VICTOR G. SPRINGER

# Revision of the Fish Genus Ecsenius (Blenniidae, Blenniinae, Salariini)

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## ABSTRACT

Springer, Victor G. Revision of the Fish Genus *Ecsenius* (Blenniidae, Blenniinae, Salariini). *Smithsonian Contributions to Zoology,* 72:1-74, 1971.—The genus *Ecsenius* comprises 18 species of Indo-Pacific reef-dwelling fishes. The species are generally characterized by a high degree of sexual dimorphism and geographic variation as indicated by statistically significant differences in average numbers of various meristic and proportional characters and color pattern types.

Keys, illustrations and diagnoses, and nomenclatural and zoogeographical discussions are provided. Four new species are described: *E. aroni* from the Gulf of Aqaba, *E. oculus* from the western Pacific, *E. bimaculatus* from Borneo, and *E. bandanus* from Banda Island.

A discussion is given of a particularly complex taxonomic problem involving three nominal species occurring in the Red Sea and Gulf of Aqaba. *E. nigrovittatus* is known only from the southern Red Sea, *E. frontalis* is known from the northern Gulf of Aqaba to the Bay of Tadjoura (Gulf of Aden), and *E. albicaudatus* is known from the northern Gulf of Aqaba to the southern Red Sea. Except for color pattern all three forms are very similar morphologically, have been collected together from one small rock, and are very different from any other species of *Ecsenius.* The problem of whether the three forms constitute one or more species is not solvable presently, but the three nominal species are treated here as color pattern forms of single species, *E. frontalis.*



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*Victor G. Springer*

# Revision of the Fish Genus Ecsenius (Blenniidae, Blenniinae, Salariini)

## Introduction

Chapman and Schultz (1952), with seventy specimens for study, last reviewed the Indo-Pacific genus *Ecsenius*. They recognized eleven species, including two species for which they had examined no specimens. Since their review five additional species of *Ecsenius* have been described (not all properly allocated to genus). Intensive collecting in recent years has made available well over one thousand specimens of *Ecsenius,* including material of all the described species and additional material of undescribed species. The new material enables the revision of *Ecsenius* presented here.

I recognize eighteen species of *Ecsenius,* of which four are new. Since some species of *Ecsenius* are restricted to poorly collected, relatively deep water, and because several of the species appear to be restricted in their geographic distribution, I believe that there will be a large increase in the number of species over that which I report when more thorough collecting has taken place. The faunistically rich Indo-Malayan region is one of the most poorly sampled for fishes, and it is therefore probable that this region will provide most of the new *Ecsenius* species collected in the future.

The species of *Ecsenius* are relatively small, not exceeding 83 mm standard length, and are known, with rare exceptions, only from coraliferous areas. They live at depths from about one meter down to at least 39 meters, although most species seem to have a relatively restricted depth range. The species may occur in the surge zone, tide pools, or the relatively quiet lagoons of atolls.

The genus is a highly specialized one, exhibiting anatomical peculiarities not found elsewhere among the blenniids (see generic discussion). Some of the species apparently are mimics, many are very colorful, while others are very somber in tone. One species, *Ecsenius bicolor,* has been maintained and bred in the laboratory (Wickler, 1965a), although it was not possible to rear the young.

Chapman and Schultz (1952) believed that the species of *Ecsenius* formed a close-knit group. I cannot agree with this. While their generic affiliation is more clear-cut than it is for the species of many blenny genera, there seems to have been an unusually high degree of adaptive radiation among the species of *Ecsenius.* Although I can recognize small groups of species within the genus, I am unable to relate the groups.

## Methods

MEASUREMENTS.—When possible, I made all measurements on the left side of each specimen, using a set of needlepoint dial calipers reading directly to the nearest tenth of a millimeter. Measurements were converted to percent of standard length.

Standard length (SL): This measurement was

*Victor G. Springer, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

taken from the midtip of the upper lip to the midlateral posterior margin of the hypural vertebra as indicated externally on the specimen. Variably, the anteriormost point of the head is in advance of the upper lip, but this portion of the head was ignored in measurements.

Nasal cirrus length (Table 10): Most species have a single, simple cirrus on the posterior rim of the anterior nostril; two species, *bicolor* and *namiyei*, also have a shorter, simple cirrus on the anterior rim of the anterior nostril. On occasion any of these cirri may bear a short secondary branch. The length of the posterior cirrus was measured as the greatest distance from the point where the cirrus joined the nostril to the distal tip of the cirrus.

Dorsal fin spine and ray lengths (Tables 5, 7, 8): These measurements were taken from the proximalmost point of the posterior axil formed by the element with the dorsal body contour to the distal tip of the element, disregarding the normal curvature of the element. In a few instances (specimens of *E. namiyei* and *E. midas* and some specimens of *E. frontalis*) the lengths of the dorsal rays and spines were taken from radiographs. This was necessary because the dark skin overlying the fin elements obscured them from view.

Longest caudal ray (Table 9): This measurement was taken from the proximalmost point of the ray, which overlaps the upper hypural plate, to the distal tip of the ray.

Dorsal fin notch (Table 5): The notch, if present, was measured as the greatest distance from the distal tip of the first dorsal ray to the distal edge of the fin membrane between the last dorsal spine and first dorsal ray. This distance was divided by the length of the first dorsal ray and the resulting proportion recorded as the nearest one-ninth of the length of the first dorsal ray. Occasionally the distal tip of the penultimate dorsal spine extended over the ultimate spine and attached to the first dorsal ray. In such instances the notch depth was measured from the point of attachment of the penultimate spine to the tip of the first ray.

Lateral line: The dorsal fin element under which the lateral line terminated was recorded (Table 6). Fin elements were numbered consecutively from the anteriormost to the posteriormost without distinguishing spines from rays. If the lateral line terminated below the space between two elements, the nearest even-numbered element was recorded. With few exceptions the lateral line terminates below the spinous portion of the dorsal fin.

MERISTIC AND OTHER COUNTABLE CHARACTERS (Tables 1–4, 6, 11, 12, 15–18).—All specimens were radiographed and counts of the dorsal, anal and caudal fin elements, caudal and precaudal vertebrae, and epipleurals were taken from radiographs. Occasionally a dorsal or anal fin ray was absent but its proximal pterygiophore was present. In such instances the ray was counted as if present. No counts of caudal vertebrae were recorded for specimens with apparent vertebral fusions. Pectoral and pelvic ray counts were made on the specimens. Counts for bilaterally paired characters are for one side only (the left, when possible, unless otherwise noted.

Dorsal spines: In some species the terminal dorsal spine is so reduced that it can be seen only on radiographs or after osteological preparation.

Dorsal rays: Each segmented element was counted separately (the last two counted as two).

Anal spines: There are invariably two, but the first in females is frequently not visible externally.

Anal rays: Each segmented element was counted separately (the last two counted as two); the terminal pterygeophore always supports a single segmented ray (unlike some other blenniids; see Springer, 1967).

Segmented caudal rays: Except for certain small specimens (see below) each segmented ray was counted, including, where they occur, the single dorsal and ventral rays with a single segmental joint. I noted that occasional specimens less than about 25 mm had one or two more segmented caudal rays than larger specimens. These additional segmented rays were usually the ventralmost and, secondarily, the dorsalmost of the segmented rays, and they never had more than two segments; they were either paired structures with right and left halves or were paired for most of their length and fused at their tips. I believe that such rays lose their segmentations with growth and become fused for much of their length. Counts for specimens under 25 mm SL are not included in Table 3 or the species descriptions.

Procurrent caudal rays: These are the unsegmented elements described by Springer (1968). As they are not bilaterally paired structures, they could be called spines. As they appear to be serially homologous with the segmented rays discussed above and usually have a bilaterally forked base, they give

evidence of having gone through a raylike stage in ontogeny. In the posteriormost procurrent ray the base may be cleft for almost half the length of the element, but the distal portion is always fused and spinelike with no evidence of a joint line extending distally from the cleft. Procurrent ray counts for specimens under 25 mm are not included in the species descriptions. In Table 3, however, total caudal element counts do include data from these specimens.

Total caudal elements: This is the sum of the dorsal and ventral procurrent caudal rays and the segmented caudal rays.

Pelvic fins: A spine and three segmented rays are always present, but the spine is imbedded, closely applied to the first pelvic ray, and not visible externally. In addition, the innermost pelvic ray is reduced and often impossible to see externally.

Vertebrae: Precaudal vertebrae are those lacking a hemal spine; the caudal vertebrae all bear a hemal spine, although that of the hypural (last) vertebra is fused with the ventral hypurals.

Epipleural ribs: The anterior epipleural ribs are not possible to count on radiographs, but from examination of cleared and stained specimens are known to begin invariably on the first vertebra (the pleural ribs begin invariably on the third vertebra). The epipleural rib count is actually a count of the number of vertebrae from the anteriormost to the posteriormost bearing an epipleural rib, regardless of whether it bears a pair or only one, and that on the right or left side. Thus, occasional vertebrae lacking epipleural ribs, that occur between vertebrae bearing epipleural ribs, are counted as if they had these ribs.

Dentary teeth (Table 4): *Ecsenius* is unique among blenniids in having two sets of canines—anterior and posterior. The anterior canines, usually a single tooth on each side, occur in line with the incisoriform, comblike teeth of the dental plate (Springer, 1968). They are usually only slightly larger than the adjacent incisor teeth and are frequently blunted and difficult to distinguish from the incisors, but in *E. midas,* and occasional specimens of other species, they are quite large, pointed, and distinct. The posterior canines (usually one or, rarely, two, in all but one species) are posterior, slightly medial to, and well separated from the anterior teeth. They are small and frequently blunted. In one species, *E. mandibularis,* there is a series of up to eight of these posterior canines on each side. In making the dentary tooth counts the anterior canines and all the incisors are included. The posterior canines were counted separately. The posterior canines frequently are not developed in specimens below 25 mm SL.

Premaxillary teeth: All the teeth in the premaxillary dental plate were counted. These counts are difficult and were made on only a relatively few specimens.

Gill-rakers and pseudobranchial filaments: All the gill-rakers on the first arch and the pseudobranchial filaments of one side were counted.

Color pattern: Unless otherwise stated, color pattern descriptions are based on preserved specimens.

Statistical tests: Student's *t*-test, two sided (Simpson, Roe and Lewontin, 1960), was employed to test the difference between means of some samples. Differences were considered to be significant when $p = .01$ or less.

Synonymies: The synonymies under each species include only references to original species descriptions.

Much of the data concerning each species is to be found under the general accounts of meristics, sexual dimorphism, etc., and is not always repeated under the individual species accounts.

Institutional abbreviations: In the material lists and acknowledgments the following abbreviations are used:

AMS—Australian Museum, Sydney; ANSP—Academy of Natural Sciences of Philadelphia; BMNH—British Museum (Natural History); BPBM—Bernice P. Bishop Museum, Honolulu; CAS—California Academy of Sciences, San Francisco (also GVF for those specimens in the George Vanderbilt Foundation collections at CAS); FMRI—Central Fisheries Marine Research Institute, Mandapam Camp, India; HUI—Hebrew University, Israel (some HUI numbers include "HUJ" as part of the catalogue number); ISZZ—Institut für Spezielle Zoologie und Zoologisches Museum, Berlin; MNHN—Museum National d'Histoire Naturelle, Paris; NFIS—Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt; RU—Rhodes University, Department of Ichthyology, South Africa; UMML—University of Miami Rosenstiel School of Marine and Atmospheric Sciences; USNM—United States National Museum of Natural History; UTAI—University of Tel Aviv, Israel; UW—University of Washington,

Seattle; ZMA—Zoologisch Museum, Amsterdam; ZITH—Zoological Institute, University of Tokyo.

Full locality citations have usually not been included in the material lists.

## *Ecsenius* McCulloch

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

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

DIAGNOSIS.—Fishes of the tribe Salariini (Springer, 1968), subfamily Blenniinae, (1) lacking an ossified median ethmoid [1], (2) having the lateral extrascapulars fused with the pterotics, (3) four circumorbital bones, (4) both anterior and posterior canines in the lower jaw (the anterior frequently difficult to distinguish from the adjacent incisors except in osteological preparations), (5) dorsomesially extending processes arising from the proximal ends of at least the third to fifth epipleural ribs, (6) all fin rays unbranched, (7) upper and/or lower caudal lobes of most mature males and many females elongated.

Characters (1), (4), and (5) distinguish *Ecsenius* from all other Blenniidae. In addition character (2) distinguishes *Ecsenius* from all blenniids except a few species in the subfamily Nemophidinae, and character (7) distinguishes *Ecsenius* from all other Salariini and Blenniini.

Further characterization: Dorsal spines 10 to 14 (rarely 10 or 11); dorsal rays 12 to 21 (rarely 12); anal elements II, 13 to 23; pectoral rays 12 to 16; pelvic elements I, 3 (but obvious pelvic rays 2 or 3); segmented caudal rays 13 or 14 (rarely 15); vertebrae 10 or 11 (9 and 12 in one specimen each) + 19 to 29 = 29 to 40; dentary incisor teeth (including anterior canines) 13 to 64; premaxillary incisor teeth 26 to 148, (usually 2 to 3 times as many upper incisors as lower incisors).

Lateral line extending posteriorly to beneath level of seventh dorsal spine to first dorsal ray. Dorsal fin varying from entire to deeply notched between dorsal spines and rays. Last dorsal and anal fin rays attached by membrane to caudal peduncle. Cirri present on anterior nostril; none on eye or nape. Distinct occipital fleshy crest absent. Circumorbital and preoperculomandibular pores in simple series (no paired pores); one mid-predorsal, supratemporal pore. Lips entire (no crenulae).

Eighteen species occurring in coraliferous areas of the Indian and western Pacific oceans and their associated seas and gulfs.

Subgenera: *Ecsenius* comprising 17 species, and *Anthiiblennius*, monotypic, differentiated in the key.

NOMENCLATURE.—Tomiyama compared *Pescadorichthys* only to the type-species of *Ecsenius*, *E. mandibularis*. All the characters, except one, that he used to differentiate the two genera vanish when all the species treated here are considered. The one character, presence of a series of canines posteriorly in each jaw, is distinctive of *E. mandibularis*. I do not believe that *Pescadorichthys* should be maintained, however, in view of the great number of pecularities exhibited by *E. mandibularis* in common with the other species here included in *Ecsenius*. Indeed, a few specimens of *E. mandibularis* have only two posterior canines on one side of the jaw, as do a few specimens of the other species, and so there is a degree of overlap in the character.

RELATIONSHIPS.—*Ecsenius* is such a highly specialized genus that it is not possible to select another genus of blenniids as its nearest relative. It is only with reluctance that I do not recognize *Ecsenius* as constituting a separate tribe of blenniids. The excavation of the premaxillaries and dentaries, the high number of premaxillary teeth, and the floating nature (Springer, 1968) of the incisor teeth of *Ecsenius* place it with the Salariini.

SEXUAL DIMORPHISM.—The species of *Ecsenius* exhibit a number of diverse morphological features that are associated with sex and, in males, with presumed degree of maturity. The primary sexual dimorphism of *Ecsenius* is that typical of all blenniids: the first anal spine in females is usually greatly reduced, not visible externally and completely included in a somewhat triangular fleshy lobe embodying a large urogenital opening and a papilla. In males the anal spines are distinct and the urogenital opening is a minute orifice at the tip of a short, slender, or truncate tube.

[1] I (Springer, 1968) erroneously reported that *Ecsenius* had a median ethmoid that was encapsulated by the lateral ethmoids and that projected into the orbital region of the skull. I have reexamined my material and additional material and find only a small amount of cartilage in the area where an ossified median ethmoid would be expected. The structure labelled as the median ethmoid in Springer (1968, plate 10, center) is actually a process on the parasphenoid.

In at least several species of *Ecsenius* there is a tendency for males to exceed females in standard length attained. In *E. gravieri* the largest male was 61 mm and the largest female was 46 mm (12 of 29 males over 24 mm exceeded 46 mm, but only 1 of 24 females over 24 mm attained that size). In *E. bicolor* the largest male was 77 mm and the largest female was 59 mm (40 of 128 males over 24 mm exceeded 55 mm, but only 2 of 110 females over 24 mm exceeded 55 mm). In *E. mandibularis* the largest male was 51 mm and the largest female was 39 mm (23 of 45 males over 24 mm exceeded 39 mm; there were 40 females over 24 mm). In *E. yaeyamaensis* the largest male was 51 mm and the largest female was 42 mm (15 of 84 males over 24 mm exceeded 42 mm; there were 71 females over 24 mm). In *E. nalolo* the largest male was 51 mm and the largest female was 43 mm (15 of 81 males over 24 mm exceeded 43 mm; there were 68 females over 24 mm). In *E. oculus, E. namiyei, E. midas,* and *E. lividinalis,* of which there were relatively few specimens, the largest specimen was a male. In *E. lineatus,* of which I had only 13 specimens (6 were males), the largest specimen was a female. In *E. frontalis* large males and females were relatively common in all three color pattern forms (see discussion under species account), but the largest female was larger than the largest male in the nigrovittatus form. The sexes attained about equal size in *E. aroni, E. pulcher,* and *E. opsifrontalis.* The list on this page gives the sizes of the largest specimen examined for each sex of each species.

| | *female* | *male* |
|---|---|---|
| *midas* | 56.0 | 83.1 |
| *frontalis* | | |
| frontalis form | 50.5 | 58.6 |
| albicaudatus form | 50.5 | 51.6 |
| nigrovittatus form | 48.3 | 44.0 |
| *pulcher* | 58.0 | 58.4 |
| *gravieri* | 46.5 | 60.8 |
| *aroni* | 40.8 | 40.8 |
| *bicolor* | 59.6 | 77.6 |
| *namiyei* | 66.5 | 81.8 |
| *lineatus* | 65.9 | 60.1 |
| *stigmatura* | 44.9 | 37.7 |
| *lividinalis* | 30.5 | 33.0 |
| *yaeyamaensis* | 42.6 | 51.9 |
| *nalolo* | 43.2 | 51.3 |
| *oculus* | 49.3 | 53.8 |
| *opsifrontalis* | 34.8 | 35.8 |
| *prooculis* | — | 39.5 |
| *bimaculatus* | — | 31.7 |
| *bandanus* | — | 31.4 |
| *mandibularis* | 39.0 | 51.1 |

These sexual differences are possibly associated with territoriality. It has been noted for freshwater fishes (Collette and Yerger, 1962, p. 220, for significant reference citations) that in those species with a well-developed territory, the males are larger. During field observations on nine different species of *Ecsenius* I noted that all appeared to have a very limited range of movement. Individuals were occasionally seen to drive off fishes (nonblenniids) that approached them, although most often the *Ecsenius* retreated. An individual *Ecsenius* occupying a hole in a rock in an aquarium would successfully drive off another attacking *Ecsenius* whether or not of the same species or of larger size. If the occupant left the hole and another individual entered it, however, the new occupant could not be driven out by the previous occupant.

In *E. bicolor* (Table 15) and Taiwan specimens of *E. namiyei* (Table 16) males have significantly ($p$ = less than .001) higher average numbers of dorsal and anal rays and caudal vertebrae than females. Ethiopian males of *E. frontaris* (frontalis form color pattern) had significantly higher average numbers of anal rays ($p$ = less than .001) and vertebrae ($p$ = between .02 and .01) than Ethiopian females (frontalis form color pattern). The other *E. frontalis* color pattern forms from Ethiopia and the frontalis and albicaudatus color pattern forms from the Gulf of Aqaba did not exhibit sexual dimorphism in these two characters. In those other species for which there were large numbers of specimens, there did not appear to be sexual dimorphism in these meristics except for numbers of dorsal rays in *E. pulcher,* where males had a significantly higher average number than females (Table 16; $p$ = .001).

Mandibular (dentary) tooth counts were examined for sexual dimorphism. Most of the species exhibited none for this character, but in three species, *E. bicolor, E. yaeyamaensis* (both Table 4), and *E. nalolo* (Table 17), females had significantly higher average numbers of teeth ($p$ = less than .001). Gulf of Aqaba and northern Red Sea speci-

mens of *E. nalolo* were considered in one test, southern Red Sea and Indian Ocean specimens in another test. Both tests were significant.

In *E. mandibularis* the third dorsal spine (Table 7) is considerably longer in males than females (only the southern Queensland specimens were checked). Though few specimens were available, it seems that the same type sexual dimorphism may also occur in *E. opsifrontalis, E. nalolo,* and *E. lineatus.*

In *E. mandibularis, E. yaeyamaensis, E. nalolo,* non-Australian *E. bicolor,* and *E. argus* the males tend to have a higher average fifth dorsal ray length than females (Table 8). There did not appear to be much difference between males and females of Australian *E. bicolor* in regard to fifth dorsal ray lengths.

Either the upper and/or lower lobes of the caudal fin in males (less so in females) of *Ecsenius* species generally become increasingly longer with increase in SL, and males of most species tend to have longer caudal fins than females (Table 9); but the two sexes are about the same in *E. gravieri* (Figure 11). In *E. mandibularis* and *E. bicolor* males and *E. aroni* females the caudal fins may reach a peak relative length well below the maximum SL and then begin to decrease in relative size with increase in SL.

Nasal cirrus lengths (Table 10) tend to be longer in males of *E. oculus, E. opsifrontalis, E. yaeyamaensis, E. nalolo,* and *E. mandibularis* than in females.

In addition to the above features the males of most, if not all, species of *Ecsenius* tend to develop thick fleshy tips on most of the anal rays (Figures 19, 33, 35, 36). Such developments may accompany sexual maturity as males of similar size within a species may or may not show such development. The fleshy ray tips appear to be a parallel of the condition found in many blenniids where the anal spines and anterior anal rays may be enveloped in rugose folds in presumably mature males.

Finally, the color pattern of preserved males is in general darker or more contrasty than that of females.

Many of the features discussed above are similarly and variously exhibited by other species of the Blenniidae. I am unable to explain why there should be meristic sexual dimorphism, especially so as there is usually a broad overlap in meristics between males and females and the average differences are frequently one element or less in a particular character. On the other hand, the longer fin elements and cirri of males are probably of importance in sex recognition and courtship.

MIMICRY.—At least two species of *Ecsenius* bear a strong, but superficial, resemblance to species of the nemophidinine genus *Meiacanthus* Norman. *E. bicolor* resembles *M. atrodorsalis* (Günther) in both color and morphology. G. Losey (in litteris) has observed the two species together at Eniwetok, where it appeared to him that *E. bicolor* was the mimic as it was the rarer of the two species. He described both species as being dark gray-blue anteriorly and bright yellow-orange posteriorly. My observations of *E. bicolor* offer some contrast to those of Losey's. At One Tree Island on the southern end of the Great Barrier Reef, I collected over 100 *E. bicolor* and only one *M. atrodorsalis,* and that one was taken in a collection where no *E. bicolor* were seen or collected. The color patterns were somewhat different also. The *E. bicolor* were bright blue anteriorly and red-orange posteriorly. The *M. atrodorsalis* was gray-blue anteriorly and yellow posteriorly. It is possible that there is population variation or that different species of *Meiacanthus* were involved.

Both *E. gravieri* and *M. nigrolineatus* Smith-Vaniz have been collected together often and are very similar in morphology and color pattern, both in life and in preserved material. There is good circumstantial evidence supporting the idea of a mimic-model relationship between these two species. In the Gulf of Aqaba the two species are represented only by pale forms; that is, with relatively little black pigment. In the southern Red Sea both species are represented only by melanistic forms. Further considerations of possible mimicry involving these two species will be discussed elsewhere (Springer and Smith-Vaniz, ms).

Starck (1969) discussed mimicry between *E. midas* and the anthiine *Anthias squamipinnis* Peters. He believed that *E. midas* was the mimic because it was much less abundant than the anthiine. He was not able to establish the basis for the mimicry but believed that the blenny, when occurring in aggregations of the anthiid, probably was protected from predation because of the difficulty a predator has in singling out a prey from a large group. My observations in the Red Sea also indicate that *E. midas* was

exceedingly rare and that *A. squamipinnis* was one of the dominant species, but I saw no predation of or interaction between these two species.

Among the blennies, the only other species reported to be involved in mimicry are the aggressive nemophidinines *Aspidontus taeniatus* Quoy and Gaimard, which mimics the cleaner wrasse *Labroides dimidiatus* (Cuvier and Valenciennes)—see Randall and Randall (1960)—and *Runula azalea* Jordan and Bollman, which aggregates with the wrasse *Thalassoma lucasanum* (Gill) where mimicry as such was not specified (see Hobson, 1969).

## Zoogeography

*Ecsenius* occurs from the Red Sea and east African coast as far west as the Tonga Islands, as far north as the Ryukyu Islands, and as far south as the southern end of the Great Barrier Reef. It has been reported questionably from the Hawaiian Islands (I doubt its occurrence there; see discussion under *E. bicolor* species account). The genus is unreported from the central and eastern Pacific and Atlantic oceans. While most of the species are inhabitants of shallow waters, they are not taken along shore. With only exceptional individuals, the species are known only from coraliferous areas.

Over half the species of *Ecsenius* are relatively restricted geographically, or form identifiable populations in different areas. Of the five species occurring in the Red Sea, *E. aroni* (Figure 2), *E. gravieri* (Figure 1), and *E. frontalis* (Figures 1 and 5) occur only there (the latter two species also occur in the contiguous Gulf of Aden). Of the other two Red Sea species, the *E. nalolo* (Figure 2) population from the Gulf of Aqaba is recognizable from the southern Red Sea and Indian Ocean populations in having more teeth, and the four Red Sea specimens of *E. midas* (Figure 2), which species is known from only 12 specimens altogether, have slightly lower vertebral counts than the six Indian Ocean specimens. However, the two specimens of *E. midas* from the Great Barrier Reef are intermediate in these counts.

Only one species of *Ecsenius, E. pulcher* (Figure 1), is known from the Persian Gulf and Arabian Sea, and it is not found elsewhere. Of the four species known from Australia (all from the Great Barrier Reef), *E. mandibularis* (Figure 3) is endemic, *E. yaeyamaensis* (Figure 2) is represented by a unique color pattern population, and the population of *E. bicolor* (Figure 2) has higher average numbers of dorsal and anal rays and caudal vertebrae than populations of the species from any other

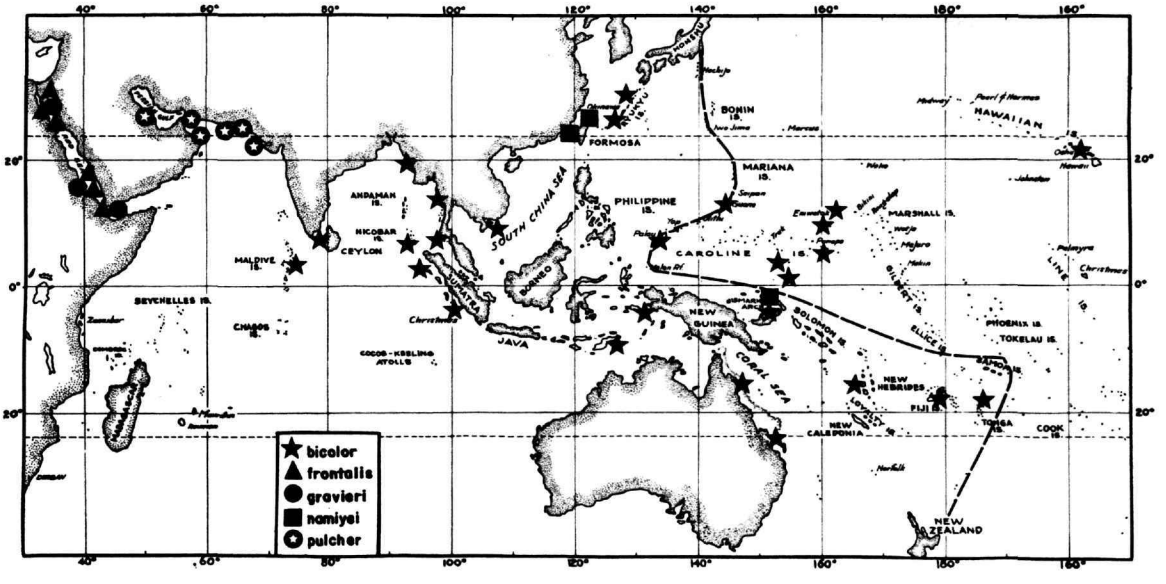


FIGURE 1.—Distribution of certain species of *Ecsenius*. Irregular broken line indicates approximate position of andesite line (see zoogeography section).

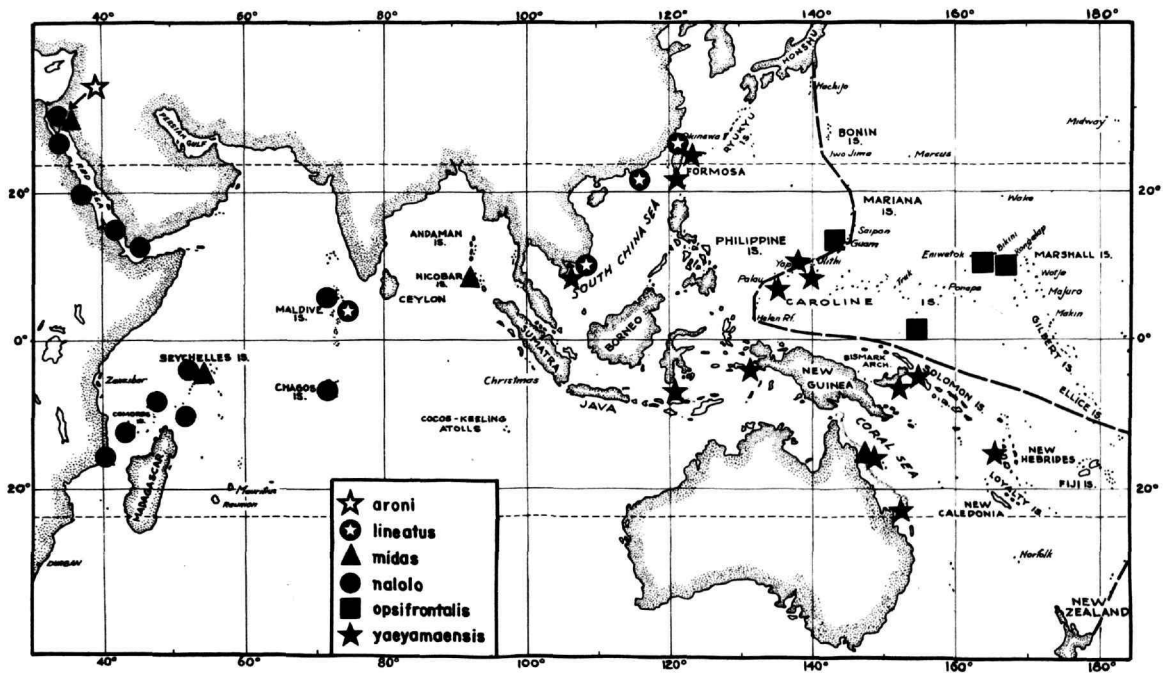


FIGURE 2.—Distribution of certain species of *Ecsenius*. Irregular broken line indicates approximate position of andesite line (see zoogeography section).

locality except the South China Sea. *E. prooculis, E. bimaculatus,* and *E. bandanus* (all Figure 4) appear to be highly restricted in their ranges, and *E. oculus* (Figure 3) comprises several recognizable color pattern populations in the Pacific.

Only three species occur in both the Indian and Pacific oceans. *E. bicolor* (Figure 1), which is widespread in the Pacific, reaches as far west as the Maldives in the central Indian Ocean. *E. oculus* (Figure 3), also moderately widespread in the Pacific, occurs along the Indian Ocean side of Sumatra, and *E. lineatus* occurs from northern Taiwan and the South China Sea to the Maldives. One might place among these species a fourth, which I have recognized as two species: *E. yaeyamaensis* (Figure 2), Pacific Ocean, and *E. nalolo* (Figure 2), Indian Ocean, which at the least are completely distinguishable based on color pattern. There is a considerable distance between the nearest known populations of these last two species.

While it is difficult to explain and may only be an artifact of collecting, only 3 of the 12 species occurring in the Pacific, *E. bicolor* (Figure 1), *E. yaeyamaensis* (Figure 2) and *E. opsifrontalis* (Figure 2) have been collected east of the andesite line (Macdonald, 1949), which separates the continental from the noncontinental rocks. The approximate position of the line, based on Menard's (1964, fig. 4.21) delineation, is indicated in Figures 1–4. Of these three species, *E. opsifrontalis* occurs only from the line eastward and *E. yaeyamaensis* has its eastern limits at or just beyond the line. The nearest relative of *E. opsifrontalis, E. oculus* (Figure 3), has its eastern limit on the line. The last two species have not been collected together.

It would appear that in the Pacific, at least, *Ecsenius* had its evolutionary origin in the older continental areas and has not been too successful in invading the more recent oceanic islands. Thus, *E. opsifrontalis* is probably a recently evolved species, perhaps a derivative of *E. oculus,* and the presence of *E. bicolor* east of the andesite line indicates a relatively recent invasion.

It is interesting to compare the distributions of the species of *Ecsenius* with those of the only other recently revised large genus of salariinine blennies,

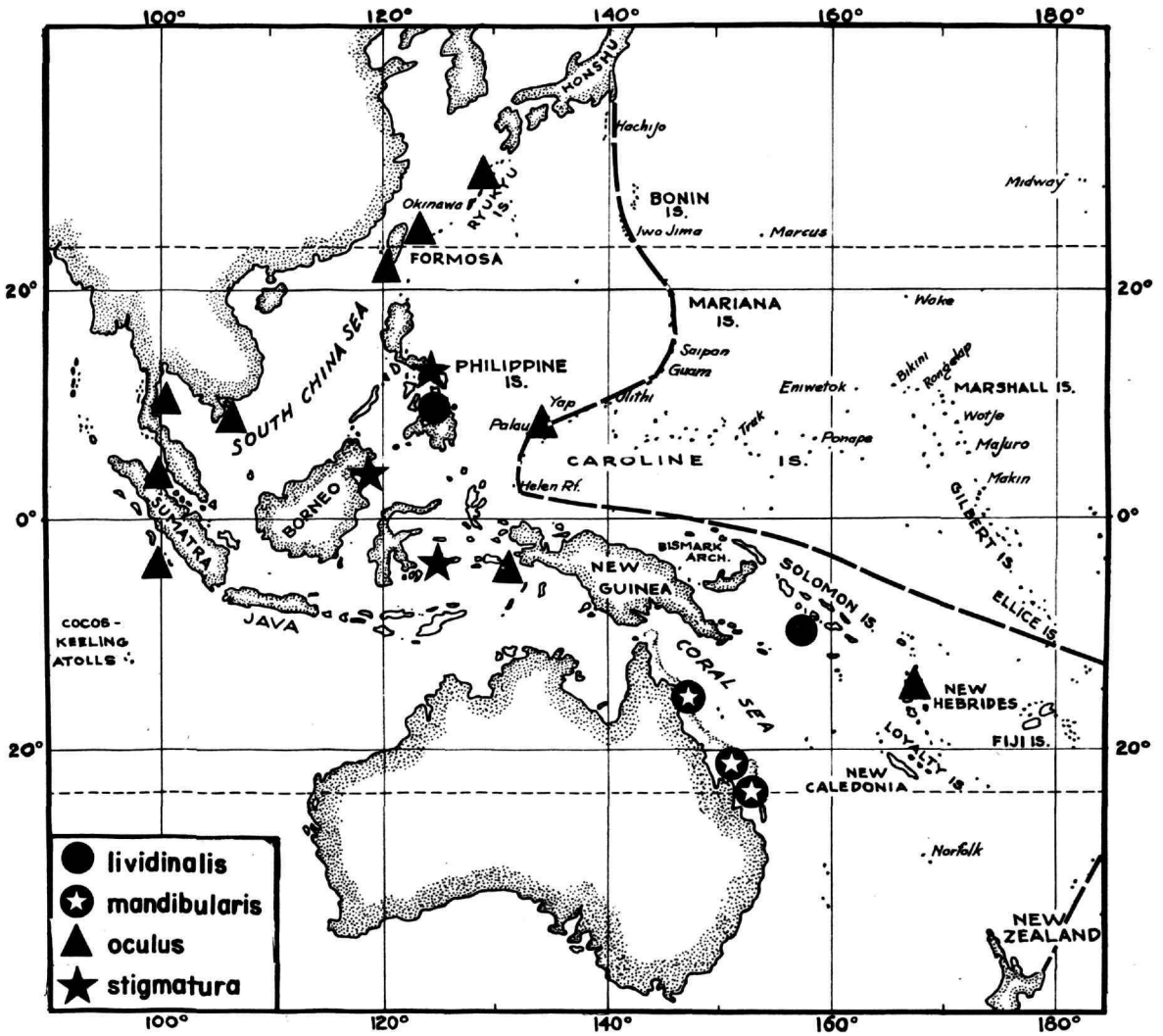


FIGURE 3.—Distribution of certain species of *Ecsenius*. Irregular broken line indicates approximate position of andesite line (see zoogeography section).

*Entomacrodus* (Springer, 1967). *Entomacrodus* occurs in waters close to rocky shores (right up to the shore line). The species are most often taken in areas where corals are sparsely or not at all present (although the corals may abound in areas adjacent to where the species occur). Species of the two genera are not often collected together, and where they are, one genus or the other usually predominates. Presumably where they are collected together, by poisoning, the poison has entered different habitats. Collectors rarely restrict themselves to a single habitat when collecting, but pick up everything killed, thus mixing the specimens so taken.

In general, the species of *Entomacrodus* are more abundant in collections and more widely distributed geographically, occurring circumtropically, than are the species of *Ecsenius*, but no species of *Entomacrodus* has been taken in the Red Sea or Persian Gulf. I collected only one specimen of *Entomacrodus* (*E. thalassinus*) at One Tree Island, Great Barrier Reef, whereas I collected hundreds

of specimens of the three species of *Ecsenius* occurring there. I collected seven species of *Entromacrodus* and four species of *Ecsenius* in Taiwan, and none were very abundant.

The overall geographic picture presented by the two genera has two parallels and several differences. Indian Ocean–Pacific Ocean species pairs are present in both genera: *Ecsenius nalolo–E. yaeyamaensis, Entomacrodus epalzeocheilus–E. niuafoouensis, Entomacrodus vermiculatus–E. decussatus.* Two species of *Entomacrodus, E. sealei* and *E. cymatobiotus,* do not occur west of the andesite line and one species, *E. stellifer,* does not occur east of it. The widespread species of *Entomacrodus* are more widespread than those of *Ecsenius,* and *Entomacrodus* is circumtropical. This may be the result of the pelagic ophioblennius larva characteristic of *Entomacrodus.* The larvae of *Ecsenius* have not been collected in the field and nothing is known of their behavior. *Entomacrodus* has eight island endemic species (22 species in the genus), whereas *Ecsenius* has only one or two (18 species in the genus), and these may be found to be more widespread when more collections are available. Two species of *Entomacrodus* have recognizable South China Sea subspecies, but none of the species of *Ecsenius* are so represented (there are few specimens of *Ecsenius* from that area). Springer (1967) noted that several species of *Entomacrodus* were peripherally distributed in the tropical western and central Pacific; only *Ecsenius mandibularis* is so limited in its distribution. *Entomacrodus* occurs in Hawaii where *Ecsenius* has been reported only once, under peculiar circumstances.

It would seem that the distributional pattern differences shown by the two genera are probably the result of their different ecological preferences and early life history. But these facts alone are insufficient to explain, on the surface, at least, why *Entomacrodus* does not occur in the Red Sea or Arabian Sea and Persian Gulf. Its absence from the latter two areas could be an artifact of collecting, but seems unlikely in view of the fact that many collections have been made in those areas and that *Entomacrodus* is an easier genus to obtain than *Ecsenius* where the two co-occur generally. The absences of *Entomacrodus* from the Red Sea and *Ecsenius* from Hawaii seem real as there has been a great collecting effort made in those areas in recent years.

Because they are more difficult to obtain, I feel certain that the ranges of the species and the number of species of *Ecsenius* reported on here will increase significantly in the course of a few years. I believe this, in part, because *Ecsenius* species frequently occur at greater depths than have usually been collected in the past; there has been relatively little collecting at depths over three meters along the coasts of the Indo-Pacific. On the other hand, I do not feel that there are many, if any, species of the shallow-dwelling genus *Entomacrodus* yet undiscovered, and the ranges of only a few of those known will increase to any significant degree with more collecting.

## Key to the Subgenera and Species of *Ecsenius*

1. Anterior canines in lower jaw obvious, more than twice size of adjacent incisoriform teeth; total incisoriform teeth + anterior canines in lower jaw 13–16; total teeth in upper jaw 26–34; caudal forked (Figure 12); mid-predorsal pore of supratemporal series in advance of level of posterior orbital margin; pseudobranchial filaments 6–12; dorsal + ventral procurrent caudal rays 18–20; epipleural ribs 22–25; postcleithra consisting of two well-separated ossifications, dorsalmost much reduced (subgenus *Anthiiblennius*)
***midas*** (Red Sea, Indian Ocean, eastern Australia)

   Anterior canines in lower jaw rarely obvious, when obvious only slightly larger than adjacent incisoriform teeth; total incisoriform teeth + anterior canines in lower jaw 30–64; total teeth in upper jaw 97–148; caudal not forked, but often with produced rays on dorsal and ventral lobes (for instance, Figures 15, 19, 20); mid-predorsal pore of supratemporal series well posterior to level of posterior orbital margin; pseudobranchial filaments 5–8 (rarely 8); dorsal + ventral procurrent rays 10–18; epipleural ribs 11–17; postcleithra consisting of two subequal articulating ossifications (subgenus *Ecsenius*) ..... 2

2. Total posterior canines in lower jaw 7–15 (2–8 on each side)
***mandibularis*** (eastern Australia)

   Total posterior canines in lower jaw 0–3 (usually 1 on each side) ..... 3

3. Segmented dorsal rays 12–15; segmented anal rays 13–17; vertebrae 29–33 ..... 4
   Segmented dorsal rays 15–20 (only 2 of 252 specimens of *bicolor* with 15); segmented anal rays 17–23 (only 1 of 258 specimens of *bicolor* with 17); vertebrae 33–39 (2 of 4 specimens of *stigmatura* and 9 of 234 specimens of *bicolor* with 33) ..... 11
4. Dark spot extending well anteriorly from anus (Figure 26); dorsal fin notched three-ninths to five-ninths length of first dorsal ray; last dorsal spine 6 to 10 percent SL; incisoriform teeth in lower jaw 30–37; segmented anal rays 13–14; caudal vertebrae 19–20; total vertebrae 29–30 ..... ***lividinalis*** (Pacific)
   No dark spot extending anteriorly from anus (occasionally black lining of gut protrudes slightly through anus giving appearance of dark ring); dorsal fin notched seven-ninths to nine-ninths length of first dorsal ray; last dorsal spine 0.4–3.1 percent SL (one specimen of 35 of *E. oculus* had length 4.6 percent); incisoriform teeth in lower jaw 41–64; segmented anal rays 14–17 (1 of 42 specimens of *opsifrontalis* with 14); caudal vertebrae 21–23; total vertebrae 31–33 ..... 5
5. Two large, distinct dark spots at caudal base extending posteriorly well out on caudal fin (Figure 31) ..... ***oculus*** (Pacific)
   Dark spots, if present at caudal base, small, scarcely encroaching on caudal fin ..... 6
6. Distinct dark stripe, stripes, or spots present on fleshy pectoral base (Figures 27–30); pseudobranchial filaments 5–8 (rarely 5) ..... 7
   Fleshy pectoral base not noticeably marked; pseudobranchial filaments 5–6 ..... 8
7. Fleshy pectoral base with at least a forked dark stripe, the arms of which extend posteriorly ..... ***yaeyamaensis*** (Pacific)
   Fleshy pectoral base with an unforked dark stripe (and usually other dark marks) ***nalolo*** (Indian Ocean; Red Sea)
8. Lateral line extending posteriorly to below level of 11th-12th (usually 12th) dorsal spine; segmented dorsal rays 13–14 (14 in only 6 of 42 specimens); segmented anal rays 14 to 16 (usually 15); nasal cirrus 2.3–5.9 percent SL ..... ***opsifrontalis*** (Pacific)
   Lateral line extending posteriorly to below level of 8th-9th dorsal spine; segmented dorsal rays 14; segmented anal rays 15–16 (usually 16); nasal cirrus 1.1–2.3 percent SL ..... 9
9. Two large dark spots on side of body in area covered by appressed pectoral fin (Figure 34) ***bimaculatus*** (Pacific)
   Body without large dark spots ..... 10
10. Side of body with alternating dark and pale longitudinal stripes (Figure 33) ***prooculis*** (Pacific)
    Side of body without distinct marks (Figure 35) ..... ***bandanus*** (Pacific)
11. Dark spot extending anteriorly from anus (Figures 24–25); dark stripe originating at ventral margin of orbit extending posteriorly across head ..... ***stigmatura*** (Pacific)
    No dark spot in region of anus; dark stripe extending posteriorly across head, if present, originating at mid-postorbital level ..... 12
12. Anterior nostril with cirri on both anterior and posterior margins; segmented caudal rays 14 (rarely 13); lateral line usually with several vertical pairs of pores beginning anteriorly ..... 13
    Anterior nostril with cirrus on posterior margin only; segmented caudal rays 13 (rarely 14 in *E. frontalis* and in some juveniles of other species under 25 mm SL); lateral line of simple pores only (rarely with a vertical pair at origin) ..... 14
13. Dorsal rays 15–18; dorsal fin notched two-ninths to seven-ninths length of first dorsal ray (usually four-ninths or more); last dorsal spine 2.5–6.9 percent SL; lateral line with vertical pairs of pores for one-third to all its length (rarely less than one-half); a dark spot on paler background on anterior dorsal fin; pseudobranchial filaments usually 6; upper nasal cirrus length usually more than 4.9 percent SL .. ***bicolor*** (Pacific and Indian Oceans)
    Dorsal rays 18–20 (rarely 18); dorsal fin unnotched; last dorsal spine 11.0–15.9 percent SL; lateral line with vertical pairs of pores, if present, rarely occupying more than anterior two-fifths its length; dorsal fin entirely black, occasionally with some obscure longitudinal stripes anteriorly; pseudobranchial filaments usually 7; upper nasal cirrus length not more than 4.8 percent SL ..... ***namiyei*** (Pacific)
14. Dorsal fin without a notch; last dorsal spine 10.7–20.8 percent SL; pectoral rays 14–16 (14 in 5 or 89 specimens) ..... ***frontalis*** (Red Sea; Gulf of Tadjourah; see discussion under species account for distinct color pattern forms.)

Dorsal fin with a notch; last dorsal spine 2.2–7.0 percent SL; pectoral rays 13–15 (15 in 5 of 87 specimens) ..... 15

15. Dorsal spines 12; pectoral rays 13 (14 in 1 of 12 specimens); body at about midlevel with a longitudinal dark stripe, either continuous or as a series of dark bars, extending length of body and entering caudal fin basally ..... ***lineatus*** (Pacific and Indian Oceans)

Dorsal spines 12–14 (12 in 9 of 201 specimens); pectoral rays 13–15 (13 in 2 of 176 specimens); body without a broad dark stripe (occasionally with a slender stripe on dorsal fourth of body, ceasing well anterior to caudal base) ..... 16

16. Mid-distal half of at least spinous dorsal fin black or with black spots in interradial membrane; dorsal and ventral lobes of caudal fin darker than remainder; usually several small dark spots on posterior third of body; usually a narrow, black longitudinal stripe on dorsoanterior portion of body ..... ***gravieri*** (Red Sea; Bay of Tadjourah)

Mid-distal half of dorsal fin not noticeably marked; dorsal and ventral lobes of caudal not darker than remainder of caudal; no black spots or longitudinal stripes on body (body uniformly dark, with a dark spot at caudal base, or with posterior half pale with irregular, vertical dark bars) ..... 17

17. Dorsal rays 17 or 18; anal rays 19 or 20; nasal cirrus 1.0–3.9 percent SL; dorsal fin notched seven-ninths to nine-ninths (usually eight-ninths) length of first dorsal ray, body uniformly dark with a darker spot at caudal base ..... ***E. aroni*** (Red Sea)

Dorsal rays 18–20; anal rays 19–23 (rarely 19 or 20); nasal cirrus 3.0–7.9 percent SL; dorsal fin notched five-ninths to eight-ninths (rarely eight-ninths) length of first dorsal ray; body uniformly dark or posterior half pale with vertical dark bars

***E. pulcher*** (Persian Gulf and northern Arabian Sea)

## The Species Groups of *Ecsenius*

The 18 species of *Ecsenius* fall into eight groups. Four of these groups are monotypic, *E. midas, E. frontalis, E. lineatus,* and *E. mandibularis,* and with the exception of *E. lineatus,* I hesitate to relate them closely to each other or to any other group. *E. lineatus* may be an offshoot of the yaeyamaensis group.

*Ecsenius midas,* as the monotypic member of the subgenus *Anthiiblennius,* is well differentiated (see key, couplet 1). It is also the most specialized of the species of the genus as evidenced by its extreme reduction in number of teeth, the increased size of the anterior canines, the reduced nature of the postcleithra, and the great anterior displacement of its dorsal fin origin. *E. frontalis* has an unnotched dorsal fin and the highest pectoral ray counts in the genus. The albicaudatus form of *E. frontalis* (see discussion of color pattern under species account) is reminiscent of that found in *E. bicolor* and *E. namiyei. E. frontalis* is separated from the latter two species, however, in having only a single nasal cirrus, 13 segmented caudal rays, and no paired lateral line pores. *E. lineatus* has no noteworthy peculiarities as found in many of the other species. Its general robustness, relatively high fin ray and vertebral counts, large size attained, and moderately notched dorsal fin separate it from the yaeyamaensis species group, to which it otherwise might belong. *E. mandibularis* is unique in its large numbers of posterior canine teeth and long third dorsal spine and fifth dorsal ray lengths. In addition, males of *E. mandibularis* develop prolongations of all the caudal rays, which in the other species are primarily restricted to the upper and lower extremities of the fin.

The pulcher species group comprises *E. pulcher, E. gravieri,* and *E. aroni.* These three species are morphologically quite similar and differ from each other primarily in color pattern, depth of the dorsal fin notch, development of caudal fin lobes, and the slightly higher meristics of *E. pulcher.* They share the pecularity of having typically 14 pectoral rays (otherwise found typically only in *E. stigmatura),* and with *E. midas* and *E. frontalis* are the only species with typically 11 precaudal vertebrae.

The bicolor species group comprises *E. bicolor* and *E. namiyei,* which are distinct from all other *Ecsenius* species in having nasal cirri on both the anterior and posterior margins of the anterior nostril and paired pores in the lateral line. They both have typically 14 segmented caudal rays.

The stigmatura species group comprises *E. stigmatura* and *E. lividinalis.* The Bornean specimen allocated to *E. stigmatura* may be recognizable as

a separate species when more specimens are known. The two species are united here in having a black spot in the anal region (found otherwise only in *E. midas*) and typically 14 segmented caudal rays, but are considerably different in other characters. *E. lividinalis* has the lowest tooth, dorsal and anal fin and vertebral counts, and the highest fin ray proportions (as percent SL) in the subgenus *Ecsenius*. The relationship of *E. lividinalis* with *E. pulcher* is questionable and possibly each should be placed in its own group.

The yaeyamaensis species group comprises *E. yaeyamaensis, E. nalolo, E. oculus, E. opsifrontalis, E. prooculis, E. bimaculatus,* and *E. bandanus*. This group comprises the more or less nondescript, small species with relatively deep dorsal fin notches and, for the most part, low vertebral and vertical fin ray counts. Within this group, there are three subgroups comprising the first two, second two, and last three species listed. The subgroups are distinguished from each other on color pattern and slight meristic or proportional differences. Each group presents certain problems.

The two species of the yaeyamaensis subgroup might, by some systematists, be considered to comprise a single species. The two species I recognize are completely differentiated by a color marking (key couplet 7) and occur in different oceans (Figure 2). In the Pacific Ocean there are also easily recognizable color pattern populations of one species. If the two species were combined the problem of what to do with these recognizable populations would remain, as the situation would then exist of having two recognizable taxa differing in color pattern with at least one of these taxa also having populations completely recognizable on the basis of color pattern (see color pattern description under *E. yaeyamaensis* species account).

The two species of the oculus subgroup are distinguished from each other on the basis of color pattern and the slightly lower meristics of one species. The two species occupy essentially allopatric ranges (Figures 2 and 3). There are indications that some recognizable populations of *E. oculus* may occur (see under species account).

The three species of the prooculis subgroup are known from 5, 3, and 1 specimens, all males. These species are distinguished from each other only by their strikingly different color patterns. They have not been collected from the same locality (Figure 4). Whether the three species comprise one highly variable species will require much more material than is available.

## Species Accounts

### *Ecsenius (Anthiiblennius) midas* Starck

FIGURE 12

*Ecsenius (Anthiiblennius) midas* Starck, 1969, p. 1 [D'Arros Island, Amirante Islands].

DESCRIPTION.—Dorsal spines 13–14 (usually 13); dorsal rays 19–21; segmented anal rays 20–23; pectoral rays 13 (12 on one side only of one specimen); segmented caudal rays 13–15 (usually 14); dorsal procurrent caudal rays 9–10; ventral procurrent caudal rays 9–10; total caudal elements 31–34; gill-rakers 10–15; pseudobranchial filaments 6–12; lower incisor teeth 13 to 16; lower jaw posterior canines 1; total lower jaw posterior canines 2; upper incisor teeth 26–34; precaudal vertebrae 11; caudal vertebrae 27–29; total vertebrae 38–40; epipleural ribs 22–25. Lateral line with no paired pores, extending posteriorly to beneath level of 7th-9th dorsal spine. Dorsal fin without notch. Third (innermost) pelvic ray obvious. One cirrus on each anterior nostril.

Color pattern: The Red Sea and Indian Ocean specimens of this species are generally dusky, darkest anteriorly, and paling on the caudal peduncle of some specimens. The lower side of the head is darker anteriorly and on some specimens a dusky stripe occurs on each side proceeding dorsoposteriorly from the side of the lower jaw and curving upward along the membranous margin of the branchiostegal membrane. A few specimens exhibit a diffusely dusky stripe beginning just behind the ventroposterior border of the eye and extending back across the opercle. One specimen had some diffuse vertical bands on the body. The most conspicuous mark is a dark spot enveloping the anus and extending anteriorly for a short distance. The dorsal fin bears a narrow, dark distal stripe beginning anteriorly on the spinous portion and extending to the anterior dorsal rays. This fin is usually dark anteriorly, making it difficult or impossible to count the spines externally. The anal fin is pale dusky, slightly darker on the spines and, in some specimens, along its distal edge. The caudal fin varies from immaculate to evenly dusky with its dorsal and ventral margins narrowly, darkly pig-

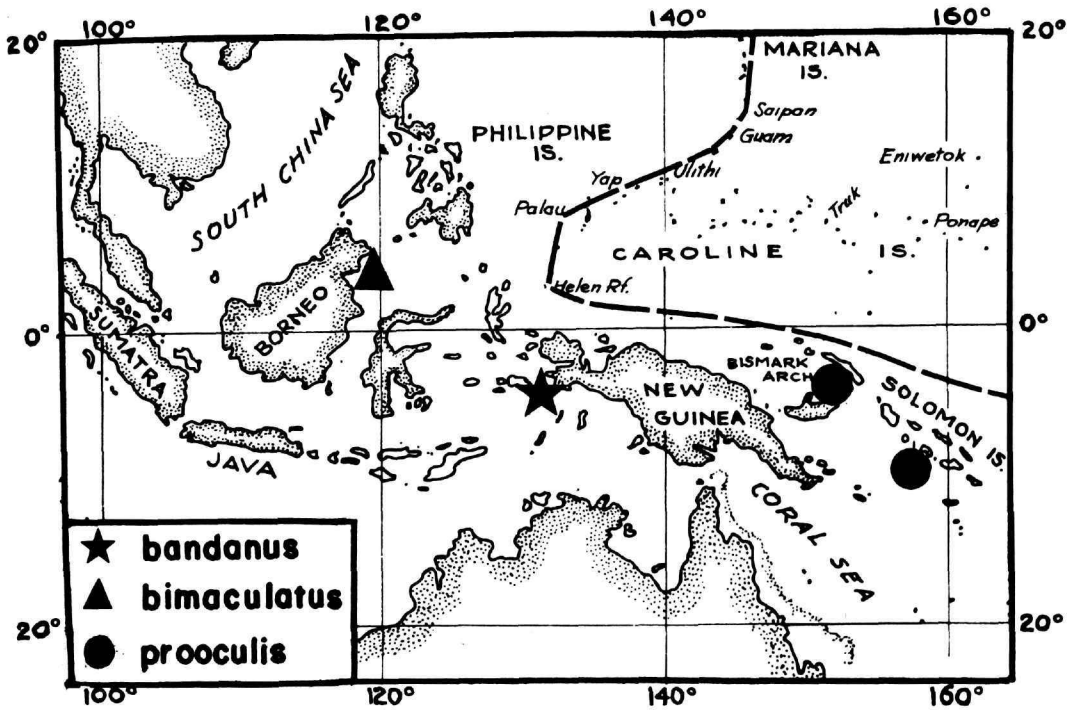


FIGURE 4.—Distribution of certain species of *Ecsenius*. Irregular broken line indicates approximate position of andesite line (see zoogeography section).

mented. The pectorals are generally pale with the rays sometimes narrowly and darkly pigmented. The pelvics are dusky. The two small Great Barrier Reef specimens differed from the others most noticeably in having the dorsal fin dusky, but with the distal portion of the segmented ray part of the fin unmarked and the edge of the dusky area much darker than the remainder in the region below the unmarked part.

Starck (1969) reported the life color to be golden yellow, darker dorsally except for a fine black marginal line on the dorsal fin and a black blotch around the anus. The color of a freshly killed female (USNM 204550) I collected in the Red Sea was somewhat different. The head was pale orange-dusky with a narrow, pale yellow-green stripe extending posteriorly from the orbit to the opercle margin. The underside of the head was pale white except for the dark dusky lower jaw. The sides of the body were pale purple-dusky overlying orange. The venter was chartreuse. The dorsal, anal, and caudal fins were orange-yellow. The pectoral fins were pale yellow-green.

GEOGRAPHIC VARIATION.—There are too few specimens of *E. midas* to draw firm conclusions, but it appears from the fact that the four Red Sea specimens have 27 caudal vertebrae and the six Indian Ocean specimens have 28 or 29 caudal vertebrae, that population differences occur. The two Great Barrier Reef specimens have 27 and 28 caudal vertebrae and are thus intermediate between the specimens from the other two areas.

MATERIAL.—Gulf of Aqaba, Sinai coast, Dahab, UTAI 4221 (71.2) and USNM 204707 (77.1); Ras Muhammad, southern tip of Sinai Peninsula, USNM 204550 (45.1) and 204551 (68.9); Amirantes Islands, D'Arros Island, ANSP 111148 (74.4, holotype of *E. midas*), 111149 (48.7), 111854 (33.5, cleared and stained), and USNM 202422 (56.0); Nicobar Islands, NFIS 9579 (83.1); Nicobar Islands, Tillanchong, NFIS 9577 (44.4); Australia, Queensland, Escape Reef, ANSP 109686 (2:28.5–29.0).

### *Ecsenius (Ecsenius) frontalis* Ehrenberg

FIGURES 13–15

*Salarias frontalis* Ehrenberg in Cuvier and Valenciennes, 1836, p. 328 [Massawa, Red Sea].

*Salarias nigrovittatus* Rüppell, 1838, p. 136 [Massawa, Red Sea].

*Ecsenius albicaudatus* Lotan, 1969, p. 372 [Marsa Murach, Gulf of Aqaba].

DESCRIPTION.—Dorsal spines 10–13 (rarely 10, 11, or 13); dorsal rays 17–21 (rarely 17 or 21); segmented anal rays 17–22 (rarely 17, 18, or 22); pectoral rays 14–16 (usually 15); segmented caudal rays 13 (rarely 14); dorsal procurrent caudal rays 6–8; ventral procurrent caudal rays 6–9 (rarely 9); total caudal elements 25–30 (rarely 25 or 30); gill-rakers 11–17 (rarely 11, 12, or 17); pseudobranchial filaments 5–7 (usually 6); lower incisor teeth 40–53; lower jaw posterior canines 0–1; total lower jaw posterior canines 0–2 (usually 2); upper incisor teeth 124–130 (4 counts); precaudal vertebrae 10–12 (rarely 10 or 12); caudal vertebrae 23–26 (rarely 23); total vertebrae 34–37 (rarely 34); epipleural ribs 11–16 (usually 12–14). Lateral line without paired pores, extending to below level of 8th-12th dorsal element (usually 9th–11th). Dorsal fin without notch (one of several hundred specimens had dorsal fin notched two-ninths length of first dorsal ray). Third (innermost) pelvic ray varying from obvious to not obvious (usually not obvious). One cirrus on each anterior nostril, each cirrus occasionally forked.

Color pattern: There are three basic color patterns found in *E. frontalis*. See discussion following, concerning the systematic status of these patterns. The smallest specimen examined was a postlarva, 15.0 mm SL, from the Gulf of Aqaba. It was not possible to assign this specimen to one of the three color pattern types. The specimen was pale with several irregular vertical bands composed of spots. A few small bright yellow individuals of *E. frontalis* were also seen in the Gulf of Aqaba. It may be that the banded and yellow forms represent the preadult color of the two color pattern forms found in the Gulf of Aqaba (more below).

## The Problem of *Ecsenius frontalis, E. albicaudatus, and E. nigrovittatus*

Although I have placed *E. albicaudatus* and *E. nigrovittatus* in the synonymy of *E. frontalis,* I am uncertain that my action is correct. In the discussion that follows I treat the three nominal species as color pattern forms of a single species, *E. frontalis,* and present the evidence on which my action is based.

*Ecsenius frontalis* and *E. nigrovittatus* were described from Massawa, Ethiopia, and *E. albicaudatus* was described from the Gulf of Aqaba, each from a single specimen. While the types of *E. frontalis* and *E. nigrovittatus* are in poor condition, data from these types, together with the distinctive color patterns given in the original descriptions, make it possible to identify recently collected specimens from Massawa with both these nominal species. The holotype of *E. albicaudatus* is in excellent condition. Its distinctive color pattern has been found in numerous recently collected specimens from near the type locality.

The morphology and meristics of the three nominal species are very similar, but the species differ consistently in color pattern. (In Figures 13–15 the apparent morphological differences exhibited in these illustrations are individual variations; when series of each color form are examined complete morphological overlap is encountered.) I have observed all three color pattern forms alive in their natural habitat. The frontalis form is generally brown, darkest anteriorly, grading into yellow-orange posteriorly, with a bright yellow-orange caudal fin. The head and body of the albicaudatus form are black with a narrow area of variable width at the caudal peduncle completely unmarked and pale (sometimes the pale area extends onto the dorsal fin); the caudal fin is immaculate except for a faint pink tinge observable only in freshly preserved specimens. The nigrovittatus form is usually brown with a black stripe on the body bordered by pale dorsal and ventral margins; the caudal fin is slightly tinged with orange. Occasional individuals of the nigrovittatus form have yellow-orange heads.

Two individuals, I believed at the time of capture to be the frontalis form, were brought to the laboratory alive. When the individuals were placed in an aquarium there appeared one frontalis form and one albicaudatus form, which was dark brown with a yellow-orange caudal—the only albicaudatus form I have collected with these colors. These and other individuals of both color pattern forms held in the aquarium paled considerably after several days, and it was not possible to tell one form from the other.

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The geographical distributions of the albicaudatus and frontalis forms are nearly identical (Figure 5). The frontalis form has been taken widely in the Gulf of Aqaba, in the southern Gulf of Suez, widely in the Red Sea and in the Bay of Tadjoura (Gulf of Aden, just outside the southern entrance to the Red Sea). The albicaudatus form has a similar distribution to that of the frontalis form, but it has not been taken outside of the Red Sea or in the Gulf of Suez. It was observed by me in the Gulf of Suez, however. The nigrovittatus form has been taken only in the southern Red Sea, on and off the coast of Ethiopia.

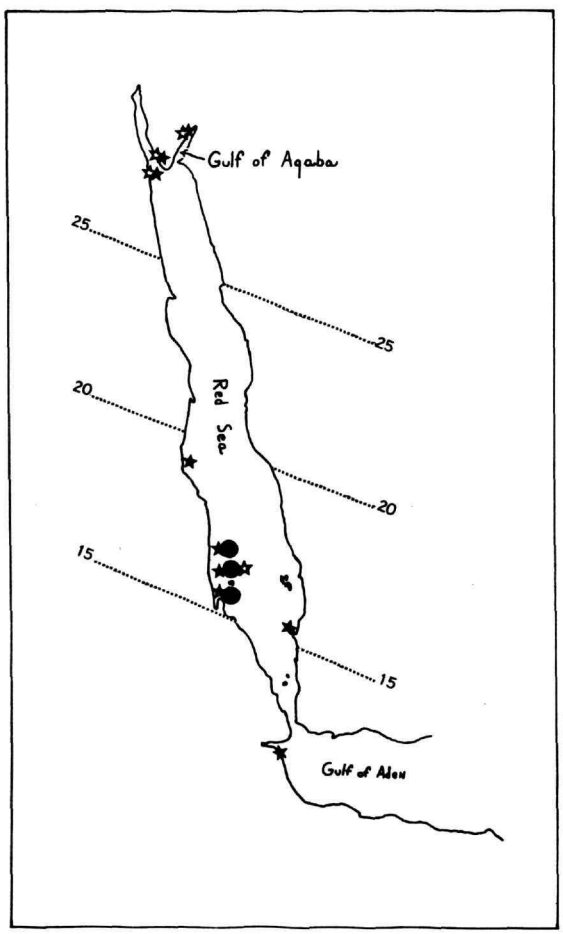


FIGURE 5.—Distribution of the three color pattern forms of *Ecsenius frontalis:* ★ = frontalis form, ☆ = albicaudatus form, ● = nigrovittatus form.

I obtained all three forms in the same collection (poison) from a coral rock outcrop estimated to be about 3 meters in height and 8–10 meters in circumference; water depth was about 4 meters. The specimens in this collection included 55 frontalis forms, 25 nigrovittatus forms, and 6 albicaudatus forms. My six collections (all made at depths of 7 meters or less) in Ethiopian waters, where the frontalis and nigrovittatus forms were always taken together, yielded three times as many frontalis forms as nigrovittatus forms, and the frontalis forms were always more abundant. The six albicaudatus forms mentioned are the only ones known from Ethiopian waters.

In the Gulf of Aqaba and Gulf of Suez collections, where only the frontalis and albicaudatus forms were seen or taken, the frontalis form was generally dominant in the shallower waters and the albicaudatus form was generally dominant in the deeper waters. The depth of each collection and the number of specimens of each form taken in the poison collections that I made in Israeli waters are listed below. Because the poison spread, it was not possible to limit collections to a particular depth. The collections were all made during the day, July-September 1969.

| *Approximate depth* (meters) | *Albicaudatus form* | *Frontalis form* |
|---|---|---|
| 0–3 | 10 | 37 |
| 0–18 | 11 | 3 |
| 0–15 | 5 | 9 |
| 0–16 | 14 | 2 |
| 0–7.5 | 3 | 0 |
| 0–10.5 | 4 | 1 |
| 0–10 | 1 | 31 |
| 0–3.5 | 1 | 8 |
| 9–12 | 18 | 1 |
| 21–27 | 3 | 0 |
| 0–9 | one seen | 9 (seen commonly) |

I observed both the frontalis and albicaudatus forms together and common at depths of about 3–12 meters on the coral reef preserve at Eilat, Israel. I cannot say whether one form was much more dominant than the other; my impressions varied from day to day.

The frontalis and albicaudatus forms were commonly observed together in the Gulf of Aqaba, and the frontalis and nigrovittatus forms were

commonly observed together at Massawa, Ethiopia. I have not seen all three forms together, although as noted above, I have collected all three from the same rock. The three forms inhabit live and dead coral and are not found over the sandy bottom. They are frequently out from under cover, on top of the coral. They dart, but only rarely swim freely, and then for only a few centimeters. Their movements are only moderately jerky. They feed by nipping at the rocky substrate. Gut contents consist of unidentifiable calcareous granules less than 0.3 mm in diameter, particulate organic matter, ostracods, and foraminifera. I noted no differences in behavior of the three forms, which appeared to be identical and different from the behavior of the other species of *Ecsenius* that occur together with them in the same general area. For instance, *E. gravieri* spends much of its time swimming freely over sandy bottom, where it feeds by nipping into the sand; *E. nalolo* was never seen out from under cover or swimming freely, and its movements are very jerky; *E. aroni* is somewhat similar in behavior (but not morphology or color pattern) to *E. frontalis,* but it usually occurs at greater depths and spends more time under cover; *E. midas,* which was not seen alive, was reported by Starck (1969) to swim with other fishes and to feed on plankton.

Certain morphological and meristic characters are given with frequency distributions in Tables 11 and 12 for each of the three forms for the different localities where they occur. Examination of the data indicates the possibility of sexual dimorphism and also that Israeli specimens of the color forms have higher numbers of certain meristic characters than Ethiopian specimens of the same forms. To determine if the differences noted are statistically significant it is, therefore, necessary to test the data for the same forms, sexes separated, from the two areas, and for different forms from the same area, sexes separated.

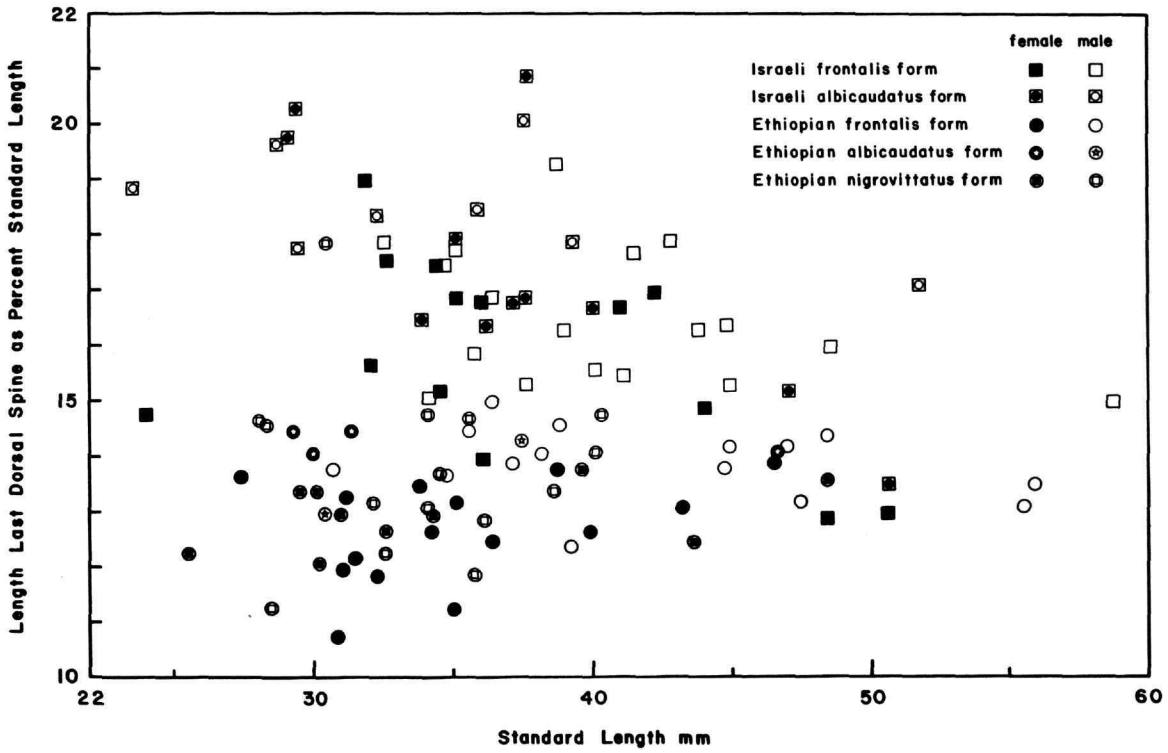


FIGURE 6.—Graph showing relationship of last dorsal spine length to standard length in the three color pattern forms of *Ecsenius frontalis.*

Data for specimens of the frontalis form from Sanganib Reef (Sudan) and the Gulf of Aden and for specimens of the albicaudatus form from Ethiopian waters were not included in the tests because the numbers of specimens were small and the localities were well removed from Israel or Ethiopia.

The following significant differences were found:

Israeli frontalis form males and females have higher average numbers of teeth, segmented dorsal rays, segmented anal rays, and caudal vertebrae than Ethiopian frontalis form males and females.

Ethiopian frontalis form males have higher average numbers of segmented anal rays than Ethiopian frontalis form females.

Ethiopian frontalis form males have a close to significantly ($p$ = between .02 and .01) higher average number of caudal vertebrae than Ethiopian frontalis form females.

Grouped data (Tables 13 and 14) of proportional characters also indicate differences among the three forms. These data were also graphed and the following differences noted:

Israeli frontalis form males have a relatively longer caudal fin than Israeli frontalis form females (Figure 10).

Israeli albicaudatus form males have a relatively longer caudal fin than Israeli albicaudatus form females (Figure 10).

Israeli frontalis form males have a relatively longer caudal fin than Ethiopian frontalis form males (Figure 10).

Ethiopian nigrovittatus form males have a relatively longer caudal fin than Ethiopian nigrovittatus form females (Figure 9).

Ethiopian nigrovittatus form males have a relatively longer caudal fin than Ethiopian frontalis form males or females (Figure 9).

Specimens of less than 30 mm SL of the Israeli frontalis and albicaudatus forms have relatively longer nasal cirri than specimens of any of the three Ethiopian forms (Figures 7 and 8).

Specimens of the Israeli frontalis and albicaudatus forms have a relatively longer last dorsal spine than any of the three Ethiopian forms

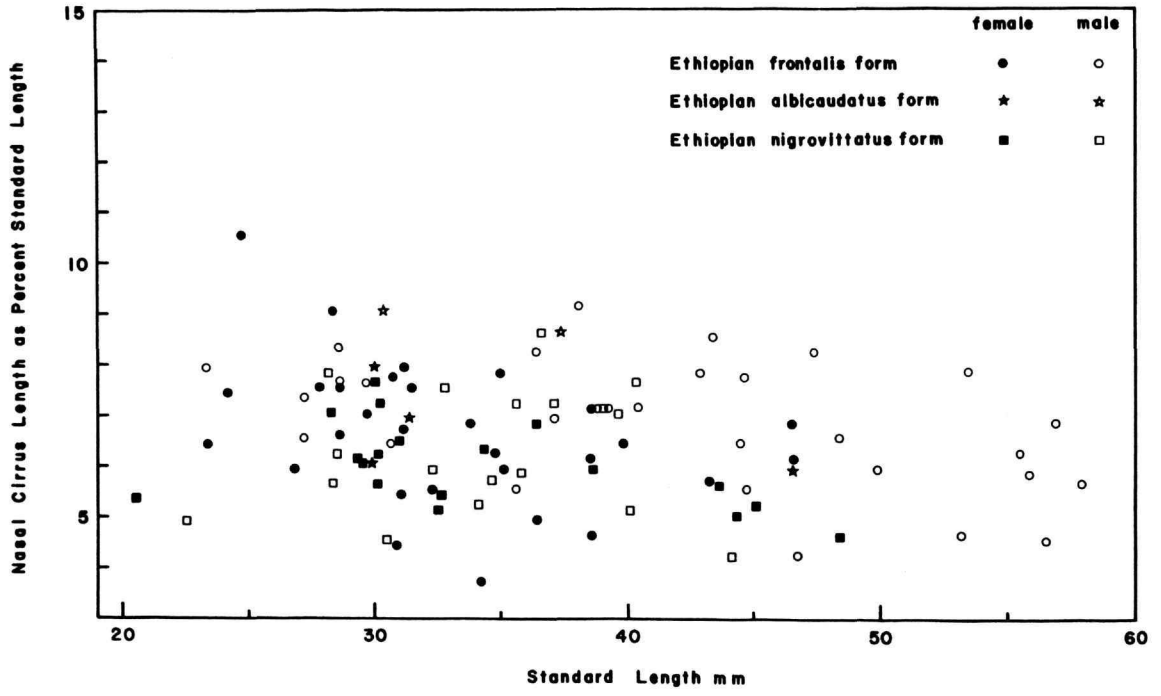


FIGURE 7.—Graph showing relationship of nasal cirrus length to standard length in the three-color pattern forms of *Ecsenius frontalis* from Ethiopian coastal waters.

(Figure 6). The same relationship exists between the relative lengths of the third dorsal spine and fifth dorsal ray of the Israeli frontalis and albicaudatus forms compared with the lengths of these elements for the three Ethiopian forms (study graphs).

There is some indication that Israeli frontalis form males have a relatively longer caudal fin than Israeli albicaudatus males (Figure 10).

Aside from the fact that there are differences between the Israeli and Ethiopian populations of the frontalis form, the above data provide only limited support for the concept that the three color pattern forms are different species: The nigrovittatus form exhibits sexual dimorphism in the length of the caudal fin, which the sympatric frontalis form does not (but the allopatric Israeli frontalis form does); nigrovittatus form males have a longer caudal fin than sympatric males of the Ethiopian frontalis form (but not longer than the allopatric Israeli frontalis and albicaudatus form males), and possibly the Israeli frontalis form males have longer caudal fins than Israeli albicaudatus form males. (This does not seem to be true of Ethiopian frontalis form males versus Ethiopian albicaudatus form males even though there are only a few specimens of the latter.)

The fact that the Gulf of Aqaba populations of the frontalis and albicaudatus color pattern forms have higher average numbers of each meristic character than their Ethiopian counterparts is probably due to the cooler water temperatures of the Gulf of Aqaba relative to those of the Ethiopian coast (Oren, 1962). The same type variation has been reported for other Gulf of Aqaba-Red Sea blenniids (Smith-Vaniz and Springer, in press).

There is, then, no consistent basis other than color pattern on which to recognize *E. frontalis* and *E. albicaudatus* as separate species. One might recognize *E. nigrovittatus* as a separate species, based on the small differences noted and the fact that it does not occur at the northern end of the Red Sea (Gulf of Aqaba).

There are other data that influence the recognition of the three forms as one species. There are no other species of *Ecsenius* that appear to be closely related to the three forms and speciation, if such occurred, would seem of necessity to have taken place in the Red Sea. The Red Sea is a relatively small body of water with a limited amount of coral reef habitat. It is difficult to postulate how three species so similar as the three color pattern forms could have evolved sympatrically, especially when there does not appear to be a difference in feeding habits or microhabitat preference.

There are other species of *Ecsenius* that have apparently evolved different color pattern forms that occur sympatrically. These forms are, however, more obviously derivative of the same basic form than are the Red Sea color pattern forms of *E. frontalis*. *Ecsenius pulcher* has a solid color form and one in which the melanophores have been suppressed in portions of the posterior region of the body, thus forming vertical dark and pale stripes (Figure 16). This form is somewhat similar to the albicaudatus form in which the melanophores on the caudal peduncle have been suppressed. *Ecsenius bicolor* has three basic color pattern forms: one that is completely dark, one that is paler (either gradually or abruptly, Figures 20 and 21), and one that has a diffuse, dark stripe on its side. Although these three forms duplicate the forms found in *Ecsenius frontalis,* they generally are not so strikingly different from each other, and the striped form is very rare. The life colors of the three *E. bicolor* forms are very much the same as opposed to the differences noted in the frontalis forms. It seems, therefore, that the tendency for species of *Ecsenius* to exhibit different color pattern forms is a trait of the genus.

Information on breeding behavior and the color patterns of the offspring are necessary for reaching a final solution to the problem of the taxonomic level that should be accorded the three color pattern forms of *E. frontalis.*

I know of no situation involving fishes that is exactly comparable with that reported here for *E. frontalis.* Although only slightly similar, the circumstances Stephens (1963) reported for *Acanthemblemaria crockeri* Beebe and Tee-Van (Chaenopsidae) is of interest. *A. crockeri* is represented by two color pattern forms in the Gulf of California, the only area where the species occurs. Only one form was found in the northern end of the Gulf, and its relative abundance gradually decreased toward the south until it was not found to occur in the southern end of the Gulf. The other form was the only one at the southern end of the Gulf and it decreased in relative abundance toward the northern end of the Gulf. The two forms occurred

together in the midportion of the Gulf. Stephens was unable to explain the basis for these circumstances. The situation is somewhat paralleled by two of the *E. frontalis* color forms. The albicaudatus form is abundant at the northern end of the Red Sea (Gulf of Aqaba) and rare at the southern end. The nigrovittatus form is common at the southern end of the Red Sea but absent from the northern end. I hesitate to place much emphasis on these similarities.

MATERIAL (localities abbreviated).—Gulf of Aqaba: USNM 204535 (3 albicaudatus, 25.4–30.5), USNM 204536 (3 albicaudatus, 19.8–24.2; 1 post larva, 15.5), USNM 204685 (1 albicaudatus, 51.6; 8 frontalis, 29.2–44.8), USNM 204684 (9 albicaudatus, 18.0–44.4; 37 frontalis, 16.8–43.7), USNM 204534 (18 albicaudatus, 16.6–36.1; 1 frontalis, 36.7), USNM 204650 (11 albicaudatus, 18.0–37.7; 3 frontalis, 18.7–48.4), USNM 204533 (14 albicaudatus, 19.5–37.5; 2 frontalis, 19.5–21.7), HUI HUJ-F-3540 (holotype of *E. albicaudatus*, 43.0), HUI E-60/96.16 (albicaudatus, 46.9), HUI HUJ-F-4375 (2 albicaudatus, 19.1–21.4), HUI HUJ-F-3544 (2 frontalis, 40.2–42.1), HUI E-64/34 (4 frontalis, 32.0–41.0), HUI E-64/3013 (frontalis, 40.0), UTAI NS-3582 (albicaudatus, 43.8); Gulf of Suez, Et Tor: USNM 204651 (9 frontalis, 29.5–44.7); Egypt, Strait of Jubal: USNM 200613 (1 albicaudatus, 50.5; 6 frontalis, including one cleared and stained, 23.9–58.6); Egypt, Al Ghardaqa: NFIS 5118 (frontalis, 43.9); Sudan, Sanganeb Reef: NFIS 8236 (3 frontalis, 40.6–47.4); Ethiopia, Massawa: ISZZ 1947 (5 damaged syntypes of *Salarias frontalis*), NFIS 1680 (holotype of *Salarias nigrovittatus*, 29.0), USNM 204517 (4 nigrovittatus, 24.2–36.0; 8 frontalis, 21.2–34.6); Ethiopia, Harat Island: USNM 204490 (6 albicaudatus, 29.2–46.5; 25 nigrovittatus, 20.4–48.3; 55 frontalis, 21.9–61.4); Ethiopia, Dahlak Islands: HUI E-62/424A (21 frontalis, 16.3–47.3), HUI E-62/1280 (2 nigrovittatus, 32.5–34.2), HUI E-62/428 (2 nigrovittatus, 18.9–40.2), HUI E62/604 (nigrovittatus, 39.2), HUI E-62/3678A (nigrovittatus, 39.5), HUI E-62/1280A (8 frontalis, 30.8–48.3), HUI E-62/417H (18 nigrovittatus, 16.7–38.5), NFIS 8757 (7 nigrovittatus, 23.8–44.0); Ethiopia, Zubair Island: HUI HUJ-F-4628 (4 frontalis 29.4–35.0); Gulf of Aden, Bay of Djibouti, French Somaliland: MNHN 04-318 (3 frontalis, 37.8–47.3).

Numerous other uncataloged specimens from the Gulf of Aqaba and Ethiopia in the USNM collections were examined in order to obtain data on frequencies of occurrence of the color pattern forms. In Ethiopian waters, the following localities for this material are as follows: Isola Delemme (35°54′E, 15°30.5′N), Sciumma Island (40° 00′00″ E; 15°32′ 31″N); Melita Bay (39°49′E; 15°15′N); Difnein Island (39°20′E, 16°36′N). The frontalis and nigrovittatus forms were present in all these collections.

### *Ecsenius (Ecsenius) pulcher* (Murray)

FIGURE 16

*Salarias pulcher* Murray, 1887, p. 23 [Manora Rocks, Karachi].
*Salarias phntasticus* Boulenger, 1897, p. 422 [Mekran Coast, Persia].
*Salarias anomalus* Regan, 1905, p. 327 [Mekran Coast, Persian Gulf].

DESCRIPTION.—Dorsal spines 12–14 (usually 13); dorsal rays 18–20; segmented anal rays 19–23 (usually 21–22); pectoral rays 14–15 (usually 14); segmented caudal rays 13 (rarely 14 in specimens over 25 mm SL; when 14, lowermost ray has only one segmental line); dorsal procurrent caudal rays 7–8; ventral procurrent caudal rays 5–8 (usually 7–8); total caudal elements 26–29 (rarely 26); gill-rakers 13–17 (usually 14–15); pseudobranchial filaments 6–7; lower incisor teeth 44–53; lower jaw posterior canines 0–1 (rarely 0); total lower jaw posterior canines 0–2 (usually 2); upper incisor teeth 107–116 (three counts); precaudal vertebrae 11, caudal vertebrae 26–28; total vertebrae 37–39; epipleural ribs 13–14. Lateral line with no paired pores, extending to below level of 8th to 12th dorsal spine (usually 9th or 10th). Dorsal fin notched five-ninths to eight-ninths (rarely eight-ninths) length first dorsal ray. Third (innermost) pelvic ray varying from not obvious to obvious (usually not obvious). One cirrus on each anterior nostril, rarely forked.

Color pattern: There are two basic color patterns found in adult and young adult specimens. These two patterns are so strikingly different as to have been the basis for species descriptions, and the uninformed worker sorts collections containing both types into different lots. Chapman and Schultz (1952) believed that the two color patterns were sex linked, but I find that both sexes exhibit both types of color pattern.

The most common color pattern, based on museum specimens, is that in which the head and body are uniformly dark or dusky brown. Occasional specimens of this form are paler posteriorly on the body. A marking slightly darker than the ground color frequently occurs behind the eye. The underside of the head may also be slightly darker anteriorly.

In the other color pattern (Figure 8) the head and anterior half of the body are similar to that of the form described above, but the posterior half of the body bears separated pigmentless areas setting off dark vertical bars of different sizes and intensities. The number of dark bars ranges from 5 to 8 on each side of the body. The smallest specimen exhibiting this pattern was 32.9 mm SL.

Below about 20 mm SL, specimens may be uniformly dark or bear 7 or 8 pairs of diffuse vertical bands on each side and irregular dark marks on the head. Both uniform and banded small specimens occurred in the same collections.

In both adult type color patterns the spinous dorsal bears a dusky stripe basally and an immaculate area distally. The dusky stripe extends onto the soft dorsal where it becomes separated into a darker area suprabasally and a paler area basally. The distal portion of the rayed dorsal is mostly unmarked. The anal fin is uniformly pale dusky. The other fins are variably marked with immaculate and pale dusky areas.

A color photograph of a living specimen of *E. pulcher,* barred form, appears in Axelrod and Emmens (1969).

NOMENCLATURE.—*Salarias phntasticus* was not compared with any other species. I have examined the two syntypes and find them to be the striped form of *E. pulcher.* (An obvious typographical error is involved in the specific epithet and the name is usually spelled *phantasticus.*)

*Salarias anomalus* was not compared with any other species. I have examined the syntypes and find them to be the uniformly dark form of *E. pulcher.*

MATERIAL (localities abbreviated).—Persian Gulf: USNM 201572 (36.5, cleared and stained), 201571

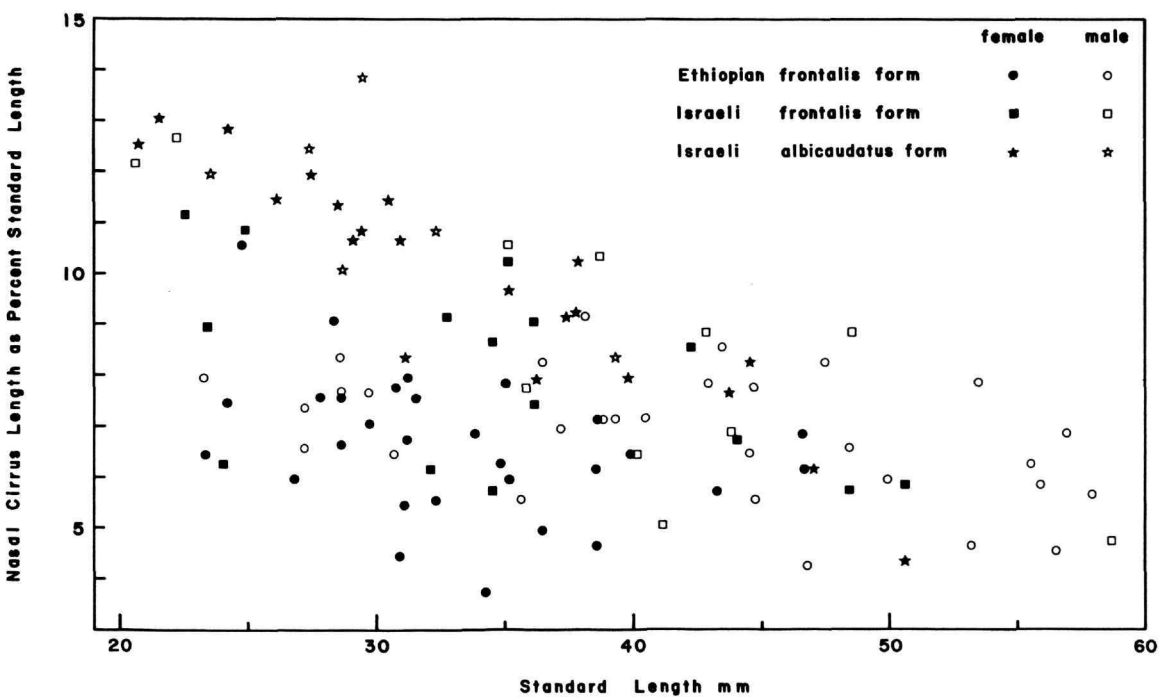


FIGURE 8.—Graph showing relationship of nasal cirrus length to standard length in the two color pattern forms of *Ecsenius frontalis* from Israeli coastal waters and one of these forms from Ethiopian coastal waters.

(32.9), 196505 (2: 42.2–52.1), 196506 (52.3), BMNH 1900.5.9.47–56 (16: 31.4–46.3, syntypes of *Salarias anomalus),* 1898.6.29.163 (57.4), 1932.2.18.43 (39.7); Gulf of Oman: BMNH 1912.11.26.1 (51.2), 1899.5.8.94 (2: 28.7–34.0); Mekran Coast, Persia: BMNH 1897.9.22.20–21 (2: 54.5–57.9, syntypes of *Salarias phntasticus);* Karachi, Pakistan: BMNH 1887.9.22.59–60 (2: 44.3–44.5, syntypes of *Salarias pulcher*), USNM 201867 (3: 38.9–58.0), 201816 (48.3), NFIS 8239 (37.3); Rupan Coast, India; FMRI uncataloged (4: 18.4–30.6, in two lots); Gulf of Kutch, India: USNM 201863 (16.6); India: NFIS 5120 (9: 21.7–54.6).

### *Ecsenius (Ecsenius) gravieri* (Pellegrin)

FIGURES 17, 18

*Salarias gravieri* Pellegrin, 1906, p. 5 [Bay of Tadjourah].
*Ecsenius klausewitzi* Lotan, 1969, p. 371 [Entedebir, Dahlak Archipelago].

DESCRIPTION.—Dorsal spines 12–14 (usually 13); dorsal rays 16–19 (rarely 16 or 19); segmented anal rays 18–21 (rarely 18 or 21); pectoral rays 13–15 (rarely 13); segmented caudal rays 13; dorsal procurrent caudal rays 7–9 (usually 8); ventral procurrent caudal rays 7–9 (usually 8); total caudal elements 27–31; gill rakers 12–16; pseudobranchial filaments 6–8 (rarely 8); lower incisor teeth 44–54;

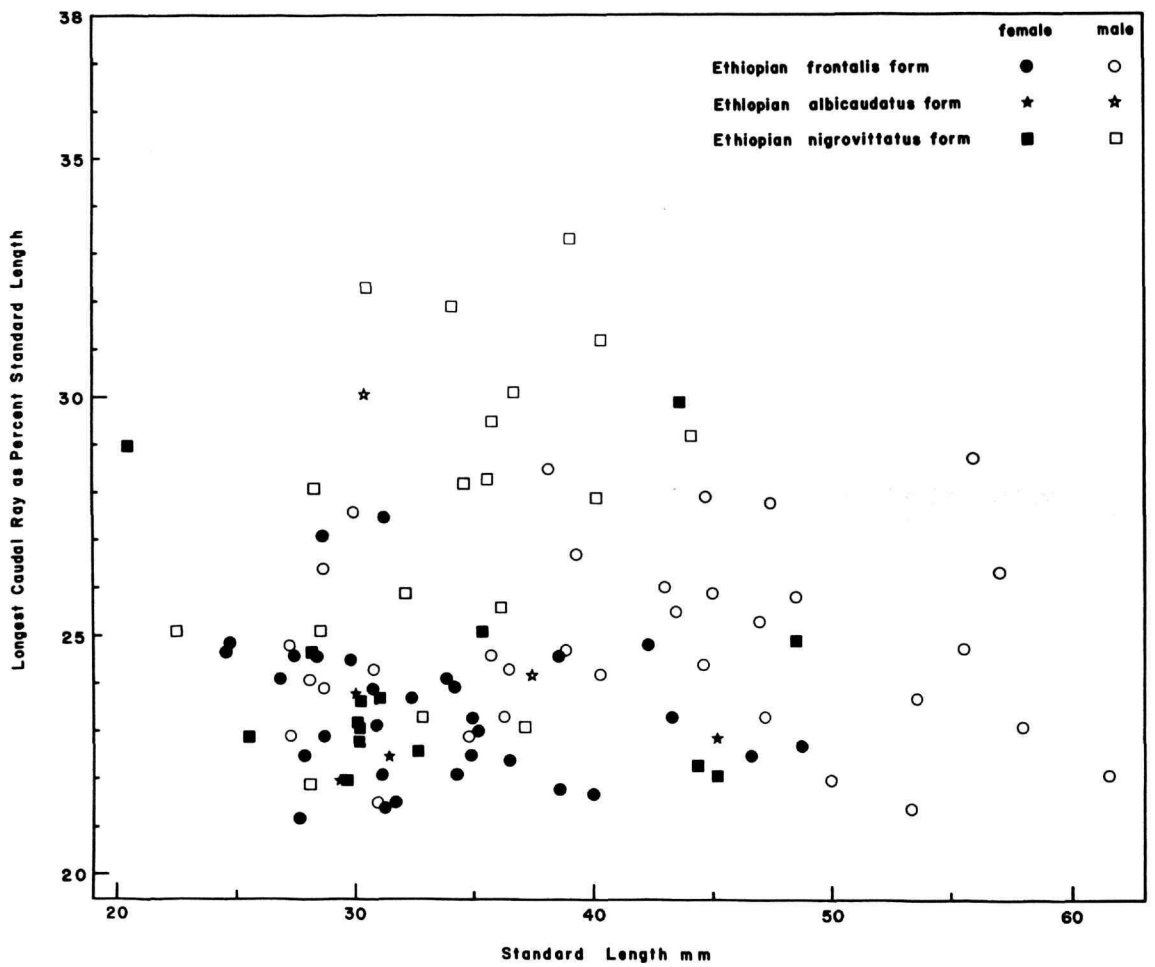


FIGURE 9.—Graph showing relationship of longest caudal ray length to standard length in the three color pattern forms of *Ecsenius frontalis* from Ethiopian coastal waters.

lower jaw posterior canines 0–1; total lower jaw posterior canines 0–2 (usually 2); precaudal vertebrae 10–11 (rarely 10); caudal vertebrae 24–26 (rarely 24); total vertebrae 35–37 (rarely 35); epipleural ribs 12–15. Lateral line with no paired pores, extending posteriorly to below level of 8th to 10th (rarely 8th) dorsal spine. Dorsal fin notched two-ninths to six-ninths length of first dorsal ray. Third (innermost) pelvic ray not obvious in specimens over 25 mm SL. One cirrus on each anterior nostril.

Color pattern: This is a distinctively marked species. In Gulf of Aqaba, Gulf of Suez, and northern Red Sea specimens, 17.5–60.8 mm SL, the head is relatively dark with the intensity of the pigment decreasing gradually on the body and becoming quite pale posteriorly. At about the midposterior margin of the orbit of most specimens there is a dark stripe, or diffuse evidence of one, that extends posteriorly across the head, darkens greatly on the body, and usually extends to below at least the middle of the spinous dorsal fin, but terminates anterior to the caudal peduncle. At its termination the stripe continues as a row of variably spaced dark spots to the base of the dorsal caudal rays. There are also a variable number of dark spots posteriorly on the body. In a few specimens the dark stripe or the spots (but not both) may be absent.

The spinous dorsal fin bears a jet black row of dark spots, restricted mostly to the interspinous fin membranes. These spots decrease in size and intensity posteriorly and may extend onto the interradial membrane of the rayed dorsal for a varying distance. There is no pigment distally on the rayed dorsal or anal fins. The upper and lower lobes of the caudal are dusky.

Specimens from the southern Red Sea and the Bay of Tadjourah, outside the entrance to the Red Sea, differ from those described above in having the dark pigment generally blacker and covering more area. The stripe on the body may be almost completely obscured anteriorly by the surrounding body pigment, but the stripe is absent in the holotype (see Smith, 1959, fig. 12, for an illustration of the holotype). In addition, some specimens exhibit dark pigment at the tips of some of the dorsal and anal rays. Specimens from the northern and southern Red Sea (including the Bay of Tadjourah, type locality) are easily distinguishable (Figures 17 and 18). I do not believe that the northern populations merit nomenclatural distinction, however, as there is a good possibility that the two forms gradually merge somewhere in the midportion of the Red Sea. There are no specimens available from the approximately 1500 km between the southernmost collections of the northern form and the northernmost collections of the southern form.

The two types of color pattern described here are paralleled in the unrelated blenniid genus *Meiacanthus*, which co-occurs with *E. gravieri* (see discussion of mimicry on page 6).

In life, *E. gravieri* is generally slate blue anteriorly grading into pale yellow posteriorly. The black markings are black.

REMARKS (see also discussion under *E. aroni*).—In the northern Red Sea and Gulf of Aqaba, *E. gravieri* occurs commonly in depths of 2 to 10 meters, but is rarely seen at greater depths. The species is frequently seen swimming freely, but such activity is punctuated by long periods of rest on the bottom. *E. gravieri* is apparently territorial and during several periods of observation, individuals were noticed to have a few favorite perching spots. An individual might leave one of these spots and swim around, up to about 5 meters distance from such a spot, but it always returned to one of the favored spots to perch.

Klausewitz (1960) illustrated *E. gravieri* but identified the specimen as *E. nigrovittatus*, a synonym of *E. frontalis*.

Lotan (1969) compared *E. klausewitzi* with *E. gravieri*, differentiating *E. klausewitzi* by its having a black line on the body, which the holotype of *E. gravieri* lacked. The presence or absence of such a dark line is variable, as noted in the color pattern description above. The holotype of *E. klausewitzi* is a small specimen of the southern Red Sea dark form of *E. gravieri*.

MATERIAL (localities abbreviated).—(Pale form) Gulf of Aqaba: UTAI NS–3580 (3: 20.4–48.1), HUI HUJ–F–4382 (38.6), HUJ–F–4377 (2: 20.4–21.0), E–64/30A (2: 20.0–32.4), USNM 204542 (9: 32.1–55.9), 204555 (15: 19.3–33.2), 204546 (9: 17.5–23.3), 204544 (22: 20.2–52.7), 204543 (3: 19.5–60.8); Ras Muhammad, southern tip of Sinai Peninsula, Red Sea: USNM 204545 (9: 27.8–44.1), 204547 (2: 27.8–41.3); Et Tur, Sinai Peninsula, Gulf of Suez: USNM 204548 (3: 50.1–54.7); Al Ghardaqa, Egypt, northern Red Sea: NFIS 5122–23 (2: 29.6–34.6).

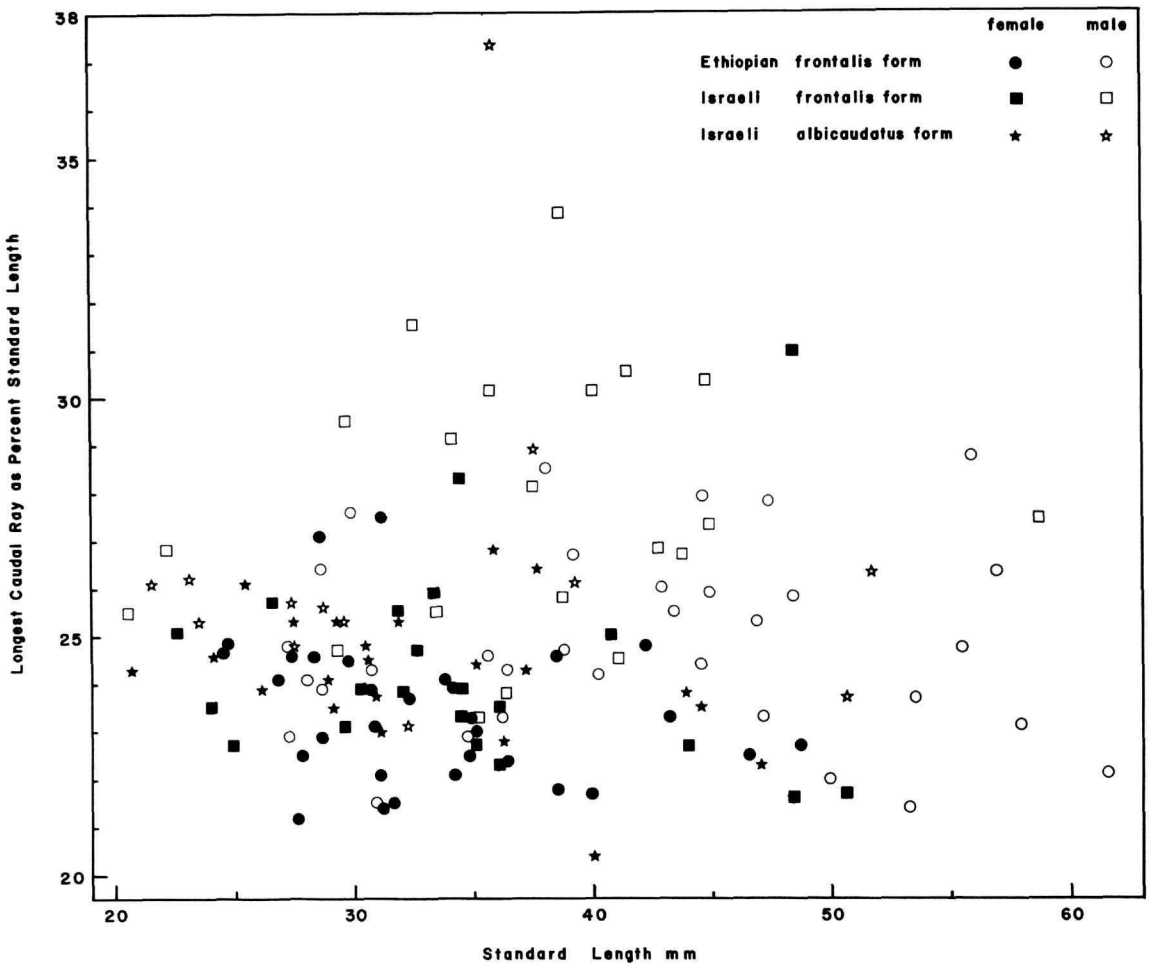


FIGURE 10.—Graph showing relationship of longest caudal ray length to standard length in the two color pattern forms of *Ecsenius frontalis* from Israeli coastal waters and one of these forms from Ethiopian coastal waters.

(Dark form) Dahlak Archipelago, Red Sea: HUI E–62/3708 15.1, holotype of *Ecsenius klausewitzi*); Isola Delemme (15°30.5′ N, 39°54′ E), Red Sea: USNM 204479 (56.5); Sheikh el Abu (16°08′ N, 39°36.5′ E), Red Sea: USNM 204480 (3: 30.5–40.1); Bay of Tadjourah: MNHN 04–319 (54.2, holotype of *Salarias gravieri*).

In addition to the above, a large number of uncataloged USNM specimens I collected in the Gulf of Aqaba were examined for color pattern and ecological data.

### *Ecsenius (Ecsenius) aroni*, new species

FIGURE 19

DESCRIPTION.—Dorsal spines 12–14 (usually 13); dorsal rays 17–18; segmented anal rays 19–20; pectoral rays 13–15 (usually 14); segmented caudal rays 13; dorsal procurrent caudal rays 6–9 (usually 7 or 8); ventral procurrent caudal rays 6–9 (usually 7 or 8); total caudal elements 25–30; gill-rakers 12–15; pseudobranchial filaments 6–7; lower incisor teeth 46–57; lower jaw posterior canines 0–1; total lower

jaw posterior canines 0–2 (usually 2); upper incisor teeth 130–132 (three counts); precaudal vertebrae 10 or 11 (rarely 10); caudal vertebrae 23–26 (rarely 23); total vertebrae 34–37 (rarely 34); epipleural ribs 11–14. Lateral line with no paired pores, extending to below level of 8th to 10th dorsal spine (usually 9th or 10th). Dorsal fin notched six-ninths to nine-ninths length first dorsal ray. Third (innermost) pelvic ray barely or not obvious. One cirrus on each anterior nostril.

Color pattern: The color pattern of preserved specimens is not very variable. The head is dark brown, but pale underneath. The body is generally dusky brown with a dark spot on the caudal peduncle that extends well onto the caudal fin. For most of its length, the dorsal fin bears a narrow suprabasal dusky stripe, but is otherwise scarcely marked. The anal fin is generally dusky and in mature males the tips of the rays are pale. The other fins are pale or unmarked.

In life the body is generally dark tan with a black spot with blue overtones at the base of and on the caudal fin. Some individuals exhibited a bright orange stripe along the dorsal body contour. The head and anal fin are dark brown. The other fins are pale or unmarked.

HABITAT AND DISTRIBUTION.—*Ecsenius aroni* is known only from the Red Sea and Gulf of Aqaba coasts of the Sinai Peninsula. It occurs in coral areas only and is commonest at depths greater than 10 meters. It was only rarely seen or taken at depths as shallow as 3 meters. The species was seen (but not collected) at the nature preserve in Eilat at depths as great as 36.6 meters, but was not found at greater depths, down to 45.7 meters (two dives planned primarily to search for the species). It prefers the undersides of ledges and pockets in the reefs and was not seen in the open areas above or about the reefs.

RELATIONSHIPS.—*Ecsenius aroni* is closely related to *E. gravieri,* with which it generally occurs in the Gulf of Aqaba, and *E. pulcher,* which occurs in the Persian Gulf and northern Arabian Sea. With these two species it shares the following unique combination of characters: typically 13 dorsal spines, a notched dorsal fin, 11 precaudal vertebrae, typically 14 pectoral rays, and 13 segmented caudal rays. It differs from these two species primarily in color pattern, proportions and meristics as indicated in key couplets 16 and 17. In addition it differs from the sympatric *E. gravieri* in that caudal filaments are primarily restricted to males (well developed in both sexes in *E. gravieri*), and in males the longest caudal ray tends to increase in relative length regularly with increase in standard length (Figure 11). In general, for either sex, *E. aroni* has a relatively shorter caudal than *E. gravieri* (Figure 11). *E. aroni* attains a much smaller maximum size than either *E. gravieri* or *E. pulcher* (Figure 11).

*E. aroni* occurs more commonly in greater depths than the sympatric *E. gravieri,* which is usually found in less than 10 meters depth. The two species behave quite differently. *E. gravieri* is an obvious species on the reef and is frequently seen swimming above the bottom over open sandy areas closely adjacent to the reef. *E. aroni* is secretive and was seen (rarely) free swimming only within small holes in the reef.

ETYMOLOGY.—This species is named for Dr. William Aron of the Smithsonian Institution in appreciation for his making possible my field work in the Red Sea. The results of that work form an invaluable contribution to this and other of my studies.

HOLOTYPE.—USNM 204468, male, 36.8 mm SL, bay at El Himeira, Sinai Peninsula, Gulf of Aqaba. Depth of collection, to 18 meters. Collected by V. G. Springer et al., 16 July 1969. Original field number, VGS 69–2.

PARATYPES (all Sinai Peninsula).—USNM 204690 (12:18.5–40.8), collected with the holotype; USNM 204560 (21:19.4–31.5), 204550 (2:21.4–27.0), 204558 (24.7), all collected in same vicinity as holotype but on different dates and at different depths; USNM 204557 (2:21.3–35.4), Marsa Muqabila, Gulf of Aqaba; USNM 204556 (33.1), bay between Marsa Mokrakh and El Himeira; USNM 204561 (40.8) and 204562 (7:25.8–40.5), Ras Muhammad, Red Sea. Some paratypes will be deposited with the Hebrew University after publication of this paper.

### *Ecsenius (Ecsenius) bicolor* (Day)

FIGURES 20, 21

*Salarias bicolor* Day, 1888, p. 798 [Saddle Island, off Kyoukphyoo, Arakan, Burma].

*Salarias furcatus* Johnstone [not of De Vis], 1904, p. 213 [Chilaw Paar, Ceylon].

*Salarias burmanicus* Hora and Mukerji, 1936, p. 34 [Maungmagan, Tavoy District, Lower Burma].

*Salarias melanosoma* Regan, 1909, p. 406 [Christmas Island, Indian Ocean].

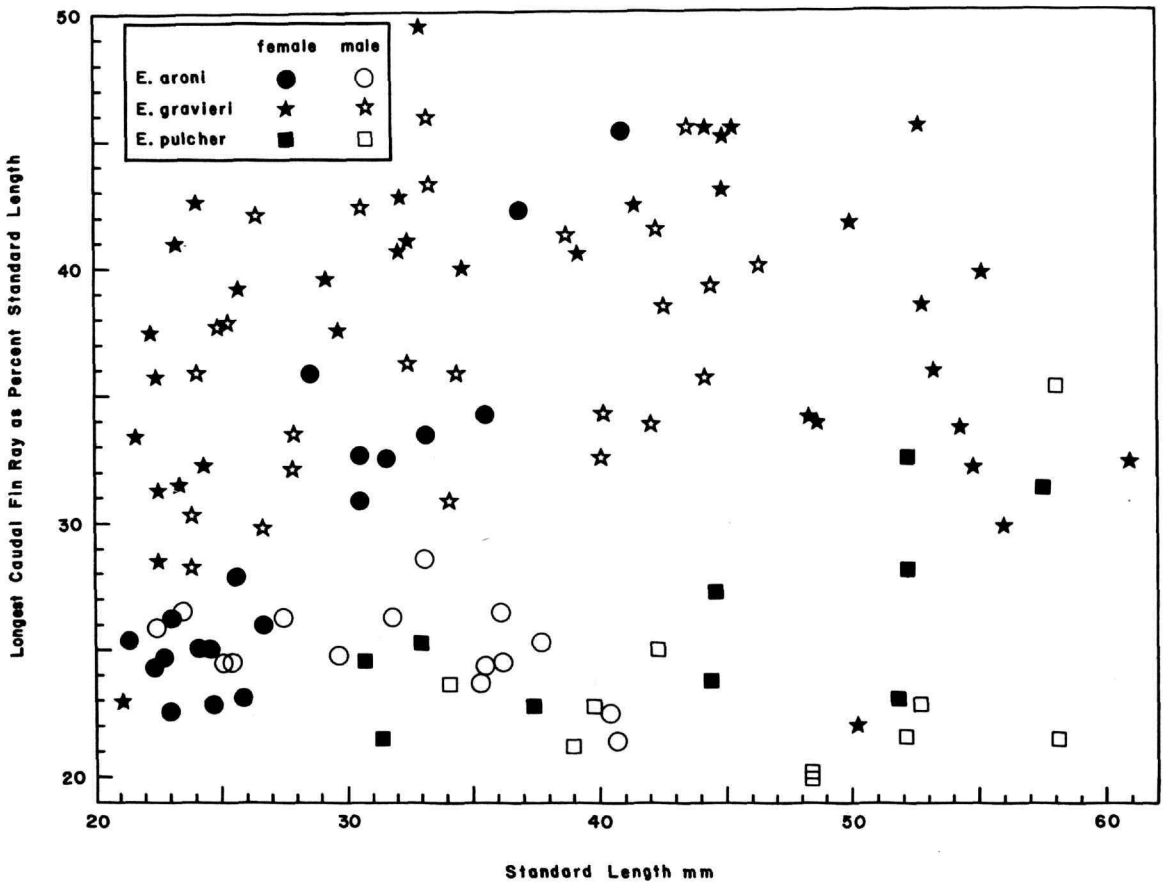


FIGURE 11.—Graph showing relationship of longest caudal ray length to standard length in species of the *E. pulcher* species group.

*Ecsenius hawaiiensis* Chapman and Schultz, 1952, p. 526 [Pearl Harbor, Oahu, Hawaii; a possible introduction from Guam].

DESCRIPTION.—Dorsal spines 11–12 (rarely 11); dorsal rays 15–18 (rarely 15); segmented anal rays 17–21 (rarely 17 or 21); pectoral rays 12–14 (rarely 12 or 14); segmented caudal rays 13–14 (rarely 13; 15 in one specimen 20.7 mm. SL); dorsal procurrent caudal rays 6–9 (rarely 6 or 9); ventral procurrent caudal rays 6–8; total caudal elements 26–31 (rarely 26 or 31); gill rakers 12–18 (rarely 12 or 18); pseudobranchial filaments 5–8 (rarely 5 or 8); lower incisor teeth 36–46 (one of 243 specimens with 32); lower jaw posterior canines 0–1; total lower jaw posterior canines 0–2 (usually 2); upper incisor teeth 114–129 (11 counts); precaudal vertebrae 10 (one specimen of 233 with 11); caudal vertebrae 23–25; total vertebrae 33–35; epipleural ribs 12–17 (rarely 12 or 17). Lateral line with vertically paired pores for one-quarter to all its length (rarely less than one-half length), extending posteriorly to beneath level of 10th–13th dorsal fin element (rarely to 13th). Dorsal fin notched two-ninths to seven-ninths (rarely less than four-ninths) length first dorsal ray. Third (innermost) pelvic ray varying from obvious to not obvious (usually obvious). Two cirri on anterior nostril, one each arising from anterior and posterior margins.

Color pattern: *Ecenius bicolor* is one of the more variably pigmented species of *Ecsenius*. Three of the nominal species referable to the synonymy of *E. bicolor* are merely color pattern variants. There are, however, two basic color patterns found in preserved specimens, which, with modifications, grade into each other. On the basis of life color variations exhibited by a single individual reported by Wickler (1965A) and in a group of specimens reported by Strasburg (1967), it appears that life color variations may be fixed at the time of preservation. Of the two basic patterns, either one or the other greatly predominates in individual collections from any locality. While either type may occur as the predominant form in individual collections from the same general locality, collections indicate that one form or the other is much more often collected.

In one of the basic patterns the head and body are, for the most part, completely dark dusky, occasionally slightly less intensely so on the posterior half of the body. There may be a dark spot just posterior to the eye. The spinous dorsal fin is dusky or bears a dusky band on its ventral half with a black spot between the first and third spines. The black spot is rarely absent. The rayed dorsal is more faintly dusky than the spinous dorsal and slightly darker basally. The anal is dusky, frequently paler basally and on the tips of the rays. The caudal bears a faint to dark dusky triangular mark centrally, the base of the triangle vertically aligned with the caudal base. The uniformly dark color pattern is the type exhibited by the holotype of *S. melanosoma*. A variation of this pattern, wherein there are several vertical, pale streaks on the body and the corners of the mouth are pale, was the basis for the description of *E. hawaiiensis*. In some specimens there is a broad, dark dusky longitudinal stripe extending from the level of the pectoral axil posteriorly to some point anterior to the caudal peduncle. The stripe may be broken into as many as five portions.

The other basic color pattern is similar to the first in that the head and body anteriorly are more or less uniformly dark, but at some point no further anteriorly than below the level of the third or fourth dorsal ray, the body gradually or abruptly becomes paler or completely lacks melanophores. A colored photograph of a freshly dead specimen of this color pattern type occurs in Axelrod and Emmens (1969). In many specimens there are one to three narrow, vertical, diffusely dusky bars in the pale area on the body. (One of these is slightly apparent in figure 21.) A number of specimens examined also exhibited the longitudinal dark stripe on the body as described above.

Wickler (1965A) illustrated and discussed life color variations in *E. bicolor,* based on aquarium specimens presumably from Ceylon. He ascertained that these patterns reflected emotional states. He described life color generally as dark gray-brown anteriorly and yellow or orange-red posteriorly.

Strasburg (1967) reported on life coloration and noted that the lengthwise stripe (described above) was two toned, black and white, with the white color turning black in preservative. Strasburg reported that *E. bicolor* from Eniwetok was bright ultramarine, sometimes tinged with violet anteriorly, and orange-yellow posteriorly. G. Losey (in litteris) described *E. bicolor,* also from Eniwetok, as blue-gray anteriorly and yellow-orange posteriorly. At One Tree Island, Great Barrier Reef, specimens I saw in life were electric blue anteriorly and yellow-orange posteriorly. One individual was seen with a rose-colored area posterior to the eye. (Such rose-colored marks are found in excited specimens, according to Wickler.) The illustration in the Tickell manuscript of the Zoological Society of London, upon which Day based his description of *S. bicolor,* is rich blue anteriorly and red-orange posteriorly.

GEOGRAPHIC VARIATION.—Average numbers of dorsal and anal rays and caudal vertebrae (usually correlated characters) tend to vary from one locality to another (Table 15). In general, the highest averages occur in the Australian specimens. Australian specimens also appeared to have average longer posterior nasal cirri and shorter fifth dorsal rays (Tables 8 and 10) than specimens from other localities. The nasal cirri were sexually dimorphic in size in the Australian specimens but not in the others. The length of the fifth dorsal ray was sexually dimorphic in non-Australian specimens but was either not dimorphic or only slightly so in Australian specimens.

REMARKS.—In Figure 1 the acceptable literature records for *E. bicolor* entered on the map were those reported in Day (1888), Hora and Mukerji (1936), and Kamohara and Yamakawa (1965).

Wickler (1965A, B, C, D) has given a detailed discussion on the behavior and biology of *E. bicolor,*

including a list of moving picture films deposited with the Encyclopedia Cinematographica.

Strasburg (1967) reported that *E. bicolor* occurred in the lagoon at Eniwetok at depths from about 1 to 7.5 meters, being more common at the latter depth. In contrast, I collected the species at One Tree Island only on the ocean side of the island at depths of about 4 and 12 meters and found the species common at both depths. Most collections of the species, however, appear to have come from the lagoon side of atolls in shallow depths, although Randall collected a specimen in Guam from a depth of 21.3 meters.

Chapman and Schultz (1952) mentioned that *E. bicolor* (as *E. hawaiiensis*) might have been introduced into Hawaiian waters from Guam, where the species is known to occur, as its collection in Hawaii was made under peculiar circumstances. They discarded the possibility, however, as they believed the species to be endemic to Hawaii. Strasburg (1956) believed that the species probably was brought to Hawaii from Guam in the fouling on the bottom of a barge, and thus was not a Hawaiian endemic, but possibly had become established in Hawaiian waters as a consequence of its introduction. Strasburg did not recognize the species as *E. bicolor,* but accepted the name *E. hawaiiensis.*

Considerable collecting in Hawaiian waters in recent years has produced no additional material of *E. bicolor* other than that reported by Chapman and Schultz. In view of this and the fact that Hawaii is considerably removed from the nearest known locality where *E. bicolor* occurs, I believe that the Hawaiian specimens were introductions and that the species has not become established in Hawaii.

NOMENCLATURE.—The description of *Salarias bicolor* was based on a short description and colored illustration in a handwritten manuscript by Colonel S. R. Tickell, dated 1875, and titled: "Fishes collected in the seas and fresh waters of British Burma from 1851 to 1864, vol. 1." The manuscript is housed in the library of the Zoological Society of London. Many of the descriptions contained in the manuscript are the sole bases of many of F. Day's new species descriptions. The specimens on which Tickell based his descriptions were evidently not retained as can be inferred from comments in the manuscript.

The colored illustration of *S. bicolor* in the manuscript is of a fish 1⅜ (35 mm) inches long. The specimen is rich blue anteriorly below the rayed portion of the dorsal fin; thence it is red-orange. The species is portrayed as having a deep notch in the dorsal fin between the spinous and rayed portions, somewhat deeper than for any specimen I have seen. The species is described as having no tentacles, but a statement was included to the effect that if there were any tentacles they "were very likely to be overlooked." The dorsal fin formula was given as 11 + 18, the anal as 18.

The distinctive life color in combination with the notched dorsal fin and a dorsal spine count of at least 11 leaves little doubt of the identification of Tickell's figure with the species treated here as *E. bicolor.* The only blenny that approximates the appearance of *E. bicolor* is the nemophidinine *Meiacanthus atrodorsalis* (Günther), which does not have a notched dorsal and has fewer than 11 dorsal spines (Tickell's count is probably in error and the reduced last—12th—dorsal spine was probably missed). From my observations *M. atrodorsalis* is more yellow than orange posteriorly. It would probably be well to designate a neotype for *S. bicolor,* but as I have no material from the same geographic area from which *S. bicolor* was described, it is not possible.

*Salarias furcatus* was not compared with any other blenny and the description and illustration leave no doubt that it is a synonym of *S. bicolor.* I have been unable to locate the holotype.

*Salarias burmanicus* was compared only with *S. anomalus* (= *S. pulcher*). The illustration and description clearly indicate *bicolor* as the species. W. F. Smith-Vaniz examined the holotype in the Indian Museum in Calcutta. It bears the number F 11872/1, type 429.

*Salarias melanosoma* was compared only with *S. anomalus.* I have examined the syntypic material and find all specimens to be the same as *S. bicolor.*

*Ecsenius hawaiiensis* was compared with *E. bicolor,* but it was thought that the pale bars on the sides were distinctive. Wickler (1965A) has described and illustrated the various color patterns exhibited by *E. bicolor,* of which the pale barred form is but one of several. He concluded that *E. bicolor* and *E. hawaiiensis* were the same species. My examination of the type material of the latter indicated no morphological differences between that material and other specimens I assign to *E. bicolor.*

MATERIAL (localities abbreviated).—Christmas Island, Indian Ocean: BMNH 1909.3.4.52–57 (5: 30.0–48.8, syntypes of *Salarias melanosoma*), USNM 157373 (40.7, syntype of *Salarias melanosoma*); Ceylon: USNM 204623 (43.3), NFIS 5256 (6: 35.4–59.0, specimens reported by Wickler, 1965A, presumably from Ceylon); Maldive Islands: NFIS 9578 (49.1); Nicobar Islands: NFIS 9576 (41.4); Pulo Penju, Indonesia: USNM 201864 (3: 23.4–52.1); Patong, Phuket, Thailand: USNM 201755 (5: 25.0–45.0); Ilot du Sud, South China Sea: CAS GVF–2113 (9: 48.3–61.3); Ryukyus: BPBM 7467 (46.4); Guam: BPBM 7851 (2: 26.0–35.1); Timor: ZMA 109.064 (36.9); Banda Sea: USNM 195718 (2: 36.8–42.0); Palau Islands: CAS GVF–740 (5: 20.7–48.5), GVF–1450 (59.5); Kapingamarangi: CAS GVF–424 (5: 22.0–46.9), GVF–452 (38: 18.5–56.7); Mortlock: ZSZM 5152 (41.5); Marshall Islands: BPBM 5895 (20: 32.3–67.6), USNM 201472 (8: 16.1–56.6), 201473 (43.9), 201475 (23.4), 201476 (5: 38.0–59.3), 201477 (3: 26.1–48.3), UW 12008 (3: 34.0–0–54.0); Ponape Island: CAS GVF–496 (20: 24.5–61.0), GVF–497 (50.7); New Britain: USNM 201813 (3; 47.7–49.8); Neiafu, Tonga Islands: USNM 203334 (2: 39.6–44.1); Fiji Islands: USNM 201827 (41.9); Espiritu Santo, New Hebrides: USNM 144293 (2: 29.5–47.5), 144294 (2: 52.2–62.0), 144716 (7: 27.1–45.0), CAS GVF–1826 (24.5); One Tree Island, Queensland, Australia: USNM 201368 (74: 38.5–69.3, including two cleared and stained); Endeavour Reef, Queensland, Australia: ANSP 109699 (2: 31.4–37.7); Oahu, Hawaii: USNM 112293 (66.5, holotype of *Ecsenius hawaiiensis*), 112294 (12: 48.0–77.0).

### *Ecsenius (Ecsenius) namiyei* (Jordan and Evermann)

FIGURE 22

*Salarias namiyei* Jordan and Evermann, 1902, p. 362 [Pescadores Islands].

DESCRIPTION.—Dorsal spines 11–12; dorsal rays 18–20; segmented anal rays 20–22; pectoral rays 13 (one specimen each with 11 and 12, and two with 14, on one side only); segmented caudal rays 13–14 (usually 14); dorsal procurrent caudal rays 7–8; ventral procurrent caudal rays 6–8; total caudal elements 26–30 (usually 28–29); gill-rakers 12–17; pseudobranchial filaments 6–8 (usually 7); lower incisor teeth 35–45; lower jaw posterior canines 0–1 (usually 1); total lower jaw posterior canines 1–2 (usually 2); upper incisor teeth 129 (one count); precaudal vertebrae 10–11; caudal vertebrae 25–27; total vertebrae 36–37; epipleural ribs 12–14. Lateral line with vertically paired pores for none to one-half its length, usually some pairs present, extending posteriorly to beneath level of 10th–13th dorsal fin element (usually 11th–12th). Dorsal fin without notch. Third (innermost) pelvic ray obvious. Two cirri on each anterior nostril, one each arising from anterior and posterior margins.

Color pattern: (Taiwan specimens) The body, head, and dorsal and anal fins are dark black, with the exception that in the caudal peduncular region the melanophores are less densely distributed, and that area is paler. The bodies of some specimens exhibit three or four short, narrow, pale, vertical, widely spaced marks on each side, similar to marks that are found in some specimens of *E. bicolor*. Most of the specimens exhibit a row of microscopic pale spots along the midportion of the body in the region where the lateral line might be expected to occur. Still others have a few small oblong intensely dark spots that underlie the dark surface pigment on the sides. The spinous dorsal fin bears irregular deeply pigmented lines below the dark surface pigment. The anal fin bears an indistinct darker stripe along its midlength. The caudal, pelvic, and pectoral fins are dusky with a greater concentration of pigment along the rays.

The life coloration of the female illustrated in Figure 13 (preserved color pattern), which had been in an aquarium for an indefinite period not exceeding a few weeks, was as follows: head and body dark brown; caudal peduncle grading into yellow-amber and then orange on proximal portion of caudal fin. Body with eight small, midlateral, blue-white spots beginning in the pectoral fin axil and extending no farther than the level of the last dorsal rays. Similar spots on pectoral base and on dorsal body contour, where they were less obvious than the midlateral spots. Upper lip with blue-white bands separated by dark interspaces. Pale stripe from behind eye to lip. Some pale blue dashes on cheek. There is no evidence of the blue-white markings on the preserved specimen.

REMARKS.—Tomiyama (1955) has given a thorough redescription of the holotype of *E. namiyei*.

On the north end of Taiwan I collected this

species from depths of about one to three meters very close to shore.

The specimens, one each, from New Britain and nearby Kerward Island, are very similar to those from Taiwan, but the color of their caudal peduncles is of about the same intensity as the rest of the body. An anal ray count was possible for only one of these specimens. The count was 20 and is lower than for any of the Taiwan specimens. The damaged specimen had a dorsal ray count of 18, lower than for any Taiwan specimen. These facts probably indicate racial variation.

MATERIAL.—Pescadores Islands: ZITU 5726 (49.5, radiograph of holotype of *Salarias namiyei*); Taiwan (north end): USNM 203125 (63.6, cleared and stained), 203126 (2: 58.0–63.2), 203127 (5: 62.0–80.4), 203128 (5: 55.4–81.8), 204478 (9: 59.0–76.3); New Britain: USNM 201865 (47.7); Kerward Island: USNM 201866 (49.0).

### *Ecsenius (Ecsenius) stigmatura* Fowler

FIGURE 23

*Ecsenius lineatus* Klausewitz, 1962, p. 145 [Madewaru Island, Fadiffulu Atoll, Maldive Islands].

DESCRIPTION.—Dorsal spines 12; dorsal rays 17–18; segmented anal rays 19–20; pectoral rays 13 (one specimen each with 12 and 14 on one side only); segmented caudal rays 13; dorsal procurrent caudal rays 5–8 (one specimen each with 5 and 8; all others had 7); ventral procurrent caudal rays 6–8; total caudal elements 25–28 (one had 25, none had 26); gill-rakers 13–16 (one had 16, none had 15); pseudobranchial filaments 6–7 (one had 7); lower incisor teeth 45–49; lower jaw posterior canines 1; total lower jaw posterior canines 2; upper incisor teeth 125 (one count); precaudal vertebrae 10–11 (two had 11); caudal vertebrae 24–26; total vertebrae 34–36 (usually 35); epipleural ribs 13–15. Lateral line with no paired pores, extending posteriorly to below 10th dorsal spine. Dorsal fin notched six-ninths to seven-ninths length first dorsal ray. Third (innermost) pelvic ray obvious. One cirrus on each anterior nostril.

Color pattern: The commonest color pattern, except as noted below, is that illustrated in Figure 23. The dark midlateral spots on the side of the body are always nine in number (the anteriormost spot is actually part of a continuous stripe extending to the eye). In the holotype and one small specimen, 20.5 mm SL, the spots are not evident, but instead there is a single, broad, uninterrupted, dark midlateral stripe on the side. In another specimen the spots are connected and are distinguishable only as slight constrictions along the length of the stripe. Usually the area of the body below the stripe, or row of midlateral spots, is abruptly and uniformly pale, and there is no evidence of a thin pale stripe below the row of dark spots as in Figure 23. The thin pale stripe above the row of spots is also frequently obscured. The presence of the tear-shaped spot on the caudal peduncle with the tip extending onto the central base of the caudal fin is distinctive of this species.

There is some variation in the markings on the head. The narrow pale stripes paralleling the dark postorbital stripe are not always distinguishable. The underside of the head is most noticeable for a pale area covering the lower lip and the region just behind the lip. The remainder of the underside of the head is variably dusky, sometimes with indistinct evidence of diffuse dark spots on both sides. The upper lip may be uniformly or irregularly dusky, sometimes with three bands anteriorly separated by narrower, paler interspaces.

In life the dark areas are various shades of brown and black and the pale areas are faintly yellow. A field assistant described one fresh-caught specimen as having much bright yellow color, but fading rapidly after preservation.

REMARKS.—*E. lineatus* co-occurs with *E. namiyei* in northern Taiwan. It was collected at depths of about 1 to 9 meters, the latter depth somewhat deeper than that from which specimens of *E. namiyei* were obtained.

MATERIAL (localities abbreviated).—Maldive Islands: NFIS 5532 (65.9, holotype of *Ecsenius lineatus*); north end of Taiwan: USNM 203129 (4: 42.1–48.2, including one cleared and stained), 203130 (2: 48.6–55.4), 203131 (54.9), 203132 (2: 44.9–49.5), 204477 (60.1); Pratas Reef, South China Sea: CAS GVF-1749 (20.5); Vietnam: CAS GVF-2116 (46.6).

### *Ecsenius (Ecsenius) stigmatura* Fowler

FIGURES 24, 25

*Ecsenius stigmatura* Fowler in Chapman and Schultz, 1952, p. 514 [Dammi Island, but see remarks section below].

DESCRIPTION.—Dorsal spines 12; dorsal rays 16–17; segmented anal rays 18–19; pectoral rays 13–15 (13

on only one side of one of the four specimens); segmented caudal rays 14; dorsal procurrent caudal rays 7–8; ventral procurrent caudal rays 6–7; total caudal elements 27–28; gill-rakers 15–17; pseudobranchial filaments 6; lower incisor teeth 37–40; lower jaw posterior canines 1; total lower jaw posterior canines 2; upper incisor teeth 107 (one count); precaudal vertebrae 10; caudal vertebrae 23–24; total vertebrae 33–34; epipleural ribs 12 (one count). Lateral line with no paired pores, extending posteriorly to beneath level of 9th dorsal spine. Dorsal fin notched six-ninths to seven-ninths length of first dorsal ray. Third (innermost) pelvic ray varying from obvious to not obvious. One cirrus on each anterior nostril.

Color pattern: The ground color of the head and body is evenly dusky brown. There is a narrow dark stripe that begins at the posteroventral margin of the eye and extends posteriorly across the opercle. Below the opercular portion of the stripe is a narrow pale stripe that is in line with a similar area margining the upper fleshy pectoral base. A large dark spot extends anteriorly from the anus. Another large dark spot occurs on the middle of the caudal peduncle and extends onto the bases of the caudal rays. The stripe has a pale margin anteriorly. The fins are variably dusky.

Three of the four specimens available are females. One female is from Masbate, Philippine Islands, and the others are from Tomahu Island in the Moluccan Sea. The fourth specimen, a male from Borneo, may not be the same species. The male differs from the females in lacking the pale stripe below the dark stripe on the head and in lacking the large spot on the caudal peduncle. Whether these differences are an indication of sexual dimorphism, individual variation, or population differences cannot be decided at present.

A color sketch of the holotype made during the *Albatross* expeditions indicates that the specimen was generally reddish brown in life. The dark streak behind the eye was deep blue and the pale streak below this was orange. The pupil was surrounded by a narrow orange border and this surrounded by a reddish-brown ring. The anal spot was black with deep blue overtones. The caudal spot was black with a pale lavender margin. The spinous dorsal was reddish brown basally and orange-brown distally. The rayed dorsal and most of the caudal were pale slate gray. There is a narrow orange-brown stripe along the dorsal body contour extending from the anterior end of the dorsal to the caudal base.

REMARKS.—In the original published description accredited by Chapman and Schultz (1952) to Fowler, the holotype and one paratype of *E. stigmatura* are reported to have been taken at Dammi Island, between Jolo and Tawi Tawi straits, at a depth of 244 fathoms (ca. 443 meters) on 21 September 1909. In an unpublished manuscript kindly lent me by J. E. Böhlke, however, Fowler stated that he was unable to ascertain the type locality. How the published locality was arrived at is not now known. I became suspicious of the published locality because no salariinine blenniids are known from depths nearly as great as 244 fathoms.

The original watercolor illustration upon which the published illustration of *E. stigmatura* was based is in the files of the Division of Fishes, National Museum of Natural History. This illustration bears a number, 2131, that corresponds with a number written on a silk tag that was tied to the holotype. Also written on the illustration was the following: Tomahu Id, 12/11–09 see color notes. I have been unable to locate the color notes or any other record of the tag number 2131, but the locality and date (interpreted as 11 December 1909) agree with the published information (Anonymous, 1910, p. 92) for a collection made by the steamer *Albatross* (depth given as 2–15 feet) at Tomahu Island. A handwritten ledger in the files of the Division of Fishes, recorded during the *Albatross* collections, indicates that blennies were collected at this station.

The published locality and date for the holotype of *E. stigmatura* are also in agreement with a published *Albatross* station (Anonymous, 1910, p. 82), but the ledger does not record that any blennies were collected at that station and they would not be expected from such a depth (ca. 443 meters).

In view of the above information I prefer to ascribe the Tomahu Island locality to the holotype and one paratype of *E. stigmatura*. In addition, as the second paratype, according to the locality records, came from either beach seining or dynamiting at a depth up to about 4.5 meters, and no salariinine is known to have a very extensive depth range, it seems much more probable that the species is restricted to shallow depths.

MATERIAL.—Tomahu Island: USNM 99379 (45.9, holotype of *Ecsenius stigmatura*), 111878 (36.6);

Cataingan Bay, east of Masbate Island, Philippines: USNM 122444 (36.5); Pulav Gaya, Darvel Bay, Borneo: USNM 201815 (37.7).

### *Ecsenius (Ecsenius) lividinalis* Chapman and Schultz

FIGURE 26

*Ecsenius lividinalis* Chapman and Schultz, 1952, p. 517 [Munda, New Georgia, Solomon Islands].

DESCRIPTION.—Dorsal spines 12; dorsal rays 12–14 (one each with 12 and 14); segmented anal rays 13–14; pectoral rays 13–14 (one of 11 with 14 on one side only); segmented caudal rays 13–15 (usually 14); dorsal procurrent caudal rays 5–6; ventral procurrent caudal rays 4–6; total caudal elements 23–26; gill-rakers 12–14; pseudobranchial filaments 5–7 (usually 6); lower incisor teeth 30–37; lower jaw posterior canines 1 (2 on one side in one specimen); total lower jaw posterior canines 2–3 (3 in one specimen); upper incisor teeth 98–111 (four counts); precaudal vertebrae 10–11 (one of 10 with 11); caudal vertebrae 19–20; total vertebrae 29 or 30; epipleural ribs 11–13. Lateral line with no paired pores, extending posteriorly to below level of 9th–11th dorsal spine. Dorsal fin notched three-ninths to five-ninths length of first dorsal ray. Third (innermost) pelvic ray obvious. One cirrus on each anterior nostril.

Color pattern: The available specimens of *E. lividinalis* are all old and to some degree faded. They appear to have been uniformly dark when fresh, with the fins perhaps paler than the body. The most obvious mark is a dark spot that envelops the anus and extends a short distance anterior from the anus.

MATERIAL (localities abbreviated).—New Georgia: USNM 144723 (33.0, holotype of *Ecsenius lividinalis*), 144292 (6:22.1–26.8, including one cleared and stained), 144291 (3:22.1–30.5); Philippine Islands: ANSP 109211 (26.0).

### *Ecsenius (Ecsenius) yaeyamaensis* (Aoyagi)

FIGURES 27–29

*Salarias yaeyamaensis* Aoyagi, 1954, p. 213 [in part, Iriomote Island, Riukius].

DESCRIPTION.—Dorsal spines 12–13 (rarely 13); dorsal rays 13–15 (usually 15); segmented anal rays 15–17 (usually 16); pectoral rays 12–14 (rarely 12 or 14); segmented caudal rays 13 (14 in one of 120 specimens); dorsal procurrent caudal rays 6–9 (usually 7–8); ventral procurrent caudal rays 6–8 (usually 7); total caudal elements 25–30 (rarely 25 or 30); gill-rakers 11–16 (rarely 11 or 16); pseudobranchial filaments 5–8 (rarely 5 or 8); lower incisor teeth 43–56; lower jaw posterior canines 0–1 (usually 1); total lower jaw posterior canines 0–2 (usually 2); upper incisor teeth 97–127 (6 counts); precaudal vertebrae 10; caudal vertebrae 21–23 (usually 22); total vertebrae 31–33 (usually 32); epipleural ribs 11–14 (rarely 11); lateral line without paired pores, extending posteriorly to beneath level of 10th–12th dorsal spine (one specimen each, of 110, to 8th and 12th spine). Dorsal fin notched seven-ninths to eight-ninths length first dorsal ray (usually eight-ninths). Third (innermost) pelvic ray varying from obvious to not obvious (usually not obvious). One cirrus on each anterior nostril.

Color pattern: Aside from a complex and variable color pattern, *E. yaeyamaensis* comprises several geographic populations that are distinguishable only on color pattern. Although treated here as a separate species, *E. nalolo* may more properly be placed with *E. yaeyamaensis*. In contrast with the color pattern populations of *E. yaeyamaensis*, which are generally of limited geographic occurrence, *E. nalolo* occurs over most of the Indian Ocean and Red Sea with little noticeable geographic variation in color pattern.

The major feature of the color pattern that links all the populations of *E. yaeyamaensis* is a dark, forked stripe on the fleshy pectoral base. The arms of the stripe extend onto the bases of the fin rays; no other species of *Ecsenius* has such a mark. (*E. nalolo* has a single, unforked, stripe on the fleshy pectoral base.)

The commonest color pattern is best typified by that illustrated in Figure 27. This color pattern is found in specimens from the South China Sea, Taiwan, the Ryukyus, Palaus and adjacent islands, New Britain, and New Georgia. The illustrated specimen has a fully developed pattern. Other specimens from the localities just cited are quite variable and are allied by lacking specific features that are found in specimens from other localities.

Banda Sea: A single specimen is available (Figure 29), which has a pattern unlike that from any other locality. The distinctive features are two long, narrow, dark stripes on the body below the anterior

dorsal rays, continuous as dark dashes and ultimately as four dark spots on the caudal peduncle. (A single, badly faded specimen of *E. yaeyamaensis* was available from Flores. Only faint remnants of the forked stripe on the pectoral base were visible. In view of the color pattern exhibited by the specimen from the Banda Sea, which is relatively close to Flores, it would be important to know what color pattern is exhibited by specimens of *E. yaeyamaensis* from the various islands surrounding the Banda Sea.)

New Hebrides: Three specimens (none illustrated), with two aligned, lengthwise rows of short, dark dashes on the body grading into spots below the posterior dorsal rays. If the dashes were to fuse anteriorly, they would form stripes as in the preceding form. The fact that the Banda Sea and the New Hebrides are quite distant from each other and that almost midway between these two localities, at New Britain and New Georgia, the common color pattern occurs, leads me to conclude that the populations are probably distinct.

Australia: All of a considerable number of specimens (not all cited in the material list) from the Capricorn group of islands at the southern end of the Great Barrier Reef and Endeavour Reef, off northern Queensland, exhibit numerous fine, dark spots on the posterior half of the body (Figure 28). These spots occur in at least two horizontally aligned rows, but there is usually a sprinkling of unaligned spots both above and between the rows. All of the specimens are larger than those from the New Hebrides and it may be that Australian specimens of sizes equal to those from the New Hebrides will be similar in color pattern.

REMARKS.—In Figure 2, a literature record for *E. yaeyamaensis* is included, based on Aoyagi's (1954) record from Iriomote Island, Ryukyus. For geographic variation see color pattern description above.

NOMENCLATURE.—Aoyagi (1954) described *Salarias yaeyamaensis* on the basis of three specimens: two males, 49.4 and 46 mm total length from Iriomote Island, and a female, 49 mm total length from Ishigaki Island. Both Islands are in the southern Ryukyus. Aoyagi wrote that the description was based on the 49.4 mm male, but he also described the female. A male, presumably the 49.4 mm specimen, was illustrated as was also the female. No holotype was specifically designated. No indication of where the type material was deposited was given, and I have been unable to locate Aoyagi's specimens. The male, well illustrated, is clearly the species that I treat here as *E. yaeyamaensis*. The female, also well illustrated, is clearly the species I describe below as *Ecsenius oculus*. (Aoyagi believed that color pattern differences between the males and female were indicative of sexual dimorphism.) In order to fix the name of Aoyagi's species, I here designate the larger male, 49.9 mm total length, as lectotype of *Salarias yaeyamaensis* Aoyagi.

MATERIAL (localities abbreviated).—South end of Taiwan: USNM 203133 (35.2), 203134 (2: 38.5–39.0), 203135 (42.0), 203136 (2: 39.7–42.6), 203137 (10: 26.5–49.0), 203138 (4: 37.7–41.8); Vietnam: CAS GVF-2072 (38.8); Flores: ZMA 109.100 (33.4); Banda Sea: USNM 202477 (26.6); Yap: CAS GVF-894 (11: 21.9–34.3), GVF-794 (9: 26.1–51.9), GVF-1912 (4: 28.7–34.8), GVF-1913 (25.0), GVF-1915 (36.7), GVF-1924 (31.7), GVF-1946 (37.7), GVF-1923 (2: 34.5–39.9); Palaus: CAS GVF-735 (46.4), GVF-740 (11: 31.9–43.0), GVF-802 (2: 24.7–29.8), GVF-807 (39.9), GVF-843 (4: 30.0–39.0), GVF-1450 (6: 31.6–43.6), GVF-1868 (46.2), GVF-1869 (41.5); Western Caroline Islands, Sorol Atoll: CAS GVF-993 (31.6); Bougainville: USNM 201824 (2: 30.4–39.8); New Britain: USNM 200428 (3: 38.2–38.7, including one cleared and stained), 201812 (32.3); New Hebrides: USNM 195787 (3: 20.6–26.0); One Tree Island, Great Barrier Reef: USNM 201818 (29: 32.1–46.8), 201822 (15: 34.1–45.4), 201836 (4: 32.0–36.0); Endeavour Reef, Great Barrier Reef: ANSP 109691 (31: 20.0–46.6), 109690 (52: 13.5–37.8).

### *Ecsenius (Ecsenius) nalolo* Smith

FIGURE 30

*Ecsenius nalolo* Smith, 1959, p. 245 [Pinda, Mozambique].
*Ecsenius minutus* Klausewitz, 1963, p. 357 [Addu Atoll, Maldive Islands].

DESCRIPTION.—Dorsal spines 11–13 (rarely 11 or 13); dorsal rays 12–15 (usually 13 or 14); segmented anal rays 14–17 (rarely 14 or 17); pectoral rays 12–13 (rarely 12); segmented caudal rays 12–14 (rarely 12 or 14); dorsal procurrent caudal rays 6–9; ventral procurrent caudal rays 5–9 (rarely 5 or 9); total caudal elements 25–31; gill rakers 12–17 (rarely 12

or 17); pseudobranchial filaments 6–8; lower incisor teeth 42–63; lower jaw posterior canines 0–1 (usually 1); total lower jaw posterior canines 0–2 (usually 2); upper incisor teeth 132 (one count); precaudal vertebrae 10; caudal vertebrae 21–23; total vertebrae 31–33; epipleural ribs 11–14 (usually 12–13). Lateral line without paired pores, extending posteriorly to below level of 8th–11th dorsal spine (rarely 8th). Dorsal fin notched seven-ninths to eight-ninths length of first dorsal ray. Third (innermost) pelvic ray varying from obvious to not obvious. One cirrus on each anterior nostril.

Color pattern (see also description under *Ecsenius yaeyamaensis*): Description of the color pattern of *E. nalolo* is difficult because of individual variation and the complexity of the pattern itself. The most consistent feature is the presence of a dark stripe on the fleshy pectoral base that extends onto the fin rays. Occasionally there are dark spots above and/or below the stripe on the fleshly base and, frequently, on the bases of the rays. The stripe is never forked as in *E. yaeyamaensis*.

The head typically bears a dark stripe, varying in intensity along its length, and extending from the midposterior margin of the orbit across the top of the opercle to the posterior bony margin of the opercle. Above this stripe is a parallel narrow pale stripe, then a stripe paler than the first described stripe, then a broad pale stripe and next a thin, narrow, dusky stripe just lateral to the midline of the top of the head. The last listed stripe may intensify as a dark spot just anterior to the level of the dorsal fin origin. Below the midorbital stripe the cheek may be pale dusky or, in some non-Red Sea males, peppered with tiny dark spots (Figure 30). The snout region is variably pale to dark dusky. The underside of the head in males may be almost black with a sharply defined, pale, triangular area, apex directed posteriorly, just behind the lower lip. In other males and females the underside of the head is dusky with a similar pale triangular area and a dorsally curving dark line on each side that extends from behind the corner of the lower lip up along the posterior margin of the opercle.

The dark stripes on the head may continue onto the body anteriorly where they usually break up into short, broad, dark dashes. Below these dashes in the region above the venter, there are a variable number of dark lines and splotches. The remainder of the body is variably dusky with pale spots.

The pectoral fin and base were described above. There is usually a dark or dusky spot in the pectoral axil (also found in *E. yaeyamaensis* and to lesser extent in *E. oculus*). The pelvics are pale to dark dusky. The caudal is not noticeably marked, but may be dusky basally. The dorsal fin is dusky basally, mostly unmarked otherwise. The anal is pale dusky in males, with the tips of the rays noticeably paler in presumably mature males.

Females are paler overall than males and the body of the female may be almost completely unmarked.

GEOGRAPHIC VARIATION.—Mandibular tooth counts (Table 17) of specimens from the northern Red Sea (including the Gulf of Aqaba) are usually much higher than those for specimens from the southern Red Sea and Indian Ocean. (See also discussion of this under *E. oculus*, geographic variation.)

REMARKS.—Specimens as small as 13.1 mm SL were examined; they were not ophioblennius type larvae, but were typical juveniles.

NOMENCLATURE.—*Ecsenius minutus* was not compared with any other species of fish. I have examined the holotype and find it to be a young specimen of *E. nalolo*.

MATERIAL (localities abbreviated).—Gulf of Aqaba: USNM 204571 (39: 13.1–46.4), 204568 (20: 15.3–38.4), 204569 (61: 16.1–42.5), HUI E-63/36 (3: 18.8–25.1), HUJ-F-3531 (25.1), HUJ-F-4376 (6: 14.5–32.0), HUJ-F-3542 (31.6), E-63/33 (2: 26.2–28.2), HUJ-F-3553 (3: 22.0–33.8), HUJ-F-4384 (35.9), HUJ-F-3551 (3: 17.5–34.8). Red Sea: southern tip of Sinai Peninsula, USNM 204570 (36: 21.8–44.9); Egypt, NFIS 5119 (38.0), USNM 200602 (4: 30.3–45.0, including one cleared and stained), 201825 (28.1), 201754 (2: 32.3–43.1); Sudan, NFIS (36.6); Zubair Island, HUI HUJ-F-4622 (25.2); Ethiopia, USNM 204481 (9: 16.6–31.4). Aden: USNM 203954 (16.8). Indian Ocean: Amirantes Islands, USNM 201845 (7: 28.8–47.6), ANSP uncataloged (35.8); Farquhar Island, USNM 203955 (48.7); Aldabra Atoll, USNM 203072 (15: 29.9–46.0), 203075 (11: 27.7–38.7), 201828 (6: 22.9–51.3); Comoro Islands, USNM 201826 (2: 30.1–31.9), 201521 (31.4); Mozambique, RU BP2127C (39.2, holotype of *Ecsenius nalolo*), BP2127B (34.3), BP2127A (33.4), BP1924 (29.7), RU uncataloged (5: 25.2–39.2, Pinda; 31.0, Ilha); Maldive Islands, NFIS 6363 (20.0, holotype of *Ecsenius minutus*);

Chagos Archipelago, USNM 203071 (43.2), 203073 (2: 30.9–49.2).

### *Ecsenius (Ecsenius) oculus*, new species

FIGURE 31

*Salarias yaeyamaensis* Aoyagi, 1954, p. 213 [in part, Ishigaki Island].

DESCRIPTION.—Dorsal spines 12; dorsal rays 12–15 (usually 13–14); segmented anal rays 14–17 (usually 15–16); pectoral rays 13–14 (rarely 14); segmented caudal rays 12–14 (rarely 12 or 14); dorsal procurrent caudal rays 7–10 (usually 8–9); ventral procurrent caudal rays 6–9 (usually 7–8); total caudal elements 27–32 (usually 28–30); gill-rakers 12–18 (usually less than 16); pseudobranchial filaments 5–6; lower incisor teeth 47–64; lower jaw posterior canines 0–1; total lower jaw posterior canines 1–2 (rarely 1); upper incisor teeth 138–148 (two counts); precaudal vertebrae 10; caudal vertebrae 21–24 (usually 22–23); total vertebrae 31–34; (usually 32 or 33); epipleural ribs 11–14 (rarely 11). Lateral line with no paired pores, extending to below level of 10th spine to first dorsal ray (usually beyond 11th spine). Dorsal fin notched nine-ninths length first dorsal ray (one specimen of 46 had notch seven-ninths). Third (innermost) pelvic ray obvious (not obvious in one specimen only). One cirrus on each anterior nostril, occasionally branched.

Color pattern: The color pattern of this species is variable, but most specimens are characterized by having at least three pairs of large, dark, pale margined spots on each side of the body. The most common pairs of spots are on or just above the midline of the body. These spots frequently give the appearance of sunglasses. Occasionally there are similar pairs of smaller dark spots with pale margins along the dorsal body contour in line with the pairs lower on the sides; sometimes only the dorsal pairs of spots are present. The general body color is less dark than the spots and is punctuated with pale areas of various sizes and shapes. There is invariably a vertical pair of dark marks (sometimes fusing, but always recognizable) on the caudal peduncle, extending onto the caudal fin and there decreasing in intensity. The dorsal spot of the pair extends diagonally downward on the caudal fin, tapering posteriorly, and the ventral spot extends horizontally, also tapering posteriorly. The extensions frequently meet posteriorly. These two spots are characteristic of the species. The caudal is otherwise clear or variably pale dusky.

The head pattern is variable, but frequently there is a middorsal pale stripe extending from just anterior to the dorsal fin to between the eyes. There is a broader dusky stripe (sometimes represented posteriorly only, as a dark spot) on either side of the median pale stripe, followed laterally by another pale stripe, then a broader dusky stripe, another narrower pale stripe, and then a broader dark stripe. This last stripe begins at about the posterior midorbital level and extends posteriorly onto the body for a short distance. Sometimes there is another thin, pale stripe ventral to this last dark stripe. The cheeks are irregularly dusky with pale marks. The corners of the upper lip may be darker than the surrounding color. Occasionally the ventral margin of the opercle is dark, and this darkness extends as a stripe onto the lower surface of the head, meeting a similar mark from the other side. The underside of the head is otherwise dusky except for a pale unmarked area around the lower lip.

The fleshy pectoral base is dusky with indications of one, rarely two, darker dusky stripes, the more dorsal of which may be bordered by pale areas. The pectoral fin is mostly unmarked except for a dusky area basally on the rays. The pelvic fins are pale to dark dusky. The dorsal may bear a basal or subbasal dusky stripe with the color mostly restricted to the membrane or to the fin elements. The anal fin is mostly uniformly dusky, paling at the distal tips of the rays.

There are some striking variations from the commonest type color pattern described above. It is probable that some of these represent population differences as they are in some degree paralleled by meristic and tooth count differences (Table 18).

Three specimens (USNM 195716) collected by Longley and presumably from the Banda Sea area (see appendix) are somewhat faded, but the two spots at the caudal peduncle extending onto the caudal fin are still apparent, as are pairs of large dark spots on the dorsal half of the body. These specimens differ in having four dark spots in a longitudinal series posteriorly on the ventral half of the body. These spots are of about equal size and intensity as those of the upper half of the body.

Four specimens from the New Hebrides (AMS I–6521–24) are similar to those from the Banda Sea, but exhibit about 6 to 8 dark spots on the ventral half of the body. The dark spots on the dorsal half of the body are not segregated as pairs but appear as a somewhat irregularly linear series.

The single specimen available from the Palau Islands (CAS GVF–880) differs from all others of the species in having three large, dark, saddle-like spots with pale ventral margins posteriorly on the dorsal body contour. Each spot is separated from the next by a slightly paler dark spot, which is darker than the ground color of the body. The two spots at the caudal base are relatively larger than those for any other specimen.

A specimen from Ilot du Sud, South China Sea (CAS GVF–2113), is unique in having only a single dark spot on the body, on the dorsal body contour at the end of the dorsal fin. The body color is generally dark, but paler than the spot, and is punctuated with rows of pale, round or oblong spots. The spots at the caudal base are normal. The fleshy pectoral base bears a dark bar with a shallow fork at its posterior end. The anterior end grades into the dusky color of the pectoral base. Above and below the bar are pale spots. The color pattern is, in general, somewhat intermediate between that of typical *E. oculus* and *E. yaeyamaensis*. Other specimens from the South China Sea are more normal.

GEOGRAPHIC VARIATION.—In addition to color pattern variation (see above), there is some evidence that populations from various localities differ in meristics and tooth numbers (Table 18). Until more specimens from more localities are available, it is not possible to say definitely what the cause of this variation is. There is a tendency for the meristic characters to gradually decrease in numbers toward the south to the equator and then to increase south of the equator. Tooth numbers seem to exhibit a sharp break near the northern end of the range of the species.

A possible explanation for the observed meristic variation may be the fact that water temperatures tend to increase in a north-south direction to the equator and decrease southward from the equator. It has been demonstrated often in fishes that meristics decrease in numbers with increase in water temperatures, but tooth numbers have not been examined for such a correlation. In this respect the tooth numbers of *Ecsenius nalolo* specimens from the northern Red Sea including the Gulf of Aqaba) are higher than those of the southern Red Sea and Indian Ocean specimens (Table 12). Gulf of Aqaba water temperatures average lower than those of the southern Red Sea (and Indian Ocean) during every month (Oren, 1962).

REMARKS.—Aoyagi (1954) illustrated a female *E. oculus* from the Ryukyus that he identified as *E. yaeyamaensis,* and Kamohara (1954) illustrated a male, from Takarajima, northern Ryukyus. Kamohara's record is included on Figure 3 although the specimen was not seen.

RELATIONSHIPS.—*Ecsenius oculus* is most closely related to *E. opsifrontalis,* from which it is distinguished in usually having more dorsal and anal rays (Table 1), usually shorter third and last dorsal spines (Tables 5 and 7), and in overall color pattern (compare Figures 31 and 32).

ETYMOLOGY.—The specific name *oculus* is Latin for eye, and refers to the eyelike spots on the body of the species.

HOLOTYPE.—USNM 203140, male, 53.8 mm SL, immediately south of cut between large outstanding rock and Ch'uan-fan-shih, south end of Taiwan. Collector V. G. Springer, et al., 24 April 1968. Depth approximately 6 meters. Original field number VGS 68–3.

PARATYPES.—USNM 203923 (7: 38.0–52.4), collected with the holotype. USNM 203142 (4: 43.9–50.5,) just north of type locality. USNM 203141 (45.5), northwest of swimming beach of Sha Toa, south end of Taiwan. USNM 203139 (3: 40.8–42.7), just south of Chin-chiao-wan, south end of Taiwan. BPBM 7464 (19.5), Taketoni Island, Ishigaki, Ryukyus. BPBM 7468 (13: 19.7–47.6), Ishigaki City Harbor, Ishigaki, Ryukyus. CAS GVF–2113 (41.3), west shore Ilot du Sud, South China Sea. USNM 201811 (4: 26.2–32.5), Goh Huyong, Similand Island, Thailand. USNM 201560 (2: 30.4), Pulo Jara, Strait of Malacca, Indonesia. USNM 201522 (3: 31.8–39.9), Pulo Mega, Mentawei Islands, Indonesia. CAS GVF–880 (40.7), vicinity of Garudowaishi Point, Nardueis Island, Palau Islands. USNM 195716 (3: 31.0–37.8), Banda Sea. AMS I.6521–24 (4: 34.7–41.8), New Hebrides.

Much additional field data is available for the specimens listed above from Taiwan and those bearing California Academy of Sciences numbers. The data are on my field data sheets for the year

1968 (in the files of the Division of Fishes, National Museum of Natural History) and the George Vanderbilt Foundation register sheets at the California Academy of Sciences.

### *Ecsenius (Ecsenius) opsifrontalis* Chapman and Schultz

FIGURE 32

*Ecsenius opsifrontalis* Chapman and Schultz, 1952, p. 521 [Rongelap Island, Marshall Islands].

DESCRIPTION.—Dorsal spines 12; dorsal rays 13–14 (usually 13); segmented anal rays 14–16 (usually 15); pectoral rays 12–13 (rarely 12); segmented caudal rays 13; dorsal procurrent caudal rays 8–9; ventral procurrent caudal rays 7–8; total caudal elements 28–30; gill rakers 12–15; pseudobranchial filaments 5–6; lower incisor teeth 43–50; lower jaw posterior canines 0–1; total lower jaw posterior canines 1–2; upper incisor teeth 127 (one count); precaudal vertebrae 9–10 (rarely 9); caudal vertebrae 21–22 (usually 22); total vertebrae 31–32 (usually 32); epipleural ribs 12 (one count). Lateral line with no paired pores, extending to below level of 11th–12th dorsal spine (usually 12th). Dorsal fin notched eight-ninths to nine-ninths length of first dorsal ray. Third (innermost) pelvic ray not obvious. One cirrus on each anterior nostril.

Color pattern: This is usually a faintly marked species. The most noticeable and consistent marking is a narrow stripe extending posteriorly from the orbit across the top of the opercle and, broadening and becoming fainter, along the upper portion of the body, sometimes onto the bases of the caudal rays. The body portion of the stripe is frequently absent in part or completely. The second most frequent and obvious marking is a dark edging of the anterior margin of the lower lip. The head is otherwise variably dusky, sometimes with one or two dusky stripes connecting the orbits across the anterior interorbital region. A second longitudinal stripe occasionally occurs along the ventral half of the body, extending onto the bases of the caudal rays. Characteristic of many specimens are up to 10 faint to dark dusky, narrow, vertical stripes on the upper two thirds of the body. Except for the anal fin, which is dusky, and the body stripes extending onto the base of the caudal, the fins are essentially unmarked. In some specimens the black lining of the intestine everts at the anus and gives the appearance of a black ring in this region.

MATERIAL.—Guam: USNM 203742 (25.5); Kapingamarangi: CAS GVF–440 (23: 15.6–32.4), GVF–468 (5: 17.8–33.8), GVF–446 (3: 18.6–28.7), GVF–452 (6: 21.9–35.8); Marshall Islands: USNM 142065 (29.7, holotype of *Ecsenius opsifrontalis*), 142066 (26.1), 152978 (34.8), 202548 (32.3).

### *Ecsenius (Ecsenius) prooculis* Chapman and Schultz

FIGURE 33

*Ecsenius prooculis* Chapman and Schultz, 1952, p. 519 [Munda Lagoon near Sassavelle, New Gorgia, Solomon Islands].

DESCRIPTION.—Dorsal spines 12; dorsal rays 14; segmented anal rays 15–16; pectoral rays 13; segmented caudal rays 13; dorsal procurrent caudal rays 7; ventral procurrent caudal rays 6–8; total caudal elements 26–28; gill-rakers 11–13; pseudobranchial filaments 6; lower incisor teeth 41–49; lower jaw posterior canines 1; total lower jaw posterior canines 2; precaudal vertebrae 10; caudal vertebrae 21–22; total vertebrae 31–32; epipleural ribs 12 (one count). Lateral line with no paired pores, extending posteriorly to below level of 8th–9th dorsal spine. Dorsal fin notched eight-ninths length of first dorsal ray. Third (innermost) pelvic ray obvious. One cirrus on each anterior nostril.

Color pattern: This species is characterized by a pattern of three dark stripes, separated by pale dusky interspaces, extending the length of the body. The dorsalmost stripe extends along the dorsal body contour. The second and darkest stripe extends along the midlength of the body, and the ventralmost, and least dark of the three, extends along the ventral body contour. The dorsalmost stripe gradually diminishes in intensity anteriorly and fades into the head. The middle stripe extends anteriorly onto the head (entering just below the dorsal level of the opercle) as a narrow dark line that reaches the posterior margin on the eye. The ventralmost stripe broadens anteriorly and may spread over much of the venter. All three stripes extend onto the bases of the caudal rays where the stripes fuse and form a crescentic dusky area. Just above the head portion of the middle stripe there may be an indication of a dark spot, which

in one specimen is faintly continuous with a spot on the dorsal margin of the opercle. The under surface of the head is generally paler than the sides of the head and there is faint indication in all specimens of a dusky stripe extending a short distance posteriorly from the anteriormost mandibular sensory pore on each side. The stripe on each side shows indications of two concentrations of pigment, which make the stripe appear as two diffusely connected spots.

The holotype exhibits some dark spots on the head not found in the other specimens. There is a spot behind each anterior nostril and five spots in the interorbital region: two anteriorly, two posteriorly, and one in the midline slightly closer to the anterior pair.

The rayed portion of the dorsal fin bears a diffuse dusky stripe in its lower third. Otherwise the fin bears only some melanophores basally. The anal fin is uniformly dusky, except for the tips of the rays, which are pale. The pelvics are pale dusky and the pectorals are clear except that the rays are faintly overlain with melanophores.

REMARKS.—see under *Ecsenius bandanus*.

MATERIAL.—New Georgia: USNM 144722 (39.5, holotype of *Ecsenius prooculis*); New Britain: USNM 201819 (4:28.2–34.0).

### *Ecsenius (Ecsenius) bimaculatus*, new species

FIGURE 34

DESCRIPTION (data for holotype followed in parentheses by data for largest and smallest paratypes, if different).—Dorsal spines 12; dorsal rays 14; segmented anal rays 16 (16, 15); pectoral rays 13 (13, 12—but 13 on opposite side); segmented caudal rays 13; dorsal procurrent caudal rays 7 (7, –); ventral procurrent rays 6 (6, –); total caudal elements 26 (26, –); gill-rakers 12 (14, 14); pseudobranchial filaments 6; lower incisor teeth 42 (42, 41); lower jaw posterior canines 1; total lower jaw posterior canines 2; precaudal vertebrae 10; caudal vertebrae 22; total vertebrae 32; epipleural ribs – (–, 12). Lateral line with no paired pores, extending to below level of 10th dorsal spine (9th, 10th). Dorsal fin notched eight-ninths length of first dorsal ray. Third (innermost) pelvic ray obvious. One cirrus on each anterior nostril.

Color pattern: The head is dusky above the level of the upper third of the eye. Immediately below this dusky area is a dark stripe that encompasses the two circumorbital pores at the midposterior orbital margin. This stripe extends posteriorly across the head along the dorsal opercular margin and enters the body, where it narrows and becomes diffuse, ending below the third or fourth dorsal spine. The head is less dark below the stripe than above. One specimen exhibited a dark spot on either side of the head at the dorsoposterior margin of the eye just above the dark stripe. There are two dusky spots on each side of the ventral surface of the head. The anterior spot of each pair is just behind the anteriormost pore of the mandibular series, and the posterior is a little medial to the fifth pore of this series.

The body is generally dusky, slightly darker anteriorly above the level where the head stripe enters the body. Just below the body portion of the stripe, the body pales abruptly or gradually. There are two distinct, dark, oblong spots on each side just below the midlevel of the body under the third or fourth through ninth dorsal spines. There is a narrow dark line at the dorsal body contour that continues on the base of the spinous dorsal only. The rayed portion of the dorsal is clear basally and has a diffuse stripe extending along its length just above the clear area. The anal fin is evenly dusky except for a paling at the distal ends of the rays. The caudal is faintly sprinkled with melanophores except for a faint crescentric concentration of melanophores at its base. The pectorals are marked similarly to the caudal; the pelvics are unmarked.

RELATIONSHIPS.—See under *Ecsenius bandanus*.

MATERIAL.—Holotype, USNM 201817, male, 31.0 mm SL, Pulav Bohidulong, Darvel Bay, east end of Borneo. Fringing coral reef on eastern (outer) side of island; depth ca. 1.5–3.6 meters; 2 February 1965, Te Vega Cruise 6, station 216.

PARATYPES.—USNM 203922, two males, 31.7 and 30.6 mm SL collected with the holotype.

ETYMOLOGY.—The name *bimaculatus* refers to the characteristic two dark spots on the side of the body.

### *Ecsenius (Ecsenius) bandanus*, new species

FIGURE 35

DESCRIPTION (holotype and only known speci-

men).—Dorsal spines 12; dorsal rays 14; segmented anal rays 16; pectoral rays 13; segmented caudal rays 13; dorsal procurrent caudal rays 8; ventral procurrent caudal rays 7; total caudal elements 28; gill-rakers 13; pseudobranchial filaments 6; lower incisor teeth 43; lower jaw posterior canines 1; total lower jaw posterior canines 2; precaudal vertebrae 10; caudal vertebrae 21; total vertebrae 31. Lateral line with no paired pores, extending posteriorly to below level of 9th dorsal spine. Dorsal fin notched eight-ninths length of first dorsal ray. Third (innermost) pelvic ray obvious. One cirrus on each anterior nostril.

Color pattern: Distinctive markings appear only on the head of this species, which has as its most noticeable marking a broad stripe extending posteriorly from just behind the eye across the top of the opercle. On the right side of the specimen there is faint indication of a continuation of this stripe on the body to just beyond the level of the pectoral base. There is also faint evidence anteriorly that the stripe continues dorsally following the margin of the eye and meeting in the interorbital region the stripe from the other side. There is a faint, narrow band in the anterior interorbital region connecting the two orbits, and a dark sprinkling of melanophores around the anterior nostrils. On each side of the undersurface of the head there is a dusky spot encompassing the anteriormost two pores of the mandibular series and a similar spot just medial to the fifth pore of this series. The rayed portion of the dorsal fin has a faintly dusky stripe extending the length of the fin on its basal half. The anal is dusky except for the unmarked basal half. The specimen is otherwise evenly dusky.

Relationships and remarks.—*Ecsenius bandanus* is most and very closely related to *E. bimaculatus* and *E. prooculis*: the prooculis species subgroup of the yaeyamaensis species group. The species of this subgroup differ from one another only in matters of color pattern, and in this they are strikingly different from one another (Figures 33–35). The species are rare in collections and all known specimens are males. The species occupy different geographic areas (Figure 4).

Divergence of the species probably occurred as a result of isolation in the different island groups, either by differentiation of an ancestral founding species that invaded new island areas, or after the breaking up of the geographic range of a widespread ancestral species. The distribution of the three species correlates somewhat with biogeographic areas recognized for terrestrial organisms. Thorne (1963) prepared a biogeographical analysis of the islands of the Pacific based on terrestrial organisms. The tropical portion of the Pacific was called the Oriental Region, which was divided into five subregions. Each subregion was divided into provinces and some provinces were divided into districts. *E. bimaculatus* occupies the Bornean District of the Malayan Province of the Indo-Malayan Subregion. *E. bandanus* occupies the Moluccan Province of the Papuan Subregion, and *E. prooculis* occupies the Bismarckian and Solomonian Districts of the Bismarckian Province of the Papuan Subregion. If these distributions are indicative of distributional patterns generally, then additional species in the prooculis subgroup can be expected to occur in other provinces and subregions.

Holotype.—USNM 195717, male, 31.4 mm SL, Banda Sea, Indonesia (see discussion of Banda Sea locality in Appendix).

Etymology.—Named for the area from where the holotype is believed to have come.

### *Ecsenius (Ecsenius) mandibularis* McCulloch

Figure 36

*Ecsenius mandibularis* McCulloch, 1923, p. 122 [Masthead Island, Australia].

Description.—Dorsal spines 12 (rarely 11 or 13); dorsal rays 14–16 (usually 15); segmented anal rays 16–18 (rarely 18); pectoral rays 13 (rarely 12); segmented caudal rays 13; dorsal procurrent caudal rays 6–7 (one of 53 with 8); ventral procurrent caudal rays 5–7; total caudal elements 24–27; gill-rakers 12–16 (usually 14); pseudobranchial filaments 6 (rarely 7); lower incisor teeth 45–53; lower jaw posterior canines 2–8 (usually 5–7); total lower jaw posterior canines 7–15; upper incisor teeth 120–121 (two counts); precaudal vertebrae 10 (one of 91 specimens with 11); caudal vertebrae 22–23 (rarely 21 or 24); total vertebrae 31–34 (usually 32–33); epipleural ribs 12 or 13 (rarely 11 or 14). Lateral line with no paired pores, extending posteriorly to below 10th–11th dorsal spine. Dorsal fin notched seven-ninths to eight-ninths length of first dorsal ray (usually eight-ninths). Third (innermost) pelvic ray obvious to not obvious (45 of 51 specimens with

ray obvious). One cirrus, rarely forked, on each anterior nostril.

Color pattern: Specimens may range from almost uniformly pale, with no distinct marks, to quite dark anteriorly, grading into moderately dusky posteriorly with two longitudinal rows of dark spots on the body. When the spots are present the upper row usually begins between the dorsal fin origin and the lateral line and terminates at some point below the dorsal fin rays. The ventral row of spots begins at about the midlateral line of the body no farther anteriorly than the level of the anus and extends to the caudal base. The upper row of spots may be obscured by the dark color of the body. I have seen collections from One Tree Island taken within a week of each other in which almost all the specimens in one collection exhibited spotting and almost none of the specimens in the other exhibited spotting. While not so restricted, the spotting seems to be found predominantly in males.

In many specimens there is a narrow, dark stripe extending from the posterior margin of the orbit across the top of the opercle. There may also be a narrow, dark stripe on each side of the underside of the head, beginning somewhat behind the tip of the lower jaw and extending to the margin of the branchiostegal membrane, thence continuous along the ventral margin of the fleshy pectoral base. The anterior margin of the lower jaw may be dark in pale as well as dark specimens. Some nonspotted specimens exhibit adumbrations of several vertical dusky bars on the upper half of the body.

The fins are not distinctively marked, usually having an overall dusky appearance. Melanophores usually concentrate along the fin elements. The caudal is darker along its midlength; the tips of the anal rays may be pale, especially in mature males; there may be a dark crescentic area at the base of the pectoral rays.

REMARKS.—At One Tree Island *E. mandibularis* was collected with *E. yaeyamaensis* (also rarely with *E. bicolor*). Superficially the two species are very similar and difficult to tell apart in the field. They can be separated readily, however, by the fact that *E. yaeyamaensis* always has a dark forked stripe on the fleshy pectoral base. This mark is not present in *E. mandibularis*.

MATERIAL.—Australia, Queensland: Endeavour Reef, ANSP 109694 (2:28.1–35.2), 109692 (30.3), 109696 (14:21.4–37.2), 109698 (20.6); Little Hope Island, ANSP 109693 (4:27.3–37.1), 109695 (18.6); Big Hope Island, ANSP 109697 (29.8); Gillett Cay, Swains Reef, AMS IB–6222 (4:28.5–35.7), IB–6237 (2:15.6–17.9); Masthead Island, Capricorn Group, AMS I–7112 (48.4, holotype of *Ecsenius mandibularis*, I–7114–6 (6: 33.6–50.6); One Tree Island, Capricorn Group, USNM 201367 (2 of 56: 31.5–44.3, cleared and stained), 201821 (57:29.7–49.1); Hoskyn Island, Bunker Group, AMS IA–3585 (35.0). In addition, several series of specimens at USNM from One Tree Island were cursorily examined in preparing the color pattern description, and one specimen from USNM 201820, also One Tree Island, was used for preparation of figure 36).

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## Literature Cited

Anonymous
1910. Dredging and Hydrographic Records of the U.S. Fisheries Steamer *Albatross* during the Philippine Expedition, 1907–1910. *Department of Commerce and Labor,* Bureau of Fisheries Document, 741:3–97.

Aoyagi, H.
1954. Description of One New Genus and Three New Species of Blenniidae from the Riu-Kiu Islands. *Dobutsugaku Zasshi,* 63(5):213–217.

Axelrod, H. R. and C. W. Emmens
1969. *Exotic Marine Fishes.* 607 pages.

Boulenger, G. A.
1897. Descriptions of New Fishes from the Mekran Coast, Persia. *Annals and Magazine of Natural History,* series 6, 20:420–422.

Chapman, W. M. and L. P. Schultz
1952. Review of the Fishes of the Blennioid Genus *Ecsenius,* with Descriptions of Five New Species. *Proceedings of the United States National Museum,* 102(3310):507–528.

Collette, B. B. and R. W. Yerger
1962. The American Percid Fishes of the Subgenus *Villora. Tulane Studies in Zoology,* 9(4):213–230.

Cuvier, G. and A. Valenciennes
1836. *Histoire Naturelle des Poissons.* Volume 11, 506 pages.

Day, F.
1888. Supplement to the Fishes of India. Pages 779–816.

Hobson, E. S.
1969. Possible Advantages to the Blenny *Runula azalea* in Aggregating with the Wrasse *Thalassoma lucasanum* in the Tropical Eastern Pacific. *Copeia,* 1969, 1:191–193.

Hora, S. L. and D. D. Mukerji
1936. Notes on Fishes in the Indian Museum. XXVII. On Two Collections of Fish from Maungmagan, Tavoy District, Lower Burma. *Records of the Indian Museum,* 38(1):15–39.

Johnstone, J.
1904. Report on the Marine Fishes Collected by Professor Herdman, at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manar,* 2(15):201–222.

Jordan, D. S. and B. W. Evermann
1902. Notes on a Collection of Fishes from the Island of Formosa. *Proceedings of the United States National Museum,* 25(1289):315–368.

Kamohara, T.
1954. A List of Fishes from the Tokara Islands, Kagoshima Prefecture, Japan. *Publications of the Seto Marine Biological Laboratory,* 3(3):265–299.

Kamohara, T. and T. Yamakawa
1965. Fishes from Amami-Oshima and Adjacent Regions. *Reports of the Usa Marine Biological Station,* 12(2): 1–27.

Klausewitz, W.
1960. Fische aus dem Roten Meer. V. Über einige Fische der Gattung *Ecsenius* (Pisces, Salariidate). *Senckenbergiana Biologica,* 41(5–6):297–299.
1962. *Ecsenius lineatus* n. sp. von den Malediven. *Senckenbergiana Biologica,* 43(2):145–147.
1963. *Ecsenius minutus* n. sp. von Malediven. *Senckenbergiana Biologica,* 44(5):357–358.

Longley, W. H.
1918. Habits and Coloration of Hawaiian Brachyura and Fishes, with a Note on the Possibility of Submarine Color Photography. *Carnegie Institution of Washington, Yearbook,* 17:158–163.
1920. The Fishes of Samoa. *Carnegie Institution of Washington, Yearbook,* 19:195–197.
1927. Preliminary Report of Observations upon Fishes of the Pacific Ocean and East Indies. *Carnegie Institution of Washington, Yearbook,* 26:280–281.

Lotan, R.
1969. Systematic Remarks on Fishes of the Family Salariidae in the Red Sea. *Israel Journal of Zoology,* 18: 363–378 (publ. 1970).

MacDonald, G. A.
1949. Hawaiian Petrographic Province. *Bulletin of the Geological Society of America,* 60:1541–1596.

McCulloch, A. R.
1923. Fishes from Australia and Lord Howe Island. No. 2. *Records of the Australian Museum,* 14(2):113–125.

Menard, H. W.
1964. Marine Geology of the Pacific. 271 pages.

Murray, J. A.
1887. New Species of Fish from Kurrachee and the Persian Gulf. *Journal of the Bombay Natural History Society,* 2(1):47–49.

Oren, O. H.
1962. A Note on the Hydrography of the Gulf of Eylath. *State of Israel, Ministry of Agriculture, Division of Fisheries, Sea Fisheries Research Station, Bulletin,* 30:3–14.

Pellegrin, J.
1906. Sur un *Salarias* nouveau de la Baie de Tadjourah. *Bulletin du Museum National d'Histoire Naturelle de Paris,* 12:93–94.

Randall, J. E. and H. A. Randall
1960. Examples of Mimicry and Protective Resemblance

in Tropical Marine Fishes. *Bulletin of Marine Science of the Gulf and Caribbean*, 10(4):444–480.

Regan, C. T.
1905. On Fishes from the Persian Gulf, the Sea of Oman, and Karachi, Collected by Mr. F. W. Townsend. *Journal of the Bombay Natural History Society*, 18: 318–333.
1909. A Collection of Fishes Made by Dr. C. W. Andrews, F.R.S., at Christmas Island. *Proceedings of the Zoological Society of London*, 1909:403–406.

Rüppell, E.
1838. *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig*, 12 (21–37) :81–148.

Schultz, L. P.
1966. *Pseudorhegma diagramma*, a New Genus and Species of Grammid Fish, with a Key to Genera of the Family and to the Species of the Subfamily Pseudogramminae. *Ichthyologica*, 37(4):185–194.

Simpson, G. S., A. Roe and R. C. Lewontin
1960. *Quantitative Zoology*. Revised edition, Harcourt, Brace and Company, 440 pages.

Smith, J. L. B.
1959. Fishes of the Families Blenniidae and Salariidae of the Western Indian Ocean. *Rhodes University, Ichthyological Bulletin* 14:229–252.

Smith-Vaniz, W. F. and V. G. Springer
In press. Synopsis of the Tribe Salariini, with Descriptions of Five New Genera and Three New Species (Pisces: Blenniidae). *Smithsonian Contributions to Zoology*.

Springer, V. G.
1967. Revision of the Circumtropical Shorefish Genus *Entomacrodus* (Blenniidae: Salariinae). *Proceedings of the United States National Museum*, 122(3582):1–150.
1968. Osteology and Classification of the Fishes of the Family Blenniidae. *United States National Museum, Bulletin* 284:1–85.

Starck, W. A., II
1969. *Ecsenius (Anthiiblennius) midas*, a New Subgenus and Species of Mimic Blenny from the Western Indian Ocean. *Notulae Naturae*, 419:1–9.

Strasburg, D. W.
1956. Notes on the Blennioid Fishes of Hawaii with Descriptions of Two New Species. *Pacific Science*, 10(3): 241–267.
1967. *Gunnellichthys monostigma* and *Ecsenius bicolor*, New Fish Records from the Marshall Islands. *Copeia*, 1967, 4:839–841.

Stephens, J. S., Jr.
1963. A Revised Classification of the Blennioid Fishes of the American Family Chaenopsidae. *University of California Publications in Zoology*, 68:1–133.

Thorne, R. F.
1963. Biotic Distribution Patterns in the Tropical Pacific. Pages 311–350 in *Pacific Basin Biogeography*, edited by J. L. Gressitt, Bishop Museum Press.

Tomiyama, I.
1955. Notes on Some Fishes, Including One New Genus and Three New Species from Japan, the Ryukyus and Pescadores. *Japanese Journal of Ichthyology*, 4(1-3):1-15.

Wickler, W.
1965. Zur Biologie und Ethologie von *Ecsenius bicolor* (Pisces Teleostei, Blenniidae). *Zeitschrift für Tierpsychologie*, 22:36–49.
1965. *Ecsenius bicolor* (Blenniidae) Schwimmen und Fressen. *Encyclopaedia Cinematographica*, E 520/1963: 397–400.
1965. *Ecsenius bicolor* (Blenniidae) Balz. *Encyclopaedia Cinematographica*, E521/1963:363–365.
1965. *Ecsenius bicolor* (Blenniidae) Kampfverhalten. *Encyclopaedia Cinematographica*, E522/1963:401–405.

## Appendix

NOTE ON BANDA SEA LOCALITIES.—After W. H. Longley's death in 1937, the Carnegie Institution of Washington presented his fish collections to the Smithsonian Institution. The only localities associated with Longley's specimens were general ones accompanying the containers holding his fishes (Schultz, 1966, p. 194). In general, these localities seem applicable, but it is known that some mixing of specimens from different localities did occur.

During his lifetime Longley collected marine fishes from only two general areas: Dry Tortugas, Florida, and the western tropical Pacific Ocean. Many of Longley's unlabeled specimens were obviously tropical western Atlantic species and a number of these were saved and cataloged into the collections of the Division of Fishes, National Museum of Natural History, as having come from Tortugas. Some of this group of specimens, however, were discarded when they were found mixed with obviously Pacific Ocean species.

The remainder of Longley's collections were obviously tropical western Pacific in origin, and all but a small lot were accorded the same general locality by L. P. Schultz, formerly curator, Division of Fishes, when they were entered into the collections: Dutch East Indies. The small lot (catalog numbers 160665–160717) was catalogued with the locality datum only of Hawaii. At least one species in this lot, *Enchelyurus brunneolus* (Jenkins), is a Hawaiian endemic.

Prior to 1926, Longley (1918, 1920) made one or two trips to the tropical western Pacific where he spent time observing fishes at Pukoo, Molokai, Hawaiian Islands, and Pago Pago, Samoa. There is no information that he did any collecting on these

trips. During 1926–27 Longley (1927) made another trip to the tropical western Pacific. On this trip he spent two weeks at Pukoo, nine weeks at Pago Pago, one week at Amboina, and eight weeks at Banda Island (the last two localities are in the Banda Sea and are about 250 km apart) collecting and making field observations on the habits of fishes. He also stopped in Sydney, but mentioned nothing about his work there.

I have been unable to locate any of Longley's specimens that bear Samoan locality data, although on the basis of his handwritten field notes in the files of the Division of Fishes, National Museum of Natural History, he definitely made collections of fishes in Samoa. Because some of the containers holding Longley's fishes did have specimens from obviously mixed localities, one cannot exclude the possibility that the Dutch East Indies locality may be erroneous for any particular specimen.

Longley appears to have made field notes on almost every specimen he collected during his 1926–27 trip. On the basis of his color pattern description of a blenny from Banda Island, I feel fairly confident that the specimen I list in the material of *E. yaeyamaensis* as having come from the Banda Sea in fact came from Banda Island.

With regard to the specimens of *E. bicolor, E. oculus,* and *E. bandanus* that I list as having come from the Banda Sea, I am less certain, but I believe that none of these came from the Hawaiian Islands or Samoa.

*Ecsenius bicolor* has been reported from the Hawaiian Islands only under unusual circumstances (see remarks under *E. bicolor* species account) and has never been found in Hawaii subsequent to the original report despite considerable collecting in that area in recent years. Samoa has been fairly well collected since Longley was there and no specimens of *Ecsenius* have been taken there. *Ecsenius* generally does not occur much farther west than 170° east longitude, and Samoa is located at approximately 170° west longitude. It is possible that the wide-ranging *E. bicolor* may turn up in Samoa as it is the only species that comes close to that island group. The Banda Sea, however, is well within the range of *E. bicolor,* and *E. oculus* and *E. bandanus* are most typical of species that seem to be limited to west of 160° west longitude.

As Longley collected only at Amboina and Banda in the Dutch East Indies, his *Ecsenius* specimens from this area could have come from either island. The two islands are close together and I have elected to use the locality "Banda Sea" for his *Ecsenius* specimens.

It is probable that proof of a Banda Sea (Amboina or Banda) locality for Longley's *Ecsenius* specimens will never be possible. Strong evidence favoring the Banda Sea would be the re-collection of the species described herein as *Ecsenius bandanus,* and also the re-collection of the peculiar color pattern forms of *E. oculus* and *E. yaeyamaensis* reported here as occurring in the Banda Sea. Longley's specimens are much too valuable to discard because of the locality data problem. Aside from their intrinsic value as specimens, I wish to use the present circumstances as a test of the predictive value of systematic work.

TABLE 1.—*Frequency distributions for certain meristic characters in species of* Ecsenius

| *Species* | *Dorsal spines* | | | | | *Dorsal rays* | | | | | | | | | | *Anal rays* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10 | 11 | 12 | 13 | 14 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
| *midas* | | | | 11 | 1 | | | | | | | | 6 | 5 | 1 | | | | | | | | 1 | 5 | 4 | 2 |
| *frontalis* | 1 | 10 | 261 | 5 | | | | | | | 3 | 108 | 96 | 59 | 3 | | | | | 1 | 9 | 97 | 118 | 45 | 1 | |
| *pulcher* | | | 3 | 58 | 5 | | | | | | | 11 | 38 | 16 | | | | | | | | 1 | 3 | 21 | 37 | 1 |
| *gravieri* | | | 4 | 77 | 6 | | | | | 4 | 45 | 38 | 1 | | | | | | | | 3 | 44 | 36 | 3 | | |
| *aroni* | | | 2 | 45 | 1 | | | | | | 22 | 26 | | | | | | | | | | 11 | 36 | | | |
| *bicolor* | | 2 | 251 | | | | | | 2 | 54 | 164 | 32 | | | | | | | | 1 | 33 | 163 | 59 | 2 | | |
| *namiyei* | | 2 | 23 | | | | | | | | | 1 | 9 | 15 | | | | | | | | | 1 | 12 | 11 | |
| *lineatus* | | | 13 | | | | | | | | 10 | 3 | | | | | | | | | | 4 | 8 | | | |
| *stigmatura* | | | 4 | | | | | | | 2 | 2 | | | | | | | | | | 2 | 2 | | | | |
| *lividinalis* | | | 11 | | | | 10 | 1 | | | | | | | | 3 | 8 | | | | | | | | | |
| *yaeyamaensis* | | | 208 | 4 | | | 11 | 186 | 24 | | | | | | | | | 17 | 182 | 12 | | | | | | |
| *nalolo* | | 1 | 127 | 4 | | 1 | 26 | 103 | 1 | | | | | | | | 3 | 30 | 93 | 2 | | | | | | |
| *oculus* | | | 48 | | | 2 | 12 | 31 | 3 | | | | | | | | 1 | 12 | 32 | 3 | | | | | | |
| *opsifrontalis* | | | 41 | | | | 36 | 6 | | | | | | | | | 1 | 37 | 4 | | | | | | | |
| *prooculis* | | | 5 | | | | | 5 | | | | | | | | | | 1 | 4 | | | | | | | |
| *bimaculatus* | | | 3 | | | | | 3 | | | | | | | | | | 1 | 2 | | | | | | | |
| *bandanus* | | | 1 | | | | | 1 | | | | | | | | | | | 1 | | | | | | | |
| *mandibularis* | | 2 | 90 | 3 | | | | 21 | 65 | 3 | | | | | | | | | 35 | 56 | 5 | | | | | |

**(For sexual dimorphism and geographic variation see individual species accounts and section on sexual dimorphism.)**

TABLE 2.—*Frequency distributions for number of vertebrae in species of* Ecsenius

| *Species* | *Precaudal vertebrae* | | | | *Caudal vertebrae* | | | | | | | | | | | *Total vertebrae* | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 9 | 10 | 11 | 12 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 |
| *midas* | | | 12 | | | | | | | | | | 5 | 5 | 2 | | | | | | | | | | 5 | 5 | 2 |
| *frontalis* | | 1 | 282 | 1 | | | | | 2 | 80 | 158 | 34 | | | | | | | | | 1 | 94 | 169 | 32 | | | |
| *pulcher* | | | 44 | | | | | | | | | 4 | 30 | 8 | | | | | | | | | | 4 | 30 | 8 | |
| *gravieri* | | 2 | 83 | | | | | | | 5 | 49 | 31 | | | | | | | | | | 6 | 49 | 29 | | | |
| *aroni* | | 1 | 47 | | | | | | 1 | 9 | 34 | 4 | | | | | | | | | 1 | 9 | 35 | 3 | | | |
| *bicolor* | | 237 | 1 | | | | | | 9 | 145 | 82 | | | | | | | | | 9 | 145 | 82 | | | | | |
| *namiyei* | | 21 | 4 | | | | | | | | 4 | 13 | 8 | | | | | | | | | 1 | 15 | 9 | | | |
| *lineatus* | | 11 | 2 | | | | | | | 3 | 9 | 1 | | | | | | | | | 1 | 11 | 1 | | | | |
| *stigmatura* | | 4 | | | | | | | 2 | 2 | | | | | | | | | | 2 | 2 | | | | | | |
| *lividinalis* | | 8 | 2 | | 2 | 7 | | | | | | | | | | 1 | 9 | | | | | | | | | | |
| *yaeyamaensis* | | 202 | 2 | | | | 10 | 179 | 15 | | | | | | | | | 10 | 179 | 15 | | | | | | | |
| *nalolo* | | 124 | | | | | 17 | 94 | 10 | | | | | | | | | 17 | 94 | 10 | | | | | | | |
| *oculus* | | 37 | | | | | 4 | 23 | 19 | 1 | | | | | | | | 4 | 23 | 19 | 1 | | | | | | |
| *opsifrontalis* | 1 | 34 | | | | | 3 | 33 | | | | | | | | | | 4 | 32 | | | | | | | | |
| *prooculus* | | 5 | | | | | 2 | 3 | | | | | | | | | | 2 | 3 | | | | | | | | |
| *bimaculatus* | | 3 | | | | | | 3 | | | | | | | | | | | 3 | | | | | | | | |
| *bandanus* | | 1 | | | | | 1 | | | | | | | | | | | 1 | | | | | | | | | |
| *mandibularis* | | 90 | 1 | | | | 1 | 34 | 49 | 6 | | | | | | | | 1 | 33 | 50 | 6 | | | | | | |

**(For sexual dimorphism and geographic variation see individual species accounts and section on sexual dimorphism.)**

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TABLE 3.—*Frequency distributions for certain characters in species of* Ecsenius

| *Species* | *Pectoral rays* | | | | | *Segmented caudal rays in specimens over 25 mm SL* | | | | *Total caudal rays* | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 13 | 14 | 15 | 16 | 12 | 13 | 14 | 15 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 |
| *midas* | 1 | 11 | | | | | 1 | 7 | 4 | | | | | | | | | 1 | 1 | 7 | 3 |
| *frontalis* | | | 15 | 236 | 27 | | 190 | 6 | | | | 7 | 21 | 116 | 37 | 26 | 2 | | | | |
| *pulcher* | | | 60 | 4 | | | 31 | 2 | | | | | 2 | 7 | 9 | 7 | | | | | |
| *gravieri* | | 1 | 62 | 6 | | | 51 | | | | | | | 5 | 13 | 47 | 5 | 4 | | | |
| *aroni* | | 1 | 39 | 3 | | | 29 | | | | | 1 | 5 | 12 | 13 | 10 | 3 | | | | |
| *bicolor* | 4 | 231 | 4 | | | | 2 | 268 | | | | | 2 | 21 | 29 | 100 | 13 | 4 | | | |
| *namiyei* | 1 | 23 | 1 | | | | 3 | 22 | | | | | 1 | 4 | 8 | 9 | 2 | | | | |
| *lineatus* | | 11 | 1 | | | | 12 | | | | | 1 | – | 9 | 2 | | | | | | |
| *stigmatura* | | 1 | 2 | 1 | | | | 4 | | | | | | 1 | 2 | | | | | | |
| *lividinalis* | | 10 | 1 | | | | 2 | 5 | 1 | 2 | – | 5 | 2 | | | | | | | | |
| *yaeyamaensis* | 4 | 119 | 3 | | | | 113 | 1 | 1 | | | 2 | 8 | 36 | 18 | 13 | 1 | | | | |
| *nalolo* | 2 | 67 | | | | 1 | 84 | 1 | | | | 4 | 4 | 9 | 9 | 24 | 5 | 1 | | | |
| *oculus* | | 44 | 1 | | | 1 | 40 | 4 | | | | | | 2 | 12 | 8 | 11 | 2 | 1 | | |
| *opsifrontalis* | 2 | 39 | | | | | 25 | | | | | | | | 3 | 4 | 3 | | | | |
| *prooculis* | | 5 | | | | | 5 | | | | | | 1 | 2 | 1 | | | | | | |
| *bimaculatus* | 1 | 2 | | | | | 3 | | | | | | 2 | | | | | | | | |
| *bandanus* | | 1 | | | | | 1 | | | | | | | | 1 | | | | | | |
| *mandibularis* | 2 | 65 | | | | | 87 | | | | 6 | 23 | 26 | 11 | | | | | | | |

TABLE 4.—*Frequency distributions for number of dentary incisor teeth (including anterior canines) in species of* Ecsenius

| *Species* | *Number of teeth* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 13 | 14 | 15 | 16 | 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 |
| *midas* | 2 | – | 2 | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *frontalis* | | | | | | | | | | | | | | | 1 | 1 | 1 | 4 | 9 | 22 | 40 | 39 | 51 | 28 | 32 | 9 | 12 | 3 | | | | | | | | | | | | | |
| (see also table 12) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *pulcher* | | | | | | | | | | | | | | | | | | | 2 | 3 | 7 | 9 | 10 | 3 | 8 | 11 | 2 | 1 | | | | | | | | | | | |
| *gravieri* | | | | | | | | | | | | | | | | | | | 2 | – | 3 | 8 | 10 | 11 | 14 | 13 | 3 | 4 | 1 | | | | | | | | | | |
| *aroni* | | | | | | | | | | | | | | | | | | | | | 1 | – | – | 1 | 1 | 2 | 8 | 9 | 8 | 4 | 4 | 1 | | | | | | | |
| *bicolor* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| male | | | | | | | | | | | 1 | 2 | 4 | 13 | 53 | 32 | 26 | 3 | 3 | 1 | | | | | | | | | | | | | | | | | | | |
| female | | | | | | | 1 | – | – | – | – | – | – | 2 | 13 | 22 | 36 | 15 | 14 | 1 | 1 | | | | | | | | | | | | | | | | | | |
| *namiyei* | | | | | | | | | | 1 | 1 | 1 | 1 | 2 | 3 | 5 | 4 | 3 | 3 | 1 | | | | | | | | | | | | | | | | | | | |
| *lineatus* | | | | | | | | | | | | | | | | | | | | 4 | 1 | 2 | 5 | 1 | | | | | | | | | | | | | | | |
| *stigmatura* | | | | | | | | | | | | 1 | 2 | – | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *lividinalis* | | | | | 1 | – | 1 | 1 | 4 | 3 | – | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *yaeyamaensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| male | | | | | | | | | | | | | | | | | | | 1 | 2 | 13 | 10 | 12 | 18 | 12 | 2 | 3 | 1 | | | | | | | | | | | |
| female | | | | | | | | | | | | | | | | | | 1 | – | – | 2 | – | – | 6 | 6 | 14 | 8 | 11 | 6 | 4 | 2 | 1 | | | | | | | |
| *nalolo* | | | | | | | | | | | | | | | | | 1 | 1 | 2 | 4 | 4 | 9 | 15 | 6 | 8 | 10 | 11 | 14 | 16 | 16 | 12 | 13 | 12 | 11 | 7 | 5 | 3 | 2 | |
| (see also table 17) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *oculus* | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | 3 | – | 2 | 3 | 4 | 3 | 3 | 3 | 5 | 4 | 4 | 2 | 3 | 1 | 1 |
| (see also table 18) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *opsifrontalis* | | | | | | | | | | | | | | | | | | 1 | 3 | 6 | 3 | 15 | 9 | – | 3 | | | | | | | | | | | | | | |
| *prooculis* | | | | | | | | | | | | | | | | | | 2 | – | – | 1 | – | – | 1 | | | | | | | | | | | | | | | |
| *bimaculatus* | | | | | | | | | | | | | | | | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| *bandanus* | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| *mandibularis* | | | | | | | | | | | | | | | | | | | | 4 | 4 | 7 | 17 | 18 | 10 | 6 | 2 | 1 | | | | | | | | | | | |

TABLE 5.—*Frequency distributions for depth of dorsal fin notch (to nearest ninth of length of first dorsal ray) and length of last dorsal spine as percent standard length in species of* Ecsenius

| *Species* | *Notch depth* | | | | | | | | | | *Last dorsal spine length (lower class limits)* | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0.0 | 1.0 | 2.0 | 3.0 | 4.0 | 5.0 | 6.0 | 7.0 | 8.0 | 9.0 | 10.0 | 11.0 | 12.0 | 13.0 | 14.0 | 15.0 | 16.0 | 17.0 | 18.0 | 19.0 | 20.0 |
| *midas* | 12 | | | | | | | | | | | | | | | | | 1 | 1 | 5 | 2 | 1 | | | | | | | | | |
| *frontalis* | 277 | – | 1 | | | | | | | | | | | | | | | | | | 1 | 6 | 18 | 25 | 21 | 9 | 15 | 10 | 3 | 3 | 3 |
| *pulcher* | | | | | | 14 | 18 | 5 | 1 | | | | 2 | 17 | 9 | | | | | | | | | | | | | | | | |
| *gravieri* | | | 2 | 2 | 17 | 33 | 7 | | | | | | | 6 | 15 | 20 | 9 | 4 | 1 | | | | | | | | | | | | |
| *aroni* | | | | | | | | 1 | 24 | 1 | | 6 | 26 | 1 | | | | | | | | | | | | | | | | | |
| *bicolor* | | | 2 | 1 | 9 | 42 | 45 | 13 | | | | | 2 | 15 | 37 | 12 | 2 | | | | | | | | | | | | | | |
| *namiyei* | 24 | | | | | | | | | | | | | | | | | | | | | 2 | 1 | 9 | 8 | 3 | | | | | |
| *lineatus* | | | | | | | 3 | 10 | | | | | 7 | 5 | | | | | | | | | | | | | | | | | |
| *stigmatura* | | | | | | | 1 | 3 | | | | | 2 | 2 | | | | | | | | | | | | | | | | | |
| *lividinalis* | | | | 4 | 3 | 1 | | | | | | | | | | | 1 | – | 1 | – | 1 | | | | | | | | | | |
| *yaeyamaensis* | | | | | | | | 7 | 101 | | 2 | 27 | 64 | 7 | | | | | | | | | | | | | | | | | |
| *nalolo* | | | | | | | 3 | 14 | 40 | 19 | 1 | 26 | 42 | 2 | | | | | | | | | | | | | | | | | |
| *oculus* | | | | | | | | 1 | – | 45 | 21 | 13 | – | – | 1 | | | | | | | | | | | | | | | | |
| *opsifrontalis* | | | | | | | | | 4 | 18 | 4 | 16 | 3 | | | | | | | | | | | | | | | | | | |
| *prooculis* | | | | | | | | | | 5 | 1 | 3 | 1 | | | | | | | | | | | | | | | | | | |
| *bimaculatus* | | | | | | | | | 1 | 2 | | 3 | | | | | | | | | | | | | | | | | | | |
| *bandanus* | | | | | | | | | 1 | | | 1 | | | | | | | | | | | | | | | | | | | |
| *mandibularis* | | | | | | | | 7 | 55 | | | 34 | 22 | 4 | | | | | | | | | | | | | | | | | |

TABLE 6.—*Frequency distributions for certain characters in species of* Ecsenius

| *Species* | *Lateral line extends posteriorly to below level of dorsal fin element* | | | | | | | *Pseudobranchial filaments* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| *midas* | 2 | 8 | 2 | | | | | | 1 | – | 1 | 3 | 5 | 1 | 1 |
| *frontalis* | | 3 | 36 | 161 | 25 | 1 | | 5 | 81 | 3 | | | | | |
| *pulcher* | | 4 | 15 | 35 | 4 | 1 | | | 28 | 8 | | | | | |
| *gravieri* | | 3 | 41 | 30 | | | | | 10 | 4 | 1 | | | | |
| *aroni* | | 7 | 13 | 25 | | | | | 7 | 3 | | | | | |
| *bicolor* | | | | 51 | 64 | 46 | 1 | 4 | 163 | 26 | 2 | | | | |
| *namiyei* | | | | 1 | 5 | 16 | 1 | | 3 | 18 | 3 | | | | |
| *lineatus* | | | | 13 | | | | | 10 | 1 | | | | | |
| *stigmatura* | | | 3 | | | | | | 4 | | | | | | |
| *lividinalis* | | 1 | 3 | 5 | 2 | | | 1 | 7 | 1 | | | | | |
| *yaeyamaensis* | | 1 | – | 74 | 34 | 1 | | 2 | 77 | 38 | 1 | | | | |
| *nalolo* | | 1 | 9 | 66 | 27 | 1 | | | 21 | 24 | 3 | | | | |
| *oculus* | | | | 2 | 3 | 37 | 5 | 11 | 17 | 1 | | | | | |
| *opsifrontalis* | | | | | 3 | 24 | | 5 | 16 | | | | | | |
| *prooculis* | | 2 | 3 | | | | | | 5 | | | | | | |
| *bimaculatus* | | | 1 | 3 | | | | | 3 | | | | | | |
| *bandanus* | | 1 | | | | | | | 1 | | | | | | |
| *mandibularis* | | | 1 | 28 | 12 | | | | 45 | 2 | | | | | |

TABLE 7.—*Frequency distributions of third dorsal spine length as percent standard length in species of* Ecsenius

| *Species* | *Percent SL (lower class limits)* | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7.0 | 8.0 | 9.0 | 10.0 | 11.0 | 12.0 | 13.0 | 14.0 | 15.0 | 16.0 | 17.0 | 18.0 | 19.0 | 20.0 | 21.0 | 22.0 |
| *midas* | | | | | | | | | | | | | | | | |
| Males | 2 | 2 | 1 | – | – | 1 | | | | | | | | | | |
| Females | 1 | 1 | 2 | – | 1 | | | | | | | | | | | |
| *frontalis* | | | | | | | | | | | | | | | | |
| Males | | | | 1 | 13 | 9 | 13 | 6 | 5 | 3 | 1 | | | | | |
| Females | | | | 3 | 10 | 9 | 7 | 9 | 3 | 3 | | | | | | |
| *pulcher* | | | | | | | | | | | | | | | | |
| Males | | | | | 7 | 3 | | | | | | | | | | |
| Females | | | | 1 | 6 | 2 | – | – | 1 | | | | | | | |
| *gravieri* | | | | | | | | | | | | | | | | |
| Males | | | | 1 | 5 | 12 | 11 | 4 | | | | | | | | |
| Females | | | | 1 | 8 | 7 | 3 | 2 | | | | | | | | |
| *aroni* | | | | | | | | | | | | | | | | |
| Males | | | | | | 5 | 7 | 1 | | | | | | | | |
| Females | | | | | 2 | 5 | 8 | | | | | | | | | |
| *bicolor* | | | | | | | | | | | | | | | | |
| Males | | | 2 | 14 | 23 | 16 | | | | | | | | | | |
| Females | | | 1 | 8 | 8 | 5 | 1 | | | | | | | | | |
| *namiyei* | | | | | | | | | | | | | | | | |
| Males | | | | 4 | 3 | 5 | 1 | | | | | | | | | |
| Females | | | 1 | – | 3 | 2 | 1 | 1 | | | | | | | | |
| *lineatus* | | | | | | | | | | | | | | | | |
| Males | | | | 1 | – | 5 | 1 | | | | | | | | | |
| Females | | | | | 3 | 2 | | | | | | | | | | |
| *stigmatura* | | | | | | | | | | | | | | | | |
| Females | | | | | | | 1 | 2 | | | | | | | | |
| *lividinalis* | | | | | | | | | | | | | | | | |
| Males | | | | | | | | 1 | – | – | – | 1 | 1 | | | |
| Females | | | | | | | | | 1 | 2 | 1 | 1 | | | | |
| *yaeyamaensis* | | | | | | | | | | | | | | | | |
| Males | | | | 4 | 17 | 25 | 11 | | | | | | | | | |
| Females | 1 | – | 1 | 2 | 10 | 22 | 5 | 2 | | | | | | | | |
| *nalolo* | | | | | | | | | | | | | | | | |
| Males | | | | | 2 | 5 | 10 | 13 | 2 | – | 1 | | | | | |
| Females | | | | | 1 | 4 | 16 | 3 | | | | | | | | |
| *oculus* | | | | | | | | | | | | | | | | |
| Males | | | 1 | – | 3 | 7 | 6 | 2 | | | | | | | | |
| Females | | | 1 | 3 | 3 | 5 | 2 | | | | | | | | | |
| *opsifrontalis* | | | | | | | | | | | | | | | | |
| Males | | | | | | | | 2 | 3 | – | 1 | | | | | |
| Females | | | | | | 2 | 5 | 4 | 1 | | | | | | | |
| *prooculis* | | | | | | | | | | | | | | | | |
| Males | | | | | | | 1 | 3 | | | | | | | | |
| *bimaculatus* | | | | | | | | | | | | | | | | |
| Males | | | | | | | | 1 | 2 | | | | | | | |
| *bandanus* | | | | | | | | | | | | | | | | |
| Males | | | | | | | | | 1 | | | | | | | |
| *mandibularis* | | | | | | | | | | | | | | | | |
| Males | | | | | | | | | | 2 | 2 | 5 | 4 | 8 | 6 | 2 |
| Females | | | | | | | 3 | 4 | 6 | 2 | 1 | | | | | |

TABLE 8.—*Frequency distributions of fifth dorsal ray length as percent standard length in species of* Ecsenius

| *Species* | *Percent SL (lower class limits)* | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10.0 | 11.0 | 12.0 | 13.0 | 14.0 | 15.0 | 16.0 | 17.0 | 18.0 | 19.0 | 20.0 | 21.0 | 22.0 |
| *midas* | | | | | | | | | | | | | |
| Males | | 2 | 1 | 2 | | | | | | | | | |
| Females | 1 | 1 | 1 | | | | | | | | | | |
| *frontalis* | | | | | | | | | | | | | |
| Males | | | 1 | 2 | 4 | 7 | 17 | 10 | 5 | 1 | 1 | – | 1 |
| Females | | | 2 | 4 | 5 | 8 | 9 | 7 | 6 | 1 | – | 2 | |
| *pulcher* | | | | | | | | | | | | | |
| Males | | | 3 | 3 | 3 | 2 | | | | | | | |
| Females | | | 3 | 5 | 1 | – | 1 | | | | | | |
| *gravieri* | | | | | | | | | | | | | |
| Males | 1 | 5 | 1 | 10 | 7 | 5 | – | 1 | | | | | |
| Females | 1 | 1 | 5 | 4 | 3 | 7 | 2 | | | | | | |
| *aroni* | | | | | | | | | | | | | |
| Males | | | | | 2 | 6 | 6 | | | | | | |
| Females | | | | 1 | 2 | 7 | 4 | | | | | | |
| *bicolor* non-Australian | | | | | | | | | | | | | |
| Males | | | | | 6 | 13 | 9 | 7 | 2 | | | | |
| Females | | | | 1 | 2 | 6 | 4 | | | | | | |
| *bicolor* Australian | | | | | | | | | | | | | |
| Males | | 1 | 1 | 3 | 9 | 1 | 4 | | | | | | |
| Females | | 1 | 2 | 4 | 6 | 3 | | | | | | | |
| *namiyei* | | | | | | | | | | | | | |
| Males | | | | 3 | 3 | 5 | 3 | 1 | | | | | |
| Females | | | | 1 | 2 | 2 | 1 | 1 | | | | | |
| *stigmatura* | | | | | | | | | | | | | |
| Males | | | | | | | | | | 1 | | | |
| Females | | | | | 2 | – | 1 | | | | | | |
| *lividinalis* | | | | | | | | | | | | | |
| Males | | | | | | | | | | 2 | – | 1 | |
| Females | | | | | | | | 1 | 2 | 1 | | | |
| *yaeyamaensis* | | | | | | | | | | | | | |
| Males | | | | 1 | 9 | 26 | 14 | 3 | 2 | | | | |
| Females | | | | 6 | 19 | 14 | 1 | | | | | | |
| *nalolo* | | | | | | | | | | | | | |
| Males | | | | | 2 | 1 | 13 | 9 | 3 | | | | |
| Females | | | | 1 | 3 | 10 | 8 | 1 | | | | | |
| *oculus* | | | | | | | | | | | | | |
| Males | | | 3 | 4 | 4 | 4 | 4 | | | | | | |
| Females | | 1 | 3 | 6 | 3 | 1 | | | | | | | |
| *opsifrontalis* | | | | | | | | | | | | | |
| Males | | | | | 1 | 1 | – | 1 | 4 | | | | |
| Females | | | | 2 | 4 | 3 | 1 | 2 | | | | | |
| *prooculis* | | | | | | | | | | | | | |
| Males | | | | | | 2 | 2 | – | – | 1 | | | |
| *bimaculatus* | | | | | | | | | | | | | |
| Males | | | | | | | | 1 | 2 | | | | |
| *bandanus* | | | | | | | | | | | | | |
| Males | | | | | | 1 | | | | | | | |
| *mandibularis* | | | | | | | | | | | | | |
| Males | | | | | | | | 2 | 5 | 5 | 6 | 5 | 6 |
| Females | | | | | | 3 | 4 | 6 | 2 | 1 | | | |

TABLE 9.—*Frequency distributions of length of longest caudal ray as percent standard length in species of* Ecsenius

| *Species* | *Percent SL (lower class limits)* | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 18.0 | 20.0 | 22.0 | 24.0 | 26.0 | 28.0 | 30.0 | 32.0 | 34.0 | 36.0 | 38.0 | 40.0 | 42.0 | 44.0 | 46.0 | 48.0 | 50.0 | 52.0 |
| *midas* | | | | | | | | | | | | | | | | | | |
| Males | | | | 1 | 2 | – | – | 3 | | | | | | | | | | |
| Females | | | | | 2 | 2 | | | | | | | | | | | | |
| *frontalis* | | | | | | | | | | | | | | | | | | |
| Males | | 4 | 13 | 26 | 13 | 12 | 11 | 3 | – | 1 | | | | | | | | |
| Females | | 10 | 49 | 32 | 5 | 2 | | | | | | | | | | | | |
| *pulcher* | | | | | | | | | | | | | | | | | | |
| Males | | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | | | | | | | | | |
| Females | 1 | 4 | 3 | 1 | | | | | | | | | | | | | | |
| *gravieri* | | | | | | | | | | | | | | | | | | |
| Males | | | 2 | – | 4 | 4 | 2 | 7 | 5 | 3 | 4 | 6 | 4 | 4 | – | 1 | | |
| Females | | | | | | 2 | 2 | 4 | 4 | 3 | 2 | 3 | 3 | 2 | | | | |
| *aroni* | | | | | | | | | | | | | | | | | | |
| Males | | | 4 | 9 | 1 | – | 1 | 3 | 2 | – | – | – | 1 | 1 | | | | |
| Females | | 1 | 2 | 8 | 2 | 1 | | | | | | | | | | | | |
| *bicolor* | | | | | | | | | | | | | | | | | | |
| Males | | 1 | 2 | 5 | – | 2 | 4 | 7 | 6 | 10 | 6 | 8 | 2 | 2 | 1 | 3 | 3 | 3 |
| Females | | 4 | 17 | 11 | 6 | 3 | 2 | 3 | – | – | 1 | | | | | | | |
| *namiyei* | | | | | | | | | | | | | | | | | | |
| Males | | | | 4 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | | | | | | | |
| Females | | | 2 | 3 | 4 | – | 1 | | | | | | | | | | | |
| *lineatus* | | | | | | | | | | | | | | | | | | |
| Males | | 3 | 2 | 1 | | | | | | | | | | | | | | |
| Females | 2 | 3 | | | | | | | | | | | | | | | | |
| *stigmatura* | | | | | | | | | | | | | | | | | | |
| Males | | | | | | | | | | 1 | | | | | | | | |
| Females | | | 1 | 1 | 1 | | | | | | | | | | | | | |
| *lividinalis* | | | | | | | | | | | | | | | | | | |
| Males | | | | | 2 | 1 | | | | | | | | | | | | |
| Females | | | | | 4 | | | | | | | | | | | | | |
| *yaeyamaensis* | | | | | | | | | | | | | | | | | | |
| Males | | | 8 | 26 | 4 | 3 | 4 | | | | | | | | | | | |
| Females | | 2 | 29 | 11 | | | | | | | | | | | | | | |
| *nalolo* | | | | | | | | | | | | | | | | | | |
| Males | | | 2 | 14 | 6 | 3 | 2 | 3 | 1 | 2 | | | | | | | | |
| Females | | | 11 | 13 | 2 | | | | | | | | | | | | | |
| *oculus* | | | | | | | | | | | | | | | | | | |
| Males | | 1 | 2 | 5 | 5 | 2 | 1 | 1 | 1 | | | | | | | | | |
| Females | | 1 | 12 | 2 | | | | | | | | | | | | | | |
| *opsifrontalis* | | | | | | | | | | | | | | | | | | |
| Males | | | 1 | 3 | 2 | 2 | | | | | | | | | | | | |
| Females | | | 5 | 5 | | | | | | | | | | | | | | |
| *prooculis* | | | | | | | | | | | | | | | | | | |
| Males | | | | 1 | – | – | – | 1 | – | 2 | | | | | | | | |
| *bimaculatus* | | | | | | | | | | | | | | | | | | |
| Males | | | | | 1 | 1 | – | – | 1 | | | | | | | | | |
| *bandanus* | | | | | | | | | | | | | | | | | | |
| Males | | | | 1 | | | | | | | | | | | | | | |
| *mandibularis* | | | | | | | | | | | | | | | | | | |
| Males | | | | | 2 | 4 | 3 | 6 | 3 | 4 | 1 | 2 | 2 | | | | | |
| Females | | | 8 | 6 | 1 | | | | | | | | | | | | | |

TABLE 10.—*Frequency distributions of nasal cirrus length as percent standard length in species of* Ecsenius

| *Species* | *Percent SL (lower class limits)* | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.0 | 1.0 | 2.0 | 3.0 | 4.0 | 5.0 | 6.0 | 7.0 | 8.0 | 9.0 | 10.0 | 11.0 | 12.0 | 13.0 |
| *midas* | | | | | | | | | | | | | | |
| Males | | | | 1 | 1 | 3 | 1 | | | | | | | |
| Females | | | | 2 | 1 | 1 | 1 | | | | | | | |
| *frontalis* | | | | | | | | | | | | | | |
| Males | | | | 1 | 7 | 15 | 15 | 21 | 10 | 3 | 6 | 2 | 2 | 1 |
| Females | | 1 | 1 | 1 | 2 | 17 | 29 | 14 | 11 | 6 | 6 | 5 | 1 | |
| *pulcher* | | | | | | | | | | | | | | |
| Males | | | | 1 | 4 | 4 | 1 | 1 | | | | | | |
| Females | | | | 3 | 3 | 3 | 2 | | | | | | | |
| *gravieri* | | | | | | | | | | | | | | |
| Males | | 1 | 6 | 7 | 14 | 3 | | | | | | | | |
| Females | | | 7 | 7 | 7 | | | | | | | | | |
| *aroni* | | | | | | | | | | | | | | |
| Males | | 1 | 9 | 4 | | | | | | | | | | |
| Females | | 2 | 10 | 3 | | | | | | | | | | |
| *bicolor* non-Australian | | | | | | | | | | | | | | |
| Males | | | | | 7 | 20 | 9 | 3 | 1 | | | | | |
| Females | | | | 2 | 5 | 9 | 5 | 1 | 1 | | | | | |
| *bicolor* Australian | | | | | | | | | | | | | | |
| Males | | | | | 1 | 2 | 9 | 5 | 1 | | | | | |
| Females | | | | | | 2 | 2 | 5 | 4 | 1 | | | | |
| *namiyei* | | | | | | | | | | | | | | |
| Males | | | | 9 | 6 | | | | | | | | | |
| Females | | | 1 | 4 | 3 | | | | | | | | | |
| *lineatus* | | | | | | | | | | | | | | |
| Males | | | | 1 | 1 | 3 | 1 | | | | | | | |
| Females | | | | | 2 | 4 | | | | | | | | |
| *stigmatura* | | | | | | | | | | | | | | |
| Males | | | | | | | 1 | | | | | | | |
| Females | | | | | 1 | – | 2 | | | | | | | |
| *lividinalis* | | | | | | | | | | | | | | |
| Males | | 1 | 2 | | | | | | | | | | | |
| Females | 1 | – | 1 | 2 | | | | | | | | | | |
| *yaeyamaensis* | | | | | | | | | | | | | | |
| Males | 1 | 27 | 32 | 2 | | | | | | | | | | |
| Females | 1 | 29 | 17 | | | | | | | | | | | |
| *nalolo* | | | | | | | | | | | | | | |
| Males | | 2 | 17 | 17 | 4 | 1 | | | | | | | | |
| Females | | 5 | 24 | 2 | | | | | | | | | | |
| *oculus* | | | | | | | | | | | | | | |
| Males | | | 4 | 4 | 8 | 2 | 1 | | | | | | | |
| Females | | | 8 | 6 | 1 | | | | | | | | | |
| *opsifrontalis* | | | | | | | | | | | | | | |
| Males | | | | 1 | 4 | 2 | | | | | | | | |
| Females | | | 2 | 6 | 3 | 1 | | | | | | | | |
| *prooculis* | | | | | | | | | | | | | | |
| Males | | 5 | | | | | | | | | | | | |
| *bimaculatus* | | | | | | | | | | | | | | |
| Males | | 2 | 1 | | | | | | | | | | | |
| *bandanus* | | | | | | | | | | | | | | |
| Males | | | 1 | | | | | | | | | | | |
| *mandibularis* | | | | | | | | | | | | | | |
| Males | | 3 | 16 | 6 | | | | | | | | | | |
| Females | 3 | 13 | 1 | 1 | | | | | | | | | | |

(In *E. bicolor* and *E. namiyei*, which have two cirri on each nostril, the posterior cirrus was measured.)

TABLE 11.—*Frequency distributions for certain characters of the three color pattern forms of* Ecsenius frontalis

| *Locality and form* | *Dorsal spines* | | | *Dorsal rays* | | | | | *Anal rays* | | | | | *Precaudal vertebrae* | | | *Caudal vertebrae* | | | | *Pectoral rays* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 11 | 12 | 13 | 17 | 18 | 19 | 20 | 21 | 18 | 19 | 20 | 21 | 22 | 10 | 11 | 12 | 23 | 24 | 25 | 26 | 14 | 15 | 16 |
| **Israel** | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | |
| males | 4 | 36 | | | 4 | 18 | 17 | 2 | | 3 | 21 | 14 | | 1 | 37 | | | 4 | 24 | 10 | 2 | 30 | 8 |
| females | 1 | 28 | | | | 15 | 14 | | | | 18 | 10 | 1 | | 29 | | | | 23 | 6 | 2 | 24 | 4 |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | | |
| males | 2 | 26 | | | | 11 | 16 | | | | 14 | 10 | | | 27 | | | | 21 | 6 | | 21 | 7 |
| females | 2 | 25 | 3 | | 3 | 15 | 11 | 1 | | 1 | 19 | 10 | | | 31 | | | 1 | 23 | 6 | | 26 | 5 |
| **Sudan** | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 1 | | | | 1 | | | | | 1 | | | | 1 | | | | 1 | | | 1 | |
| females | | 2 | | | 1 | 1 | | | | | 2 | | | | 2 | | | | | 2 | | 2 | |
| **Ethiopia** | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 40 | | 2 | 22 | 16 | | | 2 | 22 | 16 | | | | 40 | | | 16 | 24 | | 3 | 35 | 2 |
| females | 1 | 45 | | | 36 | 10 | | | 3 | 32 | 11 | | | 1 | 45 | | | 30 | 16 | | | 45 | 1 |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 2 | | | 1 | 1 | | | | 1 | 1 | | | | 2 | | | | 2 | | 1 | 1 | |
| females | | 4 | | | 4 | | | | 1 | 3 | | | | | 4 | | | 3 | 1 | | 1 | 3 | |
| nigrovittatus form | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 25 | | 1 | 18 | 6 | | | 1 | 18 | 5 | | | | 25 | | 1 | 12 | 12 | | 2 | 22 | |
| females | 1 | 24 | 2 | | 19 | 8 | | | 2 | 17 | 7 | | | | 26 | 1 | 1 | 14 | 10 | 2 | 4 | 23 | |
| **Gulf of Aden** | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 2 | | | | 1 | 1 | | | | 2 | | | | 2 | | | | | 2 | | 2 | |
| females | | 1 | | | | 1 | | | | | 1 | | | | 1 | | | | 1 | | | 1 | |

**Data from Egyptian and Gulf of Suez localities are combined with data from Israel; data from all southern Red Sea localities are combined with data from Ethiopia.**

TABLE 12.—*Frequency distributions for certain characters of the three color pattern forms of* Ecsenius frontalis

| *Locality and form* | *Total caudal fin rays (procurrent and principal)* | | | | | | *Dentary incisor teeth (including anterior canines)* | | | | | | | | | | | | | *Lateral line terminates below level of dorsal spine* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 25 | 26 | 27 | 28 | 29 | 30 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 8 | 9 | 10 | 11 | 12 |
| Israel | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 4 | 10 | 1 | 2 | | | | | | | | 2 | 3 | 4 | 6 | 9 | 3 | 5 | 1 | 2 | 6 | 22 | 1 | |
| females | | 1 | 10 | 1 | 2 | | | | | 1 | – | – | – | 2 | 3 | 7 | 6 | 4 | 3 | 2 | | 7 | 18 | 1 | |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | 1 | 1 | 7 | 3 | 2 | | | | | | | | | 3 | 4 | 1 | 8 | | | | | 3 | 7 | 2 | |
| females | | 3 | 10 | 2 | 3 | | | | | | | | 1 | 5 | 8 | 2 | 7 | 2 | 4 | | | 6 | 12 | 1 | |
| Sudan | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | | | 1 | | | | | | | | | 1 | | | | | | | | 1 | | |
| females | | | 1 | 1 | | | | | | | | | 1 | 1 | | | | | | | | 1 | | | |
| Ethiopia | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | 1 | 3 | 25 | 7 | 3 | | 1 | – | 1 | 1 | 3 | 6 | 12 | 6 | 7 | 2 | | | | | | 2 | 27 | 6 | |
| females | 1 | 6 | 23 | 9 | 6 | 1 | | | | 1 | 4 | 8 | 12 | 4 | 10 | 5 | 1 | | | | 1 | 1 | 34 | 8 | |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | | 1 | – | 1 | | | | | | | | 1 | – | 1 | | | | | | | 1 | 1 | | |
| females | 1 | – | 1 | 1 | 1 | | | | | | | | | 2 | 1 | | | | | | | | 4 | | |
| nigrovittatus form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | 1 | – | 12 | 8 | 3 | | | 1 | – | 1 | 1 | 3 | 5 | 7 | 3 | 3 | 1 | | | | | 7 | 17 | 1 | 1 |
| females | 1 | 2 | 13 | 3 | 3 | | | | | | 1 | 4 | 5 | 5 | 9 | 2 | | | | | | 2 | 15 | 5 | |
| Gulf of Aden | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | 1 | 1 | | | | | | | | | | 1 | 1 | | | | | | | | | | 2 | | |
| females | | | 1 | | | | | | | | | | | 1 | | | | | | | | | 1 | | |

Data from Egyptian and Gulf of Suez localities are combined with data from Israel; data from all southern Red Sea localities are combined with data from Ethiopia.

TABLE 13.—*Frequency distributions for measurements of certain fin elements of the three color pattern forms of* Ecsenius frontalis (see also figure 6)

| *Locality and form* | *Third dorsal spine length as percent SL* — *Lower class limits* | | | | | | | | *Last dorsal spine length as percent SL* — *Lower class limits* | | | | | | | | | | | *Fifth dorsal ray length as percent SL* — *Lower class limits* | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10.0 | 11.0 | 12.0 | 13.0 | 14.0 | 15.0 | 16.0 | 17.0 | 10.0 | 11.0 | 12.0 | 13.0 | 14.0 | 15.0 | 16.0 | 17.0 | 18.0 | 19.0 | 20.0 | 12.0 | 13.0 | 14.0 | 15.0 | 16.0 | 17.0 | 18.0 | 19.0 | 20.0 | 21.0 | 22.0 |
| **Israel** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 3 | 1 | 2 | 4 | 4 | 1 | | | | | | 1 | 5 | 5 | 4 | – | 1 | | | | | 1 | 3 | 6 | 3 | 1 | | | | |
| females | | 1 | 1 | 3 | 4 | 2 | – | 1 | | | 2 | 1 | 2 | 3 | 5 | 1 | 1 | | | | | 1 | 2 | 3 | 5 | – | 1 | | | | |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | 2 | 1 | 1 | 2 | | | | | | | | | 3 | 1 | 1 | 1 | | | | | | 3 | 1 | – | 1 | – | 1 |
| females | | 1 | 2 | 1 | 4 | 1 | 3 | | | | | 1 | – | 1 | 5 | 1 | 1 | 1 | 2 | | | 1 | 1 | 1 | 1 | 6 | – | – | 2 | | |
| **Sudan** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 1 | | | | | | | | | | 1 | | | | | | | | | | 1 | | | | | | | | |
| females | 2 | | | | | | | | | 1 | 1 | | | | | | | | | 1 | 1 | | | | | | | | | |
| **Ethiopia** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | 1 | 3 | 3 | 4 | 1 | | | | | | 1 | 7 | 7 | | | | | | | | | | 3 | 8 | 1 | | | | | |
| females | | 3 | 2 | 2 | | | | | 1 | 3 | 5 | 6 | | | | | | | | | | 3 | 1 | 2 | | | | | | |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | | 1 | – | 1 | | | | | | | 1 | – | 1 | | | | | | | | | | | 2 | | | | | | |
| females | 1 | – | 1 | 1 | 1 | | | | | | | 1 | 3 | | | | | | | 1 | – | – | 1 | 2 | | | | | | |
| nigrovittatus form | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| males | 5 | 5 | 4 | | | | | | | 2 | 2 | 4 | 6 | | | | | | | 1 | 2 | 3 | 3 | 4 | – | 1 | | | | |
| females | 5 | 3 | | | | | | | | | 6 | 4 | 1 | | | | | | | | 3 | – | 3 | 1 | – | 1 | | | | |

**Data from Egyptian and Gulf of Suez localities are combined with data from Israel; data from all southern Red Sea localities are combined with data from Ethiopia.**

TABLE 14.—*Frequency distributions for measurements of nasal cirrus and longest caudal ray of the three color pattern forms of* Ecsenius frontalis (see also figures 7–10)

| *Locality and form* | *Nasal cirrus length as percent SL* — *Lower class limits* | | | | | | | | | | | | | *Longest caudal ray length as percent SL* — *Lower class limits* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1.0 | 2.0 | 3.0 | 4.0 | 5.0 | 6.0 | 7.0 | 8.0 | 9.0 | 10.0 | 11.0 | 12.0 | 13.0 | 20.0 | 22.0 | 24.0 | 26.0 | 28.0 | 30.0 | 32.0 | 34.0 | 36.0 |
| Israel | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | 1 | 1 | 6 | 3 | 3 | – | 3 | 2 | 1 | | | 2 | 4 | 4 | 3 | 6 | 1 | | |
| females | | | | | 5 | 5 | 2 | 3 | 2 | 1 | 1 | | | 2 | 10 | 6 | – | 1 | | | | |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | | | 1 | 1 | 1 | 1 | 3 | – | 1 | 1 | | 1 | 5 | 2 | 1 | – | – | – | 1 |
| females | | | | 1 | – | 1 | 1 | 6 | 3 | 4 | 4 | 1 | | 1 | 9 | 7 | 3 | | | | | |
| Sudan | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | |
| males | | | 1 | | | | | | | | | | | | | | | | 1 | | | |
| females | 1 | 1 | | | | | | | | | | | | 1 | 1 | | | | | | | |
| Ethiopia | | | | | | | | | | | | | | | | | | | | | | |
| frontalis form | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | 4 | 7 | 7 | 10 | 4 | 1 | | | | | 3 | 8 | 13 | 6 | 3 | | | | |
| females | | | 1 | 2 | 5 | 14 | 6 | 1 | 1 | 1 | | | | 5 | 15 | 17 | 2 | | | | | |
| albicaudatus form | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | | | | | 1 | 1 | | | | | | | 1 | – | – | 1 | | | |
| females | | | | | | 2 | 1 | 1 | | | | | | 1 | 3 | | | | | | | |
| nigrovittatus form | | | | | | | | | | | | | | | | | | | | | | |
| males | | | | 2 | 7 | 1 | 7 | 1 | | | | | | 1 | 2 | 3 | 1 | 5 | 3 | 2 | | |
| females | | | | | 7 | 7 | 4 | | | | | | | | 11 | 2 | – | 1 | | | | |

Data from Egyptian and Gulf of Suez localities are combined with data from Israel; data from all southern Red Sea localities are combined with data from Ethiopia.

TABLE 15.—*Sexual dimorphism and geographic variation in frequencies of some meristic characters as indicated by specimens of* Ecsenius bicolor *from selected localities*

| *Locality* | *Dorsal rays* | | | | | *Anal rays* | | | | | | *Caudal vertebrae* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15 | 16 | 17 | 18 | Av. | 17 | 18 | 19 | 20 | 21 | Av. | 23 | 24 | 25 | Av. |
| Australia | | | | | | | | | | | | | | | |
| Males | | | 21 | 20 | 17.5 | | | 12 | 28 | 1 | 19.7 | | 7 | 28 | 24.8 |
| Females | | 2 | 31 | 2 | 17.0 | | 1 | 28 | 6 | | 19.1 | | 20 | 13 | 24.4 |
| 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 | | | 8 | | 17.0 | | | 6 | 2 | | 19.2 | | 7 | 1 | 24.1 |
| Females | | 9 | 4 | | 16.3 | | 11 | 2 | | | 18.2 | 6 | 7 | | 23.5 |
| Marshall Islands | | | | | | | | | | | | | | | |
| Males | 1 | 2 | 24 | | 16.8 | 1 | 1 | 22 | 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 | | | 2 | 5 | | 19.7 | | 2 | 4 | 24.7 |
| Females | | | 2 | 1 | 17.3 | | | | 3 | | 20.0 | | 1 | 2 | 24.7 |
| Malacca Straits | | | | | | | | | | | | | | | |
| Males | 1 | 1 | | | 15.5 | | | 2 | | | 19.0 | | 2 | | 24.0 |
| Females | 1 | 2 | | | 15.7 | | 1 | 2 | | | 18.7 | | 3 | | 24.0 |
| Christmas Island (Indian Ocean) | | | | | | | | | | | | | | | |
| Females | | | 5 | | 17.0 | | | 4 | 1 | | 19.2 | | 3 | 1 | 24.2 |

TABLE 16.—*Sexual dimorphism in frequencies of some meristic characters as indicated by specimens of* Ecsenius namiyei *from Taiwan and* Escenius pulcher

| *Species* | *Dorsal rays* | | | | *Anal rays* | | | | | | *Caudal vertebrae* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 18 | 19 | 20 | Av. | 19 | 20 | 21 | 22 | 23 | Av. | 25 | 26 | 27 | 28 | Av. |
| *namiyei* | | | | | | | | | | | | | | | |
| Males | | 1 | 13 | 19.9 | | | 4 | 10 | | 21.7 | 1 | 5 | 8 | | 26.5 |
| Females | | 7 | 1 | 19.1 | | | 8 | | | 21.0 | 1 | 7 | | | 25.9 |
| *pulcher* | | | | | | | | | | | | | | | |
| Males | 3 | 17 | 14 | 19.3 | 1 | – | 11 | 21 | 1 | 21.6 | | 1 | 21 | 5 | 27.1 |
| Females | 7 | 17 | 2 | 18 8 | | 1 | 9 | 14 | | 21.5 | | 3 | 9 | 3 | 27.0 |

TABLE 17.—*Frequency distributions for numbers of dentary incisor teeth (including anterior canines) in* Ecsenius nalolo

| *Locality* | *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 |
| Northern Red Sea and Gulf of Aqaba | | | | | | | | | | | | | | | | | | | | | | |
| Males | | | | | | | | | | | 6 | 8 | 14 | 15 | 13 | 4 | 2 | 2 | | | | |
| Females | | | | | | | | | | | | 3 | 1 | 1 | 4 | 9 | 7 | 9 | 7 | 5 | 3 | 2 |
| Middle Red Sea | | | | | | | | | | | | | | | | | | | | | | |
| Females | | | | | | | 1 | – | – | 1 | | | | | | | | | | | | |
| Southern Red Sea | | | | | | | | | | | | | | | | | | | | | | |
| Males | | | | 1 | – | 2 | 2 | 1 | – | 2 | | | | | | | | | | | | |
| Females | | | | | | | 1 | 1 | | | | | | | | | | | | | | |
| Indian Ocean | | | | | | | | | | | | | | | | | | | | | | |
| Males | 1 | 1 | 2 | 2 | 3 | 6 | 7 | 3 | 4 | 3 | 1 | | | | | | | | | | | |
| Females | | | | 1 | 1 | 1 | 4 | 1 | 4 | 4 | 4 | 3 | 1 | | | | | | | | | |

TABLE 18.—*Variation in meristic characters and number of dentary incisor teeth (including anterior canines) in populations of* Ecsenius oculus

| *Locality* | *Dorsal rays* | | | | *Anal rays* | | | | *Caudal vertebrae* | | | | *Dentary incisor teeth* | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 13 | 14 | 15 | 14 | 15 | 16 | 17 | 21 | 22 | 23 | 24 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 |
| Ryukyus | | | 12 | 2 | | | 11 | 3 | | 4 | 9 | 1 | | | | | | | | 1 | – | – | – | 3 | 2 | 1 | 1 | 2 | 1 | 1 |
| Taiwan | 1 | 3 | 12 | | | 3 | 13 | | 1 | 11 | 3 | | | | | | | | | | 1 | 3 | 3 | 2 | 2 | 3 | 1 | 1 | | |
| Ilot du Sud | | | 1 | | | | 1 | | | | 1 | | | | | | | | | | | | | | 1 | | | | | |
| Thailand | | 3 | 1 | | | 3 | 1 | | 1 | 3 | | | | 1 | – | 1 | – | 1 | – | 1 | | | | | | | | | | |
| Palau | | 1 | | | | 1 | | | | 1 | | | | | | | | 1 | | | | | | | | | | | | |
| Mentawei Island | | 3 | | | | 3 | | | 1 | 2 | | | | | | 1 | – | – | – | 1 | | | | | | | | | | |
| Strait of Malacca | 1 | 1 | | | 1 | 1 | | | 1 | 1 | | | 1 | – | 1 | | | | | | | | | | | | | | | |
| Banda Sea | | 1 | 1 | 1 | | 1 | 2 | | | 1 | 2 | | | | | | | | 1 | – | 2 | | | | | | | | | |
| New Hebrides | | | 4 | | | | 4 | | | | 4 | | | | | 1 | – | – | 2 | 1 | | | | | | | | | | |

Localities arranged from north to south. Dashed line separates localities north of equator from those south of equator.

FIGURES 12–36

383-026 O - 70 - 5

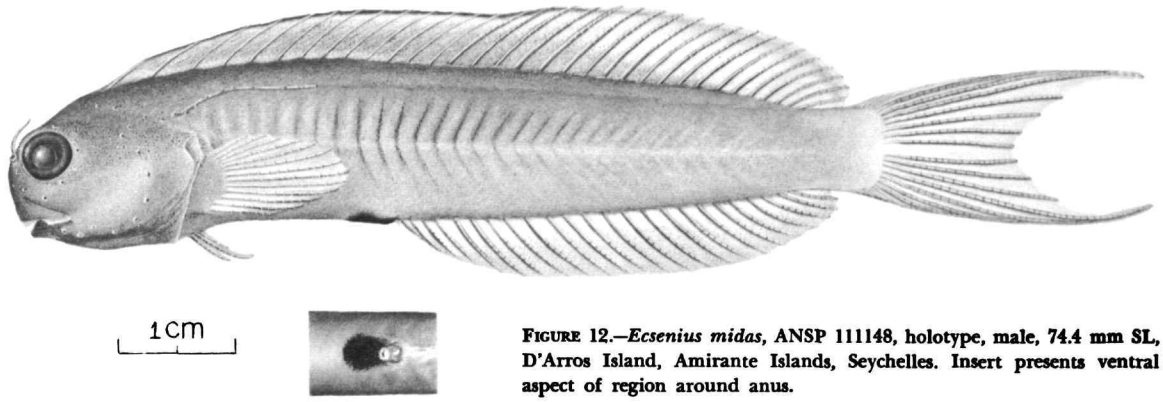



FIGURE 12.—*Ecsenius midas*, ANSP 111148, holotype, male, 74.4 mm SL, D'Arros Island, Amirante Islands, Seychelles. Insert presents ventral aspect of region around anus.

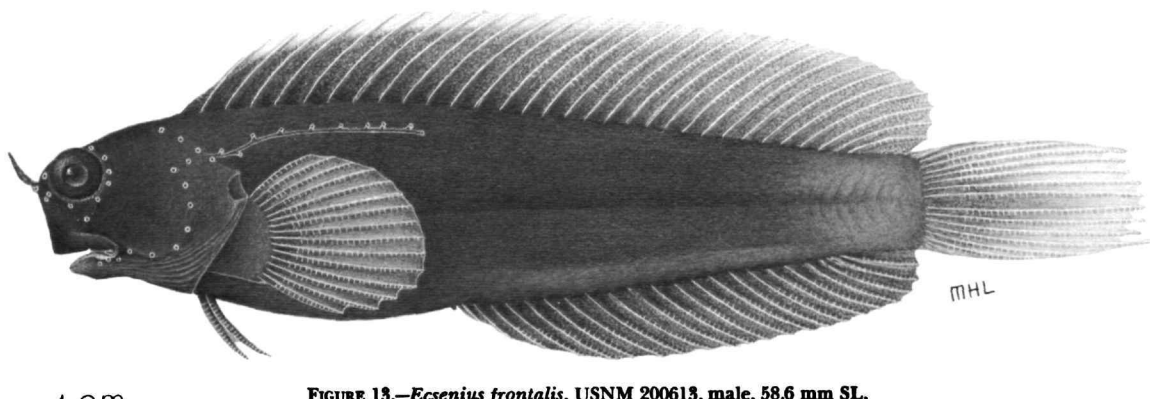



FIGURE 13.—*Ecsenius frontalis*, USNM 200613, male, 58.6 mm SL, frontalis color pattern form, Strait of Jubal, Egypt, Red Sea.

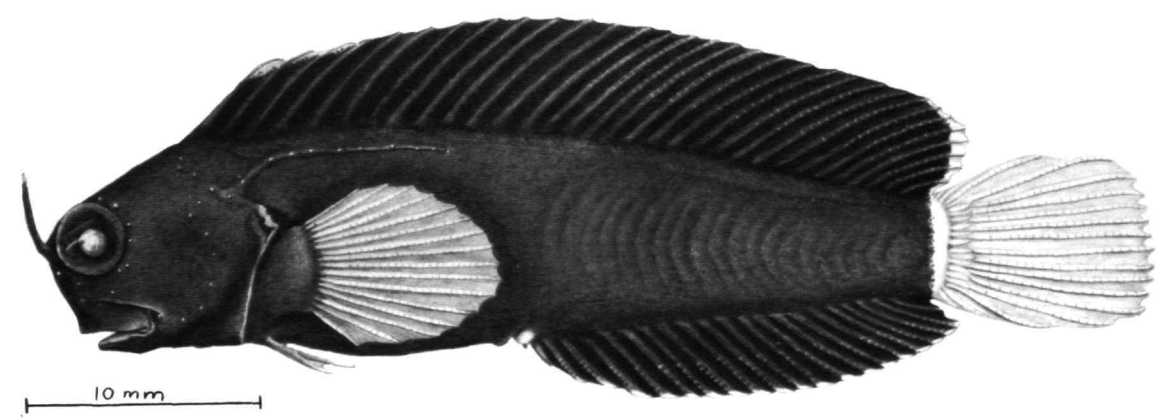



FIGURE 14.—*Ecsenius frontalis*, USNM 204650, female, 37.3 mm SL, albicaudatus color pattern form, El Himeira, Sinai Peninsula, Gulf of Aqaba.

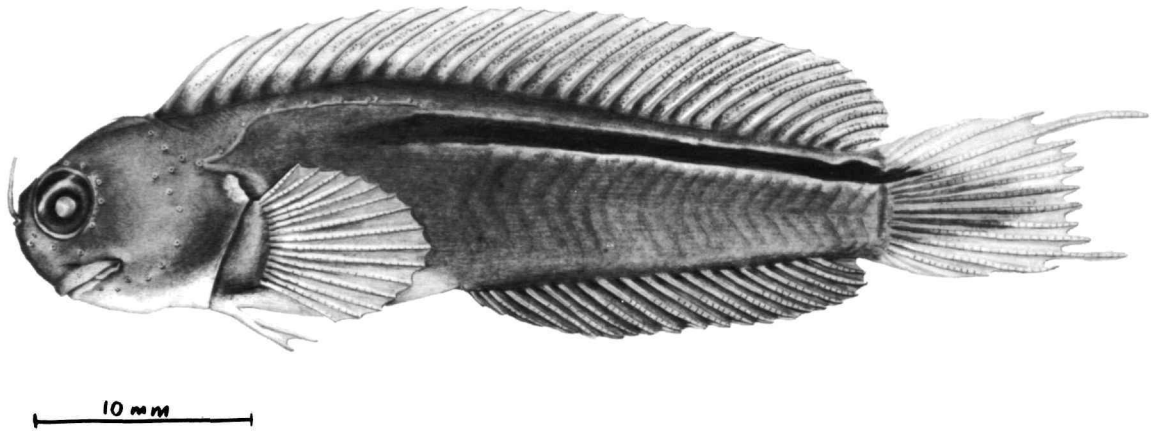



FIGURE 15.—*Ecsenius frontalis*, USNM 204490, male, 38.7 mm SL, nigrovittatus color pattern form, Sheikh el Abu, Ethiopia, Red Sea.

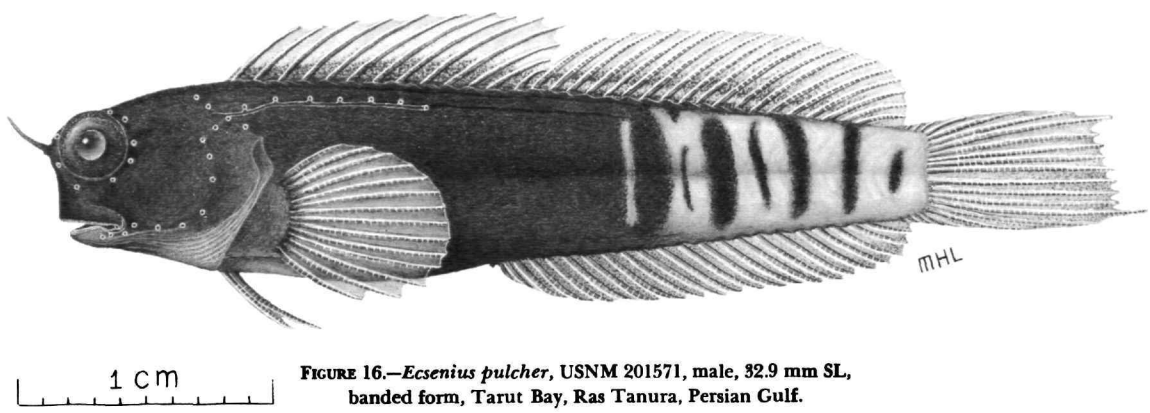



FIGURE 16.—*Ecsenius pulcher*, USNM 201571, male, 32.9 mm SL, banded form, Tarut Bay, Ras Tanura, Persian Gulf.

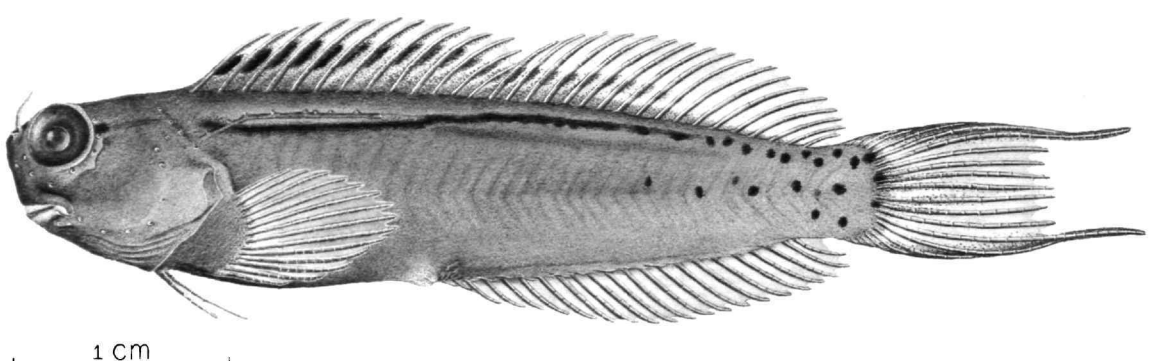



FIGURE 17.—*Ecsenius gravieri*, HUI HUJ-F-4382, male, 38.6 mm SL, pale form, Dahab, Sinai Peninsula, Gulf of Aqaba.

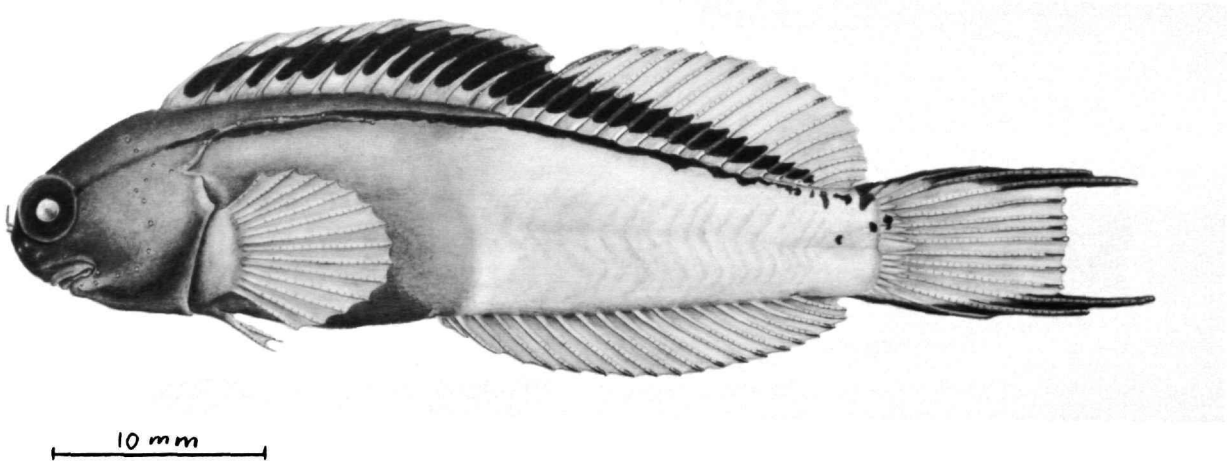



FIGURE 18.—*Ecsenius gravieri*, USNM 204480, female, 40.1 mm SL, dark form, Sheikh el Abu, Ethiopia, Red Sea.

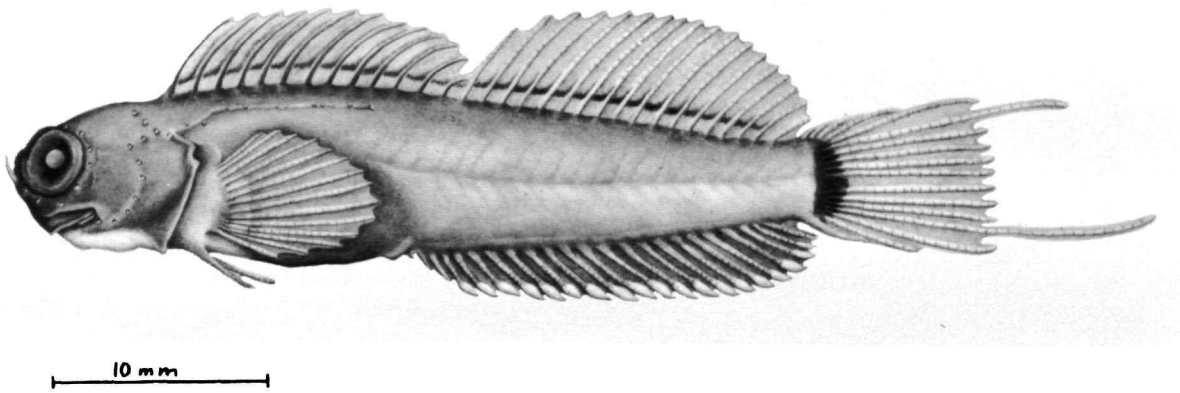



FIGURE 19.—*Ecsenius aroni*, USNM 204468, male, 36.8 mm SL, El Himeira, Sinai Peninsula, Gulf of Aqaba.

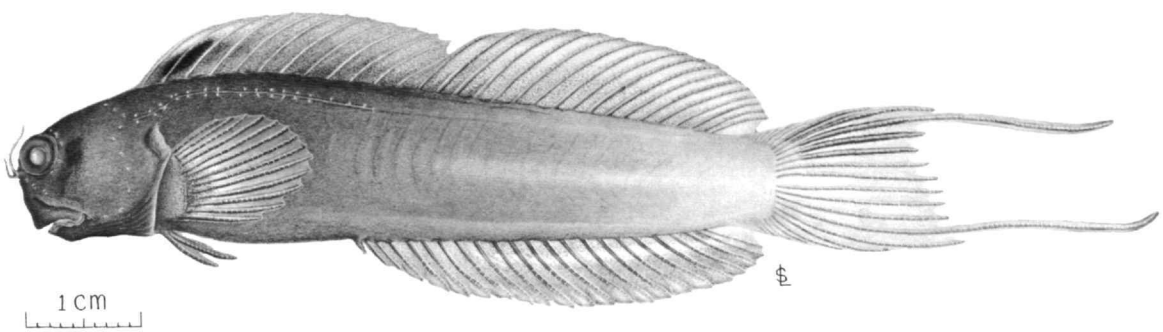
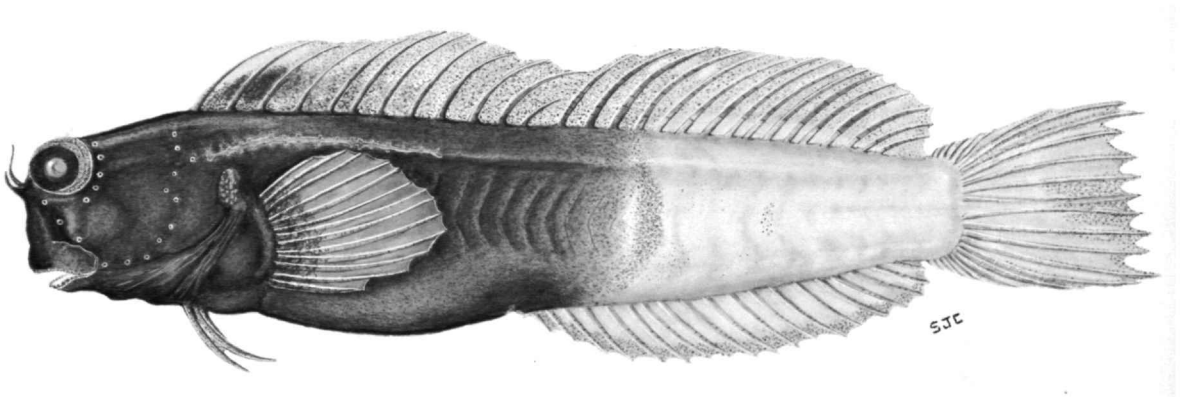



FIGURE 20.—*Ecsenius bicolor*, USNM 201368, male, 66.3 mm SL, One Tree Island, Queensland, Australia.

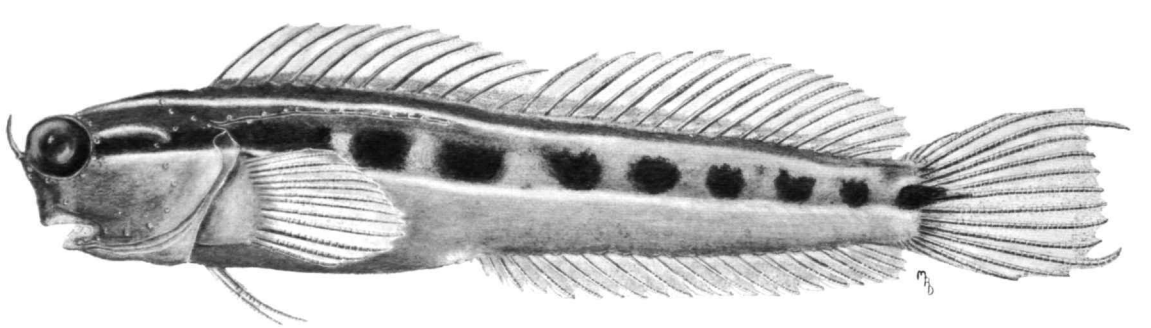



1 cm

FIGURE 21.—*Ecsenius bicolor*, NFIS 9578, female, 49.1 mm SL, Madewaru Island, Fadiffulu Atoll, Maldives.

1 cm

FIGURE 22.—*Ecsenius namiyei*, USNM 203125, female, 63.6 mm SL, north end of Taiwan.



1 cm

FIGURE 23.—*Ecsenius lineatus*, USNM 203129, male, 48.2 mm SL, just SW of Yeh-Liu, north end of Taiwan.

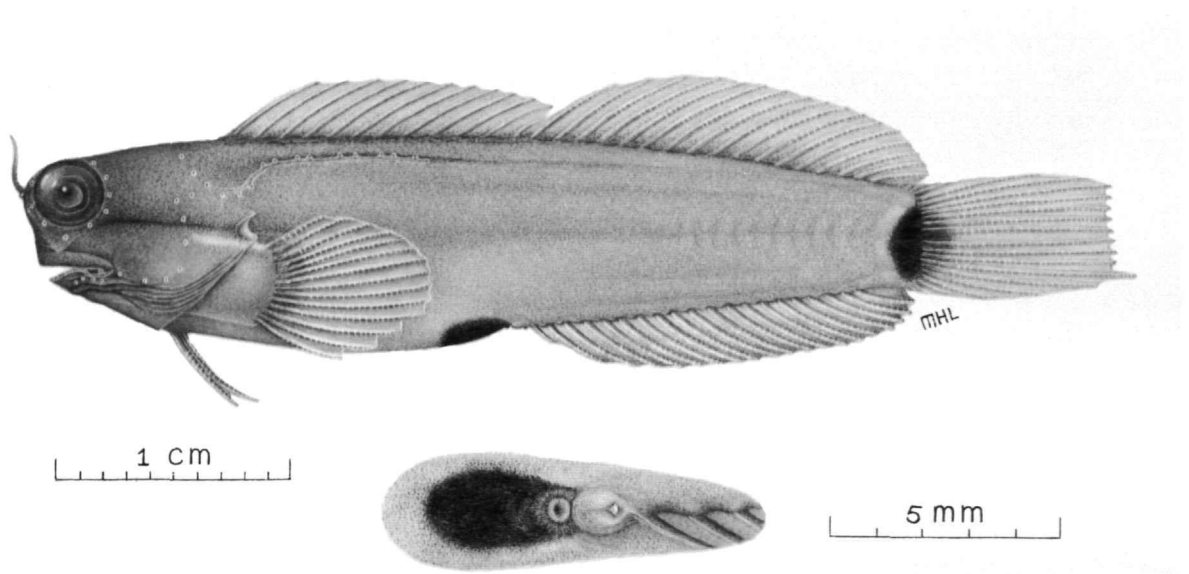



FIGURE 24.—*Ecsenius stigmatura*, USNM 111878, female, 36.6 mm SL, Tomahu Island, Indonesia. Insert presents ventral aspect of region about anus.

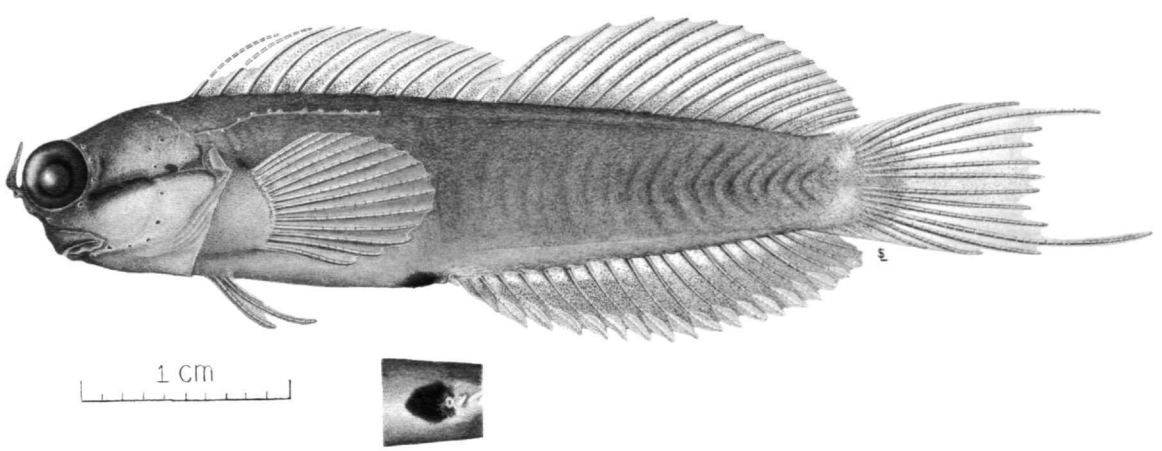



FIGURE 25.—*Ecsenius stigmatura*, USNM 201815, male, 37.7 mm SL, Pulav Gaya, Darvel Bay, Borneo. Insert presents ventral aspect of region about anus.

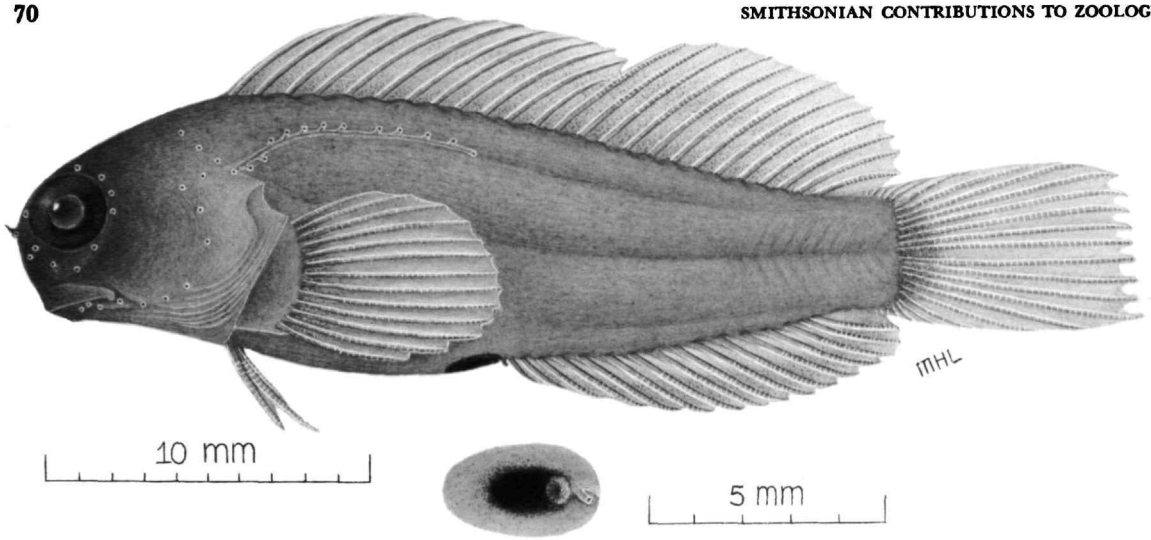



FIGURE 26.—*Ecsenius lividinalis*, USNM 144292, male, 25.8 mm SL, Munda Lagoon, New Georgia, Solomon Islands. Insert presents ventral aspect of region about anus.

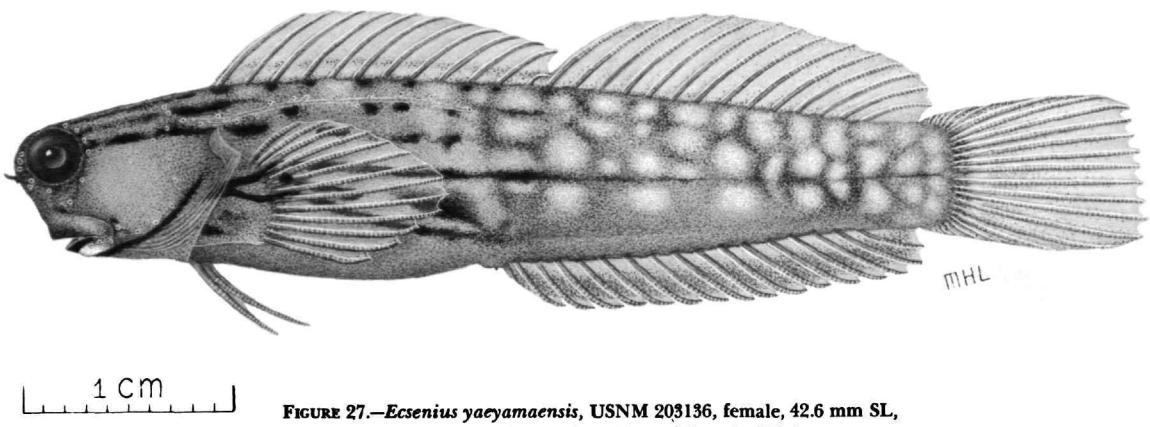



FIGURE 27.—*Ecsenius yaeyamaensis*, USNM 203136, female, 42.6 mm SL, typical color form Ch'uan-fan-shih, south end of Taiwan.

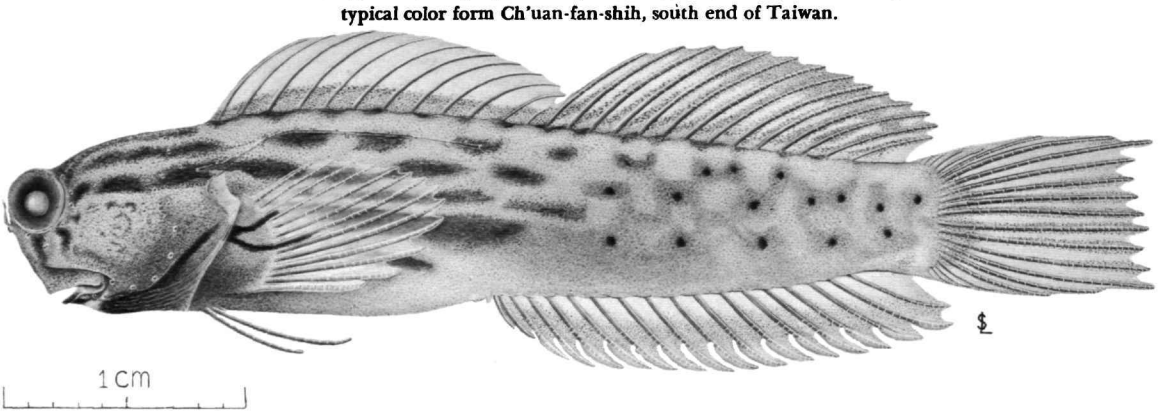



FIGURE 28.—*Ecsenius yaeyamaensis*, USNM 201818, male, 38.1 mm SL, spotted form, One Tree Island, Queensland, Australia.

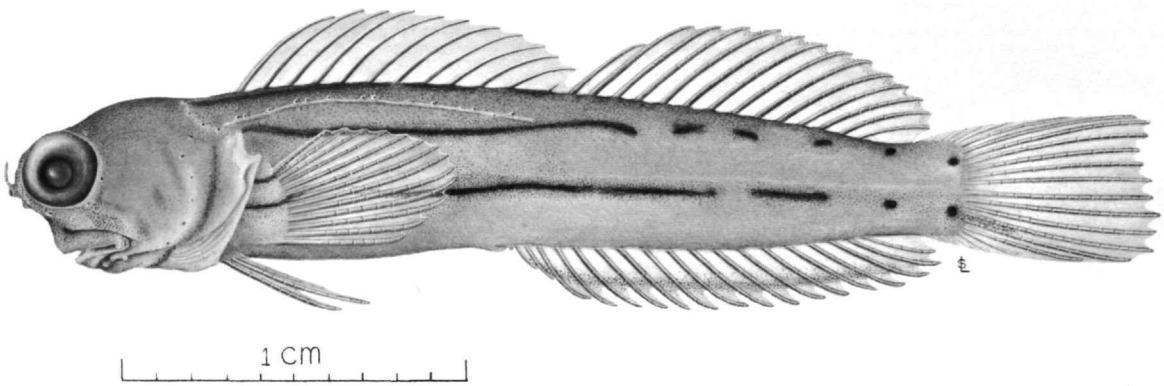



FIGURE 29.—*Ecsenius yaeyamaensis*, USNM 202477, male, 26.6 mm SL, striped form, Banda Sea, Indonesia.

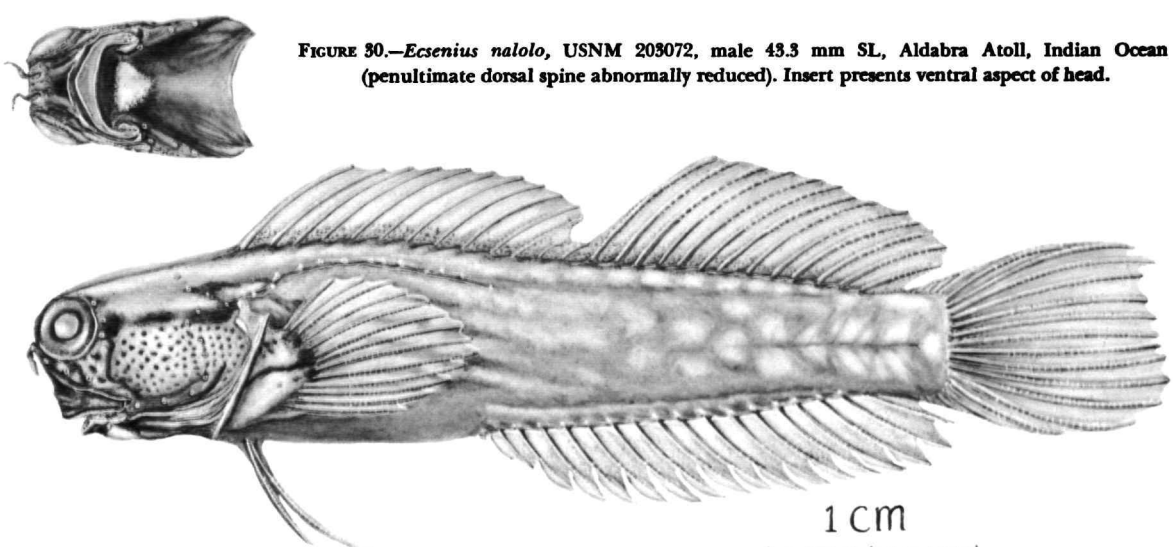



FIGURE 30.—*Ecsenius nalolo*, USNM 203072, male 43.3 mm SL, Aldabra Atoll, Indian Ocean (penultimate dorsal spine abnormally reduced). Insert presents ventral aspect of head.

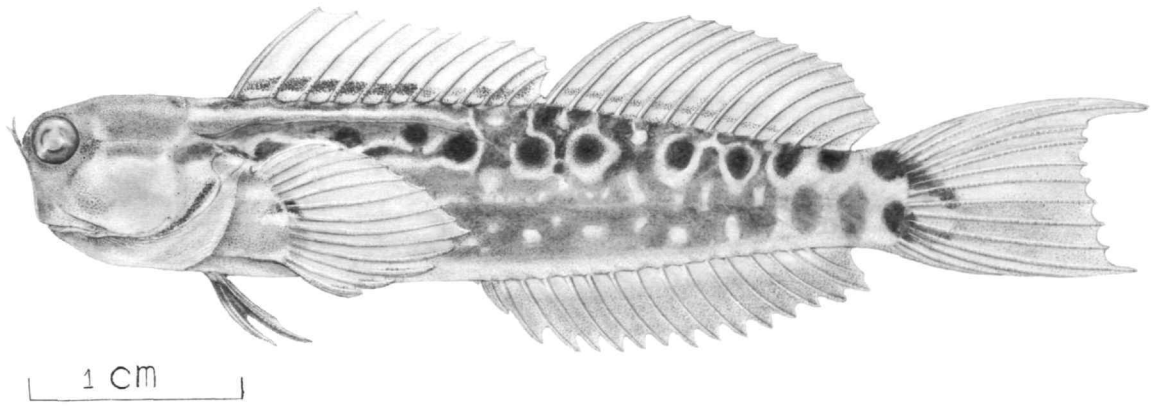



FIGURE 31.—*Ecsenius oculus*, USNM 201522, male, 39.9 mm SL, Pulo Mega, Mentawei Islands, Indonesia (forked nasal cirrus is atypical).

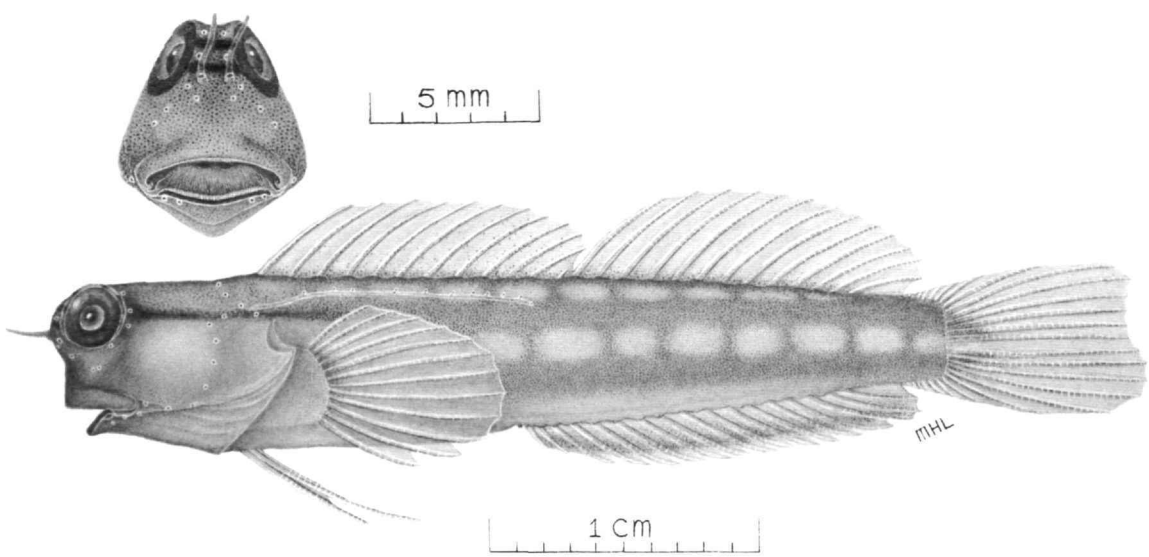



FIGURE 32.—*Ecsenius opsifrontalis*, CAS GVF-468, male, 32.5 mm SL, Kapingamarangi Atoll. Insert presents anterior view of head.

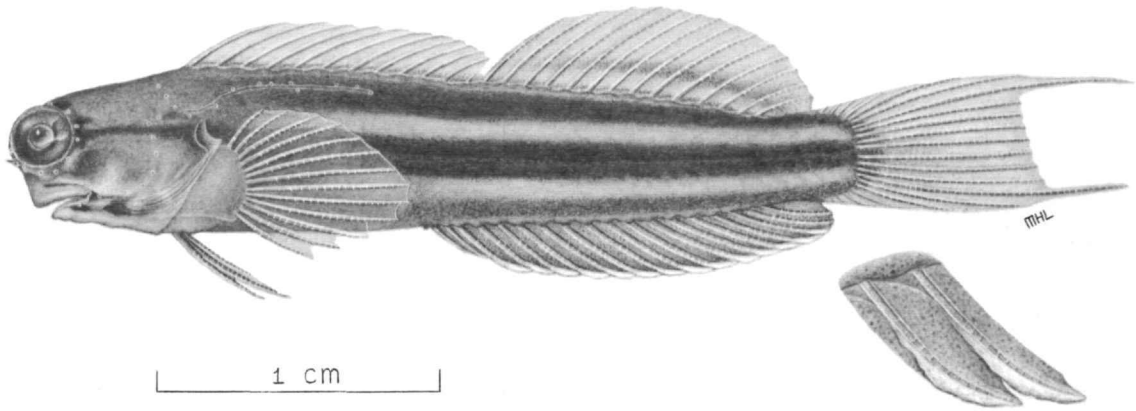
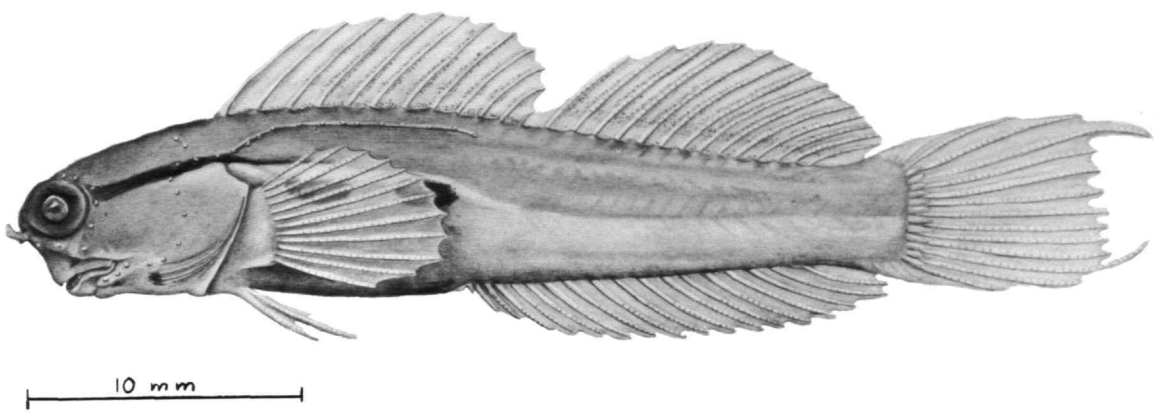



FIGURE 33.—*Ecsenius prooculis*, USNM 201819, male, 30.5 mm SL, Simpson Harbour, Rabaul, New Britain. Insert presents enlarged view of two of the anal rays exhibiting fleshy envelopment of the ray tips, a common characteristic of presumably mature males of most species of *Ecsenius*.



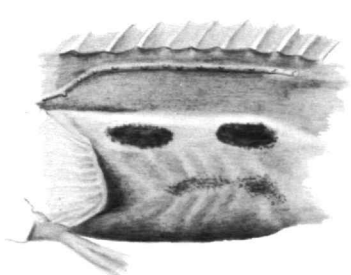



FIGURE 34.—*Ecsenius bimaculatus*, USNM 203922, male, 31.7 mm SL, Pulav Bohidulong, Darvel Bay, Borneo. Insert presents region of body hidden by pectoral fin.

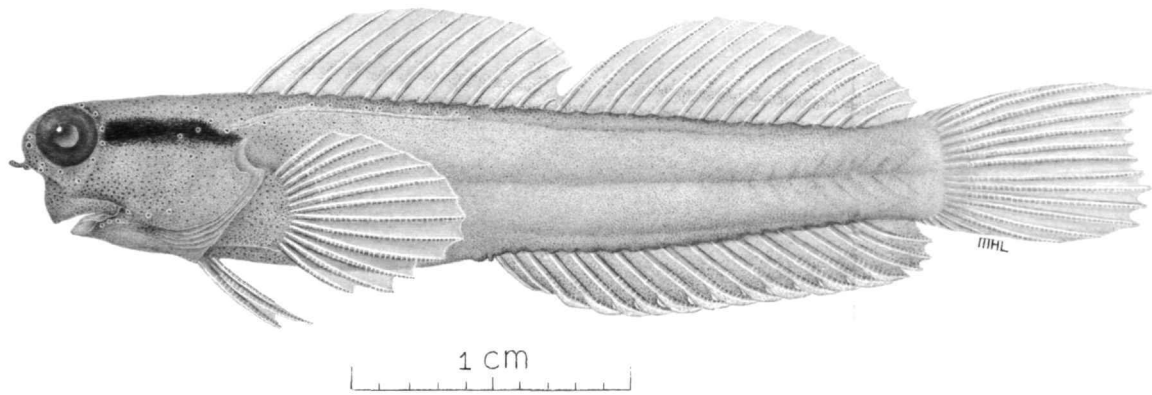



FIGURE 35.—*Ecsenius bandanus*, USNM 195717, holotype, male, 31.4 mm SL, Banda Sea, Indonesia.

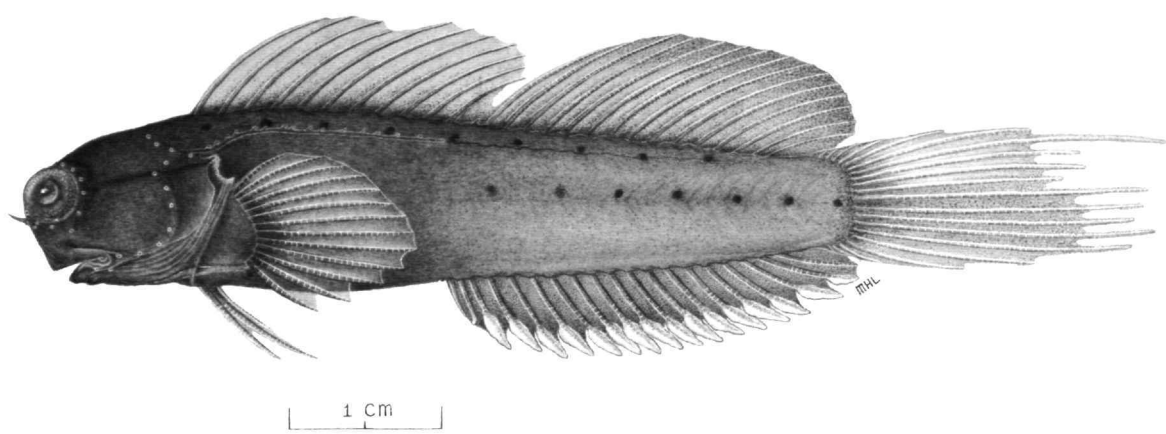



FIGURE 36.—*Ecsenius mandibularis*, USNM 201820, male, 51.1 mm SL, One Tree Island, Queensland, Australia.

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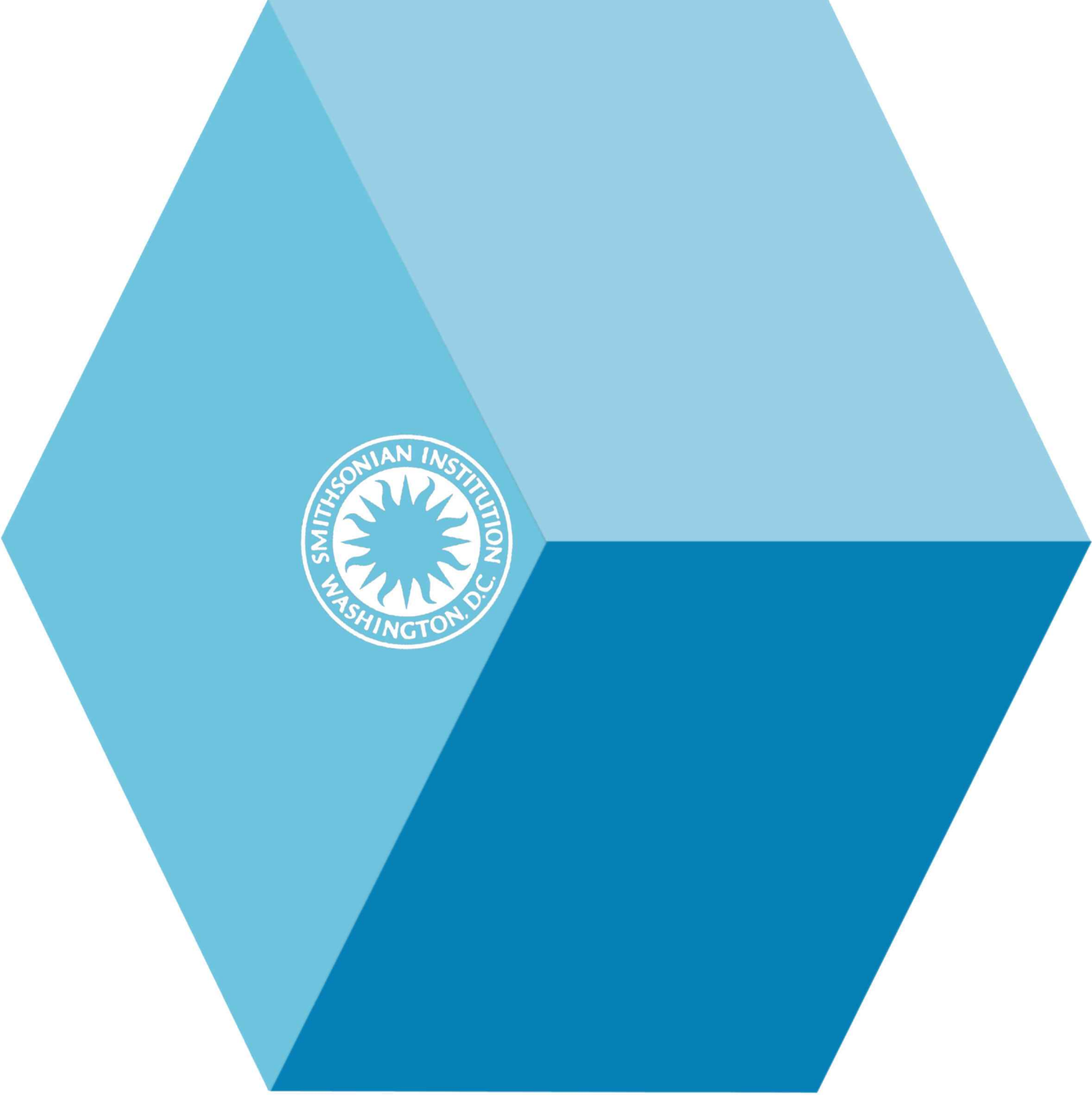
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