LOCAL RACES AND CLINES IN THE MARINE GASTROPOD *THAIS LAMELLOSA* GMELIN

A POPULATION STUDY

BY TREVOR KINCAID
Professor Emeritus in Zoology
University of Washington

THE CALLIOSTOMA COMPANY
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INTRODUCTION

In recent years considerable attention has been directed to the study of infraspecific variation in animals. Such studies have not only created a revolution in the field of taxonomy, but have also thrown considerable light upon the nature of the evolutionary process itself, which since the time of Darwin has proved a baffling problem. In the case of birds the reinterpretation of the group from this standpoint has led to the reduction in the number of recognized species in the world list from about 27,000 to approximately 8,500. The remaining trivial names either have been placed in the synonymy or reduced to the status of subspecies. In the mammals a corresponding reduction has taken place. Twenty-eight species of *Peromyscus* have been reduced to one, while the single species *Thomomys bottae* is saddled with 150 subspecific names (Burt, 1954), indicating that in this case we apparently are giving trinomial designations to local races. Similar reductions in the trivial names applied to the other groups of vertebrates have taken place, while the invertebrate phyla are being gradually subjected to the same type of critical analysis.

It is becoming increasingly evident that the Linnaean system of nomenclature, while it has served its purpose over the years, is ill adapted to express the relationships of organisms in the ever moving drama of organic evolution. To the older school of taxonomists the living world appeared as a static system only awaiting description; we now know that we are compelled to deal with situations that are highly dynamic and cannot be described in terms of traditional systematics.

The discovery that in nearly all species, when the various populations are carefully studied, the individuals present variations which tend to fall into graded series or clines, has always created problems for taxonomists, since a type must be selected from a variable series, the remaing deviations from the norm being regarded as varieties. It has also been found that when a large number of definitive populations are examned they tend to fall into graded series or clines, the so-called *Rassenkreise* of Rensch.

Since under traditional systematics all recognizable differences in organisms must be given distinctive names, usually with trivial standing, these multiplied on a grand scale. As Wagler (1912), in connection with the naming of new species of *Daphnia*, put it, "Sie sprossen wie Pilze aus die Erde."

Since the taxonomic study of most groups of animals has followed a somewhat piecemeal pattern, the discovery of their clinal relationship was not disclosed till extensive collections had been accumulated covering the geographic range of the species and the pattern formed by their local races. It was found that many species had been described which were based upon microgeographic races.

As the clinal relation of the various populations was recognized in the better known groups of animals, particularly in the vertebrates, a wholesale reduction in the number of listed species took place. In the invertebrate phyla a similar sitution exists, and as the various groups are critically studied from this standpoint the necessary readjustments are being made. When this revisionary process is carried out the already vast accumulation of synonyms will be greatly increased. In insects, on account of the magnitude and complexity of the group, a state of nomenclatorial chaos exists (Hubbell, 1954.) In some orders, as in the Coleoptera, certain authors have followed a conservative pattern, and have avoided what they instinctively recognized as local races, and as a result they have created few synonyms, while others have based their descriptions upon slight deviations from the norm, and have thereby caused a great deal of confusion, with a resulting crop of synonyms ranging in some cases up to 75 percent of their descriptions. One author dealing with sawflies redescribed the same species eighteen times. As one of my colleagues remarked regarding the description of some new species of fossils by a certain palaeontologist, "a paper might be written entitled *The Origin of Species*, with apologies to Darwin."

In most of the groups in which the nomenclatorial system has been revised from the new standpoint the change has proceeded without undue disturbance by placing large numbers of trivial names in the synonymy, and reducing others to the status of subspecies; but in the case of highly variable polytypic forms the difficulty of harmonizing the traditional systematics and the modern viewpoint has been very great. No satisfactory method has as yet been devised to give taxonomic expression to the kaleidoscopic clinal phenomena exhibited by populations and by series of local races of the "*rassenkreise*" type. Dr. H. A. Pilsbry (1912) has expressed this situation in very apt language in his monograph of the Hawaiian tree-snails where he remarks, " A philosophic method of dealing with intraspecific differentiation is one of the greatest present needs of systematic zoology." Similar difficulties have been encountered by students of insects and other groups of animals in attempting to harmonize systematics as a descriptive science and the dynamic viewpoint of the animal world as an evolving system. In plants we find similar problems, as is illustrated by the case of the tarweeds investigated by Babcock and Hall (1924). These authors in a study of a group of plants included in the genus *Hemizonia* were enabled by supplementing the usual herbarium and field examinations with detailed genetic and ecological experiments, to prove conclusively that all nine names previously assigned to this group must be regarded as variants of *Hemizonia congesta* described in 1836 by the botanist DeCandolle.

In view of the transitional state in which the science of systematics finds itself, it is not surpising that much variance exists in the treatment of taxonomic material. As yet no Moses has appeared to lead us out of the nomenclatorial wilderness.

Some authors have suggested that in such cases we should abandon the Linnean system and resort to the use of numbers to identify the various related forms. Others, as in the case of those attempting to record the protean variations in the shell banding of the garden snail *Cepea hortensis*, have resorted to the use of cabalistic insignia, which make their reports resemble the formulae of differential calculus.

In general the tendency among sytematists dealing with invertebrate groups has been to follow the procedure initiated by the ornithologists and mammalogists and reduce many of the recorded species to subspecies, and place others in the synonymy. Goodrich (1922) in an early paper dealing with the river snails of the genus *Anculosa* inhabiting the watershed of the Alabama River listed some thirty species, but in a later paper (1945) treating of the widely distributed and locally variable fresh-water snails of the genus *Goniobasis* inhabiting the area between the Great Lakes and New York, recognized the clinal relation of these forms and reduced a list of over twenty trivial names to a single species, *Goniobasis livescens*, and gives illustrations of eighteen divergent local races.

In a recent paper Herrington (1954) has presented a revision of the American forms included in the genus of small fresh-water bivalves *Pisidium*. He reduces the number of listed species from about one hundred to twenty-five. Of these only three are limited in their distribution to the United States, while twelve are circumpolar.

A classical example of the difficulties that arise in attempting to give systematic expression to a clinal group of molluscs is the case of the tree-snails of the family *Achatinellidae* inhabiting the Hawaiian Islands. The richly colored shells of these molluscs were early brought to the attention of collectors following the discovery of the islands by Captain Cook in the year 1778 who found the natives using them for ornamental purposes. The wide range of color they displayed led to numerous descriptions of supposedly new species, so when Dr. Pilsbry undertook his monographic revision of the group in 1912 he found the record cumbered by the presence of 171 trivial names that had been applied to various forms. In his revision he reduced the number of recognized species to 43.

In the meantime Gulick (1908), had called attention to the theoretical interest attaching to the achatinellids as a remarkable example of microgeographical speciation. The snails, living on the trunks of trees and relatively non-migratory, tend to form large numbers of inbred local races. Gulick interpreted these racial differences as due to isolation and random variation in the ancestral stock, the observable differences having no selective value; in other words a form of evolutionary progression in which the Darwinian principle of Natural Selection was not involved. Pilsbry offered the further suggestion that in these local races we have phenotypes representing Mendelian segregates. Both of these views are quite in line with our present interpretation of the phenomena.

The studies of Gulick and Pilsbry based upon the Hawaiian tree snails were followed by the investigation by Crampton (1916), of the terrestrial snails included in the genus *Partula* inhabiting Tahiti. He found that in this island, as in Oahu, there were a large number of microgeographical areas which were inhabited by local races of the snails. He did not find any differences in the environmental conditions which would suggest that a selective process was involved in determining the development of racial speciation.

More recently Welch (1938, 1942), has made a very detailed study of the achatinellid fauna of the island Oahu, pinpointing the microgeographical distribution of the numerous local races in great detail. He reduces the number of recognized species to six, and gives all of the clearly defined local races the status of subspecies, some of which have assigned to them as many as seven unnamed varieties. In the case of one of the species, *Achatinella apexfulva* Dixon, Welch discriminated seventy-eight named subspecies and more than sixty unnamed varieties, the majority based upon local populations differing mainly in slight deviations of color. It seems unfortunate that the literature should be burdened with such extensive taxonomic terminology to describe what is essentially an interesting biological phenomenon illustrating one phase of organic evolution. It indicates clearly however, the difficulty under which taxonomic science suffers in dealing with a problem of this type.

Another striking example of molluscan forms exhibiting polytypic tendencies is seen in the terrestrial snails of the genus *Cerion* inhabiting the coastal areas of the Bahamas, Cuba, Haiti and Porto Rico, where large numbers of localized races have been found. As usual in such cases the taxonomic history is replete with superfluous names.

In dealing with the nomenclatorial problems arising in connection with the discrimination of polytypic forms we find in the case of the mollusks a situation which is not commonly found in other groups of invertebrates.

The curator of a museum having a collection of molluscan shells in his charge naturally desires to have his specimens properly labelled, and for this purpose he depends upon the specialists in the several groups. He finds wide disagreement among the experts, and as he sadly changes his labels discovers the truth of the *bon mot* attributed to Dr. G. W. Wharton, (Allen, 1955) ", the common names of animals change from place to place, the scientific names from time to time."

Taxonomists dealing with the systematics of groups of mollusks exhibiting polytypic tendencies often find difficulty in expressing the relationships of the several forms, and usually resort to trinomials. In monographing such groups the older literature is apt to be obscure, with resulting confusion and the accumulation of many synonyms, together with the changing of many labels.

The third group of persons interested in the nomenclature of the mollusks includes what may broadly be termed amateurs. Many of these are lacking in a scientific background and take up the collection of shells as a hobby, being attracted no doubt by the endless variety and great beauty of these natural objects. Even prehistoric men and modern savage tribes have utilized shells for personal adornment and also as a medium of exchange. In ancient as well as in modern times the aesthetic appeal has provided an important stimulus for the widespread interest in these forms. The contributions of amateurs to this branch of science have been numerous and important, not only through the enrichment of the great central collections by their activities in the field, but also through the development of many specialists who have contributed greatly to this branch of science. To facilitate the exchange of specimens between collectors accurate naming was essential, and as a result the taxonomy of the group was greatly emphasized. Since rarity and unusual forms, especially those with differing color patterns or with unusual size or sculpture, led to the description of many species which have later been invalidated; it seems probable that as the polytypic character of these forms is established many additional trivial names will be suppressed.

A fourth group interested in the nomenclature of mollusks is represented by the palaeontologists, since it must be borne in mind that these forms are subject not only to spatial isolation, but to temporal isolation as well. The transition from the late Tertiary forms to those of the modern age is not sharply defined. Owing to the unique character of fossil forms the relationship between the ancient and modern types has often been obscured, and only the collection and study of ample series has enabled taxonomists to clarify the resulting confusion, especially in the case of polytypic forms.

Still another group interested in the study of poyltypic organisms includes those who see in these forms an approach to the baffling problem of speciation in the living world.

In recent years there has been inaugurated an intensive study of animal populations in an effort to determine the relative importance of genetic, ecological and spatial factors in bringing about the evolutionary differentiation of organisms. Observations in the field have been supplemented by breeding experiments, physiological studies, statistical analyses and genetic interpretations. The literature in this field has already become quite extensive: it has been thoroughly summarized by Dr. Ernst Mayr (1949), with emphasis upon spatial and other phases of isolation as factors in the evolutionary process.

The present paper is designed to place on record some of the local races of *Thais lamellosa*, which is highly polytypic and is distributed along the Pacific Coast from California to the Aleutian Islands, exhibiting an endless diversity of size, coloration and sculpture.

The writer first became interested in the marine snails of the *Thais* group at the time he entered the University of Washington as a student in 1894. At that time a group of persons known as the Young Naturalists Society maintained a meeting place and a museum in a small frame building standing upon the campus of the university, which at that time was located in downtown Seattle. The membership included several persons interested in "conchology", now known under the more dignified title of "malacology". They had accumulated a considerable collection of *Thais* material, but had been baffled in their attempts to classify them when they found the various forms shaded into one another by insensible gradations. The significance of the localized races of these forms apparently had not been realized.

With the establishment of the Puget Sound Marine Station (later renamed the Oceanographical Laboratories) under the auspices of the University of Washington, beginning in 1901, the writer was brought in contact with the rich marine fauna of the San Juan Islands. This interesting archipelago located in the Gulf of Georgia includes a large number of rocky islands of various sizes, and many reefs both emergent and non-emergent at low tide levels, and since the larger islands are freqently bordered by bold rocky headlands separated by crescentic gravelly beaches, the area is remarkably adapted for the differentiation of localized races of *Thais*. Collections made in Puget Sound, British Columbia and Alaska brought to light many additional variants.

The publication by Gulick (1905) of his paper dealing with the tree snails (*Achatinellidae*) of the Hawaiian Islands greatly stimulated our interest in the study of our local races of *Thais*, since it was at once seen that they could be interpreted as the resultant of an evolutionary process in which spatial isolation has played an important role.

In 1880 there appeared a monographic revision of the *Muricidae* of the world by George W. Tryon Jr. in which the subfamily *Purpurinae* is thoroughly reviewed. As was customary at that time he placed the forms we now include in *Thais* in the genus *Purpura* and in the subgenus *Polytropa* Swainson. A study of the material at his command led him to the conclusion that all of the forms related to *lapillus*, both in the North Atlantic and North Pacific, are variations of a single wide-spread and highly variable species. A quotation from his monograph reads as follows:-

" The quantity and variety of material before me, embracing a rich series of forms from many localities, together with the comparison of numerous descriptions and figures that have been published, induce me to include under this, the oldest name, a very large number of nominal species. As in the case of *haemastoma*, I have considered it preferable to retain some of these names as indicating growth modifications and localities; those who take a more conservative view than myself will thus have the names and descriptions at hand to designate these several forms as varieties or species, or even genera, if it so pleases them. I have also endeavored to illustrate a few of the transitional forms".

A study of abundant material indicates that all of the various forms of *Thais* found on our Pacific Coast, with the exception of *Thais lamellosa*, are completely integrated, not only among themsdlves, but also with the innumerable and varied local races of *Thais lapillus* of the Atlantic. In the case of

Thais lamellosa the writer is of the opinion it is specifically distinct. Although populations of this species are commonly found mingled with those of various forms of the *lapillus* type no clear-cut evidence of cross-breeding has been observed. In cases where the sculptural pattern of the shell in *T. lamellosa* approximates that frequently found in *T. lapillus*, this may readily be explained on the basis of their common *Purpurine* ancestry. The distinctness of the two groups is also borne out by the palaentological evidence, since both types occur in rocks of Tertiary origin.

In view of the above considerations the writer decided to deal with the problem of *Thais lamellosa* at this time, and leave the more complicated case of our west coast forms of *Thais lapillus* for future treatment.

In 1910 Miss Bertha Challis, at that time a graduate student in the Department of Zoology, became associated with the writer in the study of the *Thais* material, and eventually decided to utilize some of our findings in a thesis for the Master of Science degree. In this connection Miss Challis made a number of excellent photographs of groups of the shells of *Thais*, some of which have been utilized in the present report. The Challis report was not published, but included our findings at that time which were, as has been indicated, markedly influenced by the papers of Tryon (1880) and Gulick (1908). During the intervening years the writer has continued to accumulate representative *Thais* material from all possible areas of the Pacific Coast, as well as material from the Atlantic for comparative purposes. The writer has also had an opportunity to examine the extensive collections of *Thais* in the United States National Museum which formed the basis for the study of this group by Dr. W. H. Dall, and those in the Philadelphia Academy of Natural Sciences administered by Dr. H. A. Pilsbry. The molluscan collections in the California Academy of Sciences in San Francisco, and in the Geological Museum of Stanford University also include extensive series of *Thais* material from west coast areas.

Since the appearance of Tryon's monogaph of the *Purpurinae* in 1880 a number of important papers have been published dealing with the taxonomy, life history, ecology and genetics of this group, which have tended to modify and extend our earlier interpretations.

The photographs of *Thais* shells accompanying this paper are for the most part approximately natural size. The procedure followed has been to arrange a group of shells upon a surface measuring 5x7 inches, which were then photographed upon a film of the same size. Where there has been any departure from this scale it will be indicated in the material accompanying the several plates. Groups of shells with prevailingly pale coloration have been photographed upon a black background, otherwise a white surface has been utilized.

In selecting groups of shells for illustration the writer has attempted to show the general character of the inividuals comprising the specific populations, and also the tendency of the individuals to vary among themselves to form a local cline, either as regards sculpture or coloration, or both of these. In some cases extraneous elements appear in a population, since the degree of isolation varies with distance, tidal currents and the driving power of storms.

It is of course needless to say that our knowledge of the local races of *Thais* is far from complete. The great area of our North Pacific coast, extending from Puget Sound to Bering Sea, includes a vast number of islands, rocky promontories and reefs, very few of which have been explored by zoologists.

ACKNOWLEDGMENTS

As has already been indicated the writer is greatly indebted to Miss Bertha Challis for her fine cooperation in organizing the *Thais* collection and helping, many years ago, to lay the foundation for the present study.

The writer is greatly indebted to Mr. Walter J. Eyerdam of Seattle, Washington, for his unfailing assistance in securing local populations from areas that otherwise would have been inaccessible. Eyerdam has collected extensively in Alaska,

and has brought to light a number of interesting local races from that little known region. His extensive collection of *Thais* material has been generously placed at our disposal for study. Through the good offices of Eyerdam it was also found possible to secure on loan from the Canadian National Museum in Ottawa, an extensive collection of local races of *Thais lapillus* from the maritime provinces of Canada.

Mr. Philip Putnam of Anacortes, Washington, has provided an extensive and much appreciated series of local races, largely from areas in the Gulf of Georgia, including some localities in the Canadian islands lying in the northern part of this body of water.

Mr. I. L. Norberg of Seattle provided several sets of shells from Prince William Sound in Alaska.

From Mrs. Irma Z. Rodenhouse of Seattle, we have received an interesting series of local populations from Vashon Island in the southern section of Puget Sound.

Mr. H. Schwarz contributed a series of populations from rocky headlands on Fidalgo Island,

Mr. J. Hall furnished material illustrating the *Thais* forms occurring in the Humboldt Bay area of California.

From Dr. Allyn G. Smith of Pasadena, California, was received a set of specimens from Alameda, on San Francisco Bay.

THE GENUS THAIS

As might be expected, especially in view of their polymorphic tendencies, the marine snails of the genus *Thais* have had a long and complicated nomenclatorial history in the study of muricid gastropods, dating back into pre-Linnaean days. Dr. W. H. Dall (1909) in a paper dealing primarily with the fossil members of this group has summarized his findings in this intricate field. According to him the sequential arrangement of the historical references to the genus between 1789 and 1903 numbered thirty-eight. His analysis led him to the conclusion that the first well defined reference to the generic status of this group was in the establishment in 1798 of the genus *Thais* by Bolten.

The older records are frequently obscure and often of doubtful validity, which leads in many cases to divergent opinions among experts as to the proper application of the laws of priority governing in such cases. To the layman who lacks access to the original documents, these nomenclatorial disputations appear at times like the wrangling of lawyers over the technicalities of the civil law. No decision appears to be final.

As has been indicated Dall ascribed the founding of the genus *Thais* to Bolten, but Clench (1947) is inclined to the view that this honor belongs rather to Röding.

A similar divergence of opinion has appeared in connection with the question as to the subgeneric status of the forms of *Thais* inhabiting the North Atlantic and North Pacific areas. Dall (1915) in his revision of our west coast species placed all of these forms in the subgenus *Nucella*. Clench however on what would seem to be indisputable grounds, argues that the subgenus *Polytropa* Swainson takes precedence over *Nucella* Röding.

Dr. Clench in his survey of the forms of *Thais* representing the southern division of this genus, gives us a clear-cut analysis of this difficult group, the members of which, like many other forms exhibiting polymorphic tendencies, have received an over-supply of names, with much resulting synonomy.

As Dr. Clench has pointed out, the southern group of *Thais* differ from their northern relatives in their manner of reproduction, the young being hatched from a fixed egg-mass as a free swimming veliger larval form, which greatly increases their powers of distribution, and thus tends to form less distinctive local races except in a broadly geographic sense, as in the case of the subspecies of *Thais rustica* found upon the isolated island of St. Helena.

Clench has suggested it might be desirable to separate generically the two groups of *Thais* forms.

Although the writer has no material of the southern *Thais* for comparison, it seem probable that more detailed population studies should prove interesting.

The present paper is not designed as a taxonomic treatise, and the writer has no desire to formally synonymyze the forms of *Thais* of the *lapillus* type found upon our west coast with the Atlantic species, although he believes that would be a logical procedure.

In a paper published in 1910 Dr. E. G. Vanatta placed a considerable number of trivial names that had been applied to our west coast forms as synonyms under three species which he regarded as valid:-

Thais plicata Martyn, 1789, with a list of six synonyms, including *Buccinum lamellosum* Gmelin, 1790.

Thais lima Martyn, 1784, with five synonyms, including *Purpura canaliculata* Duclos, 1832, and *Purpura decemcostata* Middendorf, 1849.

Thais emarginata Deshayes, 1839, with several synonyms.

In the year 1915 Dr. W. H. Dall published a very detailed monographic revision of our west coast *Thaisidae*, in which he expressed his views regarding the proper classification of this group. In dealing with these highly polymorphic forms, which present intergrading series of a most far reaching nature, he followed the traditional method of dealing with such problems and initiated a series of highly artificial divisions, leaving it to the individual to fit his specimens into the system as best he might. The difficulty of harmonizing this traditional treatment with the modern trend in taxonomic procedure is quite apparent.

In his treatment of the group representing *Thais lamellosa* Dall gives an exhaustive summary of the bibliographic references to this species, tracing the permutations in the names that have been applied to this variable form by various authors through six changes in the designation of the genus and ten trivial names that have been applied since it was first called to the attention of students of the Mollusca.

In this paper Dall points out that the name of this species utilized by Vanatta is invalidated under the laws of priority, which leaves *Thais lamellosa* Gmelin as the accepted name.

Dall evidently found that the various forms of *lamellosa* were so closely intergraded it was not desirable to establish definitive subspecies, and therefore resorted to the expedient of instituting four named varieties in addition to the typical form as figured by Gmelin: *franciscana*, from San Francisco Bay; *bormica*, from Sitka Harbor, Alaska; *neptunea*, from Cook Inlet, Alaska; and *cymica*, from Port Ludlow, Washington.

These "varieties" are obviously merely descriptions of a few local races which might be extended almost indefinitely on the same basis. This has tended to increase rather than lessen the taxonomic confusion in this group, as has been indicated by Grant and Gale (1931) and others. Mrs. Ida S. Oldroyd in her survey of the molluscan fauna of our west coast (1924) cites Dall's varieties but adds the significant note "not known except from the type locality".

In dealing with the still more heterogeneous forms related to *T. lapillus* of the Atlantic, Dall differed sharply from Vanatta, since instead of the two species listed by the latter he recognizes four, with several varieties, including *lima* Martyn typical; *T. canaliculata* Duclos (1832) typical; *T. canaliculata* var. *analoga* Forbes (1850); *T. canaliculata* var. *compressa* Dall; *T. emarginata* Deshayes (1839) typical; *T. emarginata* var. *ostrina* Gould (1857); *T. emarginata* var. *projecta* Dall; *T. freycenetii* Deshayes (1841). Owing to the amount of "lumping" and "splitting" by the several authors the synonomy has become much involved.

The above arrangement by Dall has a sufficiently wide spread to make possible the labeling of a large number of divergent forms, but makes no allowance for the fact that all of these are connected by intermediate types.

Most recent authors except Mrs. Oldroyd, in dealing with this group have followed the interpretation of Vanatta rather than that suggested by Dall.

A number of fossil forms of *Thaisidae* derived from Tertiary deposits have been described under various trivial names, but most of these have been placed as synonyms under existing species.

VARIATION IN THAIS LAMELLOSA

Throughout the range of this species, which extends from the Aleutian Islands to Monterey on our western coast, there is to be found an immense number of populations which parallel if they do not exceed the profusion of local races presented by the related species *Thais lapillus* inhabiting the Atlantic.

These populations of *Thais* present a series of problems. To the taxonomist they are of interest because of the difficulty of fitting them into the traditional descriptive pattern. Unlike the tree-snails of the Hawaiian Islands, which differ mainly in their color pattern, the variants of the *lamellosa* complex differ widely in the size of the shell, its proportions and sculpture, as well as in coloration. To provide each one of these distinctive local races with appropriate latinized subspecific names, as was done with the achatinellids, would be a task of formidable proportions.

To the ecologist the group should be of interest because of the conspicuous place they occupy in the biota of the intertidal zone. Living as they do mainly on barnacles, they are provided with an ample and quickly replenished food supply, while their compact shell protects them from most ordinary enemies. There is the additional ecological interest in the question as to what extent the visible differences among the several local races may be due to environmental conditions, a much mooted problem.

To the student of microgeographical speciation as a factor in the evolutionary process, these *Thais* forms present us with an outstanding example.

Since the basic characters are obviously due to the unequal dispersal of the genic system, it seems probable they would provide interesting material for breeding experiments, a foundation for which has been provided in the thorough work upon the genetics of *Thais lapillus* by Staiger (1955).

The species of the genus *Thais* are rather exceptional among littoral marine molluscs in developing such numerous and distinctive local races, since the latter as a rule produce active free-swimming larval forms which may be carried great distances, both by their own powers of locomotion as well as by the movement of ocean currents. The only barriers to the spread and intermingling of populations of such species is in the presence of interposing land masses, the direction and force of ocean currents, contact with bodies of water with unfavorable salinities and temperatures, and the possible transport of the larval forms to areas with unfavorable ecological conditions in the littoral zone. The more distant segments of widely distributed forms of this type may diverge to form with the intermediate populations what would appear to be an extensive clinal system rather than a *rassenkreis.*

Along the borders of the continents areas may be isolated through the development of ecological conditions which are unfavorable for the majority of littoral molluscs. The most common of these is represented by embayments which receive large volumes of fresh water from inflowing rivers. In such areas there is a tendency to develop local races among the invertebrate inhabitants. The faunas of islands separated from the mainland by various distances would be another example in the same category.

The writer is inclined to believe that when the taxonomy of many of the groups of marine gastropods is revised to bring them in line with the procedure followed in recent years with the fresh-water representatives of this group, the list of trivial names will be greatly reduced, and many forms listed as species, subspecies and varieties, will be given a different and more logical interpretation.

Most of the attempts to explain the origin of the local races of *Thais* have been based upon observations made upon the Atlantic species *T. lapillus*, and the majority of the authors appear to have reached the conclusion that the observed differences are due to environmental factors, either physiological or selective.

The interpretation of the causes leading to the development of local races in *Thais* by the earlier authors is well expressed in the excellent account given by Cooke (1895: p. 91) where he states:- "The common dog-whelk (*Purpura lapillus*) of our coast is an exceedingly variable species, and in many cases the variations may be shown to bear a direct relation to the manner of life (Fig. 35). Forms occurring in very exposed situations, e. g. Land's End, the outer rocks of the Scilly Is., coasts of N. Devon and Yorkshire, are stunted, with a short spire and relatively large mouth, the latter being developed in order to increase the power of adherence to the rock and consequently of resistance to wave force. On the other hand, shells occurring in sheltered situations, estuaries, narrow straits, or even on open coasts where there is plenty of shelter from the waves, are comparatively of great size, with a well-developed, sometimes produced spire, and a mouth small in proportion to the shell surface. In the accompanying figure, the specimens from the Conway estuary and the Solent (12, 5) well illustrate this latter form of shell, while that from exposed rocks is illustrated by the specimens from Robin Hood Bay (13, 14)."

On pages 69-70 in the same article Cooke refers to the possibility that a selective factor may be involved in determining the coloration of the shell. He indicates this in the following language:- " The specimens of *Purpura lapillus* which occur in Cornwall are banded with rings of color, especially black and white, in a more striking way than any other specimens that have occurred to my notice. I am inclined to refer this peculiarity to a tendency toward protective coloration, since the rocks on which the *Purpura* occur are often banded with white and color, and variegated to a very marked extent."

Dr. W. H. Dall (1915) in his paper dealing with the forms of *Thais* belonging to the subgenus *Nucella* found on our west coast has expressed views as to the origin of the local races on purely environmental grounds as follows:- " The sheltered rocky beaches of a well protected harbor will afford slender elongated and lamellose specimens with small apertures. The outer rocks exposed to the ocean surf have short-spired relatively smooth, wide-mouthed shells, which afford the least leverage to the waves. For washed from his perch and carried to the muddy bottom off the shore by the undertow, an adult *Nucella* can hardly survive; and those offering the least friction and having the stronger hold on their situs are most likely to survive. There is also a connection between the situs and the shell which is less easily explained, and that is that, on rough surfaces such as an "oyster reef," or bar, the specimens of *lamellosa* are almost unanimously rough and laminate, while in undisturbed water on rocks with sandy surroundings the finest and most delicate development of lamellae and crenulations is to be found, according to collectors. In all cases *Nucella* seems to prefer a rocky habitat, especially if it affords young oysters or other sessile or sluggish species serving it as food."

At another point in the same paper Dall (p. 563-564) hints at the idea that inheritance may play a part in determining the character of the local races, where he remarks:- "This species (*lamellosa*) submits to such changes, incident to situs, that single specimens, or even numerous specimens from single localities, might be taken for different species, especially as specimens from a single locality often exhibit a singular uniformity of characters, even in factors which would seem not likely to be subject to influences of the environment, such as the number of the major spirals. These uniformities are probably due to inheritance from a common ancestor."

The above paper by Dall was primarily taxonomic in character, and was based largely upon 549 specimens in the U.S. National Museum. His account of the ecology of the species was rather incidental, and was based partly upon his own obseavations made in Alaska and partly on information received from his correspondents on the Pacific Coast. His views were no doubt markedly influenced by the interpretation presented by Cooke upon the allied form inhabiting the North Atlantic.

Dr. H. Colton in two papers, one published in 1916 the other in 1922, contributed some interesting observations upon the possible origin of the local races of *Thais* found upon the coast of Maine in the neighborhood of Mt. Desert Island, in which area there is a tidal movement averaging about ten feet.

In his first paper (1916) Colton dealt primarily with the phenomenon of coloration as displayed by these snails. For purposes of comparison he had available 12,000 specimens derived from 67 separate localities. He subjected this material to statistical analysis to determine whether any relation existed between the prevailing environmental conditions and the coloration of the shells.

Among the conclusions reached by Colton was the suggestion that, while the variations in color exhibited by the local races were primarily determined by the constitution of the germ cells and hence basically hereditary, there was a low-pressure selective action functioning through the activities of predators utilizing the snails for food. He found evidence that sea-gulls prey extensively on *Thais*, since considerable quantities of the shells were found upon areas frequented by the birds. He assumed that in a population that was more or less protectively colored, those individuals that were conspicuous would be most likely to be seen and devoured by the gulls, or by predatory fishes while the intertidal area was covered with water; thus in areas where the rocks were covered with barnacles dark colored specimens would be conspicuous, while on areas where mussels predominated, pale colored individuals were more apt to be seen and eliminated by predators.

Colton noted that the problem of coloration is complicated when the bulk of the population in a local race includes not only individuals with solid coloration, but those with intermediate shades and various types of banding.

In regard to sculpture Colton states that he found both imbricated and smooth varieties in protected muddy bays, which led him to the conclusion that sculpture was determined by heredity rather than by environmental factors.

In his second paper Colton dealt with the environmental relationships of *Thais* as regards form, size, sculpture and the character of the aperture. He had available material from 106 localities represented by 16,000 specimens. He was inclined to regard the size and shape of the shell as directly determined by the environment; when exposed to heavy surf action the shell becomes small and thin, while in protected areas the shell was inclined to be larger and stouter. He regarded sculpture as primarily determined by heredity, but explained the imbricated forms on the theory that this condition had a selective value, the roughened surface tending to retain debris, and thus serve as a masking device. Observing discrepancies in the existing distribution of imbricated forms he explained these as a result of changes in sea-level during the Pleistocene.

It was clearly indicated by Colton that he regarded his conclusions, based as they were upon purely observational data, as somewhat tentative, pending the evidences to be supplied by physiological experimentation and genetic studies, together with adequate cross-breeding to determine the factorial structure.

In three papers published during the years 1936-1938 Dr. Hilary B. Moore presented a very thorough and detailed account of the forms of *Thais lapillus* found upon the coast of Great Britain, including a summary of the previous work done upon this species, an observational study of 25,000 specimens derived from 67 localities, the breeding habits of the snails, their growth, their food in the wild state and under controlled conditions, and the presumed effects of chemical and physical factors; altogether a most notable contribution.

The first paper by Moore (1936) is entitled "The Biology of *Purpura lapillus*. I. Shell Variation in relation to Environment." He assumes that all observable differences seen in the local races must be due primarily to environmental influences. In this point of view he is in conformity with previous authors, since no allowance was made for the possible influence of heredity as a factor initiating variation, with isolation leading to the formation of inbred populations.

Moore however, differs sharply from Colton and others in that he minimizes the importance of wave action and selective agencies, and stresses nutritive processes as the keynote to the problem, particularly the differential utilization of the two main food materials of the snails, barnacles and mussels. *Thais* feeding exclusively upon barnacles failed to develop color in their shells, while those feeding upon mussels became pigmented. He presented rather striking evidence for this interpretation in that on placing highly colored specimens in an aquarium and forcing them to feed exclusively on barnacles, the new shell that formed was unpigmented. When the snails were returned to a diet of mussels pigmentation was restored. There were some discordant results. Yellow coloration, which presumably belongs to the same group of carotenoid pigments producing the darker shades, apparently was not influenced by dietic changes. Pale colored specimens from barnacle crusted rocks, fed upon mussels for six months, showed no signs of pigmentation. Unpigmented individuals found in populations of heavily pigmented snails were interpreted as possibly banded specimens in which the area of the mantle incapable of secreting pigment had extended entirely across that organ.

In connection with the imbricate form which Colton regarded as an ecological adjustment to shallow muddy bays, Moore found it to be absent from the intertidal zone, but present on submerged reefs in the sub-littoral area.

Moore was unable to establish any correlation between the size of the mouth opening and wave action, a point much emphasized by previous authors.

It will be noted that if we cancel out the divergencies of opinion among these several authors we have little left but the factor determining size, which all seem to be agreed upon as influenced by the relative abundance of an appropriate food supply. This is indicated by the wide prevalence of "giant" forms derived from submerged reefs, where feeding may be continuous rather than intermittent.

A new and novel approach to the problem of speciation in *Thais* populations is in the publication by Dr. Hansrudolph Staiger (1954, 1955) of two papers dealing with the differential genetic organization of local races of *Thais lapillus*. In his first paper entitled " Der Chromosomendimorphismus beim Prosobranchier Purpura lapillus in Beziehung zur Okologie der Art" Dr. Staiger gives an account of his genetic studies of a group of local races of *lapillus*, some forty-eight in number, found upon the coast of Brittany in Northern France. However, all but seven of the populations were derived from a rather limited area in the vicinity of Roscoff and the Bay of Morlaix, about twenty-two kilometers in cross-section, but with a wide range of ecological stations admirably disposed for the purpose of this study. Dr. Staiger does not give us any figures or detailed descriptions of the snails found in the local populations, the principal point emphasized being the relative thickness of the shell. From this we assume the problem was not complicated by factorial conditions involving coloration and sculpture.

As the result of his investigation of the cytological conditions in hundreds of specimens of the localized races of *lapillus* Staiger was enabled to determine that the heredity of this species is governed by a group of chromosomes which vary in number from 13 to 18. Of these 8 are present in the germ-cells of all individuals, and form the basic hereditary elements; the remaining group of chromosomes in six possible combinations providing for the diversities characteristic of local races of polytypic forms. The accompanying diagram, copied from the Staiger monograph, will give a graphic interpretation of the chromosomal organization. The eight basic or central chromosomes, technically termed acrocentric or metacentric, are numbered from 1-8; the group involved in initiating changes of a polymorphic character are numbered I-V.

While the acrocentric chromosomes are regarded as the more conservative elements in the hereditary complex, they may also play a part in initiating polymorphism, but their influence is not so readily determined.

The most surprising, and presumably unexpected result of Dr. Staiger's investigation, was the discovery that the zonal distribution of the ecological conditions in the intertidal area was paralleled by a zonation of the several types of genetic forms of *Thais*. The outer wave lashed zone was apparently occupied almost exclusively by *lapillus* with germ cells carrying 13 chromosomes, while those in the relatively undisturbed interior waters bore mainly snails bearing cells with 18 chromosomes. In the intermediate tidal areas various gradational forms were found between those of the outer zone with its pure 13-chromosome type, and the inner zone with its populations with a strictly 18-chromosome organization.

This zonal distribution of the genetic isolates of *Thais* suggests a selective factor affecting the populations, but Staiger offers no suggestion as to what this factor might be. He describes it as a case of "balanced polymorphism."

It will be recalled that Colton (1916) observed what he regarded as a zonal distribution of *Thais* in regard to coloration, which he interpreted as related to the selective activity of predatory birds and fishes. Similarly Moore (1936), observing a similar phenomenon upon the English coast, advanced evidence to prove that the differential in coloration was due to the type of food consumed by the snails. It would be of great interest to learn whether these two cases, and others like them, exhibit the same type of "balanced polymorphism" Staiger found upon the coast of Brittany. At the time of writing Dr. Staiger is entering upon a study of the genetic organization of the forms of *Thais* found upon the Pacific Coast. The results of this investigation should prove interesting, since they are likely to throw considerable light upon the relationship of the North Pacific forms to those of the North Atlantic. A majority of those who have studied large series of these forms are of the opinion there must have been an interchange of faunistic elements between the two oceans during the late Tertiary. It is well known that during this phase of geologic history there were momentous changes, both in sea level and climate.

It may well be that migration took place both along the north Eurasian coast and across the sea bordering the continent of North America. The striking similarity of many of the local races of *Thais lapillus* found in the Atlantic to related forms occurring upon our Pacific Coast, seems more than a mere coincidence. On the other hand, all of the *lapillus*-like forms of our west coast intergrade completely when examined with a large enough series, while the range of variation is not greater than that of the Atlantic forms. The tendency of taxonomists has been to gradually reduce the number of recognized species through the relegation of many of the older trivial names to the synonymy, leaving us with the three forms listed by Dall in 1915, with a number of varieties, including *lima* Martyn 1784, *canaliculata* Duclos 1832, and *emarginata* Deshayes 1839. Since these three forms intergrade completely, there seems to be no valid reason for regarding them as specifically distinct, any more than would hold for the distinctive local races of *lapillus* of the Atlantic or *lamellosa* in the Pacific. The taxonomic problem in dealing with such material, and the matter of suitable labeling, is one that is common to all cases of highly polytypic species. If the three above mentioned species were consolidated it would leave us with a single wide spread and highly polytypic species - *Thais lima* Martyn- comparable in diversity with its Atlantic relative. As to whether *lima* in its turn should be consolidated with *lapillus*, as has been suggested by several competent authorities, remains an open question.

As will be seen from the above discussion, our knowledge of the ecology and genetics of the *Thais* forms is based almost exclusively upon critical observational, physiological and genetic studies of the Atlantic species. We still await however, the experimental cross-breeding of selected forms to determine the manner in which the various hereditary factors are related.

Since up to this time no experimental observations dealing with *Thais lamellosa* are on record, the conclusions of the writer, based as they are upon purely observational data, may be regarded as somewhat tentative.

THE LOCAL RACES OF THAIS LAMELLOSA

In reviewing the various theories that have been advanced to explain the possible origin of the local races of *Thais*, one is struck by their rather contradictory character, together with the lack of emphasis upon the basic factors of heredity and spatial isolation.

In the opinion of the writer the phenomenon observed in the racial differentiation of *Thais* forms presents a classical example of geographic speciation, paralleling the situation found in many other polymorphic forms subject to some type of isolating mechanism. The genetic interpretation of such cases is gradually being brought to light, as is indicated by the summary of this subject given by Dr. Staiger in his paper on *Thais lapillus*. In view of the close relationship between *lamellosa* and *lapillus*, together with their similar type of variation, it would seem highly probable that the genetic systems of the two species should follow much the same general pattern.

The variations exhibited by *Thais lamellosa* appear to be governed by several sets of genetic elements, acting independently of one another. The resultant of these factors is then modified by environmental conditions, mostly of a nutritive character, but with the possibility of some measure of selective action through the agency of predators.

The height of the spire in proportion to the width of the shell, the writer regards as determined by heredity. Populations with high spires appear under a great variety of ecological conditions, while the same is true for low spired forms. All sorts of intermediate conditions occur, but these do not seem to bear any relation to environmental conditions.

Sculpture is also regarded as determined by genetic factors. The spiral ridges, so characteristic of most of the *lapillus*-like forms, are as a rule feebly expressed, and may be completely absent; rarely they are present as a group of many close-set ridges, and all sorts of intermediate conditions are to be found.

In some cases the major spirals, especially where these are strongly developed ,are spaced by delicate thread-like secondary spirals, which are very suggestive of the corresponding structures in *lapillus.*

The axial sculpture in *lamellosa* exhibits great extremes. The ridges may be entirely absent, presenting us with a completely smooth shell, or the ridges may be raised in conspicuous lamellae, giving rise to the imbricate type of sculpture, with all possible intermediate gradations in ornamentation.

The sculptural pattern of the shell in its turn is modified by several factors. The general type of the shell, whether long spired or short spired, tends to determine whether the lamellae will be crowded or widely spaced. The size of the adult shell appears to be determined by the basic heredity of the population and the speed of growth in reaching maturity, and in turn is related to the abundance and availability of the food supply. Snails living in the intertidal zone are more or less intermittent in their feeding operations, while those living on submerged reefs where as a rule larger types of barnacles are abundant, feed without interruption, and hence grow more rapidly and mature to a greater size. The presence of "giant" forms of this type has been noted for *lapillus* in the Atlantic, and is frequently seen in populations of *lamellosa.* In such cases the axial ridges may be widely spaced. The size of individuals in populations inhabiting different types of shore in the intertidal zone exhibit the same kind of variance. It has also been noted that colonies of *lamellosa* established upon the barnacle encrusted piles of docks usually attain a greater size than the populations inhabiting the adjacent shores, from which presumably they have been derived.

In dredging over bottoms that lie in deeper water and are covered with loose shelly debris, *Thais* material is frequently brought up containing specimens that are of moderate size; it is assumed that the conditions in such areas are unfavorable for the animals, thus retarding their growth.

The coloration of *Thais lamellosa* exhibits a very wide range. Many populations are completely devoid of color when the scum of organic matter commonly present on the shells is removed. A tinge of yellow, or a banded condition in this color, is not infrequent. The majority of the color markings are in various shades of brown, ranging from pale mahogany to dark chocolate; these occur both solid and in various types of banding. The bands may be pale on a dark background, or dark on a pale background. In some populations the banding is quite uniform throughout; more commonly a graded series is found, ranging through pale colored forms to those that are heavily pigmented, constituting a cline within the population as regards coloration.

The problem of coloration in *Thais* has given rise to considerable differences of opinion. Colton as has been noted, ascribed divergencies in color largely to selective agencies in the environment, while Moore has presented evidence leading to the conclusion that coloration in the snails is related to nutritive conditions affecting the metabolism of the animals.

The detailed and carefully controlled experiments conducted by Dr. Moore cannot be lightly set aside, but some of the results seem out of line with the conclusions, such as the failure of pale colored snails to develop pigmentation after an exposure to an exclusively *Mytilus* diet for a period of six months; likewise the occurrence of pale individuals in the midst of otherwise pigmented colonies. The failure of the yellow pigment, which belongs in the same group of carotenoid compounds as the brown coloring matter, to respond to dietary changes, is very suggestive.

In the opinion of the writer, based however upon purely observational data, the color patterns found in the local races of *Thais lamellosa* are genetically determined. The local populations, founded as they presumably were by chance migrants from established colonies, carrying elements of the highly variable ancestral stock, would eventually form inbred populations with distinctive characteristics.

The above interpretation of the phenomenon of coloration in *Thais lamellosa* would bring the conditions observed in these snails in line with the heredity of color patterns in other groups of animals in which definitive breeding experiments have been conducted. This interpretation would also appear to find confirmation in the discovery by Dr. H. Staiger of the genetic system of *Thais*, in which a group of secondary chromosomes through the translocation of their genic elements, make possible a wide range of variation in the phenotypes.

THE ISOLATING SYSTEM

I. The life history.

In *Thais lamellosa*, as in other members of the subgenus *Nucella* (*Polytropa* of some authors), the eggs are deposited in small vase-shaped capsules attached to the rocky stratum inhabited by the parent forms. The number of eggs contained in an individual capsule has not been counted, but is obviously very great. The relatively small number of embryos that complete their development within a capsule pass through the veliger stage, corresponding to the free swimming larval form of most gastropods, emerge as active, crawling young snails. The lack of a planktonic larval form tends to greatly restrict the dispersal of the snails; presumably the principal agency bringing about dispersal is the action of storms, which may break loose some of the egg capsules containing viable young and cause them to drift to suitable locations.

II. Shore conditions.

The normal habitat of *lamellosa* is upon rocky shores that provide an abundance of barnacles, which form their principal food supply. Mussels are also usually present in such areas, and may form an important element in their diet. The snails are also to be found in areas where masses of immobilized shells are present, such as occur in many oyster beds. The piles driven to support docks frequently support colonies of *Thais*.

Where areas of shore forming suitable habitats for the snails are separated by stretches consisting of mud, sand or loose gravel, the migration of the animals is inhibited, with resulting isolation. The extent of such inhibiting stretches may vary from a few hundred yards to many miles, as in the case of the great sandy beaches on the main ocean frontage. One of the commonest type of such isolating barriers is the crescentic gravelly beaches such as are frequent in the northwestern area extending from Puget Sound to Alaska.

III. Islands and reefs.

A glance at a map of the northern section of our Pacific Coast, discloses at once the existence of a vast number of islands of various sizes and types. Many of these, as for instance Vancouver Island, are sufficiently large and diversified as to shoreline to support a considerable number of local populations, and as a result the total number of these must be very great.

IV. Channels.

The width and depth of channels separating bodies of land bears directly upon the problem of dispersal. The force and direction of the tidal currents presumably determine the primary paths of migration in the establishment of new colonies, or the modification of those already in existence, and has probably been a decisive factor in determining the existing distributional pattern of the populations.

V. Submerged reefs.

Although *Thais* is regarded as primarily an intertidal form it has long been known that *Thais lapillus* can maintain an existence at considerable depths where suitable conditions exist, and the same situation holds true for *Thais lamellosa.*

Very little seems to be known regarding the extent and ecological conditions in these submerged populations, beyond the fact that in such areas "giant" forms are apt to prevail.

The lack of information regarding submerged populations of *Thais* is readily explained, since such areas are inaccessible to collectors, and are avoided by commercial fishermen operating trawls since they are destructive to their equipment. However, during a number of years of exploratory activities in the San Juan Islands a series of such reefs were located, and samples of the snails secured. Many other reefs of a similar type appeared in the records presented by echo soundings, but were not explored.

The populations of *Thais* found upon these submerged reefs do not seem to differ in any marked respect, except in the matter of size, from those occurring upon the adjacent intertidal areas. Such populations may however, play an important part as links in the migratory dispersal of the species.

Predatory birds.

It seems well agreed that predatory birds, including gulls, crows, oyster-catchers and some species of ducks, represent the most serious enemies of the snails. These birds on removing the animals from the rocks often carry them considerable distances to find a suitable place to devour them, even dropping them from a height to shatter them. Specimens escaping from the birds might readily be added to the population of another area.

Human agencies.

Although Dr. Dall failed to find remains of *Thais* in the kitchen-middens of the aborigines in Alaska, and concluded the natives did not utilize these animals for food, the writer has found an abundance of the fragmented *Thais* shells in the deposits left by the Indians in the region near Blaine, Washington. These people, in their migrations, may have unwittingly caused some dispersal.

Some colonies have been destroyed by engineering projects and pollution, while others have been established through the construction of docks, piers and breakwaters.

Oystermen and others, scowing material from one area to another, may have modified some populations.

Geologic and hydrographic factors.

For the long period of time during the Pleistocene from which we have a record of the existence of the ancestral forms of *Thais lamellosa*, there have been momentous changes in the level of the sea and the climatology of the area, which must have profoundly influenced the distribution of the species.

THE FOOD HABITS OF *Thais lamellosa*.

All who have studied the ecology of *Thais* appear to be in agreement that the basic food of the animals is barnacles. Dr. Moore has proved that *T. lapillus* can live indefinitely upon a diet of *Mytilus*, and presents evidence that this is an important factor in determining the coloration of the snails in their intertidal habitat. Moore has also expressed the view that the newly hatched snails occupy a lower zonal distribution than the parent forms, utilizing the small annelid *Spirorbis*, with other minute attached invertebrates.

Some authors have reported *lapillus* as a predator on oysters, but this belief does not appear to be well founded, and some of the other reports regarding the food habits of *lapillus* seem to have been handed down without critical examination and should be rechecked.

As regards the food habits of *lamellosa*, no critical studies appear to have been made. In all cases where individual snails were checked they were feeding on barnacles, even though clusters of *Mytilus* were close at hand, which indicates that barnacles constitute their preferential diet.

In some instances extensive reefs constituted almost exclusively of *Mytilus*, existed apparently without attracting a population of *lamellosa*.

In some areas in the San Juan Islands there are extensive submerged beds of the mytilid *Modiolus modiolus* L., but no *Thais* appear to be present.

Contrary to the reports as to the method by which *lapillus* attacks barnacles, the writer found *lamellosa* utilizing its radula to perforate the protective plates of the barnacles and the shells of mussels.

The radula of *lamellosa* is quite narrow, and as a result the aperture produced is minute. It is not known whether the snails inject a narcotizing fluid in the attack upon their prey, as is reported for some related forms.

Some fishery biologists have been inclined to regard *Thais lamellosa* as a predator upon the Olympia oyster (*Ostrea lurida*) of the Puget sound region, but the writer, in the course of more than fifty year's experience, has never seen damage to an oyster bed that could be ascribed to the activities of *Thais.* The low concrete walls enclosing the shallow oyster dikes are commonly encrusted with the small oysters in various stages of development, and in the same situation one finds immense numbers of *Thais.* In spite of this close association between the oysters and the snails, no drilled oysters were to be found. On the other hand, with the introduction of the Japanese oyster drill (*Tritonalia japonica*) a great mortality of oysters took place. Since *Thais* feeds mainly if not exclusively upon barnacles and mussels, both detrimental to the oyster, the writer would classify *Thais* as a highly beneficial organism, presumably the only invertebrate "friend" of the oyster.

ENEMIES OF *Thais lamellosa.*

As has been indicated, the principal enemies of *Thais* are various species of predatory birds, gulls, oyster catchers and ducks. Colton (1916) has given a very detailed account of the manner in which the gulls conduct their operations against colonies of *Thais lapillus,* both for their own food and that of the nesting young. The same type of behavior on the part of the birds is commonly seen on our western coast. In many populations of *T. lamellosa* considerable numbers of the snails appear in which the shells have been damaged and then repaired. The definitely notched appearance of the original fractures was not due to mechanical injury, but was produced by the beaks of birds, presumably gulls. This type of injury is illustrated on Plate XII.

Moore (1938) in his very thorough summary of this topic cites the detailed description by Dewar (1910) of the manner in which the oyster-catcher (*Haematopus ostralegus*) opens the shells of *Thais lapillus* and consumes the snails. It is presumed that our western oyster-catcher (*Haematopus bachmani*) may have similar habits, although no concrete evidence is at hand.

The white-winged scoter (*Oidemia deglandi*) frequents the intertidal zone and feeds upon an omnivorous diet of mollusks and crustaceans. On several occasions the writer has had an opportunity to examine the stomach contents of these ducks containing freshly fragmented shells of *T. lamellosa*, indicating that they habitually prey upon the snails.

Ravens (*Corvus caurinus*) are frequenters of the intertidal zone, and with their omnivorous diet probably include *Thais*.

Fishes of several species have been suggested as possible predators upon *Thais* during the periods when their habitat is covered with water, but there does not seem to be any well defined proof of this relationship.

Crabs are regarded by some observers as probable predators on *Thais*, but the evidence for this view is inconclusive, unless we regard the angular fractures found on the shells as the work of these animals rather than that of birds.

Hermit crabs are commonly found occupying the shells of the snails, but it is not believed they secure these by attacking the living animals.

A number of invertebrate animals become attached to or burrow into the shells of the snails, but none of these appear to be seriously detrimental to the *Thais*. The principal attaching forms are barnacles, which often completely cover the entire surface of the shell. The calcareous tubes of annelids and colonies of bryozoans are not infrequent, but are usually seen attached to snails inhabiting the lower tidal levels and reefs. The most striking example of attaching organisms is to be seen in areas where ths small Olympia oyster is cultivated; here the microscopic larvae of the oyster settle upon the *Thais* shell, and eventually develop into clusters, which as they mature must become an awkward burden to the snails.

The forms most often met with that excavate the shells are boring sponges and annelids of the *Polydora* type, but these are infrequent and seem to do no serious harm to the snails.

The larvae of several species of trematode worms have been reared from the snails (Miller); the adult forms are presumably parasitic in their vertebrate predators.

Certain species of minute algae, said to belong to the genera *Gomontia* and *Plectonema* (Moore, 1938) etch away the limy surface of the shell, and often obscure the more superficial sculptural details.

In a few instances specimens have been found in which the shells of the snails were covered with a coating of an alga delonging to the genus *Lithothamnion.*

TAXONOMIC INTERPRETATION

The immense number and highly localized character of the populations of *Thais lamellosa* brings into sharp focus the problem of the adequate taxonomic treatment of these and other similar infraspecific demes.

The treatment of this problem by Dall (1915), who simply selected four divergent forms which he characterized as "varieties", is obviously quite inadequate and outmoded.

These demes are obviously of the type to which the status of subspecies is commonly assigned. Some authors, as in the case of the achatinellid fauna of Hawaii dealt with by Welch (1942), have introducded large numbers of latinized subspecific names. It seems unfortunate that the literature should be burdened in such cases by names coming within the scope of the laws of priority. It appears to the writer that the trend in taxonomic procedure is definitely against this practice in dealing with highly polytypic species.

The use of the term " form" or "forma" has been utilized by some authors to designate these variant populations, but this usage suffers under the handicap that it has been used in other connections, so that it is not sufficiently distinctive.

Various additional suggestions have been offered as to a suitable taxonomic designation for these demes of polytypic species, among others "microsubspecies" (Huxley, 1940); "microraces" (Dobzhansky, 1937); "subsubspecies", (Goldschmidt, 1945), but have not been found entirely satisfactory.

Dr. J. Gordon Edwards (1954) has suggested that as a substitute for the term "form", which is meaningless apart from some correlative context, as well as for the other above mentioned expressions, the term "morph". This has the advantage of consisting of a single word instead of a compound expression, thus paralleling the terms genus and species. This also serves to replace the vague term "form" with a word of Greek origin, which is meaningful, but has not previously been used except as a significant element in a number of biological terms, such as morphology, morphogenesis, etc.

According to the suggestion of Dr. Edwards the proposed units would not be regarded as trinomials subject to the law of priority, but could be designated by explanatory spatial, genetic or ecological terminology by adding a suitable prefix.

Since the above described system seems well designed to give descriptive expression to the wide range of variants met with in the study of *Thais* material, it has been adopted for use in the present paper. The several morphs will be distinguished numerically and by pinpointing as closely as possible their microgeographical localization.

ORIGIN OF THE LOCAL RACES

The group of muricids constituting the subgenus *Nucella* (*Polytropa* according to some authors) of the genus *Thais* appears to have had its early development in the North Pacific area during the late Miocene, and undergone a considerable expansion and differentiation during the Pliocene and Pleistocene. According to Grant and Gale (1931) the stock represented by the modern *Thais lamellosa* has been in continuous existence during this entire time.

The Pleistocene, or as many geologists term it the Quaternary, while relatively short in comparison with the previous geologic epochs, presents many dramatic elements profoundly affecting the character and distribution of the present life upon our planet, including the entire span of human existence. Our existing knowledge concerning this phase of terrestrial history has recently been summarized and amply documented in an extensive monograph by Charlesworth (1957).

The Pleistocene has been characterized by a continuance of the volcanic activity that prevailed during the Pliocene, of which our North Pacific area is a good example. If carbon-14 datings have been correctly interpreted the explosive eruption of Mt. Mazama occurred about 6,500 years ago. The great eruption of Mt. Katmai in Alaska is a part of recent history.

Great changes also occurred during the Pleistocene in the distribution of both sea and land, involving according to the views of Charlesworth more than seventy percent of the surface of the planet. The presence of raised beaches, arranged frequently in step-like fashion on the coasts of all of the continents, indicates changes of level, but as to whether of sea or land has been a matter of dispute. Charlesworth would ascribe these successive steps, which range in magnitude from a few feet to one thousand feet or more, primarily to crustal changes of the type now in progress in various parts of the world. In Finland, where one generation wades the next generation plows. Hudson Bay is evidently destined to become a broad plain traversed by a river. Holland on the other hand will have to build higher dikes to hold back the sea.

On our Pacific Coast we have abundant evidence of changes of level; in California a dozen or more such steps have been noted. Similar formations, some of them at considerable altitude, have been discovered in British Columbia and Washington. One such area is exposed on the retreating eastern shore of Willapa Bay in southwestern Washington. This is illustrated on plate XIV. Not shown in the figures is a group stumps of what must have been immense trees, which from their vertical position and interlaced roots, must have grown in situ. They are now covered by the tide. The soil in which they were growing consists of glacial till containing no marine material, which must have at some earlier period formed part of the settling basin of a glacial stream.

The molluscs present in the ancient shell-bed, are conspecific with those inhabiting Willapa Bay at the present time, including *Schizothaerus nuttalii* Conrad, *Macoma nasuta* Conrad, *Venerupis staminea* Conr., *Saxidomus giganteus* Deshayes, *Clinoardium nuttallii* Conrad, *Cryptomya californica* Conrad, *Ostrea lurida* Carpenter and *Thais lamellosa* Gmelin. The type of *Thais* found in the shell bed is illustrated on Plate XVII. It does not differ materially from some of the modern representatives of this species in Willapa Bay.

The openings in the till beneath the shell-bed are the excavations of the burrowing crayfish (*Upogebia*).

Above the shell-bed there is an extensive deposit of terrace material, presumably brought into this area by the Columbia River when it was at its apex from the glacial melt.

The cause of these changes in level has been variously interpreted, but the most plausible theory appears to be that of "isostasy", which involves the concept that the continents move up and down upon an elastic substratum, somewhat after the fashion of ships loading and unloading ballast.

Whatever the causes of these changes of level may have been they must have profoundly affected the life of the intertidal and shallow water zones.

A second factor influencing the distribution of marine life upon the western coast of North America, was the advance and retreat of the great continental glaciers. According to Charlesworth there were at least four such movements, with interglacial periods having relatively warm climatic conditions, during which many of the forms driven southward by the ice returned to the north, as is indicated by the discovery of Pleistocene deposit of temperate water molluscs at Nome, Alaska, where arctic conditions now prevail.

During the periods when the northern seas were not locked in ice and the disposition of sea and land was favorable, migration was possible across the northern borders of the Eurasian and North American continents. According to Davies (1934) four gastropod genera which had been extensively developed in the North Pacific area, suddenly appear as elements in the fauna of the North Atlantic; these were *Buccinum*, *Neptunea*, *Searlesia* and *Thais* (*Nucella*), including the stock from which the modern forms of *Thais lapillus* have been derived. These facts indicate that the *Thais* fauna of the North Atlantic is little more than an extension of that found in the North Pacific, and explains why the local races of *Thais lapillus* exhibit a remarkable parallelism with those found in *Thais lima* and related forms in the Pacific.

As has been pointed out, Dr. H. Staiger found a striking example of chromosomal polymorphism in populations of *Thais* inhabiting the coast of France, the number of chromosomes ranging from thirteen to eighteen, with corresponding differences in morphology and ecological adjustments. Whether these or similar conditions exist elsewhere on the coasts of Europe, or on our eastern coast, appears to be unknown. In *Thais lamellosa* as determined by Staiger, and apparently in our other west coast forms, the chromosome number is thirty-five, which seems to be common to several muricid genera.

On the whole it would seem wise to use chromosome counts as a means of determining taxonomic relationships with due caution, especially in view of some of the recent work on chromosomal polymorphism in plants. Müntzing (1954) in a study of the local races of the grass *Poa alpina* L., which ranges from Scandinavia to the mountains of Central Europe, found chromosome counts varying from 26 to 61, with a corresponding variation in morphology and coloration.

Although the theory of isostasy may explain the major crustal movements, other factors are supposed to be involved in modifying the level of the sea. The withdrawal of vast amounts of water from the ocean to build the great continental glaciers and the eventual return of this material to the ocean must have had a very considerable effect, acting over long periods of time and presumably accounting for some of the secondary changes in level, all of which must have modified the areas inhabited by intertidal forms.

According to Flint (1957), based on Carbon-14 findings, the main continental glacier was advancing across the region of the Great Lakes about 25,000 years ago, reaching the crest of its advance at about 18,000 years. After several fluctuations it began its final retreat. About 8,000-8,500 years ago the Great Lakes were almost free of ice, and the glacier continued its long shift to the northward.

Although the glacial history of the western branch of the continental glacier, known as the Cordilleran sheet, is less completely established, its main features presumably followed the pattern of the larger ice-sheet. For many thousands of years an immense area, extending through much of Alaska, British Columbia and Washington almost to the Columbia River, was covered by a vast mass of ice, estimated to have been at least 6,000 feet thick over much of British Columbia, 3,000 feet over the Puget Sound valley between the Olympic Mountains and the Cascades.

From the above interpretation it will be seen that for a vast period of time the habitats of an immense number of our present local races of *Thais* must have been enclosed in ice or rendered uninhabitable by arctic conditions. However, to the north and to the southward of the glaciated area colonies of *Thais* were in existence, but the main groups of breeding populations were separated by wide spaces of inhospitable terrain and tended to diverge. Eventually, as the glacial conditions receded, areas suitable for colonies of *Thais* were uncovered, and eventually received migratory populations of the snails. When populations that had been separated for great periods of time and bearing differing genetic values merged, extensive variation was initiated, as is indicated by the heterogeneous character of the populations present in this intermediate zone.

It has generally been assumed by geologists that in the tectonic movements of the major continental masses we have an ample explanation for the principal changes in sea-level, while the great ocean basins have remained relatively undisturbed. Recent studies as summarized by Menard (1955) indicate that tectonic activities on a colossal scale have taken place in the Pacific. Off Cape Mendocino on the coast of California a great fault line has been discovered which extends 1,400 miles to the westward, flanked by submarine cliffs and mountains rivalling those present on the continent. The ocean floor to the south of the fault lies at a level several thousand feet below that to the north. Since several such fracture zones have been discovered it is clear that these disturbances must have profoundly affected the oceanic level. Some of the submarine mountains are flat on top, indicating they may have at one time been islands, possibly at a time when the extensive submarine canyons fronting most of our larger rivers were being excavated by rapid flowing streams.

It is clear from the above that changes in sea-level, together with the resulting terrace formations, are probably due to a variety of interacting factors.

GEOGRAPHIC DISTRIBUTION OF *Thais lamellosa*

In the older references to the distribution of this species its range is listed as extending as far southward as Santa Barbara, but it now seems to be agreed that there is no record of its presence on our coast southward of Santa Cruz in the vicinity of Monterey.

To the northward, populations of *lamellosa* are distributed along the coasts of California, Oregon, Washington, British Columbia and Alaska. In the latter area *lamellosa* appears to be present throughout the Aleutian Islands, with an extension into the Kurile Islands. All authorities appear to be in agreement that this species ranges northward along the shore of Bristol Bay to Port Clarence, but the writer has had no material for comparison from this section of Alaska.

THE CHARACTER AND DISTRIBUTION OF THE LOCAL RACES OR MORPHS OF *Thais lamellosa*

As has been indicated, the writer is of the opinion that the great diversity and localized character of the immense number of populations of *Thais lamellosa* inhabiting the Pacific Coast of North America, is due primarily to genetic segregation in an extremely unstable hereditary constitution and the effects of geographic and microgeographic isolation.

The limited powers of dispersal in this species, together with the existence of innumerable barriers in the way of deep water channels and areas of uninhabitable terrain, has lent itself to a process of speciation on a grand scale. The ability of *lamellosa* to inhabit waters subject to periods of extremely low salinity, has enabled it to form localized races in the estuaries of rivers, often separated by many miles of inhospitable terrain, as is illustrated by the populations found in Willapa Bay, Coos Bay and elsewhere.

The relationship of *Thais lamellosa* to the other species of this subgenus inhabiting the same coastal areas is evidently quite close, but although populations of *lamellosa* are commonly found associated with those of the other forms, no evidence of cross-breeding has been observed. The two groups also differ ecologically, owing to the greater ability of *lamellosa* to endure conditions of low salinity.

Although it would be premature, in the absence of any definitive experimental data, to speculate on the probable relationship between the superficial phenotypic appearances and the underlying genetic organization, it is obvious the heritage of this species must be governed by several sets of independently acting units, determining respectively, sculpture, spire form, coloration and size. We find for instance, the same type and range of coloration in populations exhibiting the greatest diversity of form and sculpture, indicating complete independence. From the fact that many populations are without pigmentation, while in others various types of banding are present, leading to forms that are heavily pigmented, suggests a genetic system comparable to that found in polymorphic terrestrial gastropods, such as *Cepaea*, *Achatinella* and *Cerion*. In the case of *Cepaea* according to Lamotte (1951) coloration is governed by several sets of alleles, the albinic condition being recessive to color, and whole color dominant to banding. In populations of *lamellosa* we commonly find a graded series ranging from pure white to heavily pigmented forms, suggesting the interaction of several allelic components. Yellow color, as is suggested by some of the observations made by Moore, apparently is governed by a separate genetic element.

The sculpture in this species appears to be governed by three independently acting genetic elements, involving the spiral bands, the vertical lamellation and the secondary spirals. The latter, which are a conspicuous feature in some of the related forms, are seldom seen in populations of *lamellosa*, and when present are feebly expressed, as may be noted in some of the specimens illustrated on Plates XVI-XIX.

The primary spirals are subject to a wide range of variation, which seems to be expressed independently of the vertical lamellae. In some cases it is sharply defined, and dominates the sculptural pattern, as may be seen in the population derived from Trinidad, California, illustrated on Plate XIX. We have here an indication of the relationship of *lamellosa* to the common muricid stem. In other cases the spirals may be so reduced as to be practically obsolete, or only feebly indicated on the terminal portion of the last whorl, as may be seen in populations such as are illustrated in Plates IX-XVIII. On the other hand the spirals may be distinct but are combined with incipient lamellae, as is illustrated by the figures in Plate XXII. In still other cases both spirals and lamellae are sharply defined so as to give the shells a cross-hatched appearance, as seen in Plate XL. In some extreme cases the vertical lamellae are more or less elevated, and the spirals are faintly indicated as modifying the contour of the lamellae: an example will be seen illustrated in Plate L.

The vertical lamellae are likewise subject to wide variation. In many populations these are completely obsolete or feebly expressed, while in others they entirely dominate the sculptural pattern, resulting in such highly imbricated forms as those shown in Plate L. Intergrading with these extremes we find every imaginable variation, not only as seen in separate populations but also within the limits of a single population, as may be seen in the specimens shown in Plates XXIX and XL., where a clinal system is developed.

The form of the spire, which largely determines the general contour of the shell, is also regarded as determined by genetic factors. The degree of acuity varies greatly, ranging from cases where the width of the shell is fully or nearly as great as its height, to forms in which the height is several times greater than the width, as appears in some of the Alaskan forms illustrated in Plates LIV, LV. Even within the same population there is often considerable variation in proportions.

Size is also determined primarily by heredity, but is influenced to an important extent by nutritive conditions in the habitat. The snails as adults feed mainly, if not exclusively, upon barnacles and mussels. Where these are abundant and the snails live upon submerged reefs, in protected coves or on the piling of docks, the growth rate is stimulated, and large or even "giant" forms are produced. The presumed differential effect of environmental conditions may be illustrated by two populations occupying contiguous areas with extremely different ecological conditions. One population (Plate XXIV) occurs in a protected cove on Brown Island in Friday Harbor, where average ecological conditions are present, and here we find individuals of average size. Across a narrow channel a short distance away there is at Point Caution a rocky, wave swept, rather barren area inhabited by a population (Plate XXV), which although of the same physical type is seemingly dwarfed. On the other hand, populations inhabiting submerged reefs, where food is abundant and the feeding process is not interfered with by storms or tidal changes, growth is speeded up and the individual snails mature to a much greater size. This condition is illustrated in Plates LVII and LVIII, where specimens are shown derived from submerged reefs that are never uncovered by the falling tide. It has also been observed that *Thais* inhabiting the piling of docks, to which great masses of barnacles and mussels are commonly attached, seem to find this situation very favorable for rapid growth, as may be seen in Plates XXXIII and XLVIII, typical of such situations.

However, even in those populations in which the relation to environmental conditions seems rather obvious, there is much variation among the individual snails, and in all populations the same is true. In some populations we find a remarkable gradation in size as shown in Plate XXI, where it will be seen that even the smallest specimens are fully mature, since the lip of the shell is fully formed. Two possible explanations suggest themselves, one that we have a common environmental condition acting upon a variable hereditary factor for size, the other that variations exist in the ecological conditions within the localized area inhabited by a group of snails, which affect the nutritive opportunities of the individual animals. It is readily seen that such ecological niches exist in the intertidal zone, and it is a question as to whether this condition is counterbalanced by the migratory powers of the snails in escaping from an unfavoable environment. At the breeding season the animals traverse considerable distances to assemble in large numbers for the deposition of their eggs. The behavior of the snails, both in their natural habitat and when confined in an aquarium, suggest considerable powers of adjustment. Even in the populations inhabiting submerged reefs the same type of size variation occurs.

The populations of *lamellosa* distributed along an extensive coastline from California to Bering Sea, exhibit the phenomenon frequently seen in polymorphic species in that populations in closely adjacent areas may be very unalike, while others although widely separated may be very similar in appearance. This would indicate that the controlling genetic elements are limited, and by chance combinations may produce similar phenotypes.

An example of divergent morphs occupying areas in close proximity is illustrated in Plates XXII and XL. Both of these inhabit areas on the west side of San Juan Island. Morph 25 is located about one mile south of Mitchell's Bay in the northern section of the coastline, and it will be noted the shells are heavily corrugated with both spiral and vertical sculpture, only a few individuals showing any indication of coloration. The lip is devoid of dentiform nodules. In Morph 7, located at False Bay, about five miles to the southward, we find a population of a sharply contrasting type. Both spiral and vertical sculpture are reduced to a minimum. The shells are uniformly tinged with a delicate brown coloration, the angle of the spire is less pronounced and conspicuous dentiform tubercles are present on the lip. A third population, Morph 24, inhabits an area at Deadman's Bay, which is located about halfway betweeen the above, is of a mixed type, presenting an intergrading series or cline, showing a transition between the two extreme forms. Many additional examples could be cited. Even the group of small islands known as the Wasps, lying between Orcas and Shaw Islands, possess in each case characteristic *Thais* populations.

In the second category, of closely similar types appearing at distant points, we also have numerous examples. The appearance of colorless forms, or those exhibiting various types of banding, appear in many populations throughout the entire range of the species. The proportional representation of the several variations in color vary from one population to another. In many cases there is a complete gradation from pure white to dark brown, in others the pale forms are nearly or completely dominant. Again the pale forms may be much in the minority. The writer has seen no indication that these variations in coloration are in any respect related to environmental influences, and regards them as primarily of genetic origin.

The populations of *Thais*, although they are extremely varied and heterogeneous in characacter, nevertheless show indications of groupings that are presumably related to the early distributional pattern of the species, when presumably it was segmented for vast periods of time as the glaciers advanced and retreated during the Pleistocene, and the shifts in the level of the ocean profoundly affected the character of the intertidal zone. With the final retreat of the ice sheet the coastline was gradually exposed, with its islands and rocky headlands. Into this biological vacuum the intertidal fauna, including the several forms of *Thais*, gradually penetrated. Among the types of *lamellosa* that had maintained itself to the southward of Cape Flattery was a form in which the sculptural pattern had become greatly reduced. Spreading through the Strait of Juan de Fuca this form established colonies on both sides of the strait, and then invaded areas in the San Juan Islands and the Canadian islands to the northward. A further extension carried it to the northern section of Puget Sound and into areas bordering on Rosario Strait. The distribution of this type of population is illustrated by the morphs shown in Plates XXVII, XXIX-XXXII. Many additional related populations are at hand.

A second invasion of the vacated area would seem to have been by a type of population which the writer is inclined to regard as more distinctly southern in origin. It is marked by a relatively blunt spire and a moderate development of the vertical lamellae. This type developed colonies in the Strait of Juan de Fuca, and extended with many modifications into the San Juan Islands, and into the Canadian islands to the northward, but became the most characteristic form throughout the extensive shoreline of Puget Sound and Hood Canal. This type of population is indicated by the morphs shown in Plates XXXIV-XXXVIII. In a group of bays in the western section of Puget Sound some populations with an extremely imbricated shell have been found (Plates XLIX, L), which would seem to be an extreme modification of this type.

A third group of populations would appear to have invaded the ice-freed area from the north. It is characterized by the presence of an elongated spire and extensive imbrication. The main center for the distribution of this group is in Southeastern Alaska, where many striking forms are present, as may indicated by the morphs shown in Plates LIII-LV, LXX, LXXII. This group is well represented in British Columbia, (Plates XLVI, LII), and extends in a modified form into some areas in the San Juan Islands (Morphs 30, 32, Plates XLV, XLVII). This form does not appear to have any well defined representatives in the Puget Sound area, although a tendency to develop an elongated spire appears in many populations wirhin the entire range of the species.

The populations occurring in the coastal region extending from Santa Cruz, California, to Cape Flattery, do not exhibit the diversity of sculpture and coloration seen in the northern forms, possibly because they have not been subjected to the disturbing effects of race-crossing with genetically different alien populations.

Although the amount of material available for study from the Aleutian Islands is unfortunately very limited, the writer is inclined to think this section also contains populations that are genetically conservative, judging by Morphs 48 and 49, shown on Plate LXXI, and beach worn specimens from Adak and Unalaska Islands. Material from Kodiak Island, Morph 51, Plate LXXIII, appears to be of an intermediate type.

The only material available from the Kuriles is a few shells from Etoro Island, Morph 52, Plate LXXIII, which appear to be very similar to the forms of *lamellosa* found in the Aleutians, and the writer has provisionally placed them with this species.

It is needless to say the writer has had available for study only a few of the innumerable populations of *Thais lamellosa* that inhabit the great range of this species, and of these it has been possible to include but a few within the limits of the present paper.

The number of specimens of the several morphs available for examination has varied from a handful to several hundred.

In selecting shells for illustration the writer decided to utilize mainly the dorsal surface, since this gives a clearer view of the characteristie sculpture and color pattern.

In some populations the shells show a remarkable uniformity indicating presumably that they have reached a state of genetic equilibrium. Such populations usually occupy isolated sites where the probability of receiving additional migrants is remote, or the migrants received may be so similar as to create no disturbance. On the other hand populations occupying areas subject to invasion by divergent alien elements are apt to be more or less heterogeneous. Artificial structures, such as docks and breakwaters, offer an interesting study from this standpoint. Many areas inhabited by populations of *Thais* are subject to destruction or profound alteration through the initiation of engineering projects.

In some instances the amount of variation within a single population is so extensive it cannot be given adequate expression within the limits of a single plate.

Many problems relating to this highly polymorphic species must remain on a tentative basis pending the initiation of adequate genetic and physiologic experimentation.

NOTES ON THE MORPHS ILLUSTRATED IN THE ACCOMPANYING PLATES

Morph 1. Plate xvi.

Long Island lies in the southern section of Willapa Bay in southwestern Washington. The primitive type of sculpture, exhibiting well defined secondary spiral bands and incipient vertical lamellae, is very suggestive of a primitive condition, pointing back to the ancestral stock.

Specimens available for study, over 200.

Morph 2. Plate xvii.

In the receding shoreline on the eastern side of Willapa Bay there is exposed an elevated bed of shells of Pleistocene origin which contains an abundance of the shells of *Thais lamellosa*. Samples of these shells are in the hands of the U. S. Geological Survey for Carbon 14 dating, but at the time of writing no report was available. As will be noted, the character of the *Thais* population of the bay has not materially changed during what must have been a considerable lapse of time.

Wood from the glacial till upon which the above shell bed lies is reported to be over 35,000 years old as determined by the Carbon-14 technique. Plate xiv.

Specimens available over 100.

Morph 3. Plate xviii.

The *Thais* populations of Willapa Bay, which is a body of water about thirty miles in length, show some tendency to develop local races, as may be seen on comparing Morph 3, which is derived from Oysterville in the northern section of the bay, with Morph 1 located a number of miles to the southward. Since this bay is the center of an active oyster industry, material containing *Thais* is apt to be shifted from one part of the area to another.

Specimens available, over 100.

Morph 4. Plate XIX.
Trinidad, California. This area is located about ten miles north of Arcata, in the Humboldt Bay region.

This morph is suggestive of the more primitive type in the species, as is indicated by the well defined secondary spirals and the very faint expression of the vertical lamellae. A tendency to develop the high spire characteristic of more northern forms is also apparent. The relationship of this morph to those found in San Francisco Bay, Willapa Bay and elsewhere in the southern range of the species is noteworthy.
Specimens available, 25.

Morph 5. Plate XX.
Alameda, San Francisco Bay, California.

Although the writer has available for study only a set of six specimens from this area, considerable range of variation is indicated, including forms with short spires and incipient vertical lamellae very suggestive of the types that dominate much of the Puget Sound area. The report by Packard published in 1918 illustrates a number of divergent forms which indicate the existence in the bay of several distinct local races, although some of these may have been affected by the extensive engineering in this body of water.

Morph 6. Plate XXI.
Port Stanley, Lopez Island, San Juan Islands.

This population is introduced to illustrate the extensive variation frequently found in local races of *lamellosa*, which indicate the probable influence of nutritive conditions in the environment determining the size of the snails on attaining maturity, as indicated by the completion of the lip protecting the aperture. It will be noted that in this population all of the individual snails are very uniform as regards form, sculpture and coloration, indicating they are not only phenotypes but also genotypically similar. Within an area inhabited by a population there are often niches which may differ in available food supply, and thus retard or accelerate the growth of individual snails. Genetic factors may also be involved.

Specimens available from the Port Stanley area, 85.

Morph 7. Plate XXII.

False Bay is a shallow, sandy body of water forming an indentation on the western coastline of San Juan Island. It is guarded at its entrance by two rocky promontories. The specimens illustrated were derived from a population inhabiting the more southerly of these capes.

In this population it will be noted there is a striking uniformity in the structure of the shells, both as regards size and sculpture. The latter exhibits a feebly expressed but balanced condition in both the spiral and lamellate striae. The coloration is uniformly a pale brown. The dentiform tubercles on the inner border of the lip are prominent, and this area of the shell is strongly tinged with purplish brown.

False Bay is also known locally as Kanaka Bay, and is so designated on the accompanying map, but this name is more properly applied to a small rocky bay located a short distance to the northeast of False Bay.

Specimens available, 75.

Morph 8. Plate XXIII.

Allan Island lies to the westward of the northern section of Fidalgo Island, in Skagit County, Washington.

In this morph it will be noted the shells are relatively small and rather uniform in size, which might be attributed to a uniform and rather unfavorable environment. Coloration is lacking. The sculpture is rather uniform and slightly expressed, with a tendency to develop the secondary spiral bands.

In this population quite a number of the shells carry the characteristic notches indicating the snails had survived the attack of some predator, presumably a bird.

Specimens available, 150.

Morph 9. Plate XXIV.

Brown Island extends across the entrance to Friday Harbor. On its outer margin it is exposed to the action of storms, while on its inner margin it is quite protected.

The shoreline of Brown Island is very irregular, and is broken into a number of niches isolated by narrow stretches of gravelly or muddy beach. As a result of this partial isolation we have in this area a number of closely related populations differing mainly in size, but with minor deviations in coloration and sculpture. Eight of these niches have been noted. The specimens figured in Plate XXIV were derived from a population inhabiting a protected cove in which favorable conditions prevailed, and as a result we find shells of a somewhat larger size than those of a similar type of sculpture and lack of pigmentation found at Point Caution, a short distance away, as shown in Plate XXV, where unfavorable growth conditions are present.

In this morph there is greater variation in sculpture than is indicated in the photograph, and all of the above eight related populations indicate a considerable interchange of genetic elements. Number of specimens available, 50.

Morph 10. Plate XXV.

Point Caution is a rocky promontory on San Juan Island at the northern entrance to Friday Harbor. The population figured inhabits a rather barren wind swept area where conditions are unfavorable, and as a result the snails at maturity produce shells of less than average size. In contrast with these a population found upon the piling of the dock at the village of Friday Harbor, in the interior of the bay, attain an unusually large size. Morph 18. Plate XXXIII.

The shells of the snails in this morph, together with those of neighboring populations, tend to exhibit a reduction in the sculptural pattern, although in some cases a clinal system is developed, ranging from strongly imbricated to perfectly smooth shells.

Specimens available, 100.

Morph 11. Plate XXVI.

Freeman's Island is a small reefy islet standing close to the northwest border of Orcas Island, in the San Juan group.

This morph is typical of an extensive series of local races found over a considerable area in the San Juan group, the shores of the mainland bordering on Rosario Strait, and parts of Puget Sound. The spire is moderately produced and the spiral sculpture is reduced to a single low ridge, while the vertical lamellae are nearly or quite obsolete. The coloration in this morph forms a pattern which is common to an immense number of local races, quite independent of morphological features. We find some individuals in which color is entirely lacking, while at the opposite extreme we have those with a uniform brown coloration. Between these we have a graded series of banded forms connecting the extremes, and thus forming what might be regarded as clines within the local races. Illustrations of this phenomenon will be seen in widely separated populations, as in morphs 12, 18, 22, 30, 37, etc.

This condition finds a ready explanation from the standpoint of genetics.

Specimens available, 100.

Morph 12. Plate XXVII.

Fidalgo Island, although it is so termed, has rather the character of a peninsula separating Rosario Strait from Padilla Bay, since it is separated from the mainland by a narrow slough.

The shoreline of Fidalgo includes several rocky capes, each of which bears a related but distinctive population of *Thais*. The morph illustrated was derived from Shannon Point which extends from the northwest border of the island. It is introduced partly to indicate that even in widely separated areas phenotypes of very similar appearance may be developed.

Specimens available, 100.

Morph 13. Plate XXVIII.

Port San Juan, otherwise known as Port Renfrew, is an indentation in the southwestern coastline of Vancouver Island. The *Thais* population of this area proved to be extremely varied, the shells differing not only in the coloration but also in sculpture and spire form, making it difficult to adequately represent the lines of variation within the limits of a single page.

It will be noted the spire varies from an extremely flattened type, such as is presented in morphs 16, 17, etc., to those in which an elevated spire is present comparable to those found in morphs 30, 37, etc. The sculpture likewise varies from a rather imbricated condition to forms that are perfectly smooth. The coloration follows the common pattern, with an integrated sequence.

Specimens available, 200.

Morph 14. Plate XXIX.

Prevost Harbor is a small bay on the northeast coast of Decatur Island, in the San Juan group. The specimens illustrated were collected from a reef on the northern border of the bay.

This morph consists of individuals in which the spire is relatively short, the sculpture is practically obsolete, and the shells are devoid of color. Their rather large size suggests favorable nutritive conditions.

Shells of this type, which appear to represent an extreme form as compared with the highly imbricate races, occur as elements in many polymorphic clines throughout the range of the species.

Specimens available, 25.

Morph 15. Plate XXX.

Ebey's Landing is located on the western shore of Whidbey Island, in Puget Sound.

This morph is a variation of the smooth type in which the sculpture is faintly indicated, and the color is very delicately banded.

Specimens available, 100.

Morph 16. Plate XXXI.

Canoe Bay is located on Vancouver Island, a short distance north of Sidney, B. C.

This morph is evidently closely related to morphs 15, 17, and many other populations in this area.

Specimens available, 100.

Morph 17. Plate XXXII.

Smith Island is an extremely isolated reefy islet, situated at the eastern end of the Strait of Juan de Fuca. The shore is covered with large glacial boulders, which constitute a rather unfavorable environment, and as a result the shells are reduced in size. This morph belongs in the large group of populations in which the sculpture is reduced and the coloration is lacking or feebly expressed.

Specimens available, 150.

Morph 18. Plate XXXIII.

The village of Friday Harbor is located on the bay bearing the same name, on the eastern side of San Juan Island. A dock has been in existence at this point for many years, and it is presumed the population of snails present on the dock piling originated from a group already present on the adjacent shore or by migrants from near-by Brown Island and Point Caution. The shells are for the most part very similar in form and sculpture to those found on adjacent areas, while their large size suggests the superior nutritive conditions commonly found in such situations.

Specimens available, 100.

Morph 19. Plate XXXIV.

North Beach is within the city-limits of Seattle. The population found here is of a type having a very wide dispersal throughout Puget Sound and adjacent areas, while forms of a very similar appearance occur in California and Alaska, indicating along with other phenomena, the common genetic background of the entire *lamellosa* complex. In this group of morphs the spire is relatively short and the sculpture is feebly developed or obsolete. In the great majority the typical graded type of color is in evidence. Illustrations given for this morph compare closely with some of those figured for morph 5 from Alameda in San Francisco Bay.

Morph 20. Plate xxxv.

Pleasant Beach is located on the southwest border of Bainbridge Island, in Puget Sound. The similarity of this morph to morphs 21, 22 and 23, will be apparent. The coloration of the shells in this population is for the most part of a pale brownish tinge, with very inconspicuous banding. The sculpture shades into an almost perfectly smooth form.
Specimens available, 150.

Morph 21. Plate xxxvi.

Wildcat Cove is an indentation at the northern border of Samish Bay in Whatcom County, Washington. In this morph we find conspicuous dark banding, with the usual range of coloration, although the small number of specimens available does not include any of the pure brown forms.
Number of specimens available, 12.

Morph 22. Plate xxxvii.

Vashon Island is located in Puget Sound, about midway between the cities of Seattle and Tacoma. The population illustrated was collected at Paradise Cove, an indentation in the southern coastline of the island. The shells in this morph are very similar in sculpture and coloration to those seen in morphs 19 and 20, which presumably indicates a comparable genetic basis.
Specimens available, 25.

In the same area there is a dock on the piling of which we find a population of an entirely different type, as shown in Plate xlviii. The shells of this morph are strongly imbricated and are of great size, indicating favorable nutritive conditions.

Morph 23. Plate xxxviii.

Deception Pass is the narrow strait which separates the north end of Whidbey Island from the mainland. The specimens illustrated were collected from a reef at the southern end of the pass.

The shells in this population are similar to those seen in related forms, but the sculpture is somewhat coarser and the size is much greater, both conditions presumably related to the favorable environment afforded by the reef. The color pattern is of the common intergrading type.

Specimens available, 25.

Morph 24. Plate XXXIX.

Deadman's Bay is a shallow indentation in the western shoreline of San Juan Island a few miles north of False Bay. Here we encounter the transition from the lightly sculptured types common in the region about Friday Harbor, and the rather heavily imbricated forms which prevail to the northward. In this population the intergrading from the relatively smooth to the imbricated type presents a sculptural cline, with the less imbricated individuals much in the minority.

Coloration in this morph is absent or very feebly expressed. The spire is moderately elongated.

Specimens available, 150.

Morph 25 Plate XL.

Mitchell's Bay is located on the northern section of the western shoreline of San Juan Island. The specimens illustrated were collected at a point about one mile south of the bay. This population is obviously closely related to Morph XXXIX, which is located a few miles to the southward, but the shells are more fully imbricated, and we find a few intruding banded forms. It will be noted this type of imbrication is developed through the almost equal elevation of both spiral and vertical striae.

Specimens available, 100.

Morph 26. Plate XLI.

North Pender Island is located to the northwest of the San Juan group, in Canadian waters. The population illustrated was collected from a reef in Shingle Bay.

In this morph it will be noted the sculpture is very similar to that seen in morphs 24 and 25, and the same type of gradational condition is in evidence, but the main spirals are more developed and the percentage of colored individuals is greatly increased.
Specimens available, 100.

Morph 27. Plate XLII.

Morse or Ship Island is a small rocky islet located at the northern end of San Juan Island.

The sculpture in this population is similar to that found in morphs 24, 25 and 26, but the imbrication is as a rule more heavily developed, and leads by a graded series to forms resembling the extreme types illustrated in morphs 34 and 35, the group forming a clinal sequence. Coloration is lacking or is feebly expressed.
Specimens available, 100.

Morph 28. Plate XLIII.

St. John's Harbor is located in the Bardwell group of islands in Milbank Sound, Alaska.

The striking similarity of this Alaskan morph to populations inhabiting the San Juan Islands, is one of the many illustrations of the appearance in this protean species, of seemingly almost identical phenotypes at widely separated points. The tendency towards the development of an elongated spire is characteristic of many of the northern forms.
Specimens available, 25.

Morph 29. Plate XLIV.

Blakeley Island is one of the larger members of the San Juan group. The specimens illustrated were collected at a point on the northern shore, northeastward of Peavine Pass.

This morph is marked by an unusual development of pigmentation, with a preponderance of banded forms. A few pale specimens present are not shown in the plate. The sculpture suggests a slight cline in the degree of imbrication.
Specimens available, 25.

Morph 30. Plate XLV.

This population was derived from the second of several reefs and rocky promontories extending from the shoreline in the vicinity of Olga, on Orcas Island in the San Juan group.

The shells in this morph exhibit considerable variation in sculpture, ranging from quite smooth to markedly imbricated forms. The spire in the majority of individuals is rather elongated. The coloration shows the widespread range from white to dark brown, with the banded forms and darker shades predominating, thus developing a cline as regards color.

Specimens available, 100.

Morph 31. Plate XLVI.

The breakwater at Victoria, on Vancouver Island is an artificial structure, and presumably has been populated by strays from neighboring colonies. As is true of many other *Thais* populations the coloration exhibits a range from brown to white, with various intermediate types of banding, indicating the compound character of the genes controlling color in these forms. The sculpture and spire form also present a wide range, as might be expected, even in the small number of shells available for comparison.

Specimens available, 25.

Morph 32. Plate XLVII.

Turn Reef is located to the eastward of Turn Island, from which it is separated by a narrow channel. Turn Island itself lies close to the eastern shore of San Juan Island.

Turn Reef is a massive group of irregular metamorphic rocks, which are for the most part exposed only at the lower tide levels, and as a result the nutritive conditions are quite favorable, and consequently the snails attain a greater than average size on reaching maturity. Along with this increased growth the sculptural elements are increased in amplitude. The coloration exhibits the common type of clinal integration.

Specimens available, 300.

Morph 33. Plate XLVIII.

Vashon Island is located in King County, Washington. The material representing this morph was collected from the piling of a dock at Paradise Cove on the western side of the island. As is commonly seen in such situations, the piles are covered by an extensive growth of marine organisms, which appear to supply the snails with an abundance of food, thus accelerating their growth and causing them to attain an unusually large size, while the imbrications are correspondingly exaggerated. Specimens available, 100.

Morph 34. Plate XLIX.

Rocky Bay is a small arm of Case Inlet, Mason County, Washington. In this population the shells are rather heavily imbricated, and present forms which resemble some of those found in the San Juan Islands and elsewhere. They also suggest a transition to the even more "frilled" variants occurring in Puget Sound, as seen in morph 35 derived from a neighboring area, as well as to the northward in Kitsap County. Variants are also present leading to forms in which the sculpture is much reduced. In this morph color is almost completely absent or feebly expressed. In the entire collection only a single specimen was found to be heavily pigmented.
Specimens available, 100.

Morph 35. Plate L.

The material representing this morph was derived from an oyster bed located in the vicinity of the town of Allyn on Case Inlet, Puget Sound.

In this population we find an example of the most extreme type of the imbricated variants. Closely related populations occur throughout Port Orchard, Sinclair Inlet, Rich Passage and the Manchester area in Puget Sound. Coloration is lacking or feebly expressed in the material at hand.
Specimens available, 25.

Morph 36. Plate LI.

Silverdale is located at the northern end of Dye Inlet, in Kitsap County, Washington.

In this population we find little variation in size or spire form, but a graded series as regards sculpture, both spiral and vertical bands varying from a sharply defined expression to forms in which both sets of bands are almost obliterated, thus forming a clinal system. The coloration is absent or obscurely indicated.
Specimens available, 25.

Morph 37. Plate LII.

Jessie Island is located in Departure Bay, British Columbia. In this morph there is present the elongated spire and balanced development of the spiral and vertical bands which are characteristic of many northern populations. The coloration of the shells follows the pattern so frequently noted of a graded series, ranging from pure white to dark chocolate. The sculpture also exhibits the graded pattern so commonly met with.
Specimens available, 100.

Morph 38. Plate LIII.

McLean's Arm is an indentation in the southeast coast of Prince of Wales Island in Alaska. In this morph the shell form is of the type common to many populations in British Columbia and Southeastern Alaska, with elongated spires and balanced sculptural pattern. In this instance coloration is almost completely lacking.

Morph 39. Plate LIV.

Thumb Bay is an indentation in the coastline of Knight Island, Prince William Sound, Alaska. This morph is notable for the extreme length of the spire in the majority of the specimens, and the tendency of some of the variants to develop close-set imbrications. The coloration is of the common type, with a graded series ranging from brown to white.
Specimens available, 50.

Morph 40. Plate LV.

Washington Bay is an indentation in the coastline of Kuiu Island, in Southeastern Alaska.

This morph is of unusual interest, since it diverges rather widely from the basic type in this species. The spire is elongated and the axial bands are, in most of the specimens, widely spaced and much elevated. The spiral bands are also reduced in number and accentuate the striking imbrication of the shell. In this population there are however, individual specimens that indicate a transition to the more normal type.

The coloration is almost without exception of the monochrome type, with various shades of orange and yellow predominating. There appears to be little indication of banding except in the case of a few seemingly intrusive types.

The size of the shells varies greatly, the larger specimens coming as usual from the deeper niches, where they grow more rapidly, with a corresponding modification of both size and sculpture as shown in Plate LV, while in less favorable situations individuals of smaller or even dwarfed size are produced, as shown in Plate LXIV.

Specimens available, 50.

Morph 41. Plate LVI.

Fossil Bay is an indentation in the southeastern border of Sucia Island in the San Juan group.

In this population we find a very heterogeneous condition, both as regards size, sculpture and coloration. In some of the shells the sculpture lacks the axial bands and has indications of the secondary spirals, which would suggest a reversion to ancestral stock, a condition found in a number of populations at widely separated points.

Specimens available 150.

Morph 42. Plate LVII.

The material representing this morph was dredged from a submerged reef off the west coast of Whidbey Island.

This population illustrates several points in the interpretation of the variation found in these snails. It will be noted that the only significant effect of the adjustment of the snails to this type of environment is apparently an increase in size, the genetically determined characters of sculpture and coloration remaining unaffected. Specimens available 25.

Morph 43. Plate LVIII.

Johns Island lies to the southeast of Stuart Island in the San Juan group. The specimens illustrated were brought up in a dredgehaul from a submerged reef in this area. We have here an additional example of the increased growth of the snails inhabiting such sites, paralleling the "giant" forms of the Atlantic species found in like situations.
Specimens available, 25.

Morph 44. Plate LIX.

The village of Neah Bay stands at the entrance to the Strait of Juan de Fuca. The specimens illustrated were derived from the piling of the dock at the village. The type presented by this population reappears with various modifications throughout the entire range of the species. The somewhat greater than average size is related to the favorable nutritive conditions commonly found in such situations.
Specimens available, 10.

Morph 45. Plate LIX.

Sitkalidak Island lies off the southern coast of Kodiak Island. This population exhibits a range in spire form and sculpture bridging the gap between the long and short spired forms.
Specimens available, 15.

Morph 46. Plate LX.

The material representing this population was collected from an area on the shore in the vicinity of Yakutat Village, on Yakutat Bay, Alaska. In this population there is a reduction in the sculptural pattern, the spire form is more obtuse, and the coloration is obscurely indicated, suggesting a combination of characters resembling some of the morphs found in the San Juan Islands and elsewhere.
Specimens available, 12.

Morph 47. Plate LX.

Craig is located on the western coast of Prince of Wales Island, Alaska.

This population is obviously very similar to the forms figured on Plate LIII, derived from another area on the same Alaskan island. It will be noted however, that the imbrication is less pronounced, while delicate color banding is in evidence This is an illustration of the delicate shading commonly found in the differences between closely allied local races.
Specimens available, 12.

Morph 48. Plate LXI.

Kagamil Island is one of a group known as the Islands of the Four Mountains, located near the center of the Aleutian Chain. The scanty material available indicates that throughout the Aleutian Islands a type prevails in which a short spire and reduced banding is in evidence, resembling quite closely some of the local races found to the south of Cape Flattery. Beachworn shells from Unalaska and from Adak Island to the westward, tend to confirm this impression.
Specimens available, 6.

Morph 49. Plate LXI.

Afognak Island lies to the northeast of Kodiak. The single pair of shells available for study indicate a type of structure comparable to that premised for the Aleutians to the westward, or to populations occurring in Puget Sound.

Morph 50. Plate LXII.

This population was collected from a reef near the village of Yakutat, in Yakutat Bay, Alaska. The striking difference between this local race and that shown on Plat LX, derived from an adjacent area, illustrates the familiar fact that very dissimilar races may inhabit closely adjoining areas, seemingly not differing greatly in tneir ecological conditions.

In the present morph it will be noted, there is exhibited a range in size, spire form, sculpture and coloration, indicating a mixture of several ancestral stocks.
Specimens available, 25.

Morph 51. Plate LXIII.

Three Saints Bay is located on the coastline of Kodiak Island, Alaska. In this population the strong development of the spiral bands, modified by a corresponding expression of the axial bands, gives the shells a rather striking sculptural pattern. There is also a tendency to develop the secondary spirals. The coloration follows the usual scheme, with the development of finely banded forms. The spire form is variable, but tends towards the shortened type.
Specimens available, 15.

Morph 52. Plate LXIII.

Etoro Island is one of the Kurile chain, which extends northward from the main Japanese archipelago.

The writer does not have sufficient Japanese material to express an opinion as to the relationship of the forms of *Thais* inhabiting the Japanese islands, and those occurring in the Aleutians. Since however, the faunal elements of the two areas are known to have much in common, they presumably were even more closely related during some parts of the Pleistocene. The only material from the Kuriles area available to the writer which can be assigned to the *lamellosa* complex are four specimens from Etoro Island, that seem to compare rather closely in their form and sculptural pattern with local races from the Aleutians. Since Etoro is located towards the southern end of the Kuriles, it would seem that *lamellosa* or closely allied forms must have a wide distribution among the islands, and along the shores of Kamchatka.

Morph. 53. Plate LXV.

Sitkalidak Island is located off the southern coast of Kodiak Island. The type of shell found in this population conforms to a widespread pattern which reappears at many points in the distribution of the species. The spire is short, and the sculptural organisation is much reduced.
Specimens available, 6.

SUMMARY

1. This paper deals with the complex group of local races of the marine gastropod *Thais lamellosa* (Gmelin) inhabiting the west coast of North America from Santa Cruz, California, to the Aleutian Islands in Alaska.

2. An account is given of the taxonomic history of the species, which illustrates the difficult nomenclatorial problem presented by extremely variable polytypic forms.

3. The biology of the species is discussed, including its life-history, food habits, means of dispersal, distributional barriers, injurious organisms, and ecological adjustments.

4. The geologic history of the forms of *Thais* inhabiting the Pacific is reviewed, and the probable relationship of these to the Atlantic species *Thais lapillus* is suggested.

5. The existing distribution of the immense number of local races of *Thais lamellosa*, differing not only among themselves, but also exhibiting great variation among the individuals comprising the local populations, is interpreted as due to a complex set of factors, including the genetic instability of the ancestral stock, geographic isolation acting over a long period of time throughout the entire range of the species, microgeographic isolation involving local topographic and hydrographic situations, and nutritive conditions in highly localized niches.

6. All of the diverse phenotypic forms are interpreted as due to the inbreeding of genetically segregated groups, which determines the form of the shell, its sculpture, including both spiral and axial bands, and its coloration. Each of these is regarded as determined by separate and independently acting genetic factors.

7. The only characteristic regarded as determined primarily by environmental conditions is that of size, which is governed by nutrition. Where food is abundant, and the feeding process is not interrupted by tidal exposure, the animals grow rapidly and attain a greater size at maturity. This tends to modify the sculptural pattern, since the several elements are given a greater spread.

8. During the Pleistocene far-reaching changes in the level of the ocean took place, as well as changes in the elevation of the land, both eustatic and tectonic, which in combination with the advance and retreat of the great continental glaciers over the northern world, must have profoundly affected the distribution and ecological adjustments of intertidal forms. These factors undoubtedly had a profound influence in determining the character of the local races of *Thais* and other intertidal forms with limited powers of dispersal.

9. The chromosome number in *Thais lamellosa* has been determined by Dr. H. Staiger to be 35, but the relationship of these elements to the variations found in the structure and coloration of the shells cannot be determined without comprehensive, controlled breeding experiments.

10. To avoid the use of an indefinite number of trinomials, the writer has adopted a suggestion offered by Dr. J. Gordon Edwards that such products of microgeographic isolation be termed "morphs", pinpointing as closely as possible the localisation of the several populations.

11. Fifty-three morphs, designed to illustrate the extensive range of variation exhibited by the local populations of *Thais lamellosa*, are figured and discussed.

NOTES AND COMMENTS

This publication is throughout an amateur production. The type was hand set and the printing was done upon a small manually operated press, one page at a time. This will explain the lack of professional touch resulting from linotype operation. All of the photographs, except a few made at an earlier date by Miss Bertha Challis, were made by the author, as is also true of the prints utilised in producing the plates.

The photographs are attached to the mounting sheets with rubber cement. If perchance any of the prints become detached they can be replaced by a few drops of this adhesive.

Corrections.

On page 48 material from Afognak Island is ascribed to the Aleutians. On page 66 this island is more properly located as one of the Kodiak group.

The reference to Goldschmidt 1945 on page 36 should be omitted.

To the previous list of acknowledgments there should be added the following:-

Mr. Verne Hayes furnished some interesting material from Liberty Bay in Puget Sound.

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Plate I

Map of Puget Sound Region

Plate II

Generalized map of the San Juan Islands
Most of the smaller islands are omitted

Plate III

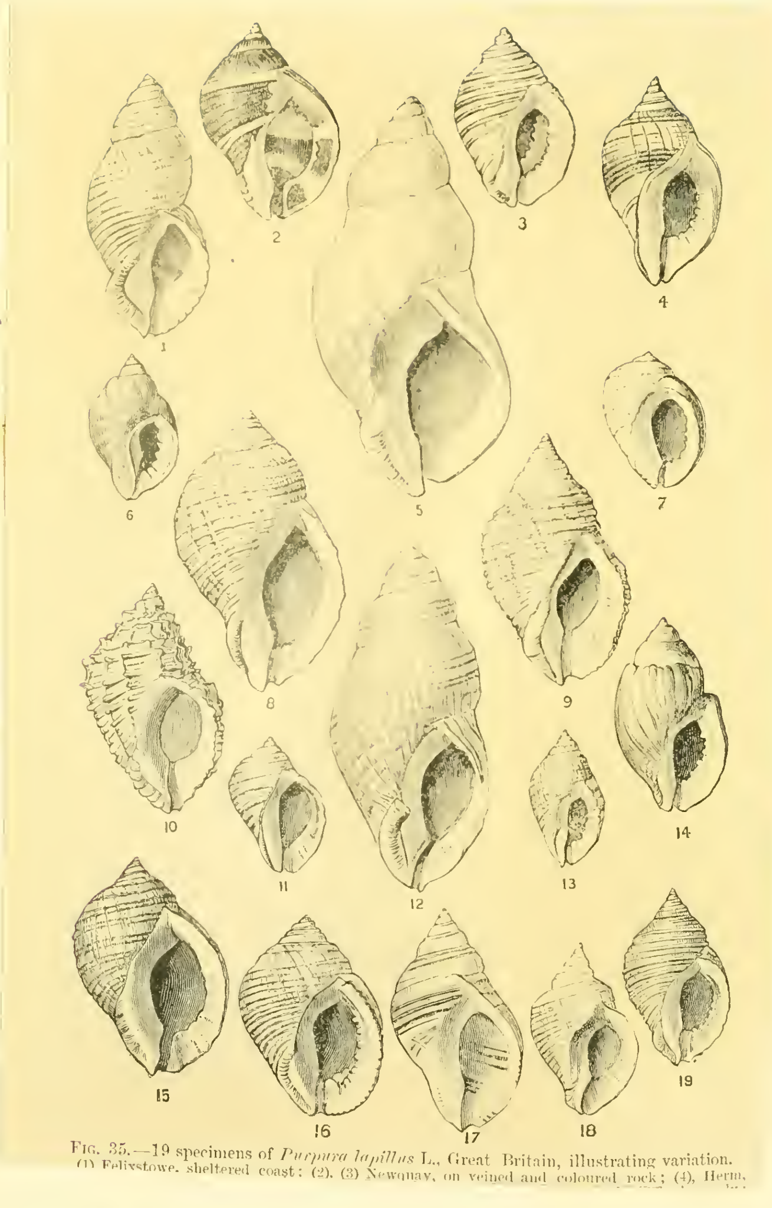


FIG. 35.—19 specimens of *Purpura lapillus* L., Great Britain, illustrating variation. (1) Felixstowe, sheltered coast: (2), (3) Newquay, on veined and coloured rock; (4), Herm,

Variation in the local races of *Thais lapillus* as illustrated by Rev. A. H. Cooke in Mollusca, v. III, Cambridge Natural History, 1895

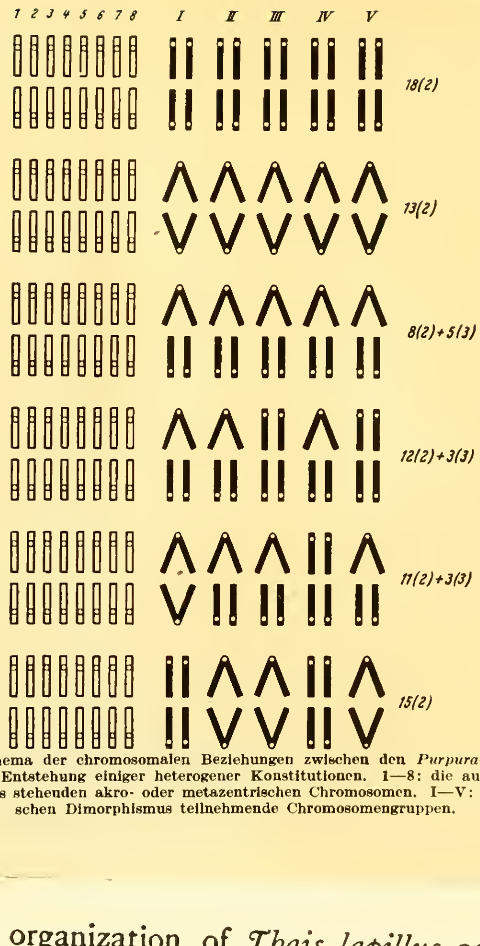
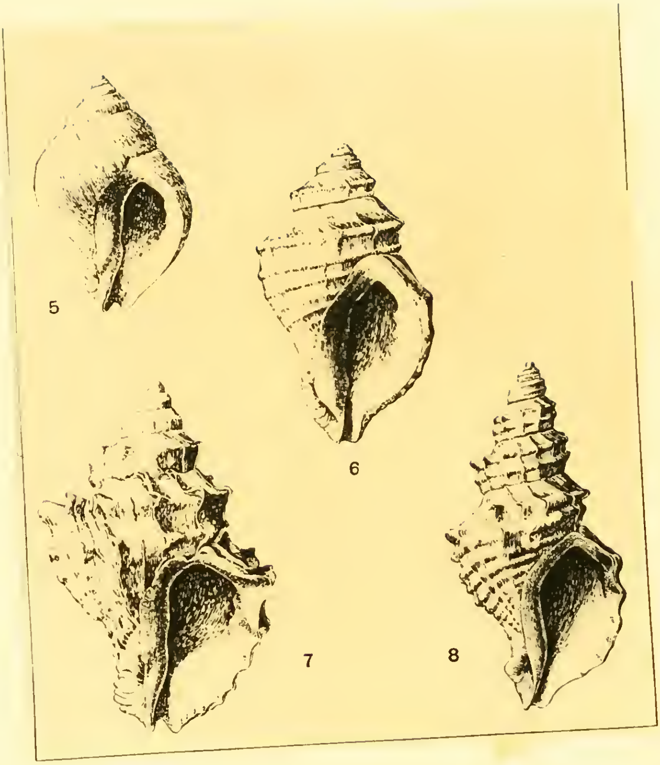


Abb. 18. Schema der chromosomalen Beziehungen zwischen den *Purpura*-Formen 13 und 18 und Entstehung einiger heterogener Konstitutionen. 1—8: die außerhalb des Dimorphismus stehenden akro- oder metazentrischen Chromosomen. I—V: am numerischen Dimorphismus teilnehmende Chromosomengruppen.

Genetic organization of *Thais lapillus* according to Dr. H. Staiger (1954). Eight basic or acrocentric chromosomes, combining with elements of ten secondary chromosomes to make possible a wide range of variation, Chromosoma, v. 6, fig. 18.

Plate V



Variation in *Thais lamellosa* as suggested by Dr. W. H. Dall (1915, pl. 74.).- 5. var. *cymica*; 6. var. *franciscana*; 7. *lamellosa* typical; 8. var. *hormica*.

Fossil form of *Thais lamellosa* from the Pleistocene of Washington. From Weaver (1942, pl. 88.)

EXPLANATION OF PLATE VI

Individual specimens from a series of local races of *Thais lamellosa*.

Top row,- Turn Reef, San Juan Islands; Orchard Rocks, Kitsap Co., Puget Sound; Allyn, Case Inlet, Puget Sound.

Second row;- McLean's Arm, Prince of Wales Island, Alaska; Vashon Island, Puget Sound; Prevost Harbor, San Juan Islands.

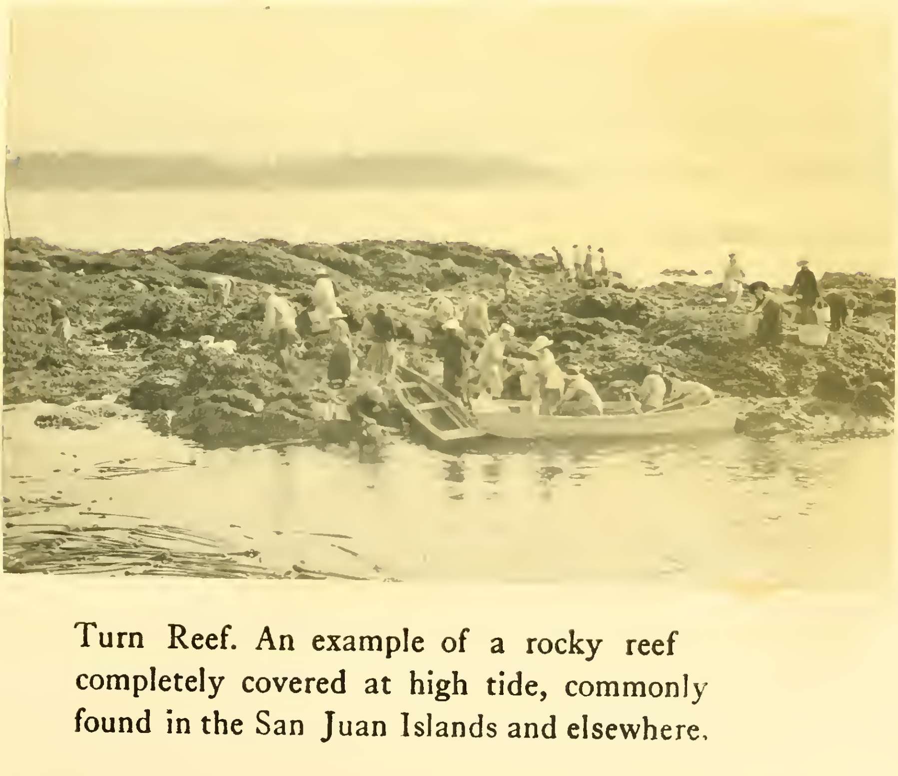
Third row,- Knob Island, San Juan Islands; Kuiu Island, Alaska; Oakland Bay, Puget Sd.; Willapa Bay, Washington.

Fourth row,- Blakeley Island, San Juan Islands; Allison Harbor, B. C.; Canoe Bay, Vancouver Island, B. C.

Plate VI

Plate VII

Characteristic rocky shore in the San Juan Islands.



Turn Reef. An example of a rocky reef completely covered at high tide, commonly found in the San Juan Islands and elsewhere.

Plate VIII

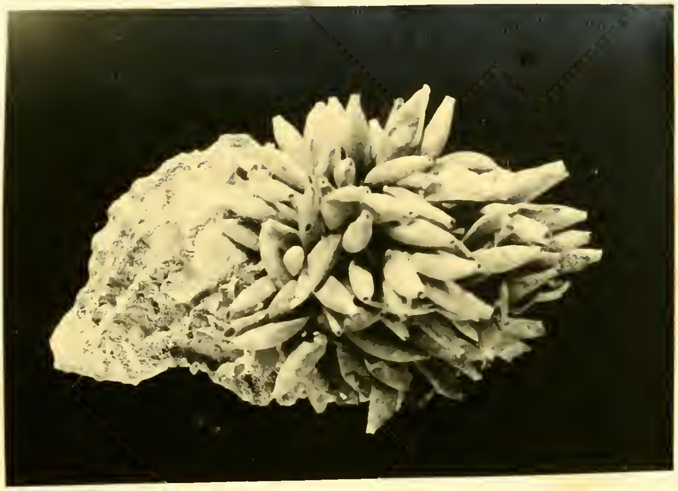
Morse Island, also known as Ship Island.
North of San Juan Island.

One of the small rocky islands characteristic of our western coast from Puget Sound to Alaska.

Plate IX

Crescent shaped beaches, composed of sand or loose gravel, serving as barriers to the migration of *Thais*.

Plate X



Clusters of the egg-capsules of *Thais lamellosa*; in this case deposited upon the back of one of the snails.

Veliger of *Thais lamellosa*, removed from one of the egg-capsules.

Organisms injurious to *Thais lamellosa.*
Upper row:- Barnacles encrusting the shells.
Middle row:- Tubes of serpulid worms. *Thais* drilled by a naticoid snail.
Bottom row:- Perforations by burrowing worms.
Injury caused by boring sponges.

Plate XII

Thais lamellosa bearing clusters of oysters (*Ostrea lurida*), Oyster Bay, Puget Sound.

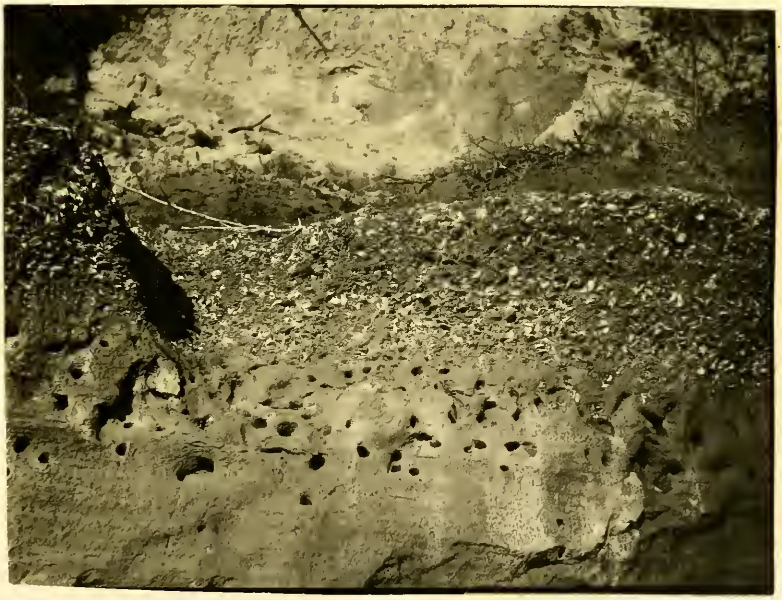
Thais lamellosa showing characteristic injury, presumably caused by predatory birds.

Thais lamellosa feeding upon the barnacle encrusted wall of an oyster dike.

Radula of *Thais lamellosa*.

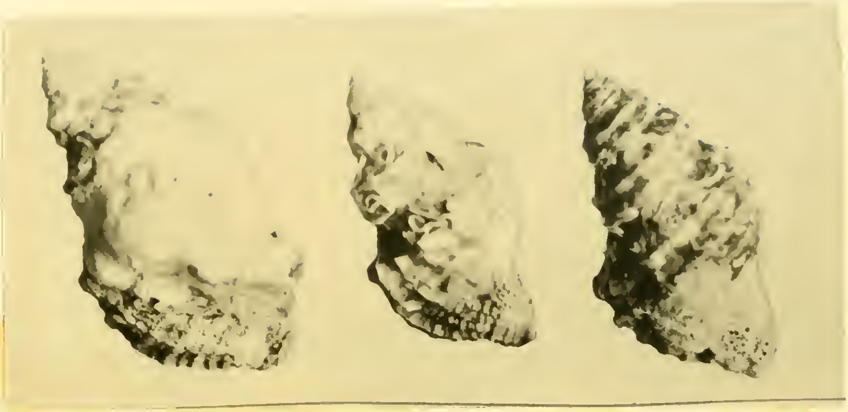
Plate XIV

Raised sea-beach on Willapa Bay, with a bed of shells containing *Thais lamellosa*, of Pleistocene origin.



Shell-bed in the Pleistocene raised beach in which may be seen the underlying glacial till, and the overlay of terrace deposits, presumably of fluviatile origin. C. 14 dating of till, over 38,000 years.

Plate XV



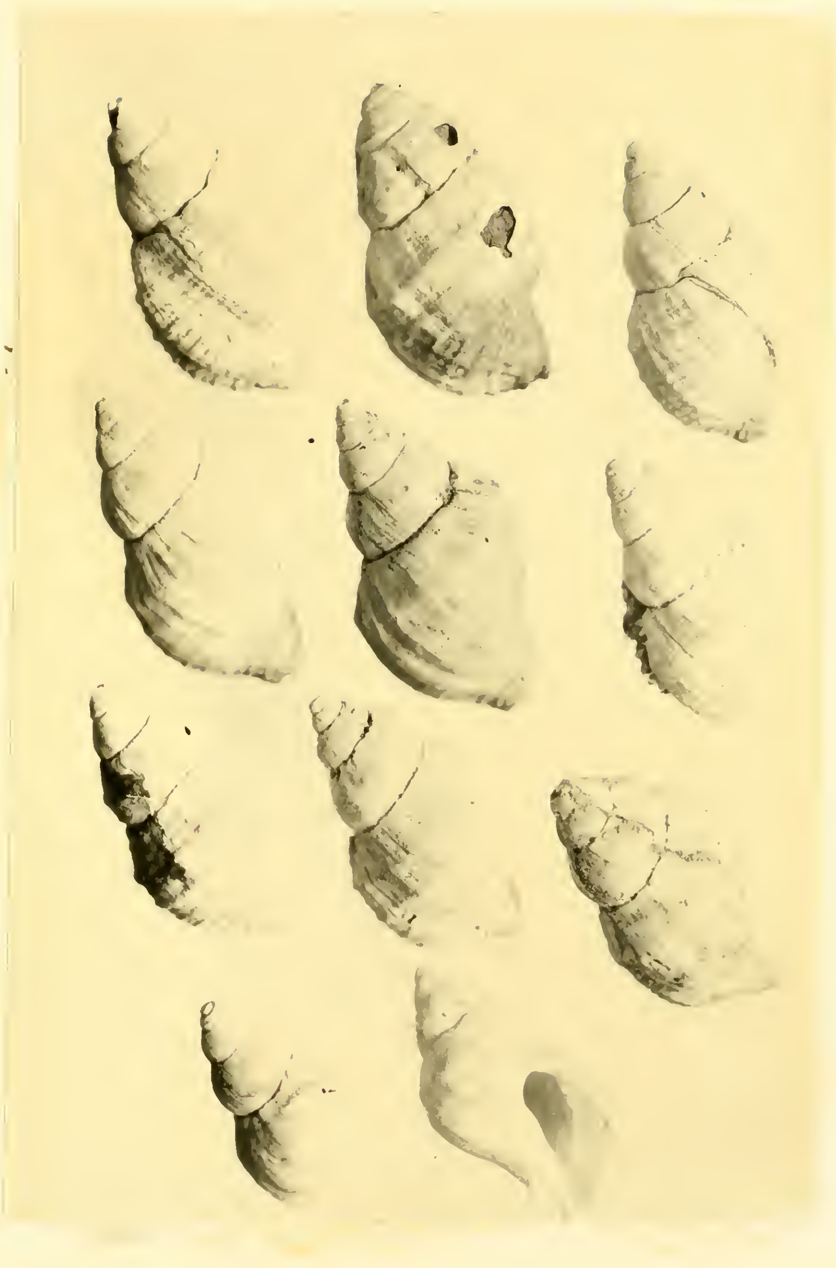
Shells of *Thais* from a submerged area encrusted with colonies of bryozoans.

Shells of *Thais* corroded by an alga.

Thais shell perforated by a boring sponge.

Plate XVI

Morph 1.
West shore of Long Island in Willapa Bay, Washington.



Morph 2.
Raised Pleistocene beach at Bay Center,
Willapa Bay, Washington.

Morph 3.
Oysterville, Willapa Bay, Washington.

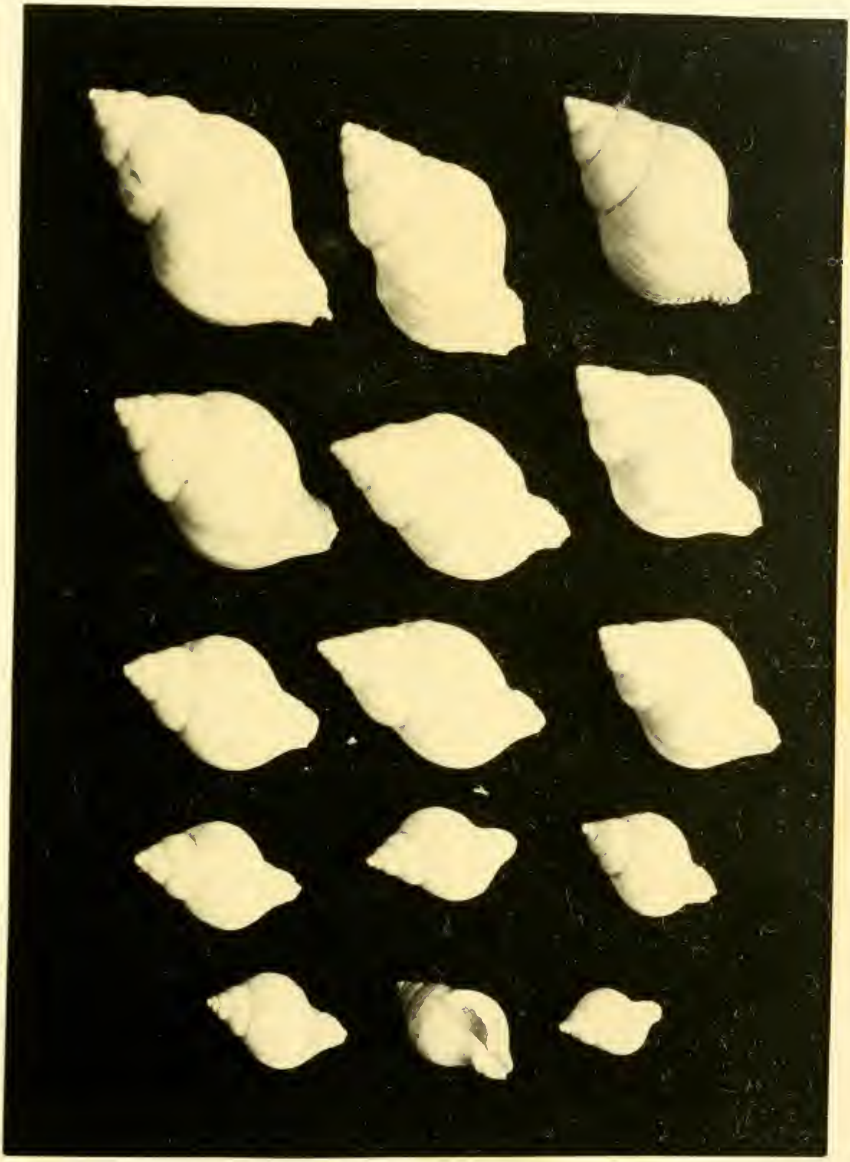
Plate XIX

Morph 4.
Trinidad, California.

Plate XX

Morph 5.
Alameda, San Francisco Bay, California.

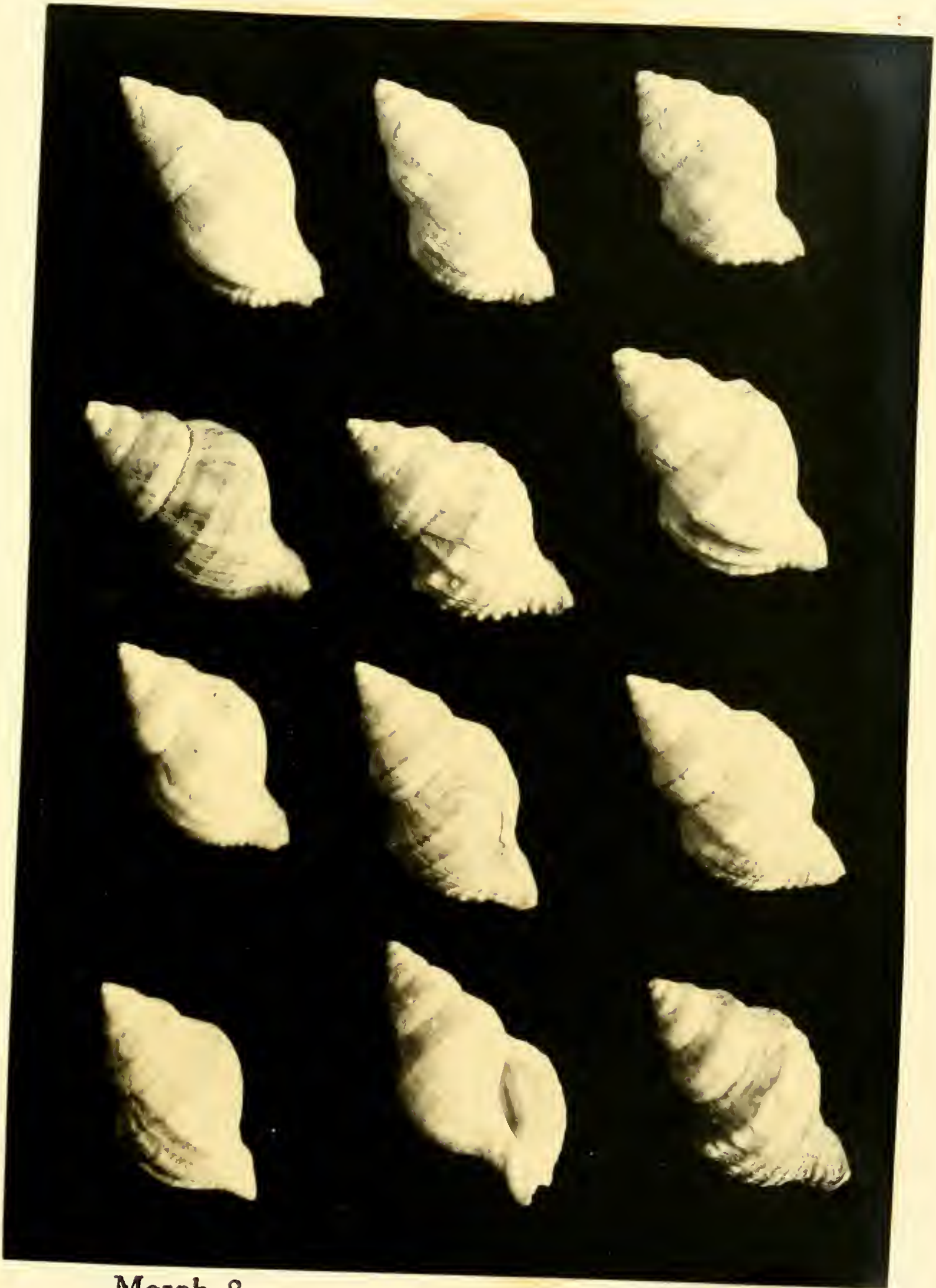
Plate XXI



Morph 6.
Port Stanley, Lopez Island, San Juan Islands.
Illustrating the variation in size found in many populations.

Morph 7.
False Bay, on the west side of San Juan Island.

Plate XXIII



Morph 8.
Allen Island, west of Fidalgo Island, Wash.

Plate XXIV

Mor ph 9.
Brown Island, San Juan Islands.

Plate XXV

Morph 10.
Point Caution, San Juan Island.

Plate XXVI

Morph 11.
Freeman's Island, north of Orcas Island.

Plate XXVII.

Morph 12
Shannon Point, Fidalgo Island.

Plate XXVIII

Morph 13
Port San Juan, Vancouver Island. British Columbia.

Plate XXIX

Morph 14.
Prevost Harbor, Decatur Island.

Plate XXX

Morph 15.
Ebey's Landing, Whidbey Island.
Puget Sound.

Plate XXXI

Morph 16.
Canoe Bay, Vancouver Island,
British Columbia.

Morph 17.
Smith Island, Straits of Juan de Fuca.

Plate XXXIII

Morph 18.
Friday Harbor Dock, San Juan Island.

Plate XXXIV

Morph 19.
North Beach, Seattle, Washington.

Plate XXXV

Morph 20.
Pleasant Beach, Bainbridge Island.

Plate XXXVI

Morph 21.
Wildcat Cove, Whatcom County,
Washington.

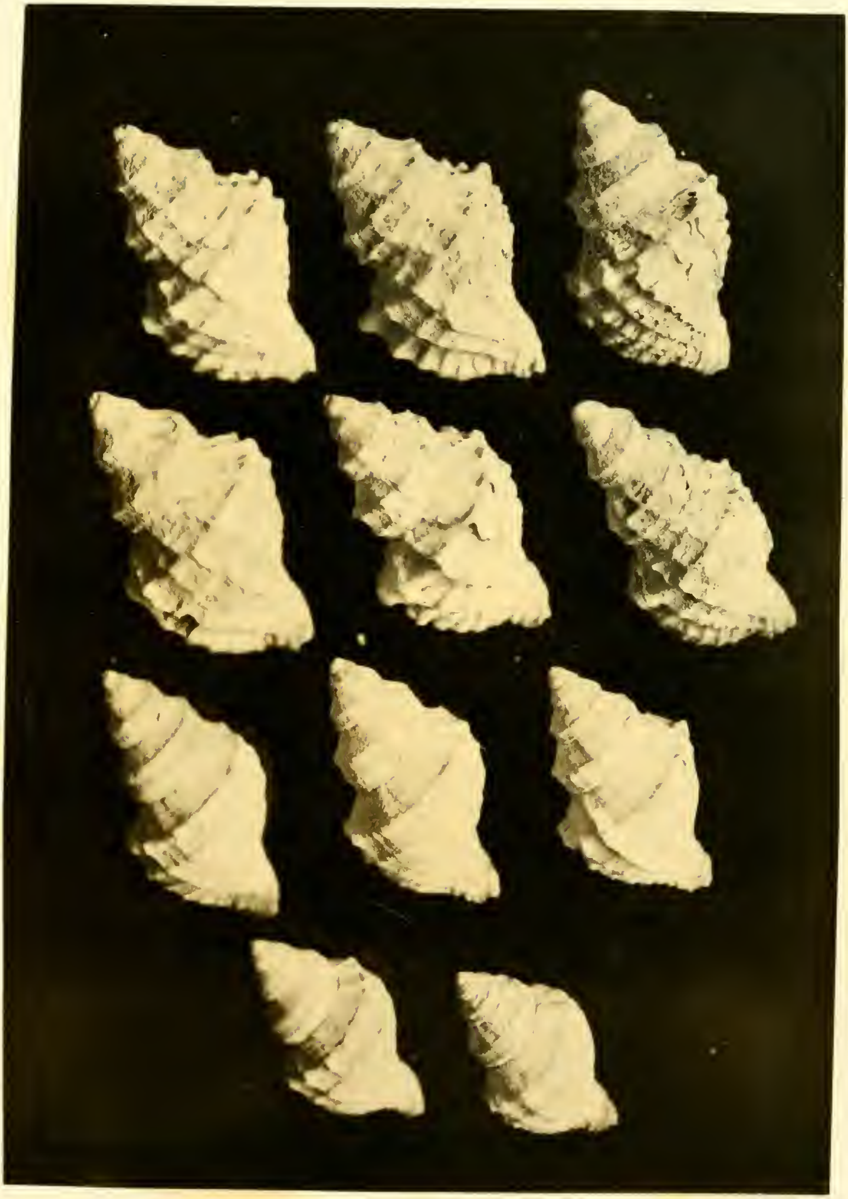
Plate XXXVII

Morph 22.
Vashon Island, Puget Sound.

Plate XXXVIII

Morph 23.
Deception Pass, Whidbey Island,
Washington.

Plate XXXIX



Morph 24.
Deadmans Bay, San Juan Island.

Plate XL

Morph 24.
Mitchell's Bay, San Juan Island.

Plate XLI

Morph 26.
Shingle Bay, North Pender Island, British Columbia.

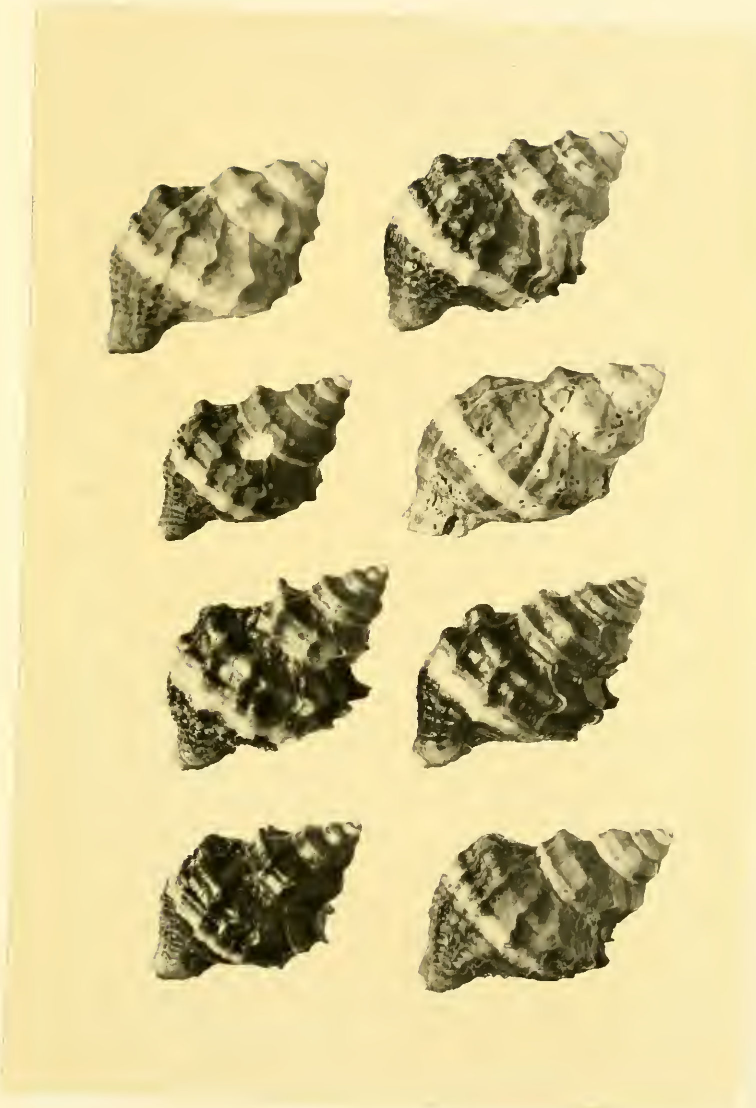
Plate XLII

Morph 27.
Morse or Ship Island, San Juan Islands.

Plate XLIII

Morph 28.
St. John's Harbor, Bardswell Group,
British Columbia.

Plate XLIV



Morph 29.
Blakely Island, north of Peavine Pass,
San Juan Islands.

Plate XLV

Morph 30.
Olga, Orcas Island, San Juan Islands.

Plate XLVI

Morph 31.
Breakwater, Victoria, British Columbia.

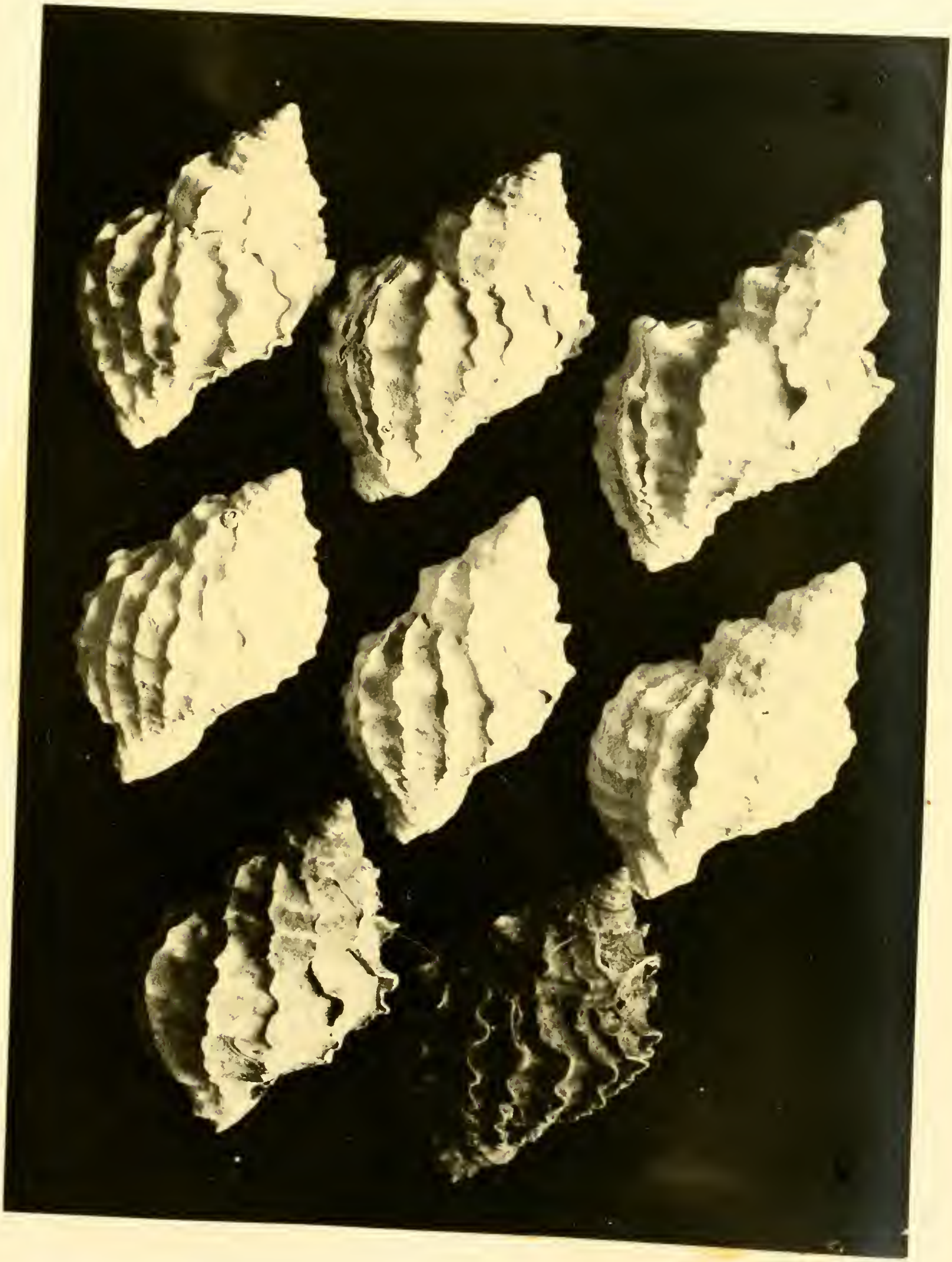
Plate XLVII

Morph 32.
Turn Reef, San Juan Islands, Washington.

Plate XLVIII

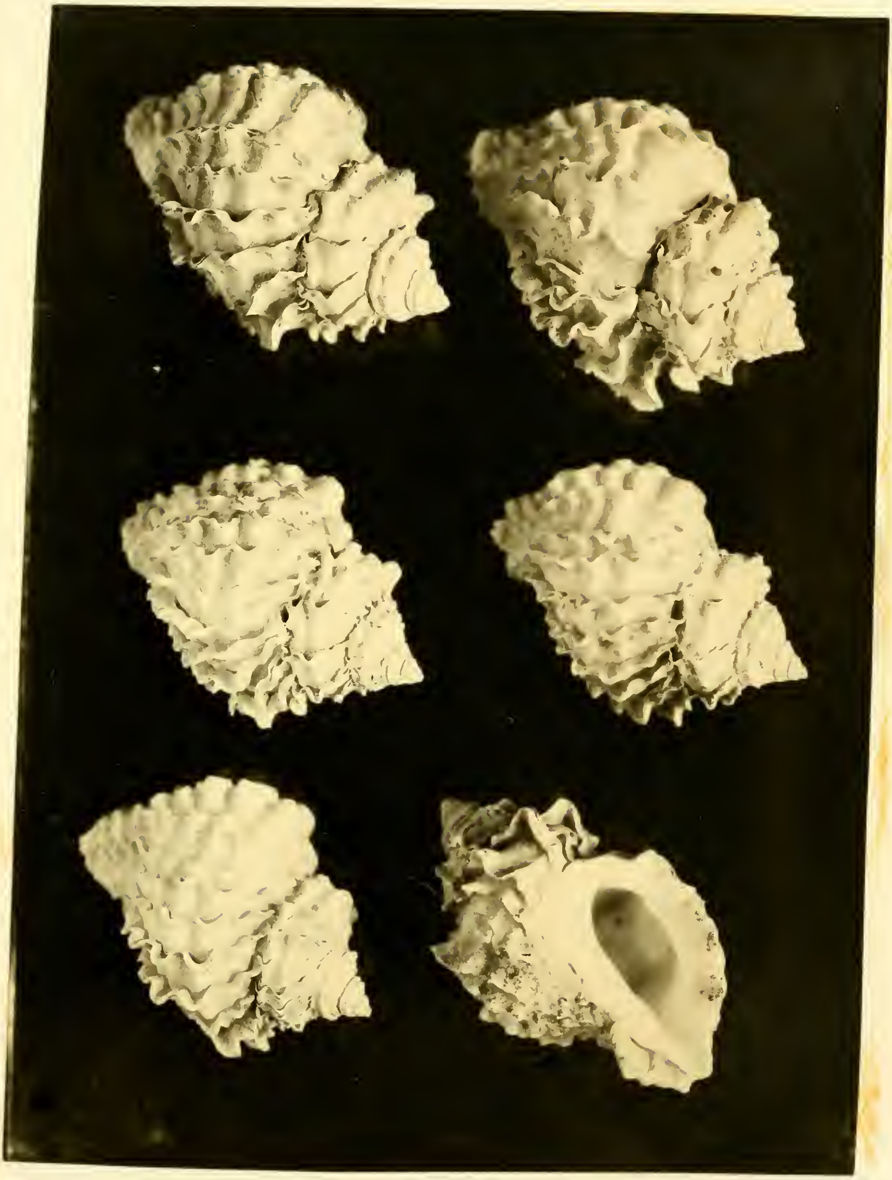
Morph 33.
Vashon Island, Puget Sound.
On the piling of a dock.

Plate XLIX



Morph 34.
Rocky Bay, Case Inlet, Puget Sound.

Plate L



Morph 35.
An oyster bed at Allyn, Puget Sound.

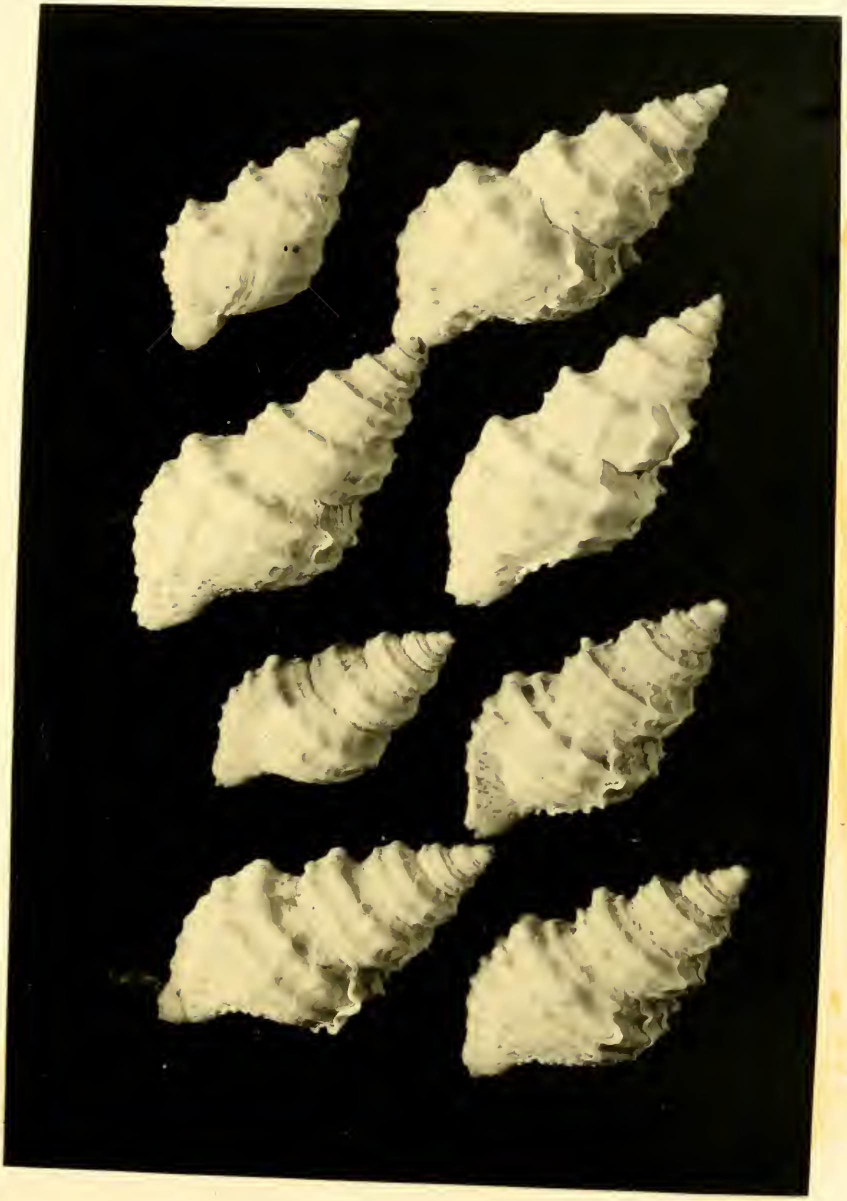
Plate LI

Morph 36.
Silverdale, Dyes Inlet, Puget Sound.

Plate LII

Morph 37.
Jessie Island, Nanaimo, British Columbia.

Plate LIII



Morph 38.
McLean's Arm, Prince of Wales Island, Alaska.

Plate LIV

Morph 39.
Thumb Bay, Knight Island, Alaska.

Plate LV

Morph 40.
Kuiu Island, Alaska.

Plate LVI

Morph 41.
Fossil Bay, Sucia Island,
San Juan Islands.

Plate LVII

Morph 42.
Submerged reef, Whidbey Island,

Plate LVIII

Morph 42.
Submerged reef, off John' Island,
San Juan Islands.

Plate LIX

Morph 44.
Neah Bay, Straits of Juan de Fuca.

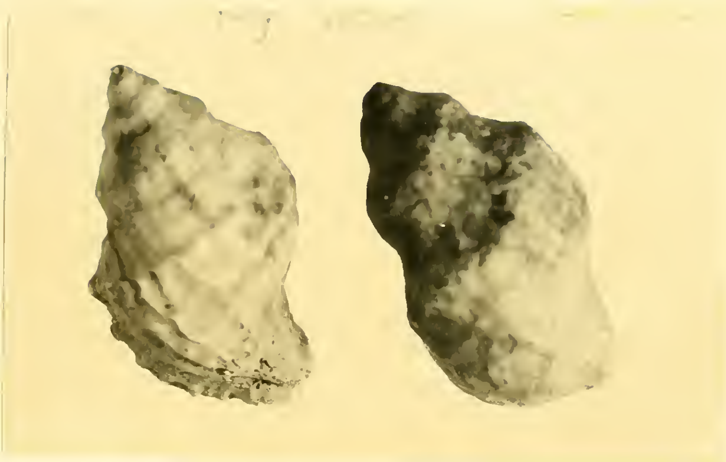
Morph 45.
Gravina Island. Alaska.

Plate LX

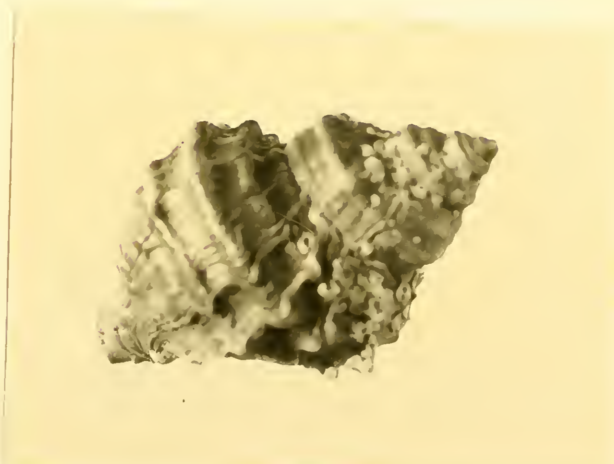
Morph 46.
Yakutat Bay, Alaska.

Morph 47.
Craig, Prince of Wales Island, Alaska.

Plate LXI

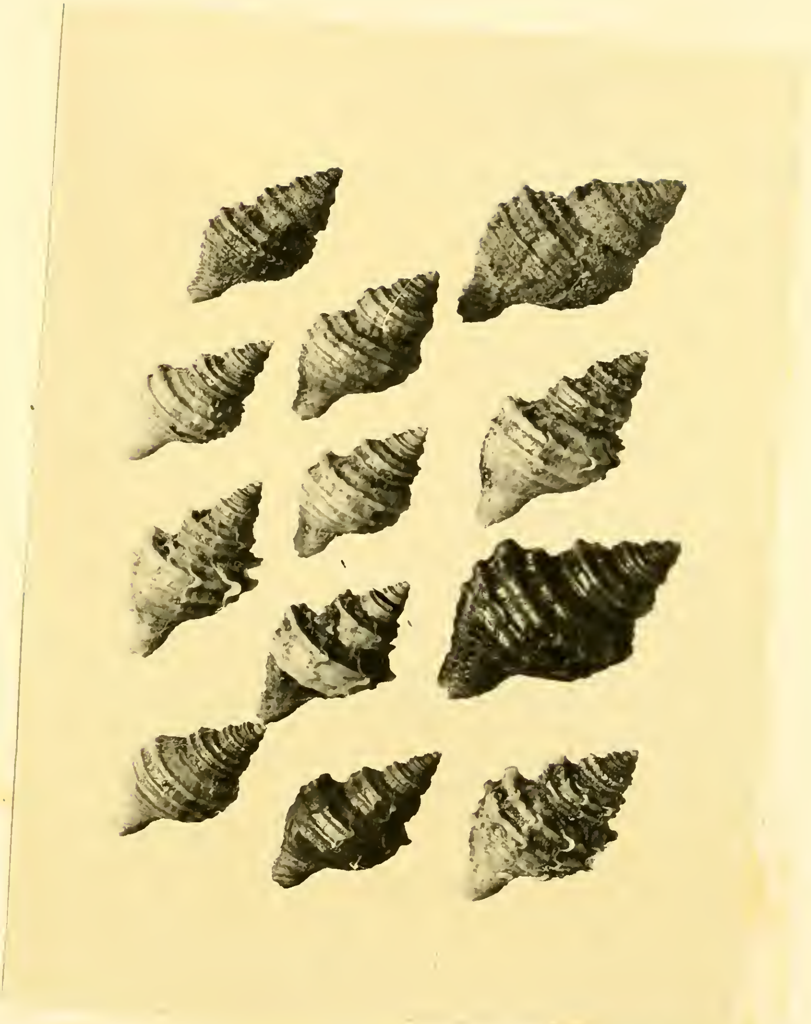


Morph 48.
Kagamil Island, Alaska.



Morph 49.
Afognak Island, Alaska.

Plate LXII



Morph 50.
Yakutat, Alaska.

Plate LXIII

Morph 51.
Three Saints Bay, Kodiak, Alaska.

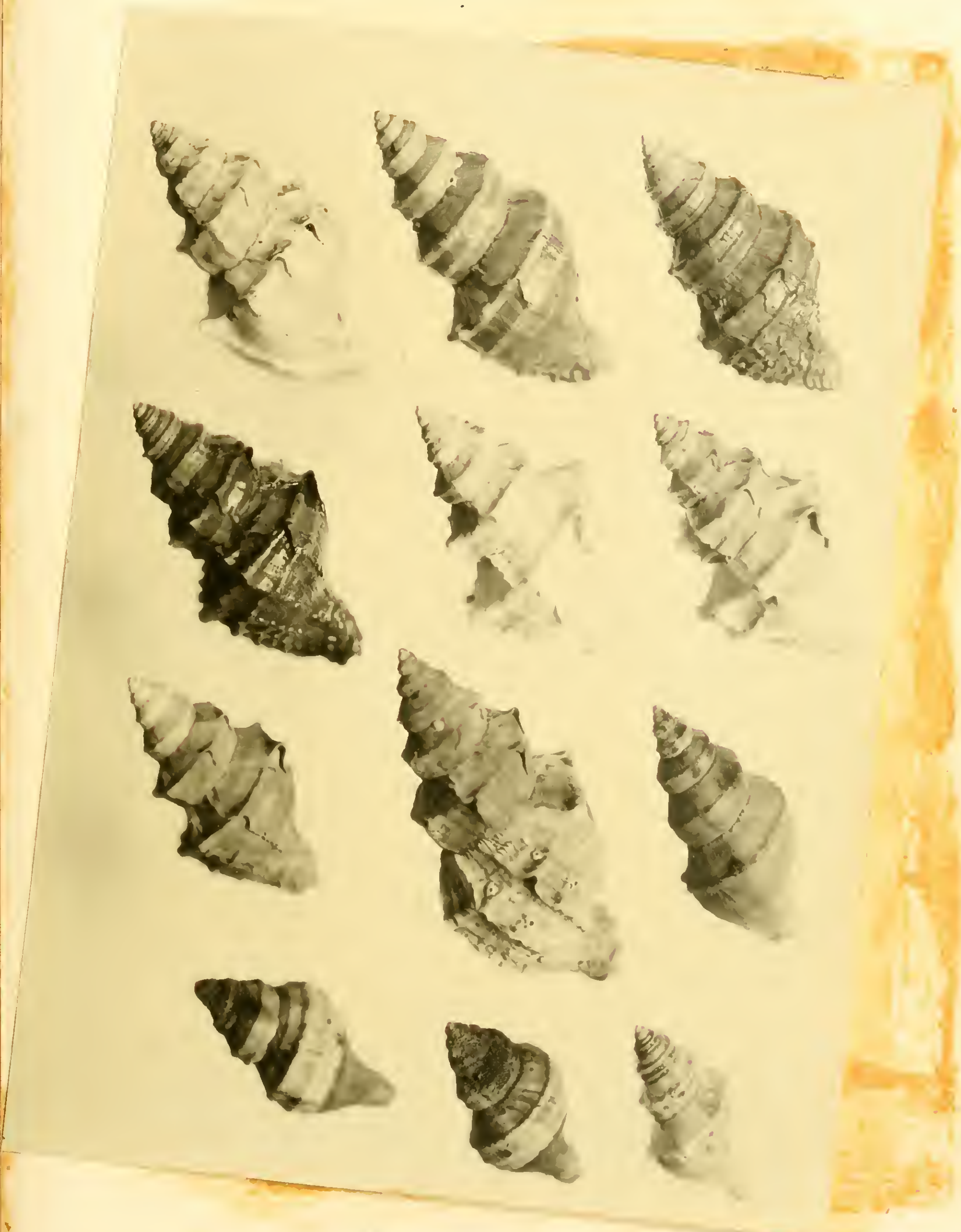
Morph 52.
Etoro Island, Kuriles, Japan.

Plate LXIV

Morph 53.
Sitkalidak Island, Alaska.

Fragmented shells of *Thais* from the intestinal tract of the White-winged Scoter (*Oidemia deglandi.*)

Plate LXV



Morph 40 A.
Kuiu Island. Alaska.