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Reprinted from the "Proceedings of Symposium on Mollusca"—Part I.

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BASIC DISTRIBUTION OF NON-MARINE MOLLUSKS

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ABSTRACT

The conventional zoogeographical realms, regions, and provinces are based upon the distribution patterns shown by birds and mammals, organisms whose major evolutionary radiation occurred during comparatively recent geological periods. An admirable summary of the world distribution into Ethiopian, Oriental, Australian, Nearctic, Palearctic, and Neotropical is given by Darlington (1957). Only in the tapirs and the families of lower vertebrates such as reptiles and amphibians, are disjunctive distributions common.

Mollusks, arthropods, and higher plant families agree in having disjunctive distributional patterns the rule rather than the exception. Although data on family and generic distributions for land and freshwater molluscs are incomplete for most zoogeographical areas, the broad patterns of distribution are clear.

The southern hemisphere areas are characterized by disjunctively distributed and relatively primitive land snail taxa, such as the Endodontidae, Acavacea, and Bulimuloidea. The Holarctic and Oriental land masses, including much of the tropical Asian and tropical African areas, have a fauna of more advanced taxa, such as the Polygyracea, Helicacea, and "zonitoid" taxa.

Faunistic boundaries of land snail distribution do not agree with those of the vertebrates. While New Guinea has an Australian vertebrate fauna, the land snails are oriental in affinities. Similarly, although the islands of Polynesia and Micronesia lack an endemic vertebrate fauna, they have a highly distinctive fauna of land snails that are endemic at the family or subfamily level.

Designation of land snail "realms, regions, and provinces" is premature, but indications of the general patterns are given.

INTRODUCTION

THE tidal wave of experimental studies on the cellular and subcellular levels, progressing from experimental physiology to biochemistry and molecular biology, which some now equate with "biology," has produced a generation of young biologists who are profoundly ignorant of such "classical" disciplines as systematics and zoogeography. I beg indulgence from my older and more classically oriented colleagues, but through sad experience realize that background information must be presented for the education of our experimental colleagues.

Zoogeography, the study of animal distribution, can be and has been approached from four different ways: (1) geographical zoology, or the distribution of particular groups of animals; (2) zoological geography, or the distribution of many animal groups in a particular area; (3) ecological animal geography, or the analysis of ecologic factors affecting animal distribution; and (4) historical animal geography, which attempts to determine the migration patterns of faunas through time and to study the origin and spread of particular animal groups. Each approach is useful and necessary, and often combinations of approaches will yield quite valuable insights. All levels of zoogeography are dependent upon systematic and faunistic data. Unless the distribution of the animals considered is well and accurately determined, the zoogeographic conclusions will be faulty at best, or erroneous. If the systematic relationships of the organisms are incompletely known, or the phylogenetic affinities incorrectly determined, then once more the zoogeographic results will be of little value.

It is no accident that the classical zoogeographic realms, regions and provinces have been determined through study of birds and mammals. These organisms are conspicuous and comparatively few in number, with only about 3,500 mammalian and 8,600 avian species. Quite understandably anthropomorphism has focused an inordinant amount of attention on their distribution and systematics. There probably have been at least 60 systematic mammalogists and ornithologists active in the last 100 years for every systematic malacologist. Thus, the mollusks, with about 100,000 species, are much more poorly known in terms of basic distribution and systematic affinities than are the over-studied birds and mammals. While students of vertebrate distribution now are able to focus on the dynamics of current distributions and have accumulated considerable data on distributions in past geological eras, the basic tasks of compiling ranges and determining systematic affinities remain to be done for mollusks and all other "invertebrate" taxa.

The classic exposition of major zoogeographic regions was by P. L. Sclater (1858), who divided the world into six major realms—Ethiopian, Nearctic, Palearctic, Neotropical, Australian, Oriental—based upon the distribution of land birds. Sclater's paper appeared before Darwin's work on evolution, and he viewed these areas as separate centers of creation. This in no way diminishes their overall utility in recognizing the basic pattern of higher vertebrate distribution. A. R. Wallace (1876) in his two-volume work, *The Geographical Distribution of Animals*, synthesized tremendous quantities of information on bird and mammal ranges. It was not until the appearance of Darlington (1957) that Wallace's study was superseded.

Between Wallace, who dealt with the present distribution of birds and mammals, and Darlington, who attempted to evaluate the average pattern of vertebrate distribution and to discuss the major faunal movements of vertebrates, zoogeographers have focused attention on several problems of a fundamental nature. Perhaps the major areas of concern have been with:

- (1) elucidation of faunal areas and determination of boundaries for these areas;
- (2) concern with the basic geologic stability or instability of land masses through time;
- (3) working out the history of major taxonomic units;
- (4) analyzing the ecologic factors determining zoogeographic distribution; and
- (5) determining the directional movements of faunal migrations.

Early attempts at recognition of faunal boundaries and areas consisted of hand compiled lists of species and distributional limits. Modern use of computers has resulted in such studies as that of Simpson (1964) in which the presence or absence of each North American mammal species was noted for quadrates 150 miles on each side, with species density contours plotted for all areas of North America.

Certain areas were recognized quite early as being zones of transition between major faunistic units. For example, a huge literature exists concerning the importance and/or reality of Wallace's and Weber's lines in separating the Oriental and Australian faunas (see Mayr, 1944). The area between Java and New Guinea is one of rapidly shifting faunal dominance, and attempts to delineate exact lines of demarcation are not particularly fruitful or important. The evolving and changing nature of faunas now is universally recognized and in the last 30 years emphasis has shifted to other features.

Of basic importance to any zoogeographical theory concerning the origin and spread of faunas is the stability or instability of the major land areas through geological history and the extent to which dry land vs. overseas dispersal is required of organisms. No branch of zoogeography has been more subject to shifting fads and fancies. In the early part of this century, the imaginary building of narrow land bridges, which extended thousands of miles across ocean deeps, was a favored activity. Such a bridge might be "required" to explain the presence of perhaps one or two small insects

or tiny land snails on remote oceanic islands. Typical of this genre, but far from being the most extreme, was the proposal of Meyrick (1926, p. 271) who explained the origin of eight Microlepidoptera on Rapa by having a land bridge extend from Fiji to Rapa. In his own words, "A rise of 12,000 feet in the sea-bottom of the South Pacific is required to show these results, but entertain no doubt that such an elevation must have existed since the Eocene period, because it is absolutely the only explanation possible." There was literally no portion of the ocean which had not been repeatedly bridged by proposed land corridors of some zoogeographer. In sharp reaction to this, during the 1930's and 1940's it became suspect for a zoogeographer to suggest changes in land area exceeding the fluctuation of the oceans related to the maximum Pleistocene glaciation.

A major school of zoogeographers considers that the present land masses have been stabilized in their present outline and position throughout the spread of currently extant animal groups. Dispersal to islands was explained through the *dei ex machina* of cyclonic winds and accidental carriage on the feathers of migratory or sea-birds. An occasional land bridge across Bering Strait; one between New Guinea and Australia; and repetitive openings and closings of the Panama land bridge were all that was required for zoogeographic proposals.

A second major school, in vogue during the 1920's and revived in full flower during the late 1950's and 1960's, was the idea of continental drift. This assumes that the major continents were in the past grouped together as one continuous land mass that subsequently broke up into the large continental fragments which slowly, or rapidly, depending on the zoogeographer, drifted to their present position. Considerable geological evidence, particularly coming from palaeomagnetism, indicates that quite possibly the continents were joined together at one time. However, I know of no animal distributions that are more simply explained by continental drift than by stability of continental mass. If drift occurred, then it must have been at a time prior to the movements of any extant families.

Particularly in respect to the mammals, where there is an abundant fossil record, we know a great deal about the history of current biotas. In a delightful book, Simpson (1953) has summarized the major features of historical biogeography as it applies to mammals. For groups in which the fossil record is absent or uninformative, data on past movements must be deduced from a combination of phylogenetic and distributional data. The tremendous effects of ecology on animal distributions have been reviewed by Hesse, Allee, and Schmidt (1951). They are not further considered in this report.

A basic problem continues to be the question of directional faunal movements. Biogeographers traditionally have been divided into two schools. Those resident in Europe and North America, perhaps subconsciously looking "downward" at the distended Southern Hemisphere on their Mercator map projections, have almost universally postulated spread from the Holarctic land mass into the Southern Continents. Biogeographers resident in South America, South Africa, Australia, and New Zealand, recognizing the many faunal elements they have in common, and possessing both a "polar" viewpoint and a sense of isolation, have tended to hypothesize a center of origin and spread from Antarctica into South America, South Africa, and Australia. This subject will be discussed later.

Recent years have seen two new important trends in study. A program of airplane and ship nettings sponsored through the efforts of J. Linsley Gressitt and reported on in various volumes of *Pacific Insects*, issued by the B. P. Bishop Museum, has provided extremely important data concerning the actuality and relative frequency of overseas dispersal in relation to arthropods. Secondly, several individuals have begun to focus on the dynamics of dispersal, colonization, and extinction of individual species in small faunal units. The resulting science of experimental biogeography now is attempting to predict faunal compositions, colonization rates, and to evolve generalized laws of biogeography. A recent summary by MacArthur and Wilson (1967) should be required reading for every potential biogeographer.

MOLLUSCAN DISTRIBUTION

As indicated earlier, the basic systematic and distributional data needed for zoogeographic surveys of mollusks are fragmentary. Any collection from south-east Asia, for example, will provide range extensions of several hundred miles and enable revisions of systematic position for many of the known species. This holds true for most areas of the world, except for much of Europe and North America, north of Mexico. I am currently finishing a revision of the Pacific Island Endodontid land snails. Ignoring Hawaii, in the larger subfamily there are 155 species level taxa. Of these, 103 were previously undescribed. In regard to particular areas, only one of 25 Endodontids found on Rapa Island was previously known and only two of 24 found on Mangareva. The classification of these species was equally poorly understood. Only five of 23 genera had been named previously, and only two of these are being used with their historic limits.

Not only are most areas incompletely explored, but the systematic work has been done from quite different philosophic viewpoints. The Australian land snail fauna has been reviewed by Iredale (1933, 1937 *a*, 1937 *b*, 1938). His concept of genera and families is so much narrower than that utilized by most other malacologists that direct faunistic comparisons on the basis of his publications are impossible (Solem, 1959, pp. 26-28). In many cases reduction of his families to generic level, and equation of his genera with superspecies is necessary for comparative studies.

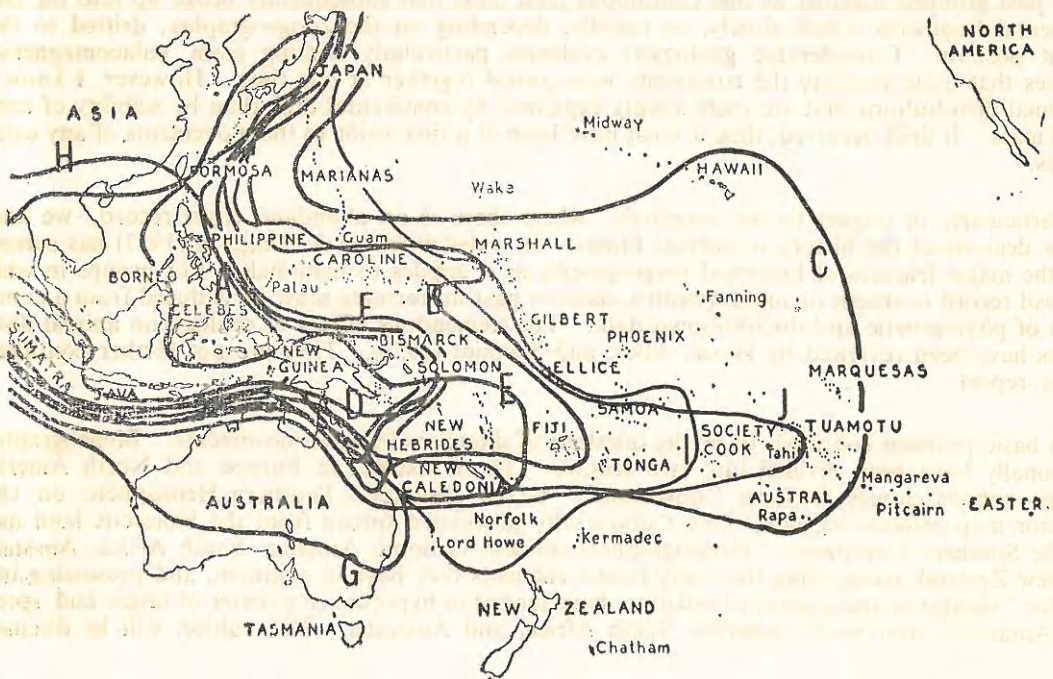


FIG. 1. Distributional limits of land snail families in Pacific region. Adapted from Solem (1959).

The families are:

- | | |
|---|---------------------|
| A, Clausiliidae; | F, Cyclophoridae; |
| B, Pupinidae; | G, Camaenidae; |
| C, Helicinidae; | H, Rathouisiidae; |
| D, larger Helicarionidae with normal shell development; | I, Diplommatinidae; |
| E, Enidae; | J, Trochomorphidae. |

Several generations of collecting and faunistic reviews combined with an equal amount of systematic revisionary work will be required before a world land snail geography can be written. Despite this, sufficient information does exist to answer a few questions. I propose to deal with two problems in this report. First, to contrast the land snail distribution in the areas from South-east Asia to the Solomon Islands with that of the terrestrial vertebrates. Secondly, to summarize what data currently available on some southern hemisphere relict land snail families tells us concerning the patterns and directions of land snail migrations.

WALLACE'S LINE AND LAND SNAILS

Although the terrestrial vertebrates show a sharp to slow transition between the Oriental and Australian faunas, in the area known as "Wallacea" no such transition is evident for vascular plants, insects, and land snails. Fairly comprehensive treatment of the general patterns of land snail distribution on the family level in this area is given in Solem (1959). Here it is proposed merely to summarize that data (Fig. 1), as slightly modified by more recent studies. It is obvious that on the family level, there is a single fauna of land snails that extends from South-east Asia to New Guinea and often on to the Solomon Islands and the tropical coast of Queensland. While some groups are also present on the islands of Polynesia and Micronesia, these consist of the smaller sized species or groups that are arboreal in habitat and therefore more apt to be transported accidentally. The larger Helicariionidae, Cyclophoridae, Camaenidae, and Clausiliidae, plus the carnivorous slugs belonging to the Rathouisiidae, are limited to the core area, except for the desert radiations of camaenids found in Australia. Departures from this pattern occur primarily on the generic level. The camaenid genus *Amphidromus* of South-east Asia to the Tenimber Islands is replaced by the *Papuina* complex in the Aru Islands, New Guinea, coastal Queensland, and the Bismarck-Solomon axis (Solem, 1959, p. 274, Fig. 20). Similarly, the helicinid genera *Geophorus* and *Palaeohelicina* (Solem, *op. cit.*, p. 277) replace each other in approximately equivalent fashion.

Very few land snail families depart from this pattern (Fig. 2). The Strobilopsidae are primarily a North American taxon with relict forms being found in the Philippines, Japan, Korea, Northern China, and Western New Guinea. The Streptaxidae are common through much of peninsular South-east Asia, Japan, Formosa, the Philippines, and Borneo, with one or two representatives reaching the Celebes. They are absent from Sumatra, Java, and the rest of Indonesia and New Guinea except for an introduced species. The Polygyracean relict family Corillidae is restricted to the mainland of South-east Asia. Figure 2 gives the distribution of two additional families, the Partulidae (D) which are restricted to the high islands of Micronesia and Polynesia with an apparently secondary invasion into the fringe of Melanesia, and the Poteriidae, found in parts of Micronesia, Melanesia, and Polynesia with their relatives being restricted to tropical Central and South America.

Many students of vertebrate distribution have either been unwilling to accept the reality of such differences, or have failed to appreciate the simple explanation for this phenomenon.

The present distribution of any animal group is the result of a historical process operating over a greater or lesser period of time. There have been terrestrial organisms since the Devonian period. With the imperfection of the fossil record, we have only the most fragmentary information concerning zoogeography of past geological eras. As we approach the present, the record becomes more complete. In regard to the mammals, which are a product of mid to late Tertiary radiations, the record is relatively comprehensive. Despite obvious limitations and inadequacies, the fossil record does show that (1) there has been a definite history of rise, dominance, decline, and extinction of animal groups; (2) many types of organisms abundant today were at one time absent or rare; and (3) some creatures that are rare today formerly were common. By the Upper Carboniferous and Permian there is evidence of a rich fauna of insects, land snails, scorpions, spiders, phalangids, and mites. Not only were these groups established, but they had diversified considerably. Pennsylvanian strata contain at least three families of land snails, and the Permian beds yield 17 orders of insects, 10 of which still exist today. The origins of these invertebrate forms must have considerably

predated the Permian and Carboniferous. Most probably the first invertebrates made the transition from freshwater to land in the Early or Middle Devonian.

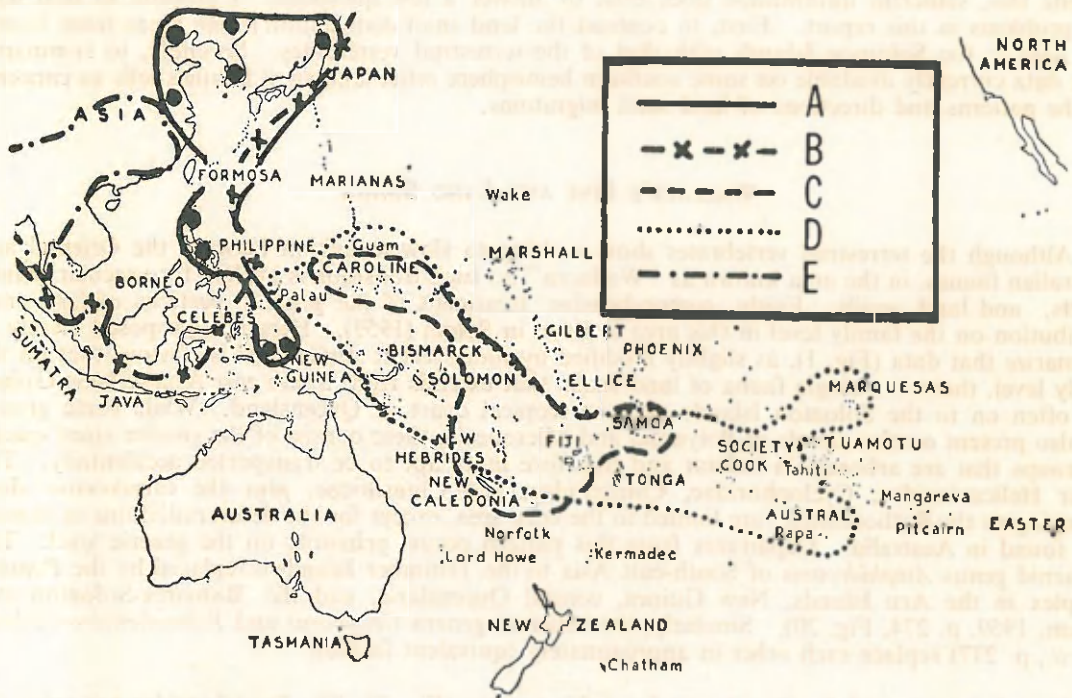


FIG. 2. Land snail families that do not conform to the basic pattern. Data from Solem (1959) and later studies. The families are:

A, Strobilopsidae;
B, Streptexidae;
C, Poteridae;

D, Partulidae;
E, Corillidae.

The basic radiation patterns of the higher vertebrates are approximately as follows: the giant amphibians became dominant in the Permian and declined at the end of the same era; reptiles had their first appearance in the late Carboniferous, an early radiation in the Permian and then produced the explosive evolution of the dinosaurs in the Mesozoic. Some time in the late Triassic, small mammals evolved from the Therapsid reptiles, with opossum-like marsupials and primitive placental mammals appearing in the late Cretaceous. Birds evolved in the Jurassic and had their major radiation in the Cretaceous. During the latter period there was the dramatic extinction of the dinosaurs. The Tertiary is characterized by the tremendous radiation of mammals and eventual evolution and rise to dominance of man.

These historical facts are clearly reflected in the differing patterns of current vertebrate distribution. When viewed at the family level, although there is an "average pattern of vertebrate distribution" (Darlington, 1957), the basic type of distribution is not unitary. If we exclude the flying mammals (bats), only a single family of recent mammals shows a disjunctive distribution—the tapirs which are found in South-west Asia and in Central and South America. Fossil tapirs still lived in Europe, Asia, and North America in the Pleistocene, so that this disjunctive pattern is of very recent origin. Otherwise families of mammals show continuous distribution within or between major zoogeographic realms. The essentially tropical nature of birds is emphasized by their distribution patterns, with numerous families showing Pantropical distribution, but are absent or sparsely represented in the temperate regions. Similar disjunctive patterns are extremely common in reptilian

families, and in addition they show a few striking examples of relict occurrences. For example, the only Old World iguanas are found in Fiji and Madagascar, while the remarkable Tuatara of New Zealand is the only living member of a major group that was widely distributed in late Mesozoic times, but are absent from fossil beds later than the Lower Cretaceous, about 135,000,000 years ago. When amphibian distribution is analyzed, there are even more striking observations, such as the New Zealand frog *Leiopelma*, whose only relative is in the Pacific North-west of the United States (*Ascaphus*). Presumably the leiopelmids were widely distributed in the past, but now survive only as these cold temperate relicts.

Since the major radiation of these groups occurred at different times in the geologic span, their initial and major radiations did not coincide. While distributional radiations occurring during the last part of the geologic time scale would be the same, barriers and land bridges present in past eras were undoubtedly different. Thus, the Oriental nature of the New Guinea plant, insect, and land snail fauna probably reflects conditions existing in the Mesozoic. Presumably at this time there was essentially dry land connections between South-east Asia and Australia via New Guinea. Long-range climatic barriers in Australia undoubtedly prevented most of these forms moving into Australia but there probably was a Mesozoic "highway" enabling colonization. During the Tertiary, the geologic history of Indonesia has been highly complex, with numerous elevations and subsidences occurring. Hence forms of comparatively late evolution and mid to late Tertiary radiations have had to try and filter across various water gaps. Thus the dramatic change in mammal and bird distributions from Java to New Guinea.

The probable nature of this historic difference has been whimsically summarised in Figs. 3 and 4, with due apologies to George Gaylord Simpson, whose earlier efforts inspired these diagrams.

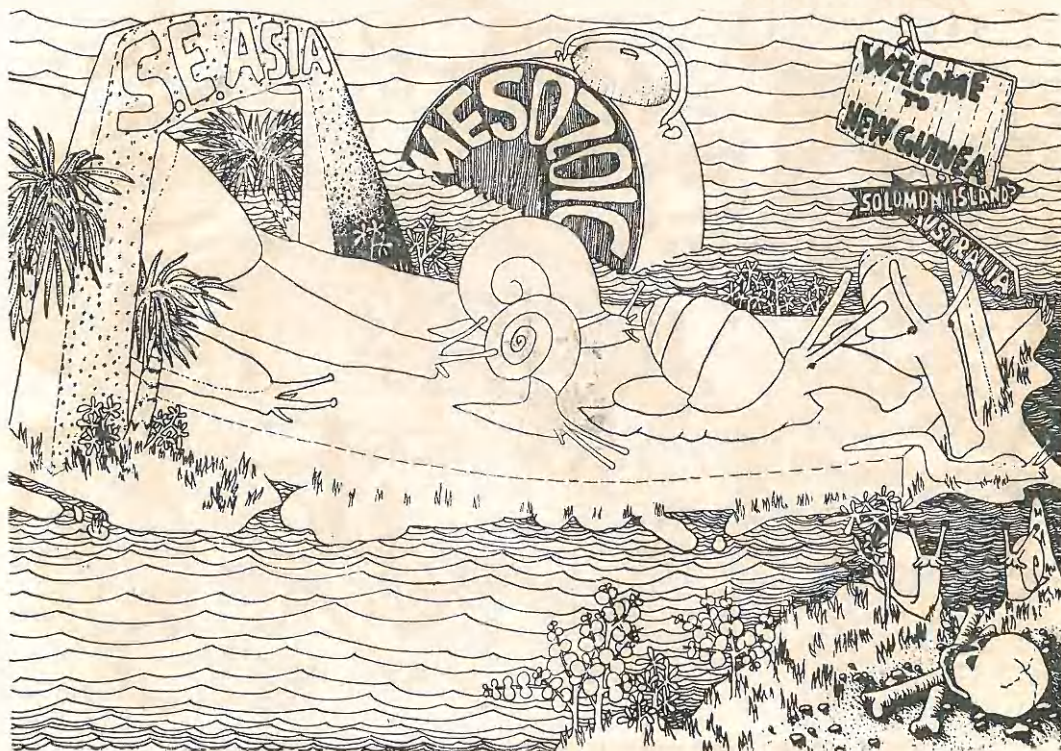


FIG. 3. South-east Asia to Australia dispersal in the Mesozoic. A cartoon by Margaret Ann Moran,

Obviously this is an enormous simplification of incredibly complex historical events, yet a basic radiation of land snails, insects, and plants through the Indonesian Archipelago to New Guinea and the Solomon Islands during the late Mesozoic does explain the vast difference from higher vertebrate distribution, which must have occurred in the presence of water barriers during the late Tertiary.

DIRECTION OF LAND SNAIL MIGRATIONS

The question of Holarctic *vs.* Antarctic origins and distributions have been outlined above. Here it is proposed to review in some detail the scanty information available concerning two superfamilies of land snails—Bulimulacea and Acavacea—that have figured prominently in nearly all Antarctic “origins” and “dispersals”.

Before discussing these taxa, it is necessary to emphasize what is the typical dispersal pattern shown by a newly evolved species or group of species. While every taxonomist can point to departures from this pattern, nevertheless it is the most frequently encountered story and less difficulties in interpretation are encountered by use of this axiom. When a species, consisting of many populations, becomes differentiated and is better adapted to conditions than neighbouring species, then it will begin to expand and sooner or later replace the less effective competitors. Then populations on the periphery of the range will be competing against less well-adapted forms and are therefore under no particular selective pressure themselves. In contrast, as the population density builds up near the original center of origin, there will be intraspecific competition which can provide a rela-



FIG. 4. Present higher vertebrate distribution, South-east Asia to Australia, A sociological impression by Margaret Ann Moran.

tively high selection pressure for greater efficiency in use of environmental resources. When continued, this will in time lead to specific level separation. The situation will thus come to resemble the model in Fig. 5a. Given time and sufficient vagility, the original Form "A" will pass over short water or montane barriers, expanding to limits beyond which it cannot pass. If subsequent widening or heightening of intermediate barriers occur, then populations but little changed from the original Form "A" will be preserved around the periphery of distribution (Fig. 5b). Under little selection pressure for change, these populations may closely resemble the primitive state of organization.

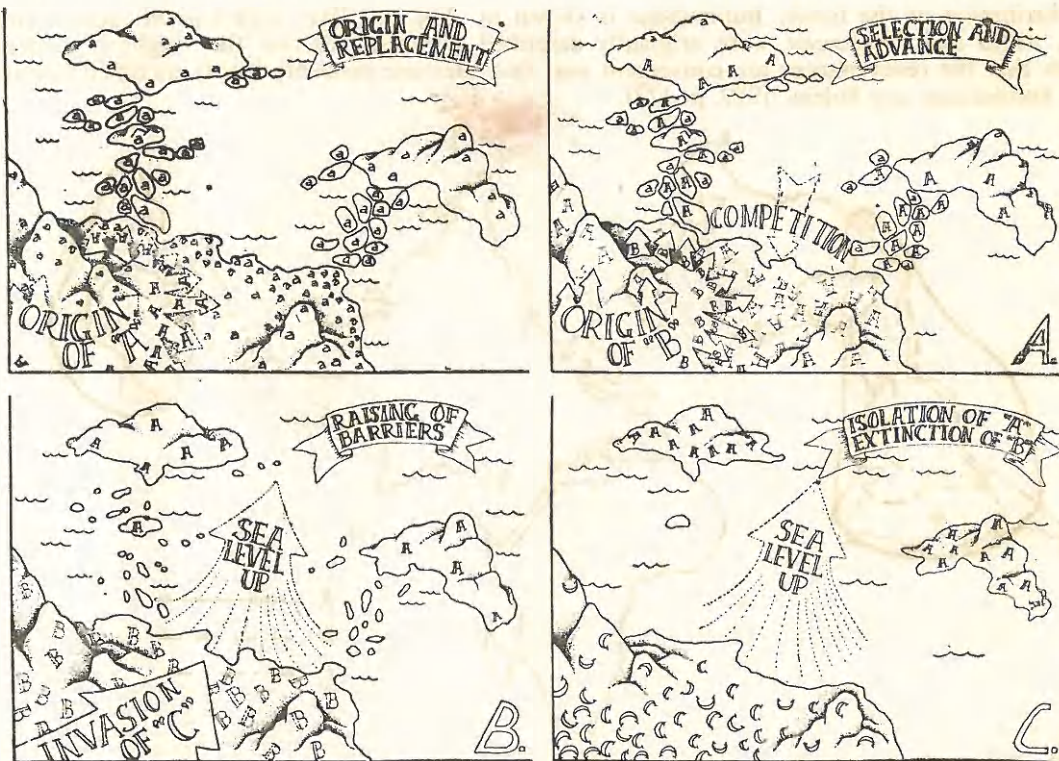


FIG. 5. Hypothetical pattern of origin, dispersal, differentiation, replacement and isolation resulting in a disjunctive relict distribution on islands. Form "A" evolved from "a" is more efficient.

Form "B" evolved from "A" under conditions of crowding and is more efficient in use of resource space, but has a lower vagility (= ability to cross barriers). Form "C" is an unrelated invader from outside the region, with great efficiency and low vagility.

Given sufficient time, forms derived in the center of evolution, such as Form "B", can, and often have been, replaced by totally unrelated organisms that are represented in Fig. 5c as Form "C". The current distributional pattern will show Form "A" limited to two isolated areas with their replacement, Form "C", occupying most of their original range. Without knowledge of their prior history, most zoogeographers would interpret this distributional pattern as Form "A" having originated in one of the areas and having been transported directly to the other, whereas historical evidence shows that they were independently derived.

Fortunately, most relict groups of organisms have a more complex and phylogenetically restricted present pattern. Under these circumstances, by determining generalized and derived taxa,

observing their distributional patterns, and assuming, unless other evidence is present, that the most primitive forms lie on the far limit of distribution with the derived taxa occurring nearer the center of origin, it is possible to deduce the probable direction of migration and areas of origin.

Although phylogenetic data on the families considered below is inadequate from the viewpoint of modern systematics, nevertheless indications are clear enough to give an extremely high probability to their Holarctic origin and subsequent spread into the Southern Hemisphere, although today they are primarily restricted to that region.

Distribution of the family Bulimulidae is shown in Fig. 6. Two little-known genera from Africa, *Aillya* and *Prestonella*, were originally described as bulimulids, but the weight of evidence suggests that the resemblances are convergent and that they are probably highly modified relatives of the Succineidae (see Solem, 1959, p. 123).



FIG. 6. Present distributional limits of the Bulimulidae. Subfamilies are: A, Bulimulinae; B, Orthaliinae; C, Odontostominae.

Probably 1,300 species of bulimulids have been described. About 110 of these are found in the Pacific area, with the remainder restricted to Neotropica with only a very few forms extending into North America. There is abundant fossil record of South American bulimulids and forms probably referable to that group have been recorded from the Eocene and Pliocene of the Rocky Mountain region. No fossils that are unquestionably bulimulid and of greater than Pliocene age are known from the Pacific region. Some controversy remains concerning major divisions within the family. Iredale (1937 a, 1944) placed the Australian-Tasmanian genus *Bothriembryon* in one family, *Placostylus* and its relatives into a second family, both of which he considered separate from the South American bulimulids. Pilsbry (1946), on the basis of dissecting specialized Solomon Island *Placostylus*, gave that group subfamily recognition. My own dissections of several *Placostylus* (unpublished data) indicate that there are no significant anatomical differences between the Austral-Melanesian bulimulids and the more generalized South American taxa. I do not accept Iredale's family level separation.

While there is no doubt that the family Urocoptidae is distinguished from the bulimulids, how to rank the major types of South American bulimulids is uncertain. Zilch (1960, pp. 473-520)

recognized the Odontostominae and Orthalicinae as separate families. Both seem to be taxa derived from the more generalized Bulimulinae. What little is known of their anatomy suggests to me that their separation is of subfamily, rather than family nature, but this is a matter of personal opinion.

In South America no bulimulids have been reported south of 46° south latitude in Chile or approximately 39° south near the Atlantic coast of Argentina. The greatest degree of generic diversification is present in Brazil and the Andean region, with a second center of diversity in Northern Central America. Very few species extend into the United States, with three species of the genus *Bulimulus* accounting for nearly all of the North American map range. A few *Drymaeus* occur in Florida. Of the derived taxa, the seemingly less specialized Orthalicinae extends from Florida and Central Mexico south along the Andean chain to Southern Peru and Bolivia, also reaching most of the Amazonian and Orinoco basins. The greatest differentiation is found in the Andean area from Colombia to Southern Peru. A few species of the more specialized Odontostominae occur north of the Amazon, even reaching coastal Venezuela, but they are primarily a group of Southern Brazil and Argentina.

No clear pattern of phylogeny is seen among the South American taxa with the fragmentary anatomical data currently available.

Data on the phylogenetic hierarchy found in the Pacific area bulimulids is presented by Solem (1959, pp. 123-147). Subsequent dissections of many additional species have confirmed basic relationships indicated in that study. The data are insufficient to allow formal taxonomic revisions to be published. Quite surprisingly, on the basis of both anatomy and shell structure the generalized taxa are the Australian genus *Bothriembryon* and the New Hebridean *Diplomorpha*. Both genera show no important qualitative differences from the more generalized South American taxa. They belong unquestionably in the subfamily Bulimulinae. Anatomical variations within *Placostylus* are simple in kind, but complex in distribution. The species from Lord Howe Island, the New Hebrides, Santa Cruz Island, and New Zealand have basically similar anatomical structures. Too few have been dissected to enable meaningful assignment of subgeneric names but they represent the same level of evolution. Species of *Placostylus* from the Loyalty Islands and New Caledonia have altered anatomic structures and seem to be intermediate between the generalized taxa mentioned above, and the very specialized species from the Solomon Islands and Fiji. In the Solomon Islands, *Placostylus* ranges through most of the Archipelago south of Bougainville, while in Fiji the genus is limited to the main groups of islands and does not reach the Lau Archipelago. The Solomon Islands and Fiji species are at a higher level of complexity than the New Caledonian taxa. Again, too few species have been dissected to enable determination of exact relationships.

The basic indications of these relationships are summarized in Fig. 7. Obviously this is a complicated picture and one which is not amenable to simple interpretation. In an early paper, Hedley (1892) hypothesized a "Melanesian continent" to explain the current distribution of *Placostylus*. This was before the relationship of *Bothriembryon* to the bulimulids was known, and before *Diplomorpha* had been removed from the Partulidae. Hedley suggested that *Placostylus* had been derived from the New Guinea region. In subsequent studies Hedley (1899, pp. 398-399) reversed his thinking and derived *Placostylus* via an Antarctic dispersal route. Bulimulids are known as fossils in the South American Paleocene, and almost certainly date from the same period in the Australian-New Zealand area. On the basis of fragmentary phylogenetic data, I would suggest an origin from the Holarctic land mass through the Indonesian Archipelago, with essentially three distinguishable waves of migration deducible. This is summarized in Fig. 8. The initial migratory wave included the ancestors of *Bothriembryon* and *Diplomorpha*. The former remained isolated in the south-western part of Australia, with a secondary radiation spreading northward in Australia and eastward into Tasmania occurring at a later time. Whether the New Hebridean *Placostylus* are direct derivatives from *Diplomorpha*, or whether they represent a secondary invasion from New Caledonia, cannot be determined at present. The second alternative is indicated in Fig. 8, since accidental spread from a New Caledonian base to Lord Howe Island and the Northern tip of New

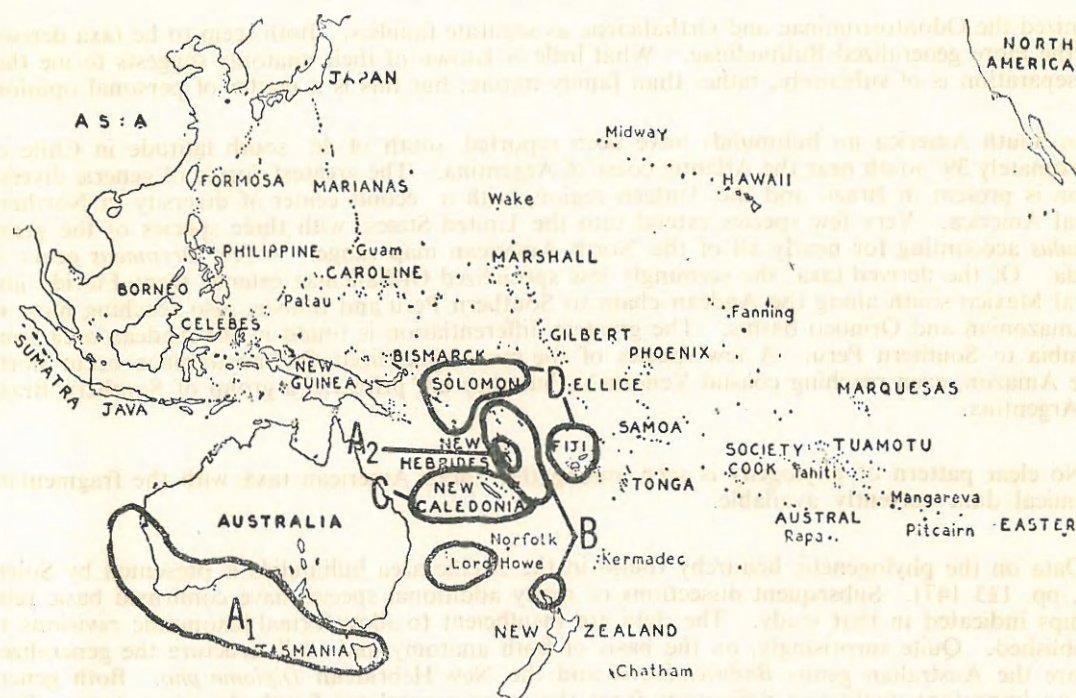


FIG. 7. Present distribution of Pacific area Bulimulinae. Taxa are: A₁—*Bothriembryon*; A₂—*Diplo-*
morpha; B—generalized *Placostylus*; C—*Placostylus* with some specializations; D—specialized
Placostylus.



FIG. 8. Hypothesized migration patterns of Pacific area Bulimulinae. Original migration is "1";
 secondary spread of *Bothriembryon* and *Placostylus* is "2"; derivation of specialized Fijian and
 Solomon Island *Placostylus* ("3") is of unknown direction and uncertain place of origin.

Zealand from the New Caledonian area seems most probable. The third major wave of colonization, coming probably from the New Guinea area, resulted in the advanced taxa reaching the Solomon Islands and Fiji. While geographic relationships would suggest a dispersal from the Santa-Cruz-New Hebrides into the Solomon Islands and Fiji independently, I suspect that a more complex derivation is required. Lack of space in Fig. 8 has resulted in an awkward placing of directional movement for this third colonization wave.

The above suggestions of origin and dispersal is admittedly speculative. However, the peripheral distribution of Pacific bulimulids in relation to the main Australian-New Guinea land mass is quite clear. Trying to derive this from an Antarctic origin would be exceedingly difficult.

Although exceedingly diverse in shell form and shape, the 16 genera grouped as the superfamily Acavacea or family Acavidae agree in numerous features of shell and anatomy. Early studies by Semper and Hedley were utilized by Pilsbry (1895, XXXII), together with dissection of new materials, to recognize a subfamily Acavinae. At this time, the South American genera, *Strophocheilus* and *Gonyostomus*, were considered bulimulids. Slightly later, Pilsbry (1900, p. 564) added the *Strophocheilinae* as a subfamily of the Acavidae. Comparatively little anatomical data have been added since this time. By far the most important paper is that of Watson in Connolly (1915) who dissected a number of South African species and analyzed the phylogenetic relationships of the Acavids. Randles (1900) dissected the Ceylonese genus *Acavus*; von Ihering (1912) gave some anatomical details on two genera that may be Acavids, but whose systematic position remains uncertain (*Macrocyelis* and *Solaropsis*); and Hylton-Scott (1939) studied *Strophocheilus oblongus lorentzianus*.

The data contained in the above papers are sufficient to indicate relative complexity in organization of the taxa, and to indicate direction of phylogeny within each area, with the exception of South America. Much of the following is condensed from Watson's excellent account. Whether the major geographic groupings are considered subfamilies or families is a matter of personal opinion, particularly until many features of the Australian and Madagascaren taxa can be examined.

A SYNOPSIS OF CLASSIFICATION

Family ACAVIDAE

Subfamily STROPHOCHEILINAE (South America)

Strophocheilus Spix, 1827

Gonyostomus Beck, 1837

Subfamily DORCASIINAE (South Africa)

Trigonephrus Pilsbry, 1905

Tulbaghinia Melville and Ponsonby, 1898

Dorcasia Gray, 1838

Subfamily CARYODINAE

Caryodes Albers, 1850 Tasmania

Anoglypta Martens, 1869 "

Hedleyella Iredale, 1914 (= *Panda* Martens, 1860 not van Heyden, 1826)

+ *Pygmipanda*, *Brazieresta*, and *Pandofella* Iredale, 1933

Pedinogyra Albers, 1860

Subfamily ACAVINAE

Clavator Martens, 1860 Madagascar

Eurystyla Ancey, 1887 "

Helicophanta Férussac, 1821 "

Ampelita Beck, 1837

Stylodon Beck, 1837 Seychelles

Acavus Montfort, 1810 Ceylon

Oligospira Ancey, 1887

The preceding review of phylogenetic trends within the Bulimulacea and Acavidae is not intended as a "formal proof" of derivation from the Holarctic land mass. These are the families that have been cited most frequently as offering proof of an Antarctic origin and dispersal. I have attempted to show that known phylogenetic trends within these groups can be interpreted more logically as indicating a northern origin. Both groups are of unquestionable antiquity, with Eocene fossils recorded. The Achatinidae of Africa and Camaenidae of South-east Asia have replaced the acavids in these areas, but in South America the camaenids are as yet a minor, although successful, constituent of the fauna (Solem, 1966). They are much more highly developed in the West Indies (Wurtz, 1955) but the long persistence of the Panama water gap denied them access to South America until comparatively recent times.

Other families that much more strongly indicate northern origin and dispersal into the southern lands are the Rhytididae and the "Endodontidae", which I am currently revising.

ACKNOWLEDGEMENTS

Preliminary systematic and faunistic studies which have contributed to the above conclusions were accomplished with the aid of National Science Foundation grants G-16419 and GB-3384. The illustrations have been prepared with the assistance of NSF grant GB-6779. I am deeply indebted to Mrs. Jane Calvin for the preparation of Figs. 1, 2, 6-10; and to Margaret Ann Moran for transferring to paper so successfully my ideas expressed in Figs. 3, 4, and 5. Manuscript preparation by Mrs. Lynda Hanke enabled completion of this paper in time for presentation at the symposium.

LITERATURE CITED

- BOETTIGER, C. R. 1936. Die Verbreitung der Land Schneckenfamilie "Acavidae" und ihre Bedeutung. *Compt. Rend. XII Congr. Internat'l. Zool., Lisbon*, : pp. 1033-1050.
- CONNOLLY, M. 1915. Notes on South African Mollusca. III. A monograph of the Dorcasinae. *Ann. S. African Mus.*, 13 (4): 120-192.
- DARLINGTON, P. J. 1957. *Zoogeography*. Wiley & Sons, New York, 675 pp.
- GERMAIN, L. 1924. La Distribution Géographique et L'origine des Mollusques de la Famille des Acavides. *Comptes Rendus de Congrès des Sociétés Savantes de Paris et des Départements*. Section des Sciences, 1924: 254-269.
- HEDLEY, CHARLES 1892. The range of *Placostylus*; A study in ancient geography. *Proc. Linn. Soc. New South Wales*, 7 (2): 335-339.
- 1899. A zoogeographic Scheme for the Mid-Pacific. *Ibid.*, 24: 391-417.
- HESSE, R., W. C. ALLEE AND K. P. SCHMIDT 1951. *Ecological Animal Zoogeography*. Wiley & Sons, New York, 715 pp.
- HYLTON-SCOTT, M. I. 1939. Estudio Anatómico del "*Borus Strophocheilus lorentziannus*". *Revista del Museo de la Plata, N.S., Zool.*, 1: 217-278.
- IREDALE, T. 1933. Systematic notes on Australian land shells. *Rec. Austr. Mus.*, 19 (1): 37-59.
- 1937 a. A basic list of the land Mollusca of Australia. *Austr. Zool.*, 8 (4): 287-333.
- 1937 b. A basic list of the land Mollusca of Australia. Part II. *Ibid.*, 9 (1): 1-39.
- 1938. A basic list of the land Mollusca of Australia. Part III. *Ibid.*, 9 (2): 83-124.
- 1944. The land Mollusca of Lord Howe Island. *Ibid.*, 10 (3): 299-334.
- MACARTHUR, R. H. AND E. O. WILSON 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, 203 pp.
- MAYR, E. 1944. Wallace's line in light of recent zoogeographic studies. *Quart. Rev. Biol.*, 19 (1): 1-14.
- MEYRICK, E. 1926. On Micro-Lepidoptera from the Galapagos Islands and Rapa. *Trans. Ent. Soc. London*, 74: 269-278.

- PILSBRY, H. A. 1895. *Manual of Conchology*, 2nd ser., 9: i-xlviii.
- . 1900. On the zoological position of *Partula* and *Achatinella*. *Proc. Acad. Nat. Sci. Philadelphia*, 1900: 561-581.
- . 1946. Notes on the anatomy of Australian and Galapagos Bulimulidae. *Notulae Naturae, Acad. Nat. Sci. Phila.*, 168: 1-4.
- RANDLES, W. B. 1900. On the anatomy of the genus *Acavus*. *Proc. Malac. Soc. London*, 9: 103-113.
- SCLATER, P. L. 1858. On the general geographical distribution of the members of the Class Aves. *J. Proc. Linn. Soc. (London), Zool.*, 2: 130-145.
- SIMPSON, G. G. 1953. *Evolution and Zoogeography*. Oregon State System of Higher Education. 64 pp.
- . 1964. Species density of North American Recent Mammals. *Systematic Zoology*, 13 (2): 57-73.
- SOLEM, A. 1959. Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana: Zoology*, 43: 1-359.
- . 1966. The Neotropical land snail genera *Labyrinthus* and *Isomeria* (Pulmonata, Camaenidae). *Ibid.*, 50: 1-226.
- VON IHERING, H. 1912. Analyse der Süd Amerikanischen Heliceen. *Jour. Acad. Nat. Sci., Philadelphia*, 2nd ser., 15: 473-500.
- WALLACE, A. R. 1876. *The Geographical Distribution of Animals*. Macmillan, London, 2 Vols.
- WURTZ, C. B. 1955. The American Camaenidae. *Proc. Acad. Nat. Sci., Philadelphia*, 107: 99-143.
- ZILCH, A. 1960. *Euthyneura* in *Handbuch der Paläozoologie*, (6), 2 (3): 401-600.

- Parsons, H. A. 1905. *Manual of Conchology*, 2nd ser., #1: 1-210.
- 1906. On the zoological position of Patella and Acanthina. *Proc. Acad. Nat. Sci. Philadelphia*, 1906: 361-381.
- 1916. Notes on the anatomy of Australian and Galesburg Helminthodes. *National Museum, Acad. Nat. Sci. Phila.*, 1916: 1-4.
- Randall, W. B. 1900. On the anatomy of the genus *Stenot*. *Proc. Acad. Nat. Sci. Philadelphia*, 1900: 103-113.
- Snyder, F. L. 1918. On the general geographical distribution of the members of the Class Aves. *A. Proc. Acad. Nat. Sci. Philadelphia*, 1918: 130-142.
- Snyder, G. C. 1921. *Evolution and Zoogeography*. Oregon State System of Higher Education, 64 pp.
- 1924. Species density of North American Recent Mammals. *American Zoology*, 13(2): 77-79.
- Snyder, A. 1928. Systematics and zoogeography of the land and freshwater Molluscs of the New World. *Evolution*, 2: 1-32.
- 1930. The Neotropical land and small genus *Lophoceros* and *Lophoceros* (Mammalia, Cervidae). *Mamm. Monographs*, 1: 1-32.
- Von Ihering, H. 1912. Analyse der Süd-Amerikanischen Helixen. *Ann. Acad. Nat. Sci. Philadelphia*, 2nd ser., 18: 473-500.
- Wallace, A. R. 1876. *The Geographical Distribution of Animals*. Macmillan, London, 2 vols.
- Waters, C. M. 1923. The American Conchology. *Proc. Acad. Nat. Sci. Philadelphia*, 1923: 99-101.
- Zinn, A. 1920. Einiges in Hinblick der Paläozoologie. (6), 2 (2): 401-600.