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THE SIGNIFICANCE OF PLEISTOCENE MOLLUSKS[1]

In the investigation of natural problems the most conspicuous or bulkiest character does not always furnish the most convincing evidence. We readily see the mass of diatomaceous earth, but we do not understand its gritty quality, nor can we appreciate its origin until we have studied the minute, individually almost negligible frustules which make it up; sandstones or limestones may form great cliffs, but it requires the comparatively insignificant fossil to finally reveal the origin and the place of the rock. Similarly, in the study of the Pleistocene we encounter gross features which have their value—we find variously comminuted and diversely arranged materials in great bulk; we find topographic and physiographic characters on a large scale; yet the best evidence which we have concerning the conditions under which certain parts of the Pleistocene formations were deposited is furnished by the fossils which usually form a small and not always conspicuous part of the deposits.

Both plant and animal fossils have been found in the various subdivisions of the Pleistocene. The former consist chiefly of the leaves and wood of gymnospermous and angiospermous trees and shrubs, mosses and diatoms; the latter of some insects, a conspicuous, though limited, mammalian fauna, and the mollusks which form the most widely distributed and most universally present group of all.

[1] Address of the vice-president and chairman of Section E—Geology and Geography—American Association for the Advancement of Science, Cleveland, 1912.

The plant remains and insects are too few and too widely scattered to form a satisfactory measure of conditions; the mammalian fauna is but little better in this respect and, moreover, consists of species which are for the most part extinct, and whose exact habits are not known; but the mollusks are not only most widely distributed in the Pleistocene deposits, but belong practically without exception to species now living whose habits may be very accurately determined. For these reasons the mollusks form the most important and most significant group of Pleistocene fossils.

Aside from the marine species of the coastal formations, which will not be here considered, the Pleistocene and modern species of mollusks naturally group into three rather well-defined divisions according to habits:

1. *Fluviatile species,* inhabiting perennial streams and lakes. These are chiefly bivalves, especially larger *Unionidæ,* and operculate gill-bearing gasteropods. A few aquatic pulmonates, like *Lymnæa emarginata* and *Planorbis truncatus,* also prefer larger bodies of water.

2. *Pond species,* inhabiting ponds, bogs and borders of smaller streams, which are likely to become dry during a part of the summer, and also the shallow swampy borders of larger bodies of water. These species are chiefly aquatic pulmonates, with a few smaller bivalves, especially of the genus *Pisidium.*

3. *Terrestrial species,* living among plants, sometimes on the bark of trees, often under leaves, sticks and stones. Among them are two operculate prosobranchs, closely related to aquatic species of the first group, but the great majority are terrestrial pulmonates. A few species, such as *Succinea retusa, Zonitoides nitidus, Vertigo ovata* and *Carychium exiguum,* naturally group with the terrestrial pulmonates, but they are commonly found in wet places, and sometimes live in the water for a time, behaving then like the aquatic pulmonates of the pond group.

The members of the pond and terrestrial groups are closely associated with plants which they require for shelter and in most cases for food. The terrestrial forms are most abundant on forested areas, but certain species, such as *Succinea grosvenorii, Cochlicopa lubrica, Vallonia gracilicosta,* etc., also extend into more open territory.

While all the terrestrial species require some moisture for activity, the amount which may be found at times under a leaf or stick, or among plants on a dewy morning, or after a rain, is entirely sufficient for the purpose. This supply of moisture is irregularly intermittent, and the mollusks remain inactive while waiting for a return of favorable conditions. Sometimes they protect themselves by a mucous epiphragm, or they creep under leaves or sticks, or burrow into the soil. Long-protracted dry seasons are fatal to many of them.

The fossil mollusks are distributed through a variety of formations. Those of the Aftonian, the Don beds, the Florencia formation and similar older Pleistocene deposits, like those of the more modern alluvial beds, present the fluviatile and pond facies in the main, though there is often a strong admixture of terrestrial forms. Those of the loesses are terrestrial in the main, with comparatively rare additions of pond types and a total absence of fluviatile forms.

Practically all of the species found in the various Pleistocene formations are living upon the continent to-day. Such exceptions as *Oreohelix ioensis* from the loess and species of *Pisidium* and *Lymnæa* recently described from indefinite alluvium, do not materially affect the truth of this statement, for these may be mere races, or a more critical study of these difficult genera may show that the apparently extinct forms are living to-day. They are certainly very closely related to existing forms, and suggest no peculiar set of conditions.

Because of the practical identity of the fossil and certain modern molluscan faunas important conclusions may be drawn concerning the conditions which existed at the time of the deposition of the fossiliferous deposits.

The first question which naturally comes to the mind of the student of Pleistocene geology in this connection is this: Could these mollusks have lived under glacial or near-glacial conditions? As in so many other cases, the measure of the past must here be sought in the present. Unfortunately, we do not anywhere have conditions which exactly parallel those which existed in the interior of our continent during the several advances of the ice-sheets. The climate of Alaska is so materially affected by warm ocean currents that no fair basis for comparison can here be established. The Antarctic region presents no partly glaciated continents, and comparisons are here impossible. Perhaps Greenland offers the nearest parallel, but even here in the study of plant and animal life we have to deal with a narrow coastal strip the climate of which is manifestly affected by the proximity of the sea.

From this narrow strip Möller reported, in 1842, four species of terrestrial mollusks (a *Vitrea,* a *Pupa,* a *Vitrina* and a *Succinea*) and three species of pond snails, two of the genus *Lymnæa* and one of *Planorbis.* These species were all represented by few widely scattered individuals, and constitute a very scant fauna. Nowhere in all the barren ground belt bordering the Arctic ice have such combinations of species been observed as we find in the various Pleistocene deposits of our country. The latter suggest rather a region very similar to the present northern part of our country, in the main, with relationship in some of the deposits with the fauna of the southern states, and in others some affinity with that of the coniferous belt to the north.

Our present knowledge of the habits and distribution of the fossil and modern mollusks forces the conclusion that the deposits containing these species are interglacial or post-glacial, and that they were formed during a period of mild climate.

The second important question concerns the immediate conditions under which the various deposits were formed. To answer this question intelligently on the basis of the molluscan fauna we must understand the habits of the mollusks as well as the conditions under which the land and fresh-water forms may mingle.

For purposes of comparison your essayist has made extensive studies of the habits of the modern molluscan fauna of the Mississippi Valley, and has compared large series of shells thrown up along the shores of larger streams and their smaller tributaries, as well as ponds and lakes, with the shells obtained from various Pleistocene deposits and from more modern alluvium, and nowhere has he found any evidence that the conditions under which the Pleistocene deposits were formed were materially different from those which are in operation in the same region to-day.

All of the Pleistocene deposits, with the exception of the loesses and certain buried sand dunes, are aquatic, and a comparison of their molluscan contents shows the same peculiarities and the same variations as are presented by the modern alluvial and water-drifted fauna.

Some of these points of similarity are brought out by a comparison of the mollusks from various deposits. Thus the Aftonian beds of Harrison and Monona counties, Iowa, have yielded 28 aquatic species and 9 terrestrial species;[2] the Don beds, 42 species, of which all but two are aquatic;[3] the Florencia formation, 30 aquatic and swamp species and 19 terrestrial species;[4] the buried silt in the Illinois Central cut in Sioux Falls, 14 aquatic and 2 terrestrial species, one of the latter doubtfully belonging to the deposit;[5] the more modern river alluvium of Harrison County yielded 18 aquatic and swamp species and 19 terrestrial species;[6] the lacustrine alluvium of West Lake Okoboji exposed by recent canal excavations, yielded 27 aquatic and swamp species, and 1 terrestrial species; modern drift along the Big Sioux River opposite Canton, South Dakota, contained 18 aquatic and 5 terrestrial species; similar drifted material along the Missouri River at Rulo, Nebraska, showed 12 pond and swamp species, and 15 terrestrial species; and drifted material on the north shore of Miller's Bay, West Lake Okoboji, Iowa, contained 14 aquatic and marsh species and 14 terrestrial species.

These lists indicate that terrestrial mollusks are not uncommon in the various alluvial deposits. It should be remembered, however, that as a rule the terrestrial species are represented by very few individuals which accidentally drifted in from adjacent land surfaces, while the aquatic species belonging to the genera *Sphærium, Pisidium, Campeloma, Valvata, Amnicola,* the larger species of *Lymnæa, Physa, Planorbis, Segmentina* and *Ancylus* occur in larger numbers.

In those case in which larger numbers of terrestrial forms occur, as in the Miller's Bay and Rulo lists, they may be traced to nearby wooded bluffs, and it is evident that the relatively large number of terrestrial forms in the Harrison County alluvium and the Florencia formation may be traced to the same source.

It is evident that the shells do not drift far in any case. The Missouri River contains few aquatic mollusks, but its smaller tributaries usually show an abundance of them. Yet rarely are fluviatile shells found in modern river drift along the Missouri, and the aquatic species are of the pond type prevailing in small ponds along the main river, as is shown in the Rulo list. Shells of terrestrial species which are limited in their distribution are also seldom found at any distance from their habitat. This is strikingly illustrated by *Helicina occulta,* which is now restricted to limited and widely separated areas. Thus at Iowa City a colony inhabits a half-acre of wooded bluff, and in thirty years your essayist has found but one fresh shell along the creek at the foot of the slope, and none along the nearby river to which the creek is tributary.

A recently discovered colony of this species in a similar situation along the Cedar River above Cedar Rapids, Iowa,[7] gives like results. Various students of mollusks have collected in this region, yet no fresh shells of this species were ever observed in the drifted material along the Cedar River. The Miller's Bay list shows that 14 species of terrestrial shells were carried across the bay from the wooded southern shore, yet repeated dredging in the bay has brought

[2] See Iowa Geol. Survey, Vol. XX., 1910, pp. 395–6.

[3] *Journal of Geology,* Vol. IX., 1901, pp. 291–2.

[4] *Am. Jour. of Science,* 4th series, Vol. IV., 1897, p. 96.

[5] For description of this cut see *Bull. of the Geol. Soc. of Am.,* Vol. 23, 1912, pp. 141–3.

[6] Iowa Geol. Survey, *ibid.*

[7] By Mr. E. G. Grissel, of Cedar Rapids, Iowa.

to light only four of these species, represented by very few individuals, which had dropped to the bottom of the bay. Terrestrial shells which drift into water are soon cast ashore.

Nearby wooded slopes frequently contribute terrestrial shells to ponds and streams, but the latter invariably supply a relatively large number of shells of aquatic species.

It is also noticeable that such species as *Zonitoides nitidus* and *Succinea retusa,* of low grounds, and *Helicodiscus parallelus, Vitrea hammonis, Bifidaria armifera, B. contracta, B. pentodon, Zonitoides arboreus* and *Z. minusculus,* which are common on timbered alluvial flats and which occur so frequently in alluvium and modern river drift, are relatively very rare in terrestrial deposits like the loesses.

Another method by which terrestrial shells sometimes find their way into alluvial deposits has been observed where shallow ponds become dry during the summer. These ponds usually contain aquatic pulmonates, and their shells remain in the alluvium of the pond. Terrestrial species then creep out over the exposed surfaces, not infrequently leaving their shells to mingle with those of the pond species. The subsequent flooding of the pond results in the inclusion of both types in the alluvium of the pond. In the alluvium of one pond of this type between the Lakes Okoboji, Iowa, 12 aquatic and 5 terrestrial species were found, the latter being represented by few individuals.

Still another method by which aquatic species may be buried at altitudes higher than the level of the free water surface may be observed in seepy places fed by permanent springs. Such spots are not uncommon even on higher slopes and they frequently contain aquatic species belonging to the genera *Pisidium, Lymnœa* and *Physa,* probably introduced by small wading birds. Terrestrial species from nearby surfaces may creep out or be carried into the bog and the shells of both will then be mingled in the deposit of the bog. In one of these small bogs near Council Bluffs, Iowa, located at an altitude fully twenty feet above the high-water level of the Missouri River and closely surrounded by a forest, 5 terrestrial and 1 aquatic (*Pisidium*) species were collected, while in another on a prairie slope near West Lake Okoboji 3 aquatic species belonging to the genera *Pisidium, Lymnœa* and *Physa* were collected at an altitude of more than forty feet above the lake. In the latter case the surrounding prairie surfaces contributed no terrestrial species.

And finally individual specimens of aquatic species of mollusks may be carried to uplands by aquatic birds and insects, where their shells may ultimately be included in terrestrial deposits.

In order that the value of these molluscan faunas may be properly measured it is necessary that they be taken collectively. A single terrestrial shell does not make a land deposit, neither does a single aquatic shell make a water deposit. In water deposits aquatic shells always form a conspicuous part of the fauna, even though locally they may not predominate. In subaerial deposits aquatic shells may occur, but they are rare and local, and the dominant types are terrestrial. Strictly terrestrial Pleistocene deposits are of two types: buried sand dunes and the loesses. Buried sand dunes are not uncommon in the upper Mississippi Valley, excellent illustrations being found near Gladstone, Illinois; north of Iowa City, Iowa; at Hooper and West Point, Nebraska, and at other points. Neither buried nor surface dunes contain shells so far as observed.

The loesses are much more satisfactory

for our purposes, because they frequently contain fossils and offer by far the best opportunity for the study of Pleistocene terrestrial mollusks. In these deposits terrestrial forms vastly predominate, and fluviatile forms are wholly wanting. So much has been written on this feature of the subject that only reiteration is here possible.

Fresh-water shells in the loess are very few. They belong to species which inhabit small ponds and boggy places. They are not of the types found in streams and lakes. They are local in distribution, and in a number of cases clearly associated with buried ponds. Ponds are not rare in high places in loess regions. They frequently contain the smaller *Lymnæa,* etc., which are sometimes found in the loess, aquatic birds and insects probably being responsible for their introduction. Such ponds, if buried by subsequent depositions of loess, would present exactly the conditions under which aquatic shells are usually found in the loess. The vastly predominating forms are terrestrial—*upland terrestrial at that.* Some have become extinct in the loess region, but occur westward and southwestward in the drier part of the continent. Such are *Pupa muscorum, P. blandi, Sphyradium edentulum* var. *alticola, Pyramidula shimekii* and *Oreohelix iowensis.* Others like *Succinea grosvenorii* and *Vallonia gracillicorta* are still found in the loess region, but they prefer dry, often open grounds. The land species which prefer wet grounds are conspicuously absent from the loess.

The usual type of the fauna of the northerly loess is well illustrated by the fossil and modern fauna of King Hill, South St. Joseph, Missouri. This elevation rises 225 feet above the Missouri River bottoms and is capped by a thick bed of yellow loess which is quite fossiliferous to the very summit. The northeastern slope is covered more or less with low shrubs and stunted trees from twenty to eighty feet below the summit, merging below into a native grove. The loess at the summit yielded nineteen terrestrial species. Of these seven were also found living on the shrub-covered northeast surface in a relatively very dry habitat. With the latter were associated six additional terrestrial species which were not found in the summit loess, but all of which are known from the loess of the Missouri Valley. The nineteen fossil and thirteen modern species are all strictly terrestrial and the six species which are common to both well characterize the habitat of the entire fauna. A more careful examination of both the loess and modern surface faunas near the summit of King Hill would no doubt reveal a larger number of species common to both.

The fossil mollusks do not enable us to determine the age of any of the Pleistocene formations. The fossils of the Aftonian are not sufficiently distinct from those of modern alluvium to permit the drawing any conclusion other than that the conditions of deposition were much the same. They do not enable us to distinguish between the loesses, for the fossils of the gray and the yellow loesses are, in larger series, essentially the same. But they give us an excellent measure of the conditions which prevailed at the time of the deposition of the various fossil-bearing Pleistocene strata.

The fact that several ice sheets advanced into the upper Mississippi Valley has been well established. The advance and retreat of these several ice sheets were in all probability very slow, resulting in a gradual transition to and from a glacial climate. This suggested the desirability of search for evidence of such gradual transition among the mollusks of the several interglacial periods. But no such evidence has as yet been found, and it is evident that the fossiliferous Pleistocene deposits were formed after the interglacial and postglacial conditions had been fully established.

In no known Pleistocene deposit is there a vertical gradation of species which can be accounted for on climatic grounds.

The variation in horizontal distribution does not in any case indicate a climate of greater severity than that which exists in the same region to-day. The determinable deposits containing fluviatile and other aquatic shells are of such limited extent north and south, and, moreover, the species which they contain are now so widely distributed that they present no evidence of climatic variation.

The terrestrial mollusks which are found in the Pleistocene deposits are also now of very wide distribution and the variation which they exhibit in species, form and size is not at all determined by latitude, but rather by the edaphic conditions under which the forms existed. In both cases the species are those of modern faunas whose habits are well known.

Variations in the Pleistocene fauna are nowhere better illustrated than in the loess, which has a wide distribution both north and south, and east and west, in the Mississippi Valley. If we begin in the northwestern part of the loess area in Nebraska and western Iowa, we find that the dominant species in the loess are *Pupa muscorum, P. blandi, Pyramidula shimeki, Succinea grosvenorii, Oreohelix ioensis, Vallonia gracilicosta, Bifidaria procera, Sphyradium edentulum alticola.* These species all belong to a fauna characteristic of the dry western regions, *Pupa muscorum* alone passing by a wide detour northward to the northeastern part of the country. Other species belonging to more easterly faunas appear, as a rule, in smaller numbers. Southward along the Missouri River, as in northwestern Missouri, larger forms, such as *Circinaria concava, Pyramidula alternata* and *Polygyra multilineata,* more characteristic of eastern and southeastern faunas, begin to appear in larger numbers. The change southward along the Mississippi is even more striking. In the northerly deposits along the Mississippi *Helieina oculta, Pyramidula striatella, Succinia ovalis* and *S. avara* are among the most common species. *Pupa decora* is also abundant in both northern and northwestern loess, and while it is largely a boreal species, like *Pupa muscorum,* it extends along the western mountains well into our dry western region.

Southward along the Mississippi the loess molluscan fauna changes in essentially the same manner as the modern fauna of the surface. At Hickman, Kentucky, the larger helices (so prominent in the southeastern modern fauna) already appear in large numbers and *Pyramidula solitaria,* carinate *Pyramidula alternata, Polygyra tridentata,* very large *P. albolabris,* large *P. profunda,* a few *P. elevata, P. fraterna, P. fraudulenta, P. appressa, Omphalina fuliginosa,* large *Circinaria concava,* more abundant *Pyramidula perspectiva* and *Gastrodonta ligera.* These species already form the most conspicuous feature of the loess fauna. *Helicina occulta* still appears, though here approaching its southern limit. Still farther south at Dyersburg, Tennessee, a similar fauna appears in the loess, but *Helicina occulta* is not common, reaching here its southern limit and *Pyramidula striatella,* so common in the north, also becomes rare. Still farther south on the west side of the Mississippi River at Helena, Arkansas, the loess fauna becomes still more characteristically southern, and in addition to the larger helices already mentioned the large form of *Succinia ovalis, Omphalina kopnodes, Vitrea placentula* and *Helicina orbiculata* appear in conspicuous numbers. The last three species are distinctively southern. *Helicina occulta* has wholly disappeared and its place has been taken by *Helicina orbiculata.* The richly fossiliferous loess of Natchez and Vicksburg, Mississippi, also contains the forms common at Hickman and Helena, and the presence of *Polygyra obstricta, P. inflecta* and *P. stenotrema* still further stamps the fauna as distinctively southern.

But in this variation in the wide loess region there is nothing which suggests a transition or change from cold climate to warm climate faunas or *vice versa.* The variation, as we find it in the loess is practically exactly duplicated in the modern fauna of the surface. The only conclusion, then, which can be drawn from the fossils of the loess is, that during the deposition of the several loesses climatic conditions were not materially different from those which exist in the various parts of the same general region to-day. Such differences as do exist point rather to a drier climate in the northern part of the loess-covered area than that of to-day.

Emphasis has sometimes been placed upon the depauperation in size of certain loess shells, as evidence that the climate in which they existed was colder than that of to-day. These depauperate shells are found only in the northern part of the loess area, in Iowa, Nebraska, etc. Their exact counterparts are found living to-day in the drier portions of the same region. And corresponding differences do not occur in more easterly series which represent differences in latitude. It is evident that the depauperation is due to drouth and not to a low temperature, and the abundance of these depauperate shells in the northern loess reinforces the evidence already noted that the climate of this region was then somewhat drier than at present.

The earlier hasty conclusion in this case illustrates only one of the difficulties which the student of geology who has not given special attention to the mollusks encounters in his efforts to determine the conditions under which various Pleistocene deposits were formed.

Another results from erroneous identifications of deposits. An illustration of this is furnished by the Otis Mill section in South Dakota opposite Chatsworth, Iowa, which has been referred to the loess. The section, in fact, consists of Aftonian silt and sand, Kansan drift and true loess. The fossils, to which reference is usually made in connection with this section are of the usual alluvial type and belong to the Aftonian part of the section only, none being found in the capping loess. Still other errors result from erroneous identifications of species. Thus *Carychium exile,* the species usually found on high ground, has been identified as *C. exiguum,* a species which is frequently amphibious. Other errors arise from the assumption that species of the same genus have the same habitats, and that their presence in various deposits indicates like conditions. This is often far from true, thus, *Zonitoides arboreus* and *Z. nitidus* are similar in appearance, and closely related, yet the former is an upland species, while the latter is found in low grounds and is sometimes amphibious. Similarly, *Succinia avara* is upland, while *S. retusa* is amphibious; *Pomatiopsis lapidaria* is terrestrial, while *P. cincinnatiensis* is found only in somewhat deeper water in large ponds and lakes; *Planorbis trivolvis* lives in shallow waters in ponds and swampy borders, while the similar *P. truncatus* is found only in the larger lakes in deeper waters. *Lymnæa palustris* and *L. emarginata* show a similar difference in habit, the latter being a deep water form; *Physa gyrina* is a species common in small ponds, while *P. integra* prefers river borders and *P. sayi* inhabits larger ponds and lakes; and similar variations in habit may be found in the species of various genera such as *Bifidaria* and *Vertigo* among terrestrial genera, and *Amnicola* and *Pisidium* among aquatic genera.

It is, therefore, not safe to jump at conclusions on the basis of mere relationship. A student of geology who would correctly measure the conditions which prevailed during the time of deposition of the various fossiliferous Pleistocene formations must not only accurately identify the fossil species, but he must learn to know the habits of the modern representatives of the same species.[8]

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RAMSAY HEATLEY TRAQUAIR

Ichthyologists all over the world have read with profound regret of the death of Dr. Ramsay Heatley Traquair, the eminent authority on fossil fishes. Dr. Traquair had long been regarded as the dean of paleichthyology, and had been revered by those in his field, both for his personality and his scientific achievements, as few men ever were. It was a shock to them to realize that he was no more among them. His work in ichthyology was of a fundamental kind, like that of Huxley or of Johannes Müller in zoology, and much of it has long since become incorporated among the established principles of the science. Indeed, Dr. Traquair may be regarded as the founder of modern paleichthyology, and his name, we believe, will stand next to that of Louis Agassiz, as the most illustrious in the history of this science.

Ramsay Heatley Traquair was born at Rhynd, Perthshire, July 30, 1840. He was the youngest son of a Scottish minister. As a boy, he was sent to a preparatory school in Edinburgh, where his quiet bearing and studiousness attracted the attention of his teachers. Almost from childhood he manifested a deep love of nature, and as a boy he frequented a small natural-history shop kept by an old woman in Edinburgh, where were displayed minerals, fossils and shellfish: these no doubt stimulated his imagination and helped to nurture a growing love of natural history. As he grew older, he would go on excursions into the hills around Edinburgh in quest of paleichthyological specimens. On one of these trips, the story runs, he found a nodule with a portion of a palæoniscid fish, and was greatly surprised to learn that no book then available gave an adequate account of it. It was his ardent love of natural history that led to his choice of medicine as a profession, for this was the only science, at that time, that afforded both a foundation for natural history studies and the means of a livelihood. He entered the University of Edinburgh as a student of medicine in his seventeenth year, and he seems to have been a good student. His holidays were spent in collecting and studying fossils. As the end of his studies approached, it became more and more plain to him that he ought not to practise his profession but seek an opening in science. He took his degree in 1862, receiving a gold medal for his thesis on the asymmetry of flatfishes. In this year, too, he published his first paper, "On the Occurrence of Trilobites in the Carboniferous Limestone of Fifeshire."

For several years after graduation he held minor posts in the school of medicine, first as prosector and later as demonstrator of anatomy. This period afforded him an opportunity of acquiring skill in making anatomical preparations, besides allowing him to be near his favorite fossil hunting grounds. During 1866–67, he held the professorship of natural history in the Agricultural College at Cirencester, where he taught botany and devoted his spare time to the study of local geology

[8] A supplementary table of mollusks, containing twelve lists of fossils and six lists of shells obtained from modern drift along streams and lakes, has been published by the author, and will be sent on application to members who are specially interested.