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An extraordinary reproductive strategy in freshwater bivalves: prey mimicry to facilitate larval dispersal

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SUMMARY

1. Females of the North American freshwater bivalve *Lampsilis perovalis* release their larvae, which are obligate parasites on fish, in a discrete mass (superconglutinate) resembling a small fish in shape and coloration. After release, the mass remains tethered to the female by a long, transparent, mucous strand and, in stream currents, displays a darting motion that further mimics a small fish.
2. Release of superconglutinates was observed in March and April at water temperatures of 14–17 °C. However, superconglutinates detached from the parent mussel were observed from March to June at water temperatures of 11–26 °C, indicating that release may occur into the summer.
3. The superconglutinate lure may function to attract a predaceous fish to ingest the mass, ensuring that the larvae are exposed to a suitable host.
4. This reproductive strategy was confirmed recently to occur in a congener, *L. subangulata* and is suspected to occur in another congener, *L. australis*.

Introduction

Most parasites are faced with the problem of encountering a specific host among a myriad of non-suitable organisms (Thompson, 1982). Freshwater bivalves of the superfamily Unionacea have a highly specialized reproductive strategy in which the modified veliger larvae (glochidia) undergo a brief period as obligate ectoparasites in the buccal cavity or on the fins of a fish. The glochidia are brooded in the interlamellar spaces (water-tubes) of the gills until mature then released through the siphons (Kat, 1984) after which they can survive only a few days before they must find a host (Neves & Widlak, 1988). Because most glochidia show narrow host specificity, attempts to parasitize non-host fish species result in rejection by the fish's immune system and death of the glochidia (Neves *et al.*, 1985). Transformation from the larval to the juvenile stage is therefore dependent not only on encountering a fish but encountering the proper species among a fish community that, in regions with high biological diversity such as the south-eastern United States, may include thirty or more species (Swift *et al.*, 1986).

Among freshwater unionacean bivalves there is a wide variety of strategies used to infect host fishes with glochidia. Some species produce prodigious numbers of glochidia that drift passively in stream currents and encounter fish in a density-dependent fashion (Dartnall & Walkey, 1979). Other species have evolved mechanisms that exploit predator–prey interactions to increase the chances of glochidia encountering a fish.

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Some release the glochidial contents of each individual gill water-tube in discrete, mucous-encased packets called conglutinates that mimic fish food items such as leeches, worms, flatworms or insect larvae (Kat, 1984; Neves & Widlak, 1988) and are foraged upon by several species of fishes (Dartnall & Walkey, 1979; Chamberlain, 1934). Mantle margins of females of several species in the subfamily Lampsilinae are pigmented in patterns resembling small fish or invertebrates and flap, undulate, or pulsate with muscular contractions thought to lure fish near the gravid mussel at which time the mussel releases a cloud of glochidia (Kraemer & Swanson, 1985; Kat, 1984; Kraemer, 1970).

We report the discovery of an elaborate method of glochidial release in which the entire contents of the gill, and hence, the entire year's reproductive effort, are presented in a highly modified external structure, a superconglutinate, that mimics a swimming fish and lures a piscivorous fish host. This strategy may reduce the parasite's dependence on population density of potential hosts and greatly lower the likelihood of glochidia encountering non-suitable hosts. We observed superconglutinate production in *Lampsilis perovalis* (Conrad), a species endemic to the Mobile Basin in the south-eastern United States, and it has recently been confirmed for *L. subangulata* (Simpson) (C. O'Brien personal communication) of the Apalachicola and Ochlockonee river systems. Based on gill morphology similar to *L. perovalis* and *L. subangulata*, we suspect that *L. australis* (I.Lea) of the Escambia and Choctawhatchee river systems also produce superconglutinates.

Materials and methods

We surveyed one site each in five streams in the upper Black Warrior River system (Mobile Basin, Cumberland Plateau physiographic region, Winston and Lawrence counties, Alabama, U.S.A.) known to harbour populations of *L. perovalis*. These streams included Sipsey Fork (sixth order), Borden Creek (fifth order), Rush Creek (fourth order), and Brown and Flannagin creeks (third order). We surveyed Rush and Brown creeks monthly during the spring in 1993–95 and approximately bimonthly from July to October 1993. We surveyed Borden Creek on 18 August and 26 October 1993, 15 April 1994, and 2 April and 17 May 1995, and Sipsey Fork on 30 September and 26 October 1993, 15 April and 11 May 1994, and 2 April and 17 May 1995. Additional observations were made at one site each on Limestone Creek, 25 June 1988, and the Pea River, 22 June 1993 (Choctawhatchee River system, Eastern Gulf Coastal Plain physiographic region, Walton County, Florida, and Coffee County, Alabama, respectively) known to harbour populations of *L. australis*. We did not survey sites within the range of *L. subangulata*.

We surveyed for mussels and superconglutinates using glass-bottomed buckets to reduce surface glare. Water temperature, current velocity, and substrate composition were recorded adjacent to mussels associated with superconglutinates. Female mussels and superconglutinates were preserved in 70% ethanol or 5% buffered formalin. Measurements of superconglutinates were made with dial calipers and a dissecting microscope with ocular micrometer. Observations on timing and mode of superconglutinate production were made in the field for three *L. perovalis* in Rush Creek on 27 March 1995 and one individual in Brown Creek on 29 March 1995. Two gravid *L. perovalis* were collected from Brown Creek on 29 March 1995 and observed in aquaria at 22 °C.

Results and Discussion

The superconglutinate of *L. perovalis* is tethered to the parent mussel by a transparent strand, 10–15 mm in diameter, originating from the excurrent siphon and extending for up to 250 cm (Fig. 1). The strand is composed of two hollow, mucous tubes lying next to each other. The terminal end of each tube is blind and encases the entire glochidial contents of a single gill. In newly produced specimens, both ends lie together, giving the impression of a single terminus. After an unknown period of time in the water, the ends disassociate and older strands assume a distinctly bifurcated appearance. The strand is pliant, allowing the terminal end containing the glochidial mass to dart with the current in a manner resembling a small fish or fishing lure. After an unknown but probably variable period of attachment to the female, the superconglutinate breaks off or may be actively released by the female. We frequently observed detached mucous strands snagged on woody debris in the stream where they continued to display fish-like motion. Detached but otherwise complete superconglutinates, ranging from 25 to 250 cm in length were found in all five streams (Table 1).

Production of the superconglutinate takes up to 8 h

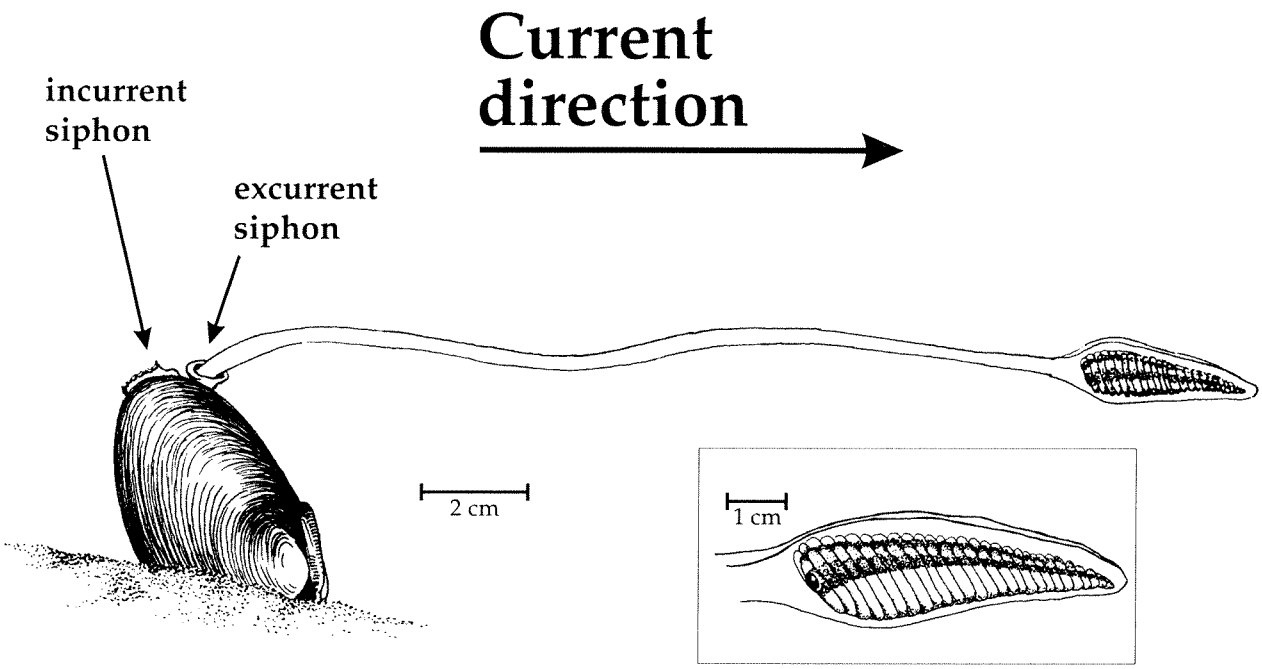

Fig. 1 Female *Lampsilis perovalis* releasing superconglutinate. The mucous strand originates from the excurrent siphon and trails downstream; the glochidial mass is deposited in the terminal end of the strand. Inset shows detail of the glochidial mass with vertical bands representing contents of individual conglutinates.

Table 1 Results of superconglutinate (SG) surveys in three streams in the upper Black Warrior River drainage, Lawrence Co., Alabama for eight dates on which SG were observed. Sample dates outside earliest and latest dates for each year produced no superconglutinate observations. NA, water temperature not available

Date	Water temp. (°C)	Stream	Number of attached SG	Number of detached SG
19 April 1993	15	Brown	2	3
	15	Rush	2	0
11 May 1993	18	Brown	0	1
17 June 1993	20	Rush	0	3
15 March 1994	11	Flannagin	0	1
12 April 1994	14	Brown	1	> 10
	17	Rush	1	> 10
20 April 1994	17	Brown	0	1
	NA	Rush	1	1
27 March 1994	16	Brown	1	> 20
	16	Rush	7	> 10
15 May 1994	21	Brown	0	1

but the rate of production is apparently related to water temperature. Initially, the glochidial contents are deposited in the blind ends of the strand, and the strand is gradually lengthened by addition from the female. Release of the superconglutinate began in the early hours of daylight for all specimens observed. Two specimens observed in the wild produced over 30 cm of mucous strand h^{-1} at 16 °C and another produced less than 10 cm of strand h^{-1} at 14 °C. In aquaria, two individuals produced 20–60 cm of strand h^{-1} at 22 °C.

In most species that release glochidia in conglutinates, the conglutinates are composed of the contents of individual gill water-tubes and maintain the shape of the tubes after release (Kat, 1984). However, glochidia of *Lampsilis perovalis* are released in masses composed of the entire contents of a single gill, including all conglutinates from marsupialized water-tubes of that gill (Figs 1 and 2). The mass is identical in shape to the marsupialized portion of the gravid gill (Fig. 2), but before release, the mass lies upside-down in the gills relative to its orientation after deposition in the mucous tube (compare Figs 1 and 2). In all of the superconglutinates examined, the contents of both gills had been deposited in the mucous tube with the contents of a single gill in the end of each tube.

Reproductive characteristics of most species of *Lampsilis* differ from superconglutinate production in *L. perovalis* in two principal ways:

1 the shape of the marsupialized portion of the gill;

2 the method of release of glochidia from the gills. The marsupialized portion of the gill of *L. perovalis* tapers at the posterior end rather being than kidney-shaped as in typical *Lampsilis* (Fig. 2). Most lampsilines release glochidia from the gills through specialized pores in the water-tubes into the mantle cavity then discharge the glochidia through the in-current siphon (Kat, 1984); *L. perovalis* releases superconglutinates through the excurrent siphon. This implies that the glochidial mass must be released into the supra-branchial chambers (Fig. 2), a method common in other genera of freshwater mussels (Kat, 1984).

The glochidial mass (Figs 1 and 2) ranged in length from 37 to 50 mm, in height from 10 to 12 mm, and in width from 5 to 7 mm. The following description is based on the orientation the mass assumes once deposited in the mucous tube (Fig. 1). In lateral view, the mass is rounded anteriorly and gradually tapers to a point posteriorly. The number of individual conglutinates present in the mass ranged from sixteen to twenty-nine. Coloration of the mass is imparted by pigments in a thin membrane that surrounds each individual conglutinate; the individual glochidia are colourless. Each conglutinate is pink at the dorsal edge and bordered below by a band of black speckling ≈ 1 mm wide that is slightly broader on the anterior-most conglutinates; the remaining ventral portion of the conglutinate is creamy white. Thus, the overall colour of the mass is creamy white below with a dark, medial stripe broadened at the anterior end, forming a distinct eyespot, and a pink wash on the upper margin. The colour pattern strongly suggests a small fish; this resemblance is strengthened by the vertical pattern of conglutinates that resemble myomeres.

Superconglutinates were observed in five streams in Gulf Coast drainages of the south-eastern United States: Rush, Brown, and Flannagin creeks (Mobile Basin) and Limestone Creek and the Pea River (Choctawhatchee system). No superconglutinates were found in the Sipsey Fork or Borden Creek. Female *Lampsilis perovalis* were observed releasing superconglutinates in March and April at water temperatures of 14–17 °C in Rush and Brown creeks (Table 1). However, in the Mobile Basin streams, superconglutinates that had become detached from the female were observed from March to June at water temperatures of 11–21 °C (Table 1), indicating that release may occur throughout the spring. One detached superconglutinate was found in Limestone Creek on 25 June 1988 at a water temperature of 26 °C and one was found in the Pea River on 22 June 1993 (water temperature unavailable), indicating that, in the Choctawhatchee River system some releases may occur well into the summer. Females releasing superconglutinates were found at depths and current velocities of 13–60 cm and 0.07–0.25 m s^{-1}, respectively, in predominantly sand and gravel substrate. All individuals releasing superconglutinates had approximately half their shell length exposed above the substrate. Most unionacean bivalves remain completely buried in the substrate except during periods of glochidial release (Kat, 1984).

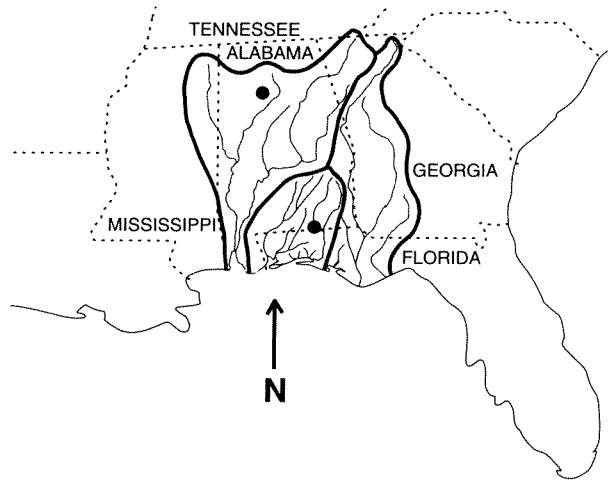

Fig. 3 Map of the south-eastern United States showing, from west to east, the approximate ranges of *Lampsilis perovalis* (Mobile Basin), *L. australis* (Escambia/Choctawhatchee river systems), and *L. subangulata* (Apalachicola/Ochlockonee river systems). The northern-most dark circle represents the location of Brown, Flannagin, Rush, and Borden creeks and the Sipsey Fork in the Mobile Basin; the southernmost circle represents the location of Limestone Creek and the Pea River in the Choctawhatchee River system.

The identification of the parents of detached superconglutinates found in the Pea River and Limestone Creek is not known because *L. perovalis* does not occur in these drainages. However, two other species of *Lampsilis* occur in the Pea River and Limestone Creek; *L. straminea claibornensis* and *L. australis*. *Lampsilis australis*, endemic to coastal drainages from the Choctawhatchee to the Escambia river systems (Heard, 1979; Clench & Turner, 1956; Fig. 3), is a likely species for superconglutinate production (Williams & Butler, 1995). Gill marsupia of *L. australis* collected in Limestone Creek and the Pea River were similar in shape to the glochidial mass of superconglutinates found at these sites and resembled the glochidial mass and

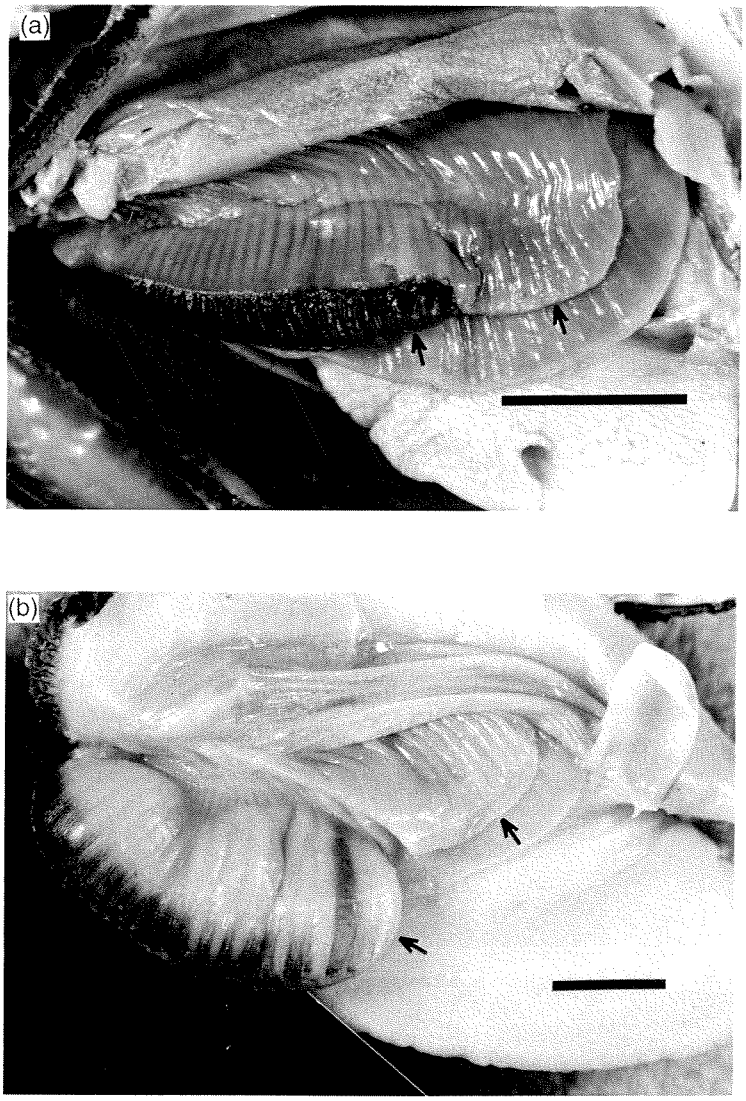

Fig. 2 Gill morphology of two species of *Lampsilis*. (a) Marsupialized outer right gill of *L. perovalis* from Browns Creek, Lawrence Co., Alabama, 19 April 1993. (b) Marsupialized outer right gill of *L. siliquoidea* from Cypress Creek, Lafayette Co., Mississippi, 5 April 1994. The suprabranchial chamber lies immediately above the gills; the mantle cavity lies immediately below the gills. Arrows indicate the marsupialized (right arrow) and unmarsupialized (left arrow) portions of the outer right gill in both figures. The scale bar represents 10 mm in both figures.

marsupial gill of *L. perovalis* (Fig. 2). *Lampsilis straminea claibornensis*, a widespread species in the south-eastern U.S.A. (Williams *et al.*, 1993), has kidney-shaped gill marsupia typical of most *Lampsilis* (Fig. 2). Specimens of *L. subangulata* collected from the Chipola River, Florida also had gill marsupial morphology similar to *L. perovalis* and *L. australis*. Recently, it has been confirmed that *L. subangulata*, an endemic of the Apalachicola and Ochlockonee river systems (Heard, 1979; Fig. 3), also produces superconglutinates (C. O'Brien, personal communication).

Species that produce or are suspected of producing superconglutinates are restricted to the Gulf Coastal Plain from the Mobile Basin east to the Apalachicola and Ochlockonee river systems (Fig. 3). One species each is found in the three major drainage groups of this region: Mobile Basin (*L. perovalis*), Escambia/Choctawhatchee systems (*L. australis*), and Apalachicola/Ochlockonee systems (*L. subangulata*). A number of clades of aquatic organisms contain sister species distributed parapatrically in these drainages (Wiley & Mayden, 1985). Zoogeographic patterns in this region are largely attributed to vicariant events related to eustatic cycles (Swift *et al.*, 1986; Warren, 1992). The parapatric distribution of this group of *Lampsilis* and the distinctiveness of the marsupial morphology and reproductive strategy suggest that these three species may have diverged from a common ancestor after isolation in coastal drainages due to changes in sea level. Although these species were widespread historically within their ranges, they are now restricted to clear headwater streams and are either federally protected or candidates for protection under the U.S. Endangered Species Act. The drastic range reduction experienced by these species may be, at least in part, related to increased turbidity in larger streams which causes the superconglutinate lure to be less conspicuous to potential host fishes.

The production of superconglutinates represents a highly specialized reproductive strategy that may increase the chances for parasitization of an appropriate fish host by freshwater bivalve larvae. All species of *Lampsilis* for which the host fish is known use a piscivorous fish (Tedla & Fernando, 1969; Zale & Neves, 1982; Waller & Hollands-Bartel, 1989). Centrarchid fishes (basses and sunfish) are common in all the streams where superconglutinates were found and these large, active, sight-feeding fishes comprise the majority of piscivorous fishes in these communities. Preliminary data suggest that basses (*Micropterus* spp.) act as hosts for *L. perovalis*. Sixty per cent of basses ($n = 11$, *M. coosae* and *M. punctulatus*) from Rush Creek and other Mobile basin tributaries that contain *L. perovalis* were infested with lampsiline glochidia that closely resemble those of *L. perovalis* (W.R. Haag and M.L. Warren, Jr., unpublished data). However, the density of *L. perovalis* was unrelated to centrarchid fish density in these streams (W.R. Haag and M.L. Warren, Jr., unpublished data). The superconglutinate is a conspicuous lure that may attract large piscivorous fishes, even when they occur at low densities, and may be too large to be ingested by small fishes. This method of glochidial release represents the most elaborate of a diverse array of strategies used by freshwater mussels to facilitate larval dispersal and may further ensure that parasitic larvae will encounter their specific host.

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