

A Description and Experimental Analysis of Batesian Mimicry between a Marine Gastropod and an Amphipod¹

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ABSTRACT: An apparent case of Batesian mimicry is described between three co-occurring species of the marine gastropod *Lacuna* (the model) and an amphipod mimic (*Stenopleustes*). Similar characteristics include size, color pattern, and locomotory behavior on eelgrass blades. Both animals inhabit subtidal eelgrass beds, but the mimic is only 1.0-4.2 percent as common as the model. Predatory fish (Cottidae, Pholidae) from the eelgrass habitat rarely eat *Lacuna* or *Stenopleustes* (shown by fecal analysis) but will readily eat *Stenopleustes* if the mimic betrays its snail disguise by swimming. Only 8.8 percent of the *Stenopleustes* (which walks along eelgrass blades and seldom swims) were eaten, compared to 62.5-percent predation of a co-occurring nonmimetic gammarid amphipod (which often swims), in laboratory predator-prey experiments. These data suggest that the amphipod, by resembling a conspicuous and relatively inedible snail, enjoys a protective advantage from predation by fish in the eelgrass habitat.

EXAMPLES OF MIMICRY among marine invertebrates appear to be exceedingly rare. To my knowledge, only one description of a possible mimetic relationship (Crane 1969) has been published. This instance reported the similarity in appearance between *Mitrella carinata*, a small gastropod abundant in the kelp beds off southern California, and the pleustid amphipod *Pleustes platypa*. The basis for mimicry rested upon similarity in color pattern and body shape. The mimic, *Pleustes*, is evidently rare but occupies the same habitat as the gastropod model.

The present report deals with another example of apparent mimicry between two marine invertebrates. The mimic, a pleustid amphipod (*Stenopleustes*), appears to resemble closely several species of snails (genus *Lacuna*). The aim of this paper is to present observations and experimental results that attempt to verify the hypothesis that *Stenopleustes* effectively mimics *Lacuna*. Wickler (1968) has pointed out that the phenomenon must be investigated in terms of

evolutionary questions concerning functional relationships between the species under study. For example, it would be interesting to know, in the amphipod-mollusk example of Crane (1969), whether the resemblance includes behavioral similarities and whether any predators are deceived by the amphipod. The following two conditions have been set forth by Wickler (1968: 50) as being necessary for proof of functional mimicry: "(1) the demonstration that a predator or other signal receiver responds to the signals involved in the manner postulated; (2) the demonstration that this response is an advantage to the organism that transmits the signals."

Stenopleustes and *Lacuna* appear to represent a case of Batesian mimicry. This form of mimicry was first proposed by Henry Bates (1862), who hypothesized that a palatable species could obtain protection from predators by resembling a distinctly marked, unpalatable species that is avoided by predators. Bates observed this false warning coloration in South American butterflies, which mimicked brightly colored, unpalatable species of the family Heliconiidae. Batesian mimicry has since been reported in many other terrestrial arthropod orders (for reviews see Cott 1957, Sheppard 1959, Holling

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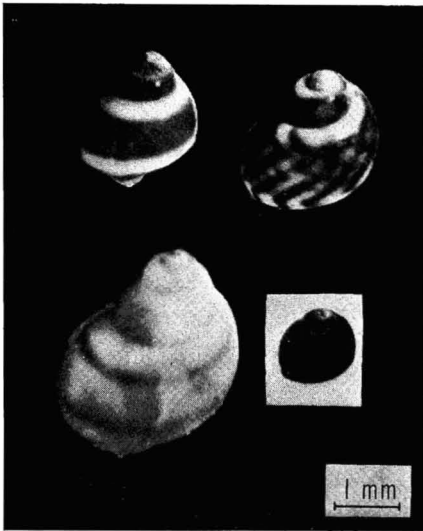


FIG. 1. Shells from the four species of *Lacuna* found in *Zostera* beds, illustrating the variety of color patterns. From left to right, top row: *Lacuna* sp., *L. variegata*; bottom row: *L. vincta*, *L. marmorata*.

1964, and Wickler 1968), but, strangely, is exceedingly rare among invertebrates in the marine environment.

MATERIALS AND METHODS

The animals were collected at Turn Island and San Juan Island, near Friday Harbor, Washington, by sweeping an 8-inch net (1 mm nylon mesh) through beds of eelgrass (*Zostera*) in the shallow subtidal zone. The pleustids were sorted from the initial samples and placed in 1-gallon tanks of fresh, circulating seawater, each containing several *Lacuna* and blades of *Zostera*. Initial observations on coloration and behavior were made on approximately 12 amphipods collected over a 2-week period.

To estimate the relative abundance of pleustids and *Lacuna* and to determine what other similar prey animals might coexist in the *Zostera* habitat, I collected 50 replicate sweep samples (using the same net) from the Turn Island location. Three additional collections were made from a boat at Beaverton Cove (San Juan Island) by sweeping the net through eelgrass beds for 5 minutes per collection. A total

of 140 pleustid amphipods were examined in this study.

A 10-foot beach seine (4-mm mesh) was pulled through eelgrass beds at Turn Island to collect fish which might be likely predators of pleustids. Collections were made on 2 separate days. All fish were isolated for 2 days in mesh-covered aquaria that were immersed in a tank of circulating seawater. At the end of this period, the feces from eight fish (representing five species and two families) were examined to determine the fishes' diets and, in particular, whether they had preyed upon amphipods or snails.

A series of feeding experiments was carried out with 18 fish of the two most common genera, *Oligocottus* and *Pholis*. Each fish was kept in an immersed, mesh-covered aquarium with various prey animals, whose survival was recorded daily for up to 3 days. Cover for the prey consisted of five *Zostera* blades per aquarium.

RESULTS

Color Pattern Similarities

A variety of colors and patterns exists in the genus *Lacuna* in the San Juan Islands, but not all of these patterns are mimicked by pleustids. Unfortunately the taxonomy of *Lacuna* has been confused by apparent hybridization among the local species. Four species have been reported by Johnson (1960), two of which hybridize (the *L. variegata*-*L. marmorata* complex) and two of which are polychromatic (*L. vincta* and *Lacuna* sp.). *Lacuna variegata* represents one extreme (a pure species) of the *variegata*-*marmorata* complex (Fig. 1). A brown checked pattern covers each whorl, on the upper border of which is a white band, just below the suture. This form and closely colored hybrids do not appear to have counterparts in the pleustid mimics. The other extreme of the hybrid complex is represented by *L. marmorata*, a small dark purple to brown snail that is evenly colored and possesses a keeled whorl and low spire (Fig. 1). *Lacuna vincta*, a polychromatic species, is distinguished from those above by its higher spire (Fig. 1) and fewer number of cusps (three to four) on the fourth lateral radular tooth (compared to five or six cusps in the *variegata*-*marmorata* complex).

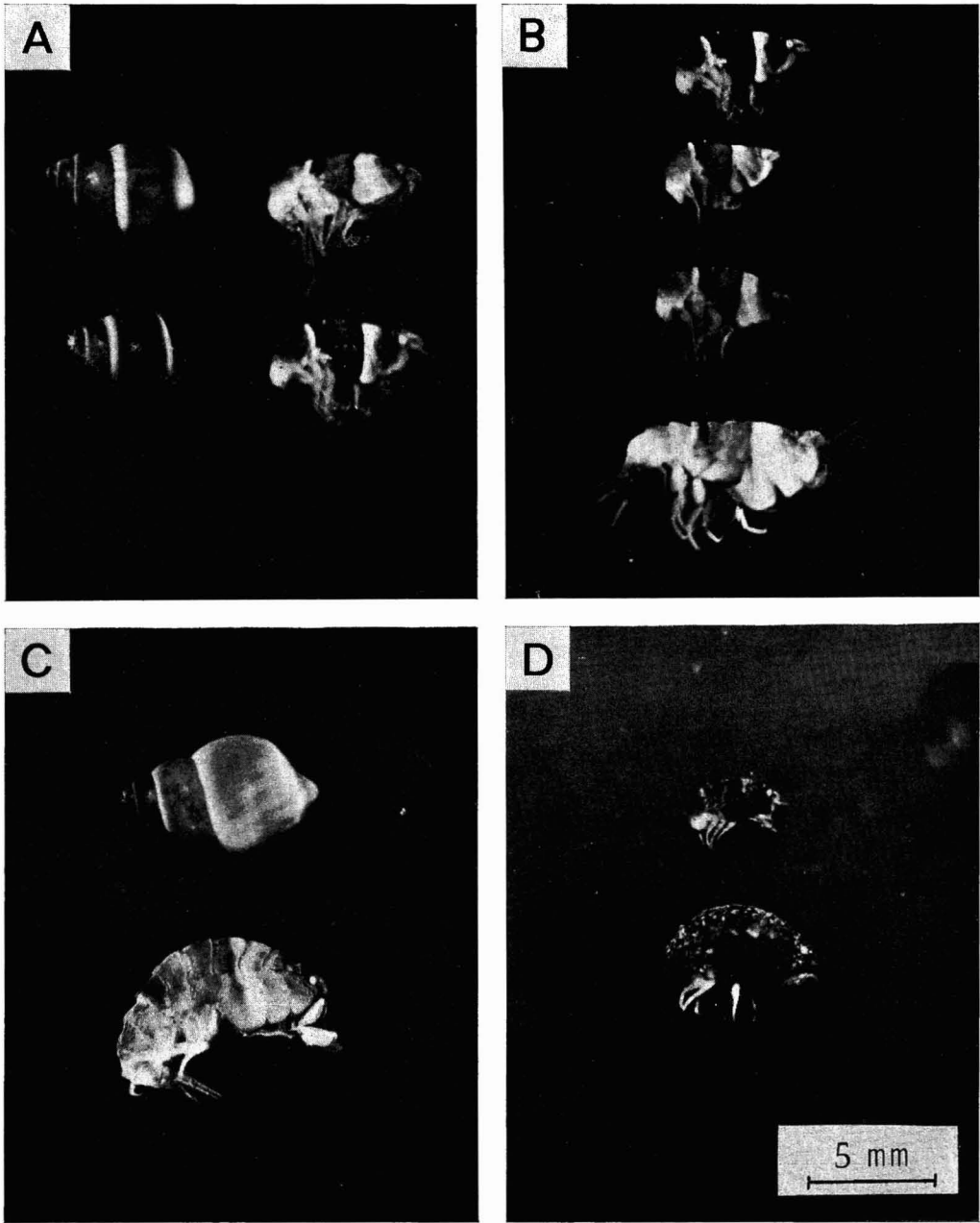


FIG. 2. Color patterns of the pleustid amphipods examined in this study, together with *Lacuna* specimens that appear to serve as models. *A*, the most common pattern, which mimics the banded forms of *L. vineta* and *Lacuna* sp.; *B*, variation in darkness of the *Stenopleustes* pattern shown in *A*; *C*, a large, light buff pleustid that resembles the more pale forms of *L. vineta*; *D*, the small dark pleustids that resemble *L. marmorata*. All of these animals were freshly killed with 5-percent formaldehyde before being photographed.

The fourth species, designated *Lacuna* sp. by Johnson (1960), is undescribed but resembles *L. vincta* in general morphology (Fig. 1). The two differ in that *Lacuna* sp. has five to six cusps on the fourth radular tooth, and the aperture has a truncate or concave anterior lip, as contrasted to the rounded aperture lip of *L. vincta*. The color pattern of these two species may be either uniform or banded. The color varies from pale buff to chestnut brown or purple.

The taxonomy of the family Pleustidae is somewhat confused, but the specimens in the present study all appear to belong to the genus *Stenopleustes*, according to the scheme of Barnard and Given (1960). Of the amphipods examined, examples were found which matched *L. marmorata*, *L. vincta*, and *Lacuna* sp. in both color and pattern. The most common form of *Stenopleustes* was the one that mimicked banded forms of *Lacuna* sp. and *L. vincta* (Fig. 2A). These amphipods varied in color from buff to dark chestnut brown, with two white transverse bands across the pereon (Fig. 2B). They ranged from 2–7 mm in total body length. Some of the larger specimens were very light buff and more or less uniform in pattern due to weak banding; these resembled the large specimens of *L. vincta* of similar pattern (Fig. 2C). Occasionally small pleustids (1–4 mm) were encountered that had a dark brown to purple-brown, unbanded appearance similar to *L. marmorata* (Fig. 2D). As judged from sample collections, all of the color patterns in both *Lacuna* and *Stenopleustes* occurred together in local populations.

Behavioral Comparisons

Lacuna were observed to glide continually along *Zostera* blades while in aquaria. The longitudinal axis of the shell was usually positioned at an angle of 60°–90° to the longitudinal axis of the grass blade (Fig. 3A). Because of the animal's ditaxic mode of locomotion, the shell would rock laterally as the snail moved forward. These positions and movements were duplicated by *Stenopleustes*. In the normal resting position (Fig. 3B), the amphipod grasped the edge of the blade with three pairs of pereopods and faced transversely on it. Locomotion was accomplished by moving laterally along the blade edge, lifting the legs sequentially (Fig. 3C). The



FIG. 3. Photographs of living *Lacuna* and *Stenopleustes* on *Zostera* blades. A, typical position of *Lacuna* during locomotion; B, *Stenopleustes* in resting position; C, *Stenopleustes* during lateral walking, showing the legs gripping the *Zostera* blade.

TABLE 1

PERCENT COMPOSITION OF ANIMALS IN SWEEP NET COLLECTIONS FROM *Zostera* HABITATS

LOCATION	HERMIT CRABS	<i>Lacuna</i>	PLEUSTID AMPHIPODS	GAMMARID AMPHIPODS	ISOPODS	SHRIMP	TOTAL NO. OF ANIMALS	RATIO (%) OF NO. PLEUSTIDS/ NO. <i>Lacuna</i>
Turn Island	0.6	67.7	0.6	28.5	1.1	1.5	2379	1.0
Beaverton Cove								
Experiment A	0.0	92.7	2.5	0.3	0.7	3.8	206	2.8
Experiment B	0.0	94.1	3.4	0.0	1.0	1.5	2806	3.6
Experiment C	0.0	94.9	3.3	0.3	0.5	1.0	913	4.2

rate of movement was not qualitatively different from that of nearby *Lacuna*. *Stenopleustes* also showed a rocking behavior, involving a dipping of the body forward and back. This often occurred while the animals were stationary, but was also evoked whenever the *Zostera* blade was tapped or moved by the observer. While walking, *Stenopleustes* would often stop and rock, then continue. This rocking behavior resulted in movements similar to the rocking of *Lacuna* during locomotion. In general, the amphipods were reluctant to leave the *Zostera* blades; gentle prodding would cause an animal to move across the blade and down onto the underside, where it would cling to the opposite edge. Only when violently prodded or when the blade was lifted out of the water would the amphipods swim, but then only for a short (2–5 cm) distance to the nearest *Zostera* blade.

Relative Abundance of Mimic and Model

The percent composition of invertebrates in the sweep net samples is shown in Table 1. Pleustids accounted for 0.6 to 3.4 percent of the individual sample totals, whereas *Lacuna* comprised 67.7 to 94.9 percent. Other invertebrates found in the collections included hermit crabs, nonmimetic gammarid amphipods, isopods, and shrimp. Table 1 indicates the ratio of pleustids to *Lacuna* in four collections that were tabulated. This ratio varied from 1.0–4.2 percent. No effort was made to separate the *Lacuna* into species for these counts.

Predator-Prey Studies

The following fish species were seined from *Zostera* beds: *Oligocottus maculosus*, *Clinocottus*

acuticeps, *Leptocottus armatus*, *Pholis laeta*, and *P. ornata*. Fecal contents of eight fish were analyzed (Table 2) to gain an idea of the natural prey of these fishes. The diets were similar, being composed primarily of small crustaceans. They differed in that only cottids ate tanaidaceans whereas only pholids ate pinnotherid crabs, foraminifera, and two *Lacuna*. Copepods were more abundant in the cottid diet, whereas shrimp were more abundant in the pholid diet. Only one pleustid amphipod was recognized; most of the amphipods were gammarids. The *Lacuna* were undigested, owing, presumably, to protection from the opercula.

Four experiments were conducted with the two most common fish (*Oligocottus maculosus* and *Pholis laeta*) being used to test for a possible protective advantage experienced by *Stenopleustes*. The experiments were replicated in pairs, each with one *Pholis* and one *Oligocottus* that had not been fed for 3 days (summarized in Table 3). *Zostera* blades served as a substrate for the amphipods or snails. In experiment A, each fish was presented with only one prey species (*Lacuna* or *Stenopleustes*). This provided maximum predatory pressure on the prey species, thus testing whether either prey was acceptable to the fish. No *Lacuna* and one *Stenopleustes* were eaten. Experiments B and C tested whether the fish would show a preferential predatory distinction between *Stenopleustes* and either *Lacuna* or a nonmimetic (gammarid) amphipod species. When paired with *Lacuna* (experiment B), no prey were eaten; but, when paired with the gammarid amphipods (experiment C), one pleustid and two gammarids were eaten. Finally, experiment D tested whether the fish would show a predation preference when the mimic,

TABLE 2

FECAL ANALYSIS OF FISH SEINED FROM *Zostera* HABITAT AT TURN ISLAND

SPECIES	FAMILY	FECAL MATERIAL	COMMENTS
<i>Leptocottus armatus</i>	Cottidae	ostracods copepods isopods assorted cuticular parts	few few few
<i>Oligocottus maculosus</i> and <i>Clinocottus acuticeps</i>	Cottidae	copepods isopods amphipods barnacles shrimp tanaidaceans	many few chelae and assorted remains appendages only one few
<i>Pholis laeta</i>	Pholidae	shrimp crabs copepods ostracod foraminiferans barnacles <i>Lacuna</i> <i>Ulva</i>	many pinnotherids few only one appendages two, undigested small bits
<i>Pholis ornata</i>	Pholidae	crabs shrimp <i>Lacuna</i> pleustid amphipod foraminiferans	pinnotherids few one, undigested one many

model, and nonmimic were all present in the same container. In this case, one *Stenopleustes* and eight gammarids were eaten, but no *Lacuna* was eaten.

Interesting observations were made on the behavior of another group of fish (*Pholis laeta* and *Oligocottus maculosus*) that were kept individually in aquaria. The reaction of the fish appeared to depend upon the behavior shown by the various prey species when one of the latter was dropped into the water. When dropped into the aquaria, *Lacuna* were watched by the fish, but no further reaction occurred. *Stenopleustes*, when dropped in, would sink to the bottom, then intermittently would swim and rest for several seconds before becoming inactive. This behavior was observed by the fish, and in one instance a *Pholis* swam over and ate the amphipod. In contrast, nonmimetic gammarid amphipods would swim immediately and for longer periods when introduced into the aquaria. Both species of predators would watch these amphipods for a short while and then would usually approach and engulf them.

DISCUSSION

Various criteria have often been used in establishing cases of Batesian mimicry (e.g., Sheppard 1960). For example, the model must have a conspicuous color pattern, a feature that is certainly applicable to *Lacuna* as it moves against the green background of *Zostera*. Also, the mimic should closely resemble the model; *Stenopleustes* not only resembles the color pattern and the range of its variation in *Lacuna* but also shows similar locomotory behavior. The mimic should be less abundant than the model; in the present instance the pleustid amphipod was less abundant by a factor of 25 to 100 times (Table 2). Finally the species under consideration should coexist in the same habitat. That this is true for *Lacuna* and *Stenopleustes* is suggested indirectly by their common presence in the sweep net samples and by the knowledge that pleustids are benthic rather than planktonic animals (Barnard and Given 1960).

However, in attempting to determine whether the apparent relationship provides a selective

TABLE 3

FEEDING EXPERIMENTS WITH FISH AND VARIOUS PREY ANIMALS

EXPERIMENT	FISH (ONE PER AQUARIUM)	PREY	NO. OF PREY ADDED	NO. OF PREY EATEN	DURATION OF EXPERIMENT (DAYS)
A	<i>Oligocottus maculosus</i>	<i>Lacuna</i>	6	0	1
	<i>Pholis ornata</i>	<i>Lacuna</i>	6	0	3
	<i>Oligocottus maculosus</i>	<i>Stenopleustes</i>	6	0	1
	<i>Pholis laeta</i>	<i>Stenopleustes</i>	6	1	3
B	<i>Oligocottus maculosus</i>	<i>Stenopleustes</i>	3	0	1
		<i>Lacuna</i>	3	0	1
	<i>Pholis laeta</i>	<i>Stenopleustes</i>	3	0	3
		<i>Lacuna</i>	3	0	3
C	<i>Oligocottus maculosus</i>	<i>Stenopleustes</i>	3	0	1
		nonmimetic amphipod	3	0	1
	<i>Pholis laeta</i>	<i>Stenopleustes</i>	3	1	2
		nonmimetic amphipod	3	2	2
D	<i>Oligocottus maculosus</i>	<i>Stenopleustes</i>	5	1	2
		nonmimetic amphipod	5	5	2
		<i>Lacuna</i>	5	0	2
	<i>Pholis laeta</i>	<i>Stenopleustes</i>	5	0	2
		nonmimetic amphipod	5	3	2
		<i>Lacuna</i>	5	0	2
PREY SPECIES		TOTAL PRESENTED	TOTAL EATEN	PERCENTAGE EATEN	
<i>Lacuna</i>		28	0	0	
<i>Stenopleustes</i>		34	3	8.8	
nonmimetic amphipod		16	10	62.5	

advantage to *Stenopleustes* in an evolutionary sense, we may find it useful to review Wickler's criteria mentioned previously. First, does the signal-receiver respond to the signals as postulated (i.e., the fish avoids predation of the model or the mimic)? It is known (from the fecal analysis) that fish from the *Zostera* habitat only rarely prey upon *Lacuna*. The few snails found were neither crushed nor digested, and it is unlikely that *Lacuna* contributes to the predator's nutrition. Since most of the crustaceans in the feces were disarticulated (hence, were possibly crushed during ingestion), it is conceivable that *Lacuna* could be rejected when a fish closes its mouth on the hard shell. In this way a fish could learn to associate the *Lacuna* color pattern with inedibility and respond accordingly. Shell hardness is assumed to be the major deterrent against *Lacuna* predation, but it should be noted that, although not demonstrated, *Lacuna* may render itself unpalatable through chemical secre-

tion. *Stenopleustes*, although apparently palatable, is rarely eaten. The results of the experiments in Table 3 suggest that fish do eat pleustids. The observations made while dropping prey species into aquaria containing fish revealed that swimming behavior is evidently an important cue that triggers feeding by the fish. Thus *Lacuna* and immobile *Stenopleustes* were ignored; but when the pleustid or the nonmimetic amphipods began to swim, they were eaten. Therefore, the signal-receiver's response (i.e., to ignore the model or mimic unless it swims) is as postulated. Swimming would appear to be the one behavior that could immediately betray the snail disguise of *Stenopleustes*. It is interesting, therefore, to note that this amphipod could not readily be provoked into swimming.

The second of Wickler's criteria would seem to be met (although only tentatively) by the same set of observations and data. In asking whether the signal-receiver's (fish) response is

advantageous to the signal-transmitter (*Stenopleustes* and *Lacuna*), one must consider two lines of evidence. The first—analysis of fish fecal material—indicated that very few signal-transmitters are eaten. The second evidence comes from experiment D in which *Lacuna*, *Stenopleustes*, and the nonmimetic amphipod were placed in aquaria with *Zostera* blades and fish predators. The results showed that *Stenopleustes* had a much smaller chance of being eaten than did its nonmimetic counterpart, under the artificial conditions of the experiment. It would be interesting to extend these experiments by testing naive predators from a different habitat. A complete demonstration of an evolutionary advantage experienced by *Stenopleustes* should involve a study of the predator-prey relationships under natural conditions. In addition to being able to observe undisturbed animals, one would also be able to conduct field experiments, such as planting mimics in a habitat that lacks the models. From the evidence gathered in the present study, it appears likely that certain species of fish from the *Zostera* habitat are deceived by the *Lacuna*-like appearance of *Stenopleustes*. These fish probably do not prey upon the pleustid amphipod unless it betrays its disguise by swimming.

It is curious that examples of mimicry appear to be rare among marine invertebrates. This does not seem to be the result of lack of investigation, since many major coastlines have been thoroughly examined by a variety of celebrated marine biologists during the past 2 centuries. A number of animals could possibly serve as models for a Batesian mimicry. Halstead (1965) described particular species of the following groups as being either toxic or venomous: sponges, hydroids, anemones, jellyfish, corals, flatworms, polychaete annelids, octopuses, snails, nudibranchs, starfish, sea cucumbers, and sea urchins. Sponges, flatworms (triclad and polyclad turbellarians), nudibranchs, and the echinoderms would seem to be especially relevant because many of the poisonous kinds are brightly colored (Halstead 1965, 1971). A number of such nudibranchs possess nematocysts, obtained through ingestion of coelenterate prey (Hyman 1940), whereas others secrete acids or noxious products (Thompson 1960, Johannes 1963). Although these nudi-

branches would appear to be likely candidates for Batesian models, Thompson (1960) found that fish rejected all nudibranch species tested (from the British coast), regardless of their coloration. It is not known how widespread this repulsion effect is among nudibranchs.

Fish, octopuses, and possibly crabs would be likely predators to serve as visual signal-receivers. The discrimination and learning abilities of the first two groups have been documented (Wells 1968, Hinde 1970). One apparent difference between the terrestrial (bird-insect) and the marine predator-prey relationships is that insects generally move much faster than the above mentioned marine invertebrates. This makes prey recognition by avian predators more difficult and therefore would allow for some inconsistencies in pattern between mimic and model prey species (which is required for the evolution of a mimicry relationship). In the marine environment the predators may have a longer period to inspect slow-moving prey animals. Since complete protection would necessitate a nearly perfect mimic-model resemblance, such a mimicry relationship may only have a minimal chance to become established through the gradual phenotypic alteration involved in the evolutionary process. Perhaps for this reason it is far more common to find examples of cryptic coloration than of Batesian mimicry among marine invertebrates.

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