curves ventrally (usually only visible when opercle is pushed aside). Adumbrations of the two pectoral-fin base stripes of *E. trilineatus* occur in the other two species of the Isos Group. Indistinct, dusky stripes or Y-shaped pectoral-fin base markings occur variously among specimens of the Oculus Group species.

Specimens of all the Yaeyamaensis Group species usually have a conspicuous dark spot on the internal (axillary) surface of the fleshy pectoral-fin base. Occasional specimens may have two dark spots on the internal surface, or the spot may be faint or diffuse. A similar spot occurs in *E. trilineatus* (Isos Group; I have no well-preserved specimens of the other two species) and a much more diffuse spot is characteristic of the Oculus Group. *Ecsenius alleni* (Opsifrontalis Group) has a relatively large round spot on the internal surface of the fleshy pectoral-fin base, but this spot appears to be the counterpart of the unique dark spot on the external pectoral-fin base and of a different origin than those of the other species.

Also common to the Yaeyamaensis Group species is the presence of up to three dark stripes, often separated by conspicuous pale stripes, on the side of the head. The ventralmost, and most commonly present, of these stripes extends posteriorly from about the mid-postorbital margin,

often extending onto the body, where it usually breaks up into a series of irregular, dark dashes. Dark head stripes, and particularly a mid-postorbital stripe, occur commonly among *Ecsenius* species with a deeply incised dorsal fin. The mid-postorbital stripe is present in many or all of the species of the Opsifrontalis, Lineatus, Oculus, Mandibularis, Pictus, and Prooculis groups, and is probably synapomorphic for these groups. A similar stripe occurs in *E. gravieri* (Pulcher Group) and in two species of the Stigmatura Group.

In *E. gravieri,* the dark mid-postorbital stripe lacks the pale bordering stripes of the other groups. I believe the stripe is an autapomorphy of *E. gravieri,* having evolved in response to that species' evolution as a Batesian mimic of a species of *Meiacanthus* (Blenniidae, Nemophini) that also has a dark postorbital stripe (Springer and Smith-Vaniz, 1972; most *Meiacanthus* species exhibit a postorbital stripe). The stripe of the two Pulcher Group species is positioned somewhat ventral to the mid-postorbital level, and bordered mainly ventrally by a bright white or orange stripe. I believe that this more ventral stripe is a synapomorphy of the two species.

In the Yaeyamaensis Group, the color pattern of the body, although highly variable and bearing species-specific markings, exhibits some features restricted to the group. Anteriorly, there are dark stripe-like marks and irregular splotches, and posteriorly a dusky ground color that is regularly punctuated with diffuse, pale, roundish spots. Often, spots and ground color alternate in a somewhat checkerboard pattern. The stripe-like markings are not duplicated in other *Ecsenius* species, but the pattern of pale spots occurs in *E. monoculus* and *E. sellifer,* and on the ventral half of the body in *E. oculus, E. paroculus,* and *E. oculus* (all Oculus Group).

Weighting heavily the unique shared presence of a pale area, which is salmon pink in life (as far as known: three of the five species), on the ventral surface of the jaw and the pale-spotted pattern on the body (not present in those Oculus Group species that have dark ocelli on the ventral half of the body), the Yaeyamaensis Group appears to be most similar to the Oculus Group, and I believe the two groups form a monophyletic pair. I treat the biogeographic implications of this hypothesized clade in Appendix I. In Appendix II, I discuss the intragroup relationships and distribution patterns of the Yaeyamaensis Group.

Ecsenius dentex, new species

FIGURE 35*d;* PLATE 8: FIGURE 4; TABLES 19, 20

Ecsenius (Ecsenius) nalolo.—Springer, 1971 [in part].

DESCRIPTION.—Dorsal fin XI–XIII,13–15 (rarely XI, XIII, or 15); incised between spinous and segmented-ray portions. Anal fin II,15–17 (rarely 17). Pectoral fin 12–14 (usually 13). Segmented caudal-fin rays 13. Vertebrae 10 + 21–23. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 49–59 in males and 53 to 63 in females, averaging more in females than males (Table 20); posterior canines 0 or 1 (usually 1). Lateral line without vertical pairs of pores, extending posteriorly to point between verticals from ninth and eleventh dorsal-fin spines (usually reaching to or beyond tenth spine). Cirrus present on posterior rim of anterior nostril; none present on anterior rim.

Color Pattern: The main features of the color pattern of *E. dentex* are those of the group and are described in the account of the Yaeyamaensis Group. There are no features of the color pattern that distinguish specimens of *E. dentex* from Red Sea specimens of *E. nalolo* (q.v.).

A color photograph (Plate 8: figure 4) of a freshly dead

TABLE 19.—Frequency distributions for numbers of segmented dorsal- and anal-fin rays and precaudal vertebrae in species of the *Yaeyamensis* Group (localities indicated only for *E. nalolo*; geographic variation not evident in other species).

Species/locality	Segmented dorsal-fin rays					Segmented anal-fin rays					Caudal vertebrae			
	12	13	14	15	$\bar{x}$	14	15	16	17	$\bar{x}$	21	22	23	$\bar{x}$
Ecsenius yaeyamaensis		31	223	12	13.9	1	34	226	4	15.9	25	220	14	22.0
Ecsenius stictus		7	105	14	14.0		7	106	10	16.0	6	104	9	22.0
Ecsenius minutus		13	24		13.6		19	19		15.5	5	32		21.9
Ecsenius dentex		24	75	4	13.8		26	73	2	15.8	8	80	12	22.0
Ecsenius nalolo														
Red Sea	1	7	4		13.2	3	8	1		14.8	8	2	1	21.4
Mozambique		2	9		13.8		4	7		15.6	1	10		21.9
South Africa		6	6		13.5		6	6		15.5	6	6		21.5
Commoro Islands			3		14.0		1	2		15.7	1	2		21.7
Aldabra		4	28		13.9		3	27	2	16.0	3	20	1	21.9
Amirante Isles		1	7		13.9		1	7		15.9	1	7		21.9
Chagos Islands		6	41		13.9		11	35		15.8	5	45		21.9
Cargados Carajos		5	39	3	14.0		7	39	2	15.9	5	36	5	22.0

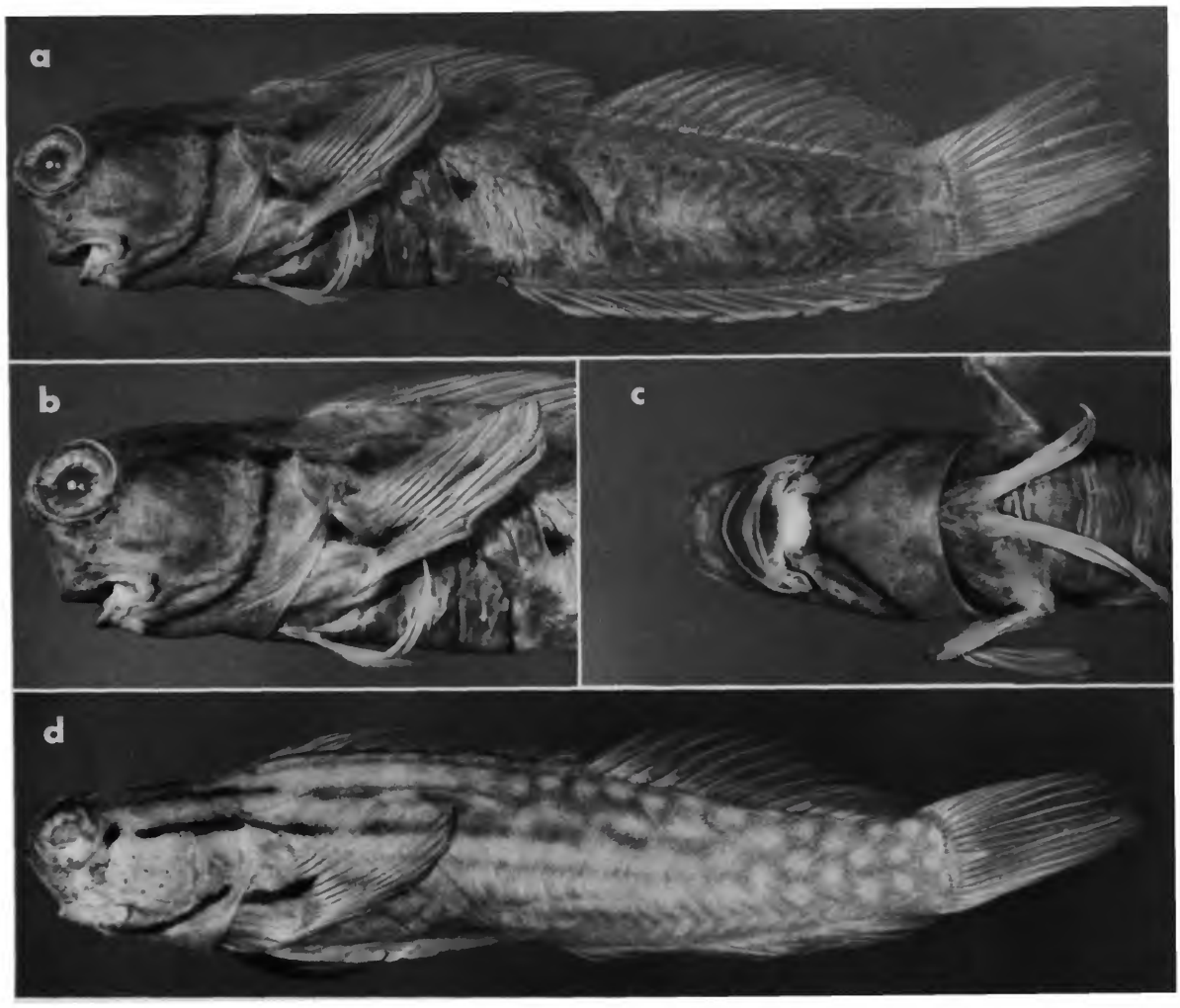


FIGURE 35.—*Ecsenius minutus: a–c,* FMNH 71367, male, 31 mm SL, South Nilandu Atoll, Maldive Islands; *Ecsenius dentex, d:* USNM 204570, female, 37 mm SL, Strait of Jubal, Ras Muhammad, Sinai Peninsula, Egypt (photographs by T.B. Griswold).

TABLE 20.—Frequency distributions for number of dentary incisor teeth in species of the *Yaeyamaensis* Group.

	Dentary incisor teeth																							
Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	$\bar{x}$
Ecsenius yaeyamaensis																								
males	1	2	2	8	8	16	18	22	21	10	6	1												47.4
females				1	2	5	9	12	13	22	14	8	5	1										49.4
Ecsenius stictus																								
males						4	3	5	8	7	1	3	-	1										49.0
females								6	4	3	6	8	3	5	2	1								51.3
Ecsenius minutus																								
males						3	5	6	4	8	2													48.5
females								2	-	2	3	1	1											50.4
Ecsenius dentex																								
males									1	-	1	7	8	15	14	14	4	3	2					54.7
females													3	2	2	4	8	6	9	7	5	3	2	58.3
Ecsenius nalolo																								
males		1	1	4	6	14	14	17	9	9	5	2												47.5
females					1	1	1	8	7	9	12	16	3	3										50.5

specimen shows the dark colors on the head and body to be shades of brown to black; cheek with fine, golden spots. Randall (1983:156) presents an illustration of a fresh, but somewhat faded specimen labelled as *Ecsenius nalolo*, which he informs me came from the Gulf of Aqaba; hence, it must be *E. dentex*.

RELATIONSHIPS.—*Ecsenius dentex* is probably most closely related to *E. nalolo* (particularly the Red Sea populations of *E. nalolo*), from which *E. dentex* appears to differ only in averaging about 7 more dentary incisor teeth in males and females. Many preserved Indian Ocean specimens of *E. nalolo* differ from *E. dentex* (and Red Sea *E. nalolo*) in having a noticeable peppering of dark spots on their cheeks and in having indistinct stripes and/or additional dark markings on the fleshy pectoral-fin base, and dark spots on the abdominal flanks. *Ecsenius dentex* may have a peppering of golden spots on its cheeks. In preservative, these spots, if they were present, are represented by fine pale spots that are easily overlooked. It is interesting that *E. stictus* also differs from its presumed sister species, *E. yaeyamaensis*, in having a higher average number of dentary incisors. Unlike *E. dentex* and *E. nalolo*, however, *E. stictus* also differs from *E. yaeyamaensis* in particulars of the color pattern on the body.

DISTRIBUTION.—*Ecsenius dentex* occurs only in the Gulf of Aqaba and northernmost portion of the Red Sea adjacent to the Gulf.

ETYMOLOGY.—The (pre-Linnean) source of the word dentex is unclear, but the word is apparently derived from the Latin *"dens,"* meaning "tooth." Dentex, meaning toothed, has been used as a specific name for several fishes; in the present case, the name refers to the most prominent characteristic of the species: it has the highest average number of teeth of all the species in the Yaeyamaensis Group.

HOLOTYPE.—USNM 276351, male, 34.3 mm SL, reef near road at Marsa Muqabila (= Muqabla), Sinai Peninsula, Gulf of Aqaba northwest coast, water depth to 4.1 m, V.G. Springer et al., 17 July 1969.

PARATYPES.—*West coast Gulf of Aqaba* (Sinai Peninsula): Marsa Muqabila, USNM 276352 (9 specimens: 15–31 mm SL, collected with holotype), 204567 (61:16–42); Elat (= Eilat), HUI E63/33 (2:26, 32), E63/36 (3:19–25); Al-Kura, HUI 3531 (1:25); Ras El Hameirah (= Hamira), BPBM 13394 (2:37, 40), HUI F-4384 (1:36); ?Ras El Hameirah, HUI F-4376 (6:~15–32); Ophir (= Ofir) Bay, HUI F-3551 (3:18–35); "Smithsonian Bay," HUI F-3542 (1:32), F-3553 (3:22–34); Ras Burqa, USNM 204571 (39:13–46); between Marset Mahash El Ala and Marset Abu Samra, USNM 204568, (20: 15–38). *Red Sea:* southern tip of Sinai Peninsula, Ras Muhammad, BPBM 29663 (5:29–42), USNM 204570 (36: 22–48); Tiran [Island], near Marsa, Shabir, ROM 43606 (4: 31–41); Al Ghardaqa [and vicinity], Egypt, SMF 5119 (1:38), USNM 200602 (4:30–45, including one cleared and stained), 201754 (3:28–43).

Ecsenius minutus Klausewitz

FIGURE 35*a–c*; PLATE 9: FIGURES 4, 5; TABLES 19, 20

Ecsenius minutus Klausewitz, 1963:357 [Addu-Atoll, Maldives; holotype, SMF 6367].
Ecsenius (Ecsenius) nalolo.—Springer, 1971:33, 34 [in part].
Ecsenius nalolo.—McKinney and Springer, 1976:11.

DESCRIPTION.—Dorsal fin XII or XIII,13 or 14 (rarely XIII); incised between spinous and segmented-ray portions. Anal fin II,15 or 16. Pectoral fin 12–14 (usually 13). Segmented caudal-fin rays 13. Vertebrae 10 + 21 or 22. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 46–51 in males and 48–53 in females, averaging more in females than males (Table 20); posterior canines 0 or 1 (usually 1). Lateral line without vertical pairs of pores, extending posteriorly to point between vertical from interspace between ninth and tenth dorsal-fin spines and vertical from eleventh spine (usually reaching to or beyond 10th spine). Cirrus present on posterior rim of anterior nostril; none present on anterior rim.

Preserved Color: The main features of the color pattern of *E. minutus* are described under the account of the Yaeyamaensis Group and in the relationships section of *E. yaeyamaensis*. The most distinctive features of the color pattern of *E. miniutus* are the disposition of the single dark stripe on the pectoral-fin base and the dark, ventroanteriorly curving line anteriorly on the opercle. The pectoral-fin base stripe is much broader anteriorly than posteriorly, and posteriorly enters the fin at some point between the seventh and eighth from dorsalmost rays. In those species of the Yaeyamaensis Group that have a similar stripe, the stripe is usually not much broader anteriorly, and posteriorly it enters the fin at a point along the vertical connecting the bases of the fifth and sixth from dorsalmost rays. Dorsally, the dark curving opercular line reaches, or just fails to reach a dark spot, which is situated at the dorsal margin of the opercle, in the position occupied by the dark mid-postorbital stripe of the other species of the Group. Another dark spot dorsal to the pectoral-fin axil is also probably a remnant of the postorbital stripe. In the other species of the Yaeyamaensis Group there is a large gap between the dorsal end of the dark opercular line and the mid-postorbital stripe, which may be almost continuous from the postorbital margin to well out on the body anteriorly. Additional note is taken here that the cheeks are not spotted in any of the specimens (occurs only in some specimens of *E. nalolo*) and that there are occasionally one or two large, dark, roundish blotches on the flanks in the abdominal area. These are darkest in males.

Live Color (Plate 9: figure 4): Based on photographs taken in the wild, the darker colors on the head and body are shades of brown. There are some diffuse golden marks on the cheeks. The ring around the pupil and spokes radiating from the pupil appear to be white. Pale spots on the body are less consipicuous than those in the other species of the Yaeyamaensis Group.

One photograph shows a specimen almost totally blanched, with an almost transparent body; the most noticeably markings include the opercular line and some spots posterior to the eye (fleshy pectoral-fin base is obscured).

RELATIONSHIPS.—I am unable to hypothesize unequivocally the sister group of *Ecsenius minutus* within the Yaeyamaensis Group. The broad anterior end of the pectoral-fin base stripe is reminiscent of the forked anterior end of the stripe in some specimens of *E. nalolo* (Figures 37*d, e*), if one imagines the area between the forks becoming filled in. The posterior end of the stripe enters the fin at about the level of the eighth from dorsalmost ray in *E. minutus*, but in *E. nalolo* it enters at the level of the fifth to sixth from dorsalmost ray.

DISTRIBUTION.—*Ecsenius minutus* is known only from the Maldive Islands.

MATERIAL.—*Maldive Islands:* Addu Atoll, FMNH 71368 (13 specimens: 27–38 mm SL), SMF 6367 (holotype of *Ecsenius minutus:* 20); South Nilandu Atoll, FMNH 71367 (21:26–36); Villingilli Island, BPBM 18055 (1:32).

Ecsenius nalolo Smith

FIGURES 36, 37; PLATE 8: FIGURES 5, 6; TABLES 19, 20

Ecsenius nalolo Smith, 1959:245 [Pinda, Mozambique; RUSI BP-2127C, holotype].

Ecsenius (Ecsenius) nalolo.—Springer, 1971:33 [in part].

DESCRIPTION.—Dorsal fin XI–XIII,12–15 (rarely XI, XIII, 12, or 15), deeply incised between spinous and segmented-ray portions. Anal fin II,14–17 (rarely 14, except Red Sea, or 17). Pectoral fin 12–14 (usually 13). Segmented caudal-fin rays 13 or 14 (rarely 14). Vertebrae 10 + 21–23. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 41–53 in males and 44 to 54 in females, averaging more in females than males (Table 20); posterior canines 0 or 1 (usually 1). Lateral line without vertical pairs of pores, extending posteriorly to a point between verticals from ninth and eleventh dorsal-fin spines. Cirrus present on posterior rim of anterior nostril; none present on anterior rim.

Preserved Color: The main features of the color pattern of *E. nalolo* are those of the group and are described in the account of the Yaeyamaensis Group. There is no single feature, or combination of features, of the color pattern that distinguishes Red Sea specimens of *E. nalolo* from specimens of *E. dentex* (restricted to Gulf of Aqaba and northernmost Red Sea). Red Sea specimens of *E. nalolo*, like *E. dentex*, lack dark spots supplemental to the the dark stripe on the pectoral-fin base and fin. Supplemental spots are typical of Indian Ocean specimens. Indian Ocean specimens of *E. nalolo* may have up to four large, well-developed dark spots on the abdominal flanks (especially noticeable in Cargados Carajos and South African specimens). Flank spots are almost inconspicuous on Red Sea and Chagos Islands specimens of *E. dentex*. Many specimens of *E. nalolo* from the Cargados Carajos lack a distinct dark stripe on the fleshy pectoral-fin base, and in some specimens that possess the stripe, it is forked anteriorly. The stripe on the pectoral-fin base may form an enlarged spot as it passes onto the rays in Indian Ocean (including Cargados Carajos) specimens.

Live Color: A photograph (Plate 8: figure 6) taken in the wild at the Seychelles shows the darker areas on the body to be shades of brown. Pale spots on the body are brilliant white.

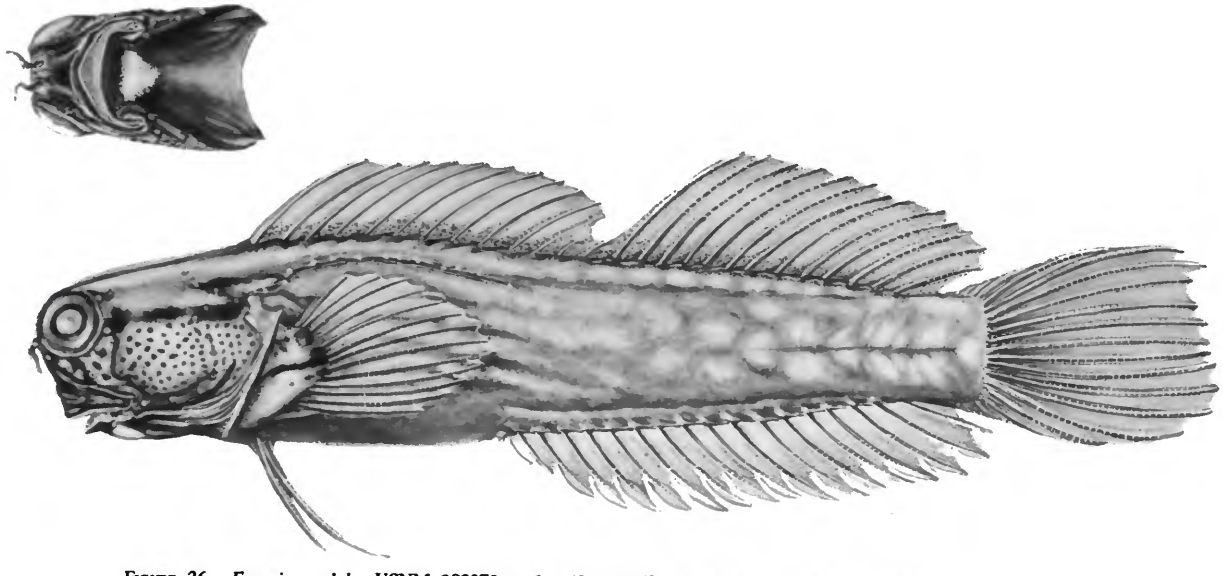


FIGURE 36.—*Ecsenius nalolo*, USNM 203072, male, 43 mm SL, Aldabra Atoll (small illustration shows underside of head; drawn by B. Holden).

Spokes in the iris radiating dorsally from the pupil are pale golden. Fine, dark-brown spots cover the cheeks. A Sudan (Red Sea) specimen (Plate 8: figure 5) is generally buff colored with paler, but not brilliant, spots on the body. Faint, golden spots are present on the cheeks.

REMARKS.—I (Springer, 1971) erroneously synonymized *Ecsenius minutus* Klausewitz with *E. nalolo*. I now conclude that Klausewitz's species is valid.

Frequency distributions of meristic elements (Table 19) indicate the possibility of geographically associated variability, with specimens from South Africa and the Red Sea having the lowest averages for these elements. These two localities are at the northern and southern extremes of the distribution of *E. nalolo*.

DISTRIBUTION.—Indian Ocean west of the Mid-Indian Ocean Ridge, south to Sodwana Bay, South Africa (~27°32'S), and Cargados Carajos (= St. Brandon's Shoals), and north to Djetta (=Jeddah), Saudi Arabia, Red Sea.

MATERIAL (* = new material).—*Saudi Arabia:* Djetta, USNM 217724* (1 specimen: 25 mm SL). *Sudan:* Sanganib Reef, SMF 8234 (1:37). Yemen: Zubair Island, HUJ F-4622 (1:25). *Ethiopia:* Difnein Island, USNM 204481 (9:17–31). *Aden:* USNM 203954 (1:17). *Amirantes Islands:* USNM 201845 (7: 29–48), ANSP 114824 (1:36). *Farquhar Island:*

FIGURE 37.—*Ecsenius nalolo*, USNM 216545, Cargados Carajos, females; *a–c*, 47 mm SL; *d*, 39 mm SL; *e*, 40 mm SL; *a*, lateral view (note conspicuous dark spots in abdominal area); *b*, close-up view of anterior end with pectoral fin rotated forward to show spots in axil; *c*, underside of head; *d* and *e*, close-up views of anterior end to show variation in markings on pectoral-fin base (note absence of abdominal spots; photographs *a–c* by K.A. Bruwelheide, *d* and *e* by T.B. Griswold).

USNM 203955 (1:49). *Aldabra Atoll:* USNM 203072 (15:30–46), 203075 (11:28–39), 201828 (6:23–51). *Comoros Islands:* Pamanzi Island, USNM 201826 (2:30, 32), 201521 (1:31). Mozambique: Pinda, RUSI BP2127C (39, holotype of *Ecsenius nalolo*), BP2127A (1:33), BP1924 (1:30), 25468? (6 [of 8?]:25–39). *South Africa:* Sodwana Bay, RUSI 76-8 (2: 38, 40), 76-9 (3:32–34), 76-10 (2:28, 30), 76-11 (2:30, 44), 76-13 (3:28–51). *Chagos Archipelago:* ROM 43823* (13: 14–43), 43834* (2:40, 46), 43825* (6:17–42), 43826* (5: 16–33), 43827* (6:15–39), 43828* (5:16–46), 43829* (4: 30–44), 43830* (4:15–33), 43831* (5:21–36), USNM 203071 (1:43), 203073 (2:31, 49). *Agalega Islands:* USNM 260329* (1:14). *Cargados Carajos:* USNM 216541* (43:31–46), ROM uncataloged* (formerly in 43805; 1:38) 216544* (5:39–44), 216545* (33:33–50).

Ecsenius stictus, new species

FIGURE 38; PLATE 9: FIGURES 5, 6; TABLES 19, 20

Ecsenius (Ecsenius) yaeyamaensis.—Springer, 1971:32, fig 28 [in part, Great Barrier Reef].

DESCRIPTION.—Dorsal fin XII or XIII,13–15 (rarely XIII;), deeply incised between spinous and segmented-ray portions. Anal fin II,15–17. Pectoral fin 12–14 (rarely 12 or 14). Segmented caudal-fin rays 13. Vertebrae 10 + 21–23. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 46–54 in males and 48 to 56 in females, averaging more in females than males (Table 20); posterior canines 0 or 1 (usually 1). Lateral line without vertical pairs of pores, extending posteriorly to point between vertical from interspace between ninth and tenth spines and vertical from base of eleventh dorsal-fin spine (rarely anterior to base of tenth spine). Cirrus present on posterior rim of anterior nostril; none present on anterior rim.

Preserved Color: The main features of the color pattern of *E. stictus* are those of the group and are described in the account of the Yaeyamaensis Group and in the relationships section of *E. yaeyamensis.* The color pattern of *E. stictus* is distinguished from all the other species of its group in having a sprinkling of widely-spaced, fine, dark spots on the posterior half of the body. These spots are aligned, more or less, in two or three rows, and may be continuous with dark dash-like marks anteriorly on the body. *Ecsenius stictus* has a Y-shaped dark mark on the fleshy pectoral-fin base, a mark it shares only with *E. yaeyamaensis.* The cheeks below the level of the midpostorbital stripe are never peppered with fine, dark spots, as occurs in some specimens of *E. nalolo.* The abdominal flanks may have one or two dark spots, but these are not particularly marked, and they appear to be aligned with the ventralmost row of dark body spots.

Live Color: The same color photograph of a living specimen in the wild appears in Debelius (1985:275, lower right, identified as *E. yaeyamaensis;* a photograph of *E. yaeyamaensis* appears on the upper right of the same page, identified as *E. mandibularis*) and Debelius (1986:96, center, also identified as *E. yaeyamaensis*). The head has alternating brown and white stripes dorsally and pale grayish cheeks with curving dark opercular line; dark Y-shaped mark on pectoral-fin base; body anterodorsally with three rows comprising from two to five dark spots, dorsal two rows in line with brown postorbital stripes; three elongate dark blotches on abdominal flanks; three rows of fine, dark spots on posterior half of body, which is otherwise pallid. Other individuals (Plate 9: figures 5, 6) are similar, but the head and body are more blanched, and the ventral pale head stripe is faintly golden. Pale spots on the body are scarcely evident in living specimens. It is possible that the blanching is a transient emotional response (fear?) that obscures normally expressed live color pattern.

RELATIONSHIPS (see also Appendix II).—Within the Yaeyamaensis Group, *E. stictus* appears to be most similar and closely related to *E. yaeyamaensis,* which differs mainly in lacking the fine dark body spots and having a slightly lower average number of dentary incisor teeth.

DISTRIBUTION.—Restricted to the Great Barrier Reef off Queensland.

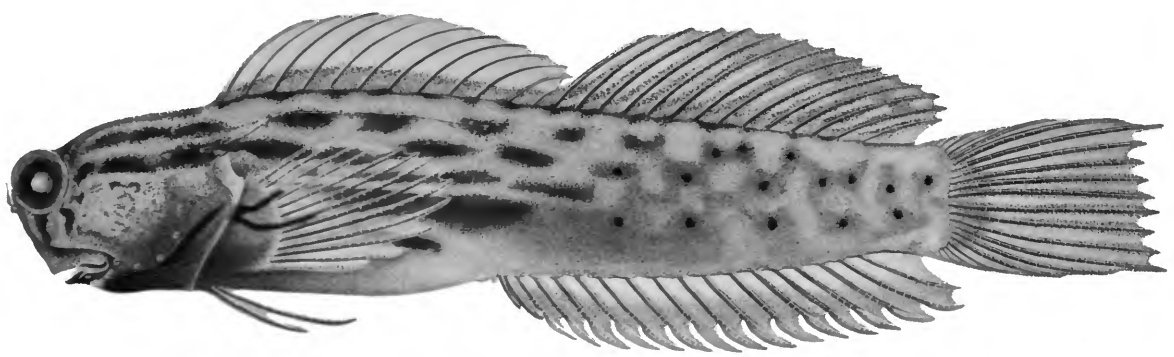


FIGURE 38.—*Ecsenius stictus,* USNM 201818, holotype, male, 38 mm SL, One Tree Island, Queensland, Australia (drawn by S.L. Chambers).

ETYMOLOGY.—The name stictus is derived from the Greek word meaning spotted, and refers to fine dark spots on the body that distinguish the species.

HOLOTYPE.—USNM 201818, male, 38.1 mm SL, south reef face about one mile (~1.7 km) from One Tree Island, Capricorn Group, Great Barrier Reef, Queensland, Australia. Collected by V.G. Springer et al., 22 November 1966; depth ~15 feet (~4.6 m). An illustration of the holotype also appeared in Springer (1971: figure 28), labelled *Ecsenius yaeyamaensis.*

PARATYPES.—*Southern Queensland:* One Tree Island, USNM 276343 (28 specimens: 32–45 mm SL; collected with the holotype, formerly included in USNM 201818), USNM 201822 (15:34–45), USNM 201836 (4:32–36); Heron Island, USNM 274539 (1:43), 274601 (1:37). *Northern Queensland:* Endeavour reef, ANSP 109690 (52:14–38), ANSP 109691 (30:20–47); Sir Charles Hardy Island, AMS I.20770-072 (18: 22–46); Escape Reef, AMS I.22574-045 (2:15, 40), I.22579-023 (1:37), I.22586-019 (1:39), I.22637-023 (1:39), ROM 40617 (1:15); Eagle Island, ROM 39674 (1:36); Lizard Island, ROM 38690 (2:37, 43), 39668 (2:39, 40), 39860 (5:14–19); Linnet Reef, AMS I.22574-045 (2:24, 26); off Cape Melville, AMS I.20755-037 (1:24).

NON-TYPE MATERIAL.—Heron Island, USNM 264121 (1: 35), 274537 (1:35), 274538 (1:13).

Ecsenius yaeyamaensis (Aoyagi)

FIGURE 39; PLATE 9: FIGURES 1–3; TABLES 19, 20

Salarias yaeyamaensis Aoyagi, 1954:213 [in part, Iriomote Island, Riukius; holotype probably destroyed].

Ecsenius (Ecsenius) yaeyamaensis.—Springer, 1971:32 [in part]; Springer, 1972:2.

Ecsenius yaeyamaensis.—McKinney and Springer, 1976:23.

DESCRIPTION.—Dorsal fin XI–XIII,13–15 (rarely XI or XIII), deeply incised between spinous and segmented-ray portions. Anal fin II,14–17 (rarely 14 or 17). Pectoral fin 12 or 13 (rarely 12). Segmented caudal-fin rays 13. Vertebrae 10 + 21 to 23. Dentary incisor teeth (includes anterior canines, which differ little, if at all, in appearance from incisors) 41–53 in males and 44–55 in females, averaging more in females than males (Table 20); posterior canines 0 or 1 (usually 1). Lateral line without vertical pairs of pores, extending posteriorly to point between verticals from tenth and eleventh dorsal-fin spines. Cirrus present on posterior rim of anterior nostril; none present on anterior rim.

Preserved Color: The main features of the color pattern of *E. yaeyamaensis* are those of the group and are described in the account of the Yaeyamaensis Group. The color pattern of *E. yaeyamaensis* is mainly distinguished by its having a Y-shaped dark mark (arms of Y directed posteriorly) on the fleshy pectoral-fin base and fin and lacking a sparse peppering of fine dark spots on the posterior half of the body. Of all the material examined, one specimen, of 21, from Tioman Island, Malaysia, had a single stripe on the fleshy pectoral-fin base on both sides, and might be confused with *E. nalolo* or *E. dentex.* In this specimen, however, the stripe enters the fins along the sixth from dorsalmost ray on one side and between the sixth and seventh rays on the other side. In *E. nalolo* and *E. dentex* the stripe enters the fin between the fifth and sixth rays. The cheeks below the level of the mid-postorbital stripe are never peppered with fine, dark spots. There is a wide gap between the dorsal end of the dark, ventroanteriorly curving opercular line and the extension of the mid-postorbital stripe at the dorsal margin of the opercle (the stripe may be interrupted and appear as an isolated spot above the opercle). The abdominal flanks may have one or two dark spots, but these are not particularly conspicuous.

Live Color (based on live and freshly killed specimens): Allen (1985, fig. 379) published a color photograph of a fresh specimen from Western Australia. In this specimen the dark pigments of the head and body are shades of brown (mid-postorbital and pectoral-fin base stripes are almost black). The upper half of the eye is much darker than the lower half, and the iris has eight evenly spaced spokes, with a perimetric pale spot in each space between spokes. The dark mid-postorbital stripe is margined dorsally by a diffuse, fine, pale stripe, and ventrally by a brighter pale stripe of lesser depth than the mid-postorbital stripe. This latter pale stripe, which is margined ventrally by a fine, brown pinstripe, expands and becomes less definite on the opercle and as it extends onto the

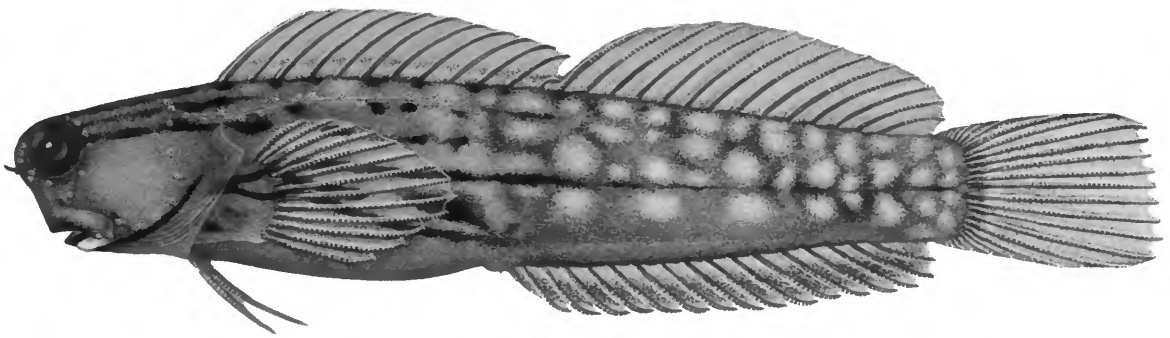


FIGURE 39.—*Ecsenius yaeyamaensis,* USNM 203136, female, 43 mm SL, Taiwan (drawn by M.H. Lester).

body. The dark opercular line is dusky and obvious only on the pale ventral surface of the head.

The color pattern of the Western Australian specimen is scarcely different from that of one from the Solomon Islands (Plate 9: figure 3), but the dark line on the opercle is obvious in the latter.

In a color photograph (Plate 9: figure 1) of a living specimen from Sri Lanka, the pale brown markings on the body ventroanteriorly are suffused with yellow, and dorsally, particularly on the head, the markings have pinkish overtones; the Y-shaped mark on the pectoral-fin base is yellow brown, rather than blackish as in preserved specimens, and other markings on the abdominal flank are also yellow brown; there is no noticeable dark curving line on the opercle. Finally, a live specimen (Plate 9: figure 2) from Palau is pallid with a highly contrasting dark opercular line and two dark, dash-like spots posterodorsally on the head.

REMARKS.—In spite of the variation in live or fresh color described above, I have not been able to detect consistent differences in the color pattern of preserved material from widely different localities.

RELATIONSHIPS (see also Appendix II).—Within the Yaeyamaensis-species Group, *E. yaeyamaensis* is most similar in external appearance and presumably most closely related to *E. stictus* in having a Y-shaped dark mark on the pectoral-fin base. It differs from *E. stictus* in lacking the sparse peppering of dark spots on the posterior half of the body and in that most populations have slightly lower average numbers of mandibular teeth (Table 20) than do populations of *E. stictus*. All the species of the Yaeyamaensis Group, except *E. minutus*, have a large gap between the dorsal end of the dark opercular line and the posterior extension of the mid-postorbital stripe. In *E. minutus*, there is at most a very narrow space separating these two markings.

DISTRIBUTION.—Ceylon east to the southern Ryukyus, Sorol Island (Carolines), and south to New Hebrides.

MATERIAL (* = new material).—*Ceylon:* USNM 206381 (9 specimens: 22–33 mm SL), 206382 (16:28–47), 206383 (8:25–31). *Malaysia:* Tioman Island, BPBM 21981* (21:24–36). *Taiwan:* USNM 203133 (1:35), 203134 (2:38, 39), 203135 (1:42), 203136 (2:40, 43), 203137 (10:26–49), 203138 (4: 38–42). *Philippine Islands:* Luzon, USNM 225051 (6:23–36)*; Siquijor, USNM 227538* (1:36); Palawan, USNM 222138* (1:33); Cuyo Islands, USNM 219312* (9:27–48)), 227539* (1:36), 227540* (1:30). Viet Nam: CAS 24487 (1:39). *Caroline Islands:* Palau, CAS 24462 (1:46), 24463 (11:32–43), 24468 (2:25, 30), 24470 (1:40), 24471 (4:30–39), 24475 (6:32–44), 24479 (1:46), 24480 (1:42); Sorol, CAS 24474 (1:32); Yap, USNM 24466 (9:26–52), 24473 (11: 22–34), 24481 (4:29–35), 24482 (1:25), 24483 (1:36.7), 24484 (2:34, 40), 24485 (1:32), 24486 (1:38). *Indonesia:* Seribu Islands, USNM 211994 (1:30); Karimundjawa, USNM 211981.(1:30); Bawean, USNM 211974 (5:20–24); Boeton, USNM 211967 (2:15, 40); Ambon, USNM 209735 (5:33–40), BPBM 18051 (1:not measured); Haruku, USNM 202381 (14: 13–33), 209603 (14:12–33); Saparua, USNM 211924 (50: 14–42); Flores, ZMA 109.100 (1:33). *Papua-New Guinea:* Madang, USNM 205706 (1:33); Basilaki Island, USNM 217564* (1:34); Watts Island, CAS 56578* (1:38) Muschu Island, USNM 221240* (13:26–41); Ninigo Islands, USNM 222968* (7:14–34), 227541* (2:24, 37), 227542* (1:38); Hermit Islands, USNM 222543* (1:29), 227544* (1:14), 227545* (3:14–28), 222546* (2:27, 32), 227547* (2:26, 32); New Britain, USNM 200428 (3:38–39, including one cleared and stained), 201812 (1:32) . *Solomon Islands:* Bougainville, USNM 201824 (2:30, 40); Guadalcanal, AMS I.17486-002 (10:not measured); Florida Island, AMS I.17497-002. *New Hebrides:* Efate, USNM 214819 (2:35, 42), BPBM 19577 (2: not measured). *Australia:* Western Austalia, Dirk Hartog Island, WAM P.27970-024*, in part (1:37); Northwest Cape area, AMS 19641-015* (2:32, 38), AMNH 33982* (11: 20–41); Montebello Islands, NTM S.10805-009* (34–48), S.10808-004* (6:22–39); Dampier Archipelago, NTM S.10809-008* (1:32), S.10814-005* (11:26–38); Northern Territory, Gove Peninsula, AMS 21963-019* (9:19–42).

OPSIFRONTALIS GROUP

This group comprises nine species: *E. alleni, E. australianus, E. axelrodi, E. bathi, E. dilemma, E. fijiensis, E. fourmanoiri, E. opsifrontalis*, and *E. tigris*.

The synapomorphies that I hypothesize as uniting the species as a monophyletic group are manifested primarily by living or freshly dead specimens: the presence on the body of pinkish to reddish to brownish-orange stripes and/or bands in at least one color-pattern form of each species. These colors may be obscured by blackish stripes and/or bands in darkly-pigmented forms, but indications of the orange pigment usually persist.

Three species of the Opsifrontalis Group (*E. axelrodi, E. bathi, E. dilemma*) have two markedly different color-pattern types, striped and banded, which I propose is a synapomorphy for these species within the Opsifrontalis Group. All the other species in the group have but one type pattern. In the three species with two patterns, the striped form lacks the orange pigment. None of the species in the other species groups of *Ecsenius* have live coloration similar to that of the Opsifrontalis Group. In the two non-Opsifrontalis Group species (*E. frontalis, E. bicolor*) with more than one type pattern and which have a striped pattern, the stripe is poorly developed and markedly different in appearance from that of the Opsifrontalis Group. Furthermore, neither of these two species exhibits a banded pattern.

In preserved specimens, the basic color pattern of the Opsifrontalis Group is one composed of two dark or dusky stripes on the body (the dorsalmore originating at the mid-postorbital margin) crossed by several dark or dusky bands (a third, less distinct stripe may be present on the dorsal body contour). The stripes and bands are present in the same relative positions on the body in all the species. The basic striped and

banded pattern is not present in other *Ecsenius* species.

The manifestations of the stripes and bands, whether uninterrupted or broken into spots, faint or intensely dark, present as two forms within a species, or other variations, usually are the main characters that define the species and clusters of species in the group. Two other color-pattern characters, which are not synapomorphies, typify the group: a dark stripe, margined dorsally and ventrally by fine pale stripes, extending posteriorly from the midpostorbital margin, and extensions of the body stripes onto the caudal fin. The postorbital stripe may be very faint in preserved specimens, but is usually noticeable in living or freshly collected specimens. The caudal extensions of the stripes may also be faint or even absent in species with both banded and striped forms.

Additional, non-synapomorphic characters defining the group are relatively small size, a deeply notched dorsal fin, and relatively low counts for fin-rays and dentary incisors. The species all lack a dark spot anterior to the anus, pale or dark spots on the ventral head surface (such as define the Prooculis group), a reddish-orange spot on the chin, and multiple posterior dentary canines, which are useful in defining other species groups of *Ecsenius*.

I have been unable to present a reasonable hypothesis of the sister-group relationships of the Opsifrontalis Group, and I have no intuitive opinion of what they might be, other than that they lie among those groups with deeply notched dorsal fins, low meristics, and dark postorbital stripes.

I also have been unable to hypothesize reasonably a complete set of interrelationships of the species within the group, although I have proposed some probable relationships in discussions under individual species accounts. I have hypothesized some partial vicariance scenarios that might explain the distributions of some of the related species (see under account of *E. australianus*).

DISTRIBUTION.—The Opsifrontalis Group species are all allopatric. There are extensive expanses of ocean lacking islands and reefs that separate various populations of a particular species of the Opsifrontalis Group. On the other hand, a species may occur at an island closely adjacent to another island inhabited by a different species of the group, indicating to me that simple dispersal cannot account for the distributions of the individual species.

The distributions of *E. fourmanoiri, E. fijiensis,* and *E. opsifrontalis* (Figure 40) relative to each other, and *E. australianus* and *E. tigris* (Figure 41) relative to each other, are probably indicative of how sharply defined are the distributions of the species of the Opsifrontalis Group.

Ecsenius fijiensis has been collected only from the reefs of the closely spaced islands of Fiji. Most of these reefs are quite close to one another reef; they are often separated by much less than 50 km. The most isolated reef, Vatoa, where *E. fijiensis* occurs is about 60 km (south) from the nearest neighboring reef. The closest known occurrence of *E. fourmanoiri* to *E. fijiensis* is at Ono-i-Lau, which is about 85 km south of Vatoa. There are no reefs between Ono-i-Lau and Vatoa. The significance of this narrow gap between the ranges of the two species is emphasized by the fact that, aside from Vatoa to the north and two small islets (Tuvana Itholo, Tuvana Ira) less than 40 km to the south of Ono-i-Lau, the closest reefs to Ono-i-Lau, other than the closely-spaced islands of Fiji (inhabited by *E. fijiensis*), are the Minerva Reefs (about 350 km south), the Tonga Islands (nearest about 350 km east), and Theva-i-Ra (= Conway Reef, about 500 km west). *Ecsenius fourmanoiri* occurs in the Tonga Islands (Tongatapu), but is unknown at the Tuvanas, Minerva Reefs, and Theva-i-Ra (no species of *Ecsenius* is known from these islands, of which only Minerva has ever been the subject of collecting). The nearest locality inhabited by *E. fourmanoiri* to the west of Ono-i-Lau is southeastern New Caledonia, about 1500 km distant. There are, however, some reefs punctuating the area between New Caledonia and Theva-i-Ra, and I predict that if a species of the Opsifrontalis Group occurs at any of those islands, the Tuvanas, Minerva Reefs, or Ceva-i-Ra, it will be *E. fourmanoiri* or a species yet unknown.

Ecsenius opsifrontalis is widely distributed among the islands of the Pacific Plate and eastern margin of the Philippine Plate. In the vicinity of Fiji, it has been taken only at Tutuila (American Samoa) and Rotuma. Rotuma is about 400 km north of Fiji (but uncollected Balmoral Reef, about 125 km northwest of Fiji and 350 km south of Rotuma, is a stepping-stone between them), and Tutuila is somewhat further northeast. However, it is possible to chart a stepping-stone route from Rotuma to Samoa with no stepping-stone separated from another by more than about 125 km (most much less), and from Samoa to Fiji or Tongatapu with no stepping-stone separated from another by more than 100 km (most much less). If simple dispersal explained the distribution patterns exhibited by the Opsifrontalis Group species, it would seem that some combination of *E. fijiensis, E. foumanoiri,* and *E. opsifrontalis* would either occur together at several localities in the vicinity of Fiji, or else there would be a mosaic of distributions of the three species. Instead, each of the species exhibits a cohesive distribution.

Ecsenius opsifrontalis also occurs at some localities that are either relatively close to, or connected by closely spaced stepping-stone islands to, localities where *E. axelrodi* occurs. If dispersal is an important factor in the distribution of the Opsifrontalis Group species, one can wonder why only *E. opsifrontalis* occurs at Pacific Plate islands, and why it is restricted to those islands (and islands along the bordering eastern margin of the Philippine Plate).

There are several islandless and reefless gaps of lengths greater than 100 km among the islands of the Pacific Plate surrounded by the known occurrences of *E. opsifrontalis.* It would be of considerable interest to determine if *E. opsifrontalis* or some other species of the Opsifrontalis Group occurs at these "isolated" islands, for example, Nauru and Ocean islands. Indeed, there are other islands and chains of islands, for example, New Hebrides and Santa Cruz (see Figure 40),

isolated by gaps of more than 100 km from the nearest locality that might be expected to harbor a species of the Opsifrontalis Group, but from which no specimens of the Group are known. All of these localities would be of importance to collect in order to reach a better understanding of the factors that resulted in the present distribution of the Group.

As for the distributions of three species discussed above, it is instructive to note the circumstances of the distributions of

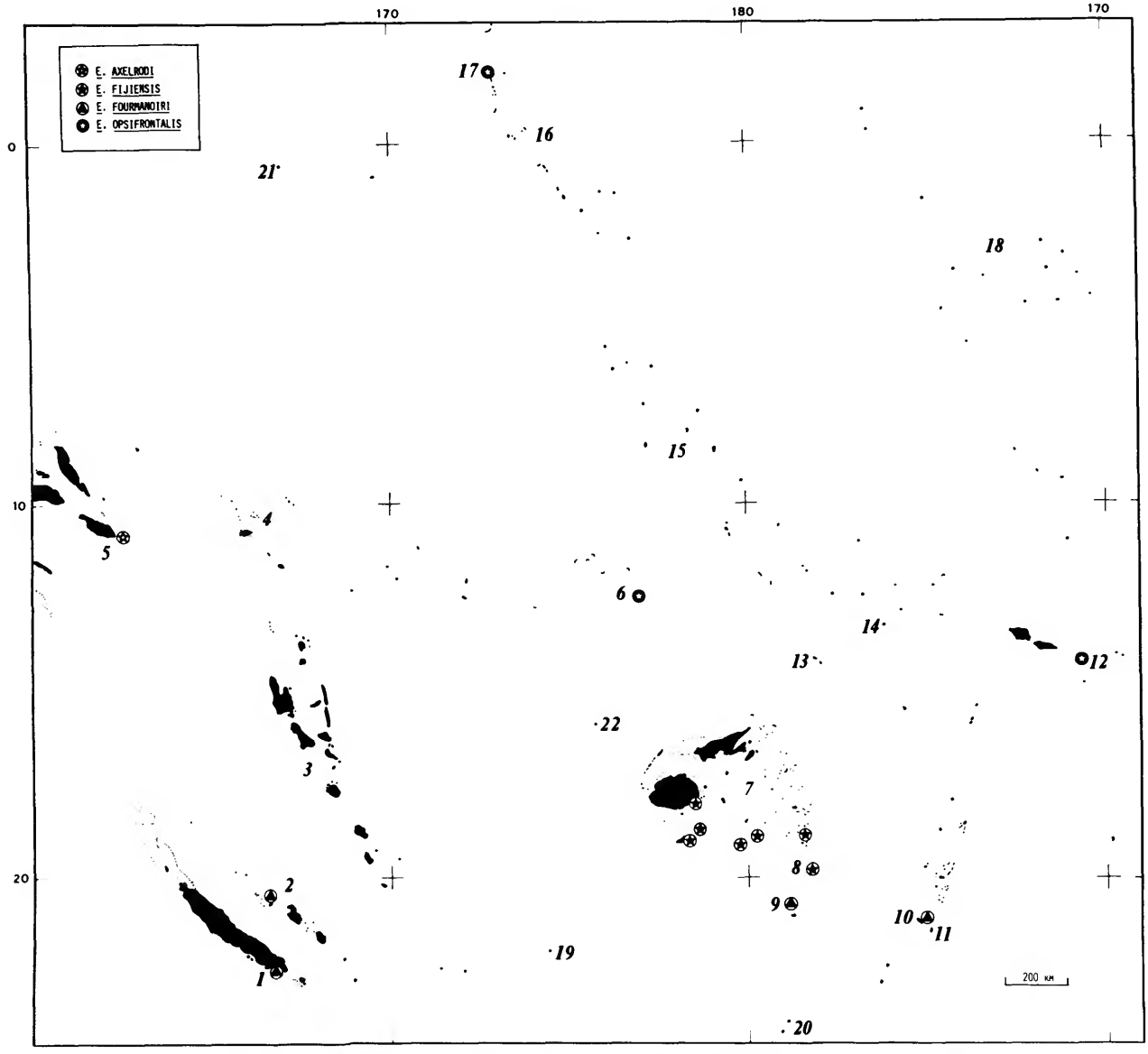


FIGURE 40.—Distributions of the (four) species of the Opsifrontalis Group occurring in a selected area of the southwest Pacific (all isolated reefs, shoals, and banks no deeper than 30 m are included—see particularly area between Santa Cruz and Samoa islands—based on Kroenke et al., 1983). Only distributions of *E. axelrodi* and *E. opsifrontalis* extend beyond area (for complete distributions of all species of the Group see Figure 11). Key to numbers on map: 1, Noumea area, New Caledonia; 2, Ouvea, Loyalty Islands; 3, New Hebrides (Vanuatu); 4, Santa Cruz Islands; 5, Santa Ana, Solomon Islands; 6, Rotuma; 7, Fiji; 8, Vatoa (Lau Group, Fiji); 9, Ono-i-Lau (Lau Group, Fiji); 10, Nukulofa, Tonga Islands; 11, Eua, Tonga Islands; 12, Tutuila, American Samoa; 13, Futuna Island; 14, Wallis Island; 15, Ellice Islands (Tuvalu); 16, Gilbert Islands (Kiribati); 17, Abaiang Atoll (Kiribati); 18, Phoenix Islands (Kiribati); 19, Theva-i-Ra (Conway Reef); 20, Minerva Reefs; 21, Nauru; 22, Balmoral Reef.

E. australianus and *E. tigris* (Figure 41). *Ecsenius australianus* occurs only on the northern Great Barrier reef. *Ecsenius tigris* is known only from the northernmost reefs of the Coral Sea Islands Territory of Australia, offshore of the Great Barrier Reef (Figure 41). The Coral Sea reefs rest on ocean bottom that comprises the Queensland Plateau (Kroenke et al., 1983; Kroenke, 1984, figure 8.1). The Queensland Plateau was once continuous with the Lord Howe Rise (Coleman, 1980:110, fig. 5; Kroenke, 1987, pers. comm.), which rise was rifted from the east coast of Australian Gondwana (Coleman, 1980, fig. 2) about 80–100 m.y.a. The Queensland Plateau appears always to have been adjacent to the coast of Australia, although the narrow Queensland and Townsville troughs separate the Plateau from the coastal Great Barrier Reef of Australia. I infer from this topography that the Plateau was rifted from the coast of Australia even though its distancing has not been great. This history might make it seem likely that *E. tigris* and *E. australianus* arose from a common ancestor whose distribution was split by the rifting. I hypothesize, however, that *E. australianus* is the sister group of *E. fourmanoiri* (see "Comparisons" and "Remarks" sections under *E. australianus*). The sister group of *E. tigris* is undecided, but there is evidence, perhaps, that it is either *E. fijiensis* or the clade of three species, including *E. axelrodi*, that exhibit two different color pattern types (see "Comparisons" and "Remarks" sections under *E. tigris*).

All the reefs in the Coral Sea that might possibly harbor *E. tigris* are shown in Figure 41. *Ecsenius tigris* is known only from three of the four northernmost reefs (Shark Reef, almost continuous with northernmost Osprey Reef, has not been

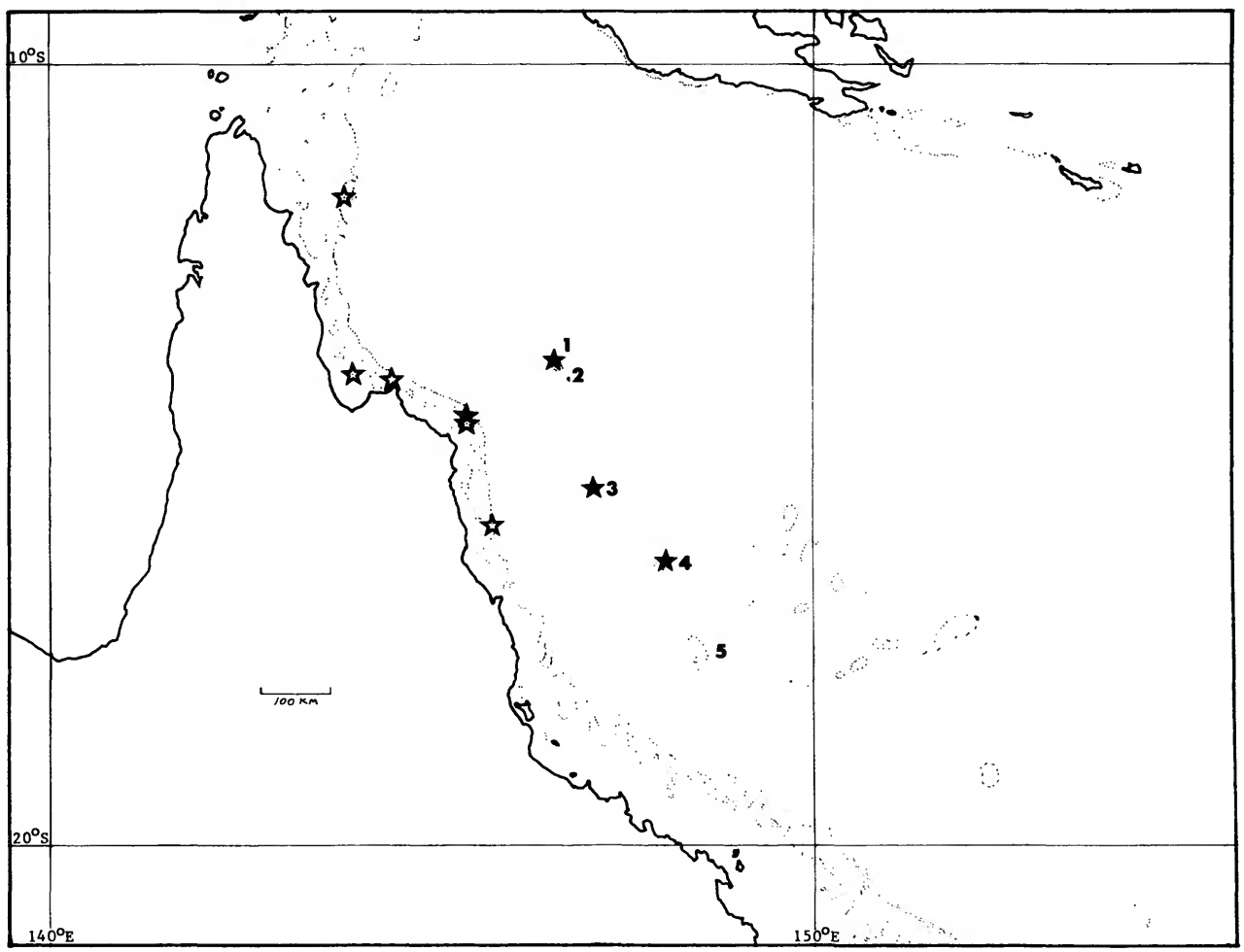


FIGURE 41.—Distribution of *Ecsenius australianus* (open stars) and *E. tigris* (closed stars), the only species of the Opsifrontalis Group recorded in the mapped area (for complete distributions of all species of the Group see Figure 11). All land and shoal areas indicated (based on Kroenke et al., 1983). 1, Osprey Reef; 2, Shark Reef; 3, Bougainville Reef (record based on photograph); 4, Holmes Reef (record based on photograph; note unnamed reef just SW); 5, Flinders Reefs.

TABLE 21.—Frequency distributions for meristic characters in the species of the Opsifrontalis Group.

Species/locality	Segmented dorsal-fin rays					Segmented anal-fin rays					Caudal vertebrae					
	12	13	14	15	$\bar{x}$	14	15	16	17	$\bar{x}$	20	21	22	23	24	$\bar{x}$
Ecsenius alleni		44	7		13.1	1	42	8		15.1		7	43			21.9
Ecsenius australianus		8	47	2	13.9		2	49	6	16.1		3	50	4		22.0
Ecsenius axelrodi	5	64	1		12.9	2	59	7		15.1		12	56	1		21.8
Ecsenius bathi																
Java		5			13.0	2	3			14.6	1	3				20.8
Komodo	1	3	1		13.0	1	4			14.8	1	1	3			21.4
Ecsenius dilemma	5	27			12.8	4	28			14.9	1	26	1			21.0
Ecsenius fijiensis		25	18		13.4		22	21		15.5		3	38	2		22.0
Ecsenius fourmanoiri																
New Caledonia			1	7	14.9				8	17.0				7	1	23.1
Uvea				1					1						1	
Ono-i-Lau			1	7	14.9			3	4	16.6				8		23.0
Ecsenius opsifrontalis	3	138	21		13.1	2	147	13		15.1		16	136	2		21.9
Ecsenius tigris		9	30		13.8		4	33		15.9			38			22.0

TABLE 22.—Frequency distributions for number of dentary incisor teeth in species of the Opsifrontalis Group.

Species/locality	Dentary Incisor Teeth																	
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	$\bar{x}$
Ecsenius alleni							3	3	9	10	8	7	2	-	-	1		44.2
Ecsenius australianus										2	-	5	5	16	10	9	1	48.2
Ecsenius axelrodi				1	-	4	7	10	21	14	2	1						42.7
Ecsenius bathi																		
Bali	1	-	-	1	1	2												38.4
Komodo			1	2	-	-	1	-	1									39.4
Ecsenius dilemma					3	5	3	5	2	1								41.0
Ecsenius fijiensis		1	-	-	-	-	1	1	1	1	3	11	16	12	4	1		46.6
Ecsenius fourmanoiri																		
New Caledonia											1	2	5	1				46.9
Uvea														1				
Ono-i-Lau											1	2	1	1	3			47.4
Ecsenius opsifrontalis																		
Anatahan												1						
Tinian										1	2							44.7
Saipan									2	4	2							44.0
Guam							1	1	1	1	2	1						45.4
Palau									1									
Ulithi										2	-	1						44.7
Kapingamarangi									1	3	5	2	14	9	-	3		46.8
Ponape											1	2	1					46.0
Enewetak									1	-	-	-	-	-	1			46.0
Bikini & Rongelap											1	1	1	1				46.5
Majuro													1					
Kwajalein													1	1	-	1		48.3
Abaiang										1	4	11	4	2				46.1
Rotuma							1	2	-	8	5	5	6	3	1			45.4
Samoa											1	1	2					46.2
Ecsenius tigris								2	4	5	6	4	2	3				44.9

sampled, but it would appear certain that *E. tigris* occurs there). The distance between Shark Reef and Bougainville Reef, the next nearest Coral Sea reef, and one where *E. tigris* occurs (documented in photographs), is approximately 160 km, whereas the closest reefs on the Australian coast, where *E. australianus* exists or can be expected, are only about 140 km from Osprey Reef. If *E. tigris* occurs at the Flinders Reefs (next reefs SSE of Holmes Reef, where *E. tigris* has also been

TABLE 23.—Lateral-line terminus in species of the Opsifrontalis Group.

Species/locality	Terminus of lateral line below dorsal-fin element*					
	9	10	11	12	13	$\bar{x}$
Ecsenius alleni		2	32	5		11.1
Ecsenius australianus		2	29	19		11.3
Ecsenius axelrodi		5	36	25		11.3
Ecsenius bathi		7	2			10.2
Ecsenius dilemma	3	12	5			10.1
Ecsenius fijiensis		1	6	20		11.7
Ecsenius fourmanoiri						
New Caledonia		2	4	2		11.0
Uvea				1		
Ono-i-Lau			3	5		11.6
Ecsenius opsifrontalis			18	65	1	11.8
Ecsenius tigris	1	-	17	9		11.2

*Numbered beginning with anteriormost dorsal-fin element. If terminus is below inter-element space, highest numbered element is recorded.

photographed but not collected), the distance from the nearest reefs on the Great Barrier Reef would only be about 120 km. The distribution of *E. australianus*, however, is not known to occur as far south as the latitude of Flinders Reefs.

The point of the present discussion is that populations of *E. tigris* are isolated from their closest conspecifics by distances greater than those that isolate them from populations of another species in the same species group. Such circumstances seem to indicate limited dispersal ability, and that, together with the fact that the species distributions correspond with geological features, leads me to believe that the distributions are reflective of vicariance events, even though there is inadequate information on which to formulate these events.

Ecsenius alleni, new species

FIGURE 42; PLATE 12: FIGURE 2; TABLES 21–23

Ecsenius nov. sp. Allen and Russell, 1986:95 [Rowley Shoals, Scott Reef].

DESCRIPTION.—Dorsal fin XII,13–14 (usually 13), deeply notched between spinous- and segmented-ray portions. Anal fin II,14–16 (usually 15). Pectoral fin 13. Caudal fin 13. Vertebrae 10 + 21–22 (usually 22). Dentary incisor teeth 41 to 50 (rarely more than 47; includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between vertical from interspace between bases of tenth and eleventhth dorsal-fin spines and vertical at base of twelfth dorsal-fin spine (usually terminating at or anterior to base of eleventh spine). Short cirrus present on posterior rim of anterior nostril, none on anterior rim.

Preserved Color: Head: snout dark; cheeks darkest dorsally with slightly darker spot at about midpostorbital margin giving rise to slender, faintly dusky stripe, which extends posteriorly to lateral-line pores at dorsoposterior margin of opercular area; cheeks ventral to dusky stripe without distinct markings. Body: broad, diffusely dusky stripe at same level as slender postorbital stripe variably present; up to 12 dark bands extending ventrally from dorsal-fin base; anteriormost band usually represented only as dusky spot at bases of first two spines; next 5 bands below spinous dorsal-fin base, usually fading out at about midside (often two offset dusky bands inserted ventrally in pale interspaces between posteriormost two of these 5 bands); next 5 bands extend ventrally from dorsal body contour below segmented-ray portion of dorsal fin, often with spotlike intensification in each band; posteriormost body band often faintly dusky or present only as dark spot continuous with diffuse, dark, posteroventrally extending marking on caudal fin; diffuse, posterodorsally extending marking on caudal fin ventral to just described marking. Pectoral-fin base and axil each with large, dark spot that extends with decreasing intensity onto fin rays basally. Dorsal fin with dusky markings along rays. Anal fin broadly dusky. Pectoral and pelvic fins unremarkable.

Live Color (Plate 12: figure 2): Head dusky brownish dorsal to mid-orbital level, with three fine, bright-white stripes extending posteriorly from postorbital margin; dorsalmost two stripes very short, ventralmost stripe extends posteriorly to posterior opercular margin; cheeks pinkish below ventralmost stripe; eye black with two bright-white stripes passing across surface and continuing around snout. Body stripes blackish, but those on posterior half of body dusky ventral to body midline; dorsal half of body darker, bluish gray anteriorly, faintly dusky pink on posterior two-thirds, row of about 8 squarish bright-white spots on ventral half. Dark spot on fleshy pectoral-fin base indigo blue anteriorly, black posteriorly; spot with narrow, bright-white anterior border. Fins unremarkable.

COMPARISONS.—Among the eight species of the Opsifrontalis Group, *Ecsenius alleni* is most similar to the banded phases of *E. axelrodi* and *E. dilemma* in having an intensely dark banded pattern on the body with occasional spot-like intensifications of pigment within the bands. It also appears to be similar to the banded phase of *E. bathi*, but the bands are much fainter in the latter species. Numerous trenchant dissimilarities in color pattern exist among these species. In particular, *E. alleni* lacks a striped phase, which is present in the other three species, and has a large, dark spot on the pectoral-fin base (and in the axil), which distinguishes *E. alleni* from all other species of *Ecsenius*.

ETYMOLOGY.—Named for my colleague Gerald R. Allen, who collected most of the specimens and recognized that they represented an undescribed species, as well as for many other courtesies extended to me.

DISTRIBUTION.—Known only from Scott Reef and Clerke and Mermaid reefs, Rowley Shoals, each about 300 km off

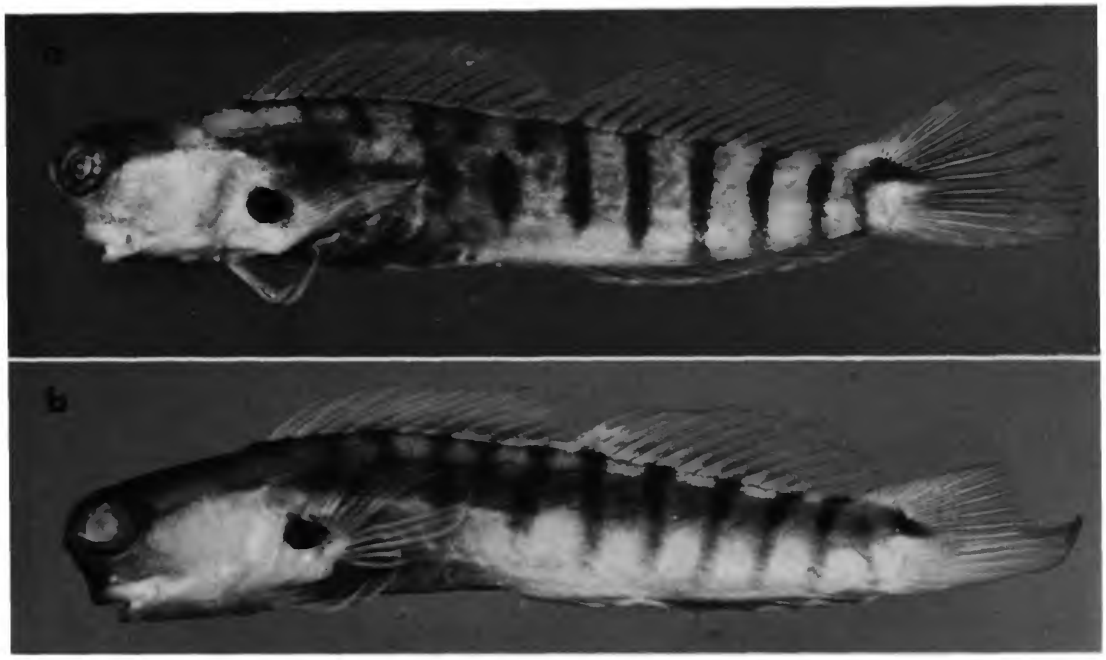


FIGURE 42.—*Ecsenius alleni: a,* WAM P27666-017, holotype, male, 28 mm SL, Mermaid Reef, Rowley Shoals, Western Australia; *b,* AMS I.21318-014, male, 27 mm SL, Scott Reef, Western Australia (photographs by K.A. Bruwelheide).

northwestern Western Australia. According to Allen, *E. alleni* was common in both lagoon and outer reef areas at depths from about 1–35 m.

HOLOTYPE.—WAM P27666-017, male, 28.2 mm SL, Mermaid Reef, central lagoon, 15–18 m, G.R. Allen, 26 July 1982.

PARATYPES.—USNM 279474 (2 specimens: 30, 32 mm SL), collected with the holotype; WAM P27665-001 (4:28–32), WAM P27668-014 (1:26), WAM P27658-013 (1:27), WAM P27663-010 (1:26), WAM P27660-009 (4:24–32), WAM P27662-026 (2:30, 33), WAM P27656-021 (1:32), WAM P28022-048 (19:22–34), all collected at Clerke Reef by G.R. Allen between 21–27 July 1982, at depths from 2 to 35 m; AMS I.21318-014 (1:27), Scott Reef, S. Talbot, 21 September 1979; NTM S.11371-047 (7:18–28), NTM S.11376-033 (3: 23–38), NTM S.11387-017 (1:28), NTM S.11389-031 (3: 22–23), all collected by B. Russell between 7–13 September 1984.

Ecenius australianus, new species

FIGURE 43; PLATE 12: FIGURE 2; TABLES 21–23

Ecsenius (Ecsenius) opsifrontalis.—Springer, 1972:4 [Great Barrier Reef].

DESCRIPTION.—Dorsal fin XII,13–15 (usually 14), deeply notched between spinous and segmented-ray portions. Anal fin II,15–17 (usually 16). Pectoral fin 13 or 14 (rarely 14). Caudal fin 13. Vertebrae 10 + 21–23 (usually 22). Dentary incisor teeth 44–51 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines usually one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 10 and 12. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Darkly pigmented specimens (Figure 43*b*) have dark stripe extending posteriorly from postorbital margin to dorsal opercular region; stripe not clearly continuous with broad, dusky stripe on body, which appears to originate posterior to opercle and extend posteriorly onto caudal fin with slight ventral deflection; stripe increasing in intensity at caudal-fin base; another broad, dusky stripe with indistinct origin posterior to pectoral-fin axil extending onto caudal fin with increase in intensity at caudal-fin base; stripes connected by broad, dusky bands, setting off two rows of pale, oblong areas, each row with 7–9 such areas; bands darkest along dorsal body contour. Some specimens exhibit a scarcely noticeable, fine, dark posterior edging of the opercle. Anal fin with broad, dusky submarginal band; other markings on head, body, and fins not distinctive. Faintly pigmented specimens (Figure 43*a*) exhibit same basic pattern but stripes and bands on body may be almost unrecognizable.

Live Color (Plate 12: figure 2; also Debelius, 1986:92, upper figure, labelled *Ecsenius opsifrontalis*): Dark postorbital head stripe brownish or blackish, bordered by narrow, bright,

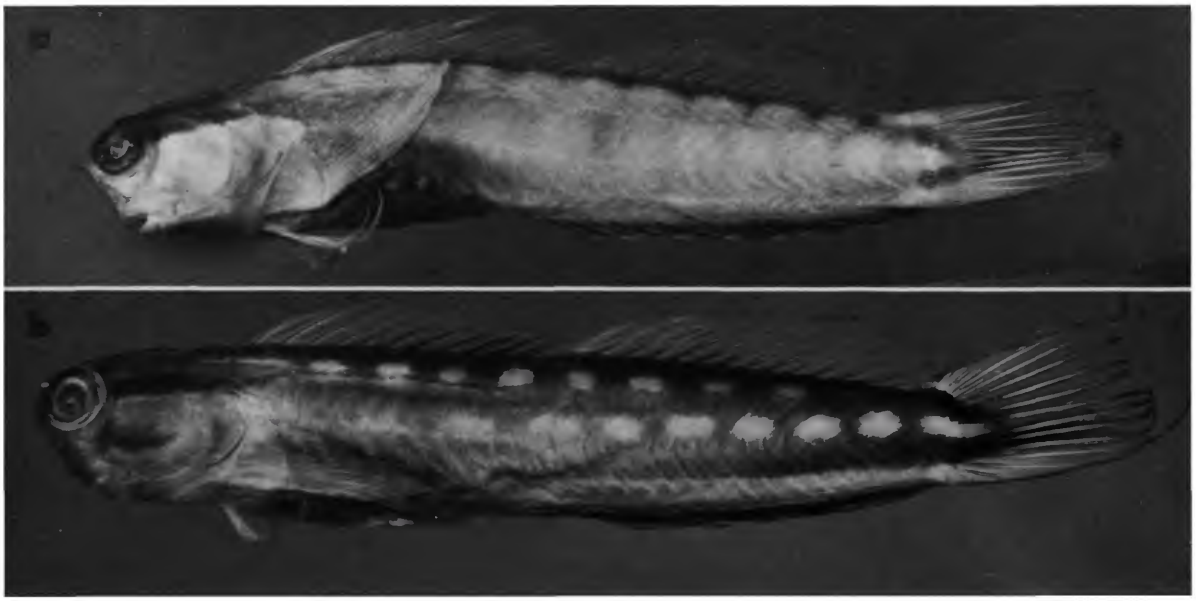


FIGURE 43.—*Ecsenius australianus*, Yonge Reef, Great Barrier Reef: *a*, USNM 278593, male, 32 mm SL; *b*, AMS I.19481-062, holotype, male, 43 mm SL (photographs by K.A. Bruwelheide).

pale stripes, which are continuous through eye dorsal and ventral to pupil; another slender, pale stripe extends short distance along dorsal head profile just above eye. Bands and stripes on body vary, according to specimen, from bright reddish orange to dark brownish pink, becoming dark gray posteriorly in all specimens; two rows of bright-white, oblong areas set off by bands and stripes, dorsal row consisting of about 11 areas and ventral row of about 10; body white below ventral stripe.

COMPARISONS.—*Ecsenius australianus* appears to be most similar (closely related?) to *E. fourmanoiri*. Within the Opsifrontalis Group, these two species have the highest averages for meristic characters. Some preserved specimens of *E. australianus* exhibit a faint dark line along the posterior opercular margin, reminiscent of the intensely dark line of *E. fourmanoiri*, but the line, when present, of *E. australianus* does not extend to the ventral surface of the head as it does in *E. fourmanoiri*. The dark opercular margin is not present in the other species of the Group and I hypothesize that it is a synapomorphy for *E. australianus* and *E. fourmanoiri*. Also, only in these two species are there adults with broad, darkly dusky bands and stripes such as illustrated in Figures 43*b* and 48 (some juveniles of *E. opsifrontalis* duplicate this pattern, Figure 50*d*). In *E. australianus* and *E. fourmanoiri* the intersections of the bands and stripes are never marked with spots or intensifications of pigment. A similar lack of intensified pigment at the intersections is characteristic otherwise only of some populations of *E. opsifrontalis*.

Ecsenius australianus differs from *E. fourmanoiri* in having lower average numbers of segmented dorsal- and anal-fin rays and caudal vertebrae (Table 21). It also differs from *E. fourmanoiri* in lacking a dark stripe on the fleshy pectoral-fin base, in having the dark line along the posterior opercular margin only faintly dusky, the dorsal body stripe indistinctly formed anteriorly in the region above the appressed pectoral fin, and in never having the body markings so intensely dark as may occur in *E. fourmanoiri*. The color-pattern of *E. australianus* is reflected in life by the preponderance of orange markings, as opposed to the blackish markings of *E. fourmanoiri*. Pale, preserved specimens of *E. australianus* are remarkably similar in color pattern to dark preserved specimens of *E. opsifrontalis* (particularly specimens from Abaiang, Kiribati, which have the darkest postorbital stripe of any population within the species). The Kiribati specimens (as is true generally for the species), however, have the postorbital stripe continuous with the dorsal body stripe, which is darker than that of *E. australianus*. Additionally, except for the northern populations, which are well removed from Australia, *E. opsifrontalis* rarely has more than 15 segmented anal-fin rays, whereas *E. australianus* rarely has less than 16.

REMARKS.—If *E. australianus* and *E. fourmanoiri* form a monophyletic group, as I believe, it would be of interest to determine the possible vicariance scenario that resulted in their divergence from a common ancestor. I assume that the common ancestor would have occupied an area that includes all, or portions, of the range of both species. The ancestral

distribution, therefore, would have included eastern Australia and, I believe, probably only New Caledonia. Geologically, the Loyalty Islands and Lau and Tonga ridges are much younger than Australia-New Caledonia, and the presence of *E. fourmanoiri* in Lau-Tonga and the Loyalties is probably more recent than its occurence in New Caledonia. The following discussion of the tectonics of the pertinent region is distilled mostly from Kroenke's (1984) important synthesis.

The oldest rocks in New Caledonia appear to have formed on the tectonically active eastern margin of Australian Gondwana during the Permian or earlier. At that time, the insular core of New Caledonia adjoined what was to become the Norfolk Ridge, which adjoined what was to become the Lord Howe Rise. In the late Cretaceous, 89–75 m.y.a., the New Caledonia-Norfolk Ridge region was rifted from the coast of Australia. Following rifting, seafloor spreading occurred, first opening the New Caledonia Basin and displacing the New Caledonia-Norfolk Ridge region to the northeast. Soon after the New Caledonia Basin began to open the Lord Howe Rise was rifted from Australia and seafloor spreading in the Tasman Basin displaced the rise to the east. There is no evidence that New Caledonia has been linked to the Australian coast subsequent to its rifting (Stevens, 1980:165).

I therefore hypothesize that the common ancestor of the *australianus-fourmanoiri* sister group existed on the pre-rifted coast of Australia about 75 m.y.a. Following rifting, a portion of the ancestral population remained in Australia and a portion accompanied the rifted segment. Divergence of the two portions of the ancestral population began after rifting, and must have been completed before the formation of the Lau-Tonga Ridge in early Miocene, about 21 m.y.a.

It is possible to account for the presence of *E. fourmanoiri* on the present-day Lau (at Ono-i-Lau) and Tonga ridges by invoking the history of Eua, now one of the southern Tonga Islands. The oldest rocks of Eua are of middle Eocene origin, about 47 m.y.a., and are anomalously much older than the rocks of any of the other Tongan islands (volcanism first began on the Lau-Tonga Ridge about 21 m.y.a.). The rocks of Eua are believed to have been sundered from the old New Caldedonia-Norfolk Ridge and displaced eastward by seafloor spreading during formation of the Loyalty and South Fiji basins. The displacement resulted in the incorporation of Eua, first on the Lau-Tonga Ridge and then on the Tonga Ridge.

The crests of today's Lau and Tonga ridges, although relatively close at the latitude of Eua, are separated there by about 400 km, a distance apparently limiting dispersal in the Opsifrontalis Group (see discussion under "Opsifrontalis Group"). These two ridges were one until about 3–5 m.y.a., when the original, Lau-Tonga, ridge began to sunder. I hypothesize, therefore, that *E. fourmanoiri* accompanied the displaced Eua as it travelled first to the ancestral Lau-Tonga Ridge and finally to its present location on the Tonga Ridge, leaving behind a population at Ono-i-Lau on the Lau Ridge. Ultimately divergence of the Lau and Tonga (and New Caledonia-Loyalty) populations can be expected. Slightly lower meristics of the Ono-i-Lau population are evidence that divergence is occurring.

The presence of *E. fourmanoiri* in the Loyalties is most easily explained by dispersal, as the the Loyalties were not formed until the late Miocene, about 10 m.y.a. At their closest, reefs in the Loyalties and New Caledonia are no more than about 50 km distant (probably less during glacial periods), within apparent dispersal distances attained by the related *E. fijiensis* within Fiji and *E. opsifrontalis* at various islands.

I have not searched the literature for corroborating distributions, but I recently noted an article by Ferreira (1986) on the chiton genus *Acanthopleura* (Phylum Mollusca). He gave the distribution of *A. araucariana* (Hedley) as Pines Island [= Ile des Pins, off southern tip of New Caledonia], Lifou Island [Loyalty Islands], and Eua and Tongatapu islands, Tonga. This distribution pattern is remarkably similar to that of *E. fourmanoiri*.

The main problem that arises from the vicariance scenario developed above is that it appears to require that *E. fourmanoiri* has remained essentially unchanged since it evolved some time between 47 and 21 million years ago. Such a condition may border on the unbelievable, but I find the only other alternative explanation, long-distance dispersal, for the distribution of *E. fourmanoiri* to be just as unbelievable, in view of the absence of *E. fourmanoiri* from the Fiji Islands.

ETYMOLOGY.—Named *australianus* in reference to its presumed endemicity in Australia.

DISTRIBUTION.—Known only from the northern portion of the Great Barrier Reef of Australia.

HOLOTYPE.—AMS I.19481-062, male, 43.4 mm SL, Yonge Reef, collected by Australian Museum party, November 1975.

PARATYPES.—AMS I.19481-018, (5:18–36 mm SL), collected with holotype; AMS I.19454-030 (2:31, 33), I.19472-017 (9:17–39), USNM 278593 (9:24–45), all with same data as holotype; AMS I.18740-018 (6:16–36), Lizard Island, collected by Australian Museum party, November 1975; ANSP 114789 (3:26–39), northern Escape Reef, 24.4–27.4 m depth, J.C. Tyler et al., 24 January 1969; AMS I.22574-026 (1:40), AMS I.22582-035 (4:~15–27), AMS 22619-014 (2:19, 29), AMS I.22621-012 (2:22, 30), AMS I.22637-016 (2:17, 35), ROM 40529 (1:29), all Escape Reef, variously collected during October and November 1981 and October 1982, at depths from 3–22 m; AMS I.20775-046 (1:37), 11°36′S, 144°01′E [near Raine Island], 11 February 1979; AMS I.20756-042 (2:22, 27), Raine Island, 11°43′S, 144°03′E, 11 February 1979; AMS I.20779-088 (7:28–39), Tijou Reef, 13°05′S, 143°57′E, 1979; AMS I.20755-038 (1:39), off Cape Melville, 14°56′S, 144°36′E, 9 February 1979.

Ecsenius axelrodi, new species

FIGURE 44; PLATE 10: FIGURES 1–3; TABLES 21–23

DESCRIPTION.—Dorsal fin XII,12–14 (usually 13), deeply notched between spinous and segmented-ray portions. Anal fin II,14–16 (usually 15). Pectoral fin 12 or 13 (usually 13).

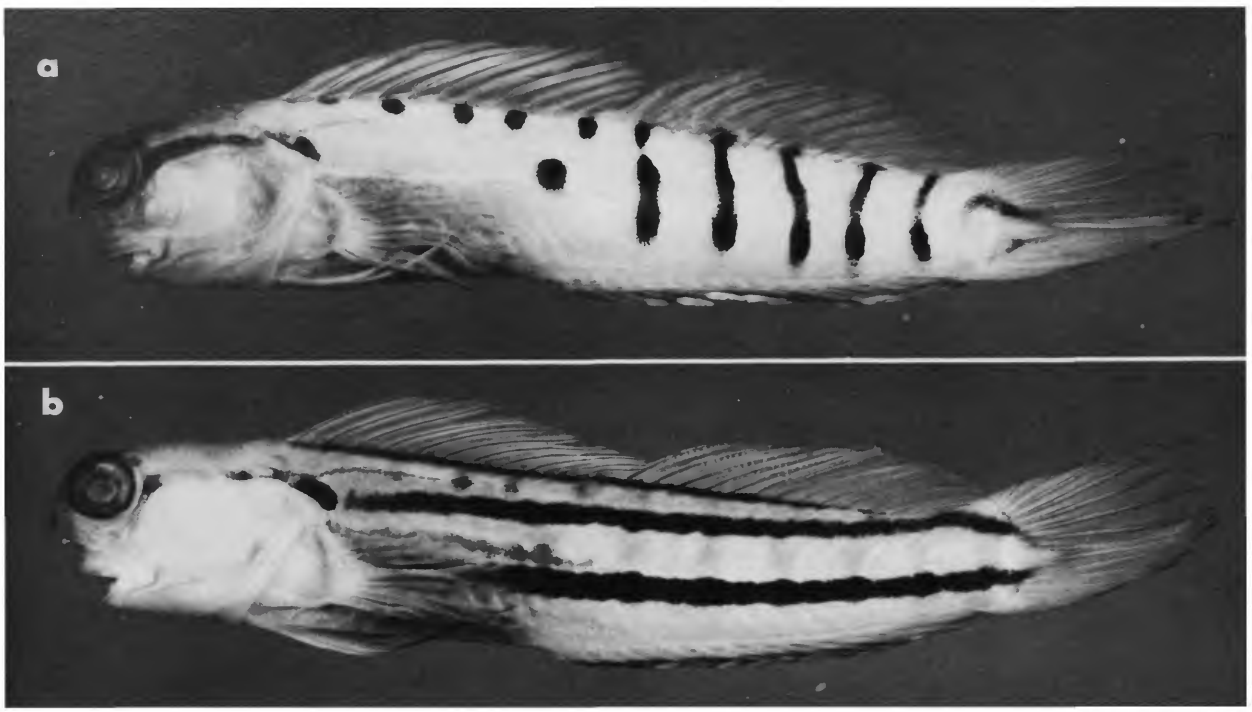


FIGURE 44.—*Ecsenius axelrodi*, USNM 220975, Hermit Islands, Papua New Guinea, males: *a*, banded form, 32 mm SL; *b*, striped form, 31 mm SL (photographs by K.A. Bruwelheide).

Caudal fin 13. Vertebrae 10 + 21–23 (usually 22). Dentary incisor teeth 38–46 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines usually one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between vertical from interspace between dorsal-fin spines 9 and 10 and vertical from spine 12. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Two markedly different color pattern types occur in *E. axelrodi:* banded (Figure 44*a*) and striped (Figure 44*b*). Of the 73 specimens available, 45 are banded and 28 are striped. Both color-pattern types were taken in the same collections and neither pattern is correlated with size or sex.

Banded Pattern: Head dusky dorsally; dusky area margined ventrally by dark postorbital stripe of variable intensity, stripe fading somewhat posteriorly on head and ending at abruptly darker, ventroposteriorly angled spot on body ventral to anterior end of dorsal fin. Cheeks pale ventral to postorbital stripe. Five slender, dark bands on body; bands restricted to region below segmented-ray portion of dorsal fin, sometimes fainter or interrupted at midside of body. Dark spot dorsally on caudal peduncle, extending as stripe onto caudal-fin rays, occasionally extending ventrally, forming faint (sixth) body band; dusky spot on caudal fin ventral to stripe. Dark spot on midside anterior to anteriormost body band; up to 6 dark spots on dorsal body contour below spinous dorsal fin; ventroposteriorly angled dark spot (mentioned above) below anterior end of lateral line, occasionally only faintly indicated, variably continuous with faint or dark stripe extending posteriorly from orbit. Head generally darker dorsal to postorbital stripe. Fleshy pectoral-fin base dusky, frequently with included immaculate, pale band; axil faintly dusky, unremarkable. Pelvic fins immaculate.

Striped Pattern: Head similar to that of banded specimens. Three intensely dark stripes, narrower than pale interspaces, on body; dorsalmost stripe extends along dorsal body contour for length of dorsal-fin base; middle stripe usually originates as dark spot posterior to orbit, decreases greatly in intensity on remainder of head, then markedly increases in intensity as slightly ventroposterior spot-like deflection below anterior end of lateral line, and continues, sometimes with slight interruption, to caudal peduncle, where it becomes ventroposteriorly directed and decreases in intensity as it continues on caudal fin; ventralmost stripe originates in pectoral-fin axil and is dusky from origin to point over posterior portion of abdomen, where stripe becomes intensely dark and extends onto caudal fin, decreasing greatly in intensity at stripe's posterior end. One to 4 dusky or dark spots in pale area between two dorsalmost stripes in region below posterior half of spinous dorsal fin, and up to 6 faint bands or faint to dark spots in pale area between two ventralmost stripes in region below

segmented-ray portion of dorsal fin; faint indications of the 6 bands may also appear in pale area between two dorsalmost stripes. Other markings similar to those appearing in banded pattern.

Live Color: Based on color photographs taken in wild at Rabaul, New Britain.

Banded Pattern: Head blackish dorsal to midorbital level; cheeks pinkish below midorbital level; blackish area with three fine, pale-white stripes extending posteriorly from postorbital margin (hence enclosing a dark stripe); dorsalmost two stripes shortest, extending anteriorly through black dorsal two-thirds of eye and across snout; ventralmost stripe extends anteriorly along suborbital margin and across snout, interrupted posteriorly at posterior opercular margin, beginning again on body and extending posteriorly to midbase of caudal fin, becoming gradually deeper posteriorly; stripe has fine, dusky dorsal and ventral margins and is interrupted by black body bands; two deep, pinkish-orange stripes on body interrupted by black bands; third, slender, orange stripe-like area along dorsal body contour below spinous dorsal fin. Orange stripe on fleshy pectoral-fin base with white dorsal and ventral margins.

Striped Pattern: Head brown suffused with yellow dorsally, anteriorly, and ventroanteriorly, cheeks pinkish; iris of eye dorsally with three black spokes alternating with three bright-yellow spokes, ventrally yellow and white; fine, bright-yellow stripe at 3 o'clock position on postorbital margin, extending short distance posteriorly; fine, bright-yellow stripe margining orbital rim ventrally, extending posteriorly to posterior margin of opercle; dusky-brown postorbital stripe between the two fine, bright-yellow stripes, extending posteriorly and gradually decreasing in intensity to posterior opercular margin; two fine, bright-yellow stripes extending transversely across snout between anterior orbital margins. Black spot with fine, bright-white ventral margin on body in area above pectoral-fin axil; fleshy pectoral-fin base with bright-orange stripe margined ventrally by fine, bright-white stripe; two black stripes on body with dusky bands between; areas dorsal to dorsalmost black stripe and between black stripes, grayish; area white ventral to ventral stripe.

Comparisons.—*E. axelrodi* appears to be most similar and closely related to *E. dilemma* and *E. bathi*, which are unique within the Opsifrontalis Group in having banded and striped forms. *Ecsenius axelrodi* is most readily distinguished from the other two species in having an oblong, dark spot (banded form) or oblong enlargement of the dark stripe in the area below the origin of the lateral line (see comparisons sections under *E. dilemma* and *E. bathi*, for more detailed comparison).

Distribution.—Admiralty Islands, New Britain, and Solomon Islands.

Etymology.—Named in honor of Dr. Herbert R. Axelrod in recognition of his numerous and continuing important contributions in support of ichthyology.

Holotype.—USNM 231432, male, 35.2 mm SL, banded color pattern, Amot Island, Hermit Islands, Bismarck Archipelago, ocean side of reef at dropoff, 3–6 m depth, V.G. Springer and party, 30 October 1978.

Paratypes.—USNM 220975 (54 specimens: 16–44 mm SL, collected with holotype); USNM 220976 (10:17–33), about 200–300 m SSE Pechu Island, Hermit Islands, reef dropoff on ocean side, about 18–21 m, V.G. Springer and party, 5 November 1978; USNM 220977 (4:15–28), same locality as holotype, about 30–36 m, V.G. Springer and party, 31 October 1978. WAM P28182-004 (2:20, 34), submarine base 7 km north of Rabaul, New Britain, G. R. Allen, 12 October 1983. CAS 56556 (2:30–33), outside of St. Mary's Harbor, near Gupuna Village, Santa Ana Island, Solomon Islands, J.E. McCosker, 1 April 1985, 25–30 ft [7.6–9.1 m] and 80–85 ft [24–26 m].

Ecsenius bathi, new species

Figure 45; Plate 11: figures 5, 6; Tables 21–23

Description.—Dorsal fin XI or XII,12–14 (XI, 12, and 14, separately, once each in ten specimens), deeply notched between spinous and segmented-ray portions. Anal fin II,14 or 15. Pectoral fin 13–14 (14 in only one of nine specimens). Caudal fin 13. Vertebrae 10 + 20–22. Dentary incisor teeth 35–43 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from interspace between dorsal-fin spines 9 and 10 and spine 11. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Banded Pattern (6 males, one female): Head darkly dusky dorsal to mid-orbital level, much paler below; dark stripe extends posteriorly across head from mid-postorbital margin, enters body and almost immediately intensifies and forms blotch-like expansion; fine, short, dark line extends posteriorly from postorbital margin just dorsal to mid-postorbital stripe, another dark line at about one o'clock position on postorbital margin, a longer dark line in mid-interorbital area; deep, diffusely pale, area (stripe) between dark mid-postorbital stripe and ventral level of orbit extends across head and enters body; deep, diffusely dusky stripe below diffusely pale stripe extends across head onto fleshy pectoral-fin base; lower lip darkly dusky, remainder of ventral head surface faintly dusky in males, immaculate in female. Body with up to 10 narrow, dusky bands extending ventrally from dorsal body contour: three or four below spinous portion, one between spinous and segmented-ray portions, four or five below segmented-ray portion; bands may have slightly less dusky margins; bands below segmented-ray portion of dorsal fin interrupted by pair of slender, diffusely dusky stripes extending posteriorly from dark blotch-like marking at dorsoanterior origin of body (same stripes margin salmon-orange stripe in life); number of bands below pair of stripes is one less than on dorsal body contour; another pair of faintly dusky stripes (also enclose a salmon-orange stripe in life), similar in appearance to those just described, extend posteriorly from pectoral-fin axil (body bands extend no further ventrally

FIGURE 45.—*Ecsenius bathi*, Bali: *a*, banded form, USNM 277665, holotype, male, 29.6 mm SL, "Liberty Wrack;" *b*, striped form, SMF 17096, female, 30.5 mm SL, Padang Bay (photographs by T.B. Griswold).

than ventralmore of pair); body abruptly pale ventral to ventralmore stripe of pair. Dorsal fin with diffuse sprinkling of melanophores basally and along elements. Anal fin of males more-or-less uniformly dusky anteriorly, becoming immaculate posteriorly; female with slender, dusky, subdistal stripe. Caudal fin with sprinkling of melanophores along rays. Pectoral fins dusky basally. Pelvic fins of males evenly dusky, female immaculate.

Striped Pattern (2 males, 1 female): Differs from banded form in having two nearly black, slender stripes on body, each covering area of pair of dusky stripes as described in banded form; stripes clearly entering caudal fin basally; a third, somewhat inapparent, dark stripe courses along the body contour below the dorsal fin in one of the two specimens; only four or five broad, extremely faint or diffuse bands restricted essentially to pale area between dark stripes; subdistal stripe in the anal fin almost black; dusky stripe on fleshy pectoral-fin base.

Live Color (from color photographs taken in wild; Plate 11: figures 5, 6): Banded form has dark postorbital stripe margined with slender, brilliant-white stripes, which pass through iris and around snout; cheeks below postorbital stripe pale gray, continuing as white on fleshy pectoral-fin base; body stripes and bands dusky gray anteriorly becoming salmon orange posteriorly; spaces between stripes and bands white; dorsal fin immaculate, anal fin broadly salmon orange distally, pale yellow basally. Striped form has bright dusky-yellow head with slender, brilliant-yellow stripes margining dark postorbital stripe; brilliant-yellow stripes pass through eye and around snout; fleshy pectoral-fin base has blackish stripe dorsally, pale area ventrally; body stripes are black, including one along dorsal body contour; area between dorsal two stripes is slate gray, between next two stripes, paler gray, and below ventralmost stripe, even paler gray; fins immaculate except dark margining of elements.

COMPARISONS.—Within the Opsifrontalis Group, *Ecsenius bathi* appears to be most closely related to *E. dilemma* and *E. axelrodi*. These three species share the presumed synapomorphy of having two distinctly different color patterns: banded and striped. Among the three species, the preserved color pattern of *E. bathi* is most similar to that of *E. dilemma*. The striped forms of these two species are indistinguishable in preserved specimens, and the banded form of *E. bathi* appears to be but a greatly faded version of that of *E. dilemma*. Life coloration, so far as known, is quite different, particularly that of the banded forms. The banded form of *E. bathi* exhibits

much more orange in the bands than either of the other two species. On first seeing the color photographs of the banded form of *E. bathi*, and without having preserved specimens available, I thought the photograph was of *E. australianus*. The head of striped forms of *E. bathi* and *E. axelrodi*, aside from the dark postorbital stripe, is yellowish, whereas that of *E. dilemma* is dusky pinkish. The striped forms of all three species have brilliant-yellow stripes margining the dark postorbital stripe. The same brilliant stripes in the banded form of *E. bathi* and *E. axelrodi* are white, whereas they are pale yellow in *E. dilemma*. It is possible that there is variation in these head colors, and forms of all three species may exhibit similar life coloration. (See also "Comparisons" under *E. dilemma* for further comments on these three species.)

DISTRIBUTION.—Known only from Bali and Toko Toko Rock or Island (N of NE corner of Komodo), Indonesia.

ETYMOLOGY.—Named for Dr. Hans Bath, prominent student of blenniid systematics, who brought the first specimens to my attention and permitted me to describe the species.

HOLOTYPE.—USNM 277665, male, 29.6 mm SL, Indonesia, Bali, "Liberty Wrack" [about 15 km NW of E tip of Bali; "wrack" is German for "wreck"], depth 7 m, R. Patzner, April, 1984.

PARATYPES.—SMF 17100, male, 25.1 mm SL; NMW 81944, male, 24.6 mm SL; both from Liberty Wrack. Female, fixed in Bouin's solution, deossified, sectioned, now in two pieces (personal collection of Dr. Robert Patzner, Zoologisches Institut der Universität, Salzburg, Austria) and SMF 17096, female, 30.5 mm SL (striped pattern), both from Bali, Padang Bay [about 25 km SW of E tip of Bali], R. Patzner, 1984. BPBM 31533, male, 30.5 mm SL (striped pattern), and BPBM 31535, three males, 28.2–36.4 mm SL, Toko Toko Rock, N of NE corner of Komodo, rubble and coral bottom, depth 6 m, J.E. Randall, 12 October 1986. CAS 59521, male, 27.7 mm SL (striped pattern), Toko Toko Island, depth 30–40 ft [9.1–12.2 m], J.E. McCosker et al., 15 September 1986.

Ecsenius dilemma, new species

FIGURE 46; PLATE 11: FIGURES 2–4; TABLES 21–23

DESCRIPTION.—Dorsal fin XII,12 or 13 (usually 13), deeply notched between spinous and segmented-ray portions. Anal fin II,14 or 15 (usually 15). Pectoral fin 12–14 (usually 13). Caudal fin 13. Vertebrae 10 + 20–22 (usually 21). Dentary incisor teeth 39–44 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines usually one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spine 9 and interspace between spines 10 and 11. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Two markedly different color-pattern types occur in *E. dilemma*, banded (Figure 46*a, b*) and striped (Figure 46*c*). Of the 32 specimens available, only two small specimens (one female, 23 mm SL, and one sex indeterminate, 18 mm SL) are striped (J.E. Randall has photographed a larger striped specimen in the wild, Plate 11: figure 3); all other specimens are banded and include males and females larger and smaller than the striped specimens, which were taken in the same collections with banded specimens. The banded color pattern is fully developed in the smallest specimen available, 13 mm SL.

Banded Pattern: Eight or nine slender, intensely dark bands on body; bands narrower than pale interspaces; bands present below both spinous and segmented-ray portions of dorsal fin. Bands may be continuous from dorsal to ventral body contours or variously interrupted; dark stripe, sometimes irregularly interrupted, extends along dorsal body contour at dorsal-fin base. Dark spot usually present on side of body below level of dorsal-fin spines 3–4; spot may be isolated or continuous with dark stripe extending posteriorly from postorbital margin; 0–3 dark or dusky spots in pale spaces between anterior body bands, in line with spot below spines 3 and 4, occasionally followed posteriorly by faintly dusky stripe (interrupted by bands) that may extend onto proximal portions of caudal-fin rays. Faintly dusky stripe, occasionally present, extending posteriorly from pectoral-fin axil, usually disappearing before reaching caudal-fin base, occasionally reappearing faintly on proximal portions of caudal-fin rays. Dusky stripe or spot on pectoral-fin base. Head darker on dorsal portion; lower lip dusky ventrally; no other conspicuous pale or dark markings on ventral surface of head or on opercle margin. Slender, dark, submarginal stripe on anal fin; various dusky markings on other fins, except pelvics, which are immaculate.

Head with short stripes extending from post-orbital margin at one and two o'clock positions; main postorbital stripe at 3 o'clock position extends across head and onto body; pale area across snout includes anterior nostril; dark band across snout includes posterior nostrils and anterior and posterior nasal pores, and impinges on iris of eye anteriorly; narrow pale area above band followed dorsally by dark interorbital area; pale streaks between postorbital stripes.

Striped Pattern: Three intensely dark stripes, narrower than pale interspaces, on body: dorsalmost stripe extends along dorsal body contour for most of length of dorsal fin; middle stripe originates at postorbital margin and extends onto proximal portions of caudal-fin rays; slight expansion of middle stripe in area below dorsal-fin spines 3 and 4 (where a dark spot occurs in banded specimens); ventralmost stripe originates in pectoral-fin axil and extends posteriorly onto proximal portions of caudal-fin rays; much less distinct stripe, in line with ventralmost body stripe, on pectoral-fin base. Other head and fin markings as in banded pattern, except snout bands not obvious, perhaps because of small size of specimens.

Live Color (live, from color photographs taken in wild, Plate 11: figures 5, 6): Striped pattern. Head with three parallel neon-yellow pinstripes; dorsalmost pinstripe extends anteriorly along dorsolateral surface of head and across dorsal surface of eye; other two pinstripes margin dark postorbital stripe and extend anteriorly through eye (dorsal and ventral to pupil),

FIGURE 46.—*Ecsenius dilemma*, Philippine Islands: *a*, banded form, USNM 220973, female, 20 mm SL, Cebu; *b*, banded form (note faint stripes), USNM 231319, holotype, male, 31 mm SL, Sombrero Island, Batangas; *c*, striped form (note faint bands), female, 23 mm SL (photographs by K.A. Bruwelheide).

turning medially across snout as they exit from eye and join same stripes from opposite side (animal's ability to rotate eye can cause offset of eye portions of stripes). Head much paler below yellow stripes, variously pinkish to brownish. Body stripes black, bands gray, pale areas encompassed by stripes and bands faint gray to almost white.

Banded Pattern: Pinstripes on head with same disposition as in striped pattern but stripes almost brilliant white with only faint indications of yellowish tinge; head otherwise similar to that of striped specimen. Two orange or brownish-orange stripes on body (in position of black stripes of striped specimens, but stripes broader) interrupted by black bands; pale areas, delimited by stripes and bands, gray.

COMPARISONS.–*Ecsenius dilemma* appears to be most similar to *E. axelrodi* and *E. bathi* (and possibly *E. tigris*). Within the Opsifrontalis Group, these three species are unique in having two distinct color-pattern types: banded and striped. *Ecsenius dilemma* is similar to *E. axelrodi* in that the stripes and bands of the two forms of each species are intensely dark, whereas in *E. bathi* only the striped form has intensely dark markings. Nevertheless, in preservation, the banded form of *E. dilemma* appears to be but an intensely pigmented variety of the banded form of *E. bathi*, and the striped forms of the two species are inseparable (see account of *E. bathi* for additional remarks and differences in life coloration between these two species).

Ecsenius dilemma and *E. axelrodi* differ from each other primarily in aspects of their color patterns. In *E. axelrodi* there is an oblique, dark spot just below the lateral-line origin on the

body, and another dark spot—in the banded phase—on the body midside perpendicular to the anus; neither spot present in *E. dilemma*. In addition, *E. dilemma* has a shorter average lateral-line length (relative to a dorsal-fin element; Table 23) than *E. axelrodi*. The striped pattern is much more common in *E. axelrodi* than in *E. dilemma*.

REMARKS.–I am unable to propose a vicariographic scenario that might explain the evolution and distribution of a clade comprising *E. dilemma, E. axelrodi,* and *E. bathi* because there is inadequate information on which to build a tectonic reconstruction and there are many areas among the distributions of these species from which no member of the Opsifrontalis Group is known (more collecting needed). In the remarks section under *E. fijiensis* I propose a scenario that accounts for the high level of endemism in the Fijian islands and that might have contributed to the evolution of the common ancestor of a *dilemma-axelrodi-bathi* clade on the one hand, and to *E. fijiensis* and *E. opsifrontalis* on the other. That scenario would probably be incongruent with one that would explain the evolution of a *tigris-fijiensis* clade or a *tigris-axelrodi* clade (questionable possibilities suggested in Remarks section under *E. tigris*).

ETYMOLOGY.—The name *dilemma,* here used as a noun in apposition, is from the Latin word meaning "two assumptions," and here alludes to the two strikingly different color pattern types exhibited by the species, as well as to problems in separating its striped form from that of *E. bathi*.

DISTRIBUTION.—Known only from the Philippine Islands.

HOLOTYPE.—USNM 231319, male, 31.3 mm SL, banded color pattern, Sombrero Island, Batangas Province, Philippine Islands, 0–10 m depth, coll. C. J. Ferraris, 23 April 1980.

PARATYPES.—USNM 225053 (10 specimens: 15–30 mm SL), collected with holotype; USNM 225052 (2:18, 19), Sombrero Island, 0–6 m, CJ. Ferraris and E.O. Murdy, 24 April 1980; USNM 228919 (1:16), Sombrero Island, predominantly coral bottom, 0–10 m, C.J. Ferraris, 23 April 1980; AMS I.21918-003 (2:18, 25), Caban Island, Batangas Province, coral, rubble, sand, 11—29 m, D.F. Hoese and E. Murdy, 25 April 1980; AMS I.21918-004 (1:19), Caban Island, 1980; BPBM 26848 (1:29), Caban Island, rubble and sand, 27–30 m, J.E. Randall and M.J. Gawel, 25 May 1981; BPBM 28481 (1:28), Caban Island, bay on east side, 7 m, J.E. Randall, 25 May 1981; AMS I.21908-021 (2:17, 20), Sombrero Island, Batangas Province, coral, 1–34 m, D. Hoese and E. Murdy, 23 April 1980; AMS I.21915-045 (2:17, 28), Sombrero Island, D. Hoese, 24 April 1980; USNM 220973 (6: 14–23), Liloan Point, S tip Cebu Island, 13–19 m, J. Libbey, 29 April 1979; USNM 220974 (3:13–36), NW side Pescador Island, 2 km from Cebu mainland, 18–24 m, J. Libbey, 7 May 1979.

Ecsenius fijiensis, new species

FIGURE 47; PLATE 12: FIGURE 3; TABLES 21–23

Ecsenius opsifrontalis.—McKinney and Springer, 1976:17–19, figs 9*d,e* [in part; Fiji Islands].

DESCRIPTION.—Dorsal fin XII,13 or 14, deeply notched between spinous and segmented-ray portions. Anal fin II,15 or 16. Pectoral fin 13 or 14 (rarely 14). Caudal fin 13. Vertebrae 10 + 21–23 (usually 22). Dentary incisor teeth 36–50 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines usually 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 10 and 12 (usually at 12). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Dark stripe extending posteriorly from postorbital margin, decreasing in intensity as it extends on anterior half of body (intensity did not decrease in one specimen, <25 mm SL); head darker above, paler below, without distinct markings below postorbital stripe. Conspicuous dark markings absent from anterior third of body. Most conspicuous markings on posterior half of body, consisting of 7–8½ vertical pairs of intensely dark spots arranged in two rows; spots usually discrete, occasionally with vertical or horizontal dusky connections, three pairs posterior to vertical through posteriormost segmented dorsal-fin ray, with posteriormost pair clearly extending onto basal portion of caudal fin; spots of dorsal row represent intensifications of postorbital stripe on body; ventral row of spots represent intensifications of dusky stripe originating near pectoral-fin axil (spots are in positions where bands of other species in group cross stripes). Dark saddle-like spots variably present dorsal to dorsal row of spots, impinging on dorsal fin basally, and often connected with dorsal row of spots. Anal fin with broad, dusky, submarginal band; other fin and body markings not distinctive.

Color pattern (based on notes and photographs of freshly collected specimens; Plate 12: figure 3). Ground color pale gray to white ventrally; head and pectoral-fin base orange brown, darker above, paler below. Narrow black stripe extends posteriorly from postorbital margin to vertical from second dorsal-fin spine, where stripe merges with broader, red-orange stripe that continues to vertical from tenth to eleventh spine; stripe then changes to gray and is punctuated by 8 black spots; narrow, pale stripe present along ventral margin of cephalic portion of black stripe. Another red-orange stripe (originating in pectoral-fin axil) changing to gray and punctuated by 8 black spots parallels other stripe; anteriormost black spot of second stripe with much red pigment, and may appear more as reddish spot. Each of the posterior 7 black spots of dorsal stripe connected by a gray bar to a spot in ventral stripe. Black spots variously irridescing bluish. Dorsal-fin base red orange anteriorly; red-orange blotch on body contour below spines 6 to 8, followed by 7 black blotches. Anal fin with broad pinkish-brown submarginal stripe.

COMPARISONS.—The two rows of prominent, essentially discrete, dark spots arranged in vertical pairs, with 3 pairs (as opposed to no more than 2 pairs) on the caudal peduncle posterior to a vertical from the posteriormost segmented dorsal-fin ray, and the essential absence of dark spots on the anterior third of the body are sufficient to distinguish *E.*

fijiensis from all other species in the Opsifrontalis Group.

Superficially, the color pattern of *E. fijiensis* could be confused with that of *E. collettei* (Figure 58; a member of the Bandanus Group). The dorsal row of spots in *E. collettei* begins below the anterior portion of the spinous dorsal fin, whereas this row of spots begins below the posterior portion of the spinous dorsal fin in *E. fijiensis*. There is no postorbital stripe in *E. collettei*, although a dark spot is present on the posterior portion of the head at about the mid-postorbital level. The elongate, curved, dark marks on the ventral surface of the head of some specimens of *E. collettei* are not duplicated in *E. fijiensis*. Finally, there does not appear to be any red-orange pigment on the body of *E. colletei* (Plate 13: figure 6).

REMARKS.—*Ecsenius fijiensis* has been collected in water of depths from 0.5–23 m, but most specimens were collected at depths of 10 m or more.

I have been unable to hypothesize reasonably the sister group of *E. fijiensis*, although on the basis of the intensely dark spots, it would appear that *E. axelrodi*, *E. opsifrontalis*, or *E. tigris* are likely candidates. On the unique basis of having two similar and distinctive color pattern types within each species, however, *E. axelrodi* appears to form a monophyletic group with *E. dilemma* and *E. bathi*. In any event, it is clear that Fiji must have been isolated from other areas of the Melanesian Borderlands (Coleman and Packham, 1976; Kroenke, 1984), which includes the island arcs extending from New Britain to Tonga, in order for an endemic species to have evolved. It is possible to propose a scenario for isolating Fiji, which has a number of endemic fish species.

The following tectonic reconstruction is extracted mostly from Kroenke (1984). (See also remarks section under *E. australianus*.)

During middle Eocene (~45 m.y.a.), the convergence boundary, where island-arc volcanism was occurring, between the India-Australian and Pacific plates included stretches along the coast of New Guinea and along the New Caledonia-Norfolk Ridge. In late Eocene-early Oligocene (~38 m.y.a.) there was an extensive northeastern shift in position of the convergence boundary, with consequent commencement of island-arc volcanism along the new boundary. Volcanic islands formed along the new boundary from late Eocene-early Oligocene to early Miocene (~21 m.y.a.), during which times the various linear island chains ranging from New Britain and New Ireland east to Fiji were formed (includes Solomons and New Hebrides). The formation of the island chains trapped a large area of the Pacific Plate between them and the margin of the India-Australian Plate.

The oldest rocks in Fiji are late Eocene-early Oligocene and occur on Viti Levu. These rocks predate the early Miocene origin of the Lau-Tonga Ridge, which at its time of formation

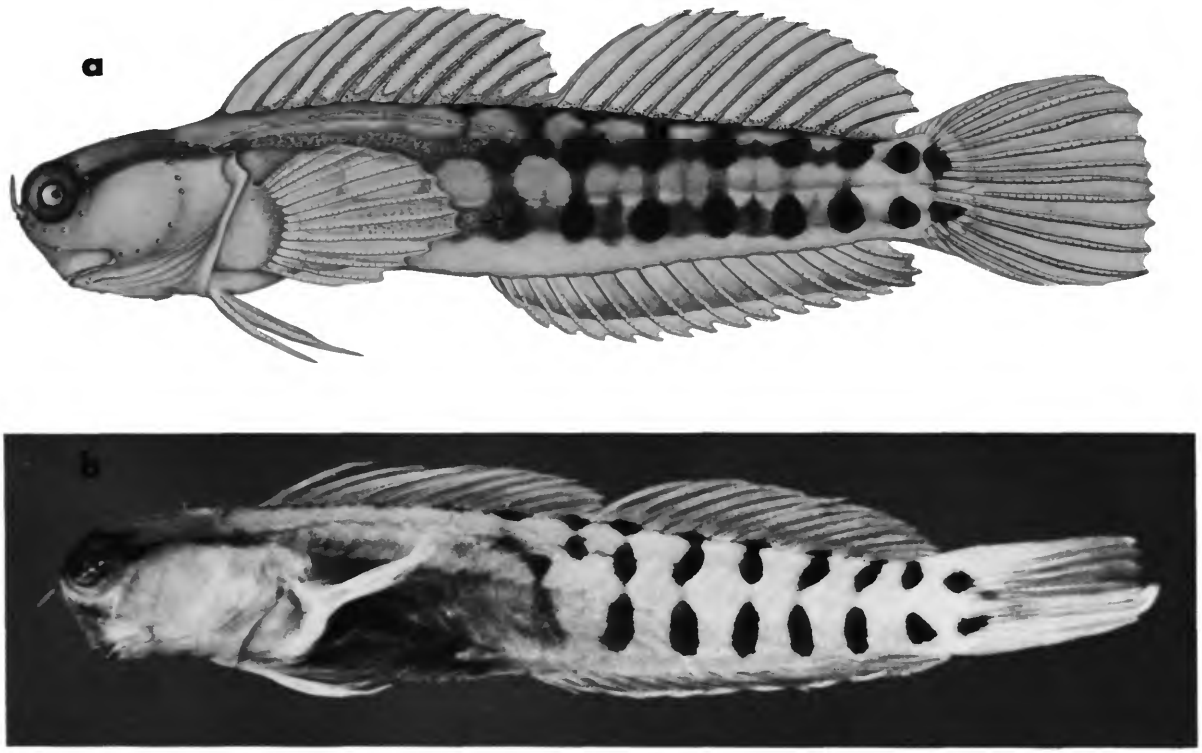


FIGURE 47.—*Ecsenius fijiensis*, Fiji: *a*, USNM 211285, holotype, male, 35 mm SL, leeward of Great Astrolabe Reef, Kadavu (drawn by J.R Schroeder); *b*, ANSP 128013, male, 38 mm SL, Viti Levu (photograph by J.F. McKinney).

was almost perpendicular to, south of, and well removed from Fiji (Viti Levu). Wood (1980) has proposed that in early Miocene the New Hebrides and Fiji may have been part of the Pacific Plate or separated from it by the Vitiaz trench.

In mid-Miocene, about 13.5 m.y.a., the Samoan Islands began forming (Natland and Turner, 1985) on the Pacific Plate just east of Fiji and just north of the northern end of the Lau-Tonga trench. I surmise that stepping-stone islands quite possibly existed between Fiji and Samoa at that time and, based on present ocean-bottom topography, probably existed between Samoa and the Santa Cruz islands (near northern New Hebrides) during the last glaciation, 18,000 years ago (Robinson, 1975:340; Gibbons, 1985a, fig. 3; 1985b:113; see also Wood [1980] for his early Miocene reconstruction). About 10 m.y.a., ocean floor (the former trapped portion of the Pacific Plate) behind the convergence zone established in late Eocene-early Oligocene began subducting the line of island arcs that had formed along the zone in those times. Consequently, the contiguous, linear chains of island arcs from New Britain through the Solomons and the New Hebrides to Fiji that were once well out on the Pacific Plate (at least surrounded by Pacific Plate) moved west and/or south, overriding the northeastern margin of the India-Australian Plate.

About 8–6 m.y.a. the New Hebrides Arc began a clockwise rotation and the Fiji Arc (Viti Levu-Vanua Levu) began a counterclockwise rotation associated with the formation of new ocean bottom in the North Fiji Basin. The effects of these rotations were to: separate Fiji from the New Hebrides and increase the distance between the two; increase the distance between Fiji and the Samoan Islands; eliminate the island stepping stones between the New Hebrides and Fiji and between Fiji and Samoa (not necessarily as a direct result, although the Mamanuca and Yasawa Islands, now on the Fiji platform, appear to have been a segment of the original New Hebrides Arc); approximate the Fiji platform (Viti Levu-Vanua Levu) to the northern end of the Lau-Tonga Ridge; disconnect the western end of the New Hebrides Arc from the eastern end of the Solomon Islands Arc, increasing slightly the distance between their adjacent ends; and to put the New Hebrides on a collision course with New Caledonia and the Loyalty Islands (with which the southern end of the New Hebrides is presently about to collide).

From these circumstances, I think it probable that the distribution of the ancestral species of the Opsifrontalis Group that first colonized Fiji probably also included the island arcs extending from New Britain to Fiji, as well as islands east on the Pacific Plate, Samoa in particular. Fiji's connections with the New Britain-to-New Hebrides portion of the previous continuous group of island arcs was broken about 8–6 m.y.a. when rotation and distancing began. Probably Fiji's linkage with Samoa (via island stepping stones on either side of the Vitiaz Trench) was broken about the same time. These disconnections resulted in biotal isolations, and, as far as the Opsifrontalis Group is concerned, resulted in the formation of at least three species: (1) *E. axelrodi* (or its ancestor) in the closely continuous Admiralties (includes New Britain, and, perhaps by dispersal the Western Admiralties) and Solomon Islands; (2) *E. fijiensis* in Fiji and (by dispersal?) the northern Lau Islands (see remarks section under *E. fourmanoiri* for explanation of why this species is present in the southern Lau Islands); and (3) *E. opsifrontalis* in Samoa, and (by dispersal and/or island movements?) other Pacific Plate islands, if this species is not a complex (see "Remarks" and "Comparisons" sections under *E. opsifrontalis*). The New Hebrides, where no member of the Opsifrontalis Group has been collected, probably is inhabited by *E. axelrodi* or another endemic species.

DISTRIBUTION.—Known only from Fiji, including the Lau Group of islands, but absent from Ono-i-Lau and Rotuma.

ETYMOLOGY.—named *fijiensis* in reference to its presumed endemicity in Fiji.

HOLOTYPE.—USNM 211285, male, 35 mm SL, fore-reef N of Alacrity Passage, leeward Great Astrolabe Reef, Kadavu (= Kandavu or Candavu), rich coral growth, depth 3–6 m, B.A. Carlson, 5 August 1973.

PARATYPES.—USNM 231668 (1 specimen: 34 mm SL), collected with holotype; USNM 210562 (1:32), Alacrity Reef, S of Alacrity Pass and due W of Yabu Island, Great Astrolabe Reef, Kadavu, depth ca. 18 m, B.A. Carlson and M. Gawel, 1 April 1972; USNM 214521 (1:37), W side Rat-tail Passage, Suva Harbour, Viti Levu, depth 0–ca. 8 m, B.A. Carlson, et al., 25 June 1975; AMS I.18354-112 (6:32–38), Bird Island, Bay of Islands, Suva, Viti Levu, B. Russell and B. Goldman, 9 July 1974; ANSP 128013 (4:33–39) E side Mbengga Island, ca. 33 km SW of Suva Harbor, Viti Levu, ca. 24 m, W.F. Smith-Vaniz et al., 14 April 1974; ANSP 128014 (1:31), ca. 100 m S of previous locality, ca. 12–18 m, same date and collectors; USNM 236009 (3:27–32), Viti Levu, ocean side of barrier reef SE side of channel to Suva, V.G. Springer et al., 19 April 1982; USNM 236011 (13:18–36), Dawson Reef, Kadavu, V.G. Springer et al, 12 May 1982; USNM 236010 (11:23–34), Totoya, ocean side of barrier reef, WSW Na'vaka Gap, V.G. Springer et al., 27 April 1982; USNM 236015 (1:29), Yagasa (=Yangasa), ocean side of barrier reef, V.G. Springer et al., 2 May 1982; USNM 279472 (1:32), Vatoa, NW outer reef, 4.5–9.4 m, A. D. Lewis et al., 14 June 1986; ROM 50029 (7: 22–34), outer reef top on E side Great Astrolabe Reef, due E of N tip of Dravuni, 6–10 m, R. Winterbottom et al., 30 March 1983; ROM 50031 (16:19–31), 200 yds S of Usborne Pass, outer reef, 8–12 m, R. Winterbottom et al., 22 March 1983; ROM 50037 (15:19–37), off Yanu-Yanu-Sau Island (just S of Dravuni), 0.5–3 m, R. Winterbottom et al., 30 March 1983.

OTHER MATERIAL.—USNM 236008 (9 specimens), Kadavu; USNM 236012 (2), USNM 236013 (2), 236014 (8), 236972 (40), all Matuku; ROM 50027 (1), NW of Dravuni; ROM 50028 (1), S coast of Vanuakula; ROM 50030 (1), Herald Pass 4.1 km N of Yanu-Yanu-Sau Island; ROM 50032 (1), 50036 (6), reef off Dravuni; ROM 50033 (6), S of Usborne Pass;

ROM 50034 (4), SW of Beagle Pass; ROM 50035 (3), between Usborn and Herald passes; ROM 50038 (5), Herald Pass.

Ecsenius fourmanoiri Springer

FIGURE 48; PLATE 12: FIGURE 4; TABLES 21–23

Ecsenius (Ecsenius) fourmanoiri Springer, 1972:5 [New Caledonia; holotype, BPBM 11416].

DESCRIPTION.—Dorsal fin XII,14 or 15, deeply notched between spinous and segmented-ray portions. Anal fin II,16 or 17. Pectoral fin 12 or 13 (rarely 12, and only unilaterally). Caudal fin 13. Vertebrae 10 + 23 or 24. Dentary incisor teeth 45–49 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines 1 on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from interspace between dorsal-fin spines 10 and 11, and vertical from spine 12. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Dark stripe extending posteriorly from posterior margin of eye, across head and body, to well out on caudal fin, where it decreases in intensity. Slender, dark stripe extending along dorsal body contour for most of dorsal-fin length. Dark stripe on lower portion of body beginning in area covered by appressed pectoral fin, extending posteriorly to well out on caudal fin, where it decreases in intensity and often coalesces with dark stripe just dorsal. About 7–10 dusky bars connect body stripes, resulting in segregation of pale spots on body; bars often offset after crossing middle body stripe. Dark stripe on fleshy pectoral-fin base extending onto basal portion of fin rays. Dark, curving line on posterior margin of opercle, extending ventroanteriorly to ventral surface of head, where it may join contralateral twin. Darkly dusky area anteriorly on ventral surface of lower jaw. Dorsal fin with dusky areas variably present in spinous and segmented-ray portions. Anal fin with broad dusky stripe at midlevel. Pelvic fin faintly dusky. Large males may have the dusky markings almost black on the head, body, and anal and pelvic fins.

Live Color (based on underwater photographs taken at New Caledonia, Solomon Islands, and Tongatabu, Tonga Islands, Plate 12: figure 4): Bright-white pinstripes with at most a tinge of yellow, pass through eye. Head pale pinkish below black postocular stripe. Dark stripes on body blackish brown; cross bands dusky orangish brown; pale spaces enclosed by stripes and bands whitish, as is venter. Dorsal, pectoral, and caudal fins colorless, transparent; dusky streaks apparent on caudal fins of all preserved specimens not apparent on specimens photographed in wild.

GEOGRAPHIC VARIATION.—There is an indication (Table 21) that average number of segmented anal-fin rays varies geographically.

COMPARISONS.—*Ecsenius fourmanoiri* is quite similar in appearance to *E. australianus*. The main differences in color pattern that distinguish the two species are the presence in *E. fourmanoiri* of the dark stripe on the pectoral-fin base, the dark, curving line on the opercular margin, and the replacement of the orangish stripes and bands, particularly anteriorly, with black pigment. In *E. australianus* the opercular line may be faintly dusky in in some specimens and just recognizable in photographs of specimens in the wild. I hypothesize that the dark marginal line of the opercle is a synapomorphy for a *fourmanoiri-australianus* clade. A possible vicariance scenario

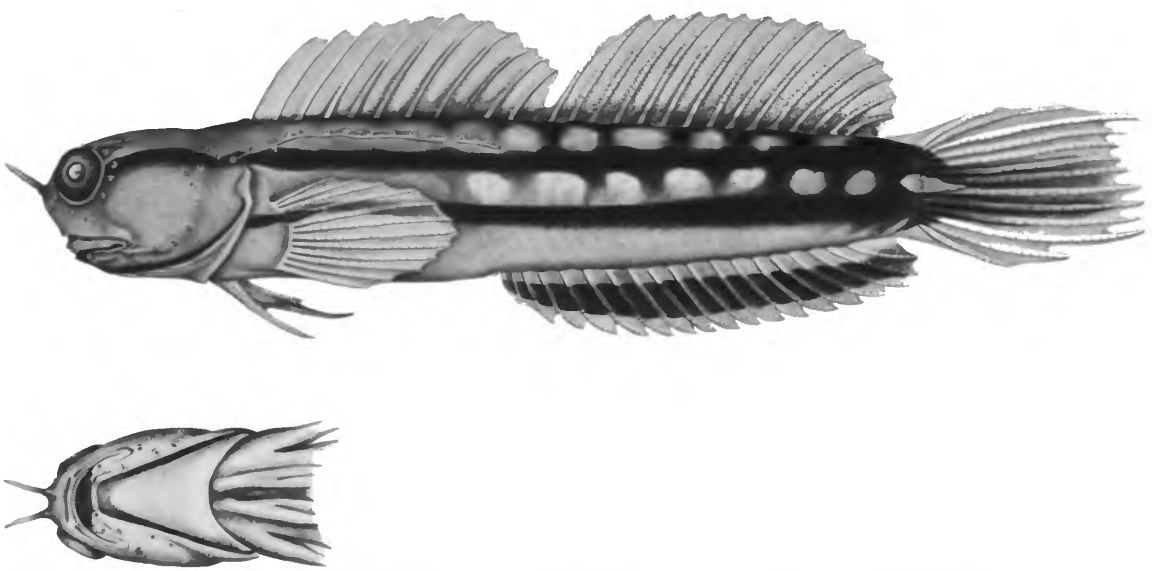


FIGURE 48.—*Ecsenius fourmanoiri*, BPBM 11416, holotype, male, 49 mm SL, off Noumea, New Caledonia (small illustration is underside of head; drawn by J.R. Schroeder).

explaining the distribution of this clade is given in the remarks section under *E. australianus*.

DISTRIBUTION.—*Ecsenius fourmanoiri* was originally described and reported only from New Caledonia, based on four specimens. Since its description, 13 more specimens have become available, extending the range of the species to include Uvea (Loyalty Islands) and Ono-i-Lau (southern Lau Islands Group of Fiji). Additionally, the presence of *E. fourmanoiri* at Tongatapu (Tonga Islands) has been documented in underwater photographs taken by J.E. Randall (Plate 12: figure 4; copies in files of BPBM and USNM), and there is an underwater photograph of the species in the files of T.F.H. Publications, Inc., purportedly taken by Wade Doak in the Solomon Islands. Confirmation of the occurrence of *E. fourmanoiri* in the Solomon Islands is desirable, but I doubt its presence there. *Ecsenius axelrodi* is present in the Solomon Islands (near the southernmost island, as well as further north), and no two species of the Opsifrontalis Group are yet known to occur sympatrically, or mosaically.

MATERIAL (* = not previously reported).—*New Caledonia:* MNHN 1980-250* (4 specimens: 38–40 mm SL), 1971-134 (2:40, 44), BPBM 11416 (holotype: 49), USNM 206456 (1:39). *Loyalty Islands, Uvea:* BPBM 27072 (1:27). *Fiji, Lau Group, Ono-i-Lau:* USNM 236016* (8:33–42).

Ecsenius opsifrontalis Chapman and Schultz

FIGURES 49–51; PLATE 12: FIGURES 5, 6; TABLES 21–23

Ecsenius opsifrontalis Chapman and Schultz, 1952:521 [Rongelap, Marshall Islands; holotype, USNM 142065].—McKinney and Springer, 1976:17 [in part; Ulithi, Guam, Saipan, Tinian, Eniwetok, Majuro, Abaiang].

DESCRIPTION.—Dorsal fin XII,12–14 (13 in 85% of specimens), deeply notched between spinous and segmented-ray portions. Anal fin II,14–16 (15 in 91% of specimens). Pectoral fin 12–14 (usually 13). Caudal fin 13. Vertebrae 10 + 21–23 (22 in 88% of specimens). Dentary incisor teeth 41 to 50 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from eleventh dorsal-fin spine and first segmented ray (rarely posterior to twelfth dorsal-fin spine). Short cirrus present on posterior rim of anterior nostril, none on anterior rim.

Preserved Color: Dusky stripe extending along dorsal body contour at base of dorsal fin. Another, often very faint, dusky stripe extending posteriorly from posterior margin of orbit across opercle, onto body, where, depending on population (see remarks section), stripe either broadens and continues posteriorly, undiminished in intensity, onto caudal fin, or becomes very faint or absent anteriorly on body, but persists posteriorly and continues onto caudal fin, often increasing in intensity. Faint, third stripe originating in area covered by appressed pectoral fin and extending posteriorly for variable distance, often increasing in intensity and passing onto caudal fin. Up to about 10 faintly dusky bars crossing ventral two body stripes; bars often offset after crossing more dorsal of the two stripes. Pigment at intersections of bars and stripes, on posterior half of body, often intensified as spots (see remarks section). Dorsal, pectoral, and pelvic fins predominantly unmarked. Anal fin with faintly to darkly dusky subdistal stripe. Caudal fin dusky where body stripes extend on fin; stripes usually converge posteriorly.

Live Color (based on color photographs taken in the wild at Enewetak and Kwajalein, Marshall Islands; Plate 12: figure 5): Top of head above horizontal midorbital level dark

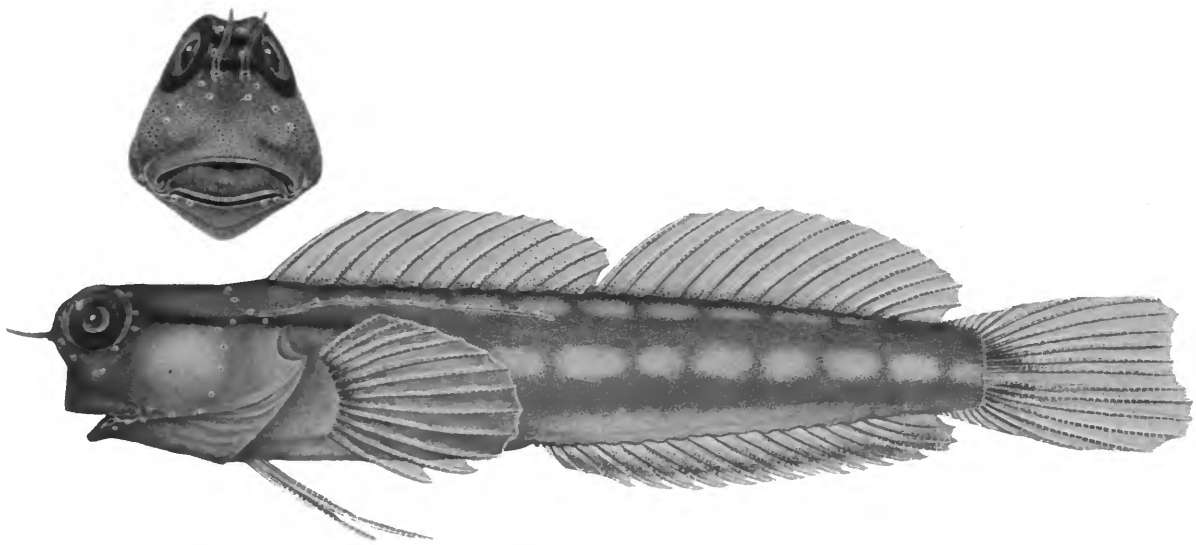


FIGURE 49.—*Ecsenius opsifrontalis*, CAS 24453, male, 32 mm SL, Kapingamarangi Atoll (small illustration shows anterior view of head; drawn by M.H. Lester).

orangish-brown with fine white stripe extending posteriorly from one o'clock position on postorbital margin to dorsal-fin origin; two other fine, bright-white stripes dorsally and ventrally bordering deeper, dusky stripe extending posteriorly from midpostorbital margin; head below postorbital stripes pale pink. Iris of eye divided sharply into dark-brown dorsal and bright-white ventral halves; dark portion punctuated with pale spots. Bands and stripes on body pinkish orange anteriorly grading to grayish orange posteriorly, with blackish spots at posteriormost three ventral crossings of bars and stripes; stripes and bands enclose pale-pinkish rectangular areas; body bright white below ventralmost pink-orange stripe. Fins clear with dusky markings except anal fin with deep, subdistal pinkish-orange stripe. A freshly dead specimen from Ulithi, Marianas, was similarly pigmented to those from the Marshall Islands, whereas fresh specimens from Ponape (Eastern Carolines) and Rotuma (Plate 12: figure 6) had the bars and stripes orangish throughout and either lacked the blackish spots posteriorly or had them only faintly and diffusely indicated.

COMPARISONS.—*Ecsenius opsifrontalis* can be distinguished from *E. alleni, E. dilemma, E. fijiensis, E. axelrodi,* and, in part, *E. bathi* in lacking a color-pattern form that bears conspicuous intensely black stripes and/or bands or spots, and from *E. axelrodi, E. dilemma,* and *E. bathi* in having essentially only one color-pattern type in a population. *Ecsenius opsifrontalis* differs from *E. fourmanoiri,* which may exhibit a pattern of conspicuous dark stripes and bars, in lacking a dark stripe on the pectoral-fin base and a dark, curving line bordering the posterior opercular margin (faintly present also in some specimens of *E. australianus*). Various meristic characters are also useful in distinguishing *E. opsifrontalis* from the other species of its group (Table 21).

The main feature of the color pattern that unites the various populations of *E. opsifrontalis,* and distinguishes them from *E. australianus,* which exhibits a color pattern that closely resembles that of some populations of *E. opsifrontalis,* is either the absence of a conspicuous, dark postorbital stripe (the stripe may be faint or absent) or, if a dark stripe is present, it continues with little or no decrease in darkness as it extends onto the body (compare Figure 43 with Figures 50 and 51). The postorbital stripe of *E. australianus* is conspicuously dark, but loses its integrity as it passes onto the body. Among the populations of *E. opsifrontalis,* the postorbital stripe is best developed in the specimens from Abaiang, Kiribati.

Of all the species of the Opsifrontalis Group, *E. opsifrontalis* has the most extensive distribution and greatest amount of geographic variation in color pattern. Within its distribution, there are numerous gaps from which no specimens are available and from which specimens might exhibit patterns intermediate to those I describe here—intermediates that I predict exist. Based on *preserved* material, the patterns I have noted are as outlined below.

Pattern 1: Rotuma and Samoa (Figure 50): with a very faint, dusky postorbital stripe or, usually, none at all, and when faint, not clearly continuous on the body; at most only faint, almost inconspicuous intensifications of pigment at intersections of bars and stripes on body posteriorly.

Pattern 2: Specimens from all the other localities usually have a noticeable dusky to dark postorbital stripe.

Pattern 2A: Ponape, Ant Atoll, (Figure 51*d*): with postorbital stripe light dusky, not or only faintly continuing on body; no conspicuous intensifications of pigment at intersections of bars and stripes on body posteriorly. This form is somewhat intermediate between pattern types 1, 2B, and C.

Pattern 2B: Kapingamarangi and Abaiang, Kiribati (Figures 49, 51*a,b*): with dark postorbital stripe, which continues on body with little decrease in intensity for most of body length; no conspicuous intensifications of pigment at intersections of bars and stripes on body posteriorly. Available specimens from Kapingamarangi are in poor condition, and I uncertain that all of them have dark postorbital stripes.

Pattern 2C: Mariana, Ulithi, Palau, and Marshall islands (Figures 51*c,e*): with dusky postorbital stripe continuing on body for variable distance; conspicuous intensifications of pigment present at three or four of the intersections between bars and ventral stripe posteriorly (often at intersections with dorsal stripe also).

The color pattern of paler specimens of *E. australianus,* which is usually characterized by having a dark postorbital stripe that greatly decreases in intensity, or loses its integrity, as it passes onto the body, and by lacking intensifications of pigment at the intersections of the bars and stripes, is difficult to distinguish from that of some Kiribati specimens of *E. opsifrontalis.* Many specimens of *E. australianus* are readily recognizable as distinct from all *E. opsifrontalis* specimens in having the bands and stripes on the body broader and generally more darkly pigmented. Some juveniles (under 25 mm SL, Figure 50*e*) of *E. opsifrontalis* adumbrate the *E. australianus* color pattern; however, the juveniles lack a dark postorbital stripe. Because the two species have strong modal differences in the number of segmented dorsal- and anal-fin rays, and because their distributions are separated by an area in which several other species of the Opsifrontalis Group occur, I believe that recognition of *E. australianus* and *E. opsifrontalis* as distinct taxa is warranted.

The possible relationships of *E. opsifrontalis* are discussed under the remarks section of *E. fijiensis.*

MATERIAL (* = new material).—*Mariana Islands:* Anatahan, USNM 289110* (2 specimens: 18–28 mm SL); Guam, UG 1542 (1:28), 1746 (1:27), USNM 203742 (1:26) 289109* (5:23–25); Saipan, UG 4892 (7:19–32), 5097 (3:27–36); Tinian, UG 5416 (16:16–30). *Palau Islands:* BPBM 20972* (1:31). *Marshall Islands:* Rongelap, USNM 142065 (holotype: 30); Bikini USNM 202548 (1:32), 142066 (paratype: 26), 152978 (1:35); Enewetak, BPBM 12896 (1:23), 17958 (1:30); Majuro, BPBM 17740 (1:25); Kwajalein, BPBM 19973* (3:25–38). *Caroline Islands:* Kapingamarangi, CAS 24458 (23:16–32), 24453 (5:18–34), 24448 (3:19–29), 24451 (6:22–36); Ant Atoll, USNM 223285* (3:19–27); Ponape, 223035* (1:26), 223317* (1:20); Ulithi, BPBM 11487 (3:23–25).

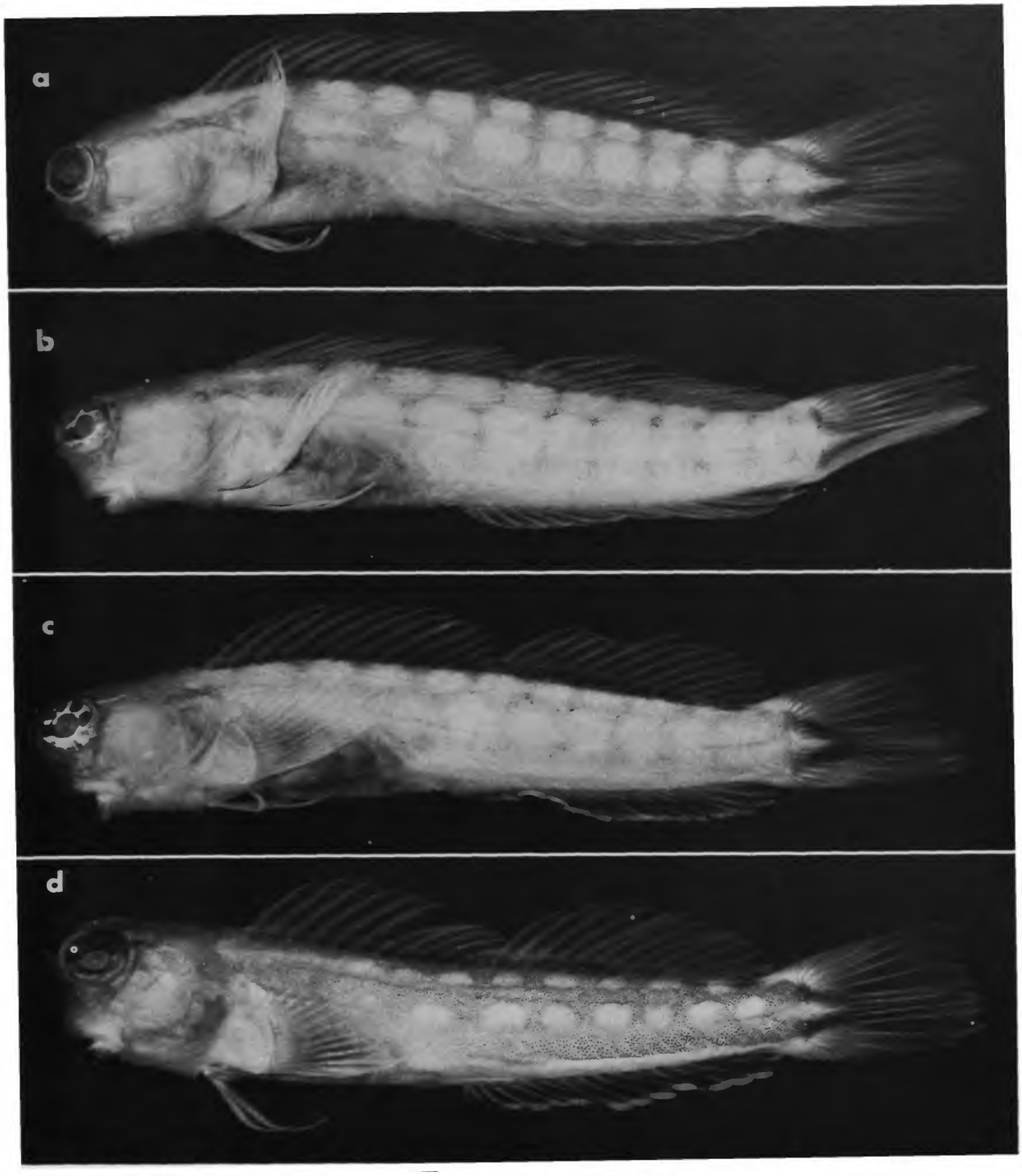
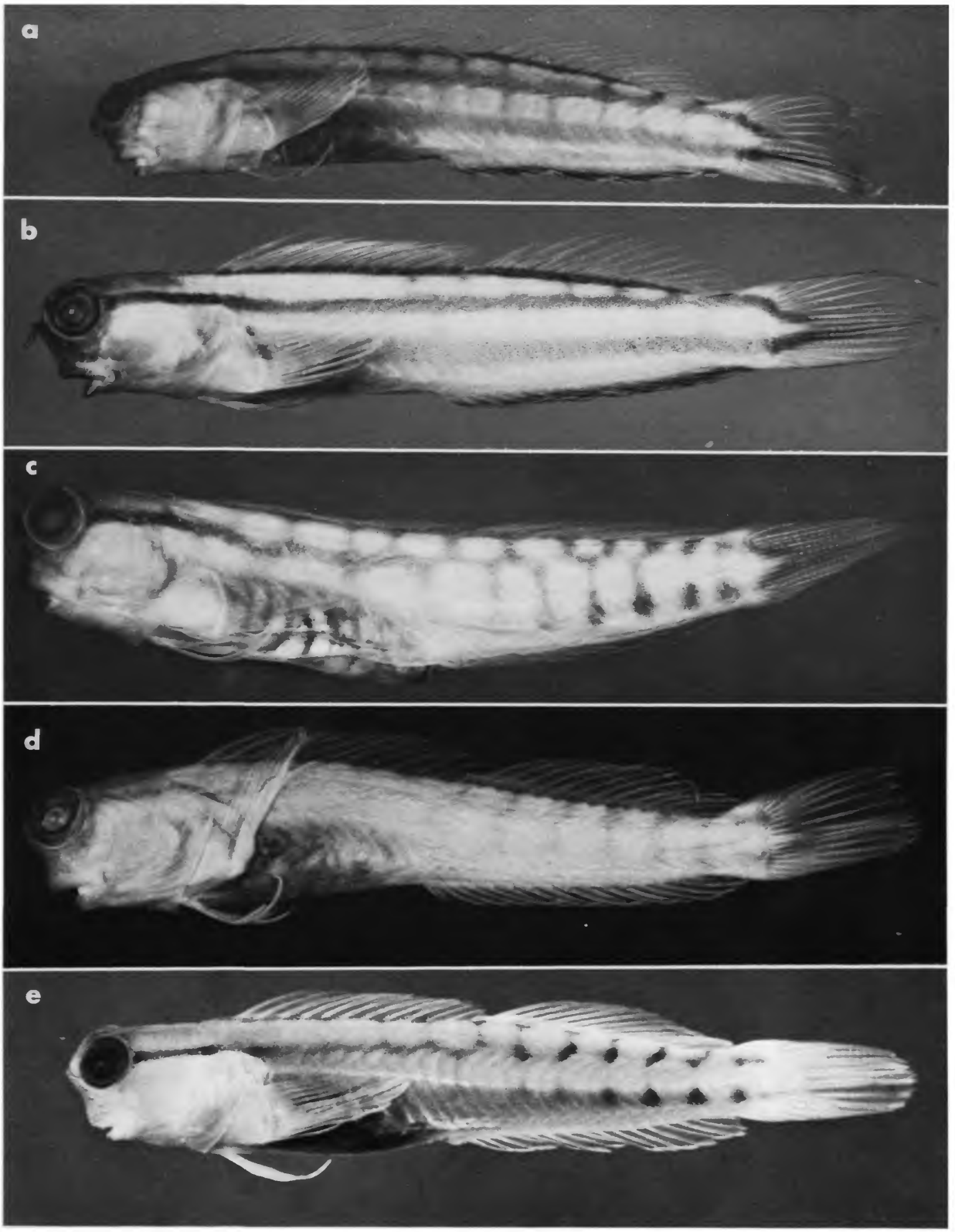


FIGURE 50.—*Ecsenius opsifrontalis*, Rotuma, males: *a,b*, USNM 278596, 37 and 33 mm SL; *c,d*, USNM 278595, 33 and 24 mm SL (photographs by T.B. Griswold).

FIGURE 51 (right).—*Ecsenius opsifrontalis: a,b*, AMS I.18051-24, males, 36 and 32 mm SL, Abaiang, Gilbert Islands (Kiribati); *c*, BPBM 17958, female, 30 mm SL, Enewetak, Marshall Islands; *d*, USNM 223285, male, 27 mm SL, Ant Atoll, Eastern Caroline Islands; *e*, UG 1746, female, 27 mm SL, Guam (photographs *a–c* by K.A. Bruwelheide; *d* by T.B. Griswold; e by J.F. McKinney).


a
b
c
d
e

Kiribati (= Gilbert Islands): Abaiang, AMS I.18051-024 (16:28–40), I.18044-004 (16:18–39). Rotuma: USNM 278595* (20:17–36), 278596* (10:28–37), 278597* (5:18–38), 278598* (2:18–32). *Samoa:* Tutuila, USNM 236063* (2:28–29), 220998* (2:22–30).

Ecsenius tigris, new species

FIGURE 52; PLATE 11: FIGURE 1; TABLES 21–23

DESCRIPTION.—Dorsal fin XII,13 or 14 (14 in 77% of specimens), deeply notched between spinous and segmented-ray portions. Anal fin II,15 or 16 (16 in 89% of specimens). Pectoral fin 12–14 (usually 13). Caudal fin 13. Vertebrae 10 + 22. Dentary incisor teeth 42–48 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior canines one on each side. Lateral line without vertical pairs of pores, terminating posteriorly at point between vertical from interspace between dorsal-fin spines 10 and 11 and vertical from spine 12. Short cirrus present on posterior rim of anterior nostril, none on anterior rim.

Preserved Color: Faintly to darkly dusky stripe (sometimes originating as dark spot) extending posteriorly from pore at about mid-postorbital margin to about origin of lateral line; dusky spot on postorbital margin sometimes present at pore just dorsal to origin of dusky stripe; two darkly dusky bars extend across anterior interorbital area; dorsal surface of sclera blackish; ventral surface of ventral lip darkly dusky. Body with 10 or 11 dark marks along dorsal body contour: anteriormost, which may be absent, spot-like, at posterior base of first dorsal-fin spine; next three spot-like, at bases of third and fifth spines and between bases of sixth and seventh spines; next six usually bar-like, between bases of ninth and tenth spines, at base of twelfth spine, between bases of second and third segmented rays, fifth and sixth rays, eighth and ninth rays, and eleventh and twelfth rays; dark spot near dorsal body contour posterior to last dorsal-fin ray; dark spot, in line with previous spot, just anterior to caudal-fin base, giving rise to dusky, ventroposterior extension on caudal fin; up to 7 small, pale-margined, faintly dusky spots in interspaces between dark marks on dorsal body contour (none apparent in most specimens); 3 or 4 dark spots on dorsal third of body below spinous dorsal fin, posteriormost spot occasionally coalescing with dark spot on dorsal body contour; deep, faintly dusky stripe extending body length, embodying dark marks on dorsal half of body; 7 or 8 dark spots on ventral third of body; anteriormost spot, when 8 are present, faintest, anterior to vertical from anus; next spot, occasionally with dorsal extension, below vertical from eleventh dorsal-fin spine; other spots, except posteriormost, below band-like spots on dorsal body contour; posteriormost spot slightly anterior to caudal-fin base, giving rise to dusky dorso-posterior extension on caudal fin; deep, faintly dusky stripe extending body length, embodying dark spots on ventral third of body; body immaculate to faintly dusky below stripe; up to 9 small, elongate, pale-margined, dusky spots along midline of body in interspaces between dark marks (none apparent in most specimens); fleshy pectoral-fin base slightly darker dorsally than ventrally.

Slender, dusky stripe extending basally along spinous dorsal fin and anteriorly along segmented-ray portion; dusky extensions from stripe extend along spines; distal margin of segmented-ray portion dusky. Anal fin with deep, darkly dusky subdistal stripe. Pectoral-fin rays lined with melanophores. Pelvic fins immaculate. Caudal-fin rays variably lined with melanophores; dusky stripe-like extensions, originating from dark body spots, meeting on fin, enclosing pale area basally.

Live Color (based on photographs taken in the wild at Osprey, Bougainville, and Holmes reefs): Iris and pupil black with fine, bright-white or pale-yellow stripes extending dorsal and ventral to pupil; three small, bright-white or pale-yellow dash-like spots on dorsal surface of eye; short stripe-like marks on head in line with and same color as eye stripes (marks border dark postorbital stripe dorsally and ventrally); fine, bright-white or pale-yellow stripe between eyes anteriorly; bright-white or pale-yellow spot dorsal to latter stripe; head dusky yellow to plain brown dorsal to midorbital level; cheeks pink. Dusky stripes on body pinkish-orange brown to brown; row of small, bright-white spots in interspaces between dorsal dark marks; another row of rectangular or dash-like bright-white spots along body midline. Fins untinted except for brownish orange stripe in anal fin.

COMPARISONS.—In preservation, if not in life, *Ecsenius tigris* appears to be most similar in color pattern to *E. fijiensis* and the banded form of *E. axelrodi*. *Ecsenius tigris* differs from *E. fijiensis* in having 5 or 6 dark spots (versus less than 3) along the dorsal body contour below the spinous dorsal-fin, in having a row of 4 (versus less than 3) dark spots on the dorsal third of the body below the previous row, and in having but 2 vertical pairs of dark spots on the caudal peduncle (versus 3 pairs), with at most only the dorsal member of the posteriormost pair noticeably encroaching on the caudal fin (versus both members clearly present on the caudal fin).

Ecsenius tigris differs most obviously from the banded form of *E. axelrodi* in having 4, approximately equally spaced dark spots anteriorly on the body that are in line and posterior to the dark postorbital head stripe, whereas the banded form of *E. axelrodi* has only 2 widely separated spots in this area, and the anterior spot is invariably at the posterior margin of the opercle, slightly anterior to the position of the anteriormost spot of *E. tigris*. *Ecsenius tigris* further differs from the banded form of *E. axelrodi* in having two vertical pairs of dark spots on the caudal peduncle, whereas *E. axelrodi* has but one dark band and indications of a pair of short, dark stripes that extend onto the caudal fin.

Similar to *E. fijiensis*, but not to *E. axelrodi*, *E. tigris* lacks a dark-striped color-pattern form, and the members of a vertical pair of body spots are either completely separate or, when linked, clearly recognizable as separate. In *E. axelrodi*

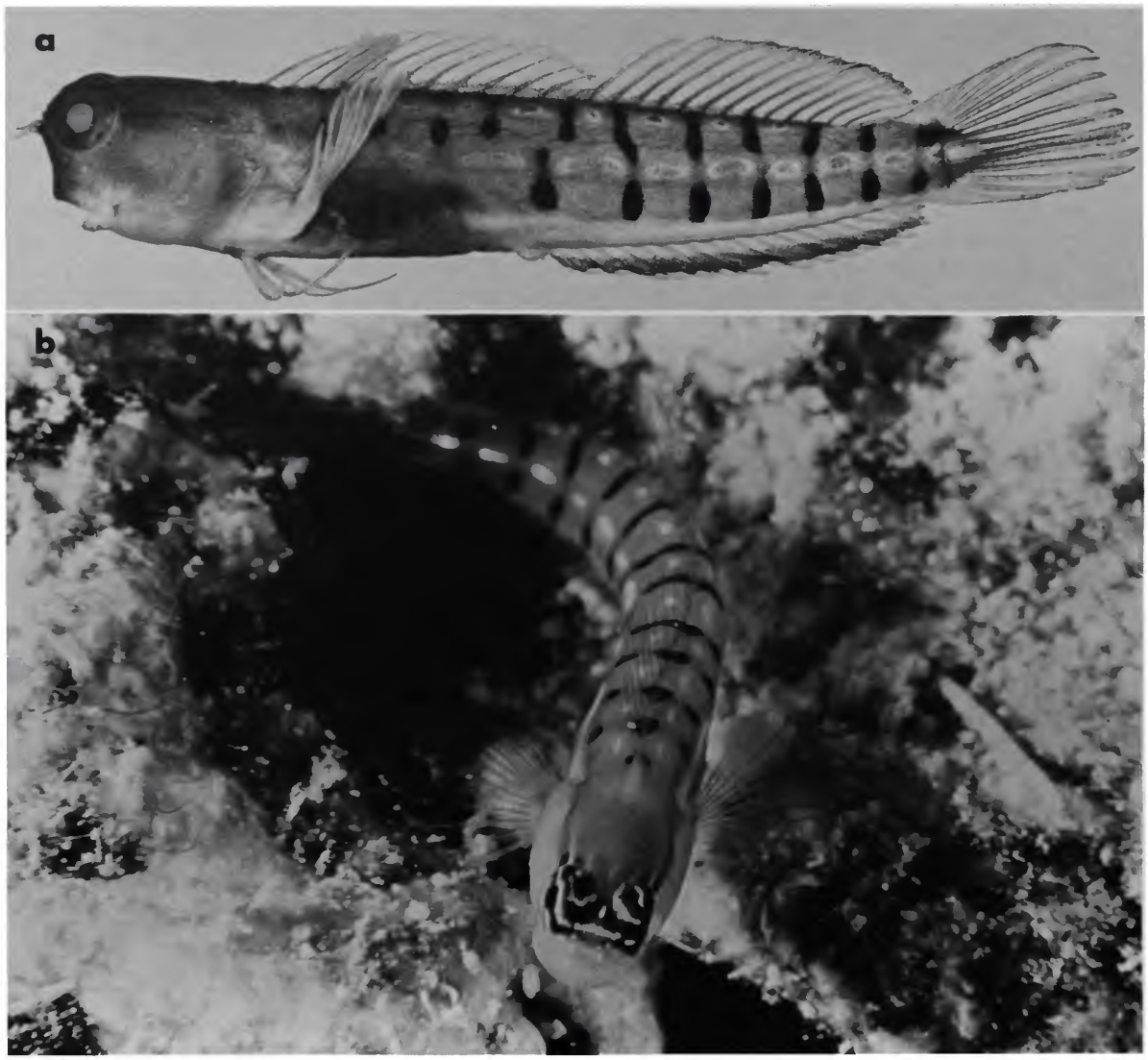


FIGURE 52.—*Ecsenius tigris*, Osprey Reef, Coral Sea: *a*, holotype, female, 28.9 mm SL; b, from a color photograph taken by J.E Randall (photographs by T.B. Griswold).

individual members of the vertical pairs of dark spots are scarcely, if at all, distinguishable in the dark body bands.

Information on live coloration is unavailable for *E. fijiensis*, and available information on freshly dead specimens is inadequate for comparisons. In live banded forms of *E. axelrodi*, the body stripes appear to be more orange than in *E. tigris*. Although *E. tigris* is most similar to *E. fijiensis* and *E. axelrodi* in overall color pattern, I am uncertain of its phylogentic relationships within the Opsifrontalis Group. I believe that the presence of two distinct color pattern types is a synapomorphy of a clade comprising *E. axelrodi*, *E. bathi*, and *E. dilemma*. This might suggest that *E. tigris* is the sister group of *E. fijiensis*, but, certainly, there are other possibilities.

HOLOTYPE.—BPBM 31034, female, 28.9 mm SL, entrance to lagoon, Osprey Reef, Coral Sea, reef in 5 m, J.E. Randall, 25 January 1987.

PARATYPES (all Osprey Reef).—BPBM 31035 (1 specimen: 19.7 mm SL) and USNM 285461 (2:21.1 and 28.4), collected with the holotype; AMS I.25110-021 (17:15.6–35.7), W edge reef flat, 8 m, 6 November 1984; AMS I.25112-025 (15:15.2–34.4), W edge 0.75 km N Osprey reef, 1 m, 8 November 1984; AMS I.25113-020 (3:14.6–30.0), West Pass inside reef, 8 November 1984, all Australian Museum Sunbird Party.

Isos Group

This group consists of three species, *E. isos*, *E. lubbocki*, and *E. trilineatus*, which share several features of a complex color pattern that are probably synapomorphic. One unique feature is the presence of two stripe-like markings on the fleshy pectoral-fin base. In *E. trilineatus* the stripes are distinct and dark, the upper positioned near the level of the interspace between the uppermost two pectoral-fin rays; the lower usually positioned at about the interspace between the sixth and seventh from dorsalmost rays. The upper stripe often bends ventrally anteriorly (bend frequently hidden by opercle); occasionally the anterior end of the lower stripe also bends ventrally. In the other two species these two stripes are usually represented by scarcely noticeable, diffuse, dusky stripes that occupy the same positions as in *E. trilineatus*.

Ecsenius trilineatus has a conspicuous ventroanteriorly curving dark line on the opercle well anterior to the posterior margin of the opercle. The line usually reaches dorsally to about the dorsal level of the opercle and ventrally extends to the ventral surface of the head, or is represented there by a disconnected dark spot. In *E. lubbocki* the line is variably well defined or diffuse. In *E. isos* the line appears to be absent, but is represented by a series of diffuse, dusky spots. Based on its position, the dark opercular line of the Isos Group is most similar to that of the Yaeyamaensis Group species (see footnote in discussion under the account of the Yaeyamensis Group).

Ecsenius trilineatus has three dark, well-defined stripes on the body, the dorsalmost extends along the dorsal body contour to the end of the dorsal fin and is the least noticeable. The two more ventral stripes break up posteriorly into a series of dashes and dots, with faint indications of dusky extensions onto the caudal fin from the vertical pair of spots at the caudal-fin base. *Ecsenius isos* exhibits diffuse dusky markings anteriorly in the position of the three stripes of *E. trilineatus*, but posteriorly the two more ventral stripes are represented by dark spots, the posteriormost vertical pair of which also continue as dusky extensions onto the caudal fin. In *E. lubbocki* the stripes are diffuse, the two more ventral stripes are relatively deep and continue very faintly onto the caudal fin.

There is a dark spot on the axillary (internal) surface of the fleshy pectoral-fin base in *E. trilineatus;* occasionally the spot is diffuse. In the other two species, of which only poorly preserved material is available, the spot is represented by a diffuse concentration of melanophores. A discrete axillary spot is otherwise found only in the species of the Yaeyamaensis Group and *E. alleni* of the Opsifrontalis Group; the species of the Oculus Group have a diffuse axillary spot.

Males, at least, of *Ecsenius trilineatus* and *E. lubbocki* have dark pigment on the pelvic fins; the fins of *E. isos* are immaculate. Dark pelvic-fin pigment occurs commonly among the species of the Oculus and Yaeyamaensis groups, and *E. fourmanoiri* (Opsifrontalis Group).

I am unable to hypothesize unequivocally the sister group of the Isos Group, but based on color-pattern characters, my putative Oculus-Yaeyamaensis clade appears to be a good candidate (see discussions of relationships under accounts of Oculus and Yaeyamaensis groups).

The three species of the Isos Group have allopatric distributions, with the distributions of *E. isos* and *E. trilineatus* being almost parapatric. *Ecsenius lubbocki* is known only from Phuket, Indian Ocean coast of Thailand; *E. trilineatus* ranges from the Moluccas east and south to the Solomon Islands; and *E. isos* ranges through the New Hebrides south and slightly west to New Caledonia.

I cannot hypothesize a single, unequivocal cladistic pattern of relationships for the three species of the Isos Group that might be used as a basis for hypothesizing a vicariographic (Springer, 1982:5) scenario. Even without such information I propose that historically there was a single ancestral species that occupied essentially the entire range of the group. At least two vicariant events are necessary to have evolved the present three species from that ancestral species. I believe that the first event either isolated an Indian Ocean population or a New Hebrides-New Caledonian population from the remainder of the distribution (population) of the ancestral species. The resulting two populations subsequently diverged. The second vicariant event isolated either an Indian Ocean population from an Indian Ocean-to-Solomon Islands population (if the first event had isolated a New Hebrides population) or a New Hebrides-New Caledonian population from a Moluccan-New Hebrides-New Caledonian population (if the first event had isolated an Indian Ocean population). The resulting two populations subsequently diverged. The three populations formed during this scenario are represented today by three species. The presence of an extensive geographic gap between the distributions of *E. trilineatus* and *E. lubbocki*, and a much smaller gap between *E. trilineatus* and *E. isos*, may be the result of collecting artifacts and/or extinction in the gap areas.

Based on the timing of various geological and climatic events, it is possible to hypothesize the nature and order of the two vicariant events that gave rise to the three species. I believe that the first event occurred between the Solomon Islands and New Hebrides, where the distributions of *E. trilineatus* and *E. isos* come closest together. This event resulted in the formation of a barrier to dispersal between these two island groups. To hypothesize such a barrier it is necessary to note that the Santa Cruz Islands, although politically part of the Solomon Islands, geologically are part of the New Hebrides Islands (Kroenke, 1984) and form the northern extension of the New Hebrides. No collections of *Ecsenius* are known from the Santa Cruz Islands, but the presence of *E. isos* in those islands would corroborate the vicariance scenario I will propose. The presence of only *E. trilineatus* in the Santa Cruz Islands would falsify the scenario, and the presence of both species in those islands would neither corroborate nor falsify the scenario.

The vicariance scenario assumes the former existence of a common ancestral species occurring in both the Solomons and New Hebrides (and possibly as far west as the Moluccas and as far south as New Caledonia). These two island arcs were

once part of a more-or-less east-west linearly continuous ridge that existed at least as recently as about 10 m.y.a.. (Packam and Andrews, 1975; Kroenke, 1984:117). During that time I hypothesize that the islands on the ridge were spaced closely enough (much less than 350 km between an island and its nearest neighbor) to have allowed the ancestral species to colonize ridge segments representing both of today's island arcs. A complex tectonic history has resulted in the present-day location and configuration of the island arcs on the original ridge. During approximately the past 6 million years, the Santa Cruz-New Hebrides portion of the originally continuous ridge rotated about 30° clockwise (Kroenke, 1984), and broke the continuous ridge between the Solomon and Santa Cruz-Solomon islands. Independent movement of the resulting ridges created what is presently an islandless gap of about 350 km between the closest Solomon and Santa Cruz islands. The length of this gap was sufficient to isolate portions of the parental population on either side and permit their subsequent divergence. The New Hebrides are currently on the verge of colliding with the Loyalty Islands, which are adjacent to New Caledonia. Dispersal from the New Hebrides to the Loyalties and then to New Caledonia could account for the occurrence of *E. isos* in New Caledonia (and it probably will be found in the Loyalties; the gaps separating the New Hebrides from the Loyalties and the Loyalties from New Caledonia are both less than the gap between the Santa Cruz and Solomon islands).

As I have shown in the discussion of the distributions of the Opsifrontalis Group species, gaps of as little as 85 km are adequate to isolate populations of different species from each other.

If this scenario explains the distribution of *E. isos* (and I believe it does), then *E. isos* must be the sister group of the other two species. It is possible to propose reasonably a vicariant event that would have isolated the Indian Ocean portion of an ancestral population that had a distribution extending from the west (Indian Ocean) coast of the Malay Peninsula to the Solomon Islands.

Present-day marine connections between the Indian and western Pacific oceans are through the very shallow Straits of Malacca or along the outer coast of the southern chain of Indonesian islands, an area in which no species of the Isos group is known to occur today. Any of the drops in sea level that have occurred during the many glacial periods of the recent Cenozoic (last occurred about 18,000 years ago) would have been sufficient to close the Strait of Malacca and dry up most of the inland seas of western Indonesia (Potts, 1983, 1984; Woodland, 1983; McManus, 1986), thus isolating the Indian Ocean from the western Pacific. Conspecific populations on either side of the barrier could then have begun to diverge.

The distribution of *Ecsenius lubbocki* is widely separated from the nearest known population of *E. trilineatus*. If this large distributional void is real, rather than apparent, it might be the result of extinction, resulting from elimination of much of the coastal area during the last glaciation, and subsequent non-recolonization by dispersal since sea level last rose.

Ecsenius lubbocki is one of the few species endemic to the eastern Indian Ocean. Another is *E. oculatus* (Oculus Group), which, however, is not sympatric with *E. lubbocki*. My hypothesized sister group of *E. oculatus*, *E. paroculus*, however, is sympatric over part of its range with *E. lubbocki*.

Jeffrey T. Williams (pers. comm.) suggested the possibility that a period of glaciation as early as Miocene could have been responsible for the isolation of *E. lubbocki*. Depending on the timing of this isolation, then, *E. lubbocki*, could be the sister group of the other two species.

Ecsenius isos McKinney and Springer

FIGURE 53; PLATE 13: FIGURE 1; TABLES 24, 25

Ecsenius (Ecsenius) yaeyamaensis.—Springer, 1971:32–33 [misidentification in part, New Hebrides].

Ecsenius (Ecsenius) trilineatus Springer, 1972:2 [in part: nonparatypic "additional material"].

Ecsenius isos McKinney and Springer, 1976:5 [New Hebrides, Efate; holotype, BPBM 12122].

DESCRIPTION.—Dorsal fin XII,14 or 15, deeply notched between spinous and segmented-ray portions. Anal fin II,16 or 17. Pectoral fin 13 or 14 (14 unilaterally only in one of seven specimens available). Segmented caudal-fin rays 13. Vertebrae 10 + 22 or 23. Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 43–51; posterior dentary canines 1 on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8 and 11. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Color Pattern: Head diffusely dusky, darker dorsally, with series of up to 4 small spots extending ventroanteriorly from opercular area; when four spots are present, dorsalmost is on opercle dorsally, and is diffusely or darkly dusky; next spot is also on opercle, mid-laterally, and is dark or diffusely dusky; next spot is on opercle just posterior to ventralmost preopercular pores, and is dark or diffusely dusky; last spot is on mid-lateral ventral surface of head, always present, dark, and most prominent of series; another, small dark or dusky spot occasionally present on cheek anterior to first from dorsalmost spot of opercular series; ventral margin of lower lip dusky anteriorly. Side of body with two longitudinal series of markings, dorsal series beginning below spinous dorsal anteriorly as diffuse, relatively deep stripe of somewhat connected blotches, gradually intensifying as dark spots in area below mid-section of segmented-ray portion of fin; terminal spot of dorsal series positioned no further posteriorly than very end of body; ventral longitudinal series of markings similar to, and paired with, dorsal series (no more than 3 or 4 pairs of dark spots). Pectoral-fin axil with noticeable dark spot or marking in well-preserved specimens, diffusely represented in poorly preserved specimens. Fleshy pectoral-fin base with dark or dusky spot dorsally and another at about level of seventh from dorsalmost ray; another spot just posterior (distal) to that at seventh ray extending from base a short distance onto fin

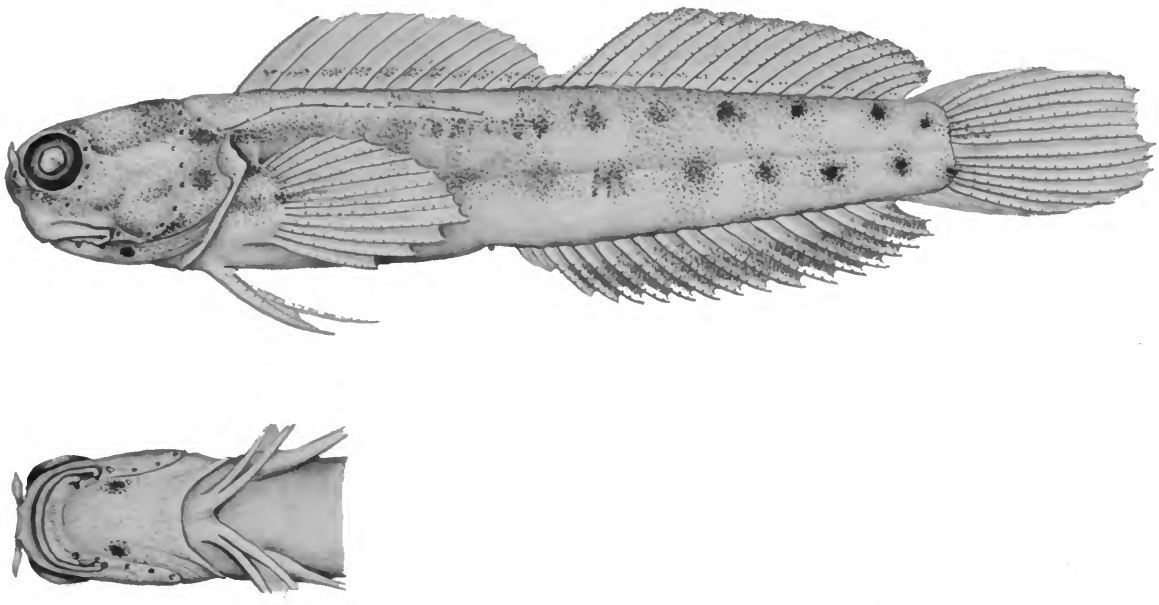


FIGURE 53.—*Ecsenius isos*, BPBM 12122, holotype, male, 26 mm SL, Efate, New Hebrides (small illustration shows underside of head and abdomen; drawn by J.R. Schroeder).

rays. Spinous-dorsal fin with a diffusely dusky stripe suprabasally, usually continuous on segmented-ray portion, which has a diffusely dusky stripe distally. Anal fin with a deep, subdistal dusky stripe. Diffuse dusky extensions from terminal pair of spots on body extend a short distance on caudal fin. Pelvic fins unmarked.

A fresh specimen, not in a good state of preservation, photographed in color (Plate 13: figure 1) exhibits little remarkable color, except for two rows of large pinkish spots on the anterior half of the body. These spots, of which there is no trace in preservation, are in the position of the two faintly dusky stripes present in preserved specimens of *E. lubbocki*.

COMPARISONS.—The color pattern of *Ecsenius isos* appears to be similar to that of *E. trilineatus*. The same basic pattern is present in both species but the markings on the body anteriorly, and on the fleshy pectoral-fin base, of *E. trilineatus* are much more intense, continuous, and discrete. The dark, curving stripe in the opercular area of *E. trilineatus* is

TABLE 24.—Frequency distributions for certain characters of the species of the Isos Group.

	Segmented dorsal-fin rays				Segmented anal-fin rays				Caudal vertebrae			
Species	13	14	15	$\bar{x}$	15	16	17	$\bar{x}$	21	22	23	$\bar{x}$
Ecsenius isos		6	1	14.1		5	2	16.3		5	2	22.3
Ecsenius lubbocki	3	5		13.6	3	5		15.6	1	7		21.9
Ecsenius trilineatus	11	37	4	13.9	9	38	5	15.9	5	38	4	22.0

	Dentary incisor teeth															
Species	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	$\bar{x}$
Ecsenius isos							1	-	1	1	-	-	-	2	1	47.5
Ecsenius lubbocki																
males	1	-	-	-	-	1	-	2								41.8
females									1	-	1	2				47.0
Ecsenius trilineatus				2	3	4	6	14	7	1						43.4

TABLE 25.—Frequency distributions for level of posterior termination of lateral line relative to a dorsal-fin spine base in species of the Isos Group (both sides of each specimen recorded for *E. isos*).

	Lateral line extends to below dorsal-fin spine				
Species	9	10	11	12	$\bar{x}$
Ecsenius isos	2	9	3		10.1
Ecsenius lubbocki		4	4		10.5
Ecsenius trilineatus		3	24	5	11.1

represented by four diffuse or dusky spots in *E. isos*, and the two dark stripes on the fleshy pectoral-fin base of *E. trilineatus* are represented by the dusky spots in the same area on *E. isos*. In some specimens of *E. trilineatus* the curving opercular stripe is interrupted near its ventroanterior end, and the "end piece" is comparable in position to the spot on the ventral side of the head in *E. isos*. include pinkish tints, as are present in *E. isos*.

Because of the bilateral pair of dark spots on the ventrolateral surface of the head, *E. isos* superficially appears to belong to the Prooculis Group, but the dark spots in the latter group of species occur only in males, whereas both males and females of *E. isos* have the dark spots. *Ecsenius isos* and *E. trilineatus* are further distinguished from the Prooculis Group in having a dark spot in the pectoral-fin axil (spot diffuse in available material of *E. isos*) and in a tendency for the lateral line to extend slightly further posteriorly.

DISTRIBUTION.—New Hebrides and New Caledonia.

MATERIAL (* = new material).—New Hebrides: Efate, BPBM 12122 (holotype: 26 mm SL); Espiritu Santo Harbor, USNM 195787 (3 specimens: 21–26). New Caledonia: Solitaire Island, BPBM 22524* (1:32); Kinde Reef, MNHN 1980-807* (1:32); Baie de Prosny [= Prony?], MNHN 1980-920* (1:32).

Ecsenius lubbocki, new species

FIGURE 54; TABLES 24, 25

DESCRIPTION.—Dorsal fin XI–XII,13 or 14 (XII,14 in 5 of 8 specimens), deeply notched between spinous and segmented-

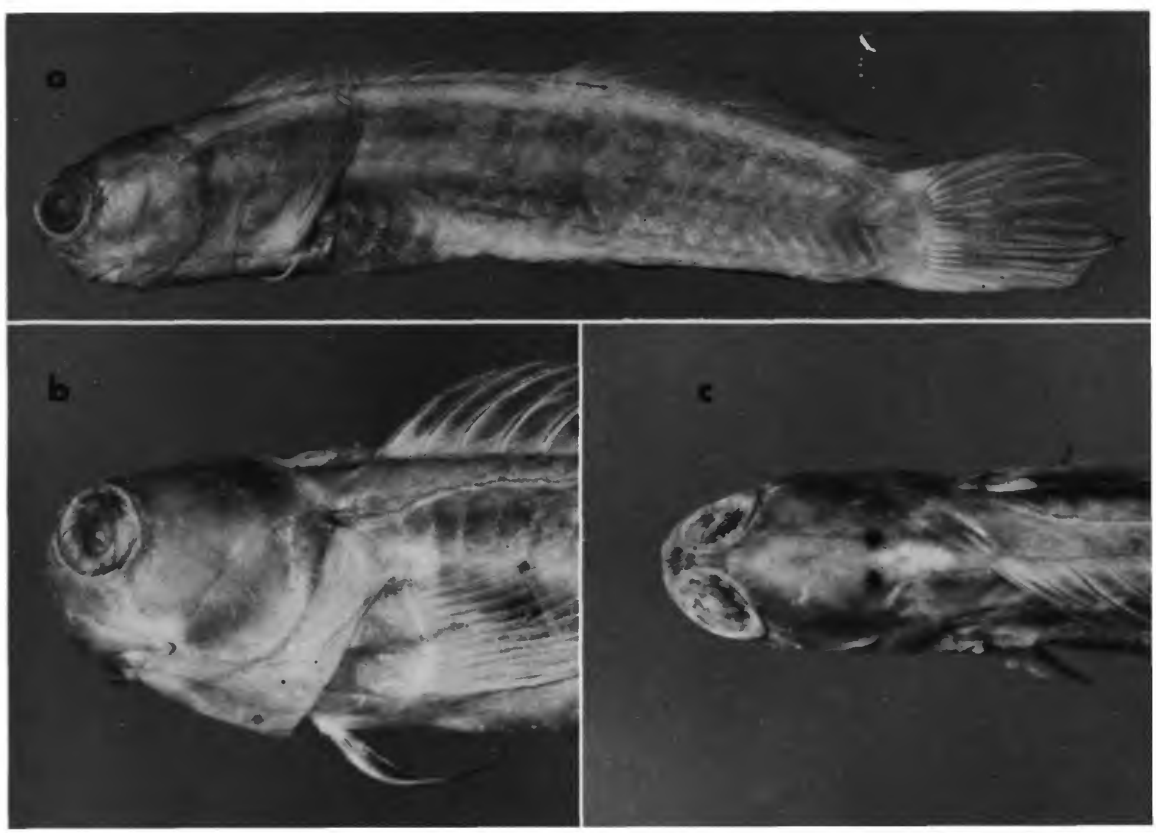


FIGURE 54.—*Ecsenius lubbocki*, males, Phuket, Thailand: *a*, USNM 217533, holotype, 31 mm SL; *b,c*, BPBM 29380, 33 mm SL: *b*, note dusky stripes on opercle and fleshy pectoral-fin base; and *c*, note dark spots on dorsal head surface (photographs by T.B. Griswold).

ray portions. Anal fin II,15 or 16 (16 in 5 of 8 specimens). Pectoral fin 13. Segmented caudal-fin rays 13. Vertebrae 10 + 21 or 22 (22 in 7 of 8 specimens). Dentary incisor teeth 37 to 48 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior dentary canines on each side 1. Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 10 and 11. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color (Note: none of the available specimens is in good condition): Ground color pale with dusky markings. Head with prominent, small, dark, round or oblong spot dorsally on each side of mid-line; dorsal margin of opercle with faintly dusky to dark spot from which faintly dusky curving line extends ventroanteriorly down middle of opercle to mid-ventral surface of head, where line is continuous with line from opposite side of head. Ventral surface of head with lower lip darkly dusky, followed posteriorly by small less dusky area, followed by slightly darker dusky area. Body with three dusky stripes, dorsalmost slenderest, extending along dorsal body contour; middle stripe extending posteriorly from spot at dorsal margin of opercle to caudal-fin base, where stripe becomes very faint, angles posteroventrally, and continues well out on fin; ventralmost stripe orginating in pectoral-fin axil and extending posteriorly to well out on caudal fin. There are very faint indications of several bands connecting the stripes on the body. Fleshy pectoral-fin base with broad, faintly dusky stripe that continues short distance onto two dorsalmost pectoral-fin rays, and another extending slightly further onto fin at about level of sixth from dorsalmost ray. Internal surface of fleshy pectoral-fin base dusky. Slender, dusky stripe courses suprabasally along interradial membranes of dorsal fin. Interradial membranes of anal fin dusky. Interradial and longest ray of pelvic fin darkly dusky.

DISTRIBUTION.—Known only from Phuket Island, on the west coast of Thailand.

COMPARISONS.—*Ecsenius lubbocki* differs from *E. isos* and *E. trilineatus* most obviously in possessing a transverse pair of dark spots on its nape and in lacking two rows of dark spots posteriorly on its body. It possibly differs from them in exhibiting sexual dimorphism in number of dentary incisor teeth. The four available males of *E. lubbocki* have 37, 42, 44, and 44 dentary incisor teeth, whereas, the four females have 45, 47, 48, and 48 teeth. Among all *Ecsenius species*, a pair of dark nape spots is found only in some members of the Oculus Group, and sexual dimorphism in number of dentary incisor teeth is known otherwise only in the Yaeyamaensis (all 5 species), Prooculis (1 of 5 species), Bicolor (both species), and Oculus (probably all 8 species) groups.

ETYMOLOGY.—This species is named for the late Roger Lubbock, who collected all the known specimens and recognized that they did not accord with any described species of *Ecsenius*.

HOLOTYPE.—USNM 217533, male, 31.0 mm SL, off Kata Beach, Laem Sai, Phuket Island, Thailand, large Porites boulder and scattered small corals, 3 m, R. Lubbock and N. Polunin, 20 March 1977.

PARATYPES.—BPBM 29380 (7 specimens: 25.3–33.1 mm SL, collected with the holotype).

Ecsenius trilineatus Springer

FIGURE 55; PLATE 13: FIGURE 2; TABLES 24, 25

Ecsenius (Ecsenius) yaeyamaensis.—Springer, 1971:32–33, fig 29 [misidentification in part, Banda Sea].

Ecsenius (Ecsenius) trilineatus Springer, 1972:2 [Trobriand Islands, Kiriwina; holotype, USNM 205705].

Ecsenius trilineatus.—McKinney and Springer, 1976:22.

DESCRIPTION.—Dorsal fin XI–XII,13–15 (XI in one, and 14 in 29, of 40 specimens), deeply notched between spinous and segmented-ray portions. Anal fin II,15–17 (16 in 29 of 40 specimens). Pectoral fin 12–14 (12 or 14 uncommonly and only unilaterally). Segmented caudal-fin rays 13. Vertebrae 10 + 21 to 23 (22 in 30 of 37 specimens). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 40–46; posterior dentary canines 1 on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 10 and 12 (from spine 11 in 23 of 29 specimens). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Head diffusely dusky with fine, dark, ventroanteriorly-curving stripe extending from mid-upper portion of opercle (well anterior to posterior margin) to underside of head (not continuous with stripe from opposite side of head); discontinuous dark spot may appear anterior to anterior end of stripe; scattered dark spots variably present on side of head; lower lip dusky followed posteriorly by paler or pigmentless area; pigmentless area not extending posteriorly beyond level of rictus. Body with three fine, dark stripes; dorsalmost stripe beginning just anterior to dorsal-fin origin, continuing on dorsal body contour to point below anterior third of segmented-ray portion of dorsal fin; middle stripe beginning just above dorsalmost point of curving stripe on side of head, sometimes diffusely continuous with curving stripe, and continuing posteriorly on upper third of body to point below segmented-ray portion of dorsal fin, thence continuing as row of dashes and spots to caudal-fin base, with diffusely dusky or dark extension of melanophores continuing from posteriormost spot ventroposteriorly onto caudal fin; ventral stripe beginning internal to pectoral-fin axil and extending posteriorly on lower third of body to point below segmented-ray portion of dorsal fin, thence continuing as row of dashes and spots to caudal-fin base, with diffusely dusky or dark extension of melanophores continuing from posteriormost spot or marking posteriorly or ventroposteriorly well out on caudal fin; up to 8 faint, diffuse, dusky bands extending from dorsal stripe to middle stripe, becoming even fainter as they extend to ventral stripe. Pectoral-fin axil with dark or dusky spot. Fleshy pectoral-fin base with pair of dark pinstripes; dorsal stripe enters fin between dorsalmost two rays, but occasionally is

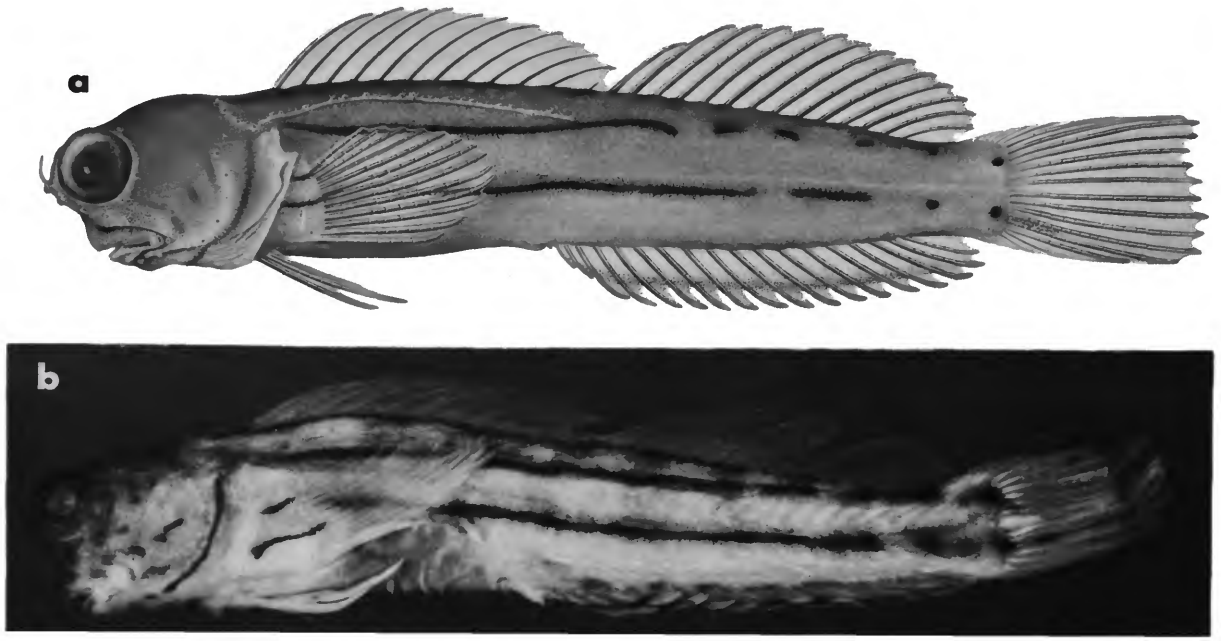


FIGURE 55.—*Ecsenius trilineatus: a,* USNM 202477, male, 27 mm SL, probably Banda Sea (drawn by S.L. Chambers); *b,* USNM 211926, female, Saparua, Indonesia (photograph by K.A. Bruwelheide).

reduced to dark spot; ventral stripe, which may be in two disconnected pieces and curve ventrally anteriorly, enters fin between sixth and seventh from dorsalmost rays. Dorsal fin of males variably with fine, diffuse, dusky stripe suprabasally in spinous portion and another distally in segmented-ray portion (both stripes absent in females). Anal fin with diffusely to darkly dusky stripe in distal third. Caudal fin with dusky extensions of body markings (described above) and faintly to darkly dusky dorsal and ventral edgings. Pelvic fin pale (both sexes) or with dark membranes and markings on rays (males only).

Live Color (based on color slides taken near Bali and at Banda; Plate 13: figure 2): Head is pinkish brown dorsally, pale pinkish below level of eye; cheeks variably with a few brownish spots; opercular stripe blackish; pupil of eye surrounded with yellow ring, which is surrounded by black iris, which contains several slender, yellow bands or spots in the sagital plane. Body stripes (including dash-like and spot-like continuations) blackish, areas between stripes greenish gray, periodically darker and lighter forming diffuse bands; row of four white spots between dorsal two body stripes (plus dashes and spots): anterior three spots bright, posterior spot pale; row of six white spots between ventral two body stripes (plus dashes and spots): anterior two spots diffusely pale, posterior four bright. All fins immaculate.

SEXUAL DIMORPHISM.—See description of color pattern.

REMARKS.—*Ecsenius trilineatus* appears to be the smallest species of *Ecsenius,* with a maximum size for both males and females of only 27 mm SL.

COMPARISONS.—See comparisons section under accounts of *E. isos* and *E. lubbocki* and discussion under Isos-species Group.

DISTRIBUTION.—Known only from various small islands from the Moluccas eastward to Florida Island, Solomon Islands.

MATERIAL (* = new material).—*Moluccas:* Saparua, USNM 211926 (17 specimens: 14–27 mm SL); Banda Islands, USNM 211930 (5:14–26), 211941 (15), 211945 (7:22–27). *Kai Islands:* 221239* (2:23, 24). *Papua-New Guinea:* Massas Island (Madang Harbor), USNM 267267* (1:24), 205704 (1:27); Trobriand Islands, USNM 205705 (holotype, 26), 206378 (3:26–27), 205703 (1:26). *Solomon Islands:* Florida Island, AMS I.17497-001 (1:26). Presumably *Banda Sea:* USNM 202477 (1:27).

PROOCULIS GROUP

This group comprises five species: *E. bandanus, E. bimaculatus, E. collettei, E. prooculis,* and *E. taeniatus,* which differ primarily in color pattern. All the species are small (attaining a maximum size of no more than 40 mm SL) and have deeply notched dorsal fins, low meristics, and short nasal cirri and lateral lines. Among the species of *Ecsenius,* they exhibit a unique sexual dimorphism in the color pattern of the ventral side of the head (here considered to be a synapomorphy): presence of dark, round spots or elongate crescentic marks in males, pale, round spots or cresentic marks in females and some males, with no evidence that these markings extend

dorsally on the side of the head. The positions of these markings are the same in both sexes. All of the species are allopatric, and all but *E. bandanus* are relatively limited in distribution. I am unable to hypothesize an unequivocal set of interrelationships for the species, although I think it probable, based on color pattern similarities, that *E. bandanus* and *E. bimaculatus* form a monophyletic group, and *E. prooculis* and *E. taeniatus* form a monophyletic group (see discussions under individual species accounts).

Ecsenius bandanus Springer

FIGURE 56; PLATE 13: FIGURE 5; TABLES 26–28

Ecsenius (Ecsenius) bandanus Springer, 1971:38 [Banda Sea, Indonesia; holotype, USNM 195717].
Ecsenius bandanus.—McKinney and Springer, 1976:2 [redescription].

DESCRIPTION.—Dorsal fin XI–XIII (XII in 98% of specimens), 13–15 (usually 14). Anal fin II,15–17 (usually 16). Pectoral fin 12–14 (13 in 97% of specimens). Segmented caudal-fin rays 13 or 14 (13 in 97% of specimens). Vertebrae 10 + 21–23 (usually 22). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 39–50; posterior dentary canines 0 to 2 (usually 1) on each side. Lateral line without pairs of pores, terminating at point between verticals from eighth to tenth dorsal-fin spines. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, upper third of head moderately to darkly dusky, usually with dark spot at one o'clock position on postorbital margin; deep, dark stripe extending posteriorly from mid-postorbital margin to dorsal portion of opercular area, ceasing there or becomming less discrete and more slender as it gradually fades completely on body under spinous portion of dorsal fin; pale, diffuse, usually imperceptible stripe margining head portion of dark mid-postorbital stripe; another, pale stripe margining ventral border of dark stripe on body, but continuing further posteriorly than dark stripe; side of head below dark stripe paler than area dorsal to stripe; ventral head surface of males usually with two pairs of dark spots, often uniformly dusky, occasionally with two pairs of pale spots, and infrequently with both dark and pale spots (see McKinney and Springer (1976:2) for frequency table); ventral head surface of females with two pairs of pale spots or, infrequently, uniformly dusky; dorsal portion of eye and interorbital region with dark spots, which may be joined to similar spots on opposite eye. Body generally dusky, darker dorsal to dark stripe and paler on posterior portion; occasionally with evidence of three or four very broad, diffusely dusky saddles dorsally. Spinous-dorsal fin generally clear, with fine melanophores along spines; segmented-ray portion similar, but males usually with slender suprabasal stripe of fine melanophores; females without stripe. Anal fin generally uniformly dusky with rays paler distally. Pectoral and pelvic fins generally unmarked. Caudal fin with fine sprinkling of melanophores basally, otherwise mostly unmarked.

Live Color (based on color photographs taken in the wild at Celebes (= Sulawesi), Bone Rate, and Banda islands (Plate 13: figure 5): Head darkly dusky above with slender, brilliant-white stripe mid-dorsally, two brilliant-white stripes pass through eye above and below pupil; ventral stripe commences on snout and continues across head onto body below dark postorbital stripe, stripe fading in region above venter; fine, diffusely pale stripe above dark postorbital stripe; cheeks below brilliant-white stripe pinkish gray or white; body area covered by appressed pectoral fin pale blue-green, remainder of body dusky olive gray, darker dorsoanteriorly, with faint indications of broad, diffuse bands dorsally.

My recorded observations of living specimens in Ceram indicate that the brilliant-white stripes on the head, described above, were brilliant yellow. Additionally, a color photograph of a freshly dead, posed specimen from the Seribu Islands shows the pale spots on the ventral surface of the head to be orange (not visible in Celebes, Bone Rate, and Banda photographs).

SEXUAL DIMORPHISM.—Other than the sex-associated color pattern differences noted above, there are statistically significant differences between the sexes in average number of dentary incisor teeth in the Seribu, Kabaena, and Ceram populations (Table 27). Females have higher averages, and even in populations where differences were not significant females had more, or averaged more, teeth. Maximum size attained by males (34 mm SL) is greater than that of females (29 mm), and relative caudal-fin lengths are longer in males than females (McKinney and Springer, 1976).

GEOGRAPHIC VARIATION.—There appears to be a shift in modal numbers of dorsal- and anal-fin segmented rays and caudal vertebrae from the populations to the east of, to those to the west of, the area separating Celebes from the Moluccas (Table 26).

REMARKS.—Springer (1971) named this species on the basis of a presumption that his material was collected by W. H. Longley at Banda (see Springer, 1971:42–43). Since my 1971 study, no specimens have been collected at Banda. A recent color photograph of *E. bandanus*, taken by J.E. Randall in the Banda Islands, now confirms the presence of that species where I predicted it would occur.

COMPARISONS.—See comparisons section under *E. bimaculatus*.

DISTRIBUTION.—From the Seribu Islands off the northwestern coast of Java eastward to Biak off the northwestern coast of New Guinea. Recorded from Bone Rate, Flores Sea, based on a photograph taken by J.E. Randall.

MATERIAL (* = new material).—*Indonesia:* Seribu Islands, USNM 211988 (1 specimen: 21 mm SL), 211993 (17:13–29), 211996 (18:16–34), BPBM 10854 (5:16–23); Karimundjawa, USNM 211979 (11:24–32); Bone Betang [NW of Ujung Padang], BPBM 26720* (3:23–29); Kabaena, AMS I.18490-001 (10: 17–29), USNM 211916 (14:22–29); Ambon, USNM 209767 (3:26–29), 211958 (1:25); Ceram, USNM 209660 (2:19,20), 210170 (24:13–29), CAS 34243 (6:15–23), BMNH

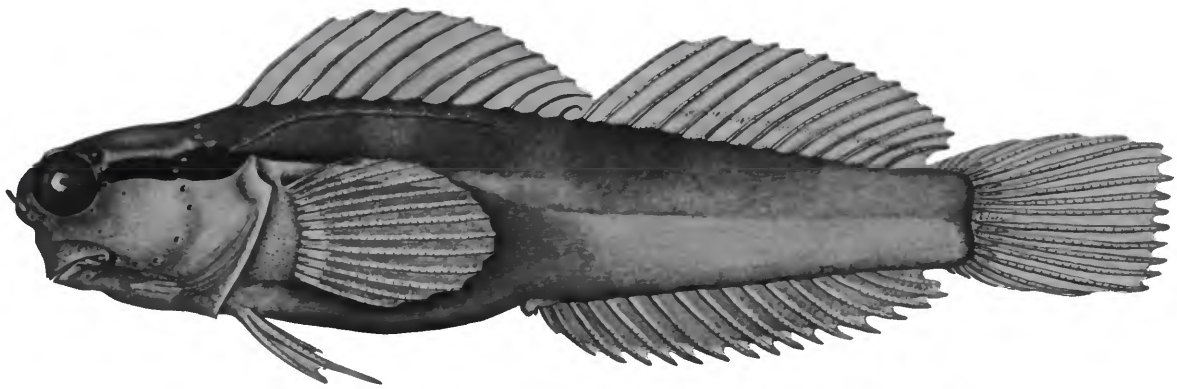


FIGURE 56.—*Ecsenius bandanus*, USNM 209767, female, 26 mm SL, Ambon, Moluccas, Indonesia (drawn by J.R. Schroeder).

1975.11.19.1–3 (3:22–25); Saparua, USNM 209991 (7: 17–31), 210111 (1:26), 210374 (1:25); presumably Banda Sea, USNM 195717 (holotype: 31); Tajandoe Island, Kai Islands, AMS* (1: not measured); near Pulau Adi (Irian Jaya), NCIP* (1: not measured; collected by B.B. Collette); Biak, USNM 221236* (6:15–32).

Ecsenius bimaculatus Springer

FIGURE 57; PLATE 13: FIGURE 6; TABLES 26–28

Ecsenius (Ecsenius) bimaculatus Springer, 1971:38 [Darvel Bay, Borneo; holotype, USNM 201817].

DESCRIPTION.—Dorsal fin XII–XIII (XIII in 2 of 15 specimens checked), 13 or 14. Anal fin II,15–17 (usually 16). Pectoral fin 12 or 13 (rarely 12, and only unilaterally). Segmented caudal-fin rays 13. Vertebrae 10 + 21 or 22 (usually 22). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 41 to 45; posterior dentary canines 0 or 1 (usually 1) on each side. Lateral line without pairs of pores, terminating at point between vertical from interspace between dorsal-fin spines 8 and 9 and vertical from spine 11 (usually at or before vertical from spine 10). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, head generally dusky, usually with dark spot or stripe extending short distance posteriorly from one o'clock position on postorbital margin; another, broader, dark stripe extending from mid-postorbital margin to point on side of body below anterior portion of spinous dorsal fin; stripe may attenuate or decrease in intensity on entering body; side of head below stripes may be noticeably paler; ventral head surface of males either uniformly dusky or (usually) with pale ventral lip and longitudinal pair of dark spots on each side; ventral head surface of females faintly

TABLE 26.—Frequency distributions for meristic characters in species of the Prooculis Group.

Species/locality	Segmented dorsal-fin rays				Segmented anal-fin rays				Caudal vertebrae			
	13	14	15	$\bar{x}$	15	16	17	$\bar{x}$	21	22	23	$\bar{x}$
Ecsenius bandanus												
Seribu	13	27		13.7	8	25		15.8	5	24	1	21.9
Karimundjawa	4	7		13.6	5	6		15.5	3	7	1	21.8
Bone Betang	1	2		13.7		2		16.0		3		22.0
Kabaena	7	17		13.7	3	21		15.9	7	15	1	21.7
Ambon	1	3		13.8		4		16.0	1	3		21.8
Saparua		8	1	14.1		8	1	16.1	1	7	1	22.0
Ceram	1	31	1	14.0		31	2	16.1	3	29	3	22.0
Biak	1	3	2	14.2	1	4	1	16.0	1	4	1	22.0
Ecsenius bimaculatus	5	10		13.7	3	11	1	15.9	2	12		21.8
Ecsenius collettei		6	2	14.2		8		16.0	2	6		21.8
Ecsenius prooculis	1	66	7	14.1	5	60	3	16.0	10	58	6	21.9
Ecsenius taeniatus		3		14.0		3		16.0		2	1	22.3

TABLE 27.—Frequency distributions for number of dentary incisor teeth in species of the Prooculis Group.

Species/locality	Dentary incisor teeth												
	39	40	41	42	43	44	45	46	47	48	49	50	$\bar{x}$
Ecsenius bandanus													
Seribu Ids.													
males	1	-	1	2	2	4	1						42.8
females			1	1	-	-	3	2	1				44.6
Karimundjawa													
males				1	3	2							43.2
females		1	-	-	-	2	1						43.3
Bone Betang													
males			1										
females					1								
Kabaena													
males		2	1	6	2								41.7
females					3	4	3	3					44.5
Ambon													
males				1	-	-	1						43.5
females							1	1					45.5
Saparua													
males				3	2	2							42.9
females						1	-	-	1				45.5
Ceram													
males		1	3	5	2	2							42.1
females						2	3	3	1				45.3
Biak													
males							1						
females							1	-	1				46.0
Ecsenius bimaculatus			2	5	2	2	2						42.8
Ecsenius collettei							2	2	-	2	1	1	47.1
Ecsenius prooculis			2	7	12	11	13	5	5	8	3		44.8
Ecsenius taeniatus						1	-	1	1				45.7

dusky with longitudinal pair of unpigmented spots on each side (pale spots often difficult to distinguish). Body sides pale to dark dusky with longitudinal pair of elongate-oblong dark spots on each side in area covered by appressed pectoral-fin; dark spots with variably recognizable, confluent, broad, pale, margins. Spinous dorsal-fin of males with fine melanophores along elements and loose sprinkling of melanophores in some interspinous areas; segmented-ray portion with fine, faintly-dusky stripe suprabasally; females with fine melanophores along spines and segmented rays, no stripe. Anal fin uniformly dusky, except distal portions of rays, which are pale. Pectoral fins with fine melanophores along rays. Pelvic and caudal fins essentially unmarked.

TABLE 28.—Frequency distributions for terminal position of lateral line in species of the Prooculis Group.

Species	Lateral line extends to vertical from dorsal-fin spine				
	8	9	10	11	$\bar{x}$
Ecsenius bandanus	5	33	29		9.4
Ecsenius bimaculatus		6	7	1	9.6
Ecsenius collettei	3	2	3		9.0
Ecsenius prooculis	19	38	13		8.9
Ecsenius taeniatus	1	1	1		9.0

Live Color (based on photograph taken in the wild in the Philippines): Head, including eye, very dark gray or black dorsally above level between four and five o'clock postions on postorbital margin, abruptly pale below this level; eye with faint, pale stripe extending from about nine to three o'clock position, brilliant white below level passing between seven and eight and four and five o'clock positions, continuing posteriorly as fine, brilliant-white stripe, which extends across head, enters body, where it deepens as it envelops longitudinal pair of elongate-oblong dark spots on body; cheeks cream colored below white stripe. Body dorsal and posterior to white stripe slate gray to pale gray; fleshy pectoral-fin base pinkish gray; fins immaculate.

SEXUAL DIMORPHISM.—See description above of preserved color pattern.

REMARKS.—*Ecsenius bimaculatus* is one of the smaller

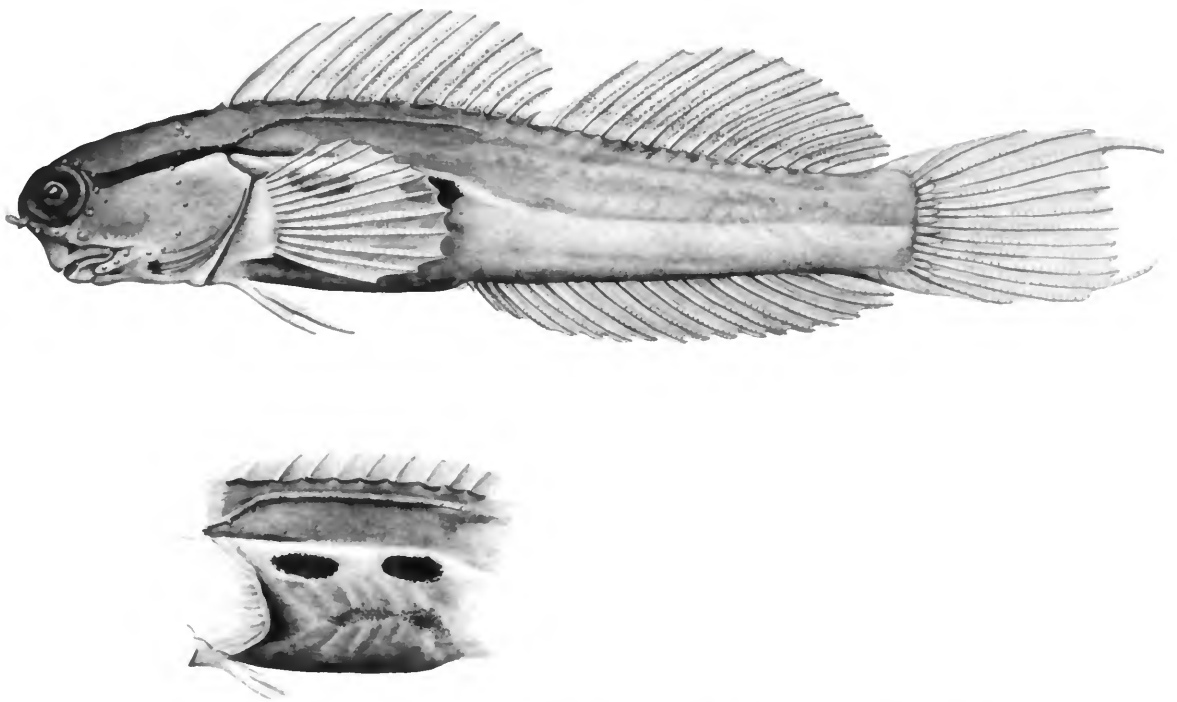


FIGURE 57.—*Ecsenius bimaculatus*, USNM 203922, male, 32 mm SL, Darvel Bay, Borneo (small drawing shows abdominal region with pectoral fin removed; drawn by J.R. Schroeder).

species in the genus: largest male is 32 mm SL, and largest female, 27 mm.

COMPARISONS AND RELATIONSHIPS.—The two dark spots on each side of the abdomen, surrounded by a bright-white area superficially appear to indicate that *E. bimaculatus* belongs to the Oculus Group. The spots of *E. bimaculatus*, however, are elongate rather than round, as they are in the Oculus Group, and the spots occur on the abdomen, a region where no such spots occur in the Oculus Group. The type of sexual dichromatism exhibited by *E. bimaculatus* (a synapomorphy of the Prooculis Group) and the lack of the color-pattern synapomorphies of the Oculus Group (see account of Oculus Group) contra-indicate inclusion of *E. bimaculatus* in the Oculus Group.

Within the Prooculis Group, *Ecsenius bimaculatus* appears to be most similar and closely related to *E. bandanus*, from which it differs in having two dark spots on each side of the body, the greatest depth of the postorbital stripe about one-third to one-quarter less than that of comparably sized specimens of *E. bandanus* (true at least of preserved material), and in lacking evidence of sexual dimorphism in numbers of dentary incisor teeth. If these two species form a monophyletic group, as I believe, it would be important to hypothesize the vicariance scenario that might have given rise to them. The ancestral population of the pair probably would have had a distribution covering both the Philippines and Indonesia, but I am unable to hypothesize the vicariance scenario that split it into two populations along a line separating the two areas.

DISTRIBUTION.—Known only from the Philippine Islands and adjacent northeast Borneo (Sabah).

MATERIAL (* = new material).—*Sabah:* Pulav Bohidulong, Darvel Bay, USNM 201817 (holotype: 31 mm SL), 203922 (2:31,32). *Philippine Islands:* NE of Bolinao (Luzon), channel W of Santiago Island, AMS I.21903-025* (2:23,25); Bolinao, USNM 225054* (3:15–25); Sombrero Island, Batangas, AMS I.21915-036* (1:29), USNM 225055* (1:27), 225056* (1: 24); Siquijor Island, USNM 219317* (1:27); Bararin, Cuyo Islands, USNM 227401* (1:26); Puerto Princessa, Palawan, and vicinity, USNM 222135* (1:21), 222136* (1:27), BPBM 30636* (1:16).

Ecsenius collettei Springer

FIGURE 58; PLATE 14: FIGURE 1; TABLES 26–28

Ecsenius (Ecsenius) collettei Springer, 1972:6 [Krankett Island, Madang Harbor, New Guinea; holotype, USNM 206379].

DESCRIPTION.—Dorsal fin XII,14 or 15. Anal fin II,16. Pectoral fin 13. Segmented caudal-fin rays 13. Vertebrae 10 + 21 or 22. Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 45 to 50; posterior dentary canines 1 on each side. Lateral line without pairs of pores, terminating posteriorly at point between

verticals from dorsal-fin spines 8 and 10. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, head dusky above with one or two, small dark spots along dorsoposterior margin of orbit; another, larger, darker spot on opercle dorsally; underside of head plain dusky (males or females) or with elongate, curved dark mark on each side (males only); dark spot variably present just anterior to each mark. Body with row of up to about 7 small, indistinct dark spots on dorsal contour, first spot surrounding base of first dorsal-fin spine, posteriormost spot anterior to mid-base of segmented-ray portion of fin; row of 8–11 dark spots beginning at level of opercular dark spot in area covered by appressed pectoral fin and continuing no further posteriorly than basalmost portion of caudal fin; another row of 6–9 dark spots on ventral quarter of body beginning no further anteriorly than about vertical at notch in dorsal fin and terminating no further posteriorly than basalmost portion of caudal fin, where terminal spot may be at body mid-line. Fleshy pectoral-fin base dusky dorsally, paler ventrally; axil uniformly, diffusely dusky, without distinct dark marking. Segmented-ray portion of dorsal with dusky suprabasal stripe; other fins varying from immaculate to generally dusky.

Live Color: A color photograph of a living specimen taken underwater was published in Burgess and Axelrod (1975, fig. 390; reproduced here as Plate 14: figure 1). The head is dusky above the ventral level of the eye and almost white below this level. The pupil of the eye is ringed with yellow and there are some yellow spots in the dark dorsal half of the iris outside the yellow ring. The body is a pale milky gray, the dark spots blackish.

Sexual Dimorphism.—In addition to the color pattern on the ventral surface of the head, males may differ from females in having elongate dorsal and ventral caudal-fin rays.

Comparisons.—The distinctive color pattern of *Ecsenius collettei* cannot be confused with that of any other species in the Prooculis Group. I am unable to hypothesize its sister group unequivocally or subjectively.

Distribution.—Known only from eight specimens all taken at Krankett Island, Madang Harbor, Papua–New Guinea.

Material (* = new material).—USNM 206379 (holotype: 30 mm SL), 206380 (1 specimen: 33), 205701 (1:22), 205702 (2:30,32), BPBM 15796* (3:28–30).

Ecsenius prooculis Chapman and Schultz

Figure 59; Plate 14: figure 2; Tables 26–28

Ecsenius prooculis Chapman and Schultz, 1952:519 [Munda Lagoon near Sassavelle, New Georgia, Solomon Islands; holotype, USNM 144722].—McKinney and Springer, 1976:21].

Ecsenius (Ecsenius) prooculis.—Springer, 1971:37 [redescription].

Description.—Dorsal fin XII or XIII (XIII in only 1 of 73 specimens checked), 13–15 (14 in 89% of specimens). Anal fin II,15–17 (16 in 89% of specimens). Pectoral fin 12–14 (rarely 12 or 14). Segmented caudal-fin rays 13. Vertebrae 10 + 21–23 (22 in 80% of specimens). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 41–49; posterior dentary canines 0 or 1 (usually 1) on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8 and 10. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Head dusky brown, noticeably paler below level of mouth; slender, dark stripe usually present, originating just below mid-postorbital margin and extending posteriorly to preopercular or opercular area; small, dark spot usually present on postorbital margin slightly dorsal to stripe; variably, other dark spots (bilaterally paired) in interorbital region, along dorsal surface of eye, and just posterior to anterior

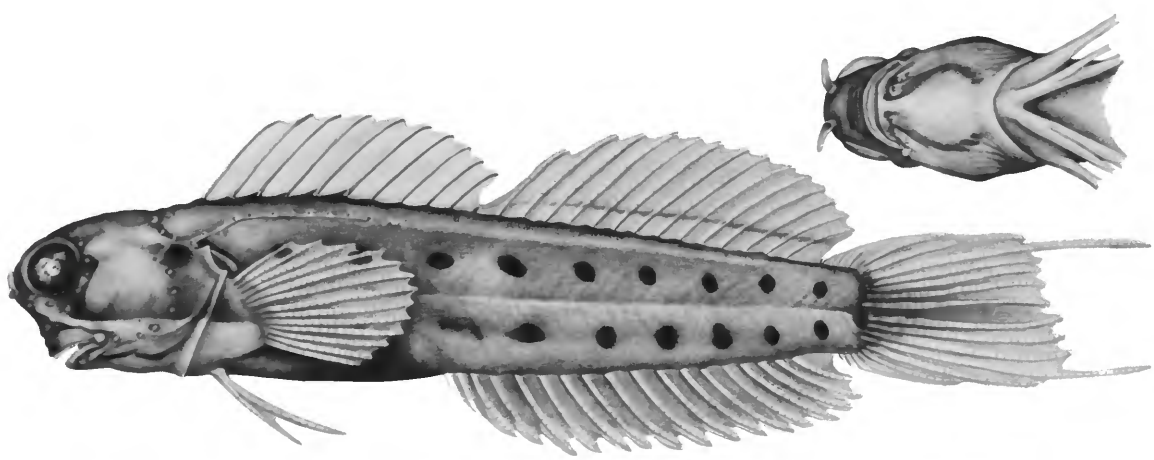


Figure 58.—*Ecsenius collettei*, USNM 206380, male, 33 mm SL, Krankett Island, Madang Harbour, Papua New Guinea (small drawing shows underside of head; drawn by J.R. Schroeder).

nostril (or dark line extending across snout just posterior to anterior nostrils); median, unpaired spot may be present in interorbital region. Pattern on ventral surface of head somewhat sexually dimorphic: males most frequently have dark, somewhat crescentic mark, or longitudinal pair of spots, of variable intensity, on each side, but these markings may be replaced by pale, unpigmented areas, or the ventral side of the head may be uniformly dusky; females never have dark markings like those found in males, but most frequently have the pale, unpigmented markings described for males, or ventral surface of head may be uniformly dusky. Body has three broad, dark stripes separated by slender ($^1/_2$–$^3/_4$ depth of middle dark stripe), pale interspaces (i.e., stripes); dorsal pale stripe is dorsal to mid-line of body; ventral pale stripe is ventral to mid-line. Dorsal fin essentially unmarked except for a fine, dusky, suprabasal stripe that is variably present in the segmented-ray portion. Anal fin is usually dusky overall, except for distal portions of rays of mature males, which may be pale. Pectoral and pelvic fins essentially unmarked. Caudal fin with dusky half-moon shaped area basally.

Live Color (Plate 14: figure 2): Color of living specimens is much like that of preserved examples, except that there is a bright-yellow ring around the pupil, and bright-yellow spokes extending out from the the dorsal half of the ring.

Sexual Dimorphism.—Aside from color pattern, described above, males differ from females in having longer dorsal-fin elements, which can be recognized when similar-sized males and females are compared. Elongate caudal-fin lobes occur only in males. Males attain a larger size than females; maximum noted: males, 39.5 mm SL; females, 30.3 mm. Of the 27 females and 57 males longer than 19 mm SL, only one female was longer than 29.9 mm SL, whereas, 13 males exceeded that length. No dimorphism was noted among meristic characters.

Comparisons.—*Ecsenius prooculis* appears to be most similar (closely related?) to *E. taeniatus*, under the account of which a comparison and possible vicariance scenario are given.

Distribution.—Hermit and Ninigo islands (western Admiralty Islands), New Britain and New Ireland (Bismarck Archipelago), New Georgia (Solomon Islands).

Material (* = new material).—*Solomon Islands:* New Georgia, Munda Lagoon, USNM 144722 (holotype: 40 mm SL). *New Britain:* Rabaul area, AMS I.17503-001 (1:27), BPBM 15719 (4:23–36), USNM 201819 (4:28–34). *New Ireland:* Nusa Island, USNM 217563* (1:31). *Admiralty Islands:* Hermit Islands, USNM 227349* (1:17), 227350* (13:16–31), 227351* (34:14–32), 227352* (12:16–29), 227353* (13:15–24), 227355* (1:19), 227357* (21:15–30); Ninigo Islands, USNM 227354* (3:28–35), 227356* (3:21–30), 227358* (8:21–33).

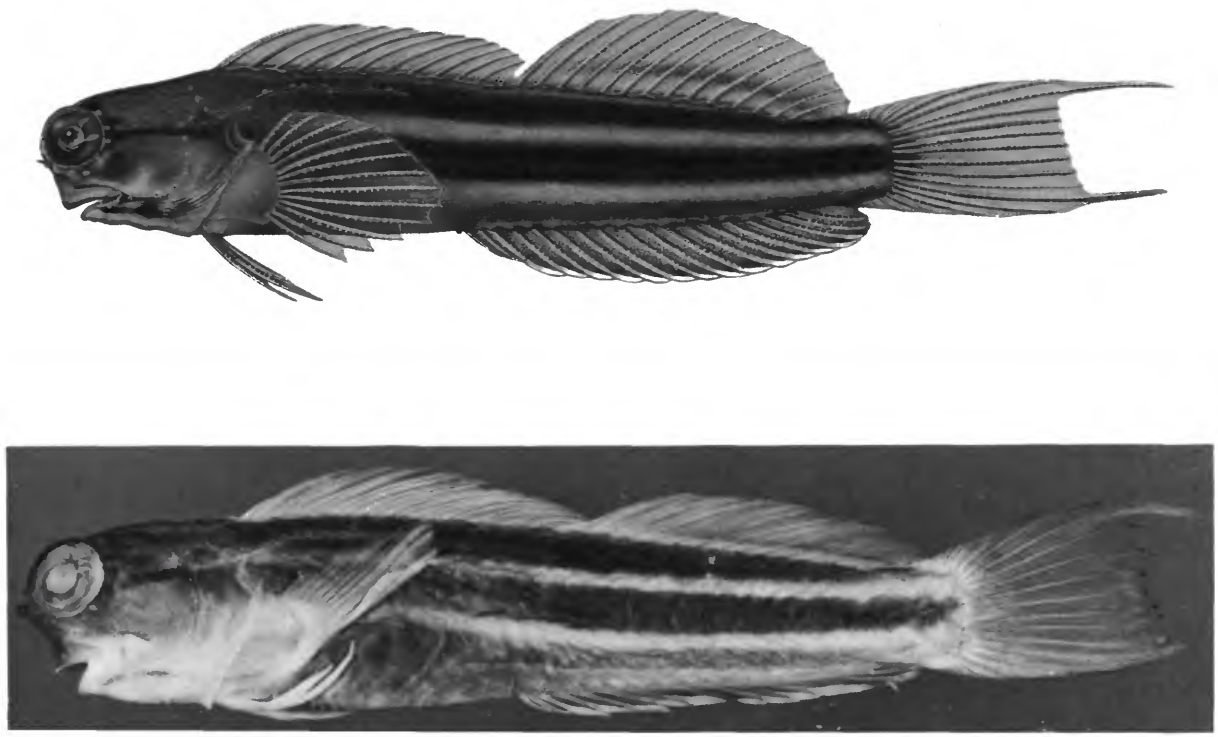


Figure 59.—*Ecsenius prooculis:* upper, USNM 201819, male, 30 mm SL, Rabaul, New Britain (drawn by J.R. Schroeder); lower, USNM 227350, male 27 mm SL, Hermit Islands (photograph by K.A. Bruwelheide).

Ecsenius taeniatus, new species

FIGURE 60; TABLES 26–28

DESCRIPTION (three specimens known).—Dorsal fin XII,14. Anal fin II,16. Pectoral fin 13. Segmented caudal-fin rays 13. Vertebrae 10 + 22 or 23. Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 44, 46, and 47; posterior dentary canines 1 on each side. Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8 and 10. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Head darkly dusky above horizontal at ventral orbital margin, pale dusky below; dark spot just posterior to postorbital margin, fading posteriorly and continuing as diffuse stripe across head; ventral surface of head faintly dusky with single, slender, curved, pale area, or linear pair of pale spots, on each side. Body with slender, pale stripe originating in region dorsal to pectoral-fin axil and extending posteriorly along body midline almost to caudal-fin base; body darkly dusky above stripe, paler below; another slender, pale stripe originating at about vertical from dorsal-fin origin, extending posteriorly between lateral line and dorsal body contour, and ending at about vertical from midbase of segmented-ray portion of dorsal fin; ventral third of fleshy pectoral-fin base pale dusky, abruptly darker on upper two-thirds. Spinous-dorsal fin with scattered melanophores basally, giving rise to dusky extensions along spines; segmented-ray portion with suprabasal slender, diffusely dusky stripe of melanophores. Anal fin almost uniformly covered with fine melanophores. Caudal fin dusky basally with diffuse extensions of melanophores along central rays. Pectoral and pelvic fins scarcely marked.

COMPARISONS.—*Ecsenius taeniatus* appears to be most similar in color pattern (most closely related to?) *E. prooculis*, with which it is easily confused on superficial examination. Both species have two pale stripes alternating with two dark stripes on the side of the body, but the dorsal pale stripe in *E. prooculis* is ventral to the level of the lateral line, whereas in *E. taeniatus* it is just dorsal to the lateral line. The ventral pale stripe of *E. prooculis* is well ventral to the mid-line of the body, whereas in *E. taeniatus* it is on the mid-line. Additionally, the pale stripes of *E. prooculis* are about twice as deep as those of *E. taeniatus*. *Ecsenius prooculis* never has a conspicuous dark spot on the mid-postorbital margin, as is present in *E. taeniatus*, but often exhibits a slender, dark postorbital stripe, which is not present in *E. taeniatus*.

These two species are allopatric. If they form a monophyletic group, as I think they may, an explanation of their origins is possibly to be found in the tectonic events that separated the islands of the Bismarck and Solomon plates from the north coast of New Guinea. Kroenke (1984:35) has written,

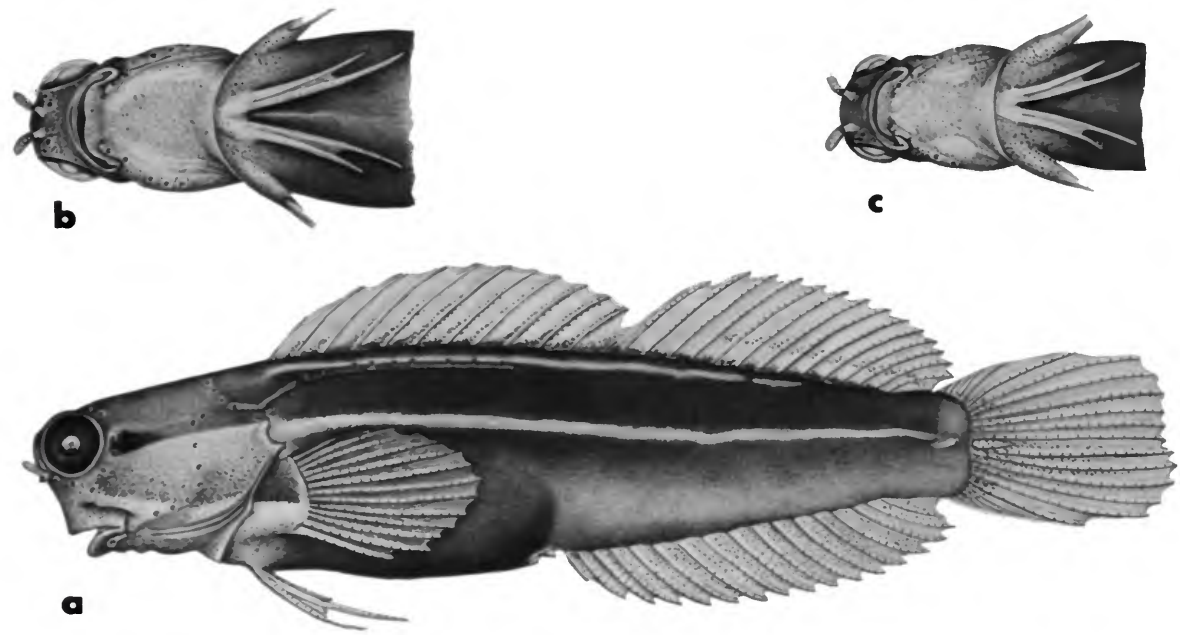


FIGURE 60.—*Ecsenius taeniatus*: *a* (lateral view) and *b* (underside of head), USNM 277494, holotype, female, 32 mm SL; *c* (underside of head), USNM 217566, male, 28 mm SL; both Milne Bay, Papua New Guinea (drawn by J.R. Schroeder).

... at 3.5 Ma ... the New Britain Arc and Papua New Guinea mainland were separated by more than 300 km. Further back in time near the Mio-Pliocene boundary (5 Ma), the New Britain Arc and the Papua New Guinea mainland [now in contact] were separated by more than 500 km and exhibited no interdependence. Thus, as they were separate entities, the pre-Pliocene development of New Britain (as part of the Manus–New Ireland–Solomon Island Arc) and that of the New Guinea mainland can be viewed independently.

These circumstances would seem to indicate that a common ancestor of the putative *prooculis-taeniatus* clade would have had to exist prior to 5 m.y.a. and would have been broadly distributed over a rather extensive range that included a connection, such as stepping-stone islands, between New Guinea and the New Britain–Manus–New Ireland–Solomon Island Arc. Subsequent loss (possibly by submergence) of the connection would have isolated New Guinea and the Island Arc, thus also isolating populations in each area that subsequently diverged. There is, however, no evidence for the existence of the necessary connection. The issue becomes even more complicated when one realizes that four of the five species of the Prooculis Group exist allopatrically either on the New Guinea coast or on the islands adjacent to the coast (the hypothesized scenario could hold if any of the three other New Guinea species, or combinations of them, is the sister group of *E. prooculis*).

DISTRIBUTION.—Known only from Goodenough Island, D'Entrecasteaux Islands, and nearby Basilaki Island, Papua-New Guinea.

ETYMOLOGY.—The species name is from the Latin taenia, meaning stripe, and refers to the stripes on the body.

HOLOTYPE.—USNM 277494, female, 32 mm SL, Papua-New Guinea, Milne Bay District, Basilaki Island; coral reef, 0–20 ft [0–6 m], Tyson Roberts, 22–25 August 1975.

PARATYPES.—USNM 217566, male, 28 mm SL, collected with the holotype. WAM P24913, male, 32 mm SL, D'Entrecasteaux Islands, Goodenough Island, G.R. Allen, 28 May 1972.

PICTUS GROUP

This group comprises a single species, *Ecsenius pictus*. I am unable to hypothesize its sister group, which is probably among those species groups that, like *E. pictus*, are characterized by having a dark postorbital stripe and deeply incised dorsal fin: Lineatus, Mandibularis, Oculus, Opsifrontalis, Prooculis, Yaeyamaensis. The Pictus Group and all these groups, except the Lineatus Group, are also characterized by having relatively low fin-ray and caudal vertebral counts (all other species groups of *Ecsenius* have high counts). The color pattern of *E. pictus* is distinctive (see description below) and sets it apart from all other species of *Ecsenius*.

It is of interest, perhaps, that among the six groups listed above, *E. pictus* comes closest to being completely allopatric to the Lineatus Group, which is the only one of the six that is monotypic. I find no character that would indicate that *E. pictus* might be more closely related to *E. lineatus* than to another of the six species groups, unless the low meristics of *E. pictus* are specializations shared with one or more of the groups that also exhibit them.

Ecsenius pictus McKinney and Springer

FIGURE 61; PLATE 13: FIGURES 3, 4; TABLE 29

Ecsenius pictus McKinney and Springer, 1976:19 [Great Banda Island, Molucca Islands, Indonesia; holotype, USNM 213853].

DESCRIPTION.—Dorsal fin XII,13–15, deeply notched between spinous and segmented-ray portions. Anal fin II,15–17. Pectoral fin 13 (rarely 12 or 14 unilaterally). Segmented caudal-fin rays 13. Vertebrae 10 + 21–23 (rarely 23). Dentary incisor teeth 40–48 (includes anterior canine teeth, which differ little, if at all, in appearance from incisors); posterior dentary canines 1 on each side (rarely 2). Lateral line without vertical pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8 and 11. Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In preservative, body dark brown with up to 8 pale pinstripes; mid-lateral pale stripe often with series of pale enlargements (spots) along its length; irregular row of pale spots often present near dorsal body contour, spots ending well before caudal peduncle; caudal peduncle with irregular, broad, pale and dark markings, sometimes appearing as alternating pale and dark bands (up to 4 pale and 3 dark). Mid-lateral pale stripe on body and another above it extend anteriorly on head to posterior margin of orbit; dark postorbital stripe often inconspicuous (see life color below). Head and cheeks dorsally as dark as body or considerably paler; underside of head less dark than dorsal surface; lower lip darkly dusky anteriorly, followed posteriorly by narrow, immaculate, pale area, and diffuse darkly dusky area. Pectoral-fin base with prominent pale stripe; irregular pale markings often present dorsal to stripe. Pectoral and caudal fins with dusky pigment along rays. Anal fin dusky with indistinct pale basal stripe. Dorsal fin dusky at base and along proximal half of rays; diffuse pale stripe may interrupt dusky basal area. Pelvic fins unmarked or faintly dusky proximally.

Live Color (based on color photographs published by Debelius (1986:92) and taken in the wild at Kakabia Island, Indonesia; augmented by photographs of fresh specimens from the Molucca and Solomon islands): Head paler than body, brownish dorsally above mid-orbital level, paler pinkish brown below; iris of eye with almost complete bright-white ring around pupil (ring with gap ventrally); about 4 bright-yellow spokes radiating dorsally from ring; bright-yellow spots in dark part of iris between spokes; fine, bright-yellow spots in two lines across front of snout; fine, bright-white stripe dorsally on each side of interorbital area; bright-yellow spot on postorbital margin at 2 o'clock position, short, fine, bright-yellow stripe at 3 o'clock position, and bright-white stripe at 4 o'clock position extending posteriorly across head onto body

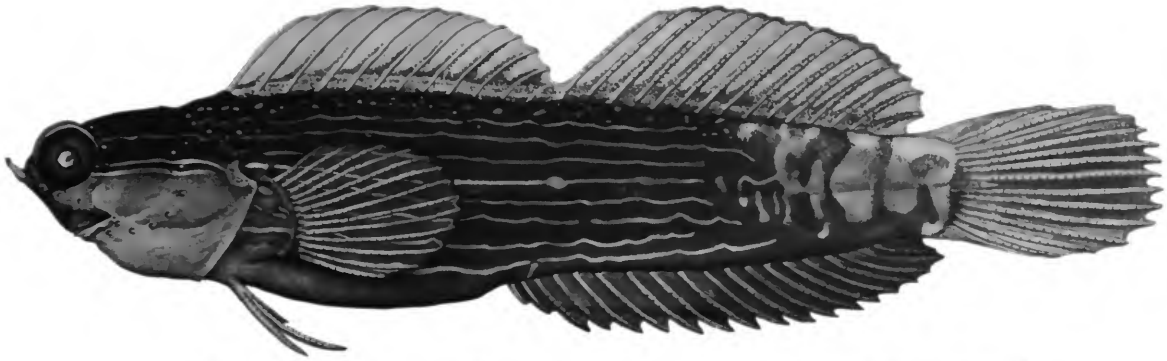


FIGURE 61.—*Ecsenius pictus*, BPBM 15612, male, 42 mm SL, Alite Reef off Malaita, Solomon Islands (drawn by J.R. Schroeder).

(3 and 4 o'clock stripes border dark postorbital stripe); ground color of body dark purplish brown; spots and pinstripes on body brilliant white, pale bands on caudal peduncle pale yellow, of which anteriormost is saddle-like and, in living individuals, brightest; bands equally yellow in freshly collected specimens.

The photograph published in Debelius (1986), shows an individual that conforms with the above description, except that there is no white ring around the pupil; instead, two fine, bright stripes, more or less continuous with the 3 and 4 o'clock stripes (see above), pass dorsal and ventral to the pupil (ventral stripe interrupted by pupil); and 3 o'clock stripe extends across head to body. In photographs of fresh specimens from the Molucca and Solomon islands, the area around the mouth and underside of the head are yellow.

SEXUAL DIMORPHISM.—Female specimens from the Philippine Islands have significantly higher average numbers of dentary incisor teeth than do males ($t = 3.03$; $p = < 0.01$; df = 23; Table 29).

GEOGRAPHIC VARIATION.—Specimens from the Solomon Islands have more dentary incisor teeth and higher average meristics than specimens from the Philippine, Molucca, and Bone Rate islands (Table 29).

REMARKS.—*Ecsenius pictus* is one of the deeper dwelling species of *Ecsenius*. All specimens have been collected at depths ranging from 10.7–40.3 m.

DISTRIBUTION.—Known only from the Philippines; Indonesia: Molucca (Great Banda, Saparua) and Bone Rate

TABLE 29.—Frequency distributions for certain characters of *Ecsenius pictus*.

Localities	Segmented dorsal-fin rays				Segmented anal-fin rays				Caudal vertebrae			
	13	14	15	$\bar{x}$	15	16	17	$\bar{x}$	21	22	23	$\bar{x}$
Philippines	6	23	1	13.8	1	26	1	16.0	5	20	2	21.9
Indonesia	5	4		13.4	4	5		15.6	5	4		21.4
Solomons			4	15.0			4	17.0		4		22.0

Localities	Dentary incisor teeth									
	40	41	42	43	44	45	46	47	48	$\bar{x}$
Philippines										
males	3	1	4	1						41.3
females	1	1	4	3	4	3				43.1
Indonesia										
males	1	1	1							41.0
females		3	1							41.2
Solomon Islands										
males							1	1		46.5
females									1	

(Telerang, Kakabia) islands; and Solomon Islands: Malaita.

MATERIAL (* = new material).—*Indonesia:* Great Banda Island, USNM 213853 (holotype: 33 mm SL), 211895 (1 specimen: 31), CAS 34245 (1:23); Saparua, USNM 210056 (1:18); Moromaho Island, CAS 59539* (1:33); Bone Rate Group, Telerang, BPBM 31513* (3:21–34), Kakabia, BPBM 31497* (1:21). *Solomon Islands:* Alite Reef off Malaita, BPBM 15612 (1:35), 15624 (1:35), 15940 (1:37); Guadalcanal, BPBM 19016 (1:20). *Philippine Islands:* Siquijor Island, USNM 219316* (1:36), 219319* (1:40), 226995* (1:16), 227001* (4:14–38); Balicasag Island, USNM 226996* (5:14–41); Solino Island, Mindanao, USNM 226997* (1:50); Negros Island, USNM 219310* (2:38, 50), 219314* (2:35, 39); Pescador Island, Cebu, USNM 226994* (2:30, 37), 226998* (3:28–36); Mactan Island, Cebu, USNM 219318* (2:18, 31), 227000* (1:25); Cebu, USNM 226999* (6:28–37).

MANDIBULARIS GROUP

This group comprises four species: *E. mandibularis, E. schroederi, E. aequalis,* and *E. kurti.* The hypothesized synapomorphy that I believe indicates the monophyly of the group pertains to the number of posterior canine teeth: in specimens over 25 mm SL, there are 4–8 posterior canine teeth on at least one side (dentary bone) of the lower jaw (usually both dentaries have at least 4). All other species of *Ecsenius* normally have only 1 posterior canine tooth on each side, and never have more than 2. The posterior canines are arranged in a row perpendicular to the row of incisoriform teeth. The only other genus of Blenniidae that normally has more than one posterior canine tooth on each side is the monotypic salariinin genus *Glyptoparus* Smith. *Glyptoparus* exhibits no other specialization that might indicate it as the sister group of *Ecsenius,* and I believe that the presence of multiple posterior canines in the two genera is homoplasious.

The species of the Mandibularis Group are moderately small, attaining a maximum SL of about 33–51 mm, and have deeply-notched dorsal fins and similar meristics. They differ primarily in color pattern. The species are allopatric for the most part, but the Great Barrier Reef portion of the range of *E. aequalis* overlaps the northern portion of the range of *E. mandibularis.* There are considerable gaps between and/or within the ranges of the species; more so than one would expect if the gaps are not collecting artifacts. I am unable to hypothesize unequivocally the intragroup relationships.

Ecsenius aequalis, new species

FIGURE 62; PLATE 14: FIGURES 3, 4; TABLE 30

DESCRIPTION.—Dorsal fin XII,13–15 (14 in 85% of specimens). Anal fin II,14–17 (16 in 84% of specimens). Pectoral fin 12–14 (rarely 12 or 14, and only unilaterally). Segmented caudal-fin rays 13. Vertebrae 10 + 21–23 (22 in 87% of specimens). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 42–51; posterior dentary canines (specimens at least 25 mm SL) 4–8 on each side (only two of 52 specimens had 8, unilaterally; specimens 20 mm SL or less have 0–4). Lateral line without pairs of pores, terminating posteriorly at point between vertical from dorsal-fin spine 9 and vertical from interspace between spines 11 and 12 (rarely reaching past vertical from spine 11). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: In Great Barrier Reef specimens: head varying from generally pale dusky (females and small males) to darkly dusky (large males), ventral surface infrequently with diffuse, faint stripe on each side extending posteriorly from just posterior to lower jaw and curving up along posterior margin of opercle (usually fading out before reaching opercle margin). body usually exhibiting three slender, dark stripes separated by about equal interspaces in region of pectoral-fin axil; stripes often variously interrupted; dorsal stripe originating in region above anterior oblique portion of lateral line or on horizontal portion of lateral line, proceeding posteriorly along lateral line, and terminating at some point below segmented-ray portion of dorsal fin; middle stripe originating no further anteriorly than intersection of oblique portion of lateral line with head and terminating as far posteriorly as caudal-fin base (usually ceasing well anterior to fin base); ventral stripe originating as far anteriorly as pectoral-fin axil and ceasing posteriorly at some point anterior to caudal-fin base; occasional specimens have stripes represented by only a few diffuse, dash-like markings, and one small specimen (21 mm SL) from the Trobriand Islands exhibited ventral two stripes anteriorly, but each appearing as row of 4 or 5 fine, dark spots posteriorly. Specimens from Osprey Reef vary from lacking body stripes to having the stripes restricted to the anterior half of the body, where they are poorly developed and frequently interrupted.

Dorsal fin: spinous portion anteriorly with fine melanophores along spines, posteriorly with melanophores partially filling interradial membranes; segmented-ray portion with slender, immaculate area basally forming stripe, from which melanophores extend dorsally along rays, concentrating ventrally and at ray tips, thus giving appearance of two, somewhat diffuse stripes (Osprey Reef specimens lack concentrations at ray tips); interradial membranes more densely pigmented in males than females. Anal fin generally dusky, but ray tips pale; melanophores often concentrating in membranes just proximal to ray tips, giving appearance of subdistal stripe. Pectoral fin with melanophores along rays. Pelvic fins ranging from immaculate to rays with sparsely distributed melanophores. Caudal-fin rays essentially unmarked except for fine, dusky margining dorsally and ventrally on each ray; membranes varying from almost clear (females) to almost uniformly dusky (large males).

A freshly collected specimen from the Great Barrier Reef, posed underwater, is shown in color on Plate 14: figure 3. The species either has no distinctive color in life or, more probably,

this particular specimen has faded. Photographs of living specimens at Osprey Reef (e.g., Plate 14: figure 4), show fishes that are generally cream colored, varying from lacking dark body stripes and pigmentation in the fins to having some dark dash-like marks on body. Most notable in the Osprey Reef specimens is the black pupil of the eye surrounded by a broad, white ring, which is surrounded by a slender, yellow ring. The yellow ring is perimital in lateral view, but the dorsal surface of the eye medial to the ring is black with fine yellow spots.

REMARKS.—Specimens from Osprey Reef differ from those from the Great Barrier Reef in size and color pattern. Randall (pers. comm.) noted that he saw only small individuals of *E. aequalis* at Osprey Reef, and the largest specimen I have from there is a mature male only 28 mm SL. Females are well developed by 21 mm SL, and the largest I have is but 23 mm. At the Great Barrier Reef, males and females attained 34 and 32 mm SL, respectively. Differences in color pattern from the two areas were noted above. I do not believe that the differences warrant naming the different populations.

The species has been collected at depths between 2 and 11 meters.

COMPARISONS.—*Ecsenius aequalis* is most similar to *E. kurti*, from which it differs primarily in color pattern. In *E. kurti*, the posterior terminus of each of the two more ventral body stripes (and often the dorsalmost stripe as well) is followed by a row of 3–6 dark spots. The posteriormost spot of the upper of the two rows is exactly at the base of the caudal fin. This condition is adumbrated only in the smaller of the two available Trobriand Islands' specimens of *E. aequalis* (see color-pattern description above). The spots in this latter specimen are not as marked as those in any of the *E. kurti* specimens, and the specimen did not have a spot at the base of the caudal fin. Furthermore, specimens of *E. kurti* often exhibit a well-defined pair of stripes under the head, whereas such stripes are only diffusely and uncommonly present in *E. aequalis*. Many specimens of *E. kurti*, particularly females, have a dusky stripe, or diffuse indications of one, on the fleshy pectoral-fin base. None of the specimens of *E. aequalis* exhibit such a stripe. Additionally, the lateral line of *E. aequalis* tends to be longer than that of *E. kurti*, and the number of dentary incisor teeth tends to be greater (Table 30).

There is a large gap between the geographic ranges of *E. aequalis* and *E. kurti* from which one might expect to find populations of *Ecsenius* that are intermediate in morphology

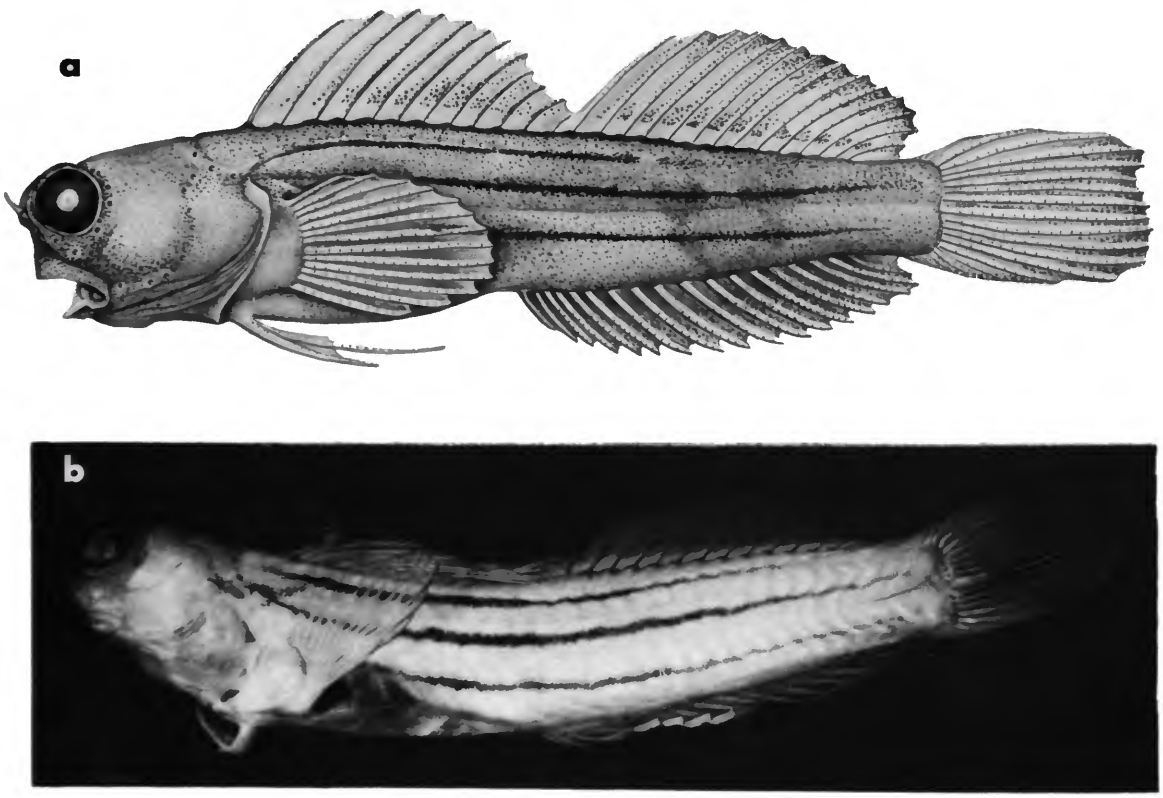


FIGURE 62.—*Ecsenius aequalis: a*, AMNH 55722, male 22 mm SL, Escape Reef, Great Barrier Reef, Australia (drawn by J.R. Schroeder); *b*, USNM 217567, male, 28 mm SL, Kiriwina Island, Trobriand Islands, Papua New Guinea (photograph by K.A. Bruwelheide).

between these two species, thus portending the invalidity of recognizing two taxa for the available specimens. The presence of *E. schroederi* in the middle of this gap (Figure 13) leads me to believe that such populations will not be found. Supporting evidence for my decision to recognize the two species may also be indicated by the fact that there are many endemic species of fishes in the Philippines, including *Ecsenius dilemma* and, essentially, *E. bimaculatus*.

Ecsenius aequalis is sympatric with *E. mandibularis* over the northern portion of the latter species' distribution. Some pale specimens of *E. mandibularis* exhibit diffuse indications of three stripes on the body and, thus, might be confused with *E. aequalis*. *Ecsenius mandibularis* usually has a postorbital stripe and/or two rows of dusky spots on the body, markings that *E. aequalis* lacks. *Ecsenius mandibularis*, in general, has higher meristics and attains a larger size than *E. aequalis*.

DISTRIBUTION.—Known only from the northern portion of the Great Barrier Reef off Queensland, Osprey Reef in the Coral Sea, and the Trobriand Islands.

ETYMOLOGY.—The name aequalis is derived from the Latin word for "equal," and refers to the approximately equal spacing of the dorsal and ventral stripes relative to the middle stripe. The name is here used as a noun in apposition.

HOLOTYPE.—AMS I.22586-076, male, 28.6 mm SL, Australia, Queensland, Escape Reef North, hole in bommie [coral head] in lagoon, 2–6 m, coral sand, 30 October 1982.

PARATYPES.—*Australia, Queensland:* Escape Reef, AMS I.22586-014 (8 specimens: 15–32 mm SL) and USNM 278048 (3:26–31, collected with holotype); AMS I.22633-017 (18: 18–34), AMNH 55723 (1:24), 55722 (4:18–24), ROM 40449 (3:30–32), 40450 (5:15–30), 40451 (3:15–25); Yonge Reef, AMS I.18740-017 (10:15–32), I.19472-016 (1:20), I.19546-024 (5:13–31); Lizard Island, AMS I.19473-065 (1:31). *Papua–New Guinea, Trobriand Islands, Kiriwina Island:* USNM 217567 (2:21, 28). *Coral Sea:* Osprey Reef, AMS I.25113 (13:16–28); BPBM 31040 (6:17–26).

Ecsenius kurti, new species

FIGURE 63; TABLE 30

DESCRIPTION.—Dorsal fin XII,13–15 (modally 14). Anal fin II,14–17 (modally 16). Pectoral fin 13 or 14 (14 in only one specimen, and only unilaterally). Segmented caudal-fin rays 13. Vertebrae 10 + 21–23 (modally 22). Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 42–46; posterior dentary canines (specimens at least 25 mm SL) 4–7 on each side. Lateral line without pairs of pores, terminating posteriorly at point between

TABLE 30.—Frequency distributions for certain characters in species of the Mandibularis Group.

Species	Segmented dorsal-fin rays					Segmented anal-fin rays					
	13	14	15	16	$\bar{x}$	14	15	16	17	18	$\bar{x}$
aequalis	8	70	4		14.0	1	9	58	1		15.9
kurti	3	7	3		14.0	1	4	7	1		15.6
mandibularis		23	67	10	14.9			33	61	5	16.7
schroederi	10	25			13.7		11	24			15.7

Species	Caudal vertebrae					Lateral line extends to vertical at dorsal-fin spine					
	21	22	23	24	$\bar{x}$	8	9	10	11	12	$\bar{x}$
aequalis	3	60	6		22.0		2	30	22		10.4
kurti	2	6	4		22.2		3	8	1		9.8
mandibularis	1	36	52	6	22.7		2	38	16	2	10.3
schroederi	3	30	2		22.0	1	5	8			9.5

Species	Dentary incisor teeth													
	41	42	43	44	45	46	47	48	49	50	51	52	53	$\bar{x}$
aequalis		1	1	2	2	7	12	18	7	9	1			47.6
kurti		1	2	4	1	4								44.4
mandibularis					5	6	12	20	22	11	8	2	1	48.5
schroederi	1	-	1	2	7	6	-	3	2	-	-	-	1	46.0

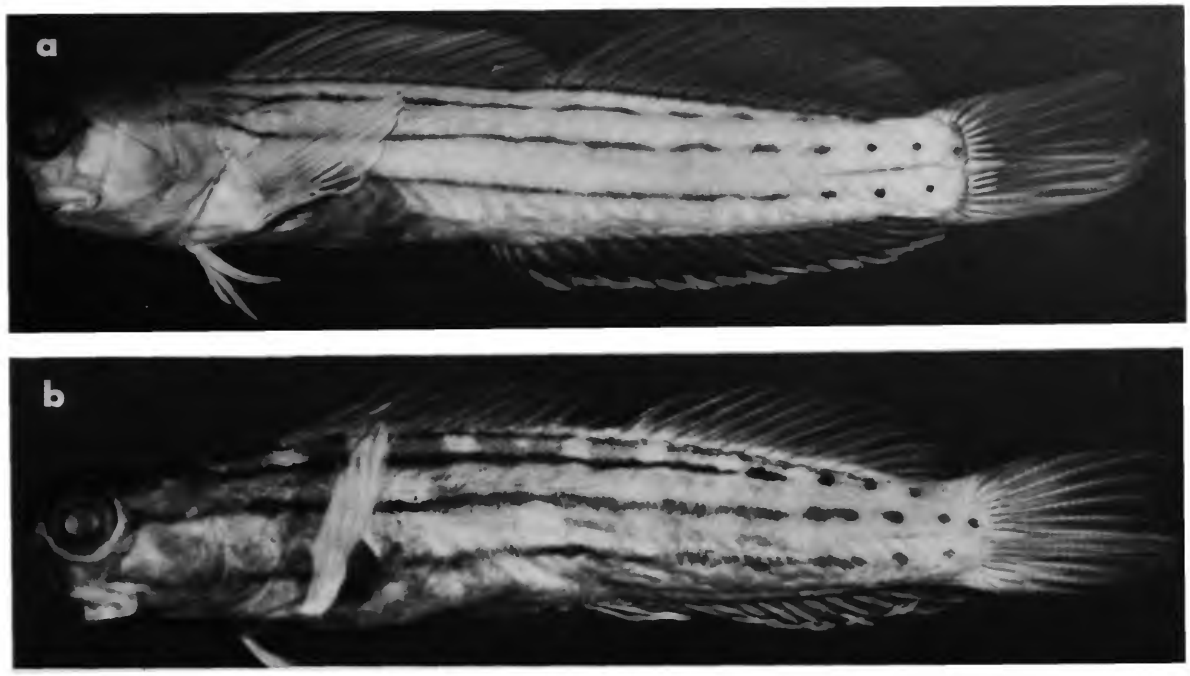


FIGURE 63.—*Ecsenius kurti*, Cuyo Islands, Philippines: *a*, USNM 227416, holotype, male, 35.0 mm SL, Bararin Island (photograph by K.A. Bruelheide); *b*, USNM 219303, female, 30 mm SL, Tagauayan Island (photograph by J.M. Clayton).

verticals from dorsal-fin spine 9 and interspace between spines 10 and 11 (modally reaching vertical from 10). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Head variable, generally pale to moderately darkly dusky (darker in males than females), often darkest above mid-orbital level; dusky spot often present at mid-postorbital margin, occasionally continuing posteriorly across head, particularly on opercle, as dark or diffuse, faintly dusky stripe, which connects with middle body stripe; some specimens with short, diffuse, dusky stripe on ventral third of opercle; ventral surface of head usually with indications of slender, dark stripe on each side extending posteriorly from just posterior to lower lip and ceasing before reaching margin of gill opening. Body with three slender, dark stripes separated by equal interspaces in region of pectoral-fin axil; stripes continuous anteriorly, changing posteriorly, usually in region below segmented-ray portion of dorsal fin, to dashes, then fine, dark spots (usually 4 or more spots in each "stripe"); dorsal stripe originating in region above anterior, oblique portion of lateral line, proceeding posteriorly along lateral line, and terminating at some point below posterior region of segmented-ray portion of dorsal fin; middle stripe originating as far anteriorly as head and terminating posteriorly as dark spot at caudal-fin base; ventral stripe originating in pectoral-fin axil and ceasing posteriorly as dark spot on caudal peduncle well anterior to caudal-fin base; some specimens exhibited 7 or 8 faintly dusky bands along dorsal body contour, extending ventrally and becoming offset in space between two ventral dark stripes. Dorsal fin: spinous portion with fine melanophores distributed along spines, least dense in interradial membranes closely adjacent to spines, and narrowly along fin base; segmented ray portion with slender, immaculate area (stripe) just above base, from which melanophores extend dorsally along rays, diffusely concentrating ventrally (giving impression of faint suprabasal stripe in males); few melanophores at ray tips (in males). Anal fin generally dusky with pale ray tips; melanophores concentrating in membranes just proximal to ray tips, giving appearance of subdistal stripe. Pectoral fin with melanophores along rays; fleshy base usually with indication of fine, dark stripe at about mid-level. Pelvic fins ranging from immaculate to rays with sparsely distributed melanophores. Caudal-fin dusky basally with rays essentially unmarked except for fine, dusky margin dorsally and ventrally on each ray; membranes of central rays variably dusky, others almost clear.

COMPARISONS.—See this section under *Ecsenius aequalis*.

DISTRIBUTION.—Known only from the Cuyo Islands, Palawan Province, Philippine Islands.

ETYMOLOGY.—*Ecsenius kurti* is named for Kurt A. Bruwelheide, former museum specialist in the Division of Fishes, who participated in much of the early work of this study.

HOLOTYPE.—USNM 227416, male, 35.0 mm SL, Philippine

Islands, Palawan Province, Cuyo Islands, Bararin Island, west side, 0–13.7 m, 23 May 1978, Smithsonian Institution and Silliman University teams.

PARATYPES.—Philippine Islands, Palawan Province, Cuyo Islands: Bararin Island, USNM 219305 (7 specimens: 12–32 mm SL; collected with the holotype), 219311 (3:26–30); Tagauayan Island, USNM 219303 (2:30, 33).

Ecsenius mandibularis McCulloch

FIGURE 64; PLATE 14: FIGURE 5; TABLE 30

Ecsenius mandibularis McCulloch, 1923:122 [Masthead Island, Australia; holotype, AMS I.7112].
Ecsenius (Ecsenius) mandibularis.—Springer, 1971:39 [redescription].

DESCRIPTION.—Dorsal fin XI–XII (XII in 96% of specimens), 14–16 (modally 15). Anal fin II,16–18 (modally 17). Pectoral fin 12 or 13 (rarely 12). Segmented caudal-fin rays 13. Vertebrae 10 or 11 (11 in only 1 of 90 specimens) + 21–24 (rarely 21, modally 23) = 31–34. Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 45–53; posterior dentary canines (specimens at least 25 mm SL) 3–8 on each side (rarely 3). Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 9 and 11 (rarely failing to reach past vertical from 9). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Specimens may range from almost uniformly pale, with no distinct marks to darkly dusky anteriorly, grading into moderately dusky posteriorly (females within a collection generally less dark than males). Occasionally, there is a dark, somewhat diffuse, stripe extending posteriorly from the orbit across the head; margining the stripe ventrally, there may be a more slender, pale stripe; on each side of the ventral surface of the head, there is usually evidence of a fine, dark stripe that extends posteriorly from the lower lip to the margin of the gill membrane; the stripe is in line with a similar, fine, dark stripe that borders the ventral margin of the fleshy pectoral-fin base; this latter stripe may extend anteriorly onto the breast area covered by the gill membrane. Many specimens exhibit two longitudinal rows of widely-spaced, small, dark spots; the upper row usually begins in the area between the dorsal-fin origin and the lateral line, terminating on the upper portion of the body at some point below the segmented dorsal-fin rays; the ventral row begins just dorsal to the midline of the body and no further anteriorly than a vertical from the anus, and extends to the caudal-fin base, where the terminal spot is on the body midline. Uncommonly, nonspotted specimens may exhibit several, faint, dusky bands dorsally on the body. Dorsal fin: of males almost uniformly dusky; spinous portion of females with melanophores mostly restricted to base and along spines, segmented ray portion with melanophores in interradial membranes just suprabasally, coursing along spines, and as narrow distal edging. Anal fin dusky, paler proximally (giving appearance of pale basal stripe) and distally. Pectoral fin dusky basally and along rays. Pelvic fins dusky. Caudal fin dusky basally; more or less uniformly dusky elsewhere in males, except melanophores very sparse over rays; females similar but interradial membranes dorsally and ventrally with clear areas.

Live or Fresh Color (Plate 14: figure 5): The main difference between preserved and live coloration is that the pale postorbital stripe and spots on the body are bluish; the color is otherwise overall buff grayish. Some over-exposed color slides taken in the wild on the Great Barrier Reef show the species to be generally buff colored with two rows of white spots on the body.

SEXUAL DIMORPHISM.—Aside from color pattern described above, large, mature males tend to have longer dorsal and anal fin elements than females (Springer, 1971), and most of the caudal-fin rays of males tend to elongate.

COMPARISONS.—Within its species group, and aside from color pattern, *E. mandibularis* is distinct in attaining a larger size (51 mm versus 36 mm SL) and in having generally higher average numbers of segmented dorsal and anal-fin rays and caudal vertebrae than the other species. See also comparisons section under *E. aequalis*.

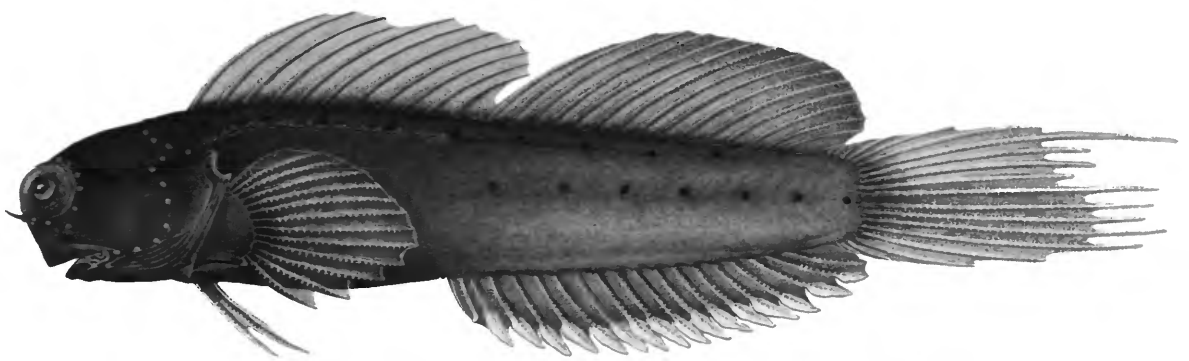


FIGURE 64.—*Ecsenius mandibularis*, USNM 201820, male, 51 mm SL, One Tree Island, Great Barrier Reef (drawn by M.H. Lester).

DISTRIBUTION.—*E. mandibularis* is restricted to the reefs on the coast of Queensland, Australia, from Haggerstone Island and Cape York Peninsula in the north to the Bunker Group reefs (due east of Gladstone) in the south.

MATERIAL (* = new material).—*Australia, Queensland:* Haggerstone Island, Cape York Peninsula, AMS I.20937.011* (1 specimen: 39 mm SL); Lizard Island, AMS I.18739-017* (1:29), I.21943-024* (1:35); Endeavour Reef, ANSP 109692 (1:30), 109694 (2:28, 35), 109696 (14:21–37), 109698 (1:21); Egret Reef, BPBM 31714* (1:38); Little Hope Island [near Endeavour Reef], ANSP 109693 (4:27–37), 109695 (1:19); Big Hope Island [near Endeavour Reef], ANSP 109697 (1: 30); Gillett Cay, Swains Reef, AMS IB.6222 (4:28–36), IB.6237 (2:16, 18); Masthead Island, Capricorn Group, AMS I.7112 (48, holotype of *Ecsenius mandibularis*), I.7114-6 (6:34–51); One Tree Island, Capricorn Group, USNM 201367 (2 of 56:32, 44, cleared and stained), 201820 (40:16–51), 201821 (57:30–49); Hoskyn Island, Bunker Group, AMS IA.3585 (1:35).

Ecsenius schroederi McKinney and Springer

FIGURE 65; PLATE 14: FIGURE 6; TABLE 30

Ecsenius schroederi McKinney and Springer, 1976:21 [Ambon; holotype, USNM 209743].

DESCRIPTION.—Dorsal fin XI–XIII (XII in 88% of specimens), 13 or 14 (modally 14). Anal fin II,15 or 16 (modally 16). Pectoral fin 13 or 14 (rarely 14). Segmented caudal-fin rays 13. Vertebrae 10 or 11 (11 in only 1 of 34 specimens) + 21 to 23 (22 in 86% of specimens) = 31–33. Dentary incisor teeth (includes anterior canine teeth, which differ little, if at all, in appearance from incisors) 41–53 (only 1 of 23 specimens with more than 49); posterior dentary canines (specimens at least 25 mm SL) 3–6 on each side (usually more than 3; one specimen had none on one side and 6 on the other; specimens 20–24 mm SL usually have 3 or 4). Lateral line without pairs of pores, terminating posteriorly at point between verticals from dorsal-fin spines 8 and 10 (rarely failing to reach past vertical from 8). Cirrus present on posterior rim of anterior nostril; none on anterior rim.

Preserved Color: Head dusky, occasionally darker dorsally and anteriorly; fine, dusky stripe often extending posteriorly from mid-postorbital margin to upper posterior edge of opercle; indistinct, fine, dusky stripe, often originating just posterior to corner of mouth and extending across lower cheek onto opercle; fine, dusky stripe often on ventrolateral surface of head, originating just medial to anteriormost mandibular sensory pore and extending posteriorly almost to margin of gill membranes. Body pale with three, dark, wavy pinstripes; dorsalmost stripe extends from supratemporal canal posteriorly along lateral line to point below segmented-ray portion of dorsal fin; middle stripe is continuation of mid-postorbital stripe (if present), dips ventrally in region covered by appressed pectoral fin and continues to, or almost to, caudal-fin base; ventral stripe originates at dorsalmost point of pectoral-fin axil and extends posteriorly to, or almost to, caudal-fin base; stripes may be variously interrupted; a few indistinct, pale spots may be present between ventral two stripes. Dorsal fin: spinous portion with strip of melanophores basally, above which is slender immaculate area from which sparsely distributed melanophores extend dorsally along spines; segmented-ray portion without melanophores basally, but with melanophores extending up rays. Anal fin generally dusky basally up to distal margin of incised interradial membranes, at which level melanophores concentrate to form diffuse stripe; ray tips paler distal to stripe. Pectoral fin dusky basally, with melanophores coursing along rays, infrequently with diffuse stripe-like marking on fleshy portion. Pelvic fins almost immaculate. Caudal fin with dusky area basally and melanophores coursing along rays.

Live Color (from color photograph taken by G.R. Allen at Rowley Shoals): Head dark gray above mid-orbital level, abruptly paler gray below, with fine, white stripe between the two areas; upper half of the eye black, lower half white; black portion with yellow spots and spokes connected to faint-yellow half ring bordering pupil dorsally. Body similar in color to dorsal portion of head, with row of five white spots along

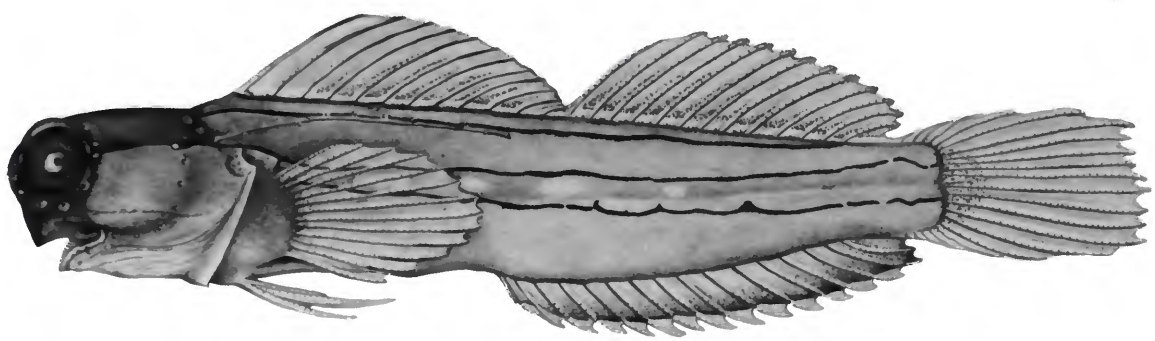


FIGURE 65.—*Ecsenius schroederi*, USNM 209743, holotype, male, 24 mm SL, Ambon Island, Moluccas (drawn by J.R. Schroeder).

dorsal contour anteriorly and row of six, larger, white spots anteriorly between two dark, ventral-body stripes. Debelius (1986:96) reproduces a color photograph of *E. schroederi* in life, much the same as that described here, except that his figure shows six white spots dorsally and seven between the dark stripes.

COMPARISONS.—*E. schroederi* has a distinctive color pattern within its group, as well as within *Ecsenius* as a whole. The striped pattern on its body might be confused with that of some specimens of *E. aequalis* and *E. kurti* that have the body stripes represented as fine lines, but the latter two species are easily separable from *E. schroederi*. In the anterior region of the body of *E. aequalis* and *E. kurti*, the space between the lower and middle stripes and that between the middle and upper stripes are about equal in depth, or the lower space is only slightly less deep than the upper space. In *E. schroederi*, in the same region of the body, the depth of the lower space is about half the depth of the upper space.

DISTRIBUTION.—Known only from the Moluccas and Scott Reef and Rowley Shoals, off northwestern Australia.

MATERIAL (* = new material).—*Indonesia, Moluccas:* Ambon Island, USNM 209743 (holotype: 24 mm SL); Ceram, Marsegoe Bay [~3°S, 128°E], AMS I.18469-132* (1:29). *Off northwestern Australia:* Scott Reef, AMS I.21315-031* (1:23), I.21316-032* (1:22), I.21318-025* (3:13–14); Rowley Shoals, Clerke Reef, WAM P.27658-014* (9:23–30), P.27665-002* (7:22–34), P.27662-025* (12:22–36).

Appendix I

Speculative Discussion of the History of the Present-day Distribution of the Oculus-Yaeyamaensis Clade

I have hypothesized a sister-group relationship for the Oculus and Yaeyamaensis groups based primarily on a few shared color-pattern characters (see discussion under account of Yaeyamaensis Group). After arriving at this hypothesis, I noted not only that all of the species within each of the two component species groups are allopatric, but also that 12 of the 13 species contained in the hypothesized clade are allopatric (Figures 9 and 10). The thirteenth species, *E. yaeyamaensis,* is broadly sympatric with six of the eight species of the Oculus Group. Considering the overall present distributions of the two species groups, I found it instructive to examine how these distributions might have developed. Obviously, the partial sympatry of the two groups is evidence for dispersal.

I am unable to hypothesize unequivocally the interrelationships of the species within each of the two groups, which, methodologically, should precede vicariance scenarious such as I will propose. I have proposed interrelationships for some of the species of the Oculus Group, however, based on color pattern and distribution of the species (see account of Oculus Group), and I will propose others for some of the species of the Yaeyamaensis Group (see Appendix II). Based on past tectonic and sea-level changes, I will also propose possible vicariance scenarios that could have resulted in the present-day distributions of some of the species of the Oculus Group and will discuss others for some of the species of the Yaeyamaensis Group (also in Appendix II).

A summary of my scenario for arriving at present-day distributions of the Oculus and Yaeyamaensis groups is given in Figure 66. This figure should be compared with the present-day species distribution maps of the Oculus and Yaeyamaensis groups (Figures 9 and 10) when assessing the discussion that follows.

I have been unable to hypothesize the sister group of the Oculus-Yaeyamaensis clade. Lacking that and information on the distribution of the sister group, I am unable to hypothesize the vicariant event (and its timing) that preceded the evolution of the common ancestor. For purposes of discussion, I have arbitrarily set the timing of the event as 80 m.y.a. (Figure 66*a;* Upper Cretaceous). Although the common ancestor may have existed earlier than 80 m.y.a., I doubt that it continued to exist much more recently than 40 m.y.a., as explained below.

I propose that the overall distribution of the common ancestor of the clade included the southeastern coasts of the Asian Plate and east coast of Africa, just as the combined distribution of the clade does today. Although I show the ancestor's distribution extending northwestward into the Eurasian Tethys, such extension would not have been necessary for my scenario if ancient land masses (e.g., island chains) stretched between eastern Africa and southeast Asia. The distribution of the common ancestor probably did not include the Red Sea, which began forming between 16 and 41 m.y.a. (time varies according to different investigators; summarized in Cochran, 1983:48). A Miocene opening, about 7–25 m.y.a., for the southern Red Sea appears to be favored (Klausewitz, 1983). The distribution also probably did not extend to Australia, which was well separated from the southeast Asian and east African areas by 80 m.y.a.

India (plus Madagascar) had separated from African Gondwana long before 80 m.y.a., and slightly before 80 m.y.a. had separated from Madagascar and begun its movement north toward Asia (Norton and Sclater, 1979). It is possible, therefore, that the distribution of the common ancestor included Ceylon, which was integral with India, by the time of Figure 66*a,* even though I first indicate the ancestor's presence in Ceylon in Figure 66*b,* 60 m.y.a.

No species of the Oculus-Yaeyamaensis clade is currently known from the coast of India or Madagascar, and I have not included these two areas in the past distribution of the common ancestor of the clade. The present absence of representatives of the clade from Madagascar is possibly a collecting artifact; few reef-fish collections have been made there. Such does not appear to be the case with India, however, which has an active community of ichthyologists. A great many extant, widely distributed, Indo-Pacific species of coral-reef associated organisms appear to be absent from the peninsular coast of India (but not the coast of Madagascar). This is due to the general absence of coral reefs on all but the southernmost portion of that coast (Sewell, 1932), which is well supplied with river deltas and sandy shores. The consequences of the absence of coral reefs on the coast of India are important and will be mentioned again below.

In Figure 67*a,* the Indian Ocean area is depicted at about 75 m.y.a. (McKenzie and Sclater, 1973). At this time the Seychelles and Mascarene Plateau were attached to India.

In Figure 66*b* (~60 m.y.a.) I propose that India's continued movement north constricted the range of the common ancestor of the Oculus-Yaeyamensis clade. Current studies (Klootwijk et al., 1986) indicate that India first collided with Asia about 60 m.y.a. The initial contact was only at the northwestern corner of India. By this time the common ancestor of the clade

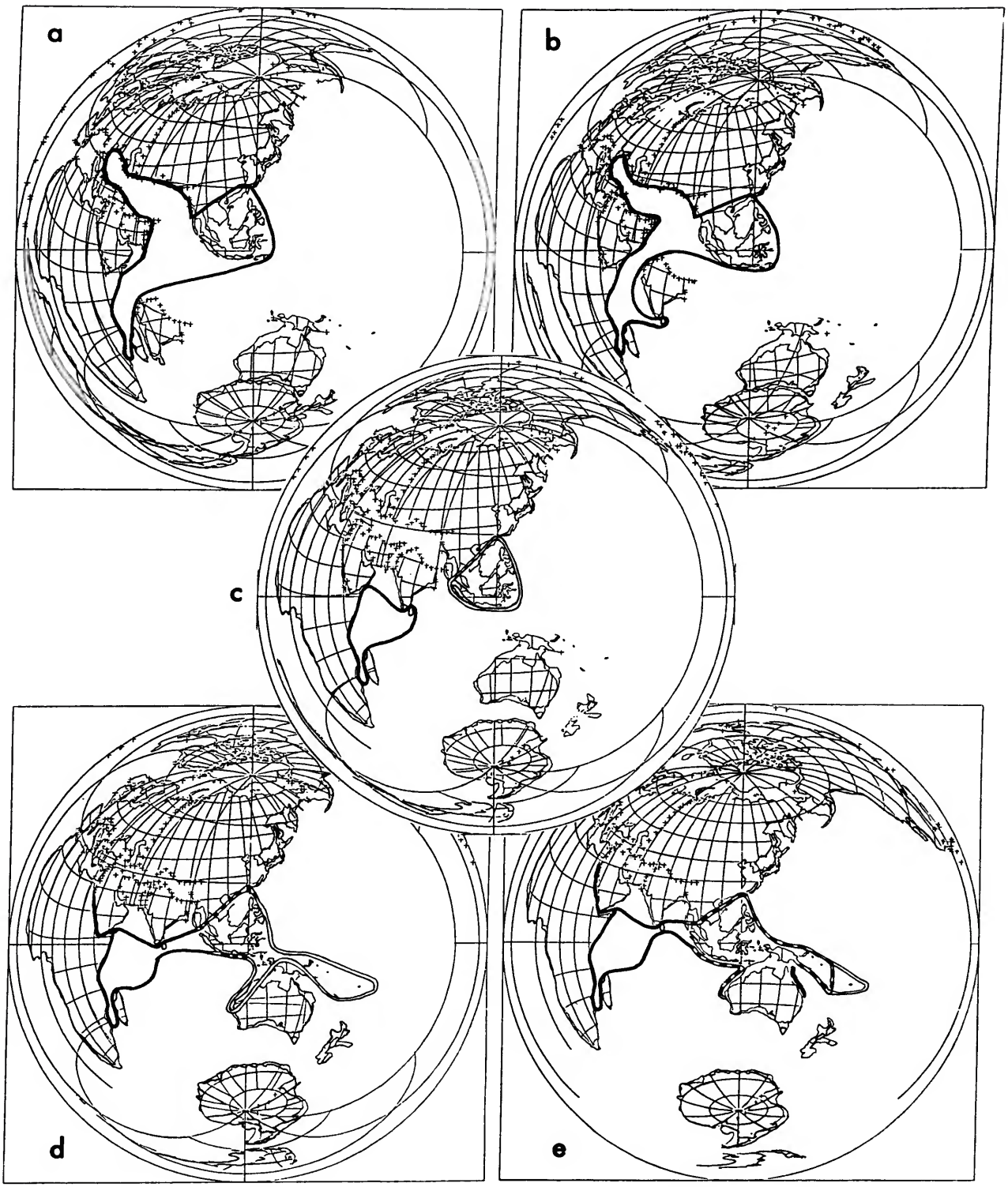


FIGURE 66.—Hypothetical reconstruction of the origin and distribution of the Oculus-Yaeyamaensis clade (see Appendix for discussion): *a*, 80 m.y.a., distribution of common ancestor (dark line) of clade; *b*, 60 m.y.a., distribution of common ancestor is being constricted by northward movement of India; *c*, 40 m.y.a., distribution of common ancestor has been divided by suturing of India to Asia, giving rise to the Yaeyamaensis (dark line) and Oculus (double line) groups; *d*, 20 m.y.a., Australia-New Guinea is about to collide with Asia, Yaeyamaensis and Oculus groups have dispersed and become partially sympatric (area of sympatry denoted by dashed line; neither group has reached eastern Australia); *e*, 0 m.y.a., collision of Australia-New Guinea with Asia is well advanced, dispersal has increased area of sympatry, only Yaeyamaensis Group has reached eastern Australia. (Base maps modified from Audley-Charles, Hurley, and Smith, 1981, figs. 3.6–3.10.)

had dispersed to Ceylon, and India-Ceylon was well separated from Madagascar and the Seychelles, a continental fragment of undecided origin. It is possible that the division of the common ancestor of the Oculus-Yaeyamaensis clade was effected by 60 m.y.a.

By 55–53 m.y.a., the suturing of India to Asia was essentially completed (Curray, et al., 1982; Klootwijk, et al., 1986) and the western Indian Ocean, if not already isolated by 60 m.y.a., was now isolated from the Indo-West Pacific. Similarly, the range of the common ancestor of the Oculus-Yaeyamaensis clade, if it was not divided by 60 m.y.a., was now divided by the Indian barrier. In Figure 66*c* (~40 m.y.a.) I show the hypothetical distribution of the Oculus and Yaeyamaensis groups after divergence. The open area between India and Asia represents the unknown portion of India that has subducted and is subducting Asia (Audley-Charles, Hurley, and Smith, 1981). Marine forms, such as the ancestor of the Oculus-Yaeyamaensis clade, in that area would have been annihilated (finding a fossil *Ecsenius* in the area would be congruent with my scenario, although it would probably be impossible to assign such a fossil to the Oculus-Yaeyamaensis clade with confidence). At 40 m.y.a., I propose that populations of the Yaeyamaensis Group existed on continental fragments or volcanic edifices, such as the Seychelles Bank, the Mascarene Plateau, and the Chagos-Maldive-Laccadive ridge. Although these fragments were not all connected, distances separating one fragment from the next adjacent fragment quite possibly were small (Figure 66*b,c;* between 39 and 35 m.y.a.; McKenzie and Sclater, 1973; Norton and Sclater, 1979). The Laccadive Islands at the northern end of the ridge, where the Yaeyamaensis Group appears to be absent today (Jones and Kumaran, 1981), have not been collected for fishes using modern methods.

I propose that the isolating effect of the suturing of India (with the unfavorable ecology of both its coasts) to Asia is the basal cause of endemism among many littoral forms, particularly coral-reef obligates, in the western Indian Ocean. I do not mean to imply, however, that all subsequent speciation in the western Indian Ocean was initiated by this event. I mean only to suggest that present-day western Indian Ocean-western Pacific Ocean sister groups should in the main owe the initiation of their divergence to the barrier formed by the suturing of India to Asia.

Hocutt (1987) was probably the first to propose that the movement of India and its suturing to Asia were the vicariant events leading to western Indian Ocean endemism. His scenario originates during the late Jurassic, about 145 m.y.a., when Africa, India, Antarctica, and Australia were joined. At that time, what was to become much of the southeast coast of Africa was not coastal. He alluded to a Tethyan biota that, he implied, extended from what would be today's eastern Mediterranean to the Malayan region. He then proposed, sequentially, that India-Madagascar's separation from Africa, India's separation from Madagascar, and India's drift north enabled the dispersal of the Tethyan biota to the newly created south coast of Africa. From Africa, the biota dispersed [via Antarctica] to Australia. Present-day similarities [and sister groups] shared by the biotas of southern Africa and western Australia are thus explained. The later joining of India to Asia isolated the western Indian Ocean. Based on Hocutt's scenario, it is possible that the sister group of the Oculus-Yaeyamensis clade was formed as a result of the separation of Africa-India-Madagascar from Australia-Antarctica about 100–120 m.y.a.

Hocutt gave a general discussion of some of the systematic and biogeographical literature that had bearing on his hypotheses. Restricting myself to the ichthyological literature, I expand upon that discussion.

Cohen (1973), in an admittedly limited analysis of endemism among Indo-Pacific shorefishes, noted that a relatively high percentage (22%) of the fishes in the western Indian Ocean are endemic. Klausewitz (1978), evaluating only the families Chaetodontidae and Pomacanthidae, corroborated Cohen's findings. Klausewitz concluded that the eastern Indian Ocean coast of the Malay Peninsula was a part of the Indian Ocean biogeographic realm, or Indian Province, which he divided into eastern and western sections. In the sense that the two sections are different, I agree with him, but my impression is that the biota of the west coast of the Malay Peninsula is only slightly separable from that of the east coast; there are relatively few endemics on the west coast (but *Ecsenius lubbocki* is one of them).

Cladistic studies of Indo-Pacific fishes, which might be used to test the biogeographical hypotheses proposed above, are uncommon. Smith-Vaniz' (1976) cladogram of the three species of the blenniid subgenus *Musgravius* (genus *Plagiotremus*) shows a branching that separates the two western Indian Ocean species from the western and central Pacific Ocean species (the other two subgenera and all other species of *Plagiotremus* are either limited to the Pacific or are widely distributed throughout the Indo-Pacific).

Smith-Vaniz (1976) indicates that only three species of the blenniid subgenus *Meiacanthus* (genus *Meiacanthus*) are present in the western Indian Ocean. All but one of the remaining species of the subgenus are restricted to the western and central Pacific. The exception ranges from the Maldives east to off Bali, and Smith-Vaniz (1987) considers it to be the sister group of a Pacific species complex (group). The sister group, or groups, of the Indian Ocean species of the subgenus *Meiacanthus* must, therefore, be in the western Pacific.

The blenniid genus *Aspidontus* consists of two species (Smith-Vaniz, 1976). One, *A. dussumieri,* is widely distributed in the Indo-Pacific; the other, *A. taeniatus,* consists of two subspecies. *Aspidontus t. tractus* ranges from the Red Sea and western Indian Ocean to the Malayan Peninsula and Pulau Seribu Islands, in the Java sea just north of Djakarta (hence, on the fringe of western Pacific); *A. t. taeniatus* ranges from Viet Nam to the central Pacific. Traditionally, the isolation and subsequent divergence of these two subspecies would be attributed to a Malayan Peninsula barrier. Although this barrier, which has been transgressed by *A. t. tractus,* may be

responsible for the divergence, I think it just as likely that the Indian barrier initiated the formation of the two subspecies and that *A. t. tractus* dispersed eastward (from Ceylon?) into the fringes of the Pacific. (The two subspecies of *A. taeniatus* are almost, if not completely separable based on color pattern; some investigators might recognize both as species.)

Vari's (1978) cladistic analysis of the genera of the Teraponidae does not indicate the existence of western Indian Ocean-western Pacific sister groups. The distributions of some of the teraponid species might indicate that such sister groups exist, but Vari's cladistic analysis did not extend below the generic level.

Winterbottom's (1985a) vicariographic analysis of the pseudochromid subfamilies Anisochrominae and Congrogadinae resulted in some unresolved relationships among the Congrogadinae, but his tentative cladogram of the species shows distinct trends with branches generally separating the western Indian Ocean genera and species from the western Pacific-eastern Indian ocean genera and species. Winterbottom hypothesized the presence of the ancestors of the anisochromin and congrogadin lines in the proto-western Indian Ocean prior to the break up of Gondwana (100–120 m.y.a.). The anisochromins (two species) are still restricted to the western Indian Ocean, but the congrogadins currently occur in both the Indian and western Pacific oceans, and, in the western Pacific, on both the India-Australian and Asian plates. To explain the distribution of the congrogadins Winterbottom (partly presaging Hocutt, 1987) proposed the following scenario.

The congrogadin ancestor dispersed (or increased its range) to include the India-Australian plate, which later separated from Gondwana, thus leading to allopatry. Three or four speciation events occurred on the India-Australian plate, which then drifted north and collided with the Asian plate. Dispersal then occurred from the India-Australian plate to the Asian plate.

Considering only the period of geologic time we both cover, Winterbottom's scenario contrasts with mine in originating Asian plate endemics subsequent to invasion from the India-Australian plate and according India no importance in isolating the eastern from the western Indian Ocean.

The scenario I am proposing (continuing below and in Appendix II, particularly for the Yaeyamaensis Group in the Indian Ocean) could be invoked to explain some of the history of the distribution patterns shown by Winterbottom's taxa. For instance, although not a coral inhabitant, *Halidesmus thomaseni* (Nielsen) has a disjunct distribution comprising essentially the northeastern and northwestern coasts of the Indian subcontinent (Winterbottom, 1985, fig. 4). If one can reasonably postulate that the species was distributed continuously across the coast of the Asian plate about 60 m.y.a., then the collision of India with the Asian plate could explain the present-day disjunction.

Smith-Vaniz (1976), Vari (1978), and Winterbottom (1985a) are the only cladistic studies of Indo-Pacific fishes I know, but they lend support to the western Indian Ocean-western Pacific vicariographic scenario I propose. I have not surveyed the non-ichthyological literature, but there are numerous western Indian Ocean endemic molluscs, for instance, that may well duplicate the trend shown by the fishes (see also Hocutt, 1987).

By 20 m.y.a. (Figure 66*d*), Australia was closely approaching the southeastern coast of the Asian Plate (Audley-Charles, et al., 1981), the Red Sea had probably opened (Cochran, 1983), and a line of island arcs (Outer Melanesian Arcs), which had begun forming about 38 m.y.a., extended along the converging margins of the Indo-Australian and Pacific plates (Kroenke, 1984). By about 25 m.y.a., this line of island arcs already included the island chains now extending from New Ireland southeast to Fiji. On Figure 66*d*, I indicate that the Yaeyamaensis Group had expanded its range into the Red Sea and into coastal southeast Asia, where it became sympatric with the Oculus Group. The Oculus Group is shown as having expanded its range along the Outer Melanesian Arc and down the northwest coast of Australia.

This portion of the scenario may have a weakness in that it requires an extensive eastward dispersal of the Yaeyamaensis Group, at least across the Bay of Bengal, if not around the bay's northern coast (improbable if the Gangetic delta existed). The form that dispersed would have been a Ceylonese endemic that was ancestral to *E. yaeyamaensis* and *E. stictus* (see discussion in Appendix 2). One might well question why there was no westward dispersal of the Ceylonese endemic (which would have resulted in sympatry of Yaeyamaensis Group species).

I have not extended the range of the Yaeyamaensis Group in Figure 66*d* to include the northwest coast of Australia because I have arbitrarily equated speciation rates in the Yaeyamaensis and Oculus groups. I believe that the extant two Oculus Group species, one (*E. paroculus*) occupying the Malayan Peninsula, Sumatra, and Java, and the other (*E. oculatus*) occupying Christmas Island and the mid-west coast of Australia, are sister species, and that their divergence occurred after the expansion of the range of their common ancestor. On the other hand, there is but a single extant Yaeyamaensis Group species sympatric with the two Oculus Group species. Because the Yaeyamaensis and Oculus groups are essentially sympatric in much of the western Pacific and have closely similar, if not identical, ecological requirements, I assume that if a Yaeyamaensis Group species had been present in Western Australia before, or contemporaneous with, the common ancestor of the two Oculus Group species, the Yaeyamaensis Group species also would have diverged recognizably. Therefore, it would have dispersed to NW Australia relatively recently, after the divergence of the Oculus Group species. (One reviewer was concerned by this proposal of "equal" evolutionary rates.)

Woodland (1986) proposed a founder-principle mechanism to explain Australia-Asian sister groups, such as *E. oculatus* and *E. paroculus*, that is compatible with Figure 66*d*. According to him, as Australia moved from temperate into tropical latitudes (before 20 m.y.a.), its northern edge became

available for colonization by tropical species from southeast Asia. At some critical distance, there was low-level colonization of Australia by a particular species, followed by rapid evolution (adaptation) of the founder colony, and, finally, exclusion by this colony of subsequent potential colonizers of the sister species. Subsequent dispersal of Australian endemics north into the Wallace's Line zone, and similar southern dispersal into northern Australia by Asian endemics accounts for sympatry of some sister groups. Woodland also indicated the possibility that changes in sea level during the recent Cenozoic could account for the distribution and evolution of some taxa in the Wallace's Line zone. It is a subjective decision as to whether one accepts a vicariance or founder principle scenario. The main difference is that founder principle must be invoked for each pair of sister-species relationships that exhibits the same distribution pattern, whereas a vicariance scenario need be invoked but once to explain a large number of such distribution patterns.

In Figure 66*d* I have not extended the range of the Oculus Group to include the northeast coast of Australia. I assume that the present-day absence of the Oculus Group from northeastern Australia indicates that there was a barrier to dispersal of the Oculus Group into that area. This presents a paradoxical problem, because the Yaeyamaensis Group is represented today by a species (endemic) in northeastern Australia (Figure 66*e*). It might be that the barrier prevented both species groups from dispersing to northeastern Australia, but when the barrier disappeared, the Yaeyamaensis Group dispersed first. Subsequent to the first dispersal, the barrier was re-established before an Oculus Group species was able to disperse. The various interglacial periods of the recent Cenozoic could have produced such a barrier, as discussed in Appendix II.

Appendix II

Interrelationships and Biogeography of the Species of the Yaeyamaensis Group

I have been unable to hypothesize unequivocally the interspecific relationships within the Yaeyamaensis Group. At most, only one of the three types of pectoral-fin base color patterns exhibited by the group can be plesiomorphic for the group. It follows, then, that the other two patterns must be apomorphic and at least one of the two must include a pattern common to two species (either *E. yaeyamaensis* plus *E. stictus* or *E. dentex* plus *E. nalolo*, of which each pair shares a common pectoral-fin base pattern). I propose below a set of scenarios that partially account for the distributions of the species of the Yaeyamaensis Group and some of the interrelationships of the species. The scenarios are based on the hypothesized monophyly of the Oculus and Yaeyamaensis groups, the hypothesized overall vicariographic history of this clade, and details of the tectonics of the Indian Ocean area and Australia-New Guinea.

The apparently recent geological appearance of the Gulf of Aqaba (post early Miocene, not more than 20–22 m.y.a. and possibly within the past 5–10 m.y.; Eyal et al. 1981) and its cul-de-sac relationship with the Red Sea, makes it probable that *E. dentex* and *E. nalolo* had a common ancestor that was distributed in both the Red Sea and the Gulf of Aqaba (as well as the Indian Ocean).

The Gulf of Aqaba is connected to the Red Sea by an extremely narrow opening of about 6–7 km. The greatest sill depth at the opening is about 300 m. During Pleistocene glacial periods, drops in the world sea level of 100–200 m have been proposed commonly. Such drops in sea level would have restricted the opening to about 2 km or less without, at the same time, much decreasing the length and width of the Gulf (estimates based on *As Suways to the Brothers*, United States Defense Mapping Agency Chart 62020, 5th Edition, August, 1976).

Ideally, it would be desirable to show that the opening to the Gulf completely closed during some past period, thus guaranteeing complete isolation of all marine organisms in the Gulf of Aqaba. Although this circumstance may have existed, I do not believe it was necessary. Considering the restricted opening to the Gulf of Aqaba, all that would be necessary would be for genetic divergence of Gulf forms to occur faster than could be offset by genetic interchange with Red Sea immigrants into the Gulf (conversely, the amount of genetic interchange between species in the Red Sea and their Gulf of Aqaba conspecific immigrants would have to be so low as to be swamped, a reasonable assumption considering the much larger area of coastline available to the species in the Red Sea).

In the present scenario, the occurrence of *E. dentex* at Ghardaqa, Egypt, slightly southwest of the southern tip of the Sinai Peninsula, would be evidence for recent dispersal of *E. dentex* out of the Gulf of Aqaba.

Ecsenius dextex is differentiated from *E. nalolo* (and all other species of its group) primarily in having considerably more mandibular teeth (Table 20). There is a relatively short expanse of coastline between Djetta, Saudi Arabia, and Ghardaqa (northernmost Red Sea record of *E. nalolo*), from which no specimens of *E. dentex* or *E. nalolo* are known. If there should be a gradual change in the number of dentary incisors in specimens from along this expanse, it might be desirable to synonymize *E. dentex* with *E. nalolo*.

There are other Gulf of Aqaba-Red Sea blenniid species that show differentiation that I have not recognized nomenclaturally. I have much less material available for most of these species, but even so there is evidence of a gradual change in their morphology from north to south (see species accounts of *Ecsenius gravieri* and, particularly, *Ecsenius frontalis*). Specimens of *E. frontalis* tend to indicate a gradual decrease in averages for meristic characters and numbers of dentary teeth from north to south (with a reversal of the trend in the Gulf of Aden; see also: Smith-Vaniz (1976) for *Meiacanthus nigrovittatus* Smith-Vaniz, and Smith-Vaniz and Springer, 1971, for *Mimoblennius cirrosus* Smith-Vaniz and Springer and *Alloblennius pictus* (Lotan)).

Winterbottom (1985*b*) reported that a step cline exists in *Haliophis guttatus* (Forsskål), a congrogadid that ranges from the Gulf of Aqaba south to Madagascar. The northernmost populations are most similar to the southernmost populations. On the other hand, he noted species in several families (Chaetodontidae, Gobiidae, Pomacentridae, Labridae) that were endemic to the northern Red Sea and had their sister group in the southern Red Sea and/or Indian Ocean. Winterbottom proposed that these examples were probably indicative of a generalized tract between the northern Red Sea and the southern Red Sea plus Indian Ocean. He argued that the most plausible explanation of this tract is a vicariant event, which was undecipherable based on information available to him. He did, however, propose the possibility that the southern Red Sea was isolated from the Indian Ocean and that conditions in the southern Red Sea then might have become unfavorable to life. Present-day occurence in the southern Red Sea of sister groups of northern Red Sea taxa would be, therefore, the result

of recent dispersal from the Indian Ocean (or Gulf of Aden).

Winterbottom's scenario contrasts with that which I proposed above, and which I prefer because it seems unlikely to me that conditions in the southern Red Sea would become unfavorable to life while conditions in the more restricted (lesser volume) northern Red Sea remained favorable. Hot, dry winds blow predominantly from the Wadi-al-Arabah, to the north, southward over the Gulf of Aqaba and Red Sea, causing great evaporation with resulting high salinities in the Gulf of Aqaba and northern Red Sea (note: the Dead Sea, almost uninhabitable to all life because of its high salinities, is at the north end of the Wadi-al-Arabah). The northern Red Sea, therefore, is more likely to become uninhabitable (at least through increased salinity) than is the southern Red Sea.

An alternative explanation to speciation in the Gulf of Aqaba might be that the oceanographic conditions of the Gulf, which is much cooler and saltier than the Red Sea, merely have had an ecophenotypic effect. Winterbottom argued strongly against this possibility, and I essentially agree with him. A solution, if there is only one, to this problem will require much more material from the middle and northern coastlines of the Red Sea than is currently available.

The circumstances that might have resulted in the formation of a *yaeyamaensis-stictus* clade are as follows. The Torres Strait (between Cape York Peninsula and New Guinea) has been opened and closed several times during the Pleistocene through changes in sea-level (Doutch, 1972). One can invoke, therefore, a land barrier to segregate a population of *Ecsenius* on the Queensland coast from a conspecific population on more western Australian coasts. Such isolation could result in subsequent divergence of one or both populations and might explain adequately the existence of *E. stictus*, except that there is no obvious reason for the ancestral Queensland population to have been (and remain) isolated from a conspecific population in eastern New Guinea, where *E. yaeyamaensis* occurs today: the Great Barrier Reef (GBR) continues across Torres Strait almost to New Guinea. A barrier to dispersal between Queensland and New Guinea appears to exist nevertheless.

A cursory survey of the literature evidenced several fishes (and there must be many more) that have similar distributions to that of *E. stictus: Ecsenius australianus* Springer, *E. mandibularis* McCulloch, *Petroscirtes fallax* Smith-Vaniz, *Meiacanthus lineatus* (De Vis) (all Blenniidae), *Rainfordia opercularis* McCulloch (Serranidae), *Corythoichthys paxtoni* Dawson and *Doryrhamphus negrosensis malus* (Whitley) (Syngnathidae), *Chaetodon rainfordi* McCulloch and probably *Chelmon muelleri* Klunzinger (Chaetodontidae), and *Stegastes apicalis* (De Vis) (Pomacentridae).

Possibly, ecological conditions prevent genetic interchange between the northern end of the GBR and the southeastern end of New Guinea, on the east side, and the Northern Territory, on the west side. The western half of the Gulf of Papua, northeast of the terminus of the GBR, receives drainage from many rivers and lacks coral reefs. Although the distance from the GBR to the nearest reefs to the east, which could serve as stepping-stones for dispersal, appears to be as little as 100–150 km, even shorter distances are known to isolate species in other *Ecsenius* species groups (for example: *E. fourmanoiri* from *E. fijiensis; E. oculus* from *E. monoculus*). The eastern Arafura Sea coast of New Guinea, just west of the northern terminus of the GBR, and the northern Gulf of Carpentaria coast along the west side of the Cape York Peninsula, also receive a large amount of river drainage and lack coral reefs. The nearest reefs to the west of the GBR are much further removed than those to the east. I hypothesize that these circumstances are major contributors to the maintenance of endemism on the GBR.

There are many species of reef fishes with distributions that are apparently unaffected by the ecological conditions that I propose. Most notably is that of *Ecsenius aequalis*, known only from the Great Barrier Reef and the Trobriand Islands (just north of the southeastern tip of New Guinea). I do not believe such distributions contraindicate my explanation of the GBR endemics. Endemism in marine fishes rarely exceeds 25–30% except in the largest areas. The Red Sea, which is about comparable in extent and number of species to the GBR, but with a more highly restricted interface with the rest of the marine realm, is only reported to have about 10% endemism among its fishes (Randall, 1983). The level of endemism exhibited by GBR fishes has not been estimated, but is probably less than 10%.

Although I am unable to hypothesize unequivocally the sister group of the fifth and final species of the Yaeyamaensis Group, the Maldive Islands endemic *E. minutus*, it is instructive to examine distributions of the Yaeyamaensis Group species in the Indian Ocean in the context of the tectonic evolution of that ocean.

Figure 67*a* illustrates the hypothetical distribution of major land and near-surface features in the Indian Ocean area about 75 m.y.a., at which time I hypothesized above that the ancestor of the Oculus-Yaeyamaensis clade had not been split (Figure 66*a*). As such, the ancestor would have occupied, among other areas, the Seychelles and Mascarene Plateau, which were attached to India. Accordingly, evolution of the Yaeyamaensis Group (and Oculus Group) species would have occurred more recently than 60 m.y.a. I propose that the common ancestor of the Yaeyamaensis Group evolved between about 60 and 40 m.y.a. (Figure 66*b,c*).

Between about 60 and about 39 m.y.a., India's movement north resulted in: the separation of the Seychelles and Mascarene Plateau from India, the formation of the Chagos-Maldive-Laccadive Ridge, which was attached initially at its southern end to the Mascarene Plateau (Figure 67*b,c*), and a distancing of this ridge from India (in particular, southern India-Ceylon) by seafloor spreading between the ridge and the coast of India. Schlich (1982) considers proposals that portions of this ridge represent rifted fragments of India as speculative, although he accepts the continental association of the ridge (hotspot traces, leaky transform faults, continental fragments of India, and mixed origin have all been proposed to explain

the ridge; Sahni, 1982). Heezen and Tharp's *World Ocean Floor* chart (United States Office of Naval Research, 1977), appears to me to indicate ocean floor spreading between India and the ridge (indications may be unclear on my much reduced reproduction of the pertinent portion of that chart, Figure 68).

Whatever the source of the ridge, it appears that a consensus would accept its closer association with the west coast of India than exists presently. In view of the occurrence of *E. yaeyamaensis* in Ceylon, but only other species of the Yaeyamaensis Group on the ridge and in other areas of the western Indian Ocean, I propose that the common ancestor of the *yaeyamaensis-stictus* clade evolved as a Ceylon endemic and as a result of the separation of the Chagos-Maldive-Laccadive Ridge from the west coast of India before 39 m.y.a. and after 60 m.y.a., based on the hypothesized time of origin of the common ancestor of the Yaeyamaensis Group (the time of the separation could be restricted further if the age of the Chagos-Maldive-Laccadive Ridge could be established).

Ecsenius minutus in the Maldives is allopatric to, and separated by a distance of about 700 km from, both the Ceylon population of *E. yaeyamaensis* and the closest resident population of *E. nalolo*, which occurs in the Chagos Islands on the Chagos-Maldive-Laccadive Ridge. Populations of *E. nalolo* also exist on the Mascarene Plateau and other shores of the western Indian Ocean and Red Sea. The interesting point about this distribution pattern (Figure 10) is that the Chagos Islands population of *E. nalolo* is approximately 1,700 km from its nearest (possible) conspecific population, on the Mascarene Plateau. Inasmuch as the Chagos Islands were formerly attached to the Mascarene Plateau (Figure 67*c*), one could propose that the Chagos population was carried to its present location by the seafloor spreading that split the Chagos-Maldive-Laccadive Ridge from the Mascarene Plateau beginning about 39 m.y.a. Considering the relative age of the split and great distance separating the Chagos Islands from the Mascarene Plateau, one also might expect to find evidence that the Chagos population of *E. nalolo* has diverged from the other Indian Ocean populations of *E. nalolo*. Especially so, as there is

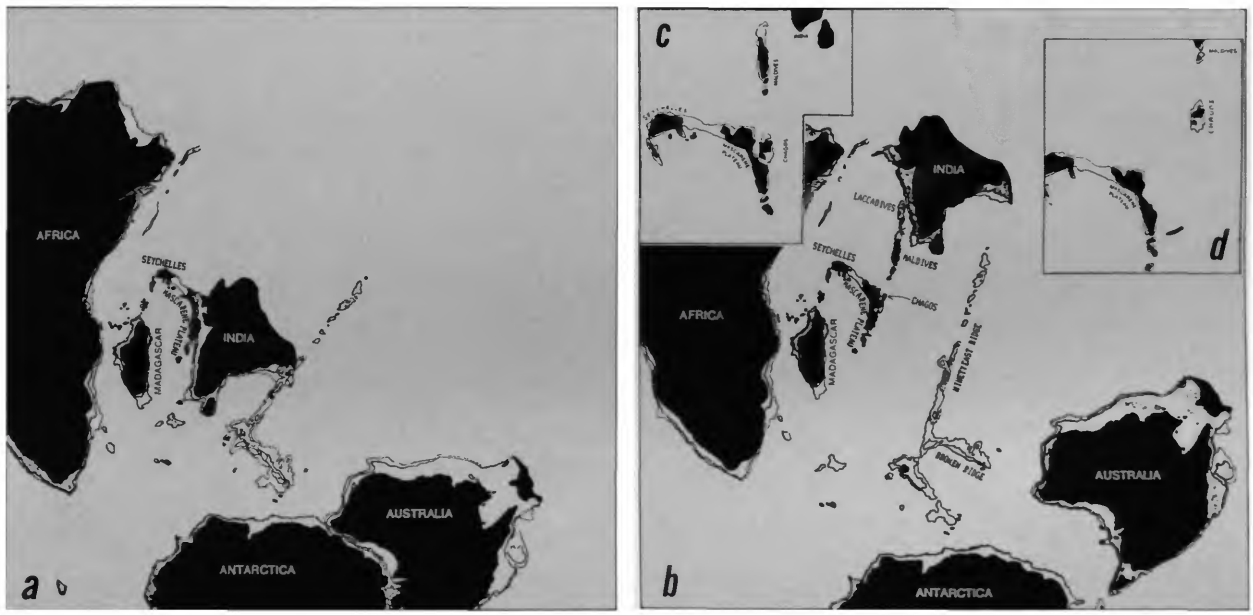


FIGURE 67.—Paleo-reconstructions of the Indian Ocean area: *a*, 75 m.y.a.: India has separated from Madagascar; the Seychelles, a continental fragment of undecided origin, and Mascarene Plateau, probably of volcanic origin, were linked to each other and India (Norton and Sclater, 1979; Schlich, 1982). *b*, 39 m.y.a.: the suturing of India to Asia has been completed; the Seychelles-Mascarene Plateau has separated from India (~65 m.y.a.; Norton and Sclater, 1979); the Chagos-Maldive-Laccadive ridge, probably of volcanic origin, has been formed in the wake of India's move north and is attached at its southern end to the Mascarene Plateau. *c*, 39 m.y.a.: magnified section of *b* showing attatchment of Chagos to Mascarene Plateau. *d*, today: ocean-floor spreading at the Mid-Indian-Ocean ridge has separated the Mascarene Plateau and the Chagos-Maldive-Laccadive ridge. (Modified from McKenzie and Sclater, 1973; however, slight shifts in the relative positions of Australia-Antarctica to India and the attachment of Chagos to the Mascarene Plateau have not been changed to accord with the findings of Norton and Sclater, 1979.) See also Figure 68 for present-day arrangement of land masses and ocean-bottom topography; note continued distancing of Chagos-Laccadive Ridge from Mascarene Plateau.

FIGURE 68.—Topography of the Indian Ocean (after B.C. Heezen and M. Tharp, 1977, *World Ocean Floor*, chart, United States Navy, Office of Naval Research).

evidence that differences appear to have developed relatively recently between the Red Sea and non-Red Sea populations of *E. nalolo,* and I have proposed equally recent speciation events to explain the occurrence of *E. dentex* in the Gulf of Aqaba and *E. stictus* on the Great Barrier Reef. I find no such divergence, however.

The puzzling occurrence of *E. nalolo* in the Chagos Islands has a parallel in the distribution of *E. yaeyamaensis.* The population of *E. yaeyamaensis* at Ceylon is approximately 1,200 km from the nearest possible coral-reef locality to the east, Andaman Islands, where a conspecific population might be expected to occur. The species is unknown in the Andamans, which have not been well collected, but I predict that *E. yaeyamaensis* exists there. The population of *E. yaeyamaensis* known to be nearest to the Ceylon population is in southern Malaysia (Figure 10), and the two populations appear to be undifferentiated. The major portion of the distribution of *E. yaeyamaensis* is east of Ceylon, in the Pacific Ocean, and, as proposed above, this species is presumed to have reached the Pacific by dispersal. One difficulty with eastward dispersal is that the ocean currents, if such were the dispersal mechanism, in the eastern Indian Ocean-Malaysian region flow predominantly westward all year long (Wyrtki, 1961), and have done so since at least the mid-Jurassic (Haq, 1984), about 180 m.y.a. Another difficulty is that Indian Ocean populations of *E. yaeyamaensis* would have been isolated from conspecific Pacific populations during the same glacial periods of lowered sea level that I have hypothesized initiated divergence of the common ancestor of the *yaeyamaensis-stictus* clade.

If the proposed *nalolo-dentex* and *yaeyamaensis-stictus* clades are real, then *E. minutus* must be the sister group of one or both of them. Even narrowing the possibilities to just these three is of little help in proposing a "clean" vicariance scenario that is consistent with currently accepted historical geology. Invoking dispersal provides similarly unsatisfactory scenarios.

The solution to these problems awaits new information and insights.

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☆U.S. GOVERNMENT PRINTING OFFICE: 1988-181-717/60026

Color Plates
1 to 14

Plate 1

FIGURE 1.—Batesian mimetic association involving *Ecsenius gravieri,* mimic (on left), and *Meiacanthus nigrolineatus,* model (note lack of dark spots posteriorly on body), Sinai Coast, Gulf of Aqaba (V.G. Springer).

FIGURE 2.—*Ecsenius gravieri,* Sinai coast, Gulf of Aqaba (V.G. Springer).

FIGURE 3.—*Ecsenius gravieri,* Gulf of Aqaba (J.E. Randall).

Plate 2

FIGURE 1.—*Ecsenius aroni,* Sudan, Red Sea (J.E. Randall).

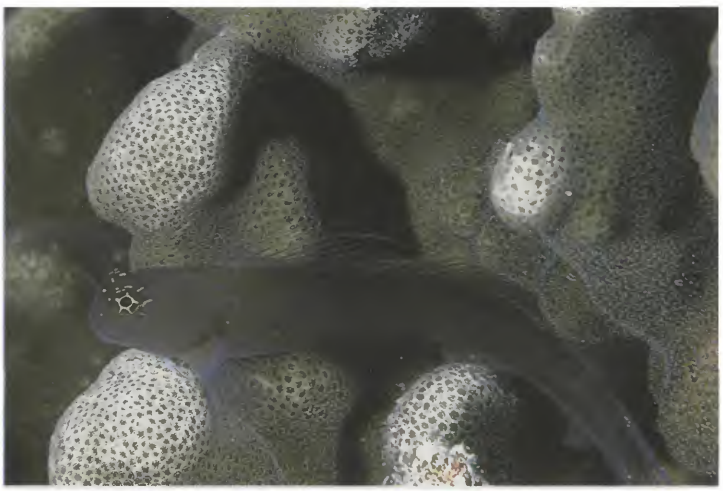

FIGURE 2.—*Ecsenius pulcher,* Bahrain, Persian Gulf, uniform pattern (J.E. Randall).

FIGURE 3.—*Ecsenius pulcher,* Bahrain, Persian Gulf, banded pattern (J.E. Randall).

FIGURE 4.—*Ecsenius pulcher,* off Manifa, Persian Gulf, horizontally bicolored pattern (J.E. Randall).

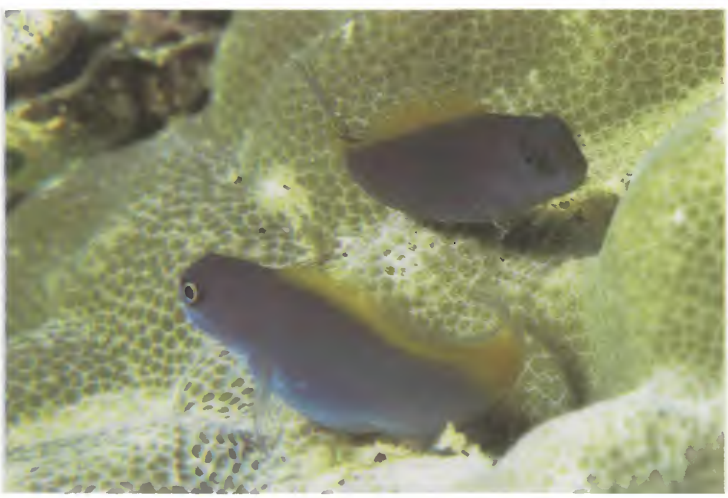

FIGURE 5.—*Ecsenius lividanalis,* off Ujung Pandang, Sulawesi (= Celebes), Indonesia, bicolored pattern (J.E. Randall).

FIGURE 6.—*Ecsenius lividanalis,* off Kampungmahu, Saparua, Indonesia, freshly collected (V.G. Springer).

Plate 3

FIGURE 1.—*Ecsenius melarchus*, Pulau Menjangan, Bali, Indonesia (J.E. Randall).

FIGURE 2.—*Ecsenius melarchus*, Pulau Menjangan, Bali, Indonesia (J.E. Randall).

FIGURE 3.—*Ecsenius midas*, Christmas Island, Indian Ocean (R.C. Steene).

FIGURE 4.—*Ecsenius midas*, Christmas Island, Indian Ocean (R.C. Steene).

FIGURE 5.—*Ecsenius midas*, Mauritius (J.E. Randall).

FIGURE 6.—*Ecsenius midas*, Sudan, Red Sea, other fishes are *Anthias squamipinnis*, which *E. midas* reportedly mimics (J.E. Randall).

Plate 4

FIGURE 1.—*Ecsenius stigmatura,* Ambon, Indonesia (G.R. Allen).

FIGURE 2.—*Ecsenius stigmatura,* Cebu, Philippines (R. Lubbock).

FIGURE 3.—*Ecsenius frontalis,* Suakin, Sudan, Red Sea, frontalis form (J.E. Randall).

FIGURE 4.—*Ecsenius frontalis,* Sharm Abhur, Saudi Arabia, Red Sea, albicaudatus form (J.E. Randall).

FIGURE 5.—*Ecsenius frontalis* Djibouti, nigrovittatus form (J.E. Randall).

FIGURE 6.—*Ecsenius bicolor,* Christmas Island, Indian Ocean, uniform pattern, pale bars are transient, presumably fright pattern (R.C. Steene).

Plate 5

FIGURE 1.—*Ecsenius bicolor,* Similan Island, Thailand, Andaman Sea, uniform pattern (R.C. Steene).

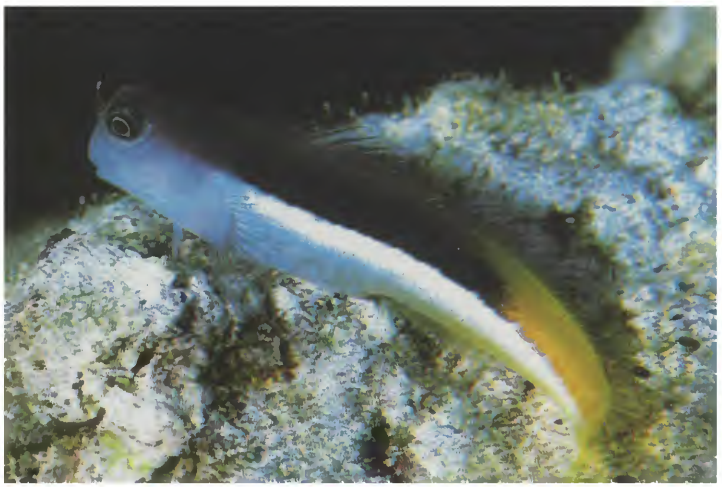

FIGURE 2.—*Ecsenius bicolor,* Christmas Island, Indian Ocean, striped pattern (G.R. Allen).

FIGURE 3.—*Ecsenius* bicolor, probably Great Barrier Reef, bicolored pattern (R.C. Steene).

FIGURE 4.—*Ecsenius bicolor,* Enewetak, Marshall Islands, bicolored pattern, black spot in spinous dorsal fin is variably present (J.E. Randall).

FIGURE 5.—*Ecsenius namiyei,* Florida Island, Solomon Islands, bicolored form, freshly collected specimen (J.E. Randall).

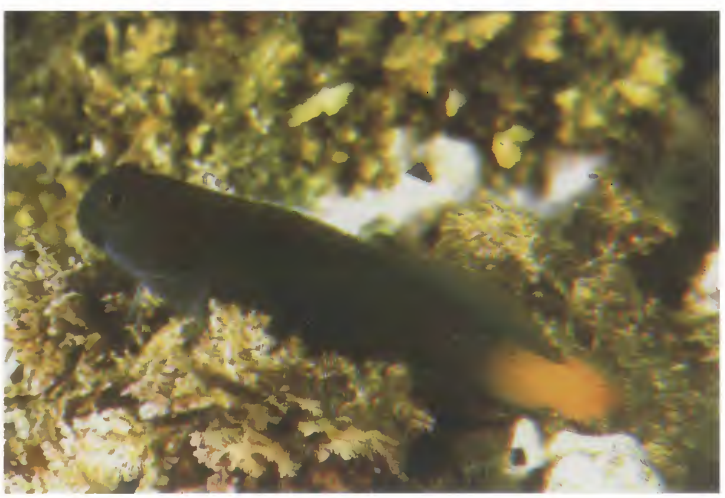

FIGURE 6.—*Ecsenius namiyei,* bicolored form (J.E. Randall).

Plate 6

FIGURE 1.—*Ecsenius namiyei*, Sumilon Island, Philippines, uniform pattern (J.E. Randall).

FIGURE 2.—*Ecsenius lineatus*, Villingilli, Maldive Islands, Indian Ocean (R.C. Steene).

FIGURE 3.—*Ecsenius lineatus*, northern Taiwan (J.E. Randall).

FIGURE 4.—*Ecsenius lineatus*, in presumably transient fright pattern (R.C. Steene).

FIGURE 5.—*Ecsenius lineatus*, Mauritius (J.E. Randall).

FIGURE 6.—*Ecsenius lineatus*, Mauritius (J.E. Randall).

Plate 7

FIGURE 1.—*Ecsenius oculatus*, Christmas Island, Indian Ocean (R.C. Steene).

FIGURE 2.—*Ecsenius paroculus*, Similan Island, Thailand, Andaman Sea (J.E. Randall).

FIGURE 3.—*Ecsenius oculus*, Ishigaki Island, Ryukyu Islands (R.C. Steene).

FIGURE 4.—*Ecsenius monoculus*, Philippines (R.C. Steene).

FIGURE 5.—*Ecsenius tessera*, New Caledonia, freshly collected specimen (J.E. Randall).

FIGURE 6.—*Ecsenius pardus*, Suva Harbor, Fiji, freshly collected specimen, about 20 mm SL (B. Carlson).

FIGURE 1.—*Ecsenius pardus*, Fiji, freshly collected specimen, about 49 mm SL (J.E. Randall).

FIGURE 2.—*Ecsenius portenoyi*, Tutuila, American Samoa (J.E. Randall).

FIGURE 3.—*Ecsenius portenoyi*, Rotuma, freshly collected specimen (J.T. Williams).

FIGURE 4.—*Ecsenius dentex*, Gulf of Aqaba, freshly collected specimen (J.E. Randall).

FIGURE 5.—*Ecsenius nalolo*, Sudan, Red Sea (J.E.Randall).

FIGURE 6.—*Ecsenius nalolo*, Seychelles (J.E. Randall).

Plate 9

FIGURE 1.—*Ecsenius yaeyamaensis*, Sri Lanka (J.E. Randall).

FIGURE 2.—*Ecsenius yaeyamaensis*, Palau (J.E. Randall).

FIGURE 3.—*Ecsenius yaeyamaensis*, Marau, Solomon Islands, freshly collected specimen (H.R. Axelrod).

FIGURE 4.—*Ecsenius minutus*, Maldive Islands (J.E. Randall).

FIGURE 5.—*Ecsenius stictus*, Great Barrier Reef, Australia (R.C. Steene).

FIGURE 6.—*Ecsenius stictus*, Great Barrier Reef, Australia (R.C. Steene).

FIGURE 1.—*Ecsenius axelrodi,* Rabaul, New Britain, striped form (R.C. Steene).

FIGURE 2.—*Ecsenius axelrodi,* Rabaul, New Britain, banded form (R.C. Steene).

FIGURE 3.—*Ecsenius axelrodi,* Rabaul, New Britain, banded form (R.C. Steene).

Plate 11

FIGURE 1.—*Ecsenius tigris*, Osprey Reef, Coral Sea (J.E. Randall).

FIGURE 2.—*Ecsenius dilemma*, Batangas, Luzon, Philippines, banded form (R.C. Steene).

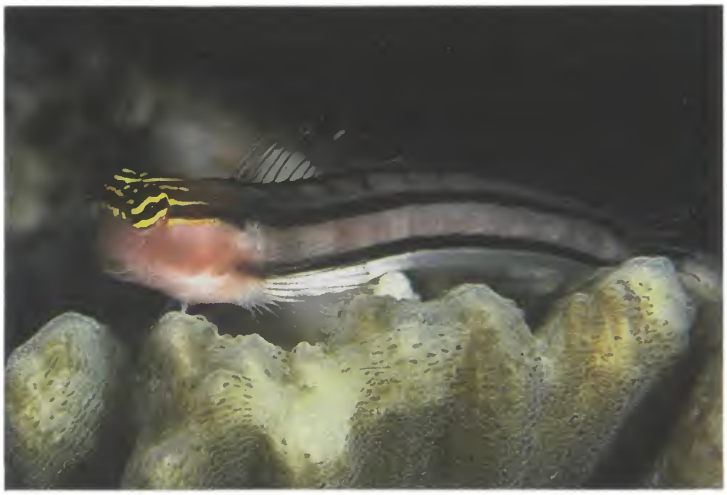

FIGURE 3.—*Ecsenius dilemma*, Batangas, Luzon, Philippines, striped form (J.E. Randall).

FIGURE 4.—*Ecsenius dilemma*, Batangas, Luzon, Philippines, banded form (J.E. Randall).

FIGURE 5.—*Ecsenius bathi*, Toko Toko Rock, Komodo, Indonesia, banded form (J.E. Randall).

FIGURE 6.—*Ecsenius bathi*, wreck of "Liberty," Bali, Indonesia, striped form (red-striped fish is a tripterygiid) (J.E. Randall).

Plate 12

FIGURE 1.—*Ecsenius alleni*, Rowley Shoals, off Western Australia (R.C. Steene).

FIGURE 2.—*Ecsenius australianus*, Great Barrier Reef, Australia, note faintly dusky posterior opercular margin (R.C. Steene).

FIGURE 3.—*Ecsenius fijiensis*, Great Astrolabe Reef, Kadavu, Fiji, freshly collected specimen (B. Carlson).

FIGURE 4.—*Ecsenius fourmanoiri*, Tongatapu, Tonga Islands (J.E. Randall).

FIGURE 5.—*Ecsenius opsifrontalis*, Kwajalein, Marshall Islands (J.E. Randall).

FIGURE 6.—*Ecsenius opsifrontalis*, Rotuma, freshly collected specimen (J.T. Williams).

Plate 13

FIGURE 1.—*Ecsenius isos*, New Caledonia, freshly collected specimen (J.E. Randall).

FIGURE 2.—*Ecsenius trilineatus*, Pulau Menjangan, Bali, Indonesia (J.E. Randall).

FIGURE 3.—*Ecsenius pictus*, Bone Rate Island, Indonesia (J.E. Randall).

FIGURE 4.—*Ecsenius pictus*, Kakabia Island, Indonesia (J.E. Randall).

FIGURE 5.—*Ecsenius bandanus*, off Ujung Pandang, Sulawesi, Indonesia (J.E. Randall).

FIGURE 6.—*Ecsenius bimaculatus*, Batangas, Luzon, Philippines (J.E. Randall).

Plate 14

FIGURE 1.—*Ecsenius collettei*, Madang Harbor, Papua New Guinea (G.R. Allen).

FIGURE 2.—*Ecsenius prooculis*, Manus, Admiralty Islands (G.R. Allen).

FIGURE 3.—*Ecsenius aequalis*, Great Barrier Reef, Australia, freshly collected specimen, posed dead (R.C. Steene).

FIGURE 4.—*Ecsenius aequalis*, Osprey Reef, Coral Sea (J.E. Randall).

FIGURE 5.—*Ecsenius mandibularis*, One Tree Island, Great Barrier Reef, Australia, freshly collected specimen (V.G. Springer).

FIGURE 6.—*Ecsenius schroederi*, Rowley Shoals, off Western Australia (R.C. Steene).

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