Reproductive Cycle and Fish Hosts of the Rabbit's Foot Mussel, Quadrula cylindrica strigillata (Mollusca: Unionidae) in the Upper Tennessee River Drainage[1]

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ABSTRACT: The reproductive biology and fish host requirements of *Quadrula cylindrica* were studied in the upper Tennessee River drainage, Virginia and Tennessee, during 1982 and 1983. Gametogenesis in this summer breeder was characterized by three stages: active gamete formation in late summer, an inactive overwintering period, and rapid gamete maturation and release (spawning) from May to July. Gravid females were collected from mid-May through early July, and mean fecundity was approximately 115,000 embryos per female. Glochidia exhibited a relatively high degree of host specificity, metamorphosing on only three cyprinids of 34 fish species tested in the laboratory. Host species identified were *Notropis galacturus, N. spilopterus* and *Hybopsis amblops*.

INTRODUCTION

The rabbit's foot mussel, *Quadrula cylindrica* (Say 1817), is widely distribu throughout the Ohio, Cumberland and Tennessee river basins in the eastern Uni States and ranges westward in the Mississippi drainage to Arkansas, Kansas and Ok homa (Ortmann, 1919). In the Tennessee River Valley, two subspecies are recogniz The headwaters form, *Q. c. strigillata* (Wright), is a compressed, highly tuberculate ty in the Clinch, Powell and Holston rivers; and *Q. c. cylindrica* (Say), a more inflat nodulate form with tubercles on the posterior ridge, occurs in the Duck River a mainstream Tennessee River below Pickwick Landing Dam.

In the early 20th century, the shells of several species of *Quadrula* were harvested the commercial shell industry of the Mississippi River basin (Lefevre and Curtis, 19 Coker, 1919; Coker *et al.*, 1921), and drastic reductions in their abundance promp preliminary studies on reproduction and host fish identification (Surber, 1913; Howa 1913, 1914; Coker *et al.*, 1921). On the basis of these early studies, the glochidia *Quadrula* species were identified as gill parasites, and several species of sunfishes (C trarchidae) and catfishes (Ictaluridae) were implicated as hosts for *Q. metanevra, Q. no lata, Q. pustulosa* and *Q. quadrula* (Fuller, 1974). However, life history information on rabbit's foot mussel has not been previously reported. Objectives of the present stu were to describe the seasonal progression of gametogenesis, document the spawning a glochidial release periods, identify fish hosts and characterize the early life stages of *c. strigillata*. This research was conducted as part of the Cumberlandian Mollusk C servation Program of the Tennessee Valley Authority (Jenkinson, 1981) to provide history information on the rabbit's foot mussel that would be applicable to biologi studies proposed for *Quadrula intermedia* and other endangered mussel species.

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MATERIALS AND METHODS

All specimens of *Quadrula cylindrica strigillata* were collected from the upper Tennes River drainage in 1982 and 1983 at the following sites and river mile (RM) locatic Grays Island (RM 233.5) and Pendleton Island (RM 226.3) on the Clinch River, S Co., Virginia; and McDowell Ford (RM 106.7) on the Powell River, Hancock C Tennessee. Except during periods of high flow and turbidity, Pendleton Island was sa pled most often and served as the major source of *Q. c. strigillata* for reproductive st ies. Mussels were obtained by snorkeling, and roughly five adult individuals were lected on each of the following sampling dates in 1982 and 1983: 21 and 30 April 10, 18, and 26 May; 16 June; 29 July; 24 August; 29 September; 7 January; March; 21 April and 21 May. These specimens, collected for histological studies, w relaxed in propylene phenoxitol, fixed in 10% buffered formalin, and preserved in 7 ethyl alcohol. The gametogenic cycle was investigated by cutting serial sections (7 thick) of gonadal tissue with a microtome and staining these glass slide preparati with standard hematoxylin-eosin techniques (Humason, 1972). The reproductive st of each specimen was described and recorded. Absence of gametes immediately afte period of reproductive maturity was assumed to indicate that spawning had occur (Zale and Neves, 1982a).

During spring and summer 1982, mussels from the Clinch and Powell Rivers w examined periodically by opening them slightly with modified O-ring expanders check for gravidity. On each sampling date, nongravid mussels were returned to river, and gravid specimens were placed in cloth bags for transport to a mobile labc tory (house trailer 3.7 m wide, 15.3 m long) downstream from Speer's Ferry (I 211.8), Clinch River, Virginia. A 3.75-hp submersible sewage pump supplied ambi river water directly to aquaria and Living Streams[2] (Frigid Units Inc., Toledo, Ohio the laboratory at a maximum flow of ca. 72,000 liters/hr.

Because conglutinates are often prematurely discharged (aborted) by female *Quadrula* species (Lefevre and Curtis, 1910), two methods of transporting and maint ing gravid females were tested to avoid or reduce abortion of glochidia. Specimen cloth bags were transported in insulated coolers with either ambient river wate crushed ice, and bags were examamined for aborted conglutinates at the laborat Mussels transported in river water were placed directly in Living Streams with r substrate or in aerated aquaria. Specimens transported on ice were transferred to 11-liter bucket with aerated, chilled river water (10 C), allowed to warm to room t perature (20 C), and then placed in Living Streams or aquaria. A sample of gravid males was aged by the external growth ring method (Chamberlain, 1931; Crow 1957). A fecundity estimate for gravid females was obtained by counting the numbe eggs, embryos or glochidia in expelled or aborted conglutinates and multiplying by mean number of water tubes used for brooding embryos in females.

Thirty-four fish species of eight families were exposed to glochidia of *Quadrula cy drica strigillata* in laboratory trials for fish host identifications. Fish for these host exp ments were collected at various river locations by backpack electroshocker or seine, regated by species, and conveyed to the laboratory in insulated coolers. Collection a for fish used in laboratory trials were as follows: Clinch River drainage—Cop Creek, Irving Branch and Stock Creek in Scott Co., Va.; Buffalo Creek, Bull F Creek and Hinds Creek in Anderson Co., Tenn.; and Mill Creek in Union Co., Te Powell River drainage—RM 65.2 in Claiborne Co., Tenn.; and RM 106.5 in Hanc Co., Tenn.; North Fork Holston River drainage—RM 6.3 and 13.4 in Scott Co., Cumberland River drainage—RM 224 in Sumner Co., Tenn. Collection sites for e fish species are tabulated in results. Fish collections were made at mussel-free sites w possible to avoid prior exposure of specimens to glochidia, and specimens were chec during collection for parasitic infestations. Likely fish hosts for glochidia of the rab foot mussel were selected by examing a list of fish species occurring where *Q. c. strigi* also occur at numerous sites in the upper Tennessee River drainage and a list of

species with glochidial infestations at those sites. Numbers of fish in each trial depend on species availability and ranged from 1-25; each fish was exposed to glochidia or once. All fish were maintained in either 76-liter aerated aquaria or Living Streams w flow-through water. Laboratory confinement of fish prior to infestation varied from 1 to 14 days, depending on availability of mature glochidia for induced infestations. Fr zen brine shrimp, commercial fish pellets, or forage fish were fed to experimental fi before and during infestation trials.

Mature glochidia were obtained from aborted conglutinates or by excision of t gills from gravid female mussels. Glochidia were tested for maturity by exposing a su sample to salt crystals; mature glochidia exhibit a closing response (Zale and Nev 1982b). In the laboratory, fish were anaesthetized with tricaine methanesulfonate (M 222), infested by pipetting several hundred glochidia into the left branchial cavity, a allowed to recover (15 min). Each species was placed in a separate aerated aquariu (19—114 liters) with filtered water and sections of plastic pipe for cover. Two fish spec with a closely bound isthmus (*Campostoma anomalum* and *Rhinichthys atratulus*) were e posed to glochidia in a 1-liter beaker for 1 min and then placed in separate aquaria.

Roughly 1.5 hr after infestation, specimens of each fish species were again anaesth tized and checked for glochidial attachment. Subsequent examinations occurred on d 2, day 3 or 4, and at irregular intervals thereafter to monitor the status of encyst glochidia. Nonhost fish usually rejected glochidia within the 1st 3 days. For all speci the last day of glochidial attachment was recorded. Material from the aquarium botte was siphoned daily through a 125-μm nylon mesh sieve beginning 1 day after infes tion. Sloughed glochidia and dead juvenile mussels were examined with a stereomici scope and preserved in 10% formalin. Live juveniles were kept for behavioral obser tions or placed in a shallow, stainless steel pan with sand-silt substrate in a flow-throu Living Stream.

Measurements of glochidia and juveniles were obtained under a stereomicrosco with an ocular micrometer; length is the maximum anteroposterior dimension paral to the hinge, and breadth is the maximum dorsoventral dimension perpendicular to t hinge.

RESULTS

The gonads of 35 males and 39 females, collected from the Clinch River on the sampling dates in 1982 and 1983, were sectioned for histological study. Several game genic stages often occurred within and among individual mussels on each sampli date. Males began active spermatogenesis in August. In the males, the gonadal tissu were characterized by widely spaced acini with numerous spermatogonia, sperma cytes and nutritive granules (Fig. 1). These active spermatogenic stages were al present in late September. No specimens were collected from October through Dece ber, but the reproductive stages of males taken in January were similar to those of ma collected in September. By March and April, the number of spermatids increased a acini were compact. Sperm were first noted in early May in 1982 and in mid-April 1983. Sperm were closely packed in the lumen by mid-May of both years, with f spermatogonia and nutritive granules. In June, sperm occurred in the ducts, and ac were less tightly packed. All males examined in late July were spent. Based upon the gonadal sections, release of sperm (spawning) probably began in mid-May and w completed by July.

Females showed initial signs of oogenesis in late July. By mid-August, nutriti granules with imbedded oogonia and thick acinal walls were evident in ovarian tiss (Fig. 2). The appearance of gonadal tissues from specimens in the September samp was similar to that of mid-August. By January, many oocytes had developed, acin walls were thinner, and ovocytes had separated from nurse cells. The lumen was fill with eggs, acini were thin-walled, and some mature eggs occurred in the follicles. T number of mature eggs increased in April and May, but few eggs remained by m

June. Eleven females collected on 10 May had not spawned, although a single fer examined on 3 May bore eggs in her gills. Gills of all females were partly or f charged in late May and June, and acini were empty in July. These gonadal sect suggest that release of eggs (spawning) probably began in mid-May and was ne completed by mid-June.

Except for the female examined on 3 May, gravid individuals of *Quadrula cylin strigillata* were collected first from the Clinch River on 13 May 1982 and from the Po River on 18 May 1982; water temperatures in these rivers were 20 C and 22 C, res tively (Table 1). Between 20 May and 26 June, 15-30% of the mussels examined f the Clinch River were gravid. Because the rabbit's foot mussel is not sexually dir phic, percent gravidity is based on all mussels examined. However, since the rando collected specimens for histological study (35 males:39 females) appear to indica roughly equal sex ratio in the population, percent gravidity among females is li double the expressed values (Table 1). Most of the females examined ranged from 102 mm in length and 10-22 years in age. The percentage of gravid females peake 30-32% in late May and then gradually declined through June. The lower percent of gravid specimens from the Clinch River observed on 16 and 23 June occurred a an extended period of high turbidity. The relatively greater number of gravid fem collected on 26 June from the Clinch River was obtained primarily from another a at the Pendleton Island site. Mature glochidia were not abundant in conglutinates u June, females apparently expelled all glochidia by late July. All specimens examinec ter July were not gravid.

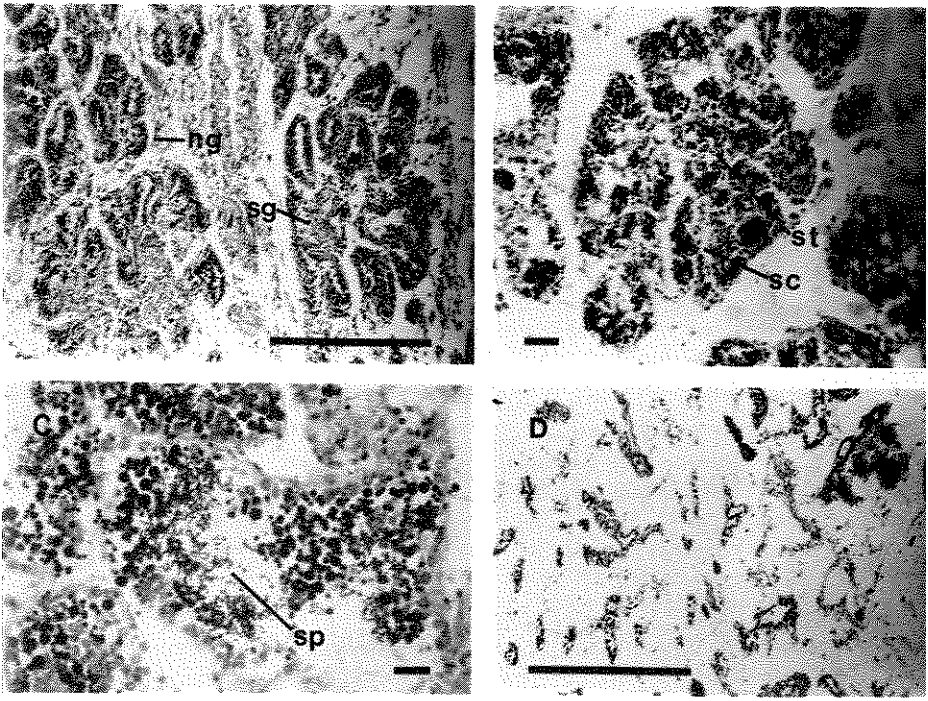

Fig. 1.—Histological sections of testes of *Quadrula cylindrica strigillata* collected 24 Au (A), 1 January (B), 29 June (C) and 29 July (D). Abbreviations: ng, nutritive granules spermatogonia; sc, spermatocytes; st, spermatids; sp, sperm. Bar = 200 μm

Fifty-three (65%) of the 82 gravid females examined from the Clinch River l glochidia in the outer demibranchs only, whereas the remaining 29 (35%) had at le part of all four gills serving as marsupia. Unfertilized eggs accounted for less than 5 of conglutinates during May and June. Fertilization success, the ratio of embryos embryos plus unfertilized eggs, was high, therefore, at this time. In contrast, gravid males examined late in the reproductive season (7 July) contained only unfertilized e in their gills. Conglutinates with embryos and immature glochidia frequently w aborted by gravid females regardless of efforts to improve transportation and hold methods. Gravid females discharged at least a few conglutinates under all field and l oratory conditions. Expulsion of conglutinates generally occurred within 1 day of ini handling or examination for gravidity or after periods of high turbidity in the fl through laboratory facilities.

Lanceolate-shaped conglutinates of immature and mature glochidia were expe through the excurrent siphon. Seven conglutinates averaged 11.5 (±0.69 SD) mm lo 1.7 (±0.23 SD) mm wide, and 0.9 (±0.07 SD) mm deep. Embryos in the conglutina were light yellow until they reached the late gastrula stage, then progressed thro light peach to reddish brown in maturing glochidia. Fully mature glochidia were nea transparent or light peach, except for a tinge of rust along the mantle margin. Th glochidia were expelled in granular-appearing whitish to reddish brown conglutina or were expelled individually as the conglutinate matrix disintegrated. The eight c glutinates contained between 375 and 505 (mean, 469±43.0 SD) embryos or glochic Mean fecundity (computed from the mean number of water tubes used for brood embryos in five sacrificed specimens, field observations of gravid females, and the m number of embryos per conglutinate) was 114,246 (±5,368 SD) embryos per female

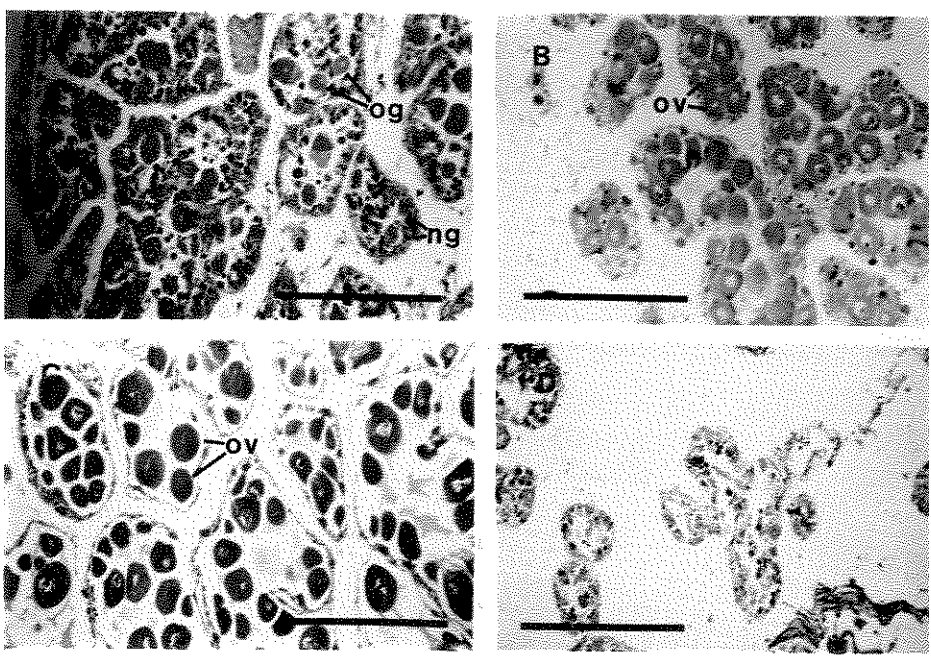

Fig. 2.—Histological sections of ovaries of *Quadrula cylindrica strigillata* collected 24 Au (A), 6 November (B), 21 May (C) and 29 July (D). Abbreviations: ng, nutritive granules; oogonia; ov, ovocytes. Bar = 200 μm

Within each conglutinate, all glochidia were at the same stage of developme Gravid females, determined to contain mature glochidia by excising and agitating gill, consistently had mature glochidia in all conglutinates. However, one female c lected on 13 May had several developmental stages in different conglutinates. S aborted several nearly mature glochidia with well-formed valves on 14 May, but pelled conglutinates of immature embryos (light yellow to peach) on 18 May.

Conglutinates with mature glochidia were easily teased or shaken apart to rele their glochidia. Colorless glochidia were not used for induced infestation trials becau they exhibited a slow closing response when exposed to salt crystals. Mean dimensic of 100 mature glochidia from four females were as follows: length, 0.22 (± 0.03 mm; breadth, 0.22 (±0.02 SE) mm; depth, 0.16 (±0.02 SE) mm; and hinge leng 0.14 (±0.02 SE) mm. Glochidia were subcircular with a truncated dorsal hinge li (Fig. 3); the single adductor muscle was readily visible.

Glochidia pipetted onto the gills of potential hosts typically attached to the dis portion of gill lamellae, although some glochidia occasionally attached to epithelial sue lining the branchial cavity. Degrees of infestations were light to moderate, deper ing on the relative size of the fish species. As few as 5-10 glochidia were seen on cyp nids and as many as several hundred on large centrarchids.

Glochidia were sloughed from the gills of 31 of the 34 species tested at mean wa temperatures between 20.0 and 23.1 C (Table 2). In these infestation trials, 19 spec sloughed glochidia within the 1st day after exposure. Several species of cyprinids

TABLE 1.—Reproductive condition of *Quadrula cylindrica strigillata* examined from the Cli and Powell rivers during 1982

Stream and date	Water temperature (C)	No. examined	Percent gravid
Clinch River			
21 April	15.6	35	0
5 May	16.7	10	0
10 May	20.0	11	0
13 May	20.0	1	100
14 May	21.1	46	0
20 May	21.4	33	15
26 May	22.2	70	30
27 May	22.2	51	29
16 June	20.6	260	5
23 June	21.1	106	6
26 June	23.0	96	15
7 July	24.0	106	8
29 July	24.0	30	0
Powell River			
5 May	17.8	9	0
18 May	22.2	31	32
25 May	21.7	13	31
18 June	22.2	3	0

tained glochidia somewhat longer than species in other fish families. For example, striped shiner *Notropis chrysocephalus* retained glochidia for up to 12 days, but no tr formed juveniles were found. All specimens of this species used in these tests ha moderate infestation of encysted trematodes, which may have affected our experime results. Glochidia of *Quadrula cylindrica strigillata* were sloughed from all rock bass (*Ar plites rupestris*) within 1 day after exposure, but a light infestation of elongate gloch (subfamily Lampsilinae) was discovered on two of these fish after 2 days. Juvenile this undetermined mussel species were collected 11-15 days later.

Three species of Cyprinidae were confirmed as suitable fish hosts for the gloch of the rabbit's foot mussel (Table 3). In three trials with a total of 13 whitetail shi (*Notropis galacturus*), 17 juvenile mussels were collected in the siphonate of aquaria. period of metamorphosis was 13-23 days at mean water temperatures between 20.5 21.6 C. One juvenile each was recovered from glochidial infestations on 12 spotfin s ers (*Notropis spilopterus*) in 20 days and from 12 bigeye chubs (*Hybopsis amblops*) i days.

Three newly metamorphosed juveniles of *Quadrula cylindrica strigillata*, probably eral hours old, averaged 0.23 mm in length, 0.23 mm in breadth and 0.16 mm depth, with a hinge length of 0.15 mm. In size and shape, they were nearly identic glochidia. Juveniles in a glass petri dish moved by slowly extending the foot a dist roughly equivalent to 50% of body length, then quickly drawing the body to the f The foot was extremely adhesive, and juveniles could hold position when nudged b dissecting probe. In the laboratory, 0.5 cm of fine silt had settled in the shallow with juveniles, and no live individuals were recovered after 28 days.

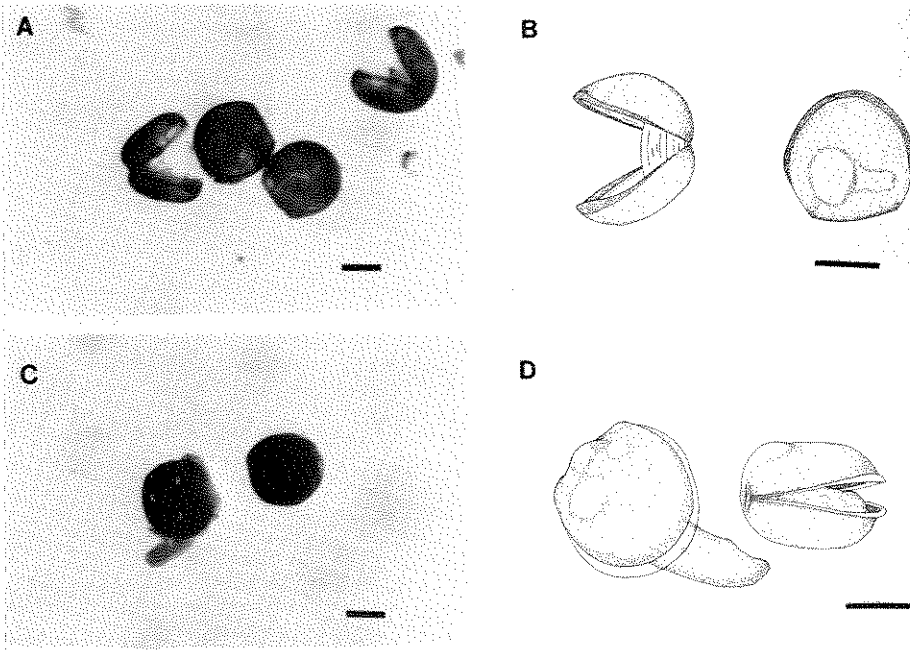

Fig. 3.—Mature glochidia of *Quadrula cylindrica strigillata* in (a) lateral and dorsal (1(and (b) schematic view (155X). Metamorphosed juvenile (c) lateral (82X); (d) schematic (165X). Bar = 100 μm

TABLE 2. — Number of fish exposed (N), maximum periods of attachment, mean water te peratures and sources of specimens in laboratory trials with glochidia of *Quadrula cylindrica s gillata* on nonhost fish species

Species	N	Period (days)	Temperature (C)	Source
Catostomidae				
Catostomus commersoni	1	3	20.8	Bull Run Creek
Hyopentelium nigricans	5	<1	21.2	Bull Run Creek
Moxostoma erythrurum	3	<1	22.8	Bull Run Creek
Centrarchidae				
Ambloplites rupestris	9	<1	22.4	Buffalo Creek
Lepomis macrochirus	5	2	22.2	Hinds Creek
L. megalotis	6	<1	22.7	Buffalo Creek
Micropterus dolomieui	2	<1	22.2	Bull Run Creek
M. punctulatus	4	<1	21.8	Bull Run Creek
Cottidae				
Cottus carolinae	7	<1	22.6	Bull Run Creek
Cyprinidae				
Campostoma anomalum	12	6	22.6	Buffalo Creek
Hybopsis dissimilis	7	<1	22.2	Powell River
Nocomis micropogon	1	<1	20.2	Powell River
Notropis chrysocephalus[a,b]	8	9-12	22.5	Hinds Creek
N. coccogenis	7	4	20.0	Stock Creek
N. leuciodus	9	2	21.9	Copper Creek
N. rubellus	9	2	21.9	Powell River
N. serrulatus	8	<1	22.4	North Fork Holston Rive
N. volucellus	3	<1	21.7	Powell River
Phenacobius uranops	3	<1	22.8	Powell River
Pimephales notatus[b]	25	4-7	22.7	Mill Creek
Rhinichtys atratulus	12	2	21.8	Irving Branch
Cyprinodontidae				
Fundulus catenatus	7	<1	22.6	Stock Creek
Ictaluridae				
Ictalurus punctatus	6	<1	22.7	Cumberland River
Noturus eleutherus	1	<1	20.8	Powell River
Lepisosteidae				
Lepisosteus osseus	1	<1	20.8	Stock Creek
Percidae				
Etheostoma blennioides	6	<1	21.6	Hinds Creek
E. jessiae	12	3	22.8	Hinds Creek
E. rufilineatum	6	<1	22.7	North Fork Holston Rive
E. simoterum	11	2	22.6	Hinds Creek
E. zonale	17	2	21.2	North Fork Holston Rive
Percina caprodes	3	<1	20.5	Hinds Creek

[a] Fish with trematode infestation
[b] Two infestation trials on this species

DISCUSSION

In the upper Tennessee River drainage, *Quadrula cylindrica strigillata* is a short-ter summer breeder (tachytictic) that spawns and releases glochidia from May to July. A though this reproductive period agrees with periods described previously for oth short-term breeders (Matteson, 1948; Yokley, 1972; Weaver, 1981), the seasonal gam togenic cycle is different. Gonadal development in the rabbit's foot mussel was chara terized by three general stages; active gametogenesis in late summer, a relatively ina tive overwintering period, and rapid gamete maturation and release from May to Ju Yokley (1972) reported early gametogenic stages in male *Pleurobema cordatum* from t Tennessee River during summer and sperm by autumn. Mature sperm were prese year-round in *Elliptio complanatus* from the Great Lakes region (Matteson, 1948) and *Pleurobema oviforme* from the Tennessee River drainage (Weaver, 1981), increasing abundance as the spawning period approached. Females of these three species also co tained mature ova during winter months, with little if any additional maturation r ported before the spring spawning. The formation of intermediate gametic stages du ing winter and rapid maturation of sex products during spring in the rabbit's fo mussel thus differed considerably from the seasonal progression of gametogenesis other summer breeders that have been studied.

The fertilization period for *Quadrula cylindrica strigillata* apparently began in mid-M and continued into June. Gravid females were collected from mid-May through ea July. This period coincides with the occurrence of gravid specimens in June and July the Cumberland River (Wilson and Clark, 1914) and with 22 May to 8 July records gravid females in Pennsylvania (Ortmann, 1919). The breeding period of this and oth *Quadrula* species is apparently similar throughout the Mississippi River basin (Lefev and Curtis, 1910; Howard, 1914), but some differences in reproductive traits are e dent. Females of *Quadrula* were reported to carry developing glochidia in all four gi (Howard, 1914; Ortmann, 1919), but we found this trait varied in the rabbit's fo mussel throughout the period of gravidity. The high percentage (65%) of females wi glochidia in the outer gills only is apparently atypical for the genus (Howard, 1914).

Unfertilized eggs are commonly found in summer breeders and are especially co mon among *Quadrula* species (Lefevre and Curtis, 1910). However, we observed hi fertilization success (>95%) through late June, particularly at the Pendleton Isla site. The abundance of *Quadrula cylindrica strigillata* at this location was greater than other known sites in the upper Tennessee drainage, and this highly successful fertiliz tion may be attributed to high population density. Coker *et al.* (1921) suggested that r lease of sperm of male mussels and their entry into females may stimulate ovulation, though no documentation has yet been presented. The females with unfertilized eggs their gills on 7 July apparently released eggs after the major spawning period of ma (late May until July). Lefevre and Curtis (1910) intimated that their collection reco

TABLE 3. — Metamorphosis of glochidia of *Quadrula cylindrica strigillata* from induced labo tory infestations on whitetail shiners (*Notropis galacturus*), spotfin shiners (*N. spilopterus*) and b eye chubs (*Hybopsis amblops*)

Fish species	No. of fish exposed	Period of metamorphosis (days)	Mean temperature (C)	No. of juvenile recovered
N. galacturus[a]	2	18	21.6	1
	10	15-23	20.6	12
	1	17	21.9	4
N. spilopterus[a]	12	20	21.0	1
H. amblops[b]	12	17	21.3	1

[a] Collected from Bull Run Creek
[b] Collected from Powell River

of *Quadrula* species provided evidence of a double spawning, first in June-July and ag in July-August; however, our field and laboratory examination of specimens provi no evidence of the bimodal occurrence of gravid females.

The gills of gravid females were clearly distended and assumed the coloration of closed conglutinates. Ortmann (1919) described the conglutinates of the rabbit's f mussel as being a yellow brown or pale orange, and we noted similar hues depend on the stage of development. The coloration of conglutinates provided a useful mean determining when mature glochidia were present and ready for release. Our measu ments of mature glochidia of *Quadrula cylindrica strigillata* were slightly larger than pr ously reported (length and height ca. 0.19 mm) by Ortmann (1919) and similar in and shape to those of *Q. metanevra* (Lefevre and Curtis, 1910; Surber, 1912). The m diagnostic character for mature glochidia of the rabbit's foot mussel was the tinge reddish brown on the mantle.

Sensitivity of gravid *Quadrula cylindrica strigillata* to handling and holding stresses c firmed earlier observations of other *Quadrula* species. Lefevre and Curtis (1910) ported that each of the *Quadrula* species they studied tended to abort embryos glochidia to varying degrees when removed from the river. Within a few hours after lection, at least partial abortion occurred in all specimens in spite of precautionary m sures. However in our flow-through holding tanks, some females retained glochidia up to 8 days under conditions of high aeration, low turbidity and adequate curr This tendency to abort was a major problem in our study and will probably handi efforts to conduct life history research on congeneric species, particularly the end gered *Q. intermedia* and *Q. sparsa*.

The mechanics of attachment and encystment by glochidia on host fish follo early descriptions of natural infestations (Arey, 1921, 1924, 1932). Sloughing glochidia by nonhost fish within a few hours after attachment appeared to involve sc degree of cytolytic disintegration. Open valves of sloughed glochidia in aquaria w generally without internal tissues. The few closed glochidia with body tissues in found in the siphonate 1 day after infestation apparently had not attached successf to gill lamellae. Meyers *et al.* (1980) noted a failure of host cells to form cyst w around glochidia of *Margaritifera margaritifera* as an initial rejection response by c salmon (*Oncorhynchus kisutch*) but did not describe the condition of rejected glochi Seemingly normal glochidia of *M. margaritifera* were rejected after infestation by a tis response of cyst formation and sloughing of tissue (Fustish and Millemann, 1978). S ilarly, glochidia of *Quadrula cylindrica strigillata* partly enclosed in nonhost fish tissue w sloughed intact with no evidence of disintegration after 9-12 days on the cyprinid *N pis chrysocephalus*. However, we were unable to document the manner of rejection f unsuitable hosts because of the relatively short sloughing period.

Glochidia of *Quadrula cylindrica strigillata* exhibited a relatively high degree of l specificity, metamorphosing on only three (all cyprinids) of the 34 fish species tes Association of the rabbit's foot mussel with members of the Cyprinidae may be rel to the co-occurrence of the mussel with these fish species in riverine habitats. A mussels were usually observed lying on their sides on a mixed cobble and gravel s strate or were only partly burrowed in the river bottom. Water velocity appeared to fluence the instream distribution of specimens, since this species was most abundan eddies along the periphery of midstream currents or adjacent to emergent or subme vegetation. It was not found in river sections with considerable current or stagnant ter. Individuals or small schools of whitetail shiners are commonly collected in riffle eas with coarse substrates immediately above and below pools or in eddies along the riphery of midstream currents (Outten, 1958). On several occasions, we colle gravid *Q. c. strigillata* with individuals of *Notropis galacturus* hovering in proximity. co-occurrence of mussel and host species in the same habitat obviously would enh the degree of infestation and reproductive success for the mussel.

The degree of overlap between the rabbit's foot mussel and the whitetail shine

their southern (Tennessee-Cumberland rivers) and western (Black, White, Saline, Qu chita and Neosho rivers) changes is noteworthy (Fig. 4). Numerous other cyprinids the subgenus *Cyprinella*, including partly sympatric species, border the southern ran of *Quadrula cylindrica*, but the rabbit's foot mussel appears to occur only in those riv drainages populated by the whitetail shiner. Ranges of *Notropis spilopterus* and *Hybop amblops* (Lee *et al.*, 1980) encircle the northern portion of the range of *Q. cylindrica*, a these fish may serve as more frequent hosts in those northern drainages. The occu rence of other forms of *Q. cylindrica* in the mainstream Tennessee and Ohio Rive where *N. galacturus* and *H. amblops* typically do not occur, and in regions not occupi by *N. spilopterus* (*e.g.*, northern Arkansas), suggests that additional hosts remain to identified. One likely candidate fish host in these other rivers would be *N. whipplei*, fo merly considered a subspecies of *N. spilopterus*, which has a range enclosing that of t rabbit's foot mussel (Lee *et al.*, 1980).

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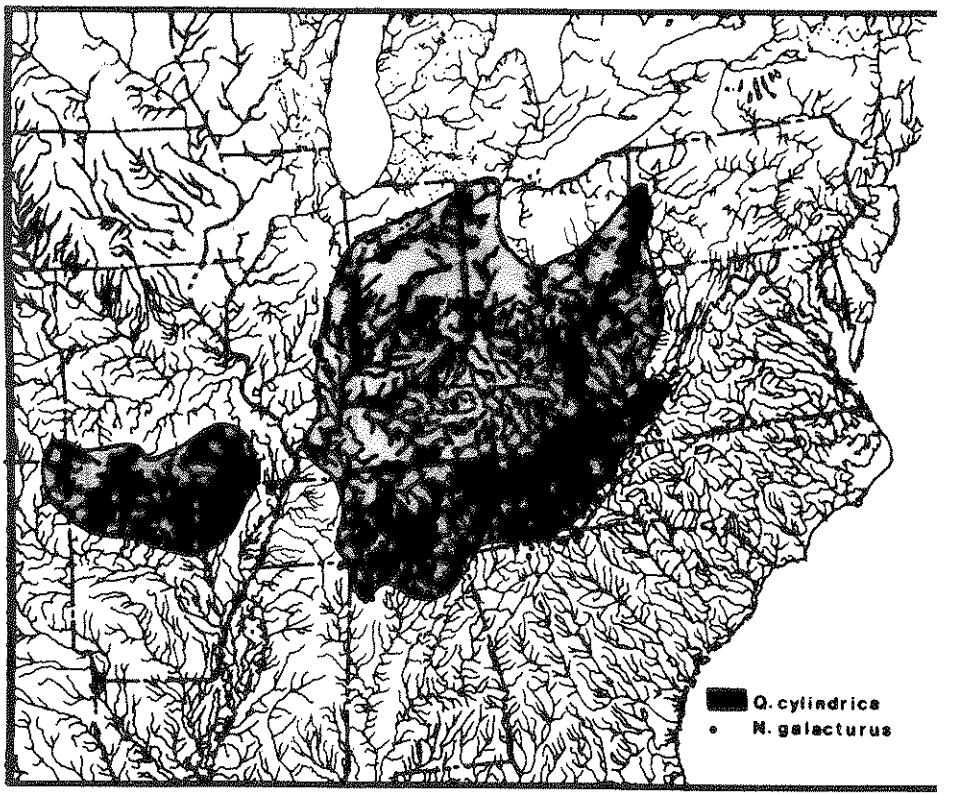

Fig. 4.—Distribution of *Quadrula cylindrica* (shaded area) and of the host fish *Notropis gal turus* (dots) in the South-central United States. Host distribution was redrawn from Lee *et* (1980)

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