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A survey of the pleurocerid gastropods of South Carolina

Robert T. Dillon, Jr.[1,3] and Eugene P. Keferl[2]

[1]*Department of Biology, College of Charleston, 66 George Street, Charleston, SC 29424 USA;*
[2]*Department of Natural Sciences & Mathematics, Coastal Georgia Community College, 3700 Altama Avenue, Brunswick, GA 31520 USA.*

ABSTRACT: The 3 large river systems in South Carolina (the Pee Dee, Wateree/Santee, and Savannah), all flow southeast through sandy hills and coastal plain to the Atlantic Ocean. Between 1986 and 1995 we surveyed 629 sites distributed evenly about the state, documenting approximately 30 *Goniobasis* populations at 44 sites. We found 11 populations of *Goniobasis proxima* (14 sites), a species widespread from Virginia to Georgia, in small streams in or near the Appalachian (Blue Ridge) foothills. Nine populations of *Goniobasis catenaria catenaria* were found at 22 sites in streams and rivers of varying size through the South Carolina midlands. The disjunct distribution of these populations suggests that this species may have been highly impacted by agricultural siltation and impoundment. We documented 6 *Goniobasis catenaria dislocata* populations at 8 sites in small streams of the Coastal Plain. Described by Thomas Say in 1822, *G. catenaria* is the second oldest nomen in the genus. The genetic relationships among its 6 subspecies, as well as its relationship to other very similar *Goniobasis* more recently described from southern Atlantic Slope drainages, would profitably bear examination.

Keywords: gastropods, *Goniobasis*, *Elimia*, South Carolina, Piedmont, Coastal Plain, surveys, conservation, siltation, erosion.

Despite early interest, the pleurocerid fauna of South Carolina has been poorly documented. *Melania* (=*Goniobasis*) *catenaria* Say 1822, was among the earliest North American freshwater mollusks to be described. The type locality for this species, Limestone Springs, St. John's, Berkeley (Say 1822), must have been Eutaw Springs, arising from a marly outcrop about 80 km NW of Charleston. The only review of the pleurocerids of the southeastern US to date has been that of Goodrich (1942). He made *G. catenaria* the type of a group including 29 species and subspecies ranging from Virginia to Texas (Burch and Tottenham 1980). Within South Carolina he recorded *G. catenaria catenaria* from "A springs of eastern South Carolina, possibly in streams southward to the Savannah River." Goodrich also listed a subspecies with a much less costate shell, *G. catenaria dislocata* (Ravenel 1834), from "A headstreams in South Carolina," as well as from counties in east-central North Carolina and Virginia. The only other pleurocerid recorded from the state by Goodrich (1942) was *Goniobasis proxima* (Say 1825), from "A highlands of North and South Carolina."

Snails of the genus *Goniobasis* are primarily inhabitants of clean, well-oxygenated lotic waters, usually with solid substrates. But as eastern North America has been settled, farmed and developed, such environments have largely disappeared. Most of South Carolina was tilled for agriculture in the 19th century, primarily for cotton, causing severe erosion and sedimentation in rivers statewide. In the present century we have seen many of the larger rivers impounded for hydroelectric power, most notably the Savannah River and the Piedmont tributaries of the Santee, Saluda, and Wateree Rivers. The giant Santee-Cooper Project, in diverting and re-diverting the Santee through Lakes Marion and Moultrie, flooded the Eutaw Springs type locality of *G. catenaria* in the 1940's. Such trends have aroused concerns for the safety of the South Carolina pleurocerid fauna as a whole.

Pleurocerid populations have played central roles in life history studies (Aldridge 1982, Huryn *et al.* 1994) and in ecosystem studies of great generality and importance (*e.g.*, Lamberti *et al.* 1989, McCormick and Stevenson 1991, Mulholland *et al.* 1991, Hill *et al.* 1995, review in Dillon 2000). By virtue of their isolation, their large population sizes, and their ease of collection, pleurocerids have proven quite useful for studies of evolutionary and population genetic processes (*e.g.*, Chambers 1982, 1987; Dillon 1984, 1988a; Dillon and Lydeard 1998, Lydeard *et al.* 1997). Yet the specific identity of many pleurocerid populations remains problematic, and their systematic relationships obscure (Dillon 1989, 1991; Lydeard *et al.* 1998). In light of the biological importance of pleurocerid snails and well-founded concerns over

[3] For correspondence contact R.T. Dillon, Jr. (Email: dillonr@cofc.edu)

their present status in South Carolina, we have conducted a broad survey of streams and rivers throughout the state. Here we report that South Carolina's pleurocerid populations have survived centuries of agriculture, impoundment, and economic development, but that remaining populations are scattered and vulnerable to extirpation.

Methods

Our study area encompasses the three physiographic provinces in South Carolina. The eastern half of the state lies in the Atlantic Coastal Plain, trending from entirely flat and swampy near the coast to gently hilly toward the midlands. The Coastal Plain is underlain by unconsolidated sedimentary beds of sand and clay, with occasional marl outcrops. Most of the western half of the state comprises the Piedmont Plateau, a region of gently rolling sandy hills underlain by igneous rocks such as granite and gneiss. At its western tip, South Carolina rises to the Blue Ridge province, a region of steep mountains composed of hard rocks such as gneiss. The state's three major river systems, the Pee Dee, the Broad/Wateree/ Santee, and the Savannah, flow southeast through the Piedmont and Coastal Plain to the Atlantic Ocean.

The authors of the present work surveyed South Carolina independently. RTD visited 202 sites during the spring and summer of 1988, primarily in connection with a small grant to assess the status of *G. catenaria*. The results of this survey were combined with those of 31 previously-visited sites (Dillon 1988b). EPK visited 447 sites in South Carolina from 1986 - 1995, primarily surveying for unionids. There was an overlap of 51 sites, yielding a combined total of 629 sites surveyed.

Pleurocerid gastropods are relatively large and conspicuous, often occurring in high density (Dillon 2000). Thus collecting them requires no specialized equipment or methods. We performed systematic searches at each site, paying special attention to solid substrates, lifting rocks and logs. The time spent at each site was variable and proportional to the size and complexity of the habitat. Each site was assigned a field number, a 1 - 3 digit number (sometimes with letter suffix) for RTD and a YY:nnn code for EPK, where YY stands for the last 2 digits of the year. Sites where pleurocerids were found have been re-numbered here for consistency. Samples were taken of all pleurocerid populations discovered. Voucher specimens for this project have been deposited in the Academy of Natural Sciences, Philadelphia.

We also searched the catalogues of the two major North American collections available on line, the Florida Museum of Natural History (http://www.flmnh.ufl.edu/databases/mala/intro.htm) and the Academy of Natural Sciences of Philadelphia (gopher://erato.acnatsci.org:70/11/.mala). The former was searched for family=Pleuroceridae and State=South Carolina, and the latter searched for Pleuroceridae or *Goniobasis* or *Elimia* and South and Carolina.

Results

Pleurocerids were found at the 44 sites numbered in Fig. 1. Locality data for these sites are presented in Appendix 1. Locality data for sites where no pleurocerids were observed may be accessed at http://www.cofc.edu/~dillonr/fwgnadata.htm.

We discovered 11 populations of *Goniobasis proxima* at 14 sites in the Western Piedmont, 9 populations of *G. catenaria catenaria* scattered in 22 sites from the Piedmont into the Coastal Plain, and 6 populations of *G. catenaria dislocata* at 8 sites in small streams of the Coastal Plain. Photos of typical shells of these 3 taxa are shown in Fig. 2.

Our online search returned no data from the ANSP, but 11 records at the FLMNH. Four of these 11 sites appear to duplicate populations collected by us: FLMNH catalog numbers 28120 and 71128 seem to correspond to our population 11p, and catalog numbers 261840 and 261841 correspond to our 5c. The remaining 7 are discussed below.

Discussion

The three pleurocerid species of South Carolina were consistently referred to the genus *Goniobasis* from the publication of Tryon (1873) up until the monograph of Burch (1982). Burch resurrected the genus nomen *Elimia* (H. & A. Adams 1854) as a prior synonym of *Goniobasis* at that time, on the basis of Pilsbry & Rhodes' (1896) type designation. However, Pilsbry subsequently reversed himself, observing that *Elimia* was described from a composite group (Walker 1918, 149). Thus we continue to use the more established *Goniobasis*.

Our documentation of numerous *G. proxima* populations in small, generally rapid flowing streams in western South Carolina confirms the report of Goodrich (1942). *Goniobasis proxima* is a widespread species of the piedmont and Blue Ridge

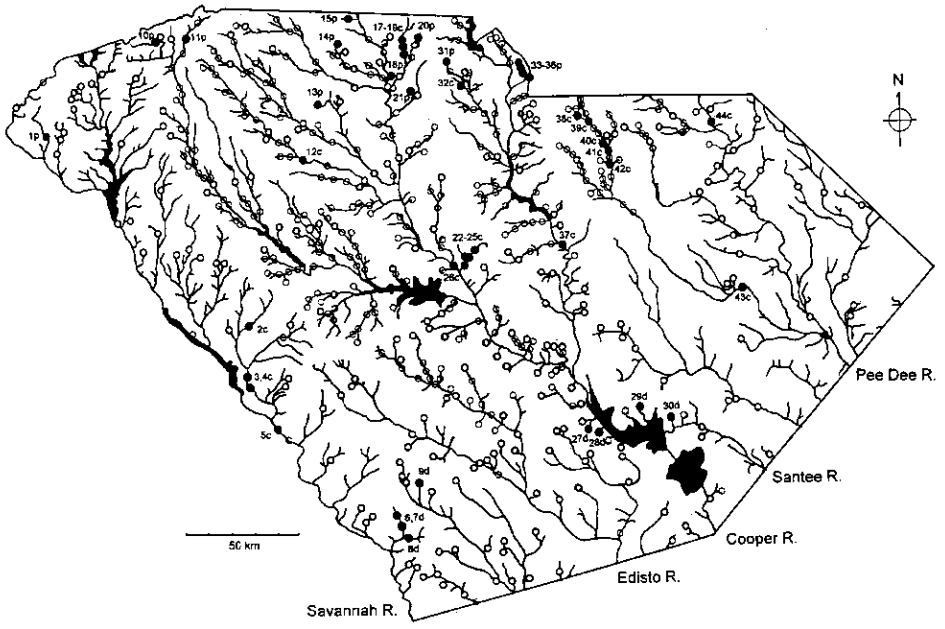

Figure 1. Map of South Carolina showing sample sites. The darkened circles (with site numbers) show where pleurocerid snails were found. Coastal areas of the state have been truncated in this depiction. Key to site number suffixes: c - *Goniobasis catenaria catenaria*, d - *G. catenaria dislocata*, and p - *G. proxima*.

mountains in the southeastern US, ranging from Virginia (south of the Roanoke River) to western Georgia, on both sides of the eastern continental divide (Dillon 1984). In South Carolina, it occurs in tributaries of the 3 main branches of the Santee River: the Saluda (10p, 11p), Broad (13-16p, 20p, 21p), and Catawba-Wateree rivers (31p, 33-36p). We also found it in one Savannah River tributary (1p).

The FLMNH collection contains one 1915 lot of *G. proxima* from "A Davis Valley near Clermont." A search of the USGS Geographic Names Information System returned no entry for Davis Valley, but found a Clermont Plantation (historical) in Kershaw County. This plantation is near the Wateree River upstream about 10-20 km from site 37c, in a region now heavily impacted by Wateree Lake. The FLMNH also contains 4 lots of *G. proxima* from the upper Keowee River drainage, a tributary of the Savannah (between sites 1p and 10p on Fig. 1): 1 collected in 1915 (75584), 1 from 1935 (75585) and 2 from 1970 (232410, 232418). Although our collections did not confirm *G. proxima* in the Keowee drainage, the patchy nature of *Goniobasis* distribution can make such populations easy to miss.

The similarity in shell morphology between *G. proxima* and *G. catenaria dislocata* is striking (Fig. 2). Both have a single spiral carination, but shells of the latter are marked with faint axial costae near the apex, disappearing after the first 2-3 whorls, while the former are entirely uncostate. The 2 taxa both inhabit small, rapidly-flowing streams, *G. catenaria dislocata* generally being found in those rather unusual regions of the Coastal Plain (often bordering large rivers) with slope and marl exposure. Whether the gross similarity of *G. proxima* and *G. catenaria dislocata* reflects a genuine genetic relationship or is the result of convergence cannot be told at present.

Goodrich (1942) recognized a total of six *G. catenaria* subspecies in the southeastern U.S., including four not found in South Carolina. In Georgia he listed *G. catenaria postellii* from the Altamaha, Ogeechee, and Canoochee rivers, and *G. catenaria inclinans* from the Flint River. From Florida he reported *G. catenaria*

Figure 2. Representative shells from the three taxa of South Carolina pleurocerids. From left, *Goniobasis catenaria catenaria* (site 3c), *G. catenaria dislocata* (site 27d), *G. proxima* (site 10p). The standard length of the *G. catenaria catenaria* shell is 18.8 mm, other two specimens to scale.

cancellata and *G. catenaria vanhyningiana*. These last three taxa have been synonymized under *G. floridensis* by Chambers (1990). It seems possible that a 2nd, rather similar *Goniobasis* species of Florida and Georgia, *G. boykiniana*, may be synonymous with *G. c. postellii* and *G. catenaria catenaria* itself. Chambers (1990) noted, "The relationship between *E. catenaria* and *E. boykiniana* is probably close and would be a highly appropriate subject for detailed analysis of shell characters and genetic analysis." It is not inconceivable that *G. catenaria* may ultimately be found to range from Virginia to Florida.

It seems that Goodrich's (1942) description of the *G. catenaria catenaria* habitat, "A springs of eastern South Carolina, possibly in streams southward to the Savannah River", was misleadingly narrow. The species can be common in medium-sized streams and even in larger rivers. The extensive Stevens Creek population (2 - 4c) seems to extend into the Savannah River (5c), and the Cedar Creek population (22-25c) extends into the Broad River west of Columbia (26c). Our discovery of a *G. catenaria catenaria* population as far west as York County's Clark Fork (17 - 19c) was most unexpected. This is a small rocky stream approximately 5 m wide, well into the Piedmont region of the state, within the range of *G. proxima*. The contrast between this habitat and that of the Lynches River south of Florence (43c), a slow, blackwater river over 20 m wide, is striking.

The FLMNH collection contains two lots of *G. catenaria* from populations not shown on Figure 1: a 1981 collection from the main Santee River (approx. 30-40 km E of 30d) and a 1955 collection from the type locality, Eutaw Springs, where the species no longer occurs. It is interesting to note that the Eutaw Springs population seems to have persisted for at least a decade after the Santee-Cooper Project brought the waters of Lake Marion just over its habitat.

It would appear that *G. catenaria catenaria* is capable of inhabiting a very broad range of stream-river environments, large and small, from piedmont to coastal plain. This leads one to question the disjunct nature of its present range. Why do populations seem to be absent from so many sites that, from their geographic location, seem otherwise suitable? We speculate that the absence of *G. catenaria catenaria* from most of the lotic habitats of South Carolina may be a consequence of the lack of suitable substrate. Most pleurocerids are adapted to graze over solid substrates, and all require solid substrates for egglaying. They can graze on unconsolidated substrate if it is firm enough to allow detritus and algal cells accumulate on its surface, but not on shifting substrates. Thus in the lower Lynches River (*e.g.*, 43c), individual *G. catenaria catenaria* are absent from most of the mud bottom, and restricted to isolated hard marl habitat.

Today many, perhaps most, of the smaller to mid-sized streams of the South Carolina Piedmont and upper Coastal Plain flow over bottoms of white sand. Even during low flow, this sand is often visibly shifting downstream. This is not natural in many cases. These sediment loads result from the intensive agricultural practices of previous generations, practices that included clearcutting of riparian vegetation and cultivation to the streambank (Trimble 1974). Topsoil eroded into the stream beds, and the decay of its organic component left the thick layers of sand that cover the naturally firm substrate of many streams today. A downward spiral of diversity was the result (Neves *et al.* 1997).

Agriculture in South Carolina today is neither as extensive nor as intensive as it has been in previous generations. Harding *et al.* (1998) have characterized the current biodiversity of the streams of the southeastern U.S. a ghost of land use past. The populations of pleurocerids that remain scattered across the state should be protected, not simply as a biodiversity resource, but also as a valuable subject for ecological, environmental, and evolutionary study.

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