



Polymorphism in Marine Mollusks
and Biome Development

ARTHUR H. CLARKE

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ABSTRACT

Clarke, Arthur H. Polymorphism in Marine Mollusks and Biome Development. *Smithsonian Contributions to Zoology*, number 274, 14 pages, 5 figures, 1978.—Many arctic marine mollusks exhibit much greater intraspecific variation in shell shape and sculpturing and greater interspecific morphological overlap than temperate or tropical species of the same families. Tropical marine mollusks ordinarily exhibit more pronounced interspecific morphological distinctness in mixed-species communities and more remarkable intraspecific polychromatism in single-species dominated communities than their temperate or arctic relatives. A number of groups do not exhibit any variability shifts with latitude but shifts opposite to those here described have not been observed. Changes in the nature and intensity of natural selection, which are deemed to occur with increased biome maturation, appear to account for these morphological trends .

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Polymorphism in Marine Mollusks and Biome Development

Arthur H. Clarke

Introduction

This paper examines aspects of variation in shell shape and shell coloration among marine mollusks. Some previous generalizations about patterns of intra- and interspecific morphological variability in arctic, temperate, and tropical mollusks are stated, pertinent data are compiled and presented, and a hypothesis is formulated to partially account for these patterns in terms of altered responses to changing selective pressures.

Viewed from the perspective of experience gained initially with New England marine mollusks and later enriched through several field expeditions in the Canadian arctic and others to the West Indies and Panama, the nature and extent of variation in arctic and in tropical marine mollusks appears quite different from each other and from those in temperate latitudes. Of course it is well known that arctic mollusks are dull in color and conservative in sculpture and that tropical mollusks are often colorful and flamboyant in sculpture. More detailed examination of these features reveals interesting correlations and trends, however, which presumably are attributable to changes in the nature and intensity of natural selection.

The literature citations in the text are included not only to document the statements made but to provide additional bases for the generalizations presented. Readers who desire additional informa-

tion, for example about the variability of arctic or tropical mollusks, are invited to refer to that literature.

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Variability in Arctic Marine Mollusks

An approximation of the relative taxonomic complexity of the families of marine bivalve and prosobranch gastropod mollusks in the arctic may be achieved by ranking them in order of the number of arctic species they contain. No overall revisions for the entire arctic exist but the regional studies by Ockelmann (1958) for East Greenland bivalves and by Macpherson (1971) for Canadian arctic prosobranchs treat what appear to be typical arctic faunas. Their data indicate that the most important arctic families of these groups are as follows:

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Bivalves (57 species): Nuculanidae (11), Astartidae (5), Mytilidae (5), Thyasiridae (4), Tellinidae (4), Cuspidariidae (4), Arcidae (3), Pectinidae (3), Cardidae (3), Thraciidae (3), Limidae (2), Saxicavidae (2), and 8 families each with 1 arctic species.

Prosobranchs (102 species): Buccinidae (36), Turridae (15), Trochidae (9), Lamellariidae (7), Rissoidae (5), Naticidae (4), Muricidae (4), Lacunidae (3), Trichotropidae (3), Acmaeidae (2), Littorinidae (2), Turritellidae (2), and ten families each with 1 arctic species.

The extreme and sometimes baffling phenotypic diversity of form in some arctic species of *Buccinum*, *Neptunea*, *Admete*, *Bathyarca*, *Mytilus*, *Astarte*, *Mya*, and *Hiatella*, among others, and the consequent difficulty in distinguishing species in several of these genera has been commented upon by several authors (e.g., Thorson, 1944; Ockelmann 1958; MacGinitie, 1959; A. Clarke, 1960, 1963; Macpherson, 1971; Petersen, 1977). (Variation in color within arctic species is not extreme and most species are white or some shade of brown.) In some published reports, however, and even in some museum collections, the fact that certain species are variable in shell shape within populations has been obscured by the segregation of various "varieties" and "forms."

MacGinitie (1959:65) has expressed well the situation pertaining to marine mollusks:

Perhaps nowhere in the world do shells consistently exhibit such marked and confusing variations as do the Arctic species. Among the gastropods the genera *Buccinum*, *Boreotrophon*, *Neptunea*, *Beringius*, and *Diaphana* and among the pelecypods *Musculus*, *Astarte*, and *Liocyma* are particularly subject to variation. Because of these great variations, species of some of these genera are extremely difficult to identify and in order to resolve these problems it will be necessary to make intensive studies at the specific level.

A. Clarke (1963) briefly commented on the extreme diversity seen in mollusks dredged from the Chukchi Sea (Arctic Ocean). In *Bathyarca frielei* (Friele), for example, in addition to great variation in shell shape, some species have short taxodont hinge teeth which are nearly perpendicular to the hinge line whereas many others possess only elongate hinge teeth which are roughly parallel to the hinge line. All intergrades also occur. The specimens with lamellate hinge teeth are almost identical, in fact, to the Ordovician species *Cyrtodonta grattanensis* Wilson (Steele and Sinclair, 1971, pls.

1-3) except that *C. grattanensis* is four times as long.

In the following table (Table 1) arctic species which exhibit marked variability within populations are compared with other taxonomically related and approximately ecologically equivalent species from the same climatic region and from other regions. The families examined have been selected because they are epifaunal and subject to visual predation and because there are enough specimens within single lots available in museum collections to enable diversity to be estimated with some confidence. All are important arctic families. The Buccinacea, in fact, are the dominant group of arctic marine gastropods and constitute about 35% of the gastropod species there. Relative diversities in particular morphological characteristics of population samples have been assessed by comparing their coefficients of variability (CV). This is the standard deviation expressed as a percentage of the mean ($CV = \frac{SD \times 100}{M}$).

It is clear from Table 1 that in the superfamilies Arcacea, Astartacea, and Buccinacea, within populations of some arctic species, variation in shell shape is unusually great. Not all arctic species in these (or other) superfamilies show such prominent polymorphism (pers. obs. and Petersen, 1977). Presumably these groups are genetically more conservative. Within the three superfamilies considered, however, no species samples were found in collections in the Smithsonian Institution or the National Museums of Canada from shallow temperate or tropical waters that exceeded, equalled, or even approached the intrapopulation variability of the most variable arctic species samples. In some other superfamilies (e.g., Trochacea: *Molleria costulata* (Møller); Veneracea: *Liocyma fluctuosa* (Gould); Myacidae: *Mya truncata* L.), however, substantial variation also appears to exist, but sufficient material is not available to statistically demonstrate it. An estimated 35% to 40% of all arctic marine mollusk species appear to be significantly more variable than their closest temperate relatives. The other arctic species appear to be approximately equally as variable as their closest temperate relatives.

Morphological distinctness between sympatric species appears to be substantially less in some

TABLE 1.—Intrapopulation variability in arctic, temperate, and tropical populations of Arcidae, Astartidae, and Buccinidae

Species	Locality	Region	Character	N	Range	Mean	CV
ARCIIDAE							
<i>Batharca pectunculoides</i> (Scacchi)	Eclipse Sound, near Bylot I., N.W.T., Canada (NMC 76123)	Arctic	Breadth/Length	28	.42-.59	.51	6.4
<i>B. glacialis</i> (Gray)	Lancaster Sound, N. of Bylot I., N.W.T., Canada (NMC - Clarke sta no 1270)	Arctic	"	30	.39-.53	.46	8.3
<i>B. glacialis</i> (Gray)	Kap Hedlund, Greenland (data from Ockelmann, 1958:47)	Arctic	"	22	.46-.65	.55	9.2
<i>Anadara ovalis</i> (Say)	Great Egg Harbor, N. J. (USNM 27311)	Temperate	"	11	.63-.71	.67	4.1
<i>A. transversa</i> (Say)	Vineyard Sound, Mass. (USNM 74047)	Temperate	"	16	.51-.60	.55	4.6
<i>A. brazillana</i> (Lamarck)	Jekyll I., Ga. (USNM 408549)	Subtropical	"	12	.66-.75	.72	3.4
ASTARTIDAE							
<i>Astarte subaequalata</i> Sby.	Icelandic Shelf, N. Atlantic (63°06.7'N 24°00.0'W) (NMC 66584)	Arctic	"	30	.48-.61	.54	6.5
<i>A. montagui</i> f. <i>warhami</i> Hancock	Silidre Fiord, Ellesmere Island, N.W.T., Canada (NMC 70005)	Arctic	"	43	.31-.44	.38	6.4
<i>A. montagui</i> f. <i>warhami</i> Hancock	East Greenland (data from Ockelmann, 1958:85)	Arctic	"	16	.35-.51	.42	9.8
<i>A. castanea</i> Say	Westerly, R.I. (USNM 463224)	Temperate	"	12	.51-.55	.53	2.6
<i>A. triangularis</i> Montagu	Guernsey, U.K. (USNM 200658)	Temperate	"	30	.50-.59	.53	3.9
<i>A. nana</i> Dall	near Ragged Key, Fla. (USNM 444915)	Tropical	"	28	.51-.61	.56	4.3
BUCCINIDAE							
<i>Neptunea ventricosa</i> Gray	Nunivak I., Alaska (USNM 222049)	Arctic	Diameter/Height	8	.53-.75	.65	10.2
<i>N. heros</i> Gray	MacKenzie R. mouth, Canada (USNM 221652)	Arctic	"	28	.50-.65	.58	6.9
<i>Colus togatus</i> Mörch	Starvation Cove, N.W.T., Canada (USNM 44746)	Arctic	"	12	.47-.61	.52	6.9
<i>C. togatus</i> Mörch	Cape Parry, N.W.T., Canada (USNM 36837)	Arctic	"	15	.45-.53	.49	4.2
<i>Buccinum glaciale</i> L.	Shumagin Islands, (USNM 221768)	Arctic	"	18	.47-.60	.54	7.6
<i>B. angulosum</i> Gray	Point Barrow, Alaska (USNM 40966)	Arctic	"	13	.57-.75	.65	7.8
<i>B. hydrophanum</i> Hancock	Sagunay River, Canada (NMC 35848)	Arctic	"	16	.49-.58	.53	4.6
<i>B. scalariformis</i> Beck	Noursoak Penin., Greenland (USNM 150736)	Arctic	"	10	.51-.57	.54	3.2
<i>Colus pubescens</i> Verrill	E. of Grand Banks, Newfoundland (NMC 23057)	Subarctic	"	17	.38-.42	.40	3.2
<i>Buccinum undatum</i> L.	Off Martha's Vineyard, Mass. (USNM 158958)	Temperate	"	18	.57-.63	.60	3.2
<i>Searlesia dira</i> (Reeve)	Sooke, B.C., Canada (NMC 1093)	Temperate	"	19	.45-.53	.49	3.9
<i>Buccinum amiantis</i> Dall	Off northern Calif. (USNM 221299)	Temperate	"	16	.59-.66	.62	3.0
<i>Neptunea arthritica</i>	Hakodate, Japan (USNM 215099)	Temperate	"	14	.58-.68	.62	4.4
<i>Cantharus undosus</i> (L)	Arue, Tahiti (USNM 672804)	Tropical	"	16	.59-.65	.63	2.2
<i>Phos senticosus</i> (L)	Okinawa, Japan (USNM 671098)	Tropical	"	16	.49-.53	.50	2.3
<i>Babylonia japonica</i> Reeve	Nogata, Japan (USNM 227348)	Tropical	"	10	.52-.58	.55	3.7
<i>Pisania pusio</i> (L)	Off Sand Key, Fla. (USNM 415138)	Tropical	"	18	.43-.49	.46	3.8
<i>Solenostrea turbinelloides</i> (Reeve)	Off Baja California, Mexico (USNM 96955)	Tropical	"	15	.63-.72	.66	3.7
<i>Antillophos candei</i> (Orbigny)	Lavaguez, Puerto Rico (USNM 161239)	Tropical	"	29	.45-.52	.49	3.6
<i>Engina zea</i> (Melvill)	Goa, India (USNM 443082)	Tropical	"	20	.48-.56	.53	3.4

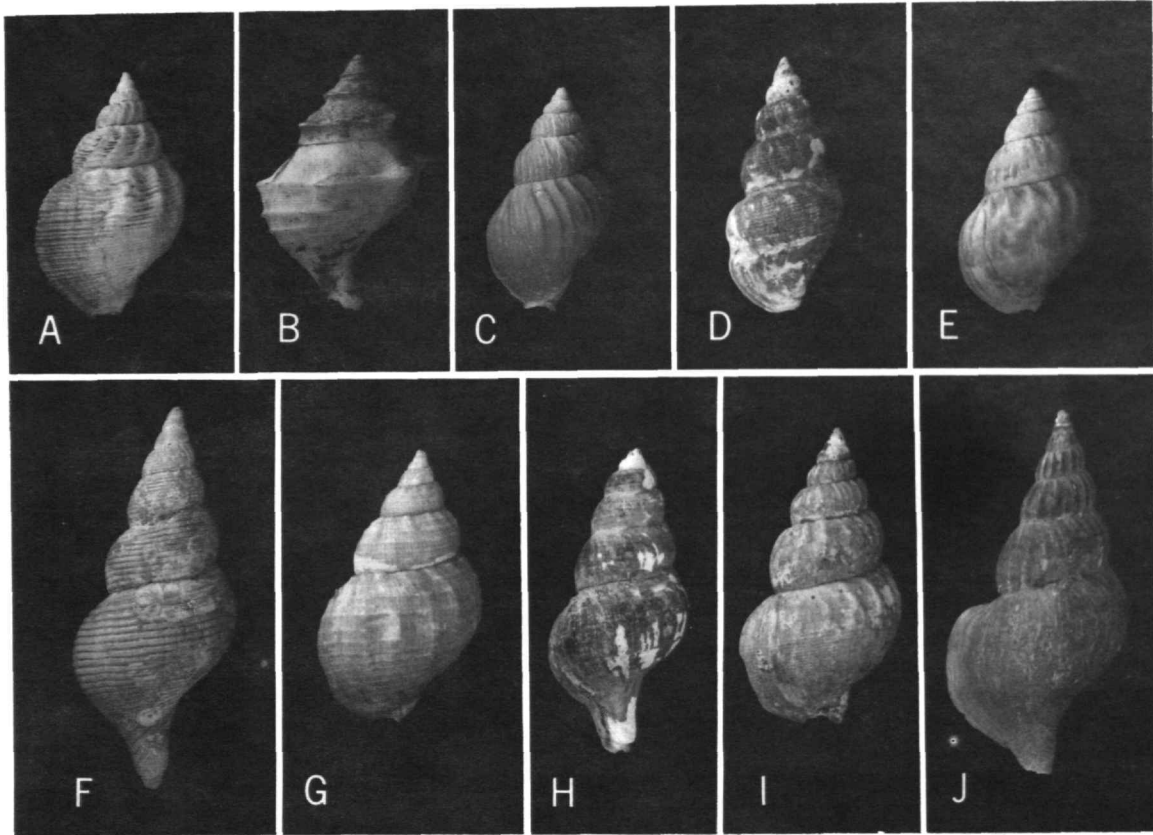


FIGURE 1.—Interspecific aspect diversity in representative Buccinidae from the Canadian Arctic: A, *Buccinum undatum* L.; B, *B. angulosum* Gray; C, *B. finmarkianum* Verkrutzen; D, *Colus tortuosus* (Reeve); E, *Buccinum cyaneum* Bruguiere; F, *Colus spitzbergensis* (Reeve); G, *Buccinum ciliatum* Verkrutzen; H, *Anomalosipho verkruzeni* Kobelt; I, *Buccinum plectrum* Stimpson; J, *Plicifusus kroyeri* (Møller).

arctic marine mollusks than in comparable temperate or tropical groups. Figure 1 illustrates, as an example, "typical" specimens of 10 arctic Buccinacea species. Figure 2 shows the amount of variation commonly encountered in individual populations of one arctic species, *Buccinum glaciale* Gray. Although this variation is rather remarkable, extreme morphs also occur in other buccinid species. Some of these morphs closely resemble species to which they do not really belong and detailed examination of somewhat obscure characters (e.g., microsculpture of nuclear whorls, fine sculpture between major sculptural elements, structure and relative size of the operculum) is necessary to distinguish them.

Numerous examples of the taxonomic importance of minute or inconspicuous characters for species discrimination in arctic Buccinacea are given by Macpherson (1971). Similar problems exist in arctic species of *Astarte*. Here gross morphologies may overlap (Ockelmann, 1958; Petersen, 1977) and examination of the microstructure of the periostracum may be necessary for positive identification (Saleuddin, 1967). Arctic *Hiatella* species may be distinguishable only by sculptural characters of the postlarval juvenile shells, but whether more than one species exist in the arctic is still open to question (Petersen, 1977). Similar difficulties that arise in distinguishing arctic species of *Admete*, *Plicifusus*, *Polinices*, *Musculus*, *Lio-*

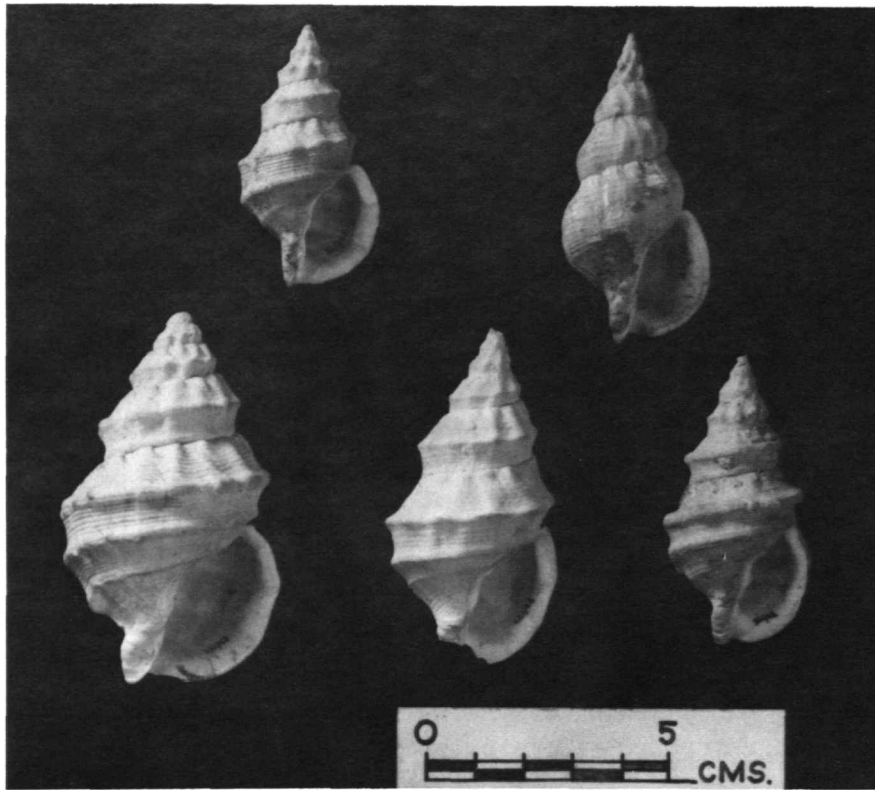


FIGURE 2.—Intraspecific variation within a population of *Buccinum glaciale* Gray from Shumagin Islands, Alaska.

cyma, and other groups have been described by MacGinitie (1959).

It must be emphasized that not all arctic groups show overlap in gross species morphologies. For example, species of Acmaeidae, Trochidae, Trichotropidae, Pectinidae, and some other families (and genera) are obviously distinct and readily identifiable. But the presence of such a large number of species in the arctic whose aspect diversities overlap with those of other sympatric species is almost certainly significant.

It should be mentioned that a number of deep-sea species also exhibit pronounced variability. The data in Knudsen (1970), which includes measurements of all hadal bivalve mollusks collected by the *Galathea* Expedition, are useful in this connection. Although most species are only represented by three specimens or fewer, some have enough specimens to enable variability estimates to be made. Those species with eight or more specimens

from a single dredge haul, or from closely spaced dredge hauls, are cited in Table 2.

It has frequently been observed that the Arctic Ocean and the deep sea have some interesting similarities in faunal composition and in physical characteristics. A large percentage of species in each region also appears to be highly variable. This indicates that biological selection in the deep sea may be of lower intensity than it is in shallow marine habitats (excluding the arctic). The survival of *Neopilina* there supports this view, as previously suggested by Parker (1962). Further consideration of the abyssal and hadal deep-sea fauna, however, is beyond the intent of this paper.

Variability in Tropical Marine Mollusks

Many tropical marine mollusks, of course, exhibit flamboyant diversity in color and in form within and between species. Masterful, encyclopedic

TABLE 2.—Variability of breadth/length in hadal deep-sea bivalve species-lots ($N > 7$) reported by Knudsen (1970)

Species	Locality	N	Range	Mean	CV
NUCULACEA					
<i>Brevinucula verrilli</i> (Dall)	Off West Africa, 3196M (3 54'N, 8 22'W)	15	0.23-0.30	0.262	8.47
<i>Nuculana pallida</i> (E. A. Smith)	Off Gabon, 4018M (4 00'S, 8 25'E)	10	0.20-0.22	0.209	3.53
<i>Nuculana vestita</i> (Locard)	Off West Africa: 2550M (1 42'N, 7 51'E) and 2770M (2 17'S, 8 10'E)	8	0.20-0.22	0.210	4.41
<i>Neilonella guineensis</i> (Thiele)	Off West Africa: 2770-4020M (3 stations)	8	0.21-0.28	0.238	9.19
ARCAEA*					
<i>Bathyarca orbiculata</i> (Dall)	Kermadec area, W. Pacific, 4410M (36 31'S, 178 38'W)	18	0.39-0.51	0.439	8.78

* Great variability is also reported in other Arcacea, e.g. in *Bathyarca asperula* (Dall) (see also Knudsen, 1967) and in two species of *Limopsis* but measurements are not given. In *Limopsis* the valves become obliquely elongated with growth and standard measurements are not meaningful.

overviews of the North American fauna have recently been produced by Keen (1971) and Abbott (1974). It is far beyond the intent of this paper to examine the diversity of tropical mollusks in detail but some data that are pertinent to the present discussion must be mentioned.

In the judgment of the writer, the most highly variable polychromatic marine species are members of six families: Phasianellidae, Neritidae, Cerithiidae, Olividae, Pectinidae, and Donacidae. North American representatives of these families are discussed below.

Tricolia (Phasianellidae) includes seven tiny, tropical North American species. Most are abundant in shallow subtidal habitats on turtle grass (*Thalassia*) and these exhibit striking diversity in colors (bright shades of red, pink, orange, yellow, green, purple, brown, and black) and color patterns (dots, bands, flamelike spots). One species (*T. thalassicola* Robertson) extends north to North Carolina and there the colors are muted. For details see Robertson (1958) and Abbott (1974).

Neritina (Neritidae) has three tropical North American species. All range south from southern Florida and are abundant in brackish and coastal freshwater habitats. Outstanding diversity in color pattern (spots of many shapes and sizes, zigzag bands, and spiral stripes) and color (brown, olive, gray, purple, and yellow) is normal in most populations and especially for the most abundant species *N. virginea* (see Figure 3). Russell (1941) and Abbott (1974) give details.

Bittium (Cerithiidae) has two abundant East

Coast species and one rare Californian species. *B. varium* (Pfeiffer) (Maryland to South America) has five common color morphs: dark purple-brown, pale purple-brown, brown, pale brown, and white. *B. alternatum* (southeastern Canada to Virginia) is more uniformly dark purple-brown and lacks the pale brown and white morphs. Both occur in incredible numbers on subtidal mud flats and eelgrass. A related West Indian species, *Batillaria minima* (Gmelin) (Family Potamididae), also occurs abundantly in intertidal mud flats and white limestone rocks, and exhibits striking variation in its black, brown, gray, and white banding.

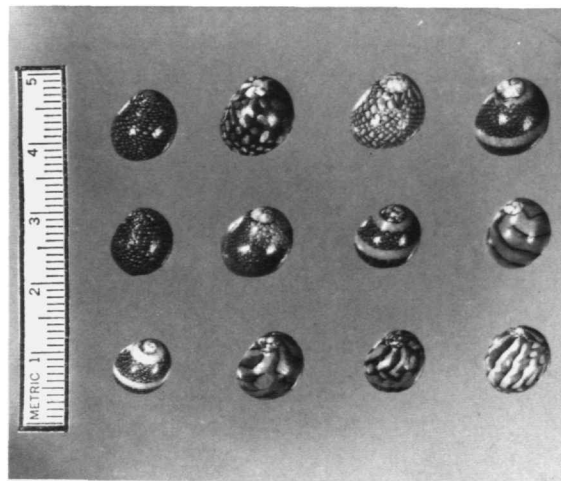


FIGURE 3.—Intraspecific variation within a population of *Neritina virginea* (Lamarck) from Parahyba River, Brazil.

Olivella (Olividae) includes about 40, mostly tropical, North American species. The most abundant (*O. mutica* (Say), *O. pusilla* (Marrat) *O. biplicata* (Sowerby)) are all highly polychromatic, shallow subtidal, and tropical. The single northern species (*O. boetica* Carpenter) (Alaska to California) is dull and brownish. See Abbott (1974) and included references for more information.

Argopecten ((Pectinidae) *Aequipecten* of many authors) contains four or five North American species; all are subtidal and most are locally abundant. All are strongly polychromatic, especially on the upper valve, and northern populations on both coasts are more subdued in color than southern populations. A cline in frequency of white lower valves (17% of specimens in the extreme northern population to 100% in most of the southern populations) has been demonstrated for the eastern *A. irradians* (Say). See A. Clarke (1965), Waller (1969), and Abbott (1974) for further details.

Donax (Donacidae) has five or more North American species. Most live in the wave zone of tropical sandy beaches and are momentarily exposed on the surface of the sand by each succeeding wave. They are often exceedingly abundant. Southern populations are incomparably variable in color and pattern (see Figure 4). Shades of bright pink, yellow, bluish, purple, mauve, and white are distributed in bands, rays, or as solid colors. The most northern species (or ecophenotype), *D. fossor* Say (New York to Virginia), is ordinarily only white. See Abbott

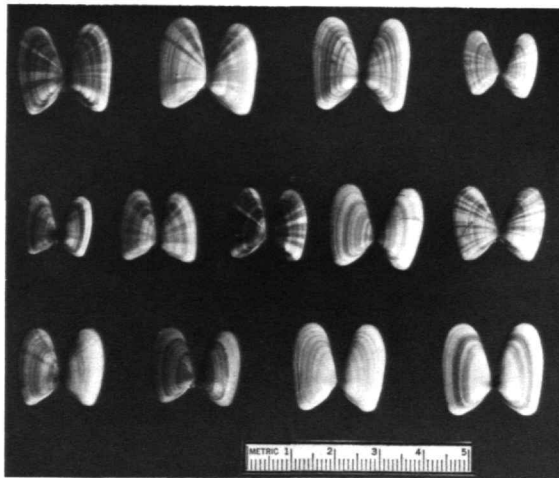


FIGURE 4.—Intraspecific variation within a population of *Donax variabilis* Say from Sarasota, Florida.

(1974) and Emerson and Jacobson (1976) for further information.

Other groups could be cited that include variable species. Among them are *Nerita*, *Littorina*, *Chlamys*, and *Tellina*. It must be emphasized that many intertidal and shallow-water tropical marine mollusks are *not* particularly variable in color, but it is certainly true that those species that are remarkably polychromatic are almost all tropical.

As mentioned above, in contrast to arctic marine mollusk faunas, conspicuous morphological distinctness between species of the same family, or in the same community, is also a characteristic of tropical marine mollusk faunas. Figure 5 illustrates this phenomenon using Philippine species of Muriidae. Inspection of any unsorted field collection of tropical marine mollusks will reveal a striking multitude of different shapes, colors, and patterns. The plates and figures in Keen (1971) and Abbott (1974) will so completely demonstrate the intraspecific diversity of tropical mollusks that further discussion here is unnecessary.

The Diversity Maturation Hypothesis

The fact that patterns of morphological variability change as they do as one moves from one climate zone in North America to another indicates that differing selective forces exist in different zones. The hypothesis presented below attempts to explain, at least in part, the possible adaptive value of these patterns. For clarity a brief statement of essential features is given first and additional supporting evidence and discussions are presented later.

The existence of a continuum of biome development is postulated but for ease of discussion three progressive phases are identified, each characterized by distinct patterns of intra- and interspecific morphological variation. The phases are not visualized as mutually exclusive but they are believed to represent a real trend.

PHASE I: INITIAL OCCUPANCY.—Any area of the world that becomes fit for occupancy by animals and plants because of ameliorating climatic conditions gradually becomes populated with more and more species. Initially, in comparison with more mature biomes, interspecific competition in this unfilled environment and selection of particular prey species by predators will be relatively unim-

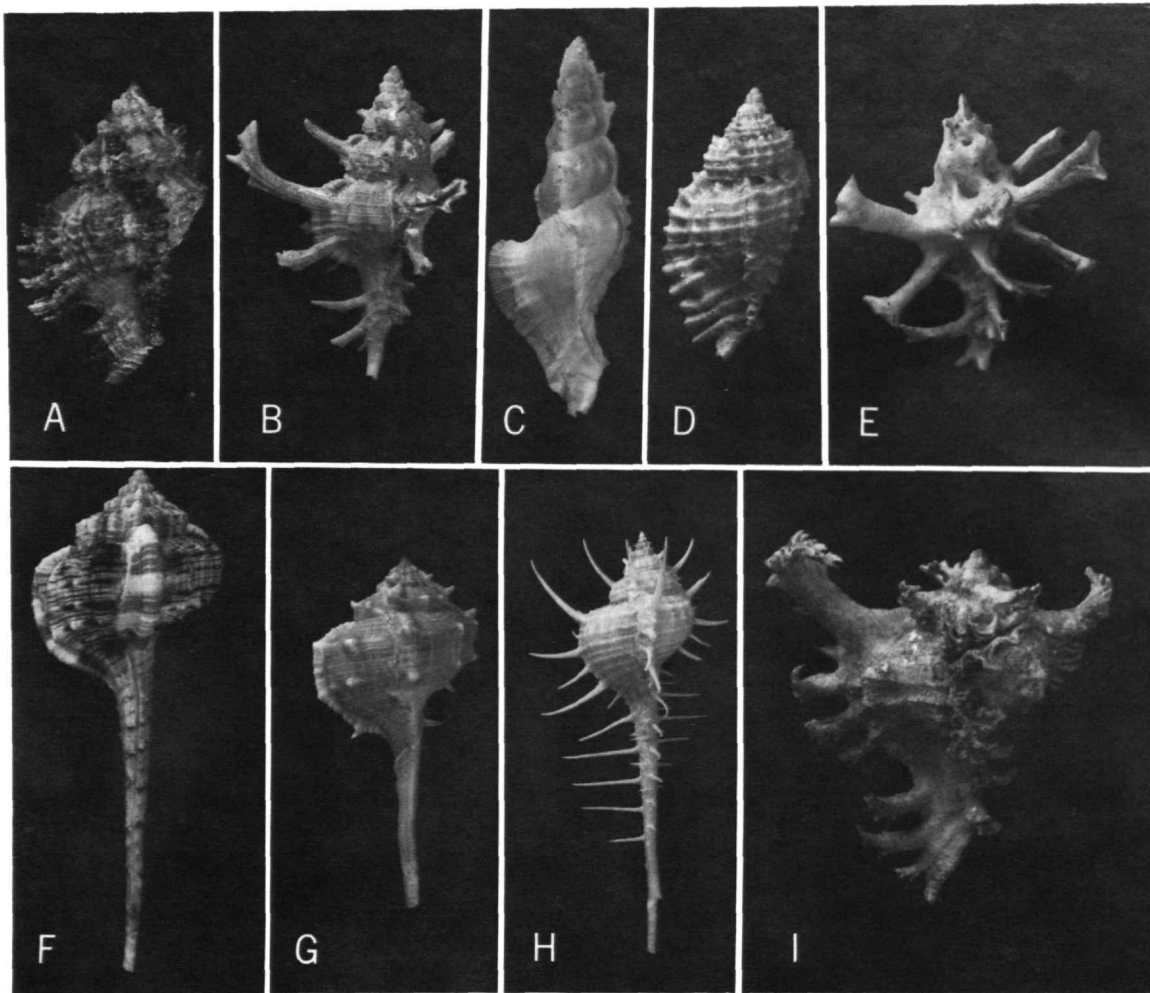


FIGURE 5.—Interspecific aspect diversity in representative Muricidae from the tropical Western Pacific (Philippine Islands to northern Australia): A, *Phyllonotus laciniatus* (Sowerby); B, *Chicoreus damicornis* (Hedley); C, *Marchia elongata* (Lightfoot); D, *Naquetia trigonula* (Lamarck); E, *Homalocantha zamboi* (Burch and Burch); F, *Haustellum haustellum* (L.); G, *Murex brevispinus* Lamarck; H, *M. tribulus* L.; I, *Chicoreus cornucervi* (Röding).

portant in limiting populations and natural selective pressures will be imposed primarily by the physical environment. As a result, many mutations will persist, morphological diversity within some prey species will be great, and instances of approximate morphological overlap between species will be numerous. The arctic and deep sea regions provide characteristic examples of this phase.

PHASE II: EARLY BIOLOGICAL SELECTION.—As more and more species enter the new environment,

and become adapted to it, intra- and interspecific competition and selection by predators will become progressively more important. In the face of increased biological selection, diversity in color, color pattern, and form will decrease among prey species because, of course, certain colors and color patterns and body forms are more efficient than others in ensuring survival. Examples of morphological overlap between species will become less frequent as large deviations from the optimum become rarer.

The temperate regions provide numerous illustrations of this transitional phase.

PHASE III: BIOME MATURATION.—After equilibrium and species saturation is established within a mature biome, and with the passage of time, special strategies for survival evolve within prey species. Many species become cryptic, such as hidden within coral reefs or overgrown by algae or bryozoans. Many noncryptic species evolve intrinsic defense mechanisms such as becoming poisonous or venomous, or evolving hidden sharp barbs, spines, teeth, or even more unique features. Predators are then under selective pressure to become more discriminating in their diets. A frequently observed manifestation of this behavior is that during any single feeding period, and after an initial trial, a predator will feed only on prey which look alike and therefore appear to belong to the same species. In turn, this brings selective pressure to bear among noncryptic prey species to evolve conspicuous diversity of two kinds. Within a community composed of many noncryptic prey species, each will tend to evolve prominent morphological features that contrast with those of neighboring species, thereby minimizing the chance of being consumed by error by a discriminating predator who is searching for another species. Within some communities composed of only one or a very few prey species, dominant species will tend to evolve diverse (and often stereotyped) contrasting color and color pattern morphs and thereby seem to mimic an assemblage of many different species. The tropical regions support many biomes in this phase of development.

Discussion

Phase I, II, and III biomes only approximate with arctic, temperate, and tropical shallow-water marine ecosystems because the former relate to levels of maturity achieved since initial colonization, whereas the latter relate to temperature. Because of recent geological history, however, there is an undeniable parallel, and since the literature may be conveniently divided on the basis of climatic zones, the following discussion is also arranged in that manner. It must be emphasized that the phenomena discussed are not simple temperature effects because arctic animals are surely as well

adapted to arctic life as tropical animals are to existence in the tropics.

The youthful nature of arctic ecosystems is undisputed (Dunbar, 1968). Evidence indicates that during the short time since deglaciation the marine mollusks (and the freshwater mollusks as well) have not yet achieved distributional equilibrium. In many species, for example, rapid range expansions appear to be going on at the present time (A. Clarke, 1973, 1974). Other marginal habitats such as the deep sea and (for terrestrial animals) deserts may be expected to exhibit similar phenomena.

Details concerning the feeding habits of most predators, and indeed the identity of the major predators of most prey species, are lacking. Such data are necessary before the adaptive significance of many characteristics of prey species can be clearly understood. It is clear, however, that many and probably most arctic predators (and even aboriginal Eskimos) are catholic, opportunistic feeders, a behavior necessitated by the seasonal and resurgent nature of populations among major prey species. This feeding behavior has been frequently observed by arctic field biologists but, with few exceptions (e.g., Holmes and Pitelka, 1968), rarely documented in the literature.

Pleistocene temperature fluctuations (see Flint, 1971) undoubtedly destabilized and shifted biotic zones in the north temperate region. The fauna there is complex and diverse. The relative lack of variability among most marine mollusks there implies that, in general, biological selection is neither as unimportant there (with respect to physical selection) as it is in the arctic nor as intense as it is in the tropics. Polychromatic populations of some mollusks and other invertebrates do occur, however, especially among (but not exclusive to) out-post populations of groups that are principally tropical, e.g. in *Donax variabilis*.

An interesting case involves the brittlestar *Ophiopolis aculeata* observed in a cove in Maine in about one inch of water (Moment, 1962). One or more species of birds and fishes are presumed to be the major brittlestar predators. This example illustrates a phenomenon that may alter the kind of morphological diversity in prey species from what would be expected in temperate ecosystems. Many predatory birds migrate and highly selective feeding habits which might have evolved in a Phase III biome, if applied in a Phase II biome, may affect

it in a discordant way. The similarities in morph distributions observed in tropical and temperate moths by Ricklefs and O'Rourke (1975) and the presence of polymorphic colonies of the intertidal mollusks *Nucella lapillus* and *N. lamellosus* in the temperate region may be partly attributable to this. Invertebrate marine assemblages in arctic Phase I biomes will be little influenced by this phenomenon because they occur almost exclusively in subtidal depths below the ice-scoured zone.

Dobzhanski (1950) has described the luxuriant taxonomic diversity of the tropics. He was also the first to make the point, albeit somewhat indirectly, that whereas natural selection in the arctic is principally mediated by the physical environment, in the tropics such selection is mediated by species interaction. He states:

The role of environment in evolution may best be described by stating that the environment provides "challenges" to which the organisms "respond" by adaptive changes. . . . Tropical environments provide more evolutionary challenges that do the environments of temperate and cold lands. Furthermore, the challenges of the latter arise largely from physical modifications and, often, by escaping into evolutionary blind alleys. The challenges of tropical environments stem chiefly from the intricate mutual relationships among the inhabitants (Dobzhanski 1950:221).

Later A. Clarke (1965:182), as part of a discussion on geographic-morphological trends in American scallops stated that "selection in the north is strongly climatic and in the south it is strongly biological."

The groups of polychromatic marine mollusks cited earlier have one obvious and highly significant feature in common: they are all extremely abundant. Individuals of *Tricolia*, *Nerita*, *Littorina*, *Bittium*, *Olivella*, *Chlamys*, and *Tellina* are often the dominant species in their respective communities. A few groups—and this includes those that exhibit the *most* flamboyant diversity in color and color pattern—exist almost alone in marginal, specialized habitats.

As mentioned previously, most species of *Donax* live in the wave zone of tropical sandy beaches and are momentarily exposed on the surface of the sand by each succeeding wave. They burrow quickly back into the sand but after each wave recedes there are always many that have not yet hidden themselves. At these recurring moments they are obvious and are the only visible mollusks present.

Species of *Neritina* live in brackish water tropical habitats and, except for *Melampus* and *Littorina*, which cling to mangroves and other solid support above the water surfaces, they are also often the only visible molluscan inhabitants.

Species of Pectinidae, such as *Chlamys nobilis* (Reeve) from Japan, may occur with other marine bottom-dwelling mollusks, but when disturbed they vigorously swim away. During the swimming stage they may be the only large mollusks occupying the water column.

The possible selective advantage of massive polymorphism in *Donax variabilis* (Say) has been discussed by Moment (1962) and Li (1962). Neither author, however, recognized the strong positive general correlation between community dominance and the occurrence of extreme intraspecific polychromatism, although other authors have noted that particular polychromatic species are abundant. That observation is critical, however, to an understanding of tropical morphological diversity. It demonstrates that in a tropical, intertidal, or shallow-water marine habitat, intraspecific aspect diversity must confer selective advantage on a population living in a monospecies community. This leads to the reasonable conclusion that interspecific aspect diversity must also confer selective advantages on populations living in a mixed-species community.

In tropical intertidal epifaunal assemblages, aspect diversity can be achieved by contrasts in color and in form. In tropical subtidal epifaunal assemblages, however, with the notable exception of burrowing species and/or those that keep their shells covered by the mantle (e.g., *Cypraea*), a number of species have their shell surfaces often heavily encrusted with epizoons and algae which obscure shell coloration. In water over a few fathoms deep reduced light penetration also severely impedes color perception. Aspect diversity there is therefore achieved principally by contrasts in shell form alone.

Some species in the Indo-Pacific area, a geologically ancient region that probably supports the most advanced Phase III biome in existence, have carried this strategy to a remarkable stage of development. Species in the genera *Delphinula*, *Stellaria*, *Lambis*, *Thatcheria*, *Tibia*, *Corculum*, and *Penicillus* illustrate this point. In other subtidal genera, aspect diversity seems to be achieved

through brilliant, contrasting color pigmentation of the mantle (e.g., *Tridacna*—see Rosewater, 1965; and *Lima*) and other exposed soft parts (e.g., nudibranchs).

The adaptive value of polychromatic variation within and among infaunal species (e.g., *Olivella* and *Tellina* species) still defies explanation, but perhaps the colorful empty shells lying on the substrate or inhabited by hermit crabs may have a role in confusing or distracting predators.

The concept of apostatic selection that is gradually emerging (Owen 1963; B. Clarke, 1962, 1969) provides an appealing explanation of the adaptive value of the brightly colored and exquisitely molded shells and bodies of tropical marine mollusks. Substantial evidence is accumulating that many predators, and especially those in the tropics, feed selectively; they hunt by sight and are able to distinguish colors and/or color patterns. Guppies, for example, tend to feed exclusively on the most abundant kind of food available until it becomes rare and then switch to another kind of food, which is then the most abundant. In such a situation any rare morph is apparently not recognized as desirable prey until, because of continued sequential predation on the more abundant morphs, the formerly rare morph itself becomes relatively abundant. Apostatic selection is "selection for variation for its own sake in which a given phenotype is favored in direct proportion to its rarity through frequency-dependent predator pressure" (Paulson, 1973:269). Such selection also may have survival value for colonies of prey animals; at least during any single feeding period a predator may be expected not to devastate a whole polymorphic colony but to move on in search of more individuals of the morph that is currently acceptable. Such a mechanism would also be expected to favor the maintenance of contrasting aspect diversity between species in a mixed-species prey assemblage (A. Clarke, 1965; Rand, 1967) and contrasting aspect diversity within those species which live alone or virtually alone.

It is not proposed that among tropical marine mollusks inter- or intraspecific aspect diversity is more important in assisting survival than classical strategies such as protective coloration or mimicry. For example, a dense population of *Neritina usnea* (Roeding) (= *N. reclinata* (Say)) was recently observed on intertidal oysters at a Gulf of Mexico

locality (north side of Dauphin Island, near Mobile Bay, Alabama) in which all individuals are olive brown and closely resemble algae-covered barnacles on the same oyster shells. Numerous other examples of such phenomena could be cited. It is believed, however, that apostatic selection may play a role among tropical shallow-water marine mollusks that is much more pervasive than has been previously suggested.

Conclusions

One of the major points of this paper is that the nature and intensity of natural selection appears to be significantly different within communities of shallow-water arctic, shallow temperate, shallow tropical, and deep-sea marine mollusks. It therefore provides a caveat against attempts to apply in one biome a hypothesis concerning natural selection or an ecological "principal" that was originally proposed to explain phenomena observed in a different biome.

Smith (1976), for example, has thoroughly studied the ecology of *Littorina obtusata* in Great Britain and Iceland. He found that the color morphs are cryptic, with various morphs being favored on different algal species in different seasons. He also tested the possibility that apostatic selection might be important in promoting color diversity in this species but found that it was not.

It probably should not be expected that apostatic selection should be clearly demonstrable in northern European littorinids. J. Allen and B. Clarke (1968) have shown that selective feeding by passerine birds does occur in England. However, decreasing color morph variability among marine mollusks correlates well with increasing latitude in the northern hemisphere and indicates that the mechanisms responsible for maintaining this variability impact more strongly on tropical than on temperate marine mollusks. Presumably one of these mechanisms is apostatic selection.

Another thoughtful study of relevance here is by Petersen (1977), who described the structure, population density, origin, and variability of the North Sea bivalve mollusk fauna. He suggests a dual origin for the fauna, one group derived from the North Pacific and the North Atlantic, partly by way of the Arctic Ocean, and characterized by containing a number of highly variable species and

genera in which species discrimination is difficult, and another group of Tethyan origin in which species are less variable and species discrimination presents few difficulties. He further suggests that the northern group may be variable because out-post populations containing mutant genes might have survived in marginal epicontinental seas and other isolated locations thus permitting these genes to become established, whereas the Tethyan fauna lacked such marginal isolated havens and mutants could not therefore survive. He concludes by suggesting that this hypothesis might be tested in Panama, which has many islands off its Caribbean side and few off its Pacific side. In such a situation the Caribbean fauna should present more taxonomic difficulties than the Pacific fauna.

Other hypotheses to account for arctic diversity could also be proposed and one soon becomes faced with Phaedrus' dilemma (Pirsig, 1975:107): plausible hypotheses can be proposed to explain any complex phenomenon in nature faster than they can be tested and evaluated.

The writer has had some field experience in Panama and taxonomic problems seem to be of comparable difficulty in both faunas except that the Pacific fauna is more diverse. Petersen's hypothesis remains to be tested, but it is doubtful if the islands of the Caribbean are sufficiently remote from each other to provide tropical species (which, in contrast to arctic species, have predominantly pelagic larvae) sufficient isolation for mutations to multiply and to become fixed in Caribbean populations. Moreover, if the biome maturation hypothesis is correct, one should not expect to find that natural selection has produced similar effects in the arctic and in the tropics.

Another explanation for the North Sea phenomenon is compatible with the biome maturation hypothesis, i.e. that lack of intense biological selection (perhaps combined with partial isolation) has enabled some arctic species to acquire and store substantial genetic variability which persists in a northern environment such as the North Sea. It is well established that in the absence of predation and interspecific competition the morphological versatility of many species will tend to increase (see Vermeij, 1973, and included references). Teth-

yan species might have been exposed to more intense biological selection that has not permitted substantial genetic variability to develop. The North Sea fauna may not yet have reached the stage of advanced equilibrium necessary for the genetic variability of the two groups to converge as a result of comparable selective pressures.

Summary

Studies on the morphological diversity of marine mollusks have shown that a relationship probably exists between the nature and extent of diversity on the one hand and biome maturation on the other. A hypothesis is developed called the Diversity Maturation Hypothesis which describes these diversity shifts and correlates them with changes in natural selection. Although viewed as a complex continuum, three general, progressive phases in biome maturation are postulated.

PHASE I: INITIAL OCCUPANCY.—A relatively few (but increasing number of) predator and prey species are present. Many of the prey species exhibit pronounced morphological diversity and individuals are frequently seen which are externally difficult to identify. Predators tend to be indiscriminate feeders and natural selection is mediated principally by the physical environment.

PHASE II: EARLY BIOLOGICAL SELECTION.—Many more predators and prey species are present. Diversity within most prey species is much reduced and species tend to be distinctive in appearance. Predator pressure is relatively great, predators are more discriminating in their diets, and natural selection is principally biological.

PHASE III: BIOME MATURATION.—Predator and prey species are both numerous. Many prey species evolve intrinsic defense mechanisms and predators tend to become selective in their diets. Many prey species become cryptic. Many noncryptic prey species evolve conspicuous aspect morphologies that contrast with those of other species in the same communities. In some marginal habitats where only one (or a very few) noncryptic prey species lives conspicuous polymorphism evolves. Both of these prey responses appear to be maintained by apostatic selection.

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