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1939

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## Distributional Studies of the Naiades as Related to Geomorphology

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THE WRITER welcomes the opportunity to publish in the Journal a few remarks on the value of Naiades in geomorphic studies. Because of limitation of space it will not be possible to treat the subject thoroughly, but two objectives may perhaps be attained: first, consideration of fallacies bearing on the methods of migration in this group; and second, introduction to papers which unquestionably indicate the significance of careful zoögeographical studies of fresh-water mussels to physiography and vice versa.

In his recent article, Johnson<sup>1</sup> states the issue: "Do these mussels require direct fresh-water connection between two streams in order to pass from one to the other?" In my paper<sup>2</sup> discussing the Naiades of the Cahaba River, this question was not answered directly, although a crossing by stream confluence was implied. For most malacologists sufficient affirmation to show that migrations of mussels take place through stream connections is already available in published reports. But, in this day of specialization, I can well appreciate the need for explanatory statements for clearing up the difficulties of those not familiar with a field as specialized as this phase of malacology. Let us first review the significance of the evidence offered by some biologists that mussels can be transported from one drainage to another by birds.

Many workers, such as Call, Mather, Gray, Fewkes, Sage, Frierson, Adams, Cotton, and others, in papers listed at the end of this article, have noticed fresh-water mussels attached to the feet of aquatic birds. Some have been content simply to record the observation, while others draw the inference that a general distribution of mussels can be explained simply on the basis of these observations. Evidently, as prominent a worker as Simpson<sup>3</sup> held this opinion. It should be pointed out, however, that so

1. Douglas Johnson, "Biologic Evidence of Capture." *Jour. Geomorph.*, Vol. 2, pp. 88-91, 1939.  
2. Henry van der Schalie, "The Naiades (Fresh-Water Mussels) of the Cahaba River in Northern Alabama." *Occ. Paper Mus. Zool. Univ. Mich.*, No. 392, pp. 23-28, 1938.  
3. C. T. Simpson, "On the Relationships and Distribution of the North American Unionidae, with Notes on the West Coast Species." *American Naturalist*, Vol. 27, pp. 353-358, 1893.

far as can be determined from accounts in the literature no one has ever established that fresh-water mussels *have actually been transported from one stream to another in this manner*. That some groups of fresh-water mollusks may be distributed by means of birds is not questioned here, but there is apparently no instance yet known where the mussels are transported across divides in this way.

Perhaps the strongest evidence against the distribution of mussels by birds is that most species of mussels have a definite and characteristic distribution pattern within one or more of the major drainage systems. Such patterns would not be likely to develop if mussels were haphazardly carried about from stream to stream by birds. Furthermore, the protagonists of passive migration of mussels by means of aquatic birds fail to take into account the life history requirements of our Naiades. All North American fresh-water mussels are parasitic in their larval stage on some species of fish, before they are capable of beginning life in the environment in which we normally find them. (One exception to this is *Simpsoniconcha ambigua* (Say) which is parasitic on the mud-puppy, *Necturus*.) Assuming that a mussel which accidentally attached itself to the foot of an aquatic bird were a gravid female, and that that mussel with its potential glochidia (also an assumption because glochidia are shed at specific periods) reached a body of water belonging to another drainage, it would yet not necessarily establish a colony of mussels there, because the particular fish host which carries that particular species of mussel would necessarily have to become parasitized to complete the life cycle of the mussel. Also, even assuming that all this did happen by chance, the ecological demands for most species of mussels are such that the young mussel dropping from the fish would have to arrive in an environment suited to it, a condition which adds materially to the hazards involved. Considering all such specific requirements in combination with the absence of substantial proof that mussels have ever been transported successfully from one drainage to another by means of aquatic birds, I believe that we can dismiss such contentions until a time when someone can more fully substantiate them.

On the other hand, there is an abundance of evidence to show that mussels make use of direct connections between streams to migrate from one to the other. An analysis of Simpson's<sup>4</sup> paper, *which is now very much out-of-date*, will perhaps best develop this idea historically, and

4. Simpson, Op. cit., Quotation on page 354.

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5. Johnson. Op. cit.  
6. Bryant Walker  
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29-34, 40-47, 191  
7. A. E. Ortman  
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S. Henry van der  
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will also more definitely answer Johnson's recent criticism on this score. Simpson wrote:

Those streams which fall into the Atlantic are peopled by an entirely different set of forms, the Appalachian chain seeming to act as a sharp barrier between the two regions. Many of the Mississippi Valley species have spread into Michigan, a few into Canada, into streams in New York that flow into the Atlantic, and two or three of these are met with in the Red River of the North, and the waters about Hudson Bay; while below the southern end of the mountain range, there is another mingling of groups.

In this quotation we note that Simpson, as a pioneer, merely calls attention to the areas in which there seems to be a "mingling of groups." He admits that the groups are quite distinct for whole areas, but he is at loss to explain why they seem to mingle in the particular regions he mentions. He had a few facts and lacked essential data, but he was willing to make a big guess (see Johnson's quotation<sup>5</sup>) as to how these faunal groups "mingled." Is it perhaps unscientific to consider it significant that those areas, which as early as 1893 were zones where the "mingling" was observed to occur, are the areas which later were definitely shown to have had connections across divides with drainages in adjoining areas?

If we analyze Simpson's paragraph we note that he finds "mingling" in the following zones: (1) Michigan, Canada and New York; (2) Red River of the North and the waters about Hudson Bay; and (3) "the southern end of the mountain range," by which he probably meant the Tennessee-Alabama River drainages. In several of these areas physiographers themselves have given us basic facts to show river connections across divides during postglacial time. This data has been used in turn by the malacologists to account for the distribution of mussels as we find them in these regions at present. Though it is admitted that we have hardly exploited these possibilities fully, there is no question but that the facts given by Walker<sup>6</sup> accounting for the distribution of Mississippi River mussels in Michigan, are essentially true. Furthermore, this account has been elaborated upon by Ortmann<sup>7</sup> and van der Schalie,<sup>8</sup> and

5. Johnson, Op. cit. See p. 90.

6. Bryant Walker, "The Distribution of the Unionidae in Michigan." pp. 7-17. Privately printed by the author, 1898.

———, "The Unionid Fauna of the Great Lakes." *Nautilus*, Vol. 27, pp. 18-23, 29-34, 40-47, 1913.

7. A. E. Ortmann, "Distributional Features of Naiades in Tributaries of Lake Erie." *Amer. Midland Naturalist*, Vol. 9, pp. 101-115, 1924.

8. Henry van der Schalie, "The Naiad Fauna of the Huron River in Southeastern Michigan." *Misc. Pub. Mus. Zool. Univ. Mich.*, No. 40, pp. 10-14, 1938.

the explanations tally accurately with the events expounded by glacial geologists and subscribed to by physiographers. In these accounts there is ample evidence to show that mussels crossed these present divides only when rivers had formerly crossed them.

Unfortunately the area in the region of the Red River of the North has never been carefully studied by anyone particularly interested in the ecology and distribution of Naiades. There is, however, already sufficient evidence to indicate that if mussels crossed the divide in this region it probably took place by way of the well known River Warren, the outlet of Glacial Lake Agassiz, past Traverse and Big Stone lakes. On the basis of the correlations already noted between such river connections and the "mingling" of the mussel fauna of the two distinct river systems, there is already a strong likelihood that careful studies in this region would give highly interesting results to both the zoögeographer and the geomorphologist.

As for the region designated by Simpson as "the southern end of the mountain range," we might safely assume this to mean the Tennessee-Alabama region. There is now some basic factual data<sup>9</sup> to support the view that mussels from the Tennessee River have crossed into the headwaters of the Alabama drainage at two different periods.

Another crucial region where a crossing of divides has been observed is in western Montana and northwestern Wyoming where fish as well as mollusks have made the crossing. *Unio luteolus* (now called *Lampsilis siliquoidea*) was long ago interpreted by Cooper<sup>10</sup> as having crossed the divide from the headwaters of the Missouri River into the drainage of the Columbia River. Since there is some question concerning the reliability of the record of *luteolus* in Spokane River, an attempt is now being made to verify this record of Cooper. Furthermore, Evermann<sup>11</sup> gives an interesting account to show that certain fishes have freely crossed this divide in an area known as Two-Ocean Pass. He says: "Evidently, Yellowstone Lake and the Upper Yellowstone River were stocked from the west, and almost certainly via Two-Ocean Pass. The probability that the outlet of Yellowstone Lake at one time was toward the Pacific, as claimed by geologists, only strengthens this solution of the problem." If fishes have freely crossed the divide at this point, mussels which are

9. Henry van der Schalie, "The Naiades (Fresh-Water Mussels) of the Cahaba River in Northern Alabama." *Occ. Paper Mus. Zool. Univ. Mich.*, No. 392, pp. 23-28, 1938.  
10. J. G. Cooper, "Shells of Montana." *Amer. Naturalist*, Vol. 2, pp. 486-487, 1868.  
11. B. W. Evermann, "A Reconnaissance of the Streams and Lakes of Western Montana and Northwestern Wyoming." *Rept. U. S. Comm. Fish.*, pp. 22-26, 1892.

parasitic on them might have been. However, certain matters make it seem questionable. A more careful study of the record given by Cooper is necessary.

Though the Naiad fauna of the application of these facts to this line have been made, the work proceeded on the basis of the work in Germany are derived from the fact that the mussels have a long history since Miocene time, and the stability which is intrinsic to the inhabitants of an area of structural characteristic maintained even though stream capture to be considered in this way Haas believe in stream connections. For to clearly detect zones of stream connection.

Since the above are strongly urged, anyone interested in the distribution and ecology of mussels should consult the references in the footnotes.

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12. C. T. Simpson, Op. cit.  
13. Fritz Haas, "Die geologische Ver. d. pr. Rheinfl."  
14. W. Kobelt, "Der etc Ver. d. pr. Rheinfl. u. W."  
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parasitic on them might have crossed as well during the confluence. However, certain matters connected with the ecology of *Unio luteolus* makes it seem questionable that this species has actually crossed this divide. A more careful study is necessary before the writer will accept the record given by Cooper, and upon which Simpson<sup>12</sup> bases his contention.

Though the Naiad fauna in Europe is comparatively meager, limiting the application of these methods considerably, basic contributions along this line have been made. Fritz Haas<sup>13</sup> has clearly stated that W. Kobelt<sup>14</sup> proceeded on the basis that the fresh-water mussels inhabiting streams in Germany are derived from former geological periods. Kobelt believed that the mussels have almost or completely remained unchanged, at least since Miocene time, and that they have passed through a large part of the history of the earth's surface as we find it today. On the basis of this stability which is intrinsic to mussels, Haas has been able to show that the inhabitants of an area in a river in which they originated, possess structural characteristics peculiar to this zone, and these peculiarities are maintained even though portions of the river concerned are separated by stream capture to become connected with another drainage system. In this way Haas believes that the Naiades serve as indicators of former stream connections. Faunal evidence along similar lines has enabled us to clearly detect zones in North America where invasions of mussels by way of stream connections have occurred.

Since the above account is far from complete, the author would strongly urge anyone particularly interested in the relation of the distribution and ecology of our fresh-water mussels to geomorphology to consult the references which follow, in addition to those mentioned in the footnotes.

#### Auszug\*

Johnson hat die Frage gestellt, ob eigentlich eine direkte Süßwasser-Verbindung nötig sei, um den Najaden die Wanderung von einem Fluss in den andern zu ermöglichen. Muschelforscher sind zur Zeit allgemein der Ansicht, dass eine solche Verbindung bestehen muss, um die erfolg-

12. C. T. Simpson, Op. cit., p. 358.

13. Fritz Haas, "Die geographischen Verbreitung der westdeutschen Najaden." *Verh. Nat. Ver. d. pr. Rheinl. u. Westf.*, Vol. 68, pp. 505-506, 1911.

14. W. Kobelt, "Der erdgeschichtliche Bedeutung der lebenden Najaden." *Verh. Nat. Ver. d. pr. Rheinl. u. Westf.*, Vol. 65, pp. 151-162, 1908.

\* Aus dem Englischen übersetzt von Kurt E. Lowenstein.

reiche Entwicklung und Verbreitung der Najaden im neuen Lebensgebiet zu gewährleisten. Obwohl das Anhängen von Süßwassermuscheln an die Füße von Wasservögeln vielfach beobachtet worden ist, so ist doch kein einziger Fall in der Fachliteratur angeführt, auf Grunde dessen bewiesen werden könnte, dass eine neue Muschelkolonie jenseits einer Wasserscheide durch derartige Vogelübertragung gegründet worden wäre. Tatsächlich wäre die beschränkte und charakteristische Verbreitung der Najaden ein höchst unwahrscheinlicher Zufall, wenn sie auf die ganz zufällige Art und Weise der Vogelübertragung von Fluss zu Fluss beruhen würde. Ausserdem sind die Möglichkeiten einer erfolgreichen Verpflanzung durch Vögel gering, da die Najadenlarven als Parasiten bestimmter Fischarten leben, und da die jungen Muscheln, sobald sie von den Fischen abfallen und somit ihre Ernährer verlassen, in geeignete Lebensverhältnisse kommen müssen. In Nord Amerika können etliche, im Mississippi Tal heimischen Muschelarten auch in Michigan, Kanada, in manchen dem Atlantischen Ozean zufließenden Strömen New Yorks, im Red River des Nordens und sogar in den Gewässern der Hudson Bay vorgefunden werden. Eine derartige Verbreitung stimmt durchaus überein mit unserer Kenntnis von den nordamerikanischen Wassernetzverbindungen in der spätglazialen und postglazialen Periode. Angeführte Beweise, dass Najaden vom Tennessee River in den Oberlauf des Alabama River übergegangen sind, mögen auf eine frühere direkte Verbindung zwischen den beiden Flussläufen hinweisen. Noch ein anderes berühmtes Beispiel ist aus dem Gebiet des Yellowstone Park bekannt, wo eine unmittelbare Wasserverbindung die Wanderung von Fischen aus dem Stillen in den Atlantischen Ozean über die Kontinentalwasserscheide hinweg ermöglicht.

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