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Rozmieszczenie błotniarek w Europie i Ameryce Północnej a teorja Wegenera.

The distribution of Lymnaeids in Europe and in North America, with relation to Wegener's theory.

[Pl. VI — XI]

Oekland (3) has recently drawn attention to certain consequences following from Wegener's theory (3), and concerning the distribution of the European and the North American fauna. Were Europe to have been connected to North America throughout the Tertiary Period, and in its northern part at the beginning of the Quaternary Period, forming one land-mass, such a state could not but have its repercussion on the distribution of the fauna. Far-reaching interpenetration of the fauna of these continents must have taken place, as a result of which a considerable number of Western European species would be found in Eastern America, and *vice versa*. Such species actually exist, but in such small number as compared with what might have been expected, that Oekland concludes that the theory of a transient existence of land-communication between Europe and America corresponds more closely to zoogeographic data than does that of Wegener.

The problem raised by Oekland should receive the consideration of specialists, who would investigate it for the various systematic groups; Oekland himself based his conclusions on rather inadequate material, and treated the matter fairly generally, appealing, however, to zoologists, in particular to those engaged in the study of arthropods to extend the material

from which he drew his conclusions. This paper is written with the object of showing that even so small a group as that of the Lymnaeids, which was, until recently denied any zoogeographical significance, can also be of use for the elucidation of this question.

Kobelt wrote as long ago as 1904: „Von den Süsswasserschnecken sind die Limnaeen geographisch am wenigsten zu verwerten. Nicht nur als Gattung, sondern auch mit allen wichtigen Untergattungen in die Kreide zurückreichend, finden sie sich so ziemlich überall, wo Wasser zum Leben vorhanden ist und die zahlreichen Formen sind ausnahmlos nur Lokalformen der altbekannten Arten, die wir wohl nach den Verhältnissen unterscheiden können, unter denen sie leben, nicht aber nach ihrer geographischer Verbreitung" (2).

This view is apparently quite correct, if we take into consideration the facility with which Lymnaeids can be transferred from one reservoir to another, in all probability by the agency of aquatic birds. It has been proved experimentally that Lymnaeid eggs can pass undamaged through the alimentary canal of swans, and can develop further after being excreted with the faeces into the water. There can be no doubt that such birds as ducks, geese, swans etc. often swallow Lymnaeid egg-capsules together with water-plants, such as *Lemna*, and carry them in their alimentary canal possibly over quite considerable distances, in this way extending the geographic limits of the given species of Lymnaeid.

In 1916 I found very large numbers of the Lymnaeid *Radix ovata* forma *B* in a small pond in the Crimean steppes. This pond had come into existence only four years previously to my arrival in the Crimea, having been formed after the sinking of an Artesian well, and was not connected with any surface reservoir, there being not even an outlet for the water. These animals could only, therefore, have been carried to this pond, probably by birds, from other ponds. Since, however, no other open water reservoir existed within a radius of 20 km., they must have been carried at least over this distance. This observation appears to be clear evidence of the rapidity with which at least certain species of Lymnaeids can be transported, and, in view of this one might expect, should Wegener's theory be correct, to find the same genera and species of Lymnaeids on both sides of the Atlantic.

Thanks to the works of F. C. Baker, of Geyer, of Annandale and Rao and of many other authors, we now know more of the systematics of this family than was possible at the time when Kobelt expressed the above-quoted view. Although we are still far from possessing an exhaustive knowledge of the whole Lymnaeid group, yet already a knowledge of the distribution of many of its representatives is not without importance for zoogeography, as will be shown in this paper.

According to F. C. Baker's monograph (1) 64 species of Lymnaeids are to be found in North America. Even should it be impossible to admit the independent existence of certain of these species, we would even so undoubtedly have here a large number of species and genera different from the European. In Europe only about 10 species [1]) are to be found. Among the considerable number of forms occurring in both continents, only three common species are to be found, viz., *Lymnaea stagnalis* (L.), *Stagnicola palustris* (Müller), and *Galba truncatula* (Müller). We shall first consider the distribution of these common species.

Lymnaea stagnalis: in almost every part of Europe, from the north of Morocco to the far north (in Scandinavia to lat. 69° N); it does not occur in Iceland; to the west this form is found in all parts of Great Britain and Ireland and to the east throughout Siberia to the Bering Sea [2]).

The distribution of this form in North America is shown on plate (map) VI, compiled according to Baker's data [3]). We see that here, too, this species is to be found from sea to sea, appearing to pass in a wide and long zone through Yukon Territory and Alaska to Asia. On the Atlantic sea-board this species does not appear in Labrador, in Nova Scotia, on the Hudson Bay coast or in Greenland.

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[1]) I have not sufficient evidence for the independent existence of the Irish species *Cyclolimnaea involuta* (Harv.), which for this reason will not here be considered.

[2]) The southern boundary in Asia does not, in this case, interest us, and, similarly as for the following species, will not be considered here.

[3]) All the maps except that on pl. VII are based upon the data of Baker; the map on pl. VII is based on my paper on *Myxas* (4) with later additions and corrections.

Stagnicola palustris has a similar distribution on both continents, perhaps on the whole a somewhat wider one than that of the preceding form. In the Old World it is to be found from North-West Africa throughout Europe to the Arctic Ocean, and from the British Isles through Siberia to the Bering Sea. In America, it is to be found further to the south, and passes in a broader belt than *Lymnaea stagn.* from ocean to ocean, reaching Hudson Bay on the East. This species also appears to cross into Asia through the Yukon Territory.

Both of the above forms passed from one continent to the other. The question arises whether this passage was over the Atlantic Ocean, or the Bering Sea. Baker, in his monograph, issued before the publication of Wegener's theory, considered the Asiatic origin of the American types more probable than the European. „The north-eastern Greenland-Iceland connection, so ably advocated by Dr. Scharff, does not appear to have been made use of by the Lymnaeas, the characteristic European species *stagnalis* and *palustris* being absent from Greenland and northeastern America" (1). Wegener's theory does not throw any further light on this matter, and at present it appears from a study of the map showing the distribution of *L. stagnalis* in America that this species could have migrated only by the trans-Pacific route. The north-western branch passing through the Yukon and Alaska towards Asia would seem clearly to indicate this, and the same applies to *Stagnicola palustris.*

Matters are not so clear for the third species, *Galba truncatula.* In the Old World this species is equally widely distributed from North Africa to the Arctic Ocean, throughout Europe and Northern Asia. Of all three species, this one reaches furthest west, since it is not limited in this direction by Scandinavia and the British Isles, but is also found in Iceland. This would appear to suggest that this form migrated to America by the trans-Atlantic route.

The absence, however, of this, on the whole, coldwater species from Greenland would tend to negative this supposition. In America, according to Baker, *G. truncatula* is to be found only in the Aleutian Islands, in Alaska and in the Yukon Territory. Should this actually be the case, this would be excellent evidence that this Lymnaeid had migrated to America from Asia

via the Pacific, and not from Europe over the Atlantic. Unfortunately, however, it appears to me that Baker divided this genus into too many species, certain of which may have to be incorporated into *G. truncatula* in this way widening the occurrence of this species. However this may be it is of striking significance that the distribution of *G. truncatula* is, similarly to that of the two preceding species, distinctly orientated towards Asia, and that it is likewise absent from Greenland, although it does not avoid cold-water ponds. These facts would seem to indicate that this species had, in the same way as the two preceding species, passed over from Asia by the trans-Pacific connection.

In this way, we see that the three species common to both continents do not support Wegener's theory. An even stronger argument against this theory is given by those species occurring in only one of these continents, but reaching to one or the other side of the Atlantic Ocean.

In Europe the most important of these are the representatives of the *Radix* genus, if only for the reason that certain species of this genus are widely distributed in the Old World, are capable of adapting themselves to the most varied conditions of existence, and are, as is shown by my above-cited observation in the Crimea, readily transported from place to place. One of the representatives of this genus, *Radix pereger* (Müller) is to be found in large numbers even in Iceland, from North Africa to latitude 70° N in Scandinavia, and from the Atlantic through Siberia to Kamchatka. Others, such as *Radix auricularia* (L.) and *R. ovata* (Drap.) are almost as widely distributed, with the exception of North Africa and Iceland. All three forms are to be found throughout the British Isles and in Scandinavia; their distribution extends, as we have seen, along almost the entire European Atlantic sea-board, including the European islands, which should, were Wegener's theory correct, have given every possibility for the representatives of this genus to pass over to North America, at the time when the two continents formed one landmass or were at least very nearly contiguous, the more so that these species are not new arrivals on the Atlantic sea-board, as at least some of them existed in England during the Pliocene. In North America, on the other hand, the genus *Radix* does not

appear at all, with the exception of the species *Radix auricularia*, which was recently imported by man.

Another genus which in Europe reaches the Atlantic is *Myxas*, species *glutinosa* (Müller). Map on pl. VII illustrates the distribution of this species in the Old World, the separate colonies in Poland and Eastern Europe being marked by black dots [according to my previons paper (4)] and the more numerous groups of colonies by crosses. We see that this genus similarly attains the Atlantic coast or North Sea in France, Ireland and Jutland. This genus also has been found in England in the upper Pliocene and the Pleistocene, and is also unknown in North America.

A third example is afforded by the genus *Leptolimnaea*, whose species *glabra* (Müller) attains the Atlantic in France, Ireland and northern England, passing through Jutland, southern Sweden and the Baltic States to the neighbourhood of Leningrad, and probably considerably further, to the Volga basin and Siberia.

In North America a considerably larger number of species are to be found on the Atlantic sea-board, which do not occur in Europe. Baker gives 18 such species (excluding those whose distribution is confined to the more southerly portions of the North Atlantic, such as the Gulf of Mexico, or which, although to be found in the vicinity of the coast, do not actually attain it, such as *Acella haldemani*). Although, as has already been mentioned, Baker took the sub-division of the genus *Galba* probably somewhat too far (it is not possible for the author without an actual examination of the North American material to state definitely to what extent this is the case), there can be no doubt that a considerable number of species are to be found on the Atlantic sea-board of North America which have not crossed over to the Old World. The list of these, given below, is according to Baker's monograph.

The most interesting from the point of view of our problem are two species occurring in Greenland. One of these, *Galba holbölli* (Beck-Müller) is to be found only on this island (it is, in my opinion, quite probable, as will be shown in the following paper, that this species constitutes merely a variety of *G. vahlii*). The second species, *Galba vahlii* (Beck-Müller) has a much wider distribution, as is shown by the dotted area on Pl. (Map) VIII — this species passes from Greenland to Labrador,

whence it is to be found in a broad belt through the whole of North America to Yukon Territory.

The remaining species do not occur in Greenland or even in Labrador. Several types of distribution, according to the magnitude and shape of the area over which these animals occur, may be distinguished. These are:

1. Species of a wide distribution similar to that of *Lymnaea stagnalis* in North America. To this type belong: *Galba caperata* (Say), which is to be found between the Atlantic and the Pacific (Map on pl. IX), but whose northern limit does not extend as far as that of *stagnalis; Galba parva* (Lea), occurring over a wide area around the Great Lakes, and extending to the Atlantic on the east, but not reaching the Pacific on the west, and not extending as far north as *caperata; Galba humilis* (Say), reaching from the Atlantic to the Pacific, and from the Gulf of Mexico to Nova Scotia and the Gulf of St. Lawrence; this species has thus a much wider range of distribution than *capereta; Galba obrussa* (Say), similarly distributed to *humilis*, but reaching further to the north.

2. The second type of distribution is represented by *Pseudosuccinea columella* (Say), found over a considerable area on the Atlantic sea-board. This species extends in the form of its sub-species considerably further to the south, but, as the southern forms do not here concern us, they are not marked on the map on pl. X.

3. The third type is exemplified by *Bulimnea megasoma* (Say), illustrated on Map on pl. XI. This species is distributed around the Great Lakes, whence it passes along the St. Lawrence River to the Gulf of St. Lawrence, whilst to the north it reaches to Hudson Bay. The limits of distribution of other species included by myself in this type are different from those of *B. megasoma* in that they mostly run along the Atlantic coast over a much greater area to the south-east of the St. Lawrence, whilst they do not extend so far to the north. These species are: *Galba elodes* (Say), grouped mainly to the south of the Great Lakes, and reaching the Atlantic in the latitude of New York State; *Galba reflexa* (Say), grouped similarly to *elodes* to the south of the Great Lakes, but in a more westerly direction, and reaching along the St. Lawrence River to the sea; *Galba catascopium* (Say), from the vicinity of the Great Lakes, and reaching fairly far to

the north (to latitude 55° N), touching the Atlantic coast over a considerable distance (from latitude 40 to 50 N); *Galba emarginata* (Say), from the Great Lakes district to the Gulf of St. Lawrence and the Atlantic coast.

4. The fourth type includes species distributed rather to the east of the Great Lakes, the centre of whose area of distribution lies between the Atlantic coast and the St. Lawrence River. This type might be considered as a variety of the preceding type. It is exemplified by *Galba umbilicata* (C. B. Adams), whose distribution is illustrated by the shaded area of map on pl. VIII. Apart from this, the following species belong to it: *G. cyclostoma* (Walker), distributed between Michihan and New York; *G. oronensis* (Baker), between the St. Lawrence River and the Atlantic. The extreme forms of this type would be those species limited practically exclusively to the Atlantic coast, such as *Galba owascoensis* (Baker), occurring only in New York State, or *G. pseudopinguis* Baker, to be found only on Long Island (N. Y.).

Finally we would mention *Galba neopalustris* Baker, occurring only in the State of Virginia.

If a comparison be made of the above data, applying to Europe and to North America, it will be seen that a surprisingly large number of species whose distribution limits lie along the Atlantic coast have not passed from one continent to the other. If it be remembered that certain of these species are very widely distributed in their continent, and that these forms readily pass from one reservoir to another, the obvions conclusion is that the distribution of European and American Lymnaeids in no way supports Wegener's theory. It is difficult to conceive how, were both continents to have been closely connected as is required by this theory, the Lymnaeid fauna could remain so distinct, and that the connection between these continents could leave no trace in the distribution of such widely spread forms as the genera *Radix*, *Pseudosuccinea*, *Myxas* and a number of species of the genus *Galba*.

The above facts agree far more satisfactorily with the theory of bridges connecting the two continents, which remained in existence barely long enough to allow those species able to extend most rapidly their limits of distribution, such as *Lymnaea stagnalis*, *Stagnicola palustris*, and *Galba truncatula*, to cross over to

another continent, but whose existence was too transient to allow the other forms to do so. As far as concerns the Lymnaeids, only the trans-pacific bridge could be considered; this family was not able, or perhaps had not time to cross the trans-atlantic bridge. They were able to cross from Europe to Iceland (*Radix pereger*, *Galba truncatula*) but apparently time did not suffice to allow them to reach America; we do not consider that climatic conditions can have been an obstacle to their passage, as both species are well able to endure low temperatures. From the other side, *Galba vahlii* reached no further than Greenland, without even attaining Iceland.

The above conclusions agree in every way with those of Oekland as to the bearing of zoogeographical data on the theory of bridges connecting the two continents and on Wegener's theory. The distribution of the fauna has certain peculiarities which fit in well with the theory of bridges, but which appear strange and incomprehensible if considered in the light of Wegener's theory.

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OBJAŚNIENIE TABLIC. — EXPLANATION OF PLATES.

Pl. VI. Rozmieszczenie *Lymnaea stagnalis* w Ameryce. — Distribution of *Lymnaea stagnalis* in America.
Pl. VII. Rozmieszczenie *Myxas glutinosa*. — Distribution of *Myxas glutinosa*.
Pl. VIII. Rozmieszczenie *Galba vahlii* (przestrzeń zakropkowana) i *G. umbilicata* (przestrzeń kreskowana). — Distribution of *Galba vahlii* (dotted) and *G. umbilicata* (shaded).

Pl. IX. Rozmieszczenie *Galba caperata*. — Distribution of *Galba caperata*.
Pl. X Rozmieszczenie *Pseudosuccinea columella*. — Distribution of *Pseudosuccinea columella*.
Pl. XI. Rozmieszczenie *Bulimnea megasoma*. — Distribution of *Bulimnea megasoma*.

STRESZCZENIE.

Autor omawia rozmieszczenie w Starym i Nowym Świecie przedewszystkiem trzech gatunków wspólnych: *Lymnaea stagnalis*, *Stagnicola palustris* i *Galba truncatula*, wykazując, że prawdopodobnie przybyły one z jednego lądu na drugi przez most transpacyficzny. Liczne pozostałe rodzaje i gatunki błotniarek, ograniczone w swem rozmieszczeniu do jednego z tych lądów, ale rozsiedlone nad Atlantykiem, i to niektóre z nich już co najmniej od końca trzeciorzędu, nie popierają ani jednym faktem teorji Wegenera; jeśliby oba lądy, zgodnie z teorją, jeszcze w końcu trzeciorzędu, a północne ich krańce nawet w początku czwartorzędu, były ze sobą połączone, musiałoby nastąpić znaczne przemieszanie fauny błotniarek obu lądów, czego nie widzimy. Wzajemna obcość i odrębność obu faun przemawia raczej przeciw wegenerowskiej teorji.

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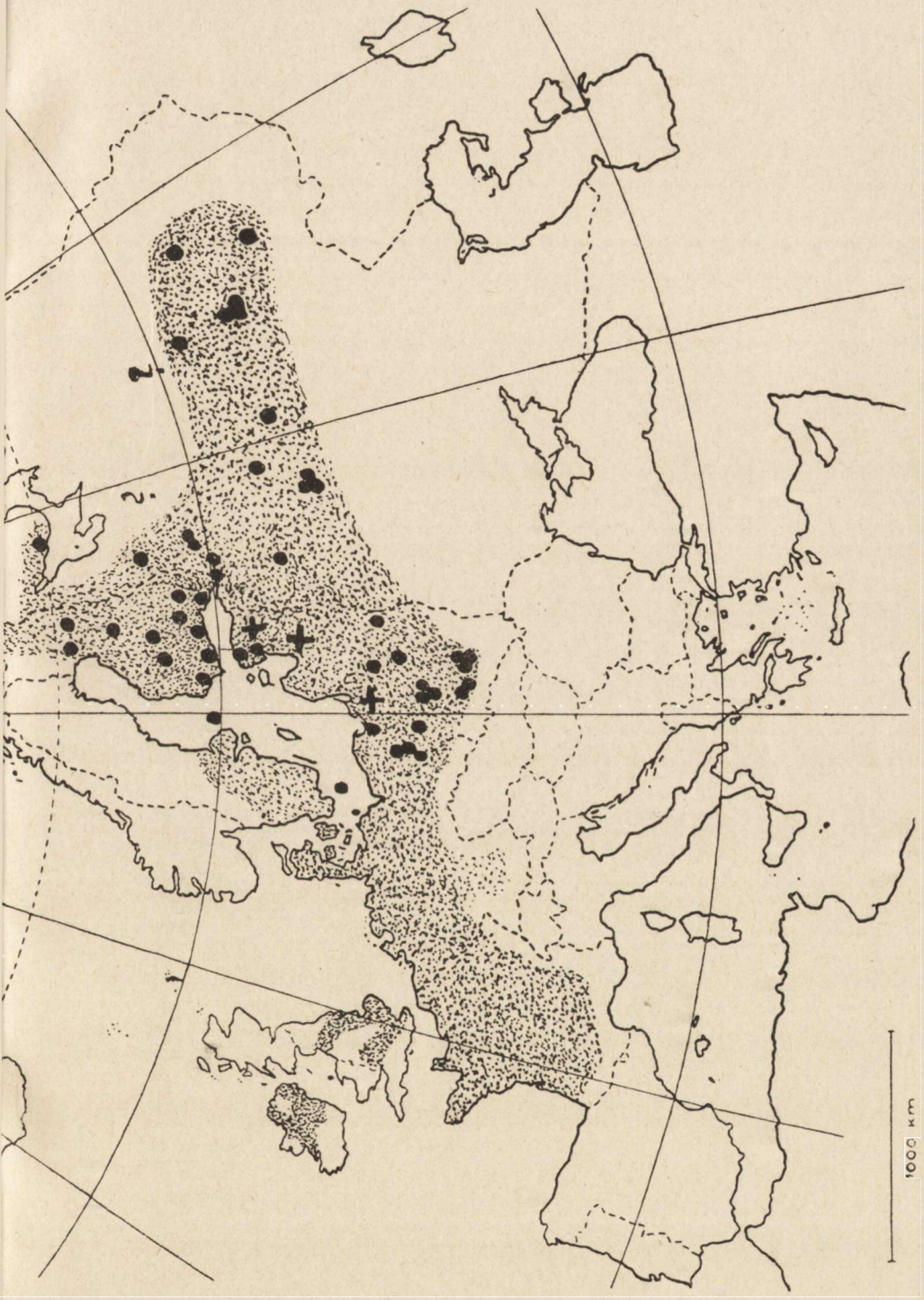
Tab. VII.



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Tab. XI.

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