

Henderson

S [Vol. 18, No. 3
skulls (*Trigonias*) from the
VIII, pp. 1-32, 1928.
North America: U. S. Geol.
and its vertebrated animals:
a of North America: *Idem.*,
aska: Jour. Acad. Nat. Sci.
Survey Monograph XXVII,
ary of the West: Bull. Amer.
do: Mem. Amer. Mus. Nat.
r. Mus. Nat. Hist., XVI, pp.
I, pp. 291-310, 1902.
U. S. Geol. Survey Bull. 361,
Hist., XXVIII, pp. 289-316,
ocene mammals: Amer. Mus.
d its Wind River and Bridger
7.
th America; iconographic type
. 1-330, 1918.
ka: U. S. Geol. Survey Mono-
k formation of Moffat County,
pp. 87-120, 1928.
e western part of the San Juan
'0, 1924.
re. New York, 1913.
niversity: Trans. Conn. Acad.
Mus., III, 1, 1929.
lorado: Proc. Colo. Mus. Nat.
Acad. Sci., XVIII, pp. 145-158.

THE UNIVERSITY OF COLORADO STUDIES

VOLUME 18, NO. 4, NOVEMBER, 1931

MOLLUSCAN PROVINCES IN THE WESTERN UNITED STATES

BY JUNIUS HENDERSON*

As early as 1885 Binney¹ recognized the fact that land-snail faunas of several portions of the United States are sufficiently distinct to warrant the division of the country into molluscan provinces, which he defined as follows:

I. Pacific Province; comprising a narrow strip between the Sierra Nevada and Cascade Mountains on the east and the Pacific Ocean on the west, extending from San Diego, California, northward to Alaska. This province he subdivided into two regions:

- a. The Oregonian Region; from Humboldt Bay, California, to Alaska.
- b. The Californian Region; from Humboldt Bay to San Diego.

II. Central Province; from Mexico to British America, between the Rocky Mountains on the east and the Sierra Nevada and Cascade Mountains on the west. He says that "paucity of species over this large area is owing to the nature of the climate and soil—causes in equal force on the western border of the Eastern Province." This was before the discovery of the rich faunas of *Oreohelix*, *Ashmunella*, *Sonorella*, *Holospira*, and other genera.

III. Eastern Province; comprising the remaining portions of the continent north of Mexico, thus presumably including all of British America except the narrow region along the Pacific Coast, as he cut off the Central Province at the British boundary. This province he subdivided into three regions, which he designated the Northern Region, the Interior Region, and the Southern Region.

Binney's provinces and regions were based upon the geographical range of selected species, not of genera. That appears to be a very unsatisfactory method. Furthermore, at that time very little was known of the mollusks of the arid or

* Professor of Natural History and Curator of the University Museum.
¹ Binney, A Manual of American Land Shells, *Bull. U. S. Nat. Mus.*, No. 28, 1885.

semi-arid, sparsely-inhabited interior basin; many species and subspecies of important genera now known to inhabit the Pacific Coast region were not yet discovered, while the recognized species and their generic relationships were but little known. He was not entirely consistent in his lists of species inhabiting the various provinces. Thus he listed eleven species which he said range "over the whole of" the Pacific Province (that is, from San Diego to Alaska inclusive), yet in giving their range in the descriptions of species in the same book he reported only two of them from north of Oregon and only one from as far south as San Diego. He stated that the snails of the Californian Region have no connection with those of Lower California, because only one or two species overlap. The genus *Micrarionta*, as now known, plainly relates the faunas of southern California and those of northern Lower California, though the occurrence of *Bulinus* and *Codacntrum* to the southward may make it advisable to divide Lower California into two districts. Binney did not take fresh-water mollusks into consideration at all. It seems quite probable, too, that in setting boundaries to his provinces he was influenced partly by climatic conditions and physiographic features, not entirely by the geographical distribution of the mollusks. However, with the limited information then at hand, and the use of species instead of genera as a foundation, the outlines of his provinces were more nearly correct than one might have expected.

With the accumulated knowledge derived from the work of many students during the intervening 45 years or more, we are now able to correct the boundaries of the provinces and to make some additional subdivisions, based upon the range of important genera of limited distribution, genera of world-wide or circumpolar distribution being of no value in this connection. Anatomical investigations have led to the establishment of several very important genera of mollusks which are confined to the West. These, together with the absence of quite a number of important eastern genera, give to the western faunas as a whole a very distinct aspect. The provinces whose delineations are based upon the more recent work have been briefly discussed in several papers,¹ but well-known conchologists have urged the publication of a more detailed and thorough discussion of the subject, which has been made possible by a study of the large amount of material and the data contained in the card index and catalogue of western fossil and recent mollusks in the University of Colorado Museum.

There are some difficulties in the working out of such provinces. In the first place, there are in the United States no sharply defined physical barriers affecting

¹ Hershkovs, "On the North American genus *Oreohelix*," *Proc. Malac. Soc. London*, XIII, 21-24, 1918; "Malacusan provinces in the western United States," *Naudin*, XII, 63-91, 1928; "Mollusca of Colorado, Utah, Montana, Idaho and Wyoming," *Park. Geol. Studies*, XIII, 58-218 (on pp. 65-66), 1924; "The non-marine Mollusca of Oregon and Washington," *Univ. Cal. Studies*, XVII, 47-190 (on pp. 47-52), 1929.

all groups of mollusks or even all the members of one group. Even the sharp crest of the lofty mountains of Colorado or of the ranges near the Pacific Coast, and the desert and semidesert areas of the interior basin are not absolute barriers for all groups. In the second place, it is highly probable that the geographic distribution of some of the most important genera was accomplished largely before the development of present climatic and physiographic areas, and numerous local living colonies have been able in favorable situations to survive changing conditions. The colonies having been isolated for a very long period, by intervening unfavorable territory, numerous species and races of very limited range, many of them confined to a single small colony, have become differentiated, as is well illustrated by the genera *Oreohelix*, *Ashmunella*, *Sonorella*, *Micrarionta*, and *Haminthologypha*.

Whatever groups of Mollusca may be chosen in prescribing boundaries of provinces in a region devoid of sharp physical barriers, there is certain to be a considerable amount of overlap. Hence the provinces must be bounded by broad zones, not by sharp lines, and no definite limits can be assigned to the broad bounding zones. They may be exhibited on a map only in a very much generalized way. Even though all may agree as to the existence of such provinces and their general outlines, there is room for much difference of opinion as to just how the details of the boundaries should be drawn and as to how many provinces should be recognized. However the boundaries may be expressed on a map, a careful study of the western molluscan faunas as a whole leaves no doubt as to the reality of such provinces.

The preparation of the statistics presented herein has involved a great deal of work. It has been necessary to determine, so far as was practicable, just what species described or recorded from the western states are entitled to recognition as members of the western faunas. The names of some species originally described from the western states prove to be synonyms. Many eastern species have been erroneously reported from the West upon incorrect identifications. By examination of large collections of material from many localities and a critical examination of hundreds of publications, it has been possible definitely to eliminate many species from the list. Future work will doubtless eliminate others, but they will be balanced by discoveries of new species and subspecies and forms not hitherto reported from the region. So the figures herein may be considered substantially correct.

MAJOR MOLLUSCAN DIVISIONS

I. EASTERN DIVISION, extending from a broad zone on the plains east of the Rocky Mountains eastward to the Atlantic Coast.

II. WESTERN DIVISION, extending from the same zone westward to the Pacific Coast.

Both Divisions extend northward into British America and southward into Mexico. The dividing zone, starting on the Canadian boundary line at about longitude 108° west, swings southwardly across the plains of eastern Montana, around to the eastward of the Black Hills of South Dakota (as shown by the occurrence of *Oreohelix* there), thence along near the eastern border of Wyoming and through eastern Colorado and eastern New Mexico to the Rio Grande.

Nearly all of the genera of the fresh-water families Lymnaeidae, Planorbidae, Physidae, Valvatidae, Amnicolidae, Anicidae, and Spiraeridae, together with the terrestrial genera *Succinea*, *Vallonia*, *Pupilla*, *Ferussacina*, *Fusulin*, *Helicostoma*, *Angustipira*, *Agrionax*, *Zonitoides*, *Escomulus*, *Reticella*, *Helicotrema*, *Cochitopa*, and others, are found in both areas. It may be noted that nearly all of the land-snail genera mentioned comprise only small species, easily transported in various ways, and most of the groups mentioned are of wide geographical distribution. On the other hand, a large number of important genera occur in one division but not in the other.

Eastern Division. In this division are found the genera *Campeloma*, *Vitipera*, *Liopira*, *Pleurocera* and several other related genera, *Helicina*, *Profundella*, *Omphalina*, *Gastrolimnaea*, and others, wholly unknown in the Western Division, aggregating a very large number of species and some of them abundant; the large operculate univalves alone probably numbering over 300 species and subspecies. *Polygona* and *Goniatina* are represented in the Eastern Division by many species and subspecies (over 100 of each) and in the Western Division by only a few species confined chiefly to Northern California, western Oregon, and Washington. The former, and possibly the latter, extends into northern Idaho and western Montana, but not into the other Rocky Mountain states and not into New Mexico, Arizona, or Nevada. The numerous genera of *brachy-shelled* pebbly fresh-water mussels (Naiades), so abundant and in some localities commercially important in the Eastern Division, are entirely absent from the Western Division, except a few found in the extreme eastern part. Simpson's 1914 recognition of 28 genera of Naiades (mostly Unionidae) in the United States, of which 27 occur in the Eastern Division, including over 500 species and subspecies, while only four genera, with nine species and subspecies, occur in the Western Division.

Western Division. Of the numerous genera of Naiades which occur in the United States, only *Goniatina* is confined to the Western Division. *Limnoidia* occurs in both divisions, represented by several species in each. *Margaritifera* is represented in the Western Division by a color form *lybata*, of the circumarctic *M. margaritifera*, which occurs in eastern Canada, New York, and New England, but is absent from the central part of North America. These three genera are all

1 Simpson, *A Descriptive Catalogue of the Mollusca of the Pacific, Farallone Islands, Channel Islands, and the Hawaiian Islands*, 1914, 160-169, plates.

thin-shelled forms. Several heavy-shelled forms, *Lompsilis* and *Aradontoides*, have been reported from northeastern Colorado, and *Unionensis* from the Arkansas Valley, along the western border of the Eastern Division. *Strophitus* has been found a little farther west, close to the western edge of the plains in Colorado. *Lowsilis* has been found in the eastern edge of the Western Division, in eastern Wyoming and Montana. *Leucopis papai* Lea has been found in the Pecos Valley, eastern New Mexico, in the western fringe of the Eastern Division. With the exception of these meager occurrences, no heavy-shelled Naiades have been found in or near the Western Division, and of them only *Lompsilis* is within that division as mapped. The region west of the Rocky Mountains, according to Simpson, is the largest area in the temperate and tropical portions of the earth devoid of heavy-shelled Unionidae.¹

Not only are there a large number of genera of the Eastern Division missing from the Western Division faunas, but some of the most important genera of the Western Division are totally absent from the Eastern Division. Exclusive of western Texas species, which might well be included in the Western Division, there are now known in this division approximately 1,000 species and subspecies of non-marine mollusks, the exact number depending upon how many may yet be eliminated as synonyms and erroneous records. Of this number, so far as can be stated at present, 504, or about one-half, belong to genera which are not found in the Eastern Division, if we except a few *Holospiras* in Texas. The list is as follows:

Terrestrial		Aquatic	
Monsaltema	15	Caridier	5
Helicobagryla	68	Pampholyx	5
Micromelania	94	Lana	8
Succinea	84	Planumbicula	11
Oreohelix	80	Aniculus	1
Ashmurella	55	Goniatina	2
Tolospira	39		
Tridacna	8		
Ammonitella	1		
Polygona	1		
Polygona	1		
Polygona	1		
Vitipustoma	2		
plus several genera	15		

Hemiphaedusa extends into Texas, but cannot be considered a genus of the Eastern Division. The Texas species are not included in the above enumeration. *Hemiphaedusa* extends into Lower California, but is a strictly Western Division genus, and the Lower California species of the genus are included in the enumeration.

¹ Simpson, *Mollusca*, VIII, 118, 118B.

The Western Division I have divided into several provinces, thus:

a. *Rocky Mountain Province*; comprising Colorado except the eastern plains region, most of Wyoming, part of Montana, southern Idaho, Utah, and tentatively Nevada. It extends northward into British America. It is characterized by the dominant land genus, *Oreobolia*, and is distinguished from the Southern Province by the absence of *Astusella*, *Sonorella*, and *Halospira*, from the Washingtonian and Oregonian provinces by the absence of *Polygona*, *Gonobasis*, *Agassiziana*, *Monadenia*, and *Haplotrema*, and from the Californian Province by the absence of *Monadenia*, *Micraria*, and *Helminthoglypta*.

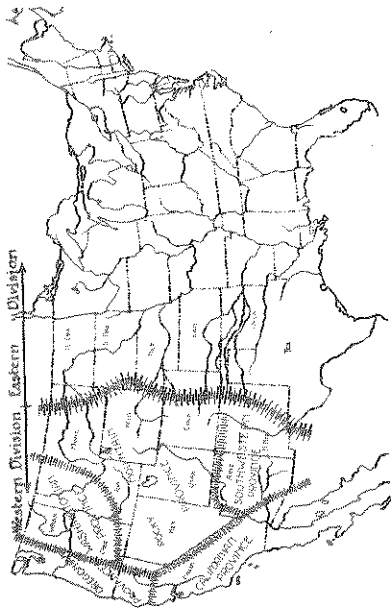


FIG. 1. Molluscan Provinces in the Western United States.

b. *Southern Province*; comprising the larger part of the states of Arizona and New Mexico and extending southward into Mexico. Though *Oreobolia* is a conspicuous element in the fauna, the province is distinguished from the Rocky Mountain Province by the large number of species and subspecies of *Astusella*, *Sonorella*, and *Halospira*, which genera are absent from the Rocky Mountain Province. It is distinguished from the Californian Province by the absence of *Micraria* and *Helminthoglypta*. *Astusella* comes nearly to the Colorado line but has not been found in Colorado. *Sonorella* comes north to the Grand Canyon in Arizona, but has not been found in Utah.

c. *Washingtonian Province*; comprising western Montana, northern Idaho, eastern Washington, Eastern Oregon, and perhaps part of the state of Nevada.

Though the genus *Oreobolia* extends westward as far as Celilo, Oregon and Ellensburg, Washington, this province is distinguished from the Rocky Mountain and Southwestern Provinces by the presence of *Polygona* of the *millasi* group, *Agassiziana*, *Gonobasis*, and *Haplotrema*, and from the Oregonian Province by the presence of *Oreobolia* and the absence of *Monadenia*.

d. *Oregonian Province*; comprising the moist coastal region of northern California, western Oregon, western Washington, and probably northward to Alaska. It is distinguished from the Californian Province by the presence of *Gonobasis* and *Polygona* and the absence of *Micraria* and *Helminthoglypta*, except for some overlapping of these in the northern part of California.

e. *Californian Province*; comprising most of California, extending into Lower California and eastward into southeastern Arizona. It is characterized by numerous species and subspecies of *Micraria* and *Helminthoglypta*, the scarcity of *Oreobolia*, and the absence of *Polygona* and *Gonobasis*.

I do not know just what to do with Nevada. Its mollusks are not very well known, and it could be placed consistently in either the Rocky Mountain or Washingtonian province, more likely the former, as *Oreobolia* occurs in the state, but *Polygona*, *Gonobasis*, *Haplotrema*, and *Agassiziana* are not known there. The apparent absence of *Micraria* and *Helminthoglypta* prevent its assignment to the Californian Province, and the absence of *Polygona*, *Gonobasis*, *Monadenia*, and *Haplotrema* prevent assignment to the Oregonian Province. It seems best, therefore, to place it in the Rocky Mountain Province, together with southeastern Oregon. I do not know how far southward *Polygona* extends in Oregon, but a new colony has been found near Pendleton, Oregon and another just across the boundary at Weiser, Idaho. Very little collecting has been done south of there in Oregon.

A separate province should be made of southwestern Texas, because of the prominence of *Bulimulus* in its fauna, and the absence of *Oreobolia*, *Astusella*, *Sonorella*, *Micraria*, *Helminthoglypta*, *Polygona*, and *Gonobasis*, as well as the absence of various genera which are prominent in the eastern faunas. However, at present I do not know where a line should be drawn to include such a province, so I refrain from designating it. One fossil form of *Oreobolia* has been found in Iowa in the loess, but of course that is not sufficient to extend the Western Division eastward. One species of *Bulimulus* is reported from extreme southern Arizona, but that does not place southwestern Texas in the Southwestern Province.

POSSIBLE GEOLOGICAL ORIGIN OF THE PROVINCES AND PROVINCES

Present differences in environmental conditions do not coincide with the present distribution of the mollusks and do not seem wholly sufficient to account for the separation of the United States into two distinct molluscan divisions. True, the

shallow streams of the western plains, with their rapidly shifting channels, are not favorable to the heavy-shelled Unionidae. The cold, rapid streams of the Rocky Mountains would perhaps present an unsurmountable barrier to such mollusks at the present time, but the Rocky Mountains have not always been there. The Continental Divide has for unknown ages been a rather effective barrier to the passage of fishes from the streams of the eastern side to those of the western slope. The Unionidae, being dependent upon rivers for distribution, would thus be prevented from passing into the Great Basin region, except for some very unusual accidental method.

However, turning to the land snails, *Oreohelix* is the only genus of large species which occurs in all of the states of the Western Division - 12 states - and northward into Canada, and is confined to that division except for the fossil subspecies (*Oreohelix*) in the loess of Iowa. It is found under a very great variety of environmental conditions, as to climate, vegetation and other cover, and rock formations. It is found in very cool, moist localities up to timber line in the mountains; under bare rocks without any cover at all; under shrubs out in broad valleys; under logs in aspen groves; under slides of limestone, granite, and volcanic rocks; under leaves of herbs on otherwise bare foothill slopes beneath the heat of the blazing sun in Utah and Idaho; in situations of all sorts, from timber line at 11,500 feet in Colorado to nearly sea level in California; from the cooler, moister parts of Montana and British Columbia to hot, dry situations at and beyond the foot of the mountains in Idaho, Utah, Nevada, New Mexico, and Arizona. Evidently there are no known environmental factors which would prevent it from flourishing at many localities in the Eastern Division if it should be carried to such localities by any agency. Likewise, there is no known reason why *Polysphaera* should not flourish in Colorado and Utah as well as it does in Idaho and Montana, if it should in any way be brought to those states.

The striking separation of the United States into two very distinct molluscan divisions suggests some profound, widespread cause, which may be found in the geological history of the continent. Perhaps more complete knowledge of the geological history of the several western provinces, and of their faunas would show that they also are the result of past geological conditions. Unfortunately, as all paleontologists know, the chances for non-marine mollusks to be buried under such conditions as to be preserved as fossils are very slender, and particularly in this case of the strictly terrestrial snails. Consequently, but little is known of the geological history of our fresh-water mollusks, and even less of our land snails.

It is known that *Oreohelix*, the dominant genus of land snails in the Rocky Mountain Province, extending over nearly the whole Western Division, had its origin at least as early as late Cretaceous time. Fossils from late Cretaceous, Paleocene, and Eocene formations show that even in the Eocene it had acquired a

range extending from Alberta to New Mexico, strongly suggesting that it had been then in existence for a considerable period. The number of species, present distribution, and center of distribution lead to the conclusion that the genus originated in what we now call Utah, Arizona, or New Mexico. Most of the species are found in the region where there are no Cretaceous rocks. It is known that during much of Cretaceous time a great interior sea extended northward from the Gulf of Mexico well into Canada, separating the continent into two large land areas. This, so far as we can tell from the evidence, was when the great development of modern non-marine molluscan faunas in North America was just beginning, though non-marine mollusks are known from formations dating far back in Paleozoic time.

It is quite possible, then, that the distinct molluscan faunas of the Eastern and Western Divisions were developing in the two separate land areas during Cretaceous time, and after the retreat of the inland sea they continued to develop along the lines then laid down.

This explanation of the origin of the two faunas leaves to be answered the query as to why the faunas have not mingled much during the long period subsequent to the withdrawal of interior marine waters. There is much evidence that conditions during Eocene time in the Rocky Mountain region and at least part of the western border of the plains were much more favorable for the extension of such faunas than at present. As we have seen, a group of fresh-water mollusks did at that time cross what is now the Great Plains area into Rocky Mountain states and became temporarily established, but failed to survive there through the Tertiary, perhaps due to changing stream conditions.

Even during the Cretaceous at times the sea temporarily retreated locally, leaving some fresh land surfaces, the streams and ponds of which were promptly invaded by eastern types of fresh-water gastropods, which were destroyed by the returning sea. At the close of the Cretaceous, with the final withdrawal of the sea from the whole interior region, heavy-shelled Unionidae, *Uniparus*, *Campylodonta*, and *Goniobasis* invaded Colorado, Wyoming, Utah, and Montana, as shown by abundant paleontological evidence, but did not long survive. *Goniobasis* was living in the Yellowstone Park region in early Cretaceous, before the division of the continent by the inland sea, and may have then crossed to the Pacific Coast. Anyhow, fossils prove that it reached Washington at least as early as the Eocene, and Oregon and California as early as middle or late Tertiary, which seems to account for this eastern genus being now represented by living species from northern California to Washington. It probably reached Idaho and Nevada during Eocene time, as it was living there during the Pliocene, after it had disappeared apparently from the Rocky Mountain and western plains region. *Polysphaera* also probably crossed to the Pacific slope during the favorable Eocene period, as it is found fossil in Tertiary deposits of the Pacific Coast region; thus account-

ing for this eastern genus in portions of the Western Division. Two other genera of large land snails of the eastern fauna, represented by living species in the Northwest, *Haplotrema* and *Anguispira*, may also have crossed at that early period. One Pacific Coast species of *Goniobasis* was long ago reported as living in western Montana, but the report has not since been confirmed and it has not been found anywhere between there and western Washington. A *Unio* was described from the John Day beds of Oregon and another from the Tejon beds of California, but they do not seem to be congeneric with any other North American forms.

Very few fossil mollusks have been found in the thick and extensive post-Eocene formations of the western plains and Rocky Mountain region, and such as have been found are confined to a few localities and are of types which cannot affect the solution of the problem. Of course, it may be argued that the absence of fossils is not at all conclusive. There is a similar scarcity of fossil plants in the same formations, yet the presence of remains of many species of mammals shows that at least locally there must have been considerable vegetation, probably of the same general character as the herbaceous plants now predominant in that region. The facts that the more important genera of land snails of the Western and Eastern Divisions failed to migrate across the Great Plains area, except one species of *Oreohelix*, as hereinbefore indicated, and that the fresh-water groups which had succeeded in crossing to the Rocky Mountains during Eocene time soon disappeared, leaving no evidence that they have existed there since the Eocene, suggest very strongly that the present unfavorable conditions in a broad area east of the Rocky Mountains, which now prevent the mingling of the faunas, have existed with but little change since Eocene time.

Oreohelix, having extended its range from British America to New Mexico during late Cretaceous and Eocene time, while conditions were more favorable than now, reached the eastern base of the Rocky Mountains and the Black Hills of South Dakota. Just how and when a single small form reached Iowa is not known, but it failed to establish permanent residence. As conditions became less favorable, isolated colonies were left stranded in small favorable stations in the western mountains, surrounded by wide expanses of unfavorable territory. Consequently in the course of time many local races became differentiated, including some rather striking forms, such as *elrodi*, the *haydeni* group, and the *idahoensis* group, characterized by heavy transverse or longitudinal ribs. It is likely that the numerous races of *Ashmunella*, *Sonorella*, *Micrarionta*, and *Helminthoglypta*, of the Southwest and Pacific Coast region, also developed because of isolation in small colonies.

The differences between the molluscan faunas of the various western provinces are not so great as the differences between the faunas of the Eastern and Western Divisions, but they are nevertheless striking. Perhaps in time the reasons for them may be discovered, but adequate causes have not yet been suggested.

FRITZ LI

Geneticists & whether the r escapable inhe as to maintain voting suffice such supreme it has seemed clear and eloq icist, Dr. Frit

What follo Fischer-Lenz pp. 471 *et seq* tion, have ki passages. R tion of the l available in York).

The differ greater tha The cultura mental equ carry it to countless d in tempera many stup cheerful, of that some saying to : spiritual c

* Professor