A systematic review of the *Pleurocera laqueata/troostiana* complex in Tennessee, Kentucky, and North Alabama.

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Note: This is a pdf separate compiled from five posts on the FWGNA Blog, slightly edited for continuity. The original dates of their web publication range from September 18, 2024 – January 14, 2025.

1. The Type Locality of *Melania laqueata*

[18Sept24] Nashville, home of the Grand Old Opry and the Brand-New Parthenon, was founded on a low hill overlooking the Cumberland River in 1779. Well situated on a deepwater port with an easy float to the Mississippi River, at the northern terminus of the Natchez Trace to walk home again, the town grew quickly. Nashville was chartered shortly after Tennessee was granted statehood in 1796, and selected as state capitol in 1843, thanks in large part due to her favorite son, Andrew Jackson.

1. Pleurocera laqueata **[1]**

My faithful readership might remember the thumbnail portrait we sketched back on [6Dec19] of a colorful character named Prof. Gerard Troost (1776 – 1850). Troost was a pioneering Dutch American geologist, the founding president of the Academy of Natural Sciences in Philadelphia, who in 1825 sailed down the Ohio River with Thomas Say to the utopian community of New Harmony, Indiana. A scant two years later, however, Troost accepted a call to the University of Nashville, becoming state geologist in 1831. From that date until his death, he travelled widely across the Volunteer State, becoming (according to the Tennessee Encyclopedia online) "the state's best-known antebellum scientist."

Meanwhile, back in New Harmony, his buddy Thomas Say kept the printing presses cranking. And in 1829 Say described a pleurocerid snail named *Melania laqueata*, as follows **[1]:**

> "Shell oblong: spire longer than aperture, elevated, conic, acute: volutions moderately convex, with about seventeen regular, elevated, equal, equidistant costae on the superior half of each volution, extending from suture to suture, and but little lower, and becoming obsolete on the body whirl; suture moderately impressed; sinus obsolete. This species was found by Dr. Troost in Cumberland River. Aside from a difference in form, it may be distinguished from *cancellata*, nob., and *catenaria*, nob., by being altogether destitute of elevated revolving lines. The young shell is carinated."

Today, of the (roughly 1,000) names for species of pleurocerid snails described from the waters of North America, Thomas Say's "*Melania laqueata*" is twelfth oldest **[2].** And populations matching the snails that Gerard Troost sent to Thomas Say from the "Cumberland River," reidentified as *"Goniobasis" laqueata* between 1862 and 1980, re-reidentified as *"Elimia" laqueata* 1980 – 2011, re-re-reidentified as Pleurocera laqueata in the modern day **[3],** have turned out to be common and widespread in rivers and streams throughout the greater Cumberland and Green River drainages, the upper Kentucky River, and Tennessee River drainages west of Chattanooga.

So, the "Cumberland River" covers a big patch of territory. Who could honor the Volunteer Spirit of Tennessee better than a malacologist stepping forward to narrow down (or "restrict') Thomas Say's type locality for *Melania laqueata* to some more precise spot? And one's natural first thought – correct me if I am wrong – would be to assume that Gerard Troost collected that first specimen of *M. laqueata* from the Cumberland River as it runs by his adopted home of Nashville. But alas.

2. Modern Nashville

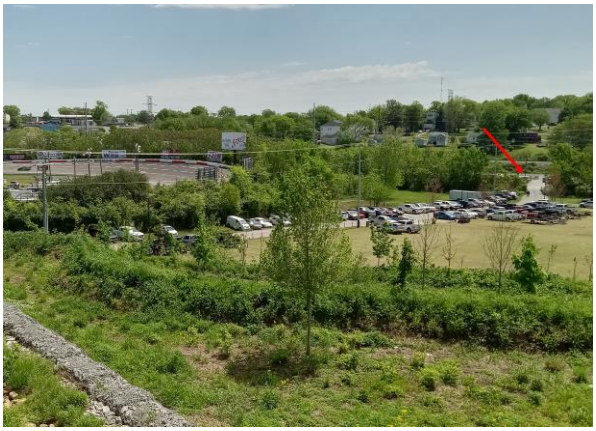
Efforts by the U.S. Army Corps of Engineers to blast the Cumberland River clear of obstacles to navigation began as early as the 1830s. The first lock and dam on the Cumberland River was constructed at Nashville in 1887, and by the 1920s a system of 15 locks and dams regulated the Cumberland River to a minimum depth of 6 feet through the entire state of Tennessee. Attention then turned to the generation of hydroelectric power, the COE constructing a series of gigantic dams in the 1940s through the 1970s, including Old Hickory Dam just 20 river miles upstream from Nashville in 1956.

A visit to the Nashville waterfront today betrays no hint of gastropod habitat, nor indeed, home for macrobenthic life of any sort or description. Downstream the Cumberland River is armored with rip rap boulders. Upstream the flow is increasingly controlled by the generation schedule at the Old Hickory Dam, daily cycles at the Edenwold Gage often reaching amplitudes of 6 feet. Slackwater extends 100 miles above the dam, essentially to the base of Lake Cordell Hull, which extends another 70 miles, essentially to Kentucky. If a viable population of pleurocerid snails of any description survives in the Cumberland River of Tennessee today, I am not aware of it.

It seems to me that we are left with no alternative but to select a tributary of the Cumberland River as the type locality for Thomas Say's *Melania laqueata*. And the tributary closest to Gerard Troost's base of operations currently inhabited by a viable population of pleurocerid snails matching Thomas Say's 1829 description would be Browns Creek, a small stream running north through the state fairgrounds to empty into the Cumberland entirely within the modern city limits of Nashville.

I visited Browns Creek at the state fairgrounds on a sunny Saturday morning this April just past, as crowds were beginning to gather for the INEX Spring Nationals at the Fairgrounds Speedway **[4].** If you examine the left margin of Figure 3 closely, you can see a supertruck practicing on the track below. Browns Creek runs under that bridge I've marked with an arrow, where the race fans have crossed to park in the field.

The stream itself doesn't stink anywhere near as bad as you might expect from its entirely urban catchment. Sure, there was garbage and litter of all sorts everywhere down in the rather narrowly incised ditch through which Browns Creek runs. But the water was clear, and coolish for April, and running over riffles, and you could flip rocks and find mayfly larvae. I've waded into much worse.



3. Tennessee State Fairgrounds

The pleurocerids were not abundant, but with an hour's effort I was able to collect N = 29 *topotypic Pleurocera laqueata laqueata* (Say 1829) from Browns Creek at the state fairgrounds, in Nashville, TN (36.1282, -86.7628). At this point I propose to **restrict the type locality of Melania laqueata Say 1829.**

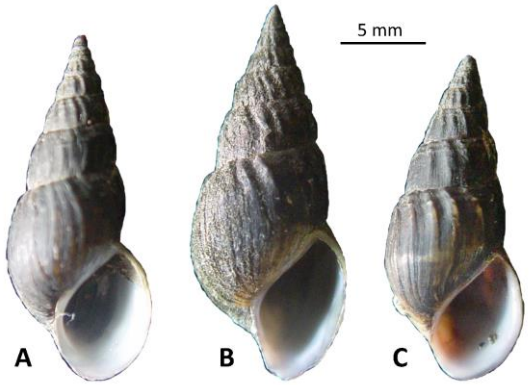
My sample demonstrated the range of shell morphological variation typical of pleurocerid populations everywhere. But before we follow that thread any further, we need to clarify some terminology.

In his original description, Thomas Say focused on the "regular, elevated, equal, equidistant costae" on the whorls of the shell. Such scallop-shaped ridges on the whorls have also been called, by other authors at other times, "costations," "plicae," or "plications." Generally, in previous posts on this blog, I have tended to prefer plications (adj. plicate) to describe that particular shell feature, so let's try to be consistent.

And Thomas Say also went on to stipulate that the shell of his *Melania laqueata* was "altogether destitute of elevated revolving lines." Such shell features have also been called, by other authors at other times, "spiral lines" or "spiral cords" or "striae" or "striations." I have generally preferred striation (adj. striate) in past essays on this blog, so again, let's stick with that. Thomas Say's holotype shell (Figure 1, way up above) demonstrates very strong plications but no striation whatsoever.

So a small sample of the shells born by the newly designated topotypic population of *P. laqueata* is shown in Figure 4. And it should come as no surprise to see significant intrapopulation variation in shell plication. All are plicate around the apex, but the body whorl of shell on the left is essentially smooth, that of the shell on the right strongly plicate, and the shell in the middle approximately half-plicate, around the top of the body whorl only.

The subject of shell plication in pleurocerid snails has come up at least three times previously in the columns of this blog, maybe more **[5],** most recently in an essay I published on *P. troostiana* back in [15Apr20]. My loyal and attentive readership may recall that Calvin Goodrich devoted #3 in his "Studies on the Pleuroceridae" series to plication way back in 1934 **[6].** The laboratory rearing experiments of Misako Urabe **[7]** returned evidence that at least some variation in the strength of shell plication may be an ecophenotypic response to substrate.



1 *4.* Topotypic *Pleurocera laqueata*

And we shouldn't let an opportunity pass to tip our caps to Thomas Say, the Father of American Malacology, as well. In a quaint nineteenth-century fashion, I think he may have tried to telegraph that he noticed intrapopulation variance in the plication of *Melania laqueata*, like a Charles Darwin on the American frontier. His figured holotype clearly shows strong plication ("costae") across the entire body whorl "from suture to suture," much like topotypic shell C above. But in his description, he specified:

> "seventeen regular, elevated, equal, equidistant costae on the superior half of each volution, extending from suture to suture, and but little lower, and becoming obsolete on the body whirl."

The wording of Say's written description about plication on "the superior half of each volution … and but little lower" implies to me a morphology more like topotypic shell B. And that final clause about plication "becoming obsolete on the body whirl" suggests more the morphology demonstrated by topotypic shell A.

Darwin's theory depended on three hypotheses: that populations vary, that such variation yields fitness differences, and that fitness differences drive evolution. The first hypothesis is the easiest to test, but historically, was the most difficult to accept. It is humbling to see a pre-Darwinian systematic biologist such as Thomas Say entertaining an hypothesis that so many 21st-century systematic biologists refuse to consider.

Ah, but. Thomas Say was very, very certain that the shell of his new *Melania laqueata* was "altogether destitute of elevated revolving lines." What is the situation with striation? Tune in next time.

Notes:

[1] Say, T. (1829) Descriptions of some new terrestrial and fluviatile shells of North America. New Harmony Disseminator of Useful Knowledge 2(18): 275 – 277.

[2] *Melania laqueata* is in a five-way tie for twelfth oldest, to be precise, with the four other pleurocerids described by Thomas Say in 1829: *semicarinata, obovata, canaliculata*, and *trilineata*.

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[3] The history of the genus of pleurocerid snails to which Say's *Melania laqueata* has been assigned is long and tortured. For a brief review, see:

- Goodbye Goniobasis, Farewell Elimia [23Mar11]

[4] The Nashville Fairgrounds Speedway is the second oldest continually operating motorsports track in the United States. It hosted Grand National / Winston Cup NASCAR races 1958 – 1984, and NASCAR Busch Series races 1984 – 2000, before being replaced on the schedule by the 1.33 mile Nashville Superspeedway in 2001. Here's a quote from the sportscaster Dave Moody (interviewing Sterling Marlin): "If they announced that five old ladies would push baby buggies around that track, 4,000 people would show up."

[5] Previous essays touching on shell plication in the Pleuroceridae:

- Semisulcospira research: A message from The East [6Jan08]
- Semisulcospira research: A second message from The East [1Feb08]
- What is a subspecies [4Feb14]
- What subspecies are Not [5Mar14]
- Huntsville Hunt [15Apr20]

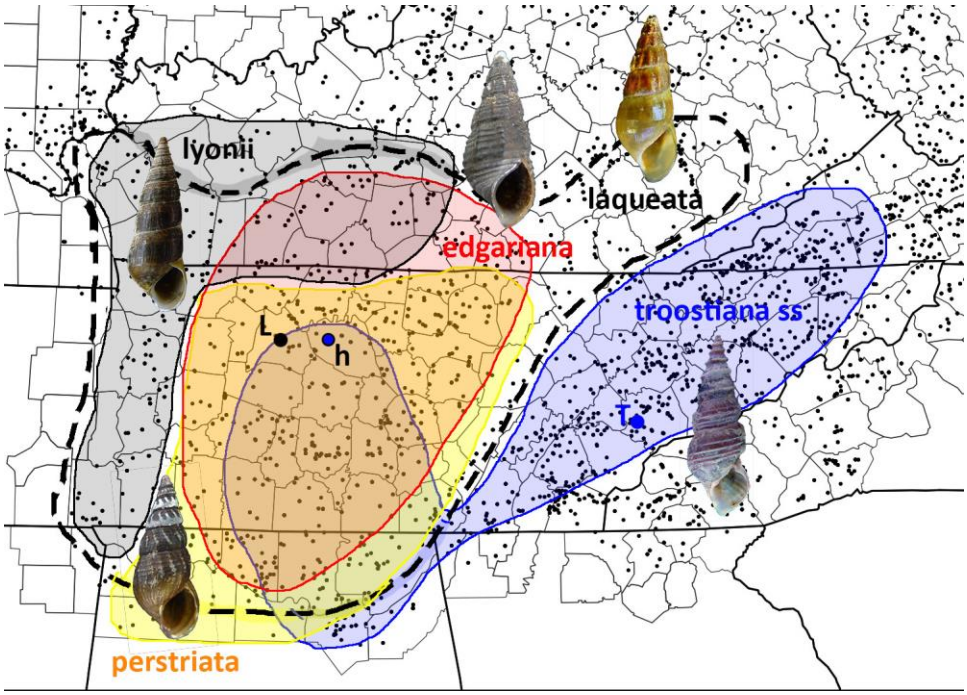
[6] Goodrich, C. (1934) Studies of the gastropod family Pleuroceridae – III. Occasional Papers of the Museum of Zoology, University of Michigan 300: 1 – 11.

[7] Urabe, M. 2000. Phenotypic modulation by the substratum of shell sculpture in *Semisulcospira reiniana* (Prosobranchia: Pleuroceridae). J. Moll. Stud. 66: 53-59.

2. Widespread hybridization between *Pleurocera laqueata and P. troostiana* in streams of the Tennessee/Cumberland

[15Oct24] In the previous essay we focused on Pleurocera laqueata, a widespread and common inhabitant of streams and rivers in Middle Tennessee, central Kentucky, and North Alabama. The species was described by Thomas Say in 1829 **[1]** from specimens collected by Prof. Gerard Troost in the "Cumberland River," an overly broad region which we ultimately restricted to Browns Creek, running through the state fairgrounds in Nashville. The topotypic population of *P. laqueata* bears shells that are variably plicate but never striate, matching Say's original description.

In direct contrast stands Pleurocera troostiana, also first collected by Prof. Troost [6Dec19] but described a bit later by Thomas Say's successor at the ANSP, Isaac Lea around 1838 **[2].** In its East Tennessee type locality, *P. troostiana* bears shells that are variably striate, but entirely without plication. In a painfully detailed and ultimately exhausting series of six essays posted on this blog between December 2019 and July 2020, we reviewed the shell morphological variation demonstrated by populations of *P. troostiana* across Tennessee, Kentucky, and North Alabama, and the elaborate taxonomy that developed in the 19th century in an attempt to capture it.



4 5. The range of *Pleurocera. laqueata* (dashed) compared to the four subspecies of *P. troostiana*

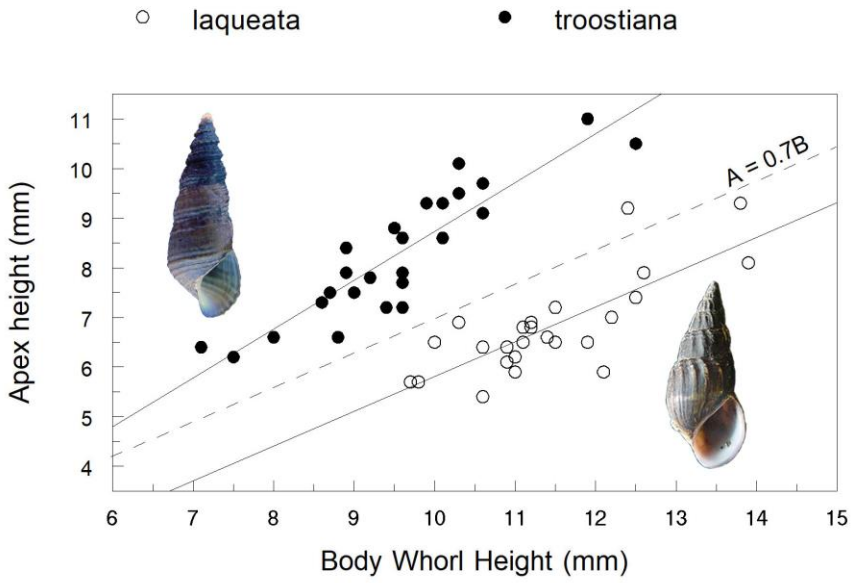
So, if you have more than a casual interest in the taxonomy, systematics, and evolution of the North American Pleuroceridae, I would encourage you to go back and click through my 2019 - 20 series on *P. troostiana* from the links at footnote **[3]** below and download the pdf summary for your files. Otherwise, here is a quick summary.

The range of variably-striate-but-never-plicate populations of *P. troostiana*, which we refer to as *P. troostiana troostiana* or *P. troostiana sensu strictu* (s.s.) is shown in blue above. That is all you will find in East Tennessee. West of Chattanooga, however, as the Tennessee River breaks through Walden Ridge into Alabama and Middle Tennessee, the range of *P. troostiana* begins to overlap with the range of *P. laqueata*, shown as a dashed line. And populations of *P. troostiana* bearing shells that are both striate and plicate, variously identified under the subspecific nomina *perstriata* (yellow), *edgariana* (red), and *lyonii* (gray), begin to predominate. This is not a coincidence.

I have hypothesized that *P. troostiana* hybridizes with *P. laqueata* several times previously on this blog, most prominently in my *P. troostiana perstriata* essay of [15Apr20]. But to show this, we will require a second, independent genetic character of some sort, beyond shell sculpture. Let me back up a couple steps and refocus this entire essay away from shell sculpture, and toward shell shape.

Quite a few 19th century authorities remarked on the "spire elevation" or slenderness of the *P. troostiana* shell. Isaac Lea, in his original description of 1838 **[2],** remarked that the shell of *M. troostiana* is "elevated." In 1841 Lea described *M. teres* (a *troostiana* synonym) as "remarkably elevated, spire much drawn out," and ditto "spire drawn out" for a second *troostiana* synonym, *M. strigosa* **[4].** John G. Anthony **[5]** described his *M. arachnoidea* (yet another *troostiana* synonym) as "rather thin, spire slender and much elevated" in 1854.

Now I daresay that no man nor beast who ever held a gastropod shell in hand, nor cracked it open with tooth, nor crushed it with claw, has ever in the history of this wide earth been more sensitive to that portion of the variance in shell shape that is not heritably genetic than the humble author of the present essay **[6].** My filing cabinets bulge with papers vividly demonstrating ecophenotypic effects on gastropod shell morphology. Bulge. I cannot close them. They remain ajar, to scar my wife's shoulders should she dare enter the sanctum sanctorum wherein I lurk, writing quaint and curious blog posts such as this.



6. Shell shape and shell sculpture in pure populations

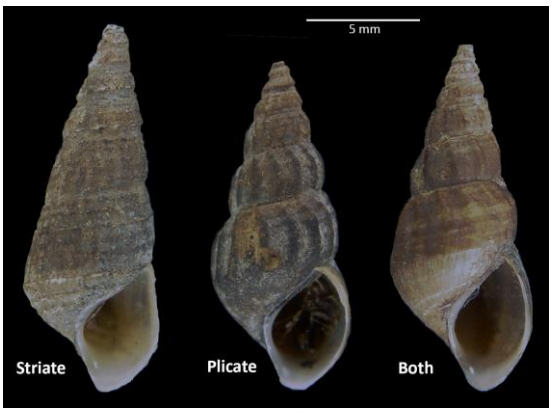
But the heritable component of shell shape in gastropod mollusks is equally undeniable. Working with *Physa acuta* in controlled conditions, I have estimated the heritability of simple shell length (SL) as h^2 = 0.429, and that of body whorl length (B) as h^2 = 0.321 **[7].** In recent years I have favored the simple regression of shell width on shell length **[8],** or body whorl height (B) on apex height (SL), as a quick and reliable method of extracting the heritable component of shell morphological variance **[9, 10]** correcting for the age structure variance inevitable in wild populations.

So, last month I reported the collection of 29 topotypic *P. laqueata* from Browns Creek in Nashville, mapped as "L" on Figure 5 up above. Of those, N = 25 were adults. I measured total shell length for each (SL) and body whorl height (B), then calculated apex height as SL – B = A. These data are plotted on Figure 6. The regression of B on A was A = 0.70B – 1.19 (R = 0.77), a good fit.

I also measured N = 25 shells from a sample of *P. troostiana troostiana* collected from Steekee Creek at Loudon, Tennessee (35.7252, -84.3482), mapped as "T" on Figure 5 **[11].** This is the type locality of J. G. Anthony's (1854) *Melania arachnoidea* **[5],** synonymized under Isaac Lea's *Melania troostiana*, see my essay of [7Jan20], FWGNA

Circular 2 [pdf], or FWGNA Volume 6: 41 – 49 [publications]. The regression of body whorl height on apex height for troostiana was A = 0.98B – 1.11 (R = 0.90), an excellent fit.

Between the two elongated clusters of shell measurements, I have drawn a dashed line corresponding to the function A = 0.7B. As a convenient approximation, it would appear that the two species can be distinguished by the ratio of shell apex height to body whorl height, greater than 0.7 for *P. troostiana* and less than 0.7 for *P. laqueata*.

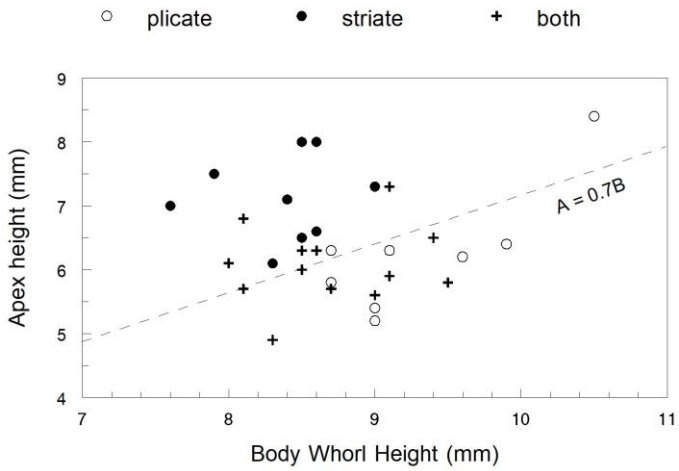


6 *7.* Example *Pleurocera* from Spring Creek

So now let's examine the *Pleurocera* in habiting Spring Creek (Wilson County, TN), a small tributary of the Cumberland River about 45 km east of the state fairgrounds in Nashville, mapped as "h" in Figure 5 way up above (36.1800, -86.2411). The Tennessee Department of Environment and Conservation took a quantitative sample of the Spring Creek macrobenthos back in August of 2014, using a kick net along three linear meters of creek bank to good effect, returning N = 185 *Pleurocera* **[12].**

I subsampled the N = 30 largest adults, measured their shells, and categorized the sculpture on their body whorl, ultimately recognizing (with some head-scratching) N = 9 striate (only), N = 8 plicate (only), and the remainder N = 13 as both striate and plicate. The result is graphed in Fig. 8 below.

There is clearly a significant relationship between shell sculpture and shell shape in this sample of 30 pleurocerid snails, such that the fraction bearing smaller body whorls for their apex height (A > 0.7B) tend to bear striation (only) on their body whorl, and the fraction bearing larger body whorls for their apex height (A < 0.7B) bear plication (only) on their body whorl. With just those two open circles misclassified above the dashed line above, the Fisher's exact probability is p = 0.002 **[13].**



7 8. Shell shape and shell sculpture in Spring Ck.

The most likely explanation for this phenomenon, which we have labeled "character phase disequilibrium" [4Jan22] is nonrandom mating. The data graphed in Figure 8 strongly suggest some sort of reproductive isolation between the slender-shelled striate pleurocerid population of Spring Creek and the fat-shelled plicate population. But the data also suggest that reproductive isolation is incomplete. The largest fraction of the sample, 13/30 = 43%, seem to be hybrids, bearing both plication and striation on their body whorls.

***Pleurocera laqueata* and *Pleurocera troostiana* are distinct, reproductively isolated, biological species that hybridize extensively** in rivers and streams throughout Middle Tennessee, southern Kentucky, and North Alabama. *Pleurocera troostiana* populations are more common in the small creeks, and *P. laqueata* in the larger rivers, and the mixed populations in streams of intermediate size may comprise more hybrids than purebreds.

In keeping with taxonomic tradition, let us reserve the name *P. laqueata* for populations bearing shells entirely without striation, and *P. troostiana troostiana* for populations entirely without plication. Then the subspecific nomina *perstriata*, *edgariana*, and *lyonii* will apply to the hybrids, according to their degree of shell sculpture.

OK, fine. What might such widespread hybridization suggest about the evolution of the Pleuroceridae in North America? Tune in next time.

Notes:

[1] Say, T. (1829) Descriptions of some new terrestrial and fluviatile shells of North America. New Harmony Disseminator of Useful Knowledge 2(18): 275 – 277.

[2] Lea, Isaac (1838-39) Description of New Freshwater and Land Shells. Transactions of the American Philosophical Society (New Series) 6: 1 – 154.

[3] Dillon, R.T., Jr. (2020) The four subspecies of Pleurocera troostiana (Lea 1838), with synonymy. FWGNA Circular 2: 1 - 5. [pdf] This is a summary document for the observations, arguments, and hypotheses I advanced in a series of six blog posts to the FWGNA Blog:

- On The Trail of Professor Troost [6Dec19]
- CPP Diary: The Many Faces of Professor Troost [7Jan20]
- Huntsville Hunt [15Apr20]
- A House Divided [10May20]
- What is Melania edgariana? [5June20]
- The Return of Captain Lyon [6July20]

[4] Brief Latinate descriptions:

- Lea, Isaac (1841) Proceedings of the American Philosophical Society 2: 11 – 15.

More complete English descriptions with figures:

- Lea, Isaac (1843) Description of New Fresh Water and Land Shells. Transactions of the American Philosophical Society 8: 163 – 250.

[5] Anthony, J.G. (1854) Descriptions of new fluviatile shells of the genus *Melania* Lam., from the western states of North America. Annals of the Lyceum of Natural History of New York 6: 80 -132.

[6] In fact, I have designated an entire topic entitled “phenotypic plasticity” in the list of “labels” at the right margin of my FWGNA Blog. If you fire your computer up and click that link you will find 24 essays (as of October 2024) touching upon the component of shell phenotype that is not heritably genetic. Among the most prominent:

- New clothes for The Emperor [7Feb23]
- Elimia livescens and Lithasia obovata are Pleurocera semicarinata [11July14]
- Pleurocera acuta is Pleurocera canaliculata [3June13]
- The Lymnaeidae 2012: A clue [9July12]
- Shell morphology, current, and substrate [18Feb05]

[7] Dillon, R. T., Jr. & S. J. Jacquemin (2015) The heritability of shell morphometrics in the freshwater pulmonate gastropod *Physa*. PLoS ONE 10(4): e0121962. [html] [pdf] For a review, see:

- The heritability of shell morphology in Physa h^2 = 0.819! [15Apr15]

[8] Wethington, A.R., J. Wise, and R. T. Dillon (2009) Genetic and morphological characterization of the Physidae of South Carolina (Pulmonata: Basommatophora), with description of a new species. The Nautilus 123: 282-292. [pdf]

[9] Dillon, R. T. & J. D. Robinson (2016) The identity of the "fat simplex" population inhabiting Pistol Creek in Maryville, Tennessee. Ellipsaria 18(2): 16-18. [pdf] For a review, see:
The fat simplex of Maryville matches type [14Oct16]

[10] Dillon, R. T. (2016) Match of *Pleurocera gabbiana* (Lea, 1862) to populations cryptic under P. simplex (Say, 1825). Ellipsaria 18(3): 10 - 12. [pdf] For a review, see:

- One Goodrich Missed: The skinny simplex of Maryville is Pleurocera gabbiana [14Nov16]

[11] I would have preferred to do these measurements on a sample of troostiana from Lea’s type locality at Mossy Creek, about 50 miles NE of Steekee Creek, but my sample size is insufficient.

[12] The gallon jug containing this (whole, unsorted) bulk sample was released to me by TNDEC-DWR personnel in Nashville on 14Jan21.

[13] Here I count cases above the line and striate = 9, above and plicate = 2, below and plicate = 6, below and striate = 0. The Fisher’s exact probability of that relationship between shell shape and shell sculpture would be p = 0.002.

3. Reticulate Evolution in the North American Pleuroceridae

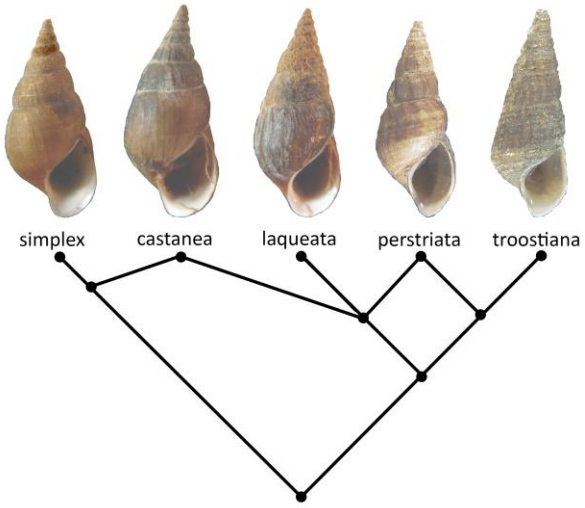
[12Nov24] In the previous essay we reviewed the evidence that populations of two pleurocerids widespread in the Greater Ohio Drainage, P. laqueata and P. troostiana, hybridize extensively in the rivers and streams of Middle Tennessee. And our most useful genetic marker was shell plication, a scallop-shaped ridging pattern characteristic of *P. laqueata*, absent from *P. troostiana* outside the *laqueata* range, but variably present in *troostiana* populations overlapping with *laqueata*.

Sharing most of those same rivers and streams with both *laqueata* and *troostiana* are populations of a third pleurocerid species, Pleurocera simplex, our old friend familiar from five previous essays, see footnote **[1]** below to refresh your memory. The FWGNA Project recognizes two subspecies of *simplex*: the typical form found in small streams throughout the greater Tennessee/Cumberland region and a paler, more heavily shelled form common in larger streams of the Cumberland drainage, extending into Central Kentucky, Pleurocera simplex ebenum.

In 1934, Calvin Goodrich **[2]** published #3 in his "Studies on the gastropod family Pleuroceridae" series, focusing on shell plication. Here is a verbatim quote from page 5:

> "*G. ebenum* (Lea), commonly a smooth species, occurs in the Cumberland River drainage basin. In the upper part of the drainage, material containing plicate shells has been taken. The only lot at hand that can be accepted as a "pure" race of these forms is from New River, Scott County, Tennessee. Of 46 shells from Straight Creek at Pineville, Bell County, Kentucky, 54.4 per cent are plicate. In the Cumberland River a few miles below Pineville, 18 per cent of 72 shells are so sculptured; 74 shells of ebenum taken just above the falls of the Cumberland are 14.8 per cent plicate. The only specimens from the river below the falls which have been seen, taken at Smith's Shoals near Burnside, Pulaski County, Kentucky, are all smooth; so also are shells of all lots of the species ranging as far to the west as streams of Dickson County, Tennessee."

Yes, all of that is true. I myself have confirmed at least seven populations of *P. simplex ebenum* bearing lightly plicate shells scattered about Middle Tennessee, in minor tributaries of the Cumberland, the Harpeth, the Red, and the Duck. We are also aware of 14 such populations in North Alabama tributaries of the Tennessee. All these populations co-occur with populations of *P. simplex* bearing normal, smooth shells and populations of (you guessed it) *P. laqueata*. The first three shells figured at left below were collected from the backs of pleurocerids inhabiting Brush Creek, a tributary of the Red-Cumberland in Robertson County, NW of Nashville (36.4342, -87.0662): an apparently pure *P. simplex*, an apparently pure *P. laqueata*, and what most certainly appears to be a *simplex/laqueata* hybrid ("*castanea*"), almost entirely smooth but bearing tiny plications around the apex.



9. Reticulate evolution in the Pleuroceridae

Exactly as is the case with *P. troostiana*, *P simplex* populations inhabiting East Tennessee, where *P. laqueata* does not occur, never bear plicate shells. Only where the ranges of *P. simplex* and *P. laqueata* overlap in Middle Tennessee and North Alabama does one find pleurocerid populations bearing fat, pear-shaped *simplex*-looking shells with tiny apical plications.

There is not a shadow of doubt in my mind that *P. simplex* hybridizes with *P. laqueata*, just as *P. laqueata* hybridizes with *P. troostiana*. The two shells at right in Figure 9 above were sampled from Spring Creek east of Nashville, carried over from last month: an apparently pure *P. troostiana* and a *laqueata/troostiana* hybrid ("*perstriata*"). **This is reticulate evolution.**

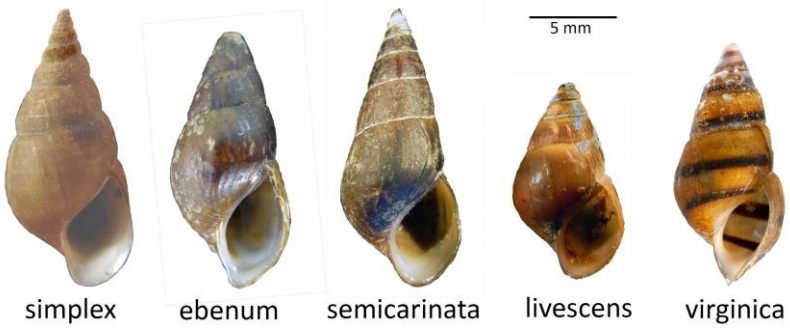
Digging back through the classic literature, it turns out that Isaac Lea described a *Melania castanea* in 1841, the shell of which appears to be a perfect match for the *simplex/laqueata* hybrid populations I have been referring to here. Lea's brief Latinate description appeared in that same early work that featured such notables as *clavaeformis, ebenum*, and *edgariana* **[3],** with a more complete English description and figure following in 1843 **[4].** Lea's type locality, "Maury County, Tenn." is in the upper Duck River drainage, where *simplex* and *laqueata* are both common. Calvin Goodrich **[5]** lowered Lea's nomen *castanea* to subspecific status under *Goniobasis laqueata* in 1940, giving its range as "Headwaters of the Duck River, Tennessee."

10. Melania castanea **[4]**

OK, fine. Given that we have recognized three subspecific names for *laqueata/troostiana* hybrids, I suppose it is only fair to recognize a subspecific name for hybrids between *P. laqueata* and *P. simplex*. So, this week I have added a new (sub)species page to the FWGNA website for Pleurocera laqueata castanea (Lea 1841), with corresponding entries in the gallery and dichotomous key for the Tennessee/Cumberland **[6].** This is the 135th species or subspecies of freshwater gastropod we have recognized as valid in our 21-state study region.

I am every bit as certain that *P. simplex* hybridizes with P. semicarinata in Kentucky and Tennessee, although I have no genetic data or photos to enter into evidence. The two species are only distinguishable by subtle differences in shell shape, the former bearing fatter shells with a larger body whorl, neither demonstrating any sort of shell sculpture (beyond a carinate upper whorl) that might serve as a discrete marker. The range *of P. semicarinata semicarinata* overlaps that of *P. simplex* broadly in the Cumberland, Green, and Kentucky Rivers, and extends much further north, up into Wisconsin, Michigan and New York, where chubby-shelled populations are referred to the subspecies P. semicarinata livescens.

And I am still amazed **[7]** by the 1994 allozyme study of Bianchi and colleagues **[8]** demonstrating hybridization between Great Lakes *P. semicarinata livescens* and the Hudson River population of Pleurocera virginica through the Erie Canal. Those two species bear strikingly different shell morphologies, have entirely distinct ranges, and could not have shared a common ancestor in many, many millions of years. Perhaps since the Appalachian Orogeny?



11. Hybridizing?

Yes, that is my next point. The architects of the Modern Synthesis generally seem to have considered hybrid zones an unstable and transitory step toward speciation **[11].** I am sympathetic with the Darwinian rationale for such an hypothesis, and admit it could certainly hold in many cases. But more recently the research emphasis seems to have shifted toward hybrid zones that give evidence of stability and permanence **[12].**

The photo below comes from the 8Mar24 issue of Science **[13].** Here's the caption: "This fish is the hybrid offspring of an alligator gar and a spotted gar – members of genera that last shared a common ancestor at least 100 million years ago."

The paper being reviewed, by Brownstein and colleagues **[14],** detailed the results of a survey of 1,105 exons over 481 vertebrate species, demonstrating exceptionally slow rates of molecular evolution in gars and sturgeons. Yet gar species last sharing a common ancestor no later than the Cretaceous still hybridize naturally in the greater Ohio and southern Mississippi drainages today.

EVOLUTION

Gars truly are 'living fossils,' massive DNA data set shows

The fish's genomes change so slowly that species separated since the dinosaurs can produce fertile hybrids today

12. Brownstein et al. **[14]**

Could some cranky, washed-up old crackpot wading those same rivers and streams, throwing snails into a bucket and measuring them with rusty calipers, achieve the same results as an international team of eight scientists from six different institutions with "massive" DNA data sets and ten different sources of funding?

The distribution of pleurocerid snails in the rivers and streams of North America is whispering a story to us in a language that we do not understand. It is an ancient story of colliding continents and earthquakes and mountains 10,000 feet high, eroding and shifting and washing into the sea. Most of the pleurocerids of the Greater Ohio drainage, including *P. simplex* and *P. troostiana*, range across the entirety of the state of Tennessee, as well as into Kentucky and North Alabama and even into SW Virginia. Then why are populations of *P. laqueata* absent East of Chattanooga? Is their dispersal capability so much worse than *P. simplex* and *P. troostiana* that they are unable to penetrate Walden's Ridge? I simply do not think so. Here is the story that I hear the pleurocerids whispering to me.

The story I hear is that the crest of the ancient Appalachians, at some point in the millions of years of their orogeny, was approximately where Walden's Ridge lies today, at the eastern edge of the Cumberland Plateau. *Pleurocera laqueata* evolved on the west side of that crest, while *P. troostiana* and *P. simplex* evolved on the East. Then the mountains eroded such that the divide shifted east, opening a hole at Chattanooga, switching the flow of the rivers in which *troostiana* and *simplex* evolved from east to west, bringing those pleurocerid populations into secondary contact with *laqueata*.

I have said it many times **[15],** but I will say it again**. A step off the creek bank in the Southern Appalachians is a step back millions of years**. Look around you, colleagues, look! Those banks are covered with mosses and liverworts, horsetails and ferns. The waters team with dragonflies and stoneflies, gars and hellbenders. And pleurocerid snails jostle each other to graze across every square inch of substrate.

Why does this entire ecosystem seem frozen in time? My hypothesis calls on three independent sets of factors: environmental, genetic and historical.

First, the freshwater environment is more stable than that of the land. Water temperatures lag behind and buffer air temperatures. That buffer is not just seasonal, it is climatological. The temperature in smaller streams, in particular, typically remains very close to that of the ground, 10 – 15 degrees Centigrade year round. Such environments are not simply protected from hot Julys, they are protected from ice ages. And the lower the temperature of the environment, I might add, the slower the generation times of its poikilothermic biota.

Rainfall and storm are similarly buffered. Droughts obviously have less effect on rivers than on the surrounding land, ditto wind and fire. The ecosystems of many (especially smaller) bodies of water are based on allochthonous input, rather than primary productivity, and life could more easily survive (let us say) a cometary impact, and a period of worldwide darkness.

Most of the above, it must be admitted, could also be said for the marine environment as well as the freshwater. This calls upon a second set of factors, which are population genetic.

13. Rock Island State Park, TN **[16]**

In two words, marine populations are gigantic and panmictic. Almost all the mollusks, for example, retain a planktonic larval stage lasting at least a couple weeks, facilitating dispersal over very long distances. Here on the Atlantic side, the population of commercially important eastern quahogs ("cherrystone" or "littleneck" clams), demonstrates no significant allelic frequency differences at multiple allozyme-encoding loci from Canada to Florida **[17].** Ditto oysters, ditto oyster drills, ditto whelks, ditto periwinkles **[18].**

Consequently, when a beneficial mutation arises in a marine population, it spreads quickly in evolutionary time. Diseases, predators, and other riders of the apocalypse spread as quickly as the angels. Speciation is quick, extinction is quick, evolution is quick. The marine molluscan fauna of the Virginia Pliocene does not look like the marine molluscan fauna of the Virginia Recent.

But for better or worse, freshwater populations are small and fragmented. Evolution does not stop, of course; the molecular clock keeps ticking **[19].** But when adaptations evolve (such as reproductive isolation, for example) they do not spread **[20, 21].** The outward appearances of such populations, then, will give the impression of morphological stasis.

So, freshwaters are more environmentally stable than the land, and the populations inhabiting those freshwaters more genetically stable than those inhabiting the sea. There is a third factor. History.

The land mass that we today identify as the "Appalachians," together with the freshwaters that drain those mountains to the ocean, is really, really old. It is clear that several orogenies have taken place, beginning with the Grenville over one billion years ago, proceeding through the Taconic (500 mybp) and the Acadian (400 mybp), culminating with the Alleghanian Orogeny at the formation of Pangaea 300 mypb.

Did Cerithiacean gastropods crawl from the sea at that time, evolve into the first pleurocerids, disperse and diverge across drainage systems as they existed in the ancient Appalachians hundreds of millions of years ago, and then sit in evolutionary stasis as the mountains wore down around them? Yes, I think so.

Next month… taxonomic implications.

Notes:

[1] See the following essays for a review of the biology of *Pleurocera simplex*, its sibling *gabbiana* and its subspecies *ebenum*:

- The cryptic Pleurocera of Maryville [13Sept16]
- The fat simplex of Maryville matches type [14Oct16]
- CPP Diary: Yankees at The Gap [4Aug19]
- CPP Diary: What is Pleurocera ebenum? [3Oct19]
- CPP Diary: The spurious Lithasia of Caney Fork [4Sept19]

[2] Goodrich, C. (1934) Studies of the gastropod family Pleuroceridae – III. Occasional Papers of the Museum of Zoology, University of Michigan 300: 1 – 11.

[3] Lea, Isaac (1841) Continuation of Mr. Lea's paper on New Fresh Water and Land Shells. Proceedings of the American Philosophical Society 2: 11 – 15.

[4] Lea, Isaac (1843) Description of New Fresh Water and Land Shells. Transactions of the American Philosophical Society 8: 163 – 250.

[5] Goodrich, C. (1940) The Pleuroceridae of the Ohio River drainage system. Occasional Papers of the Museum of Zoology, University of Michigan 417: 1-21.

[6] Alas, *Pleurocera laqueata castanea* cannot be retroactively included in the hardcopy FWGNA Volume 5, which came off the presses in the fall of 2023. In our next edition, however, *castanea* will enter at FWGNA species Number 103.2.

[7] See my essay of [3Mar22] for rankings of a broad selection of freshwater gastropod papers by international amazingness units. The paper of Bianchi et al **[8]** scored a whopping 93.2 iau, good for first place in the population genetics subdivision:

- The third-most amazing research results ever published for the genetics of a freshwater gastropod population. And the fourth-most amazing, too. [3Mar22]

[8] Bianchi, T. S., G. M. Davis, and D. Strayer 1994. An apparent hybrid zone between freshwater gastropod species *Elimia livescens* and *E. virginica* (Gastropoda: Pleuroceridae). Am. Malac. Bull. 11: 73 – 78.

[9] From left to right. *Pleurocera simplex simplex* from Brush Creek, Robertson Co, TN. *Pleurocera simplex ebenum* from the Falls of The Cumberland, Whitley Co, KY [see 3Oct19]. *Pleurocera semicarinata semicarinata* from Harrison Ck, Nelson Co, KY [see 6Sept17]. *Pleurocera semicarinata livescens* from Portage Ck, Washtenaw Co, MI **[10].** *Pleurocera virginica*, an especially chubby shell from Deer Ck, Harford Co, MD courtesy R. Aguliar.

[10] "Station 2" of Dazo, B. C. (1965) The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). Malacologia 3: 1 – 80.

[11] Dobzhansky, T. (1940) Speciation as a stage in evolutionary divergence. American Naturalist 74: 312 – 321.

[12] Barton, N.H. and G.M. Hewitt (1985) Analysis of hybrid zones. Annual Review of Ecology and Systematics 16: 113-148.

[13] Heidt, A. (2024) Gars truly are "living fossils," massive DNA data set shows. Science 383 (6687): 1041.

[14] Brownstein, Chase B, Daniel J MacGuigan, Daemin Kim, Oliver Orr, Liandong Yang, Solomon R David, Brian Kreiser, and Thomas J Near (2024) The genomic signatures of evolutionary stasis. Evolution 78: 821 – 834. https://doi.org/10.1093/evolut/qpae028

[15] Dillon, R T. and J. D. Robinson (2009) The snails the dinosaurs saw: Are the pleurocerid populations of the Older Appalachians a relict of the Paleozoic Era? Journal of the North American Benthological Society 28: 1 - 11. (Rosemary Mackay Award) [pdf]. For a review, see:

- The snails the dinosaurs saw [16Mar09]

[16] The Caney/Collins River system, impounded below Rock Island State Park, was home to at least eight species of pleurocerid snails, including P. simplex [4Sept19], *P. troostiana edgariana* [5June20] and the pleurocerid megafauna hung in Cousin Bob Winter's prehistoric necklace as depicted [5Apr22].

[17] The population genetic literature on Atlantic coastal bivalves is very large. For a review of the *Mercenaria* case, see:

- Dillon, R.T. and J.J. Manzi (1992) Population genetics of the hard clam, *Mercenaria mercenaria*, at the northern limit of its range. Canadian Journal of Fisheries and Aquatic Sciences 49:2574-2578. [pdf]

[18] For reviews of the genetics of marine gastropod populations on the Atlantic coast, see:

- Wise, J., M. G. Harasewych, and R. T. Dillon. (2004) Population divergence in the sinistral *Busycon* whelks of North America, with special reference to the east Florida ecotone. Marine Biology 145:1167-1179. [pdf]
- Dayan, N.S., and R.T. Dillon (1995) Florida as a biogeographic boundary: Evidence from the population genetics of *Littorina irrorata*. The Nautilus 108: 49-54. [pdf]

[19] An inexorable (but not especially clocklike) accumulation of neutral mutations yields the startlingly high levels of mtDNA sequence divergence often recorded among pleurocerid populations. And the crazy distribution patterns of those crazy mtDNA sequence markers come from rare long-distance dispersal events which, given hundreds of millions of years of birds wading through these streams and flying off elsewhere, do happen. For more about my Jetlagged Wildebeest Model of mitochondrial superheterogeneity, see:

- Mitochondrial superheterogeneity: What we know [15Mar16]
- Mitochondrial superheterogeneity: What it means [6Apr16]
- Mitochondrial superheterogeneity and speciation [3May16]

[20] The absence of any correlation between genetic divergence and environmental difference in isolated populations of *Pleurocera proxima*, together with strong correlations between genetic divergence and geographic distance, supports this hypothesis. See:

- Dillon, R.T. (1984) Geographic distance, environmental difference, and divergence between isolated populations. Systematic Zoology 33:69-82. [pdf]

[21] Evidence from Pleurocera proxima transplant experiments is also consistent with the hypothesis that beneficial genomes may be prevented from spread by the isolated character of southern Appalachian streams. See:

- Dillon, R.T. (1988) Evolution from transplants between genetically distinct populations of freshwater snails. Genetica 76: 111-119. [pdf]

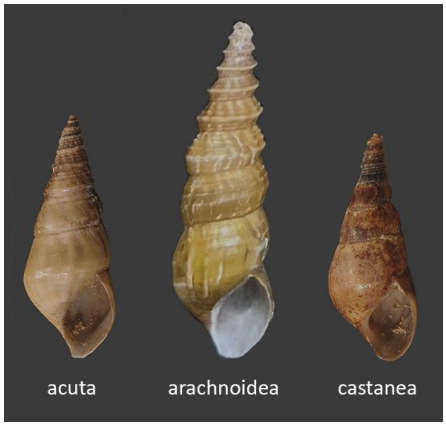
4. Taxonomy of the Pleurocera laqueata/troostiana complex. Part I, A - La.

[10Dec24] Calvin Goodrich **[1]** divided the *Goniobasis* species of the Tennessee, Cumberland, and Ohio River systems into six groups **[2]**. Prominent among those was a "Group of *Goniobasis laqueata*," with ten species and six subspecies, and a "Group of *Goniobasis catenaria*" with eight species and one subspecies. Unsurprisingly, most of the nomina in that former group are synonyms of Pleurocera laqueata (Say 1829), and most of the latter group synonyms of Pleurocera troostiana (Lea 1838).

But because *P. laqueata* and *P. troostiana* hybridize, the distinction between Goodrich's two groups has never been clear. Burch **[3]** moved three species with two subspecies from Goodrich's Group of *Goniobasis laqueata* to his understanding of the "*Elimia catenaria* Group" and separated one species/subspecies pair from Goodrich's *laqueata* group (the "*Elimia acuta* Group") as entirely distinct.

So, working alphabetically, this month we will review the first twelve of the 10 + 6 + 8 + 1 = 25 pleurocerid nomina from the Ohio, Cumberland and Tennessee allocated by Calvin Goodrich to his Groups of *Goniobasis catenaria* and *Goniobasis laqueata* combined.

The vast majority of these were described by our old buddy Isaac Lea **[4],** in eight separate papers and monographs published between 1831 and 1868. Lea described seven of the species we will review over the next two months (as "*Melania*") in brief Latinate form in the Proceedings of the American Philosophical Society of 1841 **[5],** following with more complete English descriptions and figures in the APS Transactions of 1843 **[6].** He disgorged an additional dose of seven brief Latinate descriptions (as "*Goniobasis*") in the Proceedings of the Academy of Natural Sciences of 1862 **[7],** following with complete descriptions and figures in the ANSP Journal of 1863 **[8].** Lea's descriptions of the third set of seven species were scattered in other journals at other times.



14. USNM119088 (14.9 mm), MCZ50236 (21.1 mm), USNM119217 (13.5 mm)

This catalog may become a bit tedious at times, I'm afraid, involving a lot of rather dry library scholarship, and to be quite frank, is not the kind of thing I am especially good at, not having been blessed with the lawyerly frame of mind necessary to build any reputation in the marble halls of zoological nomenclature. It's a service, I suppose.

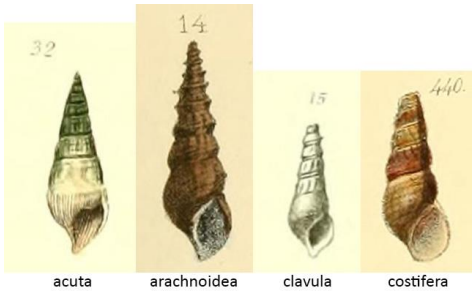
So, for a spoonful of sugar, last month I traveled up to Washington to see our good friend Ellen Strong of the USNM. Ellen and her obliging staff set aside for me Isaac Lea's type specimens **[9]** for 20 of the species that Goodrich included in his groups of *catenaria* and *laqueata* from the greater Ohio drainage. This is the first time that photos of any of those types have ever been published, as far as I am aware.

And I contacted our good buddy Gonzalo Giribet up at the MCZ Harvard, and he and Ms. Jennifer Trimble agreed to add type specimens of Conrad's *nassula*, Anthony's *arachnoidea*, and Wetherby's *plicata-striata* to their (rather lengthy) "imaging queue." And our friends at the ANSP, already on the ball, had previously uploaded and made available to the public a nice photo of Haldeman's *costifera*. Bottom line, over the next two months, we will publish fresh photos of type material for 24 of the 25 *catenaria/laqueata* group species in habiting the Ohio, Cumberland, and Tennessee River systems. And offer a coherent, modern hypothesis for both their evolutionary and their taxonomic relationships. Here we go:

Acuta. First, we must be very clear about what the pleurocerid snail that Isaac Lea described as *Melania acuta* is not. It is not that well-known inhabitant of rivers and streams of the Ohio, Great Lakes, and upper Mississippi drainages described as "Pleurocera acuta" by C.S. Rafinesque **[11]** in 1831, monographed in loving detail by Dazo **[12]** in 1965. Rafinesque's *Pleurocera acuta* was lowered to subspecific status under *Pleurocera canaliculata* by Dillon **[13]** in 2013.

Completely independent of whatever Constantine Smaltz Rafinesque was discovering and publishing in the early 19th century, on May 7, 1830 Isaac lea read a paper at a meeting of the American Philosophical Society in Philadelphia describing "*Melania acuta*" from the "Tennessee River, Prof. Vanuxem" bearing a shell whose "delicate form, furnished with undulations and transverse lines, will easily distinguish it." Lea's little 1:1 figure is reproduced in Fig. 15 at right.

A reading is not a publication, however. The front page of Volume 4 of the Transactions of the American Philosophical Society, in which Lea's paper was ultimately published **[14],** clearly states 1834. N.P. Scudder **[15]** argues, however, that Lea's paper was "issued in the latter end of 1831, and acknowledged by correspondents as received in that year, PANSP 7:243." Tryon **[16]** does not hazard a guess on Lea's publication date, Goodrich **[1]** suggests 1830 and both Burch **[3]** and Graf **[10]** accept Scudder's 1831.



15. From Lea **[14],** Anthony **[20],** Lea **[22],** Reeve **[24].**

So, the bottom line is that Rafinesque's *acuta* and Lea's *acuta* seem to have been published simultaneously. And since Lea's acuta was reassigned to Goniobasis by Tryon **[16],** and then re-assigned to *Elimia* by Burch **[3],** and then both *Goniobasis* and *Elimia* folded under *Pleurocera* by Dillon **[17],** today we have two *Pleurocera acutas*, both described in 1831, meaning entirely different things.

Rafinesque's *acuta* became prominent, however, while Lea's *acuta* receded into obscurity. A big part of the reason is that Isaac Lea's type locality was vague. Goodrich **[18]** speculated that the that the "Tennessee River" from which Vanuxem sampled that first specimen of Lea's *acuta* must have been in North Alabama, where specimens matching his description "have been taken at Muscle Shoals by Messrs. Hinkley and Smith." That malacologically rich section of the Tennessee River is long inundated and much lamented **[19].** Goodrich also reported collections from the Flint River, the Elk River, and Piney Creek, but of course, tributaries are a poor substitute for the main river itself.

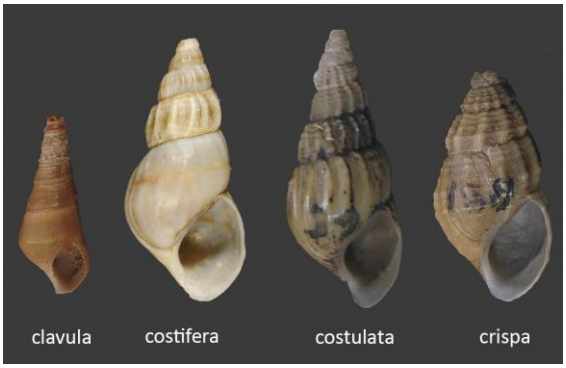
An image of the type specimen (USNM119088) was reproduced up at the top of this essay in Figure 14. Rather than join the speculation on where that shell might have been collected, or whether the population of pleurocerid snails including the individual from the back of which it was snatched almost 200 years ago might have been reproductively isolated from any of the biological species of pleurocerids we recognize today, I will simply suggest that *Melania acuta* Lea 1831 is **a junior homonym of Pleurocera acuta Rafinesque 1831**. RIP *Melania* (aka *Goniobasis*, aka *Elimia*) *acuta*.

Arachnoidea. John G. Anthony **[20]** described *Melania arachnoidea* from "a small stream emptying into the Tennessee River near Loudon, Tennessee" in 1854. Goodrich **[1]** considered it a valid species in his Group of *Goniobasis catenaria*, as did Burch **[3]** in his *Elimia catenaria* Group. We consider the nomen a junior synonym of Pleurocera troostiana troostiana (Lea 1838).

For our rationale, together with an image of a modern topotype, see Dillon **[21]** pp 41 – 49 or my essay of [7Jan20]. See Fig. 14 for an image of a lectotype (MCZ50236) and Fig. 15 for a reproduction of Anthony's original 1:1 figure. We measured and scored a sample of N = 30 shells from Anthony's *arachnoidea* type locality near Loudon for our *troostiana* regression analysis in Essay #2 of the present Circular.

Castanea. Isaac Lea's brief Latinate description of *Melania castanea* (Maury County, Tenn. Thomas H. Dutton) was published in 1841 **[5],** with a more complete English description and figure following in 1843 **[6].** In Essay #3 just previous (Fig 10) I reproduced Lea's original 1843 figure, concurring with Goodrich's **[1]** suggestion that *castanea* is a valid subspecies Pleurocera laqueata castanea (Lea 1841), and advancing the hypothesis that pleurocerid populations bearing shells of that distinctive morphology are hybrids between *P. laqueata* and *P. simplex*. A fresh image of the holotype, USNM119217, was reproduced in Fig. 14 way up above.

Clavula. *Goniobasis clavula* was described from "Jackson Co, Alabama, Dr. Spillman" by Isaac Lea **[22]** in 1868. That county, in the extreme NE corner of Alabama, lies entirely within the Tennessee River drainage. The nomen was demoted to subspecific status under *Goniobasis acuta* by Goodrich **[1, 18]** and placed in the Group of *Goniobasis laqueata*. Burch **[3]** agreed with Goodrich about the subspecific relationship but transferred *clavula* along with its parent into a separate *Elimia acuta* Group.



16. USNM121480 (10.2 mm), ANSP27434 (18.3 mm), USNM119021 (19.3 mm), USNM118463 (14.1 mm)

Lea's **[22]** original figure **[22]** is reproduced in Fig. 15 above and a fresh image of the holotype (USNM121480) is reproduced at right. The type specimen is subadult, very slender, demonstrating both striation and plication, becoming obsolete on the body whorl. We consider the nomen a junior synonym of the hybrid Pleurocera troostiana perstriata (Lea 1853).

Costifera. *Melania costifera* was described in 1841 from "Hennepin, Illinois" by S. S. Haldeman **[23].** The nomen was considered to represent a valid species by both Goodrich and Burch, in their Groups of *Goniobasis laqueata* and *Elimia laqueata*, respectively. No figure was provided originally, but Haldeman's written description "having numerous, spiral, elevated lines, crossing a series of curved ribs, on all the whorls," together with the slender figure subsequently published by Reeve **[24],** reproduced above, sound very much like *P. troostiana lyonii*.

Haldeman's original type shell (ANSP27434) is still held in the ANSP collection today, however, its image thoughtfully made available online by our friends in Philadelphia. And that image, as reproduced in Fig. 16 above, suggests that the "spiral, elevated lines" are negligible, and the body whorl relatively large, as typical for *Pleurocera laqueata laqueata*.

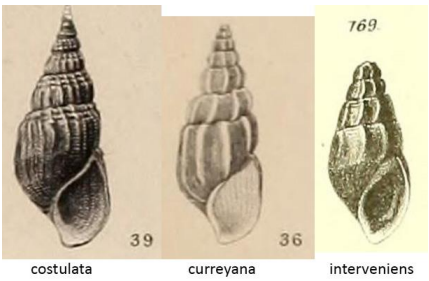
In such a situation, where the published figure and the type shell are strikingly different, it would be nice to refer to a modern topotypic collection. Alas, my review of the online catalog at the Illinois Natural History Survey returned no modern records of *costifera, laqueata, troostiana*, or any pleurocerid bearing a shell with plications or striations of any sort within 250 miles of Hennepin **[25].** Absent a tiebreaker, therefore, the actual type shell as held by the ANSP must take precedence over the Reeve's 1860 figure. *Melania costifera* (Hald 1841) would appear to be a junior synonym of Pleurocera laqueata laqueata (Say 1829).

Costulata. *Melania costulata* was described in 1841 by Isaac Lea **[5]** from the "Barren River, Kentucky." His 1843 figure **[6]** is reproduced in Fig. 17 below. Goodrich **[1]** recognized the nomen as a subspecies *of Goniobasis laqueata*, as did Burch **[3]** of *Elimia laqueata*.

Lea wrote, "In its general characters this species resembles *M. laqueata* Say. It may be distinguished in its being of less diameter and being more slender." The holotype shell (USNM119021) as freshly figured in Fig. 16 above is indeed a bit more slender than typical for *laqueata*. But it demonstrates strong striations (not noted by Lea) as well as plications, extending down to include the body whorl. We consider *costulata* a junior synonym of the hybrid taxon Pleurocera troostiana edgariana (Lea 1841).

Crispa. Isaac Lea **[7]** described *Goniobasis crispa* from "Florence, Alabama" in 1862. The nomen was lowered to subspecific status under *G. perstriata* by Goodrich **[1, 18]** and placed with its parent in the Group *of Goniobasis laqueata*. Burch **[3]** concurred with the demotion, but not the placement, transferring "*Elimia perstriata crispa*" to his *Elimia catenaria* Group. We consider the nomen a junior synonym of Pleurocera nassula (Conrad 1834). See Dillon **[21]** pp 61 – 71 or my essay of [10May20] for a copy of Lea's **[8]** original figure. A fresh image of the holotype (USNM118463) is collected in Fig. 16 above.

Curreyana. Just as was the case of *Melania costulata, Melania curryana* was described by Isaac Lea **[5]** from the "Barren River, Kentucky" in 1841. Lea's 1843 figure of curreyana **[6]** is reproduced next to his figure of costulata at right. And again, as in *M. costulata*, Goodrich **[1]** recognized *M. curryana* as a valid nomen in his Group of *Goniobasis laqueata*, as did Burch **[3]** in his *Elimia laqueata* Group.



17. From Lea **[6]**, Lea **[6],** Lea **[8].**

Unlike *M. costulata*, however, Graf **[10]** was unable to find any type material for *curreyana* in the USNM. It would appear that Lea's 1841 written description, together with his 1843 figure, are all we have for evidence today.

Lea wrote that the shell of *M. curreyana* was "Remarkable for large and strong folds," adding "It is without striae, and the body whorl is smooth, except near the suture." Those contemporary observations, together with Lea's figure of a shell absent any apparent striation, combine to suggest strongly that *M. curreyana* (Lea 1841) is a simple junior synonym of Pleurocera laqueata laqueata (Say 1829).

Decampii. Isaac Lea **[26]** described *Goniobasis decampii* from "Huntsville, Alab." in 1866. He apparently intended to include the Latinate description in his paper of Mayish **[27]** 1863, because in his follow-up paper of 1866 he stated that his original description had been published three years earlier, but it was not.

The nomen was lowered to subspecific status under *G. perstriata* by Goodrich **[1, 18]** and placed with its parent in the Group of *Goniobasis laqueata*. Burch **[3]** concurred with the demotion, but not the placement, transferring "*Elimia perstriata decampii*" to his *Elimia catenaria* Group. We consider the nomen a junior synonym of the hybrid taxon Pleurocera troostiana perstriata (Lea 1853).

For our rationale, together with a copy of Lea's **[26]** original figure, see Dillon **[21]** pp 61 – 71 or my essay of [10May20]. A fresh image of the very slender holotype shell (USNM118967), bearing light striations and plications on its upper whorls only, is collected in Fig. 18 below.

Edgariana. Isaac Lea **[5]** described *Melania edgariana* from "Cany Fork, Tenn." in 1841. Tryon **[16]** synonymized the nomen under Conrad's (1834) *nassula* **[28]** but Goodrich **[1]** resurrected it as a valid species in his Group of *Goniobasis laqueata*. Burch agreed on the specific status but transferred it to his *Elimia catenaria* Group. We consider the nomen valid at the subspecific level, Pleurocera troostiana edgariana (Lea 1841), identifying *laqueata/troostiana* hybrids with strong sculpture on the body whorl.

For our rationale, together with a copy of Lea's **[6]** original figure, an image of a modern topotypic specimen, and example shells from several additional populations, see Dillon **[21]** pp 73 – 79 or my essay of [5June20]. A fresh image of Lea's holotype (USNM118423) is collected in Fig. 18 below.

Interveniens. Isaac Lea **[7]** briefly described *Goniobasis interveniens* from "North Alabama, Prof. Tuomey" in 1862, with a more complete description and figure following in 1863 **[8].** His original 1:1 figure is reproduced in Fig. 17 above and a fresh image of the holotype (USNM118959) is collected in Fig 18 below. Both Goodrich **[1, 18]** and Burch **[3]** considered *interveniens* a valid and distinct species in their Groups of *Goniobasis laqueata* and *Elimia*

laqueata, respectively. We are at a loss to find any distinction between Lea's *interveniens* and Thomas Say's *laqueata* whatsoever, considering *Goniobasis interveniens* (Lea 1862) a simple junior synonym of Pleurocera laqueata laqueata (Say 1829).

Laqueata. *Melania laqueata* was described by Thomas Say in 1829 from "Dr. Troost in Cumberland River" **[29].** No original type material seems to have survived, although Say's written description and figure were sufficient to establish it as the type for both Goodrich's Group of *Goniobasis laqueata* and Burch's *Elimia laqueata* Group.

18. USNM118967 (17.0 mm), USNM118423 (19.0 mm), USNM118959 (17.5 mm).

As we developed at great length in Essay #1 of the present Circular, Pleurocera laqueata (Say 1829) is the oldest name for a distinct, valid, biological species of pleurocerid snail widespread in rivers and streams of Middle Tennessee, North Alabama, and southern Kentucky. We recognize three subspecies: the typical (s.s.) form, the *laqueata/simplex* hybrid *castanea* (Lea 1841) and the big river form *alveare*. See my essay of [8Aug18] for more about *P. laqueata alveare* (Conrad 1834).

Okay, twelve down. Many of you, I feel sure, will have heard that saccharine story about the young girl who finds a million starfish washed up on the beach, and begins to toss them back, one at a time. Along comes a man and asks her how she could possibly hope to save a million starfish. And she flips another starfish into the sea and replies, "Well, I saved that one."

So Dan Graf **[10]** catalogued over 1,000 pleurocerid nomina at the specific or subspecific level, washed up on the beach like starfish. In the present essay we flipped three nomina back into the ocean (*castanea, edgariana, laqueata*), bagged nine others, and threw them into the dumpster. In the final essay of this Circular, we'll dispatch 14 more, one way or the other.

Notes:

[1] Goodrich, C. (1940) The Pleuroceridae of the Ohio River drainage system. Occasional Papers of the Museum of Zoology, University of Michigan 417: 1-21.

[2] Plus a seventh set of "unknowns" and an eighth set he identified as "invasions" from the Alabama system.

[3] This is a difficult work to cite. J. B. Burch's North American Freshwater Snails was published in three different ways. It was initially commissioned as an identification manual by the US EPA and published by the agency in 1982. It was also serially published in the journal Walkerana (1980, 1982, 1988) and finally as stand-alone volume in 1989 (Malacological Publications, Hamburg, MI).

[4] For a brief biographical sketch of Isaac Lea, and a review of his contribution to our modern understanding of freshwater gastropod evolutionary biology, see:

- Isaac Lea Drives Me Nuts [5Nov19]

[5] Lea, Isaac (1841) Continuation of Mr. Lea's paper on New Fresh Water and Land Shells. Proceedings of the American Philosophical Society 2: 11 – 15.

[6] Lea, Isaac (1843) Description of New Fresh Water and Land Shells. Transactions of the American Philosophical Society (New Series) 8: 163 – 250.

[7] Lea, Isaac (1862) Description of a new genus (*Goniobasis*) of the Family Melanidae and eighty-two new species. Proceedings of the Academy of Natural Science of Philadelphia 19: 262 – 272.

[8] Lea, Isaac (1863) New Melanidae of the United States. Journal of the Academy of Natural Sciences of Philadelphia (New Series) 5: 217 – 356.

[9] All 20 of these specimens are labeled "holotype" in the USNM collection. Graf **[10]** considered most of them lectotypes, but I am not going to second-guess the USNM.

[10] Graf, D. L. (2001) The cleansing of the Augean stables. Walkerana 12(27): 1 - 124.

[11] Rafinesque, C.S. (1831) Enumeration and account of some remarkable natural objects in the cabinet of Prof. Rafinesque, in Philadelphia. Self-published, 4 pp.

[12] Dazo, B.C. (1965) The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). Malacologia 3:1-80.

[13] Dillon, R. T., Jr., S. J. Jacquemin & M. Pyron (2013) Cryptic phenotypic plasticity in populations of the freshwater prosobranch snail, *Pleurocera canaliculata*. Hydrobiologia 709: 117-127. [html] [pdf] For more, see:

- Pleurocera acuta is Pleurocera canaliculata [3June13]
- Pleurocera canaliculata and the process of scientific discovery [18June13]

[14] Lea, I. (1831/34) Observations on the naiads, and descriptions of new species of that and other families. Transactions of the American Philosophical Society (New Series) 4: 63 – 121.

[15] Scudder, N. P. (1885) Bibliographies of American naturalists – II. The published writings of Isaac Lea, LL.D. Bulletin of the US National Museum 23: 1 – 278.

[16] Tryon, G. W. (1873) Land and Freshwater shells of North America Part IV, Strepomatidae. Smithsonian Miscellaneous Collections 253: 1 - 435.

[17] Dillon, R. T., Jr. (2011) Robust shell phenotype is a local response to stream size in the genus Pleurocera (Rafinesque, 1818). Malacologia 53: 265-277. [pdf] For a review, see:

- Goodbye Goniobasis, Farewell Elimia [23Mar11]

[18] Goodrich, C. (1930) Goniobases of the vicinity of Muscle Shoals. Occasional Papers of the Museum of Zoology, University of Michigan 209: 1 – 25.

[19] The TVA closed Wheeler Dam in 1936 and Pickwick Dam in 1938, creating a pair of reservoirs that covered the North Alabama shoals of the Tennessee River under 100 miles of slackwater and muck. For my own personal lament, see the latter half of:

- The Union in Tennessee! [15Aug23]

[20] Anthony, J.G. (1854) Descriptions of new fluviatile shells of the genus *Melania* Lam., from the western states of North America. Annals of the Lyceum of Natural History of New York 6: 80 -132.

[21] Dillon, R.T., Jr. (2023b) The Freshwater Gastropods of North America Volume 6, Yankees at The Gap, and Other Essays. FWGNA Project, Charleston, SC. [publications]

[22] Lea, Isaac (1868) New Unionidae, Melanidae, etc., chiefly of the United States. Journal of the Academy of Natural Sciences of Philadelphia (New Series) 6: 303 – 343.

[23] Haldeman. S. S. (1841) A monograph of the Limniades and other freshwater univalve shells of North America. Volume 2.

[24] Reeve, L. A. (1860) Conchologia Iconica, or, Illustrations of the shells of molluscous animals. Volume 12, Plate 56.

[25] The INHS collection does hold four historic records of *"Elimia" costifera* from a creek in Hardin County, bordering the Ohio River about 250 miles south of Hennepin. The University of Michigan also holds one historic lot of *Goniobasis costifera* (UMMZ 241604) from Hardin County. Hardin County is simply too far away from Hennepin to have any bearing on this question.

[26] Lea, Isaac (1866) New Unionidae, Melanidae, etc. chiefly of the United States. Journal of the Academy of Natural Sciences of Philadelphia (New Series) 6: 113 – 187.

[27] Lea, Isaac (1863) Descriptions of fourteen new species of Melanidae and one Paludina. Proceedings of the Academy of Natural Sciences of Philadelphia 15:154 – 156. Lea apparently read his paper in May of 1863, and "May" is printed on the bottom of the published pages, but the front of the published volume says, "June and July, 1863."

[28] Conrad, T. A. (1834) New Fresh Water Shells of the United States, with coloured illustrations, and a monograph of the genus *Anculotus* of Say; also A synopsis of the American naiades. Philadelphia, Judah Dobson. 76 pp, 8 plates.

[29] Say, T. (1829) Descriptions of some new terrestrial and fluviatile shells of North America. New Harmony Disseminator of Useful Knowledge 2(18): 275 – 277.

14

5. Taxonomy of the Pleurocera laqueata/troostiana complex. Part II, Ly - Z. Or, Just 974 Starfish Left to Go.

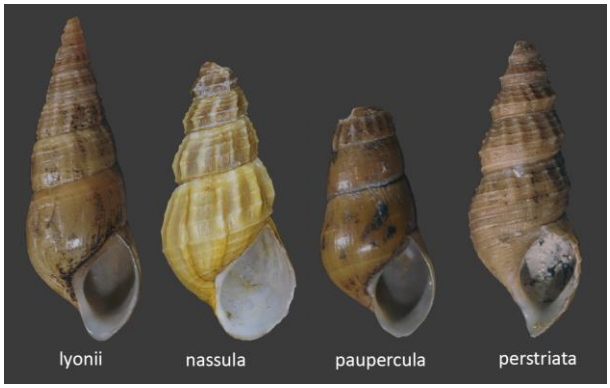
[14Jan25] We opened Essay #4 of the present Circular with a tally of the pleurocerid nomina that Calvin Goodrich **[1]** recognized as valid to describe representatives of his Groups of *Goniobasis catenaria* and *Goniobasis laqueata* in the Ohio, Cumberland, and Tennessee River systems. We observed that there are 25 such names and reviewed the first 12 of them (alphabetically), promising to finish the job here.

I did not mention it at the time, because it is a bit embarrassing, but I have found one Latin nomen useful for certain pleurocerid populations of the greater Ohio River basin that Goodrich synonymized under something else, and hence was not listed by him in 1940. So, the total is actually 26 names, and we have 14 to review here. Sorry – I know that's going in the wrong direction, and I apologize.

Lyonii. Isaac Lea **[2]** described *Goniobasis lyonii* in brief Latinate form from "Grayson County, Kentucky" in 1862. Goodrich **[1,3]** synonymized *lyonii* under *Goniobasis laqueata* and the nomen was carried passively (with a long list of other junior synonyms) into his Group of *Goniobasis laqueata*. From there it disappeared, not mentioned at all by Burch **[4],** forgotten and consigned to the boneyard.

We consider the nomen *lyonii* valid and useful at the subspecific level **[5],** Pleurocera troostiana lyonii (Lea 1862), identifying *laqueata/troostiana* hybrids at the western and northern limits of the phenomenon. For our rationale, together with a copy of Lea's **[6]** original figure and a modern topotype, see Dillon **[7]** pp 81 – 88 or my essay of [6July20]. An image of the holotype (USNM119147) is collected below.

Nassula. Timothy Abbot Conrad **[8]** described *Melania nassula* in 1834 from "the limestone spring at Tuscumbia, Alabama." Goodrich **[1,3]** considered that the taxon named a distinct and valid species in his Group of *Goniobasis catenaria*; Burch followed suit in his *Elimia catenaria* Group.



19. USNM119147 (23.1 mm), MCZ53965 (17.3), USNM118923 (13.6), USNM118429 (20.1)

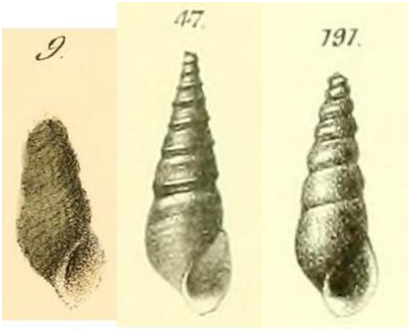
No original type material seems to have survived, according to Graf **[9],** although the MCZ holds the "possible syntype" figured at right (MCZ 53965). And a pleurocerid population matching Conrad's original 1834 description and figure (#9 below) quite well still inhabits the Tuscumbia Big Spring to the present day. It does, indeed, look very much like an Atlantic drainage (or Floridian) population of *Pleurocera catenaria* has been airlifted 300 miles west and dropped into North Alabama. This is a distinct and valid biological species, Pleurocera nassula (Conrad 1834).

Paupercula. Isaac Lea described *Goniobasis paupercula* in brief Latinate form in 1862 **[2],** giving the type locality as "North Alabama, Prof. Tuomey," with a more complete English description and figure following in 1863 **[6].** Goodrich **[1,3]** recognized it as a valid species in his Group of *Goniobasis laqueata*, as did Burch **[4]** in his *Elimia laqueata* group.

We consider the nomen a junior synonym of Pleurocera troostiana perstriata (Lea 1853) **[10]**, identifying *laqueata/troostiana* hybrids with decollate shells in North Alabama. For our rationale, together with a copy of Lea's **[6]** original figure and images of two topotypes (an adult and a juvenile, both **R**), see Dillon **[7]** pp 61 – 71 or my essay of [10May20]. An image of the holotype (USNM 118923) is collected above.

Perstriata. Isaac Lea **[10]** described *Melania perstriata* from "Coosa River, Alabama, Prof. Brumby, Huntsville, Tenn., Mr. J. Clark" in 1853. Goodrich **[1,3]** recognized it as a valid species in his Group of *Goniobasis laqueata*, restricting its type locality to the Big Spring at Huntsville, Alabama. Burch **[4]** concurred on the specific value of the nomen but transferred it to his *Elimia catenaria* group. We consider the nomen valid at the subspecific level, Pleurocera troostiana perstriata, identifying *laqueata/troostiana* hybrids with little or no costation on the body whorl.

For our rationale, together with a copy of Lea's **[10]** original figure, an image of a modern topotypic specimen, and example shells from several additional populations, see Dillon **[7]** pp 51 – 59 or my essay of [15Apr20]. An image of the holotype (USNM 118429) is collected in Fig. 19 above.



20. From Conrad **[9],** Lea **[16],** Lea **[7].**

Plicata-striata. Albert G. Wetherby's **[11]** 1876 description of *Goniobasis plicta-striata* **[12]** is very difficult to obtain today. But Walker **[13]** quotes his type locality as "Stone River and Mill Creek, Rutherford County, and Sinking Creek, Shelbyville, TN." Goodrich **[1]** assigned the nomen to his Group of *Goniobasis laqueata*. Burch re-spelled the nomen without the dash and shifted it to his *Elimia catenaria* group.

The entire main stem of the Stones River is impounded today, as is Mill Creek, but Sinking Creek is inhabited by apparently healthy populations of both *P. laqueata* and *P. troostiana edgariana*, not especially helpful for our understanding of Wetherby's taxon today.

Fortunately, Wetherby donated N = 65 paratypes "ex original lot" to Harvard's Museum of Comparative Zoology (MCZ 149453). Unfortunately, that entire lot of shells is dead collected, worn, and bleached – the poorest excuse for type material I have ever seen preserved in any collection, in my entire 50 years of professional experience.

I have some insight into the origin of this problem, although I cannot explain it. Several years ago I myself was quite stricken by a gigantic bed of relic pleurocerid shells at the bottom of Bradley Creek, a tributary of the East Fork Stones River near Lascassas. The photo below, taken through about an inch of gently flowing water, shows thousands of *P. laqueata* shells, primarily, with scattered *troostiana* hybrids, all in various stages of decomposition. Why Albert G. Wetherby would paw through such a bed, select 65 and describe them as "*Goniobasis plicata-striata*" is beyond me.


21. Bradley Creek, TN

The staff at the MCZ selected two shells from lot 149453 as exemplars to photograph for their online catalog at my request, offering seven images of the two shells from various angles. The best of those seven images is

reproduced in Fig. 22 down below. From some angles, it is possible to make out, just barely, weak plications on the top half of the shell I have figured. I cannot find evidence any striation on either exemplar shell at any angle photographed.

Therefore, *Goniobasis plicata-striata* (Wetherby 1876) appears to be a simple junior synonym of Pleurocera laqueata laqueata (Say 1829) **[26].**

Porrecta. Isaac Lea **[14]** described *Goniobasis porrecta* in brief Latinate form from "Gap Creek and Spring" (Cumberland Gap, TN) in 1863, with more complete English description and figure (#47 in Fig. 20 above) in 1866 **[15].** Goodrich **[1]** considered it a valid species in his Group of *Goniobasis catenaria*, subsuming *vittatella* (Lea 1863) under it, as did Burch **[4]** in his *Elimia catenaria* group.

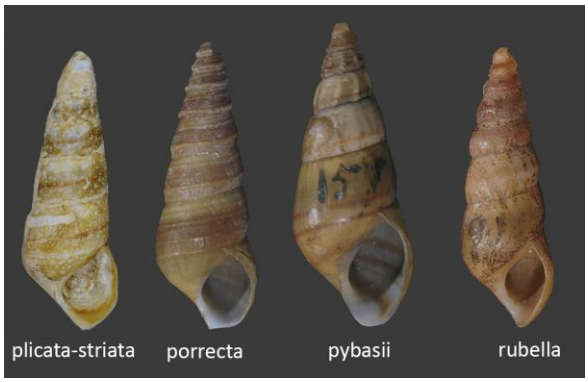
We consider the nomen a junior synonym of Pleurocera troostiana troostiana (Lea 1838). For our rationale, together with an image of a modern topotype, see Dillon **[7]** pp 1 – 7 or my essay of [4Aug19]. An image of the holotype (USNM 118834) is collected in Fig. 22 below.

Pybasii. Isaac Lea **[2]** published a brief Latinate description of *Goniobasis pybasii* from "Tuscumbia, Alabama" in 1862, with English description and figure following in 1863 **[6].** This is the third of Lea's 1862/63 "eighty-two new species" of *Goniobasis* we have reviewed in the present essay, along with *lyonii* and *paupercula*, all synonyms of the same species. A nineteenth-century malacological hat trick! There will be two more.

Goodrich **[1,3]** recognized *pybasii* as a valid species in his Group of *Goniobasis laqueata*, as did Burch **[4]** in his *Elimia laqueata* group. We consider the nomen a junior synonym of Pleurocera troostiana perstriata (Lea 1853), identifying *laqueata/troostiana* hybrid populations in North Alabama. For our rationale, together with a copy of Lea's **[6]** original figure and an image of a modern topotypic specimen (Q), see Dillon **[7]** pp 61 – 71 or my essay of [10May20]. An image of the holotype (USNM 119329) is collected below.

Rubella. This is the fourth of the "eighty-two new species" that Isaac Lea **[2]** described in 1862 we have reviewed in this Essay. Lea's original figure **[6]** is reproduced above (Fig 20, #191), and a fresh image of the holotype (USNM 119296) offered at right.

Goodrich **[1]** considered *rubella* a valid species in his Group of *Goniobasis catenaria* noting as he did, however, that the species was "reported originally from Cherokee County, North Carolina, and not found there since. May be the same as *porrecta*." Burch **[4]** did not list *rubella* but did reproduce Tryon's figure of it (#369), with the caption "E. rubella = ?E. porrecta."



22. MCZ149453 (16.1 mm), USNM118834 (17.7 mm), USNM119329 (19.8 mm), USNM119296 (16.9 mm)

Right. Lea's original description, "very near to *Melania (Goniobasis) teres* but differs in being carinate," together with his figure and type specimen, make it quite clear that *Goniobasis rubella*, like *porrecta* and like *teres*, is a simple junior synonym of Pleurocera troostiana troostiana (Lea 1838).

That said, I really think that the type locality given by Lea for his *G. rubella*, "Near Murphy, Cherokee County, North Carolina," must have been in error. The modern range of *P. troostiana* does not extend any further east up the Hiwassee drainage than Polk County, TN.

Spinella. The fifth of Isaac Lea's 1862/63 creations **[2,6]** we have reviewed this month, *Goniobasis spinella* was described from "Sycamore, Claiborne County, Tennessee" as "very nearly of the same outline *of Melania (Goniobasis) strigosa* but much smaller, slimmer, and darker color." Goodrich **[1]** considered the nomen a

subspecies of *Goniobasis arachnoidea* in his Group of *Goniobasis catenaria*, as did Burch **[4]** in his *Elimia catenaria* group.

Lea's original figure is reproduced down below (Fig. 24, #130), and his holotype (USNM 119269) freshly imaged at right. We consider *spinella* another simple junior synonym of Pleurocera troostiana troostiana (Lea 1838). For our rationale, together with an image of a modern topotype, see Dillon **[7]** pp 41 – 49 or my essay of [7Jan20].

23. USNM119269 (16.3 mm), USNM118448 (14.2 mm), USNM121603 (19.4 mm)

Striatula. Isaac Lea **[16]** described *Melania "striata"* in brief Latinate form from "Tennessee" in 1841, with English description and figure following in 1843 **[17].** He amended the name to "*striatula*" in the interim **[18].** Goodrich **[1]** considered *striatula* a valid species in his Group of *Goniobasis catenaria*, as did Burch **[4]** in his *Elimia catenaria* group.

Lea's original **[17]** figure is reproduced below (Fig. 24, #49), and a shell catalogued into the USNM collection as the holotype (USNM 118448), that Graf **[9]** referred to as a "possible syntype" is imaged at right. They do not match. Rats.

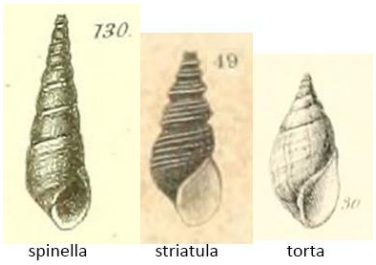
Lea's original figure showed strong striation and no plication, looking like a synonym of typical *P. troostiana troostiana*, as I myself suggested in Dillon **[7]** pp 41 – 49 and in my essay of [7Jan20]. The nominal holotype, however, shows plicae as strong as striae **[19],** looking very much like *P. troostiana edgariana*. And the locality information, simply "Tennessee," is no help resolving the discrepancy.

Turning to the letter of Lea's **[16]** original description as a tiebreaker, we read "shell striate" to lead off, with no mention of plication. But in Lea's remarks, we read "In some individuals the folds are numerous – in others the striae predominate and cover nearly all the whorls." Are the "folds" plicae?

In the end, I suppose it does not matter. *Melania striatula* (Lea 1842) is a junior synonym of Pleurocera troostiana (Lea 1838), but whether of the purebred (typical) form or the hybrid *edgariana* form, I don't think we'll ever know.

Strigosa. Another of Isaac Lea's 1841/43 classics **[16,17],** *Melania strigosa* was described as "somewhat like the *teres* herein described" from "Tennessee, Dr. Troost, Holston River Dr. Warder." Goodrich **[1]** considered it a valid species in his Group of *Goniobasis catenaria*, as did Burch **[4]** in his *Elimia catenaria* group.

In my published essay **[7]** of 2023 (pp 41 - 49] and in the 2020 blog post from which that essay was crafted [7Jan20], I offered four reasons to restrict the *strigosa* type locality to Little Flat Creek 10 miles north of Knoxville, figured a topotype, and reproduced Lea's **[17]** original figure. Lea's holotype (USNM 121603) is imaged in Fig. 23 above. We consider the nomen yet another simple junior synonym of Pleurocera troostiana troostiana (Lea 1838).



24. From Lea **[7],** Lea **[18],** Lea **[22]**

Teres. And a third time. Isaac Lea **[16]** described *Melania teres* from "Tennessee, Dr. Troost" in 1841, following with a more complete English description and figure in 1843 **[17].** Again, Goodrich **[1]** considered it a valid species in his Group of *Goniobasis catenaria*, as did Burch **[4]** in his *Elimia catenaria* group.

We considered the locality data too vague to send us on a modern day *teres*-hunt for our blog post of [7Jan20] or the published essay **[7]** derived from it (pp 41 – 49), but did reproduce both Lea's **[17]** original figure, and figure #356 from Burch **[4].** An image of Lea's holotype (USNM 119251) is collected in Fig. 25 below. We consider the nomen yet another simple junior synonym of Pleurocera troostiana troostiana (Lea

1838). So, it materializes that Isaac Lea scored malacological hat tricks in both 1841 and in 1862. Without question, Isaac Lea was the greatest of all time, of something.

Torta/tortum. Isaac Lea's brief, Latinate description of *Melania torta* from "Big Creek, Lawrence County, Tennessee" was published in 1845 **[20],** with more complete English description and figure following in 1848 **[21].** Tryon **[22]** assigned the nomen to *Pleurocera* in 1873, changing the spelling to *tortum* **[23].** Goodrich considered *tortum* a valid subspecies of *Goniobasis laqueata*, as did Burch, of *Elimia laqueata*.

Lea's original **[21]** figure is reproduced above (Fig. 24, #30), and a fresh image of the holotype (USNM 119255) collected below. Quoting him verbatim:

> "There were eight specimens of this species submitted to my examination by Mr. Clark, of Cincinnati. […] The apices of the individuals now before me are slightly eroded … one of the specimens has small folds near the apex, with decussating striae. […] The body whorl is very long."

Lea's description, original figure, and designated holotype all strongly suggest that *Melania torta* is a *laqueata/simplex* hybrid, making the nomen a junior synonym of populations we identified as Pleurocera laqueata castanea (Lea 1841) in Essay #3 of the present Circular.

Lawrence County, Tennessee, is on the Alabama line just north of Florence in the Shoal Creek subdrainage. I cannot find a "Big Creek" anywhere on modern maps, but *Pleurocera laqueata* populations bearing shells of typical morphology are widespread in that county. And the FWGNA database contains five records of *P. laqueata castanea* in Lauderdale County, AL, just south.

Troostiana. Isaac Lea **[24]** described *Melania troostiana* from "Mossy Creek, Jefferson County, Ten" quite early in his career, in 1838. Goodrich **[1]** considered it a valid species in his Group of *Goniobasis catenaria*, as did Burch **[4]** in his *Elimia catenaria* group.

25. USNM119251 (21.6 mm), USNM119255 (18.0 mm), USNM119256 (25.3 mm)

Pleurocera troostiana is the oldest name for a distinct, valid, biological species of pleurocerid snail widespread in small streams of the greater Ohio drainage from SW Virginia through most of Tennessee, North Alabama and Southern Kentucky. For a complete review, illustrated with a copy of Lea's **[24]** original figure and images of modern topotypes, see Dillon **[7]** pp 35 – 40 or my essay of [9Dec19]. An image of the holotype (USNM 119256) is collected at right.

I provided a photo of a living *P. troostiana* individual in my follow-up essay of [7Jan20], published in Dillon **[7]** pp 41 – 49. I then developed the argument that a great variety of pleurocerid nomina in East Tennessee might be junior synonyms, including *arachnoidea, porrecta, spinella, strigosa, striatula*, and *teres*, as reviewed above.

Then in a series of four essays posted on this blog between April and July of 2020, and published in 2023 by Dillon **[7]** pp 51 – 88, I recognized three subspecies **[5]** of *P. troostiana* inhabiting the waters of North Alabama, Middle Tennessee, and Kentucky: *perstriata* (Lea 1853), *edgariana* (Lea 1841), and *lyonii* (Lea 1862), synonymizing a large number of additional nomina underneath those as well. I also published a separate circular **[25]** reviewing the entire four-subspecies system, including the typical (s.s.) form.

So, we closed Essay #4 with a reference to the sanctimonious story usually entitled "Starfish on the Beach," which seems to have evolved from a 1969 essay by Loren Eiseley. Including the 12 starfish we dispatched in Essay #4, our two-month total is 26 starfish on the beach, 7 of which we tossed back into the sea. At the species level we recognize *laqueata, troostiana*, and *nassula*. At the subspecies level, all of hybrid origin, we recognize *perstriata,*

edgariana, and *lyoni*i under *troostiana* and *castanea* under *laqueata*. The other 19 starfish we have now bagged for the dumpster. Just 974 starfish left to go.

Notes:

[1] Goodrich, C. (1940) The Pleuroceridae of the Ohio River drainage system. Occasional Papers of the Museum of Zoology, University of Michigan 417: 1-21.

[2] Lea, Isaac (1862) Description of a new genus (*Goniobasis*) of the Family Melanidae and eighty-two new species. Proceedings of the Academy of Natural Science of Philadelphia 19: 262 – 272.

[3] Goodrich, C. (1930) Goniobases of the vicinity of Muscle Shoals. Occasional Papers of the Museum of Zoology, University of Michigan 209: 1 – 25.

[4] This is a difficult work to cite. J. B. Burch's North American Freshwater Snails was published in three different ways. It was initially commissioned as an identification manual by the US EPA and published by the agency in 1982. It was also serially published in the journal Walkerana (1980, 1982, 1988) and finally as stand-alone volume in 1989 (Malacological Publications, Hamburg, MI).

[5] Subspecies are populations of the same species in different geographic locations, with one or more distinguishing traits. For more, see:

- What is a subspecies? [4Feb14]
- What subspecies are not [5Mar14]

[6] Lea, Isaac (1863) New Melanidae of the United States. Journal of the Academy of Natural Sciences of Philadelphia (New Series) 5: 217 – 356.

[7] Dillon, R.T., Jr. (2023b) The Freshwater Gastropods of North America Volume 6, Yankees at The Gap, and Other Essays. FWGNA Project, Charleston, SC. [publications]

[8] Conrad, T. A. (1834) New Fresh Water Shells of the United States, with coloured illustrations, and a monograph of the genus *Anculotus* of Say; also A synopsis of the American naiades. Philadelphia, Judah Dobson. 76 pp, 8 plates.

[9] Graf, D. L. (2001) The cleansing of the Augean stables. Walkerana 12(27): 1 - 124.

[10] Lea, Isaac (1853) Description of a new genus (*Basistoma*) of the Family Melaniana, together with some new species of American Melaniae. Transactions of the American Philosophical Society (new series) 10: 295 – 302.

[11] We first met Albert G. Wetherby (1833 – 1902), author of the baffling taxon *Helisoma duryi*, back in 2020:

- The flat-topped Helisoma of The Everglades [5Oct20]

[12] Wetherby, A.G. (1876) Remarks on the variation in form of the family Strepomatidae, with descriptions of news species Proceedings of the Cincinnati Society of Natural History 1:10.

[13] Walker, B. (1918) A synopsis of the classification of the freshwater Mollusca of North America, North of Mexico, and a catalogue of the more recently described species, with notes. Univ. Mich. Mus. Zool. Misc. Publ. 6: 1 - 213.

[14] Lea, Isaac (1863) Descriptions of fourteen new species of Melanidae and one *Paludina*. Proceedings of the Academy of Natural Sciences of Philadelphia 15: 154 – 156.

[15] Lea, Isaac (1866) New Unionidae, Melanidae, etc. chiefly of the United States. Journal of the Academy of Natural Sciences of Philadelphia (New Series) 6: 113 – 187.

[16] Lea, Isaac (1841) Continuation of Mr. Lea's paper on New Fresh Water and Land Shells. Proceedings of the American Philosophical Society 2: 11 – 15.

[17] Lea, Isaac (1843) Description of New Fresh Water and Land Shells. Transactions of the American Philosophical Society (New Series) 8: 163 – 250.

[18] Lea, Isaac (1842) Minutes of the Stated Meeting of December 2. Proceedings of the American Philosophical Society 2: 237.

[19] If you are confused about striation and plication (costation), see my 2020 essay for a diagram:

- Huntsville Hunt [15Apr20]

[20] Lea, Isaac (1845) Descriptions of new fresh water and land shells. Proceedings of the American Philosophical Society 4: 162 – 168.

[21] Lea, Isaac (1848) Description of new fresh water and land shells. Transactions of the American Philosophical Society 10: 67 – 101.

[22] Tryon, G. W. (1873) Land and Freshwater shells of North America Part IV, Strepomatidae. Smithsonian Miscellaneous Collections 253: 1 - 435.

[23] At the risk of confusing the situation further. Isaac Lea also described a *Trypanostoma tortum* in 1862 from the Uchee River (Creek), a tributary of the Chattahoochee on the GA/AL border. That one was *renamed Pleurocera parkerii* by Tryon.

[24] Lea, Isaac (1838-39) Description of New Freshwater and Land Shells. Transactions of the American Philosophical Society (New Series) 6: 1 – 154.

[25] Dillon, R.T., Jr. (2020) The four subspecies of *Pleurocera troostiana* (Lea 1838), with synonymy. FWGNA Circular 2: 1 - 5. [pdf]

[26] In the original version of this blog, as posted 14Jan25, I ventured to hypothesize that Weatherby's *plicata-striata* was a junior synonym of *Pleurocera troostiana edgariana* (Lea 1841). That was before I saw the MCZ paratypes. On 10Feb25, I changed my mind.