FRESHWATER PEARLY MUSSELS: Pigtoes and Ortmann's Law

by Daniel L. Graf

The esthetic and scientific value of freshwater pearly mussels has captured the interest of collectors and biologists in North America for nearly 200 years. One difficulty inherent in the study of these bivalves is their almost unimaginable conchological variation. Since taxonomists began describing the American mussel fauna, they have debated whether differences in the shapes of various mussels were due to their belonging to different species or whether they were simply the result of within-species heterogeneity.

It has long been observed that many freshwater mussels vary clinally; that is, over the geographic range of a particular species, as the environment in which the animal lives transitions into another, so does the form of its shell. Gradual habitat variation is typical of a long reach of river: the headwaters are very different from the largest parts of the river near the mouth. The transformation from one extreme habitat to another, however, occurs incrementally along the length of the stream.

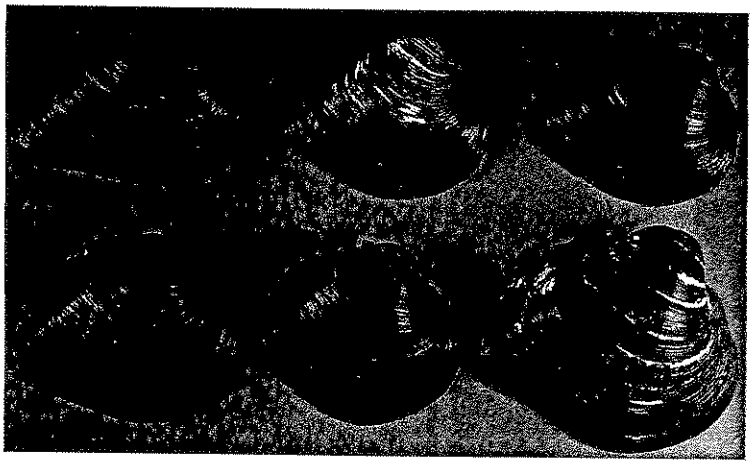
One of the earliest and most important researchers to address this phenomenon was Dr. Arnold E. Ortmann (1920). For many of the freshwater pearly mussels of the upper Ohio River, Ortmann demonstrated that, as he sampled from the headwaters to the larger river, their valves grew more laterally obese, were less elongate, and acquired more robust umbos. This type of clinal conchological variation is now known as *Ortmann's Law of Stream Station*.

An example of the effect of Dr. Ortmann's work was the change in taxonomy of *Fusconaia flava*, the Wabash Pigtoe. Historically, this species was thought to be two: *Fusconaia flava* was the laterally compressed, elongate form occurring in the headwaters and medium-sized rivers, while *F. undata* occurred downstream in larger streams. Besides the ecological difference, *F. undata* also exhibited an extreme "big river" morphology, having an obese, almost trigonal, shell. However, once it was suggested that the *flava*-type shell of the smaller rivers was connected to the "big river" *undata*-type by a series of intermediate forms, the Wabash Pigtoe was united as a single species.

A challenge to the single-species hypothesis for the Wabash Pigtoe, however, was that the "big river" *undata*-form had not been collected from the northward flowing Red River of the North of Minnesota, North Dakota, and Manitoba. This struck me as surprising since the United States' portion of the Red River drains roughly 109,000 square kilometers; the Illinois and Wabash Rivers of Illinois and Indiana drain only 72,000 km^2 and 77,000 km^2 respectively, yet the "big river" form of the Wabash Pigtoe can be found in both of these large-but-smaller streams. For science to be dealing with a single species, there must be a fundamental difference between populations of the Hudson Bay and Mississippi drainages for Ortmann's Law to operate in one basin but not in the other.

What if the Wabash Pigtoe really was two species? In that case, the absence of one species, *Fusconaia undata*, from the Red River and the presence of the other, *Fusconaia flava*, would not be so difficult to explain. Only a limited freshwater mussel fauna gained access to the Red River with the close of the last ice age; *F. undata* simply may not have made it across the continental divide while *F. flava* did. If the Wabash Pigtoe really was two species, I predicted I should be able to distinguish two distinct shell types in the upper Mississippi basin, the parental stock from which the Red River was populated.

To test this prediction, I measured hundreds of Pigtoes from the upper Mississippi and Ohio Rivers, the Great Lakes, and the Red River of the North in order to determine the geographical and ecological distribution of the various morphotypes. I used three different indices to quantify the shape of each pair of valves. The width index was calculated by dividing the lateral obesity of the shell by its anterior-posterior length; the height index was the ratio of the dorsal-ventral height to the length. These quotients enumerated the relative obesity and elongation of a shell, respectively. An index of umbo height characterized the development of the umbos and was simply the projection of the umbo above the hinge line divided by the height of the shell. The use of ratios allowed me to make comparisons among the mussels of different absolute sizes.



Shells of *Fusconaia flava* demonstrating Ortmann's Law of Stream Station. Moving across each row, we start with a creek form in the upper left, and end with a specimen from the Mississippi River in the lower right. Notice the change in shell proportions, such as higher umbos, and more inflated shell. Specimens are from Ohio State University Museum of Biological Diversity. Photo by G. Thomas Watters

I could have treated all *Fusconaia flava* equally as had been done in the past. I would surely then have accounted for every conceivable combination of shell obesity, elongation, and umbo inflation. However, the Wabash Pigtoe occurs in a variety of habitats. All *Fusconaia flava* are not equal; a headwaters Pigtoe is conchologically very different from one further downstream.

To quantify the habitat of each measured specimen, I calculated the average daily discharge of each collection locality from data made available by the U.S. Geological Survey on the World Wide Web (<http://water.usgs.gov>). Each measured Wabash Pigtoe was then assigned to one of eight discharge classes based on the average daily discharge of the locality from which it was collected: 0 (*i.e.*, lakes), 1 to 30, 31 to 80, 81 to 160, 161 to 270, 271 to 540, 540 to 2700, or greater than 2700 cubic meters per second ($m^c\ s^{-1}$). I then analyzed average width, height, and umbo height indices among discharge classes using both parametric and non-parametric statistics to determine whether variation in shell morphology varied according to changes in habitat.

Besides separating *Fusconaia flava* among habitats, I also compared them within each discharge class by plotting "scattergrams" of the umbo height index vs. the width index. By considering Wabash Pigtoes from one discharge class at a time, I greatly reduced the degree of environmental variation among specimens. This allowed me to assume that much of the variation among specimens in a particular habitat was genetic. I predicted that if *Fusconaia flava* was indeed a single species, I should only find one basic shell type per habitat and a single cluster of points on each scattergram. On the other hand, I should find two distinct shell types, and two clusters of points per discharge class if the Wabash Pigtoe was composed of two distinct, reproductively-isolated species. A more thorough account of these methods can be found in Graf (1997a).

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So what did I find? Firstly, within each discharge class, only a single cluster of morphologies was evident in the scattergrams; this led me to conclude that the Wabash Pigtoe is indeed composed of a single species: *Fusconaia flava*. I also demonstrated statistically that in the upper Mississippi and Ohio Rivers, the Great Lakes, and the Red River of the North, the shape of *Fusconaia flava* varies significantly with habitat: as average daily discharge increases, mean shell obesity and umbo development increases while the degree of elongation decreases. Ortmann's Law of Stream Station predicts exactly such a distribution of shell types. These results bring the taxonomic status of *Fusconaia flava* right back to where it was before I ever picked up a caliper, but we are still left with the question of why the "big river" *undata*-form is absent from the Red River of the North.

Having rejected the hypothesis that the Wabash Pigtoe is composed of two species, we are forced to speculate on the differences between the populations of *Fusconaia flava* in the Red River of the North and those of the upper Mississippi. Populations in the Red River may be genetically less variable than the others. I have found that the Wabash Pigtoe, among other freshwater mussel species, may have colonized the Hudson Bay drainage via stream capture; that is, mussels living in the headwaters of a tributary of the Mississippi were "captured" when that stretch of stream changed direction to flow into the Red River of the North (Graf, 1997b). The current population of *Fusconaia flava* in the Red River may have been founded by only a few individuals, and this sort of genetic "bottle-neck" may explain the observed reduction in potential phenotypes.

There are also habitat differences between the Red River and the upper Mississippi. Consider again the Red, Illinois, and Wabash Rivers. Although all three of these large rivers drain areas of equivalent size, the two Mississippi basin tributaries have average daily discharge values roughly five times greater than that of the Red River — 135 m^3s^{-1} versus 595 and 708 m^3s^{-1} for the Illinois and Wabash respectively. So, although the Red River of the North drains a large area, its average daily discharge is that of a smaller stream the size of the Scioto River of southern Ohio. The *undata*-form does not occur in that river either.

We can be satisfied that the observed morphological variability of the Wabash Pigtoe is due to environmental influences and not to two or more distinct species being lumped together as one. However, there remains the problem of the mechanism by which Ortmann's Law of Stream Station maintains this variation throughout the range of the mussel. The hypotheses of environmental and genetic differences between populations in the Red River of the North and Mississippi basins are not mutually exclusive, and they remain in need of further testing.

The Great Lakes basin may also provide further opportunity for the study of Ortmann's Law and its effect on *Fusconaia flava*. Although typical *undata*-type Pigtoes are absent from that basin as well (contrary to much of the literature), "big river" analogs can be found in such systems as the Grand River of Michigan and in Lake Erie.

Acknowledgments

This study was undertaken while I was a graduate student at Northeastern University, Boston, MA and forms part of my M.D. thesis (Graf, 1997a). Profs. E. Ruber and G.S. Jones of Northeastern and R.I. Johnson of the Museum of Comparative Zoology, Cambridge, MA served as my thesis committee and provided invaluable assistance, advice and encouragement; K.J. Boss (Harvard) and J.C. Underhill (U of MN) were also integral in getting this study off the ground. Specimens were loaned by P. Kelley (U of ND, Grand Forks); D. Ó Foighil et al. (U of MI, Ann Arbor), G. Rosenberg (Academy of Natural Sciences, Philadelphia) and R. Hershler (National Museum of Natural History). This particular facet of my thesis work was funded by the Conchologists of America, Inc. My parents made their vehicles and home available for research transportation and a field station, respectively. My thanks are extended to all of the above.

References Cited

Graf, D. L. 1997a. Morphology, Zoogeography, and Taxonomy of *Fusconaia flava* (Rafinesque, 1820) (Mollusca: Bivalvia: Unionidae) in the Upper Mississippi, Great Lakes, and Nelson River Basins. M.S. Thesis, Department of Biology, Northeastern University, Boston, MA. vii + 122 pp.

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For the Record:

Almost a year ago, at the Captiva COA convention in July 1997, amateur malacologist, book dealer, and collector of interesting malacological minutiae Dick Petit gave your editor the manuscript of the following small article, a comment on Peter Dance's "Junonia" reminiscence published in the June 1997 American Conchologist *(p. 18) in honor of the COA 1997 convention on Captiva. A bit of confusion resulted it its being filed away with another manuscript by Dick, already published. With apology to Dick for our unconscionable lateness, we offer:*

More on *Junonia*

by Richard Petit

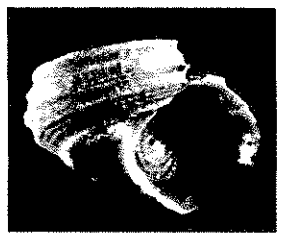
A year ago, in *American Conchologist 25(2)* there was an interesting article by Peter Dance on the appearance of *Scaphella junonia* on an Audubon plate. Dance speculated as to whether or not Sitwell (1949) may have been the first to notice this occurrence.

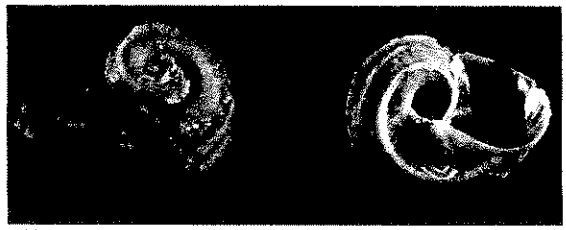
In 1913 W.G. Mazÿck published his *Catalog of Mollusca of South Carolina*. Therein, on page 10, he stated: "...the very rare *Scaphella junonia*...is in the Ravenel collection now in the Charleston Museum. Dr. Ravenel told me in 1868 or 1869 that his Sullivan's Island specimen had been drawn by Audubon on one of the plates of our shore birds for his great work on the birds of North America. A recent search for this figure has located it on plate CCCCIX in company with *Sterna havelli* Aud., one of our local gulls."

Mr. Al Sanders of the Charleston Museum has confirmed (pers. Comm., July 1997) that the Ravenal Collection in the Charleston Museum contains two specimens labeled "Sullivan's Island" bearing the catalog number ChM-R699.

WHAT IS IT?

by Kevan Sunderland





***Cyclostremiscus* sp? 5 mm. Dredged in 80 fathoms, off N coast of Colombia.**