

# ECOLOGY OF CALIFORNIA *ACMAEA*

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Except for an occasional isolated bit of information, the literature is almost entirely devoid of ecological material on species of the genus *Acmaea*, the only notable exception being the work of Hewatt ('37). It therefore seems desirable to set forth the results of a study of several years duration. This study was more extensive in scope than is suggested by this paper, since it also involved the study of the taxonomy of the genus, the results of which are to appear in a separate paper, and developed into an attempt to unravel some of the mysteries of speciation in this group (Test, '45b). It is to be hoped that other students of this group will be persuaded to contribute their observations also, to provide eventually a greater understanding of the ecology of the genus wherever species may be found. It is a firm belief of mine that only when the ecology is known will the taxonomy of the species be thoroughly understood.

This study was made while a student at the University of California, under the guidance and help of Professor S. F. Light. Further assistance in the preparation of the manuscript has been rendered by the Laboratory of Vertebrate Biology, University of Michigan. I wish to express my great gratitude to Professor Light for his encouragement and guidance, and to Professor Lee R. Dice of the Laboratory of Vertebrate Biology for his help and encouragement in getting the paper published.

The facts presented herewith and the conclusions, in many cases assumptions or hypotheses, are necessarily derived entire from field observations, with the exception of the data on distribution, which have been drawn in part from field observations, in part from materials and information available in a number of large collections which were carefully

studied. These collections were loaned or made available to me as follows: (1) nearly the entire collections of the Zoologisches Museum, Berlin; (2) extensive collections from the Riksmuseum, Stockholm; (3) large collections of the Indian Museum, Calcutta; (4) the collections of the Museum of Palaeontology, University of California, including much of the Hemphill collections; (5) the Oldroyd collection, Stanford University; (6) collections of the California Academy of Sciences; (7) the entire collections of the United States National Museum; (8) the small but excellent collection of Allyn Smith, Berkeley, California; (9) my own collection. In addition, a number of individual specimens were loaned or contributed to my collection by a considerable number of persons. These collections were utilized in determining ranges.

The specific names used herein are in agreement with those given in the taxonomic paper resulting from this same study, now in manuscript. Since the material discussed here is new to the literature on the genus, and since the terminology will not necessarily be familiar to the conchologist, it seems best to define or limit terms and categories, even at the risk of appearing elementary.

## TERMINOLOGY

*Distribution* is used in the geographic sense unless otherwise specified.

*Range* indicates the geographic extent of a given species.

*Intertidal belt* is that region of the ocean shore lying between the highest and the lowest tide line. For the purposes of this discussion it is subdivided into three zones: *high intertidal zone*, or that region exposed by the receding tides at least once daily; *intermediate intertidal zone*, or that region briefly exposed by minus tides during, at most, only a few

days in each lunar month; and *low intertidal zone*, the region exposed by ebb tides for, at most, an hour or so a few times a year; this would be approximately below the  $-1.0$  line.

*Habitat* is used here solely for subdivisions of the intertidal belt, designated according to the nature of the substrate. The only habitat favorable to species of the genus *Acmaea* is the rocky substrate, which may be conveniently considered to include three subhabitats: (1) rocky reef, (2) boulders set in sand, and (3) anchored algae, such as *Postelsia*, *Egregria*. All three subdivisions appear to be compatible with the successful existence of *Acmaea*.

*Ecologic niche* refers to the exact physical and biotic environment within the habitat in which a given species is able to maintain itself, and is understood to include all factors which affect the existence of the species as a whole, or individual members of it. Since only one or two of these factors have been determined as yet for most of the species, it has been necessary to describe ecologic niches in terms of the factors which are known. This limitation should be kept in mind in reading the ensuing discussions.

*Eurytopic* refers to the tolerance by species of a wide range of ecologic conditions, as used by German ecologists (for instance, Mertens, '34). Perhaps the most eurytopic of the California species of *Acmaea* is *pelta*, so tolerant ecologically that it succeeds equally well in the rocky reef or the floating plant sub-habitats, extends up into the high littoral and down into the low littoral zones, although it is characteristic of the intermediate zone, and is able to utilize a number of different genera of algae as food.

*Stenotopic* refers to the opposite condition, intolerance to all but optimum ecologic conditions. An example of a *stenotopic* species is *A. instabilis*, rigidly restricted to the blades of the alga *Laminaria Andersonii* Farlow. So rigid is this restriction that I have never found

even a stray individual on any other substrate. Since this alga is found only below the intertidal zone, *A. instabilis* is likewise restricted.

*Subspecies* is used solely for the geographically distinguishable forms of a species (i.e., for those races that show a recognizable geographic differential in distribution of variants). *Ecologically equivalent* species are those which occupy the same or equivalent ecologic niches in different geographic areas, whether contiguous or not. Such species need not be related. Species of the genus *Acmaea* seldom are of complete ecological equivalence (that is, their ranges usually overlap), excepting when the species are widely separated geographically. For instance, *A. limatula*, ranging from Crescent City, California, to Lower California, is fundamentally ecologically equivalent to *A. testudinalis scutum*, which ranges from Alaska to San Pedro, California, but since the ranges overlap, it is only a partial ecologic equivalent. As examples of completely ecologically equivalent species I may cite *A. testudinalis scutum* and/or *A. limatula*, of North American shores, equivalent with *A. striata*, of Asiatic shores. These species occupy equivalent niches, but are completely separated geographically.

#### THE GENUS *ACMAEA* IN CALIFORNIA

Seventeen species of *Acmaea* are known to occur along the coast of California. The exact limits of the ranges of most of these species remain somewhat in doubt. My own records are far from complete, and are in conflict in several instances with published records. This I believe to be due in part to faulty identifications by previous workers, in part to the mixing of labels, specimens, etc. (Carpenter, 1857: 162-3), and in part to the incompleteness of my own records.

Seven species unquestionably range at least the full length of the state. They are *pelta* Eschscholtz, *digitalis* Eschscholtz, *asmi* (Middendorff), *paleacea*

(Gould), *rosacea* Carpenter, *limatula* Carpenter, and *scabra* (Gould). Two others, *insessa* (Hinds) and *mitra* Eschscholtz, are accorded this range in the literature, but I have not been able to substantiate the records with localities in the collections I have studied (Test, MS., Taxonomy, Natural History and Bibliography of the Genus *Acmaea*), which of course may have been incomplete in these instances.

The ranges of the eight remaining species, *testudinalis scutum* Eschscholtz, *persona* Eschscholtz, *depicta* (Hinds), *instabilis* (Gould), *fenestrata* (Reeve) [= *A. scutum cribraria* of Oldroyd, '27], *triangularis* Carpenter, *ochracea* Dall, and *conus* Test (Test, '45) extend beyond the state line in one direction or the other, but fail to extend the entire length of the state. They are all littoral species, and with the exception of *depicta* are, like other species of the genus, limited to the rocky habitat.

Only *A. fenestrata* is successful in the subhabitat of loose boulders set in sand. On the other hand, fifteen species favor the rocky reef subhabitat, filling many diverse ecologic niches. I know of only one species of the genus, *A. depicta*, which occupies a non-oceanic habitat exclusively. This species is strictly estuarine, and its habitat is not rocky. It dwells only upon the eel grass *Zostera*, which is not dependent upon a rocky substrate.

The substrate in all the ecologic niches of the high intertidal zone is rock, and microscopic algae are the staple food. There is a niche, or possibly three closely equivalent niches, in this zone where exposure is the rule and submersion relatively rare or brief. This niche (or niches) is occupied by three competitive, related species, *A. digitalis*, *scabra*, and *conus*, which have overlapping ranges and hence are equivalent to an artenkreis of the third degree (Rensch, '34). In this niche protection from the force of wave action is an essential, and perhaps the most important, factor. In the other niches of this zone, exposure is frequent and may be of long duration, but sub-

mersion is regular. One of these niches, occupied by *A. persona*, is distinguished by an inverted horizontal substrate (the underside of overhanging rocks and ledges) and subdued light. The other niche, occupied by *A. fenestrata*, is characterized by the presence of sand around the base of rock.

Niches of the intermediate intertidal zone may be segregated into those in which the staple food is macroscopic algae, and those in which the food is microscopic. The substrate in the latter niche, occupied by *A. asmi*, is the shell of another gastropod, *Tegula funebris* (Adams), upon which algae collect. Among the niches providing macroscopic algae for food are those in which the animal moves about on the rock surface, grazing upon suitable algae with which it comes in contact, and those in which the animal's movements are limited to the specific alga upon which it feeds, or to the plant or animal upon which the food alga grows.

The first of these two categories, that in which the animal grazes on such suitable algae as are encountered, includes the niches occupied by the three most eurytopic of the California species. These niches differ principally in the staple foods and in the presence or lack of shelter. One of them is occupied by *A. pelta*, the other (which is really two equivalent niches) by two incompletely ecologically equivalent species, *A. testudinalis scutum* and *A. limatula*.

*A. pelta* is indeed so eurytopic that it is difficult to set limits to its niche. It is able to survive in all three intertidal zones, although it does not extend far into the high zone. It is very general with regard to its food habits, being able to utilize almost any, perhaps all, macroscopic algae. It has, however, definite preferences, selecting *Costaria* and *Macrocystis* when available, or *Postelsia*. It feeds at any and all times, regardless of whether the tide is in or out, the light bright or dim. Heat sufficient to cause rapid desiccation appears to be the only inhibiting factor in feeding. Individuals

which are not too large are equally comfortable on a rock substrate or a floating plant, somatic adjustments to environmental conditions taking place in the architectural pattern as growth proceeds. The one ecologic necessity of this species, aside from food and almost constant submersion, appears to be the presence of some sort of breakwater (either plant or rock), usually provided by the plants on which it feeds, to reduce the impact of the water. Perhaps this need explains the apparent preference for algae having a certain amount of stiffness or rigidity.

The intermediate zone niche (or niches) occupied by the other eurytopic species, *A. testudinalis scutum* in the northern part of the state, and *A. limatula* in the southern part of the state, is also a comprehensive one, although distinctly less so than that of *A. pelta*. This niche likewise extends into both high and low intertidal zones, but is much more characteristic of the intermediate zone. It is entirely limited, however, to a rocky substrate, and contains fewer suitable foods. Both species in this niche feed only upon the more delicate varieties of alga, such as *Ulva*, *Iridaea*, and *Enteromorpha*, probably because of a behavior habit. These animals graze with the head close to the substrate, and hence perhaps do not encounter the higher-growing *Costaria* and *Macrocystis*. Their architectural pattern precludes their using *Postelsia*, which affords only a very limited substrate. These two species, with their extremely flat architectural structure, do not need the protection of breakwaters to reduce the force of the water, and hence can do without the tougher algae utilized by *A. pelta*.

The second type of niche, involving macroscopic foodstuffs, includes several niches each occupied by a strikingly stenotopic species limited to existence upon a specific alga. *Acmaea insessa*, for instance, lives and feeds only upon fronds of *Egredia Menziesii* Aresch. The stipe of *Laminaria Andersonii* Farlow, upon which *A. instabilis* lives and feeds, forms

the substrate of another such narrow niche. Still another is restricted to the blades of the eel grass *Phyllospadix torreyi* Watson, upon the cortical cells of which *A. paleacea* feeds. Finally, there is a niche limited to coralline algae, occupied by *A. triangularis*, which feeds exclusively upon the alga *Amphiroa tuberculosa* Decaisne.

Finally, the low intertidal zone includes only two *Acmaea* niches which are peculiar to it. Owing to the brevity and infrequency of exposure in this zone, it is hardly possible to accumulate much information about the inhabitants; nevertheless a certain amount of ecologic data is presented here.

The controlling factor in one of the two niches of this zone, that occupied by *A. mitra*, appears to be the presence of mossy red (*Microcladia*) or microscopic algae for food, since this limpet is found only in locations where there is a rich accumulation of one or the other of these food materials. Shelter is provided by the mossy red alga, or by irregularities (such as urchin pits). I have found this species to be most abundant on reefs extensively pitted by the sea urchin *Strongylocentrotus purpuratus*. *A. mitra* moves into the pits and feeds upon the algae which collect on the pit surfaces. Not only have the most abundant populations been found in such situations, but also the largest individuals.

The other niche of the low zone, occupied by *A. ochracea*, appears to be limited by at least three recognizable factors: the presence of microscopic algae for food; the absence of competing or inimical forms; and permanent submersion. Individuals are found only upon rocks largely bare of other macroscopic forms, in places which are never uncovered by tidal action. Were they in exposed situations, these limpets would perhaps be more subject to predatory action than are other species, because of the extreme delicacy of the shell and the reduced adhesive power of the foot.

As is obvious from the foregoing dis-

cussion, the food of all California *Acmaea* except for at most two species is algae of one sort or another, and it is probably safe to assume that the same is true of almost all *Acmaea* everywhere. As has been shown, there is considerable specificity of feeding habits, many species feeding upon only one general kind of alga or, in certain cases, upon only one species of alga; for instance, *A. insessa* upon *Egregia Menziesii*, and *A. instabilis* upon *Laminaria Andersonii*. On the other hand, some species utilize a variety of algae as foods. For example, *A. pelta* feeds with equal readiness upon certain species of *Costaria*, *Macrocystis*, or *Postelsia*; likewise, *A. scutum* feeds upon either *Ulva*, *Iridaea*, or *Enteromorpha*. Only those algae which are sufficiently rigid to provide a good scraping surface, or which are supported by hard surfaces, as microscopic algae upon a rock or *Ulva* held against a rock by the weight of the limpet, can be utilized by these species, since all are grazers which scrape up their food by means of a well-developed radula. None are plankton feeders.

In spite of the numerous species of *Acmaea* present in small areas, interspecific competition is not common, because of the limiting ecologic factors. However, there are some cases of active competition, the most severe occurring in the high intertidal zone niche characterized by short periods of submersion and long periods of exposure. Surprisingly enough, three closely related species, *A. conus*, *A. digitalis*, and *A. scabra*, jointly occupy this niche within the considerable areas in which their ranges overlap. *A. digitalis* occurs the length of the coast from Alaska southward into Lower California. It is not so abundant in the San Diego region as farther north, but is still important. *A. scabra* extends from the Puget Sound area down around the tip of Lower California and up into the Gulf, but becomes decreasingly abundant below San Pedro. *A. conus* extends from Point Concepcion, California, around Lower California and up into the Gulf. It is

obvious that all three species are in competition from Point Concepcion to the Gulf of California, and that *A. digitalis* and *A. scabra* compete from Puget Sound southward. Competition appears to be severe among these species only in the matter of shelter, however. All three species have developed an elevated form, doubtless an adaptation for resisting desiccation, since it permits a considerably thickened body, and accommodation of an increased amount of moisture under the shell. Since the elevated shell increases the danger of their being forced loose from the rocks by wave action, these species seek shelter in protected spots, such as depressions, crevices, and irregularities of abrupt character in the rock surface. Such irregularities are scarce on the water-worn rocks at high tide line, but where present are inevitably crowded. On the other hand, large smooth expanses of rock are numerous and provide admirable surface for the growth of microscopic algae, thereby ensuring a more than plentiful supply of food for the relatively sparse population which can find shelter upon a given rock.

Another example of competition among the *Acmaea* is provided by a pair of unrelated (different subgenera) species, *testudinialis scutum* and *limatula*, which occupy equivalent niches with overlapping geographic ranges. The range of *A. testudinialis scutum* extends from Alaska to San Pedro, California, where it terminates with surprising abruptness; that of *A. limatula*, from Crescent City, California, to the tip of Lower California, although it is extremely spotty north of Santa Cruz. Indeed, it is negligible in most places, with heavy populations in isolated areas cropping up where the temperature of the water is as high as in the southerly part of the range of the species. Such an isolated population for instance, occurs in Tomales Bay, Marin County. In general, this species becomes a factor in competition only south of Santa Cruz, California. In other words, *A. testudinialis scutum* dominates the ecologic niche

in question from Alaska to Santa Cruz, whereas *A. limatula* entirely fills the same niche from San Pedro southward. In the area between Santa Cruz and San Pedro, however, the two populations, both large, offer real competition to each other. Nevertheless, they are not to be considered as fundamental competitors, but rather as ecological equivalents, which compete, as is often the case, in the area of overlap, where temperature conditions are equally favorable to both species.

These are the only two interspecific instances of competition among *Acmaea* in California. The latter is the type of competition found commonly throughout the animal world, but the former is an unusual type and therefore especially interesting. We often find ecologically equivalent species competing in the areas of overlap (incomplete ecological equivalents), but it is most unusual to find ecologically equivalent species which compete throughout their ranges. It is particularly unusual to find this condition among closely related species.

Whereas there is little interspecific competition among *Acmaea*, species must be prepared to meet competition from other genera which include grazers upon algae. In this respect the limpets are able to hold their own because of their great adhesive powers. Furthermore, severe intraspecific competition is frequently apparent in favorable areas. Such competition is more often for space than for food, I suspect, since the individuals in greatly crowded areas are frequently very large, perhaps indicating that the reason for the crowding is the presence of abundant food. However, some very crowded areas are found in which the individuals are small; perhaps this indicates strenuous competition for food as well as for space.

Undoubtedly, the lack of competition among the many species of *Acmaea* living in a given habitat is a result of the high degree of ecologic specialization shown by each species, and the consequent eco-

logic segregation. This may be illustrated by a number of species found within the confines of a single reef, such as that at Moss Beach, San Mateo County, California.

The niche at high tide line, in which infrequent and brief submersions, high rate of desiccation, and danger from the force and frequency of water impact are important ecologic factors, is occupied by *A. digitalis* Eschscholtz, and *A. scabra* (Gould). These species are characterized by the development of adaptive features compatible with such ecologic factors. For instance, the shell has a small aperture, which decreases the rate of desiccation. [With regard to mode of reduction of aperture, see Orton ('32) and discussion below.] In addition, the animals exhibit a behavior tendency which further reduces danger of desiccation, in that they move about and feed only when the light is dim, clamping tightly to the rock surface when the light is bright. The elevated structure, which compensates for the reduced aperture, appears at first thought incompatible with a niche where danger of dislodgement by water movement is great. However, this apparent incompatibility is obviated by behavior traits. The animal moves about only when the tide is in, seeking a protected crack, crevice, or depression as soon as the tide recedes. It always orients itself so that the long slope of the posterior end will receive and break the force of the water. Although the animal is not negatively phototropic, as evidenced by its preference for the upper sides and slopes of rocks, to which it is admirably suited by reason of its adaptations for resisting desiccation, it does show a tendency toward negative geotropism. This is probably a factor in preventing competition between the species of this or equivalent niches and those of the two niches next to be described.

The two niches which come below high tide line but still within the high intertidal zone are distinguished by certain factors. One of these niches, occupied

by *A. persona*, is controlled by two factors in particular: an inverted horizontal or semi-horizontal substrate, such as is offered by the roofs of caves, the undersides of rocky ledges, etc., and dim light. In addition, there is continual water movement, except during ebb tide. The adaptations shown by *A. persona* which enable it to occupy this niche successfully are chiefly behavior traits. This animal appears to be negatively phototropic, causing it to seek the most dimly lighted locations available. To compensate for its large size and large aperture which would make it particularly subject to desiccation, it selects roosting sites which minimize this hazard, and, furthermore, feeds only at night, at ebb tide, hastening back at the first dim suggestion of daylight. The habit of feeding during ebb tide undoubtedly eliminates another danger, that of removal from the substrate by the continual impact of the water. During roosting periods this danger is minimized by the animals' habit of turning the long, streamlined posterior slope of the shell toward the direction of the impact.

The third niche of the high intertidal zone is characterized by the presence of loose sand in the water. The occupant of this niche, *A. fenestrata*, is dependent for shelter upon a sandy layer around the base of the rocks or boulders which comprise the substrate, and exhibits structural adaptations and behavior traits suitable for such a subhabitat. The shell is constructed on a subcircular plan, with a somewhat elevated apex. Although admirably able to withstand the abrasive action of sand in the water, the shell would be somewhat conspicuous and subject to a high degree of desiccation on the bare rocks which *fenestrata* inhabits. However, the animal does not remain exposed but retreats down the rock as the water recedes, digging in at the base and remaining buried there until the water returns. The apical structure is admirably suited to this habit since the cone acts as a wedge, enabling the or-

ganism to push down into a dense aggregation of materials. Correlated with this habit is another, of feeding only when submerged.

Further examples of correlation of adaptive characters with the ecologic niche, especially in such stenotopic species as *A. insessa*, *A. instabilis*, *A. triangularis*, *A. asmi*, and *A. paleacea*, will be discussed below.

The great variety of ecologic adaptation has probably been the result of ecologic selection of suitable adaptive characters, genetic in origin, appearing among variants of ancestral eurytopic species. This implies extensive genetic variation of individuals within the eurytopic species, which is exactly the case. Such eurytopic species as *A. testudinialis scutum*, *A. pelta*, and *A. limatula* show a noteworthy response to varying ecologic factors with regard to shell weight, texture, sculptural emphasis, and even architectural pattern. It is because of this adaptability of the eurytopic species that the literature abounds with varietal and subspecific names, these having been applied to the many ecologic variants. I have not encountered in the literature a single justifiable use of a trinomial name among the species of *Acmaea*. Such names have been applied in every case not to geographic subspecies but to ecologic variants (that is, a group of individuals differing from the main stock in one or more respects because of peculiar ecologic factors) or individual variants (individuals varying from the normal or typical form in some respect owing to an extreme genetic make-up, a pathologic condition, feeding peculiarities at some time in life, etc.). This does not mean that there are no cases within the genus where trinomial names are justified, but merely that they have not been used correctly, the temptation to apply them to all striking, recurrent variants apparently having been too great.

As has been indicated in the previous paragraph, variability within a species in this genus may be either ecologic or indi-

vidual. Ecologic variation follows trends in certain predictable directions in correlation with ecologic factors. Conditions which are less than optimal with regard to any given factor or set of factors usually produce predictable somatic changes in the architectural pattern of the shell regardless of the species, providing only that it is one which is sufficiently eurytopic to exist in spite of somewhat unfavorable conditions. For instance, reduced salinity results in a thinner shell than is developed in environments where the salinity is normal, as is shown by *A. fenestrata* which have grown near large river mouths, and by many species grown in bays where there are no complicating factors. An additional factor usually characteristic of bays is that of reduced wave action, to which the animal makes a somatic response by still greater reduction in shell weight together with a marked (probably genetic) reduction in the magnitude of sculpturing, and a tendency toward retention of the epidermis, if ever present. Reduced wave action may not be unfavorable, but it is a complicating factor often combined with the unfavorable one of reduced salinity.

If, however, the chemical content of the water differs in any respect other than salinity from that of normal sea water, thick shells with reduced aperture and increased elevation result as a somatic response in those species in which the hereditary limitations permit. All three modifications serve to reduce the contact of the environment with soft parts of the animal. The increased elevation allows for expansion in a vertical direction to compensate for reduction in aperture and the consequent reduction in diameter. Thus the area directly in contact with the environment becomes reduced. Thickening apparently reduces the amount of diffusion which takes place through the shell. Often, perhaps usually, thickening of the shell under such conditions is augmented by further thickening resulting from infection by the fungus *Didymella conchae* Bonar ('36), which be-

comes especially prevalent on *Acmaea* shells when conditions are unfavorable for the latter. Chemical conditions which cause such developments are often found in bays where commercial activities are extensive, or in those where, because of inadequate drainage, detritus tends to accumulate.

The adaptive somatic development of increased shell height combined with reduced aperture, often called dwarfing, results not only from abnormal chemical conditions in the water; it appears, in fact, to be a common response to many unfavorable ecologic conditions. For example, it is found among species subject to more than optimum exposure, or to intensive evaporation during exposure; it may characterize individuals living under crowded conditions or near the extreme limit of the species range. This often gives rise to the illusion that a subspecies is present. This adaptive character when genetic, has served as the basis for selection of certain species in the past.

Wave action affects magnitude of sculpturing, shell weight, and architectural pattern by selecting individuals with genetic tendencies in favorably adaptive directions. Increased magnitude of sculpturing strengthens the shell; the same end is attained by increase in shell weight. At the same time, the architectural pattern which succeeds best with increased wave action is one which offers a minimum of resistance. Reduced wave action, on the other hand, permits development in the opposite direction. Excellent examples of these responses are afforded by the variants of *A. limatula* and *A. pelta* (see below). A yielding substrate, which counteracts the water impact, permits survival of individuals with thin shells, reduced sculpturing, and increased elevation resulting from lateral compression. Such a type of architecture is regularly associated with the floating plant sub-habitat, correlated with the reduced or limited substrate accommodation such as is provided for *A. pelta* by the narrow



stipe of *Postelsia*. It is seemingly upon these particular variable genetic characters of the eurytopic *A. pelta* that selection has worked to produce the stenotopic species *A. asmi*, *A. instabilis*, and *A. triangularis*, all close relatives of *A. pelta*. The principal isolating factor in the ecologic niche of each of these stenotopic species is the reduced substrate, which, together with the lack of effective water force, has also acted as a principal selective agency in their evolution.

*Acmaea pelta* affords the best example of somatic response to this particular set of ecologic factors. Individuals of that eurytopic species frequently dwell on the alga *Postelsia*, in which case they tend to have a reduced, narrowed aperture (correlated with the narrow substrate), a laterally compressed, elevated architecture, and reduced sculpture (correlated with ineffective water force). These characters may be either somatic or genetic, or both. When such individuals move onto the rocks, if the trait is somatic, a change in structural pattern is initiated, causing, in the portions of the shell developed after moving to the new site, a widened aperture, lateral expansion, and increase in magnitude of sculpturing. It is notable that only small *Postelsia*-grown individuals appear able to make the shift; at least, large variants of this kind are not found upon the rocks, and I assume that when they attempt the change they are promptly swept off. It is also unlikely that genetic variants can successfully make the change.

An extrinsic cause of variation, widespread in occurrence, and similar in its depredations upon many species, is the Ascomycete fungus *Didymella conchae* Bonar ('36). This fungus completely transforms the color pattern of the shell, giving to many different species a uniformity of appearance entirely superficial (for discussion of infection, see Bonar, '36). The color pattern produced by the the fungus is a combination of ash gray and brown in various designs, but may be plain brown, tan, ash gray, or even whit-

ish. Sometimes the darker color is present in the form of chevrons, a reticulation, concentric circles, or other patterns, many of which occur commonly among several species.

The infection not only changes the coloring, but also seriously affects the sculpturing, often completely obliterating it. It also changes the surface of the shell into a thick spongy material not at all like the normal surface. Some species are so commonly infected that it is difficult to determine just what the normal sculpturing is.

One striking phenomenon which impresses the collector of *Acmaea* is the consistent resemblance, in color, texture, and contour, of individuals to their respective substrates. The resemblance may be so close as to make the animals invisible except to an expert eye. The explanation for the absence of conspicuous individuals is to be found, I believe, in their continual selective elimination by predators which hung visually, namely, birds (Bent, '27: 293, 298, 307; '29: 308, 313, 322; Vallentin in Boyson, '24: 309; Cottam, '39: 36, 60, 77, 94, 129), notably the oyster catcher; and rodents, coons, fish, and possibly crabs (I have seen them knock off and devour limpets in aquaria). It is difficult to conceive of any other answer to this problem. The food eaten by limpets certainly does not explain their resemblance to the substrate since it is as striking in the instances where the external color pattern of shells has been determined by fungus infection, yet when the shells are freed of the fungus they have no resemblance to the substrate. This indicates, of course, that the resemblance is not an active response on the part of the animal to its environment, either through the influence of food or other factors, but that only those individuals which have a resemblance to the substrate are able to survive. This is well exemplified among eurytopic species by the striking resemblance of specimens of *A. scabra* to the kind of rock upon which each happens to have developed. Speci-

mens located upon granite have a whitish ground color marked by speckles of black, exhibiting a truly astonishing resemblance to the granite; those which have grown upon sand rock are somewhat nondescript in color, as is the rock; those upon green chert have green predominant in their own coloration. Such close resemblance might lead one to suspect the food supply, but specimens in which the normal shell characters are completely deleted or obscured have just as striking a resemblance. This is exemplified by the striking black and white marking of fungus-infected *A. digitalis* found among the *Mytilus*-barnacle beds, in contrast to the nondescript ash and tan color of infected specimens found on sand rock. The only possible explanation appears to be that offered above, namely, that there is a very effective selection proceeding at a rapid rate, and only specimens possessing a striking resemblance to the substrate are able to survive.

The fungus infection is widely prevalent among eurytopic species, in contrast to the immunity of some stenotopic species (*A. insessa*, *paleacea*, *persona*) which bear a natural resemblance to their substrate in color and texture. The freedom from infection of the latter species suggests that the susceptibility of the former to the infection may be the result of a selective process. Since eurytopic species do not bear an inherent resemblance to their substrate, they are at a disadvantage except in so far as they assume a measure of protective coloration, such as is provided by the fungus infection. This circumstance may have tended, by the elimination of immune individuals, toward the selection of a hereditary line especially liable to the infection. On the other hand, there may be no selection of hereditary tendencies at all, but simply a survival of infected animals because of their protective coloration, and, correspondingly, an elimination of ineffectively colored individuals. The same process may have taken place in the evolution of stenotopic species. This fungus

infection may therefore represent a symbiosis which in many cases is of considerable advantage, in some instances even obligatory, to the host.

#### SUMMARY

Certain general conclusions may be drawn from the foregoing:

(1) The species of *Acmaea* are highly dependent upon their structural pattern; this may be of either somatic or genetic determination in the eurytopic species, but only of genetic determination in stenotopic species, in accordance with the ecologic situation. It is therefore possible for a student of the genus who is well versed in its ecology in one part of the world to predict with reasonable accuracy, on the basis of structural types, the ecologic niche of species from another part of the world, if enough individuals from sufficient localities are considered. It is also possible to predict with reasonable accuracy ecologic peculiarities. However, unless groups of individuals are considered, individual variation or other complicating factors may easily produce an erroneous impression.

(2) Seeming geographic subspecies must be carefully considered. It is necessary to determine if they really represent true geographic subspecies, comprised of one or another extreme variant of the species which appear elsewhere in the specific range only as an occasional variant, never in large numbers, and which are not merely ecologic variants, reappearing in considerable numbers wherever the conditions are equivalent. Examples of such apparent geographic subspecies which are actually only ecologic variants are afforded in many instances by the dwarfed, humped, thin-shelled individuals to be found near the end of the range of many species, as for example, *A. ceciliansa* Gay, which is a common variant of *A. viridula* Lamarck found in the Magellanic regions. In spite of the seeming geographic segregation of these ecologic variants, dominant in that particular geographic area because of ad-

verse ecologic conditions which prevail near the end of the species range, they do not form a sound subspecies; whole populations of such deformed individuals may likewise be found anywhere in the species range in any situation in which ecologic conditions are not favorable. Such variant groups have often been given trinomial names, and may appear to be geographic races if the range has been insufficiently sampled. *A. limatula morchii* Dall, long considered a geographic subspecies, is an excellent instance. This striking variant of the species *A. limatula* appears to be geographic, occurring in a bay (Tomales Bay) somewhat distant from the regions in which the population is large. Careful examination of large series from the bay, however, reveals the presence there of complete intergradation from the variant to the normal pattern, the latter occurring at a lower vertical level than the former. Similarly, a careful study of extensive series from many other localities shows that the variant reappears wherever the unfavorable conditions are repeated, and that individuals from near the northern end of the range tend to vary in a similar manner. The southern end of the range terminates abruptly in the Gulf of California, where many complicating factors are present which require special consideration. It is clear that in this case we are dealing with an ecologic variant, and not a true geographic subspecies.

The foregoing considerations should convince the conchological taxonomist of the value, indeed, of the necessity, of a knowledge of the natural history (in the ecological sense) of the group for an intelligent interpretation of the taxonomic problems. They may also suggest to what extent his locally acquired knowl-

edge may be utilized in interpreting materials from distant and unfamiliar regions.

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