

VICTOR G. SPRINGER
and WILLIAM F. SMITH-VANIZ

*Mimetic Relationships
Involving Fishes of
the Family Blenniidae*

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SMITHSONIAN CONTRIBUTIONS TO
ZOOLOGY

NUMBER 112

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SMITHSONIAN INSTITUTION PRESS
CITY OF WASHINGTON

1972

ABSTRACT

Springer, Victor G., and William F. Smith-Vaniz. Mimetic Relationships Involving Fishes of the Family Blenniidae. *Smithsonian Contributions to Zoology*, number 112, 36 pages, 1972.—Nine different mimetic complexes involving 17 species of blenniid fishes and 4 species of nonblenniid fishes are reported. Eight of the complexes include genera of the blenniid tribe Nemophini (*Aspidontus*, two species, in one complex, *Meiacanthus* in six, *Petroscirtes* in two, and *Plagiotremus* in four), and three include a genus of the tribe Salariaiini (*Ecsenius*). Most of the study is devoted to an analysis of one complex involving three blenniid species: *Meiacanthus nigrolineatus*, *Ecsenius gravieri*, and *Plagiotremus townsendi*, from the Red Sea and Gulf of Aqaba. *M. nigrolineatus* and *E. gravieri* are almost identical in appearance. Both feed primarily on small invertebrates. *P. townsendi*, while similar in appearance to the other two species, is not a close mimic. It is a predatory species feeding primarily on the mucus and epidermis of scaled, nonpiscivorous fishes. *M. nigrolineatus* can inflict a noxious bite, which causes most native predators under laboratory conditions to reject it alive and unharmed after ingestion. *E. gravieri* is acceptable prey for native predators under laboratory conditions. *P. townsendi* is rejected as food by some species of native predators under laboratory conditions. The reasons for its rejection are unknown. The mimetic relationships among the three blenniids are involved and include elements of Batesian, Müllerian, and aggressive mimicry (in Wickler's sense: involving three or more species). *E. gravieri* is primarily a Batesian mimic of *M. nigrolineatus*. The two species are common and probably not different in relative abundance. The unusual situation of a close mimic's equaling the abundance of its model is explained in terms of the behavior of the two species, which result in the mimic's being less available than its model to predators, and the highly noxious quality of the model. *P. townsendi* is the least abundant of the three species. Quantitative information on intramimetic associations of the three species shows that they occur within less than one meter of each other a high percentage of the time and tends to support the idea that *P. townsendi* does not distinguish between either of the other two species at a distance. *M. nigrolineatus* and *E. gravieri* exhibit parallel geographic changes in color pattern.

Contribution No. 1405, University of Miami, Rosenstiel School of Marine
and Atmospheric Sciences

*Official publication date is handstamped in a limited number of initial copies and is recorded
in the Institution's annual report, Smithsonian Year.*

UNITED STATES GOVERNMENT PRINTING OFFICE
WASHINGTON : 1972

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402 - Price 50 cents (paper cover)
Stock Number 4700-0173

Contents

	<i>Page</i>
Introduction	1
Mimetic complexes	2
<i>Meiacanthus nigrolineatus</i> , <i>Ecsenius gravieri</i> , and <i>Plagiotremus townsendi</i> ..	2
Distribution	2
Color Pattern	2
Morphology	3
Toxicity of <i>Meiacanthus Bite</i>	4
Habitat and General Behavior	5
Reproduction and Growth	5
Food and Feeding	6
Nonmimetic Blenniid Associates of the Mimetic Complex	6
Species Associations within the Mimetic Complex	7
Relative Abundance	10
Methods and Results	10
Discussion	12
Predation Experiments	14
Introduction	14
Experiments with <i>Pterois volitans</i>	15
Experiments with <i>Synanceichthys</i> , <i>Scorpaenopsis</i> , and <i>Brachirus</i>	17
Experiments with <i>Epinephelus fasciatus</i>	19
Experiments with Other Serranidae	19
Experiments with Holocentridae	20
Experiments with Naive Predators	20
Summary of Feeding Experiments	20
General Discussion	21
Other Cases of Presumed or Known Mimetic Relationships	
Involving Blenniid Fishes	22
<i>Meiacanthus atrodorsalis</i> , <i>Plagiotremus laudandus</i> , and <i>Ecsenius bicolor</i>	22
<i>Meiacanthus smithi</i> and <i>Plagiotremus</i> sp.	23
<i>Meiacanthus lineatus</i> and <i>Petroscirtes</i> sp.	23
<i>Meiacanthus grammistes</i> and <i>Petroscirtes breviceps polyodon</i>	24
<i>Meiacanthus anema</i> and <i>Amblygobius linki</i>	24
<i>Thalassoma lucasanum</i> and <i>Plagiotremus azaleus</i>	24
<i>Anthias squamipinnis</i> and <i>Ecsenius midas</i>	25
<i>Labroides dimidiatus</i> , <i>Aspidontus taeniatus</i> and <i>Aspidontus filamentosus</i>	25
Acknowledgments	26
Literature Cited	27
Plates	30

*Victor G. Springer
and William F. Smith-Vaniz*

Mimetic Relationships Involving Fishes of the Family Blenniidae

Introduction

The purpose of this study is to call attention to the relatively large number of blenniid fishes that are known, or presumed, to be involved in mimetic associations with other fishes. Particular attention is given to a description of the natural history of one such mimetic association comprising three genera and three species of blenniids. We also discuss the results of laboratory experiments that provide information on the basis for the association.

Reports of mimicry among fishes are uncommon. Randall and Randall (1960) summarized the known and probable mimetic associations involving fishes. Since their publication only four reports (two refer to the same species) of additional, possibly mimetic, fish species have appeared (Tyler 1966; Starck 1969; Hobson 1968, 1969), although Springer (1971) mentioned four other species in anticipation of the present paper.

Our study evolved through a combination of circumstances beginning in 1966 when Springer, on a collecting trip to the Great Barrier Reef, confused two species of blenniids, belonging to different genera, as one species. At the same time he also noted that two other pairs of blenniid species, including a third genus, were very similar in appearance. In an osteological study, Springer (1968:50) noted that one of these genera (*Meiacanthus*) was unique among fishes in having glands associated with grooved dentary

canine teeth. He did not elaborate on their use or possible venomosity. In 1969, on a collecting trip to the Red Sea and Gulf of Aqaba, Springer frequently observed three species (in separate genera) of very similar appearing blenniids, two of which showed parallel geographic variations in color pattern. During this time, Smith-Vaniz, who is revising several of the genera we discuss below, found a number of mixed lots of similar appearing blenniids, obtained from the same localities, in museum collections that had supposedly been sorted to species. These observations and the possibility for further study of the Gulf of Aqaba mimetic complex led to the present investigation.

In the interest of stability of nomenclature, we use several new combinations of scientific names in the following discussion. These nomenclatural changes will be explained in Smith-Vaniz's revision of the relevant genera, which is now in an advanced state of preparation.

Each mimetic association is discussed separately, beginning with the association that was the subject of our work in the Gulf of Aqaba in August and September 1970. We also had the opportunity to make observations from 7-9 March 1971.

For the purposes of our study we define mimicry as the similarity in external appearance of two species of animals, at least one of which derives an advantage from the similarity. Batesian mimicry is the resemblance of a palatable (broad sense) species to an unpalatable (broad sense) species. Müllerian mimicry is the resemblance of two unpalatable (broad sense) species to each other. Aggressive mimicry is here used in Wickler's (1968) sense, involving at least three species. One is a predator that resembles a nonaggressive or useful species, such as a cleaner fish. In aggressive

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sive mimicry the similarity functions as a disguise that enables the predator to gain access to a prey (the third species) that confuses it with the nonaggressive or useful species.

Mimetic Complexes

Of the nine mimetic complexes involving blenniids that we report, eight include genera of the tribe Nemophini (*Aspidontus*, two species, in one complex, *Meiacanthus* in six, *Petrosirtes* in two, and *Plagiotremus* in four) and three include a genus of the tribe Salarini (*Ecsenius*). Nonblenniid species are involved in four of the complexes. Fourteen of the 35 species (Smith-Vaniz, ms) of the Nemophini are involved in these complexes, and it seems probable that more of the species will be found involved in mimetic associations when their biology is better known. In listing the species and presenting the illustrations for each mimetic complex, the presumed model is presented first.

Meiacanthus nigrolineatus, *Ecsenius gravieri*, and *Plagiotremus townsendi*

PLATE 2

DISTRIBUTION

Meiacanthus nigrolineatus Smith-Vaniz occurs only in the Red Sea and the tributary gulfs of Suez and Aqaba. *Ecsenius gravieri* (Pellegrin) has the same distribution as *M. nigrolineatus* except that *E. gravieri* is also known from the tributary gulf of Aden, based on a single specimen. *Plagiotremus townsendi* (Regan) is known only from the Gulf of Aqaba (including the southern tip of the Sinai Peninsula, which could be included in the Red Sea) and from a single Persian Gulf specimen. The three species are known to occur together generally only in the Gulf of Aqaba. In the Red Sea *E. gravieri* has always been collected in the same general area where *M. nigrolineatus* has been taken.

Based on field observations and collections made with poison (rotenone, discussion in relative abundance section), the three species are most abundant in the northern part of their range (Gulf of Aqaba). Only 15 specimens of *M. nigrolineatus* and 5 specimens of *E. gravieri* are known from the Red Sea proper (off Ethiopia). None of the three species were seen during several dives in August 1969, in Ethiopian

waters in habitats where the three species would be expected to occur, although a few *E. gravieri* and *M. nigrolineatus* were collected with poison in these habitats.

COLOR PATTERN

All three species are blue to blue gray on the head and anteriorly on the body. Posteriorly the body is pale yellow. The shades of the colors and the relative areas occupied by them are almost identical. *M. nigrolineatus* and *E. gravieri* usually have a black lengthwise stripe on the body, terminating below the dorsal fin, although in life the stripe of *M. nigrolineatus* is frequently unapparent. There are none to several black spots posteriorly on the body of *E. gravieri* and *M. nigrolineatus*; the spots are more abundant and rarely absent in *E. gravieri*. All three species have a black area in the dorsal fin, at least anteriorly. The extent of the black area in the dorsal fin of *E. gravieri* and *M. nigrolineatus* is much greater than it is in *P. townsendi*. *P. townsendi* differs from the other two species in having a horizontal white bar passing around the tip of the snout, and only males have a small orange spot on the anteriormost portion of the dorsal fin. Specimens of *M. nigrolineatus*, approximately 25 mm standard length (SL) or less, have a diffuse dusky blotch on the caudal peduncle and a diffuse dusky stripe anteriorly below the black stripe on the body.

The black markings of *E. gravieri* and *M. nigrolineatus* from the Gulf of Aqaba are much less extensive than they are in specimens of these two species from off Ethiopia. There is little possibility of confusing specimens from these two areas. Whether the change from one form to the other is gradual or abrupt is unknown; there are no collections of either species from the approximately 1,500 km separating the Gulf of Aqaba from the coast of Ethiopia. The single known Gulf of Aden specimen of *E. gravieri* agrees in color pattern with the Ethiopian specimens. These parallel color changes provide strong circumstantial support for a mimetic relationship between *M. nigrolineatus* and *E. gravieri*. Unfortunately, we have no specimens of *P. townsendi* from the southern Red Sea. The single known Persian Gulf specimen does not differ from the Gulf of Aqaba specimens in preserved coloration. If differences in the black marks existed, they would be apparent as, contrary to other colors,

they are not lost in preservation.

It was not possible to distinguish *M. nigrolineatus* from *E. gravieri* in the wild, on the basis of color or morphology, without considerable experience. Certain behavioral characteristics help in recognizing the three species, particularly the fact that *E. gravieri*, in contrast to the other two species, is often seen resting motionless.

The only other organisms in the Gulf of Aqaba and Red Sea that even generally resemble the color pattern of these three blenniids are the young of a labrid, *Gomphosus melanotus* Bleeker. Young *G. melanotus* are navy blue on the dorsal half of the head and body, and pale yellow posteriorly. Below the blue area, the head is white and the body and truncate tail are white to pale yellow. These colors are readily recognized by a human as different from those of the blenniids. The head shape, with a long tubular snout, and the short caudal fin lobes (of at least young individuals) are markedly different from these features in the blenniids.

The blue and yellow color of the blenniids and the leisurely free-swimming nature of *M. nigrolineatus* and *P. townsendi* make these species conspicuous members of the coral reef fish community. Conspicuous color patterns frequently serve an aposematic function. A yellow and black color pattern is one of the most frequently encountered combinations shown by aposematic animals other than fish. The blue and yellow pattern (with hues very close to those of the blenniids) was reported and figured by Darlington (1938) for certain aposematic beetles and their mimics (in contrast, however, the beetles are yellow anteriorly and blue posteriorly), so there is some precedence, although probably coincidental, for according an aposematic function to the color pattern of the blenniids.

MORPHOLOGY

Based on measurements of numerous preserved specimens, *M. nigrolineatus* attains a maximum size of about 65 mm SL, *E. gravieri*, 61 mm SL, and *P. townsendi*, 42 mm SL. Individuals of sizes near the maxima occur commonly in *E. gravieri* and *M. nigrolineatus*, but individuals over 30 mm are uncommon in *P. townsendi*.

The caudal fin lobes of *E. gravieri* and adults of *M. nigrolineatus* are greatly elongated, much more so than in *P. townsendi* and young of *M. nigrolineatus*. The

elongation of the caudal fin lobes of *P. townsendi* and young *M. nigrolineatus* are about the same. This is important if, as we believe, *P. townsendi* is primarily a mimic of *M. nigrolineatus*. Elongated caudal lobes are found in nonmimetic species of *Ecsenius*, and this character in *Ecsenius* is therefore not necessarily the result of mimetic influence on selection (some species of *Meiacanthus* lack elongated caudal fin lobes—in others the character is sexually dimorphic).

In *E. gravieri* the snout region is slanted a little off the vertical, and the eyes are about an eye diameter above the ventral head margin; in *M. nigrolineatus* the snout is obtusely rounded with the eyes slightly less than an eye diameter above the ventral head margin; in *P. townsendi* the snout is more strongly slanted than in *E. gravieri*, and the eyes are only half an eye diameter above the ventral margin of the head.

In *Meiacanthus* the canine teeth of the lower jaw, one on each side, are restricted to the rear of the jaw. Each tooth bears a deep groove along its anterior surface. In at least the base of the groove and in a depression in the dentary bone lies a gland. A diagrammatic illustration of the structure of the dentary and gland, based on a specimen of *Meiacanthus lineatus* from Australia, is given in Figure 1; this structure is the same in all species of *Meiacanthus*. The gland is covered by a sheath of fibrous connective tissue that invades the gland and divides it into several incomplete compartments. Several glands were examined grossly and in serial sections, but no duct was identified; however, pressing slightly in the region of the main body of the gland of the living *Meiacanthus* provokes a ready flow of milky fluid from the groove in the canine tooth. A histological section of a portion of the gland from a specimen of *M. grammistes* from Taiwan is given in Plate 1. Sections stained with hematoxylin and eosin show gland cells densely packed with coarse, darkly staining granules, much the same in general appearance as those illustrated by Halstead (1970, figure 22*b*) for the highly venomous scorpaeonoid fish *Synanceja horrida*. The main differences we noticed between the gland cells of *Meiacanthus* and *Synanceja* are that the cells are much smaller in *Meiacanthus* and the granules are contained in the cells themselves. In *Synanceja* the granules are contained in extracellular compartments of cellular origin (Endean 1961).

The dentition of *Ecsenius* was illustrated and described by Springer (1968, 1971). In most species of

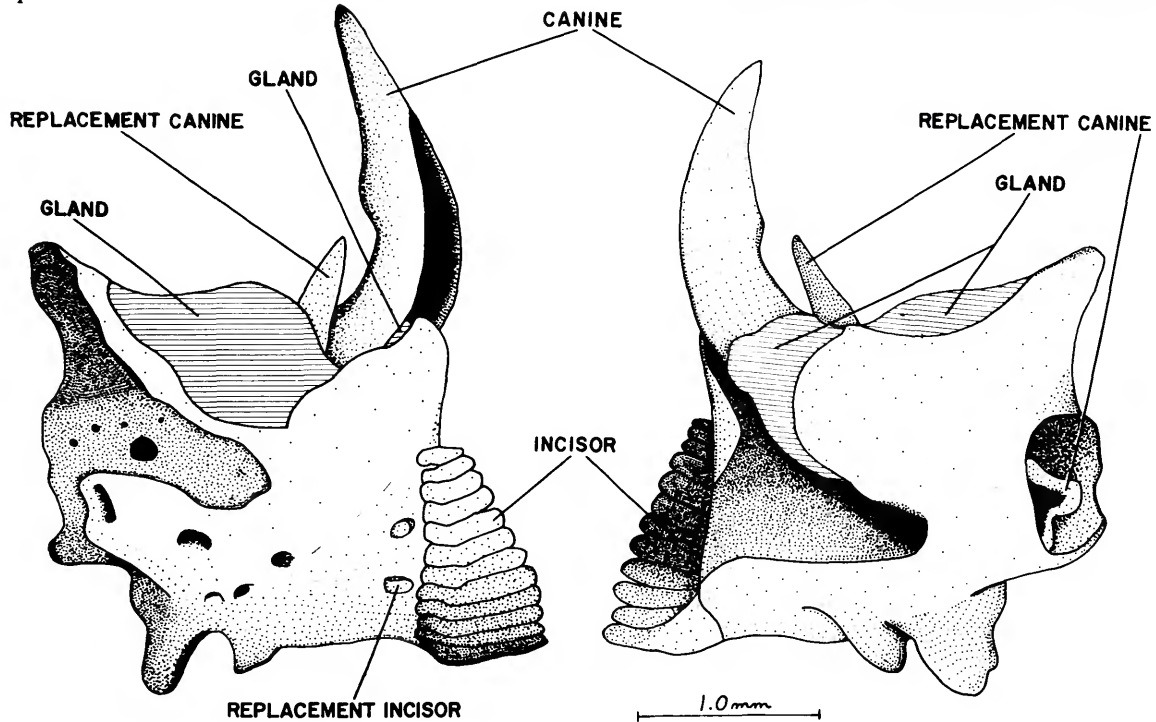


FIGURE 1.—*Meiacanthus lineatus*, lateral and internal views of right dentary bone with position of right dentary gland indicated.

Ecsenius the canines are poorly developed and scarcely distinguishable from the incisoriform teeth. One species, *E. midas* Starck, has well-developed anterior canines and can probably inflict physical damage that the other species cannot.

The dentition of *Plagiotremus* (as *Runula*) was illustrated by Springer (1968). The genus is characterized by a pair of well-developed canines in the rear of the lower jaw. While *Plagiotremus* can puncture human skin with its canines, their use in life has not been determined (see Wickler, 1962, where the genus is referred to as *Aspidontus*).

TOXICITY OF *Meiacanthus* BITE.

To test the possible toxicity of *M. nigrolineatus*, a large specimen, 61.5 mm SL, was induced to bite the fleshy side of Smith-Vaniz's midriff. Little pain was felt, but almost immediately there was an extensive, irregular reddening of a broad area about the wound, approximately 6 cm in diameter. Ten minutes later a pale

welt, 1 cm in diameter, appeared in the area immediately around the wound. For comparison, two pin pricks were made just below the reddened area using alcohol-sterilized pins. The pin pricks were separated by the same distance that separated the tooth marks. No reddened area or welt formed around these punctures. A slight flow of blood issued from both the tooth and pin wounds. Fourteen hours later all redness and swelling around the *Meiacanthus* bite had disappeared, but an area of endurance developed around the tooth marks that persisted for over 24 hours. No such formation developed around the pin-prick wounds. Color transparencies of the *Meiacanthus* and pin-prick wounds are deposited in the files of the Division of Fishes, United States National Museum of Natural History.

As a further test we later induced a specimen of *P. townsendi* to bite Smith-Vaniz on the midriff. This wound was not noticeably different in activity from the one caused by the pin pricks. At this time we caused another *M. nigrolineatus* to bite Smith-Vaniz on the

arm. Reaction to the second *Meiacanthus* bite was the same as the first, except that the area of endurance was not as well developed and did not persist as long.

On the basis of the above evidence it appears that the bite of *M. nigrolineatus* is probably toxic to a human, and that the bite of *P. townsendi* is probably not toxic. These data provide a possible basis for the rejection of active *M. nigrolineatus* after ingestion by our experimental predators, which we observed. The physiological response of various fishes to the bites of *M. nigrolineatus* and *P. townsendi* might prove a worthwhile subject for further study. It would be desirable to determine if the dentary glandular product of *Meiacanthus* is primarily toxic, causes a bad taste, or both.

HABITAT AND GENERAL BEHAVIOR

In the Gulf of Aqaba all three species of the blenniids are found at depths below one meter. *M. nigrolineatus* was twice seen at a depth of 36.6 meters, but was not seen below this depth (deepest point checked, 45.7 meters). *E. gravieri* was twice recorded to a maximum depth of 30.5 meters. We have no sight records for *P. townsendi* greater than 7.6 meters, but the species was taken in poison collections made at depths between 23.0-29.5 meters (Strasburg, et al., 1968, report sight records of Hawaiian species of *Plagiotremus*—as *Runula*—at depths up to 55 meters). The greatest abundance of the three species, between 1.5-10 meters, is correlated with maximum coral reef development in the Gulf of Aqaba. *P. townsendi* occurs almost exclusively around massive coral formations or large isolated coral heads; the other two species commonly occur in rocky areas as well.

M. nigrolineatus is usually seen swimming slowly during the day. The distance it moves appears to be related to size. Small individuals (25-30 mm) often are found swimming or hovering around the pin-cushion sea urchin (*Diadema*), occasionally making short forays two or three meters from the urchin. Young *M. nigrolineatus* are easily caught with dip nets as they tend to remain "close to home." Larger individuals (35-45 mm) may also occur near *Diadema*, but usually are found swimming over an area of several square meters. When threatened by a diver they will range over a more extensive area, perhaps ten meters in radius. The largest individuals range widely over the reef and adjacent sandy and grassy flats between

coral outcrops. They often lead a pursuing diver for at least 50 meters. These large individuals occasionally home on a tube sponge or an empty reef-attached pelecypod shell or worm tube, which they may enter for periods of a few seconds, but leave immediately when threatened (no eggs were found in the sponges, shells or tubes). *M. nigrolineatus* was never seen resting or motionless for more than a few seconds, except when cornered or exhausted. They would then flatten themselves against a rock in a crevice and assume a barred color pattern.

E. gravieri, of all sizes, are often seen around *Diadema* and in tubelike holes in the reef. They spend a large proportion of their time perching motionless on rocks and dead coral. When making brief sporadic changes in position, they frequently swim, usually for a distance less than half a meter. Each individual appears to be highly restricted to a particular spot on the reef. On occasion (see discussion under association surveys) *E. gravieri* will swim slowly and continuously for several minutes and forage over an area several meters in radius from its perch, but always returns to, or near, its original perching spot. *E. gravieri* darts into a hole when threatened.

P. townsendi was usually observed swimming slowly or hovering. When active, it usually remains farther off the bottom than the other two species, which rarely are found more than a half meter, if that much, above the substrate. Rarely, *P. townsendi* may enter a vertical tube, or hole, but does not remain there more than a few minutes. It is the easiest of the three blenniids to capture, and initially shows no fear of divers. If *P. townsendi* has not been threatened with a net, it will frequently enter the net. *P. townsendi* is attracted to divers, whom it occasionally attempts to bite.

In order to observe their night behavior, one night dive was made in an area where the three blenniids were common. The only blenniid we saw was a single *E. gravieri* in a hole. Hobson (1965) reported that *Plagiotremus azaleus* (Jordan and Bollman), which has similar habits to those of *P. townsendi*, enters a hole at night and remains there until morning.

REPRODUCTION AND GROWTH

Nothing is known of the breeding behavior or nest sites of the three blenniids; however, it was appar-

ent that when we began our observations in early August 1970, breeding had essentially ceased for both *E. gravieri* and *M. nigrolineatus*. This conclusion rests on our observation that the majority of these blenniids were about 20-25 mm standard length; relatively few smaller or larger individuals were seen. By the end of the five-week study the dominant size group for *E. gravieri* and *M. nigrolineatus* was 30-35 mm, with smaller individuals almost nonexistent. During early March 1971, all the *M. nigrolineatus* seen were 45 mm or larger. The *E. gravieri* were 35 mm or larger except for one individual estimated to be 20-25 mm. These observations indicate that both species are essentially annuals and have a similar spawning period. Growth rate and size composition of their populations are probably also similar¹. Such conditions might serve to enforce the strength of a mimetic relationship.

We noted no obvious change in the size groups of *P. townsendi* during the course of our study, but the small size of this species suggests that it too is an annual species.

Rosenblatt (1963) noted that in short-lived species (annuals for instance), the entire gene pool is reshuffled every year, and that a new genotype can be selected for with great rapidity. For this reason it is probable that the close similarity of the proposed mimic and model, *E. gravieri* and *M. nigrolineatus*, developed rapidly and is subjected to strong annual reinforcement.

FOOD AND FEEDING

M. nigrolineatus feeds primarily on annelids and other small invertebrates that it obtains from the sand

¹ It would not be surprising if spawning in these small species were suspended in the middle of the summer. Springer and McErlean (1961) demonstrated that *Gobiosoma robustum* Ginsburg (Gobiidae), a small species (maximum size 48 mm SL), was essentially an annual species that ceased spawning in July and August (the middle months between its spawning periods) in the Tampa Bay Area (latitude ca 27°45'N) of Florida, and this phenomenon could be expected for small fishes in the Gulf of Aqaba in the vicinity of Eilat (latitude about 29°33'N). An explanation of this phenomenon is provided by Harrington's (1959) demonstration that certain combinations of light and temperature are necessary for egg maturation in the low latitude fish *Fundulus confluentus* Goode and Bean. A double spawning period in spring and fall (or at least reduced spawning in midsummer) results because proper light and temperatures exist only during these two seasons.

around the base of reefs. Occasionally it appears to feed along the surface of rocks and dead coral. *E. gravieri* feeds primarily on ostracods, foraminiferans, and algae that it obtains from the surface of rocks and dead coral. Occasionally it appears to obtain food from sandy areas. *P. townsendi* feeds primarily on the mucus and epidermis of living fishes. Our examination of a large number of stomachs from individuals of ten species of *Plagiotremus* indicates that mucus and epidermis are the primary sources of food for all, because all but the empty stomachs contained fish scales.

We saw attacks by *P. townsendi* on fishes of the families Acanthuridae, Apogonidae, Chaetodontidae, Holocentridae, Lethrinidae, Mullidae, Pomacentridae, Pseudochromidae (in aquaria only), Scaridae, and Serranidae (only *Anthias squamipinnis* Peters). These fishes are scaled and, with the possible exception of some apogonids and holocentrids, nonpiscivorous. Prey fishes that were attacked (typically from behind) by *P. townsendi* usually darted away, but an apogonid (*Chilodipterus* sp.) and some pomacentrids were seen to chase the *P. townsendi* that bit them. We never saw *P. townsendi* attack known piscivores of the families Lutjanidae, Paraperidae, Scorpaenidae, Serranidae, Synodontidae, etc., which abound on the reef—nor did it attack fishes of the family Labridae, which are generally nonpiscivores and very abundant on the reef.

NONMIMETIC BLENNIID ASSOCIATES OF THE MIMETIC COMPLEX

There are 35-40 species of blenniids known from the Red Sea and its tributary gulfs. Among these are five species of *Ecsenius*, three species of *Plagiotremus*, and a single *Meiacanthus*. All nine occur together, but they exhibit strong intrageneric differences in color pattern, morphology, and, in *Ecsenius*, behavior.

None of the four other species of *Ecsenius* resemble *E. gravieri* in color pattern or degree of elongation of the caudal fin lobes. *E. aroni* Springer, an orange brown species with bluish overtones, is common only at depths where *E. gravieri* begins to decrease in abundance or is absent. *E. aroni* is relatively shy and is rarely seen out from under cover. *E. nalolo* Smith, a common mottled brown species, is never seen free-swimming or away from cover. *E. frontalis* (Ehrenberg) is a common species that has three color-pattern forms, two in the northern Red Sea and gulfs of Aqaba and Suez and three in the southern Red Sea (Springer

1971). Although *E. frontalis* is no more secretive than *E. gravieri*, it was never seen swimming or away from the reef. The commonest color pattern form of *E. frontalis* throughout its range is brown anteriorly, grading into orange posteriorly. The second commonest form in the northern part of the range (rarest in the southern part of its range) is uniformly black with an immaculate caudal fin. The third form, found only in the southern part of the range, is olive, orange, and brown with a lengthwise black stripe on the body. *E. midas* is a rare, orange yellow, free-swimming species that Starck (1969) reported as a mimic of the free-swimming serranid *Anthias squamipinnis*.

All three species of *Plagiotremus* occur in the same habitat and behave in much the same way. *P. tapeinosoma* (Bleeker), dark brown and white striped with yellow areas under the head and on the caudal fin, is more elongate than *P. townsendi* and attains over twice the size of that species. *P. rhinorhynchus*, black and blue striped, also attains a much larger size than *P. townsendi*. *P. tapeinosoma* and *P. rhinorhynchus* are much less common than *P. townsendi* in the Gulf of Aqaba. The three *Plagiotremus* species and *Ecsenius midas* are the only Red Sea species congeneric with members of the mimetic complex that occur outside the Red Sea, and, except for *P. townsendi*, their distributions extend well into the Pacific Ocean (*Ecsenius frontalis* has been recorded from the tributary Gulf of Aden).

SPECIES ASSOCIATIONS WITHIN THE MIMETIC COMPLEX

Mimetic theory generally requires that models and their mimics (not necessarily including nonmimetic forms of mimetic species) be found in the same area. Wallace (1870) first stated this condition: that the animals that resemble each other inhabit the same area and occur together on the same spot (although currently it is recognized that the occurrences need not be nearly so close). Carpenter and Ford (1933) proposed that anything that increases the conspicuousness of aposematic species (in their case, insects) would aid in the recognition (and avoidance) of these species by potential predators. They further stated that such species will often associate together "quite apart from the fact that they may be feeding on the same plant." This conclusion implies either that the aposematic forms have been conditioned to associate or that there has

been genetic selection for behavioral patterns (feeding and reproductive, for instance) that compel them to associate. It seems to us that mimics would derive similar advantages from closely associating with their aposematic models, although Carpenter and Ford did not mention this possibility.

The nature of the spatial associations of a mimic and its models are given only in very general terms in most mimetic accounts. We know of no published attempts to quantify the spatial associations of mimics with models, which as noted, must play a large part in the success of mimetic relationships.

During our dives we frequently encountered individuals of *M. nigrolineatus* closely juxtaposed to individuals of *E. gravieri*. We also observed that *P. townsendi* was usually seen in close association with one or both of these two species. To more firmly establish the basis for our impressions, we made a series of association surveys in different areas that covered various shallow reefs in the vicinity of the northern Gulf of Aqaba (Table 1). In each survey area, except area A (where only one transect was made), we each swam a transect of a different portion of the area (stations A, B, C, D were made by one of us and stations B', C', D' were made by the other). When one of the three species of blenniids was noted, we paused to observe it for up to five minutes. During this period the presence and number of each of the three species that occurred within an estimated one meter distance of each other were recorded (although an arbitrary one-meter distance was selected, the individuals of these species almost invariably approached within a very few millimeters or centimeters of each other). When an observation station was completed we swam for a sufficient distance to avoid overlap in observations of individual blenniids at our next station.

The results of the surveys (Table 1) can be summarized by the following numbered statements (see also Table 2, where the percentages are based, however, on the total number of stations in each survey area):

1. When *M. nigrolineatus* was present, at least one of the other two blenniids was also present 45.0-85.7 (av 60.7) percent of the time.
2. When *M. nigrolineatus* was present, *E. gravieri* was also present 40.0-71.4 (av 50.3) percent of the time.
3. When *M. nigrolineatus* was present, *P. townsendi* was also present 5.0-41.7 (av 23.2) percent of the time.

TABLE 1.—Seven surveys (A,B,B',C,C',D,D') in the northern Gulf of Aqaba, 15-18 August 1970, for purpose of determining frequency of associations of *Meiacanthus nigrolineatus* (M), *Ecsenius gravieri* (E) and *Plagiotremus townsendi* (P).

		SURVEY											
A		B		B'		C		C'		D		D'	
Station No.	Species M E P	Station No.	Species M E P	Station No.	Species M E P	Station No.	Species M E P	Station No.	Species M E P	Station No.	Species M E P	Station No.	Species M E P
1	1 - -	1	- 1 -	1	2 1 1	1	1 1 -	1	1 1 1	1	1 1 -	1	1 1 -
2	- 2 -	2	- 1 -	2	1 1 1	2	1 1 -	2	1 - -	2	1 1 -	2	- - 1
3	1 1 -	3	- - 1	3	1 2 1	3	1 - -	3	- 1 -	3	- - 1	3	- 1 1
4	1 1 -	4	- 1 -	4	1 1 -	4	2 1 -	4	3 1 -	4	1 1 -	4	- - 1
5	2 1 -	5	2 - -	5	1 2 -	5	1 - -	5	1 - -	5	- 1 -	5	1 2 -
6	- 1 -	6	- 1 -	6	1 1 -	6	1 1 -	6	- 1 -	6	- - 1	6	1 1 -
7	1 1 -	7	1 - 1	7	1 1 -	7	1 - 1	7	- 1 -	7	- 1 1	7	1 1 -
8	1 1 -	8	- - 1	8	1 - 1	8	- 1 1	8	- 1 1	8	1 - -	8	1 1 -
9	- 1 -	9	1 1 1	9	1 1 2	9	- 1 -	9	2 - -	9	1 1 -	9	1 1 -
10	1 - -	10	1 1 1	10	1 - 1	10	1 1 -	10	1 1 -	10	- 1 -	10	1 1 1
11	1 - -	11	1 2 -	11	2 2 -	11	- 1 -	11	- 1 -	11	1 - 1	11	2 - -
12	2 - -	12	1 - -	12	1 2 -	12	1 1 -	12	1 - -	12	1 - -	12	2 - -
13	1 - -	13	- 3 -	13	1 1 1	13	- 1 1	13	2 - -	13	1 - -	13	1 - 1
14	1 - -	14	1 1 -	14	1 - -	14	1 1 -	14	1 1 -	14	1 1 -	14	1 1 -
15	1 - -	15	1 1 -	15	2 - -	15	1 - 1	15	1 1 -	15	- 1 1	15	1 - 1
16	- 1 -	16	1 - -	16	1 1 -	16	1 - -	16	1 1 -	16	1 1 -	16	1 1 1
17	1 - -	17	1 1 1	17	1 - -	17	- 1 -	17	2 - -	17	1 1 -	17	<u>1 1 -</u>
18	2 1 -	18	- 2 -	18	- 1 -	18	1 - -	18	2 - -	18	- - 1	TOTAL	16 12 7
19	- 1 -	19	1 1 1	19	1 1 -	19	- 1 -	19	<u>1 - 1</u>	19	1 1 1		
20	- 1 1	20	1 1 1	20	1 - 1	20	- 1 -	TOTAL	20 11 3	20	- 1 1		
21	2 - 2	21	1 - -	21	1 - 1	21	1 - -			21	1 - 1		
22	1 - -	22	2 1 -	22	1 1 1	22	2 - -			22	1 - -		
23	1 1 -	23	<u>1 1 -</u>	23	1 1 -	23	1 1 -			23	- - 1		
24	1 - -	TOTAL	17 20 8	24	2 - -	24	<u>1 - -</u>			24	- 1 1		
25	3 1 -			25	<u>1 1 -</u>	TOTAL	9 15 4			25	1 - -		
26	1 - -			TOTAL	28 21 11					26	- 1 -		
27	<u>- 2 -</u>									27	1 1 -		
TOTAL	26 17 3									28	1 - -		
										29	- - 1		
										30	1 - -		
										31	- - 1		
										32	- - 1		
										33	1 1 -		
										34	1 - -		
										35	<u>1 - 1</u>		
										TOTAL	21 17 15		

Paired surveys (B, B', etc.) indicate simultaneous surveys in different sub-areas within a single general area. All non-prime areas surveyed by one investigator, all primes by the other. Frequencies are numbers of each species seen at each station and are employed only for determination of relative abundance. Further discussion under sections on relative abundance and association surveys.

TABLE 2.—*Intramimetic Associations of Meiacanthus nigrolineatus (M), Ecsenius gravieri (E), and Plagiotremus townsendi (P), based on observational surveys in Table 1.*

Stations	Survey												Total	Range %	Ave. %		
	A		B		B'		C		C'		D					D'	
	N	%	N	%	N	%	N	%	N	%	N	%				N	%
Number of stations	27		23		25		24		19		35		17		170		
Number of stations with at least M	20 (74.1)		15 (65.3)		24 (96.0)		17 (70.8)		14 (73.7)		21 (60.0)		14 (82.4)		125	60.0-96.0	73.5
Number of stations with only M	11 (40.8)		4 (17.4)		4 (16.0)		7 (29.2)		7 (36.8)		8 (22.8)		2 (11.8)		43	11.8-37.0	25.3
Number of stations with at least E	15 (55.5)		16 (69.5)		17 (68.0)		15 (62.5)		11 (57.9)		17 (48.6)		11 (64.7)		102	48.6-69.5	60.0
Number of stations with only E	6 (22.2)		6 (26.1)		1 (4.0)		5 (20.8)		4 (21.0)		3 (8.6)		0		25	4.0-26.1	14.7
Number of stations with at least P	2 (7.4)		8 (34.8)		10 (40.0)		4 (16.7)		3 (15.8)		15 (42.8)		7 (41.2)		49	7.4-42.8	28.8
Number of stations with only P	0		2 (8.7)		0		0		0		7 (20.0)		2 (11.8)		11	0.0-20.0	6.5
Number of stations with at least M+E	8 (29.6)		10 (43.5)		16 (64.0)		8 (33.3)		6 (31.6)		10 (28.6)		10 (58.9)		68	28.6-64.0	40.0
Number of stations with at least M+P	1 (3.7)		6 (26.1)		10 (40.0)		2 (8.3)		2 (10.5)		4 (11.4)		4 (23.6)		29	3.7-40.0	17.1
Number of stations with at least E+P	1 (3.7)		5 (21.7)		6 (24.0)		2 (8.3)		2 (10.5)		5 (14.3)		3 (17.6)		24	3.7-24.0	14.1
Number of stations with (M+E)+(M+P)+(M+E+P)	9 (33.3)		11 (47.8)		20 (80.0)		10 (41.7)		7 (36.8)		13 (37.6)		12 (70.5)		82	33.3-80.0	48.2
Number of stations with (E+M)+(E+P)+(E+M+P)	9 (33.3)		10 (43.5)		16 (64.0)		10 (41.7)		7 (36.8)		14 (40.0)		11 (64.7)		77	33.3-64.7	45.3
Number of stations with (P+M)+(P+E)+(P+M+E)	2 (7.4)		6 (26.1)		10 (40.0)		4 (16.7)		3 (15.8)		8 (22.8)		5 (29.4)		38	7.4-40.0	22.4
Number of stations with M+E+P	0		5 (21.7)		6 (24.0)		0		1 (5.3)		1 (2.9)		2 (11.8)		15	0.0-24.0	8.8
Number of stations with more than one species	10 (37.0)		11 (47.8)		20 (80.0)		12 (50.0)		8 (42.1)		17 (48.6)		13 (76.5)		91	37.0-80.0	53.5
Number of stations with only one species	17 (63.0)		12 (52.2)		5 (20.0)		12 (50.0)		11 (57.9)		18 (51.5)		4 (23.6)		79	20.0-63.0	46.5

4. When *E. gravieri* was present, at least one of the other two blenniids was also present 60.0-100 (av 75.5) percent of the time.

5. When *E. gravieri* was present, *M. nigrolineatus* was also present 53.3-94.1 (av 66.6) percent of the time.

6. When *E. gravieri* was present, *P. townsendi* was also present 6.7-35.5 (av 23.6) percent of the time.

7. When *P. townsendi* was present, at least one of the other two blenniids was also present 53.3-100 (av 77.5) percent of the time.

8. When *P. townsendi* was present, *M. nigrolineatus* was also present 26.6-100 (av 59.2) percent of the time.

9. When *P. townsendi* was present, *E. gravieri* was also present 33.3-66.7 (av 49.0) percent of the time.

10. *M. nigrolineatus*, *E. gravieri*, and *P. townsendi* occurred together 0.0-24.0 (av 8.8) percent of the time.

Because we lack information on the density of occurrence of the three species and the average area traversed by each species in a five-minute period, we cannot test the association survey data for statistical significance. Nevertheless, it seems noteworthy to find two or three species of fishes on a reef so closely

associated, as are the members of the proposed mimetic complex.

The associations of *M. nigrolineatus* and *P. townsendi* with *E. gravieri* or each other do not seem to be attributable to chance. Neither *M. nigrolineatus* nor *P. townsendi* was seen to approach any of the four other species of *Ecsenius* that occur in the same general habitat with *E. gravieri*, nor did *M. nigrolineatus* approach either of the two other species of *Plagiotremus* that occur in the same habitat with, and prey on the same species as, *P. townsendi*. Neither did we observe the two other species of *Plagiotremus* to approach either *M. nigrolineatus* or *E. gravieri*.

For purposes of comparison it would be of interest to qualify intraspecific associations of the mimetic complex, but the design of the association surveys precludes their use for such purposes (see discussion under relative abundance p. 10). The information in Table 1 tends to substantiate our impression that one is more likely to encounter intraspecific associations of *M. nigrolineatus* than intraspecific associations of the other two species.

The associations we report may be due in part to interspecific confusion. If the slight differences in appearance between *M. nigrolineatus* and *E. gravieri* are

not resolved by other fishes, one might expect the social reactions of other fishes to these two species to be, initially at least, almost identical. Here it is of interest to note that *P. townsendi* associates with *M. nigrolineatus* and *E. gravieri* in almost equal fashion (see statements 3 and 6 above).

That such confusion may extend to *M. nigrolineatus* and *E. gravieri* with regard to each other is indicated by the similarity of their coassociations (statements 2 and 5, above). The greater occurrence of *M. nigrolineatus* with *E. gravieri* than of *E. gravieri* with *M. nigrolineatus* is probably due to the greater mobility of *M. nigrolineatus*.

In the case of *M. nigrolineatus* we suspect that some of the attraction for other individuals of *M. nigrolineatus* was an aggressive interaction. We occasionally saw an individual *M. nigrolineatus* quickly and erringly swim a distance of several meters to meet another individual *M. nigrolineatus* of about equal size. Upon meeting there was brief agonistic encounter, whereupon the two individuals separated and swam away in different directions. This behavior was not the usual reaction when two *M. nigrolineatus* met. More often encounters were passive.

We frequently noted that when we pursued an *M. nigrolineatus* through an area in an attempt to catch it, one or two other *M. nigrolineatus* would approach the individual, and all would tend to "split off" in separate directions. Since it was frequently necessary to tire an *M. nigrolineatus* before it was possible to net it, the inability to keep sight of one's original prey, or distraction because of the seemingly easier possibility of capturing one of the attracted individuals, often contributed to failure (because of diver fatigue) to obtain a specimen on a particular foray. Such behavior might benefit *Meiacanthus* when pursued by a natural predator. Large individual *Meiacanthus* seemed to particularly attract smaller *Meiacanthus*. In general, we rarely saw more than two or three *Meiacanthus* swimming together, although on one occasion we observed a feeding cluster of seven individuals.

We rarely saw aggressive interactions between individuals of *E. gravieri*, but when they occurred they were not so strong as those we noted for *M. nigrolineatus*. They occurred occasionally when one individual, apparently inadvertently, approached too close to another, whereupon one of the two was driven off, but never so violently as with *Meiacanthus*. We never saw

aggressive interactions between individuals of *P. townsendi*, but we rarely saw two individuals in close proximity.

While we rarely saw *E. gravieri* initiate an approach to an *M. nigrolineatus*, we often noted interaction between these two species. Often when an *M. nigrolineatus* approached or swam past a resting *E. gravieri*, the *E. gravieri* would begin to swim alongside the *M. nigrolineatus* or else would swim after it once it had passed a short distance. On such occasion the *E. gravieri* would periodically nip into the sand, thus exhibiting behavior (feeding?) typical of *M. nigrolineatus*, but not of *E. gravieri*. After following the *M. nigrolineatus* for a variable but never extended period, the *E. gravieri* would return (alone) to the same or approximate spot from where it began swimming.

On some occasions when an *M. nigrolineatus* approached a *P. townsendi*, the *Plagiotremus* made a brief "attack" on the *Meiacanthus*, but the *Meiacanthus* did not seem to take particular note of the attack. Although *P. townsendi* often approached resting *E. gravieri*, we never saw aggressive interactions between these two species. The close presence of one or both of the other two species was not necessary for *P. townsendi* to successfully initiate an attack on its prey.

Intraspecific associations are frequently the result of reproductive drives. That the associations we saw were not necessarily for the purposes of breeding was based on the fact that both the intra- and interspecific associations were frequently between small individuals (juveniles) and the fact that we never saw any reproductive behavior or evidence of nests. The unusually close associations among the three species may indicate that elements of social mimicry (Moynihan 1968) are involved.

RELATIVE ABUNDANCE

METHODS AND RESULTS.—Information on the relative abundance of the three blenniids was obtained in three ways: (1) from the number of each species collected during 13 poison stations made in different areas of the Gulf of Aqaba, and one station in the Gulf of Suez, from 15 July to 28 September 1969 (attempts were made to procure all blenniids killed); (2) from two censuses, one by each of us, in different reef areas on 16-17 August 1970, made by continuously swimming a transect along the reef and recording all

individuals of each species seen (one transect was 15 minutes in duration, the other 20 minutes); (3) from the total number of each of the three blenniids recorded during the seven surveys of species associations made on 15-18 August 1970 (see also Table 1; further discussion is given in section on species associations). The association surveys were not designed for the purpose of obtaining relative abundances, but they do provide some information on the subject.

Each of the three methods is subject to certain biases, at least partly attributable to differences in behavior and niche preferences of the three species. *M. nigrolineatus* is a strong swimmer and individuals range over a fairly wide area. *P. townsendi* is a weak swimmer and individuals range over a more restricted area. *E. gravieri* is essentially a sedentary form, frequently spending much time in holes, but, when swimming, ranges over a relatively restricted area. Thus, with poison, one would expect to obtain relatively fewer of the *M. nigrolineatus* than of the *E. gravieri* and *P. townsendi* because the *M. nigrolineatus*, upon sensing the poison, would be more likely to leave the poisoned area. On the other hand, while

swimming a continuous transect, one would expect to see relatively fewer *E. gravieri* than *M. nigrolineatus* or *P. townsendi* because some of the *E. gravieri* would probably be hidden.

The association surveys have several limitations. As each observation station was initiated upon sighting any of the three blenniids, the more obvious *M. nigrolineatus* and *P. townsendi* would be favored. The fact that up to five minutes was spent making each station would offset this bias somewhat, because it would allow any hidden *E. gravieri* a better chance to appear (but it is possible that many would remain hidden for even longer periods). Because the amount of time spent making each station varied (from a few seconds to five minutes), the observations are not entirely comparable. For instance, if the station was initiated by observing all three species together at the onset, the diver moved on immediately, as he was primarily interested in what species occurred together and not in the number of each (although the number of each species seen at each station was recorded). In addition, these surveys are open to bias in favor of *P. townsendi*, which has a variable tendency to be at-

Data from the poison collections are as follows:

	NUMBER OF SPECIMENS COLLECTED														Total
	Station number														
	1	2	3	4	6	7	8	18	21	23	24	28	29	30	
<i>M. nigrolineatus</i>	4	6	7	15	1	9	13	11	3	11	3	1	8	1	93
<i>E. gravieri</i>	10	10	7	15	3	22	8	9	7	7	4	9	3	2	116
<i>P. townsendi</i>	1	2	2	0	5	10	1	2	2	1	1	9	0	1	37

Data from the two censuses are as follows:

	NUMBER OF INDIVIDUALS SIGHTED	
	15-minute census	20-minute census
<i>M. nigrolineatus</i>	19	33
<i>E. gravieri</i>	15	21
<i>P. townsendi</i>	4	16

Data from the association surveys are as follows:

	NUMBER OF INDIVIDUALS SIGHTED								Total
	Area								
	A	B	B'	C	C'	D	D'		
<i>M. nigrolineatus</i>	26	17	28	19	20	21	16	147	
<i>E. gravieri</i>	17	20	21	15	11	17	12	113	
<i>P. townsendi</i>	3	8	11	4	3	15	7	51	

tracted to a diver, occasionally making attacks on him—Randall and Randall, 1960, reported similar behavior for *Plagiotremus tapeinosoma* (Bleeker).

The results of the three methods used to estimate relative abundance agree in showing that *P. townsendi* is the least common of the three species. They also agree in showing that *M. nigrolineatus* and *E. graviori* are not very different in abundance. A t-test of the frequencies of these last two species based on the poison collections indicates that their numbers are not significantly different ($.20 < p < .30$). A chi-square test of the frequencies of these two species in each of the censuses is also not significant ($.25 < p < .10$ for the 20-minute census; $.50 < p < .25$ for the 15-minute census; a chi-square comparison of the proportions of the three species in the two censuses also indicates no significant difference: $.25 < p < .10$). The lack of statistical homogeneity in the results of the association surveys precludes statistical testing of these data, but examination of the data indicates trends that are not too different from those obtained by the other two methods. Excluding *P. townsendi*, the most different in appearance of the three species, the importance of these observations lies in the fact that the abundance of the presumed mimic, *E. graviori*, is not very different from that of its presumed model, *M. nigrolineatus*.

DISCUSSION.—Traditionally, mimetic theory holds that a Batesian mimic (which *E. graviori* seems to be) must be relatively rare compared with its model, if the mimetic association is to persist. The basis for this reasoning lies in the assumption that if a predator finds its chances of obtaining an acceptable prey are high, it will overcome its aversion to taking a possibly unacceptable prey of similar appearance. In an experimental study on mimicry involving butterflies and birds, J. Brower (1958c) concluded that if birds (predators) have had a long laboratory experience with only edible butterflies (prey), they tend to seize all butterflies offered. The implication, she reported, is that “in a situation in nature in which palatable mimics outnumber unpalatable models, mimicry would not work effectively.” J. Brower (1960), however, demonstrated experimentally in the laboratory, using artificial models and mimics, that there is a definite advantage to a mimic, even when the mimics outnumber the models 9:1. In this particular case, 17 percent of the mimics were avoided by the predators. Later, L. Brower, Cook, and Croze (1967), in a field

test using artificial mimics, concluded that “When the frequency of mimics is too great, their protection is lost either because predators become aware of the deception, or because the models are so rare relative to the mimics that the avoidance reaction is no longer adequately developed.” The apparently contradictory results of the 1960 study have not been explained.

Fisher (1930) proposed that the condition of a Batesian mimic's outnumbering its model could not be excluded on theoretical grounds if the model was extremely noxious or the mimic was an unimportant source of food, because the incentive for avoidance by predators would be changed little by increase of the mimic. Fisher made the important point that abundance relative to human collectors was not so meaningful as abundance relative to unknown selective agents that exist in nature.

The authors of recent theoretical studies (Holling 1963, 1965; Emlen 1968; Nur 1970), in postulating conditions for the development and maintenance of Batesian mimicry, have also recognized the possibility of a mimic's outnumbering its model. Excluding Holling, who was interested in relative population densities and learning characteristics of predators, the authors imply, as an integral basis for their reasoning, the special assumption that sampling error of a predator results in the death of all or many of the models sampled. We question whether this assumption is necessary or true of the majority of the reported cases of Batesian mimicry. Our experiments (see feeding experiments section) show that the predators of our models, in general, eat the models with apparent impunity (in which case mimicry serves no purpose) or reject them unharmed after ingestion. In the latter case sampling error plays little or no part in the evolution of the model away from the mimic or in controlling the size of the model population, upon which the number of mimics might be dependent. Fisher (1930) and Carpenter and Ford (1933) discussed the fact that many aposematic butterflies were protected by their toughness, but they did not consider what effect this might have on the relative abundance of models and mimics. (Holling, 1965, found valid theoretical reasons for believing that the elements of Batesian mimicry are widespread and of all degrees in nature. He considered the case of a highly unpalatable model with a dramatically similar mimic to be extreme Batesian mimicry, and therefore relatively uncommon. We accede to his

arguments but feel constrained to note that the cases of Batesian mimicry that will receive most of man's attention will be those at the extreme end of the scale.)

Wickler (1968:46-47) stated that the real meaning of the concept that models outnumber their mimics is that potential predators should encounter the mimics less often than the model, and that this concept held only when the predators had to learn to recognize the model and mimic and when positive and negative experiences carried equal weight. Wickler went on to state that learning experiments demonstrated that negative experiences can have a stronger, more lasting effect than positive experiences; thus, one should expect that the number of mimics would exceed the number of models in proportion to the predominance of negative over positive experiences.

In spite of the theoretical aspects, modern quantitative reports on relative abundance of mimics and their models (of which there are few: Poulton 1911; Ford 1946; Carpenter 1920, 1949; Brower and Brower 1962) show that models greatly outnumber mimics, except where the mimetic association is in the process of breaking down and many of the mimics do not closely resemble the models. (Sheppard, 1959, has demonstrated that in certain butterflies there is a statistically significant increase in the percent of imperfect mimics with increase in the percentage of mimics to models.) The situation with regard to *E. graviori* and *M. nigrolineatus* is rather unusual because all of the *E. graviori* are close mimics of *M. nigrolineatus*; some explanation is, therefore, necessary.

We believe that Fisher's and Wickler's ideas should be developed further. We therefore hypothesize the following situations whereby a close Batesian mimic in nature might occur in high numbers relative to its models, providing there are essentially no differences, temporal or spatial, in the geographic ranges occupied by the two species (more than one of the following may be operational in a particular situation):

1. Where the models are unharmed in the process of being tested by the predators. This permits a model to be tested repeatedly, thus increasing the effective number of models without increasing their actual number.

2. Where negative experiences of the predators have a stronger, more lasting effect than positive experiences. Duncan and Sheppard (1965), using ar-

tificial mimics, experimentally demonstrated this possibility. A correlative condition is probably also necessary: that there must be a relatively constant population of predators, as a strong, continued influx of naive predators would probably offset some of the advantages of a strong negative response by the predators.

3. Where the predators innately recognize a particular morphology or behavior as belonging to an unpalatable prey. We know of no proven cases where this condition exists.

4. Where because of certain behavioral differences:
 - a. the mimic is encountered less often than the model.

- b. the mimic is less easily caught than the model.

5. Where, temporarily, the predator population has been greatly reduced. Mimicry would break down where predators did not exist, as there is a tendency for mimics to develop nonmimetic forms (Carpenter 1920; Ford 1936; Brower and Brower 1962), and these forms would not be selected against.

6. Where temporarily the mimic population is exceptionally large (for instance, as the result of recruitment from a highly successful spawning) or the model population is exceptionally small (for instance, as the result of low recruitment from an unsuccessful spawning). Populations of annual species would be particularly sensitive to fluctuations in reproductive success.

7. Where alternative prey species, more acceptable than the mimic, exist. The results of this condition have been demonstrated theoretically by Holling (1965).

With regard to the high abundance of *E. graviori* relative to its model, we believe that conditions 1, 4a, 4b, at least, are contributing factors, varying somewhat with the species of predator.

The rejection of *M. nigrolineatus* unharmed after ingestion by certain predators has already been mentioned.

The secretive behavior of *E. graviori* in nature would probably make it less available (and thus decrease its effective abundance) than *M. nigrolineatus* to some predators. Also, the chances are better that a predator, especially a sedentary one, would encounter *M. nigrolineatus* more often than *E. graviori*. The fact that *E. graviori* is a relatively shy animal, rapidly entering small holes when disturbed, would make it

possibly more difficult for some predators to catch than *M. nigrolineatus*, which usually swims away when threatened. When vigorously and persistently pursued, by a diver, however, *M. nigrolineatus* will enter a hole.

The experimental data, so far as *Pterois volitans* Linnaeus (see also section on experiments) is concerned, offer some support for the idea that a negative experience with *M. nigrolineatus* is a strong inhibitor. Six *P. volitans* that had had a negative experience with *M. nigrolineatus* ingested none of the 19 *E. gravieri* and 10 of the 12 *M. nigrolineatus* subsequently offered them. All of the *P. volitans* ingested other food fishes after their initial negative experience and four of the six ingested an *E. gravieri* before their negative experience.

The effect of availability on the ratio of models to mimics (as modified by behavior, etc.) has generally been ignored in studies of mimicry, although Punnett (1915) in discussing a 5 to 2 ratio of models to mimics in certain butterfly species noted that the mimic was more wary and a stronger flyer than its models. It would seem that these differences in behavior would contribute heavily to the 5 to 2 ratio, which was based on a supposed random collection made by humans (Poulton 1911). We find it difficult to equate availability of mimics to humans with availability to natural predators. In general, all citations of relative numbers of mimics and models, including our own, are open to the challenge that they are not representative of the ratios in nature, because none conclusively demonstrate that the methodology for obtaining the ratios was truly random.

PREDATION EXPERIMENTS

INTRODUCTION.—To test whether any of three species of blenniids was protected from predation and could thus serve as a model in a mimetic association, experiments were made using predatory fishes held in aquaria.

Initially we intended to use only naive predators, serranids, obtained from the Mediterranean coast of Israel. The Mediterranean fish fauna is distinct from that of the Red Sea (Gulf of Aqaba) and none of the genera of the mimetic complex occur in the Mediterranean. Since the opening of the Suez Canal there has been an invasion of the Mediterranean by a few Red Sea fish species (Ben-Tuvia 1966), but no blen-

niids are among these. Our results were unsatisfactory because most of the predators, which were adversely affected by conditions associated with their capture and shipment to Eilat, refused to eat live fishes and some refused food of any kind.

Failure with the Mediterranean predators caused us to attempt experiments with Gulf of Aqaba predators. Because they were subjected to less drastic handling than the Mediterranean predators, some of these fishes were better "performers," but most did not live long enough for us to run the series of tests we would have liked. Many died within one or a few days after being placed in aquaria. Their deaths undoubtedly were caused by air bubble disease and unexpected shutdowns of the water pump.

We used prey and predators available at the time in the field. The species used, and their sizes (fishes do not have determinate growth), were the result of our efficiency in collecting. In no case, however, did we offer a predator a prey that was too large for it to ingest. The variables introduced here are, for instance, the fact that a small predator ingesting a large prey might not eat again for a longer period than if it had eaten a small prey. It is also possible that the relative sizes of both predator and presumed models might influence palatability. Actually, we have no evidence that size differences affect palatability. It is also probable that the discomfort caused by the bite of a large *M. nigrolineatus* is greater than that caused by the bite of a small individual, in which case the degree of the negative reaction experienced by a predator would affect its future reactions with the mimics and models. Suffice it to say that both large and small *M. nigrolineatus* were capable of causing large and small predators to reject them.

Other than the species of predators we used, at least two other common Gulf of Aqaba species are potential predators of the blenniids: *Synodus* sp. and *Parapercis* sp. On one occasion while observing a resting *E. gravieri*, we saw *Synodus* make an unsuccessful attack on it. On another occasion a *Synodus* took a *P. townsendi*, as it was being pursued by one of us, only moments after escaping from a net in which it had been caught. These observations were the nearest thing to natural predation on the mimetic complex that we saw.

The blenniids, food fishes, and predators were caught locally with dip nets and placed in aquaria of varying sizes (all that were available). Only one pred-

ator was put in each aquarium for the purposes of the experiments, with the exception of the single individuals of *Synanceichthys verrucosa* and *Scorpaenopsis gibbosa* (see discussion under these species). Holding tanks were maintained for reserve predators and other tanks were used to hold the blenniids and other food fishes. The experimental aquaria were shielded so that no predator could see another. (Brower, Alpert, and Glazier, 1970, demonstrated experimentally with birds that one predator can learn from observing the behavior of another.)

Prey were offered to the predators one at a time, with an interval of at least one minute between consecutive offerings. All prey so offered were allowed to remain with the predator until the end of the experiment. Frequently predators were tested two or more times during the course of a day.

Predators were allowed a maximum of 35 minutes, but usually 15 minutes or less, to attack each prey. We observed predators and prey continuously during the experiments. We report results of the experiments for each predator, using only the data obtained during the period comprising the first to the last day that the predators ate. Results are not given for the large number of experiments with predators that refused to eat. The experiments covered the period 17 August to 10 September 1970.

In introducing prey to the predators, it was often necessary to restrain the predator until the prey was well established in the tank. After a few prey introductions, some predators learned where their food was coming from and would immediately come to the surface of the aquarium on the approach of an investigator. The predator would immediately take anything that was placed near the surface of the water. For other predators it was necessary to tether the prey on a thread and tiny (No. 28) barbless hook, as the confines of the aquaria often made it impossible for the predator to catch a free-swimming prey. Even when these predators briefly swallowed the line or became briefly hooked, they did not seem adversely affected and continued to take tethered fish throughout their captivity, regardless of whether the prey was retained or rejected after ingestion. With few exceptions, it was not possible to establish the predators in aquaria under anything like natural conditions. If rocks were introduced to afford the predators cover, introduced prey would hide under the rocks and avoid being captured.

In spite of the poorly controlled nature of our experiments, a definite pattern evolved that offers substantial evidence to support the idea that *Meiacanthus nigrolineatus* is at least a Batesian model for *Ecsenius gravieri*. The position of *Plagiotremus townsendi* in the mimetic complex needs more study.

EXPERIMENTS WITH *Pterois volitans*.—*Pterois volitans* is a venomous, highly conspicuous fish of the family *Scorpaenidae*. In nature it feeds on live fish and invertebrates, although in captivity it can be induced to take a piece of flesh (squid, etc.) that is moved about in front of it. In an aquarium, *Pterois* pursues a moving fish until the fish is in a confined space. The *Pterois* blocks exit of the prey by adducting and expanding its large, fanlike pectoral fins. Unacceptable prey are frequently chased, cornered, and examined for several seconds before the *Pterois* moves away. A summary of the experiments with *Pterois* is presented in Figure 2.

Of the 12 *Pterois* tested, only 6 ingested normal individuals of *Meiacanthus nigrolineatus*. All were quickly rejected unharmed. Of the six, one (predator #9) refused the two *Ecsenius gravieri* offered during the next three days (no *Meiacanthus* offered), after which the experiment was terminated; one (#11) refused the two *E. gravieri* and two *M. nigrolineatus* offered during the next two days, after which the experiment was terminated; one (#20) refused the five *E. gravieri* offered during the next four days (no other *M. nigrolineatus* offered), after which the experiment was terminated.

Two of the *Pterois* (#22, 26) that rejected normal *Meiacanthus* each ingested and retained a *Meiacanthus* that had had its canines clipped off.

Four of the six *Pterois* ingested and retained an *E. gravieri*. Of the other two, one (#22) rejected an *E. gravieri* only after next ingesting and rejecting a *Plagiotremus townsendi* and an *M. nigrolineatus*, indicating that rejection of the *E. gravieri* was probably incidental. The other *Pterois* (#6) was offered an *E. gravieri* less than a minute after the *Pterois* had rapidly ingested and rejected a *P. townsendi* five times, also indicating that the rejection of the *E. gravieri* may have been incidental.

From these data it would appear that normal *M. nigrolineatus* are unacceptable prey for *Pterois* and that *M. nigrolineatus* and *E. gravieri* are generally avoided once a *Pterois* has ingested and rejected an *M. nigrolineatus*.

PREDATOR NUMBER	Pterois volitans
6	e a r P E E P ^X M M E P
9	e a r E E P X P X ¹ X E ^X M
11	e a r E M E M M P X E X E P ^X M M X ² M
12	e a r E P E
17	e a r P M E X ^X M X X E ^X P
19	e a r P E M X
20	e a r M X P X E X P X E P X P E E X P X ³ E P ^X X
22	e a r E ¹ E ^X M E P M P E M ¹ M M M M P E ^X P M
23	e a r P E E X
25	e a r M X E E ^X E P
26	e a r E M ¹ M ¹ X E X E P M X M
27	e a r M X E P X E E ^X M E P E P X M

FIGURE 2.—Sequence of prey offerings and responses of *Pterois volitans*. E=*Ecsenius gravieri*; E¹=*E. gravieri* rejected later after next *Meiacanthus nigrolineatus* was rejected; M=*Meiacanthus nigrolineatus*; M¹=*M. nigrolineatus* with canines clipped off; P=*Plagiotremus townsendi*; X=prey known to be acceptable; X¹=*Amphiprion bicinctus*, questionably acceptable; X²=*Plagiotremus tapeinosoma*, questionably acceptable; X³=*Labroides dimidiatus*, questionably acceptable; a=refused; e=ingested and retained; r=ingested and rejected. Vertical lines separate each day's prey offerings.

Twelve *Pterois* were offered a total of 27 *P. townsendi*. Ten of these *Pterois* ingested and rejected a total of 12 *P. townsendi*; one ingested and rejected three, and nine ingested and rejected one each. Of the seven *Pterois* that were offered two or more (up to six) *P. townsendi*, one ingested and rejected three (of four offered), four ingested and rejected one (of

two, three, three and six offered), and two refused both of the two *P. townsendi* offered. One (#11) of the two *Pterois* that refused *P. townsendi* did ingest and reject a *Plagiotremus tapeinosoma* (quite different in appearance from *P. townsendi*, but similar in behavior) while a *P. townsendi* was present in the aquarium. Of the six *Pterois* that had ingested and re-

jected an *M. nigrolineatus*, only two did not subsequently ingest a *P. townsendi* (but of these two, #11 did subsequently ingest and reject *P. tapeinosoma*).

The number of ingestions and rejections of an individual *P. townsendi* by a single *Pterois* ranged from one to twenty. In general, the behavior of *Pterois* toward *P. townsendi* seems to indicate that *Pterois* recognizes *P. townsendi* (and *P. tapeinosoma*) and considers it inedible. It may be that the *Pterois* were trying to kill or drive off the *P. townsendi*. Although we never saw a *P. townsendi* attack a *Pterois* in the field or aquarium, it is possible that such attacks occur and that the *Pterois* have come to recognize the predacious nature of *P. townsendi* and seek to drive it away. Why *Pterois* does not at the same time find *P. townsendi* edible requires additional study. Should a *Pterois* mistake an *E. graviori* for a *P. townsendi*, the *Ecsenius* would be benefited, as was perhaps the case mentioned earlier for *Pterois* specimen #6.

The only species of fish on the reef, besides those of the mimetic complex, that is blue anteriorly and yellow posteriorly is the young of the wrasse *Gomphosus melanotus* (see discussion under color pattern section). We were successful in obtaining only one young *G. melanotus*. This individual was offered to *Pterois* #9 two days after it had ingested an *E. graviori* and ingested and rejected an *M. nigrolineatus*. The next day two of the blennies and a known edible, *Chromis coeruleus* (Cuvier), were offered and refused. Before offering the *G. melanotus*, both a *Plagiotremus townsendi* and an anemone fish of questionable edibility, *Amphiprion bicinctus* Rüppell (black and yellow), were offered and refused. The *Gomphosus* was eaten, in the presence of the other two species, nine minutes after having been offered. The next day the same *Pterois* refused an *E. graviori*, but quickly ate another wrasse, *Cirrilabrus* sp. (red orange).

EXPERIMENTS WITH *Synanceichthys*, *Scorpaenopsis*, AND *Brachirus*.—All three of these genera comprise venomous species of scorpaenid fishes that are relatively sedentary in habit. *Synanceichthys* and *Scorpaenopsis* are well camouflaged and are easily overlooked in the field. *Brachirus*, while not conspicuous, is more apparent to a human observer. *Synanceichthys* is rare and is the least common of the three genera. It usually occurs only where it is well protected by cover; it attains a much larger size (at least 350 mm, Smith 1958) than the other two genera (*Brachirus*,

145 mm; *Scorpaenopsis*, 210 mm, Smith, 1957a, b) *Scorpaenopsis* and *Brachirus* are most often found resting on rocks out in the open. In captivity *Synanceichthys* waits until an unsuspecting prey is practically touching its mouth before it ingests the prey with lightning rapidity. *Scorpaenopsis* and *Brachirus* behave similarly, but will move several centimeters to engulf a prey. *Brachirus* will corner prey in a similar fashion to that of *Pterois*. A summary of the experiments with these fishes is presented in Figure 3.

One large *Synanceichthys verrucosa* (Bloch and Schneider), approximately 20 cm long, placed in a small aquarium (25×29×25 cm deep) on 31 August 1970, first ingested and retained a prey (*Meiacanthus nigrolineatus*) on 2 September. It refused further food through 6 September and appeared to be under stress in the small aquarium. On 9 September it was transferred to a larger aquarium (46×90×48 cm deep) with considerable cover and in which another *S. verrucosa* and a *Scorpaenopsis diabolus* (see discussion of this last-named individual below) had been on display for several months. On 8 September it again began to accept prey; first it ate an *Anthias squamipinnis*, then it refused an *M. nigrolineatus*, then ate a *Chromis coeruleus*, and then ignored an *E. graviori*. On 9 and 10 September it was offered only *M. nigrolineatus*, one each day, which it ingested and retained. Since that time I have been informed by Mr. David Fridman, manager of the Maritime Museum (aquarium) of Eilat, Israel, that by 8 October, this individual had ingested and retained an additional 12 *M. nigrolineatus*.

It is obvious that *M. nigrolineatus* is acceptable prey, at least for this individual. Whether smaller individuals of *S. verrucosa* would find *M. nigrolineatus* equally acceptable would be of interest. Because of the relative scarcity of *S. verrucosa* in the reef area (we encountered only three individuals during a five-week period when we were diving every day), it is doubtful that this species occupies a major role as a predator of the mimetic blenniids.

A *Scorpaenopsis diabolus* (Cuvier) that had been maintained in an aquarium together with a *Synanceichthys verrucosa* (not the one used in the experiments) for several months prior to our experiments was first offered a blenniid, *E. graviori*, on 1 September. The *Ecsenius* was ingested and retained as was an *M. nigrolineatus* offered five minutes later. The next day only an *M. nigrolineatus* was offered,

PREDATOR NUMBER	Epinephelus fasciatus
3	e E a r
5	e X E E X a E M M E P r
10	e E E E a M M P r M P M
15	e E M M M X P M M P M P E a P M M E M M E M P r
16	e E P M M M E P a r
18	e P P' M' M M E P E' P a X M r
29	e M M M E P X P P M X a r
	Epinephelus tauvina
2	e P' M' E P M X E ² P X M E X a r
	Epinephelus aeneus
4	e X E' M' E X a r
	Epinephelus guaza
8	e X P M X E X P M' X E E E X a r
	Cephalopholis nigripinnis
7	e X E a r
	Scorpaenopsis diabolus
21	e E M M X X M X X X X M X a r
	Synanceichthys verrucosa
28	e M M M X M M M X X M X M M a r
	Brachirus brachyptera
14	e E ² a r

FIGURE 3.—Sequence of prey offerings and responses of various species of predators. E=*Ecsenius gravieri*; E¹=dead *E. gravieri*; E²=*E. gravieri* rejected after next *Meiacanthus nigrolineatus* was rejected; M=*Meiacanthus nigrolineatus*; M¹=dead *M. nigrolineatus*; M²=*M. nigrolineatus* with canines clipped off; M³=*M. nigrolineatus*, badly disabled; P=*Plagiotremus townsendi*; P¹=dead *P. townsendi*; X=prey known to be acceptable; X¹=*P. tapeinosoma*, questionably acceptable; a=refused; e=ingested and retained; r=ingested and rejected; dashes indicate no prey offered; vertical lines separate each day's prey offerings.

which was snapped at but refused. On the next day the *S. diabolus* ingested and rejected an *M. nigrolineatus*, and then refused a *Cirrillabrus* sp. and a piece of squid (the usual food on which it was fed during the previous months). From 4-7 September, *M. nigrolineatus* and squid were offered daily and refused. On 8 September a *Chromis coeruleus* was ingested, an *M. nigrolineatus* was then refused, and then another *Chromis coeruleus* was ingested. On 9-10 September, *M. nigrolineatus* were again offered and refused, as was an apogonid, which was offered on 9 September.

One *Scorpaenopsis* sp. ingested and retained a freshly dead *E. graviori*, as its only prey, on the first of three days it survived in the laboratory.

A *Brachirus brachypterus* (Cuvier) refused an *E. graviori* on the first day it fed in the laboratory, but two hours later twice ingested and rejected the same *M. nigrolineatus* in a six-minute period. The next day it was offered an *E. graviori*, which it ingested immediately. Two minutes later it was offered an *M. nigrolineatus*, which it ingested immediately and quickly rejected, followed seconds later by rejection of the previously ingested *E. graviori*. Both blenniids were alive and apparently unharmed. Rejection of the *E. graviori* was probably incidental to rejection of the *M. nigrolineatus*.

EXPERIMENTS WITH *Epinephelus fasciatus*.—*Epinephelus fasciatus* (Forskål) is one of the most common and conspicuous predatory serranid fishes on the reef. It feeds on live or dead fishes and invertebrates, which it captures with its large mouth, aided by its strong swimming ability. A summary of the experiments is presented in Figure 3.

Six individuals of *Epinephelus fasciatus* ingested 18 normal *Meiacanthus nigrolineatus*. Five of these *E. fasciatus* quickly rejected unharmed 14 of the *M. nigrolineatus*. One individual (#29) retained four (of five offered). (Specimen #29 had been maintained in an aquarium for approximately six months before the experiments. It was a small juvenile, estimated at 35 mm when captured, and was about 85 mm long at the time of the experiments. Prior to the experiments it had been fed on various dead organisms, but no blenniids.) One individual (#18) ingested and retained a freshly dead *M. nigrolineatus* after it had ingested and rejected a live *M. nigrolineatus* the previous day. This same individual refused all four live *M. nigrolineatus* offered on the three days following rejection of the first live *M. nigrolineatus*.

Six *E. fasciatus* ingested and retained 9 of 18 live *E. graviori* offered. The remaining nine *E. graviori* were refused. One *E. fasciatus* (#18) ingested and retained a freshly dead *E. graviori*, but refused a live *E. graviori*. The data seem to indicate a general tendency for *E. fasciatus* to refuse live *E. graviori* once an *M. nigrolineatus* has been rejected, but the same data does not indicate any tendency to refuse subsequent *M. nigrolineatus*.

Five *E. fasciatus* ingested live *Plagiotremus townsendi*. One (#15) retained six of seven *P. townsendi* ingested (six were all that were offered after the first one was rejected). One (#16) retained all three of the *P. townsendi* ingested (and offered); one (#29) rejected the first *P. townsendi* offered and refused the next three offered; one (#10) rejected one of the two offered and refused the other offered before the rejected *P. townsendi*; and one (#18) ingested and retained one of the four offered and refused the other three, offered before and after the rejected *P. townsendi*. *E. fasciatus* (#5) refused the only *P. townsendi* offered, although it ate another food fish offered immediately afterward.

EXPERIMENTS WITH OTHER SERRANIDAE.—*Epinephelus tauvina* (Forskål) is a species similar in behavior to *E. fasciatus*; however, *E. tauvina* is not quite as common as *E. fasciatus* and is seen less often out from under cover. A summary of the experiments with *E. tauvina* is given in Figure 3.

On the first three days of the experiments it appeared that the *E. tauvina* was confused by experiences with acceptable and unacceptable dead and live blenniids. On the second day an *Ecsenius graviori* was ingested first, then a *Meiacanthus nigrolineatus* was ingested and rejected, followed by rejection of the previously ingested *E. graviori*. We consider rejection of the *E. graviori* incidental to rejection of the *M. nigrolineatus* (the *E. tauvina* did not close its widely extended mouth for seven minutes after rejecting the *Meiacanthus*). On the fourth day of the experiments the *E. tauvina* showed signs of recognizing the blenniids by refusing all those offered alive. It also refused a *Plagiotremus tapeinosoma*. On the fourth day the *E. tauvina* tossed a freshly dead *M. nigrolineatus* around with its snout for two minutes before gingerly ingesting it. This was in contrast to all but one of the other ingestions of prey, which occurred within seconds after the prey were introduced into the aquarium. The exception was an *E.*

gravieri on the second day, which was not taken for two minutes, but was not "tested" as was the dead *M. nigrolineatus*. On the fifth day two freshly dead blenniids were eaten immediately, but a canineless, somewhat disabled *M. nigrolineatus* was followed closely for four minutes before being ingested (and retained). The next three normal blenniids were ignored, but another badly disabled *M. nigrolineatus* (with canines) was ingested and retained after having been in the aquarium for only one minute. Probably encouraged by these successes, the *E. tauvina* ingested a normal *M. nigrolineatus* immediately upon its introduction into the aquarium, and almost as quickly rejected it.

Cephalopholis nigripinnis (Valenciennes) is a common, small, secretive species with feeding habits similar to those of *Epinephelus*. A *C. nigripinnis*, placed in an aquarium on 21 August, ate a piece of squid the same day. The next day it did not accept the only food, an *Ecsenius graveri*, offered it. The next day it ingested an *E. graveri* and then ingested and rejected a *Meiacanthus nigrolineatus*. The *C. nigripinnis* refused all prey (Squid, *E. graveri*, *P. townsendi*) offered during the next two days, although it showed a definite interest in the blenniids.

EXPERIMENTS WITH HOLOCENTRIDAE.—*Holocentrus diadema* Lacépède is a conspicuous, common, small species. Although frequently seen moving about in a very restricted area during the day, it is primarily a nocturnal form and probably does not feed on blenniids in nature. An *H. diadema* placed in an aquarium on 4 September ingested a *Meiacanthus nigrolineatus* the next day. It rejected the *M. nigrolineatus* one minute after ingestion. Within the next four minutes it twice ingested and rejected the same *M. nigrolineatus*.

EXPERIMENTS WITH NAIVE PREDATORS (SERRANIDAE).—Twelve serranid fishes from the Mediterranean coast of Israel, assuredly naive predators, were transported to Eilat for use in our experiments. The experiments were largely unsuccessful because most of these fish failed to eat. An *Epinephelus aeneus* (St. Hilaire), which had been placed in an aquarium about a month previously and fed on squid and pieces of atherinid fishes, refused the first blenniid (*Meiacanthus nigrolineatus*) offered it, although it did eat a piece of atherinid just before and after presentation of the blenniid. The next day it ingested a freshly dead *Ecsenius graveri* and a freshly dead *M. nigrolineatus*.

The following day it ingested a live *M. nigrolineatus*, which it rejected alive and unharmed one and one-half minutes later. The next day it refused an *E. graveri*, but ate a piece of squid. A summary of the feeding experiments with this individual is given in Figure 3.

An *Epinephelus guaza* (Linnaeus), which refused food during the first week of captivity, ingested a piece of atherinid and refused an *E. graveri* on the eighth day. It refused prey on the next day. On the tenth day it ingested an *M. nigrolineatus*, which it rejected unharmed a few seconds later. It then refused a piece of atherinid. The next day it ingested a piece of atherinid, but refused the *E. graveri* offered both before and after the atherinid. The following day it refused a *Plagiotremus townsendi*, but ate a freshly dead *M. nigrolineatus* and a piece of squid. On the next two days it refused *E. graveri*, the only prey offered. On the fifteenth day it again refused *E. graveri*, but ate a piece of squid. A summary of the feeding experiments with this individual is given in Figure 3.

Although the data are meager it appears that these two Mediterranean *Epinephelus* species respond to the blenniids much as do the Gulf of Aqaba *Epinephelus*.

SUMMARY OF FEEDING EXPERIMENTS.—Twenty individuals, representing ten species of predators, ingested 45 live *Meiacanthus nigrolineatus*. Of these 45, 33 were rejected alive and apparently unharmed. Twelve were retained, and of that number, three had had their canines clipped (the only three so altered), one was badly disabled and probably not functioning normally, four (all that were ingested) were eaten by a single *Epinephelus fasciatus*, three (all that were ingested) were eaten by a single *Synanceichthys verrucosa*, and one was eaten by a *Scorpaenopsis diabolus* (which rejected the only other *Meiacanthus* it ingested).

All of the six freshly dead *M. nigrolineatus* that were ingested (by four individuals representing four species of predators) were retained.

Sixteen individuals representing six species of predators ingested 20 live *Ecsenius graveri*. Of these 20, four were rejected alive and unharmed. Of the four rejected, three were rejected only after an *M. nigrolineatus* was next eaten and rejected, and one was rejected after a *P. townsendi* had just previously been rapidly ingested and rejected five times.

Both freshly dead *E. graviori* that were ingested (by one individual of each of two species of predators) were retained.

Twenty-four live *Plagiotremus townsendi* were ingested by 15 individuals of two species of predators (10 *Pterois volitans* and 5 *Epinephelus fasciatus*). The *Pterois* rejected alive and apparently unharmed all 12 of the *P. townsendi* ingested. (There is some question whether ingestion is properly descriptive of the behavior of *P. volitans* with regard to *P. townsendi*; see discussion under *P. volitans*). The *Epinephelus* rejected 3 of the 12 *P. townsendi* ingested.

All three freshly dead *P. townsendi* that were ingested (by one individual of each of two species of predators) were retained.

We conclude that live *Meiacanthus nigrolineatus* is a generally unacceptable prey species, whose unacceptability lies in its bite, and that *Ecsenius graviori* is a generally acceptable prey species. We also conclude that *Plagiotremus townsendi* is generally an acceptable prey for *Epinephelus fasciatus*, but not for *Pterois volitans*. The cause of this unacceptability is unknown.

GENERAL DISCUSSION

If the hypothesis that *Meiacanthus nigrolineatus*, *Ecsenius graviori*, and *Plagiotremus townsendi* form a mimetic complex is true, the following interactions, based on our limited laboratory evidence and field observations, are possible (Figure 4).

1. *E. graviori* mimics *M. nigrolineatus*. This is an advantageous situation for *E. graviori* because most predators reject *M. nigrolineatus* as prey. (*Synanceichthys verrucosa*, a rare, sedentary predator, is possibly a notable exception, but probably does not contribute significantly to the breakdown of the mimetic complex in nature). The situation here is Batesian mimicry.

2. *E. graviori* mimics *P. townsendi*. This is probably advantageous for *E. graviori* because some predators (*Pterois volitans*, at least) reject *P. townsendi* as prey. The situation is again Batesian mimicry. The fact that both species are acceptable prey for some predators would be disadvantageous for both *E. graviori* and *P. townsendi*, because it increases the chances of a rewarding experience for those predators.

3. *P. townsendi* mimics *M. nigrolineatus*. The situation is advantageous for *P. townsendi* for the same reason given in 1 (Batesian mimicry), and because some species reject both *M. nigrolineatus* and *P. town-*

sendi (Müllerian mimicry). It is also advantageous for *P. townsendi*, because *M. nigrolineatus* is nonaggressive and is allowed to closely approach other fishes (aggressive mimicry, no. 4).

4. *P. townsendi* mimics *E. graviori*. This is an advantageous situation for *P. townsendi*, because *E. graviori* is nonaggressive and not avoided by other fishes (this would be aggressive mimicry of the type involving at least three species, see Wickler, 1968).

5. *M. nigrolineatus* mimics *P. townsendi*. This is possibly an advantageous situation for *M. nigrolineatus*, because some predators (*Pterois volitans*) reject *P. townsendi* as prey (Müllerian mimicry); however, the same predators reject *M. nigrolineatus*. Even though *P. townsendi* is acceptable prey for some predators, this probably does not represent a serious disadvantage for *M. nigrolineatus*, which is rejected unharmed by most predators that happen to ingest it.

6. *M. nigrolineatus* mimics *E. graviori*. There is no evidence to support this, but the resemblance is probably not a serious disadvantage for *M. nigrolineatus* for the second reason given in 5.

In the case of a predator such as *Pterois volitans*, *E. graviori* is a Batesian mimic of both *M. nigrolineatus* and *P. townsendi*, and the last two species are Müllerian mimics. In the case of a predator such as *Epinephelus fasciatus*, *E. graviori* and *P. townsendi* are Batesian mimics of *M. nigrolineatus*. In the case of nonpiscivorous prey species such as pomacentrids, *P. townsendi* is an aggressive mimic of *M. nigroline-*

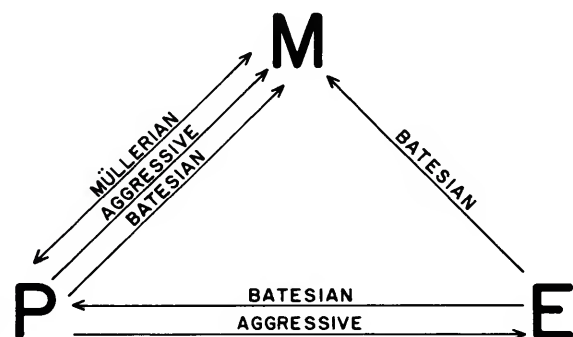


FIGURE 4.—Proposed mimetic relationships exhibited by a hypothesized mimetic complex. M=*Meiacanthus nigrolineatus*, E=*Ecsenius graviori*, P=*Plagiotremus townsendi*. Arrows point from mimics to models, which are identical in Müllerian mimicry.

eatus and *E. graviori*. In the case of a predator such as *Synanceichthys verrucosa*, the mimetic relationship probably serves no purpose.

It is difficult to ascribe quantitatively the importance of each of the above situations for the formation and maintenance of the mimetic complex because of the differences in behavior, varying densities and wide variety of potential predators on the reef, and because of the possibilities for complex feedback in the mimetic relationship. There are, however, clues in the fact that *E. graviori* and *M. nigrolineatus* more nearly resemble each other than either resembles *P. townsendi*, and that *P. townsendi* is much less abundant than either *M. nigrolineatus* or *E. graviori*.

If the mimetic relationship between *M. nigrolineatus* and *E. graviori* developed in the presence of *P. townsendi*, the similarity of *E. graviori* to *M. nigrolineatus* is of greater importance to *E. graviori* than is its similarity to *P. townsendi*. Otherwise, *E. graviori* might be expected to resemble *P. townsendi* more than it resembles *M. nigrolineatus*. In this case, the fact that *P. townsendi* resembles *M. nigrolineatus* much less than does *E. graviori* indicates a slower rate of convergence toward *M. nigrolineatus* for *P. townsendi* relative to that of *E. graviori*. This probably results from decreased predation on *P. townsendi*, which in turn apparently results from *P. townsendi*'s being an unacceptable prey for certain predators, and possibly because it is a less abundant species than *E. graviori*. Whether the similarity of *P. townsendi* to the other two species will increase is dependent on the selective weight attributable to the three types of mimetic relationship in which it is involved and on its genetic plasticity.

Fisher (1930) pointed out that Batesian mimicry can only be established when the rate of modification of the model has been less than that of the mimic. Once mimicry has been established the rate of modification of both mimics and models should be balanced if the relationship is to continue. Support for the idea of greater genetic stability of *Meiacanthus* over that of *Ecsenius* and *Plagiotremus* is found in the numbers of species and color-pattern forms in each genus. Smith-Vaniz (ms) recognizes only 11 species of *Meiacanthus*, of which only 1 species besides *M. nigrolineatus* has forms (in this case two subspecies) differing in color pattern and none have different sympatric color-pattern forms. He recognizes 9 species of *Plagiotremus*, of which at least 2 are represented by

populations varying in color pattern, but none of the color-pattern forms are sympatric (except the sexually dichromic species, including *P. townsendi*). Springer (1971) recognized 18 species of *Ecsenius*, several of which are represented by geographic populations varying in color pattern and meristics, while others are represented by markedly different sympatric color-pattern types. Whereas only one, or rarely two, species of *Meiacanthus* occur in any relatively restricted area, up to three species of *Plagiotremus* and five species of *Ecsenius* may occur together.

As Fisher (1927, 1930) has reasoned, selective pressures generally result in a Batesian mimic's developing into as close a replica as possible of its model. Müllerian mimics, however, need only to duplicate each other's appearance to the extent necessary for potential predators to recognize their distasteful (in the broad sense) qualities. Hence, given a mimetic association, one might conclude from appearance alone that *P. townsendi* is primarily a Müllerian mimic of *M. nigrolineatus*. However, if the relationship between *M. nigrolineatus* and *E. graviori* developed, or was developing, before *P. townsendi* was present, subsequent changes in the similarities of the three species must occur before it will be possible to ascribe relative importances to the various mimetic relationships.

Other Cases of Presumed or Known Mimetic Associations Involving Blennioid Fishes

Meiacanthus atrodorsalis, *Plagiotremus laudandus*, and *Ecsenius bicolor*

PLATE 3

Meiacanthus atrodorsalis atrodorsalis (Günther) is widely distributed in the tropical central Pacific Ocean with the notable exception of the Fiji Islands where it is replaced by a different subspecies. It is variably sympatric with *Plagiotremus laudandus* (Whitley) and/or *Ecsenius bicolor* (Day). The color patterns of *M. a. atrodorsalis* and *P. laudandus* are nearly identical; both are blue anteriorly and yellow posteriorly with black markings in the dorsal fin. Their similarity is further enhanced by their greatly elongated caudal fin lobes. *E. bicolor* has three, sometimes sympatric, color-pattern types, one of which is blue anteriorly and yellow posteriorly. All three types have black marks in the dorsal fin, usually restricted anteriorly (Springer, 1971, gives details on the life color of *M.*

atrodorsalis and *E. bicolor*), and elongated caudal fin lobes. It is possible that the other two color types are nonmimetic, in which case *E. bicolor* might serve as a good subject for study of breakdown of mimicry in areas where its presumed model, *M. a. atrodorsalis*, does not occur. At One Tree Island, Great Barrier Reef, large quantities of *E. bicolor* were observed and collected, all but a few of which were the blue and yellow form. Only one individual of *M. a. atrodorsalis* was encountered (and collected) at One Tree Island, and no other possible model for *E. bicolor* was seen.

The distribution of *M. atrodorsalis* and *P. laudandus* with respect to the Fiji Islands presents an interesting phenomenon. The subspecies *Meiacanthus atrodorsalis oualanensis* (Günther) and an undescribed subspecies of *P. laudandus* occur only there and are differentiated from the nominal subspecies in being entirely brilliant yellow in color, with no dark marks in the dorsal fin (Axelrod and Emmens, 1969, and Springer, 1970, present the same color illustration of *M. a. oualanensis*). No information of the life color of *E. bicolor* from the Fiji Islands is available. The single preserved specimen of *E. bicolor* available from Fiji is dark anteriorly and pale posteriorly, similar to the majority of the preserved One Tree Island specimens of *E. bicolor*, which were blue anteriorly and yellow posteriorly in life.

The possible mimetic relationship of these three species at Eniwetok, Marshall Islands, is being studied by G. S. Losey of the University of Hawaii. We predict that their mimetic relationships will be similar to those of *M. nigrolineatus*, *E. gravieri*, and *P. townsendi*.

Meiacanthus smithi and *Plagiotremus* sp.

PLATE 4 a, b

In the eastern Indian Ocean, *Meiacanthus atrodorsalis* and *Plagiotremus laudandus* are replaced by another *Meiacanthus-Plagiotremus* species pair: *Meiacanthus smithi* Klausewitz, known only from the Indian Ocean, and an undescribed species of *Plagiotremus* from Ceylon that closely resembles *M. smithi* in preserved color pattern. Although both species were not collected together, they were taken in the same general vicinity. The life color of the *Plagiotremus* was light olive buff with black markings. The life coloration of *M. smithi* is unknown. *Ecsenius bicolor* is also known from Ceylon, where a uniform dark brown

color form is common. The possibility that *E. bicolor* is involved in a mimetic relationship with *M. smithi* should be considered. If the relationship should involve only *M. smithi* and *Plagiotremus* sp., it might shed valuable light on the position of *P. townsendi* with regard to the other two Red Sea mimetic blenniids.

Plagiotremus townsendi, *P. laudandus*, and the undescribed species of *Plagiotremus* from Ceylon comprise a closely related group of species. This group is easily differentiated from the six other *Plagiotremus* species. Each of the three species in the group, including the two color forms of *P. laudandus*, is strikingly similar to a sympatric species or subspecies of *Meiacanthus*, and each of these four *Plagiotremus-Meiacanthus* pairs is allopatric. Although more documentation is needed to demonstrate that any of these pairs is actually involved in a mimetic relationship, it is difficult to attribute the parallel physical similarities and geographic occurrences of the species pairs as a whole to anything other than mimicry.

Meiacanthus lineatus and *Petroscirtes* sp.

PLATE 4 c, d

Springer observed *Meiacanthus lineatus* (De Vis) and an undescribed species of *Petroscirtes* swimming together in small schools at One Tree Island, Great Barrier Reef. At the time of these observations, 1966, he thought the schools comprised a single species, although he noted that the fish in the schools were of two types that differed only in the presence or absence of a black stripe in the dorsal fin. Both types were black, yellow, and white striped with yellow caudal fins. Examination of preserved specimens indicated that the form with the black stripe in the dorsal fin was *Meiacanthus lineatus*, and the form without the stripe was an undescribed species of *Petroscirtes*. Many museum collections were found to contain jars with a mixture of both species. Under the name *Petroscirtes lineatus* De Vis (= *Meiacanthus lineatus*), Whitley (1926) reported, "black band on dorsal present or absent." Examination of the specimens upon which Whitley's description was based revealed a mixture of the two species.

The following numbers of *M. lineatus* and *Petroscirtes* sp. were taken in eight poison collections at One Tree Island (attempts were made to obtain all blenniids killed):

NUMBER OF SPECIMENS COLLECTED

	Station number								Total
	1	4	8	9	13	14	18	19	
<i>Meiacanthus lineatus</i>	1	0	11	6	8	15	11	3	55
<i>Petroscirtes</i> sp. . . .	3	2	1	4	5	1	2	1	19

The greater abundance of *M. lineatus* and the fact that the food of the two species is similar (invertebrates, indicating a nonpredatory relationship to other fishes) leads us to propose that *Petroscirtes* sp. is a Batesian mimic of *M. lineatus*.

Meiacanthus grammistes and *Petroscirtes breviceps polyodon*

PLATE 5 a, b

Several museum collections (supposedly sorted to species), especially those from the Palau Islands, have been found to contain a mixture of *Meiacanthus grammistes* (Valenciennes) and young *Petroscirtes breviceps polyodon* (Bleeker). The geographic range of *M. grammistes* covers much of the western Pacific Ocean and completely overlaps the range of *P. b. polyodon*, which is somewhat more restricted. In life, *M. grammistes* is black, white, and yellow striped. The yellow areas are confined to the anterodorsal region and the white areas grade into pale blue posteriorly. The background color of *P. b. polyodon* is yellow, based on a colored figure in the unpublished portion of Bleeker's atlas of fishes in the files of the Leiden Museum. *M. grammistes* is more common in collections from localities where both species occur, and in view of the facts known about the relationship between *M. lineatus* and *Petroscirtes* sp. from One Tree Island, *P. b. polyodon* is probably a Batesian mimic of *M. grammistes*, if a mimetic relationship indeed exists.

Meiacanthus anema and *Amblygobius linki*

PLATE 5 c, d

Meiacanthus anema (Bleeker) and *Amblygobius linki* Herre (family Gobiidae) occur in Indonesia and the Philippine Islands. A single museum collection from Buru, Indonesia, which was supposedly sorted to species, included a mixture of these two species comprising two unrelated families. *M. anema* (as *Petroscirtes kulambangree* Herre) was reported from fresh and brackish waters (Herre 1936), a habitat not

known for any of the other species of *Meiacanthus*. Gobiids frequently occur in fresh and brackish water and these two similar species could possibly be involved in a mimetic relationship. Herre (1936) stated that the life color of *M. anema* is blue with three black stripes. A colored illustration of a presumably fresh specimen of *M. anema*, in the unpublished portion of Bleeker's atlas of fishes in the files of the Leiden Museum, indicated that the pale areas were yellow; no blue areas were indicated. In preserved specimens, mature males are much darker than females and young males, suggesting that there may be a sexual difference in color of mature individuals, which would account for the apparent discrepancy between Herre's description and Bleeker's figure. The life color of *A. linki* is unknown, and none of the specimens available to us is in good condition. Herre (1927) gives an illustration of *A. linki*, which we reproduce in Plate 5d. Inasmuch as most gobiids do not prey on fishes, the mimetic relationship, if one exists, is probably Batesian.

There is another gobiid species, *Calleleotris helsdingenii* (Bleeker), that is also as similar to *M. anema* as is *A. linki*. The distribution of *C. helsdingenii* overlaps that of *M. anema*, and the possibility that these two species are involved in a mimetic relationship should be considered. Smith (1949, plate 73) gives a colored illustration of *C. helsdingenii*.

Thalassoma lucasanum and *Plagiotremus azaleus*

PLATE 6 a, b

Hobson (1969) reported that individuals of the eastern Pacific species *Plagiotremus azaleus* (Jordan and Bollman) regularly occurred in aggregations of adult *Thalassoma lucasanum* (Gill) (family Labridae), which it superficially resembles. *P. azaleus* occurred in aggregations of no other species. Hobson supposed that *P. azaleus* possibly derived benefit from this association in two ways: the similarity of the blenny to the harmless wrasse might enable it to go unnoticed as its prospective prey passed nearby; members of an aggregation might attain a degree of protection from predators similar to that enjoyed by members of schools, as many predators find difficulty in isolating a target when confronted with a group of closely spaced prey, especially when the prey are similar in appearance (Eibl-Eibesfeldt 1962).

Anthias squamipinnis* and *Ecsenius midasPLATE 6 *c, d*

Starck (1969) discussed mimicry between the Indo-west Pacific blenniid species *Ecsenius midas* Starck and *Anthias squamipinnis* Peters (family Serranidae). He observed this blenniid among aggregations of the serranid in the Seychelles and believed that the blenniid was the mimic, because it was much less abundant than the serranid. He was not able to establish the basis for the mimetic association, but believed that the blenniid probably was protected from predation because of the difficulty a predator has in singling out a prey from a large group (Eibl-Eibesfeldt, 1962; Hobson 1969). Although we made numerous observations of *A. squamipinnis* in the Gulf of Aqaba, we never saw any *E. midas*. Rotenone collections from the Gulf of Aqaba, made by Springer in 1969, contain approximately 1,000 specimens of *A. squamipinnis*, which was only a fraction of those killed; only 2 specimens of *E. midas* were in the same collections. *A. squamipinnis* females are much more abundant than males and are generally brilliant orange in life; males are generally deep red-purple. *E. midas* is similar in color only to female *A. squamipinnis*.

Dr. L. Fishelson recently informed us that he collected a group of live *A. squamipinnis* in the Gulf of Aqaba. When the anthiids were placed in an aquarium, one *E. midas* was found among them. He stated that the *E. midas* and female *A. squamipinnis* are very similar in life color and swimming habits.

Labroides dimidiatus*, *Aspidontus taeniatus*, and *Aspidontus filamentosus

PLATE 7

One of the best known examples of mimicry (aggressive mimicry involving three or more species, Wickler, 1968) in fishes is that of the mimic blenny, *Aspidontus taeniatus* Quoy and Gaimard, and the cleaner wrasse, *Labroides dimidiatus* Bleeker (family Labridae). Both species are widespread in the Indo-west Pacific. Eibl-Eibesfeldt (1959) and Randall and Randall (1960) described this mimetic association in detail.

A. taeniatus feeds primarily on the mucus and fins of fishes, although it may also feed on annelids. *L. dimidiatus* is a cleaner fish and, as such, is able to approach predatory fishes with immunity, even enter-

ing their buccal cavities. The unusually close similarity in appearance of these two species allows the blenny to approach its potential prey and to nip its fins. No studies have been made to determine just how well protected *A. taeniatus* is from predation.

Randall and Randall (1960) and Wickler (1963, 1968) noted that *A. taeniatus* is usually successful only in attacks on young fishes. Apparently the juveniles soon learn to recognize the subtle differences between the blenny and the wrasse and to avoid the blenny. Memory of negative experiences with the blenny presumably persists in adult individuals of the blenny's prey. How long such memory persists is open to question as experimental mimetic studies have shown that a predator continues to make occasional mistakes even after repeated negative experiences with an unacceptable prey (Brower 1958a, b, c). The attack of *A. taeniatus* is not particularly destructive and a prey species would probably also have to be reminded from time to time to avoid the blenny.

Barnard (1927) first noticed the close similarity in appearance of *A. taeniatus* and *L. dimidiatus*; however, Barnard may have confused *A. filamentosus* (Valenciennes) with *A. taeniatus* (see Smith 1947), a closely related species with a similar adult color and appearance to *A. taeniatus* (see Smith, 1949, plate 21, figure 961, for a colored illustration of *A. filamentosus*). In spite of a possible error in identification, Barnard's remarks generally apply to both species. Barnard reported that southern African specimens of *A. taeniatus* and *L. dimidiatus* had forms with and without a black bar on the pectoral fin base. Actually, in the blennies the bar is on the fleshy pectoral fin base under the level of the posterior margin of the opercle. In the wrasse it is at the posteroventral corner where the fleshy pectoral base joins the body, but it is also under the level of the posterior margin of the opercle. Randall (1958) and Randall and Randall (1960) noted that there are parallel geographic color-pattern populations of both species.

With regard to the presence or absence of a black bar in the region of the pectoral fin base, we found that 93 of 95 specimens of *A. taeniatus* examined (data on some specimens furnished by J. E. Randall), from scattered localities throughout the Pacific Ocean portion of its distribution, lack such a black bar. The exceptions are two of 18 specimens from the Palau Islands that have a minute black spot on the pectoral fin base. All 7 specimens from the Red Sea and 24

from the Indian Ocean (including both the eastern and western portions) have a black bar on the pectoral fin base. Specimens from the Red Sea and Indian Ocean probably rarely, if ever, lack the black bar.

Ninety-eight of 248 specimens of *L. dimidiatus* from throughout the Pacific Ocean range of the species lack the black bar in the region of the pectoral fin base. None of those specimens with a black bar came from east of the Marshall Islands and few without a black bar came from west of the Mariana Islands. Specimens of *L. dimidiatus* with the black bar and *A. taeniatus* without the black bar commonly occurred together in collections from the Pacific Ocean. In the Indian Ocean, specimens of *L. dimidiatus* were available only from Aldabra Island, all 54 of which have a well-developed black bar. All 12 of the Red Sea specimens with adult color pattern (juveniles lack the bar) also have the black bar.

Typically, preserved specimens of *A. taeniatus* have the black body stripe ending as a large black area covering most of the caudal fin. One specimen from the Palau Islands and a few Indian Ocean specimens exhibit some evidence of the black marking on the caudal fin forming a ventrally curving hook, which is pale centrally (as illustrated in Wickler, 1968, page 161), but the central paling is not as obvious as it apparently is in life.

While our manuscript was in press, J. E. Randall sent us eight uniquely pigmented specimens of *Aspidontus taeniatus* from the Marquesas Islands. Based on a color transparency of a freshly collected specimen, their fins, except for the transparent pectorals, were pale gray. A dark lateral stripe, in the same position as in normally pigmented *A. taeniatus*, is present anteriorly, but is less intense and somewhat brown posteriorly and does not extend far onto the caudal fin. The background color of the body is pale gray, almost white ventrally. Randall observed the pale *A. taeniatus* in the vicinity of a group of similarly pigmented wrasses belonging to an apparently undescribed, endemic species of *Coris*. *Labroides dimidiatus* and typically pigmented *A. taeniatus* were also present in the area, but it is not known if the typical *A. taeniatus* also associated with the pale *Coris*.

Wickler (1968: 169) noted that blennies have a pronounced ability to change color pattern with change in emotional state. One of four such patterns of *A. taeniatus* illustrated by Wickler (1968, fig. 37c) closely approximates that of the pale Marquesas indi-

viduals. This suggests that the pale pattern is derived from the typical pattern. The apparent restriction of the pale *Coris* to the Marquesas Islands may explain the absence of the pale form of *A. taeniatus* elsewhere. Randall noted that *A. taeniatus* appeared to be more abundant in the Marquesas than elsewhere, and suggested that this might, in part, account for the apparent switchover of some individuals to another model.

All specimens of *L. dimidiatus* from Aldabra Island have the black stripe on the body continuing as a distinct ventrally curving hook on the caudal fin, pale centrally. Pacific Ocean specimens variably have the stripe ending as a large black area covering most of the caudal fin or forming a ventrally curving hook, pale centrally. Specimens with the hook usually have the black bar at the pectoral fin base, while specimens without the hook usually lack the black bar. The black hooklike mark is obvious in the caudal fins of all Aldabra specimens of *L. dimidiatus*, but the one specimen of *A. taeniatus* available from Aldabra has the stripe ending as a large black area on the caudal fin.

Aspidontus filamentosus has not been reported as a possible mimic of *L. dimidiatus*. *A. filamentosus* has much the same geographic distribution as does *A. taeniatus* and *L. dimidiatus*. We have examined 5 specimens of *A. filamentosus* from the Indian Ocean and 91 specimens from the Pacific Ocean. All of the Indian Ocean specimens, but none of the Pacific Ocean specimens, have a dark bar on the pectoral fin base. The general similarity in color pattern and the parallel geographic color-pattern changes are strong circumstantial evidence favoring a mimetic relationship between *A. filamentosus* and *L. dimidiatus*. *A. filamentosus* and *A. taeniatus* are a very closely related species pair. *A. taeniatus* feeds primarily on the mucus and fins of living fishes, although it may also feed on annelids. The stomachs were empty in all specimens of *A. filamentosus* examined, but presumably the feeding behavior is similar to that of *A. taeniatus*. If this is true *A. filamentosus* is also probably an aggressive mimic of *L. dimidiatus*.

Acknowledgments

We wish to express our appreciation to Drs. F. D. Por and the late H. Steinitz, Hebrew University, Jerusalem, for their hospitality, encouragement, and aid in administrative matters pertaining to our work in Israel. Dr. A. Ben-Tuvia, Sea Fisheries Research Station,

Haifa, was instrumental in obtaining and shipping live Mediterranean fishes to us in Eilat. Mr. David Fridman, Eilat, gave freely of his time and extensive knowledge of the behavior and distribution of local fishes. Dr. L. Fishelson, University of Tel Aviv, made several valuable suggestions for our field work. Dr. H. D. Roth and Mrs. P. J. Hicks, Smithsonian Institution, provided advice on statistical techniques. Dr. J. E. Randall, Bishop Museum, generously provided original observations, color slides, and loans of specimens pertinent to our study. Dr. C. Swift, Los Angeles County Museum, provided information on, and loans of, specimens under his care. Mr. K. Karb, Arlington, Virginia, made histological sections and photographs of the *Meiacanthus* glands.

Drafts of the manuscript were critically reviewed and substantially improved by Drs. B. B. Collette, National Marine Fisheries Research Service, L. Brower, Amherst College, L. Fishelson, University of Tel Aviv, G. S. Losey, University of Hawaii, A. A. Myrberg and C. R. Robins, University of Miami, and R. L. Jachowski, S. H. Weitzman, and G. R. Zug, Smithsonian Institution. Dr. U. Nur, University of Rochester, offered valuable comment on the relative abundance section of the manuscript.

Funds in support of this study were derived from a Smithsonian Institution Walter Rathbone Bacon Fund grant to Springer and from a Smithsonian foreign currency grant, SFC-7-1002, Drs. W. I. Aron and F. D. Por, principal investigators.

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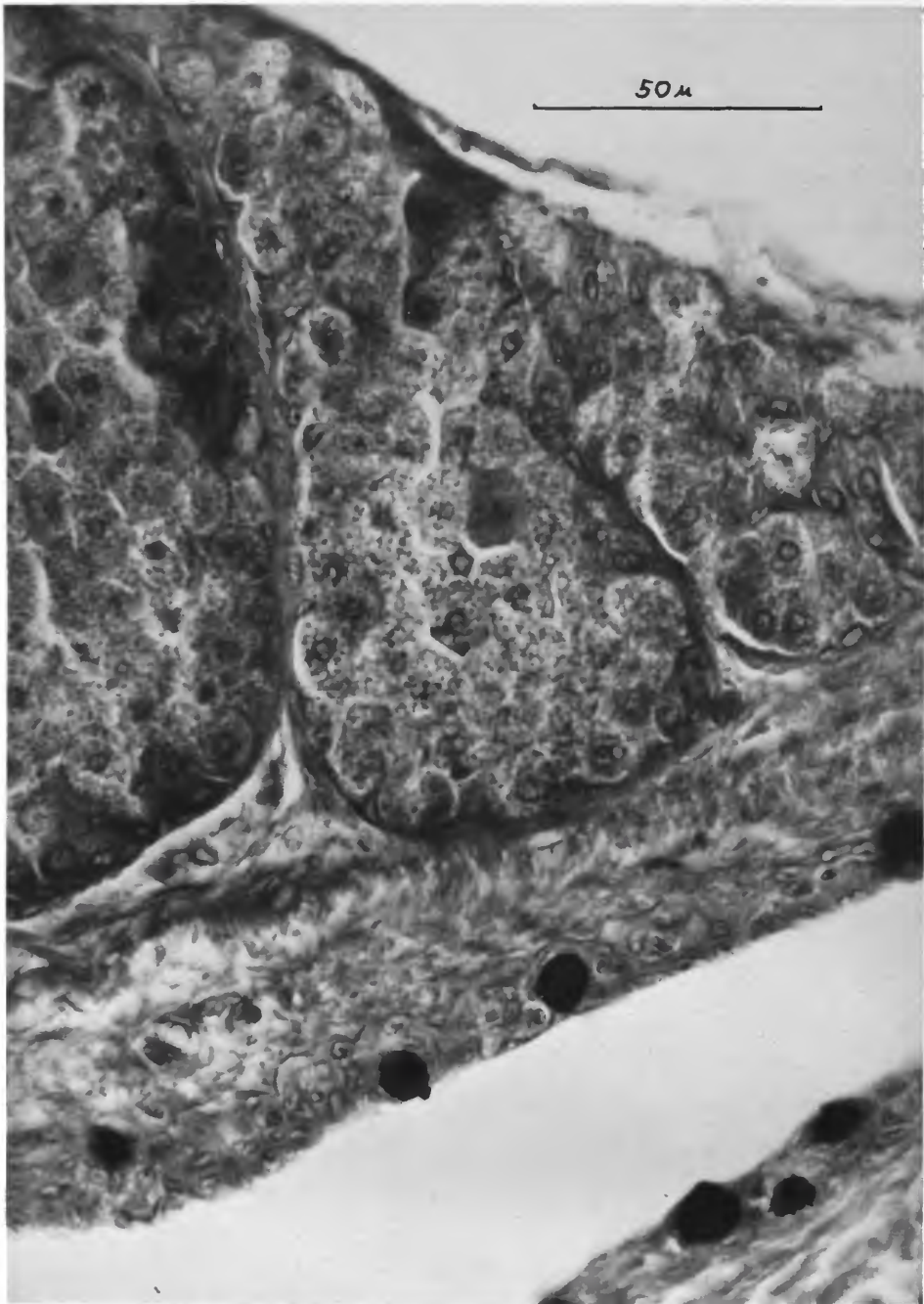


PLATE 1.—*Meiacanthus grammistes*, histological section of portion of dentary gland showing compartments separated by connective tissue. Large, dark, circular bodies at bottom of field lie in connective tissue that surrounds gland. Large, pale areas are continuous with the buccal cavity.

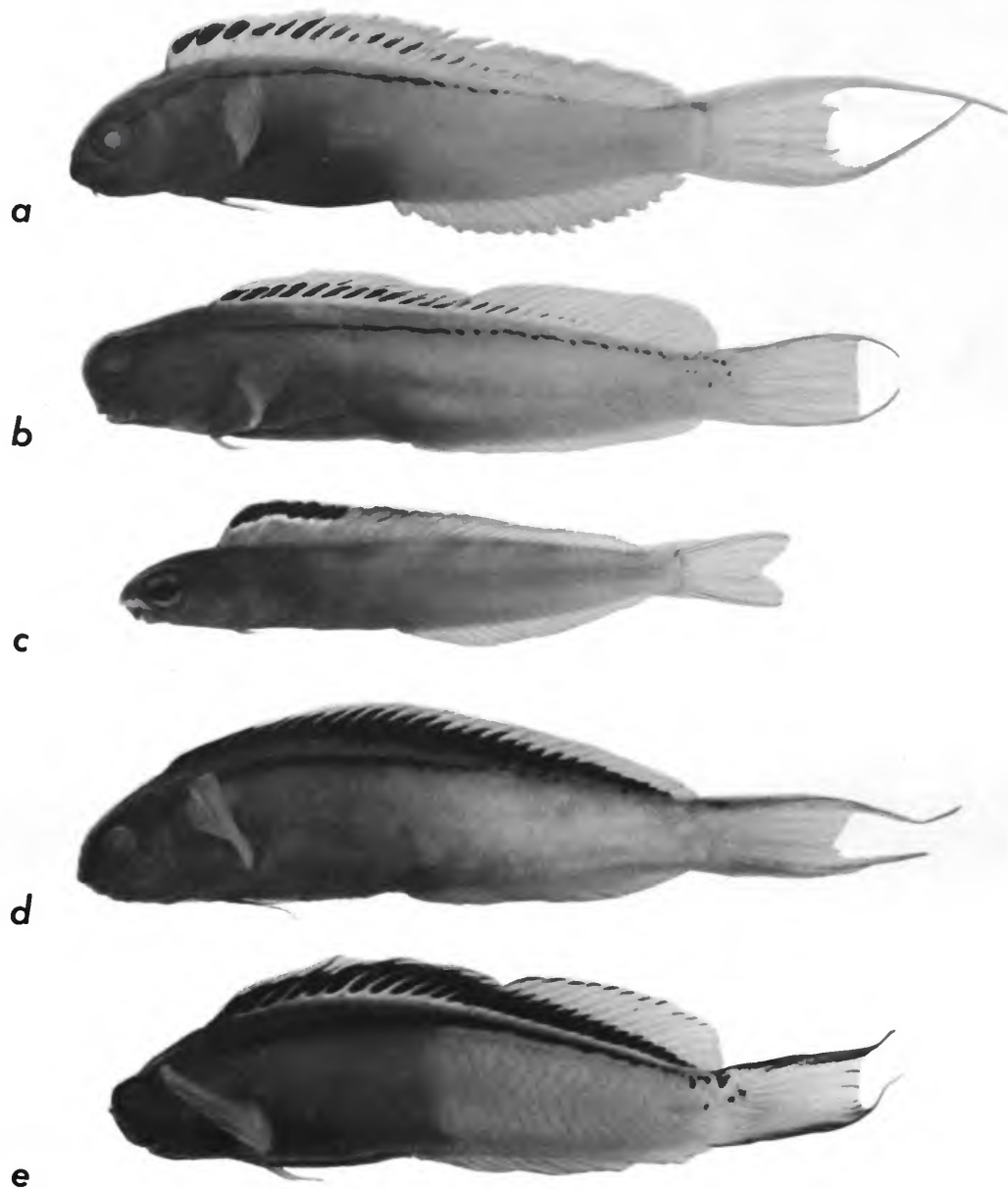


PLATE 2.—*a*, *Meiacanthus nigrolineatus*, USNM 205378, 45.6 mm SL, male, representative of darkest Gulf of Aqaba specimens; *b*, *Ecsenius gravieri*, USNM 204696, 46.2 mm SL, female, representative of darkest Gulf of Aqaba specimens; *c*, *Plagiotremus townsendi*; USNM 205379, 24.5 mm SL, female, Gulf of Aqaba; *d*, *Meiacanthus nigrolineatus*, USNM 204486, 49.3 mm SL, male, representative of palest specimens from Ethiopian coastal waters; *e*, *Ecsenius gravieri*, USNM 204480, 39.8 mm SL, female, representative of palest specimens from Ethiopian coastal waters.

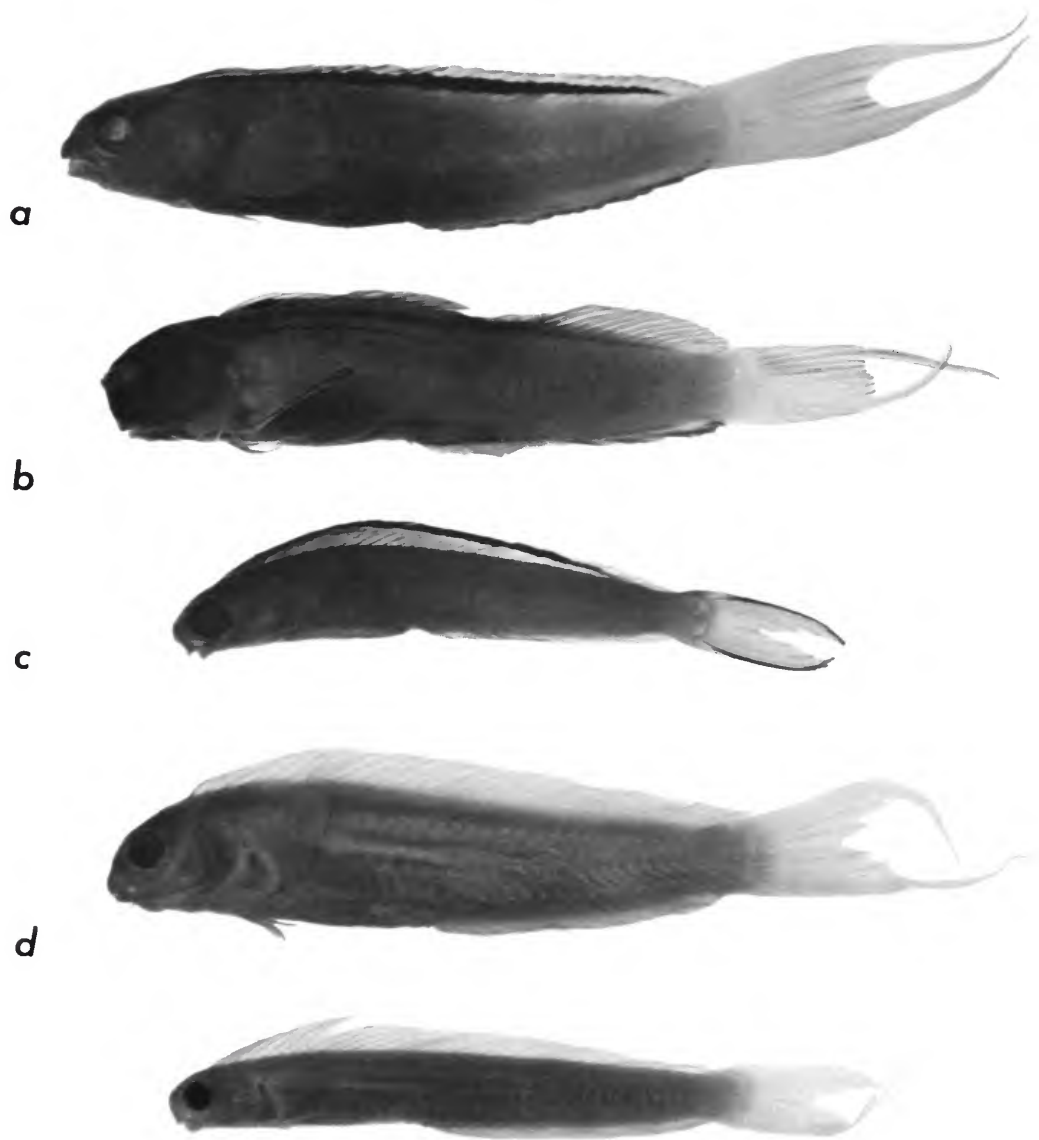


PLATE 3.—*a*, *Meiacanthus a. atrodorsalis*, USNM 201593, 50.2 mm SL, male, One Tree Island, Great Barrier Reef; *b*, *Ecsenius bicolor*, USNM 201368, male, 57.6 mm SL, One Tree Island, Great Barrier Reef; *c*, *Plagiotremus laudandus*, USNM 201413, 28. mm SL, male, Vanikoro Island, Santa Cruz Islands; *d*, *Meiacanthus atrodorsalis oualanensis*, USNM 201455, 58.5 mm SL, male, Fiji Islands; *e*, *Plagiotremus laudandus*, USNM 201676, 46.8 mm SL, female, Fiji Islands.

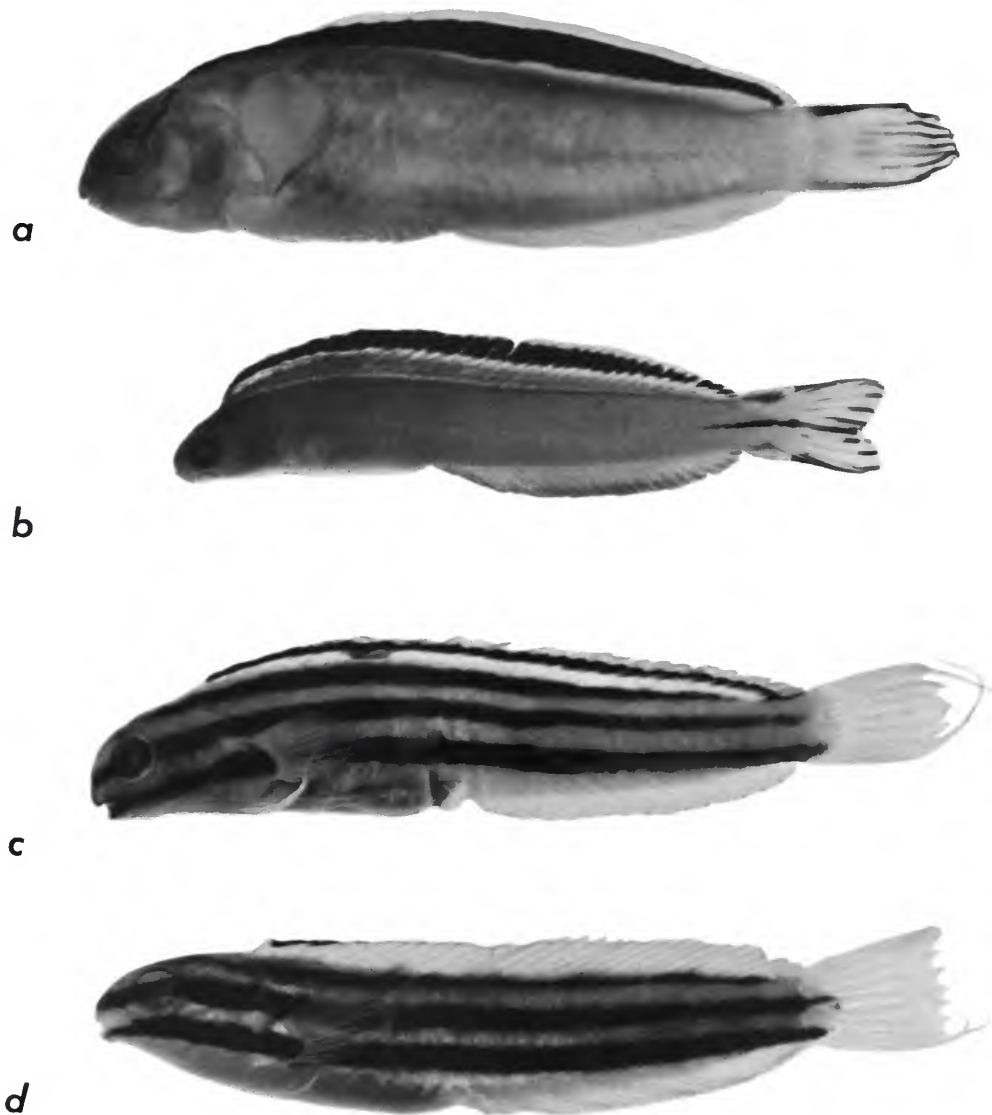


PLATE 4.—*a*, *Meiacanthus smithi*, USNM 205284, 54.2 mm SL, Trincomalee, Ceylon; *b*, *Plagiotremus* sp., USNM 204699, 34.1 mm SL, Trincomalee, Ceylon; *c*, *Meiacanthus lineatus*, USNM 201363, 62.8 mm SL, male, One Tree Island, Great Barrier Reef; *d*, *Petroscirtes* sp., USNM 201799, 54.7 mm SL, male, One Tree Island, Great Barrier Reef.

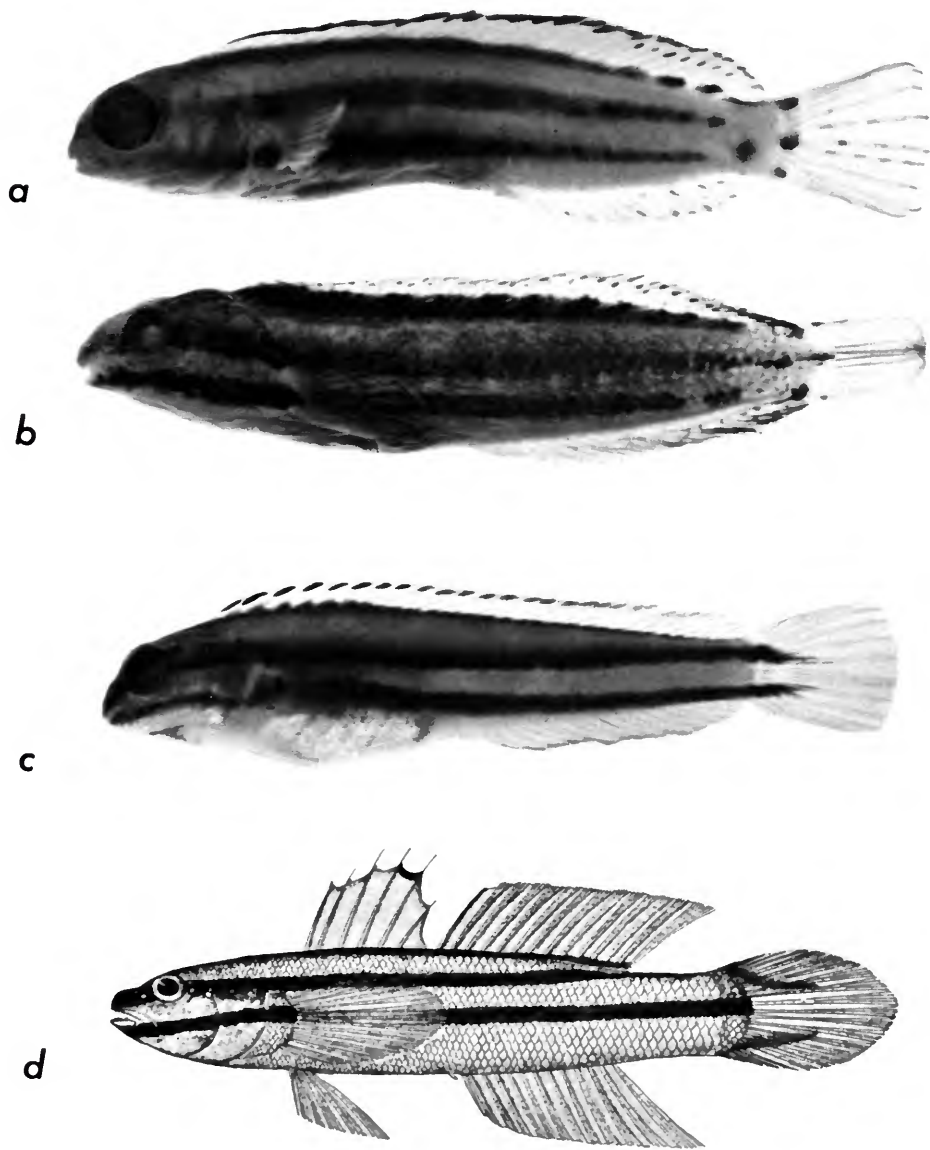


PLATE 5.—*a*, *Meiacanthus grammistes*, CAS GVF-registration no. 1397, 40.9 mm SL, female, Palau Islands; *b*, *Dasson breviceps polyodon*, BPBM 7452, 45.2 mm SL, male, Palau Islands; *c*, *Meiacanthus anema*, CAS GVF-registration no. 1820, 30.6 mm SL, female, Santa Cruz Islands; *d*, *Amblygobius linki*, after Herre (1927, plate 18: figure 4).

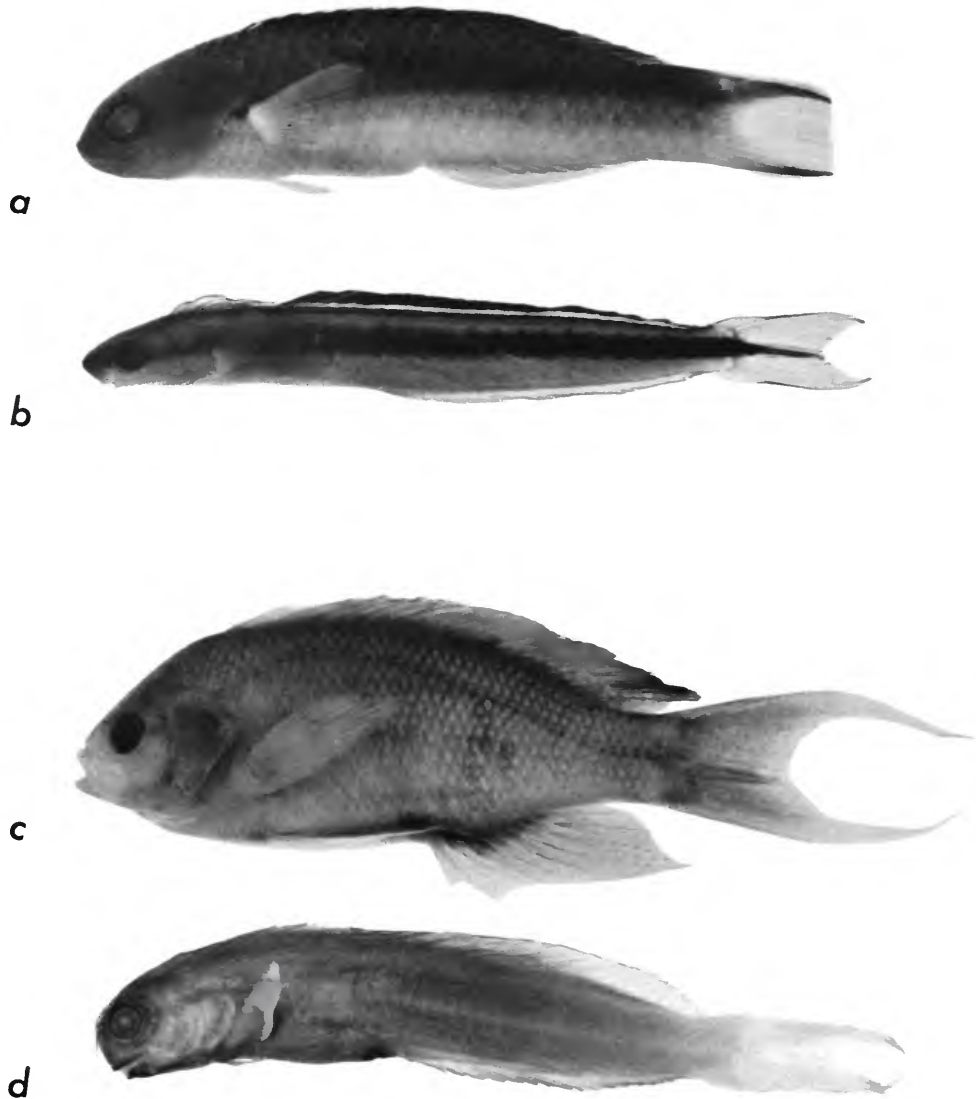


PLATE 6.—*a*, *Thalassoma lucasanum*, LACM 6894-33, 49.0 mm SL, sex indeterminate, Playa del Coco, Costa Rica; *b*, *Plagiotremus azalea*, LACM 6894-11, 52.3 mm SL, female, Playa del Coco, Costa Rica; *c*, *Anthias squamipinnis*, USNM uncat. (VGS 69-2), 74.8 mm SL, female, Gulf of Aqaba; *d*, *Ecsenius midas*, USNM 204707, 77.1 mm SL, male, Ras Muhammad, southern tip of Sinai Peninsula.

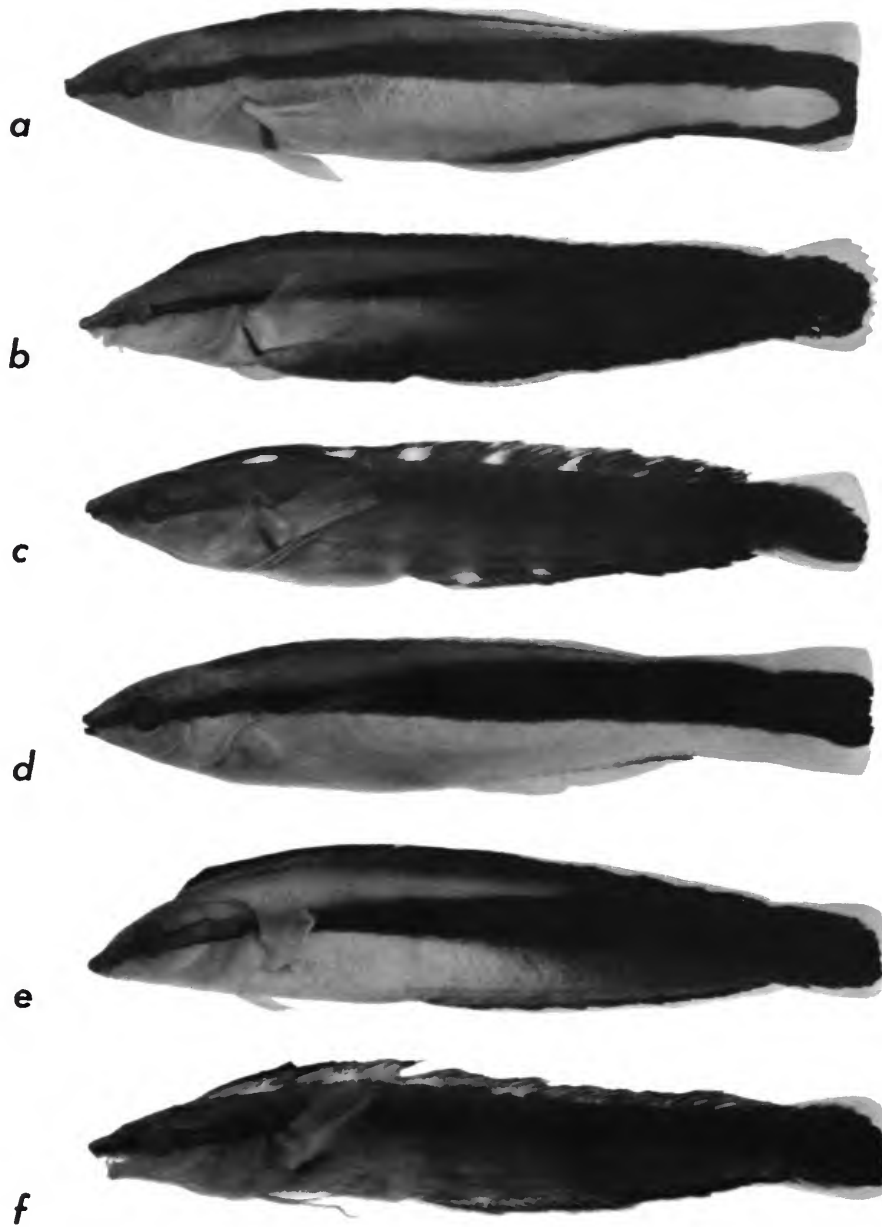


PLATE 7.—*a*, *Labroides dimidiatus*, USNM 205283, 66.2 mm SL, sex indeterminate, Aldabra Atoll; *b*, *Aspidontus taeniatus*, USNM 201563, 84.7 mm SL, male, Comoro Islands; *c*, *Aspidontus filamentosus*, USNM 199432, 48.7 mm SL, male, Comoro Islands; *d*, *Labroides dimidiatus*, USNM 205282, 64.9 mm SL, sex indeterminate, One Tree Island, Great Barrier Reef; *e*, *Aspidontus taeniatus*, ANSP 109672, 70.1 mm SL, male, Endeavour Reef, Great Barrier Reef; *f*, *Aspidontus filamentosus*, USNM 205548, 44.5 mm SL, female, Kuria Island, Gilbert Islands.

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